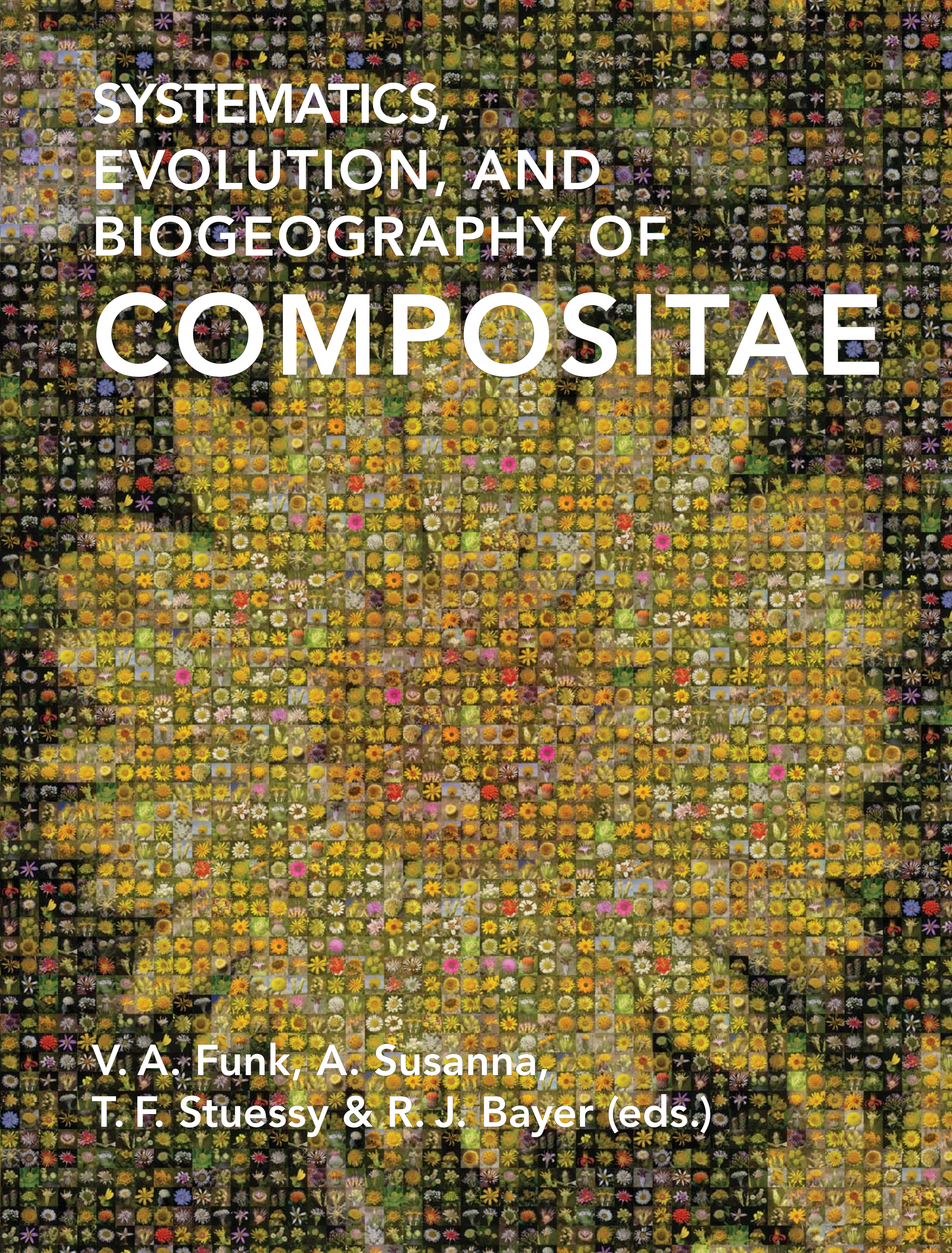

SYSTEMATICS, EVOLUTION, AND BIOGEOGRAPHY OF COMPOSITAE

V. A. Funk, A. Susanna,
T. F. Stuessy & R. J. Bayer (eds.)

Compositae

Frontispiece. *Espeletia hartwegiana* subsp. *centroandina* Cuatrec. (Millerieae) in a northern Andes páramo, a biome particularly rich in species of Compositae (Nevado del Ruiz, Departamento de Caldas, Colombia). [Photograph, J. Mauricio Bonifacino.]

Systematics, Evolution, and Biogeography of Compositae

Edited by

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INTERNATIONAL ASSOCIATION FOR PLANT TAXONOMY
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Frontcover illustration: A mosaic composed of images (most of which are contained within this book) that represent all major groups of Compositae. The image that the small photos make is of a radiate yellow head from *Grindelia orientalis* Bartoli, Tortosa & G.H. Rua (Astereae). The yellow radiate head can also be taken to represent the archetypal Compositae. The mosaic was built by J. Mauricio Bonifacino (Montevideo, Uruguay) using MacOSaiX.

Backcover illustrations (left to right and top to bottom)**:** *Helianthus annuus* L. (Heliantheae s.str.); *Centaurea stoebe* L. (Cardueae); *Bellis perennis* L. (Astereae); *Mutisia clematis* L. (Mutisieae); *Didelta spinosa* Ait. (Arctotideae); *Cichorium intybus* L. (Cichorieae). [All photographs by V.A. Funk and J.M. Bonifacino.]

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Magno amore in familiam Synantherearum captus….

(Lessing 1829)

Contents

Section I: Introduction

Section II: Character evolution at the family level

Section III: Phylogeny, classification, and biogeography of the tribes

Part 1: Asterales

Part 2: Basal clades

Part 3: Cichorioideae and Corymbioideae

Part 4: Asteroideae

Section IV: Conclusion

Section V: Appendices

Foreword

Peter H. Raven

Almost a tenth of all flowering plants belong to the great family Compositae, the subject of this wonderful book. They occur throughout the world, but are most abundant in geologically recent habitats like areas of Mediterranean (summer dry) climate, deserts and their margins, open prairies and steppes, and recently uplifted mountain ranges. Although some members of the family are widespread and a few are aggressive weeds, most of the species are relatively restricted in range, and quite a few are in danger of extinction in the face of habitat destruction and global warming. Having grown up in California where this family is especially diverse, it is interesting to see the placement of the different groups on the phylogenies presented in this volume and especially to me to puzzle over the possible origins of the Heliantheae alliance.

Although Compositae are clearly monophyletic, they are often considered 'difficult' because they are so numerous. The well-defined units that have emerged as a result of contemporary analyses make understanding the family much easier than ever before. At the same time, the discussions of the systematics and biogeography of the family and each group within it are highly informative, as are the detailed discussions of topics such as chromosomes and pollen.

Compositae are especially numerous in North America, with approximately 2500 species (an eighth of the total flora) recorded for the United States and Canada in the Flora of North America; it is the largest family in this area, and even more diverse, numerous, and better represented in Mexico. The production of treatments of this family in various floristic accounts, such as those we are coordinating at the Missouri Botanical Garden, is greatly expedited by the kinds of analyses that are so well brought up-to-date in this volume. Indeed, the family is so large that understanding it well is of particular importance in these efforts.

Finally, this new phylogenetic structure opens doors for future research and provides the basis for systematic studies, a stimulus for understanding the microevolution of individual species groups, and a clear delineation of many areas for which future molecular and morphological studies are especially desirable.

Peter H. Raven,
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Preface

This book deals with the phylogeny, classification, evolution, and biogeography of Compositae, the largest family of flowering plants. It is one of the dominant plant families on Earth, with more than 1300 genera and 23,000 species, distributed on every continent except Antarctica. To understand biodiversity across our planet's landscape requires understanding this massive, diverse, and fascinating family. It is the objective of the present book to provide this understanding.

Due to many molecular investigations on the family in recent years, new data and new phylogenies have resulted in portrayals of relationships that have impacted classification, understanding of character evolution, and interpretations of origin and diversification of the group. It has been challenging, therefore, to keep track of all new developments especially that deal with classification of tribes and subfamilies. This has been particularly burdensome for professors of systematic botany to present updated perspectives for students. It has also been relevant for researchers for asking and being able to answer significant evolutionary questions. In short, a new synthesis has been required for further progress to be made on the family. This book attempts to fill this need.

Other major syntheses on the systematics of Compositae have been published within the past 25 years. The first modern synthesis, upon which the present book has built, was based on papers from the University of Reading (UK) symposium in 1975 and published as two volumes in 1977 (Heywood et al. 1977). These focused on systematic and chemical characterizations of tribes (i.e., a taxonomic orientation). In 1994 another conference on the family was held, this time at the Royal Botanic Gardens, Kew, and these results were also subsequently published in two volumes (Hind 1996). This represented a very useful compilation of many updated topics on the family, but it lacked a comprehensive presentation of tribes. In parallel appeared the valuable book by Kåre Bremer and colleagues (Bremer 1994), which provided a morphological cladistic assessment of phylogenetic relationships for all genera of the family. This major contribution set the stage for further phylogenetic reconstructions within the family based on new molecular (DNA) data, which have been appearing virtually monthly in different journals throughout the world. In 2007 there appeared generic-level treatments of the entire Compositae in the *Families and Genera of Vascular Plants* series (series editor, Klaus Kubitzki), which provided keys, descriptions, synonymy, and protologues for every genus within the family (Kadereit and Jeffrey 2007). In 2005, a very important supertree (= metatree) for all tribes and subfamilies of Compositae was published (Funk et al. 2005), which stressed the importance of extending phylogenetic understanding for a family-wide treatment, and was the first complete evolutionary overview based on the new molecular data. This present book, therefore, builds upon these previous extensive morphological and molecular contributions and provides a new and detailed comprehensive synthesis for the entire family.

An important stimulus for arriving at final publication of this book has been the formation of The International Compositae Alliance (TICA) in 2000. The association was formed to provide links among researchers within the family and also to help further research on systematics of tribes and subfamilies. TICA held its first conference with presented papers in Albuquerque, New Mexico (USA) in 2001 and a second conference in Pretoria, South Africa, in 2003. It also hosted symposia on the family during the International Botanical Congress in Vienna, Austria, in 2005. This sustained interest led eventually to convening an international Conference on *Systematics & Evolution of the Compositae: A Symposium* in Barcelona, Spain, 3–10 July, 2006. The Barcelona meeting was an important step that led to final appearance of this book. The order of presentations at that meeting followed the previous format of the Reading Conference (Heywood et al. 1997), focusing on subfamilies and tribes. Organized by Alfonso Susanna and his team together with Vicki Funk, and hosted by the Institute of Botany located in the Barcelona Botanical Garden, the meeting was very successful, attracting individuals from many countries of the world and involving many active systematists in the family. This success suggested publication of results from the meeting, which in large measure has resulted in publication of this volume.

It was decided early, however, that a new book on relationships within the family should include more than just contents from the meeting. The present volume, therefore, builds upon the excellent papers given at the conference, but these have been greatly enlarged, improved, modified, and sometimes markedly changed to incorporate the newest viewpoints on relationships within the family. This book, therefore, is a coherent statement of the current status of Compositae systematics and evolution that goes beyond the papers presented at the conference.

Rather than attempting to present quantities of new data on the family, this book emphasizes synthesis of available data. That is, the focus has been on bringing together the vast DNA sequence information scattered in many journals and on evaluating these for a new comprehensive phylogeny of the family. This synthesis has also allowed new biogeographic hypotheses to be formulated, which were not possible prior to having the broader phylogenetic reconstructions.

It is our hope that this volume will serve as a stimulus for continued research on systematics of Compositae. In addition to research suggestions contained within each of the chapters, a concluding chapter emphasizes particular research avenues for attention. One of the most challenging is how to deal effectively with classification of the basal branches (i.e., the previous Mutisieae, s.l.). The new structure of phylogenetic relationships as revealed in the metatree will now also make possible calculation of molecular clock estimates that will help more precisely test biogeographic hypotheses. Examining character evolution within particular clades will also be more feasible, as well as within the family as a whole.

We also hope that this volume will be a useful tool by which to teach a new generation of students about the remarkable diversity of the family. Toward this objective, we have employed throughout the book a consistent mode of tree presentation, including color-coded branches reflecting geographic distributions of clades, a summary metatree inside the front and back covers, a summary classification of tribes and subfamilies, color plates of genera within each tribe representing diversity across the entire family, and a glossary of morphological features. An electronic version of the metatree as well as an electronic version of a poster suitable for classroom use are available on the IAPT (International Association for Plant Taxonomy) and TICA websites.

For uniformity, we have adopted several conventions throughout the text. First, we follow the *International Code of Botanical Nomenclature* (*ICBN*; McNeill et al. 2007) in treating Compositae (and Asteraceae) as a plural, rather than singular, noun (i.e., "Compositae are …"). Second, we employ Compositae preferentially to Asteraceae. Although the *ICBN* allows either to be used (the former being sanctioned because it lacks the correct -aceae ending, and the latter being conserved because it does not have priority), we have emphasized Compositae because of its descriptive nature and because it is the preferred label for the international alliance (TICA). It is also the personal preference of the editors! Third, authorities for names are given once in each chapter the first time they are used. Fourth, types for names are not given, except in the case of newly coined taxa (mostly new subtribes). Although it would have been useful to include this information uniformly, it represents another challenge that goes beyond the main objectives of this book.

We have added several appendices. The first is an illustrated glossary of reproductive features in the family, which should help readers understand better the descriptions. It will also be very useful in teaching. The second is an extensive bibliography of the literature on palynology of the family, which provides access to these comparative data that are scattered in many specialist journals. The third gives identifications for taxa shown in historical plates in Chapter 1. The fourth is a list of new taxa and nomenclatural combinations in the book. Although use of new names has not been encouraged, some additions have been necessary for completeness of presentations. Finally, we have also provided a combined literature cited to facilitate research in the family.

Books have a way of providing a new stepping point or level of perspective for understanding different areas of science, and it is our hope that this volume will do so for Compositae systematics. With contributions from eighty authorities, it is hard to imagine a more thorough treatment at this time. There is much left on our plate, so to speak, but so far, the meal has been gourmet, delicious, and extremely satisfying. We eagerly await the next course.

Vicki Funk, Alfonso Susanna,
Tod Stuessy, Randy Bayer

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Section I

Introduction

A history of research in Compositae: early beginnings to the Reading Meeting (1975)

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INTRODUCTION

The magnitude of the work of the great students of the Compositae in the 19th and early 20th centuries is astonishing, both in the quality and scope of their research, as well as in the great number of systematic treatments and floras they produced. Their achievements go beyond exceptional, however, when they are seen in the context of the technology that these workers had available at the time.

What follows is an attempt to gather and tie together many scattered pieces of information on their lives, work, and ideas, and to pay tribute to those individuals who have made outstanding contributions to the field. We are grateful to these men of science; their work has enabled us to see and understand the most diverse and successful plant family on Earth. This chapter covers notable synantherologists up to the 1975 conference held at Reading; a two-volume work that resulted from this meeting was published in 1977 (Heywood et al. 1977). The scientists are discussed in chronological order of the date of their major contribution(s) to our understanding of Compositae.

PRE-TOURNEFORT ERA

Compositae are such a well-defined, diverse, and conspicuous group in most areas of the world that it is perhaps not surprising to discover that even early authors such as Theophrastus (ca. 371 to 287 BC) had at least some idea about the naturalness of the group (Greene 1983: 184). As early as the mid 16th century Jean Ruel (1474–1537), a French botanist, is credited with many original observations on plants and the coining of copious new morphological terminology. He presented a description of several Compositae, clearly identifying the capitulum as being composed of several florets of different types: "*Anthemidi è rotundis capitulis flores prominent in orbem foliati, alios intus aureos flores continentibus*" ["Anthemis has its rounded capituli encircled by leafy flowers, and within these yellow ones"] (Ruel 1536, cited by Greene 1983). However, a deeper insight on the true nature of the Compositae did not come until well into the 17th century with the work of Joseph Pitton de Tournefort, Sébastien Vaillant, and Johann Le Francq van Berkhey.

Before presenting an introduction to the lives and works of these three important botanists, it seems appropriate to include a brief note on three other botanists, who albeit did not contribute to advancing the understanding of Compositae systematics, are nonetheless credited with coining the two alternative names for the family.

Michel Adanson was born April 7, 1727 in Aix-en-Provence. In 1729 the family moved to Paris. In 1763 Adanson published his *Familles des Plantes* in which he described several plant families, one of them named

Compositae. However, after the resolution adopted at the Vienna Congress in 2005 (Article 13.1, McNeill et al. 2006), the starting date for the names of families was set to August 4, 1789 (date of publication of Jussieu's *Genera Plantarum*; Jussieu 1789) and the priority of the name fell to Giseke who had published the name independently in his *Praelectiones* in 1792. Adanson died in Paris, on August 3, 1806. Biographic information on Adanson can be found in Cuvier (1861) and Bailly (1992: 127–196); see Stafleu and Cowan (1976) for a thorough list of works on the life and works of Adanson.

Paul Dietrich Giseke was born in Hamburg on December 8, 1741, the son of a merchant. He studied Medicine at Göttingen University and received his degree in 1767. Interested in the Natural System of plants, he wrote to Linnaeus for advice. Linnaeus answered that he could not give the characters of the natural orders but could explain them in person. In 1771, Giseke traveled to Uppsala where Linnaeus gave him and four other students a private lecture on these ideas; he had only done this once before, in 1764. Another student in this group was Johann Christian Fabricius (1748–1808), who later became famous as an entomologist. Fabricius and Giseke had both made records of Linnaeus' lectures, and Giseke (1792) combined them in his *Praelectiones in Ordines Naturales Plantarum* [Lectures on the natural orders of plants]. The text, partly a dialogue between the professor and his students, shows the clear insight of Linnaeus in the principles of a natural system: he recommended individuals to not use single characters to define a group (taxon)

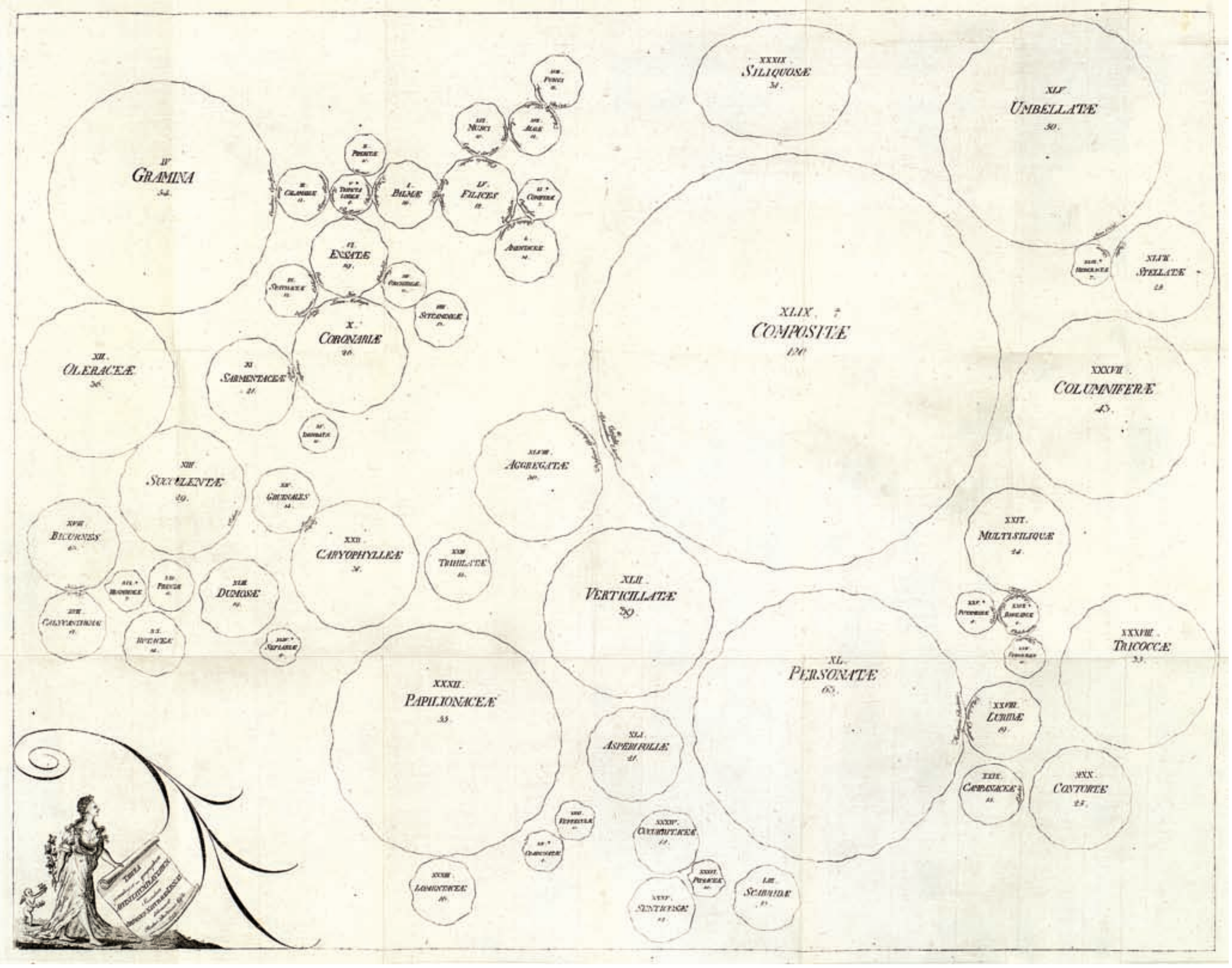


Fig. 1.1. Giseke's "Tabula genealogico-geographica affinitatum plantarum secundum ordines naturales Linnaei", where he expresses in a novel graphic mode the relationships among the plant families as envisaged by Linnaeus. The size of the circles is indicative of the number of genera considered for each order. Note the conspicuousness of Compositae. This plate, dated 1789, was also published separately and represents the first record for the name Compositae. [Taken from Giseke's *Caroli A Linne Praelectiones in Ordines Naturales Plantarum*, reproduced with the kind permission of the Linnean Society, London.]

but rather a combination of them. Compositae is taken from *Compositi* in Linnaeus' *Philosophia Botanica* (1751, cf. page 29), which in turn can be traced back to Ray's (1682) "Herbae Florae Composito". The subdivision of the family in the *Praelectiones* is the same as in Linnaeus (1751).

Probably the most interesting feature of Giseke's book is the "Tabula genealogico-geographica affinitatum plantarum secundum ordines naturales Linnaei [quam] delineavit Paulus Dietericus Giseke 1789" (Genealogical-geographical table [plate] of the relationships among plants according to Linnaeus's natural orders drawn by Paul Dietrich Giseke 1789) (Fig. 1.1), published also prior to and separately from the text. In a surprisingly modern style this copper engraving shows the Linnaean orders as circles of different sizes in relationship to the number of genera they were believed to comprise and arranged according to their presumed affinities, among them Giseke's Compositae, in fact as the circle with the largest diameter (the actual number of genera is indicated in the circle itself, which for Compositae is 120). It is a remarkable fact that Giseke is not known to have validated a single name within Compositae and is therefore listed in this contribution with some hesitation among the more important synantherologists.

When Giseke returned to Hamburg he was employed as a physician, and he became a professor of physics (meaning natural history) and poetry at the famous gymnasium of Hamburg. Giseke died on April 26, 1796 in his native town. The biographical notes on Giseke presented here were largely adapted from Schröder (1854), Schuster (1928), Hedge (1967), and Stafleu (1971).

Finally, we would like to briefly mention Ivan Ivanovich [Ivanovič] Martynov, the author responsible for coining the name Asteraceae, accepted under the current Botanical Code as the alternative name for Compositae. Little is known about the life and work of this Russian botanist born in 1771. In 1820, Martynov published a sort of botanical dictionary presenting information on terminology and nomenclature both in Latin and Russian. In this publication, *Tekhno-Botanicheskii Slovar*, Martynov (1820) validated the names of 99 plant families, Asteraceae among them, mostly through a Latinization of French names and making reference to validly published descriptions. Martynov died in 1833.

For a thorough list of all valid and invalid names applied to Compositae, see Hoogland and Reveal (2005).

JOSEPH PITTON DE TOURNEFORT (1656–1708)

Joseph Pitton de Tournefort (Fig. 1.2) was born in 1656, in the region of Aix-en-Provence. Tournefort had been interested in Botany since his youth, but his father had him pursue religious studies. When Tournefort was 22, the death of his father freed him from his religious endeavors, and from then on he devoted himself entirely to Botany. Often he collected plants in the southeast of France with Plumier. In 1679 he went to Montpellier where he followed Magnol's teaching. In 1700, Tournefort's most famous contribution, the *Institutiones Rei Herbariae*, was published (Tournefort 1700). It was an expanded Latin translation of an earlier French version entitled *Éléments de Botanique*. The *Institutiones* presented generic descriptions for more than 1500 genera of plants and displayed the encyclopedic knowledge that Tournefort had gained not only through the study of herbarium specimens but also through extensive traveling and collecting in Europe and SW Asia. Caesalpino influenced him in regard to using seeds and fruits in his classification, although he relied greatly on corollas for the definition of the main groups. Tournefort had no understanding of the role of the structures of both the androecium and gynoecium (Greene 1983). He did not believe in sexuality of plants, and this was a source of friction with Vaillant. However, the first use of the term 'pistyl' in its present sense is

Fig. 1.2. Joseph Pitton de Tournefort (1656–1708). [Engraving by L. Desrochers; courtesy of Hunt Institute.]

attributed to him, and he is recognized as one of the major contributors to the standardizing of botanical terminology in the 18th century (Stearn 1992).

With regard to his understanding of Compositae, Tournefort (1700) saw the group as a class divided into three families: *(1)* “Fleur à fleurons” (composed of species with discoid and probably disciform heads), *(2)* “Fleur à demi-fleurons” (composed of species bearing ligulate capitula), and *(3)* “Fleur radiée” (species with radiate heads). In his treatment, Tournefort included 35 detailed illustrations depicting some important groups of his native Europe, clearly showing he knew that the heads were formed by several florets, and in some cases different types of florets (Fig. 1.3). Appointed “démonstrateur et professeur de l’intérieur et de l’extérieur des plantes” at the Jardin du Roi in Paris, Tournefort died only seven months later on 28 November 1708 after a serious traffic accident in September in rue Coupeau [now rue Lacépède] near the garden. The biographic notes on Tournefort presented here were adapted from Duprat (1957), Greene (1983), and Bailly (1992: 59–126).

Fig. 1.3. Compositae as seen by Tournefort, in one of the 35 plates devoted to the family in *Institutiones Rei Herbariae*, showing impressive detail and accuracy. [Anonymous engraving taken from vol. 3, plate 251, courtesy of Smithsonian Institution, Cullman Library; for original figure legends, see Appendix C.]

SÉBASTIEN VAILLANT (1669–1722)

Another botanist, who made interesting contributions to the field, during what we call the ‘pre-Cassini era’, was Sébastien Vaillant. Vaillant (Fig. 1.4) was born on May 26, 1669 in Vigny, northwest of Paris. According to some accounts, Vaillant at age five started his own little garden in a patch of the family estate given to him by his father to grow plants he collected in the countryside around the house. One year later he was sent to study Latin and religion, where he was a very dedicated student. Apparently the strict discipline enforced by the instructors caused Vaillant to fear failure, so to avoid punishment he would use various techniques (e.g., putting a nail inside his night hat) so that he would sleep less comfortably and wake up earlier, in order to have more time to study. His dedication eventually led him to excel in all the subjects and to gain recognition from his tutors.

Vaillant’s father, seeing the great progress that his son had made, sent him to learn music at Pontoise, an activity that Vaillant seems to have particularly enjoyed, quickly mastering the pipe organ and substituting for his master in public performances. During his free time as a musician Vaillant visited the local hospital and became increasingly interested in surgery. Later he decided to become a surgeon. He succeeded in his medical studies and after a few years of practicing surgery he met Tournefort and started studying botany. After a few classes in which he was shown plants and their names, he decided to dedicate himself entirely to botany, rapidly gaining a thorough understanding of the local flora that would eventually lead to his (posthumous) publishing of the *Botanicon Parisiense* (Vaillant 1727). In 1708, he obtained a position as “sous-démonstrateur de l’extérieur des plantes” at the Jardin du Roi, and it seemed he was very much appreciated as a teacher considering that his lectures were at six in the morning and attended by hundreds of listeners.

Vaillant is remembered as a strong supporter of sexuality in plants, and he apparently contributed to the spreading of these ideas in his lectures on the subject at the Jardin du Roi. A lecture on the structure and function of flowers held in 1717 was published one year later (Vaillant 1718) both in Latin and in French (see the translation in Bernasconi and Taiz 2002). This work was an important stimulus for the young Linnaeus, who would eventually base his classification system on the sexual organs of plants. In his treatment of Compositae (Vaillant 1719–1723), Vaillant stressed the sex of individual florets but also used other characters derived from the phyllaries, receptacles, and pappus. He coined several new terms and presented magnificent illustrations of different parts of the heads and florets (Fig. 1.5). Vaillant divided Compositae into three groups; in addition to Cichorieae recognized by Tournefort, he identified Cardueae ("Cynarocéphales") and the rest of Compositae known at his time formed the remaining group known as "Corymbifères". Vaillant's contributions to Compositae made him the last serious contributor to the field before Cassini.

Sébastien Vaillant died in Paris on May 26, 1722, after suffering for several years from severe asthma, notably aggravated by excessive work. The biographic notes on Vaillant presented here were adapted from Hermann Boerhaave's preface to *Botanicon Parisiense* (Boerhaave 1727), from Small (1917), and Greuter et al. (2005). Additional information on Vaillant can be found in Rousseau (1970) and Bernasconi and Taiz (2002).

Fig. 1.4. Sébastien Vaillant (1669–1722). [Anonymous engraving taken from *Botanicon Parisiense*, courtesy of Missouri Botanical Garden Library © 1995–2009.]

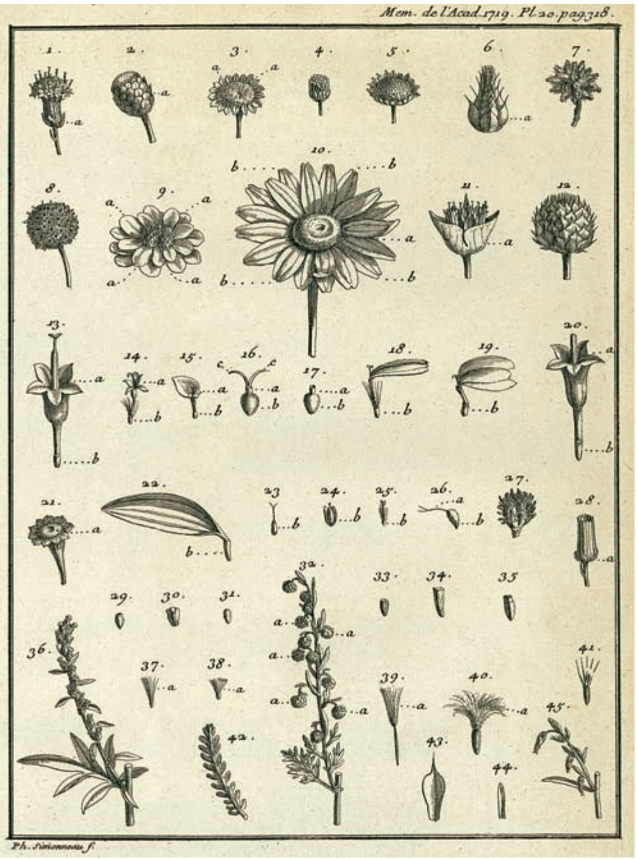


Fig. 1.5. Illustration showing different traits of "Corymbifères", the largest of the three groups in which Vaillant divided the Compositae. [Engraving by Ph. Simonneau f. taken from Vaillant's second contribution to Compositae in 1721, courtesy of Mertz Library at NYBG; for original figure legends, see Appendix C.]

JOHANNES LE FRANCQ VAN BERKHEY (1729–1812)

A short note on the Dutch naturalist Johannes Le Francq van Berkhey [Berkheij] seems appropriate since he was the first to write a book exclusively on the general features of Compositae. Berkhey was born on January 23, 1729 in Leiden and studied medicine there. His book, *Expositio Characteristica Structurae Florum qui Dicuntur Compositi* (1760) seems to be an expanded edition of his dissertation. In his *Expositio*, Berkhey (1760) described in great detail the characters of the capitula and flowers in Compositae, and their variability is shown in nine excellent copper plates (Fig. 1.6) based on his own sketches. Although the book shows good insight into the morphology of

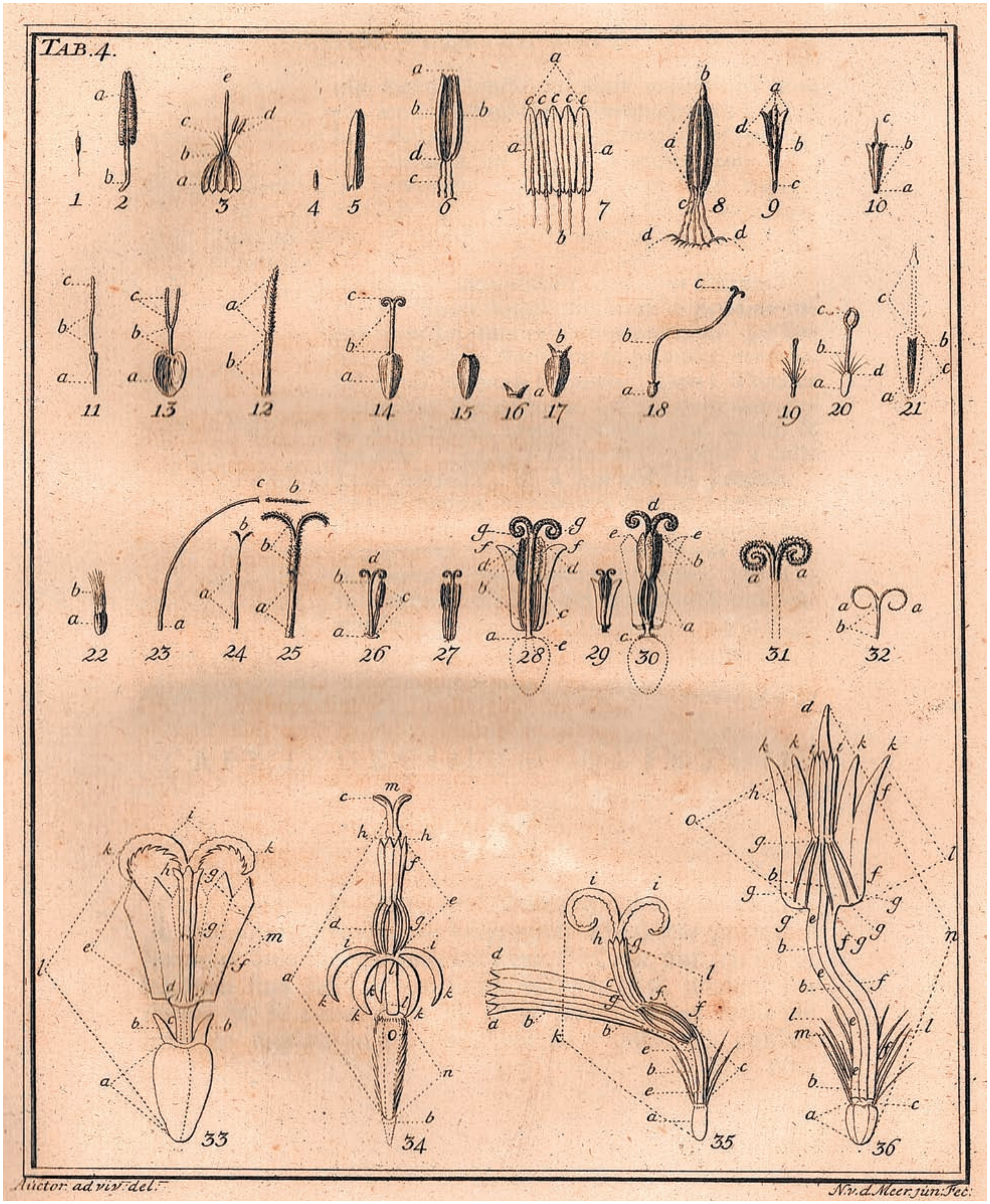


Fig. 1.6. Berkhey's *Expositio Characteristica Florum qui Dicuntur Compositi*, published in 1760 holds the status of the first book ever published exclusively about Compositae. This illustration, one of the nine magnificent plates depicting the family's morphological diversity known to him by the mid-1700s, shows Berkhey's acute level of understanding of Compositae. Berkhey's work inspired and challenged Cassini, who admitted he would have to work hard to surpass the Dutch naturalist. [Courtesy of Botanic Garden and Botanical Museum Berlin-Dahlem; for original figure legends, see Appendix C.]

the family, showing also some of the characteristic differences of the styles, it does not develop the ideas any further. Berkhey's *Expositio* was a rather rare publication, but it was known to Cassini who eulogized it generously amid some objective and constructive criticisms (Cassini 1818a). The *Expositio* inspired, and at the same time challenged Cassini's genius and he set himself to produce a more comprehensive treatise, which would eventually be destined to be more far-reaching than Berkhey's own. In Cassini's own words: "il [Berkhey] a rendu ma tâche difficile, parce que j'ai dû m'imposer l'obligation de le surpasser" (he [Berkhey] has made my task harder, because I had to impose on myself the obligation of surpassing him; Cassini 1818a).

Berkhey was a man of many talents, being known also as an artist and a poet. He was also a lecturer at the university of Leiden and wrote the monumental *Natuurlijke Historie van Holland* [Natural History of the Netherlands] in nine volumes, which unfortunately was never finished (e.g., two volumes including the part on plants were not published). Some unfortunate events towards the end of his life caused him to spend his later years in poverty and partially secluded from academic life. Berkhey died on March 13, 1812 in The Hague (The Netherlands).

The African genus *Berkheya* F. Ehrhart from the Arctotideae was named after him. This brief sketch on Berkhey was adapted from Aa (1859) and Zagwijn (2004); a wealth of information on the life and work of Berkhey can be found in Arpots (1990), and San Pío Aladrén (2007).

ALEXANDRE-HENRI-GABRIEL DE CASSINI (1781–1832)

Information on Cassini's life and work is scarce. Three of the few accounts are notable: a short biography written by Gossin (1834), an acquaintance from Cassini's judiciary circle, and located at the beginning of the third volume of Cassini's *Opuscules Phytologiques*; Cassini's own remarks at the beginning of the first volume of the *Opuscules* (Cassini 1826); and in footnotes in other works by Cassini (Cassini 1834). Cassini's work on Compositae is a masterpiece. His descriptions of organs are still valid and, for most cases, still interpreted in the same way he described and illustrated them almost 200 years ago. He is the true founder of detailed, rigorous, and systematic studies of Compositae. His modesty and respect for other botanists' works are shown repeatedly throughout his own works, but it is also evident from the comments of scientists who knew him.

It is thanks to King and Dawson (1975) and King et al. (1995a, b) that we have easy access to the amazing array of scientific works of Cassini which, for diverse reasons, appeared scattered in publications of various sorts, some of them rare and under restricted access today. These authors, working on an idea originally suggested by José Cuatrecasas, compiled most of Cassini's scattered publications in five volumes and presented them in three contributions entitled *Cassini on Compositae* I, II, and III.

A member of an illustrious family of French astronomers, Alexandre-Henri-Gabriel de Cassini (Fig. 1.7) was born on May 9, 1781, in the Royal Astronomic Observatory in Paris, the residence of his family since it was built, and four generations had lived there from the time his family had moved from its native Savoy to Paris during the reign of Louis XIV. When the revolution started, he was sent to Savoy to live with his uncle where he studied at the College of Nobles in Turin (today Italy, then the Kingdom of Sardinia). After the revolution, he returned to France, and between 1794 and 1798 he retreated to the family estate in the countryside in Thury (department of Oise) to study under his father.

It was during this time that Cassini developed his profound interest in Nature. Soon after he started observing his surroundings, young Cassini realized that he could not find in the current literature answers to many of his questions, and so he started to make observations, descriptions, and drawings of the plants, animals and fossils that were around him. Later on, following family tradition, he went to Paris to study astronomy. However, his zeal for natural history, especially botany, did not diminish, and during this time he studied botanical books, visited the Jardin des Plantes, and botanized around Paris.

According to Cassini, his lack of private fortune forced him to find an occupation that would allow him to make a living. He began to study law in 1804. He soon attracted the attention of M. Pigeau, one of his professors, who took him as an assistant and eventually a co-worker. Cassini started his career in the French judiciary system as Judge of First Instance and made his way through the system to the highest position, President of the Chamber. Under King Louis Philippe, Cassini was made 'Pair de France', then one of the most prestigious honorary positions in the country.

Cassini developed his ideas on Compositae during his leisure time. Through his *Opuscules* we learn why he eventually took up Botany from among the different fields of learning. In Cassini's own words: "The mineral kingdom was not varied and offered little interest where I lived. I also reluctantly abandoned very soon the study of animals, which interested me the most but caused me terrible disgust, because of the torments and suffering that had to be inflicted on these unhappy creatures. Therefore, I focused my entire attention on the living but insensitive beings that were so abundant around me, very variable and graceful, and that I could

Fig. 1.7. Alexandre-Henri-Gabriel de Cassini (1781–1832). [Engraving by Ambroise Tardieu; courtesy of the Department of Botany, Smithsonian Institution.]

mutilate, dissect and destroy without inspiring pity in me" [*Opuscules Phytologiques*, vol. 1, page ix]. He started studying Compositae in 1810.

In February 1812, Cassini married Agatha de Riencourt to whom he would remain loyally attached. He dedicated the genera *Agathaea* and *Riencourtia*, as a proof of his "*love, esteem, respect, and gratitude*" [*Opuscules Phytologiques* 1, page xv].

Cassini believed that, in order to truly understand the *système naturel*, it was necessary to study all the organs of a plant throughout all the species in the family without exception, and through all the phenological stages. Only after this gargantuan work has been completed could the true order of the plant groups be established. Therefore, Cassini envisaged studying one organ at a time (probably influenced by Adanson). He stated that once all the organs for Compositae were carefully described, it would be possible to tell which characters defined the groups more clearly. Cassini started his *Mémoires* with the description of the style because, according to him, this character was one of the best to infer the natural groups of Compositae. He acknowledged the fact that earlier botanists such as Jussieu, Richard, and Adanson all noticed the importance of this character, but he felt they had failed to extract all possible information from it. Cassini even presented a critique of the description of the styles by these botanists.

In April 1812, Cassini's "Observations sur le style et le stigmate des Synanthérés" was presented at one of the meetings of the Académie des Sciences. This work (Cassini 1813a) was greatly praised by Jussieu and Mirbel. Cassini believed (correctly) that the style was one of the characters with which the natural groups in Compositae could be identified. In this work, Cassini presented the descriptions of the shape and variations of the style throughout the whole family, setting a landmark in the study of the family. Cassini had a methodical way of recording his observations, giving a precise account of the genera and species he had observed in order to reach his conclusions. In a series of seminal papers that started with the one on styles and stigmas, Cassini would describe during the following seven years (Cassini 1813a–c, 1814, 1816a, b, 1817, 1818a, b, 1819a, b) the characters derived from stamens, corollas, achenes, and pappus (Fig. 1.8). In one of these papers, Cassini (1817) would lay out his first three principles governing the classification of Compositae, which he would expand the next year (Cassini 1818b) to include two extra principles. In this later paper, Cassini stated:

"1. The Compositae form so tight an assemblage, that it is absolutely impossible to divide it into a small number of large natural groups, and so in order to divide it naturally it is necessary to recognize 20 small groups or tribes.

2. The characters dividing these natural tribes are those that are based on the style, plus the stigma and sweeping hairs, stamens, corolla, and the ovary; other organs can only suggest generic characters.

3. The hermaphroditic flowers possess all the diagnostic characters that define the tribe they belong to.

4. It is impossible to assign diagnostic characters to the natural tribes except for those common in the family.

5. Many Compositae offer a mix of characters that are present in several different tribes."

In the course of the series of papers mentioned above, the survey of the different organs and the understanding of the whole group progressed at a steady rate, which lead Cassini to gradually improve his classification. At the beginning (Cassini 1813a–c) he adopted a rather conservative approach, taking up from Jussieu's classification a division of the family into three groups: Lactucées, Astérées, and Carduacées, dividing however, Astérées into nine sections. In his final classification scheme (Cassini 1819a) he would recognize 20 tribes (Table 1.1).

Most of the tribes recognized by Cassini still hold their status and are defined by the same characteristics he described near 200 years ago. Note how Cassini's placement of tribes agrees to a certain extent with current classification (in Fig. 1.9, circles in green represent tribes in a clade with lowermost branch containing Senecioneae; circles in orange represent lower branches of the tree, from Barnadesioideae to Corymbieae). Although not a novel idea, Cassini correctly placed Calyceraceae (Boopidées) as one of the closest relatives to Compositae; even his placement of the other relative, Campanulaceae, is not that far from reality, as it is currently placed in the same order Asterales. Cassini took the original idea of placing the families (or tribes in this case) in a linear sequence from Mirbel; however, to reconcile that Vernoniées and Lactucées, according to him closely related, ended up at the extremes of the linear sequence, he placed them in a circle. To show other relationships among the different tribes, he added additional lines to his diagram. The rooting of Cassini's scheme was misplaced, but in general tribes that are closely related were placed near each other. The lines connecting adjacent tribes (e.g., Centauriées and Carduacées) denote a very close relationship, more than mere contiguity would imply. Similarly, lines connecting more distant tribes denote more distant resemblances. Although when describing the figure, Cassini (1818b) mentioned Boopidées (Calyceraceae) and Goodenoviées (Goodeniaceae) as the two closely associated families, eventually he ended up publishing his figure placing Campanulaceae instead of Goodeniaceae. Cassini was not explicit on the reasons explaining why these families were placed close to Vernonieae and Lactuceae; however it seems likely that the discoid heads and the highly dissected actinomorphic corollas of mainstream Vernonieae played a major part in his assignment of a relationship towards Calyceraceae. The zygomorphic corollas of Lactuceae, in addition to the presence of latex, so characteristic in this group, most assuredly pointed a sort of natural idea of relationship between this tribe and Campanulaceae or Goodeniaceae. According to Cassini the reasons behind his decision of placing Lactuceae side by side with Vernonieae, lay on the similar style (not shared with any other tribe) and the members of Vernonieae (*Gorteria*) with zygomorphic corollas that would set a natural transition between both groups.

A note of interest is that although Compositae was his main interest and the topic of most of his printed publications, Cassini also sought to apply his method of systematics to Gramineae, and he published miscellaneous works on other botanical topics.

In 1827, Cassini was elected and appointed *Académicien libre* at the Académie Royale des Sciences. When a cholera epidemic struck Paris in 1832, Cassini became infected and soon there was no hope for him. Alexandre-Henri-Gabriel de Cassini died on April 16, 1832, having been survived by his devoted wife and his caring father. As King and

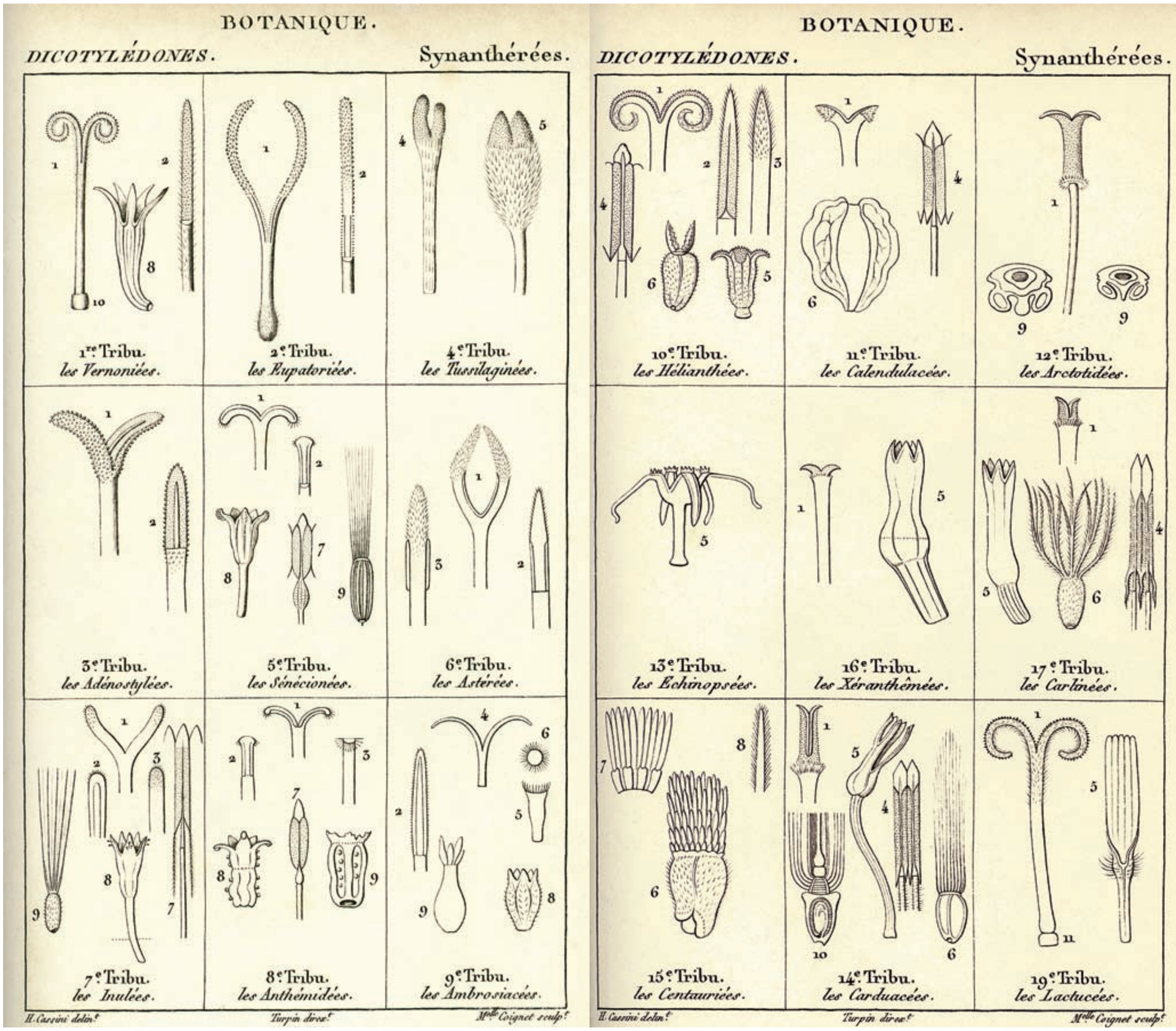


Fig. 1.8. Compositae as seen by Cassini, showing with remarkable skill and accuracy the defining traits of the tribes he recognized, most of which are still valid and defined by the same morphological traits. [Drawings by Cassini, engraving by Coignet, taken from *Opuscules Phytologiques*, vol. 1; courtesy of the Department of Botany, Smithsonian Institution; for original figure legends, see Appendix C.]

Dawson (1975) rightfully stated, because Cassini did not survive his father, he did not acquire the title of Count, which has often been assigned to him incorrectly.

Cassini's detailed descriptions of the styles, anthers, corollas, and achenes of Compositae led him to classify a complex group, which although recognized in the past, was internally in a state of chaos. When Cassini compiled some of the scattered articles that had appeared in different journals and the *Dictionnaire*, he authored the first books published on the classification of Compositae: *Opuscules Phytologiques* vols. 1 and 2, in 1826, only preceded as a book entirely dedicated to Compositae by the general book on the family by Berkhey in 1760. Cassini's generic concepts were rather narrow and comprised only a few closely allied species; also the materials he based his descriptions on correspond in some cases with plants taken from gardens, a situation that sometimes present problems for determination, which in turn can make typifications difficult. This, however, does not diminish the value of his studies; in many cases his genera eventually became sections of larger genera.

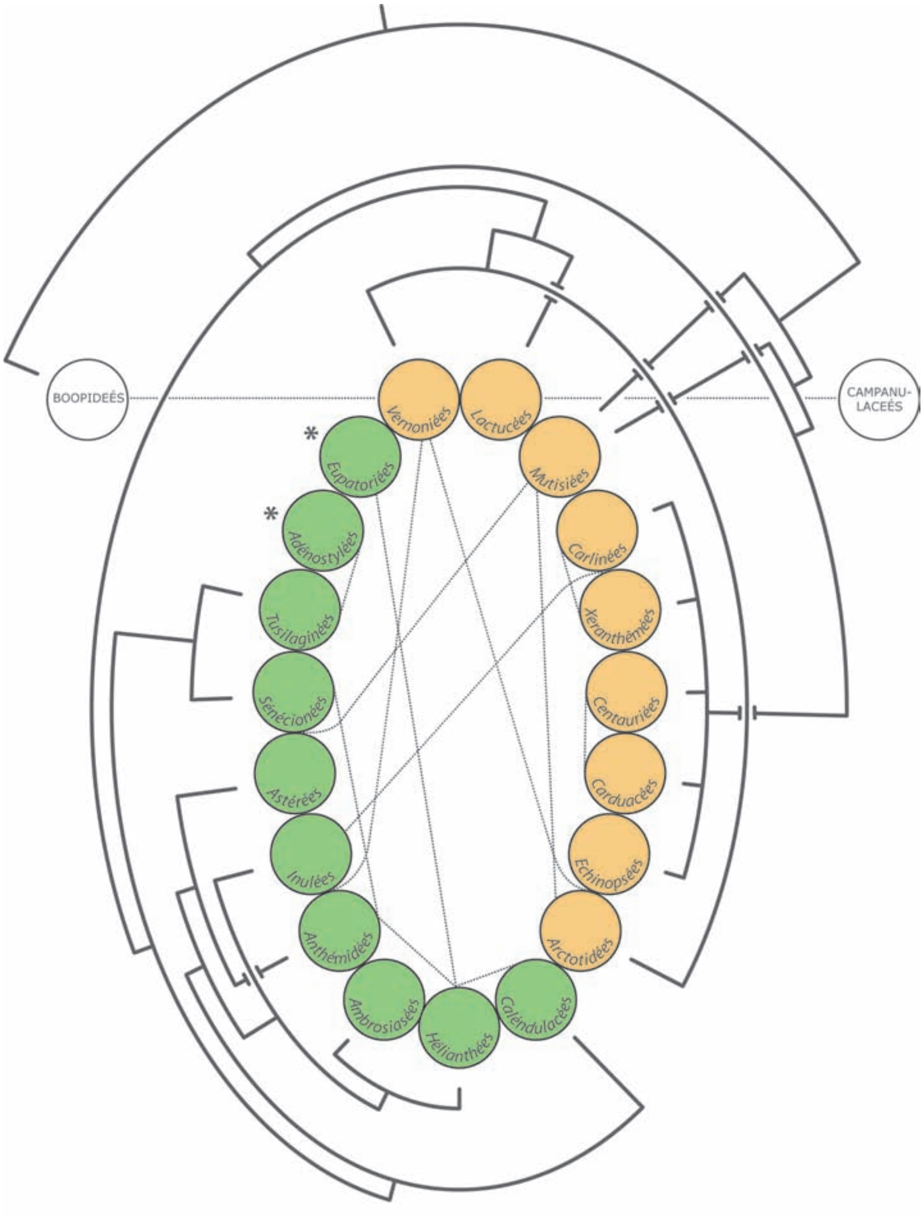
On the introduction to the (posthumously published) third installment of his *Opuscules* (Cassini 1834), dated May 9 of 1831, a rather somber Cassini proclaimed his definitive departure from the study of Compositae. The disputes with other botanists as well as the non-acceptance of his method by the current establishment and the indifference and dismissal of his classification by other

Table 1.1. During a period of six years, Cassini presented his classification of Compositae in a series of classic papers. From the table one sees the impact that his progressive study of more organs had on his classification. The modern flavor of his classification can be seen, which contains more than 15 tribes still recognized.

1813a–c 11 sects. + 1 unclassified	1814 12 sects. + 1 unclassified	1816 17 tribes + 1 unclassified	1817 19 tribes	1819a, b 20 tribes
Lactucées	Lactucées	Lactucées	Lactucées	Lactuceae
		Labiatiflores		
Carduacées	Carduacées	Carduacées	Carduinées	Carduineae
		Carlinées	Carlinées	Carlineae
			Centauriées	Centaurieae
		Xéranthémées		
		Echinopsées	Echinopsées	Echinopseae
Arctotides	Arctotides	Arctotidées	Arctotidées	Arctotideae
		Calendulacées	Calendulées	Calenduleae
				Tagétineae
Hélianthes	Hélianthes	Hélianthées	Hélianthées	Héliantheae
	Ambrosiacées**	Ambrosiacées	Ambrosiacées	Ambrosieae
Chrysanthèmes	Chrysanthèmes	Anthémidées	Anthémidées	Anthémidées
Inules	Inules	Inulées	Inulées	Inuleae
Solidages	Solidages	Astérées	Astérées	Astereae
		Sénécionées	Sénécionées	Sénécioneae
			Nassauviées	Nassauvieae
			Mutisiées	Mutisieae
Tussilages	Tussilages	Tussilaginées	Tussilaginées	Tussilagineae
			Adénostylées	Adénostyleae
Eupatoires	Eupatoires	Eupatoriées	Eupatoriées	Eupatorieae
Vernonies	Vernonies	Vernoniées	Vernoniées	Vernonieae
Hétérogynes*	Hétérandres*	Synanthérées non-classées*		

* Transitory (including unclassified species or genera); ** included as an addendum in the text discussion.

Fig. 1.9. Compositae classification by Cassini vs. current classification (cf. explanation in the text). [Modified from Cassini's *Opuscules Phytologiques*, vol. 1; circular tree adapted from the general tree for the family presented in Chapter 44.]



* nested within Helianthées and Ambrosiasées

leading synantherlogists of his time (e.g.: Kunth and Lessing) most assuredly tired this remarkable man who withdrew from studies on the family.

Cassini's classification (Fig. 1.9) has been confirmed, to a considerable extent, by modern techniques (i.e., chromosome counts, phytochemistry, SEM & TEM examinations, and DNA sequencing), a clear reminder of all that can be done with careful observation and a simple microscope. Cassini is commemorated by the generic name *Cassinia* R. Br. (Compositae). The biographic notes on Cassini presented here were adapted from Gossin (1834) and Cassini (1826, 1834).

CHRISTIAN FRIEDRICH LESSING (1809–1862)

Christian Friedrich Lessing was born on August 10, 1809 in Polnisch-Wartenberg (now Syców, Poland), which at that time was part of the Kingdom of Prussia, and remained a part of Germany until 1945. Little is known about the life of this precocious Prussian botanist. We know that his brother, Carl Friedrich Lessing, was a celebrated painter and his grandfather, Karl Gotthelf Lessing, was the brother of the famous poet and philosopher Gotthold Ephraim Lessing and that Christian Friedrich pursued medical studies in Berlin and graduated in 1832.

Beginning as a schoolboy, he had a great love for botany and enjoyed roaming the countryside much to the dismay of his father. In his youth he was a stammerer, a condition that excluded him from many positions in public life.

Lessing's contributions to the understanding of Compositae appeared as a series of papers published in the journal *Linnaea* from 1829 to 1834, the first one completed when he was still a teenager. However, the publication for which he is best known is that of a separate work on the family, which included the second classification system proposed for Compositae (after Cassini's in 1813): *Synopsis Generum Compositarum Earumque Dispositionis Novae Tentamen Monographiis Multarum Capensium Interjectis*, which appeared in July–August 1832 (Lessing 1832). He assembled the material for this work in part during his travels, and notably from the rich collection of plants in the botanical garden and the herbarium in Berlin, specifically through study of the collections of Vahl, Bergius, Ecklon, Kunth, Thunberg and others. Importantly for South American workers, Lessing had access to collections by Sellow, which resulted in the description of several new genera from that continent.

In the *Synopsis*, Lessing (1832) presented his classification of Compositae, including a total of fourteen pages dedicated to characters that defined the family. Lessing stressed the importance of the style in the classification, depicting this character in four impressive illustrations on the diversity of this feature. He recognized only eight tribes.

Other papers by Lessing refer to Compositae deposited in the Berlin herbarium (Lessing 1829, 1830a, c, d, 1831d), Compositae of the Romanzoff expedition

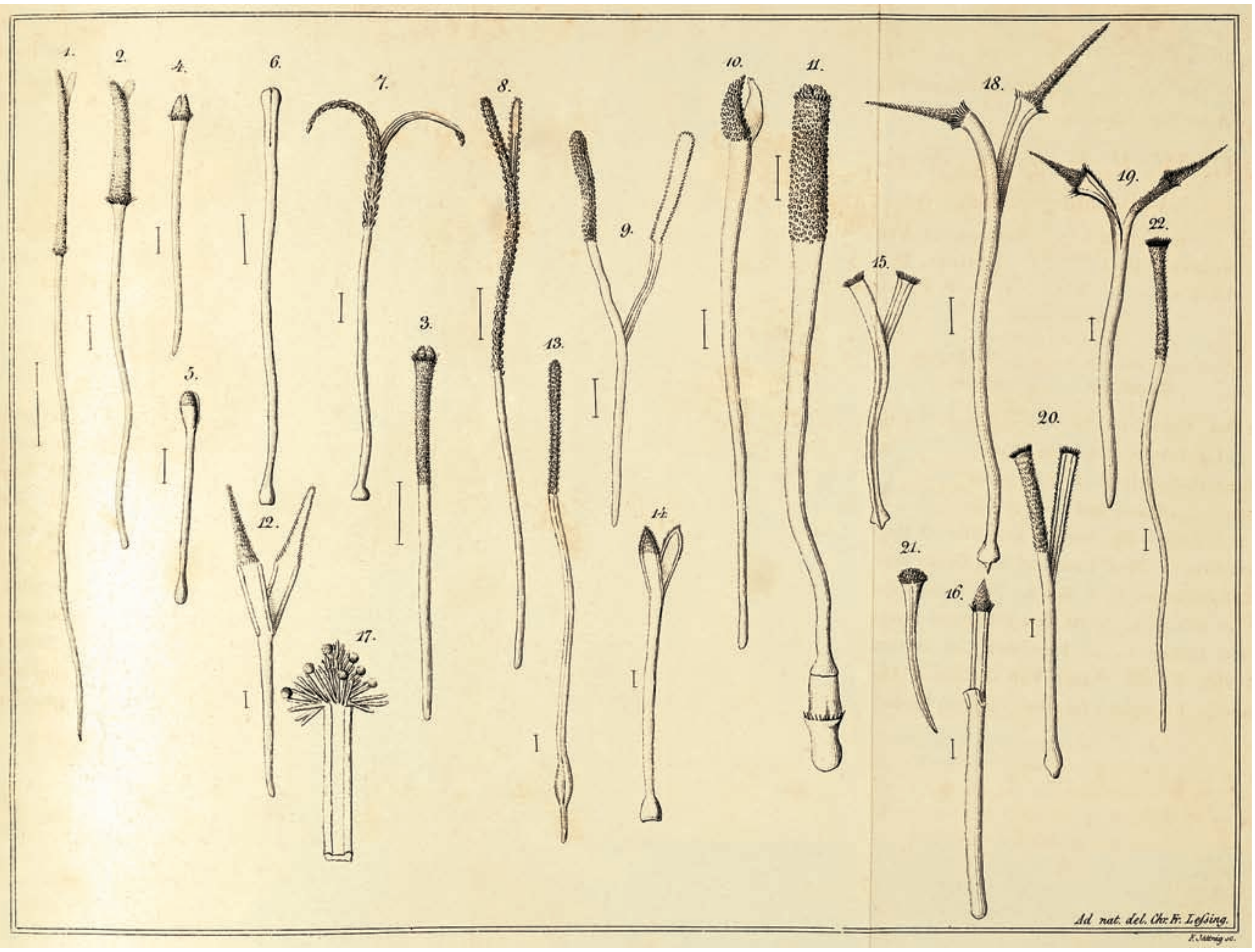
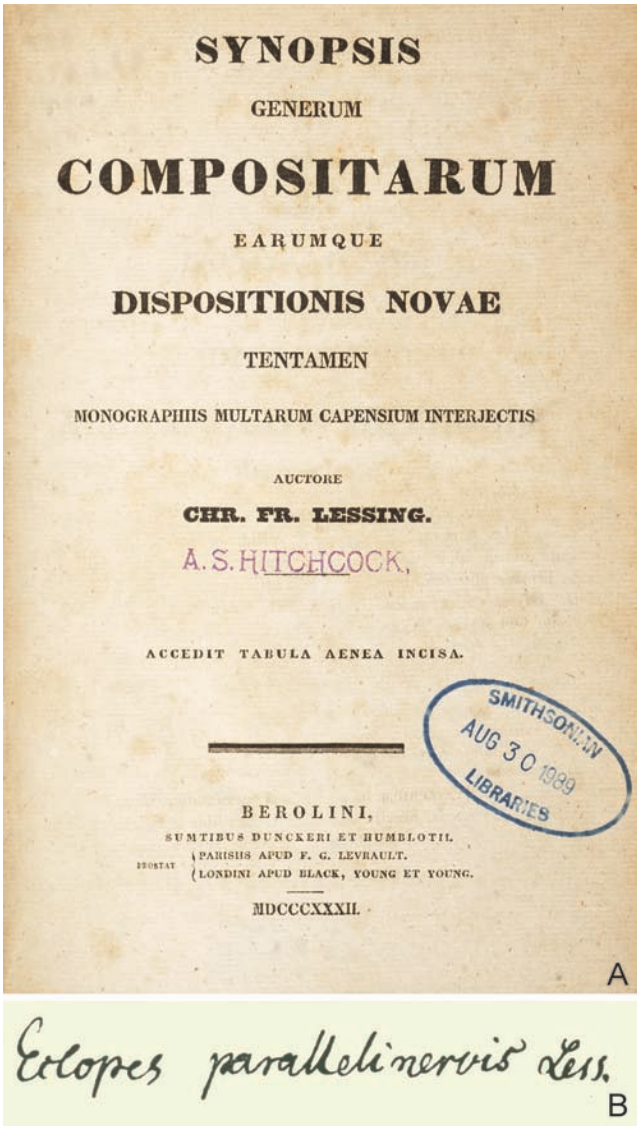


Fig. 1.10. Compositae as seen by Lessing, showing detailed morphology of styles, the character upon which he largely based his classification. [Drawings by Lessing, engraving by F. Jättnig, taken from Lessing's *Synopsis Generum Compositarum Earumque Dispositionis Novae Tentamen Monographiis Multarum Capensium Interjectis*, 1832; courtesy of Smithsonian Institution, Cullman Library; for original figure legends, see Appendix C.]

(Lessing 1831a–c), and Compositae from the collections of Schiede and Deppe in Mexico (Lessing 1830b). All these papers show a rigorous and detailed treatment of the plants considered. However, two notable characteristics of these publications deserve special mention. First, he included dichotomous keys for the identification of some genera and species; these keys are the first of their kind for the identification of genera in Compositae. Second, the illustrations (Fig. 1.10) he presented for the different characters defining the genera and the tribes are remarkable and only equaled by those of Hoffmann, which appeared almost 60 years later. Reading Lessing's work, it is evident that he based his own treatments on the findings of Cassini. However, it was remarkable that he accomplished such a large amount of work in such a short period of time.


SYNOPSIS
GENERUM
COMPOSITARUM
EARUMQUE
DISPOSITIONIS NOVAE
TENTAMEN
MONOGRAPHIIS MULTARUM CAPENSIUM INTERJECTIS
AUCTORE
CHR. FR. LESSING.
A.S. HITCHCOCK.
ACCEDIT TABULA AENEA INCISA.

BEROLINI,
SUMTIBUS DUNCKERI ET HUMBLOTII.
PROSTAT PARISIIS APUD F. G. LEVRAULT.
LONDINI APUD BLACK, YOUNG ET YOUNG.
MDCCCXXXII.

Eclopes parallelinervis Less.

Fig. 1.11. A Title page of Lessing's 1832 book on Compositae; **B** Lessing's handwriting. [A, courtesy of Smithsonian Institution, Cullman Library; B, taken from *Webbia* 32: 14. 1977.]

In 1830 Lessing traveled for seven months in the Scandinavian countries and collected specimens, somehow managing to produce a published account of his travels, including the description of the geography and vegetation, and a flora of the places he had visited. All of this was published in a 300-page volume (Lessing 1831e).

Soon after publication of his Doctoral thesis, and his book on Compositae in 1832 (Fig. 1.11A), Lessing obtained a travel stipend from Alexander von Humboldt, and went to St. Petersburg, Russia, apparently with the intention of making his future living there. This same year, he went on a longer journey to Asiatic Russia, this time thanks to the support of the Prussian and Russian states. He then explored the flora of the southern Urals and the adjoining steppes. The results of this journey (Lessing 1834) would end up being Lessing's last printed contribution; he was only 25 years old.

In these first two years in Russia, Lessing became acquainted with Prince Pastievitch who hired him as a personal physician for his gold washing operations for a period of fourteen years. It was because of this activity that Lessing ended up in Krasnojarsk, Siberia. During this time in Siberia, Lessing learned the business of gold washing in detail and this new skill along with the success of his medical practice led him to resign his position with Prince Pastievitch and start his own gold-washing operation in the Altai. He was initially successful and joined with two Russian businessmen in order to expand his operations. This decision would later result in the loss of most of his fortune and he was left with only some real estate in Krasnojarsk. He withdrew to his remaining properties and resumed his medical profession.

Eventually he was given up as lost by his family as well as his botanical friends. According to some reports he became a beer brewer in his later years. This highly gifted man fell victim to the harsh conditions of Siberian life and the selfishness of false friends. All who knew him described his character as exceptionally noble. Christian Friedrich Lessing died on March 13, 1862 in Krasnojarsk, Russia.

At the beginning of his first publication (Lessing 1829) was the quote "Magno amore in familiam Synantherearum captus atque summorum virorum auxiliis gaudens, clar. Adalb. de Chamisso et D.F.L. de Schlechtendal, qui herbaria ditissima, et sua ipsorum et regia, eximia cum benevolentia et atque confidentia mihi aperuerunt statui hanc familiam fractare, nescius quousque ducar" [Seized by a great love of the family of Compositae I have undertaken to cope with this family. I was glad to have the support of excellent men, the famous Adalb. de Chamisso and D.F.L. de Schlechtendal. With extraordinary benevolence and confidence they opened to me their own herbaria as well as the Regius herbarium, which are very rich. I do not know how far this will lead me"] and we find it inexplicable that after having so profusely declared his passion for Compositae that he should have abandoned it altogether. We can only speculate about the reasons that might have caused this highly gifted young botanist to distance himself from the study of Compositae and his family and friends. It is possible that losses in his gold mining speculations, and also his need to make a living in such a desolate region, may be the main reasons, but why did he remain in Siberia? All his papers appeared in a very short period, but after 1834 he never authored another paper on any subject.

Lessing is commemorated by the generic name *Lessingia* Cham. (Compositae). The biographic notes on Lessing presented here were adapted from Anonymous (1864), Wunschmann (1883), Herder (1888), and Buchholtz (1909). By far the most detailed report on his life is in a massive book by Buchholtz (1909) on the history of the Lessing family. Buchholtz had access to the archives and cites extensively from letters to the family and to the Secretary of the State (Minister) Altenstein. Our efforts to locate an image depicting Lessing failed, and we found only his handwriting (Fig. 1.11B). According to the information available to us and collected from Buchholtz (1909), Lessing refused his wife's wish to have him photographed.

CARL (KARL) HEINRICH SCHULTZ BIPONTINUS (1805–1867)

Born on 30 June 1805 in Zweibrücken, then Deux-Ponts, Department Mont-Tonnère, France, Carl Heinrich Schultz (Fig. 1.12) was the second son of the apothecary Carl Friedrich Schultz and his wife Marie Caroline. Since Schultz is an extremely common surname Carl Heinrich later on added the epithet "Bipontinus" (two bridges), referring to Bipontinum, the Latin name of his birthplace, hence the standardized author abbreviation "Sch.Bip."

Carl Heinrich grew up in a well-to-do family; among his uncles were Dr. Carl Ferdinand Schultz, physician in Zweibrücken, Dr. Fleschütz, physician-in-ordinary to Princess Therese of Saxony-Hildburghausen, Queen of Bavaria, and the famous Dr. Johann Gottlieb Fichte, professor of philosophy at Berlin University and its first rector. When Carl Heinrich entered the gymnasium in Zweibrücken, the Congress of Vienna had reshuffled Central Europe and his native town had become part of the Kingdom of Bavaria.

At age 20, Carl Heinrich moved to Erlangen, then also belonging to the Kingdom of Bavaria, where he started to study medicine and joined the Burschenschaft Germania. Because of the infamous Carlsbad Decrees, which had banned all student fraternities, this was both illegal and dangerous, in particular since the Germania clearly aimed for a political unification of the German speaking area and used the strictly forbidden colors black-red-gold. However, Carl Heinrich remained unharmed and later moved to Munich University where he not only continued his political activities but also finished his medical studies as early as 1829 and published a medical thesis. After having passed his biennium practicum with his uncle in Zweibrücken and as an assistant at the Hôtel de Dieu in Paris, Carl Heinrich passed his approbation examination in Munich and opened his practice in the Bavarian capital.

Nothing indicates that he took part in the Hambacher Fest, a festival celebrated in late May 1832 near Neustadt an der Weinstraße, then belonging to the Kingdom of Bavaria, with about 30,000 participants from all ranks of society, workmen, students and members of parliament. Although disguised as non-political county fair, liberty, civil rights and national unity were demanded with highly critical texts published in the local press. Political pamphlets printed in Zweibrücken and elsewhere were sent in some number to Carl Heinrich in Munich who rather unwisely made them freely available and even sold the rest to a bookseller. Back from an excursion to the Tyrol in Munich he was arrested, charged for high treason and in December 1832 found guilty of having attempted high treason as well as of committing an insult against his Majesty the King in the second degree. The sentence was severe: imprisonment of the second class for an unlimited period of time, then effectively sixteen years. A career seemed to have come to an end, in particular since Carl Heinrich' s name was listed in the Black Book of revolutionaries kept in Munich. In short he suffered a fate similar to that of the key figures of the Hambacher Fest.

The family's network of contacts plus the huge sum of 5000 guilders helped to speed up the release of Carl Heinrich, who after three years in jail returned in 1836 to his native Zweibrücken. He had learned his lesson, sent a letter of apology to the minister of the interior in Munich, and refrained from any further political activity. The same year Carl Heinrich was appointed physician of the hospital in Deidesheim, a small town in the Bavarian part of the Palatinate. For the rest of his life he maintained this position that came with an official residence in hospital. On 15 June 1837, Carl Heinrich married Carolina Giessen, the daughter of the owner of a local vine-growing estate, and had two sons and two daughters with her. He settled down in Deidesheim as a respected physician with a busy practice. His workload fluctuated depending on epidemics and the number of visits to the sick, infirm and dying, but otherwise peaceful years followed.

After a remarkably active life Carl Heinrich Schultz Bipontinus died on December 17, 1867 in Deidesheim, then Kingdom of Bavaria, and was buried in the local cemetery, survived by his two sons and younger daughter. He was also survived by his elder brother Friedrich Wilhelm, an apothecary and botanist in Wissembourg who had earlier fled his native town because of political reasons, his younger brother Wilhelm Eugen, an apothecary in Zweibrücken, and his elder sister Caroline Sophie.

Carl Heinrich seems to have developed an early taste for the natural sciences in Zweibrücken, which was further developed by the botanist Wilhelm Daniel Joseph Koch at Erlangen University. The excursion to the Tyrol was clearly a botanical one, later described in print. However, the focus on synantherology developed only later, in prison, with Julius Hermann Schultes the younger, physician in Munich, acting as his key contact. It is hard to believe but true that Carl Heinrich had not only books and letters sent into his confinement, but even Compositae achenes that he managed to raise in the prison court, a fact substantiated by a label in FI stating "culta in aula carceris regii monacensis Schultz Bip." [grown in the court of the Royal Prison in Munich]. Carl Heinrich was also permitted to send letters from prison to his botanical friends, the red lines in the four corners of the paper are evidence of the scrutiny of the censor. Even more surprising is the fact that Carl Heinrich had his first papers published while still an inmate of the infamous Fronsveste in Munich, dealing with Cichorieae, notably Hypochaeridinae.

Fig. 1.12. Carl (Karl) Heinrich Schultz Bipontinus (1805–1867). [Photograph taken from Portrait Collection, courtesy of Botanic Garden and Botanical Museum Berlin-Dahlem.]

When finally released he continued with synantherology, apparently as a hobby and alternative to his busy practice. Based in the tiny town of Deidesheim, Carl Heinrich could not rely on an institutional infrastructure but rather had to build up his own herbarium and library. This he started by asking fellow botanists for duplicates and by maintaining an extensive correspondence with many of his colleagues and the main collectors of his time, among them Willibald Lechler, Gilbert Mandon, Eduard Rüppell, the Schlagintweits, Friedrich Sello, Jules Pierre Verraux, Hugh Algernon Weddell, to name a few. Remarkably, Carl Heinrich also grew very many species from seed in a garden at Deidesheim, possibly the hospital's, and had herbarium specimens prepared from them. Little is known about his travels; he visited Vienna in 1856, London in 1866 and must have been to the Royal Herbarium in Berlin since his private herbarium contained very many fragments from specimens kept in the latter institution, including some taken from the Willdenow Herbarium. There is evidence that he also attended several meetings of naturalists in Central Europe where he lectured, mainly on Compositae.

Carl Heinrich studied the whole geographic and taxonomic range of this family, in particular Cichorieae, and published widely and extensively, mainly in journals, e.g., *Flora*, *Linnaea*, *Bonplandia* and *Jahrbuch der Pollichia*. An important contribution to the systematics of Anthemideae was his paper "Über die Tanaceteen" (Schultz Bipontinus 1844), dedicated to his mentor and friend Koch containing a new circumscription of genera such as *Chrysanthemum* L. and *Matricaria* L. using mainly fruit characters.

Several of the generic names he coined have stood the test of time; among his larger genera are *Critoniopsis* Sch. Bip., *Fleischmannia* Sch. Bip. and *Tripleurospermum* Sch. Bip. However, many other names remained unpublished and were validated by subsequent workers, which results in a long list of names having "Sch. Bip. ex" as author citation, e.g., *Laggera* Sch. Bip. ex Koch. The reason for this is not entirely clear, but the busy practice seems to have been an important cause. Overwhelmed by the steady flow of collections reaching him from all over the world, he often only published preliminary lists of names. Carl Heinrich's suprageneric and infrageneric entities are a nightmare for the monographer, being often both chaotic and confused. His single account for a flora is the treatment of Compositae for the *Histoire Naturelle* *des Iles Canaries* published between 1844 and 1850 in several installments by Philip Barker Webb and Sabine Berthelot in Paris. An extensive series of letters by Carl Heinrich to Webb on this subject is kept at the Museo di Storia Naturale in Florence, all now available on the Internet but not yet analyzed. Similarly very many more letters by Carl Heinrich, mostly in French or Latin, still await further study, e.g., those kept in the Conservatoire Botanique in Geneva, the Pfälzische Landesbibliothek in Speyer and elsewhere. Carl Heinrich published little outside Compositae. Clearly he simply did not have the time to write a magnum opus like his colleagues placed in more comfortable circumstances. With the exception of his paper "Beitrag zum Systeme der Cichoriaceen" (Schultz Bipontinus 1866), a critical synopsis of Cichorieae aiming at a global approach, his contributions refer as a rule to a single genus or a small group of genera.

After Koch's death in 1849, his chair at Erlangen University became vacant. In order to impress the selection panel Carl Heinrich seems to have quickly validated the generic name *Erlangea* Sch.Bip., and indeed the senate proposed him as full professor to the ministry responsible for university affairs in Munich. However, the ministry of the interior vetoed this move because of Carl Heinrich's political past and the whole affair came to nothing. In 1840, Carl Heinrich was among the cofounders of an association named Pollichia, which continues to the present day as the Palatinate's society to promote the study of natural history and the preservation of the country. Since 1843, he was a fellow of the famous Leopoldina, the Imperial Academy of Natural History and Medicine then based in Breslau (Wrocław) with the cognomen Henri Comte Cassini. He was made an Adjunkt [member] in 1853 and in 1865 received the order of St. Michel first class of the Kingdom of Bavaria. Late in life Carl Heinrich distributed a series of exsiccate under the title "Cichoriaceotheca", with sets in several major institutions.

Upon his death Carl Heinrich's library was sold to a bookseller in Frankfurt and broken up, while his priceless herbarium, probably the most comprehensive collection of Compositae then in existence, passed to his elder son Carl Heinrich, a wine merchant in Deidesheim. He sold it to Ernest Saint-Charles Cosson in Paris who seems to have kept it intact. In 1904, Ernest Saint-Charles's grandson Ernest Armand Durand presented his grandfather's and Carl Heinrich's collections to the Muséum National d'Histoire Naturelle in Paris where it was integrated into the Herbier Général. The specimens from Carl Heinrich were mounted with a note "Herb. Schultz Bip." added to the sheet along with all his manuscripts and annotations; this trove of information is not yet fully appreciated by many synantherologists. Specimens annotated by Carl Heinrich in his characteristic hand are often difficult to decipher; they are found in many herbaria, in particular Florence, where Webb's collections from the Canary Islands are preserved.

Carl Heinrich is commemorated by the generic name *Bipontia* S.F. Blake = *Soaresia* Sch.Bip., nom. cons. (Compositae). The biographic notes on Schultz presented here were adapted from Anonymous (1868), Becker (1932), Poeverlein (1905), Remling (1847), Spilger (1942), and Strebel (1955).

GEORGE BENTHAM (1800–1884)

Son of Samuel Bentham, a well-known British naval architect, George Bentham (Fig. 1.13) was born in Plymouth, England, on September 22, 1800. When Bentham was only five, his father was asked to build vessels for the British navy in Russian dockyards so the family moved to St. Petersburg. While in Russia, George Bentham quickly learned Russian and French, and also became interested in music. When war broke out between Russia and England in 1807, the family swiftly returned to England where they lived till 1814.

Bentham never attended school, and his education (and that of his brothers) was carried out at home through private tutors as well as his parents, who always engaged their children in varied cultural activities. It is perhaps because of this circumstance, which Bentham later regretted, that he remained a rather shy individual for the rest of his life.

After Napoleon was defeated by the allies and peace returned to continental Europe, the Benthams moved to France. Now that George's father had retired, they decided to enjoy the better climate of the continent, and at the same time they would offer their children a better education, since living abroad was much more affordable than in their own country.

The portraits of Bentham depicting him with a rather sober expression can be misleading in terms of showing his true character. Throughout his life he enjoyed getting together with friends after work and attending concerts and plays. Apparently Bentham was fond of music and theater, and even a performer of both. He seems to have particularly enjoyed the long festivities of the French Carnivals during his youth, hardly missing a single dance.

In 1817, Bentham's mother introduced him to botany when she bought De Candolle's *Flore Française* (Lamarck and De Candolle 1805) to understand the plants surrounding their recently acquired estate in southern France. Bentham was struck by the synthetic way in which the information to identify the plants was presented, and immediately started to use De Candolle's flora to identify the plants near his house. In Bentham's words, "I had not the slightest idea of what was meant by any of the commonest botanical terms. All these I had to work out from the introduction, and I spent the whole morning over the *Salvia*…."

Bentham's mother was also responsible for introducing young George into drying and preserving specimens, and he did a considerable amount of collecting during the rest of his time in France. In later years, Bentham received copious amounts of specimens from almost anywhere, becoming involved with several floristic treatments around the world. He corresponded with nearly all botanists of his time, and he visited most European colleagues at least once.

In 1826, Bentham had decided he would dedicate his life to law and science, the first to make a living and the second for recreation. That same year the family returned to England. Bentham devoted himself to the study of law and to help his uncle in his writings on logic, relegating botany for evening hours or other spare time. However, after getting married in 1833 he soon found out that it was unlikely that they would have children, and since their income was sufficient for a moderate life style, Bentham left law, and dedicated himself exclusively to botany.

Fig. 1.13. George Bentham (1800–1884). Portrait taken just before Bentham started his major undertaking, the *Genera Plantarum*. Notice Bentham's signature at the bottom and year the picture was taken. [Photograph courtesy of Hunt Institute.]

It is impossible to present a full account of Bentham's published accomplishments in this short chapter. Among his major contributions, the most well-known one is probably *Genera Plantarum* published in co-authorship with Joseph Dalton Hooker over a span of almost 20 years. This work, together with the unfinished *Prodromus* edited by the two De Candolles (De Candolle and De Candolle 1824–1873), Kunth's *Enumeratio* (Kunth 1833–1850) and Engler and Prantl's *Die natürlichen Pflanzenfamilien* (Engler and Prantl 1887–1915) ranks among the four most important taxonomic productions of the 19th century. Bentham also contributed to De Candolle's *Prodromus* (De Candolle and De Candolle 1824–1873), most notably treatments of Ericaceae, Labiatae, and Scrophulariaceae among several other minor groups during the years 1838 to 1864. In addition, mention should be made of Bentham's participation in yet another important botanical enterprise of the 19th century, Martius' *Flora Brasiliensis* with the treatment of Leguminosae from 1859 to 1876.

If this short list of only the major botanical enterprises with which Bentham was directly involved is not sufficient proof of his impressive efficiency and unparalleled capacity, along with the already-mentioned publications, we can add that he produced, in a period of fifteen years, *Flora Australiensis* (Bentham 1863–1878), a monumental treatment of some 8400 species extending over 4000 pages arranged in six massive volumes, all without a co-author.

Bentham's treatment of Compositae in the *Genera* (Bentham 1873a) is considered a classic and an unavoidable reference for any researcher of the family. Together, with Hoffmann's treatment, they constitute the two most important references at the generic level for the family extending over more than a hundred years. As a companion to his treatment, he also published a paper on the classification, history and geographical distribution of the family (Bentham 1873b). In this interesting paper, Bentham presented an account of his system and acknowledged that his system was in a way similar to that of Cassini's, having used basically the same characters, stating however that he had arrived at these conclusions independently.

Joseph Dalton Hooker (Fig. 1.14), friend and colleague in the herculean undertaking of the *Genera Plantarum*, said of Bentham: "It is difficult to give an idea of the

Fig. 1.14. Hooker and companions on a field trip in the Rockies, La Veta Pass, Colorado, 1877, 9000 feet. Left to right seated: Sir Joseph Dalton Hooker, Professor Asa Gray, Mrs. Strachey, Mrs. Asa Gray, Dr. Robert H. Lambourne, Major-General Richard Strachey and Dr. F.V. Hayden. Mr. James Stenson is standing between Dr. Lambourne and General Strachey. Although Bentham was mainly responsible for Compositae in the *Genera*, as well as for many other groups, he remarked that all changes or new proposals in the *Genera* were done in consultation with his co-author. Asa Gray (1810–1888) was one of the pillars upon which North American Botany was erected. Although Gray's field of action encompassed the whole plant realm, he started his work as a botanist on Compositae and contributed with many works on the family. A thorough account on the life and work of Asa Gray is found in Dupree (1959). [Photograph reproduced with the kind permission of the Director and the Board of Trustees, Royal Botanic Gardens, Kew.]

prodigious amount of systematic and descriptive work in phanerogamic botany that Bentham accomplished. In the *Genera Plantarum* there is hardly an order of any importance that he did not more or less remodel. His labours on the Compositae, Gramineae, Cyperaceae, and Orchidaceae are especially noticeable … His treatises on the Leguminosae are no less exhaustive and valuable; and there is not a temperate or tropical region of the globe whose floras have not been largely elucidated by him … Of his amiable disposition and his sterling qualities of head and heart it is impossible to speak too highly, though cold in manner and excessively shy in disposition, he was the kindest of helpmates and most disinterested of labourers for others."

The capacity for work that Bentham showed throughout his lifetime is one of monumental proportions as evidenced by his published record and Hooker's comment. A very inspiring note on this, however, can be found in one anecdote mentioned by Jackson in his biography of Bentham: "On Saturday, 8th August, he [Bentham] finished the work on Orchidaceae for the *Genera*, half-an-hour before the close of his day's work. Most men would have put down their pen with a sight of relief and attempted nothing fresh for the moment; not so Bentham. Without a moment's hesitation he begged one of the assistants to bring him the unnamed and doubtful specimens belonging to the next part of his task [the Cyperaceae], on which he at once commenced."

After living a long and eventful life, George Bentham died in London on September 10, 1884, just a few months after the completion of the *Genera Plantarum*.

Bentham (1873b) said of Compositae, "[They] are at once the largest, the most distinct, and the most uniform, and therefore the most natural, of all orders of Pharenogamous plants … the principal changes I have proposed in the general methods of Lessing and De Candolle [on Compositae] were determined upon and worked out long before I was aware that they were in a great measure a return to that of Cassini. The confusion which his multiplication of names had produced, and the unusual terminology of his descriptions, had excited in my mind a prejudice against him, until, after completing my work of detail, I came to study his generalizations, which showed how much better his views of affinities coincided with mine than those of his successors." Bentham will always be remembered as one of the greatest botanists of all times, and he was responsible for bringing Cassini's earlier works to the attention of the Compositae community. The biographic notes on Bentham presented here were adapted from Filipiuk (1997) and Jackson (1906).

KARL AUGUST HOFFMANN (1853–1909)

Karl August "Otto" Hoffmann was born on October 25, 1853, in Beeskow, Brandenburg, Prussia. We know very little about the life of this talented Prussian botanist who in 1872 went to Berlin University to study mathematics and natural history. Later on, he attended Göttingen University for his graduate studies; he received his Doctorate degree in February 1876, though not in botany, his thesis was on "spherical curves", a mathematical subject. Hoffmann's strong interest in mathematics during his time as a student did not deter him from devoting important time to botany. He did much more on the subject than merely attend the official field excursions, clearly defining the future of his academic botanical endeavors.

Hoffmann's contributions to botany had one striking similarity with that of Cassini's: his scientific activities, and specifically his studies on Compositae, were undertaken during whatever "spare" time he had left from his main occupation. In Hoffmann's case, he was a high school teacher. He started as a private teacher in Dresden and, beginning in October 1877 until the end of his life, he taught at the prestigious Friedrichswerdersche Gymnasium in Berlin.

He collaborated with his mentor, Wilhelm Vatke, in the study of the voluminous material from J.M. Hildebrandt from Madagascar. Later on, Hoffmann worked on some other families from the rich collections of Rutenberg, also from Madagascar. He then continued to study material collected by Major von Mechow and Teusz from the interior of Angola.

However, it is in Compositae that Hoffmann produced most of his work, and in which, within a few years, he gained a deep knowledge. He benefited from the copious material he received from travelers such as Dusen, who collected in Patagonia and Tierra del Fuego, and Chevalier, who sent him specimens collected in Sudan, but also from his own hard work.

Hoffmann published several papers on the family, but his major contribution was the treatment of Compositae in the monumental *Die natürlichen Pflanzenfamilien*, edited by Engler and Prantl (Hoffmann 1890–1894). Hoffmann's classification was very similar to that of Bentham's, but his work included new information generated since Bentham's treatment was published. His treatment also differed from that of Bentham in the impressive inclusion of 108 notably detailed figures illustrating the diversity across the family (Fig. 1.15A, B). Hoffmann's work included 806 genera and constituted the last treatment at the generic level for Compositae for a hundred years until the cladistic treatment of Bremer (1994) and the revision edited by Anderberg et al. (2007).

Hoffmann published numerous individual papers as well, and in a later publication he discussed the differences between his classification and that of Bentham. Further data were published as two "Nachträge" to the *Die natürlichen Pflanzenfamilien* (1897, 1900). Due to a lack of time, he was not able to contribute to "Nachtrag III" edited by R. Pilger in 1908. Hoffmann donated his extensive and well-curated herbarium to the Berlin Herbarium. The well-known traveler and explorer-botanist R. Schlechter named a genus from western Africa, *Hoffmanniella* (Compositae), after Hoffmann.

Hoffmann was also an extraordinarily talented musician, a good husband, and an understanding father. He died on September 11, 1909 following an appendicitis operation, almost certainly in Berlin. An image of Hoffmann still remains elusive despite looking up several sources and consulting several colleagues around the globe. The biographic notes on Hoffmann presented here were adapted from Ascherson (1910).

BENJAMIN LINCOLN ROBINSON (1864–1935)

Benjamin Lincoln Robinson (Fig. 1.16) was born in Bloomington, Illinois on November 8, 1864, the youngest of eight children. He was one year younger than his brother, the historian James Harvey Robinson. He had an early interest in natural history, entered Williams College in 1883, and transferred to Harvard College in 1884, graduating in 1887. He married Margaret Louis

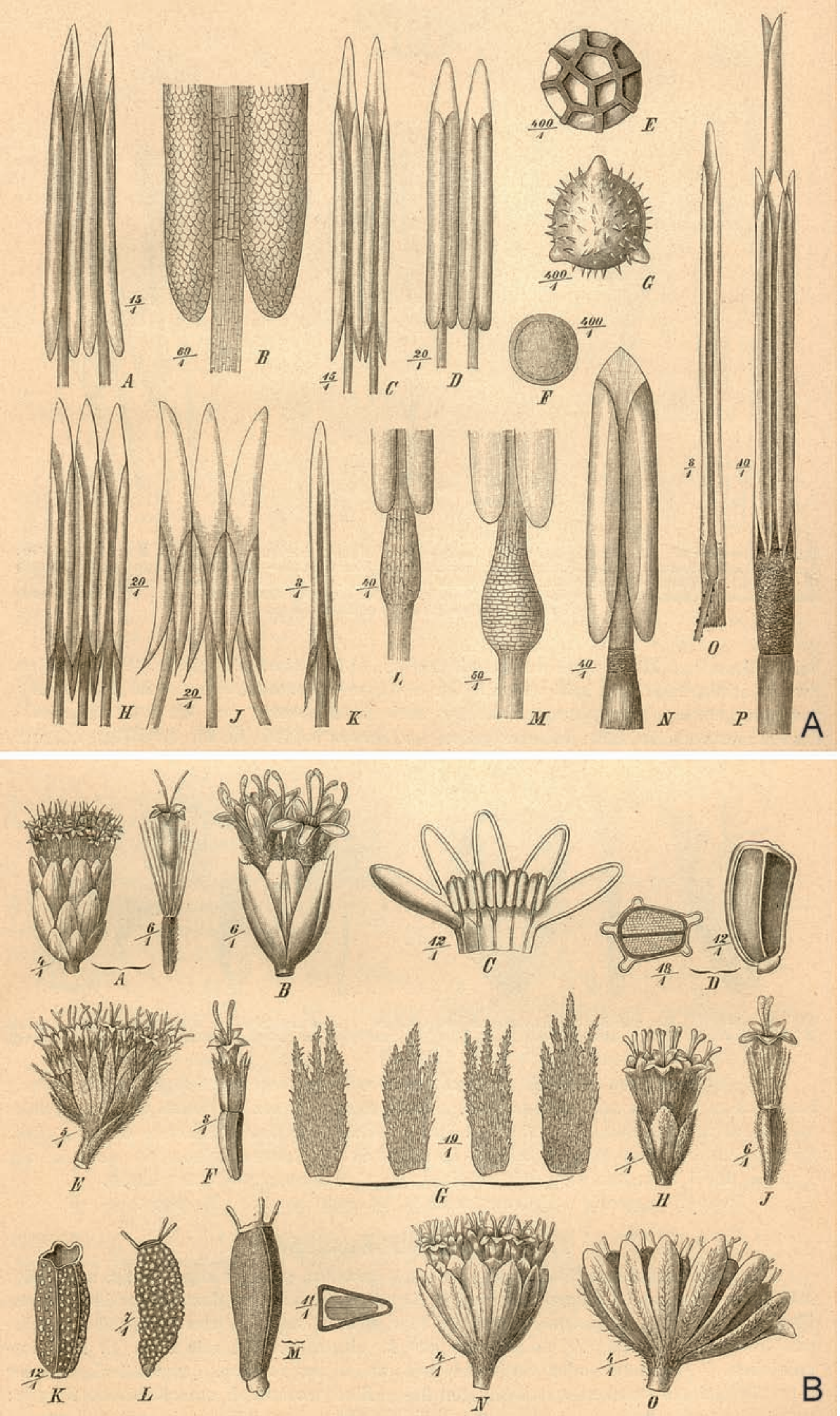


Fig. 1.15. Illustrations from Hoffmann's treatment of the Compositae for Engler and Prantl's *Die natürlichen Pflanzenfamilien*. These two figures, out of the 108 figures accompanying the text, show Hoffmann's detailed understanding of morphology in Compositae. **A** anther and pollen morphology; **B** plate depicting several Eupatorieae genera with a high degree of detail on pappus and achene structure. [From *Die natürlichen Pflanzenfamilien* 4(5); A, figure 65, page 104; B, figure 77, page 132; courtesy of MVFA herbarium; for original figure legends, see Appendix C.]

Casson in Hennepin, Illinois, and had a single child who lived only a few years. Robinson pursued graduate work at Strassburg University where he studied with Hermann Graf zu Solms-Laubach. His disseration was on plant anatomy and he graduated in 1889. Robinson returned to Cambridge, Massachusetts in 1890 where he became an assistant to Sereno Watson, then Curator of the Gray Herbarium at Harvard. He retained enthusiasm for Germanic culture and for some years conducted a course in scientific German. In 1892, Robinson was appointed successor to Sereno Watson upon the latter's death. In 1899, Robinson became the first incumbent of the Asa Gray Professorship of Systematic Botany established through a gift from Mrs. Gray.

During more than thirty years at the Gray Herbarium, Robinson improved the facility, greatly increased its budget, served as editor of the journal *Rhodora*, brought into final form the extensive manuscripts covering many families of plants in Gray's *Synoptical Flora of North America* (Gray 1878–1897), published extensively on Mexican collections of Pringle and Palmer, and completed the seventh edition of *Gray's Manual* (Robinson and Fernald 1908). Robinson encouraged collecting efforts in South America and his collaboration with South American botanists lead to his election as honorary academician of the Museo de La Plata (Argentina). In North America, Robinson was president of the Botanical Society of America (1900), vice-president of the American Association for the Advancement of Science (1905) and a member of the National Academy of Sciences.

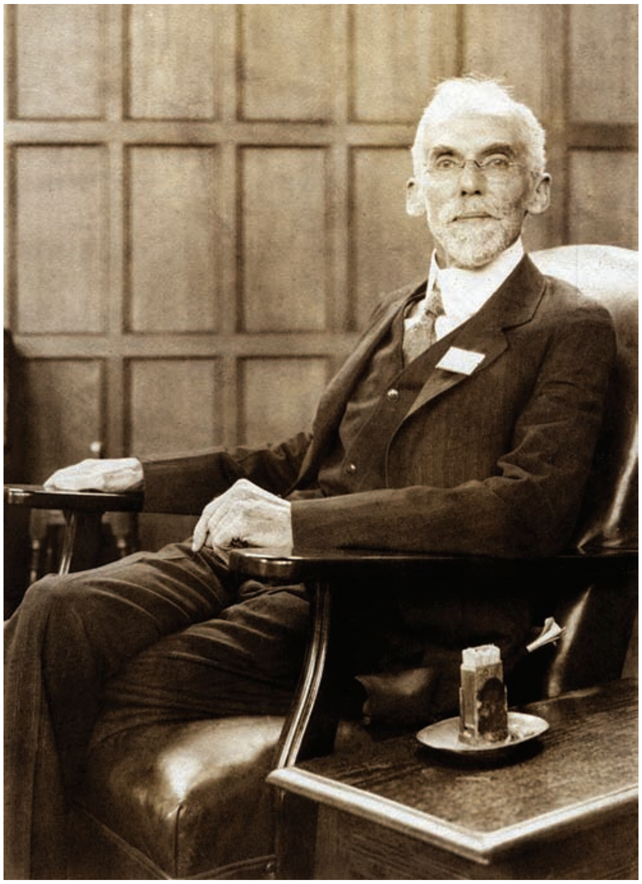


Fig. 1.16. Benjamin Lincoln Robinson (1864–1935). Photograph taken in 1926 at 4th International Botanical Congress, Ithaca, New York. [Courtesy of Hunt Institute.]

Robinson visited Europe a number of times to study type material. During International Botanical meetings, Robinson served as a member of the Commision internationale de Nomenclature botanique in 1905, as President of the International Botanical Congress at Brussels in 1910, and as a member of the Commission de Nomenclature général in 1926. Robinson was a corresponding member of the Deutsche Botanische Gesellschaft, of the Botanischer Verein der Provinz Brandenburg, a member of the Société de botanique de Genève, a foreign member of the Linnean Society of London, and a member of many other organizations.

Much of his research was devoted to the study of the Compositae tribe Eupatorieae. This included his treatments of *Eupatorium* and *Ophryosporus* in "Trees and shrubs of Mexico" (Standley 1926), and many other treatments cited in the latter work by S.F. Blake, including with Jesse Greenman on *Verbesina*. Robinson produced a series of studies on *Eupatorium*, *Mikania*, *Stevia*, and other genera for various countries in South America (see King and Robinson 1987). Benjamin L. Robinson was well aware of the artificiality of the system of classification within which he worked, for instance, in 1913 he included in the genus *Alomia* Kunth an element that he himself acknowledged was an epappose representative of *Trichogonia* DC. He (1926) comments in his description of the Mexican *Eupatorium rivulorum*: "This species in habit, habitat, foliage, and in some details of pubescence recalls *Fleischmannia arguta* (Kunth) B.L. Rob. The species if referred to *Fleischmannia* would by its indefinite (though not very numerous) pappus bristles, break down the slight distinction between that genus and *Eupatorium*. If, on the other hand it is referred to *Eupatorium* (from which on technical grounds it cannot be readily separated) its close similarity to *Fleischmannia* must render the further separation of that genus rather artificial. Neither disposition is entirely satisfactory." In discovering that his *Eupatorium dejectum* was the same as *Helogyne tacaquirensis* Hieron., Robinson (1930) questioned the distinction of the latter genus. The genera that Robinson questioned have proven to be distinct, but only after severe redelimitation of *Eupatorium*, an operation that Robinson never undertook. Robinson understood that when using an artificial system, it had to be used rigorously even in defiance of obvious relationships. The fact that Robinson found the Bentham system highly artificial at the generic level was not a surprise. By all indications, Bentham himself was fully aware of the artificiality of his system at various levels.

Robinson did very little fieldwork, apparently never visiting tropical America on whose flora he worked extensively. He did produce a number of students, including Sidney F. Blake, Merritt L. Fernald, Jesse M. Greenman, Lyman B. Smith, and at some stage Julian A. Steyermark.

Benjamin Lincoln Robinson died at Jaffrey, New Hampshire, July 27, 1935, after many years of suffering from pulmonary difficulties that ultimately developed into fibrosis. The biographic notes on B.L. Robinson presented here were adapted from Fernald (1935).

JAMES SMALL (1889–1955)

James Small was born in 1889 in Brechin, Forfarshire (United Kingdom). Beginning early in life, he was interested in plants and in 1913 he obtained his degree in pharmaceutical chemistry. Soon after graduating, he began teaching at the University of Durham, an activity that was interrupted by his participation in WWI. However, as a result of battle wounds, he left the army and was able to return to academic activities.

In 1917, Small married Helen Patisson with whom he had two sons and one daughter. Small taught in several universities across the United Kingdom, although he was also Chair of Botany at Queen's University in Belfast, Ireland, from 1920 until a few months before his death. He is mostly remembered for his *Textbook on Botany for Medical and Pharmaceutical Students* (Small 1921), his research on pH in plants (Small 1929, 1946), and his prolific production of papers on quantitative evolution. Small also conducted several ecological studies which eventually resulted in detailed floristic knowledge of several areas in the northern part of Ireland.

It was after his participation in the war that Small began his research on Compositae, research which would eventually lead to the publication of his doctoral monograph: "The origin and development of the Compositae" (Small 1917). In this contribution, Small presented a general introduction to the family with a detailed analysis of morphological characters as well as comments on the phylogenetic relationships and origins

Fig. 1.17. Photograph taken at a meeting of the British Association for the Advancement of Science held at Belfast in 1952. Seated, from left to right: N. Ferguson, J. Walton, J. Small, H. Thomas, J. Ramsbottom, G.N. Coates (seated on floor). [Courtesy of J.S. (Pat) Heslop-Harrison.]

of the family. He considered Senecioneae to be the basal group from which the rest of the family radiated. This view, although now proven incorrect, was a novelty at that time, particularly when other systematists had been considering Heliantheae as the most primitive element in the family. In his monograph, Small not only presented an updated morphological synopsis for the family but also, interestingly enough, the historical background associated with the study of each organ used in the classification of Compositae.

According to some accounts, Small was also notorious for being a rather charismatic individual who would delight audiences with provocative statements and a good sense of humor. He is also remembered for several inventions and improvisations, among which were a plant press and a leaf clasp, to aid in his daily work. He was an excellent photographer and member of three photographic societies, one of which was the Royal Photographic Society. Ironically, for someone so interested in photography, the only photograph we could find of him was from a group photo of the British Association, taken in Belfast in 1951 (Fig. 1.17).

Slightly over a year after retiring from the chair of Botany, James Small died on November 28, 1955. The biographic notes on Small presented here were adapted from Heslop-Harrison (1954, 1956).

SIDNEY FAY BLAKE (1892–1959)

Sidney Fay Blake (Fig. 1.18) was born on August 31, 1892 in Massachusetts. Natural History intrigued him early in his life: first ornithology and later, during his high school years, his passion for botany began.

Blake completed both undergraduate and graduate studies at Harvard University, having obtained his doctorate degree in 1917 with the taxonomic revision of *Viguiera* under the tutelage of B.L. Robinson. Blake was an avid collector and a keen observer of his natural surroundings; these activities led him to gain a deep understanding of the eastern North American Flora with special emphasis on Compositae, which constitute most of his more than 35,000 collections.

Barely in his early twenties, Blake was already sorting plant collections at the Smithsonian in 1913, and soon after that he was traveling through Europe visiting herbaria, a trip that was interrupted by the outbreak of WWI. Among other things, this trip to Europe resulted in Blake's returning with a massive collection of photographs of type specimens which have benefited countless botanists. Blake was soon offered two positions: one at the Smithsonian and the other at the US Department of Agriculture. Although he much preferred the position at the Smithsonian, family responsibilities forced him to accept the more "satisfactory" pay at USDA (Funk 2005). Over the years at USDA, he was heavily involved in administrative duties, a responsibility that he disliked intensely. Thus, we have in Blake yet another Compositae student that ended up doing most of his research in his spare time, a reality that did not deter him from publishing some 300 papers throughout his career.

When we look at Blake's published record, it is possible to glimpse a slight prevalence of Heliantheae taxa among his publications in Compositae; however, he worked with several other groups in the family, noticeably Astereae. His major contributions were his revisions of *Encelia* and *Viguiera*, and his treatment of the family for the "Flora of Utah and Nevada" (Tidestrom 1925), and the *Flowering Plants and Ferns of Arizona* (Kearney and Peebles 1942). However, the most important legacy of Blake's is in the hundreds of papers describing new species and reviewing small groups of Compositae both across North and South America. Blake is cited as the principal contributor of treatments to Compositae

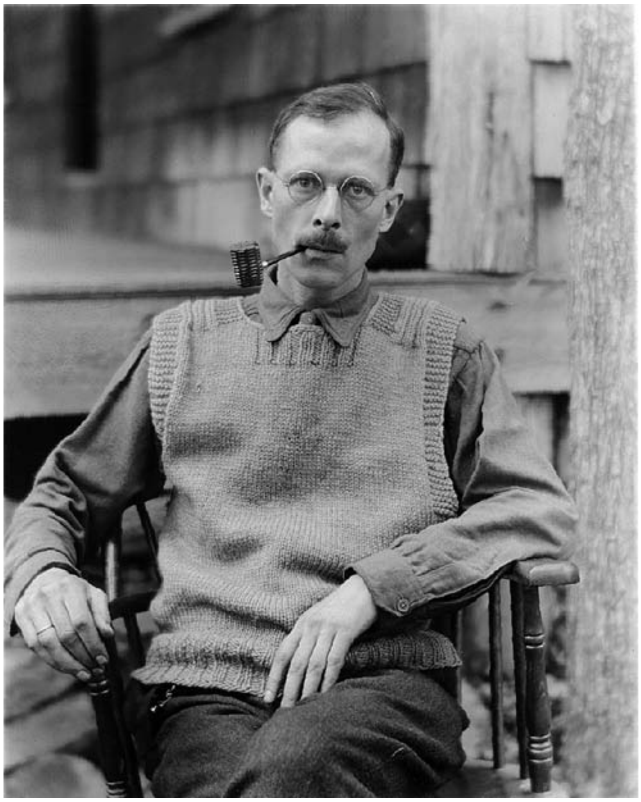


Fig. 1.18. Sidney Fay Blake (1892–1959). Photograph taken in Plummers Island (Maryland, US) at the cabin that serves as Washington Biologists' Field Club headquarters, to which Blake was elected as member in 1924 and of which he was president from 1931 to 1934. [Courtesy of Washington Biologists' Field Club.]

in Standley's (1926) "Trees and shrubs of Mexico", where he also contributed Meliaceae, Polygalaceae and Violaceae.

Thus, although Blake's contributions to botany dealt mainly with Compositae, he also published papers on other taxonomic groups, notably in Polygalaceae, a fact that clearly showed his broad botanical interest and expertise, even extending to botanical nomenclature. He also compiled a series of books on floras, the two best-known being *Guide to Popular Floras of the United States and Alaska* (Blake 1954), and *A Geographical Guide to the Floras of the World* (Blake and Atwood 1942 and 1961). This later one, produced in co-authorship with Alice C. Atwood, consisted of two volumes, the second of which was published posthumously in 1961.

Regarding phylogenetic insights, Blake (1935) cited the relationship of *Chionopappus* Benth. to *Liabum*, and as cited in Sandwith (1956) noted that *Philoglossa* DC. and *Cacosmia* Kunth were also related to *Liabum*, thus fully recognizing the entire group now placed in tribe Liabeae, which had previously been scattered among four different tribes.

Fond of poetry, Blake would recite long poems to endure long trips. In addition, he was a writer who left an unpublished notebook full of poems; he contributed to the Baker Street Journal with articles about Sherlock Holmes as well. He was a gentleman who led a quiet existence and was always held in high esteem by colleagues. Blake married a distant cousin, Doris Holmes, with whom he had one daughter.

After several years of heart trouble, possibly aggravated by too much work, Sidney F. Blake died in his USDA office of heart failure on December 31, 1959. Although his plants and some of his papers are housed at the US National Herbarium, Smithsonian Institution, his library and archives eventually ended up at the University of Texas where there is an S.F. Blake Chair that was previously held by Dr. Billie L. Turner, one of the editors of the Heywood et al. 1977 volume, and a well known synantherologist. When Turner retired, the Chair passed to Dr. Robert Jansen who was responsible for the first molecular work on Compositae (Jansen and Palmer 1987a).

Blake is commemorated by the generic name *Blakeanthus* R.M. King & H. Rob. (Compositae). The biographic notes on Blake presented here were adapted from Holmes (1960) and Funk (2005).

HERMANN MERXMÜLLER (1920–1988)

Herman Merxmüller (Fig. 1.19) was born in Munich on August 30, 1920. Merxmüller's interest in botany began very early in life. Ever since he was a school student, he collected avidly throughout Munich's surroundings and the Bavarian mountains. At the age of 17, he became a member of the Bavarian Botanical Society, where his comprehensive knowledge of the local flora immediately became evident, and this won him the respect of the botanical community. Merxmüller had to wait for WWII to end in order to proceed with his tertiary studies, which he started in 1946 at the University of Munich and finished in 1951 with a doctoral dissertation on plant distribution in the Alps.

Shortly after graduating, Merxmüller took a position as scientific assistant at the Botanische Staatssammlung, under the direction of Karl Suessenguth. It was Suessenguth who directed Merxmüller's attention to his own project of a Flora of South-West Africa. This was the starting point of a long relationship between Merxmüller and the flora of Africa.

Merxmüller's interest in complex groups led him to study European *Hieracium*, and eventually he fell under the spell of the whole Compositae family. His first contribution towards the understanding of southern African Compositae was his "Compositenstudien I" (Merxmüller 1950). This was followed by a long series of papers on Compositae, which ended with his "Compositenstudien XI" (Merxmüller 1980). Although Merxmüller centered his research on Southern Africa, he also collected extensively both in Europe and in South America.

The premature death of Suessenguth triggered important changes for Merxmüller. He first took on the position of his former director, adopting full responsibility for the South-West Africa floristic project. In a span of six years, which ended in 1972, he succeeded in publishing *Prodromus einer Flora von Südwestafrika* (Merxmüller 1966–1972). His participation in this project, accompanied by his several explorations throughout the region, led him to quickly gain notable expertise in the flora of the area. The specimens collected during these floristic endeavors fostered research on multiple fronts and initiated collaborations with many colleagues.

In 1958, Merxmüller was appointed to the Chair of Systematic Botany and founded the Institut für Systematische Botanik at Munich University. He became its first director, promoting research and re-establishing the links between German botany and the rest of the international community after the isolation that resulted from the war. In addition to his positions at the Institut and the Botanische Staatssammlung, beginning in 1969 he also assumed the position of Director of the Botanic Garden. Although not fond of bureaucracy, Merxmüller saw these executive positions as an ideal way to promote systematic research.

Merxmüller also dedicated a considerable time to the teaching of a yearly course on Systematic Botany during several years at the Institut. In 1980, he began to suffer

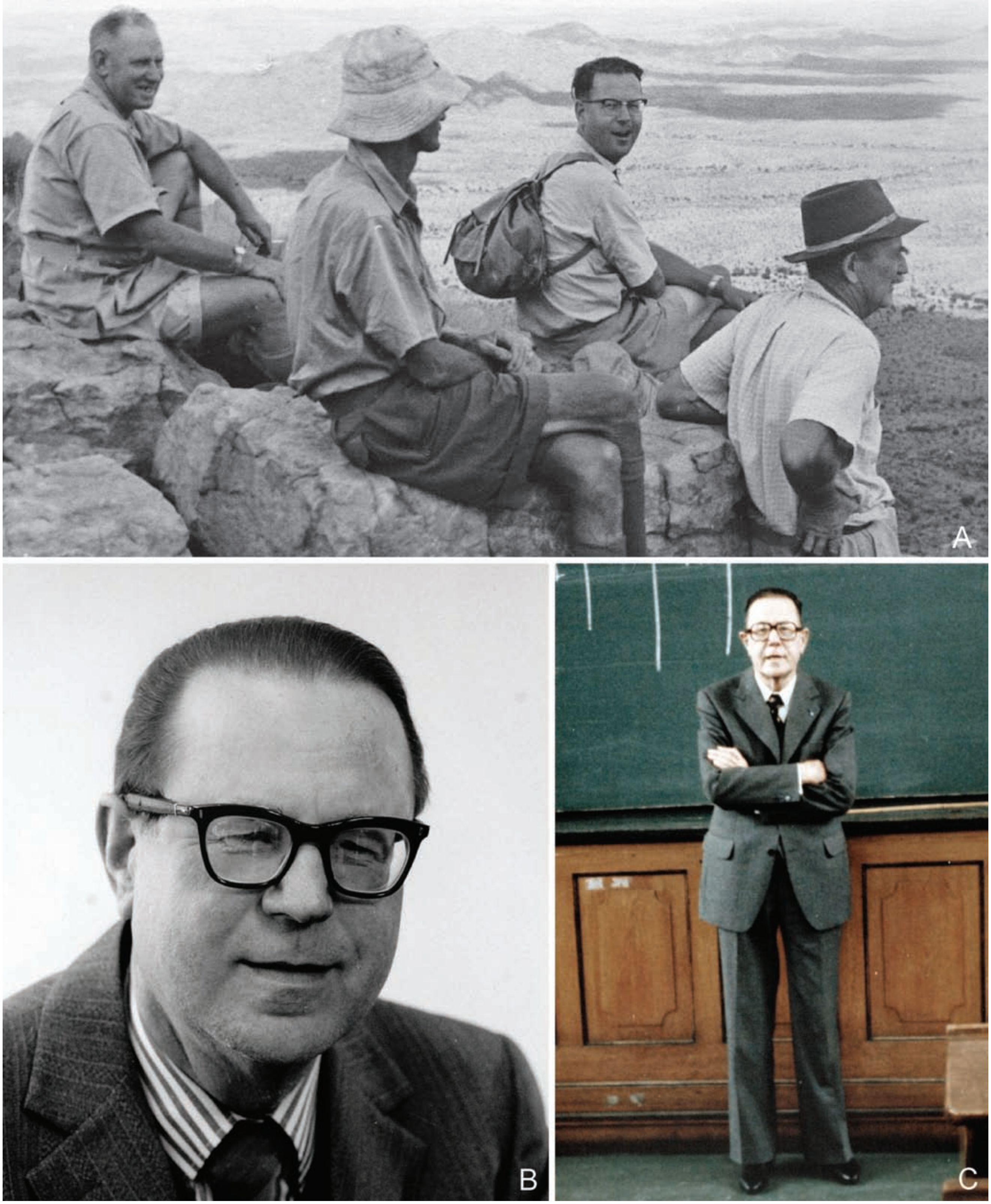


Fig. 1.19. Hermann Merxmüller (1920–1988). **A** Merxmüller (second from the right) and several colleagues in Namibia, near Brandberg in 1960, in one of his several explorations to the continent; **B** official photograph for the Institute, taken in 1980; **C** in his last class of Systematic Botany held in his institute's lecture hall in October 1985. [Photographs courtesy of Jürke Grau.]

from several health problems that forced him to resign from his positions and commitments, having presented his last lecture on systematics in October 1985 (Fig. 1.19C). Hermann Merxmüller died on February 8, 1988.

The biographic notes on Merxmüller presented here were adapted from Grau (1988) and Grau and Lippert (1988).

JOSÉ CUATRECASAS ARUMÍ (1903–1996)

José Cuatrecasas Arumí (Fig. 1.20), "Don José" as he would eventually be called, was born in Camprodon, Catalonia, Spain, on March 19, 1903. Cuatrecasas' father, a pharmacist and a judge, was responsible for teaching Cuatrecasas and the rest of his eight brothers and his one sister to read and write. It was at a young age that José Cuatrecasas developed a great interest in botany, while helping his father to gather plants for the family business. Following in his father's footsteps, he entered the Pharmacy School in Barcelona in 1918 and graduated as a Pharmacist in 1923.

A student of the renowned Pio Font Quer, Cuatrecasas obtained his doctorate at Universidad de Madrid in 1928. His dissertation was on the flora and vegetation of Macizo de Mágina (Cuatrecasas 1929), a remarkable contribution that shows the quality of Cuatrecasas' work from the very beginning. Cuatrecasas divided his time among several jobs: teaching Botany at the Universidad de Madrid, Curator of Tropical Botany at the Real Jardín Botánico de Madrid, and even director of the Jardín for two years.

In 1932, with the celebrations for the 200th anniversary of the birth of Celestino Mutis, the Spanish government sent a delegation of scientists to Colombia, including José Cuatrecasas. Cuatrecasas visited Nevado de Tolima; this first visit to Colombia and the Cordillera Central resulted in Cuatrecasas' passion for the northern Andes that would define his main botanical interests for the rest of his life.

After the end of the Spanish Civil War, and with the establishment of the *generalísimo*, it was not wise for members of the educated elite to remain in the country. At the time of the overthrow of the government Cuatrecasas was participating in the celebrations of the 400th anniversary of Santa Fé de Bogotá as an official delegate from that government. According to his journals from his 1938–39 trip to Colombia, he had friends move his family from Spain to Paris from whence they traveled to Colombia.

Cuatrecasas lived in Colombia from 1939 until 1947. In addition to the extensive field work and research he carried out during his time in the land of Mutis, he also taught at the Instituto de Ciencias Naturales de la Universidad de Colombia in Bogotá and the Escuela de Agricultura Tropical in Cali. In 1947, he moved to the United States to work at the Field Museum of Natural History in Chicago as curator of Colombian Botany. In 1955, he made his last move to Washington, D.C., where he became a Research Associate in the US National Herbarium, Department of Botany, in the National Museum of Natural History, Smithsonian Institution.

An enthusiastic collector, Cuatrecasas had passion for field botany, with a lifetime total of 40,000 collection numbers. He organized countless expeditions, and the vast majority of his copious collections are from the northern Andes, where he was captivated by the spell of the Colombian and Venezuelan páramos. In addition to his plant collecting, Cuatrecasas was a dedicated photographer taking over 20,000 images in many forms, including glass negatives, negatives, and slides. Many of his photos are of places, plants and peoples that no longer exist.

Cuatrecasas' achievements in Botany are monumental, and although he worked in several taxonomic groups such as Humiriaceae (Cuatrecasas 1961), Brunelliaceae (Cuatrecasas 1970, 1985), Malpighiaceae (Cuatrecasas 1958), and Sterculiaceae (Cuatrecasas 1964), the epicenter of his botanical enterprises resided in Compositae. The name Cuatrecasas is associated with more than 2300 records in IPNI, over 1280 of which are in Compositae, In fact, he described over 450 taxa, 348 in Compositae and over 150 taxa were named after him (not including some with the epithets of *pepi* and *tetroici*). There is hardly any large group in the family that Cuatrecasas failed to work on to some extent. However, his major interests were in Astereae (Cuatreacasas 1967, 1969), Senecioneae (Cuatrecasas 1950, 1951, 1978), and most notably in Heliantheae: Espeletiinae (Cuatrecasas, in press). Cuatrecasas had a fascination, shared by those lucky enough to have ever visited the páramos, for the "frailejones", common name given to the Espeletiinae pachycaul inhabitants in the grassy northern Andean highlands. He successfully devoted himself to seeing and studying every single species of this group in the field, noting the very interesting patterns in the distribution among the many species in this highly attractive group of Compositae. His magnum opus on Espeletiinae (a species level treatment for most of the subtribe), nearly completed at the time of his death, is now in process of being published. This large monograph has 350 illustrations and 1100 manuscript pages (Cuatrecasas, in press)

Always a visionary, and trying to boost botany wherever he was located, Cuatrecasas envisioned the idea of producing a flora for Colombia, arguably one of the most diverse countries in the New World, especially for Compositae. In 1957, Cuatrecasas' idea materialized in the creation of "Prima Flora Colombiana", of which he was the author of the first three contributions: Burseraceae

(Cuatrecasas 1957), Malpighiaceae (Cuatrecasas 1958), and Compositae: Astereae (Cuatrecasas 1969).

Another remarkable feat of Cuatrecasas was the origination of the idea of *Flora Neotropica*. He not only thought of it and helped start it, but also served as Scientific Director and President of the Organization Flora Neotropica from 1967 until 1977. It is in works like this undertaking, still in progress, that Don José's interest for advancing knowledge of Neotropical plants is strikingly evident.

José Cuatrecasas died in Washington, D.C., on May 23, 1996, ten days after his last day at work. Cuatrecasas was a true gentleman and a scholar. We find in him the 'kindred soul' of his southern South American counterpart and countryman, Ángel L. Cabrera. The two of

Fig. 1.20. José Cuatrecasas Arumí (1903–1996) on the day of his seventieth birthday in Páramo de las Moras (Cordillera Central, Colombia) holding a leaf of a "frailejón" (*Espeletia hartwegiana* Sch.Bip. ex Cuatrec.), plants for which he had a lifelong fascination. [Photograph from the Cuatrecasas Archives, courtesy of Smithsonian Institution.]

them were, for many years, the beacons of knowledge concerning Compositae of South America.

In the Compositae, Cuatrecasas is commemorated by the generic names *Cuatrecasanthus* H. Rob. and *Cuatrecasasiella* H. Rob. The biographic notes on Cuatrecasas presented here were adapted from Funk (1970, 2005, 2006), García (1997), López-Figueiras (1970), Merino (2003), Robinson (1970), and Robinson et al. (1996).

ÁNGEL LULIO CABRERA (1908–1999)

Ángel Lulio Cabrera (Fig. 1.21) was born in Madrid, Spain, on October 19, 1908. In 1925, he moved to Argentina, where his father, an eminent zoologist, was offered a professorship at the Museo de La Plata.

After joining his father on one of his first field trips to Patagonia, it became evident to Cabrera that his future was not zoology, and instead, he inclined towards botany. He focused on Compositae because he had difficulties when trying to key out specimens of this family from the La Plata area. These difficulties indicated that the taxonomy was in need of revision, and Cabrera was the individual who eventually would bring order to Compositae of southern South America.

Cabrera was a student of Lorenzo Parodi, one of the pillars of Argentine botany, and it was from the hand of Parodi that he started his career in systematics. Cabrera obtained his doctorate in 1931, and by then he had already published seven contributions on Compositae. Immediately after graduating, he started teaching at Universidad de La Plata, an activity that he would continue for most of his life, and that provided one of his most distinctive features: he always had a handful of young students under his tutelage.

Cabrera knew, like very few others, the flora of southern South America. However, he would hardly dare to express any opinion beyond the realm of his specialty, the systematics of Compositae and the phytogeography of South America. In 1945, he founded the Sociedad Argentina de Botánica, an academic society that would play a major role in fostering botany in Argentina and the rest of South America. He was also the editor of the society's journal, *Boletín de la Sociedad Argentina de Botánica*, from its beginning until 1977. Cabrera's vast academic contributions are characterized by a simple, economic, and notably informative style that brings to his publications a level of perfection that is still used as a guide for others.

Cabrera was a field botanist; he knew his daisies not only dry and mounted, but more importantly, alive in the field. On the countless field trips he undertook during his lifetime, he would often lead parties of five or even more botanists to remote areas of Argentina and neighboring countries. Showing remarkable organizational skills, Cabrera's field trips worked like well-oiled machines; orders were never given, but all participants freely took on their responsibilities. In the words of Roberto Kiesling, one of his most prominent students, and fellow during countless trips, "both in the field and in the lab, Cabrera shows no haste, but neither does he linger." These well-coordinated trips produced collections that were not only numerous, but also exemplary in quality. Visits to Europe to examine type specimens added an important aspect to Cabrera's work. The hard work during the day was compensated with enjoyable evenings at dinnertime, when Cabrera would delight his fellow botanists with countless anecdotes; nothing daunted his spirit, except for any manifested lack of enthusiasm for botany.

Ángel Lulio Cabrera died in La Plata, Argentina on July 8, 1999. He was a remarkable scholar and a passionate collector with a charismatic personality that, to this day, is remembered by every botanist who had ever met him. Cabrera's contributions to synantherology, encompassing the systematics of several groups (most notably basal Mutisieae s.l.), floristic treatments, and phytogeography, showed the diversity of Compositae in Southern South America. Among his most important contributions, there are many taxonomic revisions of genera in Mutisieae s.l. and Astereae, and most importantly his treatment of Compositae for all Argentinean regional floras up to his time such as *Flora de la Provincia de Buenos Aires* (Cabrera 1963), *Flora Patagónica* (Cabrera 1971), *Flora Ilustrada de Entre Ríos* (Cabrera 1974), and *Flora de la Provincia de Jujuy* (Cabrera 1978). Cabrera also participated in the treatment of the family in the Floras of Santa Catharina, Brazil (Cabrera and Klein 1973, 1989) and Paraguay (Cabrera 1996, 1998), and produced in co-authorship with Willink the masterpice *Biogeografía de América Latina* (Cabrera and Willink 1973). A search in IPNI reveals more than 800 records with his name, the vast majority of which are associated with taxa in Compositae, over a hundred of them representing new taxa he described, and over eighty taxa have been dedicated to him.

Cabrera not only generated an impressive published record, but a long list of notable students that still keep the spirit of this remarkable scientist alive. One of Cabrera's aspirations in his youth was to become a diplomat in order to travel to exotic places. Looking back on his academic career and successful life, it is evident that he achieved his goal, having become an ambassador for South American Compositae across the world. The biographic notes on Cabrera presented here were adapted from Crisci (1998, 2000), Katinas et al. (2007), Kiesling and Wrigh (1980), Kiesling (1999), and Múlgura De Romero and Price (1999).

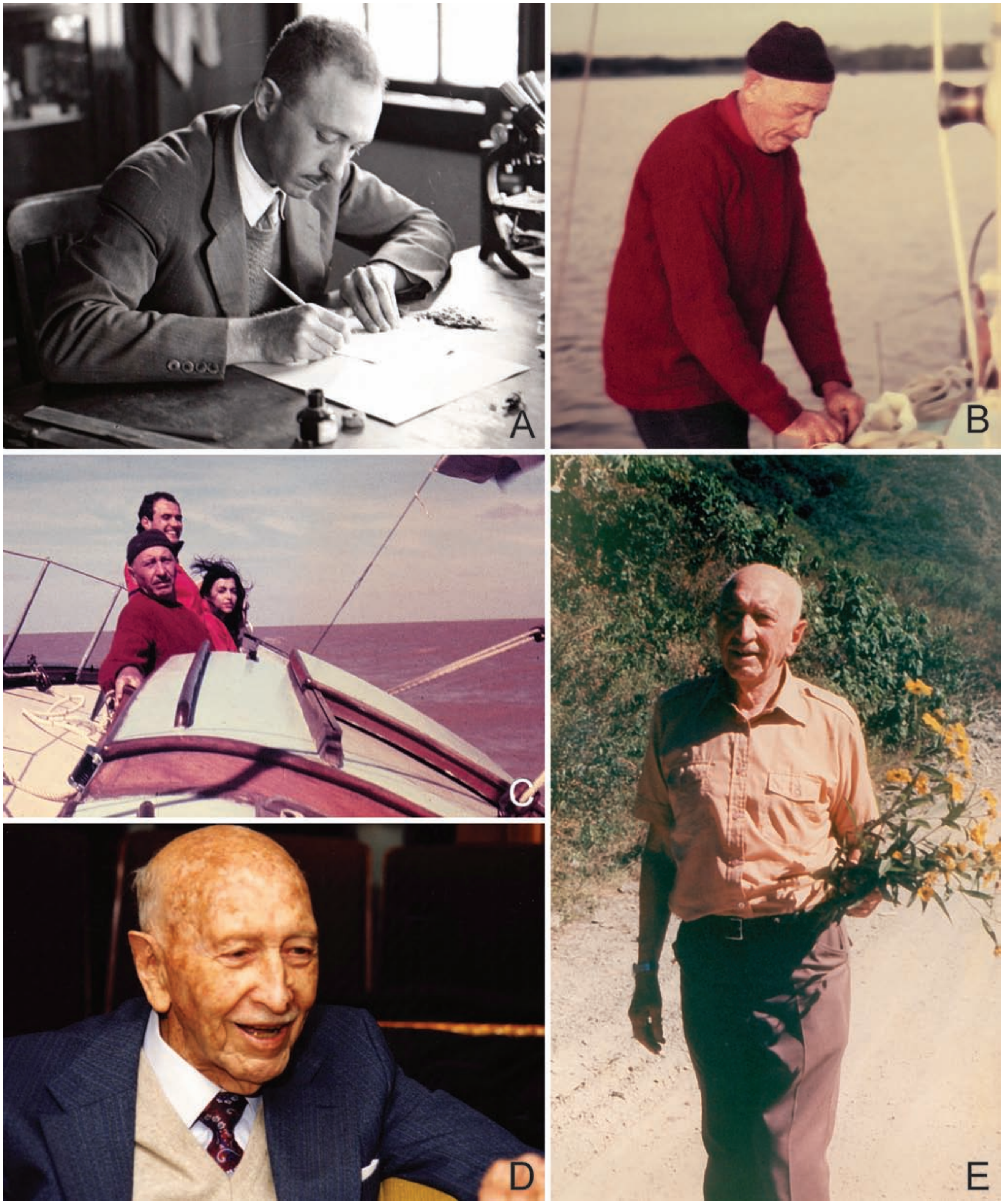


Fig. 1.21. Ángel Lulio Cabrera (1908–1999). **A** Cabrera in 1941 working at his desk in Museo de La Plata (Argentina); **B, C** Cabrera performing his roll as "the captain" of his own boat, which he used to conduct frequent botanical trips along Río de La Plata (C, together with one of his daughters and his son-in-law); **D** Cabrera aged 87 in 1995; **E** collecting comps in Jujuy, Argentina, in 1980. [A, D, photographs courtesy of J. Crisci and L. Katinas; B, C, E, photographs courtesy of R. Kiesling.]

ARTHUR CRONQUIST (1919–1992)

Arthur Cronquist (Fig. 1.22), known to his colleagues as "Art", was born on March 19, 1919 in San José, California. Much of his early years were spent in rural areas of the west coast, a situation that contributed to his affinity for outdoor activities and which left a clear imprint in someone destined to become a remarkable field botanist. As a student, Cronquist went through several summer jobs that demanded a great deal of field work; this experience eventually provided him with invaluable knowledge that he would use in the myriad of research projects undertaken during his lifetime. Cronquist's higher education was conducted in several universities, finally obtaining his doctoral degree in 1944 at the University of Minnesota.

Arthur Cronquist's life-long association with the New York Botanical Garden started in 1943, when he was invited to work as technical assistant. His areas of research encompassed a wide range of interests, from systematic and floristic projects to classification systems of the whole group of flowering plants. Cronquist believed that, given the resources available to him at the New York Botanical Garden, his time would be more productive if dedicated to the completion of floristic treatments. As a result he became the leading author for Compositae in many regional floras across North America, and contributed with several other families to other floristic projects both in the US and abroad. He is particularly remembered by his participation in the *New Britton and Brown Illustrated Flora* (Cronquist 1952; Gleason and Cronquist 1991), *Vascular Plants of the Pacific Northwest* (Hitchcock et al. 1955–1969), and the *Intermountain Flora* (Cronquist 1994; Cronquist et al. 1972, 1977, 1984; Holmgren et al. 2005).

During the year he spent in Belgium (1951–1952) he developed strong ties with European botanists and became increasingly interested in classification systems, and as a result he started publishing many papers on the subject, beginning in the late 1950s with his outline of the classification of dicotyledons (Cronquist 1957). Later on *The Evolution and Classification of Flowering Plants* would appear (Cronquist 1968), followed by *An Integrated System of Classification of Flowering Plants* (Cronquist 1981). He finally reached the climax of his career in this subject, with the second edition of *The Evolution and Classification of Flowering Plants* (Cronquist 1988). These books represent his most important productions in the realm of classification systems, and established his reputation as a botanist who worked beyond the borders of North America. Cronquist developed strong ties with his Armenian colleague, Armen Takhtajan, and in order to be able to have access to the wealth of Russian literature and better communicate with the Russian botanical community, he set himself to learn Russian, eventually becoming fluent in this language.

Cronquist's system of classification was adopted in many places and used as the system for large floristic undertakings such as the *Flora of North America* and *Flora of Australia* projects. Cronquist's understanding of the different groups of flowering plants was legendary, and he had first-hand experience with at least some element of every single family recognized in his system. Additionally, Cronquist produced a botany textbook that was widely used for over twenty years and that went through two editions.

His research on Compositae dealt with several revisionary treatments and theoretical papers, but he was largely involved with floristic treatments in North America, an activity in which he excelled. His practical knowledge of Compositae was unparalleled, proof of which can be seen in the clarity of the keys he constructed for his floras. With regards to his ideas on the internal organization of the Compositae, and more or less in the same line of thought as Bessey and Hutchinson, Cronquist viewed Heliantheae as the ancestral group in the family and set up a series of characteristics of the primitive members of the family (Cronquist 1955). Once he made up his mind he rarely changed it, but once Carlquist was able to provide him with enough data that he decided the basal members of the family were probably woody, not herbaceous (Cronquist 1977). Although many of his views

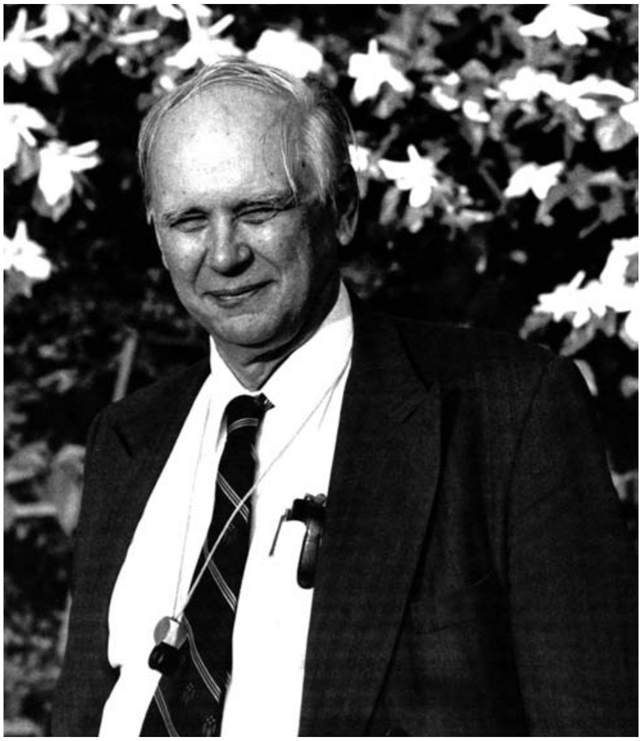


Fig. 1.22. Arthur Cronquist (1919–1992). [Photograph from *Taxon*-IAPT Archives.]

on the origin and evolution of the Compositae were not corroborated by DNA sequence data, he has left a lasting legacy in his major floristic undertakings across North America, and Cronquist will always be remembered as one of the influential figures of Compositae systematics of the 20th century.

Cronquist's towering figure, rising over two meters in height, and his profound tone of voice resulted in a "commanding" presence, which, added to his exceptional good sense of humor and his love of telling tall tales, often made him a highly agreeable individual. Arthur Cronquist died on March 22, 1992 while studying specimens of *Mentzelia* in the herbarium at Brigham Young University in Provo, Utah (US). The biographic notes on Cronquist presented here were largely adapted from Barkley (1992, 1993).

THE LATE 20th AND EARLY 21st CENTURY

As one might imagine, it was difficult to decide where to stop and who to include in this chapter. After much discussion, we decided to stop with the first meeting on the classification and evolution of the Compositae, held at Reading (UK) in 1975. This meeting sets a natural limit on synantherologists to be included in this study because it was attended by many of the scientists of that time who studied this important family, and the resulting published work, edited by Heywood, Harborne, and Turner (1977), was the standard reference for the family for many years. After over thirty years, most of those at the 1975 meeting are no longer actively working on the family, but some still are and of those, seven attended the meeting in Barcelona and eight (V.H. Heywood, C. Jeffrey, H.W. Lack, T. Mabry, B. Nordenstam, H. Robinson, J.J. Skvarla, and T.F. Stuessy) are authors on one or more chapters in this volume.

During the 20th century, in parallel with the increasing development of science as a whole, the number of researchers dedicated to the daisy family grew steadily with a significant advance in the knowledge of the family and understanding of the phylogenetic relationships at the tribal and generic level. As a simple marker of the advance in the knowledge of the family, the number of recognized genera since the treatment of Hoffmann at the end of the 19th century has doubled and it is now over 1700. The 20th century also witnessed the arrival of several techniques that increased our understanding of the family. Research methods involving counts of chromosome numbers, determining pollen structure, and understanding plant chemistry all contributed new information, and the classification of Compositae benefited from these new sets of data.

However, it is thanks to the wealth of DNA sequences accumulated during the last two decades that the relationships inside the family are now much better understood. Beginning with the seminal papers of Robert Jansen and his collaborators (Jansen and Palmer 1987a, b, 1988; Jansen et al. 1990, 1991) and increasing in number every year, the path of evolution in the family is becoming increasingly clear.

Before we finish it is critical that we acknowledge and honor all of the Compositae community, the myriad of contributors of taxonomic revisions of small groups, and the authors of regional and local floras who not infrequently are the first to draw attention to undescribed taxa and the first ones to record unknown information. They are too numerous to be mentioned here, but it is in large part due to their efforts that the savants mentioned here were able to draw their conclusions and push forward our understanding of Compositae.

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Chapter 2

The recent history of Compositae systematics: from daisies to deep achenes, sister groups and metatrees

Vernon H. Heywood

INTRODUCTION

The early history of Composite taxonomy and systematics has been covered in the introductory chapter up to the Proceedings of the 1975 symposium at the University of Reading, UK, entitled "An overture to the Compositae" (Heywood et al. 1977) and in the present contribution (Chapter 1), so I shall focus on advances in the subsequent twenty-five to thirty years during which we have witnessed a radical transformation of approaches to taxonomy and systematics and our understanding of phylogenetic relationships. Added to that have been drastic changes in the environmental, social and economic circumstances in which we practice our science.

THE SITUATION IN 1975

Life was exciting for taxonomists in the 1970s when the first Compositae symposium was held at Reading. The classification of the flowering plants was in a period of transition. Technical advances such as electron microscopy and analytical chemical techniques led to the production of new data from micromorphology, palynology and the chemistry of secondary compounds, and at the species and population level, the future direction of biosystematics and genecology was being debated—"Biosystematics at the crossroads" was the title of a symposium at the Seattle Botanical Congress in 1969, reflecting doubts about the validity of the biological species concept on both theoretical and practical grounds.

At that time, phenetic taxonomy/classification, with its emphasis on quantification of characters and character states, was part of an attempt to make the procedures of classification more explicit and reproducible, and numerical phenetics (numerical or Adansonian taxonomy) was being increasingly used to handle large datasets being produced, within the limitations of the then existing computing technology and instrumentation. Sokal and Sneath's *Principles of Numerical Taxonomy* (1963) was a highly influential text in this field and was updated as Sneath and Sokal's *Numerical Taxonomy: The Principles and Practice of Numerical Classification* (1973). Davis and Heywood's *Principles of Angiosperm Taxonomy*, which was also published in 1963, was not only the first textbook to provide a detailed analysis of the principles, issues and concepts of plant taxonomy but was essentially phenetic in its philosophy.

The phenetic approach was distinguished from the rather vague concept of evolutionary systematics sensu Mayr and from the emerging cladistic approach that was beginning to be espoused. Subsequently, during the 1960s and 1970s there was an almost endless debate regarding the relevant merits of phenetic and phylogenetic taxonomy in journals such as *Systematic Zoology*. Today the relevance of phenetic classification has been largely dismissed and often, wrongly, considered as anti-evolutionary (see discussion in Stevens, 2000) although some (myself included) would argue that it still has a significant role to play in taxonomy.

The widely used systems of classification of the flowering plants such as those of Cronquist (1968, 1981), Takhtajan (1969, 1997), and Thorne (1976, 2000, s.d.), avowedly incorporated evolutionary principles, but without using any explicit methodology and with little documentation of the processes involved or the information base used in reaching the conclusions adopted. Yet these and earlier systems, whether "phylogenetic" or not, such as those of Bessey, Bentham and Hooker, Engler, because of their recognition, description and delimitation of families (and in some cases subfamilies and tribes) provided (and still provide) the context which made later cladistic systems possible and comprehensible.

The phylogenetic approach of Hennig, although vigorously advocated by some, was at that time still little known and only slowly made any impact in botany. Likewise, biochemical systematics was then based largely on secondary compounds, and was just venturing into the macromolecular phase. In the *Biology and Chemistry of the Compositae* (Heywood et al. 1977), mention is made of the early results of Boulter and his colleagues on amino acid sequences in the family, "another neglected area", as it was called, and in his summary of the chemistry of the family, B.L. Turner was of the opinion that at the level of the tribe and above as such macromolecules would provide the only meaningful (or convincing) data!

None of the new approaches made much impact on the classification of the flowering plant families, although the circumscription and relationships of some families was affected to some extent, and no new system of classification was produced. When I produced *Flowering Plants of the World* (Heywood 1978), the sequence of families used followed that of Stebbins in his *Flowering Plants—Evolution Above the Species Level* (1974), itself largely based on Cronquist's 1968 system, but with the prophetic remark in the Preface, "… it is likely that future systems will be radically different". The treatment of the Compositae in that volume was by Charles Jeffrey (1978) who noted that the classification of the family was in a state of transition and that the arrangement into two subfamilies and twelve tribes was seen to be in need of modification in the light of new evidence.

RECENT MILESTONES IN COMPOSITAE CLASSIFICATION AND PHYLOGENY

Curiously, one of the most widely cited papers on Compositae systematics even today is Cronquist's "The Compositae revisited" (1977) which was in fact given at the 1977 symposium but which could not be included in the published volume.

Major developments since then include:

- The retreat from the traditional division of the family into two large subfamilies, the Cichorioideae and the Asteroideae, in favor of the recognition, based on both morphological and phylogenetic analyses of two very unequal sister groups: a small Barnadesioideae which is sister to the rest of the family which constitute the Asteroideae and a more narrowly circumscribed Cichorioideae.
- The publication of Bremer's *Asteraceae: Cladistics & Classification* (1994) which was described as a bible or perhaps new testament for the then current generation of Compositae students. It provided a "first approximation" of a phylogenetic system of classification of the family and an invaluable data source.
- The International Compositae Conference, held at Kew, 1994 just after publication of Bremer's book, and the Proceedings from it which covered both reviews and syntheses of the systematics and evolution of the family and its major component taxa (vol. 1. *Compositae: Systematics*, eds. D.J.N. Hind and H.J. Beentje, 1995) and a wide range of more applied aspects (vol. 2. *Compositae: Biology and Utilization*, eds. P.D.S. Caligari and D.J.N. Hind). The significance of molecular studies in the classification of the family was only just beginning to be realized at the time of this meeting (cf. Jansen and Kim 1996) and as Funk et al. (2005) note, the work of Jansen and colleagues (Jansen and Palmer 1987, 1988) on chloroplast DNA in the late 1980s led to the biggest change in Compositae systematics till then, and, as they say, "literally turned the Compositae phylogeny upside down, showing that part of the Mutisieae was the basal branch of the family and that the tribe Heliantheae s.l. was nested far up in the tree". Furthermore, their work showed that Vernonieae and Eupatorieae, long believed to be closely related, were actually in separate parts of the tree.
- The publication of new morphological and molecular studies led to further substantial reassessment of evolutionary relationships within Compositae and a new phylogenetic classification of the family was published by Panero and Funk (2002), recognizing ten subfamilies and thirty-five tribes. Then, by synthesizing a tree of the family and published and unpublished trees within the family, Funk et al. (2005) were able to produce a supertree or metatree that reflects much of the currently held views about the relationships among the major tribes and subfamilies in Compositae.
- The publication of the treatment of Compositae in Kubitzki's *The Families and Genera of Vascular Plants*

(Anderberg et al. 2007) in which over 1620 genera in thirty tribes are recognized.

- *Compositdb*—a database of molecular data for the Compositae species. A collaboration between the laboratories of Steve Knapp at Oregon State University and Richard Michelmore at UC Davis. It was initially funded by USDA ARS but is currently without support. Primarily focused on sunflower and lettuce but will expand it to include any Compositae species for which there is sufficient data and interest. It is to be hoped that this initiative will receive greater support and become more closely associated with the International Compositae Alliance.
- The proposed *Global Working Checklist of Compositae*. For details see the TICA Website. This recent development is a response to the need for family catalogues as part of the attempt to meet Target 1 of the Global Initiative for Plant Conservation which aims to produce a "widely accessible working list of known plant species, as a step towards a complete world flora". http://www.compositae.org/ and the Global Working Checklist of Compositae BIF seed Funding Project Newsletter 2, November 2006. Christina Flann has now received three years of funding for this project and has taken the lead on bringing it to completion.

REVOLUTIONS IN TAXONOMY AND SYSTEMATICS

Over the past twenty years a major shift, some would say a quantum shift, has taken place in plant taxonomy and more especially systematics. This has been as the result of:

- the publication of a large number of papers detailing morphological, anatomical and other data for various flowering plant groups
- the development of DNA sequencing technologies which have increasingly been applied to plants, leading to the production of large amounts of DNA sequence data
- the analysis of these morphological and molecular data by cladistic, phyletic, phenetic and other analytical procedures made possible by the availability of high speed computing capacity
- the development of electronic databases and information systems, as a result of advanced technology, capable of storing large amounts of data about all aspects of plants

Although often referred to as the "molecular age of systematics", the current phase of taxonomy and systematics is much wider than just the use of DNA sequence data on their own, and it would be more accurate to refer to it as the "phylogenetic (or cladistic) and bioinformatic" phase. What is remarkable is the production of large datasets of morphological as well as molecular information and the construction of tree diagrams, most frequently cladograms, from these in various combinations. Indeed the combination of disparate datasets is one of the strengths of today's systematics and classification as well as providing both philosophical and technical challenges. As we comment in the successor to *Flowering Plants of the World* (Heywood et al. 2007), these phylogenetic analyses have undoubtedly led to a much greater understanding of the evolution of flowering plants and although molecular systematics is still in its early stages, there is general agreement as to the basic framework of a phylogenetic system of classification for the flowering plants. It has led to major realignments of families, the association of families or parts of them not previously regarded as related, the splitting of some families and the merging of others. There is no room for complacency and already remarkable new alignments at the base of the angiosperm tree have been proposed as the result of work on the tiny moss-like aquatic genera *Hydatella* and *Trithuria* that comprise the family Hydatellaceae. This was previously thought to belong in the monocots and near the grasses but has now been shown to be closely related to the water-lilies (Nymphaeales), representing a new ancient lineage near the base of the angiosperm evolutionary tree (Saarela et al. 2007).

As we bring to bear new approaches in developmental genetics and genomics that will lead to a deeper understanding of the systematics, classification and relationships of the flowering plants, we may expect further modifications to our classifications both at family and lower levels.

Phenetic and phylogenetic species

At the species level, which for many of us is the frontline of taxonomy, the debate continues to rage about the nature of species, witness for example, the volume by Wheeler and Meier (2000) and the current set of commentaries by Henderson (2005, 2006) and Jensen (2006) in *Systematic Botany*. I refer also to a paper in *Nature* in which Rieseberg et al. (2006) conclude that 70 percent of taxonomic species and 75 percent of phenotypic clusters in plants correspond to reproductively independent lineages and therefore represent biologically real entities (begging the question as to what "real" means!). One could, of course, also conclude from this that traditional taxonomists are doing a good job, despite the criticisms often directed at them! And in *The Systematist*, Olivier Rieppel (2006) discusses the thesis that species and other taxa are to be considered individuals as opposed to classes or sets which are considered abstract universal concepts.

While such arcane debates (cf. Rieppel 2007) are intellectually absorbing and a logical consequence of treating taxonomy and systematics as rigorous academic disciplines (which they are, but not entirely so), one can't help wondering if more effort might not be better directed at devising more effective means of exploring and measuring populations of plants in the field and recognizing the phenetic groups we call species and which Rieseberg tells us are acceptable in most cases. Species have to be used by a wide range of interest groups and as Cracraft (2000) uncompromisingly states:

> … we should be careful in seeking justification for a particular species concept if it cannot embrace the vagaries of real-world data with aplomb. No hemming. No hawing. It must work. This does not mean that we should abandon theory and philosophy, ontology and epistemology, individuality, reality, pattern versus process, and all the other notions that orbit around discussions of species concepts. But we must keep our feet firmly planted on the ground.

I personally deplore the near demise of what one used to term biosystematic or experimental taxonomic studies in which the focus was on the nature and dynamics of species' populations and their reproductive biology and breeding relationships. Indeed, if we abandon the notion of species as representing essentially dynamic and variable populations of largely interbreeding individuals in nature, however difficult they might be to delimit, then we risk losing much of what makes taxonomy such an absorbing and valuable pursuit.

SO WHERE ARE WE NOW?

How far the transformation of systematics and in particular molecular analysis has illuminated our understanding of the Compositae is very difficult to answer. Clearly great advances have been made, but with ca. 24,000–30,000 species in over 1600–2000 genera (Funk and Robinson 2005; Funk et al. 2005; Hind 2007; Kadereit and Jeffrey 2007) it is not surprising that many problems remain at all levels and in all areas of Compositae research. There seems to be developing something of a convergence of opinion, although by no means unanimity, over the major subdivisions of the family, or at least the recognition of two sister groups, one comprising the monophyletic Barnadesioideae with a single tribe and about 100 species, and the other containing the great bulk of the family comprising a more narrow than previously circumscribed paraphyletic Cichorioideae with some 6000–7000 species and the large monophyletic Asteroideae with the remaining 18,000 or so species. Others (see Chapter 11) favor breaking up the paraphyletic Cichorioideae; only time will tell which system works the best. Hind (2007) in his treatment of the family in *Flowering Plant Families of the World*, echoes Jeffrey's remarks nearly thirty years earlier, that the classification of the family is still in a state of transition and there is no agreement yet on whether to accept monotypic subfamilies or to recognize supersubtribes sensu Jeffrey (2004) or supertribes sensu Robinson (2004).

Wagenitz (1976) observed some thirty years ago that it is remarkable that the tribes as created by Cassini in the early 19th century have not been fundamentally altered, and Per Ola Karis (2006) has recently made a similar comment regarding the Panero and Funk (2002) system, noting how it "corresponds strikingly well to the tribal system founded by Cassini almost 200 years ago".

The level of sampling of tribes and genera so far achieved in the molecular systematics of Compositae is still very low in many cases despite the impressive achievements of the past two decades, and a great deal of consolidation will be needed before we can feel comfortable with many of the new alignments.

Again, although some progress has have been made in our knowledge and understanding of structural and functional aspects of the family, the biology of the capitula, phytochemistry and biochemical pathways, the economic importance of the group, genomic evolution and analysis, and the reproductive biology and conservation status of most of its 25,000 species, there are still enormous gaps in our knowledge. We need to remember that little is known of the majority of species apart from some basic facts of their morphology and location, and their existence as coherent, repeatable population-based phenomena is only suppositional (Heywood 1988: 48). For most of them, their demography, reproductive biology, breeding system, genetic variability and so on is virtually unstudied. Yet the fact is that for many purposes, the users of our classifications require information beyond identification and description of genera and species. They may demand detailed ecogeographic and population data on the species so that effective conservation can be planned. They will need to assess the likelihood of individual species successfully migrating or surviving in the new ecoclimatic envelopes that will develop as a consequence of climate change. Already there have been calls for taxonomists to take into account the needs of conservation in designing Floras and other taxonomic outputs (Golding and Timberlake 2003; Heywood 2003; Leadlay and Jury 2006), and it is inevitable that taxonomists will be called upon to play a key role in responding to the consequences of global change. As Agapow et al. (2004) point out, the ways in which species are defined is a concern not only of the taxonomist but of the conservation biologist. The consequences of the adoption of different definitions can be serious, for example in the compilation of lists of threatened species and conservation legislation.

LOOKING TO THE FUTURE

Looking to the future, what can we expect? One view is that presented in the concluding section of Krupnick and Kress's book on *Plant Conservation* (Krupnick and Kress 2005), in which they envisage the future age of plant exploration and discovery in the 21st century. They see image-recognition software, electronic field guides, DNA bar-coding, palmtop and wearable computers, GPS receivers and web-based satellite communication. Field botanists will be able to immediately compare their newly collected plants with type specimens and reference collections archived and digitized in museums thousands of miles away. Information will be gathered and sent back to their colleagues in the laboratory to rapidly determine the genetic composition and phylogenetic position of each new species. While some of these techniques are already available, we need to consider such a scenario in the light of practicalities, cost-effectiveness, and likelihood of implementation. To repeat Cracraft's admonition, we must keep our feet firmly planted on the ground.

Although taxonomy currently is riding high on the back of the biodiversity bandwagon on the one hand and the excitement of molecular phylogenetic discovery and explanation on the other, neither is likely to retain their privileged recognition, and I agree with Olmstead (2006) that systematics will then need to reinvent itself yet again if it is to survive as a dynamic academic discipline. In the case of Compositae, at what stage or level of construction of the metatree on the one hand, and exploration and description of new taxa and revision of species-rich and/or critical groups will our paymasters and peers say, enough is enough?

Of course, there is another scenario. All the evidence suggests that the combined effects of global change (demographic, disturbance regimes, climatic), combined with unsustainable levels of consumption and use of energy will over the coming decades force dramatic changes on our current models of society and trade. This will impact on all our lives and institutions and lead to a rewriting of our priorities, not to mention research into taxonomy and systematics whether it be of plants, animals, or microorganisms, let alone Compositae systematics. What role taxonomy and systematics will play in such a world will to a large extent depend on our actions now. But until the crunch comes, let us enjoy working with these fascinating plants that give us so much pleasure.

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Chapter 3

Economic importance of Compositae

Beryl B. Simpson

INTRODUCTION

With an estimated 25,000 species, Compositae are either considered the largest plant family or a close second to Orchidaceae in number of species. Nevertheless, this high species-level diversity has not translated (in either family) into a proportional number of species directly useful to people. Poaceae, Leguminosae, and Solanaceae, all smaller families, yield more numerous and more economically important species. Purseglove (1968) in his classic work on tropical crops listed only five from Asteraceae: safflower, pyrethrum, niger seed, sunflower, and *Lactuca*. In contrast he discusses twenty from Leguminosae. He treated eleven crops from Cucurbitaceae and five from each of Brassicaceae and Solanaceae, all families much smaller than Compositae. Smartt and Simmonds' recent compendium (1995) on the evolution of crop plants included treatments of only three Compositae species: safflower, sunflower (with a brief mention of Jerusalem artichoke), and lettuce. The FAO database of world crops includes only six crop species (artichoke, chicory root, lettuce, pyrethrum. safflower, and sunflower). A recent paper by Dempewolf et al. (2008) that focused on degrees of domestication among some Compositae species also commented on the comparatively low numbers of crop plants in the family.

The major crops provided by the family are edible stem and leaf crops and seed oils (Fig. 3.1). Nevertheless composites are represented in almost all other categories of crop plants except fiber, wood, and wood products. This article explores the major economic food plants of the family and touches on plants of more minor importance used for beverages, as spices, sweeteners, insecticides, medicines, ornamentals, rubber and resin, and dyes. Of this latter group, three products, absinthe, chrysanthemums, and guayule are discussed in detail because of their particular associations with different cultures and importance relative to other members of their categories. At the local level, hundreds of species of Compositae are used as herbal medicines, dyes, ornamentals, and flavoring agents, but since it would be impossible to account here for all of these, I discuss in this overview only those that have, or had, some significant economic importance.

EDIBLE CROPS

Leaves and shoots

The major food crops in Compositae are stem and leaf crops, with those of roots and tubers (underground stems) of lesser importance. Yet, production of these crops pales in comparison with that of comparable crops in other families. For example, lettuce is the world's major salad crop but cabbage far outranks it in terms of amount grown (Table 3.1) presumably because cabbage is commonly eaten cooked as well as raw and it can be pickled as a method of preservation for use during months without fresh vegetables. Consequently, cabbage use can be extended throughout the year. Even as a fresh vegetable, cabbage keeps longer than lettuce. The same is true for the lesser leafy vegetables such as chicory and endive. Nutritionally as well, leafy crops from Asteraceae do not compare to those of other families such as Brassicaceae known for its sulfanones and antioxidant compounds, or Chenopodiaceae as a source of iron and antioxidants.

Without doubt, the major vegetative food commodity from Compositae is lettuce, *Lactuca sativa* L. (Fig. 3.1). The species is known only as a cultigen, but is undoubtedly the domesticated form of the wild *L. serriola* L., native to Asia Minor (Ryder and Whitaker 1995). The first evidence of domesticated lettuce comes from paintings of a long-leafed form on Egyptian tombs dated as 4500 BC (Harlan 1986). The plant was popular in ancient Greece and the Roman Empire from which it was spread across Europe. Lettuce was introduced into North America shortly after European contact and North America today is a primary region of production. Some researchers (Ryder and Whitaker 1994) have suggested that lettuce was first cultivated for seed oil. Harlan (1986) also stated that lettuce was grown in Egypt for seed oil and pointed out that lettuce seed oil was a commodity into the 20th century. Later selection on the species as a leafy crop would have been for non-shattering seed heads, reduction of spines on the leaves, and reduction in latex and other compounds to reduce bitterness, and paler, more tender, but crisp leaves.

The primary types of lettuce are butterhead, crisphead, latin, leaf, romaine (cos), and stem. Sometimes these are given varietal names: headed lettuces = *Lactuca sativa* var. *capitata* L., cos = *L. sativa* var. *longifolium* Lam., leaf = *L. sativa* var. *crispa* L., and stem lettuce *L. sativa* var. *asparagina* Bailey. The last, also called celtuce or asparagus lettuce, is grown for its stalk (to 1 m tall) that can be peeled,

Fig. 3.1. Several of the commercially important products from Asteraceae. From upper left spiraling around: Gerbera daisy, leaf lettuce, curly endive, dried, ground chicory root mixed with coffee, chrysanthemums, burdock root, chicory, marigolds, dandelion leaves, chamomile tea, safflower oil, sunflower oil, artichoke, Belgian endive, raddiccio.

Table 3.1. Annual worldwide production and area under cultivation of economically important crops in Compositae compared with similar crops from other families. Pyrethrum, used for its insecticidal properties, has no counterpart.

Commodity	Area harvested [ha]	Production [t]
Artichokes	121,970	1,205,505
Asparagus	1,302,886	6,647,543
Lettuce	1,015,339	22,382,600
Cabbages	3,218,971	69,782,487
Chicory root	27,446	891,554
Ginger	339,826	1,004,546
Potatoes	18,639,776	321,060,852
Safflower	813,387	776,327
Rapeseed	26,950,718	46,409,830
Sunflower seed	23,397,543	31,065,709
Groundnuts (peanuts)	25,214,451	35,907,706
Soybeans	91,299,293	209,975,643
Pyrethrum (dried flowers)	26,710	13,405

Data from the FAO database available at http://faostat.fao.org/. These are the only crops listed in the database for Compositae. Figures are for the year 2005.

sliced, and stir-fried or made into pickles. Early forms of lettuce seem to have been narrow-leaved. Headed types were products of selection in northern Europe (and later in North America) first as butterhead and then as crisphead. Romaine was developed for winter culture in the Mediterranean region.

All the different types of lettuce can exhibit variation in leaves and shoot structure. Lettuce varieties with darker colored leaves have become more diverse as their popularity grows on account of the purported antioxidant properties of the flavonoids responsible for the red colors. This trend has reduced some of the nutritional disadvantage lettuce formerly suffered relative to other greens. There has also been a huge surge in the market for "lightly processed" produce, including salad ingredients. Lettuce is cored (crisphead types), washed, sometimes shredded, and packaged. Mixtures of different kinds of lettuce (sometimes as "baby" leaves) are packaged alone or mixed with other greens—often other Compositae such as frisée, endive, or chicory.

In 1986, Jack Harlan wrote a delightful article discussing the association of the Greek (Hellenistic period) god Min with lettuce. Min is the god of fertility and procreation and is usually pictured as ithyphallic (with an erect penis) posed in front of stylized lettuce plants. Some Greeks saw lettuce as an aphrodisiac—white latex reminiscent of semen, others considered it an anti-aphrodisiac because the latex reminded them of opium poppy exudate. Unfortunately, neither of these effects pertains. The principal constituents of the latex are sesquiterpene lactones (lactucin, deoxylactucin, and lactucopicrin-6).

Chicory, *Cichorium intybus* L., (also known in various forms as Belgian endive, succory, witloof, radicchio, and coffee chicory; Fig. 3.1) is native to the Mediterranean region. Belgian endive (witloof) is a torpedo-shaped, headed form attributed to M. Bréziers of the State Botanical Garden in Brussels who in 1850 discovered some "forgotten roots" that sprouted in the dark forming white leaves (Ryder 1998). The leaves were long and loose and the product was known as *barbe de capucin*. When larger roots were forced under sand they formed tight headed chicons, or Belgian endive. Witloof was developed from the Magdebourge cultivar and became popular in France and the Netherlands, with Belgium as its cradle of culture. Dandelion chicory or puntarella is the same species as regular chicory but is a catalogna type with toothed, rather dandelion-like looking leaves. Radicchio is the name applied to headed or loosely headed forms of chicory originally developed in Italy where five different types are named for the regions of northern Italy in which they are grown. Outside of Italy, the red, round, Chioggia form is the most common and, for many, synonymous with the word radicchio. Its popularity in the United States has risen rapidly because of its color, sharp taste, and use in pre-packaged salad mixes.

Escarole, *Cichorium endivia* L. (called endive, escarole, frisée, or curly endive for the lacerate-leaved variety; Fig. 3.1) has a somewhat obscure origin according to Ryder (1998) but is known to have appeared earliest in India. Some researchers, however, consider its origin to be Sicily and it is known to have been an early salad vegetable in Egypt. The broad-leaved type is escarole or scarole, and the narrow leaved is endive or frisée, both of which can be eaten as a cooked vegetable or as a salad green.

Table 3.2 lists several additional composites that are used as vegetable greens or potherbs over substantial geographic areas.

The cardoon (*Cynara cardunculus* L.), also called the artichoke thistle, is related to the globe artichoke and may be its wild progenitor. While its immature heads can be eaten like those of the artichoke, the leaf petioles are the most commonly eaten part of the plant often (in southern Europe) after they have been blanched by being wrapped or buried in earth. When young, the petioles can be eaten raw, but the larger stalks, most commonly sold, require cooking. Because cardoon leaves can be covered with small, nearly invisible spines that can cause substantial pain, "spineless" cultivars have been developed. Given its requirements for a long (ca. five month), cool growing season, protection from frost, and substantial growing space per plant, cardoon is grown on a limited scale. Plants are highly invasive, and the species has become a noxious weed in Argentina, California, and

Australia because of its pre-adaptation to the dry climates of these areas.

Artichoke (*Cynara scolymus* L.; Fig. 3.1) is a native of the Mediterranean region and is probably the product of selection from the cardoon, *C. cardunculus*. It is one of the few plant crops in which the immature inflorescence is eaten (others being broccoli and cauliflower). The large globe artichokes are most common in North America but in Europe smaller sizes are appreciated. The size of the artichoke depends upon where it is borne, with the large heads at the top of a primary stem and smaller ones lower on the stem, often shaded by leaves. Artichokes are eaten for the starch sequestered at the base of the involucral bracts and in the receptacle. Artichokes are a "specialty" vegetable like asparagus. Both are long-lived perennials that historically had a narrow seasonal availability. With produce readily shipped today between the northern and southern hemispheres, such crops have become much more available throughout the year. It is asparagus, however, that has become the more dominant of these two (Table 3.1), perhaps because per unit weight it provides more food.

Roots and tubers

The roots of different genera of Compositae have found their way into cuisines around the world, but to a very limited extent. Roots and tubers of Compositae cannot compare to the major root and tuber crops such as manioc, true yam, potatoes, or sweet potatoes. Undoubtedly this enormous disparity comes from the fact that, as far as is known, species of Compositae do not usually store common starch in their roots and tubers. Instead, storage is primarily in the form of inulin, a fructan. Since inulin is not broken down until it reaches the large intestine, it is a poor source of calories for humans. Moreover, ingesting large amounts can lead to bloating and flatulence. Nevertheless, Compositae can boast several root and stem crops such as salsify, burdock, and the Jerusalem artichoke, each native to a different continent.

The roots of two unrelated species known as salsify (Fig. 3.1) can be used interchangeably. *Tragopogon porrifolius* L. (and other *Tragopogon* species as well), a biennial or perennial European native that has spread around the world, has a taproot that is eaten and said to taste like oysters—hence the common name of oyster plant. *Scorzonera hispanica* L., also called salsify, scorzonera, or black oyster plant is native to Europe where it is thought to have been comparatively recently brought into cultivation, probably in Spain. The root is usually cooked and, like regular salsify, it has a taste a bit like oysters or artichokes.

Burdock or gobo root (*Arctium lappa* L.) is native to Asia but has been naturalized throughout Europe and North America. It is primarily seen in Chinese cooking in soups, pickled, or as a crunchy textural component in sushi.

Helianthus tuberosus L., Jerusalem artichoke or sun choke, is, as pointed out by Heiser (1976), neither from Jerusalem nor an artichoke. It is indigenous to temperate North America. Native American Indians ate the tubers and possibly domesticated the species because there appears to have been some selection for large tuber size in cultivated plants prior to European contact. However, some authors have suggested that actual domestication is attributable to Europeans in recent times (Pickersgill 2007). It was introduced into Europe in the first part of the 17th century where it enjoyed an initial, but apparently short-lived, popularity (Heiser 1976). The tubers eaten raw have a crisp, fresh taste; cooked, they are similar to potatoes. Like other Compositae storage organs, Jerusalem artichoke tubers contain inulin that is metabolized (with the release of gas) only by bacteria in the large intestine. *Helianthus tuberosus* remains a minor crop whose major claim to fame might be that it was the species the Russians crossed with the common sunflower to increase disease resistance in the latter (Heiser 1976).

Grown on a much more limited scale is the yacon (*Polymnia sonchifolia* Poepp. & Endl.) used in Andean Colombia, Ecuador, and Peru for its crisp roots that are eaten fresh or cooked (Rubatzky and Yamaguchi 1997).

Table 3.2. Species used on a minor scale for their edible leaves, stems, and petioles (Rubatzky and Yamaguchi 1997).

Scientific name	Common name	Part used	Where used	Use
Chrysanthemum coronarium L.	Chrysanthemum	Leaves	Asia	Greens
Crassocephalum crepidioides (Benth.) S. Moore	Boloj	Leaves	West Africa	Vegetable
Cynura bicolor DC.	Cynura	Shoots and leaves	China	Vegetable, soups
Petasites japonicus (Sieb. & Zucc.) Maxim.	Butterbush	Leaf pedicels	Japan	Vegetable
Scolymus hispanicus L.	Spanish salsify	Basal leaves	Europe	Greens
Scolymus maculatus L.	Spotted golden thistle	Basal leaves	Europe	Greens
Spilanthes oleracea L.	Paragrass	Leaves	S.E. Asia	Potherb, salad
Taraxacum officinale L.	Dandelion	Young leaves	Worldwide	Greens

Seed oils

In terms of area harvested and metric tons produced, seed crops from Compositae overshadow the leafy and stem crops (Table 3.1). Most of these harvested seeds are used for the production of vegetable oil. Sunflower is a major oil-seed crop, but oil seeds across the board are minor relative to the world sustaining grains and pulses. The importance of Poaceae and Leguminosae seeds is, of course, related to their seed storage products, almost pure starch in the former and high levels of protein in the latter. Entire populations can, and do, live almost exclusively on grains supplemented with legumes. The same cannot be said of oil seeds.

The major oil seed crops from Compositae are sunflower, safflower, and niger. Oils from the seeds of any of these species can be obtained by expeller pressing or the seeds can be hulled, flaked, sometimes steamed, and then solvent extracted. The oil can then be processed by degumming (adding water and centrifuging), refining (removing free fatty acids by adding alkali), deodorized by blowing steam through the oils, and decolorizing by filtering.

Sunflower, *Helianthus annuus* L. (Fig. 3.1) ranks fourth in terms of worldwide edible oil production. It yields high quality oil and the meal left after the oil is removed is useful as animal feed (Fick 1989). There is evidence of early domestication in the 1st century BC, although some workers claim cultivation began 3000 BC. Heiser (1976) suggested it was an early camp follower of Indians of the American Southwest and now concurs that it was actually domesticated only north of Mexico (Heiser 2008), probably in the east-central part of the USA (Smith 2006; Wills and Burke 2006). While North American native people primarily used the seeds as a source of food (as nuts, flour, or mush), they also extracted oil. Heiser (1976) reports that the Iroquois would pound the seeds, heat the mash and then boil it in water to separate the oil from the meal. The water was cooled and the oil that rose to the top was skimmed off. The oil was used as a flavoring for food, to anoint the hair, and as a base for body pigments.

The most significant breeding for the large-headed cultivars important today for commercial production was undertaken in the USSR. Plants were introduced into Europe in the 1500s with Russians adopting the plant readily because its oil was not specifically forbidden during Great Lent in the Orthodox Church (Heiser 1976). Artificial selection in Russia raised the oil content of the seeds from 30% by weight in the early 1900s to 40% and finally to 50%. In addition they bred for disease resistance by crossing with *Helianthus tuberosus*, the Jerusalem artichoke. Oil constitutes 80% of the commercial value of the seed (as opposed to meal, which is comparatively more important for soybean; Fick 1989).

Sunflower oil, obtained by expeller pressing or hexane extraction, is considered a premium oil because of its light color, bland flavor, high smoke point, high level of linoleic acid, and absence of linolenic acid. Typically the unsaturated fatty acids oleic and linoleic comprise 90% of the total. The ratio of the two varies with the temperature during the growing season. High oleic (80%) oil, available since 1985, has greater oxidative stability than the traditional oil. The oil is not used as much industrially as other oils because of its higher price. However, it is used for paints, varnishes, and plastics because of good semidrying properties without yellowing. It has been considered as an alternative fuel. Non-oilseed seeds are commonly eaten as a snack. These have a gray striped pericarp as opposed to the black pericarp of the oil-seed varieties, and are comparatively higher in carbohydrate.

Safflower *Carthamus tinctorius* L. (Fig. 3.1) was not a serious oil crop until the 1930s and 1940s. Previous to this time it was a relatively minor oilseed crop because it is more difficult to grow than other seed oil species (Knowles 1989). Its native area is the Middle East where it appears to have been grown initially for its flowers. Garlands of dried safflowers have been found encircling mummies dated to 1600 BC. Oil extraction dates to Roman times.

There was much interest in safflower oil in the 1980s because it is a highly unsaturated oil and medical research had finally documented a correlation between atherosclerosis and saturated fat consumption. However, when later work showed that oils high in monounsaturated fatty acids are healthier than polyunsaturated oils, production declined. Today the oil is extracted by expeller pressing and the cake residue is used for feed. The species is highly self-pollinating, insuring a full seed crop. Breeding has been for resistance to wilt and blight, insect resistance, fewer spines, and increased yield. High linoleic (87%–89%) and high oleic (75%–80%) varieties are grown commercially. High oleic oil is superior cooking oil because it is stable and does not form a scum when used for frying (Knowles 1989), hence its frequent use for French fries. Oils with a high linoleic fatty acid content form a scum because high temperatures cause the acids to polymerize, but they are used for salads and soft margarines. Safflower oil is also used for paints and varnishes since it does not turn yellow when exposed to the air.

The last commercially important oil seed crop of Compositae is niger (also noog or noug) extracted from *Guizotia abyssinica* Cass. This oil is little known in most parts of the world, but it is important in Ethiopia, where it is probably native, and parts of India. Riley and Belayneh (1989) believe that it is derived from *G. scabra* Chiov. a morphologically very similar species that often grows as a weed in niger plots. The cultivated species has larger seeds and higher oil content. In Ethiopia (as of 1989) it was the source of 50%–60% of that country's edible oil (Riley and Belayneh 1989). It is also grown elsewhere in Africa where it is a desirable crop because it has high salt tolerance, produces a crop on waterlogged or infertile soils, and helps the soil for future crops. Plants can be grown in pure stands, with tef (*Eragrostis* spp.), or with sorghum (*Sorghum bicolor* (L.) Moench).

Niger oil is pale yellow, semidrying (moderately saturated), and slightly nutty in flavor, but it can become rancid after six months. In composition Ethiopian niger oil is similar to safflower and sunflower in its high linoleic content 75% (70%–85%) with lignoceric acid (24 : 0) making up about 2%. In India, the linoleic acid levels are lower, between 52%–74%. Although niger is primarily an edible oil it can be mixed with other oils and used for making soap or paint. In India the oil is rendered from the seeds using bullock-powered *ghanis* or in mechanized mills using expeller presses with the cake used for animal feed. Because niger is considered a minor crop there has been little breeding work for crop improvement.

Beverages

Various Compositae have been used for beverages with numerous species collected locally for making medicinal or tasty teas. Only a few species, however, have an international reputation and constitute significant economic crops. These include chamomile, chicory, cynar, and absinthe each producing a different kind of beverage: chamomile for tea, chicory as a substitute for, or additive to, coffee; cynar as an aperitif; and absinthe in a liqueur. One thing they all share is an initial use as herbal medicines.

Chamomile (Fig. 3.1) is a name applied to several different species that are used to make herbal teas, all of which are native to Eastern Europe, northern Africa, and western Asia. German chamomile is *Matricaria recutita* L., and Roman or English chamomile is *Chamaemelum nobile* (L.) All. The name chamomile is also applied to *Anthemis cotula* L., also known as dog fennel and *Matricaria matricarioides* (Less.) C.L. Porter (pineapple weed). In all cases, dried heads containing essential oils are used to brew teas. The first two species are the most commonly consumed and have been used for centuries with cultures as different as ancient Egyptians and Anglo Saxons holding them in such high esteem that both considered them a suitable offering to their gods. Before the widespread use of refrigeration, meat was sometimes soaked in chamomile tea to mask rancid tastes. Teas were also used to highlight blond tints in the hair, a practice reflected today by its inclusion in many shampoos. Although their essential oils differ, all are used today primarily as refreshing and soothing teas. The teas are considered to be calming for digestive upsets and jangled nerves, relaxing for tense muscles, and soothing to irritations of all kinds. They are drunk for many types of intestinal problems, indigestion, bloating, irritable bowel, gastrointestinal spasms, and to help with menstrual cramps. About 120 volatile oils and some flavonoids have been isolated from German chamomile, the most widely used on a worldwide basis. Two that seem to be effective are alpha-bisabolol and chamazulene. In lab studies, the flavonoid apigenin was found to inhibit *Helicobacter pylori*, now known to cause stomach ulcers.

Chicory root comes from the same species that yields the edible green chicory although the morphological form from which the roots are harvested is sometimes separated as *Cichorium intybus* var. *sativum* Bisch. Historically the juice pressed from the root was used for liver, kidney, and stomach problems, and even today it is used for indigestion. More commonly, the root of the blue-flowered perennial is dried, roasted, and ground and used as coffee substitute or mixed with coffee (often up to 30% of the mixture; Fig. 3.1).

Cynar is an Italian aperitif from Sicily produced by the Campari Company that is made using thirteen plant species, most prominently artichoke, *Cynara scolymus* L. It is a bitter and dark brown beverage with a 16.5% alcohol content. It can be drunk alone or mixed with soda water or soft drinks as a digestion aid. This latter property is due to the presence of cynarin which is one of the compounds contributing to the drink's bitter taste.

Certainly the most notorious beverage made from a member of Compositae is absinthe, a liqueur made from, or more properly flavored with, *Artemisia absinthium* L. (also used historically to flavor vermouth). *Artemisia* or wormwood has been used for millennia in Europe as a medicinal herb for overcoming bodily weakness. The species contains sesquiterpene lactones including absinthin, anabsinthin, artabsin, and the monoterpene ketone thujone. The commonly told story of its conversion into the popular liqueur centers around a Swiss doctor, Pierre Ordinaire who settled in Corvet, Switzerland and concocted a medicinal tonic for stomach ailments that became very popular. The story goes that he willed the recipe to Mère Henriod, his housekeeper and mistress (Lanier 1995; Delahaye 2001). The recipe was eventually purchased by Major Dubied whose son-in-law, Henry-Louis Pernod, used the recipe to manufacture the drink. However, Adams (2004) contends that Dr. Ordinaire's participation in the generation of the beverage is fictitious and that the original tonic, known as *l'elixir absinthe*, would more properly be traced directly to Henriette Henriod who made a tonic from infusions of *Artemisia* heads. Dubied did apparently buy the recipe from Henriod in 1797 and, with M. Pernod, set up the first commercial distillery a year later producing the alcoholic beverage that became the absinthe of commerce (Adams 2004).

Absinthe is made by placing pulverized *Artemisia absinthium* plants harvested just before the heads flower in ethanol for 24 to 48 hours and then distilling the alcohol. This initial distillate is white. The green color comes from mixing it with a powdered mixture of petite wormwood (*Artemisia pontica* L.), hyssop (*Hyssopus officinalis* L., Lamiaceae), and lemon balm (*Melissa officinalis* L., Lamiaceae), which, upon gentle heating and exposure to the air, add both volatile oils and chlorophyll to the liqueur producing a more complex flavor and the traditional green color. High quality absinthe has an alcohol content of 65%–75% (Delahaye 2001).

Originally absinthe was simply mixed with water, a combination that produces the cloudy white appearance characteristic of the beverage. Strictly speaking absinthe should not be called a liqueur because it is not sweet (Delahaye 2001). However, the method of preparation that subsequently developed produced a more liqueur-like drink by adding sugar. In fact preparation of the beverage became rather a fetish. First, ice and absinthe were placed in a glass. Then, a special perforated absinthe spoon was laid across the top of the glass and a cube of sugar placed in the center of the spoon. Ice-cold water was slowly poured over the sugar dissolving it as the water dripped through the perforations into the glass, slowly creating the cloudy, opalescent white, sweet, licorice-flavored beverage.

During the nineteenth century, absinthe became a wildly popular drink of the middle class and the art (e.g., Van Gogh, Gauguin, Manet, Degas, Toulouse-Lautrec) and literature (e.g., Verlaine, Wilde, Hemmingway) communities in France (Lanier 1995). By the end of the nineteenth century, absinthe drinking had risen to such excessive levels in France that people became concerned about high mortality rates associated with it although there was no actual determination as to whether deaths were related to absinthe itself or alcohol consumption. There was growing evidence that chronic use of absinthe led to addiction marked by epileptic attacks, delirium, and hallucinations. In 1915 selling absinthe in France was banned by presidential decree (Lanier 1995). Absinthe never gained the popularity in Germany or England that it enjoyed in France and in parts of the United States like New Orleans, the predominant location in the Americas for consuming the liqueur. Prohibition effectively stopped absinthe use in the United States.

The compound responsible for the licorice flavor in absinthe is absinthin but it is thujone that is responsible for the psychoactive properties of absinthe. It has recently been discovered that thujone acts as an antagonist to the GABA_A (G-aminobutyric acid type A) receptor (Höld et al. 2000). GABA is a neurotransmitter that causes relaxation and is antispasmodic. The antagonistic action of alpha thujone blocks the receptors leading to convulsions. In the United States, low thujone beverages containing *Artemisia* are currently again being marketed and absinthe is gaining in popularity, particularly in nightclubs.

Spices

Internationally, tarragon is the only commercially marketed herb of Compositae, but people have undoubtedly been using local species as flavorings for millennia. Other composites commonly used for flavoring are chrysanthemum and Bolivian coriander.

Tarragon, *Artemisia dracunculus* L., native to southern Russia and western Asia, was not known in ancient Greece or to the Romans. The first documented mentioned is in the 13th century by the Arabian botanist Ibnal-Baytar, a pharmacist in Spain, who listed it as a seasoning for vegetables, breath sweetener, and sleep-inducing drug (Rosengarten 1969). It became a well-known condiment only in the 16th century. By 1806 it had been introduced into California where it is now grown as a commercial crop. Distillation of tarragon yields 0.3%–1% of a pale yellow oil with an anise-like odor called tarragon oil or estragon oil—used in perfumery in France, toiletries, and in flavoring vinegar. The herb has a special affinity for chicken and lobster. In addition to this species, called "true" tarragon, there is Russian tarragon, *A. dracunculoides* Pursh. a perennial from which the young growth is harvested.

Chrysanthemum leaves called *tong ho* or *tung ho* are used in Asia as a potherb to flavor salads, soups, sukiyaki, and other dishes. Mature leaves are usually blanched (overcooking leads to bitterness) but when young they can be eaten raw.

Bolivian coriander (*pápalo*, *pápaloquete*, *quillquiña*) *Porophyllum ruderale* (Jacq.) Cassini is an annual herb used from Mexico to South America as a seasoning. It has a very pungent odor and pronounced taste that has been described as somewhat like cilantro, arugula, or rue.

Sweeteners

As far as is known, all members of Compositae store significant amounts of fructans (polymers such as inulin consisting of at least four fructose units that typically have a terminal glucose) in their underground storage organs (taproots and tubers) but not in the leaves (Roberfroid 2004). Inulin is used commercially as a sweetener in the food industry primarily because it can be converted to fructose and glucose through hydrolysis. Thus, potential sources of inulin are chicory root, elecampane (*Inula helenium* L.), dandelion (*Taraxacum officinale* L.), Jerusalem artichoke (*Helianthus tuberosus* L.), murnong (*Microseris lanceolata* Sch.Bip.), salisfy (*Tragopogon porrifolius* L. and *Scorzonera hispanica* L.), and yacon (*Polymnia sonchifolia* Poepp. & Endl.). Around 1970 researchers found that chicory root contained about 20% inulin and commenced selecting for higher yields that today reach 30%. As a consequence, virtually all commercial production of inulin is from chicory root. In addition to high yields, chicory inulin is of high quality, the roots are easy to harvest, and

Table 3.3. Approved herbs from Compositae listed in the Complete German Commission E Monographs (Blumenthal 1998) or listed in Foster and Johnson (2006).

Common name	Scientific name	Part of plant used	Use
Arnica flower	*Arnica montana* L., *A. chamissonis* Less.	Dried flowers in tincture or dried flowers in ointment	Extrernal for wounds, inflammation
Artichoke leaf	*Cynara scoymus* L.	Dried, cut leaves or pressed fresh juice	Dyspepsia
Blessed thistle	*Cnicus benedictus* L.	Leaves and stems as teas; herb	Loss of appetite, dyspepsia
Burdock	*Arctium lappa* L.	Root	Gastrointestinal, diuretic, arthritis, psoriasis
Butterbur	*Petasites hybridus* (L.) P. Gaertn., B. Mey. & Scherb.	Rhizomes and leaves	Migraines, asthma, spasms of urinary tract
Calendula flower	*Calendula officinalis* L.	Heads in infusions	External – wounds / internal – mouth and throat inflammations
Chamomile flower	*Matricaria recutita* L., *Chamaemelum nobile* (L.) All.	Heads in tea	External – inflammations / internal – gastrointestinal spasms and inflammation
Chicory	*Cichorium intybus* L.	Dried vegetative parts in teas	Loss of appetite, dyspepsia
Coltsfoot leaf	*Tussilago farfara* L.	Dried leaf in tea or fresh juice	Cough, hoarseness, mouth inflammation
Dandelion	*Taraxacum officinale* Wiggers	Cut herb, infusions	Loss of appetite, flatulence
Dandelion root	*Taraxacum officinale* Wiggers	Entire plant in liquid	Disturbances in bile, dyspepsia, stimulate diuresis
Pale purple coneflower	*Echinacea pallida* (Nutt.) Nutt.	Root tincture	Flu-like symptoms
Eastern purple coneflower	*Echinacea purpurea* (L.) Moench, *Echinacea angustifolia* DC.	Herb, juice, teas; roots	Anti-cold, respiratory chills or urinary infections / external – speed wound healing
Elecampane	*Inula helenium* L.	Rhizomes and roots	Pneumonia, asthma, diuretic
Feverfew	*Tanacetum parthenium* (L.) Sch.Bip.	Leaves, flowering heads	Fevers, migraines, rheumatism
Goldenrod	*Solidago virgauria* L.	Decoction of vegetative parts	Irrigation of inflamed urinary tract
Gumweed herb	*Grindelia robusta* Nutt. or *G. squarossa* (Pursh.) Dunal	Leaves and heads in tincture	Inflammation of respiratory tract
Milk thistle fruit	*Silybum marianum* (L.) Gaertner	Powered seeds for infusions	Dyspepsia, liver damage
Wormwood	*Artemisia absinthium* L.	Dried leaves in infusions/ decoctions	Loss of appetite, dyspepsia
Yarrow	*Achillea millefolium* L.	Dried aerial parts or juice	External – for baths for cramps / internal – gastrointestinal complaints

its inulin has a high percentage of chain lengths longer than ten.

Inulin is also considered a “prebiotic” (large molecular weight carbohydrates that are not digested in the small intestine and enter the large intestine as colonic food) that stimulates increased production of health-promoting bifidobacteria and other colonic bacteria. These bacteria are associated with an active immune function and the prevention of infectious diseases.

Stevia, *Stevia rebaudiana* (Bertoni) Bertoni, is a small herbaceous perennial native to Paraguay where native Guaraní Indians have been using it as a sweetening agent for centuries (Soejarto 2002). Stevia was introduced to Europe in 1887 and by 1909 was a cultivated crop there. The leaves contain *ent*-kaurene glycosides, stevioside and several rebaudiosides. These can be from 100–450 times as sweet as sucrose depending on the concentration. None of these substances is metabolized, so stevia is non-caloric and can be used by diabetics. Stevia has been used as a commercial sweetening agent in Asia and South America since the 1970s. In the United States it is not approved as a sugar substitute or sweetener, but can be sold as a dietary supplement (Lewis and Elvin-Lewis 2003).

NON-FOOD CROPS

Insecticides

Reflecting the association of Compositae with many insects throughout the world, it is fitting that the family is one of the few plant sources of effective commercial insecticides, known as rythrins. Rythrins are actually a mixture of pyrethrin I, and II, and cinerin I and II that are extracted from *Tanacetum cinerariifolium* (Trev.) Sch. Bip. native to south-central Europe (Purseglove 1968). Rythrins were apparently first used as an insecticide in Persia (but *Chrysanthemum coccineum* was probably the species used in that case). Initially dried heads were soaked in water to extract compounds, but later kerosene extractions proved to produce better yields. World War II saw an increased demand of pyrethrin to fight insects such as flies, fleas, lice, and mosquitoes. Pyrethrin was added to skin cream for scabies. Dried fish and meats were sometimes dipped into solutions containing pyrethrum to prevent insect infestation. The insecticide has a broad range of effectiveness, and resistance to it is low. An advantage of rythrins is that their active compounds break down rapidly and have low toxicity to mammals and birds.

Medicines

Countless species of Compositae have been used as herbal or traditional medicines for a wide array of conditions. Table 3.3 lists many of the more common of these species and their uses and Fig. 3.2 shows the distribution of the medicinal herbs (as well as poisons and species causing dermatitis) listed in Lewis and Elvin-Lewis (2004) across the tribes of Compositae. In most cases the compounds important for the use of composites as herbal medicines are sesquiterpenes, sesquiterpene lactones, and/or flavonoids. The major classes of plant-derived compounds important in modern medicine, however, are alkaloids that affect the peripheral nervous system, saponins (used as steroidal and hormone base compounds), and cardiac glycosides (used to treat congestive heart failure). Compositae are deficient in these kinds of compounds relative to species in Agavaceae, Dioscoriaceae, Leguminosae, Papaveraceae, and Solanaceae. Consequently, there are very few economically important medicinal plants from the family.

Artemisia annua L. is currently the only major medical plant belonging to Compositae (that is not classified as an herbal supplement or herbal medicine in the USA). It is native to China where it is known as *qinghao* or *huang hua hao*, and it has been used for 2000 years as an herbal remedy for fevers, headaches, and digestive complaints. In 1980 an article was published that showed the substance *qinghaosu* (artemisinin, discovered in 1972) was effective in treating malaria (Foster and Johnson 2006). Artemisinin appears to be accumulated in trichomes on the inflorescences and to a lesser extent on the leaf surfaces (Ferreira and Janick 1996). Today artemisinin and its derivatives artesunate, artemether, and dihydroartemisinin are major antimalarial drugs. It is believed that artemisinin works by entering red blood cells and, upon encountering iron in the heme, releases peroxides (free radicals) that kill the malaria plasmodium (Sullivan et al. 1996; White 2008). A recent trial study by the London School of Hygiene and Tropical Medicine demonstrated that giving young children in Tanzania a six-dose course of artemether plus lumefantrine (a traditional anti-malarial drug) cleared the malarial parasite from the blood of 99% of patients after 14 days (Arrow et al. 2004). This combination was far more effective than drugs or drug combinations conventionally used because of increased resistance of the malaria plasmodium to traditional anti-malarial drugs. Over the last two decades, artemisinin-based combination therapies (ACTs) have been very effective where they have been used, but the cost is about $2.00 per dose, much too expensive for many malaria-ravaged countries. Novartis Pharma AG, the manufacturer of Coartem™, the only ATC with reliable production figures, projected the need for 30 million treatment courses (of six doses each) in 2005 (World Malaria Report for 2005). Even at non-profit costs promised by Novartis, the revenue generated would be over $360 million annually. A National Academy of Sciences (USA) report in 2004 (Arrow et al. 2004) urged that before 2010, international organizations should begin collectively to contribute $300 million to $500 million annually to create a global subsidy that would make new combination malaria treatments available to the world's poor for as little as 10 cents per treatment course. Without significant investments in artemisinin-based combination therapies, the malaria mortality rate in Africa and Asia could double in a few decades, as the drugs used most frequently are rendered increasingly useless by rapidly spreading resistance.

Ornamentals

Many species of Compositae are used as ornamental plants, as cut flowers, potted plants, or bedding plants. Many of the more common ones are listed in Table 3.4. In the United States Department of Agriculture Floriculture database for 2004/2005 (http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1072) only three, chrysanthemums, marigolds, and Gerbera daisies are produced on a large enough scale to be included here. The potted commercial chrysanthemums are classified as *Chrysanthemum indicum* L. or as a complex hybrid composed of crosses among several annual and perennial species native to China. Though grown by the Chinese for over 2000 years, cultivars were not available in Europe until the 1800s. In Japan, the crest of the royal family is the *kiku*, or chrysanthemum.

The United States has been a site of active ornamental chrysanthemum breeding. In the 1880s, Elmer D. Smith hybridized and named over 500 cultivars. However, real development of the chrysanthemum as a pot crop has occurred since the 1940s. The chrysanthemum used in pot culture today is a hardy or semi-hardy herbaceous perennial with flowers in a wide range of colors, flower types, and plant sizes. Some types such as the pom-poms are more suited for cut flower production and others (e.g., hardy or fall mums) as bedding plants. About 100 cultivars are widely grown today as flowering pot plants with chrysanthemums constituting the third highest (after poinsettias and orchids) pot plant sold in the United States in 2004–2005 (Table 3.5). Cultivars for pot sales have been selected for a well-shaped aspect, many branches, short flowering stems, and a variety of flower shapes, forms, and colors.

Marigold is the name for several species of *Tagetes* native to Central and South America. The three most commonly cultivated species are, *Tagetes erecta* L. (African marigold), *T. patula* L. (French marigold), and *T. tenuifolia* L. (striped marigold). They are used as bedding plants

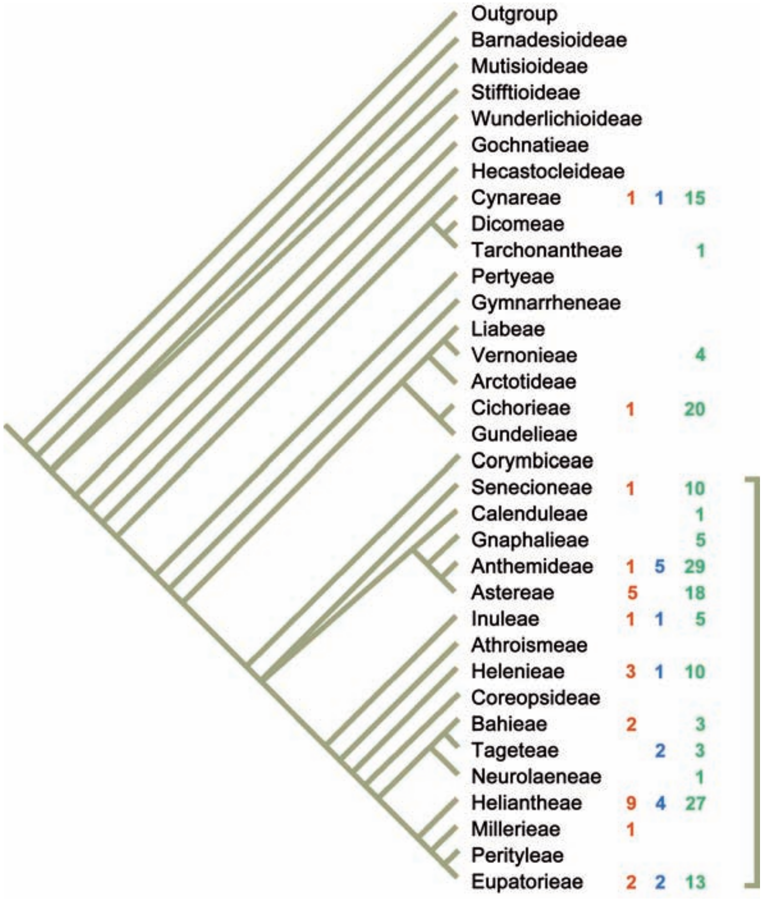

Fig. 3.2. Numbers of Compositae species (208) listed in Lewis and Elvin-Lewis (2004) as having medicinal, poisonous, or topical allergenic properties (red numbers are figures for poisonous plants, blue numbers are plants that cause disease, and green numbers list medicinal plants). The phylogenetic arrangement of tribes and subfamilies follows Panero and Funk (2008) and the website http://www.tolweb.org/asteraceae of J.A. Panero and B.S. Crozier. For simplicity, some tribes or subfamilies (without economically important taxa) have been omitted. The bar on the right spans the subfamily Asteroideae.

or as cut flowers. The Portuguese introduced them to Europe and India in the 16th century. Today, they are naturalized in the tropics and subtropics of the Old and New Worlds. They are cultivated in India and Pakistan as medicinal, flavoring, dye, and ornamental plants. Especially in India they are now part of everyday life with garlands used in festivals and burial ceremonies and as offerings to deities.

Gerbera "daisies" are one of several species of *Gerbera*. A cross between two South African species, *Gerbera jamesonii* H. Bolus ex. Hook. f. and *G. viridifolia* yielded *G.* ×*hybrida*, the most commonly grown ornamental with

Table 3.4. Compositae commonly used in the floriculture trade.

Common name	Scientific name(s)[a]	Use
Ageratum	*Ageratum houstonianum* Mill.	Bedding plant, pots
Aster	*Aster* spp.	Cut flowers, bedding plant
Bachelor button	*Cichorium intybus* L.	Bedding plant
Calendula	*Calendula arvense* L., *C. officinalis* L.	Bedding plants, cut flowers
Chrysanthemum	*Chrysanthemum indicum* L.	Cut flowers, bedding plant
Cosmos	*Cosmos sulphureus* Cav.	Bedding plant
Daisy	*Bellis perennis* L.	Cut flowers, bedding plant
Dahlia	*Dahlia hybrids*	Bedding plant, cut flowers
Gaillardia	*Gaillardia pulchella* Foug.	Bedding plant
Gerbera	*Gerbera* hybrids	Cut flowers, bedding plants
Marigold	*Tagetes* spp.	Bedding plant, cut flowers, garlands
Sunflowers	*Helianthus annuus* L.	Bedding plant, cut flowers
	H. argophyllus T. & G.	Bedding plant
	H. debilis Nutt.	Bedding plant
	H. decapetalus L.	Bedding plant
	H. ×*laetiflorus*	Bedding plant
	H. maximilianii Schrad.	Bedding plant
	H. ×*multiflorus* L.	Bedding plant
	H. salicifolius A. Dietr.	Bedding plant
Zinnia	*Zinnia elegans* Jacq.	Bedding plant, cut flowers

[a] Primary species cultivated.

Table 3.5. Major floriculture crops in the USA 2004/2005.

Potted plant species	Dollar value (wholesale)	Bedding/garden plant species (flats)	Dollar value (wholesale)	Cut flower species	Dollar value (wholesale)
Poinsettias	241,705,000	Pansy/viola	112,165,000	Lilies	77,009,000
Orchids	139,482,000	Impatiens	100,334,000	Tulips	42,121,000
Chrysanthemums	68,797,000	Petunia	94,351,000	Roses	38,969,000
Spring bulbs	55,132,000	Begonia	56,757,000	Gerbera daisies	32,314,000
Azaleas	36,750,000	Marigold	52,569,000	Gladiolas	24,074,000
Easter lilies	35,204,000	Geranium	7,763,000	Irises	20,021,000
				Chrysanthemums	17,246,000

Source: USDA Agricultural Statistics Board.

thousands of cultivars and a wide range of capitula sizes, shapes, and colors. Gerberas are sold as potted plants as cut flowers, and they can be used as a bedding plant.

Rubber

Many members of Compositae produce latex. In crops like lettuce there has been selection to reduce latex production because the latex contains bitter compounds. One species, however, guayule (*Parthenium argentatum* A. Gray), is grown expressly for its latex, which contains isoprene polymers (long chain of up to 6000 units) virtually indistinguishable from that of rubber trees *Hevea* spp. Guayule is native to the Chihuahuan Desert of SW USA and adjacent Mexico. Native Mexicans (Olmecs/Mayan) used the rubber from the plant to form balls used in the game *juego de pelota*. It is the only species of *Parthenium* that produces rubber, but unlike most other latex-producing plants, the latex is not produced in laticifers. The latex occurs in parenchyma cells throughout the plant, but primarily in the epithelial cells surrounding resin ducts formed primarily in the bark. Both rubber and resin are produced in the epithelial cells, but the resin is secreted into the ducts and the rubber remains in the surrounding cells, increasing in content until the cells die (Backhaus and Walsh 1983; Joseph et al. 1988).

Commercially, guayule plants are grown in nurseries and seedlings transplanted into the field. After about one year of age, plants can be pulled from the soil and shredded or branches can be clipped ca. 10 cm above the soil surface and processed, allowing the field plants to re-sprout. The latex is obtained by one of three methods (Ray 1993). The stems can be placed in vats in a dilute sodium hydroxide solution. The branches sink and the non water-soluble latex rises to the surface and is skimmed off. In a second method, the shredded stems are extracted with a polar solvent and the rubber separated from other compounds with hexane. The final method uses a mixture of solvents, usually hexane or pentane with more acetone added later to coagulate the rubber. Guayule could be a desirable crop in part because it is a dry land species not requiring supplemental water.

Fig. 3.3. Distribution of economically important species across the tribes of Compositae. Phylogeny as in Fig. 3.2. The bar on the right spans the subfamily Asteroideae.

Yet, Ray (1993) pointed out that guayule is not currently economical without either greater rubber yields or the identification and development of high value co-products that can be extracted, such as resin, lower molecular weight rubbers, and bagasse. Under irrigated conditions, yields of these combined products are almost at the levels needed to make guayule cultivation economically feasible. Although yields of guayule rubber are still too low for the species to be used commercially, in the early part of the 20th century several commercial operations were active in northern Mexico. One potential factor that favors guayule over *Hevea* is the absence of proteinaceous compounds in guayule that cause an allergenic reaction. Allergic reactions to *Hevea* latex products such as gloves and condoms can sometimes be life-threatening.

Dyes

Numerous Compositae have been used as sources of natural dyes. The most notable is the safflower, *Carthamus tinctorius* L. from which the red dye compound carthamin is extracted. Today carthamin, like other natural dyes, has mostly been replaced by aniline dyes, but it is still used occasionally in India for ceremonies (Purseglove 1968), for cakes, biscuits, and rouge.

Marigolds heads are used in the Asian subcontinent as a dye and in Mexico they are fed to chickens as a source of yellow pigment to insure deeply colored egg yolks.

CONCLUSIONS

Despite being one of the largest plant families, Compositae have yielded comparatively few crop plants with most economically important species concentrated in Anthemideae, Cardueae, Heliantheae, and Lactuceae (Fig. 3.3). One cannot blame this comparative low level of species utility to a poor representation of Compositae in areas where people developed agricultural systems. Composites abound in the Mediterranean Region, southern Mexico, the central Andes, and western China, all early centers of agriculture. Rather it appears that composites, in general, lack the products most desired by people and hence are usually relatively minor crops even in categories where they do provide economically important products. The major crops provided by the family are stem and leaf crops, root and tuber crops, and seed oils. Nevertheless, composites are represented in almost all other use categories except as a source of fiber, and wood, and wood products.

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Section II

Character evolution at the family level

Chapter 4

A review of chromosome numbers in Asteraceae with hypotheses on chromosomal base number evolution

John C. Semple and Kuniaki Watanabe

INTRODUCTION

> *In spite of the great variability in the chromosome numbers … a pattern can be seen when the evidence is fully reviewed.* — Robinson et al. 1981, p. 8

Asteraceae are the largest family of flowering plants and have long been of cytological interest. The first chromosome counts for members of the family were published more than a century ago (Juel 1900; Land 1900; Merrell 1900). The total number of chromosome number reports has increased dramatically with major efforts to determine chromosome numbers of large numbers of composites being conducted in the 1960–1980 period (e.g., Raven et al. 1960; Anderson et al. 1974). Prior to DNA sequence-based phylogenetic analyses, hypotheses on chromosomal base numbers in Asteraceae were hampered by a lack of understanding of which genera were basal within tribes and which tribes were basal within the family. For example, Cronquist (1981) reported that Asteraceae had a range of base numbers from $x = 2$ to $x = 19+$ and suggested that perhaps $x = 9$ was ancestral. Earlier, Solbrig (1977) had also concluded $x = 9$ was the ancestral base number of the family based on an analysis of habit and frequency of chromosome numbers. Bremer (1994) merely noted that chromosome number data were conveniently summarized in Solbrig (1977) and subsequent indices. In more recent years following the introduction of molecular techniques for analyzing phylogenies through DNA restriction fragment length polymorphisms and base pair sequence analyses, authors have compared molecular results with chromosomal basal number data in order to reach conclusions on ancestral base numbers within groups of genera and among tribes (e.g., Baldwin et al. 2002; Ito et al. 2000; Chapter 37). Accessing data in all of the tens of thousands of publications reporting chromosome numbers in Asteraceae has not been convenient until very recently, when much of the information was put online in Watanabe's (2008) *Index to Chromosome Numbers in Asteraceae* (http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html). This paper presents analyses of chromosome numbers in the online database in light of recent understanding of the phylogeny of Asteraceae (e.g., Funk et al. 2005). The first objective of the study was to compile a summary database of every genus in the family. The second objective was to determine the chromosomal base number for every genus in the family for which data were available. The third objective was to plot chromosome counts and basal chromosome numbers of every taxon onto the supertree (= metatree) phylogeny (Funk et al. 2005). The fourth object was to formulate hypotheses on patterns of chromosomal base number evolution in the family having "fully reviewed" the evidence.

MATERIALS AND METHODS

Two datasets were used as primary sources of information on chromosome numbers. The most critical of these were the data available online at http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html, Watanabe's *Index to Chromosome Numbers of Asteraceae* (2008). The database has been updated multiples times as data from additional publications are added to the matrix. Our analysis is based on entries in the database as of March 2007. This included records on more than 38,000 chromosome number reports at the time of our analysis listed by author and taxon; and 41,000 as of September 2007. Each search of counts in a genus included a summary of the number of reports, but not a calculated total of the actual numbers of counts included in the records. When a publication reported multiple counts for a single taxon, these were not listed separately. However, the information could be tallied from data presented in the search results. Also, searches for some genera include the names of taxa for which no chromosome counts have been reported in the literature. Thus, the number of "records" listed at the top of a search report needed to be recalculated to yield the actual number of individual chromosome number reports for a genus included in the summary data matrix created for this paper. The Watanabe dataset included data extracted from 4521 publications at the time of our analysis, and 4800 as of September 2007. Details on these can be accessed from the search reports generated by the web site and are not listed here. Searches of the database for this chapter were facilitated by working off-line directly from the Microsoft Excel™ data file (*.xls) created by Watanabe. Generic nomenclature in the Watanabe database follows Bremer (1994) with post March 2007 changes to reflect treatments of taxa in *Flora of North America* (Flora of North America Editorial Committee 2006).

The second data source for chromosome counts was the first author's research database files on chromosome number reports for asters, goldenrods and miscellaneous other genera of Astereae (primarily taxa of the subtribe Chrysopsidinae Nesom and miscellaneous other North American Astereae). The Semple datasets collectively included information on 10,835 individual counts at the time of our analysis and are based on individual voucher data. These were compiled for research on cytogeographic and taxonomic studies. Nomenclature in the Semple databases follows that of generic treatments of the Asteraceae in *Flora of North America* (vols. 19–21) with a data field indicating the name under which the count was originally published. These datasets are not available online. Each of the data files (*.ask) was created in askSam™ v.5.1.2.367 (Seaside Software Inc. dba askSam Systems, Perry, Florida).

A database summarizing information by genus on chromosome number data was constructed using askSam working from the Watanabe and Semple datasets plus information in generic treatments in *Flora of North America* (vols. 19–21). Eighteen data fields were included for each genus document. These are listed in Table 4.1 and included data on nomenclature and numbers of species, number of chromosome number reports (actual or estimated total number of counts), a list of chromosome numbers reported in the literature, ancestral and derived base numbers determined in this study, other cytological data (ploidy levels, aneuploidy, dysploidy and supernumerary chromosomes), geographic distribution information, and a field for miscellaneous observations, e.g., alternative sources of data, etc.

The completed generic summary database was searched to generate reports on a number of different cytological and taxonomic questions. Lists of genera with cytological data were generated for each tribe, subtribe or clade. Separate lists of all genera sorted alphabetically, by chromosomal base number, and by numbers of reports were also generated. Reports were saved as *.ask files, which can be exported as *.txt, *.rtf, *.html and several other file formats.

RESULTS AND DISCUSSION

Data on 1587 genera of Asteraceae and 15 genera of Calyceraceae and Goodeniaceae were included in the generic summary database. The results of analyses of numbers of counts and reports by genus are summarized by tribe/clade in Table 4.2 listed in the order of branching of clades on the supertree phylogeny of Funk et al. (2005). Included in Table 4.2 by tribe/clade are the numbers of genera included in this study compared with the number of genera reported for each tribe/clade in Bremer (1994), the percent of genera with at least one chromosome number report, an estimate of the number of species, and an estimate of the number of count reports.

An estimated 58,320 chromosome number reports were summarized; 58,124 of these reports were for Asteraceae. The actual number of chromosome number count determinations made on individuals is not known because this information was not always included in a publication. In some cases, a report was based on a chromosome count from a single individual of a taxon. In other cases, several hundred to more than a thousand counts were reported for a single taxon in one publication (e.g., Semple 1989). Papers reporting very large numbers of counts (>100) for a taxon were usually cytogeographic studies. At least one chromosome count has been reported for a taxon in 978 genera of Asteraceae (61.6%); no data were available for 611 genera in the family. Thirteen genera were found to have more than 1000 chromosome number reports in total (Table 4.3). The majority of genera have ten or fewer chromosome number reports (598 genera; 37.7%); 203 genera (12.8%) have been sampled only once.

The number of species of composites is estimated to be 22,472 (= total of all estimated numbers of species by genus) in 1587 genera. Cronquist (1981) estimated there to be about 1000 genera and 20,000 species in Asteraceae. Bremer (1994) recognized 1535 genera and raised the number of species to around 23,000. Bremer (1994) was the primary database on most genera included in our analysis, and thus it is not surprising that our numbers of genera and species are similar to those in Bremer (1994). The larger number of genera of Astereae reported here is the direct result of numerous DNA sequence studies published in recent years and incorporated into the generic limits followed in *Flora of North America*.

Some other errors were also undoubtedly introduced into the summary of genera in the database due to nomenclatural problems and data entry errors. The *International Plant Names Index* (http://www.ipni.org/index.html) was frequently consulted in the creation of the summary data matrix in order to reduce the number of errors due to nomenclature. Checking synonymy sometimes revealed a case of double counting of a species and including its cytological data under two genera. The case with asters is informative and indicative of possible sources of error at the time our analysis was first completed and involves the two authors of this paper. In the Watanabe database in March 2007, counts for asters were generally listed in the genus *Aster* L. under which the majority of the counts were originally reported. The online index contained 1753 records for *Aster* s.l. and one record for the North America aster genus *Symphyotrichum* Nees. The Semple database had 4578 reports for *Symphyotrichum* and only about 100 reports for the Eurasian genus *Aster* s.str. (clearly reflecting a geographic bias in data entry to date). However, when the numbers of reports were tallied for the Eurasian species included in the Watanabe database, it contained 2128 reports for 27 Eurasia species of *Aster* s.str. The number of reports for North American species of *Symphyotrichum* was larger in the Semple database than the Watanabe database because the former included more than 600 unpublished counts to be reported in unfinished cytogeographic studies. The conclusion to draw from the asters case is simple: anyone searching a database on chromosome numbers must pay attention to the generic concepts followed in entering the data. Many of these kinds of potential errors were sorted out using the synonymy in generic treatments in *Flora of North America*. We are pleased to note that changes to the nomenclature of asters in the Watanabe database post March 2007 were made so that reports of counts for North American species of asters are listed when searching *Doellingeria*, *Eurybia*,

Table 4.1. Data fields included in the summary database on genera.

PHYL [	Number for phylogenetic ordering of clades/tribes in reports 0–37
TRIBE [	
CLADE [	Any major but informal subtribal groupings
SUBTRIBE [	
GENUS [	
AUTH [	Authority(-ies) of generic name
SPP [	Number of species
REPS [	Number of published reports in on-line Index Chromo Asteraceae
X= [	Base number (not always obvious)
X2= [	Derived base numbers (not always obvious)
2n= [	All sporophytic numbers, meiotic and mitotic
POLY [	Yes/no polyploidy present
PLEVELS [	2*x*, 4*x*, 6*x*, etc.
DYSP [	Yes/no dysploidy present; base number shift up or down
ANEU [	Aneuploid numbers reported (interpretation of Index data)
SUPERS [	Yes/no supernumeraries (fragments, B's, etc.)
LOC [	General information on distribution; continent, country; state or province for North American taxa
OBS [	Notes on cytology, classification, problems to check; some synonyms

Table 4.2. Summary of numbers of genera with and without chromosome data by tribe/clade.

No.	Tribe	Included in this study	No. of genera in Bremer (1994)	% of total genera included[a]	Genera with counts	Genera without counts	% genera included with counts	Estimated number of species	Estimated number of count reports
Basal Grade									
1	Barnadesieae	9	9	100%	6	3	67%	92	28
2	*Stifftia* clade	3	2	150%	1	2	33%	18	1
3	Mutisieae	55	58	95%	27	28	49%	685	238
4	Gochnatieae	3	3	100%	2	1	67%	77	2
5	*Hecastocleis* clade	1	1	100%	1	1	100%	1	1
Carduoideae									
6	Dicomeae	7	7	100%	3	4	43%	103	5
7	Oldenburgieae	1	1	100%	1	0	100%	4	3
8	Tarchonantheae	2	2	100%	2	0	100%	17	3
9	Cardueae	83	83	100%	53	30	64%	2,557	4,093
10	Pertyeae	4	4	100%	2	2	50%	69	58
11	Gymnarrheneae	1	1	100%	1	1	100%	1	2
Cichorioideae									
12	Gundelieae	2	2	100%	2	0	100%	3	9
13	Cichorieae	100	98	102%	80	20	80%	1,850	11,635
14	Arctotideae	17	17	100%	8	9	47%	209	66
15	Liabeae	14	14	100%	12	2	86%	159	88
16	Vernonieae[b]	105	98	107%	42	63	40%	897	1001
17	unassigned	3	3	100%	1	2	33%	30	3
Asteroideae									
18	Senecioneae	120	120	100%	65	55	54%	3,196	2,784
19	Calenduleae	8	8	100%	6	2	75%	112	194
20	Gnaphalieeae	181	162	112%	95	86	52%	2,014	1,419
21	Astereae	215	170	126%	140	75	65%	2,638	20,052
22	Anthemideae	110	109	101%	69	41	63%	1,732	4,598
23	Inuleae	67	67	100%	35	32	52%	716	729
24	Athroismeae	3	3	100%	2	1	67%	27	2
Helenieae–Helianthoid clade									
25	Helenieae	13	13	100%	12	1	92%	117	441
26	Coreopsideae	24	20	120%	16	8	67%	420	980
27	Neurolaeneae	1	2	50%	1	0	100%	13	11
28	Tageteae	33	32	103%	23	10	70%	265	598
29	Chaenactideae	3	3	100%	3	0	100%	20	101
30	Bahieae	18	18	100%	17	1	94%	73	240
31	Polymnieae	2	2	100%	2	0	100%	9	67
32	Heliantheae	132	108	122%	95	37	72%	1,350	3,010

Table 4.2. Continued.

No.	Tribe	Included in this study	No. of genera in Bremer (1994)	% of total genera included[a]	Genera with counts	Genera without counts	% genera included with counts	Estimated number of species	Estimated number of count reports
33	Millerieae	34	38	89%	25	9	74%	358	737
34	Madieae	36	36	100%	36	0	100%	200	1,445
35	Perityleae	5	5	100%	4	1	80%	76	177
36	Eupatorieae	168	170	99%	89	79	53%	2,350	3,316
Incertae sedis									
	Galeana	1	1	100%	0	1	0%	3	0
	Villanova clade	2	2	100%	1	1	50%	10	2
	Welwitschiella	1	1	100%	0	1	0%	1	0
Totals		1,587	1,493		978	611	61.6%	22,472	58,136

[a] The total number of genera is based on Bremer (1994) or the tribal description in *Flora of North America* (2006).

[b] Number of genera counted and percentages based on data provided by Dr. Harold Robinson to update Watanabe database.

Symphyotrichum etc., rather than collectively under *Aster* s.l. The asters case demonstrates the advantage of online databases that can be updated and modified often, which is not the situation with printed databases or static online databases. The effort needed to keep a database such as Watanabe's *Index* up-to-date is large and time-consuming. For genera in other parts of the world, we have less confidence in decisions made while creating the summary of genera database. For nomenclature-related problems in genera within the same branch of the supertree of Funk et al. (2005), errors in assigning species and their chromosome counts to the correct genus have little or no significance to the tribal and family level conclusions presented below.

In Table 4.2, a wide range in the percent of genera for which at least one chromosome count has been reported among tribes/clades is presented. At least one chromosome number has been reported for all 36 primary clades in the family. All genera have been sampled in a number of the smaller tribes, e.g., Gundelieae and Polymnieae. For tribes with more than ten genera, the range of those sampled was 40%–100%. For the seven tribes with more than 100 genera, the average number of genera sampled was 60.75%. Vernonieae were the least well sampled with chromosome counts reported for only 40% of the genera using data in the Watanabe *Index* that was updated late in this study with the assistance of Dr. Harold Robinson. However, prior to assigning counts originally published under the generic name *Vernonia* to the many genera that have been segregated from it, only 23% of the genera in Vernonieae had at least one chromosome number reported. The average number of genera sampled for the six other large tribes was 64.2%, which is slightly more than for the entire family; the six tribes Senecioneae, Gnaphalieae, Astereae, Anthemideae, Heliantheae and Eupatorieae include about 57% of the genera in the family.

A very large range in chromosome numbers and chromosomal base numbers occurs in Asteraceae. More than 180 different mitotic counts have been reported: 2*n* = 4, 4+1–3, 5, 6, 6+1–2Bs, 7, 8, 8+1–6Bs, 9, 10, 10+1–2B, 11, 12, 12+1, 12+1–4Bs, 13, 14, 14+1–2, 15, 16, 17, 18, 18+1,

Table 4.3. Thirteen genera with more than 1000 chromosome count reports.

No. of reports	Genus	Tribe
4578	*Symphyotrichum*	Astereae
4549	*Solidago*	Astereae
4017	*Taraxacum*	Cichorieae
2129	*Aster*	Astereae
2128	*Crepis*	Cichorieae
1905	*Eupatorium*	Eupatorieae
1884	*Brachyscome*	Astereae
1709	*Hieracium*	Cichorieae
1605	*Senecio*	Senecioneae
1600	*Xanthisma*	Astereae
1489	*Centaurea*	Cardueae
1400	*Artemisia*	Anthemideae
1158	*Erigeron*	Astereae

18+1–4B, 18+2, 19, 20, 20+1–5, 20+1–6B, 21, 22, 22+1–3, 24, 24+1, 24+1B, 24+5–9, 25, 26, 27, 28, 29, 30, 30+2, 30+2B, 31, 32, 33, 34, 34+1frag, 35, 36, 36+1, 36+1–2, 37, 38, 39, 40, 40–45, 40–47, 40+2Bs, 42, 42–44, 44, 45, 45–50, 46, 47+3, 48, 48+1, 48+3Bs, 50, 50–52, 51, 51–52, 52, 53, 54, 54+1–5supers, 55, 56, 56–58, 57, 58, 58–59, 60, 61, 62, 63, 64, 65, 66, 67, 68, 69–72, 70, 72, 72–74, 76, 78, 80, 81, 84, 85, 86, 87, 88, 90, 92, 95, 96, 98, 100, 108, 110, 112, 114, 120, 122, 130, 138, 140, 146, 154, 160, 160+, 171, 176, 180, 184, 198, ca. 228, ca. 288, ca. 324, ca. 432. The most frequent number in the database was $2n = 18$ because it is the most frequent number reported in Astereae, which has the largest number of counts reported, and in several other larger tribes. Two species in the tribe Astereae have the very low sporophytic number of $2n = 4$, *Brachyscome dichromosomatica* C.R. Carter and *Xanthisma gracile* (Nutt.) D.R. Morgan & R.L. Hartman. The highest number reported is $2n =$ ca. 432 ($48x$; $x = 9$) for *Olearia albida* Hook. f. (Beuzenberg and Hair 1984), also in the tribe Astereae.

More than 170 different meiotic counts have been reported: $2n = 2_{II}$, 3_{II}, 3_{II}+1–8B, 4_{II}, 4_{II}+2sup, 4_{II}+1–3_{I}Bs, 4_{II}+1–2_{II}Bs, 5_{II}, 5_{II}+1, 5_{II}+1–4Bs, $5_{II}+10_{I}$, 6_{II}, 6_{II}+1–2Bs, $7_{II}+2_{I}$, 8_{II}, $8_{II}+1_{I}$, 8_{II}+1–2B, 9_{II}, 9_{II}+1–2_{I}, 9_{II}+2Bs, 9_{II}–12_{II}, 10_{II}, 10_{II}+1, 10_{II}+1–2Bs, $10_{II}+10_{I}$, 11_{II}, $11_{II}+1_{I}$, $11_{II}+8_{I}$, 12_{II}, 12_{II}+3Bs, 13_{II}, 13–14_{II}, $13_{II}+1_{I}$, $9_{II}+9_{I}$, 14_{II}, 15_{II}, 15_{II}–16_{II}, 15_{II}–17_{II}, 15_{II}+1B, 15_{II}+1frag, 16_{II}, $16_{II}+1_{I}$, $16_{II}+1_{I}$, 16_{II}–18_{II}, 17_{II}, 17_{II}–24_{II}, 17_{II}+1–4frags, $17_{II}+1_{I}$, $17_{II}+1_{II}$, $17_{II}+5_{I}$, 17_{II}+6B, 18_{II}, 18_{II}–20_{II}, 18_{II}–27_{II}, 18_{II}–20_{II}, 18_{II}+1frag, $18_{II}+1_{I}$, 19_{II}, 19_{II}+1frag, $19_{II}+1_{I}$, 19_{II}+2–3Bs, 19_{II}+2–3frag, 19_{II}+4–7B, 20_{II}, $20_{II}+1_{I}$, 20_{II}+1frag, 21_{II}, $21_{II}+1_{I}$, 22_{II}, 23_{II}, 24_{II}, 24_{II}–27_{II}, 24_{II}–30_{II}+8–20_{I}, 25_{II}, 25_{II}+1–6frag, 25_{II}+Bs, 26_{II}, 26_{II}+1–3Bs, 27_{II}, $27_{II}+6_{I}$, 27–28_{II}, 27_{II}–30_{II}, 28_{II}, $28_{II}+2_{I}$, 28_{II}–29_{II}, 29_{II}, $29_{II}+1_{I}$, 30_{II}, $30_{II}+2_{I}$, $32_{II}+1_{II}$, 32_{II}–34_{II}, 33_{II}, 33_{II}–34_{II}, 34_{II}, 34_{II}–36_{II}, $34_{II}+2_{I}$, 36_{II}, 36_{II}–38_{II}, 38_{II}, 39_{II}, 40_{II}, 41_{II}, 42_{II}–44_{II}, 43_{II}, 44_{II}, 44–45_{II}, 45_{II}, 46_{II}, 47–48_{II}, $47_{II}+3_{I}$, 48_{II}, 50_{II}, 50_{II}+1–8supers, 51_{II}, 52_{II}, 54_{II}, 59_{II}, 59–60_{II}, 60_{II}, 64_{II}, 68_{II}, 68_{II}–69_{II}, 70_{II}, 72_{II}, 80_{II}, 86_{II}, 89–96_{II}, 100_{II}, 102_{II}–108_{II}, ca. 108_{II}, ca. 110_{II}, ca. 131_{II}. The range in meiotic counts is the same as for mitotic counts with the exception of only reaching about $30x$ to $32x$. Meiotic irregularities and precocious divisions of some bivalents account for many of the reported numbers. These make determining with certainty the chromosome number of polyploid individuals more difficult. In our experience, interpreting meiosis is generally more difficult than counting mitotic chromosomes, and this is particularly true because such a large number of composites are of polyploid origin. However, growing live plants for root tip squashes to obtain mitotic counts is often not possible.

Two categories of chromosomal base numbers occur in Asteraceae. First, x numbers include the ancestral base numbers (plesiomorphies) and the base numbers derived from these via dysploidy. Dysploidy is the change in the chromosomal base number through a rearrangement of chromatin and loss or gain of a centromere without necessarily changing the amount of chromatin in the karyotype. In Asteraceae, dysploidy decreases are common to very common in some clades, while increases appear to be rare or very rare depending upon how the higher x numbers are interpreted. Base numbers of $x = 2$, 3, 4, 5, 6, 7, 8, 9, 10, and 11 occur in the family. Some of these numbers may be the result of a dysploid increase, others are undoubtedly the result of a series of dysploid decreases. There are many, many cases of dysploid series from higher to lower base numbers in Asteraceae, and these are found in nearly all of the 36 main branches of the phylogeny. Dysploidy is unknown in a few of the branches due to a lack of data (no counts or very few counts). Even some of the smaller branches with few taxa have some dysploidy. Dysploidy occurs in 102 genera with x base numbers and in 112 genera with derived x_2 base numbers. In total, dysploidy occurs in 214 genera, 21.9% of the 978 genera with counts reported.

Numerous secondarily derived base numbers (x_2) are also common in the family. These evolved in several different ways. Derived base numbers can result from allopolyploid combinations of x numbers. For example, the $x_2 = 9$ base number in *Chrysopsis* (Astereae) is derived from hybridizing $x = 4$ and $x = 5$ parental taxa and subsequent chromosome number doubling and diploidization (Semple and Chinnappa 1980). Alternatively, derived base numbers can result from autopolyploidy and subsequent diploidization of the karyotype resulting in a x_2 that is a multiple of the ancestral x number of the clade. Nearly the entire *Olearia* II clade in Astereae appears to be based on a diploidized $12x$ ploidy level (Cross et al. 2002; Chapter 37). Dysploid decreases also occur in clades with derived x_2. The following derived base numbers occur in the family: $x_2 = 19$, 18, 17, 16, 15, 14, 13, 12, 11, 10, 9, 8, 7, 6, 5, 4, and 3. Dysploidy has also occurred in polyploids of these derived numbers resulting in much larger x_2 numbers and dysploid numbers derived from them.

Polyploidy is common in Asteraceae and occurs in most major clades. In total, polyploidy occurs in 570 genera, 58.3% of the 978 genera with counts reported; this includes all genera of the major Helenioid–Helianthoid clade. Polyploidy occurs in 247 genera without x_2 base numbers, 25.3% of the 978 genera with counts reported. Polyploidy is common in the most basal branch of Asteraceae, subfam. Barnadesioideae, in which only *Schlechtendalia* is known to occur at a presumed diploid level with a dysploid derived base number. The following ploidy levels occur in Asteraceae: $2x$, $3x$, $4x$, $5x$, $6x$, $7x$, $8x$, $9x$, $10x$, $12x$, $14x$, $15x$, $16x$, $18x$, $20x$, $22x$, $24x$, $32x$, $36x$, and $48x$. Frequencies of ploidy levels are summarized in Table 4.4. Diploids are most frequent and

Table 4.4. Frequencies of ploidy levels in Compositae.

	Number of genera		% of 978 genera with counts			
Ploidy level	Only level	With other levels	Only level	With other levels	Genus	Tribe
Base numbers (*x*)						
2*x*	270	440	27.6%	45.0%		
3*x*	0	34	0.0%	3.5%		
4*x*	25	193	2.6%	19.7%		
5*x*	0	16	0.0%	1.6%		
6*x*	20	93	2.0%	9.3%		
7*x*	0	6	0.0%	0.6%		
8*x*	1	41	0.1%	4.2%	*Paragynoxys*	Senecioneae
9*x*	0	5	0.0%	0.5%		
10*x*	3	25	0.3%	2.6%		
12*x*	1	24	0.1%	2.5%	*Pachystegia*	Astereae
14*x*	0	5	0.0%	0.5%		
12*x* + 14*x*	1	4	0.1%	0.4%	*Soliva*	Anthemideae
15*x*	0	1	0.0%	0.1%	*Werneria*	Senecioneae
16*x*	0	3	0.0%	0.3%	*Antennaria*	Gnaphalieae
					Raoulia	Gnaphalieae
					Werneria	Senecioneae
18*x*	0	2	0.0%	0.2%	*Tetradymia*	Senecioneae
					Antennaria	Gnaphalieae
20*x*	0	2	0.0%	0.2%	*Antennaria*	Gnaphalieae
					Werneria	Senecioneae
22*x*	0	1	0.0%	0.1%	*Olearia* II	Astereae
32*x*	0	1	0.0%	0.1%	*Olearia* II	Astereae
36*x*	0	1	0.0%	0.1%	*Olearia* II	Astereae
48*x*	0	1	0.0%	0.1%	*Olearia* II	Astereae
Derived base numbers (x_2)						
2*x*	289	300	29.6%	30.7%		
3*x*	0	27	0.0%	2.8%	*Amauriopsis*	Bahieae (apomict)
4*x*	8	129	0.8%	13.2%		
5*x*	0	10	0.0%	1.0%		
6*x*	1	41	0.1%	4.2%	*Erechtites*	Senecioneae
7*x*	0	2	0.0%	0.2%		
8*x*	0	21	0.0%	2.1%		
9*x*	0	0	0.0%	0.0%		
10*x*	0	7	0.1%	0.7%		
12*x*	0	9	0.0%	0.9%		
16*x*	0	2	0.0%	0.1%	*Chromolaena*	Eupatorieae
					Leptinella	Anthemideae
20*x*	0	1	0.0%	0.1%	*Leptinella*	Anthemideae
24*x*	0	1	0.0%	0.1%	*Leptinella*	Anthemideae

were the only ploidy level occurring in 270 genera with x base numbers and in 289 genera with diploidized x_2 base numbers, 27.6% and 29.6% of the 978 genera with counts reported, respectively. Higher ploidy levels occur with decreasing frequency as the ploidy level increases; 7.4% (x) and 2.9% (x_2) of the 978 genera with counts reported include ploidy levels of $8x$ to $10x$; 3.9% (x), and 1.3% (x_2) of the 978 genera with counts reported include ploidy levels of $12x$ and higher levels.

Supernumerary chromosomes of various kinds have been reported in 143 genera of Asteraceae. Of these, 45 genera have been reported to have B chromosomes. It was not determined by us whether or not these reports were for true B chromosomes (Jones and Rees 1982) such as found and well studied in *Xanthisma gracile* and *X. texanum* DC. or were merely supernumerary chromosomes mislabeled as B chromosomes. Some reports may even have been errors in reporting the distal portion of the satellite chromosome as a supernumerary when the satellite was well separated from the proximal portion of the chromosome. For example, the large distal portion of the satellite chromosomes in *Eurybia* and *Symphyotrichum* (both Astereae) could easily be mistaken for separate small supernumerary chromosomes (J.C. Semple, pers. obs.) or separate autosomal chromosomes (Watanabe et al. 2007).

The frequency of aneuploidy was also analyzed. True aneuploidy is the gain or loss of single chromosomes without changing the base chromosome number. Due to the large number of ambiguous chromosome counts published as "circa" reports or as errors in reports based on sectioning techniques, it was unclear if ranges in numbers about a base number or multiple of the base number in polyploids were indications of aneuploidy occurring in a taxon or if these ranges were counting errors. Therefore, no reliable frequency of aneuploidy can be reported here.

Chromosomal base number evolution in Asteraceae

> *Speculating on base chromosome numbers offers,*
> *perhaps, the finest of all vehicles for intellectual*
> *auto-stimulation.* — e-mail from J.L. Strother
> to J.C. Semple, 16 June 2006

Ancestral base numbers for each of the 36 main branches of the supertree phylogeny (Funk et al. 2005) were determined, as were the base numbers for Goodeniaceae and Calyceraceae. The latter two families have a base number of $x = 9$ with lower base numbers of $x = 8$ and $x = 7$ derived by downward dysploidy. In the *rbcL* DNA phylogeny of Asterales (Gustaffson et al. 1996), the basal grade in Goodeniaceae included *Anthotium* R. Br., *Dampiera* R. Br., *Lechenaultia* R. Br. and *Brunonia* Smith. All four genera have base numbers of $x = 9$ (Peacock 1963). In Goodeniaceae, *Goodenia* and *Coopernookia* with $x = 8$ or 7 were in a derived position in the family (Gustaffson et al. 1996). A phylogeny of Asteraceae with ancestral chromosomal base numbers superimposed is shown in Fig. 4.1. An ancestral base number of $x = 9$ is hypothesized for Barnadesieae with $x = 8$ being derived by downward dysploidy. The genera *Arnaldoa*, *Chuquiraga* and *Dasyphyllum* have polyploid chromosome numbers with $x_2 = 27$ based on counts in Watanabe's online index and Watanabe et al. (2007). *Doniophyton* has reported numbers of $2n = 24_{II}$, 48, and 25_{II} suggesting base numbers of $x_2 = 25$ and $x_2 = 24$ derived from an ancestral $x_2 = 27$ via downward dysploidy. The hexaploid ploidy level would have reduced the rate of evolution allowing these genera to retain plesiomorphic traits for the family. Chromosome numbers reported for *Barnadesia* ($2n = 12_{II}$, 14_{II}, 25_{II}, 50–52, 52, 54, 62, ca. 50_{II}) suggest more karyotype evolution has taken place in the genus than other related genera or some of the counts are inaccurate. *Schlechtendalia* has a base number of $x = 8$, which is likely derived by dysploid decrease. However, it is difficult to infer dysploid reduction from $2n = 54$ to $2n = 18$ or 16 at a bound. Thus it is possible that the $x = 8$ base number for *Schlechtendalia* has been derived from the ancestral $x = 9$ by dysploid reduction and $2n = 54$ for *Barnadesia* and *Dasyphyllum* is a hexaploid state based on the original base chromosome number, $x = 9$. Stuessy et al. (1996) considered *Schlechtendalia* to be primitive within Barnadesioideae, but this is not supported by the derived position of the genus on the supertree (Funk et al. 2005); the phylogram in Stuessy et al. (1996) shows little similarity to the generic arrangement in the supertree. A basal position for *Schlechtendalia* based on new molecular sequence data, however, is an alternative that still cannot be refuted (see Chapter 13).

The chromosome number/habit situation in Barnadesieae looks similar to primitive angiosperm families with the high base chromosome numbers and with the woody habits in the woodland or forests (= the closed plant community). These high chromosome numbers, the woody habits (tree, shrub or liana) and their habitats in the closed plant communities are linked very closely. In contrast, the herbaceous members, *Acicarpha spathulata* (Calyceraceae), *Schlechtendalia luzulaefolia* and *Hecastocleis shockleyi* (Asteraceae) have the lower chromosome number of $2n = 16$ and their habitats are open plant communities such as the maritime coastal sand-dune (*Acicarpha spathulata*) and arid semi-desert (*Hecastocleis shockleyi*). They have very specialized morphology such as succulent (*Acicarpha spathulata*) or spiny (*Hecastocleis shockleyi*) leaves, and seeds embedded within the receptacle (*Acicarpha spathulata*). In sister families of Asteraceae, members of Goodeniaceae and Calyceraceae are herbs and have the low chromosome base number $x = 9$ and occur in open plant communities. In more basal Asteraceae, the $n = 8$

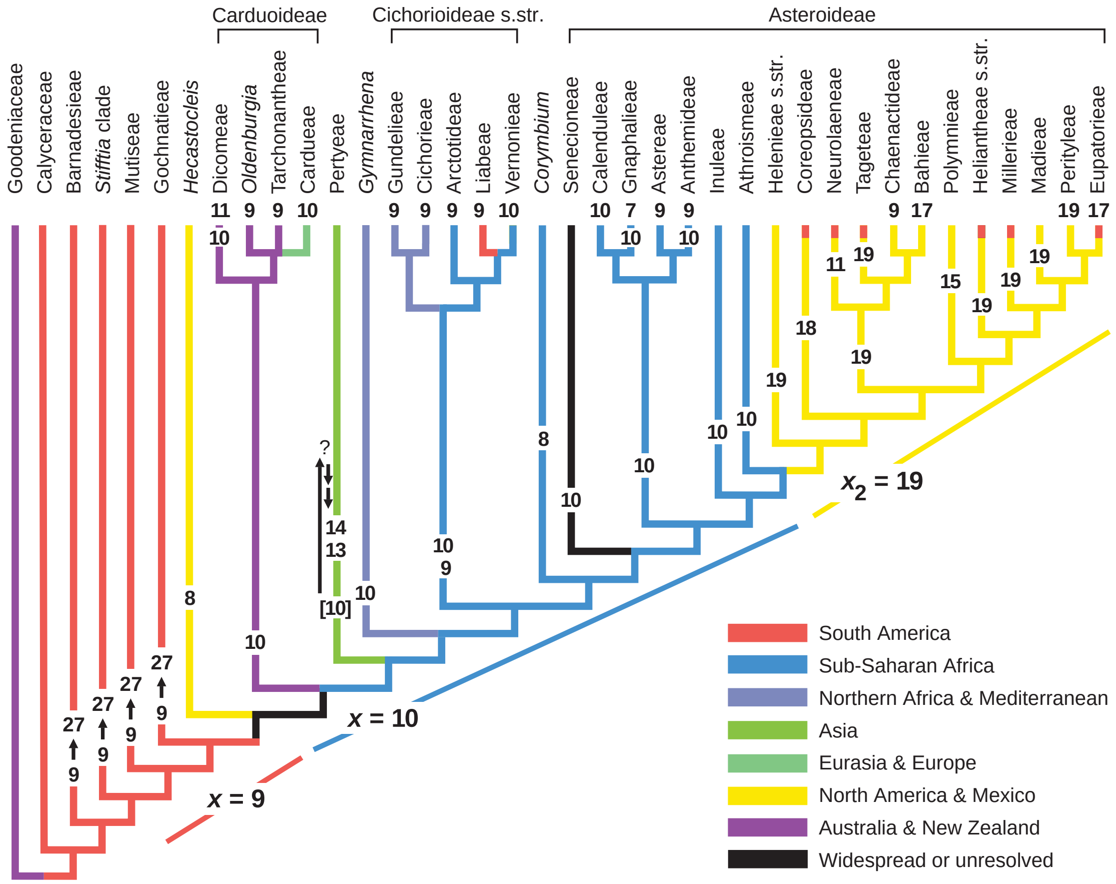

Fig. 4.1. Chromosomal base number evolution in Asteraceae. Hypothesized base numbers are superimposed on the summary tree of the supertree (= metatree) phylogeny presented by Funk et al. (2005).

for *Schlechtendalia luzulaefolia* and *Hecastocleis shockleyi* is a derived number. These specialized habitat taxa have a more restricted recombination system and more immediate fitness instead of genetic flexibility. Such a genetic system appeared to be causally connected with the dependence on ample seed production as the only means of propagation in short lived plants and with rapid population establishment in labile and briefly available habitats (Grant 1958; Stebbins 1958; Ehrendorfer 1970).

An $x = 9$ ancestral base number is hypothesized for the next three branches on the supertree (Fig. 4.1). The chromosome counts reported for the *Stifftia* clade are $2n = 54$ (Gibbs and Ingram 1982; Watanabe et al. 2007). This also is hypothesized to be a paleopolyploid with $x_2 = 27$ derived from an $x = 9$ ancestor. Additional counts for this clade are needed. Genera in Mutisieae include chromosome counts indicating that both polyploidy and dysploidy have occurred multiple times. Base numbers of x or x_2 = 8, 9, 10, 11, 12, 14, 15, 22, 23, 24, 25, 26, 27, 36 are indicated by the many counts for the tribe. We hypothesize that multiple downward dysploid events from polyploids based on $x = 9$ account for all, or nearly all, of the base numbers listed. These are the result of long dysploid series from polyploids of $x_2 = 27$. There was a reduction in chromosome number from $x_2 = 27$ (e.g., *Acourtia*) to $x_2 = 14$ and 11 (*Chaetanthera*) with a change in growth form from shrub to herb habit within Mutisieae. In Gochnatieae, four counts have been reported; $2n = 54$ for *Cyclolepis* and $2n = 54$, $2n =$ ca. 23_{II} and $2n = 44$ for *Gochnatia*. A paleopolyploid base of $x_2 = 27$ is hypothesized, again being derived from an $x = 9$ ancestor. Therefore, the basal grade of tribes native to South America all are hypothesized to have an ancestral chromosomal base number of $x = 9$. Alternatively, the *Stifftia* clade, Mutisieae and Gochnatieae could have an ancestral base number of $x_2 = 27$, with all other numbers in the three clades derived from this presumably diploidized hexaploid number. Such a possibility would then necessitate a long, and undocumented, dysploidy series from $x_2 = 27$ to $x_2 = 11$, 10, 9 and 8 in the next series of tribes/clades on the supertree. We remind the reader of Strother's comment on base numbers at this point in the discussion. If Barnadesieae were also hypothesized to be $x_2 = 27$ and this is assumed to be basal for Asteraceae, then all chromosome numbers in the family would be x_2 numbers. This does not seem likely at this time.

The next branch on the supertree includes just *Hecastocleis* with one report of $2n = 16$. A base number of $x = 8$ is indicated for this North American genus. We hypothesize that it is derived by downward dysploidy from $x = 9$. Additional chromosome counts are needed to test this hypothesis.

Funk et al. (2005) noted that next nine major branches on the supertree were likely African in origin. The red lines of the South American grade were replaced by blue, lavender and green lines on their phylogeny. Shifts from $x = 9$ to $x = 10$ and 11 are hypothesized to have occurred accompanying the shift in geography. Ancestral base numbers of $x = 10$ or 11 (Dicomeae), $x = 10$ (Cardueae, *Gymnarrhena*, Vernonieae, Senecioneae, Calenduleae, Gnaphalieae, Anthemideae, Inuleae [including Plucheeae] and Athroismeae) and $x = 9$ (*Oldenburgia*, Tarchonantheae, Gundelieae, Cichorieae, Arctotideae, Liabeae, and Astereae) are hypothesized based on the known chromosome numbers of basal members of these clades. Therefore, the base number of Carduoideae is $x = 10$. The base number of Cichorioideae could be either $x = 10$ or $x = 9$. We hypothesize that it was ancestrally $x = 10$.

The four core Asteroideae tribes also are likely to have been ancestrally $x = 10$. In Calenduleae, Nordenstam (1994) concluded a base number of $x = 10$ appeared likely, and we agree that this is most parsimonious with $x = 8$ and $x = 7$ derived by downward dysploidy. In Anthemideae and Gnaphalieae, decreases from $x = 10$ early in their histories to $x = 9$ and 7, respectively, are hypothesized. Watanabe et al. (1999) noted the difficulty in determining the ancestral base number in Gnaphalieae due to a lack of chromosome counts for African taxa. The few counts available for members of the subtribe Relhaniinae suggest base numbers of $x = 9$, 8, and 7, but the majority of genera have not yet been sampled cytologically even once. Counts with $x = 10$ have been reported in a few genera of Anthemideae. Only Astereae shifted to $x = 9$ via downward dysploidy before diversifying. However, the two most basal genera in Astereae, *Denekia* and *Printzia*, are unknown cytologically. Should either of these be found to have $x = 10$ as a base number, then Astereae also would be ancestrally $x = 10$.

Based on the preponderance of clearly downward dysploid events in Asteraceae, it seems likely that upward dysploid events are much more difficult to successfully complete. An increase in base number could result from trisomic aneuploidy of a single chromosome homologue that does not produce a lethal increase in gene product from the three copies of each gene. Aneuploidy would readily provide the new centromere needed for the increase in base number, and chromosome rearrangements and loss or suppression of critical genes could result in a stabilized new higher base number. Such an evolutionary process involves more difficult steps than simply rearranging existing chromatin on fewer centromeres to achieve a dysploid decrease. This difference in likelihood would account for the rarity of dysploid increases in the family and the relative commonness of dysploid decreases. Therefore, we have hypothesized very few ancestral dysploid increases in favor of many long dysploid series with gaps in base numbers from high to low due to extinctions or lack of discovery.

The two other tribes in this middle portion of the supertree are hypothesized to have derived base numbers. Pertyeae have chromosome numbers indicating possibly derived base numbers of $x_2 = 14$, and 13. We hypothesize that these are not derived by serial upward dysploidy from base number of $x = 10$ or 9 or 8, but rather they are derived by a series of downward dysploid events from a polyploid ancestor with $n = 20$, 18 or 16. The same series of events is a documented pattern in the Helenioid–Helianthoid clade and also appears to have occurred in Vernonieae with $x_2 = 17$ being derived from $x = 10$, 9 and 7 ancestors. This appears to be the "easier" evolutionary process than multiple dysploid increases to reach $x = 14$. *Corymbium* forms the other mid tree clade with a derived base number, but in this case $x = 8$ is indicated by the single count of $2n = 16$. Two downward dysploid events from an $x = 10$ ancestor are hypothesized in this branch of the supertree.

Numerous and sometimes well documented downward dysploid series have occurred in Cichorieae, Astereae and Gnaphalieae. Some of these cases are classical studies in cytotaxonomy and need not be discussed further here, e.g., *Crepis* and *Brachyscome*. Polyploidy is also frequent in these tribes resulting in them being some of the more intensively studied tribes cytologically over many years.

Funk et al. (2005) noted a second major geographic shift in the location of composite evolution indicated on their supertree diagram by a shift from blue, lavender and green lines to yellow lines for North American origins. This is the large terminal Helenioid–Helianthoid clade of the phylogeny. Baldwin et al. (2002) discussed this portion of the tree in detail noting the high derived ancestral base numbers for all the tribes in the clade; they hypothesized that $x_2 = 18$ was ancestral with multiple upward dysploidy events to yield $x_2 = 19$. Decades earlier, Smith (1975) and later Robinson et al. (1981) hypothesized $x = 17–19$ as basal for Heliantheae s.l., with Robinson et al. presenting arguments suggesting $x = 19$ being derived via aneuploidy from $2n = 4x = 20$. During this same pre-DNA sequence time period, base numbers of $x = 8$ or 9 (Stuessy 1977) and $x = 8–12$ (Solbrig et al. 1972) were suggested for Heliantheae s.l. We hypothesize that $x_2 = 19$ is ancestral for the entire clade (Fig. 4.1) because we believe multiple dysploid increases are much less likely than numerous dysploid decreases. In our database, $x_2 = 19$ taxa occur in Helenieae, Tageteae, Bahieae, Heliantheae, Millerieae, Madieae, and Perityleae. Dysploid derived numbers of $x_2 = 18$, 17, 15, and 11 appear to be ancestral in Coreopsideae, Eupatorieae, Polymnieae, and Neurolaeneae, respectively. The ancestral base number in Chaenactideae may be $x_2 = 9$, with $x_2 = 17$ being secondarily derived, but this is not certain (Mooring 1965; Baldwin et al. 2002).

There are several ways that $x_2 = 19$ could have evolved, and we do not favor one possibility over another due to a lack of conclusive evidence. In each scenario, downward dysploidy would have been involved, but the timing differs. Athroismeae are sister to the entire clade, and this has a base number of $x = 10$. The $x_2 = 19$ base number could be an allopolyploid derived from $x = 10$ and $x = 9$ parental taxa. The dysploid event would have occurred before the polyploid event. Alternatively, a tetraploid taxon with $n = 20$ and $x = 10$ could have undergone subsequent downward dysploidy and diploidization to yield $x_2 = 19$. There is evidence that both scenarios have occurred in other tribes, although the base numbers involved are different. Robinson et al. (1981) noted a tendency for higher base numbers to stabilize at numbers less than double the original lower base number. This observation lends support to $x_2 = 19$ evolving with polyploidy first ($2n = 4x = 20$) and subsequent disploidy and karyotype diploidization.

Within the Helenioid–Helianthoid clade, short to long downward dysploid series occur in many different genera. In most of these, gaps occur in the series, either due to a lack of data or extinction of intermediate base number taxa. Many taxa remain to be sampled cytologically and some of the gaps may be filled in with new data. Other series will likely remain incomplete.

The evolution of base numbers in Eupatorieae is striking because $x_2 = 17$ is likely both ancestral and derived (Ito et al. 2000; this study did not include any $x = 18$ taxa). Like most other tribes in the Helenioid–Helianthoid clade, a derived high ancestral base number is plesiomorphic, in this case $x_2 = 19$–18. Many subtribes within the tribe have a base number of $x_2 = 10$ derived by downward dysploid series. In some subtribes, secondarily derived base numbers of $x_2 = 20$, 19, 18, 17, 16 and 14 occur as a result of polyploidy on $x_2 = 10$ and subsequent downward dysploidy for a second time in the history of those phylads. Of note is the unusual $x = 25$ base number in one of two groups of *Neomirandea* (Watanabe et al. 1995). We choose not to speculate on the origin of this remote, high chromosome number pending further data. Without DNA sequence phylogenies, it is unlikely that such redundant patterns of karyotype evolution would have been fully resolved. The combination of morphological, cytological and molecular studies together reveal the details in the history of Eupatorieae and the family as a whole.

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Chapter 5

Secondary chemistry of Compositae

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INTRODUCTION

The great morphological and geographical diversity of Asteraceae is reflected in its ability to produce a wide range of secondary metabolites including: monoterpenes, diterpenes, triterpenes, sesquiterpenes and sesquiterpene lactones, polyacetylenes, flavonoids, phenolic acids, benzofurans, coumarins and pyrrolizidine alkaloids (these alkaloids are, with few exceptions, confined to Senecioneae and Eupatorieae). The main biosynthetic pathways are derived from acetyl coenzyme A and/or amino acids leading to a remarkable number of unique structures isolated from nearly every tribe and genus investigated. Figure 5.1 shows an example of each of the main chemical classes found in Asteraceae.

Due to the large number of species that exhibit diverse chemical profiles it is not surprising that the secondary chemistry of Asteraceae has always been an area of intense interest to plant chemists and systematists. Several researchers have made important contributions to the field of chemosystematics, that is, the application of chemical data for evolutionary studies in plants (e.g., Mabry 1973; Harborne 1977; Waterman and Gray 1987; Gottlieb 1982; Hegnauer 1996, and all of their co-workers), many of them devoting significant portions of their careers to chemical studies of this family. However, the once dynamic field of chemosystematics has been essentially displaced in the last 30 years with increasing focus on molecular-based DNA studies. The development of technology to allow rapid DNA sequencing has provided innovative approaches to plant systematics and an opportunity to re-examine phytochemical data in the context of well-resolved phylogenies for Asteraceae. The structural characterization of secondary metabolites is a necessary part of any plant chemistry investigation and with close to a century of chemical data collected for this family, researchers now have a much broader and more detailed view of the distribution and occurrences of secondary metabolites for the family.

One of the first major syntheses on the chemistry of Asteraceae was published in the 1977 volumes entitled *The Biology and Chemistry of the Compositae*. In the final chapter, Mabry and Bohlmann (1977) state that "probably every member of the family contains flavonoids and most contain volatile oils and triterpenes." They also recognized the "… presence of two unique structural classes of compounds which characterize the family; sesquiterpene lactones and acetylenes" and agreed that "… no major classes of alkaloids have been reported with the exception of pyrrolizidine alkaloids in the Senecioneae and, to a lesser extent, in the Eupatorieae." The trends observed for the distribution and accumulation of these compounds were recognized early in studies of Asteraceae and today are supported by an even larger body of chemical data.

When Mabry and Bohlmann's review (1977) was published, Barnadesieae were considered to be one of the more derived lineages in Asteraceae, whereas Heliantheae were considered a basal lineage. At the end of their chapter they summarized data for two alternative hypotheses that addressed the question "are chemically complex tribes primitive or is it chemically depauperate tribes that are primitive?" If the former concept is correct then early diverged members of Asteraceae would possess a wide range of secondary metabolites and advancement would be indicated by successive losses of compounds by more derived groups. If the latter were true then more "primitive" groups would be characterized by a simple chemical profile, while advanced groups would be represented by chemical differentiation and gains of new secondary metabolites. Indeed this topic sparked much debate for years after the 1977 paper was published!

In the late 1980s, the discovery of a chloroplast genome inversion shared by all members of Asteraceae except the subtribe Barnadesiinae confirmed its collinear position with the rest of flowering plants and clearly established its place as the primitive group within Asteraceae (Jansen and Palmer 1987). In light of the many advances made in both phytochemical and taxonomic methods since then, scientists now understand that chemical pathways have differentiated through biosynthetic simplification and/or diversification at all taxonomic levels of Asteraceae.

The next major work on the chemistry of Asteraceae was published by Zdero and Bohlmann (1990) in an article summarizing important milestones in our understanding of the chemical diversity found in the family. They outlined over 7000 constituents identified from over 5000 species studied before 1990 and provided a broad assessment of the available chemical data. The authors pointed to the special trend of accumulation of lactonized sesquiterpenes and polyacetylenes, as well as the occurrence of many highly oxidized compounds, a pattern that is now considered the signature chemical profile shared by the majority of Asteraceae.

The contributions of Bohlmann and co-workers to the field of Asteraceae chemistry continues today with an excellent online resource known as "The Bohlmann Files", which provides a searchable database for secondary metabolites found in Asteraceae (Berendsohn et al. 1998). The database was compiled from the original card catalogue created by Bohlmann and co-workers to document the thousands of secondary metabolites isolated and characterized by members of his research group.

Coinciding with the intensive chemical studies of Asteraceae in the last half of the 20th century was the development of a thriving chemosystematics program directed by the late Otto Gottlieb at the University of São Paulo in Brazil. Gottlieb believed that plant chemists should focus their efforts on examining similarities in biosynthetic pathways, not the substances produced, as an indication of phylogenetic relatedness (Gottlieb 1982). His work covered terpenoids, alkaloids, coumarins, xanthones, phenylpropanoids, polyacetylenes, iridoids among other secondary metabolites. Gottlieb's school marked the first major attempt to measure chemical evolution using phenetic methods for groups of Angiosperm taxa.

The methodology developed by Gottlieb and collaborators was greatly influenced by the classic work *Numerical*

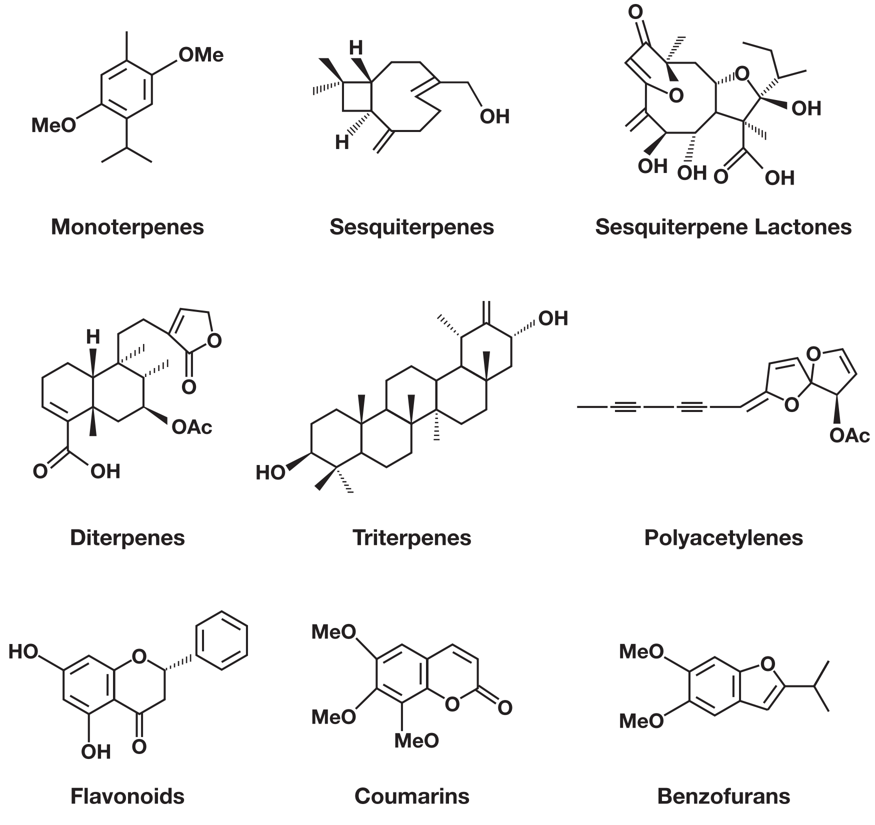


Fig. 5.1. An example of the nine major chemical classes in our chemical database represented by typical compounds found in Asteraceae. References for each compound: monoterpenes (Asfaw et al. 1999), sesquiterpenes (Macleod and Rasmussen 1999), sesquiterpene lactones (Vichnewski et al. 1999), diterpenes (Sigstad et al. 1999), triterpenes (Petrovic et al. 1999), polyacetylenes (Gonzalez et al. 1997), flavonoids (Asfaw et al. 1999), coumarins (Asfaw et al. 1999), benzofurans (Pari et al. 1998).

Taxonomy of Sneath and Sokal (1973), whose studies were based on cluster analyses using similarity matrices. Numerical taxonomy measures the gradual change in oxidation states of "micromolecules" (secondary metabolites), indicating the tendencies of the evolutionary processes that can be expressed as numeric indexes (Richardson and Young 1982; Stuessy and Crawford 1983; Emerenciano et al. 1987; Levy 1997). Another important measure of the evolutionary process in plants was calculated using probable biogenetic maps for each chemical class by observing the number of carbon-carbon connections formed or broken in a biogenetical sequence. Although Gottlieb's evolutionary approach was more phenetic than phyletic, homology of biosynthetic routes for the establishment of phylogenies would later be applied to solving taxonomic problems in Asteraceae.

Then in 1985, a doctoral student in Gottlieb's research group, Vicente Emerenciano, introduced the application of computational techniques for the organization and analysis of the chemical data (Emerenciano et al. 1985, 1986, 1987). In the last two decades the research group at the Institute of Chemistry of the University of São Paulo created a system for chemotaxonomy and structural determination of secondary metabolites found in Asteraceae. This system, called "SISTEMAT", can codify the structure of a natural product and associate the carbon skeleton, not only to the botanical origin, but also to corresponding spectral data (Gastmans et al. 1990a, b).

Using the chemical database SISTEMAT, researchers at the University of São Paulo continued their studies of Asteraceae, applying a broad range of statistical methods to establish phenetic relationships among members of the family. Earlier studies using SISTEMAT employed techniques such as PCA (Principal Component Analysis) implemented in commercially available programs (Statistica©, Unscrambler®) to examine several metabolites simultaneously, for example, in PCA analysis correlating the presence of sesquiterpene lactones and flavonoids (Emerenciano et al. 1987). Later, Emerenciano and collaborators published a PCA analysis for tribes of Asteraceae using all major classes of secondary metabolites (Alvarenga et al. 2001).

The SISTEMAT database has been employed for several other applications including testing of the redox theory in plants (Gottlieb 1993) using PLS (Partial Least Squares) analysis (Emerenciano et al. 2006), PCA analysis of Heliantheae, and analysis of hydroxylation patterns of flavonoids in tribes of Asteraceae (Emerenciano et al. 2001).

Most recently, members of Emerenciano's group, in collaboration with researchers at the University of Texas at Austin, published the first phylogenetic analysis for the entire Asteraceae based only on phytochemical data (Calabria et al. 2007). A cladistic analysis employing sesquiterpene lactones as chemical characters was previously published by Seaman and Funk (1983), however, the authors discussed only two examples from Asteraceae. The data matrix used by Calabria et al. (2007) was based on a large chemical database comprising ~400 skeletal types of secondary metabolites isolated from the family. Previous classifications based on morphological and molecular datasets were compared with new phylogenetic reconstructions based on chemical data providing a novel context for addressing questions regarding the evolution of secondary metabolism in Asteraceae.

MATERIALS AND METHODS

The chemical data were compiled by extensive inspection of *Chemical Abstracts* from 1960 to 2006 and were entered directly into an Excel file containing approximately 3024 species from 546 genera of Asteraceae, with a total of ~10,000 different chemical compounds grouped into nine major chemical classes (Fig. 5.1). Throughout this chapter the term "chemical occurrence" will be used to describe the number of times a compound of a given chemical class was reported in the literature for each species, genus, tribe, etc. For example, if two sesquiterpene lactones of the same skeletal type were isolated from *Silphium albiflorum* and one of these sesquiterpene lactones was also isolated from *Silphium perfoliatium*, then the total chemical occurrences of sesquiterpene lactones for *Silphium* would equal three, representing two different compounds, from two different species, one genus and one tribe.

Genera of Asteraceae were grouped into tribes according to the recent molecular phylogeny constructed by Panero and Funk (2002). However, we included Gundelieae as a separate tribe, and Plucheeae were placed as a monophyletic clade nested within Inuleae following the supertree (= metatree) of Funk et al. (2005), for which the Panero and Funk (2002) phylogeny served as a backbone for combining individual phylogenies for each tribe. Assignments of genera to tribes that were not outlined by Panero and Funk (2002) or Funk et al. (2005), were taken from Panero (2007). In addition, for subtribal, generic and species level analyses, we assigned genera into tribes according to Clevinger and Panero (2000). Table 5.1 shows the tribal names with the 3-letter codes used in this study and the approximate number of genera and species in each tribe compared with the number of genera and species represented in the chemical matrix. The subfamilies Hecastocleidoideae and Gymnarrhenoideae (both monotypic taxa) had no chemical reports in the literature.

Table 5.2 shows the data matrix created with the tribal arrangements used in this study and the number of occurrences of each class of secondary metabolites isolated from each tribe of Asteraceae. For figures with chemical occurrence data mapped on phylogenies for Asteraceae, the data matrix shown in Table 5.2 was converted into "one's" and "zero's" representing the "presence" or "absence" of a particular class of secondary metabolites in each taxon. "Presence" and "absence" refer to whether or not a given chemical class was reported in the literature data and, ultimately, recorded in our chemical database for Asteraceae.

RESULTS AND DISCUSSION

Here we outline our present knowledge of the distribution, abundance and diversity of secondary metabolites in Asteraceae and discuss useful approaches for detecting chemical patterns at the subfamilial, tribal, subtribal, generic and species levels. Figure 5.2 shows the total chemical occurrences for each main class of secondary metabolites found in our chemical database for Asteraceae. It is not surprising that flavonoids are nearly twice as abundant (~20,000 chemical occurrences) as any other chemical class evaluated in this study. Flavonoids serve diverse functions in plants and the subject of their ecological significance has been extensively reviewed (Bohm 1998; Seigler 1998; Bohm and Stuessy 2001). Flavonoids attract pollinators (yellow flower color predominates in Asteraceae) and seed and fruit dispersers. They provide protection against UV light and function in numerous plant-plant and plant-microbe signaling interactions. Bohm and Stuessy (2001) provide an excellent review of the distribution and occurrence of flavonoids in Asteraceae, outlining the main structural types found at different hierarchical levels; anthocyanins, chalcones, aurones, flavanones, flavones, and flavonols. Similar to their review, we found flavones and flavonols to be the most commonly occurring flavonoid structural types in our chemical database for Asteraceae.

The polyacetylenes occur over 10,000 times in our chemical database (Fig. 5.2), and although their distribution is not as consistently widespread as the flavonoids, they do tend to accumulate in large amounts in certain taxa. Four separate reviews were published (Christensen and Lam 1990, 1991a, b; Christensen 1992) outlining the distribution of polyacetylenes in the tribes Cardueae, Senecioneae, Astereae, and Anthemideae. According to our chemical database, polyacetylenes reach their maximum abundance in Anthemideae with nearly 4000 chemical occurrences, followed by Heliantheae and Astereae (both ~1000 chemical occurrences; Table 5.2). Eupatorieae, Heliantheae and Inuleae also accumulate significant amounts of polyacetylenes according to our chemical database. Polyacetylenes serve as important

Table 5.1. Tribes of Asteraceae analyzed in this study and their respective three-letter acronyms, the number of species in each tribe, and the number of species recorded in our chemical database.

Tribe	Acronym	No. of genera	No. of genera in database	No. of species	No. of species in database
Anthemideae	ANT	111	28	1800	493
Arctotideae	ARC	17	11	215	38
Astereae	AST	205	60	3080	338
Athroismeae	ATH	6	3	59	6
Bahieae	BAH	20	8	83	23
Barnadesieae	BAR	9	8	91	27
Calenduleae	CAL	12	7	120	35
Cardueae	CAR	73	28	2360	240
Chaenactideae	CHA	3	1	29	2
Cichorieae	CIC	86	23	1500	52
Coreopsideae	COR	30	10	550	137
Corymbieae	CRY	1	1	9	1
Dicomeae	DIC	7	2	100	6
Eupatorieae	EUP	182	75	2200	333
Gnaphalieae	GNA	185	24	1240	178
Gochnatieae	GOC	4	5	62	16
Gundelieae	GUN	2	2	2	2
Helenieae	HLN	13	11	120	66
Heliantheae	HLT	113	73	1500	352
Inuleae	INU	66	27	687	92
Liabeae	LIA	16	6	190	10
Madieae	MAD	36	14	200	92
Millerieae	MIL	34	24	400	80
Mutisieae	MUT	64	26	715	44
Neurolaeneae	NEU	5	5	150	16
Perityleae	PER	7	5	84	13
Pertyeae	PRY	4	4	70	2
Polymnieae	POL	1	1	3	2
Senecioneae	SEN	150	25	3500	174
Tageteae	TAG	32	9	270	30
Tarchonantheae	TAR	2	1	15	9
Vernonieae	VER	118	21	1000	117

Nomenclature for tribes follows Panero and Funk (2002), Funk et al. (2005) and Jeffrey (2007).

Table 5.2. Raw data matrix created for this study showing the number of occurrences of each class of secondary metabolites recorded in our chemical database from each tribe of Asteraceae.

Tribe	DITE	LACT	TRIT	SESQ	MONO	COUM	BENZ	POLY	FLAV	Totals
BAR	0	0	8	0	0	4	0	12	16	40
MUT	9	15	27	126	30	151	6	340	653	1,357
GOC	20	7	8	4	0	3	0	15	22	79
DIC	15	26	16	1	0	0	0	17	18	93
CAR	130	322	23	87	22	30	1	163	303	1,081
TAR	17	24	5	6	28	0	0	39	73	192
PRY	0	4	1	0	0	0	0	1	1	7
GUN	0	6	5	1	0	3	0	0	1	16
CIC	28	163	19	36	15	53	2	125	231	672
ARC	28	24	35	1	1	1	0	38	41	169
VER	288	214	174	10	24	23	1	232	290	1,256
LIA	15	37	9	8	5	0	0	22	35	131
CRY	10	0	0	0	0	0	0	0	0	10
SEN	60	111	37	837	130	24	108	1,136	2,235	4,678
CAL	94	0	11	18	7	3	7	46	81	267
GNA	301	3	29	64	145	46	19	303	577	1,487
ANT	309	810	28	236	3,454	212	4	3,934	7,840	16,827
AST	971	19	63	99	626	173	55	1,016	1,969	4,991
INU	122	242	15	271	330	36	3	655	1,295	2,969
ATH	4	21	0	0	3	0	0	3	6	37
HLN	4	359	0	4	78	1	0	83	166	695
COR	5	5	1	19	13	4	2	39	77	165
NEU	40	63	1	18	16	0	0	35	69	242
TAG	4	0	0	19	212	7	4	242	484	972
CHA	2	8	0	0	0	0	0	0	0	10
BAH	78	53	5	0	32	4	0	41	77	290
POL	16	0	0	0	0	0	1	1	2	20
HLT	883	771	45	122	302	32	177	678	1,311	4,321
MIL	528	154	8	28	91	2	2	131	254	1,198
MAD	22	16	2	8	44	9	5	68	134	308
PER	2	1	0	0	7	0	0	7	14	31
EUP	885	370	85	151	389	37	208	870	1,655	4,650
Totals	4,890	3,848	660	2,174	6,004	858	605	10,292	19,930	49,261

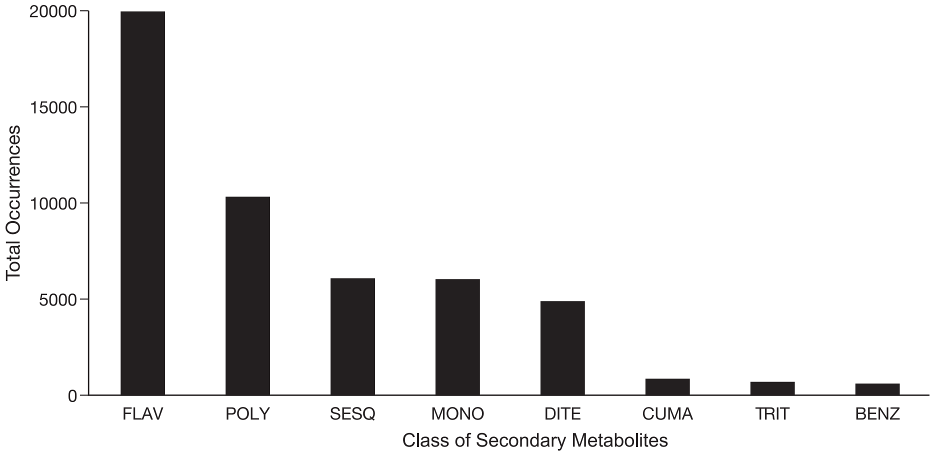
defense compounds in Asteraceae, exhibiting insecticidal and anti-feedant activities (Seigler 1998). Some polyacetylenes are considered phytoalexins; their concentration rapidly increases in response to attack by pathogenic fungi (Seigler 1998). In addition, polyacetylenes found in Asteraceae display potent phototoxic effects, killing or inactivating viruses, bacteria, fungi, nematodes and also negatively affecting herbivorous insects.

Terpenoids are the largest class of secondary metabolites found in plants, including monoterpenes (C_{10}), sesquiterpenes (C_{15}), diterpenes (C_{20}) and triterpenes (C_{30}) and are the second most common metabolites in our database for Asteraceae. Many of these compounds serve as volatile signals in plant-insect and plant-plant interactions and play essential roles in plant reproduction and defense. Sesquiterpenes (including lactones) and monoterpenes are equally abundant in Asteraceae with ~6000 chemical occurrences recorded in our database (Fig. 5.2). Diterpenes are also relatively abundant in Asteraceae, occurring ~4800 times in our chemical database (Fig. 5.2). Alvarenga et al. (2005) recently published a detailed review of the chemosystematic importance of diterpenes in Asteraceae. In addition, an extensive overview of the distribution and occurrence of diterpenes was given by Seaman et al. (1990).

The remaining classes of secondary metabolites are present in relatively low abundance in our chemical database for Asteraceae, with fewer than 1000 chemical occurrences (Fig. 5.2). Although triterpenes are one of the least abundant chemical classes, they occur in 28 of the 35 tribes of the family. This pattern of occurrence is consistent with their biological significance because triterpenes belong to the same biosynthetic group as steroid hormones and exhibit their physiological effects at very small doses. Saponins, which are the glycosidic forms of triterpenes, play important roles in the structure and function of cell membranes in addition to their role as defensive compounds against insects and pathogens.

Coumarins are well distributed in Asteraceae, but do not occur consistently in all tribes or subfamilies. The only tribes that accumulate coumarins (over 150 occurrences) are Anthemideae, Astereae and Mutisieae (Table 5.2). A group of complex coumarins known as furanocoumarins are common in the family and display a variety of biological activities against insects and pathogens. Like polyacetylenes, furanocoumarins also possess potent phototoxic properties capable of killing or inhibiting growth of pathogens, insects and nematodes (Seigler 1998). Benzofurans occur sporadically throughout Asteraceae and are the least abundant chemical class represented in our database. Figure 5.3 shows the distribution of benzofurans in tribes of Asteraceae according to Panero and Funk (2002) and Funk et al. (2005). Eupatorieae, Heliantheae and Senecioneae are the only three tribes that have more than 100 chemical occurrences of benzofurans according to our database. The distributional trend observed in Fig. 5.3 suggests that benzofurans occur more consistently in the derived lineages of Asteraceae. It is unclear, however, whether the chemical occurrence patterns observed for benzofurans represent their natural distribution or whether these compounds are investigated less frequently than other chemical classes in the family. For example, reports of triterpenes in the subtribe Engelmanniinae (Heliantheae) were limited to four genera prior to our chemical investigations, which found that every genus in this subtribe contains triterpene glycosides (data unpublished). Proksch and Rodgriguez (1983) reviewed the distribution and biological significance of benzofurans and chromenes (benzopyrans) in Asteraceae; however,

Fig. 5.2. Total chemical occurrences for Asteraceae representing each class of secondary metabolites in our chemical database.



no other major review of these compounds has been published.

The pyrrolizidine alkaloids are not represented in our chemical database for Asteraceae because of their limited occurrence. Figure 5.4 shows the distribution of pyrrolizidine alkaloids on a phylogenetic tree based on DNA data (Panero and Funk 2002; Funk et al. 2005). Historically, pyrrolizidine alkaloids were thought to accumulate only in Eupatorieae and Senecioneae, although these tribes are not phylogenetically closely related. There is evidence to support the polyphyletic origin of pyrrolizidine alkaloids in Asteraceae based on differential tissue expression of homospermidine synthase (HSS), the main enzyme involved in the biosynthesis of pyrrolizidine alkaloids (Anke et al. 2004). The authors concluded that within Senecioneae and Eupatorieae HSS is expressed in different tissue types and therefore, the ability to produce these compounds arose multiple times independently.

Since the original volumes of the *Biology and Chemistry of the Compositae* (1977) were published, alkaloids have been reported from several tribes in addition to Senecioneae and Eupatorieae; Cardueae (*Cirsium*, *Carduus*, *Echinops* and *Centaurea*) (Jordon-Thaden and Louda 2003; Chaudhuri 1992; Hymete et al. 2005; Sarker et al. 2001, respectively), Madieae (*Arnica*, *Melampodium*) (Passreiter 1992; Schüngel and Passreiter 2000), Heliantheae (*Echinacea*) (Roeder et al. 1984), and Neurolaeneae (*Neurolaena*) (Passreiter 1998). However the pyrrolizidine alkaloids in the latter three tribes are not considered "true" alkaloids, but rather β-amino acids, due to their atypical structures and biosynthesis. In addition, the methyl ester forms of these "alkaloids" were found to be artifacts derived from corresponding acids during soxhlet extraction (Passreiter 1998). Therefore, the only true alkaloids reported from Asteraceae are from Senecioneae, Eupatorieae, and Cardueae.

The occurrence of pyrrolizidine alkaloids in Senecioneae has been studied in the context of insect co-evolution (Pasteels et al. 2001). The leaf beetles *Platyphora* and *Oreina* spp. (Coleoptera: Chrysomelinae) are known to sequester pyrrolizidine alkaloids from their host plants

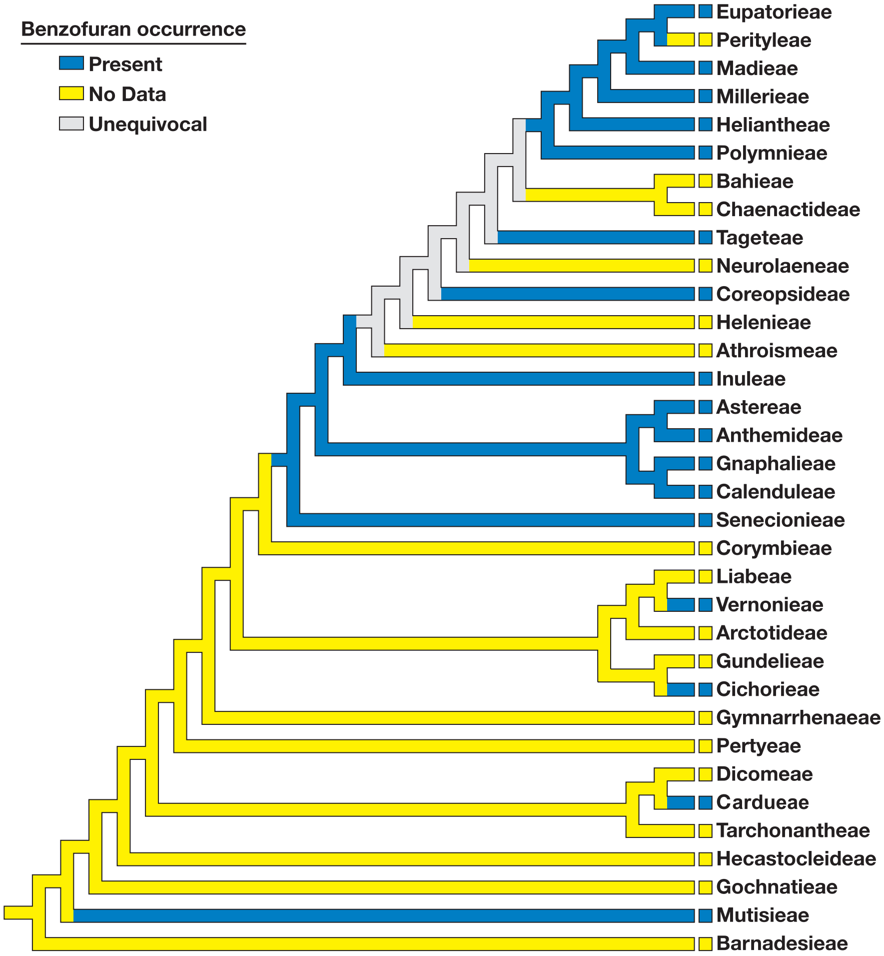


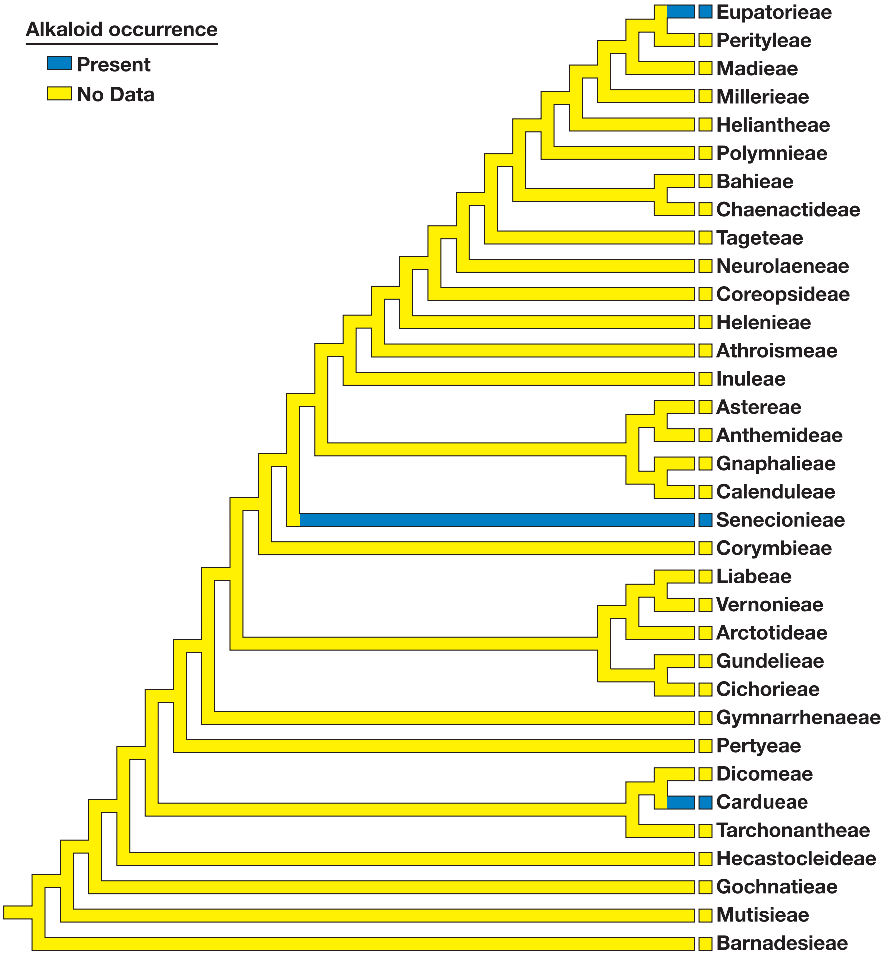
Fig. 5.3. Distribution of benzofurans viewed at the tribal level, expressed as "presence" or "absence" of chemical data recorded in our chemical database for Asteraceae. DNA-based phylogenetic framework adapted from Panero and Funk (2002) and Funk et al. (2005).

and to store these compounds as defensive secretions (Pasteels et al. 2001). Interestingly, the authors also reported the presence of saponins in the defensive secretions of *Platyphora*, but saponins were not detected in the leaf beetle's food plant, indicating these compounds are synthesized by the beetles, and not sequestered as in the case of the pyrrolizidine alkaloids. Further studies by Plasman et al. (2001) indicated that although the host plants were devoid of saponins, the triterpene precursor β-amyrin was confirmed to be present in host plant species on which the beetles fed. This suggests that insects of the genus *Platyphora* possess the necessary enzymes for transformation of β-amyrin in their food plant to the oxidized form oleanolic acid and for their subsequent glycosylation (Plasman et al. 2001). Considering that species of the leaf beetle family (with few exceptions) feed exclusively within a single plant family or even a single genus, this example shows the importance of examining chemical profiles for understanding the origin and evolution of plant-insect interactions.

Subfamilies

Total chemical occurrences for each subfamily and tribe were calculated in Excel and converted into several graphics (Figs. 5.5–5.8) showing the distribution and abundance of each chemical class. Figure 5.5 shows the occurrence of secondary metabolites in subfamilies of Asteraceae according to Panero and Funk (2002) excluding the subfamilies Hecastocleidoideae and Gymnarrhenoideae, for which no chemical data have been reported. The monophyletic Barnadesioideae, which are sister to the rest of Asteraceae, have an extremely simple chemistry characterized by the production of a relatively small number of flavonoids, polyacetylenes, coumarins and triterpenes. Similarly, chemical reviews published for Calyceraceae and Goodeniaceae, the closest relatives to Asteraceae, indicate a very simple chemical profile much like that of Barnadesioideae (Bohm et al. 1995; Ghisalberti 2004). Barnadesioideae represent only 0.4% (Jeffrey 2007) of all extant species in Asteraceae and less than 0.1% of the chemical occurrences

Fig. 5.4. Distribution of alkaloids viewed at the tribal level, expressed as "presence" or "absence" of chemical data recorded in our database for Asteraceae. DNA-based phylogenetic framework adapted from Panero and Funk (2002) and Funk et al. (2005),

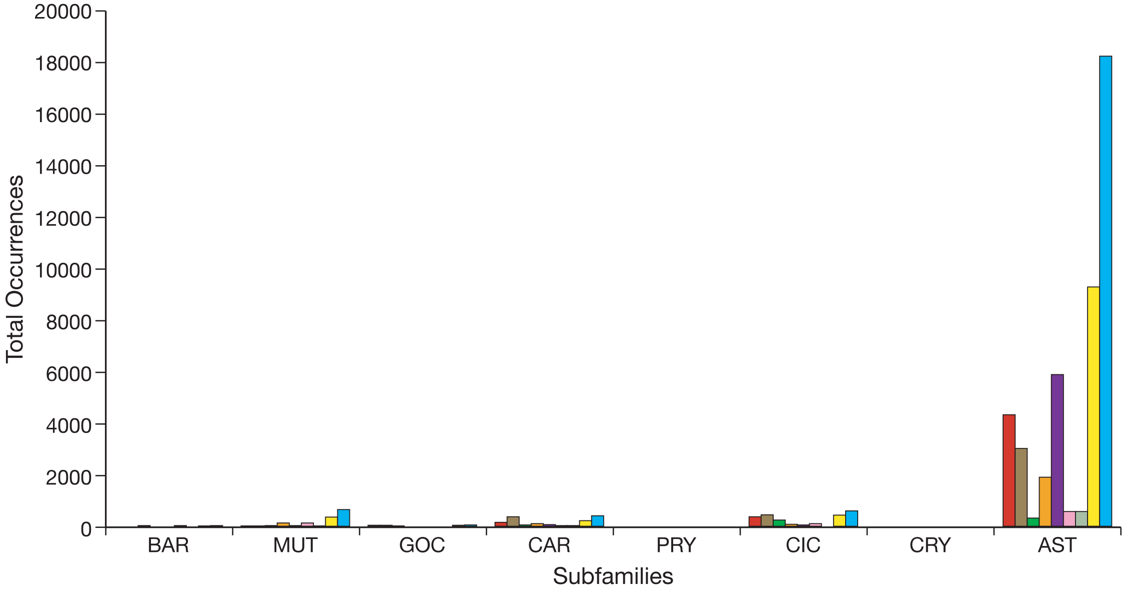


in our database. In contrast, Asteroideae are the largest subfamily in Asteraceae, containing ~72% (Jeffrey 2007) of the species in the family and have more chemical occurrences and chemical diversity than all other subfamilies combined (Fig. 5.5). Every chemical class is represented in Asteroideae, with flavonoids reported the most frequently, with over 18,000 chemical occurrences. The monoterpenes are also quite abundant, which coincides with the complex pollination systems and insect interactions in Asteroideae.

The subfamilies positioned in between Barnadesioideae and Asteroideae are clades that historically made up the large subfamily Cichorioideae (28% of the species in the family); more recently Cichorioideae were divided into several smaller subfamilies (Panero and Funk 2002). Of these subfamilies, Mutisioideae, Carduoideae, and Cichorioideae exhibit the most chemical diversity and abundance, as illustrated in Fig. 5.5.

Figure 5.6 shows the percentage of each chemical class as individual pie charts for subfamilies Mutisioideae, Carduoideae, Cichorioideae and Asteroideae. Terpenoids (including mono-, di-, sesqui-, and tri-) account for more than half of the total chemical occurrences in Cichorioideae (51%) and Carduoideae (53%), while flavonoids represent 25% of the total chemical occurrences in Cichorioideae and 29% in Carduoideae. In contrast, nearly half of the total chemical occurrences for Asteroideae (42%) and Mutisioideae (49%) are attributed to flavonoids, while terpenoids represent 15% of the total occurrences in Mutisioideae and 35% in Asteroideae.

Polyacetylenes represent the third largest component of the total chemical occurrences in all four major subfamilies (Fig. 5.6), ranging from 16% of the total chemical occurrences in Carduoideae to a maximum of 25% in Mutisioideae. In Cichorioideae and in Asteroideae polyacetylenes represent 19% and 21% of the total chemical occurrences. Benzofurans account for less than 1% of total chemical occurrences in all subfamilies, except for Asteroideae, where total occurrences slightly exceeds 1%. Mutisioideae contain an unusually large number



	BAR	MUT	GOC	CAR	PRY	CIC	CRY	AST
🟥 DITE	0	9	20	162	0	359	10	4330
🟫 LACT	0	15	7	372	4	444	0	3006
🟩 TRIT	8	27	8	44	1	242	0	330
🟧 SESQ	0	126	4	94	0	56	0	1894
🟪 MONO	0	30	0	50	0	45	0	5879
■ COUM	4	151	3	30	0	80	0	590
■ BENZ	0	6	0	1	0	3	0	595
🟨 POLY	12	340	15	219	1	417	0	9288
🟦 FLAV	16	653	22	394	1	598	0	18246

Fig. 5.5. Total occurrences for each chemical class found in our chemical database for subfamilies of Asteraceae according to Panero and Funk (2002).

of coumarins in comparison with other subfamilies of Asteraceae, representing 11% of the total chemical occurrences, whereas coumarins represent 4% of the total occurrences in Cichorioideae, 2% in Cardueae and only 1% in Asteroideae.

The chemical data presented in Fig. 5.6 illustrate how easily plants can adjust their production of secondary metabolites to adapt to changing environments. Each subfamily exhibits a distinct chemical ratio, characterized by both the expansion and reduction of different chemical classes. The ancestral state of secondary metabolite expression in Asteraceae is not known and cannot be inferred from extant species. Given the phylogenetic relationships, however, one can infer a direction in which the chemical profiles are changing. Considering that terpenoids are more expensive to manufacture per gram than most other primary and secondary metabolites (Gershenzon 1994), the benefits of devoting more than half of the total biosynthetic expenditures for secondary metabolism to produce a single class of compounds must outweigh the cost of manufacturing this one class of compounds for taxa in Cichorioideae and Carduoideae. On the other hand, the same must be true for the production of flavonoids in Mutisioideae and Asteroideae.

The observed shifts in metabolism between subfamilies are most likely the result of natural selection. However, a

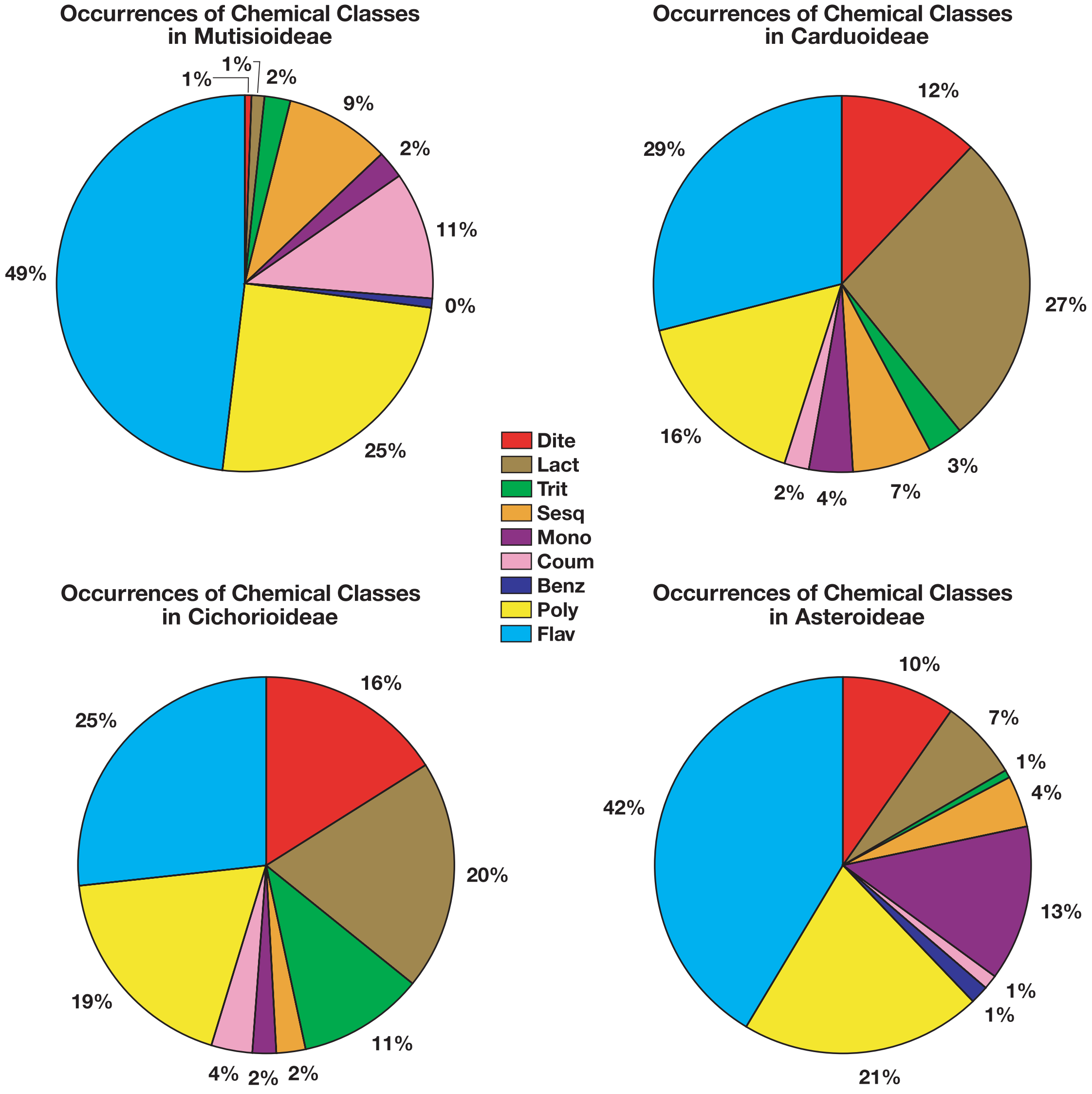


Fig. 5.6. Individual pie charts for subfamilies Mutisioideae, Carduoideae, Cichorioideae and Asteroideae representing the total chemical occurrences expressed as percentages of each chemical class found in our chemical database for Asteraceae.

single genetic mutation can sometimes drastically change the chemical properties of a plant, (i.e., taste, toxicity, etc.). The diversity and abundance of a particular chemical class could simply be artifacts of mutated enzymes with promiscuous behavior that may or may not benefit plant fitness. Furthermore, because our data are compiled from literature reports, many of which represent studies on bioactive and medicinally important compounds, we cannot be certain that the chemical occurrence patterns described here represent their natural distribution in the plants. Still, further attempts to explain these patterns should stimulate many interesting research questions that could be addressed using a combination of phytochemical, genetic and ecological data.

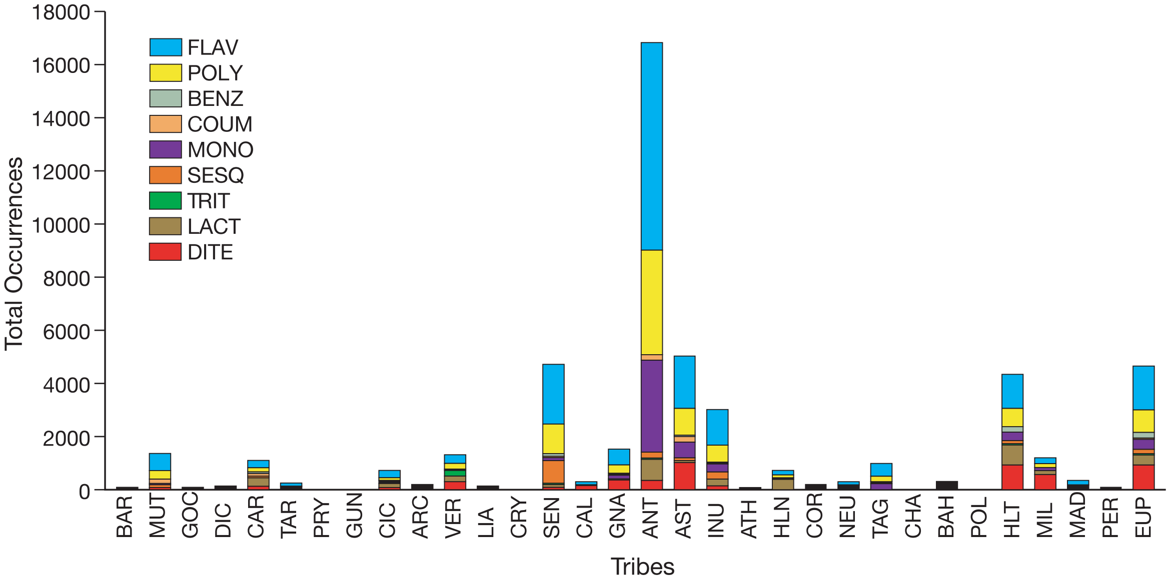


Fig. 5.7. Total occurrences of each chemical class found in our chemical database for tribes of Asteraceae. Genera were assigned to tribes according to Panero and Funk (2002), Funk et al. (2005) and Panero (2007).

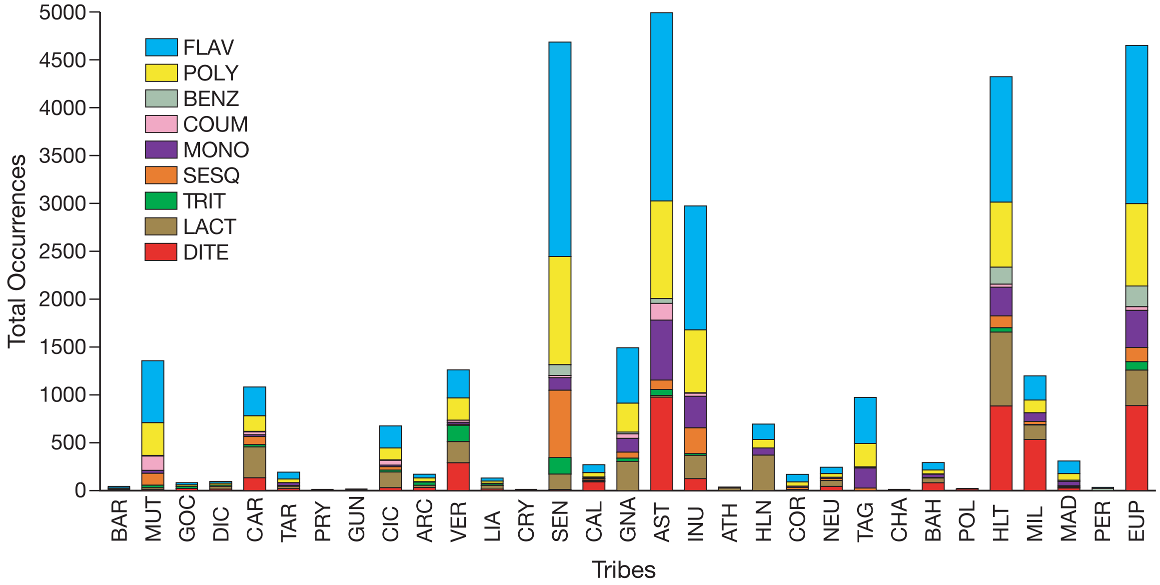


Fig. 5.8. Total occurrences of each chemical class found in our chemical database for tribes of Asteraceae, excluding Anthemideae. Genera were assigned to tribes according to Panero and Funk (2002), Funk et al. (2005) and Panero (2007).

Tribes

The distribution and abundance of each chemical class can also be viewed at the tribal level, as illustrated in Figs. 5.7 and 5.8. The maximum abundance of chemical classes is seen in Anthemideae, due to the accumulation of large amounts of flavonoids, monoterpenes and polyacetylenes and to the intensity of research devoted to medicinally important taxa from this group such as *Chrysanthemum*, *Achillea*, *Artemisia* and *Anthemis* (Teixeira da Silva 2004; Teixeira da Silva et al. 2004). When Anthemideae are excluded, the tribe with the most chemical occurrences is Astereae, as illustrated in Fig. 5.8. Flavonoids account for 2000 of the ~5000 chemical occurrences in Astereae. Polyacetylenes and diterpenes are also quite abundant in Astereae, with ~1000 chemical occurrences. All other chemical classes are represented in Astereae but in much smaller quantities then the above-mentioned classes (Fig. 5.8). Senecioneae and Eupatorieae both accumulate large amounts of flavonoids and diterpenes, but differ in their expression of sesquiterpenes and diterpenes. While Senecioneae tend to accumulate sesquiterpenes, Eupatorieae instead accumulate diterpenes.

Heliantheae show slightly fewer chemical occurrences than Eupatorieae and Senecioneae, in ratios similar to Eupatorieae. Finally, Inuleae also accumulate large amounts of secondary metabolites, mainly flavonoids and polyacetylenes and to a lesser extent, the mono-, di-, sesqui-, and sesquiterpene lactones.

All other tribes have fewer then 1500 chemical occurrences reported. Mutisieae are of particular interest because of their basal position in the family, their problematic classification, and diverse chemical profiles characterized by complex coumarins and accumulation of flavonoids, polyacetylenes, and sesquiterpenes. Vernonieae also deserve mention because they accumulate a large number of diverse triterpene skeletons.

Subtribes and genera (triterpene saponins)

The genus *Silphium* L. (tribe Heliantheae) consists of eleven species native to North America, distributed primarily in the eastern United States and extending into southeastern Canada. Recently, the phylogenetic relationship of *Silphium* and subtribe Engelmanniinae were examined using DNA sequence data (Clevinger and Panero 2000; Panero 2007). The resulting phylogeny (Fig. 5.9) will be employed here to summarize the distribution of triterpene saponins at the subtribal, generic, and species level. The oxidation patterns of triterpenes from the genus *Silphium* will also be discussed.

Silphium is the most extensively studied taxon in the subtribe Engelmanniinae, due in part to its common use as a folk medicine by several Native American tribes. In recent years, our research group at UT-Austin has focused primarily on documenting the flavonoids, phenolic acids and, more recently, the triterpene-type saponins in all species of *Silphium* (El-Sayed et al. 2002; Wojcinska et al. 2007).

Until recently, the utilization of triterpenes and their glycosidic forms, the saponins, in chemosystematic studies has been limited. One recently published excellent review outlines the evolutionary development and distribution of these compounds in higher orders of angiosperms and summarizes findings on structural and distributional data obtained for triterpenoid saponins during the last 50 years (Henry 2005). Based on these data, it is clear that saponins are restricted to advanced taxonomic groups such as Caryophyllideae, primitive Rosidae and Asteridae, but are lacking in Paleodicots and Monocots. The only exception thus far was reported by Osbourn's group (Papadopoulou et al. 1999), who used a combination of phytochemical, molecular, and genetic techniques to examine the expression patterns of naturally-occurring triterpene saponins found in oats (*Avena* spp.); these compounds proved critical in defense against pathogenic fungi.

As suggested by Gottlieb (1989) in his evolutionary studies of secondary metabolism in angiosperms, the degree of oxidation can be correlated with evolutionary advancement, with highly oxidized compounds indicating a greater capacity to utilize atmospheric oxygen (see section on Background and Historical Overview). Therefore, one would expect to see more highly oxidized compounds in more derived lineages. Early biosynthetic intermediates in the triterpene pathway, such as oleanolic acid, are represented in much greater numbers throughout the angiosperm lineages than later metabolic intermediates such as quilliac acid, implying a direction of evolution of chemical pathways in angiosperm lineages, with later biosynthetic intermediates more oxidized and primarily restricted to the more advanced groups of angiosperms, such as Asteraceae (Henry 2005). Because researchers now understand some of the main biosynthetic routes and intermediates in the production of saponins, quantitative and qualitative analyses of these different intermediates could help to clarify the role of saponins in the evolution of Asteraceae.

Through our investigation of triterpene saponins from *Silphium* we have found a range of structural types and patterns of occurrences. Some species display a rich mixture of saponins, while others contain only a few, structurally simple compounds. However, it is clear from our preliminary data that all genera of the subtribe Engelmanniinae produce saponins (data unpub.). Our results from a detailed structural analysis of triterpenes from *Silphium radula* Nutt., which belongs to the most derived clade in the genus *Silphium*, support this hypothesis based on the content of several novel triterpene saponins with high degrees of oxidation, including hydroxyl, carboxyl and aldehyde functional groups (Calabria et al. 2008). Figure 5.9 illustrates this concept showing our preliminary data on the distribution and occurrence of oxidized triterpenes in the subtribe Engelmanniinae. Although the occurrence of triterpenes in all genera in the subtribe was confirmed through our chemical investigations, a complete dataset including oxidation states is still incomplete. Therefore, Figure 5.9 shows our current knowledge of the degree of oxidation present in the subtribe Engelmanniinae and the closely related genera, *Dugesia*, *Rojasianthe*, *Podachaenium*, *Verbesina* and *Squamopappus*. The highest degree of triterpene oxidation is seen in *Lindheimera* and *Silphium*, where four to five carbons are oxidized. *Borrichia* shows three carbons oxidized and *Wyethia*, *Dugesia*, *Podachaenium* and *Verbesina* show the least degree of oxidation with only two groups oxidized. These preliminary data support the hypothesis that highly oxidized triterpenes occur in more derived taxa at the subtribal level. Further investigations of saponins at the generic and species levels are currently underway.

Species

Several species of gall wasps (Hymenoptera: Cynipidae) induce galls on *Silphium*. Gall-inducing insects are typically specialist plant feeders with most species confined to one specific host plant species. An excellent example involves several gall-inducing wasp species of the genus *Antistrophus* whose larvae induce galls in the pith and cambium of stems of *Silphium* spp. (Tooker and Hanks 2006). Of the ten or so species of *Antistrophus* native to North America, at least five form galls in either the stems or flowering heads of *Silphium* species (Tooker and Hanks 2004). For stem-inhabiting species, female gall wasps lay eggs in bolting stems and feeding by newly hatched larvae induces gall formation. A specific blend of monoterpenes emitted from the host plant is critical for female wasps to recognize their specific host plants (Tooker et al. 2005). In addition, upon emergence from galls, adult males use olfactory signals from their natal host plant species to locate their mates nested within the dead over-wintering stems of *Silphium*. This same blend of volatiles emitted

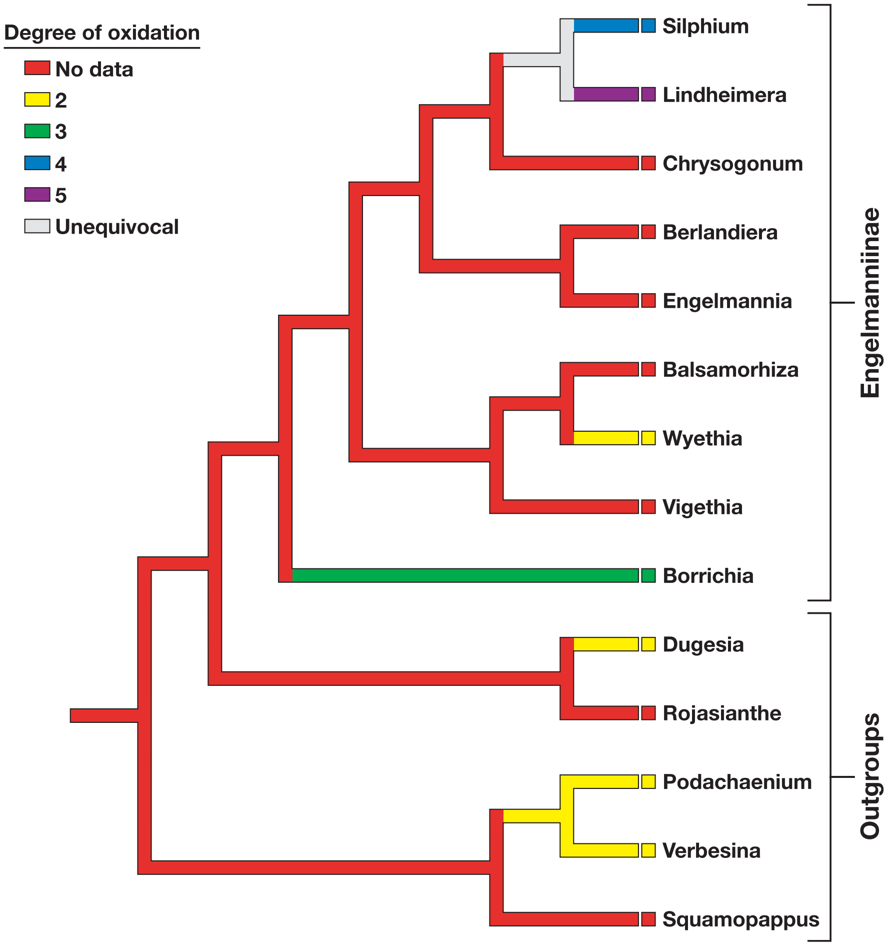


Fig. 5.9. Degree of triterpene oxidation present in the subtribe Engelmanniinae and closely related genera. DNA-based phylogenetic framework adapted from Clevinger and Panero (2000) with subtribal delineations updated by Panero (2007).

by *Silphium* also attracts the parasitic wasp *Eurytoma lutea* Bugbee (Hymenoptera: Eurytomidae), which is a natural enemy of *Antistrophus*. The larvae of *E. lutea* kill gall wasp larvae, diminishing the amount of plant damage inflicted by *Antistrophus* and allowing the plants to put resources into reproduction that would have otherwise been consumed by the gall wasp larvae. As a result, galled *S. laciniatum* plants that are able to attract *E. lutea* appear to have improved fitness relative to galled controlled plants (Tooker and Hanks 2006).

The molecular and biochemical basis for these interactions is largely unstudied. However, the manipulation of host plant's chemistry by galling (and many other) insects is well documented. Modes of action range from the induction of the hypersensitive response, suppression of genes involved in biosynthesis of defensive compounds, detoxification of active defense compounds, and even tissue-specific redistribution of secondary metabolites, to name a few. For example, the nutritive tissues lining galls often are void of secondary metabolites, whereas the exterior of the galls can have relatively high concentrations of toxins. This distribution of secondary compounds gives galling insects a toxin-free food source while providing the gall insects protection against natural enemies or herbivores that might favor plant tissue (Tooker, pers. comm.).

The story of *Silphium* and the gall wasp *Antistrophus* demonstrates how species-level chemical data can be useful for understanding plant-insect interactions in Asteraceae. To date, *Antistrophus* galls have been documented in four of the eleven species in the genus *Silphium*; the question of why these four species are the preferred host for *Antistrophus* remains to be answered. The complex tritrophic interactions described here are mediated by chemical signals produced by *Silphium* and manipulated by insects in the surrounding environment. It is our view that research utilizing both phytochemical and molecular systematic tools may help to explain such interactions. In addition, mapping chemical characters on host-plant molecular phylogenies coupled with phylogenies of their associated insects could also help to elucidate macroevolutionary patterns in both plant and insect lineages.

CONCLUSIONS

The chemical data summarized here indicate that although there are thousands of secondary metabolites described from nearly every tribe of Asteraceae, there are still many questions that could be addressed if additional chemical data were available. Furthermore, model species from Asteraceae with diverse chemical profiles are desperately needed to correlate phytochemical findings with genetic and genomic data for secondary metabolic pathways. This vision is slowly becoming a reality through the recent efforts of the Compositae Genome Project (Rieseberg and Michelmore 2003), which provides genomic resources and tools for Asteraceae, and other researcher groups developing model Asteraceae such as the *Gerbera* laboratory (Teeri et al. 2006). Considering that ~170 secondary metabolites from seven major chemical classes have been identified from the model plant *Arabidopsis thaliana* (L.) Heynh, representing a five-fold increase over the last ten years (D'Auria and Gershenzon 2005), one can imagine the potential for discovering even more secondary metabolite diversity in Asteraceae as more genomic information becomes available. With these resources, molecular biologists, chemists, ecologists, and systematists should work together to address questions about the functional importance of secondary metabolites in Asteraceae in the context of their life histories. Although DNA data provide the most reliable method for estimating evolutionary relationships and distances between taxa, these data cannot explain how or why a particular plant evolved without phenotypic information, including a broad range of morphological and chemical characters. This is an exciting time to be involved with investigations of the secondary chemistry of Asteraceae, and future studies will almost certainly shed light on the previously unknown roles of secondary metabolites in the evolution and diversification of this family.

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Chapter 6

An introduction to micro-characters of Compositae

Harold Robinson

INTRODUCTION

The "New Synantherology" (King and Robinson 1970), written to irritate the entrenched synantherology of its time, helped shift the direction of studies in Compositae toward characteristics available using the compound microscope. There was some resistance to the added difficulty of observing microscopic characters and determining their reliability. It is admitted that microscopic features can never be surveyed as easily or totally as macroscopic features, and that even the use of Hoyer's solution (Anderson 1954) requires some dissection and some facility with microscope slide preparation. A more important shortcoming of Hoyer's solution is the fact that it is not a permanent mounting medium, but it is water miscible and material can be recovered from slides that have gone bad. Nevertheless, even one slide of microscopic characters of each of the numerous species of some large genera such as *Ageratina* Spach and *Fleischmannia* Sch.Bip. in Eupatorieae allows great confidence in the results. The resistance to the microscopic approach was most surprising because a more appropriate criticism of the "New Synantherology" would have been that it was not "New".

The effective beginning of anatomical approaches to Asteraceae classification was the work of Cassini, as shown in his drawings from 1821 (see Fig. 1.8, p. 12). These summarize many of the microscopic features on which Cassini based his tribes. Of these, pronate versus recurved mature style branches, stigmatic surfaces, truncate to enlarged style appendages, bases of the anther thecae with or without tails, shape of the anther collar (L'article anthérifère of Cassini, 1814) and form of the corolla are most prominent. The stigmatic surfaces of many tribes are consistently continuous over the inner surface of the style branch (Mutisieae, Lactuceae, Vernonieae, Arctotideae, Eremothamneae, Cardueae). In other tribes the stigmatic surface is divided into two lines (Eupatorieae, Anthemideae, Astereae, most Inuleae, most Heliantheae, most Senecioneae). Within the present-day Senecioneae is a group treated by Cassini as the Tussilagineae that has the stigmatic surface continuous and lacks the ballustriform anther collars shown by Cassini for typical Senecioneae. Tails of the anther thecae were emphasized for the broadly defined Inuleae, but such tails are also found in many Mutisieae, Vernonieae, in limited form in some Senecioneae, or even in one member of Astereae (*Printzia* Cass.).

These characteristics were used by Cassini in combination with other more obvious features such as phyllotaxy, presence or absence of rays, and flower color. Style shapes and anther tails continued to be used by later authors such as Lessing (1832) and Bentham (1873), but the search for possible new characters such as endothecial cells was very casual at best, with recognition of some basic types such as radial and polar (Dormer 1962). In the last forty years, the number of micro-characters in use has greatly increased, and a partial review is appropriate.

A SURVEY OF SOME CHARACTERS

Ducts

Duct systems in Asteraceae are of some interest, both form and contents. Some have latex, some have acetylenes, and some have resins of various types. Latex in Asteraceae is usually associated with ducts. The presence of latex was once treated as a distinguishing feature of Lactuceae, but latex also occurs in many Liabeae (Robinson 1983) and some Vernonieae (Lewinsohn 1991). Latex occurs without ducts in *Parthenium argentatum* A. Gray (Perry 1945) in Heliantheae. The presence of latex associated with ducts is still a character apparently restricted to the subfamily Cichorioideae s.str. Ducts in the stems with resin can be found notably in the Mexican Senecionian genus *Pittocaulon* H. Rob. & Brettell (1973a) and in one species of the related *Roldana* La Llave in La Llave & Lag. (Robinson and Brettell 1974). Jeffrey (1987) included duct and vessel positions in the stem among the features in Senecioneae for which he proposed a stable terminology.

Pith

The pith of the stem is also sometimes useful. In Senecioneae, seemingly useful distinctions can be seen in the pitted walls of pith cells of the *Pentacalia* Cass. group in the Andes, and *Barkleyanthus* H. Rob. & Brettell of the United States and Mexico has a distinctive chambered pith (Robinson and Brettell 1974).

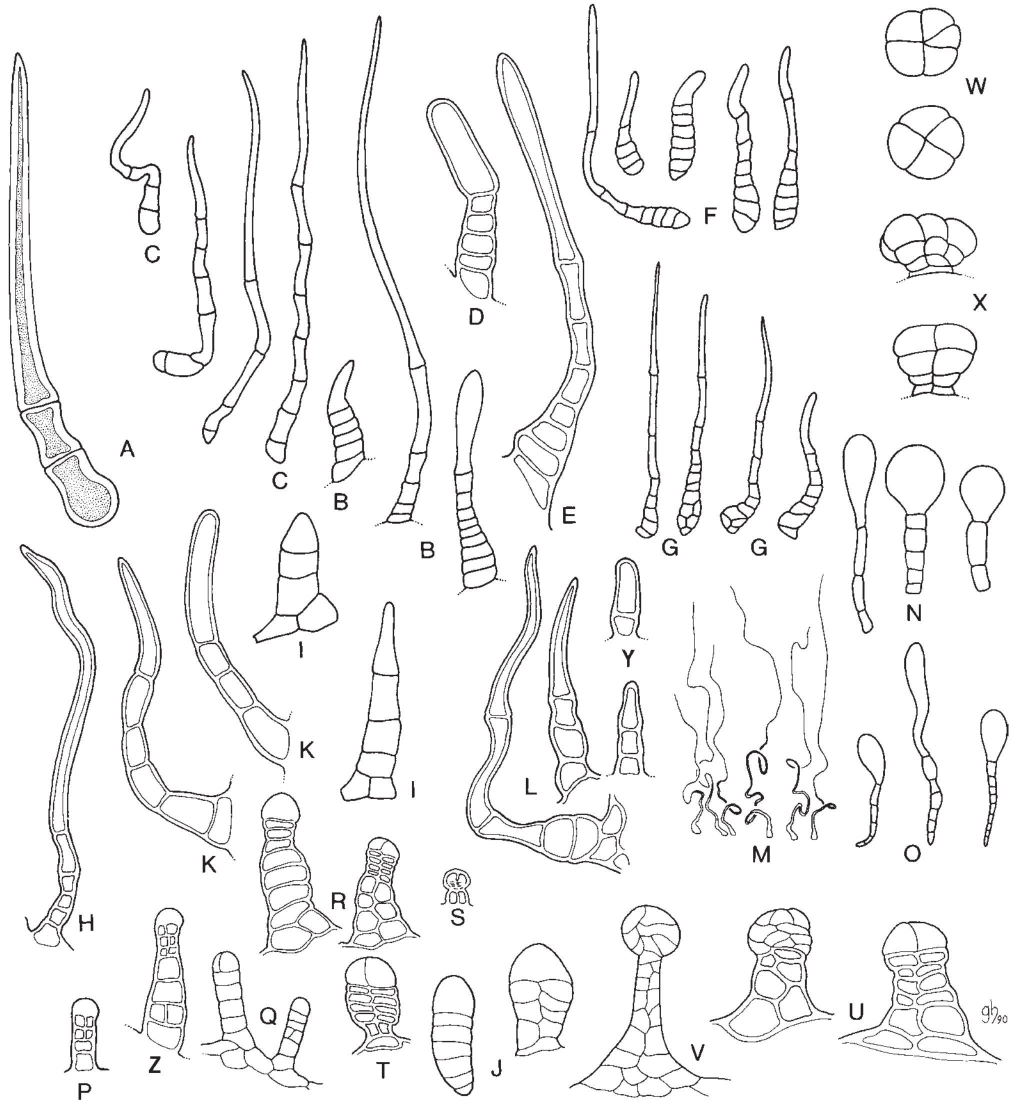


Fig. 6.1. Trichomes of Espeletiinae. [From J. Cuatrecasas (in press.), A systematic study of the subtribe Espeletiinae (Heliantheae, Asteraceae). Illustrations by G. Hormiga.]

Trichomes

Some micro-characters correlate with chemical characters. Glandular trichomes of the common short-stalked capitate type, often seen as glandular dots (Figs. 6.1W, X; 6.2A, B), tend to contain sesquiterpene lactones. Elongate, usually tapering glands with small gland tips (Fig. 6.1R, V) are usually associated with monoterpenes. The type of glands that are on the surface of vegetative parts and quickly release glutinous material are associated with clerodane and labdane derivatives. Each of these gland and chemical types is widely distributed in Asteraceae. Clerodanes and labdanes occur in at least some Eupatorieae (*Acritopappus* R.M. King & H. Rob.), Heliantheae (*Flourensia* DC.), and Astereae (*Baccharis* L.).

Both glandular hairs and the setulae ("Zwillingshaare") of the achenes are basically biseriate trichomes, and they seem to occur commonly in most genera in most of the family aside from Barnadesioideae.

Types of non-glandular hairs are useful to various degrees. In *Dresslerothamnus* H. Rob. and to a slight extent in *Urostemon* B. Nord., in Senecioneae, there are multi-tiered T-shaped hairs (Fig. 6.3) unlike anything thus far reported in other tribes. In *Dresslerothamnus angustiradiatus* (T.M. Barkley) H. Rob., in particular, the hairs differ by the different levels of cap-cells not being in one plane as in the others, but they are spreading in different directions (Fig. 6.3A), forming a unique false stellate structure (Robinson 1989).

Within American Vernonieae, stellate or variously spurred to branched or goblet-shaped trichomes (Fig. 6.4A, B) clearly support the DNA evidence (Keeley et al. 2007) for distinction of *Critoniopsis* Sch.Bip. from *Tephrothamnus* Sch.Bip. (Fig. 6.4C) and *Eremosis* (DC.) Gleason (Fig. 6.4D), which had been placed in synonymy by Robinson (1993). The tendency toward stellate, spurred, scalelike or goblet formed hairs may help define the whole subtribe Piptocarphinae, from which *Tephrothamnus* with T-shaped hairs and *Eremosis* with simple hairs would be excluded. Hair types in Old World Vernonieae are also potentially helpful, distinguishing the widespread Asian *Acilepis* D. Don with simple hairs from the *Cyanthillium* Blume group with T-shaped hairs.

The essential lack of branched or T-shaped hairs in Heliantheae and Eupatorieae is notable. The presence or absence in many other tribes is not certain, but in the subfamily Asteroideae, Senecioneae often have complex hairs (stellate in *Aequatorium* B. Nord. and *Nordenstamia* Lundin; Nordenstam 1978, 2006; Lundin 2006).

Receptacles

Receptacles have been used in the taxonomy of Asteraceae dating back to Cassini (1814), but usually in regard to only pubescence and obvious fistulosity. Additional details of fistulosity can be seen in *Packera* Löve & Löve (*P. aurea* (L.) Löve & Löve) versus typical *Senecio* L. (Fig. 6.5). The former has extensive fistulosity in the receptacles above a pair of thin diaphragms (Fig. 6.5B). The diaphragms lie together at anthesis, but move apart after anthesis to form a new cavity replacing the previous fistulosity. In typical *Senecio* (*S. vulgaris* L., *S. leucophyllus* DC.) the fistulosity is very minute (Fig. 6.5A). This is a characteristic seen best in living plants, and it needs to be surveyed in a wider selection of species.

Receptacles in Eupatorieae show variation in sclerification. Most members of the tribe have a sclerified surface and pith in the center; they are more rarely fistulose.

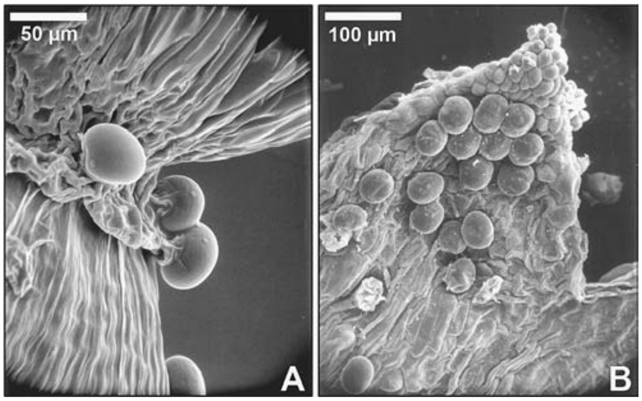


Fig. 6.2. Short-stalked capitate glands in Eupatorieae. **A** *Urolepis hecatantha* (DC.) R.M. King & H. Rob., apex of achene; **B** *Koanophyllon* sp., corolla lobe.

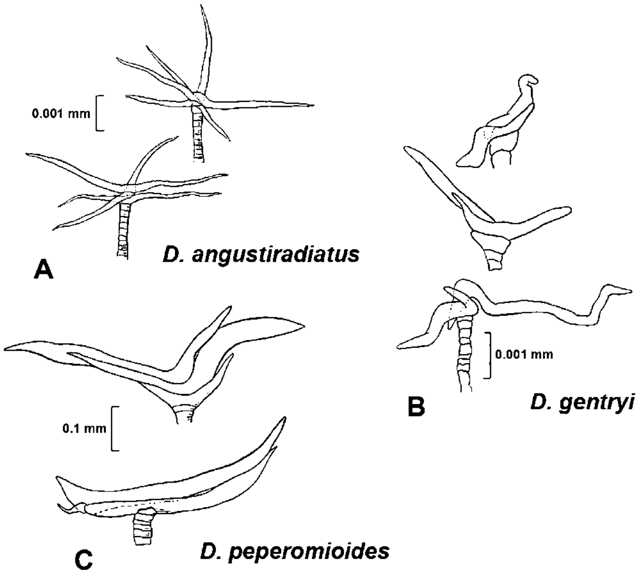


Fig. 6.3. Foliar trichomes of *Dresslerothamnus*. [Redrawn and modified from plates in Robinson 1989, *Systematic Botany* 14: 383 (A), 385 (B), 387 (C). Illustrations by A.R. Tangerini.]

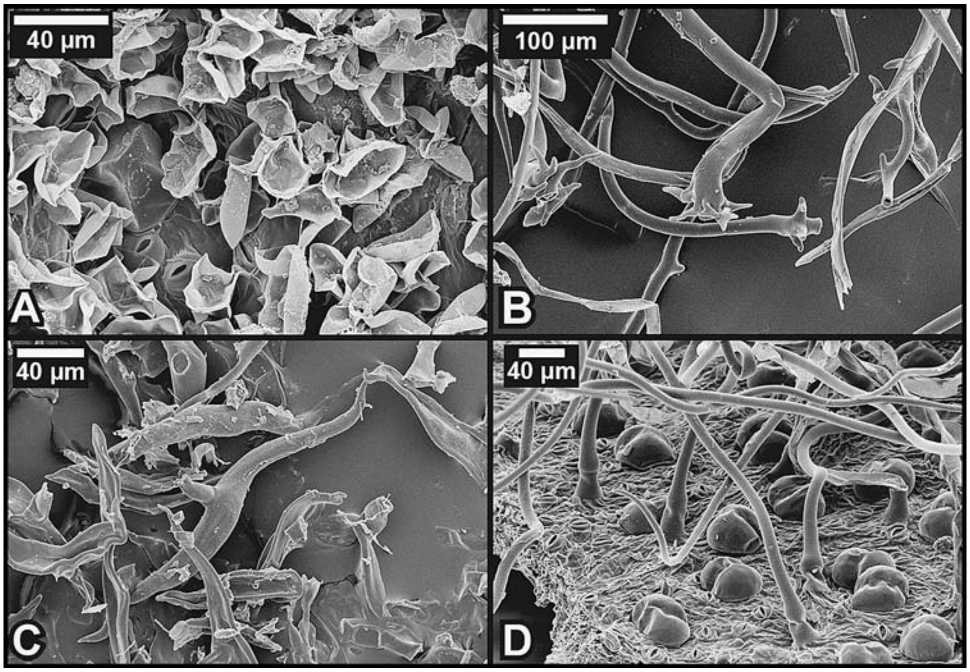


Fig. 6.4. Trichomes of Vernonieae. **A** *Critoniopsis lindenii* Sch.Bip., goblet-shaped trichomes; **B** *C. macrofoliata* H. Rob., trichomes with spurred bases; **C** *Tephrothamnus paradoxus* Sch.Bip., with T-shaped hairs; **D** *Eremosis leiocarpa* (DC.) Gleason, with simple hairs.

Most species of *Hebeclinium* DC. have a receptacle sclerified throughout, with no central pith. In *Adenostemma* J.R. Forst. & G. Forst., the receptacle surface between the florets remains scarcely sclerified, allowing the receptacle to change shape with age.

The paleae, fimbrillae, and hairs on the surface of the receptacle represent basically different structures. The hairs are often of minor taxonomic value, often correlating with hairs inside the corollas (*Neomirandea* R.M. King & H. Rob. 1987).

The fimbrillae are seen in some genera such as *Munnozia* Ruiz & Pav. in Liabeae, but true paleae are found in Liabeae only in *Chionopappus* Benth. (Robinson 1983). True paleae are structurally obvious equivalents of involucral bracts, and in many Heliantheae the structures are nearly identical. The similar situation in *Isocarpha* R. Br. of Eupatorieae was viewed by Keil and Stuessy (1981) as a developmental alteration of the heads to produce florets in the axils of all the involucral bracts. The same thing in different wording would be a partial dedifferentiation on the receptacle from the pattern of zonation between bracts and florets that is basic to head development in Asteraceae.

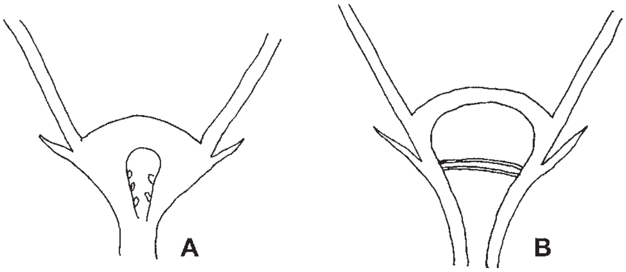


Fig. 6.5. Schematic longitudinal sections of receptacles of *Senecio* and *Packera*. **A** *Senecio vulgaris* L. and *S. leucophyllus* DC., showing small fistulosity; **B** *Packera aurea* (L.) Å. Löve & D. Löve, showing large fistulosity with paired diaphragms.

The groups in which the paleae are most highly developed are often groups with the pappus reduced or lacking (many Heliantheae). Both structures have potential protective functions. The pappus can protect the corolla and its pollen, but of the two, only the paleae can protect the achene. Therefore, it is notable that forms such as Heliantheae with the most highly developed paleae also have the most slowly maturing achenes that need long-term protection (Robinson 1981; Stuessy and Spooner 1988).

Corollas

Another familiar character needing more careful study is the corolla shape. Previously best noted is the liguliform corolla mostly seen in the latex producing Lactuceae. Such corollas are also seen, however, in *Hyaloseris* Griseb. in Mutisieae, *Stokesia* L'Hér. in Vernonieae, and *Fitchia* Hook. f. in Coreopsideae. Another corolla shape of interest is the 4-lobed outer lip of 5-lobed corollas, noted primarily in Gorteriinae of Arctotideae, but also seen in Vernonieae in *Mattfeldanthus* H. Rob. & R.M. King, and one species of *Lampropappus* (O. Hoffm.) H. Rob. (Robinson 1999a). I have referred to this as a 36° or a 10th resupination. This has been noted thus far only in bilaterally symmetrical corollas, but could occur in radially symmetrical corollas, if the lobes are turned with a sinus centered toward the periphery of the head and a lobe centered toward the center of the head. Another way to have a sinus centered to the outside is in the 4-lobed *Iltisia* S.F. Blake (Eupatorieae), *Adenostyles* Cass. (Senecioneae), and other Asteraceae with a reduced number of corolla lobes. In the latter two genera the orientation is difficult to see in dried material, except in the one species of *Iltisia* with zygomorphic corollas.

The corolla shape that proves most interesting for broad relationships is the length of the lobes (Fig. 6.6). In radially symmetrical corollas, short-lobed forms (Fig. 6.6B) are almost always restricted to Asteroideae. Short lobes do occur in modified form in some Mutisioideae (*Chaptalia* Vent.) and the Vernonian genus *Cololobus* H. Rob. (Robinson 1994). In Asteroideae, most lobes are short, but there are some with lobes much longer than wide—in Eupatorieae (*Steyermarkina* R.M. King & H. Rob., some *Neomirandea* R.M. King & H. Rob., some *Mikania* Willd.), Heliantheae (some *Calea* L., *Staurochlamys* Baker), and Senecioneae (*Charadranaetes* J. Janovec & H. Rob., *Jessea* H. Rob. & Cuatrec., *Paragynoxys* (Cuatrec.) Cuatrec., *Pojarkovia* Askerova), but they are among the exceptions in the subfamily.

One corolla micro-character of interest is not yet structurally understood. In *Vernonia* Schreb. and its immediate relatives such as *Vernonanthura* H. Rob. and *Trepadonia* H. Rob. the corolla lobes seem filled with longitudinal partitions (see Fig. 6.11A below). Whether these are ducts of some sort or simply rows of large internal cells is unknown, but they are a good phyletic character for the immediate group of genera.

The inside or adaxial surface of the corollas may be papillose or smooth, with short or elongate cells. This character has been studied in ligules of Asteraceae by Baagøe (1977). Cells inside the lobes of the disk corollas have proven taxonomically valuable in Eupatorieae, densely papillose in most Oxylobinae and Piqueriinae, with cells protruding at upper ends in Fleischmanniinae, cells elongate and not protruding, similar to those of the corolla throat in Ayapaninae and most Alomiinae, not protruding and short, clearly distinct from elongate cells of the throat in Disynaphiinae (King and Robinson 1987).

The point of insertion of the stamens on the corolla shows some interesting variations. The insertion is usually above a rather long basal tube and below an equally long or longer throat of the corolla, and I have used that position to define the limit of the basal tube and the limb (throat plus lobes) in Asteroideae (Fig. 6.6B, C). However, the position is not always so clearly delimited. In *Urbananthus* R.M. King & H. Rob. in Eupatorieae, the filaments originate almost at the extreme base of the corolla (Fig. 6.6E). In *Praxeliopsis* G.M. Barroso, the anthers are mounted at the extreme top of the throat, at the mouth of the corolla (Fig. 6.6D). In *Polyanthina* R.M. King & H. Rob., the corolla is very narrow, and the filaments are staggered in their points of insertion (Fig. 6.6F). In Eupatorieae and Heliantheae, the corolla usually shows a distinct broadening, sometimes very pronounced, at the point of the filament insertion (Fig. 6.6B, C). In Vernonieae, the point of insertion correlates with no marked change of shape of the corolla, instead being in the middle of the funnelform area

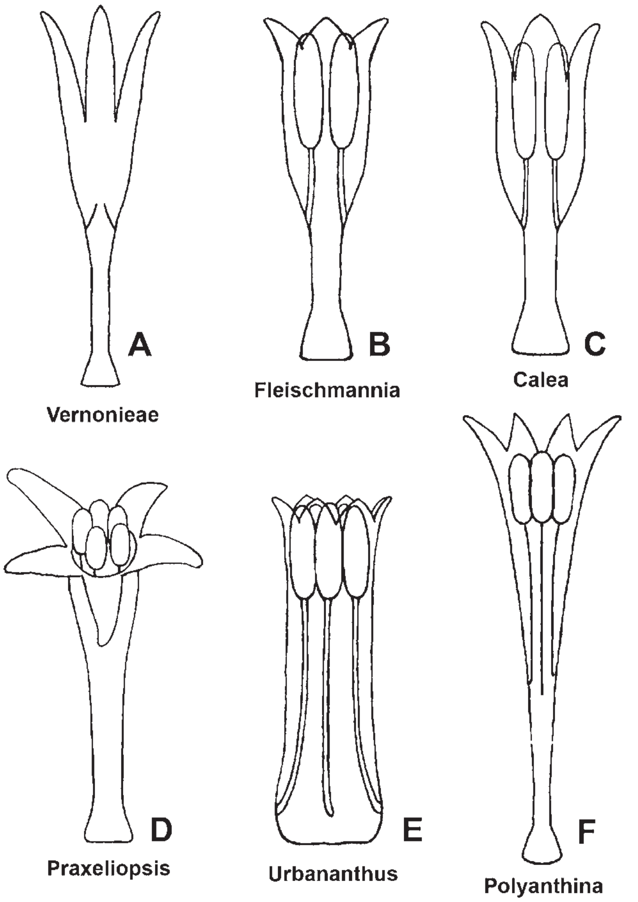


Fig. 6.6. Schematic drawings of insertions of filaments on corolla. **A** Vernonieae with insertions above distal expansion of basal tube; **B** *Fleischmannia* (Eupatorieae), and **C** *Calea* (Heliantheae), with insertions at marked basal constriction of corolla throat; **D** *Praxeliopsis* (Eupatorieae), with insertions at bases of lobes; **E** *Urbananthus* (Eupatorieae), with insertions near base of corolla; **F** *Polyanthina* (Eupatorieae), with insertions staggered in narrow corolla tube.

where the basal tube expands into the throat (Fig. 6.6A). The condition in most other tribes has not been carefully reviewed.

Anthers

On the anther, the tailed condition can be complicated by a thecal base that has been termed "spurred" or "calcarate", where the base of the pollen-bearing part of the theca extends well below the point of attachment to the filament. The true point of filament attachment may be obscured by the tendency for the collar to lie in the plane of the thecae, giving the impression that the base of the collar is the point of attachment. An anther base can be both spurred and have a tail of non-pollen-bearing tissue. Members of the subfamily Asteroideae essentially lack spurs while Cichorioideae and Mutisioideae are almost all spurred.

The endothecial cells of the anther thecae have been used in the taxonomy of Senecioneae by Robinson and Brettell (1973b) and Nordenstam (1978). The examples in the tribe were of the polarized type with thickenings on only two sides of each endothecial cell (Fig. 6.7A, C). A radial arrangement of thickenings, distributed equally on vertical and transverse walls of the cells, is seen in most Eupatorieae and in *Dahlia* Cav. of Coreopsideae.

In the "New Synantherology" (King and Robinson 1970), glands on the stamens were mentioned. At that time, stamen glands were noted for many Heliantheae and Helenieae and *Pluchea indica* L. Since that time, such glands have been seen in some Astereae and in many New World members of Vernonieae. They are absent from all Vernonieae unquestionably native to the Eastern Hemisphere. Why the character is limited to these groups remains a question since similar glands are present on corollas or other parts of plants that lack them on the stamens. It would seem that only a transfer of gene expression within the plant is involved.

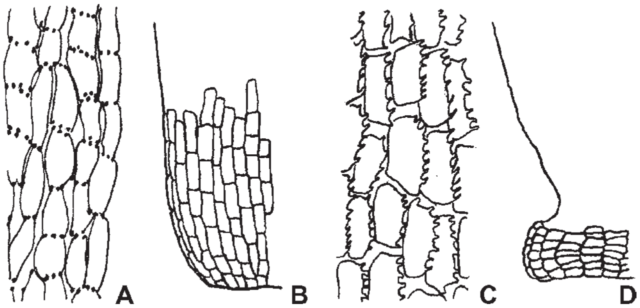


Fig. 6.7. Drawings of endothecial and carpopodial cells in Senecioneae. **A, B** *Parasenecio nikimontanus* (Matsum.) H. Koyama; **C, D** *Arnoglossum reniforme* (Hook.) H. Rob. **A, C** endothecial cells with polarized nodular thickenings; **A** thickenings on crosswalls; **C** thickenings on vertical walls. **B, D** carpopodia.

Styles

The style branches, enlarged versus tapered or truncate, with long sweeping hairs versus short scabrae, and with hairs or papillae continuous onto the upper style shaft, have long been recognized as valid characters. However, they have often not actually been properly examined, and disposition of the stigmatic surfaces was often ignored or inaccurately described (Cronquist 1968). Often the distinctly separated lateral lines in Asteroideae are noted, but the continuous stigmatic surface on the inner surfaces of the branches in Cichorioideae, Mutisioideae, Tussilagineae of Senecioneae and Helianthinae of Heliantheae have not been recognized for what they are. The stigmatic papillae are usually totally lacking in functionally male flowers, as in the male plants of *Baccharis*. The lack or near lack of stigmatic papillae and near complete lack of style branch separation in the Hawaiian genus *Hesperomannia* A. Gray shows that the genus is mostly, if not entirely, apomictic.

Shape of style tips varies greatly in Eupatorieae (King and Robinson 1987), and variations have been used by various authors (Cuatrecasas 1986; Funk 1997; Nordenstam 1978; Vincent 1996), to distinguish genera of Senecioneae.

The style is also notable for the presence or absence of a basal node. This includes various types of swellings in the lower style shaft as in most of *Ageratina* and the presence or absence of sclerified cells.

The style base or shaft in Eupatorieae may also have hairs (Fig. 6.8A, B). Such style pubescence is almost completely lacking in other tribes. Exceptions are some *Arnica* L. (Fig. 6.8D), *Chaenactis* DC., and *Chamaechaenactis* Rydb. in Helenieae (Robinson 1981). This is one reason why I have always considered *Arnica* one of the closest relatives of Eupatorieae outside of that tribe. The presence of hairs near the base of the style in *Eremanthus mattogrossensis* Kuntze seems similar, but the hairs in the latter are on the nectary, not the style (Fig. 6.8C). A character, such as hairs on the style base, which is nearly restricted to one tribe, can be useful in the overall taxonomy of the family, even when it is not consistently present within the group in which it occurs.

A character that is not strictly microscopic is what I have termed "style rotation" (Robinson 1984) (Fig. 6.9). The position of the style branches and the ovule are fixed in relation to each other, but they are not fixed in relation to the corolla. As a result the style branches of Vernonieae always spread laterally (tangentially), in the plane of the involucral bracts, while those of almost all Eupatorieae spread radially, perpendicular to the plane of the involucral bracts. In some cases, such as fertile rays of Heliantheae, the disk styles spread radially and the ray styles spread laterally. The orientation of the styles usually correlates with whether the achenes of the plant are compressed or obcompressed. Many Heliantheae have radially elongate disk achenes (laterally compressed). The ray achenes with laterally spreading style branches have tangentially elongate (obcompressed) achenes. In Eupatorieae, the few genera in Praxelinae, *Eupatoriopsis* Hieron., *Eitenia* R.M. King & H. Rob., *Praxelis* Cass., have laterally spreading style branches and the most strongly obcompressed achenes in the tribe. In Vernonieae, with laterally spreading style branches, the achenes, when flattened, are obcompressed and sometimes even laterally winged (*Dipterocypsela* S.F. Blake and *Heterocypsela* H. Rob.).

The most interesting exceptions to the direction of style branch spreading and achene compression are in Coreopsideae and *Cineraria* L. of Senecioneae. There, the achenes are obcompressed, but the style branches spread radially. As a result, the main veins leading into the style run up the middle of the flattened sides of the achene instead of up the edges as in most compressed or obcompressed achenes in Asteraceae. In spite of some exceptions as in Praxelinae, or gradations as in *Schistocarpha eupatorioides* (Fenzl) Kuntze, the character works well in distinguishing many tribes.

Achenes

Achene walls that contain phytomelanin do not have raphids (oxalate crystals). The phytomelanin layer is deposited in the intercellular spaces inside the achene walls and it has perforations where the enclosing cells connect to each other. These perforations are usually rather randomly and densely spaced, but occasionally have patterns, as in some Eupatorieae, for instance they are comparatively sparse in *Piqueria* Cav. (Fig. 6.10A) and they are arranged in transverse rows in the subtribe Disynaphiinae (Fig. 6.10B) (Robinson and King 1977). In many Heliantheae and Helenieae s.l., but never in Eupatorieae, the phytomelanin layer between the major ribs is interrupted by linear pale striations (Fig. 6.10C) (examples *Aphanactis* Wedd., *Helianthus* L., and *Arnica*). Closely related to other Helenieae, are Gaillardiinae and Marshalliinae that have no phytomelanin in the achenes, but they do have raphids. This character may not be altogether phyletically reliable, for example it differs between the otherwise almost identical genera *Psathyrotes* A. Gray and *Psathyrotopsis* Rydb. (Robinson 1981).

The presence of phytomelanin in the achene walls is mostly restricted to the supertribe Helianthodae, but it does occur in a somewhat less well-defined form in the

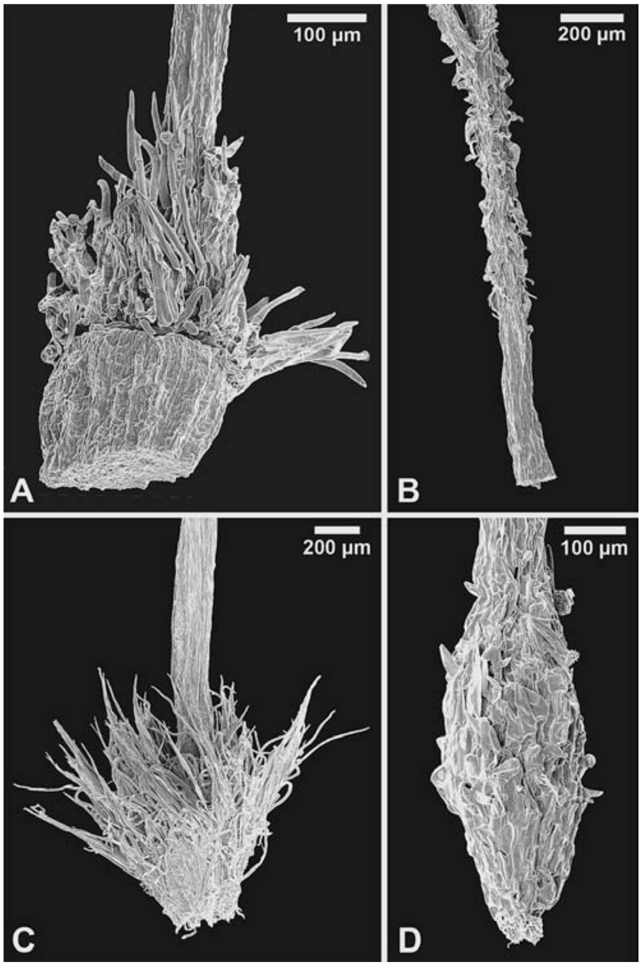
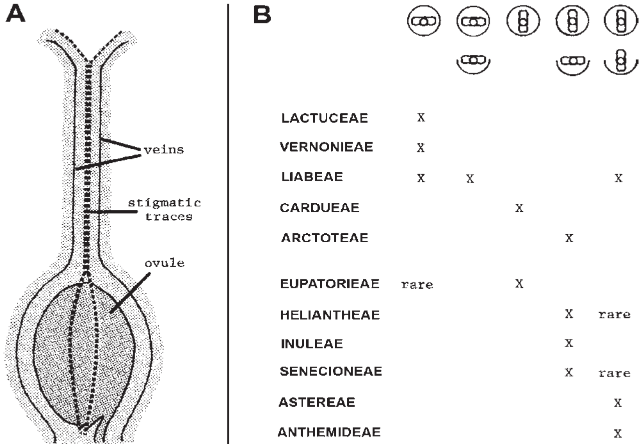


Fig. 6.8. Style bases. **A** *Gongrostylus costaricensis* (Kuntze) R.M. King & H. Rob. (Eupatorieae), with hairs on style base; **B** *Stylotrichium corymbosum* (DC.) Mattf. (Eupatorieae), with hairs on style shaft; **C** *Eremanthus mattogrossensis* Kuntze (Vernonieae), with hairs on nectary; **D** *Arnica cordifolia* Hook. (Chaenactideae), with hairs on style base.



LACTUCEAE	X				
VERNONIEAE	X				
LIABEAE	X	X			X
CARDUEAE			X		
ARCTOTEAE				X	
EUPATORIEAE	rare		X		
HELIANTHEAE				X	rare
INULEAE				X	
SENECIONEAE				X	rare
ASTEREAE					X
ANTHEMIDEAE					X

Fig. 6.9. A gynoecium of Asteraceae showing relative positions of style veins, stigmatic strands, and ovule in the style and achene; **B** Distribution of radial and tangential orientations of style branches in Asteraceae. Schematic drawings at the top with circles for disk flowers or flowers of homogamous heads, with bracts showing orientation of styles in ray flowers. [From Robinson 1984, *Taxon* 33: 401.]

subtribe Sipolisiinae of Vernonieae (Fig. 6.10D) (Robinson 1999b).

Some of the best examples of the taxonomic use of raphids in the achenes are in Senecioneae by Nordenstam (1978) and in Vernonieae by Robinson (1999b). Their shapes vary between subquadrate (Fig. 6.10E) and elongate.

Achene walls of Vernonieae often have specialized cells on the surface that I have referred to simply as idioblasts (Fig. 6.10F). They are often scattered or in longitudinal rows of three or more. In Vernonieae they can be aligned along the sides of the costae in *Linzia* Sch.Bip. and are in marked transverse rows in most *Vernoniastrum* H. Rob. (Robinson 1999a). Similar cells can be seen in *Porphyrostemma* Benth. & Oliv. of Inuleae (Bremer 1994).

The surface of the achene is often covered with biseriate trichomes, setulae or Zwillingshaare (Hess 1938), and short-stalked capitate glands. The setulae may vary in the degree to which the pair of cells is fused or unequal in length (Robinson 1999a).

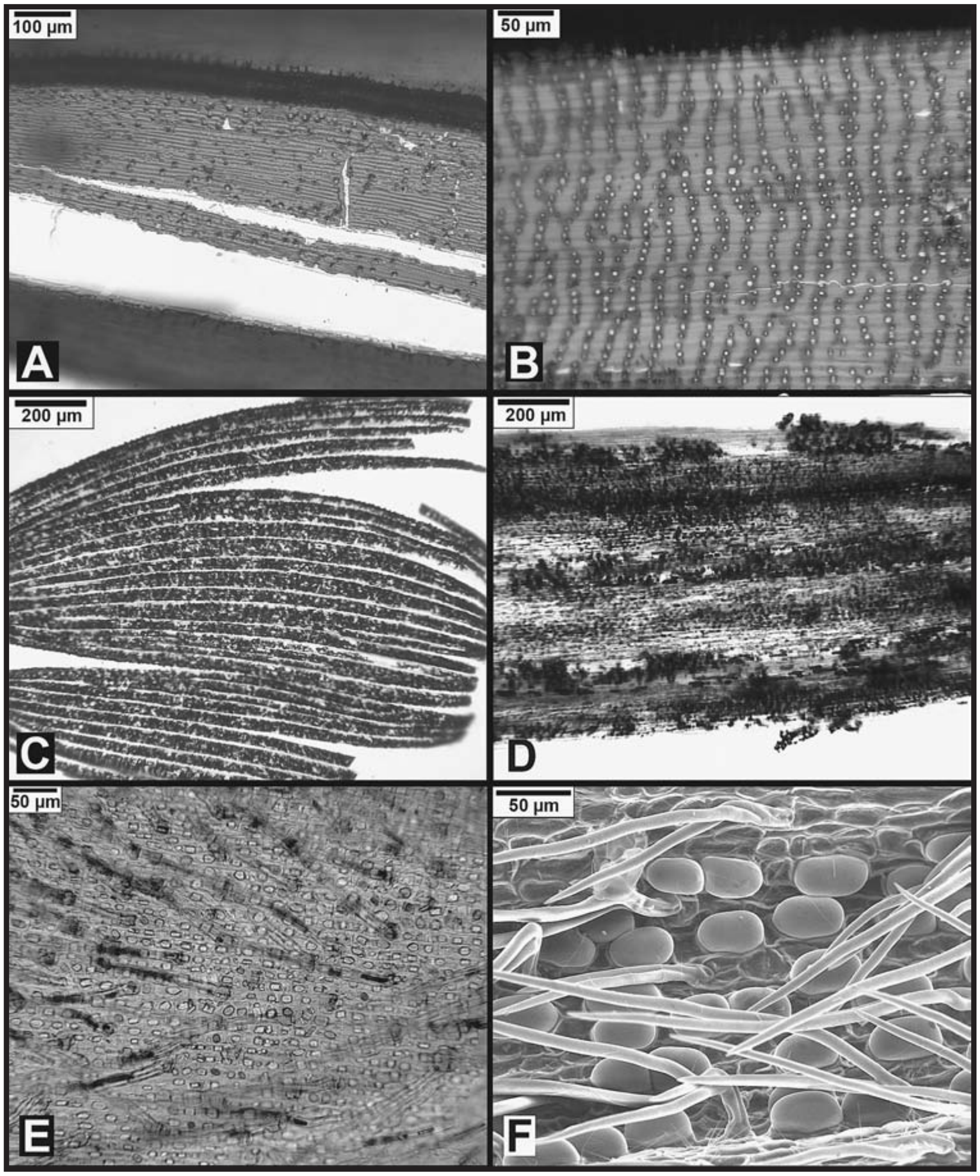


Fig. 6.10. Achene walls in Asteraceae. **A** *Piqueria trinervia* Cav. (Eupatorieae), with sparse punctations; **B** *Symphyopappus decemflorus* H. Rob. (Eupatorieae), with punctations in transverse rows; **C** *Aphanactis ollgaardii* H. Rob. (Galinsoginae), with pale striations interrupting phytomelanin; **D** *Sipolisia lanuginosa* Glaz. ex Oliv. (Vernonieae), showing phytomelanin in Cichorioideae; **E** *Heterocypsela andersonii* H. Rob. (Vernonieae), showing subquadrate raphids and setulae; **F** *Centrapalus galamensis* (Cass.) H. Rob. (Vernonieae), showing setulae and superficial idioblasts.

Elaiosomes or probable elaiosomes occur in one genus of Eupatorieae, *Cavalcantia* R.M. King & H. Rob., and in many Heliantheae (*Wedelia* Jacq.) (Strother 1991). These are located at the base of the achene above the carpopodium.

The carpopodium is the scar of the abscission zone on the base of the achene (Figs. 6.7B, D; 6.11C). It is usually pale, and has associated pale cells on the bases of the achene ribs. The structure may show taxonomically useful variations in size and shape of cells and thickness of cell walls (King and Robinson 1987). In Heliantheae, in genera such as *Wedelia*, the shape may change as the achene matures so that the carpopodium essentially bites the achene off of the receptacle. In Ayapaninae of Eupatorieae, the basal row of cells in the carpopodium can be greatly enlarged (Fig. 6.11C). The carpopodia of Vernonieae show a comparative uniformity, but one genus, *Camchaya* Gagnep. has no evident carpopodium.

Pappus

The pappus is traditionally equated with a calyx, but it is highly modified into scarious scales and bristles arising from a basal callus. The scarious pappus seems developmentally related to the twin hairs or setulae of the achene surface. Both are absent in various Helianthinae that have what are called "calvous achenes" (Robinson 1981). The pappus is considered to be lacking in many taxa where the upper callus of the achene is present (*Alomia* Kunth in H.B.K.). The complete absence of the pappus without a callus is seen in groups such as Zinniinae in Heliantheae and *Teixeiranthus* R.M. King & H. Rob. of Eupatorieae, where the corolla is directly fused to the apex of the achene (King and Robinson 1987).

The segments of the pappus, when present, are usually in one series, often arranged with stronger elements over the ribs of the achene and scales, with shorter parts, or no elements on the sides between the ribs. Many tribes such as Eupatorieae (*Ageratina* Spach), Vernonieae (*Vernonia* Schreb.), and Astereae (*Symphyotrichum* Nees) have a outer short series of fimbrillae or squamae, but these usually originate between the bases of the longer segments and are structurally of the same series. In the typical element of the genus *Senecio* L., the outer series can contain minute fimbrillae with retrorsely barbed tips called "fluked" by Drury (1966).

The pappus may also have many rows as in some Astereae, one species of *Asanthus* R.M. King & H. Rob. in Eupatorieae, and many Cardueae. In these latter cases

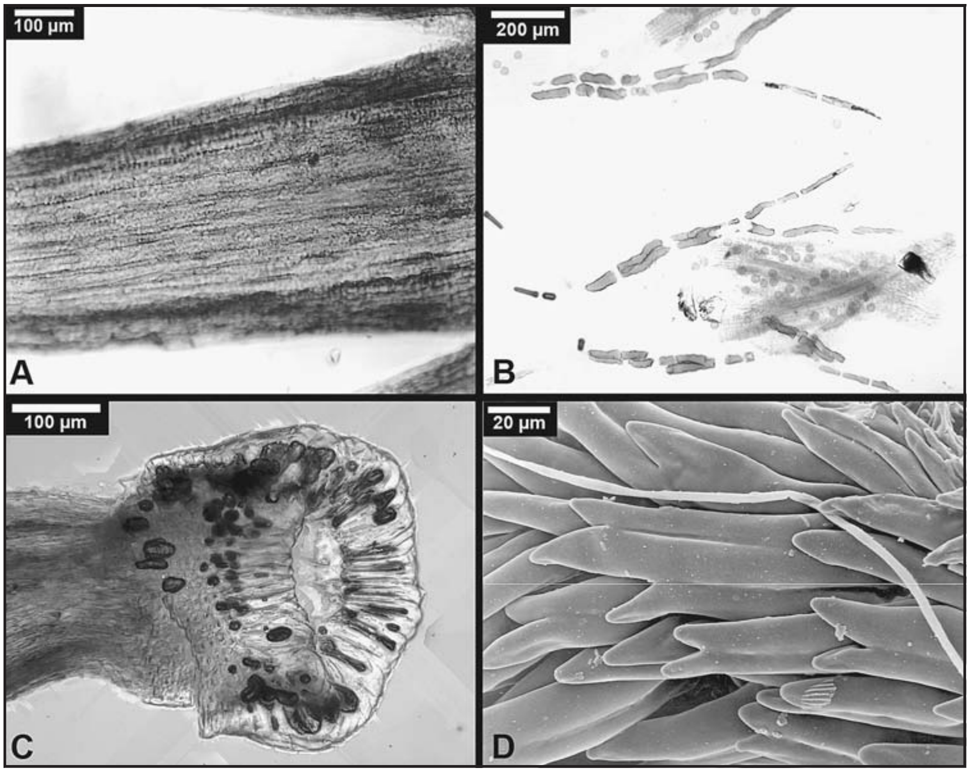


Fig. 6.11. A *Trepadonia mexiae* (H. Rob.) H. Rob. (Vernonieae), corolla lobe showing longitudinal pattern of cells characteristic of Vernoniinae s.str.; **B** *Aphanactis ollgaardii* H. Rob. (Galinsoginae), showing paired resin ducts along veins of corolla throat; **C** *Gongrostylus costaricensis* (Kuntze) R.M. King & H. Rob., (Eupatorieae), carpopodium showing enlarged basal row of cells; **D** *Hoplophyllum spinosum* DC. (Eremothamneae), sweeping hairs of style showing bi- and tri-cellular construction.

the upper callus of the achene shows its more basic nature as a highly modified primordial field with little resemblance to a calyx.

The bristles of the pappus in Eupatorieae can be slender and even fragile at the base (*Ageratina*), winged at the base (*Lasiolaena* R.M. King & H. Rob., *Stevia* Cav.), plumose (*Carminatia* Mociño ex DC., *Brickellia* Eliott), or enlarged at the tips (*Amboroa* Cabrera). Enlargement of the tips is restricted to male florets in some Gnaphalieae and Astereae (*Antennaria* Gaertn. and *Baccharis*). The outer surface may be as rough as the lateral margins or may be totally flat and lacking scabrae as in *Brickellia* of Eupatorieae and its immediate relatives (Gaiser 1954) or *Baccharoides* Moench of Vernonieae.

Bristles in a true capillary pappus are almost never vascularized, but tracheids occur in the bristles in some species as in *Helogyne* of Eupatorieae and *Tridax* in Galinsoginae. The vascularized awns and projections of many Heliantheae, especially in the subtribe Ecliptinae and *Verbesina* L., are evidently not a true pappus but are separate outgrowths of the achene. Such a false pappus sometimes occurs in the same achene with a true pappus as in *Perymenium* Schrad. and *Perymeniopsis* H. Rob. (Robinson 1981). A few Ecliptinae such as *Melanthera* Rohrb. and *Steiractinia* S.F. Blake have a true capillary pappus without a false pappus.

A true pappus is usually poorly developed in most Heliantheae. A more fully developed and more radially symmetrical, sometimes fully capillary or plumose pappus,

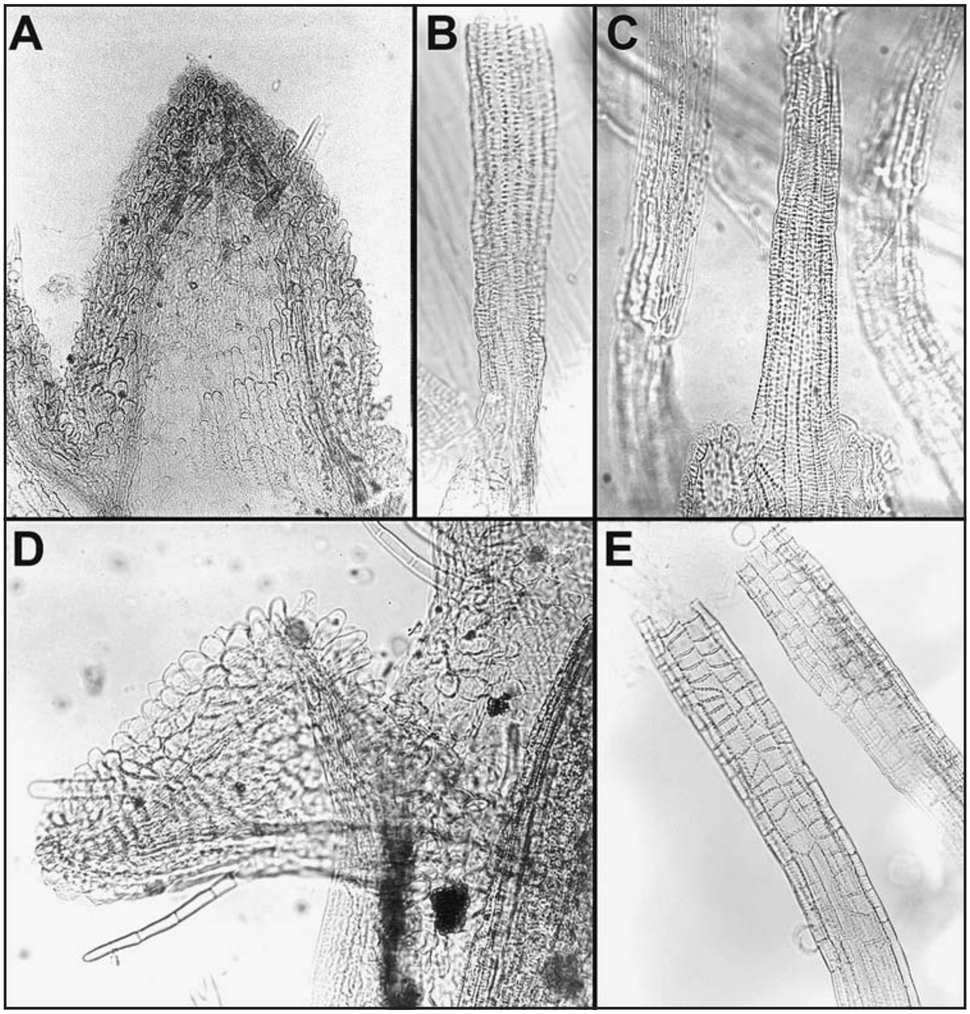


Fig. 6.12. Corolla lobes and anther collars of *Fleischmannia* and *Ageratina* (Eupatorieae). **A, B** *Fleischmannia cookii* (B.L. Rob.) R.M. King & H. Rob.; **C** *F. gentryi* R.M. King & H. Rob. **A** corolla lobe showing prorulose elongate cells projecting at upper ends on both surfaces and margins; **B, C** anther collars showing dense annular thickenings on insides of cell walls that obscure the cross-walls; **D** *Ageratina* sp., corolla lobe showing papillose inner surface and smooth outer surface; **E** *Ageratina cardiophylla* (B.L. Rob.) R.M. King & H. Rob., anther collars showing numerous subquadrate cells without obvious annular thickenings on walls.

is found in Neurolaeneae and the subtribe Galinsoginae that DNA sequences place outside of the main group of paleaceous Heliantheae (see the metatree, Chapter 44).

EXAMPLES OF MICRO-CHARACTER APPLICATION

A few examples of the successful use of micro-characters in Asteraceae taxonomy should be mentioned.

Two *Liabum* types were destroyed in Berlin in WW-II, and only small fragments were available with a photo of one type. Examination of fragments showed that *L. homogamum* Hieron. was a *Neomirandea* in Eupatorieae and *L. eupatorioides* Hieron. was the same as *Schistocarpha sinforosi* Cuatrec. (not *S. eupatorioides* (Fenzl) Kuntze).

Eremothamnus O. Hoffm. was originally placed in Senecioneae. *Hoplophyllum* DC. was long placed in Vernonieae. Karis (1992) first placed the two together. A confirming character was the longitudinally septate sweeping hairs of the styles (Fig. 6.11D) (Robinson 1992), a feature found only in those two genera of the family.

In Heliantheae, in what had been called *Calea*, species fell into at least three groups on the basis of micro-characters. One series had achenes with striations in the phytomelanin (Fig. 6.10C), yellow resin ducts paired along the main corolla veins, not fusing at the sinuses (Fig. 6.11B), and yellow resin ducts collateral with or outside the veins in the style shaft. A second series had a solid expanse of phytomelanin between the veins of the achene, single reddish resin ducts along the veins of the corolla, forking at the sinus into the adjacent lobes, and often reddish resin ducts inside the veins of the style shaft. The third type involved continuous areas of phytomelanin in the achene walls, but essentially colorless ducts in the corollas. The third type, which was not very much like other *Calea*, proved to be a *Podachaenium* Benth. ex Örsted. (*Squamopappus* R.K. Jansen, N.A. Harriman & Urbatsch), a genus related to *Verbesina* L. Of the other two groups, most species of which shared remarkably similar awn-shaped pappus segments, the first was *Alloispermum* Willd. in Galinsoginae with such genera as *Aphanactis* and *Tridax* L.; the second was typical *Calea* in Neurolaeneae.

In the traditional approach to the taxonomy of Eupatorieae, members of the presently recognized genera *Fleischmannia* and *Ageratina* were sometimes confused with each other. Even species as taxomically different as *F. microstemon* Cass. and *A. molinae* R.M. King & H. Rob. were not distinguished from each other. Nevertheless, the two genera prove to differ by corolla lobes prorulose on both surfaces (Fig. 6.12A), the anther collars narrow with cellular structure completely obscured by annular thickenings (Fig. 6.12B, C), the style base without an expanded node, the carpopodium with a projecting upper margin, and carpopodial cells having thick walls in *Fleischmannia*; versus the corolla lobes being almost always densely papillose inside, and smooth outside (Fig. 6.12D), the anther collars showing unobscured cellular structure (Fig. 6.12E), the style base almost always having an expanded node, the carpopodia without a projecting upper margin, and its cells having thin, beaded walls. *Fleischmannia* includes species with chromosome numbers of $x = 10$ or rarely 4; *Ageratina* has $x = 17$ or ca. 20. *Ageratina* also has some lesser differences of interest, the style being mounted on top of the nectary as in many other tribes rather than its base being immersed within a doughnut-shaped nectary as in most other Eupatorieae, and endothecial cells more elongate and somewhat polarized on the lateral walls, not quadrangular with radial thickenings as in most Eupatorieae.

SOME AXIOMS REGARDING THE USE OF MICRO-CHARACTERS

- It is admitted that microscopic features can never be surveyed as easily or as totally as macroscopic features. Even so, one slide of microscopic characters of each of the numerous species of some large genera, such as *Ageratina* Spach and *Fleischmannia* Sch.Bip. in Eupatorieae, allows great confidence in the results.
- From the preceeding review, a picture emerges of many characters, all of which have some value at some level. The aim is to discover the level at which each character is most useful.
- Characters that work well in one tribe can often be worthless in another. Many useful style base characters have been found in Eupatorieae (King and Robinson 1987). However, equivalent useful structures are lacking in most tribes outside of Eupatorieae, such as Astereae.
- Minute fragments can be used to identify specimens. With the destruction of the Asteraceae collection at Berlin during WW-II, some species were known only from limited photographic records and fragments obtained prior to the war by S.F. Blake. Using micro-characters, identifications were possible of two *Liabum* types mentioned above. Without such micro-character study, the latter identifications would have been impossible or uncertain.
- Use of all available characters shows that phyletic gaps between the major tribes and even subtribes are much greater than anyone had thought as little as fifty years ago (Cronquist 1955, where the Heliocentric system and the impression of a near phyletic continuum were dominant).
- There are no perfect characters to define the largest groups in the Asteraceae, neither macroscopic nor microscopic.

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Chapter **7**

Evolution of pollen in Compositae

Stephen Blackmore, Alexandra H. Wortley, John J. Skvarla and Harold Robinson

INTRODUCTION

Systematics

There has been a huge amount of progress in Compositae systematics over the past thirty years. At the Reading conference in 1975 (reported in Heywood et al. 1977), Compositae were agreed to be a natural group with well-defined limits, a diagnostic floral structure, and an accepted system of taxonomy little different in tribal limits to that of Bentham (1873). Fourteen tribes were recognized (Anthemideae, Arctotideae, Astereae, Calenduleae, Cichorieae, Cynareae, Eupatorieae, Helenieae, Heliantheae, Inuleae, Liabeae, Mutisieae, Senecioneae, and Vernonieae). These were considered to fall into two subfamilies, broadly following those of Robinson and Brettell (1973), Carlquist (1976) and Wagenitz (1976). Arctotideae, Cardueae, Cichorieae, Liabeae, Mutisieae and Vernonieae were placed in Cichorioideae. Anthemideae, Astereae, Calenduleae, Helenieae, Heliantheae and Inuleae were placed in Asteroideae, with Eupatorieae and Senecioneae seen as somewhat intermediate between the subfamilies. It was recognized at this stage that Helenieae might not be a natural group.

Ten years on, Bremer (1987) conducted the first cladistic analysis of morphological characters for the entire family, taking the fourteen accepted tribes as terminal taxa. Bremer (1994) then translated his results into a classification comprising three subfamilies and seventeen tribes. At the Kew Conference, Bremer (1996), presented a further modified version of the classification based on a growing body of morphological and molecular cladistic analyses. He recognized four subfamilies: Asteroideae, Barnadesioideae, Carduoideae, and a reduced and more clearly-defined Cichorioideae excluding Mutisieae and Cardueae. Mutisieae, considered paraphyletic, were unplaced to subfamily. Several "problem" genera (e.g., *Brachylaena*, *Eremothamnus*, *Gundelia*, *Moquinia*, and *Tarchonanthus*) were highlighted as isolated and of uncertain tribal relationship.

The 2005 supertree (= metatree; Funk et al. 2005) integrated a large number of molecular phylogenetic analyses conducted in the decade following the Kew Conference. Thirty-six tribes or tribal-level clades (some of them monogeneric) were recognized, in three main subfamilies (with many tribes unplaced to subfamily): Asteroideae (Anthemideae, Astereae, Athroismeae, Bahieae, Calenduleae, Chaenactideae, Coreopsideae, Eupatorieae, Gnaphalieae, Heliantheae, Helenieae, Inuleae, Madieae, Millerieae, Neurolaeneae, Perityleae, Polymnieae, Senecioneae, and Tageteae), Carduoideae (Cardueae, Dicomeae, Oldenburgieae, and Tarchonantheae), Cichorioideae s.str. (Arctoteae, Gundelieae, Lactuceae, Liabeae, and Vernonieae), Barnadesieae, Corymbieae, Gochnatieae, Gymnarrheneae, Hecastocleideae, Pertyeae, the *Stifftia* clade, and the Mutisieae grade. Helenieae were much reduced, and paraphyletic Mutisieae were not given formal tribal status. Several previously problematic genera and isolated small tribes were found to lie at the base of large radiations (*Cratystylis*, *Athroismeae*, *Corymbium*, *Gymnarrhena*, and *Hecastocleis*). It is on this tree that the following discussion is based.

Dedication. This chapter is dedicated to Erika Stix, pioneer palynologist of Compositae.

In sum, developments in Compositae systematics since 1975 include a more settled delimitation, topology and character concept for Asteroideae; the reassessment of Eupatorieae, previously thought to be an intermediate group between Cichorioideae and Asteroideae, as one of the most derived clades in Asteroideae; disintegration of the polyphyletic Helenieae into a number of smaller tribes including Bahieae, Madieae and Tageteae; dismemberment of the polyphyletic "dustbin tribe" Mutisieae, transferring some members to other tribes and some to their own tribes; reduction of Cichorioideae to a well-defined grouping of five tribes; erection of Carduoideae to comprise elements previously found in Mutisieae or unplaced; and placement of problematic genera including *Corymbium* and *Gymnarrhena*. Outstanding questions include the precise positions of Senecioneae and Gochnatieae; the placement of problem genera not included in the supertree (e.g, *Catamixis*, *Fitchia*, *Gladiopappus*, *Moquinia*, *Pacourina*, and *Pseudostifftia*) and the relationships of other poorly-sampled groups, such as Senecioneae and Astereae, and Asian taxa across all groups.

Palynology

Concurrent with these changes in systematics, palynological methods have also developed, shaping our current understanding of Compositae pollen. The earliest images of any angiosperm pollen were made by Nehemiah Grew in his *Anatomy of Plants* (Grew 1682), and pollen was first recognized as a useful taxonomic character by Robert Brown in 1811, but it was not until 1864 that pollen was first used as a character for defining taxa in the Compositae (in this case genera; Steetz 1864).

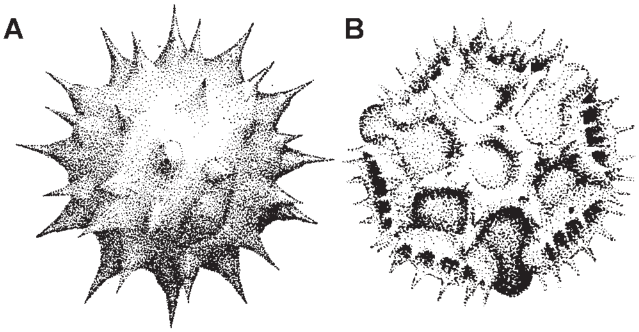


Fig. 7.1. Example drawings of Compositae pollen under LM by Roger P. Wodehouse. **A** *Helianthus annuus* L. taken from Wodehouse (1928a). Wodehouse's (1928a: 197) caption reads: "27.5 µm diam. Side view, showing the broad short furrow and long slender spines, characters which sharply differentiate it from the grains of the primitive Ambrosiaceae and likewise from those of *Parthenium* and *Parthenice*." **B** *Lepidaploa canescens* (Kunth) H. Rob. taken from Wodehouse (1928b). Wodehouse's (1928b: 932) caption reads: "34.9 µm diam. Polar view. A subechinolophate type of grain, characteristic of the bractless *Lepidaploa*. Only the paraporal crests are at all well developed. The germinal furrows, however, are well developed, as in all the *Lepidaploa*." [Reprinted with permission.]

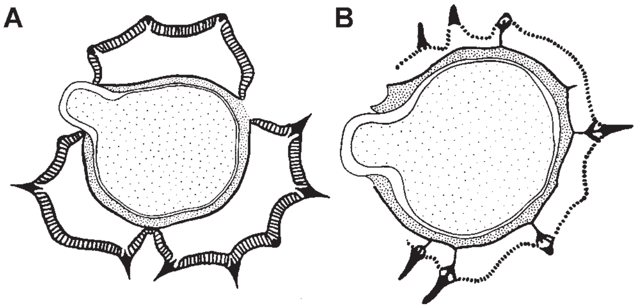


Fig. 7.2. Example drawings of cross sections of Compositae pollen under LM by Erika Stix. **A** *Helianthus debilis* Nutt. ×2000; **B** *Vernonia scorpioides* Pers. ×2000. [Taken from Stix (1960); reprinted with permission.]

Compositae pollen is typically isopolar (symmetrical about the equator) and radially symmetrical, with three compound apertures (Stix 1960). However, the pollen of basally-branching Compositae differs very little from that of the close sister groups Goodeniaceae and Calyceraceae (Skvarla et al. 1977; Gustaffson et al. 1997; Hansen 1997; DeVore et al. 2007; the sister group relationships of Compositae are discussed in more detail in Funk et al. 2005 and references therein), which renders it difficult to use pollen characters to delimit Compositae, or to use fossil pollen to date the origin of the family.

The light microscope (LM) was fundamental to establishing the foundations of modern palynology, and remains the starting point for comprehensive pollen morphological studies today. Using LM, Wodehouse (1926, 1928a, b, 1929a, b, 1930, 1935) produced accurate and beautiful drawings of Compositae pollen that are reminiscent of today's scanning electron microscope views (Fig. 7.1), and distinguished three major types of pollen—psilate, echinate and lophate. Also using LM, Stix (1960) made equally detailed and even more precise observations on the structure of the exine, recognizing a number of exine types which she represented in diagrammatic form (Fig. 7.2).

However, LM provides limited magnification, resolution and depth of focus, and the resulting images are often difficult to interpret. By the mid-1960s, the greater magnification and resolution provided by transmission electron microscopy (TEM) made it possible to build on previous work by examining ultra-thin sections of pollen exines and shadowed surface replicas. Interpreting the complex stratification of the exine remained difficult, and knowing the precise plane of a TEM section is critical to understanding it correctly. Using TEM, Skvarla and Larson (1965) and Skvarla and Turner (1966) established three principal patterns of exine stratification (Anthemoid, Helianthoid, and Senecioid; these were modified and elaborated in later works), which became widely adopted in later discussion. These were based on a combination of characters that could be seen under TEM, in particular the presence or absence of a large cavea (space) within the pollen wall and presence or absence of internal foramina (smaller spaces within individual structural elements).

From the 1970s onwards, the widespread availability of scanning electron microscopy (SEM) revolutionized palynology through the production of three-dimensional images at high magnification and resolution. There are many different methods of preparing pollen for SEM (Skvarla et al. 1988). In particular, the development of fracturing techniques (e.g., Blackmore and Barnes 1986; Robinson and Marticorena 1986) allows SEM to be used to study pollen development and examine sections through the exine as well as whole pollen grains (Fig. 7.3). However, SEM images also require skill to interpret and characterize, and both LM and TEM continue to provide valuable additional data in studies of pollen morphology.

Synthesis

The concurrent advances in systematics and palynology described above have now started to come together. Thirty years ago, when Heliantheae, and therefore the Helianthoid pollen type, were thought to represent the "primitive" state in Compositae, Skvarla et al. (1977) could find little congruence between pollen characters and classification. For example, they noted that Calyceraceae had pollen very similar to the Anthemoid type of Compositae, but admitted that palynology could not help identify the sister group of Compositae because none of the possible contenders had a Helianthoid-type exine. This led to a general perception that pollen characters were too homoplastic to be useful at family and tribal levels. However, when Bremer (1994) included palynological characters with other morphological evidence in his cladistic analysis, groups such as Barnadesieae and Mutisieae, mostly with Anthemoid pollen types, were found to form the early branches of the tree, with Heliantheae relatively derived. By the time of the Kew Conference there was a degree of congruence between the palynological evidence and the increasingly well-supported phylogeny of Compositae. This trend has continued to the present day, when palynology presents some fascinating morphological congruencies with the topology of the supertree at a variety of hierarchical levels.

MATERIALS AND METHODS

We reviewed pollen descriptions, LM, TEM and SEM images for the 402 genera in the Compositae supertree (Funk et al. 2005; Funk, pers. comm.). This was facilitated by a review of the literature on Compositae pollen (Wortley et al., this volume) which lists around 1250 references, and represents an update of the bibliography presented by Thanikaimoni (1977). In covering less than 25 percent of genera, our analysis does not attempt to provide a categorical review of Compositae pollen, but rather an indication of the variability found across the family and some of the patterns that can be seen. Fifty-two pollen characters (Appendix 7.1) were documented in one character-taxon matrix with tribes as terminals (Appendix 7.2), and additional tribal matrices with genera as terminals (not shown). It should be noted that the matrices were not designed

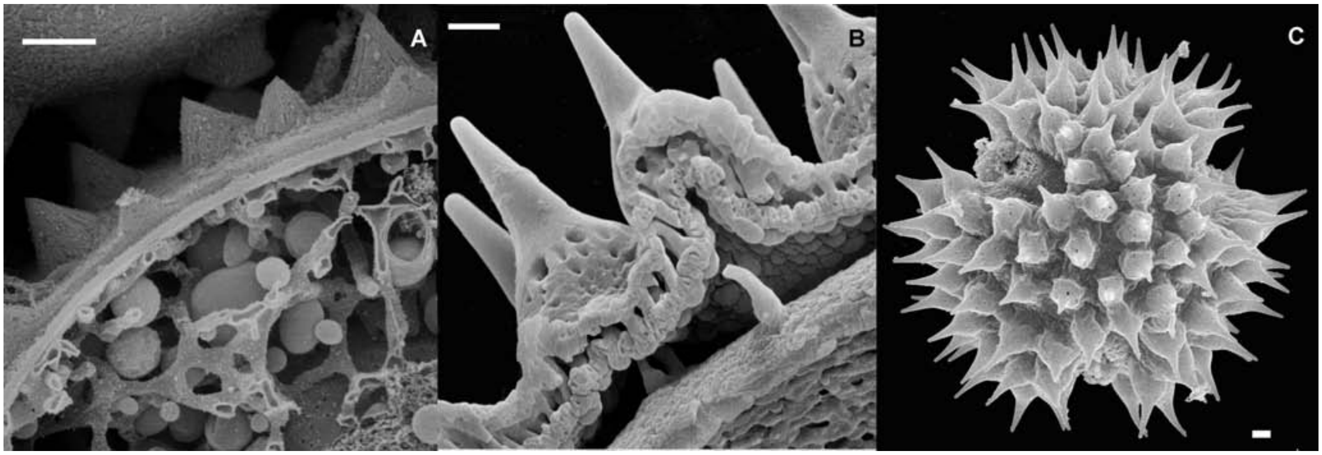


Fig. 7.3. Use of SEM to study development, exine ultrastructure and surface sculpture—examples from *Catananche caerulea* L. **A** cross section through fractured exine at early stage of pollen development; **B** cross section through fractured exine of mature pollen grain; **C** polar view of mature pollen grain. Scale bars: A, B = 1 μm; C = 2 μm.

for phylogenetic analysis, since many of the characters are known to be non-independent. The data were then optimized, character by character, as unordered multistate characters (i.e., making no assumptions about their evolution) on the supertree tree using MacClade (Maddison and Maddison 2005), to ascertain the key evolutionary changes in pollen morphology across the branches of the supertree and determine possible ancestral states relative to the outgroups Calyceraceae and Goodeniaceae. Equivocal character changes were optimized using the "show all most parsimonious character states at each node" option in MacClade.

Terminology

One constraining factor in using palynological characters is the conflicting terminologies that exist, due to the variety of descriptive terms needed for such complex micromorphologies, and the existence of alternative but not identical systems (see Fig. 7.4). In the past this has led to a tendency to use synthetic "pollen types" or "exine types," summarizing a number of characters into one statement; unfortunately these have led to more problems in analysis than they have solved. In this paper, we limit the discussion to broad-scale characters which are relevant in distinguishing Compositae at, and above, generic level. We

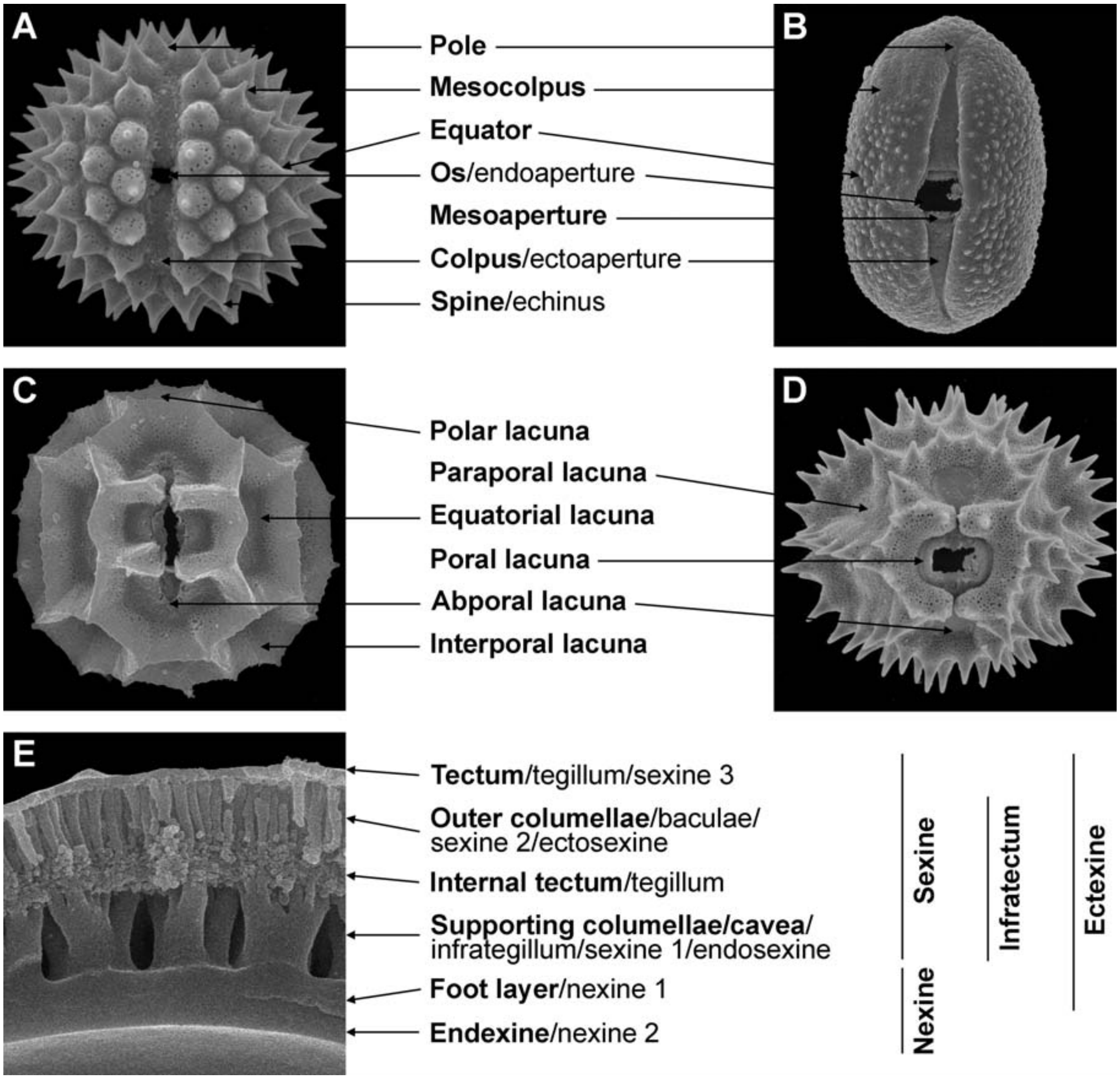


Fig. 7.4. Alternative terminologies for pollen grain surface sculpture and exine ultrastructure. **A** surface sculpture, echinate non-lophate grain (*Amellus asteroides* Druce); **B** surface sculpture, psilate non-lophate grain (*Mutisia sodiroi* Hieron.); **C** surface sculpture, psilate lophate grain (*Cullumia aculeata* (Houtt.) Roessler); **D** surface sculpture, echinate lophate grain (*Dubyaea hispida* DC.); **E** exine ultrastructure (*Nouelia insignis* Franch.). Terms in bold are those used in this paper.

take as a starting point the characters used in the *Northwest European Pollen Flora* (Blackmore 1984; Punt and Hoen, in prep.) and defined in Punt et al. (1994). We consider two major sets of characters: exine structure (in cross section) and surface sculpture (ornamentation of the pollen surface) in addition to size, shape and apertures. These are discussed below, and were formally partitioned into 52 characters with well-defined and conceptualized coded states (Appendix 7.1).

Size. — Pollen size is measured across the diameter, from spine-tip to opposite spine-tip, in the largest dimension unless stated. It varies greatly with the method of measurement, being largest when hydrated with Hoyer's Solution (Anderson 1954) and smallest (as little as two-thirds of its size when hydrated) when desiccated, such as under SEM, or acetolyzed. The acetolysis method (Erdtman 1960) has become a very common protocol for pollen preparation, and for ease of comparison with previous reviews, most of the statements in this paper are based on observations of acetolysed grains. Living pollen is architecturally optimized to accommodate these changes (Wodehouse 1935; Bolick 1991), which reflect even greater differences in volume. Pollen size is considered to vary in an informative way within Compositae, but has been only patchily documented. Across the family as a whole there is a general trend from large to small size although, as with other features, size can be affected by polyploidy or apomixis. The smallest grains are found in Eupatorieae, typically 18–20 μm diameter in Hoyer's solution (King and Robinson 1987) but in *Carterothamnus* as small as 12–16 μm. Some of the largest grains are found in Vernonieae, where they are commonly 38–42 μm and often greater than 60 μm in diameter (Robinson 1999a).

Shape. — Pollen grain shape is described using the ratio of polar to equatorial diameters (P/E; Erdtman 1952). A ratio smaller than unity is described as oblate, around unity as spheroidal, and greater than unity as prolate (we have avoided the use of sub-categories). In Compositae, grains are usually prolate in the more basal branches of the tree and spheroidal in the more derived groups. They are never more than slightly oblate (Stix 1960). Shape may also be described in terms of polar and equatorial view: in polar view grains are usually round or sub-triangular; in equatorial view they may be elliptic (oblate or prolate grains) or round (spheroidal grains). In addition, prolate grains may have blunt or protruding ("lemon-shaped") ends.

Apertures. — Aperture arrangements, also known as "pollen classes" (Faegri and Iversen 1989), vary informatively at higher taxonomic levels. Compositae grains almost always have three equatorial, compound apertures (pores; i.e., they are tri-zono-colporate), formed in pairs at six points of the tetrad during development (following Fischer's [1890] rule). Exceptions include the tricolpate grains reported in some species of *Ainsliaea* and *Hecastocleis* (Tellería and Katinas 2005). Our observations of *Hecastocleis*, as well as the drawing of Wodehouse (1929b), also suggest abnormal "exploded" apertures with no sign of an endoaperture may be common, but not universal (see Fig. 7.11B below). Pororate grains have been reported in Old World Vernonieae and *Adenanthemum* has been described as hexa-pantocolporate (Nordenstam 1976). A few aberrant taxa have tetra-colporate grains (e.g., *Calendula*) or more bizarre arrangements (*Stevia*; King and Robinson 1967). Ectoapertures (colpi) cut through the ectexine to the foot layer. Both the width and shape of the ectoaperture can be informative, particularly whether the ends are obtuse or acute. Occasionally (e.g., *Perezia*) the colpi are syncolpate (united at the poles). Endoapertures (ora) cut through the endexine and are usually lalongate (longer in equatorial than polar plane) but may be circular, square or lolongate. Occasionally (in some Cardueae) the ora are lengthened and fused into a single, continuous equatorial aperture, or endocingulum. When colpi and ora overlap at the foot layer, they sometimes form a distinct mesoaperture (Dimon 1971a, b; Tormo and Ubera 1990a).

Exine structure. — Compositae pollen grains are characterized by a thick, elaborate, multi-layered exine, divided into ectexine and endexine (Stix 1960; Skvarla and Larson 1965; Skvarla et al. 1977; Blackmore 1984; Blackmore et al. 2007). Here, discussion of ectexine stratification is limited to those characters that vary informatively in Compositae. The ectexine is divided into tectum, infratectum and cavea (if present). The tectum (outermost layer) is usually microperforate but in the basally-branching groups and outgroups it is generally imperforate, suggesting this is the plesiomorphic state for the family. In more derived groups, the tectal perforations are more pronounced and regular, becoming microreticulate. Usually the tectum covers the entire surface of the grain but in some lophate grains (e.g., many Vernonieae, *Tragopogon*) it is lost from the centres of the lacunae and sometimes from the sides of the lophae. In some species of *Distephanus* the tectum is restricted to the lacunae.

The infratectum is usually a complex, multilayered structure but may be reduced to a single layer. We found the relative thickness of inner and outer layers of the infratectum to be informative. The two layers may be distinct or indistinct, firmly-attached or free from one another. The infratectum may be columellate, spongy or granular, although there is a continuum between these states such that they are not always easy to categorise. The layers may be separated by a simple or fragmented internal tectum, which appears to be formed by branches of the columellae fusing into a contiguous layer. The columellae of the inner infratectum are highly variable in thickness and branching structure, from un-branched and more or less cylindrical to sausage-like, bifurcating (distally bifurcating), baobab- or broccoli-like (distally strongly ramified) or reticulate (branching throughout). In *Catananche* the columellae have distinctively swollen bases. Columellae may be evenly-distributed or aggregated beneath the spines, where they may group in a ring forming a spine-channel. Inside the spines there may be hanging columellae (e.g., *Didelta*; Wortley et al. 2008), columellae attached at base and top, columellae attached at the base only, or none. The elements of the infratectum may or may not contain internal foramina.

The cavea (plural caveae, adjective caveate; discussed by Blackmore et al. 1984) is a space between exine layers above the foot layer. The term acaveate is used to describe grains without a cavea (Blackmore et al. 1984). In the primexine stage of development this region is filled with material that may have a role in expansion and later it may be used for storage of pollenkitt or lipids (Rowley and El-Ghazaly 1992) or to provide buoyancy in anemophilous pollen (Harrington and Metzger 1963). Compositae grains range from fully-caveate (no columellae spanning the cavea; a condition limited to Asteroideae and most commonly seen in anemophilous taxa such as *Ambrosia*, where the cavea is an active, inflated air-space), through having a few columellae spanning the cavea (e.g., *Centaurea scabiosa* L.; Blackmore et al. 1984), to fully columellate. Interpretation of how much space constitutes a cavea is a confusing aspect of Compositae palynology; the cavea is not a simple presence/absence character.

Beneath the ectexine, cavea and foot layer (the lower part of the ectexine) is the endexine, which may vary in thickness relative to the foot layer, for example, between tribes Heliantheae and Anthemideae (Skvarla and Larson 1965).

Surface sculpture. — The sculpture elements seen in Compositae pollen grains may be divided into micro-ornaments (features smaller than 1 µm, for which SEM study is needed, such as those seen in *Gerbera*) and macro-ornaments (features greater than 1 µm, which can be seen under LM, as in most Asteroideae and many genera besides). This terminology is consistent with Punt et al. (1994), but modified from Erdtman (1952) who distinguished between spines (greater than 3 µm long) and spinules (less than 3 µm long). Thus under LM, pollen grains may be psilate (lacking macro-ornamentation) or echinate (having macro-ornamentation). At the same time they may be lophate (with the outer exine forming a pattern of ridges and depressions, as in many Cichorieae and Arctotideae) or non-lophate. Intermediate, sub-lophate grains have spines arranged in a lophate pattern although no visible ridges are present. This separation of concepts contrasts with traditional pollen sculpture types—psilate, echinate, psilolophate and echinolophate (Wodehouse 1935; Punt et al. 1994)—but we believe it allows for better representation of the likely multiple origins of both spines and lophae in Compositae pollen.

Spines can vary in shape, height, diameter, number, density and evenness of distribution; this variation is usually informative. They may also be solid or contain perforations, have a distinctly swollen base or emerge smoothly or abruptly from the surface. In addition, they may be connected by a raised tectum. The patterning of the simpler lophate types of pollen tends to be repeated across the tree, since there are a limited number of possible arrangements for ridges (lophae) and depressions (lacunae). Lacunae vary in size and shape and can be described and quantified according to their location: abporal, equatorial, interporal, paraporal, poral or polar (see Fig. 7.4). The number of abporal lacunae derived from each ectoaperture is especially characteristic.

In terms of micro-ornamentation, grains may be psilate (truly smooth, without even micro-ornamentation) or scabrate (with spinules smaller than 1 µm). Truly smooth grains are not found in Compositae, where psilate macro-ornamentation is therefore always equivalent to scabrate micro-ornamentation. Like spines, scabrae may vary in shape. The pollen surface between the scabrae may appear smooth, reticulate, striate or areolate.

RESULTS

Evolution of pollen morphology based on the Compositae supertree

Tribal descriptions are presented in Appendix 7.3. At a high hierarchical level, taking tribes as terminals, only 15 characters (29%) fail to be informative on the supertree. This is either because they do not vary at all, or are so homoplastic as to make interpretation of evolution entirely equivocal. The uninformative characters include shape in polar view, aperture number, ectoaperture separation, endoaperture shape, tectum perforation, and lacunae size and shape. In contrast, 25 characters (almost 50%) vary on the supertree in a way that is potentially informative or interesting at the inter-tribal level. Many of these characters show states that re-occur or reverse in different groups upon the tree and are therefore of little use from a classificatory point of view; others, however, display a high degree of congruence with the topology and are therefore potentially useful for defining and diagnosing groups. These will now be discussed in more detail.

The plesiomorphic shape for Compositae pollen grains is probably prolate, and a shift to spheroidal or slightly oblate grains occurred somewhere between the derivation of the *Stifftia*-*Stenopadus* clade and Hecastocleideae (Fig. 7.5). This evolutionary pattern can be interpreted as analogous to Van Campo's (1966, 1976) theory of breviaxy—a phylogenetically informative series of pollen forms ranging from subspheroidal to oblate with concurrent changes in aperture type.

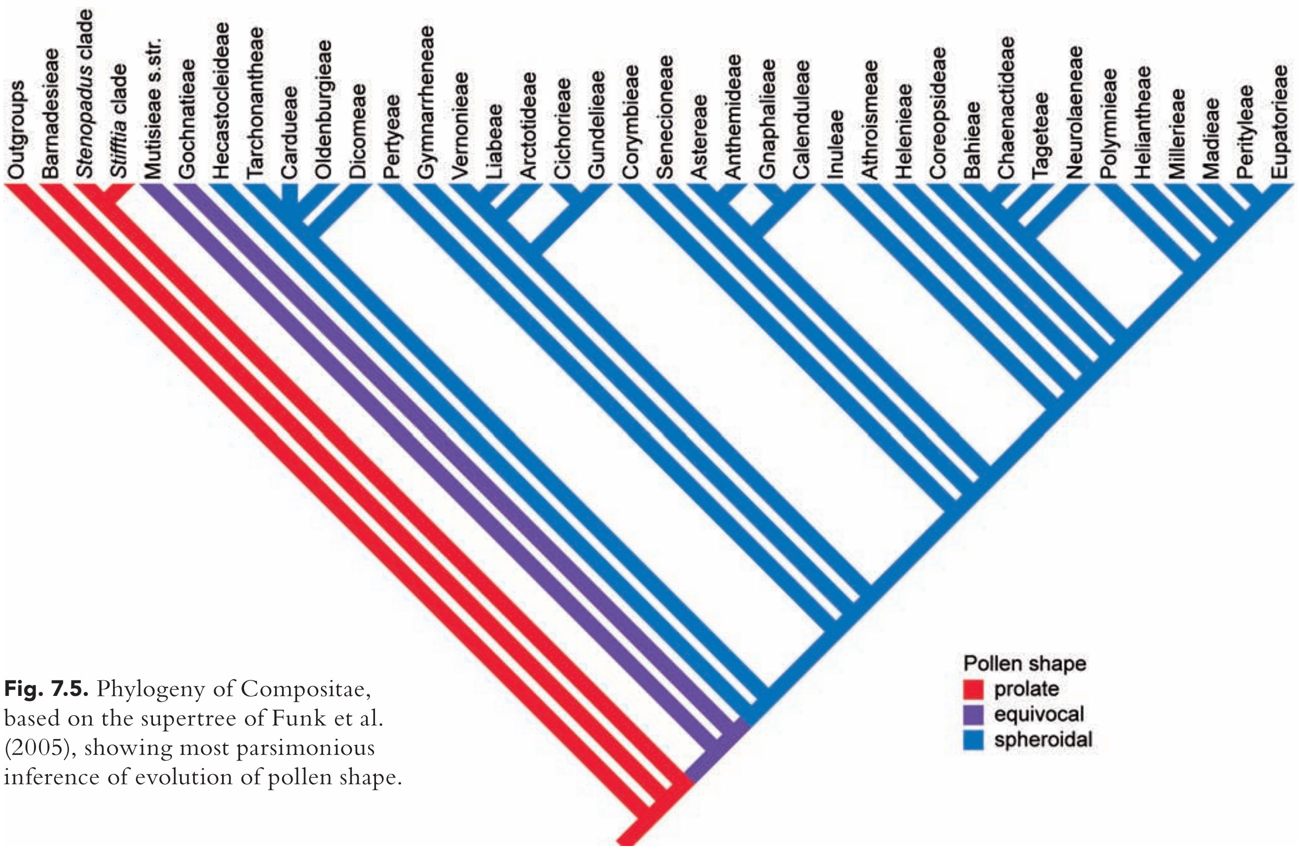


Fig. 7.5. Phylogeny of Compositae, based on the supertree of Funk et al. (2005), showing most parsimonious inference of evolution of pollen shape.

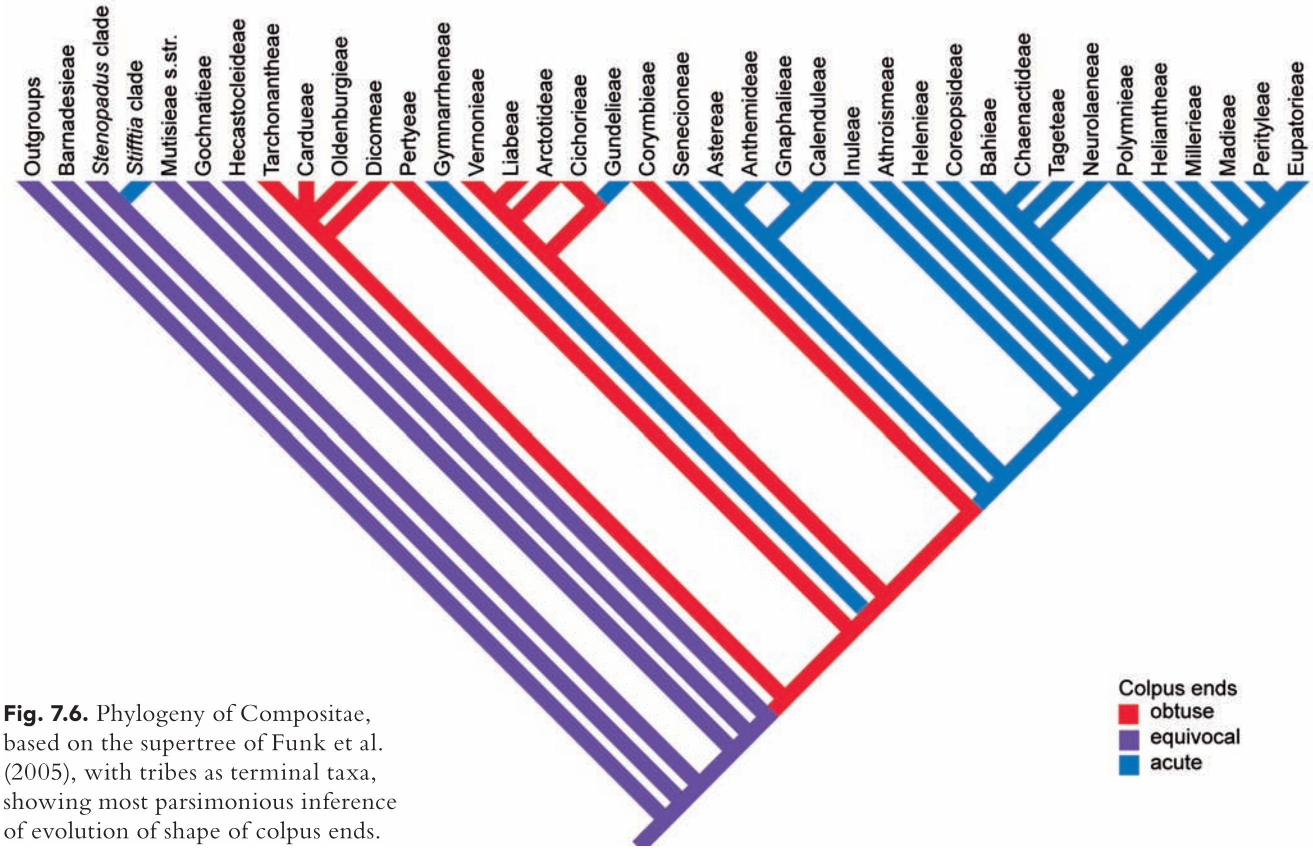


Fig. 7.6. Phylogeny of Compositae, based on the supertree of Funk et al. (2005), with tribes as terminal taxa, showing most parsimonious inference of evolution of shape of colpus ends.

The plesiomorphic state for colpus ends in Compositae is probably obtuse; acute ends provide a synapomorphy for subfamily Asteroideae, with independent derivations autapomorphic for Gundelieae, Gymnarrheneae and the *Stifftia* clade (Fig. 7.6).

Internal foramina are absent from all basal branches of the supertree and define a clade within Asteroideae. However, it is uncertain whether the precise origin occurred at the base of this subfamily or on one of the internal branches between Corymbieae and Senecioneae, or Senecioneae and the rest of the subfamily (these possibilities are all equally parsimonious). In addition, internal foramina are inferred to have been derived independently in some members of the clade containing Cardueae, Oldenburgieae and Tarchonantheae (although exactly where remains equivocal due to the presence of taxa with and without internal foramina in Cardueae) and secondarily lost in Anthemideae (Fig. 7.7).

The aggregation of columellae under the spines is a synapomorphy supporting subfamily Cichorioideae, suggesting a single transition to aggregation during the history of this group (in most Compositae and outgroups they are evenly distributed across the grain; Fig. 7.8), and a subsequent reversal to even distribution in the small tribe Moquinieae.

The development of a full cavea (i.e., without any columellae spanning the space above the foot layer), from the plesiomorphic acaveate state, is most likely to have occurred along the branch leading to the clade comprising Corymbieae and Asteroideae; thus it provides a synapomorphy linking these two groups. However, the state in Cichorioideae, Astereae and Anthemideae is equivocal and there has been a reversal (the reappearance of spanning columellae) in Neurolaeneae (Fig. 7.9).

The psilate nature of the pollen of most genera in the earliest-branching groups of Compositae and outgroups suggests that this is the plesiomorphic state of macroornamentation. Echinate pollen has evolved at least three times—in the *Stifftia* clade, in Oldenburgieae, and on the branch between Pertyeae and all higher Compositae. The state at the base of the *Stenopadus* clade and Cardueae is equivocal, both psilate and echinate grains being found in these groups (Fig. 7.10). In addition, all lophate grains (apart from an independent derivation in Barnadesieae) occur in a single subfamily, Cichorioideae, and will be discussed in more detail with reference to tribe Cichorieae. At the subfamilial level, reversals within groups render character optimization patterns entirely ambiguous when viewed on a phylogeny. Here, it is sufficient to say that not all members of Cichorioideae are lophate, suggesting

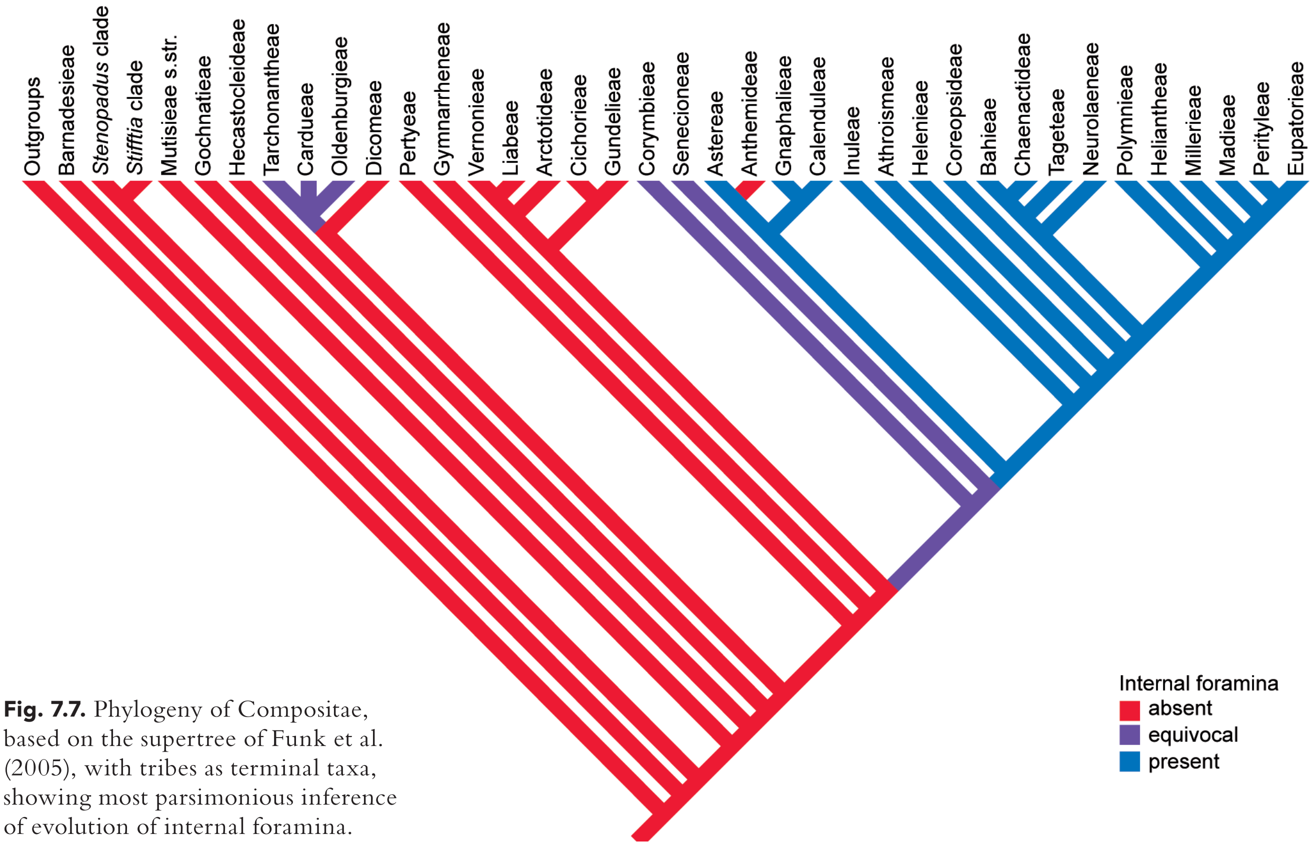


Fig. 7.7. Phylogeny of Compositae, based on the supertree of Funk et al. (2005), with tribes as terminal taxa, showing most parsimonious inference of evolution of internal foramina.

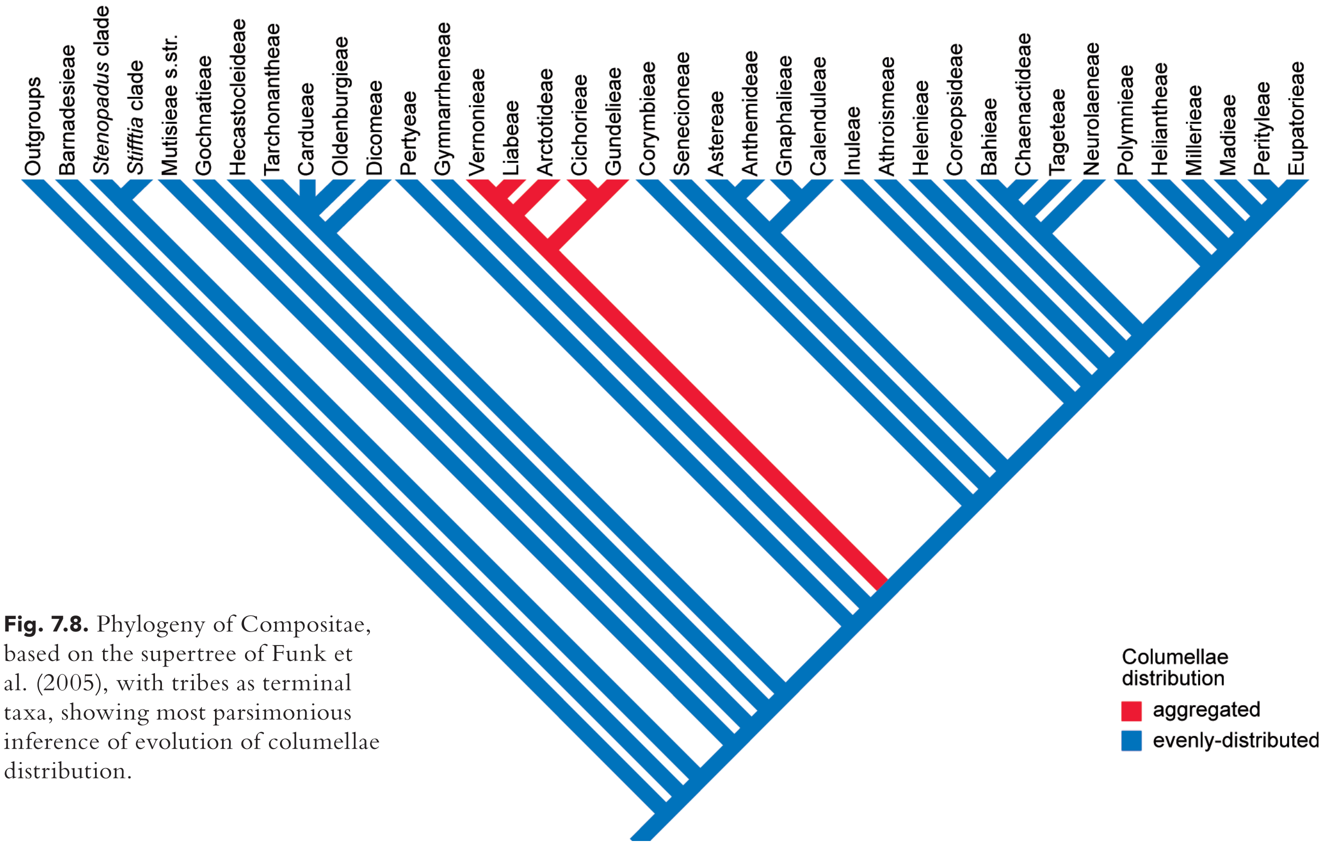


Fig. 7.8. Phylogeny of Compositae, based on the supertree of Funk et al. (2005), with tribes as terminal taxa, showing most parsimonious inference of evolution of columellae distribution.

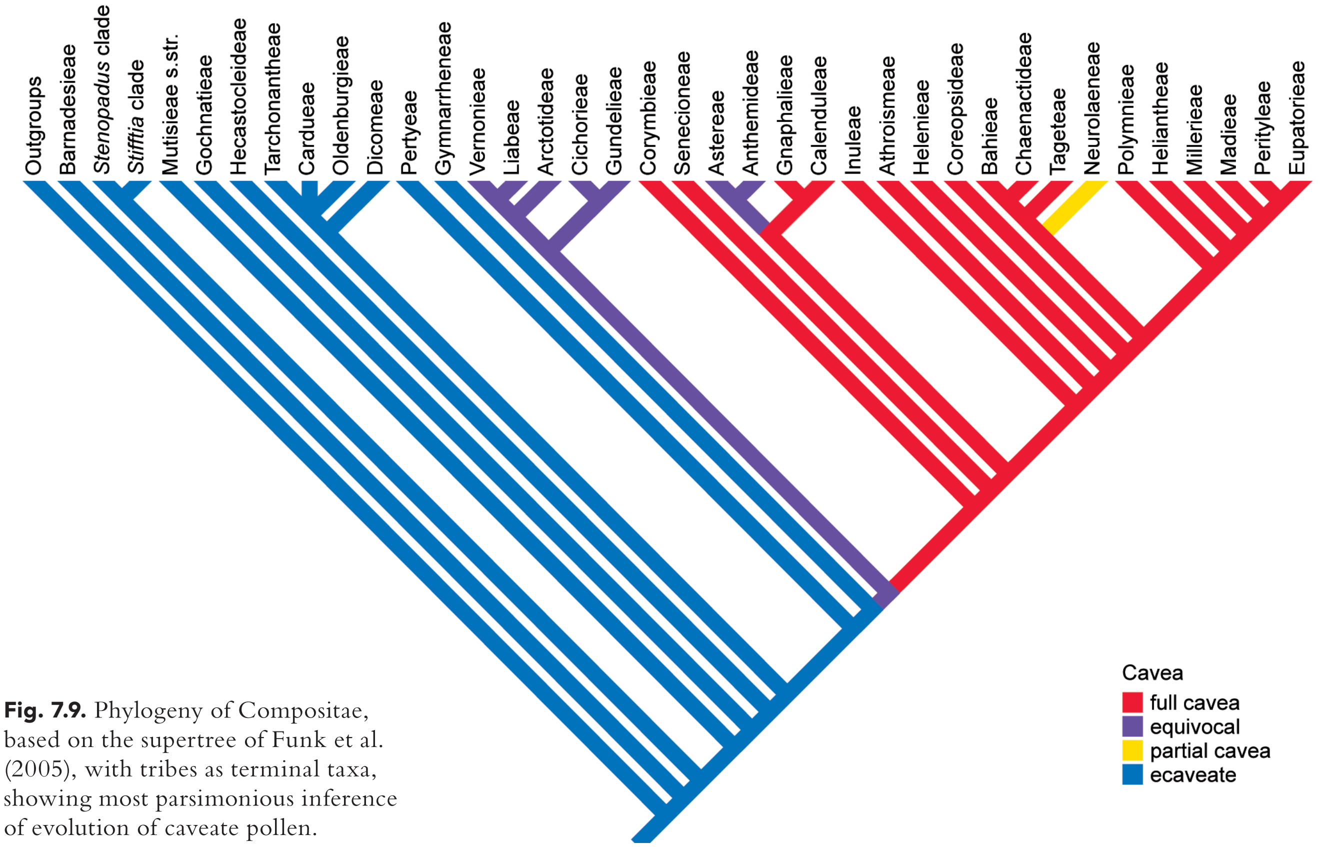


Fig. 7.9. Phylogeny of Compositae, based on the supertree of Funk et al. (2005), with tribes as terminal taxa, showing most parsimonious inference of evolution of caveate pollen.

that this character has evolved many times (supporting the conclusions of Blackmore, 1986) but that the *tendency* to develop lophae may have evolved only once. Reversals to the non-lophate state are also very common, even within genera—*Eirmocephala* (Vernonieae) comprises two sister-species, of which one has lophate pollen and the other has not.

From this selected set of examples we conclude that many of the larger-scale, structural features of pollen morphology (columellae distribution, cavea, macro-ornamentation and a number of features of the spines) have evolved in a way that is broadly coincident with phylogeny at the tribal level. These characters coincide with those that have been used to define large-scale pollen types (Skvarla and Larson 1965; Skvarla and Turner 1966; Skvarla et al. 1977).

An alternative way to investigate pollen evolution is to take a taxon- rather than character-based approach (e.g., Fig. 7.11A–D). Figure 7.11B confirms that the pollen of basally-branching Compositae is very similar to that of the outgroups Goodeniaceae and Calyceraceae (as previously reported by Patel, 1976; Avetisian 1980; Gustafsson

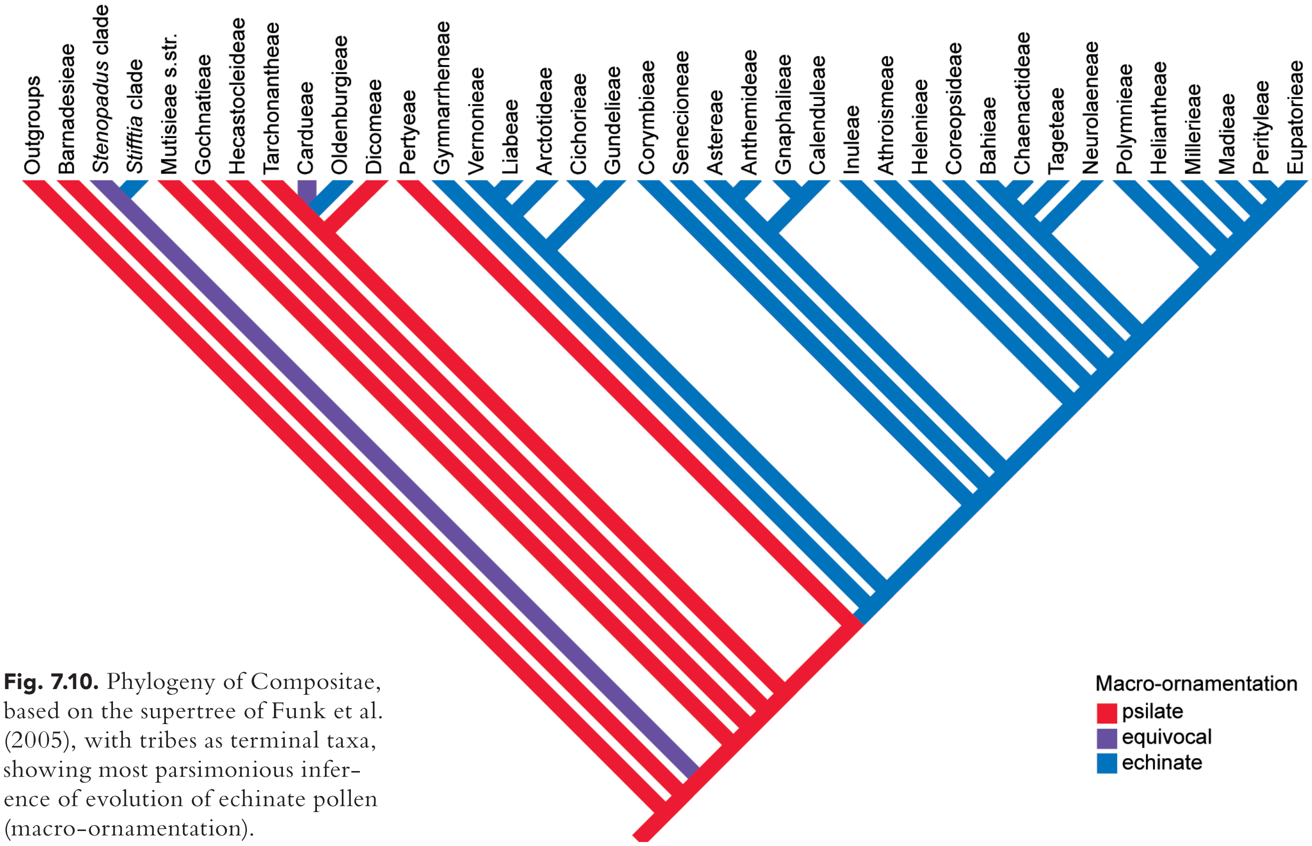
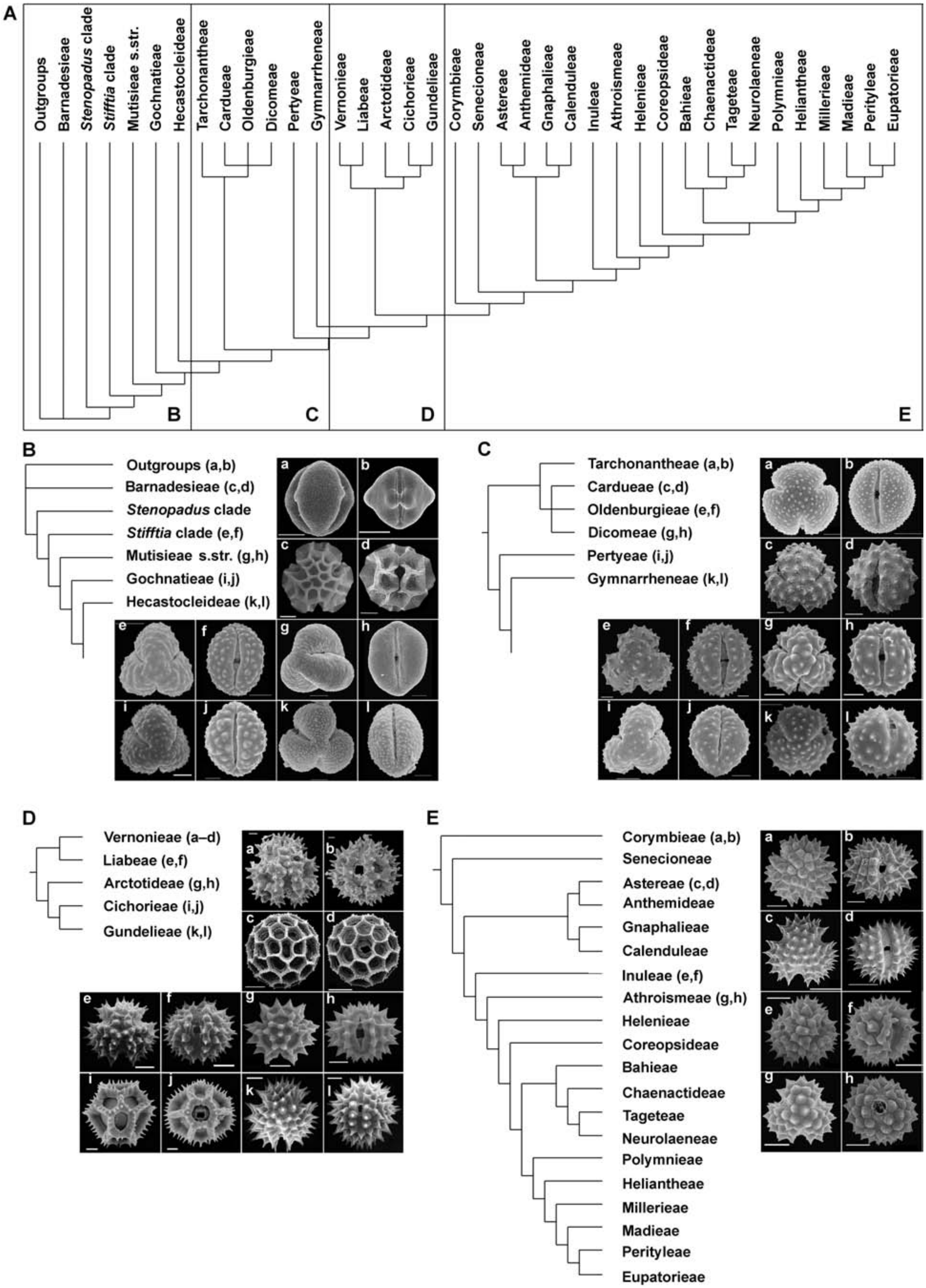


Fig. 7.10. Phylogeny of Compositae, based on the supertree of Funk et al. (2005), with tribes as terminal taxa, showing most parsimonious inference of evolution of echinate pollen (macro-ornamentation).

Fig. 7.11. Variation in pollen morphology across the Compositae supertree. **A** supertree with tribes as terminal taxa, showing compartments as in B–E. **B** Outgroups and basally-branching tribes of Compositae: outgroups, **a** *Goodenia ovata* Sm., **b** *Calycera leucanthema* (Poepp. ex Less.) Kuntze; Barnadesieae, **c** *Barnadesia pycnophylla* Muschl., **d** *B. arborea* Kunth; *Stifftia* clade, **e, f** *Hyaloseris salicifolia* Hieron.; Mutisieae, **g, h** *Gerbera crocea* Kuntze; Gochnatieae, **i** *Cnicothamnus lorentzii* Griseb., **j** *Richterago caulescens* Roque; Hecastocleideae, **k, l** *Hecastocleis shockleyi* A. Gray. **C** Carduoideae, Pertyeae and Gymnarrheneae: Tarchonantheae, **a, b** *Tarchonanthus camphoratus* L.; Cardueae, **c, d** *Alfredia cernua* Cass.; Oldenburgieae, **e, f** *Oldenburgia paradoxa* Less.; Dicomeae, **g** *Dicoma zeyheri* Sond., **h** *D. sessiliflora* Harv.; Pertyeae, **i, j** *Ainsliaea acerifolia* Sch.Bip.; Gymnarrheneae, **k, l** *Gymnarrhena micrantha* Desf. **D** Cichorioideae: Vernonieae, **a, b** *Decaneuropsis blanda* (DC.) H. Rob. & Skvarla, **c, d** *Pacourina edulis* Aubl.; Liabeae, **e, f** *Paranephelius uniflorus* Poepp. & Endl.; Arctotideae, **g, h** *Berkheya spinosissima* Willd.; Cichorieae, **i, j** *Acanthocephalus benthamianus* Regel; Gundelieae, **k, l** *Gundelia tournefortii* L. **E** Corymbieae and Asteroideae: Corymbieae, **a, b** *Corymbium africanum* L.; Astereae, **c, d** *Amellus asteroides* Druce; Inuleae, **e, f** *Cratystylis conocephala* S. Moore; Athroismeae, **g, h** *Athroisma psylloides* (Oliv.) Mattf. All scale bars 10 µm. [Photographs: 7.11Bb, 7.11Bd and 7.11Bi: courtesy Zaiming Zhao and Robert Jansen; all others by the authors.]


A
Outgroups
Barnadesieae
Stenopadus clade
Stifftia clade
Mutisieae s.str.
Gochnatieae
Hecastocleideae
Tarchonantheae
Cardueae
Oldenburgieae
Dicomeae
Pertyeae
Gymnarrheneae
Vernonieae
Liabeae
Arctotideae
Cichorieae
Gundelieae
Corymbieae
Senecioneae
Astereae
Anthemideae
Gnaphalieae
Calenduleae
Inuleae
Athroismeae
Helenieae
Coreopsideae
Bahieae
Chaenactideae
Tageteae
Neurolaeneae
Polymnieae
Heliantheae
Millerieae
Madieae
Perityleae
Eupatorieae
B
C
D
E
B
Outgroups (a,b)
Barnadesieae (c,d)
Stenopadus clade
Stifftia clade (e,f)
Mutisieae s.str. (g,h)
Gochnatieae (i,j)
Hecastocleideae (k,l)
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Tarchonantheae (a,b)
Cardueae (c,d)
Oldenburgieae (e,f)
Dicomeae (g,h)
Pertyeae (i,j)
Gymnarrheneae (k,l)
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D
Vernonieae (a–d)
Liabeae (e,f)
Arctotideae (g,h)
Cichorieae (i,j)
Gundelieae (k,l)
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Corymbieae (a,b)
Senecioneae
Astereae (c,d)
Anthemideae
Gnaphalieae
Calenduleae
Inuleae (e,f)
Athroismeae (g,h)
Helenieae
Coreopsideae
Bahieae
Chaenactideae
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et al. 1997; Hansen 1997; DeVore et al. 2007). For example, the surface of Mutisieae s.str. pollen is very like that of Goodeniaceae, but differs in exine ultrastructural characters. The pollen of these basally-branching groups is usually psilate at the macroscopic level (scabrate micro-ornamentation), and the lophate pollen of *Barnadesia* is very highly modified compared to the non-lophate taxa with which it is most closely-related. Apart from a few exceptions in Mutisieae, a general transition to echinate pollen occurs further up in this grade (Fig. 7.11C). Still further up the supertree, Cichorioideae (Fig. 7.11D) is a group in which the precise patterns of lophae and lacunae, as well as exine characters, can be highly informative for distinguishing taxa. In this clade, only Liabeae and Gundelieae completely lack lophae. The most derived part of the tree (Fig. 7.11E) generally shows much less variation in pollen than the preceding branches, with fixed characteristics including cavea, internal foramina and oblate-spheroidal, echinate grains. Two key clades in this part of the tree, Gymnarrheneae-Asteroideae and Corymbieae-Asteroideae are each defined by several character-state changes. In contrast, and as we have seen, the earlier-branching tribes have more variable characters, and optimization at this level tends to be more equivocal. Here, pollen characters may be more useful to define groups at lower hierarchical levels, such as within tribes, since they are each more closely equivalent in the hierarchy to the whole of Asteroideae (having evolved for a more comparable amount of time). For instance, Cardueae shows a huge diversity of pollen characters that are thought to differ in ways that relate to both evolutionary history and functional adaptation, and are in great need of further study (e.g., Vilatersana et al. 2001; A. Susanna, pers. comm.; see below).

Evolution of pollen morphology in exemplar tribes

A glance at the character matrix reveals that the pollen of some tribes is much more variable than others. Variability is greatest in Anthemideae, Arctotideae, Cardueae, Cichorieae, Inuleae and Vernonieae. We selected these six tribes for a more detailed analysis using genera as terminals; the results are discussed below.

Cardueae. — Variation in pollen morphology in Cardueae is perhaps greater than in any other tribe of Compositae. This variation is the subject of ongoing research, but has so far proven hard to interpret (e.g., Tormo and Ubera 1990b, 1995; Petit et al. 1996). Nonetheless, certain characters can be identified which

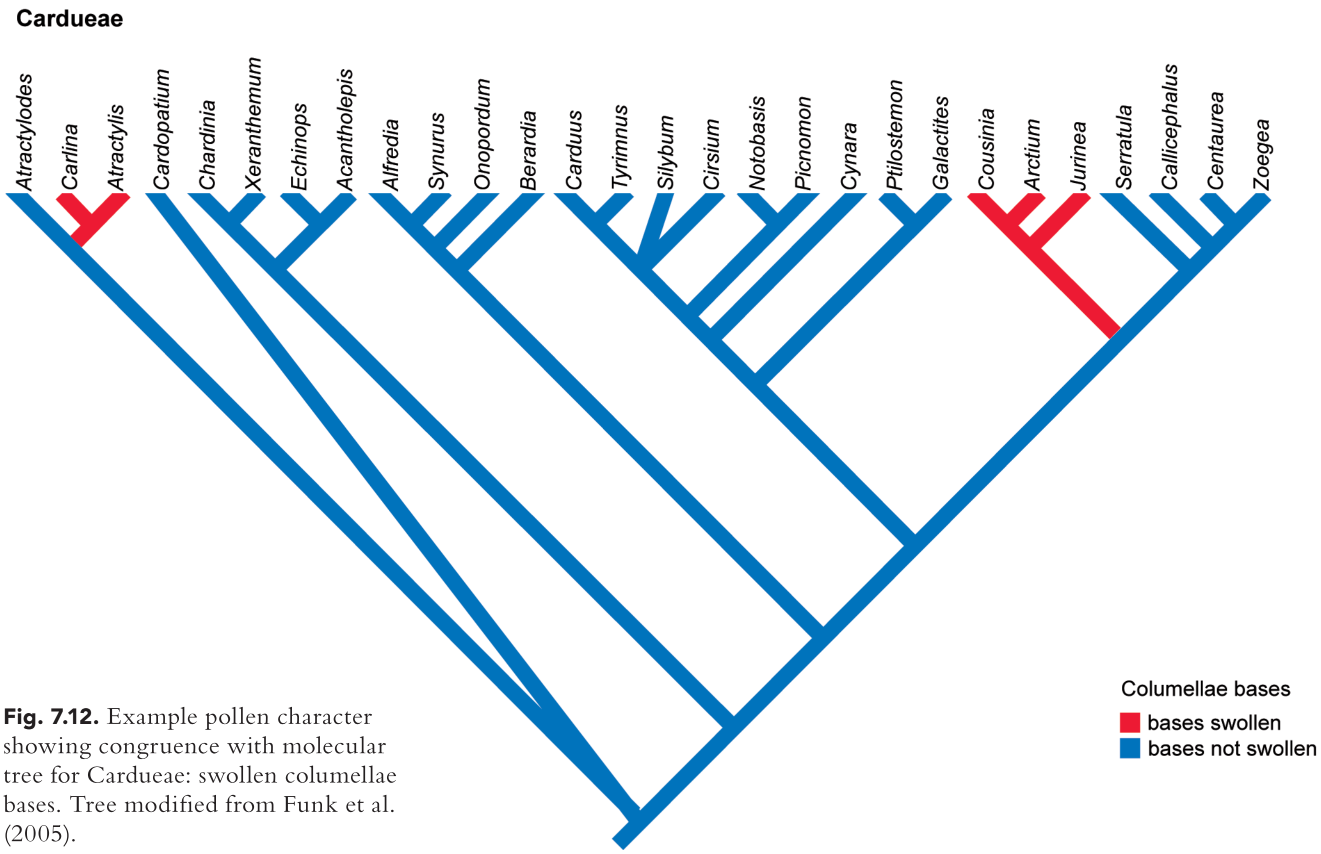

Fig. 7.12. Example pollen character showing congruence with molecular tree for Cardueae: swollen columellae bases. Tree modified from Funk et al. (2005).

define groups within the tribe. These include spine size: the group is characterized by medium-sized (2–5 µm) spines, but smaller spines (1–2 µm) define a clade from *Chardinia* to *Acantholepis.* Variation in surface structures has been linked to flower structure and pollen presentation mechanism in subtribe Centaureinae (A. Susanna, pers. comm.). Swollen-based infratectal columellae occur independently in two clades, *Cousinia-Jurinea* and *Carlina-Atractylis* (Fig. 7.12), and a thickening of the endexine occurs on the branch leading to the large clade containing *Carduus* and *Zoegea*. However, these patterns are complex: there are secondary reversals to an endexine the same thickness as the foot layer in *Carduus-Tyrimnus-Silybum*, *Notobasis*, *Galactites*, *Cousinia* and *Arctium*; *Zoegea* has an endexine thinner than the foot layer. In fact, *Cousinia* and *Zoegea* have a distinctively different exine structure with indistinct layers not separated by an internal tectum (seen in Qaid 1990; Martín Villodre and Garcia-Jacas 2000).

Arctotideae. — In contrast to Cardueae, pollen morphological characters in Arctotideae appear to vary in a systematically interesting way (Fig. 7.13). This is emphasized by the fact that a number of characters share the same distribution on the tree, particularly those defining the clade *Gazania-Gorteria-Hirpicium* (Wortley et al. 2008). These include psilate grains with a reticulate surface, broad colpi and a single-layered infratectum. Other characters, such as obtuse colpi ends and small spines clumped in a lophate pattern (further modified to become sublophate in *Didelta*), support the grouping of *Berkheya* and *Didelta*. Interestingly, the two problem genera (Funk et al. 2004) *Eremothamnus* and *Hoplophyllum* each display a large number of autapomorphies, i.e., differ significantly from the rest of the tribe.

Cichorieae. — Pollen characters can also be found to support and diagnose groups at a number of different levels in Cichorieae (Fig. 7.14). At the highest level, the first branch comprising *Scolymus* and *Catananche* (and *Hymenonema* and *Rothmaleria*, not shown) is characterized by certain exine characters including thick columellae beneath the spines and few internal tecta (Blackmore 1981). Amazingly, this group had not previously been recognized as a clade since the 1830s (Boissier 1839), until the first molecular analysis by Whitton et al. (1995). The next-branching clade in the molecular tree, *Scorzonera* and *Tragopogon* (the supertree representatives of Scorzonerinae), is supported by a large number of characters, including aperture and exine characters. The outer

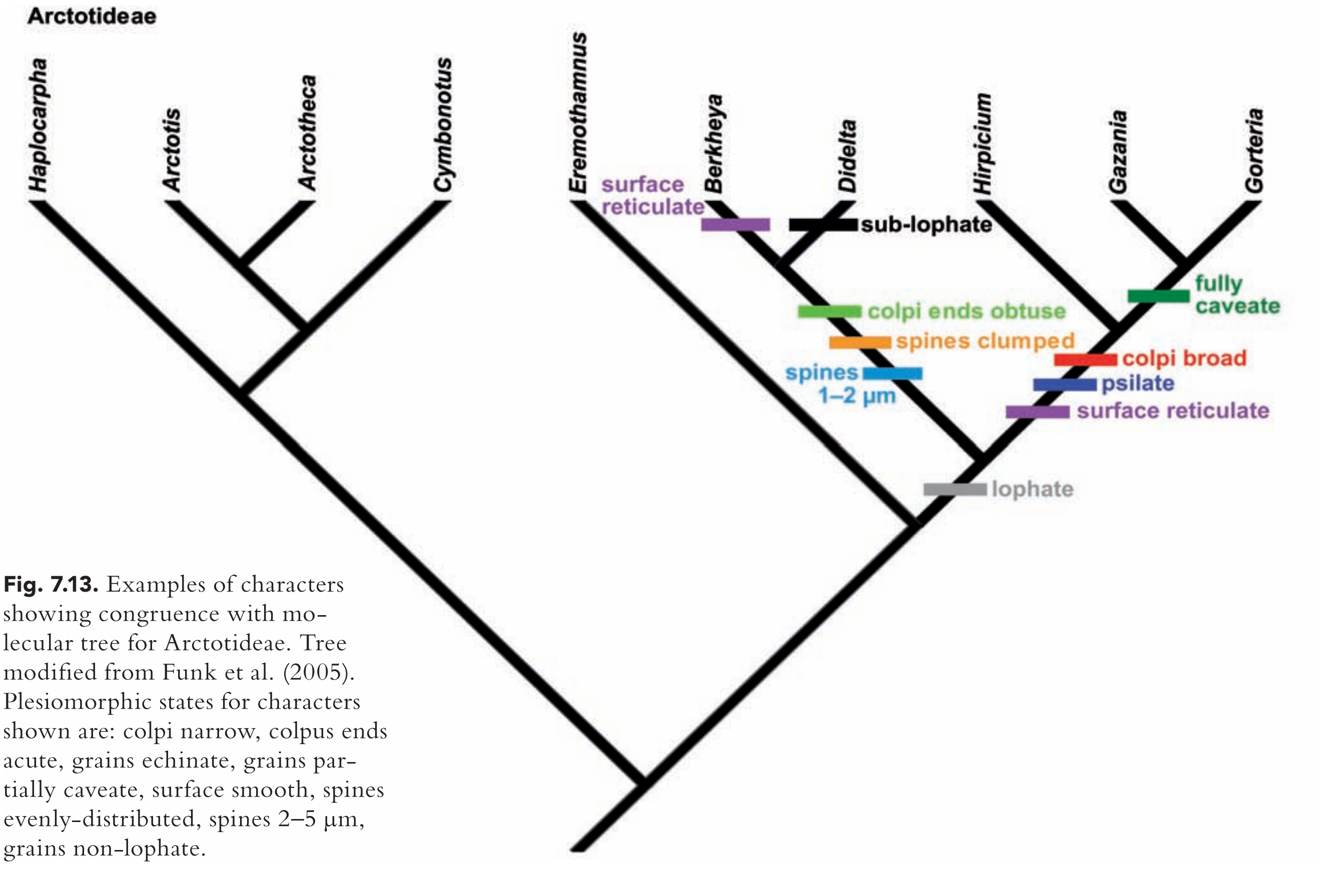

Fig. 7.13. Examples of characters showing congruence with molecular tree for Arctotideae. Tree modified from Funk et al. (2005). Plesiomorphic states for characters shown are: colpi narrow, colpus ends acute, grains echinate, grains partially caveate, surface smooth, spines evenly-distributed, spines 2–5 µm, grains non-lophate.

exine of Scorzonerinae is columellate (most Cichorieae have a spongy, highly branched outer exine), and has only a single-layered (rather than fragmented) internal tectum. However this group is also very varied—in fact all its genera except *Geropogon* can be distinguished by their pollen grains alone, and these are sufficiently distinct to pick out from Miocene and Pliocene deposits (Blackmore et al. 1986). The remainder of Cichorieae is defined by a spongy outer exine and, within this, the relationship identified by Whitton et al. (1995) between *Dendroseris* and *Sonchus* is lent further support by the fact that both have additional polar lacunae in most species. Lacunae characters are particularly useful at defining small groups within this tribe.

Vernonieae. — Vernonieae provide another example where a large number of pollen characters are congruent with the relationships presented in the supertree and provide synapomorphies for groups (Fig. 7.15). Several characters, such as round rather than sub-triangular grains in polar view, define a core clade from *Muschleria* upwards; others, such as circular ora and an endexine the same thickness as the foot layer (rather than thicker), define the clade from *Muschleria* to *Parapolydora*; and still others, the clade within this from *Polydora* to *Parapolydora* (irregularly sized, shaped and arranged lacunae). However there are often reversals from the synapomorphic state and *Parapolydora*, *Stokesia* (e.g., Bolick 1978; Robinson 1999b) and *Hesperomannia* (e.g., Marticorena and Parra 1975; Zhao 1999; Zhao et al. 2006; Wortley et al. 2007) all display a large number of autapomorphies relative to the rest of the tribe. The *Polydora-Parapolydora* clade contains a concentration of pororate grains (Robinson 1999c), which are also independently derived in *Vernoniastrum* (Robinson 1999c) and *Elephantopus* (Bolick 1978; Skvarla et al. 2005) but not known elsewhere in Compositae. There is a general trend towards increasing spine number and density with evolution through this tribe, and also to a less even (more clumped) distribution of spines.

Inuleae. — In Inuleae, despite a wide range of variability in pollen characters, very few characters support or define groups; most are instead autapomorphic for various genera. A very large number of characters (prolate, sub-triangular grains, three infratectum layers, granular internal tectum, thicker, reticulate inner columellae layer and internal foramina) separate *Cratystylis* from the rest of the tribe. *Cratystylis*, placed near Inuleae by Anderberg et al. (1992), has long been considered a morphological oddity, having unusual rows of stigmatic papillae which fuse near the base and cover nearly the entire surface (Merxmüller et al. 1977); palynological

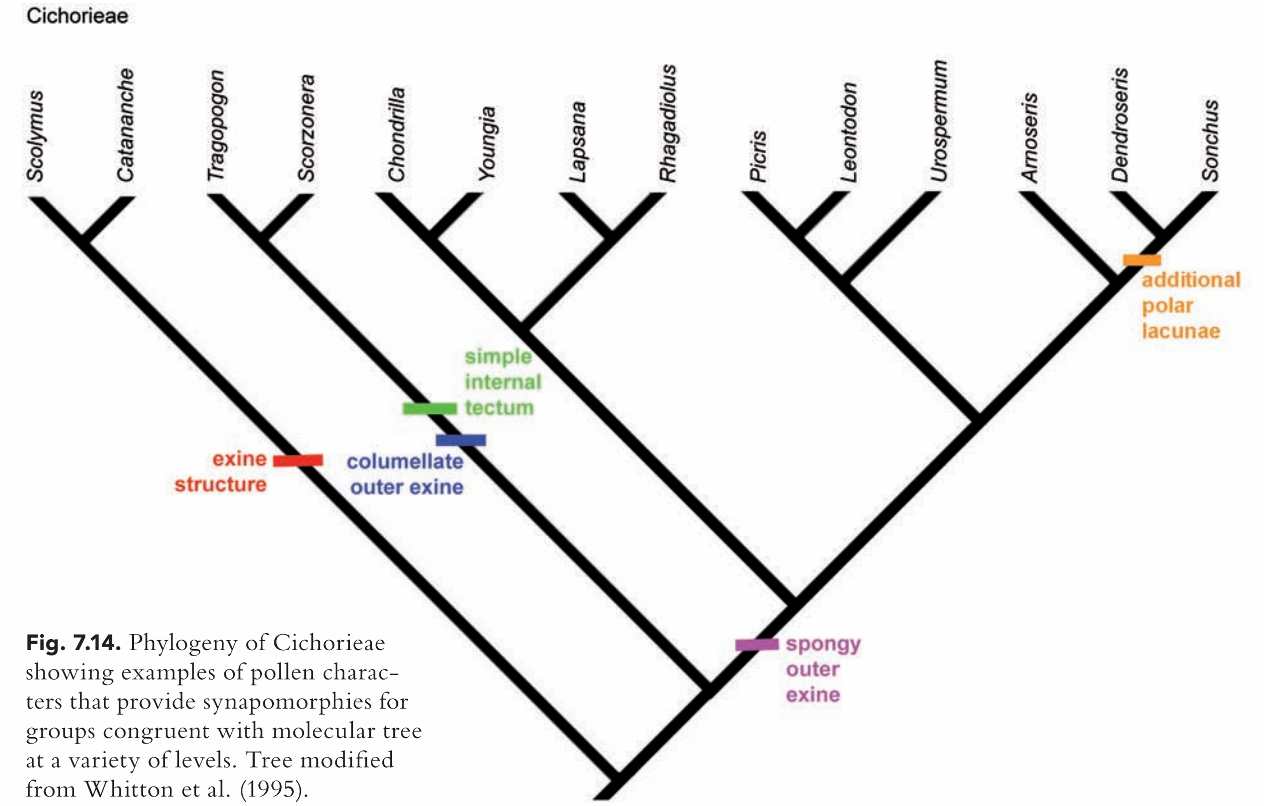

Fig. 7.14. Phylogeny of Cichorieae showing examples of pollen characters that provide synapomorphies for groups congruent with molecular tree at a variety of levels. Tree modified from Whitton et al. (1995).

characters provide further evidence of its status as a “problem genus”. Additional characters (lack of internal tectum, spongy inner infratectum, internal foramina and a deep cavea) confirm the position of *Callilepis* as the first-branching taxon in the tribe. Interestingly this taxon also, like *Cratystylis*, has internal foramina. The interpretation of pollen characters in Inuleae suggests that at infratribal level in Asteroideae the broad features of structure and sculpture that are useful in other subfamilies tend to be fixed as discussed above. However, more subtle, finer characters of exine ultrastructure can become relevant for distinguishing groups. This trend is continued in other Asteroideae tribes: even where there is a reasonable degree of variability, such as in Anthemideae, variable pollen characters tend to be highly homoplastic and fail to provide support for molecular groupings, and any trends that are seen tend to be in subtle features of exine ultrastructure.

DISCUSSION

The use of pollen types

Pollen morphology in Compositae is highly variable and provides a large number of useful characters when viewed in the context of a robust, independently-derived phylogeny such as the supertree (Funk et al. 2005; Funk, pers. comm.). Variability in pollen characters exists within genera, e.g., *Acourtia* (Cabrera and Dieringer 2003), *Chaetanthera* (Parra and Marticorena 1972; Tellería and Katinas 2004), *Gerbera* (Lin et al. 2005), *Munnozia* (Robinson and Marticorena 1986) and *Nassauvia* (Cabrera 1982) and even species, such as *Bidens gardneri* (Felippe and Labouriau 1964), and *Warionia saharae* (Petit et al. 1996).

Fifty years ago, Wagenitz (1955) and Stix (1960) recognized the fundamental importance of describing exine ultrastructure as well as surface ornamentation. However, there has since been a tendency to avoid discussing the

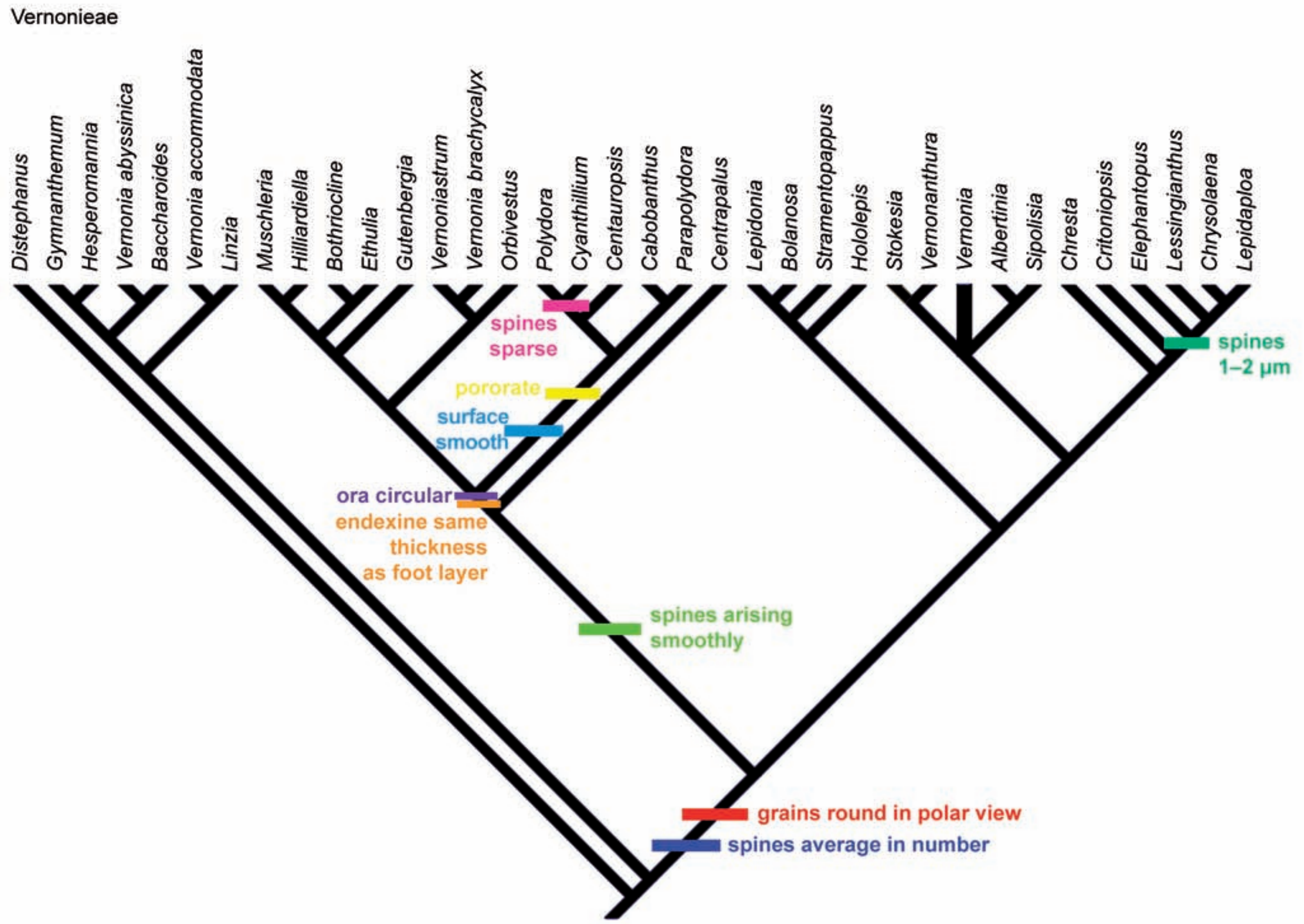

Fig. 7.15. Phylogeny of Vernonieae showing most parsimonious inference of evolution for all pollen characters that change unambiguously on the tree and provide synapomorphies for groups; autapomorphies and ambiguous characters not shown. Tree modified from Funk et al. (2005). Plesiomorphic states for characters shown are: grains sub-triangular in polar view, colporate, ora lalongate, endexine thicker than foot layer, spines few, spines 2–5 µm, spine bases swollen, surface reticulate.

complexities of palynological interpretation and terminology by the use of "pollen types" or "exine types" to compare taxa. This practice developed in two opposing directions, one culminating in the broad pollen types recognized by Skvarla et al. (1977), defined by six key characters (presence/absence of internal foramina, single/multiple-layered internal tectum, highly bifurcating/unbranched supporting columellae, presence/absence of prominent spine-channel by aggregation of columellae under spines, presence/absence of cavea and thickness of columellae); the other defining ever greater numbers of types based on increasingly subtle distinctions, for smaller groups of taxa, while still trying to avoid a description based on individual characters. For example Keeley and Jones (1977) named six pollen types (A–F) within the tribe Vernonieae based on surface morphology; more recently, Dawar et al. (2002) named three pollen types (I, II and III) within a single genus, *Inula*. Pollen types such as these have considerable relevance to the identification of dispersed pollen grains in palaeoecological studies, but in systematic studies of extant taxa they are likely to be applicable only at subtribal level or below.

At the broad scale, as described above, pollen types clearly relate to evolutionary patterns across the supertree (Fig. 7.16), with the same key characters (particularly cavea and internal foramina) being consistently informative. For this reason these characters are also most often utilized in morphological cladistic analyses (e.g., Karis 1993). Of the three major pollen types based on these two characters, most taxa with Helianthoid (caveate and foraminate) exines lie in the upper part of the tree, the Senecioid type tends to define a grade around the middle, and most of the earlier branches of the tree are characterized by acaveate grains. However, the extra criteria defining the Anthemoid type (a thick, long series of basal columellae alternating with internal tecta, a reduced endexine and thick foot layer) mean that many taxa cannot formally be ascribed to it.

The more complex pollen types become, and the more characters they incorporate, the less likely they are to form a meaningful pattern, due to the highly variable and homoplastic nature of most pollen characters at higher hierarchical levels. Thus, the subsidiary types that were later derived from the primary three types of Skvarla et al. (1977; e.g., Arctotoid) fit the tree even less well, and the process of defining minor pollen types within tribes or genera is fraught with difficulty. The logical extension of this is that we are most likely to provide useful information about the evolution of pollen morphology by describing it in the simplest way—using single characters. Even cavea and internal foramina form much more meaningful patterns on the supertree when considered in isolation (Figs. 7.7, 7.9) than when combined into pollen types (Fig. 7.16). With few exceptions (mostly in Cardueae), internal foramina (Fig. 7.7) show a simple pattern of absence/presence, although the exact branch on which the change occurs remains equivocal at present. Cavea (Fig. 7.9) show a very strong pattern whereby they are entirely

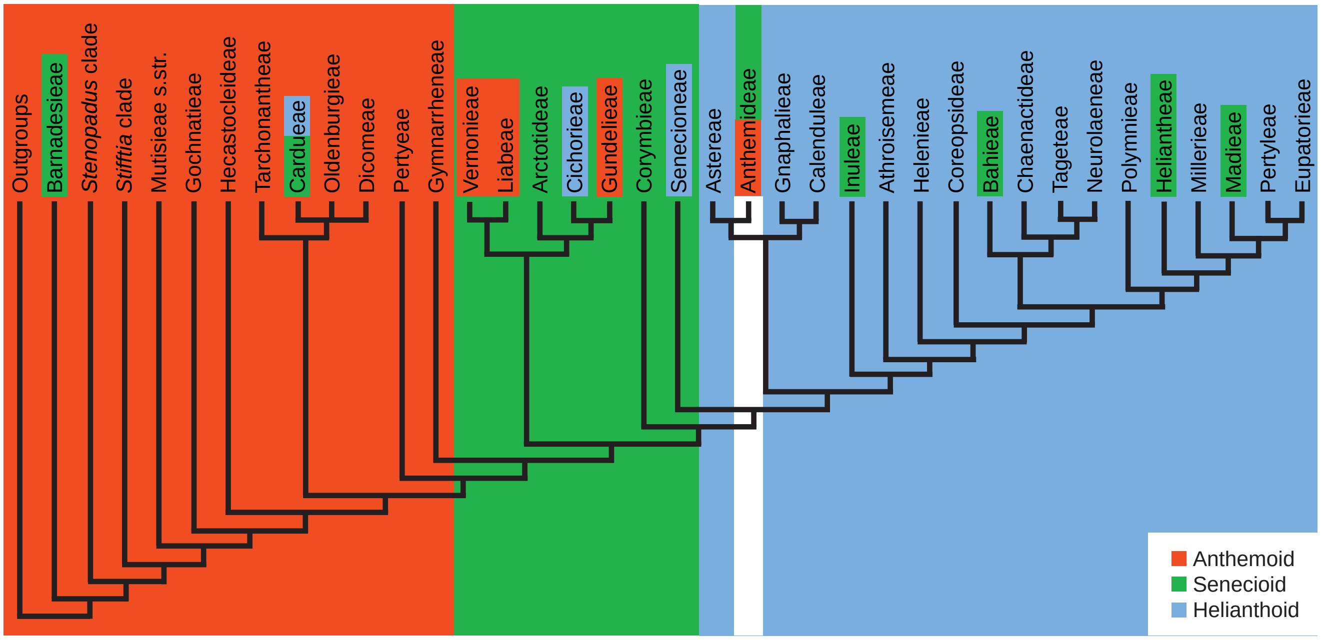

Fig. 7.16. Distribution of pollen types (Skvarla et al. 1977) on supertree of Compositae (modified from Funk et al. 2005). Pollen types here defined as: Anthemoid, acaveate and without internal foramina; Helianthoid, fully or partially caveate with internal foramina; Senecioid, fully or partially caveate without internal foramina.

lacking from the outgroups and basally-branching groups and present through the higher branches of the tree from Corymbieae to Asteroideae, with reversals in some Anthemideae; only Cichorioideae are resolved as equivocal for this character because they have a limited cavea in many taxa; there are also autapomorphic modifications in *Neurolaena*. Thus, the distribution of single characters, once their level of usefulness is known, can be more orderly (less homoplastic) than that of pollen or exine types. Even with the simplest pollen types there are some taxa that contain more than one type and others that do not conform to any type at all.

Repeated patterns

There are a limited number of palynological features on which evolution can impact, and it is therefore unsurprising to find several examples of repeated patterns or trends in pollen evolution across multiple tribes. For example, columellae aggregation defines Cichorioideae (with few reversals), but there are also trends towards aggregation in both Inuleae and Cardueae. In echinate groups there is a strong tendency for spines to become smaller or lost, or to cluster and converge into lophae; and the reduction in spine size is usually coincident with an increase in spine number and therefore density. The reasons behind these trends in pollen morphology are difficult to determine and, although it is tempting to seek functional explanations, these are difficult to prove. Some characters are potentially related to harmomegathy, for which there are many different mechanisms, all of which function successfully. The prolate pollen grains found in basally-branching groups can accommodate volume changes by folding along the colpi; the caveate pollen grains of Asteroideae by expanding or contracting the cavea (even in groups with a partial cavea spanned by columellae these columellae tend to be fine and thread-like, as if they could bend to accommodate changes in cavea size). Caveate grains have been shown to correlate with smaller grain size and a generally thinner exine (Bolick 1991), which may be modifications for wind-dispersal. A transition from entomophily to anemophily has also been linked to morphological changes such as the reduction in spines (e.g., in *Hofmeisteria*; Robinson and King 1977). More complex, specialised adaptations for harmomegathy, which are not fully understood, may be found in lophate and syncolpate-grained taxa. Lophate grains are also considered to be an adaptation for storing pollenkitt on the grain surface (Blackmore 1982) and thus may be involved in pollen-pistil interactions and self incompatibility mechanisms. There is also a high level of variability in pollen morphology in apomictic taxa such as *Taraxacum* (Blackmore 1976) and *Hesperomannia* (Marticorena and Parra 1975), perhaps related to a relaxation of adaptive constraints related to pollination.

Concurrent with the selective pressure on pollen morphology for adaptation to mechanisms of dispersal is the constant pressure for structural economy—sporopollenin deposition requires a large amount of investment on the part of the plant and the less material to be incorporated

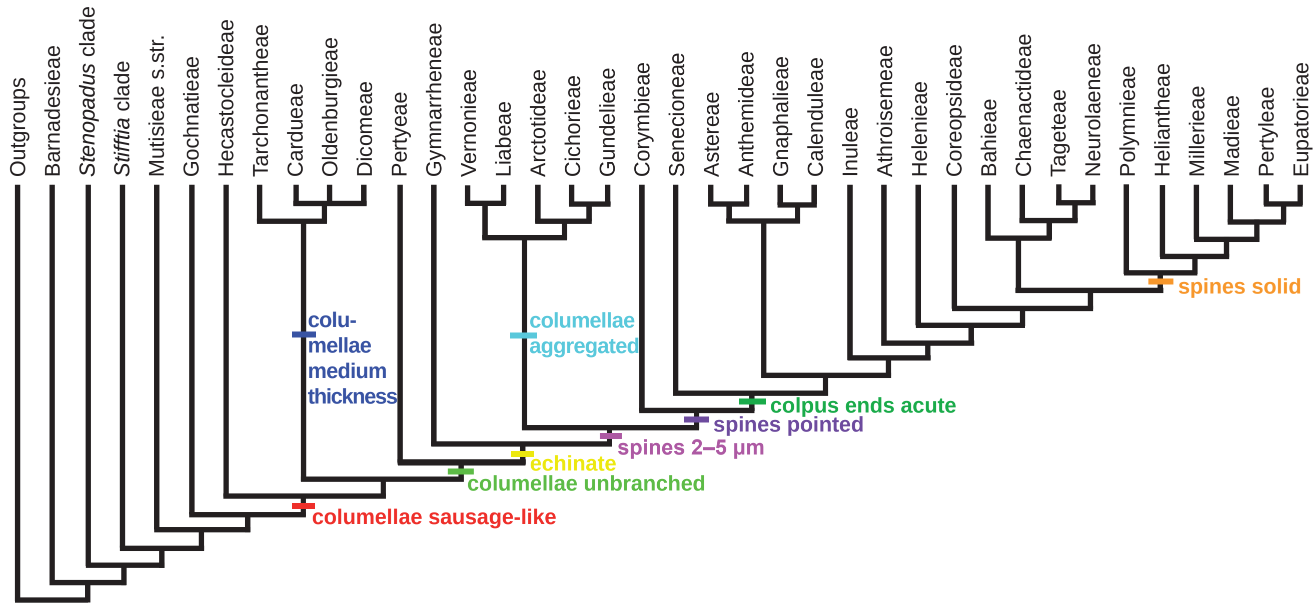

Fig. 7.17. Phylogeny of Compositae showing most parsimonious inference of evolution for all pollen characters that change unambiguously on the tree and provide synapomorphies for groups; autapomorphies for tribes and ambiguous characters not shown. Tree modified from Funk et al. (2005).

into a structure of the same strength the better. This may be a driving force behind the repeated evolution of internal foramina, hollow spines, and spongy or columellate rather than solid structures.

Most of the diversity of Compositae, in terms of species and genera, is seen in Asteroideae, particularly the lower Asteroideae which are concentrated in the Old World. However, in these groups, pollen morphology is relatively invariable. The reasons behind this canalization in pollen structure remain unclear, especially since there remains a degree of evolutionary flexibility, as seen in the loss of spines of some Eupatorieae and Anthemideae as adaptations for wind-pollination (Robinson and King 1977).

CONCLUSIONS

Although we are a long way from fully understanding the processes and mechanisms of pollen diversification and evolution in Compositae, a number of trends and evolutionary events can be inferred (Fig. 7.17), and these may become clearer as studies of evolutionary development become more commonplace, particularly given the large number of "model" species in the family (e.g., Teeri et al. 2006). When optimized on the supertree, pollen morphological characters provide a synapomorphy for almost every internal branch of Compositae phylogeny (Fig. 7.17). The earliest branching taxa and outgroups tend to have prolate, microperforate, psilate pollen grains without cavea or internal foramina. In Asteroideae the pollen is more oblate in shape, microreticulate and echinate, usually with cavea and internal foramina. On successive branches of the tree there are shifts towards a simpler exine ultrastructure with less-branched columellae, and changes in spine shape, size and internal structure (Fig. 7.17). There is a tendency to develop lophate pollen in both Barnadesieae and Cichorioideae. Contrary to the prevailing belief of the past thirty years, pollen morphological characters are highly variable and frequently congruent with the tree, providing evidence to support molecular relationships, possible diagnostic characters for tribes or sub-tribal groups, and suggesting possible relationships for genera not yet included in the supertree (Wortley et al. 2007). A key feature of this framework is that many pollen characters are highly informative when considered independently and at the correct level.

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Appendix 7.1. Characters examined (for further explanation see text)

1. *Shape.* 0, oblate (shorter in polar axis than equatorial); 1, prolate (shorter in equatorial axis than polar); 2, spheroidal (polar and equatorial axes approximately equal).
2. *Polar view.* 0, round (circular in polar view); 1, sub-triangular (broadly triangular in polar view but with rounded apices); 2, triangular (distinctly triangular in polar view); 3, triangular-concave (triangular with indentations between the apices); 4, hexagonal (six-sided in polar view).
3. *Equatorial view.* 0, round (circular in equatorial view); 1, elliptic (elliptical in equatorial view—occurs in prolate or oblate grains); 2, rectangular (very blunt-ended prolate grains that appear more rectangular than elliptic).
4. *Poles.* 0, blunt (poles rounded in a smooth progression with the rest of the grain perimeter); 1, lemon-shaped (with distinct swellings at the poles—occurs in prolate grains only).
5. *Aperture number.* 0, two (documented only in abnormal grains of *Alfredia* and *Helichrysum*); 1, three (normal state); 2, four (abnormal but fairly common state); 3, eight (abnormal state occasionally seen in *Polydora* only).
6. *Aperture type.* 0, colpate (occasionally reported in *Ainsliaea*; e.g., Tellería and Katinas 2005); 1, colporate (normal state); 2, pororate (with the ectoaperture as a pore rather than a colpus—common in a number of Vernonieae).
7. *Ectoapertures.* 0, separate (apertures not joined at the poles); 1, syncolpate (apertures joined at the poles).
8. *Ectoaperture width.* 0, narrow (this character depends on pollen treatment); 1, medium; 2, broad.
9. *Ectoaperture ends.* 0, acute (pointed); 1, obtuse (rounded).
10. *Endoaperture shape.* 0, endocingulum (single aperture extending all the way around the equator of the grain, reported in some Mutisieae and Cardueae); 1, lalongate (elliptic, longer in equatorial plane than polar one; the most common state); 2, circular; 3, square (reported in *Callilepis* and *Diplostephium*); 4, lolongate (elliptic, longer in polar plane than equatorial one; reported in *Ainsliaea*, *Linzia*, and a number of Barnadesieae); 5, irregular (reported in *Inula*).
11. *Mesoaperture.* 0, absent; 1, present
12. *Tectum.* 0, imperforate; 1, microperforate.
13. *Tectum extent.* 0, whole surface (this is particularly relevant to distinguish types of lophate taxa); 1, absent from lacunae (only occurs in lophate taxa).
14. *Infractectum layers.* 0, one (exine comprising a single layer of columellae); 1, two (exine double-layered); 2, three (exine of three distinct layers); 3, multiple (exine complex, many-layered or reticulating).
15. *Infractectum layers.* 0, distinct (exine layers clearly different or separate); 1, indistinct (exine layers merging or similar).
16. *Outer infratectum.* 0, columellate (the layer directly below the tectum comprising vertical, rod-like elements); 1, compact (this layer comprising tightly-packed material); 2, spongy (this layer comprising spongy material—this is sometimes difficult to differentiate from compact).
17. *Internal tectum.* 0, absent (no clear layer separating outer and inner columellae layers); 1, present (clear layer between outer and inner columellae).
18. *Internal tectum.* 0, single; 1, multiple (complex, fragmented or multilayered).
19. *Internal tectum.* 0, compact (solid); 1, granular; 2, spongy (sometimes difficult to differentiate from granular).
20. *Supporting layer.* 0, columellate (the lower layer of infratectum comprising more or less rod-like elements); 1, granular/spongy (layer comprising a non-columellar matrix).
21. *Supporting columellae.* 0, thin (supporting columellae much longer than they are wide); 1, medium (between thin and thick); 2, thick (supporting columellae almost as wide as they are tall).
22. *Supporting columellae.* 0, unbranched (simple); 1, bifurcating (simple with occasional straight branches from about halfway up); 2, sausage-like (similar to bifurcating but fatter, sometimes with small papillae at top); 3, baobab-like (broad, with a few broad branches towards the top); 4, broccoli-like (broad, with many small branches towards the top); 5, reticulate (with anastomosing branches at all levels).
23. *Supporting columellae.* 0, not swollen (normal state); 1, swollen at base (lower layer of columellae distinctly swollen at point of attachment to foot layer).
24. *Internal foramina.* 0, absent; 1, present (these are most easily seen in TEM).
25. *Columellae.* 0, even (spaced at equal distances throughout the exine regardless of spines or lophae); 1, uneven (not spaced evenly but not aggregated in any particular pattern—documented for some Cardueae, but hard to distinguish from aggregated or even); 2, aggregated (columellae distinctly focused under spines or lophae).
26. *Spine channel.* 0, absent (no distinct channel formed between columellae and passing through spine); 1, present (columellae forming a distinct channel under and through spine).
27. *Spine columellae.* 0, absent (columellae absent or not continuous into spine); 1, hanging (columellae hanging down from spine and remaining free from foot layer); 2, attached (columellae inside spine fully attached to foot layer at base).
28. *Cavea.* 0, columellate (no cavea, columellate layer[s] continuous between foot layer and upper infratectum); 1, partial (some columellae spanning the space between foot layer and upper infratectum); 2, caveate (complete space between foot layer and upper-infratectum, except where joined at apertures).
29. *Cavea depth.* 0, shallow (relative to other layers); 1, medium; 2, deep.
30. *Endexine.* 0, absent; 1, thinner than foot layer; 2, same thickness as foot layer; 3, thicker than foot layer (or foot layer absent).
31. *Macro-ornamentation.* 0, psilate (having no ornamentation of 1 µm or larger); 1, echinate (having ornamentation at least 1 µm in size).
32. *Spine number.* 0, few; 1, average; 2, many.
33. *Spine density.* 0, sparse; 1, average; 2, dense.
34. *Spine distribution.* 0, even (spines regularly distributed across the grain); 1, uneven (spines irregularly but randomly distributed); 2, clumped (spines clearly aggregated in certain regions—a feature that tends to correspond to echinolophate and subechinolophate grains).
35. *Spine shape.* 0, rounded (ornaments greater than 1 µm bluntly rounded); 1, conical; 2, cylindrical (spines more or less the same width for the majority of their length); 3, pointed (spines narrowing to a sharp tip).
36. *Spine size.* 0, short (1–2 µm); 1, medium (2–5 µm); 2, long (5–9 µm).
37. *Spine base.* 0, abrupt (the spine bases forming almost a right-angle with the grain surface); 1, smooth (spine bases making a smooth 45° angle running into the surface); 2, swollen (spine bases distinctly swollen).
38. *Spine perforations.* 0, absent (spines solid); 1, present (spines with holes, channels or hollow inside, usually seen under TEM).

39. *Tectum.* 0, not raised (surface flat between spines); 1, raised (surface lifted between some spines to link them).
40. *Scabra shape.* 0, rounded scabrae (surface having rounded elements smaller than 1 μm); 1, conical scabrae (surface having conical elements smaller than 1 μm); 2, pointed scabrae (surface having pointed elements smaller than 1 μm—documented for *Stoebe* but not seen).
41. *Exine surface.* 0, smooth (tectum more or less smooth between micro- or macro-ornamentation); 1, striate (surface having small lines or ridges—this is sometimes difficult to distinguish from a reticulate surface but has been documented for Liabeae; Robinson and Marticorena 1986); 2, reticulate (surface with reticulate patterning); 3, areolate (surface with indentations forming a "negative tectum").
42. *Macro-ornamentation.* 0, non-lophate (regardless of whether grains are echinate); 1, concavities (having "intercolpar concavities"—this state is restricted to Barnadesieae); 2, sub-lophate (having spines arranged in a pattern as if lophate); 3, lophate (regardless of whether grains are also echinate).

The following characters apply to lophate grains only:

43. *Lophae overlap.* 0, separate (lophae not meeting over apertures); 1, flap-like (lophae overlapping like flaps at apertures); 2, meeting (lophae meeting but not joining or overlapping at apertures, documented for some *Aynia* and *Pseudopiptocarpha* (Vernonieae)); 3, joined (all lophae completely fused).
44. *Abporal lacunae* (number of lacunae situated at the end of an aperture that is divided into two or more lacunae). 0, zero; 1, three; 2, six; 3, irregular.
45. *Equatorial lacunae* (number of lacunae situated on the equator in the mesocolpial region). 0, zero; 1, three; 2, six; 3, irregular.
46. *Interporal lacunae* (number of lacunae situated between the ends of two ectoapertures adjacent to the pole). 0, zero; 1, four; 2, six; 3, eighteen; 4, irregular.
47. *Paraporal lacunae* (number of lacunae situated in the mesocolpial region adjacent to one side of an equatorial lacuna). 0, zero; 1, four; 2, six; 3, twelve; 4, irregular).
48. *Polar lacunae* (number of lacunae situated at the poles). 0, zero; 1, two; 2, four; 3, six; 4, irregular.
49. *Poral lacunae* (number of lacunae situated around each aperture). 0, zero; 1, three; 2, six; 3, irregular.
50. *Lacunae size.* 0, 5–10 μm; 1, 10–15 μm; 2, 15–20 μm.
51. *Lacunae shape.* 0, round; 1, triangular; 2, rhomboid; 3, pentagonal; 4, hexagonal; 5, polygonal; 6, irregular
52. *Lophae over apertures.* 0, absent (colpi not dissected by lophae); 1, present (having lophae dissecting the colpi into two or more lacunae).

Appendix 7.2. Matrix of pollen morphological characters for supertree taxa, using tribes as terminals

Matrix used for character analysis (not phylogenetic analysis) as entered into MacClade (Maddison and Maddison 2005). Each of the characters, 1–52, is coded for each taxon with a number representing its state (0, 1, 2, etc.; for coding see Appendix 7.1). Where there is polymorphism within a group, all relevant states are included. Where no data were available for a group, the character is represented by "?". Where a character is inapplicable (e.g., colpus width for pororate taxa), the character is represented by "–".

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Outgroups	21	02	12	0	1	1	0	02	01	1	?	01	0	0	–	–	–	–	–	0	2	04	0	0	0	–
Barnadesieae	12	02	012	0	1	1	0	02	01	14	1	01	0	01	01	0	01	2	2	012	02	0125	0	?	0	0
Stenopadus clade	12	012	1	0	1	1	0	012	01	1	0	1	0	1	0	0	01	0	2	0	2	123	0	?	0	0
Stifftia clade	12	01	01	01	1	1	0	0	0	1	01	1	0	1	0	03	01	0	2	0	02	014	0	?	0	0
Mutisieae	12	0123	01	01	12	1	01	012	01	014	01	01	0	12	01	013	01	0	012	0	012	0135	0	0	0	–
Gochnatieae	12	012	01	0	1	1	0	12	01	1	0	01	0	123	01	012	1	0	2	012	12	1	0	?	0	0
Hecastocleideae	2	02	0	–	1	0	0	2	?	–	0	1	0	1	0	13	0	–	–	01	2	2	0	?	0	–
Dicomeae	12	02	01	01	1	1	0	1	01	1	0	1	0	2	0	01	1	0	2	0	1	2	0	0	0	0
Oldenburgieae	2	0	0	–	1	1	0	1	1	1	0	1	0	2	0	0	1	0	2	0	1	23	0	?	0	0
Tarchonantheae	12	012	01	0	12	1	0	01	01	1	0	01	0	02	0	?	1	0	2	0	1	0	0	0	0	0
Cardueae	012	012	01	0	1	1	0	012	01	0124	1	1	0	0–3	01	03	01	0	2	0	012	0–5	01	01	012	01
Pertyeae	12	01	01	0	1	130	0	02	1	14	?	01	0	2	01	01	1	0	2	0	2	0	1	?	0	–
Gymnarrheneae	2	0	0	–	1	1	0	1	0	1	?	1	0	3	0	03	1	0	0	0	2	0	0	0	0	0
Gundelieae	12	01	0	0	1	1	0	012	0	1	1	1	0	2	0	03	1	0	2	0	12	4	01	?	02	0
Cichorieae	02	014	01	01	12	1	0	12	1	12	1	1	01	23	01	03	1	02	02	0	012	01	0	01	2	1
Arctotideae	02	01	01	–	12	1	0	012	01	1	?	1	0	012	0	0	1	02	02	0	0	0	0	0	2	1
Liabeae	02	01	01	–	1	1	0	012	1	12	?	1	0	01	0	0	01	0	12	0	12	02	0	0	2	1
Vernonieae	02	01	01	–	13	12	0	012	01	124	01	01	01	01	0	03	0	–	–	0	12	0–5	0	0	02	01
Corymbieae	02	1	1	–	1	1	0	1	1	1	0	1	0	1	0	0	0	–	–	0	1	0	0	?	0	0
Senecioneae	012	01	01	0	1	1	0	012	0	12	?	1	0	0	–	0	1	0	?	–	–	–	–	01	–	0
Calenduleae	012	02	01	–	1	1	0	01	0	124	1	1	0	012	1	0	01	0	0	–	–	–	–	1	0	0
Gnaphalieae	012	01	012	0	012	1	01	012	01	1	?	1	0	1	0	0	0	–	–	2	–	–	–	1	–	01
Astereae	012	012	01	0	12	1	01	012	01	1	?	1	0	0	–	0	–	–	–	–	–	–	–	1	–	0
Anthemideae	012	01	01	0	1	1	0	012	01	13	?	1	0	012	0	0	1	012	02	0	2	1–5	01	0	02	0

continued overleaf

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
Inuleae	12	01	01	0	12	1	0	02	01	1235	?	1	0	012	01	0	01	01	02	02	01	05	01	01	02	01
Athroismeae	2	1	0	–	1	1	0	2	0	1	?	1	0	0	–	0	0	–	–	–	–	–	1	1	–	1
Helenieae	02	01	01	–	1	1	0	01	0	1	?	1	0	01	01	0	0	–	–	2	–	–	–	1	0	01
Coreopsideae	2	0	0	–	1	1	0	02	0	1	?	01	0	0	–	03	0	–	–	–	–	–	–	1	0	0
Neurolaeneae	12	?	?	?	1	1	?	?	0	1	?	?	?	0	–	0	0	–	–	–	–	–	–	1	0	1
Tageteae	012	01	01	0	1	1	0	01	0	1	?	1	0	1	01	0	0	–	–	2	–	–	–	1	0	01
Chaenactideae	12	1	01	0	1	1	0	01	0	1	?	1	0	1	1	0	0	–	–	2	–	–	–	1	0	1
Bahieae	02	0	0	–	1	1	0	0	0	1	?	1	0	0	–	0	0	–	–	–	–	–	1	01	0	01
Polymnieae	12	01	?	0	1	1	0	0	0	1	?	1	0	0	–	0	0	–	–	–	–	–	1	1	0	0
Heliantheae	02	01	0	–	1	1	0	01	0	1	?	1	0	0	–	03	0	–	–	–	–	–	1	01	0	01
Millerieae	2	0	0	–	1	1	0	2	0	1	?	1	0	0	–	0	0	–	–	–	–	–	1	1	0	1
Madieae	2	01	0	–	1	1	0	1	0	1	?	1	0	0	–	0	0	–	–	–	–	–	01	01	0	01
Perityleae	2	0	0	–	1	1	0	1	0	1	?	1	0	?	–	?	?	–	?	?	–	–	?	1	?	?
Eupatorieae	2	1	0	–	1	1	0	1	01	1	?	1	0	0	–	0	0	–	–	–	–	–	0	1	0	1

Character	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
Outgroups	1	0	–	3	0	–	–	–	–	–	–	–	0	1	0	01	–	–	–	–	–	–	–	–	–	–
Barnadesieae	?	01	0	?	01	2	2	0	1	0	1	1	0	01	013	013	3	2	1	2	3	13	1	?	3456	0
Stenopadus clade	0	0	–	23	01	12	12	0	01	0	1	01	0	01	01	0	–	–	–	–	–	–	–	–	–	–
Stifftia clade	0	0	–	13	1	12	12	0	01	01	1	0	0	0	02	0	–	–	–	–	–	–	–	–	–	–
Mutisieae	–	0	–	13	0	–	–	–	–	–	–	–	0	012	0123	0	–	–	–	–	–	–	–	–	–	–
Gochnatieae	0	0	–	2	01	1	01	0	1	01	1	1	01	12	02	0	–	–	–	–	–	–	–	–	–	–
Hecastocleideae	–	0	–	3	0	–	–	–	–	–	–	–	0	0	0	0	–	–	–	–	–	–	–	–	–	–
Dicomeae	02	0	–	3	01	1	01	0	1	0	1	1	0	0	03	0	–	–	–	–	–	–	–	–	–	–
Oldenburgieae	0	0	–	3	1	1	0	0	1	0	1	1	0	–	3	0	–	–	–	–	–	–	–	–	–	–

Tarchonantheae	–	0	–	23	0	–	–	–	–	–	–	–	0	01	0	0	–	–	–	–	–	–	–	–	–	–
Cardueae	012	012	02	123	01	012	012	01	013	012	012	01	01	01	0123	0	–	–	–	–	–	–	–	–	–	–
Pertyeae	–	0	–	0	0	–	–	–	–	–	–	–	0	01	?	0	–	–	–	–	–	–	–	–	–	–
Gymnarrheneae	2	0	–	1	1	1	1	1	13	0	2	1	0	–	0	0	–	–	–	–	–	–	–	–	–	–
Gundelieae	12	01	1	01	1	12	01	01	013	1	2	01	01	–	0	0	–	–	–	–	–	–	–	–	–	–
Cichorieae	12	01	0	3	1	12	012	2	13	1	12	1	–	–	023	03	023	2	012	02	02	013	01	01	0–6	01
Arctotideae	012	12	01	3	01	012	012	02	1	1	012	01	0	–	02	023	013	02	2	0123	12	3	12	12	35	0
Liabeae	12	01	01	3	1	012	1	01	013	12	12	01	01	–	12	0	–	–	–	–	–	–	–	–	–	–
Vernonieae	12	012	01	23	01	012	012	12	0123	012	012	01	01	0	023	023	123	0123	0123	24	0234	0124	0123	012	0–6	01
Corymbieae	2	2	0	3	1	1	1	0	3	1	1	1	0	–	2	0	–	–	–	–	–	–	–	–	–	–
Senecioneae	01	12	01	3	1	012	012	0	013	12	12	01	0	0	123	0	–	–	–	–	–	–	–	–	–	–
Calenduleae	1	12	02	3	1	012	12	0	013	01	2	01	0	–	02	0	–	–	–	–	–	–	–	–	–	–
Gnaphalieae	2	2	01	3	01	012	12	01	13	012	1	01	0	2	012	0	–	–	–	–	–	–	–	–	–	–
Astereae	12	12	012	3	1	012	12	0	13	01	012	0	0	–	023	0	–	–	–	–	–	–	–	–	–	–
Anthemideae	12	01	1	1	01	012	01	0	13	012	012	01	0	012	1	0	–	–	–	–	–	–	–	–	–	–
Inuleae	12	2	012	3	1	012	012	01	013	23	12	01	0	–	2	0	–	–	–	–	–	–	–	–	–	–
Athroismeae	2	2	2	3	1	1	02	0	0	01	2	1	0	0	?	0	–	–	–	–	–	–	–	–	–	–
Helenieae	12	2	012	3	1	01	01	01	013	12	012	01	01	0	2	0	–	–	–	–	–	–	–	–	–	–
Coreopsideae	1	2	02	3	1	12	01	01	3	12	12	01	0	–	23	0	–	–	–	–	–	–	–	–	–	–
Neurolaeneae	2	1	0	3	1	1	1	?	1	12	?	1	?	?	?	0	–	–	–	–	–	–	–	–	–	–
Tageteae	12	2	0	3	1	01	012	01	13	12	012	01	01	–	?	0	–	–	–	–	–	–	–	–	–	–
Chaenactideae	2	2	1	3	1	12	012	0	3	12	2	1	0	–	2	0	–	–	–	–	–	–	–	–	–	–
Bahieae	12	12	01	3	1	01	01	0	13	12	1	01	0	–	2	0	–	–	–	–	–	–	–	–	–	–
Polymnieae	2	2	0	3	1	01	0	1	3	1	1	0	0	–	0	0	–	–	–	–	–	–	–	–	–	–
Heliantheae	012	12	012	3	1	012	01	1	13	01	12	01	0	–	02	0	–	–	–	–	–	–	–	–	–	–
Millerieae	12	2	12	3	1	1	12	0	13	1	12	0	0	–	2	0	–	–	–	–	–	–	–	–	–	–
Madieae	012	12	12	3	1	12	012	01	013	012	12	01	01	–	2	0	–	–	–	–	–	–	–	–	–	–
Perityleae	?	2	?	?	1	2	2	0	3	1	2	0	0	–	2	0	–	–	–	–	–	–	–	–	–	–
Eupatorieae	0	2	0	2	01	1	01	0	3	01	1	01	0	–	3	0	–	–	–	–	–	–	–	–	–	–

Appendix 7.3. Pollen descriptions for tribes of Compositae

Tribes according to Funk et al. (2005).

As described in "Materials and Methods", descriptions are based on a review of pollen descriptions, LM, TEM, and SEM images for genera in the supertree (Funk et al. 2005; Funk, pers. comm.), taken from the literature listed in Appendix B.

Barnadesieae

Pollen spheroidal (lophate taxa) or prolate (non-/sub-lophate taxa), triangular, sub-triangular or round in polar view, round, elliptical or rectangular in equatorial view, blunt-ended, tricolporate; colpi separate, narrow to broad, with ends obtuse or acute, ora lalongate or lolongate, mesoaperture sometimes present; tectum imperforate or microperforate, covering whole surface of grain; occasionally echinate; where echinate spines many, dense, evenly-distributed, conical, 1 µm, smooth-based with perforations; tectum not raised, with rounded or conical scabrae and smooth, striate or areolate surface; non-lophate, with intercolpar concavities or fully lophate; where lophate having six abporal, three equatorial, six interporal, twelve paraporal, two to six polar and three poral lacunae, of variable size and shape, lophae fused, not crossing apertures; infratectum of one or two, distinct or indistinct layers, the outer layer columellate; internal tectum sometimes present, multilayered and spongy; supporting layer spongy or columellate, columellae thin or thick, unbranched, bifurcating, sausage-like or irregularly branching, bases not swollen, evenly-distributed, without spine channels or spine columellae, without internal foramina; acaveate or partially caveate, cavea shallow.

Stifftia clade

Pollen spheroidal or prolate, triangular, sub-triangular or round in polar view, round or elliptical in equatorial view, blunt-ended or lemon-shaped, tricolporate; colpi separate, narrow to broad, with ends obtuse or acute, ora lalongate, mesoaperture sometimes present; tectum microperforate, covering whole surface of grain; psilate or echinate; spines average to many, sparse to dense, evenly-distributed, conical-rounded, 1–5 µm, smooth-based, solid or with perforations; tectum not raised, with rounded or conical scabrae and exine thickenings in some species, with smooth or occasionally striate or reticulate surface; non-lophate; infratectum of two distinct layers, the outer columellate or spongy; internal tectum sometimes present, single-layered and spongy; supporting layer columellate, columellae thin or (usually) thick, unbranched, bifurcating, sausage-, baobab-, or broccoli-like, bases not swollen, evenly-distributed, without spine channels or spine columellae, without internal foramina; acaveate; endexine thicker than or same thickness as foot layer.

Mutisieae

Pollen spheroidal or prolate, triangular, sub-triangular or round in polar view, round or elliptic in equatorial view, blunt-ended or lemon-shaped, tri- (occasionally tetra-) colporate; colpi separate or syncolpate (*Perezia*), long, deep, narrow to broad, with thin margin and ends obtuse or acute, ora lalongate or an endocingulum, mesoaperture often present; tectum microperforate or imperforate, covering whole surface of grain; psilate; tectum not raised, with rounded, conical or spiky spinules and smooth, striate, reticulate or areolate surface; non-lophate; infratectum of two to three distinct (occasionally indistinct) layers, the outer columellate or spongy; internal tectum often present, single-layered and spongy, occasionally compact or granular; supporting layer columellate, columellae thin or thick, unbranched, bifurcating or baobab-like, bases not swollen, without internal foramina, evenly-distributed, without spine channels or spine columellae; acaveate; endexine thicker or thinner than foot layer.

Gochnatieae

Pollen spheroidal or prolate, triangular, sub-triangular or round in polar view, round or elliptic in equatorial view, blunt-ended, tricolporate; colpi separate, medium or broad, with ends obtuse or acute, ora lalongate; tectum imperforate or microperforate, covering whole surface of grain; psilate or echinate; spines of average number, average to sparse, evenly-distributed, conical, 1.0–1.5 µm, smooth-based, with perforations; tectum sometimes slightly raised, with conical or spiky spinules and smooth or reticulate surface; non-lophate; infractectum of two or more distinct or indistinct layers, the outer columellate or granulate; internal tectum present, single-layered and spongy; supporting layer columellate or spongy, columellae medium or thick, bifurcating, bases not swollen, evenly-distributed, without internal foramina, without spine channels or columellae; acaveate; endexine the same thickness as foot layer.

Hecastocleideae

Pollen spheroidal, round or triangular in polar view, round in equatorial view, tricolporate or tricolpate; colpi separate, broad, mesoaperture absent; tectum microperforate, covering whole surface of grain; psilate; tectum not raised, scabrate, smooth and slightly striate, with small folds carrying many scabrae; non-lophate; infratectum of two very distinct layers, not firmly attached to one another, the outer spongy, internal tectum absent; supporting layer columellate or granular, columellae thick, sausage-like (the tips slightly tapered with lots of tiny finger-like projections), bases not swollen, evenly-distributed, without internal foramina, without spine channels or columellae; acaveate; endexine thicker than foot layer.

Dicomeae

Pollen spheroidal or prolate, round or triangular in polar view, round or elliptic in equatorial view, ends blunt or lemon-shaped, tricolporate; colpi separate, medium width, with thin margin and obtuse or acute ends, ora lalongate, mesoaperture absent; tectum microperforate, covering whole surface of grain; echinate, spines of average number, fairly sparse, evenly-distributed, conical, 1–2 µm, arising smoothly from the surface of the grain, with perforations; tectum not raised, granulose, smooth or areolate-rugulate; non-lophate; infratectum of three distinct layers, the outer columellate or compact, internal tectum present, single-layered, spongy; supporting layer columellate, columellae medium, sausage-like or bifurcating, bases not swollen, evenly-distributed, without spine channels, sometimes with spine columellae, fully-attached, without internal foramina; acaveate; endexine thicker than foot layer.

Oldenburgieae

Pollen spheroidal or slightly prolate, round in both views, tricolporate; colpi separate, medium width, with ends obtuse, ora lalongate, mesoaperture absent; tectum microperforate, covering whole surface of grain; echinate, spines average in number, sparse, evenly-distributed, conical, 1 µm, arising smoothly from the surface of the grain, with perforations; tectum not raised, without micro-ornamentation, surface areolate; non-lophate; infratectum of three distinct layers, the outer columellate, internal tectum present, single-layered and spongy; supporting layer columellate, columellae medium, sausage-like or bifurcating, bases not swollen, evenly-distributed, without internal foramina, without spine channels or spine columellae; acaveate; endexine much thicker than foot layer.

Tarchonantheae

Pollen spheroidal or prolate, round, sub-triangular or triangular in polar view, round or elliptic in equatorial view, blunt-ended, tri- (sometimes tetra-) colporate; colpi separate, narrow to medium width, ends acute or obtuse, ora lalongate or circular; mesoaperture absent; tectum microperforate, covering whole surface of grain; psilate; tectum not raised, with very distinct rounded or conical spinules and smooth surface; non-lophate; infratectum of one to three distinct layers; outer layer (where present) columellate, internal tectum present beneath it, distinct, single-layered and spongy; supporting layer columellate, columellae medium and unbranched, bases not swollen, evenly-distributed, without internal foramina, without spine-channels or spine columellae; acaveate; endexine the same thickness as foot layer.

Cardueae

Pollen very diverse, prolate, oblate or spheroidal, round, sub-triangular or triangular in polar view, round or elliptic in equatorial view, always blunt-ended, (bi-) tricolporate; colpi separate, narrow to broad, with thin margin and obtuse or usually acute ends, ora lalongate, lolongate, circular or an endocingulum, mesoaperture sometimes present; tectum microperforate, covering whole surface of grain; psilate or (usually) echinate; spines few to many, sparse to dense, evenly-distributed or irregular, rounded, conical or pointed, 1–9 µm, abrupt, smooth or swollen at base, usually with perforations; tectum not raised, slightly raised or forming raised ridges between spines, with rounded granules and smooth, reticulate, striate or areolate surface; non-lophate; infratectum of one to three or more distinct or indistinct layers, outer layer (where present) columellate or spongy, internal tectum usually present, single-layered and spongy; supporting layer columellate, columellae thin to thick, unbranched, bifurcating, broccoli- or baobab-like or reticulate, with bases occasionally broadened and sometimes with internal foramina; evenly-distributed or often aggregated beneath spines forming a spine channel, with spine columellae hanging free or attached to the base layer; often partially caveate; the cavea shallow (occasionally deep); endexine thinner than, thicker than or the same thickness as foot layer.

Pertyeae

Pollen prolate or spheroidal, round or sub-triangular in polar view, round or elliptic in equatorial view, blunt-ended, tricolpate, triporate or tricolporate; colpi separate, narrow to broad, with obtuse ends, ora lalongate; tectum imperforate or microperforate, covering whole surface of grain; psilate; tectum not raised, with conical or rounded granules; non-lophate; infratectum of three distinct or indistinct layers, outer layer compact or columellate, internal tectum single-layered and spongy; supporting layer columellate, columellae thick, unbranched, slightly swollen at base, evenly-distributed, without spine channels or spine columellae; no internal foramina reported; acaveate; endexine absent.

Gymnarrheneae

Pollen spheroidal, round in both views, tricolporate; colpi separate, medium width, with acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; psilate; non-lophate; infractectum of four distinct layers; outer infratectum columellate or spongy, internal tectum single-layered, compact; supporting layer columellate, columellae thick, unbranched, bases not swollen, evenly-distributed, without spine channels, spine columellae fully-attached, no internal foramina reported; acaveate; endexine thinner than foot layer; echinate, spines of average number and density, irregularly-distributed, conical-pointed, 1–2 µm, bases swollen, with perforations; tectum not raised, without micro-ornamentation.

Gundelieae

Pollen prolate or spheroidal, round or sub-triangular in polar view, round in equatorial view, blunt-ended, tricolporate; colpi separate, narrow to broad, with thin margin and acute ends, ora lalongate, mesoaperture present; tectum microperforate, covering whole surface of grain; echinate, spines average to many, average to sparse, evenly- or irregularly-distributed, conical, pointed or blunt, 4–5 µm, swollen at base, solid or with internal foramina; tectum sometimes raised to form ridges between the spines, without micro-ornamentation, smooth; non-lophate; infratectum of three or four distinct layers, outer infratectum columellate or spongy, internal tectum single-layered and spongy; supporting columellae medium to thick, broccoli-like, bases sometimes slightly swollen, often aggregated under spines, not forming channels, hanging free or fully-attached to base layer under spines, without internal foramina; sometimes partially caveate, cavea medium; endexine absent or thinner than foot layer.

Cichorieae

Pollen oblate or spheroidal, round, sub-triangular or hexagonal in polar view, round or elliptic in equatorial view, almost always with polar thickenings, tri- (occasionally tetra-) colporate; colpi separate, medium to broad, with obtuse ends, ora lalongate or circular, mesoaperture present; tectum microperforate, covering the whole surface of the grain or lost from centre of lacunae; echinate, spines average to many, average to dense, clumped on lophae, conical-pointed, 2–5 µm, smooth or swollen at base, with perforations; tectum smooth, reticulate or areolate, usually lophate (occasionally non- or sub-lophate, e.g., *Catananche, Rafinesquia*), with lophae separate, meeting or joining but never overlapping, six abporal lacunae, up to six equatorial lacunae, zero or six interporal lacunae, zero or six paraporal lacunae, up to six polar lacunae and zero or three poral lacunae; lacunae 7–15 µm in diameter, triangular, rhomboid, pentagonal, hexagonal, elliptic or irregular in shape, sometimes with lophae over the apertures; infratectum of at least three distinct layers, outer infractectum columellate or spongy, internal tectum single or multiple, spongy; supporting layer columellate, columellae thin to medium, unbranched, bases not swollen, with or without internal foramina; aggregated under spines, not forming channels, fully-attached to base layer under spines; usually partially caveate; cavea shallow; endexine thicker than foot layer.

Arctotideae

Pollen oblate or spheroidal, round in polar view, round or elliptic in equatorial view, tri- (occasionally tetra-) colporate; colpi separate, narrow to broad, with thin membrane and acute or obtuse ends, ora lalongate; tectum microperforate, covering the whole surface of the grain; psilate or echinate, spines few to many, sparse to dense, evenly-distributed or clumped on ridges, conical, 1–4 µm, abrupt, smooth or slightly swollen at base, solid or with perforations; tectum not raised, smooth or reticulate; non-lophate, sub-lophate or lophate, with lophae joining or overlapping as flaps, zero or six abporal lacunae, six equatorial lacunae, up to 18 interporal lacunae, six paraporal lacunae, six polar lacunae and three or six poral lacunae; lacunae 10–18 µm in diameter, usually pentagonal or polygonal, sometimes with lophae over the apertures; infratectum of one (*Eremothamnus*) two or three distinct layers, outer infratectum columellate, internal tectum single or multiple, spongy or usually compact; supporting layer columellate, columellae thin, unbranched, bases not swollen, without internal foramina, aggregated under spines forming a spine channel, spine columellae hanging or fully-attached at base; caveate or partially caveate, cavea shallow to medium; endexine thicker than foot layer.

Liabeae

Pollen oblate or spheroidal, round or sub-triangular in polar view, round or elliptic in equatorial view, tricolporate; colpi separate, narrow to medium, with obtuse ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines average in number and density, usually irregularly-distributed, rounded, conical or long-pointed, 2–8 μm, usually swollen at base, solid or with perforations; tectum sometimes slightly raised between some spines, reticulate or striate; non-lophate; infratectum of one or two distinct layers, outer infratectum columellate, internal tectum present or absent, single-layered and spongy or granular; supporting layer columellate, columellae medium to thick, unbranched, bases not swollen, aggregated under spines forming a spine channel, spine columellae fully-attached at base (gazebo-like structure), without internal foramina; acaveate or partially caveate, cavea shallow to medium; endexine thicker than foot layer.

Vernonieae

Pollen variable in size and morphology, oblate or spheroidal, round or sub-triangular in polar view, round or elliptic in equatorial view, tricolporate or tri- (occasionally 8-) pororate; colpi separate, narrow to medium, with thin margin and obtuse or acute ends, ora lalongate or circular, mesoaperture sometimes present; tectum microperforate or imperforate, sometimes covering whole surface of grain, usually (in lophate taxa) restricted to lophae or parts of lophae; psilate or echinate, spines few to many, sparse to dense, distributed irregularly or clumped on lophae, conical-pointed, 1–5(–7) μm, abrupt or swollen at base, solid or with perforations; tectum occasionally slightly raised between some spines, granular with smooth, reticulate or areolate surface; non-lophate, sub-lophate or lophate, with lophae joining, meeting or overlapping as flaps, up to six abporal lacunae, up to six equatorial lacunae, six interporal lacunae, up to 12 paraporal lacunae, up to three polar lacunae and up to six poral lacunae, or lophae completely irregular; lacunae 3–20 μm in diameter, round, triangular, rhomboid, hexagonal, polygonal, or irregular, without lophae over the apertures; infratectum one- (sometimes two-) layered; outer infratectum (where present) spongy or (occasionally) columellate, internal tectum absent; supporting layer columellate, columellae thick (medium in *Vernonia brachycalyx*), unbranched, sausage- or broccoli-like or reticulate (unbranched in *V. brachycalyx*), bases not swollen, without internal foramina, usually aggregated under spines but not usually forming a spine channel; spine columellae fully-attached to foot layer; acaveate, partially or fully caveate, cavea shallow to medium; endexine the same thickness as or thicker than foot layer.

Corymbieae

Pollen oblate-spheroidal, sub-triangular in polar view, elliptic in equatorial view, tricolporate; colpi separate, medium width, with obtuse ends; ora lalongate; tectum microperforate, covering the whole surface of the grain; echinate, spines average in number and density, evenly-distributed, conical-pointed, 4–5 μm, smooth, with perforations; tectum not raised, reticulate; non-lophate; infratectum two-layered, layers very distinct, both layers columellate; internal tectum absent; columellae unbranched, medium, not swollen at base, evenly-distributed; spine channel absent, spine columellae fully-attached, no internal foramina reported; fully-caveate, cavea shallow; endexine thicker than foot layer.

Senecioneae

Pollen oblate, prolate or spheroidal, round or sub-triangular in polar view, round or elliptic in equatorial view, blunt-ended, tricolporate, colpi separate, narrow to broad, with thin margin and acute ends, ora lalongate or circular; tectum microperforate, covering whole surface of grain; echinate, spines few to many, sparse to dense, evenly-distributed, conical and blunt or pointed, 2–7 μm, smooth or slightly swollen at base, solid or with perforations; tectum not raised, with rounded granules, striate, reticulate or areolate; non-lophate; infratectum single-layered, outer layer columellate, internal tectum sometimes present, single-layered; with or without internal foramina, without spine channels; fully (occasionally partially) caveate, cavea very shallow to medium; endexine thicker than foot layer.

Calenduleae

Pollen prolate or spheroidal, round or triangular in polar view, round or elliptic in equatorial view, tricolporate; colpi separate, narrow to medium, with thin margin and acute ends, ora lalongate, lolongate or circular, mesoaperture sometimes present; tectum microperforate, covering whole surface of grain; echinate, spines few to many, average to dense, evenly-distributed, conical or long-pointed, 1–4 μm, slightly swollen at base, with perforations; tectum not raised, usually reticulate; non-lophate; infratectum single-layered, outer infratectum columellate, internal tectum usually present, single, solid, indistinct, internal foramina ubiquitous, spine channel absent, spine columellae freely hanging; fully or (occasionally) partially caveate, cavea shallow to deep; endexine thicker than foot layer.

Gnaphalieae

Pollen oblate (*Vellereophyton*), spheroidal, prolate, round or sub-triangular in polar view, round, elliptic or oblong in equatorial view, blunt-ended, tri- (bi- or tetra-) colporate; colpi separate, rarely syncolpate, narrow to medium, with acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines few to average in number, average to dense, evenly-distributed (slightly uneven in *Vellereophyton*), conical-pointed, 1–9 μm, always arising smoothly from the surface of the grain, usually with perforations; tectum not raised, occasionally with pointed granules, smooth; non-lophate; infratectum with two distinct, firmly-attached layers, outer infratectum columellate, internal tectum absent; supporting layer spongy, with internal foramina, spine channel usually absent, spine columellae fully-attached; always fully caveate, cavea shallow to medium; endexine thicker than foot layer.

Astereae

Pollen generally small, prolate, oblate or spheroidal, round, sub-triangular or triangular in polar view, round or elliptic in equatorial view, blunt-ended, tri- (or tetra-) colporate; colpi separate or syncolpate, narrow to broad, with thin margin and obtuse or acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines average to many, average to dense, evenly-distributed, conical-pointed, 1.5–5.0 μm, abrupt to very swollen at base, solid; tectum not raised, smooth or reticulate; non-lophate; infratectum single-layered, outer infratectum columellate, lacking internal tectum; with internal foramina, without spine channels, spine columellae hanging or fully-attached; fully or partially caveate, cavea shallow to deep; endexine thicker than foot layer.

Anthemideae

Pollen prolate, oblate or spheroidal, round or sub-triangular in polar view, round or elliptic in equatorial view, tricolporate; colpi separate, narrow to broad, with thin margin and obtuse or, usually, acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; psilate or (usually) echinate, spines few to many, sparse, evenly-distributed, conical-pointed, 1–7 µm, smooth or slightly swollen at base, with perforations; tectum not raised, with conical spinules and coarse granulate; non-lophate; infratectum of two to three distinct layers, outer infratectum of one to several layers, columellate, internal tectum present, single- to multi-layered, spongy; supporting layer columellate, columellae thick, sausage- or broccoli-like, bases not swollen, without internal foramina; evenly-distributed, without spine channels, with spine columellae hanging freely or fully-attached; acaveate except for *Ursinia*; endexine thinner than foot layer, often only present around apertures.

Inuleae

Pollen prolate or spheroidal, round or sub-triangular in polar view, round or elliptic in equatorial view, blunt-ended, tri- (tetra-) colporate; colpi separate, very long, narrow to broad, with thin margin and acute ends, ora lalongate or circular; tectum microperforate, covering whole surface of grain; echinate, spines average in number, sparse to dense, conical, rounded or pointed, 2.5–6.0 µm, sometimes swollen at base, with perforations; tectum not raised, reticulate; non-lophate; infratectum of two to three distinct or indistinct layers, outer infratectum columellate, internal tectum present or absent, single-layered and spongy or compact; supporting layer spongy or columellate, columellae thin to medium, unbranched (occasionally ramified), bases often swollen, evenly-distributed or, often, only present under the spines, internal foramina present in some species, absent or vestigial, with spine channels, spine columellae hanging freely; fully caveate, cavea shallow to deep; endexine thicker than foot layer.

Athroismeae

Pollen spheroidal, round or sub-triangular in polar view, round in equatorial view, tricolporate; colpi separate, broad, with thin margin and acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines of average number, sparse to dense, evenly-distributed, conical, blunt, 1–5 µm, with slightly swollen bases and perforations; tectum not raised, coarse granulate; non-lophate; infratectum single-layered, outer infratectum columellate, internal tectum absent, columellae with irregular thickenings towards the base under spines, with internal foramina and spine channels, spine columellae fully-attached to base layer; fully caveate; cavea deep; endexine thicker than foot layer.

Helenieae

Pollen oblate or spheroidal, round (occasionally sub-triangular) in polar view, round or elliptic in equatorial view, tricolporate; colpi separate, narrow (rarely medium), with thin margin and acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines few to average, sparse to average, usually irregularly-distributed, conical or pointed, 4–9 µm, usually swollen at base, solid or with perforations; tectum often raised between some spines, coarse-granulate or reticulate; non-lophate; infratectum of one or two distinct layers, outer infratectum columellate, internal tectum absent; supporting layer spongy where present, with internal foramina, evenly-distributed, with or without spine channels, spine columellae freely hanging or fully-attached to base layer; fully caveate, cavea shallow to deep; endexine thicker than foot layer.

Coreopsideae

Pollen spheroidal, round in both views, tricolporate; colpi separate, broad, with thin margin and acute ends, ora lalongate; tectum microperforate or imperforate, covering whole surface of grain; echinate, spines average in number and density, irregularly-distributed, conical to long-pointed, 3.5–8.5 µm, bases smooth or swollen, solid or with perforations; tectum not raised, reticulate; non-lophate; infratectum one-layered, outer infratectum spongy or columellate, without internal tectum; with internal foramina, without spine channels, spine columellae hanging freely; fully caveate, cavea deep or shallow; endexine much thicker than foot layer.

Neurolaeneae

Pollen prolate or spheroidal, tricolporate; colpi with thin margin and acute ends, ora lalongate; echinate, spines average in number and density, conical, 3–7 µm, with perforations; non-lophate; infratectum single-layered, columellate, without internal tectum, spine columellae fully-attached, with internal foramina; partially caveate; endexine thicker than foot layer.

Tageteae

Pollen prolate, oblate or spheroidal, round or sub-triangular in polar view, round or elliptic in equatorial view, tricolporate; colpi separate, narrow to medium, with thin margin and acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines few to average, sparse to dense, evenly-distributed, conical to long-pointed, 3–7 µm, bases abrupt to swollen, solid; tectum sometimes slightly raised between spines; non-lophate; infratectum of two indistinct layers, outer infractectum columellate, internal tectum absent; supporting layer spongy, with internal foramina, with spine channels, spine columellae hanging; fully caveate, cavea shallow; endexine thicker than foot layer.

Chaenactideae

Pollen prolate or spheroidal, sub-triangular in polar view, round or elliptic in equatorial view, blunt-ended, tricolporate; colpi separate, narrow to medium, with acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines average to many, dense to sparse, evenly-distributed, conical to long-pointed, 4–8 µm, bases slightly swollen, with perforations; tectum not raised, reticulate; non-lophate; infratectum of two indistinct layers, outer infratectum columellate, internal tectum absent; supporting layer spongy, with internal foramina, with spine channels, spine columellae fully-attached; fully caveate, cavea of medium depth, endexine thicker than foot layer.

Bahieae

Pollen spheroidal, round in both views, tricolporate; colpi separate, narrow, with thin margin and acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines few-average, sparse-average, evenly-distributed, conical to long-pointed, 1–5 µm, with smooth bases, solid or with perforations; tectum not raised, reticulate; non-lophate; infratectum one-layered, outer infratectum columellate, columellae bases swollen, internal tectum absent, with internal foramina in most species, sometimes with spine channels, spine columellae hanging or fully-attached; fully or partially caveate, cavea shallow to medium; endexine thicker than foot layer.

Polymnieae

Pollen prolate or spheroidal, round or sub-triangular in polar view, blunt-ended, tricolporate; colpi separate, narrow, with thin margin and acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines few to average, sparse, irregularly-distributed, pointed, 4–5 µm, with smooth bases, solid; tectum not raised, smooth; non-lophate; infratectum one-layered, outer infratectum columellate, columellae bases swollen, internal tectum absent, with internal foramina, without spine channels, spine columellae fully-attached; fully caveate, cavea shallow; endexine thicker than foot layer.

Heliantheae

Pollen spheroidal, round or sub-triangular in polar view, round in equatorial view, tricolporate; colpi separate, narrow to medium, with thin margin and acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines few to many, sparse to average, irregularly-distributed, conical to long-pointed, 1–5 µm, bases smooth or swollen, solid or with perforations; tectum not raised, smooth or reticulate; non-lophate; infratectum one-layered, outer infratectum columellate or spongy, columellae bases swollen, internal tectum absent, internal foramina present or absent, spine channels present or absent, spine columellae hanging or fully-attached; partially or fully caveate, cavea shallow to deep; endexine thicker than foot layer.

Millerieae

Pollen spheroidal, round in both views, tricolporate; colpi separate, broad, with acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines average in number and density, evenly-distributed, conical-pointed, 2.5 µm, bases smooth or swollen, solid; tectum not raised, reticulate; non-lophate; infratectum one-layered, outer infratectum columellate or spongy, columellae bases swollen, internal tectum absent, with internal foramina, with spine channels, spine columellae hanging or fully-attached; fully caveate, cavea medium to deep; endexine thicker than foot layer.

Madieae

Pollen spheroidal, round in both views, tricolporate; colpi separate, medium, with thin margin and acute ends, ora lalongate; tectum microperforate, covering whole surface of grain; echinate, spines average to many, average to dense, evenly- or irregularly-distributed, conical, blunt or long-pointed, 1–7 µm, bases swollen, solid or with perforations; tectum not raised, reticulate; infratectum one-layered, outer infratectum columellate, columellae bases swollen, internal tectum absent, internal foramina present in most species, with spine channels, spine columellae hanging or fully-attached; partially caveate, cavea medium to deep; endexine thicker than foot layer.

Perityleae

Pollen spheroidal, round in both views, tricolporate; colpi separate, medium, with acute ends, ora lalongate; tectum microperforate, covering whole surface of grain, echinate, spines very many and dense, evenly-distributed, pointed, 4 µm, bases swollen, solid; tectum not raised, reticulate; non-lophate; with internal foramina; caveate.

Eupatorieae

Pollen small compared to all other Compositae, oblate or spheroidal, sub-triangular in polar view, round in equatorial view, tricolporate; colpi separate, medium, with thin margin and obtuse ends (acute in *Ageratina*), ora lalongate; tectum microperforate, covering whole surface of grain; echinate or rarely subpsilate, spines average in number, sparse (average in *Ageratina*), evenly-distributed, pointed, short, 1.0–2.5 µm, bases smooth, solid or with perforations; tectum not raised, areolate; non-lophate; infratectum one-layered; outer infratectum columellate, columellae bases not swollen, internal tectum absent, with spine channels but few spine columellae; internal foramina often present; fully caveate, cavea shallow; endexine about as thick as foot layer.

Chapter 8

Evolution of Compositae flowers

Charles Jeffrey

INTRODUCTION

Since the Reading conference, there have been notable advances in our understanding of the sister group relationships of Compositae and its subfamilies and tribes (Bremer 1987, 1994, 1996; Hansen 1991, 1997; Lammers 1992; Olmstead et al. 1992; Chase et al. 1993; Gustafsson 1996; Gustafsson et al. 1996; Jansen and Kim 1996; Bayer and Starr 1998; Baldwin et al. 2002; Panero and Funk 2002; Lundberg and Bremer 2003; Anderberg et al. 2005; Funk et al. 2005; Panero 2005; Kadereit and Jeffrey 2007). We have also extended our knowledge of the ontogeny of capitula and florets (Leins and Erbar 1987, 2000; Claßen-Bockhoff 1992; Harris 1995; Palmer 1996; Erbar and Leins 2000) and refined descriptive terminology of capitular and corollar forms (Bremer 1994; Kadereit and Jeffrey 2006). Our knowledge of pollination and breeding systems has also increased. It is appropriate, therefore, to once again consider the evolution of the capitulum as a functional unit, the floret as a functional unit of the capitulum, and, in many cases, the synflorescence as a further functional unit. It is to be emphasized that the hypotheses below in nearly all cases lack experimental verification, but they are offered in hopes of stimulating functional and adaptational perspectives regarding taxonomically important characters in the family.

CAPITULUM

The capitulum as a functional unit has to maintain a dynamic equilibrium (Harris 1999), balancing morphological and physiological demands under diverse evolutionary pressures, and providing successfully for nutrition, defense, breeding systems, pollination, dispersal, germination and seedling establishment; below these requirements are discussed in more detail.

Nutrition

The developing ovule is a powerful sink requiring a rapid supply of nutrients over a comparatively short time. The efficiency of the supply mechanism and the length of the supply path are therefore important factors. Apart from a few derived C_4 (Smith and Turner 1975) and CAM (Fioretto and Alfani 1988) representatives, the members of Compositae possess an advanced apoplastic type of leaf terminal bundle, in which the phloem is loaded from the apoplast (cell walls and intercellular spaces) by means of transfer cells (Gamalei 2004). This mechanism is characteristic of advanced herbaceous eudicotyledons and is also found, for example, in subfamily Faboideae of Leguminosae and in many, but not all, representatives of Umbelliferae, Scrophulariaceae and Boraginaceae. Thus, there is no advantage here for Compositae in terms of energy expenditure over such herbaceous competitors, nor over Gramineae with their different but equally effective supply mechanisms. The condensation of the inflorescence into a capitulum, however, certainly has the effect of shortening the supply route. Competing fructan-producing families, apart from Calyceraceae, have rarely evolved the capitate inflorescence (Harris 1999), and as far as is known, apart from Boraginaceae already mentioned, they have only a less advanced type of apoplastic phloem loading. Compositae alone combine a constant capitate inflorescence, a constant advanced apoplastic type of phloem loading, and the constant production of fructan as storage carbohydrate. The evolutionary significance of the last was pointed out by Hendry (1996) at the Kew Compositae conference. In this unique combination, in conjunction with their well-developed chemical defense mechanisms, may well lie at least one of the explanations for the evolutionary success of the family.

Supply may be made yet more effective by surrounding the capitulum (as in *Aedesia*, Vernonieae) or a group of capitula (as in *Leontopodium*, Gnaphalieae) by a rosette of enlarged foliage leaves. The same effect may be obtained by enlargement of the outer phyllaries, but here phyllary modification is functionally constrained by other demands upon the involucre (e.g., defense, pollinator attraction). The further condensation of capitula into syncalathia may also be partly a reflection of this nutritional adaptive theme. When the number of florets in a capitulum is reduced to very few or one, the initial advantage of flower aggregation is largely lost, unless the synflorescence itself becomes condensed.

Defense

The capitulum with many flowers and fruits concentrated in one place may be an energy-efficient development from the nutritional point of view, but it provides a convenient food reserve for predators. A considerable selective role is played by pest pressure (Gillett 1962). The evolution of effective defense mechanisms is therefore an essential corollary of the evolution of the capitulum. Chemical defenses are variously well-developed in Compositae, and the involucre is an obvious site in which defensive secondary metabolites might be concentrated. Even so, physical protection against phytophagous invertebrates and herbivorous vertebrates plays an important role, leading to the evolution of various types of protective armature, indumentum (including chemically-defensive glands), phyllary orientation (including complete enclosure of achenes by phyllaries, as in *Acanthospermum*, *Melampodium* and *Milleria*, Millerieae), connation, and sclerification. In syncalathia, the protective role of the phyllaries may be supplemented by or transferred to more peripheral structures.

The defensive role of the pappus has been discussed in detail (Stuessy and Garver 1996). These authors contend that the pappus may have had originally only a defensive role, but subsequently developed a dual role for defense and dispersal. This may well be the case for non-barnadesioid Compositae, but the pappus in Barnadesioideae appears to be primarily an adaptation for dispersal. In Barnadesioideae, the pappus elements bear the same type of hair as found on all other floral parts, and this suggests that the barnadesioid pappus is derived from some extra-corollar structure, perhaps a synsepalous calyx. It early develops as a ring meristem in *Arnaldoa*, Barnadesieae (Leins and Erbar 2000). The varying times of initiation of the pappus primordia in non-barnadesioid Compositae suggest that at least some types of pappus in this group may be homologues of enations or trichomes of a calycular or epicalycular structure; the vascularization sometimes observed (Tamanshian 1956) in their pappus-elements appears to be a derived condition, perhaps a result of reactivation of neotenically-suppressed genes. Thus the pappus appears to have been differently and independently derived in Barnadesioideae and in the non-barnadesioid Compositae. Other pappus types in the latter, the primordia of which appear very late in floral development around the apex of the developing ovary, probably represent de novo developments and are not to be considered homologues of those that are initiated in the early stages of floret ontogeny.

RECEPTACLE

Receptacles are often provided with various vascularized or non-vascularized outgrowths between the florets, such as hairs, bristles, squamellae, elevated alveolar margins, and scales (Stuessy and Spooner 1988). Their function is also largely defensive, especially against desiccation of the florets during early stages of development. Particular evolutionary interest has been accorded to the vascularized receptacular scales (paleae), which exhibit generally a one-to-one relationship with the florets and have therefore been regarded as homologues of inflorescence bracts subtending florets. As such, they have sometimes been considered plesiomorphic in Compositae and therefore indicative of primitiveness of those tribes in which they frequently occur, especially Heliantheae s.l. (Cronquist 1955, 1977). However, both our current hypotheses of sister group relationships in the family and our knowledge of floral development (Harris 1995; Palmer 1996) indicate that the receptacular scales are derivative, not ancestral, structures and are not the homologues of flower-subtending bracts. When receptacular scales are present, they are commonly initiated along with the floret as a single primordium; in some cases, the floret primordium is initiated first. Only rarely does the scale primordium appear before the floret primordium, as would be expected if the scale were a homologue of a flower-subtending bract.

ACHENES

The achenes of Calyceraceae show distinct structural-morphological similarities to those of Compositae (Muradian 1991). Possibly these are parallelisms, rather than synapomorphies, but the difference between parallelism and synapomorphy is merely one of degree, not of kind; the change in genetic information-content may be the same in both processes of acquisition.The physical defensive role of the pericarp-testa complex (Grau 1980) is constrained by equally important adaptations facilitating dormancy (Linington et al. 1996; Seiler 1996), germination (Widell and Vogelmann 1985; Takaki and Gama 1998), and seedling establishment. The phytomelanin layer developed in the pericarp of the achenes of most Heliantheae (for the members of which it is probably a synapomorphy) and a few Vernonieae may also be defensive against insect attack or as a barrier to visible light protecting the embryo from premature breaking of dormancy.

Defense may also be attained by the strategy of not putting all one's eggs in one basket, i.e., by the production of very numerous achenes in many small, simple capitula in diffuse synflorescences. This strategy may also be adaptive for seedling establishment and stand maintenance (as in *Artemisia tridentata*; Young and Mayeux 1996). In this strategy, the advantage of a short supply path is largely lost. Changes in relative selection pressures may be responsible for a cyclic pattern of capitular aggregation and de-aggregation. The rare heterocalathial monoecy developed in Ambrosiinae may have resulted from an interplay of such selective pressures, favoring nutrition and defense in the pistillate capitula, and wind pollen dispersal in the staminate capitula. It should be borne in mind, however, that once it has attained the status of a functional flower, the syncalathium will be subject to the same epigenetic and selectional constraints as the simple capitulum.

ANTHERS

The apical anther appendage usually present in Compositae may also have a defensive function. In a number of groups of non-asteroid Compositae, it is sclerified. Interestingly, ornithophily is practically confined in the family to representatives of such groups. The sclerification can then be considered not only as a defensive response to pest pressure but also as a pre-adaptation to pollination by large, robust vectors, such as birds, which might well damage an entirely soft anther structure. The alternative hypothesis, that ornithophily is plesiomorphic in Compositae, is, on available evidence, less likely (see Chapter 13). The derived sclerification in some members of Heliantheae s.l. is most likely an adaptation partly as a support to the elongating style and partly as a defensive modification in the earlier developmental stages; in these plants, entomophily is already evolutionarily fixed.

BREEDING SYSTEM

The majority of Compositae are sporophytically self-incompatible. The incompatibility is strong but not absolute, and self-compatibility is also not uncommon. Perfect florets are protandrous but the capitulum as a whole is protogynous when the outer florets (bilabiato-radiate, radiate, or filiform) are pistillate or functionally so. The breeding system may be based on one type of capitulum (sexually homocalathial) or on more than one type (sexually heterocalathial). In homocalathial species, the following systems are met with: monocliny (all florets perfect); gynomonoecy (outer florets pistillate, inner perfect); and monoecy (outer florets pistillate, inner functionally staminate). Andromonoecy (some florets perfect, others functionally staminate) is rare. In heterocalathial species, we find: dioecy (some capitula pistillate, others staminate, borne on different plants); gynodioecy (some capitula with pistillate florets, others with perfect florets, borne on different plants); and monoecy (as in dioecy, but the sexually different capitula borne on the same plant). Androdioecy (some capitula with perfect florets, others with staminate florets, borne on different plants) is rare. From this diversity, it is clear that, in comparison with a simple solitary flower, the capitulum as the functional floral unit of Compositae is pre-adapted to flexibility in breeding system evolution. The genus *Cavea* (incertae sedis) is apparently unique in that its populations consist of a mixture of homocalathial monoecious and heterocalathial dioecious individuals (Ling and Chen 1965). In radiate capitula, the ray florets are sometimes sterile or neuter and function only to attract and/or provide a landing-stage for pollen vectors. The capitulum functioning as a single flower provides a more flexible basis for breeding system evolution than does the single flower as such.

FLORETS

Outgroup (Calyceraceae, Goodeniaceae, and non-barnadesioid Compositae) comparison with Barnadesioideae indicates that homocalathial monocliny is probably the ancestral condition in Compositae and the other types derived (Stuessy and Urtubey 2006; Torices et al. 2006). Lane (1996) notes that the central florets of such a monoclinous capitulum rarely set fruit since there are no staminate-phase florets remaining to attract bees when these florets are in the pistillate phase (pollinators are attracted only by staminate-phase florets, which provide nectar and pollen, not provided by pistillate-phase florets). Reduction of the inner florets to a functionally staminate condition avoids energy expenditure on non-functional gynoecia, a factor which undoubtedly played a part in the evolution of homocalathial monoecy.

The bilobed style with stigmatic surfaces on the inside of the initially adpressed style-arms is a synapomorphy for the members of Compositae; the outgroup families Calyceraceae and Goodeniaceae have undivided styles with a terminal, at most shortly bilobed, stigma. The Compositae stylar mechanism serves to delay the onset of the pistillate phase in floret development and so provides protandry of the perfect florets. Pollen is no longer shed onto the stigmatic surface, thus reducing the likelihood of premature selfing and inbreeding. The divided style is also an integral part of the secondary pollen presentation mechanism.

Cleistogamy as a supplement (or rarely as an alternative) to chasmogamy has developed infrequently; the different types of capitula are usually spatially and/or temporally separated. Obligate selfing in chasmogamous capitula and the various forms of apomixis that are commonly observed in Compositae are obviously derived states, and homoplasious.

POLLINATION

The pollination biology of Compositae was admirably summarized by Lane (1996) at the Kew Compositae conference in 1994. The most important pollen vectors are solitary bees, but fly pollination is also widespread (see, e.g., Johnson and Midgley 1997). Attraction mechanisms are visual (colors and patterns in both visible and UV light; see, e.g., Baagøe 1977, 1978, 1980), chemical (floral scent), and nutritive (pollen and nectar). The capitulum functions visually as a single flower and as such may be provided with a floral (pseudobilabiato-radiate, bilabiato-radiate, radiate, enlarged outer ligulate or enlarged outer radiant) or an extra-floral (colored involucral bracts) pseudocorolla.

NEOTENY AND EVOLUTION OF THE CAPITULUM

The evolution of the capitulum from a more diffuse inflorescence type is an example of neoteny, the curtailment of development to what is essentially a bud stage, brought about by the suppression or inactivation of genes. As was pointed out by Takhtajan (1969), the importance of neoteny lies in the attainment of maximum phenotypic effect by means of minimal genetic change. This was accompanied by a similar curtailment of the development of the corollas of individual flowers, from what could have been a bilabiate (2/3) or ligulate (0/5) condition, as exhibited by the more distant outgroup family Goodeniaceae, to a tubular, actinomorphic (5/0) condition, which is typical in Calyceraceae and Barnadesioideae (Stuessy and Urtubey 2006). While the further evolution of the capitulum as a functional unit was inevitably constrained by strong epigenetic canalization under pollinator selection pressure for capitular symmetry (Moller and Eriksson 1995), this was not the case with the corollas of individual florets in the early stages of the evolution of Compositae. Differential reactivation of neotenically suppressed genes gave rise to a wide range of corolla types, providing the raw material for stabilization under the influence of various selective pressures associated with pollination. The main corolla types now occurring are regular (5/0), pseudobilabiate (1/4), and ligulate (0/5) in Barnadesioideae; bilabiate (2/3) and regular (5/0) in Mutisioideae; regular (5/0) in Carduoideae; regular (5/0) and ligulate (0/5) in Cichorioideae; and regular (5/0) and radiate (0/3) in Asteroideae. The general evolutionary trend is toward stabilization of corolla types in the capitulum and a reduction in their diversity, no doubt associated with a parallel stabilization of relationships with pollen vectors. Stabilization reaches its peak in Asteroideae, for which the radiate capitulum with 0/3 outer and 5/0 inner florets is basic, probably adaptive and probably a synapomorphy for its members. In the crown group of asteroid tribes (Gnaphalieae, Astereae, Anthemideae, Inuleae, Heliantheae; also Senecioneae) a new corolla type, the filiform pistillate (here conventionally denoted as 0/0) developed, as a device by which capitular protogyny and homocalathial monoecy could be more efficiently provided. Loss of rays has repeatedly led to the development of disciform and secondarily discoid capitula. The development of rays in some non-asteroid tribes (e.g., Dicomeae, Liabeae, Arctotideae) is an obvious parallelism, exemplifying Vavilov's Law of Homologous series (Vavilov 1951). The symmetry of the capitulum is usually radial (actinomorphic), only rarely, as in a few Dicomeae, Pertyeae and Vernonieae, bilateral (zygomorphic).

Previous (Jeffrey 1977) postulation of the bilabiate (2/3) corolla type as plesiomorphic in Compositae was based on the assumption that the capitulum represented a reduced simple raceme. However, as shown by Erbar and Leins (2000) in their investigation of floral development in *Arnaldoa* (Barnadesioideae), the loose arrangement of floral primordia, the variable floret orientation and the not perfectly spiral sequence of floret initiation indicate that the capitulum is most likely derived from an originally more complex type of lax, indeterminate inflorescence, perhaps a thyrse, which, according to Carolin (1967), is the primitive inflorescence type in Goodeniaceae. In this respect it is interesting to note that, as Takhtajan (1966) wrote, a new, more advanced group originates not from the more recent and specialized representatives of the ancestral group, but from very ancient and primitive ones. This "principle of the unspecialized" may be expressed more succinctly thus: synapomorphy precedes autapomorphy. In the closest outgroup, Calyceraceae, the corollas are more or less regular (5/0). In the next outgroup, Goodeniaceae, the corollas are mostly bilabiate (2/3) or ligulate (0/5), but in *Brunonia*, where the inflorescence is a capitulum, the corolla type is regular (5/0). This analogy shows the expected reduction of the corolla to an actinomorphic (5/0) type consequent upon the condensation of the inflorescence into a capitulum.

SECONDARY POLLEN PRESENTATION

With the exception of a few anemophilous species, secondary pollen presentation, involving an anther-style complex (Thiele 1988), is universal (and ancestral) in Compositae. Secondary pollen presentation serves to limit the amount of pollen removed by a pollinator in the course of a single visit (Leins and Erbar 1990; Ladd 1994; Erbar and Leins 1995), thus increasing the probability of successful pollen transfer and optimizing the pollination process. It occurs in a number of families of Asteridae, including the outgroup families Goodeniaceae and Calyceraceae. The former exhibit a specialized stylar cup deposition mechanism, the latter a simple deposition mechanism, in which the pollen grains held together by pollenkitt are deposited onto the top of the style. In Compositae, three variants may be distinguished. From the anther-tube, into which it is shed, the pollen may be dragged out by adherence to papillae-like microhairs on the outside of the style shaft and style arms, brushed out by sweeping hairs on the outside of the style arms and very often also on the upper part of the style shaft (even on an apical appendage to the style arms), or pumped out by spreading sweeping hairs on the apex of the style arms. The drag mechanism is apparently plesiomorphic and is characteristic of Barnadesioideae, many Mutisioideae and a few Carduoideae, the brush mechanism of most Carduoideae, Cichorioideae and many Asteroideae, and the pump mechanism of many Asteroideae. However, the brush and pump mechanisms are homoplasious, appear to have evolved independently many times, and reversals have apparently occurred.

DISPERSAL, GERMINATION AND ESTABLISHMENT

Strategies of dispersal, germination and establishment are interdependent, and their interplay is reflected in the evolutionary modifications exhibited by Compositae in their fruiting capitula and achenes. Wind dispersal of individual achenes, facilitated by the development of a pappus of hairs, appears to be plesiomorphic in Compositae. Evolutionary developments within the family include modification and loss of the pappus, change in achene structure, development and modification of receptacular bracts (Stuessy and Spooner 1988), heterocarpy, synaptospermy and amphicarpy. These modifications are associated with shifts in dispersal strategy to, e.g., dispersal by ants (the development of elaiosomes), water (the development of corky ribs), or vertebrates (the development of drupaceous fruits, or of hooks, barbs or sticky knobs or glands on the achenes or other disseminules). Nearly all such modifications have occurred in parallel in different tribes, beautifully exemplifying the operation of Vavilov's Law of Homologous series (Vavilov 1951), and only rarely are they group-definitive at the higher taxonomic levels. Exceptions include Calenduleae, in which loss of pappus is accompanied by increase in achene size and complexity (with the development of winged or drupaceous fruits) and heterocarpy, and Anthemideae, in which loss of pappus is associated with reduction in achene size (small epappose achenes may be wind-dispersed, splash-dispersed or dispersed by adherence to mud or soil on the feet of birds and other vertebrates). The inconsistently deciduous capillary pappus often observed in Compositae appears to be a mechanism for achieving a mixed dispersal strategy, in which some achenes remain in the vicinity of the fruiting plant (Schmida 1985).

Heterocarpy is an extremely widespread phenomenon in Compositae (Voitenko 1989; Beneke et al. 1992), in which the position effect (Takhtajan 2001) in the individual capitula facilitates its development. The different achene morphs may exhibit different dispersal, dormancy, survival and germination strategies and thus enable the species to take advantage of a wider range of environmental conditions and/or better survive periods of adverse conditions. Compared with the simple solitary flower, the capitulum may be considered a pre-adaptation to the development of heterocarpy.

Synaptospermy (Murbeck 1920; Claßen-Bockhoff 1996), in which the achenes are retained in the involucre, is most characteristic of Compositae of semi-arid and arid areas (Gutterman and Ginott 1994). It may be partial (when some of the achenes are dispersed singly) or complete (when all the achenes are retained in the capitulum).

Amphicarpy (the ability to produce subterranean as well as subaerial fruits) is confined in Compositae, as far as is known, to the monotypic genus *Gymnarrhena* and is thus definitive of the monotypic tribe Gymnarrheneae (Panero and Funk 2002). Amphicarpy likewise appears to be an adaptive mechanism developed as a response to unreliable moisture availability (Koller and Roth 1964).

SUMMARY AND CONCLUSION

Compositae are the most evolutionarily successful family of angiosperms in terms of numbers of genera and species (over 1620 and about 23,000, respectively). They are unique in Asteridae in exhibiting a constant combination of advanced apoplastic phloem loading, capitular inflorescence, divided style, fructan carbohydrate reserve, and highly-developed chemical defenses. If this combination is the reason for their success, then floral features have undoubtedly played a significant part. The greater evolutionary plasticity of the capitulum as a functional flower, in comparison with the simple solitary flower, is important in this respect. The most adaptively and evolutionarily advanced subfamily, Asteroideae, is also the largest (over 1200 genera and about 17,000 species), within which the similarly most advanced tribe, Heliantheae, is also the largest (480 genera and over 5600 species). In supersubtribe Eupatoriodinae of this tribe, which accounts for about 180 of its genera and over 2000 of its species, a shift to a new adaptive peak has occurred, and they have proliferated in a niche in which the basically yellow-radiate, little-scented or scentless helianthoid capitulum has been replaced by a discoid, non-yellow, usually scented capitulum in which the prominent appendages of the style-arms are often the main visual attractant. Most of their diversity is exhibited in the New World (as is true for Heliantheae as a whole), where representatives of the tribes Cardueae, Gnaphalieae, Inuleae and Anthemideae are comparatively few. As a result of this adaptive shift, the taxon has become highly autoapomorphic, and it has been customary to recognize it at tribal rank. But as I have pointed out (Jeffrey 2002), while autapomorphies have their place in systematics, that place is in the descriptions of taxa, not in the according to the taxon concerned of a higher rank such that another taxon would be rendered paraphyletic. It is therefore preferable to recognize this taxon, like the other major lineages of the tribe Heliantheae, at supersubtribal and not tribal rank (Jeffrey 2004). As it would be a pity to mask the evolutionary success of the robustly monophyletic Compositae and Asteroideae by splitting them into smaller families and subfamilies, respectively, so it would be a pity to mask the similar success of the equally monophyletic Heliantheae by splitting it into smaller tribes.

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Chapter 9

Genetic diversity in Asteraceae endemic to oceanic islands: Baker's Law and polyploidy

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INTRODUCTION

The diversity of endemic plants found on oceanic islands is the result of the three processes of dispersal, establishment, and the evolutionary diversification of progeny of the colonizers (Carlquist 1974). As emphasized by Carlquist (1974: 20–21), "Factors assisting rapid evolution on oceanic islands include lack of competitors and predators, presence of a wide spectrum of ecological opportunities, and presence of isolating mechanisms (ridges, etc.) that favor small, rapidly changing populations". The important implications of Carlquist's (1974) statement are that evolution can occur rapidly following dispersal and establishment of a colonist, and open habitats on islands allow the establishment and radiation of a range of recombinant progeny that may not have been successful under the stronger selection of competitors and predators present in many continental habitats (Fig. 9.1A). Asteraceae possess several attributes that account for their high representation (Skottsberg 1921; Wiggins and Porter 1971; Wagner et al. 1990; Cronk 2000) in the endemic floras of oceanic islands. Their fruits have mechanisms that facilitate dispersal, they are effective colonizers, and they can be pollinated by a variety of vectors, which means they do not require specialized pollinators in the islands (Carlquist 1966, 1974). While both dispersal and colonization are obviously critical components of the entire process, they do not necessarily mean that progeny of the colonizers will diversify. Indeed, invasive species (such as weeds) of oceanic islands are good dispersers and colonizers, and Asteraceae are very successful invasives of oceanic islands (e.g., Wagner et al. 1990; Swenson et al. 1997). The attributes of colonizers that favor the dispersal and establishment phases in island archipelagos on the one hand, and evolution and diversification of their progeny on the other hand may be quite different. If dispersal events are rare, as no doubt would be the case for remote, small islands, then single propagules of self-compatible (henceforth, SC will designate both the adjective self-compatible and the noun self-compatibility) colonizers would be at a selective advantage for dispersal to and establishment of sexually reproducing populations in oceanic archipelagos. By contrast, colonizers from self-incompatible (SI) continental populations would presumably be at a selective disadvantage for dispersal and establishment because more than one dispersal event would be required; however, the greater genetic diversity of the colonizers would facilitate radiation and evolution in oceanic archipelagos. The basic purpose of this chapter is to discuss certain aspects of these different processes in the evolution of island lineages of Asteraceae.

Breeding system of colonizers

The breeding system of a colonizer is an important factor in determining whether it has the potential to diversify into an endemic insular lineage. With regard to dispersal, Baker (1955) argued that self-compatible colonizers would have an advantage over SI ones because only one propagule is required to establish a sexually reproducing population following long distance dispersal. In addition, SC would facilitate rapid population growth by sexual reproduction. By contrast, the likelihood of two or more propagules of SI yet cross-compatible plants being independently dispersed in time and space such that they could exchange genes is less likely. Baker's (1955) hypothesis that SC colonizers would be favored for establishment and dispersal was dubbed "Baker's Law" by Stebbins (1957).

Carlquist (1966) held that the progeny of SC, and especially autogamous, colonizers would be at a disadvantage

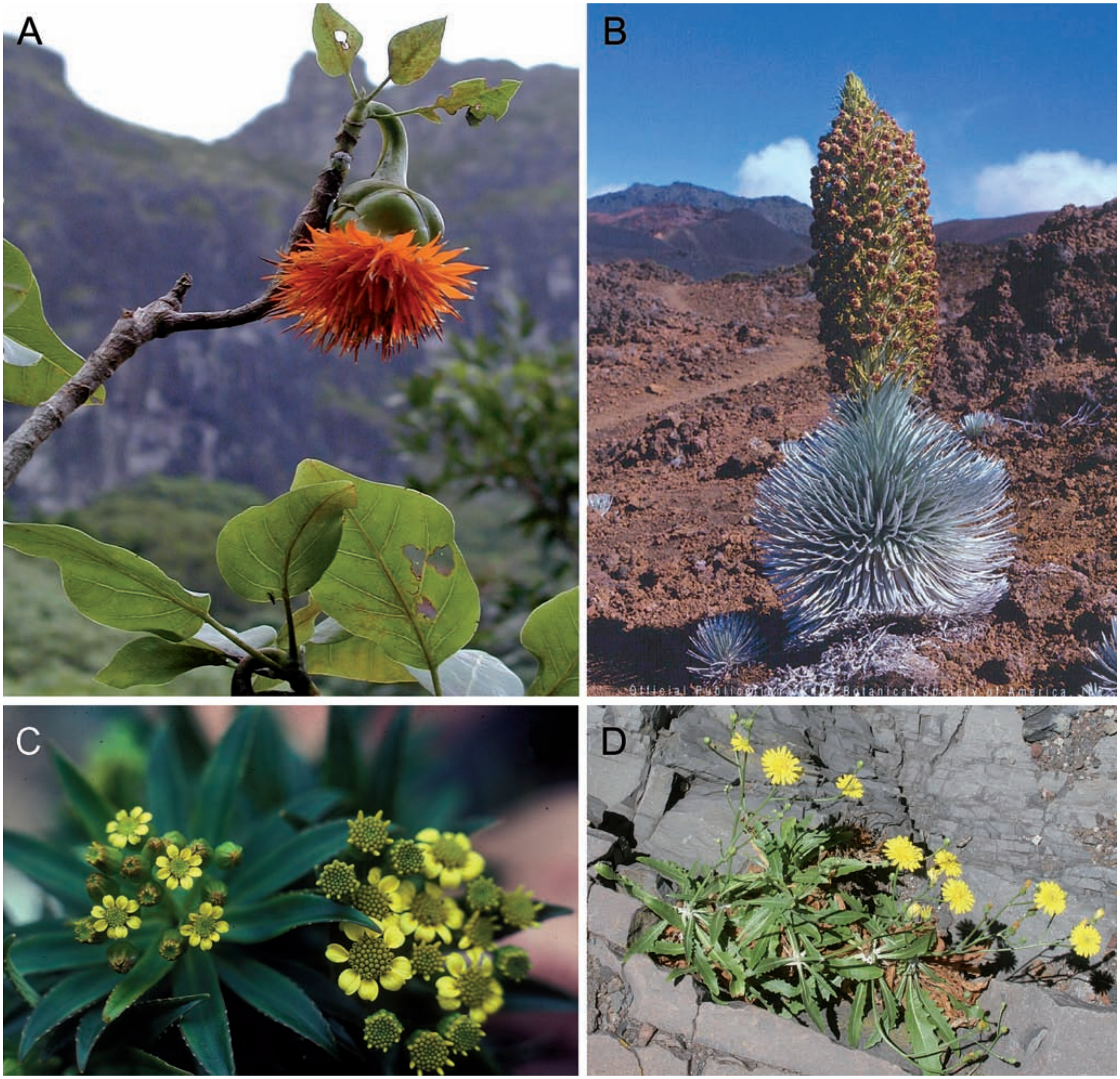

Fig. 9.1. Representative Asteraceae of oceanic islands. **A** *Fitchia nutans* Hook. f from Rapa, Austral Islands, French Polynesia; **B** *Argyroxiphium sandwicense* DC. subsp. *macrocephalum* (Gray) A. Meyrat from Haleakala National Park, Hawaii; **C** *Robinsonia gracilis* Decne on Masatierra, Robinson Crusoe Islands; capitula of female flowers on the left and male flowers on right (all species of genus are dioecious); **D** *Tolpis crassiuscula* Svent. on Tenerife in the Canary Islands. [Photographs: A, courtesy of K. Wood; B, S. Carlquist, with permission from Botanical Society of America; C, T.F. Stuessy; D, J.K. Archibald.]

once established because they would not have the genetic diversity necessary to evolve and diversify morphologically and ecologically in the island setting. Carlquist (1966, 1974: 525) did not downplay the potential advantages of autogamous colonizers, and Baker (1967), while reducing his "law" to a "rule", conceded that it is likely that not all populations are the result of a single propagule. It is important to stress that the present discussion of the breeding systems of the ancestors of insular Asteraceae will not focus on whether Baker or Carlquist is more often correct. Rather, the issues raised by them will be used to focus on the variety and complexity of the breeding systems of endemic Asteraceae This information for extant endemics will in turn be employed to infer the breeding systems of their continental ancestors. Concentration will be on the seeming conflict between the optimal breeding system for the successful establishment and growth of a sexually reproducing population from a colonizer on the one hand, and for the diversification and evolution of progeny of the colonizer on the other hand.

Polyploid colonizers

In addition to breeding system, we consider the potential role of polyploidy as a mechanism for increasing the genetic diversity of colonizers. Crawford and Stuessy (1997), Carr (1998), and Barrier et al. (1999) provided brief discussions of the ploidy of island colonists. Crawford and Stuessy (1997) observed that lineages of Asteraceae in several oceanic archipelagos originated from polyploid colonizers, and suggested that the greater genetic diversity of the polyploid (relative to diploid) colonizers was important in the evolution and diversification of their progeny. Carr (1998) discussed the high incidence of polyploidy (80 percent) for the 33 percent of the native Hawaiian species for which chromosome counts are available. He emphasized that polyploidy in the Hawaiian flora "reflects mainly paleopolyploidy inherent in the ancestors of Hawaiian species" rather than polyploids that evolved autochthonously. Stuessy and Crawford (1998) also argued that the origin of polyploids in the insular setting is rare. Like Crawford and Stuessy (1997), Carr (1998) also proposed that the high incidence of polyploidy in Hawaiian colonizers reflects selection for the increased diversity the polyploid genome affords the colonizers and their progeny as they undergo bottlenecks during establishment after long-distance dispersal. The observations of Crawford and Stuessy (1997) and Carr (1998) on polyploidy in the ancestors of insular endemics motivated the more thorough investigation of chromosome numbers in endemic Asteraceae presented in this chapter.

MATERIALS AND METHODS

Selection of archipelagos and plants

In this chapter, we review information on the breeding systems and ploidy of the ancestors of endemic Asteraceae from the Canary Islands, Galápagos Islands, Hawaiian Islands, Robinson Crusoe Islands, and St. Helena. These islands and archipelagos were selected for several reasons, having to do both with the islands themselves and their floras. The archipelagos differ in distances from continental source areas and in age, and include representatives from both the Atlantic and Pacific (Table 9.1). While information is far from complete for all of these island systems, there are relatively more data for their Asteraceae than for many other archipelagos. We included lineages with two or more species, and excluded single endemic taxa. Single endemics are indicative only of successful dispersal and establishment, and divergence from a continental ancestor (Stuessy et al. 2006; it is possible that a single species could be the remnant of a once-large lineage, but this is largely unknowable). The presence of two species in a lineage, while not indicative of an extensive radiation, at least demonstrates there was sufficient diversity in the colonizer to facilitate divergence and speciation. Although we will focus on breeding system and polyploidy, we are well aware that other factors could and probably do impact the level of genetic diversity in colonizing ancestors, and several will be mentioned as appropriate.

Chromosome numbers and polyploidy

Chromosome numbers were taken from the primary literature, from two web sites (http://www.lib.kobe-u

Table 9.1. Distance to closest source area, age, and area of island systems.

Archipelago (ocean)	Nearest continental source area [km]	Age [Myr]	Area [km^2]
Canary Islands (Atlantic)	100	1.0–21.0	7,500
Galápagos Islands (Pacific)	1,000	5.0	7,900
Hawaiian Islands (Pacific)	4,000	0.4–5.0	16,800
Robinson Crusoe Islands (Pacific)	670	1.0–5.8	100
St. Helena (Atlantic)	1,930	14.6	122

.ac.jp/products/asteraceae/index.html) and http://mobot.mobot.org/pick/search/ipcn.html), and from Goldblatt and Johnson (2006) and other publications in that series. Recent analyses in which chromosome numbers were mapped onto a phylogeny of Asteraceae (Funk et al. 2005) indicate that the ancestral base number for the family is $x = 9$ (or possibly 8) but that the base number is likely $x = 19$ for the Helianthoids (Semple and Watanabe, this volume). In the discussion of Helianthoids, we classify plants as polyploids only if there has been at least one polyploid event in their ancestry subsequent to the ancient genome duplication in the common ancestor of all Helianthoids; the reason for using this criterion for polyploidy will be discussed later.

Breeding systems

Data for breeding systems of insular endemics were taken from the literature, from personal communications, and from our unpublished results. Inferences on breeding systems of continental colonizers were made from several lines of evidence. Phylogenetic studies in which the sister group of the island lineages can be identified (with various levels of precision) represent the strongest evidence, although not without limitations (Weller and Sakai 1999). Also, if SI taxa occur in an island lineage (a monophyletic group), it is assumed that the ancestral colonist(s) expressed some level of SI. This assumption is strengthened by phylogenetic studies showing that within small monophyletic groups such as island lineages the direction of change is from expression of SI to breakdown of the system to produce SC plants (Barrett et al. 1997; Beck et al. 2006). Mulcahy (1984) presented a cogent argument for the direction from SI to SC being unidirectional within small lineages.

RESULTS AND DISCUSSION

Chromosome numbers and polyploidy in endemic island lineages

Consider first the occurrence of polyploids in the different archipelagos. The Canary Islands have the largest number of lineages and highest representation of tribes of any of the archipelagos included in this review (Table 9.2). Among the sixteen lineages we have included, only five appear to be polyploid, with three found in Cardueae, one in Gnaphalieae, and one in Senecioneae (Table 9.2).

Chromosome counts are available for the three lineages in the Galápagos (Table 9.2). Two of the three genera are in Heliantheae, and thus are paleopolyploids. *Lecocarpus* has not experienced a subsequent polyploid event whereas *Scalesia*, by far the largest composite genus in the archipelago, has a chromosome number of $n = 34$ and is a secondary polyploid (Table 9.2). The sole non-Helianthoid genus is *Darwinothamnus*, with both species diploid (Table 9.2).

In Hawaii, members of the Helianthoid tribes Coreopsideae, Eupatorieae, Heliantheae, and Madieae are paleopolyploids (Carr 2003; Semple and Watanabe, this volume). In addition, in *Bidens*, *Lipochaeta*, and the silversword alliance (Fig. 9.1B) there has been at least one subsequent (secondary) polyploid event (Table 9.2). In Astereae, the largest genus, *Tetramolopium*, has radiated at the diploid level (Table 9.2; Lowrey 1986) whereas the two much smaller genera *Keysseria* and *Remya* are polyploids (Table 9.2).

In the Robinson Crusoe Islands, the three lineages belong to different tribes. All of them are polyploids; the two endemic and largest genera, *Dendroseris* (Cichorieae) and *Robinsonia* (Senecioneae; Fig. 9.1C), are tetraploid, and all six endemic species of *Erigeron* (Astereae) are hexaploid (Table 9.2). Finally, in St. Helena, species of the endemic genus *Commidendrum* (Astereae) are polyploids (Table 9.2).

The significance of polyploid colonizers in the evolution of insular lineages

For a given polyploid lineage in an archipelago, a basic question is whether the colonizers were polyploid or whether polyploidy originated in the insular setting prior to or during radiation and diversification. With rare exceptions, there has not been robust documentation of the ploidy of colonists. Barrier et al. (1999) provide a convincing argument that the ancestors of the silversword alliance in Hawaii were allopolyploids. The difficulty of documenting the ploidy of ancestors is illustrated by the genus *Scalesia* in the Galápagos Islands. The molecular study of Schilling et al. (1994) indicated that the genus *Pappobolus* is sister to *Scalesia*, and that only $n = 17$ is known in the former genus, leading them to suggest that the later polyploid event may represent an synapomorphy for the genus. However, Schilling et al. (1994) cautioned that this relationship to *Pappobolus*, as well as the relationship of *Scalesia* to the genus *Simsia* and a section of *Viguiera*, are not well resolved. Given that $n = 34$ is known for some members of *Viguiera*, the data are inconclusive as to whether the colonizing ancestor was $n = 17$ or 34. However, for purposes of argument we will assume that insular polyploid lineages of *Scalesia* originated from polyploid ancestors based primarily on the conclusion that there is little evidence of the origin of polyploids during the evolution of lineages in oceanic archipelagos (Stuessy and Crawford 1998), and thus there is little reason to believe that a polyploid lineage would evolve from a small founding diploid population.

The overall pattern that emerges from a survey of chromosome numbers in Asteraceae of the five archipelagos is the much lower occurrence of polyploidy in

Table 9.2. Chromosome numbers, ploidy and breeding system of lineages in different island systems.

Island system	Tribe	Genus or lineage	Endemic species	Chromosome number / ploidy	Breeding system of colonizer[a]
Canary Islands	Anthemideae	*Argyranthemum*	19	*n* = 9 / diploid	SI
		Gonospermum-Lugoa-Tanacetum	8	*n* = 9 / diploid	?
	Cardueae	*Atractylis*	2	*n* = 10 / diploid	?
		Carduus	3	*n* = 16 / polyploid	?
		Carlina	4	*n* = 10 / diploid	?
		Cheirolophus	15[b]	*n* = 16 /polyploid	SC
		Onopordum	2	*n* = 17 / polyploid	?
	Cichorieae	*Andryala*	2	*n* = 9 / diploid	?
		Reichardia	3	*n* = 8 / diploid	?
		Tolpis	10	*n* = 9 / diploid	SI
		Woody *Sonchus* alliance	27	*n* = 9 / diploid	SI
	Gnaphalieae	*Helichrysum*	3	*n* = 14 / polyploid	?
	Inuleae	*Allagopappus*	2	*n* = 10 / diploid	?
		Asteriscus	3	*n* = 7 / diploid	SC
	Senecioneae	*Pericallis*	13	*n* = 30 / polyploid	?
		Canariothamnus	3	*n* = 10 / diploid	?
Galápagos Islands	Astereae	*Darwinothamnus*	2	*n* = 9 / diploid	SC
	Heliantheae	*Lecocarpus*	3	*n* = 11/diploid	SC
		Scalesia	11	*n* = 34 / polyploid	SI
Hawaiian Islands	Astereae	*Keysseria*	3	*n* = 27 / polyploid	?
		Remya	2	*n* = 18 / polyploid	SC
		Tetramolopium	11	*n* = 9 / diploid	SC
	Coreopsideae	*Bidens*	30	*n* = 36 / polyploid	SC
	Heliantheae	*Lipochaeta*	6	*n* = 26 / polyploid	SC
		Melanthera	14	*n* = 15 / diploid: paleopolyploid[c]	SC
	Madieae	Silversword alliance	30	*n* = 13, 14 / polyploid	SI
	Vernonieae	*Hesperomannia*	3	*n* = 10 / diploid: paleopolyploid[c]	SC
Robinson Crusoe Islands	Astereae	*Erigeron*	6	*n* = 27 / polyploid	SI
	Cichorieae	*Dendroseris*	11	*n* = 18 / polyploid	SI
	Senecioneae	*Robinsonia*	8	*n* = 20 / polyploid	SI
St. Helena	Astereae	*Commidendrum*	4	*n* = 18 / polyploid	SI

[a] SC = self-compatible; SI = self-incompatible, but see text for discussion of pseudo-self-fertility in the SI lineages; ? = breeding system unknown.

[b] Three species undesdribed.

[c] See text for explanation of distinction between ancient polyploid event in common ancestor of Helianthoids, and subsequent polyploidy.

the Canarian endemic flora as contrasted with the other four island systems. Any discussion of reasons for this must consider several factors. One obvious difference between the Canaries and the other island systems is their much closer proximity to a continental source area (Table 9.1). Carine et al. (2004) provide an excellent discussion of not only the present proximity (95 km) of the closest island in the Canaries to North Africa but also consider how distances could have been even less in the past. This contrasts sharply with the greater distances of the other archipelagos to potential continental source areas, with Hawaii constituting the best evidence for distant isolation (Table 9.1). Carine et al. (2004) discuss several instances of both multiple colonizations of Macaronesian islands as well as a few cases of back colonizations to a continent. While they emphasize that most endemic groups (primarily genera) appear to be monophyletic, they suggest that the close proximity of the Canaries to North Africa and the Mediterranean has facilitated multiple colonizations.

We suggest that the arguments made by Carine et al. (2004) and others may have some bearing on the success that diploid colonizing ancestors have had in the Canaries as compared to Pacific archipelagos and to St. Helena. In particular, we hypothesize that the colonizing ancestors of various endemic lineages in the Canaries may be the result of more than one colonization. This hypothesis is not in conflict with the documented monophyly of numerous endemic genera and groups of genera in the Canaries (Silvertown et al. 2005) if the dispersal events, presumably from different populations of the same species, occurred in close temporal proximity such that the multiple early colonizations could not be detected with the DNA sequences normally employed in molecular phylogenetic studies. Multiple early colonizations may have been a factor in the higher allozyme diversity seen in Canary Island plants as compared to plants from Pacific archipelagos (Francisco-Ortega et al. 2000; Crawford et al. 2001; Silvertown 2004; Silvertown et al. 2005). Beyond the general situation of the Canaries being close to potential source areas, it would be useful to look at the most probable geographic origins for particular groups; that is, to ascertain whether the ancestors did, in fact, come from the nearest potential source areas. There are several lineages for which there is sufficient information to indicate whether their ancestors were from the nearest continental areas such as the western Mediterranean or North Africa or from more distant areas. Recent compilations are given by Andrus et al. (2004) and Carine et al. (2004), and the present discussion is based largely on those two papers. Available data suggest that several of the larger lineages in the Canaries such as *Argyranthemum*, the *Gonospermum* alliance, *Tolpis* (Fig. 9.1D), and the woody *Sonchus* alliance have closest relatives in nearby source areas, although the sister group and the exact areas have been determined with various levels of rigor. All of these lineages are diploid (Table 9.2). The genus *Cheirolophus*, which is a relatively large lineage of over ten species, is polyploid (Table 9.2) and has its closest relatives in the western Mediterranean (Susanna et al. 1999). In contrast, *Pericallis*, one of the larger Canarian lineages with over twelve endemic species, is a high polyploid (hexaploid), and available evidence suggests that its colonizing ancestors did not come from a near source area, but rather may have been from North America (Panero et al. 1999; Bain and Golden 2000) or East/South Africa (Pelser et al. 2002; Swenson and Manns 2003).

In summary, most of the large endemic Asteraceae lineages in the Canary Islands originated from diploid colonizers. This situation contrasts sharply with the other four archipelagos where polyploid colonists have given rise to species-rich groups. We hypothesize that the proximity of the Canaries to continental source areas facilitated early multiple colonizations. Multiple introductions would have increased the genetic diversity in the early founding populations such that diversification and radiation could occur, and therefore there would not have been such a high premium on the genetic diversity of polyploid colonizers. However, two of the more successful lineages, *Cheirolophus* and *Pericallis*, ostensibly originated from polyploids. It may well have been that frequency of diploid colonizers was much higher than polyploid colonizers in the Canaries, and if they were not at a selective disadvantage because of low genetic diversity, they would have become established. In contrast, in more remote archipelagos where effective multiple colonizations were essentially impossible, then the genetic diversity of polyploids would have had a significant advantage over single diploid colonizers.

An important distinction that must be made for polyploid colonizers is whether they are paleopolyploids or are of more recent origin. Although ancient polyploid events may have been important in the diversification of a lineage (e.g., the Helianthoids), the paleopolyploids could have become highly diploidized (see below) and not offer the advantages of colonizers of more recent polyploid origin. In the following discussion of the advantages of polyploidy, it will be argued that the colonizers are of recent polyploid origin. Early evidence from enzyme electrophoresis for lineages such as *Bidens* (Helenurm and Ganders 1985) and the silversword alliance (Witter 1988; Witter and Carr 1988) in Hawaii, and *Dendroseris* (Crawford et al. 1987) and *Robinsonia* (Crawford et al. 1992) in the Robinson Crusoe Islands showed complex banding patterns resulting from expression of duplicate gene loci. These results indicate that there has been little if any silencing of expression at duplicate enzyme loci in the endemics. This suggests that their ancestral colonists were of recent origin rather than paleopolyploids, in which silencing would be expected (e.g., Wilson et al. 1983; Gastony 1991). In the Hawaiian silversword alliance, each of two duplicate copies of two floral homeotic genes are most similar to different members of North American diploid tarweeds (Barrier et al. 1999), indicating that the silverswords are of relatively recent allopolyploid origin relative to the divergence time between their continental diploid progenitors.

There has been a recent explosion of studies on the evolution of polyploids, from their ecology to their genomics. Naturally occurring polyploids of recent origin and synthesized polyploids have been studied, and in some instances comparisons have been made between the two (Adams and Wendel 2005; Soltis et al. 2003, 2004; Comai 2005). It is evident from these and other studies that rapid and dramatic changes may occur in synthesized polyploids and in polyploids of recent natural origin. For example, Pires et al. (2004) demonstrated differences in gene expression levels for late and early flowering at a locus known to be involved in regulation of flowering in *Brassica*, with flowering time differences in turn associated with chromosome rearrangements. Adams et al. (2003) documented complex patterns of gene expression changes in synthetic *Gossypium* tetraploids, some of which matched and some of which did not correspond to patterns seen in the natural polyploids. Differences in gene expression levels, including both silencing and novel expression relative to the diploid parents, have been shown for natural *Tragopogon* polyploids of very recent origin (Soltis et al. 2004).

With regard to island Asteraceae, Barrier et al. (2001) demonstrated accelerated rates of protein evolution in floral regulatory genes in the silverswords compared to their North American tarweed relatives. Barrier et al. (2001) showed that the accelerated evolution cannot be attributed to a general increase of neutral mutation rates in the Hawaiian endemics. Purugganan et al. (2003) caution that while it has not been demonstrated that observed molecular changes at these loci in the silverswords are responsible for the diversity of phenotypes of capitula structure and arrangement of capitula, the results are suggestive of cause and effect. The results for silverswords and other polyploids indicate that the diversity seen in insular lineages could occur rapidly following the establishment of colonizers.

Many studies now available for polyploid plants indicate their evolutionary potential. The rapid changes possible with polyploids, especially relatively "young" ones, make them excellent ancestors for rapidly diverging island lineages. An important factor is whether the polyploid colonists are paleopolyploids or of more recent origin. Although admittedly scanty, available evidence for large lineages in the Hawaiian, Robinson Crusoe, and the Galápagos islands indicates that the colonists are recent polyploids. In some instances it is difficult to know from chromosome numbers alone whether there has been recent polyploidy. For example, without a phylogenetic analysis, it could be difficult to infer secondary polyploidy for the silversword alliance (Carr 2003). Polyploidy, particularly allopolyploidy, could be especially important for selfing colonists such as *Bidens* in Hawaii (Table 9.2).

Sporophytic self-incompatibility and pseudo-self-fertility: general considerations

Asteraceae are one of the very few families of flowering plants with a sporophytic self-incompatibility system (SSI) instead of the more common gametophytic self-incompatibility (GSI). In contrast to GSI where only the haploid genotype of the pollen controls incompatibility, with SSI the diploid or sporophytic genotype of the parental anther determines compatibility (Hiscock and Tabah 2003). The difference between the two incompatibility systems has important implications for the founding of sexual populations from few propagules; because two alleles rather than one control incompatibility in the SSI, there would be fewer compatible matings compared to GSI. Thus, Asteraceae, with SSI, would appear to be at a disadvantage as colonizing ancestors of insular lineages. Genetic studies in several members of the family over fifty years ago demonstrated that SSI is controlled by one complex locus (S-locus) with multiple alleles (S-alleles) (Hiscock 2000a). However, "anomalous" compatible crosses are sometimes possible; the genetic basis of these has not been explained, although it has been suggested that "gametophytic elements" acting in particular genetic backgrounds or other modifier loci may influence compatibility (Hiscock 2000b). Regardless of the mechanisms facilitating successful matings, the result is to produce seeds from what are largely incompatible crosses, such as selfing or crossing between plants sharing the same S-allele. Diploid control of pollen incompatibility in SSI allows for dominance interactions among S-alleles. There may be complete or co-dominance among alleles, or tissue-specific dominance in either the pollen or stigma (Brennan et al. 2003). Dominance among S-alleles will increase the number of compatible matings within a population compared to allelic co-dominance because the recessive S-alleles are masked. Tissue-specific allelic dominance (pollen or stigma) may be manifested by compatibility differences between reciprocal crosses. Dominance is one mechanism for ameliorating the restrictive conditions for compatible matings for plants with SSI.

As indicated above, SI species sometimes "anomalously" set some seed in incompatible crosses, and this has been referred to as "leakiness" in the system. Other terms applied to the phenomenon are pseudo-self-compatibility (East 1927; Mulcahy 1984) or pseudo-self-fertility (PSF will be used to indicate both the noun pseudo-self-fertility and the adjective pseudo-self-fertile) (Levin 1996).

Despite the aforementioned lack of knowledge of the genetic basis of PSF, several factors may promote it. Forced inbreeding can result in the production of increased numbers of PSF progeny (Hiscock 2000a). Bottlenecks may promote the dissolution of SSI and thus increase the level of PSF within a small population (Reinartz and Les 1994). One nongenetic influence on the level of PSF is temperature, and there may be fluctuations in PSF during the growing season (Levin 1996). As emphasized by Levin (1996), PSF differs from true self-fertility (TSF) in several respects. One is the lower seed production of selfed plants than outcrossed plants with PSF whereas in TSF plants seed set is similar with both types of crosses. Also, seed set in TSF plants is not affected by all the factors just mentioned for PSF plants. Mulcahy (1984) also emphasized that another important difference between PSF and TSF is that levels of PSF are reversible and subject to selection whereas TSF may not be reversed to SI. Bixby and Levin (1996) were able to select for higher and lower levels of selfed seeds in a species of *Phlox*. A multitude of factors, and especially dominance relationships and PSF, could act individually or in concert to increase compatible matings in small founder populations. The extensive studies of the SI *Senecio squalidus* have demonstrated how complex dominance relationships among S-alleles can be, and low levels of PSF have allowed the species to be an effective colonizer despite very low diversity of S-alleles (Hiscock 2000a, b; Hiscock and Tabah 2003; Brennan et al. 2003).

Levin (1996) discussed the advantages of PSF for the founding of new populations and for increasing the number of compatible matings in small populations, and both of these attributes would be especially important for single colonizers on remote oceanic islands. A single founder capable of some level of PSF could establish a sexual population via selfing, and subsequently some crosses between progeny sharing the same S-allele would be compatible. The severe bottlenecks associated with the founding of new populations could also function to increase compatible matings. In perennial plants, as represented by the genera included in this chapter, it is plausible that a founder could establish on an island, and with time mutations at the S-allele could increase the number of compatible matings (Carr et al. 1986).

Although PSF colonizers would not build up population sizes as rapidly as SC colonizers on oceanic islands, their big advantage over selfers is that they could carry higher levels of diversity because they originated from outcrossing continental populations. Thus, PSF colonizers could facilitate the establishment of sexual populations from one or a few founders and thus satisfy Baker's rule (Baker 1955), while at the same time they provide a solution to Carlquist's concern (Carlquist 1966, 1974) about colonizers having the diversity necessary to facilitate diversification following dispersal and establishment. Given the potential advantages of PSF colonizers, a question of considerable interest is whether there is evidence that insular lineages of Asteraceae did, in fact, orignate from PSF ancestors.

Breeding systems in colonizers of oceanic archipelagos

Consider the breeding systems of the colonizing ancestors of lineages in the different archipelagos. The number of lineages for which breeding systems are known in Canary Island Asteraceae is somewhat limited, but information is available for several of the larger lineages, most of which apparently originated from SI or PSF ancestors. For example, the genus *Argyranthemum* in tribe Anthemideae (Table 9.2) had generally been considered SC (Humphries 1975; Borgen 1976), but the unpublished results mentioned in Francisco-Ortega et al. (1997) suggest that the lineage is primarily SI, with SC "very limited". While no data are presented, the comments indicate that there is likely some level of PSF in *Argyranthemum*. Francisco-Ortega et al. (1997) cite earlier studies showing strong SI in several continental relatives of *Argyranthemum*, thus providing additional support for the hypothesis that the ancestors of this insular group were highly SI, but the possibility of some level of selfing is at least present. *Argyranthemum* is thus an attractive group for more detailed studies of breeding system variation at the population and species levels.

The genus *Cheirolophus* (Cardueae), with fifteen endemic species and three undescribed species (Susanna et al. 1999; Santos-Guerra, unpubl.), is one of the larger lineages in the Canaries (Table 9.2). Published data for the genus are scanty; Calero and Santos (1988, 1993) reported abundant seed production for one species and indicated that another species is SC. Teresa Garnatje (pers. comm.) indicates that none of the species with which she has worked is SI. While the data are not extensive, they suggest that the genus is SC and that the ancestor of the lineage was also SC, or possibly PSF.

Tolpis (Cichorieae; Fig. 9.1D) is one of the larger lineages in the Canaries with ten endemic as well as several undescribed species (Moore et al. 2002; Archibald et al. 2006; Crawford et al. 2006; Santos-Guerra, unpubl.). Jarvis (1980) provided preliminary data on SC and PSF for several species, and reported wide variation within some species. Additional studies (Crawford et al., unpub.) have extended and confirmed his results and shown various levels of PSF in most species, as suggested by Jarvis (1980). Also, evolution of TSF was demonstrated for one endemic species. The ancestor of *Tolpis* in the Canary Islands probably was SI with some level of PSF.

The woody *Sonchus* alliance (Cichorieae) is a large and diverse monophyletic lineage in the Canaries (Kim et al.

1996a, b; Lee et al. 2005). Available evidence indicates that members of the complex are highly SI (S.-C. Kim, pers. comm.), but there are no studies of the occurrence or level of PSF in this lineage.

The *Asteriscus* alliance (Inuleae) presents an interesting situation because there have been two introductions of the group into the Canaries, with two species in one group and one in another (Goertzen et al. 2002). All three species are SC (Borgen 1984; Halvorsen and Borgen 1986).

In the Galápagos, *Scalesia* is the only lineage with more than ten species (Table 9.2). Initial studies (Rick 1966; McMullen 1987; McMullen and Naranjo 1994) reported several species of *Scalesia* as SC and autogamous. Nielsen et al. (2000) found seed set in isolated manually self-pollinated capitula of *Scalesia divisa* but the fruits were smaller and had a lower germination percentage than seeds produced from open-pollinated controls. A later study of another species, *Scalesia affinis*, demonstrated partial SI (Nielsen et al. 2003); this species had been reported as SC and autogamous in one of the earlier studies. There is little question that there is variation in the degree to which SI has broken down within and among species of *Scalesia*, and the results of Nielsen et al. (2000, 2003) document PSF in two species. The best evidence indicates that the ancestor of this genus was SI or PSF (Nielsen et al. 2000, 2003). Philipp et al. (2004) examined one of the three species of *Lecocarpus* (which is endemic) and documented that it is SC. One of the two species of the endemic genus *Darwinothamnus* was reported as SC and autogamous by McMullen (1987, 1990).

Only three lineages of Asteraceae have more than five species in the Robinson Crusoe Islands. The largest genus *Dendroseris* (Cichorieae), which is nested within elements of *Sonchus* (Kim et al. 2006), almost certainly originated from SI ancestors, possibly with some level of PSF. Anderson et al. (2001) and Bernardello et al. (2001) demonstrated that two species are totally SI whereas one species sets over 50 percent seed set when selfed, indicating a partial breakdown of SI in at least one species during the radiation of the genus. *Robinsonia* (Senecioneae; Fig. 9.1C), which is nested within *Senecio* in a molecular phylogeny (Pelser et al. 2006), is dioecious, a condition that is extremely rare in Senecioneae (B. Nordenstam, pers. comm.). Given the very common condition of SI in Senecioneae, it seems most likely that the ancestors of *Robinsonia* were highly SI (B. Nordenstam, pers. comm.). The species of *Erigeron* in the Robinson Crusoe Islands are monophyletic and likely originated from a single introduction (Valdebenito et al. 1992). As judged from floral morphology, all species appear to be outcrossers because they lack the suite of features normally associated with agamospermy or selfing in this large genus where outcrossing predominates and SI is important in promoting it (Noyes et al. 1995; Noyes 2000; R.D. Noyes, pers. comm.).

The genus *Commidendrum* is endemic to St. Helena, with four very rare species (Cronk 2000). Two species are highly SI but with low levels of PSF (Eastwood et al. 2004; A. Eastwood, pers. comm.), suggesting that their ancestors were likewise largely SI but exhibited some level of PSF.

In Hawaii, nearly all of the larger endemic lineages apparently arose from SC ancestors, the one notable exception being the most spectacular radiation of all, the silversword alliance (Table 9.2; Fig. 9.1B). Carr et al. (1986) first demonstrated that some members of the silversword alliance are highly SI whereas others exhibit various levels of self-fertility. Carr et al. (1986) suggested that the silverswords may have originated from a PSF colonizer, namely a tarweed from California. Alternatively, they suggested that the original colonizer may have been SI but because it was a rhizomatous, long-lived perennial it could exist until there was a mutation at the incompatibility locus. Subsequent phylogenetic studies support the hypothesis of a SI or PSF colonizer (Barrier et al. 1999; Baldwin 2003). The molecular phylogenetic studies of Lowrey and Whitkus (unpub.) demonstrate that the sister group to Hawaiian *Tetramolopium* is SC and thus there seems little question that the original colonizer(s) were likewise SC. Sun and Ganders (1988) are of the view that the ancestor of Hawaiian *Bidens* was SC (Table 9.2).

SUMMARY AND CONCLUSIONS

When considering the two factors ploidy and breeding system of ancestral colonizers together from the five archipelagos, two things are most evident. First, the Canary Islands are exceptional because of the frequency of diploid colonizers compared to the other island groups (Table 9.2). The hypothesis advanced to explain this is the much closer proximity of the Canaries to a continental source area than the other island systems; thus, multiple early introductions may have reduced the selective advantage of the greater genetic diversity afforded the single polyploid propagules dispersed to more remote archipelagos.

The other notable observation is the greater frequency of SC ancestors for Hawaii relative to the other island systems (Table 9.2). It is tempting to suggest that the higher frequency of SC colonizers in Hawaii is due to the greater distance to source areas; however, the most spectacular radiation in Hawaii, the silversword alliance, originated from SI or PSF ancestors (Table 9.2). An equally large radiation in Hawaii, but perhaps not as spectacular in terms of ecological and morphological diversity as the silverswords, is *Bidens* where the thirty species originated from a SC ancestor (Table 9.2). *Bidens* in Hawaii is a high polyploid (Table 9.2), so a single ancestor colonist could have carried extensive diversity to the island. Although species of *Bidens* are SC, there has been evolution of sexual expression in the lineage, including factors that promote outcrossing, with the net result that species exhibit a mixed mating system (Ritland and Ganders 1985; Sun and Ganders 1986, 1988).

One of the lineages that seems to "break the rules" for Hawaii, and indeed for the other four archipelagos, is *Tetramolopium*. The colonizing ancestor of this ecologically and morphologically diverse lineage (Lowrey 1986, 1995; Lowery et al. 2005) was both SC and diploid (Table 9.2). The progenitor of Hawaiian *Tetramolopium* is from New Guinea and possible dispersal mechanisms are birds and wind; the pappus and glandular trichomes on the fruits could facilitate adherence to the feathers and feet of birds (Lowrey 1995; Lowrey et al. 2005). Though highly speculative, it is suggested that there may have been multiple fruits in a single dispersal event, and *Tetramolopium* evolved from more than a single colonizer. *Tetramolopium* is an illustration of the limitation of attempting to interpret the genetic diversity of colonizers with only two variables of ploidy and breeding system. While the dispersal agent of Asteraceae is normally the individual fruit, this does not mean that single dispersal events involve only one fruit, as was admitted by Baker (1967). However, an important point with regard to *Tetramolopium*, and other lineages originating from SC colonizers, is that if a single dispersal event included more than one fruit from the same selfing population, then the multiple fruits may not collectively contain significantly more genetic diversity than a single fruit. In contrast to multiple propagules from selfing source populations, dispersal of multiple fruits in a single event from an outcrossing source population would enhance genetic diversity in a founding population relative to a single propagule. This may explain why the colonizing ancestors of so many island lineages were SI (or more likely PSF) regardless of whether there was one or multiple propagules in a single dispersal event. Despite the limitations of considering only the two variables of ploidy and breeding system, observations for the five archipelagos show that both polyploidy and SI accompanied by PSF are common attributes of successful lineages. It seems reasonable to hypothesize that these two factors, both alone or in concert, provide colonizers with the requisite diversity necessary for radiation and speciation in an archipelago. There are plausible hypotheses to explain the two notable exceptions to the above generalizations, the paucity of polyploidy in the Canary Islands and SC colonizers in Hawaii.

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Section III

Phylogeny, classification, and biogeography of the tribes

Section III Part 1

Asterales

Chapter 10

Asteraceae and relationships within Asterales

Johannes Lundberg

THE SEARCH FOR THE SISTER OF ASTERACEAE

At the Compositae Conference at Kew in 1994 ("Compositae: Systematics, Biology, Utilization"), DeVore and Stuessy (1995) argued in favor of a sister group relationship between Asteraceae and Calyceraceae, mainly drawing evidences from morphology. Even if a close relationship between Asteraceae and Calyceraceae had been repeatedly suggested ever since Cassini described the latter family (as Boopideae; Cassini 1816), it was perhaps not until the Compositae Conference at Reading in 1975 ("The Biology and Chemistry of the Compositae"), that this relationship was seriously corroborated (Turner 1977), mainly based on similarities in pollen morphology (Skvarla et al. 1977). This hypothesis further gained strength with the identification of the subtribe Barnadesiinae (now subfamily Barnadesioideae) in Mutisieae as the sister group to the rest of the family (Bremer 1987; Jansen and Palmer 1987; Bremer and Jansen 1992; Olmstead et al. 1992). However, the Asteraceae-Calyceraceae sister group relationship was soon challenged by Goodeniaceae (all these taxa, except Asteraceae of course, will be presented in some detail below). Since then there have been three competing hypotheses: a clade of Asteraceae + Calyceraceae with Goodeniaceae (if sampled) as its their sister group (Gustafsson and Bremer 1995; Kim and Jansen 1995; Downie et al. 1996; Jansen and Kim 1996; Bremer and Gustafsson 1997; Carlquist and DeVore 1998; Kårehed et al. 1999; Olmstead et al. 2000; Albach et al. 2001; K. Bremer et al. 2001; B. Bremer et al. 2002; Lundberg and Bremer 2003; Winkworth et al. 2008), or a clade of Goodeniaceae + Calyceraceae with Asteraceae as its sister group (Michaels et al. 1993; Olmstead et al. 1993; Cosner et al. 1994; Savolainen et al. 2000; Soltis et al. 2000, 2007), or a clade of Asteraceae + Goodeniaceae with Calyceraceae (if sampled) as its sister group (Gustafsson and Bremer 1995; Gustafsson et al. 1996). It is possible to find at least some characters in favor of any of these relations (as well as contradicting them), but as shown by DeVore and Stuessy (1993), Hansen (1997), and Lundberg and Bremer (2003), the morphology is mainly in favor of the Calyceraceae-Asteraceae sister group relationship, while it is largely some molecular markers that suggested the other two alternatives. Furthermore, the two best-sampled analyses to date (Lundberg and Bremer 2003; Winkworth et al. 2008) both support the Calyceraceae-Asteraceae sister group relationship. This contribution does not argue for this sister group relationship, but instead gives an overview of what I think is the most likely phylogeny of the Asteraceae alliance, covering the entire order Asterales (sensu APG II 2003; Fig. 10.1; Table 10.1).

PLESIOMORPHIC ASTERACEAE

The family Asteraceae, the focus of this volume, hardly needs any introduction. Instead I will try to give a review of possible plesiomorphic character states that might be

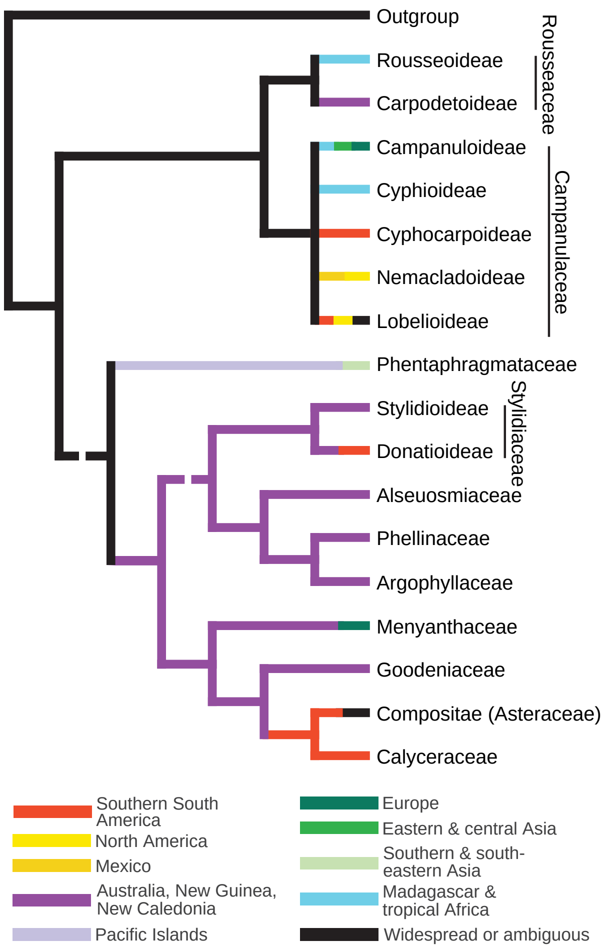

Fig. 10.1. Suggested phylogeny of Asterales, mainly based on the phylogeny presented by Winkworth et al. (2008). The two dotted branches are well supported (posterior probabilities least 0.95) in the Winkworth et al. (2008) Bayesian analysis, but the position of Pentaphragmataceae relative to Core Asterales and Campanulaceae/Rousseaceae, and that of Stylidiaceae relative to the MGCA clade and the APA clade, differ in other analyses of Asterales phylogeny (e.g., Kårehed et al. 1999; K. Bremer et al. 2001; B. Bremer et al. 2002; Lundberg and Bremer 2003).

of interest when discussing the clades most closely related to Asteraceae. Much information is obtained from Jeffrey (2007), some also from Stevens (2001 onwards), Hellwig (2007), and Carolin (2007a).

Spirally, alternate leaves are probably plesiomorphic; opposite leaves are found in some younger clades (e.g., Heliantheae, Liabeae, and some other), and also in some Barnadesioideae (e.g., *Schlechtendalia*, *Duseniella*, and some *Chuquiraga*), but not in Calyceraceae and only in a few Goodeniaceae (some *Scaevola*). It is somewhat more difficult to establish the plesiomorphic growth form; in both Barnadesioideae and Goodeniaceae there are annual and perennial herbs as well as shrubs (and in Barnadesioideae even trees up to 20 m tall), but in Calyceraceae perennial herbs dominate (in addition to a few annual herbs). The *wood* in Asteraceae is, with the exception of obviously secondary woody members, more or less indistinguishable from that of other woody sympetalous families, indicating that at least some woodiness is plesiomorphic, perhaps shrubs or subshrubs. In many Asteraceae, *internal secretory systems* are present, either as articulated laticifers or laticiferous cells (with a triterpene-rich latex), or as schizogenous secretory canals (resins). These are absent from some genera of Barnadesioideae and Mutisioideae, as well as Calyceraceae and Goodeniaceae, and it is possible that their absence is the ancestral state for Asteraceae.

The capitulum is perhaps the most prominent feature of the family. Capitula are, however, also known from Calyceraceae (in various forms from all genera) and from Goodeniaceae (most well known is *Brunonia*, but some *Dampiera* and *Scaevola* species also have tight head-like inflorescences), as well as many other more distantly related families. The capitula of Asteraceae are indeterminate, in contrast to most capitula of Calyceraceae that are determinate. However, the capitulum of *Acicarpha* differs from all other Calyceraceae in being indeterminate, but the position of this genus within Calyceraceae is still not known with certainty, and the plesiomorphic state for Calyceraceae is uncertain. It seems quite likely, however, that an indeterminate inflorescence is the plesiomorphic state for Asteraceae. The *corolla is initiated* as a ring meristem (Erbar and Leins 1996). This state is shared with nearly all investigated members of the campanulids and is most certainly the plesiomorphic state, with the irregular successive development that has been reported for bilabiate and ligulate corollas in non-asteroid tribes (Harris 1995) only recently evolved. Asteraceae have five stamens with connate anthers (only some wind-pollinated species have free anthers) and free filaments (with very few exceptions, among others some *Barnadesia*). Also Calyceraceae have anthers that are connate, although often only at the base, but with the filaments partly united forming a tube. In Goodeniaceae the filaments are free, but the anthers might be more or less connate (*Anthotium*, *Brunonia*, *Dampiera*, *Diaspasis*, and *Lechenaultia*) or free (all other genera). At least partly connate anthers (and free filaments?) thus seem to be the plesiomorphic state for Asteraceae. The upper part of the filaments form a filament collar, also reported from Calyceraceae and thus probably plesiomorphic for Asteraceae. The plesiomorphic *ovary wall vascularization* (Jeffrey 2007) may consist of a ring of ten vascular bundles (with five fused laterals, and five median bundles), in addition to the four carpellary bundles extending into the style. This pattern can be found in some Barnadesioideae (e.g., *Schlechtendalia*), Stifftieae, and Vernonieae. A similar pattern is also found in Calyceraceae (Gustafsson 1995). In most other Asteraceae, a more reduced pattern with five ovary wall bundles (two entering the style), in addition to one bundle entering the ovule, is found. Further reductions are also present. The style is single in all Asteraceae, generally with two style arms and papillose, dry stigmatic areas. Since also Calyceraceae (with a single club-like stylar head) and Goodeniaceae (with their peculiar stylar indusia) have a papillose, dry stigma, it is quite safe to assume that this is the plesiomorphic state for Asteraceae. The ovules are anatropous, unitegmic and tenuinucellate and the inner epidermis of the integument differentiates into an integumentary tapetum, all states shared with many other Asterales (Tobe and Morin 1996). The endosperm development is *ab initio* cellular in most Asteraceae, but nuclear in Cardueae and some other groups. In Calyceraceae the endosperm development is likewise *ab initio* cellular, but both nuclear and cellular developments are found in Goodeniaceae (Tobe and Morin 1996). The *ab initio* cellular endosperm development is, however, the most common state also in the rest of Asterales (but note that the endosperm development, as many other embryological characters, are not known for some of the smaller, less well-known families), and it seems fairly clear that this is the plesiomorphic state for Asteraceae. As in Calyceraceae and Goodeniaceae (as well as Menyanthaceae) no endosperm haustoria are formed (Tobe and Morin 1996).

The mature pollen grains are 3-celled, in contrast to Calyceraceae and Menyanthaceae where the pollen grains are 2-celled when shed (Tobe and Morin 1996), and the 3-celled pollen grains might be an apomorphy for Asteraceae. Spinulate (or smooth) pollen grains are shared between Barnadesioideae and Mutisioideae; they are also found in Calyceraceae and some other families, and are thus probably plesiomorphic in Asteraceae (Hansen 1991;

Table 10.1. The major clades of Asterales, with information on number of genera, species, and distribution.

Clade name	Genera	Species	Distribution
Rousseaceae	4	6	
Carpodetoideae	3	5	E Australia, New Guinea, New Zealand, Solomon Is.
Rousseoideae	1	1	Mauritius
Campanulaceae	84	ca. 2400	
Campanuloideae	50	ca. 1050	Cosmopolitan (Old World)
Cyphioideae	1	64	Africa
Cyphocarpoideae	1	3	Chile
Lobelioideae	29	ca. 2000	Cosmopolitan (New World)
Nemacladoideae	3	15	SW USA, NW Mexico
Pentaphragmataceae	1	30	SE Asia to New Guinea
Core Asterales			
Stylidiaceae	6	ca. 245	
Donatioideae	1	2	Australia, New Zealand, South America
Stylidioideae	5	ca. 245	Australia, New Zealand, (SE Asia, S America)
APA clade			
Alseuosmiaceae	5	10	E Australia, New Zealand, New Caledonia, New Guinea
Argophyllaceae	2	ca. 20	E Australia, Lord Howe Is., New Caledonia, New Zealand, Rapa Is.
Phellinaceae	1	11	New Caledonia
MGCA clade			
Menyanthaceae	5	ca. 60	Almost cosmopolitan
Goodeniaceae	11	ca. 440	Mainly Australia
Calyceraceae	4	ca. 60	Southern South America
Asteraceae	>1600	ca. 23,000	Cosmopolitan

Urtubey and Tellería 1998). In some Calyceraceae and Barnadesioideae, intercolpar concavities are found, but it is still uncertain if they represent a symplesiomorphy for the two families (and thus are plesiomorphic in Asteraceae). Associated with the *secondary pollen presentation*, the tapetum forms pollen kit that facilitates the presentation and transfer of the pollen to the pollinator. Pollen kit production is also found in Calyceraceae, a family that shares a similar pollen-presentation mechanism (Leins and Erbar 1990; DeVore and Stuessy 1995; Erbar and Leins 1995). Also Goodeniaceae have secondary pollen presentation, but involving a structure (the indusium) that is apomorphic for Goodeniaceae. Pollen kit and secondary pollen presentation are thus both probably plesiomorphic for Asteraceae.

The fruits of Calyceraceae and Asteraceae are achenes, that is single-seeded dry fruits formed by a unilocular, inferior ovary often described as indehiscent (but at least in some Asteraceae are split open by the growing embryo at preformed dehiscence lines), crowned by the persistent and more or less modified calyx. Also Goodeniaceae have dry fruits, but both indehiscent and dehiscent fruits (as well as drupes) can be found. In *Brunonia* (Goodeniaceae) a modified persistent calyx is present on top of the dry one-seeded fruit and aids in the dispersal. A dry inferior, one-seeded and basically indehiscent fruit with persistent and modified calyx thus seems to be plesiomorphic for Asteraceae.

The chemistry of Asteraceae is rich and complex, but much of this complexity has evolved after the origin of the family; the chemistry of early-branching clades such as Barnadesioideae seems to be less specialized than that of younger groups. Inulin is, however, found through the family, but it is also shared with most other members of Asterales and its presence is plesiomorphic for Asteraceae. Another family of compounds, often associated with Asteraceae, are the bitter, toxic sesquiterpene lactones, but these seem to be absent from Barnadesioideae, and are thus probably an apomorphy for the non-barnadesioid Asteraceae (they are particularly complex among the asteroid tribes). The antibiotic, toxic acetylenes (earlier often referred to as polyacetylenes), mainly present in the resin ducts are also present in Goodeniaceae (although apparently not in Calyceraceae), and their presence might be plesiomorphic for Asteraceae. On the other hand, iridoids, present in Calyceraceae and Goodeniaceae as well as other families of Asterales, are absent from Asteraceae, but their absence is strongly correlated with the presence of sesquiterpene lactones as they share the same metabolic pathway.

Although the *haploid chromosome numbers* in Asteraceae range from 2 up to 120, the most common number is 9, and this has been hypothesized also to be the plesiomorphic number (e.g., Jeffrey 2007), while in Calyceraceae the plesiomorphic number is $x = 8$ (Hellwig 2007) and in Goodeniaceae both $x = 8$ and $x = 9$ are fairly common. The plesiomorphic number for Asteraceae is thus still uncertain (but see Chapter 4).

It has been suggested (e.g., DeVore and Stuessy 1995) that the ancestral, plesiomorphic distribution of Asteraceae is southern South America, the present-day distribution of many Barnadesioideae and Calyceraceae. The scanty early fossil record of Asteraceae, Calyceraceae and Goodeniaceae (Muller 1981; Graham 1996) make it difficult to date the split between Calyceraceae and Asteraceae. Based mainly on external evidence, DeVore and Stuessy (1995) and Stuessy et al. (1996) argued for the split to correlate with the increasing aridity and temperature fluctuations in southern South America during early Oligocene. Thus the area for the split could have been the zone between the northern tropical/subtropical forests and the cool temperate forests to the south, perhaps just north of the then partly submerged Patagonia (Stuessy et al. 1996). Molecular dating of the split between Asteraceae and Calyceraceae have given older time estimates for the split; Kim et al. (2005) dated the split to mid Eocene (approximately 42–49 Ma), with a major radiation within Asteraceae during the Oligocene, coinciding with the rapid cooling of the Antarctic region following the final separation of the Australian continental block from Antarctica ca. 35 Ma (Li and Powell 2001).

If we speculate, we can thus hypothesize an ancestral Asteraceae as a subshrub or small shrub with alternate, spirally inserted leaves, growing in what today is southern South America just north of Patagonia, sometime around middle or late Eocene. Secretory systems were absent (but some precursors might have been present). The flowers were numerous and in an indeterminate capitulum, with the corolla initiated as a ring meristem, and the sympetalous corolla had five lobes. The five stamens had free filaments but more or less connate anthers, and the upper parts of the filaments were differentiated into an anther-collar. The ovary vascularization consisted of five lateral and five median bundles in the ovary wall, and four carpellary bundles extending into the single style. There were two style arms, with papillose, dry stigmatic areas. The single ovule was anatropous, unitegmic, tenuinucellate with an integumentary tapetum and *ab initio* cellular endosperm development. The mature pollen grains were 3-celled, somewhat sticky by the presence of pollen kit, and presented to the pollinator by the style. The pollen were spinulate and had intercolpar concavities. The fruit was an achene, crowned by a modified calyx that aided in dispersal. Inulin was present as a storage compound. Sesquiterpene lactones were not present, but polyacetylenes might have been. Iridoids were probably absent. The basic chromosome number might have been $x = 8$ or $x = 9$.

With this very hypothetical first Asteraceae in mind, we will visit all the major clades in Asterales, discussing relevant characters.

CALYCERACEAE AND ASTERACEAE

The sister group to Asteraceae is the small family Calyceraceae (Fig. 10.2A; four genera and some sixty species). They are endemic to southern South America where they are mostly found in high-altitude arid habitats, especially in the Andes (Hellwig 2007). They are annual or perennial herbs, with the flowers in capitula surrounded by the involucral bracts. This is not the only similarity with Asteraceae; other potential synapomorphies can be found in the stamens (the filament collars), pollen (spinulate or smooth pollen with intercolpar concavities and presence of pollen kit), ovaries (unilocular ovaries with a single ovule), the mechanisms of the secondary pollen presentation, and the fruits (achene with a persistent, modified calyx). There are also dissimilarities that are not easily explained; most notable is the orientation of the single ovule in the ovary. Asteraceae have a basal and erect ovule, while Calyceraceae have a pendulous ovule, and this difference in orientation has been used as an argument against a sister group relationship between the two families (e.g., Cronquist 1981).

GOODENIACEAE, CALYCERACEAE AND ASTERACEAE

The sister to the Calyceraceae-Asteraceae clade is the medium-sized, largely Australian family Goodeniaceae (Fig. 10.2B; eleven genera including *Brunonia*, Brunoniaceae, ca. 440 species; Carolin 2007a). The species with a distribution outside Australia are mainly found in coastal subtropical and tropical areas, apparently the results of recent long-distance dispersals. Goodeniaceae are mostly herbs or shrubs, but small trees and scramblers are also known. The variation of inflorescences is greater in Goodeniaceae than in its sister-clade; here we find cymes, thyrses, racemes, spikes, heads, subumbels and solitary flowers. Based on some striking similarities (polysymmetric flowers in a dense head, connate anthers, lack of endosperm, ovary with a single and basal ovule), it has earlier been speculated that *Brunonia* may be the closest relative to Asteraceae, but with the more likely placement of *Brunonia* as sister to one of the two major clades of Goodeniaceae (see, e.g., Gustafsson et al. 1996), these similarities are better explained as parallelisms and thus apomorphies for *Brunonia*. The other Goodeniaceae have zygomorphic flowers with petal wings (i.e., delicate, marginal appendages of the corolla lobes; Gustafsson 1995), bilocular and often more or less inferior ovaries, and a peculiar, unique form of secondary pollen presentation (lost in *Brunonia*): the pollen are collected in a cup-shaped structure, the indusium, at the top of the style, from where the pollen are presented to the pollinator. The often many-seeded fruits are variable within the family, but mostly consisting of laterally dehiscing capsules, although also drupes and nuts can be found. There are some possible synapomorphies for the Goodeniaceae-Calyceraceae-Asteraceae clade. The presence of secondary pollen presentation might be one (although the mechanisms differ within the clade, and as we will see it is also found in other more distantly related members of Asterales), as may a dry and more or less papillate stigma, and a persistent calyx (but in Goodeniaceae not modified). The split between Goodeniaceae and the Calyceraceae-Asteraceae clade might date back to the onset of the cooling at the end of the Early Eocene Climate Optimum (approximately 50 Ma; Zachos et al. 2001) and correlate with the break-up of Australia from Antarctica (starting 95 Ma, but with land contact between Australia and Antarctica maintained through the South Tasman Rise until about 40 Ma; Li and Powell 2001).

THE MGCA CLADE: MENYANTHACEAE, GOODENIACEAE, CALYCERACEAE AND ASTERACEAE

The sister clade to the three families described above is Menyanthaceae (Fig. 10.2C). This small family of five genera and ca. sixty species of aquatic and marshland herbs has an almost cosmopolitan distribution (Kadereit 2007). The two monotypic genera, *Menyanthes* and *Nephrophyllidium*, have an exclusively northern hemisphere distribution, and probably form a clade separated from the three remaining, mainly southern-hemispheric genera (Lundberg and Bremer 2003; *Liparophyllum* not sampled). *Villarsia* and the monotypic *Liparophyllum* are both nearly exclusively Australian, while *Nymphoides* is primarily tropical in distribution, but with a few species in the north temperate regions. Menyanthaceae are all glabrous herbs with rootstocks or rhizomes, and the leaves are often forming rosettes. The flowers are actinomorphic and in several species quite large (some *Nymphoides* species are cultivated as ornamentals in ponds and have thus been widely introduced) with sympetalous corolla and sometimes delicate petal wings similar to those in Goodeniaceae (Gustafsson 1995). The more or less superior ovary is unilocular (but bicarpellate), and the fruit is generally a capsule (rarely a berry) with few to many seeds. Not known from the other Asterales is the heterostyly found in all genera but *Liparophyllum*, often combined with self-incompatibility.

Fig. 10.2. Selected Asterales. **A** *Calycera herbacea* Cav. (Calyceraceae), Argentina; **B** *Lechenaultia formosa* R. Br. (Goodeniaceae), Western Australia; **C** *Nephrophyllidium crista-galli* Gilg (Menyanthaceae), northwestern North America; **D** *Argophyllum grunowii* Zahlbr. (Argophyllaceae), New Caledonia; **E** *Platyspermation crassifolium* Guillaumin (Alseuosmiaceae), New Caledonia; **F** *Phelline* sp. (Phellinaceae), New Caledonia; **G** *Donatia novae-zelandiae* Hook. f. (Stylidiaceae), Tasmania; **H** *Stylidium schoenoides* DC. (Stylidiaceae), Australia; **I** *Pentaphragma aurantiaca* Stapf (Pentaphragmataceae), Borneo; **J** *Carpodetus serratus* J.R. Forst. & G. Forst. (Rousseaceae), cultivated at University of Oxford Botanic Garden; **K** *Roussea simplex* Sm. (Rousseaceae) visited by a

Phelsuma cepediana gecko (Gekkonidae), Mauritius; **L** *Campanula persicifolia* L. (Campanulaceae), Sweden. [Photographs: A, J.M. Bonifacino; B, G. Watson, from Watson and Dallwitz 1992 onwards; C, A. Tasler; D, R. Amice; E, F, D. and I. Létocart; G, M.G. Hanna; H, P. Mann; I, T. Rodd; J, T. Waters; K, D. Hansen; L, C. Johansson.]

The clade with Menyanthaceae, Goodeniaceae, Calyceraceae and Asteraceae (the MGCA clade of Lundberg and Bremer 2003) is well-supported both by molecular and morphological data, and there are several possible synapomorphies: the presence of petal lateral veins, the absence of (micropylar) endosperm haustoria, and a thick and multilayered integument (Inoue and Tobe 1999). Other suggested synapomorphies include the presence of scalariform perforation plates, the frequent occurrence of sclerified idioblasts, binucleate mature pollen and multinucleate tapetal cells, and the at least partial fusion of lateral veins of adjacent petals, but their occurrences are either not known in sufficient detail among other Asterales outside the MGCA clade, or can equally well be interpreted as parallelisms within the clade. The similarity in the petal wings of Goodeniaceae and Menyanthaceae suggests that they are an apomorphy for the clade, but structures reminiscent of petal wings are also found in other closely related clades.

THE CORE ASTERALES CLADE: MGCA, STYLIDIACEAE AND APA

If the MGCA clade is well supported and present in all recently published molecular phylogenies, its sister group is more difficult to identify. Kårehed et al. (1999), as did Lundberg and Bremer (2003), suggested that Stylidiaceae (including *Donatia*) are the sister group to the MGCA clade, with the three families Alseuosmiaceae, Phellinaceae, and Argophyllaceae (the APA clade of Lundberg and Bremer 2003) as their successive sister group. Albach et al. (2001), on the other hand, in a sparsely sampled analysis suggested a clade with the two families Argophyllaceae and Alseuosmiaceae as the sister group to the MGCA clade with *Donatia* as their successive sister (Phellinaceae not sampled), while B. Bremer et al. (2002) suggested the APA clade together with *Donatia* to form a clade sister to the MGCA clade (with Stylidiaceae s.str., i.e., without *Donatia*, in both Albach et al. (2001) and B. Bremer et al. (2002) as sister to Campanulaceae). In a recent large-scale Bayesian phylogeny of the angiosperms, Soltis et al. (2007) found the APA clade to be sister to the MGCA clade, with Stylidiaceae s.l. as their successive sister group. Another, but more densely sampled, Bayesian analysis focusing on the campanulids (Winkworth et al. 2008) obtained a clade with Stylidiaceae s.l. together with the APA clade as the sister group to the MGCA clade (Fig. 10.1). In summary, it seems quite likely that the sister group to the MGCA clade is either the APA clade (Albach et al. 2001; Soltis et al. 2007), Stylidiaceae (Kårehed et al. 1999; Lundberg and Bremer 2003), or a clade of Stylidiaceae (and/or *Donatia*) together with the APA clade (Bremer et al. 2002; Winkworth et al. 2008). Even if the phylogeny suggested by Winkworth et al. (2008) is the most robust suggested up to now (a total of nine DNA markers, but not very densely sampled among Asterales), a trichotomy with the MGCA clade, the APA clade, and Stylidiaceae (incl. *Donatia*) is still the best representation of the present understanding of the phylogeny. These three major clades constitute the "Core Asterales" of Lundberg and Bremer (2003). This Core Asterales clade is well supported by molecular data (e.g., Lundberg and Bremer 2003; Soltis et al. 2007; Winkworth et al. 2008), although reliable morphological synapomorphies are yet to be identified.

STYLIDIACEAE

The medium-sized family Stylidiaceae (Fig. 10.2G, H; five genera including *Donatia*, ca. 245 species) is mainly distributed in Australia (in particular its southwestern parts) and New Zealand, with a few species in southeastern Asia and South America. The family can be divided into two subfamilies (Lundberg and Bremer 2003; Carolin 2007b; but see Wege, 2007, for the alternative view of treating the subfamilies as separate families), Donatioideae with *Donatia* (two species) only, and Stylidioideae with the remaining four genera (*Forstera*, *Levenhookia*, *Stylidium* including *Oreostylidium*, and *Phyllachne*). There are some marked differences between the two subfamilies, but also possible synapomorphies. Most prominent of the latter are the imbricate petals (all other Asterales have valvate petal bud aestivation) and a reduction in the numbers of stamens (three stamens in *Donatia fascicularis*, and two stamens in all other Stylidiaceae). Other suggested synapomorphies include unilacunar nodes, the absence of wood rays, the presence of extrastaminal floral nectar disc, and extrorse anthers. The differences in favor of a recognition of the two subfamilies as distinct families include the sympetalous corolla in Stylidioideae in contrast to the free petals in *Donatia*, the floral column formed by the stamens united with the style and found only in Stylidioideae but not in *Donatia* (where the stamens are free but close to the style), and some differences in vegetative anatomy (Rapson 1953; e.g., the replacement of the stem epidermis by a hypodermis in *Donatia*, scalariform vessel element perforation plates in *Donatia* but simple perforations in Stylidioideae, and stomata paracytic in *Donatia* but anomocytic in Stylidioideae). Most if not all of these differences can be interpreted as apomorphies for either Donatioideae or Stylidioideae (with the contrasting states as plesiomorphies). The flowers of *Donatia* and a few Stylidioideae are actinomorphic, but in the other species more or less zygomorphic. The floral column, the most striking feature of Stylidioideae, is active in the transfer of pollen to the pollinator, and very active indeed in the genus *Stylidium*, the trigger-plants. In this genus the column is touch-sensitive, so when the pollinator brushes the column it is triggered and very rapidly strikes the pollinator, at the same time depositing pollen from the anthers or picking them up onto the stigmata. Self-pollination is prevented in many species by protandry. After being triggered, the column slowly resets, to be triggered again by the next visitor. In *Levenhookia*, the column is released only once, and the pollen is sprayed over the pollinator. Within Stylidioideae, it appears that *Forstera* and *Phyllachne* are paraphyletic with respect to each other, and *Phyllachne* might better be merged into *Forstera* (Wagstaff and Wege 2002).

THE APA CLADE: ALSEUOSMIACEAE, PHELLINACEAE AND ARGOPHYLLACEAE

The third major clade in Core Asterales is the APA clade, consisting of the three small families Alseuosmiaceae, Phellinaceae, and Argophyllaceae. This clade is well-supported by molecular data (Kårehed et al. 1999; Lundberg and Bremer 2003; Winkworth et al. 2008), but it has been difficult to identify synapomorphies for it. This is at least partly due to lack of information on these three families, but so far serrate and gland-toothed leaves (Stevens 2001 onwards) and 3-nucleate mature pollen (Lundberg and Bremer 2003) have been suggested. All three families are woody (shrubs or small trees) with alternate leaves and a similar distribution: Alseuosmiaceae (five genera with ten species) are present in eastern Australia, New Zealand, New Caledonia, and New Guinea; Argophyllaceae (two genera with some twenty species) in eastern Australia, New Zealand, New Caledonia, Lord Howe Island, and Rapa Island; and Phellinaceae (one genus with eleven species) are endemic to New Caledonia. It is possible that Argophyllaceae and Phellinaceae are sister to each other, but also here only a few synapomorphies have been identified to date (presence of subepidermal cork, a short style, apotropous ovules, and crassinexinous and rugulose pollen; Stevens 2001 onwards; Lundberg and Bremer 2003). Alseuosmiaceae (Fig. 10.2E) are shrubs (or sometimes small trees or subshrubs) with spirally arranged leaves and, possibly a synapomorphy for the family, small tufts of rusty brown, multicellular uniseriate hairs in the leaf axils (in *Platyspermation*, probably sister to the rest of Alseuosmiaceae, these hairs are not restricted to the leaf axils but are more dense there). Except for *Platyspermation* with short corolla tube and spreading corolla lobes, the flowers are funnel-shaped or more or less bell-shaped, and the corolla lobes in all genera have more or less prominent appendages or papillae, somewhat reminiscent of petal wings (Gustafsson 1995; Kårehed 2007a). Also Argophyllaceae (Fig. 10.2D) are shrubs or small trees, but the petals are only connate at the base and have fringed appendages on the inner surfaces near the base (corolline ligules; Eyde 1966; Gustafsson 1995; Kårehed 2007b). Peculiar for Argophyllaceae, and giving *Argophyllum* its name, are the T-shaped hairs found on most parts of the plants (Al-Shammary and Gornall 1994), and especially on the lower surface of the leaves where they can give a silvery or whitish impression. Phellinaceae (Fig. 10.2F) are also small trees or shrubs with the leaves sometimes densely arranged in pseudo-whorls, but with free petals without any appendages (Barriera et al. 2007). It is possible that other synapomorphies will be discovered when more is known about the distribution of anatomical, embryological, phytochemical and karyological characters as well as the reproductive systems. The fruits in the APA clade are berries (most Alseuosmiaceae), drupes (Phellinaceae, *Corokia* in Argophyllaceae) or capsules (*Platyspermation* and Argophyllaceae except *Corokia*).

PENTAPHRAGMATACEAE

Although the support for Core Asterales is high, its sister group is still not known with any certainty. The most recently published phylogeny suggests Pentaphragmataceae as sister to Core Asterales, followed by a clade with Campanulaceae and Rousseaceae as sister to all remaining Asterales (Fig. 10.1). This relationship was obtained in the Bayesian analysis of Winkworth et al. (2008), but their sampling was made with the phylogeny of the entire campanulids in mind, and not to resolve relationships within the orders. The most likely alternatives to this hypothesis are either a clade with Pentaphragmataceae together with Campanulaceae as the sister group to Core Asterales followed by Rousseaceae as sister to all other Asterales (Kårehed et al. 1999; B. Bremer et al. 2002, but with *Stylidium* as the closest sister to Campanulaceae!), or a clade with Pentaphragmataceae as sister to Campanulaceae followed by Rousseaceae as sister to these two families only (Lundberg and Bremer 2003). *Pentaphragma* (with ca. 30 herbaceous species of southeastern Asia, the Malay Archipelago, and New Guinea) is the sole genus in Pentaphragmataceae (Fig. 10.2I; Lammers 2007b), and was for a long time closely associated with Campanulaceae, by some authors even included in this family. It differs from Campanulaceae in many respects, most markedly in its asymmetrical leaf bases (somewhat reminiscent of *Begonia*) and the flowers in helicoid cymes, but also in wood anatomy, lack of secondary pollen presentation and associated syndromes, pollen morphology, embryology (endosperm with single-celled micropylar haustoria only), and floral structures (the hypanthium is adnate to the ovary only by five longitudinal septa, perhaps of filamental origin, thus creating five nectariferous pits; Vogel 1998). In *Pentaphragma*, the fruit is a berry with numerous seeds. Unfortunately, almost nothing is known about the phytochemistry or reproductive systems, including dispersal, of this genus.

THE BASAL DIVISION: CAMPANULACEAE AND ROUSSEACEAE

As noted above, the sister to all other Asterales might be a clade with Campanulaceae and Rousseaceae (Winkworth et al. 2008; Fig. 10.1). Campanulaceae (Fig. 10.2L), the bellflowers and lobelias, hardly need any lengthy introduction (see Lammers 2007a, for more information). Its 84 genera (and nearly 2400 species) are shared among five subfamilies of markedly unequal size. Unfortunately, neither the relationships between the subfamilies, nor among the genera within the subfamilies, are particularly well known even if some recent progress has been made (e.g., Eddie et al. 2003; Antonelli 2007). Two of the subfamilies, Cyphioideae with *Cyphia* (64 species in Africa) and Cyphocarpoideae with *Cyphocarpus* (three species in Chile), are monogeneric, Nemacladoideae have three genera and fifteen species endemic to southwestern United States and adjacent parts of Mexico, while the two cosmopolitan subfamilies Lobelioideae (with 29 genera and almost 1200 species, most of them in South America) and Campanuloideae (with 50 genera and about 1050 species, most of them in Africa, Asia, and Europe), share the greater part of the species diversity. Most Campanulaceae are herbs (although there are some woody species forming trees up to 15 m tall) with alternate, spirally arranged leaves (rarely opposite or whorled). A network of articulated laticifers is associated with the phloem, and the latex produced is milky and white (or sometimes colored), and in Lobelioideae rich in pyridine alkaloids (replaced by polysterols in Campanuloideae). Neither iridoids nor sesquiterpene lactones are produced in Campanulaceae. The flowers of the subfamilies are quite different in symmetry, but are often showy and larger than those found in many other families of Asterales. The ovary is often inferior with the hypanthium adnate to it, and the fruits are often capsular, dehiscing by valves, slits or pores, but also indehiscent dry, papery fruits or berries are present. Various forms of secondary pollen presentations are found in Campanulaceae (Leins and Erbar 2006). In Campanuloideae, with mostly actinomorphic corollas of various shapes, the pollen is released from the introrse anthers and collected by hairs on the growing style. These hairs are commonly invaginating, thus facilitating the transfer of the pollen to the visiting pollinator. In Lobelioideae, with more or less zygomorphic flowers and coherent anthers forming an anther tube, a pump mechanism is present. The pollen is collected by a ring of stylar hairs just below the stigmatic lobes, and is then pushed up through the anther tube by the growing style. Species of *Cyphia* (the sole genus of Cyphioideae) lack stylar elongation, but collect the pollen in a "pollen box" formed by the emptied anthers as the walls and the stylar tip furnished with a ring of rigid hairs at the bottom. The pollination biology of Nemacladoideae and Cyphocarpoideae is much less studied. The pump mechanism of Lobelioideae, together with the presence of inulin as storage compound (present in the whole family), has inspired hypotheses about a close relationship between Asteraceae and Lobelioideae, but it seems fairly certain that the secondary pollen presentation of both clades are parallelisms, and that the presence of inulin is a plesiomorphy shared with many other (perhaps all?) members of Asterales.

The sister of Campanulaceae might be the small woody family Rousseaceae (Fig. 10.2J, K; Winkworth et al. 2008; but see the discussion above). Rousseaceae s.l. (Lundberg 2001; but see Koontz et al. 2007, and Gustafsson 2007) consists of two subfamilies, Rousseoideae with the genus *Roussea* (one species endemic to Mauritius) and Carpodetoideae with three genera (and five species in eastern Australia, New Guinea, New Zealand, and the Solomon Islands). They are shrubs or trees (to 20 m tall) or climbers (*Roussea*) with alternate or opposite (*Roussea*) and gland-toothed leaves. The petals are clearly connate in *Roussea*, but becoming free early in the development in the other genera. The flowers are also much larger in *Roussea* than in the other genera. In *Roussea* the petals are thick and fleshy, revolute at the apex, and the flowers produce copious amounts of nectar. It seems that the flowers are pollinated by geckos that also aid in dispersing the seeds by eating the berries (D. Hansen, pers. comm.). In Carpodetoideae the fruits are either berries (fleshy in *Abrophyllum* and leathery in *Carpodetus*) or loculicidal capsules (*Cuttsia*). The ovaries are superior in *Roussea*, *Abrophyllum* and *Cuttsia*, but more or less inferior in *Carpodetus*, and in all genera commonly 5(–7)-locular with numerous ovules. In Asterales, multilocular ovaries are otherwise almost only restricted to some Campanuloideae.

With the dichotomy between the Campanulaceae-Rousseaceae clade on one side, and the Pentaphragmataceae-Core Asterales clade on the other, we have reached the basal node of Asterales. Only some few uncertain synapomorphies for Asterales have so far been suggested (K. Bremer et al. 2001; Lundberg and Bremer 2003), including valvate aestivation (also frequently found outside Asterales and thus perhaps a plesiomorphy), presence of inulin (not investigated for several important clades, most notably the Rousseaceae and the APA clade), a base chromosome number of $x = 9$ (only a few chromosome counts are available for Rousseaceae and the APA clade), and secondary pollen presentation (probably better interpreted as of two apparently independent origins within Asterales, one for Campanulaceae and one for the Goodeniaceae-Asteraceae-Calyceraceae clade, respectively). It is, however, possible that there are other synapomorphies to be identified when the embryology, palynology and phytochemistry of the badly known clades in Asterales and its immediate relatives among the campanulids are more studied.

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Chapter 11

Classification of Compositae

Vicki A. Funk, Alfonso Susanna, Tod F. Stuessy and Harold Robinson

INTRODUCTION

The Compositae (Asteraceae) family is nested high in the Angiosperm phylogeny in Asterideae/Asterales. The family contains the largest number of described, accepted, species of any plant family, ca. 24,000, with estimates of the total number reaching 30,000. There are 1600–1700 genera distributed around the globe except for Antarctica. Assuming that there are 250,000–350,000 species of flowering plants, then one out of every eight to twelve species is in Compositae (about 10%). That the family is monophyletic has never been in question. Every early worker in plant classification recognized Compositae as a group at some level (i.e., Tournefort 1700; Berkhey 1760; Vaillant 1719–1723) and in every type of analysis the family is monophyletic (i.e., Small 1919; Bremer 1987; Jansen and Palmer 1987; Hansen 1991; Michaels et al. 1993; Lundberg and Bremer 2003).

The family is characterized by florets arranged on a receptacle in centripetally developing heads and surrounded by bracts, by anthers fused in a ring with the pollen pushed or brushed out by the style, and by the presence of achenes (cypselas) usually with a pappus (Fig. 11.1). Although the family is well-defined, there is a great deal of variation among the members: the habit varies from annual and perennial herbs to shrubs, vines, or trees, although few are true epiphytes; species grow in just about every type of habitat from forests to high elevation grasslands, however, they are less common in tropical wet forests and more common in open areas. Most groups in the family contain some useful and some noxious species as well as common and rare taxa. However, the general perception of this family as "weedy" is not correct. Certainly there are members that benefit from disturbance, such as a few species of dandelions and thistles, and a few global pests (e.g., *Chromolaena odorata* (L.) R.M. King & H. Rob.), but most species have a restricted distribution and just about every 'at risk' habitat in the world contains members of this family that are an important part of the flora.

From the beginning, those who studied this family thought that presence of both ray and disk florets (Fig. 11.1A) represented the basic head pattern. In his classic illustration, Cassini (1816; Chapters 1, 6 and 41) placed Heliantheae at the center, Vernonieae and Eupatorieae at one end, and Mutisieae and Cichorieae (Lactuceae) at the other. The treatment by Bentham (1873a) had 13 tribes (the most frequently used suprageneric rank), which remained more or less the same until the 1980s; although some of the concepts changed, especially in Vernonieae, Liabeae, Senecioneae and Helenieae. Bentham's work was developed independently from that of Cassini (e.g., 1826), but the 13 tribes of Bentham do correspond to many of the 19–20 tribes of Cassini. Hoffmann's treatment of Compositae (1890–1894) essentially repeated the classification of Bentham (Turner 1977; Bremer 1994). Bentham (1873b), and more recently Cronquist (1955, 1977) and Turner (1977), all thought that Heliantheae were the most primitive tribe of the family, and accordingly assumed that the ancestor was a perennial herb with opposite leaves and a yellow-flowered, radiate capitulum. In 1977 Cronquist changed his mind and allowed for a woody ancestor, as suggested by Carlquist (1966, 1976). Carlquist (1966) proposed changes to the system of Bentham, but

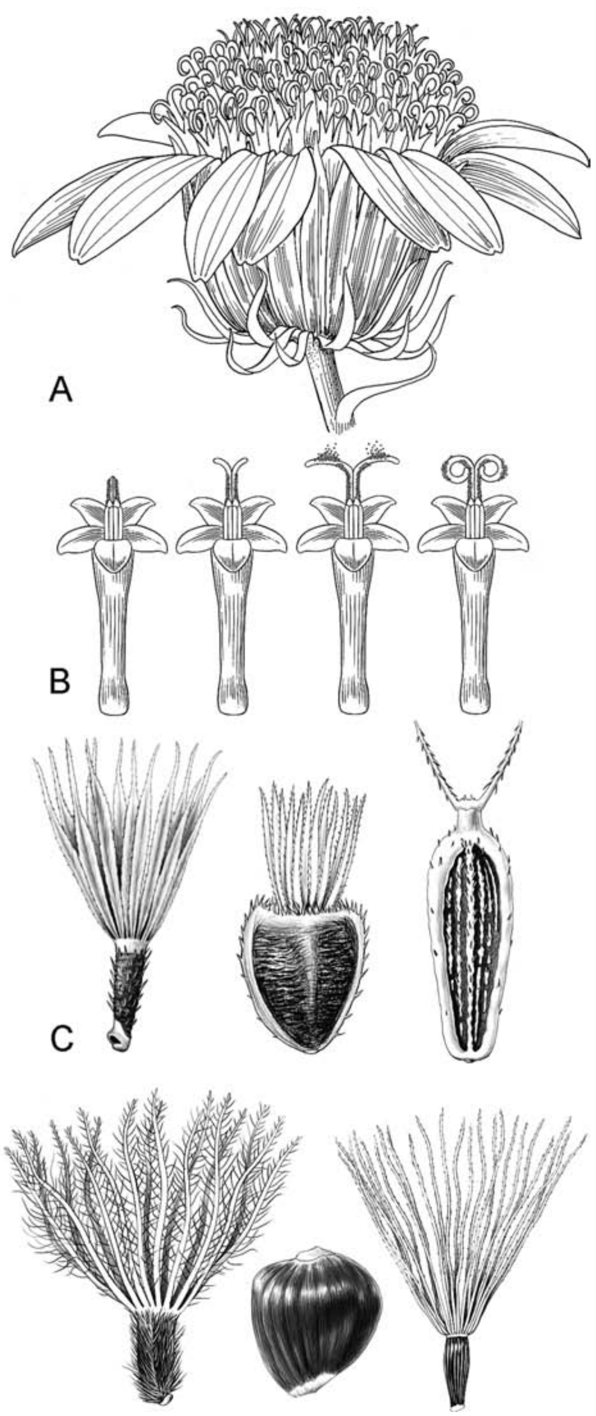


Fig. 11.1. Characters of Compositae. **A** The head with ray florets arranged around the perimeter, disc florets in the center, and an involucre with bracts (phyllaries) surrounding the outermost florets. **B** The pollen is released via the style pushing out through the anthers, which are fused at the margins; sometimes the style branches are recurved and come in contact with the style shaft. **C** Some of the achene (cypsela) and pappus types found in Compositae. [Drawings by Alice Tangerini (US); figure from Funk et al. 2005; achene drawings from Robinson 1981.]

they were not often used and acceptance of the basic 13 tribes continued. In 1975, a meeting on "The Biology and Chemistry of the Compositae" was held in Reading, England (Heywood et al. 1977). The proceedings from that meeting are interesting in that the book used the Bentham system, but several of the chapters made it clear that the data did not fit this classification. A good example is the pollen paper by Skvarla (1977), where he mentions that the pollen structure of Mutisieae is more like closely related families and very different from Heliantheae.

Abandonment of the stand-alone Lactuceae in the subfamily Cichorioideae was inevitable. Poljakov (1967) provided a fair approximation of the modern two groups of tribes with Cichorieae-Arctotideae more basal and Anthemideae-Heliantheae derived. Robinson (1973), Carlquist (1976), Wagenitz (1976), and Jeffrey (1978) all divided Compositae into two groups approximating Asteroideae and non-Asteroideae of recent treatments. Of these authors, only Carlquist and Jeffrey applied the subfamily names Asteroideae and Cichorioideae in their revised sense, and both erred in their placement of Eupatorieae because of its superficial resemblance to Vernonieae.

The biggest change in Composite systematics took place in the late 1980s and early 1990s; it was based on the molecular work by Jansen and Palmer (1987, 1988), Jansen et al. (1991a, b), and Jansen and Kim (1996). They literally turned the Compositae phylogeny upside down, showing that part of Mutisieae was the basal branch of the family and that the tribe Heliantheae s.l. was nested far up in the tree. Furthermore, their work showed that Vernonieae and Eupatorieae, long believed to be closely related, were actually in separate parts of the phylogeny. At the same time, Bremer's analysis (1987) based mostly on morphological data, for the most part agreed with the molecular findings. However, Bremer's analysis placed Eupatorieae close to Astereae and not Heliantheae.

Understanding the phylogeny of Compositae has come a long way since the papers of Jansen and Palmer (1987) and Bremer (1987). The advent of new techniques and new markers has greatly increased the amount of sequence data available. Using published trees for the family as a whole, and published and unpublished trees for individual clades, we have constructed a metatree for the family, a tree of trees (Chapter 44). It illustrates the current thinking about the relationships among the major tribes and subfamilies in Compositae. A summary tree shows the position of the major branches (Fig. 11.2). The basal group, which is monophyletic and the sister group to the rest of the family, is the distinctive subfamily Barnadesioideae, which contains less than 1% of the species in Compositae. Also monophyletic is the highly nested subfamily Asteroideae, which contains ca. 65% of the species in the family. Intercalated between the two monophyletic subfamilies are groups that used to be included in the subfamily

Cichorioideae (ca. 35% of the species in the family) and that vary in their morphological and molecular characters. Recently a new higher classification system was proposed for the family (Baldwin et al. 2002; Panero and Funk 2002, 2007, 2008) that recognized new and previously described subfamilies and tribes so that now there are 12 and 43, respectively; two or three are not supported by currently available morphological data and it remains to be seen whether or not these few taxa will be accepted by the Compositae community (see Chapter 12).

Chapter 1 covers the work of many of the scientists who provided early classifications of the family up until 1977 when the Heywood et al. volumes were published. Since that time there have been only two treatments of the whole family, Bremer (1994) and Kadereit and Jeffrey (2007), both of which were based on a mixture of morphological and molecular data. The Bremer book retained the three subfamilies but acknowledged that Cichorioideae were most likely paraphyletic. The Kadereit and Jeffrey treatment included the latest information available at the time. For instance, it broke up Heliantheae into twelve tribes that reflected the current state of knowledge. However, other areas of the family were still in flux (e.g., Mutisieae s.l.) and while some groups such as Pertyeae and Dicomeae were recognized on an informal level, others did not have sufficient data available to make a decision on their placement. Each of these works advanced our knowledge of the family and with this volume we hope to do the same. Our current classification is built on the foundation laid by others from Cassini to Kadereit and Jeffrey.

The treatments in this book are based on our attempt to combine the morphological and molecular data into a meaningful classification.

COMPOSITAE GISEKE (1792) [ASTERACEAE MARTYNOV (1820)]

Family description (adapted from Jeffrey 2007)

Often annual herbs, also biennial or perennial herbs, subshrubs, shrubs, vines or trees, monocarpic or polycarpic, leptocaul or sometimes pachycaul, usually terrestrial (rarely epiphytic or aquatic), sometimes succulent, usually with one or more of various types of glandular and eglandular hairs, commonly the glandular biseriate and the eglandular uniseriate; tissues usually with schizogenous secretory canals (resin-ducts) and/or with articulated lacticifers. Leaves alternate or opposite, rarely whorled, usually simple but often lobed or divided, exstipulate. Unit of inflorescence a capitulum (head), with rare exceptions surrounded by an involucre of one to several series of protective bracts (phyllaries), capitula sometimes solitary at the apices of more or less leafless stems (scapes) but usually few to many in often corymbiform cymose inflorescences (capitulescences, synflorescence) of various types, sometimes aggregated into often involucrate capituliform syncephalia of the second or even third order. Receptacle either naked or hairy and smooth, areolate with polygonal areoles or alveolate with depressions in which the florets are inserted, or paleate with persistent or caducous vascularized scales (paleae, pales, chaff) subtending some or all of the florets, fimbrilliferous with non-vascularized fimbrils or scale-like processes surrounding the bases of the florets. Florets (flowers) small, 1–1000 or more per capitulum, sessile or subsessile; calyx a pappus associated with the fruit (see below); corolla gamopetalous, of (3–)5(–6) united petals, more or less regular (actinomorphic) and equally or unequally (3–)5(–6)-lobed or -toothed with the lobes or teeth valvate, or filiform with the lobes reduced or absent or with a minute ray, or variously zygomorphic, bilabiate with a 2-lobed internal (adaxial) lip and a 3-lobed external (abaxial) lip, pseudobilabiate with an unlobed internal (adaxial) lip and a 4-lobed external (abaxial) lip, ligulate with an apically 5-dentate abaxial ligule, or radiate with an abaxial 0–3(–4)-dentate ray, the different types variously arranged within the capitulum, the florets either all alike (homomorphic, isomorphic, capitulum homogamous) and all regular (capitulum discoid), all ligulate (ligulate capitulum) or all bilabiate, or of more than one type (heteromorphic, anisomorphic, capitulum heterogamous) with the inner (disc florets) regular (or rarely bilabiate) and perfect (bisexual, hermaphrodite) or functionally staminate (male) and the outer (ray florets) radiate, often pistillate (female) or sometimes sterile (neuter), in one or more series (capitulum radiate), or the outer filiform pistillate, usually in several series, and the inner regular, perfect or functionally staminate (capitulum disciform), rarely the corolla absent from the pistillate florets, occasionally all the florets pistillate or staminate and the plants dioecious or monoecious, rarely the florets variously otherwise arranged. Stamens with the filaments inserted on the corolla-tube, equal in number to and alternating with the corolla lobes; filaments usually free, rarely connate, the upper part of the filament usually with thick-walled cells, forming a split cylindrical or balusterform anther-collar (or filament-collar); anthers united into a tube surrounding the style, very rarely free, dithecal, introrse, dehiscent by longitudinal slits, usually with an apical appendage, rounded, sagittate, calcarate or tailed at the base; tapetum integumentary; pollen mostly tricolporate, usually echinate (spiny), sometimes echinolophate or lophate (with a pattern of raised ridges) or spinulate (microechinate, spinulose), often caveate; nectary a thickened scale or cup surrounding the style base; style solitary, elongating through the anther-tube and extruding the pollen at its summit, apically divided (except sometimes

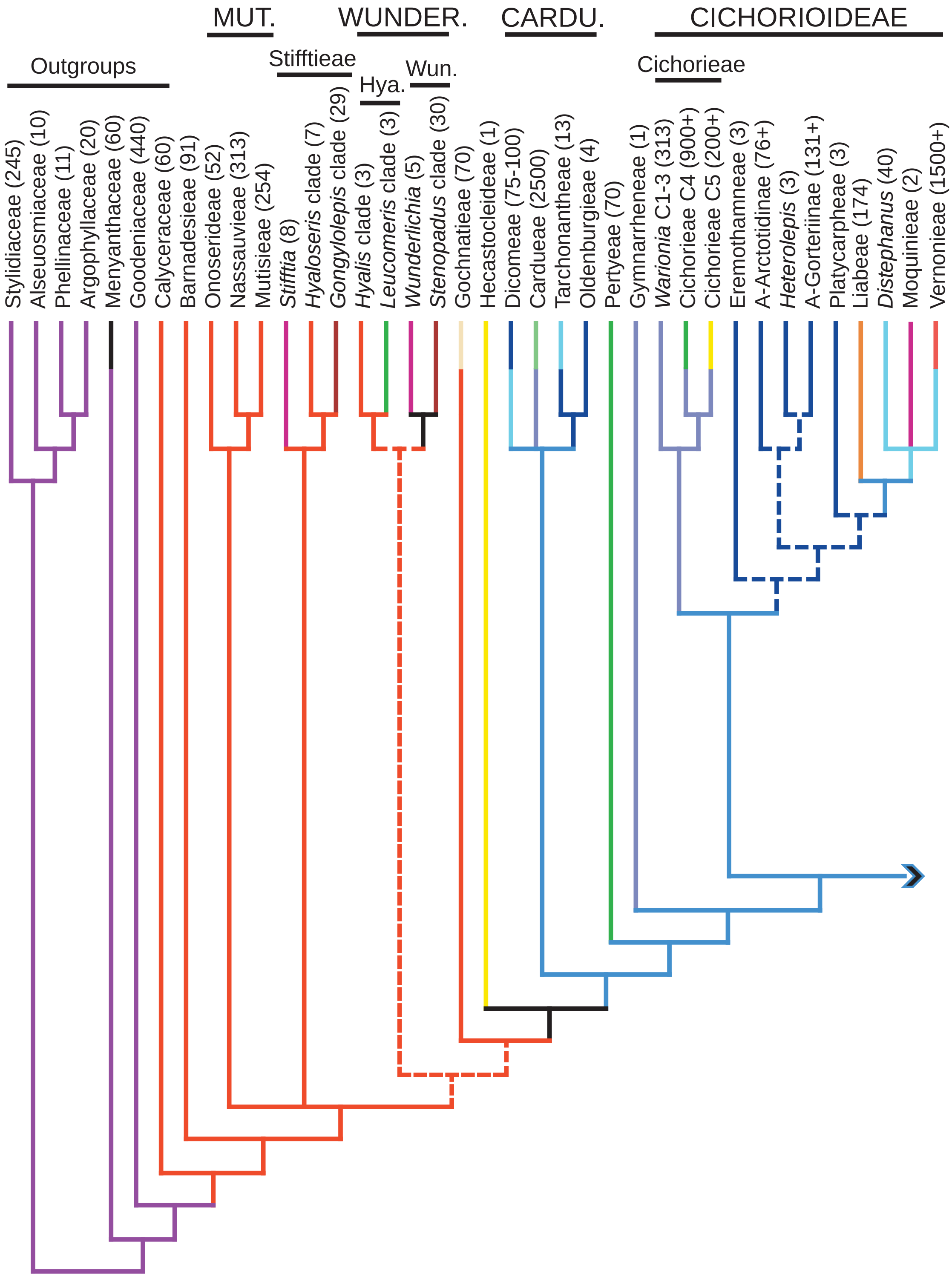
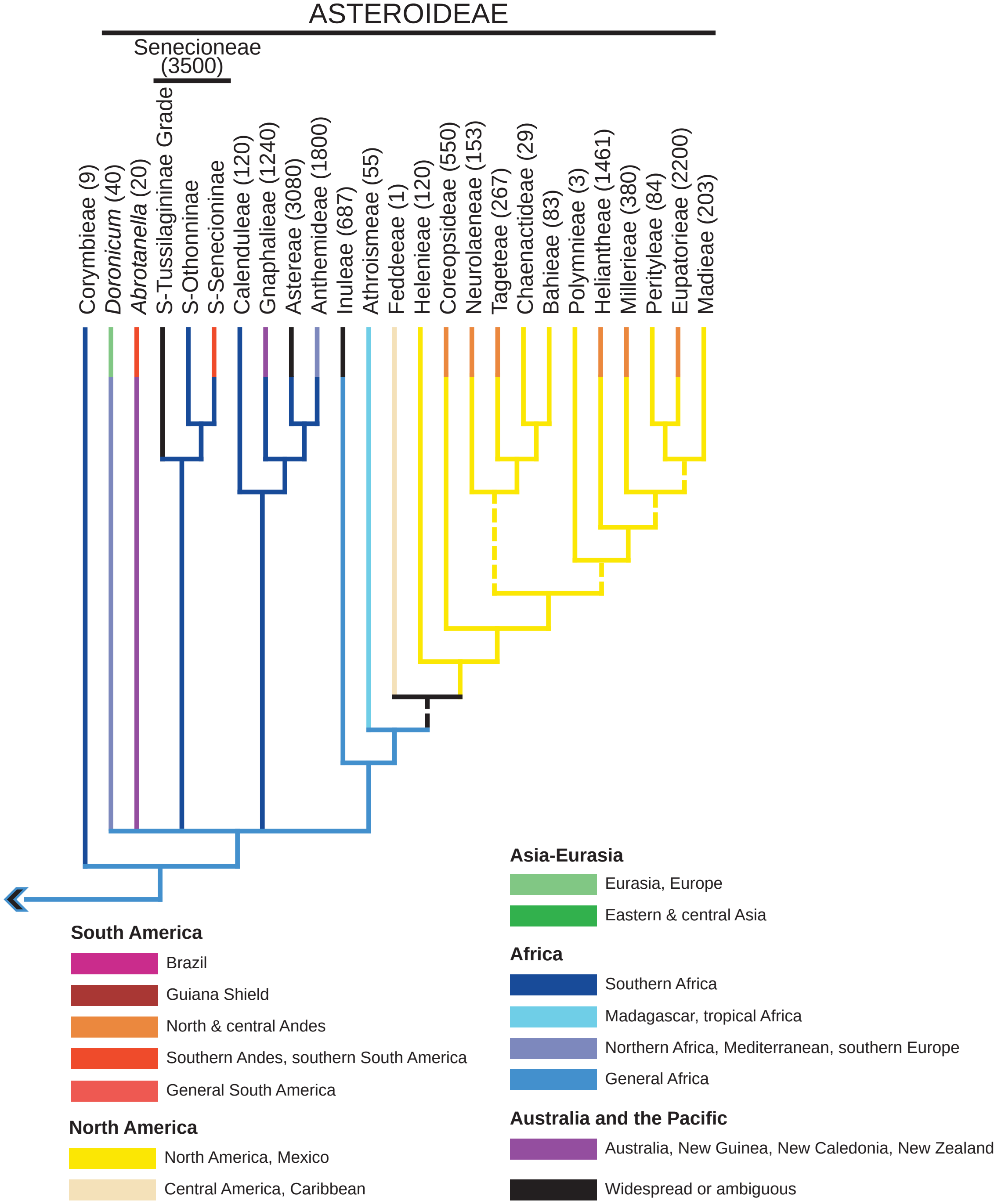


Fig. 11.2. A summary tree based on the metatree (Figs. 44.3–44.7). The tribes or clades have been represented by one to four branches. The branches and internodes were colored according to the distribution of the taxon or the optimization of those distributions. The numbers by the terminal taxa reflect the number of species in that clade. Note that some areas have been combined (e.g., Mexico and North America) and that the red color in Vernonieae represents Tropical America. Subfamilies that have more than one tribe are indicated in capital letters (see classification in this chapter). A = Arctotideae; CARDU. = Carduoideae; Hya. = Hyalideae; MUT. = Mutisioideae; S = Senecioneae; Wun. = Wunderlichieae; WUNDER. = Wunderlichioideae.



in functionally staminate or apomictic florets) into two (rarely three) short to long branches (style arms) with stigmatic areas on their inner (adaxial) surfaces, the apices of the style arms acute to rounded, truncate or with various appendages; stigmas dry, papillose; ovary inferior, of two (rarely three) united carpels, unilocular, with one erect, basal ovule; ovule anatropous, tenuinucellate, unitegmic; fruit, 1-seeded, indehiscent, usually an achene (cypsela), very rarely a drupe, crowned by a pappus formed of (1–)2 to many awns, scales (squamae, squamulae), setae or hairs in one or more series, homomorphic or heteromorphic, or by a more or less coroniform or auriculiform structure, or the pappus caducous or completely absent; abscission scar surrounded by a carpopodium, distinguished by the form of its cells and the texture of its surface, of one to many rows of cells, indistinct to prominent, sometimes apparently absent; embryo straight; endosperm scant, forming a thin layer around the embryo.

Current classification

(★ = under discussion, see Chapter 12. Recent investigations show that Corymbieae, Gymnarrheneae, Hecastocleideae, Pertyeae, and Wunderlichieae were not validly published in 2002. A republication of these suprageneric names with a Latin diagnosis will be submitted shortly.)

I. Barnadesioideae (D. Don) Bremer & Jansen (1992)
    1. Barnadesieae D. Don (1830)
II.★ Stifftioideae (D. Don) Panero (2007)
    2.★ Stifftieae D. Don (1830)
III. Mutisioideae (Cass.) Lindl. (1829)
    3. Mutisieae Cass. (1819)
    4. Onoserideae (Bentham) Panero & V.A. Funk (2007)
    5. Nassauvieae Cass. (1819)
IV.★ Wunderlichioideae Panero & V.A. Funk (2007)
    6. Wunderlichieae Panero & V.A. Funk (2007)
    7.★ Hyalideae Panero (2007)
V. Gochnatioideae (Benth. & Hook. f.) Panero & V.A. Funk (2002)
    8. Gochnatieae (Benth. & Hook. f.) Panero & V.A. Funk (2002)
VI. Hecastocleidoideae Panero & V.A. Funk (2002)
    9. Hecastocleideae Panero & V.A. Funk (2002)
VII. Carduoideae p.p. Cass. ex Sweet (1826)
    10. Dicomeae Panero & V.A. Funk (2002)
    11. Oldenburgieae S. Ortiz (2009)
    12. Tarchonantheae Kostel. (1833)
    13. Cardueae Cass. (1819)
VIII. Pertyoideae Panero & V.A. Funk (2002)
    14. Pertyeae Panero & V.A. Funk (2002)
    Catamixis incertae sedis
IX. Gymnarrhenoideae Panero & V.A. Funk (2002)
    15. Gymnarrheneae Panero & V.A. Funk (2002)
X. Cichorioideae (Juss.) Chevall. (1828)
    16. Cichorieae Lam. & DC. (1806)
    17. Arctotideae Cass. (1819)
    18. Eremothamneae H. Rob. & Brettell (1973)
    19. Liabeae (Cass. ex Dumort.) Rydb. (1927)
    20. Vernonieae Cass. (1819)
    21. Platycarpheae V.A. Funk & H. Rob. (2009)
    22. Moquinieae H. Rob. (1994)
    Heterolepis incertae sedis
XI. Corymbioideae Panero & V.A. Funk (2002)
    23. Corymbieae Panero & V.A. Funk (2002)
XII. Asteroideae (Cass.) Lindl. (1829)
    24. Senecioneae Cass. (1819)
    25. Calenduleae Cass. (1819)
    26. Gnaphalieae (Cass.) Lecoq. & Juillet (1831)
    27. Astereae Cass. (1819)
    28. Anthemideae Cass. (1819)
    29. Inuleae Cass. (1819)
    30. Athroismeae Panero (2002)
"Heliantheae alliance"
    31. Feddeeae Pruski, P. Herrera, Anderb. & Franc.-Ort. (2008)
    32. Helenieae Lindl. (1829)
    33. Coreopsideae Lindl. (1829)
    34. Neurolaeneae Rydb. (1927)
    35. Tageteae Cass. (1819)
    36. Chaenactideae B.G. Baldwin (2002)
    37. Bahieae B.G. Baldwin (2002)
    38. Polymnieae (H. Rob.) Panero (2002)
    39. Heliantheae Cass. (1819)
    40. Millerieae Lindl. (1929)
    41. Madieae Jeps. (1901)
    42. Perityleae B.G. Baldwin (2002)
    43. Eupatorieae Cass. (1819)

As an aid to understanding the system of classification, short descriptions of tribes with diagnostic features and geographic distribution are provided below. Characters follow a uniform order; + denotes small tribes with only one or two genera. The tribes are broken into two large groups, the Non-Asteroideae (a grade) and the subfamily Asteroideae (a clade). Within the subfamily Asteroideae there is the well recognized clade, the Heliantheae Alliance. The primary providers of the information for most of the tribes are listed; those without attribution are by V.A. Funk. An online key to the tribes can be found on www.compositae.org.

Group 1: 'Non-Asteroideae' grade

Tribes *not* contained in the subfamily Asteroideae usually have: stigmatic surface solid on inner surface of style branch; pollen bearing part of anther extending well below the insertion of the filament (spurred; calcarate) and with tails (caudate); pollen psilate, lophate or echinate (Liabeae, some Lactuceae, some Cardueae); disc corollas in many forms but lobes usually longer than wide (deeply lobed); 3-lobed "true ray corollas" are found only in Liabeae and some Arctotideae; leaves alternate except for most Liabeae. Base chromosome number $x = 9$ or 10.

1. Barnadesieae. — (information provided by Estrella Urtubey): Trees, shrubs, subshrubs, perennial or annual herbs without latex; leaves alternate, opposite, fasciculate or whorled; heads discoid or radiate or ligulate, 1-numerous; involucre from cylindrical to widely campanulate, bracts in several series, chartaceous; receptacle usually pilose, occasionally paleous or glabrous; florets usually hermaphroditic, white, yellow, orange, pink, purple to violet; corollas tubular, split, doubly split, ligulate, sub-bilabiate (4 + 1), rarely bilabiate (3 + 2), often villous; anther apical appendage rounded to obtuse or acute, emarginated to bilobed, thecae with or without spurs (calcarate or ecalcarate) and with or without tails (caudate or ecaudate); pollen with or without depressions, spinulate, microechinate, scabrate-microspinulate, granulate, smooth or rarely lophate; styles vary from thick to slender, shortly bilobed or bifid, apex rounded, papillose rarely pilose, style branches rarely recurving; achenes densely villous, with "barnadesioid trichomes"; pappus in a single whorl, plumose, barbellate, setaceous or rarely absent.

Diagnostic features: axillary spines frequently present; absence of short, stalked, capitate glands (sesquiterpenes lacking); filaments free or rarely fused; absence of twin hairs on achenes, instead they have "barnadesioid trichomes"; and involucral bracts often spine-tipped.

Distribution: southern South America, the Andes, and Brazil.

2. Stifftieae

***Stifftia.* —** Trees, shrubs or vines, without latex; leaves alternate; heads discoid, 1–40 florets; involucre corymbose to paniculate, bracts multiseriate, subimbricate, margins not hyaline; receptacle epaleate, plane; florets isomorphic, bisexual, corollas whitish, actinomorphic, tubular-funnelform, deeply 5-lobed, the lobes completely coiled or only near the apex; anther apical appendages acuminate, thecae with spurs (calcarate) with long, smooth to sometimes papillose tails (caudate); pollen prolate, minutely spinulose; styles thick, glabrous, shallowly divided, apex rounded to shortly acute, branches dorsally smooth to slightly rugulose at the apex, never reflexed; achenes glabrous to weakly puberulent; pappus of scabrid bristles, capillary to somewhat paleaceous, the innermost slightly apically broadened and longer.

Diagnostic features: heads discoid; pappus showy, whitish, yellowish or reddish with ca. 100 capillary bristles in 4–5 series; florets actinomorphic, white with corolla lobes rolled; and styles glabrous, shallowly divided, apex rounded to shortly acute.

Distribution: five species are endemic to Brazil and one is endemic to French Guiana.

***Hyaloseris* clade. —** Shrubs or small trees without latex; leaves alternate to opposite, clustered in brachyblasts; heads discoid or ligulate, small to large; involucres cylindrical to funnelform, bracts imbricate, multiseriate, inner longer than outer, without hyaline margins, in 4–6 series; receptacle epaleate, surface unknown; florets isomorphic or with transitional corollas in the same head, bisexual, corollas yellow, white, purplish, ligulate corollas with shallowly 5-dentate limb, occasionally some segments partially connate, sub-bilabiate (4 + 1 corolla lips), rarely bilabiate; anther apical appendages acute, theceae with spurs (calcarate) and with long laciniate, papillose tails (caudate); pollen psilate, subprolate; styles slender, bifid, branches dorsally papillose, remainder of style glabrous, recurving when mature; achenes obovate, angled in cross-section, glabrous to pubescent; pappus of scabrid, capillary bristles.

Diagnostic features: two genera of woody plants of south-central South America with leaves clustered in brachyblasts; heads ligulate.

Distribution: Bolivia and Argentina.

***Gongylolepis* clade. —** Trees or shrubs, rarely subshrubs, without latex; leaves alternate; heads discoid and one-flowered, or radiate, or homogamous and bilabiate, or homogamous and isomorphic (ligulate or bilabiate) or heteromorphic (ligulate and bilabiate), 1–150 florets; involucre cylindrical or hemispherical or campanulate, bracts imbricate but sometimes subequal; receptacle naked or hirsutulous, may be smooth or pitted or foveolate or clavate; florets perfect, corollas zygomorphic or bilabiate (some actinomorphic in *Quelchia*), red or reddish, pale yellow, or white with apices lilac, magenta, or red, outer lip 3-lobed, inner lip 2-cleft (rarely 3-cleft) and coiled or flexuous; anther acute or acuminate at apex, theceae bases calcarate and tailed (caudate), the tails long and free or connate with adjacent anthers; pollen prolate to spheroidal-subprolate, microechinate, echinate, or almost psilate; styles bifid, white, red or purple, branches dorsally smooth, erect, ascending, or recurved; achenes prismatic or cylindrical or cylindrical-turbinate, glabrous to densely pubescent; pappus of setae, multiseriate or few-seriate.

Diagnostic features: woody plants with zygomorphic or bilabiate corollas; 2-cleft inner lip that is often much coiled and so is shorter than outer lip; and styles bifid and dorsally smooth.

Distribution: predominantly on the Guiana Shield with one monotypic genus in the Dominican Republic.

3. Mutisieae. — (information provided by G. Sancho): Herbs usually perennial, often scapose and stout, or less commonly trailing shrubs or subshrubs, without latex; leaves alternate; heads radiate (less commonly disciform or discoid), small to large (6 to ca. 200); involucre usually campanulate, bracts imbricate, margins not hyaline; receptacle naked, alveolate; floret corollas white, yellow, cream, pink, purple, blue, orange, or red; marginal corolla when present, strap-shaped with three teeth, bilabiate, sub-bilabiate, or rarely tubular; disc corollas bilabiate or tubular, shallowly lobed, the lobes equal or unequal in length; anther apical appendage not constricted or demarcated from the thecae (rarely demarcated), acute, thecae rarely with spurs (calcarate) but with tails (caudate); pollen usually prolate, exine almost psilate; style slender, shallowly bilobed to bifid with two long branches, rounded at the apex, usually dorsally papillose only above the style bifurcation point, papillae rounded, never acute; achene oblong to sub-obovate, truncate, attenuate to rostrate at the apex, glabrous to pubescent, often glandular, sometimes dimorphic with the marginal achenes conspicuously larger than the central ones; pappus of one to more series of bristles, scabrid to plumose, usually capillary, or absent.

Diagnostic features: corollas often brightly colored; marginal corollas usually bilabiate; disc corollas bilabiate or tubular, shallowly lobed, lobes equal to unequal; anther apical appendage not constricted or demarcated; anthers ecalcarate and caudate; and style shallowly bilobed to bifid, rounded at the apex, usually dorsally papillose only above the style bifurcation point, papillae rounded, never acute.

Distribution: predominately southern South America with outliers in Africa and Asia.

4. Onoserideae. — (information provided by L. Katinas): Annual or perennial herbs, shrubs, sometimes dioecious, without latex; leaves alternate; heads radiate, medium to large; involucre campanulate to hemispheric, bracts imbricate; receptacle naked, alveolate; corollas red, orange, purple, pink, white, or bicolor white-purple; ray corolla bilabiate with a 3-toothed outer lobe and a 1–2-toothed inner lobe, rarely absent; disc corollas with five lobes, the lobes short to long, equal or unequal in length; anther apical appendage acute or truncate, thecae with spurs (calcarate) and tails (caudate); pollen psilate; styles thick, apex rounded, glabrous, rarely papillose on abaxial surface of style arms; achenes elliptical to turbinate; pappus of 2–4-seriate bristles.

Diagnostic features: involucral bracts imbricate; corollas often brightly colored; ray corolla bilabiate (rarely absent); disc corollas tubular with five lobes equal or unequal in length; anther apical appendage acute or truncate, thecae calcarate and caudate; styles thick, apex rounded, glabrous, rarely papillose; achenes elliptical to turbinate, glabrous or pubescent; and pappus of 2–4-seriate bristles.

Distribution: southern South America but also in the Andes.

5. Nassauvieae. — (information provided by L. Katinas): Herbs, subshrubs, shrubs or vines without latex; leaves alternate sometimes rosulate; heads discoid or radiate, small to medium size; involucre cylindric to campanulate, bracts imbricate; receptacle naked or paleate, alveolate; corollas white, yellow, red, blue, orange, purple, violet; ray corolla bilabiate with a 3-toothed outer lip and 1–2-toothed inner lip, outer lip short or long; disc corolla bilabiate (rarely with five lobes of equal size); anther apical appendage acute, thecae with spurs (calcarate) and tails (caudate); pollen psilate, spheroidal and suboblate; styles thick, apex truncate, rarely rounded, arms with an apical crown of sweeping hairs; achenes elliptic to turbinate, glabrous or pubescent; pappus of capillary, paleaceous, scabrose, or plumose bristles, one to more than one series, or absent.

Diagnostic features: all corollas bilabiate; style apex truncate, the only pubescence is on the arms, which have a unique apical crown of sweeping hairs; pollen exine distinctly bilayered, with the ectosexine and the endosexine clearly columellate.

Distribution: mostly southern South America.

6. Wunderlichieae. — Trees, shrubs, or subshrubs without latex; leaves alternate; heads discoid, 5–100 florets; involucre cylindric to hemispherical, bracts imbricate or less commonly subimbricate; receptacle epaleate to strongly paleate; disc florets perfect, corollas cream-colored to yellow to magenta with five lobes of equal size, deeply cut; anther apical appendages acute to acuminate, spurs (calcarate), base tailed, tails free to connate with tails of adjacent stamens; pollen prolate or subprolate, psilate, spinulose, or echinate with short spines; styles smooth or slightly asperulous at apex, dorsally papillose or dorsally rugulose to papillose much below the bifurcation point; achenes prismatic and glabrous to pilose; pappus of multiseriate bristles or setae.

Diagnostic features: woody; leaves clustered near stem apex, actinomorphic corollas; styles smooth or slightly asperulous at apex, dorsally papillose or dorsally rugulose to papillose much below the bifurcation point.

Distribution: Guiana Shield and Brazil.

7. Hyalideae. — (information provided by G. Sancho): Small trees, shrubs, or subshrubs without latex; leaves alternate; heads homogamous or heterogamous, radiate or discoid, small to relatively large (5 to ca. 75 florets); involucre cylindrical to campanulate or turbinate, bracts imbricate to sub-imbricate, inner bracts longer than outer, usually in 3–10 series, green with darker or lighter margins but not hyaline, sometimes scabrous (*Leucomeris*); receptacle naked, flat or alveolate; florets dimorphic or isomorphic, bisexual, corollas whitish, pink, or purple, rarely yellow; marginal florets, when present, bisexual or female, sometimes with staminodes (*Ianthopappus*), corollas bilabiate with lobes coiled; central florets one (*Hyalis*) to ca. sixty, bisexual, corollas tubular, deeply 5-lobed, the lobes equal in length and coiled; anther apical appendage apiculate, acute to acute-apiculate, thecae sagittate (spurs; calcarate) with long laciniate or papillose tails (caudate); pollen sub-prolate to prolate, elliptic, exine psilate (to nearly psilate); styles thick to slender, shallowly divided (1.5 mm), glabrous, apex rounded or subrounded, usually with an extension of the stigmatic surface (*Ianthopappus*), style branches never recurving; achenes fusiform, cylindrical, ribbed, villose; pappus of 2- or 3-seriate, scabrid to smooth (occasionally plumose at the apex) capillary bristles, outer ones shorter.

Diagnostic features: marginal corollas usually present, bilabiate; central corollas tubular, deeply lobed; anther apical appendages apiculate; styles glabrous; and pappus of 2- or 3-seriate, scabrid or occasionally plumose at the apex capillary bristles with a reduced number of outer shorter bristles.

Distribution: South America and Asia.

8. Gochnatieae. — (information provided by G. Sancho): Trees, shrubs, subshrubs, or perennial herbs without latex; leaves alternate sometimes rosulate; heads solitary (or 2–3) or several, homogamous or heterogamous, radiate or discoid (occasionally disciform), small to large (ca. 5–300 florets); involucre oblong to campanulate or turbinate, bracts imbricate in 3–10 series, margins not hyaline; receptacle naked, alveolate; corollas white to orange (seldom pink, lilac, or purple); marginal florets, when present, bisexual or female, usually with staminodes, bilabiate or sub-bilabiate (rarely sub-zygomorphic); central florets bisexual; disc corollas tubular, deeply lobed, the lobes equal in length; anther apical appendages apiculate, thecae with tails (caudate); pollen spheroidal to prolate or elliptic, exine almost psilate; styles slender, usually shallowly divided, glabrous, apex rounded to subrounded, usually with an extension of the stigmatic surface; achenes obovate, villose; pappus of uniseriate or 2- or 3-seriate, scabrid or occasionally plumose (at the apex) capillary bristles or less commonly some of them relatively flat.

Diagnostic features: marginal corollas, when present, bilabiate; disc corollas tubular, deeply lobed; anther apical appendages apiculate; and styles glabrous.

Distribution: America, from southern United States to Argentina and the Caribbean (especially Cuba).

9. +Hecastocleideae. — Small to medium shrub without latex; leaves alternate; heads discoid, small (1 floret); involucre cylindric to fusiform, bracts imbricate without hyaline margins; receptacle naked; corollas white to reddish to greenish white; disc corollas with five lobes of equal size, deeply divided; anther apical appendages lanceolate not elongate, thecae bases with spurs (calcarate) and slightly fimbriate tails (caudate); pollen psilate and oblong; styles slender and glabrous, branches short (0.1–0.5 mm), apices rounded, not recurving at maturity; achene terete, obscurely 4–5-nerved, glabrescent; pappus of six unequal, lanceolate or multi-toothed scales sometimes fused to form lacerate crowns.

Diagnostic features: stiff holly-like leaves; tricolpate pollen; heads that are single-flowered and re-aggregated on a secondary receptacle, each group of 1–5 heads being subtended by a relatively large spiny whitish or greenish bract.

Distribution: restricted to high elevation areas (1500–2000 m) in southern Nevada and adjacent California including Death Valley.

10. Dicomeae. — (information provided by S. Ortiz): Perennial herbs, shrubs or small trees without latex; leaves alternate; heads discoid or radiate, variable in size; involucre hemispherical to obconic, bracts imbricate often with hyaline margins: receptacle epaleate (rarely paleate), alveolate; corollas white, yellow, cream to pink or mauve; ray corollas bilabiate (inner lips coiled or not) or true rays with three teeth; disc corollas with five lobes of equal size, deeply divided; anther apical appendage acute to acuminate, thecae with spurs (calcarate), rarely without them (ecalcarate), and tails (caudate); pollen sub-oblate to prolate, micro-echinate or echinate; styles thick, deeply or shallowly divided, with a subacute to rounded apex and apical or subapical acute sweeping hairs, sometimes recurving at maturity; achenes often obconic but also narrowly oblong to broadly cylindrical with twin hairs; pappus of scabrid to plumose bristles or scales, pluriseriate, isomorphic or dimorphic.

The core group of genera (*Dicoma*, *Pasaccardoa*, *Macledium*, and *Cloiselia*) of this tribe is characterized by: pungent phyllaries without resin ducts (or ducts reduced); presence of star-shaped calcium oxalate crystals in the corollas, anther filaments and styles; anther tails long tapering; pollen slightly echinate; style branches straight and adjacent; and achenes broadly obconic to cylindrical with twin hairs and without a carpopodium. The remaining three genera (*Pleiotaxis*, *Erythrocephalum* and *Gladiopappus*) are rather different from this core group of Dicomeae and their inclusion in this tribe is provisional. *Pleiotaxis* and *Erythrocephalum* can be distinguished by the presence of phyllaries not pungent with resin ducts, calcium oxalate crystals not star-shaped, anther tails with subacute to subrounded apex, style branches separate and often curved, achenes ellipsoid and with carpopodium, whereas *Gladiopappus* is characterized by phyllaries with rounded apex, unisexual florets among the bisexual disc florets, marginal florets of the capitula being truly bilabiate with coiled adaxial lobes, and achenes broadly obconic without twin hairs.

Distribution: tropical and southern Africa, including Madagascar and two species range outward to the Arabian Peninsula, India, and Pakistan.

11. +Oldenburgieae. — (information provided by S. Ortiz): Dwarf cushion-forming shrubs to small trees without latex; leaves alternate, mainly coriaceous; heads radiate, large (up to 1000 florets); involucre campanulate to urceolate, bracts imbricate often without hyaline margins; receptacle epaleate, alveolate; corollas white, cream or pinkish-brown; ray corollas bilabiate with the inner lip coiled lobes; disc corollas often actinomorphic (rarely slightly zygomorphic), deeply 5-lobed; anthers apical appendage acuminate, thecae with spurs (calcarate) and tails (caudate); pollen sub-oblate to prolate, echinate; style rather thick with very short branches, rounded at the apex, smooth to papillose, rarely with apical acute sweeping hairs; achenes narrowly ellipsoid to linear; pappus of scabrid to plumose bristles, pluriseriate.

Diagnostic features: woody plants with coriaceous leaves; large heads; bilabiate corollas; and short rounded style branches.

Distribution: South Africa.

12. +Tarchonantheae. — (information provided by S. Ortiz): Dioecious trees or shrubs, without latex; leaves alternate; heads discoid, small (ca. 30, rarely up to 90 florets), unisexual, rarely with a few bisexual florets; involucre campanulate to obconic, bracts imbricate, often without hyaline margins; receptacle epaleate, alveolate; corollas yellowish or whitish; male florets with deeply 5-lobed actinomorphic, tubular corollas; anther apical appendage deltate, thecae with spurs (calcarate) and tails (caudate); style characters reduced; pollen oblate-spheroidal to sub-prolate, micro-echinate; female florets with 3–5-lobed actinomorphic, tubular to filiform corollas; anthers reduced or absent; style with short, often recurved, flattened branches, acute to obtuse at the apex, without sweeping hairs; achenes mainly cylindrical to ellipsoid, flattened or not; pappus of numerous barbellate bristles in 1–2 rows or lacking.

Diagnostic features: dioecious trees or shrubs often aromatic with small discoid capitula of ca. 30 florets and heads that are arranged in generally dense racemes or panicles.

Distribution: tropical Africa (mainly in the eastern part), Madagascar, and southern Africa, and one species also present in the Arabian Peninsula.

13. Cardueae. — (information provided by A. Susanna): Perennial or monocarpic herbs, often subshrubs (less often shrubs or annual herbs, very rarely large shrubs or even treelets), laticiferous ducts present in roots; leaves alternate frequently forming a rosette; heads discoid (very rarely peripheral florets with 5-lobed ligules), usually many-flowered (rarely one-flowered); involucre campanulate, bracts in many rows, often spiny (less frequently unarmed); receptacle scaly or more often setose, rarely naked, alveolate; florets all fertile or the peripherals sterile, corollas purple, pink or yellow, seldom blue, usually tubular, usually actinomorphic, straight or s-shaped, deeply divided in five lobes of equal size; anther apical appendages extending into a rigid, lignified, lanceolate appendage, thecae bases sagittate (calcarate) and tailed (caudate) often with long divisions; pollen psilate, verrucate, scabrate or echinate, oblate, spherical or more prolate; styles slender; apices rounded, at maturity style branches not recurving, shaft with some short hairs above the point where the style branches and below with a papillose-pilose thickening (functionally a pollen brush); achenes usually with hardened pericarp, blackish by presence of phytomelans; pappus of scales or bristles.

Diagnostic features: involucral bracts usually in five rows and spiny-tipped; leaves often spiny; style cylindrical with a thickened articulation below the branches bearing a short collar of stiff hairs; anthers often with laciniate basal appendages, anther filaments usually papillose; and stamens often strongly thigmotropic, making up an elaborate mechanism of pollen presentation.

Distribution: widespread in Eurasia, especially diverse in the Mediterranean region where they constitute an important characteristic of the vegetation; some species are cosmopolitan weeds.

14. Pertyeae. — Perennial herbs, subshrubs or shrubs, without latex; leaves alternate, often rosulate, clustered at the median part of the stem or on secondary short shoots; heads discoid, one to ca. 13(–16) florets; involucre cylindrical to obconic, commonly multiseriate (5–15 rows) to rarely uniseriate of few involucral bracts, usually imbricate with hyaline margins sometimes ciliolate; receptacle epaleaceous usually glabrous, rarely pilose, alveolate or not; florets usually bisexual and fertile (rarely functionally female/male or cleistogamous), corollas white or pink, 5-lobed but zygomorphic with one split deeper than the others, sometimes pseudo-bilabiate or pseudo-ligulate; anther apical appendages truncate or rounded to apiculate, more seldom emarginated, thecae with spurs (calcarate) and with tails long and smooth to pilose (caudate); pollen spheroidal or subprolate, exine microechinate, scabrous, or echinate; styles slender, branches bilobed to shortly branched, variously truncate, rounded or acute at the apex, dorsally pilose to shortly pilose, sometimes swelling slightly on upper part of style with branches recurved; achenes oblong to obovate, (9- or) 10-veined, glabrous or pilose; pappus bristles 1–3-seriate (sometimes absent in functionally male or chasmogamous florets), margins scabrid or plumose.

Diagnostic features: small discoid heads of white, pink, rose or purple florets; corollas irregularly deeply 5-lobed and therefore zygomorphic by having one sinus deeper than the others, appearing pseudo-bilabiate or pseudo-ligulate; and styles thick, branches bilobed to shortly branched, dorsally pilose to shortly pilose.

Distribution: southeast Asia.

+*Catamixis* incertae sedis. — Shrubs without latex; leaves alternate; heads ligulate, small (6 florets); involucre turbinate, bracts scarcely imbricate, gradate, without hyaline margins; receptacle naked, more or less alveolate; corollas whitish to pale yellow, ligulate with five lobes, sinuses varying in depth; anther apical anther appendages narrow-triangular, acute to somewhat rounded, thecae with spurs (calcarate) and tails (caudate), laciniate; pollen spinulose with widely dispersed spinules (<1 μm in height); styles slender, glabrous, branches relatively short (0.25 mm), apices slightly rounded, dorsally short papillose, at maturity style branches not recurving; achenes densely long-setuliferous/sericeous, apices acute; pappus setae uniseriate, long-barbellate, white.

Diagnostic features: small ligulate heads; distinctive leaves that are obovate, serrate with large teeth, pinnately veined and easily disarticulating; small pollen (30 μm); and phyllary apices, long-acute, often purplish.

Distribution: northern India and adjacent Nepal.

15. +Gymnarrheneae. — Amphicarpic annuals with no reports of latex; leaves alternate forming rosettes; subterranean heads homogamous, female, cleistogamous; florets enclosed in small involucral bracts, corolla vestigial;

pappus absent, vestigial, or of short, somewhat scale-like bristles; aerial heads congested in the center of the leaf rosette, heterogamous, disciform, functionally staminate florets in small groups, loosely connected on very short pedicels, interspersed among the small pistillate florets; corollas small, whitish; anther apical appendage absent, thecae without spurs (ecalcarate) and with tails (caudate); pollen echinate and non-lophate, the spines unevenly-distributed; female florets solitary, each enclosed in a prominent, stiff, white and green bract; corolla filiform; style arms long with rounded apex, glabrous, at maturity style branches not recurving; achenes of three types, those of pistillate florets numerous, tiny, ovoid, ciliate, villous, with long twin hairs; pappus of three types, that of female florets of long-lanceolate, ciliate, acuminate scales.

Diagnostic features: ephemeral, dwarf desert annual, amphicarpic; both chasmogamous aerial heads and cleistogamous subterranean ones and two different types of achenes; corollas 3–4-lobed; 3–4 anthers; and aerial heads clustered together and with functional male and female florets.

Distribution: deserts in northern Africa and the Middle East.

16. Cichorieae. — (information provided by N. Kilian): Annual to perennial herbs (more rarely subshrubs, shrubs, rosette shrubs and rosette treelets) with latex; leaves alternate frequently forming a rosette; heads ligulate (except for *Gundelia* and *Warionia*), homogamous, with one to over 600 florets but mostly with a few dozen; involucre cylindric, mostly differentiated into a few imbricate outer series of bracts and a longer inner series (rarely uniseriate), bracts with or without hyaline margin; receptacle areolate or alveolate, naked (rarely with scales or bristles); corolla predominantly of some shade of yellow or blue, with 5-toothed ligule, perfect; anther apical appendage elongate, smooth, filaments smooth, thecae calcarate and caudate; pollen echinolophate or echinate; style slender, usually with long, slender branches, sweeping hairs on the shaft and branches; achenes cylindrical, or fusiform to slenderly obconic, mostly ribbed, sometimes compressed or flattened, apically truncate, attenuate or beaked, often somehow sculptured, mostly glabrous, sometimes papillose or hairy, rarely villose, frequently heteromorphic; pappus of scales or scabrid to barbellate or plumose bristles, sometimes absent.

Diagnostic features: almost exclusive presence of homogamous capitula with 5-dentate, ligulate flowers; and exclusive presence of lactiferous canals in both the subterranean and aerial parts.

Distribution: nearly global with centers of diversity in the Mediterranean area and north temperate climates.

17. Arctotideae

Arctotidinae. — (information provided by P.O. Karis): Shrubs, shrublets, and herbs without latex; leaves alternate; heads radiate; involucre campanulate, cylindric or urceolate, bracts imbricate, outer with foliaceous tips, inner with scarious tips; receptacle mostly naked, smooth or shallowly honeycombed; ray florets often brightly colored, usually female, corollas 3-lobed; disc corollas shallowly 5-lobed; anther apical appendage short, rounded, soft, wrinkled, thecae with spurs (calcarate) and no tails (ecaudate), endothecium radial, collar usually inconspicuous; pollen echinate, oblate-spheroidal; styles with a thickened apical portion, sweeping hairs small patent, broadly subulate, much longer in a ring below the bifurcation; achenes flattened, ribbed, sometimes winged; pappus of uni- or biseriate scales.

Diagnostic features: radial anther endothecium, inconspicuous anther collar; apically thickened styles, small, patent and broadly subulate sweeping hairs; and pappus scale cells very long and with abaxially reinforced walls.

Distribution: mainly southern Africa.

Gorteriinae. — (information provided by P.O. Karis): Shrubs, shrublets or herbs with latex; leaves usually alternate, with spines or longitudinally striate hairs; heads generally radiate; involucre campanulate, cylindric, urceolate or obconic, bracts connate, herbaceous; receptacle deeply alveolate with projections along alveole margins; ray florets sterile, corollas usually 4-lobed; disc corollas with sclerified lobe margins; apical anther appendage firm, rather short, thecae with spurs (calcarate) and with (caudate) or without tails (ecaudate), endothecium without lateral wall thickenings or some polarized; pollen echinate, sublophate or lophate generally oblate-spheroidal; styles with clavate or subulate-ensiform sweeping hairs, longer in a ring below the bifurcation; achenes somewhat flattened, usually ribbed; pappus usually of uni- or biseriate scales.

Diagnostic features: latex; connate involucral bracts; deeply alveolate receptacles; 4-lobed, sterile ray florets; and disc corolla lobes with sclerified margins.

Distribution: southern Africa.

18. +Eremothamneae. — (information provided by H. Robinson): Erect branching shrubs without latex; leaves alternate; heads radiate or discoid, small (5 florets in *Hoplophyllum*) or medium (12–20 rays and 25–30 disk florets in *Eremothamnus*); involucre cylindric to campanulate, bracts multiseriate, gradate, distally papyraceous and usually with apical spine; receptacle naked, surface unknown; corollas yellow; ray corollas when present, strap-shaped with three short teeth; disc corollas with five linear lobes of equal size; anther apical appendage oblong, apiculate or broadly elongate, thecae with spurs (calcarate) and tails (caudate); pollen spinulose with larger spines in intercolpi and smaller crowded spines around poles; styles slender, elongated, branches narrow, upper portion of style shaft and outer surfaces of branches covered with elongate sweeping hairs formed by two or three cells separated by longitudinal walls, at maturity style branches not recurved; achenes densely sericeous; pappus of many stout scabrid-barbellate capillary bristles in 2–3 series, somewhat gradate in length.

Diagnostic features: slender style branches bearing relatively long sweeping hairs divided longitudinally into two or three cells; pollen spinulose with larger spines in intercolpi and smaller crowded spines around poles; and involucral bracts multiseriate, gradate, distally papyraceous and usually with apical spine.

Distribution: western South Africa and southern Namibia.

19. Liabeae. — (information provided by M. Dillon): Annual or perennial herbs, shrubs, or small trees usually with latex; leaves usually opposite; heads radiate (3 to ca. 320 florets); involucre campanulate, bracts graduate, without hyaline margins; receptacle alveolate, without chaff; corollas yellow (rarely red, purple, or white); ray corolla present, strap-shaped with three lobes; disc corollas with five lobes of equal size, longer than wide; anther apical appendage acute, thecae with spurs (calcarate) and tails (caudate) fringed or digitate; pollen echinate, spherical; styles slender, apex attenuate, sweeping hairs on upper style shaft and backs of branches, at maturity style branches recurving; achenes oblong or columnar; pappus of numerous long inner capillary bristles and short outer series of squamellae, sometimes with scales or plumose bristles or absent.

Diagnostic features: leaves usually opposite; latex present in most taxa; corollas usually yellow; and pollen echinate.

Distribution: tropical America with the vast majority in Peru and Ecuador.

20. Vernonieae. — (information provided by H. Robinson): Perennial herbs (few annuals), shrubs, vines or small trees, latex mostly lacking; leaves mostly alternate; heads one to many, homogamous; involucre with bracts subequal to gradate, inner persistent or deciduous, without hyaline margins; receptacles rarely paleate, with or without hairs; corollas mostly blue to reddish or purple, actinomorphic (rarely zygomorphic), 5-lobed (rarely with lobes grouped as four outer and one inner), lobes elongate; anther apical appendage oblong-ovate, thecae usually spurred, often tailed; pollen spherical, mostly 35–70 µm in diameter in medium, not caveate, usually sublophate or lophate, often with perforated tectum partially or totally missing; style branches spreading tangentially, slender and tapering, with long sweeping hairs on outer surface extending onto upper part of style shaft; achenes usually prismatic with 5–10 ribs, sometimes obcompressed, rarely winged; pappus usually capillary, often with short outer series, sometimes coroniform or lacking.

Diagnostic features: alternate leaves with pinnate venation, often with T-shaped or stellate hairs; heads without rays; corollas mostly blue to reddish or purple; slender tapering style branches, long sweeping hairs on outside extending onto upper style shaft; achenes usually with twin hairs, rarely with phytomelanin in walls, usually with raphids; pollen sublophate or lophate; and anther endothecial cells with thickenings on upper and lower ends; rich in sesquiterpene lactones, one group with 5-alkyl-coumarins.

Distribution: tropical and southern Africa, southeast Asia to Australia and the Pacific, and the Western Hemisphere.

21. +Platycarpheae. — Acaulescent perennial herbs without latex; leaves arranged around edge of secondary head; heads discoid, one- to many-flowered; involucre subglobose to cylindrical, bracts somewhat imbricate without hyaline margins; receptacle naked, alveolate; corollas purple, mauve, lilac, or pink, occasionally whitish, with five lobes of equal size; anther apical appendage acute not elongate, thecae subequally sagittate (calcarate) and without tails (sometimes with very short tails) (ecaudate or caudate); pollen echinate, spines regularly and irregularly arranged; styles slender, in *Platycarphella* apex slightly rounded and styles with a few distal hairs, otherwise glabrous, in *Platycarpha* apex slightly tapered, branches terete, with hairs nearly to tip, at maturity style branches arched but not recurved; achenes 3- or 5-sided, dark, oblong, with faint ribs, rugose or smooth, glabrous; pappus of persistent white scales.

Diagnostic features: complicated secondary head structures; leaves that are elongate and prostrate; stolons that emanate from the crown at the base of the secondary head; secondary head and leaves lying more or less flat on the ground; anthers purple; styles lavender; and pollen echinate with spines in a regular arrangement or in irregularly arranged ridges surrounding the colpi in a unique bowtie pattern.

Distribution: three species in southern Africa.

22. +Moquinieae. — (information provided by H. Robinson): Shrubs without latex; leaves alternate; heads with one or five florets, homogamous or with anthers aborted in functionally female florets; involucres cylindrical, bracts green-brown with short hairs and small hyaline margins; corollas lavender to purplish, actinomorphic, 5-lobed, lobes elongate; anthers apical appendages oblong-ovate, thecae spurred (calcarate) and short tailed (caudate); pollen spherical, echinate, non-lophate, non-caveate, with baculae not aligned with spines; styles slender below, swollen and scabrous above near branches, branches short, scabrous outside, with continuous stigmatic surface inside, branches in multiflowered heads spreading tangentially; achenes prismatic, 10–17-ribbed, with numerous twin hairs, idioblasts and raphids obscure, without phytomelanin; pappus capillary in ca. two series, outer somewhat shorter.

Diagnostic features: hairs simple; homogamous or gynodioecious florets; anthers spurred; styles swollen distally with short scabrae, continuous stigmatic surface inside; achenes without phytomelanin; pollen echinate, non-lophate, non-caveate, with non-aligned baculae; leaf blades elliptical to obovate, with pinnate veins; endothecial cells with thickenings at upper and lower ends.

Distribution: restricted to Brazil.

+*Heterolepis* incertae sedis. — Shrubs or subshrubs without latex; leaves alternate; heads, radiate, up to 6 cm in diameter; involucre broadly campanulate with 2–3 rows of bracts somewhat connate at base, apically scarious and laciniate; receptacles shallowly alveolate; corollas yellow; ray corollas female, strap-shaped with three teeth and four veins but also staminoides and a filiform lobe ventrally in the sinus of the tube; disc corollas with five lobes of equal size, deeply divided; anther apical appendages soft and oblong, thecae with short spurs (calcarate) and barely branched tails (caudate); pollen spherical, echinate with spines evenly and deeply separated; styles slender, style branches short, shaft slightly thickened below the style branches, sweeping hairs on backs of style branches acute, somewhat longer hairs in a ring below the bifurcation, apex slightly rounded with short hairs, style branches not recurving; small achenes covered with dense white twin hairs; pappus biseriate, of 1–10 yellow-brown, stout, subulate, bristle-like scales of varying length.

Diagnostic features: ray florets that generally have staminoides and a filiform lobe ventrally in the sinus of the tube; pappus of bristle-like scales which form a pom-pom-like shape in older heads; small achenes covered with dense white twin hairs; and partially connate involucral bracts.

Distribution: three species endemic to South Africa, mostly in the Cape Floristic Region.

23. +Corymbieae. — (information provided by B. Nordenstam): Scapose perennial herbs without latex; leaves alternate mainly rosulate; heads discoid, single-flowered; involucre cylindric, few-calyculate, two bracts, enclosing the floret, without hyaline margins; receptacle naked, flat; corollas pink to purplish or white with five oblong to linear lobes of equal size; anther apical appendage reduced, thecae blackish, shortly sagittate (calcarate) and without tails (ecaudate); pollen echinate, caveate, non-lophate; styles slender, apex tapering gradually to a slightly rounded point, short hairs on the back side of linear style branches and upper part of shaft, at maturity style branches recurving; achene oblong, terete or subcompressed, densely pubescent; pappus of basally connate short scales and/or discrete fine bristles.

Diagnostic features: tufted parallel-veined leaves from a silky-hairy rhizome; involucres of two bracts; single-flowered capitula; and elongated, densely hirsute ovary.

Distribution: the area occupied by the genus coincides with the Cape Floristic Region in South Africa.

Group 2: Asteroideae clade

Tribes contained in the subfamily Asteroideae usually have: stigmatic surface in two lines on inner surface of style branch; anthers without spurs (ecalcarate); pollen echinate with spines regularly or somewhat irregularly spaced; disc florets usually actinomorphic and corolla lobes are as long as wide (shallowly lobed); when a ray/disc arrangement occurs the ray corollas are 3-toothed 'true rays'; leaves alternate except for members of Heliantheae s.str. and closely related tribes, which have opposite leaves (some alternate). Base chromosome number $x = 9$ or 10, or $x = 19$ (Heliantheae Alliance).

24. Senecioneae. — (information provided by B. Nordenstam): Herbs, shrubs, lianas, epiphytes or trees, without latex; leaves alternate sometimes rosulate (rarely opposite); heads radiate, disciform or discoid, of various sizes; involucre calyculate or ecalyculate, bracts uniseriate and subequal or sometimes in two or more series; receptacle naked or fimbriate, denticulate or hairy; ray florets female, fertile (rarely sterile), corolla yellow or orange, white, pink, purple, red or blue; disc florets perfect or functionally male, corolla tubular or with a campanulate 4- or 5-lobed limb; anthers four or five, apical appendage flat, thecae basally obtuse to sagittate or caudate, endothecial tissue radial (Othonninae and Senecioninae) or polarized (Tussilagininae), filament collar balusterform (Othonninae and Senecioninae) or cylindrical and straight (Tussilagininae); pollen echinate, caveate, exine with columellae solid (rarely with internal foramina); style bifurcate or simple, sweeping hairs in apical tuft or distributed abaxially on style branches, branches apically truncate or obtuse to conical, sometimes with tuft, pencil, or appendage; achenes terete or flattened, sometimes ribbed, winged or angled; pappus of barbellate bristles, rarely a single scale, sometimes absent, white or straw-colored, red or purple.

Diagnostic features: uniseriate involucre (although not universal); di-ester type pyrrolizidine alkaloids and the eremophilane types of sesquiterpene lactones; polyacetylenes lacking; raphids not in walls of achenes, but in ovules; in *Senecio* and many other genera of Senecioninae the stigmatic surface is divided into two parallel bands, but most members of Tussilagininae have a continuous stigmatic surface.

Distribution: worldwide with the most marked center of diversity in South Africa, also with centers in Central America, the Andes (Peru to Colombia), and Southeast Asia.

25. Calenduleae. — (information provided by B. Nordenstam): herbs, shrubs, or small trees without latex; leaves alternate or opposite; heads radiate, various sizes; involucre campanulate or cup-shaped, bracts 1–3-seriate, sometimes with hyaline margins; receptacle naked, glabrous; ray corollas female fertile or sterile or neuter, yellow to orange or white, pink, purple or blue; disc corollas hermaphrodite, perfect or functionally male, 5-lobed, yellow to orange or reddish, sometimes purplish-black-tipped; anther apical appendage flat triangular-ovate, endothecial tissue polarized, thecae without spurs (ecalcarate) but with tails (caudate); pollen spinulose, exine without baculae; styles fertile or sterile, entire or bilobed, with sweeping hairs in a subapical collar or rarely extending down the style branches; achenes homo- or heteromorphic, terete or flattened, sometimes curved, rostrate, winged or fenestrate, exocarp sometimes fleshy and colored; pappus absent.

Diagnostic features: lack of pappus; sterile styles in many taxa; widespread heterocarpy; and unusual fruit structures such as fenestrate cavities and a fleshy exocarp.

Distribution: mainly Africa with a distinct center in South Africa; only *Calendula* extending outside Africa into Macaronesia, South and Central Europe, and Anatolia eastwards to Iran.

26. Gnaphalieae. — (information provided by J. Ward): Herbs, subshrubs, or shrubs, without latex; leaves alternate, entire; heads disciform or discoid (rarely radiate), size varies; involucral bracts imbricate in several rows, generally with a papery upper part (lamina) and a thickened, cartilaginous basal part (stereome); receptacle generally flat to convex, sometimes conical or peg-like, generally epaleate, rarely paleate, squamose or fimbrilliferous; female outer florets generally filiform or often absent; central florets generally perfect, sometimes functionally male; anther thecae without spurs, with tails and with endothecial tissue almost always polarized; pollen with a two-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer (“gnaphalioid” type); style branches with hairs apically or sometimes apically and dorsally (rarely dorsally only); achenes generally small and oblong to obovoid; pappus generally of plumose or barbellate to scabrid capillary bristles (occasionally of bristles and scales, only scales, or absent).

Diagnostic features: involucral bracts with a papery, often brightly colored lamina and a cartilaginous basal part (stereome); “gnaphalioid” pollen, with a 2-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer; stems generally with fibers in phloem and without resin canals; leaves entire; anthers tailed; and achenes small.

Distribution: centers of diversity in southern Africa, Australia, New Zealand, and South America.

27. Astereae. — (information provided by L. Brouillet): Annual or perennial herbs, subshrubs, shrubs, rarely trees or vines, usually without latex; leaves alternate (rarely opposite); heads radiate, disciform, or discoid, usually small to medium-sized (rarely large); involucre cylindric to campanulate (hemispheric), not calyculate, bracts in (2–)3–5(–9) rows, usually imbricate, sometimes nearly equal, without well-developed hyaline margin; receptacle usually naked, nearly always flat or convex; ray corollas white, yellow, or pink to blue or purple, usually strap-shaped (rarely bilabiate), usually female; disc corollas yellow to white, with five or four (rarely three) equal lobes, filiform to funnelform or with abruptly ampliate limb, bisexual or functionally male; anther apical appendages flat, lanceolate to deltate, rarely lacking, thecae rarely with basal tail; pollen spherical, tricolporate and echinate; style slender, style branch with acute appendage, scabrous or plumose on outer surface, stigmatic lines running up to base of lanceolate to triangular tip, sweeping hairs on entire outer surface of appendage, style branches pronate; achenes compressed and 2-nerved or angular to terete and multi-nerved (rarely obcompressed); pappus usually of 1–4 series of barbellate or rarely plumose bristles, persistent or caducous, sometimes with outer scales or awns, or lacking.

Diagnostic features: receptacle usually naked; bracts in 3–5 rows and usually imbricate; and style branches pronate, with acute appendage, scabrous or plumose on outer surface, stigmatic lines running up to base of lanceolate to triangular tip.

Distribution: worldwide with major centers of diversity in Africa, North America, and Australia.

28. Anthemideae. — (information provided by C. Oberprieler): Herbs, subshrubs or shrubs without latex; leaves usually alternate; heads various; involucres often hemispheric, bracts in 2–7 rows, imbricate and almost always with scarious margins and apex; receptacles flat, hemispherical or conical, glabrous or hairy, paleate or epaleate; ray corollas white and/or yellow (rarely blue-violet, pinkish or reddish), limbs with three lobes; outer disc florets (if present in disciform capitula) yellow, in one to several rows, corolla with 0–5 lobes; central disc corolla yellow or rarely whitish or reddish, actinomorphic with 3–6 apical lobes; anther apex usually ovate or triangular, generally rounded, thecae usually ecalcarate and ecaudate (rarely shortly tailed); pollen echinate (rarely rugose or smooth) and spherical; style slender, apex truncate with parallel stigmatic surfaces, style hairs rather short and apically rounded; achenes various; pappus never capillary.

Diagnostic features: leaves generally variously dissected, rarely entire with characteristic aromatic smell; involucral bracts with hyaline margin; no tails on anthers; tubular florets hermaphrodite or functionally male, tubular or funnel-shaped; upper part of the filament with cells with thickened walls, forming a split cylindrical or balusterform anther collar (filament collar); and achenes without a carbonized layer, often with glandular hairs, mucilage cells and resin sacs/ducts.

Distribution: mainly in southern Africa, central Asia, and the Mediterranean region.

29. Inuleae. — (information provided by A. Anderberg): Shrubs or herbs without latex; leaves alternate; heads, radiate, disciform or discoid, small to large (> 100 flowers); involucre cylindric, campanulate or cup-shaped, bracts imbricate without hyaline margins, generally in several rows; receptacle naked or paleate; corollas yellow, pink, violet or white; ray corolla when present, strap-shaped with three lobes; outer florets often filiform, tubular; disc corollas with five lobes of equal size, lobes mostly shorter than wide; anther apical appendage acute, thecae normally without spurs (ecalcarate) but generally with distinct tails (caudate); pollen spinulose, caveate with one baculate layer; styles slender or thick, apex rounded to acute, with short acute or obtuse sweeping hairs above or extending below where the style divides, style branches recurving at maturity; achenes generally homomorphic, elliptic, prismatic or quadrangular, often with glandular hairs and/or non-myxogenic twin hairs, walls without phytomelanin; pappus of capillary bristles, of bristles and scales, of scales only, of awns, or absent.

Diagnostic features for Inulinae: heads usually radiate and yellow-flowered; achenes with elongated crystal in each epidermal cell; and acute sweeping hairs on style branches.

Distribution: mainly Mediterranean, Saharo-Sindian, but also in East Africa.

Diagnostic features for Plucheinae: heads often purple-flowered, disciform with filiform; tubular florets; achenes without large epidermal crystal; and style frequently with obtuse sweeping hairs extending below style bifurcation.

Distribution: warm climate areas worldwide.

30. Athroismeae. — (information provided by A. Anderberg): Shrubs or herbs without latex; leaves alternate; heads disciform, discoid or radiate, small to medium with up to 45 florets (except for *Anisopappus* which can have 100's of florets); involucre cup-shaped to cylindrical, often much reduced, bracts imbricate without hyaline margins, in few rows; receptacle naked or paleate; corollas white or yellow; ray corolla when present, strap-shaped with three teeth; outer florets often filiform, tubular; disc corollas with five lobes of equal size; anther apical appendage acute, thecae generally without spurs (ecalcarate) but often with distinct tails (caudate); pollen spinulose, caveate with one baculate layer, or with irregularly interlaced inner layer; styles slender or thick, apex slightly rounded with short obtuse sweeping hairs above where the style divides, at maturity style branches recurving; achenes without large elongated crystals; pappus of scales, awns or missing.

Diagnostic features: heads sometimes in pseudocephalia, some achenes have phytomelanin; and anthers with tails.

Distribution: mainly Africa and Australia.

Heliantheae Alliance

Information for all tribes of the Heliantheae Alliance was provided by B. Baldwin unless indicated otherwise.

Diagnostic features: involucral bracts usually 1–3-seriate; anther thecae often blackened, without spurs (ecalcarate) or tails (ecaudate); styles usually with sweeping hairs above where the style divides, at least as terminal tuft, at maturity style branches recurving, style appendages usually shorter than stigmatic portion (except in Eupatorieae); most taxa with phytomelanin layer in the achene; and base chromosome number $x = 19$.

Distribution: Western Hemisphere.

31. +Feddeeae. — (information provided by B. Baldwin and A. Anderberg): Vine without latex; leaves alternate; heads discoid, large but few-flowered (9–12 florets); involucre cylindrical, multiseriate, bracts without hyaline margins but with median resiniferous duct; receptacle naked; corolla white with five lobes of equal size; anther apical appendage acute, thecae without spurs (ecalcarate) and with long tails (caudate); pollen spherical, spinulose, caveate, baculate with ramified basal layer, without internal foramina; styles slender, branches elongate, apex blunt, hairs inconspicuous, at maturity style branches slightly reflexed; achenes subcylindrical, glabrous, walls without large elongated epidermis crystal and without phytomelanin; pappus of uniseriate tawny capillary bristles.

Diagnostic features: white hermaphroditic florets; leathery entire leaves; multiseriate involucre; and bracts with resiniferous duct.

Distribution: confined to Cuba.

32. Helenieae. — Annual to perennial herbs (rarely shrubs) without latex; leaves alternate (rarely opposite); heads radiate or discoid, mostly medium-sized to large, sometimes small; involucre cylindric to hemispheric, bracts in two or more series, sometimes reflexed, margins (at least of outer) usually not hyaline or scabrous; receptacle usually naked (sometimes with palea-like receptacular outgrowths, rarely truly paleate) and sometimes alveolate; ray florets, if present, pistillate or sterile, corollas yellow or white to red or purple, strap-shaped with three lobes, sterile; disc corollas yellow or red to purple, tubular, with five lobes of equal size, lobes usually not longer than wide; anther apical appendage ovate to round, thecae not blackened, without spurs (ecalcarate) and with or without short sterile tails (caudate or ecaudate); pollen echinate and spherical; styles slender, branches usually truncate, with terminal tuft of hairs otherwise glabrous or papillose; achenes more or less clavate, glabrous to densely hairy, walls lack phytomelanin and usually include few, large crystals; pappus of scales or bristles (rarely absent).

Diagnostic features: combination of alternate leaves; usually epaleate receptacles; markedly lobed ray corollas;

truncate style branches; non-carbonized achenes (with large crystals in achene-wall cells); and scaly pappus.

Distribution: New World (mainly southwestern North America).

33. Coreopsideae. — (information provided by D. Crawford and M. Tadesse): Herbs or shrubs without latex; leaves opposite or alternate; heads radiate or discoid, 2–15 cm wide; involucre cylindric to hemispheric, bracts usually in two or more continuous series, outermost green, linear to lanceolate, striations dark green or brownish-black, inner with brownish-orange striations and scarious margins, usually ovate; receptacle with brownish-orange striated paleae, flat to conical; corollas mostly yellow or white; ray florets neuter or pistillate and then either sterile or fertile; disc corollas with (4–)5 lobes of equal size; anthers brown to black, apical appendage ovate, thecae without spurs (ecalcarate) and short-tailed (caudate); pollen radially symmetrical, isopolar, spherical, echinate and tricolporate; style undivided or shortly cleft to bifurcate, branches conic with short papillae on the outer surface, recurved at maturity, apex penicellate or truncate with fringes of papillae; achenes flat to quadrangular, rarely narrowed toward the apex and beaked; pappus of 2–15 smooth, antrorsely or retrorsely barbed bristles or short awns, rarely absent.

Diagnostic features: outer phyllaries differentiated from inner in color and shape, inner phyllaries with orange-brown striations (resin ducts); paleae with brownish-orange striations; and achenes flat obcompressed to quadrangular.

Distribution: centered in North and South America

34. Neurolaeneae. — Annual or perennial herbs or shrubs (rarely trees) without latex; leaves alternate or opposite (rarely whorled); heads radiate or discoid, small to medium-sized; involucre cylindric to hemispheric, bracts 1–8-seriate without hyaline or scabrous margins; receptacle usually paleate; ray florets, if present, pistillate, corollas highly reduced or well-developed, yellow to white, tubular or strap-shaped, usually 3-lobed; disc corollas yellow, tubular, usually with five lobes of equal size not longer than wide; anther apical appendage ovate to deltate, thecae usually blackened, without spurs (ecalcarate) and without tails (ecaudate); pollen echinate and spherical; styles slender, apices more or less acute with terminal tuft of hairs, remainder of style glabrous or papillose, at maturity style branches recurving; achenes usually not flattened, walls with phytomelanin layer; pappus absent or of scales, awns, or bristles, sometimes coroniform.

Diagnostic features: stems fistulose and rooting at nodes or not; paleae tightly enfolding achenes in aquatic or marsh-dwelling taxa; receptacle usually paleate; anthers usually blackened; achenes blackened.

Distribution: mainly Neotropics (few species in Paleotropics).

35. Tageteae. — Annual or perennial herbs or shrubs (rarely trees) without latex; leaves alternate or opposite; heads usually radiate (rarely discoid), size varies; involucre cylindric to hemispheric, bracts in 1–5 series; receptacle usually naked, smooth or pitted; ray florets pistillate, corollas yellow to red or white, strap-shaped with 2–3 lobes; disc corollas yellow with 5(–6) lobes of usually equal size or 1–2 lobes larger than others; anther apical appendages usually sclerified, thecae not blackened, without spurs (ecalcarate) and without tails (ecaudate); pollen echinate and spherical; styles slender, apices of style branches truncate or deltate to acuminate, usually variously papillose, recurving at maturity; achene walls striate or ribbed, with phytomelanin layer; pappus of scales and/or bristles (rarely absent).

Diagnostic features: epaleate receptacles, most with glandular pockets (dark spots); characteristic smell (monoterpenes); and if glands lacking, then achenes usually strongly 9–15-ribbed.

Distribution: warm temperate to tropical New World (1 sp. of *Flaveria* in Australia), mostly southwestern North America.

36. Chaenactideae. — Annual or perennial herbs (rarely subshrubs) without latex; leaves usually alternate; heads discoid, small to medium-sized; involucre cylindric to more or less broadly campanulate, bracts 1–2-seriate without hyaline margins; receptacle naked (rarely partially paleate), smooth; corollas of peripheral florets sometimes zygomorphic, corollas white to reddish or yellow with five lobes of equal or unequal size (peripheral lobes sometimes enlarged); anther apical appendage more or less round to ovate, thecae not blackened, without spurs (ecalcarate) and without tails (ecaudate); pollen echinate and spherical; styles slender, apices usually acute with short hairs, glabrous or hairy below style bifurcation, at maturity style branches recurving; achene walls striate, with phytomelanin layer; pappus of setose to obovate scales without thickened bases or midribs and sometimes fused at base into deciduous unit.

Diagnostic features: combination of alternate, often lobed, leaves; discoid heads; epaleate receptacles; pale or reddish (not blackened) anthers; more or less terete (not flattened), striate achenes; and unribbed and unthickened pappus scales, sometimes deciduous as a unit.

Distribution: western and southwestern North America, mainly California.

37. Bahieae. — Annual to perennial herbs (rarely shrubs) without latex; leaves alternate or opposite; heads radiate or discoid, mostly small to medium-sized, sometimes large; involucre cylindric to obconic or hemispheric, bracts imbricate, with or without hyaline margins in 1–4 series; receptacles usually naked; ray florets, if present, pistillate, corollas usually yellow to orange or white, sometimes pink to purplish, strap-shaped with usually

2–3 lobes; disc corollas yellow or white, sometimes pink to purplish, with 4–5 lobes of equal or unequal size; anther apical anther appendage usually ovate, thecae without spurs (ecalcarate) and without tails (ecaudate); pollen echinate and spherical; styles slender, apices deltate to acuminate with short hairs, style below bifurcation usually glabrous, at maturity style branches recurving; achene walls usually striate, with phytomelanin layer; pappus of scales with thickened base or midrib (if scales not thickened, then disk corollas 4-lobed) or of brownish-to-reddish, often fasciculate or hooked bristles.

Diagnostic features: combination of epaleate heads; pale or reddish (not blackened) anthers; blackened, striate, usually unflattened achenes; and pappus usually of basally thickened or costate scales or of fascicled or hooked bristles.

Distribution: mainly southwestern North America (also temperate and montane South America, tropical Africa, and South Pacific).

38. +Polymnieae. — Perennial herbs without latex; leaves opposite; heads radiate, small to medium-sized; involucre campanulate to hemispheric, bracts imbricate without hyaline margins in 2–3 series; receptacle paleate; ray corollas white, limbs 3-lobed, middle lobe longer and wider than lateral lobes; disk florets yellow, tubular with five equal lobes, functionally staminate; anther apical appendages deltate, anther thecae pale, without spurs (ecalcarate) or tails (ecaudate); pollen echinate and spherical; styles slender, branches tapering with short hairs, remainder of style glabrous, at maturity style branches not recurving; achenes dorsiventrally compressed, achene walls smooth, with phytomelanin layer; pappus absent or coroniform.

Diagnostic features: combination of opposite leaves; paleate receptacles; functionally staminate disc florets; pale anthers; and uncompressed smooth achenes.

Distribution: eastern North America.

39. Heliantheae. — Annual or perennial herbs, shrubs, trees, or vines without latex; leaves alternate or opposite; heads radiate or discoid (rarely disciform), size varies; involucre cylindric to hemispheric, bracts in 1–7 series, often foliaceous; receptacle paleate (rarely naked) with paleae enfolding achenes and usually persistent; ray florets if present pistillate or sterile, corollas usually yellowish, sometimes white (rarely orange to reddish), strap-shaped with usually three lobes; disc corollas yellow with five lobes of usually equal (rarely unequal) size; anther apical appendage usually ovate, thecae usually blackened, usually without spurs (ecalcarate), often sagittate (rarely with short tails = caudate); pollen echinate and spherical; styles slender, branches with separate or fused stigmatic lines, apices often terminated by tuft of hairs, the style glabrous below the bifurcation, at maturity style branches recurving; achenes compressed (rarely obcompressed), achene walls smooth or striate, with phytomelanin layer; pappus of awns or scales, sometimes coroniform (rarely absent).

Diagnostic features: combination of paleate receptacles, with paleae enfolding ovaries; usually blackened anthers; style apices terminated by tuft of papillae; achenes blackened, flattened; and pappus usually of awns or scales.

Distribution: mainly warm temperate and tropical New World.

40. Millerieae. — Annual or perennial herbs, shrubs, or trees without latex; leaves usually opposite; heads radiate (rarely discoid), size varies; involucre obconic to hemispheric, bracts in 1–5 series; receptacle paleate; ray florets pistillate (rarely sterile), ray corolla usually yellow or white, strap-shaped with three lobes or limb sometimes absent, sterile; disk florets bisexual or functionally staminate, corollas yellow with (4–)5 lobes of equal or sometimes unequal size; anther apical appendage usually lanceolate to ovate, thecae usually blackened, sometimes pale (green in *Guardiola*), without spurs (ecalcarate) and tails (ecaudate); pollen echinate and spherical; styles slender, apices of branches often acute to penicillate, with short hairs, remainder of style glabrous, at maturity style branches erect or recurving; achenes usually more or less terete, achene walls usually striate, with phytomelanin layer; pappus absent or of scales or bristles.

Diagnostic features: combination of usually opposite, often glandular leaves; scarious paleae; usually blackened anther thecae; more or less terete, usually striate, blackened achenes; and radially-arrayed (or absent) pappus scales or bristles.

Distribution: mainly Mexico and northern Andes (also Old World tropics, especially Africa).

41. Madieae. — Annual or perennial herbs or shrubs, trees, or vines, without latex; leaves alternate, opposite, or whorled; heads radiate or discoid (rarely disciform), mostly small to medium-sized, sometimes large; involucre cylindric or globose, bracts usually subequal in 1–2 series (rarely gradate in 3–4+ series), without hyaline margins; receptacle naked or paleate (paleae often restricted to periphery of receptacle), sometimes clasping ray ovaries, smooth; ray florets pistillate, corollas usually yellow or white, strap-shaped with usually three lobes; disk florets bisexual or functionally staminate, corollas yellow with five lobes of equal size; anther apical appendage rounded or usually more or less ovate to deltate, anther thecae pale or purplish, without spurs (ecalcarate) or tails (ecaudate); pollen echinate and spherical; styles slender, deeply divided or sometimes undivided, branches truncate to subulate with short hairs, remainder of style glabrous (except in *Blepharipappus*); achenes compressed, obcompressed, or terete, achene walls often striate, with phytomelanin layer; pappus of scales or bristles, sometimes absent.

Diagnostic features: combination of often glandular foliage; usually subequal phyllaries (often with one phyllary per ray ovary and with phyllary at least partially clasping ray ovary); epaleate or often partially paleate receptacle (with paleae limited to periphery of receptacle, between ray and disc florets); often deeply 3-lobed ray corollas; often dark purple (not blackened) anther thecae; often flattened ray achenes; and often striate, blackened disc achenes.

Distribution: mainly western North America (especially California).

42. Perityleae. — Annual or perennial herbs or shrubs of rocky sites, without latex; leaves usually opposite; heads radiate or discoid, small to medium-sized; involucre cylindric to hemispheric, bracts subequal in 1–2 series, usually navicular, without hyaline margins; receptacles usually naked, smooth; ray florets pistillate, corollas yellow or white, often 3-lobed; disc corollas yellow with 4–5 lobes of equal size; anther apical appendage usually ovate, thecae pale, without spurs (ecalcarate) or tails (ecaudate); pollen echinate and spherical; styles slender, deeply divided, apices of branches tapered to rounded with short hairs, style glabrous below the bifurcation, at maturity style branches recurving; achene walls smooth, with phytomelanin layer; pappus of (usually two) bristles and crown of scales or absent.

Unique or diagnostic features include: rupicolous herbs and shrubs; glandular foliage; subequal, usually navicular phyllaries; epaleate receptacles; usually 4-lobed disc corollas; pale, ecaudate anthers; smooth, blackened achenes; and pappus (if present) usually of (1–)2 bristles and rudimentary scales. Distribution: mainly deserts of southwestern North America (also Andes and Desventuradas Islands of South America).

43. Eupatorieae. — (information provided by H. Robinson): Annual or perennial herbs to subshrubs, scrambling shrubs or small trees, without latex; leaves opposite or alternate; heads discoid, varying in size; involucre campanulate to cylindrical, bracts persistent to totally deciduous; receptacle often conical, with or without hairs, rarely with simple paleae; florets one to many in a head, corollas white to reddish, blue or lavender, actinomorphic (rarely peripheral florets with outer one or three lobes enlarged, 4- or 5-lobed); anthers often with glands, with apical appendages hollow, reduced or lacking, thecae not spurred or tailed; style branches spreading radially (not in some *Praxelinae*), apical appendages not recurving, greatly enlarged, filiform, flattened or fusiform, often colored as in corolla, usually nearly smooth; achenes 4–10-ribbed with phytomelanin in walls, without raphids, usually with twin hairs; pappus usually uniseriate, of plumose bristles, scales or lacking; pollen spherical, echinate, mostly 18–25 µm in diam. (in medium), caveate.

Diagnostic features: all members of the tribe (with a few exceptions) have mono-ester type pyrrolizidine alkaloids secreted by nectaries; also with pentaynene acetylenes, some monoterpenes and sesquiterpene lactones, an ent-kaurine diterpene glycoside, kolavane derivatives, chromenes, benzofurans; raphids in the achenes are completely lacking. Other diagnostic features: mostly opposite leaves; hairs simple; heads discoid; corollas actinomorphic and whitish to reddish or lavender (never yellow); anther appendages hollow or poorly developed; and style branches with enlarged "club shaped" appendages that are often the color of the corolla. Distribution: Western Hemisphere with a few pantropical genera.

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Note added in proof

A recent paper has shown that two separate base pair deletions link *Catamixis* with the Pertyoideae. Panero, J. 2008. Shared molecular signatures support the inclusion of *Catamixis* in subfamily Pertyoideae. *Phytologia* 90: 418–424.

Section III Part 2

Basal clades

Chapter 12

The basal grade of Compositae: Mutisieae (sensu Cabrera) and Carduoideae

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INTRODUCTION

There is no doubt that understanding Mutisieae (sensu Cabrera 1977) is key to understanding the systematics, early evolution, and biogeography of Compositae, because in all molecular and recent morphological studies its members occupy the first branches of the family phylogeny (Fig. 12.1 on p. 200). In the last few years there have been various definitions of the tribe and all parts of it have been placed in informal groups, subtribes, or subfamilies by a variety of authors (Bremer 1994; Katinas 1994; Panero and Funk 2002, 2007, 2008; Hind 2007; Katinas et al. 2008). In this discussion, the taxon Mutisieae (sensu Cabrera) is meant to represent the historic circumscription of the tribe as defined by Cabrera in 1977. This is in no way meant as a negative reflection on the many contributions of Cabrera (see Chapter 1), in fact, his 1977 paper is a classic—one that is always cited as the first comprehensive treatment of the tribe. Within this paper he had many insights and some of his groups have a direct correlation to the results of the molecular analyses. In science, and especially in taxonomy, we all "stand on the shoulders of giants" and Cabrera's contributions are certainly the foundation for all modern work in the tribe. The results of the most recent and comprehensive molecular work (Panero and Funk 2002, 2007, 2008) established many new super-generic taxa and the relationships between the morphological and molecular treatments are not always clear. In this discussion, taxa will be referred to as various clades, groups, or their proper scientific names depending on the context. A detailed comparison with all the current and past super-generic names can be found in Tables 12.1 and 12.2.

The need for a re-evaluation of Mutisieae (sensu Cabrera) has been clear since the work of Jansen and his collaborators. Many have tackled this difficult group and much has been accomplished using characters from morphology, palynology, and DNA sequencing. The major goals of these studies were to: *(1)* find morphological synapomorphies that support the monophyly of proposed groups, *(2)* establish the position of some problematic genera within the phylogeny, *(3)* circumscribe the various taxonomic groups (be they subtribes, tribes, or subfamilies), *(4)* investigate the differences between the morphological and molecular results, and hopefully *(5)* agree on a placement of all species once housed under the umbrella of Mutisieae (sensu Cabrera).

The synantherology community has been partially successful in accomplishing these goals and this discussion attempts to summarize those results and identify those goals that are yet to be achieved. This chapter has four parts:

1. An explanation of Mutisieae (sensu Cabrera) based on morphology and molecular data.
2. A discussion of groups of proposed clades from

former Mutisieae (sensu Cabrera) that are not found in other chapters or that require some additional information (orphan clades).

3. A treatment of *Catamixis* incertae sedis.
4. An introduction to the subfamily Carduoideae, which is nested within Mutisieae (sensu Cabrera).

Finally, this treatment also serves as a guide to the chapters that follow, which treat clades that were once considered part of Mutisieae (sensu Cabrera).

MUTISIEAE (SENSU CABRERA 1977)

Morphological data

Beginning with Lagasca (1811), who recognized a group of genera with bilabiate florets under the name Chaenanthophorae, through Cassini (1819) who described the group as Mutisieae, to Cabrera (1977) who provided the first full modern treatment of the group, taxonomists have used the broadest concept of the tribe. There were comments as to the lack of overall agreement on morphology and statements about which subtribes or groups of genera were distinct, but there was little fluctuation in the number of genera and species according to the different authors. The main taxonomic categories and generic groups recognized by modern authors are shown in Table 12.2. The first modern circumscription was that of Cabrera (1977) who defined the tribe by its bilabiate corollas, caudate anthers, and characteristic style shape. However, he indicated that many genera housed in the tribe did not fit morphological descriptions, and he stated that it was difficult to accurately circumscribe the tribe. Cabrera recognized four subtribes: Barnadesiinae, Gochnatiinae, Mutisiinae, and Nassauviinae. Of these subtribes, he felt that Nassauviinae were the most distinct and natural. The other three were, according to Cabrera (1977), more heterogeneous and would require much investigation before the natural position of their genera would be known with any degree of certainty. Furthermore, Cabrera established some possible generic relationships showing some evolutionary lines from primitive to evolved genera for some, but not all, of the genera.

Before Cabrera, the morphological heterogeneity of Mutisieae was emphasized by authors such as Jeffrey (1967; Table 12.2), who broke the tribe up into twelve groups or series. Jeffrey (1967) did not recognize subtribal categories, and his informal series were mostly based on style features.

The first morphological phylogenetic analysis of the tribe by Hansen (1991) accepted a monophyletic Mutisieae alleging the type of ray epidermal cells as a synapomorphy of the tribe. Hansen accepted the exclusion of Barnadesiinae from Mutisieae on the basis of Bremer's (1987) cladogram of Compositae. He also excluded several genera to achieve a better circumscription of the tribe; these exclusions are, with the exception of *Adenocaulon*, currently supported by the molecular data. Many of Hansen's generic groups have provided the morphological basis for many tribes or subfamilies recognized by further molecular phylogenies.

Another morphology-based analysis of Compositae, with emphasis on the basal groups, was by Karis et al. (1992). These authors made it clear that the tribe was most likely paraphyletic. This analysis showed that the separation between subtribes Mutisiinae and Gochnatiinae was not justified. Based on this morphological work and the molecular studies of Jansen and Palmer (1987), Bremer (1994) accepted only two subtribes (Mutisiinae and Nassauviinae) and discussed several generic groups within them. Bremer stated that although Mutisieae seemed clearly paraphyletic, there was no basis at that time for splitting the tribe into smaller monophyletic tribes. He also noted that understanding the relationships among the branches of Mutisieae would provide an understanding of the basal branches of the entire family.

Hind (2007), in the *Asterales* volume of *The Families and Genera of Vascular Plants* (series ed.: K. Kubitzki), split Mutisieae (sensu Cabrera) into twelve units, some of them recognized formally as subtribes, and others only informally as generic groups. In the same treatment, Jeffrey (2007) produced a general classification of Compositae where Mutisieae (sensu Cabrera) are recognized at the level of subfamily, a category suggested by others (e.g., Bremer 1996; Panero and Funk 2002). However, some examination of the history of the Mutisieae treatment is required in order to understand the different concepts in this present book. This is particularly so because some contemporaneous and more recent accounts are critical of the infratribal taxa proposed, the genera included within them, and even the tribe Mutisieae. Although largely based on morphological data, Hind's account (Hind 2007) was in part based on an unpublished draft of the 'supertree'. Unfortunately, when the 'supertree' was finally published (Funk et al. 2005) a disagreement had led to the removal of approximately 20 taxa. This removal of taxa resulted in the collapse and realignment of some clades/grades. Consequently, Jeffrey (2007) suggested there were a number of 'misplaced' genera, simply because the location of these genera differed between the draft and the published 'supertree'. As a result, Jeffrey (2007) should not be considered as a different treatment of taxa. Editorial demands, and limitations of space, precluded any explanation of the background to the concepts employed in the Kubitzki series volume accounts. Similarly, much of the text discussing genera, and informal groups, was considerably shortened or removed. To this end, any explanation as to the inclusion of the Carduoid groups, such as the *Dicoma* group, and the *Pertya* group, etc., was not provided. Importantly, at that time the authors of Cardueae were understandably somewhat reluctant to add them to their account, hence the inclusion of genera 82 (*Oldenburgia* Less.) to 91 (*Myripnois* Bunge) within the broad concept of Mutisieae. Because the guidelines of the Kubitzki series precluded the formalizing of any new taxa within the volume, a number of taxa were left as informal groups. More importantly, perhaps, is that the subsequent analyses, including many additional genera, has further realigned some groups (Panero and Funk 2008). Also, recognition of the clades Gochnatieae, Hecastocleideae, and Pertyeae, as well as the alignment of Tarchonantheae, Oldenburgieae, and Dicomeae within Carduoideae, has been subsequently supported by on-going molecular analysis.

Katinas et al. (2008) produced a monograph including all genera considered by previous modern authors to be part of Mutisieae (excluding Barnadesieae), describing and evaluating morphological and palynological characters of taxonomic value. They used subfamilial status, and Mutisioideae were divided into the three tribes Mutisieae, Nassauvieae, and Stifftieae on the basis of style features. Katinas et al. (2008) recognized some generic groups within the tribe Mutisieae without giving them formal status. Style morphology was found to be helpful in circumscription of the subfamily, approaching that of Cabrera's (1977) concept, although excluding some genera.

Molecular data

The advance of molecular techniques deeply changed the systematic organization of the entire family (Fig. 12.1). First, the concept of evolution in the family was turned upside down by the work of Jansen and Palmer (1987): gone was the 'Heliocentric' (as mentioned by Robinson 1981: 4) view of the family. Mutisieae (sensu Cabrera) were now at the base and Heliantheae s.l. and Eupatorieae were highly nested. The subtribe Barnadesiinae was removed from Mutisieae (sensu Cabrera) by Bremer and Jansen (1992) and raised to subfamilial status, taking into account its unique morphology and the absence of a large chloroplast DNA inversion present in remaining Compositae (Jansen and Palmer 1987).

The results of the phylogenetic analyses by Kim et al. (2002) and Panero and Funk (2002), based on the sequencing of different markers of cpDNA, clearly showed the non-monophyletic character of Mutisieae. Principally the cladograms of Panero and Funk (2002), followed by Funk et al. (2005) and Panero and Funk (2008) (Fig. 12.1), displayed Mutisieae (sensu Cabrera) made up of several clades, which were then described as different subfamilies and tribes. Many of these new taxa represent groups that had already been mentioned by some workers as being different or separate from core Mutisieae, e.g., clades identified by Hansen (1991) and others: *Ainsliaea* group, *Dicoma* group, Tarchonantheae, etc., as well as confirmation of the unusual nature of some genera such as *Hecastocleis* A. Gray.

Table 12.1 gives the molecular assignment of all genera of Mutisieae (sensu Cabrera), lists where they fall in the molecular study (Panero and Funk 2008), and indicates how the placement differs from the treatments of Cabrera (1977). Detailed discussions of most of the taxa included in former Mutisieae (sensu Cabrera) are included elsewhere in this volume (Chapters 13–19, 21). There are, however, a few taxa (e.g., Stifftieae) that are left out of these chapters because they fall into clades in the molecular studies that have not been previously proposed as separate groups, some of which are difficult to support morphologically. There is also one unplaced genus, *Catamixis*.

ORPHAN CLADES

Most clades from former Mutisieae (sensu Cabrera) are covered in other chapters: Barnadesioideae, Barnadesieae (Chapter 13); Mutisioideae, Mutisieae s.str., Onoserideae, Nassauvieae (Chapter 14); Wunderlichioideae p.p, Hyalideae (Chapter 15); Gochnatioideae, Gochnatieae (Chapter 15); Hecastocleidoideae, Hecastocleideae (Chapter 16); Carduoideae, Dicomeae (Chapter 17), Tarchonantheae (Chapter 18), Oldenburgieae (Chapter 19), Cardueae (Chapter 20), and Pertyoideae, Pertyeae (Chapter 21). However, there are three clades that are part of the basal grade of Compositae that are not treated in other chapters of this book and they will be discussed here (Fig. 12.1): *(1)* the molecularly circumscribed tribe Stifftieae (subfamily Stifftioideae; not in agreement with any morphological treatment), *(2)* the tribe Wunderlichieae (agreeing with the *Wunderlichia* clade in the morphological analysis of Katinas et al. 2008), and *(3)* the subfamily Wunderlichioideae (Wunderlichieae + Hyalideae clade; not found in any morphological treatment). These clades contain members of Compositae that are found on the Guiana Shield as well as in South America and Asia (see Chapter 44 for a detailed phylogeny).

Two of the clades mentioned above have members from the Guiana Shield of northeastern South America. The high elevation areas (up to ~3000 m) of the Shield (also referred to as the Guayana or Guiana Highlands) have generated considerable interest among plant biologists because of their unique flora, high levels of endemism, and biogeographic isolation. This area is home to more than 50 tabletop mountains, each known as a *tepui* (Huber 1995). Some genera of Mutisieae (sensu Cabrera) that are found on this Shield are among the most fascinating members of the family. The tepui-centered genera, that were known to science at the time, were treated in

Table 12.1. Current taxonomy of Mutisieae (sensu Cabrera 1977) based on results of the molecular analyses (numbers in parentheses refer to literature references at the end of the table).

Molecular placement	Placement by Cabrera
I. Barnadesioideae (Chapter 13)	
Barnadesieae	
Arnaldoa Cabrera (2,6)	Barnadesiinae
Barnadesia Mutis (2,3,6)	Barnadesiinae
Chuquiraga Juss. (2,3,5,6)	Barnadesiinae
Dasyphyllum Kunth (2,3,6)	Barnadesiinae
Doniophyton Wedd. (2,3,5,6)	Barnadesiinae
Duseniella K. Schum. (5,6)	Gochnatiinae
Fulcaldea Poir. ex Lam. (2,6)	Barnadesiinae
Huarpea Cabrera (2,6)	Barnadesiinae
Schlechtendalia Less. (2,6)	Barnadesiinae
II. Mutisioideae (Chapter 14)	
Mutisieae s.str. or Mutisieae clade	
Adenocaulon Hook. (1,3)	Not listed
Amblysperma Benth.	New
Brachyclados D. Don (3,5)	Mutisiinae
Chaetanthera Ruiz & Pav. (1,3,5)	Mutisiinae
Chaptalia Vent. (1,3)	Mutisiinae
Chucoa Cabrera	Gochnatiinae
Eriachaenium Sch.Bip.	Not listed
Gerbera L. (1,3)	Mutisiinae
Leibnitzia Cass. (1)	Mutisiinae
Lulia Zardini	New
Mutisia L. f. (1,3,5)	Mutisiinae
Pachylaena D. Don ex Hook. & Arn. (1,3,5)	Mutisiinae
Perdicium L.	Mutisiinae
Trichocline Cass. (3)	Mutisiinae
Uechtritzia Freyn	Mutisiinae
Onoserideae or *Onoseris* clade	
Aphyllocladus Wedd. (1,3)	Gochnatiinae
Gypothamnium Phil.	Gochnatiinae
Lycoseris Cass. (3)	Gochnatiinae
Plazia Ruiz & Pav. (1,3)	Gochnatiinae
Onoseris Wedd. (1,3)	Gochnatiinae
Urmenetia Phil. (5)	Gochnatiinae
Nassauviinae or *Nassauvia* clade	
Acourtia D. Don (1,3)	Nassauviinae
Ameghinoa Speg. (5)	Nassauviinae
Berylsimpsonia B.L. Turner	New
Burkartia Crisci	New
Calopappus Meyen	Nassauviinae
Cephalopappus Nees & Mart.	Nassauviinae
Criscia Katinas	New
Dolichlasium Lag. (3)	Nassauviinae
Holocheilus Cass. (5)	Nassauviinae
Jungia L. f. (1,3,5)	Nassauviinae
Leucheria Lag. (1,3,5)	Nassauviinae
Leunisia Phil.	Nassauviinae
Lophopappus Rusby (3)	Nassauviinae
Macrachaenium Hook. f.	Nassauviinae
Marticorenia Crisci	Nassauviinae
Moscharia Hook. f. (5)	Nassauviinae
Nassauvia Comm. ex Juss. (1,3,5)	Nassauviinae
Oxyphyllum Phil.	Nassauviinae
Pamphalea Lag. (5)	Nassauviinae
Perezia Lag. (1,3,5)	Nassauviinae
Pleocarphus D. Don	Nassauviinae
Polyachyrus Lag. (5)	Nassauviinae
Proustia Lag. (1,3,5)	Nassauviinae
Triptilion Ruiz & Pav. (1,5)	Nassauviinae
Trixis P. Browne (1,3)	Nassauviinae
*III. Stifftioideae (Chapter 12) Stifftieae	
Stifftia genus	
Stifftia J.C. Mikan (1,3)	Gochnatiinae
Gongylolepis clade	
Achnopogon Maguire	Mutisiinae
Duidaea S.F. Blake (1,3)	Mutisiinae
Eurydochus Maguire & Wurdack	Mutisiinae
Glossarion Maguire & Wurdack	Mutisiinae
Gongylolepis R.H. Schomb. (3)	Mutisiinae

Table 12.1. Continued.

Molecular placement	Placement by Cabrera
Neblinaea Maguire & Wurdack	Mutisiinae
Quelchia N.E. Br.	Mutisiinae
Salcedoa F. Jiménez Rodr. & Katinas	New
Hyaloseris clade	
Dinoseris Griseb. (3)	Mutisiinae
Hyaloseris Griseb. (3)	Mutisiinae
*IV. Wunderlichioideae	
Wunderlichieae or *Wunderlichia* clade (Chapter 12)	
Chimantaea Maguire (3)	Gochnatiinae
Stenopadus S.F. Blake (3)	Gochnatiinae
Stomatochaeta (S.F. Blake) Maguire & Wurdack (3)	Gochnatiinae
Wunderlichia Riedel ex Benth. (3)	Gochnatiinae
*Hyalideae (Chapter 15)	
Hyalis clade	
Ianthopappus Roque & D.J.N. Hind (3)	Gochnatiinae
Hyalis D. Don ex Hook. & Arn. (3)	Gochnatiinae
Leucomeris clade	
Leucomeris D. Don (3)	Gochnatiinae
Nouelia Franch. (3)	Gochnatiinae
V. Gochnatioideae (Chapter 15)	
Gochnatieae	
Cnicothamnus Griseb. (1,3)	Gochnatiinae
Cyclolepis D. Don (3)	Gochnatiinae
Gochnatia Kunth (1,3)	Gochnatiinae
Pentaphorus D. Don	Gochnatiinae
Richterago Kuntze (3)	Gochnatiinae
VI. Hecastocleidoideae (Chapter 16)	
Hecastocleideae	
Hecastocleis A. Gray (1,3)	Gochnatiinae
VII. Carduoideae p.p.	
Dicomeae (Chapter 17)	
Cloiselia S. Moore (1)	Gochnatiinae
Dicoma Cass. (1,3)	Gochnatiinae
Erythrocephalum Benth. (4)	Gochnatiinae
Gladiopappus Humbert	Gochnatiinae
Macledium Cass. (3,4)	Gochnatiinae
Pasaccardoa Kuntze (1,3,4)	Gochnatiinae
Pleiotaxis Steetz (4)	Gochnatiinae
Oldenburgieae (Chapter 19)	
Oldenburgia Less. (2,3,4)	Gochnatiinae
Tarchonantheae (Chapter 18)	
Tarchonanthus L. (1,3,4)	Not listed
Brachylaena R. Br. (3,4)	Not listed
Cardueae (Chapter 20) – Thistles – not Mutisieae s.l.	
VIII. Pertyoideae (Chapter 21)	
Pertyeae	
Ainsliaea DC. (1,3)	Gochnatiinae
Diaspananthus Maxim.	Gochnatiinae
Macroclinidium Maxim.	Gochnatiinae
Myripnois Bunge (1)	Mutisiinae
Pertya Sch.Bip. (1,3)	Gochnatiinae
Catamixis Thompson, incertae sedis	Mutisiinae

The left column has the taxa arranged according to Panero and Funk (2002, 2007, 2008) and the supertree of Funk et al. (2005). The right column is the placement in Cabrera (1977). Some genera were listed by Cabrera but are now placed in other sections of the family phylogeny: *Hesperomannia* Gray (Vernonieae), *Moquinia* DC. (Moquinieae), and *Warionia* Benth. & Coss. (Cichorieae).

"New" indicates taxa described or resurrected since 1977 and "Not listed" indicates taxa that Cabrera did not include in his tribe Mutisieae; * = under discussion. Names in bold indicate genera for which there are no known sequence data.

1 = Kim et al. 2002 [*ndhF*]; 2 = Gustafsson et al. 2001 [ITS & *trnL*]; 3 = Panero & Funk 2008 [ten chloroplast gene regions]; 4 = Ortiz et al., unpub. [ITS & *ndhF*]; 5 = Katinas et al. 2008 [ITS]; 6 = Gruenstaeudl et al. 2009 [ITS & nine chloroplast gene regions].

the tribe Mutisieae by Bentham (1873) and subsequent authors. Don (1830) described the tribe Stifftieae to include the Brazilian-centered *Stifftia* and some species of *Gochnatia*. Later on, similarities between *Stifftia* and some tepui-centered genera were noted by several authors (e.g., Baker 1884; Maguire 1956; Maguire et al. 1957). Indeed, Maguire (1956; Maguire et al. 1957), who extensively studied these genera, included *Chimantaea*, *Quelchia*, *Stifftia*, *Stenopadus*, and *Stomatochaeta* in Gochnatiinae, and *Achnopogon*, *Duidaea*, *Neblinaea*, *Glossarion*, and *Gongylolepis* in Mutisiinae, both subtribes of Mutisieae. This alignment was followed by Cabrera (1977), who placed the tepui-centered genera with actinomorphic tubular corollas in the subtribe Gochnatiinae and those with bilabiate corollas in the subtribe Mutisiinae.

Previous to Cabrera's treatment of Mutisieae, Jeffrey (1967) divided Mutisieae into twelve series. All of the tepui-centered genera were placed in the *Stifftia* series, which also contained the mainly Brazilian genera *Stifftia* and *Wunderlichia*, the Bolivian-Argentine *Cnicothamnus*, the more widespread *Gochnatia*, the Asian *Nouelia*, and the African *Oldenburgia*. Pruski (1991) thought that the tepui-centered genera belonging to subtribe Gochnatiinae as well as those once placed in subtribe Mutisiinae shared a

Table 12.2. Main morphological taxa delimited within Mutisieae (sensu Cabrera) by modern authors. Only those genera considered to be part of groups are cited (in some cases with numbers in parentheses); genera currently placed in Barnadesioideae are not cited.

Author	Main taxonomic category	Generic groups and species
Jeffrey (1967)	Tribe Mutisieae	*Chionopappus* series: *Chionopappus*
		Anisochaeta series: *Anisochaeta*
		Pleiotaxis series: *Achyrothalamus*, *Erythrocephalum*, *Pasaccardoa*, *Pleiotaxis*
		Pertya series: *Hesperomannia*, *Macroclinidium*, *Moquinia*, *Myripnois*, *Pertya*
		Dicoma series: *Ainsliaea*, *Catamixis*, *Dicoma*, *Hochstetteria*, *Leucomeris*
		Mutisia series, *Gerbera* subseries: *Brachyclados*, *Chaetanthera*, *Chaptalia*, *Chucoa*, *Gerbera*, *Leibnitzia*, *Lycoseris*, *Macrachaenium*, *Perdicium*, *Piloselloides*, *Trichocline*, *Uechtritzia*, *Urmenetea*; *Onoseris* subseries: *Gypothamnium*, *Onoseris*, *Plazia*; *Mutisia* subseries: *Mutisia*; *Pachylaena* subseries: *Pachylaena*, *Proustia*
		Trixis series: *Cyclolepis*, *Jungia*, *Lophopappus*, *Trixis*
		Nassauvia series: *Ameghinoa*, *Leucheria*, *Moscharia*, *Nassauvia*, *Oxyphyllum*, *Panphalea*, *Perezia*, *Polyachyrus*, *Triptilion*
		Seris series: *Gladiopappus*, *Hecastocleis*, *Hyalis*, *Richterago*
		Hyaloseris series: *Dinoseris*, *Hyaloseris*
		Stifftia series, *Gochnatia* subseries: *Achnopogon*, *Cnicothamnus*, *Gochnatia*, *Nouelia*, *Oldenburgia*; *Wunderlichia* subseries: *Wunderlichia*; *Stifftia* subseries: *Stifftia*, *Stomatochaeta*; *Quelchia* subseries: *Duidaea*, *Glossarion*, *Gongylolepis*, *Quelchia*
		Barnadesia series
Cabrera (1977)	Tribe Mutisieae	
	Subtribe Barnadesiinae	
	Subtribe Gochnatiinae	(1) *Actinoseris*, *Chucoa*, *Cyclolepis*, *Gochnatia*, *Pleiotaxis* (2) *Chimantaea*, *Quelchia*, *Stenopadus*, *Stomatochaeta*, *Wunderlichia*
	Subtribe Mutisiinae	(1) *Chaptalia*, *Gerbera*, *Leibnitzia*, *Perdicium*, *Piloselloides*, *Trichocline*, *Uechtritzia* (2) *Achnopogon*, *Duidaea*, *Eurydochus*, *Glossarion* (syn. *Guaicaia*), *Gongylolepis* (syn. *Cardonaea*), *Neblinaea*
	Subtribe Nassauviinae	
Hansen (1991)	Tribe Mutisieae	
	Subtribe Barnadesiinae	
	Subtribe Gochnatiinae	*Gochnatia* group: *Actinoseris*, *Cyclolepis*, *Gochnatia* (incl. *Leucomeris*), *Hyalis*, *Nouelia* *Ainsliaea* group: *Ainsliaea*, *Myripnois*, *Pertya* *Plazia* group: *Aphyllocladus*, *Gypothamnium*, *Plazia* Guayana group: *Chimantaea*, *Quelchia*, *Stenopadus*, *Stomatochaeta*
	Subtribe Mutisiinae	Guayana group: *Achnopogon*, *Duidaea*, *Eurydochus*, *Glossarion*, *Gongylolepis*, *Neblinaea*
	Subtribe Nassauviinae	
	Excluded	African genera: *Achyrothalamus*, *Erythrocephalum*, *Pasaccardoa*, *Pleiotaxis* *Adenocaulon*, *Anisochaeta*, *Berardia*, *Brachylaena*, *Chionopappus*, *Dicoma*, *Gladiopappus*, *Hochstetteria*, *Tarchonanthus*, *Warionia*

Table 12.2. Continued.

Author	Main taxonomic category	Generic groups and species
Bremer (1994)	Tribe Mutisieae	
	Subtribe Mutisiinae	*Stenopadus* group: *Achnopogon*, *Chimantaea*, *Duidaea*, *Glossarion*, *Gongylolepis*, *Neblinaea*, *Quelchia*, *Stenopadus*, *Stomatochaeta* *Gochnatia* and relatives: *Actinoseris*, *Chucoa*, *Cyclolepis*, *Hyalis*, *Gochnatia*, *Nouelia* *Ainsliaea* group: *Ainsliaea*, *Macroclinidium*, *Myripnois*, *Pertya* *Brachylaena* and *Tarchonanthus* *Plazia* group: *Aphyllocladus*, *Gypothamnium*, *Plazia* *Dicoma* group: *Achyrothalamus*, *Dicoma*, *Erythrocephalum*, *Gladiopappus*, *Pasaccardoa*, *Pleiotaxis* *Onoseris* and *Urmenetea* *Mutisia* and *Hyaloseris* *Chaetanthera* group: *Brachyclados*, *Chaetanthera*, *Pachylaena* *Gerbera* group: *Chaptalia*, *Gerbera*, *Leibnitzia*, *Perdicium*, *Trichocline*, *Uechtritzia*
	Subtribe Nassauviinae	*Proustia* group: *Acourtia*, *Burkartia*, *Lophopappus*, *Proustia* *Leucheria* group: *Holocheilus*, *Leucheria*, *Macrachaenium*, *Moscharia*, *Nassauvia* (incl. *Calopappus*), *Oxyphyllum*, *Panphalea*, *Perezia*, *Polyachyrus*, *Triptilion* *Adenocaulon* and *Eriachaenium*
	Excluded	*Warionia*
Hind (2007)	Tribe Mutisieae	
	Stifftia group	*Hyaloseris*, *Stifftia*, *Wunderlichia*
	Stenopadus group	*Achnopogon*, *Chimantaea*, *Eurydochus*, *Glossarion*, *Gongylolepis*, *Neblinaea*, *Quelchia*, *Salcedoa*, *Stenopadus*, *Stomatochaeta*
	Subtribe Nassauviinae	*Acourtia*, *Adenocaulon*, *Ameghinoa*, *Berylsimpsonia*, *Burkartia*, *Cephalopappus*, *Criscia*, *Dolichlasium*, *Eriachaenium*, *Holocheilus*, *Jungia*, *Leucheria*, *Leunisia*, *Lophopappus*, *Macrachaenium*, *Marticorenia*, *Moscharia*, *Nassauvia*, *Oxyphyllum*, *Panphalea*, *Perezia*, *Pleocarphus*, *Polyachyrus*, *Proustia*, *Triptilion*, *Trixis*
	Subtribe Mutisiinae	*Aphyllocladus*, *Brachyclados*, *Chaetanthera*, *Chucoa*, *Cnicothamnus*, *Cyclolepis*, *Gypothamnium*, *Hyalis*, *Ianthopappus*, *Lulia*, *Lycoseris*, *Mutisia*, *Onoseris*, *Pachylaena*, *Plazia*, *Urmenetea*
	Subtribe Gerberinae	*Amblysperma*, *Chaptalia*, *Gerbera*, *Leibnitzia*, *Perdicium*, *Trichocline*, *Uechtritzia*
	Subtribe Gochnatiinae	*Gochnatia*, *Pentaphorus*, *Richterago*
	Hecastocleis group	*Hecastocleis*
	Nouelia group	*Leucomeris*, *Nouelia*
	Catamixis group	*Catamixis*
	Subtribe Tarchonanthinae	*Brachylaena*, *Tarchonanthus*
	Dicoma group	*Dicoma*, *Erythrocephalum*, *Gladiopappus*, *Oldenburgia*, *Pasaccardoa*, *Pleiotaxis*
	Pertya group	*Ainsliaea*, *Macroclinidium*, *Myripnois*, *Pertya*
Katinas et al. 2008	Subfamily Mutisioideae	
	Tribe Mutisieae	(1) *Ainsliaea*, *Macroclinidium*, *Myripnois*, *Pertya* (2) *Adenocaulon* and *Eriachaenium* (3) *Hecastocleis* (4) *Achnopogon*, *Duidaea*, *Eurydochus*, *Glossarion*, *Gongylolepis*, *Neblinaea*, *Salcedoa* (5) *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, *Nouelia*
	Tribe Stifftieae	*Chimantaea*, *Quelchia*, *Stifftia*, *Stomatochaeta*, *Stenopadus*, *Wunderlichia*
	Tribe Nassauvieae	
	Excluded	*Brachylaena*, *Cloiselia*, *Dicoma*, *Dicomopsis*, *Erythrocephalum*, *Gladiopappus*, *Hesperomannia*, *Macledium*, *Moquinia*, *Pasaccardoa*, *Pleiotaxis*, *Tarchonanthus*, *Warionia*

common ancestry and formed a monophyletic group. In addition, close relationships among tepui-centered genera and *Wunderlichia* and *Stifftia* were also indicated by Robinson (1991) and Pruski (1991).

Katinas et al. (2008), based on morphological studies with an emphasis on the corolla, style and pollen features, redefined Don's (1830) tribe Stifftieae to include *Chimantaea*, *Quelchia*, *Stenopadus*, *Stifftia*, *Stomatochaeta*, and *Wunderlichia* with mostly actinomorphic deeply 5-lobed corollas and rugulose styles. The remaining tepui-centered genera with bilabiate or ligulate corollas and glabrous styles were kept in their redefined tribe Mutisieae. For the sake of clarification, the actinomorphic corolla tepui genera are referred to as the *Stenopadus* clade (after Bremer 1994) and the non-actinomorphic group is referred to as the *Gongylolepis* clade. This clarification is necessary because the molecular data produced different results.

Molecular studies using ten regions of chloroplast DNA (Panero and Funk 2008) indicated two monophyletic groups that contain tepui-centered clades (Fig. 12.1). The first is tribe Stifftieae (subfamily Stifftioideae), which can be divided into three clades, the basal branch which has only the Brazilian-centered genus *Stifftia* (actinomorphic

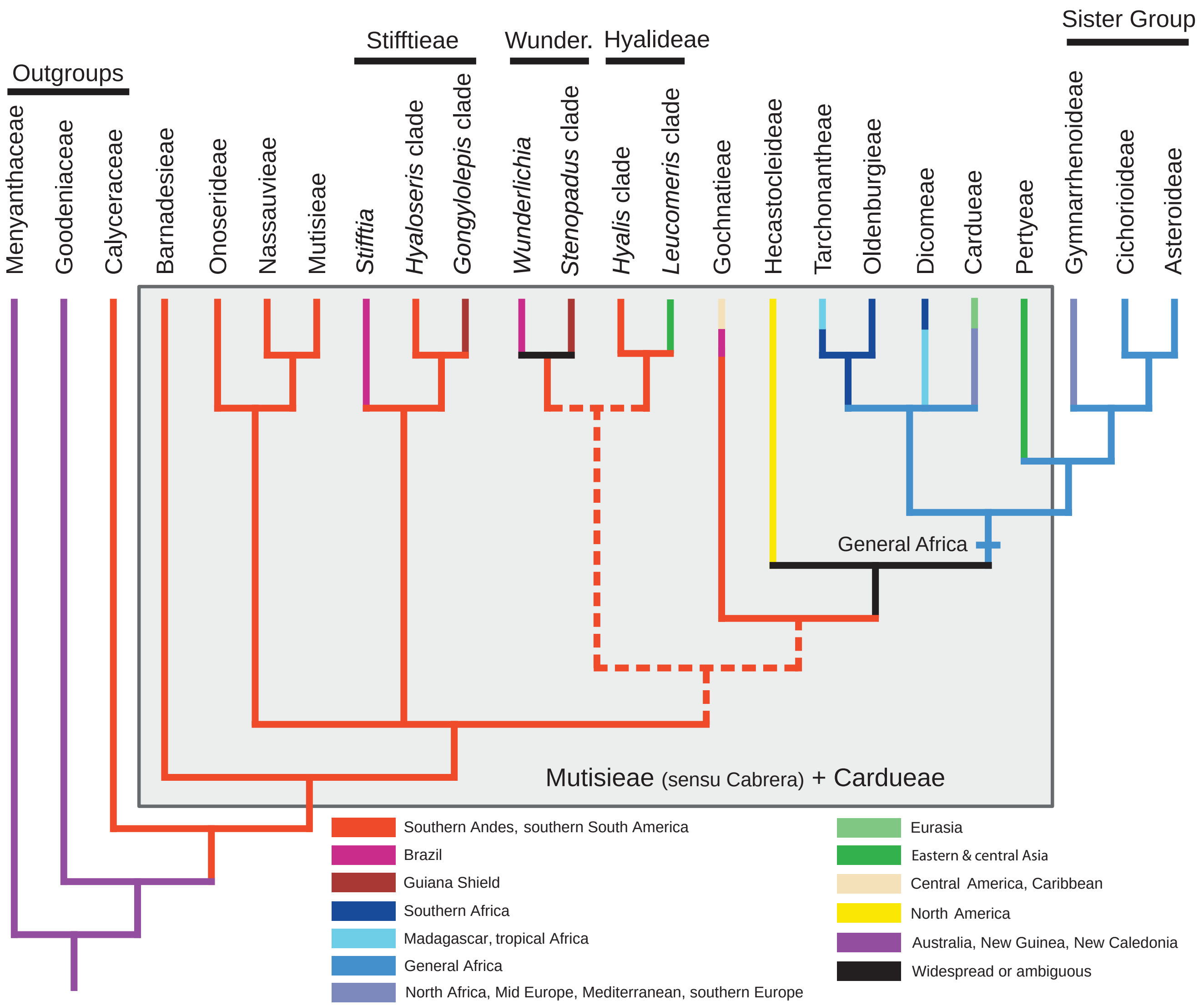

Fig. 12.1. A section of the Compositae phylogeny that highlights the basal grade of the family. A generic-level phylogeny can be found in Chapter 44. Wunder. = Wunderlichieae; the gray box denotes Mutisieae (sensu Cabrera). Cabrera never put Cardueae or Tarchonantheae into Mutisieae. Dashed lines indicate branches that are not as well supported as the remainder of the tree (Panero and Funk 2008): Wunderlichioideae have 52% bootstrap support in the parsimony tree and 91 posterior probability in the Bayesian tree; the branch connecting Wunderlichioideae to the rest of the family collapses in the parsimony tree and has a 97 posterior probability; the Gochnatieae branch has 65% bootstrap support and 100 posterior probability.

corollas; Fig. 12.2C–E), and two sister clades, the tepui-centered *Gongylolepis* clade (bilabiate corollas, rarely somewhat ligulate; Fig 12.2.A, B, F and Fig. 12.3B–E), and the Bolivian-Argentine *Hyaloseris* clade (ligulate or nearly ligulate, sub-bilabiate, or rarely bilabiate corollas; Fig. 12.3A) containing *Dinoseris* and *Hyaloseris.* Each of these three clades has a distinct morphology and there are no known apomorphic morphological characters that group the three together. The second group is tribe Wunderlichieae, including the tepui-centered *Stenopadus* clade (Fig. 12.4D, E and Fig. 12.5A–D) and the Brazilian genus *Wunderlichia* (Fig. 12.4A–C). This clade is well-supported by the morphology (Katinas et al. 2008). However, the subfamily Wunderlichioideae has both Wunderlichieae and its sister group the tribe Hyalideae, a clade containing the southern South American genera *Ianthopappus* (Fig. 12.6B, C) and *Hyalis* (Fig. 12.6A), and an Asian clade with *Leucomeris* and *Nouelia* (Fig. 12.7; see also Chapter 21; Table 12.1).

Currently there are no known morphological or palynological synapomorphies that support grouping the three molecular clades of Stifftioideae, the two tribes of Wunderlichioideae, or the two clades of the tribe Hyalideae (Table 12.1). For example, genera with actinomorphic and zygomorphic corollas, as well as glabrous and rugulose or papillose styles, are found in more than one clade.

Descriptions

Wunderlichieae (*Wunderlichia* clade). — Actinomorphic, tubular florets, receptacles commonly paleate, and styles bullate or rugulose beyond the bifurcation point of branches: *Chimantaea* (9 species), *Stenopadus* (15 species), *Stomatochaeta* (6 species), and *Wunderlichia* (6 species). These genera, the *Stenopadus* clade, plus *Stifftia* (the genus that molecular data placed with the *Gongylolepis* and *Hyaloseris* clades) have been traditionally related based on morphology (e.g., Maguire 1956; Maguire et al. 1957). On the other hand, recent studies show that the molecularly defined clade Wunderlichieae is the only basal clade with style branches that are papillose below the bifurcation and paleaceous receptacles, and that *Stifftia* does not have either of these (Roque, pers. comm.). Other characters such as the presence of more than 100 bristles in the pappus (Wunderlichioideae and Stifftioideae) and acute appendages on the anther connective (Wunderlichieae and Stifftioideae) show some signs of being useful, and all of these need to be further investigated (Roque, pers. comm.).

Floral venation in genera of the *Wunderlichia* clade was analyzed by Carlquist (1957) and summarized by Bremer (1994); it showed that the venation in the corollas of the species of *Stenopadus* was considered by Carlquist (1957) to be one of the most complex found in Compositae. There are various degrees of union among the lateral veins (they extend from the lobe margins into the corolla tube), the median veins (they do or do not extend into the tube from the middle of each lobe), and the subsidiary veins (may be present or not; they branch from the lateral veins at various points). The fusion between veins led to complex patterns resulting in 2–5-veined corolla lobes and in 10–15-veined corolla tubes in the different species of *Stenopadus*.

Many features of members of this clade, such as the tubular corollas with 3-veined lobes and paleaceous receptacles of *Stenopadus* and *Wunderlichia*, have been regarded as primitive (Cronquist 1955; Carlquist 1957, 1976; Wagenitz 1976), in fact, Bremer (1994) hypothesized a "*Stenopadus* like" ancestral morphology for Compositae. However, this is ambiguous in the current molecular analysis and therefore difficult to speculate at this time.

Pollen of the *Wunderlichia* clade is heterogeneous, with three different exine types being found in this clade: *Mutisia*, *Stenopadus*, and *Wunderlichia* types (Katinas et al. 2008; Tellería 2008). Only the *Stenopadus* type, with two layers of single columellae in concordant pattern, appears as exclusive of some species of this genus; the remaining exine types are shared with genera of other taxonomic groups.

Hyalideae. — This tribe includes two clades, the South American genera *Hyalis* (2 species) and *Ianthopappus* (1 species), which are labeled on Fig. 12.1 as the *Hyalis* clade, and the Asian genera *Leucomeris* (2 species) and *Nouelia* (1 species) referred to on Fig. 12.1 as the *Leucomeris* clade. These genera have been considered part of the *Gochnatia* group together with *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, and *Gochnatia* (Freire et al. 2002; Roque and Hind 2001) on the basis of apiculate anther appendages and smooth style branches. However, the large number of pappus bristles in the Hyalideae genera is similar to Wunderlichieae and not Gochnatieae (Roque, pers. comm.). This tribe is discussed in Chapter 15.

***Stifftia*. —** This genus is the sister group of the *Gongylolepis* and *Hyaloseris* clades (Fig. 12.1; Fig. 12.2C–E; Table 12.1). It is a genus of seven species occurring in Brazil and French Guiana; its members have actinomorphic corollas and glabrous (rarely sub-rugulose) styles. As mentioned above, *Stifftia* is generally believed to be related to the tepui-centered genera with tubular corollas. The somewhat rugulose styles observed in some species (e.g., *Stifftia chrysantha* Mikan; Katinas et al. 2008) would also support this relationship. However glabrous styles were also found in some of its species as well as other representatives of the *Gongylolepis* clade. However, such characters as pollen features, a large number of pappus bristles, glabrous achenes (except *Chimantaea*), and acute connectival appendages of anthers do link *Stifftia* with members of the *Gongylolepis* clade and with the *Wunderlichia* clade (Katinas et al. 2008; Tellería 2008; Roque, pers. comm.).

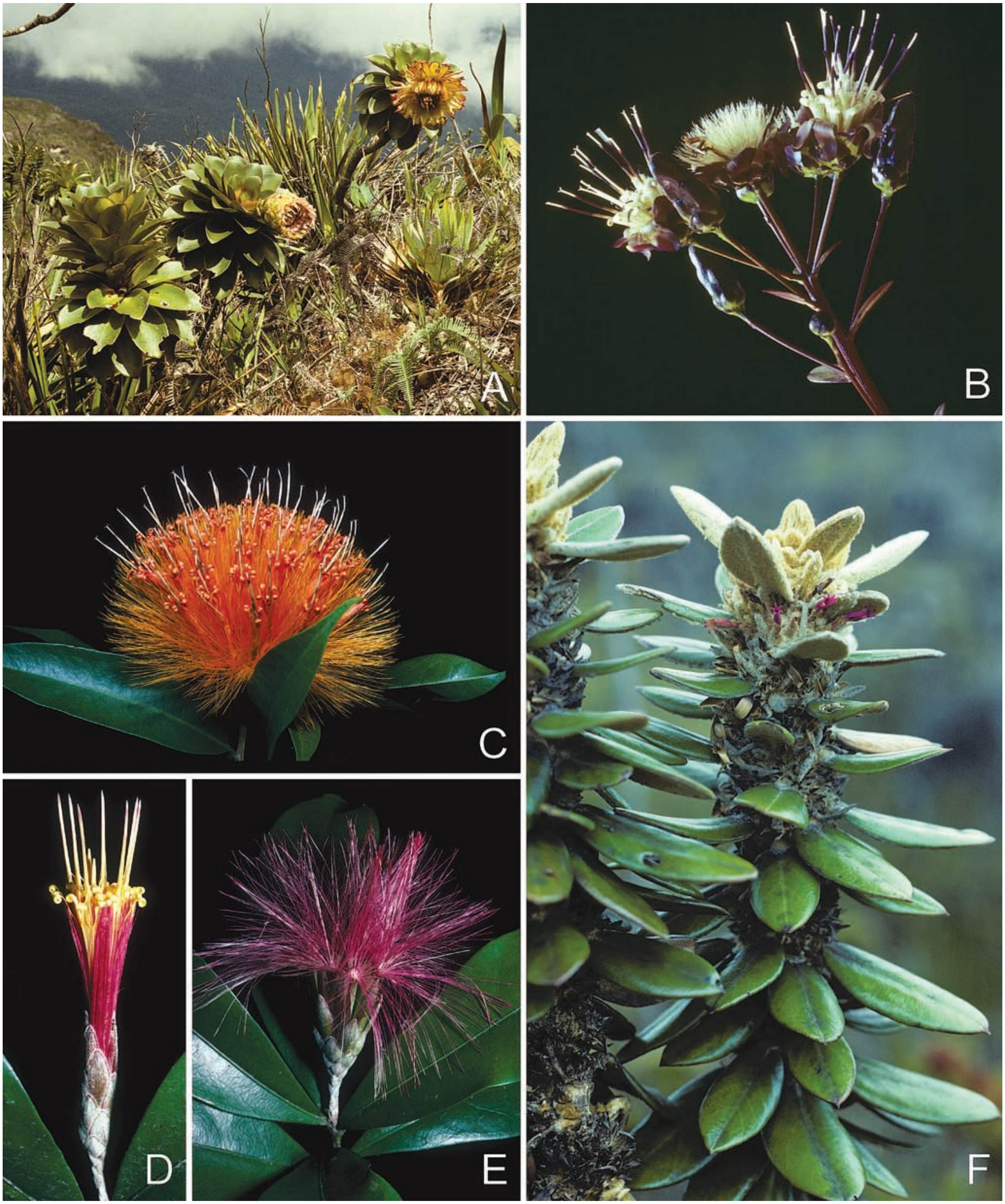

Fig. 12.2. A *Gongylolepis jauaensis* (Aristeg., Maguire & Steyerm.) V.M. Badillo (Venezuela: Cerro Coro Coro); **B** *Gongylolepis huachamacari* Maguire (Venezuela: Neblina; *Funk 6725*); **C** *Stifftia chrysantha* Mikan var. *flavicans* Toledo ex Dedecca (Brazil); **D, E** *Stifftia fruticosa* (Vell.) D.J.N. Hind & Semir (Brazil); **F** *Quelchia eriocaulis* Maguire, Steyerm. & Wurdack (Venezuela: Chimantá massif). [Photographs: A, F, O. Huber; B, V.A. Funk; C–E, G. Lewis.]

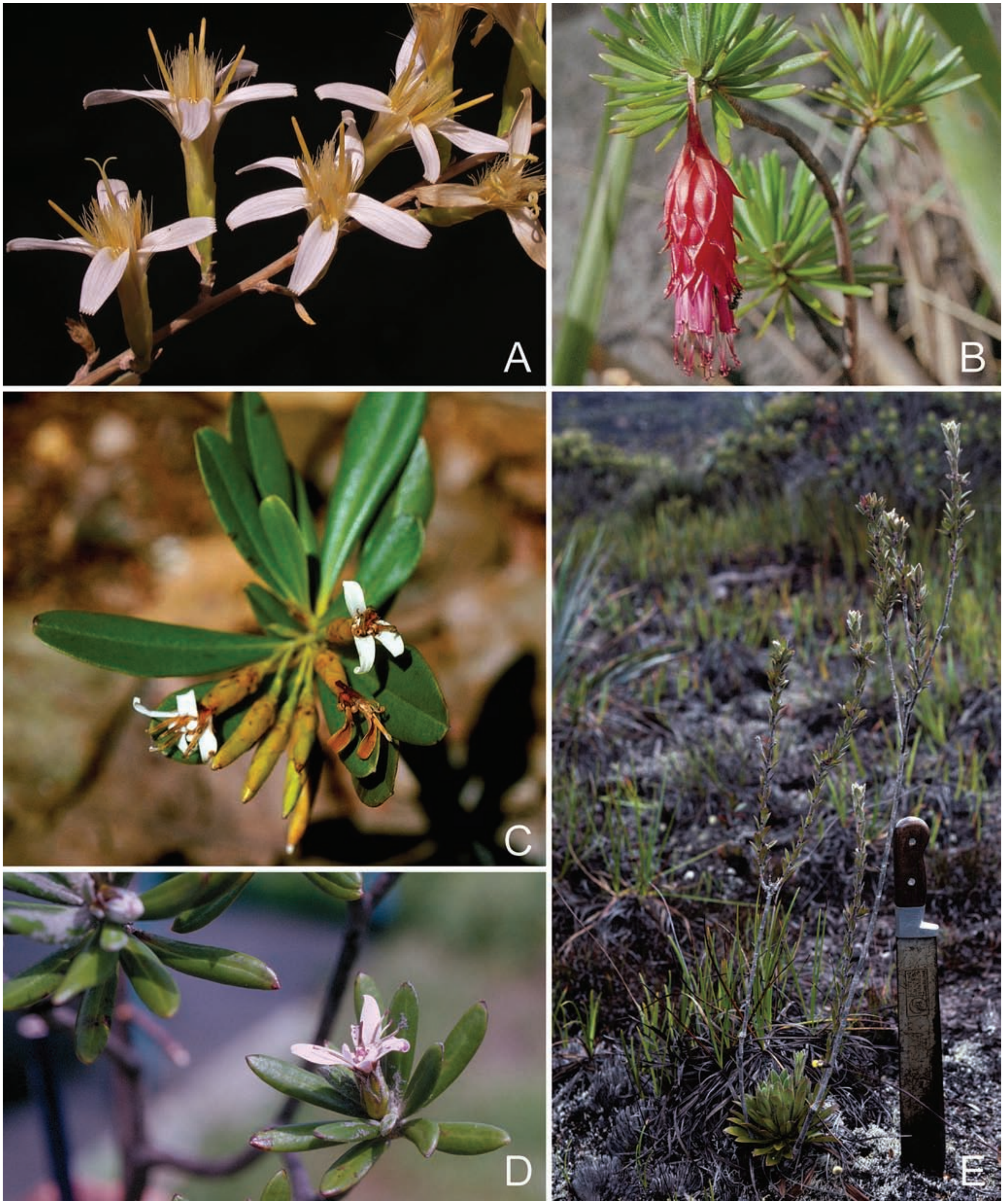

Fig. 12.3. **A** *Hyaloseris cinerea* (Grieseb.) Grieseb. (Argentina, La Rioja, near Chilecito); **B** *Duidaea rubriceps* S.F. Blake (Venezuela: Duida; *Fernández et al. 8010*); **C** *Neblinaea promontoriorum* Maguire & Wurdack (Venezuela: Neblina); **D** *Duidaea marahuacensis* Steyerm. (Venezuela: Duida; *Fernández et al. 8194*); **E** *Achnopogon virgatus* Maguire, Steyerm. & Wurdack (Venezuela, Chimantá massif). [Photographs: A, J.M. Bonifacino; B–D, V.A. Funk; E, O. Huber.]

***Gongylolepis* clade. —** This clade includes genera with all bilabiate florets, epaleate (but pilose) receptacles, and smooth style branches (Fig. 12.2A, B, F; Fig. 12.3B–E): *Achnopogon* (2 species), *Duidaea* (4 species), *Eurydochus* (1 species), *Glossarion* (2 species), *Gongylolepis* (14 species), *Neblinaea* (1 species), *Quelchia* (4 species plus one hybrid), and the more recently added (Jiménez Rodríguez et al. 2004) *Salcedoa* (1 species). Species of *Quelchia* have 1-flowered capitula, and the corollas range from tubular, slightly zygomorphic to bilabiate. The particular venation of the bilabiate genera, such as *Gongylolepis* with additional veins in the 3-lobed limb that branch off at the sinuses, led Carlquist (1957) to interpret this condition as a reflection of the vascular system of the actinomorphic corolla, which is generally assumed to be ancestral to the zygomorphic condition. The stem anatomical studies of Carlquist (1958) showed the presence of laticiferous cells in species of *Gongylolepis*, *Neblinaea*, and *Quelchia*. The presence and distribution of sclerenchyma in stems and involucral bracts as well as the presence or absence of laticiferous cells in the genera analyzed were viewed by Carlquist (1958) as significant in differentiating the genera with tubular corollas from the genera with bilabiate corollas.

Pollen of the genera of this clade was recently analyzed in detail (Zao et al. 2006; Katinas et al. 2008; Tellería 2008). Within this group, the exine *Gongylolepis* type relates the genera *Duidaea*, *Glossarion*, *Quelchia*, and *Gongylolepis*. The exine *Wunderlichia* type characterizes *Eurydochus* and *Salcedoa*, whereas the *Mutisia* exine type characterizes *Neblinaea* (Tellería 2008). Pollen features partially support the *Stifftia*-*Gongylolepis* clade since *Stifftia* has *Mutisia* exine type with microechinate or slightly echinate sculpture (such as the pollen of *Neblinaea*) whereas *Gongylolepis* presents a *Gongylolepis* exine type, which is mainly characterized by strong spines and a very perforate exine surface as occurs in many Cardueae (Tellería 2008).

***Hyaloseris* clade. —** It is not surprising that the two southern South American (Bolivia–Argentina) genera *Dinoseris* (1 species) and *Hyaloseris* (7 species; Fig. 12.3A) appear as sister taxa, since *Dinoseris salicifolia* Griseb. was originally a species of *Hyaloseris* (Ariza Espinar 1973). Both genera share opposite leaves (sometimes alternate in *Hyaloseris*), homogamous capitula, epaleate receptacles, all isomorphic bisexual florets, and usually ligulate corollas with shallowly 5-dentate limbs (occasionally the corollas in species of *Hyaloseris* have their segments partially connate producing sub-bilabiate or bilabiate corollas); both genera have pollen with an exine of a *Mutisia* type: microechinate (Tellería and Katinas 2004; Katinas et al. 2008). Roque reports that the styles are bifid and the style branches are long and papillose below the bifurcation (Roque, pers. comm.).

Similarities and differences between the molecular and morphological studies can be summarized using Tables 12.1 and 12.2. All the clades recovered in the molecular data are reasonable, although perhaps more finely divided than the morphology would suggest (with the exception of those mentioned above). As pointed out above, with the exception of few authors (e.g., Jeffrey 1967; Pruski 1991), the tepui-centered genera have been regarded as belonging to two different groups based on their morphology (Maguire 1956; Maguire et al. 1957; Cabrera 1977; Hansen 1991). Building on those data, Katinas et al. (2008) redefined the two groups pointing out that the main characters to distinguish them are style and secondly corolla shape. Those genera with rugulose styles beyond the bifurcation point of branches and deeply cleft actinomorphic corollas have been included in one of the groups: the *Stenopadus* clade. These genera are, in part, represented in the tribe Wunderlichieae obtained by molecular data (Panero and Funk 2008). The second group, the *Gongylolepis* clade has glabrous styles and bilabiate corollas and this clade is found in one group within the molecularly defined Stifftieae. The sister group (in the molecular data) to the *Gongylolepis* clade, the *Hyaloseris* clade, has mostly ligulate corollas and styles dorsally papillose only at the branches. This type of corolla and style is different from the other members of the molecularly defined Stifftieae, which have actinomorphic or bilabiate corollas and styles glabrous or subrugulose beyond the bifurcation point of branches. Usually *Hyaloseris* and *Dinoseris* have been regarded as related to *Mutisia* (Cabrera 1965; Bremer 1994) in which papillose style branches and often ligulate corollas occur.

Finally, the placement of the *Wunderlichia* clade as the sister group to the *Hyalis* clade is unusual since the characteristics of styles and corollas are very different in both groups of genera (see Chapter 15). The *Hyalis* clade is usually thought to be related to the Gochnatieae (Hansen 1991; Bremer 1994; Freire et al. 2002; Katinas et al. 2008), by the presence of glabrous styles, apiculate apical appendages of the anthers, and epaleate receptacles, among other characteristics. However, *Hyalis* and *Ianthopappus* have pappus and achene characters that are different from Gochnatieae (Roque, pers. comm.). The *Hyalis* clade (Table 12.1; Fig. 12.6A) and *Wunderlichia* clade (Figs. 12.4 and 12.5) differ also in pollen features. In Hyalideae, pollen characters are more or less homogeneous given that most genera share the *Mutisia* exine type (Katinas et al. 2008) whereas in Wunderlichieae three types of exine can be found (Katinas et al. 2008; Tellería 2008).

In summary we can point out that Cabrera (1977) recognized four subtribes: Barnadesiinae, Gochnatiinae, Mutisiinae, and Nassauviinae. The first and the last have remained largely intact, with the former now a subfamily and the latter a tribe. Mutisiinae are somewhat redefined but largely intact as a subfamily with three tribes (Mutisieae, Onoserideae, Nassauvieae; Panero and Funk

Fig. 12.4. A, B *Wunderlichia mirabilis* Riedel (Brazil: Minas Gerais, Serra do Cipó; *Roque 1622*); **C** *Wunderlichia senaei* Blaz. (Brazil: Minas Gerais, Diamantina; *Roque 1649*); **D** *Stomatochaeta acuminata* Pruski, habit only (Venezuela: Chimantá massif); **E** *Stomatochaeta cymbifolia* (S.F. Blake) Maguire & Wurdack (Venezuela: Chimantá massif). [Photographs: A–C, N. Roque; D, E, O. Huber]

Fig. 12.5. **A** *Chimantaea eriocephala* Maguire, Steyerm. & Wurdack; **B** *Chimantaea humilis* Maguire, Steyerm. & Wurdack; **C** *Chimantaea mirabilis* Maguire, Steyerm. & Wurdack; **D** *Stenopadus chimantensis* Maguire, Steyerm. & Wurdack. All from Venezuela, Chimantá massif. [Photographs: A, B, C. Brewer; C, D, O. Huber.]

Fig. 12.6. **A** *Hyalis argentea* D. Don ex Hook. & Arn. (Argentina: Mendoza, near Tunuyán); **B, C** *Ianthopappus corymbosus* (Less.) N. Roque & D.J.N. Hind (Brazil: Rio Grande do Sul, Reserva Biológica de Ibirapuitã; *Deble and Oliveira-Deble 7993*). [Photographs: A, J.M. Bonifacino; B, C, L.P. Deble & A.S. Oliveira.]

2008). Gochnatiinae, which contained most of the taxa with actinomorphic corollas, have fragmented into many smaller groups that in the molecular data are now recognized as different tribes and subfamilies (Table 12.1). Most of the clades have morphological characters that define them but some do not.

CATAMIXIS INCERTAE SEDIS

The genus *Catamixis* (Fig. 12.8) is monotypic and found only in the northern part of India and adjacent Nepal. Its DNA has not been sequenced, and it was not discussed by Panero and Funk (2002, 2008). Recent morphological treatments have not made a definite recommendation on where it should be placed. Bremer (1994) put this genus in his large, paraphyletic Mutisiinae (including Gochnatiinae). Katinas et al. (2008) placed it in a more restricted Mutisieae but did not feel strongly that it belonged there, and Freire (Chapter 21) did not include it in the *Pertya* clade (Pertyeae). Jeffrey (2007), however, did place *Catamixis* into the tribe Pertyeae. The major features that are used to place taxa in Mutisieae (sensu Cabrera) using morphology are the corolla shape, style pubescence, and style apex. The corolla of *Catamixis* is ligulate with five shallowly divided lobes, but the lobes are irregular in shape and size (Fig. 12.8F, O, P). Since this is probably an independently derived character, an autapomorphy, it is not useful for grouping. The shaft of the style of *Catamixis* is, for the most part, glabrous except for a few scattered hairs near the base (Fig. 12.8I). The style branches are relatively short and slightly rounded at the apex (not acute or attenuate) and are short-papillose (Fig. 12.8J).

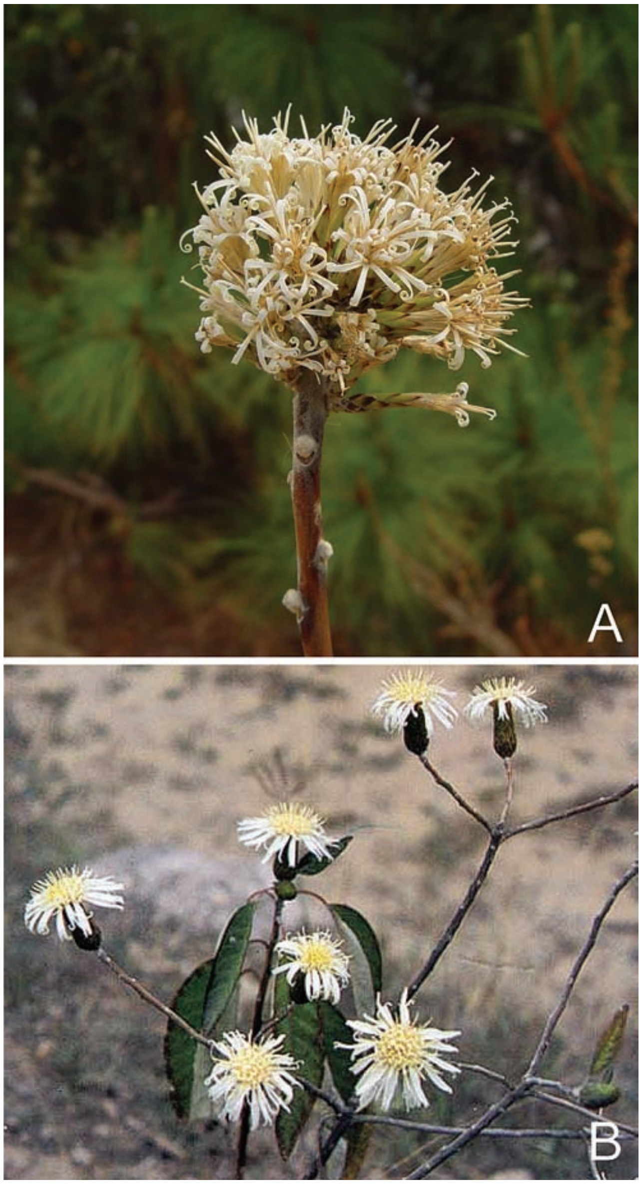

Fig. 12.7. A *Leucomeris* sp. (China: Yunnan); **B** *Nouelia insignis* Franch. (China: Yunnan). [Photographs: A, Wang Hong; B, Tao Guoda.]

The pollen grains of *Catamixis* (Fig. 12.9) have 3-colporate apertures and 2-layered exine with a surface that is spinulose with widely dispersed spinules (< 1 μm in height). The surface of the grain (Fig. 12.9B) is microperforate and spinose, and part of a fractured section (Fig. 12.9C) shows a 2-layered exine exposing a broad and thickened lower (proximal) layer of columellae and an upper (distal) layer of considerably denser and shorter columellae. The grains are rather small, 30–35 μm. The pollen characteristics tell us that *Catamixis* is definitely a member of one of the clades of former Mutisieae (sensu Cabrera), but many of the clades have similar pollen so it does not offer any immediate help with determining its position on the phylogeny. A more detailed study may provide additional data.

Catamixis, therefore, shares with Pertyeae the dorsally short papillose nature of the style branches and the ligulate corollas of some of Pertyeae, although the corolla limbs of Pertyeae are deeply 5-lobed (vs. shallowly 5-lobed in *Catamixis*); the distribution of *Catamixis* might also suggest a Pertyeae affinity. However, there are no data that clearly place *Catamixis* in any of the existing groups and at this time it seems best to list it as 'unplaced' until fresh material has been obtained so that its DNA can be sequenced.

Catamixis T. Thomson in J. Linn. Soc. Bot. 9: 342. 1865 – Type: *C. baccharoides* T. Thomson.

Small erect, poorly branched shrub. Stems densely tomentose at first, later glabrescent. Leaves alternate, petiolate, petiole winged, lamina simple, obovate, base long-cuneate, midrib prominent beneath, margins coarsely

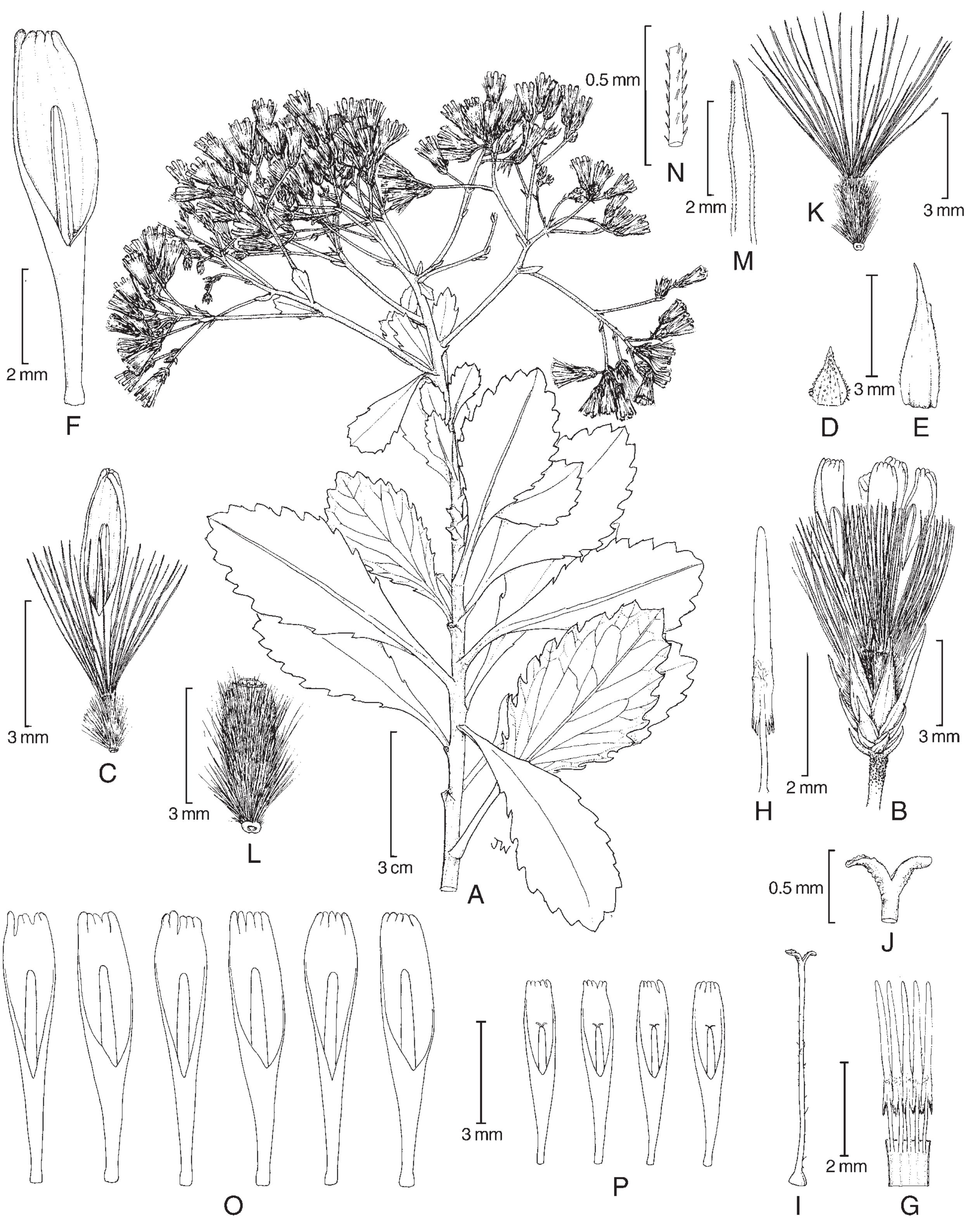

Fig. 12.8. *Catamixis baccharoides* T. Thomson. **A** habit; **B** head; **C** floret with pappus; **D** outer involucral bract; **E** inner involucral bract; **F** floret; **G** anthers opened; **H** close up of anther; **I** style; **J** style branches and stigmatic surface; **K** achene with pappus; **L** mature achene; **M, N** pappus bristles; **O, P** corolla variation in size and depth of lobes. A–F, K–N & P from *Upendranath Kanjilal 1020*; G–J & O from *Stewart 209/BS* syntype. [Drawing by J. Beentje.]

serrate, apices obtuse to sub-acute. Inflorescences terminal, eventually overtopped by vegetative branches, corymbose, well-branched, capitula pedunculate, pedicels subtended by short linear bracteole at base, pubescent with numerous short hairs; capitula homogamous, ligulate, numerous; involucres 4–5-seriate, scarcely imbricate, turbinate; phyllaries, gradate, margins ciliate and laciniate, apices long-acute, often purplish; receptacle convex, glabrous, epaleate, ± alveolate. Florets few (6), hermaphrodite, corollas whitish to pale yellow, glabrous, ligule teeth equal or unequal; apical anther appendages narrow-triangular, about three times longer than wide, apices sub-acute, somewhat rounded, anther collar indistinguishable from filament; basal anther appendages tailed, laciniate; style shaft commonly glabrous, style base with basal node; style arms relatively short, dorsally short papillose, apices slightly rounded. Achenes densely long-setuliferous/sericeous, apices acute; carpopodium distinct, annular, pappus setae uniseriate, long-barbellate, white. (Description provided by Hind, pers. comm.; Figs. 12.8 and 12.9.)

Catamixis is endemic to the Eastern Himalaya region (see discussion at http://www.biodiversityscience.org/publications/hotspots/Himalaya.html) and is listed as "vulnerable" on the list of 'Threatened Plants of Uttaranchal' (http://www.wii.gov.in/nwdc/threatened_plants_uttaranchal.pdf). It has no known chromosome counts and it has no known common names or uses.

SUBFAMILY CARDUOIDEAE CASS. EX SWEET (1826)

Perennial, biennial or less often annual herbs, shrubs or rarely trees, rarely scandent. Leaves alternate, usually simple, entire, serrate, denticulate or lobulate, especially in herbaceous members often spiny. Capitula homogamous or heterogamous, discoid or discoid with marginal florets sterile and radiant, rarely bilabiate-radiate, radiate or ligulate. Involucre narrowly cylindrical to urceolate-subglobose, phyllaries 3- to many-seriate, imbricate, often spiniferous. Receptacle epaleaceous and very often setulose, rarely paleaceous. Florets 1- to many, 5-merous, all or inner regular or subregular, outer sometimes radiant, rarely bilabiate-radiate or radiate, very rarely all ligulate; corolla lobes long, those of inner lip of bilabiate florets straight or with incurved apex, very rarely coiled. Anthers calcarate and caudate, very rarely ecalcarate, tails usually long, sometimes pilose or fringed. Pollen usually ecaveate, spiny or microechinate. Style arms short to long, obtuse to rarely acute, glabrous or with dorsal hairs, sometimes not divergent for most of their length, with stigmatic papillae covering all inner surface; style shaft often with an articulation at or below the branching point, marked by a ring of hairs and/or an increase in diameter, glabrous below the articulation, usually hairy above it. Achenes with twin hairs, simple hairs, or glabrous. Pappus usually present, of bristles or scales, isomorphic or heteromorphic. (Description adapted from Jeffrey, 2007.)

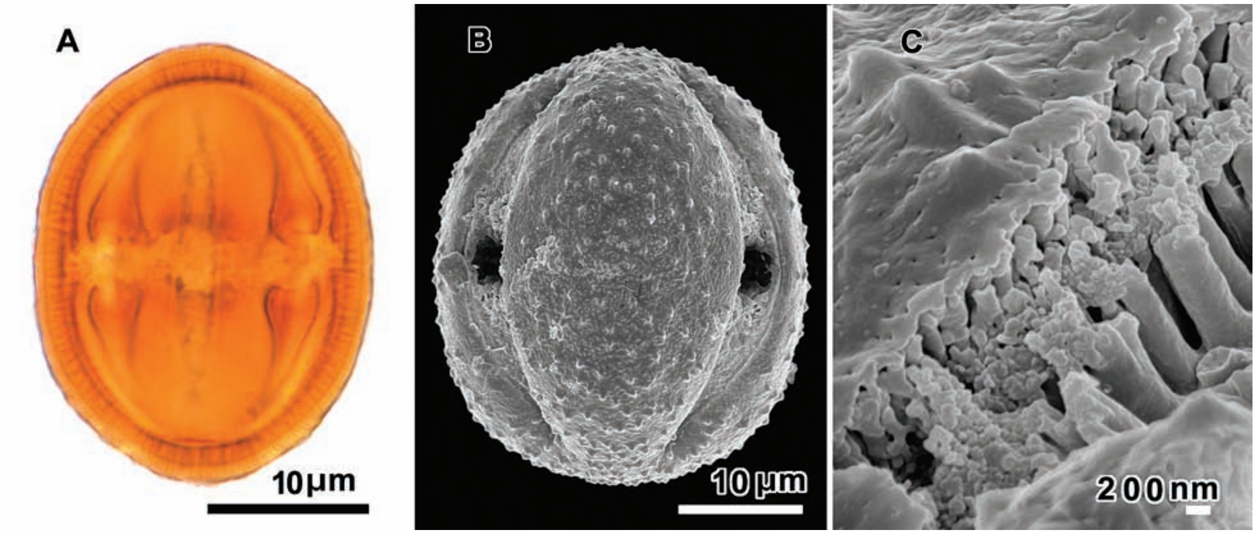

Fig. 12.9. *Catamixis baccharoides* T. Thomson. **A** Light micrograph (LM). Lateral (equatorial) view showing 3-colporate apertures and 2-layered exine. **B** Scanning electron micrograph (SEM) of pollen surface (orientation similar to LM in Fig. 12.9A) showing relatively few and widely dispersed spinules (< 1 µm in height) and colporate apertures. **C** SEM of broken grain showing microperforate and spinose surface and part of a fractured section through 2-layered exine (as described in Fig. 12.9A) exposing a broad and thickened lower (proximal) layer of columellae and an upper (distal) layer of considerably denser and shorter columellae. [Photographs, A. Wortley.]

Carduoideae comprise at least 93 genera and 2600 species, mostly in the Old World. The subfamily as here circumscribed includes all mutisioid genera that in molecular studies come out in a clade with Cardueae s.l. (Fig. 12.10). The constancy of the *Gochnatia* type of testa epidermal cell wall thickening (Grau 1980) or its derivatives define the subfamily. Although this type of cell wall thickening also occurs in some Mutisieae, possibly as a parallelism, it is there associated with different style and/or pollen types.

All the available phylogenetic information indicates that the origin of the great tribe Cardueae, centered in the Old World, can be tracked to African representatives of old Mutisieae s.l. (presently tribes Dicomeae, Tarchonantheae and Oldenburgieae), following progressive drying up of the African climate at the end of the Tertiary. These changes led to a rapid deforestation of the continent. Perhaps the best candidate with the most plesiomorphic characters in Carduoideae is tribe Dicomeae, which has some characters that are generalized among Cardueae, but are usually missing in Mutisieae s.str.

The most important characters of Cardueae are: *(1)* leaves with spiny apices (*Dicoma paivae* S. Ortiz & Rodr. Oubiña, *Dicoma tomentosa* Cass., *Macledium canum* (Balf. f.) S. Ortiz, *Macledium spinosum* (L.) S. Ortiz, etc.); *(2)* coriaceous phyllaries with spiny tips (*Dicoma*, *Macledium*, *Pasaccardoa*), and *(3)* achenes obconical (*Cloiselia*, *Dicoma*, *Gladiopappus*, *Macledium*) or broadly cylindrical (*Erythrocephalum*, *Pasaccardoa*), often with pericarp reinforced with strips of sclerenchyma and apical groove below insertion of the pappus. One of the taxa with the largest number of plesiomorphic characters, *Pleiotaxis*, shows oblong, scarcely sclerified achenes without an apical groove, similar to the achenes of most primitive Cardueae. *Pleiotaxis*

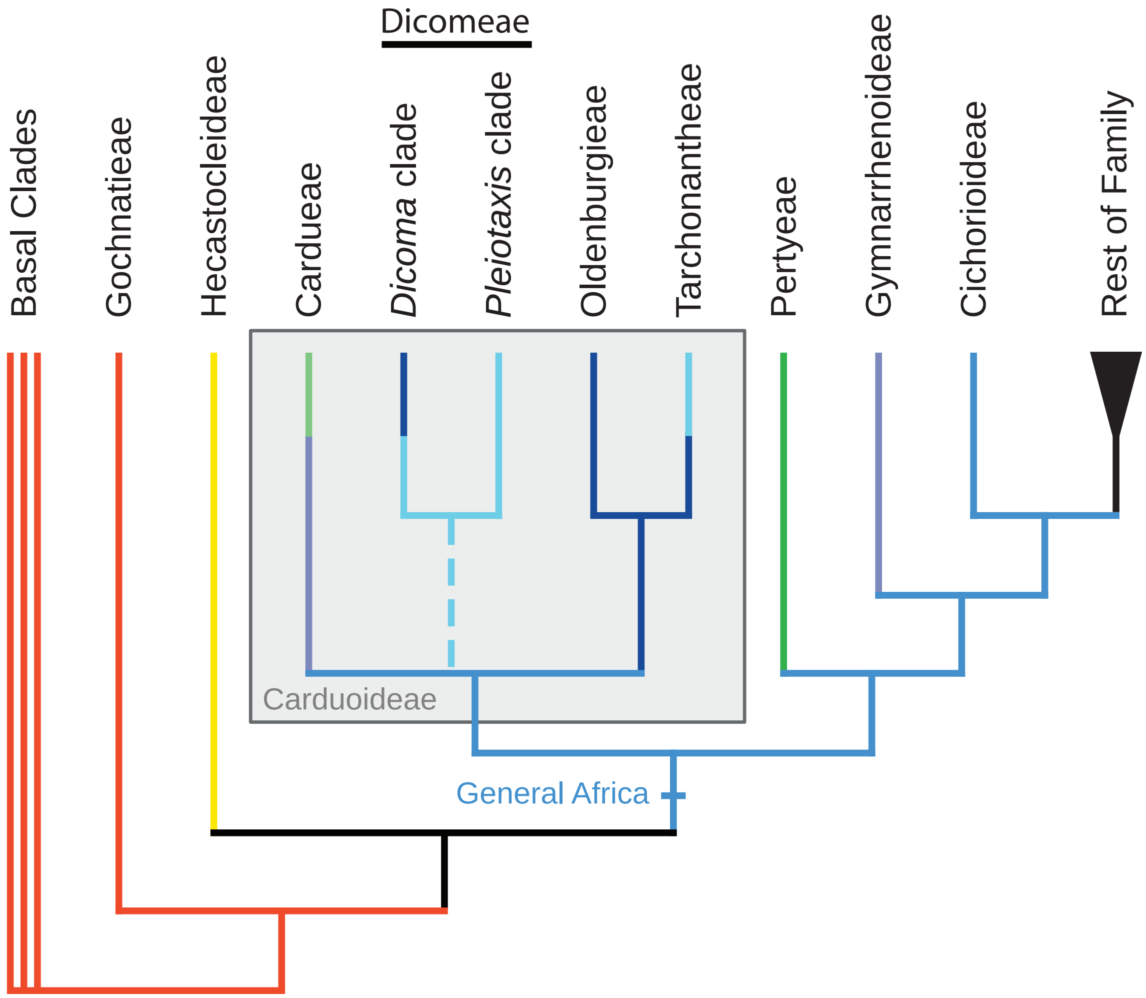

Fig. 12.10. A section of the Compositae phylogeny emphasizing relationships within the subfamily Carduoideae. The gray box denotes Carduoideae. For color chart see Fig. 12.1.

or other related genera could be the intermediates between Dicomeae and Cardueae. Achenes of Cardueae and Dicomeae would have evolved in parallel ways leading to the presently widespread sclerified type.

CONCLUSION

If we return to the overall goals of this ongoing research effort, we find that some have been met while others require further attention. In particular, some molecular clades have strong morphological support but some have no support or they conflict with the morphology; many genera have been satisfactorily placed on the phylogeny but some have not; and some super-generic taxa (be they subtribes, tribes, or subfamilies) are easy to recognize and have been accepted by most synantherologists (e.g., Nassauvieae, Wunderlichieae, Pertyeae) and some have not (e.g., Stifftieae). There are many possible reasons for these discrepancies and a better understanding of what characters are plesiomorphic would help us to understand the placement of some genera. We must also keep in mind that: some difficult taxa have only one set of sequences available, and the possibility of error exists; taxa are missing from the analyses and their addition might change the topology; and some of the branches are not as strongly supported as one would like. Each new study brings additional data and insights on relationships.

Acknowledgements. We were saddened to learn of the recent death of Chong-Jiang Zhao, a 27-year-old botanist at Xixhuangbanna Tropical Garden (Chinese Academy of Sciences), who fell from a cliff while trying to collect *Nouelia* for a Chinese colleague. The untimely death of this dedicated botanist is regretted by all who work in the family. Crisci, Katinas, Sancho, and Tellería acknowledge the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina. Funk and Bonifacino acknowledge the Smithsonian Institution's Postdoctoral Fellowship program. Other than the authors, photographs were supplied by: Otto Huber and Charles Brewer Carias, both experts on exploring and studying the flora of the tepuis and whose specimens are mainly at VEN; Gwilym Lewis (K); and Wang Hong and Tao Guoda from Xishuangbanna Tropical Garden, Academia Sinica, Yunnan, China (HITBC). We thank them all. In addition, we thank Alexandra Wortley (E) who kindly provided the unpublished pollen images and John Skvarla (OKL) who assembled the images into what is now Figure 12.9. Authorship of this paper is alphabetical after the first author.

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Note added in proof

A recent paper has shown that two separate base pair deletions link *Catamixis* with Pertyoideae. Panero, J. 2008. Shared molecular signatures support the inclusion of *Catamixis* in subfamily Pertyoideae. *Phytologia* 90: 418–424.

Chapter 13

Barnadesieae (Barnadesioideae)

Tod F. Stuessy, Estrella Urtubey and Michael Gruenstaeudl

INTRODUCTION

Subfamily Barnadesioideae (Bremer and Jansen 1992) comprises 91 species in nine genera and is entirely restricted to South America. It is clearly distinguishable from other sunflowers by possession of axillary spines (reviewed in Ezcurra 1985), pubescence of unbranched three-celled hairs ("barnadesioid trichomes"; Cabrera 1959; Erbar and Leins 2000), peculiar types of testa-epidermis (Grau 1980), and various pollen features (Parra and Marticorena 1972; Skvarla et al. 1977; Hansen 1991a; Urtubey and Tellería 1998; Zhao et al. 2000). Above all, the lack of two DNA inversions found in the chloroplast genome of all other Asteraceae supports a separated position of Barnadesioideae within the family (Jansen and Palmer 1987; Kim et al. 2005).

The nine genera of Barnadesioideae are quite diverse in species number, habit and ecology (Figs. 13.1, 13.2). Four of them are monotypic (*Duseniella* K. Schum., *Fulcaldea* Poir. ex Lam., *Huarpea* Cabrera, and *Schlechtendalia* Less.) and endemic to narrow areas in Argentina, Peru, Ecuador, and Uruguay. *Fulcaldea laurifolia* (Bonpl.) Poir is a tall arching shrub with whitish aggregations of flowering heads. *Huarpea andina* Cabrera is a very short (ca. 5 cm tall) subshrub with a thick root system, and it is relatively rare, having been collected only a few times. *Schlechtendalia luzulaefolia* Less. is a perennial herb that is striking for having long, narrow leaves that resemble those of the genus *Luzula* DC. (Juncaceae). *Duseniella patagonica* O. Hoffm., which occurs on the Patagonian steppe, is the only annual in the subfamily. The two species of *Doniophyton* Wedd. (Katinas and Stuessy 1997) are herbs that grow in dry areas of the Puna, Monte desert, and Patagonian steppe. *Arnaldoa* Cabrera comprises three shrubby species (Stuessy and Sagástegui 1993; Ulloa et al. 2002) that occur in southern Ecuador and northern Peru; the single arborescent species of *Fulcaldea* grows in the same region (Ståhl et al. 1999). *Chuquiraga* Juss. is a genus of 23 species of evergreen shrubs (Ezcurra 1985; Harling 1991; Sagástegui and Sánchez 1991; Granda 1997), with varying habits and sizes and arrangements of capitula, and a prominent member of the xeric flora in high Andean elevations and in Patagonian semideserts. Members of *Dasyphyllum* Kunth and *Barnadesia* Mutis ex L. f. are also distributed along the Andes, but additionally occur in tropical forests of Argentina, Brazil and Paraguay. *Barnadesia* consists of 19 species of arching shrubs and trees (Chung 1965; Urtubey 1999), most of which are restricted to elevations of 1800–3400 m. The largest genus of the subfamily, *Dasyphyllum*, with 40 species (Cabrera 1959, 1962, 1977; Sagástegui 1980; Sagástegui and Dillon 1985; Zardini and Soria 1994), occurs at lower elevations and shows a disjunct distribution matching its two subgenera. The arborescent subgenus *Archidasyphyllum* Cabrera is confined to the relict coastal *Nothofagus*-forests of central Chile, whereas the shrubs of subgenus *Dasyphyllum* are distributed from the Andes eastwards into tropical Argentina, Brazil, and Paraguay. Section *Macrocephala* Cabrera of subgenus *Dasyphyllum* is adapted to the warmer and more humid conditions in the uplands of Eastern Brazil and Paraguay, whereas section *Microcephala* Cabrera occurs in a north-south arc following the Andes northward into Venezuela and Colombia and extending southward into central-eastern Brazil.

HISTORICAL OVERVIEW

Barnadesioideae were first introduced by David Don (1830), who described it as one of nine tribes in Compositae. Don's Barnadesieae merely included the two genera *Barnadesia* and *Chuquiraga*. Shortly thereafter, Lessing (1832) presented tribe Mutisiaceae subtribe Mutisieae, which comprised *Barnadesia*, *Chuquiraga*, *Dasyphyllum*, *Fulcaldea* and his new genus *Schlechtendalia* (as well as *Bacasia* Ruiz & Pav., *Diacantha* Less., and *Flotovia* Spreng., later regarded as generic synonyms). *Fulcaldea* had already been described by Poiret (1817). De Candolle (1838) followed with a subtribe Mutisieae and within that, as Division I, Barnadesieae. Weddell (1855) introduced a new genus, *Doniophyton*, based on *Chuquiraga anomala* D. Don. Bentham (1873) upgraded the complex to subtribal status as Barnadesiinae within tribe Mutisieae. Hoffmann (1893) then dissolved the barnadesioid complex again, but kept the genera within tribe Mutisieae, moving *Chuquiraga* and *Doniophyton* to subtribe Gochnatiinae and *Barnadesia* and *Schlechtendalia* to subtribe Mutisinae; *Dasyphyllum* was not mentioned. Cabrera (1961) followed Bentham (1873) in resurrecting the group once again as a distinct subtribe. He also added the new genera *Huarpea* and *Arnaldoa* in 1951 and 1962, respectively. This remained the perspective in subsequent Asteraceae volumes (Cabrera 1977) and into the early 1990s.

DNA restriction site and nucleotide sequence data have provided new phylogenetic perspectives and suggested a sister relationship between Barnadesiinae and the rest of the family (Jansen and Palmer 1987; Olmstead et al. 1992, 2000; Kim and Jansen 1995; Gustafsson et al. 1996; Lundberg and Bremer 2003). The barnadesioid group was consequently elevated to subfamilial status coordinate with the two other subfamilies Cichorioideae (Juss.) Chev. and Asteroideae (Cass.) Lindl. (Bremer and Jansen 1992). This perspective was maintained by Bremer (1994). More recently, in context of additional molecular data and supertree (= metatree) analyses, eleven monophyletic groups, set up as subfamilies, have been recognized (Panero and Funk 2002; Funk et al. 2005). The most recent phylogenetic analysis, based on ten chloroplast loci (Panero and Funk 2008), retains Barnadesioideae as the most ancient extant branching event within the family and at the subfamilial level.

DESCRIPTION OF SUBFAMILY

Trees, shrubs, subshrubs, perennial or annual herbs. Leaves alternate or fasciculate, simple, entire, mostly pinnatinerved, sometimes xeromorphic. Axillary spines frequently present. Synflorescences variable. Receptacle usually pilose. Involucre from cylindrical to widely campanulate; phyllaries in several series. Capitula homog-

Fig. 13.1. Habit of representative genera of Barnadesioideae. **A** *Arnaldoa weberbaueri* (Muschl.) Ferreyra; **B** *Barnadesia dombeyana* Less.; **C** *Chuquiraga jussieui* J.F. Gmel.; **D** *Dasyphyllum* sp.; **E** *Doniophyton weddellii* Katinas & Stuessy; **F** *Duseniella patagonica* (O. Hoffm.) K. Schum.; **G** *Fulcaldea laurifolia* Poir.; **H** *Schlechtendalia luzulaefolia* Less. [Photographs: A–C, E, G, H, T.F. Stuessy; D, J.W. Kadereit; F, J.M. Bonifacino.]

amous or heterogamous, isomorphic or anisomorphic, discoid or radiate or ligulate, sessile or pedunculate, usually hermaphroditic. Florets 1-numerous, white, yellow, orange, pink, purple to violet. Corollas tubular, split, doubly split, ligulate, subbilabiate (4 + 1), bilabiate (3 + 2), often villous. Stamens 5 (3–5 in the central flowers of some species of *Barnadesia*); filaments free or rarely fused (in *Barnadesia* only), inserted at base, throat, or between both regions; anthers ecaudate to tailed, with apical connective entire, emarginate or bifid. Style shortly bilobed or bifid. Achenes densely villous, with "barnadesioid trichomes." Pappus in a single whorl, simple, barbellate, plumose, scaly, or rarely absent (disc floret in *Huarpea andina*). Pollen with or without depressions, rarely lophate (*Barnadesia* and *Huarpea*); microechinate, scabrate-microechinate, microgranulate, spinulose, or smooth. $2n = 16$, 24, 48, 50, 54, 62, ca. 100, 108.

Barnadesioideae comprise nine South American genera: *Arnaldoa* (Fig. 13.1A), *Barnadesia* (Fig. 13.1B), *Chuquiraga* (Fig. 13.1C), *Dasyphyllum* (Fig. 13.1D), *Doniophyton* (Fig. 13.1E), *Duseniella* (Fig. 13.1F), *Fulcaldea* (Fig. 13.1G), *Huarpea*, and *Schlechtendalia* (Fig. 13.1H). See also Figs. 13.3–13.11.

Morphology and anatomy

Habit. — The majority of species of Barnadesioideae are woody plants but some are herbaceous. *Arnaldoa*, *Chuquiraga* and *Fulcaldea* are shrubs, *Barnadesia* and *Dasyphyllum* are usually arching shrubs (but the two species of subg. *Archidasyphyllum* are trees to 30 m tall), some species of

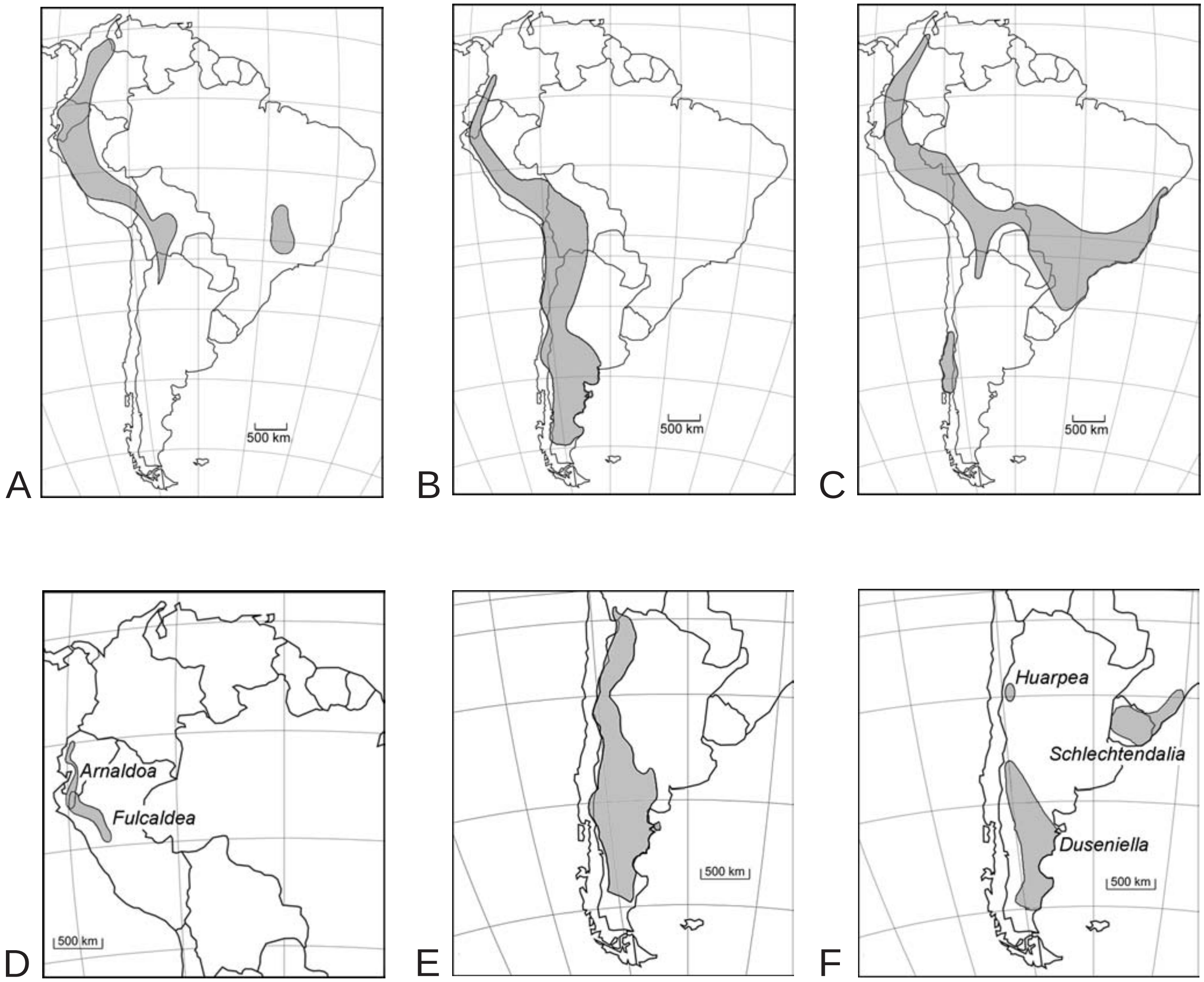
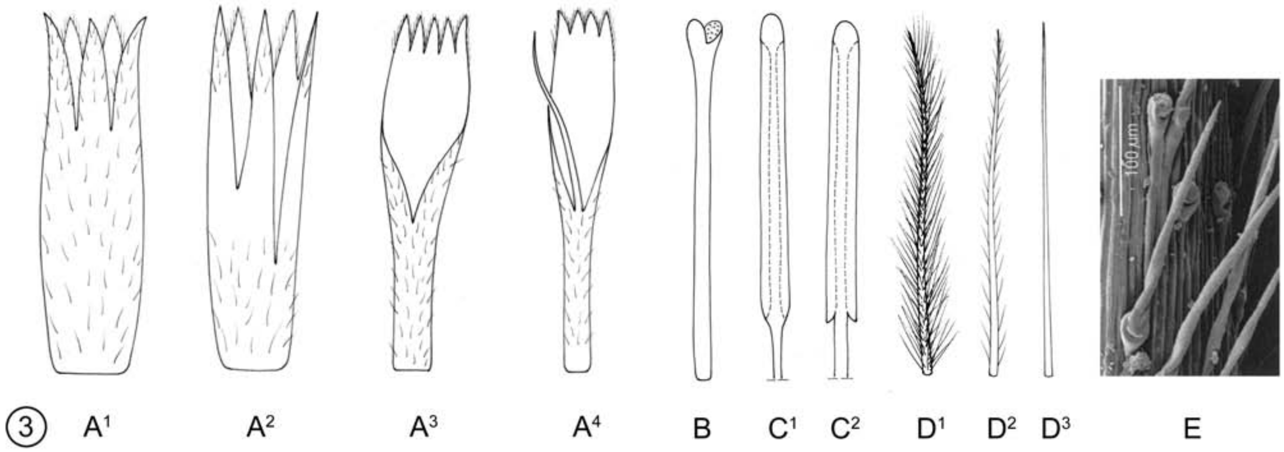


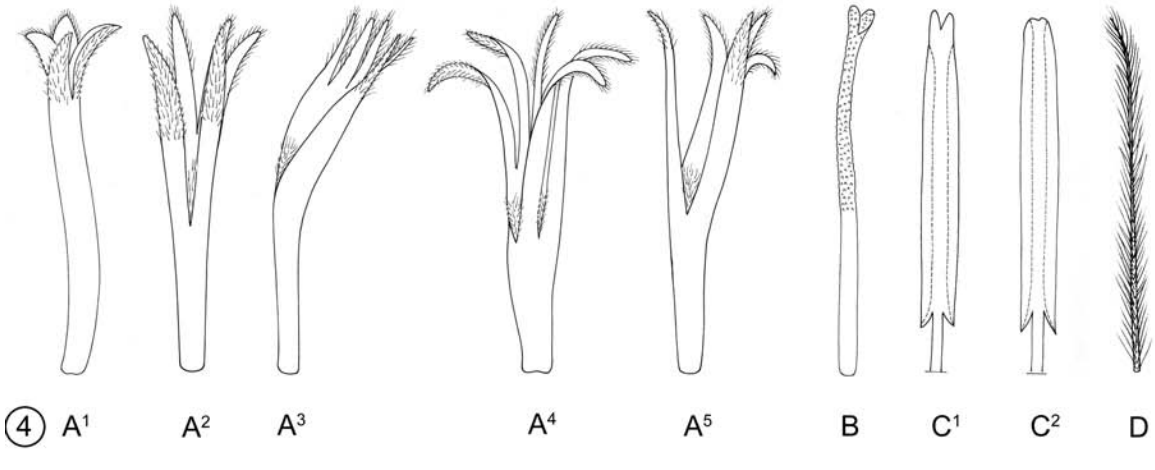
Fig. 13.2. Distributions in South America of **A** *Barnadesia* Mutis; **B** *Chuquiraga* Juss.; **C** *Dasyphyllum* Kunth; **D** *Arnaldoa* Cabrera and *Fulcaldea* Poir.; **E** *Doniophyton* Wedd.; and **F** *Duseniella* K. Schum., *Huarpea* Cabrera and *Schlechtendalia* Less.

Dasyphyllum are also vines, and *Huarpea* is a small subshrub no more than 6 cm tall. On the herbaceous side, *Doniophyton* and *Schlechtendalia* are perennials and *Duseniella* is an annual.

Leaves. — The leaves are arranged alternately or in fascicules. This character was used by Urtubey (1999) in *Barnadesia* to differentiate subgenus *Bacasia* (Ruiz & Pav.) Urtubey from subgenus *Barnadesia*. The petiole is absent in some species whereas in others the leaf is short-petiolate or petiolate. The blade is always entire, but the shape varies from linear to ovate, elliptic, oblong or slightly obovate. The apex is usually mucronate, but in many species of Barnadesioideae the blade extends into a spine. The leaves are commonly pinnatinerved, but in *Huarpea andina* and some species of *Chuquiraga* they are uninerved.

Many species of Barnadesioideae reflect morphological adaptations to dry environmental conditions. These are manifested, among other characters, by reduction of leaf surface, dorsivental or isolateral mesophyll, and amphistomatic or hipostomatic stomatal dispositions. In *Doniophyton* and *Huarpea* the margins of the leaves are involute, but in some species of *Chuquiraga* (e.g., *C. erinacea* D. Don) the leaf is linear, having resulted from maximum reduction and involution of the blade.

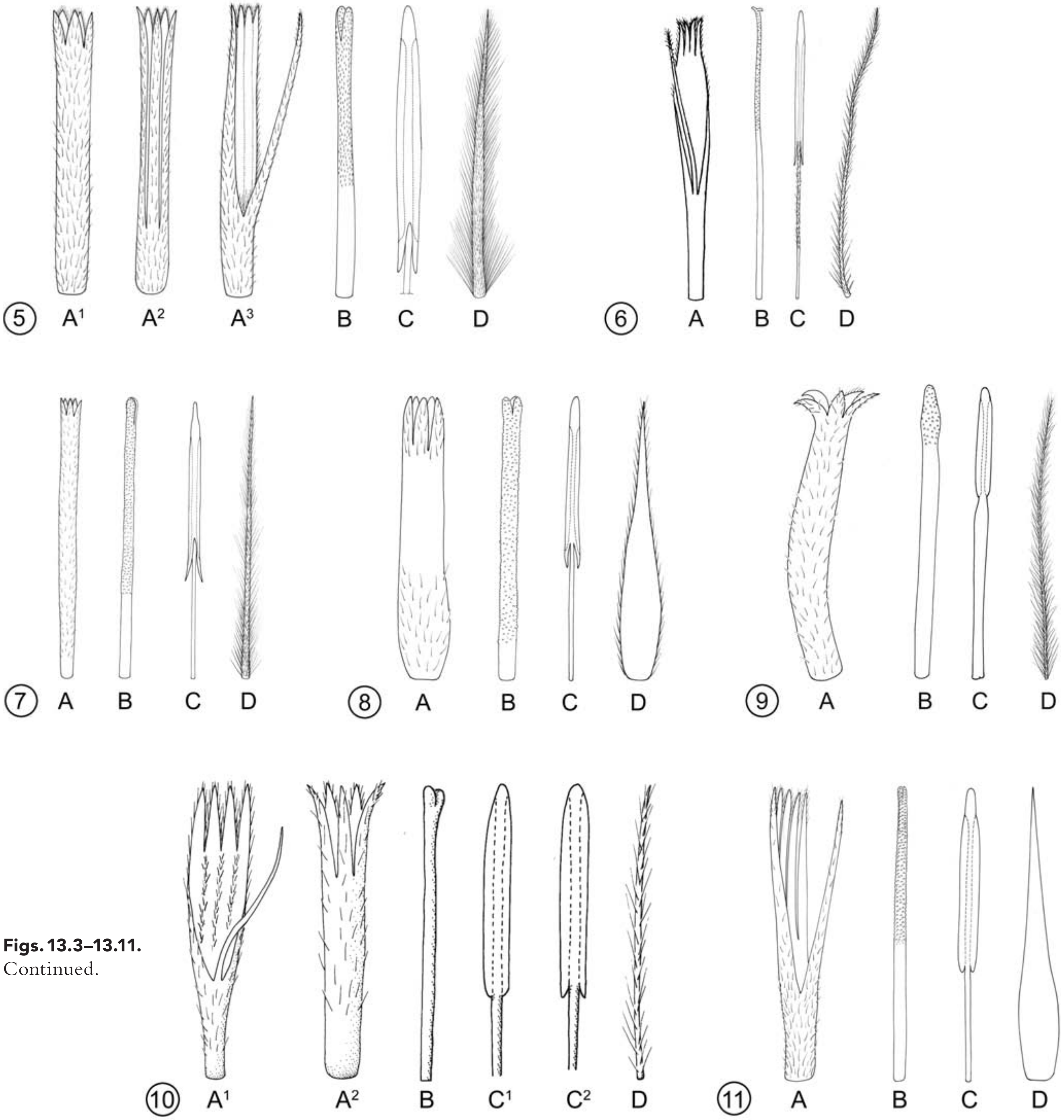




Figs. 13.3–13.11. Morphological features of genera of Barnadesioideae (**A** corollas; **B** styles; **C** anthers; **D** pappus scales, bristles or awns). **Fig. 13.3.** *Barnadesia* (A^1, corolla tubular; A^2, split; A^3, ligulate; A^4, subbilabiate. C^1, anthers adnate; C^2, shortly sagittate. D^1, pappus plumose; D^2, barbellate; D^3, setaceous. **E** "barnadesioid trichomes". *B. odorata* Griseb., A^3, A^4, B, C^2, D^3; *B. parviflora* Spruce ex Benth. & Hook. f., A^1, C^1, D^1; *B. pycnophylla* Muschl., A^2; *B. spinosa* L. f., D^2). **Fig. 13.4.** *Dasyphyllum* (A^1, corolla tubular; A^2, split; A^3, ligulate; A^4, doubly split; A^5, subbilabiate. C^1, anthers shortly sagittate and with bifid connective appendages; C^2, with emarginate connective appendages. *D. excelsum* (D. Don) Cabrera, C; *D. ferox* (Wedd.) Cabrera, A; *D. maria-lianae* Zardini & N. Soria, E; *D. tomentosum* (Spreng.) Cabrera, D; *D. velutinum* (Baker) Cabrera, B). **Fig. 13.5.** *Chuquiraga* (A^1, corolla tubular; A^2, doubly split; A^3, subbilabiate. *C. erinacea* D. Don, A^1; *C. jussieui* J.F. Gmel., A^3; *C. spinosa* D. Don, A^2; *C. straminea* Sandwith, B–D). **Fig. 13.6.** *Arnaldoa macbrideana* Ferreyra. **Fig. 13.7.** *Doniophyton anomalum* Kurtz. **Fig. 13.8.** *Duseniella patagonica* (O. Hoffm.) K. Schum. **Fig. 13.9.** *Fulcaldea laurifolia* Poir. **Fig. 13.10.** *Huarpea andina* Cabrera (A^1, corolla subbilabiate; A^2, tubular. C^1, stamen with adnate anthers, C^2, stamen with shortly sagittate anthers). **Fig. 13.11.** *Schlechtendalia luzulaefolia* Less.

Spines. — All species of *Barnadesia*, *Doniophyton*, *Fulcaldea*, and *Arnaldoa* and some of *Chuquiraga* and *Dasyphyllum* have straight or curved axillary spines. These spines are arranged at the nodes, in pairs (geminate spines) or in fascicles. These structures have vascular tissue and are considered as reduced leaves (Ezcurra 1985; Urtubey 1999).

Pubescence. — In all species of Barnadesioideae the indument is represented by "barnadesioid trichomes" (Cabrera 1959, 1977; Bremer 1987; Bremer and Jansen 1992) (Fig. 13.3E). These are 3-celled trichomes characterized by a long apical cell, an isodiametric basal cell, and an attached epidermal cell. These trichomes are present both on vegetative and reproductive structures. In *Fulcaldea*, malpighiaceous trichomes (those with apical cells with dorsal insertion) occur on the abaxial surface of the corollas. In some xeromorphic leaves of *Chuquiraga*,



Figs. 13.3–13.11. Continued.

there are biarmed trichomes that protect the opening of the stomates (Ezcurra 1985).

Involucre. — The most common shape of involucre is campanulate, but transitions occur to cylindric. The involucre can be sessile or pedunculate. The size of the involucre has been used by several authors to define infrageneric taxonomic units, e.g., Cabrera (1959) distinguished sections *Microcephala* and *Macrocephala* within *Dasyphyllum* subg. *Dasyphyllum*. Ezcurra (1985) in her revision of *Chuquiraga* differentiated series *Chuquiraga* and *Parviflorae* C. Ezcurra within section *Chuquiraga* in part by the size of heads. The involucres consist of phyllaries arranged in many rows, and they terminate in a mucro or spine. The phyllaries range from densely villous in some species to glabrous in others. In some species of *Chuquiraga* and *Barnadesia*, the phyllaries have an attractive color, although this is not typical for the subfamily.

Florets. — The number of florets varies from only one in *Fulcaldea*, to 5–50 in *Chuquiraga*, 6 (5 marginal florets, 1 disc floret) in *Huarpea*, 6 to 60 in *Dasyphyllum*, 9 or 16 (8 or 13 marginal, 1 or 3 disc) in *Barnadesia*, 9–41 (4–16 marginal, 5–25 disc) in *Duseniella*, 40–135 (10–40 marginal, 30–95 disc) in *Doniophyton*, 30–95 in *Arnaldoa*, and 50–100 in *Schlechtendalia*.

Corollas. — Stuessy and Urtubey (2006) published a detailed study on the morphology, vascularization, and evolution of corollas in Barnadesioideae. Six types of corollas were defined with the actinomorphic or tubular corolla with (3–4)–5 lobes judged ancestral for the subfamily (based on comparison with Calyceraceae R. Br. ex Rich.; DeVore 1994). The other types of corollas are somewhat to strongly zygomorphic: split corolla (with one deep longitudinal division), doubly split (with two deep longitudinal divisions), ligulate (flattened with one deep division), subbilabiate (flattened with two deep divisions, with four lobes on one side and one lobe on the other side), and bilabiate (with three deep longitudinal divisions producing an outer three-lobed lip and an inner divided two-lobed lip). All types of corollas are present in *Dasyphyllum* (Fig. 13.4A^1–A^5). In *Chuquiraga* the only type missing is the bilabiate corolla (Fig. 13.5A^1–A^3). In *Barnadesia* the bilabiate corolla (3 + 2) is rare and the doubly split condition is lacking (Fig. 13.3A^1–A^4). *Doniophyton*, *Duseniella* and *Fulcaldea* have tubular corollas (Figs. 13.7A, 13.8A, 13.9A), *Arnaldoa* and *Schlechtendalia* have subbilabiate corollas (Figs. 13.6A and 13.11A), and *Huarpea* (Fig. 13.10A) has subbilabiate (marginal flowers) and tubular corollas (central flower).

Variation in vascularization of corollas occurs in the number of bundles and their mode of terminating either free or fused in the apex of the lobes. Six types have been defined (Stuessy and Urtubey 2006): *(1)* five lateral and five central bundles, all united at the apex; *(2)* five lateral bundles fused at the apex; *(3)* five lateral bundles and five central bundles free at the apex; *(4)* five lateral bundles remaining free at the apex; *(5)* similar to type 3, but the lateral bundles are entirely separate; and *(6)* ten bundles free at the apex. The most common type of vascularization is type 4, which is present in almost 60 species of *Chuquiraga*, *Dasyphyllum*, *Doniophyton* and *Duseniella*. *Chuquiraga* and *Dasyphyllum* also contain type 6 and *Duseniella* also has type 3. *Arnaldoa* has types 5 and 6. Type 1 occurs in *Barnadesia* and *Fulcaldea* and type 2 in *Barnadesia* and *Huarpea*. The ancestral type has been hypothesized (Stuessy and Urtubey 2006), based on Calyceraceae (Gustafsson 1995), as being a tubular corolla with five lateral and five central bundles united at the apex.

The corollas are usually pubescent. "Barnadesioid trichomes" (Fig. 13.3E) are distributed on the outer (abaxial) side of the corolla toward the throat apex, on the lobes, or toward the base; on the inner (adaxial) surface the trichomes may cover the entire area or only the throat or only at the base.

Sexuality. — The flowers of Barnadesioideae are usually hermaphroditic. The androecium or gynoecium atrophies in the central flower of *Huarpea* and some species of *Barnadesia*. A tendency to dioecy via atrophy of the androecium exists in some species of *Dasyphyllum* (Cabrera 1959), resulting in some plants with female flowers and others with hermaphroditic flowers (gynodioecy). *Doniophyton* and *Duseniella* have female marginal flowers and hermaphroditic central flowers.

Stamens. — Stamens exhibit different features of filaments, connective appendages, and antheropodia (Pesacreta and Stuessy 1996; E. Svoma et al., unpub.). There are (3–4)–5–(6) stamens, with introrse anthers forming a tube and with the filaments usually free. In some species of *Barnadesia*, however, the filaments are fused into a tube. The apical connective appendage is entire, and rounded and/or acute in *Arnaldoa* (Fig. 13.6C), *Barnadesia* (Fig. 13.3C^1, C^2), *Chuquiraga* (Fig. 13.5C), *Duseniella* (Fig. 13.8C), *Fulcaldea* (Fig. 13.9C), *Huarpea* (Fig. 13.10C^1, C^2), and *Schlechtendalia* (Fig. 13.11C). It is acute to slightly apiculate in *Doniophyton* (Fig. 13.7C), bifid in *Dasyphyllum* subg. *Dasyphyllum* (Fig. 13.4C^1), and emarginate in subg. *Archidasyphyllum* (Fig. 13.4C^2). The base of the anthers is with obtuse basal appendages or slightly sagittate in *Barnadesia* (Fig. 13.3C), *Fulcaldea* (Fig. 13.9C), and *Huarpea* (Fig. 13.10C). In the remaining genera, basal appendages can be very short and/or long-sagittate, and with or without pollen sacs extending into them. The antheropodia can be shorter than, equal to, or longer than the basal appendages.

Styles. — Stigmatic branches are shortly bilobed, but in some species of *Dasyphyllum* the lobes can be deeper. In all species of Barnadesioideae, the style ornamentation is shortly papillose (Figs. 13.3B–13.11B).

Fruits. — The achenes vary from cylindric to broadly obovate. All species are villous except for *Dasyphyllum hystrix*, which has "barnadesioid trichomes" only at the apex.

Pappus. — The plumose pappus is the most common condition in the subfamily. This type is present in *Arnaldoa* (Fig. 13.6D), *Chuquiraga* (Fig. 13.5D), *Dasyphyllum* (Fig. 13.4D), *Doniophyton* (Fig. 13.7D), *Fulcaldea* (Fig. 13.9D), *Huarpea* (Fig. 13.10D), in *Barnadesia* subg. *Barnadesia* (Fig. 13.3D^1), and in the marginal flowers of *Barnadesia* subg. *Bacasia*. The monotypic genera *Duseniella* (Fig. 13.8D) and *Schlechtendalia* (Fig. 13.11D) have ciliate and glabrous pappus scales, respectively. The central flowers of *Barnadesia* have a plumose, barbellate or setaceous pappus (Fig. 13.3D^1–D^3). The central flower of *Huarpea* has a single villous bristle or is without a pappus.

Pollen

The pollen grains of Barnadesioideae, including comparisons with related families of Asterales, have been treated by several authors (Wodehouse 1928; Skvarla et al. 1977; Gamerro 1985; Hansen 1991a, 1992; Urtubey 1997; DeVore et al. 2000, 2007; Zhao et al. 2000; Polevova 2006). The most comprehensive studies have been done by Urtubey and Tellería (1998) who proposed three main types of pollen: *(1)* lophate (*Barnadesia* and *Huarpea*; Fig. 13.12B, K); *(2)* with depressions (in *Arnaldoa* four paraporal depressions per mesocolpus, Fig. 13.12A; *Schlechtendalia*, one equatorial depression per mesocolpus, Fig. 13.12L;

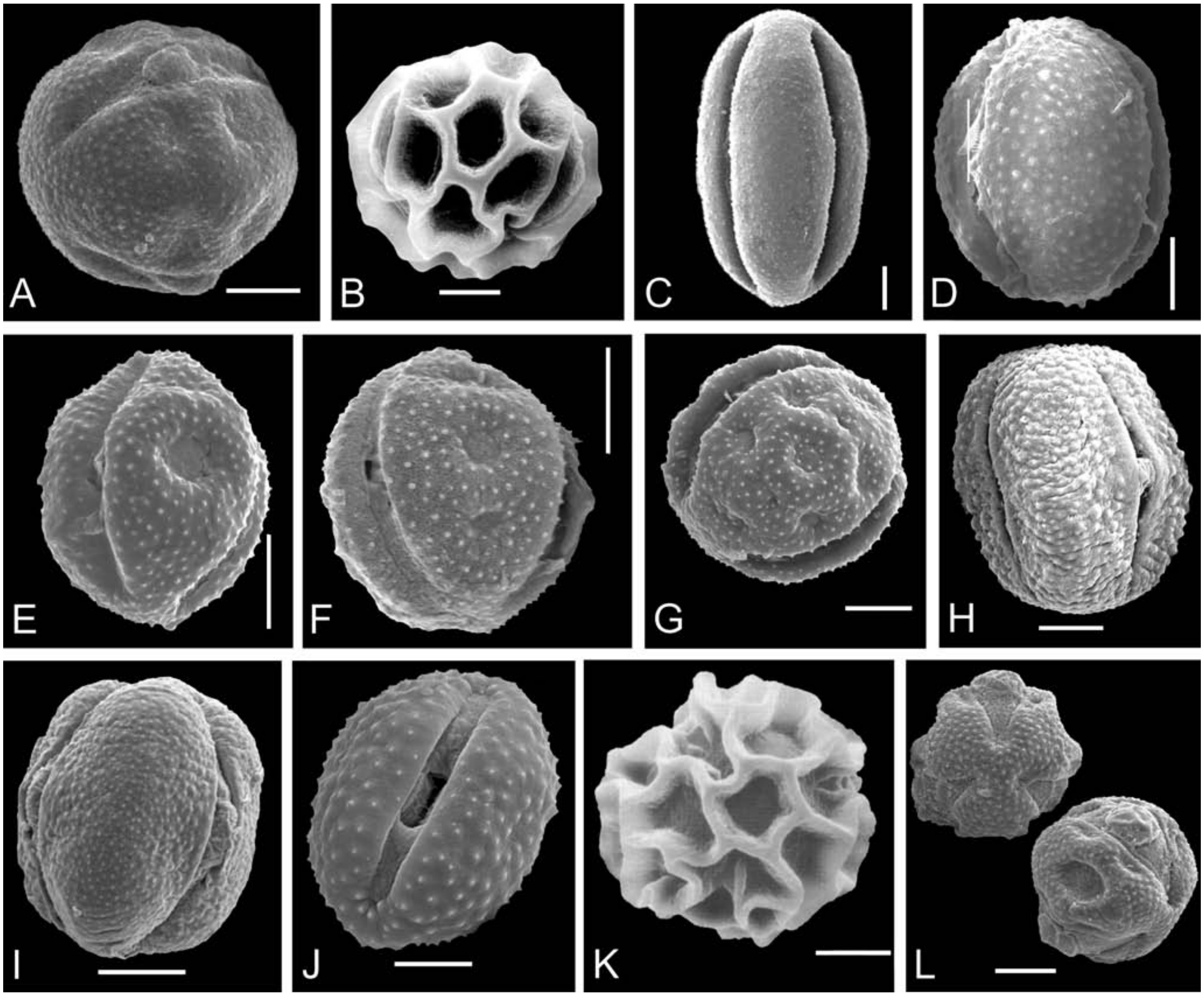


Fig. 13.12. Representative pollen grains in genera of Barnadesioideae. **A** *Arnaldoa macbrideana* Ferreyra; **B** *Barnadesia spinosa* L.f.; **C** *Chuquiraga straminea* Sandwith; **D–G** *Dasyphyllum*, showing different numbers of depressions per mesocolpus (**D** no depressions, *D. donianum* (Gardn.) Cabrera; **E** one depression, *D. floribundum* (Gardn.) Cabrera; **F** three depressions, *D. brasiliense* (Spreng.) Cabrera; **G** many depressions, *D. trichophyllum* (Baker) Cabrera; **H** *Doniophyton anomalum* (D. Don) Kurtz; **I** *Duseniella patagonica* (O. Hoffm.) K. Schum.; **J** *Fulcaldea laurifolia* Poir.; **K** *Huarpea andina* Cabrera; **L** *Schlechtendalia luzulaefolia* Less. Scale bars: 10 μm.

some species of *Dasyphyllum* with equatorial or equatorial and abporal depressions, varying one, two, three or more depressions per mesocolpus, Fig. 13.12E–G); and *(3)* without depressions (*Chuquiraga*, Fig. 13.12C; *Doniophyton*, Fig. 13.12H; *Duseniella*, Fig. 13.12I; *Fulcaldea*, Fig. 13.12J; some species of *Dasyphyllum*, Fig. 13.12D).

Detailed aspects of sculpturing and structure of the pollen grains also vary among genera of the subfamily (Fig. 13.12A–L). The sculpturing may be psilate (*Barnadesia* and *Huarpea*), microechinate (*Arnaldoa*, *Chuquiraga* and *Duseniella*), sparsely microechinate (*Dasyphyllum*), microgranulate and sparsely microechinate (*Schlechtendalia*), spinulose (*Fulcaldea*), and scabrate microechinate (*Doniophyton*). As for structure, the ektexine is always well developed, and it can be differentiated into two columellar-granulate layers in *Chuquiraga*, *Doniophyton* and *Duseniella*; the same structure occurs in three layers in *Schlechtendalia*. The pollen grains have a single columellar layer in *Arnaldoa*, *Dasyphyllum* and *Fulcaldea*, and it is spongy in *Barnadesia* and *Huarpea*. Cavea occur in *Arnaldoa*, *Barnadesia* and usually in *Dasyphyllum*. Palynologically, *Barnadesia* and *Huarpea* are very distinct with their smooth sculpturing and lophate pollen.

Chromosome numbers

Information on chromosome numbers is incomplete, but the available counts indicate that multiple polyploidization events have occurred during Barnadesioideae evolution. The following haploid numbers have been reported (reviewed in Stuessy et al. 1996): *Arnaldoa*, 24–27 [imprecise count]; *Barnadesia*, 12, 24, 25, 31, ca. 48, ca. 50; *Chuquiraga*, 27, 54; *Dasyphyllum*, $2n = 54$ (Watanabe et al. 2007); *Doniophyton*, 24, 25; *Schlechtendalia*, 8.

A base number of $x = 8$ or 9 for the subfamily, as suggested by most of these counts, would coincide with an hypothesized basal position of *Schlechtendalia*, being the only extant diploid or completely diploidized taxon. In this context, *Chuquiraga*, *Doniophyton* and *Dasyphyllum* might possess hexaploid genomes also derived from $x = 8$. *Barnadesia*, on the other hand, seems based on $x = 12$, but polyploidization in this genus has occurred as well. The only count reported for *Arnaldoa* ($n = 24–27$, *A. weberbaueri*; Stuessy and Sagastegui 1993) is sufficiently imprecise to preclude suggesting a base relationship, but its close relationship to *Dasyphyllum* would not reject an $x = 8$ hypothesis. To distinguish between auto- and allopolyploid origins of species and for a better understanding of chromosomal evolution in Barnadesioideae, more counts are needed.

Chemistry

Surveys of the occurrence of flavonoids in seven genera of Barnadesioideae (*Duseniella* and *Huarpea* lacking) have been completed by Bohm and Stuessy (1995, 2001) and Mendiondo et al. (1997, 2000). The flavonoid profiles of genera of the subtribe are quite simple, being dominated by the common flavonols kaempferol and quercetin. The pattern of glycosylation is also simple with 3-O-glucosides and 3-O-rutinosides dominating with traces of 3-O-glucuronide. The flavanone, eriodictyol glycoside, also occurs in three species of *Barnadesia* (*B. aculeata* [trace], *B. arborea*, and *B. parviflora* Spruce ex Benth. & Hook. f.). Flavonoids in the related Calyceraceae are somewhat more diverse, as reported by Bohm et al. (1995). Among the five genera analyzed (*Acicarpha* Juss., *Boöpis* Juss., *Calycera* Cav., *Gamocarpha* DC., *Nastanthus* Miers), derivatives of kaempferol and quercetin dominate. *Acicarpha* has the same flavonoid profile as in Barnadesioideae. Zdero et al. (1987) reported triterpenes in selected species of *Barnadesia*, *Chuquiraga*, *Dasyphyllum*, and *Schlechtendalia*. Despite the abundance of sesquiterpene lactones in the family (Yoshioka et al. 1973; Seaman 1982), no reports exist for Barnadesioideae. Sequiterpene lactones likewise have not been found so far in Calyceraceae (N.H. Fischer, pers. comm.).

PHYLOGENETIC RELATIONSHIPS

Phylogenetic relationships among genera of Barnadesioideae were initially investigated in several morphological studies. In an intuitive assessment of the subfamily's intergeneric relationships, Cabrera (1959) proposed *Dasyphyllum*, particularly subgenus *Archidasyphyllum*, as most ancient, and suggested four independent lineages (leading towards *Chuquiraga*, *Barnadesia*, *Fulcaldea* and *Schlechtendalia*). Comparison of palynological and floral characters also led him to conclude that *Doniophyton* descended from *Chuquiraga*, and *Huarpea* from *Barnadesia*. Hansen (1991b) performed the first explicit cladistic analysis utilizing eleven morphological characters, but obtained a largely unresolved consensus tree. A fully resolved cladogram of intergeneric relationships in Barnadesioideae was presented by Bremer (1994). He emphasized close relationships between *Doniophyton* and *Duseniella* and between *Barnadesia* and *Huarpea*, respectively. He also highlighted the isolated position of *Schlechtendalia luzulaefolia*. A more detailed morphological cladistic analysis of the subfamily as well as a hypothesis on its geographic evolution was produced by Stuessy et al. (1996). Their results corroborated close relationships between *Chuquiraga*, *Doniophyton* and *Duseniella*, between *Barnadesia*, *Huarpea* and *Fulcaldea* and basal positions for *Schlechtendalia* and *Dasyphyllum*. Results of their biogeographic analysis indicated a southern South American origin for the subfamily. The most comprehensive morphological cladistic analysis was performed by Urtubey and Stuessy (2001), who investigated 31 morphological characters in over half of all the subfamily's species.

Their results confirmed monophyly for some of the clades identified in previous studies (*Chuquiraga*-*Doniophyton*-*Duseniella*, *Barnadesia*-*Huarpea*) and reemphasized the basal position of *Schlechtendalia* in the subfamily. Contrary to previous studies, however, *Dasyphyllum* was inferred to be derived within Barnadesioideae.

The only previous molecular phylogenetic study of Barnadesioideae was completed by Gustafsson et al. (2001). DNA sequence variation of the *trnL* intron and nuclear ribosomal DNA confirmed the close relationships between *Chuquiraga* and *Doniophyton* and between *Barnadesia* and *Huarpea*. Furthermore, monophyly of all the subfamily's genera was validated—with the exception of *Dasyphyllum*, whose subgenera were separated into two unrelated clades in their analysis. Gustafsson et al. also found that, contrary to previous investigations, *Schlechtendalia luzulaefolia* was not the sister group to the rest of the subfamily.

A recent molecular phylogenetic investigation of the subfamily (Gruenstaeudl et al. 2009) employed an expanded character set as well as parsimony and model-based tree-inference methods. The character set comprised DNA sequence data of nine chloroplast markers (*atpI*-*atpH* IGS, *matK*, *psbA*-*trnH* IGS, *rbcL*, partial *rpoC1* gene + intron, *rps16*-*trnK* IGS, partial *trnK* intron, *trnL* intron, *trnL*-*trnF* IGS), the entire nuclear ribosomal ITS region (ITS1, 5.8S, ITS2), recoded DNA insertions/deletions, and selected morphological characters from previous investigations. A summary tree resulting from their combined analyses is given in Fig. 13.13.

Analyses of the new molecular data confirm most of the intergeneric relationships indicated by Gustafsson et al. (2001). Subfamily Barnadesioideae is found sister to all other Asteraceae and divided into two monophyletic groups: *Chuquiraga*, *Doniophyton* and *Duseniella* comprise one clade; *Arnaldoa*, *Barnadesia*, *Dasyphyllum*, *Fulcaldea*, *Huarpea* and possibly *Schlechtendalia* the other. The first clade has strong bootstrap and posterior probability support; monotypic *Duseniella* is at its base and *Doniophyton* sister to *Chuquiraga*. The second clade is subdivided further: *Barnadesia* and *Huarpea* form a fully supported monophyletic group, to which isolated *Schlechtendalia* is sister in model-based analyses. *Dasyphyllum*, together with *Arnaldoa* and *Fulcaldea*, comprises the other group, but it is itself paraphyletic without the latter two. *Arnaldoa* and *Fulcaldea* are sister to *Dasyphyllum* subg. *Archidasyphyllum*, all of which are located west of the Andes. Their clade has strong bootstrap and posterior probability support. Equally strongly supported is its sister clade of subgenus *Dasyphyllum*, which is distributed east of the Andes. These subgeneric separations in *Dasyphyllum* coincide with their geographic disjunctions on the western and eastern sides of the Andes. Generic status for each of the subgenera, therefore, appears to be recommended, but more species in the genus need to be sampled for molecular data before final taxonomic action is taken.

Monotypic *Schlechtendalia* constitutes the only genus for which phylogenetic placement remains unresolved. Nuclear data indicate a basal position within the subfamily, whereas chloroplast markers favor a sister relationship to *Barnadesia* and *Huarpea*. Gustafsson et al. (2001) recovered *Schlechtendalia* in yet other phylogenetic positions, namely as sister to *Chuquiraga* and *Doniophyton* in analysis of the *trnL* intron, and as sister to the *Arnaldoa*-*Fulcaldea*-*Archidasyphyllum* clade using ITS. Neither of these four placements was rejected through likelihood-based topology evaluations using Shimodira-Hasegawa and Approximately-Unbiased tests.

Cytologically, the most plausible phylogenetic position of *Schlechtendalia* is at the base of Barnadesioideae. *Schlechtendalia* has the only diploid chromosome complement ($2n = 16$) of any species of the subfamily so far examined (Ciadella and López de Kiesling 1981). This number is also found in Calyceraceae (DeVore 1994), the sister family of Asteraceae. Phylogenetic inference using model-based methods, which partially account for long-branch attraction, point to a derived position, however. Further analyses using comprehensive cytological data may indicate the true phylogenetic placement of this cryptic taxon.

BIOGEOGRAPHY

Barnadesioideae are endemic to South America (Fig. 13.2), mainly distributed in arid and desert regions along the Andean mountains from Venezuela to Chile, northwestern Argentina and Bolivia, and also in the Patagonian steppe. Another important concentration of Barnadesioideae is in Brazil. *Dasyphyllum*, with 40 species, has the broadest and most disjunct distribution; only two species (subg. *Archidasyphyllum*) are restricted to the *Nothofagus* forests of central Chile and the neighboring central-western part of Argentina. The remaining 38 species in subgenus *Dasyphyllum* inhabit the Andean mountains from Venezuela to northwestern Argentina, occupying arid regions such as the Puna but also extending to the humid Yungas and into Brazil. Brazil has the greatest number of species of *Dasyphyllum* (ca. 20) distributed in the *Araucaria* forests and the cerrado. *Chuquiraga* grows in xeric soils of the higher Andean mountains, from Colombia to Bolivia and Central Chile and also in the Patagonian steppe. The greatest number of species of *Chuquiraga* (ca. 15) is in Argentina. *Barnadesia* comprises 18 species restricted to the Andean mountains (mostly in xeric soils but also in the humid Yungas forests) with only one species reaching Brazil (*Barnadesia spinosa* L.f). The highest specific concentration of this genus is in

Peru with approximately 14 species. *Doniophyton* occurs in the Patagonian steppe plus Puna and Monte, whereas *Duseniella* is found centered in Argentinean Patagonia. The former grows in the western part (in the Monte and Puna) whereas the latter occurs eastward. The monotypic genera *Fulcaldea*, *Huarpea*, and *Schlechtendalia* have the most restricted distributions. *Fulcaldea* and *Arnaldoa* grow in Ecuador and northern Peru, and *Huarpea* inhabits the Alto Andina (High Andean) province in San Juan (Argentina). The only genus absent from the arid part of

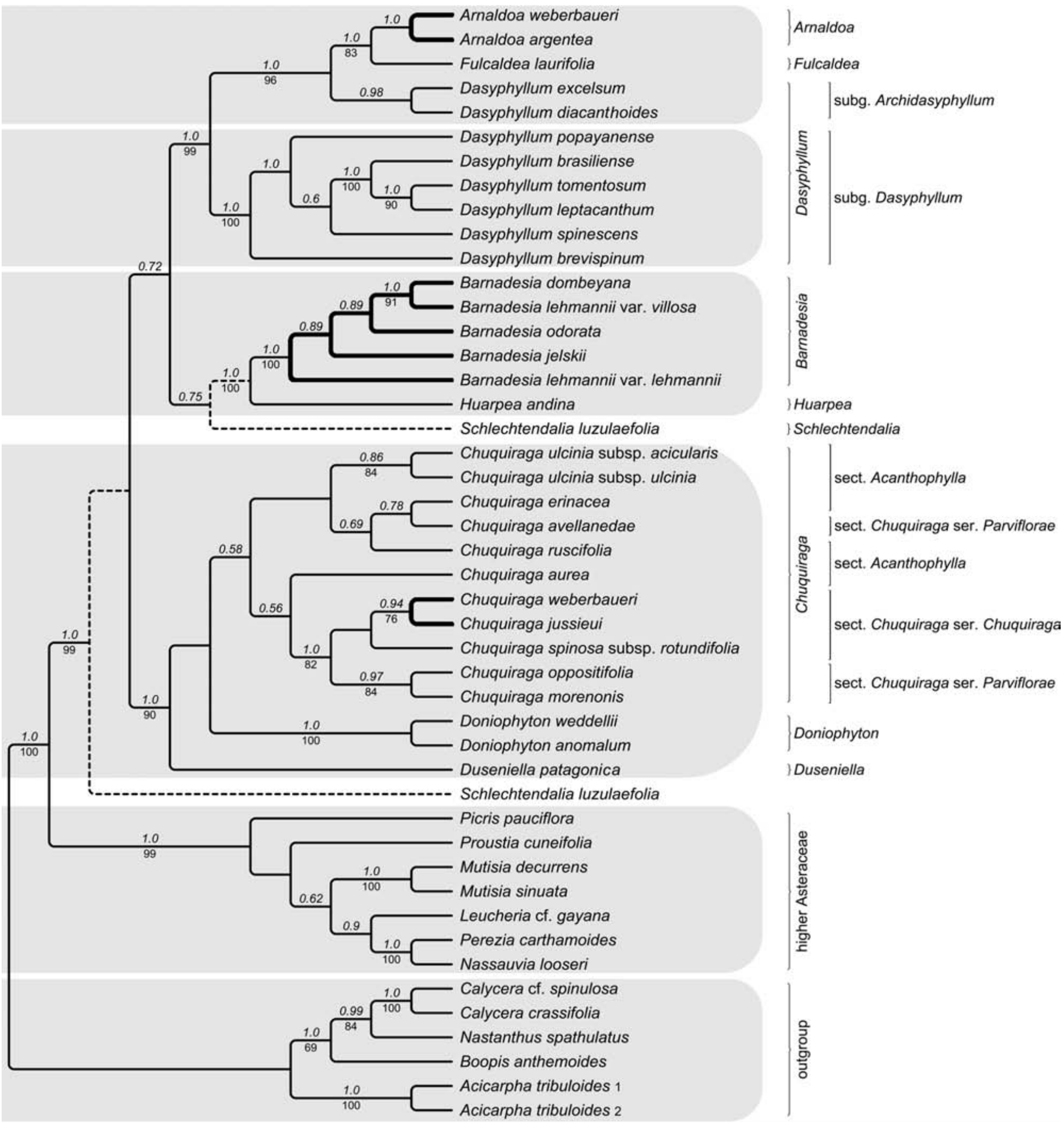


Fig. 13.13. A summary tree presenting phylogenetic relationships in Barnadesioideae based on combined analyses of chloroplast and nuclear DNA sequence variation, recoded insertions/deletions of those markers, and selected morphological characters. Bold tree branches indicate clades with known or suspected hummingbird pollination within the subfamily; dashed lines indicate alternative branch placements; numbers above lines are posterior probabilities and those below are bootstrap percentages. [Modified from Gruenstaeudl et al. (2009).]

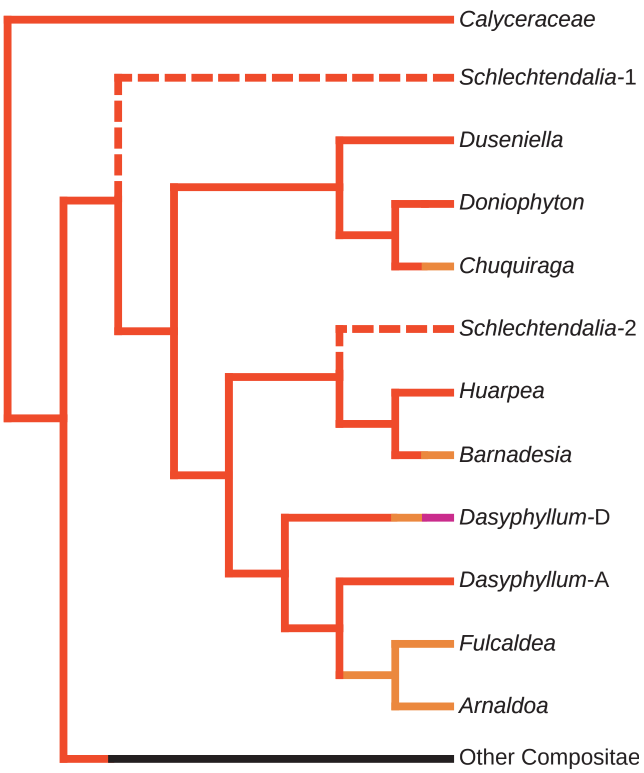


Fig. 13.14. Distribution patterns within Barnadesioideae displayed on a simplified summary tree based on total evidence analyses. Red = southern South America; orange = central and northern Andes; purple = Brazil.

the continent is *Schlechtendalia*, which is centered in the steppe of Uruguay with extensions into southern Brazil (SE Rio Grande du Sul) and adjacent Argentina (E Entre Rios).

Several geographic origins for Compositae have been proposed (reviewed in DeVore and Stuessy 1995), but the South American hypothesis has received most support. From this origin, Asteraceae have undergone extensive diversification by colonization of diverse habitats around the globe during no more than 40 Myr (DeVore and Stuessy 1995; Bremer and Gustafsson 1997; Kim et al. 2005; Panero and Funk 2008). Stuessy et al. (1996) hypothesized that the ancestor of today's Asteraceae and Calyceraceae separated in southern South America during the early Oligocene. Reasons for this are unknown, but the global climate became distinctly cooler at approximately 33.5 million years ago (the Eocene-Oligocene transition; Dupont-Nivet et al. 2007; Zanazzi et al. 2007). At the very minimum, recent analyses of fossil pollen in Patagonia document presence of Barnadesioideae at 23 Ma (Katinas et al. 2007; Palazzesi et al. 2009). During the Miocene, prototypic taxa of extant Barnadesioideae differentiated, and as late as the Pliocene with the final uplift of the Andes, the modern genera emerged. In this context, *Barnadesia* may have evolved into the montane forests on the eastern slopes of the central Andes, whereas *Dasyphyllum* developed further south and subsequently spread north into temperate-subtropical zones. *Chuquiraga* may have appeared in the northern Chilean deserts. A dispersal-vicariance (Ronquist 1996, 1997) analysis (Gruenstaeudl et al., 2009) agrees with the proposed hypothesis for *Barnadesia* and indicates an ancestral distribution area at high elevation (over 2000 m) along the central Andes. The same area is also identified as the most parsimonious origin for the clade *Arnaldoa-Fulcaldea-Dasyphyllum*. This implies that species of subgenus *Dasyphyllum* moved into lower elevations and more humid conditions during their evolution, whereas subgenus *Archidasyphyllum* was displaced southwards into the Chilean *Nothofagus* forests. Further, the extremely dry Monte region is proposed as the geographic origin of *Chuquiraga*. *Doniophyton* and *Duseniella*, phylogenetically closely allied to *Chuquiraga*, share the same distributional area. Several morphological character traits in Barnadesioideae correlate with this proposed distributional history in dry mountainous habitats. Xeromorphic leaf morphology, such as leaf-area reduction, involute leaf margins and stomata in pits, are likely adaptations to the high elevation habitats. The emergence of acicular, prickly leaves and axillary spines, as seen best in *Chuquiraga*, were likely triggered by mammalian grazers living in arid mountainous regions (Ezcurra 2002). Further, adaptation to alpine pollinators affected capitulum morphology. A pollinator-shift from insects to high elevation hummingbirds might have caused the emergence of large and conspicuous heads in several genera (*Arnaldoa*, *Barnadesia*, *Chuquiraga*).

EVOLUTION

Chromosome evolution

Barnadesioideae are also of interest with respect to chromosome evolution. The most common haploid chromosome number in Asteraceae is $n = 9$, and this has been cited as the plesiomorphic chromosome number for the family as a whole (Solbrig 1977; Jeffrey 2007; see also Chapter 4). This specific number has not been reported in Barnadesioideae, however. Although only a sparse chromosome number record for the subfamily exists (summarized by Stuessy et al. 1996), $n = 8$ in *Schlechtendalia luzulaefolia* (Ciadella and López de Kiesling 1981) is the lowest number recorded and seems basic for the subfamily. Likewise, a haploid chromosome number of $n = 8$ is found in Calyceraceae (DeVore 1994). This, and the basal position of *Schlechtendalia luzulaefolia* in analyses of morphological and combined molecular sequences, suggests that a base chromosome number of $x = 8$ might be plesiomorphic for Compositae, followed by multiple polyploidization events during evolution of

Barnadesioideae (n = 12, 24, 25, 31, ca. 48 and ca. 50 in *Barnadesia*, n = 27 and 54 in *Chuquiraga*; reviewed in Stuessy et al. 1996). Refer to Chapter 4 for further discussions on the base number of the entire family.

Pollination

Two pollination vectors are present in Barnadesioideae: hummingbirds and insects. Insect pollination is ancestral in Barnadesioideae and also found in Calyceraceae (DeVore 1994). Species of *Barnadesia*, however, have been reported on several occasions to be pollinated by hummingbirds (Delpino 1890; Goebel 1932; Urtubey 1999, and references therein). In *Chuquiraga*, the northern and central Andean lineage sect. *Chuquiraga* ser. *Chuquiraga* was found to be visited by hummingbirds (Ezcurra 2002). Based on its large red and orange heads, hummingbird pollination has also been postulated in *Arnaldoa* (Erbar and Leins 2000). These genera do not share a common ancestor other than at the origin of the subfamily (Gruenstaeudl et al. 2009). Thus, the new analyses contradict any suggestion that bird pollination might be plesiomorphic in Asteraceae and show that within Barnadesioideae at least three independent pollinator shifts from insects to hummingsbirds have occurred (Gruenstaeudl et al. 2009; clades with hummingbird pollination highlighted in Fig. 13.13).

ECONOMIC USES

Members of Barnadesioideae have little direct economic value. What little has been recorded comes from anecdotal information on herbarium labels of *Barnadesia* and *Chuquiraga*. The former is used in popular medicine for child spasms (*B. odorata* Grieseb.), for firewood (*B. odorata*), and as a hedge (*B. dombeyana* Less.). In *Chuquiraga*, *C. jussieui* J.F. Gmel. and *C. avellanedae* Lorentz have been used for different medicinal purposes, such as a tonic, and against fever, malaria, and sore throat. *Chuquiraga spinosa* D. Don subsp. *huamanpinta* C. Ezcurra has been used as a dye (yellow coloring), and *C. atacamensis* Kuntze has been employed also for making incense. Species of sect. *Chuquiraga* ser. *Chuquiraga* have also been reported as serving as ornamentals, with *C. calchaquina* Cabrera being used in flower arrangements.

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Chapter 14

Mutisieae sensu stricto (Mutisioideae sensu stricto)

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INTRODUCTION

Mutisieae include the beautiful mutisias and gerberas. A few taxa are widely distributed but the majority occur in South America. The members of Mutisieae are particularly interesting because of their basal placement in the family along with the subfamily Barnadesioideae. One of the major challenges that synantherologists have faced has been finding an accurate classification of Mutisieae since, despite the use of several types of data such as morphology, palynology, and different molecular markers, there is not a general agreement on where all of the genera should be placed.

From the establishment by Cassini in 1817 until recently, the broadest concept of the tribe (Mutisieae s.l.) has been the prevailing one, with little fluctuation in the number of genera and species according to the different authors. However, the wide morphological diversity that the genera of Mutisieae display has always made it difficult to circumscribe the tribe. With the advance of the molecular techniques some changes were made, starting with the exclusion of one of its subtribes, the Barnadesiinae (Bremer and Jansen 1992). Further molecular analyses (Kim et al. 2002; Panero and Funk 2002) suggested a non-monophyletic tribe and the need of narrowing the concept of the Mutisieae through the exclusion of many of its genera. The molecular phylogenetic study of Funk et al. (2005) examined the distribution and evolution of the family and established several independent clades for traditional Mutisieae. These studies were complemented by Panero and Funk (2007, 2008) (see Chapter 44 for a phylogeny of the group). However, it is still very difficult to find morphological characters that could be called synapomorphies for some of these clades.

There are currently two main taxonomic concepts of Mutisieae that are in use. One is the concept of the tribe Mutisieae sensu lato (which will be called hereafter Mutisieae s.l.), based mainly on morphological grounds. This is the concept employed, for example, by Cabrera (1977), Bremer (1994), Jeffrey (2007, as subfamily Mutisioideae), Hind (2007), and Katinas et al. (2008, as subfamily Mutisioideae) with some variation in the included genera in each circumscription. These authors recognized various groups, some of which were proposed at various times as distinctive "generic groups", associations, tribes, or subfamilies based on morphological and/or molecular data.

The other concept, based on phylogenies obtained with chloroplast molecular data (e.g., Panero and Funk 2002, 2007, 2008 as subfamily Mutisioideae; Funk et al. 2005), is that of the tribe Mutisieae sensu stricto (which will be called hereafter Mutisieae s.str. or the Mutisieae clade; see Table 12.1 in Chapter 12). In this paper Mutisieae s.str. contain three main clades: the *Onoseris* clade, the *Mutisia* clade, and the *Nassauvia* clade. Elsewhere in this volume these three clades are referred to as the subfamily Mutisioideae which contains the same three clades as tribes: Onoserideae, Mutisieae, and Nassauvieae (see Chapters 11 and 12 for further discussion).

At this time a brief historical review of the tribe Mutisieae s.l. is warranted in order to provide a context for the analysis of the systematics, morphology, floral biology and evolution of Mutisieae s.str. Since the name "subfamily Mutisioideae" is employed by several authors in different senses, we will restrict the use of this term only when necessary. The genera included in Mutisieae s.str. are listed in Table 14.1 of this chapter.

HISTORICAL OVERVIEW

Cassini (1817, 1819) proposed the tribe Mutisieae to include the genera with bilabiate corollas considered by Lagasca (1811) in his Chaenanthophorae, and by De Candolle (1812) in his Labiatiflorae. Cassini (1819) emphasized the style characteristics over the corolla morphology and established two related tribes: Mutisieae and Nassauvieae. The tribe Mutisieae included genera with short style branches externally covered by short hairs. Nassauvieae included genera with long, truncate style branches, with a crown of collecting hairs at the apex (Cassini 1819).

After Cassini, Lessing (1832) also emphasized style features and divided Mutisieae into three subtribes (Mutisiinae, Leriinae, Facelidinae), and Nassauvieae into two subtribes (Nassauviinae, Trixidinae).

Bentham (1873) divided the tribe Mutisieae into the five subtribes Barnadesiinae, Onoseridinae, Gochnatiinae, Gerberinae, and Nassauviinae that were reduced to three by Hoffmann in 1893 (Gochnatiinae, Mutisiinae [Gerberinae in the key] and Nassauviinae) using a wider spectrum of morphological characters than did previous authors. He emphasized types of capitula in his classification and included genera in Mutisieae with types of corolla other than bilabiate, such as ligulate and tubular.

Jeffrey (1967) revised African Mutisieae and established twelve informal series for the whole tribe mainly based on style morphology. Some of Jeffrey's series, such as the *Dicoma* Cass., *Pertya* Sch.Bip., and *Pleiotaxis* Steetz series, were the basis, with much rearrangement, of some generic groups that would be recognized by further authors (e.g., Hansen 1991; Bremer 1994).

Crisci (1974a, 1980) treated the subtribe Nassauviinae, completing morphological and palynological studies, and established its monophyly and the relationships among its genera.

Cabrera's paper on Mutisieae (1977) can be viewed as the first, modern, systematic review of the whole tribe Mutisieae. Mutisieae were defined by Cabrera as having bilabiate corollas, caudate anthers, and characteristic style shape. Cabrera divided Mutisieae into four subtribes on the basis of corolla and style features: Barnadesiinae, Gochnatiinae, Mutisiinae, and Nassauviinae, the last considered by Cabrera the most natural subtribe, morphologically homogeneous, and geographically well-defined. He pointed out, however, that several genera of Mutisieae differ by their actinomorphic or ligulate corollas, and ecaudate anthers (the last feature in some genera of Barnadesiinae). Cabrera concluded that certain genera should be excluded from the tribe or transferred to other subtribes or that perhaps genera of other tribes should be included in Mutisieae. As circumscribed by Cabrera (1977), Mutisieae included 83 genera and about 950 species mainly from America with some representatives in southern Asia and Africa, and one species in Australia.

When Jansen and Palmer (1987) found that a large chloroplast DNA inversion present in Compositae was absent in all three sampled genera of Barnadesiinae and in related families, this subtribe was removed from Mutisieae and established as the subfamily Barnadesioideae (Bremer and Jansen 1992), the sister group of the rest of the family. Also in 1987, Bremer presented the first cladistic analysis of Compositae involving 81 characters of morphology, anatomy, chromosomes, chemistry, and the chloroplast DNA inversion. This cladogram showed Barnadesioideae as basal, followed by a non-monophyletic Mutisieae.

Hansen (1991) considered Mutisieae to be monophyletic on the basis of a petal epidermal pattern he called "mutisioid" (tabular cells with crested outer cell walls), if Barnadesiinae and several Old World genera of Gochnatiinae (sensu Cabrera 1977) were excluded from the tribe. Hansen proposed to exclude from Mutisieae the genera *Dicoma*, *Erythrocephalum* Benth., *Gladiopappus* Humbert, *Pasaccardoa* Kuntze, and *Pleiotaxis* (and their current synonyms), later called the *Dicoma* group by Bremer (1994). Hansen also suggested that the genera *Adenocaulon* Hook., *Brachylaena* R. Br., *Tarchonanthus*, and *Warionia* Benth. & Coss. should be excluded from Mutisieae. The "mutisioid" ray corolla epidermal cells are now known to occur in Barnadesioideae and in some Arctoteae (Bremer 1994).

Karis et al. (1992) performed a morphology-based cladistic analysis of the Compositae family with an emphasis on the subfamily Cichorioideae using 53 taxa and 72 characters; Barnadesioideae served as the outgroup. Their tree supported the placement of a non-monophyletic tribe Mutisieae as a basal assemblage to the rest of Compositae. The genera of Mutisieae, *Ainsliaea* DC., *Gochnatia* Kunth, *Hesperomannia* A. Gray, *Stenopadus* S.F. Blake, and *Wunderlichia* Riedel ex Benth. & Hook.f. appeared as isolated clades at the base of one of the two equally parsimonious final trees; *Actinoseris* (Endl.) Cabrera, *Brachylaena*, and *Cnicothamnus* Griseb. were sister to most Mutisieae; *Gongylolepis* Schomb., *Hyaloseris* Griseb., *Pertya*, and *Stifftia* J.C. Mikan were basal to the rest of Cichorioideae and Asteroideae.

In Bremer's (1994) treatment of the family Compositae, Mutisieae included 76 genera and ca. 970 species. In this publication Bremer formally abolished the limits between Mutisiinae and Gochnatiinae. Thus, Mutisieae included only two subtribes: Mutisiinae s.l. (Mutisiinae s.str. plus Gochnatiinae) and Nassauviinae. The artificial taxonomic separation of Mutisiinae and Gochnatiinae was also confirmed by palynological evidence (Tellería et al. 2003). Within Mutisiinae, Bremer presented a tentative arrangement of generic groups, some of them already suggested by previous authors: the *Stenopadus* group (*Achnopogon*, Maguire, Steyerm. & Wurdack *Chimantaea* Maguire, Steyerm. & Wurdack, *Duidaea* S.F. Blake, *Glossarion* Maguire & Wurdack, *Gongylolepis*, *Neblinaea* Maguire & Wurdack, *Stenopadus*, *Stomatochaeta* (S.F. Blake) Maguire & Wurdack); *Gochnatia* and related genera (*Actinoseris*, *Chucoa* Cabrera, *Cyclolepis* Gillies ex D. Don, *Gochnatia*, *Hyalis* D. Don ex Hook. & Arn., *Nouelia* Franch.); the *Ainsliaea* group (*Ainsliaea*, *Macroclinidium* Maxim., *Myripnois*, *Pertya*); *Brachylaena* and *Tarchonanthus* L.; the *Plazia* group (*Aphyllocladus* Wedd., *Gypothamnium* Phil., *Plazia* Ruiz & Pav.); the *Dicoma* group (*Achyrothalamus* O. Hoffm., *Dicoma*, *Erythrocephalum*, *Gladiopappus*, *Pasaccardoa*, *Pleiotaxis*); *Onoseris* DC. and *Urmenetea* Phil.; *Mutisia* L.f. and *Hyaloseris*; the *Chaetanthera* Ruiz & Pav. group (*Brachyclados* D. Don, *Chaetanthera*, *Pachylaena* Don ex Hook. & Arn.); the *Gerbera* group (*Chaptalia* Vent., *Gerbera* L., *Leibnitzia* Cass., *Perdicium* L., *Trichocline* Cass., *Uechtritzia* Freyn). The genera *Catamixis* Thomson, *Cnicothamnus*, *Hecastocleis*, *Hesperomannia*, *Lulia* Zardini, *Lycoseris* Cass., *Oldenburgia*, *Stifftia*, and *Wunderlichia* were regarded as isolated within the tribe Mutisieae. Again, the monophyly of Nassauviinae and the non-monophyly of Mutisiinae s.l. were recognized. Bremer (1996) later modified the traditional scheme of the subfamily Cichorioideae, establishing the subfamily Carduoideae with the tribe Cardueae. Although implicit in the cladogram, Mutisieae were not raised to subfamilial level: it remained as an unresolved grade awaiting their reclassification, at the base of the family tree above Barnadesioideae.

Molecular phylogenetic studies (Kim et al. 2002; Panero and Funk 2002, 2008) investigated the circumscription of Mutisieae. Kim et al. (2002) used DNA sequences of the chloroplast gene *ndhF* from 31 genera and obtained a strict consensus tree showing that Mutisieae were non-monophyletic and that the genera *Tarchonanthus*, *Brachylaena*, *Dicoma*, *Pasaccardoa*, *Ainsliaea*, *Pertya* and *Myripnois* are related to Cardueae. Results of Panero and Funk (2002) using eight chloroplast genes and molecular markers supported the establishment of three new subfamilies: Gochnatioideae (*Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Richterago*, possibly *Chucoa*), Hecastocleidoideae (*Hecastocleis*), Pertyoideae (*Ainsliaea*, *Diaspananthus* [=*Ainsliaea*; Freire 2007], *Macroclinidium*, *Myripnois*, *Pertya*). The tribes Dicomeae (*Dicoma*, *Erythrocephalum*, *Gladiopappus*, *Macledium*, *Cloiselia*, *Pasaccardoa*, *Pleiotaxis*), Tarchonantheae (*Brachylaena*, *Tarchonanthus*), and the genus *Oldenburgia* were included in Carduoideae. Remaining Mutisieae were recognized as the *Stifftia* group, and a basal, unresolved clade referred to as Mutisioideae. Further, more defined molecular phylogenies of the family Compositae (Funk et al. 2005; Panero and Funk 2008) showed approximately the same branching sequence of Panero and Funk's (2002), with a Mutisieae clade containing three clades: the *Onoseris* clade, the *Mutisia* clade, and the *Nassauvia* clade. Based on these results, Panero and Funk (2007) established the following new taxa: the subfamily Stifftioideae, the subfamily Wunderlichioideae with the tribe Hyalideae (see Chapter 15), and the tribe Onoserideae of Mutisioideae with the genera *Aphyllocladus*, *Gypothamnium*, *Lycoseris*, *Plazia*, *Onoseris*, and *Urmenetea*.

The systematic treatment by Hind (2007) recognized a tribe Mutisieae s.l., and although he did not recognize the tribal and subfamily classification of Panero and Funk (2002), he did use most of the clades at different levels, some formal and others just informal groups. Hind divided the tribe Mutisieae into five subtribes (Nassauviinae, Mutisiinae, Gerberinae, Gochnatiinae, and Tarchonanthinae) and seven groups (*Catamixis*, *Dicoma*, *Hecastocleis*, *Nouelia*, *Pertya*, *Stenopadus*, and *Stifftia* groups) and recognized two genera, *Adenocaulon* and *Eriachaenium* as having a problematic placement.

Katinas et al. (2008) performed a morphological analysis of Mutisieae s.l., analyzing all the genera included in the tribe by Cabrera (1977) and Bremer (1994). They circumscribed the subfamily Mutisioideae with 74 genera arranged in three tribes: *(1)* Mutisieae, including those genera with smooth styles, or with dorsally papillose styles with the papillae distributed above the branch bifurcation point, sometimes extending somewhat below the bifurcation (43 genera, ca. 500 species); *(2)* Stifftieae, including those genera with rugulose or papillose styles above and below the branch bifurcation point, almost reaching the style base (6 genera, 48 species); and *(3)* Nassauvieae, including the genera with the papillae gathered in a tuft at the apex of the style branches (25 genera, ca. 315 species). Their circumscription agreed with previous authors in the exclusion of the following genera from Mutisioideae: *Brachylaena* and *Tarchonanthus* (Chapter 18), *Cloiselia*, *Dicoma*, *Erythrocephalum*, *Gladiopappus*, *Macledium*, *Pasaccardoa*, *Pleiotaxis* (Chapter 17), *Hesperomannia* (Chapter 28), *Moquinia* (Chapter 30), and *Warionia* (Chapter 24). This circumscription, on the other hand, disagreed with the exclusion of Stifftioideae (Chapter 12), Wunderlichioideae (Chapter 12), Hyalideae and Gochnatieae (Chapter 15), Hecastocleidoideae (Chapter 16), *Oldenburgia* (Chapter 19), and Pertyoideae (Chapter 21). Katinas et al. (2008) concluded that the styles smooth, rugulose and papillose with relatively short and rounded papillae

Table 14.1. Genera of Mutisieae s.str. sorted into the three main clades obtained by Funk et al. (2005), with the number of species, main literature, geographic distribution, main morphological features (Katinas et al. 2008), and chromosome number (K. Watanabe, Kobe University, site: http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html).

Taxa	Species number	Literature	Distribution	Main morphological features	Chromosome numbers
***Mutisia* clade**					
Adenocaulon Hook.	5	Bittmann (1990a, b)	Argentina, Chile, Guatemala, Mexico, N USA, S Canada, Asia	Perennial, scapiform herbs, glandular, anthers basally auriculate, style branches papillose, pappus absent	$n = 23, 46$; $2n = 20, 38, 42, 46, 48$
Brachyclados D. Don	3	Cabrera (1971)	C Chile, Patagonia, W Argentina	Shrubs with brachyblasts and macroblasts, corollas bilabiate, style branches papillose	$n = 23, 23+1B$; $2n = 46$
Chaetanthera Ruiz & Pav.	45	Cabrera (1937)	Andes from Peru to S Argentina and Chile	Usually herbs, monoecious, gynodioecious or dioecious, corollas bilabiate, subbilabiate or tubular-bilabiate, style branches papillose	$n = 14$; $2n = 22, 24, 28$
Chaptalia Vent.	ca. 70	Burkart (1944), Nesom (1995), under revision by Katinas	America from S USA to C Argentina	Perennial, scapose herbs, florets trimorphic, without staminodes, style branches papillose, achenes rostrate to attenuate	$n = 16, 24, 25$, ca. 50; $2n = 48$, ca. $48, 50$, ca. 58
Chucoa Cabrera	2	Ferreyra (1995), Sancho et al. (2005)	NW Peru	Shrubs, corollas tubular, style branches papillose	No data
Eriachaenium Sch.Bip.	1	Cabrera (1971)	Patagonia in Argentina and Chile	Perennial, dwarf herbs, corollas tubular, the marginal 4-lobed, anthers basally auriculate, style branches papillose	$2n =$ ca. 36
Gerbera L.	29	Hansen (1985a, b, 1988)	Africa, Asia, America	Perennial scapose herbs, florets dimorphic or trimorphic, staminodes, style branches papillose	$n = 12, 23, 24, 25$; $2n = 24, 46, 50$
Leibnitzia Cass.	6	Nesom (1983), Hansen (1988)	N and C America, Asia	Perennial, scapose herbs, chasmogamous or cleistogamous capitula, corollas bilabiate to filiform, style branches papillose	$n = 23$; $2n = 46$
Lulia Zardini	1	Zardini (1980)	S Brazil	Caulescent herbs, leaves linear, parallel-veined, corollas bilabiate, the marginal ones expanded, style branches papillose	No data
Mutisia L. f.	63	Cabrera (1965)	Andes from Colombia to Argentina and Chile, S Brazil and adjacent regions	Shrubs or subshrubs, stout to trailing, leaves simple to pinnately-compound, corollas bilabiate, subbilabiate, or ligulate, style branches papillose	$n = 13$, ca. $23, 23, 24$, ca. $26, 26$, ca. $27, 27$; $2n = 46, 52$
Pachylaena Hook. & Arn.	1	Katinas (2008)	Andes of Argentina and Chile	Perennial, prostrate herbs, leaves rosulate, corollas bilabiate, the marginal ones expanded, style branches papillose	No data
Perdicium L.	2	Hansen (1985c)	S Africa	Perennial, scapose herbs, corollas bilabiate, the central ones tubular to bilabiate, style branches papillose	No data

Trichocline Cass.	22	Zardini (1975)	S Peru to C Argentina and Chile, Australia	Perennial herbs usually scapose, corollas bilabiate, the marginal ones expanded, with staminodes, style branches papillose	$n = 18, 20$; $2n = 36$
Uechtritzia Freyn	3	Hansen (1988)	S Russia, N Afghanistan, Kashmir, N China, Armenia, NW India	Perennial, scapose herbs, corollas bilabiate, the marginal ones expanded, with staminodes, style branches papillose, achenes shaggy	No data
***Onoseris* clade**					
Aphyllocladus Wedd.	5	Cabrera (1951)	Andes of Argentina, Bolivia, and Chile	Shrubs, leaves caducous, marginal corollas bilabiate expanded, and central ones tubular, deeply 5-lobed, anther apical appendage truncate, style branches papillose	No data
Gypothamnium Phil.	1	Cabrera (1951)	N Chile	Shrubs, leaves linear, marginal corollas bilabiate expanded, and central ones tubular, deeply 5-lobed, anther apical appendage truncate, style branches papillose	$2n = 72$
Lycoseris Cass.	11	Egeröd & Stähl (1991)	America, from Guatemala to Brazil and Bolivia	Dioecious shrubs, marginal corollas true ray to sub-bilabiate and central ones tubular to tubular-bilabiate, style branches papillose	No data
Onoseris Willd.	31	Ferreyra (1944), Sancho (2004)	America, from S Mexico to NW Argentina and Brazil	Herbs or subshrubs, leaves often rosulate, corollas all sub-bilabiate or marginal bilabiate expanded and central ones tubular to tubular-bilabiate, style branches papillose	$n = 9, 12, 15, 18$
Plazia Ruiz & Pav.	3	Cabrera (1951)	Andes of Argentina, Bolivia, Chile and Peru	Shrubs, leaves clustered at the stem apex, marginal corollas bilabiate expanded and central ones tubular-subcampanulate, anther apical appendage truncate, style branches papillose	$n = 27$
Urmenetea Phil.	1	Cabrera (1978)	Andes of Chile and NW Argentina	Perennial, subscapose herbs, marginal corollas bilabiate expanded and central ones tubular-bilabiate, style branches papillose	No data
***Nassauvia* clade**					
Acourtia D. Don	ca. 80	Bacigalupi (1931)	S USA to El Salvador	Herbs or subshrubs, base of stems with a tuft of rust-colored trichomes, corollas bilabiate, rarely tubular, style branches crowned by apical papillae	$n = 26, 27, 28$; $2n = 54$
Ameghinoa Speg.	1	Cabrera (1971)	Patagonia of Argentina	Shrubs, leaves palmately-veined, corollas bilabiate, style branches crowned by apical papillae	$n = 26$

Table 14.1. Continued.

Taxa	Species number	Literature	Distribution	Main morphological features	Chromosome numbers
***Nassauvia* clade** (continued)					
Berylsimpsonia B.L. Turner	2	Turner (1993)	Cuba, Haiti, Puerto Rico, and Dominican Republic	Clambering, spiny shrubs, corollas bilabiate, style branches crowned by apical papillae	No data
Burkartia Crisci	1	Crisci (1976a)	Patagonia of Argentina	Cushion-like shrubs, leaves subulate, corollas bilabiate, style branches crowned by apical papillae, pappus of capillary bristles	No data
Calopappus Meyen	1	Crisci & Freire (1986)	C Chile	Cushion-like shrubs, leaves subulate, corollas bilabiate, style branches crowned by apical papillae, pappus of narrowly paleaceous bristles	No data
Cephalopappus Nees & C. Mart.	1	Baker (1884)	E Brazil	Perennial, scapose herbs, corollas bilabiate, style branches crowned by apical papillae, pappus absent	No data
Criscia Katinas	1	Katinas (1994)	NE Argentina, S Brazil, Uruguay	Perennial, scapose to scapiform herbs, corollas bilabiate, style branches crowned by apical papillae, achenes rostrate	No data
Dolichlasium Lag.	1	Cabrera (1971)	Andes of Argentina	Dwarf shrubs, leaves pinnatisect, corollas bilabiate, style branches crowned by apical papillae	No data
Holocheilus Cass.	7	Cabrera (1968)	S Brazil, Paraguay, Uruguay, N Argentina	Perennial, scapiform herbs, involucre 1–2-seriate, corollas bilabiate, style branches crowned by apical papillae	$n = 9, 11, 18$
Jungia L. f.	28	Harling (1995)	From SW Mexico to N Argentina	Herbs, shrubs or subshrubs, leaves stipulate to exstipulate, receptacle paleate, corollas bilabiate, style branches crowned by apical papillae	$n =$ ca. 18, 20, 21
Leucheria Lag.	47	Crisci (1976b)	Andes from Peru to S Argentina, Patagonia	Annual or perennial, scapiform herbs, receptacle paleate or epaleate, corollas bilabiate, style branches crowned by apical papillae	$n = 19, 20$; $2n = 40$
Leunisia Phil.	1	Reiche (1905)	Andes of C Chile	Shrubs, corollas bilabiate, style branches crowned by apical papillae, pappus paleaceous-setaceous	No data
Lophopappus Rusby emend. Cabrera	6	Cabrera (1953a)	Andes from Peru to Argentina	Shrubs with brachyblasts and macroblasts, corollas bilabiate or tubular, style branches dorsally papillose	No data

Macrachaenium Hook f.	1	Cabrera (1971)	SW Argentina and Chile	Perennial, scapiform herbs, corollas bilabiate, style branches dorsally papillose	No data
Marticorenia Crisci	1	Crisci (1974b)	C Chile	Shrubs, receptacle paleate, corollas bilabiate, style branches crowned by apical papillae	*n* = 22
Moscharia Ruiz & Pav.	2	Crisci (1974c)	C Chile	Annual herbs, basal leaves sub-rosulate, pseudocephalia, receptacle paleate, corollas bilabiate, style branches crowned by apical papillae	*n* = 20; 2*n* = 40
Nassauvia Comm. ex Juss.	38	Cabrera (1982)	Andes of S Bolivia and Argentina, Patagonia	Herbs, subshrubs or shrubs, leaves imbricate, corollas bilabiate, style branches crowned by apical papillae, pappus usually narrowly paleaceous	*n* = 11, 22, ca. 44
Oxyphyllum Phil.	1	Reiche (1905)	N Chile	Shrubs, leaves pinnatisect to reduced to 3-parted spines, corollas bilabiate, style branches crowned by apical papillae	No data
Panphalea Lag.	9	Cabrera (1953b)	S Brazil, E Paraguay, Uruguay and NE Argentina	Annual or perennial, scapiform herbs, corollas bilabiate, style branches crowned by apical papillae, pappus absent	*n* = 8
Perezia Lag.	32	Simpson Vuilleumier (1970)	Andes of Colombia to S Argentina, and Uruguay	Perennial, scapiform herbs, involucre multiseriate, corollas bilabiate, style branches crowned by apical papillae	*n* = 4, 8, 12, 14, ca. 16, 18, 19, 27, 28; 2*n* = 16, 24, 26, 54
Pleocarphus D. Don	1	Gay (1847)	C and N Chile	Shrubs, leaves linear to linear-lanceolate, receptacle paleate, corollas bilabiate, style branches crowned by apical papillae	2*n* = 52
Polyachyrus Lag.	7	Ricardi & Weldt (1974)	Peru, N and C Chile	Subshrubs, basal leaves rosulate, pseudocephalia, receptacle paleate, corollas bilabiate, style branches crowned by apical papillae	2*n* = 42, 54
Proustia Lag.	3	Fabris (1968)	Andes of Peru, Bolivia, C Chile, and Argentina	Shrubs to little trees with brachyblasts and macroblasts, often with thorns, corollas bilabiate, style branches dorsally papillose	2*n* = 52
Triptilion Ruiz & Pav.	7	Katinas et al. (1992)	Chile and SW Argentina	Annual or perennial herbs, capitula 5-flowered, corollas bilabiate, style branches crowned by apical papillae, pappus of three paleaceous bristles, apically plumose	2*n* = 20
Trixis P. Browne	38	Anderson (1972), Katinas (1996)	From S USA to C Chile and Argentina	Shrubs, subshrubs or herbs, corollas bilabiate, style branches crowned by apical papillae	*n* = ca. 27, 27, 28; 2*n* = 47+3, 54

of Mutisioideae differ clearly from the carduoid, arctotoid, and vernonioid styles, and is the main character for delimiting the subfamily Mutisioideae. These style types of Mutisioideae are shared with Barnadesioideae, which used to be included in Mutisieae of Cabrera (1977) and some previous authors. One might argue that these style characters are symplesiomorphic, but the recognition of apomorphic states in this character depends on the choice of the outgroup (Calyceraceae, Goodeniaceae, Menyanthaceae).

Finally, Katinas et al. (2008) performed a molecular phylogenetic analysis of Nassauviinae based on the nuclear ITS and plastid *trnL-trnF* regions, with a sampling of 46 species of Mutisieae s.l. The study shows the monophyly of Nassauviinae and a partial agreement with the tree of Funk et al. (2005) concerning generic relationships within the subtribe.

SYSTEMATICS

After the results of the molecular phylogenetic studies mentioned above, some taxonomic decisions were made concerning the basal clades of Compositae. Mutisieae s.str. (or the Mutisieae clade) was identified as the subfamily Mutisioideae by Panero and Funk (2008; 44 genera and 630 species). It contains three main branches corresponding to tribes: Mutisieae (= *Mutisia* clade), Onoserideae (= *Onoseris* clade), and Nassauvieae (= *Nassauvia* clade), and it does not include the Asian or African Mutisieae or *Hecastocleis*. Table 14.1 shows the main morphological characters of each genus of all three clades, together with other information. We will present a brief summary of these clades, since they were already discussed in previous works by Panero and Funk (2007, 2008). The concept of Mutisioideae of Panero and Funk (2008) does not necessarily agree completely with other circumscriptions of the same taxon, for example, Katinas et al. (2008) support a wider concept of the subfamily Mutisioideae (with 74 genera, 865 species).

Subfamily Mutisioideae Panero and Funk (2008)
(= Mutisieae s.str., Mutisieae clade)
This subfamily, as recognized by Panero and Funk (2008), contains approximately 44 genera and 630 species. It was characterized by the disc corollas with deeply dissected lobes, some of its members having bilabiate corollas, capitula with imbricate phyllaries, anthers calcarate and caudate with strongly sclerified anther appendages, and styles usually well-exserted from the floret and essentially glabrous. Most species are annual or perennial herbs, although shrubs, small trees and vines are present.

The subfamily contains three tribes: Mutisieae, Nassauvieae, and Onoserideae.

Tribe Mutisieae (= *Mutisia* clade), Panero and Funk (2008) (Fig. 14.1). The tribe contains approximately 14 genera and more than 200 species distributed mostly in South America, with representatives in Central and North America, Asia, Africa, and Australia (Table 14.1). It roughly corresponds to the circumscription of subtribes Gerberinae and Mutisiinae by Hind (2007), but excluding Onoserideae. There are perennial herbs, shrubs and vines that present a great variability in their corollas (bilabiate, subbilabiate, tubular, filiform, ligulate), sometimes the marginal corollas are conspicuously expanded, the style branches are papillose.

List of genera: *Adenocaulon*, *Brachyclados*, *Chaetanthera*, *Chaptalia*, *Chucoa*, *Eriachaenium*, *Gerbera*, *Leibnitzia*, *Lulia*, *Mutisia*, *Pachylaena*, *Perdicium*, *Trichocline*, *Uechtritzia*.

Tribe Onoserideae (= *Onoseris* clade), Panero and Funk (2007, 2008) (Fig. 14.2). The tribe contains six genera and approximately 52 species distributed mostly in the Andes (Table 14.1). According to Panero and Funk (2008), there are herbs and shrubs (sometimes dioecious), commonly with solitary or few capitula, ray florets female, corollas bilabiate, disc florets hermaphrodite or functionally staminate, corollas 5-lobed, and pappus 2–4-seriate, mostly heteromorphic.

List of genera: *Aphyllocladus*, *Gypothamnium*, *Lycoseris*, *Onoseris*, *Plazia*, *Urmenetea*.

Tribe Nassauvieae (= *Nassauvia* clade), Panero and Funk (2008) (Fig. 14.3). It is an American group with 25 genera and more than 300 species distributed mainly in the Andes and Patagonia (Table 14.1). The tribe has been traditionally viewed as a natural group (as subtribe Nassauviinae). Most of its genera have capitula with only bilabiate corollas, the style papillae form a tuft restricted to the branch apex, the pollen exine is microechinate, distinctly bilayered, and both the ecto- and endosexine are clearly columellate, with delicate columellae separated by an internal tectum (Crisci 1974a, 1980; Tellería et al. 2003; Katinas et al. 2008).

The latest molecular studies involving genera of the tribe analyzing ITS (Katinas et al. 2008) and combined analyses of ten chloroplast DNA loci (Panero and Funk 2008) support its monophyly. Despite the different sampling in both analyses, there is some agreement regarding generic relationships. For example, the generic pair *Proustia* and *Lophopappus* with rounded and dorsally papillose style branches and mostly tubular corollas is sister to the rest of the tribe.

List of genera: *Acourtia*, *Ameghinoa*, *Berylsimpsonia*, *Burkartia*, *Calopappus*, *Cephalopappus*, *Criscia*, *Dolichlasium*, *Holocheilus*, *Jungia*, *Leucheria*, *Leunisia*, *Lophopappus*, *Macrachaenium*, *Marticorenia*, *Moscharia*, *Nassauvia*, *Oxyphyllum*, *Pamphalea*, *Perezia*, *Pleocarphus*, *Polyachyrus*, *Proustia*, *Triptilion*, *Trixis*. The genus *Calorezia*, containing two species of *Perezia*, was recently proposed by Panero (2007) based

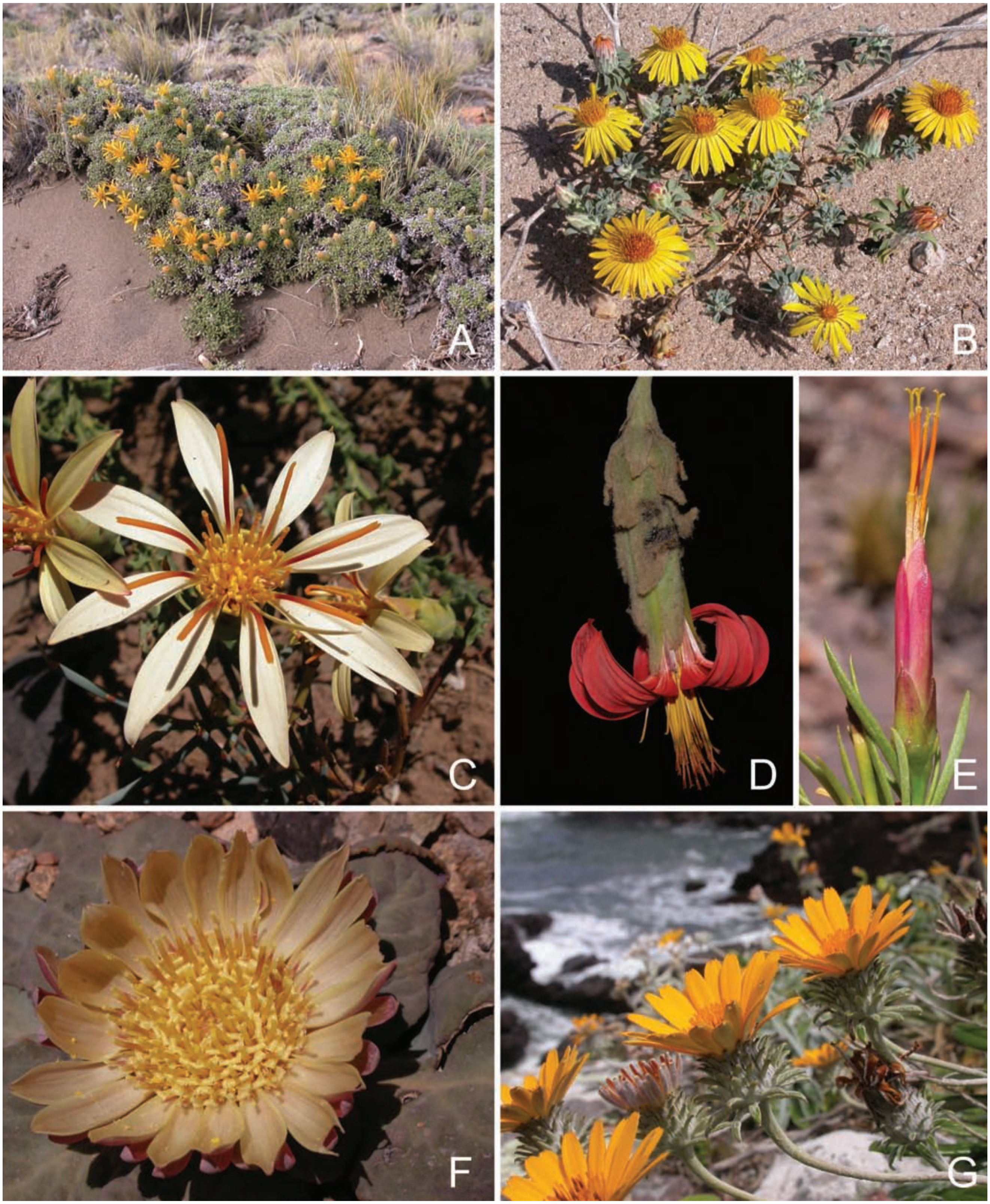

Fig. 14.1. Photographs of some members of the *Mutisia* clade. **A** *Brachyclados caespitosus* (Phil.) Speg.; **B** *Chaetanthera glabrata* (DC.) F. Meigen; **C** *Mutisia sinuata* Cav.; **D** *Mutisia clematis* L. f.; **E** *Mutisia linifolia* Hook.; **F** *Pachylaena atriplicifolia* D. Don ex Hook. & Arn.; **G** *Trichocline incana* Cass. [Photographs, J.M. Bonifacino.]

on a chloroplast DNA coding regions study (Panero et al., in prep.). Since there are no clear morphological characters that support this new genus, it is not included in Table 14.1.

MORPHOLOGY

The key morphological characters, i.e., corolla, style, and pollen, of Mutisieae s.l. were analyzed by Katinas et al. (2008). This discussion is confined to the three clades recognized by Panero and Funk (2008; *Mutisia*, *Onoseris*, and *Nassauvia* clades) and evaluates their degree of support and the relationships with other clades.

Corolla

The corolla shape is highly variable in the group under study (Fig. 14.4A–J). Several corolla types can be described with some intermediate states.

Bilabiate (3+2 corolla lips). Zygomorphic, with an external 3-dentate lip, radiating (Fig. 14.4A) or not radiating (Fig. 14.4B), and an internal 2-cleft lip. This is the

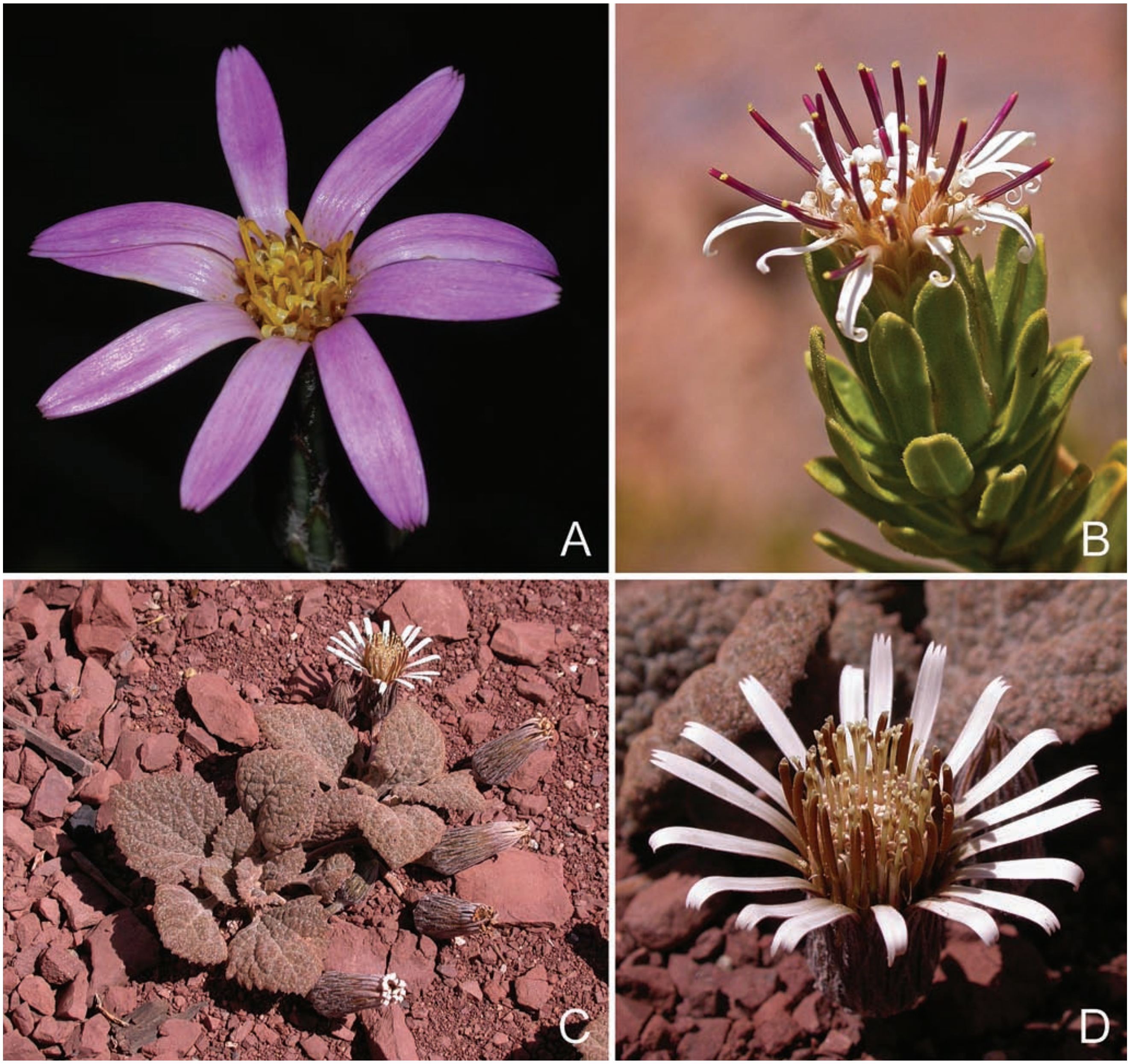

Fig. 14.2. Photographs of some members of the *Onoseris* clade. **A** *Onoseris weberbaueri* Ferreyra; **B** *Plazia daphnoides* Wedd.; **C, D** *Urmenetea atacamensis* Phil. [Photographs, J.M. Bonifacino.]

Fig. 14.3. Photographs of some members of the *Nassauvia* clade. **A** *Leucheria achillaeifolia* Hook. & Arn.; **B** *Perezia purpurata* Wedd.; **C** *Nassauvia glomerulosa* (Lag. ex Lindl.) D. Don.; **D** *Dolichlasium lagascae* D. Don; **E** *Criscia stricta* (Spreng.) Katinas. [Photographs, J.M. Bonifacino.]

most common type of corolla, but it is not present in all the genera of Mutisieae s.str. The genera of the *Nassauvia* clade, with few exceptions (e.g., *Acourtia*, *Lophopappus*), have capitula with all bilabiate corollas. *Pachylaena* and *Trichocline* are examples of the *Mutisia* clade having capitula containing solely bilabiate corollas. Members of the *Onoseris* clade, for example *Gypothamnium*, species of *Onoseris*, and *Plazia* have mostly marginal bilabiate corollas and central tubular corollas.

Tubular (0+5 corolla lobes). Actinomorphic, limb 5-lobed at the apex (4-lobed in *Eriachaenium*), the lobes usually short (Fig. 14.4C) and less commonly deeply or very deeply incised (Fig. 14.4D). These corollas are usually funnelform, with a tube gradually expanding into a limb or less frequently sub-campanulate with the tube abruptly expanding into a limb. Genera with exclusively tubular corollas are *Chucoa* and *Eriachaenium*, otherwise this type of corolla is placed in the center of the capitulum.

Ligulate (5+0 ligule lobes). Zygomorphic, with a short and narrow tube expanding into an apically 5-lobed ligule, the lobes shallowly incised (Fig. 14.4E). Examples are some species of *Mutisia* with all ligulate florets.

True ray (3+0 limb lobes). Zygomorphic, with a short and narrow tube expanding into a shallowly 3-lobed limb (Fig. 14.4F). This type occurs, for example, in the margin of the capitula of *Chaptalia*, and some species of *Chaetanthera* and *Lycoseris*.

Filiform. Irregular or zygomorphic, a very narrow, reduced tubular corolla with an irregularly-cleft short apical portion. Filiform corollas may approach other types of corollas (e.g., filiform-bilabiate, filiform-tubular, filiform-true ray) (Fig. 14.4G). Examples are *Chaptalia* and *Leibnitzia*.

Tubular-bilabiate (intermediate between 3+2 and 0+5 corolla lobes). Zygomorphic, transitional type with erect and short lip-lobes and unequal corolla incisions that result in a slightly bilabiate corolla (Fig. 14.4H, I).

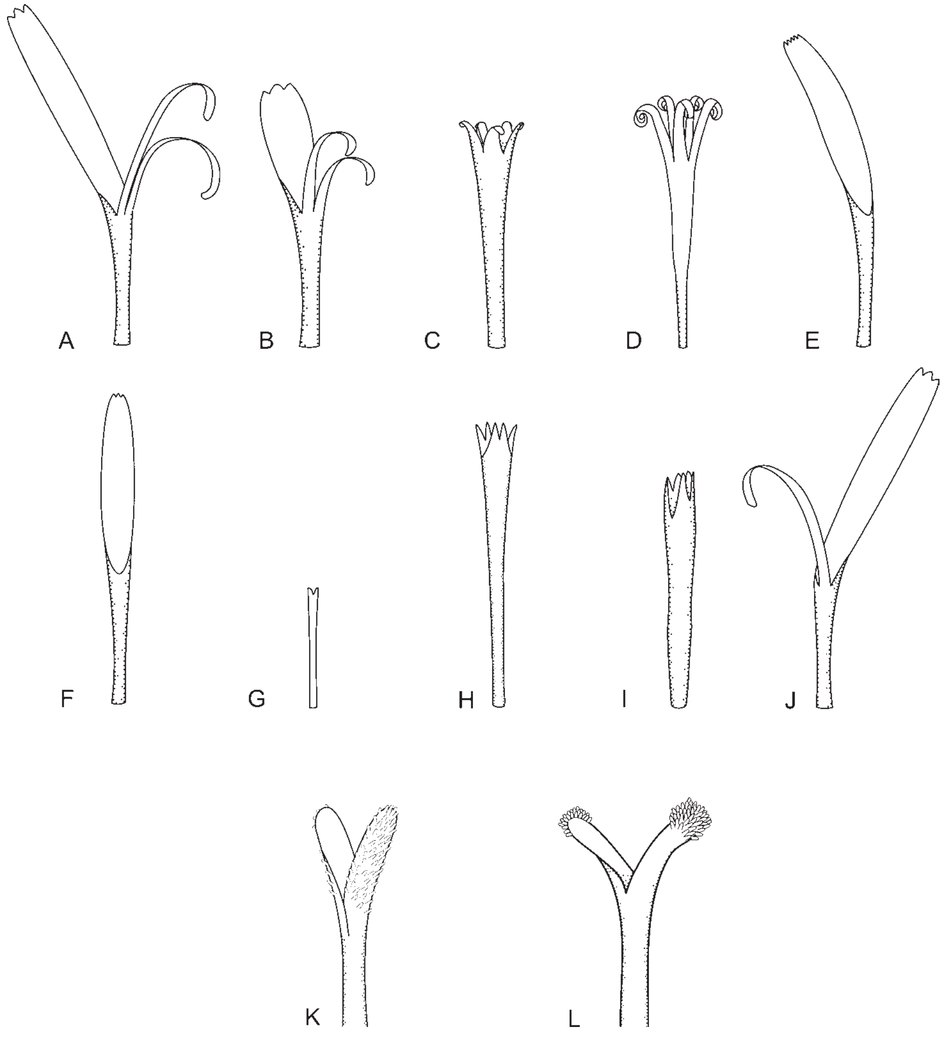

Fig. 14.4. Floral characters of Mutisieae s.str. **A–J** Corollas: **A** bilabiate radiating (*Onoseris alata* Rusby); **B** bilabiate (*Criscia stricta* (Spreng.) Katinas); **C** tubular shallowly lobed (*Onoseris hastata* Wedd.); **D** tubular deeply lobed (*Plazia daphnoides* Wedd.); **E** ligulate shallowly lobed (*Mutisia linifolia* Hook.); **F** true ray (*Chaptalia nutans* (L.) Pol.); **G** filiform (*Chaptalia nutans*; **H** tubular-bilabiate (*Chaptalia nutans*); **I** sub-bilabiate (*Urmenetea atacamensis* Phil.); **J** sub-bilabiate radiating (*Onoseris acerifolia* Kunth). **K, L** Styles: **K** style branches dorsally papillose (*Onoseris alata*); **L** style branches apically papillose with papillae forming a tuft (*Holocheilus hieracioides* (D. Don) Cabrera). [Drawings, G. Sancho.]

These are the typical central corollas of many genera such as *Chaptalia*, *Lycoseris*, *Onoseris*, and *Perdicium*.

Sub-bilabiate (or pseudobilabiate, sensu Bremer 1994; 4+1, 3+1 corolla lips). Zygomorphic, probably derived from a bilabiate corolla with different degrees of fusion among the teeth. The most common types are corollas with an external 3-dentate or 4-dentate lip and one entire, untoothed, internal lip (Fig. 14.4J). This type of corolla is very common in the margins of capitula in members of the *Onoseris* clade.

Corolla morphology does not help to distinguish Mutisieae s.str. from clades previously considered part of Mutisieae s.l. For example, bilabiate and sub-bilabiate corollas are common in *Oldenburgia* and some genera of Gochnatieae; tubular corollas are found in Gochnatieae, Hecastocleideae, and the *Stifftia* clade. Ligulate, 5 shallowly lobed corollas are found in the *Stifftia* clade. Only filiform corollas are exclusively found in Mutisieae s.str.

Style

Mutisieae s.str. are characterized by genera with papillose styles, and with the papillae or the relatively short hairs apically rounded. The stigmatic area is continuous, shortly papillate, covering the whole inner surface of the style branches.

In the *Mutisia* clade, the style branches can be very short (styles bilobed, e.g., *Trichocline*), or long (styles bifid, e.g., *Chaptalia*). Variation of the style branch length, short or long, may occur within the same genus (e.g., *Chaetanthera*, *Chaptalia*). Dorsally, the style branches are papillose in all genera (Fig. 14.4K). The papillae or short hairs may be somewhat variable in length, but they are always rounded at the apex. The papillae are distributed above the style bifurcation point in most taxa, covering the whole branch or restricted to the terminal, apical portion of the branch. Occasionally the papillae extend below the style bifurcation point (e.g., *Pachylaena*). The styles of the genera of the *Onoseris* clade are typically papillose as are those of the *Mutisia* clade.

In the *Nassauvia* clade most of the styles have relatively long branches, and the papillae form a tuft restricted to the branch apex (Fig. 14.4L). Exceptions are *Lophopappus* and *Macrachaenium*, which have styles with dorsally papillose branches. Crisci (1974a) determined four style types in the subtribe Nassauviinae according to differences in branch length, apex shape, and papilla length.

The type of style in the genera of the *Nassauvia* clade is restricted to this group. Styles of Mutisieae s.str., other than those of the *Nassauvia* clade, are shared with other groups. For example, apically papillose styles are found in Pertyeae and in *Oldenburgia*. However, the rounded apex of the papillae distinguishes these clades from other clades with acute hairs such as Dicomeae, Tarchonantheae, Cardueae, *Gymnarrhena*, and Cichorioideae. Styles with rounded papillae such as those of the Mutisieae clade are also found in Barnadesioideae.

Pollen

Within the great diversity of pollen of Compositae, the pollen of Mutisieae s.str. can be characterized by having generally tricolporate aperture; size ranging from small to large; spheroidal to prolate shape; sculpture with microspines or microgranules; structure with two columellate layers and tectum imperforate or few-perforate (Tellería et al. 2003; Zhao et al. 2006; Katinas et al. 2008; see Chapter 7). The sculpture and the structure of the exine are of the greatest taxonomic value while apertures, and to some extent the shape and size of the pollen grains, are of secondary significance.

In the *Mutisia* clade the sculpture is microechinate or microgranulate, whereas the structure consists of two columellate layers separated by an internal tectum. The inner layer has always stout and clearly ramified columellae, and the outer has a compact or slightly columellate aspect (Fig. 14.5A). This exine type is shared with the *Onoseris* clade (Tellería and Katinas 2004; Tellería 2008) and with members of Mutisieae s.l. such as some Guayana Highland genera, Gochnatioideae, Hecastocleidoideae and Pertyoideae

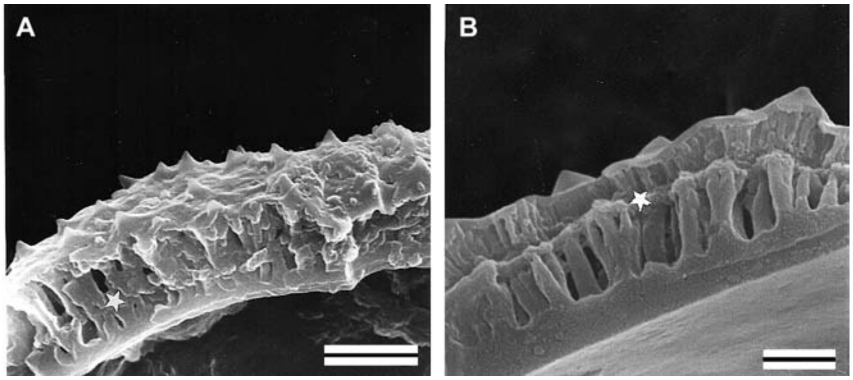

Fig. 14.5. SEM of two types of exine structure within Mutisieae s.str. **A** *Mutisia* exine type (*Mutisia* and *Onoseris* clades) showing the endosexine with stout and ramified columellae, and the ectosexine with single columellae; **B** *Cephalopappus* exine type (*Nassauvia* clade), showing the two layers of columellae sexine, separated by internal tectum parallel to the nexine. Asterisks: internal tectum. Scale bars: 2 µm.

(Katinas et al. 2008), and with Anthemideae (*Artemisia* type) (Skvarla et al. 1977) and Cardueae (*Centaurea* type) (Wagenitz 1955; Nordenstam and El-Ghazaly 1977; Pehlivan 1995; Tormo and Ubera 1995).

The pollen exine in genera of the *Nassauvia* clade is microechinate, distinctly bilayered, and both the ecto- and endosexine are clearly columellate, with delicate columellae separated by an internal tectum (Fig. 14.5B). Within this broad pattern, different exine types that characterize one genus or group of genera can be distinguished on the basis of the ratio between ecto- and endosexine and tectum internal orientation (Crisci 1974a; Tellería et al. 2003). The *Nassauvia* clade is the only one well supported by pollen features.

FLORAL BIOLOGY AND POLLINATION

Capitula and floral diversification

Radiate capitula with specialized marginal florets have been seen as more attractive to pollinators by increasing the capitulum surface (Lane 1996). In Mutisieae s.str., the species of *Gerbera*, *Mutisia* (Fig. 14.1C–E), and *Trichocline* are examples of having beautiful and conspicuous marginal radiating corollas. In the genus *Onoseris* (Fig. 14.2A), most species have showy, solitary, radiate capitula. However, a few derived species in this genus (e.g., *O. onoseroides*) have capitulescences of numerous eradiate or sub-radiate capitula (Sancho 2004). It could be hypothesized that multi-headed thyrsoid capitulescences replace the colorful solitary capitula that serve to attract pollinators in most other species of *Onoseris*. It has to be pointed out that marginal radiating corollas and inflorescence size have independent effects on total display and are distinct targets for pollinators (Lane 1996). In some cases, reduced outer lips of marginal corollas as in *Chaetanthera* (e.g., *C. apiculata* (J. Rémy) F. Meigen, *C. gnaphalioides* (J. Rémy) I.M. Johnst.) seem to be replaced by showy phyllaries that function as attractant of pollinators (Tellería and Katinas 2004). *Chaptalia* and *Leibnitzia* display cleistogamy together with chasmogamy, and the reduction of their corollas is notable when compared with the other chasmogamous genera of the *Gerbera*-complex (Hansen 1990; Katinas 2004) such as *Gerbera* and *Trichocline* (Fig. 14.1G). Usually self-pollinating species have smaller and fewer flowers because attraction of pollinators is not necessary. The production of large and showy flowers, therefore, will be selected against as a drain on energy supplies for no reproductive gain (Weberling 1989; Proctor et al. 1996).

Pseudocephalia could be seen as extreme aggregation of capitula in secondary inflorescences and have been described in several tribes. Pseudocephalia in Nassauviinae were described (Crisci 1974c; Cabrera 1982; Katinas et al. 1992, 2008; Katinas and Crisci 2000) for *Moscharia* and *Polyachyrus* and species of *Nassauvia* and *Triptilion* and have been seen as an advanced evolutionary feature when compared to a regular capitulum. According to Stebbins (1967), aggregation of capitula in pseudocephalia could increase the size of the functional inflorescence. The conspicuousness and attractiveness of small heads are heightened by their aggregation into compound capitula (Leppik 1977).

Bird pollination

Hymenoptera, especially Apoidea (bees), are, by far, the most important pollinators of Compositae. However, birds, although rarely, have been indicated as pollinators for the family, and especially in Mutisieae and Barnadesioideae, when the capitula are properly shaped for hummingbird visitation (Lane 1996). Many species of Mutisieae s.str. are known by their showy capitula, and one of the most spectacular representatives with attractive capitula is the genus *Mutisia* (Fig. 14.1C–E). The capitula of *Mutisia* have been classified by Leppik (1977) within the "cupulate" or "cup-shaped" type in his classification of the capitula of Compositae. The capitular shape of *Mutisia*, its vivid colors (especially scarlet or purple), and abundant nectar (Leppik 1970), are some of the features indicated as characteristic of bird pollinated plants. Hummingbird pollination in *Mutisia* was reported for: *M. acuminata* Ruiz & Pav. (Wester and Claßen-Bockhoff 2006), *M. alata* Hieron. (Knudsen et al. 2004), *M. campanulata* L.f. (Buzato et al. 2000), *M. clematis* L.f. (Gutiérrez 2005), *M. coccinea* A. St.-Hil. (Sazima and Machado 1983; Buzato et al. 2000), *M. speciosa* Ait. ex Hook. (Buzato et al. 2000), and *M. viciifolia* Cav. (Leppik 1970). Stamens and styles protruding from the corolla tube also have been indicated as characteristic of ornithophilous plants (Proctor et al. 1996). *Gerbera* is another genus reported as bird pollinated (Lane 1996). The position of *Mutisia* and *Gerbera* in separate clades (Panero and Funk 2008) would suggest that the bird pollination syndrome evolved independently in Mutisieae.

Nectar

Nectar of Compositae is usually hexose-rich, which is characteristic of hymenopteran-pollinated species (Lane 1996). However, *Mutisia viciifolia*, indicated as ornithophilous (Leppik 1970; Faegri and Van der Pijl 1979), reveals a predominance of sucrose in its nectar composition (Percival 1961). According to Torres and Galetto (2002), species of *Trichocline* and *Trixis* have nectar with a great variation of sucrose proportions. These authors have found correlations between corolla length and nectar sugar composition in Compositae. Thus, they pointed out that longer corolla tubes tend to have higher nectar sucrose proportions and to circumscribe the type of pollinators as occurs, for example, in *Mutisia coccinea* (Galetto 1995). Early-branching species of Compositae tend to have longer corolla tubes, higher sucrose proportions and lesser diversity of floral visitors than late-branching species. Considering that those corolla and nectar characteristics may indicate some specialization in the pollination system, Torres and Galetto (2002) suggested that there is an evolutionary tendency toward generalist pollination systems within the family.

BIOGEOGRAPHY

The genera of the Mutisieae s.str. are found in all continents except Europe and Antarctica, but the majority of species are concentrated in South America. The genera of the *Mutisia* clade are mainly South American, but they are also represented in Asia, Africa, and Australia (Fig. 44.3). There are a few monotypic genera or genera with a few species in the *Mutisia* and *Onoseris* clades that are endemic to restricted areas. Some examples of these genera are: *Gypothamnium* from northern Chile, *Perdicium* from southern Africa, and *Lulia* from southern Brazil. Genera that are well represented in the Andean mountain ranges are *Aphyllocladus*, *Chaetanthera*, *Chucoa*, *Onoseris*, *Pachylaena*, and *Plazia*. There are also many widespread genera, for instance *Chaptalia* from southern United States to central Argentina; *Gerbera* in Africa, southern Asia, and America; *Onoseris* from Central America to northern Argentina, and *Mutisia* from the Andes of Colombia to southern Argentina and Chile, and southern Brazil and adjacent regions.

The *Nassauvia* clade is exclusively distributed in the Neotropical region sensu Cabrera and Willink (1973), with mostly monotypic, endemic, Andean, Chilean, and Patagonian genera. Largely Andean-Patagonian centered genera are *Dolichlasium*, *Leucheria*, *Lophopappus*, *Nassauvia*, and *Perezia*. Exclusively Patagonian genera are *Ameghinoa* and *Burkartia*, whereas *Macrachaenium* inhabits the *Nothofagus* forest in western Patagonia. Central and northern Chile, a hot spot in South America, hosts many endemic genera such as *Calopappus*, *Leunisia*, *Marticorenia*, *Moscharia*, *Oxyphyllum*, *Pleocarphus*, *Polyachyrus*, and most species of *Triptilion*. Only *Jungia* and *Trixis* are widespread genera ranging from North and Central America to southern Argentina. On the other hand, *Acourtia* and *Berylsimpsonia* are not South American, occurring in North and Central America, and in the West Indies, respectively.

The great concentration of genera in South America, mainly in Patagonia and the Andean ranges, together with the resulting phylogenies of Compositae basal groups (e.g., Funk et al. 2005; Panero and Funk 2008), and the recent findings of fossil pollen in Patagonia (see Fossil pollen and early evolution below) would support a probable origin of this group in these areas.

ADAPTATION TO DRY ENVIRONMENTS

The concentration of genera and species of Mutisieae s.str. in dry areas such as the Andes, Patagonia, and central and northern Chile is significant, and many taxa of this group show some morphological adaptations to these environments.

Pollen

The genus *Chaetanthera*, of the *Mutisia* clade, shows particular pollen adaptations to dry and cold environments (Tellería and Katinas 2004). *Chaetanthera* is centered in two main habitats: the high elevations of the Puna and Altoandean provinces and in lower elevations of the Central Chilean province (Cabrera and Willink 1973). The Puna province is a large plateau between the Andean cordillera and the eastern mountain ranges (Precordillera), from 3400 to 4000 meters. The Altoandean province corresponds to the highest elevations of the Andes above 4000 meters. Climate in the Puna and Altoandean provinces is dry and cold, and the low temperatures and associated snow cover are crucial to plant adaptation. The Central Chilean province is a low central valley between the two cordilleras in Chile, between 32°–37° south latitude. The extreme summer drought, characteristic of Mediterranean climates, plays a key role in the strategies of survival of the plant communities. The pollen of *Chaetanthera* seems to be adapted to these dry environments: *(1)* the exine is very thick and the internal tectum is well developed in some species to increase the resistance area of pollen, reducing the tendency to buckle; *(2)* the endoapertures are united in an equatorial band or endocingulus that would increase the plasticity of the pollen walls allowing rapid hydration; and *(3)* some species have a parasyncolpus, which can be viewed as another strategy in pollen hydration because the cracks of the exine that delimit the apocolpial field would increase the flexibility of the grain during the process. In this way, the pollen of *Chaetanthera* combines characteristics against desiccation along with mechanisms that ensure quick hydration in dry environments.

These findings contrast with the palynologic analysis performed in *Mutisia* (Tellería and Katinas, submitted), which comprises 63 species endemic to South America (Cabrera 1965). The major concentration of species occurs in the Andes, from Colombia to southern Chile and Argentina, and in Central Chile, but eleven species inhabit southern Brazil, Paraguay, Uruguay and northeastern Argentina. The species of *Mutisia* grow in distinct habitats including, but not limited to, different latitudes of the Andes (yungas, lomas formation, montane forests, subantarctic forests, paramos, altoandean vegetation), tropical forests in southern Brazil and adjacent areas, the Puna or Altiplano, arid areas of Patagonia in southern

Chile and Argentina, and in the Mediterranean area of Central Chile. Several species (e.g., *M. clematis*, *M. decurrens* Cav., *M. ledifolia* Decne. ex Wedd., *M. subulata* Ruiz & Pav.) have considerable chromosomal and morphological variability, and there are reports of hybrid species and polyploids (diploids and tetraploids) in the genus (Cabrera 1965). The palynologic study of most species of *Mutisia* (Tellería and Katinas, submitted) shows that the pollen has a basic morphology, shared by all species, but at the same time, it is very polymorphic within and among species. Despite the fact that most species of *Mutisia* grow in arid places, the pollen morphology in the genus does not show adaptive environmental features as found in *Chaetanthera*.

Clustering of capitula

As previously mentioned, the genera *Moscharia*, *Nassauvia*, *Polyachyrus*, and *Triptilion* of the *Nassauvia* clade represent a morphologically distinctive group because of the aggregation of their capitula into secondary inflorescences or pseudocephalia which have been also viewed as an adaptation to arid environments. *Moscharia* and *Polyachyrus* grow in the Mediterranean central valley of Chile, the Atacama desert, and the dry littoral in Chile and Peru, all areas characterized by their extreme summer drought. *Triptilion* and *Nassauvia* (Fig. 14.3C) grow in both dry and more mesic areas and have species with and without pseudocephalia. Heads enclosed by a keeled, conduplicate bract, such as those of *Moscharia* and *Polyachyrus*, are dropped off as a whole without releasing the achenes before germination, a phenomenon called synaptospermy (Murbeck 1920) that is commonly found in genera of Compositae with pseudocephalia (Claßen-Bockhoff 1996). The bracts of the involucre are also attached to the achenes and they are deciduous with them, protecting the fruits from ground predators prior to germination and keeping moisture around the achene in arid climates (Katinas and Crisci 2000). The evolution of pseudocephalia in Nassauviinae was recently reconsidered by Katinas et al. (2008) who suggested the hypothesis that there was a reduction in complexity of the pseudocephalia. This reduction principally involved loss of capitula and rearrangement of phyllaries and flowers, perhaps in response to a shift from arid to more mesic conditions in the late Tertiary and Pleistocene.

Achene twin hairs

Traditionally, authors have agreed that the presence of twin hairs on the achenes is found exclusively in Compositae (Hess 1938; Ramayya 1962; Roth 1977). Morphology and ontogeny of twin hairs in the *Nassauvia* clade was analyzed by Freire and Katinas (1995). Twin hairs are made up of two short basal cells, one sometimes reduced, and two elongated, cylindrical or elliptical hair cells. From the basic shape, a great variation of twin hair morphology can be found, although they always share the same ontogeny. Hess (1938) postulated that water absorption was an important function of the achene twin hairs, mainly by those with thickened walls. According to him, the abundance of pits leads to a quick and uniform distribution of the absorbed humidity. Some types of twin hairs contain mucilage that extrude under the occasional humid conditions, and the achenes become sticky. For example, typical, mucilaginous, twin hairs were found in most species of the genus *Trixis* (Anderson 1972; Katinas 1996), whereas those species inhabiting very humid places (e.g., *T. glaziovii*, *T. lessingii*) have modified twin hairs without mucilage. Twin hairs were also reported in corollas of species of *Trichocline*, *Onoseris* and *Uechtritzia* growing in dry and semiarid environments (Sancho and Katinas 2002). These hairs are distributed generally in corollas of disk florets being more efficient in the humidity retention than if distributed in the more exposed marginal florets.

FOSSIL POLLEN AND EARLY EVOLUTION

The importance of Mutisieae, because of its position as the sister group to the remainder of the family, is widely recognized. The resolution of its taxonomy is fundamental to generate reliable evolutionary and biogeographical hypotheses. Southern South America was postulated as the most likely area of origin of Compositae (Stuessy et al. 1996; Funk et al. 2005; Panero and Funk 2008). Therefore, it has been pointed out that the finding of fossils in this area is fundamental to trace the fossil history of the family (Graham 1996). The fossil pollen evidence shows old records of the family Compositae belonging to *Tubulifloridites* spp. and *Mutisiapollis* spp., all related to genera of the *Mutisia* clade (e.g., *Gerbera* type, *Mutisia*), from the Oligocene (Muller 1981; Barreda 1993, 1997; Graham 1996) from well-dated deposits in the southern Hemisphere. Some older fossil records related to Mutisieae, from the Eocene, were recovered from offshore and onshore localities of southern Africa (Zavada and De Villiers 2000; Scott et al. 2006), suggesting an African origin of Compositae (Zavada and De Villiers 2000). However, these Eocene pollen records need taxonomic and/or stratigraphic confirmation (Scott et al. 2006). Those reported as *Mutisiapollis* spp. from the Late Eocene of the Gulf coast of Mexico (Elsik and Yancey 2000) might be the oldest ones, but neither description nor illustration was provided to date (T.E. Yancey, pers. comm.) to confirm their identification.

New fossil pollen discoveries of Mutisieae s.l. and Barnadesioideae were reported from marine deposits of Patagonia, in southern Argentina (Katinas et al. 2007;

Barreda et al. 2008). A minimum age of 28–23 Ma (Late Oligocene, Chattian) for fossil pollen related to the extant genera of the *Gochnatia* clade, and 23–20 Ma (Early Miocene, Aquitanian) for fossil pollen of the *Nassauvia* clade and Barnadesioideae were reported (Katinas et al. 2007). Fossil pollen records of the Late Miocene (11–9 Ma) in Patagonia show high abundance and diversity of Nassauviinae associated with pollen of Astereae and Barnadesioideae. It is interesting to note that the chronological order of appearance of these groups in Patagonia, first Mutisieae s.l. and second Barnadesioideae, differs from the branching order of the current accepted phylogenies, i.e., first Barnadesioideae and second Mutisieae s.l.

Many molecular biologists have used and are using fossils in their analyses as a way of providing a calibration point for evolutionary models used to approximate ages for the nodes of the phylogenetic trees. Opinion remains divided as to how best to use temporal (stratigraphic) data in phylogenetic reconstruction (see the online debate from 1998 at http://www.nature.com/nature/debates/fossil/). Some authors think that the order of stratigraphic appearance of taxa in the fossil record should play a role in phylogenetic tree-building. In such cases stratigraphic order is used from the outset to influence and direct branching relationships by maximizing the congruence between the age of a taxon's first occurrence in the fossil record and how early it branches from a phylogenetic tree. Others see stratigraphy as irrelevant to phylogeny, and dismiss mismatches between the fossil record and phylogenetic hierarchy as a result of an inadequate fossil record. The role of stratigraphy is then restricted to post hoc dating of branching events. If we see the last pollen findings (e.g., Katinas et al. 2007) through the former position (despite the fact that the age of fossils is considered the minimum age), they contradict the branching pattern of the current hypotheses on the evolution of Compositae. If we see these findings through the latter position, hopefully, they will help to calibrate more precisely the phylogenetic trees involving Compositae.

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Chapter 15

Gochnatieae (Gochnatioideae) and Hyalideae (Wunderlichioideae p.p.)

Gisela Sancho and Susana E. Freire

HISTORICAL OVERVIEW

Traditionally, the members of the tribes Gochnatieae (Gochnatioideae; Panero and Funk 2002) and Hyalideae (Wunderlichioideae; Panero and Funk 2007, 2008) have been thought to be related on the base of shared morphological characters (Table 15.1). The recognition of Gochnatieae (Panero and Funk 2002) was the result of resolving the polyphyly of Mutisieae suggested on the base of morphology (Cabrera 1977; Hansen 1991b; Karis et al. 1992) and supported by molecular data (Kim et al. 2002; Panero and Funk 2002). The American tribe Gochnatieae comprises (Panero and Funk 2002) four genera: *Cnicothamnus* Griseb., *Cyclolepis* Gillies ex D. Don, *Gochnatia* Kunth, and *Richterago* Kuntze (including *Actinoseris*), and probably a fifth one, *Chucoa* Cabrera, not sampled in their analysis.

The taxa of Gochnatieae of Panero and Funk (2002) were previously included within the subtribe Gochnatiinae of Mutisieae (Cabrera 1961, 1977). Cabrera (1971) considered *Actinoseris* (Endl.) Cabrera, *Cyclolepis*, and *Gochnatia* as closely related to *Pleiotaxis* Steetz because of their apiculate anther appendages. Later, Cabrera (1977) associated *Chucoa* to *Gochnatia*. Hansen (1991b), however, considered only *Actinoseris* and *Cyclolepis* of Cabrera's group of related genera to be close to *Gochnatia*, excluding *Pleiotaxis* and *Chucoa*, but including *Hyalis* D. Don ex Hook. & Arn. and *Nouelia* Franch. in what he called the "*Gochnatia* group", characterized by its cone-like involucre. Bremer (1994), agreed with Hansen in regarding *Actinoseris*, *Cyclolepis*, *Hyalis*, and *Nouelia* as closely related to *Gochnatia*. Roque and Hind (2001) added to Hansen's group the *Chucoa*, *Cnicothamnus*, and the new genus *Ianthopappus* Roque & D.J.N. Hind.

Roque and Pirani (2001) reinstated the genus *Richterago* to include *Actinoseris* together with the species of *Gochnatia* sect. *Discoseris* (Endl.) Cabrera. Later, the *Gochnatia* complex was morphologically defined by Freire et al. (2002) to include genera with glabrous styles and apiculate anther appendages, i.e., *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia* (including the sections *Discoseris* and *Leucomeris* D. Don), *Hyalis*, *Ianthopappus*, and *Nouelia*. Freire et al. (2002) excluded *Chucoa* from the *Gochnatia* complex due to its papillose styles and acute apical appendages.

Recently, Hind (2007) considered *Leucomeris* and *Pentaphorus* D. Don as two genera independent from *Gochnatia*, both previously treated by Cabrera (1971) as sections of this large genus. Moreover, Hind grouped *Leucomeris* and *Nouelia* in a "*Nouelia* group". *Cnicothamnus*, *Cyclolepis*, *Hyalis*, and *Ianthopappus* were placed by him in his subtribe Mutisiinae. Only *Gochnatia*, *Pentaphorus* (formerly a section of *Gochnatia*), and *Richterago* remained together in what Hind called subtribe Gochnatiinae.

PHYLOGENY

Phylogenetic studies based on morphological (Karis et al. 1992) and molecular characters (Jansen and Kim 1996; Kim et al. 2002; Panero and Funk 2002, 2008) showed

Gochnatia and its relatives as an independent lineage of the rest of Mutisieae. On the base of molecular data, the tribe Gochnatieae and the subfamily Gochnatioideae were described by Panero and Funk (2002). According to the tree obtained by Funk et al. (2005) and Panero and Funk (2008), the Gochnatioideae clade is basal to most Asteraceae, excluding the Barnadesioideae, Stifftioideae, Mutisioideae, and Wunderlichioideae clades.

Recently, the subfamily Wunderlichioideae was described by Panero and Funk (2007) based on a molecular study using ten chloroplast loci (Panero and Funk 2008). According to this new treatment, the genera *Hyalis*, *Ianthopappus*, *Leucomeris*, and *Nouelia*, traditionally related to *Gochnatia*, are included in the subfamily Wunderlichioideae, tribe Hyalideae. This grouping disagrees with that proposed by Panero and Funk (2002) in the placement of *Nouelia* and *Leucomeris* formerly placed by them in the Mutisioideae clade.

The Gochnatioideae clade of Panero and Funk (2008) is highly supported and shows *Cyclolepis* as sister to the remaining genera of the subfamily with *Richterago* and *Cnicothamnus* sister to *Gochnatia*.

The Wunderlichioideae clade of Panero and Funk (2008) shows the tribes Hyalideae and Wunderlichieae as monophyletic, although support for that phylogenetic relationship is low.

A generic-level phylogeny of the family can be found in Chapter 44.

TRIBE GOCHNATIEAE

Taxonomy and biogeography

Tribe Gochnatieae Panero & Funk in Proc. Biol. Soc. Wash. 115: 915. 2002 – Type: *Gochnatia* Kunth

Trees, shrubs, subshrubs, or perennial herbs, monoecious, seldom gynodioecious or polygamo-dioecous. Leaves alternate or rosulate, simple, variously linear to orbicular, pinnately veined, coriaceous or subcoriaceous, margins entire or more rarely spinose-dentate. Capitula solitary (or 2–3) at the tip of the branches or several and clustered in pseudo-corymbs, pseudo-racemes or pseudo-panicles; short-pedunculate and glomerulose to long-pedunculate and scapiform. Involucre oblong to campanulate or turbinate, 3–10-seriate, sometimes with bracteolate peduncles. Receptacle epaleate. Florets with corollas variously white to orange, seldom pink, lilac, or purple; few (4–6) to numerous (ca. 300); isomorphic (usually bisexual with tubular actinomorphic corollas deeply to very deeply 5-lobed), subdimorphic (central bisexual florets with tubular actinomorphic corollas, and marginal female florets with tubular, subzygomorphic corollas) or dimorphic (marginal corollas bilabiate or subbilabiate and central corollas tubular, all florets bisexual or the marginal female and central florets bisexual). Anthers 5, with apical appendages apiculate; tails long, smooth to pilose. Style bilobed to shortly branched, lobes rounded at the apex and dorsally glabrous. Achenes pilose. Pappus bristles

Table 15.1. *Gochnatia* and its related genera according to different authors.

Authors	Related genera
Cabrera (1971, 1977)	*Actinoseris*, *Chucoa*, *Cyclolepis*, *Gochnatia*, *Pleiotaxis*
Hansen (1991b)	*Actinoseris*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Nouelia*
Bremer (1994)	*Actinoseris*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Nouelia*
Roque and Hind (2001)	*Actinoseris*, *Chucoa*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, *Nouelia*
Panero and Funk (2002)	*Richterago (including Actinoseris)*, *Chucoa*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*
Freire et al. (2002)	*Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, *Nouelia*
Hind (2007)	*Gochnatia*, *Pentaphorus* (as *Gochnatia* sect. *Pentaphorus* in Cabrera 1971), *Richterago*
Panero and Funk (2007)	*Richterago* (including *Actinoseris*), *Chucoa*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia* (*Hyalis*, *Ianthopappus*, *Leucomeris*, and *Nouelia* treated as subfamily Wunderlichioideae, tribe Hyalideae)
Katinas et al. (in press)	*Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, *Nouelia*
Present paper	*Richterago* (including *Actinoseris*), *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, *Leucomeris*, *Nouelia*

uniseriate with all bristles of the same length or 2- or 3-seriate with a reduced number of outer short bristles, usually all thin (seldom some of them relatively wide and flat) and sometimes with the longest plumose at the apex.

The tribe Gochnatieae (Panero and Funk 2002) comprises four genera (*Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Richterago*) with ca. 88 species in South America, many in the West Indies and a few in Mexico and the United States.

Cnicothamnus Griseb. has two species (*C. azafran* (Cabrera) Cabrera, *C. lorentzii* Griseb.) of shrubs or small trees with large capitula and showy radiating orange marginal corollas. It lives in the subtropical forests of Bolivia and northwestern Argentina in hard and dry soils, between 550 and 2200 m in elevation.

Cyclolepis D. Don. is monotypic. *Cyclolepis genistoides* Gill ex D. Don, (Fig. 15.1A) is shrubby, spiny, subaphyllous, and gynodioecious with discoid capitula of whitish or often pinkish corollas. It is characteristic of salty soils from Paraguay to northern Patagonia in Argentina, between 900 and 1900 m in elevation.

Gochnatia Kunth is the largest genus of the tribe, comprising ca. 65 species of shrubs, or more rarely subshrubs or trees, monoecious, gynodioecious or polygamo-dioecious with discoid capitula of predominantly yellow or cream (more rarely orange or pink) corollas.

Thirty species occur in West Indies: twenty species live on old rocky limestones and serpentines of Cuba, in dry scrubs or diverse forests (Pérez Camacho and Ventosa

Fig. 15.1. **A** *Cyclolepis genistoides* D. Don (tribe Gochnatieae); **B** *Gochnatia polymorpha* (Less.) Cabrera (tribe Gochnatieae); **C** *Gochnatia foliolosa* (D. Don) D. Don ex Hook. & Arn. (tribe Gochnatieae); **D** *Hyalis argentea* D. Don ex Hook. & Arn. (tribe Hyalideae). [Photographs, J.M. Bonifacino.]

Rodriguez 2002) (*G. attenuata* (Britton) Jervis & Alain; *G. calcicola* (Britton) Jervis & Alain; *G. cowellii* (Britton) Jervis & Alain; *G. crassifolia* (Britton) Jervis & Alain; *G. cubensis* (Carabia) R.N. Jervis & Alain; *G. ekmanii* (Urb.) Jervis & Alain; *G. elliptica* (Léon) Alain; *G. gomezii* (Léon) Jervis & Alain; *G. ilicifolia* Less.; *G. intertexta* (C. Wright ex Griseb.) Jervis & Alain; *G. maisiana* (Léon) Jervis & Alain; *G. microcephala* (Griseb.) Jervis & Alain; *G. montana* (Britton) Jervis & Alain; *G. mantuensis* (C. Wright ex Griseb) Jervis & Alain; *G. obtusifolia* (Britton) Jervis & Alain; *G. parvifolia* (Britton) Jervis & Alain; *G. recurva* (Britton) Jervis & Alain; *G. sagraeana* Jervis & Alain; *G. shaferi* (Britton) Jervis & Alain; *G. wilsonii* (Britton) Jervis & Alain); three species live in Dominican Republic (*G. buchii* (Urb.) Jiménez; *G. enneantha* (S.F. Blake) Alain; *G. oligantha* (Urb.) R.A. Howard); four species live in Haiti (*Gochnatia buchii* (Urb.) Jiménez; *G. oligantha* (Urb.) R.A. Howard; *G. picardae* (Urb.) Jiménez; *G. tortuensis* (Urb.) Jiménez); two species live in Bahamas Islands (*G. ilicifolia* Less.; *G. pauciflosculosa* (C. Wright ex Hitchc.) Jervis ex Cabrera); one species occurs in Puerto Rico (*G. ilicifolia* Less.).

Only one species occurs in dry scrublands of southern United States (*G. hypoleuca* (DC.) A. Gray).

Six species inhabit dry and rocky soils and thickets of Mexico (*G. arborescens* Brandegee; *G. hiriartiana* Medrano, Villaseñor & Medina; *G. hypoleuca* (DC.) A. Gray; *G. magna* M.C. Johnst. ex Cabrera; *G. purpusii* Brandegee; *G. smithii* B.L. Rob. & Greenm.).

The rest of the species of *Gochnatia* are from South America, distributed in Argentina (seven species occurring usually in dry slopes of central and northwestern Argentine ranges, dry sandy cliffs, scrublands, or borders of low forest in the North East country: *Gochnatia argentina* (Cabrera) Cabrera; *G. cardenasii* S.F. Blake; *G. cordata* Less.; *G. curviflora* (Griseb.) O. Hoffm.; *G. glutinosa* (D. Don) D. Don ex Hook. & Arn.; *G. palosanto* Cabrera; *G. polymorpha* (Less.) Cabrera, Fig. 15.1B); Brazil (twenty species, mostly occurring in sunny, open, and rocky habitats of eastern Brazil: *G. argyrea* (Dusén ex Malme) Cabrera; *G. barrosoae* Cabrera; *G. blanchetiana* (DC.) Cabrera; *G. cordata* Less.; *G. densicephala* (Cabrera) Sancho; *G. discolor* Baker; *G. floribunda* Cabrera; *G. gardneri* (Baker) Cabrera; *G. hatschbachii* Cabrera; *G. haumaniana* Cabrera; *G. mollisima* (Malme) Cabrera; *G. oligocephala* (Gardner) Cabrera; *G. orbiculata* (Malme) Cabrera; *G. paniculata* (Less.) Cabrera; *G. polymorpha* (Less.) Cabrera; *G. pulchra* Cabrera; *G. ramboi* Cabrera; *G. rotundifolia* Less.; *G. sordida* (Less.) Cabrera; *G. velutina* (Bong.) Cabrera); Bolivia (seven species occurring mainly in thickets or open forests of mountain slopes: *G. angustifolia* Sancho, S.E. Freire & L. Katinas; *G. boliviana* S.F. Blake; *G. cardenasii* S.F. Blake; *G. curviflora* (Griseb.) O. Hoffm.; *G. palosanto* Cabrera; *G. pulchra* Cabrera; *G. rusbyana* Cabrera); Chile (one species from low ranges of the country, reaching habitats near the sea coast: *G. foliolosa* (D. Don) D. Don ex Hook. & Arn., Fig. 15.1C); Guyana (one species occurring in dry forests: *G. oligocephala*); Paraguay (five species living in open and sunny places or on borders of low forests: *Gochnatia barrosoae* Cabrera; *G. cordata* Less.; *G. haumaniana* Cabrera; *G. pulchra* Cabrera; *G. polymorpha* (Less.) Cabrera); Peru (five species from intermontane regions of the country, between 1600 and 3000 m elevation: *G. arequipensis* Sandwith; *G. patazina* Cabrera; *G. rusbyana* Cabrera; *G. vargasii* Cabrera; *G. vernonioides* Kunth; Uruguay (two especies: *G. cordata* Less.; *G. polymorpha* (Less.) Cabrera); and Venezuela (one species occurring in dry forests: *G. oligocephala*).

Richterago Kuntze comprises 17 species of predominately herbs to subshrubs with long-pedunculate capitula solitary, or arranged in scapose pseudo-corymbs. Its capitula may be homogamous or heterogamous, and discoid, with white, yellow or lilac corollas, or radiate, with white or purple marginal corollas. The genus *Richterago* was recently reinstated to include *Actinoseris* and *Gochnatia* sect. *Discoseris* (Roque and Pirani 2001). However, Cabrera's concept of *Actinoseris* (1970) does not include the species of sect. *Discoseris* of *Gochnatia*. Cabrera's concept was followed in later treatments based on morphological characters as habit, capitulum, pappus, and pollen features (Cabrera 1971; Freire et al. 2002; Sancho et al. 2005). These characters would link *G.* sect. *Discoseris* to *Actinoseris* as well as to other representatives of *Gochnatia*. Molecular data (Panero and Funk 2008), however, show *Richterago* as monophyletic.

Currently, *Richterago* includes the species originally belonging to *Actinoseris* (*R. angustifolia* (Gardner) Roque, *R. arenaria* (Baker) Roque, *R. hatschbachii* (Zardini) Roque, *R. polymorpha* (Less.) Roque, *R. polyphylla* (Baker) Ferreyra, *R. radiata* (Vell.) Roque, *R. stenophylla* (Cabrera) Roque), the three species that belonged to *Gochnatia* sect. *Discoseris* (*R. amplexifolia* (Gardner) Roque, *R. discoidea* (Less.) Kuntze, *R. suffrutescens* (Cabrera) Roque) and seven recently described new species (*R. campestris* Roque & J.N. Nakaj., *R. petiolata* Roque & J.N. Nakaj., *R. caulescens* Roque, *R. conduplicata* Roque, *R. elegans* Roque, *R. lanata* Roque, *R. riparia* Roque; Roque 2001; Roque and Nakajima 2001). The species of *Richterago* occur in sandy and rocky soils of "campos rupestres", in sunny and grassy places mainly of Minas Gerais ranges, Brazil.

Morphology

Capitula and sexual arrangements. — Gochnatieae may be monoecious, gynodioecious, or polygamo-dioecious. Thus, in monoecious species, plants have homogamous capitula with all bisexual florets (as in some species of *Richterago*, *Cnicothamnus*, and most species of *Gochnatia*) or heterogamous capitula with female or functionally female (with staminodes) marginal florets and bisexual central florets (as in some species of *Richterago*). *Richterago* was described by Cabrera (as *Actinoseris*, 1970) as having both marginal and central florets bisexual; since then, staminodes have been described for the marginal florets of *Richterago*, which were regarded as functionally female (e.g., Roque and Pirani 2001; Roque and Hind 2001). Gynodioecious species, as in *Cyclolepis* and *Gochnatia* sect. *Moquiniastrum*, have homogamous capitula with all female florets in one plant and capitula with all bisexual florets in other plant. (e.g., *G. blanchetiana*, *G. floribunda*, *G. paniculata*). Gynodioecy has been seen as an advanced character compared to monoecious species since it represents specialization of capitula (Hansen 1991b). Polygamodioecious species, as in *Gochnatia* sect. *Moquiniastrum*, have homogamous capitula with all female florets in one plant and heterogamous capitula with marginal functionally female florets (with staminodes) and central bisexual florets in other plant (e.g., *G. haumaniana*, *G. orbiculata*, *G. sordida*). Occasionally, in polygamous species, capitula with all bisexual florets may be also found as in, e.g., *Gochnatia polymorpha*.

Corollas and sexual arrangements. — Within the same capitulum, corollas of Gochnatieae may be isomorphic, subdimorphic, or dimorphic. Isomorphic corollas are actinomorphic, tubular, and deeply 5-lobed with the lobes coiled (the lobes straight in most Caribbean species of *Gochnatia*). These corollas are characteristic of discoid capitula of *Gochnatia* (Fig. 15.2C) (except in *Gochnatia* sect. *Moquiniastrum*, which has nearly disciform capitula) and a few species of *Richterago* (e.g., *R. amplexifolia*, *R. discoidea*, and *R. suffrutescens*, all of them once belonging to *Gochnatia* sect. *Discoseris*). Subdimorphic corollas may be in the same head in disciform heterogamous capitula of many species of *Gochnatia* sect. *Moquiniastrum*, or they may be in heads of different plants as in the gynodioecious *Cyclolepis*. *Gochnatia* is very stable in features of corolla and sex arrangement (i.e., discoid capitula with all bisexual florets of tubular deeply 5-lobed corollas). However, only its section *Moquiniastrum* is variable in sex arrangement of capitula and corolla shape, which varies from the standard actinomorphic tubular corollas of the rest of *Gochnatia* (i.e., marginal subzygomorphic corollas with one or two deeper lobes; Fig. 15.2D) (Sancho 2000). Subdimorphic corollas of *Gochnatia* could represent an initial step to the specialization of capitula. In *Cyclolepis*, bisexual plants have heads with typical tubular deeply 5-lobed corollas, whereas female plants have heads with tubular, relatively shallowly 5-lobed corollas (Fig. 15.2B). Dimorphic corollas are in radiate homogamous (i.e., *Cnicothamnus*; Fig. 15.2A) or heterogamous capitula (some species of *Richterago*; Fig. 15.2E). Marginal florets have bilabiate corollas with an external 3-dentate lip and internal 2-cleft lip (e.g., *R. campestris*) or subbilabiate ("pseudobilabiate" according to Bremer, 1994) corollas with an external 3-dentate lip and one entire internal lip (e.g., *Cnicothamnus*, *R. hatschbachii*, *R. polyphylla*; Fig. 15.2A, E). Central florets of radiate capitula have tubular, deeply 5-lobed corollas, with the lobes coiled.

Anthers. — The anthers of Gochnatieae are basally caudate and have an apical appendage not constricted at the base (Fig. 15.3A–D). Anther tails are free, laciniate, in one or both sides (e.g., *Cyclolepis*, most species of *Gochnatia*, *Richterago*; Fig. 15.3B–D) or they are smooth (e.g., most Caribbean species of *Gochnatia*, some species of *G.* sect. *Hedraiophyllum*, *Cnicothamnus* [Fig. 15.3A]). The anther apical appendages have been described as apiculate and show further variation in its shape. Apiculate apical appendages of anthers, common to all species of *Gochnatia* and its traditional relatives, have been strongly considered to be an advanced character within Mutisieae in its wide concept (Cabrera 1977; Karis et al. 1992; Bremer 1994).

Style. — Style branches of Gochnatieae are apically rounded and dorsally smooth (Fig. 15.3I–L). The inner surface of style branches is completely covered by stigmatic papillae, which in some cases prolong into a ridge over the outer surface (Fig. 15.3J, L).

Pappus. — All the members of Gochnatieae have a pappus of scabrid bristles. However, variation on bristle features leads to identify different types of pappus. According to Freire et al. (2002), pappus variation of *Gochnatia* has, indeed, allowed the distinction of sections within this genus. Freire et al. (2002) established five types of pappus in Gochnatieae and its morphologically related Hyalideae. Four of those five types of pappus are present in Gochnatieae, i.e., type A, with all bristles of the same length and width (Caribbean species of *Gochnatia*, and *Richterago*); type B, with half of its bristles shorter than the others (South American species of *Gochnatia*); and type D, with the longest bristles relatively wide and flat (*Gochnatia* sect. *Pentaphorus* and *Cnicothamnus*); and a variant of this type, i.e., type E, with longest bristles plumose at the apex (*Cyclolepis*).

Vestiture. — Gochnatieae has interesting and rich variations in trichome morphology (Fig. 15.3Q–V). Freire et al. (2002) have identified four types of leaf trichomes: *(1)* 3- to 5-armed hairs (*Gochnatia barrosoae* and *G. rusbyana* of sect. *Moquiniastrum*) (Fig. 15.3Q); *(2)* 2-armed hairs (e.g., *Gochnatia* sect. *Moquiniastrum*, *G. cordata*, *Cyclolepis* (Fig. 15.3R, S); *(3)* oblique septate hairs (e.g., in most species of *Gochnatia*, *Cnicothamnus*, and *Richterago*) (Fig. 15.3T–V); *(4)* biseriate glandular hairs (present in most species of Gochnatieae). Achenial pubescence also shows high variation. Besides twin hairs, the typical achenial trichomes of Compositae, leaf-like hairs (i.e., 2-armed hairs in *Gochnatia orbiculata*, and oblique-septate hairs in, e.g., *G. cubensis*, *G. ramboi*) and biseriate glandular hairs have been found covering the achenial surface.

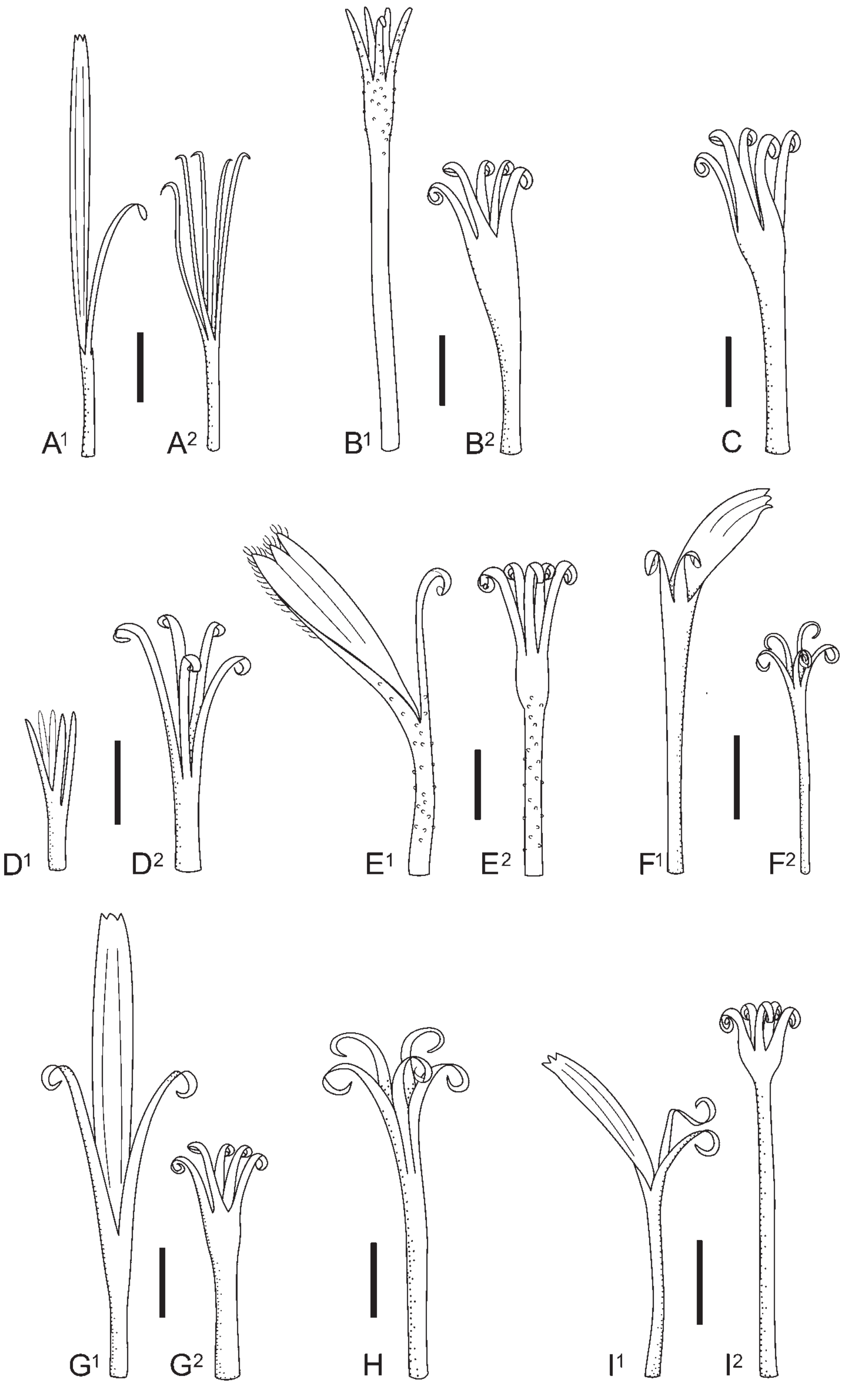

Fig. 15.2. Corollas. **A–E** Gochnatieae. **A** *Cnicothamnus lorentzii* Griseb. (*Cabrera et al. 22576*, LP). **B** *Cyclolepis genistoides* D. Don: B^1, corolla of female floret (*Stuckert 4606*, LP); B^2, corolla of bisexual floret (*Cabrera 6641*, LP). **C** *Gochnatia magna* M.C. Johnst. ex Cabrera (*Cronquist 11277*, NY). **D** *Gochnatia polymorpha* (Less.) Cabrera (*Hashimoto 624*, LP). **E** *Richterago polyphylla* (Baker) Ferreyra (*Hatschbach 35304*, LP). **F–I** Hyalideae. **F** *Hyalis lancifolia* Baker (*Schinini 16098*, LP). **G** *Ianthopappus corymbosus* (Less.) Roque & D.J.N Hind (*Palacios and Cuezzo 2304*, LP). **H** *Leucomeris decora* Kurz. (*Maung Mya 5309*, LP). **I** *Nouelia insignis* Franch. (*Maire 2516*, NY). Superscripts in A, B, D–G, I: 1 = marginal corollas; 2 = disc corollas. Scale bars: A = 6 mm; B, C, E = 2 mm; D, F, H, I = 5 mm; G = 3 mm. [Modified from Freire et al. 2002.]

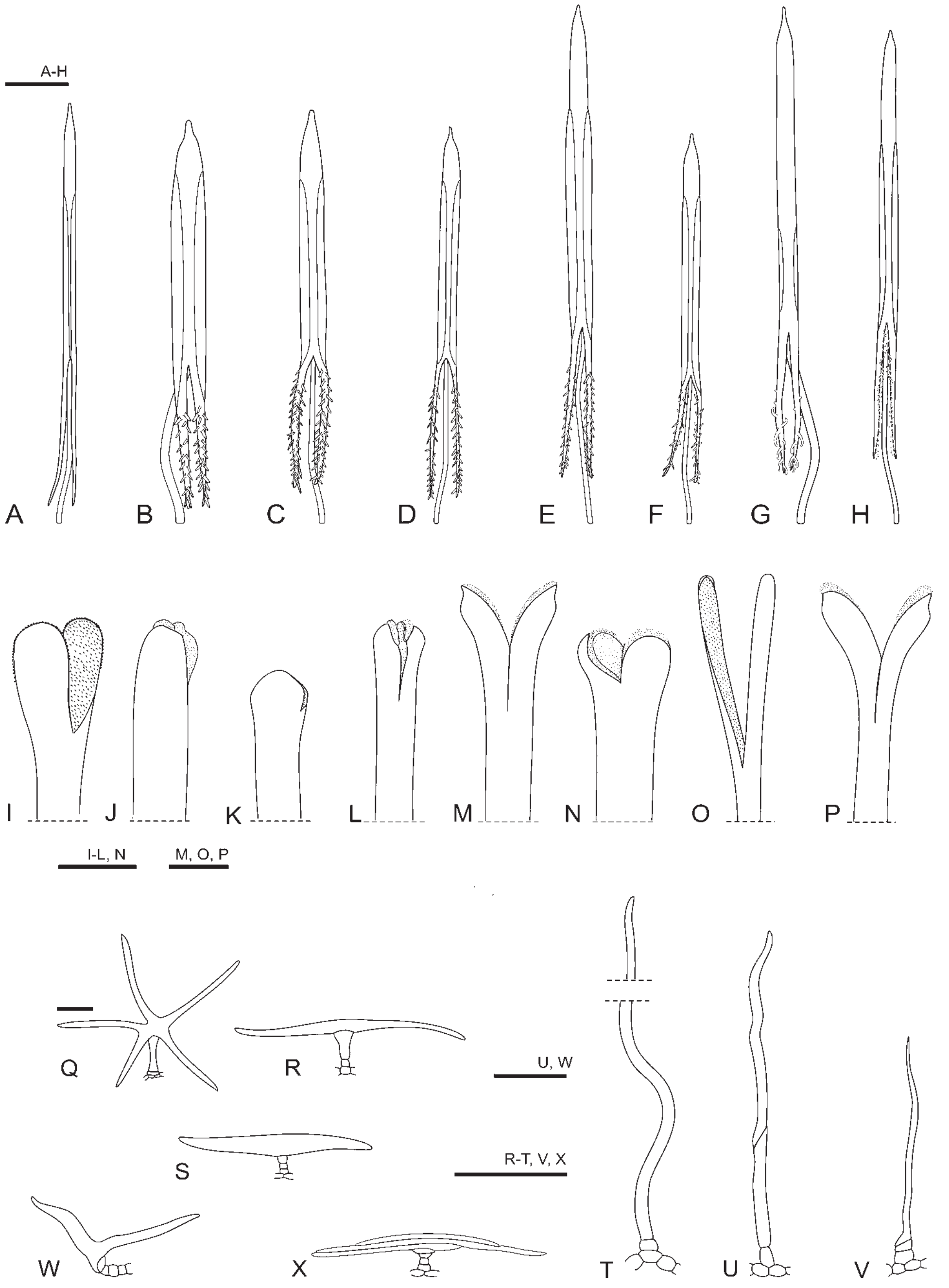

Fig. 15.3. A–H Stamens. **A–D** Gochnatieae. **A** *Cnicothamnus azafran* (Cabrera) Cabrera (*Cabrera et al. 26287*, LP); **B** *Cyclolepis genistoides* D. Don (*Correa and Nicora 3172*, LP); **C** *Gochnatia vernonioides* Kunth (*López and Sagástegui 3354*, LP); **D** *Richterago radiata* (Vell.) Roque (*Hatschbach 690*, LP). **E–H** Hyalideae. **E** *Hyalis lancifolia* Baker (*Cabrera 4083*, LP); **F** *Ianthopappus corymbosus* (Less.) Roque & D.J.N. Hind (*Palacios and Cuezzo 2304*, LP); **G** *Leucomeris decora* Kurz. (*Maung Mya 5309*, LP); **H** *Nouelia insignis* Franch. (*Maire 2516*, NY). **I–P** Style branches. **I–L** Gochnatieae. **I** *Cnicothamnus lorentzii* Griseb. (*Ruiz et al. 14162*, LP); **J** *Cyclolepis genistoides* (*Zardini and Kiesling 114*, LP); **K** *Gochnatia cordata* Less. (*Rambo 545*, LP); **L** *Richterago angustifolia* (Gardner) Roque (*Hatschbach 28756*, LP). **M–P** Hyalideae. **M** *Hyalis argentea* D. Don ex Hook. & Arn. (*Ruiz et al. 3701*, LP); **N** *Ianthopappus corymbosus* (*Palacios and Cuezzo 2304*, LP); **O** *Leucomeris decora* (*Maung Mya 5309*, LP); **P** *Nouelia insignis* (*Maire 2516*, NY). **Q–X** Trichomes. **Q** *Gochnatia barrosoae* Cabrera (*Hatschbach 16945*, LP); **R** *Gochnatia polymorpha* (Less.) Cabrera (*Pedersen 8587*, LP); **S** *Cyclolepis genistoides* (*Correa and Nicora 3172*, LP); **T** *Cnicothamnus lorentzii* (*Padaci 84*, LP); **U** *Gochnatia tortuensis* (Urb. J. Jiménez Alm. (*Ekman H-3553*, S); **V** *Richterago polyphylla* (Baker) Ferreyra (*Hatschbach 35304*, LP); **W** *Nouelia insignis* (*Maire 2516*, NY); **X**, *Ianthopappus corymbosus* (*Palacios and Cuezzo 2304*, LP). Scale bars: A = 2.5 mm; B, C = 0.8 mm; D, F = 1.2 mm; E, G, O = 1 mm; H = 1.8 mm; I–N, P = 0.5 mm; Q–X = 0.1 mm. [Modified from Freire et al. 2002.]

Pollen

Pollen of some species of *Gochnatia* was first studied by Parra and Marticorena (1972). Subsequent studies also analyzed the pollen features of some members of Gochnatieae (Roque and Silvestre-Capelato 2001; Tellería and Forcone 2002; Lin et al. 2005; Zhao et al. 2006). Recently, Katinas et al. (2008) completed an analysis of pollen of Mutisieae s.l. including all representatives of the tribe Gochnatieae.

Pollen grains of Gochnatieae have been described as spheroidal to prolate, elliptic or spheroidal in equatorial view, circular in polar view, medium to large size, tricolporate, colpi relatively short or long, with acute or obtuse ends, endoaperture lalongate, exine *Mutisia* type or *Wunderlichia* type in some species of *Gochnatia* (Tellería et al. 2003; Katinas et al. 2008), scabrous, microechinate, or equinate, thickened or not at the mesocolpium.

Pollen features of *Gochnatia* sect. *Discoseris* (now placed in *Richterago*) have been indicated as somewhat different from those typical of the genus (Roque and Silvestre-Capelato 2001), although, in *Gochnatia*, features as pollen size, exine thickness, and spine height highly vary along the whole genus and its different sections (Sancho et al. 2005; Katinas et al. 2008).

According to Lin et al. (2005), the pollen of some species of *Gochnatia* shows similarities with that of *Nouelia* (tribe Hyalideae), specifically in exine sculpturing (macrogranulate in both genera). On the other hand, exine sculpturing of pollen of *Gochnatia* differs from that of *Leucomeris* (once regarded as *Gochnatia* sect. *Leucomeris*), i.e., macrogranulate in *Gochnatia* and fine granular in *Leucomeris*.

Chromosome number

Karyological data are available for three genera of Gochnatieae. *Cnicothamnus lorentzii* was recorded with $2n = 44$ (Cristóbal 1986), which may indicate a basic number of $x = 4$, *Cyclolepis genistoides* with $2n = 54$ (Covas and Schnack 1947), with an apparent basic number $x = 9$, and *Gochnatia vernonioides* with $n = 23$ (Carr et al. 1999), with an apparent basic number of $x = 23$.

Chemistry

An extensive compilation of information and new studies of chemistry of the old "subtribe Gochnatiinae" (that included the present tribes Hyalideae and Gochnatieae among others) has been provided by Catalán et al. (1996). Sampling of that work is not complete but some remarks are worthy: *(1)* the presence of sesquiterpene lactones in Gochnatieae (e.g., germacranolides and guaianolides in *Cnicothamnus*, germacranolides in *Richterago*, and germacranolides, guaianolides, and eudesmanolides in *Gochnatia*); *(2)* acetylenic compounds and tiophenes derivatives in *Cnicothamnus* and *Gochnatia*; and *(3)* diterpenes in *Gochnatia*.

Floral biology

Floral biology has not been well studied in Gochnatieae. However, two types of pollination syndromes have been indicated in the group: bird pollination and Hymenoptera pollination. Bird pollination is not usual in Compositae and has been described only in a few members mainly of the tribes Mutisieae and Cardueae (Leppik 1977). One of the few representatives of Compositae where pollination by birds occurs is the genus *Cnicothamnus* (Leppik 1977). The large size of its capitula, colorful deep orange or red radiating marginal corollas, and colorful protruding anthers are features that coincide with those indicated for bird pollinated plants (Proctor et al. 1996). Pollination by Hymenoptera is the most common and widespread in Compositae (Lane 1996). Within *Gochnatia*, pollination by bees (*Apis mellifera*) has been described in *Gochnatia polymorpha* (Sancho 2000). Moreover, pollen of this species as well as *Gochnatia paniculata* and *Richterago amplexifolia* has been indicated as a source for bees (Faria 1994; Barth and Fernandes Pinto da Luz 1998). The main rewards for Hymenoptera are pollen and nectar. Nectaries were described in *Gochnatia polymorpha* (Sancho and Otegui 2000). The nectary of this species is placed at the base of the style, is not vascularized, and exudes nectar through stomata, as those described for the family (Fahn 1979; Gopinathan and Varatharajan 1982).

Economic uses

Economic uses in tribe Gochnatieae have been poorly recorded. Bark of *Gochnatia polymorpha* subsp. *ceanothifolia* has different industrial applications (Arechavaleta 1906). The leaves of this same subspecies were indicated as anticatarrhal and medicinal for respiratory diseases (Cabrera 1971; Arambarri et al. 2006). Plants of *Cnicothamnus* with its showy and colorful capitula could be used as ornamental. From pollen analysis of honey from some areas of Brazil (Barth and Fernandes Pinto da Luz 1998) it is known that pollen of *Gochnatia polymorpha* is an important melliferous resource, and then a possible source for production of organic honey.

TRIBE HYALIDEAE

Taxonomy and biogeography

Tribe Hyalideae Panero in Phytologia 89: 358. 2007 – Type: *Hyalis* D. Don ex Hook. & Arn.

Small trees, shrubs, or subshrubs, monoecious. Leaves alternate, simple with margins entire or denticulate, variously linear to ovate or obovate, pinnately-veined or 3-veined (actinodromus), herbaceous or subcoriaceous. Capitula solitary (2 or 3) at the tip of the branches or several and arranged in pseudo-corymbs, short-pedunculate and glomerulose or long-pedunculate and scapiform.

Involucre oblong to campanulate or turbinate, several-seriate (7–10 rows) or more commonly few-seriate (3–6 rows). Receptacle epaleate. Florets with corollas white, pink, or purple, rarely yellow; few (4–6) to many (30–50); isomorphic (bisexual with tubular corollas deeply 5-lobed) or dimorphic (marginal corollas bilabiate and central corollas tubular, all florets bisexual or marginal florets female and central florets bisexual). Anthers 5, usually with apical appendages apiculate; tails long, pilose. Style branches bilobed to shortly branched, rounded at the apex and dorsally glabrous. Achenes pilose. Pappus bristles 2- or 3-seriate with a reduced number of outer shorter bristles, all thin and sometimes with the longest plumose at the apex.

The new tribe Hyalideae (Panero and Funk 2007), includes four South American and Asian genera (*Hyalis*, *Ianthopappus*, *Leucomeris*, and *Nouelia*).

The genus **Hyalis** D. Don ex Hook. & Arn., comprises two species (*H. argentea* D. Don ex Hook. & Arn., *H. lancifolia* Baker) of subshrubs with homogamous capitula, radiating pink marginal corollas, and only one central floret with also pink corolla. It grows in sandy areas or hard and clayish soils on herbaceous plains. It is also found in forests of northern and western Argentina, Bolivia, and Paraguay. Its species usually form extensive populations recognizable by their pink flowers (Fig. 15.1D).

The genus **Ianthopappus** (Less.) Roque & D.J.N. Hind. contains only one species (*I. corymbosus* (Less.) Roque & D.J.N. Hind) of subshrubs with heterogamous capitula, radiating white marginal corollas and purple central corollas. It lives in eastern Argentina, southeastern Brazil, and northwestern Uruguay, growing in steppes and steppe-like savannas.

Leucomeris D. Don includes two species of small trees living in dry deciduous forests of southeastern Asia: *L. decora* Kurz (China, Burma, India, Laos, Thailand, and Vietnam) and *L. spectabilis* D. Don. (India, Nepal, Pakistan, Burma). The species of *Leucomeris* have isomorphic small capitula grouped in capitulescences, and all actinomorphic florets with whitish tubular corollas. These features, in addition to style and anther characteristics, place together *Leucomeris* and *Gochnatia*. Indeed, Cabrera (1971) regarded these two Asian species as a section of *Gochnatia* (*G.* sect. *Leucomeris*) due to its dorsally glabrous phyllaries. *Nouelia*, the other Asian representative of Hyalideae, shares with *Leucomeris* glabrous styles and apiculate anthers. However, the large, solitary, and dimorphic capitula with several-seriate involucres and bilabiate marginal corollas of *Nouelia* are different from those capitula of *Leucomeris*.

The Asian **Nouelia** Franch. includes one species (*N. insignis* Franch.) of shrubs or small trees with homogamous, dimorphic, large and showy capitula. The capitula have conspicuously several-seriate involucres, white radiating, marginal bilabiate corollas, and yellow, tubular central corollas. It is endemic to forests of Sichuan and Yunnan provinces of China. *Nouelia insignis* is an endangered species and most of the populations are seriously threatened, some of them even at the brink of extinction (Luan et al. 2006)

Morphology

Capitula and sexual arrangements. — Hyalideae is monoicous (*Leucomeris*; Fig. 15.2H). Thus, plants have homogamous capitula with all bisexual florets (*Hyalis*, *Leucomeris*, and *Nouelia*) or heterogamous capitula with functionally female (with staminodes) marginal florets and bisexual central florets (*Ianthopappus*).

Corollas and sexual arrangements. — Within the same capitulum, corollas of Hyalideae may be isomorphic or dimorphic. Isomorphic corollas are actinomorphic, tubular, and usually deeply 5-lobed with the lobes coiled (*Leucomeris*). Dimorphic corollas are in radiate homogamous (*Hyalis*, *Nouelia*; Fig. 15.2F, I) or occasionally heterogamous capitula (*Ianthopappus*; Fig. 15.2G). Marginal florets have bilabiate corollas with an external 3-dentate lip and internal 2-cleft lip. Central florets of radiate capitula have tubular, deeply 5-lobed corollas, with the lobes coiled.

Anthers. — The anthers of Hyalideae are basally caudate and have an apical appendage not constricted at the base. Anther tails are free and laciniate, in one or both sides (Fig. 15.3E–H). The anther apical appendages have been described as apiculate and show further variation in shape.

Style. — Style branches of Hyalideae as in Gochnatieae are apically rounded and dorsally smooth (Fig. 15.3M–P). The inner surface of style branches is completely covered by stigmatic papillae, which in some cases prolong into a ridge over the outer surface (Fig. 15.3N, P).

Pappus. — All the members of Hyalideae have a pappus of scabrid bristles. Among the five types of pappus established by Freire et al. (2002) in Gochnatieae and its morphologically related genera (including Hyalideae), only two are present in Hyalideae, i.e., Type B, with half of its bristles shorter than the others, and Type C (a variant of Type B) with the longest bristles plumose at the apex (only present in *Ianthopappus*).

Vestiture. — Four types of leaf trichomes were identified in Hyalideae (Freire at al. 2002) (Fig. 15.3): *(1)* 2-armed hairs (e.g., *Hyalis argentea*, *Nouelia*; Fig. 15.3W); *(2)* Multistoried 2-armed hairs (present only in *Ianthopappus*; Fig. 15.3X); *(3)* oblique septate hairs (e.g., *Leucomeris*); *(4)* biseriate glandular hairs (present in most species of Hyalideae).

Multistoried 2-armed hairs of *Ianthopappus* seem to come from consecutive division of the apical cell of 2-armed hairs, although studies of the ontogeny of these trichomes have not been performed.

Pollen

Pollen of some species of Hyalideae was studied by, e.g., Hansen (1991a), Lin et al. (2005), Tellería et al. (2003), and Zhao et al. (2006). Pollen grains of Hyalideae have been described as subprolate to prolate, elliptic in equatorial view, circular or subtriangular in polar view, large size (seldom medium size), tricolporate, colpi relatively long, endoaperture lalongate, exine *Mutisia* type (Tellería et al. 2003; Katinas et al. 2008), scabrate or microechinate.

Exine sculpturing has been described as macrogranulate in *Nouelia* and fine granulate in *Leucomeris*.

When compared with Gochnatieae, an infratectum thicker than tectum was indicated in *Ianthopappus* (Roque and Silvestre-Capelato 2001). On the other hand, pollen features of *Leucomeris* (formerly *Gochnatia* sect. *Leucomeris*) have been indicated as somewhat different from those typical of *Gochnatia*, whereas pollen of *Nouelia* and *Gochnatia* has shown similarities in exine sculpturing (Lin et al. 2005).

Chromosome number

Karyological data are available for two of the four genera of Hyalideae, i.e., *Leucomeris decora* with $2n = 54$ (Peng et al. 2002), and *Nouelia insignis* with $2n = 54$ (Peng et al. 2002).

Chemistry

Chemistry in tribe Hyalideae has been very poorly recorded. Recently, two new diterpenes have been isolated in *Nouelia insignis* (Hu et al. 2008).

DISCUSSION AND CONCLUSION

Molecular and morphological data combined support the tribe Hyalideae as well as the tribe Gochnatieae. All four genera of the new tribe Hyalideae have a pappus of thin bristles, some of the outermost shorter, dorsally glabrous style branches and corollas white to purple. *Hyalis, Ianthopappus and Leucomeris* have 3–6-seriate involucres and capitula arranged in pseudo-corymbs. These characteristics are lacking in *Nouelia* (that has several-seriate involucres and capitulescences of only 2 or 3 capitula), but *Nouelia* shares with *Leucomeris* the chromosome number $2n = 54$, and with *Hyalis* and *Ianthopappus* the bilabiate corollas.

Molecular phylogeny gives strong support to monophyly of the tribe Gochnatieae, and two morphological characteristics support this clade, i.e., dorsally glabrous style branches and apiculate apical appendages of anthers, in combination with deeply 5-lobed corollas. Molecular data also support the monophyly of *Richterago* as proposed by Roque and Pirani (2001).

Morphological and recent molecular data (Panero and Funk 2008) suggest different relationships for tribe Hyalideae. While morphological characters as well as pollen features (in the case of *Nouelia*; Lin et al. 2005) group the tribes Gochnatieae and Hyalideae, molecular data group Hyalideae to some genera centered in the Guayana Highland (e.g., *Chimantaea*, *Stomatochaeta*) and *Wunderlichia*. From a morphological point of view, the tribes Gochnatieae and Hyalideae together constitute a unit. Apiculate anther apical appendage and round smooth style branches are the diagnostic characters that support the relationships of *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, *Leucomeris*, *Nouelia* and *Richterago*. These two characters are present in the two tribes together with other characters as deeply 5-lobed corollas and 2-armed hairs, this last in some of the representatives of both tribes. This combination of characters is unique in Asteraceae. Although some of these characters could be found in some other groups or genera (i.e., glabrous styles, deeply 5-lobed corollas, etc.), they never are found all together as in Hyalideae and Gochnatieae. Value of all these characters can be discussed in terms of apomorphies or plesiomorphies, although in some cases that could depend on the most basal group that is taken in consideration. There are other characters as type of pappus (i.e., Type B, shared by Hyalideae and South American species of *Gochnatia*; Freire et al. 2002), corolla color (e.g., whitish in *Gochnatia rotundifolia* and *Leucomeris*, pink in *Gochnatia foliolosa* and *Hyalis*; Fig. 15.1C, D), number of series of phyllaries (e.g., few series, 3 to 4, in for instance *Cyclolepis*, *Hyalis* and *Leucomeris*; or many series, 7 to 10, in *Cnicothamnus*, some Caribbean species of *Gochnatia*, and *Nouelia*), chromosome numbers (i.e., $2n = 54$ in *Cyclolepis*, *Nouelia* and *Leucomeris*; Peng et al. 2002), and pollen features (e.g., macrogranulate exina present in *Nouelia* and some species of *Gochnatia*; Lin et al. 2005) that are also shared by members of both Hyalideae and Gochnatieae. However, molecular studies have provided new hypotheses, showing these two tribes in different clades. From this new point of view, the set of morphological characters shared by both tribes could be explained by parallel evolution.

As previously pointed out, recent molecular studies (Panero and Funk 2008) have recovered in the same clade the tribes Hyalideae and Wunderlichieae that includes the Brazilian *Wunderlichia* and some genera centered in the Guayana Highland (i.e., *Chimantaea*, *Stenopadus*, *Stomatochaeta*). Hyalideae and Wunderlichieae share apiculate apical appendages of anthers, although anther appendices of the included Guayana-centered genera have been also treated as "acuminate". In contrast, these Guayana-centered genera together with *Wunderlichia* have totally different styles (i.e., dorsally rugulose even beyond to the bifurcation point of branches; Katinas et al. 2008) and pollen features (Katinas et al. 2008) as well as different receptacles (e.g., commonly paleate or partially paleate in *Wunderlichia* and its related Guayana-centered genera vs. epaleate in Hyalideae) and pappus (some or all bristles relatively wide and flat at the base or at the apex in

Wunderlichieae vs. all thin bristles in Hyalideae; Freire et al. 2002; Katinas et al. 2008).

The diagnostic characters of style and anthers of the tribe Gochnatieae support morphologically the exclusion of *Chucoa*, which was doubtfully placed in this tribe (Panero and Funk 2002). Until now, molecular data have not elucidated the placement of *Chucoa*, which based on its morphological characters (i.e., acute anther apical appendages, papillose styles, and shallowly 5-lobed tubular corollas), could be treated within the Mutisioideae clade (Chapter 14), may be close to *Onoseris* and relatives.

As in the case of *Chucoa*, little is known about monophyly of *Gochnatia*. Morphologically *Gochnatia* s.l. (including all of Cabrera's sections) is easely recognized by its discoid capitula, apiculate anther apical appendages, and smooth and round style branches, together with all deeply 5-lobed corollas, which are constant and always present in all the species of this large genus. However, some groups of species (treated as sections) are morphologically well defined and identifiable (Cabrera 1971; Freire et al. 2002). Even if some sections of *Gochnatia* are treated as genera (e.g., *Leucomeris*, *Pentaphorus*) other groups remain to be addressed. Taking this into account, a profound analysis carried out on the whole genus and considering all the identifiable groups of *Gochnatia* is needed to define phylogenetic relationships of this intriguing group.

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Chapter 16

Hecastocleideae (Hecastocleidoideae)

Vicki A. Funk and D.J. Nicholas Hind

HISTORICAL OVERVIEW AND MORPHOLOGY

Hecastocleis shockleyi A. Gray was described in 1882 and its unusual morphology and restricted distribution has made it sought after for herbarium specimens. This shrub is easily identified because of its single flowered heads that are re-aggregated on a receptacle in groups of one to five heads; each group of heads is subtended by a relatively large spiny whitish or greenish bract (Fig. 16.1). Gray (1882) commented that is was "a remarkable addition to the few known North American Mutisieae, to stand near *Ainsliaea* DC. but altogether *sui generis* and of peculiar habit." According to Williams (1977) the generic name *Hecastocleis*, "… comes from the Greek roots, *ekastos* meaning 'each' and *kleio* meaning 'to shut up' ", referring to each flower having its own involucre. The species was named after William H. Shockley one of the first botanical collectors from Nevada (Barneby 1977). Bremer (1994) placed the genus in the tribe Mutisieae subtribe Mutisiinae, and Hind (2007) placed it in Mutisieae in a group by itself.

PHYLOGENY

Hecastocleis has always been placed in Mutisieae (Cabrera 1977). The first molecular evidence concerning the relationship of the genus was presented by Panero and Funk (2002, 2008); they reported that the genus did not belong in any existing tribe or subfamily and placed it in its own tribe, Hecastocleideae, and subfamily, Hecastocleidoideae. The monotypic genus occupies the node just below the Carduoideae—'rest of the family' split (see Chapters 12 and 44) and this placement has 100% bootstrap support. Its current position is supported by its distinct morphology and strong support from molecular data. Its nearest downstream neighbor, however, is somewhat tenuous, because the position of the branch just below it (Gochnatieae) has only 65% bootstrap support (Panero and Funk 2008) and might collapse into a polytomy with Mutisieae s.str. If one does the phylogenetic analysis without *Hecastocleis*, there is no change in the phylogeny of the family.

TAXONOMY

The genus is monotypic and has always been recognized as such since its original description by Gray (1882).

Subfamily Hecastocleidoideae

Tribe Hecastocleideae Panero & V.A. Funk in Proc. Biol. Soc. Wash. 115: 909–922. 2002 – Type: *Hecastocleis shockleyi* A. Gray in Bot. Gaz. 7: 100–101. 1882.

Subshrubs or shrubs to 40–80(–150) cm. Leaves alternate, cauline, sessile, blades linear to narrowly ovate with three main veins, stiff, margins entire, apex acute usually with a spine, base attenuate, margins with a few spines, surfaces glabrous or minutely tomentose. Heads single-flowered, clustered in second-order heads, each cluster with 1–5 heads and subtended by ovate to orbiculate bracts with spiny margins. Involucres (each enclosing one floret) cylindric to fusiform, 10 mm. Receptacle flat, naked. Florets 1, bisexual, fertile; corollas reddish purple

Fig. 16.1. *Hecastocleis shockleyi* A. Gray. **A** Red Pass, high point on the road to Titus Canyon, Death Valley, California, USA, *Hecastocleis* in the foreground; **B** habit; **C** close up of florets, involucre tightly appressed to single-flowered heads and bracts (greenish); **D** close up of several single-flowered heads, corollas deeply lobed, pink turning white, bracts whitish. [Photographs, V.A. Funk of *Funk et al. 12487–12488*.]

to greenish white, actinomorphic, deeply 5-lobed; stamens 5, anther basal appendages slightly fimbriate, apical appendages lanceolate to acute; style branches short (0.1–0.5 mm), apices rounded. Achene terete, not beaked, obscurely 4–5-nerved, glabrescent; pappus of six unequal, lanceolate or multi-toothed scales sometimes fused to form lacerate crowns. — Information for this description was taken from several sources (Keil 1993; Panero and Funk 2002; Simpson 2006; Hind 2007, and pers. obs.).

Hecastocleis is obviously a well-defined genus without close relatives and confined to high elevations (ca. 5000 ft) in southern Nevada and adjacent California (Fig. 16.1A). It is easily recognizable from a distance by its relatively large whitish to greenish bracts that subtend the clusters of single flowered heads (Fig. 16.1A–D).

POLLEN

The pollen of *Hecastocleis* is psilate and tricolpate (Fig. 16.2). The presence of colpate pollen is believed to be unusual in the family (it has never been surveyed for this character), and its presence in this genus was first pointed out by Tellería and Katinas (2005); Fig. 16.2 confirms this finding and shows the colpi to contain "pebbly" or "scabrate" particles. Figures 16.2B–D do not indicate a pore in the colpi, but the good pollen preservation may actually be covering it up. Figure 16.2E is important because if a pore were present, it would show in this "inside" view of the colpus, and it does not. The exine of the pollen of *H. shockleyi* is scabrate-microechinate with small puncta; the exine is regularly thickened over the complete grain (Tellería and Katinas 2005).

Wodehouse (1929), based on his examination of the pollen and the literature, stated that "*Hecastocleis* is a monotypic genus with no close connections in the tribe, but is regarded as closest to *Ainsliaea*; its pollen grains are rather dissimilar to any in the tribe, but show greatest similarity to those of *Ainsliaea*". Tellería and Katinas (2005) stated that the tricolpate pollen supported the previous hypothesis that *Hecastocleis* and *Ainsliaea* were related but noted that the psilate, regularly thickened exine, did not support

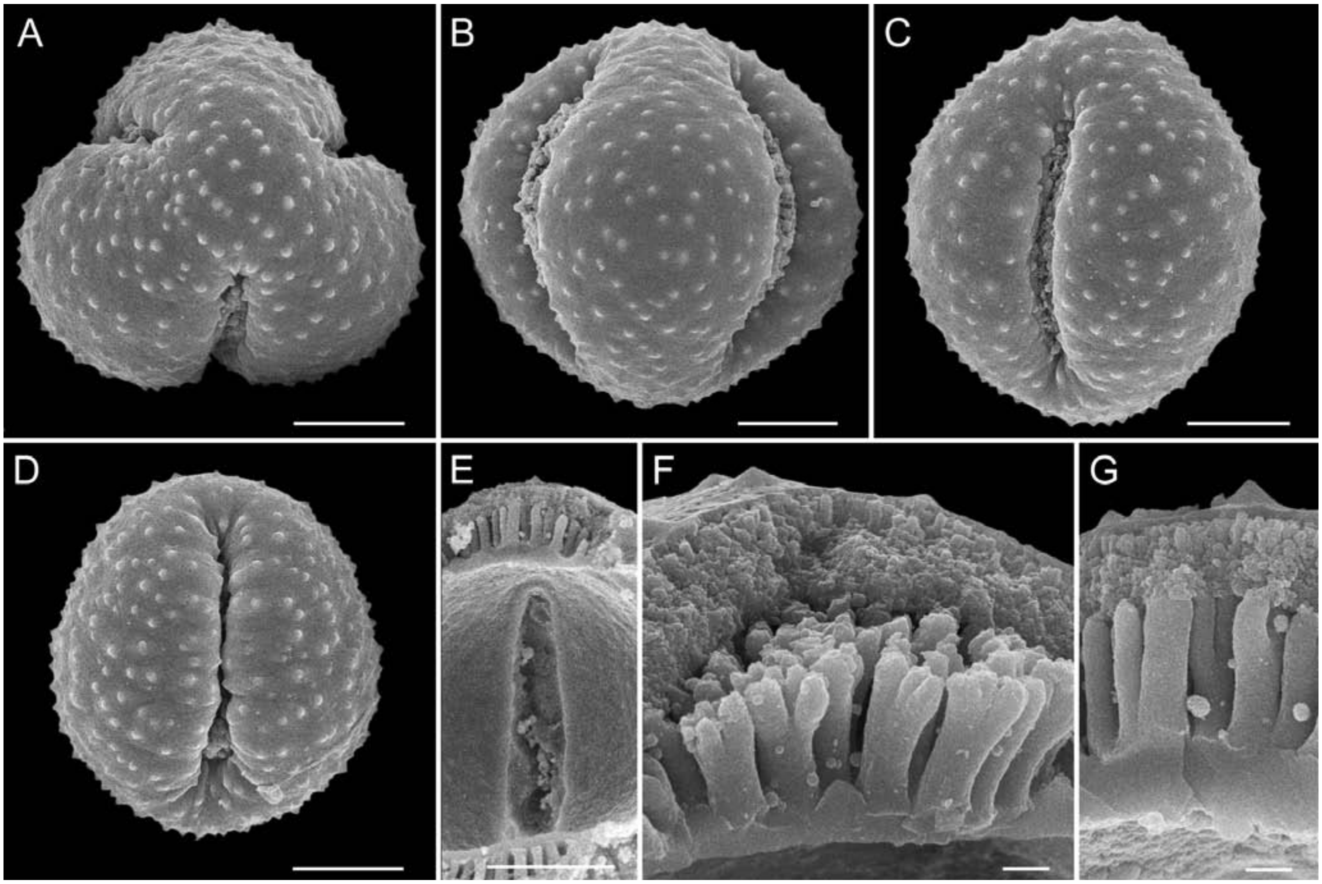

Fig. 16.2. Scanning electron micrographs of pollen of *Hecastocleis shockleyi* A. Gray. **A** polar view; **B** lateral view; **C, D** apertural views; **E** internal apertural view of fractured grain; **F, G** fractured grains. Scale bars: A–E = 10 µm; F, G = 1 µm. [SEM photographs by J. Skvarla of *Funk et al. 12487*, US.]

this relationship but is similar to more basal lineages in the family (e.g., Mutisieae, Gochnatieae).

The most recent phylogeny of the family, based on cpDNA (Panero and Funk 2002, 2008), indicates that *Hecastocleis* is separated from *Ainsliaea* by intervening Carduoideae. In fact, *Hecastocleis* is bracketed by African Mutisieae (Dicomeae, *Oldenburgia* Less., Tarchonantheae) plus Cardueae on one side and Gochnatieae on the other. Over all, the pollen seems to resemble that of the basal grade, especially Gochnatieae, which has somewhat variable pollen.

CHROMOSOME NUMBER

The basic chromosome number is estimated to be $x = 8$, based on one count of $2n = 16$ (Powell et al. 1974).

CHEMISTRY

No information is available on the chemistry.

BIOGEOGRAPHY

The distribution of *Hecastocleis* is confined to the southwestern USA. It has been collected from the mountains surrounding Death Valley and on many of the isolated mountains in southern Nevada. In fact, just about every local flora that is published from the southern Nevada/Death Valley area lists this species as occurring in its range, i.e., Charleston Mountains (Clokey 1951), Nevada Test Site (Beatley 1976), Grapevine Mountains (Kurzius 1981), and the flora of the Desert National Wildlife Range (Ackerman 2003). In general, it seems to be widespread in the southern Nevada and adjacent California area but growing in small isolated populations. The easiest place to see it is on the way to Death Valley, at Red Pass, the highest point on the dirt road from Beatty, Nevada to Leadfield and Titus Canyon, California (Fig. 16.1A).

Hecastocleis is an anomaly in the area cladogram for Compositae (see metatree, Chapter 44). Below the node where one finds this genus, the branches are estimated to have a southern South American distribution. Above *Hecastocleis* the more highly nested clades have radiations in Africa and Asia but most resolve to Africa, especially southern Africa. What happened in the past, therefore, that has left this pattern where a plant from southern Nevada is on the main stem of the cladogram between the basal South American grade and the African and Asian explosions? There are several possible explanations, two of which are equally likely based on the area cladogram: *(1)* there was a dispersal event from South America to North America and then one from North America to Africa, or *(2)* there was a dispersal event from South America to North America followed by radiation across North America and Europe and down into Africa and over to Asia followed by extinction of all northern taxa except the ancestor of *Hecastocleis*. Dispersal from South America to North America has happened in several of the groups in this part of the tree, for instance, *Gochnatia hypoleuca* (DC.) A. Gray is a member of the Gochnatieae tribe which is found at the node below *Hecastocleis*. There is, of course, a third possibility, that the placement of *Hecastocleis* is incorrect. It is a rather long branch and there might be some 'long branch attraction' affecting the phylogeny. However, bootstrap support for the separation of *Hecastocleis* from Gochnatieae is strong (100%).

BIOLOGY, ECOLOGY, ETHNOBOTANY

Very little is known about the biology of *Hecastocleis*; no pollinators were seen during visits to the Red Pass/Titus Canyon populations. Since the florets and bracts are whitish, perhaps they attract night visitors. Likewise, there is no information on the ecology or ethnobotany. It does not appear to be invasive nor does it have any commercial uses. The common name is prickeleaf.

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Chapter 17

Dicomeae (Carduoideae)

Santiago Ortiz, Rodrigo Carbajal, Miguel Serrano and Antonio X. P. Coutinho

HISTORICAL OVERVIEW

The tribe Dicomeae comprises the majority of the African and Malagasy genera traditionally included in Mutisieae, with the notable exception of *Gerbera* L. and related taxa (Hoffmann 1893; Cabrera 1977). This group of eight genera was considered by Jeffrey (1967) as one of the most distinct within Mutisieae. Grau (1980) considered their testa highly characteristic among other Mutisieae, although he did not mention that the testas of species of *Dicoma* Cass. now included in the genus *Macledium* Cass. are, in fact, similar to those of other Mutisieae. Hansen (1991) suggested that most of the genera of this group be moved from Mutisieae to tribe Cynareae (Cardueae). His arguments for this included *(1)* the cuticular ornamentation of corolla epidermal cells characterized by a "rugose pattern of longitudinal bands" ("intestine like", sensu Karis et al. 1992), not mutisioid; *(2)* corolla of disc florets bell-shaped, divided into a narrow tube and a broader limb; *(3)* bilabiate flowers with upper limb lobes short and uncoiled or absent (except in *Gladiopappus* Humbert, in which they are long and coiled; Humbert 1963); *(4)* style branches with subapical sweeping hairs (although this is not always the case in some genera such as *Macledium*); and *(5)* achene turbinate or turbinate-cylindrical and frequently with conspicuous ribs (although this is not the case in *Macledium* and *Pleiotaxis* Steetz).

Bremer (1994) referred to this group of genera as the "*Dicoma* group". He considered it to be one of the most difficult groups to evaluate phylogenetically within Mutisieae. According to his study, however, the species of the *Dicoma* group are characterized by a corolla distinctly divided into a narrow tube and wide limb, a non-mutisioid ray floret epidermial pattern, acuminate apical anther appendages, and mostly subapically pilose style branches. This group of genera was studied in a morphological phylogenetic analysis by Ortiz (2000), who concluded that the two genera, *Pleiotaxis* and *Erythrocephalum* Benth., formed a monophyletic group and that the genus *Dicoma* was paraphyletic and should be split into several genera.

Kim et al. (2002), in their phylogenetic analysis of the tribe Mutisieae based on sequencing of the chloroplast DNA marker *ndhF*, concluded that some African Mutisieae are more related to Cardueae than to Mutisieae s.str. Their analysis placed the genera *Cloiselia* S. Moore (*Dicoma carbonaria* (S. Moore) Humbert) and *Pasaccardoa* Kuntze within a clade including the tribes Tarchonantheae (*Tarchonanthus* L. and *Brachylaena* R. Br.) and Cardueae.

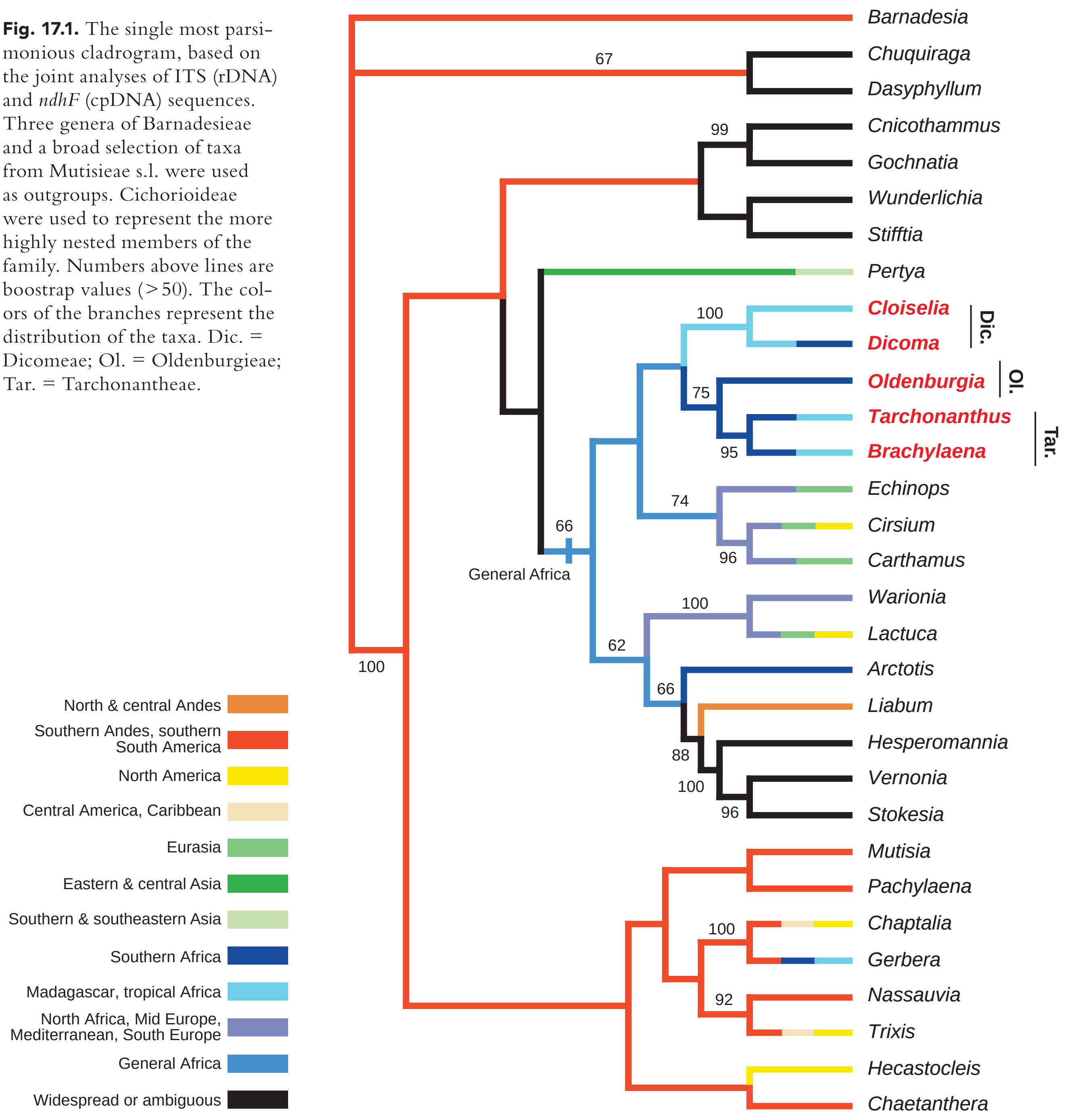
The topology of the phylogenetic tree obtained by the analysis of Panero and Funk (2002, 2008), using ten chloroplast DNA markers, supports the establishment of new subfamilies and tribes from the paraphyletic Mutisieae s.l. One of the new taxa proposed by these authors is the tribe Dicomeae, which comprises most of the African genera previously included in the tribe Mutisieae. Panero and Funk (2002) also suggested that Dicomeae and the tribes Tarchonantheae and Cardueae constituted the subfamily Carduoideae, but they did not have data for *Oldenburgia* Less. Funk et al. (2005) likewise proposed the tribe Dicomeae as the sister group of the remaining members of Carduoideae but with the relationship among *Oldenburgia*, Tarchonantheae and Cardueae unresolved. Panero and Funk (2008) had two results: *(1)* from a parsimony analysis Tarchonantheae

+ *Oldenburgia* form a clade that is in a polytomy with Cardueae and Dicomeae; and *(2)* from the Bayesian analysis, which also places Tarchonantheae + *Oldenburgia* as a clade but differs in that this clade is the sister group to Dicomeae (Cardueae is the sister group to the other three groups; this latter option does not have strong support). Obviously, the relationships among these four taxa are yet to be fully resolved. (See Chapter 44 for a complete metatree.)

PHYLOGENY

With the aim of extending our understanding of the phylogenetic relationships of Mutisieae s.l. of Africa and Madagascar, Ortiz et al. (unpub.) performed various phylogenetic analyses using sequence data from ITS (rDNA) and *ndhF* (cpDNA). In their parsimony analyses they included a selection of genera from the basal groups of Compositae.

Fig. 17.1. The single most parsimonious cladrogram, based on the joint analyses of ITS (rDNA) and *ndhF* (cpDNA) sequences. Three genera of Barnadesieae and a broad selection of taxa from Mutisieae s.l. were used as outgroups. Cichorioideae were used to represent the more highly nested members of the family. Numbers above lines are boostrap values (> 50). The colors of the branches represent the distribution of the taxa. Dic. = Dicomeae; Ol. = Oldenburgieae; Tar. = Tarchonantheae.



The tree produced using *ndhF* and ITS combined gives the best basis for the discussion of not only Dicomeae but also Tarchonantheae (Chapter 18) and Oldenburgieae (Chapter 19) (Fig. 17.1). In this tree three genera from Barnadesieae and a selection of genera from Mutisieae s.l. were used as outgroups. Carduoideae (s.l.) are a monophyletic group with Cichorioideae (s.str.) as sister. Of course, because Cichorioideae here represent the remainder of the family, one must keep in mind that this diagram tells us that Cardueae are sister to the rest of the family and not the sister group of Cichorioideae. However, the relationships among taxa of Cardueae are interesting in that they agree with the Bayesian analysis of Panero and Funk (2008), but with little support. Similar results for the monophyly of Carduoideae were obtained from the analysis using the *ndhF* marker alone (Ortiz et al., unpub.).

In the consensus tree obtained from analyses using the ITS marker, the Dicomeae genera *Macledium*, *Cloiselia*, *Dicoma*, and *Pasaccardoa* form one monophyletic group while *Pleiotaxis* and *Erythrocephalum* form another. These two clades fall in different locations based on the outgroup used. In Fig. 17.2, the outgroup was Barnadesioideae and the selected genera of Mutisieae s.l. and the two clades of Dicomeae are in separate clades with the *Pleiotaxis* + *Erythrocephalum* clade as the sister group of *Warionia* Benth. and Coss. and *Lactuca* L. In a separate analysis, when only taxa from Mutisieae s.l. were used as outgroup, and Barnadesioideae were excluded, both clades are in a polytomy with Cichorioideae s.str. (representing all the rest of the family), two thistle clades, and the *Warionia* + *Lactuca* clade (Fig. 17.3). In both of these analyses the *Oldenburgia* taxa and Tarchonantheae were located outside of the clade containing Dicomeae (Ortiz et al., unpub.).

The topology of the trees supports the split of *Dicoma* into three genera (*Dicoma* s.str., *Macledium*, and *Cloiselia*), as was proposed by Ortiz (2000) in his morphological phylogenetic analysis. Figure 17.4 shows the relationships among the various groups now accepted as three (and possibly four) different genera (Ortiz 2000, 2001, 2006).

TAXONOMY

Tribe Dicomeae Panero & Funk in Proc. Biol. Soc. Wash. 115(4): 916. 2002 – Type: *Dicoma* Cass. (Figs. 17.5–17.7)

Perennial herbs, shrubs or small trees. Leaves alternate, entire. Involucre hemispherical to obconic, pluriseriate, phyllaries often coriaceous and acuminate, pungent. Receptacle alveolate, often epaleate, rarely paleate. Capitula homogamous or heterogamous, solitary or often arranged in lax corymbs or racemes, discoid or radiate. Marginal florets white to red, bilabiate, with the inner lips coiled or not, or ray; disc florets actinomorphic or rarely zygomorphic, deeply 5-lobed; corolla white, yellow, cream to pink or mauve, glabrous to pubescent with different types of glandular, or rarely eglandular, hairs; anthers 5, caudate and calcarate, rarely ecalcarate, with long tapering or subobtuse tails, ramified, with often acute branches, rarely obtuse, these being retrorse along the tail and lacking or antrorse at the apex, apical appendage acute to acuminate, endothecial tissue polarized, pollen smooth to echinate; style short or long bifid, with

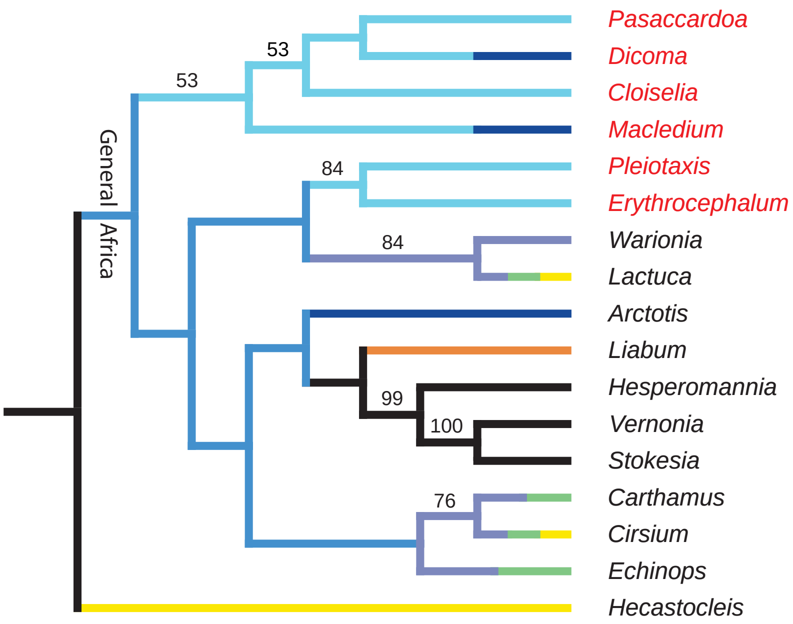


Fig. 17.2. Part of the strict consensus tree of three equally most parsimonious cladograms, based on analysis of ITS (rDNA) sequences (Ortiz et al., unpub.). Three genera of Barnadesieae and a broad selection of taxa from Mutisieae s.l. were used as outgroups. Cichorioideae were used to represent the more highly nested members of the family. Numbers above lines are bootstrap values (> 50). The colors of the branches represent the distribution of the taxa. The genus *Oldenburgia* and the tribe Tarchonantheae formed a monophyletic group that was the sister group to the clade shown here. See Fig. 17.1 for color chart.

the branches subacute to rounded, separating or not, with apical or subapical, acute sweeping hairs and the stigmatic area covering the entire ventral side. Achene often obconical but also narrowly oblong to broadly cylindrical, conspicuously ribbed or not, sometimes with an apical groove below the insertion of the pappus, often densely covered by twin eglandular hairs with a dichotomous apex and sometime with superficial glands between the ribs or all around the achene; pappus of scabrid to plumose bristles or scales, isomorphic or dimorphic, persistent, rarely absent or caducous, testa of *Dicoma*, *Erythrocephalum*, *Perezia* Lag., *Gochnatia* type (Grau 1980) or *Dicoma welwitschii* type (Ortiz 2000).

Panero and Funk (2002) recognized seven genera in their tribe Dicomeae: *Dicoma*, *Macledium*, *Cloiselia*, *Pasaccardoa*, *Pleiotaxis*, *Erythrocephalum*, and *Gladiopappus*. The first four genera form a monophyletic group, as noted above, and seem very closely related to each other morphologically. They share many characters, including: pungent phyllaries without resin ducts or these reduced; presence of star-shaped calcium oxalate crystals in the corollas, anther filaments and styles; anther tails long tapering; pollen slightly echinate; style branches straight and adjacent; and achenes broad and without a carpopodium. Also related to this group is the unpublished genus "*Dicomopsis*" from the Angolan plateau, which shares some characters with *Pasaccardoa* and some with *Dicoma*, and which also has some exclusive characters such as distinctive achene and testa morphology. This new genus would include the principally Angolan species *Dicoma welwitschii* O. Hoffm. (also present in the Democratic Republic of Congo), and *Pasaccardoa baumii* O. Hoffm.

The remaining three genera are rather different from this core group of Dicomeae and were included in this tribe by Panero and Funk (2002, 2008), based only on morphology, since they were not able to include material of these genera in their phylogenetic analysis. *Pleiotaxis* and *Erythrocephalum* form a monophyletic group, morphologically quite different from the other genera, and in view of the phylogenetic analysis using ITS are either unresolved in their relationship or are situated outside Dicomeae. These genera show various characters that separate them from the remaining genera of Dicomeae, including phyllaries not pungent, anther tails with subacute to subrounded apex, style branches separate and often curved, achenes narrowly ellipsoid and with carpopodium, and testa of the *Erythrocephalum* type (Grau 1980) (Fig. 17.5). Further molecular analyses will be necessary to confirm or reject this position and to perhaps delimit an additional tribe for these genera within the African Mutisieae assemblage.

Regarding *Gladiopappus*, no one has yet obtained recent collections of this taxon, and hence no sequence data are available. Morphologically it differs markedly from the core group of Dicomeae, including phyllaries with rounded apex, presence of unisexual florets among the bisexual disc florets, marginal florets of the capitula true bilabiate with coiled adaxial lobes, and achenes without twin hairs. Thus, its inclusion within Dicomeae is provisional.

In view of the above, we can therefore tentatively recognize the following genera within the tribe Dicomeae:

Dicoma Cass. is the largest genus of the tribe, with nearly 30 species of annual and perennial herbs, shrubs and small trees (Figs. 17.5A–C, 17.6). This genus was split

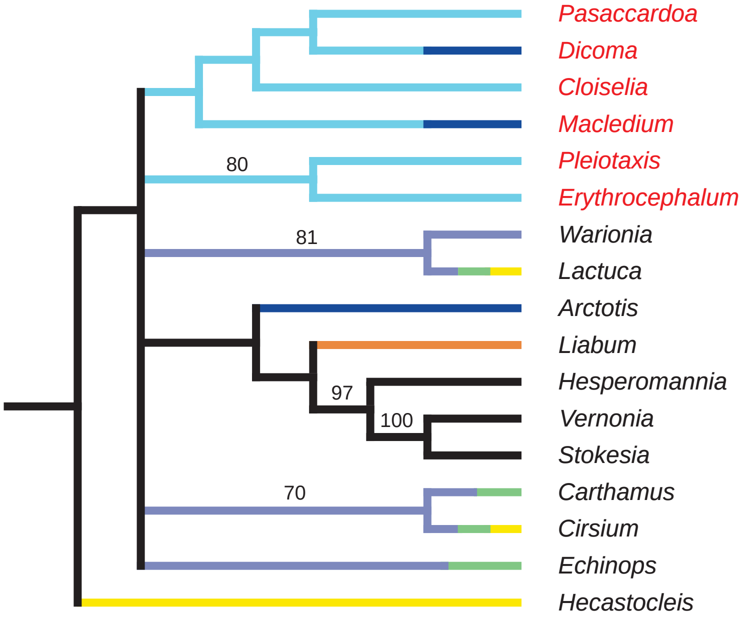


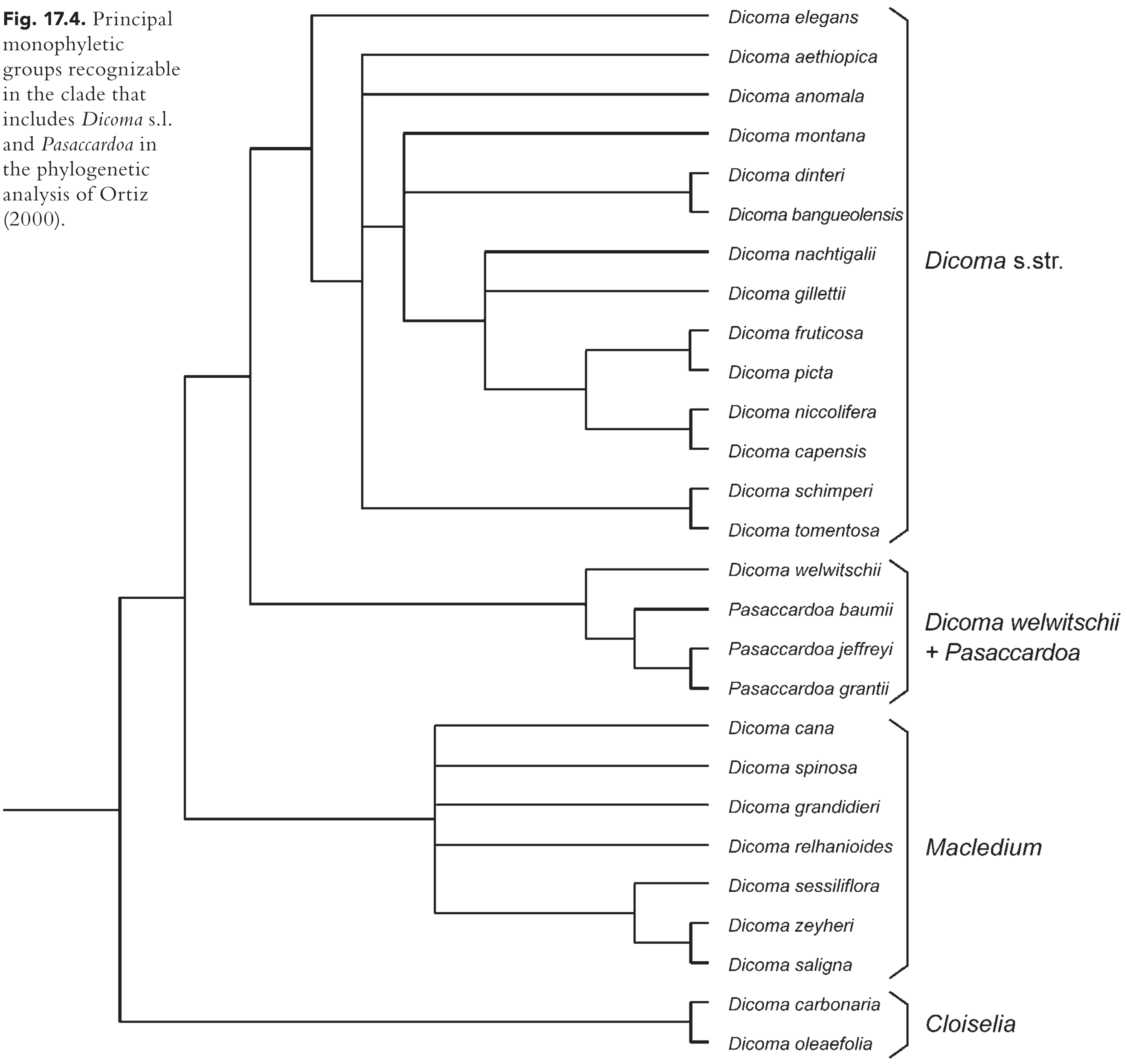
Fig. 17.3. Strict consensus tree of eight equally most parsimonious cladrograms, based on the analysis of ITS (rDNA) sequence (Ortiz et al., unpub.). A broad selection of taxa from Mutisieae s.l. was used as outgroups. Cichorioideae were used to represent the more highly nested members of the family. Numbers above lines are bootstrap values (> 50). The colors of the branches represent the distribution of the taxa. The genus *Oldenburgia* and the tribe Tarchonantheae formed a monophyletic group that was sister to the clade shown here. See Fig. 17.1 for color chart.

by Ortiz (2000) in view of its paraphyletic character if *Pasaccardoa* is not included and the marked synapomorphies that support the main subgroups recognized by Ortiz's morphological phylogenetic analysis (Fig. 17.4). Some of the diagnostic features of this genus are phyllaries with conspicuous midrib and longitudinal dark stripes, style branches long, achenes with superficial glands on the ribs and twin hairs between the ribs, and testa of the *Dicoma* type (Grau 1980). The monotypic genus *Hochstetteria* DC. (*D. schimperi* (DC.) Baill. ex Hoffm.) should, in our opinion, be included in *Dicoma*, as proposed by Hansen (1991) and Bremer (1994), and as supported by the phylogenetic analysis of Ortiz (2000).

Macledium Cass. includes 20 species of perennial herbs and shrubs (Fig. 17.7A–C). Following the above-mentioned phylogenetic analysis by Ortiz (2000), the same author (2001) reinstated this genus, well characterized with respect to *Dicoma* by many characters, including innermost phyllaries entirely scarious and shorter than the contiguous outer series, marginal vascular tissue of corolla lobes broad and surrounded by sclerenchymal fibers, achenes without superficial glands and with twin hairs bulbous-glandular at the base and distributed all around the achene, and testa of the *Gochnatia* type.

Cloiselia S. Moore is a reinstated genus of shrubby to arboreal species endemic to Madagascar (Fig. 17.5E). In a

Fig. 17.4. Principal monophyletic groups recognizable in the clade that includes *Dicoma* s.l. and *Pasaccardoa* in the phylogenetic analysis of Ortiz (2000).



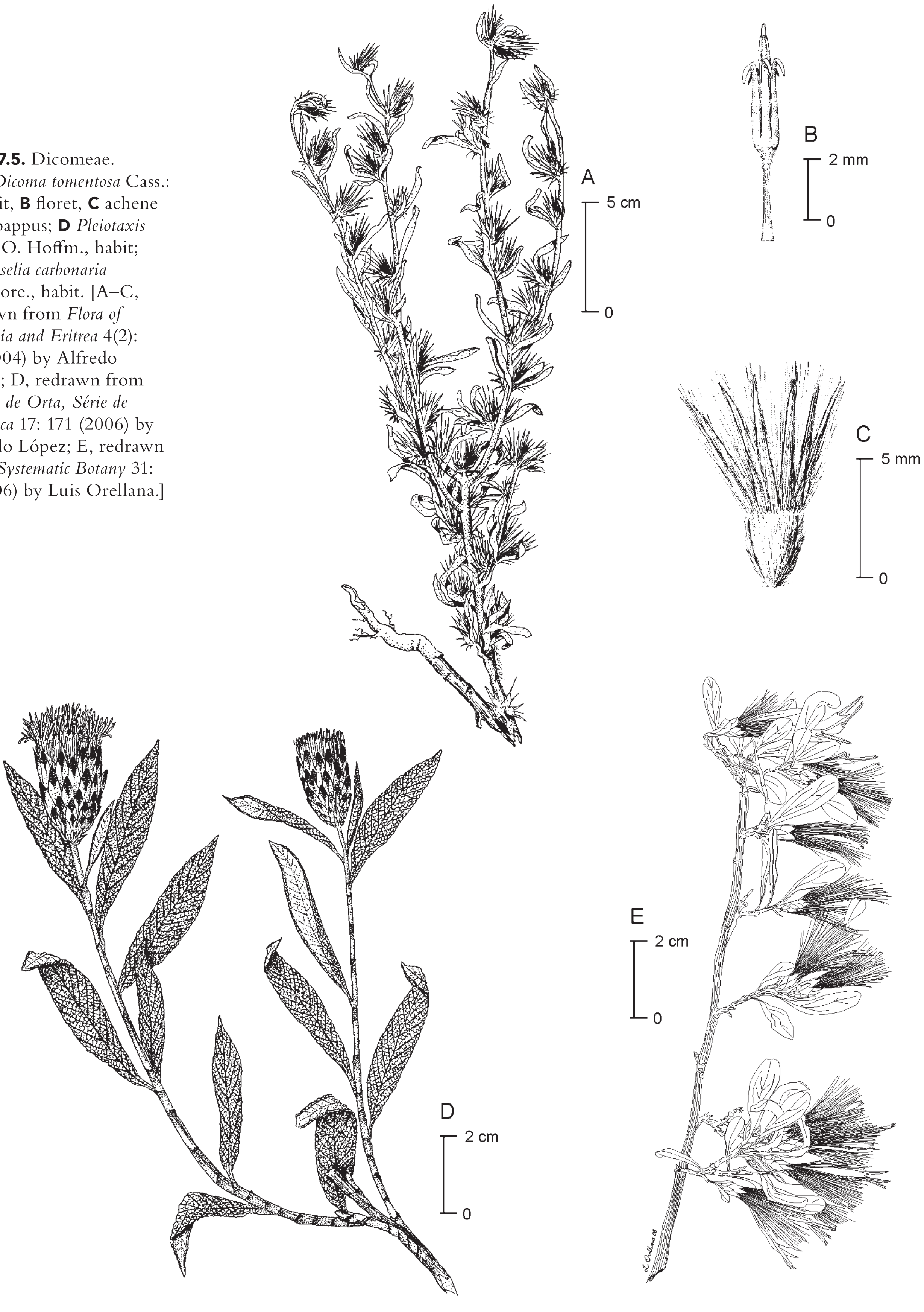


Fig. 17.5. Dicomeae. **A–C** *Dicoma tomentosa* Cass.: **A** habit, **B** floret, **C** achene with pappus; **D** *Pleiotaxis rugosa* O. Hoffm., habit; **E** *Cloiselia carbonaria* S. Moore., habit. [A–C, redrawn from *Flora of Ethiopia and Eritrea* 4(2): 12 (2004) by Alfredo López; D, redrawn from *García de Orta, Série de Botanica* 17: 171 (2006) by Alfredo López; E, redrawn from *Systematic Botany* 31: 4 (2006) by Luis Orellana.]

Fig. 17.6. *Dicoma*. **A** *Dicoma schinzii* O. Hoffm. (Namibia: *Funk and Koekemoer 12702*); **B, E** *Dicoma capensis* Less. (Namibia: *Funk and Koekemoer 12664*); **C** *Dicoma elegans* Welw. ex O. Hoffm. (Angola: *S. Ortiz et al. 881*); **D** *Dicoma welwitschii* O. Hoffm. (Angola: *S. Ortiz et al. 861*); **F** *Dicoma welwitschii* O. Hoffm. (Angola: *S. Ortiz et al. 866*). [Photographs: A, B, E, V.A. Funk; C, D, R. Carbajal; F, S. Ortiz.]

systematic review, Ortiz (2006) recognized four species. *Cloiselia* shows a few characters that are otherwise almost exclusively seen in certain primitive South American Asteracean groups, namely the tribe Barnadesieae and the *Stenopadus* group (tribe Stifftieae) of the tribe Mutisieae s.l. These characters are: corolla zygomorphic, generally tubular, with five lobes, and often with one sinus much longer than the others; marginal nerves of the adjacent lobes separate from the corolla base, rather than joined until near the sinuses as is usual in Compositae; corolla often villous, with long eglandular (not twin) hairs; stamens inserted at the corolla base, and adjacent anther tails connate. A priori, this might be taken to suggest some sort of relationship between *Cloiselia* and these other groups; however, in view of the different phylogenetic studies cited above, it must be concluded that these apparently plesiomorphic characters could be a result of isolation and protection from competition, as seen in many other plant and animal lineages on Madagascar. Besides these characters, others clearly separate this genus from the other genera of the Dicomeae core group, including corolla much longer than the involucre, anthers protruding beyond the corolla, style with four veins, achenes with superficial glands in a continuous layer, testa of the *Perezia* type (Grau 1980), and pappus overtopping the involucre and spreading at maturity.

Pasaccardoa Kuntze includes three species of suffrutescent and annual herbs. It is well characterized with respect to the previous genera by its disc corolla tube abruptly dilating into the limb, corolla lobes with sclerified margins, disc floret achenes ellipsoid, achenes of marginal florets with a rostrum, twin hairs of the achenial base conspicuously larger than those of the other parts of the achene, and superficial achene glands situated in the intercostal grooves. It has a testa of the *Gochnatia* type (Grau 1980), rather similar to that of *Macledium*. As noted above, *P. baumii* O. Hoffm., known from the Angolan provinces of Bie and Kuando-Kubango, should be included in the unpublished genus "*Dicomopsis*".

Pleiotaxis Steetz includes about 25 species of perennial herbs and subshrubs, with annual stems from woody rootstocks (Figs. 17.5D, 17.7D). The principal diagnostic characteristics of this genus are the phyllaries with subacute to rounded apices (in Dicomeae this type of phyllary is only present in *Gladiopappus* and two species of *Erythrocephalum*), anther tails ecalcarate, and achenes narrowly cylindric. Within this genus are two easily recognizable different groups: one of them with capitula solitary or in lax corymbs and with purplish florets, the other with capitula arranged in panicles and with yellowish to cream florets. These two groups should probably be treated as sections or subgenera.

Erythrocephalum Benth. comprises about 14 species of annual herbs or subshrubs, with annual stems from woody rootstocks. It is well characterized by phyllaries generally long-acuminate and dentate-lacerate, receptacle paleate, achenes broadly ellipsoid with bifurcating twin hairs, and a pappus that is caducous or absent. Ortiz and Coutinho (2001) suggested that *Achyrothalamus* O. Hoffm., with its sole species *A. marginatus* O. Hoffm., should be included in the genus *Erythrocephalum*. These authors found that the only important difference with *Erythrocephalum* was the absence of pappus, whereas the remaining 82 characters studied were almost entirely coincident. Phyllary apex morphology has been used previously as a valid character by which to segregate *Achyrothalamus* (obtuse and entire phyllaries), in contrast to phyllaries being acute and dentate-lacerate in *Erythrocephalum*. *Erythrocephalum jeffreyanum* S. Ortiz & Rodr. Oubiña, however, described from Tanzania, shows all the normal characteristics of the genus but with obtuse and entire phyllaries (Ortiz and Rodríguez-Oubiña 1998), invalidating the efficacy of this character.

Gladiopappus Humbert is a monotypic genus endemic to Madagascar. As indicated above, its morphological differences from the Dicomeae core group are marked, principally the phyllaries with rounded apices, bilabiate marginal florets with coiled adaxial lobes (as is normal in many true American Mutisieae), and presence of unisexual florets in addition to bisexual florets of the disc. The morphology of disc corollas, stamens, style and achenes, however, are similar to those of the core group.

MORPHOLOGY

With its current definition, including all the genera cited above, the tribe Dicomeae is morphologically heterogeneous. Nevertheless, the tribe as delimited could be defined by a combination of features including: involucral phyllaries pluriseriate; capitulum disc with bisexual florets, these with long lobes and bell-shaped corollas; corolla epidermal cell cuticle ornamentation longitudinally striate and transversely ondulate to nearly smooth; endothecial tissue polarized; anther appendage acuminate to apiculate; anther tails long and with retrorse branches; and styles with narrow, acute sweeping hairs. Alternatively, if the last three genera (*Pleiotaxis*, *Erythrocephalum*, and *Gladiopappus*) not belonging to the core group are excluded, morphological delimitation of the tribe would be clearer, as discussed above.

POLLEN

In accordance with Wodehouse (1929), Stix (1960), Perveen (1999), and Coutinho and Ortiz (in prep.), pollen grains of tribe Dicomeae (all genera except *Gladiopappus*

Fig. 17.7. *Macledium* and *Pleiotaxis*. **A** *Macledium zeyheri* (Sond.) S. Ortiz (South Africa, Gauteng: *Funk and Koekemoer 12431*); **B** *Macledium plantaginifolium* (O. Hoffm.) S. Ortiz (Angola: *S. Ortiz et al. 879*); **C** *Macledium plantaginifolium* (O. Hoffm.) S. Ortiz (Angola: *S. Ortiz et al. 879*); **D** *Pleiotaxis rugosa* O. Hoffm. (Angola: *S. Ortiz et al. 840*). [Photographs: A, V.A. Funk; B, S. Ortiz; C, J. Rodríguez-Oubiña; D, R. Carbajal.]

which was not studied) are isopolar, radially symmetrical, sub-oblate to prolate (P/E = 0.86–1.46), elliptic to subcircular in meridian optical section, sub-circular in equatorial optical section, acaveate, 3-zonocolporate, with a tripartite apertural system (ecto-, meso-, and endoaperture). The ectoapertures (colpi) are 12.0–40,5 μm long, sub-terminal, the mesoapertures lolongate or lalongate, and the endoapertures (ora) lolongate or lalongate, 9.4–25.0 μm wide. The exine is 4.7–13.0 μm thick, the sexine (1–)1.5–2 times thicker than the nexine, with a structured, micro-perforated tectum and an anthemoid pattern. Sculpture is micro-echinate or echinate, with spines widely conical, acute or blunt at the apices. P = 34–75 μm, E = 33–67 μm.

CHROMOSOME NUMBERS

Dicoma: *D. tomentosa* Cass., $n = 11$ (Bhandari and Singhir 1977; Razaq et al. 1988); *D. schimperi*, $n = 10$ (Khatoon and Ali 1993); *D. schinzii* O. Hoffm., $2n = 22$ (Goldblatt 1989). *Pleiotaxis*: *P. huillensis* O. Hoffm. subsp. *huillensis*, $2n = 20$ (Paiva and Leitao 1989).

CHEMISTRY

Several sesquiterpene lactones (germacranolides, eudesmanolides and elemanolides) have been identified from *Dicoma* species of southern Africa by Zdero and Bohlmann (1990). Several acetylene compounds of *Pleiotaxis rugosa* O. Hoffm. were studied by Bohlmann and Zdero (1982), who concluded that this genus is more closely related to Cardueae than to Mutisieae, because it has compounds including certain acetylenes and guaianolides that are typical of the former tribe.

ECOLOGY

Species of Dicomeae most commonly occur in desert to semi-desert bushlands or grasslands, miombo woodlands, and open woodlands and grasslands; more rarely they are found in swamp forests and on rocky outcrops and coastal cliffs. *Dicoma tomentosa* Cass. behaves like a weed.

BIOGEOGRAPHY

The tribe Dicomeae is widely distributed in tropical Africa, from Senegal and Egypt in the north to southern Africa and Madagascar. It is also present in Asia, where there are two species of *Dicoma*: *D. tomentosa* in India and Pakistan, and *D. schimperi* in the Arabian Peninsula (Table 17.1). Countries with the highest diversity and most endemic taxa are: Angola (high diversity and numerous endemics in the genera *Macledium*, *Pleiotaxis*, *Pasaccardoa* and *Dicoma*), Democratic Republic of Congo (high diversity in *Macledium*, *Pleiotaxis*, *Pasaccardoa* and *Erythrocephalum*, with many endemics in *Pleiotaxis*), and Tanzania (high diversity and many endemics in *Erythrocephalum*). Other countries such as Zambia (with high diversity but few endemics) and South Africa and Somalia (both with high diversity and many endemics in *Dicoma*) are also worth noting (Table 17.2).

EVOLUTION

It is not easy to find a relationship between the African tribe Dicomeae and the most primitive Compositae, which for the most part are American. Certainly, the Madagascan genus *Cloiselia* shows some characters that are otherwise almost exclusively seen in certain primitive South American Compositae. These plesiomorphic characters, however, could probably be a result of parallelism in isolation in Madagascar. In accordance with the hypothesis presented in other chapters of this book (see introductions to Chapter 12, Mutisieae s.l. and Chapter 20, tribe Cardueae) an origin of Cardueae occurred when Africa was covered by Tertiary forests. It is probable that the most mesophyllous members of Dicomeae (e.g., *Pleiotaxis*) originated at the end of the Tertiary and the more xerophyllous plants (e.g., many of the species of *Dicoma* and *Pasaccardoa*) probably originated when a progressive deforestation and desertification of Africa was happening.

Table 17.1. Geographical distributions of the genera of Dicomeae.

Genus	Distribution
Cloiselia S. Moore	Madagascar
Dicoma Cass.	Widely distributed in tropical and southern Africa, Madagascar, Arabian Peninsula, India and Pakistan
Erythrocephalum Benth.	Tropical Africa: from Kenya to Angola and Mozambique
Gladiopappus Humbert	Madagascar
Macledium Cass.	Widely distributed in tropical and southern Africa and Madagascar
Pasaccardoa Kuntze	Tropical Africa: Tanzania, Democratic Republic of Congo, Zambia and Angola
Pleiotaxis Steetz	Widely distributed in tropical Africa and southern Africa (Namibia and Botswana)

Table 17.2. Distribution of the species of Dicomeae by countries and genera (considering only those genera with more than five species).

Country/Genus	*Dicoma*	*Macledium*	*Cloiselia*	*Pasaccardoa*	*Pleiotaxis*	*Erythrocephalum*	*Gladiopappus*	Total
Angola	**10(4)**	**7(2)**	0	**2(1)**	**16(9)**	2(1)	0	**37(17)**
Botswana	6	0	0	0	1	0	0	7(0)
Dem. Rep. Congo	2	**7(1)**	0	**3**	**22(11)**	**3**	0	**37(12)**
Madagascar	1(1)	1(1)	**4(4)**	0	0	0	**1(1)**	7(7)
Malawi	2	4	0	0	1	**3**	0	10(0)
Mozambique	4	4	0	0	1	2	0	11(0)
Namibia	9(1)	1	0	0	1	0	0	11(1)
Somalia	**10(8)**	0	0	0	0	0	0	10(8)
South Africa	**12(5)**	**6(5)**	0	0	0	0	0	18(10)
Tanzania	2	5	0	1	6(1)	**11(5)**	0	**25(6)**
Zambia	4	6	0	**3**	**9(1)**	2	0	24(1)
Zimbabwe	6	1	0	0	1	2	0	9(0)

Number of endemic species shown in parentheses. The three countries with highest diversity are shown in bold; in addition, for each genus the three highest species numbers are shown in bold.

ETHNOBOTANY

Roots of *Dicoma anomala* Sond. subsp. *anomala* are used in Zambia (Fowler 2006), Zimbabwe (Gelfand et al. 1985) and South Africa (Watt and Breyer-Brandwijk 1962) as a remedy for fever. Dried and powdered tissue of *Macledium sessiliflorum* (Harv.) S. Ortiz subsp. *sessiliflorum* and *M. kirkii* (Harv.) S. Ortiz were successfully used in Malawi to protect stored grain against insects (Chimbe and Galley 1996), while the whole plants of the other subspecies (*M. sessiliflorum* subsp. *stenophyllum* (G.V. Pope) S. Ortiz) is very bitter and used as a febrifuge, particularly for children, in Nigeria (Burkill 1985). Root decoctions and leaf juice of *Erythrocephalum longifolium* Oliv. are drunk as an antimalarial in Tanzania (Haerdi 1964).

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Chapter **18**

Tarchonantheae (Carduoideae)

Santiago Ortiz

HISTORICAL OVERVIEW

The genera *Tarchonanthus* L. and *Brachylaena* R. Br. have been included in diverse tribes over the years. Cassini (1828) included them in the tribe Vernonieae based on style morphology. Kosteletzky (1833) included these two genera in a tribe of their own (Tarchonantheae). De Candolle (1836) included them in his Asteroideae. Bentham (1873) put them in Inuleae in view of the structure of the female florets, as did Hoffmann (1890). Skvarla et al. (1977) included them in Anthemideae based on pollen characteristics; Leins (1971), however, also on the basis of pollen characteristics, included them in Mutisieae. This latter placement of the two genera was accepted by many botanists and supported both by Grau (1980), who studied the testa of both genera, and by Zdero and Bohlmann (1990), who studied their chemical composition. Moreover these latter authors suggested placement of the two genera in a separate tribe. Placement in Mutisieae was also followed by Karis et al. (1992) and Bremer (1994). Hansen (1991), however, proposed that they should be removed from Mutisieae and included in Cardueae. This proposal was based principally on style morphology and the cuticle ornamentation of corolla epidermal cells, and was subsequently supported by the phylogenetic analysis of the family by Kim and Jansen (1995). Their trees were based on sequences of the cpDNA marker *ndhF*, which placed *Tarchonanthus* among clades of the tribe Cardueae.

Keeley and Jansen (1991), based on an analysis of chloroplast restriction site variations, proposed placement of these two genera in their own tribe (Tarchonantheae), but they were unaware of the priority of Kosteletzky's name. This proposal is supported by the phylogenetic analyses of Kim et al. (2002), based on sequencing of *ndhF*, and those of Panero and Funk (2002, 2008), and Funk et al. (2005) based on nearly 14,000 base pairs of cpDNA. In the latter three analyses, the tribe Tarchonantheae is one of the members of subfamily Carduoideae. Panero and Funk have placed the genus *Oldenburgia* in Tarchonantheae, but this hypothesis is not supported by morphology, and Tarchonantheae here are treated as containing only two genera, *Tarchonanthus* and *Brachylaena*.

PHYLOGENY

In a recent molecular phylogenetic analyses using ITS (rDNA) and the cpDNA gene *ndhF* (Ortiz et al., unpub.) the tribe Tarchonantheae is always a monophyletic group, with bootstrap values ranging from 50% to almost 100% (see Dicomeae, Chapter 17 for additional details).

In the single most parsimonious cladogram obtained from the analysis performed with the ITS + *ndhF* (Ortiz et al., unpub.), using three genera of Barnadesieae and a selection of taxa from Mutisieae s.l. as outgroups (Chapter 17: Fig. 17.1), the Tarchonantheae + Oldenburgieae clade is placed as sister group to Dicomeae within a monophyletic subfamily Carduoideae, although bootstrap values are lower than 50% for some of the branches. Using the *ndhF* gene only and the same outgroups, the tribe Tarchonantheae is an isolated clade in a polytomy that represents the subfamily Carduoideae and also includes the tribes Oldenburgieae, Dicomeae and Cardueae. Of course, since Cichorioideae here represent the remainder of the family, one must keep in mind that this diagram tells us that the tribe Cardueae is the sister group to the rest of the family, and not that it is the sister group of Cichorioideae.

In both of the ITS trees (Fig. 18.1A rooted with Barnadesieae + Mutisieae s.l.; Fig. 18.1B rooted with only Mutisieae s.l.), the monophyletic group of *Oldenburgia* + Tarchonantheae is supported. However, in contrast to the *ndhF* + ITS tree, the *Oldenburgia* + Tarchonantheae clade is situated far from the other members of the subfamily Carduoideae, the tribes Dicomeae and Cardueae, and is, in fact, the sister group to the large clade formed by *Hecastocleis*, Dicomeae, Cardueae, and the rest of the family. Although it seems likely that *Oldenburgia* is the sister group of Tarchonantheae, it also seems clear that the exact position of this clade is still unresolved.

TAXONOMY

Tribe Tarchonantheae Kostel., Allg. Med.-Pharm. Fl. 2: 668. 1833 – Type: *Tarchonanthus* L. (Figs. 18.3–18.4)

Dioecious trees or shrubs, often aromatic. Leaves alternate, entire or three-lobed at apex. Involucre campanulate to obconic, of one to several rows of phyllaries; phyllaries ovate to lanceolate or elliptic, glabrous to densely white-tomentose. Receptacle flat, epaleate. Capitula small, on thyrsoid racemes or panicles, unisexual, rarely with a few bisexual florets, discoid, often with less than 30 florets, rarely up to 90, yellowish or whitish. Male florets with deeply 5-lobed actinomorphic, tubular corollas, anthers exerted, caudate and calcarate, apical appendage deltate, style filiform, minutely bifid at the tip or undivided, ovary abortive, with reduced pappus in one row. Female florets with 3–5-lobed, actinomorphic, tubular to filiform corollas; anthers reduced to staminodes or absent; style exerted with short, often recurved branches, flattened near the tip, without sweeping hairs, the stigmatic area covering the entire ventral side. Achene mainly cylindrical to ellipsoid, flattened or not, angled or few-ribbed, pubescent, sometimes glandular, pappus of numerous barbellate bristles in 1–2 rows or lacking, testa of *Gochnatia* type (Grau 1980).

The phylogenetic position of *Tarchonanthus* and *Brachylaena* justifies their placement in a separate tribe (Tarchonantheae) within the grouping constituted by African Mutisieae s.l., as proposed by Keeley and Jansen (1991). Specifically, in the analyses of Funk et al. (2005), and in the consensus tree of a recent study (Ortiz et al., unpub.), using sequence data from the *ndhF* gene, these genera are placed in a clade separate from the other members of the subfamily Carduoideae. In the consensus trees using ITS (Fig. 18.1) and ITS + *ndhF* (Chapter 17: Fig. 17.1) Oldenburgieae is placed in a monophyletic group with Tarchonantheae. This does not justify the inclusion of *Oldenburgia* in this tribe, however, since this genus shows very marked morphological differences from *Tarchonanthus* and *Brachylaena*, and the resulting tribe would be excessively heterogeneous. The same topology was recently obtained from the analysis of Panero and Funk (2008) using several chloroplast markers, but bootstrap support for the monophyletic group including Tarchonantheae and *Oldenburgia* is the lowest obtained for any recognized tribes in that analysis.

The genera *Tarchonanthus* and *Brachylaena* (Figs. 18.2–18.3) are accepted by most authors (Bremer 1994; Hind 2007), although Hansen (1991) suggested that they might be congeneric. A recent phylogenetic analysis of the two genera presented at the International Botanical Congress (Vienna, 2005) and the Botanical 2004 meeting (Kimball et al., unpub.; Crawford, pers. comm.) have reported the results of their detailed analysis of this clade involving all of the species of *Brachylaena* and *Tarchonanthus*. In this analysis, using the markers ITS and ETS (rDNA) and *rpl16* (cpDNA), the authors concluded that *Tarchonanthus* is nested within *Brachylaena*. Nevertheless, these data are

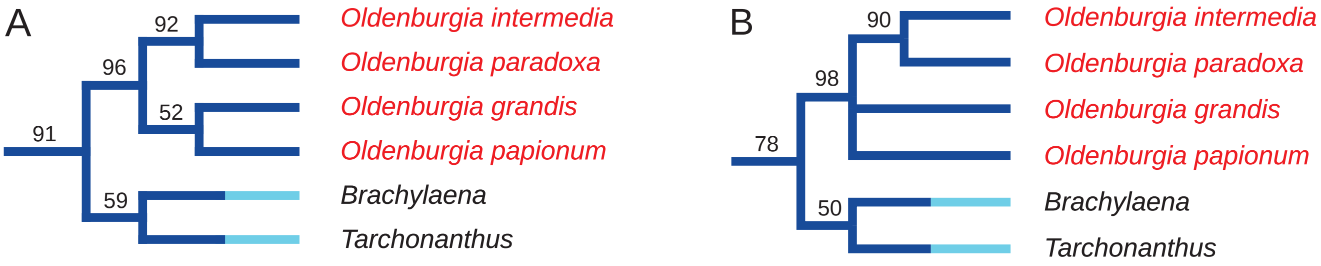

Fig. 18.1. Part of the strict consensus tree of three equally most parsimonious cladograms based on the analysis of ITS (rDNA) sequences (Ortiz et al., unpub.). **A** three genera of Barnadesieae and a broad selection of taxa from Mutisieae s.l. were used as outgroups; **B** a broad selection of taxa from Mutisieae s.l. was used as outgroup. Numbers above lines are bootstrap values (>50). The colors of the branches represent the areas of the world where the taxa are found. Dark blue = southern Africa; light blue = tropical Africa and Madagascar.

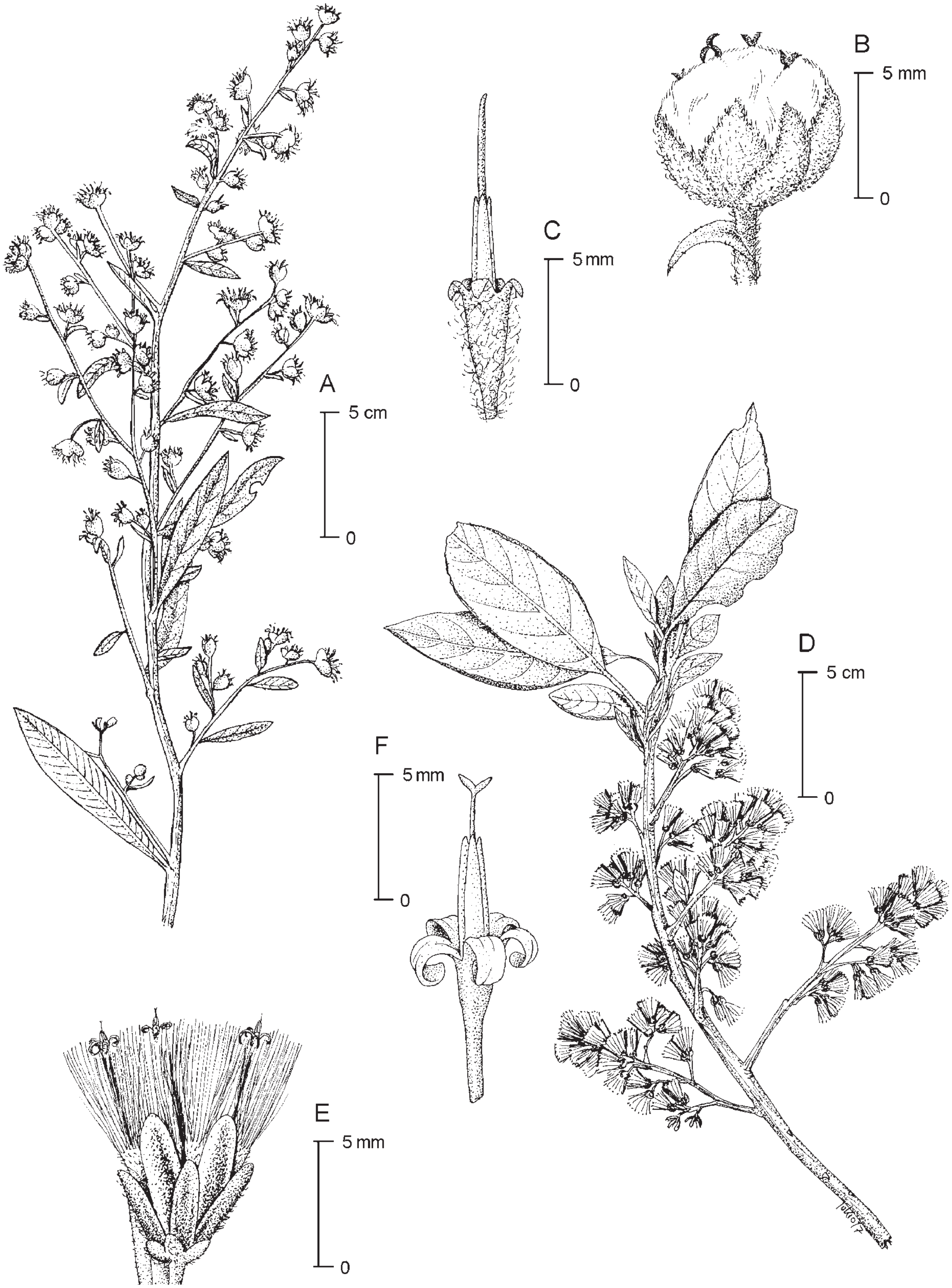

Fig. 18.2. A–C *Tarchonanthus camphoratus* L.: **A** habit of a male specimen; **B** female capitulum; **C** male floret. **D–F** *Brachylaena huillensis* O. Hoffm.: **D** habit of a female specimen; **E** female capitulum; **F** male floret. [Modified from *García de Orta, Série de Botanica* 17: 169, 170 (2006), drawn by Alfredo López "Tokio".]

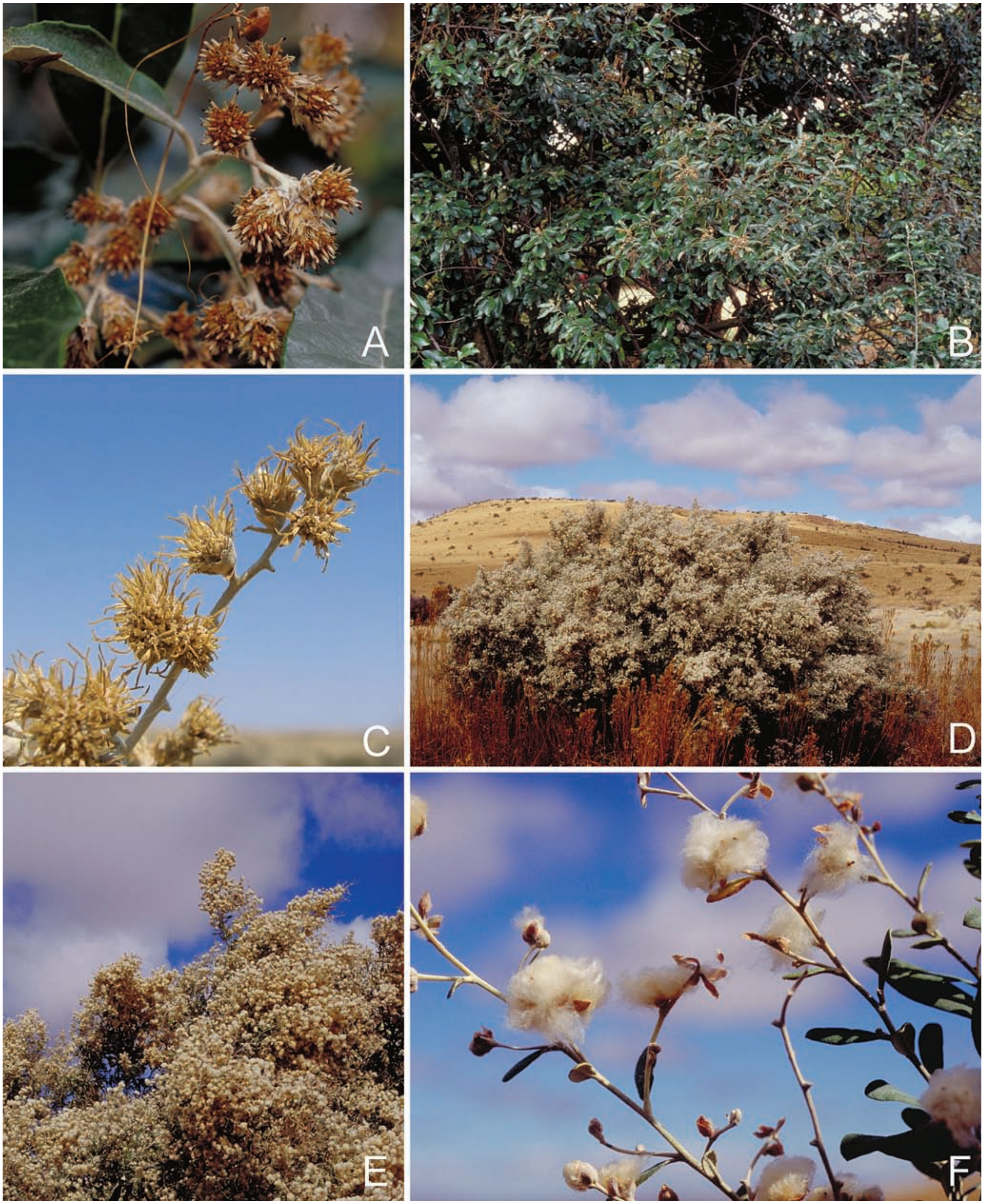

Fig. 18.3. *Brachylaena* and *Tarchonanthus*. **A, B** *Brachylaena transvaalensis* Hutch. ex Phillips & Schweick (South Africa, Gautaung: *Koekemoer and Funk 1970*); **C** *Tarchonanthus camphoratus* L. (Namibia); **D–F** *Tarchonanthus camphoratus* L. (South Africa, Northern Cape: *Koekemoer and Funk 1967*) [Photographs: A, B, D–F, V.A. Funk; C, C.A. Mannheimer.]

unpublished, and since Beentje (1999) considers that there are morphological differences between the two genera (in the number of phyllary rows, the shape of the achenes, and the presence/absence of pappus), it seems best to keep them separate at this time.

Within *Tarchonanthus* most authors recognize two species, including Beentje (1999) who completed the last complete revision of the genus. Herman (2002), however, who reviewed the variability of *T. camphoratus* L. in southern Africa, identified several differences among populations of this species (in synflorescence morphology, flowering times, leaf shape and margin, and distribution), and recognized a total of six species in the genus.

The taxonomy of the genus *Brachylaena* has been studied by several authors (Paiva 1972; Cilliers 1993; Herman 1998). The last revision was that of Beentje (2000), who recognized eleven species.

MORPHOLOGY

Morphological differences between the tribes Tarchonantheae and Oldenburgieae are substantial, as noted, the latter being dwarf shrubs to small monoecious trees, with large, radiate capitula of very numerous (80–1000) florets, the capitula solitary or arranged on small ramified peduncles.

The principal morphological characters separating Tarchonantheae from Dicomeae are basically the same as those separating Tarchonantheae from Oldenburgieae.

POLLEN

As noted by Leins (1971) and Cilliers (1991), pollen grains in Tarchonantheae are isopolar, radially symmetrical, oblate-spheroidal to sub-prolate (P/E = 0.95–1.20), elliptic in c.o.m., sub-circular in c.o.e., acaveate, and 3(4)-zonocolporate. The ectoapertures (colpi) 10–20 × 0.8–2.5 μm, with acute or rounded ends; the endoapertures are (ora) lalongate. The exine is 1.5–3.2 μm thick, the sexine is (1.2–)2–2.6 times thicker than the nexine, with a structured, micro-perforated tectum and an anthemoid pattern. Sculpture is micro-echinate or nano-echinate. P = 25–50 μm, E = 20–35 μm.

CHROMOSOME NUMBERS

Tarchonanthus: *T. camphoratus*, $n = 36$ (Keeley and Jansen 1991). *Brachylaena*: *B. discolor* DC. var. *discolor* $n = 9$ (Keeley and Jansen 1991); *B. discolor* var. *rotundata* (S. Moore) Beentje (*B. discolor* S. Moore), $n = 18$ (Keeley and Jansen 1991).

CHEMISTRY

Zdero and Bohlmann (1990), in their article on systematics and evolution of Compositae, included information on the systematic relationships of Tarchonantheae based on several chemical compounds (including triophene derivatives of tridecapentaynene, guaianolides, and other sesquiterpene lactones, plus triterpenes). In the genus *Tarchonanthus* several compounds have been studied (Bohlmann and Svwita 1979; Brown and Gray 1988) including the tarchonanthuslactone isolated by Bohlmann and Svwita (1979) from *Tarchonanthus trilobus* DC. Due to interest in the biological activities of this compound (including plant growth inhibition, as well as antifeedent, antifungal, antibacterial, and antitumor properties; Garaas et al. 2002), it was more recently obtained by synthesis (Garaas et al., 2002; Enders and Steinbusch, 2003).

Zdero and Bohlmann (1987) and Zdero et al. (1991) isolated several sesquiterpene lactones, including different guaianolides, from aerial parts of *Brachylaena* species. Vieira et al. (1991) obtained five sesquiterpenes from the bark of *Brachylaena huillensis* O. Hoffm. and described their antibacterial activity. Two triterpene esters and five triterpenoids were isolated by Chaturvedula et al. (2002) from small twigs of *Brachylaena ramiflora* (DC.) Humbert.

ECOLOGY

Tarchonanthus species occur in woodland, wooded grassland, vegetation fringing streams, bushland, acacia scrub, and rocky outcrops. Elevation ranges from 30 to 2700 m (Beentje 1999).

In Madagascar, *Brachylaena* species occur in diverse habitats including rain forest, deciduous forest, moist forest, dry bushland, rocky hillsides, and riparian sites. Outside Madagascar *Brachylaena* species are found in dry evergreen forest, semi-deciduous forest, dune forest, woodlands, riverine forest and bush, bushland, and rocky hillsides and outcrops. Elevation ranges from sea level to 2000 m (Beentje 2000).

BIOGEOGRAPHY

The tribe Tarchonantheae is distributed throughout tropical Africa, principally in the eastern part, southern Africa and Madagascar. It is also present in the Arabian Peninsula.

Tarchonanthus is distributed in the southwestern Arabian Peninsula, East Africa, the southern part of south tropical Africa, and southern Africa (Beentje 1999).

Brachylaena is principally distributed in southern Africa and Madagascar (including the Comoro Islands). The species *B. huillensis* is also present in Uganda, Kenya, Tanzania, Mozambique, Zimbabwe, and Angola, and *B. discolor* in Mozambique (Beentje 2000).

ETHNOBOTANY

Leaves of *Tarchonanthus camphoratus* are used for bedding and as a deodorant by pastoral peoples. They are also used against inflammation (Kling 1923; Roberts 1990), for asthma, cough, bronchitis, fever and chest illnesses (Hedberg and Staugård 1989; Koenen 1996), in toothache remedies (Palmer and Pitman 1972; Hutchings and Van Staden 1994), as an insect repellent (Roberts 1990), and as a narcotic (Pappe 1868). Essential oils of this tree proved moderately useful as a repellent of *Anopheles gambiae*, the principal vector of malaria in Africa (Omolo et al. 2004). The wood is used in house-building, boat-building, for fence posts, walking sticks, musical instruments and cabinet work, and formerly for bows, arrow-shafts, and spear-shafts (Palmer and Pitman 1972; Coates Palgrave 1977; Beentje 1999; Herman 2002).

Several species of *Brachylaena* also have good, dense wood, much used in furniture building and construction. *Brachylaena microphylla* Humbert wood smells like sandalwood and has been used as substitute (Beentje 2000). Leaf decoctions of *Brachylaena huillensis* are used to treat bilharzia and gonorrhoea (Chhabra et al. 1989), and the leaves show activity against the bacteria *Staphylococcus aureus* and *Klebsiella pneumoniae*, which can cause various illnesses including pneumonia, meningitis and urinary infections (Chhabra et al. 1981).

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Chapter 19

Oldenburgieae (Carduoideae)

Santiago Ortiz

HISTORICAL OVERVIEW

The tribe Oldenburgieae includes only the genus *Oldenburgia* Less. (Ortiz et al., unpub.). This genus was described by Lessing (1830) for the new species *O. paradoxa* Less. in honor of F.P. Oldenburg, a German explorer and collector in the Cape region of South Africa. Subsequently, Harvey (1865) recognized three species of this genus in his revision for *Flora Capensis*.

In 1987 Bond published a revision of the genus and described an additional species. She considered that morphologically the genus was not closely related to the other African Mutisieae genera, and associated it with the South American genera *Wunderlichia* Riedel ex Benth., *Chimantaea* Maguire, Steyerm. & Wurdack and *Cnicothamnus* Griseb. However, in the trees obtained by morphological phylogenetic analysis of Mutisieae by Karis et al. (1992), *Oldenburgia* was situated far from these three genera, though also outside the African Mutisieae clades. In view of these unclear relationships, Bremer (1994) considered *Oldenburgia* to be one of the isolated genera of Mutisieae, probably an ancient relict.

Funk et al. (2005) proposed the tribe Dicomeae as the sister group to the remaining members of Carduoideae but with the relationship among *Oldenburgia*, Tarchonantheae and Cardueae unresolved. Panero and Funk (2008) had two results, one from a parsimony analysis in which Tarchonantheae + *Oldenburgia* formed a clade that is in a polytomy with Cardueae and Dicomeae, and one from the Bayesian analysis that also placed Tarchonantheae + *Oldenburgia* as a clade but differed in being the sister group to Dicomeae, and that Cardueae were sister to the other three groups (this latter option does not have strong support). Obviously, additional work needs to be done to determine the exact relationship among these taxa.

PHYLOGENY

The molecular phylogenetic analyses (Ortiz et al., unpub.) show the genus *Oldenburgia* in one of two places: in *(1)* a monophyletic group within tribe Tarchonantheae (with high bootstrap values, possibly beeing sister to Dicomeae); or *(2)* in an unresolved clade (see Chapter 17 on Dicomeae for additional details).

The tree resulting from combined *ndhF* and ITS and presented in the Dicomeae chapter (Chapter 17: Fig. 17.1) uses three genera from Barnadesieae and a diverse selection of those from Mutisieae s.l. as outgroups. The results show that Carduoideae (s.l.) is a monophyletic group with Cichorioideae (s.str.) as the sister group (Ortiz et al., unpub.). Of course, since Cichorioideae here represent the remainder of the family, one must keep in mind that this diagram tells us that Cardueae are sister to the rest of the family and not that they are sister to Cichorioideae.

In the consensus trees obtained from the analysis performed with ITS sequences (Ortiz et al., unpub.), the four species of *Oldenburgia* form a monophyletic group with bootstrap values near 100%; part of this tree is shown in Fig. 19.1. Since the four species are very diverse morphologically, there had been some doubts as to the monophyly of the genus, but the close relationships among the species is well supported by the

Ortiz et al. (unpub.) analysis. In both of the ITS trees (Fig. 19.1A, rooted with Barnadesieae + Mutisieae s.l.; Fig. 19.1B, rooted with only Mutisieae s.l.) the monophyletic group of *Oldenburgia* + Tarchonantheae is supported. However, in contrast to the *ndhF* + ITS tree, the *Oldenburgia* + Tarchonantheae clade is situated far from the other members of the subfamily Carduoideae, the tribes Dicomeae and Cardueae, and is, in fact, the sister group to the large clade formed by *Hecastocleis*, Dicomeae, Cardueae, and the rest of the family. Although it seems likely that *Oldenburgia* is the sister group of Tarchonantheae, the exact position of this clade is still unresolved. For a generic-level phylogeny of the family see Chapter 44.

TAXONOMY

Tribe Oldenburgieae S. Ortiz in Compositae Newslett. 47: 2. 2009 – Type: *Oldenburgia* Less. (Fig. 19.2)

Dwarf cushion-forming shrubs to small trees. Leaves alternate, entire, mainly coriaceous. Involucre campanulate to urceolate, pluriseriate; phyllaries coriaceous and acuminate, pungent, white-tomentose. Receptacle flat, alveolate, epaleate. Capitula large, solitary or on scarcely ramified peduncles, homogamous, radiate. Marginal florets white, bilabiate with the inner lip of two linear-coiled lobes, with sterile stamens and the style as in disc florets; disc florets very numerous (80–1000), white, cream or pinkish-brown, often actinomorphic, rarely slightly zygomorphic, with narrow tube and limb, deeply 5-lobed; anthers 5, caudate and calcarate, with long tapering tails, ramified, with obtuse branches, being these retrorse along the tail and antrorse at the apex, apical appendage acuminate, endothecial tissue polarized, pollen smooth to echinate; style with very short branches, rounded at the apex, smooth to papillose, rarely with apical acute sweeping hairs, the stigmatic area covering the entire ventral side. Achene narrowly ellipsoid to linear, ribbed, glabrous to densely hairy, with barbellate to plumose pappus, testa of the *Gochnatia* type (Grau 1980).

The phylogenetic position and the morphologic distinctness of *Oldenburgia* justify its inclusion in a separate tribe probably as the sister group of Tarchonantheae. Most likely this clade resides in Carduoideae with other African Mutisieae s.l. (Ortiz et al., unpub.). The analyses of Funk et al. (2005) and the consensus tree of the unpublished phylogenetic analysis using the marker *ndhF* (Ortiz et al. unpub.) suggest that this new tribe is situated in a separate clade and is not nested in any other tribe. Its placement as a monophyletic group sister to Tarchonantheae, as seen in the consensus trees of the above-mentioned analyses, does not invalidate the proposal to place it in its own tribe, especially considering the marked morphological differences between the two tribes.

Two of the four species of *Oldenburgia*, *O. paradoxa* and *O. intermedia* Bond, are morphologically very similar to one another; they are both dwarf cushion-forming shrubs. In the phylogenetic analysis performed with the ITS marker (Figs. 19.1), these two species are placed in the same clade. On the other hand, *O. papionum* DC. and *O. grandis* (Thunb.) Baill. form either a trichotomy or a resolved arrangement with the clade of the former two species (Figs. 19.1); these two species are medium-sized shrubs to small trees and are less morphologically similar to one another. Similar results were obtained in a morphological phylogenetic analysis performed to verify the phylogenetic relationships among the four species of *Oldenburgia* (Ortiz et al., unpub.).

MORPHOLOGY

The morphological differences between the tribes Tarchonantheae and Oldenburgieae are well marked, bearing

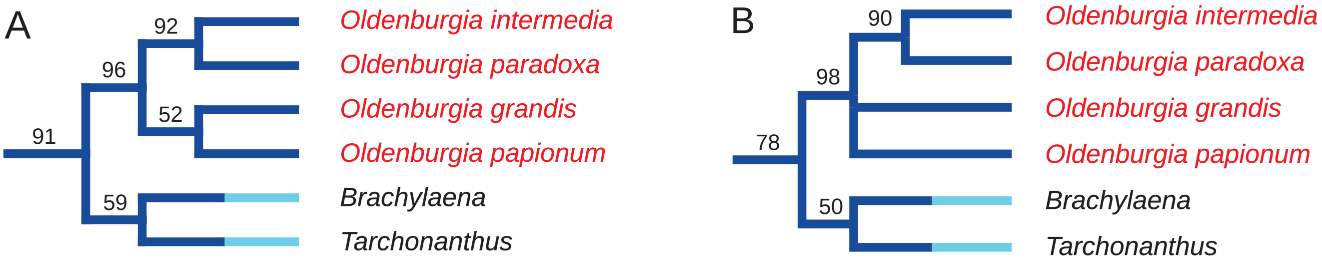

Fig. 19.1. Part of the strict consensus tree of three equally most parsimonious cladograms based on the analysis of ITS (rDNA) sequences (Ortiz et al., unpub.). **A** three genera of Barnadesieae and a broad selection of taxa from Mutisieae s.l. were used as outgroups; **B** a broad selection of taxa from Mutisieae s.l. was used as outgroup. Numbers above lines are bootstrap values (> 50). The colors of the branches represent the areas of the world where the taxa are found. Dark blue = southern Africa; light blue = tropical Africa and Madagascar.

Fig. 19.2. *Oldenburgia*. **A, E** *Oldenburgia grandis* (Thunb.) Baill., habit and habitat (South Africa); **B, C** *Oldenburgia grandis* (Thunb.) Baill., showing early (C) and late (B) flowering stages (garden in Waiuku, New Zealand); **D** *Oldenburgia papionum* DC. (South Africa, Western Cape Province). [Photographs: A, E, S. Proches; B, C, Serenithyme; D, S. Ortiz.]

in mind that the former comprises mainly dioecious trees (although also shrubs) with small discoid capitula of fewer than 30 flowers (rarely up to 90), the capitula arranged in generally dense racemes or panicles.

The morphological differences between Oldenburgieae and the tribe Dicomeae are not well marked, due to the relative heterogeneity of the latter, already noted in the corresponding chapter. However, differences between Oldenburgieae and the core group of Dicomeae are marked, principally in the corolla shape of marginal and disk florets, and achenial shape.

POLLEN

Pollen grains are isopolar, radially symmetrical, suboblate to prolate (P/E = 0.86–1.46), elliptic in meridian optical section, sub-circular in equatorial optical section, acaveate, 3-zonocolporate, with a tripartite apertural system (ecto-, meso-, and endoaperture). The ectoapertures (colpi) 60–85 × 2.5–6.0 μm; the mesoapertures are lolongate; the endoapertures are (ora) lalongate. The exine is 8–14 μm thick, the sexine is 2.5–4.0 times thicker than the nexine, with a structured, micro-perforated tectum and an anthemoid pattern. Sculpture is echinate, with blunt spines, 2–4 × 2.5–6.0 μm. P = 90–127 μm, E = 70–107 μm. [Data for pollen of *Oldenburgia grandis* (Thunb.) Baill.]

CHROMOSOME NUMBERS

Oldenburgia paradoxa, $2n = 36$; *O. papionum*, $2n = 36$; *O. grandis*, $2n = 36$ (all from Goldblatt 1987).

CHEMISTRY

Bohlmann and Zdero (1977) identified 5-methylcoumarin in *O. grandis*, a compound that they thought characteristic of tribe Mutisieae, in which the genus *Oldenburgia* was placed.

ECOLOGY

Oldenburgia lives mainly in mountain habitats ranging from 250 to 1500 m elevation. *Oldenburgia paradoxa*, *O. intermedia* and *O. papionum* colonize principally rocky sandstone outcrops, while *O. grandis* colonizes quartzite outcrops (Bond 1987).

BIOGEOGRAPHY

The four species of *Oldenburgia* are endemic to the Cape Floristic Region of South Africa. Three species (*O. paradoxa*, *O. intermedia* and *O. papionum*) are present in the Western Cape Province while *O. grandis* is present in the Eastern Cape Province (Bond 1987).

Goldblatt (1987) considers *Oldenburgia* a paleotetraploid, and Goldblatt and Manning (2002) suggest that it is a paleoendemic of the Cape Region. The ancient nature of this genus was probably inferred from its isolated situation in the Cape Region, and the fact that Bond (1987) considered its closest relatives to be among the most ancient members of South American Mutisieae s.l. However, the results of the known phylogenetic analysis do not support these relationships with ancient South American Mutisieae. In accordance with Goldblatt (1978), and independent of the geological epoch in which the genus originated, it is possible that its apparent relict character is related to the climatic fluctuations that occurred in South Africa after late Pliocene. This coincides with glacial and interglacial periods that must have been responsible for extinction on a large scale and that gave rise to many relicts confined to the coastal and mountain belts from the Cape to Natal.

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Chapter 20

Cardueae (Carduoideae)

Alfonso Susanna and Núria Garcia-Jacas

HISTORICAL OVERVIEW

The tribe Cardueae is one of the largest in Compositae, with some 2400 species in 73 genera (Susanna and Garcia-Jacas 2007). It is also one of the most complicated because of great morphological diversity and because it comprises some of the largest genera of the family. Cardueae were usually divided into four taxonomic entities, but rank and delimitation of these units has always been problematic, as we shall explain briefly. The earliest classification of the tribe by Cassini (1819) recognized three separate tribes, Echinopseae, Carlineae, and Cardueae, the latter with two subtribes, Carduinae and Centaureinae. Bentham (1873) and Hoffmann (1893), in contrast, suggested a broadly defined Cardueae comprising four subtribes: Echinopsinae, Carlininae, Carduinae, and Centaureinae. This treatment was generally accepted until Wagenitz (1976) segregated Echinopseae as a separate tribe, a proposal that was reintroduced by Petit in 1988. Dittrich (1977) returned to Cassini's views and segregated both Echinopseae and Carlineae. In view of this lack of agreement, Bremer (1994) adopted the more conservative approach and recognized only one tribe. Finally, mainly on the basis of molecular data (Susanna et al. 2006) but also on morphological grounds, Susanna and Garcia-Jacas (2007) adopted the broad concept of a single tribe with four subtribes of Bentham (1873) and Hoffmann (1893) plus one recovered fifth subtribe, Cardopatiinae, which we shall discuss below.

All molecular analyses have concluded that Cardueae are monophyletic, including the most often segregated subtribes Carlininae and Echinopsinae. Despite deep differences in habit, floral morphology, and achene anatomy, all Cardueae share some characters that are not found elsewhere in Compositae. The key is the style morphology, characterized by a thickened articulation below the branches of the upper region usually provided with a collar of hairs, and internal stigmatic surface. Notwithstanding some claims of deep differences (Duistermaat 1996; Häffner 2000), all the style variants within the tribe can be explained as variations of this basic architecture.

Most of the difficulties for assigning tribal or subtribal rank have originated in subtribes Carlininae and Echinopinae, which are rather different from the core Cardueae (the subtribes Carduinae and Centaureinae). Carlininae show some very archaic features: *Atractylis* L. and part of *Carlina* L. have true ligules (Fig. 20.2A below), which are not found elsewhere in the Cardueae. Most species of *Carlina* share a complicated involucral structure that has been interpreted as a third-order syncephaly (Meusel and Kohler 1960; Meusel and Kästner 1994), an interpretation rejected by Petit (1988). Echinopinae are a monotypic subtribe, *Echinops* L., which is characterized by uniflowered capitula grouped in second-order heads (Fig. 20.2E, F below). This structure was the main reason for the segregation of Echinopinae as a different tribe by Wagenitz (1976), Dittrich (1977), and Petit (1988, 1997). Homologies of the synflorescence of *Echinops* are extremely difficult to establish, as is usually the case with highly derived syncephalies (Stuessy and Spooner 1988), for example, two genera of troublesome position within Compositae, *Gundelia* L. and *Hecastocleis* A. Gray, are syncephalous. In fact, contradictory results obtained by different authors in cladistic analyses of morphologic data (compare Karis et al., 1992, versus Petit, 1997) could be partly attributed to different points of view in addressing the problem of homologies of the receptacular structures of *Carlina*, *Echinops*, and related genera.

In addition to the problematic delimitation of Cardueae, the boundaries between the classic four subtribes were also difficult to establish. For example, previous classifications (Bentham 1873; Hoffmann 1893; Dittrich 1977; Bremer 1994) placed *Amphoricarpos* Vis., *Cardopatium* Juss., *Chardinia* Desf., *Cousiniopsis* Nevski, *Siebera* J. Gay, *Staehelina* L., and *Xeranthemum* L. within Carlininae, whereas Petit (1997) moved *Cardopatium* and *Cousiniopsis* to Echinopseae (to which he assigned tribal rank) and the rest of genera to Cardueae-Carduinae. Other genera have been very difficult to classify, such as *Berardia* Vill., included among Cardueae by Bremer (1994), placed in Mutisieae by Dittrich (1996a) and moved back again to Cardueae-Carduinae by Garcia-Jacas et al. (2002).

Finally, there are the problems of generic delimitation posed by some large genera of the tribe: *Carduus* L. (90 spp.), *Cirsium* Mill. (250 spp.), *Centaurea* L. (400 spp. in older classifications), *Cousinia* Cass. (600 spp.), *Jurinea* Cass. (200 spp.), and *Saussurea* DC. (300 spp.). The natural delimitation of *Centaurea* was achieved by Garcia-Jacas et al. (2000, 2001, 2006), some approximations to the limits of *Carduus* and *Cirsium* were made by Häffner and Hellwig (1999), and systematics of the *Arctium* complex has received an important impulse recently (López-Vinyallonga et al. 2009), but the rest of the problems persist. Many small genera from central and west Asia have been described on the basis of splitting *Jurinea*. For example, *Diplazoptilon* Ling, *Hyalochaete* Dittrich & Rech. f., *Jurinella* Jaub. & Spach, *Himalaiella* Raab-Straube, *Modestia* Iljin, and *Outreya* Jaub. & Spach are doubtful segregates merged into the larger genus by Susanna and Garcia-Jacas (2007).

PHYLOGENY

Tribes or subtribes? Molecular evidence

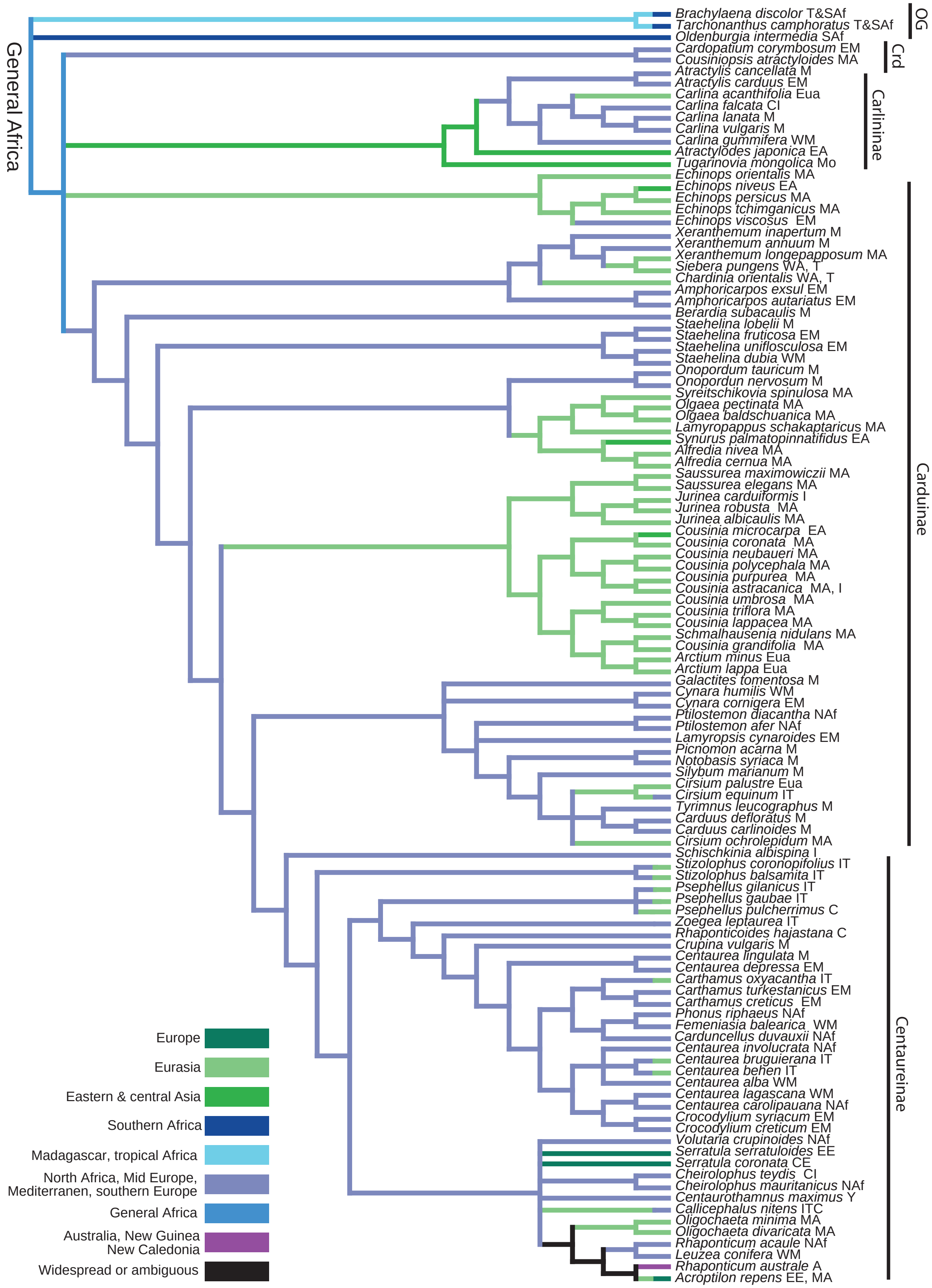
The latest molecular survey (Susanna et al. 2006) (Fig. 20.1), based on three different regions of the genome (*matK*, *trnL-F*, and ITS) and a better outgroup selection, established that the tribe was monophyletic and the subtribal rank was appropriate for the five subtribes that must be recognized (the classic four, Carlininae, Echinopsinae, Carduinae, and Centaureinae, plus one restored subtribe, Cardopatiinae). Indeed, the three basal subtribes (Carlininae, Cardopatiinae, and Echinopsinae) could be segregated from core Cardueae (Carduinae plus Centaureinae) as independent monophyletic tribes, but we do not favor such a fragmented classification. We must acknowledge that our proposal of classification is not a perfect solution, for two reasons: firstly, sister relationships among basal tribes (Carlininae sister to the rest of the tribe, and Cardopatiinae and Echinopsinae successive sisters to the other subtribes) are weakly supported by parsimony (fig. 2 in Susanna et al. 2006) and unsupported by Bayesian analyses (Fig. 20.1); secondly, Carduinae are a paraphyletic assemblage if we split from this subtribe monophyletic Centaureinae. However, alternative, stricter solutions are impracticable (Susanna and Garcia-Jacas 2007). The broad synthetic approach would group together Centaureinae and Carduinae in a single colossal subtribe encompassing 90% of the 2500 species of Cardueae. A narrow analytical approach would keep Centaureinae as a distinct subtribe at the price of splitting present Carduinae into at least seven new subtribes (many of them presently unsupported): Xerantheminae, Staehelininae, Berardiinae, Onopordinae, Carduinae, Arctiinae, and Saussureinae (Fig. 20.1). With our present state of knowledge, we do not favor this splitting, even though future studies could finally lead to it. Quoting Jeffrey (1967), the classic, conservative classification adopted here "is purely artificial without doubt, but it has the merit of some convenience". Chapters 12 and 44 contain overviews of the family and placement of Cardueae.

TAXONOMY

Tribe Cardueae Cass. in J. Phys. Chim. Hist. Nat. Arts 88: 155. 1819 – Type: *Carduus* L., Sp. Pl. 2: 820. 1753

Perennial, biennial, or monocarpic herbs or shrubs, less often annual herbs, very rarely small trees, often spiny. Leaves alternate, frequently forming a rosette, rarely in terminal whorls. Resin-ducts always present in roots, less frequent in aerial parts; laticiferous cells often present but only in aerial parts. Capitula scapose-solitary or diversely corymbose, often aggregate, usually many-flowered, rarely glomerate in secondary capituliform compound

Fig. 20.1. Bayesian inference tree from Susanna et al. (2006) showing the accepted subtribal classification of Cardueae (Crd = Cardopatiinae; OG = outgroup). Branch colors indicate distribution based on color chart using general areas. Abbreviations at the end of taxon names indicate the more specific distribution: C = Caucasus; CE = central Europe; CI = Canary Islands; EA = eastern Asia; EE = eastern Europe; EM = eastern Mediterranean; Eua = Eurasia; I = Iran; M = Mediterranean; MA = middle Asia; Mo = Mongolia; NAf = northern Africa; SAf = southern Africa; T = Turkey; TAf = tropical Africa; WM = western Mediterranean; Y = Yemen.


General Africa
Brachylaena discolor T&SAf
Tarchonanthus camphoratus T&SAf
Oldenburgia intermedia SAf
Cardopatium corymbosum EM
Cousiniopsis atractyloides MA
Atractylis cancellata M
Atractylis carduus EM
Carlina acanthifolia Eua
Carlina falcata CI
Carlina lanata M
Carlina vulgaris M
Carlina gummifera WM
Atractylodes japonica EA
Tugarinovia mongolica Mo
Echinops orientalis MA
Echinops niveus EA
Echinops persicus MA
Echinops tchimganicus MA
Echinops viscosus EM
Xeranthemum inapertum M
Xeranthemum annuum M
Xeranthemum longepapposum MA
Siebera pungens WA, T
Chardinia orientalis WA, T
Amphoricarpos exsul EM
Amphoricarpos autariatus EM
Berardia subacaulis M
Staehelina lobelii M
Staehelina fruticosa EM
Staehelina uniflosculosa EM
Staehelina dubia WM
Onopordum tauricum M
Onopordun nervosum M
Syreitschikovia spinulosa MA
Olgaea pectinata MA
Olgaea baldschuanica MA
Lamyropappus schakaptaricus MA
Synurus palmatopinnatifidus EA
Alfredia nivea MA
Alfredia cernua MA
Saussurea maximowiczii MA
Saussurea elegans MA
Jurinea carduiformis I
Jurinea robusta MA
Jurinea albicaulis MA
Cousinia microcarpa EA
Cousinia coronata MA
Cousinia neubaueri MA
Cousinia polycephala MA
Cousinia purpurea MA
Cousinia astracanica MA, I
Cousinia umbrosa MA
Cousinia triflora MA
Cousinia lappacea MA
Schmalhausenia nidulans MA
Cousinia grandifolia MA
Arctium minus Eua
Arctium lappa Eua
Galactites tomentosa M
Cynara humilis WM
Cynara cornigera EM
Ptilostemon diacantha NAf
Ptilostemon afer NAf
Lamyropsis cynaroides EM
Picnomon acarna M
Notobasis syriaca M
Silybum marianum M
Cirsium palustre Eua
Cirsium equinum IT
Tyrimnus leucographus M
Carduus defloratus M
Carduus carlinoides M
Cirsium ochrolepidum MA
Schischkinia albispina I
Stizolophus coronopifolius IT
Stizolophus balsamita IT
Psephellus gilanicus IT
Psephellus gaubae IT
Psephellus pulcherrimus C
Zoegea leptaurea IT
Rhaponticoides hajastana C
Crupina vulgaris M
Centaurea lingulata M
Centaurea depressa EM
Carthamus oxyacantha IT
Carthamus turkestanicus EM
Carthamus creticus EM
Phonus riphaeus NAf
Femeniasia balearica WM
Carduncellus duvauxii NAf
Centaurea involucrata NAf
Centaurea bruguierana IT
Centaurea behen IT
Centaurea alba WM
Centaurea lagascana WM
Centaurea carolipauana NAf
Crocodylium syriacum EM
Crocodylium creticum EM
Volutaria crupinoides NAf
Serratula serratuloides EE
Serratula coronata CE
Cheirolophus teydis CI
Cheirolophus mauritanicus NAf
Centaurothamnus maximus Y
Callicephalus nitens ITC
Oligochaeta minima MA
Oligochaeta divaricata MA
Rhaponticum acaule NAf
Leuzea conifera WM
Rhaponticum australe A
Acroptilon repens EE, MA
OG
Crd
Carlininae
Carduinae
Centaureinae
Europe
Eurasia
Eastern & central Asia
Southern Africa
Madagascar, tropical Africa
North Africa, Mid Europe, Mediterranen, southern Europe
General Africa
Australia, New Guinea New Caledonia
Widespread or ambiguous

inflorescences and then one-flowered. Involucral bracts in many rows, spiny or unarmed, foliaceous or membranous, often prolonged into a membranous, variously fimbriate, lacerate or pectinate, spiny or unarmed appendage. Receptacle variously chaffy or more often setose, rarely naked (*Alfredia* Cass. pro parte, *Dolomiaea* DC., *Onopordum* L., *Myopordon* Boiss., *Russowia* C. Winkl., and *Tugarinovia* Iljin). Florets usually tubular, very rarely peripheral florets with true rays (*Atractylis* and *Carlina* [Fig. 20.2A]); all fertile or the peripherals sterile through abortion and radiant sterile peripheral florets often absent (especially in subtribe Carduinae). Corollas usually almost actinomorphic, very rarely zygomorphic, divided into a tube and a campanulate limb, straight or s-shaped. Anthers sagittate, apically extending into a rigid, lignified, lanceolate appendage, basally caudate, often with long divisions; anther filaments glabrous or papillose; in many derived groups (especially in subtribe Centaureinae) the stamens are strongly thigmotropic making up an elaborate mechanism of pollen presentation. Style with a papillose-pilose thickening (functionally a pollen brush) below the branches; stigmatic areas only in the inner surfaces of the branches; nectary present at the base of the style. Achenes very variable, with parenchymatous pericarp (in Carlininae, Cardopatiinae, and Echinopsinae, rarely in Carduinae) or radially lignified (in Carduinae and all Centaureinae), usually hirsute in subtribes Carlininae, Cardopatiinae, and Echinopsinae, glabrous in most of Carduinae and Centaureinae. Insertion areole basal, basal-lateral or lateral. Pappus of scales or bristles, directly attached to the pericarp wall in the subtribes Cardopatiinae, Carlininae, and Echinopsinae, and in the genera *Berardia*, *Staehelina*, and the *Xeranthemum* group of Carduinae, or fixed through a parenchymatous ring to the apical plate in remaining Carduinae and all Centaureinae; pappus usually in two structurally different rows (double pappus) in Centaureinae. Pinnules shorter than width of palea (scabrate), as long as width of palea (pinnulate), or much longer and capillar (plumose). Apical caruncle present in many genera of Carduinae, basal elaiosome in Centaureinae, associated with myrmecochory. Pollen tricolporate, oblate, spherical or more prolate; ektexine formed by two layers of columellae, sometimes caveate (in subtribe Centaureinae), spiny, verrucate, scabrate or almost smooth.

Currently there are 72 accepted genera (73 in Susanna and Garcia-Jacas 2007; *Ochrocephala* Dittrich and *Takeikadzuchia* Kitag. & Kitam. moved to synonymy, *Archiserratula* L. Martins added), ca. 2400 species.

A general description of the morphology, karyology, pollen and distribution of the tribe is a complicated task due to the extreme heterogeneity in every aspect. Annuals, unarmed or spiny perennial herbs, subshrubs, shrubs, treelets, trees, alpine meadows or tropical savannahs; there is no habit or habitat alien to Cardueae, which makes it difficult to discuss overall trends. As a result, apart from the synthetic description and general comments above, each one of the five groups with distinctive characters in which the tribe is hereby divided into is discussed below. The five subtribes will have its own detailed description of morphology, chromosome numbers, biogeography, and diversification.

SUBTRIBAL CLASSIFICATION

Carlininae

Perennial herbs or shrubs, less often annual plants. Leaves usually spiny, deeply pinnatisect, rarely unarmed and entire. Capitula frequently subtended by pectinate leaf-like bracts, homogamous or heterogamous, sometimes with radiate florets (Fig. 20.2A). Inner involucral bracts often showy, radiant, and colored (Fig. 20.2B). Receptacle densely covered with large scales, absent only in *Tugarinovia*. Anther filaments glabrous, appendages long and sericeous. Corolla and style very short. Achenes with parenchymatous pericarp, densely sericeous. Pappus of plumose bristles, often connate into stout scales, persistent or deciduous.

The only genera presently included in Carlininae are *Atractylis*, *Atractylodes*, *Carlina*, *Thevenotia* (maybe not specifically different from *Carlina*), and *Tugarinovia* (Susanna and Garcia-Jacas 2007). No molecular phylogeny is yet available for the subtribe, only a reconstruction by Susanna et al. (2006) on a small sample of all the genera, which finally confirmed that *Tugarinovia* was related to *Carlina* as suggested by Dittrich et al. (1987). The curious and puzzling *Tugarinovia* is the only dioecious genus in the tribe.

Carlininae are mainly an eastern Mediterranean group, extending into Eurasia in the north and into North Africa in the south; some species of *Carlina* are widespread in the Eurosiberian climatic region, from the Pyrenees to the Urals. *Atractylis* is more centered in North Africa. The presence of two isolated genera in Middle and East Asia is very remarkable: *Tugarinovia* in Mongolia and *Atractylodes* in Japan and Korea. A probable new genus is presently being studied (Q. Liu, pers. comm.) from the Qinghai-Tibetan plateau, which could fill the gap between the easternmost range of *Carlina* and the East Asian representatives of the subtribe.

The subtribe appears to have had an African origin because Carlininae are probably the basal lineage of Cardueae (Fig. 20.1), and the other tribes of Carduoideae sister to them, Oldenburgieae and Tarchonantheae, are African. Previous hypotheses on the archaic character of insular endemics of *Carlina* in Crete and Macaronesia must be rejected.

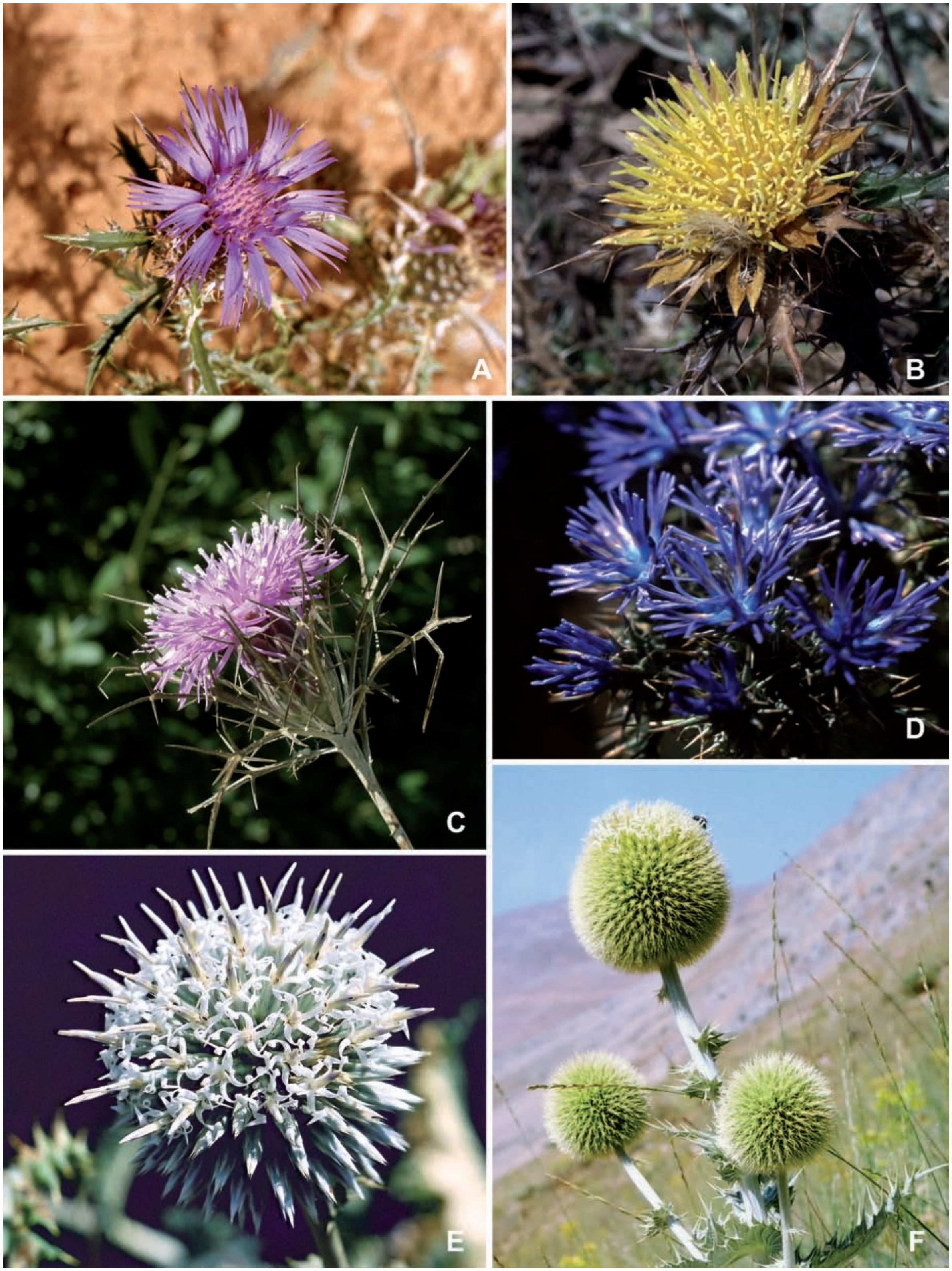


Fig. 20.2. Basal subtribes. Carlininae: **A** *Atractylis carduus* C. Chr. showing true ray florets; **B** *Carlina vulgaris* L.; **C** *Carlina comosa* (Spreng.) Greuter. Cardopatiinae: **D** *Cardopatium corymbosum* Pers. with few-flowered heads grouped in corymbs. Echinopsinae: **E** *Echinops viscosus* Rchb.; **F** *Echinops emiliae* Schwarz ex P.H. Davis and its stunning green-flowered large synflorescences up to 20 cm diameter. [Photographs, authors.]

Cardopatiinae

Spiny perennial or annual herbs. Leaves spiny-dentate or pinnatisect. Capitula either few-flowered and clustered in corymbs, or many-flowered. Involucral bracts with spiny pectinate-fimbriate appendages. Anther filaments glabrous. Florets deep blue, filiform. Style very shortly bilobed. Achenes with parenchymatic pericarp, densely sericeous; pappus double, of two rings of short scales.

Cardopatiinae, as first defined, included only the monotypic genus *Cardopatium*. Later, Nevski (1937) described another monotypic genus, *Cousiniopsis*, closely related to *Cardopatium* (it was first described as *Cardopatium atractyloides* C. Winkler). Classic monographers of Compositae consistently placed both genera among Carlininae, but the only characters that connect these two groups are achenes, which could equally relate *Cardopatium* and *Cousiniopsis* to Echinopsinae. Petit (1997) interpreted the corymbose inflorescence of *Cardopatium*, formed by very small, few-flowered capitula (Fig. 20.2D), as a first step towards the syncephaly of *Echinops* and thus placed *Cardopatium* and *Cousiniopsis* in Echinopsinae. This relationship is unsupported by molecular analyses and we favor interpreting these similarities as convergence, especially since the same trend towards syncephaly appears in all subtribes of Cardueae (Garcia-Jacas et al. 2002). Anyway, Cardopatiinae range among the oldest subtribes, together with Carlininae (Fig. 20.1).

Cardopatiinae show a disjunct distribution. Perennial *Cardopatium corymbosum* grows in central and eastern Mediterranean (from Sicily and North Africa to Greece and Anatolia). In contrast, annual *Cousiniopsis* grows in the deserts of Kara Kum and Kyzyl Kum in Turkmenistan, Kazakhstan, and Uzbekistan.

Echinopsinae

Annual or perennial herbs, spiny or unarmed. Leaves entire or mostly dentate to lobed-pinnatisect, spiny or rarely almost unarmed. Capitula one-flowered, subtended by a tuft of bristles, aggregate in globose secondary heads subtended by small bracts. Involucral bracts in many rows. Outer bracts strongly keeled, winged, apically remotely fimbriate; middle ones more broadly winged, spinose; innermost usually green or green-brown, shiny, linear-lanceolate, often partly or totally connate with only the apical appendages free, not spinose. Length of the bracts varies according to the position of the single-head in the secondary head. Florets violet-blue or greenish. Petals often apically scariose, densely denticulate. Anther filaments glabrous, basal appendages short, laciniate. Achenes with parenchymatous pericarp, oblong, densely sericeous. Pappus of broad, basally connate short scales directly attached to the pericarp.

Our results have demonstrated that Echinopsinae include only *Echinops* s.l. (Fig. 20.2E, F). The only other genus that was usually recognized in the subtribe, *Acantholepis* Less., is a reduced, unarmed species of *Echinops* (Garnatje et al. 2005) as it was originally described (*Echinops acantholepis* Jaub. & Spach).

The origin of the compound inflorescence of *Echinops* cannot be tracked on molecular grounds because the subtribe does not show affinity to any other group. Cardopatiinae and Carlininae are the best candidates for being sister to subtribe Echinopsinae. The structure of the achenes of Cardopatiinae and Echinopsinae is very similar (Dittrich 1977), but this character is also shared with Carlininae and must be considered a synplesiomorphy.

Geographic distribution of Echinopsinae is centered in the Mediterranean, with some taxa widespread in temperate Eurasia and a secondary centre of speciation in west tropical Africa.

Carduinae

Perennial, biennial or annual spiny herbs or subshrubs, rarely unarmed. Capitula homogamous, very rarely peripheral florets sterile and radiant. Bracts usually spiny, innermost exappendiculate or with rudimentary appendages. Achenes with radially sclerified pericarp (absent in *Staehelina* and the *Saussurea* group), often carunculate with apical caruncle. Insertion areole straight or lateral-abaxial. Apical plate very often inclined adaxially. Pappus inserted on a parenchymatous ring in the apical plate, simple or in many undifferentiated rows, deciduous.

Carduinae are a paraphyletic assemblage if we recognize Centaureinae as a different subtribe (Fig. 20.1). Accepting a widely defined subtribe Carduinae, even paraphyletic, seems the most appropriate solution because Carduinae plus Centaureinae would count for ca. 2200 of the 2500 species of the tribe.

Distribution is mainly Mediterranean and secondarily cosmopolitan as extremely noxious weeds (species of *Carduus*, *Cirsium*, *Onopordum*, *Silybum*, and *Notobasis*). The mountains of Central Asia constitute the eastern boundary, and only a few genera (*Cirsium*, *Saussurea*, and *Synurus* Iljin) extend beyond, and only *Cirsium* and *Saussurea* cross into North America.

There are some informal groups within Carduinae, very well-delineated on the basis of morphology and molecular analyses (Susanna and Garcia-Jacas 2007). The more notable are the following ones.

***Xeranthemum* group.** — Unarmed annual herbs, rarely dwarf shrubs. Leaves always entire, velvety underneath. Capitula heterogamous. Receptacle with large scarious scales. Anther filaments glabrous, anther appendages short, laciniate. Corolla lobes very short. Achenes often dimorphic, with pappus of long-tapering or subulate scales, rarely reduced to a corona in *Chardinia*.

Amphoricarpos, *Chardinia* Desf., *Siebera* (Fig. 20.3B), and *Xeranthemum* (Fig. 20.3A) are variations on a theme; this is one of the easiest groups to identify because of the very peculiar pappus of the achenes and the papery silver-white phyllaries. Classically placed in Carlininae, the *Xeranthemum* group appears in our latest molecular analyses (Susanna et al. 2006) as part of Carduinae, sister to the rest of the subtribe with low support but indeed in an isolated position. Cassini (1819) granted them even the tribal status ("Xeranthemées") and if a fractioning of Carduinae should ever be accepted, the *Xeranthemum* group definitely would be one of the best-defined natural subtribes.

Three genera of the group (*Chardinia*, *Siebera*, and *Xeranthemum*) are formed only by annual colonizers of arid and wasteland throughout the Mediterranean and Irano-Turanian regions, especially in the East where, according to genus and species diversity, lies the origin of the group. In contrast, species of the dwarf shrubby genus *Amphoricarpos* are narrow mountain endemics in the eastern Mediterranean (the Balkans, Anatolia, and the Caucasus) and are sister to the rest of the genera.

***Berardia* and *Staehelina*. —** *Berardia* is an acaulescent, unarmed perennial herb. Leaves rounded, entire or denticulate, densely woolly, with veins prominent beneath, white above. Capitula solitary, sessile, homogamous. Involucral bracts subulate, scarious, woolly, ending in a slender flat point. Receptacle areolate. Florets yellowish or pinkish. Staminal connective very long, apiculate. Achenes oblong, glabrous, slightly sulcate. Pericarp not sclerified. Pappus of scabrid cylindrical bristles retrorsely twisted, directly attached to the apical plate.

Species of *Staehelina* are unarmed dwarf shrubs or subshrubs. Leaves entire or dentate-pinnatifid, linear to obovate, dark green above, white-woolly beneath. Capitula corymbose or rarely solitary, homogamous. Involucral bracts ovate to lanceolate, mucronate, sometimes minutely hirsute. Receptacle with wide, basally connate scales. Florets whitish or pink-purple. Corolla lobes very long. Anther filaments glabrous; basal appendages very long, sericeous. Achenes linear-oblong, glabrous or sericeous, with minute apical coronula. Pappus of bristles basally connate into broader paleae, more or less divided apically into pinnulate fimbriae (into capillary hairs in *Staehelina dubia* L. and *S. baetica* DC.), always overtopping involucre, sometimes deciduous in a ring.

Both genera are extreme isolates with no affinities to any other genus of Carduinae, and some molecular analyses suggest without strong support that they could be relatives. *Berardia* was ranked among Mutisieae s.l. on the basis of achenial characters (Dittrich 1977, 1996a) because the pericarp wall is very similar to the type found in tribe Gochnatieae. Curiously, the pericarp of *Staehelina* is also "gochnatioid" (Dittrich 1996a), which could support this faint relationship. However, we cannot say whether this similarity is convergence or a very old character conserved in these two strange genera.

Staehelina was usually placed among Carlininae (Bentham 1873; Hoffmann 1893; Dittrich 1977; Bremer 1994), but Petit (1997) proposed moving it to Carduinae on the basis of floral morphology, which was later confirmed on molecular grounds (Susanna et al. 2006). For Dittrich (1996b), the two species of *Staehelina* with hirsute pericarp (*S. fruticosa* L. and *S. lobelii* DC.) should be classified in a distinct genus, *Hirtellina* Cass. Nevertheless, morphological differences other than achene pilosity are virtually non-existent and we prefer to keep a single genus with *Staehelina* and *Hirtellina* recognized with sectional rank (Susanna and Garcia-Jacas 2007).

Berardia is a very narrow endemic of the maritime Alps in southern France, recently migrated from its coastal glacial refuge. *Staehelina* grows only in the Mediterranean region, from the Iberian Peninsula, France, and Italy to the southern Balkans, Crete and adjacent Anatolia.

***Onopordum* group. —** There are two lineages. *(1)* *Onopordum* s.str. (Fig. 20.3F) consists of stout, erect, very spiny biennial herbs with winged stems, rarely acaulescent. Leaves dentate-pinnatisect or pinnatilobed, rarely undivided, spiny. Capitula solitary or rarely corymbose. Receptacle foveolate. Involucral bracts very deeply serrulate, spiny. Florets reddish, purple or pink. Achenes obovoid-oblong, somewhat tetrangular, glabrous, often transversally fringed, sometimes with a short apical rim. Pappus of plumose, barbellate or scabrid bristles. *(2)* *Ancathia*, *Alfredia*, *Lamyropappus* Knorr & Tamamsch., *Olgaea* Iljin (Fig. 20.3E), *Syreitschikovia* Pavlov, *Synurus*, and *Xanthopappus* C. Winkl.: perennial herbs with entire spiny-toothed leaves, sometimes lobate-pinnatifid. Receptacle usually foveolate. Heads usually solitary or less often corymbose, often nodding at anthesis, with spiny-tipped bracts, the outer ones usually recurved, dark red. Florets cream, yellow, reddish, purple, or pink. Achenes smooth or rugulose.

The usual definition of this group is founded on the absence of receptacular bracts. A pitted, naked receptacle is rare in the tribe. However, not all species of *Alfredia* show epaleate receptacles. In addition to this character, achenes are also peculiar with the pericarp diversely pitted, wrinkled, or rugulose (Susanna and Garcia-Jacas 2007), seldom smooth. The group has negative impact because species of *Onopordum* include some highly noxious weeds widespread in the Mediterranean region, such as *O. acanthium* L. and *O. nervosum* Boiss., giant thistles that can reach up to 3 m high. *Onopordum* is a genus of colonizing biennials, and molecular phylogenies suggest that all the species described in the genus are extremely young and diverged probably in the Pliocene-Pleistocene when the Mediterranean climate first appeared (Suc 1984). In contrast, species of the Central Asian genera of perennial herbs have been dated from the upper Miocene by Wang et al. (2007).

Generic definitions in the group are unclear. All the middle-Asian small genera form a polytomy with a polyphyletic genus *Olgaea*. The inclusion of more species of *Olgaea* and representatives of all the small genera of the group (Garcia-Jacas et al. 2008) has not improved the definition of the genera, besides confirming that *Takeikadzuchia* is a synonym of *Olgaea* as hinted by Dittrich (1977), Bremer (1994) and Susanna and Garcia-Jacas (2007). The only solutions are either lumping all the genera in a single genus *Alfredia*, either redescribing many small segregates from *Olgaea* as distinct genera.

Geographic distribution is very interesting. Species of *Onopordum* are weedy colonizers along the Mediterranean (and other regions with a Mediterranean climate). The remaining genera are narrow endemics in the Tian Shan and Altai mountains, from Mongolia to Tajikistan. Only *Ancathia* has an extended area to Siberia from Tibet.

***Cynara* group. —** Spiny stout perennial herbs. Leaves pinnatisect, very spiny (unarmed in cultivated *C. cardunculus* L.). Capitula large, globose, solitary or clustered in lax corymbs, less often corymbose. Involucral bracts oval or lanceolate, entire, often coriaceous, usually spine-tipped. Receptacle often fleshy, densely setose. Florets pink, purplish or violet. Anther filaments papillose. Achenes glabrous, faintly angular or smooth, globose (*Cynara* and *Ptilostemon*) or linear; apical rim and nectary absent (present only in *Lamyropsis*). Pappus of very long plumose bristles basally connate in a ring.

This group has been recently segregated from the thistles, to which it is closely related (Susanna and Garcia-Jacas 2006). It comprises the genera *Cynara* L. (Fig. 20.3C), *Lamyropsis* (Kharadze) Dittrich, and *Ptilostemon* Cass. They share floral and leaf characters and a peculiar biogeography. Some species of the *Cynara* group are ruderal colonizers with wide areas of distribution like most of the thistles. However, all the genera have undergone intense speciation in the Mediterranean region with narrow endemics in conserved habitats. *Cynara* and *Lamyropsis* show greater species differentiation in the eastern Mediterranean. In contrast, *Ptilostemon* is maybe one of the rare genera of the Carduinae that has most of its endemic taxa in the western Mediterranean (the Iberian Peninsula, southern Italy, and north Africa), even though it ranges from Ukraine to Spain (Greuter 1973).

***Carduus-Cirsium* group. —** Perennial, biennial or annual herbs. Leaves dentate-pinnatisect, spiny, sometimes entire, often semi-amplexicaul. Stems often spiny-winged (especially in *Carduus*). Outer involucral bracts few, spiny; inner bracts without spines, leaf-like, often appendiculate, and colored. Florets red, purple or pink, rarely yellow. Achenes obovoid-oblong, smooth, glabrous, with an apical rim and a small obconical caruncle. Pappus of plumose or barbellate bristles, usually deciduous as a single piece.

This is the large complex of very spiny plants which are usually called "thistles" (Fig. 20.4C, F). All of these have medium or large-sized heads, very spiny leaves, and achenes with apical nectary and a long pappus detachable as a single piece. Our molecular results indicate that at least the largest part (*Carduus* L., *Cirsium* Mill., *Notobasis* Cass., *Picnomon* Adans., *Silybum* Adans., and *Tyrimnus* Cass.) are a natural group (Fig. 20.1). The rest of the genera traditionally placed among thistles (*Cynara*, *Lamyropsis*, and *Ptilostemon*) should rather be positioned in a separate group, the *Cynara* group (see above). *Galactites* Moench probably belongs to the *Carduus-Cirsium* group, but molecular data do not support this. This genus has only two species and shows some intriguing features that are very unusual, not only among thistles, but also in Carduinae: a hygrophanous pericarp and a capitulum with well developed radiant sterile florets very similar to those of Centaureinae, in a fine example of convergence (Fig. 20.3D).

As pointed out by Häffner and Hellwig (1999) and Garcia-Jacas et al. (2002), phylogenetic relationships and generic boundaries within the clade are obscure. One of the reasons for this is the co-existence of annual or biennial species (most of *Carduus*, *Galactites*, *Picnomon* Adans., *Silybum*, and *Tyrimnus*) together with perennials (many species of *Cirsium* and some *Carduus*), which hinders the assessment of the two aspects from a molecular standpoint because of the different mutation rate of annuals and perennials (discussed for annual species of *Cousinia* in López-Vinyallonga et al. 2009; see also references therein). The *Carduus* group, together with the *Jurinea-Saussurea* group, requires a more comprehensive molecular analysis.

Distribution of the group is cosmopolitan. *Cirsium* is mainly Eurasian, with some species native to North America from Canada to Mexico. *Carduus* shows many successful adaptations to the Mediterranean region, where it is ubiquitous. Both *Carduus* and *Cirsium* range among the few genera of Cardueae that have radiated to tropical Africa (Jeffrey 1967). The rest of the genera of the group are mono- or ditypical, constituted by active colonizers in the Mediterranean region s.l. and extremely noxious weeds in other regions of the world with a Mediterranean-type climate.

***Arctium-Cousinia* group. —** Perennial herbs, rarely biennial, exceptionally annuals, spiny or less often unarmed. Receptacle scales are always twisted. Achenes tigrine (with darker wavy stripes), very often winged, without apical nectary. Pappus formed by free deciduous bristles, contrary to most of the thistles in which pappus is usually detached as a single piece.

This is a very well-defined natural group formed by the genera *Arctium* L., *Cousinia* Cass. (Fig. 20.4D, E), *Hypacanthium* Juz., and *Schmalhausenia* C. Winkl. One of them, *Cousinia*, is the largest of the tribe and one of

Fig. 20.3. Carduinae. **A** *Xeranthemum annuum* L. and **B** *Siebera pungens* J. Gay (*Xeranthemum* group) with bright-colored involucral bracts mimicking ray florets; **C** *Cynara humilis* L., a wild relative of artichoke; **D** *Galactites tomentosa* Moench with showy sterile peripheral florets; **E** *Olgaea petri-primi* B.A. Sharipova; **F** *Onopordum nervosum* Boiss. (*Onopordum* group). [Photographs, authors.]

Fig. 20.4. Carduinae. **A** *Jurinea olgae* Regel & Schmal. with florets sharply bent outwards mimicking ligules; **B** *Jurinea* sp.; **C** *Cirsium sairamense* O. Fedtsch. & B. Fedtsch.; **D** *Cousinia ferruginea* Kult.; **E** *Cousinia lanata* C. Winkl.; **F** *Cirsium arvense* (L.) Scop. [Photographs, authors.]

the largest of the whole Compositae with 600 species. New analyses including the ITS and *rpS4-trnT-trnL* region of a very large sample of more than 200 taxa (López-Vinyallonga et al. 2009) have failed in giving a solution to the limits of *Arctium* and *Cousinia*. There are two main lines in the *Arctium* group, the Arctioid clade and the Cousinioid clade, segregated by molecular data, chromosome numbers, and pollen type, but this grouping is not consistent with morphology: two genera of the group, *Schmalhausenia* and *Hypacanthium*, are part of *Arctium* on the basis of pollen, chromosomes, and DNA sequences, but are morphologically much closer to *Cousinia*. In addition to an "Arctioid" group of *Cousinia*, there is also a "Cousinioid" group of *Arctium*. A deep morphological survey is presently ongoing within the Arctioid group to verify whether a natural delineation of genera is possible, but it is highly probable that *Arctium*, *Cousinia* subgenera *Cynaroides* and *Hypacanthodes*, *Hypacanthium*, and *Schmalhausenia* will have to be grouped in *Arctium*.

The distribution of this group shows three patterns. The first one is exemplified by *Arctium*, extended in temperate Eurasia as a colonizer. It has been hypothesized that the biennial habit is a key character for the colonizing success of *Arctium* (López-Vinyallonga et al. 2009) and this is also exemplified in other noxious weeds of Carduinae such as *Onopordum* (Garcia-Jacas et al. 2008) and *Silybum*. The second pattern is the xeric adaptation of *Cousinia* s. str., extended through the Irano-Turanian region in one of the most explosive radiations in the Compositae with ca. 500 species in a limited territory (semideserts and steppes of Afghanistan, Iran, Iraq, and Turkestan). The third pattern appears among the taxa of the Arctioid group with the exclusion of *Arctium* (*Cousinia* sect. *Cynaroides* and *Hypacanthodes*, and the genera *Hypacanthium* and *Schmalhausenia*). Species of this group are very narrow endemics in the mountains of Central Asia, mainly in the Tian Shan.

***Jurinea-Saussurea* group. —** Unarmed perennial herbs or subshrubs; only two annual herbs. Leaves entire or pinnatisect, often silver-white below and glabrous above, sometimes hirsute-scabrid. Capitula cylindrical or globose, often paniculate, homogamous. Anther filaments glabrous. Achenes not lignified, soft. Pappus of very long (longer that involucral bracts), showy, usually pure white plumose bristles, basally connate in a ring; sometimes with a shorter, pinnulate deciduous pappus connate to a globose nectary (*Jurinea*). Three genera, ca. 500 species.

This group was extremely difficult because of the unclear generic boundaries between the larger genera *Jurinea* and *Saussurea* and the high number of small segregates: sixteen genera have been described within the complex. However, this figure should be reduced to three: *Dolomiaea*, *Jurinea*, and *Saussurea*. As hypothesized in the latest survey of the tribe (Susanna and Garcia-Jacas 2007), the last doubtful segregates *Diplazoptilon*, *Frolovia*, and *Himalaiella* should be placed in *Jurinea* s.l. on the basis of the molecular data contributed by Wang et al. (2007)

Geographic distribution of this group is peculiar. *Jurinea* is mainly Mediterranean, ranging from Iran to the Iberian Peninsula and North Africa, and has a middle-Asian nucleus in the mountains of the Tian Shan, connecting to the area of Sino-Tibetan *Dolomiaea*. *Saussurea* is mainly Eurasian reaching the extreme east Asia (Japan) and is one of the scarce genera of the tribe that is present in North America, with six species. A single rare species of *Saussurea*, *Saussurea lyrata* (often classified as a different genus *Hemistepta*), is one of the only two taxa of the tribe that are native in Australia.

Centaureinae

Perennial, biennial or annual unarmed herbs, shrubs or very rarely treelets, rarely spiny. Capitula often heterogamous with sterile radiant florets, rarely homogamous. Involucral bracts often with a diversely scarious, fimbriate, pectinate, spiny or unarmed appendage; innermost bracts always with a scarious appendage. Achenes with sclerified pericarp. Insertion areole concave, lateral-adaxial, very rarely (*Crupina*) straight, often with an elaiosome. Apical plate straight. Pappus inserted on a parenchymatous ring in the apical plate, double, formed by two rows of differently pinnulate bristles, rarely single by abortion, deciduous or persistent.

Subtribe Centaureinae has been subject of many studies in every aspect: morphology, chromosome numbers, pollen types and, more recently, comprehensive molecular surveys. As a result, the main problem of the group (the natural delineation of the large genus *Centaurea*) was finally solved (Garcia-Jacas et al. 2000, 2001; Greuter et al. 2001). The evolution of the characters seems also clear and is very illustrative.

Floral morphological evolution. — Evolution of morphological characters in the subtribe is extremely complicated due to the frequent reversals of character states and parallelisms (Wagenitz and Hellwig 1996; Vilatersana et al. 2000a; Garcia-Jacas et al. 2001). The main three trends are: the development of marginal sterile radiant florets (Fig. 20.5C) which, in the most primitive groups, still have staminodes (Fig. 20.5D); the specialization towards myrmecochory by means of a basal elaiosome, combined with the change from a basal hilum of the seed to a lateral hilum; and the trend towards the development of complicated appendages in the phyllaries (Dittrich 1968; Wagenitz and Hellwig 1996; Garcia-Jacas et al. 2001, 2006). Convergence, however, is always present in many of the lines: e.g., peripheral sterile florets has appeared in different lineages of Centaureinae (even in an unrelated genus of the thistles group of Carduinae, *Galactites*, Fig. 20.3D).

Fig. 20.5. Centaureinae, basal genera. **A** *Cheirolophus junonianus* (Svent.) Holub; **B** *Rhaponticum serratuloides* (Georgi) Bobrov; **C** *Amberboa moschata* (L.) DC.; **D** *Mantisalca salmantica* (L.) Briquet & Cavill. (the arrow indicates the showy staminode in the sterile peripheral florets); **E** *Psephellus* sp., a cultivated ornamental hybrid; **F** *Rhaponticoides africana* (Lam.) M.V. Agab. & Greuter. [Photographs, authors.]

Besides macromorphology, the character that best describes the evolution of Centaureinae is pollen type.

Pollen evolution. — Wagenitz (1955) described eight pollen types in the subtribe Centaureinae. The *Serratula* L. type is found in the basal genera of subtribe Centaureinae and in subtribe Carduinae. The *Crupina* type is restricted to the genus *Crupina* (Pers.) Cass. The *Rhaponticoides* (= *Centaurea centaurium*) pollen type is found in the genera *Rhaponticoides* Vaill. and *Stizolophus* Cass. The *Psephellus* (= *Centaurea dealbata*) type is diagnostic of the genus *Psephellus* Cass. The *Centaurea Cyanus* and *Centaurea Montana* pollen types are limited to *Centaurea* sect. *Cyanus*. The *Acrocentron* (= *Centaurea scabiosa*) type is characteristic of sect. *Acrocentron* in its widest sense (Wagenitz and Hellwig 1996). The *Centaurea Jacea* pollen type occurs most frequently in the genus and is the basis of present, natural circumscription of *Centaurea*.

Wagenitz (1955) gave an evolutionary ranking to the pollen types with *Serratula*, *Crupina*, and *Rhaponticoides* as the most primitive, *Psephellus* (*Centaurea dealbata*), *Centaurea Cyanus*, and *Centaurea Montana* types as intermediate, and *Acrocentron* and *Centaurea Jacea* pollen types as the most advanced. The evolution followed two independent processes, as confirmed on molecular grounds (Garcia-Jacas et al. 2001).

The first trend runs from a spiny pollen type (*Serratula* or similar pollen type) to a smooth pollen type. This evolution is paralleled in the stigma and is caused by the development of a pollen presentation mechanism. As thoroughly described by Briquet (1902), the fertile florets in many species of *Centaurea* are strongly thigmotrophic. If an insect touches a floret, the anther papillae react instantly contracting the anther tube and the brush at the base of the stigma drags the pollen from inside the anther tube. Contrary to the usual view, the anther tube is dragged downwards by the contracting anther filaments, not the style tube that extends trough the tube. This dragging mechanism is universally present in the tribe (the brush at the base of the stigma is a critical tribal character), but only the most evolved groups exhibit this ability for such a fast reaction (studied in depth by Briquet, 1902). Minimizing the run of the anthers for a fast and repeatable pulling out of the pollen implies a very short stigma, which could not accommodate the long papillae associated with spiny pollen: instead, a sticky gum is secreted and the pollen becomes smooth.

This evolution from spiny to smooth pollen type in correlation with instantaneous pollen presentation has occurred in parallel at least in two different lines in two subtribes: in Centaureinae (Garcia-Jacas et al. 2001) and in the *Arctium* group of Carduinae. In this complex, the species of *Arctium* and related genera have spiny pollen type, long stigmas, and no pollen presentation mechanism. To the contrary, *Cousinia* has smooth pollen, short stigmas, and reactive pollen presentation (López-Vinyallonga et al. 2009).

The second trend in the evolution of the pollen of Centaureinae runs from an anthemoid exine pattern to the development of a cavea. This is a generalized trend in many groups of Centaureinae, but is poorly studied in Cardueae. The cavea is certainly related to the adaptation of mesophyllous taxa to the hard conditions of the Mediterranean and Irano-Turanian climate and the need to accommodate harmomegathy for extreme oscillations in temperature and humidity. A good example is found in the genera *Myopordon* and *Oligochaeta* K. Koch (studied in depth by Hidalgo et al. 2008). Species of the small genus *Myopordon* evolved from mesophyllous taxa closely related to *Rhaponticum* Vaill. (Hidalgo et al. 2006) with *Serratula* pollen type. Adaptation to extreme high mountain conditions and warmer climate led to the development of caveate pollen types in some species of *Myopordon* in a fine recompilation of the parallel similar evolution in other groups of Centaureinae. An indirect proof of this hypothesis on the origin of caveate pollen are the intermediate types *Carthamus* L. (Vilatersana et al. 2001), *Crupina*, and *Rhaponticoides* (= *Centaurea centaurium* pollen type of Wagenitz, 1955). Exine structure of these three pollen types is intermediate between the *Serratula* exine type, with a dense basal stratum of columellae, and the caveate types where the columellae are strongly reduced. In the three cases, adaptation to extreme conditions is the driving force: the three genera derive certainly from mesophyllous plants that evolved into species adapted even to the Iranian desert, such as *Rhaponticoides lachnopus* or into genera wholly adapted to the most extreme xeric and hot conditions in the Mediterranean and Irano-Turanian region, such as *Carduncellus* Adans., *Carthamus*, and *Crupina*. Figure 20.6 reflects pollen evolution on a phylogeny of Centaureinae, showing the deep correlations between pollen types and overall evolution.

Chromosomal evolution. — The subtribe shows a complex dysploid chromosome series, with base chromosome numbers ranging from $x = 16$ to $x = 7$ (Garcia-Jacas et al. 1996). Correlation between this series and the phylogeny suggested by both pollen type and molecular data is good. The limit between primitive and derived can be placed at $x = 12$ (Garcia-Jacas et al. 1996): base numbers above $x = 12$ are found among the basal grade of the subtribe, whereas numbers of $x = 12$ and lower are found in the most evolved groups (Fig. 20.6). Descending dysploidy was interpreted as an adaptation to arid habitats by favoring shorter life cycle in *Nonea* (Boraginaceae) by Selvi and Bigazzi (2002) and in *Pogonolepis*, *Sondottia*, and *Trichanthodium* (Gnaphalieae and Plucheeae) by Watanabe et al. (1999). Thus, we hypothesize that general trend towards descending dysploidy in Centaureinae is correlated with the trend already detected towards the development

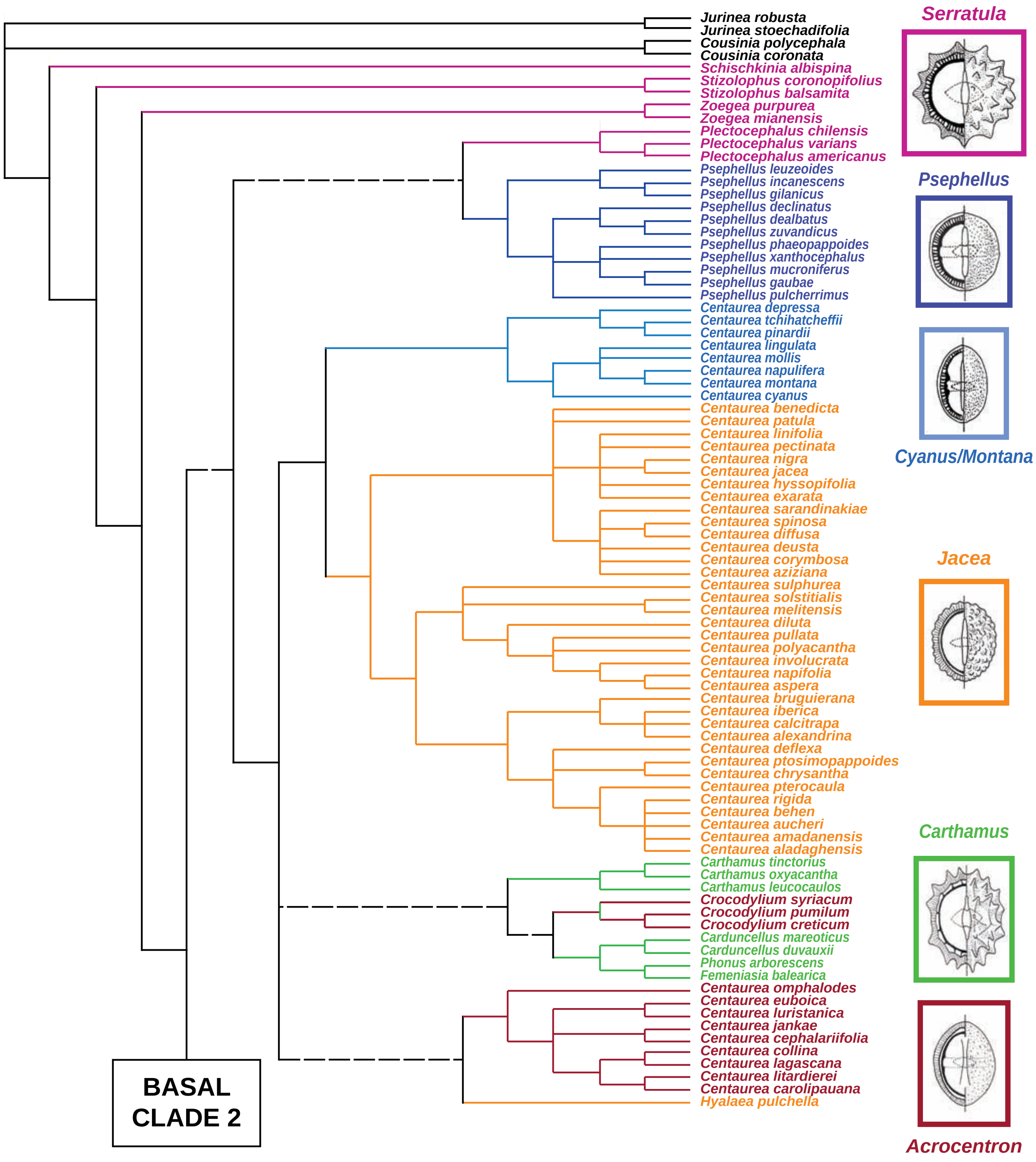
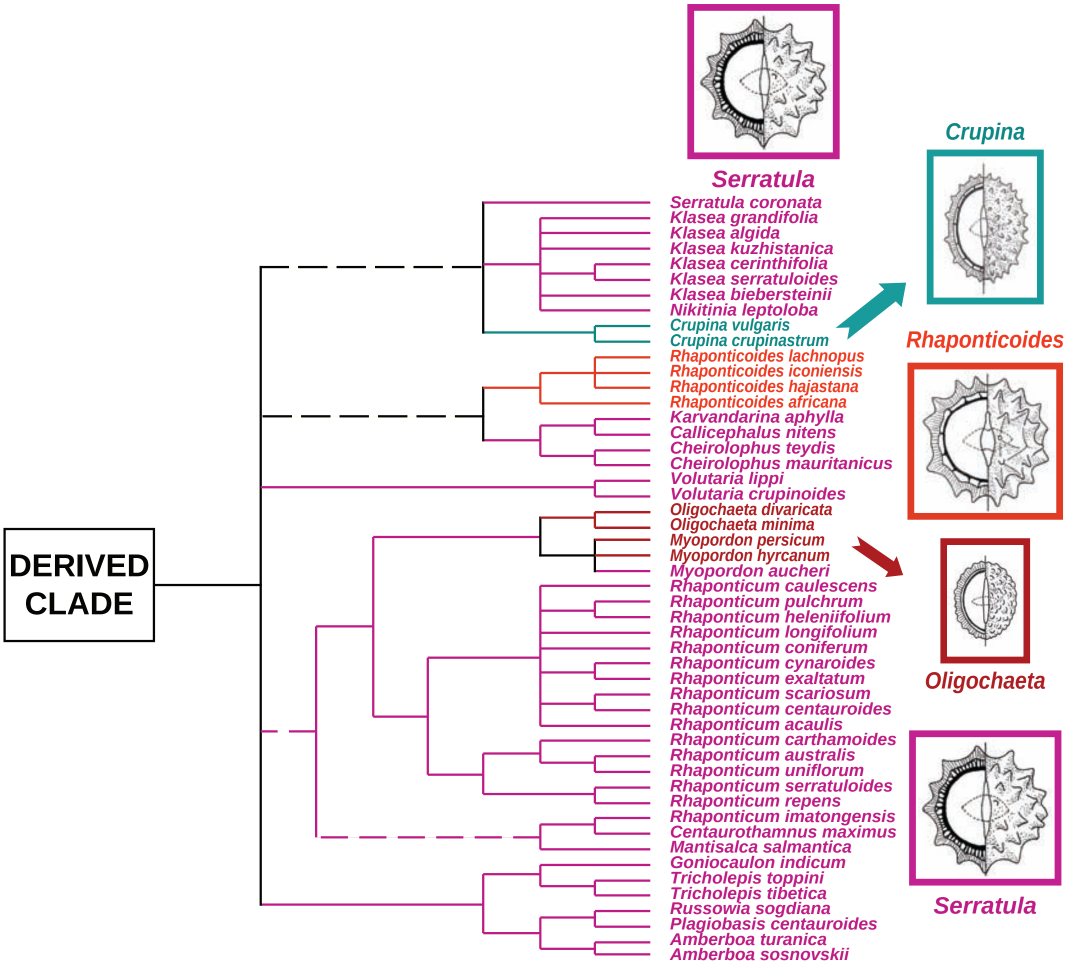


Fig. 20.6. Tentative phylogeny of Centaureinae (basal clade above, derived clade on opposite page) reconstructed on the basis of Garcia-Jacas et al. (2001, 2006) and Hidalgo et al. (2006), showing correlation between pollen types and evolution of the subtribe. Dashed lines indicate unsupported clades.



of caveate pollen. Adaptation of mesophyllous taxa to the xeric conditions of the Mediterranean would be the trigger of changes that, in the case of Centaureinae, are very well correlated with other morphological changes and hence to taxonomy. Other examples in Carduinae could confirm this trend. In the *Xeranthemum* group, perennial and mesophyllous mountain species of *Amphoricarpos* have $x = 14$, whereas annual xerophytes of the genera *Chardinia*, *Siebera*, and *Xeranthemum* show a complex dysploid series from $x = 12$ to $x = 5$ (Garnatje et al. 2001). Within the *Arctium* group, the mesophyllous Arctioid clade has $x = 18$ and the thermophyllous Cousinioid clade $x = 13$, 12, 11, 10, and 9 (López-Vinyallonga et al. 2009).

Polyploidy is also frequent and involves both auto- and allopolyploidy. A classic example of alloploidy is *Carthamus* sect. *Atractylis* (Vilatersana et al. 2000b). However, hybrids between taxa with the same number are usually homoploid (Garcia-Jacas and Susanna 1992). Among some monophyletic groups showing dysploidy, hybrids between species with different number are known and even one of them was found to be fertile: e.g., *Centaurea* ×*losana* Pau ($2n = 54$) is a naturally occurring fertile cross between *C. lagascana* Boiss. with $2n = 66$ and *C. cephalariifolia* Willk. with $2n = 40$ (cf. Fernández Casas and Susanna 1986).

Major groups in the subtribe Centaureinae. — On the basis of pollen types (Wagenitz 1955), morphology (Wagenitz and Hellwig 1996; Susanna and Garcia Jacas 2007), DNA sequence analysis (Susanna et al. 1995; Garcia-Jacas et al. 2000, 2001, 2006; Vilatersana et al. 2000a), and karyology (Garcia-Jacas et al. 1997, 1998a, b), some informal groups have been recognized in the subtribe. Some taxa cannot be placed in any group and remain isolated close to the base of the tree (Garcia-Jacas et al. 2001). Besides these unclassified genera, the major informal groups that have been defined are *Carthamus*-*Carduncellus*, *Centaurea* s. str., *Klasea* Cass., *Rhaponticum*, and *Volutaria* Cass. (Wagenitz and Hellwig 1996; Susanna and Garcia-Jacas 2007).

The unclassifiable rogue annuals. — Three small genera of annuals are placed as successive sister to the rest of Centaureinae, which are mostly perennial herbs: *Schischkinia* Iljin (Iran and Turkestan), *Stizolophus*, and *Zoegea* L. (Iran and Anatolia). Whether this position reflects true sister relationships or this is an artifact caused by the annual habit, we cannot say. On morphological grounds, the three genera are very isolated. In this case, pollen type is of little help. *Zoegea* has the *Serratula* type, the most primitive. *Stizolophus* shows a pollen type very similar to the *Carthamus* and *Rhaponticoides* types, but certainly this must be the result of convergence. Pollen type of *Schischkinia* is unknown.

Unrelated genera of the basal grade. — The genera *Centaurodendron*, *Cheirolophus* Cass., *Crupina*, *Plectocephalus*, *Psephellus*, *Rhaponticoides*, and *Serratula* are noteworthy isolates. The newly described *Archiserratula* (Martins 2006) probably belongs here, too.

Reconstructing affinities and relationships among these genera is very difficult. In this sense, the problem posed by *Psephellus* (Fig. 20.5E) is intriguing. *Psephellus* is very probably at the origin of the subgenus *Centaurea* subg. *Cyanus* on the basis of geographic distribution (eastern Mediterranean) and pollen type (smooth, not caveate). The achenial characters (hylum lateral and persistent pappus) should place *Psephellus* among the derived group of Centaureinae. However, this is utterly unsupported in all our molecular analyses. A similar close relationship is suspected between *Plectocephalus* and *Psephellus*, also unconfirmed by molecular data.

As could be expected from the oldest stock in the subtribe, many species of the basal genera are relicts. Species of *Cheirolophus* (Fig. 20.5A) grow in the Western Mediterranean and Macaronesia from Malta to Madeira (Susanna et al. 1999). *Plectocephalus* shows one of the most striking disjunctions in the tribe: one species lives in Ethiopia; two more in Siberia (if *Phalacrachena* Iljin is confirmed as a synonym of *Plectocephalus* as was suggested by Susanna and Garcia-Jacas 2007); two species in North America; and two more in South America. Closely related to the South American *Plectocephalus*, the monotypic genus *Centaurodendron* grows in the Juan Fernández archipelago (Bernardello et al. 2006). *Rhaponticoides* (Fig. 20.5F) is a steppe-related genus with many isolated and some widespread taxa ranging from the Tian Shan to the Iberian Peninsula. *Serratula* is Eurosiberian in its widest sense; in the Mediterranean region it grows only in the mountains. *Crupina* is an invader of eastern Mediterranean origin widespread in the Mediterranean and Irano-Turanian region that has become a weed in the western United States.

***Klasea, Rhaponticum,* and *Volutaria* groups. —** This complex of genera includes most of the "basal grade" of Centaureinae. Relationships of the three groups are obscure but, according to the molecular survey of Hidalgo et al. (2006), *Klasea* is sister to the *Volutaria* plus *Rhaponticum* groups. Recently, Martins (2006) described a new genus in the complex, *Klaseopsis*. The new genus must be included in *Rhaponticum* (Fig. 20.5B), as could be expected from morphology of the bracts and structure of the pappus, and this has been confirmed by DNA analyses (Hidalgo 2006).

Genus delineation is now clear, but some incongruences persist. Maybe the most vexing is the impossibility of confirming monophyly of the *Volutaria* group with molecular data. The *Volutaria* group is formed by the genera *Amberboa* Less. (Fig. 20.5C) *Goniocaulon* Cass., *Mantisalca* Cass. (Fig. 20.5D), *Plagiobasis* Schrenk, *Russowia*, *Tricholepis* DC., and *Volutaria*, according to Susanna and Garcia-Jacas (2007). On the basis of morphology (bract appendages, peripheral sterile florets, and achenes), there is little doubt regarding its monophyly. However, all the molecular analyses carried out to date place *Mantisalca* and *Volutaria* in an unsupported position within other clades (Susanna et al. 2006; Hidalgo et al. 2006).

Species of the *Volutaria* group cover a very broad area in the Mediterranean (*Mantisalca* and *Volutaria*) and Irano-Turanian regions (*Amberboa*, *Plagiobasis*, and *Russowia*). *Goniocaulon* is an annual colonizer in India that was reported in Sudan and Ethiopia by Jeffrey (1967). *Tricholepis* is the only genus of Centaureinae that has radiated principally in East Asia, from the Himalayas and north India to Myanmar.

The *Rhaponticum* group is better resolved, and its monophyly has been confirmed. It comprises the genus *Rhaponticum* (ca. 25 spp.), which, according to Hidalgo et al. (2006), should also include the genera *Acroptilon* Cass. and *Leuzea* DC. The genus *Ochrocephala* is probably part of *Rhaponticum*. Other smaller genera of the complex are monotypic *Centaurothamnus* Wagenitz & M. Dittrich and *Karvandarina* Rech. f. (placed in the *Volutaria* group by Susanna and Garcia-Jacas 2007), and *Myopordon* (5 spp.) and *Oligochaeta* (4 spp.). Species of the group are characterized by achene characters and by the usually papery silver-white involucral bracts. Nevertheless, habit and morphology are extremely variable.

Distribution of the group is also diverse. Most of the species of *Rhaponticum* (Fig. 20.5B) are mountain endemics in Eurasia, from Siberia to the Iberian Peninsula and north Africa. *Rhaponticum australe* (Gaudich.) Soják is the other only native Australian species of Cardueae, and as was the case with *Saussurea lyrata*, its natural presence in Australia is difficult to explain. *Myopordon* is a small genus of dwarf shrubs from the alpine zone of the mountains of the Middle East (Lebanon, Turkey, and Iran) at heights of 3500–4000 m. *Oligochaeta* comprises only frail annuals from the lowlands of the Irano-Turanian region from the Caucasus to west India. Finally, *Centaurothamnus* is a monotypic endemic from Yemen very closely related to the only species of *Rhaponticum* from Ethiopia (Hidalgo et al. 2006), formerly *Ochrocephala*.

The highly-evolved grade. — This group comprises the most highly nested taxa of the subtribe and they are defined by a series of characters: the basis of chromosome numbers ($x = 12$ or less), the achenial anatomy (lateral hilum in all the cases), and the presence of well-developed sterile peripheral florets without staminodes (with the exception of the *Carthamus-Carduncellus* complex, which exhibits some unusual archaic features).

***Carthamus-Carduncellus* group.** — This complex is formed by four genera, *Carduncellus* Adanson (Fig. 20.7B), *Carthamus* L., *Femeniasia* Susanna, and *Phonus* Hill. The subtribe position of this complex within Cardueae has been traditionally difficult because most species in the complex have spiny leaves, a frequent characteristic in Carduinae, but highly unusual in Centaureinae. The caducous single pappus found in some species of *Carduncellus* (Cassini 1819; Dittrich 1969) and *Femeniasia* (Susanna 1988) is more representative of the subtribe Carduinae than the tribe Centaureinae. However, the spiny habit could be easily attributed to secondary adaptation against predators; and the reduction from a double to a single pappus occurs frequently in the subtribe Centaureinae, thus it provides minimal systematic value (Dittrich 1968, 1969; Wagenitz and Hellwig 1996). Classification of the complex among Centaureinae is now undisputed, despite primitive traits, such as spiny habit, not caveate pollen, long stigmas, and the absence of peripheral specialized florets (Fig. 20.7B). These characters are in acute contrast with the position of the group within the more advanced groups of the subtribe (Garcia-Jacas et al. 2001; Susanna et al. 2006).

A fifth genus could be part of this group, *Crocodylium* Cass. (Fig. 20.7D), according to Vilatersana et al. (2000a), but without any support. *Crocodylium* (as *Centaurea* sect. *Aegialophila*) was related by Wagenitz and Hellwig (1996) to *Centaurea* subg. *Acrocentron*, from which it was excluded on molecular grounds by Font et al. (2002). In some aspects (pollen type and peripheral sterile florets with sterile "achenioids"), *Crocodylium* could be intermediate between *Carduncellus* and *Centaurea* subg. *Acrocentron*.

Carduncellus centers in the western Mediterranean (the Iberian Peninsula and North Africa, eastward to Greece and Egypt) and grows usually in conserved habitats (garrigues, macchia, and stony places in mid-mountains). In contrast, *Carthamus* centers in the eastern Mediterranean and comprises only colonizers and invaders in waste places. *Crocodylium* grows in the eastern Mediterranean and the Middle East; *Phonus* is endemic to southern Spain and Morocco, and monotypic *Femeniasia* is a very narrow endemic to Menorca (Balearic Islands).

***Centaurea* s.str.** — The natural delineation of *Centaurea* was achieved only on the basis of molecular data (Susanna et al. 1995; Garcia-Jacas et al. 2000, 2001). The group was recognized as unnatural, from Cassini (1819) to Susanna et al. (1995). The main problem was the position of the type of the genus, a species from a small group of ca. 25 taxa without relationship with the bulk of the genus (ca. 250 species). Nomenclatural consequences of a redefinition of the genus were so dramatic that only the confirmation of the relative position and the boundaries of the natural groups by DNA sequence analyses led to a proposal of a new type for the genus (Garcia-Jacas et al. 2000, 2001; Greuter et al. 2001). As presently circumscribed (Susanna and Garcia-Jacas 2007), it comprises three subgenera: *Centaurea* (formerly the *Jacea* group; Fig. 20.7C, F), with ca. 120 species; *Acrocentron* (Fig. 20.7E) with ca. 100 sp., and *Cyanus* (Fig. 20.7A) with ca. 30. Sister relationships of *Cyanus* and *Centaurea* are firmly established, but the connections of these two subgenera and subgenus *Acrocentron* are unclear.

The distribution of this very large genus is mainly Mediterranean with some taxa widespread in the mountains of temperate Eurasia and many cosmopolitan weeds such as *Centaurea cyanus* L., associated with wheat cultivation since the development of agriculture in the Neolithic (Rösch 1998). According to the well-established origin of subgenera *Acrocentron* (Font et al., in prep.), *Cyanus* (Borşič et al., in prep.) and *Centaurea* (Garcia-Jacas et al. 2006), *Centaurea* has an eastern Mediterranean origin (Anatolia and the Caucasus).

CHEMISTRY

Secondary metabolites include predominantly lipophilic compounds (especially sesquiterpene lactones); hydrophilic compounds are scarcely represented. Only some genera have been investigated in depth (*Centaurea*, cf. Trendafilova et al. 2007 and references therein; *Cirsium*, cf. Chen et al. 2007 and references therein). Subtribes Carduinae and mainly Centaureinae show higher chemical differentiation than the remaining subtribes (Wagner 1977; Bohm and Stuessy 2001). It is interesting that the increased chemical weaponry of Centaureinae is correlated to the loss of the spines so characteristic of thistles. Centaureinae and especially the genus *Centaurea* relies more on chemical than on mechanical deterrents for protection from herbivorous predators.

BIOGEOGRAPHY

The tribe is mainly Mediterranean in its widest sense (including the Irano-Turanian region) with three main centers of diversification: one in Anatolia, the Balkans, and the Caucasus; a second one in the Irano-Turanian area (Afghanistan, Iran, Iraq, and Turkistan) that reaches the mountains of Central Asia; and a western Mediterranean center encompassing the Iberian and Italian peninsulas, the Balearic and Tyrrhenian islands,

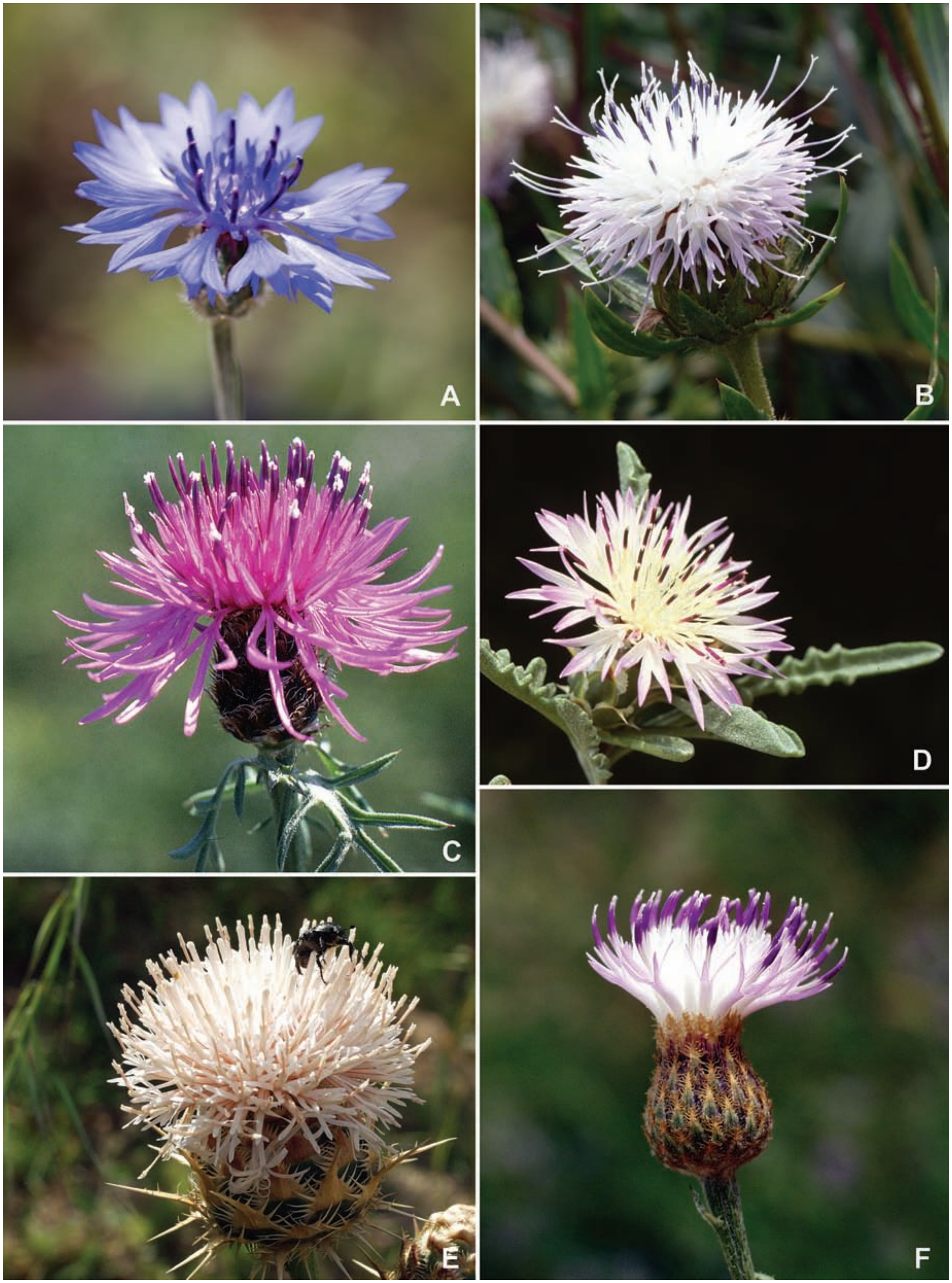


Fig. 20.7. Centaureinae, more highly nested genera. **A** *Centaurea montana* L. from subgenus *Cyanus*; **B** *Carduncellus dianius* Webb with long stigmas (a primitive character!); **C** *Centaurea corymbosa* Pourr. from subgenus *Centaurea*; **D** *Crocodylium pumilio* N. Garcia & Susanna; **E** *Centaurea lydia* Boiss. from subgenus *Acrocentron*; **F** *Centaurea exarata* Boiss. ex Coss., which lacks the sterile peripheral florets by secondary loss. [Photographs, authors.]

and North Africa. The mountains of Central Asia (Tian Shan, Pamir, and the Himalayas) constitute the eastern boundary for most of the genera. The tribe becomes less frequent in central Africa and only a few genera reach equatorial Africa (*Centaurea*, *Carduus*, *Cirsium*, and especially *Echinops*; cf. Jeffrey 1967). Three genera are native to North America (*Cirsium*, *Plectocephalus*, and *Saussurea*), only two to temperate South America (*Centaurodendron* Johow. and *Plectocephalus* D. Don), and two species are doubtfully native to Australia. The tribe contains many subcosmopolitan and noxious weeds. We shall give more details on geographic distribution for each subtribe and group.

ORIGIN AND AGE

According to Panero and Funk (2008), the sister groups of Cardueae are the tropical-African tribes Tarchonantheae and Oldenburgieae (see Chapters 18 and 19). It is generally accepted that the Mediterranean flora contains a tropical mesophyllous component lately adapted to the peculiar climate of the region (Takhtajan 1986). According to the confirmed relationships to African tribes of the subfamily Carduoideae, Cardueae count among this tropical element of African origin of the Mediterranean flora. In fact, as all the studies of the Mediterranean vegetation have pointed out, Cardueae are one of the most characteristic elements in this landscape (Takhtajan 1986).

Regarding the date of differentiation, most of the tribes were already separated by the end of the Oligocene, between 35–22 Ma (Funk et al. 2005). On the basis of ITS divergence, Wang et al. (2007) suggested a date of 29–24 Ma for the separation of the tribe from African Carduoideae. A more precise date of 10 Ma was offered by López-Vinyallonga et al. (2009) for the *Arctium-Cousinia* group, based both on molecular data and fossil records. All the dates being largely coincident, Cardueae originated as part of the Tertiary flora and benefited extensively from the new habitats that were open during the deep climate and geological changes during the Miocene (Cox and Moore 2004).

ECONOMIC USES

Economic importance of Cardueae is enormous, but more due to negative reasons than because of their use. Some of the more noxious weeds of Compositae belong to this tribe. The list of invaders in the Mediterranean and temperate regions of the globe is impressive: *Carduus pycnocephalus* L.; *Carthamus lanatus* L.; *Centaurea amara* L., *C. diffusa* Lam., *C. solstitialis* L., and *C. stoebe* L. [“*maculosa*”]; *Cirsium arvense* (L.) Scop., *C. palustre* (L.) Scop., and *C. vulgare* (Savi) Ten.; *Onopordum acanthium* and *O. nervosum*; *Rhaponticum* [“*Acroptilon*”] *repens* (L.) Hidalgo; *Picnomon acarna* (L.) Cass.; and *Silybum marianum* (L.) Gaertn. (DiTomaso 2000). In contrast, species with medicinal or industrial importance are scarce. Common artichoke (*Cynara scolymus*) and cardoon (*Cynara cardunculus*) are widely cultivated as a vegetable, especially in Italy and Spain and on a smaller scale in California. *Silybum marianum* is also cultivated in Mediterranean countries because of its lactones silybin and silymarin, powerful liver protectors used in the treatment of chronic hepatitis. *Carthamus tinctorius* (safflower) was very popular in olden times as a substitute for the culinary herb saffron, and now it is becoming an important crop as a source of vegetable oil in subtropical climates (Vilatersana et al. 2000a). Finally, some species are (or have been) cultivated as garden plants: *Amberboa moschata*, *Centaurea babylonica* (L.) L., *C. cyanus* [“bachelor’s button”], *C. montana* L., and *Plectocephalus americanus* D. Don [“basket flower”].

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Note added in proof

The engimatic genus *Dipterocome*, formerly placed in Calenduleae, belongs to Cardueae (see Anderberg et al., *Compositae Newsletter* 45, 2007, and page 535 of this book). More detailed analyses of morphology and molecular data are still lacking, but both floral characters (e.g., the heterogamous heads with outer bilabiate florets) and preliminary analyses of DNA sequences (kindly provided by A. Anderberg) point towards a close relationship with the *Xeranthemum* group.

Chapter 21

Pertyeae (Pertyoideae)

Susana E. Freire

HISTORICAL OVERVIEW

The tribe Pertyeae, recently described by Panero and Funk (2002), is a relatively small tribe with Asian distribution. It comprises four genera, *Ainsliaea* DC. *Macroclinidium* Maxim., *Myripnois* Bunge, and *Pertya* Sch.Bip., which were previously classified in Mutisieae (Cabrera 1961, 1977). Hansen (1991) additionally considered these genera as a monophyletic group within Mutisieae. Bremer (1994) also recognized the monophyly of this group, i.e., "*Ainsliaea* group", principally by its three-veined leaves, few-flowered capitula, and short dorsally pilose style branches.

Kim et al. (2002), using a molecular approach, confirmed the monophyly of the group (adding two morphological synapomorphies: homogamous capitula arranged laterally on the branches) and suggested that the Asian clade could be recognized as a distinct tribe. Simultaneously, Panero and Funk (2002), also based on molecular studies, arrived at congruent results with Kim et al. (2002), and proposed the exclusion of the Asian lineage from Mutisieae and its inclusion in the new subfamily Pertyoideae, tribe Pertyeae. In the Compositae supertree (= metatree; Funk et al. 2005), and in the base tree for the family (Panero and Funk, 2008), the Asian Mutisieae clade appears above Cardueae (Thistles) and below the Cichorioideae + Asteroideae clade.

PHYLOGENY

Morphological and palynological data support molecular phylogenetic studies (Panero and Funk 2002, 2008) that recognize the Asian Mutisieae clade as the tribe Pertyeae. The monophyly of Pertyeae is based on the possession of unique characters, i.e., three-veined leaves, homogamous capitula with one to few florets, style branches dorsally pilose, pollen grains with two exclusive exine types, and corollas zygomorphic with one sinus deeper than the others and glabrous.

The presence of pseudo-bilabiate corollas in *Pertya* and *Myripnois*, which are a modified type of the typical ones found in Mutisieae s.l., as well as the pollen "type *Mutisia*" present in *Pertya*, *Myripnois* and some species of *Ainsliaea*, relate Pertyeae to Mutisieae s.l. In addition, the presence of some characters that resemble the structure of the Cardueae, such as venation of corollas and echinate exine of *Macroclinidium*, is also consistent with the position of the Pertyeae clade above Carduoideae in the molecular studies. See Chapter 44 for a generic-level tree of the family.

TAXONOMY

Tribe Pertyeae Panero & Funk in Proc. Biol. Soc. Wash. 115: 915. 2002 – Type: *Pertya scandens* (Thunb.) Sch. Bip.

Herbs, subshrubs or shrubs, monoecious, seldom dioecious. Stems simple or branched. Leaves rosulate, clustered at the median part of the stem or on secondary short shoots or alternate; simple, variously entire to lobed, more rarely partite, three-veined or sometimes palmately-veined or pinnately-veined. Capitula solitary, or more usually on lateral short branches to terminal and numerous, spicate, racemose, paniculate, or more seldom corymbose. Involucre cylindrical to obconic, commonly multiseriate (5–15 rows) to rarely uniseriate of few involucral bracts; sometimes with peduncles (or pseudopeduncles) bracteolate with upper bracts passing to involucre. Receptacle usually glabrous, rarely pilose. Florets 1 to ca. 13 (16), isomorphic, usually bisexual and fertile or more rarely functionally female or male; corollas zygomorphic, pseudo-bilabiate or pseudo-ligulate with one split deeper than the others. Anthers 5, with apical appendages truncate or rounded to apiculate, more seldom emarginate; tails long, smooth to pilose. Style branches bilobed to shortly branched, variously truncate to acute at the apex, dorsally pilose to shortly pilose. Achenes oblong to obovate, (9- or) 10-veined, glabrous or pilose. Pappus bristles usually uniseriate, more rarely biseriate (sometimes absent in functionally male florets or occasionally in chasmogamous florets), margins scabrid or plumose.

Four genera with ca. 80 species in southeastern Asia.

Ainsliaea DC. (including *Diaspananthus* Miq.) (Fig. 21.1A–C) is the largest genus of the tribe, comprising 49 species of usually perennial herbs, with its main center of species concentration in China (Freire 2007). In fact, 37 of the total species are found in this country, principally in Yunnan and Sichuan provinces. Followed by Japan (9 spp.), Taiwan (8 spp.), India (5 spp.), Vietnam (5 spp.), Bhutan (4 spp.), Thailand (3 spp.), Bangladesh (3 spp.), Indonesia (2 spp.), Myanmar (2 spp.), Nepal (2 spp.), Pakistan (2 spp.), South Korea (2 spp.), Afghanistan (1 sp.), Kashmir (1 sp.), and the Philippines (1 sp.).

Macroclinidium Maxim. (Fig. 21.1D) comprises only six species of perennial herbs, each with restricted distributions in Japan.

Myripnois Bunge contains only one shrubby species endemic to China.

Pertya Sch.Bip. (Fig. 21.2) has about 23 species of shrubs or subshrubs. Most of the species are found in China but four occur in Japan, two in Afghanistan and one each in Taiwan and Thailand.

MORPHOLOGY AND ANATOMY

Habit and phyllotaxis

In Pertyeae there are four types of habit: Perennial herbs with simple stems and leaves congested at the median part of the stem (*Ainsliaea* spp. and *Macroclinidium*); perennial herbs with simple stems and rosulate leaves (*Ainsliaea* spp.); small shrubs having branched stems with alternate leaves (*Ainsliaea pertyoides*); shrubs or subshrubs with long primary branches, having alternate leaves, and short lateral branches, having leaves clustered (*Myripnois*, *Pertya*). In *Myripnois* and *Pertya* the leaves on the primary and lateral branches are commonly different in shape, i.e., heterophylly, which is very conspicuous in dioecious species (Ling 1948; Koyama 1975).

Leaves

The leaves of Pertyeae are mainly three-veined, more rarely pinnate or palmately-veined. The leaf blades are simple with a great diversity of shape (linear to palmatisect in *Ainsliaea*; linear to ovate in *Pertya*; ovate to trilobed in *Macroclinidium*, and ovate to elliptic in *Myripnois*), sessile to shortly petiolate (e.g., *Ainsliaea mairei* H. Lév., *A. spicata* Vaniot, *Myripnois dioica* Bunge, *Pertya* spp.) or mostly distinctly petiolate with petioles winged (e.g., *Ainsliaea bonatii* Beauverd, *A. latifolia* (D. Don) Sch.Bip. or wingless (e.g., *Ainsliaea acerifolia* Sch.Bip., *A. apiculata* Sch.Bip., *Macroclinidium robustum* Maxim., *M. trilobum* (Makino) Makino).

Leaf non-glandular pubescence in Pertyeae may be divided into four types (Koyama 1975; Freire 2007): *(1)* T-shaped with one to four long apical cells transversely elongated (Fig. 21.3A, H); *(2)* long-straight, uniseriate or multiseriate trichomes, with apical cells thick (Fig. 21.3B, F, G); *(3)* long-straight trichomes, with apical cells thin (Fig. 21.3C, E); and *(4)* long flagellate, septate, oblique trichomes (Fig. 21.3D). The structure of the long-straight trichomes and T-shaped ones seems closely related as was pointed out by Koyama (1975). In fact, the T-shaped trichomes have the same patterns as the long-straight trichomes, where the cells of the apical part develop horizontally in two directions or in one direction, respectively.

Capitula

In Pertyeae the capitula are subradiate to radiate (*Ainsliaea*, *Macroclinidium*) or discoid (*Pertya* and in some species of *Ainsliaea* with cleistogamous florets). The capitula may be solitary and terminal, *Pertya monocephala* W.W. Sm., or more usually on lateral short branches in *Pertya*, e.g., *Pertya scandens*, *P. sinensis* Oliv., and *Myripnois*, or glomerate on terminal long branches (e.g., *Pertya cordifolia* Mattf.). In *Ainsliaea* and *Macroclinidium* the capitula are arranged in spikes, racemes, or panicles. The involucral bracts may be few to numerous and in several rows. In *Myripnois*, there are only five or six. In *Ainsliaea* the involucral bracts are frequently 5–7-seriate (Freire 2007). In *Pertya*, the involucral bracts are usually 5–8-seriate, but there are some species with only 7–11 involucral bracts (e.g., *Pertya mattfeldii* Bornm., *P. uniflora* (Maxim.) Mattf.). Whereas in *Macroclinidium* the involucre is typically multiseriate with 6 to 15 rows. In *Ainsliaea* the typical number of florets is three, but there are some species with five, e.g., *Ainsliaea spanocephala* Y.C. Tseng, or with only ones, e.g., *A. lancangensis* Y.Y. Qian (Freire 2007). Most species of *Pertya* and *Macroclinidium* have between 4- and 13-flowered capitula, but there are some species with single-flowered capitula,

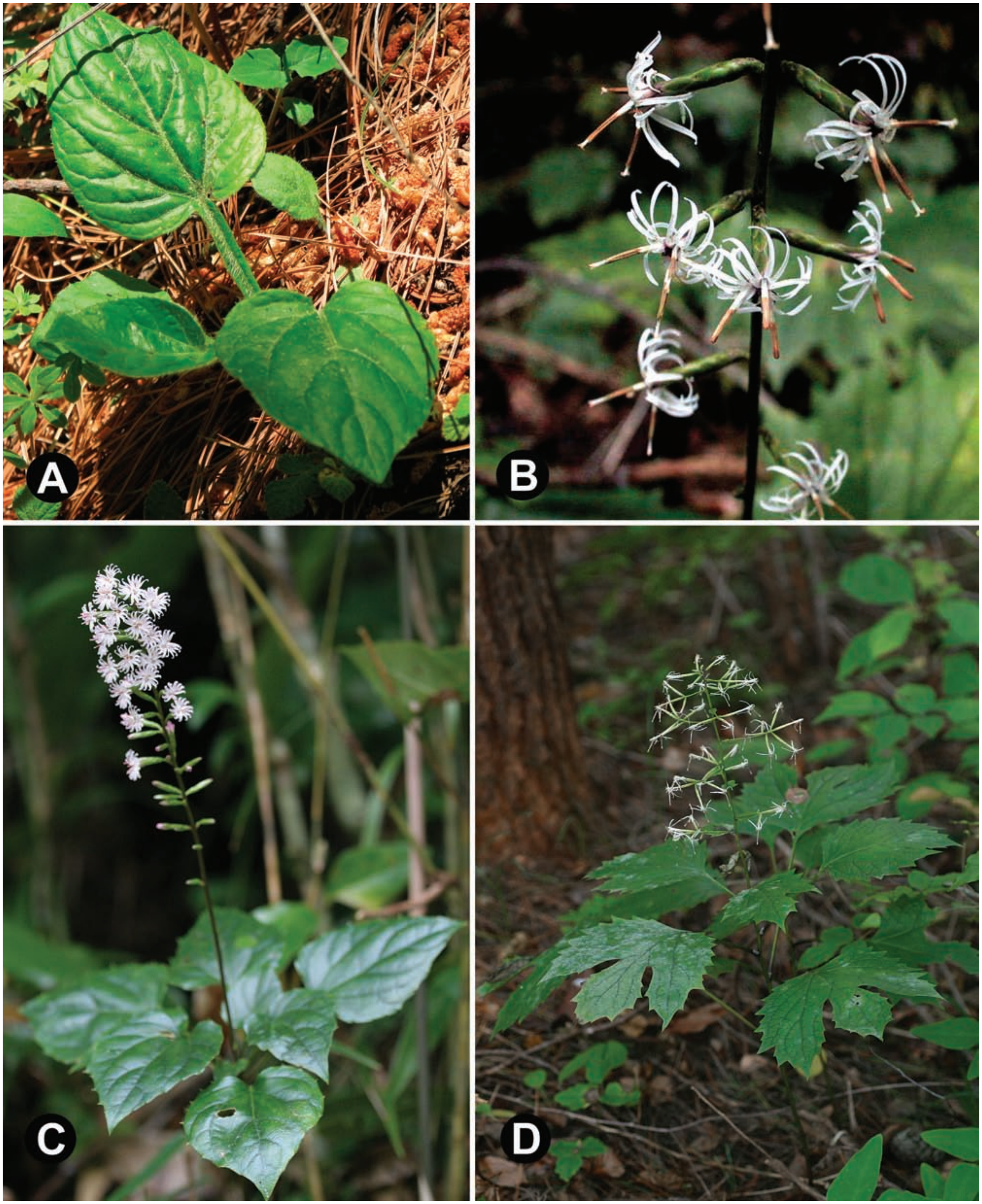

Fig. 21.1. **A** *Ainsliaea latifolia* (D. Don) Sch.Bip., China, Yunnan, habit; **B** *A. acerifolia* Sch.Bip. var. *subapoda* Nakai, Japan, capitula; **C** *A. macroclinidioides* Hayata, habit; **D** *Macroclinidium trilobum* (Makino) Makino. [Photographs: A, S. Freire; B, Shu Suehiro; C, M. Toguchi, Ocean Exposition Commemorative Park Management Foundation; D from http://www.plantsindex.com/plantsindex/demo_html/demo_db/result58860.htm.]

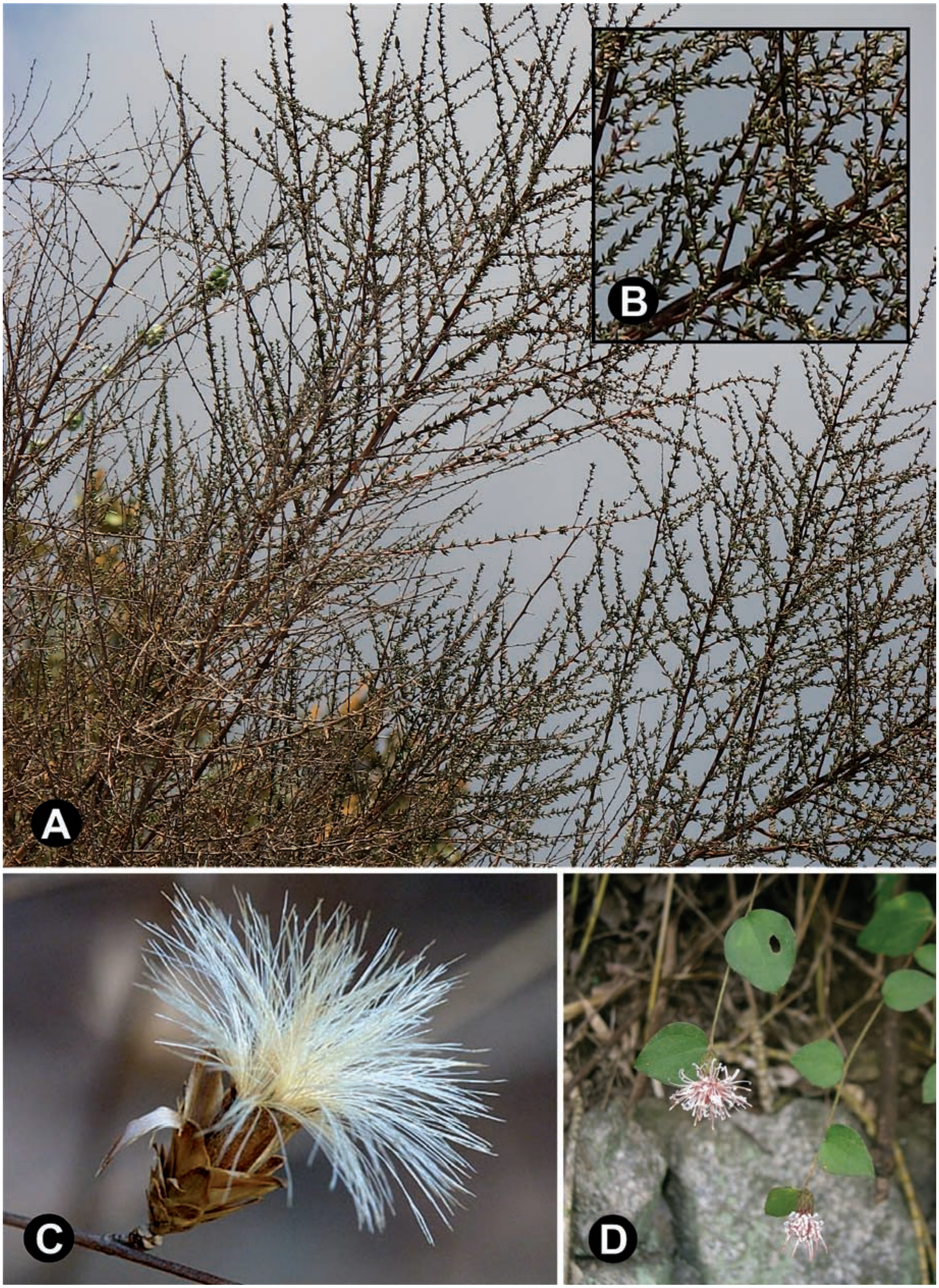

Fig. 21.2. A, B *Pertya phylicoides* Jeffrey, China, Yunnan: **A** habit; **B** leafy branch. **C, D** *Pertya ovata* Maxim.: **C** capitula in fruiting; **D** habit. [Photographs: A, B, S. Freire; C, S. Aoki from http://aoki2.si.gunma-u.ac.jp/BotanicalGarden/HTMLs/kouyabouki.html; D from http://commons.wikimedia.org sub *Pertya scandens*.]

as in *Pertya bodinieri* Vaniot, *P. desmocephala* Diels, and *Macroclinidium koribanum* Nakai. In *Myripnois* the capitula are 5- or 6-flowered.

Corollas

The corollas of the species of Pertyeae, were traditionally considered actinomorphic, 5-lobed for *Pertya*, *Macroclinidium*, and *Ainsliaea*, or zygomorphic and bilabiate for *Myripnois* (Mattfeld 1931). However, Koyama (1975) in *Pertya* and more recently, Freire (2007) in *Ainsliaea*, interpreted these corollas irregularly deeply 5-lobed as zygomorphic by having one sinus deeper than the others. The corolla of *Pertya* is considered by Koyama (1975) to be a variant of bilabiate corolla which occurs markedly in the tribe Mutisieae. In this treatment, the corollas of *Pertya* are interpreted as pseudo-bilabiate, slightly zygomorphic, with an external 3-cleft lip and an internal 2-cleft lip. The corollas of *Ainsliaea* and *Macroclinidium*, with unilateral and usually reflexed lobes which are irregularly 5-cleft, are considered to be pseudo-ligulate corollas. These corollas resemble the corollas found in some species of the genus *Dasyphyllum* Kunth (*D. inerme* (Rusby) Cabrera, *D. argenteum* Kunth) of

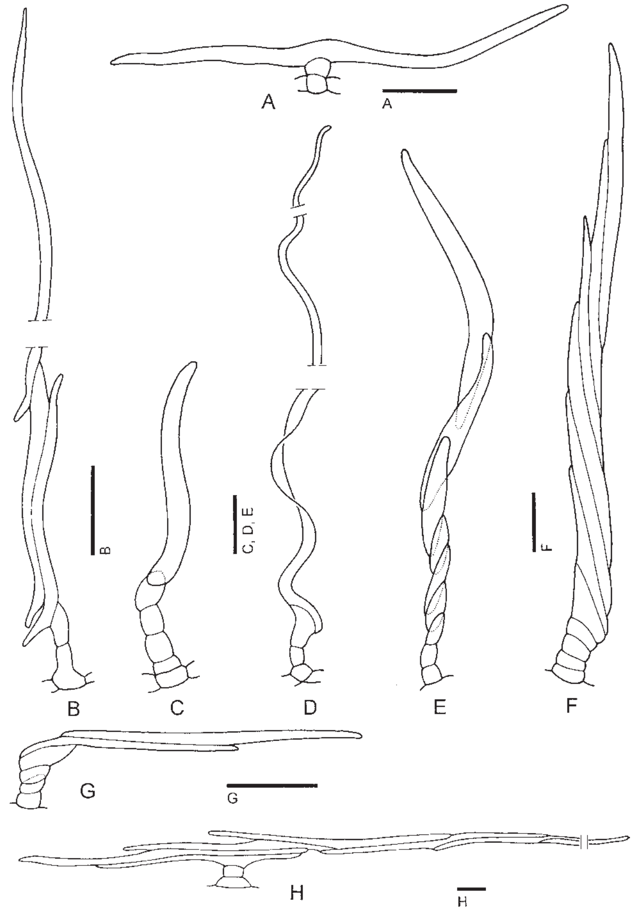

Fig. 21.3. Trichomes. **A** *Myripnois dioica* Bunge (*Chow 75099*, NY), T-shaped trichome; **B** *Pertya phylicoides* (*Forrest 12635*, K), straight trichome; **C** *Macroclinidium robustum* (*Murata 19207*, KYO), straight trichome with apical cell thin; **D** *Ainsliaea latifolia* (*Koyama et al. 30524*, C), oblique septate flagellate trichome; **E** *A. oblonga* Koidz. (*Elliott 1104*, S), straight trichome with apical cell thin; **F** *A. fragrans* Champ. ex Benth. (*Lau 111*, AAU), straight trichome; **G** *A. chapaensis* Merr. (*Petelot 2068*, NY), straight trichome; **H** *A. macrocephala* (Mattf.) Y.C. Tseng (*Rock 5773*, US), T-shaped trichome. Scale bars: A–E = 50 μm; F–H = 100 μm.

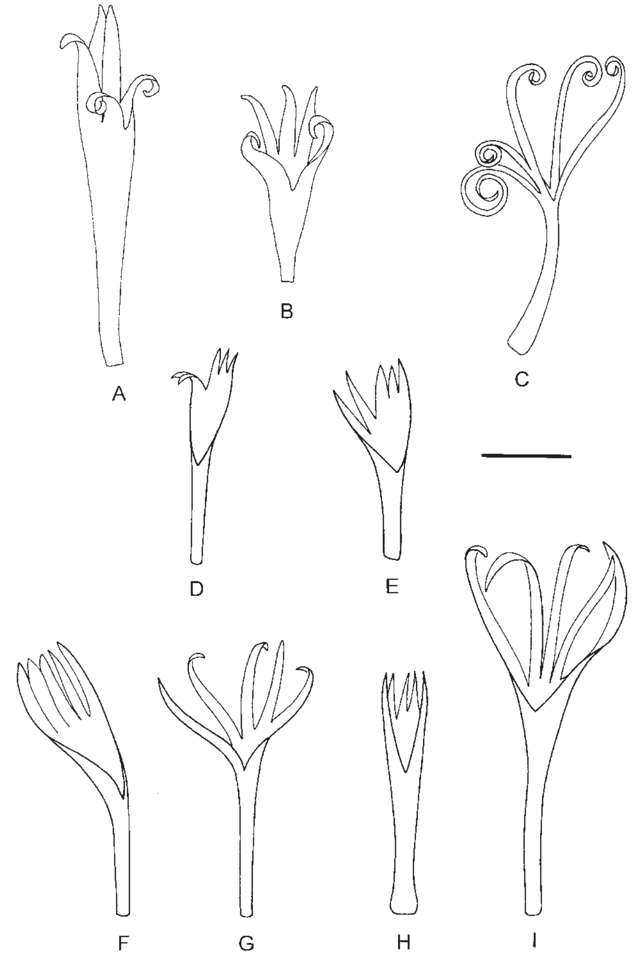

Fig. 21.4. Corollas. **A** *Pertya aitchisonii* C.B. Clarke (*Edelberg 1778*, W), pseudo-bilabiate corolla; **B** *P. discolor* Rehder (KUN 0732464), pseudo-bilabiate corolla; **C** *P. simozawai* Masam. (*Simozawa* in 1942, KYO), pseudo-bilabiate corolla; **D, E** *Myripnois dioica* Bunge, **D** pseudo-ligulate corolla of the female floret (*Sheehan 8*, K), **E** pseudo-ligulate corolla of the male floret (*Sheehan 6*, K); **F** *Ainsliaea spanocephala* (*Hennipman 3608*, BKF), pseudo-ligulate corolla of the chasmogamous floret; **G** *A. aptera* DC. (*Koelz 1789*, NY), pseudo-ligulate corolla of the chasmogamous floret; **H** *A. glumacea* Sch.Bip. (*Hooker f. et Thomsom s.n.*, US), pseudo-ligulate corolla of the cleistogamous floret; **I** *Macroclinidium robustum* (*Wawra 1527*, NY), pseudo-ligulate corolla. Scale bars: A, B = 2.5 mm; C = 3 mm; D, E = 3.5 mm; F, G, I = 5 mm; H = 1.2 mm.

Barnadesioideae, but lack the common hairs on the lobes. A closer examination in *Myripnois* reveals that the corollas are usually pseudo-ligulate but it is possible to find corollas pseudo-bilabiate in the same specimen. (Fig. 21.4).

As in most Compositae, the venation corresponds to the "discoid" type (Koch 1930a, b) with five longitudinal veins at the base that separate at each sinus of the lobes and united at the apex. Occasionally in some species of *Pertya*, e.g., *P. cordifolia*, *P. discolor*, additional longitudinal veins appear between these typical ones. Similar corolla venation is present in the genus *Cnicus* L. of the tribe Cardueae (Manilal 1971).

Anthers

The anthers of the genera *Macroclinidium*, *Myripnois*, and *Pertya* are uniform, having pilose long tails and apical appendages that are acute to apiculate. The anthers in *Ainsliaea* show tails variously smooth to pilose, and apical appendages rounded to apiculate, and seldom emarginate or retuse, e.g., *A. linearis* Makino, *A. walkeri* Hook. f., resembling the anthers found in some Arctotideae and Barnadesioideae (Fig. 21.5).

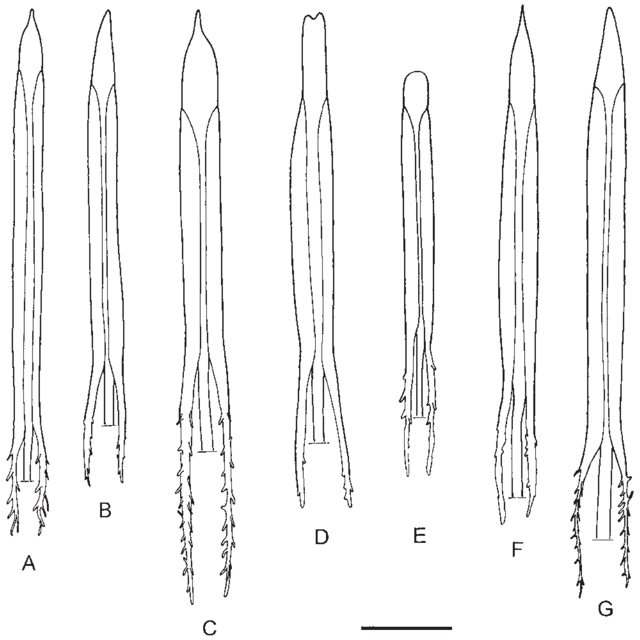

Fig. 21.5. Stamens. **A** *Pertya scandens* (*Arimoto* in 1903, MO), anther appendage apiculate; **B** *Myripnois dioica* (*Sheehan 6*, K), anther appendage acute; **C** *Macroclinidium robustum* (*Wawra 1527*, NY), anther appendage apiculate; **D** *Ainsliaea walkeri* (*Ching 8246*, UC), anther appendage emarginate; **E** *A. glabra* (*Liu 15451*, CANB), anther appendage truncate; **F** *A. lancangensis* (*Qian 3343*, SMAO), anther appendage apiculate; **G** *A. uniflora* Sch.Bip. (*Maximowicz* in 1863, S), anther appendage apiculate. Scale bars: A–C, F, G = 1.2 mm; D, E = 0.8 mm.

Style

Pertyeae have styles (Fig. 21.6) shallowly divided at the apex or shortly bifid, usually with hairs above the point of bifurcation or sometimes hairy below, e.g., *Pertya scandens*, *P. simozawai*, *Macroclinidium rigidulum*. Sometimes slightly swelling on upper part of style below branches, i.e., *Ainsliaea chapaensis*, *Macroclinidium* spp., *Pertya simozawai*, that resembles the Arctotideae-type and *Dicoma*-

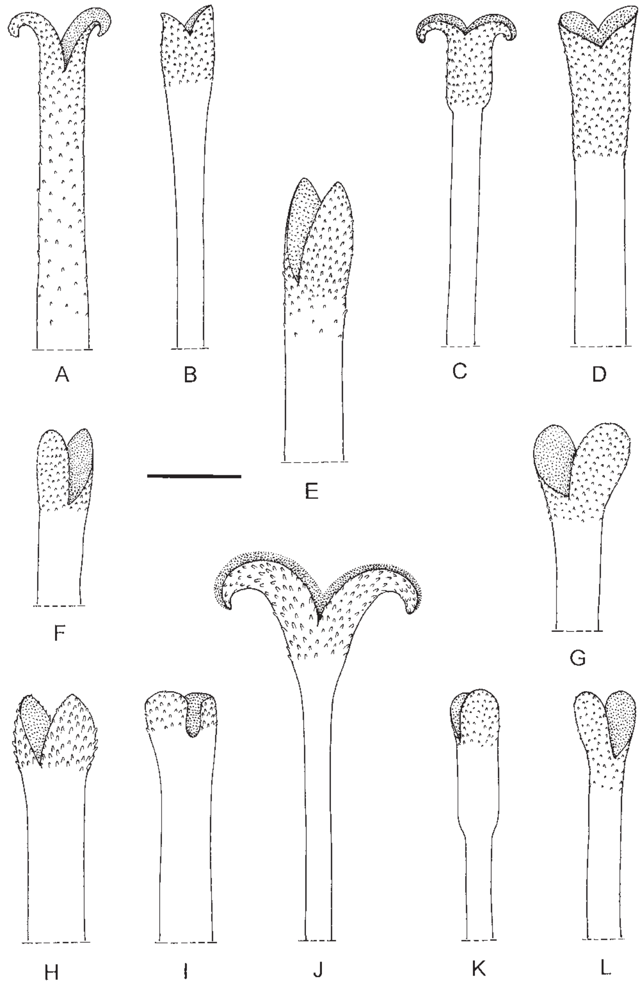

Fig. 21.6. Upper portion of style. **A** *Pertya scandens* (*Arimoto* in 1903, MO), hairy below branches; **B** *P. pungens* (*Wang 38778*, MO), style branches acuminate; **C** *P. simozawai* (*Simozawa* in 1942, KYO), slightly swollen above; **D** *P. corymbosa* (*Steward et Cheo 972*, NY), shallowly divided; **E** *Myripnois dioica* Bunge (*Sheehan 8*, K), style branches acute; **F** *Pertya discolor* (*Smith 5786*, MO), style branches obtuse; **G** *P. bodinieri* (*Bodinier et Ducloux* in 1897, P), style branches rounded; **H** *Ainsliaea cordifolia* (*Furuse* in 1956, C), style branches acute; **I** *A. elegans* (*Henry 10391*, MO), style branches truncate; **J**, *Macroclinidium rigidulum* (*Sato* in 1978, KYO), slightly swollen above; **K** *Ainsliaea chapaensis* (*Petelot 2068*, NY), slightly swollen above; **L** *A. walkeri* (*Ching 8246*, UC), style branches rounded. Scale bar = 0.8 mm.

type. The tip of the style branches may be acuminate, e.g., *Pertya pungens* Y.C. Tseng, resembling the style of some Cardueae, e.g., *Amphoricarpos* Vis. spp., or acute, e.g., *Ainsliaea pingbianensis* Y.C. Tseng, *Macroclinidium* spp., *Myripnois dioica*, or more commonly rounded to truncate (in most species of *Ainsliaea*), resembling the style of Mutisieae s.str., e.g., *Trichocline sinuata* (D. Don) Cabrera, *Brachyclados megalanthus* Speg.

POLLEN

Examination of the taxonomic value of the pollen for Pertyeae began with Wodehouse (1929) who suggested the close relationship between *Ainsliaea* and *Pertya.* Later, Marticorena and Parra (1975) added sampled species of *Macroclinidium* and *Myripnois*. Recent publications (Lin et al. 2005; Tellería and Katinas 2005) provide additional exine structure studies.

Pollen of Pertyeae are spheroidal to prolate (*Ainsliaea*), spheroidal to suboblate (*Macroclinidium*), spheroidal to elliptic (*Myripnois*), or elliptic (*Pertya*). Tricolpate (*Ainsliaea* spp.) or more commonly tricolporate (*Ainsliaea* spp., *Macroclinidium*, *Myripnois*, *Pertya*). Three types of exine are present (Lin et al. 2005; Tellería and Katinas 2005): the *Ainsliaea* type (only in some species of *Ainsliaea*), with exine microechinate, ectosexine and endosexine weekly differentiated; the *Mutisia* type (present in *Ainsliaea* spp., *Myripnois*, and *Pertya*), with exine scabrous to microechinate, tectum imperforate or scarcely perforate, ectosexine and endosexine differentiated; and the *Macroclinidium* type (only in *Macroclinidium*), characterized by its exine echinate, long spines usually with compact tip, and tectum very perforate. This last exine structure resembles that of the South American genera *Gongylolepis* Schomb. and *Wunderlichia* Riedel ex Benth. & Hook. f. and that of Cardueae, differing in the spines that are solid in *Macroclinidium*, and with an apical channel in Cardueae as well as in those South American genera (Tellería 2008).

CHROMOSOME NUMBERS

Arano (1965) suggested that *Ainsliaea* and *Pertya* may be considered phylogenetically closely related from a karyological perspective. It was pointed out that the basic number $n = 13$ in *Ainsliaea* (Arano 1963; Watanabe et al. 1992) seems to have been derived from $n = 14$ in *Pertya* by aneuploid reduction. In this sense, the haploid number $n = 12$, more recently reported for two species in *Ainsliaea* (Mehra et al. 1965; Malla et al. 1977; Peng and Hsu 1977, 1978; Gupta et al. 1989) appears also to be aneuploid derived from $n = 13$.

HYBRIDIZATION

Makino (1906) reported hybridization events among species of the genera *Macroclinidium* and *Pertya* giving rise to intermediate forms, i.e., *Pertya ×hybrida* Makino [=*Macroclinidium robustum* × *Pertya ovata*], where each parental pair includes one species with simple stem and one with stems branched. A natural hybrid between taxa within *Macroclinidium*, i.e., *Macroclinidium ×suzuki* Kitam. [=*M. trilobum* × *M. rigidulum*] was reported by Kitamura (1938). Within *Ainsliaea*, Sugimoto (1957) suggested hybridization between *A. linearis* and *A. apiculata*, i.e., *Ainsliaea ×hybrida*.

ECOLOGY AND FLORAL BIOLOGY

Pertyeae as a whole are of ecological interest because their species apparently occur in two areas. On the one hand, they live in wet conditions along shaded stream banks and in swampy thickets. In the region from southeast China to Ryukyu Islands (Japan), four species of *Ainsliaea* (i.e., *A. linearis*, *A. oblonga*, *A. trinervis* Y.C. Tseng, *A. walkeri*) exhibit narrow leaves as an adaptation to river bank environments where they are periodically covered with floodwater after heavy rains (Mitsui et al. 2007). On the other hand, there are other species (e.g., *Ainsliaea hypoleuca* Diels, *A. macrocephala*, *Pertya phylicoides*, *P. discolor*) growing in dry conditions, principally Yunnan (China) where they are found in full sun, in forest margins or in light gaps.

In the genus *Ainsliaea*, cleistogamous heads with involucres completely closed until the mature achenes are released, occur simultaneously or alternating with chasmogamous heads (Freire 2007).

BIOGEOGRAPHY AND EVOLUTION

The species of the tribe Pertyeae show a tropical to subtropical distribution pattern. They occur from north of Sumatra at the latitude of 5° N to about 40° N in Japan as the northern limit of the tribe. The highest elevation, about 4000 m, is recorded in southwest China (Yunnan, Sichuan) and the Himalayan region. The lowest elevation, i.e., near sea level, is recorded in east China and Japan.

The largest diversity in species is found in northwestern Yunnan, within the Meridional Ranges (Upper Yangtze) of China. Hu (1958), recognized the Meridional Ranges through the provinces of Yunnan, Sichuan, and Gansu, as having the highest degree of endemism in Compositae, both on generic and specific levels.

Pertyeae are present in three floristic regions (Takhtajan 1986): Eastern Asiatic Region, Malesian Region (Indonesia,

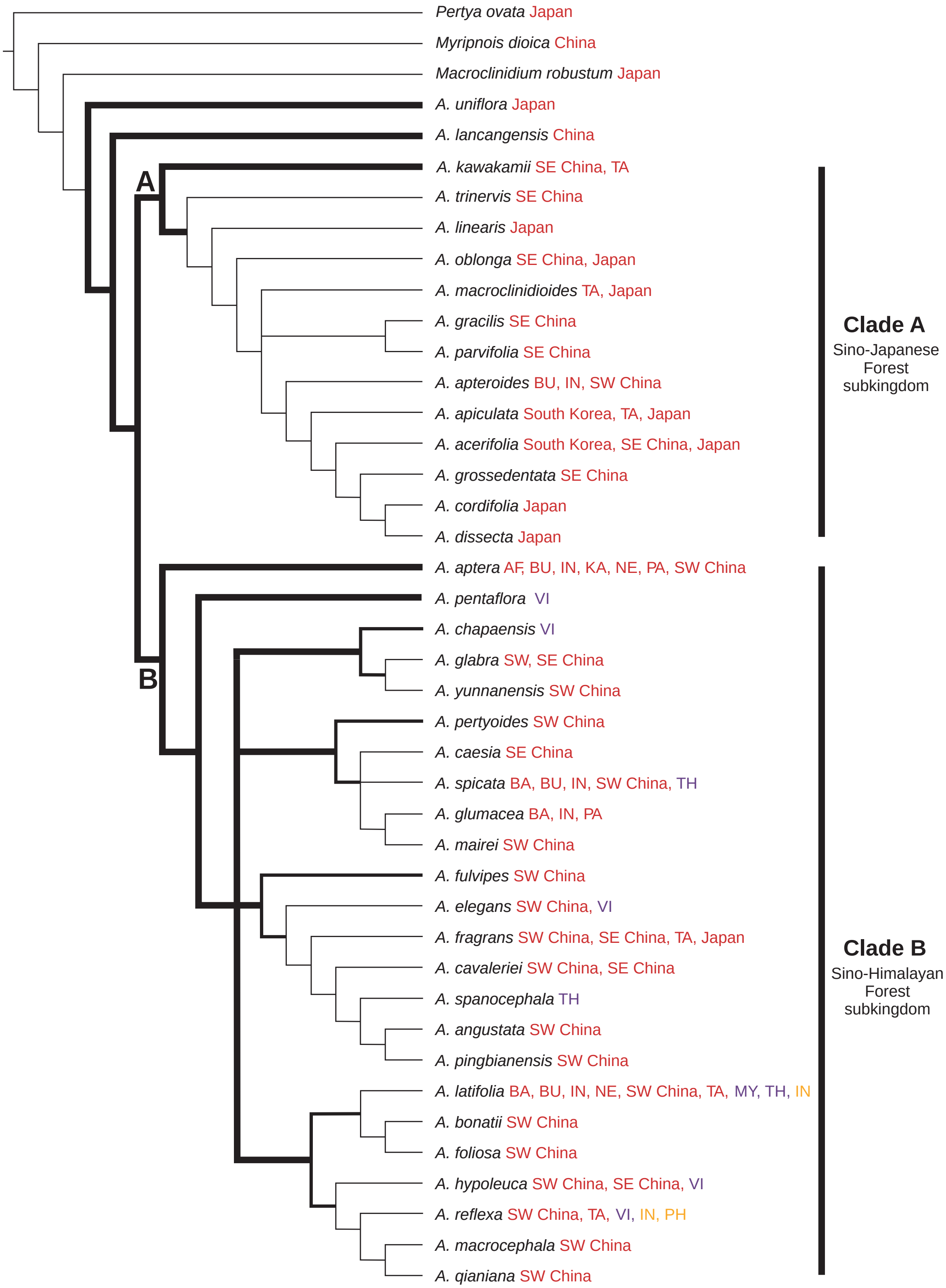

Fig. 21.7. Strict consensus cladogram of *Ainsliaea* with the geographic occurrence of the species labeled. The Eastern Asiatic Region is shown in red; Indochinese Region is shown in violet; Malesian Region is shown in orange. AF = Afghanistan; BA = Bangladesh; BU = Bhutan; IN(red) = India; IN(yellow) = Indonesia; KA = Kashmir; MY = Myanmar; NE = Nepal; PA = Pakistan; PH = Philippines; TA = Taiwan; TH = Thailand; VI = Vietnam; clades A an B indicate the subkingdoms of Wu and Wu (1996). Thickened branches of the cladogram refer to the clades illustrated in Fig. 21.8. [Modified from Freire 2007.]

Philippines), and Indochinese Region (Vietnam, Thailand, Myanmar). The close relationship between these areas was previously reported by Zhu et al. (2003).

The molecular phylogeny of the genus *Ainsliaea* (Mitsui et al. 2007) and the phylogeny based on morphological characters (Freire 2007) agree in general with the two subkingdoms proposed by Wu and Wu (1996) within the Sino-Japanese kingdom (= Eastern Asiatic Region, sensu Takhtajan), i.e., Sino-Himalayan Forest subkingdom on the western side ranging from the Himalayas to SW China, SE Asia and Taiwan, and Sino-Japanese Forest subkingdom on the eastern side ranging from southeast China to mainland Japan and Korean Peninsula through Ryukyu Islands and Taiwan (Figs. 21.7–21.8).

As was pointed out by Mitsui et al. (2007), the present moist monsoon climate of the Sino-Japanese kingdom was created by the uplifting of the Himalayas and the Tibetan Plateau in the late Paleocene about 55 Ma to the

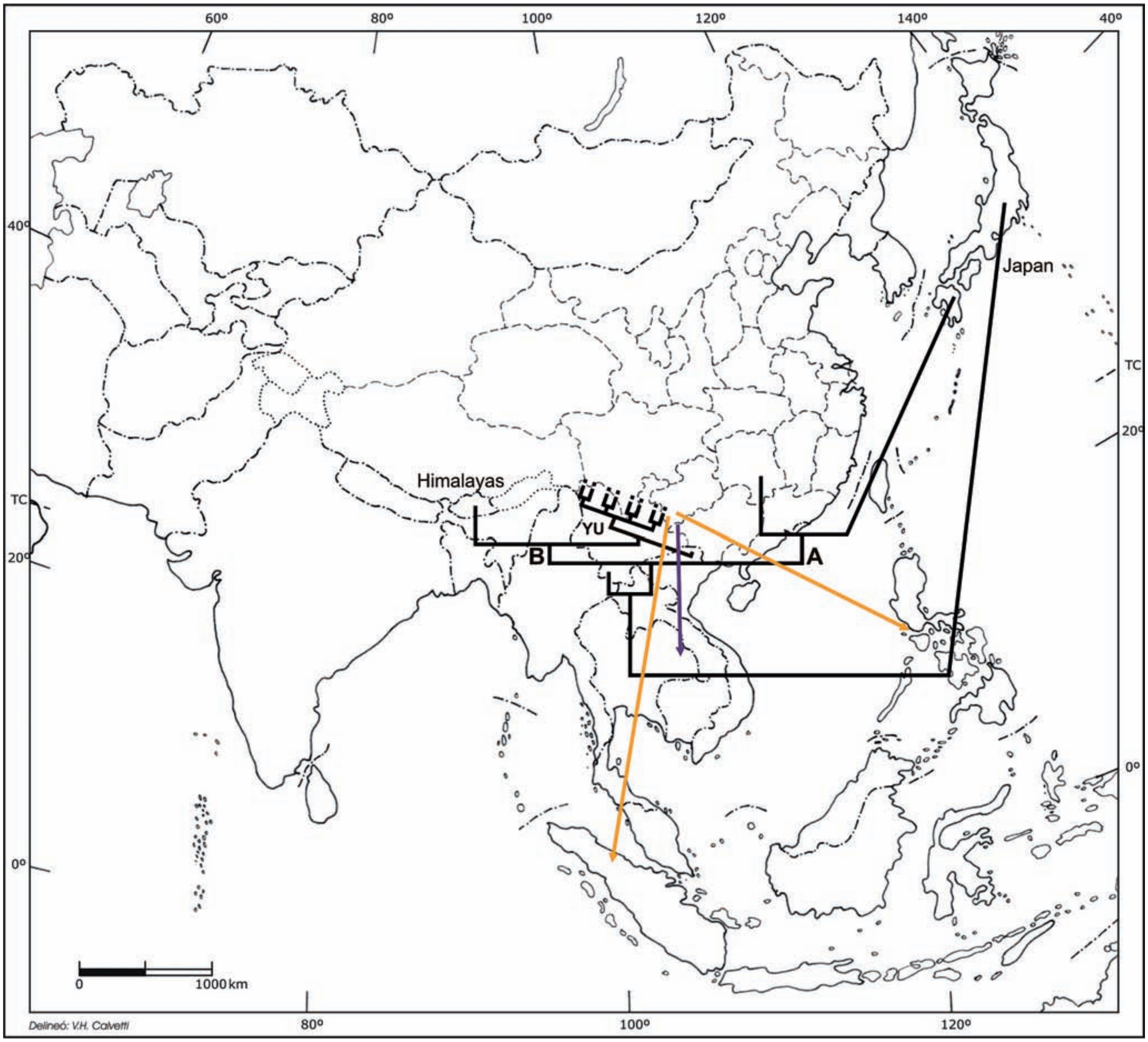

Fig. 21.8. Distribution of *Ainsliaea* species in relation to their simplified phylogeny based on Fig. 21.7. YU = Yunnan. **Clade A** Basal species of this clade are from eastern China, indicating a possible origin in the mainland for this group. Three species are endemic to Japan (see Appendix 21.1). The phylogeny of this clade suggests migration or dispersal from southeast Asia mainland to moist habits in the Pacific islands. **Clade B** There are two basal vicariant events (which separate Himalayas first and then Vietnam). Other vicariant events developed in Yunnan with most of the diverse lineages found there. Dispersal (indicated by arrows) towards Indochina, Indonesia and Philippines, probably occurred many times in combination with speciation.

early Pleistocene, as a result of the collision of Eurasia, the India subcontinent, and the Burma-Malaya Geoblock. According to Mitsui et al. (2007), the origin of the lineages of *Ainsliaea* estimated at around 1.1 Ma, during the late Pliocene or early Pleistocene, and suggests that climatic oscillations and topographical changes may have led to allopatric speciation in the genus.

ETHNOBOTANY

Even if there are no species of commercial importance within Pertyeae, many of them are known for their ethnobotanical uses. In the Indian Himalayas, the dried heads and leaves of *Ainsliaea aptera* were used in the past as tinder in fire lighting by the inhabitants of this region (Shah 1996). Many others species of *Ainsliaea* from China, such as *A. elegans*, *A. fragrans*, *A. glabra*, and *A. latifolia* are used in traditional medicine (Namba et al. 1990; Huang and Ling 1996). *Ainsliaea bonatii* has long been used in Tibetan folk medicine for the treatment of rheumatism, lumbago and gonitis (Pu et al. 2004). A few species, i.e., *Ainsliaea aptera* and *A. walkeri*, have been mentioned in horticultural treatments (Nicholson 1938: 93–94; Synge 1956: 68) due to their decorative value.

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Note added in proof

A recent paper has shown that two separate base pair deletions link *Catamixis* with the Pertyoideae. Panero, J. 2008. Shared molecular signatures support the inclusion of *Catamixis* in subfamily Pertyoideae. *Phytologia* 90: 418–424.

Appendix 21.1. List of the taxa of Pertyeae and their distribution

Species	Distribution
Ainsliaea DC.	
acerifolia Sch.Bip.	China, Japan, South Korea
angustata C.C. Chang	China
apiculata Sch. Bip.	Japan, South Korea, Taiwan
aptera DC.	Afghanistan, Bhutan, China, India, Kashmir, Nepal, Pakistan
apteroides (C.C. Chang) Y.C. Tseng	Bhutan, China, India
bonatii Beauverd	China
brandisiana Kurz	Myanmar
caesia Hand.-Mazz.	China
cavaleriei H. Lév.	China
chapaensis Merr.	Vietnam
cordifolia Franch. & Sav.	Japan

Appendix 21.1. Continued.

Species	Distribution
crassifolia C.C. Chang	China
dissecta Franch. & Sav.	Japan
elegans Hemsl.	China, Vietnam
foliosa Hand.-Mazz.	China
fragrans Champ. ex Benth.	China, Japan, Taiwan
fulvipes Jeffrey & W.W. Sm.	China
glabra Hemsl.	China
glumacea (Fr.) Sch.Bip.	Bangladesh, India, Pakistan
gracilis Franch.	China
grossedentata Franch.	China
henryi Diels	China, Taiwan
hypoleuca Diels ex H. Limpr.	China, Vietnam
kawakamii Hayata	China, Taiwan
lancangensis Y.Y Qian	China
latifolia (D. Don) Sch.Bip.	Bangladesh, Bhutan, China, India, Indonesia (Sumatra), Myanmar, Nepal, Taiwan, Thailand
linearis Makino	Japan
macrocephala (Mattf.) Y.C. Tseng	China
macroclinidioides Hayata	Japan, Taiwan
mairei H. Lév.	China
nana Y.C. Tseng	China
nervosa Franch.	China
oblonga Koidz.	China, Japan
parvifolia Merr.	China
paucicapitata Hayata	Taiwan
pentaflora S.E. Freire	Vietnam
pertyoides Franch.	China
pingbianensis Y.C. Tseng	China
qianiana S.E. Freire	China
ramosa Hemsl.	China
reflexa Merr.	China, Indonesia (Sumatra), Philippines, Taiwan, Vietnam
rubrinervis C.C. Chang	China
smithii Mattf.	China
spanocephala Y.C. Tseng	Thailand
spicata Vaniot	Bangladesh, Bhutan, China, India, Thailand
trinervis Y.C. Tseng	China
uniflora Sch.Bip.	Japan
walkeri Hook. f.	China
yunnanensis Franch.	China
Macroclinidium Maxim.	
hybridum (Makino) Matsum.	Japan
koribanum Nakai	Japan
rigidulum (Miq.) Makino	Japan
robustum Maxim.	Japan
suzuki Kitam.	Japan
trilobum (Makino) Makino	Japan
Myripnois Bunge	
dioica Bunge	China
Pertya Sch.Bip.	
aitchisonii C.B. Clarke	Afghanistan, Pakistan
angustifolia Y.C. Tseng	China
berberidioides (Hand.-Mazz.) Y.C. Tseng	China
bodinieri Vaniot	China
cordifolia Mattf.	China
corymbosa Y.C. Tseng	China
desmocephala Diels	China
discolor Rehder	China
henanensis Y.C. Tseng	China
hossei Craib. ex Hoss.	Thailand
macrophylla Nakai	Japan
mattfeldii Bronm.	Afghanistan
monocephala W.W. Smith	China
ovata Maxim.	Japan
pubescens Ling	China
phylicoides Jeffrey	China
pungens Y.C. Tseng	China
scandens Sch.Bip.	China, Japan
simozawai Masam.	Taiwan
sinensis Oliv.	China
tsoongiana Ling	China
uniflora (Maxim.) Mattf.	China
yakushimensis H. Koyama & Nagamasu	Japan

Chapter 22

Gymnarrheneae (Gymnarrhenoideae)

Vicki A. Funk and Ori Fragman-Sapir

INTRODUCTION

Gymnarrhena is an unusual member of Compositae. It is an ephemeral, amphicarpic, dwarf desert annual. Amphicarpic plants have two types of flowers, in this case aerial chasmogamous heads and subterranean cleistogamous ones, and the different flowers produce different fruits. In *Gymnarrhena*, the achenes produced from these two types of inflorescence and the seedlings that germinate from them, differ in size, morphology, physiology and ecology (Koller and Roth 1964; Zamski et al. 1983). The plant is very small and has grass-like leaves, and the aerial heads are clustered together and have functional male and female florets. The familiar parts of the Compositae head have been modified extensively, and most of the usual identifying features are missing or altered (Fig. 22.1). Currently there is one species recognized, *Gymnarrhena micrantha* Desf., but there is some variation across the distribution, and it should be investigated further.

HISTORICAL OVERVIEW

As might be imagined, the history of this taxon reflects its unusual morphology. Bentham (1873), Hoffmann (1890–1894), and Cronquist (1955) put this genus in Inuleae s.l. Hoffmann and Cronquist both mention the similarity to *Geigeria*; Bentham's alternate choice was Astereae. Small (1917–1919) considered Inuleae to be linked to *Centaurea* of Cardueae. Leins (1973), in his examination of the pollen of Inuleae, stated that *Gymnarrhena* did not belong in that tribe and suggested Cynareae-Carlininae. Merxmüller et al. (1977) agreed that *Gymnarrhena* was not in Inuleae and cited Leins (1973). Skvarla et al. (1977) acknowledged a superficial resemblance between *Gymnarrhena* and Cardueae but pointed out that it had Anthemoid type pollen (also found in Senecioneae and other tribes) and did not belong in Inuleae or Astereae. Skvarla et al. further acknowledged that, based on the pollen, the genus was difficult to place. Bremer (1994) listed the genus as belonging to Cichorioideae s.l. but as "unassigned to tribe" along with several other problem genera.

PHYLOGENY

Anderberg et al. (2005), in a study of Inuleae using *ndhF*, determined that *Gymnarrhena* did not belong in Asteroideae but rather was part of the then paraphyletic Cichorioideae s.l. or sister to the entire Asteroideae. In the most recent broad-scale cladograms, *Gymnarrhena* is in a clade by itself and is consistently located below the Cichorioideae s.str.–Corymbieae–Asteroideae clade and above the Cardueae and Pertyeae clades (Panero and Funk 2002, 2008; Chapter 44 of this volume). Its position means that it cannot be placed in any of the other suprageneric taxa and is now recognized as an independent lineage. This position is supported by the fact that *Gymnarrhena* lacks the '9 base pair deletion' in the *ndhF* gene identified by Kim and Jansen (1995) and subsequently used by Bremer (1996) as a molecular characteristic in support of the recognition of the Cichorioideae-Corymbioideae/Asteroideae clade (Chapter 44). In the

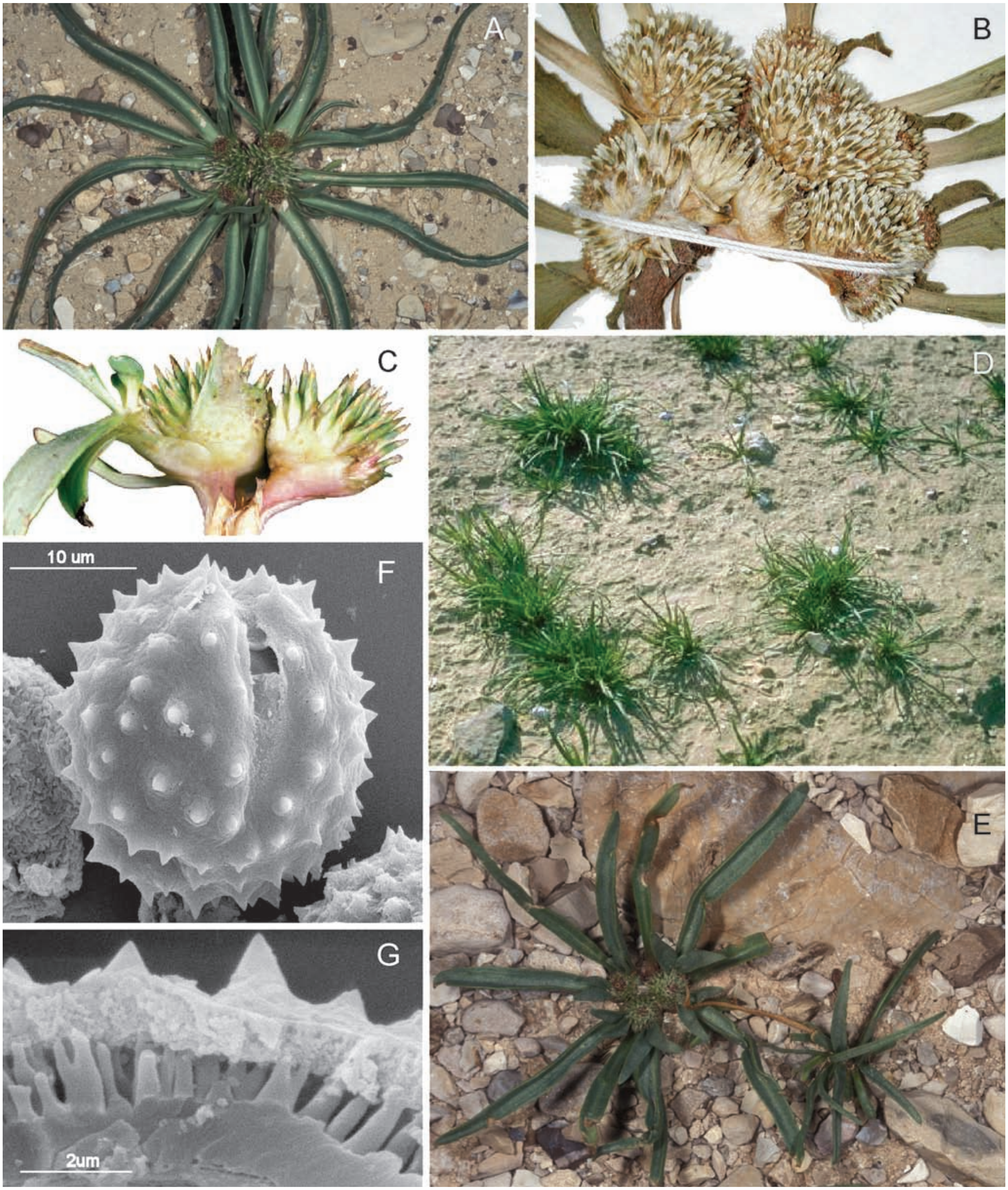

Fig. 22.1. *Gymnarrhena micrantha* Desf. **A, D, E** habit showing rocky substrate and clustered heads; **B** clustered above-ground heads with green (fading to brown) and white bracts; **C** subterranean heads; **D** population showing grass-like growth form; **F, G** pollen showing polar view and a broken grain. [Photographs: A, D, E, O. Fragman-Sapir taken in the Jerusalem Botanical Gardens; B, herbarium specimen, *Mandeville 157*, US; C, underground head, with permission from Brown and Böer (2005); F, G, SEM's, H. Robinson.]

most recent taxonomic overview for the family the tribe *Gymnarrheneae* was accepted by Jeffrey (2007) based on the molecular results reported above.

TAXONOMY

Subfamily Gymnarrhenoideae Panero & V.A. Funk
Tribe Gymnarrheneae Panero & V.A. Funk in Proc. Biol. Soc. Wash. 115: 763–764. 2002 – Type: *Gymnarrhena micrantha* Desf. in Mém. Mus. Hist. Nat. iv.: 1, t. 1. fig. 1. 1818

Annual amphicarpic herbs with a prostrate rosette, no more than a few centimeter high; no reports of milky sap. Leaves simple, forming a dense rosette, sessile, smooth, narrowly lanceolate to narrowly ovate, apex narrowly acute to attenuate, margins denticulate, base truncate, surfaces smooth and glabrous. Subterranean heads homogamous, female, cleistogamous, surrounded by the leaf bases; florets enclosed in involucral bracts, corolla vestigial; achenes relatively large, laterally flattened, blackish, sparsely hairy, remaining below the soil surface on the dead parent plant; pappus absent, vestigial, or of short, basally flattened, somewhat scale-like bristles. Aerial heads congested in the center of the leaf rosette, heterogamous, disciform; involucral bracts imbricate in several series, chartaceous, whitish, acute; receptacle convex, marginally bristly, with a few rows of chartaceous phyllaries. Functionally staminate florets in small groups, loosely connected on very short pedicels, interspersed among the small pistillate florets, corollas small, 3–4-lobed, whitish; stamens 3–4, anthers calcarate, ecaudate, without apical appendage. Pistillate florets solitary, each enclosed in a prominent, stiff, white and green bract; corolla filiform, style arms long, with rounded apices. Achenes of functionally staminate florets vestigial, pappus of a few irregularly lacerate scales or absent; achenes of pistilate florets numerous, tiny, ovoid, ciliate, villous, with long twin hairs, cell walls thin, pappus of long-lanceolate, ciliate, acutely acuminate scales.

A second species *G. balansae* Cross. & Durieu was based on two collections from near the coast in Tunisia and Algeria, and they appear to be somewhat different from the collections from the Middle East and further inland in Algeria. However, a more detailed study will have to be made to determine the validity of this taxon.

Gymnarrhena has been collected from North Africa to the Middle East. It is a winter annual and its flowering depends on the rain but usually takes place in March and April (May). According to Gutterman (1989) the life span of the plants is around 67 days out-of-doors (full sun) where it produces both types of heads, and 140 days in the greenhouse (eight hours of light) where it produces only aerial heads.

MORPHOLOGY

The male florets are not always grouped in the center of the head as previously described, in fact some groups of male florets are found at the outer edge of the receptacle. It seems more likely that the aerial heads are actually groups of heads some of which are few-flowered male heads and others are single-flowered female heads so these could represent dioecious heads grouped on a common receptacle. The subterranean heads flower first, their petals protruding just above the soil surface. Later the aerial inflorescences appear. Likewise the fruits of the two types of heads of *Gymnarrhena* have different developments, the larger subterranean fruits developing first and the aerial fruits being produced later and only in wet years. The aerial fruits are wind-dispersed while the subterranean fruits germinate underground. On the aerial heads, the scales of the pappus as well as the bracts surrounding the achenes are hydrochastic (open when wet), and the achenes are dispersed by wind (Gutterman 2002).

Gymnarrhena exhibits "dimorphic cleistogamy" or "true cleistogamy", in that it has two different flower types: chasmogamous and cleistogamous (Culley and Klooster 2007). While about 228 genera of angiosperms have some type of cleistogamous flowers, only 168 are dimorphic. It is estimated that dimorphic cleistogamy has evolved less than 40 times, and most of the lineages have very few species (Culley and Klooster 2007).

ANATOMY

The only anatomical data found is from Zamski et al. (1983) who examined the taproot of *Gymnarrhena* and found that it starts to contract soon after emergence. Ultimately, this contraction causes retraction of the main shoot apex from the soil surface to a depth of about 10 mm.

POLLEN

Gymnarrhena pollen was examined by Wortley et al. (2007; Fig. 22.1F, G), and they report that it is spheroidal, round in polar and equatorial view, and tricolporate. The colpi are separate with acute ends. The grains are echinate and non-lophate, the spines unevenly distributed, conical-pointed, 1–2 μm long, with bases slightly swollen and with internal cavities. The tectum is microperforate, covering the whole surface of the grain. The infratectum comprises two distinct layers that are not clearly attached to one another; the outer layer is columellate or spongy, the inner supporting layer made up of thick, unbranched, solid columellae, evenly distributed around the grain. The grains are ecaveate and the endexine is thinner than the foot layer. Despite the sparse spines and lack of a cavea, the ultrastructure of these grains, with unattached layers of evenly distributed columellae, does not fit into Cichorioideae (Anderberg et al. 2005) and is suggestive of the characteristics of Corymbieae, the sister group of Asteroideae (Wortley et al. 2007). This is not as far from the position on the molecular tree as it might seem, since *Gymnarrhena* is the branch just below Cichorioideae, and *Corymbium* is nested one node higher than Cichorioideae. Zhao et al. (2006) commented that *Gymnarrhena* pollen shared the multilevel columellae with Mutisieae s.l., but they noted that this character is found elsewhere in the family including Anthemideae and Cardueae; they concluded that it did not belong in Mutisieae s.l. because of its spinate pollen. Pollen characters, therefore, do not place the genus in any of the existing suprageneric taxa and are, therefore, consistent with recognizing it in its own tribe and subfamily.

CHROMOSOME NUMBERS

There are two different published chromosome counts; Murín and Chaudhri (1970) from Iraq and Kamel (1999) from Egypt; both report $2n = 20$, each from a single plant. Nikulina and Kotseruba (1999) report $2n = 18$.

CHEMISTRY

There is no information on the chemistry of Gymnarrheneae.

ECOLOGY AND REPRODUCTIVE BIOLOGY

Gymnarrhena is an amphicarpic herb (Fig. 22.1B, C) of the Mediterranean biome of North Africa and the Middle East, growing in dry, mostly bare, sandy areas and resembling a grass (Fig. 22.1A, D, E). Research on the reproductive biology of this unusual plant is summarized by Koller and Roth (1964) and in the description above. There are three aspects to its reproductive biology that are most interesting: seed heteromorphism, the presence of aerial as well as subterranean heads, and the presence of both chasmogamous and cleistogamous flowers.

Seed heteromorphism, that is, the production of seeds with variable morphologies and ecological strategies, represents an allocation of different fractions of seed output to different ends, and most examples are found in four flowering plant families, one of which is Compositae (Harper 1977). Seed heteromorphism appears to be largely restricted to relatively short-lived, fugitive species, particularly weeds. Venable and Burquez (1989) say that it might be a form of 'bet hedging' in response to environments that vary spatially or temporally. These morphological heteromorphisms are important because they may be associated with ecological strategies that have evolutionary significance, such as dispersal, dormancy, differential competitive performance, within or among year timing of germination, vulnerability to predators, and seedling growth and survival or fecundity (see many references cited in Chmielewski 1999).

The presence of aerial as well as subterranean heads has several different explanations. Koller and Roth (1964) reported that mean weight of *Gymnarrhena* aerial fruit was only 5%–6% of the weight of a subterranean fruit and that six-day-old subterranean seedlings were six times the weight of aerial seedlings. They reported that the survival was considerably greater for these subterranean seedlings and that plants under dry conditions may fail to produce aerial heads. On the other hand, according to Brown and Böer (2005) the species occurs on firm sometimes rocky, substrates that are generally hostile to plant growth. The above-ground fruits are small and possess a small pappus to aid in their dispersal so they can travel some distance from the parent plant. The one or two large underground fruits (nearly 20 times the weight of the aerial ones) lack a pappus and stay close to the parental plant. It is their opinion that the underground fruits ensure that when the mother plant dies later in the year, the same favorable location is re-colonized. Gutterman (1989) thinks that the underground location protects the seeds from predation. Zeide (1978) described dual strategies for *Gymnarrhena micrantha* in the Negev desert of Israel. He determined that the subterranean fruits were produced according to a "pessimistic strategy", whereby fruit production begins as soon as possible concurrent with continued vegetative growth. The aerial fruits, on the other hand, were produced according to a more "optimistic strategy" (in order to maximize yield, the vegetative stage precedes a last and full switchover to heavy fruiting). Cheplick and Quinn (1982) felt that the pessimistic strategy must therefore arise from other considerations such as unpredictable environments as it is at odds with optimality models of resource allocation in annuals. They summarize by saying that there are three arguments that have been supported for *Gymnarrhena*: *(1)* the seedlings arising from the larger propagules are more tolerant to stress or competition, *(2)* these subterranean seedlings have a higher probability of surviving to produce seed, *(3)* genotypes with an early production of subterranean seed may be the only ones to produce seed under stress (Evenari 1963; Koller and Roth 1964; Zeide 1978). And another has been suggested (Cheplick and Quinn 1982): *(4)* the larger subterranean seed may show a greater return on energy invested than an aerial seed. Other explanations that have been provided are the protection afforded by burial against catastrophes, and the placement of subterranean seed in the same microhabitat occupied by the parental plant, providing protection from the risks of random dispersal (Evenari 1977; Koller and Roth 1964). Cheplick and Quinn (1982) concluded that the early production of few larger seeds followed by the later production of many small seeds was presumably the result of the variable and unpredictable length of their growing periods and to their role as a fugitive species.

There are about 50 amphicarpic species worldwide, approximately one in every 5000 species of flowering plants; most of them occur in either frequently disturbed and/or stressful habitats. Eight of these are found in Israel, which has only 2500 species in its known flora, i.e., 1 in ca. 310 species, a very high ratio compared to flowering plants in general (Kaul et al. 2000; Lev-Yadun 2000). Given the suggested reasons above, Lev-Yadun (2000) adds that many of the amphicarpic annuals are found in disturbed areas that are the result of drought, fire and grazing. He thinks this indicates a long history of disturbances in the eastern Mediterranean region that pre-dates human impact.

The cleistogamous aspect of the subterranean florets is more easily explained in that such flowers are invariably cleistogamous (Kaul et al. 2000).

Additional information can be found in the recent book by Gutterman (2002).

APPLIED ASPECTS

Gymnarrhena is listed on the web in the “Global Compendium of Weeds” as being on a list of weeds from Egypt (www.hear.org/gcw/species/gymnarrhena_micrantha/), however, an examination of the book (Boulos and el-Hadidi 1984) yielded no mention of the species.

In a study of the areas of Kuwait that were damaged by oil towards the end of the Gulf War in 1991, the area covered by oil or by tar tracks is largely sterile. However, *Gymnarrhena* was one of the taxa found in this area growing in the control sites and in areas where the sand has blown out from under the tar tracks indicating that it has the ability to move into disturbed habitats (Brown and Porembski 2000). But perhaps the most interesting study involving pollution and *Gymnarrhena* concerns the copper mining and smelting activities of the Nabatean, Roman and Byzantine periods in the southern Jordanian desert that has, for 2000 years, continued to exert an influence on the plants and animals, and no doubt the people, of the area (Pyatt et al. 2000). Khirbet Faynan (believed to be the Roman city of Phaino) was a major center of metal-working in the ancient world and left huge deposits of slag containing copper and lead. Testing of recent soil, plants, and animals show enhanced concentrations of this lead and copper: one of the two plants with the highest concentrations was *Gymnarrhena*, which is one of the favorite plants for the grazing goats in the area. The goats, in turn, also showed elevated levels of lead and copper (Pyatt et al. 2000). Past levels were certainly much higher and possibly impacted the plants, animals and humans for 2000 years. Anthropologists have a wonderful ability to meld interesting science with drama, and so the final words of Pyatt et al. (2007) are worth repeating:

> The copper and lead rich wadis of southern Jordan … saw industrial pollution on a scale which would have been familiar to the inhabitants of Victorian Sheffield …. Small wonder then that in Romano-Byzantine times the mines of Phaino were seen as a place to send recalcitrant criminals. Eusebius of Caesarea in his “Martyrs of Palestine” describes such a scene; “they demanded that he should be sent away to the mines, and not just any mines but to that of Phaino where even a condemned murderer is hardly able to live a few days.”

Nothing else has been found on either this topic or any other applied aspects of this species.

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Section III Part 3

Cichorioideae and Corymbioideae

Chapter 23

Introduction to Cichorioideae

Vicki A. Funk and Raymund Chan

INTRODUCTION

In the first significant attempt to subdivide Compositae above the generic level, Cassini (1816, 1819), relied on a series of rather well delimited tribes, and since then tribes have remained the most useful level of classification within the family. In contrast, subfamilies such as Hoffmann's (1890–1894) invalidly described Labiatiflorae (bilabiate Mutisieae), Liguliflorae (Cichorieae) and Tubuliflorae (all Compositae with actinomorphic corollas) were only broadly and often inaccurately applied. A meaningful use of a subfamily classification within Compositae is comparatively recent. From the time of the re-delimitation (Poljakov 1967; Robinson and Brettell 1973; Carlquist 1976; Wagenitz 1976; Robinson 1977) of the previously artificially applied subfamily names Cichorioideae (Chevallier 1828) and Asteroideae (Lindley 1829) until 1992, only the two subfamilies were recognized. Using molecular data, Jansen and Palmer (1987) discovered that a small group of taxa that at the time was a subtribe in tribe Mutisieae (included then in Cichorioideae) was actually the sister group to the rest of the family. In 1992 Bremer and Jansen described this subtribe as a separate subfamily with only one tribe (Barnadesioideae; Barnadesieae), and from then until 2002 there were three subtribes: Barnadesioideae, Cichorioideae, and Asteroideae.

As currently interpreted, the subfamily Asteroideae is a well-defined group both morphologically and molecularly with many large tribes; indeed most species in the family (62%) are found within the clades of Asteroideae (20 tribes, 1229 genera, 15,500 species; see Chapter 33). The Barnadesioideae are also easy to distinguish using both molecular and morphological characters; since Cabrera (1977) it has been recognized as an informal group or subtribe. Compared to Asteroideae, they are a small group: one tribe, nine genera, and 92 species (< 0.004% of the species in the family; Chapter 13). The subfamily Cichorioideae, on the other hand, started out containing only one tribe, Cichorieae. (Cichorieae Lam. & DC. [1806] has priority over Lactuceae Cass. [1819].) The subfamily grew in size through the work of a number of individuals (Poljakov 1967; Robinson and Brettell 1973; Carlquist 1976; Wagenitz 1976; Robinson 1977) until it encompassed all tribes that were not in Asteroideae (until Barnadesioideae were split off from Cichorioideae).

Bremer in his morphologically based cladistic treatment of the family (1994) recognized three subfamilies, Barnadesioideae, Cichorioideae and Asteroideae, but he acknowledged that the Cichorioideae subfamily was not monophyletic but rather a grade in which Asteroideae were nested. There are a number of characters that have been proposed to support monophyletic Cichorioideae including deeply divided disc corollas, sweeping hairs on the upper part of the style, calcarate bases of the anther thecae, and base chromosome numbers of 9 or 10, but all of these characters have proven to be plesiomorphic (Bremer, 1994, 1996).

Kim and Jansen (1995) used the results of an *ndhF* study to suggest that the four tribes of their Cichorioideae s.str. (Arctotideae, Cichorieae, Liabeae, Vernonieae) formed a monophyletic group that was the sister group of Asteroideae and that the tribes Cardueae and Mutisieae did not belong in Cichorioideae. Karis et al.'s (1992) morphological cladistic analysis resulted in the formation of the same clade as reported by Kim and Jansen (1995), even though the tribe Arctotideae and the subfamily Cichorioideae s.str. were not monophyletic. Subsequently, this clade was given the informal name "the Vernonioid group" (Bremer 1994, 1996). Bremer (1996) accepted that Mutisieae and Cardueae should be removed from Cichorioideae, and he placed Cardueae in Carduoideae but left Mutisieae as "unknown" in regard to its monophyly.

As more molecular data became available (Bayer and Starr 1998; Panero and Funk 2002, 2008; Funk et al. 2005) it became clear that Cichorioideae would need to permanently decrease in size, and now most synantherologists agree that the tribes Mutisieae (sensu Cabrera) and Cardueae do not belong in redefined Cichorioideae. In addition, the genera *Gymnarrhena* Desf. and *Corymbium* L. have also been placed in subfamilies of their own (see Chapters 22 and 32). The subfamily Cichorioideae now contains eight super-generic taxa, four of which are reasonably sized tribes (Vernonieae, Liabeae, Arctotideae, Cichorieae; Table 23.1). The recent molecular works of Panero and Funk (2002, 2008) show this group to be a strongly supported clade that appears in all resulting trees. Also in this subfamily are three small clades (Platycarpheae, Moquinieae, Eremothamneae) and one difficult-to-place genus (*Heterolepis*); these clades were not in the Panero and Funk (2008) study but have been included in other analyses (Funk et al. 2004; Funk and Chan, unpub.).

The delimitation of Cichorioideae suggested by the molecular data is, however, not clearly supported by morphological characters. In fact, there are few characters that might provide apomorphies for the redefined subfamily Cichorioideae, and those characters are not consistent across the subfamily. For instance, lophate pollen is almost exclusive to this subfamily (also present in two genera of Barnadesioideae) but is not found in all groups (e.g., Liabeae and Arctotideae-Arctotidinae); latex is found in several clades (Cichorieae, Arctotideae-Gorteriinae, Liabeae) but sometimes inconsistent where it is found and missing in nearly all Vernonieae. Another possible character, the vernonioid style (Bremer 1996), is present only in Cichorioideae but does not occur in Arctotideae. Perhaps one could use the presence of the three characters above (lophate pollen, latex, vernonioid style) together, and at least one of them could be found in nearly all of the taxa of the subfamily. Blackmore et al. (Chapter 7) have suggested that "pollen grains with aggregated columellae" might serve as a synapomorphy for the subfamily, and this needs to be investigated across all taxa.

MOLECULAR PHYLOGENETIC ANALYSIS

Panero and Funk (2008) used very few taxa from Cichorioideae in their analysis; they were primarily interested in Mutisieae (sensu Cabrera 1977) and had only a few samples for each of the other tribes. However, in the last few years several detailed molecular analyses have focused on Cichorioideae or its tribes: Arctotideae (Funk et al. 2004), Arctotideae-Arctotidinae (McKenzie et al. 2006; Funk et al. 2007; McKenzie and Barker 2008), Arctotideae-Gorteriinae (Funk and Chan 2008), Cichorieae (Gemeinholzer et al., unpub.), Vernonieae (Keeley et al. 2007), Liabeae (Funk and Chan, unpub.). Available molecular data from these studies, as well as additional data generated specifically for this project, were used to investigate possible phylogenies for the subfamily (Figs. 23.1, 23.2). Materials and methods followed those described in Funk and Chan (2008).

Table 23.1. Cichorioideae tribes and their approximate number of genera and species, and general distribution. Gundelieae are included within Cichorieae (see Chapter 24).

Tribe	No. of genera	No. of species	Distribution
Cichorieae Lam. & DC. (Chap. 24)	86	ca. 1500	Mediterranean, Europe, Eurasia, Asia, North America
Arctotideae Cass. (Chap. 25)	17	215	Southern Africa with three species in Australia
Eremothamneae H. Rob & Brettell (Chap. 26)	2	3	Southern Africa
Liabeae (Cass. ex Dumort.) Rydb. (Chap. 27)	18	190	Central Andes to Mexico and the Carribean
Vernonieae Cass. (Chap. 28)	120	+1000	Tropical Africa, Asia, and the Americas
Platycarpheae V.A. Funk & H. Rob. (Chap. 29)	2	3	Southern Africa
Moquinieae H. Rob. (Chap. 30)	2	2	Brazil
Heterolepis Cass. (Chap. 31)	1	3	South Africa
Total	248	+2916	

PHYLOGENY

ITS, *trnL-F*, *ndhF* sequence data were used for this study. One hundred and fifteen representatives from the outgroups, each tribe, and the unplaced genus *Heterolepis* were included: ingroups: Cichorieae, 8 species; Arctotideae 25; Liabeae 33; Vernonieae 25; Platycarpheae 3; Moquinieae 2; Eremothamneae 2; *Heterolepis* 2; outgroups: Mutisieae s.str. 2; Gochnatieae 4; Carduoideae 8; Corymbieae 1. All three sets of sequence data were available for all taxa with the exception of *Eremothamnus* O. Hoffm., which was missing the ITS sequence. The results of these analyses are summarized in Figs. 23.1 and 23.2.

There is an ongoing discussion about the exact relationship between the tribe Gundelieae (*Gundelia* L. and *Warionia* Benth. & Cross.; sensu Panero and Funk 2008) and the rest of Cichorieae. Both genera are always found at or near the base of Cichorieae (Karis et al. 2001; Panero

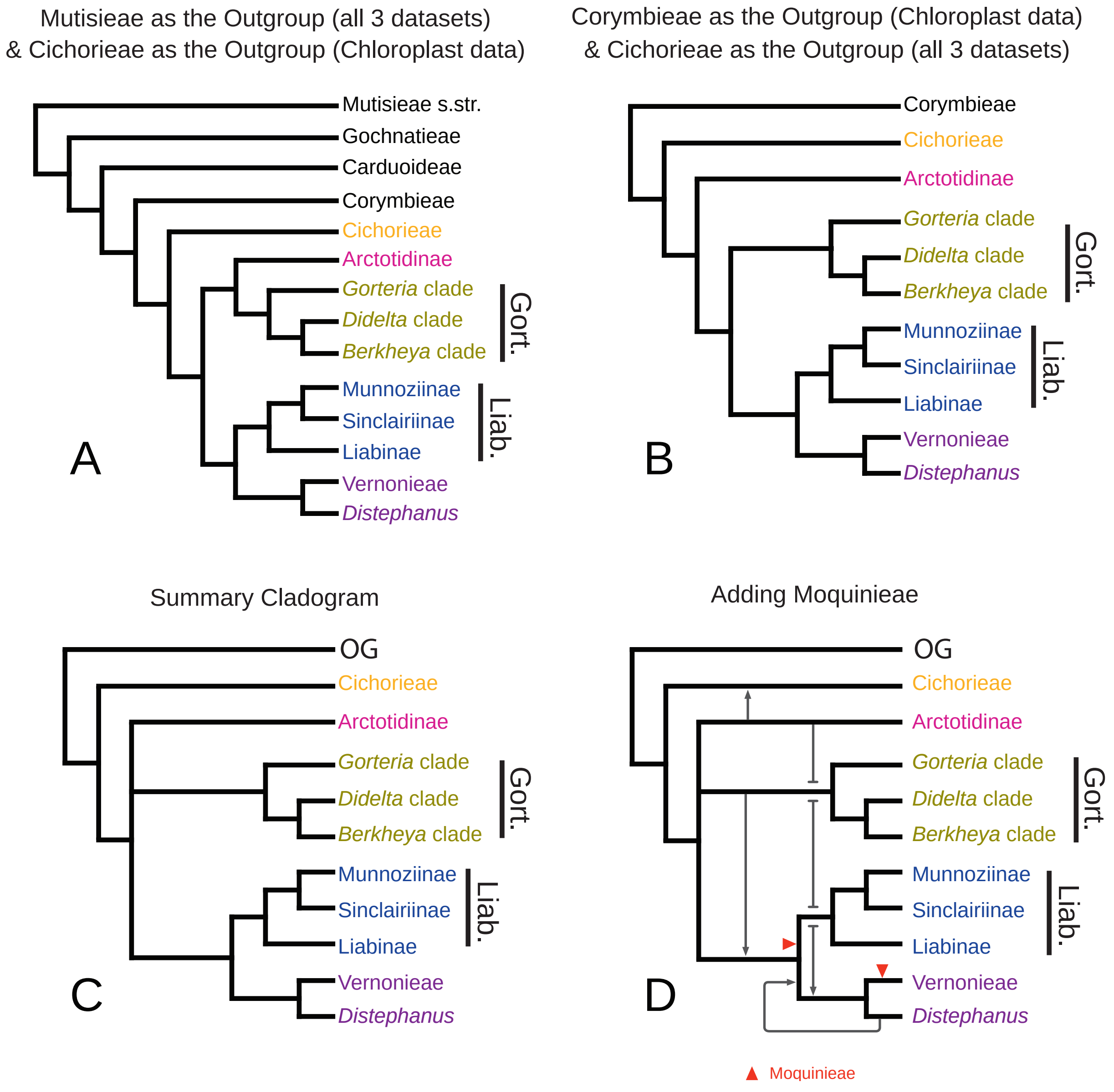

Fig. 23.1. Phylogenies showing some of the relationships among the four core tribes of the subfamily Cichorioideae: Arctotideae subtribe Arctotidinae, Arctotideae subtribe Gorteriinae, Cichorieae, Liabeae and Vernonieae (including the basal branch, *Distephanus*). **A** and **B** are strict consensus trees for separate analyses; **C** is the resulting summary diagram formed when A and B are combined; **D** illustrates what happens when one of the problem/small groups (Moquinieae) is added to the analysis using a variety of outgroups. Liab. = Liabeae; Gort. = Gorteriinae. Colors indicate clades.

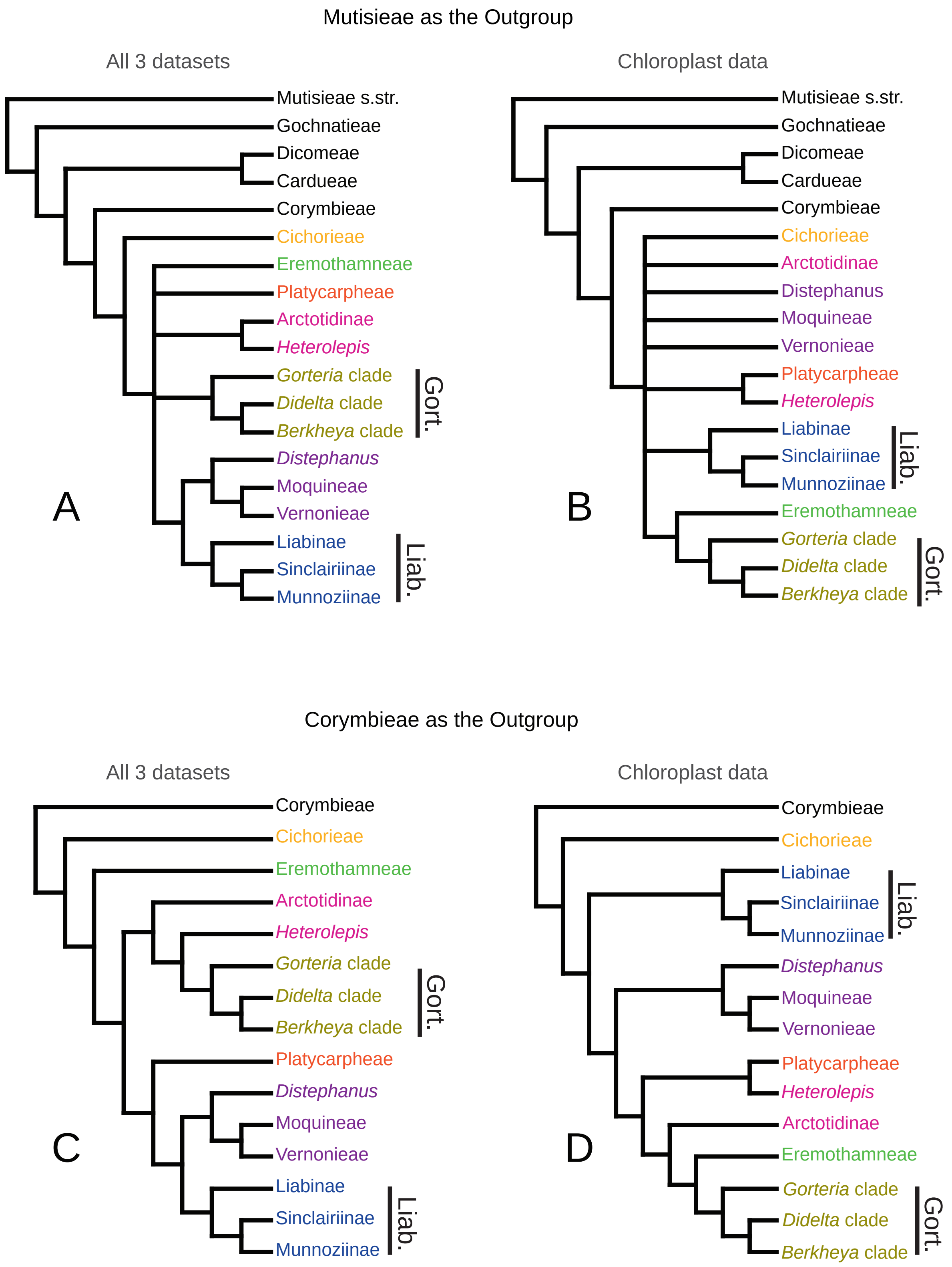

Fig. 23.2. Strict consensus trees showing some of the relationships among the four core tribes of the subfamily Cichorioideae: Arctotideae subtribe Arctotidinae, Arctotideae subtribe Gorteriinae, Cichorieae, Liabeae and Vernonieae (including the basal branch, *Distephanus*) and the four problem groups (Eremothamneae, *Heterolepis*, Moquinieae, Playtcarpheae). Liab. = Liabeae; Gort. = Gorteriinae. Colors indicate clades.

and Funk 2002, 2008; Gemeinholzer et al., unpub.) and can be sister taxa or separate clades depending on selection of terminals, type of data, and mode of analyses. Both genera were included in this analysis so their exact position does not affect the results of this study, although it does effect the placement and acceptance of the tribe Gundelieae (see Chapter 24). For this chapter we are following the results of Kilian et al. (Chapter 24) and Gemeinholzer et al. (unpub.), which show *Warionia* as the basal taxon of the tribe Cichorieae and *Gundelia* nested further up the phylogeny but still near the base.

If the data are analyzed using just the four main tribes, three of them have constant positions; Liabeae and Vernonieae are nearly always sister groups and Cichorioideae are always the basal branch. The two subtribes of Arctotideae (Arctotidinae and Gorteriinae), although monophyletic, do not always group together; their placement is dependent on the outgroup(s) that is (are) used. Figure 23.1A, B shows the strict consensus trees that are the most frequent results of the various analyses. Figure 23.1C is a summary of Fig. 23.1A, B and occurs occasionally as a strict consensus tree. Although many more taxa were used in this study than in Funk et al. (2004), these results are not in conflict with those presented in that paper.

After the initial analysis, data from the four small groups mentioned above were added: Platycarpheae (all three species), Moquinieae (two species, one from each genus), Eremothamneae (two species, one from each genus), and *Heterolepis* (two species out of three). It was hoped that the addition of these four groups would help determine their phylogenetic placement. However, the addition of these taxa resulted in a broader array of resulting strict consensus trees. Specifically, different trees resulted when the outgroup(s) (Mutisieae s.str., Gochnatieae, Carduoideae, and/or Corymbieae) were changed. As an example, Fig. 23.1D shows what happens when just Moquinieae are added. Depending on the outgroups used, Moquinieae only had two positions; they were the sister taxon of core Vernonieae joining the clade above the genus *Distephanus* Cass., or they formed a polytomy consisting of four branches: Liabeae, Vernonieae, *Distephanus*, and Moquinieae (Fig. 23.2); they always stay close to the base of Vernonieae. Unfortunately, the addition of Moquinieae had a big impact on other taxa. For instance, in some cases Arctotidinae grouped with Vernonieae + Moquinieae, leaving *Distephanus* out of the clade; in other circumstances Arctotidinae were the sister taxon of Cichorieae, or Gorteriinae formed a clade consisting of Liabeae + Vernonieae + Moquinieae (Fig. 23.1D). This type of reaction to the addition of one of the problem taxa was first noticed in 2004 (Funk et al.) but with a much smaller dataset. The other small taxa cause even more disruption. The results of the analyses are summarized in Fig. 23.2, which shows four of the resulting strict consensus trees. Three clades are always present: the tribe Liabeae, and the two subtribes of Arctotideae, although the two subtribes only group together about half the time and only when other taxa are present in the clade. In addition, all taxa of Vernonieae always group together, except one genus, *Distephanus*.

The real problems are Eremothamneae, Platycarpheae, and *Heterolepis*. A sample of the strict consensus trees is presented in Fig. 23.2, and they show that these taxa can be found in a variety of locations. The Eremothamneae taxa are the most volatile in their placement, holding the position as the sister group to all but Cichorioideae (Fig. 23.2C), as sister to the subtribe Gorteriinae in two trees (Fig. 23.2B, D), where in the latter case Arctotideae s.l. are monophyletic, or in a mostly unresolved relationship (Fig. 23.2A). Platycarpheae and *Heterolepis* are also found in different places (Fig. 23.2), and when added, signally result in the movement of other tribes. Similar results are found when using only ITS data.

If all the consensus trees are combined, the resulting tree shows all of the groups to be monophyletic (with the exception of Vernonieae with *Distephanus*) but with little resolution as to the relationships among them. Having examined hundreds of phylogenies and strict consensus trees in an attempt to bring resolution to this problem, we can only say that Fig. 23.1C, which is a summary diagram formed from the two most common strict consensus trees, is the best phylogeny to use for the main tribes. For all of the taxa in the subfamily, Fig. 23.2C occurs frequently and can be used as a reference. But as a conclusion, it can only be stated that we need more data and perhaps additional methods to try to resolve the tree. One observation is that all of the problem taxa have distinct sets of molecular and morphological data and reside on rather long branches compared to the rest of the taxa, and it is possible, therefore, that the difficulties are caused by long branch attraction. If so, additional data may help. We have added *matK* to the database, but we are still missing some critical taxa. We hope to report further resolution of this subfamily in the near future.

TAXONOMY

Subfamily Cichorioideae (Juss.) Chevall., Fl. Gén. Env. Paris 2(2): 513. 1828, based on Family Cichoriaceae Juss., Gen. Pl.: 168. 1989, nom. cons.

Subfamily Lactucoideae (Cass.) Lindl. in J.C. Loudon, Encycl. Pl.: 1073. 1829, based on Tribe Lactuceae Cass., Dict. Sci. Nat. 20: 355. 1821.

Nomenclature follows Reveal (1997) and the subfamily description is modified from that of Jeffrey (2007).

Perennial, biennial or annual herbs, shrubs or trees, rarely scandent, very rarely aquatic. Leaves alternate or opposite, usually simple, entire to deeply lobed, sometimes spiny. Capitula homogamous to heterogamous, discoid, ligulate or radiate. Involucre narrowly to broadly cylindrical or campanulate to subglobose, phyllaries (1–)2 to many-seriate, usually imbricate. Receptacle epaleaceous, often alveolate, or paleaceous. Florets 1 to many; usually 5-merous, corolla lobes usually long, not coiled. Anthers calcarate, caudate or ecaudate, tails usually unbranched. Pollen ecaveate or sometimes appearing caveate, spiny, sometimes echinolophate, psilolophate or lophate, globose; columellae aggregated. Style arms commonly long, tapered, acute, with sweeping hairs dorsally continuing below the bifurcation, or with longer sweeping hairs in a ring below the bifurcation; stigmatic papillae covering all of the inner surface. Achenes with twin hairs. Pappus usually present, of bristles or scales, sometimes heteromorphic.

The subfamily Cichorioideae s.str. is well-defined by the molecular data (e.g., 100 boostrap support in all trees; Panero and Funk 2008). Currently the subfamily has seven tribes and one unplaced genus (Table 23.1) with ca. 2900 species (ca. 12% of the species in the family) placed in ca. 240 genera (over 14%) and seven tribes (only 2%).

As mentioned above, there is only one character (pollen grains with aggregated columellae) that is a potential synapomorphy for the subfamily at this time, and readers are directed to the descriptions in each of the chapters pertaining to this subfamily for diagnostic characters of the tribes as well as the unplaced genus *Heterolepis* (Table 23.1).

CHROMOSOME NUMBERS

A base chromosome number of $x = 9$ is found for most tribes in the subfamily, although $x = 10$ is often, yet less frequently, reported. Within the individual clades such as Vernonieae, Liabeae, Arctotideae, and Cichorieae, both reduction series and polyploidy are found. The taxa that are difficult to place have either not been counted (Platycarpheae, Eremothamneae, and Moquinieae) or have an unusual base chromosome number (*Heterolepis*, $x = 6$).

CHEMISTRY

Very little is known about the secondary plant chemistry of this subfamily except for Cichorieae, Vernonieae, and Platycarpheae (Chapters 24, 28, 29). In Cichorioideae there has been quite a bit of work in the economically important groups, but little in other groups (Bohm and Stuessy 2001). According to Bohlmann and Jakupovic (1990), Vernonieae have a characteristic chemical signature and certain groups of compounds could be diagnostic at the generic level and higher. Platycarpheae, on the other hand, share some similarities with Cardueae and also with Corymbieae, but none with Vernonieae (Bohlmann and Zdero 1977).

BIOGEOGRAPHY

The subfamily Cichorioideae has a nearly worldwide distribution, but most of its clades have their basal branches in Africa. All of the Northern Hemisphere temperate taxa are deeply nested in the various clades. An area optimization analysis on a metatree of the family (Chapter 44) suggests an African origin for Cichorioideae with only two of the eight taxa having non-African affinities at their base (Liabeae, Moquinieae), and those are nested within the remainder of the clades. It is interesting to note that the tribes are in different parts of the continent, for instance the origin of extant members of Vernonieae appears to be tropical Africa; Arctotideae, Platycarpheae, Eremothamneae, and *Heterolepis* in southern Africa; and Cichorieae in Northern Africa and the Mediterranean. The two new world clades (Liabeae in the Andes and Moquinieae in Brazil) are both associated with the base of Vernonieae and appear to have originated from independent long distance dispersal events from Africa to South America.

PLACEMENT OF PROBLEMATIC GENERA

In 1994 Bremer listed some genera in the subfamily Cichorioideae that “cannot be placed in any of the existing tribes”, and after nearly 15 years it is interesting to see what we know (and don’t know) about these genera: *(1) Warionia* is now known to be related to Cichorieae, possibly as the basal branch of the tribe; *(2) Eremothamnus* and *(3) Hoplophyllum* DC. are sister taxa and are on a long branch that is unplaced but definitely in Cichorioideae; *(4) Corymbium* is outside of the subfamily Cichorioideae, in a subfamily by itself, and is the sister taxon of Asteroideae; *(5) Cratystylis* S. Moore is also outside of the subfamily and now placed in Inuleae; *(6) Gymnarrhena* is outside of the subfamily and now the sister group of the clade containing Cichorioideae + Corymbioideae + Asteroideae. In addition, other problematic taxa were discovered: *(7) Platycarpha* Less. has been separated into two genera, removed from Arctotideae, and placed in a tribe of its own that is possibly related to, but not part of, the Vernonieae + Liabeae clade or the sister taxon of the Arctotideae + Liabeae + Vernonieae clade; *(8) Heterolepis* has been temporarily removed from Arctotideae, not only because its position is uncertain, but also because its morphology does not fit the descriptions of either of the two well-supported subtribes, but its final placement has not been determined; *(9) Moquinia* and *Pseudostifftia* H. Rob. (sometimes combined in the genus *Moquinia*) were placed in the tribe Moquinieae, but that branch is somewhat unstable in its position, but consistently located near the base of Vernonieae.

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Chapter 24

Cichorieae

Norbert Kilian, Birgit Gemeinholzer and Hans Walter Lack

INTRODUCTION

Cichorieae (also known as Lactuceae Cass. (1819) but the name Cichorieae Lam. & DC. (1806) has priority; Reveal 1997) are the first recognized and perhaps taxonomically best studied tribe of Compositae. Their predominantly Holarctic distribution made the members comparatively early known to science, and the uniform character combination of milky latex and homogamous capitula with 5-dentate, ligulate flowers, makes the members easy to identify. Consequently, from the time of initial description (Tournefort 1694) until today, there has been no disagreement about the overall circumscription of the tribe. Nevertheless, the tribe in this traditional circumscription is paraphyletic as most recent molecular phylogenies have revealed. Its circumscription therefore is, for the first time, changed in the present treatment.

The easy recognition of the members of the tribe comes along with a major drawback: the tribe is not only conspicuously poor in morphological features, but extensive parallel evolution of features further renders the recognition of natural groups difficult. This situation has given rise to considerable differences in the generic and suprageneric classification of the members of the tribe by various students of Cichorieae.

Molecular phylogenetic studies have essentially improved our understanding of a few groups of the tribe since the 1990s. But only now the results of the molecular phylogeny of a large dataset (428 taxa of 83 genera; Gemeinholzer et al., in prep.), representing the entire tribe, have become available, and this has enabled us to provide an essentially revised treatment of Cichorieae. While the general lines seem sufficiently clear so far, our knowledge is still insufficient regarding a good number of questions at generic rank as well as at the evolution of the tribe.

HISTORICAL OVERVIEW

Tournefort (1694) was the first to recognize and describe Cichorieae as a taxonomic entity, forming the thirteenth class of the plant kingdom and, remarkably, did not include a single plant now considered outside the tribe. This reflects the convenient recognition of the tribe on the basis of its homogamous ligulate flowers and latex. He called the flower “flos semiflosculosus”, paid particular attention to the pappus and as a consequence distinguished two groups, the first to comprise plants with a pappus, the second those without.

Tournefort’s pupil, Vaillant, coined for his teacher’s thirteenth class the name “Cichoracées” (Vaillant 1719) and distinguished five “sections” based on features of the habit, pappus, and receptacle, the first including all scapose taxa irrespective of their pappus, the second including those with a pappus of trichomes or scales and a naked receptacle, the third those with a plumose pappus and a naked receptacle, the fourth those lacking a pappus, and the fifth those with receptacular trichomes or paleae (Vaillant 1723; for an evaluation of Vaillant’s work on Compositae see Greuter et al. 2005).

Lamarck and De Candolle (1806) validated Vaillant’s pre-Linnaean name for the tribe and subdivided Cichorieae into four subtribes according to pappus features. The lasting merit of these and the other 19th century authors dealing with the systematics of the Asteraceae in general and the tribe Cichorieae in particular, namely Cassini (1827, 1830), Don (1828), Lessing (1832), De Candolle (1838), Bentham (1873), and Hoffmann (1890–1894), is their analysis, comparison, description, and classification in species and genera of the enormously increased plant diversity that successively became known to science in the course of this century, rather than their suprageneric systems of subdividing the tribe. All attempts had in common classifications based on one or a few key features, pappus and receptacle characters having been particularly highly appreciated (for further details see Stebbins 1953: 65–67). Extensive convergent evolution, especially in the pappus of the Cichorieae, however, condemned the resulting systems from Tournefort in 1694 up to Hoffmann in 1894 to be largely artificial.

Hoffmann's (1890–1894) subdivision of the tribe, which had been influential until well into the 20th century, illustrates the stagnation in the development of the suprageneric classification from the late 17th to the late 19th century. He coined the name pair "Liguliflorae (Cichorioideae)" and "Tubuliflorae" (Hoffmann 1890–1894: 118) and separated Cichorieae as Liguliflorae on subfamily rank from all other tribes, which he united as Tubuliflorae. Hoffmann divided the tribe into five subtribes, of which his three larger subtribes are entirely based on pappus features: Cichoriinae unite all genera without or with non-setaceous pappi, Leontodontinae include all New and Old World genera with plumose pappus, and Crepidinae include all genera with setaceous, non-plumose pappus. In addition, he placed *Scolymus* in a subtribe of its own and united *Dendroseris* and *Fitchia* (the latter actually an odd liguliflorous Heliantheae; Carlquist 1947) because of their arborescent life form.

In the middle of the 20th century, a fruitful cooperation of two American botanists, Stebbins and Babcock (Babcock and Stebbins 1938), revolutionized our understanding of Cichorieae, as of plant systematics in general. Studying the American species of *Crepis*, they discovered the crucial role of hybridization and formation of polyploid complexes in the evolution of species. In the course of their subsequent cytological and taxonomic work in Crepidinae s.l., they re-established and monographed Cassini's Asian genus *Youngia* (Babcock and Stebbins 1937, 1943). Stebbins studied also the Asian *Crepis* relatives *Ixeris* (Stebbins 1937c), *Dubyaea* and *Soroseris*, hereby making fundamental contributions to our knowledge of the vascularization of the ovary (Stebbins 1940). The pair also investigated the genera *Lactuca* and *Prenanthes* (e.g., Stebbins 1937a, b) and provided a survey of karyology and phylogeny in Cichorieae (Stebbins et al. 1953). By then Babcock had completed his monumental taxonomic revision of *Crepis*, which takes karyological, morphological, and biogeographical data into account (Babcock 1947). Stebbins (1950), one of the key figures of the Modern Evolutionary Synthesis, crowned his studies in Cichorieae with a new subtribal classification, based on a phenetic multi-evidence approach by considering morphology (in particular pappus, shape of the stigma branches, pollen, and indumentum), geographical distribution, and chromosomal data (Stebbins 1953). In contrast to previous classifications, Stebbins considered "each genus separately, placing it nearest to those genera which it most nearly resembles in respect to the largest number of characteristics of external morphology, plus the nature of the chromosomes and the geographic distribution" (Stebbins 1953: 69). He arranged the 62 genera recognized by him into eight subtribes, thereby grouping genera with no pappus together with genera possessing a pappus, which, however, resemble one another in other characteristics. Within these groups the genera not always feature common characters but are sometimes united by transitional genera. Stebbins recognized the close affinity of the endemic New World genera and placed them into two new subtribes, Malacothricinae and Stephanomerinae, which are distinguished by geographic distribution and chromosome numbers.

Jeffrey (1966), in another phenetic approach undertaken in the context of his studies of Cichorieae in tropical East Africa, considered additional micro-morphological characters (length of collecting trichomes on the style, trichome shapes on stigmatic surfaces, and pubescence of the corolla tube), which he incorporated in his system to improve Stebbins's classification. He defined groups and subgroups but refrained from providing a formal taxonomic classification due to the "uncertain status of the ligulate Compositae within the family" (Jeffrey 1966: 428). Jeffrey's classification of five groups, eight subgroups and eighteen series resulted in several natural groupings, especially on the lower taxonomic levels. However, sometimes features are placed into a doubtful evolutionary context, e.g., he grouped the *Scorzonera* subgroup within the *Hypochaeris* group due to the paleaceous/plumose pappus and medium to long style-arms, and the *Crepis* subgroups within the *Cichorium* group due to long style-arms and large collecting trichomes, not taking into account the possible different evolutionary pathways by which these homologous characters could have evolved.

Bremer (1994) provided the first cladistic analysis of the tribe, based on morphological characters, by studying a selection of 23 from altogether 98 genera recognized, which either represent presumed monophyletic groups, or distinct or isolated taxa. As result of this, he divided the tribe in eleven subtribes, establishing the new subtribes Catananchinae, Malacothricinae, and Sonchinae, and left two genera, *Cichorium* and *Scolymus*, unassigned to a subtribe. Due to the isolated position of *Scolymus*, he stated the necessity of a separate subtribe; however, in his treatment, monogeneric subtribes were avoided. For *Cichorium* he proposed a relationship close to Crepidinae, or Stephanomeriinae, or to the basally branching lineages within the tribe.

Bremer's major achievement towards a more natural classification is the subdivision of former Crepidinae s.l. (Stebbins 1953) into the subtribes Crepidinae s.str., Lactucinae, and Sonchinae, although their exact circumscriptions need revision. His treatment of the basically New World genera in the three subtribes Malacothricinae, Microseridinae, and Stephanomeriinae, in contrast, constitutes a moderate improvement only, since none of them has been found to be monophyletic in later molecular analyses (compare Lee et al. 2003: 620, fig. 1). Bremer's recognition of the subtribe Hieraciinae, which corresponds to Jeffrey's *Tolpis* group (except *Koelpinia*, which on palynological evidence is correctly placed in Scorzonerinae), maintains the advantages of Jeffrey's (1966) classification over that of Stebbins (1953). His Catananchinae, comprising *Catananche*, *Hymenonema*, and *Rothmaleria*, are an artificial unit.

Although molecular analyses in Cichorieae date back to the early 1990s (Jansen et al. 1991; Crawford et al. 1992; Kim et al. 1992; Sang et al. 1994), the data were still too meager to play a role in Bremer's classification. Molecular analyses in Cichorieae were initially focused on the phylogeny of selected subtribes, apart from a single early approach by Whitton et al. (1995) using chloroplast DNA restriction site variation upon 60 Cichorieae taxa. Whitton et al. (1995) addressed relationships among major lineages of the tribe, and their results agree very well with the only other, most recent attempt by Gemeinholzer et al. (in prep.), using DNA sequences of the nuclear ITS region and covering 438 taxa. Both analyses revealed similar major lineages and confirm that groups and basal branches are better resolved with increasing number of taxa.

Molecular analyses at subtribal rank have been carried out for the Sonchinae/Dendroseridinae (Crawford et al. 1992; Sang et al. 1994; Kim et al. 1996, 1997, 1999a, b, 2004, 2007; Lee et al. 2005), Lactucinae (Koopman et al. 1998, 2001), Hypochaeridinae (Samuel et al. 2003, 2006; Tremetsberger et al. 2005), Scorzonerinae (Mavrodiev et al. 2004) and the predominantly North American subtribes (Jansen et al. 1991; Lee et al. 2003). They have added a wealth of new data, provided some new insights into the phylogeny, which led to a number of taxonomic changes regarding the circumscription of genera. The more prominent examples are *Sonchus* (paraphyletic and either to include all its previous segregates plus the Pacific islands endemics *Dendroseris* and *Thamnoseris*, or, alternatively, to be split in several monophyletic units to be newly established), *Scorzonera* (polyphyletic and to be divided up by re-establishing several former segregates), *Leontodon* (diphyletic, making re-establishment of *Scorzoneroides* necessary), *Lactuca* (paraphyletic or polyphyletic depending on circumscription, but none of the existing morphological genus concepts being monophyletic) and *Malacothrix* (diphyletic). Further details are provided in the sections on phylogeny and taxonomy, below.

The most recent overview of Cichorieae is the treatment by one of us (Lack 2007) for the *Families and Genera of Flowering Plants*, which broadly followed the classification of Bremer (1994), with more substantial modifications restricted to Sonchinae (inclusion of the Dendroseridinae and with a wider circumscription of *Sonchus*, based on the work by Kim et al. 1996, 1997, 1999a, b) and Lactucinae (wider circumscription of *Lactuca* based on Koopman et al. 1998). In the light of the most recent molecular studies, we provide an essentially updated classification here.

Circumscription of Cichorieae

The traditional circumscription of Cichorieae as a conveniently recognized tribe, diagnosed by the unique combination of homogamous capitula with 5-dentate, ligulate flowers and the presence of milky latex, has been altered recently on the basis of molecular data (Gemeinholzer et al., in prep.) to accommodate two genera hitherto variously placed: *Gundelia* and *Warionia*. Both have milky latex but otherwise homogamous capitula with tubular flowers only. By inclusion of these genera the homogamous capitula with 5-dentate, ligulate flowers no longer characterize all the members of the tribe. On the other hand, although milky latex is otherwise present in some genera of Arctotideae, Cardueae, Liabeae, Mutisieae, and Vernonieae (Carlquist 1976), and in a few cases in Asteroideae, the presence of lactiferous canals in both the subterranean and aerial plant parts seem to be an exclusive feature of Cichorieae as circumscribed here (Augier and Mérac 1951; Wagenitz 1976; Bremer 1987, 1994). Homogamous capitula with 5-dentate, ligulate flowers are present in a few genera of Mutisieae (*Catamixis*, *Glossarion*, *Hyaloseris*; Bremer 1987, 1994) and, quite evidently by convergent evolution, in Heliantheae-Coreopsidinae (*Fitchia*) of subfamily Asteroideae (Carlquist 1957); 5-dentate, ligulate marginal flowers occur in Vernonieae (*Stokesia*; Bremer 1987, 1994).

Both *Gundelia* and *Warionia* share the presence of both (functional) oil ducts and latex canals in the roots (Augier and Mérac 1951), which has been reported otherwise from only two Cichorieae genera, viz. *Scolymus* and *Scorzonera* s.l. (Tieghem 1872; Col 1903–04). The two species of *Gundelia*, with a much-derived synflorescence of one-flowered capitula aggregated to secondary capitula, have spiny leaves and pollen (Blackmore 1981; Robinson 1994) similar to *Scolymus*. *Gundelia* has been shown to form a monophyletic trichotomy with *Scolymus* and the rest of Cichorieae (Karis et al. 2001;

based on *ndhF* data). *Warionia* has been shown to form a sister group relationship to the Cichorieae by Funk et al. (2004; based on *trnL-F*, *ndhF* and ITS data) and the basalmost branch of Cichorieae clade by Goertzen et al. (2003: fig. 3; based on ITS data). A rather conservative taxonomic conclusion from these results was drawn by Jeffrey (2007), who re-established a separate tribe Gundelieae near to Cichorieae to include both genera. Formerly *Gundelia* had been associated with Arctotideae and *Warionia* with Mutisieae.

Our new molecular-based analyses using the nuclear ITS and the plastid *matK* region with a much larger dataset (including 428 taxa belonging to 83 genera), and especially the inclusion of several basally branching taxa in the analyses, revealed that both genera cluster within Cichorieae, which now are monophyletic, statistically supported by 100% bootstrap value and 1.0 posterior probability. *Gundelia* clusters with *Catananche*, *Hymenonema*, and *Scolymus* (Gemeinholzer et al., in prep.) in Scolyminae, however, only supported by posterior probability (1.0). The monospecific *Warionia*, with densely pilose achenes (rare in Cichorieae but also occuring, e.g., in many species of *Scorzonera*), is branching off basally and is found to be the sister group to all Cichorieae (*Gundelia* included). For *Warionia* a new subtribe of its own is established (see Appendix 24.1). These results do not contradict earlier studies (Karis et al. 2001; Funk et al. 2004) but reveal the closer relationship of both genera to Cichorieae than to any other tribe, which therefore justifies the treatment presented here.

For outgroup selection an alignment comprising the ITS region of 214 Cichorieae taxa and 103 GenBank sequences of potential outgroup taxa was analyzed (Arctotideae 37 sequences, Gnaphalieae 36, Inuleae [incl. Plucheeae] 14, Liabeae 5, Carduoideae 4, Barnadesioideae 2, Mutisieae 2, Vernonieae 2, Anthemideae 1). Statistical support for the monophyly of Cichorieae including *Warionia* and *Gundelia* was strong, supporting the statement of Goertzen et al. (2003) that a key factor for a successful ITS alignment is the large sample of sequences included. The same ingroup branching pattern within Cichorieae was also revealed with a reduced outgroup selection to nine taxa comprising *Brachylaena discolor* DC. AY826236, *Cardopatium corymbosum* Pers. AY826238, *Ericentrodea corazonensis* S.F. Blake & Sherff AY429088, *Ericentrodea decomposita* S.F. Blake & Sherff AY429089, *Heterolepis aliena* Druce AY504700, *Geigeria ornativa* O. Hoffm. U84774, *Oldenburgia intermedia* Bond AY826303, *Pluchea indica* (L.) Less. AF430795, and *Saussurea maximowiczii* Herder AY826324. Further reduction of outgroup taxa or selection of only the nearest neighbors (as shown by Karis et al. 2001 and Panero and Funk 2002 for cpDNA-analyses) resulted in unresolved branching patterns, provided unstable tree topologies, and/or changed the ingroup relationships considerably.

PHYLOGENY

The major clades within Cichorieae and the recognition of subtribes

Recent molecular analyses of a large dataset (428 taxa of 83 genera) of Cichorieae (Gemeinholzer et al., in prep.) revealed the existence of five major clades, with a total of eleven subclades, within the tribe (Fig. 24.1).

The first three main clades branching off basally are in general not very species-rich. Clade 1 is sister group to the remainder and includes solely *Warionia* (Clade 1, recognized as a new subtribe Warioniinae; see Appendix 24.1). Clade 2 represents the subtribe Scorzonerinae, which is statistically well supported and sister to clades 3–5. Clade 3 represents the subtribe Scolyminae, which is sister group to clades 4–5 (Fig. 24.1). The monophyly of Scolyminae is supported by a posterior probability of 1.0 but features no bootstrap support and comprises the former subtribe Catananchinae (Bremer 1994; Lack 2007). The remaining two large clades 4 (Fig. 24.2) and 5 (Fig. 24.3) comprise roughly 80% of the species (microspecies not considered) of the tribe. Clade 4 includes the subtribes Chondrillinae, Crepidinae, Hyoseridinae, Hypochaeridinae, and Lactucinae. Clade 5 includes the subtribes Cichoriinae, Hieraciinae, and Microseridinae s.l.

Clade 1. — The monospecific genus *Warionia* is the only member of Clade 1, Warioniinae (Fig. 24.1). *Warionia* is closer to Cichorieae than to any other tribe of Compositae according to molecular and morphological characters, but it is so distinct from all other genera within the tribe that it requires a separate subtribe Warioniinae. *Warionia* is endemic to SE Morocco and NW Algeria. The genus and subtribe is characterized by a frutescent habit, latex, essential oils, the presence of both oil ducts and latex canals in the roots (Augier and Mérac 1951; Carlquist 1976: 481; Ramaut et al. 1985), homogamous capitula with slightly zygomorphic 5-dentate, tubular, yellow flowers with 10 corolla bundles (see Morphology and anatomy below), densely pilose achenes with a pappus of coarse, scabrid bristles, and a basic chromosome number of $x = 17$ (Reese 1957; Humphries et al. 1978; Oberprieler and Vogt 1993).

Clade 2. — Scorzonerinae (Fig. 24.1) form a well-supported clade in all phylogenetic analyses of the tribe based on morphological (Bremer 1994) and molecular data (Mavrodiev et al. 2004; Gemeinholzer et al., in prep.). The molecular data with high statistical support of monophyly confirm its recognition as subtribe Scorzonerinae in its traditional morphological characterization and circumscription (Stebbins 1953, but lacking *Koelpinia*; Blackmore 1981; Bremer 1994; Lack 2007). Scorzonerinae are characterized by predominantly linear-lanceolate and parallel-veined leaves, an indumentum being soft or absent, uni- to multiseriate involucral bracts,

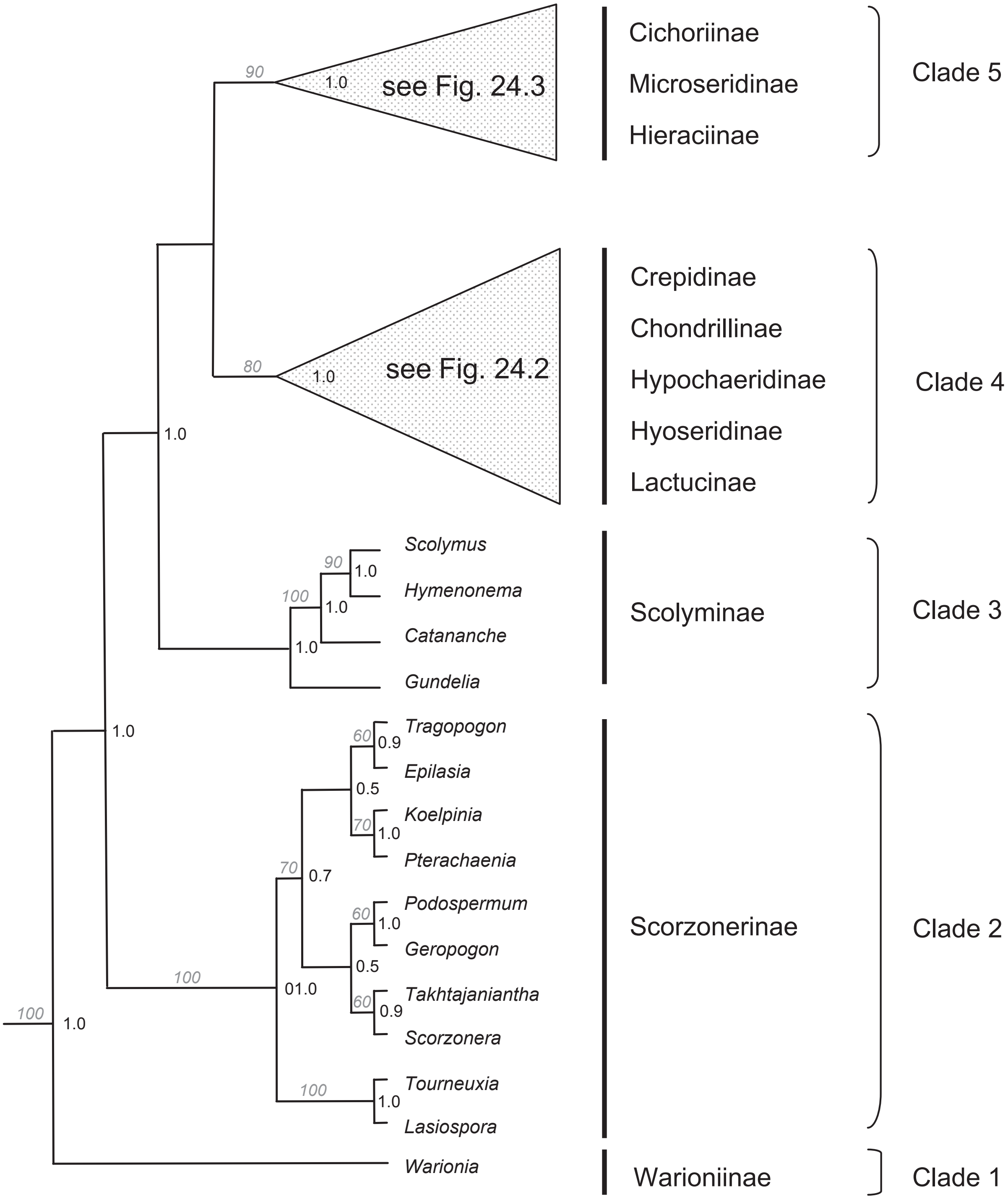

Fig. 24.1. Scheme of the molecular phylogeny of Cichorieae based on the nuclear ITS region (ITS1, 5.8S rDNA, ITS2) presenting the relationships of Cichorieae as well as within clades 1–3. Clades 4 and 5 (triangles within the tree) are only schematic here; relationships within these clades are presented in Figs. 24.2 and 24.3. This scheme, as well as the ones in Figs. 24.2 and 24.3, are inferred from majority consensus phylograms of partitioned Bayesian analyses (Ronquist and Huelsenbeck 2003) calculated on a GRID network (4 × 4 independent unlinked chains, all model parameters being unlinked, gamma distribution rate variation among sites, 10 million generations of the MCMC chains, trees saved every 100 generations and burn-in of the first 2500 trees). Numbers at branch nodes represent posterior probabilities. The topology is in large part congruent to the calculated MP analysis with 1000 bootstrap replicates (not shown), branches statistically supported <50% are depicted in italics along the branches. Only genera for which molecular data are available are presented here.

plumose pappus rays with soft pinnulae, and distinct types of echinolophate pollen (with equatorial ridges replaced by a lacuna, the aperture being divided into two lacunae, and with a characteristic exine stratification). If the pappus is absent as in *Koelpinia*, the characteristic pollen type of this alliance still allows unequivocal placement (Blackmore 1981).

Generic delimitation within the subtribe has been controversial, mainly regarding the circumscription of *Scorzonera* and the recognition of the segregates *Epilasia*, *Podospermum*, *Pterachaenia*, *Takhtajaniantha*, and *Tourneuxia*. A recent molecular phylogeny of the subtribe by Mavrodiev et al. (2004) confirmed the polyphyly of *Scorzonera* and provided support for recognition of the aforementioned segregates as well as for the separation of *Geropogon* from *Tragopogon*. Further molecular analyses of the subtribe (Gemeinholzer et al., in prep.), including more sequences from the core of *Scorzonera*, revealed paraphyletic groupings even within *Scorzonera* s.str. (Mavrodiev et al. 2004). However, due to the yet incomplete taxon sampling, the paraphyletic status of *Scorzonera* is presented here (see Appendix 24.1) without a revised taxonomic treatment, as this is still subject to ongoing studies (Gemeinholzer et al., in prep.).

Clade 3. — Within Scolyminae (Fig. 24.1), *Catananche* is sister group to *Hymenonema* and *Scolymus*. *Gundelia* is sister group to this monophyletic group with high posterior probability (1.0), however, with no bootstrap support (for discussion see Circumscription of Cichorieae, above). *Rothmaleria* formerly has also been associated with the first three genera for palynological reasons (Blackmore 1981) and has been placed together with *Catananche* and *Hymenonema* in a separate subtribe (or informal entity, respectively; Jeffrey 1966; Bremer 1994; Lack 2007). According to our molecular data, *Rothmaleria* is not related to *Catananche* and *Hymenonema* but to *Tolpis* as Stebbins (1953) and Jeffrey (1966) already assumed from morphological data.

Morphologically clade 3 is characterized by an annual or perennial life form, entire to pinnatifid-pinnatisect or coarsely lobed-pinnatisect, spiny leaves, receptacular scales or bristles, and the pappus being either absent or of denticulate-fimbriate scabrid bristles or lanceolate scales. Both *Gundelia* and *Scolymus* are laticiferous spiny leafy herbs with sessile capitula or syncalathia, respectively.

Clade 4. — This clade (Fig. 24.2) is by far the largest, with about 900 species or roughly 2/3 of the entire tribe (microspecies not considered). Its monophyly is supported by bootstrap value (80) and posterior probability (1.0). In all of our analyses of this clade, five subclades, although with weak support, can be delimited. However, there is little resolution of relationships among most major lineages within clade 4 for parsimony and Bayesian analyses, although not as result of an overall lack of resolution, but due to the uncertain placement of only few genera (e.g., *Phitosia*, *Prenanthes*, and *Urospermum*). The analyzed nuclear and plastid markers of these genera reflect different phylogenetic relationships, perhaps pointing to hybridization across lineages, possibly with former chloroplast capture and backcrossing to one parent. This might explain the overall weak support of the lineages within this clade. However, it could also be due to rapid diversification. As nuclear markers in general better resemble morphological characters, and as additional evidences for the placement of the uncertain genera are supported by morphological characteristics, we decided on the group delimitations featured in Fig. 24.2.

Subclade 4-1. The Lactucinae subclade as found in our analyses deviates considerably from the subtribe Lactucinae as previously circumscribed by Bremer (1994) and Lack (2007), which has been revealed to be polyphyletic. In the cladogram presented in Fig. 24.2 the Lactucinae are monophyletic and received bootstrap support of 80% and 1.0 posterior probability.

The delimitation of *Prenanthes* from *Lactuca* has puzzled generations of botanists, but the former is not a member of Lactucinae. In fact *Prenanthes* s.l. has been a dustbin for a number of totally unrelated elements with a combination of plesiomorphic characters. Re-circumscription on the basis of morphological data has been recently attempted by Shih (1987), who not only re-established *Nabalus* Cass. for chiefly the North American members but also removed East Asian species from *Prenanthes* and placed them in the new genus *Notoseris* on the basis of morphological analyses. Sennikov (2000) and Sennikov and Illarionova (2000) morphologically further narrowed down the circumscription of *Prenanthes*. Sennikov and Illarionova (2001), however, returned to the former, very wide circumscription of *Prenanthes*, giving the similar achene anatomy of all *Prenanthes* segregates. Our molecular phylogenies based on both nuclear and plastid markers confirm a very narrow circumscription of *Prenanthes* (perhaps being even monospecific), which, however, is not part of Lactucinae. *Prenanthes* species of the former circumscription now belong in large part to the subtribe Crepidinae (see *Nabalus*), minor parts to genera of Lactucinae (*Cicerbita*, *Lactuca* s.l., *Notoseris*) and Cichoriinae (see *Erythroseris*), which is supported by the nuclear and plastid phylogenies. For *Prenanthes* s.str. the molecular data revealed a surprising affinity to Hypochaeridinae for the nuclear marker, but in the chloroplast analysis (not presented here) it appeared to branch off basally to Lactucinae with very low posterior probability (0.50). The deviating molecular patterns of markers from different origin most likely reflect ancient hybridization with other members of the tribe, but further investigations are needed to find parental relationships.

Syncalathium, included into Lactucinae by Bremer (1994) and Lack (2007), is diphyletic according to the

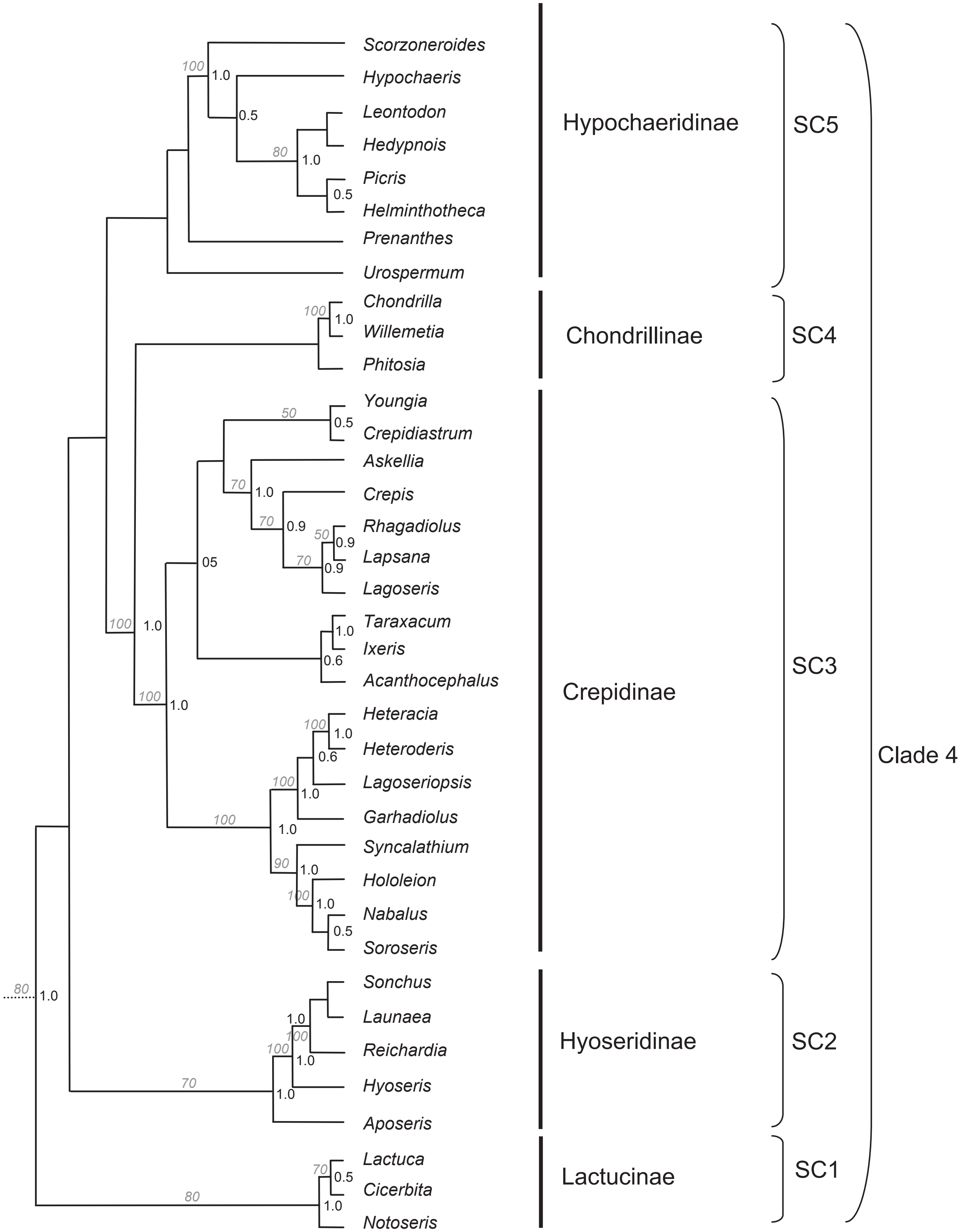

Fig. 24.2. Clade 4 as scheme of the molecular phylogeny of Cichorieae based on the nuclear ITS region (for details see legend in Fig. 24.1). SC = subclade; clades and subclades correspond to descriptions in section Phylogeny.

molecular phylogenies (Gemeinholzer et al., in prep.). The larger group of species has 5-ribbed achenes, includes *S. disciforme* (Mattf.) Y. Ling, *S. porphyreum* (C. Marquand & Airy Shaw) Y. Ling, and *S. kawaguchii* (Kitam.) Y. Ling (= *S. sukaczevii* Lipsch, providing the type of the genus name) and belongs to Crepidinae with a relationship to *Nabalus* and *Soroseris* (Fig. 24.2). The other part of the genus, represented by *S. souliei* (Franch.) Y. Ling, has achenes with one rib on either side, and belongs in Lactucinae close to *Notoseris*. This finding has also been corroborated by a recent karyological study (Zhang et al. 2007), where *S. souliei* was found to have the same chromosome number ($2n = 16$) as *Syncalathium* s.str. (represented by *S. kawaguchii*) and *Soroseris*, but with a karyotype formula quite different from them. Blackmore and Persson (1996), who included *S. porphyreum* in their palynological studies and phylogenetic analysis based on morphological data, also found an affinity with Crepidinae and not with Lactucinae, but revealed a relationship with *Ixeris* and *Youngia* rather than with *Soroseris*.

What remains in the subtribe Lactucinae is a morphologically rather diverse alliance, in which the morphological delimitation of natural entities at generic rank has posed almost insolvable problems. A key issue is the circumscription of *Lactuca*, as has already been discussed by Koopman et al. (1998), who provided an initial molecular study. Combined molecular-morphological analyses by Kilian and Gemeinholzer (in prep.) on the basis of a much enlarged sample will provide a new approach of generic subdivision of the *Lactuca* alliance; however current results provide only a preliminary taxonomy.

Subclade 4-2. This subclade comprises a re-circumscribed subtribe Sonchinae, to be named Hyoseridinae. In the cladogram presented in Fig. 24.2, subclade 2 is sister group to subclades 3–5, with monophyly supported by bootstrap values of 70% only and posterior probability of 1.0. As already stated earlier (Kim et al. 1996, 1997, 1999a, b, 2004, 2007), Bremer's (1994) subtribe Sonchinae needs to include *Dendroseris* to become monophyletic, a solution also favored by Lack (2007). Meanwhile the inclusion of the monospecific, less known genus *Thamnoseris*, which has been closely associated to *Dendroseris* (Jeffrey 1966; Bremer 1994; Lack 2007), has been confirmed by molecular analysis (Kim, pers. comm., March 2007).

The core of the subtribe consists of the *Sonchus*-*Launaea* alliance including *Reichardia*, with a monophyly supported by 100% bootstrap value and 1.0 posterior probability. The recently described Central Asian monospecific genus *Hexinia* has been placed within *Launaea* by Kilian (1997) based on morphological evidences, which are confirmed by molecular data (Kilian, in prep.). The various species-poor genera, established within the *Sonchus* alliance on often vague morphological grounds for species of the Canary Islands (*Chrysoprenanthes*, *Babcockia*, *Lactucosonchus*, *Sventenia*, *Taeckholmia*, *Wildpretia*) and of Australia/New Zealand (*Actites*, *Embergeria*, *Kirkianella*), were placed within *Sonchus* in all recent molecular studies (Kim et al. 1996, 1997, 1999a, b, 2004, 2007). The same has been confirmed for the monospecific Mediterranean *Aetheorhiza* as well as for *Dendroseris* and *Thamnoseris*, which are endemic to the Pacific Juan Fernández and Desventuradas Islands off the coast of Chile (Kim et al. 2007; S.-C. Kim, pers. comm., March 2007). A reconsideration of *Sonchus* s.l., aiming at recognition of monophyletic, morphologically delimited entities at generic or subgeneric rank, is in preparation by Kim and Mejías (pers. comm., March 2007).

Our own recent results (Gemeinholzer et al., in prep. and see Fig. 24.2) revealed also that *Aposeris* and *Hyoseris* have to be included in Sonchinae. Blackmore (1981) stated that the palynological evidence is inconclusive for the placement of *Hyoseris*, reflecting a possible relationship to the *Hypochaeris* alliance as likely as to the *Sonchus*-*Launaea* alliance. The placement of *Hyoseris* along with *Aposeris* within the *Hypochaeris* alliance was chosen by Jeffrey (1966), Bremer (1994), and Lack (2007). In contrast, molecular data revealed that neither species is related to the *Hypochaeris* alliance (Samuel et al. 2003) but form a sister group relationship to the *Sonchus*-*Launaea* alliance (Gemeinholzer et al., in prep.; Kim, unpub., pers. comm., March 2007). *Aposeris*, lacking a pappus, is sister to all other genera of this subtribe, which are rather closely related to each other, while *Hyoseris*, with an inner pappus of basally strongly widened bristles, is sister group to the clade including the *Sonchus*-*Launaea* alliance. Inclusion of *Hyoseris* unfortunately requires a change of name of the subtribe from Sonchinae to Hyoseridinae because of priority.

Subclade 4-3. Here redefined Crepidinae (Fig. 24.2 and Appendix 24.1) are monophyletic with high statistical support (bootstrap value 100%, posterior probability 1.0). They comprise two subclades (Fig. 24.2). The first subclade is predominantly Asian, with *Heteracia* and *Heteroderis* as sister groups (bootstrap value 100% and posterior probability 1.0) sharing a common ancestor with *Lagoseriopsis* (0.6 posterior probability), and all three being sister group to *Garhadiolus* (bootstrap value 100% and posterior probability 1.0). The sister group to these four genera comprises *Nabalus* and *Soroseris* sharing a common ancestor with *Hololeion* (bootstrap value 100% and posterior probability 1.0) and all three being sister to *Syncalathium* (bootstrap value 90% and posterior probability 1.0). The second subclade comprises predominantly Eurasian taxa: here newly included *Lapsana* and *Rhagadiolus* (monophyly with 50% bootstrap value and 0.9 posterior probability) are sister group to *Lagoseris* (70% bootstrap value and 0.9 posterior probability) in a monophyletic group with *Crepis* (70% bootstrap value and 0.9 posterior probability). The genus *Askellia* has been separated from *Crepis* and is basal to those four genera and forms a sister group relationship to *Crepidiastrum* and *Youngia* with bootstrap value of 70% and 1.0 posterior probability. The other branch of this second subclade comprises *Taraxacum* next to *Ixeris* featuring a common ancestor with *Acanthocephalus* (posterior probability 0.6). The phylogenetic relationships of *Dubyaea*, *Ixeridium*, and *Lapsanastrum* are yet uncertain.

With ca. 360 species (the *Taraxacum* microspecies not counted), comprising 2/5 of the species of clade 3 and more than 1/4 of the tribe, the subtribe Crepidinae is the largest of Cichorieae. We mentioned the removal of the *Chondrilla* alliance as a separate subtribe and the addition of *Nabalus* and *Syncalathium* formerly placed into Lactucinae. Molecular analyses (Whitton et al. 1995; Gemeinholzer et al., in prep.) show that the genera *Garhadiolus* and *Rhagadiolus* formerly placed in subtribe Hypochaeridinae (Bremer 1994; Lack 2007), and *Hololeion* formerly placed in subtribe Hieraciinae (Bremer 1994; Lack 2007), belong to Crepidinae. The recognition of *Nabalus* as a genus separate from *Prenanthes*, including all North American and several Central and East Asian members of the latter genus, as suggested by our analysis, confirms Stebbins (1940: 63). He concluded from studies of the achene vascularization that the species of *Nabalus* are much closer to *Dubyaea* and *Soroseris* than to *Prenanthes purpurea*, which provides the type of *Prenanthes*. The previously assumed placement of the little known monospecific genera *Dianthoseris* and *Lagoseriopsis* in Crepidinae (Bremer 1994; Lack 2007) has been confirmed by our molecular analyses (Fig. 24.2; Gemeinholzer et al., in prep.), *Dianthoseris*, however, has been found to be a congener of *Crepis*, see below.

The relationship of *Syncalathium* (s.str., compare subclade 1, above) with *Nabalus* and *Soroseris* revealed in our analyses has 1.0 posterior probability and 90% bootstrap value.

Our molecular analyses (Fig. 24.2; Gemeinholzer et al., in prep.) revealed *Crepis* sensu Babcock to be polyphyletic. Several *Crepis* species (e.g., *C. bupleurifolia* (Boiss. & Kotschy) Freyn & Slint., *C. elymaitica* Bornm.) are of uncertain position within Crepidinae and will have to be tested against a greater sampling of species in the subtribe and morphologically investigated to assign their definitive status. *Crepis* species from Babcock's sections *Intybellia*, *Lagoseris*, *Microcephalum*, *Phaecasium*, and *Pterotheca* cluster in the nuclear and plastid analyses in a monophyletic group as sister group to *Lapsana* and *Rhagadiolus* (Enke and Gemeinholzer 2008). To make *Crepis* monophyletic, this would either necessitate recognition of *Lagoseris* as a separate genus in the tradition of Bobrov and Tzvelev (1964), or inclusion of *Lapsana* and *Rhagadiolus* in *Crepis*. *Lagoseris* differs distinctly from the latter two genera in fruit morphology, but the absence of a pappus in *Lapsana* and *Rhagadiolus* is not regarded as decisive, since a loss of pappus occurs also in *Crepis*. The achenes of *Lapsana* are strongly compressed and the achenes of *Rhagadiolus* are presented in a star-like way; neither of these forms is known from *Crepis* s.l. *Lapsana* is traditionally considered to be closely related to *Crepis*, both belonging to the *Ixeris*-*Youngia* line (Stebbins 1953), the *Crepis* series (Jeffrey 1966) and Crepidinae (Bremer 1994). After separation of the former East Asian members from *Lapsana* as the new genus *Lapsanastrum* by Pak and Bremer (1995) for chiefly carpological reasons, *Lapsana* is monospecific (only comprising *L. communis* L.), which is supported by our molecular results.

The Central Asian and North American species of *Crepis* sect. *Ixeridopsis* are clearly isolated from *Crepis* s.str. and have been transferred to *Askellia* based on morphological dissimilarities in overall habit, involucral shape and flower number per capitulum as well as on molecular, cytological and biogeographical data (Sennikov and Illarionova 2007; Enke and Gemeinholzer, in press). *Askellia* clusters as sister group to the clade comprising *Crepis* s.str., *Lagoseris*, *Lapsana*, and *Rhagadiolus* on one branch, and *Ixeridium*, *Ixeris*, *Paraixeris*, *Taraxacum*, and *Youngia* on the other branch. Babcock (1947) already recognized the intermediate position of *Askellia* between *Crepis* and *Ixeris*, even though most of the species (e.g., *A. nana*, *A. flexuosa*) used to be treated under *Youngia* to which they were recently reassigned (Adylov and Zuckerwanik 1993). However, *Askellia* features terete achenes and a basic chromosome number of $x = 7$ (otherwise not present in *Crepis*), while the achenes of *Youngia* are compressed and angular and the chromosome number is $x = 8$. Other members of Crepidinae, e.g., *Ixeridium* (Pak and Kawano 1992), even though having a basic chromosome number of $x = 7$ such as *Askellia*, differ by their fusiform and flattened achenes. *Ixeris* is, in achene morphology, similar to *Ixeridium* and differs from *Askellia* in chromosome number and number of flowers per capitulum, which are both higher in *Ixeris*, confirming the close relationship of *Ixeridium*, *Ixeris*, and *Youngia*, a clade to which also *Paraixeris* and *Taraxacum* have to be added, based on molecular evidence, achene morphology, and base chromosome number range of $x = 8, 7, 6, 5$.

The monospecific afroalpine *Dianthoseris*, according to Blackmore and Persson (1996) with distinct pollen characteristics (subechinolophate pollen grains with rudimentary paraporal lacunae, rounded abporal lacunae) more similar to *Dubyaea* and *Soroseris* than to *Crepis* (echinolophate pollen grains, tricolporate, ectocolpi divided into three lacunae, somewhat angular, large abporal lacunae), is nested in our analyses right within *Crepis* s.str. (Enke et al. 2008; Gemeinholzer et al., in prep.).

Subclade 4-4. This subclade is not statistically supported, but is recognized by us as subtribe Chondrillinae comprising the genera *Chondrilla*, *Phitosia*, and *Willemetia*. The former two genera have been hitherto treated as members of subtribe Crepidinae (Bremer 1994; Lack 2007).

Chondrillinae (subclade 4) and Crepidinae (subclade 3) form a monophyletic group of 100% bootstrap value and posterior probability of 1.0 (Fig. 24.2). Since the sister group relationship of Crepidinae and Chondrillinae presented here has been proven less stable when combining different molecular datasets (*matK* and ITS; Gemeinholzer et al., in prep.), we have refrained from treating subclades 3 and 4 as a single subtribe Crepidinae. Next to *Chondrilla* and *Willemetia*, the third genus in subclade Chondrillinae is *Phitosia*, a monospecific genus recently established for a species removed from *Crepis* for cytological and carpological reasons (Kamari and Greuter 2000).

Subclade 4-5. This subclade comprises subtribe Hypochaeridinae in the sense of Bremer (1994) and Lack (2007) but excluded are *(1) Aposeris* and *Hyoseris*, which group with the *Sonchus-Launaea-Reichardia* alliance (subtribe Hyoseridinae), *(2) Garhadiolus* and *Rhagadiolus* (subtribe Crepidinae), and *(3) Arnoseris* (its relationship to the *Tolpis* alliance rather than to the *Hypochaeris* alliance is confirmed; see Cichoriinae).

The core of this subtribe (0.5 posterior probability) is formed by the *Hypochaeris-Leontodon-Picris* alliance (Fig. 24.2). Its relationship has been well resolved in a number of molecular studies (e.g., Samuel et al. 2006). *Hypochaeris*, which has a curious disjunct distribution with ca. twelve species in the Mediterranean and Europe, one species in Asia and forty species in South America (Cerbah et al. 1999), is monophyletic and has colonized South America apparently via long-distance dispersal (Samuel et al. 2003; Weiss-Schneeweiss et al. 2003, 2008; Tremetsberger et al. 2005). *Hedypnois*, the only genus in this alliance with a scabrid instead of plumose pappus, is nested right within the alliance (Samuel et al. 2006), indicating a reverse development of the plumose pappus, which is plesiomorphic in Cichorieae, back to a scabrid pappus. *Picris* and the closely related *Helminthotheca* are both monophyletic, whereas *Leontodon* in its current circumscription is diphyletic (Samuel et al. 2006), which necessitates recognition of *L.* subg. *Oporinia* as separate genus *Scorzoneroides* (Greuter et al. 2006).

Prenanthes purpurea L. (providing the type of the name *Prenanthes*) and *Urospermum* are included in subclade 5, but statistical support is missing most likely as result of ancient hybridization across lineage resulting in intermediate positions: *P. purpurea* is sister group to core Hypochaeridinae and *Urospermum* sister group to the latter two. In case of the bispecific *Urospermum*, this result is not unexpected, since the predominantly Mediterranean *Urospermum* with its plumose *Hypochaeris* type pappus, the hispid indumentum, and a pollen type very similar to *Hypochaeris* and *Picris* (Lack and Leuenberger 1979) has in spite of the uniseriate, basally connate involucre and its unique achenes, unequivocally been placed into Hypochaeridinae since Hoffmann (1890–1894). In contrast, *Prenanthes* has never been associated with Hypochaeridinae, and morphology does not provide any support for this placement. Reticulate hybridization events with one parent from Hypochaeridinae and the other from Crepidinae or some other members within clade 4 could be possible explanations for the statistically uncertain placement of the genus. At present we provisionally place it within Hypochaeridinae to which it most commonly clusters based upon our molecular results, but further investigations reassessing its phylogeny are needed. The chloroplast marker (*matK*) indicates a basal branching position within Lactucinae.

Clade 5. — The monophyly of this clade is statistically supported by bootstrap value of 90% and posterior probability of 1.0. Within this clade three monophyletic groups can be detected. Hieraciinae are sister to a clade including *(1)* the principally North American genera plus the South American *Picrosia* (Microseridinae), and *(2)* Cichoriinae (Fig. 24.3).

Subclade 5-1. Hieraciinae (bootstrap value 100% and posterior probability 1.0) represent the subtribe in the circumscription of Lack (2007) but without *Tolpis*, which clusters with *Cichorium*, and without *Hololeion*, which according to our analysis is a member of Crepidinae. *Hololeion*, with a basic chromosome number of $x = 8$, was odd within the subtribe as otherwise all taxa feature a basic chromosome number of $x = 9$. With its exclusion, the basic number of $x = 9$ is characteristic for the subtribe. Hieraciinae sensu Bremer (1994) also included *Arnoseris*, a genus that Lack (2007) placed into Hypochaeridinae, but which clusters in our analysis (Gemeinholzer et al., in prep.) with *Cichorium*, too. *Hieracium intybaceum* Lam., which is restricted to the siliceous Alps, was separated in the 19th century as the genus *Schlagintweitia*, which is in our analyses (Fehrer et al. 2007; Gemeinholzer et al., in prep.) sister to the rest of the alliance, comprising *Andryala*, *Hieracium*, *Hispidella*, and *Pilosella* (bootstrap value 80% and posterior probability 1.0; see Fig. 24.3). This result necessitates the re-establishment of *Schlagintweitia* as a segregate of *Hieracium*, with which, however, it produces fertile hybrids (C. Zidorn, pers. comm., May 2007). Intergeneric hybridization within Hieraciinae resulting in cytoplasmic inheritance has also been reported in earlier studies, e.g., from *Hieracium* subg. *Chionoracium* to *Pilosella* and from the introgressed *Pilosella* lineage to *Andryala* (Fehrer et al. 2007), and has been revealed by incongruent topologies of nuclear and chloroplast analyses inferred from chloroplast (*trnT-trnL*, *matK*) and nuclear (ITS) sequence data. In general, the ITS data analysis is in accordance with morphological and other evidence and, therefore, is assumed to reflect species relationships. Hereby, a sister group relationship between *Pilosella* and *Hispidella* (bootstrap value 80% and posterior probability 1.0) and a joint clade of these and

Hieracium (*H.* subg. *Hieracium* and *H.* subg. *Chionoracium* [= *Stenotheca*]) (100% bootstrap value and 0.7 posterior probability) is revealed (Fig. 24.3). *Andryala* represents a third major lineage of the clade including *Pilosella*, *Hispidella*, and *Hieracium*, which has 80% bootstrap support and 1.0 posterior probability.

Subclade 5-2. Sister group to Hieraciinae is a clade supported by posterior probability of 0.7 (Fig. 24.3), which includes the North American genera plus the South American *Picrosia* in one clade (bootstrap value of 80% and posterior probability of 0.8 support the monophyly) and Old World Cichorieae in a second clade sister

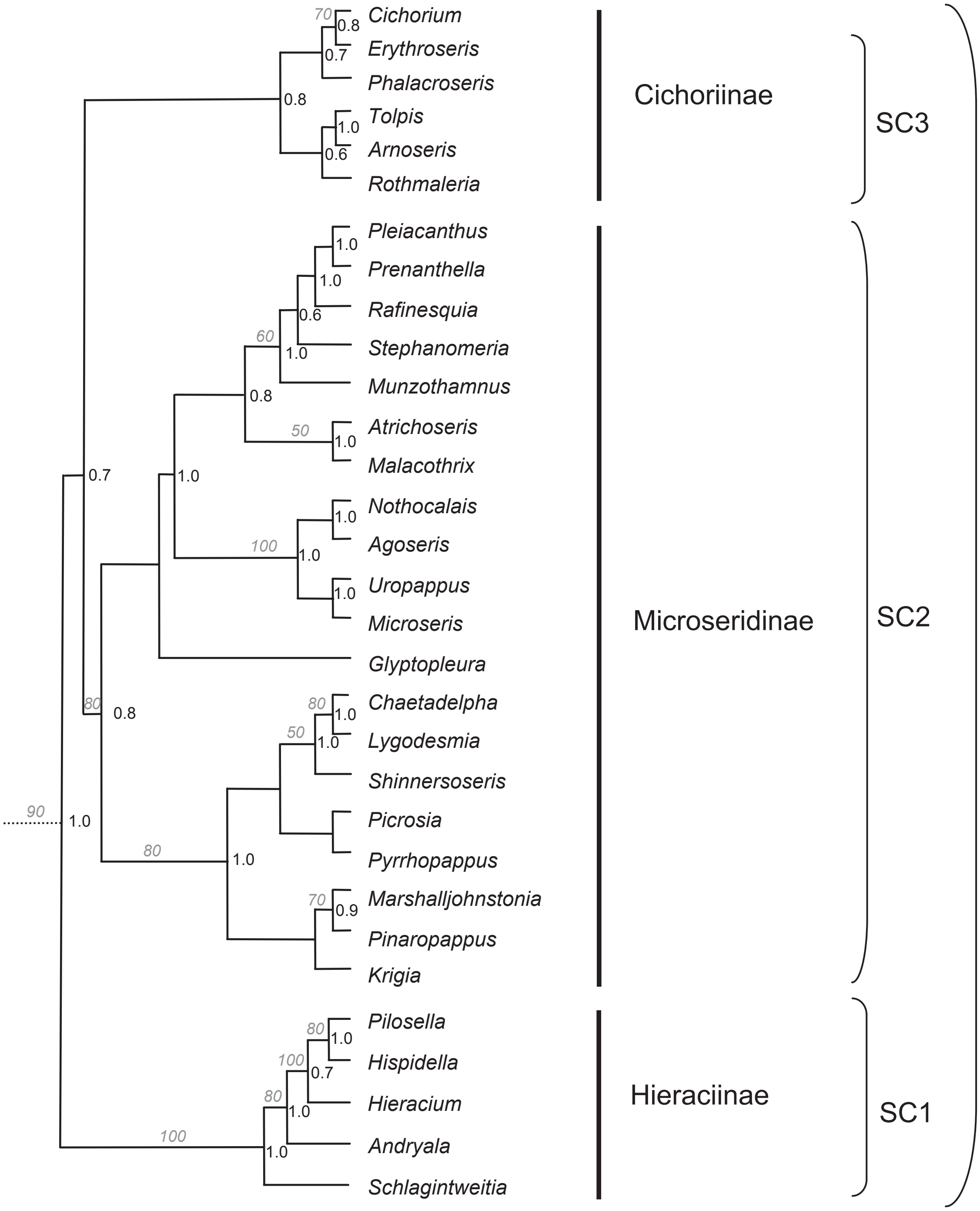

Fig. 24.3. Clade 5 as scheme of the molecular phylogeny of Cichorieae based on the nuclear ITS region (for details see legend in Fig. 24.1). SC = subclade; clades and subclades correspond to descriptions in section Phylogeny.

to the former (0.8 posterior probability). The radiation of the principal American Cichorieae genera from a single common ancestor as found by Lee et al. (2003) has been confirmed by our analyses of a much larger dataset, in which the sequences of the American clade by these authors were included, with the odd exception of *Phalacroseris*. This monospecific localized NW American genus, which is sister to the remainder of the American clade in the analyses by Lee et al. (2003), is nested in our analyses within Cichoriinae (Gemeinholzer et al., in prep.).

The American clade has previously been treated as two (Jeffrey 1966), three (Stebbins 1953; Bremer 1994; Lack 2007) or, based on the recent molecular evidence, as nine (Lee and Baldwin 2004) subtribes or informal entities, respectively. Apart from *Phalacroseris*, the suprageneric classification of the American clade by Lee and Baldwin (2004) best corresponds to the available datasets. It is, however, much more consistent with the phylogeny and the suprageneric classification of the entire tribe to reserve the subtribal rank for the American clade as such and to apply Lee and Baldwin's classification to a subordinate informal rank. We therefore recognize the American clade of our analyses as a single subtribe Microseridinae.

Subclade 5-3. Cichoriinae (Fig. 24.3) comprise six genera, four of which, viz. *Arnoseris*, *Cichorium*, *Rothmaleria*, and *Tolpis*, were united already by Stebbins (1953) in subtribe Cichoriinae with, however, other unrelated genera. Later classifications (Jeffrey 1966; Bremer 1994; Lack 2007) split these four elements apart. The relationship of *Arnoseris* with *Tolpis* (Stebbins 1953; Jeffrey 1966; Bremer 2004) rather than with the *Hypochaeris* alliance (Lack 2007) is morphologically supported by short style branches with short trichomes, corolla tubes covered externally with crisped trichomes, and has otherwise been supported by palynological data (Blackmore 1981) featuring small pollen grains with double rows of spines on the equatorial ridges. To these four genera our analyses added as sister group to *Cichorium* the genus *Erythroseris*, a genus most recently established for two species from the Horn of Africa and Socotra Island formerly placed in *Prenanthes* (Kilian and Gemeinholzer 2007), and the localized North-West American monospecific *Phalacroseris* (posterior probability 0.7), which features oblong-ellipsoid, unbeaked achenes and no pappus.

Monophyletic Cichoriinae (supported by posterior probability of 0.8 but no bootstrap support) are divided into two subclades (Fig. 24.3). In the first subclade (supported by posterior probability of 0.7 but no bootstrap support) *Erythroseris* is sister group to *Cichorium*, forming a monophyletic group (bootstrap value 70%, posterior probability 0.8), while *Phalacroseris* branches off basally to both. In the other subclade (being supported by posterior probability of 0.6) *Arnoseris* is sister to *Tolpis* (posterior probability of 1.0 but no bootstrap support), while *Rothmaleria* is sister group to *Arnoseris* plus *Tolpis*, which is supported by 0.6 posterior probability only. The chloroplast analyses of Whitton et al. (1995), Park et al. (2001), and Gemeinholzer et al. (in prep.) reveal *Tolpis* (and *Arnoseris*; Gemeinholzer et al., in prep.) not to cluster at all within the *Cichorium-Tolpis* clade but within clade 4. The deviating phylogenies of the nuclear and the chloroplast markers, with different underlying modes of inheritance, can only be explained by reticulate evolution with an unknown parent most likely being a precursor of one of the today's species of clade 4 preceding generic and species divergence of *Tolpis* and *Arnoseris*, resulting in subsequent chloroplast capture. All molecular analyses feature different sampling of ingroup and outgroup taxa and result in slightly different placements of *Tolpis*, which is, however, most often closely related to *Hyoseris* and *Urospermum*; this could be indicative for the former potential hybrid partners. The most comprehensive sample was carried out by Gemeinholzer et al. (in prep.), where, in contrast to Park et al. (2001), *T. staticifolia* (All.) Sch.Bip. as well as *T. capensis* (L.) Sch.Bip. cluster right within the *Tolpis* group in the nuclear as well as the chloroplast analysis, most likely as result of a broader taxa sampling size.

Two possible relationships have been suggested in the past for the monospecific SW Mediterranean genus *Rothmaleria*, namely either *Catananche* and *Hymenonema* (Jeffrey 1966; Bremer 1994; Lack 2007) or *Cichorium* (Stebbins 1953; Lack et al. 1980). The latter relationship is not only favored by our molecular results, it is also morphologically supported by similar achenes, the non-aristate paleaceous pappus, and the long collecting trichomes of the style (Lack et al. 1980).

TAXONOMY

Tribe Cichorieae Lam. & DC. (1806)

= Lactuceae Cass. (1819), Catanancheae D. Don (1829), Crepideae Lindl. (1829), Hieracieae D. Don (1829), Hypochaerideae D. Don (1829), Scorzonereae D. Don (1829), Taraxaceae D. Don (1829), Gundelieae Lecoq & Juillet (1831), Hyoserideae Kostel. (1833), Scolymeae Kostel. (1833), Chondrilleae W.D.J. Koch (1837), Leontodonteae (Sch.Bip.) W.D.J. Koch (1834), Picrideae Sch.Bip. (1834), Tragopogoneae Sch.Bip. (1834), Urospermeae Sch.Bip. (1834)

In the present treatment the tribe includes ca. 93 genera. Of these, 90 genera comprise approximately 1400 species, while 3 genera (*Hieracium*, *Pilosella*, and *Taraxacum*) have larger numbers of hybridogenous and/or apomictic species (*Hieracium*: ca. 770 sexually reproducing species + 5200 apomictic microspecies [pers. comm.

G. Gottschlich, April 2007]; *Pilosella*: ca. 110 sexually reproducing species + ca. 700 apomictic microspecies and weakly competitive hybrids [pers. comm. G. Gottschlich, April 2007]; *Taraxacum* ca. 1600 apomictic species [Sterk 1987, IPNI 2007]).

The new, revised classification of the tribe summarized here recognizes eleven subtribes based on the molecular and morphological analyses as discussed in the preceding part. Compared to the most recent treatments of the tribe by Bremer (1994) and Lack (2007), several subtribes are not maintained, two subtribes are newly recognized (Chondrillinae, Warioniinae) and the circumscription of most of the remaining ones as well as of several accepted (or provisionally accepted) genera has changed. It has thus been found appropriate to provide, in Appendix 24.1, a complete taxonomic overview of the tribe, including synonymies and type designations, to serve as a basis for further work. Generic delimitation in several cases is not yet fully settled; the number of genera may therefore still change in the future. Brief notes to the subtribes preceding the list of genera address such remaining problems in generic delimitation or classification.

MORPHOLOGY AND ANATOMY

Habit

The perennial herb, acaulescent (Fig. 24.4D, E, G) or scapose to caulescent (Fig. 24.4F), sometimes stoloniferous, represents the predominant habit of the tribe. Besides many pauciennial and annual herbs, more rarely subshrubs, (spiny) shrubs (Fig. 24.4B), rosette shrubs (Fig. 24.4A) to rosette trees (Fig. 24.4C) and, exceptionally, scandent vines occur. The available molecular phylogenies indicate that the perennial herbaceous growth is plesiomorphic in the tribe and that both the annual and frutescent habits are derived. Annual species have evolved in all subtribes (apart from monospecific Warioniinae). In general, habit types are systematically valuable only on the species level.

Frutescent growth occurs in several subtribes (Cichoriinae: *Erythroseris*, *Tolpis*; Crepidinae: *Crepis kilimandscharica*; Hyoseridinae: *Launaea*, *Reichardia*, *Sonchus*; Hypochaeridinae: *Hypochaeris oligocephala* (Svent. & Bramwell) Lack only; Lactucinae: *Lactuca* s.l.; Microseridinae: *Marshalljohnstonia*, *Munzothamnus*, *Pleiacanthus*, *Stephanomeria*; Scorzonerinae: *Scorzonera* s.l.; Warioniinae: *Warionia*). Four reasons indicate the apomorphy of the frutescent growth in the tribe: *(1)* All forms of frutescent growth in Cichorieae are modifications of the growth and function of the rosette axis (= caudex; see Babcock 1947: 43). The rosette shoot (= caudical axis with extremely reduced internodes) is either increased in its growth, lignification and its branching, leading to the growth form of the rosette shrublets, shrubs and trees (Fig. 24.4A, C). Alternatively the rosette axis is to some minor or larger extent disintegrated while lignified, leading to subshrubby to shrubby growth forms in which the long-articulate flowering stems are more or less included in the system of lignified caudical axes, present in the spinescent (Fig. 24.4B), scoparious or otherwise non-rosette subshrubs and shrubs of, e.g., *Scorzonera*, *Lactuca*, *Launaea* (Kilian 1997: 28–32). *(2)* The molecular phylogenies of Hyoseridinae (Kim et al. 1996, 1997, 1999a, b, 2004, 2007), which include the most spectacular and extensive occurrence of frutescent taxa, strongly indicate that the frutescent taxa have evolved independently at different times from herbaceous ancestors. *(3)* The frutescent growth occurs independently and is correlated with similar environmental conditions in different branches of the tribe. *(4)* The frutescent growth is restricted to *(a)* species on oceanic islands (see Carlquist 1974), mainland cliff habitats or, rarely, the tropical alpine zone (the rosette shrublets, rosette shrubs or rosette trees [Fig. 24.4C] of *Launaea*, *Reichardia*, and *Sonchus* s.l. [incl. *Dendroseris* and *Thamnoseris*], in Hyoseridinae, *Crepis kilimandscharica* O. Hoffm. in Crepidinae, *Erythroseris* and *Tolpis* in Cichoriinae) and *(b)* to semiarid, often montane environments (non-rosette shrubs: *Warionia* in Warioniinae, *Scorzonera* s.l. in Scorzonerinae, *Launaea* in Hyoseridinae, *Lactuca* in Lactucinae, *Erythroseris* in Cichoriinae, *Marshalljohnstonia*, *Munzothamnus*, *Pleiacanthus*, *Stephanomeria* in Microseridinae), which do not, as far as we known, represent the primary or original habitats of the tribe (see below).

A few species of Cichorieae are scandent vines of still unresolved relationships in the *Lactuca* alliance (subtribe Lactucinae), occurring in subtropical to temperate montane rain forests and savannahs of SE Asia (E Himalaya, SE China, Sumatra) and E Africa (Stebbins 1937b, under *Lactuca* and *Prenanthes*; Tjitrosoedirdjo 2002, under *Prenanthes*).

Underground parts

Four different types of underground parts can be distinguished but are systematically valuable only on the species level. Likely plesiomorphic is *(1)* the taproot with variously developed lateral root system. From this have evolved independently several times *(2)* the rhizome (e.g., present in Crepidinae: *Crepis* (initially assumed to be the plesiomorphic condition in the genus by Babcock, 1947: 43, later recognized as apomorphic by Babcock, 1949 and also by Enke and Gemeinholzer, 2008), *Nabalus*; Hypochaeridinae: *Leontodon*, *Prenanthes*; Microseridinae: *Chaetadelpha*, *Malacothrix*, *Microseris*, *Stephanomeria*, etc.), *(3)* the tuberous roots (e.g., Crepidinae: *Nabalus*; Hyoseridinae: *Launaea*, *Sonchus*; Hypochaeridinae: *Leontodon*; Microseridinae: *Krigia*, *Pyrrhopappus*; Scorzonerinae: *Scorzonera* s.l.), and the *(4)* shoot-bearing roots (e.g., Hyoseridinae: *Launaea*, *Sonchus*; Scorzonerinae: *Tragopogon*).

Fig. 24.4. Habits of Cichorieae species. **A** *Launaea picridioides* (Webb) Engl., cushion-forming rosette shrub, Cape Verde Isl., S. Antão; **B** *L. arborescens* (Batt.) Murb., cushion-forming shrub with spinescent synflorescences, Cape Verde Isl., Boa Vista; **C** *Sonchus arboreus* DC., rosette tree to 2 m tall, Spain, Canary Isl.; **D** *Soroseris gillii* (S. Moore) Stebbins, acaulescent perennial with syncalathium, China, Hengduanshan; **E** *Soroseris umbrella* (Franch) Stebbins, acaulescent perennial with densely tufted capitula, China, Hengduanshan; **F** *Schlagintweitia intybacea* (All.) Griseb., perennial caulescent herb, Austria, Venedigergruppe; **G** *Askellia nana* (Richardson) W.A. Weber, (sub)acaulescent perennial, Russia, Altai. [Photographs: A, B, N. Kilian; C, K. Rabe; D, E, M. Smalla; F, B. Gemeinholzer; G, N. Enke.]

Excretion organs

All members of the tribe are characterized by the presence of lactiferous canals in both the subterranean and aerial parts, being identical to those occurring in the aerial parts of Arctotideae, whereas other tribes of Cichorioideae merely have lactiferous cells (Augier and Mérat 1951; Wagenitz 1976). In addition to the lactiferous canals, only a few members of the tribe possess a system of endodermal oil ducts in their roots, which are commonly present instead of the lactiferous ducts in other tribes, especially of Asteroideae. The ducts are formed within the endodermis after cell divisions having led to a dedoublement (doubling) of the endodermis. Endodermal oil ducts containing oil have been reported from *Gundelia*, *Scolymus*, *Scorzonera* s.l., and *Warionia* (Tieghem 1872; Col 1903–04; Augier and Mérat 1951). Endodermal ducts without oil have been reported from *Tragopogon* (Tieghem 1885) and *Krigia* (Holm 1926) and dedoublement of the endodermis without formation of ducts from *Cichorium* and *Lapsana* (Tieghem 1885). According to these data, functional oil ducts occur in the three basally branching clades of the tribe, while relics of them (non-functional ducts or endodermis dedoublement) occur rarely here and there among other clades. This may be indicative for a successive reduction of the endodermal oil ducts in the phylogeny of Cichorieae.

Indumentum

Stems, leaves and involucres may be glabrous or variously covered with trichomes or bristles. No systematic survey across the tribe is available, so a few examples illustrating the range of variation may be given. Glandular trichomes, in particular on the peduncles and involucres are present, e.g., in *Crepis* (Crepidinae), *Sonchus* (Hyoseridinae), and *Schlagintweitia* (Fig. 24.4F; Hieraciinae); bristles, in particular on stems, occur, e.g., in *Crepis* (Crepidinae), *Lactuca* (Lactucinae), and *Urospermum* (Hypochaeridinae), stellate trichomes on leaves, stems and involucres occur in species of *Leontodon* and *Scorzoneroides* and rigid anchor-shaped trichomes are diagnostic for *Picris* (Fig. 24.5C, Hypochaeridinae). A tomentose indumentum of simple trichomes occurs, e.g., in species of *Scorzonera* s.l. (Scorzonerinae) and is characteristic for the peduncle and basal involucre of many *Sonchus* species (Hyoseridinae). Woolly leaf axils occur, e.g., in species of *Erythroseris* (Cichoriinae), *Launaea*, and *Sonchus* (Hyoseridinae). In general, indumentum types are systematically valuable at infrageneric or specific level, and more rarely, e.g., in Hypochaeridinae (*Leontodon*, *Scorzoneroides*: see Pittoni 1973; Widder 1975; Greuter et al. 2006; *Picris*: see Lack 1975), at generic level.

Leaves

The leaves are rosulate and/or alternate (as an exception in *Shinnersoseris* the lower leaves are opposite), usually sessile (petiolate in *Sonchus* p.p. [*Dendroseris*]) and often clasping the stem, sometimes decurrent (extremely so in some species of *Lactuca* and *Scolymus*), entire to dentate or pinnatisect. As exceptions, peltate leaves occur in one of the montane scandent vines of Lactucinae (Stebbins 1937b; Ebel 1998), grasslike and parallel-veined leaves occur in some *Scorzonera* s.l. and *Tragopogon* (Scorzonerinae), and spinose leaves in *Gundelia* and *Scolymus* (Scolyminae). Apart from these exceptions, leaf shape is systematically valuable only at the species level.

Synflorescence

The capitula are variously arranged in monopodial to (partly) sympodial synflorescences containing few to very many capitula. More rarely, the capitula are borne singly on scapes (Cichoriinae: *Phalacroseris*, *Rothmaleria*; Crepidinae: *Dubyaea* p.p., *Taraxacum*; Hieraciinae: *Pilosella* p.p.; Hyoseridinae: *Hyoseris*, *Sonchus* p.p.; Hypochaeridinae: *Hedypnois*, *Hypochaeris* p.p., *Leontodon* p.p., *Scorzoneroides* p.p.; Microseridinae: *Agoseris*, *Anisocoma*, *Nothocalais*; Scorzonerinae: *Pterachaenia*). Morphological transitions to synflorescences with few capitula exist (e.g., Cichoriinae: *Arnoseris*; Hypochaeridinae: *Leontodon* p.p., *Scorzoneroides* p.p.; Microseridinae: *Pinaropappus*, *Pyrrhopappus*). It has been hypothesized by Stebbins (1974: 188) that the scapose synflorescence of *Nothocalais* (sub *Microseris*) and *Agoseris* may have evolved in response to a short growing season from branched synflorescences in the *Microseris* alliance, which is basically in line with the molecular analyses by Lee et al. (2003). The molecular analyses of the latter authors indicate that scapose synflorescences have evolved only once in the *Microseris* alliance, since *Agoseris* and *Nothocalais* form a distinct clade sister to the rest of the alliance. Within the subtribe Microseridinae the scapose synflorescence has evolved independently a second time in the *Malacothrix* alliance with *Anisocoma*. As it is evident from the list of scapose taxa given above, similar trends have occurred in most other subtribes, too.

Aggregation of the capitula by reduction of both synflorescence axes and peduncles to a secondary capitulum (= syncalathium) surrounded by leaves or bracts has, apparently independently, evolved in a few genera in alpine habitats (Crepidinae: *Soroseris*, *Syncalathium*; Lactucinae: *Lactuca* s.l.; see Fig. 24.4D). Densely tufted capitula, occurring in acaulescent taxa in both alpine and savannah habitats (e.g., Crepidinae: *Dubyaea*, *Soroseris* [Fig. 24.4E]; Hyoseridinae: *Launaea*, *Sonchus*; Lactucinae: *Lactuca* s.l.) may be seen as morphological transitions to syncalathia. Some correlation of the aggregation of capitula with acaulescent habit and habitats in which the latter preferably have evolved is notable. Although in all those cases the individual capitula are still easily discernable within the syncalathium, another case of syncalathia is unique in the tribe: *Gundelia* (Scolyminae) possesses syncalathia in which usually six one-flowered capitula (with much reduced involucres) form a secondary capitulum, of which again a few dozen are aggregated in what appears to be the real capitulum (Fig. 24.5B) but actually represents a second order syncalathium (Claßen-Bockhoff et al. 1989).

Induration and lignification of the usually divaricately branched synflorescence axes after the capitula have performed their function and fallen off (and transformation of the peduncles into subulate, more or less spine-like terminal segments), occurs most conspicuously in *Launaea* (see Fig. 24.4B subtribe Hyoseridinae), otherwise, and in a

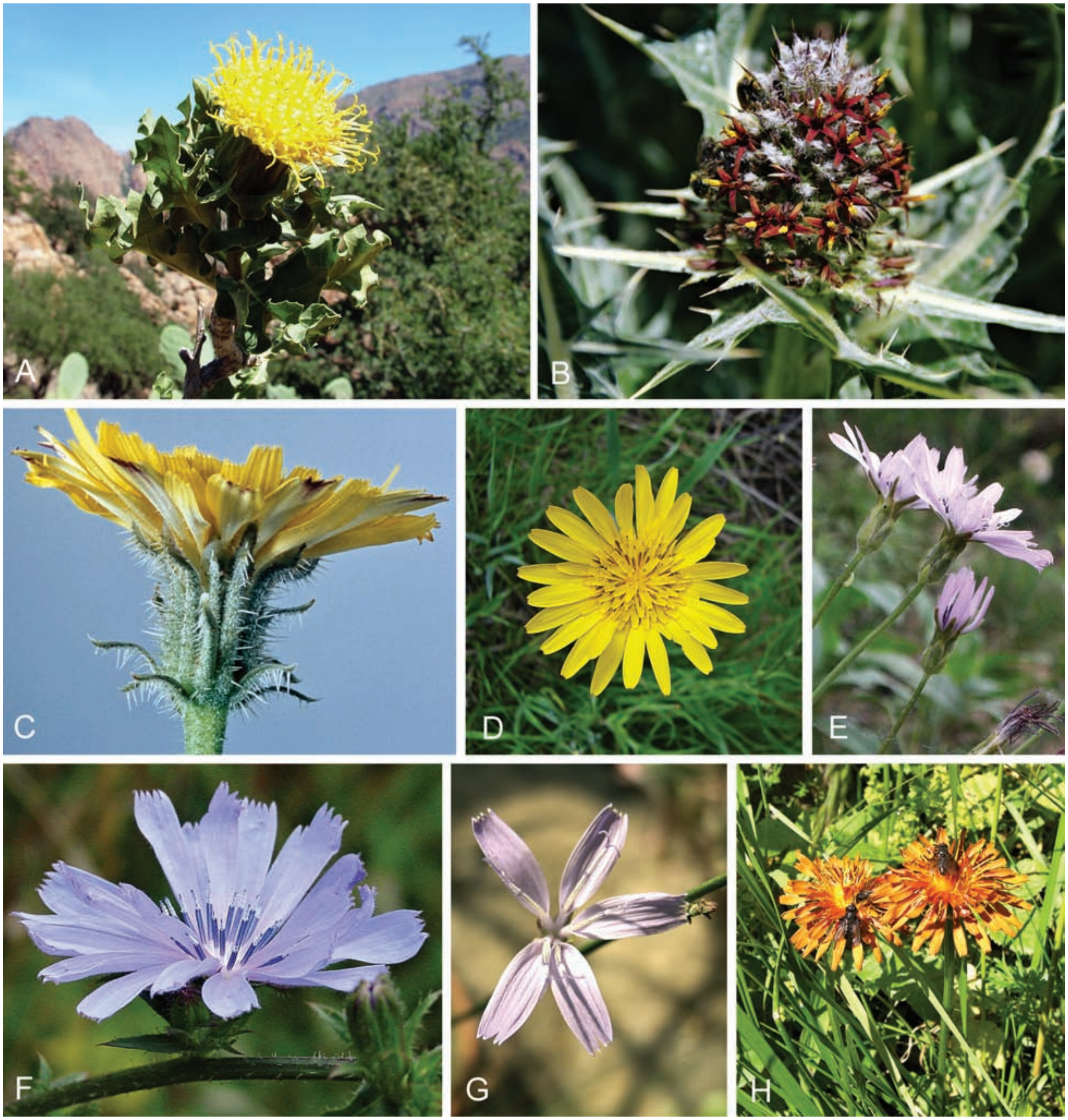

Fig. 24.5. Capitula of Cichorieae species. **A** *Warionia saharae* Benth. & Coss., Morocco, Antiatlas; **B** *Gundelia* aff. *tournefortii* L., Armenia, Mt. Aragats; **C** *Picris scabra* subsp. *abyssinica* (Sch.Bip) Smalla, cult. BG Berlin from Yemen; **D** *Tragopogon pratensis* L., Germany, Graswangtal; **E** *Podospermum purpureum* (L.) W.D.J. Koch & Ziz, Germany, at Deetz; **F** *Cichorium intybus* L., Germany, Quedlinburg; **G** *Lactuca triquetra* (Labill.) Boiss., cult. BG Berlin from Cyprus; **H** *Crepis aurea* (L.) Cass., Austria, Venedigergruppe. [Photographs: A, J. Mutke; B, E. Vitek; C, E. Dieckmann; D–F, H, B. Gemeinholzer; G, N. Kilian.]

less pronounced way, in *Cichorium* (subtribe Cichoriinae), *Lactuca* s.l. (subtribe Lactucinae), and *Scorzonera* s.l. (subtribe Scorzonerinae). Independent evolution of spinescence in these cases seems apparent and has been corroborated by the molecular analysis of *Launaea* even within a single genus (Kilian, in prep.). The case of *Cichorium spinosum* L., which strongly differs from the closely related *C. intybus* by its spinescent habit, has been thoroughly studied by Gemeinholzer and Bachmann (2005). The surprising result of their molecular phylogenetic study is that all methods applied (ITS, AFLP, microsatellites) failed to significantly discriminate between the two easily recognized species, indicating that apparently for the spinescent trait only mutations in a few crucial loci are responsible (Gemeinholzer and Bachmann 2005).

In general, the synflorescence type can systematically be valuable at generic, infrageneric and species levels.

Peduncle

The peduncle is the terminal segment of the capituliferous axis. Mostly the peduncle is not further differentiated from the preceding part of the axis. In several cases (e.g., Cichoriinae: *Arnoseris*; Hieraciinae: *Hispidella*; Hypochaeridinae: *Picris humilis* DC.; Microseridinae: *Microseris*; Scorzonerinae: *Tragopogon*) the peduncle is somewhat inflated, which has been interpreted in the context of diaspore dispersal, since the inflated peduncle provides more contact surface area for the wind to shake the achenes off the capitulum (Hoffmann 1890–1894: 114). In other cases (e.g., Hyoseridinae: *Launaea*; Hypochaeridinae: *Leontodon*; Microseridinae: *Microseris*) the peduncle is nodding in bud and/or in fruit, in the latter case evidently serving in diaspore dispersal. A particular specialization of the peduncle is its modification into subulate spine-like segments, treated above under synflorescence types. The peduncle types are systematically valuable only at the species level.

Capitula

The capitula of Cichorieae are homogamous, of perfect flowers only. The number of flowers per capitulum ranges from one in *Gundelia* (primary capitulum) to 3–5(–7) in a number of taxa (e.g., Cichoriinae: *Cichorium*; Crepidinae: *Ixeris*, *Soroseris* [Fig. 24.4D], *Syncalathium*; Hypochaeridinae: *Picris*; Lactucinae: *Lactuca* s.l. [Fig. 24.5G], *Notoseris* s.l.), and to more than 600 in *Sonchus* s.l. However, the capitula mostly comprise one dozen to several dozens of flowers (see Fig. 24.4–24.5). The molecular phylogenies provide some indication that both the very large and the very small capitula in terms of flower number are derived. The first is clearly demonstrated by the phylogenetic reconstruction of Hyoseridinae and *Sonchus* s.l. (Kim et al. 1996, 1997, 1999a, b, 2004), where *Sonchus* s.l., with generally rather large capitula, is the most terminal member of the subtribe, and where within *Sonchus* the taxa with the largest capitula also occur predominantly in more terminal clades. The second is less obvious, since species with very few flowers per capitulum occur rather scattered in several genera or alliances. In the case of the *Lactuca* alliance, where very few-flowered species such as *Lactuca muralis* (L.) Gaertn. and *L. viminea* (L.) J. Presl. & C. Presl. hold rather terminal positions in their corresponding clades, it seems very likely that these species are derived (Kilian and Gemeinholzer, in prep.).

Involucre

The involucre, as in all Asteraceae, basically consists of a number of spirally arranged, more or less imbricate bracts. At least at anthesis, the involucre is differentiated in most cases into inner and outer series of bracts, the outer series often grading into the bracts of the peduncle.

Involucre characters are systematically valuable at generic, infrageneric or species level.

In a minority of cases across the tribe (e.g., in species of *Catananche*, *Crepis*, *Dubyaea*, *Rothmaleria*, *Scorzonera*), the inner and outer series are not differentiated in length, so that the involucre is fully imbricate.

Otherwise, those of the (usually single) inner series are of equal length and evoke the impression of standing in one row; those of the outer series increase in length centripetally. The differentiation of the outer series from the inner ones varies considerably: the bracts of the outer series may be strongly imbricate, and the innermost bracts of the outer series may equal the inner series in length, or, to the other extreme, the outer series may not infrequently be reduced to a tiny single row (then termed “calyculus” by some authors), often with intermediate forms present in the same genus. More striking is the unique case of *Helminthotheca* (Hypochaeridinae), where the ca. 5 ovate outer bracts in one row are equal in length to the inner row of lanceolate bracts, with a third row of tiny bracts in between (Holzapfel 1999). Conspicuous are the several cases where the involucre has become uniseriate by abortion of the outer series and where the bracts of the remaining inner series may be connate at its base (Cichoriinae: *Arnoseris*, *Phalacroseris*; Crepidinae: *Syncalathium*; Hypochaeridinae: *Urospermum*; Microseridinae: *Picrosia*; Scorzonerinae: *Epilasia*, *Geropogon*, *Koelpinia*, *Tragopogon*).

The texture of the involucral bracts ranges from fully herbaceous to herbaceous with a scarious margin (more distinctly so, e.g., in several *Launaea*, *Reichardia* of subtribe Hyoseridinae, or in *Anisocoma* of subtribe Microseridinae), to, rarely (*Catananche*), scarious except for the (basal) midvein region.

The involucre mostly reaches its final length during anthesis. However, in several cases the involucre (or at least the inner row of involucral bracts) continues its longitudinal growth after flowering, simultaneously with the ripening of the fruit (e.g., in species of *Scorzonera*, *Podospermum*, *Tragopogon* [Scorzonerinae], *Launaea* [Hyoseridinae], *Lactuca* s.l. [Lactucinae], *Anisocoma* [Microseridinae]). The longest involucres occur in *Tragopogon*, measuring up to 80 mm in *T. porrifolius* L. and up to 90 mm in *T. paradoxus* S.A. Nikitin (Borisova in Bobrov and Tzvelev 1964).

After anthesis the innermost involucral bracts in several annual species may become indurate, ranging from having a hardened main rib (e.g., Hyoseridinae: *Hyoseris radiata* L.; Hypochaeridinae: *Picris asplenioides* L.; Lack 1975) to a transformation into an entirely sclerophyllous structure (e.g., Crepidinae: *Heteracia szovitsii* Fisch. & C.A. Mey., *Rhagadiolus stellatus* (L.) Gaertn.; Voytenko 1989). In addition, the innermost involucral bracts may become keeled and enclose partly or completely the outermost achenes, resulting in indehiscent star-like structures of various forms with the broad-based achenes coalesced to the receptacle; the epithet "stellatus" (star-like) alludes to this situation. In these cases the outermost achenes will not easily become detached from the involucrum and will not be dispersed by wind like the central achenes. The apotheosis of this development is found in involucral bracts that are provided with massive, hard hooks and which at fructification tightly enclose all achenes. The generic name *Acanthocephalus* ("head of spines"; Crepidinae) very appropriately refers to this situation. The solid hooks are reminiscent of those on the achenes in some species of *Koelpinia* (Scorzonerinae): both structures are best interpreted as an adaptation to epizoochorous dispersal, possibly by ungulates. Since these specializations have been observed only in annual species native to Eurasia and N Africa scattered widely over two subtribes, there is reason to assume that they should be interpreted as derived characters.

Receptacle

The receptacle is usually flat, slightly convex or concave and usually rather indistinctly areolate or alveolate (= areoles bordered by a ridge or membranous fringe, e.g., in *Warionia* and some *Crepis*). Receptacular paleae (= scales or bristles) are present in several cases. Receptacular scales occur in Cichoriinae: *Rothmaleria*; Crepidinae: *Crepis* p.p.; Hypochaeridinae: *Hypochaeris*; Microseridinae: *Pinaropappus*, *Agoseris* p.p.; Scolyminae: *Scolymus*, *Hymenonema*; receptacular bristles are restricted to Crepidinae (*Lagoseris*), Microseridinae (*Malacothrix* alliance: *Agoseris* p.p., *Anisocoma*, *Calycoseris*, *Malacothrix* p.p.), and Scolyminae (*Catananche*). Receptacular paleae were regarded as apomorphic in Asteraceae (Bremer 1987) but as plesiomorphic in Cichorieae (Bremer 1994: 165). As it has been shown repeatedly that the genetic basis of the presence or absence of receptacular paleae is rather simple (e.g., in the case of the receptacular scales in *Crepis*; Collins 1924; Babcock and Cave 1938), rather frequent and repeated reversals regarding this character have to be taken into consideration. Since receptacular paleae occur in only one of the three basally branching clades (Scolyminae) but in both terminal clades (clades 4 and 5, see Phylogeny), Bremer's assumption appears plausible.

Flower morphology

The corolla is divided into a tube and the 5-dentate ligule in all but two genera, the ratio of tube and ligule being of some variation within the tribe. The ligule may be longer than the tube, equaling it in length, or be shorter than the tube; different ratios may be taxonomically valuable on the specific and perhaps generic level; they seem, however, of no phylogenetic significance.

The flowers of *Gundelia* (Fig. 24.5B, Scolyminae) and *Warionia* (Fig. 24.5A, Warioniinae) markedly deviate from the typical Cichorieae flower by being entirely tubular instead of ligulate. The tubular corolla of *Warionia*, which is divided in its upper wider half into five very long teeth, is not radially symmetrical. Instead, the incisions between the teeth are of different lengths; the two incisions opposite to the longest incision are the shortest and the ones neighboring the longest one are intermediate in length. It is evident from the phylogeny of the family that the typical ligulate Cichorieae flower is derived from a tubular flower (Bremer 1994: 43, 157), and it is safe to assume from the molecular phylogenies that the tubular flowers of *Gundelia* and *Warionia*, the former also with five very long teeth but being radially symmetrical, are plesiomorphic within the tribe. This is further confirmed by the flower anatomy of *Warionia* with a primitive type of venation (see below).

Flower color. — The flower color is predominantly of some shade of yellow (= "xanthic") between the rather rare extremes cream (whitish yellow; Fig. 24.4E, F) and deep orange-yellow (Fig. 24.5H). The marginal flowers show abaxially often longitudinal stripes of a grayish-bluish-purplish tinge (Fig. 24.5C). Corollae of some shade of blue (incl. purple and whitish so = "cyanic", Fig. 24.5E–G) occur in the following subtribes and genera (exclusively or together with yellowish-flowered species): Cichorieae: *Cichorium*, *Erythroseris*; Crepidinae: *Crepis*, *Dubyaea*, *Ixeris*, *Nabalus*, *Syncalathium*, *Taraxacum*; Hyoseridinae: *Launaea* (?); Hypochaeridinae: *Prenanthes*; Lactucinae: *Cicerbita*, *Lactuca* s.l., *Notoseris*; Microseridinae: *Atrichoseris*, *Chaetadelpha*, *Glyptopleura*, *Lygodesmia*, *Malacothrix*, *Munzothamnus*, *Picrosia*, *Pinaropappus*, *Prenanthella*, *Rafinesquia*, *Shinnersoseris*, *Stephanomeria*; Scolyminae: *Catananche*, *Gundelia*; Scorzonerinae: *Epilasia*, *Geropogon*, *Scorzonera* s.l., *Tragopogon*. Exclusively yellowish-flowered taxa are thus only Chondrillinae, Hieraciinae, and Warioniinae. Bluish flower colors in two of the three basally branching clades, as well as in most of the other clades, seem to indicate the presence of this feature already in the early phylogeny of the tribe. This appears plausible also considering the particularly frequent occurrence (compared to the Asteroideae) of bluish corollae in the subfamilies Barnadesioideae and Cichorioideae (Wagenitz 1976; Bremer 1994). Both the abaxial bluish-purplish stripes of the corolla in very many of the yellow-flowered species as well as the common presence of bluish and yellowish corollas in several alliances may be taken as an indication for a rather limited number of mutations responsible for the corolla color in Cichorieae to change, as was already assumed by Cronquist (1955: 488).

Usually the capitula are uniform in their flower color, but in several cases a color differentiation between the center and the remainder of the capitulum occurs. This effect is present in the cases where the corolla is pale yellow or pale bluish, because of the usually concolorous but darker anther tubes (see, e.g., *Hololeion maximoviczii* Kitam., *Ixeris chinensis* (Thunb.) Nakai in Lee 2006: 374, 376). It is more marked in cases where the anther tube color differs from that of the ligules as, e.g., in *Taraxacum coreanum* Nakai with pale bluish ligules and yellow anther tubes (see Lee 2006: 371). Only in a few cases the corolla itself is bicolored: in *Hispidella hispanica* Lam. (Hieraciinae), *Reichardia tingitana* (L.) Roth (Hyoseridinae), and *Tolpis barbata* (L.) Gaertn. (Cichoriinae) the basal part of the ligule and the upper part of the tube are blackish-red or blackish-brown while the remainder of the corolla is yellow, providing the flowering capitulum with a dark center.

Corolla epidermis. — The micromorphology of the corolla epidermis in Cichorieae has been investigated by Baagøe (1980). The ligules in the tribe are characteristically rather thin, stomata-free, without mesophyll, with cell wall thickenings rather rare, and with anticlinal walls usually septate. Papillae, which are usually hooked and point distally, are formed on the distal end of mostly oblong cells, and any differentiation of the adaxial epidermis begins at or above the middle of the ligule. The differentiation in cell shape and cuticle type across the tribe cannot easily be interpreted from a phylogenetic point of view (Bremer 1994).

Anthers. — The anthers of Cichorieae are in general calcarate (i.e., the fertile part of the thecae is prolonged on either side below the point of filament insertion) and caudate (i.e., with tails of sterile tissue at the thecae basis on either side of filaments) and have a soft apical appendage, but no systematic survey of anther morphology and micromorphology across the tribe is available. The anthers vary considerably in length, but this variation probably occurs repeatedly within many genera and is therefore only of taxonomic relevance on the species level.

Style. — The style of Cichorieae is of the so-called vernonioid type (Hoffmann 1890–1894: 106; Bremer 1994: 32), which is generally slender, with long, filiform style branches and collecting trichomes continuing from the style branches further down the style shaft. The new members of the tribe, *Gundelia* and *Warionia*, also have this type of style. Shorter style branches, however, occur in several cases (e.g., within Microseridinae), and are probably apomorphic.

Floral anatomy. — The vascular anatomy of most of the Cichorieae flowers is of the *Lapsana* type (Koch 1930: 948): the corolla tube is traversed by five veins, one of which divides immediately at the split in the tube so that six veins continue into and traverse the ligule; two run along the margins and four towards the sinuses between the five teeth. The five veins represent each the fused lateral veins of neighboring petals.

Since the pseudomonomeric, unilocular but actually bicarpellate inferior ovary of Compositae is formed by the adnation of the basal parts of the sepals, petals and stamen whorls to the gynoecium, the vascular bundles of the ovary wall are the product of various fusions (Carlquist 1962: 132–140): one inner series represents the bundles of the two carpels, which continue as two strong separate bundles into the style and its branches; one of two outer series of originally five bundles each represents the "principle bundles" and is homologous with the united median calyx bundles, the fused lateral corolla lobe bundles and the stamen bundles; the other series represents the "supernumerary bundles" and is homologous with the united lateral calyx and median corolla bundles (Stebbins 1940: 55–64). The five principal and five supernumerary bundles continue in the ten corolla veins, which are still present in some members of the family (Koch 1930). With the successive reduction of the median corolla veins in the phylogeny of the family, the supernumerary bundles end at the ovary apex.

In Cichorieae, with only two known exceptions, the median corolla veins are absent. The first, remarkable exception, confirming the aforementioned evolutionary trend postulated by Koch (1930), is the tubular flower of *Warionia* (Warioniinae): besides the lateral bundles fused at the sinuses of the teeth as in all Cichorieae and Compositae, the median bundles of all five corolla lobes are present from the tip of the teeth to the base of the corolla, so that the *Warionia* corolla has the primitive constitution of ten corolla bundles. In the single other tubular flower of the tribe, in *Gundelia* (Scolyminae), in contrast no median corolla bundles are extant. The second exception is among the ligulate flowers, where *Dubyaea atropurpurea* Stebbins (Crepidinae) is reported by Stebbins (1940: 56) to have relics of median bundles in the teeth of the corolla lobes.

Within Cichorieae, the number of supernumerary as well as of the principal bundles in the ovary wall apparently has undergone successive reduction, as was discovered by Stebbins (1940: 55ff). He found a complete series of reduction from ten supernumerary and principal to only five principal bundles in the genus *Dubyaea* (Crepidinae) and a further reduction from only five principal bundles to two in *Lactuca* (Lactucinae) (Stebbins 1940). The data available from Crepidinae (*Crepis*, *Dubyaea*, *Nabalus*, *Soroseris*: Babcock and Stebbins 1937; Stebbins 1940; Babcock 1947; Milstead 1964), Hyoseridinae (*Launaea*: Kilian 1997), and Lactucinae (*Lactuca* alliance: Stebbins 1940; Milstead 1964; Kilian 2001; Kilian and Hand 2004) corroborate the trend of a reduction in the number of bundles. These findings seem largely congruent with the molecular phylogenies. In subtribe Crepidinae, the genera with the highest numbers of supernumerary bundles, i.e., *Nabalus* and *Soroseris*, are more basally branched than *Crepis*, which is usually without supernumerary bundles, and in the *Lactuca* alliance the species with five principal bundles are more basally branched than those with only two to three principal bundles.

Pollen

Wodehouse (1935) was the first to provide detailed descriptions of the basic morphology of Cichorieae pollen by light microscopic studies. He described these pollen grains as "globular, generally tricolpate, occasionally tetracolpate, or being sometimes abnormal, with higher numbers of furrows" comprising an outer exine that is raised in a pattern of echinate ridges (lophae) surrounding depressions (lacunae), which he named "echinolophate". In contrast, "echinate" pollen types, having less elaborate spine patterns, are regarded as being plesiomorphic in the tribe and according to Blackmore (1981) occur in almost all subtribes, which makes this feature an unreliable indicator of affinities.

The complex apertures of Cichorieae pollen have been interpreted in a variety of ways by different taxonomists (e.g., Erdtman 1952; Faegri and Iversen 1975; El-Ghazaly 1980) and various terminologies have been proposed, which are discussed and reviewed by Blackmore (1982a) who recommended retaining Wodehouse's (1935) terminology, which therefore is applied here. Blackmore (1982b, 1984) distinguished seven pollen types in the tribe: *(1) Scorzonera humilis* L. type (echinate), *(2) Scorzonera laciniata* L. type (echinolophate, and two equatorial lacunae per mesocolpium), *(3) Tragopogon pratensis* type (echinolophate, and one equatorial lacuna per mesocolpium), *(4) Sonchus oleraceus* L. type (echinolophate, and three lacunae at each pole), *(5) Lactuca sativa* L. type (echinolophate, and polar area a triradiate ridge), *(6) Arnoseris minima* (L.) Schweigg. & Körte type (echinolophate, and broad equatorial ridges with two rows of echinae), and *(7) Cichorium intybus* type (echinolophate, and narrow equatorial ridges with one row of echinae). The last type is by far the most common pollen type in the tribe; types 1–3 are restricted to the subtribe Scorzonerinae. A somewhat modified system of nine pollen types is given by Blackmore (1986). Although useful for pollen identification, these pollen types are often not congruent with taxonomic entities recognized by molecular and other morphological characters. Nevertheless, pollen morphological characters were successfully used for certain taxonomic decisions, e.g., on tribal level as by Stebbins (1940, 1953) and Jeffrey (1966), or for subtribal delimitation, e.g., by Blackmore (1981, 1982b) (see Phylogeny, above).

Achenes

The achenes of Cichorieae are in many cases indispensable for the identification of the genera and species and provide the systematically most valuable features on all taxonomic levels. Its analysis, however, has to consider that heterocarpy occurs in several alliances (Voytenko 1989; Voytenko and Oparina 1990) and may involve size, ribbing pattern, base, apex, shape, surface and anatomy, separately or in combination, resulting in two or more morphs within a single capitulum.

Achene size. — Variation in achene size across the tribe is tremendous, ranging from less than 1 mm length in *Tolpis* to a maximum of 45–55 mm length (without pappus) in *Tragopogon porrifolius* and *T. paradoxus* (Borisova in Bobrov and Tzvelev 1964; Blanca and Díaz de la Guardia 1997); the commonest size class is probably 2.5–5 mm. In contrast to the more common trend towards size reduction, *Tragopogon*, as a derived genus of subtribe Scorzonerinae (Mavrodiev et al. 2004 and see Phylogeny), illustrates an evolutionary trend towards increased size of capitula, flowers and fruits, as has already been stated by Stebbins (1950: 495).

Ribbing patterns. — The principal bundles of the ovary wall (see Flower anatomy, above) usually seem to correspond to the longitudinal main ribs of the achene, since the latter are formed above these bundles (Babcock and Stebbins 1937: 10; Kilian 1997: 47). The plesiomorphic constitution is thus an achene with five main ribs according to the originally five principal bundles of the ovary wall. The main ribs, however, are frequently differentiated, and each may be subdivided resulting in a less defined and smaller secondary rib on either side (Kilian 1997), which is a particularly frequent pattern in the tribe. Fusion of neighboring secondary ribs in the ontogeny of the achene explains the not infrequent pattern of ten equal ribs, as is the case, e.g., in *Ixeridium*, where five principal ovary wall bundles are also present (Pak and Kawano 1990a: 52–53). Rib numbers that are not a multiple of the number of principle ovary wall bundles or main ribs, occur not infrequently by incomplete differentiation into single main ribs, in particular when the achene body is not isodiametric in cross section.

The ribs, or single ribs, are transformed to (narrow) wings in several cases in the tribe, e.g., in the Crepidinae (*Ixeris* p.p., Pak and Kawano 1990a; *Youngia* p.p., Babcock and Stebbins 1937), Hyoseridinae (*Hyoseris*), Lactucinae (*Lactuca* p.p. = *Pterocypsela*), and Scorzonerinae (*Pterachaenia*, *Tourneuxia*).

In the *Lactuca* alliance (Jeffrey 1966; Tuisl 1968; Beliaeva and Boyko 1980; Kilian 2001; Kilian and Hand 2004) the number of main ribs is reduced from five down to the minimum of two in the tribe, corresponding to the reduction in the number of the principal ovary wall bundles; the achenes with only two main ribs are often strongly flattened (but see *Heteracia*; Voytenko 1989) and the ventral and dorsal surfaces show one or a few secondary ribs on each side.

Achene base. — The achene of Cichorieae is connected to the receptacle by a stipelike projection, usually from the centre of the achene base. As a rule, the peripheral achene wall is basally somewhat protruding and loosely attached to the receptacle. No in-depth survey of the achene base in Cichorieae is available, but in most cases only the main ribs somewhat protrude and they may be somewhat spreading, straight or incurved, and connate to different extents (Haque and Godward 1984). Such differences are usually of systematic value on the specific level only. However, there are at least two cases were the achene base is valuable on a higher systematic level: *(1)* the *Lactuca* alliance (Lactucinae) is characterized by an achene base forming a callose annulus or somewhat funnel-shaped carpopodium; *(2)* the genus *Podospermum* (Scorzonerinae) is characterized by an extreme, tubular carpopodium of up to 1/3 the achene body length.

Achene apex. — The achene apex is either truncate or variously attenuate (cuspidate) to rostrate. Both attenuation of a sculptured achene apex and formation of a beak (=rostrum), usually understood as a thin, unsculptured, distal part of the achene, are evidently functional for wind dispersal and have therefore evolved convergently in many genera and in seven of the eleven subtribes of Cichorieae. Presence or absence of beaks have been extensively used systematically but are actually of no systematic value unless at species level. Attenuate or beaked achenes are present in Chondrillinae (e.g., *Chondrilla*), Crepidinae (e.g., *Crepis*, *Heteracia*, *Ixeridium*, *Taraxacum*), Hyoseridinae (e.g., *Launaea*), Hypochaeridinae (e.g., *Hypochaeris*, *Leontodon*, *Urospermum*), Lactucinae (e.g., *Lactuca*) and Microseridinae (e.g., *Agoseris*, *Calycoseris*, *Picrosia*, *Pyrrhopappus*); Scorzonerinae (*Geropogon*, *Tragopogon*); no beaks are present in Cichoriinae, Hieraciinae, Scolyminae, and Warioniinae.

The achene apex in species of *Lapsanastrum*, where 2–4 main ribs are prolonged into apical hooks (Pak and Bremer 1995), is unique in Cichorieae. This also applies to the achenes in *Urospermum*, possessing a diaphragm separating the seed containing part from the hollow distal part of the achene.

Achene body shape. — The shape of the achene body shows considerable variation in the tribe. Cross sections range from isodiametric and terete or angled to a variety of anisodiametric shapes due to unilateral, median or dorsiventral flattening of the achenes. Bremer (1994: 166) distinguished three types of cross sections, which appears rather simplistic, in particular since even within a single capitulum the cross section shape often varies from center to periphery. The shape is therefore one of the systematically least valuable feature of the achene, usually being of certain value on the specific level but already of much limited value on the generic level.

Ornamentation of the achene surface. — The achene surface may be glabrous, variously hairy, papillose or scaly. Conspicuously villous achenes are present in *Scorzonera* s.l. (Scorzonerinae) and in *Warionia* (Warioniinae), a considerable diversity of papillose achenes, ranging from short papillose over densely papillose to papillosely winged, is present in *Launaea* (Hyoseridinae); minutely scaly achenes are found, e.g., in *Lactuca* (Lactucinae). The sculpturing of the achene surface shows similar variation and includes striking hooks for epizoochorous dissemination in *Koelpinia* species (Scorzonerinae). In general the achene surface features are taxonomically valuable, mainly at species level, and more rarely concur with supraspecific delimitation.

Pericarp anatomy. — Pericarp cross sections have proven so far to be of some relevance for the circumscription of genera and infrageneric entities in Cichorieae and have been published in particular for Crepidinae (Pandey et al. 1978; Beliaeva and Boyko 1980; Pak and Kawano 1990a, b; Pak 1991, 1993; Pak and Bremer 1995; Sennikov and Illarionova 2007), Hyoseridinae (Lavialle 1912; Aldridge 1978; Pandey et al. 1978; Kilian 1997), and Lactucinae (Tuisl 1968; Pandey et al. 1978; Zhu et al. 2006). The data available cover only parts of the tribe and their analysis in a phylogenetic context is still lacking.

Testa epidermis. — Since the seed of Compositae is not exposed but covered by the pericarp, the testa has no protective function. Its micromorphological diversity is therefore potentially of phylogenetic and taxonomic relevance. A comparative morphological survey of the testa epidermis has been conducted by Tegel (2002), but a phylogenetic analysis of the considerable morphological diversity observed has still not been done. It merits attention that larger parts of the tribe are rather similar, possessing a "fenestrate type" of testa epidermis (most Chondrillinae, Crepidinae, Hyoseridinae, Hieraciinae, and Lactucinae), whereas in Crepidinae, *Taraxacum* shows a distinctly different type. A "reticulate type" is found in part of Hypochaeridinae and otherwise in *Krigia* sect. *Krigia* (Microseridinae). A "helicoid type" characterizes Scorzonerinae and is otherwise present in *Rothmaleria* (Cichoriinae). Other specialized types, as well as an unstructured type, exist and complicate the picture.

Pappus

No other morphological feature has received so much attention in the systematics of Cichorieae as the pappus, which had long been used as the key feature for subdividing the tribe (see History, above). Since it is, in fact, of some systematic value at all ranks in the tribe, a brief comparative overview, not available so far, is given here.

The pappus of Cichorieae is either paleaceous or setaceous, or absent. If present, it may be homomorphic or heteromorphic. However, terminology is still unsatisfactory: "homomorphic" means both *(1)* the pappus of all achenes in a capitulum is homogeneous, and *(2)* all elements in the pappus of a single achene are equal or very similar; "heteromorphic" means *(1)* the pappus in the capitulum differs, which is a character often but not always correlated with heterocarpy (see above), and *(2)* the elements in a single pappus differ from each other. Heteromorphy involves differences in length, diameter, and/or structure of the pappus elements, or a combination of them. Heteromorphic pappuses have been studied in some detail in Hyoseridinae (*Launaea*; Kilian 1997) and Hypochaeridinae (*Picris*; Lack 1975). The largest pappus (up to 35 mm length) is found in *Tragopogon* (Borissova in Bobrov and Tzvelev 1964).

Paleaceous pappus. — A paleaceous pappus (Fig. 24.6) may resemble most the presumed homologues, the calyx lobes, and often also comprise five elements, which may be more or less keeled and/or aristate. Paleaceous pappuses are present in the subtribes Scolyminae (Fig. 24.6D–H, *Catananche*, *Hymenonema*), Cichoriinae (*Cichorium*, Kiers 2000: 12–15, fig. 2.1a–h; *Rothmaleria*, Lack et al. 1980; Fig. 24.6A–C) and Microseridinae, where the largest variety is present: in *Krigia*, predominantly with a setaceous pappus, the outer series may consist of small scales; in *Malacothrix* the pappus may consist of a scaly corona, or be otherwise either setaceous or missing; in the *Microseris* alliance (*Microseris*, *Nothocalais*, *Uropappus*) aristate scales are present apart from setaceous pappus, and in *Chaetadelpha* the pappus consists of bristles and awns. No attempts have been made yet to discuss possible homologies, in particular since it is unclear to what extent the pericarp is part of these structures.

The presence of the paleaceous pappus in three subtribes and two of the five major clades of the tribe, of which only the Scolyminae clade is among the basally branching ones, is inconclusive regarding its interpretation as plesiomorphic within Cichorieae (Stebbins 1974: 186). The same applies to the distribution of the paleaceous pappus within the subtribes and genera. The morphological similarity of, e.g., the aristate scaly pappus in Scolyminae with that of Microseridinae and with the non-aristate scaly pappus of *Rothmaleria* in Cichoriinae leaves little doubt that they represent homologous structures, and this may count for both their common origin and plesiomorphy. The distribution of a paleaceous pappus within the subtribes and genera provides strong indication for the homology of the paleaceous and the setaceous pappus, and furthermore, that the genetic differences between both cannot be too large. The morphological differences between the paleaceous and the setaceous pappus elements are of rather minor nature, because both are built of largely the same cell types. The main difference between bristles and scales is the lateral extension of the latter. This also explains the morphological transitions, which occur particularly in Microseridinae. In subtribe Cichoriinae such morphological transitions can be seen in the line from *Rothmaleria* (with 5 large, keeled scales) to *Cichorium* (with mostly tiny, numerous irregular scales) and further to *Erythroseris* (with larger inner and an outer series of in part laterally fused minute bristles, see Fig. 24.7A and Kilian and Gemeinholzer 2007).

Setaceous pappus. — The setaceous pappus (Fig. 24.7) in Cichorieae is either *(1)* scabrid (= rough), denticulate (= toothed), or barbellate (= long-toothed), i.e., with lateral projections not or at most few times longer than the diameter of the seta (= bristle), see Fig. 24.7A, B, or *(2)* plumose (meaning feather-like), i.e., with side projections (= fimbriae) many times longer than the seta diameter (Fig. 24.7C). As first observed by Lack (1975, 1984) and much later applied to the whole tribe (Lack 2007: 82), three variants of the so-called plumose pappus exist in Cichorieae: *(1)* the *feather-like fimbriate pappus* (Fig. 24.7D) has the pinnae arranged in one plane as is the case in a true feather; *(2)* the *stiffly fimbriate pappus* (Fig. 24.7E) has stiff fimbriae pointing in all directions like a bottle-brush, each fimbria consisting of a single giant tubular cell resembling a macaroni; *(3)* the *softly fimbriate pappus* (Fig. 24.7F) has soft and often intertwined fimbriae pointing in all directions and consisting of a row of flattened cells resembling cotton fibers or knitting wool along the seta. The *feather-like fimbriate pappus* is exclusively present within the principally American Cichorieae clade of Microseridinae s.l., the *stiffly fimbriate pappus* is exclusively restricted to Hypochaeridinae, and the *softly fimbriate pappus* is exclusively restricted to Scorzonerinae. In all three subtribes, however, besides the respective plumose pappus variant, also other pappus types (non-plumose setaceous or even non-setaceous types) are present and the achenes may also lack a pappus altogether.

The diameter of the setae, its surface structure, and the number of cells involved varies and requires further study. The brittleness of the setae, e.g., in *Hieracium*, as well as the varying length and density of the fimbriae have long been known and used as traditional characters for rapid generic identification but have not been investigated further.

The setaceous pappus is usually homomorphic, i.e., all bristles are roughly of the same type, diameter and length. In several cases, however, a differentiation between outer and inner series of the pappus has occurred. In, e.g., *Hypochaeris radicata* L. and *Leontodon hispidus* L.

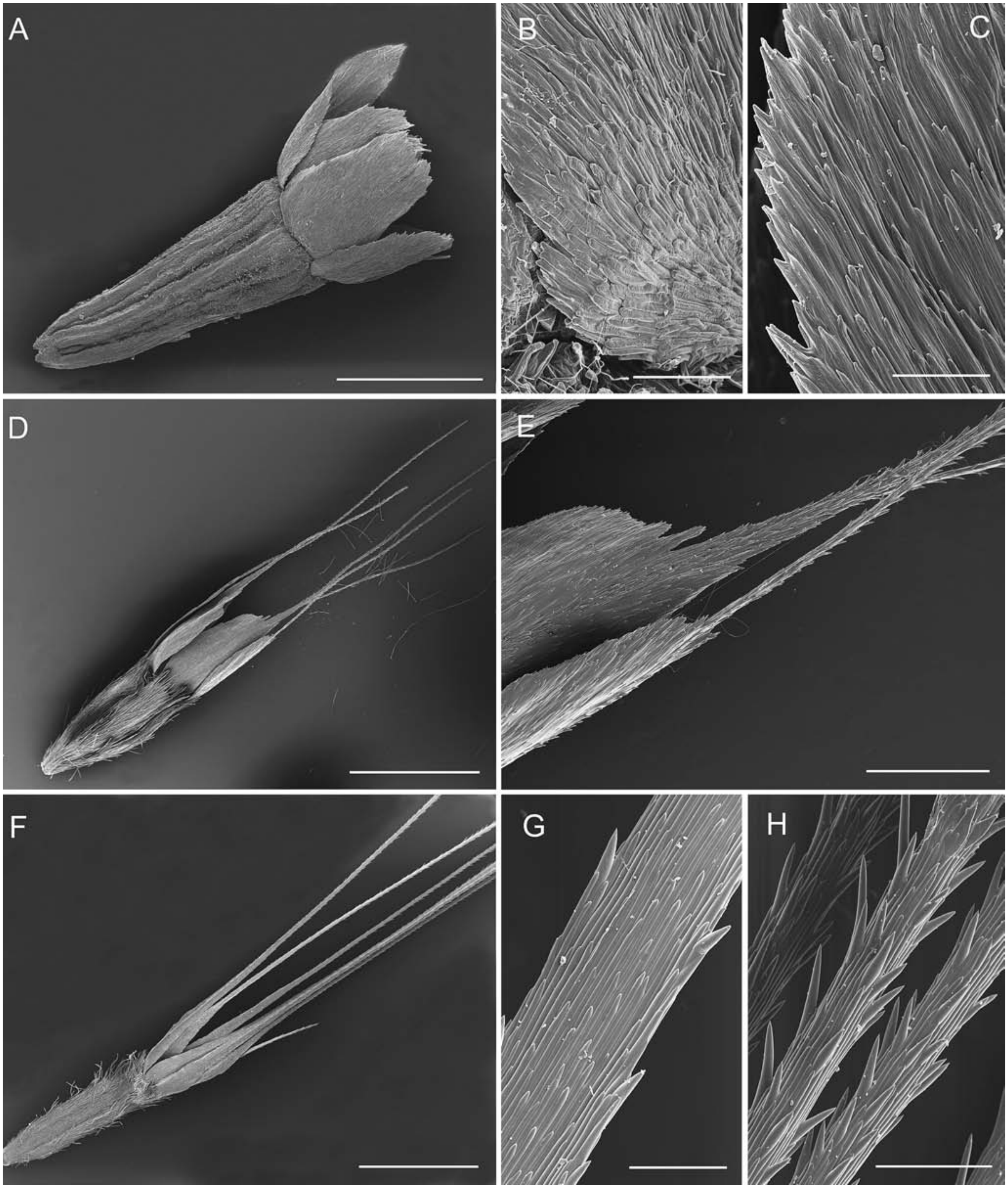

Fig. 24.6. Pappus types 1. **A–C** *Rothmaleria granatensis* (DC.) Font Quer, paleaceous pappus, overview (Spain, *Bourgeau 1261*, B), proximal portion (A), detail (B), distal portion, detail (C); **D, E** *Catananche caerulea* L., awned paleaceous pappus, overview (Morocco, *Oberprieler 1845*, B), median portion (D), detail (E); **F–H** *Hymenonema graecum* (L.) DC., lanceolate paleaceous-setaceous pappus, overview (Greece, *Heldreich 1055*, B), proximal paleaceous portion (F), detail (G), distal setaceous portion, detail (H). Scale bars: A = 2 mm, B, C, G = 100 µm, D, F = 3 mm, E = 600 µm, H = 200 µm.

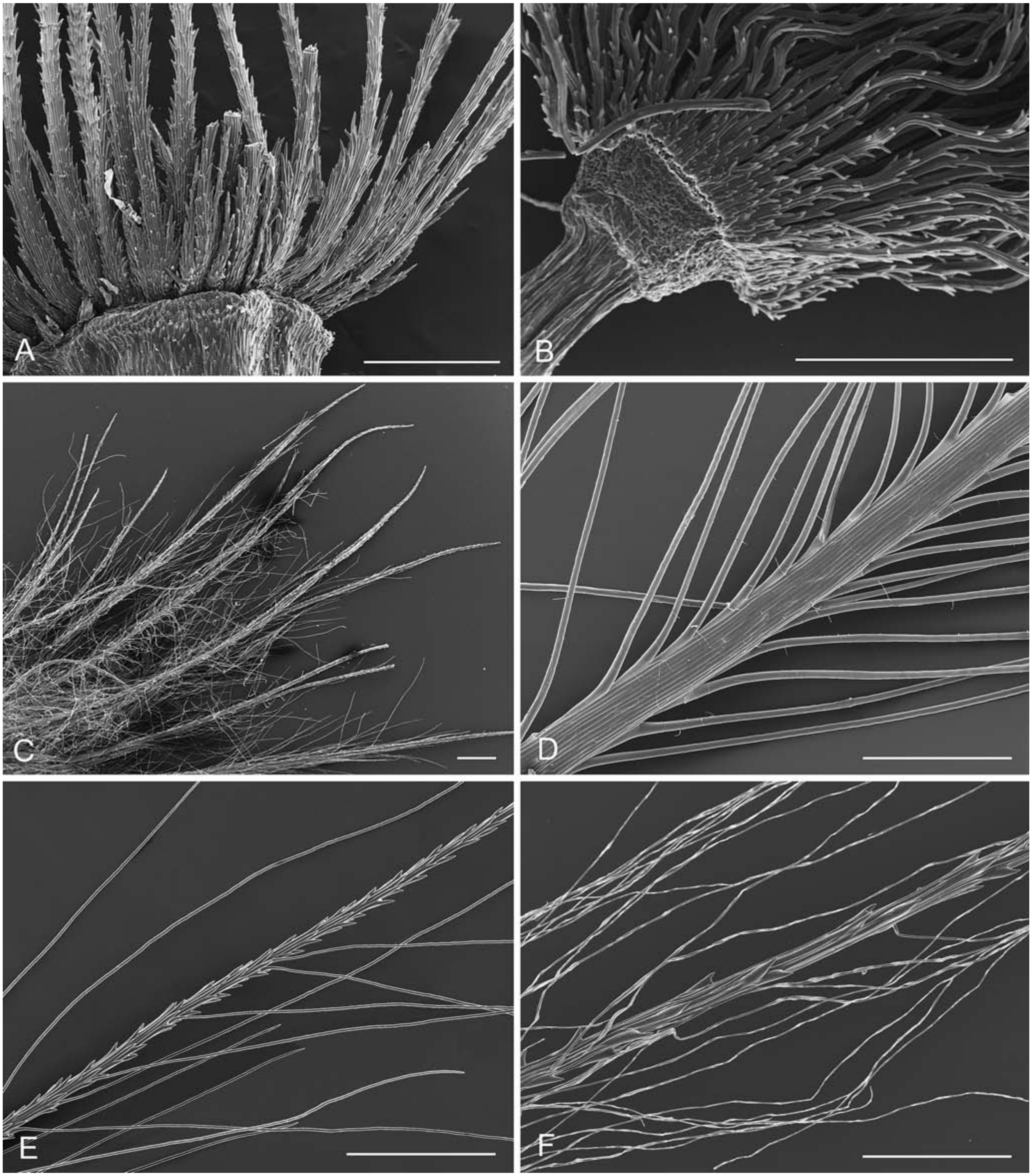

Fig. 24.7. Pappus types 2. **A** *Erythroseris somalensis* (R.E Fr.) N. Kilian & Gemeinholzer, scabrid setaceous pappus with basally partly fused bristles, proximal portion, detail (Somalia, *Thulin 4260*, UPS); **B** *Lactuca triquetra* (Labill.) Boiss., scabrid setaceous pappus, proximal portion, detail (Cyprus, *Buttler 32460*, B); **C** *Scorzonera ulrichii* Parolly & N. Kilian, proximally plumose, distally barbellate to scabrid setaceous pappus, overview (Turkey, *Ulrich 2/53*, B); **D** *Anisocoma acaulis* Torr. & A. Gray, feather-like fimbriate plumose pappus, detail (USA, *Rose 37071*, B); **E** *Hypochaeris achyrophorus* L., stiffly fimbriate plumose pappus (Greece, *R. et E. Willing 134.057*, B); **F** *Scorzonera mollis* M. Bieb., softly fimbriate plumose pappus (Greece, *R. and E. Willing 156.025*, B). Scale bars: A, D, F = 300 µm, B = 500 µm; C = 1 mm.

(Hypochaeridinae), only the inner pappus setae are plumose, whereas the marginal are denticulate (much shorter in the latter species). In many species of *Launaea* and *Sonchus* (Hyoseridinae), the inner bristles are stiff and strong, whereas the outer pappus elements are shorter, downy and flexible. In Lactucinae, besides the bristles of the inner series, frequently an outer series of tiny hairlike elements occurs.

Moreover, the setaceous pappus may be persistent or deciduous; in the latter case it either detaches as a single piece (e.g., in *Launaea* p.p. together with the pappus disk) or the bristles separate singly or in groups.

Absence of pappus. — The pappus is entirely absent in a number of taxa (*Arnoseris*, *Cichorium calvum* Asch. and *Phalacroseris* in Cichoriinae; *Acanthocephalus*, *Heteracia epapposa* (Regel & Schmalh.) M. Popov, *Lapsana*, *Lapsanastrum* and *Rhagadiolus* in Crepidinae; *Hispidella* in Hieraciinae; *Aposeris* in Hyoseridinae; *Atrichoseris* and *Krigia cespitosa* (Raf.) K.L. Chambers in Microseridinae; *Koelpinia* in Scorzonerinae); this is evidently a secondary trait, which has occurred repeatedly across the tribe.

Besides presumably having a protective property (providing a barrier for the immature fruit against predatory insects and water), the pappus is related to fruit dispersal. The assumption that in this function the pappus is a primary target of selection pressure and therefore subject of various modifications has been addressed by Carlquist (1966: 44–46) for Pacific Cichorieae. In the context of a loss of dispersability on oceanic islands, he noticed a tendency towards size reduction and deciduousness of pappus elements in the Juan Fernández taxa, the significance of which gained great support from the recent molecular data, identifying these taxa as close allies of the Old World *Sonchus* species (Kim et al. 2004). In *Hypochaeris oligocephala* (Hypochaeridinae; Lack 1978), a local endemic of Tenerife with somewhat succulent leaves, this is paralleled by the reduced number of fimbriae of its plumose pappus. The similar evolution of such antiteleochoric (= preventing long distant dispersal) properties, affecting both the achene and pappus, in arid environments with contracted vegetation is long known and was summarized, e.g., by Zohary (1950) and Voytenko (1989). It has been considered more recently by Lack (1975) in the case of *Picris*, where morphs with very short pappus and incurved outer achenes occur, and by Kilian (1997: 317) in case of *Launaea*, where morphs with deciduous pappus on long-beaked achenes occur. The dramatic short-term shifts in the achene and pappus morphology towards reduced dispersability found by Cody and Overton (1996) in weedy Cichorieae species on small Pacific near-shore islands in Canada strikingly prove the significance of selection pressure for the shaping of the pappus. Using the considerable variation in macromorphology of the pappus in Cichorieae uncritically in systematic analyses consequently leads easily astray and is, in fact, responsible for numerous former artificial groupings or delimitations on the suprageneric as well as on the generic level.

CHROMOSOME NUMBERS

The chromosome numbers of Cichorieae range between the extremes of $2n = 14x = 126$ in *Sonchus novae-zelandiae* (Hyoseridinae; Beuzenberg and Hair 1984), which is one of the very few Cichorieae in New Zealand and the rare case of a high ploidy level in the tribe, and $2n = 2x = 6$ in a few species of *Crepis* (Crepidinae; for references see Watanabe 2008) and *Hypochaeris* (Hypochaeridinae; for references see Watanabe 2008). The report of an even lower number of $2n = 2x = 4$ (see Jeffrey 1966; Jeffrey and Beentje 2000; Lack 2007) allegedly found in *Dianthoseris schimperi* A. Rich. (according to our analyses a congener of *Crepis*, Crepidinae; see Enke et al. 2008) is erroneous, the only counts obtained and published for this species are $2n = 8$ (Hedberg and Hedberg 1977: 24; compare Watanabe 2008).

The basic number in the majority of the subtribes is $x = 9$ or a descending series starting with $x = 9$: Hypochaeridinae $x = 9, 8, 7, 6, 5, 4, 3$; Microseridinae $x = 9, 8, 7, 6, 5, 4$; Hyoseridinae $x = 9, 8, 7, 6, 5$; Lactucinae $x = 9, 8$ (basic numbers of 7 and 6 published seem erroneous); Hieraciinae and Cichoriinae $x = 9$. In the Chondrillinae only the numbers $x = 9, 7, 5$ are known. In contrast, in Crepidinae the series starts with $x = 8$ and runs to $x = 3$; in Scorzonerinae only $x = 7$ and 6 are known. Scolyminae with the basic numbers $x = 10$ and 9 and Warioniinae with its only species *Warionia saharae* having the basic number $x = 17$ (Reese 1957; Humphries et al. 1978; Oberprieler and Vogt 1993) are more strongly deviating.

The ancestral basic chromosome number of Cichorieae (and Compositae in general) has been assumed to be $x = 9$ by Stebbins et al. (1953: 416), Tomb (1977: 1076), and Tomb et al. (1978: 721), but $x = 5$ (or 4) and successive aneuploid reduction from the tetraploid level were suggested by Turner et al. (1961: 219, in adnot.) mainly for the reason that this would explain the frequent gaps in the series between $x = 4$ and 5 and $x = 8$ and 9 observed at that time. Since the numbers in Cichorieae known today do not exhibit such gaps and $x = 9$ is the number present in most genera and subtribes, and since a higher karyotype symmetry has been found in species with higher basic numbers compared to lower numbers in the same genus (e.g., in *Crepis* with $x = 6$ to 3, see Babcock 1947; in *Launaea* with $x = 9$ to 5, see Kilian 1997: 80), an original basic number of $x = 9$ appears to be the more parsimonious explanation. The case of *Warionia* ($x = 17$) may hypothetically be explained through dysploid reduction from

$2n = 18$ and subsequent autopolyploidization; the same number is also present in American species of *Lactuca* (e.g., *L. canadensis* L., *L. graminifolia* Michx.; see Tomb et al. 1978: 719), which otherwise have a basic number of $x = 9$ and 8. The basic number of *Scolymus* ($x = 10$) may be explained correspondingly and is paralleled by species of *Krigia* (*K. biflora* (Walt.) Blake, $x = 5,10$; *K. montana* (Michx.) Nutt., $x = 10$, 15; see Tomb et al. 1978: 718; Kim and Turner 1992), which have as basic numbers $x = 9$, 6, 5, 4.

CHEMISTRY

Typical secondary chemical compounds within Cichorieae are glycosides of simple sesquiterpene lactone derivates mainly of the lactucin type (Zidorn 2006, 2008), flavonoids (for review see Bohm and Stuessy 2001), phenolic acids and in particular derivates of caffeic acid (Giner et al. 1993; Manez et al. 1994), simple coumarins, and triterpenes such as taraxasterol and their fatty acid esters. The latter compounds are frequently found in high amounts in the milky latex (Hegnauer 1964). Sugars and polysaccharides have extensively been studied in the economically important chicory (*Cichorium intybus*; e.g., Monti et al. 2005; Van Laere and Van den Ende 2002).

Only few studies deal with secondary metabolites in a chemosystematic context covering the tribe or individual subtribes (Bohm and Stuessy 2001; Zidorn 2006, 2008; Zidorn et al. 2006). In some cases chemical compounds have been used for intrageneric delimitations (e.g., in *Leontodon* and *Hieracium*; Zidorn and Stuppner 2001a, b; Zidorn et al. 2002) or findings on individual taxa have been discussed in a tribal context (e.g., Zidorn et al. 2005, 2006). More often the compounds of economically important taxa such as *Cichorium intybus*, *Lactuca sativa*, *Scorzonera hispanica* L. and *Tragopogon porrifolius* have been analyzed (e.g., Sessa et al. 2000; Bischoff et al. 2004; Kisiel and Zielinska 2001; Van Beek et al. 1990; Zidorn et al. 2000, 2005). Several publications deal with new chemical compounds isolated from different taxa (for review see Bohm and Stuessy 2001 and Zidorn 2006), while only few studies are concerned with phytochemical variation on the populational level (e.g., Grass et al. 2006).

Flavonoids have been comparatively well sampled throughout several groups of Cichorieae (for review see Bohm and Stuessy 2001). Common flavonoid compounds within most members of the tribe are derivates of luteolin, apigenin, kampferol and quercetin or their simple *O*-methyl ethers. As presence and quantity of flavonoids often depend on the origin of the plant, time of collection, and method of analysis, González (1977) recommended the cautious application of this character for chemotaxonomic purposes. The phenolic compounds have been reported as important characters for intraspecific, interspecific, and generic delimitation within Cichorieae (Crawford 1978; Zidorn et al. 2002), as the flavonoid structure can be altered by only few gene mutations (Fiasson et al. 1991). An exemplary evaluation of the efficacy of flavonoid data for Cichorieae systematics on higher taxonomic levels, provided in the context of a synopsis of the flavonoids in Asteraceae (González 1977; Bohm and Stuessy 2001), revealed, however, that the available data are of limited value for chemotaxonomic delimitations on the generic as well as on the subtribal level. This, for example, accounts for the presence of the "most unusual flavonoid in the tribe" (Bohm and Stuessy 2001), the 5,7,2′,4′,5′-pentahydroxyflavone (isoetin), which has been identified from *Crepis*, *Hedypnois*, *Hieracium*, *Hispidella*, *Hypochaeris*, *Leontodon*, *Picris*, *Reichardia*, and *Sonchus*, thus from genera throughout Cichorieae.

In contrast, clade 4 (Figs. 24.1–24.2), comprising Chondrillinae, Crepidinae, Hyoseridinae, Hypochaeridinae, and Lactucinae, seems to be characterized by *(1)* the flavonoid 6-hydroxyapigenin (scutellarein), which has up to now solely been detected in *Reichardia*, *Hedypnois*, *Hypochaeris* and *Leontodon* (Bohm and Stuessy 2001), *(2)* the occurrence of hypocretenolides in *Crepis aurea*, *Hedypnois cretica* (L.) Dum. Cours., *Hypochaeris cretensis* (L.) Bory & Chaub., *Leontodon hispidus* (Bohm and Stuessy 2001), and *L. rosani* (Ten.) DC. (Zidorn et al. 2007), and *(3)* in addition to the flavonoids, by the occurrence of the costus lactone type guaianolide β-D-glucopyranoside ixerin F (Zidorn 2006), which is known from species of, e.g., *Crepis*, *Lactuca*, *Picris* (Zidorn et al. 2006 and literature cited therein).

Zidorn (2006) established a hierarchical cluster analysis of sesquiterpene lactones (mainly of the guaiane type) from Hypochaeridinae sensu Bremer by summarizing phytochemical data. In concordance to our re-classification of Cichorieae, *Urospermum* turned out to be most dissimilar from all other taxa of Hypochaeridinae sensu Bremer (1994), a fact supported by the presence of *Urospermum*-type germacranolides, otherwise absent within the subtribe. *Scorzonera* and *Tragopogon* yielded numerous bibenzyl derivatives, including unique tyrolobibenzyls, which seem to be restricted to the genus *Scorzonera* (Zidorn et al. 2000, 2002, 2003, 2005; Paraschos et al. 2001).

BIOGEOGRAPHY

Cichorieae are mainly distributed in the temperate zone of the northern hemisphere, both in the Old and New Worlds (Fig. 24.8–24.10). Three main centers of diversity exist: Central to Eastern Asia, the Mediterranean Basin including SW Asia, and, to a lesser extent, western North America. Some genera are found native also in tropical and southern Africa, (e.g., species of *Crepis*, *Lactuca*, *Launaea*, *Picris*, *Sonchus*, and *Tolpis*), tropical Asia (e.g., species of *Ixeridium*, *Ixeris*, *Launaea*, *Youngia*), Australia and New Zealand (few species of *Launaea*, *Microseris*, *Picris*, *Sonchus* s.l., and *Youngia*), South America (species of *Hypochaeris*, *Hieracium*, *Microseris*, *Picrosia*, and *Taraxacum*). Several genera have reached oceanic islands, radiated there and developed endemic taxa, some of them spectacular, indeed, notably the southeastern Pacific archipelagos of Juan Fernández and Desventuradas (*Sonchus*), but also the mid-Atlantic archipelagos (Azores, Madeira, Canary and Cape Verde islands; *Lactuca*, *Launaea*, *Leontodon*, *Sonchus*, *Tolpis*). Most Cichorieae occur in moderately humid climates, some extend into semiarid to arid environments (e.g., *Lactuca*, *Launaea*), others inhabit mountains up to the alpine zone (e.g., *Soroseris*, *Taraxacum*), but they are almost absent from the humid tropics and from aquatic habitats.

Babcock (1947) was the first to address in more detail the question of the geographical origin of the tribe. He proposed an origin of Crepidinae sensu Stebbins (comprising genera from our Hieraciinae, Crepidinae, Hyoseridinae and Lactucinae) in the Angara region northeast of Lake

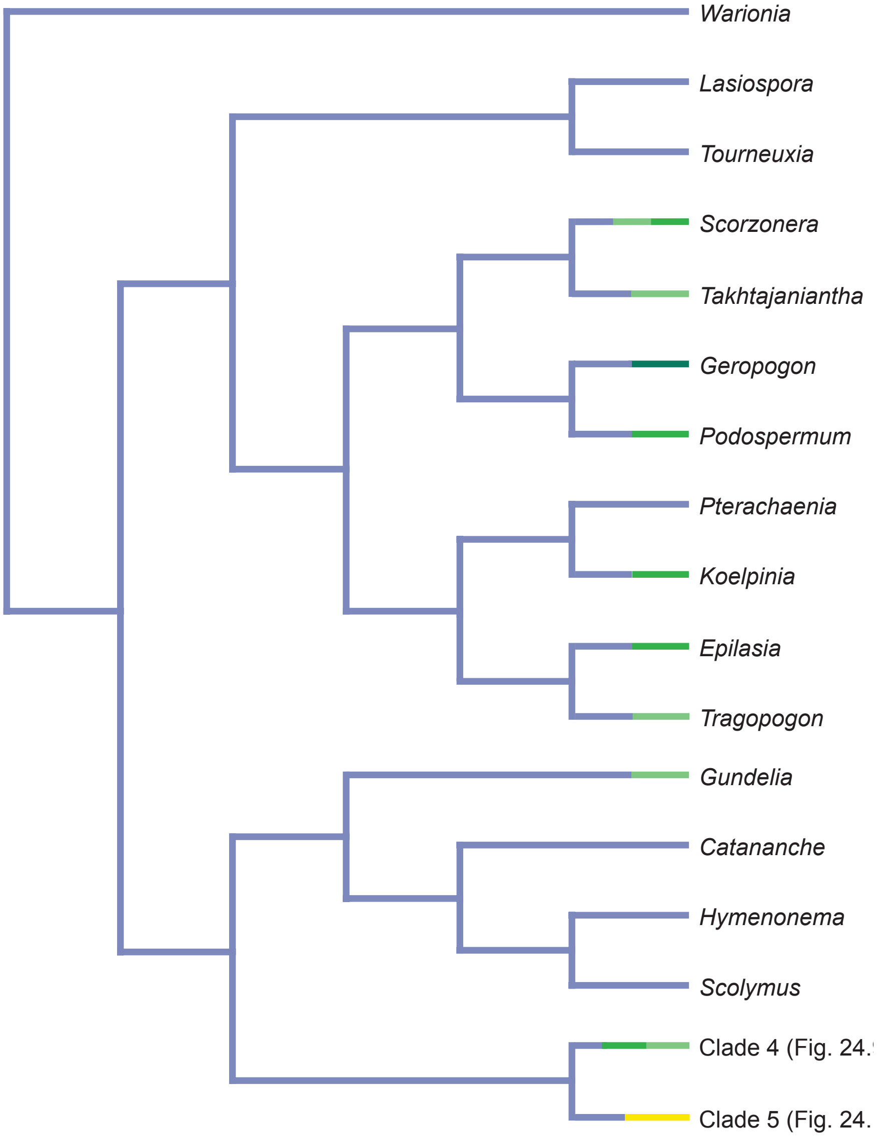

Fig. 24.8. Biogeography of the tribe Cichorieae mapped on the scheme of the ITS phylogeny in Fig. 24.1. Included are only genera for which molecular data are available. — Abbreviations: c1 = clade 1, Warioniinae; c2 = clade 2, Scorzonerinae; c3 = clade 3, Scolyminae; c4 = clade 4, including Crepidinae, Chondrillinae, Hypochaeridinae, Hyoseridinae and Lactucinae; c5 = clade 5, including Cichoriinae, Microseridinae and Hieraciinae. See Fig. 24.10 for color chart and Chapter 44 for the complete metatree.

Baikal and particularly in the Altai, where he presumed the origin of the angiosperms, although he stated that *Crepis*, *Launaea*, *Sonchus*, *Tolpis*, and *Taraxacum* have their most primitive species in the western Mediterranean region. Based on the latter assumption, Babcock proposed an alternative hypothesis of a western Eurasian origin with early migration of the Crepidinae of the pre-Tertiary arctic flora into the region of the northern Ural Mountains and subsequent migration into *(1)* northern Europe in the early Eocene, where one line was driven southwards by the cooling climate in the Tertiary, whereas another line *(2)* migrated into North Central Asia and became established in the Altai-Tien Shan region.

Based on a morphological cladistic analysis, Bremer (1994) indicated an origin of the Cichorieae in the Mediterranean region or Central Asia, due to the highest distribution density of the basally branching genera. In a parsimony optimization analysis of the Asteraceae

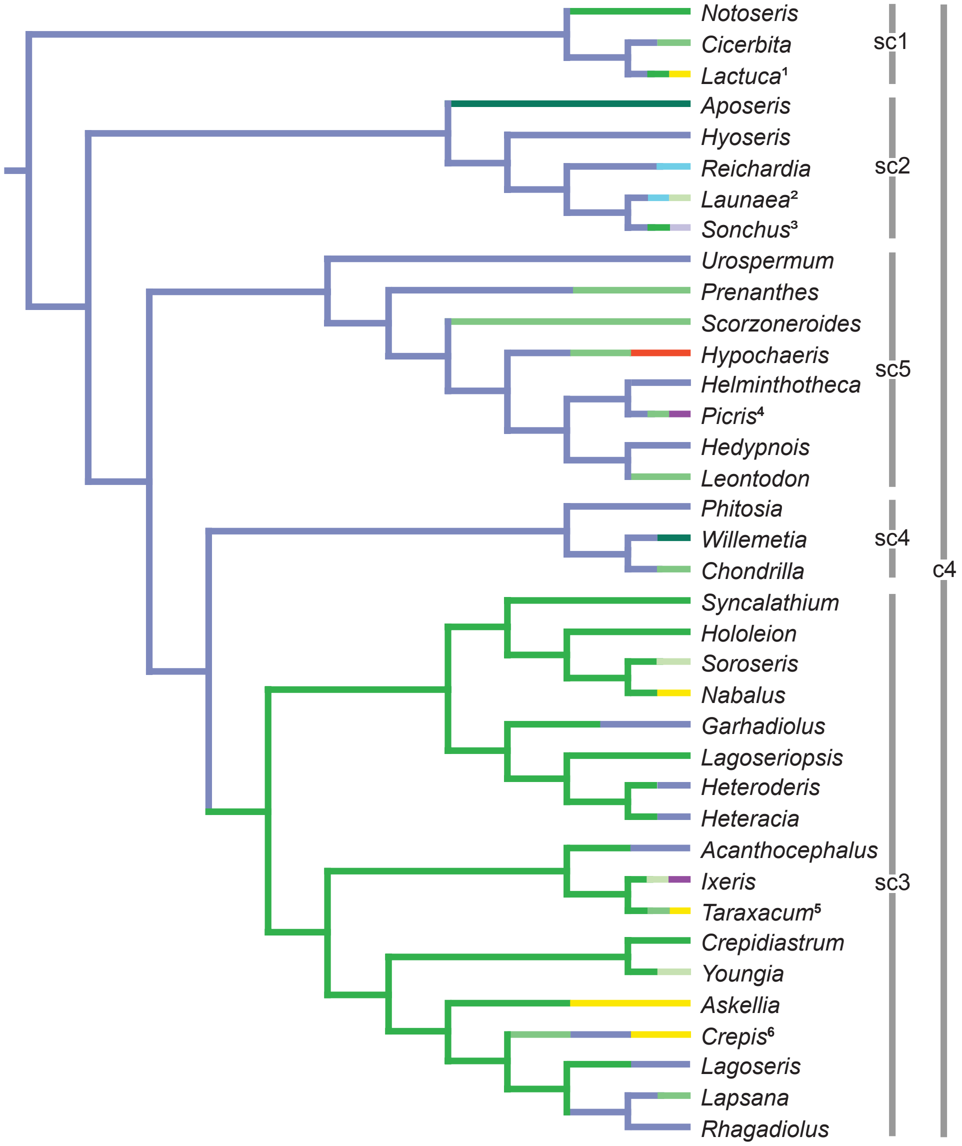

Fig. 24.9. Biogeography of clade 4 of the tribe Cichorieae mapped on the scheme of the ITS phylogeny in Fig. 24.2. Included are only genera for which molecular data are available. — Abbreviations: c4 = clade 4; sc1 = subclade 1, Lactucinae; sc2 = subclade 2, Hyoseridinae; sc3 = subclade 3, Crepidinae; sc4 = subclade 4, Chondrillinae; sc5 = subclade 5, Hypochaeridinae. — Notes: [1]also in tropical Africa and Eurasia; [2]also in Central and East Asia and Western Australia; [3]also in tropical Africa, South and Southeast Asia, Australia and New Zealand; [4]also in tropical Africa; [5]also in North and South America; [6]also in tropical Africa, Central and East Asia and Mexico. See Fig. 24.10 for color chart.

supertree (=metatree), Funk et al. (2005) inferred a North African–Mediterranean origin of Cichorieae, as they form a clade together with the tribes Arctotideae, Liabeae and Vernonieae, which are thought to be of African origin, too (Funk et al. 2004, 2005). From North Africa and the Mediterranean, Cichorieae repeatedly spread into Eurasia and also reached North America where a monophyletic radiation took place (Lee et al. 2003; Funk et al. 2005).

Up to now, no ancestral area analysis for the tribe has been carried out. As for the distribution of the three basally branching subtribes, subtribe Warioniinae is restricted to northwestern Africa, Scolyminae to the Mediterranean region, while Scorzonerinae to the Mediterranean and Eurasia (Fig. 24.8).

The distribution of the terminal-branching clade 4, including five subtribes, is predominantly Mediterranean and Central/Eastern Asian but frequently with extensions

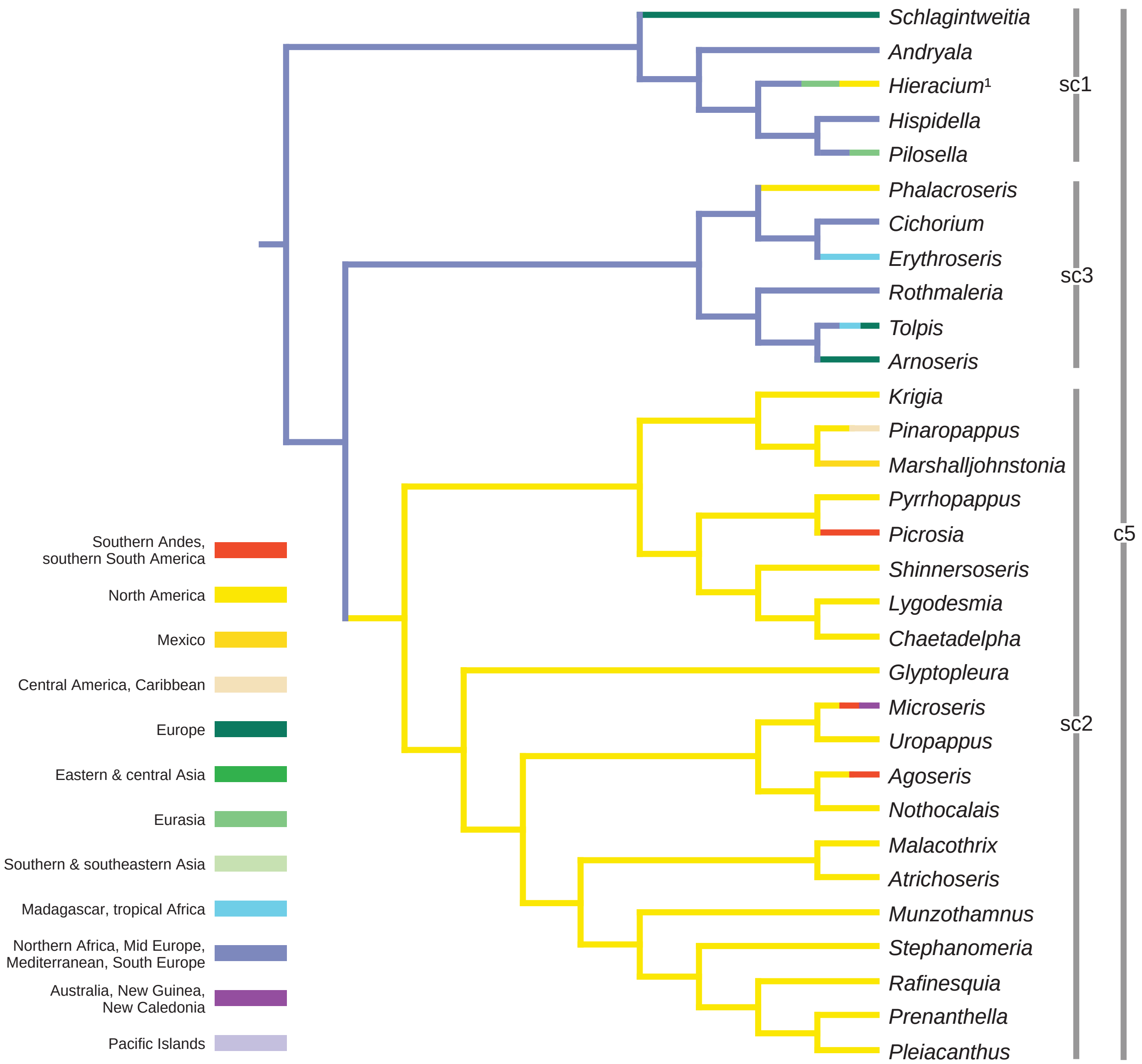

Fig. 24.10. Biogeography of clade 5 of the tribe Cichorieae mapped on the scheme of the ITS phylogeny in Fig. 24.3. Included are only genera for which molecular data are available. — Abbreviations: c5 = clade 5; sc1 = subclade 1, Hieraciinae; sc2 = subclade 2, Microseridinae; sc3 = subclade 3, Cichoriinae. — Notes: [1]also in tropical Africa, Central and East Asia and South America.

beyond this range (Fig. 24.9). Lactucinae have a Eurasian, African and North American distribution, commonly inhabiting montane to alpine, sub-boreal and boreal regions as well as steppe habitats, generally favoring cooler climatic conditions (Fries 1949; Meusel and Jäger 1992). Crepidinae have their highest species and generic diversity in Eurasia, with centers of distribution in Central/Eastern Asia and the Mediterranean region, but *Crepis* and *Taraxacum* extend to Africa and North America, the latter genus also to South America. Chondrillinae have a Eurasian distribution. Hyoseridinae have their centre of diversity in the Mediterranean region (*Aposeris*, *Hyoseris*, *Launaea*, *Reichardia*, *Sonchus*) extending to the mid-Atlantic Islands, Central and North-Eurasia, tropical Africa, Southwest and South-Asia, Australia/New Zealand, North America and the South Pacific Juan Fernández and Desventuradas Islands. Hypochaeridinae are centered in the Mediterranean region and Southwest Asia; only *Hypochaeris*, *Leontodon*, and *Picris* considerably extend beyond this area into the non-tropical part of Eurasia: *Leontodon* reaches the Ural Mountains (Meusel and Jäger 1992), *Hypochaeris* East Siberia (Vasilliev in Bobrov and Tzvelev 1964), and *Picris* extends even further eastwards to Kamchatka and Attu Island in the Aleutian archipelago but does not occur in North America (Stebbins 1971; Lack 1979). *Hypochaeris* (South America to Tierra del Fuego) and *Picris* (Australia, Tasmania and New Zealand; Holzapfel 1999) reached the southern hemisphere.

The distribution of the terminal-branching clade 5, including five subtribes, is chiefly Mediterranean/South West Asian and North American (Fig. 24.10). Cichoriinae are chiefly Mediterranean-Southwest Asian distributed but extend to North Europe, the mid-Atlantic Islands and South Africa, and with the exception of *Phalacroseris*, which occurs in western North America and traditionally has been treated as a member of the North American subtribes of Cichorieae (e.g., Lee et al. 2003; Bremer 1994). Microseridinae s.l., for which a single origin from their Old World ancestors has been supported by molecular analyses (Lee et al. 2003; Funk et al. 2005; and our results), are concentrated in southwestern North America, while species of some genera also occur in South America (e.g., *Microseris*, *Agoseris*). One genus is endemic to South America (*Picrosia*) and *Microseris* also reached Australia and New Zealand via long distance dispersal and diversified there (Van Houten et al. 1993). Hieraciinae are mainly Eurasian distributed but also occur in Africa and the Americas.

Lactuca, although not being the largest genus of the tribe, has perhaps the widest distributional area, being natively spread across the temperate and warm regions of the northern hemisphere and extending south of the equator in Africa and Asia (the distribution given by Lebeda et al. 2004, however, is partly erroneous due to uncritical inclusion of a number of species actually not belonging to *Lactuca* even in its widest sense). *Lactuca* is particularly species-rich and diverse in southern Eurasia, the African tropics, and in eastern North America (Meusel and Jäger 1992), with an altitudinal range from sea level to the alpine zone.

Also widely distributed is *Sonchus*, extending from the Mediterranean region to the mid-Atlantic Islands, temperate Eurasia, tropical Africa, Australia/New Zealand, North America and, apparently by long-distant dispersal, to the South Pacific Juan Fernández and Desventuradas Islands.

Hieracium and *Taraxacum*, the genera with the highest species number (if microspecies are considered) in the tribe, show distributional patterns similar to one another, occurring in Europe, Asia, North Africa and North and South America in boreal, temperate, humid, semiarid and arid regions, with a present center of diversity in Europe and the region between the Mediterranean and the eastern Himalaya, being synantropic in the southern parts of Africa, Australia and New Zealand. *Hieracium* has its center of diversity in the mountains of central and southern Europe in woody montane or alpine zones; in the Andes it can reach altitudes up to 4300 m. *Taraxacum* most often populates open habitats, reaching altitudes of up to 6000 m in the Himalayan region.

Genera with disjunct distribution in North America and Eurasia are *Askellia*, *Crepis*, *Hieracium*, *Lactuca*, *Nabalus*, and *Taraxacum*, with *Hieracium* also found in South America as far as Tierra de Fuego and the Falkland/Malvinas Islands. The species of *Agoseris* and *Microseris* are present in North and South America, while a remarkable South American-Eurasian disjunction occurs in *Hypochaeris*.

EVOLUTION

On a molecular base, Cichorieae are monophyletic if the variously placed genera *Gundelia* and *Warionia* are included; however, there is not a single morphological, anatomical or karyological autapomorphy characterizing Cichorieae. Wagenitz (1967) already referred to the convergent evolutionary traits of milky latex and flower symmetry in other tribes of Compositae allowing for two possible scenarios to explain the tribal evolution, either indicating a fast radiation in the early stage of the development of the tribes with incomplete lineage sorting, or hybridization events across lineages in the early stage of tribal development. The close relationships of Cichorieae within Compositae are weakly resolved as transitional characters indicative of relationships are scarce, pointing to adjacent independent evolutionary developments of the tribe with taxa of the basal lineages being descendants of this evolutionary scenario.

Despite that large amounts of molecular variation could be detected in the ITS region (478 characters in total of which 374 are parsimony informative), there is little resolution of relationships among major lineages within the tribe. Of five statistically well supported major lineages, two (clades 4 and 5) comprise more than 80% of the species of the tribes, indicating that repeated rapid radiation and diversification must have taken place in several evolutionary stages of Cichorieae.

Tremetsberger et al. (submitted) aimed at providing the best estimate of the age of Cichorieae and its subtribes based on available fossil evidence and DNA sequences. From the fossil record three different types of echinolophate pollen, i.e., the *Cichorium intybus* type (age 22–28.4 Myr), the *Scorzonera hispanica* type (min. age 3.4 Myr), and the *Sonchus oleraceus* type (min. age 5.4 Myr) were used to calibrate the phylogenetic tree, and estimates were calculated by using an uncorrelated relaxed molecular clock approach (Drummond et al. 2006). The results indicate a most probable origin of the tribe in the Late Eocene or Oligocene (25.8–36.2 Ma) in North Africa with a subsequent divergence of the main groups during the Late Oligocene or Early Miocene (Scolyminae 18.9–23.6 Ma; Scorzonerinae 17.4–21.2 Ma; and the core group of Cichorieae, comprising the species-rich clades 4 and 5, 19.9–24.9 Ma), which might be associated with the land bridge formation between the Afro-Arabian and Eurasian plates as result of northward drift of the Afro-Arabian plate. The subtribes of the core group diversified in the Middle and Late Miocene, a time of changing geological setting and climate in the Mediterranean region and Eurasia (e.g., uplift of the Alps, the Messinian Salinity Crisis and others; Mai 1995)

Four dispersal events to America seem to have occurred during the Miocene and Pliocene, the first resulting in a fast radiation and diversification of genera and species of Microseridinae in North America. Tremetsberger et al. (submitted) hypothesize that this radiation was associated with the uplift of mountain ranges along the west coast of North America and subsequent changes in climate and vegetation. Other dispersal events to America were restricted to genera that radiated at the specific level either in North America (*Crepis*), South America (*Hypochaeris*), or on both continents (*Hieracium*) involving hybridization, polyploidization and/or apomixis. Different distribution routes seem to have been involved; of these only those resulting in *Hypochaeris* on South America have been elucidated in detail (Samuel et al. 2003). Similar events led to the radiation of the otherwise Eurasian genus *Picris* in Australia. Only one tribe, Hyoseridinae, has an almost cosmopolitan distribution being present in Eurasia, Northern and Southern Africa, Australia, New Zealand and on some Pacific Islands, indicating accelerated molecular evolution, especially in the island endemics.

Parallel evolutionary trends of several characters suggest that hybridization across lineages and repeated rapid diversification played an important role in the evolution of and across several clades, which is indicated by first molecular analyses investigating maternal lineages and by comparison with nuclear data being bi-parentally inherited. Intergeneric hybridization events between ancestral lineages that resulted in cytoplasmic transfer from *Hieracium* subg. *Chionoracium* to *Pilosella* and from the introgressed *Pilosella* lineage to *Andryala* could be detected by Fehrer et al. (2007) and might also account for conflicting phylogenies of *Tolpis* (Kim et al. 1999b; Whitton et al. 1995; and this study), while it still needs to be examined for *Phitosia*, *Urospermum*, *Prenanthes* and possibly *Phalacroseris*.

Additional investigation within Cichorieae are still pending concerning their worldwide success, tendency to weediness, lack of apparent ability to move into tropical regions, and other factors that account for their present distribution and evolution.

ECONOMIC USES

Looking at Cichorieae as a whole, the number of agricultural species is rather small. *Mansfeld's Encyclopedia* (Jeffrey 2001) lists species belonging to *Chondrilla*, *Cichorium*, *Crepidiastrum*, *Gundelia*, *Hololeion*, *Ixeridium*, *Lactuca*, *Launaea*, *Pterocypsela* (= *Lactuca*), *Reichardia*, *Scolymus*, *Scorzonera*, *Sonchus*, *Taraxacum* and *Tragopogon*, all of them restricted in distribution to the Old World. For taxa occurring in the former Soviet Union an in-depth analysis lists a few more genera (Sokolov 1993). Only species of *Cichorium*, *Lactuca* and *Scorzonera* are cultivated widely; all other species seem to be of local importance only, although it is often difficult to get a clear view on the economic importance of plants used mainly as salads, potherbs, spinach and animal fodder, but rarely traded to any extent.

Basically Cichorieae are grown either for their leaves or their roots. Selection has led in some cases to cultivars with soft green leaves free of bitter substances, e.g., in lettuce (*Lactuca sativa*), or with colored leaves poor in bitter substances, e.g., in radicchio cultivars of chicory (*Cichorium intybus*). In other cases the ability to synthesize bitter substances persists, but is suppressed by keeping the plants during the development of their rosettes in the dark; this results in solid, blanched-leaf heads, e.g., the chicons in chicory. In other cases unblanched leaves are eaten as a cooked vegetable, e.g., in endive (*Cichorium endivia* L.) or only the soft innermost bleached leaves of the rosette are consumed, e.g., in dandelion (*Taraxacum officinale* Wigg. s.l.). The underground parts of several species are edible, but only Spanish salsify (*Scorzonera hispanica*) and salsify (*Tragopogon porrifolius*) are cultivated to any extent for this purpose. The use of the sweet roots of *Scorzonera deliciosa*

Guss. candied and eaten as confectionary is mentioned as a curiosity (Jeffrey 2001). The dried and roasted roots of chicory have been used historically as a substitute for roasted coffee beans, a habit made famous by the Viennese satirist Johann Nestroy, and are still used as an ingredient of caffeine-free instant coffee substitutes.

Diversification into cultivars is particularly marked in lettuce with considerable to hardly any heading, in chicory and in Indian lettuce (*Lactuca indica* L.; see Jeffrey 2001, as *Pterocypsela indica* (L.) S. Shih). Other plant parts are only occasionally used, e.g., juvenile flower heads of *Gundelia tournefortii* collected locally in the wild in the Near East and eaten as a cooked vegetable (Lev-Yadun and Abbo 1999).

In the Soviet Union under Stalin, during the period in which the political concept of economic autarky prevailed, the cultivation of perennial species of *Chondrilla*, *Scorzonera tau-saghyz* Lipschitz & Bosse and *Taraxacum kok-saghyz* Rodin as sources of milky sap for the production of rubber was a major issue. Not being in the position to grow tropical *Hevea brasiliensis* (A. Juss.) Müll. Arg. and at the same time needing large quantities of the commodity to develop the country further, great efforts were made both to better understand the taxa involved (e.g., Iljin 1930), all of them native in Central Asia, and to select and grow on a large scale variants with a high rubber content, the "Vavilon" in Leningrad acting as coordinating center (Rodin 1968). Nazi Germany under Hitler was equally focused on autarky and faced similar problems, but possessed no potential candidates for the production of rubber in its own flora. When parts of the Soviet Union were occupied by Nazi Germany, many *Taraxacum kok-saghyz* collections were therefore confiscated and subsequently grown and tested by researchers of the Kaiser-Wilhelm-Gesellschaft. Among others, prisoners from the concentration camp of Auschwitz did the work, with key political figures directly involved in the project (e.g., Heim 2003). The results being unsatisfactory, the cultivation of Cichorieae as a source for rubber has since been discontinued.

Whereas agricultural and horticultural species possess positive economic importance, weeds are best characterized as plants with negative economic importance. Among the 104 "world weeds" (Holm et al. 1997), no less than five belong to Cichorieae, all of them native in temperate Eurasia, but found today on all five continents. They are of no importance in their region of origin but only outside. Skeleton weed (*Chondrilla juncea* L.), introduced into Australia in the 1900s, may act as an example. It quickly infested huge areas of pastures and agricultural land reducing crop yields, regenerating from deep, branched taproots and seriously interfering with the wheat harvest. Other weedy Cichorieae, e.g., prickly sowthistle (*Sonchus asper* (L.) Hill), are pioneer species, invade disturbed sites, and infest the sites heavily due to copious seed production and a root system with numerous root buds, which develop after fragmentation of the root system to root-born shoots and new, independent plants (Rauh 1937: 460–461). Rusts, e.g., *Puccinia chondrillina* Bubák, and gale mites, e.g., *Aceria chondrillae* Canestrini, have been shown to be the most effective organisms to control these most noxious plants, which under suitable conditions are reported to spread at considerable speed, e.g., an average of 24 km/yr has been indicated for skeleton weed in southeast Australia. Several other Cichorieae, among them *Cichorium intybus*, corn sowthistle (*Sonchus arvensis* L.) and prickly oxtongue (*Helminthotheca echioides* (L.) Holub), behave also as aggressive weeds, notable in western North America and in Australia competing with crops and garden plants. Dandelion (*Taraxacum officinale*) seems to cause less economic loss than has been usually assumed, although it is a plant of some concern to those in search of a perfect lawn, with garden manuals recommending these weeds to be "cut out by hand using a knife or [be] killed by a herbicide applied with a 'spot-weeder'" (Huxley 1992).

Even for the enthusiast, Cichorieae are not very spectacular plants and less so for the horticulturalist who tends to focus on bright contrasting flower colors, unconventional form, special texture of leaves and stems or other showy characters as well as pleasant scent. In addition, the uninitiated is inclined to regard members of this tribe simply as weeds, which may have lessened horticultural interest in the group. Considering further that the tribe is a predominantly northern hemisphere group with comparatively few strictly tropical species, it is no surprise that only a limited number of taxa are of major horticultural importance, and all of these in use only in gardens of the temperate zone. Brickell (1999), dealing with very important "plants suitable for growing in temperate gardens world wide", lists only six genera of *Cichorieae*, i.e., *Catananche*, *Cicerbita*, *Cichorium*, *Crepis*, *Hieracium* and *Tolpis*. It seems that typical flower heads of the tribe with bright yellow ligules reminiscent of ubiquitous "weeds" such as *Taraxacum officinale* or *Picris hieracioides* L. were considered too trivial by the horticulturalist, who was and is attracted to species with *(1)* ligules in other colors, i.e., sky blue (*Catananche caerulea*; *Cicerbita alpina* (L.) Wall., *C. bourgaei* (Boiss.) Beauverd; *Cichorium intybus*), pink (*Crepis incana* Sm., *C. rubra* L.) or bright orange (*Crepis aurea*; *Pilosella aurantiaca* (L.) F.W. Schultz & Sch. Bip.), or *(2)* in flower heads with differently colored centers, e.g., in *Reichardia tingitana* or *Tolpis barbata*; a potential candidate with this character to further enrich gardens is *Hispidella hispanica*.

Although the much more comprehensive *New Royal Horticultural Society Dictionary of Gardening* (Huxley 1992) lists several more genera, e.g., the tomentose *Andryala* and the thistle-like *Scolymus*, as well as many more species of Cichorieae suitable for cultivation, the fact remains that the tribe comprises few ornamentals of any economic importance. Extremely few genera restricted in distribution to North America, i.e., *Agoseris*, *Nabalus* and *Krigia*, have ever been used as ornamentals. Furthermore, anthropogenic differentiation of species into cultivars is quite limited in the tribe, present, e.g., in *Catananche caerulea* and *Tragopogon porrifolius*.

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Appendix 24.1. Subtribal classification of Cichorieae

Suprageneric nomenclature is essentially based on Reveal (1997). Genera are listed in alphabetical order within the subtribes; their synonyms are listed in chronological order. The types, so far designated, are given for all generic names, including synonyms; in certain cases where such clarification appeared helpful, synonyms are added for the typifying binomials.

(1) Warioniinae Gemeinholzer & N. Kilian, **subtr. nov.**
Subtribus monogenerica et monospecifica insignis, a subtribibus ceteris capitulis multifloris homogamis tubulifloris corollis luteis leviter zygomorphis differt. Typus: *Warionia* Benth. & Coss.
1 species/1 genus – NW Africa
Warionia Benth. & Coss. (1872) [type: *W. saharae* Benth. & Coss.], monospecific

(2) Scorzonerinae Dumort. (1827)
ca. 300 species/10 genera – Europe, N Africa, SW to Central and and E Asia; several species introduced elsewhere
Note: The circumscription of *Scorzonera* is not yet fully settled and its revision in progress (Gemeinholzer, Kilian & Marhold, in prep.).
Epilasia (Bunge) Benth. (1873) [lectotype (designated by Lipschitz in Bobrov & Tzvelev, Fl. SSSR 29: 111. 1964): *E. hemilasia* (Bunge) C. Clarke]
Geropogon L. (1763) [lectotype (designated by Steudel, Nomencl. Bot., ed. 2, 1: 681. 1840): *G. glabrus* L. = *G. hybridus* (L.) Sch. Bip.], monospecific
Koelpinia Pall. (1776) [type: *K. linearis* Pall.]
Lasiospora Cass. (1822) [lectotype (designated by Tzvelev, Fl. Partis Eur. URSS 8: 45. 1989): *L. hirsuta* (Gouan) Cass.]
= *Pseudopodospermum* (Lipsch. & Krasch.) Kuth. [type: *P. molle* (M. Bieb.) Kuth.]
Podospermum DC. (1805) [type (cons.): *P. laciniatum* (L.) DC.]
Pterachaenia (Benth.) Lipsch. (1939) [type: *P. stewartii* (Hook. f.) R.R. Stewart], monospecific
Scorzonera L. s.str. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 177. 1929): *S. humilis* L.]
= *Gelasia* Cass. (1818) [type: *G. villosa* (Scop.) Cass.]
?= *Achyroseris* Sch.Bip. (1845) [type: *A. macrosperma* (DC.) Sch. Bip.]
?= *Avellara* Blanca & C. Díaz (1985) [type: *A. fistulosa* (Brot.) Blanca & C. Díaz]
Takhtajaniantha Nazarova (1990) [type: *T. pusilla* (Pall.) Nazarova]
Tourneuxia Coss. (1859) [type: *T. variifolia* Coss.], monospecific
Tragopogon L. (1753) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 313. 1913): *T. pratensis* L.]

(3) Scolyminae Less. (1832)
= Gundeliinae Benth. (1873), Catananchinae K. Bremer (1993)
12 species/4 genera – S Europe, N Africa, and SW Asia
Catananche L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *C. lutea* L.]
Gundelia L. (1753) [type: *G. tournefortii* L.]
Hymenonema Cass. (1817) [type: not designated]
Scolymus L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *S. maculatus* L.]

(4) Lactucinae Dumort. (1827)
ca. 230 species/3 genera – Europa, Africa, SW, Central and E Asia, North America; few species introduced elsewhere
Note: The generic arrangement provided here is still tentative and a revised classification (Kilian & Gemeinholzer, in prep.) in progress.
Cicerbita Wallr. (1822) [lectotype (designated by Kirpicnikov in Bobrov & Tzvelev, Fl. SSSR 29: 352. 1964): *C. alpina* (L.) Wallr.]
= *Mycelis* Cass. (1824) [type: *M. angulosa* Cass., nom. illeg. = *M. muralis* (L.) Dumort.]
= *Melanoseris* Decne. (1843) [lectotype (designated by Pfeiffer, Nomencl. Bot. 2: 259. 1874): *M. lessertiana* (DC.) Decne.]
= *Cephalorrhynchus* Boiss. (1844) [type: *C. glandulosus* Boiss.]
= *Chaetoseris* C. Shih (1991) [type: *C. lyriformis* C. Shih]
= *Zollikoferiastrum* (Kirp.) Kamelin (1993) [type: *Z. polycladum* (Boiss.) Kamelin]
Lactuca L. (1753) [type: *L. sativa* L.]
= *Mulgedium* F.W. Schmidt (1795) [lectotype (Shih in Acta Phytotax. Sin. 26: 390. 1988): *M. tataricum* (L.) DC.]
= *Scariola* F.W. Schmidt (1795) [type: *S. viminea* (L.) F.W. Schmidt] ≡ *Phaenixopus* Cass. 1826 [lectotype (designated by Pfeiffer, Nomencl. Bot. 2: 659. 1874): *P. decurrens* Cass., nom. illeg. = *L. viminea* L.)]
= *Steptorhamphus* Bunge (1852) [type: *S. crambifolius* Bunge]
= *Lactucopsis* Vis. & Pančić (1870) [lectotype (designated here): *L. aurea* Vis. & Pančić]
= *Lagedium* Soják (1961) [type: *L. sibiricum* (L.) Sojak]

= *Pterocypsela* C. Shih (1988) [type: *P. indica* (L.) C. Shih]
= *Lactucella* Nazarova (1990) [type: *L. undulata* (Ledeb.) Nazarova], monospecific
Notoseris C. Shih (1987) [type: *N. psilolepis* Shih]
= *Paraprenanthes* C. Shih (1988) [type: *P. sororia* (Miquel) C. Shih]
= *Stenoseris* C. Shih (1991) [type: *S. graciliflora* (DC.) C. Shih]
= *Kovalevskiella* Kamelin (1993) [type: *K. zeravschanica* (Kovalevsk.) Kamelin]

(5) Hyoseridinae Less. (1832)
= Dendroseridinae Benth. (1873), Sonchinae K. Bremer (1993)
ca. 150 species/5 genera – Europa, Africa, Asia, Australia, New Zealand, North America, S Pacific Juan Fernández and Desventuradas Islands off the coast of Chile; several species introduced elsewhere
Note: A revision of *Sonchus* s.l. (see Phylogeny) aiming at the morphological delimitation of monophyletic entities (compare Kim et al. 2007) at generic or subgeneric rank is in preparation by Kim & Mejías (pers. comm., March 2007).
Aposeris Cass. (1827) [type: *A. foetida* (L.) Less.], monospecific
Hyoseris L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *H. radiata* L.]
Launaea Cass. (1822) [type: *L. bellidifolia* Cass.]
= *Rhabdotheca* Cass. (1827) [type: *R. sonchoides* Cass.]
= *Brachyrhamphus* DC. (1838) [lectotype (designated by Britton & Wilson, Bot. Porto Rico 2: 276. 1925): *Lactuca intybacea* Jacq.]
= *Paramicrorhynchus* Kirp. (1964) [type: *P. procumbens* (Roxb.) Kirp.]
= *Hexinia* H.L. Yang (1992) [type: *H. polydichotoma* (Ostenf.) H.L. Yang]
Reichardia Roth (1787) [lectotype (designated by Britton, Fl. Bermuda: 382. 1918): *R. tingitana* (L.) Roth]
Sonchus L. (1753) [type: *Sonchus oleraceus* L.]
= *Aetheorhiza* Cass. (1827) [type: *A. bulbosa* (L.) Cass.]
= *Atalanthus* D. Don (1829) [lectotype (designated by Pfeiffer, Nomencl. Bot. 1: 321. 1873): *A. pinnatus* (L.f.) D. Don ≡ *Prenanthes pinnata* L. f. = *Sonchus leptocephalus* Cass.] ≡ *Taeckholmia* Boulos (1967), nom. illeg.
= *Dendroseris* D. Don (1832) [type: *D. macrophylla* D. Don]
= *Thamnoseris* Phil. (1895) [type: *T. lacerata* (Phil.) Johnst.]
= *Sventenia* Font Quer (1949) [type: *S. bupleuroides* Font Quer]
= *Kirkianella* Allan (1961) [type: *K. novae-zelandiae* (Hook.f.) Allan]
= *Babcockia* Boulos (1965) [type: *B. platylepis* (Webb) Boulos]
= *Embergeria* Boulos (1965) [type: *E. grandifolia* (Kirk) Boulos]
= *Lactucosonchus* (Sch.Bip.) Svent. (1969) [type: *L. webbii* (Sch. Bip.) Svent.] ≡ *Wildpretia* U. Reifenb. & A. Reifenb. (1996), nom. illeg.
= *Actites* Lander (1976) [type: *A. megalocarpa* (Hook.f.) Lander]
= *Chrysoprenanthes* (Sch.Bip.) Bramwell (2003) [type: *C. pendula* (Webb) Bramwell]

(6) Crepidinae Dumort. (1827)
= Lapsaninae Dumort. (1829), Rhagadiolinae Benth. (1873), Syncalathinae Lipsch. (1956), Taraxacinae Tzvelev (2007), Ixeridinae Sennikov (2008)
ca. 360 species apart from *Taraxacum* (with ca. 1600 apomictic species [Sterk 1987; IPNI 2007])/26 genera – Europe, Africa, Asia, North America; several species introduced elsewhere
Note: The re-circumscription of *Crepis* as a monophyletic genus (see Phylogeny) is not settled yet: parts of the genus are sister to *Lapsana* and *Rhagadiolus* (see Enke & Gemeinholzer 2008) and would necessitate the recognition of a morphologically ill-circumscribed separate genus *Lagoseris*, or, inclusion of *Lapsana* and *Rhagadiolus* in *Crepis*, or acceptance of *Crepis*, *Lapsana* and *Rhagadiolus* as paraphyletic genera, the first solution certainly being the worst. Very recently three new genera from central Asia, *Crepidifolium*, *Sonchella* and *Tibetoseris*, have been published by Sennikov (in Tzvelev 2007 and Sennikov and Illarionova 2007); molecular analyses of their status and systematic position are under way (Kilian & Gemeinholzer, in prep.).
Acanthocephalus Kar. & Kir. (1842) [type: *A. amplexifolius* Kar. & Kir.]
Askellia W.A. Weber (1984) [type: *A. nana* (Richardson) W.A. Weber]
Crepidiastrum Nakai (1920) [lectotype (designated by Pak & Kawano in Mem. Fac. Sci. Kyoto Univ., Ser. Biol. 15(1-2): 50. 1992): *C. lanceolatum* (Houtt.) Nakai]
= *Paraixeris* Nakai (1920) [lectotype (designated by Stebbins in J. Bot. (London) 75: 44. 1937): *P. denticulata* (Houtt.) Nakai]
?***Crepidifolium*** Sennikov (2007) [type: *C. tenuifolium* (Willd.) Sennikov] ≡ ***Geblera*** Kitag. (1937), nom. illeg., non Fisch & C.A. Mey. (1835)
Crepis L. (1753) [type: *C. biennis* L.]
= *Zacintha* Mill. (1754) [type: *Lapsana zacintha* L.]
= *Aracium* Neck. (1790) [type: *A. paludosum* (L.) Dulac]
= *Barkhausia* Moench (1794) [lectotype (designated by Cassini, Dict. Sci. Nat. 48: 429. 1827): *B. scariosa* Moench, nom. illeg. = *C. alpina* L.]
= *Wibelia* G. Gaertn. & al. (1801) [type: *W. foetida* (L.) Sch.Bip.] ≡ *Hostia* Moench
= *Berinia* Brign. (1810) [type: *B. andryaloides* Brign.]
= *Rodigia* Spreng. (1820) [lectotype (designated by Steudel, Nomencl. Bot., ed. 2, 2: 462. 1841): *R. commutata* Spreng.]
= *Psilochenia* Nutt. (1841) [type: *P. occidentalis* (Nutt.) Nutt.]
= *Dianthoseris* A. Rich. (1848) [type: *Dianthoseris schimperi* A. Rich.] ≡ *Nannoseris* Hedberg, nom. illeg (1957)
Dubyaea DC. (1838) [lectotype (designated by Stebbins in Mem. Torrey Bot. Club 19(3): 9. 1940): *D. hispida* (D. Don) DC.]
Faberia Hemsl. (1888) [type: *F. sinensis* Hemsl.]
= *Faberiopsis* C. Shih & Y.L. Chen [type: *F. nanchuanensis* (C. Shih) C. Shih & Y.L. Chen]
Garhadiolus Jaub. & Spach (1850) [lectotype (designated by Vassilczenko in Bobrov & Tzvelev, Fl. SSSR 29: 231. 1964): *G. angulosus* Jaub. & Spach]
Heteracia Fisch. & C.A. Mey. (1835) [type: *H. szovitsii* Fisch. & C.A. Mey.]
Heteroderis (Bunge) Boiss. (1875) [lectotype (designated by Leonova in Bobrov & Tzvelev, Fl. SSSR 29: 589. 1964): *H. pusilla* (Boiss.) Boiss.], monospecific
Hololeion Kitam. (1941) [type: *H. krameri* (Franch. & Sav.) Kitam.]
Ixeridium (A. Gray) Tzvelev (1964) [type: *I. dentatum* (Thunb.) Tzvelev]
Ixeris (Cass.) Cass. (1822) [type: *I. polycephala* Cass.]
= *Chorisis* DC. (1838) [type: *C. repens* (L.) DC.]
Lagoseriopsis Kirp. (1964) [type: *L. popovii* (Krasch.) Kirp.], monospecific
?***Lagoseris*** M. Bieb. (1810) [type: *L. crepoides* M. Bieb., nom. illeg. = *L. purpurea* (Willd.) Boiss.]
= *Pterotheca* Cass. (1816) [type: *P. nemausensis* Cass.]
= *Intybellia* Cass. (1821) [type: *I. rosea* Cass. = *C. purpurea* (Willd.) M. Bieb.] ≡ *Myoseris* Link (1822)
= *Trichocrepis* Vis. (1826) [type: *T. bifida* Vis.]
= *Phaecasium* Cass. (1826) [type: *P. lampsanoides* Cass., nom. illeg. =? *C. pulchra* L.] ≡? *Isianthes* Desvaux (1827) [type: *C. pulchra* L.] ≡ *Sclerophyllum* Gaudin (1829)
= *Cymboseris* Boiss. (1849) [type: *C. palaestina* Boiss.]

Lapsana L. (1753) [type: *L. communis* L.], monospecific

Lapsanastrum J.H. Pak & K. Bremer (1995) [type: *L. humile* (Thunb.) J.H. Pak & K. Bremer]

Nabalus Cass. (1825) [lectotype (designated by Britton & Brown, Ill. Fl. N.U.S., ed. 2, 3: 334. 1913): *N. trifoliolatus* Cass.]

Rhagadiolus Juss. (1789), nom. cons. [type: *R. edulis* Gaertn.]

?Sonchella Sennikov (2007) [type: *S. stenonema* (DC.) Sennikov]

Soroseris Stebbins (1940) [type: *S. glomerata* (Decne.) Stebbins]

= *Stebbinsia* Lipsch. (1956) [type: *S. umbrella* (Franch.) Lipsch.]

Spiroseris Rech. f. (1977) [type: *S. phyllocephala* Rech. f.], monospecific

Syncalathium Lipsch. (1956) [type: *S. sukaczevii* Lipsch. = *S. kawaguchii* (Kitam.) Y. Ling]

Taraxacum F.H. Wigg. (1780) [type: *T. officinale* F.H. Wigg.]

?Tibetoseris Sennikov (2007) [type: *T. depressa* (Hook. f. & Thomson) Sennikov]

Youngia Cass. (1831) [lectotype (designated by Sennikov in Komarovia 5: 108. 2008): *Y. lyrata* Cass.]

(7) Chondrillinae (W.D.J. Koch) Lamotte (1847)

28 species/3 genera – Central Europe, Mediterranean, SW, Central and E Asia; one species introduced elsewhere

Chondrilla L. (1753) [type: *C. juncea* L.]

Phitosia Kamari & Greuter (2000) [type: *P. crocifolia* (Boiss. & Heldr.) Kamari & Greuter], monospecific

Willemetia Neck. (1777–78) [type: *W. hieracioides* Neck., nom. illeg. ≡ *W. stipitata* (Jacq.) Dalla Torre] ≡ *Calycocorsus* F.W. Schmidt, nom. illeg.

(8) Hypochaeridinae Less. (1832)

= Leontodontinae Sch.Bip. (1834), Picridinae Sch.Bip. (1834)

ca. 150 species/8 genera – Europa, N, W and E Africa and Asia, with secondary evolutionary centers in Australia (*Picris*) and S South America (*Hypochaeris*).

Notes: For the time being *Prenanthes* s.str. has been placed with a question mark in this subtribe, based exclusively on data of the nuclear ITS region, while morphology does not provide any convincing support. Since the chloroplast marker furthermore indicates a basal position within Lactucinae, the ancestor of *P. purpurea* may most likely be hybridogenous, with one parent from Hypochaeridinae and the other from some other member of Clade 4 (see Phylogeny).

Hedypnois Mill. (1754) [lectotype (designated by Ferris in Abrams & Ferris, Ill. Fl. Pacific States 4: 587. 1960): *H. annua* Ferris ≡ *Hyoseris hedypnois* L. = *H. rhagadioloides* (L.) F.W. Schmidt]

Helminthotheca Zinn (1757) [type: *Picris echioides* L. ≡ *H. echioides* (L.) Holub] ≡ *Helminthia* Juss. (1789)

Hypochaeris L. (1753) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 309. 1913): *H. glabra* L.] ≡ *Achyrophorus* Adans. (1763)

= *Seriola* L. (1763) [lectotype (designated by Steudel, Nomencl. Bot., ed. 2, 2: 568. 1841): *S. laevigata* L.]

= *Trommsdorffia* Bernh.(1800) [type: *T. maculata* (L.) Bernh.]

= *Robertia* DC. (1815) non Scop. (1777) [type: *R. taraxacoides* (Loisel.) DC.]

= *Distoecha* Phil. (1891) [type: *D. taraxacoides* Phil.]

= *Heywoodiella* Svent. & Bramwell (1971) [type: *H. oligocephala* Svent. & Bramwell]

Leontodon L. (1753) [type (cons.): *L. hispidus* L.]

= *Apargia* Scop. (1772) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 310. 1913): *A. incana* (L.) Scop.]

Picris L. (1753) [type: *P. hieracioides* L.]

= *Spitzelia* Sch.Bip. (1833) [*S. aegyptiaca* Sch.Bip., nom. illeg. ≡ *P. asplenioides* L.]

= *Deckera* Sch.Bip. (1834) [lectotype (designated by Pfeiffer, Nomencl. Bot. 1(2): 1022. 1874): *D. asplenioides* (L.) Sch.Bip.]

Scorzoneroides Moench (1794) [type: *L. autumnalis* L. ≡ *S. autumnalis* (L.) Moench] ≡ *Oporinia* D. Don (1829)

= *Kalbfussia* Sch.Bip. (1833) [type: not designated]

Urospermum Scop. (1777) [type: *U. picroides* (L.) F.W. Schmidt ≡ *Tragopogon picroides* L.]

= *Daumailia* Arènes (1948) [type: *D. spinulosa* Arènes = *U. picroides* (L.) F.W. Schmidt]

Inclusion questionable: ***Prenanthes*** L. (1753) [lectotype (designated by Cassini in Cuvier, Dict. Sci. Nat. 34: 96. 1825): *P. purpurea* L.], monospecific?

(9) Hieraciinae Dumort. (1827)

ca. 20 species besides *Hieracium* (with ca. 770 sexually reproducing species + 5200 apomictic microspecies) and *Pilosella* (with ca. 110 sexually reproducing species + ca. 700 apomictic microspecies and weakly competitive hybrids [pers. comm. G. Gottschlich, Tübingen, April 2007], see also Bräutigam & Greuter 2007)/5 genera – Eurasia and extending to Africa, North and South America

Andryala L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *A. integrifolia* L.]

= *Pietrosia* Nyár. (1999) [lectotype (designated by Sennikov in Komarovia 1: 77. 1999): *P. laevitomentosa* Sennikov]

Hieracium L. (1753) [lectotype (designated by Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3: 328. 1913): *H. murorum* L.]

= *Stenotheca* Monnier (1829) [lectotype (designated by Garland in Taxon 39: 121. 1990): *S. subnuda* Monnier]

Hispidella Lam. (1789) [type: *H. hispanica* Lam.], monospecific

Pilosella Hill. (1756) [type: *Hieracium pilosella* L.]

Schlagintweitia Griseb. (1853) [type: *S. intybacea* (All.) Griseb.]

(10) Microseridinae Stebbins (1953)

= Stephanomeriinae Stebbins (1953), Malacothricinae K. Bremer (1993), Glyptopleurinae Joongku Lee & B.G. Baldwin (2004), Krigiinae Joongku Lee & B.G. Baldwin (2004), Lygodesmiinae Joongku Lee & B.G. Baldwin (2004), Pinaropappinae Joongku Lee & B.G. Baldwin (2004), Pyrrhopappinae Joongku Lee & B.G. Baldwin (2004)

ca. 115 species/22 genera – North and South America, one species *(Microseris)* in Australia and New Zealand

Note: The principally North American genera plus the South American *Picrosia*, excepting *Phalacroseris*, are treated as a single subtribe, considering their radiation from a single common ancestor (see Phylogeny). The suprageneric classification of the American clade by Lee & Baldwin (2004) should thus be applied at an informal subordinate rank. Generic circumscription is in several cases still disputable, affecting, e.g., *Malacothrix*, which has been shown to be polyphyletic (Lee et al. 2003).

Agoseris Raf. (1817) [lectotype (designated by Jones in Abrams & Ferris, Ill. Fl. Pacific States 4: 562. 1960): *A. glauca* (Pursh) Raf.]

Anisocoma Torr. & A. Gray (1845) [type: *A. acaulis* Torr. & A. Gray], monospecific

Atrichoseris A. Gray (1884) [type: *A. platyphylla* (A. Gray) A. Gray], monospecific

Calycoseris A. Gray (1853) [type: *C. wrightii* A. Gray]

Chaetadelpha S. Watson (1873) [type: *C. wheeleri* S. Watson], monospecific

Glyptopleura D.C. Eaton (1871) [type: *G. marginata* D.C. Eaton]

Krigia Schreb. (1791) [type (cons.): *K. virginica* (L.) Willd.]

Lygodesmia D. Don (1829) [lectotype (designated by Pfeiffer, Nomencl. Bot. 2: 183. 1874): *L. juncea* (Pursh) Hook.]

Malacothrix DC. (1838) [type: *M. californica* DC.]

Marshalljohnstonia Henrickson (1976) [type: *M. gypsophila* Henrickson], monospecific

Microseris D. Don (1832) [type: *M. pygmaea* D. Don]

= *Apargidium* Torr. & A. Gray (1943) [type: *A. boreale* (Bong.) Torr. & A. Gray]

= *Stebbinsoseris* K.L. Chambers (1991) [type: *S. heterocarpa* (Nutt.) K.L. Chambers]

Munzothamnus P.H. Raven (1963) [type: *M. blairii* (Munz & I.M. Johnst.) P.H. Raven], monospecific

Nothocalais (A. Gray) Greene (1886) [type: *N. troximoides* (A. Gray) Greene]

Picrosia D. Don (1832) [type: *P. longifolia* D. Don]

Pinaropappus Less. (1832) [type: *P. roseus* (Less.) Less.]

Pleiacanthus (Nutt.) Rydb. (1918) [type: *P. spinosus* (Nutt.) Rydb.], monospecific

Prenanthella Rydb. (1906) [type: *P. exigua* (A. Gray) Rydb.], monospecific

Pyrrhopappus DC. (1838) [type: *P. carolinianus* (Walter) DC.]

Rafinesquia Nutt. (1841) [type: *R. californica* Nutt.]

Shinnersoseris Tomb (1973) [type: *S. rostrata* (A. Gray) Tomb], monospecific

Stephanomeria Nutt. (1841) [type (cons.): *S. minor* (Hook.) Nutt.]

Uropappus Nutt. (1841) [lectotype (designated by Chambers in Contr. Dudley Herb. 4: 276. 1955): *U. lindleyi* (DC.) Nutt.]

(11) Cichoriinae Dumort. (1829)

= Phalacroseridinae Joongku Lee & B.G. Baldwin (2004)

ca. 25 species/6 genera – Europe, N, E and S Africa, Middle Atlantic Islands, SW Asia, SW North America

Note: The placement of the enigmatic SW North American *Phalacroseris* in subtribe Cichoriinae according to the molecular data (see Phylogeny) deserves further consideration in the light of morphology and phytogeography.

Arnoseris Gaertn. (1791) [type: *A. pusilla* Gaertn., nom. illeg. ≡ *A. minima* (L.) Dumort.]

Cichorium L. (1753) [lectotype (designated by Green, Prop. Brit. Bot.: 178. 1929): *C. intybus* L.]

Erythroseris N. Kilian & Gemeinholzer (2007) [type: *E. amabilis* (Balf. f.) N. Kilian & Gemeinholzer]

Phalacroseris A. Gray (1868) [type: *P. bolanderi* A. Gray], monospecific

Rothmaleria Font Quer (1940) [type: *R. granatensis* (DC.) Font Quer] ≡ *Haensleria* DC. (1838), non Lag. (1816), nom. illeg.

Tolpis Adans. (1763) [type: *T. barbata* (L.) Gaertn.]

= *Chlorocrepis* Griseb. (1853) [type: *C. staticifolia* (All.) Griseb.]

Chapter **25**

Arctotideae

Per Ola Karis, Vicki A. Funk, Robert J. McKenzie, Nigel P. Barker and Raymund Chan

HISTORICAL OVERVIEW

The tribe Arctotideae, described by Cassini (1819), was merged with the thistles by Lessing (1831, 1832), who gathered an unnatural assemblage of taxa into a large tribe Cynareae (now Cardueae). Bentham (1873a) re-established the tribe Arctotideae and recognized three subtribes later known as Arctotidinae (Figs. 25.1–25.4), Gorteriinae (Figs. 25.5–25.10), and Gundeliinae (Chapter 24). Hoffmann (1890–1894) approved Bentham's classification, although with some differences in generic circumscriptions. Beauverd (1915) surveyed the subtribe Arctotidinae while Lewin (1922) made a more comprehensive revision of this subtribe. Gorteriinae were monographed by Roessler (1959, 1973). Norlindh (1977) retained the three Benthamian subtribes, but he also included the monotypic subtribe Eremothamninae, as first proposed by Leins (1970) based on palynological data. Since Norlindh's (1977) review, studies of achene anatomy (Reese 1989), ray limb epidermis (Baagøe 1978), embryology (Ahlstrand 1992), external achene morphology (McKenzie et al. 2005), and a cladistic analysis of Gorteriinae morphology (Karis 2006) have been published. Molecular studies have been published on Arctotideae (Funk et al. 2004) and the two well-supported subtribes, Arctotidinae (McKenzie et al. 2006c; Funk et al. 2007; McKenzie and Barker 2008) and Gorteriinae (Funk and Chan 2008).

Bremer (1987) undertook a cladistic analysis of Asteraceae based on morphology using tribes or subtribes as terminals. Arctotideae were united with Cardueae due to the alleged synapomorphies of dissected, spiny leaves, and styles with a ring of sweeping hairs below the bifurcation. However, all molecular analyses, starting with the study by Kim and Jansen (1995), have yielded a monophyletic subfamily Cichorioideae s.str. wherein Arctotideae are nested, and so this chapter deals only with that placement. Early molecular studies containing Arctotideae representatives (Jansen et al. 1990; Bergqvist et al. 1995; Kim and Jansen 1995) included only 2–4 terminals from the tribe and so could not effectively deal with the question of monophyly. This was not the case in the morphological analysis by Karis et al. (1992). Here, *Eremothamnus* and *Arctotis* were united and placed in a large clade comprising Cichorieae, Liabeae, and Asteroideae, whereas *Berkheya* was placed as the sister taxon to this clade. One very uncommon family character indicated to be a synapomorphy for the clade *Eremothamnus* + *Arctotis* was soft anther appendages. However, the placement of genera was rather unstable in the analysis by Karis et al. (1992), and *Berkheya* was furthermore erroneously coded as not having arctotoid disc floret styles, i.e., with longer hairs in a ring well below the bifurcation. Admittedly, this feature is not so conspicuous in all species of *Berkheya*. Bremer conducted a morphological analysis (1994) of Arctotidinae and Gorteriinae as well as *Gundelia*, *Heterolepis*, and *Platycarpha*, and he used genera as terminals. Consequently, the monophyly of the genera could not be tested. Regardless of the choice of outgroup, the subtribes were monophyletic with *Platycarpha* sister to Arctotidinae, while Gorteriinae also included *Gundelia*. Karis et al. (2001) included one species each of *Arctotis*, *Haplocarpha* (both are Arctotidinae), *Berkheya*, *Didelta*, *Gazania* (all three are Gorteriinae), *Eremothamnus* and *Hoplophyllum*, in a study based solely on DNA sequence data from the chloroplast region *ndhF*.

All these terminals were united into a clade with 69% parsimony jack-knife support. Furthermore, the subtribes Arctotidinae and Gorteriinae, and the *Eremothamnus* + *Hoplophyllum* clade received 100%, 69%, and 100% parsimony jackknife support, respectively, but the three clades were united into a trichotomy.

PHYLOGENY

Funk et al. (2004) surveyed phylogenetic relationships in Arctotideae utilizing two chloroplast DNA regions (*ndhF*, *trnL-F*) and one nuclear DNA region (ITS). The dataset was considerably expanded in comparison with previous molecular investigations and included six terminals from Arctotidinae, eighteen from Gorteriinae, as well as all "problem genera" (see below; Table 25.1). It was indeed not straightforward to analyze the full dataset using many other Cichorioideae s.str. as the closest outgroup in different combinations (Funk et al. 2004). Yet, the subtribes received strong bootstrap support, whereas the support for Arctotideae including *Heterolepis*, and *Eremothamnus* + *Hoplophyllum* (the latter two genera are herein classified in Eremothamneae; see Chapter 26) was below 50%. The strong morphological (Bremer 1994; Funk et al. 2004; Karis 2006, 2007) and molecular support (Funk et al. 2004) for both subtribes as well-supported clades, in combination with an increased number of researchers studying these taxa, subsequently led to separate phylogenetic analyses of the subtribes (see Biogeography section below). *Heterolepis* (Chapter 31), *Eremothamnus* and *Hoplophyllum* (Eremothamneae; Chapter 26), *Platycarpha* (Plathycarpheae; Chapter 29), and *Gundelia* (Cichorieae; Chapter 24) were all at one time placed within Arctotideae. However, they are herein treated as separate clades (see Chapter 23 for an overview) and will not be considered further in this chapter.

Arctotidinae

Species relationships within Arctotidinae have been the focus of several recent molecular phylogenetic studies based on non-coding and coding cpDNA and ITS sequence data (Funk et al. 2004; McKenzie et al. 2006c; Funk et al. 2007; McKenzie and Barker 2008). A simplified phylogeny summarizing the major lineages in the subtribe is shown in Fig. 25.4. These studies demonstrated that *Arctotis* and *Haplocarpha* are polyphyletic as presently circumscribed. A combined analysis of the published sequences resolved nine major clades or monotypic lineages, each with strong bootstrap and Bayesian posterior probability support. Species that are currently placed in *Haplocarpha* were distributed among five lineages and two sections within *Arctotis* (sects. *Anomalae* and *Austroorientales*) and need to be removed in order to render the genus monophyletic. The *Landtia* clade comprises three *Haplocarpha* species, two of which (*H. nervosa* (Thunb.) Beauverd and *H. rueppellii* (Sch.Bip.) Beauverd) were previously placed in the segregate genus *Landtia* (e.g., Lessing 1831, 1832; Bentham 1873b), and is sister to the rest of the subtribe. *Haplocarpha oocephala* (DC.) Beyers, *H. scaposa* Harv. and *Dymondia margaretae* Compton comprise monotypic lineages diverging towards the base of the phylogeny. Most of the extant diversity in Arctotidinae is found in three major lineages that are indicated to have diverged rapidly; the nodes linking these lineages are weakly supported. The *Cymbonotus* clade contains the three Australian-endemic species as well as the southern African *Arctotis arctotoides* (L.f.) O. Hoffm. species complex and the East African *Haplocarpha schimperi* (Sch.Bip.) Beauverd. The clades *Arctotheca*, *Haplocarpha* s.str. and *Arctotis* sect. *Anomalae* form a well-supported lineage (McKenzie et al. 2006c; McKenzie and Barker 2008). *Arctotis* is the largest clade in Arctotidinae, comprising "perennial" and "annual" clades well supported by ITS data, and with the annual *A. breviscapa* Thunb. sister to both of these clades (Fig. 25.4). At present, few morphological synapomorphies supporting the major clades have been identified; instead, the clades are supported by combinations of morphological characters (R.J. McKenzie, unpub.).

Gorteriinae

Funk and coworkers (Funk et al. 2004; Funk and Chan 2008; Fig. 25.10) used nuclear and chloroplast DNA sequence data and obtained the same pattern within Gorteriinae throughout all analyses, viz. two groups, one containing *Gazania*, *Gorteria*, and *Hirpicium* (the *Gorteria* clade), a second comprising *Berkheya*, *Cullumia*, *Cuspidia*, *Didelta* and *Heterorhachis* (the *Berkheya* clade).

Funk and Chan (2008) furthermore obtained two well-supported sister groups within the *Berkheya* clade, viz. one containing the two species of *Didelta* plus *Berkheya spinosissima* Willd., and the other including the rest of the sampled taxa. Funk and Chan (2008) sampled 46 species with more than one terminal from all non-monotypic genera, and most monotypic genera were represented by more than one accession, which allowed monophyly of the genera to be examined. *Berkheya* and *Hirpicium* proved to be paraphyletic. This study also indicated that *Cullumia* might be paraphyletic since *Berkheya cruciata* Willd. was placed as sister to two *Cullumia* species, with three others in turn as their sister group. *Hirpicium* may have experienced past hybridization because *H. echinus* Less. has different sister groups in the nuclear and chloroplast data (Fig. 25.10). However, several strongly supported clades were found in *Berkheya* and the monotypic genera did not fall within any of them. Furthermore the study showed that some of the series recognized by Roessler (1959) corresponded to well-supported clades.

Table 25.1. Different classifications of Arctotideae. Estimated current number of species in each genus shown within parentheses. Modified after Funk et al. (2004).

Bentham 1873b (modified)	Heywood et al. 1977	Bremer 1994	Karis 2007	Barcelona 2008
Subtribe Arctotidinae Less.				
Arctotheca Vaill. (5)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Arctotis L., paraphyletic (60–70)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Cymbonotus Cass. (3)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Dymondia Compton (1)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Haplocarpha Less., paraphyletic (9)	Arctotinae	Arctotinae	Arctotidinae	Arctotidinae
Subtribe Gorteriinae Benth.				
Berkheya Ehrh., paraphyletic (79+)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Cullumia R. Br., paraphyletic? (15)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Cuspidia Gaertn. (1)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Didelta L'Hér. (2)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Gazania Gaertn. (17)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Gorteria L. (3)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Heterorhachis Sch.Bip. ex Walp. (1)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Hirpicium Cass., paraphyletic (13)	Gorteriinae	Gorteriinae	Gorteriinae	Gorteriinae
Heterolepis Cass. (3)	Gorteriinae (Norlindh) Mutisieae (Merxmüller)	Unassigned to subtribe	Unassigned to subtribe	Gorteriinae(?) or unassigned to subtribe
Subtribe Gundeliinae Benth.				
Gundelia L. (1)	Gundeliinae	Gorteriinae	Gundelieae DC. ex Lecoq & Juillet (Jeffrey)	Gundelieae
Eremothamnus O. Hoffm. (1)	Eremothamninae Leins	Unassigned to tribe	Unassigned to subtribe	Eremothamneae
Hoplophyllum DC. (2)	Vernonieae	Unassigned to tribe	Unassigned to subtribe	Eremothamneae
Platycarpha Less. (3)	Cynareae (Norlindh, rejected by Dittrich)	Unassigned to subtribe	Unassigned to subtribe	Platycarpheae

Morphological data from 43 ingroup terminals (Karis 2006) obtained the same sister group relationship between the *Gorteria* clade and *Berkheya* clade, but relationships within the latter remained uncertain. Again, *Berkheya* and *Hirpicium* were indicated to be paraphyletic. Karis (2006) found that several floral micromorphological characters were phylogenetically informative, and both sister groups were therefore defined by sets of diagnosing synapomorphies derived from anthers and styles, as well as from external morphology. As expected, the morphologically well-diagnosed small genera *Cullumia*, *Cuspidia*, *Didelta*, and *Heterorhachis* were all entrenched in the vast, paraphyletic *Berkheya* (Funk et al. 2004; Karis 2006; Funk and Chan 2008). Likewise, the morphologically diverse genus *Hirpicium* is split between two lineages in the *Gorteria* clade. In a separate study Howis (2007) reconstructed a phylogeny of *Gazania* based on sequences from nuclear ribosomal DNA (ETS, ITS) and four non-coding cpDNA regions. Of the fifteen species sampled, only seven were supported as being monophyletic; the remaining species formed a large, poorly resolved clade. This study only partially supported Roessler's (1959) morphology-based species circumscriptions in *Gazania*.

Phylogenetic investigations focused on the *Gorteria/Hirpicium* clade (F. Stångberg and P.O. Karis, unpub.), *Berkheya* clade (N. Netnou et al., unpub.), and *Cullumia* and *Didelta* (V.A. Funk and M. Koekemoer, unpub.) are in progress.

SUBTRIBAL TREATMENTS

Much of the taxonomy was covered in Karis (2007). Table 25.1 summarizes the current classification and number of species per genus. Since the two subtribes differ substantially in morphology, we have chosen to treat them separately throughout. As a result, there are two subtribal descriptions, rather than one disparate tribal description.

ARCTOTIDINAE

Taxonomy

Subtribe Arctotidinae (Cass.) Dumort., Anal. Fam. Pl.: 32. 1829 – Type: *Arctotis* L. (Figs. 25.1–25.4)

Leaves entire or lobed to pinnatisect, usually with woolly hairs. Heads pedunculate or scapose, but sessile in *Dymondia*, radiate. Scapes woolly, often with uniseriate septate hairs. Involucral bracts free, outer with foliaceous tips, inner obtuse with scarious tips. Ray florets usually 3-lobed, disc florets usually shallowly lobed, styles with a markedly thickened, basally truncate or tapering, apical part with broadly subulate sweeping hairs. Anthers distinctly ecaudate, apical appendages usually obtuse or rounded, soft, ± wrinkled, endothecium radial, collar usually inconspicuous, cells not reinforced. Achenes dorsiventrally asymmetric, usually with conspicuous abaxial ribs or wings, pericarp with subepidermal sclerifications of 1–2 oblong (cross-section) cell layers, testa epidermis with reinforcements, with twin hairs, short uniseriate or unicellular hairs. Pappus scales of very elongate, narrowly oblong cells, in 1–2 series, rarely coroniform or absent.

Arctotidinae can generally be distinguished in the field by their radiate capitulum, the free, scarious-margined inner involucral bracts, the rather shallowly lobed disc floret corolla, the dorsiventrally asymmetric, and often ribbed or winged, achenes, and the scaly pappus (which is absent in a few species). Another set of morphological and anatomical features can be considered to be synapomorphies and many of them are found in the anthers (McKenzie et al. 2006c; Karis 2007), viz. no tails, the short, blunt, soft and wrinkled apical appendage, inconspicuous filament collar (with *Cymbonotus* an exception), and radial endothecial tissue. Another probable synapomorphy is the small, subulate-ensiform sweeping hairs of the style (Karis 2006).

Norlindh (1977) accepted five genera in the subtribe Arctotidinae (Table 25.1): *Arctotheca*, *Arctotis*, *Cymbonotus*, *Dymondia*, and *Haplocarpha*. This taxonomy was retained by Karis (2007). However, recent molecular studies (Funk et al. 2004, 2007; McKenzie et al. 2006c; McKenzie and Barker 2008) have resulted in Fig. 4, which demonstrates that this classification does not reflect the evolutionary history of the group and significant taxonomic changes are needed. In addition, the alpha taxonomy of southern African Arctotidinae, particularly that of *Arctotis*, is confused and blighted by nomenclatural problems, which are in the process of being resolved (McKenzie et al. 2006a, b, 2008a, b; McKenzie and Barker 2007).

Morphology

Habit and life history. — Perennial shrublets and shrubs are common in Arctotidinae (Figs. 25.1–25.3). The orientation of the vegetative shoots in these species ranges from obligately prostrate through to erect in different species. Many of the prostrate species form adventitious roots to varying degrees (Fig. 25.3A). A truly rhizomatous habit is rare in Arctotidinae, and a significant number of the herbs are scapose (species of *Arctotheca*, *Arctotis*, *Cymbonotus*, and *Haplocarpha*) (Figs. 25.1–25.3). Fire is an important factor in the ecology of fynbos in South Africa (Cowling 1992). Many of the fynbos-endemic Arctotidinae respond to fire cycles by resprouting from either rhizomes or woody subterranean rootstocks (e.g., *Arctotis acaulis* L., *A. semipapposa* (DC.) Beauverd), or reseeding through seed germination. Species with an annual life history comprise a minority in the subtribe but notably comprise an important clade

Fig. 25.1. Arctotidinae: *Arctotis*. **A** *Arctotis arctotoides* (L.f.) O. Hoffm. (South Africa, Western Cape coast); this species is a member of a vegetatively polymorphic species complex centered in southeastern South Africa and Lesotho. **B** *A. acaulis* L. (South Africa, Northern Cape: *Funk and Koekemoer 12548*). **C** *A. acaulis* (South Africa, Northern Cape: *Koekemoer and Funk 1948*); the free involucral bracts of this species are characteristic of the subtribe. [Photographs: A, R.J. McKenzie; B, C, V.A. Funk.]

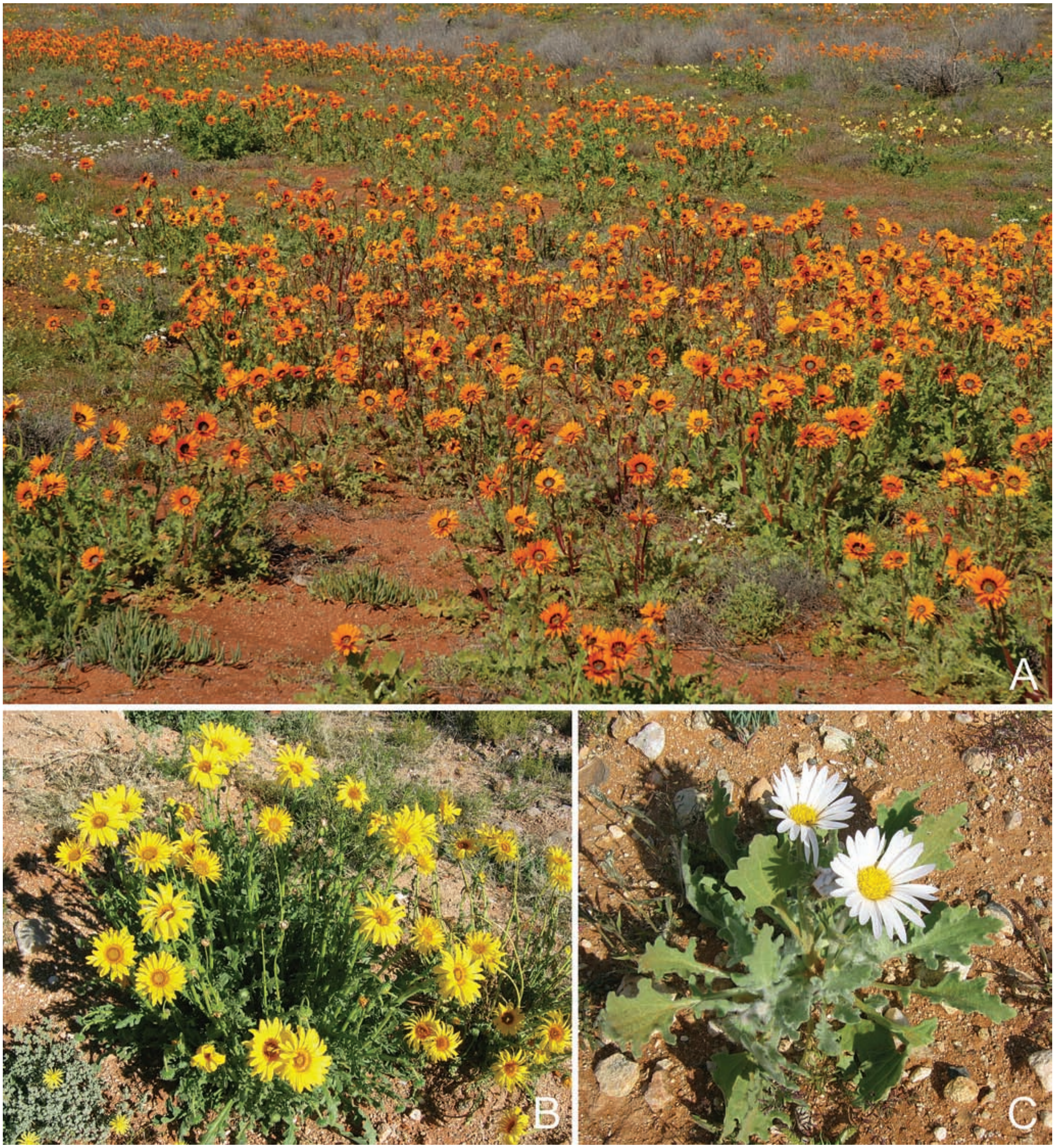
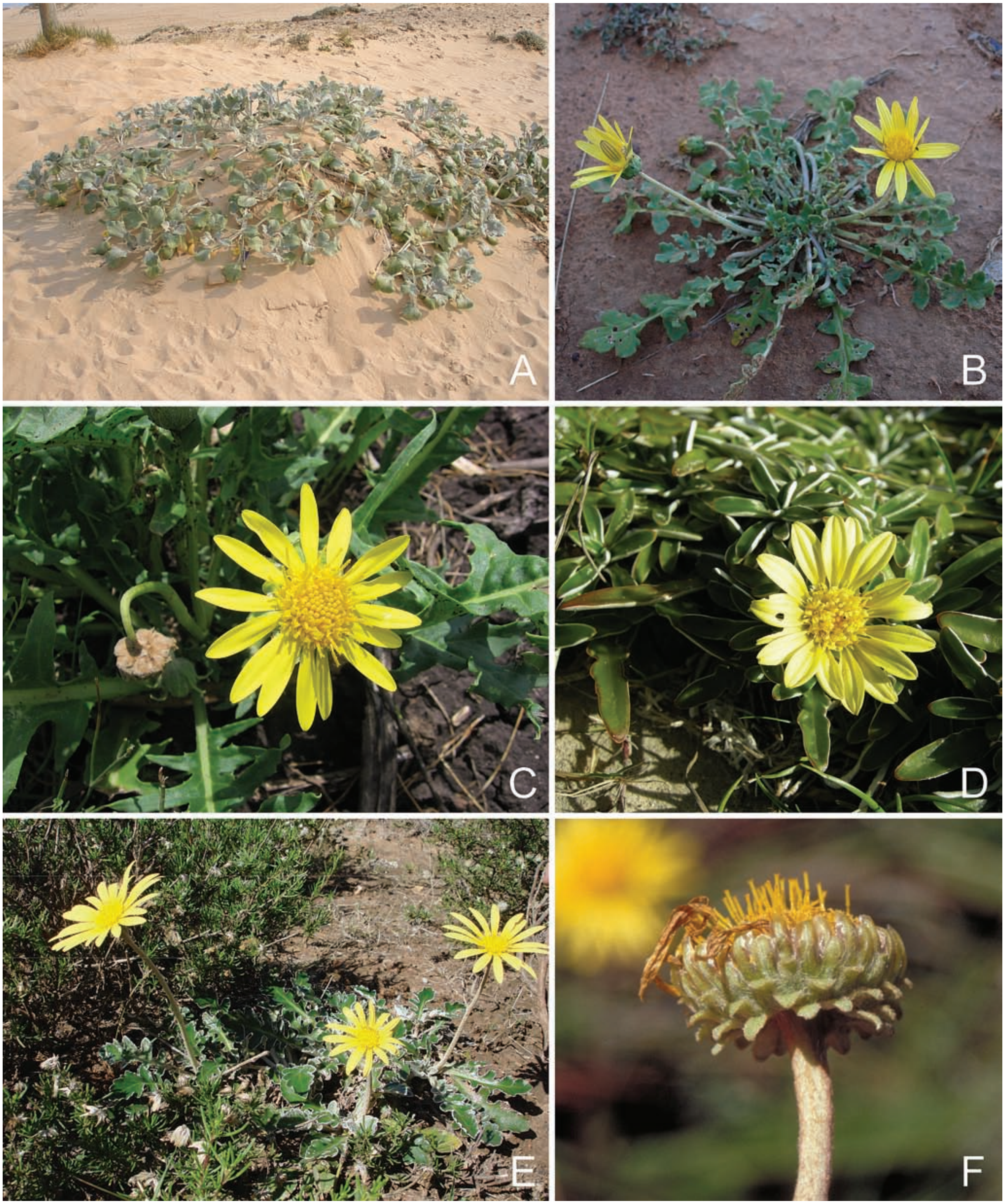


Fig. 25.2. Arctotidinae: *Arctotis* (continued). **A** *Arctotis fastuosa* Jacq. (South Africa, Northern Cape: *Funk and Koekemoer 12646*); *Arctotis* is one of the major components of the spectacular spring flower displays in the winter-rainfall region of southern Africa. **B** *Arctotis* sp. (Namibia). **C** *A. leiocarpa* Harv. (Namibia). [Photographs: A, V.A. Funk; B, C, C.A. Mannheimer.]

Fig. 25.3. Arctotidinae: *Arctotheca*, *Cymbonotus*, *Dymondia*, and *Haplocarpha*. **A** *Arctotheca populifolia* (P.J. Bergius) Norl. (South Africa, Eastern Cape); this semi-succulent species is a primary colonizer of coastal dunes. **B** *Arctotheca calendula* (L.) Levyns (South Africa, Eastern Cape); commonly known as "capeweed", this weedy annual has naturalized in numerous countries in



both hemispheres. **C** *Cymbonotus maidenii* (Beauverd) A.E. Holland & V.A. Funk (Australia, Queensland). **D** *Dymondia margaretae* Compton (South Africa, Western Cape). **E** *Haplocarpha lyrata* Harv. (South Africa, Eastern Cape). **F** *Haplocarpha scaposa* Harv. (South Africa, Free State: *Funk and Koekemoer 12406*); this species, like the others in this subtribe, has free involucral bracts. [Photographs: A, B, E, R.J. McKenzie; C, T. Bean; D, P. Sollinger; F, V.A. Funk.]

in *Arctotis* centered in the semi-arid parts of the winter-rainfall region of southern Africa.

Leaves. — All Arctotidinae have alternate leaves, but the scapose taxa have a more or less pronounced leaf rosette. Leaf shape varies considerably between and even within some species (e.g., *Arctotis arctotoides*) from simple and entire to pinnately compound in varying degrees. Certain *Arctotis* species (*Arctotis argentea* Ait., *A. linearis* Thunb.) inhabiting the Cape Floristic Region (Linder 2003) have xeromorphic linear leaves. Unlike Gorteriinae, no Arctotidinae species has spiny leaves. Owing to the tri- or multi-lacunar nodes it is common that three (often more) separate veins are distinguished already when entering the leaf in most Arctotidinae, regardless of whether the leaves are entire or dissected. Some *Arctotis* species have decurrent or auriculate leaf bases.

Trichomes. — As in all other tribes, various kinds of trichomes are common. Woolly hairs (Drury and Watson 1966) are commonly found on the stems, leaves, and involucres in all genera, if not in all species. These woolly hairs are frequently longitudinally oriented along the stem and form a felt-like indumentum. Uniseriate, often reddish-purple, septate hairs of differing length are abundant on the stems, peduncles, outer involucral bracts and sometimes along the leaf veins in some Arctotidinae. Both uniseriate glands of various length and biseriate, often short glands are common on various organs in the subtribe. There is a striking diversity of trichomes on the achenes of Arctotidinae (McKenzie et al. 2005), which is unparalleled in the rest of the tribe, or in fact, in most other clades of the family (see Achenes).

Capitula, involucres and receptacles. — All Arctotidinae have radiate capitula. In general, the heads are solitary in both herbs and woody members of the subtribe (Figs. 25.1–25.3). The general pattern is of female ray florets and hemraphroditic disc florets, but *Arctotheca* and *Arctotis* sect. *Anomalae* have sterile ray florets and in *Arctotis* s.str. the central disc florets are male or sterile while the outermost one or two series are hemraphroditic (McKenzie et al. 2005, 2006c). The involucres commonly comprise graded involucral bracts in numerous series (Fig. 25.1C). The involucral bracts are free and the outer bracts have foliaceous tips, whereas the inner bracts have a conspicuous, obtuse or rounded, scarious lamina (Fig. 25.1C). Arctotidinae have a smooth or shallowly honeycombed receptacle, and in some *Arctotis* species long, bristle-like scales are borne on the shallow alveoles.

Corollas. — Arctotidinae have "true" ray florets with a 3-lobed and 4-veined limb (Figs. 25.1–25.3) (Bremer 1988). Baagøe's (1978) survey of the ray floret corolla epidermis revealed that the epidermal cells in general are larger in Arctotidinae than in Gorteriinae, and that Arctotidinae have longitudinally striate cuticle ornamentation. Many Arctotidinae have yellow ray florets, but considerable diversification in ray floret color has occurred in *Arctotis* s.str. often within the same species. A contrasting darker or yellow spot at the base of the ray floret limb is especially common in *Arctotis* s.str. Typically, the disc corolla is yellow, but in many *Arctotis* s.str. and a few other species, the unopened disc corolla lobes are blackish, in contrast with the ray color. The disc corollas are shallowly lobed. In *Arctotis* s.str. species the abaxial surface of each disc floret corolla lobe bears a ± applanate, thickened elaboration so that the unopened florets form a flat, interlocking central disc; in other Arctotidinae the elaboration is ± tuberculate.

Stamens. — As in most clades outside the subfamily Asteroideae, the anthers of Arctotidinae are calcarate and without exception ecaudate (also noted by Lewin 1922). The short, soft and wrinkled apical anther appendages have long been noticed (Bremer 1994). An unusual attribute of Arctotidinae is their inconspicuous filament collar where the cells are devoid of wall reinforcements (although rather conspicuous in *Cymbonotus*), while all other taxa of the tribe investigated have elaborate collars with conspicuous wall reinforcements (Karis 2006, 2007; McKenzie et al. 2006c). A few species, notably the *Arctotheca* + *Haplocarpha* s.str. + *Arctotis* sect. *Anomalae* clade, have papillose filaments (Bremer 1994; McKenzie et al. 2006c). Ornamented or even hairy filaments otherwise occur in disparate taxa of Asteraceae (e.g., Cardueae, mutisioid clades, Coreopsideae). Another unusual characteristic of all Arctotidinae investigated so far is the radial endothecial tissue, i.e., the cells have reinforcements on the anticlinal walls all around the cells, which differ with the interpretation for at least Senecioneae, where radial reinforcements are confined to the inner anticlinal walls (Vincent and Getliffe 1988).

Styles (disc floret). — Even though the arctotoid style has been mentioned as a plausible synapomorphy for the tribe, there are subtle or even obvious differences both between and within the subtribes (Bremer 1994; Karis 2006, 2007). The only feature all arctotoid styles have in common is the ring of longer sweeping hairs well below the bifurcation, but the sweeping hairs themselves differ in size and shape, and they are ca. 20 µm long, patent and broadly subulate in Arctotidinae. Arctotidinae have disc floret styles with a thickened apical portion, and this is emphasized by a truncate base in *Arctotheca* and *Arctotis* sect. *Anomalae*, while it is less pronounced in the rest of the subtribe with their rounded to tapering bases. Many Arctotidinae style branches are uneven, or even markedly 3-lobed (*Dymondia*). Robinson (1984) examined style rotation of Asteraceae, i.e., the orientation of the style branches in relation to the orientation of the flowers in the head. The only representative of Arctotideae studied was *Haplocarpha scaposa*, which has radial disc styles but tangential ray styles, a combination otherwise found only in the subfamily Asteroideae (Robinson 1984). All styles throughout the tribe have an entire stigmatic surface that is safe to say must be plesiomorphic.

Achenes. — Almost all taxa of the tribe conform to the most common pattern of the family, where the pericarp is well developed, often lignified, and makes up the main protective envelope for the embryo. Reese (1989) studied achene anatomy of representative species from most genera of the tribe. The pericarp of Arctotideae is developed centripetally and is only a few cell layers thick, although it may be considerably thicker in ribs or ridges.

The pericarp of all investigated Arctotidinae have oblong (in cross-section) sclerified cells in one or two subepidermal layers. Reese (1989) observed that all Arctotidinae have a prominent, persistent testa epidermis with different reinforcement patterns. Crystals occur in the mesocarp in at least some Arctotidinae. The diversity of achene forms and trichomes in Arctotidinae is especially extraordinary considering the size of the clade. McKenzie et al. (2005) surveyed external achene and pappus morphology in Arctotidinae by means of SEM and concluded that it was possible to align the 40 investigated species into 13 more or less distinguished groups. The specific achene morphology is diagnostic for many species. The achenes of most Arctotidinae have a marked dorsiventral symmetry, and most of the species have two adaxial ribs and three abaxial, more or less pronounced ribs or wings of different size and shape. In the *Arctotis* s.str., *A.* sect. *Anomalae* and *Cymbonotus* clades the achenes have two or three well-developed wings that form either one or two furrows or "cavities" (Beauverd 1915; Lewin 1922; McKenzie et al. 2005). Four *Haplocarpha* species have rather smooth achenes with more weakly developed ribs, of which two species have a variable number of ribs in each achene (Reese 1989). The achenes of only a few species are entirely glabrous (McKenzie et al. 2005). Trichome diversity is wide in Arctotidinae (Lewin 1922; Herman 2001; McKenzie et al. 2005). Twin hairs are often present as a basal ring (or "coma", a term more often applied for hair tufts on seeds) associated with the carpopodium (Lewin 1922; McKenzie et al. 2005). Twin hairs also cover the achene surface in *Haplocarpha* s.str. (*H. lanata* Less. and *H. lyrata* Harv.), whereas most other Arctotidinae bear either uniseriate clothing trichomes with a long whip-like terminal cell, which often form a dense, woolly indumentum on at least part of the achene surface, or short uniseriate or unicellular trichomes of several forms (McKenzie et al. 2005).

The almost ubiquitous pappus in the form of scales of different sizes and shapes has been noted since Cassini (1819). However, some clades or species are devoid of a pappus, as in most of the *Cymbonotus* clade, a few *Arctotis* and two *Arctotheca* species (McKenzie et al. 2005). The scales are arranged in one or two, usually unequal series, and in three species the scales are at least partially fused forming a coroniform pappus (McKenzie et al. 2005; Karis 2006). So far as is known, all scales in Arctotidinae are composed of very elongate, narrowly oblong cells with thinner adaxial walls (Lewin 1922), thus enabling hygrochastic movement of the scales. At least in some *Haplocarpha* species, the scales have a thicker central part that continues into a narrow, almost bristle-like apical point. Most other Arctotidinae generally have obovate scales with an obtuse or rounded apex.

Pollen

Palynological data are not easily interpreted in terms of homologies, and Arctotideae do not depart from this general statement. Arctotideae pollen has cavities in the foot layer, but these are not confined to the areas between the apertures, as is the case in most caveate Asteroideae (Skvarla et al. 1977; Bremer 1987). However, it has also been suggested that a range of Arctotideae in fact share an ecaveate pattern (Bolick 1978, 1991; Bolick and Keeley 1994), but that this pattern should have evolved from an ancestral caveate type common to the entire vernonioid clade (Skvarla et al. 2005). Skvarla et al. (1977) recognized an "arctotoid" pollen type that was confined to the investigated samples of Arctotidinae. Subsequently, Vezey et al. (1994) characterized at least *Arctotis* pollen to be of the "lactucoid" exine stratification type, i.e., with an internal tectum of more than one layer (also found in Cardueae).

A recent paper described the pollen of all the major lineages of Arctotideae and discussed the pollen characteristics in detail (Wortley et al. 2008). From that work we find that the pollen of tribe Arctotideae is oblate-spheroidal and tricolporate, with a perforated tectum (Fig. 25.11). The pollen of the two subtribes differs in several ways.

The pollen of subtribe Arctotidineae is in general 16–27 μm in diameter, with narrow colpi (Fig. 25.11). The infratectum is 0.8–1.3 μm thick and comprises two columellate layers. The columellae are usually aggregated beneath the spines (except in *Dymondia*) and the grains are at least partially caveate. Arctotidineae pollen is echinate, with between 40 and 80 spines each 2–4 μm high and 3–4 μm in basal diameter, perforated throughout. The pollen of this subtribe may be distinguished by its smooth tectum and outer infratectum thinner than the inner infratectum.

Chromosome numbers

Arctotheca and *Arctotis* have a chromosome number of $2n = 18$, which is common in Asteraceae (Karis 2007). The heterogeneous *Haplocarpha* has $2n = 10$, 12, and 18 (Karis 2007) but has also been reported to display $2n = 30$ (*H. rueppellii*) and $2n = 36$ (*H. schimperi*) (Hedberg and

Hedberg 1977). This is consistent with the polyphyly of the genus (McKenzie et al. 2006c; McKenzie and Barker 2008).

Chemistry

Very little is known about the chemistry of Arctotidinae except that there are sesquiterpene lactones in *Arctotis arctotoides* (Sultana and Afolayan 2003).

Ecology

Dymondia margaretae may be a clonal species as it rarely, if at all, sets seeds in the field. *Dymondia* inhabits vlei edges and pans and withstands seasonal inundation and extreme drought conditions (Rourke 1974). The capitula of *Haplocarpha nervosa* and *H. schimperi* are "actively geocarpic", i.e., they bury their mature heads into the ground after anthesis and thus mature achenes may have little or no opportunity for dispersal (Barker 2005). The coastal primary-dune colonizer *Arctotheca populifolia* is "passively geocarpic", i.e., following anthesis the peduncle coils and often the heads are buried by subsequent accumulation of sand, creating a suitable habitat for germination without dispersal of the achenes (Barker 2005). McKenzie and Barker (2008) suggested running water may be an effective achene-dispersal vector in *H. nervosa* and *H. rueppelii*, which often grow in mesic habitats such as bogs or beside streams. The effectiveness of the pappus scales for dispersal of *Arctotis* achenes over long distances has been questioned (Lewin 1922). In some Arctotidinae, notably the *Cymbonotus* and "annual *Arctotis*" clades, the achenes are small and the pappus is lost or highly reduced. Despite their seemingly poor dispersability, both clades (especially the former) have achieved wide geographic distributions.

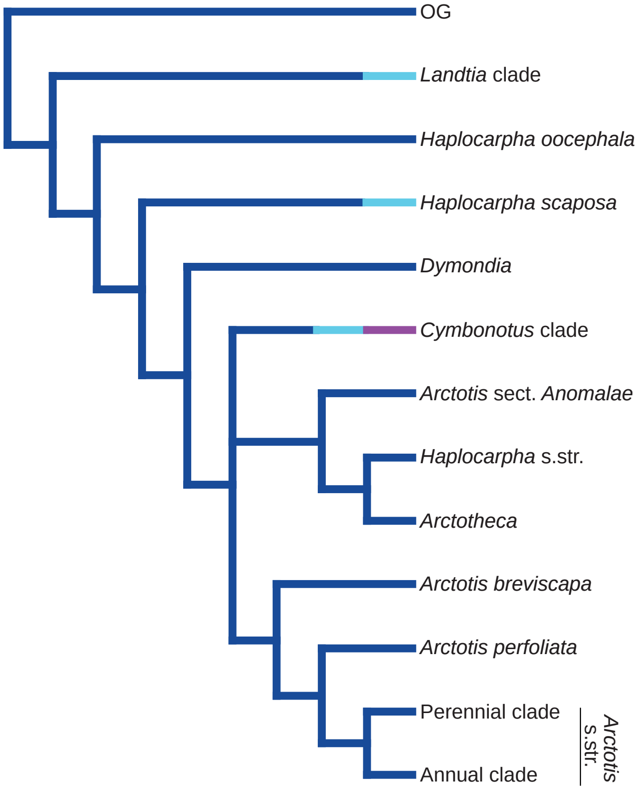


Fig. 25.4. Simplified phylogeny of Arctotidinae. The tree is adapted from McKenzie and Barker (2008) and Funk et al. (2007). Dark blue = southern Africa; light blue = tropical Africa and Madagascar; purple = Australia. See Chapter 44 for metatree of the family.

Biogeography

The phylogeny for Arctotidinae (Fig. 25.4) is color-coded for distribution, and it is clear that the extant major clades originated in southern Africa. Biogeographic relationships within Arctotidinae were explored by McKenzie and Barker (2008). In this subtribe the basalmost extant lineages are often found in mesic habitats and the accrual of xerophytic adaptations and invasion of semi-arid regions are indicated to be nested more highly in the phylogeny. The basal lineages have an afromontane-afroalpine distribution and tend to occur in mesic climates or perennially wet habitats, such as bogs, stream banks and seepages. The next extant lineage to diverge, *Dymondia margaretae*, inhabits seasonally flooded and summer-arid vleis on the Agulhas Plain, South Africa. One interpretation is that a preference for mesic habitats might be plesiomorphic in Arctotidinae (McKenzie and Barker 2008). The divergence of these lineages might have coincided with the establishment of a more humid regime during the early mid-Miocene (Dingle and Hendey 1984), which persisted in southern Africa until the late Miocene (Partridge 1997).

Most of the extant diversity in Arctotidinae is resolved into three well-supported lineages that are indicated to have diverged during a rapid radiation in southern Africa possibly during the late Miocene (McKenzie and Barker 2008). These lineages are centered in the Fynbos and Succulent Karoo biomes, which together correspond with what some authors define as the Greater Cape Floristic Region (GCFR; e.g., Born et al. 2007). McKenzie and Barker (2008) hypothesized that this radiation coincided with the trend towards increasingly seasonal rainfall and aridification in southern Africa following increased glaciation in Antarctica 14 Ma (Zachos et al. 2001) and strengthening of the South Atlantic high-pressure cell (Linder 2005), resulting in the dramatic speciation of the *Arctotis* s.str. clade in the currently winter-rainfall and presently more arid regions. Divergence of a clade within *Arctotis*, centered in semi-arid Namaqualand and with an exclusively annual life history was likely to have been an adaptation to the greater aridity and seasonal rainfall in that region.

A remarkable and well-corroborated example of long-distance dispersal from southern Africa to Australia is that of the *Cymbonotus* clade (Holland and Funk 2006; McKenzie et al. 2006c; Funk et al. 2007; McKenzie and Barker 2008). It is worth pointing out the huge distance involved, viz. well over 7000 km in a direct line for the two closest points (Funk et al. 2007). Within the same clade, migration from southern Africa to East Africa has given rise to *Haplocarpha schimperi* (McKenzie et al. 2006c; McKenzie and Barker 2008). One wonders what it is about the morphology of *Cymbonotus* clade that allows it to travel so far while others in the clade do not.

Economic uses

A few species are used in traditional medicine. In the Eastern Cape, extracts from *Arctotis arctotoides* are used by small-scale farmers to treat heart water in goats (Dold and Cocks 2001) and by Xhosa people to treat a variety of human ailments (Watt and Breyer-Brandwijk 1962). Compounds produced by *A. arctotoides* and *A. auriculata* Jacq. have microbial-inhibitory activity (Salie et al. 1996; Afolayan et al. 2002, 2007; Afolayan 2003; Sultana and Afolayan 2003).

Arctotis species have been hybridized to create a range of half-hardy perennial hybrids, which are popular ornamentals worldwide. The annual species *A. fastuosa* and *A. venusta* Norl. are also of horticultural importance.

Invasives

A number of Arctotidinae species have naturalized abroad principally in regions experiencing a Mediterranean-type climate. It is significant to note that each of these species exhibit weedy tendencies in their native ranges. Only one species, *Arctotheca calendula*, which is commonly known as “capeweed”, is classified as invasive, viz. in Australia (Groves et al. 2003) and California (Brossard et al. 2000). In Australia, *A. calendula* is a widespread weed on pastoral and agricultural land, and there has been much research into its ecology (e.g., Arnold et al. 1985; Thomson et al. 1998; Dunbabin and Cocks 1999). A bipyridyl herbicide-resistant biotype is known in Victoria, Australia (e.g., Powles et al. 1989). *Arctotheca prostrata* Britten is naturalized, but not declared to be invasive, in many of the same countries where *A. calendula* is found. In California it is reported to be “usually sterile” (Mahoney and McKenzie 2008) and therefore largely dependent on clonal spread. *Arctotis stoechadifolia* P.J. Bergius has naturalized on parts of the Australian coastline due to its popularity as a garden ornamental plant and its use as a dune stabilizer (Mahoney and McKenzie, 2008). In Australia the species is classified as a minor problem weed in natural ecosystems (Groves et al. 2003), where it may outcompete smaller indigenous plants and alter dune topography.

GORTERIINAE

Taxonomy

Subtribe Gorteriinae Benth., Gen. Pl. 2: 167, 211. 1873 – Type: *Gorteria* L. (Figs. 25.5–25.10)

Herbs or shrubs (rarely small trees in *Didelta spinosa* Ait.) with latex. Leaves entire or lobed to pinnatisect, spiny sometimes unarmed but then often tomentose-hispid with longitudinally striate hairs, usually also with woolly hairs. Capitula pedunculate, scapose or sessile, radiate, rarely discoid, receptacle deeply alveolate. Peduncles woolly, sometimes also with short or long glands. Involucral bracts connate to different degrees (free in *Didelta*), usually graded, spiny, spinulose, and glabrous or variously hairy. Ray florets usually 4-lobed, sterile disc florets deeply lobed, usually with sclerifications along the lobe margins. Anthers inconspicuously or conspicuously caudate, or ecaudate, apical appendage short to long, firm, endothecium usually without lateral wall thickenings or with some polarized, collar conspicuous. Achenes somewhat dorsiventrally asymmetric, usually ribbed, enclosed to different degrees in the receptacle alveoles, pericarp with subepidermal sclerifications of 1–2 roundish (in cross-section) cell layers, testa weakly developed only in *Gorteria*, usually with twin hairs, sometimes glandular. Pappus of small to large scales in 1–2 series, rarely absent.

In the field, Gorteriinae are recognized as latex-containing herbs or shrubs with leaves that either are spiny or tomentose to hispid, having more or less connate involucral bracts, sterile ray florets with often 4-lobed limbs, deeply alveolate receptacles, and a pappus of scales.

Norlindh (1977; Table 25.1) accepted nine genera in Gorteriinae. Karis (2007) maintained this taxonomy, but *Heterolepis* was unassigned to a subtribe. It is clear from recent studies (Funk et al. 2004; Karis 2006; Funk and Chan 2008) that *Berkheya* and *Hirpicium*, and maybe also *Cullumia*, are not monophyletic. Especially problematic is the circumscription of the largest genus *Berkheya*. Revisions of all genera are currently in progress.

Within Gorteriinae, *Gazania*, *Gorteria*, and *Hirpicium* made up a well-diagnosed clade in Bremer’s (1994) cladistic analysis of Arctotideae, and this was in line with earlier suggestions by Roessler (1959) and Leins (1970). Due to the approach of using genera as terminals, Bremer (1994) could only suggest that the large and heterogeneous genus *Berkheya* probably is paraphyletic. *Berkheya cruciata* was united with *Cullumia* in Funk and Chan’s (2008) extended analysis of Gorteriinae, which agrees with the placement of *B. cruciata* in Roessler’s (1959) treatment and in Karis’s (2006) tree, although the composition of the clades in question differs between the two cladistic studies. Two noteworthy features, viz. “endothecial wall thickening plate displaced towards the connective-facing

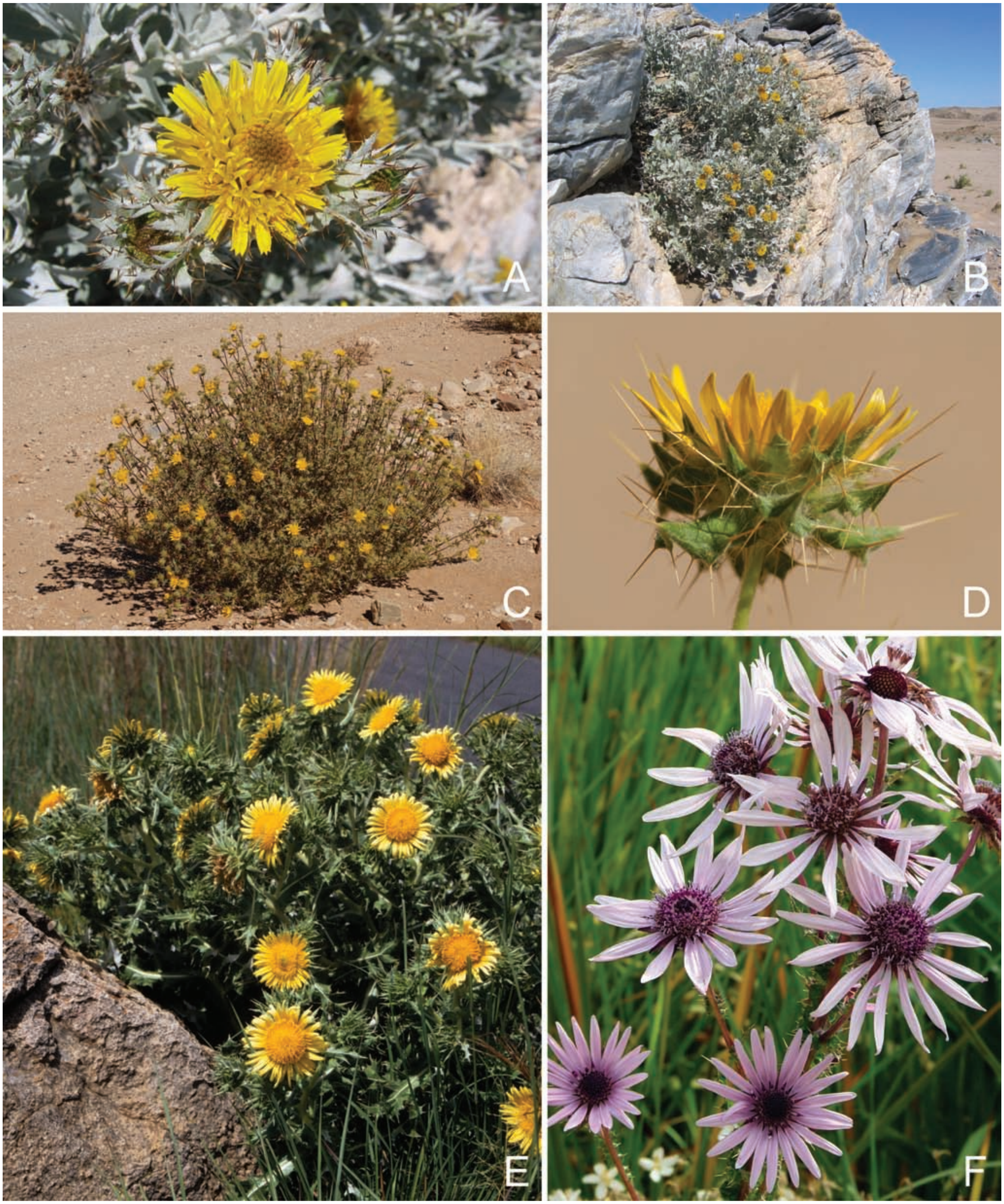


Fig. 25.5. Gorteriinae: *Berkheya*. **A, B** *Berkheya canescens* DC. (Namibia); the ray flowers of this subtribe often have four teeth, a character that is unique to Gorteriinae; the tomentose leaves are common in this tribe when taxa are found in very dry environments; as with many members of this tribe in Namibia, it grows in dry and/or rocky areas. **C, D** *Berkheya spinosissima* Willd. (Namibia: C, *V.A. Funk and M. Koekemoer 12694*; D, *V.A. Funk and M. Koekemoer 12692*); two individuals of this species were

side, ± sickle-shaped" and glabrous achenes, supported this small clade comprising *Cullumia* and *B. cruciata* (Karis 2006).

Morphology

Habit and life history. — Perennial shrublets and shrubs are common in the Gorteriinae, but *Cuspidia*, *Gorteria*, and some *Hirpicium* species are annuals. A truly rhizomatous habit is most common in *Berkheya* and *Gazania* and a few species of *Hirpicium* are scapose. As in the Arctotidinae, different adaptations to fire have arisen among fynbos endemics. For instance, *Berkheya barbata* (L. f.) Hutch. is a common re-sprouter on the Western Cape mountains, where young, often multi-stemmed exemplars are found in burnt areas, whereas *Berkheya cruciata* and *Heterorhachis* are examples of re-seeders.

Leaves. — Most Gorteriinae have alternate leaves, and the scapose taxa have a more or less pronounced leaf rosette, but a few species in the *Berkheya* clade have opposite leaves. Leaf shape varies considerably between and even within some species (e.g., *Gazania krebsiana* Less.) from simple and entire to pinnately compound to varying degrees. It is common that three (often more) separate veins are distinguished already when entering the leaf in some Gorteriinae, regardless of whether the leaves are entire or dissected. Some shrublet species inhabiting the Succulent Karoo and Fynbos biomes have xeromorphic, rather narrow leaves (e.g., *Hirpicium alienatum* Druce, *H. integrifolium* Less., *Berkheya angusta* Schltr., *B. angustifolia* (Houtt.) Merr., *Cullumia patula* Less., and *C. squarrosa* R. Br.), a situation paralleled in many plant groups inhabiting regions with a Mediterranean-type or semi-arid climate. *Didelta* usually has more or less succulent leaves. Field collection of specimens of many Gorteriinae generally renders bloodshed owing to their spinescent, often thistle-like character. Spiny leaves diagnose the *Berkheya* clade (although spines are found on the involucral bracts in *Didelta carnosa* Ait.) and the majority of the armed species have spines along the leaf margins and midribs, but a few species are also spiny on the upper leaf surface and stems. Some species of *Cullumia* have peculiar leaves with a sclerified margin in the form of a "frame" provided with a double or single row of spines. A few species of *Berkheya* have decurrent or auriculate petiole bases and some have strongly convex leaves and/or leaf lobes.

Trichomes. — As in Arctotidinae, various kinds of trichomes occur in Gorteriinae. Woolly hairs are commonly found on stems, peduncles, leaves, and involucres in all genera, if not in all species. These woolly hairs are frequently longitudinally oriented along the stem, but in some genera they are felted (e.g., *Gorteria*) or even floccose (some *Gazania*). Longitudinally striate hairs are one of the distinguishing features of the *Gorteria* clade (also containing *Gazania* and *Hirpicium*; Karis 2006, 2007). These hairs are sometimes very similar to the leaf hairs of Heliantheae, viz. rigid and provided with a flat or more raised multicellular base, but the 'Heliantheae' hairs are always uniseriate (Karis 2006, 2007). The corollas in *Gorteria* and some *Hirpicium* species have short, longitudinally striate hairs. Both uniseriate glands of various length and biseriate, often short glands, are common on various organs.

Capitula, involucres and receptacles. — Only ca. 15 species of the *Berkheya* clade are discoid while all remaining Gorteriinae are radiate. The heads are, in general, solitary and the size span is very large between the smallest species of *Gazania* and the large-headed *Berkheya* species. All Gorteriinae have sterile ray florets and the disc florets are hermaphroditic. The involucres commonly comprise graded involucral bracts in many series, but they are dimorphic in *Didelta* and even trimorphic in *Heterorhachis*. The involucral bracts are more or less connate (free in *Didelta*), usually acute, and they are all armed in the *Berkheya* clade but furnished with longitudinally striate hairs in the *Gorteria* clade. When the achenes are ripe the combination of fused involucral bracts and a lignified receptacle results in a hard, seed-bearing structure in all Gorteriinae but it is much less evident in *Berkheya*. More or less deeply alveolate receptacles distinguish all Gorteriinae, where the alveolar margins often are provided with projections in the form of teeth or smooth spines (Fig. 25.7B).

Corollas. — All Gorteriinae usually have 4-lobed, 5-veined ray florets (Figs. 25.5–25.9). However, the numbers of lobes is not consistent in a capitulum or on a plant and 2- or 3-lobed ray florets also occur. Most species of the *Berkheya* clade and several species of the *Gorteria* clade have yellow ray florets (Figs. 25.5–25.9). In *Gazania* and *Gorteria*, the ray floret color may vary profoundly within the same species and it is common for the ray floret limbs to have a contrasting, mostly darker, often ocellated spot at the base (Figs. 25.6E, F, 25.8). This reaches its most intriguing level of development in *Gorteria diffusa*, where in many populations one, two, three, or four of the rays bear

found in a dry river bed along the dirt road from Aus to Helmeringhausen; they were the only plants in bloom; note spiny involucral bracts and unique ray florets. **E** *Berkheya cirsiifolia* (DC.) Roessler (South Africa, Free State: *Funk and Koekemoer 12409*). A bushy herb of 5 meters with large heads, this species can have either yellow or white corollas. **F** *Berkheya purpurea* (DC.) Mast. (South Africa); the purple color of the florets is unusual in this genus; other *Berkheya* species are yellow or occasionally white. [Photographs: A, B, C.A. Mannheimer; C–F, V.A. Funk; E, M. Koekemoer.]

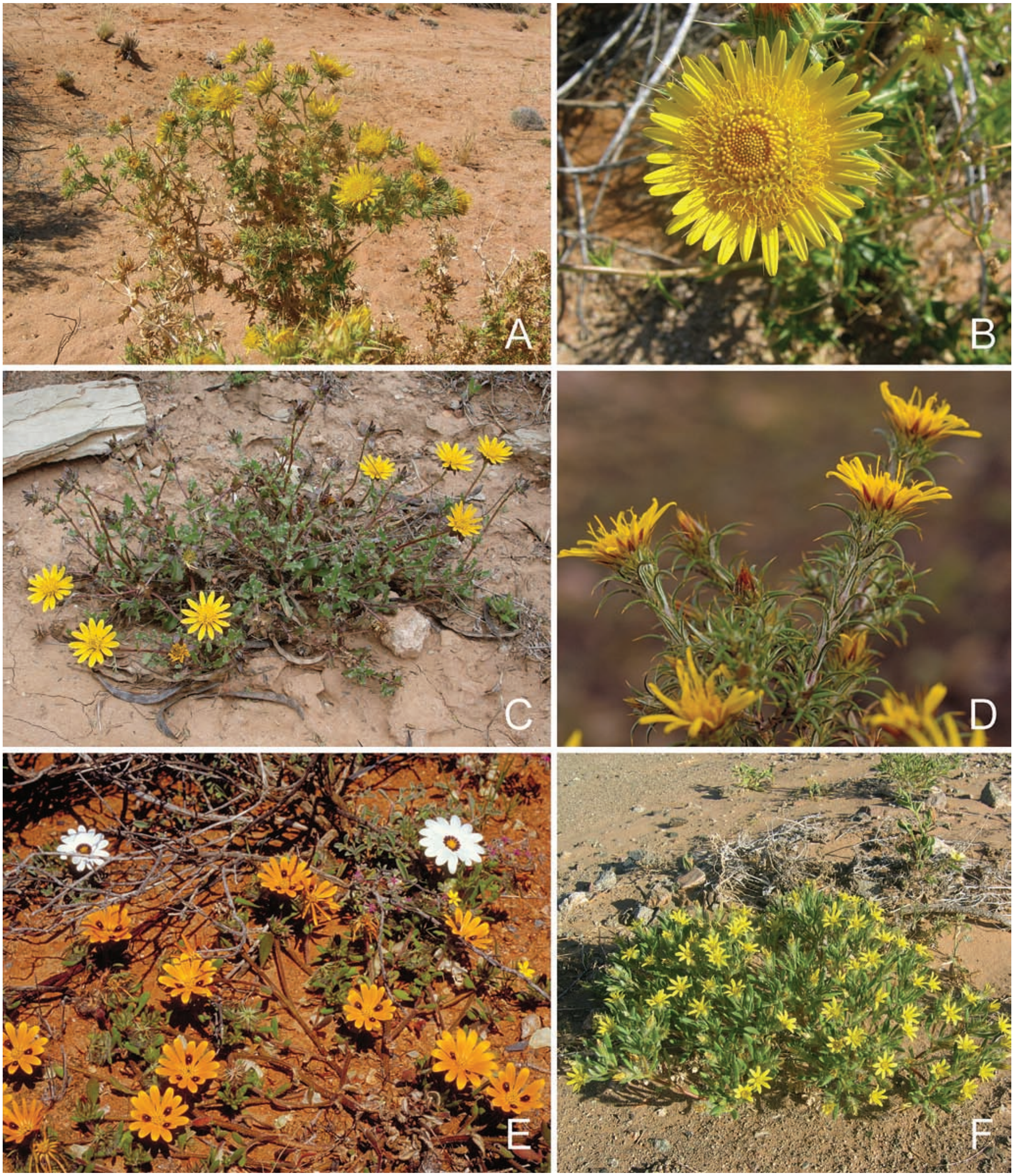


Fig. 25.6. Gorteriinae: *Berkheya*, *Cuspidia*, and *Gorteria*. **A, B** *Berkheya chamaepeuce* (S. Moore) Roessler (Namibia); this species is one of the very spiny, large-headed species. **C** *Cuspidia cernua* (L. f.) B.L. Burtt (South Africa, Eastern Cape: *McKenzie 1426*); this monotypic genus is the only annual in the *Berkheya* clade. **D** *Cullumia bisulca* Less. (South Africa: *Funk and Koekemoer 12271*); the leaves of this genus have spiny apices. **E** *Gorteria diffusa* Thunb. (South Africa: *Koekemoer and Funk 1945*); the dark spots on florets are believed by some to attract pollinators. **F** *Gorteria corymbosa* DC. (Namibia). [Photographs: A, B, F, C.A. Mannheimer; C, R.J. McKenzie; D, E, V.A. Funk.]

Fig. 25.7. Gorteriinae: *Didelta spinosa* Ait. **A** (South Africa, Northern Cape: *Funk and Koekemoer 12641*); this species is often a large shrub that is locally common. **B** Same as A; this species has an alveolate receptacle, which is common in this subtribe. **C** (South Africa, Western Cape: *Koekemoer and Funk 1936*); the corollas are entirely yellow. [Photographs, V.A. Funk.]

Fig. 25.8. Gorteriinae: *Didelta*, *Gazania*. **A** *Didelta carnosa* Ait. var. *tomentosa* (Less.) Roessler (Namibia: *Funk and Koekemoer 12685*); this collection was found growing on large sand dunes west of Lüderitz, Namibia; the leaves were covered with tomentum; this species has dark tips on the disc corollas, the head fragments into 3–5 parts, and each part has dark, stiff hairs; the heads of this plant had five parts. **B** *Didelta carnosa* Ait. var. *carnosa* (South Africa, Northern Cape: *Funk and Koekemoer 12648*);

a bulging, blackish spot that mimics a Bombyliid bee-fly species (Figs. 25.6E, F) (Johnson and Midgley 1997; Yamamura 2006). Almost all Gorteriinae have sclerified disc corolla lobe margins, and in general they are broad in the *Berkheya* clade but notably narrower in the *Gorteria* clade (Karis 2006).

Stamens. — The Gorteriinae anthers are calcarate, and are caudate with somewhat branched tails in the *Berkheya* clade (except in *Didelta*), while the *Gorteria* clade with few exceptions have ecaudate anthers. The appendages are also in general rather short compared with other non-Asteroideae clades and those in the *Gorteria* clade have seemingly fringed margins (Karis 2006). In contrast with the endothecium of Arctotidinae, the endothecium is highly variable in Gorteriinae (Karis 2006). Those in the *Gorteria* clade mostly display cells without plates, i.e., inner periclinal walls without reinforcements, while most members of the *Berkheya* clade have plates that in turn may be furnished with pores or slits. It should be pointed out that it is the outer pollen sacs that show different endothecial patterns, while the inner ones always are polarized.

Styles. — The sweeping hairs are ca. 50 μm long and erecto-patent, clavate to more acute but always mammillate in the *Berkheya* clade, and ca. 30 μm long, subulate-ensiform in the *Gorteria* clade (Karis 2006). In the *Gorteria* clade the sweeping hairs are arranged more or less in longitudinal rows. All style branches in Gorteriinae are tapering towards the apex.

Achenes. — Only a few Gorteriinae have oblong (in cross-section) sclerified cells in one or two subepidermal layers in the pericarp (Reese 1989), while the rest of the investigated species have cells about as long as wide (Reese 1989; Karis 2006). *Gorteria* has a weakly developed, disintegrating testa epidermis, which is coupled to the fact that the receptacle itself is the main protective cover for the embryo. Many Gorteriinae have subepidermal crystals in the testa (Reese 1989; Karis 2006). *Cullumia* is devoid of a carpopodium, and is further diagnosed by possessing elaiosomes, although they are rather inconspicuous. Gorteriinae achenes have a rather inconspicuous dorsiventral symmetry, often bear less conspicuous ribs, and are enclosed within the receptacular alveolae to differing degrees between the genera (Karis 2006). This is least apparent in *Gazania* (Karis 2006), while *Gorteria* has a strongly lignified receptacle enclosing the achenes, which have a much reduced pericarp. Only a few species are reported to be entirely glabrous (Karis 2006), and the hairy achenes all bear twin hairs of different form, length and color (Karis 2006, 2007). Only *Cuspidia* differs with twin hair-like uniseriate trichomes, and similar hairs are found in Arctotidinae (see above; McKenzie et al. 2005). Many of the Gorteriinae twin hairs are conspicuously forked or have very unequally long cells, and in *Cullumia* they are rarely deeply cleft. *Gorteria* has long, twisted, curly twin hairs, while *Gazania* have very long, straight hairs. Most achenes in *Gazania* and *Hirpicium* have large, globose glands in distinct rows, but smaller glands are also present in *Gorteria* (Karis 2006, 2007).

Some clades or species are devoid of a pappus, such as some *Berkheya* and most *Cullumia* species (Karis 2006, 2007). The scales are arranged in one or two series, sometimes more in some species, that may be alike or dimorphic, and in some cases they are pigmented. The pappus scales in Gorteriinae consist of short cells that do not show a trace of the anatomy found within Arctotidinae, but the diversity is nevertheless large. It is not surprising that the pappus is reduced or absent in the more or less enclosed achenes of some Gorteriinae (*Gorteria*, *Cullumia*).

Karis (2006) reported latex (the actual milky juice) or laticifers (the cells producing or containing the latex) from 26 investigated species of Gorteriinae. It may be safe to conclude that laticifers are present in all Gorteriinae, but so far as is known latex is absent in all other Arctotideae taxa. The presence of latex is not so evident in the field in, e.g., ericoid species such as *Hirpicium alienatum*, *H. integrifolium*, *Cullumia* and *Cuspidia*, whereas some *Gazania* and many *Berkheya* species really "bleed" if a leaf or a branchlet is broken.

Pollen

Echinate pollen is common in the subtribe, but many species and genera have lophate pollen. The latter kind of grain, which is found only outside the subfamily Asteroideae, was surveyed throughout the family by Blackmore (1986). Lophate pollen in many Gorteriinae is distinguished from similar pollen in other clades in that it has tectal microperforations of two considerably different sizes, instead of just one. Leins and Thyret (1971)

this collection was found in Namaqua National Park; its leaves are glabrous and the head fragments into three parts. **C** *Gazania krebsiana* Less. (South Africa, Northern Cape: *Koekemoer and Funk 1947*); this species is extremely variable in the color of the ray limb. **D** *Gazania* sp. (South Africa, Northern Cape, Nieuwoudtville: US); the spectacular displays of the winter rainfall area of southern Africa consist of many different members of Compositae; in this photo there are at least five tribes represented: *Gazania* and *Gorteria* (Arctotideae), *Cotula* (Anthemideae), *Monoculus* (Calenduleae), *Senecio* (Senecioneae), and *Felicia* (Astereae). **E** *Gazania leiopoda* (DC.) Roessler (South Africa, Northern Cape). **F** *Gazania* ×*rigens* Gaertn. "Sunshine Mix" or "Treasure Flowers" (native to South Africa, cultivated: OKL Greenhouse); *Gazania* is widely cultivated and hybrids can have brightly colored corollas. [Photographs: A–E, V.A. Funk; F, C. Lemke.]

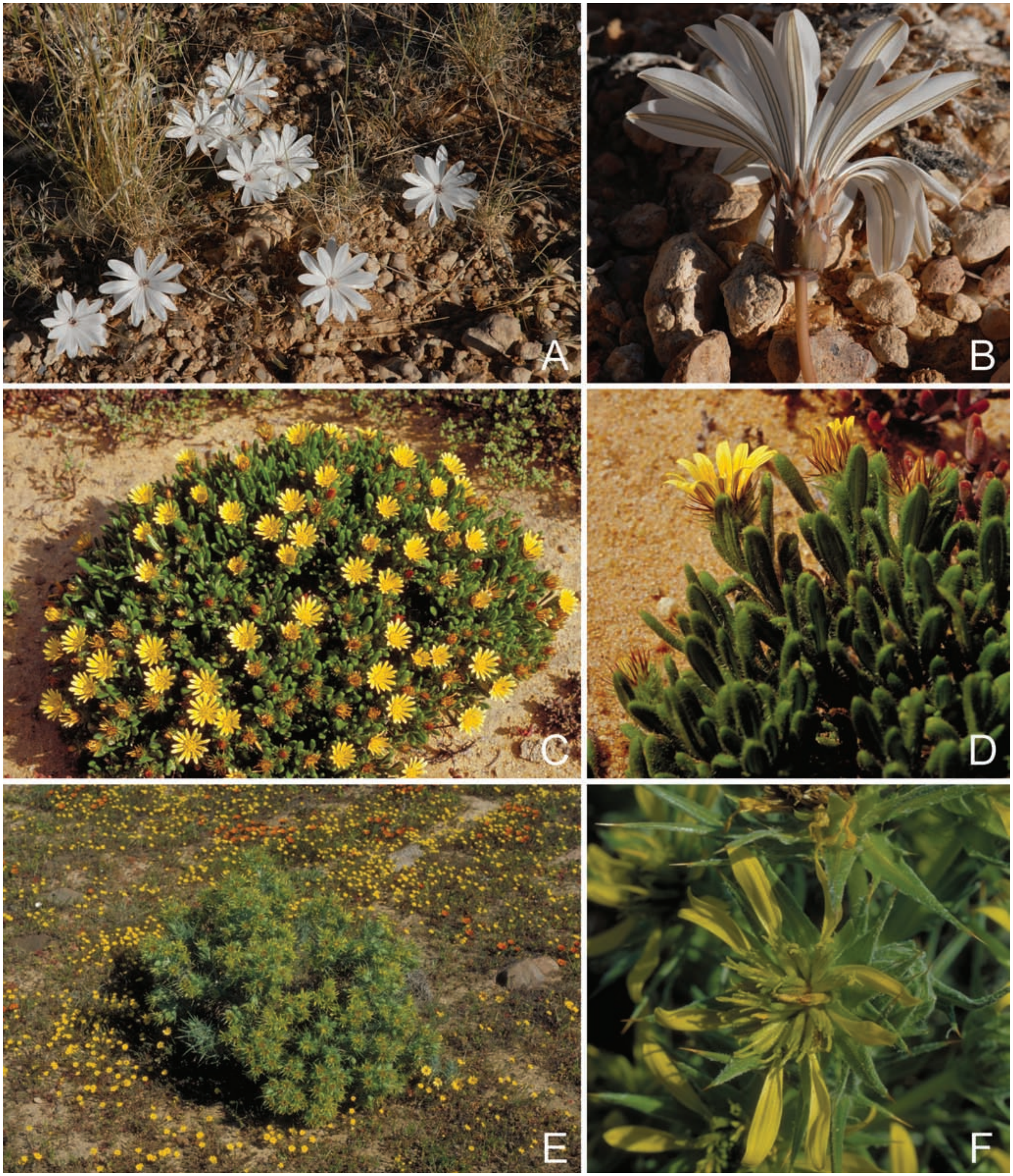


Fig. 25.9. Gorteriinae: *Gazania*, *Hirpicium*, *Heterorhachis*. **A, B** *Gazania jurineaefolia* DC. subsp. *scabra* (DC.) Roessler (Namibia: *Funk 12687*); this small annual was growing along a very dry roadside between Aus and Lüderitz; **B** the involucral bracts are fused and there are stripes on the undersurface of the ray corollas. **C, D** *Hirpicium alienatum* Druce (South Africa, Northern Cape: *Koekemoer and Funk 1956*). **E, F** *Heterorhachis aculeata* (Burm. f.) Roessler (South Africa, Northern Cape: *Funk 12550*); the flowers are greenish in color and the plants have a spiny habit; collected on old farm land near Nieuwoudtville. [Photographs, V.A. Funk.]

identified a "*Gazania* pollen type" that was characteristic for the *Gorteria* clade, but Blackmore (1986) found the same exosculpturing (psilolophate grains) in *Berkheya acanthopoda* (DC.) Roessler. Pollen anatomy shows significant diversity in the large, paraphyletic genus *Berkheya*, where echinate, echinolophate, and psilolophate pollen is found.

The pollen of subtribe Gorteriinae is more variable than that of Arctotidinae (Wortley et al. 2008), although it is usually lophate or sublophate (with the exception of *Berkheya cuneata*) (Fig. 25.11). It is generally larger than that of Arctotidinae, 20–60 μm in diameter. The infratectum is 0.5–2.5 μm thick and comprises one or more columellate layers. The grains are at least partially caveate and may be psilo- or echino-lophate. In the latter case there are 50–80 spines, 1–6 μm in height and 1.5–7.0 μm in diameter, perforated throughout except in *Heterorhachis* where they have a solid apex. For lophate grains there are always six equatorial and six polar lacunae; the numbers of other lacunae are variable.

Chromosome numbers

Gazania has a variety of chromosome numbers, viz., 2*n* = 10, 12, 14, and 16, but here the variation rather owes

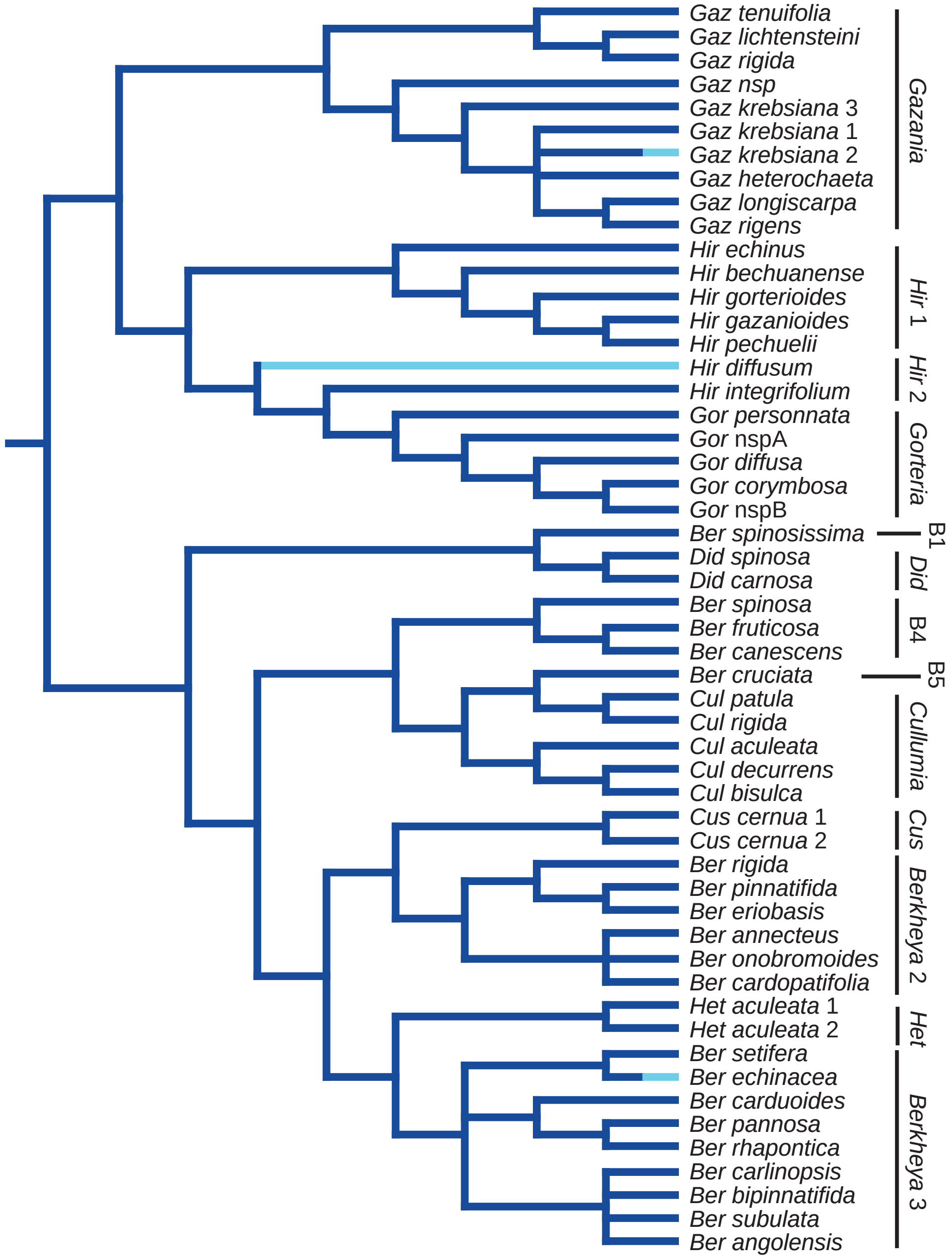


Fig. 25.10. Phylogeny of Gorteriinae with branches color-coded for distribution and clades indicated (phylogeny from Funk and Chan 2008) [Ber = *Berkheya*; Cul = *Cullumia*; Cus = *Cuspidia*; Did = *Didelta*; Gaz = *Gazania*; Gor = *Gorteria*; Hir = *Hirpicium*]. Dark blue = southern Africa; light blue = tropical Africa and Madagascar.

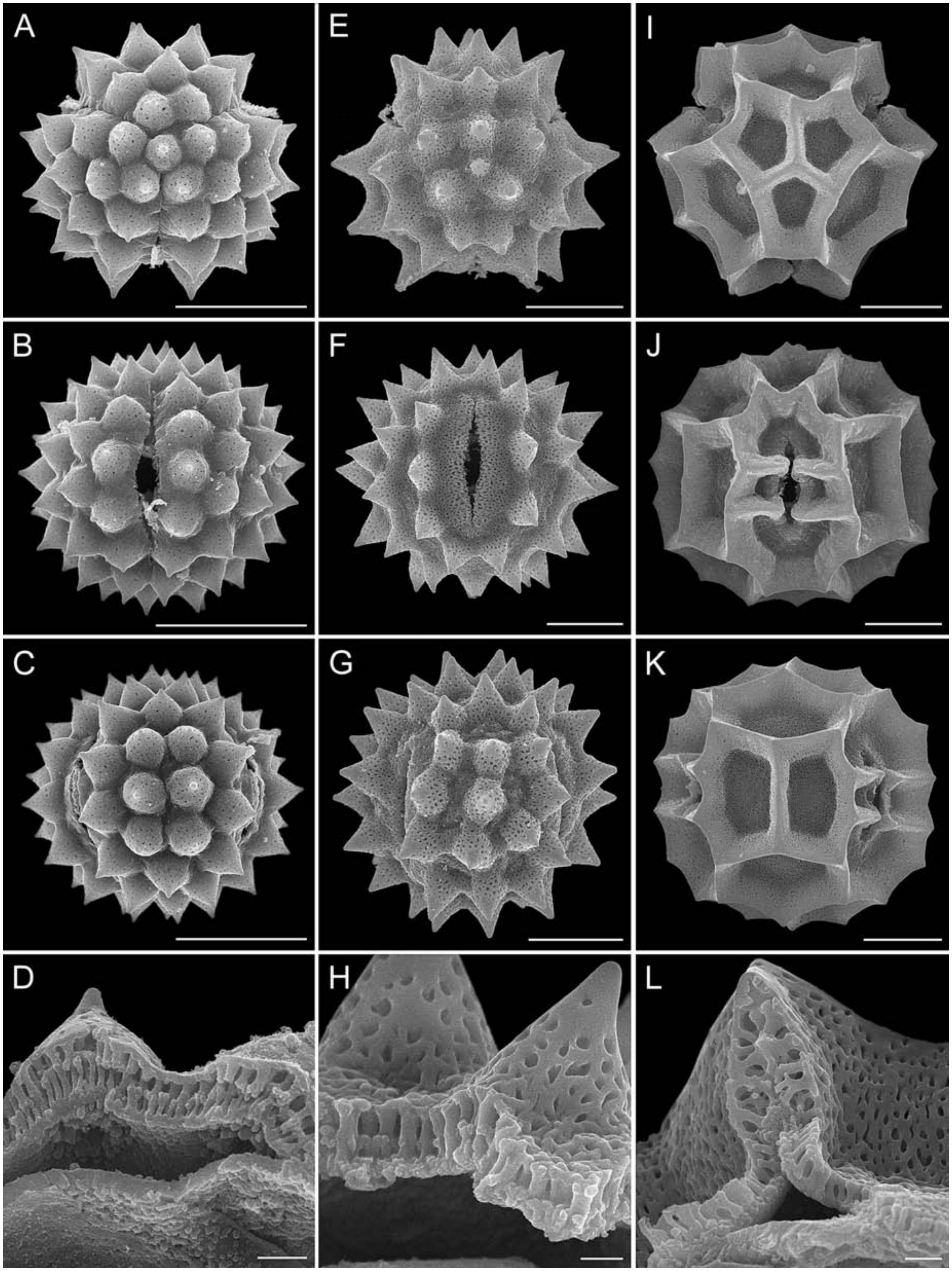


Fig. 25.11. Pollen of Arctotideae. **A** *Arctotis decurrens* Jacq., polar view; **B** *A. glandulosa* Thunb., apertural view; **C** *A. decurrens*, equatorial view; **D** *A. decurrens*, fractured grain; **E** *Didelta spinosa* Harv., polar view; **F** *D. carnosa* Ait., apertural view; **G** *D. spinosa*, equatorial view; **H** *D. carnosa*, fractured grain; **I** *Berkheya rigida* (Thunb.) Bolus & Wolley-Dod ex Levyns, polar view; **J** *B. rigida*, apertural view; **K** *B. rigida*, equatorial view; **L** *B. rigida*, fractured grain. [From Wortley et al., 2008, by permission of the authors.]

to complicated patterns of relationships including possible hybridization events. *Berkheya* has 2*n* = 14 and 16, and *Hirpicium* 2*n* = 10 (Karis 2007).

Chemistry

There is no information on the chemistry of Gorteriinae.

Ecology

In most Asteraceae the achenes act as diaspores, but in *Gorteria* the entire, lignified heads fall off and constitute diaspores. In *Didelta carnosa*, the lignified receptacles with adnate withered involucral bracts break apart into three to five separate diaspores. In both these cases, the ca. 1–5 seedlings germinate directly out of the old heads/parts of heads. This mode of dispersal is apparently not the case in *Cuspidia* and *Heterorhachis*, two other Gorteriinae taxa with more or less lignified receptacles.

Pollination has been investigated primarily in *Gorteria* (Johnson and Midgley 1997; Yamamura 2006). The capitula of *G. diffusa* (Fig. 25.6E) contain a variable number of raised dark spots at the base of the ray floret limbs. Johnson and Midgley (1997) hypothesized that the spots mimic resting individuals of the bee-fly pollinator, *Megapalpus nitidus* (Bombyliidae). Evidence for this hypothesis was supported by the mere removal of spotted rays, which resulted in a major decrease in pollination (Johnson and

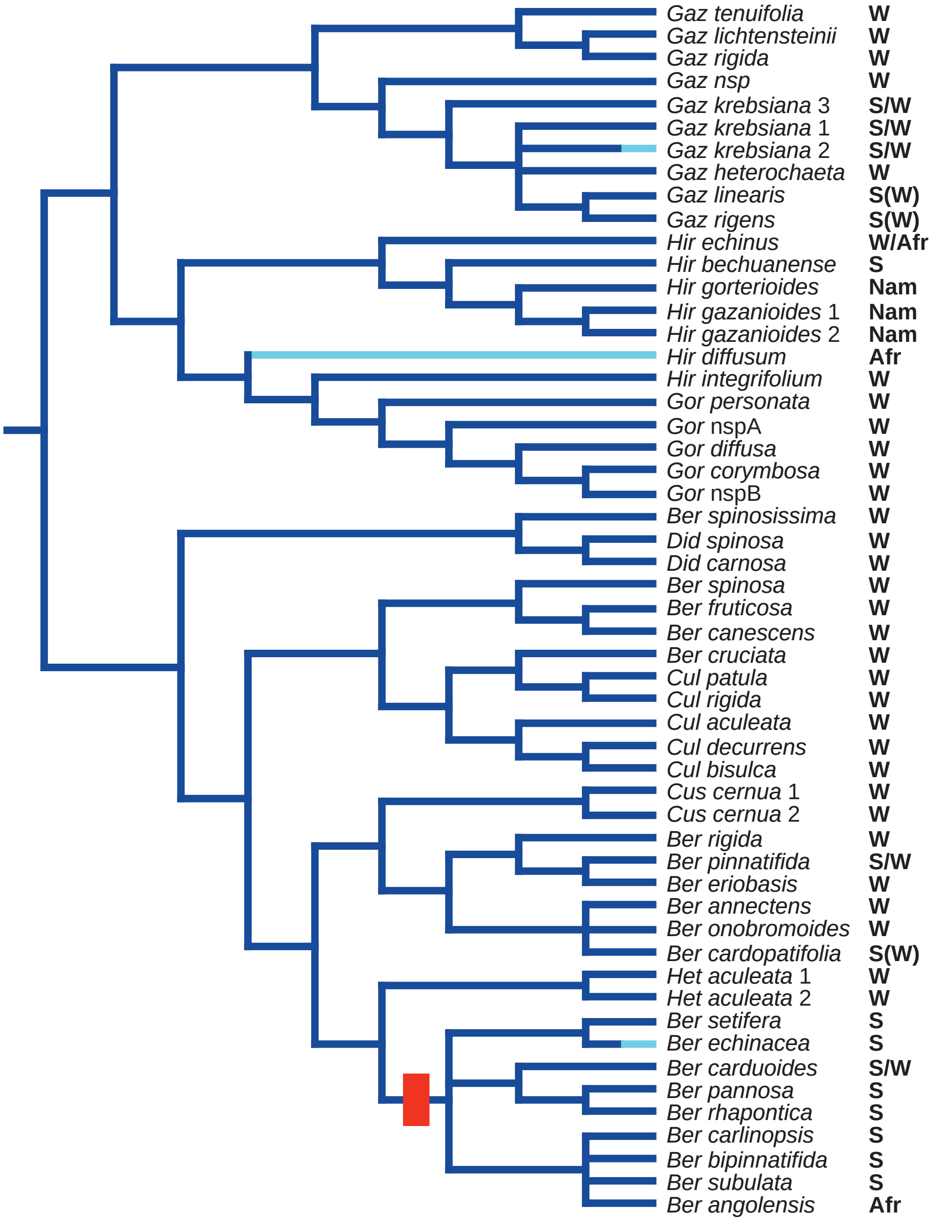


Fig. 25.12. Phylogeny of Gorteriinae showing rainfall area for each terminal taxon (phylogeny from Funk and Chan 2008). Ber = *Berkheya*; Cul = *Cullumia*; Cus = *Cuspidia*; Did = *Didelta*; Gaz = *Gazania*; Gor = *Gorteria*; Hir = *Hirpicium*; Afr = Africa outside South Africa/Namibia; Nam = Namibia (outside the winter-rainfall area); S = summer rainfall; W = winter rainfall (includes southern Namibia). The red box indicates a probable radiation of species in the summer-rainfall region. Dark blue = southern Africa; light blue = tropical Africa and Madagascar.

Midgley 1997). However, *G. diffusa* is visited by a number of other insects as well, not only this particular bee-fly (F. Stångberg and P.O. Karis, pers. obs.).

Biogeography

To date, no study with the aim of untangling the phytogeography of Gorteriinae has been attempted, other than a recent investigation focused on the genus *Gazania* (Howis 2007). Much of the following discussion is based on the geographical distribution of the terminals in the phylogenies at hand. Although the sampling is not fully congruent, both molecular (Funk and Chan 2008) and morphological (Karis 2006) data support a 'derived' radiation of many summer-rainfall species and the few tropical species of the *Berkheya* clade (Fig. 25.12). Thus both possible summer-rainfall radiation events are well embedded within apparent GCFR clades (Greater Cape Floristic Region). *Berkheya* has a significant representation in the GCFR (24 spp.), but the centre of diversity is in the summer-rainfall region (at least 46 spp.). The picture in the *Gorteria* clade is less clear due to more limited sampling in both these studies (Karis 2006; Funk and Chan 2008), but only five of the species are restricted to summer-rainfall or tropical Africa. Howis (2007) reconstructed a phylogeny of *Gazania* based on sequences from nuclear ribosomal DNA (ETS, ITS) and four non-coding cpDNA markers and hypothesized an origin for *Gazania* in the arid and/or semi-arid winter-rainfall regions of southern Africa with migration southwards and eastwards during periods of aridification. Two summer-rainfall/tropical *Gazania* species are subsumed well within the clade (Fig. 25.12). Both in the *Gorteria* clade and the subtribe as a whole, the presence of two large sister groups obscures possibilities to evaluate geographical 'origin', owing to the lack of obvious basalmost lineages containing one or few species only. However, at this point it is safe to hypothesise a GCFR (including adjacent arid areas) origin of Gorteriinae and most likely in the winter-rainfall area, but evaluation of finer phytogeographical details must await additional studies based on larger sampling.

Table 25.2. List of characters discussed in the text and "optimized" on the tree in Fig. 25.13.

1. Latex/laticifers
2. Leaf spines
3. Ray florets neuter/female sterile
4. Anthers ecaudate
5. Apical anther appendages soft
6. Arctotoid styles, sweeping hairs in a ring below the bifurcation
7. Pappus scales
8. Longitudinally striate hairs
9. Longitudinally grooved leaves
10. Involucral bracts connate
11. Inner involucral bracts apically with a scarious lamina
12. Receptacle deeply alveolate
13. Ray florets 4-lobed
14. Ray florets with an adaxial, narrow lobe
15. Disc corolla lobes short(?)
16. Disc corolla lobes with sclerified margins
17. Anther filament collar inconspicuous
18. Apical anther appendages with fringed margins
19. Anther endothecium radial
20. Anther endothecium without a plate
21. Inner periclinal wall of anther endothecium cells with band-like thickenings in lower half of cells
22. Pollen of the *Gazania* type
23. Sweeping hairs small, patent
24. Sweeping hairs oblong, erecto-patent, mammillate
25. Sweeping hairs subulate-ensiform
26. Sweeping hairs two or three together
27. Pericarp with tannic substances
28. Testa with subepidermal crystals
29. Pappus scale cells very long, abaxial wall reinforced

Economic uses

Berkheya speciosa O. Hoffm. and *B. spekeana* Oliver are used traditionally to treat numerous human ailments in several African countries (Chifundera 1998; Sparg et al. 2000; Cos et al. 2002; Fennell et al. 2004). *Berkheya spekeana* possesses antiviral activity (Cos et al. 2002).

Only a few Gorteriinae species are of horticultural significance. The most commonly cultivated are *Gazania krebsiana*, *G. linearis* Druce, *G. rigens* and their hybrids, which are widely grown as ornamentals (Fig. 25.8F). *Berkheya coddii* Roessler has potential use for phytoremediation of sites contaminated with toxic metals, as it is a nickel hyperaccumulator and has been used to treat soil contaminated with nickel (Robinson et al. 2003). In addition, certain *Berkheya* species (e.g., *B. purpurea* and *B. multijuga*) and both *Didelta* species are available from horticultural suppliers.

Invasives

Berkheya rigida is a declared weed of coastal scrubland in parts of Australia (Parsons and Cuthbertson 2001). *Gazania* species, principally *G. linearis* and *G. rigens*, have naturalized widely abroad on coastal dunes, roadsides and waste areas (e.g., McClintock 1993; Groves et al. 2003), but none have been declared to be invasive or noxious weeds.

CHARACTER EVOLUTION

During recent decades, some characters of Arctotideae have been discussed as alleged synapomorphies (Table 25.2) for the tribe, and possible character evolution of some features is illuminated in Fig. 25.13. The tree is based on the results of Funk and Chan (2008) and on unpublished data.

The evolution of characters included here may indeed show complicated patterns within taxa from outside Arctotideae and which are displayed here as single terminals. The sister group of Cichorioideae, viz., subfamily Asteroideae, is included in the tree.

Latex/laticifers probably evolved in parallel in Cichorieae and in Gorteriinae; this appears to be the case regardless if latex is considered to be ancestral for Liabeae or not. At this point, the absence of latex can be considered plesiomorphic; on the other hand, latex/laticifers diagnose Gorteriinae, as has previously been suggested (Bremer 1994; Karis 2006).

Spiny leaves appear no less than five times on the cladogram.

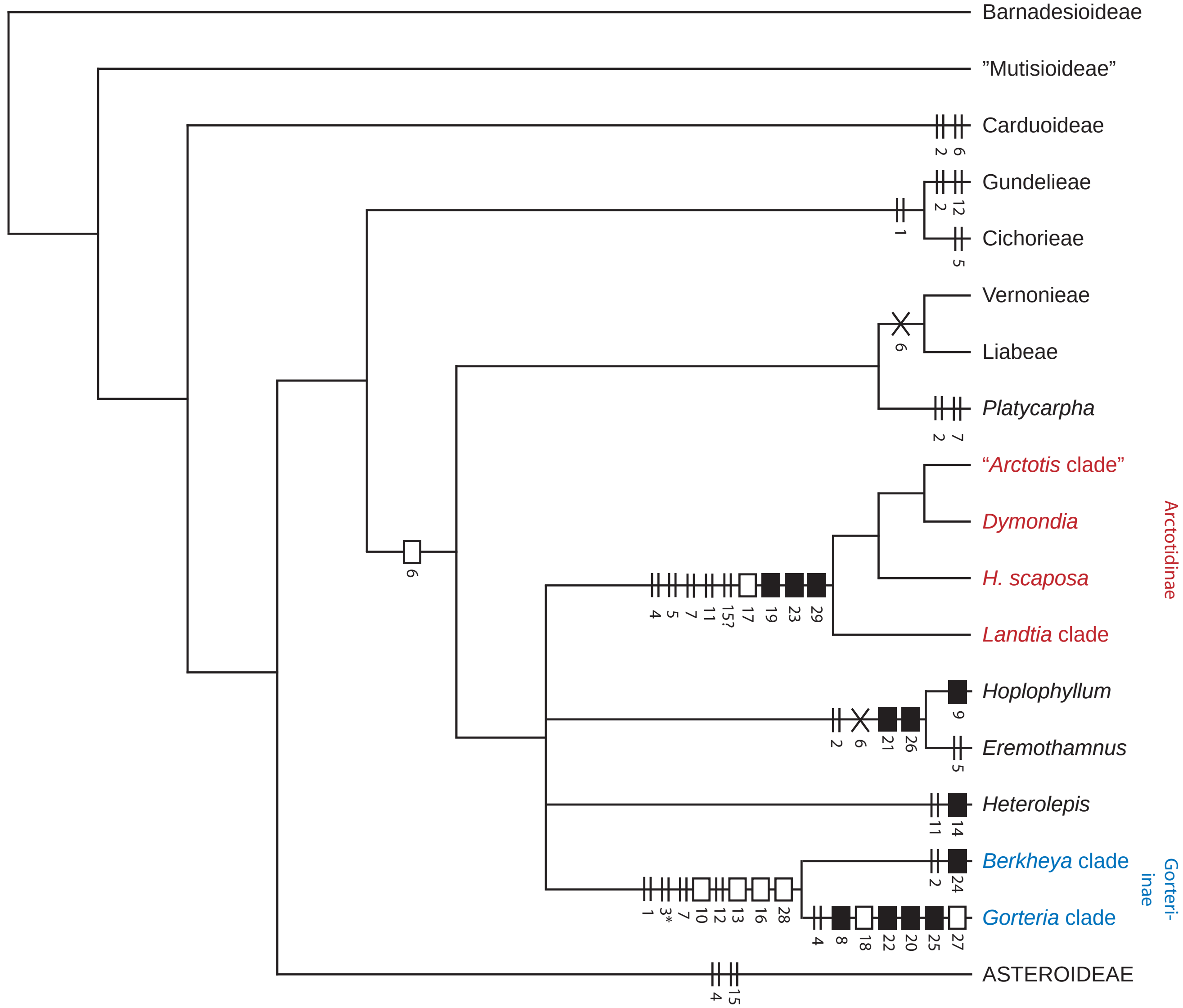


Fig. 25.13. Selected characters mapped onto a cladogram of Compositae with emphasis on Cichorioideae. Characters are listed in Table 25.2. Black boxes are synapomorphies, white boxes are homoplasious characters, parallel bars are parallelisms.

Inner involucral bracts with an apical, scarious lamina diagnose Arctotidinae, but are also typical of *Heterolepis*.

Sterile ray florets apparently evolved independently in the common ancestor to Gorteriinae and within Arctotidinae, viz., in the ancestor of the *Arctotheca* + *Haplocarpha* s.str. + *Arctotis* sect. *Anomalae* lineage (with a reversal in *Haplocarpha* s.str.) and within the *Landtia* clade (*H. parvifolia* (Schltr.) Beauverd p.p.).

Ecaudate anthers have three independent origins: in Arctotidinae, in the *Gorteria* clade, and it is also most likely ancestral for the subfamily Asteroideae. It should be noted that ecaudate anthers and "shortly lobed disc floret corollas" are the only features that also involve discussion on the corresponding character states in Asteroideae.

Soft apical anther appendages arose independently in Arctotidinae and in *Eremothamnus*.

The ring of sweeping hairs below the style bifurcation is interpreted to be a parallelism found in the thistles (Cardueae) and in Cichorioideae (Karis et al. 1992; Bremer 1994). The possible placement of *Platycarpha* on the Liabeae-Vernonieae branch would force reconsideration of the evolution of the arctotoid style in Cichorioideae.

The scaly pappus is a feature that has evolved at least three times in parallel. The most parsimonious interpretation of pappus scales in Arctotidinae is that they evolved in the common ancestor to the group. The Arctotidinae pappus scales are distinctive, with very long cells furnished with an abaxially thickened cell wall, and the scales are anatomically different from those in the other clades. The combination of these two facts makes more sense if a parallel gain of pappus scales is hypothesized.

The often enumerated synapomorphies for the subtribes and clades therein (see above; Bremer 1994; Funk et al. 2004; McKenzie et al. 2006c; Karis 2006, 2007) are also displayed on the tree (Fig. 25.13), but it should be emphasized that some characters are not investigated for all, or even many, species in all clades. Even though a phylogeny and precise patterns of relationships are not yet established in Arctotideae, it is clear that some morphological/anatomical features need to be re-evaluated in terms of homologies. One obvious example is the pappus scales, which are so fundamentally different in Arctotidinae and in the rest of the clades.

CONCLUSION

There are striking differences in morphology in virtually every part and organ between the two subtribes, but this fact alone is not evidence enough to argue that these taxa might not be one another's closest relatives. Current molecular data do not refute either hypothesis, they merely provide alternative solutions. The large morphological and anatomical diversity displayed in both subtribes might indeed be the result of repeated adaptations to similar environmental conditions, pollinators, etc., but which has been expressed in different ways in the two lineages. Hopefully, ongoing work will clarify the taxonomy and our understanding of the evolution and biogeography of Arctotideae.

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Chapter 26

Eremothamneae

Harold Robinson and Vicki A. Funk

HISTORICAL OVERVIEW AND MORPHOLOGY

The tribe Eremothamneae was first described by Robinson and Brettell (1973) on the basis of *Eremothamnus marlothianus* O. Hoffm. of Namibia. The combination of yellow rays and capillary pappus caused Hoffmann (1890–1894) to place the genus in the tribe Senecioneae and in the subtribe Liabinae (currently tribe Liabeae), at that time appended to Senecioneae (Figs. 26.1–26.2). Liabinae with its opposite leaves, milky sap, and mostly neotropical distribution was an unusual place for the alternate-leaved *Eremothamnus*. At the time Liabinae included the then mostly African, alternate-leaved, *Newtonia* O. Hoffm. (= *Distephanus* Cass.), but all these entities have now been excluded from Senecioneae. In Robinson and Brettell (1973) the basic differences in stigmatic surfaces, lengths of disk corolla lobes, and elongated or calcarate bases of the anther thecae were noted, characters that distinguish all the members of the subtribe Liabinae from most Senecioneae. The differences now seem to be important distinctions of the subfamily Cichorioideae (in the present sense, Vernonieae, Liabeae, Arctotideae, Cichorieae plus smaller tribes) from Asteroideae to which Senecioneae, Astereae, Heliantheae, etc., belong (see Chapter 1). There have been suggestions that *Eremothamnus* be placed in the African genus *Pteronia* L. of the tribe Astereae (Muschler 1911; Hutchinson and Phillips 1917; Dinter 1927), or possibly in Inuleae (Moore 1929), along with the suggestion that it be returned to the overly broad tribe Senecioneae (Merxmüller 1954). Nevertheless, all more recent comparisons of *Eremothamnus* have been with members of Cichorioideae, especially Arctotideae (Leins 1970). Leins and Thyret (1971) suggested that *Eremothamnus* should form a monogeneric subtribe in Arctotideae and in one case, on the basis of achene anatomy, Reese (1989) seemed to agree that *Eremothamnus* was in the subfamily Cichorioideae, but not in Arctotideae.

Robinson and Brettell (1973) discovered two particularly distinctive features in *Eremothamnus*. One was the structure of the endothecial cells, with annular thickenings on the lower half but none on the upper half. A second and more striking character was the rather long sweeping hairs divided longitudinally into two or three cells, each cell with its own point (Fig. 26.3). These sweeping or collecting hairs are borne on slender style branches and are distributed on the style as in Vernonieae and Liabeae with no sharp basal delimitation. They differ from the shorter, single-celled sweeping papillae on broader style branches and upper shafts in Arctotideae. The latter's scabrae end below in an abrupt basal collar.

Karis (1992) discovered that a second genus, *Hoplophyllum* DC., from western South Africa, was related to *Eremothamnus*. The position was confirmed by Robinson (1992, 1994) in studies of the sweeping hairs and the pollen (Fig. 26.4). The type species of *Hoplophyllum* had a much longer history than *Eremothamnus*, being described as *Pteronia spinosa* L. f. in 1781. Placement in *Pteronia* (Astereae), in the wrong subfamily, was the only taxonomic placement that *Eremothamnus* and *Hoplophyllum* shared before the study by Karis (1992). *Pteronia spinosa* was transferred by De Candolle (1836) to his new genus *Hoplophyllum* which was placed in Vernonieae. In spite of its yellow florets (Fig. 26.2), it was left in Vernonieae until the study by Karis (1992). It should be noted that

Fig. 26.1. *Eremothamnus marlothianus* O. Hoffm. **A** habit, note prostrate shrubby nature and dry rocky, sandy habitat; **B** flowering heads during a year (2006) of unusually high rainfall, note the large number of florets; **C** flowering heads during a year (2007) of low rainfall, note the small number of florets. [Photographs: A, B, C. Mannheimer; C, V.A Funk, *Funk 12684*; all from the same population.]

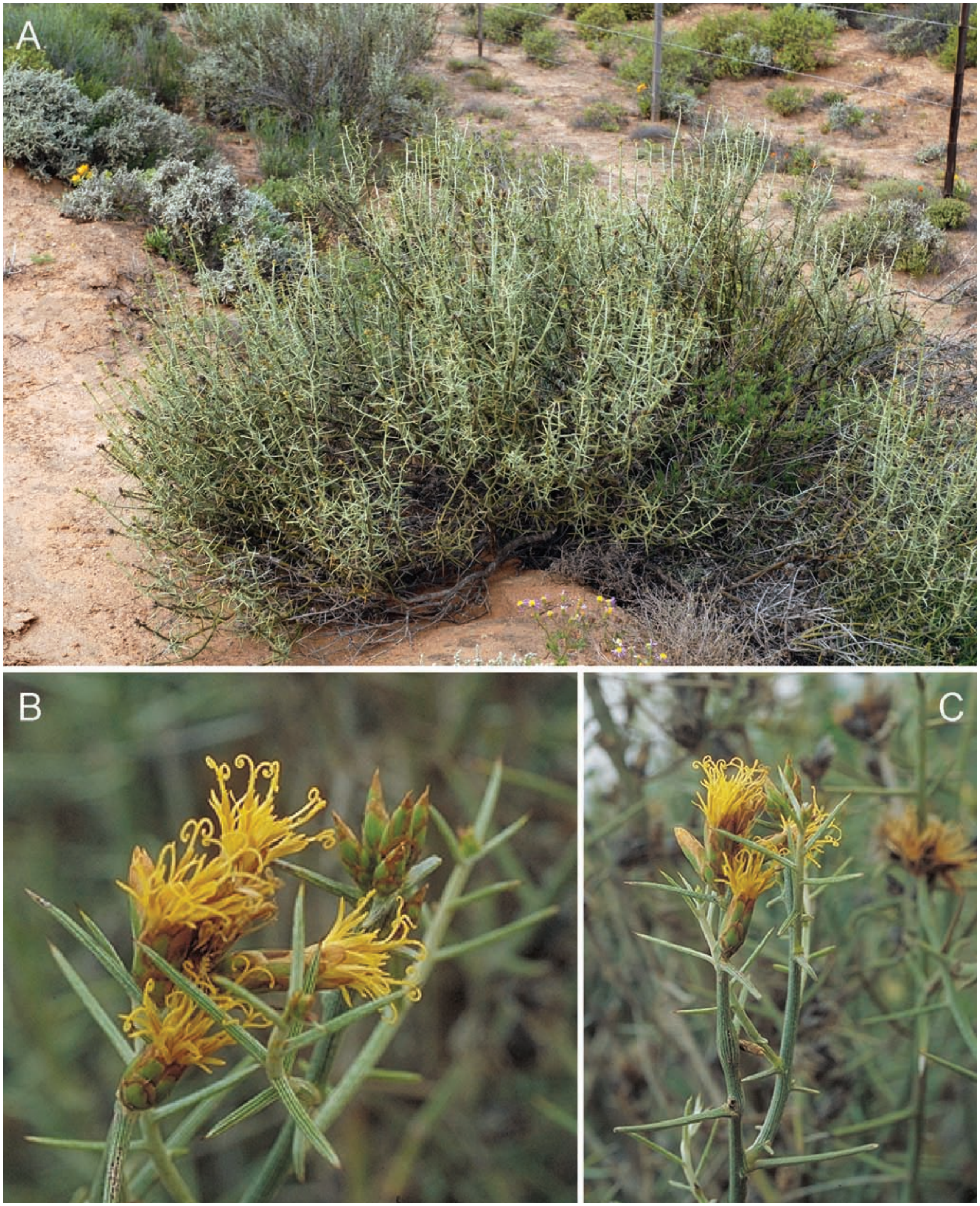

Fig. 26.2. *Hoplophyllum spinosum* (L. f.) DC. **A** habit; **B** flowering heads, note absence of ray florets; **C** involucral bracts, note hyaline margins. Taxon can be locally common in somewhat disturbed areas. [Photographs, V.A. Funk; *Funk 12650*.]

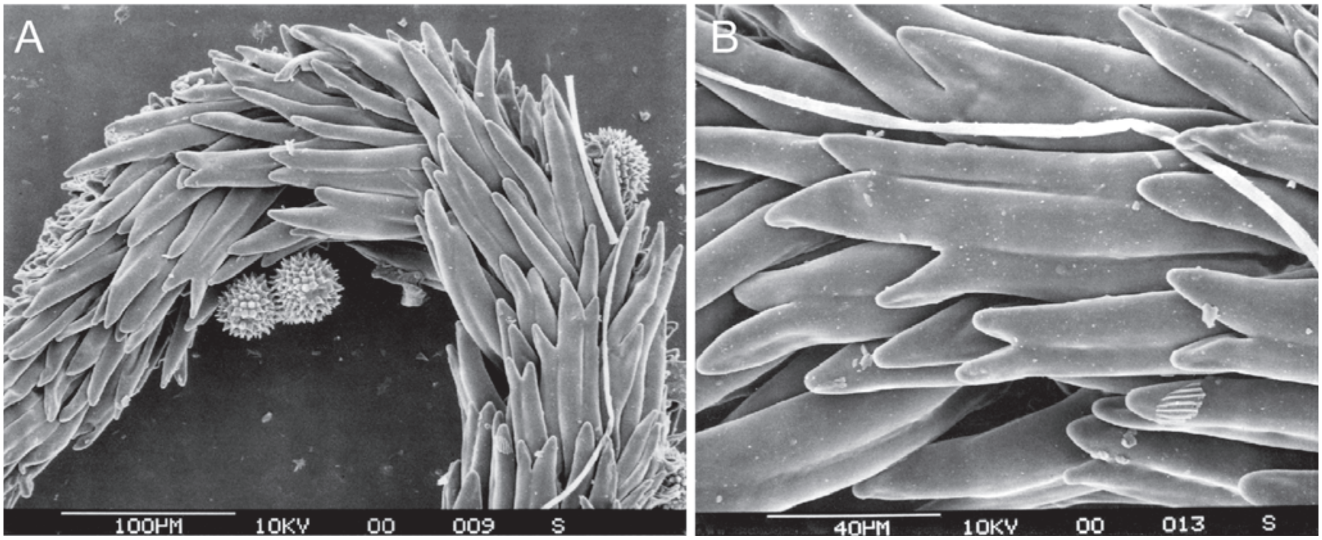

Fig. 26.3. Sweeping hairs. **A, B** *Hoplophyllum spinosum* (L. f.) DC. (B detail from A). Note the slender style branches bearing comparatively long sweeping hairs that are divided longitudinally into two or three cells. [Photographs, H. Robinson; *Barker 9757*, US.]

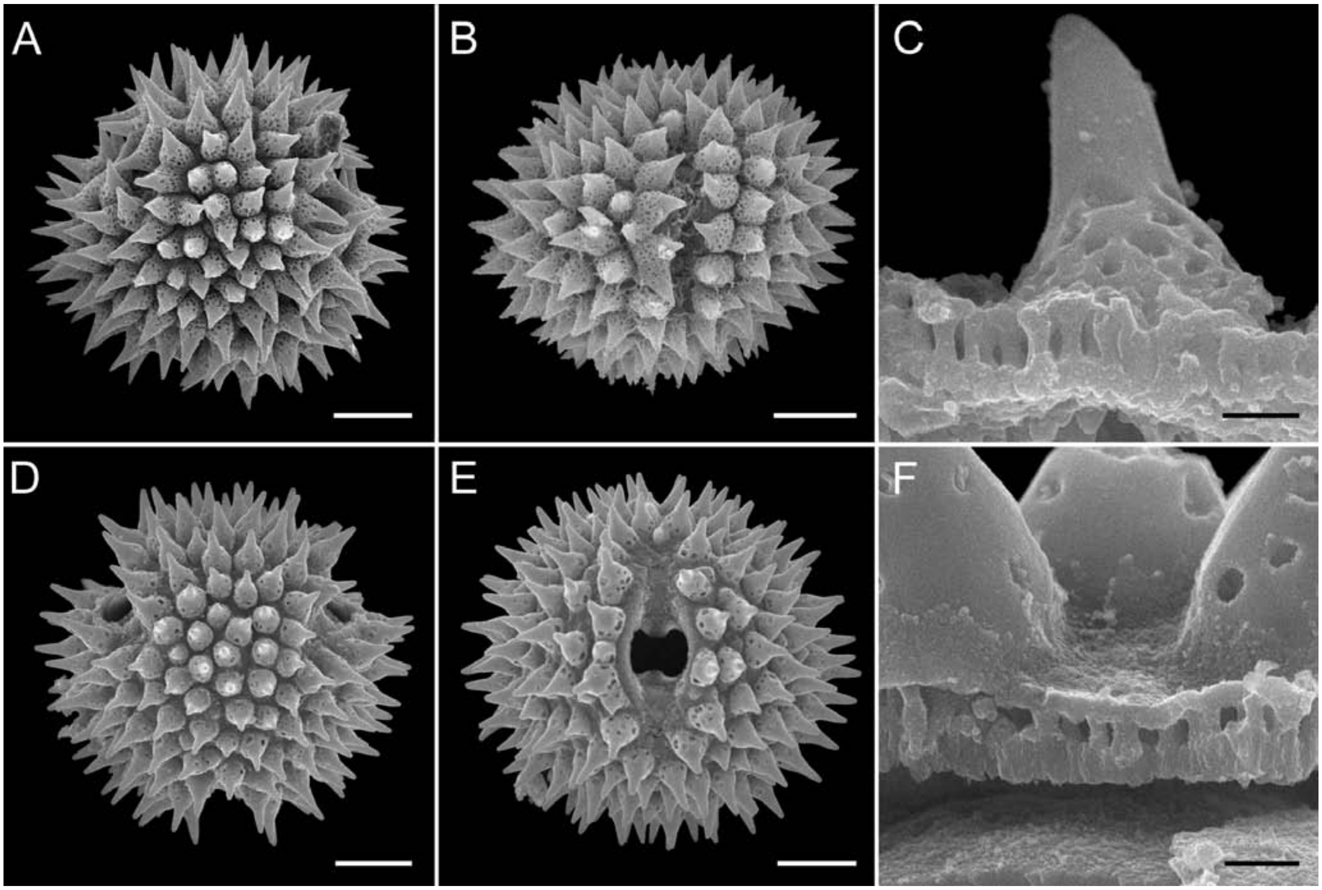

Fig. 26.4. Pollen. **A–C** *Eremothamnus marlothianus* O. Hoffm.; **D–F** *Hoplophyllum spinosum* (L. f.) DC. The pollen grain structure is unique in the family but obviously shared between the two genera. Scale bars for A, B, D, E = 10 μm; scale bars for C, F = 1 μm. [Photographs: A–C, J.J. Skvarla, *Geiss and Vauuren 710*, PRE; D–F, J.J. Skvarla, *Koekemoer 2045*, PRE.]

the two genera had such different histories primarily because *Eremothamnus* had ray florets and *Hoplophyllum* did not (Figs. 26.1–26.2). As pointed out by Karis (1992), the genera also share spinose or spiniform leaves, as seen in many Arctotideae and Cardueae, and they share caveate pollen (Fig. 26.4), a feature most common in the subfamily Asteroideae, but found in a few Cichorioideae such as some Liabeae (Robinson and Marticorena 1986) and Vernonieae (*Ethulia* L.; Bolick 1978).

PHYLOGENY

Karis et al. (1992) performed a cladistic analysis of Cichorioideae s.l. based on morphological data and concluded that *Eremothamnus* was related to *Arctotis* (the only sample from Arctotideae) but the sampling was very limited. In a separate paper in 1992 (p. 197) Karis concluded that "*Hoplophyllum* … is more closely related to *Eremothamnus* than to any taxon in the Vernonieae. The unique endothecial configuration shared with *Eremothamnus* constitutes a synapomorphy for these two taxa." Another putative synapomorphy is the accessory apical vein in the lobes of the disc florets, occurring in both genera. He also mentioned that Robinson (pers. comm.) had pointed out the unique hairs (Fig. 26.3). In 1995 Bergqvist et al. used chloroplast DNA restriction site data and showed that *Eremothamnus* was the sister group to *Gazania*, however, again, the sampling was limited to only one member of the tribe Arctotideae. In 2001 (Karis et al.) the chloroplast gene *ndhF* was used to investigate the placement of *Eremothamnus* and *Hoplophyllum*. The analysis included five species of Arctotideae and it resulted in a poorly supported trichotomy among the two subtribes of Arctotideae and the *Eremothamnus*-*Hoplophyllum* clade.

Recent molecular studies involving a large selection of taxa and several additional gene regions support the hypothesis that *Eremothamnus* and *Hoplophyllum* are sister taxa (Funk et al. 2004). However, the taxa are found on a long branch that can be found in more than one place on the phylogeny depending on the outgroups selected and the gene regions used in the anlaysis. In fact, at this point, the molecular data give more information about where the clade does not belong than where it does belong. Certainly it is in the subfamily Cichorioideae and not in any of the tribes of Asteroideae. Within the subfamily it is never found within Vernonieae, Liabeae or Cichorieae. Furthermore, it does not fit in either of the well defined subtribes of Arctotideae. Sometimes it can be found as the weakly supported sister group of one or the other of these two subtribes, most often Gorteriinae, but at other times it is the sister group of the unplaced genus *Heterolepis* or in various polytomies with all of the tribes except Cichorieae. To add to the problem, the monophyly of Arctotideae is not well supported (Funk et al. 2004), and the two subtribes sometimes fall into sister group relationships with other tribes. In summary, one can say that the subfamily analysis (Chapter 23) indicates that Eremothamneae is close to, but probably not in, the tribe Arctotideae (or its subtribes), and for now it is best to leave it in its own tribe.

TAXONOMY

Tribe Eremothamneae H. Rob. & Brettell in Phytologia 26: 164. 1973 – Type: *Eremothamnus* O. Hoffm.

Erect branching shrubs, stems very sparsely puberulous in *Hoplophyllum* to densely tomentose in *Eremothamnus*, hairs of tomentum long and simple, highly contorted, uniseriate, multicellular, crosswalls oblique; pith solid. Leaves alternate, spiniform in *Hoplophyllum*, or obovate with few short spines on distal margins and somewhat succulent in *Eremothamnus*. Heads solitary and terminal or in upper axils, or in terminal clusters, sessile or subsessile; involucral bracts multiseriate, gradate, distally papyraceous and usually with apical spine; receptacle epaleaceous. Corollas yellow; without ray florets and with ca. 5 disk florets in *Hoplophyllum*, with 12–20 rays and 25–30 disk florets in *Eremothamnus*, rays when present without anthers, with 3 short apical teeth; disc florets regular, deeply 5-lobed, lobes linear, outside with glands and few hairs; anther thecae calcarate at base and shortly tailed; endothecial cells oblong with annular thickenings crowded in basal half, lacking from distal half; apical appendage oblong with apiculate tip in *Hoplophyllum*, soft and broadly elongate in *Eremothamnus*; style base partly immersed in nectary, without enlarged basal node; branches narrow with stigmatic papillae covering entire inner surfaces; upper scape of style and outer surfaces of branches not broadened, covered with elongate sweeping hairs formed by two or three cells separated by longitudinal walls. Achenes prismatic, densely and sericeously setuliferous, with long biseriate setulae not or scarcely divided at tips, with thick cell walls, achene surface smooth, shape slightly trigonous to pentagonal, walls without phytomelanin, with linear raphids; pappus of many capillary bristles in 2–3 series, somewhat gradate in length, tapered at tips.

Eremothamneae are presently seen to include the two genera *Eremothamnus* and *Hoplophyllum*, from Namibia and adjacent South Africa. *Eremothamnus* is monotypic with one species, *Eremothamnus marlothianus* O. Hoffm., restricted to one area in Namibia, and *Hoplophyllum* has two species, *Hoplophyllum spinosum* (L. f.) DC. and *H. ferox* Sond.; the former is the more common of the two being found occasionally in the Western and Northern Cape Provinces along roadsides, while the latter is restricted in its distribution to the Western Cape. The general taxonomic position determined by Robinson and Brettell

(1973) and expanded by Karis (1992) has proven correct. The structure of the anthers with calcarate bases, the long lobes of the disk corollas, the stigmatic papillae covering the entire inner surface of the style branches and the pollen place the tribe definitely outside of what is now recognized as the subfamily Asteroideae.

The Southern African distribution is reminiscent of groups such as Arctotidinae in Cichorioideae with which Leins (1970) and others have compared *Eremothamnus*. However, the structure alone shows a form of narrow style and unique form of sweeping hairs (Fig. 26.3) that would preclude inclusion of Eremothamneae in Arctotideae, Platycarpheae, or in a relationship with *Heterolepis* Cass.

POLLEN

The grains are spherical, tricolporate, spinulose with larger spines in intercolpi and smaller crowded spines around poles, with microperforations in exine and an interior of exine caveate, with thin foot-layer, individual spines fistulose at the base (Fig. 26.4). It is unique in the family and shared by both genera.

BIOGEOGRAPHY

Because the Eremothamneae clade is small and its placement is not secure, it is not possible at this time to discuss its biogeography, but its presence in Cichorioideae strengthens the overall African presence of this subfamily (see Fig. 44.4).

CHROMOSOME NUMBERS, CHEMISTRY, BIOLOGY, ECOLOGY, ETHNOBOTANY

Nothing is known.

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Chapter 27

Liabeae

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HISTORICAL OVERVIEW

Liabeae and Barnadesieae (Compositae) are the only major tribes with entirely Neotropical distributions, both having their greatest generic and specific representation in the Andean Cordillera of western South America (Funk et al. 1995). Liabeae are concentrated in the northern and central Andes (Table 27.1) and Barnadesieae are mostly in the southern Andes. Liabeae contain approximately 165 species arranged in 18 genera and represent one of the smaller tribes in the family Compositae. The history of the classification of Liabeae reflects the difficulty in tribal placement encountered by early workers. Cassini (1823, 1825, 1830), Lessing (1832), De Candolle (1836), Weddell (1855–57), and Bentham in Bentham and Hooker (1873) all variously treated groups of taxa that are now placed in this tribe as members of Vernonieae, Heliantheae, Helenieae, Senecioneae and Mutisieae. Rydberg (1927) formally proposed tribal status for the genera of the North American Flora area.

Bentham's classification, which placed the majority of taxa in one genus, *Liabum*, in Senecioneae, was essentially adopted by Hoffmann (1890–1894). Despite work by Rydberg (1927), who established the tribe and recognized genera from Mexico, Central America, and the West Indies, and isolated works by Blake (1935), Cabrera (1954), and Sandwith (1956), which recognized the Liabean affinities of other genera, the tribe Liabeae was not adopted. Instead, Bentham's classification was retained more or less intact and accepted by many modern floristic and taxonomic workers (D'Arcy 1975; Cronquist 1955; Carlquist 1976). Nash and Williams (1976) accepted Bentham's concept of a single genus but placed the genus in Vernonieae. It was not until Robinson and co-workers published a series of papers bringing the genera together into one tribe (Robinson and Brettell 1973, 1974; see Robinson 1983a for additional references) that the accepted taxonomy began to change. Nordenstam (1977) followed Robinson's tribal circumscription and, although it was included in the same chapter as Senecioneae, he recommended recognition at the tribal level. Robinson (1983a) provided the first modern view of the tribe including a detailed review of previous classification efforts and relevant literature.

Since Robinson's generic review (1983a), there has been some research activity within the tribe, especially discussions of generic boundaries and the description of additional species. For example, the status of Rydberg's (1927) four closely related Mexican and Central American Liabeae genera (*Sinclairia*, *Sinclairiopsis*, *Megaliabum*, *Liabellum*) has been investigated. McVaugh (1984) reverted to earlier work and treated the seven species from southwest Mexico as belonging to a broadly interpreted *Liabum*. Turner (1989) revised the group and recognized three evolutionary lines within the genus *Sinclairia*; one of which equaled the genus *Liabellum*, which was reduced to sectional status. Although the two genera were combined, Turner's treatment essentially agreed with those of Rydberg (1927) and Robinson (1983a) in recognizing the *Sinclairia*–*Liabellum* lineage as distinct from *Liabum*. The question of the hierarchical structure within the *Sinclairia* complex remains controversial (Robinson 1990a). In the most recent treatment Bremer (1994) followed Turner's inclusion of *Liabellum* in *Sinclairia*. Turner (2007) recently treated the tribe for the flora of Mexico and reported one species of *Liabum* and all others referred to *Sinclairia*.

Robinson has described new species in *Liabum*, *Ferreyranthus*, and *Munnozia* (Robinson 1983b, 1990a, b, 1994). Dillon and Sagástegui (1994a) revised *Ferreyranthus* and described new species in *Chrysactinium* (Sagástegui and Dillon 1994) and *Oligactis* (Dillon and Sagástegui 1994b), both from northern Peru. Zermoglio and Funk (1997) have described a new species of *Chrysactinium* from northern Peru and revised the genus (Funk and Zermoglio 1999). Moran and Funk (2006) revised *Erato* and described a new species from Costa Rica. Funk and Robinson (2001) described a new genus, *Dillandia*, and transferred species from Colombia and Peru that formally were classified as *Munnozia*. *Sampera* (Funk and Robinson, in prep.) has been established for a group of eight species previously classified in *Oligactis* subgenus *Andromachiopsis*.

The tribe was treated in the published results from the International Compositae Conference held at Royal Botanic Gardens, Kew in 1994 (Funk et al. 1996). Most recently, the tribe was treated in Kubitzki and Jeffrey's treatment of the Asterales (Funk et al. 2007).

DISTRIBUTION AND DIVERSITY

Liabeae are distributed throughout much of the Neotropics, but they exhibit their greatest generic and specific concentration in western South America and the most likely place of origin of the modern-day tribe is in the Andean Cordillera. The center of generic diversity is in Peru where 13 of the 18 genera are found, followed by Ecuador (8 genera), Colombia (7 genera), Bolivia (6 genera), Costa Rica (5 genera), Panama (5 genera), Venezuela (4 genera), Mexico (4 genera), Argentina (4 genera), Guatemala (2 genera), El Salvador (2 genera), Honduras (2 genera), Nicaragua, and Caribbean (Cuba, Hispaniola, Jamaica) with one genus each. Recently, *Liabum acuminatum* Rusby was identified (by H. Robinson) from a 1968 collection from Acre, Brazil (*Prance, Ramos and Farias 7310*, US) making it the first confirmed record of the tribe from that country; subsequently *L. amplexicaule* Poepp. & Endl. was recorded from the region (*Daly et al. 9631*, US) (Gutiérrez, pers. comm.). Figure 27.1 illustrates the overall distribution of the tribe within the neotropics and indicates generic diversity for each country where the tribe is represented. The majority of genera possess rather limited distributions (Table 27.1), often confined to small geographic areas and narrow ranges of environmental conditions. Members of the tribe typically occupy sites in forest communities from Mexico to Central America, the West Indies, and throughout western South America from Venezuela to central Argentina (50–4750 m). A few species in several genera are found in open or disturbed habitats associated with rivers, road cuts, or tree falls. More rarely, a few species occupy seasonally dry scrub or desert habitats in both North and South America. A number of genera are associated with essentially alpine habitats well above forested zones, including *subpáramo*, *páramo*, *jalca*, and *puna* environments (>3000 m) (Dillon 2005).

For purposes of discussion, the genera will be presented as they are arrayed within the strict consensus cladogram (Fig. 27.2) derived from the molecular analysis (Funk and Chan, in prep.). The analysis utilized data from ITS, *trnL-F*, and the 3' end of *ndhF*.

Clade A, contains three *Cacosmia* species, all shrubs and primarily restricted to open habitats in northern Peru and southern Ecuador (1500–3200 m; Funk and Brooks 1991; Fig. 27.3A). The combination of characters, including sheathing leaf bases, opposite, denticulate leaves with adaxial bullate surfaces and densely tomentose abaxial surfaces, loosely aggregated capitula with cylindrical, multiseriate involucres, only five, yellow ray florets, and achenes lacking a pappus, make this a distinctive element of the central Andes (Dillon 2005).

Clade B, containing *Ferreyranthus-Dillandia-Oligactis-Sampera-Liabum*, contains ca. 36.8% of the species diversity and its representatives occur from Mexico to northwestern Argentina (Gutiérrez 2003). *Ferreyranthus* contains eight species which grow from central Peru to central Ecuador in wet to seasonally dry montane habitats. They range in size from small suffrutescent shrubs to small trees seldom over four or five meters (Dillon and Sagástegui

Fig. 27.1. Generic diversity in Liabeae by country.

1994a) (Fig. 27.3B, C). *Dillandia* contains three species of herbs with bullate leaf surfaces, pale yellow anther thecae, solitary to few capitula on long scapes, and is recorded from Colombia, Ecuador and northern Peru (Funk and Robinson 2001) (Fig. 27.3E–G). *Liabum*, *Oligactis*, and *Sampera* are concentrated in South America but range into Central America (Table 27.1). *Liabum* (Fig. 27.3D, H, I) possesses the widest overall distribution of any genus in the tribe stretching from central Mexico and the West Indies to the border between Bolivia and Argentina (Gutiérrez 2003). It is the only genus represented in the West Indies, with five species found in lowland to upland moist forests associated with limestone areas in Cuba, Hispaniola, and Jamaica (150–1400 m) (Gutiérrez and Katinas 2006). A single *Liabum* species (*Liabum bourgeaui* Hieron.) occurs in various types of forest from Mexico to Panama (1000–2000 m); the species diversity of *Liabum* increases in South America where the Andean Cordillera is home to 26 species (200–3000 m). *Oligactis* (s.str.) contains seven species confined to cloud forests from Venezuela, Colombia and Ecuador (1200–3500 m), and two species reaching the oak forests of Panama and Costa Rica (1750–2500 m). *Sampera* was described to accommodate a group of eight species of scandent shrubs and vines from Colombia to Peru that were previously classified as *Oligactis* subgenus *Andromachiopsis* (Funk and Robinson, in prep.)

Clade C, containing *Sinclairia*-*Sinclairiopsis*-*Liabellum*, contains ca. 15% of the species diversity of the tribe and is essentially a northern hemispheric group with considerable radiation. Its three closely related, and sometimes synonymous genera, *Sinclairia*, *Liabellum*, and *Sinclairiopsis*, are all found in Mexico and Central America with the exception of the widespread species *Sinclairia polyantha* (Klatt) Rydb., which is found in southern Mexico, Central America, and Colombia (Table 27.1). *Sinclairiopsis* is a monotypic Mexican genus and the sister taxon to the remainder of the *Sinclairia* complex. *Sinclairia* (including *Megaliabum*) and *Liabellum* form the *Sinclairia* complex, which contains approximately 20 species, principally confined to moist forests of Mexico and Central America (150–2500 m), with one common species reaching western Colombia (1600–1900 m) (Fig. 27.4). A few of the Mexican species are found in more arid environments associated with tropical scrub and deciduous forests. Turner (1989) treated *Megaliabum andrieuxii* (DC.) H. Rob. & Brettell, *M. pringlei* and *M. moorei* as *Sinclairia*, and these taxa do not all share sister taxa relationships (Fig. 27.2). The status of

Table 27.1. Genera, species diversity, distribution, and latitudinal range of Liabeae.

Genus	Species	Country distribution	Latitudinal range
Bishopanthus	1	Peru	3°S–7°S*
Cacosmia (*Cac*)	3	Ecuador, Peru	0°–10.5°S
Chionopappus (*Chi*)	1	Peru	7°S–13°S
Chrysactinium (*Chr*)	8	Ecuador, Peru	0.5°N–11.0°S
Dillandia (*Dil*)	3	Colombia, Peru	1.37°N–5.7°S
Erato (*Era*)	5	Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia	11°N–18.5°S
Ferreyranthus (*Fer*)	8	Ecuador, Peru	1°S–15°S
Liabellum (*Lib*)	5	Mexico	27°N–19.5°N
Liabum (*Lia*)	27	Mexico, Caribbean, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, Argentina	21.5°N–23°S
Microliabum (*Mic*)	5	Bolivia, Argentina	19°S–33°S
Munnozia (*Mun*)	46	Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina	11°N–23.5°S
Oligactis (*Oli*)	7	Ecuador, Colombia, Venezuela, Costa Rica, Panama	10°N–4°S
Paranephelius (*Par*)	7	Peru, Bolivia, Argentina	3°S–22.5°S
Philoglossa (*Phi*)	5	Colombia, Ecuador, Peru, Bolivia	0.5°N–17°S
Pseudonoseris (*Psu*)	3	Peru	3°S–17°N
Sampera (*Sam*)	8	Colombia, Ecuador, Peru	4°N–6°S
Sinclairia (*Sin*)	20	Mexico, Guatemala, El Salvador, Honduras, Costa Rica, Panama, Colombia	23°N–4°N
Sinclairiopsis (*Sio*)	1	Mexico	17°N–18°N

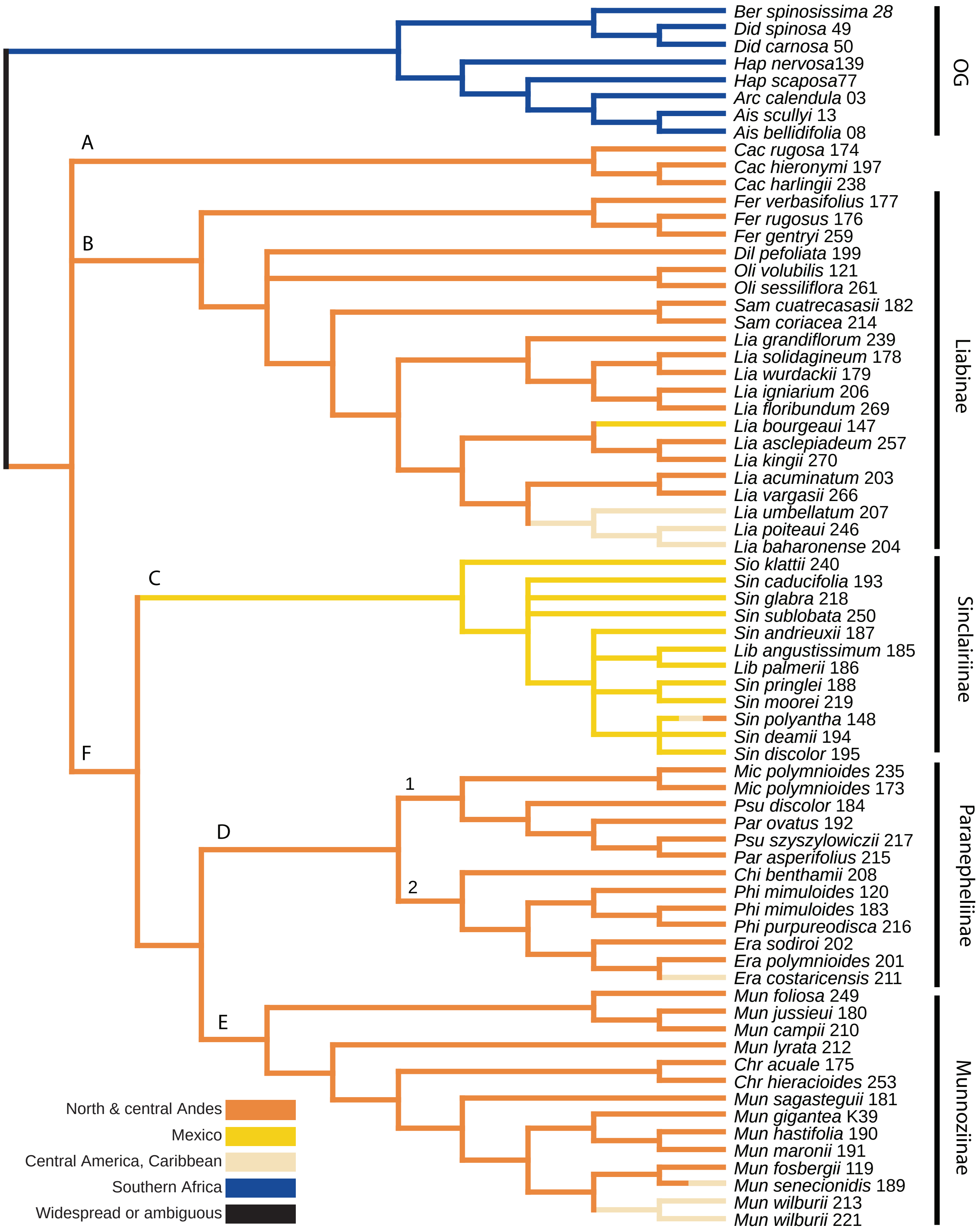

Fig. 27.2. Strict consensus cladogram from molecular studies incorporating sequence data from ITS, *trnL-F*, and the 3′ end of *ndhF* markers (Funk and Chan, in prep.). Numbers refer to accessions in the molecular studies. Colors refer to the distribution of the terminal taxa. Generic abbreviations correspond to labels in Table 27.1. See Chapter 44 for complete metatree.

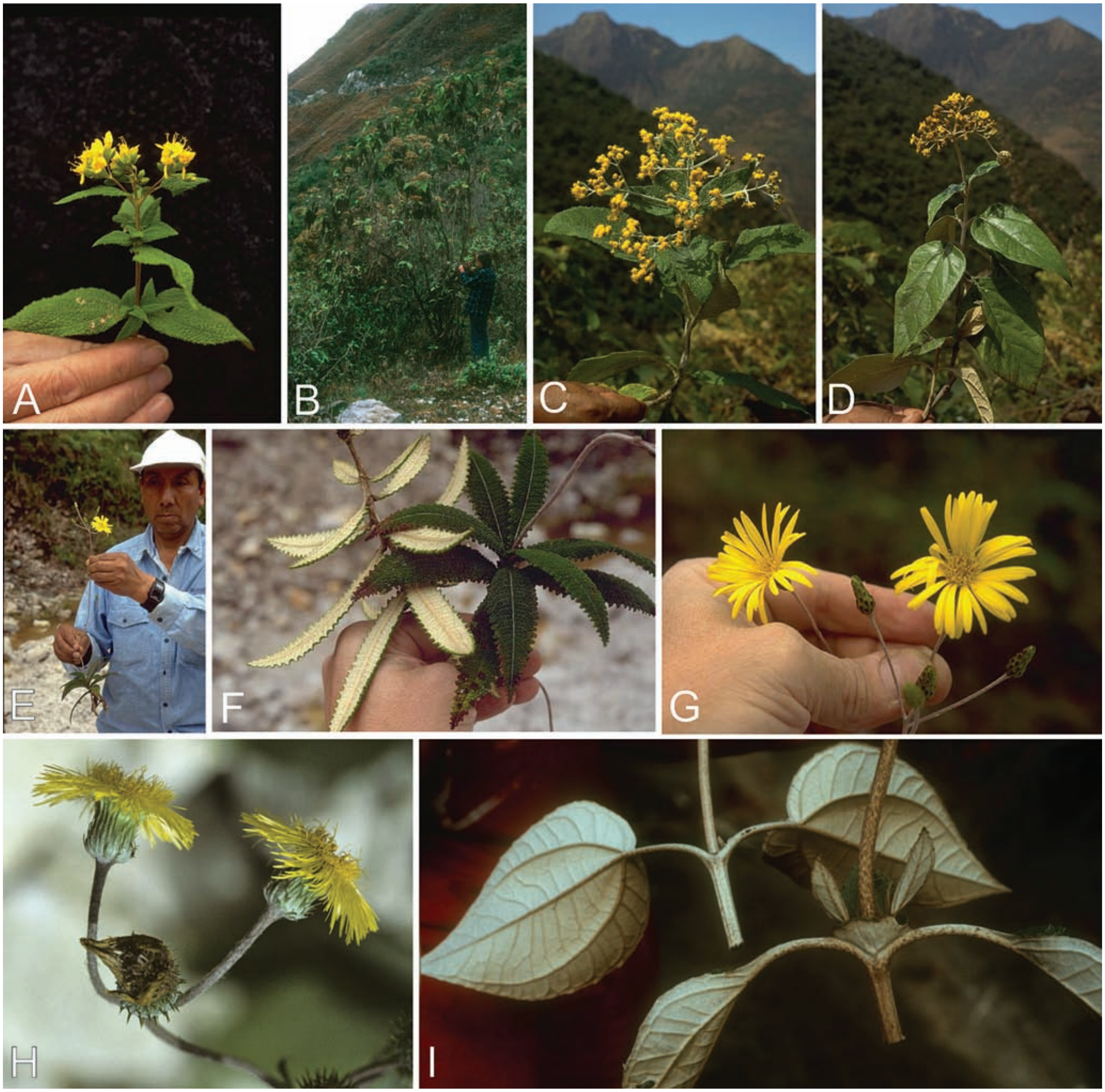

Fig. 27.3. A *Cacosmia rugosa* Kunth, a subshrub with bullate leaves and capitula with 5–6 ray florets; **B** *Ferreyranthus excelsus* (Poepp. & Endl.) H. Rob. & Brettell, a weak tree to 6 m tall with radiate capitula; **C** *F. verbascifolia* (Kunth) H. Rob. & Brettell, a large shrub with bullate leaves; **D** *Liabum solidagenium* (Kunth) Less., a large shrub with smooth leaves; **E** *Dillandia subumbellata* (Rusby) V.A. Funk & H. Rob., a weak herb with scandent habit with long peduncles and few capitula; **F** *D. subumbellata*, bullate upper leaf surfaces and densely tomentose lower surface; **G** *D. subumbellata*, capitula with ca. 40 ray florets; **H** *Liabum barahonense* Urban, capitula with nearly 50–75 ray florets with filiform limbs; **I** *L. amplexicaule* showing interpetiolar pseudostipular foliar tissue.

Megaliabum is under evaluation. *Liabellum* is comprised of perhaps five species, mostly restricted to seasonally dry sites in west-central Mexico (1000–2000 m). The group is here formally recognized at the subtribal rank, Sinclairiinae H. Rob. (cf. Appendix 27.1).

Clade D, containing *Microliabum-Pseudonoseris-Paranephelius-Chionopappus-Philoglossa-Erato*, has ca. 15.5% of the species diversity of the tribe and, with the exception of one species of *Erato* in Costa Rica, is entirely South American in distribution. The most southern genus, *Microliabum*, has five species distributed from southern Bolivia to northwestern Argentina (2800–3300 m; Funk and Brooks 1991). *Paranephelius*, with seven species, is found in upper elevation sites (*jalca* and *puna*) from northern Peru to Bolivia and extreme northern Argentina (2200–4600 m) (Fig. 27.5). *Pseudonoseris* contains three species, one, the type, is confined to a narrow distribution in southern Peru (3200–3500 m) and another two restricted to northern Peru (1800–2600 m) (Fig. 27.6A–C). *Philoglossa* with five species is represented by one found in inter-Andean sites from Colombia through the interior of Peru to Bolivia (200–3100 m), and four species restricted to the coastal *lomas* formations or valleys of coastal Peru (100–700 m) (Fig. 27.7E, F). *Erato* has five species, one endemic to Costa Rica, another that ranges from Costa Rica (1200–2500 m) to Venezuela, Colombia, and Ecuador, and another three that are confined to Ecuador, Peru, and Bolivia (900–2900 m) (Fig. 27.7C, D). *Chionopappus* is monotypic and restricted to central Peru (1600–2500 m) and occasionally recorded from coastal *lomas* formations (400–500 m) of northern Peru (Fig. 27.7B). *Bishopanthus*, a monotypic genus tentatively associated with Clade D since it approaches *Chionopappus* in capitular morphology; it has only been recorded once at a site east of the Rio Marañón and has not been included in any molecular studies to date (2000 m) (Fig. 27.7A).

Clade E, containing *Munnozia*-*Chrysactinium*, contains ca. 31% of the species diversity in the tribe and with a few exceptions represents an Andean group in a wide variety of habitats. *Munnozia* ranges from Costa Rica and Panama, where two species are known, to Andean South America from Venezuela to Bolivia and Argentina where 45 species have been recorded (600–3800 m) (Fig. 27.8C–H). *Chrysactinium*, confined to Ecuador and Peru, has eight species and is predominately found in open, upper elevation sites (*páramo*) and occasionally at the margins of cloud forests (1700–4300 m) (Fig. 27.8A, B).

PHYLOGENY AND SYSTEMATICS

A cladistic analysis was performed, using data from ITS, *trnL-F*, and the 3′ end of *ndhF*, and those results are illustrated in Figure 27.2 (cf. Funk and Chan, in prep.). The placement of *Cacosmia* as the sister taxon to the remainder of the tribe was found in ITS trees and in the combined analysis; however, it was never strongly supported. In the chloroplast trees the position of *Cacosmia* varied depending on the outgroup(s) used. Sometimes it was the sister group to Clade B (our preferred placement based on morphology), and other times it was in a polytomy with Clade B and the remainder of the tribe [Clades (C(D, E))]. At this point, it seems best to keep the least resolved tree, the polytomy, as the working cladogram. Additional markers are being added in an effort to increase resolution of putative relationships.

Subfamily, tribal and subtribal relationships

Until recently Liabeae have resided in the subfamily Cichorioideae s.l., whose members share deeply lobed disk corollas, long-spurred or calcarate anther bases, continuous stigmatic surfaces on the inside of the style branches, long sweeping hairs that cover the outer surface of the style branches and the upper style shaft, and spherical spinose pollen, along with Mutisieae, Cardueae, Lactuceae, Vernonieae, and Arctoteae and miscellaneous small tribes (Robinson and Funk 1987; Bremer 1994; Jansen et al. 1991). However, this definition of the subfamily has been shown to be non-monophyletic, and the most recent circumscription excludes paraphyletic Mutisieae and thistles. As a result, most of the characters that previously united the subfamily are now considered plesiomorphic. Some characters appear to be apomorphic, such as the tendency to produce latex or at least to have the anatomical characters that would allow it to do so. However, this character is missing in most Vernonieae and so is not reliable in determining which taxa 'belong' in this monophyletic group. Another potential apomorphy, the presence of calcarate anthers is either plesiomorphic for the family as a whole or it may be two independent apomorphic characters. Although the characterization of the subfamily is ongoing, it is clear that the four main tribes in the subfamily are Arctotideae, Lactuceae, Liabeae, and Vernonieae. They, along with several small tribes (see Chapter 23), form a strongly supported monophyletic group within the subfamily in every analysis. It also seems clear that the sister group of Liabeae is Vernonieae and/or Arctotideae. The molecular data of Vernonieae (especially the ITS) are so different from Liabeae that they make a poor outgroup, and so Arctotideae were used in the phylogenetic analysis. Lactuceae are always sister to the Liabeae-Vernonieae-Arctotideae clade. The distribution of characters makes it difficult to determine the exact relationships among these three tribes. The presence of latex is shared by Lactuceae and Liabeae and Arctotideae; vernonioid type styles are shared by Vernonieae and Liabeae; and the absence of rays and presence of mostly blue flowers group Vernonieae and Lactuceae. Most present-day taxonomists consider Liabeae to be most closely related to Vernonieae (Chapter 23). However, at present, this grouping is only moderately supported, and the placement of several smaller tribes may alter its position, and as a result, the relationships within this subfamily will require additional study.

Robinson (1983) provided the first efforts to established a subtribal classification, where three subtribes

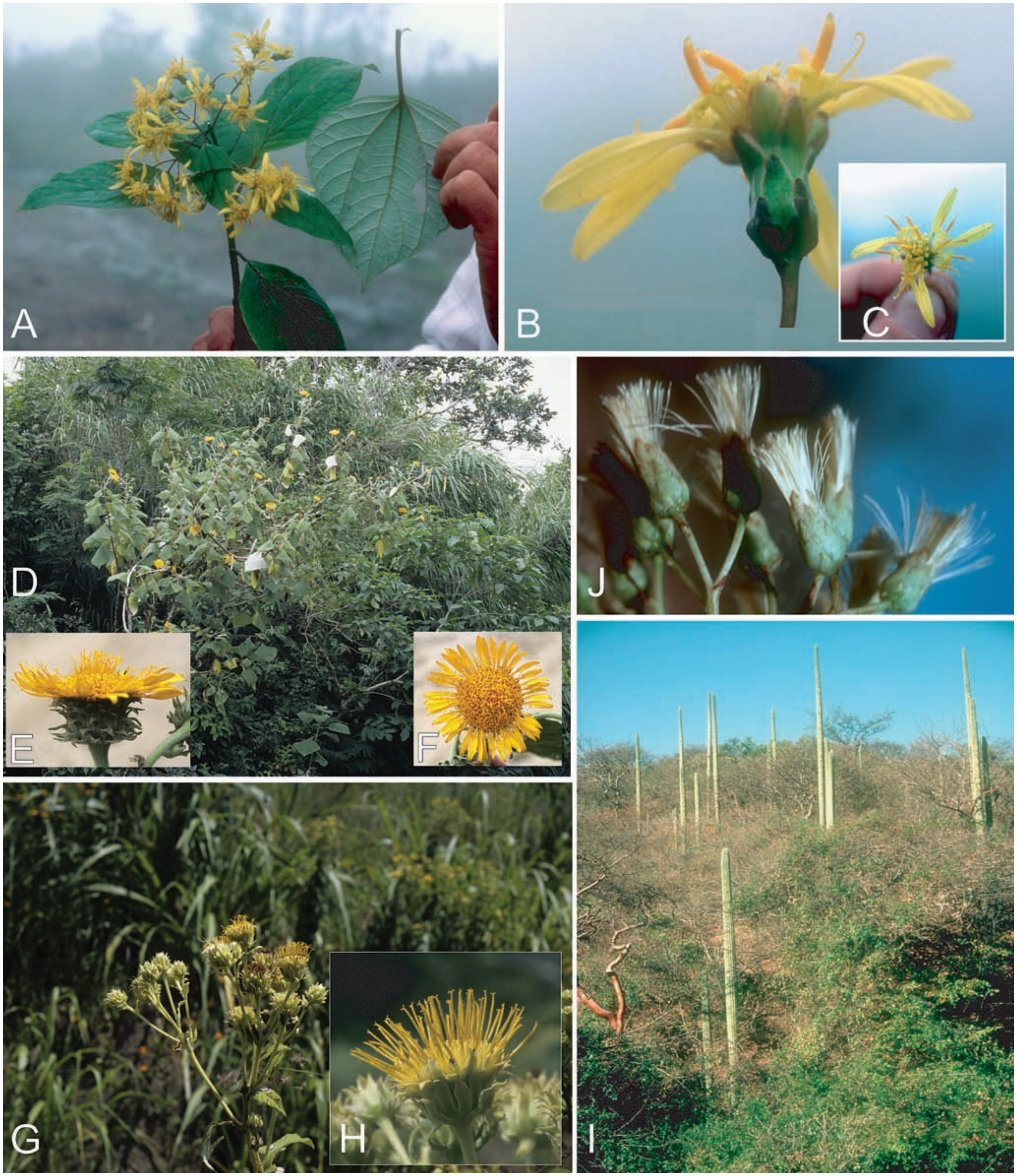

Fig. 27.4. *Sinclairia* taxa from Mexico. **A** *Sinclairia polyantha* (Klatt) Rydb., leaf underside and capitulescence; **B** *S. polyantha*, lateral view of capitulum illustrating multiseriate involucre; **C** *S. polyantha* capitulum showing loose radiate capitulum; **D** *Sinclairia* (*Megaliabum*) *andrieuxii* (DC.) H. Rob. & Brettell; **E** *S.* (*Megaliabum*) *andrieuxii*, lateral view of capitulum showing herbaceous phyllaries; **F** *S.* (*Megaliabum*) *andrieuxii* radiate capitulum; **G** *S.* (*Megaliabum*) *pringlei* (B.L. Rob. & Greenm.) Rydb. herbaceous, erect perennial; **H** *S.* (*Megaliabum*) *pringlei*, discoid capitulum; **I** *S. caducifolia* (B.L. Rob. & Bartlett) Rydb., habit and habitat; **J** *S. caducifolia*, discoid capitula.

were recognized, i.e., Munnoziinae, Liabinae, and Paranepheliinae, largely based upon overall morphology and distribution of endothecial cells. Our knowledge of the internal structure of the tribe is expanding, and the strong support for the monophyletic group represented by *Sinclairia* and its closest putative relatives, i.e., *Sinclairiopsis*, *Megaliabum*, and *Liabellum*, has led to description of Sinclairiinae (Fig. 27.1, cf. Appendix 27.1). Further, the current bounds of Paranepheliinae are expanded to include the other members of the strongly supported Clade D containing *Paranephelius*, *Pseudonoseris*, *Microliabum* and the sister group containing *Chionopappus*, *Philoglossa*, and *Erato*. As with relationships at higher levels, the internal classification of Liabeae is still a work in progress.

Fig. 27.5. **A** *Paranephelius uniflorus* (Poepp. & Endl.) Sch.Bip. with pinnately divided basal leaves and bullate upper leaf surfaces; **B** *P. uniflorus*, capitula; **C** *P. ovatus* Wedd. with entire leaves and smooth upper leaf surfaces; **D** *P. ovatus*, capitulum.

MORPHOLOGY AND ANATOMY

Liabeae have a series of characters that make it relatively easy to identify; however, as in most tribes, there are taxa with exceptions to some of the tribal characters. The tribe is diagnosed by a combination of morphological characters: the leaves are invariably opposite, but some genera possess leaves in a rosette or congested on short stems so they appear to be whorled (e.g., *Chrysactinium*, *Paranephelius*, *Pseudonoseris*, and rarely *Liabum*); leaves are often strongly trinervate (pinnatifid in *Ferreyranthus*, *Oligactis*, *Paranephelius*; palmate in *Erato*) and white-tomentose beneath (strigose or pilose in *Erato*; glabrous in *Philoglossa*), yellow ray and disk florets (reddish in *Chionopappus* and one species of *Pseudonoseris*; white in two species of *Munnozia*), disc florets numerous, hermaphroditic with narrowly funnelform limbs and

Fig. 27.6. A *Pseudonoseris discolor* (Muschl.) H. Rob. & Brettell, habit and habitat; **B** *P. discolor*, capitulum (photographs of *Quipuscoa 3338*, Sandia, Puno, Peru); **C** *Pseudonoseris szyszylowiczii* (Hieron.) H. Rob. & Brettel capitulum (*Dillon et al. 6485*); **D** *Microliabum candidum* (Griseb.) H. Rob. capitulum; **E** *M. polymnioides* (R.E. Fries) H. Rob. illustrating interpetiolar pseudostipules and white latex from cut stem. [Photographs: D, E, D. Gutiérrez.]

deeply lobed corollas; oblong or columnar achenes usually with a biseriate pappus of outer scales and inner scabrous bristles (absent in *Cacosmia*; bristles only in *Paranephelius*), and the frequent occurrence of white latex (apparently absent in *Ferreyranthus*, *Liabum*, and *Oligactis*).

Other characters are moderately useful such as involucres are cylindrical to hemispherical with 3 to many, subimbricate phyllaries, and receptacles are alveolate, naked or more often with projecting squamellae or points (true paleae are only known in *Chionopappus*); the capitula have pistillate ray florets (absent in *Liabellum* and some *Sinclairia*) with well-developed, 3-lobed lamina.

Some characters are quite variable or otherwise uninformative including the habit which comes in a wide range of forms including cauline, annual to perennial herbs, lianas, shrubs, or small trees, or more rarely acaulescent or short-stemmed herbs; the capitula can be solitary and scapose to sessile, or more often weakly to densely cymose

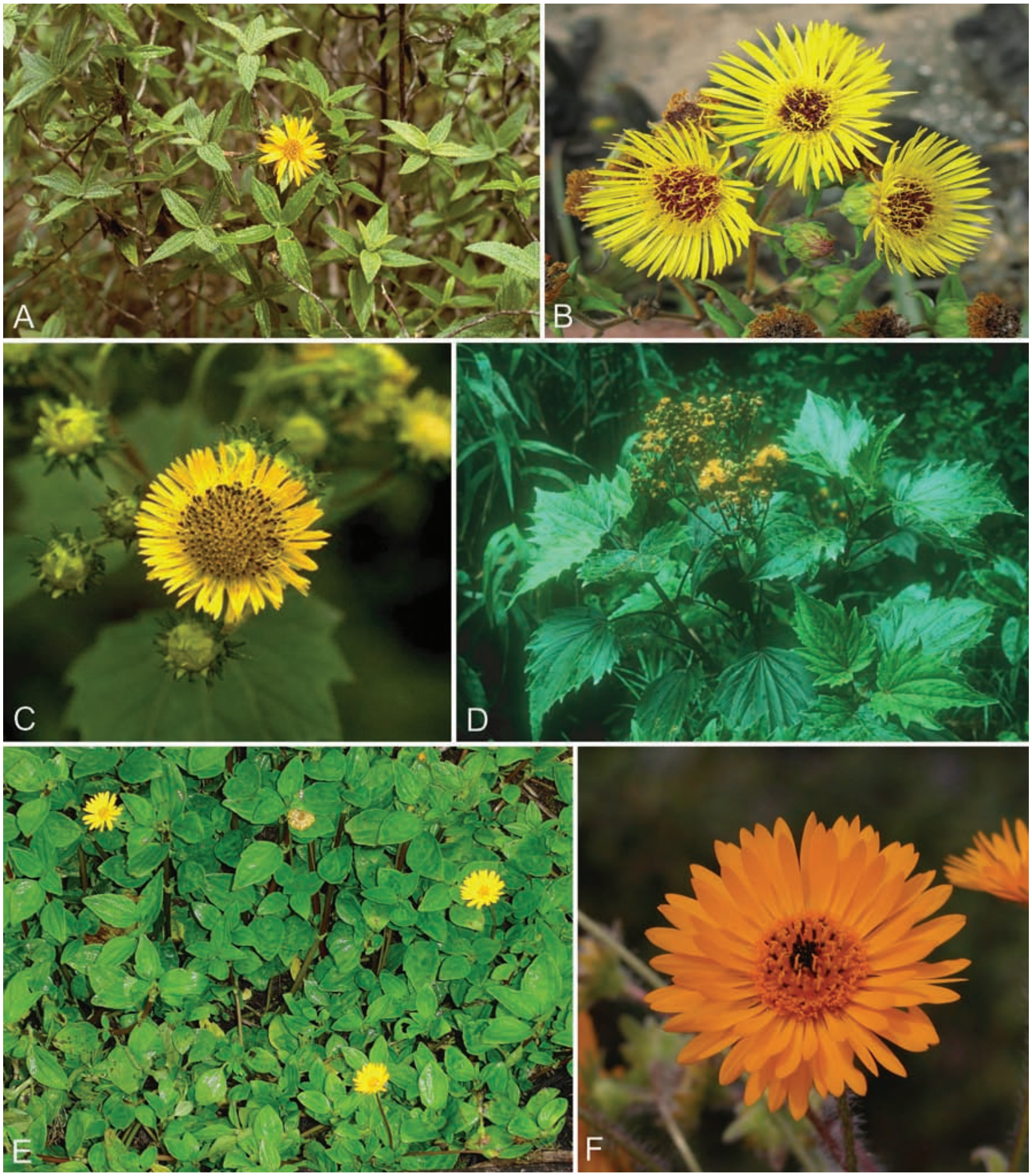

Fig. 27.7. **A** *Bishopanthus soliceps* H. Rob.; **B** *Chionopappus benthamii* S.F. Blake; **C** *Erato stenolepis* (S.F. Blake) H. Rob.; **D** *E. polymnioides* DC.; **E** *Philoglossa mimuloides* (Hieron.) H. Rob. & Cuatrec.; **F** *P. peruviana* DC.

to corymbose-paniculate; anther thecae are usually pale, or occasionally black (e.g., *Chrysactinium*, *Erato*, *Munnozia*, *Philoglossa*), the bases calcarate and tailed or rounded, and the terminal appendages oblong-ovate; style branches in most genera are relatively short and with narrowly obtuse or rounded apices; the inner stigmatic surfaces are undivided and outer branch surfaces and upper shafts are often pubescent with acute trichomes. Achenes (cypselas) are oblong, fusiform, or columnar, with (2–)4–10 ribs, the surfaces are glabrous or pubescent with glandular and/or elongate trichomes. When present, the biseriate pappus can have an inner pappus of numerous long, scabrid capillary bristles, plumose bristles (*Chionopappus*), or broad squamellae (one species of *Microliabum*). The outer pappus is often a series of shorter bristles or squamellae, but it can also be reduced to awns in *Erato* and some *Philoglossa* species, or totally absent in Paranepheliinae, much of Munnoziinae, *Cacosmia* and *Chionopappus*.

Fig. 27.8. **A** *Chrysactinium hieracioides* (Kunth) H. Rob. & Brettell, habit and habitat; **B** *C. rosulatum* (Hieron.) H. Rob. & Brettell, capitulum; **C** *Munnozia sagasteguii* H. Rob., habit; **D** *M. sagasteguii*, capitulum; **E** *M. sagasteguii*, fleshy roots; **F** *Munnozia senecionidis* Benth., leaves and capitula (*Quipuscoa 1099*, San Martin, Peru); **G** *M. jussieui* (Cass.) H. Rob. & Brettell, habit; **H**. *M. jussieui*, close-up of capitula.

POLLEN

Liabeae pollen grains are tricolporate with ectoapertures meridionally elongate and endoapertures transversely short and ovoid; spherical to oblate-spheroid in shape; approximately 25–40 μm (occasionally up to 50 μm) in diameter with *Liabum* and *Oligactis* the smallest and *Sinclairia* and *Liabellum* the largest. Stix (1960) and Robinson and Marticorena (1986) should be consulted for detailed measurements of: aperture length and width, exine layer thicknesses, spine dimensions, exine diameters with and without spines, length and diameter

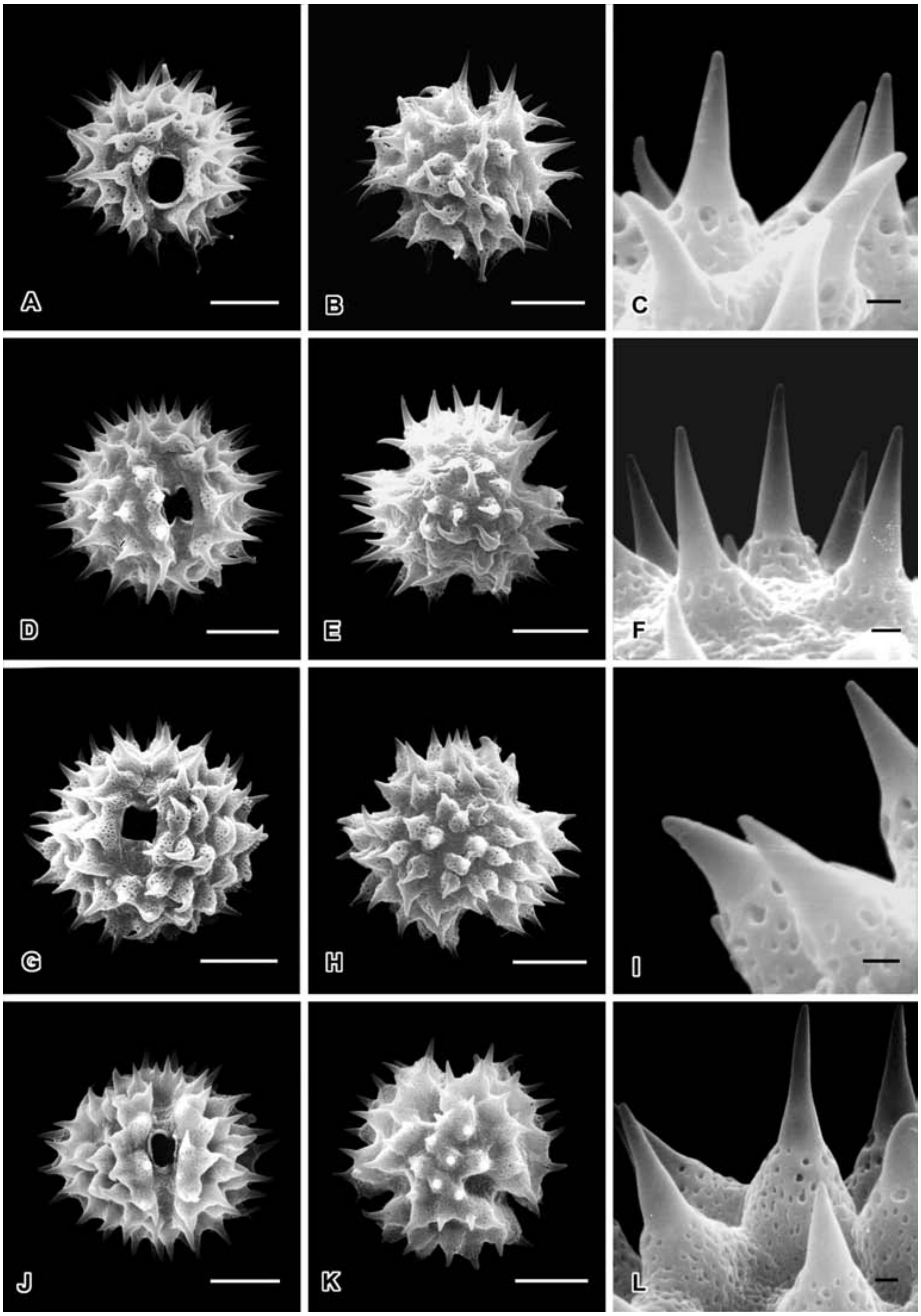

Fig. 27.9. A–C *Philoglossa peruviana* DC.; **D–F** *Philoglossa purpureodisca* H. Rob.; **G–I** *Philoglossa mimuloides* (Hieron.) H. Rob. & Cuatrec.; **J–L** *Erato polymnioides* DC. Scale bars for A, B, D, E, G, H, J, K = 10 μm; for C, F, I, L = 1 μm.

of columellae, etc. The exine surface (tectum) is highly perforate and echinate with both regular and irregularly organized spines and with spine bases either distinct or overlapping (*Philoglossa*, Figs. 27.9A–I; *Erato*, Fig. 27.9J–L; *Munnozia*, Fig. 27.10A–C; *Liabum*, Fig. 27.10D–F; *Sinclairia*, Fig. 27.10G–I; *Chionopappus*, Fig. 27.10J–L). It is noteworthy, as emphasized by Robinson and Marticorena (1986) and Funk et al. (2007), that the irregular organization of the spines and spine bases does not attain the lophate or psilate condition(s) present in putative tribes Vernonieae, Senecioneae and Lactuceae.

SEM of fractured grains shows prominently thickened basal columellae that are attached proximally to a narrow foot layer (Fig. 27.11C–E, H, J, K) and distally terminate in two levels of lateral and essentially parallel branches. The upper branch is the highly perforate exine surface (tectum, Figs. 27.9A–L, 27.11A–L) and is connected to the lower branch (inner tectum) by

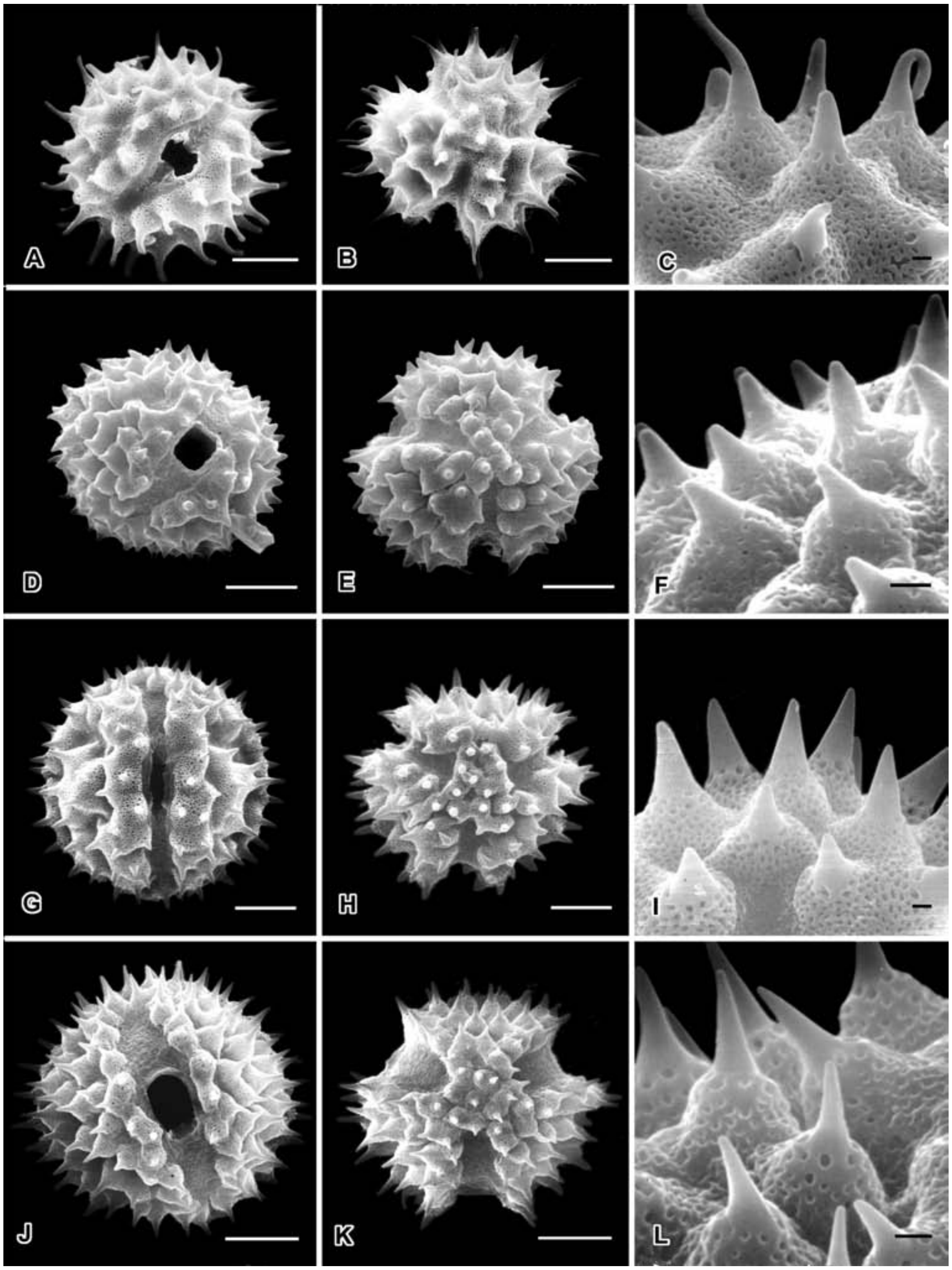

Fig. 27.10. **A–C** *Munnozia lanceolata* Ruiz & Pav.; **D–F** *Liabum ignarium* (Kunth) Less.; **G–I** *Sinclairia caducifolia* Rydb.; **J–L** *Chionopappus benthamii* S.F. Blake. Scale bars for A, B, D, E, G, H, J, K = 10 µm; for C, F, I, L = 1 µm.

short columellae <1.0 µm in length (Fig. 27.11A–K). Acute spines project from the exine surface in either orderly or unorganized arrangements as well as having bases that are distinct from adjacent spines or confluent with them (Figs. 27.9A–L, 27.11A–L). Basal columellae are either grouped under the spines or are coalesced into hollow cylinders (Fig. 27.11A–K; Robinson and Marticorena 1986) with one cylinder per spine (Funk et al. 2007: Fig. 27.41D). The particular organization of the spines on the exine surface, spine base independence and confluence, and the relationship of basal columellae with spines are characters found only in Liabeae and are considered by Robinson and Marticorena (1986) as major distinctions from Vernonieae pollen where single solid basal columellae span the exine from foot layer to spine tip, a relationship also common in other tribes

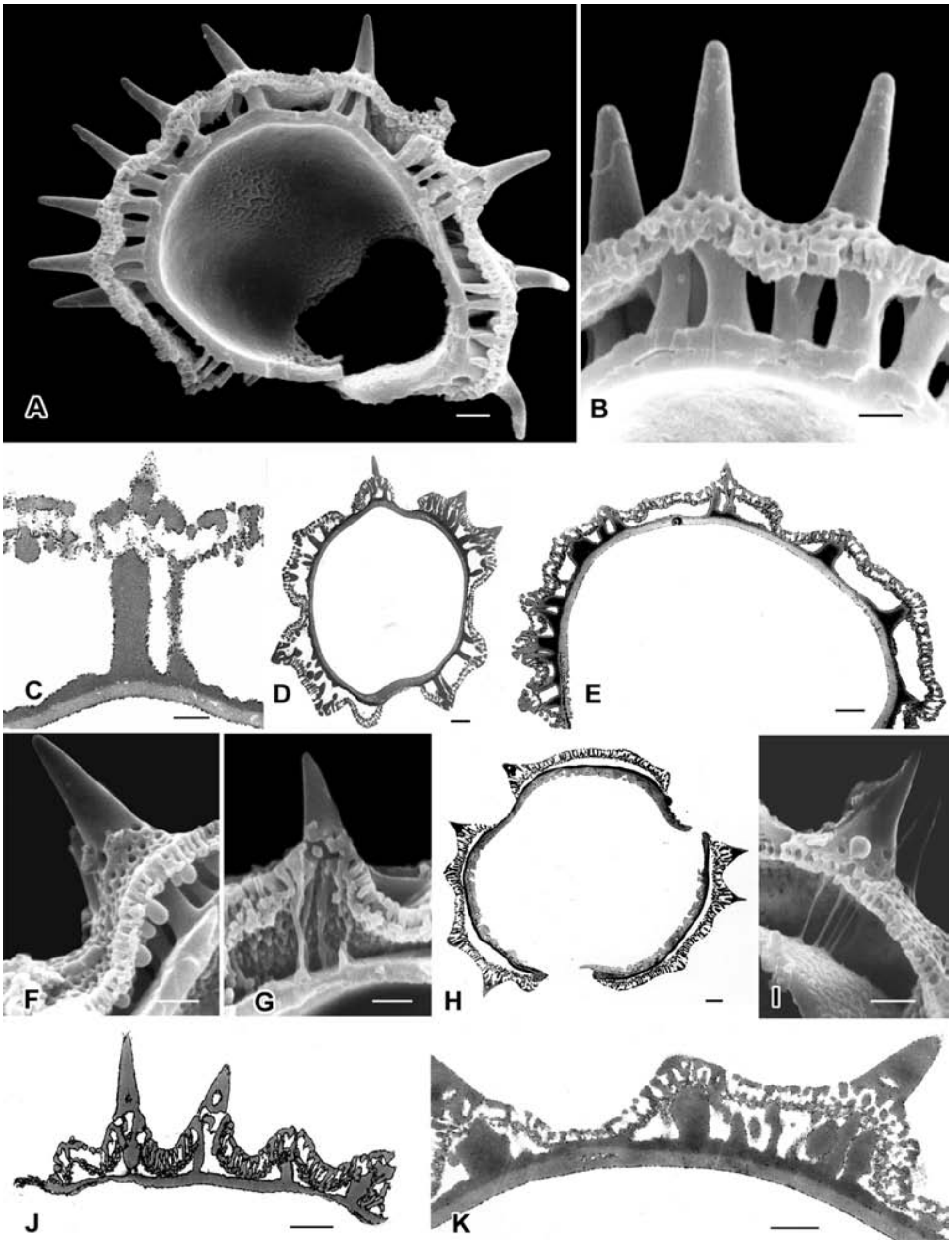

Fig. 27.11. A, B *Cacosmia rugosa* Kunth; **C, D** *Ferreyranthus rugosus* (Ferreyra) H. Rob. & Brettell; **E** *Liabum solidagineum* Less.; **F** *Sinclairia polyantha* Rydb.; **G** *Pseudonoseris discolor* (Muschl.) H. Rob. & Brettell; **H** *Paranephelius asperifolius* (Muschl.) H. Rob. & Brettell; **I** *Philoglossa peruviana* DC.; **J** *Chrysactinium acaule* (Kunth) Wedd.; **K** *Munnozia lanceolata* Ruiz & Pav. Scale bars for A, D, E, H–K = 2 µm; for B, C, F, G = 1 µm.

such as Mutisieae (Zhao et al. 2006), Anthemideae and Cardueae (Skvarla et al. 1977). Extremely thin columellae (ca. <0.5 µm in width) support the internal tectum (Fig. 27.11G–I). While common in Liabeae (Feuer and Dillon 1982; Robinson and Marticorena 1986), slender columellae are also present in Vernonieae (Skvarla et al. 2005) and Lactuceae (Blackmore 1981, 1982). The presence of columellae, both thickened and slender (Figs. 27.11A–K), interrupt what otherwise would be a continuous open space or cavus (Skvarla and Turner 1966) in the exine whereby the outer exine (i.e., lower part of the internal tectum) is separated from the foot layer and with the only union of these layers being at the three aperture margins. The result is what is known as a caveate pollen structure and is characteristic of tribes such as Heliantheae, Senecioneae, Eupatorieae and Helenieae The caveate feature is problematic only in *Paranephelius* (Fig. 27.11H; Stix 1960; Skvarla et al. 1977) and some species of *Munnozia* (Robinson and Marticorena 1986) In all other Liabeae pollen, the comparable areas are partially occupied by distinctive columellae between the foot layer and the lower part of the internal tectum and we have used the term "pseudocaveate" to describe it.

TEM sections of *Ferreyranthus* (Fig. 27.11C, D), *Liabum* (Fig. 27.11E), *Paranephelius* (Fig. 27.11H), *Chrysactinium* (Fig. 27.11J) and *Munnozia* (Fig. 27.11K), as already indicated, reinforce the data from fractured pollen grains examined in SEM (Fig. 27.11A, B, F, G, I). Especially important are the electron stain differences that indicate a consistently thicker endexine immediately beneath a slightly narrower foot layer (i.e., Fig. 27.11C, K) for all of the Liabeae taxa examined. Globose structures attached to the lower margin of the internal tectum as noted in TEM (Fig. 27.11C) and SEM (Fig. 27.11F) were earlier described for *Liabum barahonense* Urban (Robinson and Marticorena 1986) and *Munnozia tenera* (Sch.Bip.) H. Rob. & Brettell (Funk et al. 2007) and are in need of clarification but appear to be the swollen bases of the short columellae that connect the two tectal layers.

Observations based on SEM and TEM were made on the pollen of 11 genera and 17 species of the tribe (Figs. 27.9–27.11). Liabeae taxa reported earlier include *Dillandia* pollen (Funk and Robinson 2001: Figs. 1–2; Funk et al. 2007: Fig. 41C), *Microliabum* (Funk et al. 2007: Fig. 41A) and *Chrysactinium* (Funk et al. 2007: Fig. 41B). Complimenting these reports is the comprehensive study by Robinson and Marticorena (1986), where they described by SEM whole and fractured pollen grains of *Paranephelius*, *Pseudoseris*, *Bishopanthus*, *Chionopappus*, *Austroliabum*, *Cacosmia*, *Ferreyranthus*, *Sinclairia*, *Liabellum*, *Liabum*, *Oligactis*, *Erato*, *Philoglossa*, *Chrysactinium* and *Munnozia*. *Sampera* is comprised of taxa originally classified as *Oligactis*, and its species have been examined (Robinson and Marticorena 1986).

Structural features described from sectioned pollen from other studies also are in agreement with TEM in Fig. 27.11C–E, H, J, K as indicated by an LM microtome section of *Chionopappus* (Robinson and Marticorena 1986: Fig. 68), the extensive LM/ultraviolet study by Stix (1960) wherein she recognized three structural types based on differences in columellae morphology and TEM of *Cacosmia* and *Liabum* (Skvarla et al. 1977). In the latter study, a distinct morphological difference was noted in exine morphology of *Liabum ovatum* (Wedd.) J. Ball (= *Paranephelius ovatus* Wedd.) as compared to other species of *Liabum*, and Robinson and Marticorena (1986) should be consulted for a detailed explanation of this discordant morphology.

In summary, within Liabeae morphological distinctions have been noted primarily based upon size, spine organization and separation or overlapping of spine bases on the exine surface, tectum layering, and columellae relationships with overlying spines (Robinson and Marticorena 1986). These characters are considered to be unique to Liabeae and distinguishing it from other tribes. Robinson and Marticorena (1986) present in-depth discussions of all of the characters mentioned. The final contribution in this volume (Bibliography of Pollen Literature in Compositae) provides additional references for Liabeae pollen.

CHROMOSOME NUMBERS

Chromosome numbers in the tribe are known from twelve genera, base numbers are $x = 7$, 9, 12, 14, 16, and 18 (Robinson et al. 1985; Carr et al. 1999). A base number of $x = 9$ has been proposed for the tribe (Turner et al. 1967; Robinson et al. 1985). For purposes of discussion, the reported counts are discussed as they are plotted upon a simplified cladogram (Fig. 27.12) derived from the strict consensus cladogram (Funk and Chan, in prep.) (Fig. 27.2). *Cacosmia* has uniformly been reported as $n = 7$ with bivalents of the same size and potentially one small fragment.

In **Clade B,** *Ferreyranthus* species have been recorded with counts of $n =$ ca. 18, or 19 heteromorphic bivalents (Robinson et al. 1985) and a count of $n = 24$–27 for *F. excelsus* (Poepp. & Endl.) H. Rob. & Brettell, which must be interpreted as a polyploid derivative (Sundberg and Dillon 1986). Other members of the clade, i.e., *Liabum*, *Oligactis*, and *Sampera* have a hypothetical base number of $x = 9$. *Liabum* with 38 species has counts of $n = 17$–20 reported (Robinson et al. 1985; Goldblatt and Johnston 1990; Carr et al. 1999) and a hypothetical base number of $x = 9$. Its sister genus, *Sampera*, with eight species, has only one recorded count of $n =$ ca. 39 (*S. pichinchensis* (Hieron.) V.A. Funk & H. Rob.; Jansen and Stuessy 1980) with a base number of $x = 9$. It is distributed farther south than *Liabum*, restricted to Colombia, Ecuador, and Peru. No taxa within *Oligactis* s.str. or *Dillandia* have been counted to date.

In **Clade C,** *Liabellum* (five species) and *Sinclairiopsis* have no recorded counts, and *Sinclairia* (20 species) consistently has reports of 15–18 bivalents. The ancestor of the species of this clade was probably from Mexico or northern Central America and according to Turner (1989) it was most likely a shrub.

In **Clade D-1,** *Microliabum-Pseudonoseris-Paranephelius-Chionopappus-Philoglossa-Erato*, a wide array of recorded chromosome numbers ranging from *n* = 9 to *n* = 29 have been reported. *Microliabum* has counts of *n* = 12, 14, and 15; *M. polymnioides* (R.E. Fries) H. Rob. *n* = 12 (Rozenblum et al. 1985), *M. candidum* (Griseb.) H. Rob. *n* = 14 (Bernardello 1986; Hunziker et al. 1989) and *n* = 15 (Wulff et al. 1996). The sister taxon to *Microliabum* is Paranepheliinae with *Paranephelius* and *Pseudonoseris*. As discussed in detail below, the interpretation of counts is made more difficult by the putative hybridization documented in *Paranephelius* with counts of *n* = 9, 14 and 15 (Robinson et al. 1985; Sundberg et al. 1986) and another of *n* = ca. 29 (Sundberg and Dillon 1986). The report *n* = 12 by Dillon and Turner (1982) for *Pseudonoseris szyszylowiczii* (Hieron.) H. Rob. & Brettell was termed "anomalous" in Robinson et al. (1985), and the count was questioned first as to the authenticity of the voucher and secondly, that there were no immature heads on the duplicate voucher deposited at US. It was further implied that the count actually was made on material of *Chrysactinium*. Given that it has been unequivocally shown that *P. szyszylowiczii* is an intergeneric hybrid product involving *Paranephelius* and another element in *Pseudonoseris*, it seems prudent to accept the count of *n* = 12 as within the realm of possibility and given that *n* = 12 has been reported in what can be considered its sister taxon, *Microliabum*.

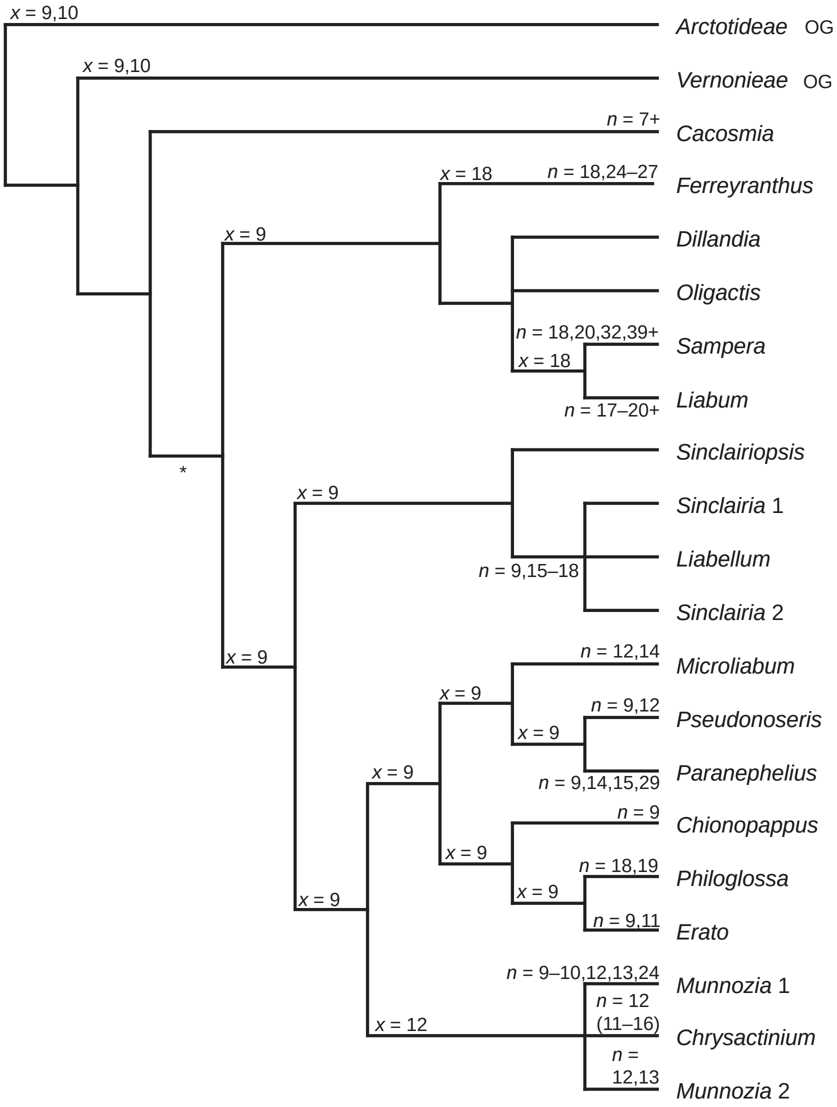

Fig. 27.12. Reported chromosome numbers plotted upon the strict consensus cladogram (Fig. 27.2) collapsed for simplification.

The genera in **Clade D-2** appear to be centered on $x = 9$. *Erato* has recorded counts of $n = 9$ (Robinson et al. 1985), $n = 11$ (Sundberg and Dillon 1986; Goldblatt and Johnson 1990), and $2n = 9–12$ bivalents (Carr et al. 1999). *Philoglossa* with five species has counts of $n = 18$ (Robinson et al. 1985) and $n = 19$ (Sundberg and Dillon 1986). *Chionopappus* has one count of $2n = 18–20$ which has been interpreted as $x = 9$. Munnoziinae have two genera. *Chrysactinium* with 8 species has recorded counts of $n = 12, 13, 14$ (Sundberg and Dillon 1986) or even 15–16 (Carr et al. 1999) and its paraphyletic sister genus, *Munnozia*, with 46 species has reported counts of $n = 10, 11, 12$, ca. 13, ca. 24 (Carr et al. 1999). The one genus that could not be placed in one of the aforementioned groups was *Bishopanthus*. The highly variable nature of counts from throughout Liabeae suggests that polyploidy and chromosomal evolution may have played a role in speciation for the group.

BIOGEOGRAPHY

Since Liabeae find their greatest generic and specific diversity in the Andean Cordillera from 12°N to 24°S latitude, any discussion of biogeography and speciation should include an examination of Andean orogeny. The Andean Cordillera is thought to be of recent origin, formed by the Nazca plate colliding with the South American plate along the Peru-Chile trench (James 1973; Jordan et al. 1983; Orme 2007). We have divided the Cordillera into four areas; the first two are the northern areas, the northeastern zone that begins in western Venezuela and extends to central Ecuador, and the somewhat overlapping zone, the northwestern zone, which extends from northwestern Colombia to northern Peru. The third area is the central zone that stretches from southern Peru to northern Argentina and adjacent Chile. The fourth area, the southern zone, occupies the border between southern Chile and Argentina and does not contain any members of the tribe. The central zone contains almost half the species and most of the genera of the tribe and is the oldest of the three zones containing Liabeae (James 1973; Jordan et al. 1983; Taylor 1991; Windley 1984). The central zone of the Andes is thought to have had its major uplift in the Oligocene (ca. 30 Ma) in northern Chile and southern Peru (James 1973; Jordan et al. 1983). The northern Andes have experienced their primary uplift in the last 5 Myr (Hammen 1974; Gentry 1982) and the *páramo-puna* area (the northeastern zone) is considered the most recent, appearing during the Quaternary (2.0–0.1 Ma; Vuilleumier 1969; Simpson Vuilleumier 1975). The northeastern zone is separated from Peru by the Huancabamba Deflection (also known as the Huancabamba Depression or North Peruvian Low), which has affected distributions of high elevation plants and animals (Fjeldsa and Krabbe 1990; Haffer 1974, 1981; Pennell 1951; Simpson Vuilleumier 1970; Vuilleumier and Simberloff 1980). However, the Huancabamba Deflection appears to have had an impact only on Liabeae concentrated in the northeastern zone. Those found in the northwestern zone (the majority) are distributed on both sides of the divide, although the more localized genera tend to have most of their species on one side or the other.

Two million years ago the isthmus of Panama was not complete (Gentry 1982) so that the Pacific and West Indies were joined, and in the last million years the sea has repeatedly intruded far into the Orinoco and Amazon basins. As little as 12,000 years ago, the sea level was lowered and as a result the climatic zones in the Andes were lowered (Simpson Vuilleumier 1975). This recent alteration of habitats is believed to have provided ample opportunity for allopatric speciation and may hold the key for current species diversity in Liabeae.

The patterns of generic richness (Fig. 27.1) suggest that the center of the extant diversity of Liabeae is northern Peru and to a lesser extent, Ecuador. This information, in conjunction with an examination of the colored branches of the strict consensus tree (Fig. 27.2), indicates that it is most likely that the extant members of the tribe originated in the central Andes (especially Peru) and repeatedly spread north into the northwestern and northeastern areas and south into Bolivia and Argentina. The non-Andean groups of Liabeae are clearly derived from radiations from Andean ancestors. These include the dispersal of the ancestor of the *Sinclairia* group into Mexico (with one species making it back to South America), which was a single event, and of repeated dispersals of *Erato* (1 sp.), *Oligactis* (1 sp.) and *Munnozia* (2 spp.) into Costa Rica and in the case of *Liabum* into Mexico (1 sp.), and also into the West Indies (one introduction, 6 spp.).

There are two types of migrations northward from Andean South America. The oldest one resulted in the establishment of the *Sinclairia* clade (Clade C), a good example of dispersal (most likely) followed by radiation. A more detailed study of this clade is being planned. A single introduction, possibly into pre-isthmian Central America, followed by radiation in Mexico and Central America is the most likely explanation (Funk et al. 1996). The second pattern has multiple migrations from the Andes to Costa Rica (*Erato*, *Munnozia*, *Oligactis*) all of which are highly nested. There is no evidence that any of these resulted in speciation. Because none of these three genera are sister groups it appears that each of the three genera invaded Central America across the isthmus of Panama separately. The fourth genus, *Liabum*, migrated farther north and is the only genus of the Liabeae to make it to the West Indies having taxa on Jamaica, Cuba, and Hispaniola. *Liabum* also has one species from Costa Rica up into southern Mexico (*L. bourgeaui*). Since *L. bourgeaui* is not the sister group of the West Indian clade, it is most likely a separate introduction. *Liabum* is the most interesting of the recent migrants and a detailed study of its relationships is planned. Thus, the species of Liabeae that inhabit North America, Central America and the Caribbean are most likely the result of nine independent events of dispersal or vicariance.

The results of this analysis support the idea that all of the clades except one originated in the Central Andes, most likely northern Peru or possibly Ecuador. And the exception, the *Sinclairia* clade, had its origin in the Central Andes as well.

EVOLUTION

Until recently, no documented evidence of interspecific or intergeneric hybridization had been reported for Liabeae, and traditionally it was felt that this was unlikely because the genera were either chromosomally, geographically, and/or elevationally separated. However, there is now evidence of interspecific and intergeneric hybridization in northern Peru between *Paranephelius* taxa and between *Paranephelius* and *Pseudonoseris*.

Soejima et al. (2008) utilized *trnL-F* and ITS markers in an analysis of the subtribe Paranepheliinae. This study found strong support for the monophyly of the subtribe Paranepheliinae, and placed *Pseudonoseris discolor* (Muschl.) H. Rob. & Brettell as the sister taxon to the remainder of *Pseudonoseris* and all *Paranephelius* species. *Pseudonoseris szyszylowiczii* exhibited intraspecific divergence suggesting intergeneric hybridization between it and *Paranephelius*. *Pseudonoseris szyszylowiczii* and *P. striata* (Cuatrec.) H. Rob. & Brettell, with similar comparative morphology, are hypothesized to be putative hybrid products between *P. discolor* (Fig. 27.6A) and an unknown element in *Paranephelius*. Further studies are necessary to confirm the origin and timing of this intergeneric hybridization event.

In addition to this instance of intergeneric hybridization, it appears that there has been considerable gene flow in the *Paranephelius* clade as well (Soejima et al., pers. comm.). Hybridization appears to have occurred at several sites in northern Peru and has been responsible for taxonomic confusion and misapplication of names. Currently, two highly variable and polymorphic taxa are recovered with molecular markers within *Paranephelius* roughly corresponding to *P. ovatus* and *P. uniflorus* (Poepp. & Endl.) Sch.Bip. (Fig. 27.5). The taxonomic status of other described entities in *Paranephelius* is under investigation.

The lack of apparent hybridization in most taxa may be a clue to the small size of the tribe. While in many environments, two or more genera exist in full sympatry, for example, *Erato*, *Munnozia* and *Liabum* are recorded from many sites within the Andes. Genera within the tribe that do have broader distributions (i.e., *Munnozia*, *Liabum*, *Sinclairia*) are the only taxa that appear to have polyploids.

CONCLUSIONS

The development of robust phylogenies with high confidence levels has improved our vision of intertribal relationships in Liabeae. While there may continue to be some disagreement among the various proposed phylogenies, there are a number of groups common to all of them.

The position of *Cacosmia* and its three species as separate from the other main clades was not predicted by cladistic analysis utilizing a morphological dataset (Funk et al. 1996). Examination of the sister group relationships within the clades reveals four major clades: Clade B—*Ferreyranthus-Dillandia-Oligactis-Sampera-Liabum* containing about 64 species; Clade C—*Sinclairia-Sinclairiopsis-Megaliabum-Liabellum* containing about 26 species; Clade D—*Microliabum-Pseudonoseris-Paranephelius-Chionopappus-Philoglossa-Erato* containing about 27 species, and Clade E—*Munnozia-Chrysactinium* containing about 54 species.

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Appendix 27.1. Description of subtribe Sinclairiinae

Sinclairiinae H. Rob., **subtr. nov.**
Plantae perennes herbaceae vel scandentes ad arborescentes laticiferae; radices tuberosae, caules et folia plerumque abaxialiter albo-tomentosa. Folia opposita vel ternata petiolata, laminis trinervatis vel lobatis. Capitula interdum eradiata, bracteis involucri imbricatis multiseriatis apice appressis vel patentibus; thecae antherarum base vix crenulatae ecaudatae; basi stylorum non noduliferi; raphidis acheniarum elongatis. Grana pollinis 33–50 µm in diametro, irregulariter spinulosa, columellis subspinosis ca. 4.

Plants are almost exclusively Mexican and Central American. Perennials, with white latex, small herbs to scandent shrubs or trees to 10 meters tall. Roots with distinct tubers at least in early stages. Stems and undersurfaces of leaves usually with white tomentum. Leaves sometimes absent at anthesis, opposite or ternate, with petioles, petioles sometimes winged with wings perfoliate, leaf blades lanceolate to ovate or triangular, venation triplinerved or spreading into narrow lobes, undersurface usually with sparse or dense white tomentum. Inflorescences terminal at stems of branches, more rarely partially axillary, corymbiform or pyramidal, with short or long peduncles. Heads with few to many flowers; involucral bracts imbricate in many series, with appressed or spreading tips; receptacles epaleaceous, glabrous; ray florets present or absent, female; disk florets bisexual, lobes elongate; anther thecae pale, spurred, scarcely crenulate at base, without tails; endothecial cells with strap-shaped sclerified shields ending in one or two nodes on transverse walls; apical appendages smooth; nectary sometimes elongate; style base without an enlarged node or only slightly enlarged; style branches shorter than the hispid part of the upper style shaft, stigmatic surface continuous. Achenes prismatic with 8–10 ribs; raphids of achene walls elongate; pappus of 30–50 capillary bristles, not or slightly enlarged distally, with outer series of 15–40 short scales. Pollen grains 33–50 µm in diam. in fluid irregularly spinulose, with cluster of separate columellae under each spine (gazebiform).

Type genus: *Sinclairia* Hook. & Arn.

The subtribe Sinclairiinae has two tendencies not seen elsewhere in Liabeae, i.e., ternate leaves and eradiate heads. However, neither of these character states is widespread in the subtribe. A few consistent characteristics of the subtribe are the tuberous roots and the lack of an enlarged node on the base of the style.

Chapter 28

Vernonieae

Sterling C. Keeley and Harold Robinson

HISTORICAL OVERVIEW

Circumscription of tribe Vernonieae remains relatively unchanged since its initial delimitation (Cassini 1816, 1819, 1828). Subsequent treatments (Lessing 1829, 1831; De Candolle 1836; Bentham 1873) have resulted in minor modifications, most notably for the placement of tribes Plucheeae and Liabeae. Liabeae are, in fact, sister to Vernonieae (Keeley and Jansen 1991, 1994; Kim and Jansen 1995) and Plucheeae are only distantly related to both tribes (Keeley and Jansen 1991; Funk et al. 2005). The relationship between Liabeae and Vernonieae is unique within the family as it pairs a tribe of Old World origin with a tribe of New World origin, Vernonieae and Liabeae, respectively (Funk et al. 2005; Keeley et al. 2007). Molecular studies (Keeley and Jansen 1991, 1994; Kim and Jansen 1995; Kim et al. 1998; Keeley et al. 2007) have confirmed the monophyly of Vernonieae. Vernonieae, Liabeae, Cichorieae and Arctoteae together with several smaller tribes form the monophyletic subfamily Cichorioideae (Funk et al. 2005).

Subtribal structure and the *Vernonia* problem

While tribal circumscription has always been straightforward, the same cannot be said for that of the subtribes. This has been largely due to the size and distribution of the core genus, *Vernonia*. For most of the history of the tribe, approximately 1000 of the 1500 species were placed in *Vernonia* (Jones 1977). The genus also encompassed much of the variation within the tribe as a whole and was defined largely by the absence of characters, rather than by any suite of uniting characters (Robinson 1999a). As a result of this "*Vernonia* problem" (Bremer 1994), only genera with autapomorphic or unusual character combinations were given separate recognition (i.e., *Stokesia*, the only member of the tribe with ligulate flowers), and their relationships to each other and to *Vernonia* were uncertain. The nearly all-encompassing variation within *Vernonia* was reflected in Bentham's (1873) treatment where he recognized two large subtribes for Vernonieae, Euvernonieae for those taxa with separate heads, and Lychnophoreae for those with aggregated heads and secondary glomerules.

Work by Jones (1977, 1979a, 1981a), Robinson and collaborators (Robinson et al. 1980; Robinson and Kahn 1986; Robinson and Funk 1987), and Jeffrey (1988) spurred subtribal reorganization. In synoptic treatments of *Vernonia*, Jones (1979a, 1981a) recognized two subgenera: subgenus *Vernonia* in the New World (Jones 1979a) and subgenus *Orbisvestus* in the Old World (Jones 1981a), based on combinations of morphological, cytological, palynological, and chemical characters. Each subgenus was comprised of sections, subsections and series. Jeffrey (1988) recognized similar (but not identical) groups to those of Jones (1981a) within African *Vernonia*. He felt that most of these should be recognized as genera, although he did not remove them due to concern for nomenclatural confusion when no good framework existed into which they could be placed at that time. In addition to suggesting likely generic segregates from within African *Vernonia*, Jeffrey (1988) also made a significant contribution to the concept of subtribal realignment. He proposed that there was likely a greater relationship among taxa within the Old World and among taxa in the New World hemispheres, respectively, than between members of the genus *Vernonia* worldwide. Subtribal rearrangements would be the logical outcome of recognizing distinct lineages in the two hemispheres. Morphological studies by Robinson and coworkers (Robinson 1999a–c, 2007) and molecular phylogenetic studies (Keeley and Jansen 1994; Kim et al. 1998; Keeley et al. 2007) have led to the recognition of 21 subtribes, 15 in the New World and 6 in the Old World.

Among the most significant taxonomic changes resulting from these studies was the reduction in the size and distribution of the core genus, *Vernonia*. The genus now includes twenty-two species from eastern North America (including the type species, *Vernonia noveboracensis* (L.) Willd.), five from central Mexico, and two from South America (Robinson 1999a, c). As a consequence there are many newly described and resurrected genera. Table 28.1 lists the 126 currently recognized genera along with their subtribal placements, chromosome numbers, and secondary chemistry. Recent molecular work (Keeley et al. 2007) provides evidence to support changes in generic status for additional taxa (Robinson et al. 2008). Since Old World generic concepts are not as well resolved as those in the New World, many species remain in *Vernonia*, even though this is clearly not where they ultimately belong.

One remaining feature after the extensive revision of *Vernonia* is the large number of monotypic and small genera that remain in the tribe (Table 28.1). There are over 50 monotypic genera and an additional 35 genera with fewer than three species. Many of these such as *Stokesia* and *Rolandra* have now been accorded their own subtribes (i.e., Stokesiinae, Rolandrinae) on the basis of their distinctive morphological features (Robinson 1999a–c, 2007). While a large number of monotypic genera is not without parallel in some of the other tribes (i.e., Senecioneae), it does pose problems for understanding relationships within the tribe. It is hoped that more material will become available in the future, particularly for molecular studies, to resolve relationships among these genera.

Regional Vernonieae taxonomy

Most taxonomic treatments of Vernonieae, like those of other large Compositae tribes, are generally for particular floristic and geographic regions. The following is a list of representative recent taxonomic publications for major regions of the New and Old World. Other references may be sought in the sections devoted to morphology, chemistry, palynology, ethnobotany and ecology in this chapter and in Robinson (1999a, c). — Geographic areas:

- Continental United States, Mexico and Central America (Clonts and McDaniel 1978; Jones 1979c, 1981b, 1982a; Carvajal 1981; Jones and Stutts 1981; Kirkman 1981; Turner 1981; Keeley 1982, 1987; McVaugh 1984; Robinson and Funk 1987; Rzedowski and Calderon 1995; Barkley et al. 2006);
- West Indies (Keeley and Jones 1977a; Keeley 1978; Stutts 1981; Stutts and Muir 1981; Urbatsch 1989; Borhidi 1992);
- Argentina, Brazil and Paraguay (Cabrera 1978; Leitão-Filho and Semir 1979; Cabrera and Klein 1980; Coile and Jones 1981, 1983; Smith 1981, 1982, 1985; Jones 1981b; 1982b; Soares Nunes 1982; Macleish 1984a, b, 1985a, b, 1987; Macleish and Schumacher 1984; Stutts 1988; Semir 1991; Esteves 1993; Hind 1993, 1994; Ariza-Espinar 1994; Matzenbacher and Mafioleti 1994; Dematteis 2003, 2006a–c; Semir and Jesus 2004; Freire et al. 2005; Smith and Coile 2007);
- Northern South America (Jones 1980; Stutts and Muir 1981; Dillon 1982; Badillo 1989; Pruski 1992, 1996; Robinson 1992; Beltran and Granda 2003);
- Africa (Wild and Pope 1977, 1978; Wild 1978; Kalanda 1981, 1982, 1986; Kalanda and Lisowski 1981; Isawumi 1984, 1989, 1993, 1995; Gilbert 1986; Lisowski 1987, 1992; Gilbert and Jeffrey 1988; Jeffrey 1988; Pope 1992; Ayodele and Olorode 2005);
- Madagascar (Humbert 1960);
- Southeast Asia (Koster 1935; Kirkman 1981; Koyama 1984; Kress et al. 2003).

PHYLOGENY

Hypotheses of subtribal relationships have rarely been suggested for Vernonieae. One of the few attempts to understand broad-scale patterns was made by Gleason (1923a) when he proposed a scheme of evolutionary relationships among the leafy-bracted and bractless sections of North American, Central American, and West Indian *Vernonia*. He suggested that putative ancestors were in South America (Gleason 1906, 1922, 1923a, b) and also noted two subtribal lines for Old and New World *Vernonia*. Additional evolutionary relationships were not suggested until Jones (1979a, 1981a) provided sectional, subsectional, and series divisions within *Vernonia* in the New and Old Worlds. Jeffrey (1988) amended the latter treatment slightly, suggesting close relationships among genera within each hemisphere, but gave few specifics.

The first study to include both New and Old World *Vernonia* was that of Keeley and Turner (1990). They conducted a morphologically-based cladistic analysis of all of the recognized sections and subsections of *Vernonia* s.l. (Jones 1979a; 1981a; Jeffrey 1988). Keeley and Turner (1990) identified the Madagascan/southern African taxa, in what is now *Distephanus* Cass. of subtribe Distephaninae, as sister to the remainder of the tribe. In addition, the cladogram revealed that Old World species diverged before New World species, and that there were two largely geographically separate lineages. Prior to Keeley and Turner (1990), it was thought that the putative

Table 28.1. Genera of Vernonieae with number of species, subtribes, distribution, chromosome number and secondary chemical compounds.

Genus	No. of species	Subtribe	Geographical distribution	Chromosome number[a]	Secondary chemical compounds
Acanthodesmos C.D. Adams & M.C. du Quesnay	1	Unplaced	Jamaica		
Acilepidopsis H. Rob.	1	Mesanthophorinae	Eastern South America	2*n* = 72	Liganes, triterpenes (Bohlmann et al. 1981)
Acilepis D. Don.	~10	Centrapalinae	India, southeastern Asia		
Adenoon Dalzell	1	Linziinae	India	2*n* = 20	
Aedesia O. Hoffm.	3	Linziinae	Tropical Africa	2*n* = 20	
Ageratinastrum Mattf.	5	Erlangeinae	Tropical Africa		
Albertinia Spreng.	1	Vernoniinae	Eastern Brazil		
Ambassa Steetz	~3	Erlangeinae	Eastern Africa		
Anteremanthus H. Rob.	1	Lychnophorinae	Brazil		
Aynia H. Rob.	1	Lepidaploinae	Peru		
Baccharoides Moench	~30	Linziinae	Tropical Africa, southern Asia	*n* = 10	Elemanolides (Bohlmann and Jakupovic 1990)
Bechium DC.	~2	Centrapalinae	Madagascar		
Bishopalea H. Rob.	1	Sipolisiinae	Northern Brazil		
Blanchetia DC.	1	Piptocarphinae	Northeastern Brazil		
Bolanosa A. Gray	1	Leiboldiinae	Southern Mexico		
Bothriocline Oliver ex Benth.	30	Erlangeinae	Africa	*n* = 9, 10, 18–20	5-alkylcoumarins (Bohlmann and Jakupovic 1990); guaianolides, r-alkylcoumarins (Jakupovic et al. 1987); 5-methylcoumarin, glaucolides (Ahmed et al. 1991); cadinolides (Bazon et al. 1997)
Brachythrix Wild & G.V. Pope	6	Erlangeinae	Africa		
Brenadendron H. Rob.	3	Gymnantheminae	Tropical western and central Africa		
Caatinganthus H. Rob.	2	Elephantopinae	Northern Brazil		
Cabobanthus H. Rob.	2	Centrapalinae	Tropical east Africa		
Camchaya Gagnep.	6	Linziinae	Thailand, Laos, southern China	2*n* = 20	
Centauropsis Boj. ex DC.	8	Centrapalinae	Madagascar		
Centrapalus Cass.	2	Centrapalinae	Africa		Glaucolides (Perdue et al. 1993; Zdero et al. 1990); elemanolides (Robinson 2006, 2007)
Centratherum Cass.	3	Centratherinae	Tropical America, Philippines, Australia	Old World: *n* = 9, 10; 2*n* = 18; New World: *n* = 16; *n* = 32 (6)	Guaianolides (Bohlmann et al. 1980); goyazenolides (Valdés et al. 1998a, b); terpenoids, furoheliangolides (Robinson 2007)
Chresta Vell. ex DC.	11	Chrestinae	Bolivia, Brazil		Glaucolides and furoheliangolides, guaianolides (Bohlmann and Jakupovic 1990)

Table 28.1. Continued.

Genus	No. of species	Subtribe	Geographical distribution	Chromosome number	Secondary chemical compounds
Chronopappus DC.	1	Lychnophorinae	Brazil		
Chrysolaena H. Rob.	9	Lepidaploinae	Brazil to Argentina, Peru	*n* = 10, 20, 30–32; 2*n* = 40, 60, 80	Guaianolides (Bohlmann and Jakupovic 1990); glucolides (Bardon et al. 1993); hirsutianolides, lignans (Borella et al. 1998)
Cololobus H. Rob.	3	Vernoniinae	Eastern Brazil		
Critoniopsis Sch.Bip.	~45	Piptocarphinae	Mexico, Central and South America	*n* = 10 (?); *n* = 17 (?) 2 species	Glaucolides (Bohlmann and Jakupovic 1990)
Cuatrecasanthus H. Rob.	3	Piptocarphinae	Ecuador, Peru		Glaucolides (Bohlmann and Jakupovic 1990)
Cyanthillium Blume	7	Erlangeinae	Old World tropics	*n* = 9, 18; 2*n* = 18	5-alkycoumarins, 5-methylcoumarins (Bohlmann and Jakupovic 1990); vernolides (Chea et al. 2006)
Cyrtocymura H. Rob.	6	Vernoniinae	Mexico, Central America, West Indies, eastern South America	*n* = 15, 17; 2*n* = 33	Glaucolides, piptocarphols, costunolide, eudemolides (Borkosky et al. 1996); glaucolides (Bohlmann and Jakupovic 1990)
Dasyandantha H. Rob.	1	Piptocarphinae	Venezuela		
Dasyanthina H. Rob.	2	Vernoniinae	Eastern Brazil		
Decaneuropsis H. Rob. & J. Skvarla	1	Unplaced	Madagascar		
Decastylocarpus Humbert	1	Erlangeinae	Madagascar		
Dewildemania O. Hoffm.	7	Centrapalinae	Tropical Africa		
Diapractanthus Humbert	1	Erlangeinae	Madagascar		
Dipterocypsela S.F. Blake	1	Dipterocypselinae	Colombia		
Distephanus Cass.	~50	Distephaninae	Africa, India, south and southeast Asia		Elemanolides (Bohlmann and Jakupovic 1990)
Echinocoryne H. Rob.	6	Lepidaploinae	Brazil		
Eirmocephala H. Rob.	3	Vernoniinae	Central America to central Andes	*n* = 16, 17	Glaucolides, piptocarphols (Borkosky et al. 1996); glaucolides (Bohlmann and Jakupovic 1990)
Ekmania Gleason	1	Piptocarphinae	Cuba		
Elephantopus L.	~28	Elephantopinae	Eastern North America, and pan tropical	*n* = 11	Dilactones (Bohlmann and Jakupovic 1990)
Eremanthus Less.	27	Lychnophorinae	Eastern Brazil, Bolivia	*n* = 15; 2*n* = 36	Goyazensikudem ermantholide (Sakamoto et al. 2005); furoheliangolides (Bohlmann and Jakupovic 1990)
Eremosis Gleason	~25	Unplaced	Mexico	*n* = 10, 17, 19	Glaucolides (Bohlmann and Jakupovic 1990)
Erlangea Sch.Bip.	~10	Erlangeinae	Tropical Africa	*n* = 10; 2*n* = 20	

Table 28.1. Continued.

Genus	No. of species	Subtribe	Geographical distribution	Chromosome number	Secondary chemical compounds
Ethulia L.	19	Erlangeinae	Africa, southern and southeastern Asia	$n = 16, 20$	5-methylcoumarins (Mahmoud et al. 1998); 5-alkylcoumarins (Bohlmann and Jakupovic 1990)
Gorceixia Baker	1	Unplaced	Brazil		
Gutenbergia Sch.Bip.	~20	Erlangeinae	Africa	$n = 10, 20$, ca. 30 (1)	Guaianolides, alkylcoumarins (King 1986; Jakupovic et al. 1987); eudesmanolides, gutenbergin germacranolide, idomain (Fujimoto et al. 1987)
Gymnanthemum Cass.	~24	Gymnantheminae	Africa, southern and southeastern Asia	$n = 10, 20$; $2n = 30, 40$	Elemanolides (Bohlmann and Jakupovic 1990)
Harleya S.F. Blake	1	Lepidaploinae	Central America		
Herderia Cass.	1	Erlangeinae	Tropical West Africa		
Hesperomannia A. Gray	3	Hesperomanniinae	Hawaii	$n = 10$	
Heterocoma DC.	1	Sipolisiinae	Southeastern Brazil		Guaianolides (Bohlmann and Jakupovic 1990)
Heterocypsela H. Rob.	1	Dipterocypselinae	Eastern Brazil		
Hilliardiella H. Rob.	~8	Centrapalinae	Southern and eastern Africa	$n = 10$; $2n = 20$	Glaucolides (Bohlmann and Jakupovic 1990)
Hololepis DC.	2	Sipolisiinae	Southeastern Brazil		
Huberopappus Pruski	1	Piptocarphinae	Venezuela		
Hystrichophora Mattf.	1	Erlangeinae	Tanzania		
Iodocephalus Thorel ex Gagnep.	1	Centrapalinae	Laos, Thailand, Viet Nam		
Irwinia G.M. Barroso	1	Piptocarphinae	Northeastern Brazil		Glaucolides (Bohlmann and Jakupovic 1990)
Joseanthus H. Rob.	5	Piptocarphinae	Colombia, Ecuador		
Kinghamia C. Jeffrey	5	Erlangeinae	Tropical Africa		
Koyamasia H. Rob.	1	Centrapalinae	Thailand		
Lachnorhiza A. Rich.	1	Linziinae	Cuba		
Lampropappus (O. Hoffm.) H. Rob.	3	Gymnantheminae	Angola, Congo, Malawi, Zambia		
Leiboldia Schltdl. ex Gleason	2	Leiboldiinae	Southern Mexico	$n = 19$	
Lepidaploa (Cass.) Cass.	~140	Lepidaploinae	Mexico, Central and South America, West Indies	$n = 10,16, 17$, 34 (2), 51	Glaucolides, goyazensolides piptocarphins, cadinolides (Valdés et al. 1998a; Borkosky et al. 2003); tricin (Jacobs et al. 1986); glaucolides (Bohlmann and Jakupovic 1990)
Lepidonia S.F. Blake	7	Leiboldiinae	Southern Mexico	$n = 19$	Glaucolides (Bohlmann and Jakupovic 1990)
Lessingianthus H. Rob.	~102	Lepidaploinae	Brazil, Argentina, Colombia, Venezuela	$n = 16, 17$, 34, ca. 52, 67, 68; $2n = 32$	Hirsutanolides (Bohlmann et al. 1980); glaucolides (Bohlmann and Jukupovic 1990)

Table 28.1. Continued.

Genus	No. of species	Subtribe	Geographical distribution	Chromosome number	Secondary chemical compounds
Linzia Sch.Bip. ex Walp.	~7	Linziinae	Africa	*n* = 10	Elemanolides (Bohlmann and Jakupovic 1990)
Lychnophora Mart.	30	Lychnophorinae	Eastern Brazil	*n* = 17, 18, 19; 2*n* = 34, 36, 38, 39	Eudesmanolides, goyazenolides, furoheliangolides (Borella et al. 1992); eremantholides, guaianolides (Cunha et al. 1995); furoheliangolides (Bohlmann et al. 1980)
Lychnophoriopsis Sch.Bip.	4	Lychnophorinae	Southeastern Brazil		
Manyonia H. Rob.	1	Dipterocypselinae	Tanzania		
Mattfeldanthus H. Rob. & R.M. King	2	Lepidaploinae	Eastern Brazil		Glaucolides (Bohlmann and Jakupovic 1990)
Mesanthophora H. Rob.	2	Mesanthophorinae	Bolivia, Paraguay		
Minasia H. Rob.	5	Lychnophorinae	Eastern Brazil	*n* = 17	
Monosis DC.	7	Unplaced			
Msuata O. Hoffm.	1	Centrapalinae	Central tropical Africa		
Muschleria S. Moore	1	Erlangeinae	Southern tropical Africa	*n* = 9	
Myanmaria H. Rob.	1	Gymnantheminae	Myanmar		
Neurolakis Mattf.	1	Linziinae	Cameroon, Chad		
Oiospermum Less.	1	Centratherinae	Northeastern Brazil		
Oliganthes Cass.	9	Centrapalinae	Madagascar		
Omphalopappus O. Hoffm.	~3	Erlangeinae	Angola		
Oocephala (S.B. Jones) H. Rob	2	Erlangeinae	Tropical Africa		
Orbivestus H. Rob.	~4	Erlangeinae	Tropical and southern Africa	*n* = 10, 20	Sesquiterpene lactones (Abegaz et al. 1994); 5-methylcoumarins (H. Rob., pers comm.)
Orthopappus Gleason	1	Elephantopinae	Tropical America	*n* = 11	Dilactones (Bohlmann and Jakupovic 1990)
Pacourina Aubl.	1	Pacourininae	Central and South America		
Parapolydora H. Rob.	1	Erlangeinae	Africa		
Paurolepis S. Moore	3	Erlangeinae	Africa		
Phyllocephalum Blume	~9	Centrapalinae	India, Malaysia	*n* = 10	
Piptocarpha R. Br.	43	Piptocarphinae	Tropical America	*n* = 17; 2*n* = 34	Glaucolides (Bohlmann and Jakupovic 1990)
Piptocoma Cass.	18	Piptocarphinae	Greater Antilles, northern South America		Furoheliangolides (Bohlmann and Jakupovic 1990)
Piptolepis Sch.Bip	~6	Lychnophorinae	Southeastern Brazil		Furoheliangolides (Bohlmann and Jakupovic 1990)
Pithecoseris Mart. ex DC.	1	Chrestinae	Eastern Brazil		
Pleurocarpaea Benth.	1	Linziinae	Australia		
Polydora Fenzl	8	Erlangeinae	Tropical Africa	*n* = 9, 18	Glaucolides (Bohlmann and Jakupovic 1990)

Table 28.1. Continued.

Genus	No. of species	Subtribe	Geographical distribution	Chromosome number	Secondary chemical compounds
Prestelia Sch.Bip.	1	Lychnophorinae	Southeastern Brazil		
Proteopsis Mart. & Zucc. ex Sch.Bip.	1	Lychnophorinae	Southeastern Brazil		Furoheliangolides (Bohlmann and Jakupovic 1990)
Pseudelephantopus Rohr	2	Elephantopinae	Tropical America	$n = (11), 13$	Glaucolides and guaianolides (Bohlmann and Jakupovic 1990)
Pseudopiptocarpha H. Rob.	2	Lepidaploinae	Colombia		
Quechualia H. Rob.	4	Vernoniinae	Peru to Argentina		Glaucolides (Bohlmann and Jakupovic 1990)
Rastrophyllum Wild & G.V. Pope	2	Erlangeinae	Tropical Africa		
Rolandra Rottb.	1	Rolandrinae	Tropical America		Terpenoids, furoheliangolides, eudesmane derivatives (Robinson 2007); glaucolides (Bohlmann and Jakupovic 1990)
Sipolisia Glaz. ex Oliver	1	Sipolisiinae	Southeastern Brazil		
Soaresia Sch.Bip.	1	Chrestinae	Brazil		Elemanolides (Robinson 2007)
Spiracantha Kunth	1	Rolandrinae	Tropical America	$2n = 16$	
Stenocephalum Sch.Bip.	5	Lepidaploinae	Central and South America	$n = 12, 17$	Gluacolides-A, B, C, D, E, F, G, H (Jones et al. 1979c)
Stilpnopappus Mart. ex DC.	20	Lepidaploinae	Brazil, Venezuela		Glaucolides (Bohlmann and Jakupovic 1990)
Stokesia L'Her.	1	Stokesiinae	Southeastern USA	$n = 7$; $2n = 14$	(Glaucolide-A,B reported in error, Robinson 2007)
Stramentopappus H. Rob. & V. Funk	1	Leiboldiinae	Southern Mexico	$n = 19$	Glaucolides-A, B, F, and marginatin (Jones 1979c)
Strobocalyx (Blume ex DC.) Spach.	~10	Unplaced	South and southeast Asia	$n =$ ca. 30	
Struchium (L.) Kuntze	2	Lepidaploinae	Pan tropical	$n = 16$; $2n = 32$	Glaucolides (Bohlmann and Jakupovic 1990)
Tarlmounia H. Rob., S. Keeley, J.J. Skvarla & R. Chan	1	Unplaced	Thailand and southeast Asia		
Telmatophila Mart. ex Baker	1	Mesanthophorinae	Northeastern Brazil		
Tephrothamnus Sch.Bip.	1	Unplaced	Venezuela		
Trepadonia H. Rob.	2	Vernoniinae	Peru		
Trichospira Kunth	1	Trichospirinae	Tropical America		
Vernonanthura H. Rob.	~70	Vernoniinae	Tropical America	$n =$ (ca. 8), 16, 17, ca. 34; $2n =$ ca. 51	Glaucolide-A, 5 other glaucolides, hirsutinolides, 1-deoxyhirsutinolides, vernomargolides, eudesmanolides (Borkosky et al. 1997); *Elephantopus* type sesquiterpene lactones (Pollora et al. 2003, 2004); glaucolides (Bohlmann and Jakupovic 1990)
Vernonia Schreb.	22	Vernoniinae	Eastern North America, Mexico, Bahamas, South America	$n = 17, 18$	Glaucolides (Bohlmann and Jakupovic 1990)

Table 28.1. Continued.

Genus	No. of species	Subtribe	Geographical distribution	Chromosome number	Secondary chemical compounds
Vernoniastrum H. Rob.	8	Erlangeinae	Tropical Africa	*n* = 10	
Xerxes J.R. Grant	2	Sipolisiinae	Southeastern Brazil		Eudesmanolides (H. Rob., pers. comm.)
Xiphochaeta Poepp.	1	Lepidaploinae	Amazon & Orinoco Basins		

[a]Chromosome numbers from *Index to Chromosome Numbers in the Compositae* (http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html) and *Index to Plant Chromosome Numbers* (w^{3}Tropicos, http://mobot.mobot.org/W3T/).

ancestral taxa were New World in origin since the family itself originated in South America (Raven and Axelrod 1974; Jansen and Palmer 1987), and Vernonieae were considered among its primitive tribes (Jones 1977). Thus it was surprising to discover that basal Vernonieae were Old World rather than New World. Equally surprising was the fact that the basal genus (*Distephanus*) was morphologically unlike nearly all other members of the tribe. *Distephanus* species are yellow-flowered with trinervate leaf venation (Fig. 28.1C), whereas most Vernonieae are characterized by white, pink, blue or purple florets and pinnate leaf venation (Jones 1977; Fig. 28.1B, D, F, L, H). The basal position of *Distephanus* (as *Vernonia populifolia*) and early divergence of Old World taxa was also supported by the cpDNA restriction site study of Keeley and Jansen (1994) and sequence data (Keeley et al. 2007). In hindsight, the yellow flower color and leaf venation provide a morphological link to members of Liabeae, which we now know is sister to Vernonieae (Jansen et al. 1991; Keeley and Jansen 1991, 1994; Bremer 1994; Kim and Jansen 1995).

Keeley et al. (2007) generated the first phylogeny for the tribe using nucleotide sequence data from cpDNA (*trnL-F*, *ndhF*) and nuclear (ITS) for a variety of genera as well as species of *Vernonia* (Fig. 28.2). Initial analyses using the tribe Liabeae as the outgroup confirmed the basal position of *Distephanus* within Vernonieae, as previously found by Keeley and Turner (1990) and Keeley and Jansen (1994). Hence, the origin of Vernonieae was established as Old World. *Distephanus* was then used as the outgroup for computational reasons in further analyses as the topology did not change when it was substituted for Liabeae (Keeley et al. 2007).

In this phylogeny two strongly supported sister clades were identified, one entirely Old World and the other with both New and Old World subclades. This is similar to the finding of Keeley and Turner (1990) and Keeley and Jansen (1994). The African genera *Baccharoides*, *Gymnanthemum*, and *Linzia*, and the Hawaiian genus *Hesperomannia* (Fig. 28.2) form the first subclade. The Australian genus *Pleurocarpaea* has since been found to group with these taxa as well (unpub. data). The other subclade of African genera, *Brachythrix*, *Bothriocline*, *Cabobanthus*, *Ethulia*, *Hilliardiella*, *Muschleria*, *Orbivestus*, *Parapolydora*, *Vernoniastrum* and the Madagascan *Centauropsis*, is sister to New World taxa. In the New World there are two sister subclades that each include species from South, Central and North America (Fig. 28.2). Among the two sister clades, members of the Brazilian subclade that includes the syncephalous *Eremanthus*, *Sipolisia*, *Gorceixia* as well as the non-syncephalous *Albertinia* and *Centratherum*, form a sister group to the subclade in which *Vernonia* s.str. occurs (Robinson 1999a). The relationship of Brazilian and Central American species in the genus *Vernonanthura* suggests further data are needed, however, as there is not a clear progression from Brazil to Central America to North America, although that is the broad outline of proposed relationships. The other New World subclade, including *Critoniopsis* and *Lepidaploa* similarly suggests patterns of radiation from South to Central and North America, but likely along a different pathway of dispersal, as *Critoniopsis* species sensu Cuatrecasas (1956) are strictly Andean.

One of the most interesting and challenging portions of the phylogeny (Fig. 28.2) is the clade that includes both Old and New World taxa, i.e., *Strobocalyx* and *Vernonia* from Malaysia with *Eremosis*, *Lepidonia*, *Leiboldia* and *Stramentopappus* (Leiboldiinae) from Meso-America and *Stokesia* from North America. This clade appears to be ancestral to purely New World taxa and is derived from Old World species. The position of the Leiboldiinae taxa between New and Old World clades was also found in studies by Keeley and Jansen (1994) and Kim et al. (1998). Another instance of a bihemispheric clade occurred with the genus *Elephantopus*. In this case species from Singapore and Hawaii are found with North American taxa in an otherwise purely New World subclade (Fig. 28.2).

While much remains to be discovered about the relationships among Vernonieae worldwide the general pattern is of New World taxa derived from Old World species and of two lineages that have radiated independently within their respective hemispheres. However, there are some New World taxa that are more closely related to Old World taxa than they are to others in their own hemisphere and vice versa. To test the current hypotheses of relationships will require the addition of taxa from south and southeast Asia, as well as from South America and Mexico. It is hoped that such data will be forthcoming in the near future.

TAXONOMY

Tribe Vernonieae Cassini in J. Phys. Chim. Hist. Nat. Arts 82: 132. 1816 – Type: *Vernonia noveboracensis* (L.) Willd. in Sp. Pl., ed. 4, 3: 1632. 1803 = *Serratula noveboracensis* L., Sp. Pl.: 818. 1753.

Annual or perennial herbs, shrubs, vines or trees; stems and foliage variously pubescent. Leaves alternate, rarely opposite or whorled; blades sessile or petiolate, entire or rarely lobed. Inflorescences cymes, corymbiform or paniculate, sometimes greatly reduced. Heads homogamous, 1–400-flowered, sessile or pedunculate, free or more rarely syncephalous, with or without subtending bracts. Florets perfect; corollas typically actinomorphic, funnelform, limbs longer than wide (rarely zygomorphic with unequal limbs), typically erect; deep purplish-red to lavender, pink, blue or white, rarely yellow. Involucres campanulate to cylindrical; involucral bracts typically imbricate in 3–9 series, scarious or leafy, persistent or deciduous. Receptacle flat or subconvex, smooth or pitted, sometimes with pales, spines or partitions. Anthers calcarate with a sagittate base, auricles obtuse or acute, often tailed, the apical appendage flat, with or without glands.

Fig. 28.1. Selected Vernonieae. **A** *Piptocarpha oblonga* Baker, Brazil; **B** *Vernonia noveboracensis* (L.) Michx., USA; **C** *Distephanus divaricatus* (Steetz) H. Rob. & B. Kahn, Africa; **D** *Stokesia laevis* (Hill) Greene, USA; **E** *Hesperomannia arborescens* A. Gray, Hawaiian Islands; **F** *Lychnophora* sp. (syncephalous), Brazil; **G** *Vernonia kotschyana* Sch.Bip. ex Walp., Africa; **H** *Lepidaploa tortuosa* (L.) H. Rob., Costa Rica. [Photographs: A, G.L. Smith; B, H, S.C. Keeley; C, G, S.B. Jones, Jr.; D, P. Redfearn; E, G.L. Carr; F, V.A. Funk.]

Style branches spreading, semi-cylindrical, slender, tips acute or obtuse sometimes recurved, outer surface with acute or blunt trichomes, inner surface with stigmatic papillae. Style base with or without a sclerified or expanded node, glabrous. Achenes terete, angled or occasionally flattened, rarely dimorphic, typically with 3–20 ribs, outer surface glabrous or pubescent and often resiniferous, walls, typically golden-brown, rarely black, may contain raphids. Pappus persistent or deciduous, usually of capillary bristles, rarely coroniform, squamellose or with flattened or twisted segments; typically arranged in two series with a short outer pappus of bristles or squamellae and a long inner series, less commonly pappus of one to several series or lacking. Pollen highly ornamented, lophate, sublophate, echinate or psilate.

Subtribes

Centrapalinae H. Rob. (1999c) – Type: *Centrapalus galamensis* Cass. = *C. pauciflorus* (Willd.) H. Rob.

Herbs to subshrubs; hairs simple or T-shaped; leaves alternate, venation pinnate. Heads separate; involucral bracts persistent; receptacle with or without pales. Florets 10–50 in a head; corollas lavender to bluish or whitish; anthers without glands; sweeping hairs acicular. Achenes with raphids short or elongate, without phytomelanin; pappus usually of capillary bristles. Pollen tricolporate and sublophate with perforated tectum continuous between colpi or triporate with irregularly arranged polar lacunae and perforated tectum restricted or lacking. *n* = 9, 10. Mostly glaucolides. Some with abundant fatty acids or epoxy oils. Mostly Africa. Twelve genera, three monotypic.

Centratherinae H. Rob., F. Bohlmann & R.M. King (1980) – Type: *Centratherum punctatum* Cass.

Herbs; hairs simple or T-shaped; leaves alternate, venation pinnate. Heads usually solitary, terminal, subtended with foliose bracts; involucral bracts persistent; receptacle without pales. Florets 25–50; corollas lavender, with numerous stipitate glands on tube; anthers without glands. Achene with subquadrate raphids, without phytomelanin; with or without easily deciduous capillary pappus bristles. Pollen tricolporate, echinate, sublophate, perforated tectum continuous between colpi. *n* = 16. Glaucolides, goyazenolides, furoheliangolides. Tropical America, introduced in Australia and Philippines. Two genera, one monotypic.

Chrestinae H. Rob. (1999a) – Type: *Chresta sphaerocephala* DC.

Herbs or subshrubs, rosuliform to caulescent; hairs simple or T-shaped; leaves alternate, venation pinnate to nearly longitudinal. Inflorescences sometimes spicate, heads sessile in dense clusters; involucral bracts persistent; receptacles without pales; florets few in a head; corollas lavender; anthers without glands. Achenes without phytomelanin; pappus of capillary or slightly broadened bristles, usually persistent. Pollen tricolporate, echinate; sublophate or weakly lophate, perforated tectum continuous between colpi. *n* = ? Glaucolides, goyazenolides, furoheliangolides. Mostly Brazil. Three genera, two monotypic.

Dipterocypselinae S.C. Keeley & H. Rob., **subtr. nov.** – Type (designated here): *Dipterocypsela succulenta* S.F. Blake

Plantae herbaceae, pilis simpliibus vel T-formibus. Inflorescentiae valde seriate vel scorpioide cymosae; capitula discreta; receptacula epaleata. Flores 20–70 in capitulo peripherales interdum differentiatae; corollis lavandulis, antheris interdum glanduliferis. Achaenia saepe alata non phytomelaninifera, raphidis quadratis dense dispositis.

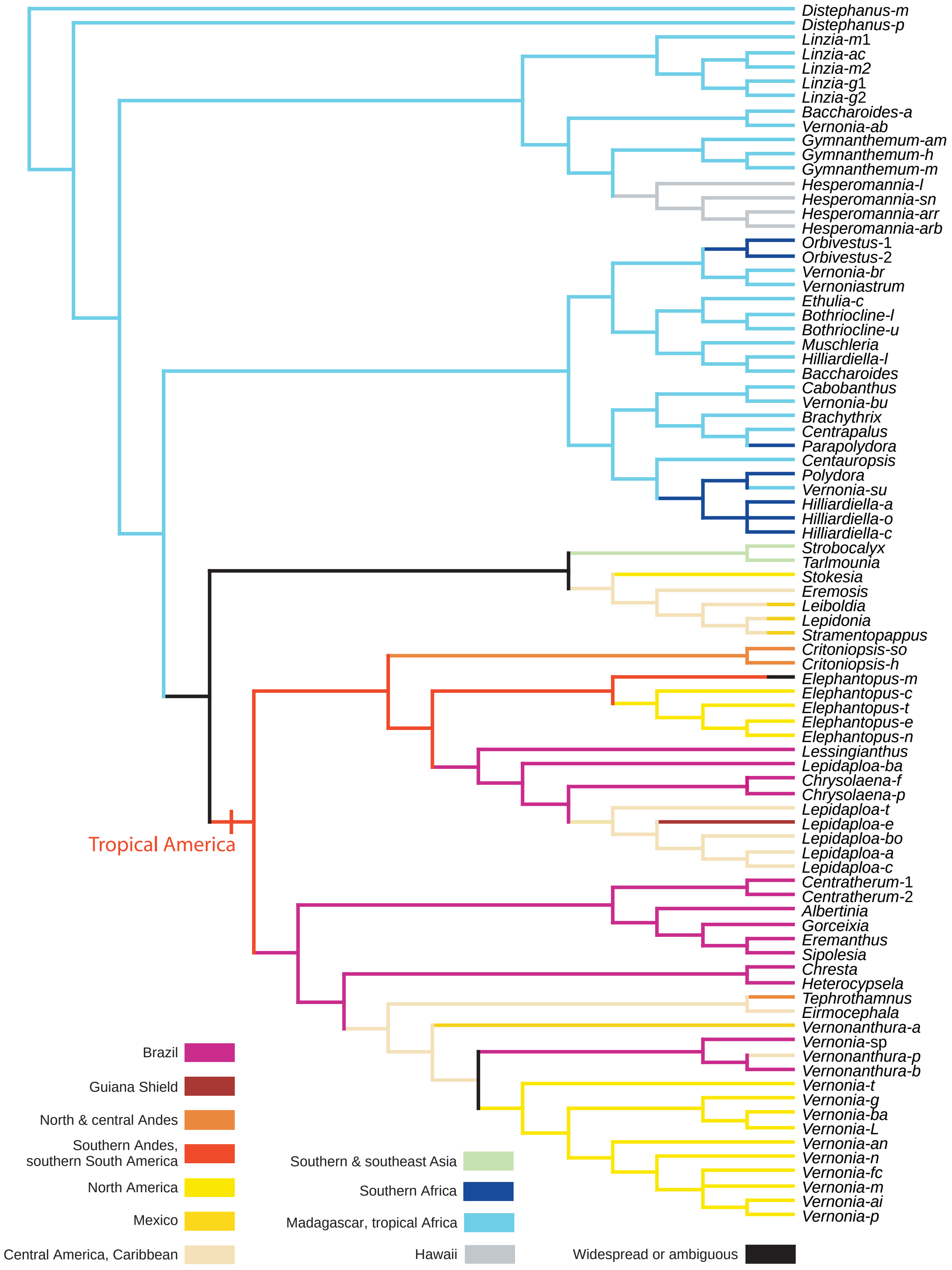
Caulescent herbs, hairs simple or T-shaped; leaves alternate, venation pinnate. Inflorescences strongly seriate- or scorpioid cymose, heads separate; involucral bracts mostly persistent; receptacles without pales. Florets 26–70 in a head; corollas lavender; anthers with or without glands. Achenes without phytomelanin, often with wings, with very dense subquadrate raphids; pappus of short or long capillary bristles, usually persistent. Pollen tricolporate to subtriporate, echinate, strongly sublophate to lophate, perforated tectum continuous or not continuous between colpi. *n* = ? Mostly glaucolides. Colombia, Brazil. Three genera, three monotypic.

Distephaninae S.C. Keeley & H. Rob., **subtr. nov.** – Type (designated here): *Conyza populifolia* Lam.

Plantae frutescentes vel arborescentes vel scandentes, pilis simplicibus. Folia alterna plerumque trinervata vel triplinervia. Capitula discreta; receptacula epaleata. Corollae plerumque flavae; antherae eglanduliferae. Achaenia non phytomelaninifera.

Vines, shrubs or trees; hairs simple; leaves alternate, venation often trinervate or triplinervate. Heads separate; involucral bracts mostly persistent; receptacles without pales.

Fig. 28.2. Bayesian analysis of combined datasets for DNA sequences of ITS, *ndhF*, *trnL-F* for 90 taxa of Vernonieae. [Redrawn, from Keeley et al. (2007: fig. 2) with the following name changes: *Gymnanthemum humblotii* = *Vernonia humblotii* (Drake) H. Rob., *Hilliardiella pinifolia* = *Vernonia capensis* (Less.) H. Rob. and *Tarlmounia elliptica* = *Vernonia elliptica* (DC. in Wight) H. Rob. S.C. Keeley, J.J. Skvarla & R. Chan.]. For a complete metatree see Chapter 44.


Distephanus-m
Distephanus-p
Linzia-m1
Linzia-ac
Linzia-m2
Linzia-g1
Linzia-g2
Baccharoides-a
Vernonia-ab
Gymnanthemum-am
Gymnanthemum-h
Gymnanthemum-m
Hesperomannia-l
Hesperomannia-sn
Hesperomannia-arr
Hesperomannia-arb
Orbivestus-1
Orbivestus-2
Vernonia-br
Vernoniastrum
Ethulia-c
Bothriocline-l
Bothriocline-u
Muschleria
Hilliardiella-l
Baccharoides
Cabobanthus
Vernonia-bu
Brachythrix
Centrapalus
Parapolydora
Centauropsis
Polydora
Vernonia-su
Hilliardiella-a
Hilliardiella-o
Hilliardiella-c
Strobocalyx
Tarlmounia
Stokesia
Eremosis
Leiboldia
Lepidonia
Stramentopappus
Critoniopsis-so
Critoniopsis-h
Elephantopus-m
Elephantopus-c
Elephantopus-t
Elephantopus-e
Elephantopus-n
Lessingianthus
Lepidaploa-ba
Chrysolaena-f
Chrysolaena-p
Lepidaploa-t
Lepidaploa-e
Lepidaploa-bo
Lepidaploa-a
Lepidaploa-c
Centratherum-1
Centratherum-2
Albertinia
Gorceixia
Eremanthus
Sipolesia
Chresta
Heterocypsela
Tephrothamnus
Eirmocephala
Vernonanthura-a
Vernonia-sp
Vernonanthura-p
Vernonanthura-b
Vernonia-t
Vernonia-g
Vernonia-ba
Vernonia-L
Vernonia-an
Vernonia-n
Vernonia-fc
Vernonia-m
Vernonia-ai
Vernonia-p
Tropical America
Brazil
Guiana Shield
North & central Andes
Southern Andes, southern South America
North America
Mexico
Central America, Caribbean
Southern & southeast Asia
Southern Africa
Madagascar, tropical Africa
Hawaii
Widespread or ambiguous

Florets 10–75 in a head; corollas mostly yellow; anthers without glands. Achenes without phytomelanin; pappus persistent, of capillary bristles. Pollen tricolporate, sublophate or lophate with continuous perforated tectum between colpi. *n* = 10. Elemanolides. Africa, Indian Ocean to Yunnan, China. One genus, ca. 45 species. (Fig. 28.1C)

Elephantopinae Less. (1830) – Lectotype: *Elephantopus scaber* L.

Herbs; hairs simple; leaves alternate, often rosulate. Inflorescence cymiform to spiciform; heads contiguous in groups, often in secondary heads; involucral bracts persistent, 4, decussate; receptacle without pales. Florets 4; corollas lavender, often zygomorphic; anthers without glands, bases of thecae often not calcarate. Achenes with raphids elongate, without phytomelanin; pappus of few to many capillary bristles or awns, sometimes highly distorted. Pollen tricolporate to subtriporate, echinate, usually lophate with rather irregular polar lacunae, perforated tectum usually restricted to muri. *n* = 11, 13. Dilactones. Pantropical. Four genera, one monotypic.

Erlangeinae H. Rob. (1999c) – Type: *Erlangea plumosa* Sch.Bip.

Herbs; hairs simple or T-shaped; leaves alternate to opposite or ternate, venation pinnate. Heads separate; involucral bracts persistent; receptacle usually without pales. Florets 3–150 in a head; corolla bluish to whitish; anthers without glands; sweeping hairs acicular. Achenes with raphids short or elongate, without phytomelanin; pappus usually of capillary to subplumose bristles, sometimes coroniform or lacking. Pollen tricolporate and non-lophate or often triporate and lophate with irregular polar lacunae, perforated tectum continuous between colpi in non-lophate forms, restricted to colpi or lacking in lophate forms, echinate to psilate. *n* = 9, 10, 18, 20. 5-methylcoumarins, glaucolides, guaianolides. Africa, Asia, one or two weedy in America. Twenty-two genera, six monotypic.(Fig. 28.1G).

Gymnantheminae H. Rob. (1999c) – Type: *Baccharis senegalensis* Pers. = *Gymnanthemum coloratum* (Willd.) H. Rob. & B. Kahn

Shrubs or trees; hairs simple, bottle- or retort-shaped in a felt, or T-shaped; leaves alternate, venation pinnate. Heads separate or closely clustered; involucral bracts persistent to mostly deciduous; receptacle usually without pales. Florets 1–50 in a head; corollas lavender to whitish; anthers without glands; sweeping hairs pointed or blunt. Achenes with or without raphids, without phytomelanin; pappus usually of capillary bristles often thickened distally, sometimes lanceolate segments. Pollen tricolporate, echinate, usually sublophate, rarely lophate with regularly arranged polar lacunae, rarely with perforated tectum restricted to muri. *n* = 10, 20, 30. Elemanolides. Africa, Asia, Indian Ocean. Four genera, one monotypic.

Hesperomanniinae S.C. Keeley & H. Rob., **subtr. nov.** – Type (designated here): *Hesperomannia arborescens* A. Gray

Plantae arborescentes. pilis ampulliformibus. Folia alterna pinnatinervata. Capitula discreta, bracteae involucri persistentibus Flores ca. 75 in capitulo; corollae flavae; antherae non glanduliferae; styli non vel pauce divisi, papillis stigmaticis non vel paucis. Achaenia non phytomelaninifera non raphidifera. Grana pollinis tricolporata non lophata minute spiculifera.

Trees; hairs bottle- or retort-shaped in a felt on stems; leaves alternate, venation pinnate. Heads separate; involucral bracts persistent; receptacle without pales. Florets ca. 75 in a head; corollas yellow; anthers without glands; style branches with only papillae outside, no sweeping hairs, branches unseparated or scarcely separated at tip, with little or no stigmatic tissue. Achenes without raphids, without phytomelanin. Pollen tricolporate, non-lophate, thin-walled, minutely spiculiferous. *n* = 10. Hawaii. One genus, three species. (Fig. 28.1E).

Leiboldiinae H. Rob (1999a) – Type: *Leiboldia serrata* (D. Don) Gleason

Herbs or subshrubs; with white tomentum, hairs simple; leaves alternate; venation pinnate. Heads solitary or separate in groups, involucral bracts persistent; receptacles usually without pales. Florets 100–120 in a head; corollas lavender; anthers without glands. Achenes without phytomelanin, apical callus partially to mostly unsclerified, sometimes forming raised ring inside of pappus; pappus of weakly attached or highly deciduous capillary bristles. Pollen tricolporate, echinate, sublophate, perforated tectum continuous between colpi. *n* = 19. Eudesmanolides, glaucolides. Mexico. Five genera, two monotypic.

Lepidaploinae S.C. Keeley & H. Rob., **subtr. nov.** – Type (designated here): *Vernonia albicaulis* Pers. = *Lepidaploa glabra* (Willd.) H. Rob.

Plantae herbaceae vel suffrutescentes, pilis simplicibus vel T-formibis. Inflorescentiae plerumque valde seriate cymosae. Capitula discreta, bracteae involucri valde persistentibus; receptacula epaleata. Corollae albae vel lavandulae; antherae saepe glanduliferae. Achaenia non phytomelaninifera, raphidis elongatis vel subquadratis. Grana pollinis tricolporata plerumque lophata, lacunis polaribus regulariter dispositis.

Herbs or subshrubs, rarely shrubs; hairs simple or T-shaped; leaves alternate, rarely opposite or ternate, venation pinnate. Inflorescence usually with seriate cymose branches, heads separate or crowded; involucral bracts usually highly persistent; receptacle without pales. Florets

(4–)10–35(–70) in a head, lavender or whitish; anthers often with glands. Achenes without phytomelanin, with elongate or subquadrate raphids; pappus persistent, usually capillary bristles, some a corona or scale-like. Pollen tricolporate, echinate, usually lophate with regularly arranged polar lacunae and with perforated tectum restricted to muri, sometimes sublophate with perforated tectum continuous between colpi. *n* = 12, 14,16, 17, 24–34. Glaucolides, goyazensolides, piptocarphines, cadinolides. Western Hemisphere, *Struchium* a pantropical weed. Fourteen genera, five monotypic. (Fig. 28.1H).

Linziinae S.C. Keeley & H. Rob., **subtr. nov.** – Type (designated here): *Linzia vernonioides* Sch.Bip ex Walp.

Plantae herbaceae, pilis simplicibus vel T-formibus. Inflorescentiae corymbiformes vel leniter cymiformes. Capitula discreta, bracteae involucri persistentibus; receptacula plerumque epaleata. Corollae saepe azurae; antherae non glanduliferae. Achaenia non phytomelaninifera; setae pappi persistentes capilliformes vel late taeniiformes. Grana pollinis tricolporata saepe lophata, lacunis polaribus regulariter dispositis.

Coarse herbs; hairs simple or T-shaped; leaves alternate, venation pinnate. Involucral bracts persistent; receptacle usually without pales. Florets (8–)20–100 in a head; corollas bluish; anthers without glands; sweeping hairs pointed. Achenes without phytomelanin; pappus of persistent capillary or flattened segments. Pollen tricolporate, usually lophate with regular polar lacunae and perforated tectum restricted to muri. *n* = 9, 10. Elemanolides. Africa. Eight genera, four monotypic.

Lychnophorinae Benth. & Hook. f. (1873) – Type: *Lychnophora salicifolia* Mart.

Perennial herbs to shrubs or candelabriform trees; hairs simple, bottle- or retort-shaped as in felt, or T-shaped; leaves alternate, venation pinnate or sublongitudinal. Heads usually sessile in compact clusters; involucral bracts persistent to somewhat deciduous; receptacles usually without pales, Florets 5–23(–ca. 60) in a head; corollas lavender to whitish; anthers without glands. Achene with raphids subquadrate, without phytomelanin; pappus of capillary or broad sometimes twisted segments, often easily deciduous, with or without outer pappus series. Pollen tricolporate, echinate, sublophate, perforated tectum continuous between colpi. *n* = 9, 15, 17, 18. Furoheliangolides, goyazensolides, eudsmanolides, eremantholides. Mostly Brazil. Nine genera, four monotypic. (Fig. 28.1F).

Mesanthophorinae S.C. Keeley & H. Rob., **subtr. nov.** – Type (designated here): *Mesanthophora brunneri* H. Rob.

Plantae herbaceae, pilis simplicibus vel nullis. Inflorescentiae saepe seriate cymosae. Capitula discreta; bracteae involucri persistentibus. Corollae albae vel lavandulae; antherae non glanduliferae. Grana pollinis triporata subpsilata sine tectis perforatis, lacunis polaris irregulariter dispositis.

Herbs; hairs simple; leaves alternate, venation pinnate. Heads separate, axillary or from middle of internodes; involucral bracts persistent; receptacles without pales. Florets 4–100 in a head; corolla lavender to whitish; anthers without glands. Achenes with raphids elongate or lacking, without phytomelanin; pappus of capillary bristles or ca. 8 short laciniate scales. *n* = 36. Brazil to Argentina and Bolivia. Three genera, two monotypic.

Pacourininae H. Rob. (1999b) – Type: *Pacourina edulis* Aubl.

Subaquatic herbs; hairs minute, simple; leaves alternate, venation pinnate. Heads seriate and sessile in axils of full-sized leaves, large; involucral bracts persistent; receptacle without pales. Florets ca. 50 in a head; corollas lavender, lobe tips and anther appendages sclerified, anthers without glands; sweeping hairs acicular. Achenes with corky surface, without raphids or phytomelanin; pappus bristles short, deciduous, outer squamellae persistent. Pollen triporate, psilate, lophate, with no perforated tectum. *n* = ? Tropical America. One genus, monotypic.

Piptocarphinae H. Rob., F. Bohlmann & R.M. King (1980) – Type: *Piptocarpha brasiliensis* Cass.

Shrubs, vines, and trees; hairs usually stellate or armed at base; leaves alternate or opposite, venation pinnate. Heads in branching panicles or axillary glomerules; involucral bracts mostly deciduous; receptacles without pales. Florets mostly 3–12 in a head, rarely 20 or more; corollas lavender to whitish; anthers rarely with glands; sweeping hairs often blunt and septate. Achenes with raphids short or subquadrate, without phytomelanin; pappus of capillary bristles or awns, rarely a corona or lacking, usually persistent. Pollen tricolporate, echinate, sublophate, perforated tectum continuous between colpi. *n* = 17. Glaucolides, furoheliangolides. Tropical America. Ten genera, five monotypic. (Fig. 28.1A).

Rolandrinae Cass. ex Dumort. (1829) – Type: *Rolandra argentea* Røttb.

Herbs or subshrubs; hairs simple; leaves alternate, venation pinnate. Inflorescence with heads sessile in globose clusters; involucral bracts 2–6, rather persistent; receptacle without pales. Florets 1 in a head; corollas lavender; anthers without glands; sweeping hairs acicular. Achenes 5-nerved, without setulae, with raphids minute or lacking, without phytomelanin; pappus of short scales or bristles. Pollen triporate, with rather irregular polar lacunae, echinate, perforated tectum usually restricted to muri. *n* = 8. Glaucolides. Tropical America. Two genera, both monotypic.

Sipolisiinae H. Rob. (1999a); Type – *Sipolisia lanuginosa* Glaz. ex Oliv.

Coarse herbs, tomentose or lanate, hairs stellate or stellate at base; leaves alternate, venation pinnate. Heads solitary or clustered and separate; involucral bracts persistent; receptacle with pales or spines; florets 20–50 in a head; corollas lavender; anthers without glands. Achenes usually with phytomelanin, rarely with raphids; pappus deciduous, of capillary or broadened bristles. Pollen tricolporate, echinate, sublophate, perforated tectum continuous between colpi. *n* = ? Furoheliangolides. Brazil. Five genera, three monotypic.

Stokesiinae H. Rob. (1999b) – Type: *Stokesia cyanea* L'Her. nom. illeg. = *Stokesia laevis* (J. Hill) E.L. Greene

Herbs, hairs simple, arachnoid, mostly on stems; leaves alternate, venation pinnate. Heads solitary or in lax cymes; involucral bracts persistent, outer filiform, with spinose margins; receptacles without pales. Florets numerous in heads; corollas bluish, mostly liguliform; anthers without glands; styles with glands, with acicular sweeping hairs. Achenes with raphids, without phytomelanin; pappus of 4 or 5 deciduous pales. Pollen tricolporate, nearly psilate, lophate, with crosswalls in colpi, perforated tectum restricted to tops of muri. *n* = 7. Abundant fatty acids and epoxy oils. Southeastern United States. One genus, monotypic. (Fig. 28.1D).

Trichospirinae Less. (1831b) – Type: *Trichospira menthoides* Kunth in H.B.K. = *Trichospira verticillata* (L.) S.F. Blake

Creeping herbs; hairs simple, arachnoid; vegetative leaves alternate, in inflorescence subopposite, venation pinnate. Heads axillary; involucral bracts persistent, subequal; receptacle with few pales. Florets ca. 10; corollas lavender, 4-lobed; anthers without glands, thecae shortly calcarate at base; sweeping hairs acute. Achenes strongly compressed, cuneate, bicornute distally, spicules on surface, without raphids or idioblasts, without phytomelanin; pappus of small awns. Pollen tricolporate, sublophate, perforated tectum continuous between colpi. *n* = ? Tropical America. One genus, monotypic.

Vernoniinae Cass. ex Dumort. (1829) – Type: *Serratula noveboracensis* L. = *Vernonia noveboracensis* (L.) Michx.

Herbs or shrubs; hairs simple or T-shaped; leaves alternate, venation pinnate. Inflorescence cymiform or with cymiform branches, sometimes seriate cymose; heads separate; involucral bracts persistent; receptacle without pales. Florets 8–120 in a head; corollas usually lavender, lobes often filled with longitudinal chambers or ducts; anthers often with glands. Achenes with raphids usually subquadrate, without phytomelanin; pappus usually of many persistent capillary bristles. Pollen tricolporate, echinate, usually sublophate, with perforated tectum continuous between colpi. *n* = 15, 16, 17, 18. Glaucolides, eudesmanolides, guaianolides. Western Hemisphere, one genus in Africa. Nine genera, one monotypic. (Fig. 28.1B).

MORPHOLOGY AND ANATOMY

Morphological characters are variable and overlapping in most Vernonieae genera. As a result, there are no morphological characters that can be used for tribal-wide phylogenetic reconstruction (Funk et al. 2005; Keeley et al. 2007). Despite these difficulties, studies by Robinson and others (see treatments in Robinson, 1999a, c, for a review) have revealed useful combinations of characters, such as inflorescence type, number of flowers per head, leaf indument, and others which can be used with success to delimit subtribes, genera and species within geographically defined regions. (The latter often necessary because of nearly complete morphological overlap by species in South America and Africa, for example). This situation is largely responsible for the historical persistence of the large core genus *Vernonia*. The value of each of these characters varies with the group. That is, trichomes may be significant for recognition of species in some genera and insignificant in others. The most detailed discussion of morphological features is that given in Robinson (1999a). This work provides comparative figures illustrating the details of character states in the subtribes and genera for New World taxa along with a complete synonymy. Similarly, descriptions of characters and character states are also provided for Old World Vernonieae in Robinson (1999c).

Vegetative characters that have been used for taxonomic resolution include leaf venation (pinnate versus trinervate), phyllotaxy, the presence and type of trichomes (unicellular, multicelluar, glandular, branched, stellate, peltate, etc.; presence on abaxial, adaxial leaf surfaces and on petioles), habit and within the latter whether or not a xylopodium is present. Varying environmental conditions reveal substantial morphological plasticity in many species (Keeley 1982). Anatomical characters such as wood or leaf anatomy appear to be useful in individual cases, but have not been widely applied (see Jones 1977; Robinson 2007).

Reproductive characters have long been the standard in Vernonieae taxonomy as elsewhere in the family (Fig. 28.3). In general, inflorescence type provides useful separations at the subtribal and generic levels (Gleason 1906 1923a; Jones 1977, 1979a, 1981a; Robinson 1999a, c). Inflorescences fall into one of several categories including cymose (scorpioid, seriate cymose) and paniculate with or without bracts subtending the heads, and highly condensed spicate forms. Syncephaly is a feature of some Brazilian subtribes (Lychnophorinae, Sipolisiinae, Piptocarphinae,

Fig. 28.3. *Dasyanthina* spp. **A–H** *D. palustris* (Gardn.) H. Rob.: **A** habit; **B** head; **C** corolla showing anthers and style; **D** section of corolla showing tailed anthers, glands on connective and short hairs on inner surface of corolla; **E** short hairs on inner surface of corolla throat; **F** style showing enlarged basal ring; **G** achene; **H** raphids from cells of achene wall. **I** *D. serrata* (Less.) H. Rob., hairs from inner surface of corolla throat. [From Robinson 1999a; drawing by A. Tangerini.]

Chrestinae) and the widespread Elephantopinae found in the Old and New Worlds. Persistence of involucral bracts is variable at the level of the subtribe, genus and species with deciduous phyllaries particularly prominent in the New World Chrestinae, Lynchnophorinae and Piptocarphinae and the Old World Gymnantheminae. Corollas vary with regard to the length of the petal lobes relative to the tube and whether or not they reflex at maturity. There are frequently glands and trichomes on the outer surface of the corolla, but less commonly on the interior (*Dasyanthina* H. Rob., Fig. 28.3). The anther base is variable and useful at the subtribal and generic levels. For example, the sharply elongate and sclerified anther base of Piptocarphinae contrasts with the more typically blunt and often non-tailed condition of Vernoniinae genera. Apical appendages are important among New World taxa being variously glandular or thickened, but are uniform among Old World taxa. Like many of the other floral characters, sweeping hairs on the style are useful for recognizing genera and species. The sweeping hairs vary from acicular to obtuse, or glandular, for example among genera in Old World Centrapalinae. The receptacle is often slightly pitted and only infrequently paleaceous. Achenes supply characters useful at many levels, again, varying with the group. The only phytomelanin containing achenes are found in Sipolisiinae, but the distribution of raphids can separate tribes (Lychnophorinae) and genera (*Vernonia*, *Vernonanthura*, *Lepidaploa*). Similarly, the type and persistence of the pappus is useful at the generic level within a subtribe (i.e., Chrestinae, Lychnophorinae, Piptocarphinae).

POLLEN

Vernonieae pollen morphology is highly variable and has been used extensively in taxonomic delimitations at the generic and subtribal levels (Kingham 1976; Keeley and Jones 1977b, 1979; Bolick and Keeley 1994) (Fig. 28.4.). In general, grains are lophate or sub-lophate, tricolporate or triporate, with either a continuous or discontinuous punctate or emicropunctate tectum, and with or without spines. Keeley and Jones (1979) identified six basic types to which additional variations have been added (see Robinson 1999a, c, 2007, for additional examples). Initially it appeared as if pollen types could be correlated with geographical areas (Keeley and Jones 1979), however, with additional study (Kingham 1976; Robinson 1999a, c, 2007) it has become apparent that this is not the case. The overlap in pollen types and the lack of geographical partitioning have made it difficult to use pollen morphology directly for phylogenetic reconstruction. However, pollen is routinely included in the basic descriptions of subtribes and genera as it is useful at these taxonomic levels.

CHROMOSOME NUMBERS

Jones (1977) reported an apparent dichotomy in chromosome number between Old and New World Vernonieae. Old World taxa routinely had $n = 9$, 10 while New World species had $n = 14$, 16, 17, 18. At that time the frequency of $n = 17$ counts suggested this was the likely base number for the New World (Jones 1977). Additional counts, reported in the *Index to Chromosome Numbers in the Compositae* (http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html) and the *Index to Plant Chromosome Numbers* (W^{3}Tropicos, http://mobot.mobot.org/W3T/Search/ipcn.hmtl) have altered this picture.

Species with counts of $n = 10$ have been reported for a number of South American taxa, i.e., *Lepidaploa bakerana* (Britton) H. Rob. (Olsen 1980) and *Chrysolaena platensis* (Spreng.) H. Rob. (Galiano and Hunziker 1987) in subtribe Lepidaploinae and for *Vernonia pacchensis* Benth. (= *Vernonanthura patens* (H.B.K.) H. Rob.) in subtribe Vernoniinae (Turner et al. 1967). These taxa have been separated out from *Vernonia* s.str., which is characterized by $n = 17$ (Table 28.1). Higher numbers based on $n = 10$ have also been reported for *Chrysolaena flexuosa* (Sims) H. Rob. (as *Vernonia flexuosa* Sims.; $2n = 40$ and $n = 30$(–32); Dematteis 1998b), and additional counts for *C. platensis* ($2n = 40$, 60, 80; Dematteis 1997). These are presumably polyploids based on $x = 10$.

Additional variations in chromosome number among New World taxa do not follow the general patterns in either hemisphere. The monotypic *Stokesia laevis* (Hill) Greene, for example, has a haploid number of $n = 7$ (Jones 1974) and that of *Spiracantha cornifolia* H.B.K. is $n = 8$ (Semple 1974). *Eremanthus* species are reported consistently as $n = 15$ (Turner et al. 1979; Jones 1982c), a count found in no other genus in either the New or Old World. Similarly, subtribe Elephantopinae (*Elephantopus* L., *Orthopappus* Gleason, and *Pseudelephantopus* Rohr) found in the New World (and pantropically) are the only taxa with $n = 11$ or 13 (Table 28.1). *Stramentopappus pooleae* (B.L. Turner) H. Rob. & V. Funk, *Lepidonia callilepis* (Gleason) H. Rob. & V. Funk, *Lepidonia jonesii* (B.L. Turner) H. Rob. & V. Funk, *Leiboldia arctoides* (Less.) Schltdl. are all reported to be $n = 19$ (Turner 1981; Sundberg et al. 1986) along with *Eremosis obtusa* var. *parkeri* (Gleason) S.B. Jones and *E. steetzii* (Sch.Bip.) Gleason (Jones 1973). Several species of *Lychnophora* are reported as having counts of $n = 18$ and $n = 19$ (Jones 1973; Buechler 2001). Turner (1981) proposed that $n = 19$ arose as an aneuploid reduction from $2x = 20$ or possibly by ancestral amphiploidy ($19 = x_9 + x_{10}$). Presumably, $n = 18$ would be a doubling on a base of $x = 9$. Higher numbers in New World Vernonieae are consistent with a pattern of members invading new geographical areas. Since New World taxa are clearly derived (Fig. 28.1), part of their success may be due to increased genetic diversity achieved through higher chromosome number and hybridization (see below).

Unlike New World taxa, there is very little variation in chromosome number among Old World species reported to date. For example, taxa in subtribes Centrapalinae, Distephaninae, Erlangeinae, Gymnantheminae and Linziinae (Table 28.1) are based on $n = 9$, 10. *Bothriocline* Oliver ex Benth. and *Gutenbergia* Sch.Bip., with $n = 20$ and ca. 30 (Jones 1979b) and *Strobocalyx* (Blume ex DC.) Spach with $n =$ ca. 30 (Jones 1982c) are presumably polyploids. With the exception of *Vernonia appendiculata* Less. ($n = 7$) (Rabakonandrianina and Carr 1987), and *Elephantopus* ($n = 11$), and which is likely New World in origin (Keeley et al. 2007), all other Old World taxa appear to fit Jones' (1977) conclusion that the base numbers for this hemisphere are $x = 9$, 10. This uniformity may be an artifact of the relatively low number of species sampled from the Old World compared to New World.

One other factor that impacts the understanding of chromosomal variation is uneven representation of taxa. Some genera have been counted many times as is the case for *Centratherum* and *Elephantopus* (e.g., Sharma and Sakar 1967–68; Jones 1979b; Mathew and Mathew 1983, 1988; Gupta and Gill 1984, 1989), *Lychnophora* (Coile and Jones 1981; Buechler 2001; Mansanares et al. 2002; Mansanares 2004) and *Vernonia eleagnifolia* DC., *V. bourneana* W.W. Sm., and *V. albicans* DC. (Mathew and Mathew 1976, 1982, 1983, 1988), while other large genera such as *Gutenbergia* (Jones 1979b; Gill and Omoigui 1992), *Gymnanthemum* (Ayodele 1999) and *Piptocarpha* (Turner et al. 1979; Smith

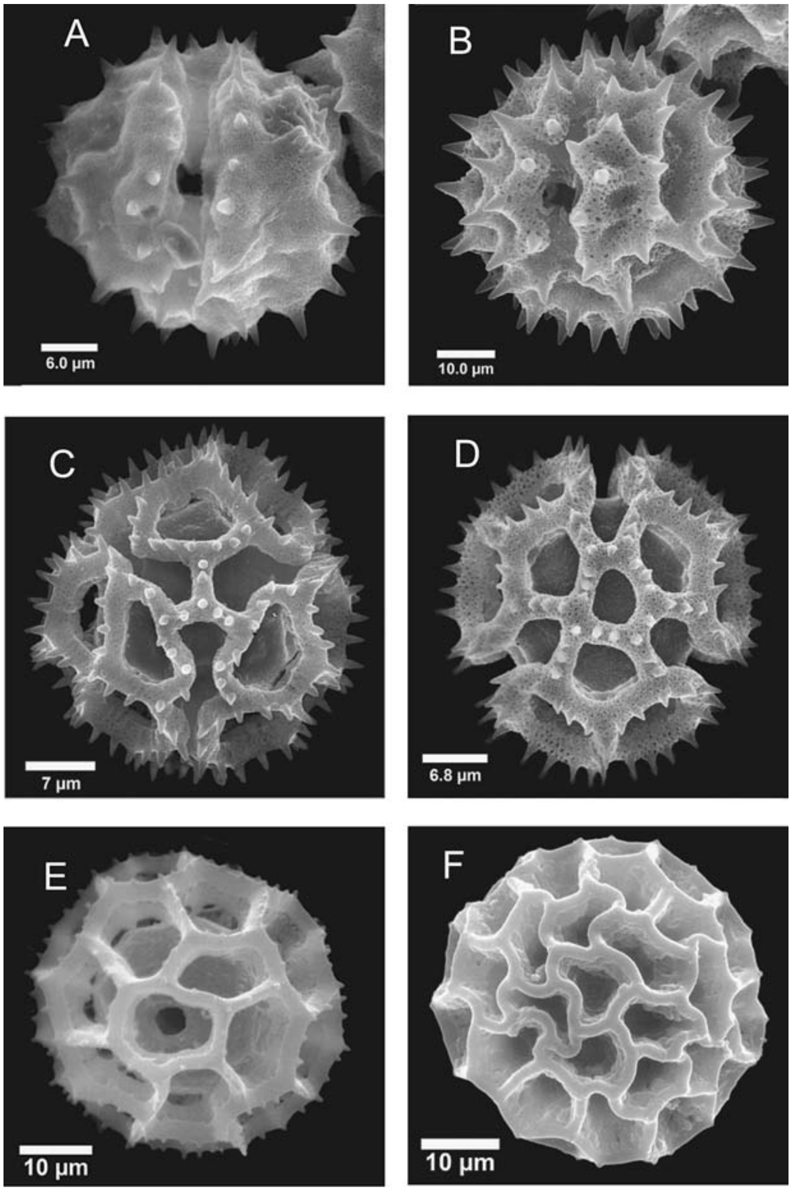


Fig. 28.4. Selected pollen types of Vernonieae. **A** non-lophate, *Distephanus divaricatus* (Steetz) H. Rob. & B. Kahn; **B** non-lophate, *Eirmocephala megaphylla* (Hieron.) H. Rob.; **C** lophate, tricolporate, *Lepidaploa psilostachya* (DC.) H. Rob.; **D** lophate, tricolporate, *Lepidaploa salzmannii* (DC.) H. Rob.; **E** lophate, triporate, *Phyllocephalum scabridum* (DC.) K. Kirkman; **F** psilate, *Pacourina edulis* Aubl.

and Jones 1987) have very few counts (Table 28.1). The picture is not entirely bleak, however. Recent work in Brazil, the New World center of diversity, by Dematteis and colleagues (e.g., Dematteis and Robinson 1997; Dematteis 1997, 1998a–c, 2002) has provided new counts for a number of genera. More research in this area is clearly needed as chromosome number can provide valuable information at the subtribal and generic levels.

CHEMISTRY

Sesquiterpene lactones, bitter tasting compounds in the leaves and stems of many Vernonieae, have been the principal secondary chemicals used in tribal systematics. Bohlmann and Jakupovic (1990) compiled the most complete survey of Vernonieae chemistry to date. They found that there was a characteristic chemical signature for the tribe, and that certain groups of compounds could be diagnostic at the generic level and higher. The commonly occurring compounds in Vernonieae include the sesquiterpene lactone glaucolides, germacranolides, guaianolides, hirsutinolides, furoheliangolides, eremanolides and elemanolides along with nerolidol derivatives and the nonsesquiterpene lactone coumarins (Harborne and Williams 1977; Seaman 1982; Bohlmann and Jakupovic 1990). Robinson (1999a, c, 2007) found these compounds useful at the subtribal level. For example, dilactones are found in Elephantopinae, furoheliangolides and goyazenolides in Lychnophorinae, both from the New World. The relatively uncommon 5-methylcoumarins are in Old World Erlangeinae. Similarly, compounds such as elemanolides are found in basal Distephaninae, Linziinae and Gymnantheminae, but not in New World taxa (Robinson 2007). Other compounds have been recognized since Bohlmann and Jukupovic (1990), i.e., piptocarphins (Valdés et al. 1998a; Borkosky et al. 2003) in Piptocarphinae and gutenbergin (Fujimoto et al. 1987) in Erlangeinae, that may be useful in confirming subtribal boundaries (Table 28.1).

Harborne and Williams (1977), Seaman (1982) and Seaman and Funk (1983) found that the sesquiterpene lactone chemistry of New and Old World species differed. These differences were enough to suggest two separate lineages, supporting the treatments of Jones (1979a, 1981a), Jeffrey (1988) and Robinson (1999a, c). The data also showed that New World *Vernonia* species were more closely related to each other and to *Stokesia* (Hill) Greene than they were to Old World species (Seaman 1982; Seaman and Funk 1983), and that North American species appeared to be derived from South American species, as supported in recent findings (Keeley et al. 2007). Additionally, their work supports the recognition of subtribe Lepidaploinae (here), as the *Lepidaploa* group represents a distinct line that was separate from other New World Vernonias.

Other secondary compounds such as epoxy oils and vernolic acid have been investigated for phylogenetic signal, but on a more limited basis (Harborne and Williams 1977; Jones 1977; Bohm and Stuessy 2001). Epoxy oils are found in large amounts in particular taxa, e.g., *Stokesia laevis* (New World) and the Old World taxa *Vernonia galamensis* and *Baccharoides anthelmintica* (L.) Moench, but most work in this area has centered on commercial uses (see below). Flavonoids have also been investigated in selected species groups (for recent summary see Bohm and Stuessy, 2001), but have so far been little used in Vernonieae systematics as patterns of inheritance are difficult to elucidate. More remains to be understood in the area of secondary chemical constituents.

ECOLOGY

Secondary chemistry is responsible for anti-herbivore defenses in some New World Vernonieae. In eastern North America *Vernonia* species with glaucolide-A, for example, were shown to deter feeding by rabbits and deer, to reduce larval feeding in three species of army worms and to affect insect life cycles (Burnett et al. 1974; Jones 1977; Jones et al. 1979). *Vernonia mollissima* D. Don ex Hook. & Arn., *V. nudiflora* Less., *V. rubricaulis* H.B.K. and *V. squarrosa* Less. were responsible for liver toxicity and death in cattle and sheep in Mato Grosso do Sul and Rio Grande do Sul in Brazil and areas of nearby Uruguay, presumably due to secondary chemical accumulation (Brum et al. 2002).

While some animals are poisoned by Vernonieae, others appear to have co-evolved with the toxic compounds and are unaffected. Insect interactions reported include those with aphids, ants, treehoppers and various pollinator species. Five closely related species of eastern North American *Vernonia* (*V. angustifolia* Michx., *V. baldwinii* Torr., *V. fasciculata* Michx., *V. interior* Small, *V. noveboracensis* (L.) Michx., *V. maxima* Small) are host plants for the Vernonia aphid, *Aphis vernonia*, and *V. baldwinii* and *V. noveboracensis* are also hosts for the treehopper *Pubilia reticulata*, both insects tended by ants (Bristow 1984). Ants milk aphids and build houses for them out of leaves or shoots of *Vernonia guineensis* Benth. (= *Gymnanthemum coloratum* (Willd.) H. Rob. & B. Kahn) in the Ivory Coast; it appears that different ant species create different styles of houses for their aphids as well (Duviard 1969, 1970a, b). Hind (pers. comm.) also noted ants occupying the hollow peduncles beneath the heads of post-flowering *Pithecoseris pacourinoides* Mart. ex DC. in Bahia State, Brazil. In Costa Rica the moth species *Pericopus leucophaea* Walker is a voracious herbivore of *Vernonanthura patens* (H.B.K.) H. Rob. (Young 1981). A number of beetles and bugs have been noted on *V. interior* (Schwitzgebel and Wilbur 1942a, b, 1943). Vernonieae are also closely associated with tephridid flies (Diptera:

Tephritidae) in both North and South America. These flies infest the heads of numerous eastern North American *Vernonia* species reducing the number of mature achenes (Jones 1977). Studies by Prado and co-workers (Prado et al. 2002, 2004; Prado and Lewinsohn 2004) reported similar infestations in numerous Vernonieae genera of the cerrado and campo rupestre habitats of Brazil. The flies were able to distinguish between taxa of subtribes Centratherinae, Lychnophorinae and Vernoniinae, laying eggs only in the heads of members of the particular subtribe with which they have co-evolved; *Cyrtocymura* had two insects not associated with any other plant. Genera for which specific associations were reported (above) included *Chresta*, *Chrysolaena*, *Cyrtocymura*, *Eremanthus*, *Lessingianthus*, *Lychnophora*, *Lychnophoriopsis*, *Minasia*, *Piptolepis*, *Proteopsis*, *Vernonia*, and *Vernonanthura*.

Jones (1977) reported that a wide variety of bees, butterflies, flies and wasps visited *Vernonia* gathering pollen and nectar from florets that are often sweet smelling and aggregated into showy inflorescences. Savannah species *Vernonanthura brasiliana* (L.) Druce, *V. constricta* N.I. Matzenbacher & S.I. Mafioleti (*Lessingianthus*?), and *Lepidaploa remotiflora* (Rich.) H. Rob. in Brazil were similarly reported to have a number of different types of generalist pollinators (Ramirez 2004). In northern Brazil (Bahia) *Lepidaploa arenaria* (Mart. ex DC.) H. Rob. was visited by seven species of bees, while *L. edmundoi* (G.M. Barroso) H. Rob. was visited by only two and *Stilpnopappus scaposus* DC. by only one (Viana and Kleinert 2006). In the latter study, the generalist nature of pollinator relationships appeared to be responsible for maintaining species diversity in this sandy coastal area. The extent of generalists versus specialist (and possibly obligate) pollinator relationships remains to be further studied in virtually all areas where Vernonieae are native.

Decaneuropsis vagans (DC.) H. Rob. & Skvarla (as *Vernonia scandens* DC.) was reported as a bat roosting habitat in India (Balasingh et al. 1993, 1995). *Cynopterus sphinx* bats made day-roost tents by chewing twigs of this species. No other such reports were encountered.

Another ecological feature of Vernonieae is a strong tolerance for heavy metal soils such as serpentine, bauxite and dolomite. Vernonieae species are among the most tolerant of serpentine soils of South African species in the Greenstone Belt (Smith et al. 2001). The first author has also observed this tolerance (and possible preference) in numerous locations in Central and South America and the West Indies. Additionally, many taxa grow on karst and volcanic substrates and derive their common name, iron weeds, from their preference for iron rich soils in eastern North America (along with the toughness of their stems, which is sometimes said to be the origin of the name).

One additional aspect of Vernonieae soil relationships is the apparent ability to improve soil fertility, at least in some areas of Africa. *Bothriocline tomentosa* (S. Moore) Gilbert was reported to increase soil fertility when planted and when naturally occurring in Tanzania as did *Vernonia subligera* O. Hoffm. (Wickama and Mowo 2001). For the latter species, areas previously under *V. subligera* were easier to cultivate, produced healthier crops, and better retained soil moisture (Wickama and Mowo 2001).

Many Vernonieae are also tolerant of burning and flooding, particularly in grassland and savannah locations in Central and South America (Jones 1977; pers. obs.). Burning can increase seed set in some species (Hoffmann 1998). *Lessingianthus rubricaulis* (Humb. & Bonpl.) H. Rob. and other species grow in seasonally inundated savannahs in Venezuela, Brazil and nearby areas (pers. obs.). African species are also anecdotally reported to survive well where grasslands are regularly burned, i.e., South Africa. Specific studies of these responses are needed to confirm these reports.

Urban (1973) reported a co-evolutionary relationship among autoecious rust species and North American Vernonieae. Each species of rust was found only on closely related Vernonieae, i.e., *Puccinius longipes* on species of *Vernonia* subsection *Paniculatae verae* while *P. semiinsculpta* was found on species of subsection *Paniculatae umbelliformae* (Urban 1973). *Puccinia* species were also found to be specific to taxonomic subgroups of *Piptocarpha* in all but a few cases (Smith and Coile 2007). Given the taxonomically useful nature of this information, a more systematic investigation into Vernonieae fungal symbiosis would likely prove valuable.

BIOGEOGRAPHY

Long distance dispersal has played an important role in the distribution of Vernonieae. That this is undeniably the case can be seen by the relationship of the Hawaiian endemic, *Hesperomannia*, to taxa in Madagascar 12,000 km away (Kim et al. 1998; Keeley et al. 2007). The Hawaiian Islands are among the most distant landmasses in the world (ca. 4000 km from the closest source area) and are the result of oceanic volcanoes rising from the sea floor. The islands were bare lava when they emerged from the sea and have never been connected to a continent yet are the home of a rich flora (Wagner et al. 1999). Australia, with the endemic *Pleurocarpaea* Benth., has also been isolated with no direct connection to another landmass within the time frame for Compositae evolution (maximum age ca. 60 Myr; Zavada and De Villiers 2000). It is 8000 km from Australia to Africa where the nearest relatives of *Pleurocarpaea* are found. Additionally, many endemic species are found on islands in the West Indies (Keeley 1978) and other areas around the world.

There have been at least two long-distance dispersal events between the New and Old Worlds. Two species from southeast Asia, *Strobocalyx arborea* and *Vernonia elliptica* (now *Tarlmounia elliptica* (DC. in Wight) H. Rob. S.C. Keeley, J.J. Skvarla & R. Chan), are most closely related to species from Meso-America (*Lepidonia*, *Leiboldia*, *Stramentopappus* [subtribe Leiboldiinae]), *Eremosis* and North America (*Stokesia*) (Fig. 28.2). The clade in which these taxa are found is derived from Old World species and is found between clades that are otherwise composed of Old World and New World species, respectively (Fig. 28.2). The unusual position of Leiboldiinae between Old and New World taxa was also noted by Keeley and Jansen (1994) in a cpDNA restriction site study and by Kim et al. (1998) in a sequencing study of the *ndhF* and ITS regions. On the basis of the evidence to date, it seems most likely that dispersal was from the Old World to the New World (Keeley et al. 2007). In addition, *Elephantopus*, now found in both hemispheres, has its origin among New World taxa (Fig. 28.2). Dispersal from the New to the Old World is the most likely explanation for the current distribution. Long-distance dispersal from Africa to South America has been reported for *Hypochaeris* (Lactuceae) (Tremetsberger et al. 2005) and from Mediterranean Europe to western North America for *Senecio* (Senecioneae) (Coleman et al. 2003). It is likely that other long distance dispersal events remain to be documented among Vernonieae and for other Compositae tribes.

Biogeographic patterns within each hemisphere are only beginning to be understood for Vernonieae. Brazil is the New World center of diversity, for example, but relationships among the many genera and former *Vernonia* species have only been touched upon so far. It is also not clear how many lineages may have radiated northward to Central America, the West Indies and North America or if there has been back dispersal. Meso-America is an area where relictual habitats persist and presumably at least some of the species that colonized them in the distant past have remained there. Relict habitats are surrounded by more recent ones, especially along the Andes and the mountain ranges extending up through Central America to Mexico (Rzedowski 1993), and there have been many opportunities for exchanges from north to south and for intermixing (Keeley et al. 2007). Further, the connection between Andean Vernonieae and species now found in Argentina, Uruguay, Paraguay, Bolivia, Brazil and Venezuela, and their spread to the north remains unclear as well, but could be important to larger biogegraphic patterns (i.e., as in *Elephantopus*). Among Old World Vernonieae, many of the same kinds of questions about dispersal remain unresolved. For example, the relationships of Madagascan/African taxa to those in India remain unknown, but are likely given their geographical proximity. There are many endemic Vernonieae in the Western Ghats and Sri Lanka; the relationships of these to taxa further east also are unknown. Further, given that Malaysian Vernonieae are found in the same clade as Meso-American species and their position is between Old and New World clades, the inclusion of more Old World taxa from this region has the potential to greatly alter our understanding of subtribal relationships. As there are other Compositae tribes found in Africa and southeast Asia this information could impact our understanding of the biogeography of the family as a whole.

Molecular clock estimates date dispersal from the Old World to the Americas at between 20 and 14 Ma (Keeley et al. 2007). This is similar to the timing for the dispersal from Africa of the ancestor of the Hawaiian endemic, *Hesperomannia* (Kim et al. 1998), roughly when Midway was a high island. Many wind-dispersed seeds are produced each year by 100s of thousands of plants in Africa, North, Central and South America, India, Asia, on oceanic islands in the New and Old Worlds and in countless microhabitats throughout the world. Given the millions of years over which flowering, fruiting and dispersal have occurred, the odds of a propagule landing in a receptive habitat from time to time are certainly within reason. Lineages of different ages and sizes with some widespread and others only narrowly distributed would be expected. Distribution includes islands and continents in tropical regions worldwide and a much smaller number in temperate areas (i.e., eastern North America). Vernonieae are not found north of the Himalayas, in Europe or in western North America, all areas where high elevation mountain ranges, glaciations, or rainshadows appear to have halted their movement. Given the lack of taxa in some of these areas and the derived nature of North American species at least one possible land based dispersal scenario, the boreotropical route (Tiffney 1985), seems unlikely for Vernonieae.

The emerging picture of Vernonieae biogeography is of an origin in the region of Madagascar/southern Africa with radiations north and east to southern and southeast Asia and to the Americas (Keeley et al. 2007). These radiations gave rise to two major lineages, one Old World and one New World with centers of diversity in east Africa and Brazil, respectively. The result is a particularly wide geographic distribution and one that can provide information on radiation for the family as a whole. For example, broader patterns emerge when distributions match those of other tribes while non-concordance could suggest differences in timing or nature of dispersal. Vernonieae comprise the only Old World tribe within Compositae with a New World sister tribe (Liabeae), and Vernonieae are found among the tribes near the base of the family phylogeny (Funk et al. 2005). Further refinement of the dispersal scenarios for Vernonieae will provide improved understanding of the pathways and the timing of Compositae radiation worldwide.

EVOLUTION

In addition to obvious dispersal capabilities within the tribe, there are several other features of Vernonieae biology that have no doubt contributed to its success. One important attribute is the ability to become established in marginal habitats, particularly on serpentine, dolomite, bauxite and other soils with unusual mineral content, as well as on cliff faces, volcanoes, and soil slips. Many members of Vernonieae have developed fire-survival strategies, such as woody rootstocks that allow them to thrive in savannahs and grasslands.

In addition, species appear to persist once established, and there are many instances of adaptive radiation in the tribe. Few Vernonieae are weedy even if widespread, and the number of monotypic genera and genera found in relictual habitats in Central and South America and Africa suggest that specialized adaptations have allowed Vernonieae to remain as conditions around them changed. It is unclear if the general lack of weediness is due to poor competitive ability in areas already occupied by other plants or to the lack of suitable habitat (or both). More studies in the field are definitely needed.

Vernonieae can hybridize readily among closely related species and polyploidy is common, allowing for a rapid increase in genetic variability. This could be particularly important when habitats are disrupted as they would likely be in disturbed and environmentally marginal areas. Vernonieae taxa are often visited by a suite of different pollinators, often generalists themselves, whose behavior may promote gene exchange. Although poorly studied, it is also possible that relationships with specific pollinators may account for persistence within given environments. Additionally, many Vernonieae are exceptionally well defended by a battery of bitter-tasting sesquiterpene lactones and other compounds that deter insect and mammalian herbivores. These attributes have no doubt been combined in different ways through time, playing off one another, fostering radiations in some lineages at some times while leaving others to languish. When combined with a talent for widespread dispersal, it is no wonder that Vernonieae are found in all but a few areas of Eurasia and North America where high mountains have prevented their movement. They are plentiful everywhere else, on islands and continents, and include virtually every habitat type and growth form. Vernonieae truly represent an evolutionary success story, helping to make Compositae the largest and most widespread flowering plant family in the world.

Hybridization is potentially of significance in the evolution of Vernonieae taxa, although the frequency and extent are documented for a limited number of species. The ability of closely related *Vernonia* species to hybridize was demonstrated in studies by Jones (Jones 1966, 1967, 1968, 1972; Jones et al. 1970; Faust 1972; Urbatsch 1972) for North American species and by Smith (1971) for some African species. In general, crosses among closely related taxa produced fertile F_1s with some breakdown in the second generation. Wider crosses resulted in weak and sterile first generation progeny. The extent to which outcrossing and selfing affect taxa within the tribe is only poorly known. Jones (1977) reported that 45 New World and about 8 African species were self-incompatible. *Vernonia cinerea* (now *Cyanthillium cinereum* (L.) H. Rob.), is self-fertile as are some *Vernonia anthemintica* (now *Baccharoides anthemintica* (L.) Moench) individuals (Jones 1977). *Vernonia galamensis* Willd. (now *Centrapalus pauciflorus* (Willd.) H. Rob.) is primarily selfing, with less than 20% seed set from outcrossed plants (Baye and Becker 2004). In some cases wide experimental hybridizations caused normally self-incompatible species to self (Jones et al. 1970). Counts such as $n = 19$ in Leiboldiinae could suggest an ancient hybridization event ($n = 9 + n = 10$), for example, but this remains unknown. The degree of selfing versus outcrossing is also poorly known.

WEEDS

Only a small number of Vernonieae taxa are reported to be weedy. These are typically found in disturbed areas such as pastures, croplands and along roadsides. Most Vernonieae species with weedy characteristics are shrubs or herbaceous perennials, only one, *Cyanthillium cinereum* (L.) H. Rob., is an annual. In North America, *Vernonia baldwinii* Torr. is considered a weed in rangelands and pastures throughout the great plains and extending as far north as Minnesota and as far south as Texas, and east to Arkansas and Louisiana (USDA PLANTS Database, http://plants.usda.gov; GRIN, Germplasm Resources Information Network, http://www.ars-grin.gov). It is the tough nature of the roots and stems that makes it difficult to remove these plants and causes problems for ranchers and farmers. Related species such as *V. altissima* Nutt. (Venal Ironweed) (Mann et al. 1983) and *V. gigantea* Trel. (Tall Ironweed) (USDA PLANTS Database; TNC GISI, Global Invasive Species List, http://tncweeds.ucdavis.edu/global/australia/ast.html) are weedy in some areas as well. In grasslands used for grazing in South America, a few species have also been reported as weedy. This is the case for *Vernonanthura brasiliana* (L.) H. Rob. and close relatives such as *V. polyanthes* Less. (now *V. phosphorica* (Vell.) H. Rob.) (Filho et al. 1997), *V. westiniana* (Less.) H. Rob. (Mendonca 2004) and *V. ferruginea* (Less.) H. Rob. (Fujisaka et al. 1997). *Vernonanthura chamaedrys* (Less.) H. Rob. has also been reported as a grassland weed in Corrientes province in Argentina (Kurtz et al. 2006). In Africa, *Vernonia galamensis* is considered a weed in fields, woodlands and in many agroecological conditions (Baye and Becker 2005). Other

Vernonia spp. may invade savannah areas when intensified cereal-based cropping fields lose soil fertility (Webber et al. 1995). *Polydora poskeana* (Vatke & Hildeb.) H. Rob. occurs in heavily grazed dryland ecosystems in the Kalahari, Botswana (Thomas et al. 2000) and as a weed of maize cultivation (FAO, http://www.fao.org/ag/agp/agpp/IPM/Weeds). *Vernonia ambigua* L. has been reported as a weed in Nigerian farmlands (Kayode 2003) and roadsides. *Vernonia amygdalina*, *V. colorata*, *V. cinerea*, *V. galamensis* and *V. tenoreana* were also reported in the latter habitat (Kayode 2005a). *Struchium sparganophorum*, evidently New World in origin (Robinson 1999a), is now widely distributed in the Old World tropics (Uniyal 1995).

Major weeds of agricultural areas in the tropical southern and western Pacific include the now pantropical *Vernonia cinerea* (L.) Less. (now *Cyanthillium cinereum* (L.) H. Rob.), *Elephantopus mollis* Kunth and *Pseudelephantopus spicatus* (Juss.) Baker (Waterhouse 1997). Wu and Wang (2005) considered the latter two taxa invasive in Taiwan. *Cyanthillium cinereum*, in addition to being found in many disturbed locations, is also found in rice paddies in the Philippines (Marcos et al. 2000) and as a weed in cotton and maize fields (Science and Technology Information Network of the Philippines, http://scinet.dost.gov.ph) and appears to be a vector for the spread of phytoplasma diseases in Australia (Davis et al. 2006). Overall, however, Vernonieae species are not highly invasive and appear to have few negative economic or ecological effects.

ETHNOBOTANICAL AND MEDICINAL USES

The number and variety of studies on the uses of Vernonieae have increased by several orders of magnitude since the last review of the tribe by Jones (1977). These studies show the powerful effects of sesquiterpene lactones and other secondary chemical compounds on everything from soil fertility and improved agricultural production to curing illness in chimpanzees and humans. Several species are particularly important within countries and geographical regions and may have multiple effects while others may be used on a much more limited basis.

In Africa, *Vernonia amygdalina* Del. (now *Gymnanthemum amygdalinum* (Del.) Sch.Bip. ex Walp.) stands out for its multiple uses (Erasto et al. 2006). This species is widespread and is used in West, Central and East Africa (Angola, Ethiopia, Guinea, Nigeria, Tanzania, Ghana, Sierra Leone, and W. Cameroon). It is an anthelmintic used to treat a variety of trematode and other worm infections in people and animals and for the treatment of schistosomiasis (Dalziel 1937; Kokwaro 1976, 1993; Burkill 1985; Hamill et al. 2000; Alawa et al. 2003; Fichtl 2005). It also has a variety of other medicinal uses: as a substitute for quinine in the treatment of malaria and to lower fevers in general, as a heart stimulant as it contains a cariotonic glycoside comparable to digitalin, to reduce blood sugar, to cure urinary infections, diarrhea and as a purgative, to treat skin disorders, and as a general pain reliever (Watt and Breyer-Brandwijk 1962; Akah and Okafor 1992; Kayode 2002, 2005b; Abosi and Raseroka 2003), and it is used as a treatment for sexually transmitted diseases in Zimbabwe (Kambizi and Afolayan 2001). The edotides in an aqueous extract of the leaves have been shown to be effective against the growth of breast cancer cells and including it in the diet may delay or prevent breast cancer (Izevbigie 2003; Izevbigie et al. 2003, 2004, 2005). Ashes of wood and leaves were effective in preventing mycelial growth of wheat rust (Enikuomehin et al. 1998). Additionally, it is eaten as a leafy vegetable and helps provide micronutrients, vitamin C, and carotenoids to local populations (Akachuku 2001; Adeboye et al. 2005) and improves the nutrition of cattle when added to teff straw (Bonsi et al. 1995a, b). It is also used as a flavoring agent in the production of beer and wine (Lasekan et al. 1999). An interesting use of *G. amygdalinum* is by animals rather than by humans. Chimpanzees have been seen to self-medicate by eating the pith of young stems, and sesquiterpene lactones with medicinal effects have been identified from this species (Huffman and Seifu 1989; Ohigashi et al. 1991, 1994; Jisaka et al. 1992a, b, 1993a, b; Koshimizu et al. 1993, 1994; Huffman et al. 1996, 1997; Huffman 2001, 2003; Krief et al. 2005). Hind (pers. comm.) noted that this species has also been described from Brazil (as *Vernonia condensata* Baker and *V. bahiensis* Toledo), where it appears to have been transported by African slaves.

Anthelmintic properties similar to those of *V. amygdalina* are found in a number of other Old World Vernonieae taxa as well. For example, *V. anthelmintica* L. (now *Baccharoides anthelmintica* Moench) is commonly used in India to treat a variety of worm infections, as its name would suggest (Iqbal et al. 2006) and for the treatment of skin diseases (*Botanical Dermatology Database*, http://bodd.cf.ac.uk). *Vernona auriculifera* Hiern. is used as an anti-trypanosomal for treatment of malaria and sleeping sickness, an effect backed up by scientific tests (Freiburghaus et al. 1996; Hamill et al. 2000). *Vernonia brachycalyx* Hoffm. (East Africa) is used by Masai and Kipsigis for treatment of parasitic diseases (Watt and Breyer-Brandwijk 1962; Kokwaro 1993; Beentje 1994), and has been shown to be effective against malaria schizonts, and against the promastigotes that cause leishmaniasis (Beentje 1994; Oketch-Rabah et al. 1997, 1998, 1999). Similarly, *V. cinerea* (*Cyanthillium cinereum*) extracts were effective against chloroquine-resistant *Plasmodium falciparum* and are widely used in the pharmaceutical industry as antibacterial, antiviral, and anticancer treatments (Chea et al. 2006). Like *Gymnanthemum amygdalinum*, *Cyanthillium cinereum* also functions as a general pain and inflammation reliever. An extract of *Vernonia subuligera* O. Hoffm. (now *Gymnanthemum myrianthum* (Hook.)

H. Rob.) was demonstrated to be effective against the trypanosome that causes sleeping sickness (Wickama and Mowo 2001). Other Old World taxa that have many of these same uses and properties include *Gymnanthemum coloratum* (Willd.) H. Rob. & B. Kahn (Kelmanson et al. 2000), *Bothriocline* spp. (Wickama and Mowo 2001), *Gutenbergia cordifolia* Benth. ex Oliver (Mungarulire et al. 1993), *Struchium sparganophorum* L. (Oboh 2005), *Vernonia cinerea* (Mendes et al. 1999; Hamill et al. 2000), *V. auriculifera* Hiern. (Freiburghaus et al. 1996), *V. chinensis* Less. (Chen et al. 2005, 2006), *V. kirungae* R.E. Fr. (Chifundera 1998), *V. lasiopus* O. Hoffm. (Njoroge 2004), *V. pachyclada* Baker (Williams et al. 2005), *V. pogosperma* Klatt., *V. thomsoniana* Oliver & Hiern ex Oliver, and *V. tufnellaei* S. Moore (Mungarulire et al. 1993).

In the New World, anthelmintic and anti-trypanosomal effects have been demonstrated for a number of taxa. *Vernonia brasiliana* L. extracts are effective against both human and rodent malarial *Plasmodium* spp. (Carvalho et al. 1991; Carvalho and Krettli 1991; Alves et al. 1997). *Piptocarpha rotundifolia* Baker, *Stilpnopappus ferruginea* Mart., *Eremanthus erythropappus* (Sch.Bip.) MacLeish and *V. eremophila* Mart. sesquiterpenes and extracts were effective against the snails that carry bilharzias (Alarcon et al. 1990; Cunha et al. 1995, 1999; Mendes et al. 1999). Extracts of *Lychnophora pinaster* Mart. and *L. granmongolense* (Duarte) D.J.N. Hind killed trypanosomes of Chagas disease in the blood (Chiari et al. 1996; Grael et al. 2000, 2005; Alcantara et al. 2005; Silveira 2005). *Elephantopus spicatus* Juss. ex Aubl. (*Pseudelephantopus spicatus* (Juss. ex Aubl.) Rohr) is one of the most widely used cough remedies in middle America (Heinrich et al. 1998), and it is applied topically for skin infections. *Elephantopus mollis* Kunth is chewed for toothache relief (Sequeira 1994) while *E. scaber* L. is useful in the treatment of urinary problems, and extracts have been shown to be effective against carcinomas (Heinrich et al. 1998). *Vernonathura tweediana* (Baker) H. Rob. roots are used locally for treatment of fungal infections and skin irritations; an extract was found to be effective in inhibiting growth in eleven species of fungi (Portillo et al. 2001, 2005). *Vernonia scorpioides* Lam. extracts were shown to inhibit growth of *Penecillium* and *Aspergillis* (Freire et al. 1996). A variety of antimicrobial and analgesic properties were reported for various additional species of Brazilian Vernonieae (Lopes 1991). Among North American Indians, *Vernonia glauca* (L.) Willd. and *V. noveboracensis* (L.) Michx. were used by the Cherokee for pain relief, especially associated with menstruation and childbirth, to improve the blood and for loose teeth (Hamel and Chitoskey 1975). *Vernonia missourica* Raf. was used by the Kiowa for treatment of dandruff, as a candy, a dye plant, and for fiber (Vestal and Schultes 1939). *Vernonia fasiculata* Michx. was used as an analgesic for body aches and in ceremonies by the Yuchi (Jackson 2000).

ECONOMIC USES

Vernonieae species are used in the manufacture of a number of products benefited by epoxy oils and epoxy acids. The most widely cultivated species for production of naturally epoxidizing (non-volatile) oils and vernolic acid is the African species *Vernonia galamensis* (*Centrapalus pauciflorus* (Willd.) H. Rob.). Oils and resins are used to reduce emissions of volatile organic compounds in the manufacture of alkyd paints, as an additive to PVC, in the manufacture of plasticizers, polymers and coatings, and has cosmetic and pharmaceutical applications (Bhardwaj et al. 2000, 2007). *Vernonia anthelmintica* (*Baccharoides anthelmintica* Willd.) and *V. cinerea* (*Cyanthillium cinereum*) are also used in India to produce vernolic acid for commercial paints, plastics, coatings and additionally, from the latter species, soaps and emulsifying agents, animal feed and dietary supplements (Viswanathan and Singh 1996). *Vernonia volkameriaefolia* DC. (now *Monosis volkameriaefolia* (DC.) H. Rob. & Skvarla) has also shown to have high levels of epoxy acid (Siddiqi et al. 1984). The widely used *Vernonia amygdalina* (*Gymnanthemum amygdalinum*) is grown to produce an anticorrosive (Avwiri and Igho 2003). *Stokesia laevis* of eastern North America is also grown as a potential crop for production of epoxy acids (Callan and Kennedy 1995). The high concentration of fructans and fructose in the roots of the Brazilian *Chrysolaena herbacea* (Vell.) H. Rob. make it of potential commercial value in the production of high-fructose syrups and inulins (Vullo et al. 1991; De Carvalho and Dietrich 1993; De Carvalho M.A.M. et al. 1997, 1998; De Carvalho, M.G. 1999; Pessoni et al. 1999, 2005).

Centratherum punctatum and *Stokesia laevis* are used widely as ornamentals in the United States (USDA-GRIN, Germplasm Resources Information Network), http://www.ars-grin.gov). Several South African species are grown for their showy flowers that attract butterflies (Koekemoer, pers. comm.) and a number are also cultivated in Europe (Hind, pers. comm.).

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Chapter 29

Platycarpheae

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HISTORICAL OVERVIEW

Thunberg (1800) described the type species of *Platycarpha* as a thistle, *Cynara glomerata*, and mentioned its spiny pinnately divided leaves. Lessing (1831) did not think it belonged in the thistles and described the genus *Platycarpha* based on the Thunberg species. De Candolle (1836) placed *Platycarpha* in Vernonieae. Bentham moved *Platycarpha* from Vernonieae into a subtribe of its own in reestablished Arctotideae (1873a, b) and Hoffmann agreed (1890–1894). There it remained until Stix (1960) suggested that *Platycarpha* should be in Mutisieae based on pollen morphology. Robinson and Brettell (1973) put *Platycarpha* in Cardueae (thistles) based on the pollen's "… prominent complex columnar structure in the thickened rather smooth exine" and the lack of stomates on the corolla lobes; both characters are similar to what they found in Cardueae.

In the book *The Biology and Chemistry of the Compositae* (Heywood et al. 1977), Dittrich (1977), in his treatment of the thistles (Cardueae), rejected *Platycarpha* and returned it to Arctotideae without explanation. In the same volume, Norlindh (1977) reviewed Arctotideae and he excluded *Platycarpha* citing the evidence of Robinson and Brettell (1973).

The most recent classifications of Arctotideae (Bremer 1994; Karis 2007) accepted *Platycarpha* in the tribe but listed it as "unassigned to subtribe". Based on molecular and morphological data the clade has recently been proposed as a tribe: Platycarpheae. Furthermore, two of the species are placed in a new genus, *Platycarphella*, based on morphology (Funk and Robinson 2009).

PHYLOGENY

What are now Platycarpheae have always been recognized as distinct morphologically, however, they never really fit in the tribe Arctotideae. The analysis of the DNA sequence data showed that the three species form a monophyletic group on a long branch (Funk et al. 2004; Funk and Chan, unpub.) within the subfamily Cichorioideae. The placement of Platycarpheae within the subfamily differed slightly in the analyses of the nuclear and chloroplast DNA (see Chapter 12). The combined analysis produced results that placed Platycarpheae as the sister group to the Liabeae-Vernonieae clade, however, while the individual clades within the subfamily were present in all the parsimony trees, they collapsed into a polytomy in the bootstrap analysis. New markers are being added in an attempt to better resolve the relationships among the clades.

TAXONOMY

Tribe Platycarpheae V.A. Funk & H. Rob. in Compositae Newslett. 47: 25. 2009

Platycarpha Less. in Linnaea 6: 688. 1831 – Type: *Platycarpha glomerata* (Thunb.) Less.

Perennial herbs (Fig. 29.1), prostrate, acaulescent, stoloniferous, forming clonal mats or individual rosulate plants in close proximity, no milky sap. Leaves prostrate, radiating from central portion of plant, in 2–6 rings with oldest leaves and larger in the lowermost ring; blades oblanceolate, lanceolate, elliptic, or linear, varying in

Fig. 29.1. Species of Platycarpheae. **A** *Platycarpha glomerata* Less., note the spiny leaves, large primary and secondary heads (3–10 cm in diam., this one is 8 cm), and the long styles; **B** *Platycarphella carlinoides* (Oliv. & Hiern.) V.A. Funk & H. Rob., note the leaves flat on the ground and the large secondary head (2–10 cm in diam., this one 10 cm) with many small primary heads; **C** *Platycarphella parviflora* (S. Moore) V.A. Funk & H. Rob., note the small size of the plant, small secondary heads (1–2 cm diam., this one 2 cm), and the entire leaves. [Photographs: A, B, M. Koekemoer; C, V.A. Funk.]

length (1–35 × 0.5–11.0 cm), margins entire, dentate, or pinnatisect, adaxially green and mostly glabrous, with or without spines; abaxially with dense, white tomentum. Inflorescence sessile, one- to many-headed, grouped in a secondary head on a crown, secondary receptacle 2–10 cm in diameter. Heads subglobose to cylindrical, discoid, 3–25 mm in diameter. Involucral bracts (phyllaries) 7–40 in 3–5 series, lanceolate to linear, usually glabrous (some collections of *Platycarphella carlinoides* with tufts of tomentum at apices), outer bracts 6–20 × 1–5 mm, inner bracts becoming smaller and more slender with innermost bracts resembling pales; margins entire, apices acuminate. Disc florets 3–60, bisexual; corollas purple, mauve, lilac, or pink, occasionally white, varying in size from 8 to 23 mm long, lobes 3.0–3.5 mm long with glands on abaxial surface of apex of each lobe; tubes sparsely hispid at distal end; anthers purple, 4–13 mm long, tailed; styles lavender, varying in length, 9–29 mm long, in longer form (*Platycarpha*) the branches terete, with hairs nearly to tip, in shorter branches (*Platycarphella*) slightly tapered with hairs scarcely developed distally. Achenes 3- or 5-sided, dark. Pappus of 7–12 persistent white scales 2–6 mm long, apex acuminate.

There are two genera, *Platycarpha* (one species) from the Eastern Cape and KwaZulu-Natal of South Africa and *Platycarphella* (two species) from central South Africa to the highlands of Namibia. They can be distinguished by an impressive list of characters: pollen type, corolla and style length, primary and secondary head size and leaf type (Funk and Koekemoer, unpub.; Funk and Robinson 2009).

MORPHOLOGY

Perhaps the most interesting aspect of this tribe is its growth pattern. The secondary heads are the crown of the plant with the roots emanating from the base of the crown; the leaves are produced at the narrow circular perimeter. The heads are strongly attached and even embedded in the surface of the secondary receptacle. The crown is woody. The heads of any one secondary receptacle are of different ages, so while some are in flower, new small heads are forming at the base of old heads. In addition, once a secondary head is past flowering, a new crown can form with another secondary head. At other times, a stolon will form from below an old secondary head and grow some distance before developing a new secondary head. Thus, once an individual becomes established, it can spread over a large area by means of these rhizomes. The leaves usually lie flat on the ground and spread out around the central portion of the plant like the spokes of a wagon wheel, however, when crowded they arch in *Platycarpha*. In *Platycarphella* sometimes the secondary heads are close together and they push one another upward. The receptacles have narrow pales (receptacular bracts); the discoid heads have 3 to possibly 100 florets, the corollas are purple to pink and they are deeply divided; the anthers are tailed, and the styles have a small swelling just below the base of the style branches that is covered with small hairs; the achenes are only faintly ribbed, and the pappus is composed of 7–12 scales, 2–6 mm long.

Platycarpheae have recently been revised; for additional information see Funk and Koekemoer (unpub.) and/or Funk and Robinson (2009).

POLLEN

The pollen morphology of *Platycarphella parviflora* (Fig. 29.2E–H) and *P. carlinoides* (Fig. 29.2I–L) is identical. As described in greater detail elsewhere (Wortley, Funk and Skvarla, 2008), the pollen is echinate with spines approximately 1 μm in height and 2.5–3 μm across their bases and with more than 100 spines distributed over a smooth and minutely perforate surface. The apertures are tricolporate and occasionally syncolpate at the poles. In structure, the pollen is ecaveate (Figs. 29.2H, L) with an infratectum comprised of two distinct columellae layers separated by multilayered internal tecta. The outer layer consists of fine columellae and is approximately 1.2 μm in thickness; the inner columellae layer is over 2 μm in thickness and consists of thickened columellae that are prominently branched at the distal ends.

The pollen of *Platycarpha glomerata* (Fig. 29.2A–D) is in marked contrast to that of *Platycarphella parviflora* and *P. carlinoides*. The minutely perforate exine surface consists of distinct but irregularly arranged ridges separated by lacunar areas that somewhat resemble the lophate pattern common to pollen in Vernonieae but the grains are prenanthoid, with fused mura continuous around the colpus, bowtie-shaped, at waist fused across the pore dividing it into two pores. Spines and spine bases are somewhat greater than in *P. parviflora* and *P. carlinoides*. The apertures are tricolporate with surrounding ridges commonly obscuring the pore region. There is some structural similarity to *P. parviflora* and *P. carlinoides* in that the lower (inner) columellae are similarly thickened and distally branched (Fig. 29.2D); however, these branches appear to both support as well as form a finer (i.e., weaker) and less complex tectum. This is especially noteworthy in the lacunar areas.

According to Wortley et al. (2007), the *Platycarphella* pollen provides no evidence to link the species to any other group in the subfamily Cichorioideae; that statement was written prior to the discovery of the even more unusual pollen of *Platycarpha*.

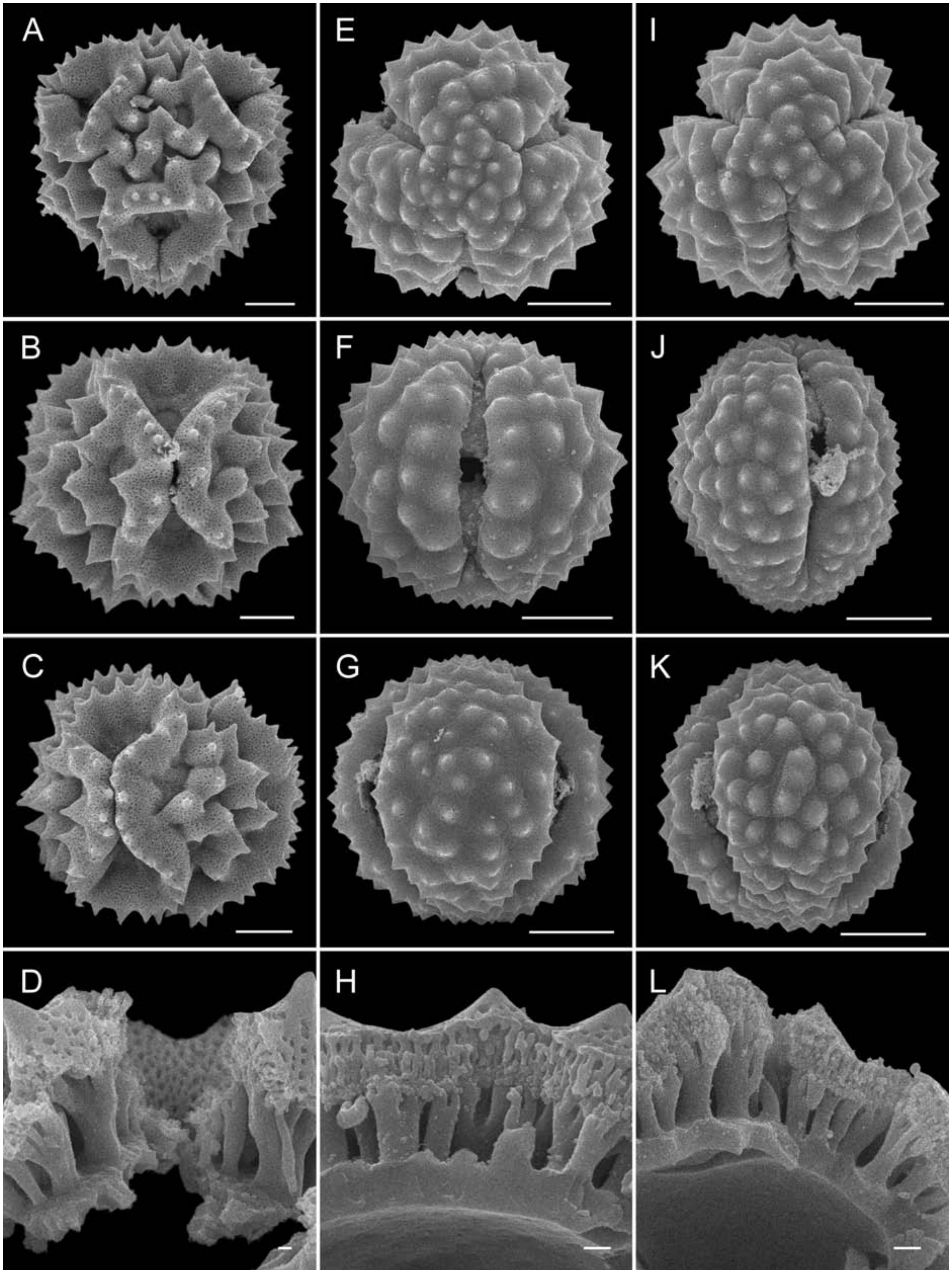

Fig. 29.2. Scanning electron micrographs of Platycarpheae pollen. **A–D** *Platycarpha glomerata* Less.; **E–H** *Platycarphella parviflora* (S. Moore) V.A. Funk & H. Rob.; **I–L** *Platycarphella carlinoides* (Oliv. & Hiern.) V.A. Funk & H. Rob. **A, E, I** polar view; **B, F, J** apertural view; **C, G, K** lateral view; **D, H, K** fractured grains. Scale bars: whole grains = 10 µm; fractured grains = 1 µm.

CHROMOSOME NUMBERS

There are no known chromosome counts for members of Platycarpheae.

CHEMISTRY

The chemical compounds of two species have been sampled. Bohlmann and Zdero (1977) reported that *Platycarpha glomerata* had five thiophenes and a diol that were isolated from roots, and two germacranolides were isolated from aerial parts, and in Zdero and Bohlmann (1989) they reported that "The chemical investigation of *P. glomerata* gave in addition to thiophenacetylenes, typical of *Berkheya*, some germacranolides." Their examination of aerial parts of *Platycarphella carlinoides* (Oliv. & Hiern.) V.A. Funk & H. Rob. gave the ent-kaurene derivatives 1, 2, 3a and 4–10, the nor-kaurenes 13–15, the thiophene derivatives 16, ent-16β-hydroxy-kaurane-19-oic acid and the germacranolide 17. The high concentration and the degree of variation in the diterpenes in *P. carlinoides* may indicate a relationship to *Atractylis* (tribe Cardueae, subtribe Carlineae) where nor-kaurene derivatives and their glycosides are present, though in these compounds a 4-methyl group is missing. Diterpenes link *Platycarpha* to *Corymbium* (not in Cichorioideae) and exclude a placement in Vernonieae, where so far no diterpenes or thiophenes such as 16 have been isolated. The latter have so far only been reported from *Berkheya* (Arctotideae) species, which also contain germacranolides. Due to these findings, Zdero and Bohlmann (1989) concluded that the results supported the proposed position of Platycarpheae [*Platycarpha*] intermediate between Arctotideae and Cardueae. In summary, the chemistry is no more helpful than the molecular or pollen data at placing this unique clade.

BIOGEOGRAPHY

The members of Platycarpheae are native to central and southern Namibia and South Africa. The monotypic *Platycarpha* is found in the Eastern Cape and KwaZulu-Natal provinces of South Africa. *Platycarphella* has two species in the South African provinces of The Free State, Mpumalanga, Northern Cape, and Northwest Province and in Namibia (Funk and Koekemoer, submitted). The fact that this tribe is endemic to southern Africa strengthens the concept of an African origin for the Cichorioideae (see Chapter 23).

BIOLOGY AND ECOLOGY

The tribe Platycarpheae is found from the low elevations in the coastal areas of South Africa up to 1800 meters in the high central plateau of Namibia. Its members often grow in open disturbed areas with rocky and sandy soil, in full sun. All of the taxa are apparently unpalatable for grazing animals.

Nothing definite is known about the pollination of this genus, and the only records are photographs of several populations with ants crawling on them. Moreover, there are large nectaries on the abaxial surface at the apex of the lobes of the corollas which may be an attractant for pollinators (Funk and Koekemoer, unpub.).

All three species are allopatric and flower at different times during the year. The diversificaiton within the tribe may be a response to the most recent uplift of the Great Escarpment, which isolated what is now *P. glomerata* around 5 Ma (Linder, pers. comm.).

ETHNOBOTANY

Platycarpha glomerata has several common names in KwaZulu-Natal: 'imbozisa' (Gordon-Gray 2003), 'inyathelo' and 'imbozisayabesuthu', and it is believed to have some magical powers; a concoction of the whole plant (called 'intelezi') is sprinkled in the yard around a homestead to protect against lightning strikes (pers. comm. Mkhipheni Ngwenya, Zulu Botanical Knowledge Project). Raymond (2002) and Hutchings (1996) report the Zulu name as 'imboziza', and Pooley (1998) cites it as 'usiphahluka'. Plant infusions are known to be used as sprinkling charms against evil spirits (Arnold et al. 2002). *Platycarpha* is apparently not eaten by livestock and feeding tests were negative (Watt and Breyer-Brandwijk 1962), which agrees with our field observations (for all three species): it can be found in pastures and roadsides where all palatable plants have been consumed.

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Chapter 30

Moquinieae

Harold Robinson

HISTORICAL OVERVIEW

A member of Moquinieae first entered the taxonomic record as *Conyza racemosa* Spreng. (1826) and was first recognized at the generic level by Lessing (1832) under the later homonym *Spadonia*. The same species was redescribed as *Baccharis avicenniaefolia* by De Candolle (1836). It was again recognized at the generic level, under the name *Moquinia*, by De Candolle (1838), based on *Conyza racemosa* Spreng. *Moquinia* was considered congeneric with the Mutisian *Gochnatia* Kunth in H.B.K. by many authors from Bentham (1873) through the earlier works of Cabrera (1950, 1959). Later, Cabrera (1969) redelimited *Moquinia* as one species, separate from *Gochnatia*, describing, and in part, illustrating the differences in the stamens, styles and pollen. Cabrera (1969) offered no comment on any tribal distinction from *Gochnatia*. Robinson (1979) established the new genus *Pseudostifftia*, without reference to or recognition of relationship to *Moquinia*. *Pseudostifftia* was initially placed in Vernonieae, although the style and pollen were considered anomalous in that tribe (Robinson and Marticorena 1986). *Moquinia* (Figs. 30.1–30.2) and *Pseudostifftia* (Fig. 30.3) were first placed together and monographed by Gamerro (1990) under the one genus *Moquinia* in Vernonieae. A distinct tribe was described by Robinson in 1994, and maintained in Robinson (2007) with recognition of two genera.

PHYLOGENY

Moquinieae have most recently been placed in or near Vernonieae, first as a genus (Robinson 1979), then as a subtribe (Robinson et al. 1989), and finally as a segregated tribe (Robinson 1994). DNA sequences (see metatree, Chapter 44) confirm a position close to but outside of Vernonieae. Using the principle of definability, the structure of the style and pollen mandates recognition of Moquinieae as a tribe separate from Vernonieae.

TAXONOMY

Tribe Moquinieae H. Rob. (1994) [Tribe Vernonieae, Subtribe Pseudostifftiinae H. Rob, R.M. King & F. Bohlmann (1989)] (Figs. 30.1–30.4)

Monoecious or gynodioecious, moderately branched shrubs or small trees mostly 1.5–5.0 m tall. Stems not fistulose. Leaves alternate, short-petiolate, blades coriaceous, obovate, cuneate, margins entire, apices rounded to slightly retuse, surfaces with glandular dots, undersurfaces whitish to pale-yellowish tomentose or lepidote, venation pinnate. Inflorescence terminal, pyramidally thyrsoid, branches racemiform or ending in corymbiform clusters of heads; peduncles 2–3 mm long. Heads homogamous; involucre narrowly campanulate, bracts in 4–5 series, gradate, inner bracts deciduous; receptacle epaleaceous. Florets 1–5 in a head; corollas regular, lavender to purple, narrowly funnelform, glanduliferous outside, throat short, lobes 5, linear, smooth; anther thecae calcarate, with short tails; endothecial cells with broad longitudinal median band usually narrowed at each end to one point; apical appendages 3–4 times as long as wide, with cell walls not thickened, anthers sometimes aborted in functionally female florets. Style base broadly

Fig. 30.1. *Moquinia racemosa* (Spreng.) DC. **A** habit; **B** head; **C** corolla, showing tips of anthers and style; note deeply divided lobes; **D** corolla in long section, one lobe removed, showing anthers and style; **E** style, showing basal node, swollen upper shaft, showing scabrid surface consisting of short sweeping hairs on upper shaft and backs of lobes, and undivided stigmatic surface inside of branches; **F** anther, showing long calcarate and shortly tailed bases, and apical appendage; **G** achene with setulae and capillary pappus. [Drawing by Alice Tangerini.]

abruptly noduliferous, upper part of style becoming broadened, upper shaft and outer surface of branches scabrid with short sweeping hairs; branches narrowly triangular, shorter than scabrous part of upper style shaft, with inner surface completely covered by stigmatic papillae. Achenes densely setuliferous, 10–17-costate, idioblasts obvious or obscure, raphids obscure, phytomelanin lacking, carpopodia annuliform to stopper-shaped, with quadrate cells in 3–17 series, cell walls thickened; pappus of many capillary bristles in ca. 2 series, outer setae irregularly shorter.

The two genera have a generally similar habit (Figs. 30.2.A, 30.3A) and leaf form (Figs. 30.2C, 30.3B), but differ strongly in form of the inflorescence (Figs. 30.1A, 30.2A, B, 30.3B) and number of florets in the heads.

Style. — (Figs. 30.1C–E, 30.3C–F) The distal shaft of the style is swollen and the branches are short with a continuous stigmatic surface inside. The sweeping hairs are short and spiculiform. The swollen and spiculiferous distal style shaft is generally like many in Mutisieae, Arctotideae and Platycarpheae, but differs from the slender style with long sweeping hairs found in Vernonieae, Liabeae, Lactuceae, and Eremothamneae. The resemblance of the style to Arctoteae and various Mutisian types is not complete. The transition between the lower style shaft and the scabrid upper portion of the shaft is more gradual, not abrupt.

POLLEN

Grains are spherical, tricolporate, echinate with long spines, not lophate or sublophate, exine noncaveate with solid bacula distributed randomly, not grouped or

Fig. 30.2. *Moquinia racemosa* (Spreng.) DC. (Brazil, Bahia, Morro do Chapéu). **A** inflorescence; **B** inflorescence showing flowers; **C** leaves. [Photographs, N. Roque.]

positioned directly under the spines (Fig. 30.4). The shape of the grains and the size of the spines in Moquinieae differ from the usually prolate and often subpsilate grains of *Gochnatia* and Mutisieae. The noncaveate condition differs from the caveate form in most members of the subfamily Asteroideae. The nonlophate and nonsublophate condition differs from the form in almost all Vernonieae. The random distribution of the bacula is different from the condition in Vernonieae and Liabeae, and the solid form of the bacula is different from the form in Liabeae.

CHEMISTRY

Guaianolides have been reported by Bohlmann et al. (1982) and Bohlmann and Jakupovic (1990).

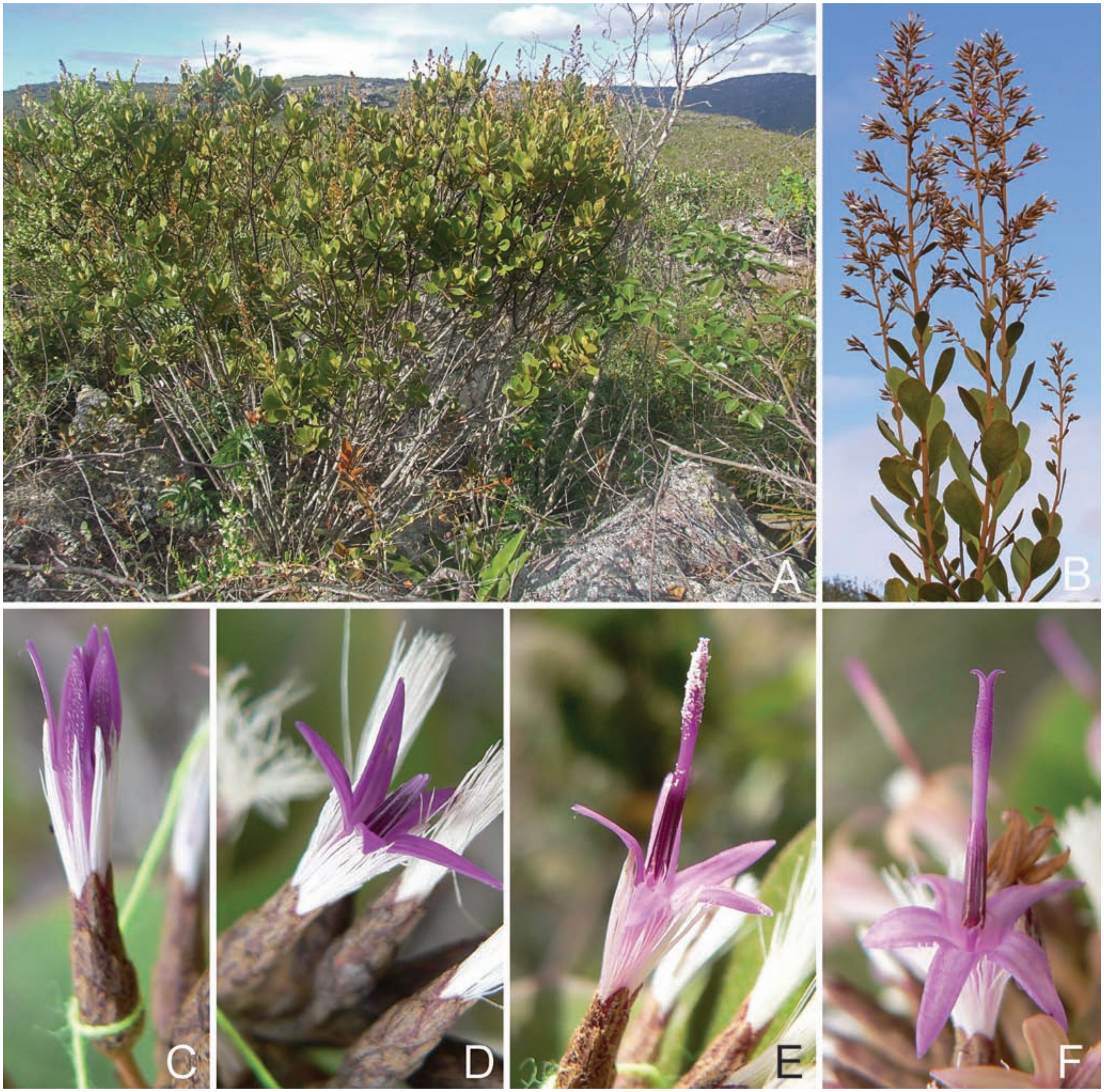

Fig. 30.3. *Pseudostifftia kingii* H. Rob. (Brazil, Bahia, Mucugê). **A** habit; **B** inflorescence architecture; the series of photos in **C–F** show the development of the male and female flowers (J.H. Souza, pers. comm., unpub.). [Photographs: A, B, J.H. Souza; C–F, A. Morse.]

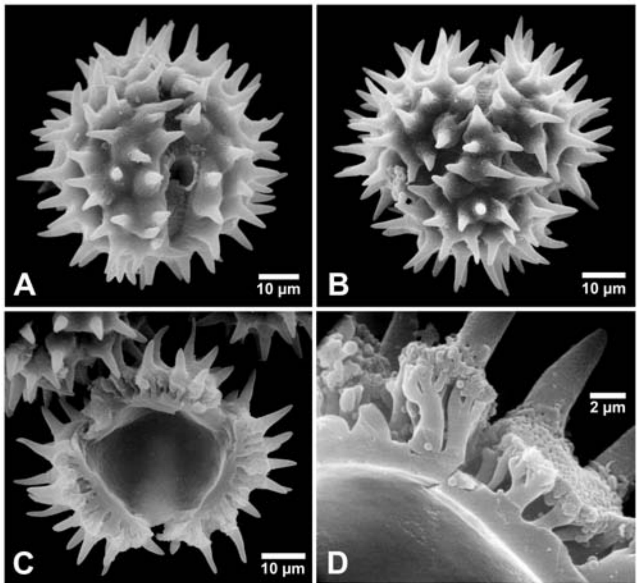

Fig. 30.4. SEM of *Pseudostifftia kingii* H. Rob. pollen (*R.M. King et al. 8145*, Brazil). **A** colpar view; **B** polar view; **C** cross section of pollen grain; **D** broken grain showing irregularly distributed bacula.

BIOGEOGRAPHY

The relationship of Moquinieae to Vernonieae seems obvious. The geographic distribution of Moquinieae is clearly Brazilian, but the style structure is unlike that of any other New World Cichorioideae, and it is more like African members of the subfamily. The oldest members of Vernonieae, to which DNA studies most closely relate to Moquinieae, also occur in Africa and the Indian Ocean area. On the basis of such evidence, the closest relationship of the New World Moquinieae seems to be with Old World Cichorioideae. Biogeography trees can be found in Chapter 44.

Very little else is known about the tribe, and there are no chromosome counts.

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Chapter 31

Heterolepis: an unplaced genus

Vicki A. Funk and Per Ola Karis

HISTORICAL OVERVIEW AND MORPHOLOGY

The three species of *Heterolepis* Cass. are found in southern South Africa and especially in parts of the Succulent Karoo and almost throughout the Cape Floristic Region (CFR; Linder 2003). One of the species, *H. aliena* (L. f.) Druce, forms a small shrub covered with large yellow heads and is often cultivated. The genus has been moved from tribe to tribe. Cassini (1816, 1821) described *Heterolepis* and placed it in the tribe Arctotideae. Lessing (1832) treated the whole tribe Arctotideae along with Calenduleae and some Senecioneae, as part of a large Cynaroideae. Bentham (1873) reestablished Arctotideae but he placed *Heterolepis* in Inuleae; Hoffmann (1890–1894) followed Bentham. Robinson and Brettell (1973a) returned *Heterolepis* to Arctotideae, and Norlindh (1977) placed it in the subtribe Gorteriinae. Merxmüller et al. (1977) in his treatment of Inuleae agreed that *Heterolepis* did not belong in that tribe and suggested a placement in Mutisieae, but nearly everyone has left it in Arctotideae.

In truth, *Heterolepis* never fit very well in Arctotideae, and Bremer (1994) pointed out that it did not have all the diagnostic characters of the subtribe Gorteriinae, where it was placed by Norlindh (1977). In comparison to both subtribes of Arctotideae, there is little reason to include it. It has none of the putative synapomorphies of Gorteriinae, for instance, it lacks latex, the involucral bracts are only slightly connate, the receptacle is not deeply alveolate, it has female ray florets where the lamina is 3-toothed and 4-veined, and finally it has a pappus of bristle-like scales. In the subtribe Arctotidinae the anthers are without exception ecaudate, while in *Heterolepis* the anthers are caudate with barely branched tails (somewhat similar to those of the *Berkheya* clade of Gorteriinae). The anther apical appendages of *Heterolepis* are soft but longer and quite unlike the shorter but likewise soft ones of Arctotidinae. Also *Heterolepis* has anthers with a polarized endothecium, or many cells have a plate but no polarized pattern, which is similar to the endothecium in some species of the *Berkheya* clade of Gorteriinae. In contrast, Arctotidinae have a consistently radial endothecium.

Bremer's (1994) morphological cladistic analysis placed *Heterolepis* as the sister group to the *Platycarpha*-Arctotidinae clade or in a trichotomy with the two main subtribes depending on the outgroup used. Based on this analysis Bremer decided to list *Heterolepis* as belonging to Arctotideae but unassigned to subtribe, and the same approach was followed by Karis (2007). In Funk et al. (2004) and Funk and Chan (2008) *Heterolepis* was sometimes linked with the base of Gorteriinae but with very weak support.

It is interesting to note that Ahlstrand (1992) studied the embryology of species from both subtribes as well as *Heterolepis aliena* and *H. peduncularis*. He found that while representatives of Arctotidinae and Gorteriinae all shared a possibly plesiomorphic monosporic *Polygonum* type of embryosac development, *Heterolepis* species displayed a bisporic embryosac development. All other examples of bisporic embryo sac development are confined to the subfamily Asteroideae (Asplund 1978; Ahlstrand 1992). However, *Heterolepis* has other symplesiomorphic morphological characters that demonstrate its affinity to groups outside of Asteroideae, such as deeply lobed disc corollas, an entire stigmatic surface, and a style with a ring of longer sweeping hairs below the bifurcation. In addition, *Heterolepis* also lacks the apomorphic length mutation of the *rbcL* gene (Karis, pers. obs., sequence from Forest et al. 2007), and which is found in all Asteroideae (Bremer 1994).

PHYLOGENY

The subtribes Arctotidinae and Gorteriinae as currently defined are monophyletic. In order to accomplish this, three taxa (nine species) had to be removed: *Heterolepis* and the tribes Eremothamneae, and Platycarpheae. The most recent analysis has not resolved the placement of *Heterolepis* within the subfamily (Chapter 23).

TAXONOMY

Heterolepis Cass. in Bull. Sci. Soc. Philom. Paris 1820: 26. 1820, nom. cons. [information taken from Karis 2007; Hermann et al. 2000, and pers. obs.] (Fig. 31.1)

Small, rounded, sometimes sprawling, densely leafy sub-shrubs to ca. 0.5 m tall with woody rootstocks; sometimes scented. Leaves linear-oblong, 15–40 mm long, ericoid; apex linear to acute, base tapering, margins entire or apically dentate, abaxial surface densely woolly, adaxial surface glabrous. Heads pedunculate, radiate, up to 6 cm in diameter. Involucral bracts in 2–3 rows, somewhat connate at base, outer lanceolate, foliaceous, acute; inner bracts rounded-truncate, apically scarious and laciniate; receptacle areolate. Florets yellow; ray florets female, fertile, generally with staminoides, with a filiform lobe ventrally in the sinus of the tube, lamina apically 3-lobed; disc florets bisexual, fertile, corolla deeply 5-lobed; anthers calcarate, shortly caudate, with a long collar of reinforced cells, apical appendages soft, oblong; styles slender, style branches short; slightly thickened below the style branches, sweeping hairs acute, somewhat longer in a ring below the bifurcation. Achenes small, ca. 3 mm long, oblong-obovoid, densely sericeous with twin hairs and without ribs. Pappus of 1–10 yellow-brown, stout, subulate, bristle-like, marginally barbellate or subplumose scales of varying length up to 10 mm, usually in two rows (Fig. 31.1).

Heterolepis is a well-defined genus confined to South Africa. *Heterolepis aliena* is easily recognizable from a distance by the large number of flowering heads that almost completely cover the plant (Fig. 31.1B), and the pom-pom like shape of the older heads is typical for all three species (Fig. 31.1A). On a more detailed scale it can be identified by its ray florets, which generally have staminodes and a filiform lobe ventrally in the sinus of the tube (Fig. 31.1D), its pappus of 1–10 irregular length bristle-like scales (Fig. 31.1A insert), and its small achenes covered with dense white twin hairs (Fig. 31.1A insert).

The genus name *Heterolepis* is derived from the Greek *hetero* meaning dissimilar and *lepis* a scale.

POLLEN

Spherical, ca. 30–35 μm in diameter (dry), tricolporate, echinate with spines evenly and deeply separated, tips of spines solid, sides with distinct microperforations; internally nearly totally caveate, with sparse slender, sometimes branched columellae under sides of spines, outer exine with well-developed layer of columellae with distinct underlying inner tectum. Spines fistulose under apex, fistula bordered by a few enlarged columellae (Fig. 31.1E, F. Additional photos and comments on the pollen can be found in Wortley et al. (2008).

CHROMOSOME NUMBERS

The only count reported is $x = 6$ (Strother et al. 1996), probably $2n = 12$. The TROPICOS database reports this number and reference as does the Compositae chromosome website maintained by Watanabe (http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html). There is a report of $x = 10$ in Hermann (2000), but that appears to be an error as we have searched all of the listed references and can find only the Strother et al. count.

CHEMISTRY

We found no information on the chemistry of *Heterolepis.*

BIOGEOGRAPHY

Heterolepis aliena occurs on rocky sandstone slopes, in crevices and on outcrops from the Cedarberg Mountains to the Witteberg and Hermanus (pers. obs.; Goldblatt and Manning 2000). It is most often found on steep, sunny, north or northeast-facing slopes or well-drained, rocky outcrops on shallow soils, in dry fynbos as well as in areas that receive high rainfall, such as Franschhoek. *Heterolepis peduncularis* DC. grows on plains near rocky slopes, has smaller heads on longer peduncles than *H. aliena*, and it is scented. It has a wider distribution, but it is less common. The third species, *H. mitis* DC. occurs in the Eastern Cape, but it has not been collected for a considerable time.

Fig. 31.1. *Heterolepis aliena* (L.f.) Druce. **A** head in late flower/early fruit, note "pom-pom" like appearance of head; **insert** achene, note small size, white pubescence, and irregular bristle-like pappus; **B** plant in full flower; **C** lateral view of heads and narrow leaves; **D** close-up of flowering head; **E** internal view of pollen, note that it is nearly totally caveate, with sparse slender, sometimes branched columellae under sides of spines; **F** external view of pollen. [Photographs: A–D, A. Notlen; E, F, from Wortley et al. 2008.]

ECOLOGY, CONSERVATION, HORTICULTURE

Along with members of both subtribes of Arctotideae, *Heterolepis* grows in the succulent karoo and CFR. It is xeromorphic with rather narrow leaves (Fig. 31.1A, C), a situation paralleled in many plant groups inhabiting vegetation in regions with Mediterranean climate.

Victor and Dold (2003) list *Heterolepis mitis* DC. as a plant that is "Near Threatened (NT)" in that it does not meet the criteria for being listed as threatened with extinction but could qualify in the future.

Heterolepis aliena (Rock Daisy or Rotsgousblom) makes a very attractive garden plant and if one can mimic the hot, dry, sunny, well-drained habitat it normally inhabits, it will thrive almost anywhere although standing water should be avoided. It will propagate from seed and from cuttings (Notten 2007).

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Chapter 32

Corymbieae

Bertil Nordenstam and Vicki A. Funk

HISTORICAL OVERVIEW AND TRIBAL RELATIONSHIPS

The generic name *Corymbium* was employed by Linnaeus in *Corollarium Generum Plantarum* (Linnaeus 1737), *Hortus Cliffortianus* (Linnaeus 1738), and *Genera Plantarum* ed. 2 (Linnaeus 1742) and ascribed to Gronovius (in Burman's *Rariorum Africanarum Plantarum*, 1738–39). With valid publication in *Species Plantarum* (Linnaeus 1753) the official name became *Corymbium* L. Linnaeus placed the genus in his Syngenesia Monogamia together with *Jasione*, *Lobelia*, *Viola* and *Impatiens* on account of the unusual capitular and floral morphology, but in his outlines of a natural system he placed the genus with the other members of Compositae. Thus in the *Fragmenta Methodi Naturalis*, which appeared as an appendix in the Paris edition of the *Genera Plantarum* (1743), he placed *Corymbium* in "XXI Ordo", comprising all genera that he would later refer to as Compositae.

Cassini (1818, 1829) referred *Corymbium* without hesitation to Vernonieae, where it has since traditionally been placed (Lessing 1832; De Candolle 1836; Harvey 1865; Bentham 1873a, b; Hoffmann 1890–1894; Jones 1977; Weitz 1989, 1990), although the genus has never fit comfortably in that tribe. Bentham (1873b) noted that the pistil of *Corymbium* has a distinct ovary that is long, cylindrical, and densely hirsute, and very short style branches, while in typical Vernonieae the ovary is not densely hirsute and the style branches are long and slender (Jones 1977). Bolick (1978) also noted that *Corymbium* pollen differed from that of other Vernonieae. Based on significant differences in sesquiterpene lactones and diterpenes, Bohlmann and his collaborators (Zdero and Bohlmann 1988; Bohlmann and Jakupovic 1990) suggested *Corymbium* be removed from Vernonieae. Bremer (1994) in a cladistic analysis of Compositae found *Corymbium* morphologically anomalous in Vernonieae and removed it from the tribe. In his treatment *Corymbium* was placed in subfamily Cichorioideae but without a tribal assignment. Similarly, Robinson (1996) excluded *Corymbium* from Vernonieae based on the chemistry and morphology, but proposed no other tribal placement.

Molecular data (Panero and Funk 2002, 2008) reflect the morphological, palynological and chemical disparities noted by earlier workers (described above). Sequence information showed that *Corymbium* did not belong in any existing tribe or subfamily and so was placed in its own tribe, Corymbieae, and its own subfamily, Corymbioideae (Panero and Funk 2002) (see the metatree in Chapter 44). In addition, *Corymbium* was strongly supported as the sister group to the entire subfamily Asteroideae which contains 65% of the genera within the family. The removal of *Corymbium* from Vernonieae has been accepted by the systematic community (Nordenstam 2007) and the recent molecular phylogeny of Vernonieae by Keeley et al. (2007) did not include this genus.

TAXONOMY

Although reported on in the 1600s (Breynius 1680; Plukenet 1696), the first valid publication of the genus was by Linnaeus (1753) who recognized a single species, *Corymbium africanum* L. Later Linnaeus (1767a, b) distinguished two species, *C. scabrum* L. and *glabrum* L., and abandoned the name *africanum*, which is not in agreement with present rules of nomenclature. The first taxonomic revision after Harvey (1865, with seven species) was published by Markötter (1939), who accounted for twelve species. Jones (1977) stated the number of species to be seventeen. In the latest revision by Weitz (1989, 1990) nine species, four subspecies and five varieties are recognized.

Fig. 32.1. *Corymbium glabrum* L. var. *glabrum*. Note the narrow leaves with parallel veins, the densely hirsute ovary, and the single floret per head. [Illustration (as *C. nervosum* Thunb.) by Ethel Dixie and Joseph Pohl in Marloth (1932: pl. 55).]

Tribe Corymbieae Panero & Funk (2002)

Scapose perennial herbs with a stout, silky-hairy rhizome. Leaves alternate, mainly rosulate, sessile, entire, linear-lanceolate to narrowly elliptic-oblong, flat or conduplicate, parallel-veined, more or less coriaceous, sometimes cartilaginous or herbaceous, acute to acuminate, narrowing toward the base, glabrous or pubescent, sometimes glandular; cauline leaves gradually smaller. Capitula pedunculate or rarely sessile, several to many in corymbs to panicles terminating a stout erect bracteate scape, discoid, single-flowered. Involucre cylindrical, calyculate; involucral bracts 2, enclosing the floret, narrowly oblong to lanceolate, flat or keeled, 3-nerved, glabrous or glandular, sometimes scabrid, often with a purplish tinge, apically 2–3-fid or fimbriate; outer bracts 2 or 3, short. Receptacle flat, naked. Florets hermaphroditic; corolla 5-lobed, pink to purplish or white; corolla lobes linear to oblong, spreading, apically cucullate and dorsally papillate. Stamens 5; anthers tetrasporangiate with blackish thecae, shortly sagittate; apical appendage reduced. Style bifurcate with linear branches; style branches and uppermost part of shaft hairy. Achenes narrowly oblong, somewhat compressed, densely pubescent. Pappus of basally connate short scales and/or discrete fine bristles.

Corymbium is obviously a well-defined genus without close relatives. At first sight the plants may give a monocotyledous impression. They are perennial tufted herbs with a fibrous rhizome covered by silky hairs. The rosulate, entire, linear to lanceolate leaves are parallel-veined (Figs. 32.1, 32.2). The narrow capitulum consists of two involucral bracts enclosing the single floret, which is white, pink or purplish, never yellow.

POLLEN

The pollen grains of *Corymbium* are caveate, in contrast to those of Vernonieae (Bolick 1978). A caveate exine structure is commonly found in subfamily Asteroideae but only occasionally in Cichorioideae (Nordenstam and El-Ghazaly 1977; Skvarla et al. 1977; Robinson and Marticorena 1986).

CHROMOSOME NUMBERS

The basic chromosome number is estimated to be $x = 8$, based on a single count of $2n = 16$ in *C. congestum* E. Mey. ex DC. (Weitz 1989).

Fig. 32.2. *Corymbium*. Note the single-flowered heads and grass-like leaves. **A, B** *C. glabrum* L. (South Africa); **C** *C. laxum* Compt. subsp. *laxum* (South Africa, Cedarberg Tafelberg); **D** *C. africanum* L. (South Africa). [Photographs: A, B, N. Bergh; C, B. Nordenstam, *Nordenstam 9607*; D, J. Manning.]

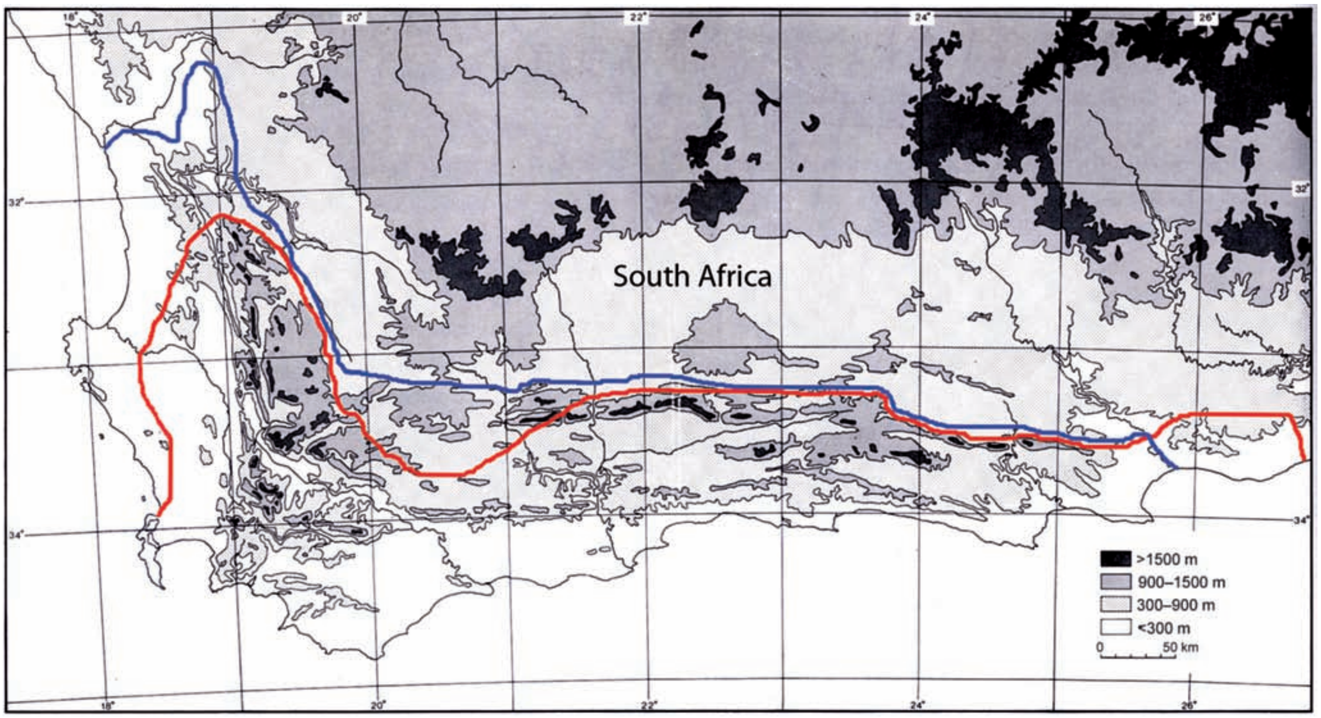

Fig. 32.3. Distribution of the genus *Corymbium* (red) and range of the Cape Floristic Region (blue). [Compiled from data in Weitz (1989) and Goldblatt and Manning (2000).]

CHEMISTRY

Corymbium possesses macrolide diterpenes and lacks sesquiterpene lactones, by these characters differing markedly from Vernonieae (Zdero and Bohlmann 1988; Bohlmann and Jakupovic 1990; Alvarenga et al. 2005).

BIOGEOGRAPHY

The distribution of *Corymbium* is confined to the southwestern and southern Cape Province and coincides remarkably well with the range of the Cape Floral Kingdom, or Cape Floristic Region of South Africa (Fig. 32.3). The habitats are poor sandy soils of Table Mountain Sandstones and coarser soils derived from granitic and phyllitic formation (Bokkeveld and Malmesbury series), sometimes clayey soil or even marshes (Weitz 1989). The members of the genus are found from sea level up to 1850 m in the Cedarberg and the mountains of Ceres and Worcester districts. The complete metatree showing the position of *Corymbium* can be found in Chapter 44.

BIOLOGY

Corymbium species produce copious nectar, which has rendered them the vernacular name "heuningbossie", although this name is used also for other nectar-bearing plants (Smith 1966). "Plampers" is another, more unequivocal name given to *Corymbium* species (Smith 1966). Bees, wasps, beetles and ants are reported as visitors and likely pollinators (Weitz 1989). It has been reported that the species of this genus flower during the first few years after fire. Fire adaptation is a common phenomenon in the Cape flora (cf. e.g., Linder and Ellis 1990; Schutte et al. 1995; Cowling et al. 1996; Campbell and Van der Meulen 2004).

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Section III Part 4

Asteroideae

Chapter 33

Introduction to Asteroideae

Pieter B. Pelser and Linda E. Watson

INTRODUCTION

Asteroideae are comprised of ca. 15,500 species (over 60% of the species in the family) placed in ca. 1229 genera (over 70%) and 20 tribes (approximately 60%), and is the largest subfamily of Compositae (Table 33.1). It is well characterized by morphological and molecular characters (reviewed by Bremer 1994). The flower heads of Asteroideae can be heterogamous and then radiate or disciform, or homogamous and discoid. The central florets (disc florets) are usually actinomorphic and perfect (hermaphrodite) or rarely male, whereas the marginal florets are radiate or actinomorphic and most commonly female. The corolla lobes of the disc florets are typically short. The anthers mostly have thecae that do not extend below the insertion of the filament (ecalcarate) and often lack a tail of sterile cells at their base (ecaudate). The style arms frequently have two adaxial bands of stigmatic surface separated by a sterile zone. The columellae in the pollen wall are usually partly separated from the foot layer (caveate), although most Anthemideae have ecaveate pollen. Latex is only rarely produced. In addition to these morphological characters, Asteroideae are characterized by a duplication in the *rbcL* region of the plastid genome (Kim et al. 1992).

THE DELIMITATION OF ASTEROIDEAE AND ITS PHYLOGENETIC POSITION

It is only fairly recently that Asteroideae have been recognized in its current form. In the 1960s and 1970s the notion of the existence of two tribal alliances emerged in a series of papers by, amongst others, Carlquist (1961: 135–140, 1976), Poljakov (1967), Robinson and Brettell (1973b), and Wagenitz (1976). Carlquist (1976) formally recognized these alliances as subfamilies Cichorioideae and Asteroideae. He considered Eupatorieae a member of Cichorioideae. Wagenitz (1976), however, correctly pointed out that, in contrast to traditional views (e.g., Cassini 1818; Lessing 1832; Bentham 1873a; Cronquist 1955), Eupatorieae was only distantly related to Vernonieae (now placed in Cichorioideae sensu Bremer 1996) and assigned Eupatorieae to his "Group 2" of Asteroideae, which otherwise conforms to Carlquist's delimitation of the subfamily. Similarly, the assumed close relationship between species of Liabeae and Senecioneae (e.g., Bentham 1873a, b) did not pass the test of time as they also proved to belong to different subfamilies.

Although the delimitation of Cichorioideae changed markedly (Bremer 1996) after phylogenetic analyses showed it to be a paraphyletic assemblage (Bremer 1987; Jansen et al. 1988; Palmer et al. 1988; Karis et al. 1992; Kim and Jansen 1995), Asteroideae were proven to be a well-supported monophyletic group (Jansen et al. 1988, 1990; Kadereit 1989; Bremer and Jansen 1992; Bremer 1994; Kim et al. 1992; Panero and Funk 2008) and largely retained its original circumscription. DNA sequences of the plastid genome indicate that *Corymbium* from the Cape region of South Africa is sister to Asteroideae (Panero and Funk 2002, 2008; see metatree in Chapter 44). Some authors prefer to place *Corymbium* in a separate subfamily (Corymbioideae), whereas others include it in Asteroideae (Jeffrey 1995, 2007a, c) with which it shares caveate pollen (Nordenstam 2007) and ecaudate anthers (Panero and Funk 2002). *Corymbium* is, however, different from most, but not all, members of Asteroideae in having disc florets with relatively large corolla lobes (Nordenstam 2007) and slightly calcarate anthers (Panero and Funk 2002).

Plastid data place the clade formed by Corymbioideae and Asteroideae sister to Cichorioideae sensu Bremer (1996) (Panero and Funk 2008). The tribes currently included in Asteroideae are listed in Table 33.1.

TRIBAL DELIMITATION

A recent revision of the tribal delimitation of Asteroideae, mainly on the basis of the results of phylogenetic analyses of DNA sequence data (Baldwin et al. 2002; Panero and Funk 2002, 2008; Anderberg et al. 2005; Cariaga et al. 2008), resulted in the recognition of 20 tribes in the subfamily (Table 33.1). Tribes Anthemideae and Astereae have seen relatively few changes in their circumscription since they were first described. After some debate (reviewed in, e.g., Robinson and Brettell 1973b; Watson et al. 2000; Oberprieler et al. 2007), *Cotula* and *Ursinia* are now well-accepted members of Anthemideae (Chapter 38). *Geissolepis*, *Isoetopsis*, *Novenia*, *Olivaea*, *Plagiocheilus*, *Printzia*, *Rigiopappus*, *Sheareria*, and *Welwitschiella* were added to traditional Astereae (Bayer and Cross 2002; Nesom and Robinson 2007; Chapter 37). In contrast to Anthemideae and Astereae, the small tribe Calenduleae has been subjected to many changes in its delimitation. Although recognized as a tribe early on (Cassini 1816), its species have also been placed in Astereae, Cynareae, and Senecioneae (Lessing 1832; De Candolle 1836–1838; Harvey 1865; Cronquist 1955; Anderberg et al. 2007), and several genera have been erroneously placed in Calenduleae (Chapter 35). Until Nordenstam presented a new delimitation of Senecioneae at the Reading symposium in 1975 (Nordenstam 1977), Senecioneae was a heterogeneous assemblage, which traditionally included, amongst others, genera now placed in Calenduleae, Helenieae, and Heliantheae (e.g., Lessing

Table 33.1. Asteroideae tribes and their approximate number of genera and species, and general distribution.

Tribe	No. of genera	No. of species	Distribution
Senecioneae (Chapter 34)	150	3000	Worldwide
Calenduleae (Chapter 35)	12	120	Mainly southern Africa
Gnaphalieae (Chapter 36)	185	1240	Worldwide
Astereae (Chapter 37)	222	3100	Worldwide
Anthemideae (Chapter 38)	111	1800	Mainly Old World
Inuleae (Chapter 39)	66	687	Mainly Eurasian and east and south African
Athroismeae (Chapter 40)	5	59	Mainly paleotropics
Feddeeae[a]	1	1	Cuba
Heliantheae alliance (Chapter 41)	477	5600	Worldwide
Bahieae (Chapter 41)	20	83	Mainly North America and Mexico
Chaenactideae (Chapter 41)	3	29	North America and Mexico
Helenieae (Chapter 41)	13	120	New World
Heliantheae (Chapter 41)	113	1500	Mainly pantropical
Madieae (Chapter 41)	36	200	Mainly North America and Mexico
Millerieae (Chapter 41)	34	400	Mainly New World
Neurolaeneae (Chapter 41)	5	150	Mainly New World tropics
Perityleae (Chapter 41)	7	84	Mainly North America and Mexico
Polymnieae (Chapter 41)	1	3	North America
Tageteae (Chapter 41)	32	270	Mainly North America and Mexico
Coreopsideae (Chapter 42)	30	550	Worldwide
Eupatorieae (Chapter 43)	182	2200	Mainly New World

[a] Feddeeae can be placed inside or outside the Heliantheae alliance.

1832; Turner and Powell 1977). Also Liabeae, now in subfamily Cichorioideae (Chapter 23), was previously regarded as an element of Senecioneae (e.g., Bentham 1873a; Small 1917–1919) and only later was realized to be distinct (Rydberg 1927; Robinson and Brettell 1973a; Nordenstam 1977). Gnaphalieae was regarded as an element of Inuleae by Merxmüller et al. (1977), but on the basis of morphological (Bremer 1987; Anderberg 1989; Karis et al. 1992; Karis 1993) and molecular data (Kim and Jansen 1995; Jansen and Kim 1996) is now considered to be separate from newly defined Inuleae (Anderberg 1989, 1996; Chapter 36). Inuleae now include former Plucheeae, a tribe that was segregated from Inuleae s.l. together with Gnaphalieae when Inuleae were discovered not to be monophyletic (Bremer 1987; Anderberg 1989, 1996; Karis et al. 1992; Karis 1993). Plucheeae were first assumed to be a monophyletic sister group of Inuleae s.str. (Anderberg 1996), but Anderberg et al. (2005) presented evidence that Plucheeae are nested within Inuleae s.str., and therefore decided not to maintain Plucheeae as a separate tribe (Anderberg and Eldenäs 2007). Furthermore, phylogenetic analyses using cpDNA sequences indicated that three genera formerly placed in Inuleae (*Anisopappus*, *Athroisma*, and *Blepharispermum*; Merxmüller et al. 1977) form the sister group of Feddeeae plus the Heliantheae alliance (Kim and Jansen 1995; Eldenäs et al. 1999; Panero and Funk 2002, 2008; Cariaga et al. 2008). These genera, together with *Centipeda* (previously placed in Anthemideae, Astereae, and Inuleae; Nesom 1994; Panero 2005, 2007a; Chapter 40) and *Leucoblepharis*, are now recognized as tribe Athroismeae (Panero and Funk 2002; Panero 2005), which is mainly defined on the basis of DNA sequences (Panero 2007a). Feddeeae is a recently described monospecific tribe that accommodates *Feddea cubensis*, a singular species of which the phylogenetic position in Asteroideae was only recently resolved (Cariaga et al. 2008). The remainder of the tribes in Asteroideae is commonly referred to as the Helianthoid group or alliance (Bremer 1996; Chapter 41), which is characterized by a phytomelanin layer in the achenes. The present tribal delimitation in this group is very recent (Baldwin et al. 2002; Panero and Funk 2002) and resulted from dissatisfaction with the clearly artificial circumscription of the traditional Helenieae and Heliantheae (e.g., sensu Bentham 1873a; Cronquist 1955, 1977; Carlquist 1976; Robinson 1981). Also the large and clearly defined tribe Eupatorieae is part of this assemblage, and in order to arrive at monophyletic Helenieae and Heliantheae while maintaining Eupatorieae, the Heliantheae alliance was subdivided into twelve tribes (Baldwin et al. 2002; Panero and Funk 2002; Panero 2007b) (Table 33.1; Chapter 41). Of these, Coreopsideae, Millerieae, Neurolaeneae, and newly described Polymnieae (Panero and Funk 2002) are segregates of traditional (paleate) Heliantheae, which are now recognized in a narrower sense. Classic (epaleate) Helenieae were split up in much more narrowly defined Helenieae s.str. plus Madieae, Tageteae, Bahieae, Chaenactideae, and Perityleae, of which the latter three tribes were recently described by Baldwin et al. (2002).

The tribal affiliations of several Asteroideae genera remain uncertain. *Doronicum*, for example, may be a member of Senecioneae and sister to the remainder of the tribe; however this hypothesis is poorly supported by DNA sequence data (Pelser et al. 2007) and some datasets suggest that this genus is more closely related to Astereae and Gnaphalieae (Goertzen et al. 2003). Although *Centipeda* is here considered a member of Athroismeae, it is presently unclear whether this genus should be included in the tribe (Panero 2005) or if it should be positioned elsewhere among Athroismeae, Feddeeae, and the Heliantheae alliance (Wagstaff and Breitwieser 2002). Panero (2007a) suggests that *Symphyllocarpus*, another genus of uncertain tribal affiliation (Jeffrey 2007c), may be sister to *Centipeda*. *Nanothamnus* is treated here as Inuleae, but its affinities may also be elsewhere in Asteroideae (Chapter 39). *Callilepis* (incl. *Zoutpansbergia*) has been placed in Inuleae s.l. (Merxmüller et al. 1977) and Gnaphalieae (Bayer et al. 2007), but the results of phylogenetic studies using *ndhF* sequence data indicate that this genus is more closely related to Athroismeae, Feddeeae, the Heliantheae alliance, and Inuleae (Anderberg et al. 2005; Cariaga et al. 2008). Jeffrey (2007b) listed *Cavea* as a carduoid genus of uncertain placement, but also suggested that it may be related to Inuleae or is positioned elsewhere in the family. *Diodontium* and *Staurochlamys* were tentatively considered as members of Coreopsideae by Panero (2007c), but he indicated that *Diodontium* may well belong to Astereae or Anthemideae, and that *Staurochlamys* might be best placed in Neurolaeneae. Panero (2007d) treated *Guardiola* as a subtribe (Guardiolinae) of Millerieae, but underscored this placement as tentative awaiting more detailed studies.

TRIBAL PHYLOGENY

Early views of the evolutionary relationships between Asteraceae lineages are often in sharp contrast with our current understanding. This pertains to many tribes, including those now placed in subfamily Asteroideae. Heliantheae were, for instance, long regarded to be one of the earliest tribes that arose and closest in morphology to the ancestor of Asteraceae (e.g., Bentham 1873a; Bessey 1915; Hutchinson 1916; Cronquist 1955; Turner 1977). Also Senecioneae has been mentioned as one of the basal groups of the family, a view partly derived from the notion that *Senecio* is the largest genus in the family (Small 1917–1919). More recent studies, however, have shown these tribes and other members of Asteroideae to be in a more derived position in the family (e.g., Panero and Funk 2002, 2008; Funk et al. 2005).

Various hypotheses of intertribal phylogenetic relationships for Asteroideae have been published using morphological, chemical, restriction fragment length polymorphism (RFLP), and DNA sequence data. Bremer (1987) published the first cladistic study of the tribal relationships in Asteraceae using a morphological dataset, although he also coded several chemical characters and the presence/absence of a 22 kb cpDNA inversion characterizing all Asteraceae except Barnadesioideae (Jansen and Palmer 1987). This analysis showed that Eupatorieae is not a basal member of the subfamily as was hypothesized by Robinson (1981) and King and Robinson (1987). Instead, Inuleae appeared as the sister group to the remainder of Asteroideae, a result also found by Karis (1993, 1996) using morphological data. Except for Eupatorieae, which was placed sister to Astereae, the other members of the Heliantheae alliance (as defined here) formed a clade nested within a grade formed by the other tribes (Bremer 1987) (Fig. 33.1). Palmer et al. (1988) used cpDNA RFLPs to resolve tribal relationships and found Eupatorieae nested within the Heliantheae alliance. Inuleae (incl. Gnaphalieae) were resolved as sister to a clade formed by Anthemideae and Astereae in this study. Similar results were obtained in another RFLP study (Jansen et al. 1990, 1991) (Fig. 33.1). In contrast to previous studies, however, Jansen et al. (1990; 1991) calculated bootstrap support values for their phylogenetic hypotheses. These analyses indicated that within Asteroideae only the Heliantheae alliance is well supported as a monophyletic group. This was also concluded in studies that followed (e.g., Kim et al. 1992; Bayer and Starr 1998) until analyses of *ndhF* sequence data revealed strong support for a sister group relationship between Athroismeae and the Heliantheae alliance and a clade formed by these two lineages and Inuleae (excl. Gnaphalieae; Kim and Jansen 1995; Eldenäs et al. 1999) (Fig. 33.1). In addition, these studies indicated that Anthemideae, Astereae, Calenduleae, and Gnaphalieae comprised a well supported clade. As in several other studies (Karis 1993, 1996; Palmer et al. 1988; Jansen et al. 1990 (p.p.); Kim et al. 1992; Bayer and Starr 1998), Anthemideae were resolved as the sister clade of Astereae, although with low bootstrap and jackknife support. These phylogenetic patterns were further strengthened by Panero and Funk (2002, 2008), who employed a large multi-locus cpDNA sequence dataset to study the intertribal phylogeny of Asteraceae (Fig. 33.1). In addition, their data indicated that Gnaphalieae are sister to the Anthemideae-Astereae clade and provided more resolution and support within the Heliantheae alliance. Recently, *ndhF* sequences and morphological data supported the recognition of Feddeeae, which proved to be the immediate sister group of the Heliantheae alliance (Cariaga et al. 2008) (Fig. 33.1). None of the phylogenetic studies to date has resulted in a well supported phylogenetic position of tribe Senecioneae. This tribe is, most likely, sister to either the rest of Asteroideae, a clade formed by Anthemideae, Astereae, Calenduleae, and Gnaphalieae, or the clade composed of Inuleae, Athroismeae, Feddeeae, and the Heliantheae alliance. The short branches that connect Senecioneae with its putative sister clades (e.g., Kim et al. 2005; Hershkovitz et al. 2006) suggest that the difficulty of placing Senecioneae may be due to a lack of synapomorphies with these clades, perhaps as a consequence of rapid diversification early in the evolutionary history of Asteroideae.

In contrast to cpDNA RFLP and sequence data, data from the nuclear genome have only been scarcely used to study the phylogeny of Asteraceae at the tribal level. To date, only ITS sequences have been employed for phylogeny reconstruction in this context (Baldwin et al. 2002; Wagstaff and Breitwieser 2002; Goertzen et al. 2003), and this resulted in mostly alternative, yet weakly supported, hypotheses with respect to the relationships between the tribes. ITS data have, however, played an important role in delimiting the tribes of the Heliantheae alliance (Baldwin et al. 2002) (Chapter 41). This is partly because the ITS region contained more variable characters than single cpDNA regions and therefore allowed for a larger taxon sampling than was feasible in multi-locus cpDNA studies. Hopefully, the development of single-copy nuclear markers for the family (e.g., Álvarez et al. 2008) will stimulate studies employing nuclear sequence data, resulting in a well-resolved and supported nrDNA phylogeny that can be contrasted with cpDNA phylogenies.

BIOGEOGRAPHY AND AGE

Subfamily Asteroideae has a nearly worldwide distribution. An area optimization analysis on a supertree (=metatree) of the family suggests a sub-Saharan origin of Asteroideae (Funk et al. 2005). Africa is also the continent where all tribes except for Feddeeae and those of the Heliantheae alliance had their origin. From there, other continents were colonized, resulting in an almost cosmopolitan distribution for Astereae, Senecioneae, Gnaphalieae, and to a lesser extent, Anthemideae (Table 33.1). Feddeeae are endemic to Cuba and a western North American-Mexican origin is assumed for the Heliantheae alliance (Baldwin et al. 2002; Funk et al. 2005). Several of the Helianthoid tribes dispersed to South America and some colonized Old World areas (e.g., Coreopsideae).

Assuming a date of 128 Ma for the crown Asteridae and employing a penalized likelihood analysis of *ndhF* data, Hershkovitz et al. (2006) estimated the crown age

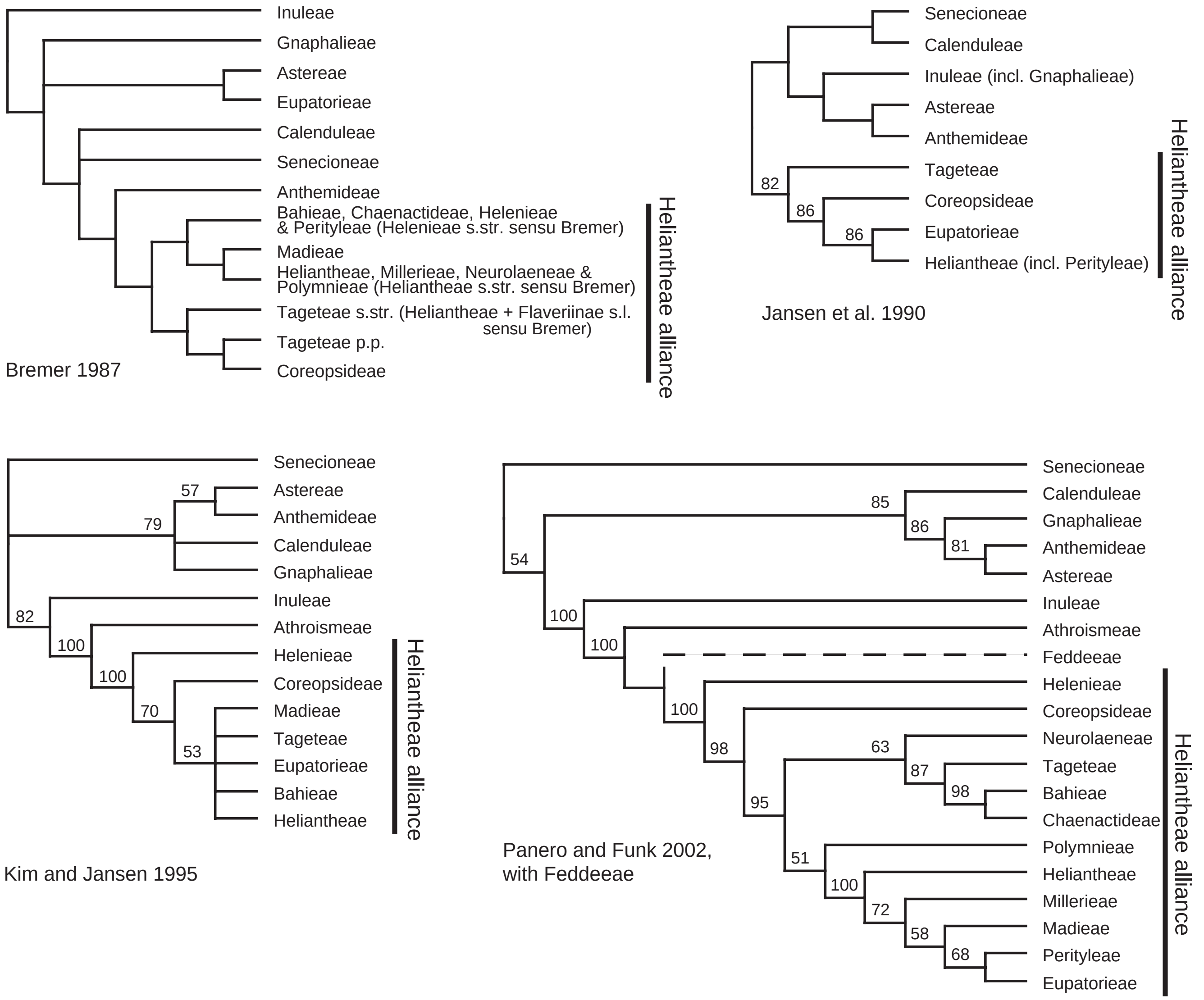

Fig. 33.1. Comparison of hypotheses of intertribal relationships in Asteroideae. Cladograms are redrawn from Bremer (1987: Fig. 5, mainly morphological data), Jansen et al. (1990: Fig. 4, cpDNA RFLF data), Kim and Jansen (1995: Fig. 2, *ndhF* sequence data), and Panero and Funk (2002: Fig. 1, multiple cpDNA sequence regions). Taxonomy follows the tribal delimitation used in this book. Bootstrap values above 50% as reported in the original papers are placed above the branches. Bootstrap support was not presented for the cladogram in Bremer (1987). The phylogenetic position of Feddeeae according to Cariaga et al. (2008) is indicated with a dashed branch in the cladogram of Panero and Funk (2002). Bootstrap values in the latter cladogram refer to those presented with the original tree of Panero and Funk (2002), which did not include Feddeeae. The complete metatree of Compositae can be found in Chapter 44.

of Asteroideae to be ca. 29–30 Myr. Kim et al. (2005) used nonparametric rate smoothing in their molecular dating study of *ndhF* data and *Cornus* as an internal calibration point and arrived at an estimate for the subfamily of 26–29 Myr. Their age estimate for Asteroideae derived from average synonymous nucleotide substitutions using the same dataset and substitution rates for Poaceae and Oleaceae was 35–39 Myr (Kim et al. 2005). These studies and unpublished data for Senecioneae (Pelser et al., in prep.) further indicate that the Heliantheae alliance and all Asteroideae tribes outside of it are 17 Myr or older and the result of a family-wide rapid Oligocene-Early Miocene diversification. These results are roughly in line with other molecular dating studies in Asteraceae (e.g., Wikström et al. 2001; Wagstaff et al. 2006) and palaeopalynological data (e.g., Katinas et al. 2007), although the latter source of data generally results in somewhat lower age estimates for Asteraceae lineages.

CHROMOSOME NUMBERS

A base chromosome number of $x = 9$ is found for most tribes in Asteroideae, although $x = 7$ to 10 are also often, yet less frequently, reported. The base chromosome number of $x = 18$ has been postulated for the Heliantheae alliance (Baldwin et al. 2002), but considering the numbers found elsewhere in the subfamily, $x = 9$ seems to be a more likely candidate for the base chromosome number of the Heliantheae alliance and the subfamily as a whole. Both dysploid reduction and polyploidy seem rampant and complicate the interpretation of chromosome numbers. These changes appear to coincide with shifts in life history strategies, such as between annual and perennial, and herbaceous and woody habits (Baldwin et al. 2002; Jeffrey 2007a) (Chapter 41).

CHEMISTRY

Sesquiterpene lactones are characteristic for the family as a whole, but their chemistry seems to be more complex in Asteroideae than in other subfamilies (Jeffrey 2007a). These secondary metabolites are, however, absent in Tageteae and Calenduleae and rare in Astereae. Another phytochemical characteristic of the subfamily is the production of benzopyrans and benzofurans (Proksch and Rodriguez 1983; Proksch 1985). In addition, external flavonoid accumulation is much more abundant in Asteroideae than elsewhere in the family (Wollenweber and Valant-Vetschera 1996). Thymol derivatives are present in all Asteroideae except for Senecioneae and most Astereae (Jeffrey 2007a). Within Asteroideae there are several chemical synapomorphies for some of the clades identified using morphological and molecular characters. In both Anthemideae and Astereae, for instance, C_{10}- and C_{17}-acetylenes and umbelliferone derivatives are reported, and the close affinities between Eupatorieae and Heliantheae s.l. are evident in the shared presence of 8 β-substituted germacranolides and special aromatic compounds (Zdero and Bohlmann 1990).

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Chapter 34

Senecioneae

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HISTORICAL OVERVIEW

The taxonomic history of tribe Senecioneae began when Henri Cassini laid the foundation for the tribal classification of "Synantherées", i.e., family Compositae (Asteraceae), in four Mémoires delivered to the Académie des Sciences in 1812–1817 (Cassini 1812, 1813a–c, 1814, 1816, 1817). In his third Mémoire (Cassini 1816), he distinguished 17 "natural" tribes including Senecioneae ("Les Senécionées"), plus an "artificial" 18th tribe of three genera, which could not be classified in the natural tribes. In his sixth Mémoire (Cassini 1819), he recognized 20 tribes and for the first time used their Latin denominations such as Senecioneae (see Chapter 1).

Senecioneae were originally comprised of *Cacalia*, *Cineraria*, *Othonna*, and *Senecio* (Cassini 1816). However, in a final paper, Cassini (1829) included a total of 35 genera in the tribe. Additional genera that are presently in Senecioneae were placed by him in two separate tribes, Tussilagineae and Adenostylineae. Tussilagineae included three genera (*Tussilago*, *Nardosmia*, and *Petasites* [Fig. 34.1I]) and Adenostylineae included six (*Senecillis* with a question mark, *Ligularia* [Fig. 34.2A–C], *Celmisia*, *Homogyne*, *Adenostyles*, and *Paleolaria*). *Doronicum* was originally listed among the genera not assigned to a natural tribe (Cassini 1816), but it was later included in Senecioneae together with *Arnica* (Cassini 1829).

In his description of tribe Senecioneae, Cassini (1819) stressed floral characters such as: bifurcate styles with separated stigmatic areas on the inside of style branches, apically truncate with sweeping hairs ("collecteurs"); anthers ecaudate; fruits 10- or 20-striate with alternating glabrous and papillate-hairy areas; pappus of white filiform barbellate bristles. The characteristics of Tussilagineae included: style branches with continuous stigmatic areas, corolla lobes equalling the tube in length, an ecalyculate involucre, and leaves developing after anthesis. Tribe Adenostylineae was defined, *inter alia*, by styles dorsally covered by sweeping hairs and separated stigmatic areas, an ecalyculate involucre, and a reddish corolla. Cassini remarked that the two latter tribes may need to be united.

The works of Lessing (1832) and De Candolle (1836–1838) resulted in little improvement in tribal classification. Lessing recognized eight largely artificial tribes. His tribe "Senecionideae" was broadly defined and included eleven subtribes covering Anthemideae, Tageteae, Ambrosieae, Helenieae, Heliantheae, etc. His subtribe "Chrysanthemeae" included not only most of Anthemideae but also Calenduleae and some elements presently in Senecioneae. Lessing's subtribe Senecioneae was likewise ill-defined with anomalous genera such as *Lessingia*, *Charieis*, *Schistocarpha*, *Neurolaena* and *Arnica* included, and senecioid elements such as *Othonna* excluded (and referred to tribe Cynareae). De Candolle essentially adopted the general outline of Lessing's scheme with some refinements regarding generic disposition. Bentham (1873a) provided a less artificial arrangement similar to that of Cassini. However, his tribe Senecioneae was not well-defined in the light of present knowledge. He included Liabeae as one of four subtribes, as well as a number of helianthoid (or helenioid) genera such as *Arnica*, *Neurolaena*, *Psathyrotes*, and *Schistocarpha*. This unnatural classification persisted well into the 20th century (e.g., Hoffmann 1890–1894; Small 1919), when several authors

Fig. 34.1. Diversity in life-form and morphology in Senecioneae. **A** *Senecio vulgaris* L. (short-lived annual, Senecioninae); **B** *Senecio cadiscus* B. Nord. & Pelser (syn. *Cadiscus aquaticus* E.Mey. ex DC.; aquatic herb, Senecioninae); **C** *Curio rowleyanus* (H. Jacobsen) P.V. Heath (creeping succulent perennial, Senecioninae); **D** *Senecio hakeifolius* Bert. ex DC. (perennial herb, Senecioninae); **E** *Dendrosenecio kilimanjari* (Mildbr.) E.B. Knox (pachycaul tree-like herb, or "dendroforb", Senecioninae); **F** *Pittocaulon praecox* (Cav.) H. Rob. & Brettell (subsucculent precocious shrub or small tree, Tussilagininae s.str.); **G** *Senecio haworthii* Sch.Bip. (succulent perennial, *Senecio medley-woodii* Hutch.–*Brachyglottis* clade); **H** *Crassocephalum crepidioides* (Benth.) S. Moore (annual herb, Senecioninae); **I** *Petasites frigidus* (L.) Fries (perennial herb with hysteranthous leaves, Tussilagininae s.str.). [Photographs: A, C, D, H, P.B. Pelser; B, E. van Jaarsveld; E, J. de Vries; F, P. Carillo-Reyes; G, I, B. Nordenstam.]

still included *Arnica* and many other helenioid elements in Senecioneae.

Bentham's division of Senecioneae into four subtribes was based on characters of the style and involucre, and apart from Liabeae, he distinguished Eusenecioneae, Othonneae (with *Othonna* and *Euryops* [Fig. 34.3A–C] as major components), and Tussilagineae as subtribes. Also Hoffmann (1890–1894) considered Liabeae as a subtribe of Senecioneae ("Liabinae"). However, he did not recognize Tussilagininae as distinct from Senecioninae. Other than Liabinae and Senecioninae, Hoffmann (1892) considered Othonninae a subtribe.

Current views on tribal delimitation of Senecioneae have largely been based on the Compositae symposium held in Reading in 1975. During this meeting, Turner and Powell (1977) argued for a wide circumscription of the tribe to include most of the dismantled Helenieae, such as Chaenactidinae, Eriophyllinae, Flaveriinae, and Peritylinae, which included the arnicoid group (*Arnica*, *Psathyrotes*, etc.). Nordenstam (1977), however, presented a narrower concept of Senecioneae, excluding *Arnica* and all other helenioid genera. He listed 18 characters from morphology, anatomy, embryology, cytology, and chemistry used to exclude the arnicoid group. He also excluded Liabeae, which prior to the Reading symposium was already recognized as a separate tribe with affinities to Vernonieae (Rydberg 1927; Robinson and Brettell 1973a, 1974b). To this day, this narrower tribal concept of Senecioneae (Nordenstam 1977) has largely been followed.

Nordenstam (1977) distinguished only two subtribes in Senecioneae: Senecioninae, which also included the genera others assigned to Othonninae and Tussilagininae, and Blennospermatinae for four small and morphologically somewhat aberrant genera (*Abrotanella*, *Blennosperma*, *Crocidium*, and *Ischnea*). Blennospermatinae sensu Nordenstam (1977) are characterized by a biseriate rather than uniseriate involucre and, when present, ray florets that are mostly without a tube. Pappus is absent in this subtribe, or composed of a few bristles or teeth. The basic chromosome number in Blennospermatinae is $x = 7$, 8 or 9.

On the basis of morphological and cytological characters, Nordenstam (1977) informally distinguished two loosely defined complexes within Senecioninae which emerged from the studies of Pippen (1968) and Robinson and Brettell (1973e, 1974a), viz. the senecioid and cacalioid complexes. Due to the ambiguity of the rejected name *Cacalia*, the term tussilaginoid was later introduced for the latter complex (Jeffrey 1992; Barkley 1999). Members of the senecioid complex typically have radiate and yellow capitula with calyculate involucres (Fig. 34.3D, F). This complex is further characterized by balusterform filament collars, radial endothecial tissue, style branches with two separate areas of stigmatic tissue, and a basic chromosome number of $x = 10$. In contrast, the tussilaginoids are characterized by capitula that are often white and discoid, and have an ecalyculate involucre (Figs. 34.1I, 34.2B, F). Tussilaginoid anthers have polarized endothecial cell wall thickenings, and the shape of the filament collar is typically cylindrical (or semi-cylindrical with involute margins). The style branches in this complex have continuous stigmatic areas, and the basic chromosome number is frequently $x = 30$ or a derivative thereof. Jeffrey and Chen (1984) recognized these two complexes as subtribes Senecioninae and Tussilagininae, respectively. Mainly on the basis of somewhat deviating chromosome numbers compared to other tussilaginoids, these authors erected subtribe Tephroseridinae for *Nemosenecio*, *Sinosenecio*, and *Tephroseris*.

Bremer (1994) published a phylogenetic analysis using morphological characters that were frequently used to distinguish senecioids and tussilaginoids, and the resulting phylogeny supported their monophyly. He agreed with Jeffrey and Chen (1984) in recognizing subtribes Senecioninae and Tussilagininae, in addition to subtribe Blennospermatinae. In the absence of sufficient distinguishing characters, Bremer included the genera of Tephroseridinae in Tussilagininae.

Robinson et al. (1997) followed Bremer (1994) in recognizing subtribes Blennospermatinae, Senecioninae, and Tussilagininae. On the basis of clear morphological differences from the group composed of *Blennosperma*, *Crocidium*, and *Ischnea*, the genus *Abrotanella* was, however, excluded from Blennospermatinae and established as the monogeneric subtribe Abrotanellinae. Robinson et al. (1997) erected subtribe Adenostylinae for five genera previously placed in Senecioninae sensu Bremer (*Adenostyles*, *Caucasalia*, *Dolichorrhiza*, *Iranecio*, and *Pojarkovia*). This alliance was termed the "Quadridentate Group" by Jeffrey (1992) and is characterized by the presence of a four-lobed disc floret corolla.

The 1970s were not only the starting point for a new, much narrower concept for the tribe and for developments that resulted in a new delimitation of its subtribes, but also marked the start of a renewed interest in the generic delimitation of Senecioneae and in particular of *Senecio*—by far the largest genus in the tribe. *Senecio* was traditionally composed of ca. 3000 species (Jeffrey et al. 1977), but eventually this concept was generally perceived as highly artificial (Bremer 1994; Vincent 1996), in the sense that many species traditionally assigned to *Senecio* s.l. were thought to be more closely related to species of other genera. Following detailed morphological and karyological studies, several anomalous species were removed from *Senecio* and placed in new or resurrected genera (e.g., Robinson and Brettell 1973b–e, 1974a; Robinson 1974; Nordenstam 1978), and these efforts have been continued (e.g., Jeffrey and Chen 1984; Jeffrey 1986,

Fig. 34.2. Representatives of the main clades of Senecioneae. **A–C** *Ligularia dentata* (A. Gray) Hara (Tussilagininae s.str. clade); **D–F** *Acrisione denticulata* (Hook. & Arn.) B. Nord. (*Senecio medley-woodii–Brachyglottis* clade). [Photographs, P.B. Pelser.]

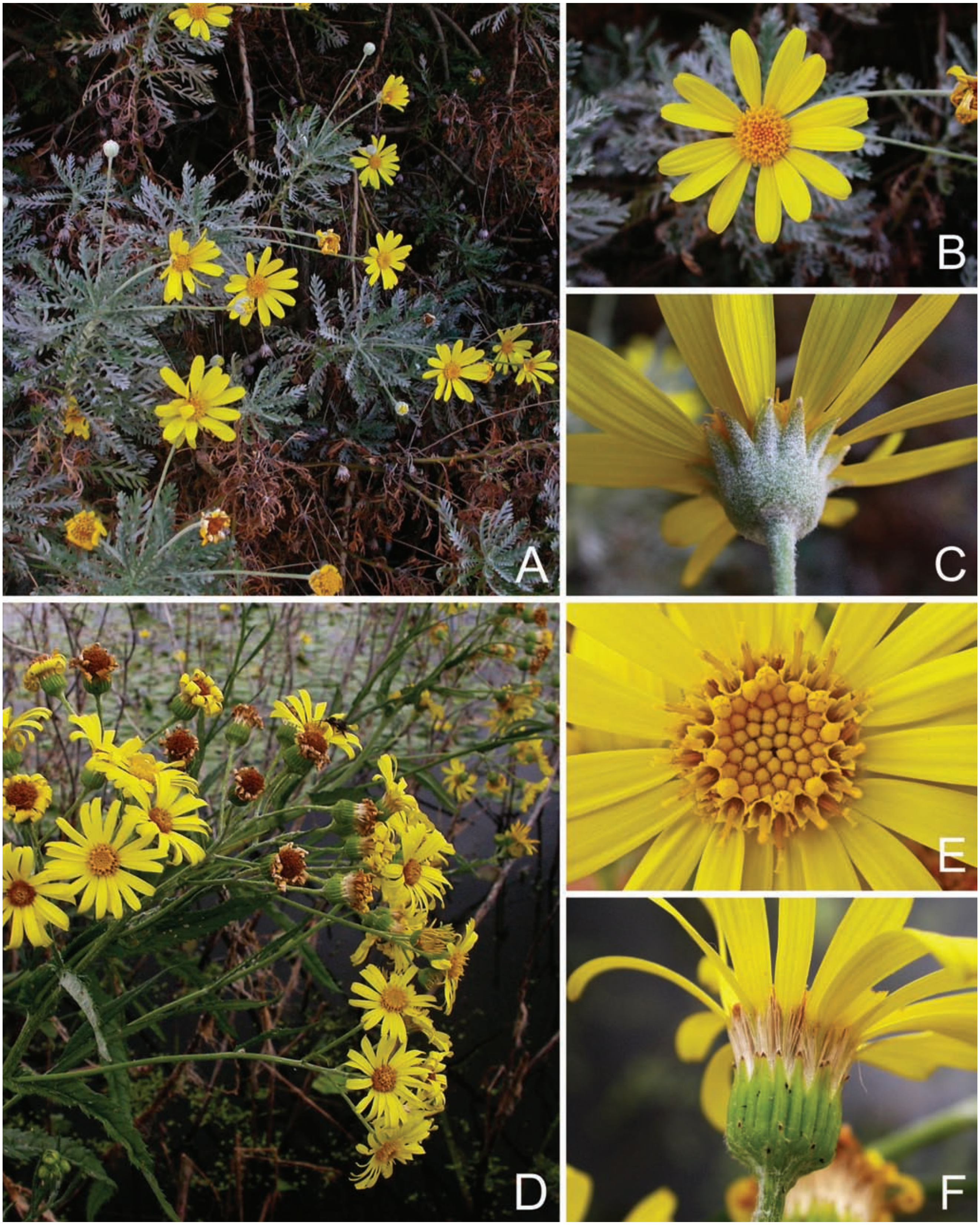


Fig. 34.3. Representatives of the main clades of Senecioneae. **A–C** *Euryops pectinatus* (L.) Cass. (Othonninae); **D–F** *Jacobaea paludosa* (L.) G. Gaertn., B. Mey. & Scherb. (Senecioninae clade). [Photographs, P.B. Pelser.]

1992; Nordenstam 1985, 1989, 1997, 2002, 2003, 2006c, d; Nordenstam and Lundin 2002).

In the late 1980s and onwards, morphological data for the tribe were supplemented by data from restriction site maps of chloroplast DNA (e.g., Palmer et al. 1988; Jansen et al. 1991; Knox and Palmer 1995; Kadereit and Jeffrey 1996; Knox 1996) and nucleotide sequence data (e.g., Bain and Jansen 1995; Panero et al. 1999; Bain and Golden 2000; Pelser et al. 2002; Bain and Jansen 2006). These molecular phylogenies provided an additional stimulus to redefine the generic delimitation of Senecioneae (e.g., Nordenstam and Pelser 2005; Cron et al. 2006; Nordenstam 2006a, b; Pelser et al. 2006). As *Senecio* gradually became more narrowly defined, declining to an estimated number of approximately 1000 species in 2007 (Pelser et al. 2007), the number of genera in the tribe steadily increased from 110 in Jeffrey (1992) and 120 in Bremer (1994) to 150 in the most recent overview (Nordenstam 2007). Despite considerable efforts and progress in redefining the generic delimitation of Senecioneae, a limited number of new genera remain to be defined, and some recognized and generally accepted genera need to be transferred into *Senecio* to arrive at a monophyletic generic concept. Furthermore, the limits and taxonomy of other genera in the tribe (e.g., *Ligularia* [Fig. 34.2A–C], *Parasenecio*, *Roldana*, *Monticalia*, *Pentacalia*, *Dendrophorbium*, *Othonna*) need to be revised.

PHYLOGENY

Traditionally, tribe Senecioneae was placed as sister to tribe Calenduleae (Bayer and Starr 1998). This view was supported by chloroplast restriction site (Jansen et al. 1991) and Internal Transcribed Spacer (ITS) sequence data (Goertzen et al. 2003). In contrast, DNA sequence data of the chloroplast *trnL* intron and *trnL-F* intergenic spacer regions identified tribe Gnaphalieae as its closest relative (Bayer and Starr 1998; Liu et al. 2002). However, other datasets provided different hypotheses for the phylogenetic position of Senecioneae within subfamily Asteroideae (Kim et al. 1992; Liu et al. 2002; Panero and Funk 2002, 2008; Funk et al. 2005) or were inconclusive (Kim et al. 1992; Kim and Jansen 1995). In general, these studies indicate that Senecioneae appear most likely sister to either a clade formed by all other tribes in subfamily Asteroideae, a clade formed by tribes Anthemideae, Astereae, Calenduleae, and Gnaphalieae, or a clade composed of Athroismeae, Feddeeae, Inuleae, and the Heliantheae alliance. The short branches that connect Senecioneae with its putative sister clades (e.g., Kim et al. 2005; Hershkovitz et al. 2006) suggest that the difficulty of placing Senecioneae may be due to rapid diversification early in the evolutionary history of Asteroideae.

Knowledge regarding the subtribal and intergeneric evolutionary relationships within tribe Senecioneae has been highly fragmented until very recently. With the exception of Bremer (1994) and Kadereit and Jeffrey (1996), who focused on studying the monophyly of subtribes Senecioninae and Tussilagininae, and Bain and Jansen (2006) who discussed the phylogenetic significance of a hair-pin structure in the *psbA-trnH* region of chloroplast DNA, intergeneric relationships in Senecioneae had only been studied within the context of resolving phylogenies of select genera or sections of *Senecio* with all of these studies containing only relatively few genera and species of Senecioneae (Knox and Palmer 1995; Bain and Jansen 1995; Sang et al. 1995; Knox 1996; Swenson and Bremer 1997, 1999; Panero et al. 1999; Bain and Golden 2000; Álvarez Fernández et al. 2001; Comes and Abbott 2001; Pelser et al. 2002; Coleman et al. 2003; Swenson and Manns 2003; Wagstaff and Breitwieser 2004; Kadereit et al. 2006; Liu et al. 2006; Wagstaff et al. 2006).

A first attempt at constructing a comprehensive phylogeny for the tribe was completed by Pelser et al. (2007). In this study, DNA sequences of the ITS region were compiled for 614 species representing 114 of the 150 Senecioneae genera recognized by Nordenstam (2007) and included 186 sampled species of *Senecio*. Several plastid regions were also sequenced for a subset of the 614 sampled species. In addition to providing new insights into evolutionary relationships at the intergeneric level, phylogenies were used to propose a new delimitation for *Senecio*, and resulted in transferring the species of *Aetheolaena*, *Culcitium*, *Hasteola*, *Iocenes*, *Lasiocephalus*, and *Robinsonia* into *Senecio*, and removing several *Senecio* species and species groups that are only distantly related to the core of *Senecio*.

Here we discuss the subtribal and intergeneric relationships of Senecioneae using a condensed version of the ITS phylogeny of Pelser et al. (2007) in which detailed information about intrageneric relationships has been omitted (Fig. 34.4). In this modified version, branches were collapsed for clades for which the parsimony and Bayesian analyses of the original dataset resulted in conflicting topologies. Although phylogenetic analyses of the plastid and combined ITS/plastid datasets (Pelser et al. 2007) provide additional information about intergeneric relationships in the tribe (sometimes supporting and sometimes contradicting the ITS trees), these datasets contain a much smaller selection of genera. Therefore, we use only the ITS tree as the basis for the discussion of relationships within the tribe. Although this tree is not fully resolved and contains clades that are only weakly supported by bootstrap values and posterior probabilities, it allows for several conclusions regarding the subtribal delimitation and intergeneric relationships of the tribe.

Delimitation of tribe Senecioneae

Although most genera currently regarded as members of Senecioneae form a well-supported clade in the ITS (100% bootstrap support and a posterior probability of 1.00; Fig. 34.4), plastid, and combined-data trees (Pelser et al. 2007), there is little nodal support for the inclusion of *Doronicum* and *Abrotanella* in the tribe. In fact, using ITS data, Goertzen et al. (2003) demonstrated that *Doronicum* is only distantly related to tribe Senecioneae and instead appears to be closer to tribes Astereae and Gnaphalieae. On the basis of unpublished analyses of plastid DNA sequences, Panero (2005) concurred and formally placed this genus in a monogeneric tribe Doroniceae, and further suggested affinities to tribe Calenduleae. We therefore regard the tribal affiliation of *Doronicum* as uncertain. Although the phylogenetic position of *Abrotanella* remains relatively poorly supported by our data, we still consider it to be a member of Senecioneae in the absence of evidence for an alternative tribal affiliation.

Subtribal relationships

Subtribe Blennospermatinae sensu Nordenstam (1977; Bremer 1994) included four genera, *Abrotanella*, *Blennosperma*, *Crocidium*, and *Ischnea*, but its monophyly is not supported by molecular data. Swenson and Bremer (1999) and Wagstaff et al. (2006) utilized ITS, *ndhF*, and 5' *trnK/matK* sequence data and their resulting phylogenies placed *Abrotanella* distantly related to the other three genera of this subtribe. This was confirmed in the ITS phylogeny of Pelser et al. (2007), which placed *Abrotanella* near the base of Senecioneae (Fig. 34.4A). The latter study resolved a clade of *Blennosperma*, *Crocidium*, and *Ischnea* nested within subtribe Tussilagininae sensu Bremer (1994) (Fig. 34.4A). Thus *Abrotanella* may be best placed in the monogeneric subtribe Abrotanellinae (Robinson et al. 1997), whereas the remaining three genera of Blennospermatinae should be considered members of subtribe Tussilagininae.

The ITS, plastid, and combined-data trees of Pelser et al. (2007) indicate that subtribe Tussilagininae sensu Bremer (1994) (apart from *Doronicum*) is paraphyletic with subtribes Othonninae and Senecioninae nested within it. The tussilaginoid genera occur in three distinct clades. The first clade, informally named Tussilagininae s.str., is composed of 34 genera of which 31 are considered characteristic elements of the subtribe (e.g., *Ligularia* [Fig. 34.2A–C], *Parasenecio*, *Roldana*, *Petasites* [Fig. 34.1I], and *Tussilago*; Fig. 34.4A). It also includes the three genera of Blennospermatinae. Tussilagininae s.str. contains the three genera that comprise Jeffrey and Chen's (1984) subtribe Tephroseridinae (*Nemosenecio*, *Sinosenecio*, and *Tephroseris*; Fig. 34.4A). Except for a slightly deviant chromosome number, Tephroseridinae is hardly distinguishable from Tussilagininae (Bremer 1994), and is therefore best included in this subtribe. A second tussilaginoid clade, referred to as the *Senecio medley-woodii*–*Brachyglottis* clade (Pelser et al. 2007), is formed by *Brachyglottis* and eight allied genera along with some African succulent species formerly assigned to *Senecio* (the *Senecio medley-woodii* group; Figs. 34.1G, 34.4A). The third clade is composed solely of *Chersodoma* species. The phylogenetic position of *Chersodoma*, however, remains elusive in the trees presented by Pelser et al. (2007), and is sister to either the Tussilagininae s.str. clade or the *Senecio medley-woodii*–*Brachyglottis* clade (ITS data), or alternatively sister to a clade of the remaining genera of Tussilagininae sensu Bremer (1994), Othonninae, and Senecioninae (plastid and combined datasets). In Fig. 34.4A, the relationships between these three subgroups of Tussilagininae are, therefore, presented as a polytomy.

Subtribe Othonninae consists of five to seven genera (*Euryops* [Fig. 34.3A–C], *Gymnodiscus*, *Hertia*, *Lopholaena*, *Othonna*, and perhaps *Bafutia* and *Oligothrix*; Fig. 34.4A) and is sister to subtribe Senecioninae (Fig. 34.4A, B)—the largest subtribe of Senecioneae, of which representatives of 64 recognized genera were included in the analyses (Pelser et al. 2007). Subtribe Senecioninae includes a clade of the five genera of subtribe Adenostylinae sensu Robinson et al. (1997; *Adenostyles*, *Caucasalia*, *Dolichorrhiza*, *Iranecio*, and *Pojarkovia*; Fig. 34.4B). Because of its nested position within subtribe Senecioninae, the genera of Adenostylinae should be reassigned accordingly.

Intergeneric relationships

In addition to providing new insights into subtribal delimitations and relationships in Senecioneae, the ITS phylogenies of Pelser et al. (2007) also improved the understanding of evolutionary relationships on the inter- and intrageneric level, especially for *Senecio*.

Tussilagininae s.str. — The Tussilagininae s.str. clade is composed of four subclades. However, the relationships among these subclades are unresolved, due to conflicting results in parsimony and Bayesian analyses (Pelser et al. 2007). *Endocellion*, *Homogyne*, *Petasites*, and *Tussilago* form a well-supported subclade (Fig. 34.4A). Its members have a predominantly northern temperate/boreal distribution in Eurasia with a single representative in North America, viz., the polymorphic *Petasites frigidus* (cf. Cherniawsky and Bayer 1998) (Fig. 34.1I). The second subclade of Tussilagininae s.str. has a mainly New World distribution and includes among others *Cacaliopsis*, *Lepidospartum*, *Luina*, *Rainiera*, and *Tetradymia* (Fig. 34.4A). These five North American genera form a clade sister to the three Blennospermatinae genera (*Blennosperma* from South and North America, *Crocidium* from North America, and *Ischnea* from New Guinea). The third subclade is an exclusively New World clade. It is well supported by ITS, plastid, and combined data (Pelser et al.

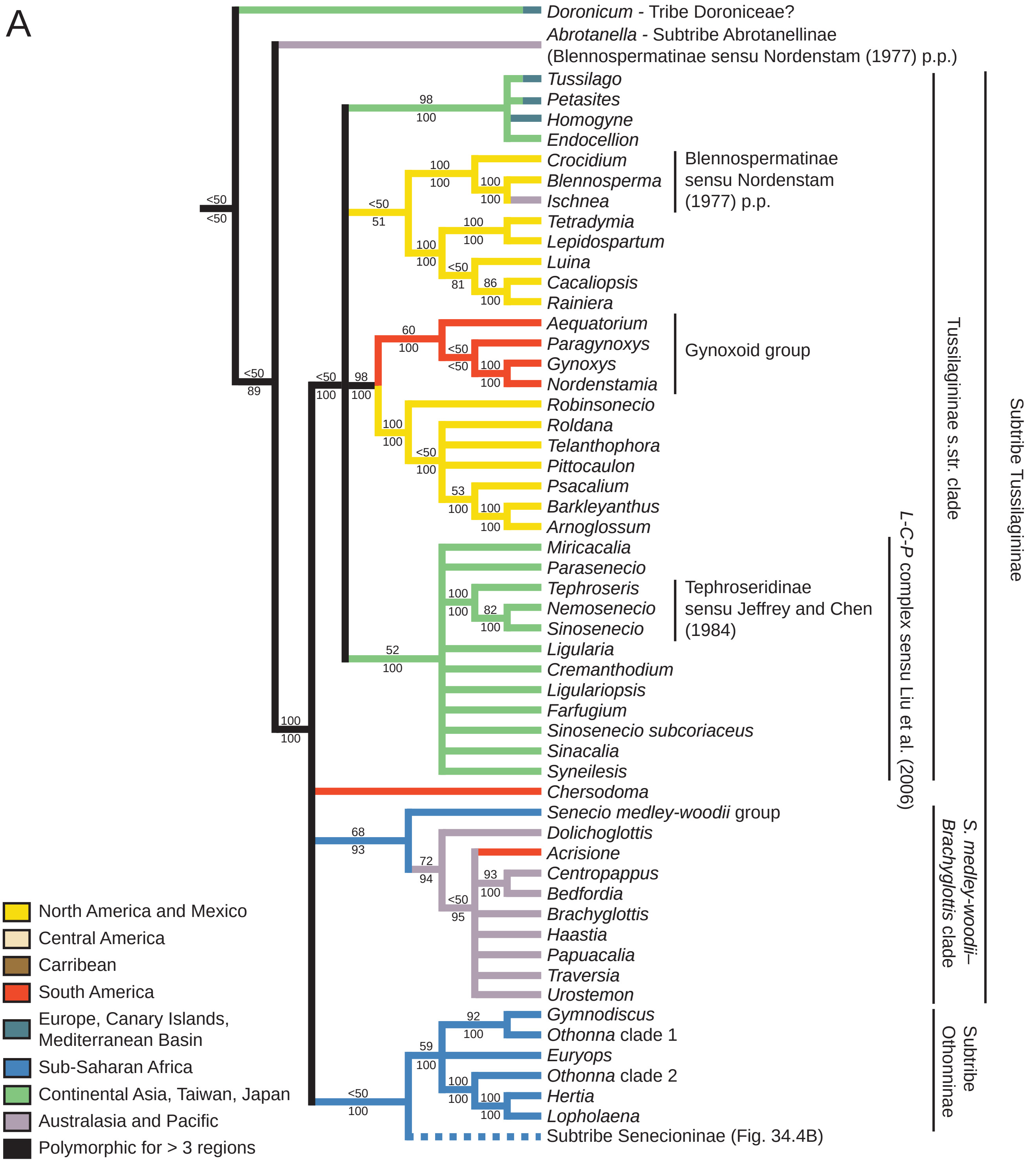
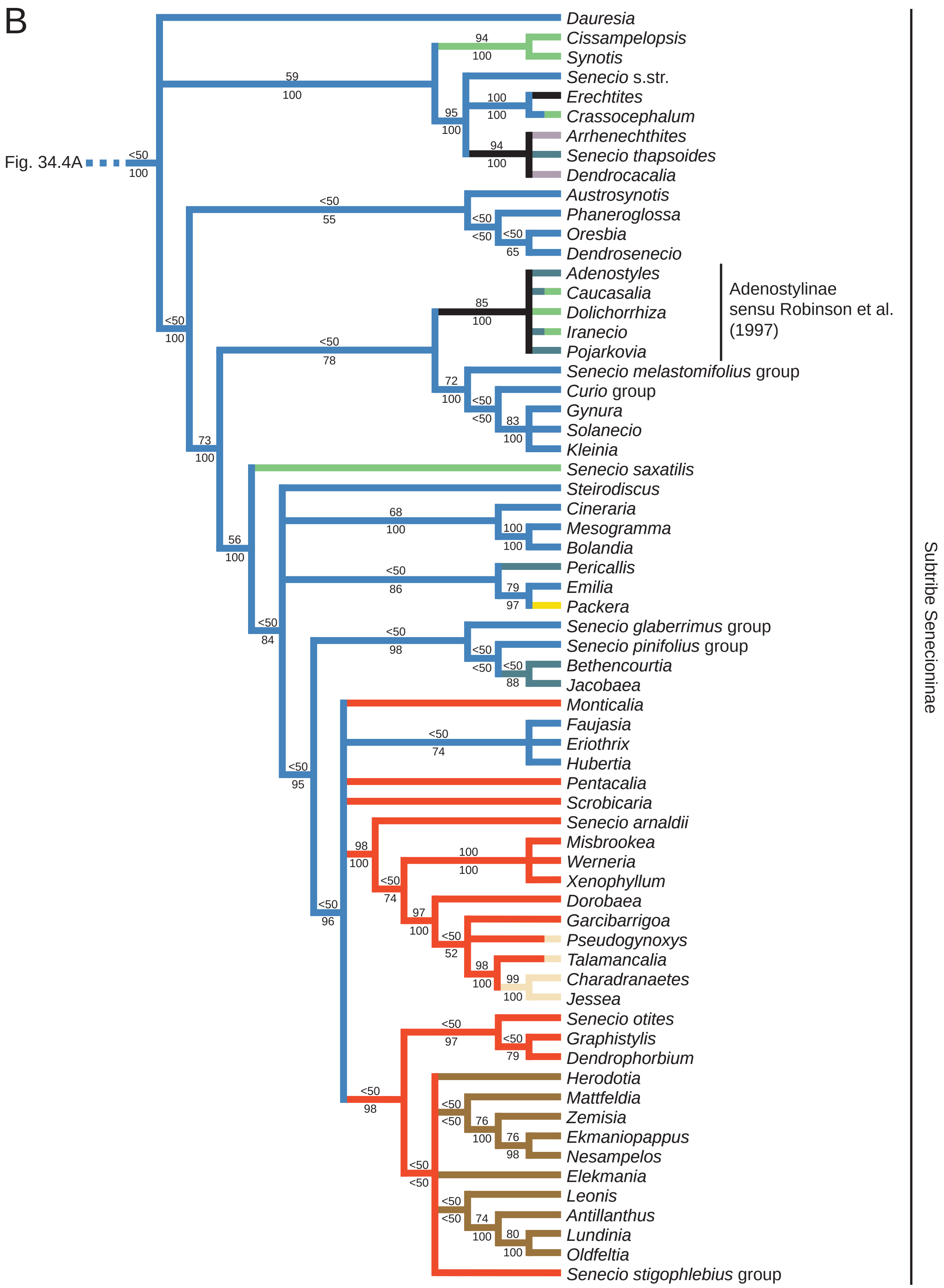


Fig. 34.4A, B. Condensed version of the ITS phylogeny of Pelser et al. (2007). Branches were collapsed for clades for which the parsimony and Bayesian analyses of the original dataset resulted in conflicting topologies. Bootstrap values are indicated above the branches and Bayesian consensus percentages (posterior probabilities ×100) below the branches. Branches are colored to show the results of an area optimization analysis using MacClade. See Chapter 44 for the metatree of the family.


B
Fig. 34.4A
<50
100
Dauresia
59
100
94
100
Cissampelopsis
Synotis
Senecio s.str.
95
100
100
100
Erechtites
Crassocephalum
94
100
Arrhenechthites
Senecio thapsoides
Dendrocacalia
<50
55
Austrosynotis
<50
<50
Phaneroglossa
<50
65
Oresbia
Dendrosenecio
<50
100
85
100
Adenostyles
Caucasalia
Dolichorrhiza
Iranecio
Pojarkovia
Adenostylinae
sensu Robinson et al.
(1997)
<50
78
72
100
Senecio melastomifolius group
<50
<50
Curio group
83
100
Gynura
Solanecio
Kleinia
73
100
Senecio saxatilis
56
100
Steirodiscus
68
100
Cineraria
100
100
Mesogramma
Bolandia
<50
86
Pericallis
79
97
Emilia
Packera
<50
84
<50
98
Senecio glaberrimus group
<50
<50
Senecio pinifolius group
<50
88
Bethencourtia
Jacobaea
Monticalia
<50
74
Faujasia
Eriothrix
Hubertia
<50
95
Pentacalia
Scrobicaria
98
100
Senecio arnaldii
<50
74
100
100
Misbrookea
Werneria
Xenophyllum
<50
96
97
100
Dorobaea
<50
52
Garcibarrigoa
Pseudogynoxys
98
100
Talamancalia
99
100
Charadranaetes
Jessea
<50
97
Senecio otites
<50
79
Graphistylis
Dendrophorbium
<50
98
Herodotia
<50
<50
Mattfeldia
76
100
Zemisia
76
98
Ekmaniopappus
Nesampelos
<50
<50
Elekmania
<50
<50
Leonis
74
100
Antillanthus
80
100
Lundinia
Oldfeltia
Senecio stigophlebius group
Subtribe Senecioninae

2007) (Fig. 34.4A) and contains a clade with the South American genera *Aequatorium*, *Gynoxys*, *Nordenstamia*, and *Paragynoxys*, which is sister to a clade with seven genera from Central and North America (e.g., *Arnoglossum*, *Pittocaulon*, *Psacalium*, and *Roldana*). The fourth subclade of Tussilagininae s.str. is the *Ligularia*-*Cremanthodium*-*Parasenecio* complex (*L-C-P* complex; Liu et al. 2006) (Fig. 34.4A). This subclade is largely Asian and is composed of eleven genera, some of which are not monophyletic. One of the few assemblages within the *L-C-P* complex that receives high support in the ITS and plastid trees of Liu et al. (2006) and Pelser et al. (2007) is subtribe Tephroseridinae of Jeffrey and Chen (1984), which is composed of *Nemosenecio*, *Sinosenecio*, and *Tephroseris*.

***Senecio medley-woodii–Brachyglottis* clade. —** The monophyly of the *Senecio medley-woodii*–*Brachyglottis* clade is well supported by ITS data (Fig. 34.4A). It includes a mostly southern Australasian subclade of *Bedfordia*, *Brachyglottis*, *Centropappus*, *Dolichoglottis*, *Haastia*, *Papuacalia*, *Traversia*, and *Urostemon* as well as the South American genus *Acrisione* (Fig. 34.2D–F) (Wagstaff and Breitwieser 2004). Sister to the *Brachyglottis* alliance is a subclade composed of succulent species from South Africa presently assigned to *Senecio* (*S. haworthii* Sch.Bip. [Fig. 34.1G], *S. medley-woodii* Hutch., *S. pyramidatus* DC., and *S. scaposus* DC.), but resembling other tussilaginoid lineages in micromorphological characters (Pelser et al. 2007).

Othonninae. — *Euryops* (Fig. 34.3A–C) and *Othonna* are the main elements of subtribe Othonninae, in addition to *Gymnodiscus*, *Hertia*, and *Lopholaena* (Fig. 34.4A). This subtribe was recognized by Bentham (1873a) and Hoffmann (1890–1894), although South American *Werneria* was also included. Our analyses support the distinction of Othonninae as a subtribe separate from Senecioninae s.str. Additionally, species of *Othonna* fall into two clades that are also morphologically distinct. Their phylogenetic positions and taxonomy are currently under investigation (Nordenstam and Devos, in prep.).

Senecioninae. — Low support values and incongruence between ITS, plastid, and combined datasets indicate that the affinities of many of the lineages and genera in subtribe Senecioninae are insufficiently known (Pelser et al. 2007). Thus the phylogenetic position of the genera in this subtribe presented in the ITS tree (Fig. 34.4B) should be viewed with caution.

Thus far, the small Namibian genus *Dauresia* appears to be one of the earliest lineages that arose in subtribe Senecioninae, although its precise phylogenetic position remains elusive (Fig. 34.4B). It may be related to *Cissampelopsis* and *Synotis*, with which it shares macro- and micromorphological characters (Nordenstam and Pelser 2005; Pelser et al. 2007). The latter two genera form a clade sister to a well-supported clade containing *Arrhenechthites*, *Crassocephalum* (Fig. 34.1H), *Dendrocacalia*, *Erechtites*, *Senecio* s.str., and *Senecio thapsoides* DC. (Fig. 34.4B). The latter singular species appears to be more closely related to *Arrhenechthites* and *Dendrocacalia* than to *Senecio*, from which it should therefore be excluded.

The genera *Aetheolaena*, *Culcitium*, *Hasteola*, *Iocenes*, *Lasiocephalus*, and *Robinsonia* are found nested in *Senecio* s.str. (Pelser et al. 2007) (Fig. 34.4B) and should be included in that genus. On the other hand, several lineages hitherto assigned to *Senecio* prove to be more closely related to other genera in Senecioninae and will have to be excluded from *Senecio*, as outlined below.

The African genera *Austrosynotis*, *Dendrosenecio* (Fig. 34.1E), *Oresbia*, and *Phaneroglossa* form a weakly supported clade that is placed by the ITS data in a relatively basal position in the subtribe (Fig. 34.4B). Plastid and combined data, however, indicate a more nested position within Senecioninae (Pelser et al. 2007).

In addition, the phylogenetic position of the clade composed of *Adenostyles*, *Caucasalia*, *Dolichorrhiza*, *Iranecio*, and *Pojarkovia* (i.e., the "Quadridentate Group", or subtribe Adenostylinae) is incongruent between ITS and plastid data. Whereas the plastid and combined-data trees suggest a position close to, among others, *Cineraria*, *Emilia*, *Misbrookea*, *Monticalia*, and *Pericallis* (Pelser et al. 2007), ITS data place this clade sister to a predominantly succulent clade formed by *Kleinia* and allied genera (Fig. 34.4B). In turn, *Kleinia* is most closely related to *Gynura* and *Solanecio*. In ITS, plastid, and combined trees, these three genera form a well-supported clade together with two subclades of succulent species (the *Senecio melastomifolius* Baker- and *Curio* groups [Fig. 34.1C]) that are most commonly placed in *Senecio* (Pelser et al. 2007). Also *Senecio saxatilis* Wall. ex DC., a representative of the Indian *Senecio* sect. *Madaractis* (DC.) Hook. f., is only remotely related to *Senecio* and needs to be excluded from the genus.

Due to conflicting topologies obtained from parsimony and Bayesian analyses of the ITS dataset (Pelser et al. 2007), *Steirodiscus* is placed in a polytomy with a clade formed by *Bolandia*, *Cineraria*, and *Mesogramma*, a weakly-supported clade composed of *Emilia*, *Packera*, and *Pericallis*, and a clade that includes *Bethencourtia*, *Jacobaea* (Fig. 34.3D–F), two lineages of species usually ascribed to *Senecio* (the *S. glaberrimus*- and *S. pinifolius* groups), a Madagascan clade (*Eriothrix*, *Faujasia*, and *Hubertia*), and most Central and South American genera of subtribe Senecioninae (Fig. 34.4B). These New World lineages receive high branch support, especially the clade formed by *Charadranaetes*, *Dorobaea*, *Garcibarrigoa*, *Jessea*, *Misbrookea*, *Pseudogynoxys*, *Senecio arnaldii*, *Talamancalia*, *Werneria*, and *Xenophyllum* (Fig. 34.4B). Within this clade, the subclade composed of *Misbrookea*, *Werneria*, and *Xenophyllum* is sister to a strongly supported subclade formed by *Charadranaetes*, *Dorobaea*, *Garcibarrigoa*, *Jessea*, *Pseudogynoxys*, and *Talamancalia*.

TAXONOMY

Tribe Senecioneae Cass. (1819)

Herbs, shrubs, lianas, epiphytes, treelets, or trees. Monoecious, rarely dioecious. Leaves usually alternate, rarely opposite; sessile or petiolate; entire or variously lobed or dissected; sometimes succulent or spiny. Inflorescence terminal or lateral; composed of a single capitulum or capitula organized in corymbose, paniculate, or thyrsoid synflorescences. Capitula homo- or heterogamous; often yellow flowered. Involucre usually uniseriate; additional smaller bracts (calyculus) present or absent. Involucral bracts mostly free, sometimes partially connate. Receptacle epaleate; usually without projections; hairy or glabrous. Marginal florets of heterogamous capitula female, sometimes sterile; radiate or disciform. Florets of homogamous capitula and central florets of heterogamous capitula perfect or functionally male, rarely female; discoid. Corolla of discoid and disciform florets tubular to funnel-shaped or with a campanulate limb; 5- or rarely 4-lobed. Anthers 5, rarely 4; tetrasporangiate, rarely bisporangiate; apical appendage flat; ecalcarate; ecaudate or sometimes caudate; endothecial tissue radial or polarized, rarely transitional; filament collar cylindrical with uniformly shaped cells, or balusterform with larger cells basally. Pollen caveate (columellae in the pollen wall partly separated from the foot layer); columellae usually solid (senecioid), sometimes with internal foramina (helianthoid). Style bifid or unbranched; apex truncate, rounded, or conical, sometimes with elongated appendage; papillate or hirsute, or only apically with short sweeping hairs or minute papillae, sometimes with a central tuft or pencil of hairs or fused papillae; stigmatic areas in two bands or partly or entirely continuous. Achenes terete, elliptic-oblong, or obovoid; sometimes triquetrous flattened, winged, or angled; often ribbed; glabrous or variously pubescent; carpopodium distinct or indistinct, ring-like. Ovary wall crystals often present, variously sized, often prismatic, isodiametric or longer than wide, sometimes drusiform. Pappus usually of few to many bristles, occasionally reduced to scales, sometimes absent; persistent or caducous; bristles uni- to multiseriate, barbellate to subplumose, usually white.

Subtribal classification

Recent phylogenetic analyses of DNA sequence data provide evidence for a revised subtribal classification. The core of former Blennospermatinae should be included within subtribe Tussilagininae s.str., which includes many genera traditionally placed in this subtribe. *Abrotanella*, however, forms a subtribe of its own: Abrotanellinae. Subtribes Adenostylinae and Tephroseridinae should be abolished, because they are deeply nested within subtribes Senecioninae and Tussilagininae s.str., respectively. The subtribal affiliations of *Chersodoma* and the *Senecio medley-woodii*–*Brachyglottis* may merit status as separate subtribes, but further investigations are needed before taxonomic changes on this level are made. On the other hand, subtribe Othonninae seems well supported and worth distinction from Senecioninae s.str. If future studies show that *Doronicum* is part of Senecioneae, this genus is best placed in a monogeneric subtribe Doronicinae. In summary, Abrotanellinae (monogeneric), Othonninae, Senecioninae, and Tussilagininae are the only subtribes supported by molecular data (Pelser et al. 2007). All remaining previously described subtribes should be abolished due to a nested position.

Generic classification

Ongoing studies into the generic delimitation of Senecioneae have resulted in many taxonomic changes in the past decades. In the search for monophyletic generic concepts, including *Senecio*, many genera have been newly described or resurrected for segregate lineages, and some previously distinguished genera have been synonymized. The revision of the generic delimitation of Senecioneae has not yet been completed, however. Segregates of several genera are still to be accommodated in new or already named genera. Here we give an overview of the taxonomic changes since Bremer's account of the tribe (1994) and highlight some species assemblages which are in need of revision.

New and resurrected genera. — In Bremer (1994) 120 genera of Senecioneae were recognized. The latest overview of the tribe by Nordenstam (2007) recognized 151 genera (150 numbered genera plus *Jacobaea*). In total 32 genera have been added in a relatively short period of time and these are listed in Table 34.1.

Most of the newly added genera are segregates of *Senecio*, and it is noteworthy that ten of these are from the Greater Antilles, where indigenous species of *Senecio* s.str. are absent. Five new genera segregated from *Senecio* (*Charadranaetes*, *Jessea*, *Robinsonecio*, *Talamancalia*, and *Villasenoria*) are from Central America including Mexico. Other elements removed from *Senecio* are *Dauresia* and *Curio* (Fig. 34.1C) in southern Africa and *Caucasalia* in Eurasia.

The Andean genus *Werneria* has been divided into three genera with *Misbrookea* and *Xenophyllum* distinguished as new. The African genus *Cineraria* has been more accurately defined, resulting in the recognition of two new genera, *Bolandia* and *Oresbia*. *Nordenstamia* has been segregated from *Aequatorium*, and *Ligulariopsis* from *Ligularia* (Fig. 34.2A–C), the latter split perhaps on questionable grounds, because *Ligulariopsis* appears to be nested within *Ligularia* (Liu et al. 2006; Pelser et al. 2007). Only one new genus is an entirely new discovery, viz., the singular *Caxamarca* from Peru. Four old generic names have been placed into use for genera now resurrected, viz., *Bethencourtia*, *Jacobaea* (Fig. 34.3D–F), *Mesogramma*, and *Centropappus*. A single genus, *Haastia*, has been transferred in from another tribe,

Table 34.1. Genera of Senecioneae added since 1994.

Antillanthus B. Nord. (Nordenstam 2006c)

Bethencourtia Choisy (syn. *Canariothamnus* B. Nord., resurrected by Nordenstam 2006b, e)

Bolandia Cron (Cron et al. 2006)

Caucasalia B. Nord. (Nordenstam 1997)

Caxamarca Dillon & Sagástegui (Dillon and Sagástegui-Alva 1999)

Centropappus Hook. f. (resurrected by Nordenstam 2007)

Charadranaetes J. Janovec & H. Rob. (Janovec and Robinson 1997)

Curio P.C. Heath (Heath 1997)

Dauresia B. Nord. & Pelser (Nordenstam and Pelser 2005)

Ekmaniopappus A. Borhidi (Borhidi 1992)

Elekmania B. Nord. (Nordenstam 2006c)

Haastia Hook. f. (Wagstaff and Breitwieser 2002, 2004; Breitwieser and Ward 2005)

Herreranthus B. Nord. (Nordenstam 2006c)

Ignurbia B. Nord. (Nordenstam 2006d)

Io B. Nord. (Nordenstam 2003)

Jacobaea Mill. (resurrected by Pelser et al. 2006; Nordenstam 2006a) (Fig. 34.3D–F)

Jessea H. Rob. & Cuatrec. (Robinson and Cuatrecasas 1994)

Leonis B. Nord. (Nordenstam 2006c)

Ligulariopsis Y.L. Chen (Chen 1996)

Lundinia B. Nord. (Nordenstam 2006c)

Mesogramma DC. (resurrected by Nordenstam and Pelser 2005)

Misbrookea V.A. Funk (Funk 1997a)

Nesampelos B. Nord. (Nordenstam 2006c)

Nordenstamia Lundin (Lundin 2006)

Oldfeltia B. Nord. & Lundin (Nordenstam and Lundin 2002)

Oresbia Cron & B. Nord. (Cron and Nordenstam 2006)

Pseudojacobaea (Hook. f.) R. Mathur (Rao et al. 1988)

Robinsonecio T.M. Barkley & J.P. Janovec (Barkley and Janovec 1996)

Talamancalia H. Rob. & Cuatrec. (Robinson and Cuatrecasas 1994)

Villasenoria B.L. Clark (Clark 1999)

Xenophyllum V.A. Funk (Funk 1997b)

Zemisia B. Nord. (Nordenstam 2006c)

viz., Astereae, where the genus had been misplaced since its description. In addition there are two name changes, *Capelio* B. Nord. for *Alciope* DC. (Nordenstam 2002) and *Psednotrichia* Hiern for *Xyridopsis* B. Nord. (Anderberg and Karis 1995).

Synonymized genera. — As a result of our phylogenetic analyses (Pelser et al. 2007), a number of genera need to be sunk into *Senecio*. These include some well-known and long recognized genera, but also some taxa of previously uncertain status.

Robinsonia of the Juan Fernández Islands has long been regarded as a taxonomically isolated endemic genus, characterized by its shrubby to arboreal habit and dioecious capitula, and was at some time even regarded as three different genera (*Robinsonia*, *Rhetinodendron*, and *Symphyochaeta*; Skottsberg 1953). Its members are nested within *Senecio* s.str. and *Robinsonia* will be sunk in *Senecio*.

The Andean genera *Aetheolaena*, *Culcitium*, and *Lasiocephalus* have been notoriously difficult to define and distinguish from each other and from *Senecio*. The molecular data place them strongly nested within *Senecio*. The same is true for the Patagonian genus *Iocenes*. These four genera were defined by apomorphic characters of floret color and style morphology, or adaptive features typical of high montane habitats, such as nodding and discoid capitula, and dense pubescence. The North American *Hasteola* was distinguished by its rhizomatous habit and the narrow discoid capitula with white florets, but its affinities are clearly with *Senecio* sect. "*Triangulares*" (Jeffrey 1992), which comprises North American species such as *S. triangularis* Hook. and *S. eremophilus* Phil.

Anticipated taxonomic changes. — Our phylogenetic analyses (Pelser et al. 2007) suggest that approximately eight to ten species or species groups still remain to be removed from *Senecio* in order to achieve a monophyletic *Senecio*. These include the South American sections *Adamantina* (with *S. adamantinus* Bang., *S. stigophlebius* Baker, etc.), *Paranaia* (with *S. hemmendorffii* Malme, *S. paranensis* Malme, etc.), and *Otites* (with *S. otites* Kunze ex DC.); the Central Asian sect. *Madaractis* (with *S. grahamii* Hook. f., *S. saxatilis*, etc.); and the African sections *Pinifolii* (*S. pinifolius* Lam., *S. triqueter* Less.), *Plantaginei* (with *S. glaberrimus* DC.,, *S. latifolius* DC., *S. retrorsus* DC., etc.) and *Aphylli* (*S. junceus* (Less.) Harv. = *Brachyrhynchos juncea* Less.). For a few of these groups generic names are already available, such as *Madaractis* DC. and *Brachyrhynchos* Less., whereas others will need new names.

In addition to the above segregates, there are two succulent species groups that need to be segregated from *Senecio*: the *Curio* group (Fig. 34.1C) and the *S. medley-woodii* group (Figs. 34.1G, 34.4). The *Curio* group includes most of the African succulents, variously and inconsistently referred to as *Senecio*, *Kleinia* (including *Notonia* and *Notoniopsis*), or *Curio*. Many southern and tropical African, as well as

Malagasy species, belong to this assemblage, which requires further study. The *Senecio medley-woodii* group, consisting of a handful of South African succulent taxa, is more clearcut and will be described as a new genus.

The most confused generic taxonomy within the tribe is found in the *Brachyglottis* assemblage, which includes taxa from New Zealand and Australia (*Bedfordia*, *Brachyglottis*, *Centropappus*, *Dolichoglottis*, *Haastia*, *Papuacalia*, *Traversia*, and *Urostemon*), as well as *Acrisione* (Fig. 34.2D–F) from Chile and *Papuacalia* from New Guinea. The genus *Haastia*, a recent transfer from tribe Astereae (Wagstaff and Breitwieser 2002; Breitwieser and Ward 2005) is also nested within this group. As presently circumscribed, *Brachyglottis* is not monophyletic (Wagstaff and Breitwieser 2004; Pelser et al. 2007). The concept of *Brachyglottis* may have to be narrowed to include only the trees *B. repanda* J.R. Frost & G. Frost and *B. arborescens* W.R.B. Oliv., whereas the predominantly shrubby and herbaceous species may belong to four different genera. Even the small and highly specialized genus *Haastia* is not monophyletic in recent studies (Wagstaff and Breitwieser 2004; Pelser et al. 2007).

Among other Senecioneae genera in need of taxonomic revision are the genera that form the *Ligularia-Cremanthodium-Parasenecio* complex (Liu et al. 2006), *Dendrophorbium*, *Monticalia*, *Othonna*, *Pentacalia*, and *Roldana* (Pelser et al. 2007).

MORPHOLOGY

Tribe Senecioneae is characterized by the shape and position of the bracts that surround the capitulum. This involucre is usually composed of a single row of bracts, equal to each other in size and shape. In contrast, the tribe exhibits remarkable variation in other morphological characters, such as leaf shape and arrangement, indument, inflorescence type, and flower color (Barkley 1978).

Life forms

Senecioneae are represented in most habitats, from lakes and marshes to deserts, mountaintops, and forests. An amazing range of habits and life forms occur within the tribe, which are clearly adaptations to the variety of habitats occupied by its members.

Herbs are common in many lineages, especially in the core genus *Senecio*. The aquatic *Cadiscus* of South Africa has floating strap-shaped leaves and white-flowered capitula borne above the water surface (Fig. 34.1B). *Stenops* is semi-aquatic with stems rooting at nodes and with linear leaves. Annual herbs have evolved repeatedly in the Old World senecioids, as well as New World tussilaginoid groups. Thus annuals are common within *Senecio* (including the type, *S. vulgaris* L.) and *Emilia*, and occur in several African genera, viz., *Bafutia*, *Emiliella*, *Mesogramma*, *Oligothrix*, *Psednotrichia*, *Steirodiscus*, and *Stilpnogyne*. It is remarkable that the large African genus *Euryops* (Fig. 34.3A–C) with 100 species of shrubs also includes a single annual species in South Africa. A somewhat parallel case is found in *Othonna* (biphyletic, with ca. 120 species), a genus of perennial species, whereas the few species of the closely related *Gymnodiscus* are annual. A remarkable range of morphological variation is found in the two *Othonna* clades: herbs with or without stem or root tubers, herbs and shrubs with succulent stems or leaves, subterranean or aerial stolons, and stems with protuberances, scales or spines. Among the tussilaginoids only two genera, *Blennosperma* and *Crocidium*, are annuals. These have affinities with, and are probably derived from, genera of perennial herbs.

Shrubs are found throughout the tribe and represent the most common life form in Tussilagininae, the *Brachyglottis* assemblage, Othonninae, and Senecioninae in some areas. Scandent shrubs, or vines and lianas, are found in several unrelated groups, e.g., *Delairea* and *Mikaniopsis* of Africa, *Humbertacalia* of Madagascar, *Cissampelopsis* of southeast Asia, and also West Indian *Leonis* and *Nesampelos*, and South and Central American *Dresslerothamnus*, *Paracalia*, and *Pseudogynoxys*. The large neotropical genus *Pentacalia* consists of both lianas and epiphytes. The latter are otherwise rare in the tribe but found also in *Nelsonianthus*, *Solanecio*, *Urostemon* and the Malagasy species *Senecio francoisii*.

Trees have evolved in different groups of the tribe. In Tussilagininae s.str. they occur in genera of the gynoxoid group, viz., *Aequatorium*, *Gynoxys*, *Paragynoxys*, and especially in *Nordenstamia*, where they can attain 18 meters in height. In the largely Australasian *Brachyglottis* group, small trees are found in various genera, such as in *Acrisione* (Fig. 34.2D–F), *Bedfordia*, *Brachyglottis*, *Papuacalia*, and *Urostemon*. Yet, in the same group are the cushion-plants of *Haastia* in New Zealand, sometimes called “vegetable sheep”. The remarkable trees of St. Helena, *Lachanodes* and *Pladaroxylon*, must also be mentioned; their relationships are still unknown. The well known “tree groundsels” of the tropical African mountains, *Dendrosenecio*, are regarded as “woody herbs”, secondarily derived tree-like plants with herbaceous ancestors (Fig. 34.1E). Such “dendroforbs” are also found in Andean *Dendrophorbium* species.

Pubescence

Senecioneae exhibit wide variation in indument types, which may be taxonomically useful on different hierarchical levels (Drury and Watson 1965; Ali 1969; Sahu 1983; Vincent and Wilson 1997; Pelser et al. 2004), but will not be discussed at length here. Truly stellate hairs are rare and serve to characterize the New World genera

Aequatorium and *Dresslerothamnus*, whereas *Nordenstamia* differs from *Aequatorium* by pseudo-stellate trichomes, which are variously and irregularly branched and non-peltate. Stellate hairs have also been recorded occasionally in other lineages (e.g., *Euryops anthemoides* B. Nord.). The Australasian *Bedfordia* was erroneously reported in early literature (e.g., Bentham 1873a, b) as possessing a stellate tomentum, but its trichomes are actually unbranched (Mattfeld 1940; Willis 1967; Drury 1973). Achene hairs of the duplex type (twin hairs), common in the family (Hess 1938), are widespread in the tribe. They are typically three-celled with two parallel cells and a smaller basal cell. Sometimes they are myxogenic, i.e., have mucilaginous properties when soaked in water, especially in taxa of arid regions (*Dauresia*, *Dolichoglottis*, *Euryops*, *Jacobaea* species, *Mesogramma*, *Senecio* species, among others).

Floral micromorphology and anatomy

Floral microstructures provide the most important diagnostic characters in the tribe, as in the family at large. The endothecial tissue of the stamens has characteristic and distinct thickenings along the cell walls (Dormer 1962). If these thickenings are concentrated to the short latitudinal cell walls, the endothecium is termed polarized, and if distributed along the longitudinal walls, termed radial. In subtribes Senecioninae and Othonninae, the endothecium is radial in all genera except *Dauresia*, *Graphistylis*, and perhaps *Synotis*. In Tussilagininae s.str. a polarized endothecium is the rule, but the radial type has been recorded in several genera (*Tephroseris*, *Nemosenecio*, *Psacaliopsis*, *Psacalium*, *Arnoglossum*); in *Sinosenecio* both types and an intermediate pattern seem to occur (Jeffrey and Chen 1984).

The filament collar is the upper part of the filament, shaped as a grooved cylinder or baluster with a distinct cellular structure. A cylindrical (or semi-cylindrical) collar of uniformly shaped cells is found in all tussilaginoid genera including the *Senecio medley-woodii*–*Brachyglottis* clade. The senecioid genera have a balusterform collar, which is more or less distinctly basally swollen with larger cells. Sometimes the basal dilation is very prominent (e.g., *Oligothrix*, *Pericallis*, *Stenops*). The anthers are non-calcarate throughout the tribe, and the anther base may be rounded, acute or sagittate, or caudate, sometimes with long branching tails. *Senecio* s.str., as defined by Pelser et al. (2007), has ecaudate anthers. Caudate anthers are characteristic of the synotoid groups (Jeffrey 1979, 1992) and *Dauresia*, which may be closely related to one of the synotoid groups including *Austrosynotis*, *Cissampelopsis*, *Mikaniopsis*, and *Synotis*. The other synotoid clade, which is restricted to the Malagasy region (*Faujasia*, *Hubertia*, etc.), likewise has caudate anthers, which also occur in various other unrelated lineages, e.g., in the West Indian group (*Jacmaia*, *Odontocline*, *Oldfeltia*, *Lundinia*), in the Macaronesian *Bethencourtia*, and in the Australasian *Brachyglottis* clade (*Urostemon*).

The styles of the disc florets provide useful taxonomic characters at different hierarchical levels. The typical senecioid style, as found in *Senecio* s.str., is two-branched with two parallel stigmatic bands on the inside (adaxially), and the glabrous style branches are truncate with apical sweeping hairs. Although this type is found in many senecioid genera, there is much variation, and continuous stigmatic areas are found in different lineages, e.g., in South African *Phaneroglossa* and *Lamprocephalus*, tropical African *Dendrosenecio* (Fig. 34.1E), Madagascan *Io*, and several Caribbean genera (*Antillanthus*, *Jacmaia*, *Odontocline*, etc.). Continuous stigmatic surfaces are the rule in Tussilagininae s.l., but there are exceptions. Separate stigmatic areas are found in *Crocidium* and in some genera the stigmatic areas are separated for their greater part but apically fused (*Brachyglottis* spp., *Cacaliopsis*, *Luina*). Stylar structure is variable also in other respects. The style branches are often glabrous except for the apical sweeping hairs, but in some taxa they are distinctly hirsute or papillate abaxially (*Hertia*, *Lopholaena*, a.o.). Apical appendages are often present as elongated glabrous, papillate, or hairy structures (*Dicercoclados*, *Gynura*, *Jacmaia*, *Lamprocephalus*) or a central tuft or hair pencil (*Arbelaezaster*, *Bolandia*, *Pseudogynoxys*, *Senecio* spp.). The sterile styles of *Othonna* and *Gymnodiscus* are undivided and often have a terminal conical appendage.

Calcium oxalate is often present in the ovary walls of the achenes (Dormer 1961), sometimes as prismatic plate- or needle-like crystals, sometimes as irregular druses. Their taxonomic value has not yet been fully explored, but it is noteworthy that the *Gynura*-*Solanecio*-*Kleinia* subclade (Fig. 34.4B) has drusiform crystals (Nordenstam 1978; Jeffrey 1986), whereas distinct plate- or needle-like crystals are found in *Pericallis*, *Senecio* s.str., and many other senecioid as well as tussilaginoid genera (Nordenstam 1978).

The pappus consists of barbellate bristles, which may be persistent or caducous, usually white but sometimes colored (yellowish, tawny, red, or purple), mostly slender but sometimes coarse and stiff. Rarely the pappus is reduced to a few scaly bristles (*Cadiscus*) or reduced to a single scale (*Emiliella*). Loss of pappus has occurred independently in many different lineages, such as Abrotanellinae, Blennospermatinae, Othonninae (*Euryops* p.p., *Stenops*), and Tussilagininae (*Pippenalia*).

Several members of the tribe possess resin ducts (schizogenous secretory canals) in tissues of stems, leaves and roots, sometimes also in floral parts, and even in cotyledons. The resin production may be copious and easily noted as stickiness and exudates on vegetative parts. This occurs in the tussilaginoid group (*Brachyglottis adamsii* (Cheesem.) B. Nord., *Centropappus*, *Traversia*) as well as in senecioids (*Euryops*, *Othonna*).

POLLEN

The pollen grains in the tribe generally lack internal foramina in the exine. This is often referred to as the senecioid (senecionoid) pollen type (Bain et al. 1997; Bain and Golden 2000). The helianthoid type, defined by the presence of small internal foramina, is present in a few genera of Senecioneae, notably *Doronicum*, *Farfugium*, *Gynura*, *Pericallis*, and *Packera* (Bain and Walker 1995; Liu 2000; Skvarla and Turner 1966; Skvarla et al. 1977). The tribal position of *Doronicum* is not yet finally resolved, as mentioned elsewhere in the present paper. ITS phylogenies indicate that *Pericallis* and *Packera* are related to each other (Panero et al. 1999) and form a weakly supported senecioid clade also including *Emilia* (Pelser et al. 2007; Fig. 34.4). However, the pollen of *Emilia coccinea* (Sims) G. Don has been reported as senecioid (Skvarla et al. 1977). Further investigations of exine pattern and structure in this group are needed.

CHROMOSOME NUMBERS

The original basic chromosome number in Senecioneae is probably $x = 10$ (cf. Ornduff et al. 1963; Nordenstam 1977; Robinson et al. 1997). From this basic number, higher as well as lower levels have been derived by polyploidization and stabilization of secondary basic numbers, by reduction through loss of chromosomes, and by haploidization to $x = 5$. The latter number has, from time to time, been suggested as the basic number in the tribe (e.g., Turner and Lewis 1965; Dematteis and Fernàndez 1998; López et al. 2005), but is probably secondarily derived from $x = 10$. It occurs only in some unrelated lineages, such as within *Crassocephalum* (Fig. 34.1H) and *Gynura*, and in some annual species of *Emilia*.

The basic karyologic pattern is $x = 10$ in the senecioid assemblages and $x = 30$ or numbers derived from that number in the tussilaginoid groups. The reduction series from $x = 30$ can be exemplified by the following genera (although some early published counts may not be reliable; cf. Liu 2004): *Barkleyanthus*, *Dendrocacalia*, *Digitacalia*, *Pittocaulon*, *Robinsonecio*, *Roldana*, and several others, $n = 30$; *Ligularia*, *Parasenecio*, $n = 30, 29$; *Endocellion*, *Homogyne*, $n = 30, 29, 28$; *Miricacalia*, $n = 30, 27, 26$; *Cremanthodium*, *Ligulariopsis*, *Sinacalia*, $n = 29$; *Rugelia*, $n = 28$; *Arnoglossum*, $n = 28, 27, 26, 25$; *Syneilesis*, $n = 26$.

Further reduction seems to have taken place in the tephroserioid lineage, where $n = 24$ and 23 frequently occur in *Nemosenecio*, *Sinosenecio*, and *Tephroseris*.

A stepwise reduction from other levels, viz., $n = 10$ or 20, has occurred independently in some groups. Examples are $n = 9$ in the tussilaginoid *Blennosperma*, *Crocidium*, and *Ischnea* (where also $n = 7$ and 16 are recorded), and in the senecioid *Gymnodiscus*, which is close to *Othonna* with $x = 10$. Dysploid reduction is a phenomenon occurring in arid regions in connection with speciation within the family (Jeffrey 2007: 68), and there may be a correlation with the evolution of an annual life form (*Blennosperma*, *Crocidium*, and *Gymnodiscus* are all annuals that are closely related to perennial taxa).

The unusual $n = 19$ is known in *Lordhowea*, a few species of *Senecio* (incl. *Hasteola*), and also *Adenostyles* and *Caucasalia*, undoubtedly derived independently by dysploid reduction from the common $n = 20$.

Instances of polyploidy are scattered throughout the tribe (*Othonna*, *Senecio*, *Tephroseris*, etc.). The *Werneria* group in the high Andes (i.e., *Misbrookea*, *Werneria*, *Xenophyllum*) have an especially complicated karyology with high polyploid and aneuploid numbers in the range $n = 21$–111, but frequently around 50–58.

CHEMISTRY

The tribe is well characterized by the presence of pyrrolizidine alkaloids (PAs) of the macrocyclic senecionine type (Hartmann and Witte 1995; Pelser et al. 2005), which, unlike most plant alkaloids, are derived from the amino acid ornithine. These PAs are a deterrent and are toxic to most vertebrates and insects (Boppré 1986; Schneider 1987; Macel 2003). They provide plants with a chemical defense against herbivores, causing loss of livestock in some regions; well-known examples are provided by *Jacobaea vulgaris* Gaertn., an important invasive weed in many countries, various *Senecio* species in southern Africa (Watt and Breyer-Brandwijk 1962), and members of the *Senecio glaberrimus* group, which does not belong in *Senecio* s.str. The alkaloid contents can be very high; in *Senecio riddellii* Torr. & A. Gray 18% alkaloid content of leaf dry weight has been reported (Hegnauer 1989). PAs of the macrocyclic senecionine type comprise a diverse class of more than 100 structures, the distribution of which in Senecioneae appears to be largely incidental with lineages showing large intra- and interspecific qualitative and quantitative variation (Pelser et al. 2005). PAs are therefore probably not taxonomically very useful within the tribe.

The sesquiterpene lactones known as eremophilanes and furanoeremophilanes are excellent phytochemical markers of the tribe (Hegnauer 1989). They are highly diverse and variation of their chemical structure may prove useful in subtribal and generic classification. Other sesquiterpenes that may be characteristic of the tribe are oplopanone derivatives, which have been reported from *Acrisione* (Fig. 34.2D–F), *Arnoglossum*, *Euryops* (Fig. 34.3A–C), *Kleinia*, *Rugelia*, and *Senecio* (Abdel Aal et al. 1988; Hegnauer 1989).

Polyacetylenes are widespread and common in the family, but practically absent from Senecioneae (Robins 1977). They have been reported in *Doronicum*, which has been mentioned as perhaps anomalous in the tribe. *Doronicum* is otherwise phytochemically very close to other Senecioneae, having sesqui- and triterpenes, thymol and tremetone derivatives (like some *Senecio* spp.), and notably pyrrolizidine alkaloids (Hegnauer 1989).

Coumarins, which are common in asteroid tribes, are also absent from Senecioneae (Zdero and Bohlmann 1990). Chinoid compounds of chinol type have been found in *Cineraria*, *Emilia*, *Jacobaea* (Fig. 34.3D–F), *Senecio*, and *Tephroseris* (Hegnauer 1989); their taxonomic value is not known. The copious resin of *Euryops* and a few other genera contains esters of acids like butter acid (Hegnauer 1964).

The most complex flower pigment has been isolated from the florist's Cineraria, *Pericallis hybrida* B. Nord. (Goto et al. 1984), and the color variation among its cultivars is indeed striking.

BIOGEOGRAPHY

Although the tribe has a worldwide distribution, there are some marked centers of generic diversity (Fig. 34.5) and speciation. These areas include temperate and subtropical arid or montane regions, continental as well as insular. The centers coincide with some of the recognized "hot-spots" of biodiversity, although tropical forests are not represented. Very few Senecioneae inhabit tropical forests and almost none are found in rainforests. *Senecio* is the only nearly cosmopolitan genus in the tribe.

Mesoamerica

A large number of tussilaginoid genera occur in Central America, with a center of diversity in Mexico (Fig. 34.4A). *Digitacalia* (5 spp.), *Pittocaulon* (6 spp.; Fig. 34.1F), and the monotypic genera *Pippenalia* and *Villasenoria* have so far only been recorded from Mexico, whereas *Nelsonianthus* (2 or 3 spp.), *Psacaliopsis* (6 spp.), and *Robinsonecio* (2 spp.) also occur in Guatemala. Similar ranges with extensions northwards into the United States and/or southwards to Panama are found in *Barkleyanthus* (1 sp.), *Lepidospartum* (3 spp.), *Psacalium* (ca. 40 spp.), *Roldana* (ca. 65 spp.), and *Telanthophora* (14 spp.).

A small group of senecioid genera of this region have another and quite different biogeographical pattern with southern affinities (Fig. 34.4B). The monotypic *Charadranaetes* is endemic to Costa Rica, and the closely related *Jessea* (4 spp.) is distributed in Costa Rica and Panama. Also the related *Talamancalia* occurs in Costa Rica and Panama with two species, but has a disjunct distribution with another two species in Ecuador and Peru. Further studies are needed to ascertain if the species referred to *Talamancalia* are congeneric. *Dresslerothamnus* (ca. 5 spp.), found in Costa Rica and Panama as well as Colombia, should also be referred to this group. Although not yet included in the molecular analyses, its affinities are probably with the other genera mentioned.

Western and southern USA

Close to the Mesoamerican center, a number of tussilaginoid genera have a more northerly distribution, but are not represented in Mesoamerica. These include *Luina* (2 spp.) and *Tetradymia* (10 spp.), the latter of which is closely related to *Lepidospartum* (cf. above; Fig. 34.4A), and the monotypic *Cacaliopsis*, *Crocidium*, and *Rainiera*. Some genera fall slightly outside this pattern through a more southern or eastern distribution in the USA, viz. the monotypic genera *Rugelia* and *Yermo*, and *Arnoglossum* (8 spp.). Because of the obvious affinities in geographic ranges and evolutionary relationships, this region of tussilaginoid diversity may be regarded rather as a subcenter of the Mesoamerican center.

The West Indies

Until recently the majority of the West Indian species of the tribe were placed in *Senecio*, but as a result of recent revision (Nordenstam 2006c) this genus is no longer represented as indigenous in the area. Instead a substantial number of endemic genera have been recognized. They all belong to the senecioid group (subtribe Senecioninae s.str.), which is in sharp contrast to the dominance of tussilaginoid genera in the Mesoamerican center of the tribe. The West Indian genera form a close-knit group with affinities to some South American genera, and are only remotely related to *Senecio* s.str (Fig. 34.4B).

The West Indian genera are confined to the three western islands of the Greater Antilles. Jamaica is the home of *Jacmaia* (1 sp.), *Odontocline* (6 spp.), and *Zemisia* (1 sp.). Considerable diversity is found in Cuba, with four endemic genera and two genera shared with Hispaniola (*Leonis* and *Lundinia*). The largest endemic genus is *Antillanthus* with 17 species, whereas *Herreranthus*, *Oldfeltia*, and *Shafera* are monotypic, as are *Leonis* and *Lundinia*. Hispaniola has the greatest generic diversity in the region with six endemic genera, viz., *Ekmaniopappus* (2 spp.), *Elekmania* (10–12 spp.), *Nesampelos* (3 spp.), and the monotypic genera *Herodotia*, *Ignurbia*, and *Mattfeldia*, plus the two genera shared with Cuba (*Leonis* and *Lundinia*).

Andes of South America

In South America the tribe is well represented by genera of different lineages. They are mainly distributed along the High Andes, and are often shrubs or trees, although there are also some specialized herbs adapted to high mountain conditions.

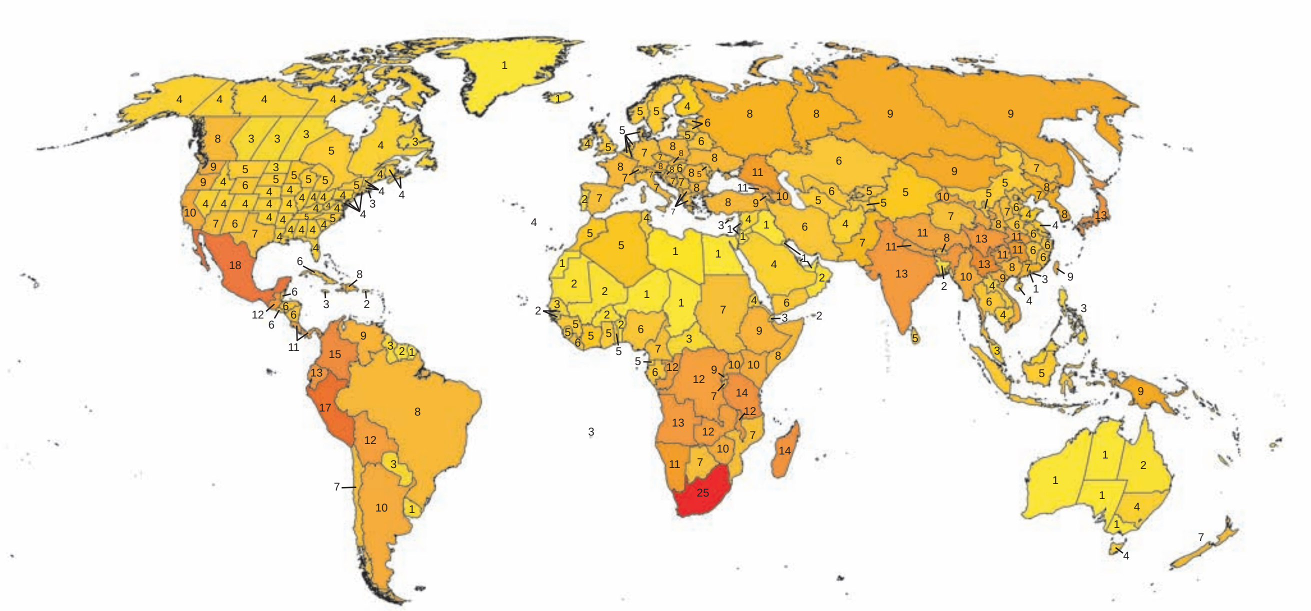


Fig. 34.5. Generic diversity of tribe Senecioneae. Numbers indicate the number of genera in each of the outlined geographic regions. The color coding of these regions ranges from light yellow (1 genus) to dark red (25 genera). The foremost center of generic diversity is South Africa (25 genera), followed by Mexico (18), Peru (17) and Colombia (15).

Within the tussilaginoid assemblage, there is a gynoxoid group consisting of *Aequatorium* (ca. 12 spp.; Ecuador to Venezuela), *Gynoxys* (> 100 spp.), *Nordenstamia* (ca. 20 spp.), *Paracalia* (2 spp.; Bolivia, Peru), and *Paragynoxys* (12 spp., Colombia, Venezuela) (Fig. 34.4A). They are erect trees or shrubs, or occasionally scandent (*Paracalia*). Two distantly related tussilaginoid genera are *Chersodoma* with nine species from Argentina to Peru, and *Acrisione* (2 spp.; Fig. 34.2D–F), which is endemic to Chile but closely related to *Brachyglottis* in New Zealand and to several other Australasian genera (Fig. 34.4A).

Within Senecioninae, a coherent group of related species comprises *Misbrookea* (1 sp.), *Werneria* (25–30 spp.), and *Xenophyllum* (21 spp.; Fig. 34.4B). They are mainly mat- or cushion-forming plants of high altitudes in the Andes.

Dorobaea (3 spp.) and *Garcibarrigoa* (2 spp.) are herbaceous Andean genera of restricted distribution in Peru and Ecuador to southern Colombia and are related to *Pseudogynoxys* (14 spp.; Fig. 34.4B). The latter genus contains scandent herbs and subshrubs and has a wider distribution from Bolivia and Brazil to Central America and Mexico. It is also allied to *Talamancalia*, which as presently defined, has two species in Ecuador and Peru and another two in Central America. The herbaceous monotypic genera *Arbelaezaster* from Colombia and *Caxamarca* from Peru need further study to identify their phylogenetic position, as does the opposite-leaved scandent shrubby *Cabreriella* (2 spp.; Colombia).

Three large South American senecioid genera are *Dendrophorbium* (ca. 75 spp.), *Pentacalia* (ca. 200 spp.) and *Monticalia* (ca. 70 spp.). The latter two are no doubt polyphyletic as presently circumscribed. They are widely distributed along the Andes, with some taxa extending north to Central America.

Southern Africa

Tussilaginoid genera in the strict sense are absent in Africa, but two interesting genera with tussilaginoid features are endemic to South Africa, viz., the shrubby Cape genus *Capelio* (3 spp.) and the *Senecio medley-woodii* group of succulent species (generic name pending; Fig. 34.1G). According to ITS data, the latter group belongs in the *S. medley-woodii–Brachyglottis* assemblage (Fig. 34.4A), which has its center of diversity in Australasia and also includes the bispecific Chilean genus *Acrisione* (Fig. 34.2D–F).

Senecioids are well represented in southern Africa with a large number of endemic genera. Some of them belong to the mainly African subtribe Othonninae (Fig. 34.4A) including the small genus *Gymnodiscus* (2 spp.), endemic to the Cape Province, and a closely allied larger genus of ca. 20–25 species presently included in *Othonna*. The true *Othonna* species (perhaps > 80 spp.) are allied to *Lopholaena* (18 spp.) and confined to southern Africa, whereas the related genus *Hertia* (ca. 10 spp.) has a wider range extending to North Africa, southwest Asia and Iran. *Euryops* (100 spp.; Fig. 34.3A–C) also belongs in the Othonninae and has a marked center in South Africa, although the genus extends with a few species outside Africa to Socotra and the Arabian peninsula.

Oresbia and *Phaneroglossa* are herbaceous or suffruticose monotypic genera endemic to the Cape and have obscure relationships (Fig. 34.4B). *Cadiscus* (1 sp.; Fig. 34.1B), *Delairea* (1 sp.), *Lamprocephalus* (1 sp.), *Oligothrix* (1 sp.), and *Steirodiscus* (5 spp.) are small endemic Cape genera of various and partly insufficiently known affinities. *Cadiscus* is an aquatic herb with white flowers (Fig. 34.1B), but despite its unusual appearance, it may be close to *Senecio* s.str. *Delairea* is presumably closely related to species of the *Curio* group (Fig. 34.4B), which also has its greatest diversity in southern Africa.

A singular genus, perhaps related to the Asian genera *Cissampelopsis* and *Synotis* (Nordenstam and Pelser 2005; Pelser et al. 2007), is *Dauresia* (2 spp.; Namibia; Fig. 34.4B). Two other South African endemic genera, *Bolandia* (2 spp.) and *Mesogramma* (1 sp.), are clearly closely related, and their affinities are with *Cineraria*, an African genus (ca. 35 spp.) with a distinct center in South Africa. *Stilpnogyne* (1 sp.; endemic to the Cape) probably also belongs to the same alliance.

Tropical continental Africa

The remarkable tree-groundsels of *Dendrosenecio* (11 spp.; Fig. 34.1E) are endemic to east Africa and adapted to high altitude conditions on the tropical mountains. Very different life forms are represented by the modest aquatic or semi-aquatic herbs of *Stenops* (2 spp.) and the small annuals of *Bafutia* (1 sp.; Cameroon), *Psednotrichia* (2 sp.; Angola), and *Emiliella* (5 spp.; Angola and Central Africa). The latter is related to *Emilia*, which is a large herbaceous genus (ca. 100 spp.) with a center in tropical Africa. *Austrosynotis* (1 sp.), *Mikaniopsis* (15 spp.), *Solanecio* (16 spp.) and *Crassocephalum* (24 spp.; Fig. 34.1H) are other tropical African genera with different affinities and life forms. The two latter genera extend into Madagascar and Yemen. Also *Kleinia* is mainly African although represented in the Canary Islands, Arabia, Sri Lanka and India.

Madagascar and Mascarenes

Different endemic senecioid lineages are found in this important center of biodiversity. One group consists of obviously related shrubby genera that share a common ancestor. *Humbertacalia* (9 spp.) and *Hubertia* (ca. 25 spp.) occur in Madagascar and La Reunión. Some genera absent from Madagascar occur on Mauritius and La Reunión, viz., *Faujasiopsis* (3 spp.) and *Parafaujasia* (2 spp.). *Eriothrix* (2 spp.) and *Faujasia* (4 spp.) are restricted to La Reunión.

An endemic genus of uncertain affinity is the monotypic *Io* from Madagascar. A group of about 20 succulent species still placed in *Senecio* (*S. melastomifolius*, *S. crassissimus* Humbert, etc.; Group XVI in Humbert 1963) may constitute a new genus related to *Curio* (Fig. 1C), *Gynura*, *Kleinia*, and *Solanecio* on the African continent.

Southeast Asia and Japan

This is an important center with a rich diversity in the tussilaginoid group. Large genera with a wide distribution have centers of diversity in this region (*Ligularia* [Fig. 34.2A–C], *Parasenecio*, *Tephroseris*), and there are a number of endemic genera. The largest of these is *Sinosenecio* with ca. 40 species restricted to southwest China (when species from Korea and Canada are removed that have been previously included). Others are *Nemosenecio* (6 spp.; China, Japan), *Farfugium* (3 spp.; China, Korea, Taiwan, Japan), *Sinacalia* (4 spp.; China), *Syneilesis* (7 spp.; east Asia), and the monotypic genera *Dendrocacalia* (Japan), *Dicercoclados* (China), *Ligulariopsis* (China; doubtfully distinct from *Ligularia*), and *Miricacalia* (Japan).

The senecioid genus *Cissampelopsis* (10 spp.) falls slightly outside of the core geographic range and as well as being divergent in its relationships (Fig. 34.4B). It is distributed in East Asia to Indonesia and has close affinities to the mainly central Asian *Synotis*.

Australia–New Zealand

The *Brachyglottis* alliance has its center of diversity in Australasia. There are several elements endemic to New Zealand, Tasmania, and mainland Australia. *Brachyglottis*, as presently defined (30 spp.), is endemic to New Zealand and polyphyletic. Related monotypic genera, sometimes included in *Brachyglottis*, are *Centropappus* (Tasmania) and *Urostemon* (North Island of New Zealand). *Traversia* (1 sp.; New Zealand), *Bedfordia* (2 spp.; Australia), and *Dolichoglottis* (2 spp.; New Zealand) are also related, in addition to the peculiar and highly apomorphic genus *Haastia* (3 spp.; New Zealand; Fig. 34.4A).

Additional insular endemism

There are many examples of insular endemism in the tribe, some of which are included in the scheme above (West Indies, Japan, Australia–New Zealand, Madagascar and Mascarenes). Additional examples are found in Macaronesia, where *Pericallis* (15 spp.) is endemic to the Canary Islands, Madeira and the Azores, whereas *Bethencourtia* (3 spp.) is endemic to the Canary Islands.

New Guinea has three endemic genera, viz., *Brachionostylum* (1 sp.), *Ischnea* (4 spp.), and *Papuacalia* (14 spp.). Also *Arrhenechthites* (6 spp.) is well represented on New Guinea but has outliers in Indonesia (Celebes) and southeast Australia.

Finally, two interesting monotypic genera are endemic to St. Helena, viz., *Lachanodes* and *Pladaroxylon*. Their phylogenetic position in the tribe has not yet been investigated, and like other St. Helena endemics they are white-flowered trees.

To place patterns of distribution for Senecioneae in a historical biogeographical context, the general distribution of the genera was optimized onto the molecular phylogeny (Fig. 34.4). This area optimization was carried out under maximum parsimony with the "Trace" routine in MacClade v. 4.06 (Maddison and Maddison 2003). Eight areas were defined for this area optimization analysis: *(1)* North America, *(2)* Central America, *(3)* the Caribbean Basin, *(4)* South America, *(5)* Europe and the Mediterranean Basin (the countries included in EURO+Med area: http://www.euromed.org.uk), *(6)* sub-Saharan Africa, *(7)* continental Asia, Taiwan and Japan, and *(8)* Australasia and the Pacific. This area optimization analysis supports a close association between evolutionary relationships and patterns of geographical distribution in various parts of the cladogram. Although the analysis could not confirm an African origin for the tribe as postulated by Funk et al. (2005), it indicates a strong African influence throughout the evolutionary history of Senecioneae, predominantly in subtribes Senecioninae and Othonninae. This is also clear in the nearly cosmopolitan genus *Senecio*. The results of Pelser et al. (2007) indicate that this genus originated in sub-Saharan Africa and colonized other continents multiple times independently.

EVOLUTION

Tribe Senecioneae is one of the largest tribes in Compositae. It has a worldwide distribution, contains more than 3000 species in 151 genera (Nordenstam 2007), and harbors one of the largest genera of flowering plants: *Senecio* (approximately 1000 species in the strict sense). The genus has successfully colonized most parts of the world and has become almost cosmopolitan. In Mediterranean climates, such as South Africa, Chile, and the Mediterranean region, the genus has undergone prolific speciation, contributing strongly to the enormous size of the genus. *Senecio* is less well represented in Australasia and Mesoamerica. In the West Indies the genus has no indigenous species.

Although the evolutionary success of the tribe is striking, as measured by its tremendous number of species and its incredible morphological diversity, the cause(s) of its success remain largely unknown and unexplored. Bremer (1994) suggested that the prosperity of Senecioneae might be due to their poisonous pyrrolizidine alkaloids. This hypothesis has, however, not been further examined, presumably because of the previous lack of a robust phylogeny for Senecioneae and the limited availability of comparative pyrrolizidine alkaloid data for its species. Others have linked diversifications of Senecioneae lineages to geological and climatological changes, such as the uplift of the Cordilleran mountain regions in North America, glaciations during the Pleistocene, and a drying trend throughout the Tertiary (e.g., Barkley 1988, 1990; Bain and Golden 2000; Coleman et al. 2003).

ECONOMIC USES

The economic uses of Senecioneae are mainly within horticulture. Species of *Brachyglottis*, *Doronicum*, *Ligularia* (Fig. 34.2A–C), *Petasites*, *Pseudogynoxys*, *Senecio*, and other genera are used as outdoor garden plants, whereas *Pericallis hybrida* has become a popular pot plant. *Curio* and *Kleinia* species and succulent *Senecio* species are frequently grown in greenhouses (Fig. 34.1C, G).

Several members of the tribe are used in traditional herbal medicine, e.g., *Emilia* and *Ligularia* in China, *Packera* in North and Central America, and *Psacalium* and *Roldana* in Central America. *Tussilago farfara* L. is a well known medicinal plant in China and Europe since ancient times. It is used as a treatment for cough and asthma, but because of the alkaloid content caution in its use is recommended in several countries. The use of *Petasites* root extract (butterbur) is widespread and has been tested as an effective remedy for migraines. Two alkaloid-producing (platyphyllin) species of *Caucasalia* are cultivated in Russia for medicinal purposes. Nowhere is there a trade of great economic importance, and examples of registered and accepted medicines based on Senecioneae are rare or non-existent.

Species of *Crassocephalum*, *Emilia*, *Farfugium*, *Gynura*, *Ligularia*, *Petasites*, and *Tussilago* are used in some countries as a vegetable, and *Petasites hybridus* (L.) G. Gaertn., B. Mey. & Scherb. is cultivated experimentally in Russia as a potential crop for fodder (Hanelt 2001).

CONCLUSION

The last decade has witnessed an increased interest in the systematics of Senecioneae, and a wealth of new data has been accumulated. A phylogenetic outline of the tribe has been achieved by analysis of molecular data, and for the first time a concept of a monophyletic *Senecio* has been developed. Although further generic revision is necessary in some lineages, it can be now be postulated that the number of genera in the tribe is around 160. The relationships of most of them have been presented in a phylogenetic tree, which in the near future will be completed and refined to serve as a basis for the formal recognition of subtribes and monophyletic genera. However, much work remains before the evolutionary history of the tribe can be described in full detail with accuracy and confidence.

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Chapter 35

Calenduleae

Bertil Nordenstam and Mari Källersjö

HISTORICAL OVERVIEW

The small tribe Calenduleae was already recognized by Cassini (1816), as "8. Tribu. Les Calendulacées", one of seventeen tribes in the family Asteraceae and comprising the genera *Calendula* L. and *Osteospermum* L. He emphasized the outgrowths on the fruits and the lack of a pappus as characteristic for the tribe (Cassini 1817a, 1819). He also described the style morphology of the hermaphrodite fertile disc florets, as found, for example, in *Dimorphotheca* Vaill. (by Cassini referred to as *Meteorina* Cass., *Arnoldia* Cass., and *Castalis* Cass.), and he noted the distinctly caudate anthers. He further remarked on the characteristic odor of all plants examined, and suggested that this character might be exclusive for this tribe. Cassini (1821, 1824, 1829) recognized nine genera, only four of which are recognized today, viz., *Calendula*, *Osteospermum*, *Garuleum* Cass. and *Gibbaria* Cass. The remainder are synonymized with *Dimorphotheca* (*Blaxium* Cass., plus those three mentioned above) or *Chrysanthemoides* Fabr. (*Eriocline* Cass.).

Lessing (1832) reduced the tribe Calenduleae to a small subtribe of Cynareae and included only three genera, viz., *Calendula*, *Oligocarpus* Less., and *Tripteris* Less. He referred *Osteospermum* to another subtribe Othonninae (as "Othonneae") and treated *Dimorphotheca* in a subtribe Chrysantheminae ("Chrysanthemeae") of the tribe Senecioneae ("Senecionideae"). Furthermore, he moved *Garuleum* to still another tribe, Astereae ("Asteroideae"), and placed *Gibbaria* among the insufficiently known genera. His disposition of Calenduleae genera was thus highly artificial, although he did contribute to the generic taxonomy by adding the new genera *Tripteris* and *Oligocarpus*.

De Candolle (1836–1838) largely followed Lessing's unnatural scheme, keeping Calenduleae (including Othonneae) as a small subtribe of Cynareae, and like Lessing he referred *Dimorphotheca* to Senecionideae and *Garuleum* to Asteroideae. He also added some new genera (*Acanthotheca* DC., *Xenismia* DC. and *Xerothamnus* DC.), none of which is recognized today. De Candolle was the first to circumscribe *Calendula* to become a strictly Northern Hemisphere genus.

Harvey in *Flora Capensis* (1865) recognized a subtribe Calenduleae of Senecionideae and included five genera, among them *Dimorphotheca*, thereby creating a natural group. With Bentham (1873a), who adopted much of Cassini's system, Calenduleae were recognized as a tribe again. However, Bentham added three genera, *Ruckeria* DC., *Dipterocome* Fisch. & Mey., and *Eriachaenium* Sch. Bip., none of which now belongs there. *Ruckeria* is a synonym of *Euryops* (Cass.) Cass. in Senecioneae (Nordenstam 1968). *Dipterocome* and *Eriachaenium* were included in Calenduleae by Norlindh (1943), who later excluded the latter genus, but kept the former in the tribe (Norlindh 1977a).

The South American monotypic genus *Eriachaenium* was for some time considered to belong to Inuleae, but finally placed in Mutisieae by Robinson and Brettell (1973), where it is now generally accepted (Bremer 1994). *Dipterocome* was excluded from the tribe by Nordenstam (1994a), but its tribal position remained uncertain until recently, when it was convincingly shown to belong in Cardueae (Anderberg et al. 2007).

Hoffmann (1890–1894) followed Bentham (1873a) and recognized the tribe as a group of eight genera including *Dipterocome* and *Eriachaenium*.

Norlindh in a series of papers (e.g., Norlindh 1943, 1960, 1962, 1963, 1977a, b) contributed much to the systematic knowledge of the tribe. He made many changes on the generic level, such as sinking *Tripteris* and *Oligocarpus* in *Osteospermum*, moving sect. *Blaxium* (Cass.) T. Norl. from *Dimorphotheca* to *Osteospermum*, and re-establishing the genera *Castalis*, *Gibbaria* and *Chrysanthemoides*. Much of his generic taxonomy relied on single diagnostic characters in floret sexuality or fruit morphology and anatomy, and many of his generic dispositions have recently been challenged.

Nordenstam (1994a, b, 1996) transferred sect. *Blaxium* back from *Osteospermum* to *Dimorphotheca*, relying on convincing evidence from morphology, cytology and phytochemistry, and this move has since been confirmed also by molecular data. Further changes in generic delimitation were introduced by the recognition of *Tripteris* and *Oligocarpus* as separate genera.

More recently, attempts have been made to define more monophyletic groups within the tribe by separating the new genera *Norlindhia* B. Nord., *Monoculus* B. Nord., and *Inuloides* B. Nord. from *Tripteris* (Nordenstam 2006), and *Nephrotheca* B. Nord. & Källersjö from *Gibbaria* (Nordenstam et al. 2006). It has also been pointed out that *Chrysanthemoides* is poorly defined against sections *Polygalina* DC., *Homocarpa* T. Norl., and *Coriacea* T. Norl. of *Osteospermum*, calling for further revision of generic limits (Wood and Nordenstam 2003).

The most recent overview of the tribe recognizes twelve genera (Nordenstam 2007), but as will be discussed below, further changes seem inevitable.

PHYLOGENY

The first cladistic study of the tribe was published by Nordenstam (1994a), based on morphological characters. *Dipterocome* was not accepted in the tribe, but nevertheless included in the analysis. In the resulting cladogram *Dipterocome* was found at the base and well separated from strongly supported Calenduleae, which fell into two major clades. One placed *Gibbaria* and *Garuleum* together as sister to *Dimorphotheca* (including *Castalis* and sect. *Blaxium*). The second clade comprised *Chrysanthemoides*, *Tripteris*, *Osteospermum*, *Oligocarpus* and *Calendula*.

A molecular study was undertaken in order to further investigate relationships in the tribe. The phylogeny was investigated using sequences from two chloroplast genes, *ndhF* (the 3' end) and *trnL-F*, and from the nuclear rDNA ITS-region (Källersjö et al., in prep.). The study included 47 terminals, representing all presently recognized genera, and attempting to cover the considerable morphological variation in the group. In many cases sequences from more than one specimen per species were investigated, to confirm the correct sequence. *Dipterocome* was not included as it does not belong in the tribe (Bremer 1987, 1994; Nordenstam 1994a), and its position has now been shown to be in Cardueae (Anderberg et al. 2007).

Nordenstam (1994a) used Senecioneae as an outgroup for his study, since at the time Senecioneae and Calenduleae were thought to be closely related. Later studies have shown that this is not the case (Panero and Funk 2002, 2008), and instead, for the molecular study one representative each of Astereae, Gnaphalieae and Anthemideae were selected as outgroups. The combined analysis of all three genes comprised almost 3000 sites, of which 424 were phylogenetically informative. A parsimony analysis produced six equally most parsimonious trees. A condensed tree of their strict consensus is shown in Fig. 35.1. Support for nodes was assessed using parsimony jackknifing (Farris et al. 1996). The combined data were also analyzed using Bayesian inference as implemented in MrBayes (Huelsenbeck and Ronquist 2001).

This analysis produced the same topology as in Fig. 35.1, with one exception (see below). Apart from that, there was no supported difference between the parsimony jackknife and the Bayesian analyses. Further discussions will focus on the parsimony analysis only.

As can be seen in Fig. 35.1, the strict consensus tree is well resolved and major groups are well supported. *Garuleum* is sister to all other Calenduleae, supported at 100%. *Dimorphotheca*, including sect. *Blaxium*, *Castalis* and *D. pinnata* (Thunb.) Harv. (syn. *Osteospermum pinnatum* (Thunb.) T. Norl.; Nordenstam 2006) is monophyletic (100%) and sister to the remaining Calenduleae (98%). The recently recognized *Nephrotheca* (Nordenstam et al. 2006) follows as sister to a large clade composed of three major groups (100%). The first (*Calendula-Tripteris*) is supported at 100%, has a basal trichotomy consisting of a monophyletic *Calendula* (100%), a poorly supported (53%) group of *Tripteris microcarpa* Harv. and some *Osteospermum*, and finally a group, supported at 99%, comprising *Tripteris* and *Osteospermum* species with *Norlindhia* and *Monoculus* nested among them.

It is within this major clade we find the only conflict between the parsimony and the Bayesian analyses. In the parsimony analysis the position of *Calendula* is unresolved in the relation to the other clades in the *Calendula-Tripteris* group, due to a conflict between the *ndhF* and the *trnL-F* datasets. In the *ndhF* tree *Calendula* is sister to the other two groups. In the *trnL-F* tree *Calendula* is most closely related to the *Tripteris-Osteospermum-Monoculus-Norlindhia* group. In the Bayesian analysis a third alternative is supported, viz. *Calendula* as sister to the small group of *Tripteris*, although the posterior probability is only 0.93. It can also be noted that the type of *Osteospermum* (*O. spinosum* L.) is found within the *Tripteris*-*Osteospermum*-*Monoculus*-*Norlindhia* group. The second major clade (*Oligocarpus* – *Gibbaria*) consists of *Osteospermum* species with *Oligocarpus* and *Gibbaria* s.str. nested among them. The support is 97%. The third major clade (*Inuloides*-*Chrysanthemoides* is supported at 100%. In it the monotypic *Inuloides* is sister (97%) to a large group with species of *Osteospermum* and *Chrysanthemoides*. Within this group the support values are very low, but it can be noted that representatives of *Chrysanthemoides* do not group together, but instead they are found intermixed with different species of *Osteospermum*.

The molecular phylogeny resolved or confirmed many issues in Calenduleae, but it also pointed out new or unresolved questions. The tree topology is in many ways different from that of Nordenstam (1994a), but this is not surprising since the studies differ in many ways. Nordenstam's study included the anomalous *Dipterocome* and used Senecioneae as outgroup. Also genera, rather than species, were used as terminals.

The position of *Garuleum* as sister to all other Calenduleae is well supported. To test if *Garuleum* is indeed a member of Calenduleae, or if it would be better placed in another tribe, an analysis was performed using *ndhF* sequences from a large range of taxa, including representatives of all Asteraceae tribes (Källersjö et al., in prep.). The study placed *Garuleum* together with other Calenduleae. The close association of *Osteospermum pinnatum* to *Dimorphotheca*, where it was transferred by Nordenstam (2006), is confirmed by the molecular information. The close connection between some groups of *Osteospermum* (sections *Homocarpa*, *Polygalina*, and *Coriacea*) and *Chrysanthemoides* pointed out by Wood and Nordenstam (2003) is also confirmed. The DNA sequences for the two former *Gibbaria* species (Norlindh 1943) were found to be highly divergent and not surprisingly they end up far apart in the tree. This led to the recognition of the new genus *Nephrotheca* (Nordenstam et al. 2006).

The main remaining problems in the tribe concern the delimitation of the two larger genera *Osteospermum* and *Tripteris*. Clearly neither is monophyletic. Nordenstam aimed to improve the definition of *Tripteris* by removing taxa that lacked the typical three-winged and three-fenestrate achenes. However, in the molecular tree, taxa with other kinds of achenes are nested among typical *Tripteris* species and further revision will be necessary for this group. Likewise, the boundaries between *Oligocarpus*, *Chrysanthemoides* and *Osteospermum* p.p. need further study.

TAXONOMY

After the exclusion of the anomalous elements *Eriachaenium* and *Dipterocome*, the tribe is now a well-defined natural group. About 120 species are known and presently referred to twelve different genera. Some of these are polyphyletic as presently circumscribed.

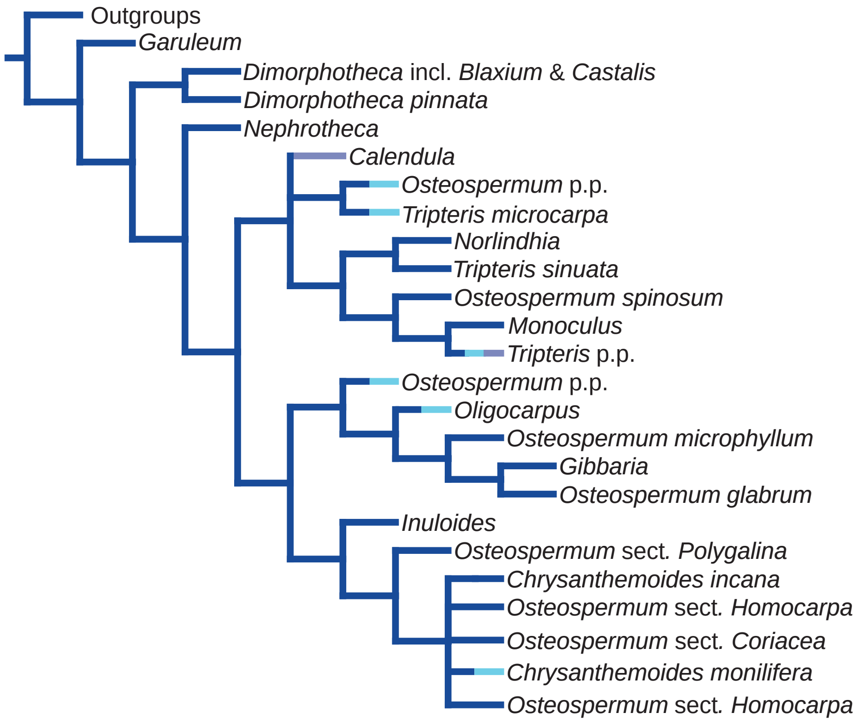

Fig. 35.1. A condensed consensus tree resulting from parsimony analysis of the two chloroplast genes *ndhF*, *trnL-F* and the nrDNA ITS region. Numbers below nodes represent parsimony jackknife frequencies. The analysis included 47 taxa of the tribe, which have been condensed to show mainly genera and some sections of *Osteospermum*. Colors of the branches indicate the native range of the terminal taxa: dark blue = southern Africa; medium blue = Mediterranean; light blue = tropical Africa. For the complete metatree see Chapter 44.

The exclusively Northern Hemisphere genus *Calendula* (Fig. 35.2A, 35.3A, B) is a well-defined and natural group, but its infra-generic taxonomy is complex and not sufficiently known. Species limits are difficult and sometimes vague, and the number of species has been estimated to be anything from 10 to 30. The complex karyology with diploid numbers ranging from $2n = 14$ to over 80 no doubt contributes to the taxonomic difficulties.

With the transfer of the St. Helena endemic *Osteospermum sanctae-helenae* T. Norl. to *Oligocarpus* (Nordenstam 2006), this genus is no longer monotypic and not restricted to South Africa. On the other hand, the bispecific *Gibbaria* has been divided into *Gibbaria* s.str. and the new genus *Nephrotheca* (Nordenstam et al. 2006). This rendered *Gibbaria* monotypic, but on morphological and molecular evidence *Osteospermum glabrum* N.E. Br. has to be transferred to *Gibbaria* (cf. Fig. 35.1 and Discussion, below):

Gibbaria glabra (N.E. Br.) B. Nord. & Källersjö, **comb. nov.** Basionym: *Osteospermum glabrum* N.E. Br. in Bull. Misc. Inform. Kew 1901: 125. 1901 – Type: South Africa, Cape Province: Riversdale distr., summit Muiskraal Ridge near Garcias Pass, 1897, *Galpin 4217* (K lectotype, selected by Norlindh 1943; BOL, GRA, PRE isotypes).

Norlindh (1943) noted the distinctness of *Osteospermum glabrum* in the genus and created a section for it, viz., sect. *Acerosa* T. Norl. The crowded linear acicular leaves, the narrowly lanceolate acuminate involucral bracts and the sessile capitula are unusual features in *Osteospermum* but strongly reminiscent of *Gibbaria scabra*. There is no doubt that *O. glabrum* is closely related to *G. scabra*, as also corroborated by the molecular evidence (Fig. 35.1) and the unusual rudimentary pappus sometimes present in both species (cf. below).

Dimorphotheca has received a broader circumscription by the inclusion of the genus *Castalis* and the section *Blaxium* of *Osteospermum*, as well as *O. pinnatum* (Fig. 35.4A, B, 35.5.A; Nordenstam 1994, 2006). Nevertheless, *Dimorphotheca* is a natural and monophyletic group, well supported by morphological, cytological, chemical and molecular data.

Three small genera, *Inuloides*, *Monoculus* (Fig. 35.3E) and *Norlindhia* (Fig. 35.5C), have been newly described, leaving *Tripteris* better defined (e.g., with achenes always three-winged and with an apical trifenestrate cavity; Fig. 35.3F), although not necessarily monophyletic.

Osteospermum in its present circumscription is clearly polyphyletic. A sizeable part of the genus (including sections *Homocarpa* and *Coriacea*) is closely related to *Chrysanthemoides* (Fig. 35.3C, D), and the generic limits of this assemblage need revision.

Garuleum deviates in many respects from the other Calenduleae genera (Norlindh 1977a, b), but is certainly best retained in the tribe, where it has a basal position in the phylogenetic tree.

MORPHOLOGY

There is much variation in sex distribution in the capitulum within the tribe. The ray florets, which are always present, may be female-fertile, female-sterile or neuter. These characters were much emphasized by some earlier authors. The genus *Castalis* was defined by its sterile or neuter marginal florets, but there is nothing else to distinguish it from *Dimorphotheca*. The disc florets are hermaphroditic, either perfect or functionally male. Perfect disc florets are only found in two genera, viz., *Garuleum* and *Dimorphotheca*. Norlindh (1943) restricted the latter genus to include only species with perfect disc florets, but it is obvious that taxa with functionally male florets (sect. *Blaxium* and *D. pinnata*) also belong there (cf. above). Style morphology provides important characters in Calenduleae as in most tribes of the family Asteraceae. The disc floret styles are characteristically only shortly bilobed or bifid, and styles of sterile pistils may be undivided (*Calendula*). A subapical collar of short sweeping hairs is usually present at the base of the style lobes. Only in *Garuleum* the style is differently shaped, with long branches, that are dorsally distinctly papillate or hirsute.

The stamens are caudate throughout the tribe, and the apical appendage is distinct, flat, triangular-ovate. There is no significant variation in the endothecial tissue, which is invariably polarized.

The tribe is well known for the great variety of achene structures. The achenes may be compressed, winged, or provided with outgrowths like beaks, horns, or prickles. Heterocarpy occurs in genera with such varied fruit morphology, with *Calendula* as the best known example (Fig. 35.3A, B), but also *Oligocarpus*. Cavities may be present in the fruits, either ventrally (*Gibbaria*, *Nephrotheca*) or apically (*Tripteris*, *Monoculus*, etc.; Fig. 35.3E, F). Cavities mean reduced weight and often occur in conjunction with large wings, as adaptations to wind dispersal. The apical cavity may be fenestrate, i.e., covered by a translucent window. In *Monoculus* there is a single window (Fig. 35.3E), whereas the achenes of *Tripteris* are always trifenestrate (Fig.35.3F).

The genus *Chrysanthemoides* was distinguished on the single character of having fruits with a fleshy exocarp (Fig. 35.3C, D). These fruits have often been referred to as drupes and regarded as unique for this genus in the family. However, a more or less fleshy exocarp is also found in species of *Osteospermum* (e.g., *O. junceum* P.J. Bergius), and there is a variation from distinctly fleshy to

Fig. 35.2. A *Calendula officinalis* L. (cultivated, Uruguay); **B** *Dimorphotheca ecklonis* DC. (cultivated, Uruguay); **C** *Dimorphotheca sinuata* DC. (Namibia); **D** *Tripteris glabrata* (Thunb.) Harv. (South Africa: Namaqualand). [Photographs: A, B, J.M. Bonifacino; C, C.A. Mannheimer; D, V.A. Funk.]

Fig. 35.3. Fruits of Calenduleae. **A** fruiting capitulum of *Calendula officinalis* L. (cultivated, Uruguay); **B** worm-like achenes of *Calendula officinalis* (cultivated, Uruguay); **C** drupaceous achenes of *Chrysanthemoides monilifera* (L.) T. Norl. (South Africa: Eastern Cape); **D** Silvereye (*Zosterops lateralis* Latham) feeding on *Chrysanthemoides monilifera* achenes (Australia: New South Wales, Newcastle, introduced); **E** fruting capitulum of *Monoculus monstrosus* (Burm. f.) B. Nord. (South Africa: Western Cape, Hondeklipbaai); achenes trialate, unifenestrate; **F** trialate trifenestrate achenes of *Tripteris glabrata* (Thunb.) Harv. (South Africa: Western Cape, Riethuis). [Photographs: A, B, J.M. Bonifacino; C, R. McKenzie; D, M. Kibby; E, F, M. Koekemoer.]

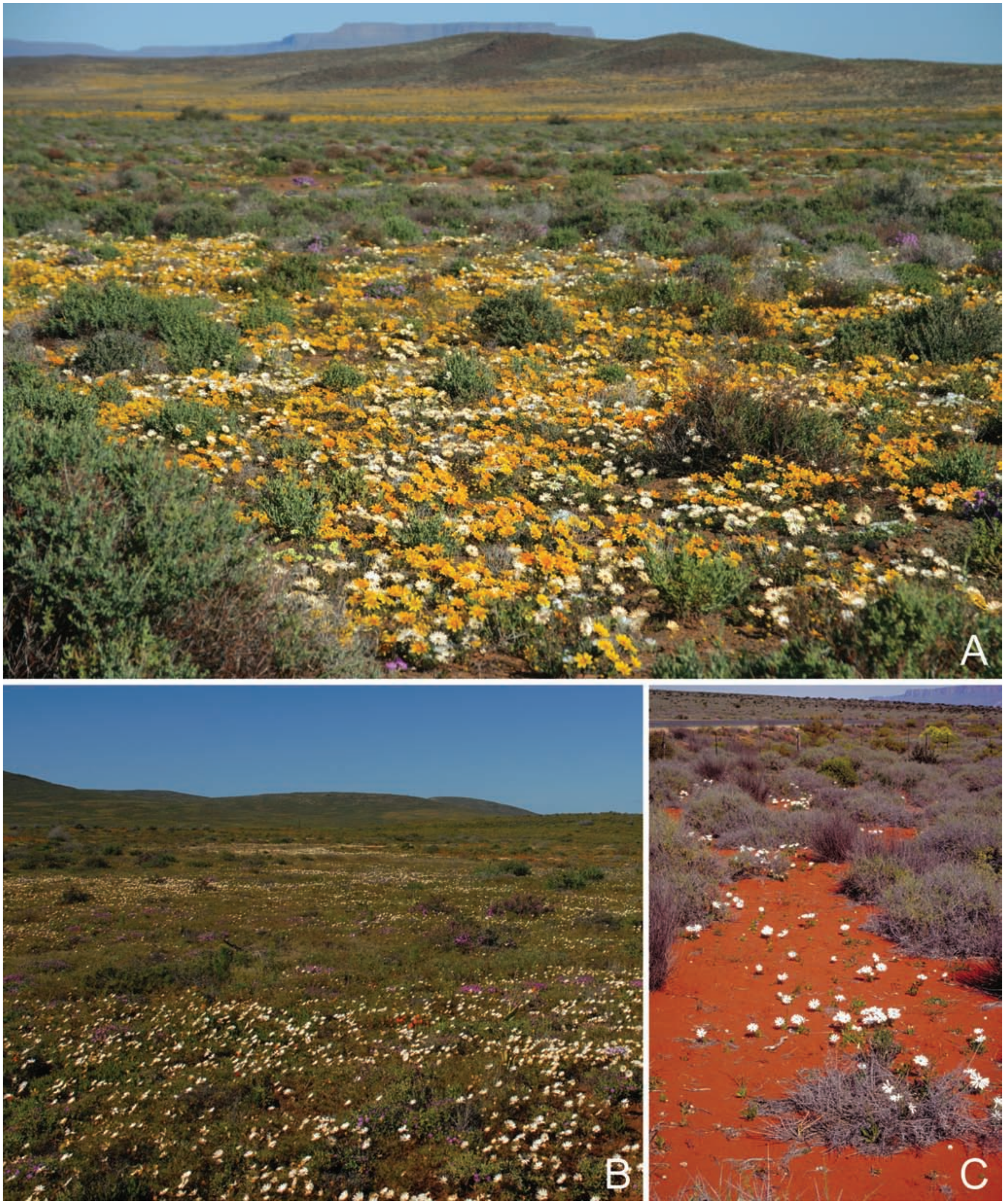

Fig. 35.4. A display from winter rainfall area with *Dimorphotheca pinnata* (Thunb.) Harv. (white) and *Gazania lichtensteinii* Less. (tribe Arctotideae, yellow) (South Africa: Northern Cape, Tankwa Karoo National Park); **B** display with *Dimorphotheca pinnata* (South Africa: Northern Cape, Tankwa Karoo National Park); **C** blooming display with *Dimorphotheca pluvialis* (L.) Moench (South Africa: Namaqualand). [Photographs: A, B, M. Koekemoer; C, V.A. Funk.]

thinner, soft or membranous skins on the achenes (Wood and Nordenstam 2003). These features are not readily seen in herbarium material, but need to be observed in nature.

Glandular hairs of a characteristic shape, with a narrow stalk and a dark-colored apical gland, are found on stems, leaves and involucres in several genera (*Norlindhia*, *Monoculus*, *Tripteris*, *Calendula*, etc.). Corolla venation has proved useful in the generic taxonomy, especially the distribution of sclerenchymatic strands in the corolla lobes (e.g., well developed in *Tripteris* and *Monoculus*).

One of the important characters defining the tribe is the lack of a pappus. However, in *Gibbaria scabra* the ovaries of the disc florets are sometimes provided apically with a minute corona, which can be interpreted as a rudimentary pappus. This feature was observed already by Cassini (1817b), and mentioned by Norlindh (1943), who dismissed it as having no taxonomic value. However, the presence of a quite similar rudimentary pappus or corona in *Osteospermum glabrum* is certainly interesting, in light of the transfer of the latter species to *Gibbaria* (cf. above).

Fig. 35.5. A *Dimorphotheca pinnata* (Thunb.) Harv. (Namibia); **B** *Dimorphotheca pluvialis* (L.) Moench (South Africa: Namaqualand); **C** *Norlindhia amplectens* (Harv.) B. Nord. (South Africa: Namaqualand). [Photographs: A, C.A. Mannheimer; B, C., M. Koekemoer.]

POLLEN

The pollen grains of Calenduleae are oblate-spheroidal, tectate and caveate, with exine sculpture spinose or spinulose and lacking distinct infratectal bacula. Praglowski and Grafström (1980) recognized five pollen types within the rather stenopalynous tribe. One type was completely aberrant, found in *Dipterocome*, which is now excluded from the tribe. *Calendula* is well characterized palynologically, having large pollen grains with large and distinct ora and long and slender solid spines. *Garuleum* has a pollen type distinct from *Osteospermum*, *Dimorphotheca* etc., having numerous dense spines, wide colpi and dense caveae.

The remainder of the taxa studied by Praglowski and Grafström (1980) did not provide clear palynotaxonomical data, partly because of the unnatural generic taxonomy applied. The *Osteospermum* species in their study are now referred to five different genera, and *Dimorphotheca* species were listed under *Castalis* as well as *Osteospermum*. Although the authors distinguished a *Gibbaria* type, the two taxa were found to differ in several respects, which is not surprising in the light of present taxonomy where they belong to different genera (*Gibbaria scabra* (Thunb.) T. Norl. and *Nephrotheca ilicifolia* (L.) B. Nord. & Källersjö).

It is also worth noting that the types of *Tripteris* and *Osteospermum* "are easily distinguishable on pollen morphological criteria" (Praglowski and Grafström 1980: 183). This observation may be useful in future refinement of generic classification in the tribe.

CHROMOSOME NUMBERS

The most complex karyology is found in *Calendula*, with $n = 7, 8, 9, 11, 14, 15$ and higher reported. The basic number $x = 8$ is known in *Monoculus*, *Osteospermum*, and possibly *Tripteris* (where $2n = 36$ has been recorded), whereas $x = 9$ occurs in *Tripteris*, *Osteospermum*, *Chrysanthemoides*, and one species of *Dimorphotheca*. The latter genus is otherwise characterized by $x = 10$, which is also reported repeatedly for *Chrysanthemoides*. Since no chromosome counts have been reported for *Garuleum*, the most basal genus in the phylogeny, we think it would be premature to postulate a basic number for the tribe.

CHEMISTRY

Some secondary compounds of Calenduleae are useful as chemotaxonomical markers. *Dimorphotheca* is characterized by the presence of cyanoglycosides such as linamarin, which has been found in eight species and is probably occurring constantly in the genus (Hegnauer 1964). Cyanoglycosides occur also in other tribes (Anthemideae, Cardueae, Mutisieae s.l.) but the biosynthetic pathway is different from that in Calenduleae (Hegnauer 1989).

The achenes of many Calenduleae contain a unique fatty oil, which has received the name dimorphecolic acid (Smith et al. 1960; Hegnauer 1964). This oil has received much attention for its commercial potential in technical industry (see below). Another unique fatty acid, calendic acid, occurs in *Calendula*, *Osteospermum* and *Chrysanthemoides* (Valadon 1977).

Diterpenes, which are otherwise rare or scattered in the family, occur in many (or perhaps all) species of Calenduleae, mainly of a type called pimaranes (Hegnauer 1989; Alvarenga et al. 2005). *Garuleum* and *Osteospermum* have very similar types of pimaranes, which confirms the position of the former genus in the tribe.

BIOGEOGRAPHY

The tribe has a very marked center in southern Africa, where all genera but one and ca. 80% of the species occur. Only *Calendula* has a Northern Hemisphere distribution, mainly in the Mediterranean region and extending eastwards as far as Iran. In the west the genus occurs in Macaronesia, with one species, *Calendula maderensis* DC., endemic to Madeira. The genus reaches its southern limits in two outlying ranges in the Hoggar Mountains and in the mountains of Yemen, respectively (Norlindh 1946).

Six genera are endemic to southern Africa, and three of them are confined to the Cape Floristic Region, viz., *Nephrotheca*, *Inuloides* and *Gibbaria*. Another three are mostly found in the Karoo-Namib Region, viz., *Monoculus*, *Norlindhia* and *Garuleum*.

Dimorphotheca in its revised circumscription encompasses taxa both of the Cape and the Karoo-Namib Regions and extends into Zimbabwe and Angola. Still wider ranges are found in *Osteospermum* and *Tripteris*, both of which are distinctly centered in South Africa but have scattered taxa in tropical and northern Africa and extend into Arabia (*Tripteris* also in Jordan). Also *Chrysanthemoides monilifera*, which is a polymorphic species complex, has a wide distribution from the Cape along eastern Africa to the Equator. The gaps in the somewhat discontinuous range are congruent with the Zambesi and Limpopo intervals (Norlindh 1946). Even larger disjunctions are found in the range of *Osteospermum muricatum* E. Mey., which is widely distributed in southern Africa and has isolated occurrences in Somalia and Yemen.

An interesting disjunction is presented by *Oligocarpus*, with one species in South Africa and another endemic to

St. Helena. The African connection in the endemic flora of St. Helena has been discussed by various authors (e.g., Bentham 1873b; Cronk 1987, 1990, 1992). It has been suggested that relatives of the most ancient endemics have become extinct on the African mainland by climatic changes in Miocene and Pliocene. However, *Oligocarpus burchellii* (Hook. f.) B. Nord. (until recently known as *Osteospermum sanctae-helenae* T. Norl.; cf. Nordenstam 2006) belongs to the low altitude St. Helena endemics and is regarded as a more recent endemic dating from arid periods in the Pliocene and Pleistocene. Cronk (2000) estimates its age to less than 2.4 million years (whereas the age of the island is estimated to some 14 million years). It is an annual that grows in the hottest and driest parts of St. Helena, and it is interesting to note that its single close relative, *Oligocarpus calendulaceus* (L. f.) Less., inhabits hot and arid regions of the Northern, Western and Eastern Cape Province. Also Ashmole and Ashmole (2000) list *Oligocarpus burchellii* (Hook. f.) B. Nord. (as *Osteospermum sanctae-helenae*) among the young endemic species with closest relatives in southern Africa together with *Hydrodea cryptantha* (Hook. f.) N.E. Br., *Hypertelis acida* (Hook. f.) K. Müll., *Pelargonium cotyledonis* (L.) L'Hér. and *Eragrostis saxatilis* Hemsl.

EVOLUTION

Some of the most interesting evolutionary aspects of Calenduleae are connected with dispersal. To compensate for the complete loss of the pappus, various adaptations of the achene to different modes of dispersal have evolved. The strong heterocarpy in *Calendula* and *Oligocarpus* is noteworthy, with some achenes curved and larva-like (Fig. 35.3B), others beaked or provided with different outgrowths. The larva-shaped fruits have sometimes been interpreted as adaptations to bird dispersal, an arguable hypothesis. Nevertheless, the occurrence of different fruit types within a single capitulum may contribute to effective dispersal by different agents and to different distances from the mother plant.

However, the drupaceous fruits of *Chrysanthemoides* (Fig. 35.3C) are undisputably dispersed by birds (Rowan 1967; Keith et al. 1992; Fig. 35.3D). In their natural habitats in southern Africa it may even be difficult to find mature achenes, since they are quickly taken by various birds. Also in countries where *Chrysanthemoides* was introduced, bird dispersal occurs, as in St. Helena, where the likewise introduced Indian Myna birds are actively dispersing the fruits (Ashmole and Ashmole 2000), and in Australia, where Silvereye birds feed on the fruits (Fig. 35.3D). The drupe-like fruits are also eaten by mammals including rodents, foxes, monkeys and people (Palmer and Pitman 1972; Weiss 1986).

As noted above, the development of a fleshy exocarp is not restricted to *Chrysanthemoides* (as presently defined), but also occurs in species of *Osteospermum*. Sometimes, as in *O. junceum*, the fruits are most likely bird-dispersed (cf. Fig. 6 in Wood and Nordenstam 2003). Other taxa with less prominent but soft and sometimes juicy exocarp may be adapted to dispersal by ants. This could be the case in, e.g., *Osteospermum potbergense* A.R. Wood & B. Nord., *O. asperulum* (DC.) T. Norl., *O. corymbosum* L., *O. subulatum* DC. and *O. triquetrum* L. f., but remains to be investigated in nature (cf. Wood and Nordenstam 2003). Also other *Osteospermum* species have been reported as ant-dispersed, especially in the fynbos biome (Bond and Slingsby 1983).

The winged achenes in *Tripteris* and other genera (Fig. 35.3E, F) are no doubt adaptations to wind dispersal, sometimes enhanced by a reduction in weight by the development of cavities in the achene.

ECONOMIC USES

The common marigold (*Calendula officinalis*, Fig. 35.2A, 35.3A) has been used in horticulture since ancient times and is not known as wild in nature. More recently, several cultivars of *Dimorphotheca* spp. (Fig. 35.2B) have found an increasing market as pot plants and for outdoor planting (often marketed under the name of *Osteospermum*).

The unusual oils of *Dimorphotheca* have special properties and are of potential interest in technical industry (Barclay and Earle 1965; Van Soest 1990; Hof 1996). The problem with low oil content has been successfully addressed by experiments to select for increased oil contents in *D. pluvialis* (Hof et al. 1999).

Members of the tribe, especially *Calendula*, have been used in traditional medicine in Europe and China, and also for flavoring and coloring in cheese and butter, and as a salad ingredient (Hanelt 2001).

Some species of *Dimorphotheca* are highly toxic to sheep and other animals in southern Africa, causing hydrocyanic acid poisoning ("geilsiekte") (Watt and Breyer-Brandwijk 1962).

Garuleum bipinnatum (Thunb.) Less. had a reputation among the early settlers in the Cape Colony as an effective remedy for snakebites and also found various other uses in traditional medicine (Watt and Breyer-Brandwijk 1962).

Chrysanthemoides monilifera has become a noxious weed in especially Australia (where it was initially planted for stabilization of sand dunes; Fig. 35.3C, D) and New Zealand, and also to some extent in southern Europe, California, and St. Helena.

CONCLUSIONS

Although Calenduleae constitute one of the smaller tribes and have been rather thoroughly studied in various respects, their taxonomy is not yet well known. This is a valid statement for the tribal affinities, and is especially true for the generic taxonomy, where further changes will be necessary. On the infrageneric level the genus *Calendula* is notoriously difficult, whereas the species of other genera are better known, although new taxa are continuously being discovered and described especially in southern Africa.

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Chapter 36

Gnaphalieae

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INTRODUCTION

The Gnaphalieae are a moderately large tribe whose members were traditionally included in the tribe Inuleae. It has only been relatively recently that the tribe has been shown to be isolated from the remainder of "old" Inuleae (Anderberg 1989, 1991a). The approximately 180–190 genera of Gnaphalieae are most numerous in the southern hemisphere, with the strong centers of diversity in Australia, southern Africa, and South America (Anderberg 1991a; Bayer et al. 2007).

HISTORICAL OVERVIEW

The Inuleae were established as a section by Cassini (1812) in an account of the style and stigma in Compositae, then enumerated (Cassini 1815) and described (Cassini 1818) as one of 17 then 20 tribes in a new classification of Compositae. In a synopsis of Inuleae (Cassini 1822), the 77 recognized genera were organized into three sections, of which the first, Inuleae-Gnaphalieae, was reserved for taxa with scarious bracts, truncate style branches and long-tailed anthers and contained mainly genera of Gnaphalieae sensu Anderberg (1991a). The second section, Inuleae-Archetypae, contained in addition to genera of today's Inuleae, the *Filago* group which also belongs to the modern tribe Gnaphalieae. The third section, Inuleae-Buphthalmeae, contained only nine genera which are distributed across four modern tribes but with none in Gnaphalieae.

Lessing's classification of Compositae (1832) is largely regarded as artificial, and he placed Cassini's Inuleae into two different tribes, viz., Senecionideae and Asteroideae, based largely on characters of the styles. Although his classification system was mostly ignored by students of Compositae who followed him, Lessing is remembered as the first person to point out that Inuleae of Cassini were an unnatural group. De Candolle (1836) adopted Lessing's classification of Inuleae and in doing so shared Lessing's view of the unnaturalness of Cassini's tribe. Bentham (1873a) returned to Inuleae that, in its circumscription, was largely a Cassinian one. His Inuleae had nine subtribes, in which the majority of modern Gnaphalieae were contained in his subtribes Filagineae, Gnaphalieae, Angianthieae, Relhanieae and Athrixieae. Although Bentham's (1873a) Inuleae were also an unnatural assemblage, his classification of the tribe and other tribes has persisted until the present day largely because his tribes were easy to perceive morphologically, and their readily recognized characters made them easy to distinguish in a key. Hoffmann's treatment for *Die natürlichen Pflanzenfamilien* (Hoffmann 1890–1894) was largely an adoption of Bentham's treatment, recognizing nine subtribes in Inuleae.

The first modern account of Inuleae was that of Merxmüller et al. (1977). Beginning with the Benthamian classification, they considered cytological, phytochemical, and palynological information, in addition to classical morphological characters, to produce a classification that recognized only three subtribes, viz., Inulinae, Gnaphaliinae, and Athrixiinae. By excluding and transferring some genera from Inuleae, Merxmüller et al. (1977) demonstrated that they believed that Benthamian Inuleae were artificial to some extent; nevertheless, their classification remained largely an unnatural one. Bremer (1987) and Anderberg (1989), using morphological cladistics, were the first to clearly demonstrate that "old" Inuleae were not monophyletic, and Anderberg (1991a–c) proceeded to redefine Inuleae s.l. as three presumably monophyletic tribes, Inuleae s.str., Plucheeae, and Gnaphalieae. Based on his analysis, Anderberg (1991a) proposed that the tribe Gnaphalieae be composed of five monophyletic groups or subtribes, largely recircumscribed from two of the subtribes of former Inuleae, viz., Gnaphaliinae and Athrixiinae of Merxmüller et al. (1977). While recognized by most as a phenomenal effort and good starting point toward a modern reclassification of Gnaphalieae, Anderberg's classification (Anderberg 1991a) has come under some criticism with regard to the cladistic methodology that was used and the scoring of characters that were used to produce it (e.g., Puttock 1994a).

PHYLOGENY

Circumscription and affinities at the tribal level

The modern history of phylogenetic study of Gnaphalieae begins with its removal from Inuleae based on morphological differences (Anderberg 1989, 1991a–c; Karis 1993) and DNA sequences (Kim and Jansen 1995; Bayer and Starr 1998; Wagstaff and Breitwieser 2002; Goertzen et al. 2003). A series of papers provided alternative hypotheses of relationships between Gnaphalieae and other tribes. Karis (1993) recovered them as sister to a clade containing Astereae and Anthemideae in a phylogenetic analysis of morphological characters. Jansen et al. (1991a) described them as the sister group of Inuleae (represented by *Inula* L.) on the basis of chloroplast DNA restriction site analysis. Keeley and Jansen (1991) showed them as the sister group of a clade consisting of Inuleae and Plucheeae also using chloroplast DNA restriction site analysis. In contrast Kim and Jansen (1995) included Gnaphalieae in a clade containing Calenduleae, Astereae, and Anthemideae in an analysis of *ndhF* sequences. Bayer and Starr's (1998) analysis of *trnL* intron and *trnL-trnF* intergenic spacer sequences suggested Gnaphalieae to be the sister group of Senecioneae. Goertzen et al. (2003), through the use of ITS sequences, suggested Gnaphalieae to be the sister group of Astereae, whereas the Compositae supertree (= metatree; Funk et al. 2005) showed them as the sister group of Calenduleae. A ten-region chloroplast sequence study (Panero and Funk 2008) provides strong bootstrap support for the placement of Gnaphalieae as the sister group to a clade including Anthemideae and Astereae. The discrepancies among these studies reflect the fact that in all of them branch lengths grouping Gnaphalieae with any other tribe are short. They are therefore potentially impacted by sampling error, idiosyncratic lineage sorting of ancestral polymorphisms (Avise and Robinson 2008), or reticulate evolution among species of an ancestral group, or systematic bias in the datasets.

Phylogenetic analysis has also led to the exclusion of several genera from Gnaphalieae and their transfer to other Compositae tribes. *Oxylaena acicularis* (Benth.) Anderb. has been recognized as conspecific with *Gibbaria scabra* (Thunb.) Norl., a member of Calenduleae (Koekemoer, pers. comm.). Bayer and Cross (2002) used DNA, chemical, and morphological evidence to show that *Isoetopsis* and *Printzia* should be transferred to Astereae. The New Zealand endemic genus *Haastia* Hook. f. has sometimes been included in Gnaphalieae (see Breitwieser and Ward 2005), but DNA sequence data (Wagstaff and Breitwieser 2004) and morphological studies (Breitwieser and Ward 2005) show it to be closely related to *Brachyglottis* J.R. Forst. & G. Forst. (Senecioneae). The genus *Callilepis* belongs to the major clade of Compositae that includes the tribes Heliantheae s.l. and Inuleae (incl. Plucheeae), but its exact position remains unresolved (Anderberg et al. 2005). The tribal position of *Denekia* is near *Printzia* in the basal part of Astereae (see Chapter 37).

Phylogenetic relationships within the tribe

The principal works attempting to recover broad phylogenetic relationships above the generic level within Gnaphalieae are the cladistic analyses of morphological data by Anderberg (1991a) and of DNA sequences by Bayer et al. (2000, 2002). Based on his cladistic analyses, Anderberg (1991a) recognized five subtribes. The monophyly of four of these subtribes (Cassiniinae, Gnaphaliinae, Loricariinae, Relhaniinae), however, is strongly inconsistent with subsequent molecular data, and re-analysis of the morphological dataset has yielded markedly different but shorter trees (Puttock 1994a). Furthermore, Anderberg's tribes united some genera that have since been shown to have only superficial morphological similarity and differ widely in morphology, chemistry and DNA sequence data (Ward and Breitwieser 1998). Bayer et al. (2000) sampled the *trnL* intron and the *trnL-trnF* intergenic spacer sequences from South African Gnaphalieae and aimed to test the monophyly of both Anderberg's (1991a) subtribe Relhaniinae and the South African species of the genus *Helichrysum*. Both these taxa were found to be non-monophyletic, as were the South African members of Anderberg's subtribes Cassiniinae and Gnaphaliinae, although support for many alternative clades was weak. Bayer et al. (2002) attempted to recover phylogenetic relationships among genera of Australian Gnaphalieae using the *trnL* intron, *trnL/trnF* intergenic spacer, *matK*, and ETS. The trees presented show little resolution of major clades, although some small clades of two or a few terminal taxa were supported (e.g., that comprising *Pycnosorus* and *Craspedia*).

For this work a new analysis has been conducted of a subset of the available chloroplast DNA sequences for *matK*, the *trnL* intron, and the *trnL-trnF* intergenic spacer using the Bayesian approach implemented in MrBayes 3.1.2 (Ronquist and Huelsenbeck 2003). The principal improvement of this over previously published DNA sequence phylogenies for Gnaphalieae is that it includes a broad (but far from complete) sampling of genera from Africa and Australasia together with a few important genera from other continents.

The data were treated as two partitions, *matK* on one hand and the combined *trnL* intron and *trnL-trnF* on the other. Gaps in aligned sequences were treated as missing data, and regions of the *trnL* intron and *trnL-trnF* intergenic spacer that were not readily alignable were omitted from the analysis, leaving an alignment of 2518 sites. A general time reversible (GTR) substitution model was independently estimated for each partition. Among site rate variation was modelled using gamma distributed rate classes for each partition, and for *matK* a proportion-of-sites-invariant parameter was also estimated. These models received the best scores in hierarchical likelihood ratio tests conducted with MrModelTest 2.3 (Nylander 2004) and had the highest Akaike information criterion score. Results from analyses using other appropriate models yielded essentially similar trees (not shown) and the clades discussed below were also recovered using other phylogenetic analysis methods (Smissen, unpub.). The trees shown were generated from two independent MCMC runs of two million generations, sampling trees every thousand generations, and post-run analysis conducted with the first 200 trees (200,000 generations) discarded to allow for convergence ("burn-in") after examining the log probabilities of observing the data for the tree samples. Four further runs of one million generations converged on the same tree topology. The following discussion draws not only on this analysis, but on previously published studies and some unpublished analyses. Overall, little resolution of phylogenetic relationships is achieved with confidence, but a number of important groups are evident.

Most importantly, a clade including some members of Relhaniinae (sensu Anderberg 1991a) along with some other African species that appeared as "basal taxa" of Gnaphalieae in the cladistic analysis of morphological characters by Anderberg (1991a) is the sister group to the rest of the tribe (Figs. 36.1, 36.2). Both this "*Relhania* clade" (Fig. 36.3.) and the split between it and the remainder of Gnaphalieae are recovered with high posterior probability (1.0) and supported by numerous informative characters represented by relatively long branch-lengths in Fig. 36.3. A clade of similar composition to this "*Relhania* clade" (differing only because of slightly different taxon sampling) was also observed in the DNA sequence phylogeny of South African Gnaphalieae based on *trnL* intron and *trnL-trnF* intergenic spacer of Bayer et al. (2000). It is possible that this group could form the basis of a revised subtribe Relhaniinae, but additional taxon sampling is required to test which species are part of this clade, and it would have a substantially different circumscription to Relhaniinae of Anderberg (1991a). It is also possible that additional taxon sampling will result in a grade of taxa at the base of the tribe, making a simple split into two subtribes problematic. In contrast to the main clade of Gnaphalieae (see discussion of "crown radiation" below), there appears to be robust resolution of relationships among the sampled genera of the "*Relhania* clade" (all clades supported by posterior probabilities of 1.0).

With the exclusion of the "*Relhania* clade" described above, the next clade to diverge in the present analysis comprises two southern African species, *Dolichothrix ericoides* (Lam.) Hilliard & B.L. Burtt and *Phaenocoma prolifera* D. Don (Figs. 36.3, 36.4E). These species appeared as part of Anderberg's (1991a) Relhaniinae. As in the "*Relhania* clade", the position of these species in the present analysis is supported by a large number of characters (relative to most of the internal branches in the tree), and recovered with a posterior probability of 1.0.

The remainder of the sequences included in the analysis contribute to a poorly resolved "crown radiation" (Fig. 36.3) of Gnaphalieae. This "crown radiation" includes genera assigned to all five of Anderberg's subtribes and some of the "basal taxa". Although Bayer et al. (2002) discussed a number of clades within Australian Gnaphalieae based on analysis of chloroplast *matK*, *trnL* intron, *trnL-trnF* intergenic spacer, and nuclear ETS sequences, as in that presented here the analysis largely failed to provide robust resolution of phylogenetic relationships except for small clusters of terminal taxa.

Comparison of the analysis described here with published and unpublished phylogenetic analyses suggests that relationships among the majority of genera of Gnaphalieae will be difficult to discern. Challenges to phylogenetic analysis of the "crown radiation" include highly uneven rates of nucleotide substitution among lineages and the short internal branches in phylogenies consistent with a rapid radiation of many extant lineages (Fig. 36.3). Phylogenetic incongruence among morphology, chloroplast DNA sequences and nuclear DNA sequences is extensive in some taxa within the "crown radiation" (Smissen et al. 2004; Smissen and Breitwieser 2008), further complicating the interpretation of phylogenies generated from DNA sequences (see discussion of *Raoulia* alliance below). Further practical and analytical problems are created for studies of genera or groups of genera by the presence in the tribe of doubtfully monophyletic genera.

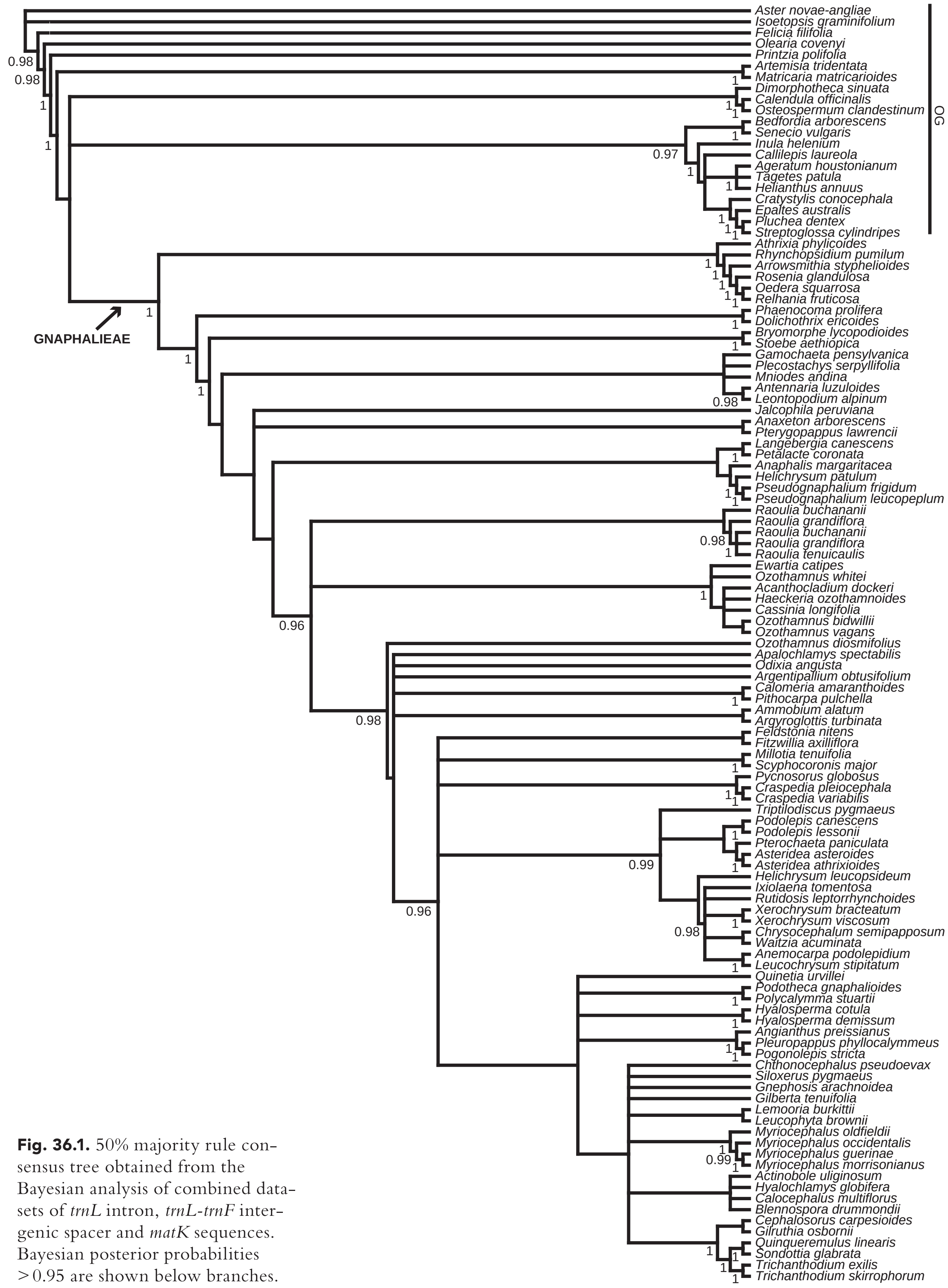

Fig. 36.1. 50% majority rule consensus tree obtained from the Bayesian analysis of combined datasets of *trnL* intron, *trnL-trnF* intergenic spacer and *matK* sequences. Bayesian posterior probabilities > 0.95 are shown below branches.

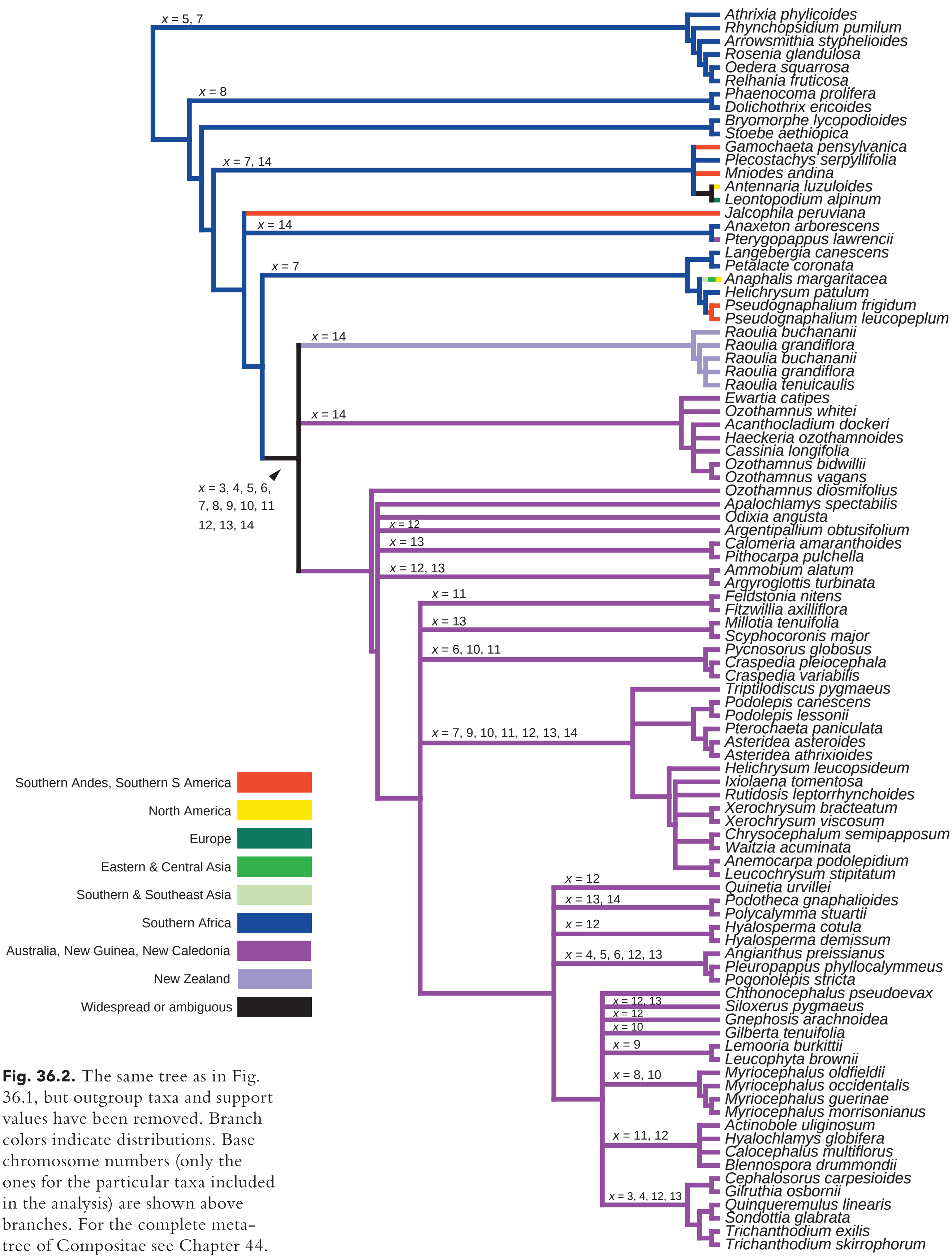

Fig. 36.2. The same tree as in Fig. 36.1, but outgroup taxa and support values have been removed. Branch colors indicate distributions. Base chromosome numbers (only the ones for the particular taxa included in the analysis) are shown above branches. For the complete metatree of Compositae see Chapter 44.

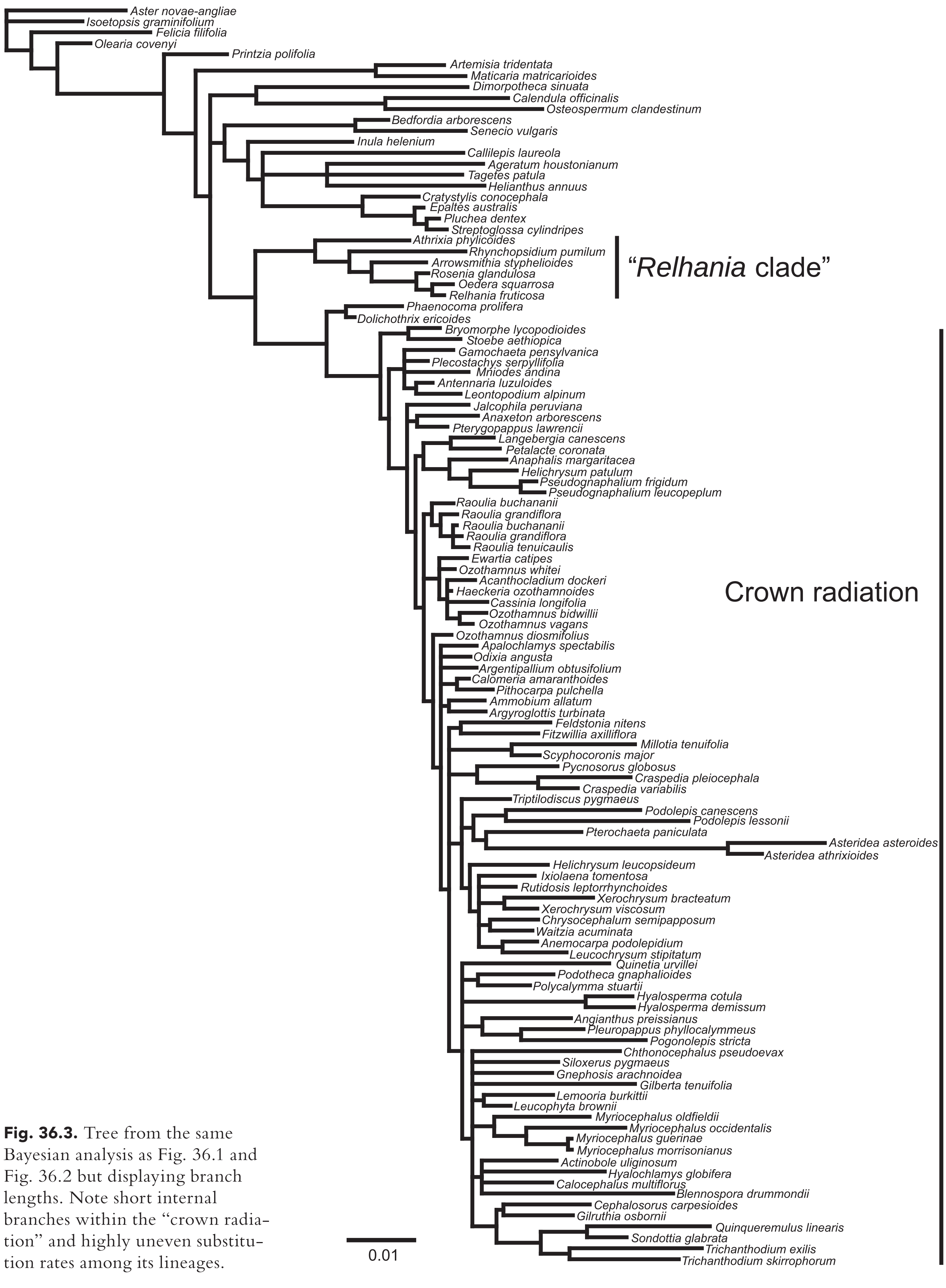

Fig. 36.3. Tree from the same Bayesian analysis as Fig. 36.1 and Fig. 36.2 but displaying branch lengths. Note short internal branches within the "crown radiation" and highly uneven substitution rates among its lineages.

For this and other reasons, published phylogenetic studies analyzing Gnaphalieae DNA sequences might be criticized as fragmentary and incompletely sampled. By and large they are also characterized by poor resolution as a result of inadequate sampling of nucleotides, although there are notable exceptions. Some studies with a genus level focus are discussed below to illustrate where progress has been made and the problems encountered in some groups that may prove general or common. The impact of cladistic analysis of morphological characters in the tribe is discussed in the Taxonomy section of this chapter.

Phylogenetic studies on genera

Trans-specific polymorphism and phylogenetic incongruence are significant and serious issues in phylogenetic inference that are well-documented in Compositae as a whole (e.g., Jansen et al. 1991b; Comes and Abbot 2001; Guo et al. 2004; Fehrer et al. 2007). Within Gnaphalieae they are best illustrated by studies of *Raoulia* and allied genera from New Zealand and Papua New Guinea. Despite initially promising results, improved sampling of genes, individuals, and species has resulted in a progressive discrediting of phylogenetic inference in the *Raoulia* alliance rather than progress toward a meaningful "species tree". Glenny and Wagstaff (1997) and Breitwieser et al. (1999) used nuclear ITS sequences to investigate the phylogenetic relationships among New Zealand genera of Gnaphalieae. These studies confirmed the presence of several independently derived lineages of Gnaphalieae within New Zealand, one of these being a group of genera including *Anaphalioides*, *Ewartiothamnus*, *Leucogenes* (Fig. 36.5C), *Rachelia*, *Raoulia* (Figs. 36.5A, B), and the New Zealand species currently assigned to *Helichrysum* (henceforth, the *Raoulia* alliance). However further sampling of ITS sequences suggested unexpected and unlikely relationships among species within the *Raoulia* alliance (Smissen et al. 2003), and chloroplast DNA sequence phylogenies were incongruent with these (Smissen et al. 2004). Intraspecific sampling of chloroplast sequences revealed extensive trans-specific (and indeed, trans-generic) polymorphism in the group (Smissen et al. 2004). Non-monophyletic groups of chloroplasts were sampled from within several species that are well defined by morphology and sometimes by independent genetic data (Smissen and Breitwieser 2008). Conversely, derived chloroplast lineages were found to be shared by morphologically dissimilar species (e.g., Smissen et al. 2006). The evolution of ITS sequences also appears to be idiosyncratic in the group; for example *Leucogenes grandiceps* Beauverd displays two ITS sequence types, differing by 18 substitutions (Smissen and Breitwieser 2008). These sequence types sometimes co-occur in the same specimen, although there is a geographic component to the distribution of the sequences. Some other common New Zealand species within the complex are comparatively uniform in their ITS and chloroplast sequences across their range (Smissen et al. 2006). The early support from ITS sequences for the monophyly of the *Raoulia* alliance was also undermined by further sampling of ITS sequences from additional species of *Raoulia* (Smissen et al. 2004). In general there is little congruence between chloroplast and ITS sequence-based phylogenies in the *Raoulia* alliance, and in turn little correspondence between these and taxonomic concepts based on morphology or multi-locus DNA fingerprint data (Smissen et al. 2004; Smissen and Breitwieser 2008). Many of the species of the *Raoulia* alliance form wild hybrids (see Hybridization, this chapter), often across generic boundaries (McKenzie et al. 2003, 2004, 2008; Smissen et al. 2003, 2004, 2007), but it has not been clearly demonstrated that the phylogenetic incongruence in the group is the result of hybridization.

In the analysis presented here the *Raoulia* alliance is represented by five sequences from three species of *Raoulia*. These sequences are representative of those found in other genera in the alliance. Although the *Raoulia* sequences appear as a clade in the tree presented here, support for this is weak, and the branch uniting them is short. In fact, the degree of difference between different chloroplast sequences sampled from within *R. buchananii* Kirk or *R. grandiflora* Hook. f. is similar to the degree of difference represented by the length of many internal branches in the phylogeny presented here (Fig. 36.3). To what extent similar results may ultimately be found in genera of Gnaphalieae outside New Zealand remains to be seen, but analyses of nuclear and chloroplast DNA sequences for a few Australian *Ozothamnus* and *Cassinia* species show similar incongruities (Smissen, unpub.).

The removal of Australian and New Zealand species from *Helichrysum* (see Hilliard and Burtt 1981; Anderberg 1991a; and Taxonomy section below) is largely supported by DNA sequence phylogenies and can therefore be viewed as an area where these have contributed to the taxonomy of the tribe, but the lack of phylogenetic structure within the "crown radiation" makes outgroup selection for any test of generic monophyly problematic. The New Zealand species are clearly related to members of the *Raoulia* alliance of genera (Breitwieser et al. 1999; Smissen et al. 2004) and need to be accommodated within those genera or in a new genus. The Australian species have mostly been apportioned among a series of segregate genera (see Taxonomy section below). Galbany-Casals et al. (2004a) further reduced *Helichrysum* by removing two aberrant species (*H. frigidum* (Labill.) Willd. and *H. montelinasanum* Em. Schmid) to a new genus *Castroviejoa* principally on the basis of phylogenetic analysis of nuclear ITS sequences (Galbany-Casals et al. 2004b). In their phylogeny, Mediterranean and Asian *Helichrysum* (including the type species *H. orientale* Gaertn.) were nested within a

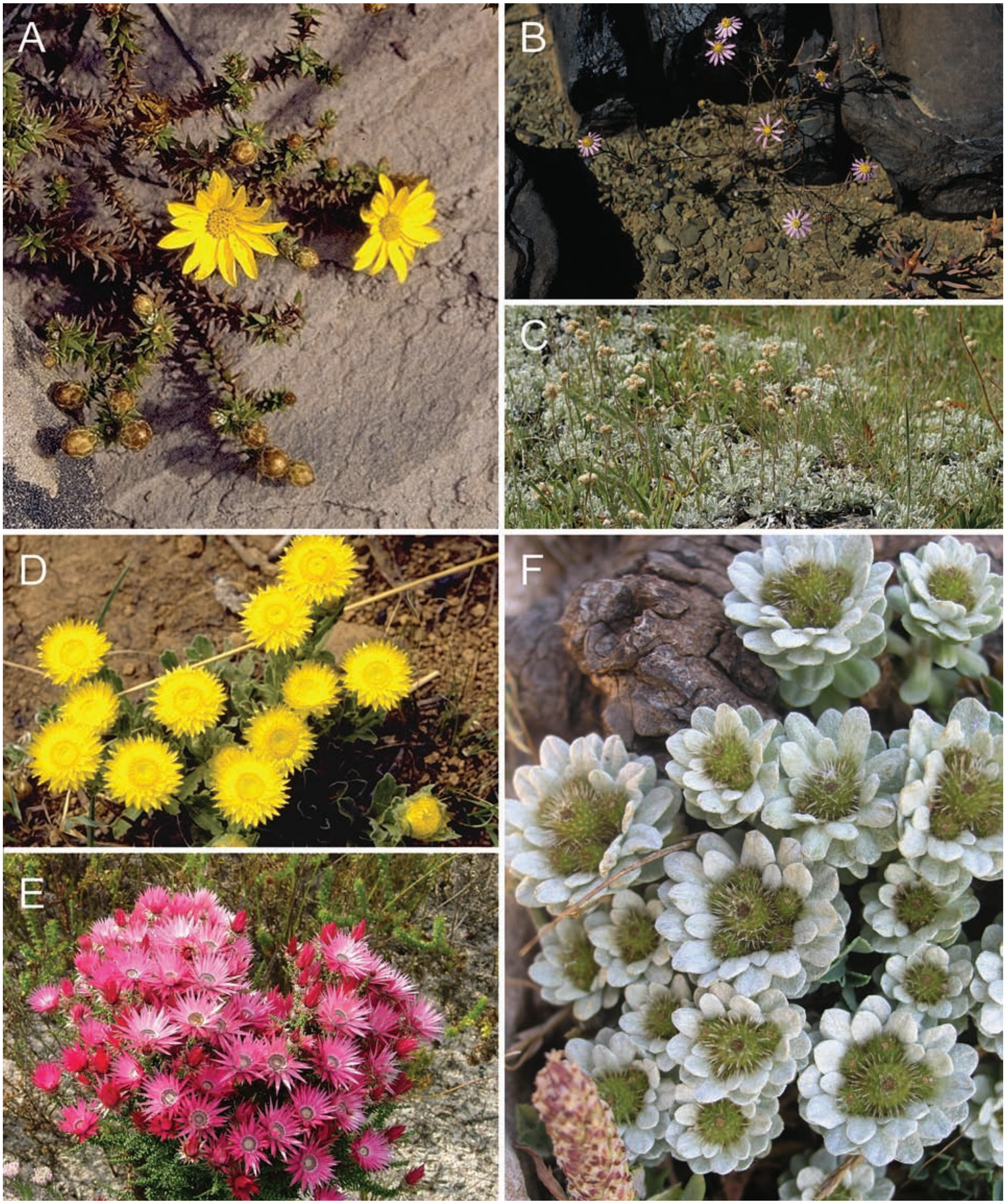

Fig. 36.4. Gnaphalieae, habit. **A** *Arrowsmithia styphelioides* DC., decumbent ericoid shrub with heterogamous radiate capitula, southern Africa; **B** *Alatoseta tenuis* Compton, annual with heterogamous radiate capitula, perhaps misplaced in Gnaphalieae, southern Africa; **C** *Antennaria umbrinella* Rydb., dioecious perennial herb with pronounced sexual dimorphism, North America; photo is of the sexual tetraploid cytotype ($2n = 56$); **D** *Helichrysum aureum* (Houtt.) Merr., perennial herb with discoid heterogamous capitula and bright yellow, showy, papery involucral bracts, southern Africa to Angola; **E** *Phaenocoma prolifera* D. Don, ericoid shrub to one meter with discoid heterogamous capitula and bright rose-pink, showy, papery involucral bracts, southern Africa; **F** *Filago* [*Evax*] *pygmaea* L., annual herb with clustered, heterogamous capitula surrounded by a ray of modified leaves, Mediterranean. [Photographs: A, C, D, R. Bayer; B, J. Manning; E, M. Koekemoer; F, M. Galbany-Casals.]

Fig. 36.5. Gnaphalieae, habit. **A, B** *Raoulia eximia* Hook. f., cushion shrub, New Zealand; **C** *Leucogenes grandiceps* Beauverd, decumbent herb, dense clusters of capitula surrounded by ring of showy modified leaves, New Zealand; **D** *Bryomorphe aretioides* (Turcz.) Druce, ericoid shrub, capitula with radiate outer florets, South Africa; **E** *Xerochrysum bracteatum* (Vent.) Tzvelev, upright herb, colorful papery involucral bracts, Australia; **F** *Leucochrysum albicans* (A. Cunn.) Paul G. Wilson, mat-forming herb, white papery involucral bracts, Australia; **G** *Mniodes pulvinulata* Cuatrec., suffruticose cushion, Peru; **H** *Gnaphalium supinum* L., stoloniferous rosette herb, inconspicuous involucral bracts, Eurasia. [Photographs: A–C, F, J. Lovis; D, M. Koekemoer; E, R. Bayer; G, M. Dillon; H, I. Breitwieser.]

poorly resolved and probably paraphyletic group of southern African *Helichrysum* (Fig. 36.4D) species together with *Pseudognaphalium luteoalbum* (L.) Hilliard & B.L. Burtt. However, no studies have been able to include adequate taxon sampling to properly test the monophyly of the remaining species of *Helichrysum*. Although alignment of ITS sequences across the tribe is problematic, analysis of those available in GenBank provides support for the inclusion of at least part of *Pseudognaphalium* (Fig. 36.6D) and *Anaphalis* in this *Helichrysum* (Fig. 36.4D) clade but does not establish if they fall within *Helichrysum* or merely close (Smissen, unpub.). A clade comprising two species of *Pseudognaphalium* and the southern African species *Helichrysum patulum* (L.) D. Don is supported by the analysis of chloroplast sequences presented in this chapter (PP 1.0), and this clade is in turn weakly associated with *Anaphalis margaritacea* (L.) Benth. & Hook. f. (Fig. 36.1). Therefore, it does appear that there is some consistent signal from both nuclear and chloroplast genomes for a lineage within the "crown radiation" that includes at least the bulk of the species still classified in *Helichrysum*, and an as yet unknown number of species from other genera. Further work is required to fully establish the composition of this clade, particularly better sampling of sequences from *Anaphalis*, and it appears that circumscribing a monophyletic *Helichrysum* will remain problematic at least until these data are available.

Well resolved phylogenies have been produced for the Australasian genera *Podolepis* (using nuclear ITS and chloroplast *matK* sequences; Konishi et al. 2000) and *Craspedia* (using nuclear ITS and ETS, and chloroplast *psbA-trnH* intergenic spacer sequences; Ford et al. 2007). These two studies illustrate that phylogenetic analysis of DNA sequences has particular potential in lineages that are part of the unresolved "crown radiation" but have relatively high rates of nucleotide substitution (compare branch lengths in Fig. 36.3). In the first study, the monophyly of *Podolepis* was supported only with the exclusion of *P. kendallii* (F. Muell.) F. Muell. and *P. georgii* Diels. The second study showed New Zealand's endemic species of *Craspedia* to be monophyletic and nested within one of three Australian *Craspedia* clades. However, phylogenetic incongruence was observed between chloroplast and nuclear datasets for *Craspedia*, and two species for which more than one specimen was sampled appeared to be non-monophyletic. In the absence of independent data, Ford et al. (2007) were unable to establish whether this species' non-monophyly was the result of idiosyncratic behavior of nrDNA loci or the specimens were not conspecific as believed.

Phylogenies of *Antennaria* (Fig. 36.4C) were produced from both morphological and ITS data matrices (Bayer 1990; Bayer et al. 1996). The trees from these analyses had similar topology, and for the first time distinct lineages were delimited within the genus. *Antennaria* is composed of two major lineages, the Leontipes group, which consists of species that are generally restricted in their distributions to western North America, and the Catipes group occurring throughout the Northern Hemisphere and South America (Bayer et al. 1996). The Leontipes group is composed of species that are amphimictic (sexually reproducing) and primarily diploid (tetraploids are known only in *A. dimorpha* (Nutt.) Torr. & A. Gray and *A. pulcherrima* (Hook.) Greene; Bayer and Stebbins 1987). The Catipes group contains both amphimictic diploids and tetraploids and polyploid agamic complexes derived from them. The relationships of *Antennaria* to other genera have not been firmly established, but it is associated with *Leontopodium* in the trees presented here, which is consistent with ITS sequence analyses (Bayer et al. 1996; Smissen, unpub.).

TAXONOMY

Tribe Gnaphalieae (Cass.) Lecoq & Juillet, Dict. Rais. Term. Bot.: 296. 1831 – Type: *Gnaphalium uliginosum* L.

Herbs, subshrubs or shrubs, generally unarmed. Stems generally with fibers in phloem (Fig. 36.7A), without resin canals. Leaves alternate, rarely opposite, generally entire, and generally tomentose at least on the lower surface. Capitula heterogamous disciform, or homogamous discoid, rarely heterogamous radiate, solitary or variously grouped, sometimes forming dense secondary capitula. Involucral bracts (Fig. 36.7B, C) generally papery, generally brightly colored or hyaline and with a thickened, cartilaginous basal portion (the stereome) composed of compact sclerenchyma sometimes divided by an unthickened, translucent central region (Fig. 36.7B). Receptacles generally epaleate. Female outer florets generally filiform or often absent. Central florets generally perfect, sometimes functionally male. Anthers ecalcarate, with tails (Fig. 36.7D); endothecial tissue almost always polarized. Pollen (Fig. 36.7E) with two-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer ("Gnaphalioid" type). Style branches with hairs apically (Fig. 36.7F), sometimes apically and dorsally (Fig. 36.7G), or rarely dorsally only; stigmatic rows generally separated (Fig. 36.7F). Achenes generally small and oblong to obovoid, usually hairy; pericarp generally with 2–3 or 5 vascular bundles. Pappus generally of plumose or barbellate to scabrid capillary bristles, occasionally of bristles and scales, only scales, or absent. Base chromosome number variable, but often $n = 7$ (in some groups 8 or 9). Phytochemistry: sesquiterpene lactones usually absent. 180–190 genera and about 1240 species, cosmopolitan, but most diverse in Australia and southern Africa.

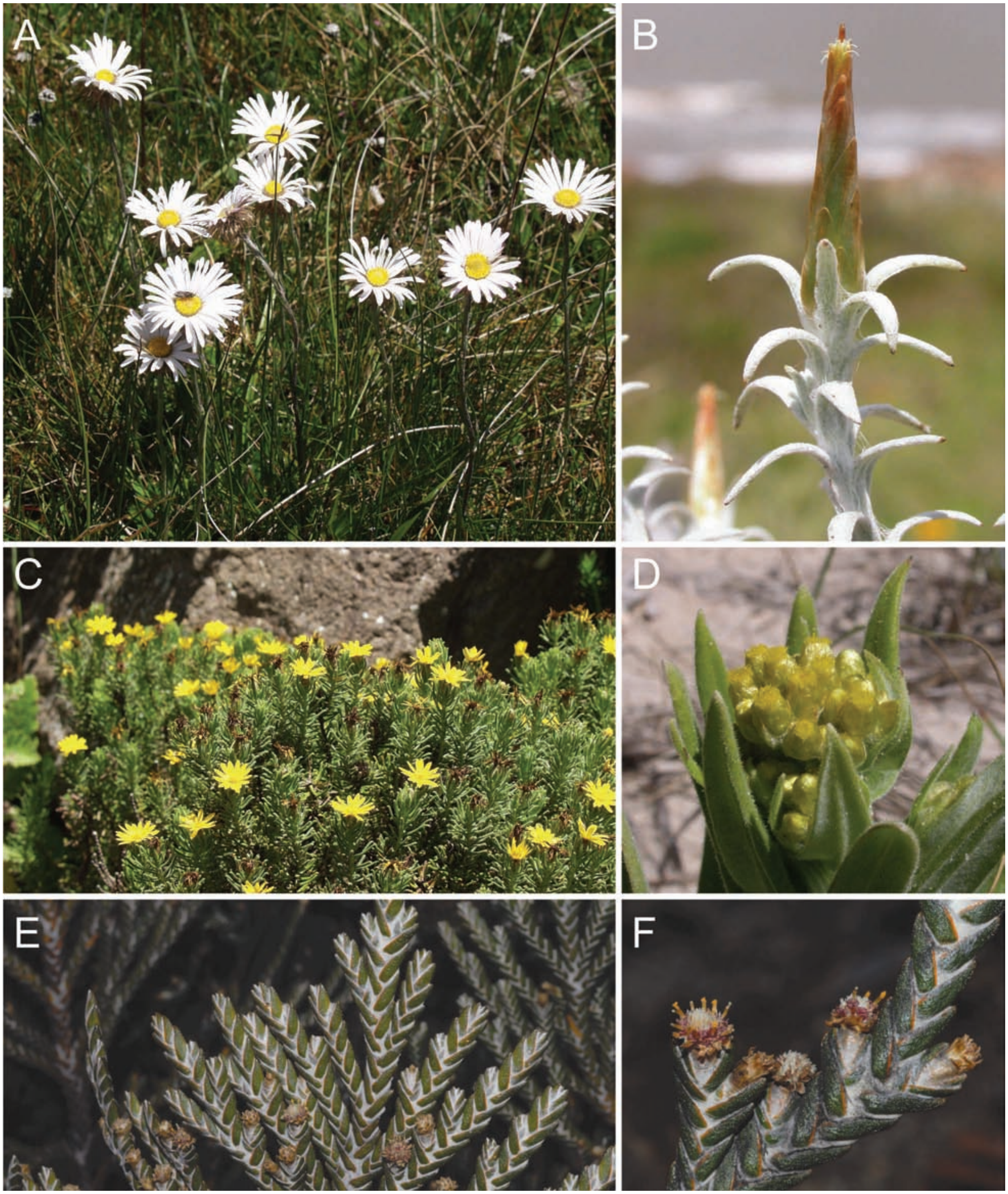

Fig. 36.6. Gnaphalieae, habit. **A** *Athrixia fontana* MacOwan, perennial herb of Anderberg's (1991a) "*Relhania* group" with solitary, radiate, white-rayed, heterogamous capitula, southern Africa; **B** *Lucilia acutifolia* Cass., woolly perennial herb with solitary, heterogamous, discoid capitula, South America; **C** *Macowania hamata* Hilliard & B.L. Burtt, ericoid shrub of the "*Relhania* group" with solitary, radiate, yellow-rayed, heterogamous capitula, southern Africa; **D** *Pseudognaphalium cheiranthifolium* (Lam.) Hilliard & B.L. Burtt, perennial herb with heterogamous capitula borne in small clusters, South America; **E, F** *Loricaria* sp., dioecious ericoid shrub with unisexual capitula borne in leaf axils or terminally, South America. [Photographs: A, C, R. Bayer; B, D–F, J.M. Bonifacino.]

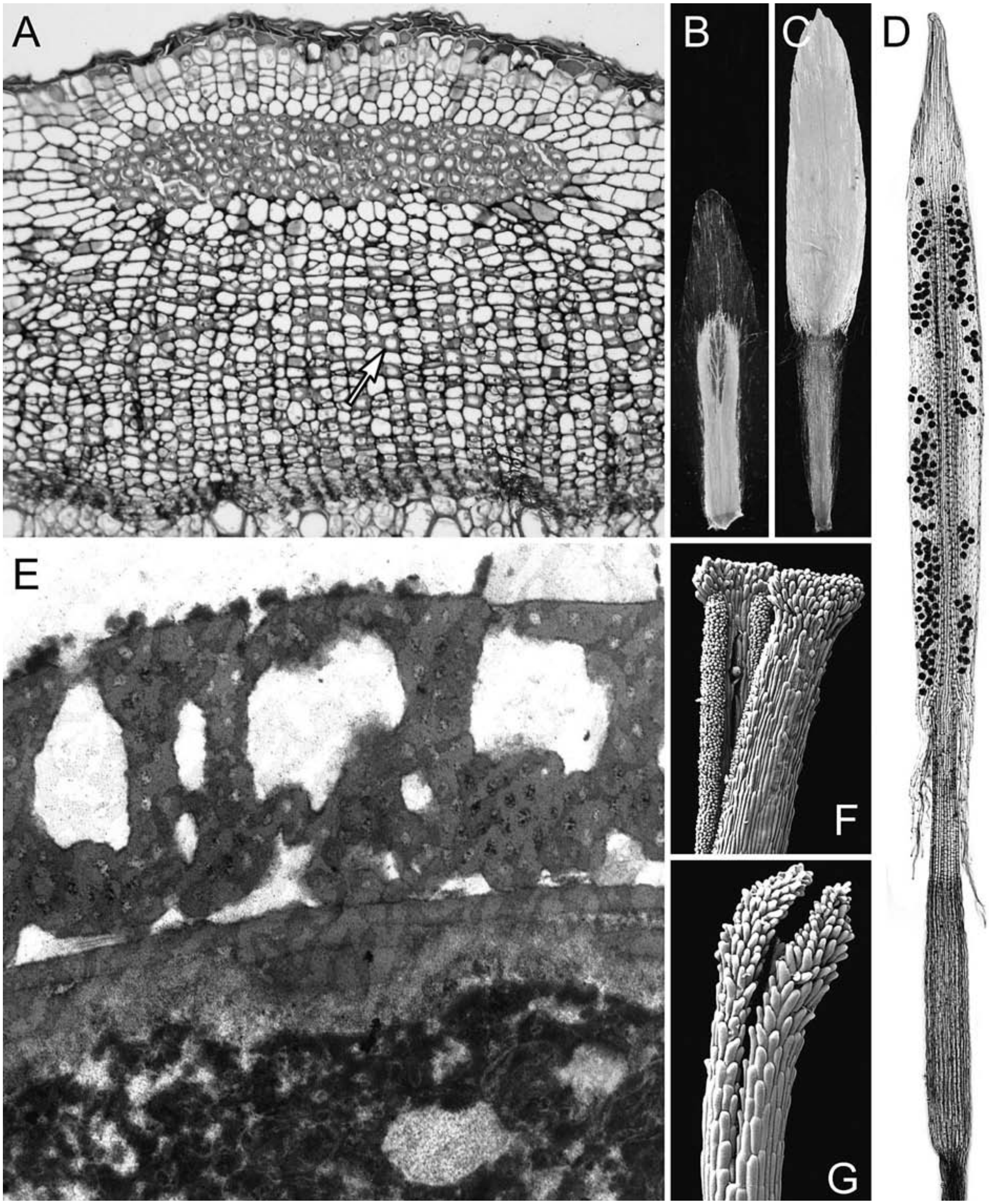

Fig. 36.7. Gnaphalieae, tribal characters. **A** fibers (arrow) within phloem, *Helichrysum lanceolatum* (Buchanan) Kirk (*Wilton 174*), TS stem (×213); **B, C** papery involucral bracts, **B** *Pseudognaphalium luteoalbum* (L.) Hilliard & B.L. Burtt (*Ward 88295*), hyaline lamina, divided stereome (×18), **C** *Anaphalioides bellidioides* (G. Forst.) D. Glenny (*Ward 94006*), showy lamina, undivided stereome (×9); **D** stamen with ecalcarate, tailed anther (×67), *Helichrysum depressum* (Hook. f.) Benth. & Hook. f. (*Ward 93028*); **E** pollen with 2-layered ectexine, *Anaphalis margaritacea* (L.) Benth. & Hook. f. (cultivated, *Ward 91199*), TEM section (×4650); **F, G** style branches from central florets, **F** *Ozothamnus leptophyllus* (G. Forst.) Breitw. & J.M. Ward (*Ward 96079*), separate stigmatic rows, hairs located apically (SEM ×115), **G** *Ewartia catipes* (DC.) Beauverd (*Ward 94086*), hairs placed apically and dorsally (SEM ×112.5).

INFRATRIBAL CLASSIFICATION

A satisfactory infratribal classification of Gnaphalieae does not exist, and understanding of phylogeny is as yet insufficient for proposing such a classification with confidence. However, recent revision at the generic level has been extensive, and much is known about relationships within small groups of genera. An account of taxonomic revision within the tribe since Merxmüller et al. (1977) is therefore provided here. Because there is no acceptable taxonomic framework in which to present this information, and because the vast majority of genera concerned are either endemic to a particular region or almost so, revisions are arranged under regional headings (Southern Africa, Australia, New Zealand, South and Central America and Mexico, and North America and Northern Old World). Large, wide-ranging revisions (and genera) precede these regional treatments. Revisions in Floras are excluded except for descriptions of new genera. Where transfers between genera are listed, the species name is generally given in the genus from which it was transferred, but not in the genus to which it was transferred unless the specific epithet is different (apart from gender). This is to facilitate finding which species have recently been transferred, and to where, especially from large genera such as *Helichrysum* and *Helipterum*.

Table 36.1 shows the recognized genera of Gnaphalieae in alphabetical order, with number of species, geographical distribution, chromosome number where known, and position in the phylogenetic analyses of Bayer et al. (2000, 2002) and the infratribal classifications of Anderberg (1991a) and Merxmüller et al. (1977). Genera accepted by Merxmüller et al. (1977) or proposed since then but not currently recognized for the tribe are listed with only their present status (included in another genus, excluded from the tribe, or an illegitimate name which has been replaced).

In the thirty years since the publication of *The Biology and Chemistry of the Compositae*, generic revision in Gnaphalieae has proceeded at an extraordinary rate compared to the previous century, fuelled by the increase in information from phylogenetic analyses and by the preparation of major floristic works such as the *Flora of Australia*. This period has seen the publication of revisions of some 40 genera, the description of 48 new genera and the reinstatement of a further 22. Most revisions have been regional, but two have had far-reaching effects.

The first one, that of Hilliard and Burtt (1981), focused on the flora of southern Africa, refining the concepts of a number of widespread genera, notably *Gnaphalium* (Fig. 36.5H), *Helichrysum* (Fig. 36.4D), and *Pseudognaphalium* (Fig. 36.6D). The longstanding problem of the separation of *Gnaphalium* and *Helichrysum* by a single character was discussed and revised concepts of both genera were presented. These are of general interest because both genera are large, widespread, polyphyletic and partway through the long process of being divided into monophyletic genera.

For *Gnaphalium* (Fig. 36.5H), a tentative redescription was based on the type species group and another shown to be congeneric, the *G. declinatum* L.f. group (including *Amphidoxa*). These are small, weak-stemmed herbs with flat, woolly, mostly spathulate to oblanceolate leaves, brown, buff or creamy-white involucral bracts with undivided stereomes, and heterogamous capitula. Variable features include floral ratio, achene hairs and pappus. Hilliard and Burtt found that the status of *Euchiton* and *Omalotheca* in relation to *Gnaphalium* was debatable and required further study, *Synchaeta* was not distinct from *Omalotheca* even at sectional level, and there was insufficient evidence to exclude *Gamochaeta* from *Gnaphalium*. The situation in *Gnaphalium* has been improved by Hilliard and Burtt (1981) and later authors with the recognition of segregate genera such as *Anaphalioides*, *Argyrotegium*, *Gnaphaliothamnus*, *Gnomophalium* and *Pseudognaphalium*, the transfer of anomalous species to existing genera such as *Chionolaena*, *Galeomma*, and *Lasiopogon* and to newly described genera such as *Plecostachys*, *Troglophyton*, and *Vellereophyton*, and regional revisions such as that of Hilliard (1981a) for Africa and Madagascar. However, many species in *Gnaphalium* may still need to be transferred to other genera such as *Pseudognaphalium* and *Gamochaeta* (Anderberg 1991a). *Euchiton* is now widely accepted at generic level whereas *Synchaeta* and *Omalotheca* are regarded as part of *Gnaphalium* by most authors (but see Nesom 1990e), and agreement has not been reached on *Gamochaeta*.

Hilliard and Burtt (1981) built up a general concept of *Helichrysum* (Fig. 36.4D) by considering the features of the type species, *H. orientale* (itself typical of a large group of Mediterranean and western Asian species) and then the features shared with most of the numerous and diverse African species, namely flat or revolute leaves, involucral bracts with a divided stereome, hairs abaxially on corolla lobes and achene hairs of the common duplex type or absent, with any deviations from this pattern requiring careful study. Special attention was given to features that had been used to characterize genera: pappus form, ratio of female to hermaphrodite florets and presence of receptacular paleae. The urgent need for the extension of the generic survey to Madagascar and Australia was noted. Since then the entire Australasian component has been excluded from *Helichrysum* and most of the species have been relocated in other genera. Many anomalous species in Africa and Eurasia have been accommodated by Hilliard and Burtt (1981) and later authors in *Achyrocline*, *Atrichantha*, *Castroviejoa*, *Chiliocephalum*, *Dolichothrix*, *Edmondia*, *Plecostachys*, *Syncarpha*, *Troglophyton* and *Vellereophyton*, and there has been some regional revision (Mesfin Tadesse and

Table 36.1. Genera of Gnaphalieae. Presented are the recognized genera of Gnaphalieae, number of species per genus, geographical distribution, haploid chromosome number(s), and phylogenetic and classical taxonomic affinities. Genera that have lapsed from recognition in Gnaphalieae since 1977 are listed by name and status only. The last five columns show clades in Bayer et al. (2000) and Bayer et al. (2002) (SAf., South Africa; Aus., Australia; subtribes (subtr.) and basal taxa with named groups if any in Anderberg (1991a); subtribes (I, Inulinae; II, Gnaphaliinae; III, Athrixiinae) and groups, then group numbers, in Merxmüller et al. (1977); nd, not described; nr, not recognized; nt, not in tribe; sa, semi-accepted.

				Bay. et al.		And.	Merxm. et al.	
Genus	No. of species	Geographical distribution	Haploid chromosome number	SAf.	Aus.	subtr. + group	subtr. + group	group
Acanthocladium F. Muell.	1	Australia			E	C–	II Hel?	14 (sa)
Achyrocline (Less.) DC.	32	Tropical Africa, Madagascar, Central and S. America	12, 14			G–H	II Gna	9
Acomis F. Muell.	3	Australia			D	A–	II Sch	16
Actinobole Fenzl ex Endl.	4	Australia	10, 11 or 12		J	A–A	II Ang	18
Alatoseta Compton	1	Southern Africa				B–	III Ala	22
Aliella Qaiser & Lack	3	Morocco	7, 9			B–Ph		nd
Ammobium R. Br.	3	Australia	12, 13		G	C–	II Hel	14
Amphidoxa DC. — included in *Gnaphalium*								
Amphiglossa DC.	11	Southern Africa				R–M	III Amp	21
Anaphalioides (Benth.) Kirp.	7	New Zealand, New Guinea	14, 28, 42			C–A	II Ana	10 (sa)
Anaphalis DC.	~110	Asia, North and South America	7, 13, 14, 21, 24			C–A	II Ana	10
Anaxeton Gaertn.	10	Southern Africa		S		C–A	III app	24
Ancistrocarphus A. Gray	1	North America				G–F		nr
Anderbergia B. Nord.	6	Southern Africa		S		nd		
Anemocarpa Paul G. Wilson	3	Australia			I	nd		
Angianthus J.C. Wendl.	17	Australia	6, 12, 13		J	A–A	II Ang	18
Anisochaeta DC.	1	Southern Africa				B–	III Prit	19
Anisothrix O. Hoffm.	2	Southern Africa	7	F		B–Pe	I Inu	1 (sa)
Antennaria J. Gaertn.	~40	Asia, Europe, North and South America	14, 21, 28, 35 42, 49, 56, 70, ~84			C–A	II Ana	10
Antithrixia DC.	1	Southern Africa				R–R	III Athr	20
Apalochlamys Cass.	1	Australia			G	C–C		nr
Argentipallium Paul G. Wilson	6	Australia	12		G	nd		
Argyroglottis Turcz.	1	Australia	12		G	C–	II Hel?	14 (sa)
Argyrotegium J.M. Ward & Breitw.	4	Australia, New Zealand	14			nd		
Arrowsmithia DC.	1	Southern Africa		F		B–Ma	III Athr	20

Artemisiopsis S. Moore	1	Southern Africa				B–D	II Gna	9
Asteridea Lindl.	9	Australia	7, 9		I	A–W		nr
Athrixia Ker Gawl.	14	Southern Africa		E		B–A	III Athr	20
Atrichantha Hilliard & B.L. Burtt	1	Southern Africa				R–M		nd
Basedowia Pritzel	1	Australia				C–	II Ang	18
Bellida Ewart	1	Australia	9		G	A–	II Scho	16
Belloa Remy	1	South America	12			G–L	II Luc	11
Berroa Beauverd	1	South America				G–L	II Luc	11
Blennospora A. Gray	2	Australia	11		J	A–A		nd
Bombycilaena (DC.) Smoljan.	3	Asia, Europe, North America	14			G–F	II Fil	13 (sa)
Bracteantha Anderb. & L. Haegi — illegitimate name for *Xerochrysum*								
Bryomorphe Harv.	1	Southern Africa		D		R–M	III Amph	21
Callilepis DC.	5	Southern Africa				B–	III Cal	23
Calocephalus R. Br.	11	Australia	12, 14, 28		I,J	A–A	II Ang	18
Calomeria Vent.	1	Australia			G	A–	II Hel	14
Calotesta P.O. Karis	1	Southern Africa				R–M		nd
Cassinia R. Br.	> 40	Australia	14		E	C–C	II Hel	14
Castroviejoa Galbany, L. Sáez & C. Benedí	2	Corsica, Sardinia	14			nd		
Catatia Humbert	2	Madagascar				G–	II Hel?	14
Cephalipterum A. Gray	1	Australia	12, 14		I	A–	II Ang	18
Cephalosorus A. Gray	1	Australia	12		J	A–A		nr
Chamaepus Wagenitz	1	Afghanistan				G–F		nd
Chevreulia Cass.	~6	South America				G–L	II Luc	11
Chiliocephalum Benth.	1	Ethiopia				G–H		nr
Chionolaena DC.	20	South America	14			C–A	II? Luc	11
Chondropyxis D.A. Cooke	1	Australia				nt		nd
Chrysocephalum Walp.	~5	Australia	12, 24, ~38		I	A–W		nr
Chthonocephalus Steetz	6	Australia			J	A–A	II Ang	18
Cladochaeta DC.	2	Eurasia	8, 9			G–S	II Hel	14 (sa)
Comborhiza Anderb. & K. Bremer	2	Southern Africa	7			nd		

Table 36.1. Continued.

Genus	No. of species	Geographical distribution	Haploid chromosome number	Bay. et al.		And.	Merxm. et al.	
				SAf.	Aus.	subtr. + group	subtr. + group	group
Comptonanthus B. Nord. — included in *Lasiopogon* and *Ifloga*								
Craspedia G. Forst	~20	Australia, New Zealand	11, 22, 33, 44, 55, 70+		J	A–	II Ang	18
Cremnothamnus C.F. Puttock	1	Australia				nd		
Cuatrecasasiella H. Rob.	2	South America				G–L		nd
Cymbolaena Smoljan.	1	Middle East, Asia				G–F	II Fil	13
Decazesia F. Muell.	1	Australia	14		J	A–A	II Ang	18
Denekia Thunb. — excluded from tribe								
Dielitzia P.S. Short	1	Australia	13			A–A		nd
Disparago Gaertn.	9	Southern Africa	8, 9	D		R–M	III Amp	21
Dithyrostegia A. Gray	2	Australia	7		D	A–		nr
Dolichothrix Hilliard & B.L. Burtt	1	Southern Africa		E		R–M		nd
Edmondia Cass.	3	Southern Africa		S		G–S		nr
Elytropappus Cass.	8	Southern Africa		D		R–M	III Amp	21
Epitriche Turcz.	1	Australia	5			A–A		nr
Eriochlamys Sond. & F. Muell.	1	Australia	14		G	A–A	II Ang	18
Eriosphaera Less. — illegitimate name for *Galeomma*								
Erymophyllum Paul G. Wilson	5	Australia	11, 12, 14		J	A-		nd
Euchiton Cass.	21	Western Pacific	14			G–G	II Gna	9 (sa)
Evacidium Pomel	1	South-eastern Europe and northern Africa				G–F	II Fil	13
Evax Gaertn. — included in *Filago*								
Ewartia Beauverd	4	Australia	14, 28		E	C–A	II Gna	9
Ewartiothamnus Anderb.	1	New Zealand	14			C–A		nd
Facelis Cass.	4	South America	14			G–L	II Luc	11
Feldstonia P.S. Short	1	Australia	11		J	A–A		nd
Filago L.	46	Asia, Europe, North Africa and North America	7, 9, 13, 14			G–F	II Fil	13
Fitzwillia P.S. Short	1	Australia			I	A–A		nd
Galeomma Rauschert	2	Southern Africa				G–	II Hel	14

Gamochaeta Wedd.	~50–80	South America	14			G–	II Gna	9 (sa)
Gamochaetopsis Anderb. & Freire	1	South America				nd		
Gilberta Turcz.	1	Australia	10		J	A–		nr
Gilruthia Ewart	1	Australia	13		J	A–A	II Hel?	14
Gnaphaliothamnus Kirp. — included in *Chionolaena*								
Gnaphalium L.	~80	Cosmopolitan	7, 8, 9, 10, 14, 21, 26, 28			G–G	II Gna	9
Gnephosis Cass.	16	Australia	6, ~11, 12, ~13, 14		I,J	A–A	II Ang	18
Gnomophalium Greuter	1	North Africa and Asia				G-H	II Gna	9 (sa)
Gratwickia F. Muell.	1	Australia				A–W	II Hel	14 (sa)
Haastia Hook. f. — excluded from tribe								
Haeckeria F. Muell.	2	Australia			E	C–C		nr
Haegiela P.S. Short & Paul G. Wilson	1	Australia				nd		
Haptotrichion Paul G. Wilson	2	Australia	12			nd		
Helichrysopsis Kirp.	1	Southern Africa				G–S	II Gna	9 (sa)
Helichrysum Mill.	~600	Africa, Europe, Asia	4, 7, 9, 14, 21, 28	S		G–H	II Hel	14
Helipterum DC. — illegitimate name for polyphyletic taxon								
Hesperevax (A. Gray) A. Gray	3	North America				nr		nr
Homognaphalium Kirp. — illegitimate name for *Gnomophalium*								
Humeocline Anderb.	1	Madagascar				G–		nd
Hyalochlamys A. Gray	1	Australia			I	A–A		nr
Hyalosperma Steetz	9	Australia	8, 11, 12		J	A–A		nr
Hydroidea P.O. Karis	1	Southern Africa				R–M		nd
Hypelichrysum Kirp. — included in *Pseudognaphalium*								
Ifloga Cass.	6	Africa, Asia, Europe, Middle East	7			G–	II Hel?	14
Isoetopsis Turcz. — excluded from tribe								
Ixiolaena Benth.	1	Australia			I	B–Mi	II Hel?	14
Ixodia R. Br.	2	Australia	13		G	C–C	II Hel	14
Jalcophila M.O. Dillon & Sagást.	3	South America				G–L		nd
Lachnospermum Willd.	3	Southern Africa		E		R–M	II Hel?	14
Langebergia Anderb.	1	Southern Africa		S		C–A		nd

Table 36.1. Continued.

Genus	No. of species	Geographical distribution	Haploid chromosome number	Bay. et al.		And.	Merxm. et al.	
				SAf.	Aus.	subtr. + group	subtr. + group	group
Lasiopogon Cass.	8	Africa and Middle East	7	P		G–	II Gna	9
Lawrencella Lindl.	2	Australia	8, 11		I	A–		nr
Leiocarpa Paul G. Wilson	10	Australia	20, ~21, 30, ~38, ~40			nd		
Lemooria P.S. Short	1	Australia			J	A–A		nd
Leontonyx Cass. — included in *Helichrysum*								
Leontopodium R. Br. *ex* Cass.	58	Asia and Europe	7, 12, 13, 14, 22, 24, 25, 26, 52			G–	II Ana	10
Lepidostephium Oliv.	2	Southern Africa				B–A		nr
Leptorhynchos Less.	8	Australia	12		D	A–W	II Hel?	14
Leptotriche Turcz. — type included in *Myriocephalus*								
Leucochrysum (DC.) Paul G. Wilson	5	Australia	9		I	nd		
Leucogenes Beauverd	4	New Zealand	14, 28, 56			G–	II Gna	9
Leucopholis Gardner — included in *Chionolaena*								
Leucophyta R. Br.	1	Australia	9		J	A–A		nr
Leysera L.	3	Southern Africa	4, 8			nr	II Luc	11
Logfia Cass.	9	Europe, North Africa, Middle East,	14	F		R–R	III Athr	20 (sa)
Loricaria Wedd.	19	South America	14, ~14			L	II Lor	12
Lucilia Cass.	12	South America	14			G–L	II Luc	11
Luciliocline Anderb. & Freire	13–16	South America				nd		
Luciliopsis Wedd. — type species excluded from tribe, others in *Cuatrecasasiella*								
Macowania Oliv.	12	Southern Africa				B–Ma	III Athr	20
Metalasia R. Br.	52	Southern Africa	8	E		R–M	II Hel?	14
Mexerion G.L. Nesom	2	Mexico				nd		
Micropsis DC.	~5	South America				G–	II Fil	13
Micropus L.	1	Europe, North Africa	14			G–F	II Fil	13
Millotia Cass.	11	Australia	8, 10, 11. 13		J	B–Mi	II Scho	16
Mniodes (A. Gray) Benth.	4	South America				L	II Luc?	11
Myriocephalus Benth.	12	Australia	8, 10, 12, 14		I,J	A–	II Ang	18

Nablonium Cass. — included in *Ammobium*								
Neotysonia Dalla Torre & Harms	1	Australia				A–	II Hel	14
Nestlera Spreng.	1	Southern Africa	5			nr		nr
Odixia Orchard	2	Australia			G	C–C		nd
Oedera L.	18	Southern Africa	7	F		R–R		nt
Oligandra Less. — type sp. in *Lucilia*, others in *Chionolaena*								
Omalotheca Cass. — included in *Gnaphalium*								
Oreoleysera K. Bremer	1	Southern Africa		S		R–R		nd
Oxylaena Benth. ex Anderb. — excluded from tribe								
Ozothamnus R. Br.	~50	Australia, New Zealand, New Caledonia	14	E,G		C–C		nr
Paenula Orchard	1	Australia				nd		
Parachionolaena M.O. Dillon & Sagást. — included in *Chionolaena*								
Parantennaria Beauverd	1	Australia			B	C–A	II Gna?	9
Pentatrichia Klatt	4	Southern Africa		F		B–Pe	III Prit	19
Petalacte D. Don	1	Southern Africa		S		C–A	III app	24
Phaenocoma D. Don	1	Southern Africa	8	E		R–M	III app	24
Phagnalon Cass.	43	Western Asia, southern Europe, tropical + northern Africa	9			B–Ph	III app	25
Philyrophyllum O. Hoffm.	2	Southern Africa				B–Pe	III Prit	19
Pithocarpa Lindl.	2	Australia	13		G	A–	II Hel	14
Planea P.O. Karis	1	Southern Africa				R–M		nd
Plecostachys Hilliard & B.L. Burtt	2	Southern Africa		S		G–		nd
Pleuropappus F. Muell.	1	Australia			J	A–A		nr
Podolepis Labill.	20	Australia	3, 7, 8, 9, 10, 11, 12, ~12, 20, ~30		I	A–W	II Scho?	17
Podotheca Cass.	6	Australia	13, 14, 26		J	B–Mi	II Scho	16
Pogonolepis Steetz	2	Australia	4, 5, 6, ~10, 12		I	A–A		nr
Polycalymma F. Muell. & Sond.	1	Australia	14		J	A–		nr
Printzia Cass. — excluded from tribe								
Pseudognaphalium Kirp.	~90	Africa, Asia, Central, North + South America, New Zealand	7, 8, 9, 10, 14, 20			G–H	II Gna	9 (sa)
Pseudoligandra M.O. Dillon & Sagást. — included in *Chionolaena*								
Psilocarphus Nutt.	8	North and South America	14			G–F	II Fil	13

Table 36.1. Continued.

Genus	No. of species	Geographical distribution	Haploid chromosome number	Bay. et al.		And.	Merxm. et al.	
				SAf.	Aus.	subtr. + group	subtr. + group	group
Psychrophyton Beauverd — included in *Raoulia*								
Pterochaeta Steetz	1	Australia	12		I	nr		nr
Pterothrix DC. — included in *Amphiglossa*								
Pterygopappus Hook. f.	1	Australia	14		E	L	II Gna?	9
Pycnosorus Benth.	~6	Australia	6, 10		J	nr		nr
Quinetia Cass.	1	Australia	12		J	A–	II Scho	16
Quinqueremulus Paul G. Wilson	1	Australia			J	A–		nd
Rachelia J.M. Ward & Breitw.	1	New Zealand	14			nd		
Raoulia Hook. f.	23	New Zealand	14, 28, 42, 56			C–	II Gna	9
Raouliopsis S.F. Blake	2	South America				L	II Luc?	11
Relhania L'Herit.	13	Southern Africa	7	F		R–R	III Athr	20
Rhodanthe Lindl.	45	Australia	5, 7, 8, 10, 11, 14		I	A–		nr
Rhynchopsidium DC.	2	Southern Africa	5	F		nr		nr
Rhynea DC. — illegitimate name for *Tenrhynea*								
Rosenia Thunb.	4	Southern Africa	7, 14, 28	F		R–R	III Athr	20
Rutidosis DC.	9	Australia	11, 12, 13, 19, 21, 22, 23, 26, 33, 36		I	A–	II Hel?	14
Schoenia Steetz	5	Australia	12			A–	II Scho	16
Scyphocoronis A. Gray	2	Australia	13		J	B–Mi	II Scho	16
Siloxerus Labill.	3	Australia	~12 or 13		I,J	A–A		nr
Sinoleontopodium Y.L. Chen	1	China				L		nd
Sondottia P.S. Short	2	Australia	3		J	A–A		nd
Stenocline DC.	3	Madagascar, (?)Mauritius				G–	II Gna?	9
Stenophalium Anderb.	3	South America				G–		nd
Stoebe L.	34	Eastern and southern Africa, Madagascar, La Réunion	8	D		R–M	III Amph	21
Stuartina Sond.	2	Australia			E	G–G	II Ang?	18
Stuckertiella Beauverd	2	South America	11 or 12			G–	II Gna	9
Stylocline Nutt.	7	North America	14			G–F	II Fil	13

Syncarpha DC.	28	Southern Africa	7, 11	S		G–S		nr
Syncephalum DC.	25	Madagascar				G–	II Hel?	14
Synchaeta Kirp. — included in *Gnaphalium*								
Taplinia Lander	1	Australia				A–		nd
Tenrhynea Hilliard & B.L. Burtt	1	Southern Africa		S		G–	II Hel	14
Thiseltonia Hemsl.	1	Australia				A–A	II Scho	16
Tietkensia P.S. Short	1	Australia				nd		
Toxanthes Turcz.	3	Australia			D	B–Mi	II Scho	16
Trichanthodium Sond. & F. Muell.	4	Australia	3, 4, 7		I J	nr		nr
Trichogyne Less.	8	Southern Africa				G–		nr
Triptilodiscus Turcz.	1	Australia	10, ~12		I	A–W		nr
Troglophyton Hilliard & B.L. Burtt	6	Southern Africa				G–G		nd
Vellereophyton Hilliard & B.L. Burtt	7	Southern Africa		S		G–G		nd
Waitzia J.C. Wendl.	5	Australia	10, 12		I	A–W	II Scho	16
Xerochrysum Tzvelev	6	Australia	11, 12, 13, 14, 15		I	A–		nd

Reilly 1995; Galbany-Casals et al. 2006). Nevertheless the circumscription of *Helichrysum* in relation to other large genera such as *Pseudognaphalium*, *Achyrocline*, and *Anaphalis* remains a problem (see also Phylogeny, this chapter).

Pseudognaphalium (Fig. 36.6D) was maintained as a genus by Hilliard and Burtt (1981) on the grounds that it has little affinity with *Gnaphalium* s.str. and would form an atypical appendage to *Helichrysum*. Salient features are involucral bracts with a divided stereome (with one exception), short involucral bracts, and female florets outnumbering the hermaphrodite and usually filiform. Achenes are usually glabrous and pappus hairs scabrid with bases cohering by patent cilia. Hilliard and Burtt (1981) transferred nine representative species from *Gnaphalium* to *Pseudognaphalium* (previously monotypic), and Anderberg (1991a) added over 70 more. The widespread Linnaean species *Gnaphalium luteoalbum* L., put in a new section of *Gnaphalium*, sect. *Calolepis* Kirp., by Kirpichnikov (1960) and excluded from *Gnaphalium* by Merxmüller et al. (1977), was shown by Hilliard and Burtt (1981) to have allied species in America, Africa and Asia. This group was shown to resemble but remain distinct from *Pseudognaphalium* and was given subgeneric status as *Pseudognaphalium* subg. *Laphangium* Hilliard & B.L. Burtt (not *Calolepis* as it is too similar to *Callilepis* for convenience if it is ultimately necessary to raise the section to generic rank). It was raised to generic rank by Tzvelev (1994) and this change was accepted for the Euro+Med Checklist (Greuter 2003) but not by Bayer et al. (2007). Unpublished phylogenetic analyses of DNA sequences suggest *Pseudognaphalium luteoalbum* is at least a close relative of part of *Pseudognaphalium* s.str.

Anderberg (1991a) presented the only recent worldwide revision of Gnaphalieae, in which 167 genera were recognized. Of the 102 genera accepted by Merxmüller et al. (1977) in their subtribes Gnaphaliinae and Athrixiinae, 96 were accepted by Anderberg (1991a) into Gnaphalieae (three of them under different names, due to replacement of illegitimate names, *Eriosphaera* by *Galeomma* (Rauschert 1982), *Rhynea* by *Tenrhynea* (Hilliard and Burtt 1981) and *Helipterum* by *Syncarpha* in Africa (Nordenstam 1989) and *Rhodanthe*, etc., in Australia (Wilson 1992a). Of the six genera not accepted by Anderberg (1991a), four had been (or were about to be) reduced to synonymy (*Comptonanthus* by Hilliard and Burtt 1981, *Leucopholis* by Freire 1993, *Nablonium* by Anderberg 1990, and *Oligandra* by Freire 1989), for the fifth (*Luciliopsis*) the type species had been excluded from the tribe and the other two species transferred to a new genus, *Cuatrecasasiella* (Robinson 1985), and the sixth (*Haastia*) was not mentioned.

Of the nineteen genera "semi-accepted" by Merxmüller et al. in Gnaphaliinae and Athrixiinae, Anderberg (1991a) recognized thirteen, seven from the *Gnaphalium* group (*Anaphalioides*, *Euchiton*, *Gamochaeta*, *Gnaphalioth-

amnus, *Helichrysopsis*, *Homognaphalium* and *Pseudognaphalium*), four from the *Helichrysum* group (*Acanthocladium* (Fig. 36.8G), *Argyroglottis* (Fig. 36.8D), *Cladochaeta* and *Gratwickia*) and the remaining two, *Bombycilaena* and *Logfia*, from the *Filago* group. Of the six semi-accepted genera of Merxmüller et al. not recognized by Anderberg (1991a), four were from the *Gnaphalium* group (*Amphidoxa*, *Hypelichrysum*, *Omalotheca* and *Synchaeta*), one from the *Helichrysum* group (*Leontonyx*) and one from the *Filago* group (*Evax*; Fig. 36.4F). In addition, Anderberg recognized *Anisothrix* (semi-accepted in Merxmüller et al. in Inuleae-Inulinae) as a basal genus in Gnaphalieae s.l.

As well as recognizing these 110 genera accepted or semi-accepted by Merxmüller et al., Anderberg (1991a) described six new genera: *Oxylaena*, monotypic, from southern Africa and in the basal *Macowania* (Fig. 36.6C) group; *Langebergia* from southern Africa and *Ewartiothamnus* from New Zealand, both monotypic and in the *Anaphalis* group; *Humeocline*, monotypic, from Madagascar and probably close to *Stenocline* s.str.; *Stenophalium* to accommodate the three South American species excluded from *Stenocline*; and (with L. Haegi) *Bracteantha* for the Australian *Helichrysum bracteatum* (Vent.) Andrews group. The name *Bracteantha* was superfluous because in the preceding year Tzvelev (1990) had erected *Xerochrysum* to accommodate *H. bracteatum* (Fig. 36.5E).

Most of the ten genera not accepted in Merxmüller et al. (1977) and listed by Anderberg (1991a) as again recognized at the generic level were the result of revision in Australia, particularly the redistribution of species formerly in *Helichrysum* (*Chrysocephalum*, *Lawrencella*, *Ozothamnus*) and *Helipterum* (*Gilberta*, *Hyalosperma*, *Rhodanthe*). *Polycalymma* was segregated from *Myriocephalus* following floristic treatments in South and Western Australia and *Leptotriche* was tentatively resurrected by Anderberg for species formerly in *Gnephosis* (Fig. 36.8H) and under revision at that time by Short. The remaining two, *Trichogyne* and *Psychrophyton*, resulted from Anderberg's breakup of *Ifloga* and *Raoulia*. The sections of *Ifloga* that had been redefined and raised to subgenera by Hilliard (1981b) were recognized as separate genera. Two of the three subgenera of *Raoulia* were recognized as *Raoulia* while the third was raised to generic level as *Psychrophyton* and moved to the new cushion-plant containing subtribe Loricariinae.

A further 19 genera not accepted in Merxmüller et al. (1977) were recognized by Anderberg (1991a). Two, *Oedera* and *Isoetopsis*, were transfers from other tribes and the remainder were the result of revisions since Merxmüller et al., mostly of Australian genera (*Apalochlamys*, *Asteridea*, *Blennospora*, *Cephalosorus*, *Dithyrostegia*, *Epitriche*, *Haeckeria*, *Hyalochlamys*, *Leucophyta*, *Pleuropappus*, *Pogonolepis*, *Siloxerus* and *Triptilodiscus* from Australia, *Ancistrocarphus* from North America, *Chiliocephalum* from East Africa, and *Edmondia* and *Lepidostephium* from southern Africa).

Apart from the replacements for illegitimate names mentioned above, 22 genera published since Merxmüller et al. (1977) were accepted by Anderberg (1991a). Most of these were from southern Africa and Australia (*Atrichantha*, *Calotesta*, *Dolichothrix*, *Hydroidea*, *Oreoleysera*, *Planea*, *Plecostachys*, *Troglophyton* and *Vellereophyton* from southern Africa, *Dielitzia*, *Erymophyllum*, *Feldstonia*, *Fitzwillia*, *Lemooria*, *Odixia*, *Quinqueremulus* and *Sondottia* from Australia, *Cuatrecasasiella* and *Jalcophila* from South America, *Aliella* from North Africa, *Chamaepus* from Afghanistan, and *Sinoleontopodium* from China).

Anderberg (1991a) recognized five subtribes in Gnaphalieae and within these a number of informal groups. The subtribes are Loricariinae, comprising six alpine cushion plant genera from Australia, New Zealand, South America, and China; Relhaniinae with twenty genera including six in the *Relhania* group and fourteen in the *Metalasia* group; Cassiniinae with twenty-two genera including six in the *Cassinia* group and eleven in the *Anaphalis* group; Angianthinae with fifty-one genera including six in the *Waitzia* group and twenty-four in the *Angianthus* group; and Gnaphaliinae with forty-seven genera, including six in the *Helichrysum* group, four in the *Syncarpha* group, seven in the *Lucilia* group and ten in the *Filago* group. Also included in the tribe but outside the subtribes were twenty-one genera called "basal taxa".

The most recent general account of Gnaphalieae (Bayer et al. 2007) includes 185 genera, generally following Anderberg (1991a). Bayer et al. (2007) did not arrange the genera in subtribes, finding Anderberg's subtribes not monophyletic, and there was not yet sufficient phylogenetic evidence to recircumscribe them. Of the 167 genera recognized by Anderberg for Gnaphalieae, 164 are included in Bayer et al. (2007). *Psychrophyton* is returned to *Raoulia*, and *Printzia* and *Isoetopsis* are excluded from the tribe. In their treatment fifteen new genera are included, nine for Australia, two each for southern Africa and South America and one each for Mexico and New Zealand (*Anemocarpa*, *Argentipallium*, *Chondropyxis*, *Cremnothamnus*, *Haegiela*, *Haptotrichion*, *Leucochrysum*, *Taplinia*, *Tietkensia* [Australia], *Anderbergia*, *Comborhiza* [southern Africa], *Gamochaetopsis*, *Luciliocline* [South America], *Mexerion* [Mexico] and *Rachelia* [New Zealand]). Six genera in synonymy in Anderberg (1991a) are again recognized: *Hesperevax* (from *Filago*), *Nestlera* and *Rhynchopsidium* (from *Relhania*), *Pterochaeta* (from *Waitzia*), *Pycnosorus* (from *Craspedia*), and *Trichanthodium* (from *Gnephosis*, under *Leptotriche*).

Three genera remain to be mentioned here. *Pseudoligandra*, described in 1990, was included in *Chionolaena* by Anderberg (1991a) and Bayer et al. (2007). *Parachionolaena*, described in 1991, was included in *Chionolaena* by Freire (1993) and Bayer et al. (2007). *Haastia*, accepted in part for Gnaphalieae by Merxmüller et al. (1977), not mentioned

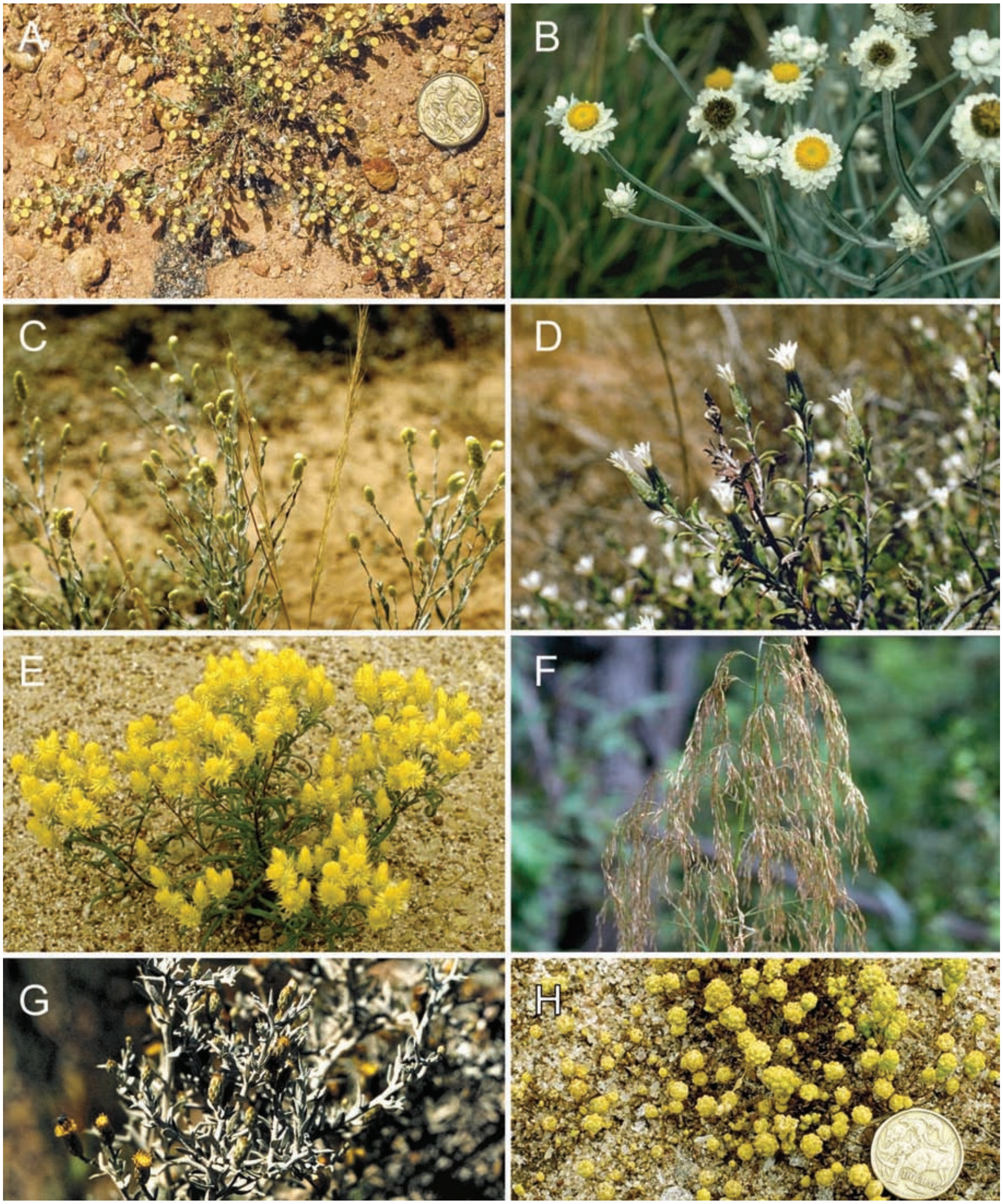

Fig. 36.8. Australian Compositae, tribe Gnaphalieae, habit. **A** *Gilruthia osbornii* Ewart & Jean White, annual herb with discoid homogamous terminal capitula; **B** *Ammobium alatum* R. Br., perennial herb with discoid homogamous capitula and white, showy, papery involucral bracts; **C** *Angianthus tomentosus* J.C. Wendl., annual with cylindrical secondary capitula composed of homogamous primary capitula; **D** *Argyroglottis turbinata* Turcz., shrub with solitary homogamous discoid capitula and involucral bracts with radiating papery, white laminae; **E** *Waitzia acuminata* Steetz, annual with homogamous discoid capitula and teretely-clawed, brightly-colored involucral bracts; **F** *Calomeria amaranthoides* Vent., biennial herb with panicles of numerous, few-flowered, drooping, homogamous capitula; **G** *Acanthocladium dockeri* F. Muell., silvery, armed shrub with heterogamous discoid capitula; having been last collected in 1910 and presumed extinct (five new populations were recently discovered in South Australia in 1999); **H** *Gnephosis cassiniana* P.S. Short, annual with golden, clavate, secondary capitula composed of homogamous primary capitula. [Photographs, R. Bayer.]

by Anderberg (1991a) and of uncertain tribal position in Bremer (1994), is a member of Senecioneae (Breitwieser and Ward 2005; Nordenstam 2007).

Four new genera have been proposed since the descriptions were written for Bayer et al. (2007): *Argyrotegium* (Ward et al. 2003), *Castroviejoa* (Galbany-Casals et al. 2004a), *Leiocarpa* (Wilson 2001) and *Paenula* (Orchard 2005b). Descriptions in the same format are provided in Appendix 36.1. Another recent change is the exclusion of *Callilepis* from the tribe (Bayer et al. 2000; Anderberg et al. 2005). Two further tribal exclusions not yet published are *Denekia* (see Chapter 37) and *Oxylaena* (Koekemoer, pers. comm.).

Southern Africa

Southern Africa is one of the centers of taxonomic diversity in Gnaphalieae and in the 30 years since the publication of *The Biology and Chemistry of the Compositae* (Heywood et al. 1977), it has also been one of the most active areas of taxonomic revision.

***Relhania* group.** — The *Athrixia* group of Merxmüller et al. (1977) comprised seven genera of which four (*Relhania*, *Antithrixia*, *Leysera* and *Rosenia*) were found by Bremer (1976, 1978a) to constitute a monophyletic group defined by its adaxially pubescent (or secondarily glabrous) and furrowed leaves. (Leaf pubescence in Gnaphalieae is commonly abaxial or on both surfaces, sometimes absent, but rarely adaxial only.) The four genera were defined by pappus characters in a reduction series: *Antithrixia* with many barbellate bristles and no scales; the other three with only scales in the female florets, in the hermaphrodite florets scales and usually five bristles in *Leysera*, scales and usually 1–2 bristles in *Rosenia* and scales only in *Relhania*. *Leysera* was also distinguished by solitary capitula on long peduncles. *Leysera montana* Bolus, which possessed this derived feature but had a pappus of barbellate bristles as in *Antithrixia*, was excluded from *Leysera* and subsequently placed in the new monotypic genus *Oreoleysera* (Bremer 1978b), defined by the solitary pedunculate capitula and the specialized montane habit (a cushion shrub).

Oedera, a southern African genus of six species, was transferred by Anderberg and Källersjö (1988) from Anthemideae to Gnaphalieae on the basis of the characteristic pollen wall structure of Gnaphalieae and the many derived character states shared with *Relhania* and associated genera. Anderberg (1991a) placed these six genera in the *Relhania* group. He maintained *Oreoleysera* but redefined it as possessing minute pappus scales but lacking two synapomorphies of *Leysera*, plumose pappus bristles and receptacular scales adaxial to the florets.

This *Relhania* group was revised by Anderberg and Bremer (1991) based on a parsimony analysis of morphological data. *Relhania* was reduced from 29 to 13 species, poorly defined as a group but mostly with adaxially pubescent, abaxially glandular-punctate leaves, solitary capitula and a diploid chromosome number of fourteen. *Leysera* was reduced from four to three species, characterized by a pappus of plumose bristles and scales, and diploid chromosome numbers of eight and sixteen. *Comborhiza* was proposed for two species, one from *Relhania* and one from *Leysera*, with thick subterranean rhizomes, adaxially glabrous and abaxially glandular-hairy leaves, and a diploid chromosome number of fourteen. *Nestlera* was reinstated for a single biennial species from *Relhania* with almost glabrous achenes and a diploid chromosome number of ten. *Rhynchopsidium* was reinstated for two annual species from *Relhania* with densely hairy achenes with long, apically-coiled hairs and with a diploid chromosome number of ten. *Oedera* was expanded from six to eighteen species, with twelve transferred from *Relhania*, and characterized by generally glabrous, glandular-punctate leaves, generally cymose-corymbose to congested capitula and a diploid chromosome number of fourteen. *Antithrixia* (monotypic), *Oreoleysera* (monotypic), and *Rosenia* (four species) were unchanged. Bayer et al. (2000), in an analysis of South African Gnaphalieae based on two noncoding chloroplast sequences, found that this *Relhania* group was monophyletic if *Oreoleysera* was excluded. They suggested that *Oreoleysera* is probably misplaced in Anderberg's subtribe Relhaniinae due to its reduced morphology and alpine habit convergence.

***Metalasia* group.** — Hilliard and Burtt (1981) made several changes to *Metalasia* and allied genera. *Lachnospermum*, with two species, had previously been distinguished from *Metalasia*, with 33 species, by the presence of receptacular paleae. *Metalasia imbricata* (P.J. Bergius) Harv. which lacks these paleae, was transferred to *Lachnospermum* and the defining differences in *Lachnospermum* became the few, large, campanulate heads, multicellular hairs on the outside of the corolla lobes, long, unicellular hairs on the achenes, and a rim or shallow cup at the top of the achene, within which the pappus arises. The remaining 32 species in *Metalasia* were found to be remarkably uniform in involucre, pappus and corolla characters except for *M. schlechteri* L. Bolus, noted as perhaps needing more critical study. A new genus *Atrichantha* was proposed for two species of *Helichrysum*, *H. gemmiferum* Bolus and an apparently closely allied new species *A. elsiae* Hilliard, both clearly out of place in *Helichrysum* and more closely allied to *Metalasia*, but differing substantially from both *Metalasia* and *Lachnospermum*. Another new genus *Dolichothrix* was proposed for *Helichrysum ericoides* (Lam.) Pers., a species allied to *Lachnospermum* but with some striking differences (Hilliard and Burtt 1981).

Metalasia was monographed by Karis (1989) who recognized 52 species, all endemic to southern Africa and 14 of them newly described in this work. The genus is defined by two uniquely derived characters, testa epidermal cells with sinuose walls and apical cells of pappus bristles markedly fused. *Metalasia schlechteri*, which lacks both these features, was excluded. Karis (1990) proposed three new monotypic genera: *Planea* for *Metalasia schlechteri*, *Hydroidea* for *Atrichantha elsiae*, characterized by rather large, solitary, white capitula and thick-walled apical pappus cells, and *Calotesta* for a new species sharing with *Metalasia*, *Atrichantha* and *Hydroidea* a glabrous corolla and a well-developed testa, but with the epidermal cells of the testa covered by a thick, greenish cuticle and lacking the brownish, inversely U-shaped outgrowths found in the other three genera.

Disparago, with seven species all endemic to southern Africa, was revised by Koekemoer (1991, 1993) who maintained six of the existing species and described three new ones. *Disparago* is distinguished from *Stoebe* and *Elytropappus* by the presence of ray florets. *Bryomorphe* (Fig. 36.5D), a monotypic genus with a distinctive moss-like habit, may not be generically distinct from *Disparago*.

Amphiglossa, with four species all endemic to southern Africa, was revised by Koekemoer (1999) who described four new species and broadened the concept of the genus to include the three species of *Pterothrix*. The two genera had been separated by the presence of ray florets in *Amphiglossa* and their absence in *Pterothrix*, but were united on the basis of shared pappus and achene features: a pappus of many fine plumose bristles interlocking in the central parts and a papillose achene with a germination strategy unique in Relhaniinae.

***Gnaphalium*, *Helichrysum* and associated genera.** — Hilliard and Burtt (1981), in conjunction with revising the concepts of the widespread genera *Gnaphalium* (Fig. 36.5H) and *Helichrysum*, made substantial changes to other genera in southern Africa.

The genus *Edmondia* (Cassini 1818), included in *Helichrysum* by Merxmüller et al. (1977), was reinstated with two species. A third species was added later (Hilliard 1983). *Edmondia* has distinctive subulate to linear-lanceolate leaves with strongly involute margins and tomentum on the adaxial but not the abaxial surface, the reverse of the usual condition in *Helichrysum*. It is endemic to the S.W. Cape.

A new genus *Troglophyton* was proposed for six species, one from *Gnaphalium* and one from *Helichrysum* formerly separated by different sex ratios, and four new, undescribed species (subsequently described by Hilliard 1983). *Troglophyton* is endemic to southern Africa and characterized by damp, shady habitats, filiform stems, petioles and peduncles, involucral bracts with undivided stereomes, the innermost bracts concave on the inner face and embracing the adjacent floret, and a precise form of pappus unmatched in *Gnaphalium* or *Helichrysum*.

A new genus *Vellereophyton* was proposed for one species from *Gnaphalium* and two from *Helichrysum* as well as several undescribed species (four described subsequently by Hilliard 1983). They are woolly herbs of damp places, with capitula congested into glomerules, involucral bracts with divided stereomes, the innermost bracts concave on the inner face and embracing the adjacent floret, and the entire upper part of the pappus subplumose. Also recognized as separate from *Gnaphalium* and *Helichrysum* were two species (*G. polifolium* Thunb. and *H. serpyllifolium* (Berg.) Pers.) placed in the new genus *Plecostachys*.

The concept of "*Helipterum*", with usually undivided stereomes and plumose pappus bristles (cf. *Helichrysum*), was widened to include the *Helichrysum paniculatum* (L.) Willd. (five species) and *Helichrysum vestitum* (L.) Willd. (three species) groups. Formal transfers were not made because *Helipterum* is antedated by other names and the southern African species were under revision by Nordenstam, who subsequently transferred these and sixteen species in *Helipterum* to the reinstated genus *Syncarpha* (Nordenstam 1989). He later recognized and recombined two more species in the *Helichrysum paniculatum* group and added two more species, one newly described (Nordenstam 2003), bringing the number of species in *Syncarpha* to twenty-eight.

Achyrocline, a primarily Central and South American genus, was reinstated for those African species earlier transferred to *Helichrysum* by Moeser (1910), as well as an additional species of *Helichrysum*, with a note that it was provisionally maintained for taxonomic convenience rather than conviction.

Less reliance on pappus differences in favor of other more numerous similarities led to expanded concepts of *Eriosphaera* and *Lasiopogon*. *Eriosphaera*, with linear-lanceolate involucral bracts with strongly acute tips and a divided stereome, was expanded to accommodate *Gnaphalium stenolepis* S. Moore. Rauschert (1982) proposed the name *Galeomma* to replace *Eriosphaera* Less., a later homonym of *Eriosphaera* F. Dietr. *Lasiopogon* was expanded from two to seven species, two from *Gnaphalium*, two from *Comptonanthus*, and one new, characterized by a biseriate involucre, blunt involucral bracts with a strongly divided stereome, and achene hairs absent or minute. An additional species, *Gnaphalium minutum* B. Nord., distinct but clearly adjacent to *Lasiopogon*, was included as a separate section.

Hypelichrysum, *Helichrysopsis*, and *Homognaphalium*, all monotypic, had been segregated from *Gnaphalium* (Fig. 36.5H) by Kirpichnikov (in Kirpichnikov and Kuprijanova 1950) and "semi-accepted" by Merxmüller et al. (1977). *Hypelichrysum*, based on *G. heterotrichum* Phil., was reduced to synonymy under *Pseudognaphalium* (Fig.36.5D). *Helichrysopsis*, based on *G. septentrionale* (Vatke) Hilliard under the illegitimate name *G. stenophyllum* Oliv. & Hiern., was accepted. It has a unique combination of strongly revolute leaves, globose achene hairs and distinctive pappus bristles with a plumose tip, a smooth shaft, and two levels of fusion. *Homognaphalium*, based on a description of *G. pulvinatum* misidentified as *G. crispatulum* Delile, was regarded as doubtfully distinct from *Eriosphaera*, so *G. pulvinatum* Delile was not transferred to *Homognaphalium*. This was, however, done later by Fayed and Zareh (1989). The generic name for *H. pulvinatum* was changed to *Gnomophalium* by Greuter (2003) (see Appendix 36.1).

Ifloga s.l. comprises about 14 species of annual or perennial herbs or shrubs with ericoid leaves. The upper surface of the leaf is white-tomentose and the lower surface and stems are covered with a thin, tissue-papery, myxogenic indumentum to which sand grains adhere. The structure of the capitulum is unusual, with the outer involucral bracts concave on the inner face and subtending and more or less enveloping the epappose female florets, whereas the inner bracts are more or less flat and surround the pappose hermaphrodite florets. Hilliard and Burtt (1981) expanded the concept of the genus to include *Comptonanthus molluginoides* (DC.) B. Nord., which resembles annual species of *Ifloga* except that the female florets are pappose and included within the main involucre.

Hilliard (1981b) revised the southern African species of *Ifloga*, recognizing twelve species including two newly described, and commented on the two or three Northern Hemisphere species, one restricted to the Canary Islands and the other polymorphic and widespread from the Canary Islands, Spain and North Africa east to Pakistan and North West India, with a segregate species from The Sinai sometimes recognized. The genus had been divided into two sections on the basis of annual or perennial habit (De Candolle 1838; Bentham 1873b), but Hilliard redefined these sections, using a remarkable number of floral characters, and raised them to subgenera, with some annual species transferred to the otherwise perennial subgenus *Trichogyne* (Less.) Hilliard. Subgenus *Ifloga* has glabrous involucral bracts, hermaphrodite florets with cylindrical corollas, scattered thickenings in the endothecial cell walls of the anthers, divided styles, usually developed achenes, and pappus bristles with basal patent cilia and regularly plumose tips in which the cell walls are unthickened; subgenus *Trichogyne* has at least the inner involucral bracts usually hairy on the outer face, hermaphrodite florets with the upper part of the corolla campanulate, polarized endothecial thickenings, undivided styles, aborted ovaries, and pappus bristles naked at the base and with shortly and irregularly plumose tips often with delicate spiral thickenings in the cell walls.

Anisothrix was revised by Anderberg (1988a) who recognized two species, one transferred from *Iphiona* Cass., and transferred the genus from Inuleae to Gnaphalieae. *Anisothrix* has apically confluent stigmatic lines as in Inuleae but has other characteristics of Gnaphalieae including obtuse (vs. acute) sweeping hairs on the style arms, a base chromosome number of 7 (vs. 9 or 10), and the definitive pollen wall structure of a two-layered sexine with an outer baculate and an inner irregularly perforated layer, although the bacula are devoid of the internal foramina common in Gnaphalieae. Anderberg (1991a) placed *Anisothrix* as a close relative of *Pentatrichia* in the "basal taxa" of Gnaphalieae.

Two new genera have been proposed for species allied to, but aberrant in, the African genera *Petalacte* and *Anaxeton*. Anderberg (1991a) proposed *Langebergia* for *Petalacte canescens* DC., which has features in common with both genera but was accepted in neither by Lundgren (1972, 1974). Nordenstam (1996) proposed *Anderbergia* for two species aberrant in *Petalacte* (*P. epaleata* (Hilliard & B.L. Burtt) B. Nord. and *P. vlokii* (Hilliard) B. Nord.) and another four species previously undescribed, all lacking the receptacular paleae and flat leaves of *Petalacte* and the corymbophore and usually glabrous upper leaf surface of *Anaxeton*. *Anderbergia* also differs from *Petalacte*, *Anaxeton* and *Langebergia* in having white to yellow rather than purple corollas.

Australia

Australia has a very large and mostly unique representation of Gnaphalieae. Of its 85 genera, only five occur outside Australia: *Gnaphalium* and two of its segregate genera, *Euchiton* and *Argyrotegium*, *Ozothamnus* in the *Cassinia* group, and *Craspedia* in Angianthinae. Angianthinae sensu Anderberg with 63 genera, contains most of the Australian Gnaphalieae and is entirely endemic except for *Craspedia*, which has dispersed across the Tasman Sea to New Zealand.

Although Australia has produced a number of relatively recent State floras, the only national flora was compiled by Bentham and published nearly one and a half centuries ago (Bentham 1867). Bentham commented with regard to Compositae that the large genera run into each other so much as to make it difficult to circumscribe them, and that the number of published monotypic genera was most excessive, requiring the suppression of more than eighty of them. A new *Flora of Australia* is partway through publication, and the prospect of a new and unified treatment for Australian Compositae has greatly stimulated taxonomic activity, with many revisions published in the thirty years since Heywood et al. (1977), especially in Gnaphalieae, most notably by Short and Wilson in Angianthinae sensu Anderberg and Orchard in the *Cassinia* group. One noticeable outcome of all this revisionary work is the high numbers of monotypic or ditypic genera, both reinstated and newly described.

Thirty years ago the two largest Compositae genera in the Australian flora were *Helichrysum* (Fig. 36.4D) and *Helipterum*. Australian species of *Helichrysum* were effectively excluded from the genus as redefined by Hilliard and Burtt (1981) and *Helipterum* was an unwieldy combination of size, polyphyly and an illegitimate name. Nearly all Australian species from both *Helichrysum* and *Helipterum* have now been relocated in other genera.

Anderberg's (1991a) subtribes of Gnaphalieae are unevenly represented in the Australian flora. There are four genera of Gnaphaliinae, one of Loricariinae, fourteen of Cassiniinae, and sixty-three of Angianthinae, and one group of genera which appeared as part of his basal grade (the *Millotia* group). Revisionary work has been predominantly in Angianthinae and the *Cassinia* group, with the *Millotia* group and the genus *Nablonium* also receiving attention, as well as some genera shared with (and reviewed under) New Zealand.

The *Millotia* group comprises *Ixiolaena*, *Podotheca*, *Millotia*, *Toxanthes*, and *Scyphocoronis*, all of which have undergone taxonomic changes. *Ixiolaena* was reduced to one species, with the other seven transferred to *Leiocarpa* (Wilson 2001). *Podotheca*, a genus of annual herbs found mainly in Western Australia, was revised by Short (1989a). Of the six species recognized in Grieve and Blackall (1975), three were retained, two were excluded and one was reduced to synonymy. Three new species were described. Distinguishing features of the genus are involucral bracts in several series with the outer ones leaf-like, a pappus of one, five or ten bristles, and long, bisexual florets in large capitula. The fruit has a prominent stipe but this is not exclusive to *Podotheca*.

Millotia, *Toxanthes*, and *Scyphocoronis* are all annual herbs with a more or less uniseriate involucre, discoid capitula and a more or less deflexed corolla. *Scyphocoronis* has two species, both with a distinctive apical cup on the achene, and *Toxanthes* conventionally has two species (three in Anderberg 1991a) with extremely long achenes (a feature also found in some species of *Millotia*). Many similarities have been noted between species in the different genera (Schodde 1963), and Short et al. (1989) found the anatomy of fruits of species in all three genera to be similar. Short (1990c) reduced *Toxanthes* and *Scyphocoronis* to synonymy under *Millotia* and described a new species to bring the number of species in *Millotia* to ten. Anderberg (1991a) recognized the three separate genera but commented that they would be better treated as one, otherwise *Millotia* is paraphyletic. Short (1995) subsequently revised *Millotia*, describing six new species and recognizing sixteen in total including those previously in *Toxanthes* and *Scyphocoronis*. A cladistic analysis of morphological data (Short and Anderberg 1995) showed the two traditional species of *Toxanthes* and the two species of *Scyphocoronis* as two monophyletic groups within *Millotia*. Bayer et al.'s (2002) analysis of DNA sequences recovered a well supported clade of *Scyphocoronis major* (Turcz.) Druce and *Millotia tenuifolia* Cass., but was not consistent with a close relationship between these species and *Toxanthes perpusilla* Turcz.

Cassinia group. — Discussing the delimitation of *Cassinia* and associated genera, Orchard (1981) wrote "It is not possible to fully represent within a formal nomenclatural system the interwoven relationships of these taxa." Again, nearly two and a half decades later (Orchard 2005b), he remarked that they showed a braided series of interrelationships, where characters usually thought to be diagnostic seemed to be segregating independently of each other. Consequently species have been moved among genera as different characters were considered diagnostic of phylogenetic relationship. In the last thirty years taxonomic papers have been published on *Ixodia* (Orchard 1981; Copley 1982), *Odixia* (Orchard 1981), *Cremnothamnus* (Puttock 1994b), *Haeckeria* (Orchard 2004a), *Cassinia* (Orchard 2004b–d, 2005a, 2006), and *Paenula* (Orchard 2005b). *Ozothamnus*, included in *Helichrysum* as a section by Bentham (1867, 1873b) and as a subgenus by Burbidge (1958), is now widely accepted as a distinct genus (e.g., Anderberg 1991a; Wilson et al. 1992; Bayer et al. 2007). A comprehensive modern revision is not yet published.

Orchard (1981) compared *Ixodia*, *Haeckeria*, *Ammobium* (Fig. 36.8B), *Cassinia*, and *Ozothamnus* (as *Helichrysum*) and found that they exhibited a mosaic of character states. He proposed a new genus *Odixia* for the two Tasmanian species of *Ixodia*, which he found to be distinct from the type (and only other species) of *Ixodia* and not congeneric with any other species to which they showed similarities, but closely allied to *Cassinia* and *Haeckeria*. Distinctive features of *Odixia* include densely matted hairs and a yellow exudate on the lower surface of the leaves, homogamous capitula with 5–6 florets and disarticulating below the involucre to be shed as a unit, inner involucral bracts with narrow white tips, receptacular paleae similar to the involucral bracts or absent, and pappus absent but a small rim or ring of papillose hairs forming a pseudopappus at the top of the achene.

Copley (1982) revised *Ixodia* and described a second species. Distinctive features of *Ixodia* include inner involucral bracts with a white, papery, petaloid, radiating lamina, involucral bracts that more or less envelop the florets, and pappus absent but sometimes a shallow, shortly ciliate cup present on the achene.

In the course of revising *Ozothamnus*, Puttock came across a species of small shrub, *Helichrysum thomsonii* F. Muell., that differed considerably from all four genera, *Helichrysum*, *Lawrencella*, *Basedowia*, and *Ozothamnus*, with which it had been associated. To estimate its generic affinities he scored it for the 84 morphological and anatomical characters used by Anderberg (1991a), and added the data to Anderberg's matrices which he then reanalyzed. Results suggested that *Helichrysum thomsonii* was neither congeneric with nor closely related to any of the above genera and required a new genus, for which he proposed the name *Cremnothamnus*. Its affinities appear to be with *Argyroglottis* (Fig. 36.8D) and *Xerochrysum* (Fig. 36.5E) in Angianthinae (Puttock 1994b).

Orchard (2004a) commented that generic limits in *Haeckeria* and related taxa have been problematic for 150 years. In a reassessment of *Haeckeria*, he distinguished between *Apalochlamys*, biennial herbs with soft, stem-clasping leaves, with both pappus and receptacular paleae, and with 4–16 florets per capitulum; *Calomeria* (Fig. 36.8F), also biennial herbs with soft, stem-clasping leaves, but without pappus or receptacular paleae, and with only 2–4 florets per capitulum; *Haeckeria*, short-lived shrubs with fleshy, more or less terete to linear leaves which are not stem-clasping, are hemispheric, trigonous or cruciform in section and have dark-colored pit-glands embedded in all surfaces, without pappus or receptacular paleae; *Cassinia*, shrubs with relatively stiff, dorsiventral leaves not clasping the stem, with pappus and receptacular paleae, and with incurved tips on the inner involucral bracts; and *Ozothamnus*, again shrubs with relatively stiff, dorsiventral leaves not clasping the stem and with pappus, but without receptacular paleae and with inner involucral bracts either incurved or with a spreading lamina. *Haeckeria* was revised and restricted to two species. A useful nomenclatural summary of taxa presently and formerly referred to *Haeckeria*, *Humea* and *Calomeria* was provided. Detailed field study of the third, excluded species of *Haeckeria*, *H. ozothamnoides* F. Muell., revealed three more or less distinct geographic variants with receptacular paleae and with a facultative ability to develop a pappus. They were transferred to *Cassinia* as three species making up a distinctive *Cassinia ozothamnoides* (F. Muell.) Orchard group, which was accorded its own section, *Venustae*, in *Cassinia* subg. *Cassinia* (Orchard 2004b). In an ongoing series of papers (five to date) revising *Cassinia*, Orchard has discussed in detail the differentiation between *Cassinia* and *Ozothamnus* and provided an infrastructure for *Cassinia* of two subgenera, seven sections and five series. He estimates there will be over 40 species, of which 27, 16 of them new, have so far been recognized and described (Orchard 2004b–d, 2005a, 2006).

In the course of revising *Cassinia*, Orchard came across an unnamed species that caused him to revisit the *Ixodia* complex. The specimen had the terete-trigonous leaves with dark, sunken pit glands characteristic of *Haeckeria*, *Cassinia*-like capitula with white involucral bracts incurved at the tip, no pappus as in *Haeckeria*, *Ixodia* and *Odixia*, and the peculiar sheathing paleae characteristic of *Ixodia*. Since it did not fit well in any of the existing genera, Orchard described the species under a new, monotypic genus, *Paenula* (Orchard 2005b). It has not been rediscovered in the wild and Orchard suggested it may be short-lived and dependent on habitat disturbance for re-establishment.

Anderberg (1991a) found that most of the genera discussed above occurred together in one clade that he called the *Cassinia* group (*Apalochlamys*, *Haeckeria*, *Ixodia*, *Odixia*, *Ozothamnus*, and *Cassinia*). *Calomeria* (Fig. 36.8F), however, was far removed in Angianthinae.

Nablonium. — The monotypic genus *Nablonium*, which has a distinctive morphology and a limited distribution in Tasmania and the islands of Bass Strait, was reduced to synonymy under *Ammobium* (Fig. 36.8B) by Anderberg (1990). This was based on a cladistic analysis, using 10 morphological characters, which showed *Nablonium* as sister to one of the two species of *Ammobium*, thus rendering *Ammobium* paraphyletic if *Nablonium* was maintained. Orchard (1992) presented an alternative view, comparing the three species in detail, reinterpreting some of Anderberg's characters, demonstrating that the two species of *Ammobium* were far more similar to each other than either was to *Nablonium*, and maintaining that this is best reflected by keeping the two genera apart. Anderberg (1992) replied with a second cladistic analysis, utilizing Orchard's data to generate a cladogram in which *Nablonium* showed a large number of autapomorphies but was again sister to one of the species of *Ammobium*. In line with a general trend to avoid paraphyletic genera, *Nablonium* has become one of many distinct genera to lapse into synonymy.

Angianthinae. — The years from 1983 to 1990 saw the publication of a large body of work on Angianthinae, including six generic revisions from Short, the description of eleven new genera, and the start of the dismemberment of *Helipterum* by Wilson.

Angianthus (Fig. 36.8C) was revised by Short (1983a, b) who recognized fifteen species, four of which were new. Fourteen are annual herbs and one is a perennial shrub. All are homogamous, with compound capitula. A distinctive feature in 14 of the 15 species is the four involucral bracts, the outer two variably concave and surrounding the two flat inner ones. Short later described two more new species (Short 1990c).

Short reinstated eight genera that had been reduced to synonymy under *Angianthus* by Bentham (1867), and revised seven of them. All are annual herbs with homogamous, compound capitula. *Siloxerus* has three species with a general receptacle (for the aggregated capitula) covered with long silky hairs, rigid, opaque involucral bracts, florets each subtended by a single bract, a pappus of jagged scales joined to a greater or lesser extent in a ring and a small obovoid, pink or purple, non-myxogenic achene. Six species, three of them new, were recognized for *Chrysocoryne*, characterized by scale-like glandular hairs on the leaves, no conspicuous general involucre, and a small, obovoid, pink or purple, non-myxogenic achene. *Pogonolepis* was reinstated but not revised. The remaining five genera were all recognized as monotypic:

Cephalosorus with leaves uniquely opposite and petiolate at least in the lower half of the plant and an achene with a cellular, diaphanous pellicle; *Hyalochlamys* with scale-like glandular hairs on the leaves and an achene with a carpopodium appearing as a distinct white band; *Dithyrostegia* with a unique concave and stem-clasping leaf, two overlapping or connate leaf-like bracts subtending the compound capitulum, a general receptacle covered with long silky hairs and an achene clothed in long hairs; *Pleuropappus* with rigid, opaque involucral bracts, an oblique, scale-like pappus and an achene attached obliquely to the corolla tube; and *Epitriche*, known only from the type collection and with characters not well-known, but with a distinctive ring of hairs at the apex of the achene. Three species of uncertain affinity, *Angianthus axilliflorus* W. Fitzg. ex Ewart & Jean White, *A. burkittii* (Benth.) J.M. Black, and *A. connatus* W. Fitzg., were excluded from all the above genera, with *A. burkittii* returned for the time being to *Gnephosis* (Fig. 36.8H), where it had been placed by Bentham (1867).

Actinobole was revised by Short (1985) who recognized four species, two of them new and delimited mainly by anther length and pollen/ovule ratio. All are annual herbs, three endemic to Western Australia and one widespread through central and southern Australia. All have a distinctive pappus, with five bristles fused at the base, tapering towards the apex, plumose for most of their length and ending in a shortly stalked plumose tuft, about as long as the corolla tube and strongly reflexed when the fruits are shed, shooting them out of the capitulum.

Pogonolepis was revised by Short (1986) who recognized two species based on anther length and pollen/ovule ratio. They are annual herbs of Western and southern Australia, with the unique feature of papillose apices on the involucral bracts. Other cytotypes exist in the genus but have not been given specific status because they cannot be distinguished morphologically.

While working on *Gnephosis* (Fig. 36.8H), Short discovered that *Gnephosis tenuissima* Cass., the type species, is conspecific with *Chrysocoryne pusilla* (Benth.) Benth. *Gnephosis* has priority, so he transferred the other five species of *Chrysocoryne* to *Gnephosis* (Short 1987a). He remarked that it was likely that *Gnephosis* (Fig. 36.8H) when revised would include only these six species. However he later (1990c) broadened his concept of the genus to include two species referred to *Gnephosis* by Bentham (*G. brevifolia* (A. Gray) Benth. and *G. eriocephala* (A. Gray) Benth.) and two newly described (*G. setifera* P.S. Short and *G. cassiniana* P.S. Short). All species are united by achene and involucral bract characters. Achenes are small, pink or purple, glabrous or with scattered papillae, and with a pericarp that lacks sclerenchyma and has two vascular bundles. Involucral bracts are all essentially hyaline with ciliate or long-ciliate margins.

Anderberg (1991a), for the purposes of his analysis, listed the species excluded from Short's concept of *Gnephosis* under *Leptotriche*. He did not recombine them, as they were under review, and in fact recombined a species from *Calocephalus* as *G. angianthoides* (Steetz) Anderb. One of the species he listed, *G. skirrophora* Benth., is the type species of the reinstated genus *Trichanthodium* and another two, *G. baracchiana* Ewart & Jean White and *G. exilis* W. Fitzg., were transferred to that genus (Short 1990a). Another, *G. pygmaea* (A. Gray) Benth. (= *L. perpusilla* Turcz., the type species of *Leptotriche*) was transferred to *Myriocephalus* by Short (2000), thus placing the name *Leptotriche* in synonymy under *Myriocephalus*. Six have not been formally transferred out of *Gnephosis* (Fig. 36.8H) and are listed under that genus in FloraBase (Western Australian Herbarium 1998 onwards).

Blennospora was reduced to synonymy under *Calocephalus* by Bentham (1867) but is readily distinguished from *Calocephalus* s.str. (i.e., *C. citreus* Less. and *C. lacteus* Less.; Short 1987b) by its annual (vs. perennial) habit, involucral bract lamina that is not colored and opaque (vs. opaque white or yellow), and a suite of five achene characters (Short 1981, 1987b). Short (1987b) revised *Blennospora* in which he recognized two species.

The monotypic genus *Trichanthodium* was reduced to synonymy under *Gnephosis* (Fig. 36.8H) by Bentham (1867) but reinstated and revised by Short (1990a) who recombined two more species (see above) and described one as new. The genus is distinguished from *Gnephosis*, and all others, by the combination of its involucral bract morphology and absence of capitulum-subtending bracts. All four species form ectomycorrhizal associations (Warcup 1990).

Bentham (1867) recognized three species in *Chthonocephalus*, *C. pseudevax* Steetz, *C. pygmaeus* (A. Gray) Benth., and *C. tomentellus* (F. Muell.) Benth., and Willis (1952) described a fourth species *C. multiceps* J.H. Willis. Short (1983b) transferred *C. pygmaeus* to *Siloxerus*. He revised *Chthonocephalus* (Short 1990b), excluding *C. multiceps* with the comment that it is close to *Calocephalus aervoides* (F. Muell.) Benth., and both should probably be referred to a separate genus. They share the distinctive feature of paleae confined to the center of the receptacle and partly fused at the base. He added four new species of *Chthonocephalus* to the two that were retained. All six species are annual herbs, five endemic to Western Australia and one spread across southern Australia. They are distinguished from other compound-headed Australian Gnaphalieae by their brown ovoid achene with a thin pericarp and testa lacking a collenchyma or sclerenchyma layer and with two vascular bundles in the pericarp. The involucral bracts are in a single row and usually predominantly green and opaque.

Eleven new genera were proposed for Angianthinae sensu Anderberg (1991a) in the short period 1987–1990.

Wilson in 1987 described a Western Australian endemic species of annual herb with compound heads under the name *Quinqueremulus*. It has an extraordinary pappus of five scales alternating with the corolla lobes, small, erect, and fleshy at anthesis but becoming greatly enlarged, radiating, woody, and persistent in fruit. *Quinqueremulus* has much in common with a group of species in *Myriocephalus*, *M. stuartii* (F. Muell. & Sond.) Benth., *M. morrisonianus* Diels and *M. guerinae* F. Muell., which Wilson noted should probably be segregated under the reinstated name *Polycalymma*. *Polycalymma* was recognized by Cooke (1986) and Anderberg (1991a) but with only the type species *P. stuartii* F. Muell. & Sond. Inclusion of the other two species is not supported by fruit anatomy (Short et al. 1989; Short 2000) and the recombinations have not been made.

Taplinia was proposed by Lander (1989) for a Western Australian endemic species of perennial herb with discoid capitula arranged in terminal corymbs, multiseriate, papery involucral bracts with broad translucent margins, ecaudate anthers, and style arms with a terminal tuft of collecting hairs from which projects a shaft of fused epidermal cells. Anderberg (1991a) commented that it seemed to be related to *Lawrencella*. *Dielitzia*, *Feldstonia*, *Fitzwillia*, *Lemooria*, and *Sondottia* were described by Short (1989b). All except *Sondottia* are monotypic, all except *Lemooria* are Western Australian endemics, and all are annual herbs with compound capitula and only one or two florets per capitulum. *Dielitzia* has three unique features: a general involucre of cartilaginous bracts, a cup-like general receptacle, and involucral bracts in two rows, the outer bristle-like and the inner marbled. Its tufted habit with a cluster of compound heads surrounded by linear leaves is otherwise seen only in *Isoetopsis*. The single species was newly described. *Feldstonia* was also erected for a newly described species, differing in its semicartilaginous bracts of the general involucre and its combined fruit, pappus and involucral bract features from other genera of Gnaphalieae. *Fitzwillia* was erected to accommodate a species earlier excluded from *Angianthus* s.l., *A. axilliflorus* (Short 1983a). The fruits have a distinctive sclerified apical cap (also found in *Epitriche*) and the leaf-like bracts subtending the capitulum, the conduplicate involucral bracts, and probably the translucent white florets are unique to the genus. *Lemooria* was proposed to accommodate another species excluded from *Angianthus* s.l. and temporarily returned to *Gnephosis* (Fig. 36.8H) as *G. burkittii* Benth. (Short 1983a), but possessing a unique combination of bract and fruit characters. *Sondottia* contains the third species excluded from *Angianthus* s.l. (Short 1983a), *A. connatus*, as well as one newly described species. The cartilaginous capitulum-subtending bracts are apparently unique to the genus. Other distinctive features are opposite, connate leaves and intertwined long hairs at the apex of the achene.

Tietkensia was described by Short (1990c) for a single species similar to *Chthonocephalus* but differing in having female florets, receptacular paleae similar to the involucral bracts, a much-branched general receptacle, and in fruit morphology.

Haegiela was erected by Short and Wilson (1990) to accommodate a single species formerly in *Epaltes* Cass. (Inuleae). Its affinities lie with *Triptilodiscus* from which it differs in having an achene with crystals in the testa and in lacking a pappus.

Bracteantha (Fig. 36.5E) was proposed by Anderberg and Haegi (in Anderberg 1991a) for a distinctive group of species in *Helichrysum*, including *H. bracteatum*. They were unaware that Tzvelev had already proposed a monotypic genus, *Xerochrysum*, for *H. bracteatum* (Tzvelev 1990). Bayer (2001) made the required recombinations in *Xerochrysum* (Fig. 36.5E) for the five remaining species in *Bracteantha* and this name lapsed into synonymy. Distinctive features of the genus are the presence of ectomycorrhiza and the large, glabrous, smooth achenes.

In 1989 Wilson published the first two of a series of papers revising the species of *Helipterum* and the part of *Helichrysum* in Anderberg's (1991a) Angianthinae and assigning them to different genera, in conjunction with revisions of related taxa. The genus *Hyalosperma* was described by Steetz in 1845 but was used for less than a decade, after which any species now referred to *Hyalosperma* (Wilson 1989a) were placed in *Helipterum*. Wilson (1989a) reinstated and revised *Hyalosperma* to contain nine species from *Helipterum* (*H. zacchaeus* S. Moore, *H. demissum* (A. Gray) Druce, *H. stoveae* D.A. Cooke, *H. glutinosum* Hook., *H. semisterile* F. Muell., *H. cotula* (Benth.) DC., *H. simplex* Steetz, *H. praecox* F. Muell., and *H. pusillum* Turcz.). Closest affinities are with the members of the "Achyroclinoides" alliance in *Helipterum* (*H. laeve* (A. Gray) Benth., *H. corymbosum* (A. Gray) Benth., *H. polycephalum* (A. Gray) Benth., and *H. forrestii* F. Muell.). *Hyalosperma* differs in its terete (vs. flat) leaves, glabrous achenes, uniseriate (vs. biseriate) corolla hairs and smooth, straight (vs. papillose and undulate) walls of the epidermal cells on the inside of the corolla. *Hyalosperma* may also be allied to *Blennospora*.

Erymophyllum was erected by Wilson (1989b) for two species from *Helipterum* sect. *Pteropogon* (DC.) Benth., *H. tenellum* Turcz., and *H. involucratum* (F. Muell.) Benth. (as *E. ramosum* (A. Gray) Paul G. Wilson), and three newly described species. Four of the five species are endemic to Western Australia and the other just reaches into southwestern South Australia. *Erymophyllum* is closest to the *Pteropogon* complex in *Helipterum*, from which it differs in its glandular-pubescent (vs. woolly) indumentum, terete (vs. flat) leaves, and in two features which may be unique in the tribe. The outer involucral bracts have a short, scarious base and a terete, leaf-like apex. There is a transition to entirely scarious inner bracts, in which the scarious base increases and the leaf-like apex decreases. The epidermal cells on the insides of the corolla lobes are narrow-oblong to linear and grouped in transverse rows (like the cells of storied wood).

Wilson (1992a–c) published three more papers revising the species in *Helipterum* and related genera, attempting to associate closely related species and to segregate as distinct genera those species or groups of species that show marked morphological discontinuity. He adopted a conservative approach in *Rhodanthe*, using sections for taxa that might later be shown to merit generic rank. The first of these three papers (Wilson 1992a) is concerned with the *Rhodanthe*, *Hyalosperma* and *Triptilodiscus* groups of species.

The *Rhodanthe* group are all annuals or short-lived perennials, characterized by inner involucral bracts with broad flat claws, anthers with fine filamentous tails and achenes with normal (mostly not thickened) twin hairs. They are not known to form ectomycorrhizal associations, except for *Rhodanthe citrina* (Benth.) Paul G. Wilson.

The genus *Rhodanthe* is circumscribed to contain the majority of the Australian species previously included in *Helipterum*. The 45 species are grouped into eleven sections: *Rhodanthe*, monotypic (*R. manglesii* Lindl.); *Monencyanthes* (A. Gray) Paul G. Wilson (probably polyphyletic), with three species; *Leiochrysum* (DC.) Paul G. Wilson, with seventeen species; *Achyroclinoides* (A. Gray) Paul G. Wilson, with nine species; *Citrinae* Paul G. Wilson, monotypic (*R. citrina*); *Synachryum* (A. Gray) Paul G. Wilson, with five species; *Helipteridium* (A. Gray) Paul G. Wilson, monotypic (*R. heterantha* (Turcz.) Paul G. Wilson); *Helichrysoides* (A. Gray) Paul G. Wilson, with four species; *Actinaria* Paul G. Wilson, with two species; *Anisolepis* (Steetz) Paul G. Wilson, monotypic (*R. pyrethrum* (Steetz) Paul G. Wilson); and *Polyphyllum* Paul G. Wilson, monotypic (*R. polyphylla* (F. Muell.) Paul G. Wilson).

Two other genera are included in the *Rhodanthe* group: *Erymophyllum*, reviewed above, and *Cephalipterum*, monotypic and similar to *Rhodanthe* sect. *Synachryum*, especially in the dense, imbricate, crystalline cover to the seed. In *Cephalipterum* only one or two seeds in a capitulum develop, but all the achenes coalesce by their barbed hairs and the entire cluster is dispersed as a unit. The developed achenes have a raised rim at the tip on the abaxial margin, a character unique in the *Rhodanthe* group.

The *Hyalosperma* group is characterized by inner involucral bracts with broad, flat claws, anthers with fine filamentous tails and achenes without normal twin hairs but with 2-celled bulbous papillae that are frequently myxogenic, and deciduous pappus that is shed entire. Species that have been examined form ectomycorrhizae (Warcup 1990). The group has two genera, *Hyalosperma*, reviewed above, and *Gilberta*, monotypic and differing from *Hyalosperma* in the arrangement of the capitula, terminal on short lateral branches, and in having five receptacular paleae around each floret.

The *Triptilodiscus* group is characterized by achenes with 2-celled, tooth-like trichomes and oblong or boat-shaped claws to the involucral bracts. *Triptilodiscus* forms ectomycorrhizal associations but the other genera have not been investigated. The group may be polyphyletic. It comprises four genera: *Triptilodiscus*, monotypic and closely related to *Haegiela*, also monotypic and differing from *Triptilodiscus* in lacking a pappus and having crystals in the testa; *Pterochaeta*, again monotypic, a southern Western Australian endemic; and *Haptotrichion*, a new genus of two Western Australian endemic species, one newly described and one, *H. conicum* (B.L. Turner) Paul G. Wilson, transferred from *Waitzia* (Fig. 36.8E). *Pterochaeta*, *Haptotrichion* and *Waitzia* all have beaked achenes with tooth-like 2-celled trichomes, but are dissimilar in other characters.

In the second paper of the 1992 series Wilson (1992b) described a new genus *Leucochrysum* (Fig. 36.5F) to accommodate *Helipterum stipitatum* (F. Muell.) F. Muell. ex Benth., *H. fitzgibbonii* F. Muell., and most of the taxa previously referred to the *H. albicans* DC. group (*H. albicans* and *H. molle* (DC.) Paul G. Wilson but not *H. saxatile* Paul G. Wilson; *H. albicans* var. *graminifolium* Paul G. Wilson was raised to species). *Leucochrysum* differs from other species from *Helipterum* in having stipe-like claws to the involucral bracts, a glabrous, translucent, two-layered pericarp, a firm testa that is distinct from the pericarp, straight, firm anther tails, and a broad-deltoid or broad-ovoid style arm apex with a thick vascular strand that forms a club-shaped mass in the tip. *Leucochrysum* is most closely related to *Waitzia* (Fig. 36.8E), as also noted by Anderberg (1991a). *Waitzia* s.str. (Wilson 1992d) differs in having an elongated neck to the achene, 2-celled, tooth-like achene trichomes in which the lower cell overtops the upper, and barbellate pappus bristles shed as a unit. *Helipterum saxatile* was excluded from the *Helipterum albicans* group on the basis of numerous character differences, and said to be apparently related to *Chrysocephalum podolepidium* (F. Muell.) Anderb.

The third paper of the series (Wilson 1992c) relates to species that were currently in both *Helipterum* and *Helichrysum*. Two new genera were described, *Anemocarpa* and *Argentipallium*. *Anemocarpa* has three species: *A. podolepidium* (F. Muell.) Paul G. Wilson from *Helichrysum*, *A. saxatilis* (Paul G. Wilson) Paul G. Wilson from *Helipterum*, and a newly described species, *A. calcicola* Paul G. Wilson. The genus is closest to *Leucochrysum* (Fig. 36.5F). It may in future be expanded to include the *Helichrysum elatum* DC. group (e.g., *H. elatum*, *H. boormanii* Maiden & Betche, *H. adenophorum* F. Muell.), which differs in having a brittle (vs. papery) pericarp, a minute (vs. prominent) carpopodium, and an ovate to acuminate (vs. round) style arm apex. Species of *Anemocarpa* and the *H. elatum* group are all perennial herbs with achenes with a papery or brittle endocarp and with lateral vascular bundles. Those investigated lack ectomycorrhizal associations, which are however found in *Chrysocephalum*, *Leucochrysum*, and *Waitzia*.

Argentipallium was described to accommodate the "*Helichrysum dealbatum*" group (*H. dealbatum* Labill., *H. spiceri* F. Muell., *H. obtusifolium* Sond., *Ozothamnus tephrodes* Turcz., and *Helipterum niveum* Steetz) as well as the rather different species *Helichrysum blandowskianum* Sond. Species of *Argentipallium* are perennial herbs that form ectomycorrhizal associations. They have involucral bracts with divided stereomes and achenes with lateral vascular bundles. *Argentipallium* is similar in floral characters to *Ozothamnus*, which differs mainly in habit (shrubs or subshrubs), size and arrangement of the capitula, and in not being ectomycorrhizal.

Wilson (1992d) revised the circumscription and content of *Waitzia* (Fig. 36.8E), including a key and full synonymy, but not species descriptions. The genus had been found to be polyphyletic by both Anderberg (1991a) and Wilson, a condition that was rectified by excluding three species, *Waitzia citrina* (Benth.) Steetz, *W. paniculata* (Steetz) Benth., and *W. conica* B.L. Turner, leaving the five closely related species *W. corymbosa* J.C. Wendl, *W. nitida* (Lindl.) Paul G. Wilson, *W. acuminata* Steetz, *W. suaveolens* (Benth.) Druce, and *W. podolepis* (Gaudich.) Benth. Distinctive characters of *Waitzia* s.str. include scarious involucral bracts, the outer with terete, glandular, stipe-like claws, the inner linear and divided, with a small lamina, achenes with a slender neck, 2-celled, tooth-like trichomes in which the lower cell overtops the upper, a thin, transparent pericarp, a thick, ruminate testa with oblong crystals, and with corrugate margins to the epidermal cells, and a pappus of barbellate bristles shed as a whole from the achene neck. The vascular bundles of the achene are lateral, and ectomycorrhizal associations are formed. Of the three excluded species, *W. citrina* was transferred to *Rhodanthe*, the monotypic genus *Pterochaeta* was reinstated for *W. paniculata*, and *W. conica* was accommodated in the newly described, ditypic genus *Haptotrichion*.

Waitzia (Fig. 36.8E) is clearly allied to *Leucochrysum* (Fig. 36.5F) and Anderberg (1991a) and Wilson (1992d) agree in associating it also with *Gratwickia*, *Chrysocephalum*, *Leptorhynchos*, *Asteridea*, *Podolepis*, and *Triptilodiscus* in a "*Waitzia* group" within subtribe Angianthinae.

As part of the reorganisation of Australian species excluded from *Helichrysum*, Wilson (1992e) reclassified the *Lawrencella* complex, including the monotypic genera *Bellida* and *Schoenia*, five species (*H. davenportii* F. Muell., *H. lindleyi* H. Eichler [=*Lawrencella rosea* Lindl.], and the *Xanthochrysum* group comprising *H. filifolium* (Turcz.). F. Muell., *H. ramosissimum* (F. Muell.) Druce, and *H. macivorii* F. Muell.) included by Bentham (1867) in *Helichrysum* sect. *Lawrencella* (Lindl.) Benth., and one species (*H. ayersii* F. Muell.) formerly placed in both *Helichrysum* and *Podolepis*. This assemblage is recognized by Wilson (1992e) as constituting a natural group clearly distinct from other Angianthinae, and with three subgroups recognized at generic rank. The first subgroup is the monotypic genus *Bellida*. The second subgroup is an expanded *Schoenia* encompassing *Helichrysum ayersii*, *H. cassinianum* Gaudich. (as *S. oppositifolia* Steetz), and the *Xanthochrysum* group of *H. filifolium*, *H. ramosissimum*, and *H. macivorii*. The third subgroup is *Lawrencella* with two species, *H. lindleyi* (as *L. rosea*) and *H. davenportii*.

Achene and pappus characters show a close relationship between *H. ayersii* and *H. cassinianum*, between these two species and the three in the *Xanthochrysum* group, and between *Bellida* and the two species here placed in *Lawrencella*. No ectomycorrhizal associations have been found in the *Lawrencella* complex.

Anderberg included *Helichrysum spiceri* and *H. obtusifolium* in the *Lawrencella* complex but Wilson considers them generically distinct (Wilson 1992e) and has included them, together with another four species, in the new genus *Argentipallium* (Wilson 1992c).

Pithocarpa was revised by Lepschi (1999) who recognized two species. They are perennial herbs or subshrubs endemic to the southwest of Western Australia. Their generic relationships are obscure: an analysis by Lepschi placed them next to *Argentipallium* and Anderberg (1991a) suggested they might be closest to *Lawrencella* s.l.

Short (2000) surveyed recent changes in *Myriocephalus* taxonomy, added two new species, and discussed the circumscription of the genus. Short (1983a) and Wilson (1987) had already noted that *Myriocephalus* as circumscribed by Bentham (1867) is an unnatural group. Short et al. (1989), in a study of fruit anatomy of Australian Gnaphalieae, suggested that *Myriocephalus* s.str. probably consists of seven species: *M. appendiculatus* Benth., *M. helichrysoides* A. Gray, *M. nudus* A. Gray, *M. pluriflorus* (J.M. Black) D.A. Cooke, *M. rhizocephalus* (DC.) Benth., *M. rudallii* (F. Muell.) Benth., and *Gnephosis pygmaea*. This last was recombined and *M. isoetes* Diels was recognized (under its correct name *M. occidentalis* (F. Muell.) P.S. Short) as a species separate from *M. rhizocephalus* (Short in Elliot and Jones 1993). Short (2000) described two new species, bringing the number of species he recognized to ten. Features that distinguish *Myriocephalus* s.str. from other compound-headed species of Gnaphalieae are narrowly ellipsoid achenes with non-myxogenic, straight twin hairs and an annular carpopodium, and a pappus of up to four bristles or bristle-like scales or absent. The genus is variable in many other features. Two species excluded from Short's concept of *Myriocephalus*, *M. guerinae* and *M. morrisonianus*, were not transferred to *Polycalymma* and remain for the time being in *Myriocephalus*.

Short et al. (1989), Anderberg (1991a) and Wilson (2001) noted that the type species of *Ixiolaena*, *I. viscosa* Benth., differed radically from the other seven species in the genus. All species except the type needed to be reassigned. Wilson (2001) investigated other genera for correct placement, in particular the features of the achene, and concluded that combined evidence from chromosome numbers, ectomycorrhizal associations and morphology showed that they belong in a new genus, *Leiocarpa*. Two species from *Chrysocephalum*, *C. semicalvum* (F. Muell.) Paul. G. Wilson and *C. serpens* J. Everett, and two from *Leptorhynchos*, *L. gatesii* (H.B. Will.) J.H. Willis and *L. panaetioides* (DC.) Benth., were shown also to belong to the new genus. One species of *Ixiolaena* s.l., *I. chloroleuca* Haegi, was reduced to synonymy under *I. leptolepis* (CD.) Benth., leaving *Leiocarpa* with ten species. *Leiocarpa*, *Ixiolaena* s.str., *Chrysocephalum* and *Leptorhynchos* differ in chromosome number, mycorrhizal association and bract, achene and pappus characters. Chromosome numbers in *Leiocarpa* appear to be based on $x = 10$, and in *Chrysocephalum* and *Leptorhynchos* on $x = 12$ (the number in *Ixiolaena* s.str. is not known). *Chrysocephalum* and *Leptorhynchos* both form ectomycorrhizal associations, *Leiocarpa* does not, and *Ixiolaena* s.str. has not been investigated. The stereome of the involucral bracts is not divided in *Ixiolaena* s.str. but is divided in the other three genera. The pappus is persistent in *Leiocarpa* and *Leptorhynchos*, shed as a whole in *Ixiolaena* s.str., and shed as individual bristles in *Chrysocephalum.* The achene surface is hispid in *Ixiolaena* s.str., has 2-celled papillae in which the lower cell overtops the upper in *Chrysocephalum* and *Leptorhynchos* and is smooth and glabrous or almost so in *Leiocarpa*, and cartilaginous with the appearance of many linear, clear windows set into the translucent wall, which probably correspond to paired myxogenic cells reported by Short et al. (1989) from transverse sections of achenes of *Leiocarpa*.

A comprehensive revision of *Craspedia* in Australia has not yet been published, but the status of *Pycnosorus* as a separate genus is widely recognized following demonstrated differences in morphology (Short et al. 1989; Everett and Doust 1992), cytology (Watanabe et al. 1999), and DNA sequences (Breitwieser et al. 1999; Bayer et al. 2002; Ford et al. 2007).

***Chondropyxis* and *Isoetopsis.* —** *Chondropyxis* was described by Cooke (1986) for a species of annual herb with disciform capitula, scarious involucral bracts in about one row, papery receptacular paleae, outer filiform florets with villose achenes and a pappus of minute bristles, and central florets functionally male with a pappus of unequal, plumose, basally connate bristles. The fruiting capitulum is woody, with persistent scales enclosing the achenes. The tribal position of *Chondropyxis* is uncertain. Cooke placed it in Anthemideae but commented it might have closer affinities with Astereae. Anderberg (1989, 1991a) suggested that *Isoetopsis*, also of uncertain tribal position and previously in Anthemideae, resembles Gnaphalieae in its divided stereome and narrow anther appendages. He placed it in his *Waitzia* group, close to *Rutidosis* which has a similar pappus. *Chondropyxis* and *Isoetopsis* both form ectomycorrhizal associations, which are almost unknown in Compositae outside the tribe Gnaphalieae. Both genera have been placed in this tribe (e.g., Anderberg 1994), but *Isoetopsis* has since been excluded (Bayer and Cross 2002).

New Zealand

Most of the 70 to 80 species of Gnaphalieae in New Zealand are endemic. Generic limits are not clearly defined (Ward and Breitwieser 1998) and *Craspedia*, *Ozothamnus*, *Raoulia* (Fig. 36.5A, B) and the species formerly in *Ewartia* and *Helichrysum* are all under review.

Merxmüller et al. (1977) recognized ten genera of Gnaphalieae in New Zealand. All but one of these (*Leucogenes*) has undergone some form of revision and two new genera have been proposed. *Gnaphalium luteoalbum* is discussed elsewhere under *Pseudognaphalium. Craspedia* is an outlier of a predominantly Australian genus, and has undergone extensive diversification in New Zealand, most of it undescribed. The New Zealand species are under revision by I. Breitwieser.

Haastia (the type species only) was accepted in the Gnaphalieae by Merxmüller et al. (1977) but not by Anderberg (1991a), who did not mention this genus, nor by Bremer (1994) who included it in the genera unplaced as to tribe. It has since been definitely placed in Senecioneae (Wagstaff and Breitwieser 2002; Breitwieser and Ward 2005; Nordenstam 2007).

The five species of *Cassinia* formerly recognized in New Zealand (Allan 1961; Anderberg 1991a) were combined by Webb (1988) into a single polymorphic species, *C. leptophylla* (G. Forst.) R. Br., which was transferred to the predominantly Australian genus *Ozothamnus* by Breitwieser and Ward (1997), thereby leaving *Cassinia* endemic to Australia.

Euchiton has a western Pacific distribution with its greatest diversity in New Zealand. Its status has been uncertain; Drury (1970, 1972) treated it as a section of *Gnaphalium*, Merxmüller et al. (1977) gave it "semi-accepted" generic status and Anderberg (1991a) and Bayer et al. (2007) recognized it as a genus. Holub (1974) had recombined the New Zealand species in *Euchiton* except for the two chamaephytic species which were recombined by Anderberg (1991a). These two species and another two from Australia differ substantially from the rest of *Euchiton* and lack its two definitive features, stoloniferous habit and achenes with paired papillae on the epidermal cells, the latter unique in the tribe. They were transferred to a new genus *Argyrotegium* by Ward et al. (2003), leaving *Euchiton* with 21 species.

Anaphalioides was "semi-accepted" as a genus by Merxmüller et al. (1977) and tentatively accepted by Anderberg (1991a) but not by Webb (1988) who felt that such a step would be premature and placed the New Zealand species of Drury's (1970) "anaphalioid cudweeds" in *Anaphalis*. *Anaphalioides* was revised by Glenny (1997) who recognized seven species, five in New Zealand and two in New Guinea, five from *Anaphalis* and two (*H. bellidioides* (G. Forst.) Willd. and *H. alpinum* Cockayne), formerly in *Helichrysum*.

The single New Zealand species of *Ewartia* was segregated from the other four species (all Australian) as the new monotypic genus *Ewartiothamnus* by Anderberg (1991a). It has been demonstrated to form fertile wild hybrids with *Anaphalioides bellidioides* (G. Forst.) D. Glenny (McKenzie et al. 2008).

New Zealand has ten species formerly in *Helichrysum*, seven from the woody section *Ozothamnus* and three from the herbaceous section *Xerochlaena* Benth. (Allan 1961; Ward et al. 1997b). The redefinition of *Helichrysum* by Hilliard and Burtt (1981) effectively excluded all New Zealand species from that genus. Anderberg reinstated the genus *Ozothamnus* and included the seven woody New Zealand species, making the necessary recombinations. These New Zealand species are, however, distinct from all other species in this predominantly Australian genus (Ward and Breitwieser 1998). They are under revision by J.M. Ward. The herbaceous New Zealand species of *Helichrysum* were informally referred by Anderberg (1991a) to the "Scorpioides" complex of *Lawrencella* in subtribe Angianthinae. Two, *H. bellidioides* and *H. alpinum*, have since been transferred to *Anaphalioides* (Glenny 1997) and the other, *H. filicaule* Hook. f., is as yet unplaced.

Raoulia, with 23 published species and several as yet undescribed (Ward 1998), is by far New Zealand's largest endemic genus, and one of its most taxonomically recalcitrant. It contains two distinct species groups, one of herbaceous mat-formers with numerous fine pappus bristles in several series and with small globose achene hairs, and the other of woody cushion-formers (Fig. 36.5A, B) with a single series of coarse pappus bristles and with elongated achene hairs. In addition there are seven species that match neither group, do not form groups themselves, and match no other genera. Merxmüller et al. (1977) placed *Raoulia* with most other New Zealand genera in the "*Gnaphalium* group". Anderberg (1991a) reinstated subgenus *Psychrophyton* as a genus and placed it in the new alpine cushion plant subtribe Loricariinae, leaving the rest of *Raoulia* in subtribe Gnaphaliinae. The division of *Raoulia* s.l. into two genera was not accepted by Ward and Breitwieser (1998) as it does not resolve the taxonomic problems in the genus.

The monotypic genus *Rachelia* was proposed by Ward et al. (1997a) for a rare, previously undescribed alpine species confined to argillite scree in a small area of the north-eastern South Island. It does not fit into any other genus, although there are similarities to *Leucogenes* (Fig. 36.5C). Unique features include the arrangement of the capitula, sessile in the axils of the uppermost, crowded leaves, and the extension of the entire outer walls of achene epidermal cells into projecting papillae.

Raoulia, *Leucogenes*, *Ewartiothamnus*, *Anaphalioides*, and the species formerly in *Helichrysum* are distributed through four of the five subtribes of Anderberg (1991a). However they are all interconnected by natural hybrids (Ward 1997; McKenzie et al. 2004, 2008). Together with *Rachelia*, which is geographically and ecologically isolated and not known to form hybrids, they constitute the "*Raoulia* alliance", which is restricted to New Zealand except for two species of *Anaphalioides* in New Guinea (Ward and Breitwieser 1998; Breitwieser et al. 1999; McKenzie et al. 2008).

South and Central America and Mexico

Seventeen genera of Gnaphalieae in South America have undergone changes in status or circumscription since 1977, including 14 of the 24 listed for South America by Dillon and Sagástegui (1991).

Luciliopsis was described by Weddell (1856a) for *L. perpusilla* Wedd., a minute Bolivian plant known only from the type, in which most of the florets are missing (Anderberg and Freire 1990b). Robinson (1985) thought it was conspecific with *Facelis plumosa* Sch.Bip. The other two species in *Luciliopsis* are quite distinct from the type and Robinson proposed for them the name *Cuatrecasasiella*. Anderberg and Freire (1990b) re-examined the type of *Luciliopsis* and transferred it to *Chaetanthera* Ruiz & Pav. (Mutisieae) as *C. perpusilla* (Wedd.) Anderb. & S.E. Freire, thus excluding it from the tribe.

Jalcophila was proposed by Dillon and Sagástegui (1986) for two new alpine species, from Peru and Ecuador, which show a general similarity to the *Lucilia* group of Merxmüller et al. (1977) but are not close to any existing genus. They are minute caespitose herbs with densely crowded leaves and sessile heterogamous capitula becoming pedunculate in fruit. Two further species have been described, one of which, *J. boliviensis* Anderb. & S.E. Freire (Anderberg and Freire 1990a), has been excluded from *Jalcophila* (Dillon and Sagástegui 1991) and transferred to *Gamochaeta* (Dillon 2003).

Lucilia (Fig. 36.6B) was revised by Freire (1986a) who recognized 22 species, reducing *Belloa* to synonymy on the grounds that it was insufficiently distinct, but recognizing *Oligandra* as a separate genus because of its heterogamous capitula with female florets outnumbering the few hermaphrodite, female-sterile florets. Later Freire (1989), finding that the female florets could be fewer or even absent and that the hermaphrodite florets could be female-sterile or fully fertile in the type species of *Oligandra*, *O. lycopodioides* Less., transferred it to *Lucilia*. Freire stated that *Oligandra* was monotypic but Dillon and Sagástegui (1990) pointed out that two other species had been described by Weddell (1856b). One of these, *O. pachymorpha* Wedd., had been transferred to *Raouliopsis* by Blake (1938) but the other, *O. chrysocoma* Wedd., was unlike the type species (now in *Lucilia*) and could not be placed in any existing genus. They placed it in a new monotypic genus, *Pseudoligandra*. It is distinguished from *Lucilia* (Fig. 36.6B) by its heterogamous capitula with female-sterile hermaphrodite florets and its glabrous achenes (Dillon and Sagástegui 1990). Anderberg (1991a) did not recognize *Pseudoligandra* because it rendered *Chionolaena* paraphyletic in the results of a cladistic analysis of morphological data carried out by Freire and published soon after (Freire 1993). Freire recombined it as *Chionolaena chrysocoma* (Wedd.) S.E. Freire.

Belloa, reduced to synonymy by Freire (1986a), was reinstated by Anderberg (1991a). Differences between results of cladistic analyses (Freire 1987; Anderberg 1991a) led to a cladistic analysis by Anderberg and Freire (1991) of the entire *Lucilia* group sensu Anderberg: *Belloa*, *Berroa*, *Chevreulia*, *Cuatrecasasiella*, *Facelis*, *Jalcophila*, and *Lucilia*. In order to achieve monophyletic genera according to the results of this analysis, it was necessary either to combine *Belloa*, *Berroa*, *Facelis*, and *Lucilia* into one large, heterogeneous, poorly defined genus or to split *Belloa* into two genera and raise *Lucilia alpina* (Poepp. & Endl.) Cabrera, which was isolated from the rest of *Lucilia*, to generic rank. Accordingly two new genera were proposed, *Luciliocline*, with five species, for *Belloa* pro parte and *Gamochaetopsis* for *Lucilia alpina* (Anderberg and Freire 1991), leaving nine species in *Belloa* and eight species in *Lucilia*. Three species of *Belloa* described by Sagástegui and Dillon (1985), *B. plicatifolia* Sagást. & M.O. Dillon, *B. turneri* Sagást. & M.O. Dillon, and *B. spathulifolia* Sagást. & M.O. Dillon, were not included in Freire (1986). Only *B. plicatifolia* was recognized by Anderberg (1991a) and included in Anderberg and Freire (1991) where it was maintained in *Belloa*. All three species were recognized in *Belloa* by Dillon and Sagástegui (1981) and subsequently transferred to *Luciliocline* by Dillon (2003). A ninth species of *Lucilia*, *L. saxatilis* V.M. Badillo, was described in 1988. Dillon (2003) lists a further three species (*L. conoidea* Wedd., *L. araucana* Phil., and *L. nivea* (Phil.) Cabrera).

Dillon (2003) expanded *Luciliocline* from five to thirteen species, transferring to it all examined species of *Belloa* except the type, *B. chilensis* Hook. & Arn., one species (*B. kunthiana* (DC.) Zardini) already transferred to *Lucilia* (Dillon and Sagástegui 1991), and another three species (*B. argentea* (Wedd.) Cabrera, *B. caespititia* (Wedd.) Cabrera, and *B. virescens* (Wedd.) Cabrera) that probably belong in *Luciliocline* but require further investigation. Dillon (2003) pointed out that the identity of *Gamochaetopsis* is problematic because it is defined by Anderberg and Freire (1991) by its achenes with short, clavate twin hairs, whereas Cabrera (1961) had described it as possessing sericeo-pubescent achenes (i.e., with elongated twin hairs). Examination of probable type material showed achenes with elongated twin hairs. Since short, clavate twin hairs are known in the *Lucilia* group only from *Belloa chilensis* J. Rémy, it is possible that Anderberg and Freire mistook this species for *Lucilia alpina* (Dillon 2003).

Chionolaena was tentatively associated with the *Lucilia* group, or perhaps the *Anaphalis* group, by Merxmüller et al. (1977). Anderberg (1991a) placed it firmly in the *Anaphalis* group, in his subtribe Cassiniinae. Dillon (2003) suggested it may be close to the *Lucilia* group; *Chionolaena* and *Lucilia* (Fig. 36.6B) both have achenes with elongated twin hairs with terminal cells that are thick-walled, acute, and never myxogenic.

Chionolaena species are small alpine shrubs or subshrubs of Central and South America, characterized by sympodial growth, reflexed leaves with revolute margins, central florets that are usually functionally male, and clavate pappus tips (Freire 1993). Merxmüller et al. (1977) give ca. eight species, Dillon and Sagástegui (1991) eight and Freire (1993), who revised the genus, seventeen including two transferred from *Anaphalis* (Anderberg and Freire 1989) and one from *Gnaphalium*, one newly described, and the inclusion of *Leucopholis*, *Pseudoligandra* and (although the genus was not included as such in the study) *Parachionolaena*. Freire reorganized the genera according to the results of a cladistic analysis based on morphological data, which showed *Leucopholis*, *Pseudoligandra*, and *Parachionolaena* (as *C. columbiana* S.F. Blake) embedded in *Chionolaena*. Freire (1993) remarked that *Chionolaena* is closely related to the Mexican genus *Gnaphaliothamnus*. This genus has had a chequered history since its proposal by Kirpichnikov (in Kirpichnikov and Kuprijanova 1950) based on *Gnaphalium rhodanthum* Sch.Bip. in Seem. It was reduced to synonymy under *Gnaphalium* by McVaugh (1984), "semi-accepted" by Merxmüller et al. (1977) and recognized as a monotypic genus by Anderberg and Freire (Anderberg and Freire 1989; Anderberg 1991a; Freire 1993). Nesom (1990a), investigating *Gnaphalium* in Mexico, identified a distinct group characterized by strongly woody habit, revolute leaves, involucral bracts with white, opaque, spreading tips, mostly heterogamous capitula, reddish corollas, achenes with minute, slightly elongated twin hairs, functionally male hermaphrodite florets and apically swollen pappus bristles. This group is confined primarily to the peaks of the highest mountains from south-central Mexico to Costa Rica and was named

Gnaphalium sect. *Rhodognaphalium* Sch.Bip. in 1856, typified by *G. rhodanthum*. As well as the type of *Gnaphaliothamnus*, it includes two species transferred from *Anaphalis* to *Chionolaena* (*C. aecidiocephala* (Grierson) Anderb. & S.E. Freire and *C. concinna* (A. Gray) Anderb. & S.E. Freire) by Anderberg and Freire (1989), three more species of *Chionolaena* (*C. eleagnoides* Klatt, *C. lavandulifolium* (Kunth ex B.D. Jacks. & Hook. f.) Benth. & Hook. f. ex B.D. Jacks., and *C. sartorii* Klatt) and four undescribed species. Nesom (1990a) compared this group with *Gnaphalium*, *Anaphalis*, *Leucopholis* and *Chionolaena* and concluded that it represents a monophyletic Mexican-Central American lineage closest to *Chionolaena* s.str. but separated by its polycephalous stems, apically mucronate leaves and sparsely, minutely pubescent achenes. He recombined the above five species of *Chionolaena* in *Gnaphaliothamnus*, described three new species and another soon after (Nesom 1990b), and recombined *Gnaphalium salicifolium* Sch.Bip., an earlier available name for *G. rhodanthum*. (This predates the same recombination made by Anderberg 1991a.) This brought the number of species in *Gnaphaliothamnus* to ten. *Chionolaena mexicana* S.E. Freire and *C. seemanii* (Sch.Bip.) S.E. Freire were reduced to synonymy under *Gnaphaliothamnus* when they were found to be conspecific with *G. concinnus* (A. Gray) G.L. Nesom and *G. salicifolius* (Bertol.) G.L. Nesom, respectively (Nesom 1994).

Nesom (2001) later accepted the concept of a single genus and the transfer of all ten species of *Gnaphaliothamnus* to *Chionolaena*, thereby emphasizing similarities in habit and microcharacters as well as apparent geographical continuity. He made the required combinations in *Chionolaena* and stressed that *C. salicifolia*, the type of *Gnaphaliothamnus*, could not be separated from the other northern species and that these ten Mexican and Central American species probably constitute a monophyletic northern segment of the genus rather than being interspersed among the South American species, as postulated by Freire (1993).

Gamochaeta is much older and larger than *Gnaphaliothamnus* but similarly uncertain in status. It was erected by Weddell (1856c), recognized as a genus by Cabrera (1961), Holub (1976), Nesom (1990c), Anderberg (1991a), Dillon and Sagástegui (1991) and Bayer et al. (2007), "semi-accepted" by Merxmüller et al. (1977) and not accepted by Bentham (1873b), Hoffmann (1890–1894), Wagenitz (1965), Drury (1970), Hilliard and Burtt (1981) or Greuter (2003). The number of species is uncertain, with 52 listed by Anderberg (1991a) and ca. 80 in Cabrera (1978), mostly in South America with five or six extending into Central America, Mexico, and North America and with species adventive in many parts of the world. A comprehensive study of *Gamochaeta* is badly needed (Nesom 1990c). Nesom (1990c) makes a case for maintaining it as a genus, pointing out that the characters that separate it from *Gnaphalium* s.str. are at least as significant as for other generally accepted genera of Gnaphalieae, that the generic identity of plants of *Gamochaeta* is immediately recognizable and that there are no species dubiously included or excluded from it. The combination of morphological features that distinguishes it includes small capitula arranged in spikes, few (2–5) hermaphrodite florets, style arm apices with a blunt-truncate cluster of collecting hairs, achenes with rounded-conic, myxogenic twin hairs, and pappus bristles that are monomorphic, eciliate, and fused at the base into a cylinder of more or less quadrate cells (cf. interlocking basal cilia in genera such as *Pseudognaphalium*). An additional feature that appears to be rare elsewhere in Gnaphaliinae is the peculiar and prominent concavity developed in the post-fruiting receptacles (Nesom 1990c).

Anderberg (1991a) remarked that *Gamochaeta* differs from *Gnaphalium* in its pappus bristles united into a ring at the base and shed as a single unit. He commented that it is poorly defined, without any synapomorphy of its own, and apparently paraphyletic, but not to be retained in *Gnaphalium*.

Mexerion was proposed by Nesom (1990d) for two species of perennial herbs from Mexico, one newly described and one recombined from *Gnaphalium sarmentosum* Klatt. They have features not found in combination in any other genus, including stoloniferous habit, large heads arranged in spikes, functionally male central florets, achenes without papillae but with short, myxogenic twin hairs, and basally fused pappus bristles.

Stenophalium was proposed by Anderberg (1991a) for three South American species of *Stenocline*, possibly related to the *Pseudognaphalium-Achyrocline* complex and distinguished from other South American taxa with divided stereomes by their homogamous, few-flowered capitula. The remaining three species of *Stenocline* are from Madagascar and Mauritius and related to *Catatia* and *Syncephalum* (Anderberg 1991a). *Novenia* S.E. Freire is a monotypic genus proposed by Freire (1986b) based on *Gnaphalium tunariense* Kuntze, which was later found to be a synonym of *Dolichogyne acaulis* Wedd. ex Benth. & Hook. f., necessitating a change of name to *Novenia acaulis* (Benth. & Hook. f. ex B.D. Jacks.) S.E. Freire & F.H. Hellw. (Freire and Hellwig 1990). It was excluded from Gnaphalieae, Inuleae, and Plucheeae by Anderberg (1991a–c) and was unassigned to a tribe in Bremer (1994). It was accepted into Astereae by Nesom and Robinson (2007). The three Andean genera *Loricaria* (Fig. 36.6E, F), *Mniodes* (Fig. 36.5G) and *Raouliopsis* were tentatively associated with the *Lucilia* group by Merxmüller et al. (1977) but Anderberg (1991a) moved them to a small new subtribe of alpine cushion plants, Loricariinae, together with *Sinoleontopodium* from China, *Pterygopappus* from Australia, and *Psychrophyton* from New Zealand.

North America and northern Old World

Gnaphalieae are primarily a Southern Hemisphere tribe but with some large genera in the Northern Hemisphere including *Anaphalis*, *Antennaria* (Fig. 36.4C), *Gnaphalium* s.l., *Helichrysum*, *Leontopodium*, *Phagnalon* and *Pseudognaphalium* (Fig. 36.6D). Recently published revisions have been few compared to the Southern Hemisphere. *Gnaphalium* (Fig. 36.5H), *Helichrysum* and *Pseudognaphalium* have already been reviewed (see early this section), as have the Central American and Mexican genera *Gnaphaliothamnus* and *Mexerion*. Other genera to appear in the taxonomic literature since 1977 include *Antennaria* (Fig. 36.4C), *Hesperevax*, and *Ancistrocarphus* in North America and *Phagnalon*, *Aliella*, *Omalotheca*, *Chamaepus*, *Chiliocephalum*, *Castroviejoa*, and *Sinoleontopodium* in the Old World.

Antennaria (Fig. 36.4C) is a genus of dioecious perennial herbs distributed throughout temperate to arctic regions of the Northern Hemisphere with three species in the southern Andes of South America. Its center of diversity is in western North America. It is taxonomically complex because agamospermy has led to the evolution of numerous microspecies (Bayer 1993). The number of species is ca. 40 (Bayer et al. 2007) although estimates vary widely. Bayer has published a long series of biosystematic papers on North American species, as well as regional revisions (Bayer and Stebbins 1982; Bayer 1993), a synopsis for North America (Bayer and Stebbins 1993), and a phylogenetic reconstruction of the genus as a whole that gives a subdivision into five informal but named monophyletic groups (Bayer 1990).

Hesperevax briefly enjoyed generic status in the nineteenth century but has usually been included in *Evax* (Fig. 36.4F), which was itself reduced to synonymy under *Filago* by Wagenitz (1969). Merxmüller et al. (1977) left *Hesperevax* in synonymy but accorded "semi-accepted" status to *Evax*. Anderberg (1991a) placed both *Evax* and *Hesperevax* in synonymy under *Filago* but commented that two aberrant species might be better treated as a separate genus *Hesperevax*. Morefield (1992) reinstated and revised *Hesperevax*, accepting three species all from the Californian floristic province. It is separated from other genera in the *Filago* group by a distinctive combination of features two of which are unique in the group: stiff, shiny, transparent bristles on the receptacle and central paleae with erect or spreading, green, ventrally pubescent tips.

The monotypic Californian genus *Ancistrocarphus*, in the *Filago* group, was reinstated by Anderberg (1991a) from synonymy under *Stylocline*. This followed the treatment of Munz (1974). Anderberg (1991a) commented that this made *Stylocline* paraphyletic and the two genera are perhaps better treated as one.

Phagnalon comprises 43 species and stretches from Macaronesia in the west to the Himalayas in the east, and from southern Europe in the north to Ethiopia in the south. Characteristic features are a small shrub or woody perennial habit, undulate or dentate leaves with revolute margins, capitula that are solitary, terminal, heterogamous, and disciform, involucral bracts with scarious margins and apices, female florets filiform and usually outnumbering the hermaphrodite florets, corollas usually hairy at the apex, and anthers ecaudate. Cassini (1819a, b) separated it from *Gnaphalium* by the involucral bracts and ecaudate anthers. Qaiser and Lack have published regional revisions of *Phagnalon* for Arabia (1985) and tropical Africa (1986a) as precursors to the revision of the genus as a whole, and Fayed (1991) has revised it for Egypt (five species) as well as *Leysera* (1991), *Filago*, *Ifloga* (Fayed and Zareh 1988), *Gnaphalium*, *Helichrysum*, *Gnomophalium* (as *Homognaphalium*), *Lasiopogon*, and *Pseudognaphalium* (Fayed and Zareh 1989). Merxmüller et al. (1977) were uncertain about the tribal position of *Phagnalon* but Anderberg (1991a) commented that it, together with *Aliella*, is clearly linked with Gnaphalieae s.str.

Aliella was proposed by Qaiser and Lack (1986b) for three species aberrant in *Phagnalon* and showing some similarities to *Gnaphalium* and *Helichrysum*. A comparison of these four genera was provided. All three species of *Aliella* are small, woody, densely hairy perennials from the high mountains of Morocco. They differ from *Phagnalon* in their tubular, not filiform, female florets, their peduncles with bracts similar in shape and texture to the involucral bracts, and their caudate anthers. A distinctive feature that separates them from *Phagnalon*, *Gnaphalium* and *Helichrysum* is waxy, cushion-like thickenings on the outside of the corolla lobes.

Omalotheca is conventionally included in *Gnaphalium* but Nesom (1990e) supports its recognition as a genus, closest to *Mexerion* and probably with affinities to *Pseudognaphalium* (Fig. 36.6D), and superficially similar to *Gamochaeta*. There are eight species, all at high altitudes, five endemic to Europe and adjacent Asia and three primarily Eurasian but reaching boreal eastern North America. *Omalotheca* is distinguished from similar genera by the combination of herbaceous, rhizomatous, fibrous-rooted perennial habit, narrow- to linear-lanceolate leaves, relatively large capitula arranged in spikes, involucral bracts with undivided stereomes, female corollas that are minutely papillate-punctate, relatively large pollen grains, achenes with imbricate papillae and myxogenic twin hairs 6–12 times as long as wide, and basally eciliate pappus bristles either free or basally connate and shed as a unit (Nesom 1990e).

Chamaepus was proposed by Wagenitz (1980) for a single species of tomentose annual herb from Afghanistan. It has few, disciform capitula congested into glomerules, boat-shaped involucral bracts folded around the female florets and scarcely hardened at maturity, female florets with the corolla attached subapically (vs. laterally in e.g., *Bombycilaena*) to the achene, and the few central florets functionally male and epappose. Wagenitz placed it in the vicinity of the old *Micropus* s.l., in the generic complex that includes *Micropus* s.str., *Bombycilaena*, *Cymbolaena* and *Stylocline*, but not fitting into any existing genus. Anderberg (1991a) placed it with these genera and others in the *Filago* group.

The monotypic Ethiopian genus *Chiliocephalum* was distinguished from *Helichrysum* (Fig. 36.4D) by the absence of pappus bristles and preponderance of female florets. Hilliard and Burtt (1973) included it in *Helichrysum* on the grounds that both its distinguishing features were found together in that genus. Anderberg (1988b) reinstated it on the grounds that its distinctness should not be concealed by submerging it in *Helichrysum* and that the lack of pappus bristles and the densely congested or matted, minute capitula seemed to be synapomorphies of *Chiliocephalum* and *Catatia* from Madagascar.

Castroviejoa was proposed by Galbany-Casals et al. (2004a) for two species of *Helichrysum* (*H. frigidum* and *H. montelinasanum*) from Corsica and Sardinia that have three features not found in combination in *Helichrysum*: biseriate, glandular hairs on the corolla tube, an undivided stereome, and dorsal as well as apical sweeping hairs on the style arms (Galbany-Casals et al. 2004c). Separation of the genus is supported by a phylogenetic analysis of ITS sequence data (Galbany-Casals et al. 2004b).

Sinoleontopodium was proposed by Chen (1985) for a single species of dioecious, pulvinate perennial herb from China. Distinctive features include female florets that are tubular, not filiform, corollas that are rather densely white-villose in the upper part, and pappus bristles that are free and persistent. The author found it reminiscent of *Antennaria* (Fig. 36.4C) and *Leontopodium* but distinct from both. Dillon (2003) has commented that the generic description could refer to a shrubby species of *Anaphalis*. Anderberg (1991a) gave a detailed description but did not see authentic material. He placed *Sinoleontopodium* in the new subtribe Loricariinae.

MORPHOLOGY AND ANATOMY

Most investigations into Gnaphalieae morphology in the last 30 years have been undertaken either to provide data for phylogenetic analyses or to elucidate relationships and establish generic boundaries in small groups of species. Broad scale non-phylogenetic studies in morphology have been less common.

Compiling information for phylogenetic analyses has produced a great deal of morphological data, but it may also have impeded understanding of morphological variation. Because characters are generally required to be reduced to a small number of discrete character states, and because there is commonly no allowance for variability within terminal taxa, much natural morphological variation has of necessity been obscured.

There have been some morphological (and anatomical) publications that are taxonomically broad and not intended directly for phylogenetic analysis. Short et al. (1989) investigated achene structure in a wide range of Australian Gnaphalieae. The taxonomic focus and the use of both scanning electron microscope images and anatomical sections combined to illustrate a remarkable number of characters, many of which demarcated related groups of species. These characters have been important in unravelling the complex relationships of Australian Gnaphalieae (especially the large number of Angianthinae sensu Anderberg, many of which have modified and reduced morphology) and redistributing species into existing, reinstated and newly described genera. Achene characters have also been valuable taxonomically in southern Africa (e.g., Hilliard and Burtt 1981; Karis 1990; Koekemoer 1999), tropical Africa (Mesfin Tadesse and Reilly 1995), South America (e.g., Freire 1986a; Dillon and Sagástegui 1991; Dillon 2003) and New Zealand (e.g., Ward et al. 1997a, 2003).

Hilliard and Burtt (1981) provided detailed notes and informative figures for characters they had found taxonomically useful in their wide-ranging study of genera in southern Africa, as well as valuable information on less taxonomically reliable characters such as white, radiating involucral bracts, and the floral sex ratio (i.e., the proportion of outer female to hermaphrodite or male inner florets in a capitulum), which had been used to separate the two large and widespread genera *Gnaphalium* and *Helichrysum*.

Two useful features of this account are the observation that described character states may be part of a continuum and the extensive use and clear explanation of a character discovered by Drury (1970) a decade earlier, the fenestration of the stereome of the involucral bracts ("divided stereome"), which has proven to be so useful in demarcating many genera of Gnaphalieae both inside and outside southern Africa. Here, too, are observations that have been confirmed in later investigations, such as the value of the type of hair on the achene and the presence or absence of hairs on the abaxial surface of the corolla lobes, and the fact that genera often show a range of related pappus forms rather then a single constant type.

Meticulous observation of large samples and observation of populations in the field have brought new insights into Gnaphalieae morphology and confirmed earlier interpretations of morphological anomalies.

In *Ifloga*, the usual arrangement of florets in the capitulum is peculiar. The outer involucral bracts are boat-shaped and each subtends an epappose female floret. The inner involucral bracts are flat and surround the terminal part of the receptacle, which bears the hermaphrodite florets. Hilliard and Burtt (1971) originally interpreted this as a compound capitulum, with each female floret in its bract representing a primary capitulum. An otherwise similar species, *Comptonanthus* (formerly *Lasiopogon*) *molluginoides*, was excluded from *Ifloga* by its conventional floral structure, with all the female florets pappose and within the main involucre. However, detailed study of another species, *Ifloga thellungiana* Hilliard & B.L. Burtt (formerly *I. ambigua* Thell.), revealed that although the female florets are generally peripheral to the hermaphrodite florets within the main involucre and pappose, occasionally there are one or two female florets in the axils of the outer involucral bracts, and these are epappose or have just one or two pappus bristles. This intermediate form links the conventional heterogamous capitulum structure to that typical of *Ifloga*, indicating not only the affinity of *Comptonanthus molluginoides* to that genus but also a reinterpretation of the *Ifloga* capitulum as simply a single capitulum in which the morphogenetic potential for the production of female flowers has moved outwards to the axils of the outer bracts (Hilliard and Burtt 1981).

During field studies of *Haeckeria*, Orchard (2004a) discovered a population with a mixture of pappose and epappose plants. Where the pappus is absent or almost so, there is at the apex of the achene a small raised rim which has small bumps in the positions of the missing pappus bristles, indicating that pappus bristles are initiated but development stops at an early stage. Clearly this species has the potential to form a pappus, and this may be expressed and suppressed even within a population. Absence of pappus has often been used to define genera (including *Haeckeria*) but evidently should be used with care.

Presence of receptacular paleae between the florets is one of the features that separates *Cassinia* from the similar and closely related genus *Ozothamnus*, but there are some species that resemble *Cassinia* except for the absence of receptacular paleae. They have only one to three florets in the capitulum (Orchard 2004b). Wakefield (1951) suggested that as the paleae were borne on the abaxial side of the florets, they would be indistinguishable from the bracts of the involucre and thus interpreted as absent. Recent field observations of the behavior of the bracts in the two- to three-flowered capitula of *C. leptocephala* F. Muell. (Orchard 2006) revealed that as the fruits ripen, the apparently involucral bracts subtending each floret reflex at the midpoint of the stereome forcing the capitulum to open, and are then shed with the fruits. The remaining bracts of the involucre do not flex and are not shed. This distinction into two types of bracts, both apparently involucral but one intimately associated with the florets and behaving quite differently, strongly supports the hypothesis that receptacular paleae are not absent from few-flowered species of *Cassinia*, but merely disguised.

One of the reiterated themes of Gnaphalieae morphology is the tendency for character states to form a reticulate pattern in a group of related genera. Such patterns make generic circumscription difficult and phylogenetic analyses uninformative (e.g., Breitwieser and Ward 2003). Many recently described monotypic genera show such patterns (e.g., Wagenitz 1980; Short 1989b; Orchard 2005b). *Paenula*, for example, has the terete-trigonous leaves with deeply sunken dark pit glands of *Haeckeria*, the white involucral bracts with a hooded and incurved tip (vs. showy, petaloid tip) typical of *Cassinia*, absence of pappus as in *Haeckeria* and *Odixia*, and the peculiar sheathing paleae of *Ixodia* (Orchard 2005b). In the *Raoulia* alliance, where this type of character state distribution is common, there is some indication of rapid species radiation involving ancestral hybridization (Smissen et al. 2004).

Perhaps the greatest advances in morphology in Gnaphalieae in the last 30 years have been the discovery of a wealth of taxonomically useful characters in the fine structure of the fruit and the increasing realization that morphological characters frequently do not fall into a tidy number of usefully discrete states, nor do they necessarily remain unchanged over long periods of time.

Although only a few anatomical studies were undertaken in the last thirty years, characters from fruit, stem and leaf anatomy were shown to be useful in classification in Gnaphalieae. Based on a more general survey of fruit characters in Australian Gnaphalieae, Short et al. (1989a) demonstrated the value of fruit characters in establishing generic limits. Fruit characters were also incorporated in revisions of several genera, e.g., *Blennospora* (Short 1987b), *Podotheca* (Short 1989a), and *Pogonolepis* (Short 1986) and for the description of the new Australian endemic genus *Cremnothamnus* (Puttock 1994b). Studies in New Zealand Gnaphalieae showed that leaf anatomy characters such as lamina structure, bundle-sheaths and bundle caps are taxonomically useful (Breitwieser 1993; Breitwieser and Ward 1998). These characters were also used in a phylogenetic analysis of Australasian Gnaphalieae inferred from morphological and anatomical data (Breitwieser and Ward 2003).

POLLEN

Skvarla et al. (1977) stated that the pollen of many genera of "Inuleae-Gnaphaliinae" has the same basic structure characterized by a two-layered ectexine comprising an outer columellate layer and an irregularly interlaced basal layer. They termed this pollen type the "inuloid pattern". Since then Anderberg (1991a) has recognized Gnaphalieae as a separate tribe and consequently referred to this same pollen type as "the gnaphalioid type", proposing all true Gnaphalieae have a gnaphalioid sporoderm pattern. Since 1977 only a few researchers have studied pollen of Gnaphalieae (Anderberg and Källersjö 1988; Anderberg 1991a; Moar 1993; El-Ghazaly and Anderberg 1995; Breitwieser and Sampson 1997a, b). Pollen morphology and ultrastructure was shown to be useful for assigning genera to the tribe. Anderberg's hypothesis that *Phagnalon* and *Aliella* belong to the "basal taxa" of the tribe was corroborated (El-Ghazaly and Anderberg 1995), while *Haastia* was found not to belong to Gnaphalieae because of its senecioid pollen as well as its single layer of internal tecta and highly bifurcating columellae bases (Breitwieser and Sampson 1997b). Pollen was also shown to provide characters which are useful in classification of New Zealand Gnaphalieae (Breitwieser and Sampson 1997a, b).

CHROMOSOME NUMBERS

Chromosome numbers are known for about 100 genera of Gnaphalieae, over half of the genera in the tribe. The following basic chromosome numbers have been recorded: $x = 3$, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, and 14. All of these are found in the Australian genera, while within Africa, Eurasia, New Zealand and New World genera counted, $x = 7$ and 14 are by far the most commonly found base numbers.

Turner (1970) proposed $x = 4$ and 5 as base numbers for the tribe, the other known base numbers appearing to be aneuploid derivatives from them. The former would have given rise to 8 and 12, and the aneuploid numbers 7 and 13, respectively; the latter would have given rise to 10, and the aneuploid numbers 9 and 11, respectively. In contrast, Watanabe et al. (1999) proposed $x = 14$ as the base number for the tribe. This was based mainly on the observation that $x = 14$ is the most commonly found base number throughout the tribe, and that it occurs within the Australian "*Millotia* group", particularly *Podotheca*, that was placed by Anderberg (1991a) within the "basal taxa" in a phylogeny based on morphology. However, the results of molecular phylogenetic analyses presented in this chapter suggest that the "*Millotia* group", including *Podotheca*, is nested within the "crown radiation" of the tribe, thus not supporting Watanabe et al.'s (1999) hypothesis.

Chromosome numbers reported in the *Index to Chromosome Numbers in the Compositae* (http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html) have been plotted on the tree in Fig. 36.2, with the purpose of providing new insight into chromosome number evolution within Gnaphalieae. However, because chromosome counts are lacking for an important portion of the species of this tree and because of little phylogenetic structure, only some tentative conclusions can be made.

Species with counts of $2n = 8$, 10 and 14 have been reported for genera of the "*Relhania* clade". Since $x = 7$ is a common base number within the tribe, and it is present in some species of the "*Relhania* clade", this seems to be a more probable base number for the whole tribe than $x = 14$ as proposed by Watanabe et al. (1999). Within this scenario, $x = 4$ and $x = 5$, found in the primarily annual genera *Leysera* and *Rhynchopsidium*, respectively, would be derived probably from $x = 7$ by descending dysploidy, whereas $x = 9$, found in *Phagnalon*, and $x = 8$, found in *Phaenocoma* and *Stoebe*, would be derived probably from $x = 7$ by ascending dysploidy.

Within the "crown radiation" most of the Eurasian and some African taxa are defined by $x = 7$ and $x = 14$. Most genera exhibit high stability in chromosome number. The main exceptions are *Leontopodium* and *Antennaria* (Fig. 36.4C), which show long polyploid series. In *Leontopodium* $2n$ numbers of 14, 24, 26, 28, 44, 48, 50, 52 and 104 have been reported. In *Antennaria* $2n$ numbers of 28, 42, 56, 70, 84, 98, 112, 140 and ca. 168 have been reported. The highest $2n$ number reported for any Gnaphalieae is ca. 168 (dodecaploid, based on $x = 14$), counted in *Antennaria soliceps* S.F. Blake (Bayer and Minish 1993).

Unlike most genera from the New World, Africa and Eurasia, many Australian genera that are part of the "crown radiation" are highly variable in chromosome number. Watanabe et al. (1999) suggested $x = 14$ as the base number of all Australian Gnaphalieae, based on its highest frequency among them, but also on other observations of morphological trends and karyotype symmetry trends in some groups of related species. Several independent dysploidy events would then lead to the different base numbers among Australian taxa. In fact, several examples of infrageneric dysploidy series are found: *Angianthus* ($n = 13$, 12, 6), *Asteridea* ($n = 9$, 7), *Millotia* ($n = 13$, 11, 10, 8) and *Pogonolepis* ($n = 6$, 5, 4), among others (Watanabe et al. 1999). However, considering the available data (Table 36.1), $x = 7$ cannot be ruled out as the possible base number for other Australian genera. Other numbers could then be explained as a combination of several dysploidy and polyploidy events. The variation in chromosome number in Australian taxa is also the result of polyploidy. For example, several species of *Craspedia* ($n = 55$, 22, 33) and *Leiocarpa* (as *Ixiolaena*) ($n = 20$), *Helichrysum scorpioides* Labill. ($n = 24$), *Calocephalus citreus* Less. ($n = 28$), *Chrysocephalum adpressum* (Fitzg.) Anderb. ($n = 24$) and *Ewartia meredithiae* (F. Muell.) Beauverd ($n = 28$) are polyploid taxa (Watanabe et al. 1999). Additionally, even infraspecific polyploidy has been recorded in some species, e.g., *Chrysocephalum apiculatum* (Labill.) Steetz ($n = 12$, 24), *Podolepis neglecta* G.L.R. Davis ($n = 20$, 40), *Leiocarpa leptolepis* (DC.) Paul G. Wilson (as *Ixiolaena leptolepis* (DC.) Benth.) ($n = 20$, 30), and *Podotheca angustifolia* (Labill.) Less. ($n = 13$, 26)

(Watanabe et al. 1999). The highest chromosome number reported for any Australian Gnaphalieae is *n* = 70+ in *Craspedia* (Turner 1970).

In New Zealand, Dawson (2000) reported species of the *Raoulia* alliance displaying 2*n* numbers of 28 or multiples of these (up to 112). A secondary base number of *x* = 14 has been inferred for them (Dawson et al. 1993). A 2*n* number of 28 was also reported for the sole New Zealand species of *Ozothamnus*, *O. leptophyllus* (G. Forst.) Breitw. & J.M. Ward, and for species of *Euchiton* and *Argyrotegium*. Lower base numbers are evident in New Zealand for the cosmopolitan species *Pseudognaphalium luteoalbum* (2*n* = 14) and the primarily Australian genus *Craspedia* (2*n* = 22).

CHEMISTRY

Although sesquiterpene lactones are usually common in other Asteroideae tribes, they are rare in Gnaphalieae (see Anderberg 1991a). They are known from only a small number of genera (*Anaphalis*, *Antennaria* [Fig. 36.4C], *Angianthus* [Fig. 36.8C], *Calocephalus*, *Helichrysum* [Fig. 36.4D]; see Seaman 1982). Other compounds of significance at the tribal level are the diterpenes. Gnaphalieae were shown to have different diterpene chemistry to Inuleae (see Alvarenga et al. 2005).

In a few cases chemistry has been able to provide supportive data to determine that some genera, previously assigned to Gnaphalieae (sensu Anderberg 1991a), need be reassigned to other tribes. For example, Bohlmann and Zdero (1978) found compounds (prinzianic acid methylester; isoprinzianic acid methylester; 15, 16H-16-oxohardwickiic acid methylester; 2-oxo-ent-manoyl oxide; 2-oxo-19-hydroxyl ent-manoyl oxide) in *Printzia* that were identical to those found in members of Astereae, specifically species of *Solidago* L. This provided supporting evidence that allowed *Printzia* to be removed from Gnaphalieae and relocated in Astereae (Bayer and Cross 2002).

In other cases chemical data were shown to be good indicators of intergeneric relationships. For example, the flavonoid chemistry of the two genera *Leucogenes* (Fig. 36.5C) and *Leontopodium*, previously regarded as sister taxa (Anderberg 1991a), did not indicate a close relationship between these two genera, a result supported by phylogenies of chloroplast (Fig. 36.1) and nuclear ITS (Breitwieser et al. 1999) sequences. *Leontopodium* contains only apigenin and luteolin glucosides (Tira et al. 1970; Dashbalyn and Glyzin 1978) while *Leucogenes* contains apigenin and luteolin, kaempferol and quercetin 3-*O*-glycosides, kaempferol and quercetin 3-methyl ethers, quercetin 7-methyl ether, galangin (Reid and Bohm, unpub.; see Bohm and Stuessy 2001).

Chemical compounds may also be characteristic for species groups. For example, the benzofuran derivatives phloroglucines are diagnostic of a group of *Helichrysum* species (see Anderberg 1991a).

Numerous papers on chemical consituents in Gnaphalieae have followed those reviewed by Harborne (1977). However, there are many problems with using chemical constituents as taxonomic characters in Gnaphalieae, particularly the lack of availability of all identified constituents of a taxon, since usually only new substances are reported (see Anderberg 1991a). Most recently though, Emerenciano et al. (2007) investigated the presence or absence of several types of flavonoids with different oxidation levels and pattern substitutions in Compositae, including 185 species of Gnaphalieae. Diterpenes were found in 87 species; 36% are labdane skeletons and 29% are kauranes (Alvarenga et al. 2005). These studies will be a useful source of taxonomic information.

ECTOMYCORRHIZAL ASSOCIATIONS

Vesicular-arbuscular mycorrhizal associations (VAM) have been demonstrated in a wide range of Compositae (Warcup and McGee 1983; Harley and Harley 1987) but ectomycorrhizal associations are generally rare in the family as a whole. Of about 150 species examined in the British flora, over 90% have records of VAM and only *Mycelis muralis* Dumort (one record of six) and *Homogyne alpina* Cass. (one record of seven) have records of ectomycorrhizae. In Australia, the discovery of an ectomycorrhizal association in a species of Compositae (*Xerochrysum bracteatum* (Vent.) Tzvelev; Fig. 36.5E) led to an investigation of other Australian Compositae by Warcup and McGee (1983). They found VAM in a wide range of Compositae but they also found ectomycorrhizae in 27 species, 26 of which were in Gnaphalieae. (The 27th was *Isoetopsis graminifolia* Turcz., a species of uncertain tribal affinity.) Occurrence of ectomycorrhizae matched generic circumscriptions except in *Helichrysum* (Fig. 36.4D) and *Helipterum*, which were known to be unnatural assemblages of species. Because this limited sample suggested that occurrence of ectomycorrhizae might be a taxonomically useful character in the tribe, the survey was extended to 180 species in 55 genera of Australian Gnaphalieae (Warcup 1990). Ectomycorrhizal associations were found in 75 species and coincided with generic circumscriptions in all except three cases. One of the 45 species of *Rhodanthe* (*R. citrina*, as *Waitzia citrina*) is recorded as having an ectomycorrhizal association. Wilson (1992a), in placing it in a monotypic section of *Rhodanthe*, commented that it was difficult to place and possibly deserves recognition as a distinct genus. *Gnephosis* has a mixture of species with and without ectomycorrhizae, but it has not yet been completely revised (Short 1990c). *Podotheca*, which has recently been revised (Short 1989a), is apparently the only genus in which presence or absence of ectomycorrhizae does not coincide with established generic boundaries. Five of the six recognized species form ectomycorrhizae and one does not.

Presence of ectomycorrhizal associations has proven to be a reliable indicator of interspecific relationships in Australian Gnaphalieae. It would appear to merit investigation in taxonomically difficult Gnaphalieae outside Australia, although all the genera that showed ectomycorrhizal associations in the survey (Warcup 1990) are endemic to Australia.

BIOGEOGRAPHY

Anderberg (1991a: 175) commented that it is difficult to discern biogeographic pattern in the tribe as a whole and that vicariance events alone would be insufficient to explain extant distributions. Given the trees presented here, an hypothesis of African origin and subsequent spread of Gnaphalieae to other continents is plausible (Fig. 36.2). However, taxon sampling in this tree is heavily biased toward Australia and Africa at the expense of Europe, Asia and the Americas, therefore any conclusions would be premature. The distributions indicated in Fig. 36.2 for the species included in the phylogenetic analysis are often not fully representative of their genera. For example the *Craspedia* and *Ozothamnus* species sampled in the phylogenetic analysis were from Australia, but both these genera also have species native to New Zealand. It must also be borne in mind that in general Gnaphalieae appear to be highly dispersible and their true history might be difficult to reconstruct. For example, at least five Gnaphalieae lineages appear to have migrated to New Zealand independently, possibly with a subsequent dispersal from New Zealand to New Guinea for *Anaphalioides* (Breitwieser et al. 1999). Given that some species are effectively cosmopolitan (e.g., *Pseudognaphalium luteoalbum*), a frequent exchange of lineages among areas through range expansion and long distance dispersal is plausible.

HYBRIDIZATION

The species of *Raoulia* (Fig. 36.5A, B) and allied genera of New Zealand have long been noted for numerous hybrid combinations between plants of strikingly different morphology (Cockayne and Allan 1934; Allan 1939, 1961; Ward 1997). Recently, some of these hybrids have had their parentage tested by detailed morphological or genetic methods (Smissen et al. 2003, 2007; McKenzie et al. 2003, 2004, 2008). McKenzie et al. (2008) showed that F_1 hybrids of the cross *Ewartiothamnus sinclairii* (Hook. f) Anderb. × *Anaphalioides bellidioides* (as *Ewartia sinclairii* × *Anaphalioides bellidioides*) have some fertility despite meiotic abnormalities, and provided morphological evidence that a wild-collected plant is a backcross based on this cross. Smissen et al. (2007) used AFLP fingerprinting to identify wild backcrosses of *Anaphalioides bellidioides* × *Helichrysum lanceolatum* (Buchanan) Kirk within a mixed population, and subsequent glasshouse study has confirmed the fertility of this backcross. These results allow the possibility that the levels of sequence polymorphism and phylogenetic incongruence in the group (see Phylogeny, this chapter) may have resulted from introgression or homoploid hybrid speciation. The only available data suggests that pre-zygotic isolation is often weak or absent and that F_1 hybrids form at high frequency for some combinations in some populations (Smissen et al. 2007). However, neither hybrid swarms, nor contemporary introgression have been convincingly documented. Hybridization among species of Gnaphalieae apparently has not received comparable attention outside of New Zealand, but as is usually the case, it is difficult to discern if this is due to its relative unimportance, the interests of individual researchers, or other biases.

HORTICULTURE

Among Gnaphalieae used as ornamentals, species of *Ammobium* (Fig. 36.8B), *Cephalipterum*, *Chrysocephalum*, *Craspedia*, *Hyalosperma*, *Lawrencella*, *Leucochrysum* (Fig. 36.5F), *Rhodanthe*, *Schoenia*, *Waitzia* (Fig. 36.8E), and *Xerochrysum* (Fig. 36.5E) from Australia are most predominant (Bailey 1975, Barker et al. 2002). Australian everlastings were taken to Europe in the late eighteenth century and rapidly became collectors' items. *Xerochrysum bracteatum* (strawflower) and *Calomeria amaranthoides* Vent. (incense plant) were first described from plants flowering in the Empress Josephine's garden at Malmaison in 1803 and 1804, and many species were grown in the Royal Botanic Gardens at Kew. *Xerochrysum bracteatum* was grown in England as early as 1791 and European horticulturalists soon produced a range of colored varieties and double forms (Schaumann et al. 1987). *Xerochrysum bracteatum* has been important in the nursery trade since that time and is probably the most widely grown species of Gnaphalieae.

Australian species are important in the dried flower trade, particularly *Xerochrysum bracteatum*, *Rhodanthe manglesii* (Swan River everlasting), *R. chlorocephala* (Turcz.) Paul G. Wilson subsp. *rosea* (Hook.) Paul G. Wilson (pink and white everlasting), *Waitzia acuminata* Steetz (orange immortelle), and *Pycnosorus globosus* Benth. (Billy buttons, drumsticks). *Ixodia achillaeoides* R. Br. regenerates *en masse* after fires and in its natural area in southeastern Australia it is an important commercial crop as an everlasting flower (Schaumann et al. 1987; Huxley et al. 1992). Many annual species of Australian and South African Gnaphalieae are difficult to germinate and need pretreatments of liquid smoke, gibberellins, or 65°C heat in order to coax germination (Barker et al. 2002).

A few species of Gnaphalieae are widely grown as general garden ornamentals including *Anaphalis margaritacea* and *A. triplinervis* Sims ex C.B. Clarke (pearly everlastings), *Anaphalioides bellidioides* (New Zealand everlasting), *Helichrysum petiolare* Hilliard & B.L. Burtt (liquorice plant), *H. italicum* (Roth.) G. Don (curry plant), *Rhodanthe manglesii* and *Xerochrysum bracteatum*, but many more are grown as rock garden plants, including various species of *Antennaria*, *Helichrysum*, *Leontopodium*, *Leucogenes*, *Lucilia* and *Raoulia* (Bailey 1975; Huxley et al. 1992). The cushion shrub species of *Raoulia* such as *R. eximia* Hook. f. (one of the famed "vegetable sheep", Figs. 36.5A, B) are highly prized by specialist alpine gardeners, and their natural hybrids, such as *R.* ×*petrimia* Kit Tan & J.D. McBeath (*R. eximia* × *R. petriensis* Kirk) and *R.* ×*loganii* Cheeseman (*R. rubra* Buchanan × *Leucogenes leontopodium* (Hook. f.) Beauverd) are becoming established in the specialist nursery trade (Ingwersen 1991; Beckett 1993).

Many more species of Gnaphalieae, especially South African taxa, would undoubtedly make fine cultivated plants. This area of horticultural research should be explored.

INVASIVENESS

Euchiton gymnocephalus (DC.) Holub, *E. involucratus* (G. Forst.) Holub, *E. sphaericus* (Willd.) Holub, *Facelis retusa* (Lam.) Sch.Bip., *Filago pyramidata* L., *Gamochaeta americana* (Mill.) Wedd., *Gnaphalium uliginosum* L., *Logfia gallica* Coss. & Germ., *Pseudognaphalium luteoalbum*, and *Vellereophyton dealbatum* (Thunb.) Hilliard & B.L.Burtt are low impact weeds, many of which have been distributed globally (Harden 2000; Flora of North America Editorial Committee 2006; R.J. Bayer, pers. obs.). In most cases, Gnaphalieae have not become major agricultural weeds.

CONSERVATION/ENDANGERED SPECIES

Several species of Gnaphalieae are considered rare, threatened or endangered including *Acanthocladium dockeri* F. Muell. (Fig. 36.8G), *Achyrocline glandulosa* S.F. Blake, *A. hallii* Hieron., *A. mollis* Benth., *Antennaria arcuata* Cronquist, *A. soliceps*, *Argentipallium spiceri* (F. Muell.) Paul G. Wilson, *Craspedia preminghana* Rozefelds, *Gamochaeta antarctica* (Hook. f.) Cabrera in M.N. Correa, *Helichrysum aciculare* Balf. f., *H. arachnoides* Balf. f., *H. balfourii* Vierh., *H. biafranum* Hook. f., *H. cameroonense* Hutch. & Dalziel, *H. mannii* Hook. f., *H. nimmoanum* Oliv. & Hiern, *H. paulayanum* Vierh., *H. rosulatum* Oliv. & Hiern, *H. sphaerocephalum* Balf. f., *H. suffruticosum* Balf. f., *Gnaphalium chimborazense* Hieron., *G. dysodes* Spreng., *G. ecuadorense* Hieron., *G. imbaburense* Hieron., *G. sepositum* Benoist, *G. sodiroi* Hieron., *Lasiopogon ponticulus* Hilliard, *Loricaria antisanensis* Cuatrec., *L. azuayensis* Cuatrec., *L. ollgaardii* M.O. Dillon & Sagást., *L. scolopendra* Kuntze, *Neotysonia phyllostegia* (F. Muell.) Paul G. Wilson, and *Rutidosis leptorrhynchoides* F. Muell. (IUCN 2007).

ETHNOBOTANY

Several species of Gnaphalieae are used for medicinal purposes. *Pseudognaphalium luteoalbum*, and several other species of *Pseudognaphalium* and *Gnaphalium* have been used as a diuretics and in the general treatment of digestive ailments (Uphof 1968). *Antennaria dioica* (L.) Gaertn. and other *Antennaria* (Fig. 36.4C) species have been used as antitussives and diuretics (Launert 1981). European *Helichrysum stoechas* DC. has been employed to treat edema, skin diseases, and worms (Uphof 1968). In Africa, *Elytropappus rhinocerotis* Less. is used to treat influenza symptoms and as an aid to digestion and loss of appetite (Van Wyk and Gericke 2000). *Helichrysum pedunculare* (L.) DC. is used by the Zulus to treat circumscision wounds and to dress septic sores (Van Wyk and Gericke 2000). The smoke from the burning of *Helichrysum odoratissimum* (L.) Sweet is used by the Zulu people as a sedative and to cure insomnia (Van Wyk and Gericke 2000).

Hottentots tea is made from an infusion of *Plecostachys serpyllifolia* (Berg.) Hilliard & B.L. Burtt (Uphof 1968); whereas Zulu and daisy tea are made from *Athrixia phylicoides* DC. and *A. elata* Sond., respectively (Van Wyk and Gericke 2000).

Branches of *Helichrysum tomentosulum* (Klatt) Merxm. are sometimes used as thatching for huts in South Africa (Van Wyk and Gericke 2000).

CONCLUSIONS

The recognition by Anderberg (1989) of the distinct tribe Gnaphalieae has facilitated progress in understanding the diversity of and relationships among this group of plants. In the nearly twenty years since then, the understanding of the major phylogenetic groups in the tribe has changed radically but is now converging on a sustainable if not finely divided arrangement. Although there is not yet the basis for a satisfactory subtribal classification, much more is known about relationships at the generic level. Generic changes have proceeded apace driven by regional treatments, leaving room for considerable global synthesis. A general trend has been to attempt to achieve monophyletic genera by splitting into smaller units rather than by merging into larger ones, with the recognition of 70 additional genera, either reinstated or newly described, in the last 30 years. Many anomalous species have been removed from large, widespread, polyphyletic genera, and the exclusion of the entire Australasian component from *Helichrysum* has to some extent simplified its circumscription. Although much remains to be done in elucidating relationships among species of such still unwieldy and ill-defined genera as *Gnaphalium*, *Pseudognaphalium*, *Helichrysum*, *Achyrocline*, and *Anaphalis*, Gnaphalieae are poised for a far more auspicious taxonomic century than the last.

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Appendix 36.1. Nomenclatural changes made since Bayer et al. (2007)

Homognaphalium Kirp. was based on a description of *G. pulvinatum* Delile misidentified as *G. crispatulum* Delile (Hilliard & Burtt, 1981). Greuter (2003) pointed out that the name *Homognaphalium* was based on the name *G. crispatulum*, which is thus the type of *Homognaphalium*, but was based on the description of *G. pulvinatum*, for which a new generic name was required. He proposed the name *Gnomophalium* and recombined *Gnaphalium pulvinatum* as *Gnomophalium pulvinatum* (Delile) Greuter.

Four new genera have been proposed since the descriptions were written for Bayer et al. (2007). Matching descriptions are appended here so they can be added to that volume.

Argyrotegium J.M. Ward & Breitw.

Argyrotegium J.M. Ward & Breitw., N. Z. J. Bot. 41: 608–9. 2003; Ward, Breitwieser & Flann, N. Z. J. Bot. 41: 603–611. 2003.

Perennial, usually mat-forming herbs. Leaves alternate, usually flat, with entire margins, tomentose on both surfaces. Capitula solitary or few together. Involucral bracts papery, stramineous or brownish, stereome usually undivided. Receptacle flat, epaleate. Outer florets filiform, purple to colorless. Central florets perfect, purple to colorless. Anthers with flat appendages. Style branches obtuse, with hairs located dorsally and apically. Achenes usually obovoid, usually glabrous. Pappus bristles capillary, scabrid, connate in groups or in a fragile ring, sometimes with patent cilia. *n* = 14. Four species, Australia, New Zealand.

Castroviejoa Galbany, L. Sáez & Benedí

Castroviejoa Galbany, L. Sáez & Benedí, Butl. Inst. Catalana Hist. Nat., Secc. Bot. 71: 133. 2004; Galbany-Casals, Garcia-Jacas, Susanna, Sáez & Benedí, Austral. Syst. Bot. 17: 241–253. 2004; Galbany, Sáez & Benedí, Austral. Syst. Bot. 17: 581–591. 2004.

Perennial herbs. Leaves alternate, usually flat, with entire margins, tomentose on both surfaces or adaxially only. Capitula solitary. Involucral bracts papery, white, stereome undivided. Receptacle flat, epaleate. Outer florets absent. Central florets perfect, yellow. Anthers with flat appendages. Style branches truncate, with hairs placed dorsally and apically. Achenes cylindrical to ovoid-cylindrical, with elongated twin hairs. Pappus bristles capillary, scabrid to barbellate, free or cohering by patent cilia. *n* = 14. Two species, Corsica, Sardinia.

Paenula Orchard

Paenula Orchard, Telopea 11: 5. 2005; Orchard, Telopea 11: 1–9. 2005.

Shrub. Leaves alternate, terete-trigonous, glabrous. Capitula many in corymbs. Involucral bracts membraneous to cartilaginous, white, stereome undivided. Receptacle paleate, paleae cartilaginous, enclosing achene and base of corolla. Outer florets absent. Central florets perfect. Anthers with flat appendages. Style branches truncate, with hairs located apically. Achenes ellipsoid, with short clavate twin hairs. Pappus absent. One species, *P. storyi* Orchard, Australia.

Leiocarpa Paul G. Wilson

Leiocarpa Paul G. Wilson, Nuytsia 13: 597. 2001; Wilson, Nuytsia 13: 595–605. 2001.

Perennial herbs. Leaves alternate, flat with entire margins, tomentose on both surfaces. Capitula solitary. Involucral bracts scarious, herbaceous or cartilaginous, pale brown, stereome divided. Receptacle usually convex, epaleate. Outer florets filiform, usually yellow, or absent. Central florets perfect, usually yellow. Anthers with concave appendages. Style branches truncate to rounded. Achenes terete, somewhat compressed, smooth or sparsely glandular and with a few minute unicellular hairs. Pappus bristles capillary, barbellate, persistent. *n* = 20, ca. 21, 30, ca. 38, ca. 40. Ten species, Australia.

Chapter 37

Astereae

Luc Brouillet, Timothy K. Lowrey, Lowell Urbatsch, Vesna Karaman-Castro, Gisela Sancho, Steve Wagstaff and John C. Semple

INTRODUCTION

Tribe Astereae, with an estimated 222 genera and ca. 3100 species (emended from Nesom and Robinson, 2007), is the second largest tribe of family Compositae. Members of the tribe range from the Arctic to the tropics, though they are more numerous in temperate regions. They are mostly found in open habitats, from salt marshes and bogs to deserts, and from sea level to the alpine zone. They are mostly characterized by their ecaudate and ecalcarate anther bases (though a few genera have caudate anther bases), and a disc floret style with two distinct marginal stigmatic lines and deltate to triangular or lanceolate style appendages that are glabrous adaxially and with sweeping hairs abaxially.

The tribe is part of subfamily Asteroideae and belongs to a clade that includes Calenduleae, Gnaphalieae, and Anthemideae, the latter often considered its sister tribe (e.g., Panero and Funk 2002, 2008), though this question is still not fully resolved (e.g., Goertzen et al. 2003). Grau (1977), Bremer (1994), Nesom (1994g), and Nesom and Robinson (2007) summarized the taxonomic history of the tribe. These authors addressed subtribal classification of Astereae, acknowledging the somewhat artificial nature of the traditional divisions. The most significant departure from the classic scheme was that of Nesom (1994g, 2000a), which culminated in the recent classification by Nesom and Robinson (2007). This classification incorporates some, but not all, the molecular phylogenetic information published between 1994 and 2004. Though an evolutionary tree was presented by Nesom (1994g), it was not based on a phylogenetic analysis of characters. The only cladistic analysis of tribe Astereae (Zhang and Bremer 1993) was subsequently used by Bremer (1994). This analysis, however, was based on a few representatives selected from the existing subtribes, using traditional morphological characters and the sampling did not allow for the assessment of whether or not the subtribes were monophyletic. Nesom (1994g) reviewed this analysis and made extensive comments on the data and conclusions.

Much of the taxonomic literature published since Grau (1977) has been summarized by Bremer (1994), Nesom (1994g, i, 2000a), Müller (2006), Flora of North America Editorial Committee (2006), and in the phylogenetic papers cited herein. This literature will not be repeated here unless necessary.

Molecular phylogenies in the tribe initially were based on cpDNA RFLP analyses, mostly of North American (Suh and Simpson 1990; Zanowiac 1991; Morgan and Simpson 1992; Morgan 1993, 1997; Lane et al. 1996; Xiang and Semple 1996; Zhang 1996; see Semple et al. 1999) or Asian genera (Gu et al. 1994; Ito et al. 1995, 1998). Few papers using cpDNA sequence data were published for Astereae (Denda et al. 1999; Bayer and Cross 2002; Liu et al. 2002; Watanabe et al. 2006; Forest et al. 2007); these data are not cumulative since different markers were used in the studies, which further used a restricted sample of taxa.

Mostly after the publication of the seminal paper by Noyes and Rieseberg (1999), phylogenies of genera or groups of genera based on the nuclear ribosomal internal transcribed spacer (ITS) were published (Morgan 1997, 2003; Noyes 2000a; Lowrey et al. 2001; Markos and Baldwin 2001; Cross et al. 2002; Fiz et al. 2002; Liu et al. 2002; Wagstaff and Breitwieser 2002; Roberts and Urbatsch 2003, 2004; Urbatsch et al. 2003; Beck et al. 2004; Brouillet et al. 2004; Eastwood et al. 2004; Field et al. 2006; Watanabe et al. 2006; Selliah and Brouillet 2008). Some papers also added the nrDNA 3′ETS region as a phylogenetic tool in Astereae (Markos and Baldwin 2001, 2002; Morgan 2003; Roberts and Urbatsch 2003, 2004; Urbatsch et al. 2003; Brouillet et al. 2004; Selliah and Brouillet 2008).

Given the large number of available ITS sequences in Astereae and the fact that no phylogeny exists for the whole tribe, we firstly present an ITS-based phylogeny of the entire tribe. The resulting lineages are discussed in relation with the pertinent literature. Secondly, we review briefly the various characters (morphological, cytological, chemical) and their distribution in the tribe. Thirdly, economic uses and biological data on Astereae are summarized. Fourthly, we examine the biogeography of the tribe in terms of the ITS phylogeny, contrasting it with hypotheses based on traditional classifications. Finally, we examine the impact of the current molecular phylogeny on generic delimitation and contrast our Astereae ITS phylogeny with the recent classification of Nesom and Robinson (2007).

MATERIALS AND METHODS

The phylogeny was reconstructed using GenBank-available nrDNA ITS sequence data for Astereae, as well as representatives of the sister tribes Calenduleae, Gnaphalieae, and Anthemideae. Details on sequencing methods and phylogenetic analyses, as well as discussions of specific results, are available in the papers where the data were initially published (cited above), as well as in papers being concurrently prepared with the present analysis (Sancho and Karaman-Castro 2008; Karaman-Castro and Urbatsch, pers. comm.; Brouillet et al., pers. comm.). To align the more than 850 available sequences, and more specifically the Astereae sequences with those of the outgroups, we used the 80%-consensus aligned sequences for the tribes of Asteraceae as determined from the ITS secondary structure by Goertzen et al. (2003). Small misalignments in the consensus sequences of Astereae, Gnaphalieae, and Anthemideae were noted in ITS1 (before helix 1A and in helix 1B) and in ITS2 (in helices 2A and 2C). These most likely resulted, for Astereae, from the fact that the sequences used by Goertzen et al. were mostly from derived genera with numerous indels, such as *Erigeron*. The availability of sequences of primitive Astereae, such as *Nannoglottis* and *Printzia* Cass., and the large number of available ITS sequences, allowed us to correct these misaligned portions. Duplicate sequences or sequences of dubious origin were removed from the matrix. The resulting matrix included 752 taxa (737 Astereae and 15 outgroup species) by 852 characters, of which 468 were parsimony informative. Gaps were treated as missing characters. Multistate data were treated as uncertainties. Given that sequences came from a number of laboratories, there were missing data, particularly in the outgroups where many lacked the 5.8S portion; otherwise, data were missing mostly from the beginning of ITS1 or the end of ITS2; missing data were usually a few bases only.

Given the size of the matrix, a PAUPRat (Sikes and Lewis 2001) parsimony analysis was carried out using PAUP*10.6b (Swofford 2002) (swap = tbr, nrep = 1, addseq = random, nchuck = 1, chuckscore = 1, wtset = 1). Subsequently, a parsimony analysis starting from the trees obtained in the 15 ratchet runs was done in PAUP* (tbr, maxtree = 20,000) in order to obtain a greater number of trees as a basis for the strict consensus tree. Base chromosome numbers and distribution (as branch color) were manually mapped onto the phylogeny.

RESULTS

Resulting parsimony trees had a length of 7928, a consistency index (non informative characters removed) of 0.15, a homoplasy index of 0.84, and a retention index of 0.79; the rescaled consistency index was 0.12. The strict consensus tree is presented in Fig. 37.1A–E, where subtribes following Nesom and Robinson (2007) are indicated to the right of the cladograms. Given the number of parsimony informative characters, much lower than the number of taxa analyzed, and the relatively recent radiations in many groups of Astereae, homoplasy is high and in part responsible for the low resolution of the trees. More localized analyses (see studies cited above), which exclude taxa from other groups or continents, often produce more resolved trees. Support for clades is usually non-significant, in large part due to the low number of characters defining each branch, particularly along the spine of the tree. The addition of phylogenetically significant indels to the analysis may increase support for individual clades (Brouillet, pers. obs.).

The ITS sequence data, as analyzed here, do not allow us to determine the relationships between Astereae and the three tribes to which it is considered closely related, Calenduleae, Gnaphalieae, and Anthemideae.

Tribe Astereae is monophyletic and resolves into a number of large clades that will each be described below; many have been the object of recent phylogenetic analyses. The phylogeny (Fig. 37.1A–E) includes a basal African grade, with disjunct Chinese, South American, and New Zealand lineages, and a polytomy of crown groups in Australasia, South America, and North America.

PHYLOGENETIC LINEAGES

Basal lineages: out of Africa, repeatedly

Printzia (Figs. 37.2A, 37.3A) and *Denekia* Thunb. (Fig. 37.3B) have been shown by Bayer and Cross (2002) and Brouillet et al. (pers. comm.) to belong to tribe Astereae and are sister to the remaining members of the tribe (Fig. 37.1A①). Using *rbcL* data, Forest et al. (2007, Supplement 3) also placed *Printzia* within Astereae, but not as sister to the genera studied. Both genera are South African, which supports the hypothesis of an African origin for the tribe (Noyes and Rieseberg 1999). The tailed anthers of *Printzia* and *Denekia* is a symplesiomorphy shared with related tribes and tends to confirm the early diverging position of the taxa in a mostly tail-less tribe. *Printzia* is placed in subtribe Hinterhuberinae by Nesom and Robinson (2007), a position not supported here. *Denekia* has traditionally been placed in tribe Gnaphalieae (e.g., Bayer et al. 2007). Placement within Astereae is novel and postdates the Nesom and Robinson classification. The capitulum morphology of *Denekia*, with its bilabiate peripheral (rays) and functionally male disc florets, appears odd in Astereae, but some aspects of its morphology certainly agree with a placement near *Printzia*, notably the tomentose abaxial leaf faces. These two genera may deserve a subtribe of their own.

Liu et al. (2002) showed that the Chinese *Nannoglottis* Maxim. is sister to other Astereae, though they postulated an African origin followed by dispersal to Asia. Our data (Fig. 37.1A②) confirm that it is one of the earliest diverging lineages and that it must have dispersed from Africa to China at some early stage of Astereae evolution.

Brouillet et al. (pers. comm.) showed that *Mairia* Nees is an isolated genus among African Astereae, between *Nannoglottis* and the Paleo South American and New Zealand clades (Fig. 37.1A③) (Paleo South American and New Zealand clades: see below). The study also confirmed the separation of *Mairia* into *Mairia* s.str., *Polyarrhena* Cass., and *Zyrphelis* Cass. (Nesom 1994a). The latter are members of subtribe Homochrominae (below). As with *Printzia*, *Mairia* was placed within the Southern Hemisphere subtribe Hinterhuberinae in the Nesom and Robinson classification, a position not supported here.

At the next node in the phylogeny (Fig. 37.1A④), *Pteronia* L. and the Homochrominae form a polytomy with the remaining Astereae. In some trees, *Pteronia* segregates first, while in others, it is sister to Homochrominae. *Pteronia* is a large genus of shrubs with discoid heads. The majority of genera in Homochrominae are radiate, although *Felicia* Cass. (83 species; Fig. 37.2B), *Amellus* L. (12 spp.), *Engleria* O. Hoffm. (2 spp.), and *Chrysocoma* L. (20 spp.) have taxa with both radiate and discoid heads. Two South African genera, *Heteromma* Benth. and *Engleria*, were not included in the present analysis. *Heteromma* is wholly discoid while *Engleria* has one discoid and one radiate species. All species in both genera are herbaceous perennials with the exception of one annual species of *Engleria*. The affinities of these two taxa are currently unknown. Broader sampling of the southern African taxa is needed to resolve the relationships between *Pteronia*, Homochrominae, and the few genera that remain to be sampled.

Subtribe Homochrominae had been called Feliciinae by Nesom (1994g). He had included the African *Felicia* group, the Asian *Lachnophyllum* Bunge group, and the American-European *Monoptilon* Torr. and A. Gray group in this subtribe. Nesom and Robinson (2007) restricted Homochrominae to the *Felicia* group, thus making it strictly African, as was done by Grau (1973). The current study confirms this circumscription, at least insofar as the genera included are concerned (Fig. 37.1A⑤). The Nesom (1994g) evolutionary tree showed Homochrominae as nested within a polytomy of subtribes mainly with Australasian and South American elements, but some European and North American as well; such affinities are not supported here. Homochrominae constitute one of the major radiations among the early diverging lineages. A major difference in the composition of Homochrominae between Nesom and Robinson (2007) and the current analysis is the inclusion of the St. Helena endemic trees and shrubs *Commidendron* Lem. and *Melanodendron* DC. In their classification, Nesom and Robinson left these genera unplaced. Nesom (1994g) had placed them within woody Baccharidinae, though noting the lack of comfortable fit in any subtribe. Noyes and Rieseberg (1999) noted the position of *Commidendron* near *Felicia* and *Amellus*, while Eastwood et al. (2004) showed a relationship of both to *Felicia*. Our phylogeny confirms the relationship between the two groups, but places *Commidendron* and *Melanodendron* as a clade sister to the *Felicia* clade. It would appear that these arborescent genera evolved from an ancestor common to the two groups. Within the *Felicia* lineage, *Felicia* does not appear to be monophyletic. *Felicia uliginosa* (J.M. Wood & M.S. Evans) Grau and *F. clavipilosa* Grau group with *Nolletia* Cass., well nested within a lineage that also includes *Amellus*, *Poecilolepis* Grau, and *Chrysocoma*. There are two other unresolved *Felicia* lineages, the *F. namaquana* (Harv.) Merxm. and *F. filifolia* Burtt Davy lineages. *Polyarrhena* and *Zyrphelis* appear related to the *F. filifolia* lineage, but it is impossible to determine whether the genera are sister to this lineage or whether *Felicia* is paraphyletic to them. *Felicia* is most likely polyphyletic as currently circumscribed and needs more study.

The Madagascan genus *Madagaster* G.L. Nesom was recently segregated from *Aster* by Nesom (1993b), who placed it in his southern Hemisphere subtribe Hinterhuberinae; he considered these taxa unrelated to *Aster*, including the African asters. As with *Printzia* and *Mairia*, our study does not support a position in this subtribe (Fig. 37.1A⑥). Instead, it is one of many isolated African lineages along the basal spine of the Astereae phylogeny. More genera from Africa need to be included in phylogenetic analyses before the position of *Madagaster* can be settled.

Conyza gouani Willd. is the only African *Conyza* Less. that does not group with Grangeinae (see below) (Fig. 37.1A⑦). Further study is required before its position can be ascertained and it can be assigned to a genus of its own. Nesom and Robinson (2007) hinted at the polyphyletic nature of *Conyza*. The morphology of this species appears quite distinct from that of other African conyzas, and its isolated position is therefore not surprising.

Nesom (1994h) and Nesom and Robinson (2007) maintained the African asters within the mainly Asian *Aster* L. s.str. but our results (Fig. 37.1A⑧) do not support such a relationship. As with several other African lineages, these asters appear to be isolated. Additional study is needed to better resolve their affinities.

Brouillet et al. (pers. comm.) have shown that subtribe Grangeinae is a monophyletic group of African and south Asian genera, and does not appear to include Australasian or American elements (Fig. 37.1A⑨). A major difference with the generic composition given by these authors is the addition of the African conyzas, *Psiadia* Jacq., and *Welwitschiella* O. Hoffm. to the subtribe. Nesom and Robinson, however, mentioned the potential relatedness of African conyzas to the subtribe. Earlier, Nesom (1994g) had suggested a relationship of the African conyzas to the *Nidorella* Cass. group of Grangeinae, as was proposed by Wild (1969a, b). Our data support this relationship, but only generally: *Nidorella* appears more closely related to *Grangea* Adans. than to the conyzas in our analysis. Nesom (1994g) had placed *Psiadia* in Baccharidinae, a relation not supported here. It was left unplaced in the Nesom and Robinson classification. Finally, *Welwitschiella*, a genus traditionally placed within Heliantheae s.l., also belongs here (Brouillet et al. pers. comm.). This genus has not been treated within Astereae before.

Fiz et al. (2002) studied the evolution of subtribe Bellidinae s.str. (Fig. 37.2C) and showed it had relationships with *Bellidiastrum* Cass. and the *Galatella* Cass. group (Fig. 37.1A⑩). The current analysis supports this view and suggests that Bellidinae should be expanded to include *Bellidiastrum* and the *Galatella* group, placed in Asterinae by Nesom and Robinson (2007) and often treated as *Aster* species in the past. Furthermore, an African origin for Bellidinae is suggested by their placement on the tree, in a polytomy with mainly African Grangeinae.

As with *Nannoglottis*, *Callistephus* Cass. (Brouillet et al. 2001; Semple et al. 2002) occupies an isolated position within the Astereae phylogeny (Fig. 37.1A⑪–C), usually within the crown group polytomy. It never groups with *Aster* s.str., in contradiction to its classification in subtribe Asterinae (Nesom 1994g; Nesom and Robinson 2007). Given that few Asiatic genera have been included in molecular phylogenetic analyses, it is difficult to reach further conclusions concerning this taxon.

Paleo South American clade

The Paleo South American clade (Fig. 37.1B) is placed in the phylogeny between the South African *Mairia* lineage (above) and the New Zealand clade (below). In more restricted phylogenies (Brouillet et al., pers. comm.), it is sometimes sister to the New Zealand clade. The interrelationships of these two clades remain to be ascertained. The clade includes taxa placed within Hinterhuberinae by Nesom and Robinson (2007). Our phylogeny shows that subtribe to be polyphyletic. The Paleo South American clade consists of two sister subclades: the *Chiliophyllum* Phil. nom. cons. and the *Oritrophium* (H.B.K.) Cuatrec. clades.

The *Oritrophium* clade (Fig. 37.1B①) includes rosette herbs that are scapose (*Oritrophium*) or acaulescent (*Novenia* S.E. Freire). They are adapted to the climatic and edaphic conditions of the puna and páramo ecosystems, respectively (Freire 1986; Torres et al. 1996). *Oritrophium* is distributed in South America and Mexico. Because of its herbaceous habit, it was considered a highly derived member of subtribe Hinterhuberinae (Nesom 1993a). Its rosulate habit, scapose inflorescences, and staminate disk florets define the genus. Recently two new species of *Oritrophium* were described from Mexico (Nesom 1992, 1998b). This is a remarkable

Fig. 37.1. Strict consensus tree of tribe Astereae based on a parsimony phylogenetic analysis of ITS sequence data. **A** (opposite page) basal grade of mostly African lineages; **B** (p. 594) Paleo South American and New Zealand clades; **C** (p. 596) Australasian lineages; **D** (p. 597) South American lineages; **E** (pp. 598–599) North American clade. Branches are colored according to geographic distribution, following the color code developed for this volume; Madagascar and St. Helena are color-coded distinctly from tropical Africa (Fig. 37.1A). Numbers along branches are basic chromosome number (*x*) for all taxa subtended by the branch, unless otherwise indicated; × on a branch indicates taxa for which chromosome numbers are lacking. Thin red lines to the right of trees indicate groups found in the unpublished ML analysis (Brouillet et al., pers. comm.). Black lines and subtribal names to the right of trees indicate subtribes according to Nesom and Robinson (2007). Circled numbers to the right refer to the groups discussed in text. For a complete biogeography tree of the entire Compositae see chapter 44.

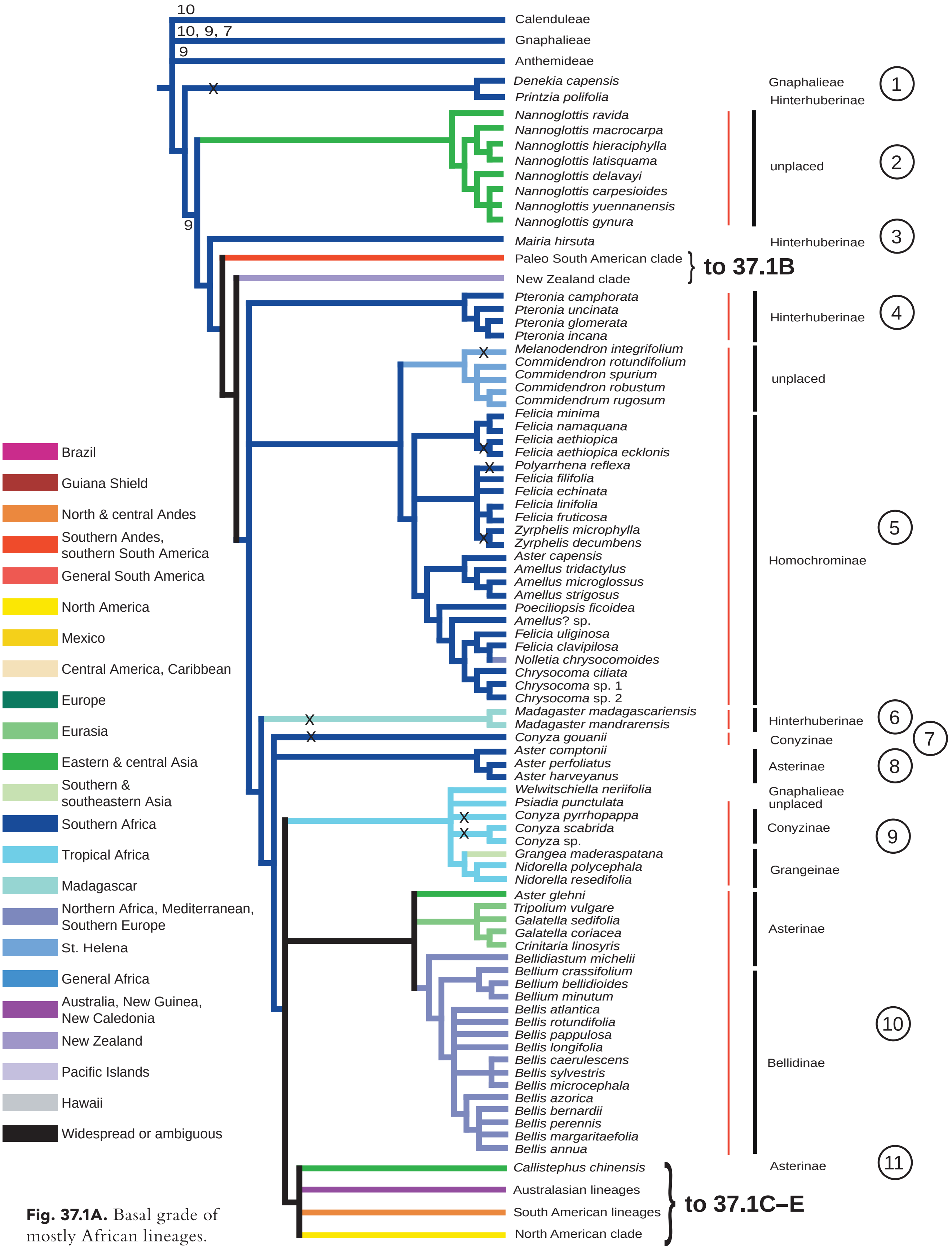


Fig. 37.1A. Basal grade of mostly African lineages.

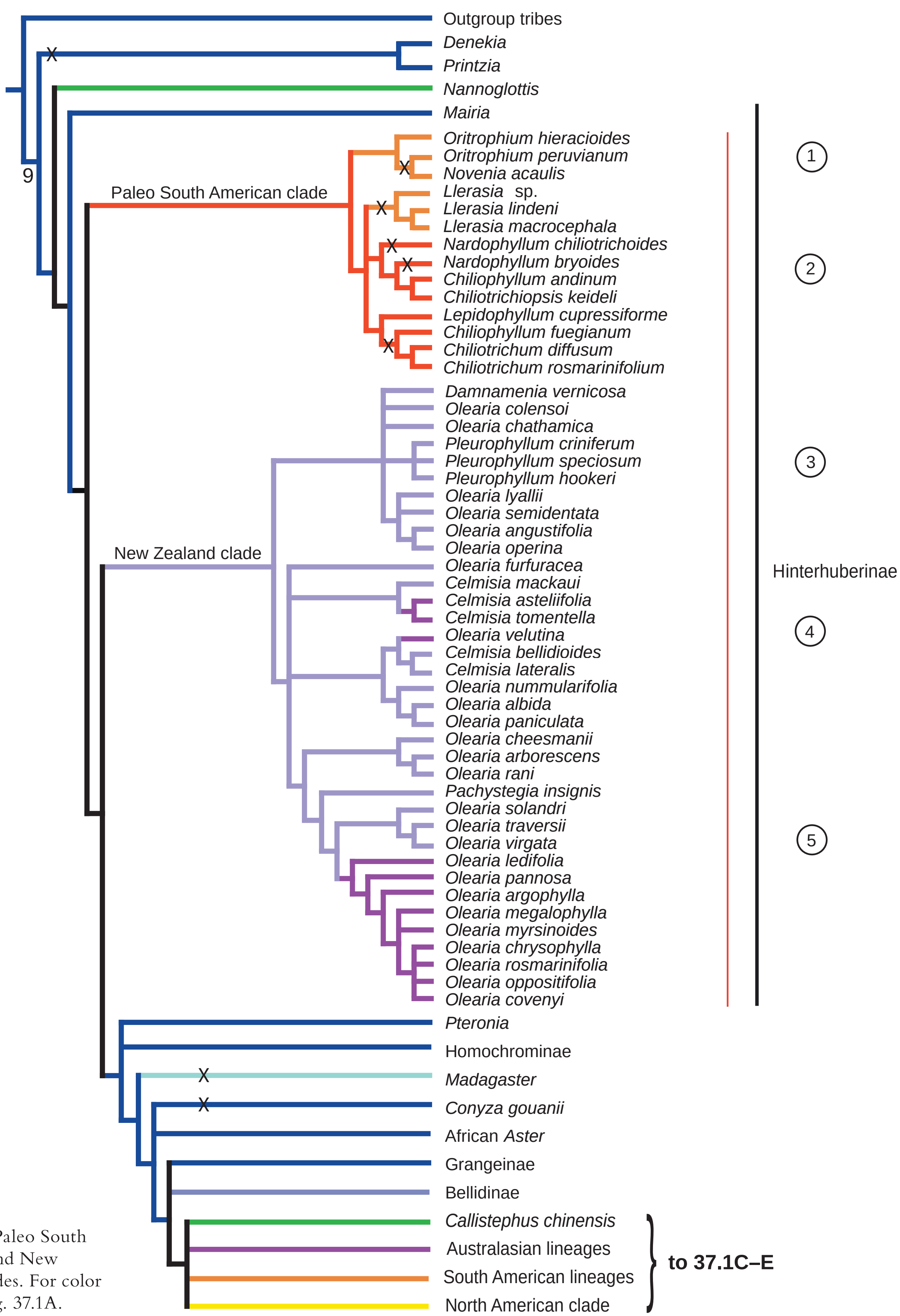


Fig. 37.1B. Paleo South American and New Zealand clades. For color chart see Fig. 37.1A.

finding because the genus has not been found in Central America. Such a disjunct distribution may be attributed to transport by birds, possibly from northern Venezuela (Cuatrecasas 1997). *Novenia*, a monotypic genus, is distributed at high elevations in the Andes from Bolivia to northern Peru and Argentina. *Novenia* is highly reduced, with rigid leaves with axillary clumps of tomentum, numerous sessile, disciform capitula in the center of the rosette, with reduced pistillate corollas and functionally staminate disk florets, and multinerved achenes with a multiseriate pappus of persistent barbellate bristles. These characters and the number of chromosomes typical of Astereae ($n = 9$) justified its transfer from Inuleae (Freire 1986; Anderberg 1991) to Hinterhuberinae (Nesom 1994g). The genus appears to be derived from within *Oritrophium*; more data are needed to evaluate the relationship of these two genera.

The *Chiliophyllum* clade (Fig. 37.1B②) includes resinous shrubby genera with usually white-tomentose leaves, radiate capitula, paleate receptacles, and bisexual disk florets (functionally staminate in *Lepidophyllum* Cass.): *Chiliotrichum* Cass. (Fig. 37.2D), *Chiliotrichiopsis* Cabrera, *Nardophyllum* Hook. & Arn., *Lepidophyllum* (Fig. 37.3C), and *Llerasia* Triana. These are mainly restricted to the arid puna region of southern Chile and Argentina (Patagonia and Tierra del Fuego). *Llerasia* is restricted to the uppermost montane forest of the Andes, below the páramo zone, in Peru, Ecuador, and Colombia. The group is characterized by a pappus of flattened bristles in one to several series. In *Nardophyllum*, pappus bristles vary from flattened to terete and widened apically, whereas pappus bristles in *Llerasia* are terete and scabrous. The presence of receptacular paleae is another defining feature for this group, but receptacles vary from epaleate in *Lepidophyllum* and three species of *Nardophyllum*, to few-paleate in *Chiliotrichum*, and *Llerasia*, to fully paleate in *Chiliotrichiopsis* and *Chiliophyllum* (Bonifacino and Sancho 2001). Variation in the number of receptacular paleae was recorded at the population level in *Nardophyllum* (Bonifacino 2005). *Lepidophyllum* is the only genus in the group with opposite leaves. *Chiliophyllum*, a genus of three species from Argentina and Chile, was traditionally distinguished from *Chiliotrichum* based on the color of ray florets, and from *Chiliotrichiopsis* based on the morphology of pappus bristles. In the present analysis, *Chiliophyllum* appeared polyphyletic. *Chiliophyllum fuegianum* O. Hoffm. in Dusén groups with *Chiliotrichum* and *Lepidophyllum*, and *Chiliophyllum andinum* Cabrera with *Nardophyllum* and *Chiliotrichiopsis*, suggesting that the defining characteristics of the genus are homoplasious (Karaman-Castro and Urbatsch, pers. comm.).

New Zealand clade

In this phylogeny (Fig. 37.1B), the New Zealand clade is located between the Paleo South American clade and a grade of African lineages (see above). A similar clade was retrieved by Wagstaff and Breitwieser (2002), who noted that Astereae are the most diverse tribe of Asteraceae in New Zealand, and by Cross et al. (2002) as their primary clade II (but including *Chiliotrichum*); it also coincides with the *Olearia/Celmisia* complex of Given and Gray (1986) and the *Celmisia* group of Nesom (1994g). The New Zealand clade is comprised of over 100 endemic species that traditionally have been placed in five genera: *Celmisia* Cass. (Figs. 37.2E, 37.3D, E), *Damnamenia* Given, *Olearia* Moench (Figs. 37.2F, 37.3F), *Pachystegia* Cheeseman (Figs. 37.2G, 37.3G), and *Pleurophyllum* Hook. f. (Fig. 37.3H) (Wagstaff and Breitwieser 2002). All have been classified within Hinterhuberinae by Nesom and Robinson (2007); this taxonomy is not supported here. *Olearia* and *Pachystegia* are woody shrubs, whereas *Celmisia*, *Damnamenia*, and *Pleurophyllum* are subshrubs or herbs that arise from a woody base. These five genera are characterized by tailed anthers, tomentose leaves, and usually large heads, features they share with the South American genus *Chiliotrichum* (Cross et al. 2002). Many of the species are showy ornamental shrubs that are widely cultivated in New Zealand. A chromosome number of $2n = 108$ is the most commonly reported for members of the New Zealand clade, but numbers as high as ca. 432 have been reported for *Olearia albida* Hook. f. (Dawson 2000). The New Zealand clade is not restricted to New Zealand since members of *Celmisia* and *Olearia* s.l. independently dispersed to Australasia. Within the New Zealand clade, two subclades can be recognized: the megaherb clade, including *Damnamenia*, *Pleurophyllum*, and the macrocephalous *Olearia* species (Drury 1968; Given 1973), and the *Celmisia* clade, including *Celmisia*, *Pachystegia*, and the remaining New Zealand *Olearia* species (including the divaricating tree daisies; Heads 1998). *Olearia* is clearly polyphyletic (Cross et al. 2002), hence well-supported clades in New Zealand will likely be recognized as distinct genera.

Members of the megaherb clade (Fig. 37.1B③), *Damnamenia*, *Pleurophyllum* (the megaherbs), and macrocephalous olearias (*Olearia* spp.), were considered related by Drury (1968) and Given (1973). All were included in the current analysis (Fig. 37.1B). In Given's taxonomic scheme, *Damnamenia* and *Pleurophyllum* are closely related to *Olearia colensoi* Hook. f. and *O. lyallii* Hook. f., while the other olearias of the group (*O. oporina* Hook. f., *O. chathamica* Kirk, *O. angustifolia* Hook. f., and *O. semidentata* Decne. ex Hook.) were related only through *Celmisia*; the Australian *Pappochroma palucidola* (S.J. Forbes) G.L. Nesom (as *Erigeron pappocroma* Labill.) (Nesom 1994f, h, 1998a) was also considered tentatively related to *Celmisia* but was not included in molecular analyses and therefore cannot be evaluated (but see *Pappochroma* Raf. in Australasian lineages below). These taxa are concentrated in the subantarctic islands of New Zealand and Australia, and in the highlands of New Zealand (Drury 1968; Given

1973 provides a map of the taxa). Our phylogeny does not support membership of *Celmisia* in this clade but all other taxa identified by Given belong here, as was also noted by Cross et al. (2002). Members of the clade are trees, shrubs or woody-based herbs, with abaxially tomentose leaves, racemose capitulescences or solitary capitula, large capitula with usually purple disc florets (yellow in *O. oporina*) and tailed anthers with prominent apical appendages, and long-villose achenes. *Damnamenia* is monotypic and based upon the distinctive subantarctic *D. vernicosa* (Hook. f.) (Given 1973). It was formerly considered as the sole member of *Celmisia* subgenus *Ionopsis*, but was recently recognized as a distinct genus. The distinctness of this taxon from *Celmisia* is confirmed here. *Pleurophyllum* includes three subantarctic island species, *P. speciosum* Hook. f., *P. criniferum* Hook. f., and *P. hookeri* Buchanan, which

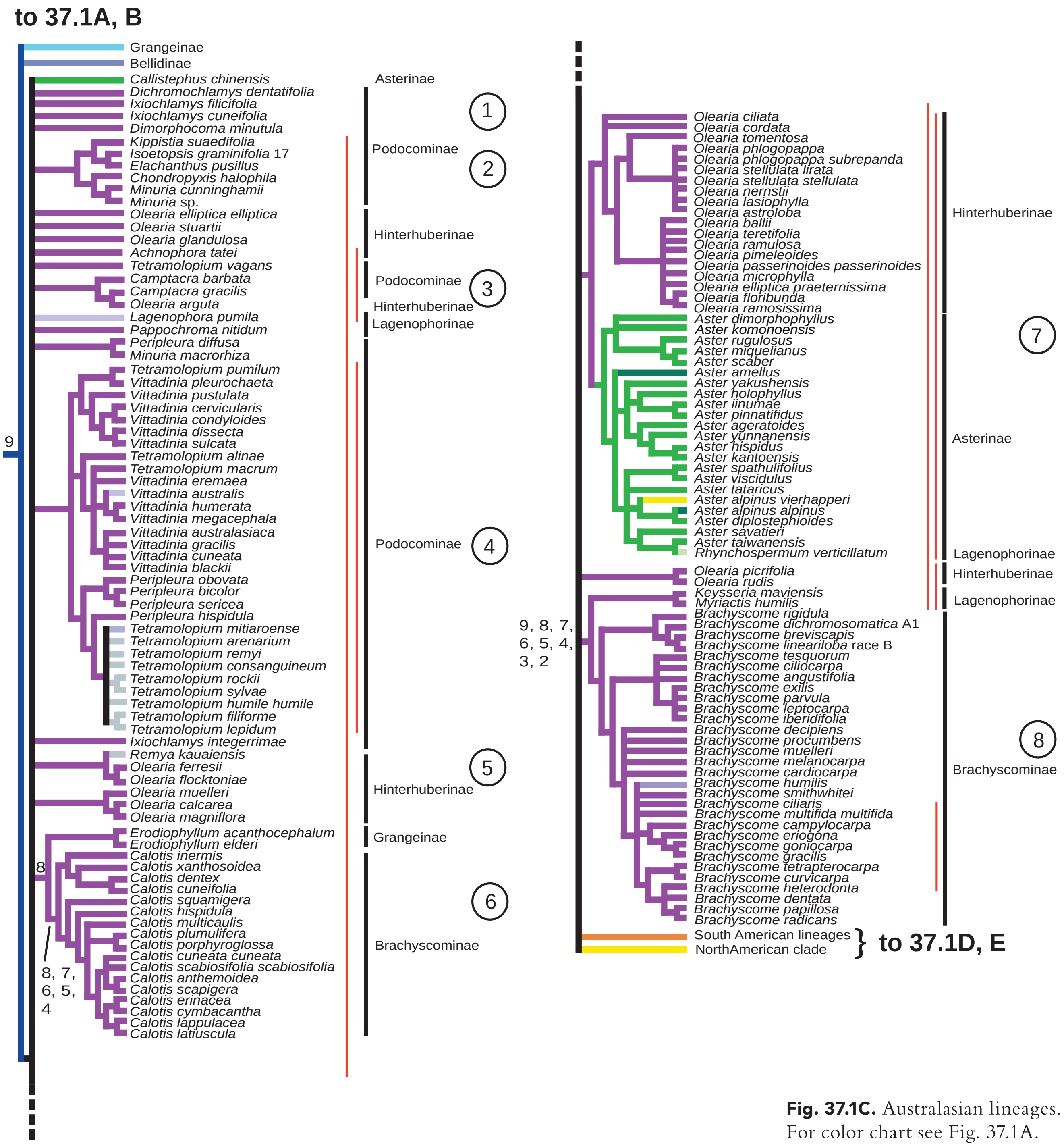


Fig. 37.1C. Australasian lineages. For color chart see Fig. 37.1A.

have purple or whitish-purple rays (Drury 1968). Drury (1968) noted the similarity of the macrocephalous olearias to *Pleurophyllum*, suggesting the inclusion of the former into the latter; Given (1973) proposed to include *O. colensoi* and *O. lyallii* in *Pleurophyllum* and to create a new genus for the others.

The genus *Celmisia* (Fig. 37.1B④) is not fully resolved in our analysis. This may be due to the fact that only about 20% of the taxa have been included so far (S. Wagstaff, pers. comm.). The clade shows a polytomy comprised of an apparently isolated *O. furfuracea* Hook. f., a large *Pachystegia* clade, and two *Celmisia* lineages, one of which is associated with the *Olearia albida* subclade (clade F of Cross et al. 2002) and the New Guinean *O. velutina* Koster (*O.* sp. WNG in Cross et al., 2002). The *Olearia* groups recognized here coincide with those of the Cross

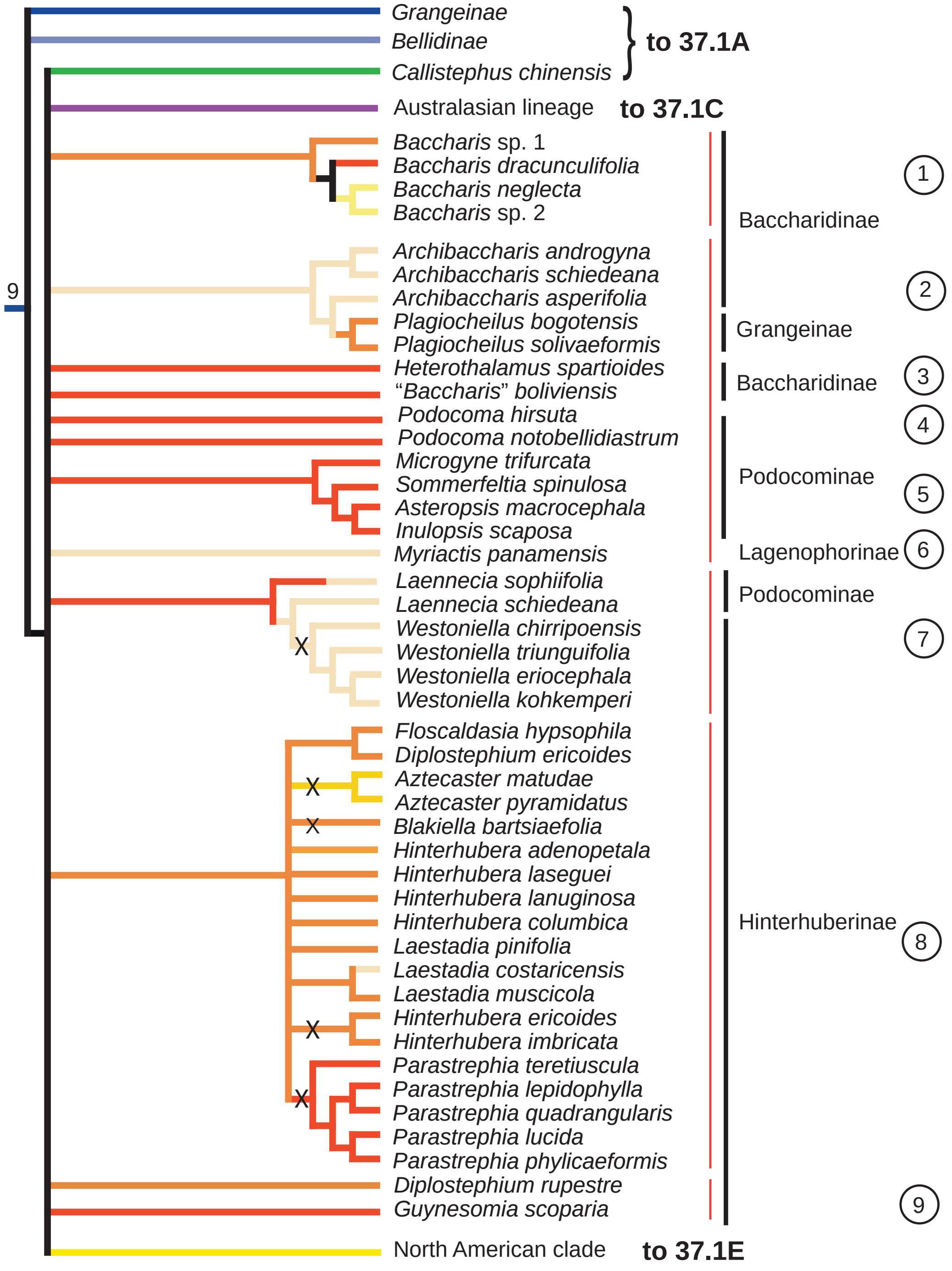


Fig. 37.1D. South American lineages. For color chart see Fig. 37.1A.

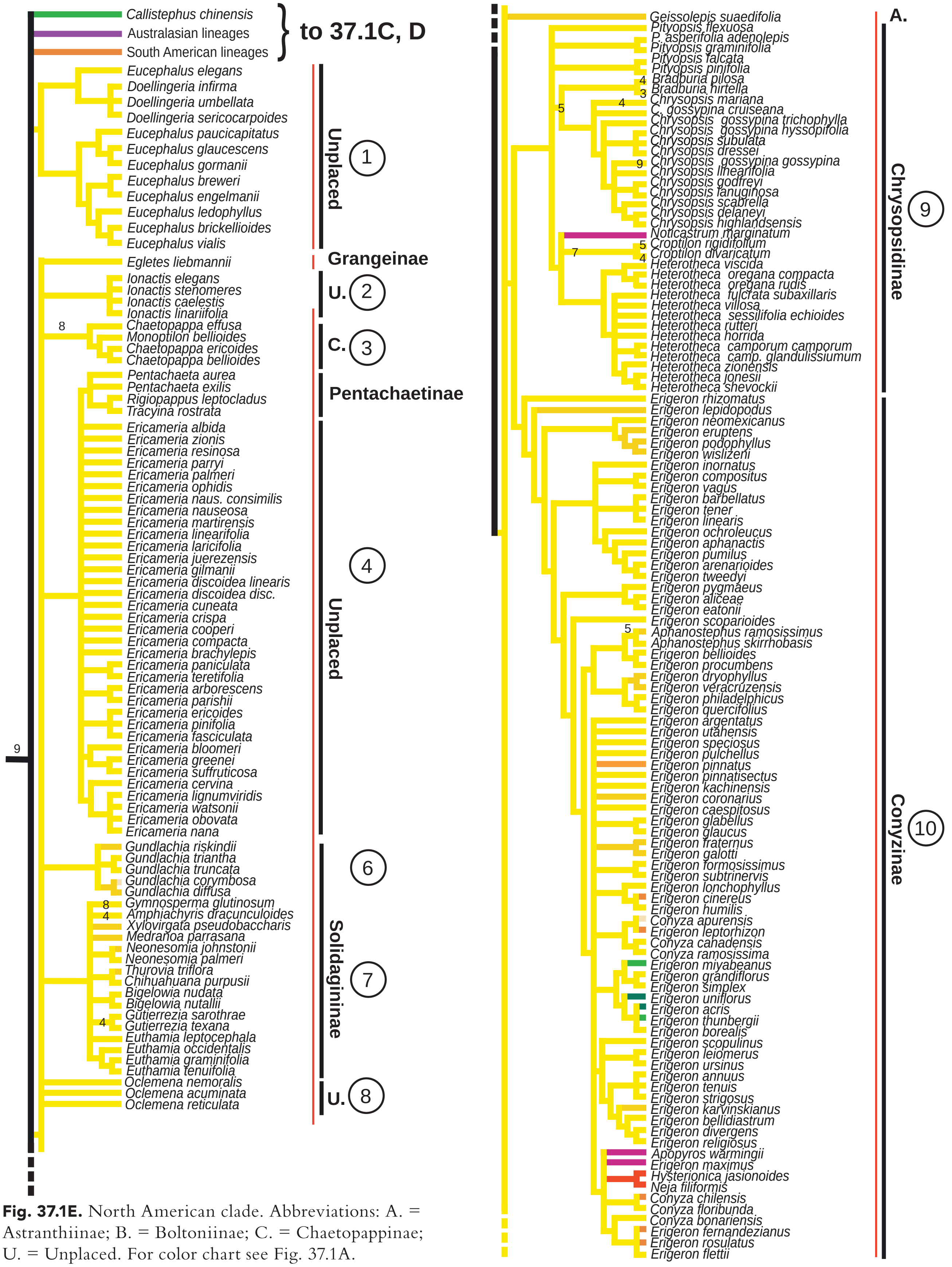


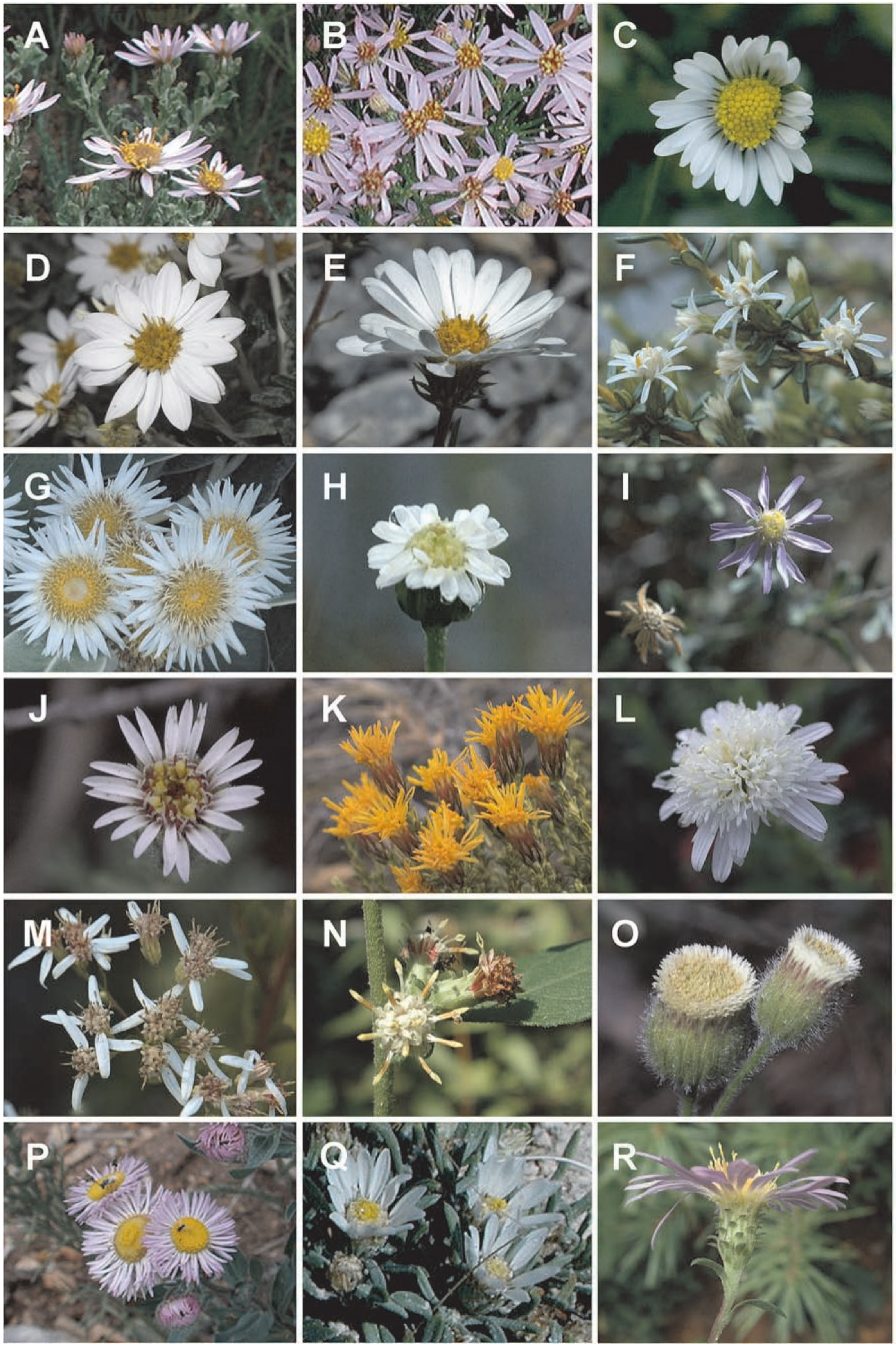
Fig. 37.1E. North American clade. Abbreviations: A. = Astranthiinae; B. = Boltoniinae; C. = Chaetopappinae; U. = Unplaced. For color chart see Fig. 37.1A.


Cuniculotinus gramineus
Sericocarpus asteroides
Sericocarpus tortifolius
Sericocarpus oregonensis
Sericocarpus linifolius
Stenotus pulvinatus
Stenotus lanuginosus
Columbiadoria hallii
Nestotus macleanii
Nestotus stenophyllus
Petradoria pumila
Toiyabea alpina
Chrysoma pauciflosculosa
Brintonia discoidea
Solidago patula
Solidago bicolor
Solidago nitida
Solidago rigida
Solidago shortii
Solidago sempervirens
Solidago petiolaris
Solidago fistulosa
Solidago canadensis
Oreochrysum parryi
Stenotus acaulis
Stenotus armerioides
Lorandersonia microcephala
Tonestus peirsonii
Lorandersonia pulchella
Lorandersonia spathulata
Lorandersonia baileyi
Lorandersonia salicina
Lorandersonia linifollia
Eastwoodia elegans
Tonestus eximius
Tonestus graniticus
Tonestus pygmaeus
Tonestus lyallii
Amphipappus fremontii spinos.
Acamptopap. sphaerocephala
Acamptopappus shockleyi
Hesperadoria scopulorum
Chrysothamnus stylosus
Chrysothamnus molestus
Chrysothamnus humilis
Chrysothamnus eremobius
Chrysothamnus visc. viscidiflorus
Chrysothamnus visc. axillaris
Chrysothamnus greenei
Chrysothamnus depressus
Chrysothamnus vaseyi
9, 5, 4, 3
Townsendia florifer
Astranthium integrifolium
Dichaetophora campestris
Batopilasia byei
Chloracantha spinosa
Boltonia asteroides
Boltonia diffusa
Canadanthus modestus
Ampelaster carolinianus
9
Almutaster pauciflorus
Psilactis brevilingulata
Symphyotrichum trilineatum
9, 4, 3
Psilactis odysseus
Psilactis asteroides
Psilactis boltoniae
Psilactis tenuis
7
Symphyotrichum chapmanii
8
Symphyotrichum urophyllum
8
Symphyotrichum texanum
8
Symphyotrichum drummondii
8
Symphyotrichum cordifolium
Symphyotrichum depauperatum
Symphyotrichum porteri
Symphyotrichum puniceum
8
Symphyotrichum parviceps
Symphyotrichum elliottii
Symphyotrichum dumosum
Symphyotrichum tradescantii
Symphyotrichum racemosum
Symphyotrichum attenuatum
Symphyotrichum foliaceum
8
Symphyotrichum subspicatum
Symphyotrichum turbinellum
Symphyotrichum boreale
5
Symphyotrichum tenuifolium
Symphyotrichum spathulatum
Symphyotrichum eulae
Symphyotrichum bracteolatum
8
Symphyotrichum hallii
Symphyotrichum eatonii
Symphyotrichum cusickii
7
Symphyotrichum frondosum
Symphyotrichum ciliatum
7
Symphyotrichum laurentianum
13
Symphyotrichum ascendens
Symphyotrichum pygmaeum
5
Symphyotrichum oblongifolium
5
Symphyotrichum novaeangliae
5
Symphyotrichum georgianum
Symphyotrichum sericeum
Symphyotrichum concolor
5
4
Symphyotrichum plumosum
Symphyotrichum ericoides
Symphyotrichum falcatum
Symphyotrichum vahlii
5
Symphyotrichum subulatum
Solidagininae
5
U.
Solidagininae
U.
Solidagininae
A.
11
B.
12
Symphyotrichinae
13
Oreostemma elatum
Oreostemma alpigenum andersonii
Oreostemma alpigenum haydenii
Herrickia horrida
Herrickia glauca glauca
Herrickia glauca pulchra
Herrickia wasatchensis
Herrickia kingii kingii
Herrickia kingii barnebyana
Eurybia paludosa
Eurybia radula
Eurybia gracilis
Eurybia avita
Eurybia furcata
Eurybia chlorolepis
Eurybia divaricata
Eurybia radulina
Eurybia sibirica
Eurybia eryngiifolia
Eurybia integrifolia
Triniteurybia aberrans
4
Machaeranthera tanacetifolia
Xylorhiza wrightii
Xylorhiza tortifolia
5
Oonopsis engelmannii
Oonopsis wardii
5
Arida parviflora
Arida turneri
Arida blepharophylla
5
Arida riparia
4
Dieteria bigelovii
Dieteria canescens
Xanthisma texanum drummondii
Xanthisma viscidum
4, 3, 2
Xanthisma gracile
4
Xanthisma spinulosum
6
Xanthisma stenolobum
Xanthisma blephariphyllum
Xanthisma gymnocephalum
Xanthisma coloradoense
Xanthisma crutchfieldii
Xanthisma rhizomatum
5
Haplopappus macrocephalus
5
Haplopappus foliosus
Haplopappus marginalis
5
Haplopappus glutinosus
Haplopappus paucidentatus
Xanthocephalum gymnospermoides
Isocoma wrightii
Isocoma acradenia
Isocoma tenuisecta
Isocoma rusbyi
Isocoma veneta
Isocoma menziesii vernonioides
Grindelia ciliata
Grindelia lanceolata
Grindelia nana
Rayjacksonia phyllocephala
Pyrrocoma clementis
Pyrrocoma lanceolata
Pyrrocoma crocea
4
Hazardia whytnei
Hazardia detonsa
6, 5, 4
Hazardia cana
Hazardia squarrosa grindelioides
Hazardia squarrosa
5
Benitoa occidentalis
Corethrogyne filaginifolia californica
Corethrogyne filaginifolia filaginifolia
Lessingia arachnoidea
Lessingia virgata
5
Lessingia ramulosa
Lessingia nemaclada
Lessingia nana
Lessingia micradenia micradenia
Lessingia micradenia glabrata
Lessingia leptoclada
Lessingia hololeuca
Lessingia glandulifera
Lessingia glandulifera peirsonii
Lessingia glandulifera glandulifera
Lessingia glandulifera tomentosa
Lessingia tenuis
Lessingia germanorum
Lessingia pectinata
Unplaced
14
Machaeranthinae
15

et al. primary clade II, except that the inclusion of more *Celmisia* species modified the relationships of group F and of *O. velutina*. The occurrence of natural intergeneric hybrids between *Celmisia* and *Olearia* species (e.g., Clarkson 1988) would lend support to a close relationship between the two taxa. *Celmisia* includes about sixty endemic New Zealand species and five Australian ones, grouped into six subgenera with eight sections (Given 1969) (the new subgenus *Ionopsis* subsequently described as *Damnamenia* by Given, 1973; see above). In our analysis, *Celmisia* is found in two clades: *(1) C. mackaui* Raoul–*C. asteliifolia* Hook. f.–*C. tomentella* M. Gray & Given, the latter two Australian, and *(2) C. bellidioides* Hook. f.–*C. lateralis* Buchanan. The first clade corresponds to the woody group of Allan (1961, as cited in Given 1969), characterized by biseriate corolla hairs widened at the tip, short pappus hairs, and few achene ribs; their living leaves are equally distributed on the stems. In Given's (1969) classification, *C. lateralis* belongs to subgenus, section, and series *Lignosae*, a group of woody, ericoid, erect subshrubs with globose receptacles, while *C. bellidioides* is a member of subg. *Caespitosae*, a group of softly woody, creeping herbs with short, oblong leaves and obconic receptacles. The relationships of this clade to various *Olearia* s.l. species needs to be explored further. The second clade corresponds to the herbaceous group of Allan, which coincides here with the subg. *Pelliculatae* of Given (1969) insofar as the species sampled are concerned. They are herbs arising from woody rootstocks with the densely compacted, pigmented leaf sheaths forming a pseudostem; the leaves are usually petiolate and firm, and are borne in rosettes at the ends of branches. *Celmisia mackaui* of New Zealand belongs to sect. *Petiolatae*, while the Australian *C. tomentella* and *C. asteliifolia* (the latter Tasmanian) are in sect. *Pelliculatae*, ser. *Linearifoliatae*, characterized by linear, rigid leaves. Gray and Given (1999a, b) report ten species of *Celmisia* in Australia, all derived from New Zealand taxa, including the two sampled species. Given our limited sample of *Celmisia* and *Olearia* species, it would be premature to conclude whether *Celmisia* is poly- or paraphyletic, however. The presence of large heads (the macrocephalous condition) in the megaherb and *Celmisia* clades suggests either that this trait was acquired in parallel in both lineages or that it is symplesiomorphic to the New Zealand clade. Cross et al. (2002) noted that either their clade F (*O. albida* subclade) or *O. furfuracea* were sister to *Celmisia*. Our analysis confirms a relation between the *O. albida* subclade and *Celmisia*, but is inconclusive concerning *O. furfuracea*. The position of *O. velutina* in our analysis as sister to *Celmisia bellioides*–*C. lateralis* contrasts with the sister relationship with the *O. cheesemanii* Cockayne & Allan clade (clade G) found by Cross et al. (2002) in a reduced analysis (it was part of the clade II polytomy in their total analysis, however). The *O. albida* subclade is characterized by stellate hairs (Cross et al. 2002), which contrasts with the usually tomentose hairs of *Celmisia*.

The *Pachystegia* clade (Fig. 37.1B⑤) includes the *Olearia cheesemanii* subclade (clade G of Cross et al. 2002), *Pachystegia*, and the *O. solandri* Hook. f. subclade (divaricating tree daisies; clade H) sister to the Australian *O. ledifolia* (DC.) Benth. subclade (clade E). It is the second most diverse group of New Zealand Astereae. Species of *Olearia* are generally recognized by their shrubby growth habit and usually dense indumentum on the lower leaf surface. However, there is remarkable diversity in phyllotaxis, leaf shape and margin, leaf hairs, position and arrangement of the inflorescences, and pappus bristles. Apart from *Pachystegia*, which has elongate intertwined hairs, all members of this clade appear to have t- or y-type hairs, suggesting the possibility of a single origin for these hair types (Cross et al. 2002). *Pachystegia* is a small genus including three species, only one of which was included here. The species taxonomy is not clearly resolved and further study may show that three variants are also worthy of species rank (Molloy and Simpson 1980). The species of *Pachystegia* are showy, medium-sized shrubs with distinctive thick, leathery leaves. They are confined to one of the driest regions in New Zealand, the northeastern part of South Island. Commonly known as Marlborough

Fig. 37.2. Structure and diversity of the capitulum in tribe Astereae. **A** *Printzia polifolia* (L.) Hutch., Western Cape, South Africa; **B** *Felicia filifolia* Burtt Davy, Western Cape, South Africa; **C** *Bellis perennis* L., lawn weed, Canterbury, New Zealand; **D** *Chiliotrichum diffusum* (G. Forst.) Kuntze, Bahía La Pataia, Tierra del Fuego, Argentina; **E** *Celmisia du-rietzii* Cockayne & Allan, Authors Pass National Park, New Zealand; **F** *Olearia solandri* Hook. f., cultivated Landcare Research experimental gardens, New Zealand; **G** *Pachystegia insignis* Cheeseman, cultivated Landcare Research experimental gardens, New Zealand; **H** *Lagenophora strangulata* Colenso, cultivated Landcare Research experimental gardens; **I** *Vittadinia gracilis* (J.D. Hook.) N.T. Burb., naturalized Godley's Head, New Zealand; **J** *Microgyne trifurcata* Less., Las Palmas, Córdoba, Argentina; **K** *Nardophyllum bryoides* (Lam.) Cabrera, Central Chubut, Argentina; **L** *Aster mongolicus* Franch., cultivated Ontario, Canada; **M** *Doellingeria sericocarpoides* Small, St. Tammany Parish, Louisiana, USA; **N** *Brintonia discoidea* (Elliott) Greene, Alabama, USA; **O** *Conyza monorchis* (Griseb.) Cabrerra, Sierra de las Animas, Maldonado, Uruguay; **P** *Erigeron subtrinervis* Rydb., Sandia Mountains, New Mexico, USA; **Q** *Townsendia gypsophila* T.K. Lowrey & P.J. Knight, White Mesa, New Mexico, USA; **R** *Eurybia spectabilis* (Ait.) G.L. Nesom, USA. [Photographs: A, B, P, Q, T.K. Lowrey; C, E–I, S. Wagstaff; D, J, K, O, J.M. Bonifacino; L, N, R, J.C. Semple; M, L. Urbatsch.]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rock daisies, they are widely cultivated. The New Zealand *Olearia solandri* subclade (sect. *Divaricaster*; Heads 1998) is supported by the opposite leaves synapomorphy (Cross et al. 2002). This group is sister to the Australian *O. ledifolia* subclade (clade E, traditionally classified in sect. *Dicerotriche*), as noted by Cross et al. (2002).

Astereae crown lineages. Australasian lineages

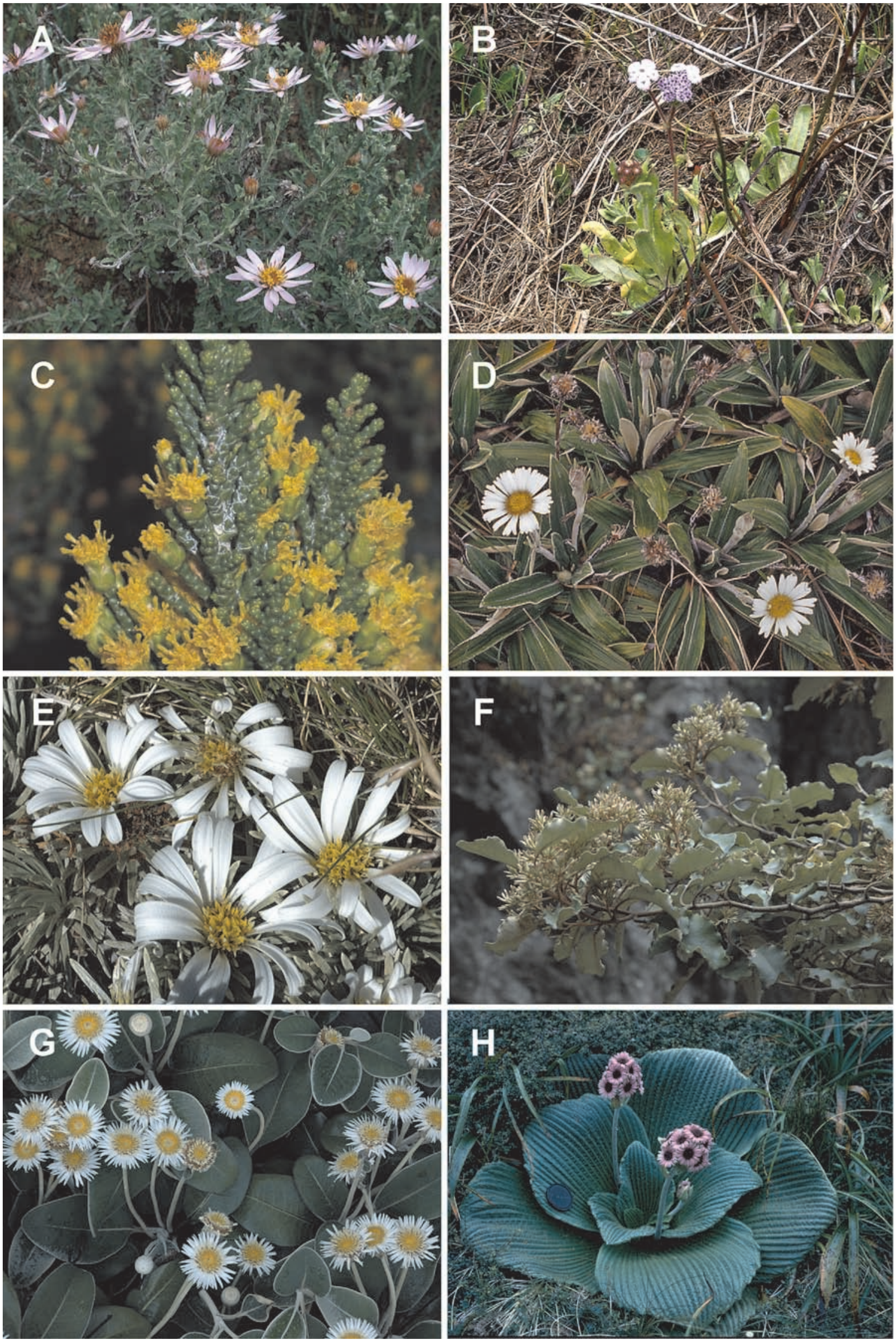
In the current analysis, Australasian lineages are part of the large polytomy at the crown of Astereae (Fig. 37.1A–C). The Australasian lineages (Fig. 37.1C) correspond with the primary clade I of Cross et al. (2002). In more restricted analyses (Brouillet et al., pers. comm.), however, the Australasian lineages sometimes form a clade that includes the mainly Asian genus *Aster* s.str. and always excludes members of the New Zealand clade discussed above. All members of *Olearia* that are not part of the latter are found here. No Australasian genus is found associated with South American members of Hinterhuberinae and Podocominae (see below; Fig. 37.1D), where they were placed by Nesom and Robinson (2007). This was also noted in analyses with a more limited taxon sampling (Cross et al. 2002; Brouillet et al., pers. comm.; Karaman-Castro and Urbatsch, pers. comm.). In the current analysis, the Australasian lineages are: *(1) Kippistia* F. Muell., *Isoetopsis* Turcz., *Elachanthus* F. Muell., *Chondropyxis* D.A. Cooke, *Pappochroma*, and *Minuria* DC. species; *(2) Olearia arguta* Benth.–*Camptacra* N.T. Burb.; *(3) Vittadinia* A. Rich.; *(4) Erodiophyllum* F. Muell.–*Calotis* R. Br.; *(5) Olearia* s.str.–*Aster* s.str.; *(6) Keysseria* Lauterbach–*Myriactis humilis* Merr.–*Brachyscome* Cass.; *(7) Remya* Hillebr.–*Olearia* species. There is also a series of ungrouped genera and species, which will be discussed where appropriate.

Two species sometimes classified in *Minuria* do not appear closely related to the genus in our analyses (Fig. 37.1C①). *Minuria macrorhiza* (DC.) N.S. Lander is sister to *Peripleura diffusa* (N.T. Burb.) G.L. Nesom, a species morphologically and molecularly distinct from other *Peripleura* (Lowrey et al. 2001). The suggestion that *Eurybiopsis* DC. should be reinstated to accommodate *M. macrorhiza* (Watanabe et al. 1996) may have merit; the status of *P. diffusa* should be considered simultaneously. *Minuria integerrima* (DC.) Benth. does not group consistently with other taxa, and particularly not with the species of *Ixiochlamys* or *Minuria* included in the analyses; the identity of the voucher may need validation. It is a polyploid apomict (Davis 1964), which partly may explain its inconsistent positioning. Brouillet et al. (pers. comm.) showed that *Ixiochlamys filicifolia* Dunlop and *I. cuneifolia* (R. Br.) F. Muell. & Sond. are paraphyletic to *Dichromochlamys*, a result not seen here. This raises the question of the distinction of *Dichromochlamys* from *Ixiochlamys*. No relationships could be identified for this clade within Australasian Astereae. *Pappochroma*, represented by *P. nitidum* (S.J. Forbes) G.L. Nesom (*Erigeron nitidus* S.J. Forbes) (Nesom 1994f–h, 1998a), has an unresolved position in the polytomy, but in more restricted analysis, it groups with the genera discussed here (Brouillet et al. pers. comm.). Nesom and Robinson (2007) classify the genus within subtribe Lagenophorinae. *Lagenophora pumila* Cheeseman also is found in this polytomy, but it groups with *Camptacra* (below) in restricted analyses, not with *Pappochroma*.

Kippistia, *Isoetopsis*, *Elachanthus*, *Chondropyxis*, *Pappochroma*, *Minuria* (Fig. 37.1C②). Some of these small Australian genera have been excluded at one time from tribe Astereae (e.g., Bremer 1994), but they are currently included by Nesom and Robinson (2007), a position that is confirmed by the analyses of Bayer and Cross (2002) and Brouillet et al. (pers. comm.), and in the current one (Fig. 37.1C). In both the latter, these genera form a small clade, with *Kippistia* sister to *Isoetopsis*-*Elachanthus* and *Minuria* to *Chondropyxis*. These data appear to confirm the segregation of *Kippistia* from *Minuria* (Lander and Barry 1980), though only two of the nine species of *Minuria* s.str. were sampled here. The current study confirms the close relationships of *Isoetopsis* and *Elachanthus* (e.g., Bruhl and Quinn 1990, 1991), though a relationship to *Kippistia* appears novel. These genera never group with South American taxa, as would be expected if they belonged to Podocominae as defined by Nesom and Robinson (2007).

Lowrey et al. (2001) and our analysis (Fig. 37.1C③) both show that *Camptacra* is paraphyletic to *Olearia arguta*. No relationship of this group suggests itself in the current analysis. Artificial intergeneric hybrids were obtained between *Camptacra* and both *Vittadinia* and Hawaiian *Tetramolopium* Nees (Lowrey et al. 2001), but *Camptacra* and *O. arguta* are isolated from these in the current study.

Fig. 37.3. Growth habit diversity among southern hemisphere members of tribe Astereae. **A** *Printzia polifolia* (L.) Hutch., perennial herb, Western Cape, South Africa; **B** *Denekia capensis* Thunb., perennial herb, Connemara Lake World's View, Nyanda, Zimbabwe; **C** *Lepidophyllum cupressiforme* (Lam.) Cass., Strait of Magellan, close to Primera Angostura, Chile; **D** *Celmisia spectabilis* Hook. f., perennial herb from stout rootstock, near Lake Lyndon, Porter's Pass, New Zealand; **E** *Celmisia sessiliflora* Hook. f., alpine cushion plant, Arthurs Pass National Park, New Zealand; **F** *Olearia paniculata* Druce, small tree, Marlborough, New Zealand; **G** *Pachystegia insignis* Cheeseman, woody subshrub, cultivated Landcare Research experimental gardens, New Zealand; **H** *Pleurophyllum speciosum* Hook. f., megaherb, Campbell Island, New Zealand. [Photographs: A, T.K. Lowrey; B, M. Hyde; C, J.M. Bonifacino; E–H, S. Wagstaff; D, C. Meurk.]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Note that *Achnophora* F. Muell. and *Olearia* are placed in Hinterhuberinae by Nesom and Robinson (2007), and *Camptacra* and *Tetramolopium* in Podocominae. Such positions are not supported here.

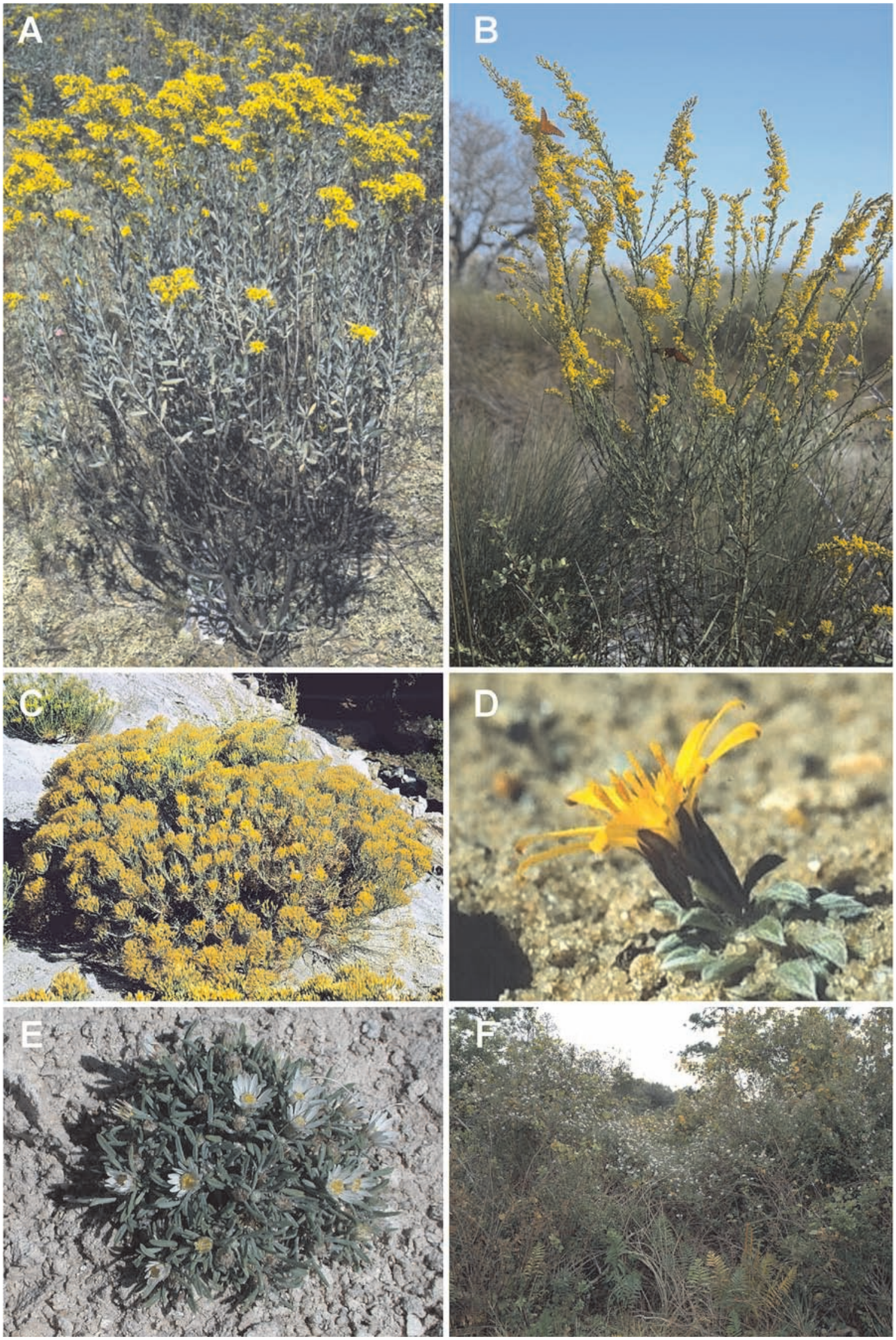
The molecular phylogeny of the *Vittadinia* lineage was discussed by Lowrey et al. (2001). In the current analysis (Fig. 37.1C④), this lineage does not appear to be closely related to a specific Australasian group. Despite small differences in the topologies shown here and in the Lowrey et al. study, the relationships among groups within the complex are congruent. Both studies show that *Tetramolopium*, *Vittadinia* (Fig. 37.2H), and *Peripleura* (N.T. Burb.) G.L. Nesom form a clade. The close relationship indicated by the molecular data is supported by morphology (Lowrey et al. 2001). Furthermore, intergeneric hybrids with varying levels of pollen fertility can be produced from among the three genera (Lowrey, Quinn, and Avritt, unpub.). The segregration of *Peripleura* from *Vittadinia* (Nesom 1994e) was rejected by Lowrey et al. (2001) and is not supported here. Highly fertile hybrids have been obtained between the Australian *Peripleura hispidula* (F. Muell. ex A. Gray) G.L. Nesom and several species of Hawaiian *Tetramolopium*. Lowrey et al. (2001) and the current study support the crossing data and indicate that *Peripleura* is sister to the Hawaiian *Tetramolopium*, contradicting the hypothesis that New Guinean *Tetramolopium* are sister to the Hawaiian taxa as suggested by Lowrey (1995) and Lowrey et al. (2005). Finally, morphology, molecular data, and crossing data strongly suggest that the three genera should be merged into a single genus. Nesom and Robinson (2007) placed *Vittadinia*, *Tetramolopium*, and *Peripleura* in subtribe Podocominae. Such a relationship is not supported here, since these genera never group with South American Podocominae.

Remya kauaiensis Hillebr. from Hawaii groups with *Olearia ferresii* (F. Muell.) Benth. and *O. flocktoniae* Maiden & Betche (Fig. 37.1C⑤). Relationships between *Remya* and these *Olearia* species need further study.

In the current analysis, as in Brouillet et al. (pers. comm.), *Erodiophyllum* appears to be sister to *Calotis* (Fig. 37.1C⑥). The molecular phylogeny of *Calotis* by Watanabe et al. (2006), was based on ITS and *matK* sequence data for 17 of the 28 species; *Erodiophyllum* was not included. The *Calotis* clade shown here expresses similar relationships to the ITS and combined trees of those authors, except that in our analysis, the *Calotis inermis* Maiden clade (their clade A) is sister to the *C. multicaulis* Druce–*C. cuneata* (Benth.) G.L.R. Davis clade (their clade B) plus *C. squamigera* C.T. White and *C. hispidula* F. Muell., both of which are unresolved in their analysis. Clade A, *C. squamigera*, *C. hispidula*, and clade B/E (except *C. anthemoides* F. Muell.) all have a base chromosome number of $x = 8$. This base number has also been reported for *Erodiophyllum* (Watanabe et al. 1996), which would tend to confirm both the symplesiomorphic status of $x = 8$ in *Calotis* and the relationship of the two genera, given that such a number would be synapomorphic in this part of the Astereae tree. Watanabe et al. (2006) noted the similar base number in the two genera and pointed out their uniqueness in Australia, without inferring a relationship between the two. Both genera are herbaceous, with convex (*Calotis*) or conic (*Erodiophyllum*) receptacles. Achenes are somewhat compressed in both and the pappus is absent; more or less developed pericarpic awns (outgrowths of the pericarp), characterize both genera. They inhabit arid areas of Australia. Collectively, these features appear to support a close relationship between the two. Relationships within *Calotis* are discussed in Watanabe et al. (2006). The placement by Nesom and Robinson (2007) of *Calotis* in Brachyscominae and of *Erodiophyllum* in Grangeinae is not supported here. In no analysis (e.g., Cross et al. 2002) does *Calotis* group with *Brachyscome*, which would be the case if both were members of Brachyscominae as hypothesized by Nesom and Robinson. Likewise, *Erodiophyllum* is the sole member of Grangeinae from Australia and seems geographically out of place in this African-south Asian group.

In analyses performed using a large number of species of *Olearia* and *Aster*, *Olearia* s.str. (including the type *O. tomentosa* (Wendl.) DC.) proves to be sister to the primarily Asian (secondarily European) genus *Aster* s.str. (including the type, the European *A. amellus* L.) (Brouillet et al. 2006a) (Fig. 37.1C⑦). Relationships between the mainly Australian *Olearia* s.str. and the Asian *Aster* s.str. (Fig. 37.2L) would indicate that *Aster* originated by dispersal from Australasia into eastern Asia. Fiz et al. (2002) suggested that *Rhynchospermum* was related to *Aster* and not to *Bellis*. Our analysis confirms their finding and places this genus as sister to *A. taiwanensis* Kitam., in a group with *A. savatieri* Makino. Asian segregate genera such as *Kalimeris* (Cass.) Cass. (Gu and Hoch 1997) (e.g.,

Fig. 37.4. Growth habit diversity among northern hemisphere members of tribe Astereae. **A** *Chrysoma pauciflosculosa* Greene, subshrub arising from woody base, Panhandle Florida, USA; **B** *Solidago sempervirens* L., perennial herb from woody rootstock, Santa Rosa Island, Florida, USA; **C** *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird, woody subshrub, San Gabriel Mountains, California, USA; **D** *Heterotheca jonesii* (S.F. Blake) S.L. Welsh & N.D. Atwood, perennial herb arising from woody taprooted rootstock, Hell's Backbone Ridge, Utah, USA; **E** *Townsendia gypsophila* T.K. Lowrey & P.J. Knight, cushion, White Mesa, New Mexico, USA; **F** *Ampelaster carolinianus* (Walter) G.L. Nesom, vine, central Florida, USA. [Photographs: A, C, D, F, J.C. Semple; B, L. Urbatsch; E, T.K. Lowrey.]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A. holophyllus Hemsl., *A. pinnatifidus* (Hook.) Kuntze, *A. miquelianus* Hara in the current analysis), *Heteropappus* Less. (e.g., *Aster hispidus* Thunb.), and *Miyamayomena* Kitam. (e.g., *A. savatieri*) are also embedded within *Aster*, which suggests that they are not phylogenetically distinct from it. Natural hybrids between *Aster ageratoides* Turcz. and *Kalimeris incisa* (Fisch.) DC. (*Aster incisus* Fisch.) (Tara 1989), for instance, and phylogenetic analyses of cpDNA RFLP data (Ito et al. 1994, 1995, 1998) support this. Indeed, Ito and Soejima (1995) included *Kalimeris* within *Aster*. Members of *Doellingeria* Nees sect. *Cordifolium* (Nesom 1993c) (e.g., *A. dimorphophyllus* Franch. & Savat., *A. komonoensis* Makino, *A. rugulosus* Maxim., *A. scaber* Thunb.), together with *A. miquelianus*, form a clade sister to the rest of *Aster* s.str. (Fig. 37.1C). The name *Doellingeria* (see Saito et al. 2007 for a recent usage) cannot be applied to Asian species since the type of the genus, *D. umbellata* (Mill.) Nees, belongs to the North American clade (Nesom 1993c); such a usage would make *Doellingeria* polyphyletic. These taxa might best be treated within *Aster*.

The *Keysseria*-*Myriactis humilis*-*Brachyscome* grouping (Fig. 37.1C⑧) has been noted first by Brouillet et al. (2006a; ML analysis, unpub.). *Keysseria* and *Myriactis* Less. were not included, however, in the Denda et al. (1999) and Field et al. (2006) phylogenetic studies of *Brachyscome*, respectively based on *matK* and ITS sequence data. All three genera are herbs (perennial, often annual in *Brachyscome*) with campanulate heads, herbaceous phyllaries in 1–2 series (rarely more), rays in one or more series, bisexual disk florets (functionally male in *K. radicans* (F. Muell.) Mattf.), achenes without pappus or with a pappus of united bristles, occasionally scale-like, and a base chromosome number of $x = 9$. These features, however, are not significant enough by themselves to confirm a relationship and the hypothesis must be investigated further, since it could be the result of insufficient taxon sampling among Australasian Astereae. *Keysseria* and *Myriactis* were placed in Lagenophorinae by Nesom and Robinson (2007). Only three genera of the subtribe are included here, *Rhynchospermum* Lindl., which is nested within *Aster* s.str. (which see), the Central American *Myriactis panamensis* (S.F. Blake) Cuatr., sometimes included in *Lagenophora* Cass., and *Lagenophora pumila*, a New Zealand species, two taxa that do not group here and in analyses (Cross et al. 2002; Karaman-Castro and Urbatsch, pers. comm.). These data imply that neither *Myriactis* nor *Lagenophora* (Fig. 37.2I) are monophyletic as currently defined. Neither *Lagenophora* species groups with *Keysseria* and *Myriactis* in any analysis, suggesting that their subtribal affinities lie elsewhere. In the absence of further representation of the subtribe it is difficult to assess its status. Relationships and evolution within *Brachyscome* recently were discussed by Denda et al. (1999) and Field et al. (2006). Short (2004) segregated *Allittia* P.S. Short, *Hullsia* P.S. Short, and *Pembertonia* P.S. Short from *Brachyscome*. *Allittia cardiocarpa* (F. Muell ex Benth.) P.S. Short (*Brachyscome cardiocarpa* F. Muell. ex Benth. here) was included in the Field et al. and the current analyses, and is appears nested within *Brachyscome* in both cases. On the basis of the sampling at hand, it would appear that *Allittia* is embedded within *Brachyscome*. Given that *Brachyscome* includes more than 110 species and that our sampling is incomplete, however, it may be premature to assess the taxonomy of the genus. It is noteworthy that long-distance dispersal occurred to New Zealand at least once, as exemplified by *B. humilis* G. Simpson & J.S. Thompson (Fig. 37.1C).

South American lineages

Parsimony (Brouillet et al. 2006a) and ML (unpub.) analyses of the ITS data (using a slightly smaller taxon set) revealed four main South American lineages: *(1) Baccharis* L. s.str. (Baccharidinae); *(2)* Podocominae plus diverse South American genera classified in Baccharidinae (excluding *Baccharis* s.str.), Lagenophorinae, and Grangeinae; *(3) Laennecia* and *Westoniella* Cuatr.; and *(4)* Hinterhuberinae genera. In the ML analysis (unpub.), these lineages form a grade to the North American clade (NAC); in the parsimony analysis (Brouillet et al. 2006a), a *Baccharis* lineage diverged prior to a Podocominae-Hinterhuberinae clade, itself sister to the NAC. In the current analysis (Fig. 37.1D), these lineages form a polytomy. In each analysis, the position of *Guynesomia* Bonif. & G. Sancho varied. Below, we discuss these lineages.

The circumscription of Baccharidinae by Nesom and Robinson (2007) includes *Archibaccharis* Heering, *Baccharis*, and *Heterothalamus* Less. In our analysis, all the species of *Baccharis* except for *B. boliviensis* (Wedd.) Cuatr. form a clade (Fig. 37.1D①). In the more restricted analyses mentioned above, these taxa all grouped with subtribe Podocominae (below), not with *Baccharis*. *Baccharis* is a large genus of about 360 species ranging from Argentina to the southern United States. The species are mostly dioecious, although monoecious or polygamo-dioecious species have been reported (Cuatrecasas 1967; Jackson 1975; Giuliano 2000; Müller 2006). The morphological variability in *Baccharis* led Hellwig (1992) to divide the genus into several segregates. In his recent monograph of Bolivian species, however, Müller (2006) maintained the wider delimitation, including *B. boliviensis*. Zanowiak (1991) conducted a cpDNA RFLP phylogenetic study of Baccharidinae, but sampling outside the subtribe was insufficient to evaluate its monophyly. Our current data, admittedly limited, do not support the monophyly of the subtribe nor of *Baccharis* s.l. They support the segregation of *Aztecaster* G.L. Nesom (Nesom 1993a) and of *Heterothalamus* from *Baccharis*, and do not support the position of Müller (2006) on this topic. A thorough phylogenetic study of *Baccharis* is needed.

As established on the basis of morphology (Nesom and Robinson 2007), Podocominae comprise South American and Australasian (above) genera. In all analyses, Australasian elements never grouped with South American ones. Therefore, Podocominae are restricted here to the South American elements that group with *Podocoma* Cass. The South American genera included by Nesom and Robinson in the subtribe are *Asteropsis* Less., *Inulopsis* O. Hoffm., *Laennecia* Cass., *Microgyne* Less. (Fig. 37.2J), *Podocoma*, and *Sommerfeltia* Less. In more restricted analysis (Brouillet et al. 2006a), the Podocominae clade comprised: *Myriactis* (*Lagenophora*) *panamensis* [Lagenophorinae] (*Podocoma hirsuta* Baker (*Baccharis boliviensis*, *Heterothalamus* [Baccharidinae]) [= the *Heterothalamus* subclade]) (*Podocoma notobellidiastrum* (Griseb.) G.L. Nesom) ((*Archibaccharis* [Baccharidinae]-*Plagiocheilus* Arn. ex DC. [Grangeinae] [= *Archibaccharis* subclade]) (*Asteropsis* clade)).

Archibaccharis (Fig. 37.1D②) is a mainly Mexican and Central American genus that probably ranges to Bolivia; it includes ca. 32 functionally dioecious species. Its resemblance to *Baccharis* was pointed out by several authors (e.g., Blake 1924; Jackson 1975; McVaugh 1984; Nesom 1994g, 2000a), but it differs by the presence of hermaphrodite florets in the center of the female capitula and by its compressed, 2-nerved achenes (vs. female capitula wholly of pistillate florets and terete, 5–10-nerved achenes in *Baccharis*). Relationships among *Baccharis*, *Archibaccharis*, and *Heterothalamus* have been recognized by authors (e.g., McVaugh 1984; Bremer 1994; Nesom 1994g) mainly based on sexuality and morphology of capitula. *Archibaccharis* and *Heterothalamus* have been seen as phylogenetically "basal" to *Baccharis* (Nesom 2000a) and functionally dioecious species of *Archibaccharis* as evolutionary stages to dioecy in *Baccharis* (Jackson 1975). In Karaman-Castro and Urbatsch (pers. comm.) as well as in our analysis (Fig. 37.1D), *Archibaccharis* is closely related to *Plagiocheilus* Arn. ex DC. (Grangeinae fide Nesom and Robinson 2007). *Plagiocheilus* includes seven species ranging from Colombia to Argentina (Ariza Espinar 1997). Some of the characteristics that have made *Plagiocheilus* difficult to place in the tribe are the deeply pinnatifid leaves, the hemispherical, heterogamous heads, the rays (outer florets) with bilabiate corollas, the functionally male disc florets with tubular corollas, and the epappose achenes. *Plagiocheilus* often has been treated in Anthemideae (e.g., Cabrera 1974; Ariza Espinar 1997), but our molecular analysis confirms its placement in Astereae, as suggested by previous authors (e.g., Robinson and Brettell 1973; Grau 1977; Bremer 1994).

Heterothalamus and *Baccharis boliviensis* form a subclade (Fig. 37.1D③). The Andean *B. boliviensis* departs from other *Baccharis* species by its female capitula with paleate receptacles and corollas with short laminae (vs. female capitula usually epaleate and female corollas apically denticulate or less commonly minutely limbed in *Baccharis*), although similar characters are sporadically present in some *Baccharis* species (Cabrera 1978; Giuliano 2000). It was originally described as a *Heterothalamus* species (Weddell 1856). Our analysis supports the distinctiveness of this species from *Baccharis*, as previously noted by other authors that treated it under *Heterothalamus* or *Psila* Phil. *Heterothalamus* is a genus of three species (Paz Deble et al. 2005) from Argentina, Brazil, and Uruguay, that are polygamo-dioecious or imperfectly dioecious glandular shrubs. The male capitula have epaleate receptacles and pistillate or neutral rays (pistillate florets), and the female have paleate receptacles and all pistillate, short-limbed rays. In the current analysis, *Heterothalamus* falls in a polytomy, while in some more restricted analyses, it groups with *B. boliviensis* and *Podocoma hirsuta*. In no instance is it related to Baccharidinae s.str.

Podocoma, with eight mainly Argentinian-Brazilian species (Nesom 1994c), has capitula with 2–3-seriate, narrow and short-limbed rays, and typical rostrate achenes. Our analysis (Fig. 37.1D④) shows a non-monophyletic *Podocoma*, in agreement with other molecular and morphological analyses (Sancho and Karaman-Castro 2008). In these, *Podocoma hirsuta* appears to be an early diverging member of the *Heterothalamus* subclade, and *P. notobellidiastrum* to both the *Archibaccharis* subclade and the *Asteropsis* clade. The genus deserves further study.

Only *Asteropsis*, *Inulopsis*, *Microgyne*, and *Sommerfeltia*, four genera with radiate and usually solitary capitula, appear to form a monophyletic group in both the current (Fig. 37.1D⑤) and the more restricted analyses. A close relationship among these genera is in agreement with other studies based on morphological and molecular data (Nesom 1994c, d; Sancho et al. 2006; Sancho and Karaman-Castro 2008).

Myriactis (*Lagenophora*) *panamensis* (Fig. 37.1D⑥) is a Central American member of Lagenophorinae sensu Nesom and Robinson (2007); the other Lagenophorinae in our analysis fall within the Australasian lineages (above). This species is a delicate rosulate herb with basal and cauline leaves, monocephalous, radiate capitula, and epappose, beaked achenes. Along with five other Central American species, it is representative of a genus otherwise known in Asia (Cuatrecasas 1982; Nesom 2000a, 2001; Pruski and Sancho, pers. comm.). Its placement within Podocominae, instead of with Australasian or African lineages, suggests that *Myriactis* as currently conceived is polyphyletic.

In the Brouillet et al. (2006a) parsimony analysis, *Laennecia*-*Westoniella* (Hinterhuberinae) were sister to Podocominae, a relationship not retrieved here (Fig. 37.1D⑦). *Laennecia* ranges from Argentina to the Dominican Republic and the southern United States (Nesom 1990; Sancho and Pruski 2004). It includes 17 species of commonly woolly or glandular herbs with usually paniculiform or spiciform capitulescences of small, mostly disciform capitula (Zardini 1981). In our analysis, *Laennecia* forms a monophyletic group with *Westoniella* (Fig. 37.1D), a genus of six species endemic to the páramos of Central America (Cuatrecasas 1977). They are reduced subshrubs, sometimes cushion-like, that inhabit rocky and humid habitats. *Westoniella* was included in the subtribe Hinterhuberinae (Cuatrecasas 1986; Nesom and Robinson 2007) based on morphological features. One of the unique features of the genus are the marginal, bulbous-tubular corollas that somewhat radiate from the capitula (Pruski and Sancho, pers. comm.). Although molecular data relate *Laennecia* and *Westoniella*, these genera differ greatly in habit, capitulescence, capitula, marginal florets, and pappus features.

As defined by Nesom and Robinson (2007), subtribe Hinterhuberinae includes 33 genera distributed in Australasia, Africa, Madagascar, and South and Central America, two genera reaching Mexico. Recent molecular analyses do not support the monophyly of the subtribe (Noyes and Rieseberg 1999; Cross et al. 2002; Brouillet et al. 2006a; unpub. ML analysis; Karaman-Castro and Urbatsch, pers. comm.). In the present analysis, South American genera previously classified in Hinterhuberinae belong mainly to two distinct lineages, the Paleo South American clade and a more restricted Hinterhuberinae (Fig. 37.1D⑧), in a polytomy with Podocominae, *Diplostephium rupestre* Wedd., and *Guynesomia*. In more restricted analyses, *Diplostephium rupestre* usually is sister to Hinterhuberinae, while the position of *Guynesomia* varies. Two subclades were recognized in restricted analyses (Brouillet et al. 2006a; unpub. ML analysis), (*Floscaldasia* Cuatrec.–*Diplostephium ericoides* (Lam.) Cabrera) (*Blakiella* Cuatrec.–*Aztecaster*), sister to *Parastrephia* Nutt. (*Hinterhubera* Sch.Bip.–*Laestadia* Kunth). In these analyses, Hinterhuberinae are sister either to Podocominae or to the North American clade. As restricted here, Hinterhuberinae have the following features: disciform or discoid capitula (radiate in *Diplostephium*), epaleate receptacles, zygomorphic to actinomorphic rays (pistillate florets) with more or less reduced laminae (in *Floscaldasia* and *Blakiella*, the laminae are well developed but the florets are minute and the capitula appear disciform), and functionally staminate disc florets (bisexual in *Guynesomia*). *Aztecaster* is the only dioecious genus within Hinterhuberinae. The subtribe includes genera of diverse habits: *Diplostephium* includes small trees and shrubs, *Floscaldasia* is a herbaceous perennial, *Laestadia* includes small subshrubs and herbaceous perennials, *Blakiella* is a subshrub, *Hinterhubera* are mainly low shrubs with more or less densely tomentose, revolute, ericoid leaves, *Parastrephia* and *Aztecaster* are tall shrubs with tomentose ericoid leaves.

Blakiella, a monotypic genus from the páramos of Colombia and Venezuela, has beaked achenes. Its recent transfer from Podocominae to Hinterhuberinae (Nesom and Robinson 2007) is supported by this analysis. Achenes in *Blakiella* are cylindrical with 3–5 nerves, unlike the compressed and usually 2-nerved achenes in Podocominae.

Aztecaster includes two similar but widely allopatric species endemic to Mexico. The dioecy in Baccharidinae and *Aztecaster* probably developed along different pathways (Nesom 1993a), which is also suggested by the current analysis (Fig. 37.1D).

Laestadia is distributed in Costa Rica, Hispaniola, Bolivia, Peru, Ecuador, Colombia, and Venezuela. The genus was considered among the most specialized members of Hinterhuberinae because of its herbaceous habit (Nesom 1994g, 2000a). Unusual features include beaked, epappose achenes, otherwise characteristic of Grangeinae, also found in Lagenophorinae. The multinerved, partially compressed achenes and disk florets with sterile ovaries nest *Laestadia* in Hinterhuberinae, while the similarity of achenes with those in Grangeinae and Lagenophorinae is a result of convergent evolution, as confirmed by the molecular analyses of Karaman-Castro and Urbatsch (pers. comm.) (Fig. 37.1D). In Brouillet et al. (2006a), *Laestadia* was intermixed with *Hinterhubera*, rendering both genera paraphyletic. In the analyses of the combined ITS and ETS datasets (Karaman-Castro and Urbatsch, pers. comm.), the two genera were monophyletic in a weakly supported clade with *Blakiella*. This deserves further investigation.

Diplostephium is a large genus of ca. 90 species, which is distributed in the páramos from Costa Rica to northern Chile. Because of its radiate capitula and partially paleate receptacles, it was thought to be related (Nesom 1994g) to genera here placed in the Paleo South American clade. The most interesting feature in the morphology of *Diplostephium* is the variation of style branch length in disk florets. Blake (1928) suggested that the evolution of the genus was directed towards development of two groups, one with subentire, slightly bifid styles and sterile disk florets, and the other with elongate styles and fertile disk florets. The two species included in the present analysis represent both types, *D. rupestre* has a merely bifid style, and *D. ericoides* has styles with elongate branches. The two taxa formed a weakly supported clade in previous analyses (Karaman-Castro and Urbatsch, pers. comm.), while our phylogeny suggests that the two groups are not immediately related and that the genus is polyphyletic.

Guynesomia (Fig. 37.1D⑨) is a monotypic genus endemic to Chile that was recently segregated from *Nardophyllum* (Fig. 37.2K), a genus of the Paleo South American clade (Fig. 37.1A), based on its disciform capitula and epaleate receptacles, versus the discoid capitula and paleate receptacles of *Nardophyllum* (Bonifacino and Sancho 2004). Its numerous capitula are arranged in paniculiform or racemiform capitulescences and have bisexual disc florets.

The placement of *Guynesomia* in the South American clade (Fig. 37.1D) strongly supports its distinctness from *Nardophyllum*, although a hypothesized close relationship of *Guynesomia* to the radiate *Diplostephium* (Bonifacino and Sancho 2004) was not confirmed in the present analysis. The relationship of *Guynesomia* to the remaining Hinterhuberinae remains unresolved (Karaman-Castro and Urbatsch, pers. comm.).

North American lineage

Relationships of the North American clade appear to be with South American Hinterhuberinae and Podocominae discussed above (Fig. 37.1D). It is yet unclear whether these clades form a grade to the North American clade or whether they form a monophyletic group sister to it.

Nesom (2000a) provided a generic conspectus and a literature review of tribe Astereae in North America, which integrated parts of the molecular phylogenetic data then published. This paper summarized his views on the subtribal classification of Astereae for the continent, a modification of Nesom (1994g) now superseded by Nesom and Robinson (2007). Most of the molecular phylogenetic analyses then published were based on RFLP of chloroplast DNA (Suh and Simpson 1990; Morgan and Simpson 1992; Morgan 1993, 1997; Lane et al. 1996; Zhang 1996; Semple et al. 1999), though some of these included ITS data as well (e.g., Morgan 1993, 1997). Semple et al. (1999, 2002) published floristic treatments for Ontario goldenrods and asters, respectively, that included phylogenetic discussions. More recently, a complete floristic treatment of North American genera north of the Mexican border was published that incorporated recent phylogenetic findings and pertinent literature (Flora of North America Editorial Committee 2006). Most of the North American genera are endemic to the continent or nearly so, and thus the North American clade has been the object of a thorough treatment at the generic and species level, except for taxa present only in Mexico and adjacent Central America, and those that migrated secondarily to Eurasia and Central and South America (species of *Erigeron* L., *Grindelia* Willd., *Gutierrezia* Lag., *Solidago* L., *Psilactis* A. Gray, and *Symphyotrichum* Nees, and South American endemic genera such as *Haplopappus* Cass. and *Noticastrum* DC.).

Noyes and Rieseberg (1999) first revealed the existence of a monophyletic North American clade, a group that had never been recognized before. Phylogenetic analyses of North American groups, based mostly on ITS data but some with cpDNA RFLPs or ETS data as well, have been published subsequently (Noyes 2000a; Markos and Baldwin 2001, 2002; Morgan 2003; Urbatsch et al. 2003; Roberts and Urbatsch 2003, 2004; Beck et al. 2004; Brouillet et al. 2001, 2004; Selliah and Brouillet 2008). These papers provide in-depth analyses and literature reviews of the studied groups. The following groups can be recognized within the North American clade.

Noyes and Rieseberg (1999) showed *Doellingeria* (Fig. 37.2M) as an early diverging taxon within the North American clade. Subsequent analyses by Brouillet et al. (2001; Semple et al. 2002) showed *Eucephalus* Nutt. and *Doellingeria* together as sister to the North American clade (Fig. 37.1E①). This complex appears to be of western North American origin, with a more recent invasion of temperate eastern North America by *Doellingeria*. *Doellingeria* as defined here excludes the Asian species (sect. *Cordifolium*) assigned to this genus by Nesom (1993b). The latter, originally treated as *Kalimeris* sect. *Cordifolium*, are part of *Aster* s.str. from Asia (above; Fig. 37.1C). Species of this clade are found in mesic to humid, temperate habitats.

The North American polytomy (Fig. 37.1E) includes clades that have been encountered in all recent phylogenetic studies, though few were strongly supported. In all studies, *Egletes* Cass. occupies an unresolved position in the North American polytomy. The clades are (subtribal names are those of Nesom and Robinson 2007): *(1)* Chaetopappinae, *(2) Euthamia* (Nutt.) Cass. clade, *(3) Ericameria* Nutt.–Pentachaetinae, *(4)* Solidagininae, *(5)* Chrysopsidinae–Conyzinae, *(6)* Astranthiinae, and *(7)* Boltoniinae–Symphyotrichinae–Machaerantherinae. The position of the aster genera *Ionactis* Greene (Fig. 37.1E②) and *Oclemena* Greene (Fig. 37.1E⑧) are ambiguous. Ecologically, both are temperate genera of mesic or humid habitats. *Ionactis* is western North American with a single eastern species (*I. linearifolia* (L.) Greene), while *Oclemena* is eastern North American.

Chaetopappinae are of uncertain position in the phylogeny (Fig. 37.1E③), but may be the earliest diverging group to a large clade including Pentachaetinae-*Ericameria*, Solidagininae, the *Euthamia* clade, and the Chrysopsidinae-Conyzinae (Brouillet et al. pers. comm.). Nesom (2000b) discussed this subtribe.

Pentachaetinae, comprising *Pentachaeta* Nutt., *Tracyina* S.F. Blake, and *Rigiopappus* A. Gray, are sister to *Ericameria* (Fig. 37.1E④). Pentachaetinae were discussed in Nesom (2000b) and Roberts and Urbatsch (2003). In the analyses of Roberts and Urbatsch (2003, 2004), *Ericameria* (Fig. 37.4C) is monophyletic and does not fall within Solidagininae. *Chrysothamnus* was shown to be polyphyletic in that it contained taxa now representative of basal Solidagininae (*Cuniculotinus* Urbatsch, R.P. Roberts & Neubig species) and more derived entities in this lineage, *Chrysothamnus* Nutt. s.str. and *Lorandersonia* Urbatsch, R.P. Roberts & Neubig, as well as four species now regarded as *Ericameria* (Urbatsch and Roberts 2004). As traditionally conceived, *Ericameria* had been considered a taxon of Mediterranean climate and desert and higher-elevation habitats, mainly of California. With the accretion of species from *Chrysothamnus* and *Macronema* Nutt., the *Ericameria* radiation now also includes Rocky Mountain habitats and the Great Basin, where certain species are among the dominant taxa of this arid shrubland. Nesom (1994g) regarded *Ericameria* as an ancient disjunct of the primarily South American subtribe Hinterhuberinae, but subsequently he and Robinson (Nesom 2000b; Nesom and Robinson 2007) gave it unplaced status. Its affinity to Solidagininae or the *Euthamia* clade is at most weakly supported. In some analyses, this clade appears sister to Solidagininae, but there is no support yet for such a relationship.

Solidagininae (Fig. 37.1E⑤) exclude the *Euthamia-Gundlachia* A. Gray lineage (below), in contrast to Nesom and Robinson (2007). Thus restricted, Solidagininae (Fig. 37.2N, 37.4A) are one of the largest groups of North American Astereae. The subtribe was investigated by Roberts and Urbatsch (2003) and Beck et al. (2004). *Cuniculotinus* and the white-rayed *Sericocarpus* Nees are basal to an essentially yellow-rayed group of genera found both in mesic and xeric habitats. *Cuniculotinus* is found at high elevations of the Sierra Nevada and adjacent ranges, and *Sericocarpus* in mesic to dry woods of western (two species) and eastern (four species) North America. Most genera of the subtribe appear to inhabit humid or mesic, though sometimes seasonally dry, habitats. *Solidago* (Fig. 37.4B), with some 100 species (77 in North America), radiated mostly in eastern North America, with a secondary radiation in mesic to dry habitats of the prairies and the West. It secondarily spread to Eurasia and South America. *Chrysothamnus* represents a major radiation in xeric habitats in western North America, apparently from mesic ancestors. The polyphyletic nature of *Tonestus* A. Nelson and *Stenotus* Nutt. are evident in the studies cited above and here (Fig. 37.1E).

Gundlachia was sister to the *Euthamia* clade (Fig. 37.1E⑥) in earlier analyses (Urbatsch et al. 2003; Beck et al. 2004) and is discussed here. Urbatsch et al. (2003) commented on the affinities of genera within the *Euthamia* clade. Within this clade, relationships are unresolved. Subsequent to the investigations by Urbatsch et al. (2003), *Xylothamia* was dissolved with the transfer of four of its nine species to *Gundlachia* (Urbatsch and Roberts 2004). The other five species were placed in the new genera *Neonesomia* Urbatsch & R.P. Roberts, *Chihuahuana* Urbatsch & R.P. Roberts, *Xylovirgata* Urbatsch & R.P. Roberts, and *Medranoa* Urbatsch & R.P. Roberts. These four genera are placed in the *Euthamia* clade rather than close to *Gundlachia*, which support their removal from this genus. In the present analysis the *Euthamia* clade and *Gundlachia* have little affinity to Solidagininae (Fig. 37.1E⑦).

In all analyses so far, *Geissolepis* Robinson is the earliest branching lineage within the clade or is sister to Conyzinae, but is never found within Astranthiinae where Nesom & Robinson (2007) placed it. Chrysopsidinae and Conyzinae are sister to each other (Fig. 37.1E). The genera included here within Chrysopsidinae (Fig. 37.1E⑨) are those grouped within the subtribe (Semple 2006): *Pityopsis* Nutt., *Bradburia* Torr. & A. Gray, *Chrysopsis* (Nutt.) Elliott, *Noticastrum* DC., *Croptilon* Raf., and *Heterotheca* Cass. (Fig. 37.4D). *Noticastrum* is South American and represents a disjunction between North and South America. Conyzinae (Fig. 37.1E⑩) include the single genus *Erigeron* (Fig. 37.2P), from which authors have segregated *Aphanostephus* DC. (the sole member of the subtribe with a reduced chromosome number of $x = 5$), *Conyza* s.str. (a polyphyletic entity in all analyses, even when excluding African species) (Fig. 37.2O), *Apopyros* G.L. Nesom, *Neja* D. Don, and *Hysterionica* Willd. (see Noyes 2000a). These segregations are not supported by molecular data since they render *Erigeron* paraphyletic (Fig. 37.1E). Early branching lineages within *Erigeron* all are North American, and Eurasian and South American lineages represent secondary dispersals. Dispersal to both continents may have occurred repeatedly in various lineages, but some South American sections of *Erigeron* and the South American segregate genera are closely related (Noyes 2000a).

Astranthiinae include *Townsendia* Hook. (Fig. 37.2Q, 37.4E), sister to *Astranthium* Nutt. and *Dichaetophora* A. Gray, but exclude *Geissolepis* (Fig. 37.1E⑪).

The Boltoniinae-Symphyotrichinae-Machaerantherinae group (Fig. 37.1E) includes the eurybioid asters (*Oreostemma* Greene, *Herrickia* Wooton & Standl., *Eurybia* (Cass.) Cass., and *Triniteurybia* Brouillet & al.), unplaced in the Nesom and Robinson (2007) classification. Boltonieae (Fig. 37.1E⑫) are sister to Symphyotrichinae and eurybioids plus Machaerantherinae. This small clade comprises *Chloracantha* G.L.Nesom & al., *Batopilasia* G.L. Nesom & R.D. Noyes, and *Boltonia* L'Hér., which confirms the findings based on cpDNA RFLP (see Nesom et al. 1991) and of Noyes and Rieseberg (1999). Relationships within Boltoniinae were discussed by Nesom and Noyes (2000). These taxa mostly inhabit wetlands, sometimes temporary ones in desert areas, of south-central North America.

Symphyotrichinae comprise, in phylogenetic order (Fig. 37.1E⑬), *Canadanthus* G.L. Nesom, *Ampelaster* G.L. Nesom (Fig. 37.4F), *Almutaster* Á. Löve & D. Löve, *Psilactis*, and *Symphyotrichum*. The first three genera all have a chromosomal base number of $x = 9$, while the latter two are cytologically variable (respectively, $x = 9$, 4, 3, and $x = 8$, 7, 5, 4). This clade had been identified in the cpDNA study of Xhang and Semple (1996). Brouillet et al. (2001) and Semple et al. (2002) have shown that *S. chapmanii* (Torr. & A. Gray) Semple & Brouillet is part of *Symphyotrichum* and not of *Eurybia* (versus Nesom 1994i), in keeping with its unusual base number ($x = 7$) and morphology. *Symphyotrichum* is the largest North American aster genus (some 90 species, 77 of which occur north of

Mexico) and one of the three largest Astereae genera on the continent. Species of *Symphyotrichum* have migrated to Eurasia (*S. ciliatum* (Ledeb.) G.L. Nesom) and to southern South America (e.g., *S. vahlii* (Gaudich.) G.L. Nesom), and have become introduced in Eurasia and other continents. Relationships within the genus are unresolved (Brouillet et al. 2001; Semple et al. 2002), in part due to its complex reticulate evolution and to frequent interspecific hybridization.

The eurybioid genera *Oreostemma*, *Herrickia*, *Eurybia* (Fig. 37.2R), and *Triniteurybia* form a grade to subtribe Machaerantherinae (Fig. 37.1E⑭). The rayless, monospecific *Triniteurybia*, until recently placed in *Tonestus*, has been shown to be sister to Machaerantherinae (Brouillet et al. 2004) (Fig. 37.1E⑮). This mesic to semi-xeric, high-elevation, rhizomatous genus with the basal number of $x = 9$, thus appears sister to a major radiation into xeric habitat by the speciose, sometimes taprooted and annual Machaerantherinae with $x = 6, 5, 4$. Relationships among the eurybioid genera are discussed in Selliah and Brouillet (2008). Subtribe Machaerantherinae has been studied recently in a molecular phylogenetic context by Lane et al. (1996), Morgan (1993, 1997, 2003); Morgan and Simpson (1992), and Markos and Baldwin (2001, 2002).

CLASSIFICATION

Generic level

Recent morphological and molecular phylogenetic studies have resolved many issues relating to generic delimitation in Astereae (e.g., *Aster* s.l., Nesom 1994g; *Chrysothamnus*, Roberts and Urbatsch 2004). Nonetheless, it is obvious from the synthesis presented here that many genera are still in need of revision. This is particularly true of *Myriactis* and *Lagenophora* (Fig. 37.2I), which display wide intercontinental disjunctions; taxonomic discussions often raise the difficulty of dealing with such genera with morphology alone, e.g., Nesom's (2000a) discussion of *Myriactis*. Likewise, *Olearia* needs a thorough re-evaluation, since it is clear that the genus artificially groups elements from two widely divergent lineages, the New Zealand clade and the Australasian group, as has been emphasized by Cross et al. (2002), as well as a number of smaller splinter entities. Phylogenetic studies encompassing a wider range of genera are the only solution to this type of problem. A narrow focus on single genera and on few representative species in Astereae can only prove counter-productive. Another example is *Baccharis*, recently revised by Müller (2006) for Bolivia based on morphology; our molecular data show that taxa such as *Heterothalamus* and *Baccharis boliviensis* cannot be included within *Baccharis*. A last example is *Erigeron* and the splinter genera recognized by Nesom and Robinson (2007), notably *Conyza*, *Neja*, *Hysterionica*, and *Aphanostephus*. All these are deeply embedded within *Erigeron* (Noyes 2000a) and furthermore, *Conyza* is shown to be polyphyletic even as more narrowly circumscribed (i.e., excluding African taxa). Recognition of these genera is mostly based on the perception of greater evolution within these lineages, leading to the acceptance of paraphyletic genera. Other taxonomists may wish to recognize a single monophyletic *Erigeron*. This philosophical difference is but one of the problems that confront systematists in Astereae. Other problems are related to character homology and evolution, and their interpretation by taxonomists. Classically, genera in Astereae were defined on the basis of overall similarity: few if any attempts were made to distinguish homoplasious from homologous characters or symplesiomorphies from synapomorphies. Another difficulty has been the relative paucity of characters that could be used in morphological taxonomic or phylogenetic analyses. Molecular phylogenetic approaches will help resolve such outstanding issues.

Subtribal level

Nesom and Robinson (2007) produced the latest classification of tribe Astereae. We are assessing this classification in terms of the phylogeny presented here (Fig. 37.1), because the subtribes often proved to be polyphyletic and thus the information is scattered in the phylogenetic discussion above. The order of discussion is that of the subtribes in the Nesom and Robinson classification.

Homochrominae. — This southern African subtribe appears monophyletic. It should comprise the unplaced St. Helena woody genera *Commidendron* and *Melanodendron*.

Hinterhuberinae. — This southern hemisphere subtribe is polyphyletic (Fig. 37.1A–D). The elements that belong with the type *Hinterhubera*, are members of one of the derived South American lineages, and they are closely related to or intermixed with some elements of Podocominae and Baccharidinae. As currently defined, the subtribe also includes members of the Paleo South American (*Chiliophyllum* and relatives) and New Zealand (*Celmisia*, parts of *Olearia*, etc.) clades, as well as members of the Australasian lineage (*Olearia* in part). Isolated African elements (*Mairia*, *Madagaster*, etc.) also are included, and notably *Printzia*, which is diverging early in our phylogeny.

Brachyscominae. — Even as narrowly defined as was done by Nesom and Robinson (2007), two of the three genera of this subtribe (*Ceratogyne* Turcz. has yet to be studied) do not form a clade in analyses of Australasian taxa. *Calotis* occurs in a position distinct from *Brachyscome* (Fig. 37.1C). The value of erecting a subtribe for the sole genus *Brachyscome* will depend on its position on the tree, which cannot be ascertained at the present time due to the large polytomy among Australasian lineages.

Bellidinae. — This subtribe is monophyletic but too narrowly defined. Elements classified in Asterinae are closer to *Bellis* (Fig. 37.2C) and *Bellium* than to *Aster* (Fig. 37.2L) (Fig. 37.1A). To be monophyletic, it should be enlarged to include *Bellidiastrum* and the *Galatella* group.

Grangeinae. — This subtribe of mainly African and south Asian elements (Fig. 37.1A) is polyphyletic when American (*Egletes*, *Plagiocheilus*; Fig. 37.1E) and Australasian (*Erodiophyllum*; Fig. 37.1C) taxa are included, as was done by Nesom and Robinson. It may prove monophyletic once these elements are removed, but the position of many south Asian taxa is still unknown. It is noteworthy that *Welwitschiella*, long considered in Heliantheae, is added to this subtribe. Likewise, African members of *Conyza* belong here, except for *C. gouani*. The unplaced *Psiadia*, and possibly unstudied genera related to it, belong here too.

Lagenophorinae. — This subtribe mostly includes parts of the Australasian lineages (Fig. 37.1C). It also comprises genera with trans-Pacific distributions, shown here to be polyphyletic, such as *Myriactis* and *Lagenophora*. *Rhynchospermum* is embedded within *Aster* (Fig. 37.1C). Many elements remain to be investigated.

Baccharidinae. — This subtribe has been characterized by unisexuality. Our phylogeny, however, indicates that this feature has originated more than once among South American lineages, independently in *Baccharis*, *Archibaccharis*, and *Heterothalamus* (Fig. 37.1D). Baccharidinae should be restricted to *Baccharis* sensu stricto.

Podocominae. — As circumscribed by Nesom and Robinson, this subtribe includes genera from South America and Australasia. In molecular phylogenies, they are mixed with members of other subtribes (Fig. 37.1C, D). Australian elements show no relationship to South American ones. The subtribe as defined is polyphyletic and should be restricted to genera clustering with *Podocoma* in phylogenies (Fig. 37.1D).

Asterinae. — This subtribe is polyphyletic, comprising isolated Asian elements such as *Callistephus* (Fig. 37.1A), the *Galatella* group and *Bellidiastrum* that clearly are related to Bellidinae (Fig. 37.1A), and a series of *Aster* segregates whose status still needs to be assessed, but most of which probably will not prove to be distinct from the primarily Asian *Aster* s.str. African *Aster* species (Fig. 37.1A), left within *Aster* by Nesom (1994i), represent a distinct, isolated lineage among the basal African diversification and should be removed from *Aster.* The relationship of *Aster* to Australasian *Olearia* s.str. (Fig. 37.1C) hints that Asterinae may have to be expanded to include elements that had not previously been considered.

Solidagininae. — With the help of molecular phylogenetic data, this subtribe was recently redefined to include only North American members (Beck et al. 2004). Nonetheless, the inclusion of the *Euthamia* lineage may make it polyphyletic since it does not form a clade with Solidagininae s.str. (Fig. 37.1E).

Pentachaetinae. — This subtribe of three genera forms a clade with the large *Ericameria*, which is unplaced in the Nesom and Robinson classification (Fig. 37.1E).

Boltoniinae. — This group of three genera is monophyletic and sister to Symphyotrichinae-Machaerantherinae (Fig. 37.1E).

Machaerantherinae. — This is a well-delimited, monophyletic group of North American taxa with $x = 6$. It has a close relationship to the $x = 9$ eurybioid grade (Fig. 37.1E) (*Oreostemma*, *Herrickia*, *Eurybia*, *Triniteurybia*, all unplaced in the classification of Nesom and Robinson); these might best be included there.

Symphyotrichinae. — This is a well-defined clade comprising most of the North American asters. It is sister to eurybioids-Machaerantherinae.

Chaetopappinae. — This group of two genera is monophyletic and early diverging in the North American clade (Fig. 37.1E).

Astranthiinae. — It includes four genera, one of which, *Geissolepis*, does not belong here but with Chrysopsidinae-Conyzinae (Fig. 37.1E). *Geissolepis* either belongs with one of these subtribes or is sister to both. With this genus removed, Astranthiinae are monophyletic.

Chrysopsidinae. — This is a monophyletic group, sister to Conyzinae.

Conyzinae. — This subtribe essentially is equivalent to a monophyletic *Erigeron*. All other genera are derived from within the latter and could be considered synonyms. As stated in Nesom and Robinson (2007), African conyzas belong to Grangeinae.

***Doellingeria, Eucephalus, Oclemena, Ionactis.* —** These unplaced North American taxa all were traditionally classified in *Aster.* Their position is unusual within the North American clade (Fig. 37.1E). *Eucephalus*-*Doellingeria* represents the most early diverging lineage. *Oclemena* and *Ionactis* are still difficult to assign, but it is likely that they will be early diverging in distinct North American clades, as yet undetermined.

The Nesom and Robinson (2007) classification does not adequately reflect the phylogeny presented here. Firstly, many of the subtribes are polyphyletic. It is worth noting that none of the subtribes with intercontinental disjunctions, except a few between New Zealand and Australia or across the Pacific Islands, have proven to be monophyletic. This would indicate that the criteria used to group genera into subtribes are not diagnostic of relationships or should be reinterpreted (e.g., convergences). Secondly, the basal African grade, with its numerous, sometimes isolated lineages, intermixed with Chinese, South American, and New Zealand lineages, is not represented in it. Thirdly, several major, monophyletic clades are not recognized in the classification, notably the Paleo

South American, New Zealand, and North American clades. Fourthly, the classification fails to recognize the phylogenetic proximity of genera from the same continent, notably the genera belonging to the Australasian and South American lineages. Finally, the classification is over-elaborate in North America, where a large number of subtribes are recognized. These groups are indeed worthy of recognition, but it must be questioned whether this should be done at the subtribal level.

At the present time, we are refraining from proposing a new classification of the tribe because many details of the phylogeny remain to be validated. Nonetheless, we would suggest that the subtribal level should be reserved for the most significant clades of the phylogeny, including the isolated African or Chinese genera or lineages where necessary. The subtribes Homochrominae, Grangeinae, and Bellidinae should be recognized but with a wider membership than defined by Nesom and Robinson (2007). Clades that deserve subtribal recognition but that currently lack a name are the Paleo South American, the New Zealand, and the North American. The name Solidagininae might be applied to the North American clade, though this would extend the concept of this subtribe beyond its traditional content; it would have the virtue of being monophyletic and of providing a name for one of the most important radiations within the tribe. The large polytomies of Australasian and of South American lineages will have to await better resolution before a classification of their elements into subtribes can be entertained. Among the Australasian lineages, the clade that will end up including *Olearia* s.str. and *Aster* s.str. will have to be called subtribe Asterinae, again a departure from past practice but a more natural assemblage. It is unclear whether this group will include all or only part of the Australasian genera. It is likely that subtribe Baccharidinae will be a significant clade, restricted to *Baccharis* s.str. The other South American lineages may either form a grade to the North American clade, or form a sister group to it; the taxonomic disposition of this group must await better supported data. Until better resolution and better support is obtained for the phylogeny of Astereae, it would be premature to propose a new classification.

MORPHOLOGY, ANATOMY, PALYNOLOGY

Since Grau (1977) published his summary, few papers have been devoted solely to the comparative morpho-anatomy or palynology of tribe Astereae, if one excepts cytotaxonomic or phylogenetic papers including morphological analyses. Wood anatomy was studied for *Melanodendron* and *Commidendron* by Carlquist (2001), *Tetramolopium* by Carlquist and Lowrey (2003), and *Heterothalamus* by De Oliveira et al. (2005). Capitulum and floret developments were studied in *Erigeron philadelphicus* L. by Harris et al. (1991), and in *Symphyotrichum laurentianum* (Fern.) G.L. Nesom by Lacroix et al. (2007). Pullaiah (1978) published on the embryology of *Solidago* and *Erigeron* (*Conyza*), and Noyes and Allison (2005) on that of sexual and apomictic members of *Erigeron strigosus* Muhl. ex Willd. Jordaan and Kruger (1993) studied pollen wall ontogeny in *Felicia muricata* Nees. Jackson et al. (2000) noted a unique pollen wall mutation in $n = 2$ *Xanthisma gracile* (Nutt.) D.R. Morgan & R.L. Hartman (as *Haplopappus gracilis* (Nutt.) A. Gray). Torres (2000) showed a correlation between pollen volume and pistil length in Asteraceae, including several species of Argentinian Astereae.

It was not possible for this paper to re-evaluate and map onto the phylogeny the morphological and anatomical characters that have been used to assess generic relationships and to delimit subtribes. The discrepancy between our molecular phylogeny and the classifications proposed for the tribe, the Nesom and Robinson (2007) classification being the most recent example, indicates that the interpretation of morphological data requires a re-assessment, notably as to whether the characters used represent convergences, or whether they are symplesiomorphic or synapomorphic. Furthermore, the lack of resolution and support of the current phylogeny would prevent us from reaching meaningful conclusions in many cases.

Nonetheless, Cross et al. (2002) suggested that the presence of a tomentum on the abaxial surface of leaves is symplesiomorphic in the tribe. Our data appear to support this hypothesis, since most groups that possess this feature are in the basal grade of Astereae. It is possible that some instances of such a character represent convergences; a detailed examination of the trichomes making up the tomentum would be needed to determine whether this is the case. Also, loss of the tomentum may have occurred independently several times during evolution of Astereae. Grangeinae as well as the crown lineages lack this feature, and the loss may have occurred a single time along the spine below the origin of these taxa. More African genera need to be incorporated in the phylogeny before we can satisfactorily address this issue.

Cross et al. (2002) also proposed that caudate or sagittate anther bases, a feature present in the sister tribes of Astereae, had evolved in parallel several times in Astereae and in those other tribes. We would suggest a different interpretation of this feature: caudate anthers, like abaxially tomentose leaves, may represent a symplesiomorphy in the tribe. Given that all lineages with tailed anthers are among primitive Astereae, being present, for instance, in *Printzia*, *Denekia*, and the Paleo South American and New Zealand clades, it would appear most parsimonious to postulate that anther tails are a primitive feature within Astereae that may have been lost repeatedly in early lineages. It was also possibly lost a single time along the spine of the phylogeny, resulting in most Astereae genera being tailless. This would explain why tribe Astereae has been traditionally described as having tailless anthers as a defining feature, with apparently random exceptions. Such exceptions are all found among early diverging groups in our phylogeny, though. Tailless anthers, instead of being an absolute defining feature of the tribe, would appear to be one that characterises relatively derived members of the tribe.

CHROMOSOME NUMBERS

There are more than 18,800 chromosome number reports for individuals of tribe Astereae (Chapter 4 and references cited therein). At least one chromosome number report has been published for 140 genera included in the tribe. Twenty genera have only been sampled once. More than 15,000 of the reports are for individuals of just six genera, due primarily to cytogeographic studies on taxa within each genus: *Symphyotrichum* (4578), *Solidago* (3451), *Aster* (2129), *Brachyscome* (1884), *Xanthisma* (ca. 1600), and *Erigeron* including *Conyza* (1370).

The tribe includes the greatest diversity in chromosome numbers and ploidy levels within the family Compositae (Chapter 4). Chromosome numbers in Astereae range from $2n = 4$ (*Xanthisma gracile* (Nutt.) D.R. Morgan & R.L. Hartm. and *Brachyscome dichromosomatica* C.R. Carter) to $2n =$ ca. 432 (*Olearia albida*). Polyploidy occurs in nearly all major clades with a decrease in frequency as ploidy level increases. Tetraploids are known in 48 genera, hexaploids in 23, and octoploids in 11. Higher ploidy levels are rarer. Decaploids are known in *Bellis*, *Boltonia*, *Brachyscome*, *Erigeron*, *Lorandersonia*, *Solidago*, and *Symphyotrichum*. Dodecaploids and higher ploidy levels are known in *Solidago* ($14x$), *Eurybia* ($14x$), and nearly all members of the New Zealand clade ($12x$, $32x$, $36x$, and $48x$). With the exception of the latter, high ploidy levels generally are known in the genera that have been sampled most extensively.

The ancestral number of Astereae is $x = 9$ (Semple 1995). The lack of a DNA-based phylogeny at the time left many of the conclusions speculative. No chromosome numbers have been reported for either *Printzia* and *Denekia*, reported here to form an early diverging lineage in the tribe. Both are native to southern Africa and were included in Gnaphalieae but unassigned to subtribe in Bremer (1994). All major clades within the tribe and the majority of species have a base number of $x = 9$. Machaerantherinae sensu Nesom and Robinson (2007) have a base number of $x = 6$. If they are expanded to include *Oreostemma*, *Herrickia*, *Eurybia*, and *Triniteurybia*, Machaerantherinae s.l. also have a base number of $x = 9$. The small subtribe Chaetopappinae in the North American clade has a base number of $x = 8$.

Dysploid decreases have occurred in several dozen genera and eight subtribes scattered throughout the tribe. Dysploidy is most frequent in the Symphyotrichinae-Machaerantherinae s.l. clade, one of the crown lineages of the North America clade, which includes numbers ranging from $x = 9$ to $x = 2$. The longest dysploid series in a single genus occurs within *Brachyscome* s.l. with $x = 9$ to $x = 2$ taxa in the Australasian clade. In the same clade, another long dysploid series is found in *Calotis* ($x = 8, 7, 6, 5, 4$), sister to *Erodiophyllum* ($x = 8$). In the basal grade, dysploidy also is known in *Amellus* ($x = 9, 8, 6$), and *Felicia* ($x = 9, 8, 6, 5$).

Three genera include derived base numbers higher than $x = 9$. *Symphyotrichum* subg. *Ascendentes* has allopolyploid-derived base numbers of $x_2 = 13, 18, 21$ with $x = 8$ and 5 as parental taxa (Brouillet et al., pers. comm.). In *Brachyscome*, counts with $x_2 = 11$ and 13 were reported (Watanabe et al. 1999). The single report for *Isoetopsis* of $2n = 17_{\mathrm{II}}$ (as $n = 17$; Turner 1970) occurs in a clade with $x = 9$ as ancestral; if correct, this may be a dysploid derived $x_2 = 17$ from a tetraploid with $2n = 36$.

New approaches have been applied to further our understanding of cytological evolution within genera, notably polymorphic heterochromatic segments (Houben et al. 2000) in *Brachyscome*, fluorescence in situ hybridization (FISH) of nuclear ribosomal DNA probes in *Brachyscome* (Adachi et al. 1997), *Aster* (Saito and Kokubugata 2004), and *Haplopappus* and *Grindelia* (Baeza and Schrader 2005), and genomic in situ hybridization in *Aster* (Matoba et al. 2007).

CHEMISTRY

The chemistry of Astereae first was summarized by Herz (1977b), who underlined the partial nature of our knowledge in terms both of the organs (mostly roots) and of the taxa surveyed. Interpretation of infratribal variation was based on the six traditionally recognized subtribes. Since then, overviews have been provided for the tribe on acetylene (Christensen and Lam 1991) and terpenoid chemistry (Herz 1996). General surveys for Compositae were published by Hegnauer (1977) and Zdero and Bohlmann (1990). The latter provided a framework useful to intrepret chemical evolution within Compositae in terms of biosynthetic pathways: chemicals derived from acetyl coenzyme A are polyacetylenes, aromatic compounds, and terpenes and saponins, and those derived from amino acids include flavonoids, phenyl propanes, pyrrolizidin alkaloids, and a few others. Specialist reviews were done on sesquiterpene lactones (Herz 1977a; Seaman 1982), diterpenes (Alvarenga et al. 2005), benzopyranes, and benzofuranes (Proksch 1985), polyacetylenes (Sørensen 1977), leaf wax alkanes (Maffei 1996), steroids (within a survey of angiosperms; Borin and Gottlieb 1993), flavonoids (Harborne 1977, 1996; Seeligman 1996; Bohm and Stuessy 2001, summarizing data on 48 genera of Astereae), and pharmaceutical uses (Wagner 1977).

Examples (our search was not exhaustive; more is also to be found in the sources above) of new chemical reports within the tribe include (and references therein): surveys of essential oils (Kalemba 1998; Zunino et al. 1997; Barbosa et al. 2005) or volatile compounds (Chung et al. 1997); matricaria esters and lactones (Lu et al. 1998); benzofuranes and terpenoids (Schmidt et al. 2003); flavonoids (Saleh and Mosharrafa 1996; Wollenweber and Valant-Vetschera 1996; Vogel et al. 2005), flavonoids and terpenes (Verdi et al. 2005), or flavonoids and quinic acid derivatives (Kwon et al. 2000; Hur et al. 2001, 2004; Choi et al. 2003; Simoes-Pires et al. 2005); heterocyclic terpenes (Li et al. 2005); cerebrosides and terpene glycosides (Kwon et al. 2003); sesquiterpene hydroperoxide (Choi et al. 2003); monoterpene peroxide glycosides (Jung et al. 2001); diterpenes (Herz et al. 1977; Hoffmann et al. 1982; Waddell et al. 1983; Warning et al. 1988; Zdero et al. 1990, 1991; Zhou et al. 1995; He et al. 1996; Ahmed et al. 2001; Choi et al. 2002; Lee et al. 2005); saponins from *Aster* s.l. (incl. *Galatella*, *Aster*, *Bellidiastrum*) species (Lanzotti 2005); and anti-inflammatory products in *Laennecia* and *Baccharis* (Cifuente et al. 2001). It is remarkable that much of this research concerns pharmaceutically active compounds and their properties (e.g., *Aster* spp.; Graham et al. 2000; Sok et al. 2003; Oh et al. 2005; Seong Il et al. 2005). Of note were the reports of the sesquiterpene lactone eudesmanolide from *Grangea maderaspatana* (Ruangrungsi et al. 1989) and *Erigeron annuus* Pers. (Li et al. 2005), added to the three known records for the tribe (Seaman 1982).

The studies cited above show that Astereae overall are characterized by a paucity of sesquiterpene lactones, usually of basic skeleton types, an absence of tridecapentaynene and derivatives, replaced by C10- and C17-acetylenes (a feature shared with Anthemideae), the presence of aromatic compounds such as prenylated p-hydroxyacetophenones, which accumulate in some Astereae, the presence of phenylpropane derivatives, the common occurrence of coumarins, both simple, prenylated or linked with terpenes or sesquiterpenes, and among diterpenes, the presence of kauranes and derivatives, including the rare abietanes, and of labdanes and clerodanes. Monoterpenoids and sesquiterpenoids are varied and widespread. Flavonoids and other phenolics are present but do not exhibit particular trends.

Taxonomic interpretation of the distribution of compounds within the tribe, however, is currently of limited usefulness because it has been based on traditional genera, many of which have been recently shown to be polyphyletic, and on traditional subtribes, also shown as artificial despite the recent classification of Nesom and Robinson (2007). For chemical data to play a significant role in our knowledge of the evolution of Astereae, the generic identity of reports will need to be reassessed and the chemical data re-interpreted within the context of both biosynthetic pathways and a well-supported phylogenetic framework. Work on the enzymes regulating biosynthetic pathways in Astereae is promising in this regard (e.g., Prosser et al. 2002, 2004). Chemical data should not be dismissed, however. An example comes from the report by Bohlmann and Zdero (1978) of new diterpenes constituents in *Printzia*, then considered an Inuleae, showing clear relationships to compounds in Astereae, a fact confirmed by the current placement of the genus as an early derived lineage of the tribe.

BIOLOGY AND EVOLUTION

Species of Astereae have been the object of numerous biological or evolutionary studies. Exemplars of recent studies are summarized below in order to show the potential of the tribe for evolutionary and ecological studies, as well as to illustrate the biology of the tribe. An overview of pollination and dispersal morphology and ecology of Indian Compositae (mostly native, some introduced), including several Astereae species (*Aster* s.l., *Centipeda*, *Conyza*, *Dichrocephala*, *Erigeron*, *Grangea*, *Microglossa*, *Myriactis*, *Solidago*), is provided by Mani and Saravanan (1999).

Interspecific hybridization has been documented repeatedly within the tribe. This has been summarized by Nesom (1994j), among others. Some reported intergeneric hybrids, such as those between *Kalimeris* and *Aster*, in fact are between members of genus *Aster* (see Australasian clade). Recently, FISH techniques (Saito and Kokubugata 2004) and molecular phylogenetic evidence (Saito et al. 2007) were used to document the hybrid origin of *Aster* ×*sekimotoi* Makino in Japan. Matoba et al. (2007) used GISH techniques to identify the parents and their contribution to genomic organization in the allotetraploid *Aster microcephalus* Franch. & Sav. var. *ovatus* (Franch. & Sav.) A. Soejima & Mot. Ito.

Gottlieb (1981) investigated the number of allozymic gene loci in species of *Almutaster*, *Psilactis*, and *Arida* (as *Machaeranthera* Nees. s.l. and *Aster* s.l.) in North America with chromosome numbers of $n = 4, 5, 9$. He concluded that the absence of multiple isozymes in the species with $n = 9$ suggested it did not arise via polyploidy. In an isozyme study of 6-phosphogluconate dehydrogenase (6PGD) in *Aster* s.str. (as *Kalimeris*), however, Nishino and Morita (1994) found a duplication within the diploids that would not reject the possibility of an allopolyploid event at the base of the $x = 9$ number in the group. If a duplication occurred, it either happened before the origin of Astereae, or it was the result of a single gene or chromosome segment duplication.

As stated above (Cytology section), polyploidy is a frequent phenomenon in tribe Astereae. Allopolyploids are the result of reticulate evolution and thus of interspecific hybridization (see Otto and Whitton, 2000 and Chapman and Burke, 2007 for reviews). Allen (1985, 1986; Allen et al. 1983) showed that *Symphyotrichum ascendens* (Lindl.) G.L. Nesom ($n = 13$) and *S. defoliatum* (Parish) G.L. Nesom ($n = 18$) originated through a series of hybridization events between *S. spathulatum* (Lindl.) G.L. Nesom ($n = 8$) and *S. falcatum* (Lindl.) G.L. Nesom ($n = 5$). Chapman and Burke (2007) reported ITS sequence distances among these parental species consistent with a model in which the likelihood of polyploid formation increases with the genetic divergence of the parents (versus in homoploid speciation). Using cpDNA, ITS, and ETS molecular phylogenetic data, Morgan (1997, 2003; Morgan and Simpson 1992) dissected reticulate evolution within the *Machaeranthera* generic complex (see Morgan and Hartman 2003), showing introgression both of chloroplast and ITS in various members.

Apomixis is known in several genera of Astereae and is usually associated with polyploidy. The process of apomixis and the relationships among diploid and polyploid populations within apomictic taxa have been studied in *Erigeron strigosus* (Noyes 2000a, b, 2006, 2007; Noyes and Allison 2005; Noyes and Rieseberg 2000), *Erigeron compositus* Pursh (Noyes et al. 1995), and *Townsendia hookeri* Beaman (Thompson and Ritland 2006; Thompson and Whitton 2006). Apomixis had also been studied from an anatomical standpoint in the Australian *Minuria integerrima* (DC.) Benth. and *Calotis lappulacea* Benth. (Davis 1964, 1968).

Genetic uniformity of *Erigeron* species in the European Alps was shown by Huber and Leuchtmann (1992) using allozymic data, as a result of recent speciation, probably during the glaciations; morphological and ecological differences between them could be the result of changes at few loci. Valdebenito et al. (1992) studied the evolution of six endemic, polyploid *Erigeron* species on the Juan Fernández Islands (Chile) using flavonoid profiles and showed all to derive from a single introduction to Masafuera, followed by colonization of Masatierra. A study of Hawaiian and Cook Islands *Tetramolopium* species based on morphology (Lowrey 1986, 1995), allozymes (Lowrey and Crawford 1985), nuclear DNA RFLP markers (Okada et al. 1997), and ITS-based phylogenetic data (Lowrey et al. 2001) showed low levels of variation within the group, supporting the hypothesis of a recent origin and rapid diversification of the morphologically distinct taxa. Microsatellites were developed to characterize populations of *Solidago sempervirens* L. in North America (Wieczorek and Geber 2002) and *Aster amellus* L. in Europe (Mayor and Naciri 2007), opening new avenues for population genetic studies in Astereae.

The population genetics of rare species of *Aster* was studied using allozymes. The population structure and genetic diversity of the autotetraploid *Aster kantoensis* Kitam. was studied (Maki et al. 1996); Inoue et al. (1998b) showed strong inbreeding depression in selfed individuals; these studies led to the suggestion of conservation measures for the species (Inoue et al. 1998a). The rare, Korean and Japanese, coastal *Aster spathulifolius* Maxim. was shown to have high overall diversity but restricted gene flow (Maki and Morita 1998). The rare, insular endemic *Aster asa-grayi* Makino from the subtropical islands of southern Japan, however, had both low allozyme genetic variability and restricted gene flow (Maki 1999).

Hunziker et al. (2002) reported permanent translocation heterozygosity in the dioecious South American shrub *Baccharis coridifolia* DC., hypothesizing that it was correlated with the maintenance of tightly linked male sex genes on four chromosomes, and that it might explain the excess of male plants in populations in ensuring a sufficient supply of pollen to insect pollinators at flowering time.

Niche ecology of *Ericameria* (as *Haplopappus* and *Chrysothamnus*) species has been studied in the Mojave desert (Cody 1978). Meyer (1997) showed a relation between achene mass variation in *Ericameria* (as *Chrysothamnus*) *nauseosa* and successional status of the community in the habitats of subspecies, accompanied by high between-individual differences. Bernard and Toft (2007) showed that seed size had important consequences on biomass, biomass allocation, and survivorship in seedlings of *E. nauseosa*, and a significant impact on subsequent life stages. Baskin and Baskin (1976) and Flint and Palmbald (1978) have shown germination dimorphism among ray and disc achenes, respectively, in *Heterotheca subaxillaris* (Lam.) Britton & Rusby and *H. grandiflora* Nutt., and Venable and Levin (1985) studied the ecology of achene dimorphism in *H. latifolia* Buckley. Gibson (2000) showed that achene dimorphism in *Grindelia* (*Prionopsis*) *ciliata* (Nutt.) Spreng. had little ecological significance but resulted in subtle genetic differences between ray and disc achene groups that could influence metapopulation architecture. Lacroix et al. (2007) studied the floral development, fruit set, and dispersal of a rare endemic saltmarsh species, *Symphyotrichum laurentianum*, showing that fruit set is mostly from ray achenes and that dispersal is limited. The growth strategy of *Tripolium vulgare* Nees (*Aster tripolium* L.) in Korea was studied by Lee and Ihm (2004). This species also showed its ability to invade turf-dominated waste landfills (Kim 2002). Gowe and Brewer (2005) demonstrated the evolution of fire-dependency of flowering in sect. *Graminifoliae* of *Pityopsis* using a morphology-based phylogeny.

Butcko and Jensen (2002) studied allelopathic activity of *Euthamia graminifolia* (L.) Nutt. and *Solidago canadensis*, two species able to form large, monospecific stands. They showed that allelopathic substances may inhibit the establishment, growth, and survival of competing species.

Associations with other organisms have been described for many Astereae genera or species, notably with insects. The papers cited below are but a sample of those available. *Aster scaber* was shown to be tolerant of the nematode *Meloidogyne hapla* (Park et al. 2004). Parker (1984) studied the foraging behavior of a specialist grasshopper (*Hesperotettix viridis*) on *Gutierrezia microcephala* (DC.) A. Gray; food depletion appears to strongly affect the insect and thus direct food selection. Parker (1985) investigated the demographic impact of two specialist insect herbivores on populations of *G. microcephala* in arid grasslands, which showed reduced plant longevity and recruitment under high attacks, and thus vulnerability to local extirpation. Parker and Salzman (1985) showed that protection from herbivory and competition increased growth and survival in *G. microcephala* juveniles. Glendinning et al. (1998) showed the role that taste receptor cells in maxillary palps of caterpillars play in rejecting allelochemical substances from *Grindelia glutinosa* (Cav.) C. Mart. Moran et al. (1999) studied the phylogenetic relationships among aphids of the genus *Uroleucon*, whose primary hosts are Compositae species, including among others *Erigeron*, *Eurybia* (as *Aster*), and *Solidago* (both North American and Eurasian species); the species attacking Astereae genera do not form a monophyletic group, even among North American taxa, and represent repeated colonizations of Astereae hosts by the aphid from other Asteraceae. Olsen (1997) studied polllination effectiveness and pollinator importance in a population of *Heterotheca subaxillaris*; pollination effectiveness was similar for both ray and disc florets, though seed set was higher in the former; the plant species was not under strong selective pressure to co-specialize with specialist visitors, though one bee species was a specialist. Torres and Galetto (2002) studied the relationship between nectar sugar composition, corolla tube length, and diversity of insect visitors on Asteraceae flowers in South America, including *Baccharis*, *Grindelia*, and *Solidago*, and showed a lack of correlation, though more derived lineages of Asteraceae (including Astereae) tended to show evolution toward more generalist pollinators.

Solidago and its insect fauna often were used as models in the evolutionary ecological study of plant-herbivore interactions. Abrahamson and Weis (1997) summarized decades of research on the relationships between the goldenrods, their insect stem gallmakers (*Eurosta solidaginis*, Tephritidae, Diptera), and their natural enemies. Several papers have been published since on the same or related topics: Meyer (1998b), Civenetti et al. (1999), Summerford et al. (2000), Cronin and Abrahamson (1999, 2001a, b), Mapes and Davies (2001a, b), Nason et al. (2002), Abrahamson et al. (2001, 2003), Eubanks et al. (2003), Stone and Schönrogge (2003), Stireman et al. (2005a, b), Williams and Lee (2005), including educational materials (Yahnke 2006). Other studies involving galling insects and Astereae species include those of Espírito-Santos and Fernandes (2002) and Rudgers and Whitney (2006) in *Baccharis*, and of Floate et al. (1996) on *Ericameria* (*Chrysothamnus*) *nauseosa*, in which insect galls were distinctive for each subspecies present in a population. Pak et al. (2004) reported midge-galls (Cecidomyiidae, Diptera) on *Aster scaber* in Korea. Fontes et al. (1994) studied the phytophagous insect guild associated with *Solidago* species in Florida. Shealer et al. (1999) showed the value of goldenrod galls as winter forage for the Eastern gray squirrel in North America.

Morrow et al. (1989) showed the response of the goldenrod leaf beetle (*Trirhabda canadensis*, Chrysomelidae) to volatile odors of the *Solidago altissima* L. host plant in the field, the insect selecting denser colonies or, when winds are strong, the first available plot upwind. Meyer (1998a) studied defoliation recovery mechanims in the same herbivore-goldenrod system. Dickens and Boldt (1985) showed the greater sensitivity of antennal receptors of *Trirhabda bacharides* (Chrysomelidae) to volatiles emanating from *Baccharis* and other Compositae species. Futuyma and colleagues (Futuyma and McCafferty 1990; Futuyma et al. 1993; Funk et al. 1995a, b; Knowles et al. 1999) studied the evolution of host-insect relationships in the endemic North American leaf beetle genus *Ophraella* (Chrysomelidae); early evolution of the group occurred on Astereae such as *Solidago* (main host), *Symphyotrichum*, and *Eurybia*; there were subsequent shifts in host plant to members of Eupatorieae, Heliantheae, and Anthemideae, shifts that appear to be genetically constrained in descendant groups due to the radical change in plant chemistry from the original Astereae hosts; a later reversal to Astereae hosts (*Heterotheca* and *Solidago multiradiata* Ait.) occurred, which were not involved in the early evolution of the beetles.

Warcup and McGee (1983) reported that the unusual, Australian annual *Isoetopsis graminifolia* Turcz. (classified as Anthemideae) formed both ectomycorrhizae and vascular-arbuscular mycorrhizae, and so does *Chondropyxis halophila* D.A. Cooke (Warcup 1990); the only other Compositae genera doing so were in Gnaphalieae. All other Australian Astereae genera investigated formed only vascular-arbuscular mycorrhizae.

BIOGEOGRAPHY

Grau (1977) and Bremer (1994) noted the distribution of Astereae in lands peripheral to the Pacific and Indian oceans. Based on his subtribal classification, Nesom

(1994g) noted the mostly Southern Hemisphere distribution of subtribes Baccharidinae, Hinterhuberinae, and of his "grangeoid complex" of seven subtribes, which repeatedly show South American-African disjunctions, and the concentration in the Northern Hemisphere of subtribes endemic to North America, to the exception of Asterinae. Southern disjunctions between South America and Australasia were also noted. These patterns were discussed in terms of Tertiary biogeography. Subsequently, the molecular phylogenetic study of Noyes and Rieseberg (1999) showed that Astereae were probably of African origin and that North American Compositae formed a clade. In their meta-analysis of Asteraceae biogeography, Funk et al. (2005) also suggested an African origin for Astereae, with an Australasian central grade and a terminal North American clade. The molecular phylogenetic studies cited in the sections above discussed various aspects of Astereae biogeography pertinent to the group studied, but were limited in geographic and taxonomic scope. It is worth noting that all tribes sister to Astereae in the meta-tree of Funk et al. (2005) are of southern African origin.

The current Astereae phylogenetic tree (Fig. 37.1) provides a more detailed hypothesis of biogeographic relationships within the tribe. The presence at the base of the tree of two South African genera, *Printzia* and *Denekia*, would indicate that the tribe indeed originated on that continent, as hypothesized by Noyes and Rieseberg (1999). The second lineage to diverge is the Chinese genus *Nannoglottis*, which suggests long-distance dispersal or rafting of members of Astereae to eastern Asia early in the evolution of the tribe (Liu et al. 2002). Another isolated, southern African genus, *Mairia*, is next to diverge. Then follow two radiations in southern hemisphere, temperate areas: southern South America (and adjacent Andes) and New Zealand (with subsequent dispersal to Australia). In various analyses, these two clades either form a grade as shown here or are sister to each other. Several scenarios may explain this pattern: *(1)* independent dispersals directly from Africa to South America and to New Zealand; *(2)* dispersal to South America followed by dispersal to New Zealand or vice versa (if the two clades are sister, for instance); and *(3)* given the fact that both southern South America and New Zealand are high-latitude, southern temperate areas, dispersal through Antarctica to southern South America and New Zealand. Members of the New Zealand clade, i.e., species of *Celmisia* and *Olearia* s.l., dispersed to Australia, with little subsequent diversification. All subsequent lineages above this segment are mainly southern African: *Pteronia*, subtribe Homochrominae, *Madagaster*, *Conyza gouani*, the African asters, and subtribe Grangeinae. Homochrominae ancestors gave rise by long-distance dispersal to the St. Helena trees, *Melanodendron* and *Commidendron* (see also Eastwood et al. 2004). Likewise, the Madagascan *Madagaster* originated from Africa via long-distance dispersal. Grangeinae are wider ranging in Africa and dispersed to southern Asia (Indian subcontinent and adjacent areas), as shown by *Grangea maderaspatana*. The fact that Bellidinae are found on a polytomy with Grangeinae would suggest that this Mediterranean–Eurasian lineage originated in Africa; after diversifying in the Mediterranean basin, it spread through the steppes of central Asia to eastern Asia. In more resolved analyses, the next lineage usually is *Callistephus*, another isolated Chinese genus without clear affinities at the present time. Is it another case of long-distance dispersal from Africa to eastern Asia, as in *Nannoglottis*, but at a later time? Above this level a major polytomy is encountered, indicating a possibly rapid series of independent colonizations and radiations in Australasia and South America. Dispersal could have occurred either directly from Africa to both continents or via Antarctica, as hypothesized above. At the present time, it is unclear whether Australia was colonized once or a few times. What is clear, however, is that Astereae strongly radiated on the continent, giving rise to unique lineages. Some of these lineages in turn migrated north through New Guinea to southeast Asia and the Pacific Islands, including Hawaii. Some species also dispersed to New Zealand, a secondary colonization of this archipelago by Astereae. It is notable that the sister group of the eastern Asian genus *Aster* s.str. (Eurasian by secondary expansion) is the Australasian *Olearia* s.str., and not genera placed by Nesom and Robinson (2007) in subtribe Asterinae: *Aster* s.str. had Australasian ancestors. This represents a fourth independent colonization of temperate eastern Asia by Astereae. Meanwhile, South America was colonized a second time by Astereae in a series of lineages that appear to form a grade in some analyses. In more resolved phylogenies, *Baccharis* appears to be the first lineage of this new colonization, followed by Podocominae and Hinterhuberinae (though these are not necessarily monophyletic), either in succession or as sister to each other. This radiation was more extensive than that of the Paleo South American lineage. Finally, members of the South American lineages gave rise to the North American clade in apparently a single event of dispersal, followed by a rapid radiation. It is unclear whether this dispersal occurred over long distances or whether the gradual closure of the Isthmus of Panama played a role. The fact that there is no apparent connection between Central American representatives of the South American lineages and the North American clade would seem to eliminate the second option.

Thus, it would appear that the biogeographic history of Astereae is that of a development in Africa both accompanied and followed by repeated dispersals, during the Tertiary, to eastern Asia and to other Southern Hemisphere continents, South America, New Zealand, and Australia, either directly or via Antarctica. Each dispersal led to more or less intense episodes of diversification in the new environments. Later, the more recent southern lineages (late African, South American, Australasian) gave rise independently to derived clades in the Northern Hemisphere: Bellidinae in the Mediterranean area from Africa, *Aster* in east Asia from Australasia, and the North American clade from South America, the latter to radiate extensively and become a center of diversity of the tribe. Subsequent dispersals occurred from Asia to North America (a single event in *Aster*) or from North America to Eurasia (*Symphyotrichum ciliatum* (Ledeb.) G.L. Nesom, *Eurybia sibirica* (L.) G.L. Nesom, *Solidago*, *Erigeron*) and, repeatedly, to South America (*Erigeron*, *Solidago*, *Grindelia*, *Symphyotrichum*, the ancestors of *Haplopappus* and *Noticastrum*). Repeated dispersals also occurred throughout the Pacific Islands from Australasia and between New Zealand and Australia, in both directions.

ECONOMIC USES

Although tribe Astereae is the second largest of Compositae, the economic importance of the group is often considered to be rather low and largely limited to garden ornamentals cultivated in temperate gardens (Bremer 1994). There are numerous Astereae that are used medicinally in various parts of the world, however. The list is too long to elaborate on any particular genus or species. Medicinal plant websites and books on economic and medicinal plants are the best sources of information. There are also a number of taxa that have great potential in several categories of economic use including perfume ingredients, commercial resins, and elastic latexes including rubber.

The southern African genus *Pteronia* contains a number of species with highly aromatic foliage. *Pteronia incana* DC. produces a yellowish oil with a strong odor (Mangena and Muyima 1999). The strongly scented oil has chemical properties that make it suitable for use as a fragrance in the perfume industry (Bruns and Meiertoberens 1987). The oil has also been shown to possess antibiotic properties that show promise for use in the cosmetic industry (Mangena and Muyima 1999.). Another aromatic species, *P. onobromoides* DC., was used by the Hottentots of southern Africa as a perfume but is yet to be studied commercially (Hutchinson and Phillips 1917).

Species of *Grindelia* from the southwestern United States and South America have generated interest as a source of diterpene resin acids (grindelic acid and others) that have the potential for uses similar to those for pine resins, which are known as "naval stores" (Hoffmann et al. 1984; Hoffmann and McLaughlin 1986). These compounds are used in paper sizing processes, the rubber industry, as ester gums for the food industry, and resins (Thompson 1990). Three species of *Grindelia* have been studied as potential resin crops including *G. camporum* Greene (native to Central Valley of California), *G. stricta* DC. (coastal estuaries of California), and *G. chiloensis* (Cornel.) Cabrera (southern and central Argentina) (Ravetta et al. 1996). A tetraploid accession of *Grindelia chiloensis* has been shown to produce the highest yield of diterpene resins (Ravetta et al. 1996). The drop in domestic production of pine resins in the United States and demand for naval stores throughout the world coupled with the high cost of petroleum may well revive interest in the commercial cultivation of *Grindelia*.

Ericameria (endemic to the western United States) includes several species that produce significant amounts of hydrocarbon compounds, of which rubber and resins are economically important (Weber et al. 1986). One of the most widespread species, *Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird, may contain up to 7% rubber as measured in dry weight (Weber et al. 1993) and as much as 35% resin (Bhat et al. 1989). The resin contains a range of terpenoid compounds some of which have potential as insect inhibitors (Weber et al. 1993) and as plastics extenders (Thames 1988).

One of the more promising sources of natural rubber that never went beyond the experimental stage is *Solidago* (goldenrod). The great inventor, Thomas Edison, dedicated the last years of his life to developing a new source of natural rubber as an alternative to the tropical tree, *Hevea brasiliensis* (Willd. ex A. Juss.) Müll.Arg. (Josephson 1959). After several years of testing numerous species from different plant families, he decided that species of *Solidago* from the Southeastern USA showed the most promise. Edison embarked on a series of selection experiments in the late 1920s and eventually developed a strain of *Solidago leavenworthii* Torr. & A. Gray that grew to a height of 14 feet and contained 12% rubber (Josephson 1959; Polhamus 1962). *Solidago* was not developed into a commercial source of rubber since it was too costly at the time, the rubber was inferior to *Hevea* rubber (Swanson et al. 1979), and natural rubber was soon superseded by synthetic rubber obtained from petroleum (Josephson 1959). The notes of Thomas Edison's experiments on rubber-producing plants including *Solidago* are archived at the LuEsther T. Mertz Library at the New York Botanical Garden.

The horticultural importance of Astereae is based on taxa from relatively few genera. In southern hemisphere gardens, *Brachyscome* from Australia and *Felicia* from southern Africa are important ornamental plants in Mediterranean climate gardens (Elliot 2003; Pienaar 2003). The genera that contain most of the species in the commercially important horticultural trade in Europe and North America include *Symphyotrichum*, *Solidago*, *Callistephus*, and *Aster* (Halevy 1999). The Asian *Callistephus chinensis* Nees, commonly known as the China aster, is the common aster of florists and flower gardens. Hybrids between *Symphyotrichum novi-belgii* (L.) G.L. Nesom and other eastern North American species have become important greenhouse crops and are currently a major horticultural export from Israel (Halevy 1999). Interspecific hybrids derived from North American species have likewise become important products in the cut-flower trade in Israel, Europe, and North America (Halevy 1999). *Aster amellus* L., native to Europe, is an important garden plant throughout Europe. Numerous other taxa of Astereae are regularly cultivated in their continent of origin but are not of major economic importance in the horticultural trade.

The negative economic impact of Astereae, as weeds, is relatively low. Several late-successional species of *Solidago* and *Symphyotrichum* may be considered weedy because they occupy old fields and may prevent succession to forests in North America (e.g., Byrnes et al. 1993; Cain 1997; De Blois et al. 2002). Three species of *Solidago* introduced into European gardens as ornamentals have escaped from cultivation and become weedy in Europe (Weber 1998). *Solidago canadensis* L. has escaped cultivation in China and is rapidly spreading in eastern provinces of the country (Dong et al. 2006). *Erigeron* (*Conyza*) *canadensis* L., one of the most widely distributed Astereae species, has been shown to reduce agricultural productivity (Buhler and Owen 1997). It has become resistant to glyphosate, currently the most commonly used herbicide with genetically modified crops, in several countries, and thus has the potential of becoming noxious (VanGessel 2001). Furthermore, it could potentially transfer its resistance to related *Erigeron* species (for a review, see Zelaya et al., 2007).

CONCLUSION

We have presented the first overall phylogeny of Astereae (Fig. 37.1A–E), based on nuclear ribosomal internal transcribed spacer (ITS) sequence data. Though the tree is not fully resolved, we believe it reflects most of the important features of the evolution of the tribe. Most significantly, we confirmed that Astereae emerged in southern Africa and dispersed early to other continents. Most early lineages diverge in sequence along the spine of the tree and are species poor, but a few provide examples of evolutionary radiations in the southern hemisphere: Homochrominae and Grangeinae (southern Africa), Paleo South American clade and New Zealand clade. An evolutionary explosion occurred among the crown lineages of Astereae, which conquered in rapid succession Australasia, South America (independently of the paleo invasion), and North America. From each of these new centers of diversification, dispersals occurred widely when opportunity arose, to Asia, the Pacific, Europe, and back to South America. What is most significant here is that radiation in each continent did not involve repeated intercontinental migrations. What is also significant is the dispersal capacity of Astereae, which show few dispersal specializations beyond anemochory.

The taxonomic consequence of this phylogenetic pattern is that, pending the identification of appropriate synapomorphies, continent of origin often reflects intergeneric relationships better than do the subtribal classification of Nesom and Robinson (2007). Despite this, we estimate that this classification, based on morphological and anatomical traits analyzed in a traditional manner, represents a significant advance in our knowledge of the tribe since it was founded on a major re-evaluation of characters and relationships. What is needed now is that character evaluation be done in a more strictly phylogenetic context. The phylogeny needs to be validated using other molecular markers, and the groups confirmed with better support and better resolution. This requires that regions both more conserved and more variable than ITS be explored. Also, the level at which subtribes are recognized will need to be discussed among specialists of the tribe to reach a proper consensus, as was done for Compositae (Panero and Funk 2002).

We have shown that potential economic usages of Astereae are greater than usually recognized, notably in domains such of pharmaceutical applications, rubber production, and horticulture. Likewise, we have shown that Astereae provide great scope for evolutionary and biological studies. Well-resolved phylogenies of the tribe, subtribe, and genera will stimulate such studies, and we hope that this overall phylogeny of Astereae will provide the impetus for further research in this field.

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Chapter **38**

Anthemideae

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HISTORICAL OVERVIEW

According to the most recent generic conspectus of Compositae tribe Anthemideae (Oberprieler et al. 2007a), the tribe consists of 111 genera and ca. 1800 species. The main concentrations of members of Anthemideae are in Central Asia, the Mediterranean region, and southern Africa. Members of the tribe are well known as aromatic plants, and some are utilized for their pharmaceutical and/or pesticidal value (Fig. 38.1).

The tribe Anthemideae was first described by Cassini (1819: 192) as his eleventh tribe of Compositae. In a later publication (Cassini 1823) he divided the tribe into two major groups: "Anthémidées-Chrysanthémées" and "Anthémidées-Prototypes", based on the absence vs. presence of paleae (receptacular scales). These two subtribes, later validly named Chrysantheminae Less. and Anthemidinae Dumort., were used by most systematists concerned with the infratribal taxonomy in the following decades (e.g., Candolle 1838; Boissier 1875; Hoffmann 1890–1894). The artificiality of this subdivision was clearly stated by Merxmüller (1954) and Wagenitz (1964), and demonstrated by Greuter (1968) when he found that in *Ammanthus*, previously classified as Chrysantheminae, the presence or absence of paleae "does not even suffice to distinguish species". Hybridization experiments among members of Anthemideae made by Mitsuoka and Ehrendorfer (1972) have shown that the inheritance of paleae is probably under simple oligogenic control.

The circumscription of Anthemideae remained relatively unchanged since the early artificial classification systems of Lessing (1832), Hoffmann (1890–1894), and Bentham (1873), and also in more recent ones (e.g., Reitbrecht 1974; Heywood and Humphries 1977; Bremer and Humphries 1993), with *Cotula* and *Ursinia* being included in the tribe despite extensive debate (Bentham 1873; Robinson and Brettell 1973; Heywood and Humphries 1977; Jeffrey 1978; Gadek et al. 1989; Bruhl and Quinn 1990, 1991; Bremer and Humphries 1993; Kim and Jansen 1995). Subtribal classification, however, has created considerable difficulties throughout the taxonomic history of the tribe. Owing to the artificiality of a subtribal classification based on the presence vs. absence of paleae, numerous attempts have been made to develop a more satisfactory taxonomy for the tribe. In this endeavour, carpological characters proved to be the most important source of phylogenetically relevant features. Despite some early findings on the relevance of carpological characters in delimitating natural genera (e.g., Schultz 1844, 1860; and in Schnitzlein 1854), the full merit for the exploitation of achene anatomy for taxonomic questions in Anthemideae is attributed to J. Briquet who used characters of the pericarp to circumscribe Mediterranean genera in the tribe (Briquet 1916a–c; Briquet and Cavillier 1916). In the following decades, detailed carpological studies have been made in the so-called "*Chrysanthemum* complex" (Giroux 1930, 1933; Horvatic 1963; Borgen 1972; Alavi 1976; Humphries 1976), the *Anthemis* complex (Humphries 1977; Benedí i González and Molero i Briones 1985), and in a more geographically

Fig. 38.1. Representative members of Anthemideae. **A** *Osmitopsis asteriscoides* (P. Bergius) Less.; **B** *Athanasia dentata* (L.) L.; **C** *Artemisia arborescens* (Vaill.) L.; **D** *Achillea cretica* L.; **E** *Anthemis rigida* Heldr.; **F** *Ismelia carinata* (Schousb.) Sch.Bip. [Photographs: A, B, Ch. Oberprieler; C–F, P. Schönfelder.]

focused study by Kynčlová (1970). The carpological survey of Reitbrecht (1974) deserves consideration as the first comprehensive tribal evaluation of achene anatomical features for the elaboration of a more natural subtribal classification, utilizing as many genera with suitable study material as possible but with a clear focus on the northern hemisphere representatives of the tribe. The latter study yielded a subdivision into seven provisional groups which were also accepted for the (informal) subtribal treatment of Anthemideae in Heywood and Humphries (1977). Triggered by these surveys, studies of achene anatomy in the following decades contributed to a better understanding of the taxonomy and phylogenetic classification of southern hemisphere genera: Källersjö (1985, 1988) used mainly carpological characters for generic circumscriptions in the *Athanasia* and *Pentzia* complexes, respectively, while Bruhl and Quinn (1990) added fruit anatomical evidence for the exclusion of several genera of "Cotuleae" from Anthemideae and the retention of *Cotula*, *Leptinella*, *Nananthea*, and *Soliva* in the tribe.

The tribe was monographed and a subtribal classification with twelve subtribes was proposed by Bremer and Humphries (1993) based on a mostly morphological phylogenetic study. However, the proposed classification showed little congruence with any of the previous classifications and with molecular phylogenies for the whole tribe (Watson et al. 2000), for the Mediterranean genera alone (Francisco-Ortega et al. 1997, Oberprieler and Vogt 2000, Oberprieler 2002, 2004a, b, 2005), or for Asian genera (Watson et al. 2002). As a consequence of these findings, Oberprieler et al. (2007a) rejected the subtribal classification of Bremer and Humphries (1993) in their recent treatment of Anthemideae in Kubitzki's *The Families and Genera of Vascular Plants*, volume 8, *Asterales* (Kadereit and Jeffrey 2007) and arranged the genera in a linear manner according to the results of Watson et al. (2000), i.e., in a primarily geographic representation of the tribe members beginning with the (basal) southern African representatives, followed by the central and eastern Asian ones, and ending with the Eurasian/Mediterranean genera; within these major biogeographical groups, genera were arranged alphabetically and/or into putative monophyletic generic groups. In the present treatment, we adopted a new subtribal classification proposed recently by Oberprieler et al. (2007b) based on phylogenetic analyses of nrDNA ITS and cpDNA *ndhF* sequence variation.

PHYLOGENY

Reconstructions of the evolutionary history of Anthemideae presented and discussed here are based on two molecular datasets: The first comprises sequence information for cpDNA *ndhF* for 62 representatives of 61 genera of the tribe (Himmelreich et al. 2008), while the second is more complete and provides sequence information for the nrDNA ITS marker for 103 of the 111 accepted genera (Oberprieler et al. 2007b). Both datasets were analyzed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian Inference (BI) as tree-constructing tools and representatives of tribes Astereae, Calenduleae, Gnaphalieae, and (in the case of *ndhF*) Inuleae as outgroups. The resulting tree topologies of the ML analyses are depicted in Figs. 38.2–38.4, along with support values from bootstrap (BS) analyses (MP and ML in the *ndhF* dataset, MP in the ITS dataset) and with posterior probabilities (PP) of the BI analyses.

Despite some minor incongruence between the phylogenetic reconstructions based on the two markers (that will be discussed in detail below), there are a seven features supported by both analyses:

1. The tribe Anthemideae in the circumscription of Bremer and Humphries (1993) and Oberprieler et al. (2007a) is strongly supported as monophyletic in both analyses (*ndhF*: BS: 87% MP, 90% ML; PP: 1.00; ITS: BS: 88% MP; PP: 1.00). Therefore, it is now clear that the tribe includes the genera *Cotula* and *Ursinia* for which a classification as independent tribes has been previously debated (Bentham 1873; Robinson and Brettell 1973; Heywood and Humphries 1977; Jeffrey 1978; Gadek et al. 1989; Bruhl and Quinn 1990, 1991; Bremer and Humphries 1993; Kim and Jansen 1995).
2. Both datasets are congruent with each other in the basal split within the tribe into three independent monophyletic lineages: (*a*) the isolated position of the genus *Osmitopsis* from southern Africa (i.e., subtribe Osmitopsidinae), (*b*) the well supported clade around *Cotula* (i.e., subtribe Cotulinae) with members showing their distributional range in southern Africa and/or the southern hemisphere (*ndhF*: BS: 100% MP, 100% ML; PP: 1.00; ITS: BS: 93% MP; PP: 1.00); and (*c*) the well supported clade comprising the rest of the tribe with further southern African genera and all Asian and Eurasian/Mediterranean representatives (*ndhF*: BS: 91% MP; PP: 1.00; ITS: BS: 88% MP; PP: 1.00).
3. A further common feature of phylogenetic trees based on both markers is a paraphyletic assemblage of southern African genera around the two genera *Athanasia* and *Ursinia* (i.e., subtribes Athanasiinae and Ursiniinae) at the base of the above-described clade (c) as opposed to the strongly supported monophyletic group (*ndhF*: BS: 90% MP, 91% ML; PP: 1.00; ITS: BS: 91% MP; PP: 1.00) comprising all northern hemisphere representatives and a closely-knit, southern African generic group around *Pentzia* (i.e., subtribe Pentziinae, see below). This is also where

the main discrepancies are found between the two datasets: in the *ndhF* analyses the clade of *Eumorphia*, *Gymnopentzia*, and *Phymaspermum* (i.e., subtribe Phymasperminae) is nested within members of the Pentziinae/northern hemisphere clade, whereas in the ITS analyses these three genera are excluded from the latter clade and form a lineage in the paraphyletic assemblage around *Athanasia* and *Ursinia*. Himmelreich et al. (2008) provide two possible explanations for this incongruence between nuclear and plastid dataset: (*a*) The progenitor of Phymasperminae may have been formed by a hybridization event between a member of the phylogenetically basal southern African group of genera as a paternal partner and either a member of the Asian groups around *Artemisia*, *Microcephala*, or *Pseudohandelia* or a member of southern African Pentziinae as the maternal (chloroplast contributing) partner, whereby the latter event seems

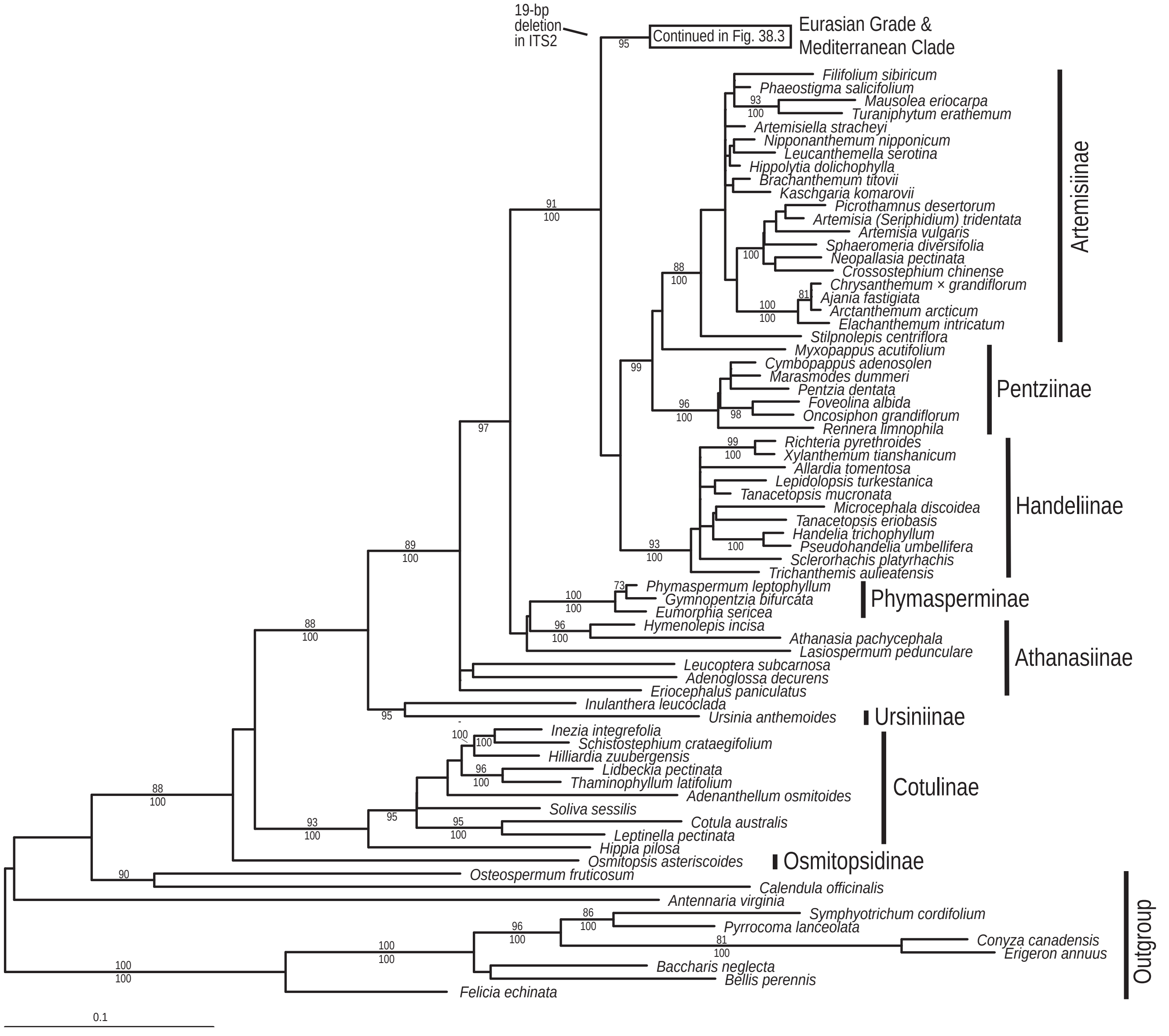

Fig. 38.2. Basal part of a phylogenetic tree from a maximum-likelihood (ML) analysis of nrDNA ITS sequence variation database on the TrN + Γ model of DNA substitution (Tamura and Nei 1993) with base frequencies, gamma distribution parameter α, and substitution rate matrix given in Oberprieler et al. (2007b). Values above branches indicate bootstrap support values from a maximum-parsimony (MP) analysis based on 100 replicates and values below branches give posterior probability (PP in percent) of clades gained from a Bayesian analysis (BI) of data.

geographically more reasonable. (*b*) Phymasperminae may hold a phylogenetically intermediate and bridging position between the more basal southern African members of the tribe and the more advanced crown group consisting of Pentziinae and all Asian and Eurasian Anthemideae, sharing the rather apomorphic chloroplast type with the latter but a relatively plesiomorphic ITS sequence with the former. As a consequence of this scenario, Phymasperminae may be a good candidate for the sister group to the clade of Pentziinae + Asian + Eurasian Anthemideae, while Pentziinae itself may exhibit a sister group-relationship to the Asian (or the Asian + Eurasian) members of the tribe.

4. Besides monophyletic Phymasperminae (no significant support for *ndhF*, but for ITS: BS: 100% MP; PP: 1.00) and Pentziinae (*ndhF*: BS: 81% MP, 83% ML; PP: 0.99; ITS: BS: 96% MP; PP: 1.00, excluding *Myxopappus*), there is also support for two generic assemblages with an Asian center of diversity. While the clade around *Handelia* (i.e., subtribe Handeliinae) receives high support values in analyses of both markers (*ndhF*: BS: 86% MP, 87% ML; PP: 1.00; ITS: BS: 93% MP; PP: 1.00), subtribe Artemisiinae is only supported by the reconstructions based on ITS (BS: 88% MP; PP: 1.00).
5. A further corresponding topological feature of all analyses is the strongly supported clade of Eurasian and Mediterranean genera comprising subtribes Anthemidinae, Glebionidinae, Leucantheminae, Leucanthemopsidinae, Matricariinae, and Santolininae. In addition to the high support values from the different sequence-based analyses (*ndhF*: BS: 95% MP, 92% ML; PP: 1.00; ITS: PP: 0.95), the monophyly of this generic assemblage is further corroborated by the synapomorphy of a 19-bp deletion in ITS2 found in all of the members of the clade.
6. Within the Eurasian + Mediterranean clade, corresponding topological features are (*a*) the sister group relationship between generic groups around *Anthemis* (i.e., subtribe Anthemidinae) and *Matricaria* (i.e., subtribe Matricariinae) (*ndhF*: BS: 78% MP, 76% ML; PP: 1.00; ITS: PP: 1.00) and (*b*) the monophyletic group formed by members of Glebionidinae, Leucantheminae and Santolininae. The latter, however, is only supported by *ndhF*-based analyses (BS: 83% MP, 86% ML; PP: 1.00). According to the ITS-based analyses, the generic assemblage around *Leucanthemopsis* (i.e.,

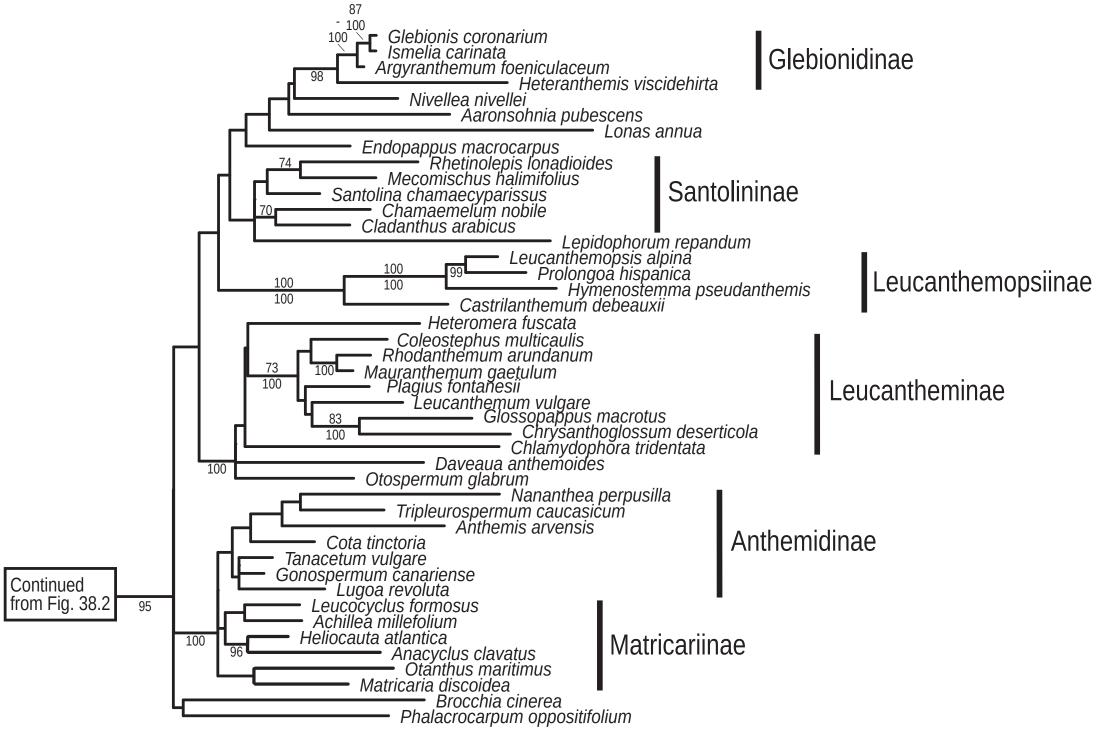

Fig. 38.3. Apical part of a phylogenetic tree from a maximum-likelihood (ML) analysis of nrDNA ITS sequence variation databased on the TrN + Γ model of DNA substitution (Tamura and Nei 1993) with base frequencies, gamma distribution parameter α, and substitution rate matrix given in Oberprieler et al. (2007b). Values above branches indicate bootstrap support values from a maximum-parsimony (MP) analysis based on 100 replicates, and values below branches give posterior probability (PP in percent) of clades gained from a Bayesian analysis (BI) of data.

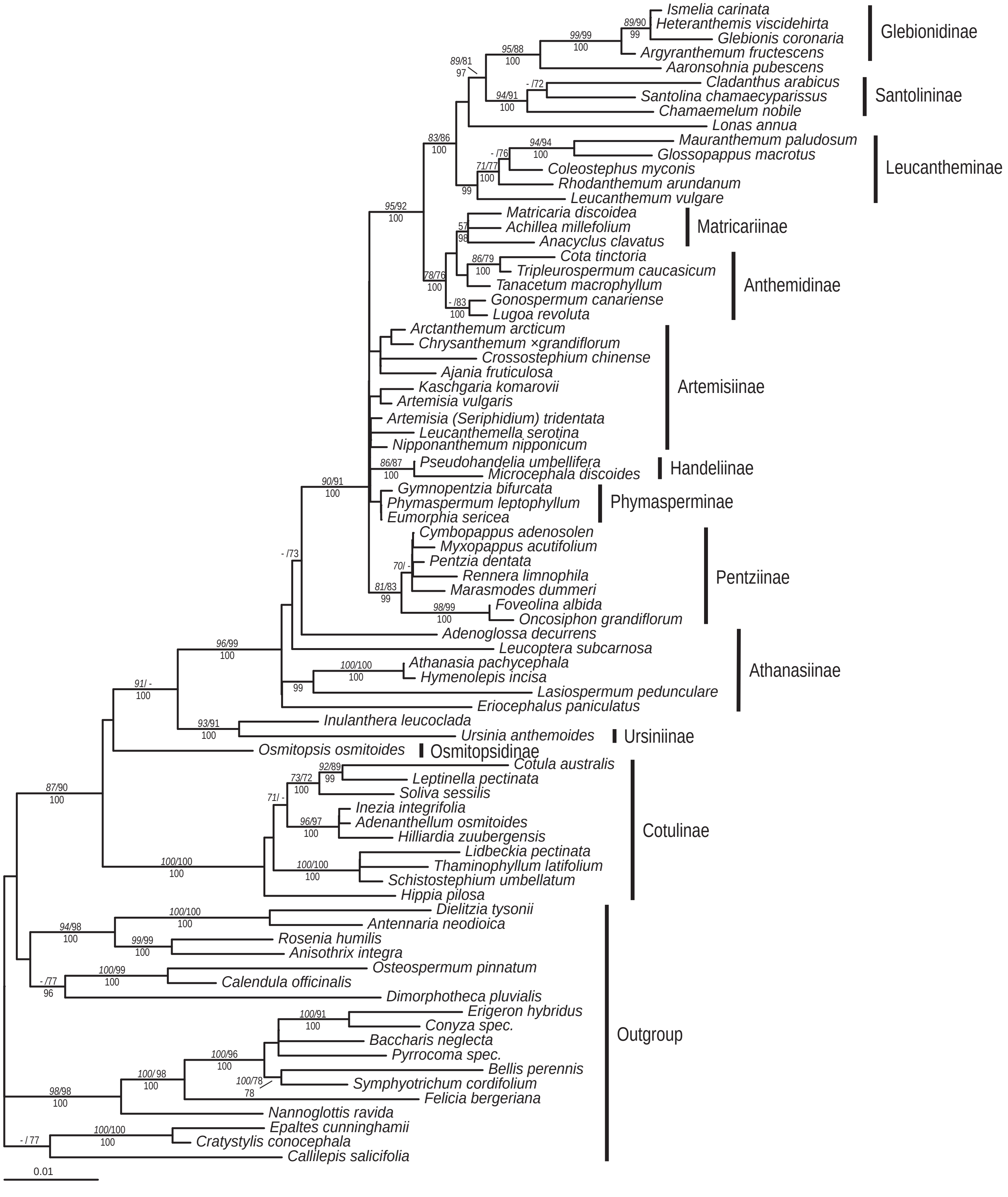

Fig. 38.4. Phylogenetic tree from a maximum-likelihood (ML) analysis based on cpDNA *ndhF* sequence information. Numbers above the lines are bootstrap values of the MP and ML analyses; numbers below the lines are posterior probabilities of the Bayesian inference (BI) approach (adapted from Himmelreich et al. 2008).

subtribe Leucanthemopsidinae), that shows strong support (BS: 100% MP; PP: 1.00) as a monophyletic group, may also belong to this clade, but there is evidence that the latter subtribe may be more basal within the Eurasian + Mediterranean clade. In previous analyses based on the cpDNA *trnL-trnF* intergenic spacer, Oberprieler and Vogt (2000) observed that members of Glebionidinae, Leucantheminae and Santolininae share an apomorphic 5 bp deletion while members of Anthemidinae, Matricariinae and Leucanthemopsidinae show the plesiomorphic condition.

7. Both datasets in the present study unequivocally show a clear biogeographic pattern with a basal position of southern hemisphere representatives of the tribe. This is in accordance with previous studies based on *ndhF* sequence variation (Watson et al. 2000; Himmelreich et al. 2008) and on ITS sequences (Oberprieler 2005).

SUBTRIBAL TAXONOMY

Based on our analyses of ITS and *ndhF* sequence variation, Oberprieler et al. (2007b) proposed a new subtribal classification of Compositae-Anthemideae. Discussion of the molecular phylogenetic analyses in conjunction with morphological, anatomical, cytological, embryological, and phytochemical evidence resulted in the recognition of 14 subtribes. Table 38.1 provides information about the subtribal placement of most genera, although some genera are missing or have equivocal molecular evidence. Following their biogeographical pattern in the phylogenetic reconstructions, the subtribes are arranged into (*1*) a southern hemisphere grade, (*2*) an Asian-southern African grade, (*3*) an Eurasian grade, and (*4*) a Mediterranean clade.

I. Southern hemisphere grade

Osmitopsidinae Oberprieler & Himmelreich in Willdenowia 37: 94. 2007

The subtribe consists of the single genus, *Osmitopsis*, that holds a basal and isolated position in the molecular analyses of ITS and *ndhF* sequence variation. It contains nine southern African species of shrubby habit with alternate and entire to lobed leaves and an indumentum of basifixed hairs. It is further characterized by radiate capitula with a paleate receptacle, ray florets with a white, many-veined limb and a pilose tube, and disc florets with a 5-lobed corolla, basally caudate anthers with non-polarized endothecial tissue and a slender filament collar. The achenes are obovoid to ellipsoid, 3–4-angled or -ribbed, and have an apex with a corona made of subulate to triangular, basally fused scales that is sometimes lacking.

The main characteristic of *Osmitopsis* is its possession of tailed anthers that led some authors (Bentham 1873; Hoffmann 1890–1894) to consider an inulean affiliation for the genus, whereas others (e.g., Cassini 1823) included it in their concept of Anthemideae. Palynological evidence (Stix 1960) and additional characters like odor, the occurrence of pluriseriate involucral bracts with scarious margins, together with the truncate style and the tendency towards the reduction of the pappus also support its inclusion in Anthemideae. This membership is also strongly supported by our present analyses based on ITS and *ndhF* sequence data.

While membership in Anthemideae is supported in both analyses, its relationship to either of the two highly supported subclades of the tribe (subtribe Cotulinae on the one hand and the remainder of the tribe on the other) remains unresolved. This corroborates observations made by Bremer (1972) and Nordenstam (1987) who already noted that the genus is systematically isolated in the tribe. The inclusion of the paleate genus *Osmitopsis* in the subtribe Thaminophyllinae by Bremer and Humphries (1993), together with the alleged closely related (epaleate) genera, *Adenenthellum*, *Inezia*, *Lidbeckia*, and *Thaminophyllum*, was mainly based on a similar habit and foliage, the occurrence of many-veined rays and a large stylopodium, the tendency towards the loss of a pappus in some species, and the (still not yet fully corroborated) base chromosome number of $x = 10$. Alternative affiliations were proposed by Reitbrecht (1974) and Baagøe (1977) who considered closer relationships of the genus to *Lasiospermum* (paleate, $x = 9$) based on morphological and ligule micromorphological grounds, respectively, and by Watson et al. (2000) who found a strongly supported sister group relationship of *Osmitopsis* with *Athanasia* (paleate, $x = 8$) in their molecular study based on *ndhF* sequence variation. Since both *Lasiospermum* and *Athanasia* are characterized, however, by deviating base chromosome numbers and anthers with polarized endothecial tissue (unpolarized in *Osmitopsis*), these alleged relationships seem unjustified. The same is true for any relationship with other genera of Anthemideae characterized by tailed anthers: neither *Inulanthera* nor *Hippolytia* are confirmed by our present analyses as closely related to *Osmitopsis*.

Cotulinae Kitt., Taschenb. Fl. Deutschl., ed. 2, 2: 609. 1844 = Thaminophyllinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 144. 1993

Cotulinae are formed by ten genera with approximately 137 species of the southern hemisphere with its center of diversity in southern Africa but also distributed and species-rich in Australia, New Guinea and New Zealand, and some species widespread and naturalized also in the northern hemisphere. While strongly supported as a monophyletic group in our molecular phylogenetic

Table 38.1. List of accepted genera of Compositae-Anthemideae, with information on number of species, distributional area, and subtribal relationships.

	Number of species	Distribution
I. SOUTHERN HEMISPHERE GRADE		
1. Osmitopsidinae Oberprieler & Himmelreich		
Osmitopsis Cass.	9	South Africa
2. Cotulinae Kitt.		
Adenanthellum B. Nord.	1	South Africa, Swaziland
Cotula L.	55	Africa, Australia, South America, Mexico, New Zealand, southern oceanic islands
Hilliardia B. Nord.	1	South Africa
Hippia L.	8	South Africa
Inezia E. Phillips	2	South Africa, Swaziland
Leptinella Cass.	33	New Guinea, Australia, New Zealand, South America, Falkland Islands, subarctic islands
Lidbeckia P.J. Bergius	2	South Africa
Schistostephium Less.	12	South Africa, Mozambique, Zimbabwe, Swaziland
Soliva Ruiz & Pav.	8	South America
Thaminophyllum Harv.	3	South Africa
3. Ursiniinae Bremer & Humphries		
Ursinia Gaertn.	39	South Africa, Namibia, Botswana, Ethiopia
4. Athanasiinae (Less.) Lindl. ex Pfeiff.		
Adenoglossa B. Nord.	1	South Africa
Athanasia L.	39	South Africa, Namibia
Eriocephalus L.	32	South Africa, Namibia, Botswana, Lesotho
Hymenolepis Cass.	7	South Africa
Lasiospermum Lag.	4	South Africa, Namibia, Lesotho, Egypt (Sinai)
Leucoptera B. Nord.	3	South Africa
5. Phymasperminae Oberprieler & Himmelreich		
Eumorphia DC.	6	South Africa, Lesotho, Swaziland
Gymnopentzia Benth.	1	South Africa, Lesotho
Phymaspermum Less.	19	South Africa, Swaziland, Zimbabwe, Namibia
Genera of the Southern hemisphere grade unassigned to a subtribe		
Inulanthera Källersjö[a]	10	South Africa, Swaziland, Lesotho, Angola, Zimbabwe, Madagascar
II. ASIAN-SOUTH AFRICAN GRADE		
6. Pentziinae Oberprieler & Himmelreich		
Cymbopappus B. Nord.	3	South Africa
Foveolina Källersjö	5	South Africa, Namibia
Marasmodes DC.	4	South Africa
Myxopappus Källersjö	2	South Africa, Namibia
Oncosiphon Källersjö	8	South Africa, Lesotho, Namibia

Table 38.1. Continued.

	Number of species	Distribution
Pentzia Thunb.	23	South Africa, Namibia, Morocco, Algeria, Chad, Somalia, Yemen
Rennera Merxm.	4	Namibia, South Africa, Botswana
7. Handeliinae Bremer & Humphries		
Allardia Decne.	8	Afghanistan, Central Asia, Mongolia, China
Handelia Heimerl	1	Afghanistan, Pakistan, Central Asia, China
Lepidolopsis Poljakov	1	Iran, Afghanistan, Central Asia
Microcephala Pobed.	5	Central Asia, Afghanistan, Iran, Pakistan, Mongolia, China
Pseudohandelia Tzvelev	1	Iran, Afghanistan, Central Asia, China
Richteria Kar. & Kir.	6	Iran, Afghanistan, Central Asia, Mongolia, China, Himalaya
Sclerorhachis (Rech. f.) Rech. f.	4	Iran, Afghanistan
Tanacetopsis (Tzvelev) Kovalevsk.	21	Iran, Afghanistan, Central Asia
Trichanthemis Regel & Schmalh.	9	Central Asia
Xylanthemum Tzvelev	8	Iran, Afghanistan, Central Asia
8. Artemisiinae Less.		
Ajania Poljakov	39	Central Asia, China, Japan
Arctanthemum (Tzvelev) Tzvelev	3	Arctic Eurasia, Siberia, Japan, Arctic North America
Artemisia L. (incl. *Seriphidium* Fourr.)	522	Northern hemisphere, South America, South Africa, Pacific Islands
Crossostephium Less.	1	Philippines, Taiwan, South Japan, China
Filifolium Kitam.	1	Siberia, Mongolia, China, Korea
Mausolea Poljakov	1	Iran, Afghanistan, Central Asia
Neopallasia Poljakov	3	Central Asia, South Siberia, Mongolia, China
Picrothamnus Nutt.	1	North America
Sphaeromeria Nutt.	9	North America, Mexico
Turaniphytum Poljakov	2	Turkmenistan, Iran, Afghanistan, Kazakhstan
Artemisiella Ghafoor	1	Ladakh, Tibet, Nepal, Bhutan, South China
Brachanthemum DC.	10	Central Asia, Mongolia, China
Chrysanthemum L.	37	Asia (Mongolia, Russia, China, Japan, Korea), East Europe
Elachanthemum Y. Ling & Y.R. Ling	1	Mongolia, China
Hippolytia Poljakov	19	Central Asia, Mongolia, China, Himalaya
Kaschgaria Poljakov	2	Mongolia, Kazakhstan, China
Leucanthemella Tzvelev	2	East Europe, Far East (Mongolia, China, Korea, Japan)
Nipponanthemum Kitam.	1	Japan
Phaeostigma Muldashev	3	China
Stilpnolepis Krasch.	1	Mongolia, China
Genera of the Asian-South African grade unassigned to a subtribe		
Ajaniopsis C. Shih[b]	1	China, Tibet
Cancrinia Kar. & Kir.[c]	4	Central Asia, Mongolia, China
Cancriniella Tzvelev[c]	1	Central Asia

Table 38.1. Continued.

	Number of species	Distribution
Hulteniella Tzvelev[b]	1	Arctic Eurasia, Arctic North America
Lepidolopha C. Winkl.[c]	9	Central Asia
Opisthopappus C. Shih[b]	2	China
Polychrysum (Tzvelev) Kovalevsk.[c]	1	Afghanistan, Central Asia
Tridactylina (DC.) Sch.Bip.[b]	1	East Siberia
Ugamia Pavlov[c]	1	Central Asia
III. EURASIAN GRADE		
9. Matricariinae Willk.		
Achillea L.	115	Europe, Asia, North Africa, North America
Leucocyclus Boiss.	1	Turkey
Otanthus Hoffmanns. & Link	1	South Europe, North Africa, Southwest Asia
Anacyclus L.	12	South Europe, North Africa, Southwest Asia
Heliocauta Humphries	1	Morocco
Matricaria L.	6	Europe, North Africa, Asia, North America
10. Anthemidinae (Cass.) Dumort.		
Anthemis L.	175	Europe, Southwest Asia, North and East Africa
Cota J. Gay	40	Europe, Southwest Asia, North Africa
Nananthea DC.	1	South Europe (Corsica, Sardinia)
Tanacetum L.	154	Europe, Asia, North Africa, North America
Gonospermum Less.	4	Canary Islands
Lugoa DC.	1	Canary Islands
Tripleurospermum Sch.Bip.	40	Europe, North Africa, Asia, North America
11. Leucanthemopsidinae Oberprieler & Vogt		
Castrilanthemum Vogt & Oberprieler	1	Spain
Hymenostemma Willk.	1	Spain
Leucanthemopsis (Giroux) Heywood	9	Europe, Northwest Africa
Prolongoa Boiss.	1	Spain
Genera of the Eurasian grade unassigned to a subtribe		
Brocchia Vis.[d]	1	North Africa, Southwest Asia
Phalacrocarpum (DC.) Willk.[e]	2	Southwest Europe
IV. MEDITERRANEAN CLADE		
12. Leucantheminae Bremer & Humphries		
Chlamydophora Ehrenb. ex Less.	1	North Africa, Cyprus
Chrysanthoglossum B.H. Wilcox & al.	2	North Africa
Coleostephus Cass.	3	Mediterranean region, Macaronesia
Glossopappus Kunze	1	Southwest Europe, North Africa
Leucanthemum Mill.	43	Europe, Siberia
Mauranthemum Vogt & Oberprieler	4	North Africa, Southwest Europe

Table 38.1. Continued.

	Number of species	Distribution
Plagius L'Hèr. ex DC.	3	South Europe (Corsica, Sardinia), North Africa
Rhodanthemum (Vogt) B.H. Wilcox & al.	14	Northwest Africa, Southwest Europe
13. Santolininae Willk.		
Chamaemelum Mill.	2	South and West Europe, Northwest Africa
Cladanthus Cass.	5	South Europe, North Africa, Southwest Asia
Mecomischus Coss. ex Benth. & Hook. f.	2	Northwest Africa
Rhetinolepis Coss.	1	Northwest Africa
Santolina L.	13	South Europe, Northwest Africa
14. Glebionidinae Oberprieler & Vogt		
Argyranthemum Webb	24	Macaronesia
Glebionis Cass.	2	South Europe, North Africa, Northwest Asia, Macaronesia
Heteranthemis Schott	1	Northwest Africa
Ismelia Cass.	1	Northwest Africa
Genera of the Mediterranean clade unassigned to a subtribe		
Aaronsohnia Warb. & Eig	2	North Africa, Southwest Asia
Daveaua Willk. ex Mariz[f]	1	Northwest Africa, Southwest Europe
Endopappus Sch.Bip.	1	North Africa
Heteromera Pomel[f]	2	North Africa
Lepidophorum Neck. ex DC.	1	Southwest Europe
Lonas Adans.	1	North Africa, South Europe
Nivellea B.H. Wilcox & al.	1	Morocco
Otospermum Willk.[f]	1	North Africa, Southwest Europe

[a] Suggested placement in Ursiniinae, [b] Artemisiinae, [c] Handeliinae, [d] Matricariinae, [e] Leucanthemopsidinae, [f] Leucantheminae.

reconstructions, the subtribe is morphologically diverse and consists of members of subtribes Matricariinae (*Cotula*, *Hilliardia*, *Hippia*, *Leptinella*, *Schistostephium*, *Soliva*) and Thaminophyllinae (*Adenanthellum*, *Inezia*, *Lidbeckia*, *Thaminophyllum*) in the sense of Bremer and Humphries (1993).

In the present circumscription, the subtribe contains mainly shrubs and perennial herbs (with annuals occurring in *Cotula*, *Leptinella*, and *Soliva*) with a plesiomorphic, basifixed indumentum. The capitula, which are arranged solitarily or in lax to dense corymbs, are radiate, disciform, or discoid. The receptacle is usually epaleate, but sometimes hairy (*Lidbeckia*, *Thaminophyllum*) or marginally paleate (*Schistostephium*). The ray florets (when present) are either white or yellow, and in *Adenanthellum*, *Inezia*, and *Thaminophyllum* confluent with the achene. In *Cotula* the ray florets or marginal female disc florets are stalked. The disc florets are usually hermaphroditic or functionally male in *Hippia*, *Leptinella*, *Schistostephium*, and *Soliva* with a 3–4- or sometimes 5-lobed (*Adenanthellum*, *Hippia*) corolla, and anthers with non-polarized endothecial tissue and a slender filament collar. The achenes of Cotulinae are highly polymorphic, with a tendency towards the reduction of rib number from 3–4 (as in *Osmitopsis* of the Osmitopsidinae) towards 2, and the transition between terete to dorso-ventrally flattened cross-sections. As an exception to this, 10-ribbed and only slightly compressed achenes are observed in *Adenanthellum*. The subtribe shows the presumably plesiomorphic base chromosome number of $x = 10$ (with descending dysploidy in *Cotula* [$x = 8, 9, 10$] but ascending dysploidy in the closely related genus *Leptinella* [$x = 13$]). The monophyly of this subtribe suggested by our molecular results may be corroborated in morphological respects by the apomorphies of epaleate receptacles and 4-lobed corollas of tubular florets (with exceptions to this in *Adenanthellum* and *Hippia*).

Evidence for the unification of members of Bremer and Humphries's (1993) two subtribes into a single subtribe was suggested by Nordenstam (1987) when describing the new genus *Hilliardia* (Matricariinae in the sense of Bremer and Humphries 1993) and connecting it with *Adenanthellum* and *Inezia* (Thaminophyllinae). These genera possess ray florets with a bifid or emarginated limb, a branching venation, a papillate upper surface, a reduced tube, and large sessile glands. Additionally, there is further support from phytochemical investigations made by Bohlmann and Zdero (1972a, 1974, 1977, 1982) who found that the guaianolide called zuubergenin from *Hilliardia* is closely related to guaianolides that have been found in *Lidbeckia* and *Inezia* (both Thaminophyllinae), and that *Thaminophyllum* is phytochemically related to *Schistostephium* (sub *Peyrousea*, Matricariinae).

Ursiniinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 91. 1993

Ursiniinae in the sense of Bremer and Humphries (1993), comprising the genera *Athanasia* (including *Asaemia*), *Eumorphia*, *Gymnopentzia*, *Hymenolepis*, *Lasiospermum*, *Phymaspermum*, and *Ursinia*, are not supported as monophyletic in our molecular phylogenetic reconstructions where we observe a deep split between *Ursinia* on the one hand and the remainder of the mentioned genera on the other hand. The circumscription of Ursiniinae in the sense of Bremer and Humphries (1993) was based mainly on phytochemical evidence, with a number of publications made by Bohlmann and co-workers (Bohlmann and Rao 1972; Bohlmann and Zdero 1972b, 1974, 1978a, b; Bohlmann et al. 1973; Bohlmann and Grenz 1975) indicating that representatives of these genera possess furanosesquiterpenes rather than the common polyacetylenes. This, in conjunction with morphological and anatomical evidence (paleate receptacles, ray floret limbs with tabular epidermis cells, anthers with partly or totally polarized endothecial tissue) was considered sufficient to suggest the monophyly of the subtribe (Källersjö 1985; Bremer and Humphries 1993), which also included *Ursinia*, a carpologically and palynologically distinct genus. However, due to its anthers with broad ovate apical appendages and baluster-shaped filament collars (Meiri and Dulberger 1986), its pollen exine without columnar structure, and its achenes with a biseriate pappus formed of scales, this genus had been formerly considered to hold a very isolated position within Anthemideae (Cassini 1816; Beauverd 1915), or as an independent tribe Ursinieae (Robinson and Brettell 1973), or even as a member of Arctoteae (Bentham 1873).

Treated here as an independent subtribe, Ursiniinae, with its sole member *Ursinia*, is a mainly southern African subtribe (with one species reaching Ethiopia) of perennial (sometimes annual) herbs or shrublets characterized by basifixed hairs and alternate, entire to 2-pinnatisect, sometimes succulent leaves, radiate or discoid capitula arranged solitarily or in lax corymbs with a paleate receptacle, yellow, orange, white or reddish ray florets and 5-lobed disc florets with polarized endothecial tissue and a baluster-shaped filament collar. The achenes are cylindrical or obovoid, straight or curved, circular in cross-section, with five ribs and a basal tuft of hairs or glabrous; their apex is furnished with a uniseriate pappus of 5–10 ovate or circular scales, or a biseriate pappus of five outer such scales and five inner subulate ones, or is rarely epappose. The genus shows a descending dysploidy with base chromosome numbers of $x = 5, 7, 8$.

Our present molecular phylogenetic reconstructions suggest a close relationship of *Ursinia* with the small, southern African genus *Inulanthera*, which was treated as a member of the polyphyletic subtribe Gonosperminae by Bremer and Humphries (1993). Since *Inulanthera* differs from *Ursinia* morphologically (anthers caudate and with slender filament collar, achenes with a pappus of small scales terminating each of the 8–10 ribs), we have refrained from including it in Ursiniinae to emphasize the isolated phylogenetic position of *Ursinia*. On the other hand, we also consider it premature to erect an independent subtribe for *Inulanthera* due to the apparently clear position of this genus as sister to *Ursinia* in the molecular phylogenetic reconstructions.

Athanasiinae (Less.) Lindl. ex Pfeiff., Nomencl. Bot. 1(1): 323. ante 12 Jul 1872

This subtribe is comprised of genera that were formerly classified as members of Matricariinae (*Adenoglossa*, *Eriocephalus*, *Leucoptera*) or Ursiniinae (*Athanasia*, *Hymenolepis*, *Lasiospermum*) sensu Bremer and Humphries (1993). Since the distinction of this group of genera from *Ursinia* is strongly supported, unification under a single subtribe Ursiniinae seems unjustified. However, the assemblage of genera around *Athanasia* is by far the most problematic in our present classification because in the ITS tree *(1)* the group appears to be paraphyletic with *Adenoglossa*, *Eriocephalus*, and *Leucoptera* being sister group to a well-supported clade of *Athanasia*, *Hymenolepis*, *Lasiospermum* plus Phymasperminae and the Pentziinae-northern hemisphere clade (*Trichanthemum* through *Glebionis*), and *(2)* Phymasperminae appear to be closely related to *Athanasia*, *Hymenolepis*, and *Lasiospermum*, making Athanasiinae even more paraphyletic. While the former findings are also supported by the analyses based on *ndhF* sequence variation, the three Phymasperminae genera hold a different position in the plastid phylogenetic reconstruction, supporting their treatment as an independent subtribe (see discussion below).

While molecular evidence is (at best) equivocal with respect to the monophyly of Athanasiinae, there is one morphological character that appears to support a close relationship among these genera: with the exception of *Eriocephalus*, all members of Athanasiinae (together with Phymasperminae) are characterized by the possession of anthers with polarized endothecial tissue. Since this character expression is apomorphic relative to the unpolarized endothecium found in the more basal Cotulinae and Osmitopsidinae, and in the more advanced subtribes, this morphological evidence may argue for a monophyly of the subtribe (and, as a consequence, the inclusion of Phymasperminae).

As circumscribed here, Athanasiinae are comprised of six mainly southern African genera with approximately 86 species (only one *Lasiospermum* species reaching the northern hemisphere). The plants are mainly shrubs or shrublets, but rarely also perennial and annual herbs (*Adenoglossa*, *Lasiospermum*). They are characterized by alternate or opposite, entire to 2-pinnatisect leaves and radiate, disciform or discoid capitula arranged in a solitary fashion or in lax to dense corymbs with a paleate or epaleate (*Adenoglossa*, *Leucoptera*) receptacle, yellow, white or reddish ray florets, and 5-lobed, hermaphroditic (functionally male in *Eriocephalus*) disc florets with anthers with polarized endothecial tissue (unpolarized in *Eriocephalus*) and a slender filament collar. The achenes are cylindrical to obovate, either terete and with 5–12(–18) ribs or dorsiventrally flattened with lateral wings (*Adenoglossa*, *Leucoptera*); their apex is marginally rounded, with a short, thickened rim (*Athanasia*), or furnished with a corona or scales (*Adenoglossa*, *Hymenolepis*, *Leucoptera*); the pericarp is glabrous or densely hairy (*Eriocephalus*, *Lasiospermum*). Base chromosome numbers are $x = 8, 9$.

Phymasperminae Oberprieler & Himmelreich in Willdenowia 37: 99. 2007

This small subtribe comprises three South African genera with only 26 species. While its monophyly is strongly supported in our phylogenetic analyses based on molecular data, its position in the tribe is rather unclear. Analyses based on ITS show a close relationship to members of Athanasiinae, while analyses based on *ndhF* consistently indicate that Phymasperminae possess a chloroplast type that is more closely related to members of the Pentziinae-northern hemisphere clade than to members of Athanasiinae. Himmelreich et al. (2008) argue that this conflict between results based on nuclear and plastid sequences is either due to a hybrid origin of the ancestor of Phymasperminae (with the plastid donor among members of the Pentziinae-northern hemisphere clade) or may indicate a sister group relationship between Phymasperminae and the Pentziinae-northern hemisphere clade that is unresolved in the ITS trees due to a lack of parallel evolution of the two markers examined.

According to Källersjö (1985) and Bremer and Humphries (1993), the monophyly of the subtribe seen in the molecular phylogenies is also strongly supported by morphology because the three genera share the apomorphies of achenes with 10–12(–18) ribs and a papillose pericarp. The possession of anthers with polarized endothecial tissue indicates a close relationship to Athanasiinae but contrasts markedly with the plastid phylogeny.

Phymasperminae are shrubs or shrublets with basifixed hairs, opposite or alternate, entire to lobed leaves, and radiate or discoid capitula arranged solitarily or in lax corymbs and with epaleate or paleate (*Eumorphia*, occasionally in *Gymnopentzia*) receptacles, white, yellow, or purplish ray florets, and hermaphroditic, 5-lobed disc florets. The achenes are cylindrical or ellipsoid, terete with 10–12(–18) ribs. The apex is truncate or furnished with an entire to dentate, thickened rim or corona. The pericarp is papillose, usually without myxogenic cells or resin sacs, but in *Phymaspermum* with ovoid myxogenic trichomes and resin sacs in some of the ribs.

II. Asian-South African grade

Pentziinae Oberprieler & Himmelreich in Willdenowia 37: 99. 2007

This strongly supported clade of six genera (with the seventh genus, *Myxopappus*, being included due to *ndhF* support) contains further southern African members of subtribe Matricariinae in the sense of Bremer and Humphries (1993). It forms a close-knit group of genera that is characterized by epaleate receptacles, anthers with unpolarized endothecial tissue and slender filament collars, basifixed hairs (medifixed in *Pentzia*), and a base chromosome number of $x = 9$ (with descending dysploidy in *Myxopappus*, *Oncosiphon*, and *Pentzia*). It unites genera of shrubby habit (*Cymbopappus*, *Marasmodes*, *Pentzia*) and annuals (*Foveolina*, *Myxopappus*, *Oncosiphon*, *Rennera*) that were all once united under a broad concept of *Pentzia*, which has been dismembered by Källersjö (1988). According to Bremer and Humphries (1993), this group may be supported as monophyletic by achenes with myxogenic cells on the abaxial surface and on the ribs of the adaxial surface (with exceptions in *Oncosiphon* and *Rennera*) and with an adaxially long auricle (with a secondary loss of a corona in *Oncosiphon*, *Rennera* and some *Pentzia* species). Despite considerable similarity in achene characters (oblong to obovoid, with 4–5 ribs, in *Myxopappus* triquetrous in cross-section and with one adaxial and two lateral ribs), putative close relationships with the northern hemisphere Matricariinae genera, *Matricaria*, *Otospermum*, or *Tripleurospermum*, were not supported by the molecular data. On the other hand, a sister group relationship with subtribe Artemisiinae receives some support (PP 0.99 in the ITS analysis, but not in the *ndhF* analysis), and may be of great importance for the further understanding of the biogeography of the whole tribe, forming a link between the strictly southern hemisphere genera of other subtribes and the northern hemisphere representatives. The occurrence of some species of *Pentzia* in northern Africa or in southwest Asia may add further evidence to this biogeographic pattern, but may, on the other hand, be interpreted equally justified as an example of independent expansion towards the north at a different time.

Handeliinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 108. 1993 ?= Cancriniinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 96. 1993

This subtribe is well supported as monophyletic in the ITS analysis (93% BS; PP 1.0) and consists of at least ten genera that have been members of Handeliinae (*Handelia*, *Lepidolopsis*, *Pseudohandelia*, *Sclerorhachis*), Cancriniinae (*Allardia*, *Richteria*, *Trichanthemis*), Matricariinae (*Microcephala*), and Tanacetinae (*Tanacetopsis*, *Xylanthemum*) in the sense of Bremer and Humphries (1993). Unfortunately, sequence information for the type of Cancriniinae (*Cancrinia* Karelin and Kir. [*Cancrinia chrysocephala* Karelin and Kir.]) is still lacking and inclusion of this subtribe in Handeliinae in the present circumscription is preliminary. However, since other members of Cancriniinae in the sense of Bremer and Humphries (1993) are well nested in this clade and appear to be closely related to *Cancrinia* (synapomorphies of Cancriniinae being the compact, scapoid habitus and involucral bracts with dark brown margins; Bremer and Humphries 1993), inclusion of this subtribe in a broad subtribe Handeliinae seems to be justified.

In its present circumscription, the subtribe Handeliinae is considerably diverse, and synapomorphies from morphology or anatomy are lacking. It contains annual, biennial (hapaxanthic) or perennial (pollacanthic) herbs or subshrubs with basifixed, rarely (in some species of *Tanacetopsis* and *Xylanthemum*) medifixed hairs, alternate, lobed to 3–4-pinnatisect leaves, and discoid or radiate capitula arranged solitarily, in lax to dense corymbs, or in a long spike-like panicle (*Lepidolopsis*). While in most members receptacles are epaleate, *Handelia* and *Sclerorhachis* have paleate receptacles. Ray florets have white, yellow, pink or violet limbs and disc florets are usually 5-lobed (4–6-lobed in *Lepidolopsis*), are sometimes hairy (*Tanacetopsis*, *Trichanthemis*, *Xylanthemum*), and possess anthers with non-polarized endothecial tissue and a baluster-shaped filament collar (slender in *Allardia* and some *Tanacetopsis* species). Achenes are cylindrical to obconical, circular to elliptical in cross-section, with 4–10 ribs, sometimes with 3–5 adaxially arranged ribs (*Microcephala*); their apex is furnished with a corona formed by 25–50 bristle-like scales (*Allardia*), a short rim, consists of laciniate scales of various shapes, or is rarely ecoronate (*Pseudohandelia*, *Sclerorhachis*); the pericarp is usually glabrous and with or without myxogenic cells, but is densely hairy in *Trichanthemis*. While $x = 9$ prevails as the base chromosome number, the dysploid number $x = 7$ is reported for a member of *Microcephala*.

Generic groupings among members of Handeliinae are largely unresolved in the molecular trees, but the similar habit of *Handelia*, *Lepidolopsis*, *Pseudohandelia*, and *Sclerorhachis*—with rather thick, basally villous stems, a soft pith, and strongly dissected leaves with filiform lobes (as apomorphic characters used by Bremer and Humphries 1993 to define their smaller Handeliinae)—may argue for a closer relationship of these entities and for an inclusion of the not yet sequenced *Polychrysum* into this monophyletic group. In addition to that, further members of the Cancriniinae sensu Bremer and Humphries (1993), i.e., *Cancrinia*, *Cancriniella*, and *Ugamia*, may be further candidates for inclusion into Handeliinae in the broad sense proposed here.

Artemisiinae Less. in Linnaea 5: 163. Jan 1830 = Chrysantheminae Less. in Linnaea 6: 167. 1831

With the exception of the recently described genus *Artemisiella* (Ghafoor 1992), the genus *Hippolytia* (from Tanacetinae in the sense of Bremer and Humphries, 1993) and two of their Leucantheminae genera (*Leucanthemella*, *Nipponanthemum*), the members of the strongly supported clade around *Artemisia* (88% BS; PP 1.0 in the ITS analysis) all belong to subtribe Artemisiinae in the sense of Bremer and Humphries (1993). This corroborates findings of Kornkven et al. (1998, 1999), Torrell et al. (1999), Watson et al. (2002), Vallès et al. (2003), and Sanz et al. (2008) who have concentrated on the phylogeny of this subtribe and, therefore, comprehensively sampled it. These studies also demonstrated that *Artemisia*, in the circumscription of Bremer and Humphries (1993), is highly paraphyletic and that *Crossostephium*, *Filifolium*, *Mausolea*, *Neopallasia*, *Picrothamnus*, *Seriphidium*, *Sphaeromeria*, and *Turaniphytum* should be sunk into its synonymy to arrive at a monophyletic genus, which is the largest in the whole tribe.

According to the cladistic analyses by Bremer and Humphries (1993), morphological evidence for the monophyly of the subtribe is considered to be the possession of medifixed or stellate rather than basifixed hairs (plesiomorphic in some species of *Ajania*, *Artemisia*, *Brachanthemum*, *Chrysanthemum*, *Leucanthemella*, and *Turaniphytum*, and in *Arctanthemum*), the anthers with triangular-linear-lanceolate apical appendages of rather thick-walled cells, and the tendency towards ecoronate, marginally rounded achenes (with exceptions in *Crossostephium*, *Nipponanthemum* and one species of *Sphaeromeria* where a pappus of small scales is observed, and in *Artemisiella* and *Hippolytia* where the achene apex is a more or less distinct rounded rim). With base chromosome numbers of $x = 7, 8, 9, 10, 11, 17$, the subtribe Artemisiinae shows an impressive and comprehensive example of descending and ascending dysploidy in Anthemideae.

The phylogeny of Artemisiinae is marked by a transition between the more basal genera with solitary to laxly corymbose arrangements of radiate, disciform or discoid capitula with insect-pollinated, hermaphroditic disc florets and spiny pollen of the so-called *Anthemis*-type, towards the advanced genera of the *Artemisia* group with densely corymbosely or paniculately arranged disciform or discoid capitula with wind-pollinated, often unisexual florets and smooth pollen of the *Artemisia*-type. In a recent molecular phylogenetic study based on nrDNA ITS and ETS sequence variation, Sanz et al. (2008) found that at the very base of the subtribe a generic group of *Brachanthemum*, *Hippolytia*, and *Nipponanthemum* receives high support as a monophyletic group. This group may also include *Leucanthemella*, and then would consist of shrubs and perennial herbs with either radiate or discoid capitula with white, female or sterile ray florets, hermaphroditic, 5-lobed disc florets, and achenes with 5–10 ribs and a pericarp without myxogenic cells (with myxogenic cells in *Brachanthemum*). A further well-supported generic assemblage is formed by the perennial genera *Ajania*, *Arctanthemum*, and *Chrysanthemum*, along with the annual *Elachanthemum*, and may also comprise two other annual, unispecific genera: the morphologically similar genus *Tridactylina* that shares involucral bracts with dark brown margins with *Arctanthemum* and *Chrysanthemum*, and the enigmatic genus *Ajaniopsis* from China and Tibet. The unispecific genus *Elachanthemum*, which has been united with *Stilpnolepis* by Bremer and Humphries (1993), was corroborated by Watson et al. (2002) and Sanz et al. (2008) as an independent genus. It shows, despite its firm position in the *Chrysanthemum* group of genera and in contrast to the yet ungrouped unispecific *Stilpnolepis*, an *Artemisia*-like pollen type with a smooth exine also shared with *Ajaniopsis* (Martín et al. 2003). Finally, Sanz et al. (2008) also succeeded in pinpointing the sister group of *Artemisia* (including all the derivatives mentioned above) to the small Central Asian genus *Kaschgaria*, which also possesses the *Artemisia* pollen type (Martín et al. 2001).

III. Eurasian grade

Matricariinae Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 92. 1870 = Achilleinae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 126. 1993

This subtribe consists of members of Achilleinae (*Achillea*, *Anacyclus*, *Leucocyclus*, *Otanthus*), Tanacetinae (*Heliocauta*), and Matricariinae (*Matricaria*) in the sense of Bremer and Humphries (1993). The group was resolved in previous molecular phylogenetic studies based on ITS sequences (Oberprieler and Vogt 2000: "Achilleinae I"; Oberprieler 2004a, b). The inclusion of *Matricaria* in this subtribe (with its nomenclatural consequences due to the priority of Matricariinae against Achilleinae) is further supported by *ndhF* sequence information, as is the exclusion of *Tripleurospermum* that was considered closely related to *Matricaria* (e.g., Applequist 2002). In our present ITS dataset, the subtribe lacks support in both the MP bootstrap and the BI analyses. There is only high support (PP = 1.0) for a monophyletic group consisting of Matricariinae and Anthemidinae together. However, while Anthemidinae could be defined as monophyletic by the apomorphic character expression of a tetrasporic embryo sac development, and this is supported at least by the topology of the nrDNA ITS phylogeny (see below), Matricariinae with their monosporic development possibly constitute a paraphyletic group relative to Anthemidinae.

The members of Matricariinae are subshrubs or perennial to annual herbs with an indumentum of basifixed hairs (in *Achillea* sometimes asymmetrically medifixed), alternate or basally rosulate, usually dentate to 4-pinnatisect, rarely entire, sometimes vermiform leaves, and radiate, disciform or discoid capitula arranged solitarily or in lax to dense corymbs. The medium to small capitula have a paleate or epaleate (*Matricaria*) receptacle, white, yellow, or pink ray florets with more or less flattened tubes, and hermaphroditic disc florets with a (4–)5-lobed, basally saccate corolla clasping the top of the achene, and anthers with non-polarized endothecial tissue and a baluster-shaped filament collar. The achenes are obovoid, terete with 3–5 weak ribs or dorsiventrally flattened and with two lateral ribs or wings; their apex is marginally rounded or with a narrow marginal corona (*Anacyclus*, *Matricaria*), and their pericarp is furnished or lacks myxogenic cells and sometimes possesses longitudinal resin ducts (*Achillea*, *Heliocauta*). All members of the subtribe show a base chromosome number of $x = 9$. The subtribe is distributed in Europe, Asia, northern Africa, and western North America.

Following results of Guo et al. (2004), the genera *Leucocyclus* and *Otanthus* should be included in a broader genus *Achillea* to achieve monophyly. Oberprieler (2004a) demonstrated that the northwestern African, unispecific genus *Heliocauta* is the sister group to the western Mediterranean genus *Anacyclus*, despite the alleged relationships (Bremer and Humphries 1993) of the former with the Asian genus *Hippolytia* of Artemisiinae (in their present circumscription). Another northern African-southwestern Asian, unispecific genus, *Brocchia*, with a single species, *B. cinerea*, which was treated as a member of *Cotula* by Bremer and Humphries (1993), is clearly a member of the Eurasian/Mediterranean clade of Anthemideae (Oberprieler 2004a). Despite its very isolated position in the molecular analyses, it may be closely related to *Matricaria* due to its achenes with four inconspicuous lateral and adaxial ribs, a marginally rounded apex, and a pericarp of elongated myxogenic cells without resin sacs.

Anthemidinae (Cass.) Dumort., Fl. Belg.: 69. 1827 = Pyrethrinae Horan., Char. Ess. Fam.: 90. 1847 = Tanacetinae Bremer and Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 99. 1993 = Gonosperminae Bremer and Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 106. 1993

The Anthemidinae are easily characterized as monophyletic by the joint possession of a tetrasporic embryo sac development that constitutes an apomophic character expression in the otherwise monosporic Anthemideae (with exceptions in *Argyranthemum* and *Heteranthemis*, Glebionidinae). As described above, Anthemidinae are closely related to the subtribe Matricariinae with which they form a well supported monophyletic clade in our ITS-based analysis (PP 1.0).

Containing the species-rich genera *Anthemis* (175 spp.) and *Tanacetum* (154 spp.), the subtribe is the second largest in Anthemideae. It comprises annuals, biennials, or short- to long-lived perennial herbs and subshrubs with an indumentum of medifixed or basifixed (*Tanacetum*, *Tripleurospermum*) hairs, radiate, disciform, or discoid capitula arranged solitarily or in lax to dense corymbs and with paleate or epaleate receptacles, white, yellow or pink ray florets, and hermaphroditic, 5-lobed (4-lobed in *Nananthea*) disc florets with anthers with non-polarized endothecial tissue and a baluster-shaped filament collar. The achenes are obovoid to obconical, either circular in cross-section and possessing 5–10(–15) ribs, or dorsiventrally flattened with 3–10 ribs on each surface (*Cota*), or sometimes triquetrous and with 3(–5) ribs (*Tripleurospermum*); their apex is furnished with a corona or an auricle, but is also sometimes ecoronate and/or marginally rounded; the pericarp usually carries myxogenic cells that are lacking in *Tanacetum*, and are devoid of resin sac or ducts, except in *Tripleurospermum* where (1–)2(–5) abaxial-apical resin sacs are observed. With a base chromosome number of $x = 9$ the subtribe is cytologically homogeneous.

While the circumscription of the subtribe as monophyletic is rather clear based on the embryological findings, the generic delimitations and the phylogenetic relationships within the subtribe remain unresolved. Despite the assessment of Bremer and Humphries (1993: 99) that "there are several segregate genera and groups of genera, possibly even whole subtribes, which are related to parts of *Tanacetum*" making it a highly paraphyletic genus, molecular phylogenetic studies thus far based on ITS sequence variation with a number of *Tanacetum* species included (Oberprieler 2005) have shown that the Mediterranean and southwestern Asian representatives of the genus are all closely related. More comprehensive, but yet unpublished, analyses (Stroka and Oberprieler, in prep.) demonstrate that only a few central Asian representatives of the genus (all of them with phylogenetic connections to Artemisiinae or Handeliinae, respectively) will have to be removed and transferred to other genera to arrive at a monophyletic genus *Tanacetum* around the type species *T. vulgare* L. Preliminary analyses based on small samples of *Tanacetum* species (Francisco-Ortega et al. 2001; Oberprieler 2005; Oberprieler and Vogt 2006), however, have already clearly shown that the Canary Island endemics, *Gonospermum* and *Lugoa*, represent derivatives closely related to the *Tanacetum* species found on this archipelago and, therefore, should be included in a monophyletic genus *Tanacetum*, and that the generic distinction between *Tanacetum* (with disciform, discoid or yellow-rayed capitula) and *Pyrethrum* (with white- or pink-rayed capitula) may not be very helpful to achieve monophyletic genera in this subtribe.

Molecular phylogenetic studies based on ITS and focussing on the delimitation and infrageneric classification of *Anthemis* (Oberprieler 2001, 2004a, 2005; Oberprieler and Vogt 2006) have demonstrated that *A.* subg. *Anthemis* is more closely related to *Tripleurospermum* and the unispecific *Nananthea* than to species formerly treated under *A.* subg. *Cota*. This has led to the acknowledgement of *Cota* as an independent genus and the transfer of a number of *Anthemis* species to this genus (Greuter et al. 2003). Again, more detailed analyses are underway (Lo Presti and Oberprieler, in prep.) to provide a better understanding of the phylogenetic relationships for the species formerly treated under *Anthemis* and other members of subtribe Anthemidinae.

Leucanthemopsidinae Oberprieler & Vogt in Willdenowia 37: 104. 2007

This small subtribe consists of the small perennial genus *Leucanthemopsis* with nine species in southwestern and Central Europe (one species in northern Africa) and the three unispecific, annual segregate genera *Castrilanthemum*, *Hymenostemma*, and *Prolongoa*, all of which are endemic to Spain and formerly treated under the subtribe Leucantheminae in the sense of Bremer and Humphries (1993; cf. Vogt and Oberprieler 1996). The members are characterized by an indumentum of medifixed hairs, solitary and radiate capitula with epaleate receptacles, yellow or white ray florets, and hermaphroditic, 5-lobed disc florets with anthers with non-polarized endothecial tissue and a baluster-shaped filament collar. The achenes are obovoid, round in cross-section and with (3–)5–10 ribs, rarely dorsoventrally compressed and with one adaxial, two lateral and two abaxial ribs (*Prolongoa*); their apex is furnished with a scarious corona or is marginally rounded (*Castrilanthemum*); the pericarp possesses myxogenic cells along the ribs and is devoid of resin sacs. The base chromosome number is $x = 9$.

As Bremer and Humphries (1993) and Vogt and Oberprieler (1996) have shown in cladistic analyses based on morphological and anatomical characters, the members of this subtribe lack the specialized achene anatomy of the *Leucanthemum* group of genera. Furthermore, molecular studies (Oberprieler and Vogt 2000, Oberprieler 2005) have shown that the monophyly of Leucanthemopsidinae is strongly supported and that they are not closely related to the *Leucanthemum* group of genera (that is treated here as subtribe Leucantheminae). Despite its well-supported monophyly in studies based on molecular characters, the subtribe is not yet well-defined by morphological or anatomical synapomorphies: while Bremer and Humphries (1993) considered the reduced number of pericarp ribs and the occurrence of a scarious, flimsy corona as possible synapomorphies for *Hymenostemma*, *Leucanthemopsis*, and *Prolongoa*, the addition of *Castrilanthemum* by Vogt and Oberprieler (1996) with its 10-ribbed and ecoronate achenes changed the circumscription enormously. In fruit morphology and anatomy, *Castrilanthemum* shows similarity to the southwestern European endemic genus *Phalacrocarpum* that has an unresolved position in the ITS analyses. However, following our present phylogenetic reconstructions, the closer relationship of the former with *Hymenostemma*, *Leucanthemopsis*, and *Prolongoa* is strongly supported.

IV. Mediterranean clade

Leucantheminae Bremer & Humphries in Bull. Nat. Hist. Mus. Lond. (Bot.) 23: 136. 1993

Leucantheminae are a group of eight genera with approximately 71 species distributed mainly in the western Mediterranean region, Macaronesia, Europe, and Asia. It consists of annual or perennial herbs and subshrubs (*Leucanthemum*, *Plagius*, *Rhodanthemum*) with an indumentum of basifixed, rarely medifixed (some *Rhodanthemum* species) hairs, entire, lobed or up to 3-pinnatisect leaves, discoid or radiate, solitarily arranged capitula with epaleate receptacles, white, yellow or red ray florets, and disc florets with a (4–)5-lobed, basally often saccate corolla clasping the top of achenes, and anthers with non-polarized endothecial tissue and a baluster-shaped filament collar. The main distinctive feature to circumscribe this subtribe is the fruit anatomy of its members: the achenes are ellipsoid and circular in cross-section, with 5–10 ribs, a marginally rounded apex sometimes furnished with a scarious and adaxially longer corona, and a pericarp with myxogenic cells along the ribs and with resin canals and vascular strands in the furrows between ribs. The apomorphic nature of these vallecular resin canals and vascular strands had been clearly worked out by Bremer and Humphries (1993). They used it to circumscribe their *Leucanthemum* group of genera, which formed the centre of their larger subtribe Leucantheminae, but also including now some unrelated generic elements (e.g., *Leucanthemella* and *Nipponanthemum* of Artemisiinae and *Hymenostemma*, *Leucanthemopsis*, and *Prolongoa* of Leucanthemopsidinae).

Despite that the subtribe Leucantheminae in the present circumscription is well-defined morphologically, there is less support provided by molecular analyses. While most of its members form a moderately to well-supported monophyletic clade in the analyses based on ITS sequences, the genus *Chlamydophora*, which shares the apomorphic achene anatomy of valecular resin canals and valecular vascular strands, is consistently found outside this clade (Oberprieler and Vogt 2000; Oberprieler 2004a, b, 2005; Vogt and Oberprieler 2006; Oberprieler et al. 2007b). Alternatively, the next, more inclusive and well-supported clade in the present analysis (PP 1.0) also contains genera (*Daveaua*, *Otospermum*, *Heteromera*) of Matricariinae in the sense of Bremer and Humphries (1993) devoid of the characteristic achene anatomy of Leucantheminae but with similarity to each other in achene anatomical respects (5-ribbed achenes with vascular strands in the ribs). As Oberprieler (2004b) has argued, this controversial morphological and molecular evidence may indicate that *Daveaua*, *Heteromera* and *Otospermum* are a paraphyletic group that gave rise to the very distinct *Leucanthemum* group of genera with its specialized achene anatomy. Due to the unclear generic relationships in the ITS analyses and the incomplete sampling in the *ndhF* analysis, Oberprieler et al. (2007b) have refrained from inclusion of these three genera in the well-circumscribed Leucantheminae and treated them as genera unassigned to subtribe.

Santolininae Willk. in Willk. & Lange, Prodr. Fl. Hispan. 2: 76. 1870

This subtribe comprises those genera of Achilleinae in the sense of Bremer and Humphries (1993) that also were found to be characterized by an apomorphic 5-bp deletion in cpDNA *trnL-trnF* spacer that they share with Glebionidinae, Leucantheminae, and a number of unassigned Mediterranean genera (*Aaronsohnia*, *Endopappus*, *Lepidophorum*, *Lonas*, *Nivellea*), but not with *Achillea*, *Anacyclus*, or *Matricaria* (Oberprieler and Vogt 2000; Oberprieler 2002). Therefore, in Oberprieler and Vogt (2000) this group was called "Achilleinae II" in contrast to "Achilleinae I", the latter being here treated as the subtribe Matricariinae (see above).

Members of Santolininae are perennial or annual herbs, subshrubs or shrubs with an indumentum of basifixed, medifixed or stellate hairs, entire or lobed up to 2–3-pinnatisect, sometimes vermiform leaves, and radiate, disciform or discoid capitula arranged solitarily or in lax corymbs. The capitula are characterized by paleate receptacles, white, yellow or orange ray florets, and hermaphrodite, 5-lobed disc florets with distinct basally saccate or spurred corollas clasping the top of achenes either laterally or adaxially, and anthers with non-polarized endothecial tissue and a baluster-shaped filament collar. Most of the members of the subtribe are characterized by achenes with a very thin pericarp that mainly consists of an epidermis formed by longitudinal rows of large mucilage cells that is devoid of resin sacs or ducts. The only exception is found in *Santolina* where some species are lacking mucilage cells altogether and the pericarp is thicker and sclerenchymatous. Since the latter condition is considered plesiomorphic, the thin pericarp is a synapomorphy that unites the four genera *Chamaemelum*, *Cladanthus*, *Mecomischus*, *Rhetinolepis*, and some of the species of *Santolina.* Putative close relationships to other genera with reduced pericarp (e.g., *Achillea* or *Matricaria* of Matricariinae or members of Artemisiinae) were not confirmed by analyses based on nuclear or plastid markers.

Glebionidinae Oberprieler & Vogt in Willdenowia 37: 106. 2007 = Chrysantheminae Bremer & Humphries in Bull. Nat. Hist. Mus. London, Bot. 23: 136. 1993, nom. illeg.

Glebionidinae consist of four mainly western Mediterranean and Macaronesian genera of 28 species of which the majority are found in the shrubby Macaronesian endemic genus *Argyranthemum* and the remainder being annual species. The close relationship of these four genera had been previously described by Heywood and Humphries (1977) and received subtribal status by Bremer and Humphries (1993) under the name "Chrysantheminae". However, since the conserved type of *Chrysanthemum* L. is now *Ch. indicum* L. (= *Dendranthema indicum* (L.) Des Moul.) the two Mediterranean annuals *Ch. coronarium* and *Ch. segetum* are now treated as members of *Glebionis* Spach, and the subtribal name Chrysantheminae Bremer and Humphries, validly published with a Latin description and designation of type, became an illegitimate later homonym of Chrysantheminae Less. As a consequence, the name of the subtribe was changed to Glebionidinae (Oberprieler et al. 2007b).

The monophyly of this group is well-supported due to the occurrence of distinctly heteromorphic achenes with achenes of ray florets being triquetrous and winged and achenes of disc florets being terete or laterally flattened. Early studies of ITS sequence variation in Mediterranean and Macaronesian Anthemideae by Francisco-Ortega et al. (1997), and more comprehensively sampled studies, revealed this generic group as a well-supported clade (Oberprieler 2005), as did studies based on *ndhF* sequence variation (Watson et al. 2000; Himmelreich et al. 2008). The latter analysis also suggested a close relationship of Glebionidinae with the northwestern African endemic, annual genus *Aaronsohnia* and may serve as an argument that the annual life-form may be plesiomorphic in the subtribe, and that the perennial life form observed in *Argyranthemum* may be best interpreted as an adaptation to the insular habitat ("insular woodiness"; Carlquist 1974). Close phylogenetic relationships of Glebionidinae to members of Anthemidinae, as suggested by Bremer and Humphries (1993) based on the alleged apomorphy of thick-walled achenes, did not receive support from the molecular analyses.

MORPHOLOGY

Habit and life form

Anthemideae comprise annual, biennial or perennial, hapaxanthic or pollacanthic herbs, subshrubs or shrubs. All presently accepted subtribes (besides basal Osmitopsidinae and more advanced Phymasperminae, which contain only shrubs or subshrubs) are characterized by transitions between perennials and annuals, either within genera or in the phylogenies of closely related genera. In *Anthemis*, for example, Oberprieler (2001) demonstrated that the distinction of perennial and annual sections within the genus was highly artificial since the annual habit evolved several times independently. The same observation was also made in a more comprehensive molecular phylogenetic study of Eurasian and Mediterranean representatives of Anthemideae (Oberprieler 2005), where it was suggested that the annual habit in this group appeared around 5 to 10 million years ago in conjunction with a progressive aridification in the area (Van Dam 2006) and the onset of a Mediterranean climate type at 3 Ma (Suc 1984). Analogous results should be expected from comparable comprehensive species-based phylogenetic analyses of the southern African representatives of the tribe, where the onset of a Mediterranean climate in the Cape Floristic Region is also dated to 5 Ma (Midgley et al. 2001; Linder 2003).

The two Asian-centered subtribes Artemisiinae and Handeliinae are mainly perennial herbs, subshrubs or shrubs. Annual representatives constitute only a minority in these groups (e.g., *Ajaniopsis*, *Microcephala*, *Elachanthemum*, *Tridactylina*, *Neopallasia*, *Stilpnolepis*, and some *Artemisia* species), which may be interpreted as adaptations to steppe habitats evolving during the Tertiary (Oligocene to late Miocene, 34–10 Ma; Willis and McElwain 2002).

Indumentum

The indumentum of Anthemideae frequently consists of short glandular hairs formed by two parallel rows of cells (biseriate) and an apical pair of enlarged cells capped with an acellular vesicle. This hair type is very common in all subtribes and seems to be of minor taxonomic and evolutionary significance (Ciccarelli et al. 2007). In contrast, eglandular hairs of Anthemideae are far more interesting phylogenetically (see reconstruction of character evolution in Fig. 38.5). While the basal subtribes Osmitopsidinae, Cotulinae, and Ursiniinae are characterized by an indumentum of basifixed hairs formed by a few basal stalk cells and a long apical cell, more advanced subtribes (especially Artemisiinae, Anthemidinae, Leucanthemopsidinae, and Santolininae) are partly or completely formed by genera characterized by medifixed or so-called dolabriform hairs (Napp-Zinn and Eble 1980; Bremer and Humphries 1993). These usually comprise a few stalk cells and a transversely arranged apical cell. In some cases (e.g., *Athanasia*, *Hymenolepis*, *Artemisia*, *Mecomischus*) stellate hairs are encountered that may be interpreted as derived from medifixed ones.

In a recent publication, Herman (2001) reported on septate hairs with oblique (or sometimes perpendicular) walls observed on fruits or paleae of *Eriocephalus*, *Lasiospermum*, *Lidbeckia*, and *Ursinia* (Athanasiinae, Cotulinae, and Ursiniinae, respectively) and also described the occurrence of hairs with spiral wall thickenings in *Ursinia.* Since Bremer and Humphries (1993) also reported on hairs with spiral thickenings on the achenes of the Asian genus *Microcephala* (Handeliinae) this may emerge as another feature of phylogenetic significance if studied in a more comprehensive sampling of genera.

Leaves

Leaves of Anthemideae are usually alternate and only a few genera have opposite leaves. While sometimes entire, or in some cases (mainly from South African representatives) ericoid and needle-like, in the majority of the tribe dentate or moderately to extremely dissected leaves are observed. As extremely dissected foliage the 3–4-pinnatisect leaves with hair-like pinnae of *Sclerorhachis* (Handeliinae) and the strongly dissected, sometimes 3-dimensional and vermiform leaves of some *Achillea* species may serve as impressive examples. While in most genera leaves are covered with glandular hairs and basifixed or medifixed trichomes, Bremer and Humphries (1993) describe secretory cavities that are otherwise only found in floral structures of a number of genera in the leaves of *Eumorphia*, *Gymnopentzia*, and *Phymasperma* (Phymasperminae) and of *Athanasia* and *Hymenolepis* (Athanasiinae).

Napp-Zinn and Eble (1978) surveyed the stomatal apparatus of species of *Eriocephalus* and a number of northern hemisphere genera and documented a number of different types. These findings, however, are very hard to utilise due to the very sporadic sampling.

Inflorescence

Capitula are arranged either solitarily or in lax to dense corymbose capitulescences. The heads are usually distinctly pedunculate, but in some cases (e.g., *Cladanthus* or *Soliva*; Weberling and Reese 1988) sessile capitula or syncephalia (clustered capitula) are observed. In subtribe Artemisiinae and in some representatives of Handeliinae, panicle- or raceme-like capitulescences with numerous, small capitula are formed.

Floral arrangement

In all presently accepted subtribes, the plesiomorphic condition of radiate, heterogamous capitula with hermaphroditic disc florets and female (or sometimes sterile or neuter) ray florets is encountered. The occurrence of capitula with reduced ray florets leading to discoid, homogamous capitula and of disciform, heterogamous flower heads with female marginal and hermaphroditic central disc florets in many of the subtribes demonstrate the plasticity of Anthemideae in this respect, and even within single species the transition between radiate and discoid capitula is often observed (e.g., *Anthemis*; Oberprieler 1998).

In subtribe Artemisiinae, the reconstruction of character evolution based on a molecular phylogeny made by Watson et al. (2002) demonstrates that homogamous discoid capitula have arisen several times in parallel from heterogamous, either radiate or disciform ones. Here, namely in the genera *Artemisia*, *Filifolium*, *Mausolea*, *Picrothamnus* and *Turaniphytum*, central disc florets with reduced female fertility leading to functionally male florets are observed. In some cases (*Elachanthemum*, *Neopallasia*) the inner tubular florets are even completely sterile.

The *Cotula* group of genera (*Cotula*, *Leptinella*, *Soliva*) in subtribe Cotulinae exhibits even more complex floral arrangements in the flower heads. While in *Cotula* capitula are either radiate, disciform, or discoid with outer female ray or tubular florets and a central mass of hermaphrodite florets, the derivative genera *Leptinella* and *Soliva* show outer female disc florets and functionally male inner disc florets. In *Leptinella*, subdioecious or even dioecious conditions are observed, while Heywood and Humphries (1977) report the gynodioecious condition in *Achillea* and the occurrence of dioecy in *Artemisia*.

Involucre and involucral bracts

The involucres encountered in Anthemideae are often hemispherical or obconical, but may (especially in smaller capitula) tend to be more cylindrical or even urceolate. The phyllaries are usually arranged in two to seven imbricate rows and almost always possess scarious margins and a scarious apex that are reduced only in a minority of genera. In *Eriocephalus* the rows of involucral bracts

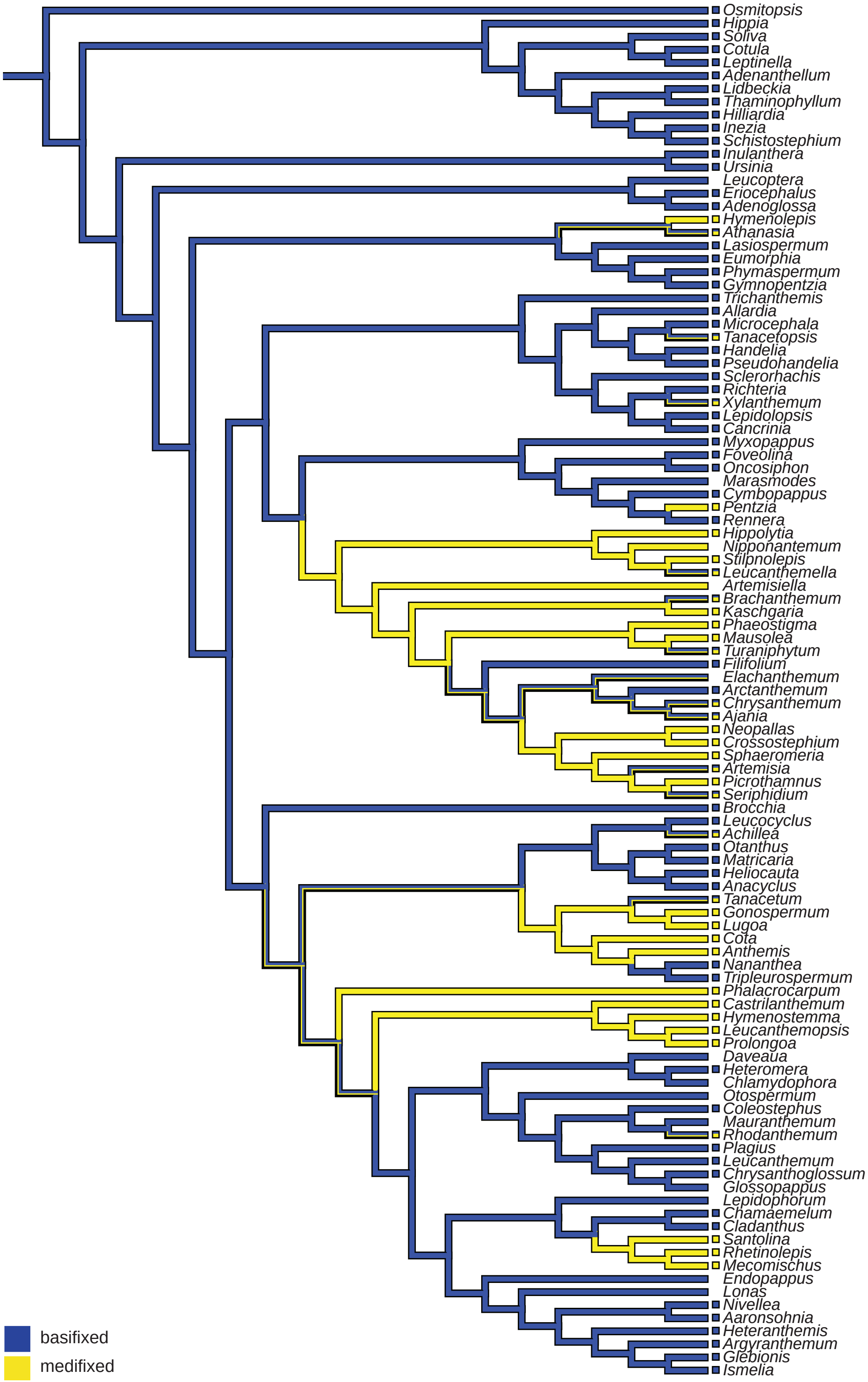

Fig. 38.5. Evolution of indumentum type (basifixed vs. medifixed hairs), as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.

are reduced to two very unequal types, the outer scarious with very wide brown to reddish scarious margins, and the inner connate and hairy that subtend the outer florets.

Receptacle

In Anthemideae the receptacles are either paleate or epaleate. This character had been used by Cassini (1823) to divide the tribe into two subtribes, later validly named Chrysantheminae Less. and Anthemidinae Dumort. The artificiality of this subdivision was clearly stated by Merxmüller (1954) and Wagenitz (1964), and demonstrated by Greuter (1968) when he found that in *Ammanthus* (now included in *Anthemis*) the presence or absence of paleae "does not even necessarily suffice to distinguish species". Hybridization experiments among members of Anthemideae made by Mitsuoka and Ehrendorfer (1972) have shown that the inheritance of pales is probably under simple oligogenic control. The observation of sporadic paleate capitula in *Glebionis* (Napp-Zinn and Eble 1978, under *Chrysanthemum*) and inclusion of paleate and epaleate species into *Athanasia* by Källersjö (1991) point in the same direction.

A reconstruction of character evolution based on the present phylogeny of the tribe is equivocal with respect to the plesiomorphy of paleate or epaleate receptacles (Fig. 38.6). With Osmitopsidinae assumed to be basal and sister to the rest of the tribe, the presence of paleae may be the plesiomorphic condition, arguing for a epaleate receptacle to constitute a synapomorphy of Cotulinae and a number of Asian, Eurasian, and Mediterranean subtribes, with reversals to the paleate conditions occurring in Anthemidinae, Matricariinae, Santolininae, and a number of other genera or infrageneric entities.

The paleae are either persistent or readily deciduous and may be flat or canaliculate, sometimes even enclosing the florets. Paleae may be also hairy or may be furnished with resin canals along their midvein.

The shape of the receptacles varies from flat or convex to conical or even narrowly conical. Usually the receptacle is filled with pith, but in some cases (e.g., *Matricaria*) it is hollow. In some cases (e.g., *Inezia*, *Eriocephalus*, and some Artemisiinae) the receptacles are pilose or densely hirsute.

Ray florets

The ray florets in Anthemideae are either female and fertile or sterile, or neuter. Their limb is usually white or yellow, but also red, orange, or pink colors are found in some genera. In some genera of Cotulinae (e.g., *Adenanthellum*, *Hilliardia*, *Inezia*) the limbs of ray florets are apically emarginate or bifid, possess a branching venation, and are characterized by a reduced tube. While most of the genera have ray florets with a helianthoid epidermal cell type (following the definitions of Baagøe, 1977), *Osmitopsis* and some representatives of Athanasiinae (*Lasiospermum*), Ursiniinae (*Ursinia*), and Phymasperminae (*Eumorphia*, *Phymaspermum*) possess the senecioid cell type with tabular cells.

Disc florets

Following Bremer and Humphries (1993) and our present phylogenetic reconstructions, the plesiomorphic type of tubular florets in Anthemideae is characterized by an unswollen, non-saccate tube and a 5-lobed limb. In Pentziinae, Anthemidinae, Leucantheminae, and Glebionidinae many representatives have basally swollen tubular florets, being conspicuously inflated and spongy at maturity. Sponginess is caused by the excessive growth of subepidermal tissue, with the cells forming long interwoven and repeatedly branched rows and large intercellulars, while the epidermal cells become indurate by sclerification of their walls. However, as observed in *Anthemis* (Oberprieler 1998), inflation of disc floret bases is often not consistently realized throughout a genus and florets with a slender base or with a base pressed flat and appearing laterally winged at maturity are found.

In Matricariinae, Leucantheminae, and Santolininae the disc florets have a more-or-less conspicuously saccate tube with either lateral or abaxial spurs clasping the top of achenes. This character expression is often correlated with the occurrence of achenes with marginally rounded apices and the lack of a pappus or corona. In a number of genera the tube is confluent with the achene and may persist on top of the mature fruits. While hairy corollas are encountered in several genera of Anthemideae, some species of *Athanasia* in Athanasiinae bear unique, long-stalked glands at the base of the disc corolla tubes that have the appearance of a bristly pappus, although not connected with the achenes.

In some subtribes the corolla has only four lobes. This is often observed in Cotulinae where only two genera (*Adenanthellum*, *Hippia*) are characterized by 5-lobed corollas, and the 4-lobed condition may be a synapomorphy of the subtribe or of a generic group within. However, corollas with reduced lobe numbers also occur in other, unrelated subtribes such as Pentziinae (*Myxopappus*, *Oncosiphon*), Handeliinae (*Lepidolopsis*), Artemisiinae (*Ajania*, *Filifolium*, *Artemisiella*), Matricariinae (*Matricaria*), Anthemidinae (*Nananthea*), and Leucantheminae (*Chlamydophora*), mainly in connection with capitula of small size and the reduction of tubular florets. In disciform capitula the outer female, tubular florets are often further diminished and provided with a reduced, sometimes slender limb without apical teeth. In *Cotula* these peripheral florets are usually stalked, while in the closely related genus *Soliva* they form several rows.

The disc floret corolla lobes are often of the same size, but in several genera (e.g, *Anacyclus* in Matricariinae)

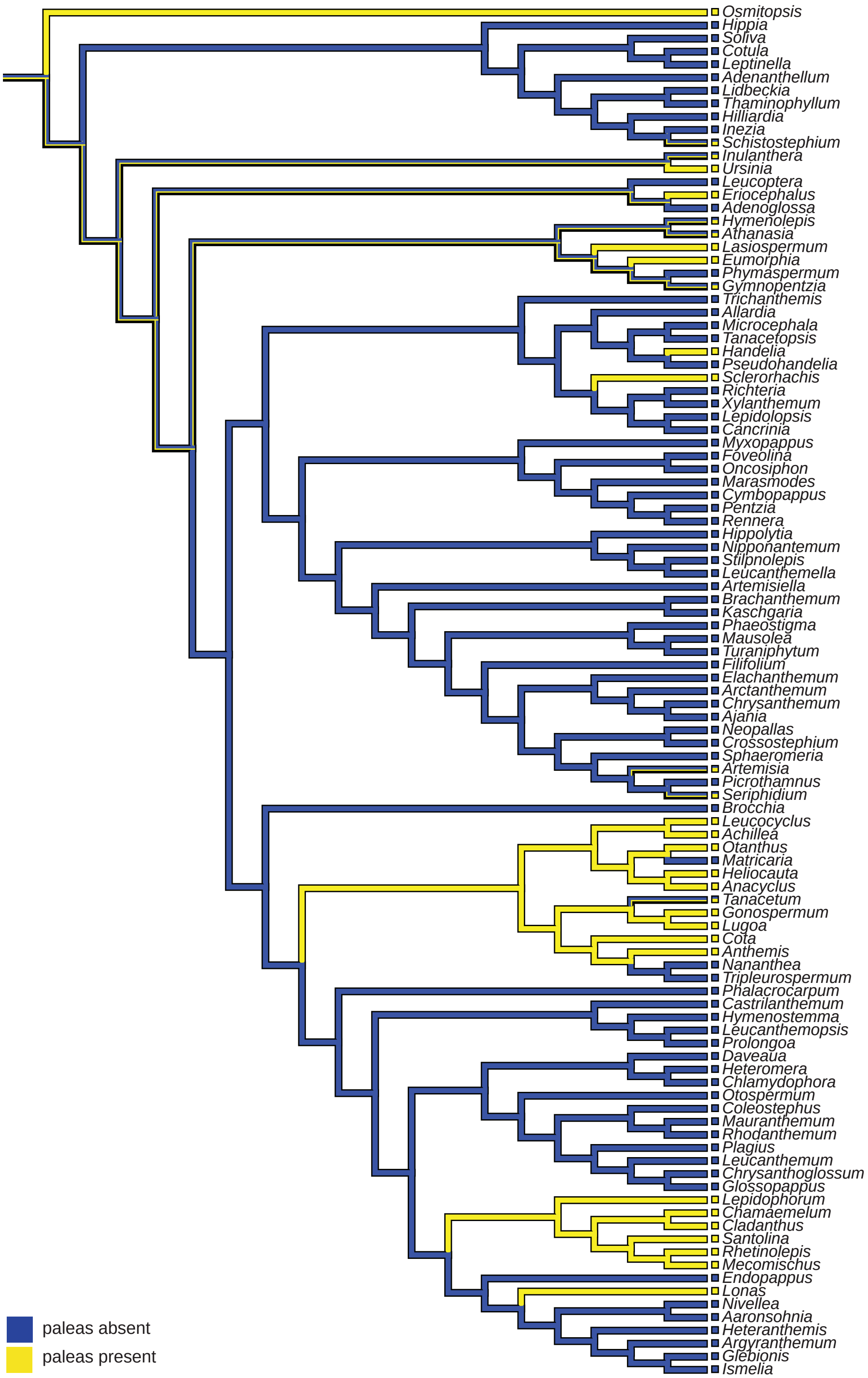

Fig. 38.6. Evolution of receptacle type (paleas absent vs. present), as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.

characteristic appendages on the abaxial side are found and may lead to asymmetrical corollas. However, Oberprieler (1998) found in *Anthemis* that these appendages are too variable to characterise species or species groups. The vascularization of corolla lobes seems to provide some useful characters, with the majority of Anthemideae genera devoid of vascular bundles along the margins of lobes but with an anastomosing vascular system in *Athanasia* (Athanasiinae). This feature, however, has been studied very fragmentarily.

Anthers

In the majority of Anthemideae the anther thecae are obtuse to slightly pointed at the base. However, in some genera of different subtribes (*Osmitopsis* [Osmitopsidinae], *Inulanthera* [unassigned to a subtribe], and *Hippolytia* [Artemisiinae]), they are tailed. The apical anther appendage is usually ovate in outline and obtuse to round apically. In Artemisiinae, however, triangular, linear, or elliptical appendages are observed that consist of rather thick-walled cells and may constitute an apomorphy of the subtribe (Bremer and Humphries 1993). The endothecial tissue is usually not polarized, i.e., its cells have wall thickenings evenly distributed over their whole length, while in the genera of Ursiniinae, Athanasiinae (with the exception of *Eriocephalus*), and Phymasperminae cells of the endothecial tissue have thickenings only apically and basally. The filament collar is either slender or widens gradually towards its proximal end ("baluster-shaped", Meiri and Dulberger 1986). It consists of cells with thickened walls and its margins are involute in cross-section. The filament proper is usually formed by large, unthickened, elongated cells.

Styles

The styles in Anthemideae are very uniform and represent the so-called senecioid type: two vascular bundles run through the cylindrical and glabrous style shaft and end in the stigmatic branches, which are truncate-penicillate, bearing two separate lines of stigmatic papillae on the inside and obtuse sweeping hairs at their apex. Usually the stigmatic branches contain elongate resin ducts with a brown or orange content. The base of the style usually becomes swollen and hardened due to enlarged and sclerified cells. In the functionally male florets of *Artemisia*, *Cotula*, *Filifolium*, *Leptinella*, *Mausolea*, *Picrothamnus* and *Turaniphytum*, the style branches are undivided and lack a stigmatic area. In *Soliva* the styles of the marginal female florets become spinescent in fruit.

Achenes

Dating back to the studies of Cassini (1823) and Schultz-Bipontinus (in Schnitzlein 1854, Schultz 1860), the paramount importance of achene morphology for the taxonomy and for the delimitation of genera in Anthemideae is well known. Achenes are often either cylindrical, ellipsoid or obovoid in outline and more or less circular in cross-section. In a number of genera or generic groups, flattened achenes are encountered. In some genera of Cotulinae, Athanasiinae, Artemisiinae, Matricariinae, and Anthemidinae dosiventrally compressed, sometimes even laterally winged, achenes are found, while in Glebionidinae laterally compressed fruits occur.

The presence, number, shape, and arrangement of ribs are variable. In the most basal representative of the tribe (*Osmitopsis* in Osmitopsidinae), achenes are 3–4-angled or ribbed. Four or five evenly arranged ribs may therefore be the plesiomorphic condition in the tribe. In dorsiventrally or laterally flattened achenes, the number of ribs may be reduced and 1–2 wing-like ribs are formed. In other cases, the number of ribs is increased and achenes with up to 18 (in *Cota* even more) ribs are encountered.

The achene apex in Anthemideae is usually furnished with a relatively large, bowl-shaped discus called either coronet, nectary, or stylopodium, respectively (Kynčlová 1970; Vogt 1991; Bremer and Humphries 1993). In *Lidbeckia* and *Thaminophyllum* (Cotulinae) this discus is very large and persistent in fruit. The apical plate is either ecoronate and truncate or marginally rounded, or it is coronate. Only in Ursiniinae and in some Handeliinae is this corona pappus-like and formed of ovate scales (*Ursinia*) or subulate to bristle-like scales (*Allardia*, *Ursinia*), but never formed of true bristles. In many cases the corona is formed by basally fused scales or is an adaxial auricle or a more-or-less thickened rim.

ANATOMY

Owing to the artificiality of a subtribal classification once based on the presence vs. absence of paleae, numerous attempts have been made to elaborate a more satisfactory taxonomy of the tribe. In this endeavour, carpological characters proved to be the most important source of phylogenetically relevant features. Despite some early findings on the relevance of carpological characters in the elaboration of naturally delimitated genera (e.g., Schultz 1844, 1860, and in Schnitzlein 1854), the full merit for the exploitation of achene anatomy for taxonomic questions in Anthemideae goes to J. Briquet who used characters of the pericarp for the demarcation of Mediterranean genera of the tribe (Briquet 1916a–c; Briquet and Cavillier 1916). In the following decades, detailed carpological studies have been made in the so-called *Chrysanthemum* complex (Giroux 1930, 1933; Horvatic 1963; Borgen 1972; Alavi 1976; Humphries 1976), in the *Anthemis* complex (Humphries 1977; Benedí i González and Molero i Briones 1985), or in a more geographically focused study by Kynčlová (1970). The carpological survey of Reitbrecht

(1974) deserves consideration as the first comprehensive tribal-wide evaluation of achene anatomy for the elaboration of a more natural subtribal classification, utilizing as many genera with suitable study material as possible but with a clear focus on the northern hemisphere representatives of the tribe. The latter study yielded a subdivision into seven provisional groups, which were also accepted for the (informal) subtribal treatment of Anthemideae in Heywood and Humphries (1977). Triggered by these studies, anatomical studies of achenes in the following decades contributed to a better understanding of the taxonomy and the phylogenetic classification of southern hemisphere genera: Källersjö (1986, 1988) used mainly carpological characters for generic circumscriptions in the *Athanasia* and *Pentzia* complexes, respectively, while Bruhl and Quinn (1990) added fruit anatomical evidence for the exclusion of several genera of "Cotuleae" from Anthemideae and the retention of *Cotula*, *Leptinella*, *Nananthea*, and *Soliva* in the tribe.

The achene wall is often several cell layers thick and partly or completely sclerified. In other cases, especially in Santolininae, the pericarp is very thin and consists only of a single cell layer that is made up of longitudinal rows of mucilage cells. In the majority of the genera of the tribe, the pericarpic ribs coincide with vascular bundles through the mesocarp. However, in some genera (e.g., in a few *Anthemis* species; Oberprieler 1998) or generic groups (such as Leucantheminae), the vascular bundles are found in the furrows between ribs, and the external ribs of the achene seem to result from the outgrowth of intervascular mesocarpic tissue.

The pericarp of achenes in Anthemideae is frequently furnished with myxogenic cells of different dimensions and different shapes. Very often these mucilage cells are localized on the ridges of achene ribs and consist of transversely compressed cells in longitudinal rows, but in other cases these specialized cells are solitarily interspersed among normal epidermal cells. In most representatives of the tribe the epicarp is furnished with short glandular hairs formed by two parallel rows of cells (biseriate) and an apical pair of enlarged cells capped with an acellular vesicle. Besides these glands, several genera of Cotulinae, Athanasiinae, Handeliinae, and Artemisiinae are characterized by normal, eglandular hairs. Extremely villous achenes are found in *Lasiospermum* (Athanasiinae) and *Trichanthemum* (Handeliinae), while achenes with a conspicuously papillose pericarp are typical for subtribe Phymasperminae.

Additionally, the pericarp of many Anthemideae representatives is furnished with resin canals or resin sacs. These may be either scattered over the whole pericarp or are found in more characteristic positions (longitudinal resin canals in or between ribs, round or ellipsoid resin sacs near the achene apex). As Oberprieler (1998) has demonstrated when discussing the differences between *Anthemis* and *Cota*, further useful characters may be found when analyzing the shape and number of calcium oxalate crystals in the epicarpic cells.

The testa epidermis of nearly half of the presently accepted genera of the tribe was studied in a comparative manner by Kneißl (1981) who classified them into three different testa epidermis types (epidermal, sclerenchymal, and parenchymal type) and a number of genera unassigned to these groups. While the parenchymal type was found to be restricted to members of the present Cotulinae, and other members of the southern hemisphere subtribes (together with members of subtribes Anthemidinae, Glebionidinae, Leucanthemopsidinae, Matricariinae, and Santolininae) are characterized by the epidermal type, the sclerenchymal type is restricted to some northern hemisphere subtribes (Anthemidinae, Artemisiinae, Handeliinae, Leucantheminae).

POLLEN

The first detailed light microscopic studies of Anthemideae pollen were made by Wodehouse (1926, 1935) on *Anthemis cotula* and *Chamaemelum nobile*. He described the pollen as tricolporate, echinate, having a coarse-granular, two-layered exine. The thicker inner layer appeared to him to be built of coarse radial striae, and the outer, much thinner layer was found to have very fine radial striae. He considered the exine sculpturing as a main difference within the tribe, with echinate pollen grains with sharply pointed spines characterizing *Anthemis* together with other insect-pollinated genera (*Leucanthemum*, *Glebionis*, *Tanacetum*) and non-echinate pollen grains with vestigial or entirely absent spines being typical for generally wind-pollinated genera like *Artemisia* (Wodehouse 1935).

Stix (1960), in her comprehensive light microscopical work on pollen morphology of Compositae, described her "*Anthemis*-type", to which she also assigned representatives of *Achillea*, *Chamaemelum*, *Glebionis*, *Leucanthemum*, *Cotula*, and *Matricaria*, as having a tegillate sexine. She found the inner, coarsely striate layer of the sexine to consist of rather thick and distantly branched infrategillary baculae, while the outer, finer striate layer is formed of fine pila with heads mostly fused together ("intertegillary baculae"). Her findings were later corroborated by transmission electron microscopy (TEM) and scanning electron microscopy (SEM) (e.g., Skvarla et al. 1977; Vezey et al. 1994; the latter authors use the term "double tectum" for the outer layer of baculae that they erroneously call "infratectal columellae", while the infrategillary baculae are called "basal columellae").

In further studies of pollen in Anthemideae by Čigurjaeva and Tereškova (1983), Benedí i González (1987), Fedorončuk and Savitskii (1988), and De Leonardis et al.

(1991), pollen grains of the "*Anthemis*-type" were found to be rather uniformly sphaeroidal, trizonocolporate and spiny, with tenuimarginate, sharply pointed colpi, and lalongate, tenuimarginate, sharply pointed ora. Detailed SEM studies by Vezey et al. (1994) demonstrated that pollen grains of *Ursinia* are qualitatively different from the common "*Anthemis*-type" because grains lack the infrategillary baculae ("basal columellae") leading to so-called caveate pollen (Skvarla and Larson 1965; Skvarla and Turner 1966; Skvarla et al. 1977). They also found that pollen grains from *Artemisia* are characterized by infrategillary baculae ("basal columellae") with complex and interwoven branches. Both conditions were interpreted as being apomorphic relative to the common "*Anthemis*-type" with vestigal infrategillary baculae observed in *Ursinia* being a reversal towards the plesiomorphic condition. A further exceptional case in Anthemideae is observed in *Adenanthellum* (Cotulinae), where the pollen is hexa-panto-colpoporate rather than tricolporate (Bremer and Humphries 1993).

Gadek et al. (1989) were able to provide light and electron microscopical (SEM, TEM) evidence for the dismembering of the former "Cotuleae", with *Cotula*, *Leptinella*, *Nananthea*, and *Soliva* having anthemoid pollen, but *Abrotanella*, *Ischnea*, and *Centipeda* having senecioid, and *Ceratogyne*, *Dimorphocoma*, *Elachanthus*, *Isoetopsis*, *Minuria*, and *Plagiocheilus* having helianthoid exines, leading to their exclusion from Anthemideae. Detailed pollen morphological studies (LM, SEM) in Artemisiinae made by Martín et al. (2001, 2003) demonstrated that besides *Artemisia* and the closely related genera *Crossostephium*, *Filifolium*, *Mausolea*, *Neopallasia*, *Picrothamnus*, *Seriphidium*, *Sphaeromeria*, and *Turaniphytum*, the more distantly related genera *Ajaniopsis*, *Kaschgaria*, and *Phaeostigma* are also characterized by smooth or microechinate pollen grains, while *Arctanthemum*, *Chrysanthemum*, *Hulteniella*, *Stilpnolepis*, and *Tridactylina* show the normal long-spined "*Anthemis* type".

EMBRYOLOGY

Anthemideae have been thoroughly, but not comprehensively, studied embryologically by Harling (1950, 1951, 1960), who concentrated mainly on northern hemisphere representatives of the tribe. Sparse information on embryo sac formation for southern hemisphere, i.e., the basal genera of the tribe (*Cotula* [Harling 1951], *Ursinia* [Ahlstrand 1978], *Lasiospermum* [Harling 1950], *Oncosiphon* [Harling 1951]), suggest that a monosporic embryo sac development is the plesiomorphic condition in the tribe (see reconstruction of character evolution in Fig. 38.7), and that the bisporic and tetrasporic modes of development are apomorphic. While the bisporic condition has been solely reported for *Argyranthemum* of Glebionidinae, the tetrasporic embryo sac development observed in *Anthemis* (Harling 1950, 1960), *Cota* (Harling 1950, 1960), *Nananthea* (Martinoli 1940), *Tanacetum* (Harling 1951), and *Tripleurospermum* (Harling 1951) constitutes an important argument for the monophyly of Anthemidinae with a parallelism found in *Heteranthemis* (Harling 1951) of Glebionidinae. As in the case of chromosome numbers and karyotypes, more extensive and taxonomically complete studies on this character are needed (especially for the southern hemisphere representatives of the tribe) to fully appreciate the power of embryology for the phylogenetic classification of Anthemideae.

CHROMOSOME NUMBERS

According to Heywood and Humphries (1977) and Bremer and Humphries (1993), $x = 9$ is the most common base chromosome number in Anthemideae. Other base numbers occur only in a few genera. Based on our present phylogenetic reconstructions with the basal position of *Osmitopsis* (Osmitopsidinae) and Cotulinae and the base chromosome number of $x = 10$ found in *Osmitopsis* (cf. Bremer and Humphries 1993) and a number of genera of Cotulinae (*Cotula*, *Hilliardia*, *Inezia*, *Soliva*, *Thaminophyllum*), the reconstruction of character evolution shown in Fig. 38.8 indicates that $x = 10$ is the most reasonable base chromosome number for the common ancestor of the tribe. A transition to $x = 9$, however, is observed very close to the base of the tree and this base chromosome number is reconstructed for most of the subtribes above Athanasiinae.

Descending dysploidy is found in *Cotula* ($x = 8, 9, 10$; Cotulinae), *Ursinia* ($x = 5, 7, 8$; Ursiniinae), *Athanasia* ($x = 8$; Athanasiinae), *Myxopappus*, *Oncosiphon*, *Pentzia* ($x = 6, 7, 8$; Pentziinae), *Microcephala* ($x = 7$; Handeliinae), and to a considerable extent in *Artemisia* ($x = 7, 8, 9$; Artemisiinae), while ascending dysploidy occurs more rarely in *Leptinella* ($x = 13$; Cotulinae) and again in *Artemisia* ($x = 8, 9, 10, 11, 17$; Artemisiinae).

Polyploidy is common in the tribe. Extensive polyploid complexes are found in *Achillea* ($2x$–$10x$), *Artemisia* ($2x$–$16x$, Pellicer et al. 2007), *Dendranthema* ($2x$–$10x$), *Leptinella* ($4x$–$12x$), and *Leucanthemum* ($2x$–$22x$, Vogt 1991).

Uitz (1970) found prominent differences in structure and total size of karyotypes among Anthemideae. However, these observations were only based on northern hemisphere representatives of the tribe. Despite the lack of a more comprehensive study on the cytogenetics of the tribe, also including representatives of the southern hemisphere and Asian subtribes, some interesting evolutionary patterns of karyotype modification were observed (Uitz 1970). The low recombination rate

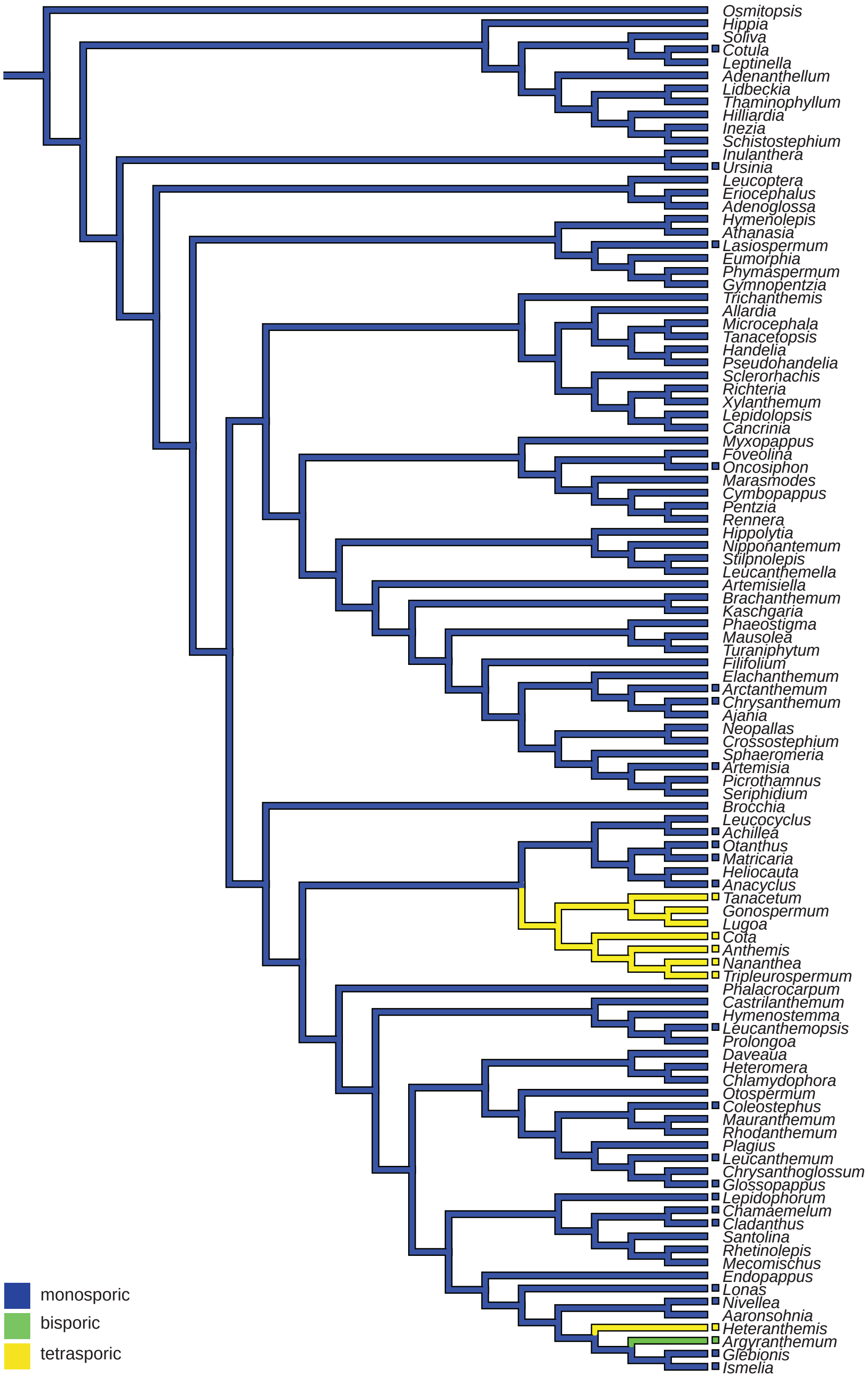

Fig. 38.7. Evolution of embryo sac development type, as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.

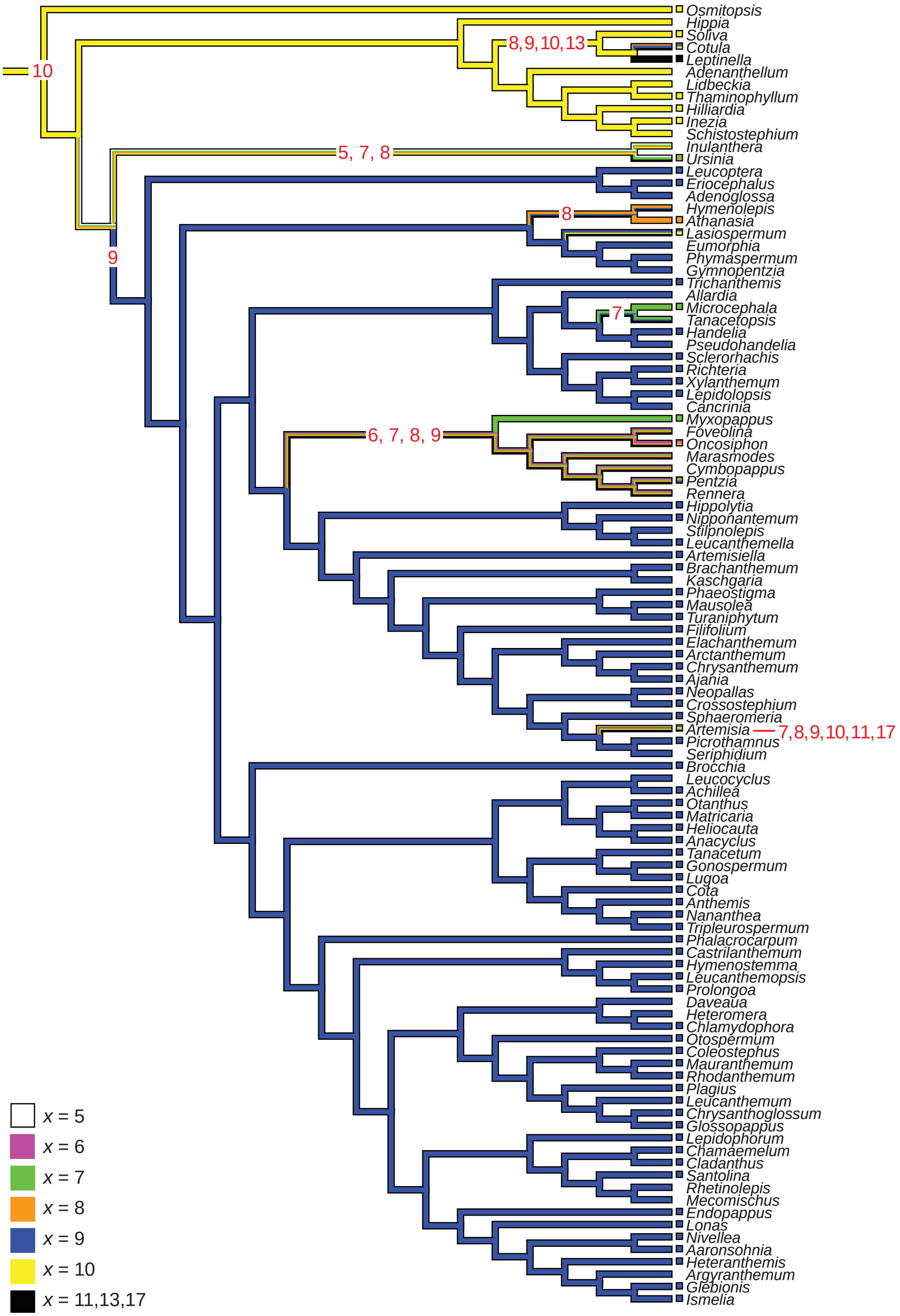

Fig. 38.8. Evolution of base chromosome numbers, as reconstructed based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2.

caused by long generation times in perennials seems to be compensated for by the prevalence of allogamy and polyploidy. The relatively high recombination rates in annuals, due to their short generation times, are compensated by the tendency towards autogamy and structural heterozygosity, along with higher cross-over frequencies during meiosis. With the exception of a cytogenetic study by Mitsuoka and Ehrendorfer (1972), who included *Pentzia* as a southern hemisphere Anthemideae member in their study, more detailed surveys on karyotype evolution in the whole tribe are lacking. Only some studies at the generic level have been made in the last three decades, e.g., Ehrendorfer et al. (1977) in *Anacyclus*, Oberprieler (1998) in *Anthemis* s.l., or Mendelak and Schweizer (1986), Oliva and Vallès (1994), Vallès and Siljak-Yakovlev (1997), Torrell et al. (2003) and Garcia et al. (2007) in *Artemisia*.

CHEMISTRY

As Christensen (1992) pointed out, the tribe Anthemideae is one of the chemically best investigated tribes of Compositae. According to Greger (1977), polyactylenes, sesquiterpene lactones, and flavonoids are the three main classes of interest to systematists. However, as Bremer and Humphries (1993) also noted, information on micromolecular substances are still difficult to utilise in a taxonomic or phylogenetic context because these data have often been collected in a rather unsystematic, uncomprehensive and sporadic manner. Further, these studies often do not indicate the absence of a particular chemical compound in a taxon. The hardly accessible, and in many cases unknown, background information on biochemical pathways further complicates exploitation of micromolecular data for systematic studies. Nevertheless, in the following we will try to give a short review of important groups of secondary compounds in the tribe.

Acetylenes and related compounds

Acetylenes and related compounds were reviewed for the tribe by Christensen (1992), who noted that a wide array of acetylenic compounds are present, including aromates, lactones, isocoumarins, cumulenes, pyrones, spiroacetal enol ethers, furans, thiophenes, thioethers, sulphoxides, alkamides, and straight chain acetylenes. Only in some southern hemisphere representatives of the tribe, namely in *Athanasia* and *Lasiospermum* of Athanasiinae, *Eumorphia*, *Gymnopentzia*, and *Phymaspermum* of Phymasperminae and *Ursinia* of Ursiniinae, acetylenes seem to be completely absent and are found substituted for by characteristic furanosesquiterpenes (see below).

An additional main pattern of chemical variation in the tribe is the predominance of C_{17}-acetylene dehydrofalcarinone and its derivates in the southern hemisphere genera of *Cotula*, *Inezia*, *Lindbeckia*, *Schistostephium*, *Thaminophyllum* (all Cotulinae), and *Eriocephalus* (Athanasiinae) and in the northern hemisphere genus *Artemisia* (Artemisiinae). Most of the northern hemisphere representatives (including *Artemisia*) also contain acetylenes of the C_{13} or C_{14} pathways (Greger 1977; Marco and Barberá 1990; Christensen 1992). It is interesting to note that the mainly southern hemisphere genus *Pentzia* (Pentziinae), which is found closely related to the northern hemisphere portions of the molecular phylogenetic tree, is also characterized by acetylenes of the C_{14} rather than the C_{17} pathway.

Other groups of acetylenes have been observed (or studied) mainly in northern hemisphere representatives of the tribe. These show only restricted phylogenetic and/or taxonomic significance. For example, thiophenes (consisting mainly of C_{10}-, C_{12}- and C_{13}-monothiophenes) are found regularly in *Artemisia* of Artemisiinae, in *Anthemis*, *Tanacetum*, and *Tripleurospermum* of Anthemidinae, in *Anacyclus* and *Matricaria* of Matricariinae, and in *Argyranthemum* of Glebionidinae. Aromatic acetylenes and furan acetylenes are mainly restricted to some Mediterranean genera of the tribe (*Anthemis* of Anthemidinae, *Leucanthemum* of Leucantheminae, *Santolina* of Santolininae, *Argyranthemum* and *Glebionis* of Glebionidinae, and in the unassigned *Lonas*), but also occur in *Artemisia* (Artemisiinae).

The presence of amides, which are frequently responsible for insecticidal activity, was considered significant for the circumscription of Achilleinae in Bremer and Humphries (1993), but it now seems that these secondary compounds are characteristic of a broader array of Mediterranean genera (*Achillea*, *Anacyclus*, *Leucocyclus*, and *Otanthus* of Matricariinae, *Chamaemelum* and *Cladanthus* of Santolininae, *Leucanthemum* of Leucantheminae, *Argyranthemum* and *Glebionis* of Glebionidinae, and the unassigned *Aaronsohnia*).

Terpenoids

The strong aromatic odors found in members of Anthemideae are caused by the presence and high concentrations of monoterpenes. In several members of the tribe (e.g., *Achillea*, *Artemisia*, *Tanacetum*) essential oils from leaves and/or flowers are used medicinally or industrially (Greger 1977). The "pyrethrins", responsible for the insecticidal properties of some Anthemideae species (especially of *Tanacetum cinerariifolium*), also belong to this group of secondary compounds. A comprehensive study of monoterpenes and their bearing on the infrageneric classification of *Artemisia* was conducted by Stangl and Greger (1980). Oberprieler and Vogt (1999) used a gas chromatographic survey of essential oils to study species delimitation in *Anthemis* from Cyprus.

Of the sesquiterpenes, bisabolol from *Matricaria recutita* has gained some pharmaceutical attention due to its antiphlogistic activity, while the occurrence of furansesquiterpenes instead of polyacetylenes in *Athanasia*, *Lasiospermum* (Athanasiinae), *Eumorphia*, *Gymnopentzia*, *Phymaspermum* (Phymasperminae), and *Ursinia* (Ursiniinae) was considered an important character to circumscribe the subtribe Ursiniinae in the sense of Bremer and Humphries (1993), which now appears to be highly polyphyletic.

Sesquiterpene lactones in Anthemideae were reviewed by Seaman (1982) in the course of his study on this group of secondary compounds as taxonomic markers in Compositae. The simplest sesquiterpene lactones are the germacranolides that are converted into more derived guaianolides and santanolides (Greger 1977). Sesquiterpene lactones are very common in the genus *Artemisia*, in which they constitute the most characteristic chemical markers (Marco and Barberá 1990). While the santanolides are only known from *Artemisia*, the other two groups are found both in the basal subtribe Cotulinae and in the more advanced ones (Pentziinae, Artemisiinae, Anthemidinae, Matricariinae, and Santolininae). Most important in phylogenetic respects is the observation reported by Seaman (1982) that many genera of the tribe are linked together by the presence of C_6 trans-lactonized guaianolides, and that these constituents are missing in the southern hemisphere genera *Osmitopsis* (Osmitopsidinae) and *Ursinia* (Ursiniinae).

Flavonoids

Information on flavonoids in Anthemideae was reviewed recently by Bohm and Stuessy (2001) in their comprehensive treatment of this group of secondary compounds for the whole family. These authors consider the tribe as moderately complex in its flavonoid chemistry and find that flavones and flavonols are about equally represented in the larger genera (Bohm and Stuessy 2001). While anthochlors (aurones and chalcones) and isoflavones have never been reported from the tribe (with the exception of a chalcone derivative reported by Huneck et al., 1985, as quoted in Marco and Barberá, 1990), only a few members were found to possess dihydrochalcones, flavanones, dihydroflavonoles, and C-glycosylflavones. When information available from Bohm and Stuessy (2001) is compared with the presently suggested subtribal classification only two interesting distribution patterns emerge. Firstly, it seems that a 4′-hydroxylation with extra oxygenation at C_6, while present in at least some genera of the other surveyed subtribes, is completely lacking from Leucantheminae, Leucanthemopsidinae, and Glebionidinae. Secondly, flavanones are absent from both the basal and the advanced subtribes and characterise the intermediate Athanasiinae (*Eriocephalus*), Phymasperminae (*Gymnopentzia*), Pentziinae (*Oncosiphon*, *Pentzia*), and Artemisiinae (*Arctanthemum*, *Artemisia*, *Filifolium*).

BIOGEOGRAPHY

Anthemideae show a mainly Old World–centered, extratropical distributional range. Primary concentrations of genera and species are observed in the steppe and semidesert vegetation of middle and southwest Asia and the areas with a winter rain, Mediterranean climate type in southern Africa, and the Mediterranean region ("etesian climate"). While both the boreal and arctic zone is inhabited by numerous species of the large genera *Artemisia* and *Achillea*, other members of the tribe (*Cotula*, *Leptinella*, and *Soliva* of Cotulinae) occur in the southern hemisphere (Jäger 1987). In addition, representatives of the tribe are also characteristic at high altitudes (Meusel and Jäger 1992). The adaptation to a winter-green and often annual growth rhythm in the Mediterranean climate types has led to the enlargement of distributional areas of numerous taxa due to their co-migration with humans as members of a segetal or ruderal flora (Meusel and Jäger 1992).

The biogeographic signal in the evolutionary history of the entire tribe is apparent (Fig. 38.9). Members of the basal subtribes Osmitopsidinae, Cotulinae, Ursiniinae, Athanasiinae, and Phymasperminae form a mainly southern hemisphere grade with a concentration of genera and species in South Africa. Only some members of Cotulinae and Athanasiinae occur outside of southern Africa. Members of *Cotula* are found also in northeastern Africa (*C. abyssinica* Sch.Bip. ex A. Rich., *C. cryptocephala* Sch. Bip. ex A. Rich.), Australia (*C. alpina* (Hook. f) Hook. f., *C. cotuloides* (Steetz) Druce), Java (*C. elongata* B. Vogel), Central and southern America (*C. mexicana* (DC.) Cabrera), and the southern oceanic islands (*C. goughensis* R.N.R. Brown, *C. moseleyi* Hemsl.) or have conquered vast areas as widespread weedy species (*C. anthemoides* L., *C. australis* (Spreng.) Hook. f., *C. coronopifolia* L.). *Leptinella*, a derivative of *Cotula*, has a center of diversity in Australia and New Zealand, and *Soliva* is mainly American and Australian with two species widespread as weeds (*S. sessilis* Ruiz & Pav., *S. stolonifera* (Brot.) Loudon). Finally, *Ursinia* of Ursiniinae and *Lasiospermum* of Athanasiinae have an extended distributional range to northeastern Africa (Ethiopia) and southwestern Asia (Sinai), respectively.

Subtribes of the intermediate Asian-southern African grade clearly demonstrate that the evolutionary history of the tribe obviously passed through phases of migrations out of Africa into Asia and/or the Mediterranean region. Pentziinae are mainly southern African, but some species of *Pentzia* are also found in northern Africa (*P. hesperidum* Maire & Wilczek, *P. monodiana* Maire) and in the Horn of Africa region (*P. somalensis* E.A. Bruce ex Thulin, *P. arabica* Thulin; Thulin 2001). Handeliinae are strictly Asian with most genera stretching their area between Iran and Afghanistan and China, while Artemisiinae (headed by *Artemisia* and its allied genera) have conquered

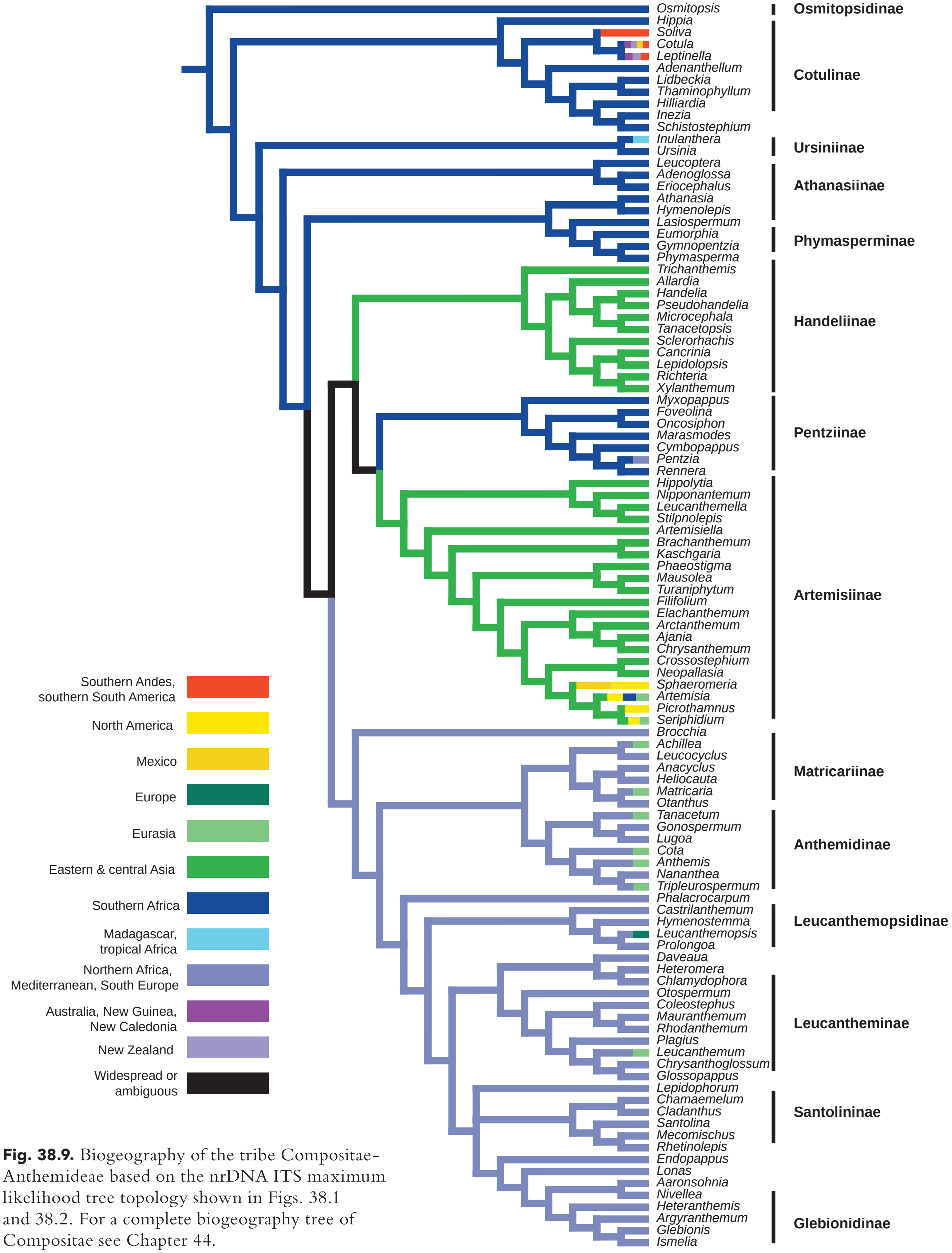

Fig. 38.9. Biogeography of the tribe Compositae-Anthemideae based on the nrDNA ITS maximum likelihood tree topology shown in Figs. 38.1 and 38.2. For a complete biogeography tree of Compositae see Chapter 44.

areas of the northern hemisphere beyond central Asia (e.g., *Arctanthemum* in arctic Eurasia and arctic America, *Chrysanthemum* and *Leucanthemella* in Japan and eastern Europe, or *Artemisia*, *Picrothamnus*, and *Sphaeromeria* in America) and made their way to the Mediterranean (*Artemisia*), South America (*Artemisia copa* Phil., *A. echegarayi* Hieron., *A. mendozana* DC.), and even back into Africa south of the Sahara (*Artemisia afra* Jacq.).

The Eurasian/Mediterranean clade of the tribe which comprises the most advanced subtribes Anthemidinae, Glebionidinae, Leucantheminae, Leucanthemopsidinae, Matricariinae, and Santolininae shows a strictly northern hemisphere distribution with a main concentration in southwestern Asia and the circum-Mediterranean region, and only four species of *Tanacetum* reaching the New World via Siberia (*T. camphoratum* Less., *T. douglasii* DC., *T. huronense* Nutt., *T. bipinnatum* Sch.Bip.). This monophyletic group of subtribes is the only part of the tribe for which detailed statistical biogeographic analyses have been carried out (Oberprieler 2005). Based on a combination of dispersal-vicariance analysis (Ronquist 1997) and molecular clock dating of calibrated, rate-smoothed maximum-likelihood trees based on ITS sequence information, Oberprieler (2005) demonstrated that the ancestor of this clade diverged from the basal African lineages in the late Early Miocene (18 Ma), presumably in conjunction with the collision of the African and Eurasian platforms. Recurrent dispersal/vicariance events during the Middle and Late Miocene (16–11 Ma), both between the eastern and western Mediterranean region and (in the latter region) between the northern and southern Peri-Tethys platforms, caused the further diversification of the clade. This led to the paramount role of the North African platform and the Anatolian region in the radiation of the tribe, causing the present-day generic richness in the western Mediterranean subclade and richness of species in the large genera *Achillea*, *Anthemis*, *Cota*, *Tanacetum*, and *Tripleurospermum* of the eastern Mediterranean subclade.

EVOLUTION

As Ehrendorfer (1970) pointed out, the main changes in evolutionary patterns and processes in Anthemideae have been observed in connection with the switch from a perennial to an annual life form. According to the survey made by Uitz (1970), perennials of the tribe are mostly self-incompatible, while annuals are nearly all self-compatible, more or less autogamous, and much more variable in karyotype length, symmetry, and chiasma frequency. In these respects, the finding made in a systematic study of *Anthemis* in northern Africa by Oberprieler (1998) may be roughly generalized to most Eurasian/Mediterranean representatives of the tribe, if not for all members of Anthemideae. Variation in perennials occurs on a larger geographical scale, and morphologically divergent forms are geographically isolated but often connected by morphological intermediates, which results in clinal patterns of morphological variation. In contrast, annual taxa show more restricted, allopatric distributional areas, and morphological variation within taxa is rather small as compared to the variation among taxa. Evolutionary divergence appears to be more rapid in the annual representatives than in the perennial ones. However, exceptions to these rules exist, and we often find narrowly restricted perennials (often paleoendemics with remnant populations or neoendemics due to polyploidization), as well as widely distributed annuals (especially weedy species that followed the human dispersal as members of a segetal or ruderal flora).

Anthemideae provide several impressive and fascinating examples of polyploid complexes in Compositae. Without exception, these are confined to perennial taxa (whole genera as in *Achillea*, *Leucanthemum*, or *Leptinella* or perennial members of polymorphic genera, e.g., as in *Anthemis*). As noted above, the most comprehensive series of polyploid chromosome numbers exist in *Achillea* (2*x*–10*x*), *Artemisia* (2*x*–16*x*, Pellicer et al. 2007), *Dendranthema* (2*x*–10*x*), *Leptinella* (4*x*–12*x*), and *Leucanthemum* (2*x*–22*x*, Vogt 1991). In *Achillea*, the best studied genus of the polyploid complexes in Anthemideae, various studies have demonstrated numerous cases of polyploidy, transition zones between species, hybridization, and excessive polymorphism (Ehrendorfer 1959; Vetter et al. 1996a, b; Saukel et al. 2004) leading to the conclusion that reticulate evolution was not only involved in recent radiations but must have been already active in the early diversification of the genus (Guo et al. 2005). On the other hand, however, studies presently underway in *Leptinella* (Himmelreich, unpub.) and *Leucanthemum* (Hößl, unpub.) demonstrate that the present polyploid species evolved mainly from their diploid ancestors during the Pleistocene. Using AFLP analyses, Guo et al. (2005) were able to decipher some relationships in the *Achillea millefolium* complex which contains species with diploid and up to hexaploid chromosome numbers.

The Macaronesian genus *Argyranthemum* of subtribe Glebionidinae with its 24 endemic species provides a spectacular example of adaptive radiation at the diploid level (Francisco-Ortega et al. 1996, 1997). Using evidence from phylogenetic analyses based on nrDNA and cpDNA, along with the characterisation of the ecology of each species, Francisco-Ortega et al. (1996, 1997) demonstrated that the primary avenue of taxonomic diversification in this group was extensive inter-island colonization between similar ecological zones, and that hybridization and diploid hybrid speciation played an important role in the evolution of the genus. In other genera of the tribe, diversification through hybrid speciation is often hypothesized on morphological grounds (e.g., in *Anthemis* by Oberprieler, 1998) but remains unproven using molecular techniques. Since intergeneric crosses between and among different genera of the tribe produce fertile or semifertile offspring (cf. experiments of Mitsuoka and Ehrendorfer, 1972, with representatives of *Anthemis*, *Chamaemelum*, *Cota*, *Matricaria*, and *Tripleurospermum*), the prerequisite for diploid hybrid speciation is highly plausible and may be responsible not only for speciation events within genera but also for the reticulate combination of characteristic morphological features of different genera of the tribe.

ECONOMIC USES

Members of Anthemideae are used and cultivated for a broad variety of purposes, mainly as ornamentals, but also for their medicinal and culinary importance, as well as other economic uses. For the southern hemisphere representatives of the tribe, cultivation as ornamentals is known for species of *Athanasia*, *Eriocephalus*, *Oncosiphon*, and *Ursinia*, while members of *Cotula* and especially of *Leptinella* are well-known carpeting plants also in the northern hemisphere. From the Asian subtribe Artemisiinae, the autumn flowering garden chrysanthemums derived from *Chrysanthemum grandifolium* (probably a complex hybrid group raised in China from *Ch. indicum*) are of high economic importance as ornamentals, followed by members of *Ajania*, *Arctanthemum*, *Artemisia*, *Leucanthemella*, and *Nipponanthemum*. Ornamentals from the Eurasian/Mediterranean clade are found in *Tanacetum* (*T. coccineum*, the garden pyrethrum), *Leucanthemum* (*L.* ×*superbum*, the oxeye daisy or marguerite), *Mauranthemum* (*M. paludosum*), and the Paris daisy *Argyranthemum frutescens*. To a lesser extent, members of *Achillea*, *Otanthus*, *Cota*, *Heteranthemis*, *Ismelia*, *Glebionis*, *Chamaemelum*, *Santolina*, and *Lonas* are also found in ornamental gardens.

Medicinal importance of Anthemideae species is mainly restricted to members of *Artemisia* and *Matricaria*, where, for example, vermifugal or antimalarian usages are described for *A. abrotanum* and *A. annua*, respectively. *Matricaria recutita* is known for its antibacterial and anti-inflammatory chemical compounds. To a lesser extent, members of *Achillea* (*A. millefolium* as an herbal treatment of arthritis), *Anacyclus* (*A. pyrethrum* as the source of 'Radix Pyrethri', pellitory), and *Tanacetum* (*T. corymbosum* providing an antibacterial oil) may be similarly used. *Artemisia* is also an important source for plant species with high culinary importance. *Artemisia absinthium* (absinth), *A. genipi*, *A. glacialis* and *A. umbelliformis* (genepi liqueur), and *A. pontica* (flavour of vermouth) are used to flavour alcoholic beverages; *A. dracunculus* (tarragon, estragon) and *A. vulgaris* are important spices.

Additional economic importance is reported for the two species of *Glebionis* that are cultivated in China and Japan due to their edible leaves and flowers, for *Crossostephium chinense* as a source of cotton-like wool that is obtained from the hairs on young leaves, for *Cota tinctoria* that produces a yellow dye, and for *Chamaemelum nobile*, the source of the "Roman Chamomile" oil that is mainly used in the cosmetics industry. Some members of Anthemideae are known for their insecticidal potential. This is mainly exploited in the case of *Tanacetum cinerariifolium*, the important source of "pyrethrum" insecticide. Some Asiatic, North African and North American species of *Artemisia* are relevant for pastures and fodder. *Pentzia* has also been introduced (with little success) in North America as a fodder plant in arid areas.

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Chapter 39

Inuleae

Arne A. Anderberg

HISTORICAL OVERVIEW

The circumscription of the tribe Inuleae has caused little controversy over the years. The presence of tailed anthers in combination with two separated stigmatic surfaces made members of Inuleae easily recognizable. Both Bentham (1873) and Hoffmann (1890) essentially followed Cassini's definition of the tribe (Cassini 1819) with only minor changes.

After the first international symposium on the biology and chemistry of Compositae in Reading in 1975, Merxmüller et al. (1977) prepared the systematic overview of the tribe identifying three major groups, Athrixiinae, Gnaphaliinae, and Inulinae. They also tried to make a tentative subdivision in smaller natural groups of the genera within each of the three subtribes. Inulinae were formed by merging the former groups Buphthalminae, Inulinae, and Plucheinae into a group diagnosed by styles of the *Inula*-type with apically confluent stigmatic bands, and pollen walls with one baculate layer but without an interlaced basal layer. The presence or absence of paleae (receptacular scales) was regarded as having no value for classification. Gnaphaliinae were diagnosed by styles of the *Senecio*-type with apical sweeping hairs and separate stigmatic bands, and by pollen-walls with an intricately interlaced inner layer. In several respects Athrixiinae were a heterogeneous assemblage of inuloid genera that did not completely fit into the two former groups. They had pollen with the interlaced basal layer in the pollen wall but the styles were more like those of Inulinae. The contribution by Merxmüller et al. (1977) was a first critical evaluation of Hoffmann's still prevailing classification of the tribe. The addition of new data from palynology, cytology, and morphology made this treatment modern, but still it was obvious that any unifying characters diagnosing Inuleae were missing. The style shape and pollen wall anatomy were different in different subtribes, and the only shared character seemed to be the tailed anthers, a plesiomorphic character that was also present in most of the Cichorioideae tribes. The treatment with its discussions and the new data gave new insights and a good start for the more analytical approach that was to follow.

Bremer (1987) presented the first cladistic analysis of tribal relationships in Asteraceae and included three different groups from Inuleae, which were found to be in a basal unresolved position within the subfamily Asteroideae. Anderberg (1989) published a more detailed analysis of major clades in Inuleae and came to the conclusion that the genera of Inuleae did not form a monophyletic group. Furthermore, it was found that the genera placed in Athrixiinae by Merxmüller et al. (1977) were mixed among those of Gnaphaliinae, and that the genera of Inulinae as circumscribed by Merxmüller et al. (1977) did not form a monophyletic group. In consequence, Anderberg proposed that Inuleae should be divided into three separate tribes: Gnaphalieae, Inuleae s.str., and Plucheeae. Three subsequent papers (Anderberg 1991a–c) tried to analyze generic relationships within each of the three tribes, respectively.

In contrast to the earlier meeting in Reading, the second international Compositae symposium in Kew 1994 presented Inuleae as a paraphyletic assemblage that should be subdivided into three smaller tribes (Anderberg 1996). DNA *ndhF* sequence analyses confirmed this view and also supported the separation of Inuleae-Gnaphaliinae as tribe

Gnaphalieae, which was demonstrated to be closer to tribes such as Astereae and Calenduleae than to Inuleae proper (Kim and Jansen 1995). This pioneer analysis of molecular data by Kim and Jansen also found with very robust support that Inuleae and Plucheeae together constituted the sister group of Eupatorieae, Heliantheae s.l., and the African *Athroisma* DC. and *Blepharispermum* Wight ex DC. (i.e., what later came to be recognized as Athroismeae), two genera formerly included in Inuleae (Merxmüller et al. 1977). In contrast, the data from *trnL/trnF* of the chloroplast genome (Bayer and Starr 1998) indicated that Inuleae (and Plucheeae) were basal in Asteroideae, as was also suggested by morphological data (Bremer 1987). Kim and Jansen (1995) included only three taxa from Inuleae and Plucheeae and so could not clarify the systematic position of Inuleae within the family; questions of tribal delimitation and generic interrelationships were left unsolved.

Eldenäs et al. (1999) tried to elucidate the evolutionary relationships between Inuleae and Plucheeae by analyzing sequences from a larger number of taxa. They showed that Inuleae and Plucheeae form two lineages, but there were still three of the investigated genera that had unresolved relationships, so an entirely clear picture did not emerge. They also found that the former Inuleae genus *Anisopappus* Hook. & Arn. grouped with *Athroisma* and *Blepharispermum* in the sister group to Heliantheae. Panero and Funk (2002, 2008) also found the group Inuleae + Plucheeae to be sister to Heliantheae and what they recognized as tribe Athroismeae (*Anisopappus*, *Athroisma*, and *Blepharispermum*).

The latest contribution to the understanding of relationships in Inuleae and Plucheeae is that of Anderberg et al. (2005). This paper showed that a number of genera from Inuleae s.str. were actually placed at the base

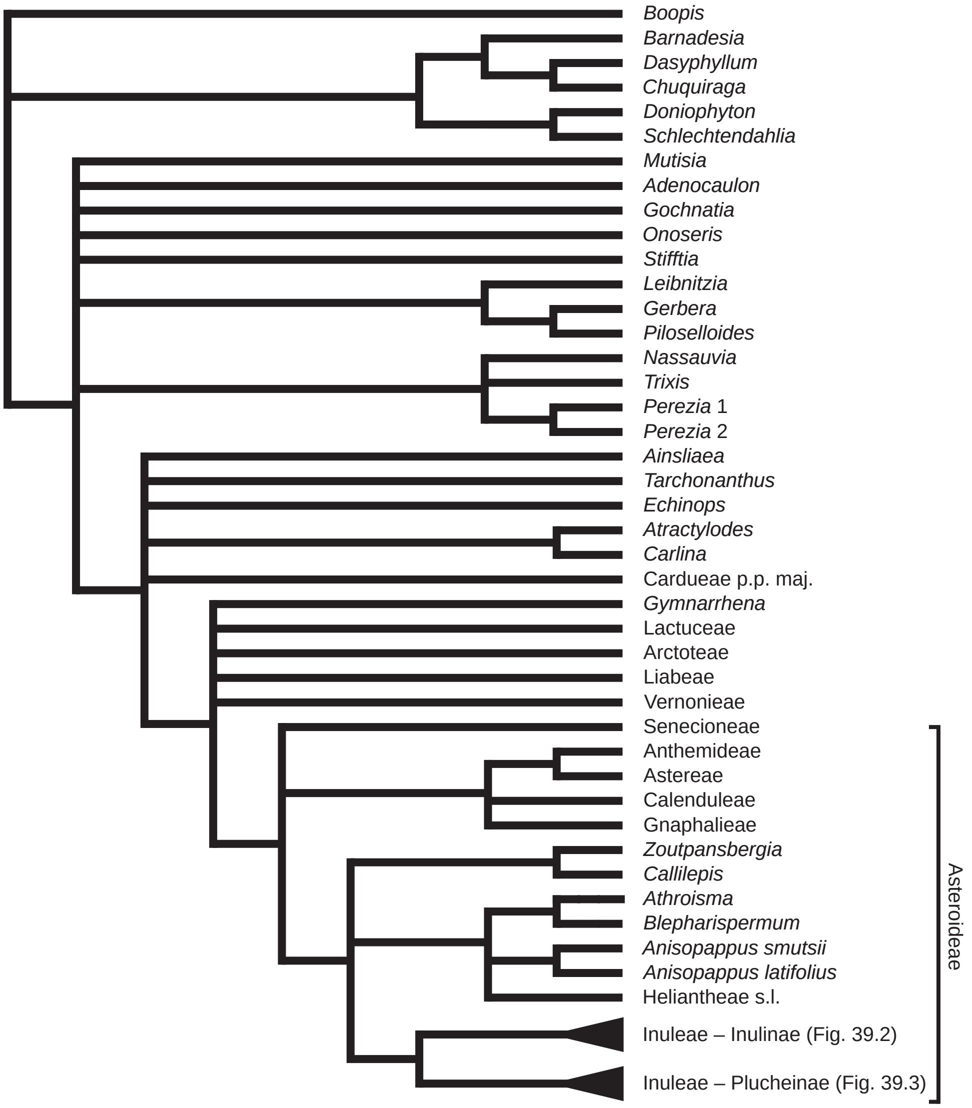

Fig. 39.1. Position of Inuleae in the family based on *ndhF* sequences (Anderberg et al. 2005).

of Plucheeae clade and they therefore concluded that Plucheeae could not be maintained as a separate tribe. They showed that Inuleae consisted of two major sister lineages: Inuleae-Inulinae and Inuleae-Plucheinae. Inuleae together with the small South African group *Callilepis* DC./*Zoutpansbergia* Hutch., and Athroismeae + Heliantheae s.l. formed a trichotomy (Fig. 39.1).

In the subsequent treatment of Inuleae, Anderberg and Eldenäs (2007) followed these new results and placed Plucheeae within Inuleae as a subtribe. As molecular data from a number of genera are still scanty, there is considerable work needed to understand the species relationships in the tribe, and the monophyly of many genera needs to be tested. Some more information has been added, i.e., the three genera *Blumeopsis* Gagnep., *Merrittia* Merr., and *Nanothamnus* Thomson have all been proven to be derived representatives of the genus *Blumea* (Pornpongrungrueng et al. 2007; Anderberg and Pandey 2008), and the enigmatic genus *Feddea* has been shown to represent a separate lineage (tribe Feddeeae; Carriaga et al. 2008) that is sister to Heliantheae s.l. Further studies on generic delimitations and systematic positions in Inuleae are one of the author's ongoing research projects.

PHYLOGENY

Inuleae-Inulinae (Fig. 39.2)

The taxa of this clade are, except for *Caesulia*, characterized by the presence of one large oxalate crystal in each achene epidermis cell. The subtribe has two well-supported main monophyletic groups, i.e., *Duhaldea* together with the *Caesulia*-*Blumea* group, and its sister group comprising all the taxa from the remaining genera, including the *Inula* and *Pulicaria* complexes, which seem to be paraphyletic in relation to other more derived genera. This large clade, including the *Inula* and *Pulicaria* complexes, has an unresolved trichotomy at the base. One clade in that trichotomy includes the genera *Rhanterium*, *Schizogyne* and *Vieria* (*Vieraea*). *Vieria* has an *Inula*-like appearance, but unlike *Inula* it has a pappus of bristles of unequal length arranged in several rows. The second clade within the trichotomy includes *Amblyocarpum*, *Carpesium*, *Chrysophthalmum*, *Inula*, *Pentanema*, and *Telekia*. This clade has *Buphthalmum* as its sister group. The third clade in the trichotomy includes the genera *Anvillea*, *Asteriscus*, *Ighermia*, and *Pallenis*, where *Anvillea* is sister to the others. These genera all have paleate receptacles, and except for *Anvillea* (pappus missing) they have a pappus of scales only. *Pulicaria* groups together with *Jasonia* and *Dittrichia*. All except for *Dittrichia* have a double pappus consisting of both bristles and scales. The pappus in *Dittrichia* consists of many barbellate capillary bristles united at the base in a cupule-like structure that is unique in the tribe.

The relationships among the taxa of Inuleae-Inulinae are still not fully understood, but the small sample of species we have included shows that the circumscription of many of its genera are problematic and may have to be revised to obtain monophyletic genera. A more detailed study of the phylogeny of Inuleae-Inulinae is another ongoing part of our present research in Asteraceae (Englund et al., in press).

Inuleae-Plucheinae (Fig. 39.3)

Many genera belonging to Inuleae-Plucheinae have styles with obtuse sweeping hairs reaching below the style bifurcation, but no species has the large oxalate crystal in the achene epidermis that is characteristic of Inuleae-Inulinae. However, several genera have styles with acute sweeping hairs ending above the style bifurcation, e.g., *Antiphiona*, *Calostephane*, *Geigeria*, *Pegolettia*, *Rhodogeron*, and *Sachsia*.

At the base of Plucheinae there is a polytomy including the South American *Stenachaenium* and groups comprising southern African genera, many of which were earlier considered members of Inulinae (Anderberg 1991a). On the next higher level of the phylogeny the relationships have not been fully resolved, and the genera belong to one of five clades in a pentatomy. The first branch is *Cratystylis*. It is an Australian genus of four species of dioecious shrubs having white, deeply lobed corollas, styles almost devoid of sweeping hairs, and a stigmatic area covering almost the entire inner surface of the style branches. Other Inuleae are not dioecious; they have short-lobed corollas, distinct sweeping hairs, and a stigmatic area separated in two lateral bands that are confluent distally. The phytochemical characteristics of *Cratystylis* are congruent with a position in Inuleae-Plucheinae (Bayer and Cross 2003; Anderberg et al. 2005).

The second part of the pentatomy is the African *Iphionopsis*. The three species of *Iphionopsis* have homogamous capitula and characteristic longitudinal resin ducts in the corolla and the mid-portion of the involucral bracts, and has also resin ducts in the non-sclerified fruit wall. The stigmatic area covers almost the entire inner surface of the style branches as in *Cratystylis*.

The third clade is formed by the mainly Caribbean genus-pair *Rhodogeron* and *Sachsia*. They consist of a few species of herbs with basal leaf rosettes and disciform or radiate capitula. The genus *Sachsia* has pollen with branching bacules (Leins 1971) and in that differs from pollen of other Inuleae-Plucheinae.

The fourth clade of the pentatomy is represented by the genus *Pterocaulon*, a New World genus, with a few species in Australia and adjacent areas. The diagnostic characters for *Pterocaulon* are heterogamous capitula with filiform female florets, generally winged stems, and capitula congested into spherical or elongated secondary aggregations.

Some species have distinct spherical or ellipsoid secondary heads, whereas others have a rather loose spike- or raceme-like arrangement of capitula that can hardly be referred to as secondary heads.

The last group in the pentatomy comprises the core plucheoid taxa, i.e., *Coleocoma*, *Cylindrocline*, *Doellia*, *Epaltes*, *Karelinia*, *Laggera*, *Pechuel-loeschea*, *Pluchea*, *Porphyrostemma*, *Pseudoconyza*, *Sphaeranthus*, *Streptoglossa*, and *Tessaria*. The relationships within this group are almost unresolved. Most taxa of this group have styles with obtuse sweeping hairs extending below the bifurcation. The capitula generally have filiform female outer florets and male or hermaphroditic central florets, but some species have discoid capitula with only hermaphroditic florets. The Australian *Streptoglossa* differs in having conspicuously radiate capitula with distinct purple ray florets.

TAXONOMY

Tribe Inuleae Cassini in J. Phys. Chim. Hist. Nat. 88: 193. 1819 – Type: *Inula helenium* L., Sp. Pl.: 881. 1753

Annual or perennial herbs, shrubs, or small trees; stems and foliage variously pubescent. Leaves generally alternate; blades sessile or petiolate, entire, rarely lobed or pinnatifid. Inflorescences solitary, cymose, corymbiform or paniculate, sometimes much reduced and forming secondary heads. Heads generally heterogamous, sessile or pedunculate, free or more rarely syncephalous, generally without subtending bracts. Florets purple, pink, yellow, cream, or white. Marginal florets (when present) female, rarely neuter; corollas filiform, miniradiate or radiate. Pappus persistent or deciduous, of bristles, awns, bristles and scales, scales only, or missing. Central florets perfect,

Fig. 39.2. Phylogenetic relationships within Inuleae-Inulinae. See. Fig. 39.3 for color chart.

or functionally male; corolla actinomorphic, funnel-shaped, rarely zygomorphic. Pappus of bristles, awns, bristles and scales, scales only, or missing. Involucres campanulate, cupuliform to cylindrical; involucral bracts typically imbricate in a few to several series, cartilaginous to leafy, sometimes only with a leafy distal portion, persistent or deciduous. Receptacle flat, subconvex, or concave, smooth or honeycombed, sometimes with scales or bristles. Anthers ecalcarate with well developed tails, rarely calcarate or ecaudate, the apical appendage flat, without glands. Endothecial tissue radial or polarized. Style branches in perfect florets spreading, semi-cylindrical or flattened, slender, tips obtuse or sometimes acute, outer surface with sharply acute or distinctly obtuse trichomes (sweeping hairs), inner surface with stigmatic papillae generally forming two distally confluent rows. Style in functionally male florets more or less undivided. Style base glabrous, often bulbous, non-sclerified. Achenes terete, ovoid, triquetrous, or quadrangular, sometimes dimorphic and flattened in ray florets, often with ten ribs, outer surface glabrous or pubescent and sometimes resiniferous, typically brown, achene epidermis with or without one large oxalate crystal in each cell. Pollen echinate, with one-layered baculate sexine, without internal foramina.

MORPHOLOGY AND ANATOMY

The majority of Inuleae (Figs. 39.4, 39.5) are subshrubs, shrubs or perennial herbs, adapted to a warm or temperate climate; some species are adapted to short vegetation periods (annuals) or arid or saline environments

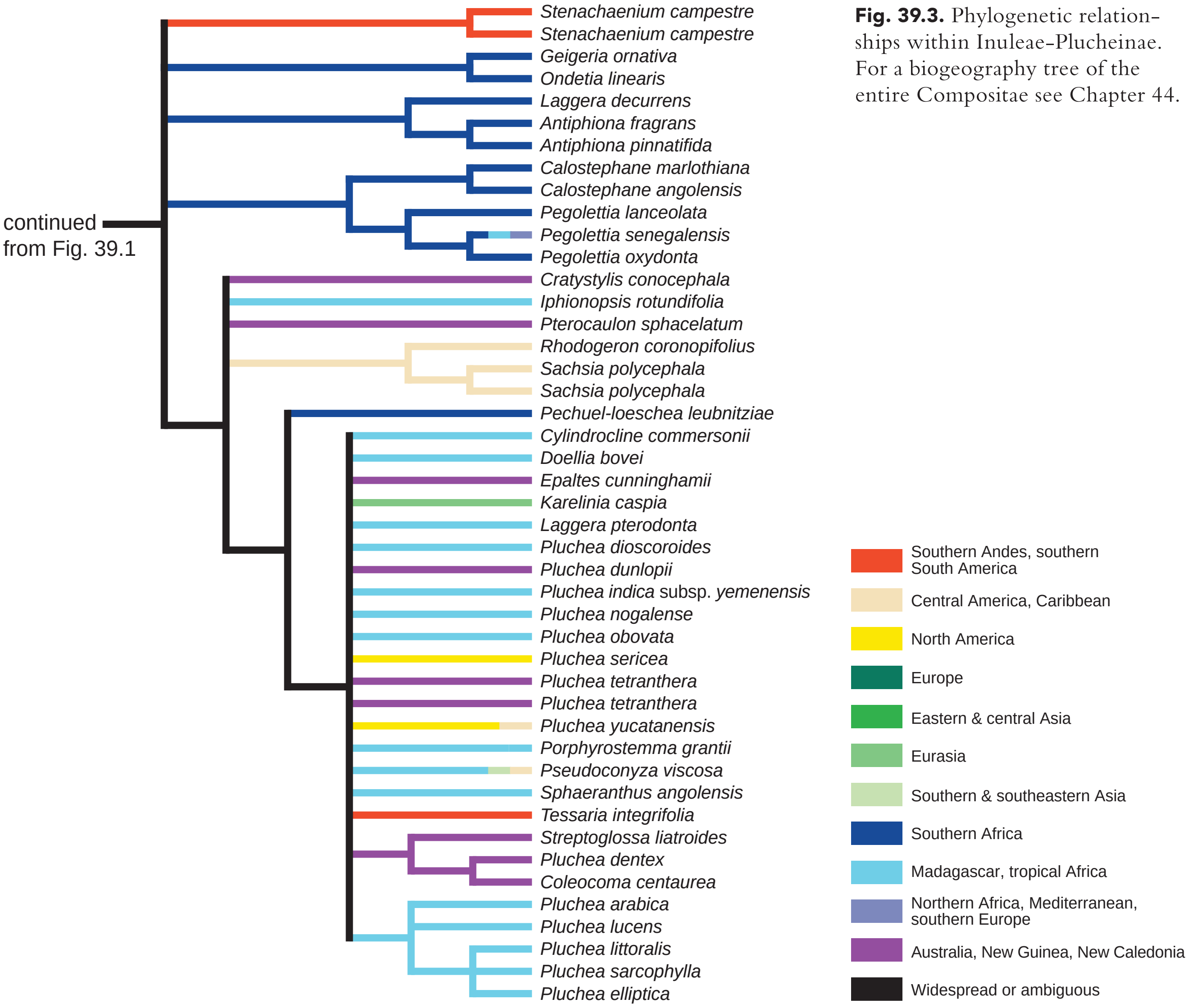

Fig. 39.3. Phylogenetic relationships within Inuleae-Plucheinae. For a biogeography tree of the entire Compositae see Chapter 44.

(succulent leaves). The leaves are alternate and generally scattered on the stem, but in genera such as *Cylindrocline* and *Monarrhenus* the leaves are confined to the tips of the branches, and in *Sachsia* and *Rhodogeron* the leaves form a basal rosette. The lamina is generally simple with entire or dentate or serrate margin, but some genera have pinnatifid or pinnatisect leaves (e.g., *Adelostigma*, *Antiphiona*, some *Iphiona*, *Perralderia*), or apically lobed leaves (some *Iphiona*, *Limbarda*). A few genera have distinctly decurrent leaf bases that may appear as winged stems (e.g., *Calostephane*, *Geigeria*, *Laggera*, *Ondetia*, and *Pterocaulon*). Stems and leaves lack spines and thorns, but the leaves in some species may be needle-like and sharply pointed. The outer bracts in *Pallenis spinosa* (L.) Cass. terminate in a short sharp thorn and this species is a notable exception. Many of the herbaceous species are rhizomatous, and sometimes with almost tuberous rhizomes (*Jasonia*).

Resin ducts are found in the stem of both Inuleae-Inulinae (e.g., *Limbarda*, *Rhanterium*, *Telekia*) and Inuleae-Plucheinae (e.g., *Doellia*, *Laggera*, *Porphyrostemma*, *Tessaria*) and several genera are also heterogeneous in this respect, e.g., *Inula*, *Pluchea*, and *Stenachaenium* (Anderberg 1991a, b). In transverse sections of stems resin exudate is visible as golden or reddish-brown drops, and the presence or absence of resiniferous ducts is a potentially informative character for resolving relationships in heterogeneous genera and should be studied more in detail. A characteristic of many genera of the tribe Gnaphalieae is the presence of fibers in the phloem, i.e., fibers mixed in the phloem, but in no representative of Inuleae-Inulinae, and only in two genera of Inuleae-Plucheinae, has this feature been found (*Neojeffreya* and some *Nicolasia*). Laticifers are not found in any member of Inuleae. The trichomes are either glandular or non-glandular, the glandular trichomes are biseriate, whereas the non-glandular trichomes are uniseriate with several cells and widened septa; in a few species woolly trichomes with a few basal cells and a long non-septate part are found (e.g., *Pterocaulon*).

The capitula are generally solitary and separate even if they are more or less congested. In some genera (*Neojeffreya*, *Sphaeranthus*, *Pseudoblepharispermum*, *Pterocaulon*, and *Triplocephalum*) capitula are aggregated into spherical or ellipsoid secondary heads and in *Pterocaulon* capitula may also be arranged in more-or-less densely congested spikes. In several genera capitula of pseudocephalia are reduced in size with reduction in the number of involucral bracts. In *Pterocaulon* the capitula are reduced to various degrees, most so in the taxa with spherical secondary heads. Florets are usually yellow in Inuleae-Inulinae, and they generally have various shades of pink, mauve or purple in Inuleae-Plucheinae except in many of the basal inuloid genera such as *Calostephane*, *Geigeria*, and *Pegolettia*.

The capitula of most genera are heterogamous with both female and bisexual florets, the outer ones female, either radiate, miniradiate, tubular or filiform. Heterogamous disciform capitula with filiform female florets are apomorphic. Homogamous capitula are frequent in genera of Inuleae but seem to have evolved several times independently as outer florets have been reduced. Normally radiate genera may also have discoid species, or in some cases the same species can be either radiate or discoid (e.g., *Anvillea garcinii* (Burm. f.) DC.). The genus *Cratystylis* is the only dioecious representative.

Ray florets are typical of most genera of Inuleae-Inulinae. In Inuleae-Plucheinae rays are found in the yellow-flowered southern African genera *Calostephane*, *Geigeria*, and *Ondetia*, whereas disciform capitula are more common in the majority of genera, except *Porphyrostemma*, *Rhodogeron*, and *Streptoglossa*, which have purple rays. Many genera of Inuleae-Plucheinae have functionally male disc florets and female filiform outer florets in several rows. The filiform female florets are generally minutely three-lobed, but in *Stenachaenium* the outer florets have a five-lobed corolla and may therefore be derived from bisexual disc florets. Both ray florets and filiform marginal florets are generally female, but a few genera (e.g., *Anvillea*, some *Iphiona*, *Jasonia*, and *Perralderia*) have neuter ray florets with well-developed lamina. The corolla epidermal cells of the ray florets are generally elongated with almost smooth or finely striated surface. Crested ray floret epidermal cells are typical of *Asteriscus* and *Pallenis*, but not found in the closely related *Ighermia*. Isodiametric cells with a papillose surface are characteristic of *Perralderia*, but not found in its closest relative, *Iphiona*.

Disc floret corollas are short-lobed as in Asteroideae in general, but some exceptions are known, i.e., *Geigeria*, *Ondetia*, and *Tessaria*. In *Geigeria* and *Ondetia*, corolla lobes have fibers surrounding the vascular bundles forming conspicuous ribs on the margin. Other taxa of Inuleae and Plucheeae have smooth or indistinctly ribbed corolla lobes. Most species have short biseriate glandular trichomes on the corolla lobes, and robust, acute trichomes occur on the corolla lobes of *Antiphiona*, *Pegolettia*, and some *Geigeria*, but otherwise the corolla lobes are smooth or provided with weak, septate trichomes. The corolla epidermis cells in the disc florets are elongated and smooth with straight or minutely undulated cell walls, but in *Iphiona* the epidermal cells have distinctly sinuous cell walls. Small crystals in various shapes may be present, but very long, needle-like crystals are only found in *Iphiona* and *Perralderia*.

The receptacles are epaleate or paleate. Receptacular scales, or paleae, were once considered diagnostic of subtribe Buphthalminae, but this was rejected by Leins (1971) and by Merxmüller et al. (1977). Paleate receptacles are found in many genera that are not closely related, but they have various shapes and have evolved in parallel in various evolutionary lineages in the tribe. In

Fig. 39.4. Representative genera of Inuleae. **A** *Anvillea garcinii* DC. (*Anderberg 549*; Ain Sefra, Annaba, Algeria); **B** *Chiliadenus lopadusanus* Brullo (*Anderberg and Anderberg L07-1*; Lampedusa, Sicily, Italy); **C** *Pallensis hierochuntica* (Michon) Greuter (Negev Highlands, Mt. Retamim, Israel); **D** *Inula helenium* L. (Stockholm, Uppland, Sweden); **E** *Pluchea sagittalis* (Lam.) Cabrera (Cuchilla Alta, Dpto. Canelones, Uruguay); **F** *Cratystylis conocephala* (F. Muell.) S. Moore (*Nordenstam and Anderberg 604*; Kalgoorlie, Western Australia, Australia). [Photographs: A, F, A.A. Anderberg; B, R. Anderberg; C, O. Fragman-Sapir; D, A.-L. Anderberg; E, J.M. Bonifacino.]

Fig. 39.5. Representative genera of Inuleae. **A** *Iphiona aucheri* (Boiss.) Anderb. (*Gharemaninejad 1506*, Hajiabad, Hormozgan Prov., Iran); **B** *Tessaria integrifolia* Ruiz & Pav. (near Gualeguaychú, Prov. Entre Ríos, Argentina); **C** *Pterocaulon lorentzii* Malme (Santa Ana, Dpto. Canelones, Uruguay); **D** *Stenachaenium megapotamicum* Baker (Sierra de las Ánimas, Dpto. Maldonado, Uruguay). [Photographs: A, F. Gharemaninejad; B–D, J.M. Bonifacino.]

Inuleae-Inulinae, paleate capitula are found in several genera, but among Inuleae-Plucheinae this character state is rare and found only in *Cylindrocline*, *Ondetia*, *Neojeffreya*, and *Pseudoblepharispermum*. Epaleate receptacles may have other kinds of structures on the surface, e.g., bristles in *Geigeria*, or knobs in some *Inula*, or unevenly incised scale-like ridges, which are found in a number of genera, e.g., *Dittrichia* and *Duhaldea*.

The anthers are ecalcarate or exceptionally calcarate as, e.g., in *Tessaria*, and in the Inuleae-Inulinae taxa *Asteriscus* and *Geigeria* they are also somewhat calcarate. The vast majority of genera are, however, ecalcarate, which is the prevailing condition in Asteroideae. The anther thecae are generally distinctly caudate, often with long and with distinct branched tails but many times with short and almost unbranched tails. A few genera are ecaudate (e.g., *Adelostigma*, *Laggera*), which in this respect make them anomalous in Inuleae. The endothecial tissue is either radial with wall thickenings on longitudinal walls, or polarized with wall thickenings confined to the proximal and distal ends of the endothecial cells, and larger heterogeneous genera may have species with either kind of wall thickenings. The apical anther appendage is flat and soft with an acute or obtuse apex, which in a few taxa is truncate or emarginate (e.g., *Duhaldea*).

The style is bifid in most taxa but may be undivided in some Inuleae-Plucheinae with functionally male florets. The style branches are generally obtuse and rather short with sweeping hairs dorsally and two apically confluent bands of stigmatic tissue ventrally. In *Cratystylis* and *Iphionopsis* the stigmatic tissue covers almost the entire inner surface of the style branches. The shape and distribution of the sweeping hairs is of taxonomic importance. They are acute in shape and confined to the upper half of the style branches, or distinctly obtuse and extending down on the shaft some distance below the style bifurcation. The former is typical of Inuleae-Inulinae whereas the latter is characteristic of many Inuleae-Plucheinae. The genus *Cratystylis*, which belongs in Inuleae-Plucheinae have almost no sweeping hairs at all and the style branches, are almost smooth. The style may contain small square crystals or star-shaped crystal druses.

The achenes are in most cases provided with five vascular strands and are more-or-less lignified and provided with a varying number of sclerenchymatous ribs in the pericarp in Inuleae-Inulinae. The achenes of Inuleae-Plucheinae genera are often less sclerified and rarely provided with distinct ribs. The achenes are fusiform, angled, quadrangular or more or less triquetrous, generally homomorphic, but ray floret achenes are often flattened in species with triquetrous disc floret achenes. Trichomes and glands are frequent and may be arranged in various ways. Elongated non-myxogenic twin hairs are common in all genera, and specialized types with anchor-shape (*Anvillea*, *Sphaeranthus*) or uncinate shape (*Lifago*, *Pseudoblepharispermum*, *Sphaeranthus*, and *Thespidium*) are known from a few genera. Biseriate glandular trichomes are often found in the portion of the fruit nearest to the pappus but may also be scattered over the entire surface. A mixture of glands and ordinary twin hairs is also found in some genera.

All genera of Inuleae-Inulinae (except *Caesulia* where the true pericarp is highly reduced to one single cell-layer) are diagnosed by the presence of one large oxalate crystal in each epidermal cell. The monophyly of this "crystal clade" has received support by molecular data from the *ndhF* gene (Eldenäs et al. 1999) and by the presence of a unique 3-base pair insertion (CCT). The 3-bp insertion is absent from all other Asteraceae, including all the genera of Inuleae-Plucheinae, notably also from the inuloid genera of that subtribe (*Antiphiona*, *Calostephane*, *Geigeria*, *Ondetia*, and *Pegolettia*). The parenchymatous part of the pericarp is often provided with larger crystals in many genera, but the distribution is far from constant and shows no pattern.

Schizogenous secretory ducts, resin canals or resin cavities, are found in a few genera. In *Limbarda* five resin ducts are present in the pericarp, an autapomorphic character used to distinguish this genus within the *Inula*-complex. *Asteriscus* is diagnosed by chambered secretory cavities along the edges of the achenes, and in *Doellia* the longitudinal secretory ducts are clearly visible on the surface of the fruit. In *Porphyrostemma* there are instead two-three celled cavities arranged in longitudinal rows.

The carpopodium in most species is symmetrical or slightly oblique, and is particularly prominent in some Inuleae-Plucheinae. The testa, endosperm, and embryo are not known to have any diagnostic features.

The pappus is normally composed of free capillary bristles (*Inula*-type) but may sometimes be connate basally, or the pappus consists of capillary bristles in combination with a row of short scales (*Pulicaria*-type). Capillary pappus bristles are usually scabrid or barbellate but distinctly plumose are derived in some *Pegolettia*. A diagnostic feature of the capillary pappus bristles in many plucheoid taxa is that the teeth are erect and adpressed towards the next upper ones, something which gives the bristles a characteristic aspect. In the two genera *Rhanteriopsis* and *Rhanterium* the bristles are much wider than in other taxa but may still be considered homologous to ordinary bristles. More difficult is the interpretation when the pappus in some genera is composed of flattened, more or less scale-like bristles, as, e.g., in the genera *Coleocoma*, *Delamerea*, and *Thespidium* of Inuleae-Plucheinae. The pappus elements are intermediate between bristles and scales, and it is not evident whether they have evolved from scales or bristles. However, in many cases such genera are placed in clades where all

Table 39.1. Genera of Inuleae with number of species, subtribes, distribution, and chromosome number.

Genus	Number of species	Subtribe[a]	Distribution	Chromosome number (2*n*)[b]
Adelostigma Steetz	2	Pl	Tropical Africa	—
Allagopappus Cass.	2	In	Africa (Canary Islands)	20
Allopterigeron Dunlop	1	Pl	Australia	—
Amblyocarpum Fisch. & C. A. Mey.	1	In	Asia (Caspian Sea area)	—
Antiphiona Merxm.	2	Pl	S Africa (Namibia)	—
Anvillea DC.	2	In	N Africa, Middle East	14
Asteriscus Tourn. ex Mill.	8	In	Mediterranean region, Macaronesia	14, 16, 18
Blumea DC.	ca. 100	In	Trop. and subtrop. Asia, Africa	16, 18, 20, 22, 30, 36, 44, 48, 54
Buphthalmum L.	3	In	Europe	20
Caesulia Roxb.	1	In	India	14
Calostephane Benth.	6	Pl	Tropical Africa, Madagascar	—
Carpesium L.	25	In	Asia, SE Europe	20, 36, 40
Chiliadenus Cass.	10	In	Mediterranean region	16, 18
Chrysophthalmum Sch.Bip.	3	In	SW Asia	—
Coleocoma F. Muell.	1	Pl	Australia	—
Cratystylis S. Moore	4	Pl	Australia	—
Cylindrocline Cass.	2	Pl	Africa (Mascarene Isl.)	—
Delamerea S. Moore	1	Pl	E Africa	—
Dittrichia Greuter	2	In	Mediterr. region, introd. Amer., Aus.	16, 18, 20
Doellia Sch.Bip.	2	Pl	Africa, Asia (Arabia)	20
Duhaldea DC.	14	In	Asia, possibly one sp. in Africa	18, 20, 40
Epaltes Cass.	14	Pl	Worldwide, trop./subtrop.	20
Geigeria Griess.	28	Pl	Africa, mainly S Africa	20
Ighermia Wikl.	1	In	NW Africa (Morocco)	14
Inula L.	ca. 100	In	Europe, Africa, Asia	16, 18, 24, 32, 36
Iphiona Cass.	12	In	NE Africa, W Asia	18, 20
Iphionopsis Anderb.	3	Pl	E Africa, Madagascar	—
Jasonia Cass.	1	In	Europe (Spain)	18
Karelinia Less.	1	Pl	Asia (Caspian Sea area)	20
Laggera Sch.Bip. ex Koch	17	Pl	Tropical Africa, Asia	20
Lifago Schweinf. & Muschl.	1	In	N Africa	—
Limbarda Adans.	1	In	Mediterranean region	18
Litogyne Harv.	1	Pl	Tropical Africa, Namibia	—
Monarrhenus Cass.	2	Pl	Africa (Mascarene Isl.)	—
Neojeffreya Cabrera	1	Pl	Madagascar, E Africa	—
Nicolasia S. Moore	7	Pl	S Africa	—
Ondetia Benth.	1	Pl	S Africa (Namibia)	—

Table 39.1. Continued.

Genus	Number of species	Subtribe[a]	Distribution	Chromosome number (2*n*)[b]
Pallenis (Cass.) Cass.	3	In	Mediterr. reg., introduced elsewhere	10, 12
Pechuel-loeschea O. Hoffm.	1	Pl	S Africa (Namibia)	—
Pegolettia Cass.	9	Pl	S Afr., 1 sp. to N Afr. & Middle East	20
Pentanema Cass.	20	In	Asia, Tropical Africa	18, 27
Perralderia Coss.	3	In	N Africa	18
Pluchea Cass.	ca. 80	Pl	Worldwide	20, 30
Porphyrostemma Benth. ex Oliv.	4	Pl	Tropical Africa	—
Pseudoblepharispermum Lebrun & Stork	2	Pl	E Africa	—
Pseudoconyza Cuatrec.	1	Pl	C America, Asia, Africa	20, 22
Pterocaulon Elliott	18	Pl	N + S America, Australasia	20
Pulicaria Gaertn.	85	In	Europe, Africa, Asia	12, 14, 16, 18, 20, 36
Rhanteriopsis Rauschert	4	In	Middle East	—
Rhanterium Desf.	3	In	N Africa to Middle East	24
Rhodogeron Griseb.	1	Pl	West Indies (Cuba)	—
Sachsia Griseb.	4	Pl	SE USA, West Indies	20
Schizogyne Cass.	2	In	Africa (Canary Islands)	18
Sphaeranthus L.	41	Pl	Old World tropics	20
Stenachaenium Benth.	5	Pl	S America	—
Streptoglossa Steetz	8	Pl	Australia	20
Telekia Baumg.	1	In	C Europe, W Asia	20
Tessaria Ruiz & Pav.	1	Pl	S America	20
Thespidium F. Muell. ex Benth.	1	Pl	Australia	—
Triplocephalum O. Hoffm.	1	Pl	Tropical Africa	—
Varthemia DC.	1	In	W Asia	16
Vieria Webb & Berth.	1	In	Africa (Canary Islands)	16

[a] Subtribes: In = Inulinae, Pl = Plucheinae.

[b] For references to chromosome numbers, see Anderberg (1991a, b), and *Index to Chromosome Numbers in the Compositae* (http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html).

other taxa have capillary bristles, and therefore it seems reasonable to assume that these scale-like structures are actually modified bristles. In some the pappus consists of fairly large scales only, particularly in many of the genera of Inuleae-Inulinae with paleate receptacles (e.g., *Asteriscus* and *Buphthalmum*). The scales are of different size and shape but never resemble bristles. In Inuleae-Inulinae there are species with both scales and bristles, and genera such as *Asteriscus*, *Ighermia*, and *Pallenis* belong to the same clade as *Pulicaria*, which has both bristles and scales. It could be hypothesized that in these genera the bristles have been lost, and that the scale in the pappus has been enlarged. *Buphthalmum*, on the other hand, is part of the *Inula* clade where all species have a pappus of bristles only. In that case it seems more parsimonious to interpret the pappus scales as modified bristles. Within the *Pulicaria* clade all species have pappus scales, except *Dittrichia*, which is close to *Jasonia*. *Dittrichia* was formerly part of *Inula* but differs in having several rows of bristles that are united into a cup basally. Considering the position of *Dittrichia* close to *Jasonia* and *Pulicaria*, it can be assumed that the outer rows of bristles are derived from the short scales typical of the double *Pulicaria*-type pappus. It seems evident that bristles can transform into scales and that scales can change into bristles.

POLLEN

In Inuleae the pollen is fairly similar between genera, but differs considerably from that of Gnaphalieae ("Inuleae-Gnaphaliinae"). Pollen in Inuleae s.l. was investigated by Leins (1971); it is caveate with an echinate, microperforate exine, which in transverse section has a tectum with one layer of columellae between the spines and two layers in the spine bases. The apical part of the spines is often provided with a minute cavity but generally lacking internal foramina. The pollen has a diameter/exine thickness ratio of 8.0 (Bolick 1991) except in *Cratystylis*, which in this respect is more similar to the Cichorioideae tribes where the ratio is lower (6.2–7.5).

CHROMOSOME NUMBERS

Chromosome numbers in Inuleae are often based on $x = 9$ or $x = 10$, and common numbers are $2n = 18$, 20, 40, but there are numerous polyploid or dysploid reductions. Some genera of Inuleae-Inulinae have lower basic number than the average, based on $x = 5$, 6, or 7 (e.g., *Anvillea*, *Ighermia*, *Pallenis* and some *Asteriscus*). Information is still missing for several genera (Table 39.1).

CHEMISTRY

Some phytochemical characteristics have been investigated in genera of Inuleae, which in general conform to the family characteristics. The oligosaccharide inuline is characteristic of the entire family, but was named after *Inula* and was first described from rhizomes of *Inula royleana* DC. Among sesquiterpene lactones, the presence of 8,12 eudesmanolides predominates in Inuleae and are also typical of their sister group (Heliantheae). Benzofurans or benzopyrans are diagnostic of the subfamily Asteroideae, and have also been found in some Inuleae-Inulinae, but not in Inuleae-Plucheinae, and this may prove to have a diagnostic value. Several genera of the latter (*Epaltes*, *Laggera*, *Pluchea*, and *Tessaria*), have the sesquiterpene cuauhtemon or its derivatives, whereas these substances have not been found in other investigated genera, i.e., *Cratystylis*, *Pechuel-loeschea*, *Pterocaulon*, and *Sphaeranthus* (Nakanishi et al. 1974), and is thus a potential synapomorphy. Further references to information on chemical components in species of Inuleae is presented by Harborne (1977) and Anderberg (1991a, b).

DISPERSAL

Most species of Inuleae release the fruit by wind as the involucral bracts are bent backwards, opening the capitulum, and allowing the pappus to carry the fruit away. Species without any pappus bristles drop fruits from the capitula as the involucres open. *Asteriscus* and *Pallenis* (e.g., *P. hierochuntica* (Michon) Greuter) have hydrochastic capitula that are closed in drought but open after rain, exposing the achenes. The woody capitula in *Anvillea* have achenes firmly subtended by the paleae, and both capitula and achenes remain attached on the plant for a long time. The rigid and solid capitulum is hardly flexible enough to allow a hygrochastic mechanism; the entire capitulum is eventually broken loose from the stem and the spinescent remains of the surrounding leaf midrib make the entire capitulum function as a burr. Germination may be depending on good conditions, and fruits of *Anvillea* in herbarium specimens are known to be viable for decades (Anderberg, pers. obs.).

BIOGEOGRAPHY

The subtribe Inulinae is here viewed as a predominantly European, North African, western Asian group with its highest generic and morphological diversity in areas around the Mediterranean (Fig. 39.2). In the subtribe many species occur in other areas, most species of *Carpesium* occur in Asia, some species of *Inula* are found as far to the east as China and Japan, several species of the *Inula* occur in tropical Africa, several *Pulicaria* have distributions in Arabia and Socotra, and one *Pulicaria* is found in South Africa. However, yet unpublished results show that these taxa must be interpreted as having extended their distribution secondarily. The subtribe has two major clades, one here with *Blumea*, *Caesulia*, and *Duhaldea* has been recently shown to contain also the tropical species of *Pentanema* (*P. cernuum* (Dalzell) Y. Ling, *P. indicum* (L.) Y. Ling, and *P. ligneum* Mesfin), the two first occurring in Asia or the Old World tropics, the latter in the Horn of Africa (Pornpongrungrueng et al. 2007). The majority of species in this clade occur in tropical Asia, although a few are found in Africa, or Australia.

The subtribe Plucheinae seems to have a much more complex biogeography (Fig. 39.3), due to the fact that the tree structure is not as resolved as the one for Inulinae, with low support values for many nodes. At the base there is a polytomy consisting of a South American clade (*Stenachaenium*) together with three southern African clades and the large group comprising taxa from many different areas. The taxon sampling is also not representative for the distribution of many genera. Species of *Pluchea* can be found in Australia, Asia, Africa, in various parts of

South America, North America and Central America and the Caribbean, and it is yet unclear if any of these areas could be ancestral. If the present tree topology is supported by additional data, it is interesting that the South American *Stenachaenium* is placed at the base of the tree together with only southern African genera.

ECONOMIC USES

No representative from Inuleae and Plucheeae are among the economically important species in the family. A few species such as *Buphthalmum salicifolium* L., *Inula britannica* L., *I. ensifolia* L., *I. helenium* L., *I. hookeri* C.B. Clarke, *I. magnifica* Lipsky, *I. oculus-christi* L., *I. orientalis* Lam., *I. racemosa* Hook. f., *I. royleana* DC., *Pallenis maritima* (L.) Greuter, and *Telekia speciosa* (Schreb.) Baumg. are frequently grown as ornamentals and sold as garden perennials. *Inula helenium* (alant) and *Pulicaria dysenterica* were formerly a source of herbal medicine in Europe. In Inuleae-Plucheinae, *Pluchea odorata* has been used for medicinal purposes in Mexico but has no importance in other areas of the world.

CONCLUSION

Since the time of the first Compositae conference in 1975, the level of understanding the family has increased considerably. First, and most important, is that the tribe Inuleae is much smaller since all the genera of Merxmüller et al.'s (1977) II. Gnaphaliinae and III. Athrixiinae have been removed to tribe Gnaphalieae. The modern circumscription of Inuleae basically comprises the genera of the groups 1–8 under I. Inulinae sensu amplo.

Their *Inula* group *(1)* belongs to Inuleae-Inulinae, except for *Calostephane* (incl. *Mollera*) and *Pegolettia* that are part of Inuleae-Plucheinae. Merxmüller et al. (1977) also included *Anisothrix* in *Pegolettia*, but that genus actually belongs in Gnaphalieae. The genus *Pelucha* has been shown to belong in Heliantheae-Helenieae (Baldwin and Wessa 2000). The *Geigeria* group *(2)* is also part of Inuleae-Plucheinae. Their *Carpesium* group *(3)* is an integrated part of the *Inula* group, since *Carpesium* is a derived ingroup in the *Inula* complex, albeit without pappus and with tubular female marginal florets. Their *Pluchea* group *(4)* contains almost all the genera that form the core Inuleae-Plucheinae. Although *Blumea* has filiform marginal florets, it does not belong in Inuleae-Plucheinae, but it is close to *Duhaldea* in Inuleae-Inulinae. The *Sachsia* group *(5)*, and *Stenachaenium* group *(5a)* both belong to Inuleae-Plucheinae, although they were both considered aberrant by Merxmüller et al. (1977). *Sachsia* and *Rhodogeron* are integrated parts of the subtribe, whereas the position of *Stenachaenium* is in the unresolved basal polytomy. The *Feddea* group *(6)* included only the monospecific *Feddea* from Cuba, which combined styles of *Inula*-type with aberrant pollen wall morphology. After being a genus incertae sedis, it has now finally been shown to be sister to Heliantheae s.l. (Carriaga et al. 2008). The *Cratystylis* group *(7)* is also an integrated part of Inuleae-Plucheinae. The *Sphaeranthus* group *(8)* also belongs to Inuleae-Plucheinae but is apparently polyphyletic, as *Athroisma* and *Blepharispermum* belong to tribe Athroismeae (Panero and Funk 2002). Its remaining genera *Cylindrocline*, *Pterocaulon*, or *Sphaeranthus* belong in Inuleae-Plucheinae, whereas *Caesulia* is a close relative of *Blumea* in Inuleae-Inulinae.

Ongoing research in Inuleae is now focused on sequencing all remaining recognized genera to test their systematic position and the monophyly of the genera. This latter goal is especially important because several of them have been shown to be paraphyletic or polyphyletic (Englund et al., in press; Anderberg, unpub.). In addition to *ndhF*, datasets for other plastid loci such as *trnL/trnF*, *psbA-trnH*, and from the nuclear markers such as ITS, ETS, and PgiC are being used to infer a phylogeny. A well corroborated hypothesis of generic relationships and generic monophyly will form an evolutionary framework for future work in Inuleae and help with revisions of generic circumscriptions.

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Chapter 40

Athroismeae

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HISTORICAL OVERVIEW

The Athroismeae Panero are a small and recently described tribe (Panero and Funk 2002), which constitutes the sister group of Feddeeae and all the clades of the Heliantheae tribal complex (Kim and Jansen 1995; Eldenäs et al. 1999). Panero and Funk (2002) recognized no less than twelve tribes within the Heliantheae tribal complex (Bahieae, Chaenactideae, Coreopsideae, Eupatorieae, Helenieae, Heliantheae s.str., Madieae, Millerieae, Neurolaeneae, Perityleae, Polymnieae, Tageteae), and consequently also gave their sister group the tribal name Athroismeae.

Few genera have been associated with Athroismeae. Analyses of DNA sequence data have so far supported that the Athroismeae clade comprises at least the genera *Athroisma* (Fig. 40.1C, D), *Blepharispermum* (Fig. 40.1A, B) and *Anisopappus* (Fig. 40.2) (Kim and Jansen 1995; Eldenäs et al. 1999). *Leucoblepharis* is morphologically very close to *Athroisma* and *Blepharispermum* and is with certainty a member of the tribe. Panero (2005) stated that his ongoing research and yet unpublished data showed that also the enigmatic genus *Centipeda* (Fig. 40.3) was part of the same clade.

Panero subdivided Athroismeae into the three subtribes Athroisminae, Anisopappinae, and Centipedinae. In a later treatment, Panero (2007) included also the enigmatic genus *Welwitschiella* O. Hoffm., which shows a superficial resemblance to *Anisopappus*. My preliminary analyses of *ndhF* and ITS showed that *Welwitschiella* is not related to *Anisopappus*, but instead nested within the tribe Astereae (Brouillet et al., submitted). Therefore, *Welwitschiella* will not be discussed further here.

The five genera of Athroismeae differ considerably from each other in many characters, and it is not evident that they are closely related, although they form three morphologically distinct groups corresponding to Panero's three subtribes. The different genera have also been treated in various ways and placed in different tribes over the years, often misplaced in previous taxonomic treatments.

De Candolle (1833, 1834) described the genera *Blepharispermum* and *Athroisma*, and later (De Candolle 1836) included both genera in Sphaerantheae of div. Conyzeae under Asteroideae-Baccharideae. Bentham placed them in tribe Inuloideae, and Hoffmann (1890) included *Athroisma* and *Blepharispermum* (incl. *Leucoblepharis*) in Inuleae-Filagininae, with which they shared filiform female florets and capitula arranged in secondary heads. Also Merxmüller et al. (1977) considered *Athroisma* and *Blepharispermum* to be close and included them in the *Sphaeranthus* group of Inuleae-Inulinae.

Eriksson (1991) was first to suggest that the so-called *Blepharispermum* group was entirely misplaced in Inuleae, and pointed out that they shared several synapomorphic character states with members of Heliantheae-Ecliptinae, such as carbonized achenes, paleate receptacles, ovate anther appendages, and anther appendages provided with an apical gland (*Blepharispermum*, *Leucoblepharis*). He also showed that the secondary heads in *Sphaeranthus* and in genera of the *Blepharispermum* group were likely to have evolved independently, as they are fundamentally different in structure. Consequently, Eriksson proposed that the genera should be included in Heliantheae, and Karis (1993) included *Athroisma* in his analysis of morphological data in Heliantheae s.l., where it was found to be a member of a basal unresolved complex in Helenieae. Bremer (1994) also placed *Blepharispermum*, *Athroisma* and *Leucoblepharis* in the tribe Helenieae, and in a later paper (Bremer 1996) he used these three genera as examples of isolated and specialized taxa of Helenieae.

Anisopappus (Fig. 40.2) was described by Hooker and Arnott (1837) who stated that the new genus had some characters resembling *Buphthalmum* (Inuleae). The same species had earlier been described by Linnaeus (1753) as *Verbesina chinensis*, and retained in that genus by De Candolle (1836) albeit with a question mark added. From a nomenclatural perspective this is an interesting case. When *Verbesina chinensis* L. became synonymized with *Anisopappus chinensis* Hook. & Arn., the Linnaean epithet was already taken, and a new epithet needed to be chosen from among those available for the taxon. A nomen novum could not be proposed since the name *A. chinensis* Hook. & Arn. was already available and legitimate. The notion that *A. chinensis* Hook. & Arn. is a new combination for *Verbesina chinensis* L. (Wild 1964; Beentje 2002) is a misconception. Bentham placed *Anisopappus* in tribe Inuloideae, and Hoffmann (1890) concurred and included *Anisopappus*, *Sphacophyllum* Benth., and *Astephania* Oliv. in Inuleae-Buphthalminae. The differences between *Anisopappus*, with well-developed scaly pappus, and other genera were merely technical. *Astephania* was devoid of pappus whereas *Sphacophyllum* had a very short scaly rim. Several workers had found the diagnostic characters of a number of genera to be unnatural, and in the revision of *Anisopappus*, Wild (1964) merged the genera and also *Astephania*, *Eenia* Hiern & S. Moore, and

Fig. 40.1. Representatives of Athroismeae. **A, B** *Blepharispermum zanguebaricum* Oliv. & Hiern; **C** *Athroisma stuhlmannii* (O. Hoffm.) Mattf.; **D** *Athroisma gracile* (Oliv.) Mattf. [Photographs: A, B, T. Eriksson of *Eriksson 604*, Kibwesi, Machakos Distr., Kenya; C, A.A. Anderberg, University of Stockholm, cult.; D, T. Eriksson of *Eriksson et al. 559*, Mwanga, Machakos Distr., Kenya.]

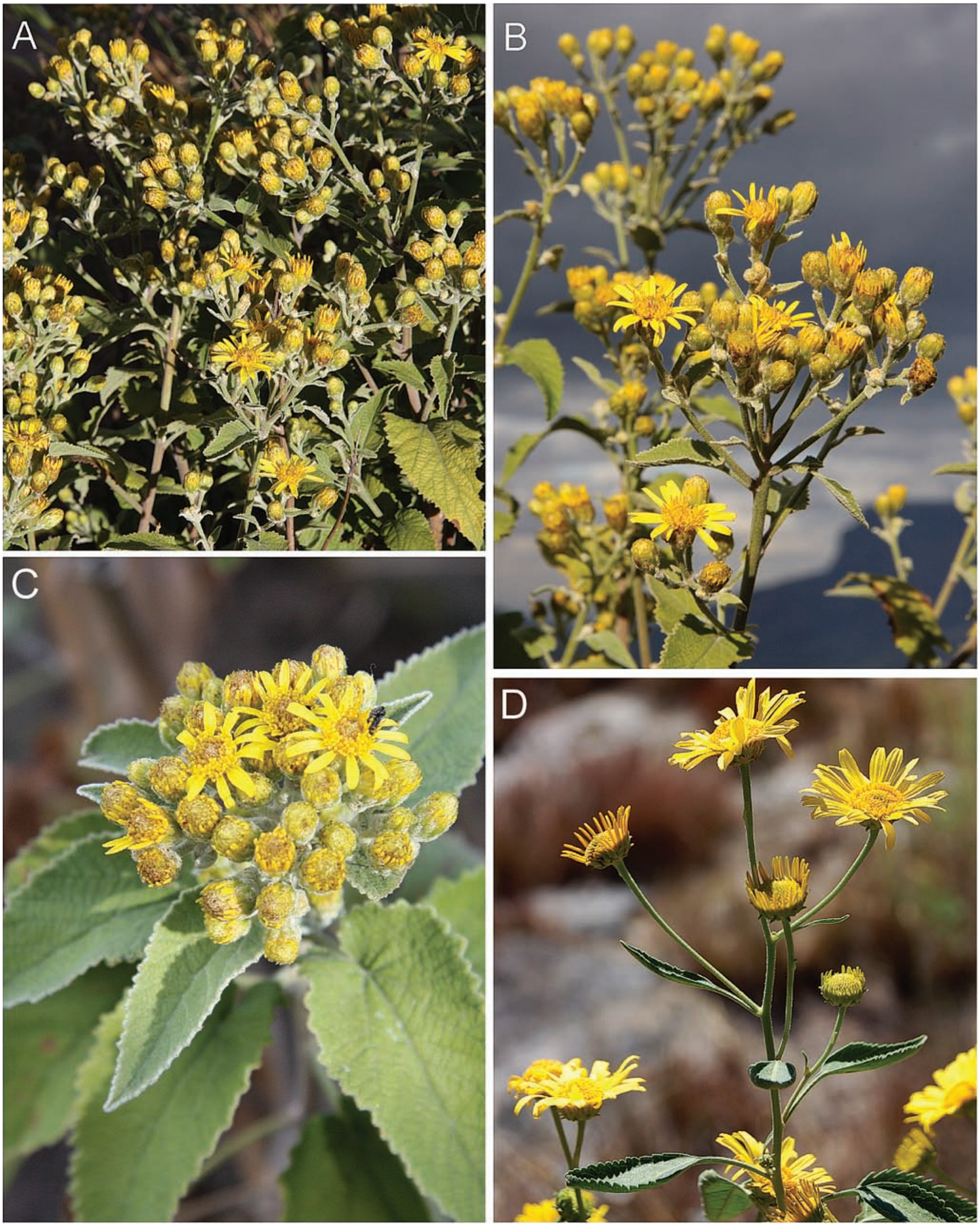

Fig. 40.2. *Anisopappus*. **A–C** *Anisopappus junodii* Hutch.; **D** *Anisopappus fruticosus* S. Ortiz & Paiva [Photographs: A–C, M. Koekemoer, South Africa; D, M. Serrano of *Ortiz et al. 885*, Angola.]

Epallage DC., *Sphacophyllum*, and *Temnolepis* Baker. It can be noted that *Epallage* had earlier been considered a member of Heliantheae-Verbesineae (Hoffmann 1890). Merxmüller et al. (1977) included *Anisopappus* in the *Inula* group of Inuleae-Inulinae, and so did Anderberg (1991) who found *Anisopappus* to be sister to all other Inuleae s.str. It was noted that it differed in several important features, e.g., lacking the typical large achene epidermis crystals and had style branches provided with obtuse instead of acute sweeping hairs. *Anisopappus* was later included in the Inuleae by Anderberg in Bremer's book (Anderberg 1994) in consequence with his earlier work in that tribe.

De Candolle (1838) included *Sphaeromorphaea* (incl. *Centipeda*) in Artemisieae under Senecionideae. The systematic position of *Centipeda* has, however, been much discussed since then, and different views on tribal placement have been put forward over the years, such as Anthemideae (Bentham 1873; Hoffmann 1892; Heywood and Humphries 1977) or Inuleae (Skvarla et al. 1977). Bremer and Humphries (1993) excluded the genus from Anthemideae, but Zhang and Bremer (1993) did not include *Centipeda* in their treatment of Astereae, whereas Nesom (1994) considered it part of the grangeoid complex of Astereae. Bremer (1994) left *Centipeda* unassigned to tribe within the subfamily Asteroideae.

PHYLOGENY

A better understanding of the phylogeny of Athroismeae has come step by step. Eriksson (1990, 1992, 1995) presented the first cladistic analyses of relationships among species of *Athroisma* and *Blepharispermum*. The analyses were based on morphological data and found *Athroisma* and *Blepharispermum* to be sisters, but also that *B. subsessile* is sister to all the other species of the latter genus. Eriksson discussed the position of this species. It lacked the diagnostic synapomorphies shared by the other *Blepharispermum* species, and its inclusion weakened the characterization of that genus, so Eriksson reinstated the monotypic genus *Leucoblepharis*. In their analysis of *ndhF* sequences, Kim and Jansen (1995) did not include *Leucoblepharis*, but they confirmed Eriksson's conclusion that the *Blepharispermum* group should be moved away from Inuleae towards Heliantheae, and showed that *Athroisma* and *Blepharispermum* took a position as sister group to the entire Heliantheae tribal complex. This reflected Karis' earlier results from analysis of morphological data that they were among the basal taxa of Helenieae. The *Blepharispermum* group, with their reduced capitula arranged in secondary heads and their tailed anthers, still proved to be closer to the Heliantheae tribal complex than to Inuleae where they had been placed until then. Robinson (1996), not at ease

Fig. 40.3. *Centipeda*. **A** *Centipeda crateriformis* N.G. Walsh; **B** *Centipeda minima* (L.) A. Braun & Asch. [Photographs: A, B. Fuher, Ilparpa claypans near Alice Springs, Northern Territory, Australia; B, M. Fagg of *Purdie 4148*, Australia.]

with the notion that the *Blepharispermum* group would be part of Heliantheae, discussed the presence of phytomelanin in Heliantheae and other groups, and noted that Kim and Jansen (1995) had placed the *Blepharispermum* group just outside of the Heliantheae tribal complex.

Eldenäs et al. (1999) found that *Anisopappus* (*A. latifolius* (S. Moore) B.L. Burtt, *A. smutsii* Hutch.) also belonged to the same clade as the members of the *Blepharispermum* group, and as sister to *Athroisma* and *Blepharispermum*. They proposed that *Anisopappus* and the genera of the *Blepharispermum* group should be treated as members of Heliantheae pending further studies in that tribal complex. Eldenäs and Anderberg (1996) had previously studied species relationships in *Anisopappus* by cladistic analysis of morphological data and concluded that *A. latifolius*, the only epaleate species of the genus, was sister to the rest.

The first molecular data from *Centipeda*, a study of ITS sequences (Wagstaff and Breitwieser 2002), indicated with strong support (98% jackknife and 87% bootstrap) a position of *Centipeda cunninghamii* (DC.) A. Braun & Asch. as sister to a clade formed by the *Athroisma* group (*Athroisma hastifolium* Mattf., *Blepharispermum zanguebaricum* Oliv. & Hiern, and *Anisopappus smutsii*) together with the genera of the Heliantheae tribal complex. Panero (2005) stated from results of his ongoing research that data from several coding DNA regions supported the inclusion of *Centipeda* in Athroismeae, thus contradicting the ITS results of Wagstaff and Breitwieser, and this is supported also by my own ongoing work (Anderberg, unpubl. *ndhF* sequence data). The species relationships within *Centipeda* are yet to be investigated in a phylogenetic context (part of my ongoing research).

TAXONOMY

Tribe Athroismeae Panero in Proc. Biol. Soc. Wash. 115: 917. 2002 – Type: *Athroisma laciniatum* DC., Prodr. 5: 369. 1836

Perennial or annual herbs, shrubs or small trees. Leaves alternate, sometimes in fascicles on brachyblasts, petiolate or sessile, entire, serrate, dentate, or sometimes pinnatifid. Capitula solitary, in dense or loose corymbs, or congregated in secondary heads (*Athroisma*, *Blepharispermum*, *Leucoblepharis*), pedunculate or sessile, terminal, or axillary (*Centipeda*); radiate, disciform or discoid. Involucral bracts often in few rows. Receptacle paleate (*Athroisma*, *Blepharispermum*, *Leucoblepharis*, most *Anisopappus*) or epaleate (*Centipeda*, *Anisopappus latifolius*). Marginal florets female, often radiate, sometimes filiform; corolla yellow or white. Central florets hermaphroditic or functionally male; corolla yellow or whitish, sometimes with purple tinge. Stamens 4–5, shortly calcarate or ecalcarate, with long or short sterile tails basally, anther appendix sometimes with an apical gland (*Blepharispermum*, *Leucoblepharis*). Style with marginal, sometimes apically confluent stigmatic lines, sometimes undivided. Achenes subterete, turbinate or sometimes flattened or triquetrous, in some genera with phytomelanin carbonization (*Athroisma*, *Blepharispermum*, *Leucoblepharis*). Pappus of scales or a short crown of scales (*Anisopappus*), bristle-like scales (*Athroisma*, *Blepharispermum*, *Leucoblepharis*), or missing (*Anisopappus*, *Centipeda*).

Athroismeae comprise only 55 species, and taxonomic revisions have been published for all genera. Wild (1964) revised *Anisopappus* and recognized 29 species, whereas Ortiz and coworkers (Ortiz et al. 1996; Ortiz 2005) recognized only 17 species. Eriksson (1990, 1992, 1995) revised *Leucoblepharis* (1 sp.), *Blepharispermum* (15 spp.), and *Athroisma* (12 spp.), and Walsh (2001) revised *Centipeda* (10 spp.) (Table 40.1).

MORPHOLOGY

The striking morphological variation between genera in Athroismeae makes any effort to characterize the tribe very difficult. All of the genera have also been associated, albeit misplaced, with other groups, and never with each other. An insignificant, but still noteworthy detail is that some taxa have achene twin hairs that are apically coiled or anchor-shaped, something that is not common in the

Table 40.1. Genera of Athroismeae with number of species, distribution, and chromosome numbers.

Genus	Species	Distribution	Chromosome number (2*n*)
Anisopappus Hook. & Arn.	17	Africa, one species in China	28
Athroisma DC.	12	Africa, one species in SE Asia	20
Blepharispermum Wight ex DC.	15	Africa, Arabia, India, Sri Lanka	20
Centipeda Lour.	10	Australia, New Zealand, SE Asia, S America, Madagascar	10, 20
Leucoblepharis Arn.	1	India	—

family. Coiled hairs occur in *Centipeda pleiocephala* N.G. Walsh (Walsh 2001: fig. 1) and *Anisopappus rhombifolius* Wild (Eldenäs 1996: fig. 3A), and anchor shaped twin hairs are found in many *Athroisma* (Eriksson 1995).

POLLEN

The pollen grains are spinulose and caveate as in most Asteraceae. Pollen of *Blepharispermum* and *Athroisma* have been described as being similar to that of *Sphaeranthus* (Inuleae-Plucheinae) and conforming to the basic Inuleae-type, as with pollen of *Anisopappus* (Leins 1971), i.e., with a simple or double columellate sexine. The simpler baculate sexine in *Blepharispermum*, *Athroisma* and *Anisopappus* (in comparison to *Centipeda* pollen ultrastructure) is probably symplesiomorphic, as it is also found in all investigated taxa of Inuleae.

The difference in pollen ultrastructure between *Centipeda* and the other genera is striking. The pollen of *C. cunninghamii* differs profoundly from that of the other genera, in that the wall has a complex structure of highly ramifying columellae that gives an interlaced impression and more resembles that of Gnaphalieae, certain Heliantheae, or Helenieae. Skvarla et al. (1977) considered the structure of the pollen wall in *Centipeda* to suggest a relationship with Inuleae, but this would only apply to taxa that are today placed in Gnaphalieae (Inuleae-Gnaphaliinae), and not to Inuleae proper, where this kind of interlaced structure is not found.

CHROMOSOME NUMBERS

The basic chromosome number in *Anisopappus* is estimated to be $x = 7$ ($n = 7$, $2n = 28$) from counts in *A. anemonifolius* (DC.) G. Taylor and *A. chinensis* (= *Anisopappus africanus* (Hook. f.) Oliv. & Hiern, and *A. dalzielii* Hutch.) (Auquier and Renard 1975; Rabakonandrianina and Carr 1987; Gill and Omoigui 1992; Morton 1993). The basic chromosome number in *Athroisma* and *Blepharispermum* is $x = 10$ ($2n = 20$) based on counts from *Athroisma hastifolium*, *A. gracile* (Oliv.) Mattf., and *A. stuhlmannii* (O. Hoffm.) Mattf., *Blepharispermum xerothamnum* Mattf. and *B. zanguebaricum* (Eriksson 1992, 1995). The basic chromosome number in *Centipeda* is $x = 10$ based on counts from *Centipeda aotearoana* N.G. Walsh, *C. cunninghamii*, *C. elatinoides* (Less.) Benth. & Hook. f. ex O. Hoffm., *C. minima* (L.) A. Braun & Asch. (De Lange and Murray 2002), and *C. thespidioides* F. Muell. (Bruhl 1990).

Inuleae have a basic chromosome number of $x = 9$, or 10 ($2n = 18$, or 20), and it seems that this is also the case in Athroismeae, and thus a possible symplesiomorphy, but with a reduction in *Anisopappus*. Without a clear picture of generic phylogeny in the tribe, it is difficult to ascertain the base number.

CHEMISTRY

As with morphological variation, there seems to be no chemical characteristic uniting the genera of Athroismeae, and no evidence has been presented for a tribal relationship of any genus. Zdero et al. (1991) found the presence of thymol and ent-labdane in *Athroisma* and *Blepharispermum* uninformative as indicator of tribal position in Inuleae or Heliantheae. *Athroisma* shares a thymol that was thought to be an indication of a relationship with *Sphaeranthus* L. and members of Inuleae, whereas the chemistry of *Blepharispermum* was more stated to be complex and difficult to interpret. *Athroisma* also contained a menthene diol that had previously been found in *Eupatorium* L., but neither genus contained compounds shared specifically with Heliantheae-Ecliptinae, and the similarity in the thymol observed between *Athroisma* and *Sphaeranthus* can be viewed as symplesiomorphic similarity.

Sørensen (1977) described the chemistry in *Centipeda* to be anomalous from other Anthemideae, where it was placed at the time, by having tridecapentaynene, but this is a compound that is otherwise widespread in the family. Bohm and Stuessy (2001) tentatively proposed a position in Astereae, but stated that the flavonoids did not contribute any diagnostic information. Several members of Athroismeae contain biologically active substances that have been used in ethnopharmacology for treatment of fungus infections, colds and skin disorders (Baerts and Lehmann 1991; Agarwal et al. 2000; Walsh 2001).

DISPERSAL

None of the genera of Athroismeae have a bristly pappus and therefore are less likely to be dispersed by wind. The scaly pappus in many *Anisopappus* may act to promote fruit dispersal by zoochory, and the distal anchor-shaped fruit hairs in some *Athroisma* may perhaps also promote zoochory. The scaly or awn-like pappus of *Blepharispermum* and *Leucoblepharis* are less indicative of any particular fruit dispersal mode. In neither case this has been studied experimentally, whereas for *Centipeda*, Walsh (2001) described seeds of all species to be buoyant and floating around after flooding by means of spongy distal tissue in fruits. This often results in a zone of *Centipeda* around seasonally water-filled depressions. The fruits also have inrolled hairs and viscid exudates that promote long distance dispersal by attachment to animal fur or feathers. In some species capitula disintegrate at fruit maturity and fruits are released.

In other species capitula remain intact after the plant has withered, thus extending the release period, and in a few species the entire capitulum may act as a dispersal unit.

BIOGEOGRAPHY

The majority of species of Athroismeae occur in Africa (seventeen *Anisopappus*, eleven *Athroisma*, twelve *Blepharispermum*, and one *Centipeda*). *Anisopappus chinensis* occurs also in China, *Athroisma laciniatum* DC. from India to SE Asia, *Blepharispermum petiolare* DC. in India and Sri Lanka, and *B. hirtum* Oliv. and *B. yemense* Deflers in the Arabian peninsula. Only *Leucoblepharis subsessilis* Arn. (India) and *Centipeda* have their main distributions outside Africa. *Centipeda* is concentrated in Australia and New Zealand and adjacent areas, but it occurs also in Madagascar, southern South America, and in Asia.

Although the distribution of the tribe is mainly African, with a few species occurring in the Arabian peninsula and further eastward in Asia, the range seems to indicate a once much larger distribution for Athroismeae. If *Centipeda* is monophyletic, which seems reasonable, then its wide distribution may also support this idea. If the ancient distribution were much broader in the Old World, then this would also be of interest, as the group is sister to a predominantly New World Heliantheae tribal complex.

For a biogeography tree of the entire Compositae see Chapter 44.

ECONOMIC USES

Members of Athroismeae are not used as ornamentals, and except for the ethnopharmacological uses mentioned above, they are not known to produce anything that has been of economic importance.

Acknowledgements. I would like to thank Tod Stuessy and Vicki Funk for inviting me to write this paper on Athroismeae. I am also grateful to Marinda Koekemoer, Bruce Fuher, Murray Fagg, Miguel Serrano, and Torsten Eriksson for providing photos. Financial support was received from the Swedish Research Council (Vetenskapsrådet).

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Chapter 41

Heliantheae alliance

Bruce G. Baldwin

HISTORICAL OVERVIEW

The "Heliantheae alliance" sensu Panero (2007a) or "Helianthoid group" sensu Bremer (1996) contains ca. 5500 species or ca. 20%–25% of the species recognized in Compositae, including sunflowers, sneezeweeds, and eupatoriums. The clade occurs principally in the New World, with limited representation elsewhere. Extensive variation in morphological characters often used for higher-level classification in Compositae (e.g., presence/absence of paleae, types of pappus elements, anther color and apices, and style branch shapes) helps to explain the dynamic taxonomic history of the Heliantheae alliance and the difficulty of achieving a practical higher-level classification of the lineage that reflects monophyletic groups and preserves tribal status for the highly diverse and long-recognized Eupatorieae (see Baldwin et al. 2002; Panero and Funk 2002; Panero 2007a).

Cassini's (1819) tribal system for Compositae (Fig. 41.1), based in part on micro-synantherological characters, was a major step forward in classification of Helianthoid taxa. Membership of his tribe Heliantheae ("Helianthées") comes close to recent circumscriptions of Heliantheae sensu lato (s.l.) (e.g., Robinson 1981) and was far more natural than subsequent treatments by Lessing (1832) and De Candolle (1836–1838). Cassini's placement of *Ambrosia* and relatives in a separate, adjacent tribe ("Ambrosiacées" or "Ambrosiées") is understandable in light of the highly modified reproductive morphology of those plants, associated with evolution of wind pollination (e.g., free anthers; heteromorphic, unisexual heads). His placement of Eupatorieae ("Eupatoriées") in a position far removed from Heliantheae s.l. (but connected by a line) is also understandable; Eupatorieae was not strongly associated with Heliantheae s.l. until molecular phylogenetic analyses were undertaken in the 1980s and 1990s (e.g., Jansen et al. 1990; Kim et al. 1992).

Bentham's (1873) widely followed tribal treatment for Compositae (Fig. 41.2) also focused in part on micro-synantherological characters and converged on Cassini's system. An important departure from previous classifications of Compositae in Bentham's treatment was recognition of Helenieae ("Helenioideae") for epaleate taxa with scaly pappus that were mostly placed by Cassini within Heliantheae. Bentham also moved epaleate taxa with bristly pappus elements in Cassini's Heliantheae to Senecioneae.

Bentham's Helenieae have the distinction of being the only tribe in his classification of Compositae that was abandoned by most synantherologists in the mid-to-late 20th Century. Helenieae came to be widely regarded as an unnatural assemblage of epaleate taxa that should be treated either within Heliantheae (e.g., Cronquist 1955) or within Heliantheae and other tribes, especially Senecioneae (e.g., Stuessy 1977; Turner and Powell 1977). Nordenstam (1977), however, in his review of Senecioneae for the Reading Symposium proceedings, concluded that various epaleate genera, such as *Arnica*, that were placed by Bentham (1873) and subsequent authors within Senecioneae, are more closely related to Heliantheae s.l.

Robinson (1981) incorporated all of the epaleate taxa excluded from Senecioneae and assigned provisionally to Heliantheae by Nordenstam (1977) in a completely re-evaluated Heliantheae (s.l.), with 14 principally epaleate subtribes arrayed consecutively in a linear sequence meant to approximate relationships within the tribe. The epaleate subtribes of Robinson's (1981) system include the bulk of epaleate genera included by Bentham (1873) in his Helenieae, as well as those taxa of Cassini's (1819) Heliantheae that Bentham placed in Senecioneae. Robinson (1981: 26) expressed support for "…more phyletic integrity among the epaleaceous Heliantheae than is generally recognized by recent workers."

Subsequent phylogenetic analyses helped to refine general hypotheses of relationships in the Heliantheae alliance. Karis's (1993) morphology-based cladistic analysis of Heliantheae s.l. resolved an epaleate grade of helenioid taxa, part of which was placed sister to paleate (core) Helianthoids, with members of Eupatorieae in an unresolved position or shallowly nested among helenioid lineages. Based on those findings and the desirability of continued recognition of Eupatorieae, Karis and Ryding (1994) provisionally recognized a paraphyletic Helenieae s.l. until additional evidence about relationships among genera of Helenieae s.l. would allow for a revised tribal treatment.

Kim and Jansen's (1995) phylogenetic analysis of *ndhF* sequence data for Compositae yielded a well-supported clade consisting of Heliantheae s.l. (including helenioid taxa) and Eupatorieae, with representatives of core Helenieae (i.e., Gaillardiinae sensu Karis and Ryding)

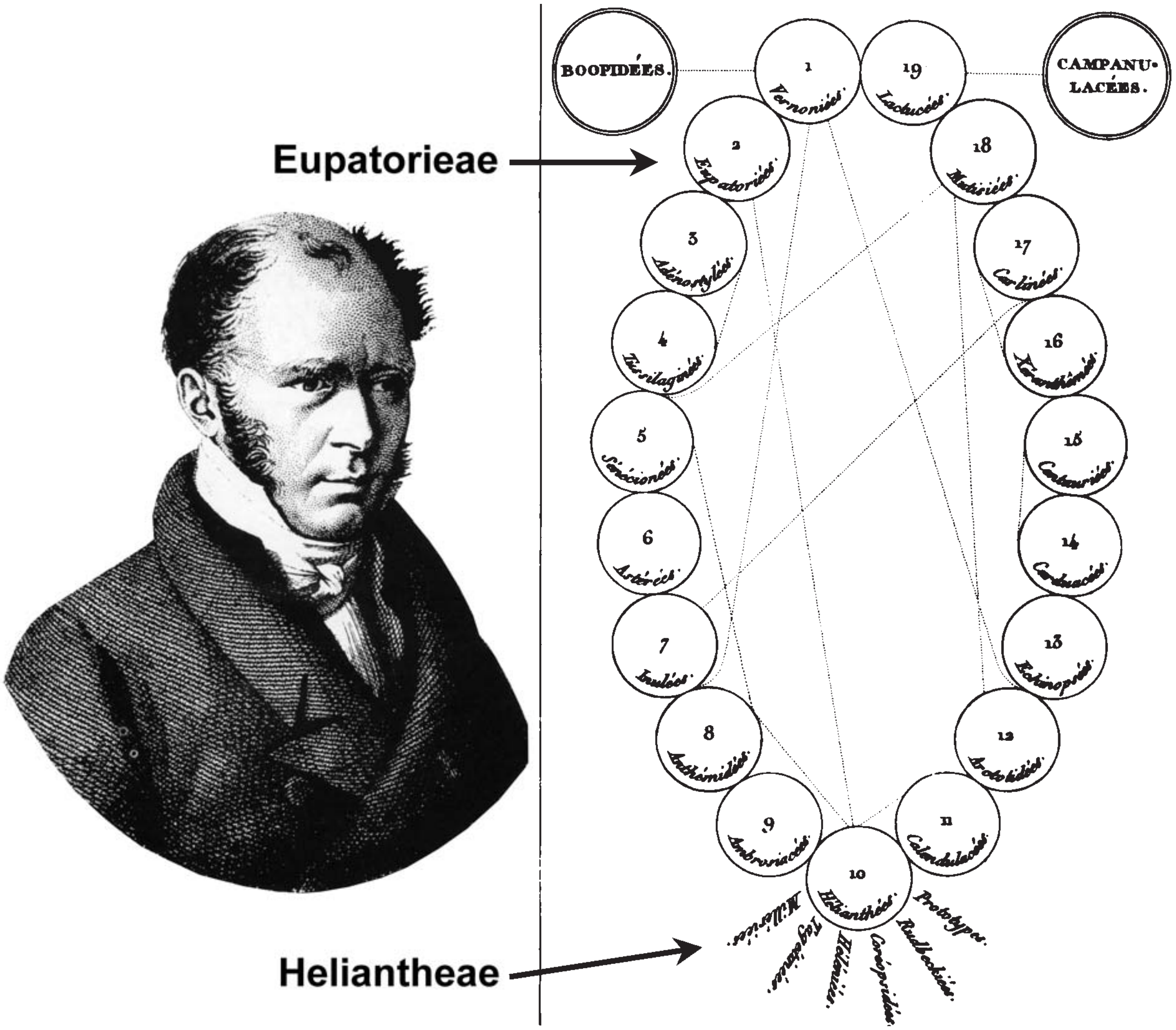

Fig. 41.1. Cassini's (1817) tribal diagram of Compositae ("Synanthérées"). Note the broadly circumscribed Heliantheae ("Helianthées"), including the mostly epaleate "Héléniées" and "Tagétinées" (but not "Ambrosiacées" or "Eupatoriées"). Upon formal description of the tribes, Cassini (1819) recognized Tageteae ("Tagétinées") as a tribe distinct from Heliantheae ("Helianthées"). Engraved portrait of Alexandre Henri Gabriel de Cassini by Ambroise Tardieu, 1827.

sister to the rest of Heliantheae s.l. plus Eupatorieae (Fig. 41.3). Although relationships among most members of Heliantheae s.l. and the precise position of Eupatorieae were unresolved, Kim and Jansen's (1995) tree established that the "*Athroisma* group", a lineage once placed in tribe Inuleae, is sister to Heliantheae s.l. plus Eupatorieae. Eriksson (1991) earlier established that the "*Blepharispermum* group" (= "*Athroisma* group"), a lineage of paleotropical, African and Asian genera with compound heads (now recognized as part of a distinct tribe, Athroismeae; see Panero 2007b), belongs to Heliantheae s.l., as indicated by blackened fruits and ovate, basally constricted, apical anther appendages (Fig. 41.4). Recognition that Athroismeae are sister to other Helianthoid taxa paved the way for more detailed phylogenetic studies of Heliantheae s.l. plus Eupatorieae by identifying the best outgroup for such analyses.

RECONSIDERATION OF HELENIEAE

Baldwin et al. (2002) undertook a phylogenetic analysis of 18S-26S rDNA internal transcribed spacer (ITS) region sequences in the Heliantheae alliance, with sampling concentrated on epaleate genera and Madiinae, in order to improve understanding of the relationships of tarweeds

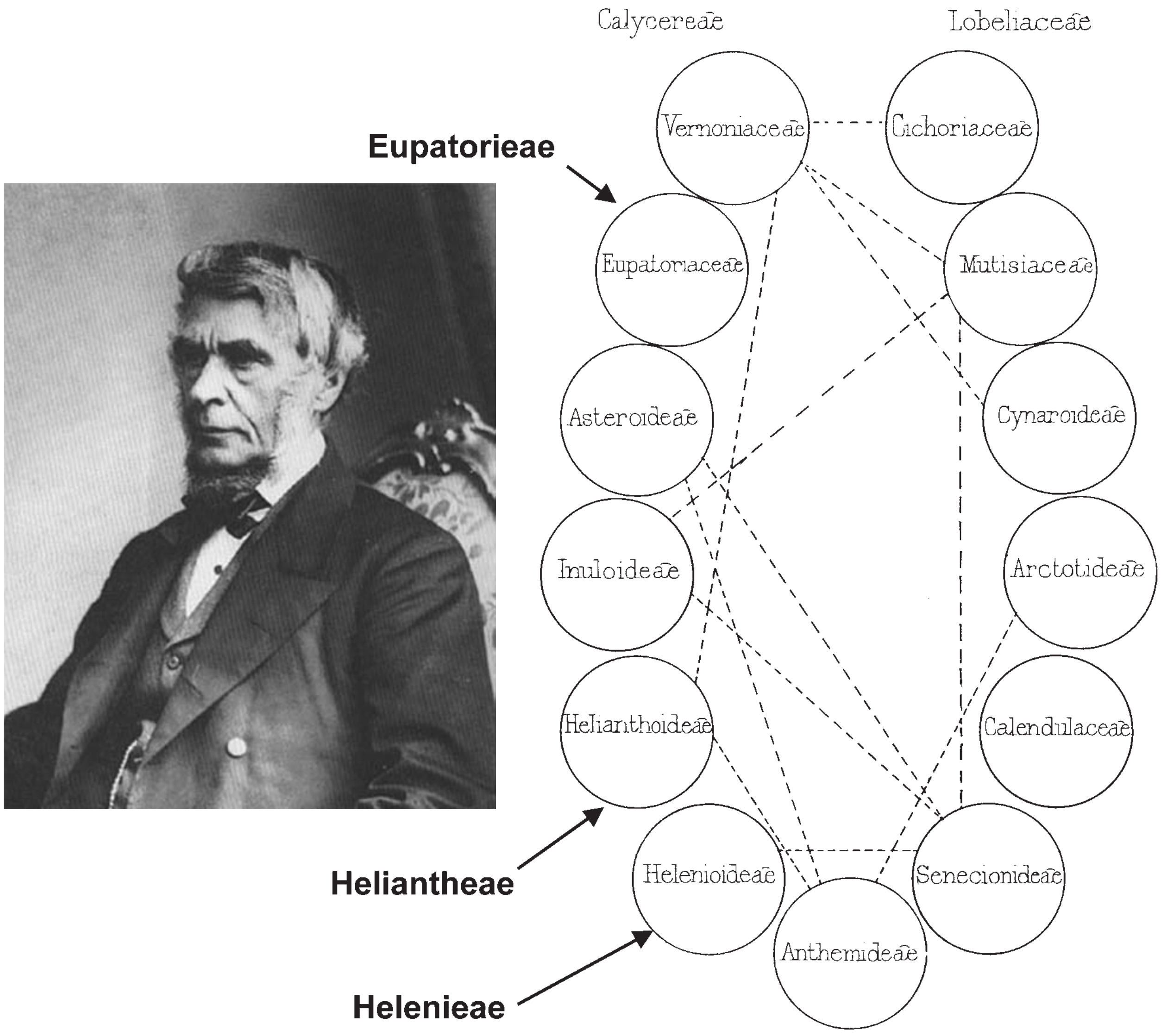

Fig. 41.2. Bentham's (1873) tribal classification of Compositae. Note the similarities with Cassini's system (and diagram), except for recognition of Helenieae ("Helenioideae") as a tribe. Adjoining photograph of George Bentham.

and silverswords (Madiinae) and the constitution of helenioid lineages. Panero et al.'s (2001) extensive sampling of cpDNA variation for the Helianthoid group included a broad representation of both paleate and epaleate genera. In general, resultant ITS and cpDNA clades of epaleate taxa correspond closely to previously recognized subtribes or tribes, especially in Robinson's (1981) and Karis and Ryding's (1994) system. As in Kim and Jansen's (1995) *ndhF* trees, a clade of core Helenieae (= Gaillardiinae sensu Karis and Ryding 1994) was resolved as sister to other members of Heliantheae s.l. and Eupatorieae (see Fig. 41.5); Goertzen et al. (2003) corroborated that result with a family-wide phylogenetic analysis of ITS sequences that were aligned based on an rRNA secondary structure model. Unlike other ingroup (and outgroup) lineages of the Heliantheae alliance, core Helenieae (Helenieae sensu Baldwin) comprises taxa that have raphides or druses rather than phytomelanin in the cypselae walls (i.e., the fruits are not "blackened"). Based on the phylogenetic results, presence of those epidermal-cell crystals is probably a derived condition in Helenieae, although lack of achenial phytomelanin may be ancestral; Panero (2005, 2007a, b) noted that two of three subtribes (i.e., Anisopappinae and Centipedinae) of the most basally divergent tribe of the Helianthoid group, Athroismeae, also lack fruit blackening, as in tribe Inuleae, which may be most parsimoniously interpreted as indicating independent expressions of phytomelanin in subtribe Athroisminae and in the bulk of the Heliantheae alliance (i.e., in the sister group to Helenieae). Cariaga et al.'s (2008) finding that the Cuban genus *Feddea* (Feddeeae), with unblackened fruits (and lacking epidermal-cell crystals), is sister to all other members of the Heliantheae alliance except Athroismeae strengthens the hypothesis of two origins of achenial phytomelanin expression in the Helianthoid clade and ancestral absence of blackened fruits in Helenieae.

Within tribe Helenieae, four principal, morphologically distinct lineages were indicated by ITS findings (Fig. 41.6) and given subtribal status (Baldwin and Wessa 2000a; Baldwin et al. 2002): Gaillardiinae, Tetraneurinae, Psathyrotinae, and Marshalliinae, in addition to the monotypic Plateileminae (*Plateilema palmeri*, of southern Texas and northern Mexico). Panero and Funk (2002) and Panero (2007c) also recognized those subtribes.

Subtribe Gaillardiinae in the revised sense is restricted to *Balduina*, *Gaillardia* (blanket flowers or firewheels), and *Helenium* (sneezeweeds), in accord with previous hypotheses that the three genera represent a natural group (Parker and Jones 1975; Bierner 1989). Members of Gaillardiinae usually have widely spreading or reflexed phyllaries and

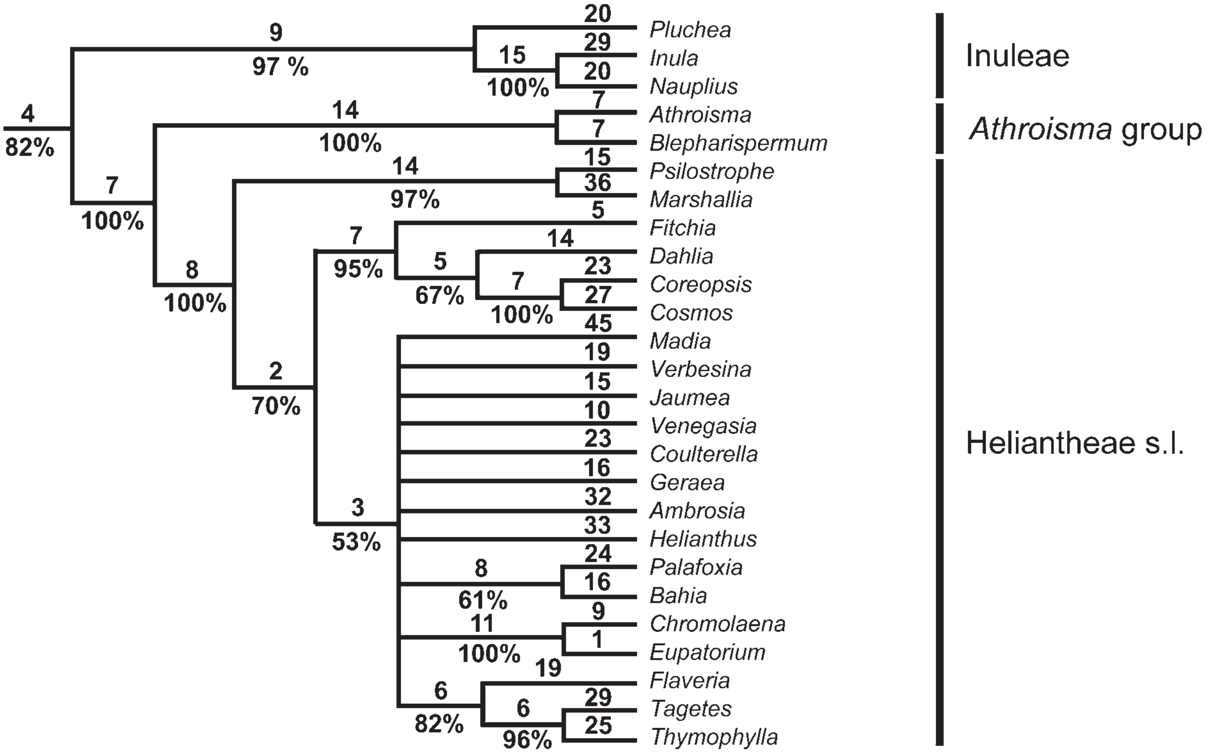

Fig. 41.3. The clade of Kim and Jansen's (1995) chloroplast (*ndhF*) DNA tree of Compositae containing members of Inuleae and the Heliantheae alliance. Note the early diverging positions of the "*Athroisma* group" and representatives of Helenieae in the current sense (i.e., *Marshallia* and *Psilostrophe*). [Reproduced with permission of the National Academy of Sciences, USA.]

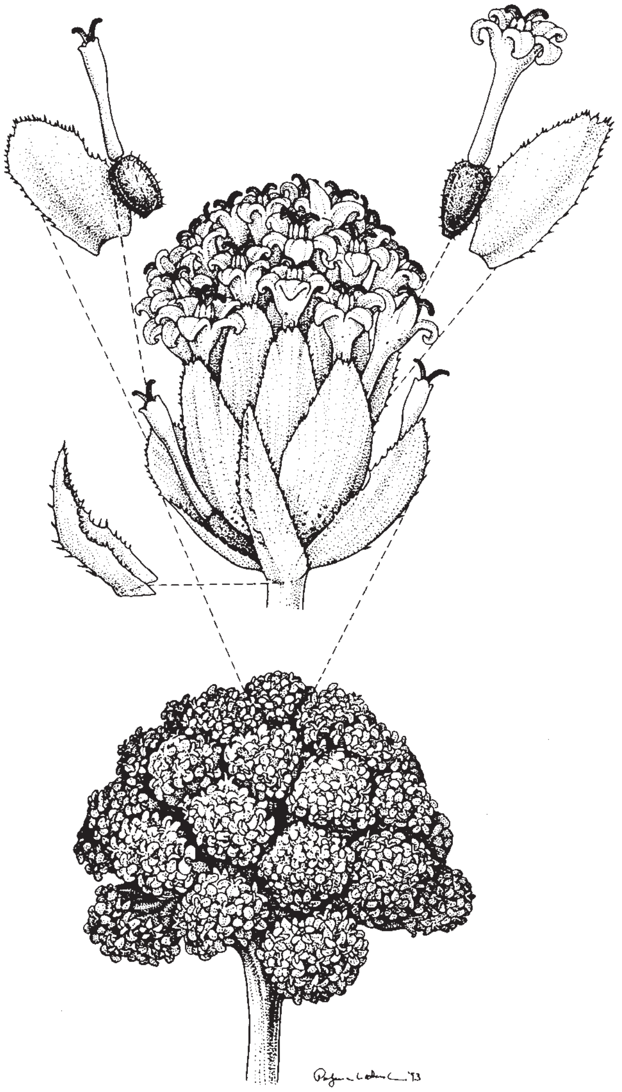

Fig. 41.4. Capitulescence and head of *Athroisma hastifolium* Mattf. (Athroismeae). Note spherical secondary heads and "blackened" ovaries. [Reproduced from Eriksson (1995), with permission from Elsevier.]

often enlarged, pitted, or spinose receptacles, occasionally with paleae near the margins. *Balduina* and *Gaillardia*, with receptacular pits or projections, are evidently sister taxa, as implied earlier by Rock (1957). At least some members of both genera occur in dry habitats; *Helenium* is found mostly in mesic situations. *Gaillardia* (15+ spp.) and *Helenium* (ca. 32 spp.; Fig. 41.7A) occur widely, in North America and South America; *Balduina* (3 spp.) is restricted to the southeastern USA. Historical biogeographic analysis of *Gaillardia* based on molecular phylogenetic data led Marlowe and Hufford (2007) to conclude that the genus arose in the Chihuahuan Desert and underwent multiple northward and eastward range expansions.

Subtribe Tetraneurinae, as revised, is the most diverse subtribe of Helenieae and corresponds in part with Gray's illegitimate Riddelliinae and Turner and Powell's (1977) informal "Psilostrophinae" by including *Baileya* (3 spp.) and *Psilostrophe* (7 spp.), with persistent, papery ray corollas (sometimes called paper flowers). Persistent ray corollas are also common in the bitterweed genera *Hymenoxys* (including *Dugaldia*, *Macdougalia*, and *Plummera*, 25 spp.) and *Tetraneuris* (9 spp.), and may be diagnostic (synapomorphic) for the subtribe. Bierner's (1990) hypothesis that the morphologically and biochemically anomalous, monotypic *Amblyolepis* (Huisache-daisy) is closely related to *Hymenoxys* s.l. (including *Tetraneuris*) was upheld by ITS data (Baldwin et al. 2002), as was Bierner and Jansen's (1998) subsequent treatment of *Tetraneuris* as distinct from *Hymenoxys*. Most members of Tetraneurinae occur in arid or semi-arid habitats of southwestern North America; some bitterweeds are found in more mesic, often montane or alpine settings and extend geographically to Canada and South America.

Subtribe Psathyrotinae comprises three southwestern North American desert genera (*Pelucha*, *Psathyrotes*, and *Trichoptilium*) that only recently have been placed in the same tribe. Members of the subtribe have discoid heads and pappus of multiseriate, fascicled, or coalesced bristles. Prior

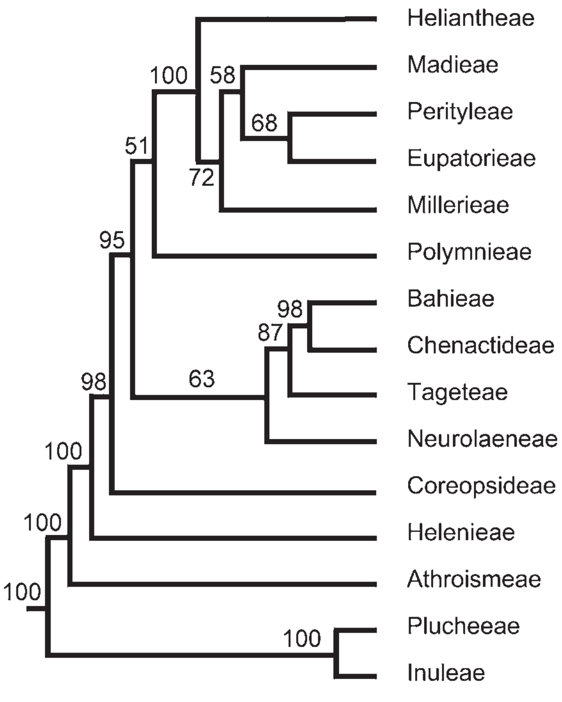

Fig. 41.5. Relationships among tribes of the Heliantheae alliance based on chloroplast DNA sequence data (Panero et al., 2001) and the tribal classification of Panero and Funk (2002). [Reproduced from Panero and Funk (2002), with permission of The Biological Society of Washington.]

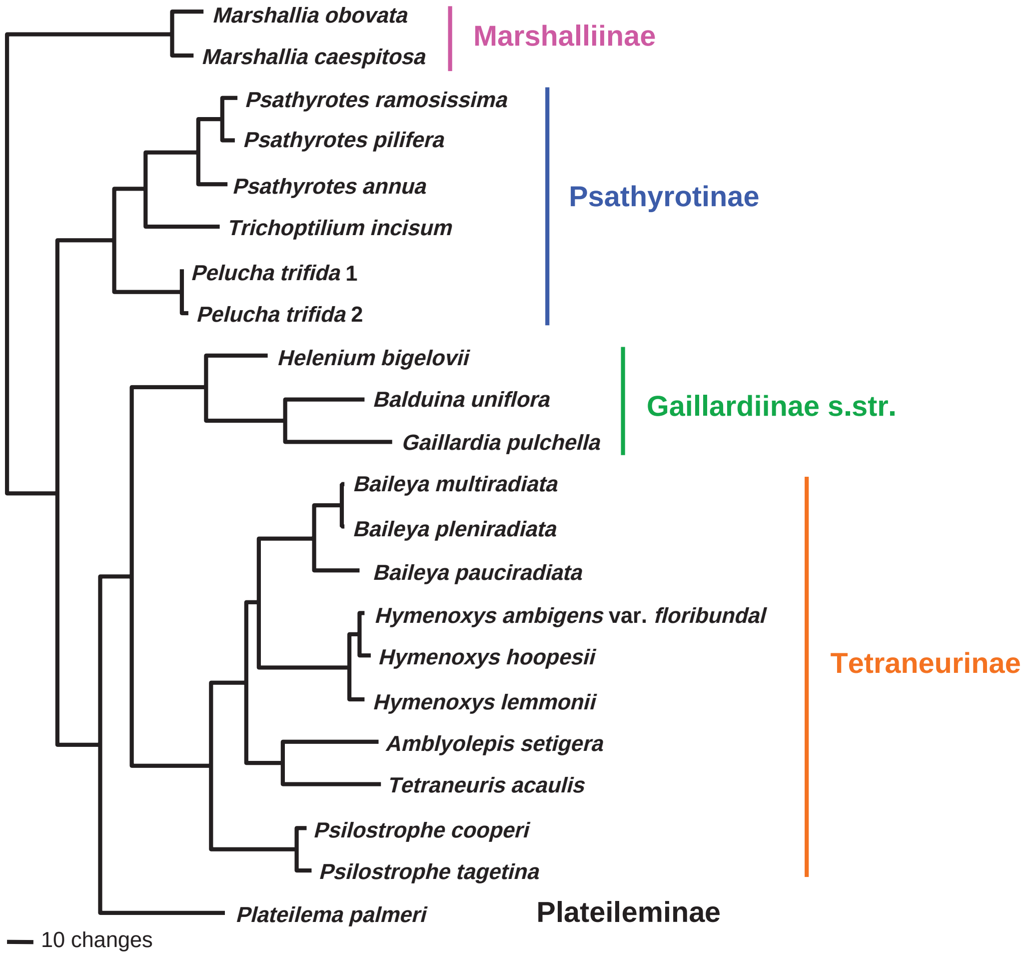

Fig. 41.6. Phylogenetic hypothesis for Helenieae s.str. based on rDNA internal transcribed spacer region (ITS) sequences (Baldwin and Wessa, 2000a). Tree was rooted with sequences of Athroismeae (*Athroisma hastifolium* Mattf. and *Blepharispermum zanguebaricum* Oliv. & Hiern). Note clades corresponding to subtribes, including re-delimited Gaillardiinae.

to Baldwin and Wessa's (2000a) study, the monospecific *Pelucha* was treated as a member of Inuleae or Plucheeae, although Anderberg (1994) questioned that placement and Strother (1994) suggested that the genus belonged in Heliantheae s.l. Members of *Psathyrotes* (turtle plants, 3 spp.; Fig. 41.7B) were long included in Senecioneae, along with other epaleate members of the Heliantheae alliance with a bristly pappus (see "Systematic Background" above). Robinson (1981) associated *Psathyrotes* and *Trichoptilium* with taxa treated here in Helenieae and recognized a close relationship between the two genera, which do appear to be sister taxa (Baldwin and Wessa 2000a). *Psathyrotes* and *Trichoptilium* are mostly herbaceous; *Pelucha* is a well-developed shrub. Baldwin and Wessa (2000a) suggested that if *Pelucha* evolved on islands in the Gulf of California, where most populations are found, then conceivably the shrubby habit may reflect selection under insular conditions, as in various other lineages of island plants, including a wide diversity of clades in Compositae (see, e.g., Baldwin et al. 1998; Panero et al. 1999a).

Subtribe Marshalliinae includes only the strange genus *Marshallia* (Barbara's buttons, 7 spp.), of the central and eastern USA. Relationships of *Marshallia* have been confusing because of morphological and chemical similarities with various groups of Compositae, such as the exclusively discoid heads and white or cyanic corolla color (as in Eupatorieae); strongly thickened, green-margined receptacular projections that have been interpreted as paleae (as in core lineages of Heliantheae) but could be interpreted as enations (as in *Gaillardia*); violet anthers (as in *Palafoxia* or Madiinae); prenyl flavonoids (as in Heliantheae and Inuleae); and a low chromosome number ($x = 9$) relative to other putatively Helianthoid taxa that lack phytomelanin in the fruit walls. Karis's (1993) morphological phylogenetic analysis placed *Marshallia* with core Helenieae, as did Kim and Jansen's (1995) analysis of *ndhF* sequences. The results of ITS analyses (Baldwin and Wessa 2000a; Baldwin et al. 2002) are consistent with Karis's (1993) and Kim and Jansen's (1995) findings and with Robinson's (1981) placement of Marshalliinae adjacent to Gaillardiinae s.l. in his subtribal classification of Heliantheae s.l. Based on available data, a sister group relationship between *Marshallia* and other core Helenieae cannot be ruled out.

HOMOPLASY AND TAXONOMIC RETHINKING OF EPALEATE CLADES

Morphological and chemical similarities between members of core Helenieae and epaleate taxa assigned by Robinson (1981) and Karis and Ryding (1994) to subtribe Chaenactidinae earlier led to questions about a possible close relationship between the two groups (see Robinson 1981). For example, Robinson (1981) noted strong morphological similarities between *Psathyrotes* (Psathyrotinae, Helenieae) and *Psathyrotopsis* (Chaenactidinae sensu Robinson 1981), sometimes treated as congeneric (see Strother and Pilz 1975). *Marshallia* (Marshalliinae, Helenieae) and *Bahia*, *Florestina*, and *Palafoxia* (Chaenactidinae sensu Robinson 1981) also were suggested to be possible close relatives (e.g., Turner and Powell 1977). Sesquiterpene lactone similarities between *Arnica* (Chaenactidinae sensu Robinson 1981) and core Helenieae (see Bohlmann 1990) provided other potential evidence for close relationship between Helenieae s.str. and Chaenactidinae s.l. (see Robinson 1981). These intriguing possibilities, in addition to concerns about polyphyly of Chaenactidinae s.l. (Karis and Ryding 1994) and indications from earlier molecular studies of close molecular similarity between some taxa of Chaenactidinae s.l. (*Arnica* and *Hulsea*) and the tarweed

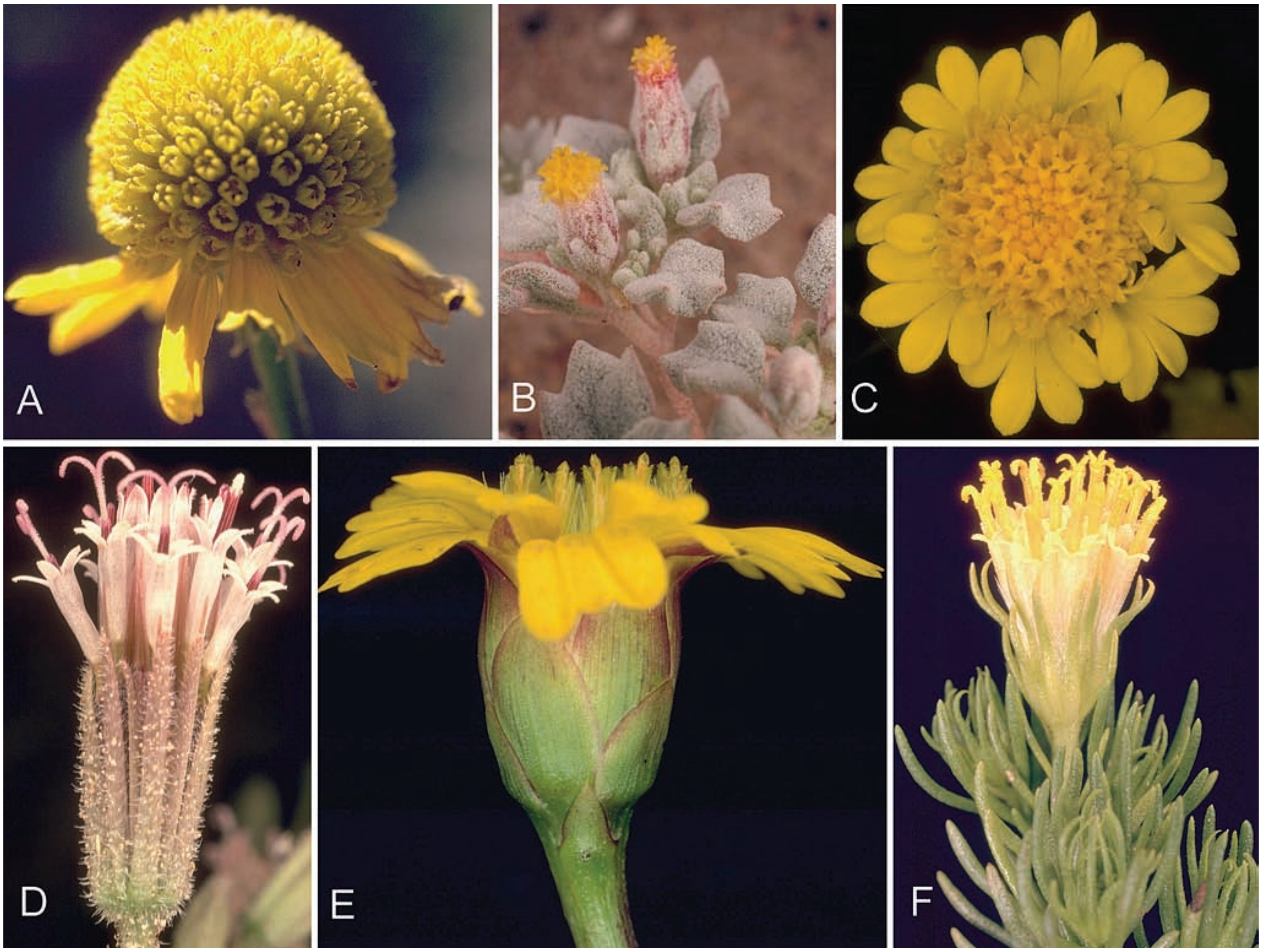

Fig. 41.7. Representatives of some predominantly epaleate tribes of the Heliantheae alliance. **A** *Helenium bigelovii* A. Gray (Helenieae); **B** *Psathyrotes annua* (Nutt.) A. Gray (Helenieae); **C** *Chaenactis glabriuscula* DC. (Chaenactideae); **D** *Palafoxia arida* B.L. Turner & M.I. Morris (Bahieae); **E** *Chaetymenia peduncularis* Hook. & Arn. (Bahieae); **F** *Peucephyllum schottii* A. Gray (Bahieae). [Photographs, B. Baldwin.]

subtribe Madiinae (Baldwin 1992, 1996), led Baldwin et al. (2002) to extensively sample taxa within those subtribes in their phylogenetic analyses of ITS sequence data. Results of that study confirmed that Chaenactidinae s.l. was polyphyletic, although the vast majority of genera previously assigned to the group belonged to only four major clades, one of which also contained the partially to (sometimes) fully paleate subtribe Madiinae (tarweeds and silverswords). Phylogenetic data for those clades helped to resolve patterns of character evolution and historical biogeography in epaleate lineages in general and allowed for initiation of tribal revision of the Heliantheae alliance (Baldwin et al. 2002). Panero and colleagues (Panero et al. 2001; Panero and Funk 2002; Panero 2005, 2007a) reinforced and greatly extended tribal revision of the Heliantheae alliance based on ca. 25,000 bp of cpDNA data from ca. 120 genera, with excellent representation of paleate as well as epaleate groups.

Four tribes are now recognized that include at least some elements of Chaenactidinae sensu Robinson (1981): Chaenactideae, Bahieae, Madieae, and Tageteae. These four tribes are discussed in detail below, as is the mostly-epaleate Perityleae; members of all five tribes were previously included in Helenieae s.l. (e.g., Karis and Ryding 1994).

Tribe Chaenactideae

Tribe Chaenactideae is limited to a well-supported, divergent clade of three mostly herbaceous, discoid genera: *Chaenactis* ("pincushions", 18 spp.; Fig. 41.7C) and the monotypes *Dimeresia* and *Orochaenactis* (Baldwin et al. 2002; see also Panero 2007d). Members of the tribe have usually petiolate, often lobed to dissected leaves and usually cyanic or white corolla coloration, with a pappus of scales that lack a medial costa or basal thickening or with bristle-like elements that are deciduous as a unit (*Dimeresia*). Relationships of the three genera, especially *Dimeresia*, were debatable prior to molecular study (Fig. 41.8). *Chaenactis* was once understandably regarded as closely related to the monotypic *Chamaechaenactis* (Preece and Turner 1953), which has pappus scales with well-developed medial costas, unlike *Chaenactis* and *Orochaenactis*. *Dimeresia* has been treated in Senecioneae (e.g., Bentham 1873) and in a monotypic subtribe, Dimeresiinae, within Heliantheae (Robinson 1981). *Orochaenactis thysanocarpha* (A. Gray) Coville, originally included in *Chaenactis*, and *Dimeresia* both have basally connate pappus elements that are shed as a unit (a possible homology). Some members of *Chaenactis* have enlarged, bisexual, marginal ray corollas that appear somewhat ray-like (Fig. 41.7C). The tribe is restricted to western North America, with most species occurring at least in part in California.

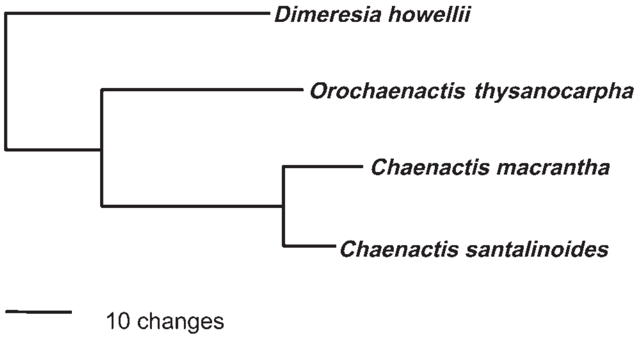

Fig. 41.8. The most parsimonious tree for Chaenactideae based on rDNA internal transcribed spacer region (ITS) sequences (data from Baldwin et al. 2002). Tree was rooted with sequences of Bahieae.

Tribe Bahieae

Tribe Bahieae includes most genera of Bahiinae sensu Stuessy (1977) and all genera of one of Robinson's (1981) two informal groups within his Chaenactidinae (Baldwin et al. 2002; see Panero 2007e). The tribe differs from Chaenactideae in having pappus scales that each have a medial costa or basal thickening or in having pappus awns or bristles that are fascicled or apically hooked. Cypselae walls in Bahieae may be striated, as in most of the genera, or not, as in *Hymenopappus*, which evidently belongs in the tribe, in accord with Stuessy's (1977) placement of that problematical genus in his subtribe Bahiinae.

Most diversity in the tribe is encompassed by the "Bahia clade" (Baldwin et al. 2002) (Fig. 41.9), which is being studied in more detail with rDNA external transcribed spacer (ETS) sequences (Baldwin et al., unpub.). Results to date indicate that phyllotaxy is even more conservative evolutionarily in the "Bahia clade" than implied by Ellison (1964), who recognized two principal groups of the genus *Bahia* based largely on phyllotaxy ("Alternifoliae" and "Oppositifoliae"). The ITS + ETS trees resolve two sister lineages in the "Bahia clade" that differ in phyllotaxy, with alternate-leaved and opposite-leaved bahias each placed with taxa of other genera that share the same leaf arrangement (i.e., *Bahia* sensu Ellison is not monophyletic). For example, the alternate-leaved members of *Bahia* are evidently more closely related to the alternate-leaved genera *Florestina*, *Hymenothrix*, and *Palafoxia* (Fig. 41.7D) than to the opposite-leaved bahias.

ITS + ETS trees also indicate that *Apostates*, endemic to the remote South Pacific island of Rapa Iti (Austral Islands), belongs to the opposite-leaved lineage of the "Bahia clade" (Baldwin et al. unpub.). The sole species, *A. rapae* (F. Brown) N.S. Lander, a broad-leaved shrub, was originally described in *Olearia* (tribe Astereae) and has been of uncertain tribal placement. Based on morphological studies of available herbarium specimens, Karis (1998) proposed that the genus should be treated as part of the Heliantheae alliance and that close relatives might be sought in Chaenactidinae s.l., in accord with the molecular findings. An extreme long-distance dispersal event from the New World to Rapa Iti must be hypothesized to account for this South Pacific lineage, which is well nested within an otherwise American clade.

Another instance of extreme long-distance dispersal in Bahieae can be inferred for the "Chaetymenia clade" (Baldwin et al. 2002), which comprises three genera of long-uncertain relationship: the New World monotypes *Chaetymenia* (Fig. 41.7E) and *Espejoa*, and the African *Hypericophyllum* (ca. 12 spp.). The two New World genera constitute a paraphyletic group in the ITS trees (Fig. 41.9), with African *Hypericophyllum* nested therein (sister to *Chaetymenia*), in accord with trans-Atlantic dispersal from Mexico or Central America to Africa and subsequent diversification in the new continental setting. Bentham (1873) treated taxa now included in the above three genera within his circumscription of *Jaumea*, based in part on the common characteristic of broad, hyaline-margined phyllaries, which likely is diagnostic (synapomorphic) for the "Chaetymenia clade" and evidently of independent origin in *Jaumea* s.str. (Tageteae).

Robinson's (1981) conclusion that extensive morphological similarities between *Psathyrotopsis* and *Psathyrotes* (Helenieae) are misleading about relationships of the two genera was corroborated by ITS findings (Baldwin et al. 2002). *Psathyrotopsis* belongs to Bahieae and was resolved as sister to *Peucephyllum* in ITS trees (Fig. 41.9); both genera were placed by Robinson (1981) in his Chaenactidinae, which also included most other genera now treated in Bahieae, as noted above. Unlike the vast majority of other continental taxa of Bahieae, the sole species of *Peucephyllum*, *P. schottii* A. Gray (Fig. 41.7F), is a robust shrub, commonly called "pygmy cedar" and appearing juniper-like at a distance. *Peucephyllum* occurs in extreme desert environments, where evolution of extensive above-ground woodiness from an ancestrally herbaceous condition might not be expected, although an herbaceous ancestry was inferred for the genus from rDNA

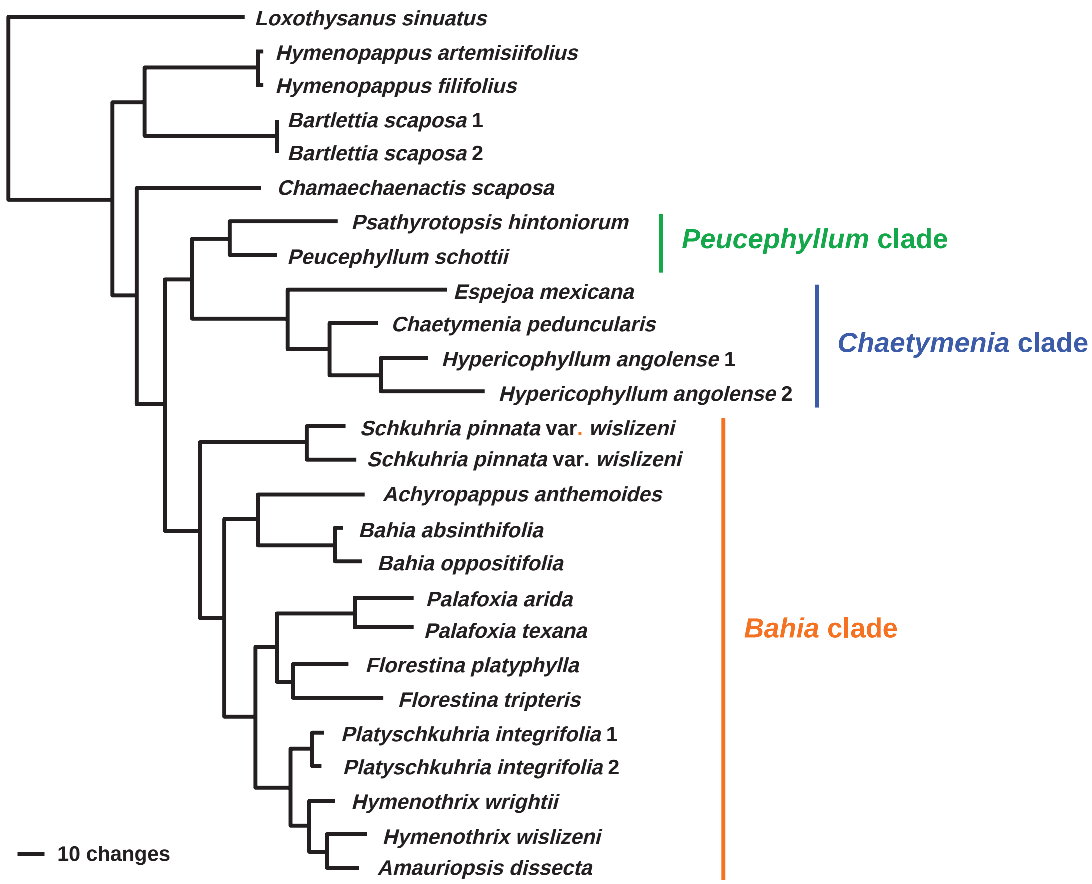

Fig. 41.9. The most parsimonious tree for Bahieae based on rDNA internal transcribed spacer region (ITS) sequences (data from Baldwin et al. 2002). The tree was rooted with sequences of Chaenactideae. Note informal clades for some groups of genera, which have not been given subtribal status because relationships of other genera in Bahieae are still under investigation (Baldwin, unpub.).

trees (Baldwin et al. 2002). Carlquist (1962a) noted that stem wood of *Peucephyllum* shows diverse specializations to xeric conditions shared with other woody desert taxa of Compositae (e.g., *Tetradymia*; Senecioneae) that also can be inferred to be secondarily woody based on phylogenetic data (see Chapter 34).

Tribe Madieae

Tribe Madieae unites the tarweeds and silverswords (Madiinae) with the woolly sunflowers (Baeriinae) and an "arnicoid" grade (Arnicinae, Hulseinae, and Venegasiinae). Prior to Baldwin et al. (2002), Madieae and Madiinae were used in similar senses depending on whether tarweeds were regarded as warranting tribal or subtribal status. Members of Baeriinae and Madiinae generally have uniseriate involucres with one ray floret (when rays are present) per phyllary and have chromosome numbers that range widely across taxa, from 3 to 19 pairs; members of Arnicinae, Hulseinae, and Venegasiinae are morphologically heterogeneous and consistently have 19 pairs of chromosomes or (in *Arnica*) are neo-polyploids based on $x = 19$ (see Baldwin and Panero 2007).

Subtribe Madiinae (24 genera, 120 spp.) was circumscribed by Carlquist (1959a) to include not only the traditionally recognized tarweeds (such as *Layia*; Fig. 41.10A), a group of mostly annual or ephemeral herbs of low-elevation, summer-dry settings in the California Floristic Province, but also the alpine and subalpine western North American perennial herbs in *Raillardella* s.l. and the trees, shrubs, rosette plants, cushion plants, and lianas that constitute the endemic Hawaiian silversword alliance (*Argyroxiphium* [Fig. 41.10B], *Dubautia*, *Wilkesia*; 31 spp.), a premier example of long-distance dispersal and insular adaptive radiation (see Carlquist et al. 2003).

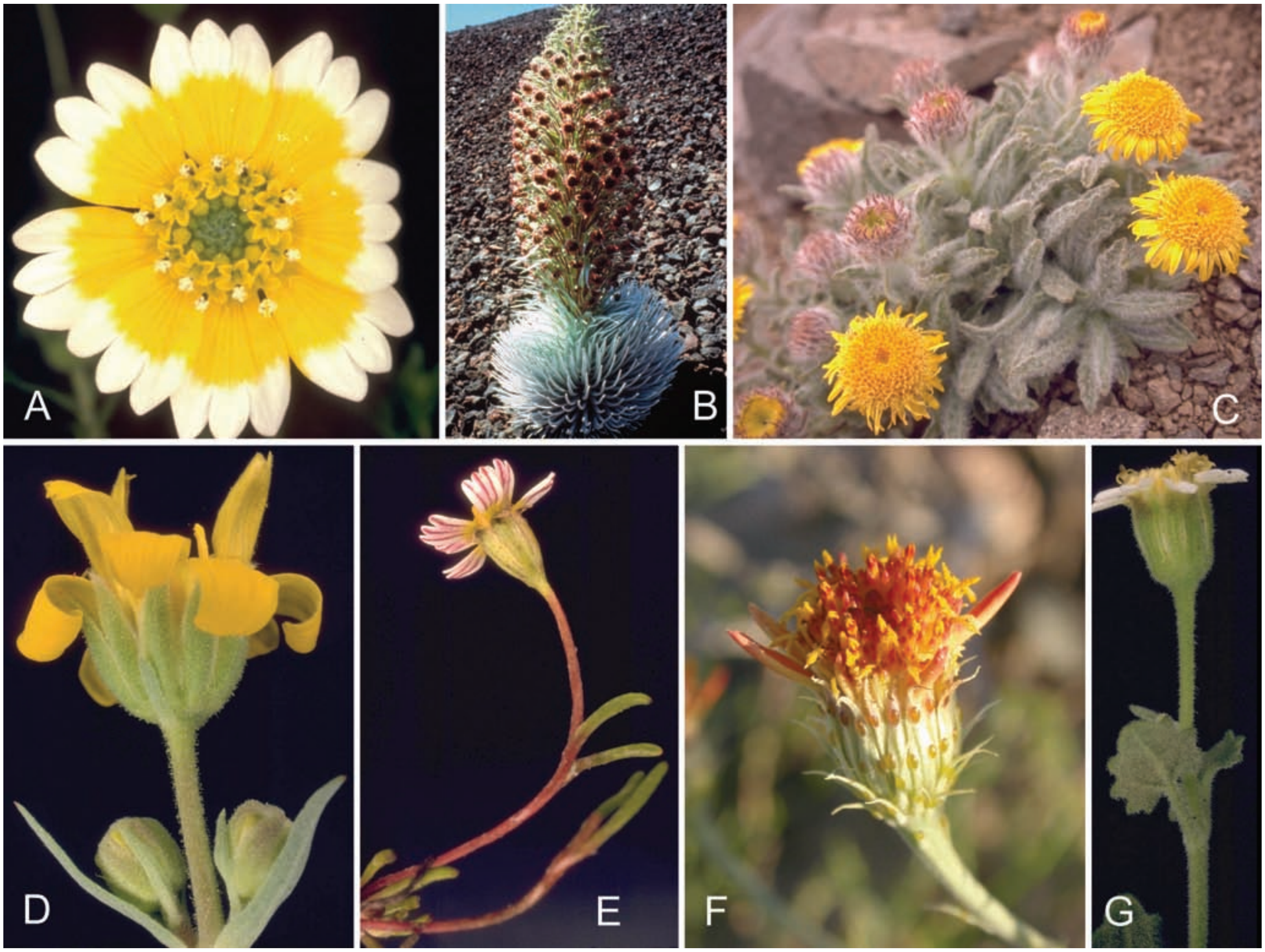

Fig. 41.10. Additional representatives of predominantly epaleate tribes of the Heliantheae alliance. **A** *Layia fremontii* Torr. & A. Gray ex A. Gray (Madieae); **B** *Argyroxiphium sandwicense* DC. (Madieae); **C** *Hulsea algida* A. Gray (Madieae); **D** *Arnica dealbata* (A. Gray) B.G. Baldwin (Madieae); **E** *Syntrichopappus lemmonii* (A. Gray) A. Gray (Madieae); **F** *Adenophyllum cooperi* (A. Gray) Strother (Tageteae); **G** *Eutetras palmeri* A. Gray (Perityleae). [Photographs: A, C–E, G, B. Baldwin; B, D.W. Kyhos; F, J. Andre.]

Keck (1936), who first recognized that the Hawaiian silversword genus, *Argyroxiphium* (in which he included *Wilkesia*), and the Hawaiian endemic *Dubautia* (including *Railliardia*) represent a common insular lineage, rejected Gray's (1852) placement of *Argyroxiphium* in Madiinae, with the Californian tarweeds. Keck (1936) stated, "By thus divorcing *Argyroxiphium* from the American genera to which it has been thought related, the most persistently proposed connection between the ancient element in the Hawaiian flora and the New World has been shattered." Molecular phylogenetic data upheld Carlquist's (1959a) hypothesis by showing that the monophyletic Hawaiian silversword alliance is highly nested within a Californian tarweed grade (Baldwin et al. 1991; see Baldwin 2003a) (Fig. 41.11). The woody or semi-woody Hawaiian taxa were found to belong to the otherwise herbaceous "Madia" lineage, one of four major lineages of Madiinae (Baldwin 1996, 2003a), and to be an unequivocal example of insular evolution of extensive above-ground woodiness and of long-distance dispersal from temperate North America to Hawaii, a previously underappreciated biogeographic pattern (see Fosberg 1948).

Subtribe Arnicinae contains only the circumboreal and montane genus *Arnica* (29 spp.; Fig. 41.10D), in-

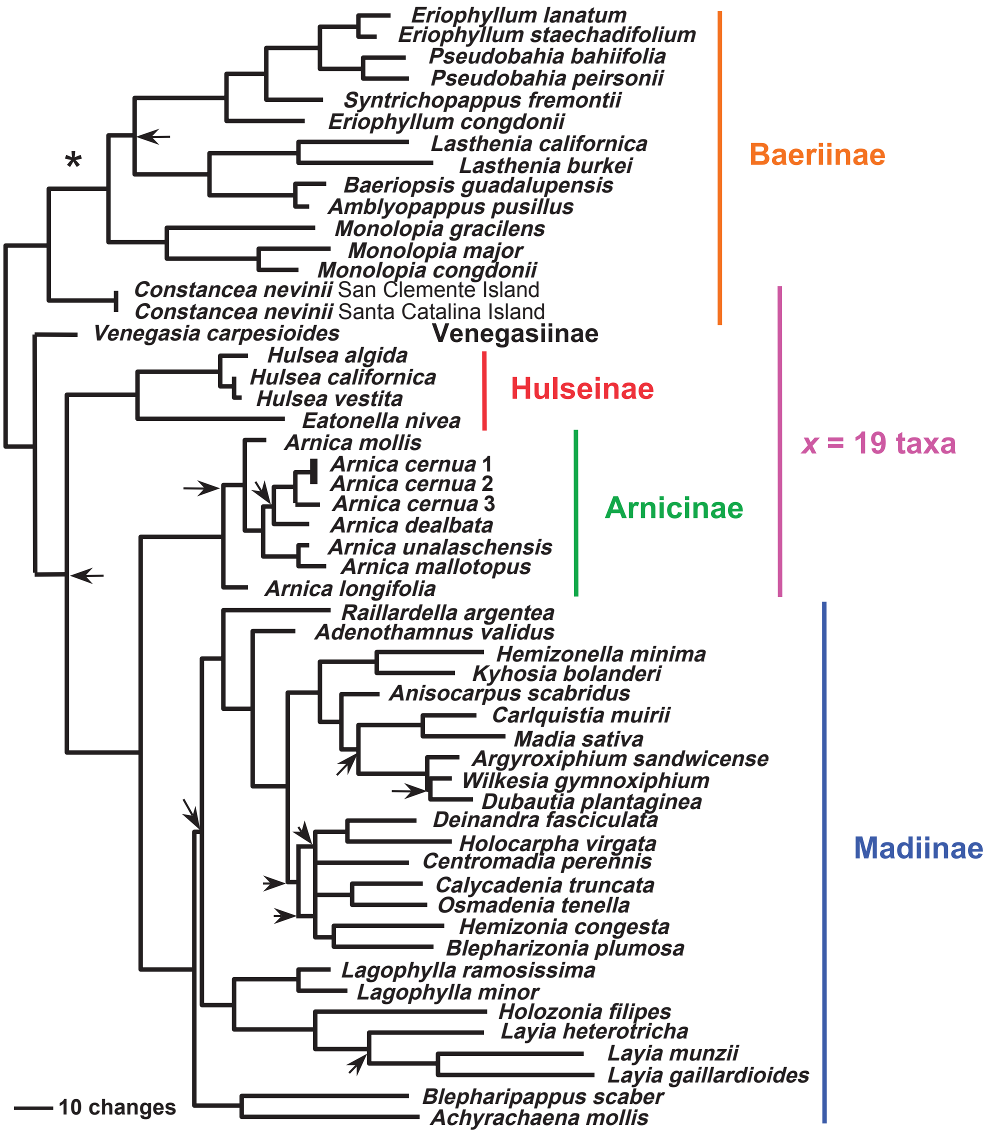

Fig. 41.11. One of 300 maximally parsimonious trees for Madieae based on rDNA internal transcribed spacer (ITS) sequences (Baldwin and Wessa 2000b). Arrows indicate branches that collapse in the strict consensus tree. The tree was rooted based on analyses of Baldwin et al. (2002); the asterisk (*) indicates an alternative, nearly equally parsimonious, rooting of the tree. Evident taxonomic problems in *Eriophyllum* and relatives are subjects of continuing investigation (Baldwin, unpub.).

cluding the nested monotypes *Mallotopus* and *Whitneya*. Resolution of a robust sister group relationship between *Arnica* and the tarweed–silversword lineage (Madiinae) (Fig. 41.11) simultaneously solved two long-standing problems in Compositae systematics (Baldwin and Wessa 2000b; Baldwin et al. 2002). *Arnica*, without paleae and with a pappus of bristles, was long treated in Senecioneae (following Bentham 1873) until Nordenstam (1977) removed the genus from the tribe, along with other taxa treated subsequently by Robinson (1981) in an expanded Heliantheae. Members of Madiinae, with usually only one ring of paleae (between ray and disc florets), had been of uncertain relationship to other taxa of the Heliantheae alliance and were earlier (and understandably) suggested to be either transitional between epaleate and paleate groups (Robinson 1981) or sister to other paleate lineages, with all of the paleate taxa (including Madiinae), in turn, nested within an epaleate grade (Karis and Ryding 1994).

Striking similarities between *Arnica* and the subalpine-to-alpine tarweed genus *Raillardella* in morphology, ecology, and chromosome number may reflect homologous and ancestral (plesiomorphic) states within Arnicinae and Madiinae; *Raillardella* was resolved as sister to other members of Madiinae, with *Arnica*, in turn, sister to all of Madiinae, in combined rDNA+cpDNA analyses (Baldwin 2003a). Bentham (1873) placed *Arnica* and *Raillardella* in his opposite-leaved group within Senecioneae, where the two genera remained in close taxonomic association until Carlquist (1959a) moved *Raillardella* to Madiinae. Some shared traits of *Arnica* and the three species of *Raillardella*, such as occurrence in seasonally frigid and often wet environments; rhizomatous perennial habit; bristly or bristle-like pappus elements (except the epappose *A.* [*Whitneya*] *dealbata* (A. Gray) B.G. Baldwin); and high base chromosome numbers ($x = 19$ in *Arnica*; $x = 17$ or 18 in *Raillardella*) are otherwise highly unusual among the ca. 90 species of continental Madiinae (see Baldwin 2003b), wherein a shift to summer-dry and often hot environments was evidently accompanied by evolution of annual or ephemeral habit and associated dysploidization to chromosome numbers as low as $2n = 4_{II}$, in *Calycadenia* and *Holocarpha*.

Subtribes Hulseinae and Venegasiinae reinforce the above interpretation that occurrence in montane or mesic settings, perennial habit, and high base chromosome number are ancestral traits in much or all of Madieae. Hulseinae (ca. 8 spp.) comprise the western North American montane genera *Eatonella* and *Hulsea* (Fig. 41.10C); Venegasiinae include the monotypic *Venegasia*, from riparian habitats and canyons in the coastal southern California Floristic Province. All members of both subtribes have $2n = 19_{II}$ and only the monotypic *Eatonella* (sister to *Hulsea*) is strictly annual. In ITS trees, Hulseinae and Venegasiinae constitute a clade with Arnicinae and Madiinae (Baldwin and Wessa 2000b; Baldwin et al. 2002) (Fig. 41.11).

Subtribe Baeriinae (8 genera, 44 spp.) includes the woolly sunflowers (*Eriophyllum*), goldfields (*Lasthenia*), and other less diverse genera of western North America, with most species in the California Floristic Province. *Constancea*, a recent segregate of *Eriophyllum*, is a shrub endemic to the southern Channel Islands, with $2n = 19_{II}$ and other putatively plesiomorphic or ancestral characteristics for Baeriinae and perhaps Madieae in general (Baldwin 1999a). *Baeriopsis* is a shrublet of the California Islands, endemic to Guadalupe Island and sister to an annual, coastal Californian and insular monotype, *Amblyopappus*, which together constitute the sister group of the goldfields (*Lasthenia*) based on ITS data (Baldwin et al. 2002) (Fig. 41.11), in accord with Howell's (1942) suggested relationships among the three genera based on morphological considerations. Perennial members of *Eriophyllum* appear to be more closely related to the annual genera *Pseudobahia* and *Syntrichopappus* (Fig. 41.10E) than to annual members of *Eriophyllum* (Baldwin et al. 2002; Baldwin, unpub.). Perenniality in *Baeriopsis* and in some members of *Lasthenia* and *Eriophyllum* appears to be independently derived from the annual habit in each genus based on parsimony mapping of habital states on molecular trees (Chan et al. 2001; Baldwin et al. 2002; see below). Extreme reduction of ray laminae in one lineage of the Baeriinae genus *Monolopia* explains earlier confusion about the relationships of *M. congdonii* (A. Gray) B.G. Baldwin, which has been treated in *Eatonella* (Hulseinae) and *Lembertia*; the 4-lobed corollas of marginal florets in *M. congdonii*, easily misinterpreted as disciform, reflect a 3-lobed vestigial ray lamina and an opposing lobe that is easily seen in the other, more obviously radiate members of *Monolopia* (Baldwin 1999b; Baldwin et al. 2002).

Evolutionary flexibility in ecologically important traits, such as life-form, inferred from phylogenetic data for Baeriinae, extend to fine-scale levels of evolutionary divergence in the subtribe, as in the *Lasthenia californica* DC. ex Lindl. complex. Chan et al. (2002) found that *L. californica*, the common goldfields, included two cryptically distinct, non-sister lineages that can be distinguished macro-morphologically only when pappus is present (both lineages include epappose individuals or populations). In some areas, the two cryptic lineages—now treated as distinct taxa, *L. californica* subsp. *californica* and *L. gracilis* (DC.) Greene—occur in close parapatry and are restricted to distinct soils (e.g., serpentine vs. non-serpentine), where they were earlier noted to represent distinct flavonoid races (Bohm et al. 1989). Rajakaruna et al. (2003a, b) determined that *L. californica* subsp. *californica* and *L. gracilis* each include populations representative of the two flavonoid races and constitute an example of parallel evolution in flavonoids and associated edaphic specialization.

Tribe Tageteae

Tribe Tageteae (32 genera, ca. 270 spp.) comprises the marigold subtribe Pectidinae, as well as other principally New World taxa not included in the tribe until molecular data became available (Baldwin et al. 2002; Panero 2007f). "Core" members of Tageteae, such as *Pectis*, *Porophyllum*, *Tagetes*, and *Thymophylla*, with pellucid secretory cavities or pustules and distinctive secondary chemistry, have been treated as a tribe (e.g., Strother 1977) or subtribe (as Pectidinae; e.g., Robinson 1981; Karis and Ryding 1994; Panero 2007f) since Cassini (1819) segregated Tageteae from his previously more broadly delimited Heliantheae (Cassini 1816).

Family-wide phylogenetic analyses of *rbcL* (Kim et al. 1992) and *ndhF* (Kim and Jansen 1995) variation provided initial cpDNA evidence for a close relationship between Pectidinae ("core" Tageteae) and *Flaveria*, which both include examples of evolution of C_4 photosynthesis (Smith and Turner 1975; McKown et al. 2005) and were earlier suggested to be "very close(ly)" related on the basis of secondary chemistry (Rodríquez and Mabry 1977: 796). Phylogenetic analyses based on ITS sequences (Baldwin et al. 2002) and diverse cpDNA regions (Panero and Funk 2002; Panero 2007f) from an expanded sampling of taxa in the Heliantheae alliance corroborated and extended the earlier cpDNA results by resolving a clade encompassing Pectidinae and Flaveriinae sensu Turner and Powell (1977), i.e., *Flaveria*, *Haploësthes*, and *Sartwellia*, as well as other taxa sometimes included in Flaveriinae based in part on their similar, 10-ribbed achenes, e.g., *Clappia*, *Jaumea*, *Pseudoclappia*, and *Varilla* (Bremer 1987; Karis and Ryding 1994), or previously suggested to be closely related to members of Flaveriinae s.l. or Pectidinae, such as the bizarre, semi-succulent shrub *Coulterella* (Stuessy 1977; Robinson 1981) (Fig. 41.12). Neither ITS nor cpDNA results support monophyly of Flaveriinae s.l. (Fig. 41.12), so recognition of additional subtribes (e.g., Jaumeinae and Varillinae) of Tageteae is warranted (Baldwin et al. 2002; Panero 2007f). Panero (2007f) noted that most of the glandular and eglandular members of Tageteae in the current sense share highly sclerified anther appendages, striate achenes with prominent carpopodia, and bristly or

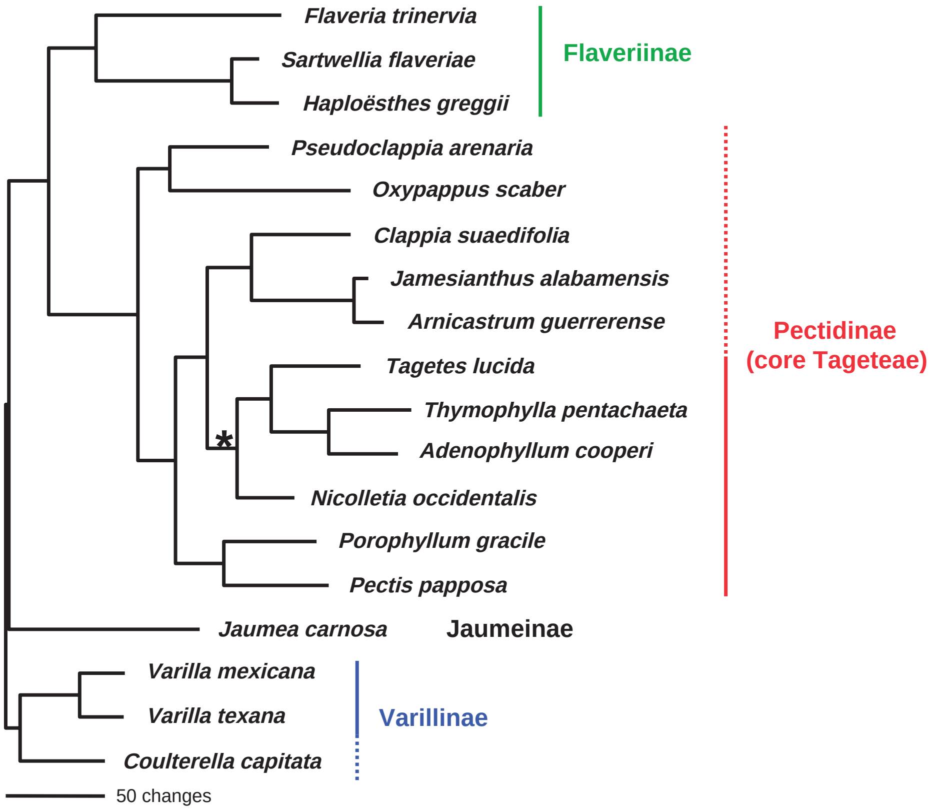

Fig. 41.12. One of two maximally parsimonious (MP) trees for Tageteae based on rDNA internal transcribed spacer (ITS) sequences (data from Baldwin et al. 2002). The clade of *Arnicastrum* + *Jamesianthus* and *Clappia* is sister to *Adenophyllum* + *Thymophylla* and *Tagetes* (but not *Nicolletia*) in the other MP tree; the asterisk indicates the branch that collapses in the strict consensus tree. Rooting of the tree is based on broader-scale analyses of Baldwin et al. (2002).

dissected pappus elements. Based on unstated similarities, Nordenstam (1977: 823) earlier noted that Flaveriinae "seem(s) to lead over to the Tageteae".

Some taxa included in Tageteae by Baldwin et al. (2002) and Panero (2007f) have long been of uncertain relationship. For example, *Arnicastrum* (Sierra Madre, Mexico) and *Jamesianthus* (southeastern USA), previously considered closest relatives (Sherff 1940; Turner and Powell 1977) and recently treated in Chaenactidinae s.l. (Robinson 1981; Karis and Ryding 1994), were sampled for ITS variation and resolved as a clade sister to *Clappia* (Baldwin et al. 2002) (Fig. 41.12); the three genera have similar involucres, pappus, and capitulescence characteristics and two of the three genera (*Clappia* and *Jamesianthus*) have an unusual chromosome number ($n = 16$) for Tageteae (no counts are known for *Arnicastrum*).

Loockerman et al. (2003) investigated relationships among the glandular ("core") members of Tageteae (in Pectidinae) based on ITS and *ndhF* sequences and found that the highly distinctive, C_4 genus *Pectis* is most closely related to *Porophyllum*, in contrast to the dominant view since Bentham (1873) that *Pectis* is an outlier in the tribe (see Smith and Turner 1975; Strother 1977). Strother's (1986) treatment of members of *Dyssodia* s.l. in seven genera (*Adenophyllum* [Fig. 41.10F], *Boeberastrum*, *Boeberoides*, *Comaclinium*, *Dysodiopsis*, *Dyssodia* s.str., and *Thymophylla*) and his suggestion that *Dyssodia jelskii* Hieron. be included in *Schizotrichia* were strongly supported by Loockerman et al.'s (2003) data, which showed *Dyssodia* s.l. to be polyphyletic. *Porophyllum* and the marigold genus *Tagetes* also were found to not be monophyletic; Loockerman et al. (2003) recognized a Baja Californian genus *Bajacalia* for *Porophyllum tridentatum* Benth. and relatives, and treated *Adenopappus* and *Vilobia* as members of *Tagetes*.

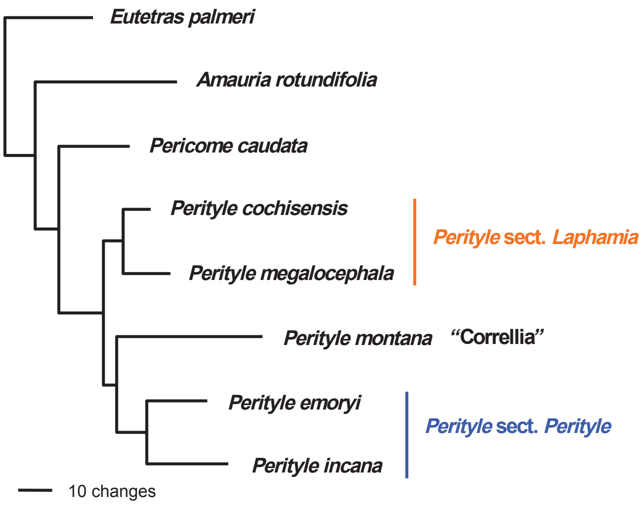

Fig. 41.13. The most parsimonious tree for "core" Perityleae (Perityline) based on rDNA internal transcribed spacer (ITS) sequences (data from Baldwin et al. 2002). The tree was rooted with sequences of *Galeana* and *Villanova* (Galeaninae).

Tribe Perityleae

Tribe Perityleae represents a principally epaleate clade that largely corresponds with a long-recognized group, the rock-daisies (*Perityle* and relatives), most of which are confined to cliff faces, other rocky exposures, or coarse soils in semi-arid regions of southwestern North America. Four-lobed disc corollas and epaleate heads readily identify Peritylinae (4 genera, 72 spp.), which has the same circumscription as the group proposed informally by Powell (1968a, b) and formally named as a subtribe by Robinson (1981). Molecular phylogenetic data from both rDNA (Baldwin et al. 2002) and cpDNA (Panero and Funk 2002) strongly support the monophyly of Peritylinae sensu Robinson (Figs. 41.5, 41.13). The other subtribe with four-lobed disc corollas, Lycapsinae, comprises a single, paleate species (*Lycapsus tenuifolius*) from the remote, floristically depauperate Desventuradas Islands of northern Chile. On the basis of cpDNA findings, Panero (2007g) expanded the circumscription of Perityleae to include a third, southern subtribe, Galeaninae (2 genera, 11 spp.), from Mexico, Central America, and South America, with 5-lobed disc corollas.

Robinson's (1981) interpretation that the "*Perityle*-type" layer of fruit carbonization is diagnostic for a clade including all genera of Peritylinae except *Eutetras* was upheld by molecular phylogenetic data (Baldwin et al. 2002), as were Powell's (1968a, 1973) hypotheses that *(1) Perityle* is more closely related to *Correllia* and *Laphamia* (now both treated as synonyms of *Perityle*) than to *Pericome* and *(2) Perityle* and *Pericome* are more closely related to one another than to *Amauria* or *Eutetras* (Fig. 41.13). Molecular data also support Powell's (1974) conclusion that the robust, shrubby *Nesothamnus* (= *Perityle incana*) from Guadalupe Island (Baja California, Mexico) belongs to *Perityle* sect. *Perityle* (Baldwin et al. 2002). Traits of *Perityle* [*Nesothamnus*] *incana* regarded by Powell (1974) as anomalous for *Perityle* may well have evolved on Guadalupe Island, where an example of neo-endemism and diversification is evident in the closely related Madieae, i.e., in *Deinandra* (Baldwin 2007), and where a genus of Madieae, *Baeriopsis*, is endemic (see above discussion of Baeriinae; see also Moran 1996).

THE CLOSEST RELATIVES OF EUPATORIEAE

Molecular phylogenetic studies focused on the Heliantheoid group have allowed for more detailed assessment of the relationships of Eupatorieae. Earlier family-wide analyses of Compositae indicated that Eupatorieae, although monophyletic, is nested among taxa traditionally placed in Helenieae s.l. and Heliantheae s.l. (Kim and Jansen 1995; Jansen and Kim 1996; Bayer and Starr 1998). ITS analyses based on a more extensive sampling of taxa in the Heliantheae alliance did not result in a robust resolution of the position of Eupatorieae, but did weakly unite the tribe with a subset of epaleate clades and Madiinae (Baldwin et al. 2002). Analysis of the full, compartmentalized ITS dataset placed Eupatorieae in a polytomy with tribes Bahieae, Madieae, and Perityleae; a set of smaller-scale ITS analyses that included different exemplars of Helianthoid tribes most often placed Eupatorieae with either Madieae or Perityleae (Baldwin et al. 2002). A much more extensive analysis of cpDNA sequences of the Helianthoid group placed Eupatorieae as sister to Perityleae, with both tribes in turn sister to Madieae (Panero and Funk 2002; Panero 2007a) (Fig. 41.5), in accord with ITS results. Those findings are consistent with putatively paleopolyploid base chromosome numbers of $x = 19$ for Madieae (Baldwin and Wessa 2000b), $x = 18$ for Perityleae (Robinson et al. 1981; Baldwin et al. 2002), and ca. $x = 17$ for Eupatorieae (Watanabe et al. 1995; Schilling et al. 1999; Ito et al. 2000). A 10–25-fold higher level of species diversity in Eupatorieae (ca. 2200 spp.) compared to Perityleae (84 spp.) or Madieae (203 spp.) may reflect accelerated diversification of Eupatorieae, possibly as a result of one or more key innovation(s) associated with entry into tropical habitats. Robinson et al. (Chapter 43) provides a detailed perspective on relationships and classification of lineages within Eupatorieae.

PHYLOGENETIC AND TRIBAL REASSESSMENT OF PALEATE LINEAGES

In contrast to the longstanding uncertainty and disagreement about tribal/subtribal affiliation and relationships of epaleate ("helenioid") taxa of the Heliantheae alliance, most synantherologists since Cassini (1819) have treated paleate members of the alliance in tribe Heliantheae, with some exceptions, such as occasional treatment of coreopsids in Coreopsideae (see Chapter 42), ragweeds (Ambrosiinae) in Ambrosieae, and the mostly partially-paleate tarweeds and silverswords (Madiinae) in Helenieae or Madieae (see above). A revised perspective on relationships of these paleate lineages has recently emerged as a result of J.L. Panero's efforts in sequencing of ca. 25,000 base pairs of cpDNA for ca. 120 genera of the Heliantheae alliance (Panero et al. 2001), with an extensive sampling of both paleate and epaleate genera (see Panero and Funk 2002; Panero 2007a). The resulting cpDNA tree of the Heliantheae alliance (Fig. 41.5) has indicated that all previous taxonomies of Compositae that have treated Eupatorieae as a tribe have also recognized a non-monophyletic Heliantheae.

Based on cpDNA findings of Panero et al. (2001), Panero and Funk (2002) proposed a new tribal classification of the Heliantheae alliance that adheres to the criterion of monophyly and allows for continued recognition of Eupatorieae as a tribe, by recognizing five tribes of mostly paleate taxa in addition to the principally epaleate tribes (including Madieae) proposed in Baldwin et al. (2002) and Athroismeae (Fig. 41.5). Panero and Funk's (2002) system, discussed in more extensive detail by Panero (2007a), retains Coreopsideae in nearly the traditional sense (Panero 2007h; see Chapter 42), Heliantheae in a more limited sense than in previous classifications, and three new or reconstituted tribes for taxa previously included in Heliantheae: Millerieae, Neurolaeneae, and Polymnieae.

Tribe Heliantheae

Tribe Heliantheae (113 genera, ca. 1461 spp.), as redelimited by Panero and Funk (2002), still encompasses the majority of paleate taxa and a wide diversity of woody lineages in the Heliantheae alliance (see Panero 2007i) (Fig. 41.5). The tribe occurs mostly in the New World, especially in Mexico, Central America, and South America, and includes commercially important temperate North American plants, such as sunflowers and Jerusalem artichokes (*Helianthus*) and purple coneflowers (*Echinacea*). Panero (2007i) noted that members of Heliantheae sensu Panero and Funk (2002) often have flattened achenes, with paleae folded around the fruits and pappus elements arrayed in an oval or narrowly rectangular pattern on the fruit apex, rather than having ± terete fruits and radiating pappus, as are often found in the most diverse segregate tribe, Millerieae (see below). He concluded from cpDNA data (Panero et al. 2001) that extensive homoplasy in macro- and micro-morphological characters had previously complicated recognition of natural groups within Heliantheae s.str., without the aid of molecular evidence, and resulted in understandable problems in earlier subtribal circumscriptions. Panero's (2007i) system of 14 subtribes includes the long-recognized, highly distinctive Ambrosiinae and Helianthinae (including *Phoebanthus*) and Robinson's (1978) Montanoinae and Rudbeckiinae; other subtribes are either novel (Chromolepidinae, Dugesiinae, Enceliinae, Rojasianthinae, and Spilanthinae) or of revised circumscription (Ecliptinae, Engelmanniinae, Verbesininae, Zaluzaniinae, and Zinniinae) based in part on clades resolved with cpDNA data (e.g., Panero et al. 1999b, 2001; Clevinger and Panero 2000; Urbatsch et al. 2000).

Recent systematic studies also have led to improved understanding of relationships and revised generic circumscriptions within various subtribes of Heliantheae. In Ambrosiinae, *Ambrosia*, *Iva*, and *Hymenoclea* were each concluded to be non-monophyletic based on morphological and cpDNA investigations (Karis 1995; Miao et al. 1995); *Hymenoclea* has been subsequently treated as a synonym of *Ambrosia* (Strother and Baldwin 2002) (Fig. 41.14C) and multiple genera (e.g., *Hedosyne*) have been recognized for members of *Iva* s.l. (Strother 2000; Panero 2005, 2007i). In Helianthinae, Schilling and Panero (2002) concluded from congruent ITS and cpDNA trees that *Viguiera* in all previous senses was not monophyletic; they adopted a more limited circumscription of *Viguiera* and recognized *Bahiopsis*, *Calanticaria*, *Heliomeris*, and *Hymenostephium* for other members of *Viguiera* s.l. In Rudbeckiinae, Urbatsch et al. (2000) concluded from cpDNA and ITS data that *Dracopis* is nested among lineages of *Rudbeckia* and should be treated within *Rudbeckia*; they also corroborated Robinson's (1978) conclusion that coneflowers are polyphyletic by showing that *Echinacea* (now in Zinniinae) is more closely related to *Zinnia* and relatives than to *Rudbeckia* and *Ratibida*. Phylogenetic studies of *Balsamorhiza/Wyethia* (Engelmanniinae; Moore and Bohs 2007), *Encelia* (Enceliinae; Fehlberg and Ranker 2007), *Helianthus* (Helianthinae; Rieseberg et al. 1988, 1991; Schilling 1997; Schilling et al. 1998; Linder et al. 2000), *Montanoa* (Montanoinae; Plovanich and Panero 2004), *Silphium* (Engelmanniinae; Clevinger and Panero 2000), and *Verbesina* (Verbesininae; Panero and Jansen 1997) exemplify other recent work that has elucidated evolutionary and biogeographic questions and taxonomic issues at fine-scale taxonomic levels in Heliantheae sensu Panero and Funk (2002). The huge body of cutting-edge

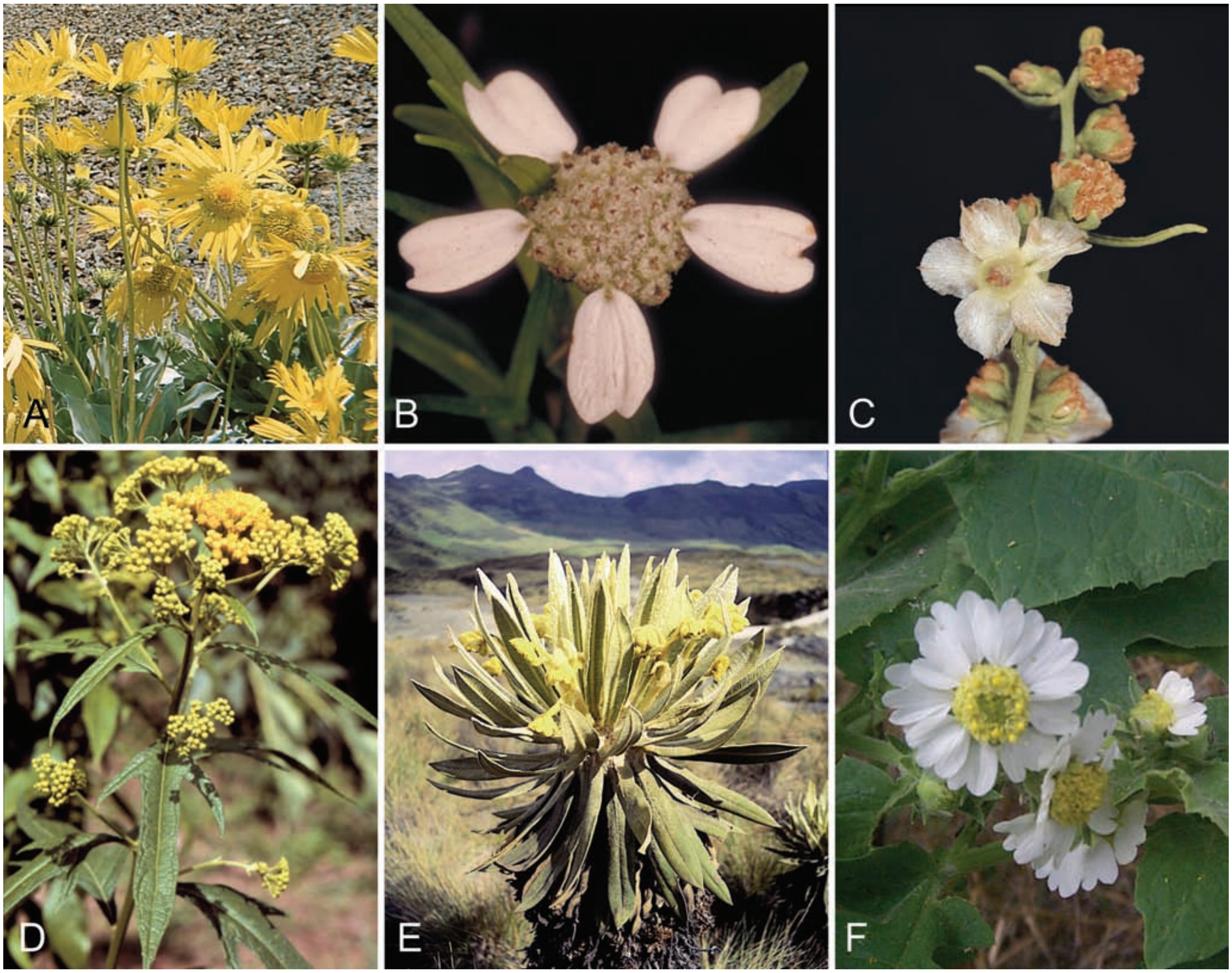

Fig. 41.14. Representatives of predominantly paleate tribes of the Heliantheae alliance. **A** *Enceliopsis covillei* (A. Nelson) S.F. Blake (Heliantheae); **B** *Trichocoryne connata* S.F. Blake (Heliantheae); **C** *Ambrosia salsola* (Torr. & A. Gray) Strother & B.G. Baldwin (Heliantheae); **D** *Neurolaena lobata* (L.) R. Br. (Neurolaeneae); **E** *Espeletia hartwegiana* Cuatrec. ex Herzog (Millerieae); **F** *Polymnia canadensis* L. (Polymnieae). [Photographs: A, G. Norvell; B, C, B. Baldwin; D, M. Balick (courtesy of New York Botanical Garden); E, J. Rauscher; F, D. Reed.]

evolutionary work on *Helianthus* by L. Rieseberg and colleagues provides especially detailed insights into evolutionary patterns and processes, including the importance of hybridization and genomic reorganization in adaptation and diversification (see, e.g., Rieseberg 2006).

Tribe Millerieae

Recognition of tribe Millerieae (34 genera, ca. 380 spp.) was based on cpDNA evidence for a closer relationship of the group to Eupatorieae, Madieae, and Perityleae than to a clade corresponding to Heliantheae s.str. (Panero et al. 2001; Panero and Funk 2002). Millerieae are the most diverse of the new, principally paleate tribes described by Panero and Funk (2002) and comprise eight subtribes of mostly Mexican and neotropical taxa previously placed under Heliantheae (see Panero 2007j). Robinson (1981) recognized six of those subtribes (Desmanthodiinae, Espeletiinae, Galinsoginae, Guardiolinae, Melampodiinae, and Milleriinae), with the same or somewhat different circumscriptions, in his revision of Heliantheae s.l.; Panero (2005) proposed two additional subtribes (Dyscritothamninae for *Bebbia*, *Cymophora*, *Dyscritothamnus*, *Tetragonotheca*, and *Tridax*; and Jaegeriinae for *Jaegeria*). Dyscritothamninae and Jaegeriinae comprise taxa with a base chromosome number of $x = 9$ that were treated in Galinsoginae by Robinson (1981) and resolved as distinct clades by Panero et al. (1999b, 2001). Galinsoginae sensu Panero (2007j) corresponds to a well-supported $x = 8$ clade. Panero (2007j) also recognized Melampodiinae (for *Acanthospermum*, *Lecocarpus*, and *Melampodium*) in a narrower sense than in previous taxonomies (e.g., Robinson 1981) based on cpDNA evidence for a closer relationship of *Ichthyothere* and *Smallanthus* to members of Milleriinae than to *Melampodium* and relatives (Panero et al. 1999b, 2001).

Within Milleriinae, the mostly herbaceous, neotropical genera *Ichthyothere* and *Smallanthus* appear to be the closest relatives of the spectacular Andean rosette-shrubs and trees of the "*Espeletia* complex" (Espeletiinae) based on both cpDNA and ITS data (Panero et al. 1999b; Rauscher 2002). Rauscher (2002) concluded that woodiness in *Espeletia* (Fig. 41.14E) and relatives is likely a derived state for that páramo clade and, based on timing of Andean uplift and levels of ITS sequence divergence, that diversification of the ca. 90 species of the complex may have occurred within the estimated timeframe for diversification of another lineage of the Heliantheae alliance noted for derived woodiness and evolution of alpine rosette-shrubs; namely, the Hawaiian silversword alliance of Madieae (Baldwin and Sanderson 1998) (Fig. 41.7). Millerieae also includes a putative example of diversification on oceanic islands, *Lecocarpus* (Melampodiinae), endemic to the Galapagos Islands. Other geographical outliers in Millerieae that provide evidence for long-distance dispersal in the tribe include the paleotropical genera *Guizotia* (Africa)—the source of niger-seed oil (*G. abyssinica* (L.f.) Cass.)—and *Micractis* (e. Africa and Madagascar).

Tribe Neurolaeneae

Tribe Neurolaeneae (5 genera, ca. 153 spp.) was recognized by Panero and Funk (2002) in light of cpDNA evidence for a closer relationship of the group to Bahieae, Chaenactideae, and Tageteae than to Heliantheae or other paleate tribes (Panero et al. 2001). Neurolaeneae comprise three mostly neotropical subtribes of perennial (rarely annual) herbs that were previously recognized by Robinson (1981) within Heliantheae: Enydrinae sensu Robinson (1981), for *Enydra*; Heptanthinae in a restricted sense, for *Heptanthus*; and Neurolaeninae in a restricted sense, for *Calea*, *Greenmaniella*, and *Neurolaena* (Fig. 41.14D) (see Panero 2007k). Panero et al.'s (1999b) cpDNA evidence for a clade corresponding to subtribe Neurolaeninae in the current sense also indicated a more distant relationship between tribe Neurolaeneae and tribe Millerieae than might be assumed from previous classifications, wherein various genera of Galinsoginae and Dyscritothamninae (both in Millerieae) were treated in Neurolaeninae (e.g., *Bebbia*, *Schistocarpha*). Based on results of Panero et al. (2001), *Calea*, which constitutes >80% of the species diversity in Neurolaeneae, is sister to both *Greenmaniella* and *Neurolaena*; in turn, those New World genera are sister to the pantropical, aquatic or semi-aquatic *Enydra*.

Tribe Polymnieae

Tribe Polymnieae comprises three species of eastern North American herbs in the genus *Polymnia* (Fig. 41.14F), which also constitute Robinson's (1981) subtribe Polymniinae. Panero and Funk's (2002) recognition of a tribe for *Polymnia* was based on cpDNA data indicating that the genus is deeply divergent within the Heliantheae alliance, i.e., sister to all members of the group except the more basally divergent Athroismeae, Helenieae, and Coreopsideae (Panero et al. 2001; see Panero 2007l). *Polymnia canadensis* has been studied extensively as an unusual example of variation among annual, biennial, and perennial life-histories in temperate deciduous forests of North America (see Bender et al. 2003).

EVOLUTION

Capitular characteristics

Evolution of some capitular characteristics that were emphasized in previous classifications have been reevaluated on the basis of ITS and cpDNA trees of the Heliantheae alliance.

As discussed under "Systematic Background" (above), presence or absence of paleae or receptacular bracts has been variously regarded by synantherologists as a criterion for higher-level classification in the Heliantheoid group. Although Bentham (1873) evidently overemphasized the importance of paleae (or lack thereof) in his concepts of Heliantheae and Helenieae, evolutionary shifts between paleate and epaleate conditions have been sufficiently rare during diversification of the Heliantheae alliance to allow for use of presence or absence of paleae, in combination with other characters, to diagnose major clades, including those reflected by subtribes, tribes, or even groups of tribes (Baldwin et al. 2002; Panero and Funk 2002). For example, absence of paleae in most members of Eupatorieae appears to be homologous with the epaleate condition in much of Madieae and Perityleae. On the other hand, expression of paleae has apparently evolved recently in some otherwise epaleate genera, such as *Chaenactis* (Chaenactideae), *Helenium* (Helenieae), and *Hymenophyllum* (Bahieae), and paleae were evidently lost recently in *Trichocoryne* (Heliantheae; Fig. 41.14B) (Urbatsch et al. 2000; Baldwin et al. 2002). In Madieae, the partly (sometimes fully) paleate heads of tarweeds and silverswords (Madiinae) do not represent a transitional stage in the evolution of fully paleate heads in other tribes of the Heliantheoid group, such as Heliantheae; the Madiinae lineage is highly nested among epaleate lineages of Arnicinae, Baeriinae, and Hulseinae and evidently represents an origin of the expression of paleae that is independent from the evolution of paleae expression in other taxa (Baldwin and Wessa 2000b; Baldwin et al. 2002).

Pappus evolution in the Heliantheae alliance has been highly dynamic. In particular, bristles or bristle-like pappus elements have evolved repeatedly from scales or awns and, as concluded by Robinson (1981), have been given too much weight in higher-level taxonomic decisions. As noted under "Systematic Background", Bentham's (1873) circumscription of Senecioneae included a wide diversity of epaleate taxa with a bristly pappus that Nordenstam (1977) excluded from Senecioneae and Robinson (1981) included in Heliantheae s.l.; molecular data corroborate membership of those taxa in the Heliantheae alliance (Baldwin and Wessa 2000b; Baldwin et al. 2002; Panero and Funk 2002). Examples of epaleate Helianthoid genera with a pappus of bristles or bristle-like scales that have been regarded as representatives of tribes outside the Heliantheae alliance include *Arnica* (Madieae), *Bartlettia* (Bahieae), *Dimeresia* (Chaenactidinae), *Haploësthes* (Tageteae), *Pelucha* (Helenieae), *Peucephyllum* (Bahieae), *Psathyrotes* (Helenieae), *Psathyrotopsis* (Bahieae), and *Raillardella* (Madieae).

Vegetative morphology

Extensive above-ground woodiness has evidently evolved repeatedly from an ancestrally herbaceous state in the Heliantheae alliance, based on parsimony mapping of life-history on molecular trees (Baldwin et al. 2002; Panero and Funk 2002), in addition to shifts from woodiness to herbaceousness. Some examples of derived woodiness, such as *Baeriopsis*, *Constancea*, and the silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*) of tribe Madieae, are associated with dispersal to oceanic islands, in accord with the increasingly well-documented hypothesis that natural selection under insular conditions may favor shrubby or arborescent growth forms in angiosperms, including a broad diversity of Compositae (see Carlquist 1962b, 1974; Baldwin et al. 1998; Panero et al. 1999a).

Although molecular data indicate that the annual habit usually has been derived from an ancestrally perennial state in the Heliantheae alliance, some perennial herbaceous and even shrubby lineages evidently descended from annual ancestors in the group. In *Chaenactis* (Chaenactideae), perennial herbaceous and suffrutescent lineages are nested within a grade of annuals, including *Dimeresia* and *Orochaenactis* (Baldwin et al. 2002; Baldwin, unpub.), and may represent evolution of perenniality under montane conditions. Perennial herbs in *Lasthenia* (Baeriinae; Madieae) are restricted to cool, foggy, maritime settings, where climatic equability may have selected for vegetative persistence; the perennials *L. californica* subsp. *macrantha* and *L. ornduffii* are endemic to the immediate Pacific coast of North America and are nested within a grade of otherwise annual *Lasthenia* taxa (Chan et al. 2001, 2002). The closely related shrublet *Baeriopsis*, from the immediately coast of Guadalupe Island, also appears to have evolved perenniality from an annual ancestry in a maritime situation (Baldwin et al. 2002). In the paraphyletic *Eriophyllum* (Baeriinae; Madieae), shrubby taxa of a wide variety of habitats, from coastal and alpine environments, constitute a clade nested within a grade of annuals, in *Eriophyllum*, *Pseudobahia*, and *Syntrichopappus*. The above examples are consistent with Carlquist's (1974) views on conditions favoring evolution of persistence and woodiness in plants and with his conclusions based on wood anatomy of various members of the Heliantheae alliance (Carlquist 1958, 1959a, b).

Chromosome evolution

Exceptionally elegant work on structural evolution of chromosomes has been focused on members of the Heliantheae alliance from both classical cytogenetic and molecular genetic perspectives (e.g., Kyhos 1965; Carr and Kyhos 1986; see Rieseberg 2006). Extreme descending dysploidy is strongly evident in some lineages of the Heliantheae alliance based on molecular trees (e.g., Baldwin et al. 2002) and appears to be in part associated with evolution of the annual habit, as suggested earlier for Heliantheae s.l. by Robinson et al. (1981) and for annuals in general by Stebbins (1950). For example, in tribe Madieae, parsimony mapping of chromosome numbers onto ITS trees indicates a putatively paleopolyploid base-chromosome number of $x = 19$, which is shared by various, mostly perennial taxa (e.g., *Arnica*, *Constancea*, *Hulsea*, *Venegasia*), with numbers decreasing to as few as four pairs of chromosomes in some annual members of Madiinae (in *Calycadenia* and *Holocarpha*) and as few as three chromosomal pairs in annual members of Baeriinae (in *Pseudobahia*). Conversely, chromosome number rise via polyploidization was associated with a shift from annual to perennial habit in some lineages of the same subtribes, as in *Eriophyllum* (Baeriinae) and in the Hawaiian silversword alliance (Madiinae). Such oscillations in chromosome number cloud the distinction between diploids and polyploids in Madieae and other groups in the Heliantheae alliance (Baldwin and Wessa 2000b; Baldwin et al. 2001; see also Chapter 4).

BIOGEOGRAPHY

As discussed by Funk et al. (2005) and Panero (2007a), an African or Asian origin of the Heliantheae alliance and early dispersal to the New World of the common ancestor of all Helianthoid tribes except Athroismeae is evident from cpDNA trees (Kim and Jansen 1995; Panero et al. 2001; see Panero and Funk 2002); i.e., from the sister group relationship of Athroismeae (Old World) to the other, principally New World Helianthoid tribes and the sister group relationship of the Heliantheae alliance (including Athroismeae) to the mostly Old World tribe Inuleae.

Biogeographic analyses of ITS and cpDNA trees each yield a common resolution of a North American—and possibly southwestern North American—onset of diversification of the Helianthoid group within the New World (Baldwin et al. 2002; Panero and Funk 2002), in agreement with Rzedowski's (1972) suggestion of a southwestern North American origin for Helenieae s.l. Cariaga et al. (2008) noted that their finding of a sister group relationship between the monospecific, Cuban *Feddea* and all other New World members of the Heliantheae alliance supported a North American origin of the New World clade, in light of the proximity of Cuba to North America. Southward incursions into the neotropics, i.e., into southern Mexico, Central America, and/or South America, appear to have occurred in a wide diversity of lineages and were followed by major diversification of Heliantheae, Millerieae, and Eupatorieae there (see Panero 2007a, i, j). Madieae represent a major example of diversification in the California Floristic Province and other dry temperate areas of western North America (Baldwin et al. 2002). Based on cpDNA findings of Panero et al. (2001), Madieae and Perityleae conceivably represent examples of temperate North American groups of subtropical or tropical origin within the Heliantheae alliance. Both tribes also include examples of amphitropical dispersal from western North America to southern South America, i.e., *Lasthenia kunthii* (Less.) Hook. & Arn., *Madia sativa* Molina, and *Perityle emoryi* Torr. (Raven 1963; Ornduff 1966; Chan et al. 2001; Baldwin, unpub.).

Dispersal out of the New World evidently has occurred repeatedly within the Heliantheae alliance, as discussed in part above. Members of Coreopsideae have been especially widely dispersed (see Chapter 42), as have members of Heliantheae s.str., such as the pantropical genera *Acmella*, *Blainvillea*, *Melanthera*, *Sphagneticola*, *Spilanthes*, and *Wedelia* (see Panero 2007i). Pantropical genera of other tribes include *Adenostemma* (Eupatorieae), *Enydra* (Neurolaeneae), and *Sigesbeckia* (Millerieae) (see Hind and Robinson 2007; Panero 2007j, k). Old World endemics that stem ultimately from dispersal events out of the New World include *Exomiocarpon* (Madagascar), *Fenixia* (Phillipines), *Guizotia* (Africa), *Hoffmanniella* (Africa), *Hypericophyllum* (Africa), *Micractis* (Africa/Madagascar), *Pentalepis* (Australia), Australian species of *Eclipta* and *Flaveria*, and Eurasian species of *Arnica* and *Eupatorium* (see Baldwin et al. 2002; Hind and Robinson 2007; Panero 2007e, i, j).

Members of the Heliantheae alliance are well represented in oceanic island floras of the Pacific and constitute some excellent examples of insular adaptive radiation. In the Hawaiian Islands, the silversword alliance (*Argyroxiphium*, *Dubautia*, *Wilkesia*; Madieae), *Lipochaeta* (Heliantheae), and endemic species of *Bidens* (Coreopsideae) represent the three most diverse radiations of Compositae and nearly 60% of all indigenous Hawaiian species of the family (see Baldwin 1998). *Scalesia* (Heliantheae) is arguably the best example of plant adaptive radiation in the Galapagos Islands (see Carlquist 1974), where other members of Heliantheae, such as *Trigonopterum* and species of *Delilia* and *Encelia*, are endemic, as is *Lecocarpus* (Millerieae). Other oceanic-island endemics of the Heliantheae alliance include *Apostates* (Bahieae; Rapa Iti, French Polynesia), *Baeriopsis* (Madieae; Guadalupe Island, Mexico), *Constancea* (Madieae; Channel Islands, USA), and *Lycapsus* (Perityleae; Desventuradas Islands, Chile).

A biogeography tree of the entire Compositae can be found in Chapter 44.

CONCLUSIONS

Considerable work remains to understand phylogenetic patterns across the Heliantheae alliance, especially at finer-scale levels of evolutionary divergence. As that knowledge improves and genomic resources for *Helianthus* and other members of Compositae are further developed, e.g., by Loren Rieseberg and other participants in the

Compositae Genome Project (http://compgenomics.ucdavis.edu/), the stage will be set for particularly interesting explorations of trait evolution and development, and of process-oriented evolutionary questions in the group (see, e.g., Kane and Rieseberg 2007). Evolutionary dynamism in vascular anatomy, chromosome structure and number, bract expression, pappus characteristics, phenology, secondary chemistry, and physiology make the Heliantheae alliance an exceptionally promising subject for a wide diversity of comparative evolutionary and developmental investigations.

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Chapter 42

Coreopsideae

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HISTORICAL OVERVIEW AND PHYLOGENY

Morphological data

A synthesis and analysis of the systematic information on tribe Heliantheae was provided by Stuessy (1977a) with indications of "three main evolutionary lines" within the tribe. He recognized fifteen subtribes and, of these, Coreopsidinae along with Fitchiinae, are considered as constituting the third and smallest natural grouping within the tribe. Coreopsidinae, including 31 genera, were divided into seven informal groups. Turner and Powell (1977), in the same work, proposed the new tribe Coreopsideae Turner & Powell but did not describe it. Their basis for the new tribe appears to be finding a suitable place for subtribe Jaumeinae. They suggested that the previously recognized genera of Jaumeinae (*Jaumea* and *Venegasia*) could be related to Coreopsidinae or to some members of Senecioneae.

In his revision of the tribal and subtribal limits of Heliantheae, based on morphology, anatomy and chromosome studies, Robinson (1981) kept Coreopsideae as a synonym of Coreopsidinae. Bremer (1987), in his studies of tribal interrelationships of Asteraceae, provided Coreopsideae as a subset of Heliantheae. He retained many of the genera assigned to Coreopsidinae by Stuessy (1977a) except for *Guizotia* (placed in Milleriinae), *Guardiola* (in a new tribe Guardiolinae; Robinson 1978), *Jaumea* (placed in Jaumeinae), *Selleophytum* (as a synonym of *Coreopsis*), *Staurochlamys* (placed in Neurolaeninae), and *Venegasia* (in Chaenactidinae).

In a cladistic analysis of morphological features of Heliantheae by Karis (1993), Coreopsidinae were reported to be an ingroup within Heliantheae s.l. The group was represented in the analysis by *Isostigma*, *Chrysanthellum*, *Cosmos*, and *Coreopsis*. In a subsequent paper (Karis and Ryding 1994), the treatment of Coreopsidinae was the same as the one provided above except for the following: *Diodontium*, which was placed in synonymy with *Glossocardia* by Robinson (1981), was reinstated following the work of Veldkamp and Kreffer (1991), who also relegated *Glossogyne* and *Guerreroia* as synonyms of *Glossocardia*, but raised *Glossogyne* sect. *Trionicinia* to generic rank; *Eryngiophyllum* was placed as a synonym of *Chrysanthellum* following the work of Turner (1988); *Fitchia*, which was placed in Fitchiinae by Robinson (1981), was returned to Coreopsidinae; *Guardiola* was left as an unassigned Heliantheae; *Guizotia* and *Staurochlamys* were placed in Melampodiinae; *Jaumea* was put in Flaveriinae; *Microlecane* was kept as a synonym of *Bidens* following the work of Mesfin Tadesse (1984); *Sphagneticola* was assigned to Verbesininae; and *Venegasia* was placed in Chaenactidinae. Stuessy (1988) transferred two species of *Oparanthus* and one species of *Petrobium* to *Bidens*. Shannon and Wagner (1997) reinstated *Oparanthus* and recognized four species in the genus. The genera recognized in this chapter are the same ones recognized by Karis and Ryding (1994) with the exceptions that *Megalodonta* is not segregated from *Bidens* and *Selleophytum* is segregated from *Coreopsis*.

The first cladistic analysis focusing on Coreopsideae was by Ryding and Bremer (1992). Parsimony analysis recovered three major groups, which were treated as subtribes Coreopsidinae, Petrobiinae, and their new Chrysanthellinae. The monospecific genera *Dicranocarpus* and *Goldmanella* were eventually excluded from their analyses because they occurred in various positions on the cladograms, and inclusion of the genera produced so many shortest trees that computer memory was exhausted. Of special interest, the largest genus *Bidens* occupied various positions in the shortest trees, including occurrence in the two different subtribes Coreopsidinae and Petrobiinae. Karis and Ryding (1994) essentially followed the treatment of Ryding and Bremer (1992) but recognized the entire group as subtribe Coreopsidinae with the three subtribes of Ryding and Bremer (1992) treated as informal groups.

Tribes/subtribes based on molecular data

Jansen et al. (1991) were probably the first to apply comparative cpDNA data to the evaluation of phylogenetic relationships within Asteraceae as a whole. Coreopsideae were represented by *Coreopsis* and *Dahlia*, and cpDNA data supported the segregation of Coreopsideae from the core of Heliantheae. Based on complete sequences of the *rbcL* gene for 25 species of Asteraceae, Kim et al. (1992) did not find strong support for relationships between the tribes but stated that Tageteae, Coreopsideae, Heliantheae and Eupatorieae are close, and maintained Coreopsideae as a tribe. Using chloroplast *ndhF* sequences from *Dahlia*, *Coreopsis* and *Cosmos* of Coreopsidinae, Kim and Jansen (1995) showed that this group is embedded within a clade of Heliantheae s.l., (i.e., including Helenieae, Coreopsideae, Eupatorieae, and Tageteae). Bayer and Starr (1998), using two non-coding chloroplast sequences (*trnL* intron, and *trnL/trnF* intergenic spacer), showed the same relationship between Tageteae, Heliantheae and Eupatorieae as Kim and Jansen (1995). Heliantheae were represented only by *Helianthus* in their analysis. Panero and Funk (2002) used a combined dataset of chloroplast sequences totaling over 13,000 bp to produce a phylogeny-based subfamilial classification for Asteraceae with Coreopsideae treated as a tribe. In the supertree (= metatree) of Funk et al. (2005), Coreopsideae were retained at the tribal level.

Genera based on molecular data

The following observations regarding resolution of relationships within Coreopsideae can be generalized from the morphological studies conducted through the early 1990s. All studies recognized as monophyletic those taxa with C_4 photosynthesis (the *Chrysanthellum* group). *Goldmanella* was placed within Coreopsideae, but was recognized as a somewhat discordant element in the tribe (Stuessy 1977a; Robinson 1981). Without doubt, however, the biggest impediments to understanding relationships within Coreopsideae have been the two largest genera *Bidens* and *Coreopsis*. Reservations have continually been expressed for decades not only about distinguishing the two genera from each other, but also regarding the monophyly of each genus (Wild 1967; Agnew 1974; Mesfin Tadesse 1984b, 1986, 1993). One of the shortcomings of the phylogenetic analysis of Ryding and Bremer (1992), which they readily acknowledged, is that both *Bidens* and *Coreopsis* were each accepted as "good" genera in their analyses even though neither is likely monophyletic. It was necessary for Ryding and Bremer (1992) to accept both genera because it was beyond the scope of their study to examine these large complex genera in depth. It is evident that until there is better resolution of relationships within and among elements of *Bidens* and *Coreopsis*, as well as clarification of their relationships to other genera, it will not be possible to reach a proper understanding of phylogenetic relationships within Coreopsideae.

Kim et al. (1999) used ITS sequences to provide the first molecular phylogenetic study of *Bidens* and *Coreopsis*. The two shortcomings of the study were limited taxonomic sampling in *Bidens* and inclusion of only representatives of the two genera as the ingroup. Despite the shortcomings, the results of Kim et al. (1999) indicated strongly that neither *Bidens* nor *Coreopsis* was monophyletic. Ganders et al. (2000) used ITS sequences to examine relationships in *Bidens*, with emphasis on ascertaining the continental relatives of Hawaiian and Marquesan members. Their results produced groups of *Bidens* similar to those detected by Kim et al. (1999), but since no other genera were included in the ingroup, the monophyly of *Bidens* was not tested.

Kimball and Crawford (2004) conducted a molecular phylogenetic study of Coreopsideae using ITS sequences from 20 of 24 genera (Table 42.1). Taxon sampling in *Bidens* and *Coreopsis* included representatives of clades recovered by Kim et al. (1999) and Ganders et al. (2000). The tree presented in Fig. 42.1 was constructed with maximum likelihood (ML) analyses of ITS sequences and includes exemplar taxa for clades present in the analysis of Kimball and Crawford (2004). While prior studies used maximum parsimony for tree construction, Mort et al. (2008) and Mort et al. (unpub.) show high congruence between maximum likelihood and maximum parsimony analyses, and only the likelihood tree is shown. All ITS sequences are available in GenBank and have been previously published. Plastid sequences are available for some taxa (Mort et al., 2008) but will be mentioned only when they provide additional insights into relationships or results incongruent with the ITS tree. The only monophyletic group not collapsed in the tree is *Bidens*-2, 3, and the reason for this will be discussed.

The first split in the ingroup is between the small South American genus *Ericentrodea* (Table 42.1; Robinson 1993) and the remainder of the sampled taxa. Two of

Table 42.1. Currently recognized genera of Coreopsideae, giving number of species sampled for construction of Fig. 42.1 (followed by approximate total number of species sequenced for ITS in parentheses and total number of species in genus, known chromosome numbers, and assessment of monophyly of each genus with reference to most comprehensive study.

Genus	Taxa	Chromosome number (*n*)	Monophyletic; reference
1. *Bidens* L.	11(25)/340	10, 11, 12, 16, 17, 18, 22, 23, 24, 34, 36, 38, 40, 48, 72, ca. 73	N; Kimball and Crawford 2004
2. *Chrysanthellum* Rich.	1(1)/13	8, 12	?; –
3. *Coreocarpus* Benth.	4(7)/7	9, 11, 12	N; Kimball et al. 2003
4. *Coreopsis* L.	16(55)/86	6, 7, 8, 9, 10, 12, 13, 14, 24, 26, 28, 32, 39, 56	N; Kimball and Crawford 2004
5. *Cosmos* Cav.	3(3)/36	11, 12, 17, 22, 23, 24, 33, 36	Y; Kimball and Crawford 2004
6. *Cyathomone* S.F. Blake	0/1	–	N/A; –
7. *Dahlia* Cav.	3(33)/35	16, 17, 18, 32	Y; Saar et al.; 2003; Kimball and Crawford 2004
8. *Dicranocarpus* A. Gray	1/1	10	N/A; –
9. *Diodontium* F. Muell.	0/1	–	N/A; –
10. *Ericentrodea* S.F. Blake	2(2)/6	–	Y; Kimball and Crawford 2004
11. *Fitchia* Hook. f.	1(3)/6	35–40, 45	Y; W.L. Wagner, pers. comm.
12. *Glossocardia* Cass.	1(1)/12	12	?; –
13. *Goldmanella* Greenm.	1/1	–	N/A; –
14. *Henricksonia* B.L. Turner	1/1	18	N/A; –
15. *Heterosperma* Cav.	2(2)/5–11?	9, 11, 13, 24, 25	N; Kimball and Crawford 2004
16. *Hidalgoa* La Llave & Lex.	1(1)/5	15, 16, 17	?; –
17. *Isostigma* Less.	1(1)/13	9, 12	?; –
18. *Moonia* Arn.	0/1	–	N/A; –
19. *Narvalina* Cass.	1/1	60	N/A; –
20. *Oparanthus* Sherff	1(4)/4	–	Y; W.L. Wagner, pers. comm.
21. *Petrobium* R. Br.	1/1	–	N/A
22. *Selleophytum* Urban	1/1	32	N/A
23. *Thelesperma* Less.	3(5)/15	8, 9, 10, 11, 12, 20, 22, 24, 30	Y; Kimball and Crawford 2004
24. *Trioncinia* (F. Muell.) Veldkamp	0/1	–	N/A

Y = yes; N = no; N/A = not applicable; ? = not determined; – = not studied.

the six *Ericentrodea* species were included by Kimball and Crawford (2004), and they form a strongly supported monophyletic group (Fig. 42.1). Features of the fruits, in particular, characterize the genus (see generic diagnosis; Robinson 1993; Karis and Ryding 1994). Stuessy (1977a) included this genus in his large group 1 (which includes *Cyathomone* and *Narvalina*), and it was placed near both *Cyathomone* and *Narvalina* in the morphological phylogeny of Ryding and Bremer (1992). As far as we are aware, *Cyathomone* is known only from the meager type specimen, and there is some question as to whether it is distinct from *Ericentrodea* (see below). Available molecular data offer no clues to the closest relatives of *Ericentrodea*, but if appropriate material were available, it would be instructive to include *Cyathomone* in future analyses.

The small Mexican-Central American genus *Hidalgoa* branches next and is weakly placed (< 50% bootstrap) as sister to the remaining ingroup taxa (Fig. 42.1). Because only one species was sampled, it is not possible to assess the monophyly of *Hidalgoa*. However, the present analysis clearly indicates that the genus is not closely allied with *Petrobium*, as suggested by Ryding and Bremer (1992).

Previous analyses using ITS (Gatt et al. 2000; Kimball and Crawford 2004) and ITS-ETS sequences (Saar et al. 2003) provided strong support for the monophyly of the large genus *Dahlia* (Fig. 42.2G, K). However, somewhat

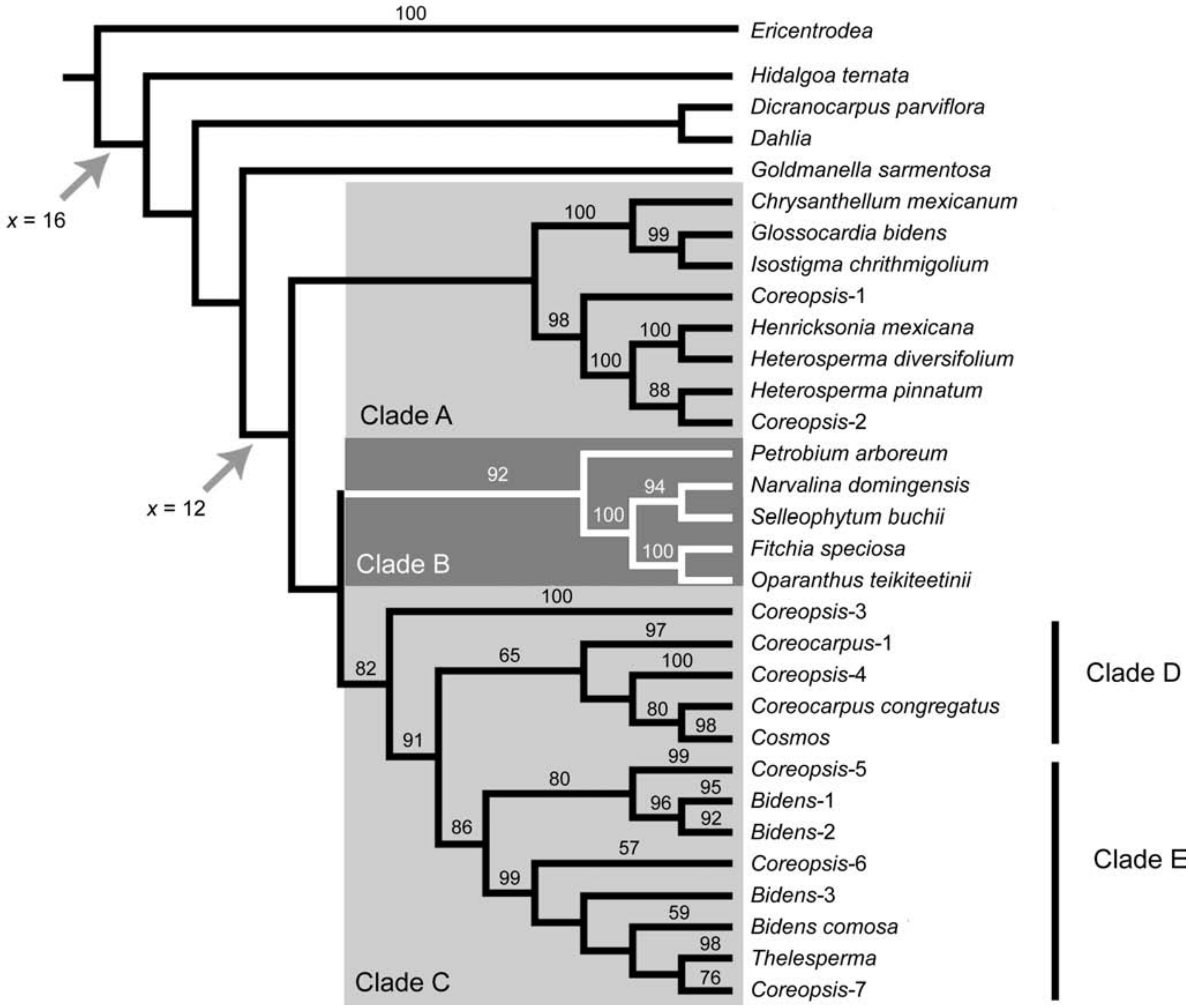

Fig. 42.1. Maximum likelihood (ML) topology inferred from analyses of nrDNA ITS spacers. Well-supported, monophyletic taxa have been collapsed to a single terminal (see Table 42.2 for clade composition). Relative support as assessed via ML bootstrap analyses indicated above branches. MacClade reconstructions of ancestral base chromosome numbers for two clades are indicated by arrows. For a biogeographic analysis see Chapter 44.

unexpected was the recovery of *Dahlia* and the monospecific genus *Dicranocarpus* as sister taxa (Fig. 42.1). We are not aware that a close relationship between these two genera has previously been suggested, obstensibly because they contrast in several morphological features (cf. generic diagnoses below). The results of the molecular study should be viewed with caution, however, because there is not strong support (< 50% bootstrap) for this clade (Fig. 42.1). However, the grouping of *Dahlia* and *Dicranocarpus* is strongly supported (100%) in both maximum likelihood and maximum parsimony analyses of plastid sequences, and in the analyses of the combined ITS/cpDNA dataset (Mort et al., submitted). If indeed the two genera are sister taxa, as the plastid and the combined ITS/cpDNA evidence suggest, then they have diverged significantly from their common ancestor in many features (see generic diagnoses).

The monospecific genus *Goldmanella* was placed in Coreopsideae by both Stuessy (1977a) and Robinson (1981). The former author recognized its distinctive morphology by placing it in its own group, while the latter commented that the genus is best placed in Coreopsideae despite several unusual features (see generic diagnosis). The molecular phylogenetic analysis supports the inclusion of *Goldmanella* in Coreopsideae, but offers no insights into its closest relatives in the tribe (Fig. 42.1).

The vast majority of taxa in Coreopsideae occur in a clade composed of two subclades, one of which (B plus C) is much larger than the other (A) (Fig. 42.1). The smaller subclade (A) in turn contains two highly supported subclades, one consisting of three genera belonging to Stuessy's (1977a) group 3 and the *Chrysanthellum* group of Ryding and Bremer (1992) and Karis and Ryding (1994). Robinson (1981) likewise recognized the *Chrysanthellum* group as natural, with one of the unifying features the Kranz syndrome (C_4 photosynthesis). The molecular phylogenetic analysis confirms prior assessments of the monophyly of the group (Fig. 42.1).

Sister to the *Chrysanthellum* group is a strongly supported clade (98%) comprising two sections of mostly Mexican *Coreopsis* (*Coreopsis*-1, -2; Table 42.2), the monospecific Mexican genus *Henricksonia*, and two representatives of the small southwestern United States, Mexican, and Central American genus *Heterosperma* (Fig. 42.1). The present analysis is concordant with Kimball and Crawford (2004) in showing that neither the two sections of *Coreopsis* nor the two species of *Heterosperma* form monophyletic groups. A cladistic analysis of morphological characters for North American *Coreopsis* (Jansen et al. 1987) did not recover the two Mexican *Coreopsis* sections as sister taxa. To our knowledge, there has been no previous doubt expressed about the monophyly of *Heterosperma*; it has been defined by the dimorphic achenes (see generic diagnosis; Karis and Ryding 1994). A range of chromosome numbers has, however, been reported for the genus (Table 42.1; Robinson et al. 1981). Further studies are needed, including sequencing of additional species and morphological investigations, to resolve relationships among species assigned to *Heterosperma*. *Henricksonia* was described primarily on the basis of the unusual paleaceous scales comprising the pappus of the disc florets (see generic diagnosis; Turner 1977). Turner (1977) suggested *Coreopsis* sections *Electra* and *Anathysana* (*Coreopsis*-1, -2; Figs. 42.1, 42.2J), among others, as closest relatives of *Henricksonia*. While not suggesting a close affinity, Turner (1977) did indicate that *Henricksonia* would key to *Heterosperma* in the generic key of Sherff and Alexander (1955) for North American Coreopsidinae; available molecular data suggest a close phylogenetic relationship between *Henricksonia* and *Heterosperma* (Fig. 42.1).

The last large clade contains two subclades (B and C; Fig. 42.1) that receive moderate to strong support (92% and 82% bootstrap, respectively). Clade B consists entirely of plants endemic to oceanic archipelagos. Within this clade, the monospecific *Petrobium* from St. Helena in the south Atlantic is sister to a well-supported (100% bootstrap) clade comprising the other four genera (Fig. 42.1); noteworthy, the placement of *Petrobium* is well-resolved in the current analysis whereas it was not in Kimball and Crawford (2004). This difference is the result of modifiying the alignment of the ITS sequence data. Various workers have considered *Petrobium* and the two Polynesian genera *Fitchia* (Fig. 42.2A) and *Oparanthus* (Fig. 42.2M) as closely related, and in particular, have viewed the latter two genera as close (Carlquist 1974, 2001; Cronk 1992; Ryding and Bremer 1992; Shannon and Wagner 1997). In the analysis of Ryding and Bremer (1992), *Petrobium*, *Fitchia* and *Oparanthus* are united by several non-homoplastic characters, with the former genus sister to the latter two genera. *Narvalina* was far removed from the other three genera in the trees of Ryding and Bremer (1992), and *Selleophytum* (which was placed in *Coreopsis* by Sherff and Alexander, 1955, but has recently been resurrected by Mesfin Tadesse and Crawford 2006) was not included as a separate element in their study. We are unaware of non-molecular studies suggesting a close relationship between the two monospecific genera *Narvalina* and *Selleophytum*, and the other three insular genera. The common ancestor of this clade may have possessed characters that contributed to their success in dispersal to and establishment in the insular setting. The molecular phylogeny offers no support for the hypothesis that any of the island genera are derivatives of *Bidens* (Carlquist 1974, 2001; Stuessy 1988; Shannon and Wagner 1997) because they are not nested within any of the *Bidens* clades (Fig. 42.1).

The last clade (C, Fig. 42.1) contains about 80% of the species in Coreopsideae, including all representatives of *Bidens* (Fig. 42.2C, D), *Coreocarpus*, *Cosmos* (Fig.

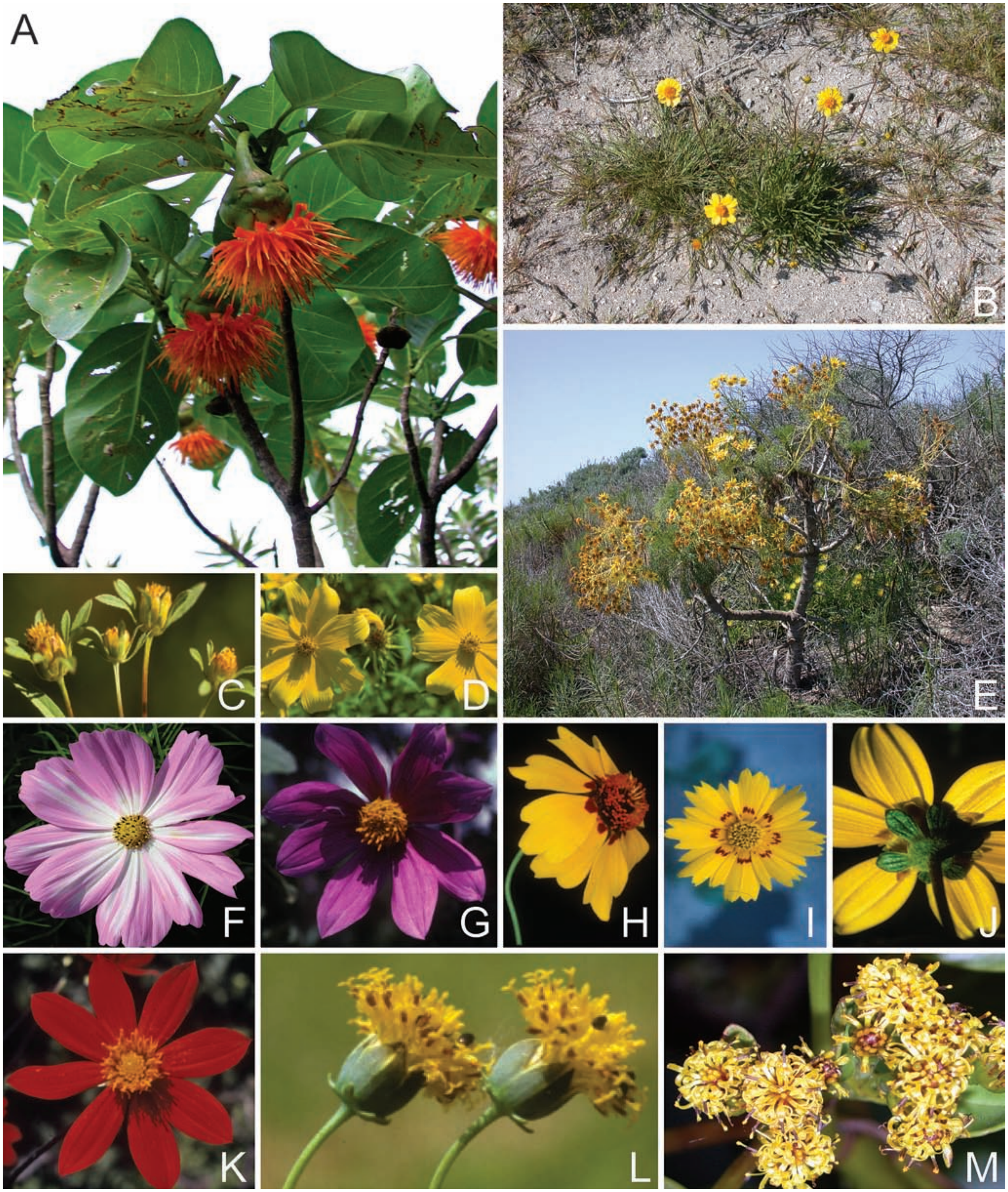

Fig. 42.2. Representatives of Coreopsideae. **A** *Fitchia nutans* Hook. f.; **B** *Coreopsis californica* (Nutt.) H. Sharsm.; **C** *Bidens frondosa* L.; **D** *Bidens aristosa* (Michx.) Britton; **E** *Coreopsis gigantea* (Kellogg) H.M. Hall; **F** *Cosmos bipinnatus* Cav.; **G** *Dahlia pinnata* Cav.; **H** *Coreopsis tinctoria* Nutt.; **I** *Coreopsis nuecensis* A. Heller; **J** *Coreopsis mutica* DC., showing outer and inner involucral bracts; **K** *Dahlia coccinea* Cav.; **L** *Thelesperma megapotamicum* (Spreng.) Kuntze, showing fused inner involucral bracts; **M** *Oparanthus coriaceus* (F. Br.) Sherff. [Photographs: A, M, K. Wood; B, E, M. Mort; C, D, G, K, L, C. Freeman; E, H–J, D. Crawford; F, J. Archibald.]

42.2F), and *Thelesperma* (Fig. 42.2L), as well as the majority of *Coreopsis* species (Fig. 42.2H, I). Within clade C, *Coreopsis*-3 (100% bootstrap) is sister to all other taxa and consists of eight species in three sections, all of which are largely restricted to California (Table 42.2; Fig. 42.2B, E). This clade has long been considered a "natural" group (Sharsmith 1938; Smith 1984), and it was the subject of a recent molecular phylogenetic study (Mort et al. 2004) that provided strong support for monophyly. Mort et al. (2004) present the diagnostic characters for this clade and discuss character evolution within it.

Sister to *Coreopsis*-3 in clade C is a very strongly supported clade (91%) that is composed of two major subclades D and E (Fig. 42.1). Subclade D is weakly supported (65% bootstrap) and contains all or some elements of three genera, including *Coreocarpus* (Fig. 42.1). Though a relatively small genus (see generic diagnosis; Table 42.1), delimiting *Coreocarpus* has posed significant problems (Smith 1989; Melchert and Turner 1990; Kimball et al. 2003; Kimball and Crawford 2004). Various combinations of characters including corky achene wings, monomorphic phyllaries, and neutral ray florets have been used with little success to delimit the genus. The molecular phylogenetic study by Kimball et al. (2003) identified a "core" *Coreocarpus* (*Coreocarpus*-1; Fig. 42.1; Table 42.2) that excluded three species. Two of the excluded species were transferred to *Bidens* by Melchert and Turner (1990); this is consistent with the molecular data that grouped the two species with other Mexican *Bidens* (Kimball et al. 2003; Kimball and Crawford 2004). The most enigmatic species in the genus is *Coreocarpus congregatus* (S.F. Blake) E.B. Smith, which was originally described as a *Coreopsis* but was transferred (with some reservations) to *Coreocarpus* by Smith (1983). Molecular phylogenetic studies using ITS sequences indicate that *C. congregatus* is sister to *Cosmos* (Kimball et al. 2003; Kimball and Crawford 2004; Fig. 42.1). Plastid sequences group *C. congregatus* with *Bidens*-1, 2 (with less than 50% bootstrap support) while the combined nuclear and plastid data partitions show over 80% bootstrap support for it as sister to *Cosmos* (Mort et al., 2008). Although DNA sequence data indicate that *C. congregatus* is sister to *Cosmos*, comparative morphological studies are to be desired to identify diagnostic characters for the clade.

Cosmos is shown as monophyletic by both nuclear and plastid sequences (Kimball and Crawford 2004; Mort et al., 2008); although present taxon sampling is limited (three species), there is strong support for the monophyly of the genus (98% bootstrap; Fig. 42.1). Pubescent filaments serve as a synapomorphy for the genus (see generic diagnosis; Robinson 1981; Ryding and Bremer 1992; Karis 1993). While the three species of *Cosmos* receive strong support as monophyletic, sequences from additional taxa are needed to provide a more thorough assessment of monophyly.

The last element of subclade D to be considered is *Coreopsis*-4, and it will be discussed together with *Coreopsis*-5 of subclade E (Fig. 42.1). *Coreopsis*-4 is well supported (100% bootstrap) and consists of members of *Coreopsis* sect. *Pseudoagarista* from Mexico (Table 42.2). *Coreopsis*-5 includes species of the same section from South America (Table 42.2) and is a well-supported lineage (99% bootstrap). *Coreopsis* sect. *Pseudoagarista* consists of woody perennials, and has been defined by the pubescent achenes with basally attached paleae (Mesfin Tadesse et al. 1995a, 2001). While ITS sequences place Mexican and South American species of the section in different

Table 42.2. Definition of the major clades recovered by ML analyses of the nrDNA internal transcribed spacers shown in Fig. 42.1.

Clade name	Section(s) and their general distribution
Bidens-1	Sects. *Campylotheca*, *Greenmania*, and ***Psilocarpaea***; Caribbean, Hawaii, Mexico, South America, South Pacific
Bidens-2	Sects. ***Psilocarpaea*** and unassigned; Africa
Bidens-3	Sects. *Bidens* and *Hydrocarpaea*; north temperate
Coreocarpus-1	All species except *C. congregatus* (see Fig. 42.1)
Coreopsis-1	Sect. *Electra*; Mexico, Central America
Coreopsis-2	Sect. *Anathysana*; Mexico
Coreopsis-3	Sects. *Leptosyne*, *Pugiopappus*, and *Tuckermannia*; mostly California
Coreopsis-4	Sect. ***Pseudoagarista***; Mexico
Coreopsis-5	Sect. ***Pseudoagarista***; South America
Coreopsis-6	Sects.*Gyrophyllum* and *Silphidium*; eastern North America
Coreopsis-7	Sects. *Calliopsis*, *Coreopsis* and *Eublepharis*; eastern North America

Sections of genera that are found in multiple clades (i.e., not monophyletic) are indicated in bold. Excluded from this list are monospecific genera.

clades (Fig. 42.1; Kimball and Crawford 2004), all members of sect. *Pseudoagarista* from the two geographical areas occur together in a moderately robust clade (83% bootstrap) with plastid sequences (Mort et al., 2008). However, combining the two data partitions, as with the ITS data alone, places taxa from the two areas in separate clades (Mort et al., 2008). Additional nuclear sequence data from unlinked loci are required to test rigorously the phylogenetic placement of the Mexican and South American elements of sect. *Pseudoagarista*. Furthermore, comparative morphological studies are needed to ascertain whether diagnostic characters for species in each of the geographical areas can be identified.

In addition to *Coreopsis*-5, the remaining moderately supported subclade E (86%) contains *Bidens* (the largest genus in the tribe), *Thelesperma*, and two other elements of *Coreopsis* (Fig. 42.1). Within subclade E there is moderate support (80% bootstrap) for a lineage comprising the aforementioned *Coreopsis* sect. *Pseudoagarista* from South America (*Coreopsis*-5), southern tropical and subtropical *Bidens* (*Bidens*-1) and *Bidens* from Africa (*Bidens*-2; Table 42.2). Mesfin Tadesse et al. (1995a) mentioned similarities between some species of African *Bidens* and those of Mexico and South America, and it was suggested that these similarities are indicative of a close relationship between the two elements. North temperate *Bidens* (*Bidens*-3; Table 42.2) do not occur with the two other groups of *Bidens*, but rather are in a strongly supported clade (99% bootstrap) with north temperate *Coreopsis* (*Coreopsis*-6, -7; Table 42.2) and *Thelesperma* (Fig. 42.1). Mesfin Tadesse et al. (1995a) commented on the differences in fruits between north temperate and other *Bidens*.

All molecular phylogenetic studies (Kim et al. 1999; Kimball and Crawford 2004; Crawford and Mort 2005) indicate that the three sections comprising *Coreopsis*-7 (Table 42.2) constitute a monophyletic group, as does *Thelesperma* (Kimball and Crawford 2004) (Fig. 42.1). However, neither the two sections comprising *Coreopsis*-6 (Table 42.2) nor the north temperate *Bidens* (*Bidens*-3, *Bidens comosa*; Table 42.2) receive strong support, and relationships among the four groups (*Coreopsis*-6, -7, *Bidens*-3, *B. comosa*, and *Thelesperma*) in this clade likewise do not enjoy strong support (Fig. 42.1). This entire group is in need of additional morphological and molecular studies.

Molecular phylogenetic studies have made valuable contributions toward elucidating phylogenetic relationships in Coreopsideae. Arguably, the most important contribution has been the recovery of strongly supported smaller clades, which in some instances correspond to recognized genera (e.g., *Cosmos*, *Dahlia*, and *Thelesperma*; Fig. 42.1; Table 42.1). On the other hand, molecular data have documented that the two largest genera, *Bidens* and *Coreopsis*, are not monophyletic, a result that is not surprising. However, it is noteworthy that many of the recovered clades correspond to geographically-confined sections or groups of sections of *Bidens* and *Coreopsis* (Fig. 42.1; Table 42.2). With rare exceptions, for example the *Chrysanthellum* group (Fig. 42.1), the larger clades do not correspond to prior views of taxonomic relationships (Stuessy 1977a) or to clades recovered by cladistic analyses of morphological characters (Ryding and Bremer 1992; Mesfin Tadesse et al. 2001). Mapping of morphological-anatomical characters onto molecular phylogenies indicates that many of the characters that have been used taxonomically are quite labile (Kimball and Crawford 2004; Mort et al. 2004; Crawford and Mort 2005).

Future molecular phylogenetic studies should have two major foci. One focus is additional taxon sampling. Efforts should be made to obtain sequences from monospecific genera such as *Cyathomone*, *Diodontium*, *Moonia*, and *Trioncinia* that have not yet been sampled. Additional representatives of poorly sampled genera such as *Chrysanthellum*, *Cosmos*, *Glossocardia*, *Heterosperma*, and *Isostigma* should be sequenced to test their monophyly. Also, taxon sampling has been quite limited in Mexican and South American *Bidens*, and additional sequences are needed to resolve relationships in many complex groups and to assess the monophyly of *Bidens*-1 (Fig. 42.1; Table 42.2). Support for larger clades (along the spine) is not high (Fig. 42.1), and additional sequences are to be desired to test whether these are "good" clades (i.e., receive stronger support).

While not proposed here, it is apparent that taxonomic changes are needed to reflect relationships recovered by the molecular phylogenetic studies. Recent analyses show that clades present in ITS topologies (Kimball and Crawford 2004) (Fig. 42.1) are also seen in trees generated from plastid sequences, and resolution and support for clades are often enhanced from analyses of combined ITS-cpDNA datasets (Mort et al. 2004; Crawford and Mort 2005; Mort et al., 2008). While we have hesitated to make taxonomic changes based solely on sequences from one region of one genome (ITS), it is now clear that nuclear and plastid sequences, with several exceptions, each produce trees with similar topologies. A major challenge will be to identify diagnostic characters or unique combinations of characters for the clades recovered with strong support in the molecular phylogenetic studies.

TAXONOMY

Characters and character states useful in the diagnosis of the tribe and the genera are in italics.

Tribe Coreopsideae Turner & Powell (1977). Basionym: Coreopsidinae Less. in Linnaea 5: 153. 1830 – Type: *Coreopsis* L., Sp. Pl. 2: 907. 1753

Includes: *Bidens* L. (ca. 340 species), *Chrysanthellum* Rich. (13 species), *Coreocarpus* Benth. (7 species), *Coreopsis* (ca. 86 species), *Cosmos* Cav. (36 species), *Cyathomone* S.F. Blake (1 species), *Dahlia* Cav. (35 species), *Dicranocarpus* A. Gray (1 species), *Diodontium* F. Muell. (1 species), *Ericentrodea* S.F. Blake & Sherff (6 species), *Fitchia* Hook. f. (6 species), *Glossocardia* Cass. (12 species), *Goldmanella* (Greenm.) Greenm. (1 species), *Henricksonia* B.L. Turner (1 species), *Heterosperma* Cav. (ca. 5–11 species), *Hidalgoa* La Llave & Lex (5 species), *Isostigma* Less. (13 species), *Moonia* Arn. (1 species), *Narvalina* Cass. (1 species), *Oparanthus* Sherff (4 species), *Petrobium* R. Br. (1 species), *Selleophytum* Urban (1 species), *Thelesperma* Less. (15 species), and *Trioncinia* (F. Muell.) Veldk. (1 species).

Herbs, shrubs or rarely small trees or vines, up to 10 m high, glabrous to variously hairy, hairs uniseriate. Leaves opposite or alternate, basal or cauline, simple with entire margins to tripinnatisect, Capitula heterogamous or homogamous, radiate or discoid, solitary to cymose or corymbose, pedunculate. Involucre cylindric to hemispheric, with one-to-many-seriate phyllaries. Outer phyllaries green, linear to ovate, inner phyllaries with *few to many brownish-orange striae* and scarious margins. Receptacle flat to conical, *paleaceous*. Paleae linear to lanceolate, with few *brownish-orange striae*, continuous with inner phyllaries. Ray florets, when present, bright to pale yellow, orange, white, pink, purple, neuter, pistillate and sterile or pistillate and fertile. Disc florets bisexual and fertile or functionally male; corolla yellow, orange or yellow-orange, tubular or "opening by a sinus traversing the ventral side (*Fitchia*), (4–)5-lobed at apex, lobes short triangular, glabrous or with short hairs or papillae, sometimes tinged purple, red or pink; anthers (4–)5, brown or black, rarely yellowish, short tailed at base; style undivided or with short cleft to bifurcate, branches conic with short papillae to penicellate. Achenes *dorsally flattened to columnar*, black, brown, rarely yellowish-brown or reddish-brown, smooth to striated, with or without wings. Pappus of 2–15 smooth, *antrorsely or retrorsely barbed* bristles, or of short awns.

Coreopsideae are primarily centered in North and South America. The genera *Diodontium*, *Glossocardia*, and *Trioncinia* are Australian. *Moonia* is known only from India and Sri Lanka, and it is hypothesized to be derived from either *Dahlia* or *Hidalgoa* by long distance dispersal and isolation (Stuessy 1975). *Bidens* and *Chrysanthellum* have cosmopolitan weedy members.

1. *Bidens* L. (1753), rev. Sherff (1937), Mesfin (1984b, 1993)

Herbs or shrubs. Leaves *opposite, simple to bipinnatisect*. Capitula *heterogamous, radiate, rarely homogamous, discoid*, small to large. Involucre cylindric to hemispheric; phyllaries 2–3-seriate, outer green, linear to oblanceolate, rarely leafy, inner membranous with scarious margins. Paleae membranous. Ray florets *neuter*, rarely *pistillate or pistilloid*, yellow, white, pink or purple, *apex 3-dentate or 3-fid*. Disc florets yellow, *fertile*; corolla *5-lobed, rarely 4-lobed*. Achenes linear-oblong, ellipsoid to oblanceolate, *flat to 3- or 4-angled*, with raised ribs, *wings* present or absent. Pappus of 2–5 *antrorsely or retrorsely* barbed *aristae*, rarely absent.

Distribution: Worldwide, mostly in North and Central America; ca. 340 species.

Habitat: moist forest margins, grassland, wooded grassland, rarely dry bush-land or shrub-land, roadside ditches, margins of cultivations; 1–3600 m (highest record from Ethiopia, lowest from Hawaii).

2. *Chrysanthellum* Rich. (1807), rev. Turner (1988)

Herbs with erect or *prostrate stems*. Leaves *alternate or rosulate*, simple to tripinnatisect. Capitula *heterogamous, radiate*, small. Involucre campanulate; phyllaries 1–3-seriate, rarely absent, linear-lanceolate to ovate with scarious margins. Receptacle flat to convex. Ray florets yellow or orange-yellow, *female, fertile, apex entire or bifid*. Disc florets *dimorphic*, pale yellow to orange-yellow, *rarely white* (outer series), brown or *reddish-brown* (inner series), fertile or *functionally male*; *corolla 4–5-lobed*. Achenes *dimorphic*: ray achenes *thickened*, clavate, epappose, *not winged*, columnar or *curved*; disc achenes, when present, flat, with *thick* or *corky wings*. Pappus *absent* (of ray florets), or of two minute *awns*, or a crown (of disc florets).

Distribution: North America: Mexico (9 endemic species), Central America (2 species), West Indies (1 species), Galápagos Islands (1 endemic species); total of 13 species (Veldkamp and Kreffer 1991).

Habitat: limestone hills, short grassland, "thorn forest", coastal dunes; 0–3500 m.

3. *Coreocarpus* Benth. (1844), rev. Smith (1989)

Herbs or shrubs. Leaves *opposite*, pinnatifid to bipinnatisect. Capitula *heterogamous, radiate*, rarely *homogamous, discoid*, small. Involucre campanulate, 1–2-seriate, monomorphic; outer phyllaries narrowly spathulate or linear, green, inner ovate, or all similar in shape. Receptacle flat. Ray florets yellow (*2-toned in some*, upper half lemon-yellow, lower half golden yellow) or white, *female* and *fertile or neuter, rarely absent*. Disc florets yellow, bisexual, *sometimes functionally male*. Achenes monomorphic, obovate to oblong or spathulate, *winged*, wings thin or *corky and incurved*, entire or *narrowly dissected into oblong to obdeltoid teeth*. Pappus of 1–2 *smooth, antrorsely* or *retrorsely* barbed aristae, or absent.

Distribution: North America (Arizona and Mexico): 7 species (2 species transferred to *Bidens* by Melchert and Turner 1990).

Habitat: rocky slopes in open pine-oak forest, with sparse vegetation, rocky cliffs, shores and canyons, near streams; 5–2200 m.

4. *Coreopsis* L. (1753); rev. Sherff (1937)

Herbs or shrubs. Leaves *opposite* to *alternate*, simple to pinnatisect. Capitula *heterogamous, radiate*. Involucre cylindric to hemispheric; phyllaries 2-seriate, outer green, herbaceous, equal to or shorter than the inner, inner membranous with scarious margins. Receptacle flat to convex. Ray florets *neuter* or *female and sterile or fertile*, pure *yellow* or with median or basal *orange or reddish blotches*. Disc florets fertile, bisexual; corolla yellow, rarely lobes red-brown to purple, (4–)5-lobed. Achenes *oblong to elliptic*, with or without wings, *wings* thin or corky. Pappus of two *nude or antrorsely* barbed aristae, or absent.

Distribution: North and South America, introduced as ornamental garden plants elsewhere; ca. 86 species.

Habitat: glades in deciduous woodland, pine barrens, peaty bogs, swamps, pond margins, floodplains, prairies, coastal bluffs and dunes, secondarily on roadside ditches, disturbed places; 0–4700 m.

5. *Cosmos* Cav. (1791), rev. Sherff (1932, 1955)

Herbs. Leaves *opposite*, simple to pinnatisect. Capitula *heterogamous, radiate*. Involucre subhemispheric; phyllaries 2-seriate, outer green, herbaceous, spreading, linear-lanceolate, inner membranous, pale at margins. Ray florets *neuter, white, yellow, pink, purple to dark red-purple*. Disc florets *fertile*, bisexual, *yellow*. Anther *filaments hairy*. Achenes *dark brown* to *black, linear, fusiform-tetragonal*, tapering into a slender *beak, much elongated in the inner ones, erect or slightly curved, 4-lobed in cross-section*. Pappus of 2–4(–6) *retrorsely barbed* aristae.

Distribution: North, Central and South America; ca. 36 species (Melchert 1968; 59 sp. in IPNI, www.ipni.org).

Habitat: dry, rocky mixed pine-oak woodland, wooded grassland; 2–3300 m.

6. *Cyathomone* S.F. Blake (1923)

Shrub or subshrub with *scandent* branches. Leaves opposite, ternate to biternate, membraneous. Capitula 7–15, cymose, nodding, long-pedunculate. Involucre campanulate, 2-seriate, glabrous. Receptacle convex. Outer phyllaries linear-oblong; inner wider with scarious margins. *Flowers unknown*. Achenes (submature) dorso-ventrally compressed, narrowly obovate, *glabrous, brownish*, widely *winged* with cilia all along the wing margins, contracted at apex. Pappus of *two retrorsely* barbed aristae.

Distribution: Ecuador, 1 species: *C. sodiroi* (Hieron.) S.F. Blake

Habitat: subtropical woods along the Rio Pilaton.

Note: This may not be different from *Ericentrodea* S.F. Blake & Sherff. The constricted achene neck of *E. davidsmithii* H. Rob. (Robinson 1993) (Fig. 42.1D) and that of *C. sodiroi* S.F. Blake (Blake 1923) (Fig. 42.1D) are similar except for number of pappus members. The leaf descriptions of the two "species" are also similar.

7. *Dahlia* Cav. (1791), rev. Sørensen (1969); Saar et al. (2003)

Herbs, subshrubs or *epiphytic* lianas. Roots *tuberous*. Leaves with *stipels*, sometimes *petioles hollow*. Leaves opposite or *whorled*, simple to tripinnate. Capitula *heterogamous, radiate, large*. Involucre hemispheric, 2-seriate; outer phyllaries *fleshy*, green, linear to ovate or obovate, inner membranous, *red, reddish-brown or brown*, margins scarious, ovate. Receptacle flat. Ray florets *neuter* or *female, sterile, white, pink, purple or yellow*. Disc florets *fertile*, yellow or yellow with pink or purple lobes or limbs; corolla 5-lobed. Achenes *gray* or *black*, linear to linear-oblanceolate or spathulate, *flat or 3-angled* (in cross-section), finely striated. Pappus *absent* or of two minute teeth or flexuous *threads*.

Distribution: Mexico, Cental America, northeastern South America; 35 species (Saar et al. 2003).

Habitat: cool cloud forests to sclerophyllous forests, oak-pine woodland, roadsides and margins of fields; 350–3100 m.

8. *Dicranocarpus* A. Gray (1854)

Annual herb. Leaves *opposite, once or twice pinnate* with *linear-filiform* segments. Capitula *heterogamous, radiate*, solitary or few and cymose, small. Involucre cylindric, distinct; outer phyllaries 1 or 2, linear, similar to bracts; inner 3–5, lanceolate with scarious margins. Receptacle convex. Ray florets *female*, ca. 1 mm long, *yellow, fertile*. Disc florets yellow, 3–5, *functionally male*; corolla *5-lobed*. Achenes linear, *yellowish-brown*, ribbed, striated. Pappus of ray achenes 2, large, *widely divergent/spreading to recurved* and *smooth* aristae, almost *perpendicular to body*, those of disc florets often undeveloped.

Distribution: North America (southwestern USA and northern Mexico); 1 species: *D. parviflorus* A. Gray.

Habitat: dry desert, soil alkaline or with gypsum; 900–1700 m.

9. *Diodontium* F. Muell. (1857), rev. Veldkamp and Kreffer (1991); Veldkamp (1992)

Herb with *bushy* habit. Leaves *opposite*, simple, linear or filiform. Capitula *homogamous, discoid*. Involucre (shape not described); phyllaries 2-seriate, outer lanceolate, longer than inner, *inner ca. 2*, ovate, margins not scarious. Ray florets *absent*. Disc florets *bisexual, fertile, yellow*, 3–10; corolla *5-lobed*. Achenes obovoid, *narrowly winged* below, glabrous, *smooth, not ribbed, yellow or yellowish-brown*. Pappus of *two aristae, glabrous* except for barbs at the apex.

Distribution: Australia, Nothern Territory; 1 species.

Habitat: granite and sandstone hills; known from the type, which was collected between Sturt Creek and Victoria River.

Diodontium filifolium F. Muell., distinguished from *Glossocardia* by habit, leaf arrangement, and achene characters.

10. *Ericentrodea* S.F. Blake & Sherff (1923), rev. Robinson (1993)

Herbs or shrubs with *scandent branches* or *vines climbing over shrubs and trees*, clasping *by petioles*. Leaves *opposite*, simple to quadri-ternate, *coriaceous*. Involucre campanulate, *2-seriate*; outer phyllaries herbaceous, linear to oblong, shorter than inner, inner oblong, reddish-yellow. Receptacle flat. Capitula *heterogamous, radiate or homogamous, discoid*. Ray florets, when present, *female and fertile, bright yellow*. Disc florets *bisexual, fertile, pale yellow*; corolla *5-lobed*, up to *18 mm long*. Achenes obovoid, margins *winged*, wings densely fringed with bristles. Pappus of *6–15 retrorsely* barbed aristae, *in two series*.

Distribution: South America (Ecuador, Colombia, Peru); 6 species.

Habitat: forests in river valleys; 2000–3300 m.

11. *Fitchia* Hook. f. (1845), rev. Carlquist (1957)

Shrub or *tree*. Stem with *prop roots*. Leaves *opposite-decussate, simple*, margins entire or serrate (when young), *petioles half to almost the length* of the blade. Capitula *homogamous, discoid*, solitary 2–3 each on *recurved* peduncles. Involucre campanulate, 4–5-seriate; phyllaries *leathery to woody*, large, graded monomorphic, inner with scarious margins. Receptacle flat. Florets *yellow-orange*, all similar; corolla *5-lobed*, sinuses between lobes *a third* (*F. nutans* Hook. f.) *to as deep as the ventral sinus* (*F. tahitensis* Nadeaud). Style *cleft into two tiny branches* at the tip. Achenes flat, winged, *40–45 mm long*, light brown, sparsely bristled in middle. Pappus of two *antrorsely* barbed, *vascularized, bristles* continuous with the wings, often *longer than body of achene*.

Distribution: Polynesia: 6 species, Tahiti (2 species), Raiatea Island (1 species), Mangareva (1 species), Rapa Island (1 species), and Rarotonga Island (1 species); *Fitchia speciosa* Cheesman introduced in Hawaii (O'ahu – Honolulu) and has not spread elsewhere (Wagner et al. 1990).

Habitat: "Island slopes" suggested by Ewan (1958) based on the illustrated prop roots of *F. speciosa* Cheesman in Carlquist (1957); *F. nutans* and *F. tahitensis* "swales above 3,000 feet" (Carlquist 1957: 63).

12. *Glossocardia* Cass. (1817), rev. Veldkamp and Kreffer (1991), Veldkamp (1992)

Herbs. Leaves *alternate or basal*, simple to pinnatisect. Capitula *heterogamous, radiate*. Involucre *irregularly* 1–2-seriate (*number of phyllaries variable*); outer phyllaries *few or absent*, linear to ovate; inner phyllaries lanceolate to ovate, 3–7. Receptacle flat. Ray florets 0–12, *female or sterile*, yellow, white, bluish, pink, reddish, violet, or purple. Disc florets *functionally male or bisexual*; corolla 4- or 5-lobed, white, yellow, lilac or pale purple. Achenes oblong to linear-lanceolate, ribbed, black. Pappus of *two short glabrous aristae* or coroniform.

Distribution: Africa (Chad and Niger, 1 species; Tanzania, 1 introduced species; cf. Mesfin Tadesse 1990), Asia (India to Japan and Taiwan), West Pacific Islands south to Australia; 12 species.

Habitat: grassland, coastland, wooded grassland, stream banks, along margins of plantations; 0–1165 m.

13. *Goldmanella* (Greenm.) Greenm. (1908)

Herb with *scandent branches*. Leaves *alternate, simple, oblique* or *assymetrical* at base, margins sharply serrate. Capitula *heterogamous, radiate*, axillary and *leaf-opposed*, long-pedunculate. Involucre campanulate, *3–4-seriate*; outer phyllaries yellowish with reddish-brown nerves, ovate, inner oblong, margins scarious. Receptacle *conical*. Ray florets *female*, 5–8, white or yellow. Disc florets yellow; corolla 5-lobed. Achenes *reddish-brown*, glabrous with rough surface, prismatic. Pappus of 2–4 short thick *awns*.

Distribution: Mexico, Belize; 1 species: *G. sarmentosa* (Greenm.) Greenm.

Habitat: wet clearings; moist open areas in tropical evergreen forest.

14. *Henricksonia* B.L. Turner (1977)

Subshrub. Leaves *opposite*, ternately parted, segments lanceolate. Capitula *heterogamous, radiate*, solitary. Involucre hemispheric, 2-seriate; outer phyllaries green, linear; inner linear-lanceolate, brownish, scarious at margins. Receptacle flat. Ray florets *female, fertile*, yellow, 8–12. Disc florets bisexual, *fertile*, yellow; corolla 5-lobed. Achenes *dimorphic*: of ray florets dorso-ventrally flattened, broadly *obovate*, winged, apex with *2(–3) short awns*; of disc florets *linear-quadrangular*, ribbed, apex with 4 persistent *paleaceous scales*.

Distribution: Mexico; 1 sp.: *H. mexicana* B.L. Turner.

Habitat: vertical cliffs in dry canyons, ca. 1320 m.

15. *Heterosperma* Cav. (1794, cf. *Index Kewensis*)

Annual herbs. Leaves *opposite*, simple to pinnately compound with elongate linear segments. Capitula *radiate*, solitary or few and cymose. Involucre cylindric, 2-seriate, distinct; outer phyllaries linear to filiform, green, often exceeding involucre, inner membranous and pale yellow or purple, oblong or ovate. Receptacle flat or concave. Ray florets *female, fertile*, pale yellow. Disc florets yellow, *bisexual, fertile*; corolla 5-lobed. Achenes *dimorphic*, of ray florets ellipsoid or obovoid, *winged*, wings corky or pectinate, surfaces tuberculate, glabrous; of disc florets obovoid or tapered and beaked above (innermost the longest, purplish), *not winged*. Pappus *absent* (outermost) or of 2–3 *spreading and retrorsely* barbed *aristae* (inner).

Distribution: Southwest US (Arizona, New Mexico, Texas), Mexico, Central and South America, West Indies (introduced); ca. 5–11 species.

Habitat: stream banks in pine-oak wooded grassland, roadside ditches, open mountain slopes; 650–3200 m.

16. *Hidalgoa* La Llave & Lex. (1824), rev. Sherff and Alexander (1955), Sherff (1966)

Woody climbers, the stems *climbing* using *petioles*. Leaves *opposite, 3-foliolate to palmately 5-parted*, leaflets ovate. Capitula *radiate*, solitary or few, axillary. Involucre *campanulate*; phyllaries 3–4-seriate, distinct, outer linear-lanceolate to oblanceolate, herbaceous, spreading, inner oblong-ovate, thicker. Receptacle flat. Ray florets *female, fertile*, yellow, orange, purple or reddish. Disc florets yellow, *sterile*; corolla *4-lobed*. Achenes of ray floret (immature) flat, oblong, *dark brown*; pappus of two blunt *awns*; of disc florets not seen.

Distribution: North and South America (Mexico, Guatemala, Costa Rica, Panama, Colombia, Ecuador, and Peru); 5 species.

Habitat: Wet mountain forest, cloud forest; 200–1800 m.

17. *Isostigma* Less. (1831), rev. Sherff (1926, 1931); Peter (2004, 2006)

Herbs or subshrubs, stem often a *corm*. Leaves *rosulate* or *alternate*, rarely opposite, simple to pinnatisect with filiform, linear or lanceolate segments. Capitula radiate or discoid, solitary. Involucre campanulate or subglobose, 2–4-seriate; outer phyllaries linear, green; inner ovate, brown with scarious margins. Receptcle flat to convex. Paleae *keeled* at base. Ray florets *female*, yellow, *purple* or *white*. Disc florets *bisexual, perfect*, yellow or purple, corolla 5-lobed. Achenes *graded-monomorphic, lengthening inwards*, linear, flattened, with 1–3 ribs and striate-sulcate in between ribs, narrowly winged, brown or black with yellow apex, base and wings. Pappus of two erect or slightly divergent, short, *smooth or shortly antrorsely barbed aristae*, rarely absent.

Distribution: South America (northeastern and central Argentina, southern Brazil, southeastern and central Bolivia, Paraguay and northwestern Uruguay); 13 species.

Habitat: arid and semi-arid to moist grasslands, subhumid open fields, glades in forests; ca. 400–600 m.

18. *Moonia* Arn. (1836), rev. Stuessy (1975)

Herb (*annual*, fide Karis and Ryding 1994; *shrubby, stems erect*, fide Stuessy 1975). Leaves *opposite*, simple and ovate with broadly dentate margins to pinnately compound with up to five segments. Capitula *radiate*, small. Involucre *campanulate*, 2–3-seriate; outer phyllaries green, *elliptic* to oblanceolate, inner phyllaries narrowly ovate, brownish. Receptacle convex. Ray florets *female, fertile*, yellow. Disc florets yellow, 10–15, *sterile*; corolla *4-lobed, anthers 4*, style *linear, undivided*. Achenes (of ray florets) *black*, obovate, glabrous. Pappus *absent*.

Distribution: India, Sri Lanka (Ceylon); 1 species: *M. heterophylla* Arn.

Habitat: wet montane forests; 1500–2150 m.

19. *Narvalina* Cass. (1825)

Shrub to 2 m. Leaves *opposite, simple, coriaceous*, margins sharply dentate. Capitula radiate, small, corymbose. Invoucre cylindric, irregularly 2–3-seriate; outer phyllaries few, green, leaf-like; inner phyllaries *coriaceous*, light brown with scarious margins, *stiff at post-anthesis*. Receptacle flat. Paleae *coriaceous*. Ray florets *female, fertile*, yellow. Disc florets yellow, *fertile*, 10–15; corolla *5-lobed*. Achenes black, *winged*, monomorphic, *elliptic*, dorso-ventrally flattened, wings white, margins antrorsely barbed. Pappus of *two retrorsely* barbed aristae.

Distribution: Haiti and Dominican Republic; 1 species: *N. domingensis* (Cass.) Less.

Habitat: broad-leaved forest, arid thickets; 350–1300 m.

20. *Oparanthus* Sherff (1937), rev. Stuessy (1977b), Shannon and Wagner (1997)

Shrubs or trees. Leaves *opposite, simple*, ovate, thin to *leathery, margins entire*. Capitula radiate, solitary to cymose. Involucre campanulate, *1–2-seriate*. Receptacle convex. Phyllaries and paleae *coriaceous*. Ray florets *female, fertile*, white, yellow to yellowish-green, 1–2-seriate. Disc florets white or yellow, *sterile or fertile*, ovary filiform with 1–2 narrow awns; *corolla 4-lobed; stigma undivided* or only *slightly bifid* at apex. Achenes (of ray florets) flattened, elliptic to narrowly elliptic, *narrowly winged* on one or both margins, *glabrous*; pappus of 2, *smooth or ciliolate awns*, confluent with wings; of disc florets with 1–2 linear awns.

Distribution: Southeast French Polynesia (4 species): Marquesas Islands (2 species) and Rapa in the Austral (Tubuai) Islands (2 species).

Habitat: mesic to wet humid forests with two species approaching the cloud zone; 50–1200 m.

21. *Petrobium* R. Br. (1817), nom. cons. Nicholson (1997), Brummitt (2000)

Tree, dioecious or *gynodioecious*. Leaves *opposite, simple*, ovate, *membranous*, margins dentate. Capitula *discoid*, corymbose. Involucre (shape not known), 3-seriate; phyllaries and paleae *coriaceous*. Receptacle (shape not known). Florets yellow, *fertile; corolla 4-lobed*. Achenes flat to trigonous, narrow, oblong, *scabrid-hispid*. Pappus of 2–3 stiff aristae.

Distribution: St. Helena (Atlantic Ocean); 1 species: *P. arboreum* (J.R. Forst. & G. Forst.) Spreng.

Habitat: "damp, relict tree-fern thicket or cabbage-tree woodland" (Cronk 2000: 82)

22. *Selleophytum* Urban (1915), rev. Mesfin and Crawford (2006)

Shrub. Leaves *simple, opposite, sessile*, oblong-lanceolate to narrowly ovate, glabrous, *coriaceous*, margins entire or inconspicuously undulate. Capitula solitary or up to three terminating main stem or branches, *radiate*. Involucre campanulate, 2-seriate, *coriaceous*, glabrous, outer phyllaries green; inner orange-red. Receptacle flat. Ray florets *female*, yellow, *fertile*. Disk florets *fertile, yellow or purple*; corolla *5-lobed*. Achenes oblong-linear, gray brown, subquadrangular, not winged, densely short-setose at the margin and near the apex, striate-sulcate on both surfaces. Pappus of two *antrorsely* barbed aristae.

Distribution: Haiti and Dominican Republic; 1 species: *Selleophytum buchii* Urban.

Habitat: open pine forest on limestone cliffs; 800–2550 m.

23. *Thelesperma* Less. (1831)

Herbs (*annual* and perennial) or subshrub. Leaves *opposite*, mostly basal, once to thrice pinnate with linear or filiform segments. Capitula *radiate* or *discoid*, solitary or in loose corymbs. Involucre hemispheric to urceolate; phyllaries distinct, leathery, 2–3-seriate; outer phyllaries linear, green, short, inner phyllaries oblong-ovate, *connate for up to 3/4 of their lengths*. Receptacle flat or convex. Ray florets, when present, *sterile, neuter, yellow, red-brown or bicolored* (yellow and red-brown). Disc florets *fertile, yellow or red-brown*; corolla *5-lobed*. Achenes black or gray (dark red-brown), *smooth or verrucose wrinkled, margins winged*; outer *incurved, dorsally rounded, shorter*, inner *linear-oblong, columnar*. Pappus of two *divergent, white, thick, retrorsely* barbed aristae.

Distribution: North (southern and western US, Mexico) and South America; 15 species.

Habitat: desert scrub, limestone ridges, alpine meadow; 0–3650 m.

24. *Trioncinia* (F. Muell.) Veldk. (1991), rev. Veldkamp and Kreffer (1991); Veldkamp (1992)

Perennial herb with woody *taproot*. Leaves *basal and closely imbricate, alternate*, pinnatifid to bipinnatisect, upper simple. Capitula radiate, few. Involucre (shape not recorded). Receptacle (shape not recorded). Phyllaries 1–3-seriate; outer ovate to ovate-oblong with scarious margins. Paleae flat, lanceolate. Ray florets *female*, sterile, probably yellow. Disc florets probably yellow; *corolla 4-lobed*. Achenes lanceolate, slightly incurved, glabrous, *ribbed, not winged, dark brown or black* with many *transverse ridges*. Pappus of *three retrorsely* barbed aristae.

Distribution: Australia; 1 species: *T. retroflexa* (F. Muell.) Veldk.

Habitat: "basaltic plains" (Veldkamp and Kreffer 1991: 481). The taxon is known from the single type specimen and possibly from one additional specimen from "black soil at Blair Athol" (Veldkamp 1992: 743) in Australia.

ANATOMY

The capitulum, with much emphasis given to the structure of the corolla, is the portion of the plant of Coreopsideae that has been studied in depth anatomically, cf. Koch (1930a, b), Carlquist (1957, 2001), Baagøe (1977), Burtt (1977), Jeffrey (1977), Leppik (1977), and Stebbins (1977). There is very little addition to these works. Mesfin Tadesse (1984b) provided foliar and trichome anatomy and micro-characters of ray floret papillae and anthers for *Bidens*. The occurrence of Kranz anatomy has been reported for the three genera *Chrysanthellum*, *Glossocardia*, and *Isostigma* (Smith and Turner 1975; Turner 1988; Veldkamp and Kreffer 1991; Peter and Katinas 2003).

POLLEN

The pollen in Heliantheae s.l. is uniform and hence there are only few additions to the original studies by Skvarla and Turner (1966), Skvarla et al. (1977) and Thanikaimoni (1977). Pollen morphology for *Bidens*, *Glossocardia* and *Coreopsis* is presented by Mesfin Tadesse (1984, 1990) and Mesfin Tadesse et al. (1995b), respectively. Jose (1993) provided pollen morphology for two species each of *Bidens*, *Coreopsis*, *Cosmos*, *Dahlia* and one species of *Glossocardia*.

CHROMOSOME NUMBERS

Chromosome numbers for genera of Coreopsideae are given in Table 42.1. These numbers are taken from Robinson et al. (1981), Goldblatt and Johnson (2006) and other publications in the series, the *Index to Plant Chromosome Numbers Data Base* of the Missouri Botanical Garden (http://mobot.mobot.org/W3T/Search/ipcn.html) and from the website *Index to Chromosome Numbers in Asteraceae* maintained by K. Watanabe at Kobe University (http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html). As far as we can determine, chromosome counts are lacking for eight of the genera (Table 42.1). All numbers that have been reported are presented unless there is strong reason to believe they are erroneous. As discussed by Semple and Watanabe (Chapter 4), the common ancestor of all Helianthoids was tetraploid, so all Coreopsideae are of polyploid origin. Therefore, in the discussion of numbers, only those taxa with higher numbers that ostensibly result from secondary polyploid events will be designated as polyploids.

Chromosome number evolution within Coreopsideae was inferred using MacClade 4.06 (Maddison and Maddison 2003) and optimizing known numbers on the phylogeny using the default settings (e.g., unordered characters of equal weight) (Fig. 42.1). Certain species within Coreopsideae are known to have multiple base chromosome numbers; these were scored as polymorphic characters and included in the reconstruction. Because terminals were collapsed in the present discussion, we will limit our comments to broad patterns of chromosomal change across the clade; however, future focused studies of chromosomal evolution within lineages could prove informative. The ancestral base number for the tribe is inferred to be $x = 16$, with the ancestral number for the large clade (consisting of clades A, B, and C) inferred as $x = 12$ (Fig. 42.1). The genera *Dahlia* and *Hidalgoa* (counts available for only one species), which are two of the first taxa to diverge in the ITS phylogeny, have several chromosome numbers in common in the range of $n = 16–18$; with the more typical low numbers of $n = 12$ and 13 being absent from these basal groups (Fig. 42.1; Table 42.1). Clearly, there has been a dysploid reduction in *Dicranocarpus* (Fig. 42.1; Table 42.1). Polyploidy occurs in *Dahlia*, and both polyploidy and dysploidy have been associated with evolution and diversification in the genus (Gatt et al. 1998, 2000).

Comparison of chromosome numbers in Table 42.1 with the phylogeny in Fig. 42.1 allows several observations to be made with regard to the evolution of chromosome numbers within the large clade consisting of clades A, B, and C. Assuming that $x = 12$ is the ancestral base number for this clade, the first generalization is that the majority of species have retained this number. Over half of the terminals in clades A and C include taxa with $n = 12$, and in most instances this number is the most common one for taxa represented by these terminals. Within clade C, four of the five *Coreopsis* terminals (*Coreopsis*-4 to -7) are composed entirely or nearly so, of $n = 13$ taxa or polyploids based on that number. Thus, two prevalent patterns seen at the "diploid" level are retention of the ancestral number ($x = 12$) and dysploid increase to $x = 13$, and this is especially true in clade C.

Within clade A, there have been several independent dysploid reductions (*Chrysanthellum*, *Isostigma*, and *Heterosperma*) as well as increase to $x = 14$ in *Coreopsis*-1 from the presumed ancestral $n = 12$ (Fig. 42.1; Table 42.1). The three small genera *Chrysanthellum*, *Isostigma*, and *Heterosperma* could prove most interesting subjects for molecular phylogenetic and chromosome studies, given the different chromosome numbers reported for them. For example, the two species of *Heterosperma* included in molecular phylogenetic studies are not sister species (Fig. 42.1; Kimball and Crawford 2004), and they differ in chromosome number with one $n = 9$ and the other $n = 25$. Thus, both dysploidy and polyploidy are known among taxa that have been included in *Heterosperma* (Table 42.1), and only a combination of phylogenetic and cytogenetic studies will elucidate the evolution of chromosome numbers in the genus. With present data, it is impossible to infer whether the number of $n = 18$ for *Henricksonia mexicana* B.L. Turner is the result of secondary polyploidy, or dysploid increase from $n = 12$ or some lower number.

Available chromosome numbers for Clade B, the island endemics, indicate that they are polyploids (Fig. 42.1; Table 42.1). Because chromosome numbers apparently are not known for the genera *Oparanthus* and *Petrobium*, and only one species of *Fitchia* has been counted (Table 42.1), it is not possible to infer whether all genera evolved from a common polyploid ancestor or polyploidy originated several times. For the two sister genera *Narvalina* and *Selleophytum* in the Caribbean, the former has approximately twice as many chromosomes as the latter (Table 42.1), indicating that an additional polyploid event occurred in *Narvalina* subsequent to divergence from its common ancestor with *Selleophytum*.

As indicated above, most taxa represented by terminals in the large clade C have numbers of $n = 12$ or 13, or are polyploids based on those numbers. Despite the preponderance of these numbers, it is evident from Table 42.1 that a wide array of "diploid" numbers occurs in several genera, especially in the two largest genera *Bidens* and *Coreopsis*. However, since neither genus is monophyletic, it is instructive to examine whether the diversity is a reflection of different numbers between clades or variation within clades. Within *Bidens*, the vast majority of species are $n = 12$ and polyploids based on that number; reports of $n = 10$ and 11, and their polyploid derivatives are quite rare. However, species in the African clade (*Bidens*-2; Table 42.2) are noteworthy because they lack the lower numbers (10, 11, and 12) found in the other two clades of *Bidens*, and instead exhibit a series of higher numbers with $n = 16$, 17, 18, 21, 23, 24, and 36 (Mesfin Tadesse 1984; Mesfin Tadesse and Hedberg 1986). It is not apparent whether the series of numbers (excluding 36, which is polyploid) was generated by both polyploidy and dysploidy, or only by dysploid increase. In *Coreopsis*, only section *Electra* with $x = 14$ has a number not detected in other clades of the genus. The numbers $n = 6$, 7, 8, 9, and 10 are found in the two closely related species *C. nuecensis* A. Heller and *C. nuecensoides* E.B. Smith of section *Coreopsis* (Smith 1974), and the common numbers $n = 12$ and 13 (Smith 1975) occur in several clades. In the relatively large and apparently monophyletic genera, *Cosmos* and *Thelesperma*, both dysploidy and polyploidy have been associated with evolution and diversification (Table 42.1).

The variety of chromosome numbers that have been reported indicates that much could be learned about chromosomal evolution from a detailed analysis of Coreopsideae. Molecular phylogenetic analyses of many of the clades, combined with the extensive knowledge of chromosome numbers, would provide refined insights into the evolution of chromosome numbers at smaller taxonomic scales. Such studies could be valuable in elucidating common and contrasting patterns of chromosome evolution in different lineages. In addition, there are small genera such as *Isostigma* where the few counts available reveal different numbers (Table 42.1), and suggest that additional counts together with phylogenetic studies could prove interesting with regard to understanding chromosome number evolution. Also, one third of the genera have no reported chromosome counts, and efforts should be made to obtain the counts. For example, no counts are available for *Ericentrodea*, which is sister to all other ingroup taxa, and knowing the number for this genus would be valuable for reconstructing the evolution of chromosome numbers.

CHEMISTRY

The most characteristic chemical feature of Coreopsideae is the accumulation of flavonoid compounds known as anthochlors, which include both chalcones and aurones. These pigments are important in imparting the yellow color to floral tissues. The most extensive review of anthochlors in Coreopsideae and in Asteraceae as a whole is given by Bohm and Stuessy (2001). While anthochlors are not restricted to Coreopsideae, it is the only group of Asteraceae where they are present in a very high percentage of genera now placed in the tribe (Robinson 1981). Bohm and Stuessy (2001) provide a comprehensive discussion and synthesis of the use of anthochlors and other flavonoid compounds at various taxomonic levels in Coreopsideae.

The use of DNA sequence data for phylogenetic reconstruction has largely replaced earlier attempts to infer phylogeny from the distribution of secondary compounds in plants, including members of Coreopsideae (e.g., Stuessy and Crawford 1983). It would be of interest to map the distribution of structural variation of secondary compounds, flavonoids and otherwise, onto phylogenies generated from DNA sequence data. The major impediment to such a study is finding a group where both a phylogeny and adequate chemical data are available. In Coreopsideae, these two conditions are met for *Dahlia*, where the extensive flavonoid data of Giannasi (1975) could be mapped onto the phylogeny of Saar et al. (2003).

ECONOMIC USES

Bidens

The genus *Bidens* is commonly noted for its weedy habit and for the relative ease in the dispersal of some of the species owing to the nature of the sticky fruits. A few species have also been noted to be of some economic importance: *B. aurea*, both disc and ray florets are bright yellow and keep on producing flowers until late autumn "Bees love them"; Dijk 1997; *B. cernua* (nodding stick-tight, bur-marigold), the fruits (achenes) have been reported as damaging gill arches and bringing about severe fungal infection to young salmon (Allison 1967, cited in Voss 1996: 382); *B. frondosa* (beggar-ticks, stick-tight), used in herbal therapy to prevent the "irritation, inflammation, pain, and bleeding of the urinary tract mucosa", to treat "benign prostatic hypertrophy" and to "increase excretion of uric acid, decreasing the risk of gout attacks"(M. Moore 1993, cited in Strother and Weedon 2006: 212); *B. prestinaria* (Adey Abeba), a native of North East Africa, is the symbol of the beginning of the new year in Ethiopia and bouquets of this as well as related species, obtained from their natural growing sites, are presented to families and friends as gifts. The species has also been reported to be used medicinally in abetting blood clotting in southeastern Ethiopia and also as an insecticide; Mesfin Tadesse 1984); *B. pilosa* L. (blackjack, stick-tight) with its large white flowers, is being considered as an important source of nectar for butterflies in Levy County, Florida (Robert Dirig, pers. comm.).

The following species of *Bidens* have been grown in well-drained soils in Mexico and Arizona in the USA from late spring to early fall: *B. aequisquamea* (Fernald) Sherff, disc florets yellow, ray florets red to purple or purplish-pink, the flower heads open up successively; *B. ferulifolia* (Jacq.) DC. (golden goddess), both disc and ray florets are yellow and the flower heads open up successively; *B. triplinervia* H.B.K., both disc and ray florets are bright yellow.

The following species of *Bidens* are noted for their weediness: *B. pilosa* (worldwide, apparently a very recent introduction to North America, north of Mexico, absent from many floras and manuals, e.g., Gleason and Cronquist 1991) and recently recorded from only some states (cf. Strother and Weedon 2006); *B. biternata* (Lour.) Merr. & Sherff (Africa and Asia), and *B. bipinnata* L. (Spanish needles; Asia, southern Africa, Europe and North and South America).

Coreopsis

Members of this genus grow well in any public or residential garden and bloom in summer and fall. The following species are known from cultivation: *C. auriculata* L. (lobed tickseed), disc and ray flowers yellow; *C. basalis* (Dietr.) S.F. Blake, disc flowers yellow, ray flowers yellow with basal red-brown blotch; *C. bigelovii* (A. Gray) H.M. Hall, both disc and ray florets yellow; usually cultivated in southern California (as *C. stillmanii* (A. Gray) S.F. Blake); *C. californica* (Nutt.) H. Sharsm., both disc and ray florets yellow; cultivated in southern Arizona, southern California and northern Baja California (as *C. douglasii* (DC.) H.M. Hall); *C. grandiflora* Hogg in Sweet (big-flowered tickseed), both disc and ray florets yellow, widespread in warm tropics, the name often misapplied for large-headed *C. lanceolata* L.; *C. lanceolata* (long-stalk tickseed), both disc and ray florets yellow, widespread also in Europe and Africa, cultivar "Grandiflora" is applied to large-headed specimens or mistakenly to *C. grandiflora*; *C. tinctoria* Nutt. (golden tickseed, plains tickseed), the most commonly cultivated annual species, disc flowers are dark red, purple, brown-purple, reddish, ray flowers are yellow with brown-purple base or entirely yellow, brown or purple-red, cultivar "Nana" are low compact annuals; *C. verticillata* L. (thread-leaf tickseed), disc and ray florets yellow; very distinctive in its narrowly cut leaves.

Cosmos

This genus has a few species in cultivation throughout the world: *C. atrosanguineus* (Hook.) A. Voss in Vilmorin (black cosmos, chocolate cosmos), ray florets are dark maroon with chocolate scent, leaves are few-lobed and tinged pale purple; *C. bipinnatus* Cav. (common cosmos, Mexican cosmos), leaves are feathery, ray florets are white, pink or crimson, cultivars with multiple series of ray florets and florets with strips of colors have been produced from this species; *C. sulphureus* Cav. (yellow or orange cosmos), the yellow or orange ray florets and the wider leaves set this apart from the previous species.

Dahlia

This is one of the most important garden ornamental plants that is selected for its large, showy ray florets and green lustrous leaves. Sørensen (1969) and Foulis et al. (2001) state that probably two or three species, including *D. coccinea* Cav. and *D. pinnata* Cav., are the sources of the thousands of the named cultivars and hybrids. Dwarf hybrids of *D. pinnata* are "forced for Easter and Mother's Day" (Graf 1974). The hybrids are grouped into ten different groups (Foulis et al. 2001) or twelve (Bailey and Bailey 1976) on the basis of the size, number, and shape of the ray florets making up the flower head. Important species include: *D. coccinea* (common or garden dahlia), described by Sørensen (1969: 405) as the most complex species of the genus, is widely cultivated, disc florets are yellow or scarlet at the apices, ray florets lemon-yellow, orange, scarlet, sometimes variegated yellow and orange; *D. pinnata* (common or garden dahlia), the disc flowers are yellow, sometimes with light purple veins, and the ray florets are pale purple or lavender-purple, often with a basal rosy or yellow spot; *D. imperialis* Roezl (tree or candelabra dahlia), disc flowers are yellow, ray flowers are lavender-pink, large solitary capitula, ray florets in one series and the thick bamboo-like stems are distinctive of this species.

The following species are planted along highway or roadside slopes: *Thelesperma simplicifolium* A. Gray in California (Strother 2006: 201); *Cosmos bipinnatus* (Kiger 2006: 204; MesfinTadesse, pers. obs. in Ohio)

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Chapter **43**

Eupatorieae

Harold Robinson, Edward Schilling and José L. Panero

INTRODUCTION

The majority of the taxonomic history of the non-radiate, non-yellow-flowered Eupatorieae (Figs. 43.1–43.3) has depended on broad generic concepts such as those in Bentham (1873), Hoffmann (1890–1894), and B.L. Robinson (1913). Some rather well-defined genera were recognized such as *Brickellia* Elliot, *Mikania* Willd. and *Stevia* Cav., but the core of the tribe consisted of a broad concept of *Eupatorium* L. and many artificial segregates based on variations in pappus and anther appendages. Redefinition of the core group into reasonably phyletic units was the aim of studies by King and Robinson summarized in the treatment of 1987.

PHYLOGENY

The present study takes the biosystematic, phenetic study of Eupatorieae by King and Robinson (1987), based on morphology, anatomy, cytology, and secondary metabolite chemistry, and compares it with preliminary results of DNA sequencing, a method not available for the 1987 study. The DNA sequence results presented here are derived mostly from the work of Schilling et al. (1999), Schmidt and Schilling (2000), and Ito et al. (2000a, b). Two phyletic trees are presented here, one an extract from the big tree made available for the Barcelona Symposium, and a second tree derived through the efforts of Dr. Funk and Dr. Chan including additional generic data available from GenBank. Some problems in the latter effort arise from different sites that have been examined by different workers: Ito et al. (2000a, b) use nrDNA ITS regions and cpDNA RFLP, Schmidt and Schilling (2000) use nuclear ITS sequence data, and Schilling et al. (1999) use chloroplast DNA restriction site data. Though genera sampled are limited, some generalizations on phylogeny can be made.

As seen in the Eupatorian part of Helianthodae in the Big Tree (Fig. 43.4), Eupatorieae are not the most plesiomorphic group in the Helianthian relationship (supertribe Helianthodae) as suggested in King and Robinson (1987). Structurally, the tribe could already be seen as highly derived in its enlarged stylar appendages and its tendency for reduced and hollow apical anther appendages.

The genera of Eupatorieae come out as a natural group among the various elements of the supertribe Helianthodae, nested within groups that have been traditionally treated as Helenieae (Bentham 1873; Hoffmann 1890–1894). On the basis of structure, particularly hairs on the style base, closest relatives outside of the tribe would be *Arnica* L., *Chaenactis* DC., and *Chamaechaenactis* Rydb. of Chaenactidinae (Robinson 1981). Closest relative on the basis of secondary metabolite chemistry could be *Arnica* L., which shares the presence of pyrrolizidine alkaloids with Eupatorieae (C. Jeffrey, oral statement at Kew Symposium, 1994). The most closely related group to Eupatorieae according to DNA sequencing, based on ITS regions, is Peritylinae (Fig. 43.4). Structurally the two groups are not close. The most plesiomorphic elements of Eupatorieae, Hofmeisteriinae and Oaxacaniinae, already show highly subimbricated, graduated involucres, no ray florets, lack of yellow pigmented corollas, 5-merous florets, and

Fig. 43.1. Eupatorieae: Disynaphiinae and Adenostemmatinae. **A** *Disynaphia calyculata* (Hook. & Arn.) R.M. King & H. Rob., Uruguay; **B** *Acanthostyles buniifolius* (Hook. & Arn.) R.M. King & H. Rob., Uruguay; note style appendages; **C** *Grazielia brevipetiolata* R.M. King & H. Rob., Uruguay; **D** *Gymnocoronis spilanthoides* (D. Don.) DC., Argentina. [Photographs and plate preparation, J.M Bonifacino.]

well-developed style appendages, differing from the few subequal involucral bracts, presence of rays, commonly yellow pigmented corollas, 4-merous florets, and unexpanded style appendages in Peritylinae.

Within Eupatorieae, the overall sequence of subtribes in King and Robinson (1987), and the implied phylogeny prove completely inverted on the basis of DNA sequence data. In the 1987 work, the wide-spread $x = 10$ was regarded as basic to the tribe, and the genera with higher numbers were considered derived. According to the DNA sequence data (Schilling et al. 1999), the large element of the tribe with stabilized chromosome base numbers of $x = 10$ is apparently derived. It is the groups with higher basic chromosome numbers that are more plesiomorphic,

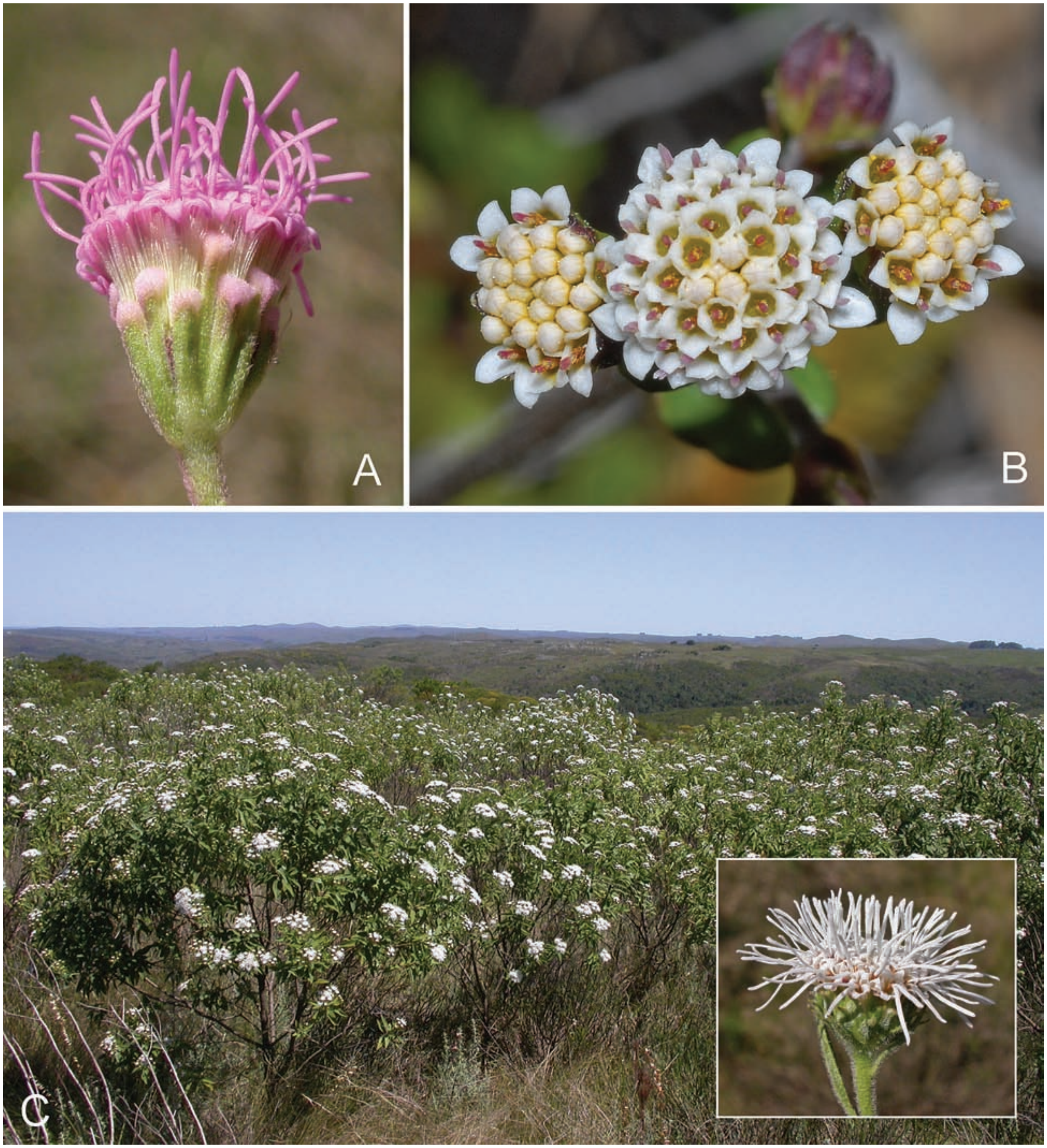

Fig. 43.2. Eupatorieae: Gyptidinae and Ageratinae. **A** *Gyptis pinnatifida* Cass., Uruguay; **B** *Iltisia repens* S.F. Blake, Costa Rica, note 4-lobed corollas; **C** *Radlkoferotoma cistifolia* (Less.) Kuntze, Uruguay. [Photographs and plate preparation, J.M. Bonifacino.]

Fig. 43.3. Eupatorieae: Eupatoriinae and Ageratinae. **A** *Eupatorium hyssopifolium* L.; **B** *Conoclinium coelestinum* (L.) DC., eastern United States. [Photographs, E.E. Schilling; plate preparation, J.M. Bonifacino.]

a situation seen also in several genera of Heliantheae and Helenieae (Robinson et al. 1981). The polyploid origin of the tribe is confirmed by Ito et al. (2000b).

DNA studies have provided some additional results. Schilling et al. (1999) have shown that *Eupatorium* must be interpreted much more narrowly than the traditional view (Benth. 1873). DNA studies by Schmidt and Schilling (2000) and Ito et al. (2000a) provide more concentrated surveys of *Eupatorium* in the strict sense with its closest relatives.

The intent of the King and Robinson (1987) study was to stabilize generic concepts, and generic concepts have not been altered by DNA data presently available. This is in spite of the fact that some generic elements are, and were then, seen as slightly paraphyletic. Definability of concepts is not sacrificed here to minor concerns about paraphylesis. Excessively paraphyletic elements, those defined only by what they are *not*, rather than by what they *are*, have been rejected.

SUBTRIBAL CLASSIFICATION

The major taxonomic changes in Eupatorieae that can be anticipated from DNA data involve the sequence of the subtribes. There are also some evident alterations in the limits of the subtribes, as might be expected where limits tend to depend on one character or even lack of specialized characters. In contrast to the sequence given in King and Robinson (1987) beginning with Adenostemmatinae and Eupatoriinae, the subtribes are treated below in the order suggested by the available DNA (Figs. 43.5–43.10). Subtribes without known DNA sequences are included in the sequence on the basis of structural or cytological data.

Oaxacaniinae. — $x = 18$. Two genera, *Oaxacania* B.L. Rob. & Greenm. and *Carterothamnus* R.M. King & H. Rob. No DNA reports are available, but proximity to Hofmeisteriinae seems certain. Both groups are primarily Mexican. The most significant difference from Hofmeisteriinae is the paleaceous receptacles of the present group.

Hofmeisteriinae. — (Fig. 43.6). $x = 17?, 18, 19$. The subtribe is basal in Eupatorieae among the groups for which DNA has been sequenced. The epaleaceous receptacles, the pseudowhorled leaves subtending the peduncles, and the sometimes shortened apical appendages of the anthers are distinctive. The pollen of the subtribe is the most nearly smooth of any in Eupatorieae (King and Robinson 1966).

Neomirandeinae. — (Fig. 43.6). $x = 17, 20, 24, 25$. DNA sequence data place the subtribe in a cluster that includes Oxylobinae and Trichocoroninae. Higher chromosome numbers in the group seem to be plesiomorphic. Previous assumptions of close relation to Critoniinae seem incorrect based on data from *Critonia*. Relation to the subtribe Hebecliniinae remains in question, since DNA sequence data are not available for the latter. The most obvious difference between Neomirandeinae and Hebecliniinae is the specialization for epiphytism and highly organic soils in the former and the presence of

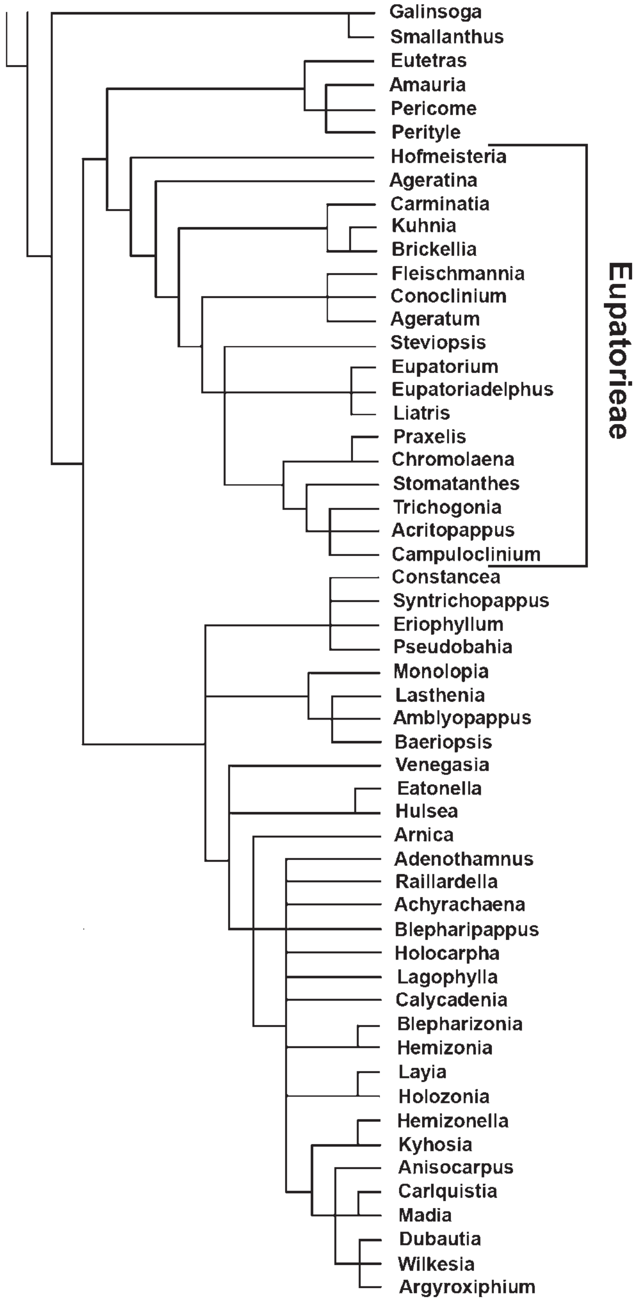

Fig. 43.4. Segment of "Big Tree" showing Eupatorieae (*Hofmeisteria–Campuloclinium*) as a well-defined group within the supertribe Helianthodea. Position of Eupatorieae shown as closest to Peritylinae within various elements of the old tribe Helenieae. Tree derived from ITS data in GenBank.

both $x = 10$ and $x = 16$ chromosome base numbers in the latter. Receptacles and inner surfaces of the corollas in Neomirandeinae are often pubescent as in some Hebecliniinae and a few Critoniinae.

The subtribe is credited with one genus, but two clear subgroups can be seen. Typical *Neomirandea* includes both the epiphytic *N. araliifolia* (Less.) R.M. King & H. Rob. and its close relatives with the habit of a Strangler Fig, plus the terrestrial forms. The strictly epiphytic *Neomirandea eximia* (B.L. Rob.) R.M. King & H. Rob. and its relatives are distinct, having no hairs on the receptacle or on the inner corolla surfaces and no enlarged style bases.

Trichocoroninae. — (Fig. 43.6). $x =$ ca. 15. In this group of three genera, *Trichocoronis* A. Gray, *Sclerolepis* Cass., and *Shinnersia* R.M. King & H. Rob., DNA sequences are only published for *Sclerolepis* (Ito et al. 2000b). The group is notable for its aquatic and semi-aquatic nature and rather distinctive chromosome number. Structurally, the subtribe might seem a reduced close relative of Ageratinae, but sequence data indicate that relationship is remote. Distribution is in Mexico and the eastern United States.

Oxylobinae. — (Fig. 43.6). $x = 16$, 17, ca. 40. DNA has been sequenced for the largest genus, *Ageratina* Spach, with well over 200 species (Robinson 2006b). From limited DNA results, the subtribe is in a group with Neomirandeinae and Trichocoroninae. The group appears variously coequal with or basal to Mikaniinae. In the latter case it appears basal to the rest of the tribe above Hofmeisteriinae. This reinforces the conclusion

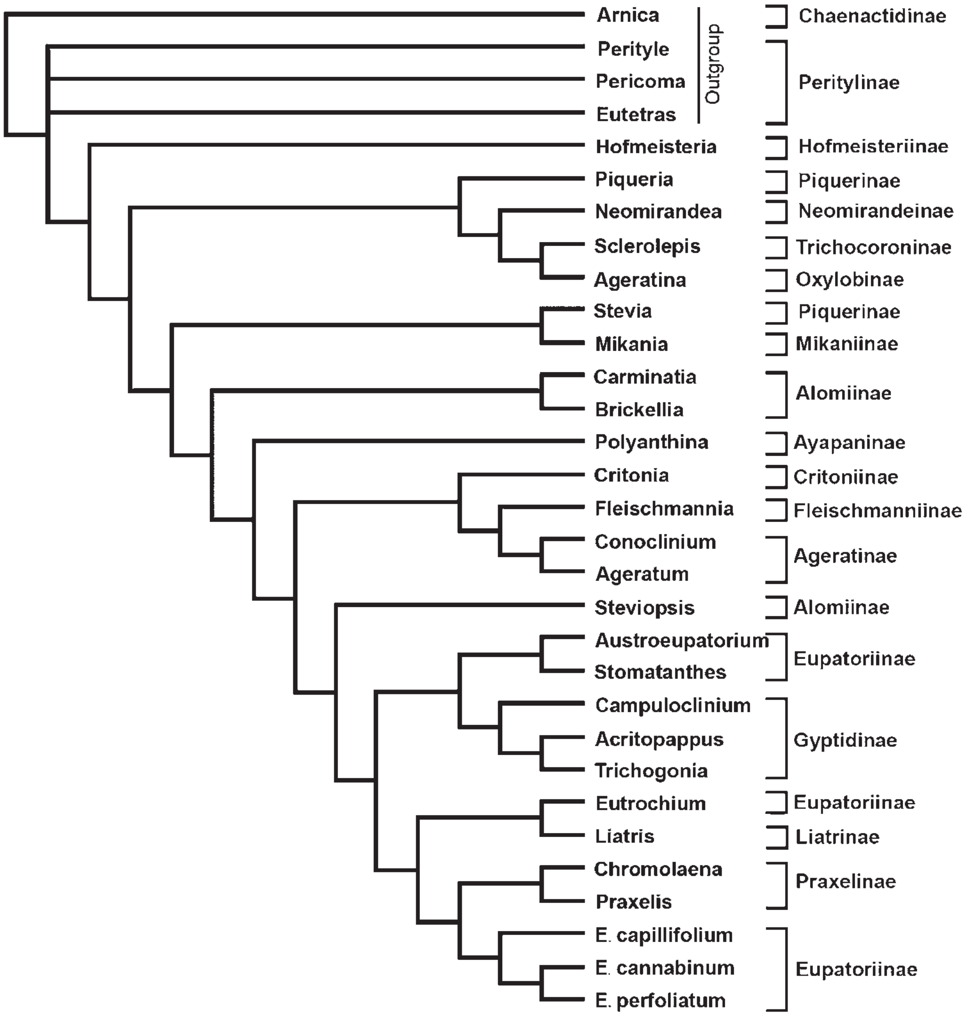

Fig. 43.5. Phyletic tree of the tribe Eupatorieae with selected outgroups based on ITS data from GenBank with additional genera intercolated on the basis of their positions in the cpDNA RFLP results of Ito et al. (2000b). Tree prepared by V.A. Funk and R. Chan. Excluded here, but included in the text, members of the subtribes Adenostemmatinae, Disynaphiinae, Hebecliniinae, and Oaxacaniinae, for which no DNA data are available. A biogeographic tree of Compositae can be found in Chapter 44.

that higher chromosome numbers are plesiomorphic in Eupatorieae. There is no particular close resemblance between Mikaniinae and Oxylobinae except their higher chromosome numbers and great number of species. Oxylobinae more closely resemble the members of the tribe that follow Mikaniinae in this sequence. The group is geographically concentrated in the western parts of North and South America with a few intrusions into eastern North America and the West Indies. A number of the species seem to be apomicts, speciating like *Taraxacum* Weber in F.H. Wigg. and *Hieracium* L. in Cichorieae.

Piqueriinae. — (Fig. 43.7). *Stevia/Piqueria* group. $x = 11, 12, 13$. DNA sequences place the group among the basal subtribes of Eupatorieae, and the chromosome numbers fall outside of the stabilized $x = 10$ that is widespread in the remainder of the tribe. Some features are the often reduced number of 3–5 florets and involucral bracts that equal each other in number, and the totally reduced or obovate and irregularly-margined apical appendages of the anthers. In the most complete DNA sequence results used here, *Piqueria* Cav. and *Stevia* Cav. are separated, the former closer to *Ageratina* Spach and the latter closer

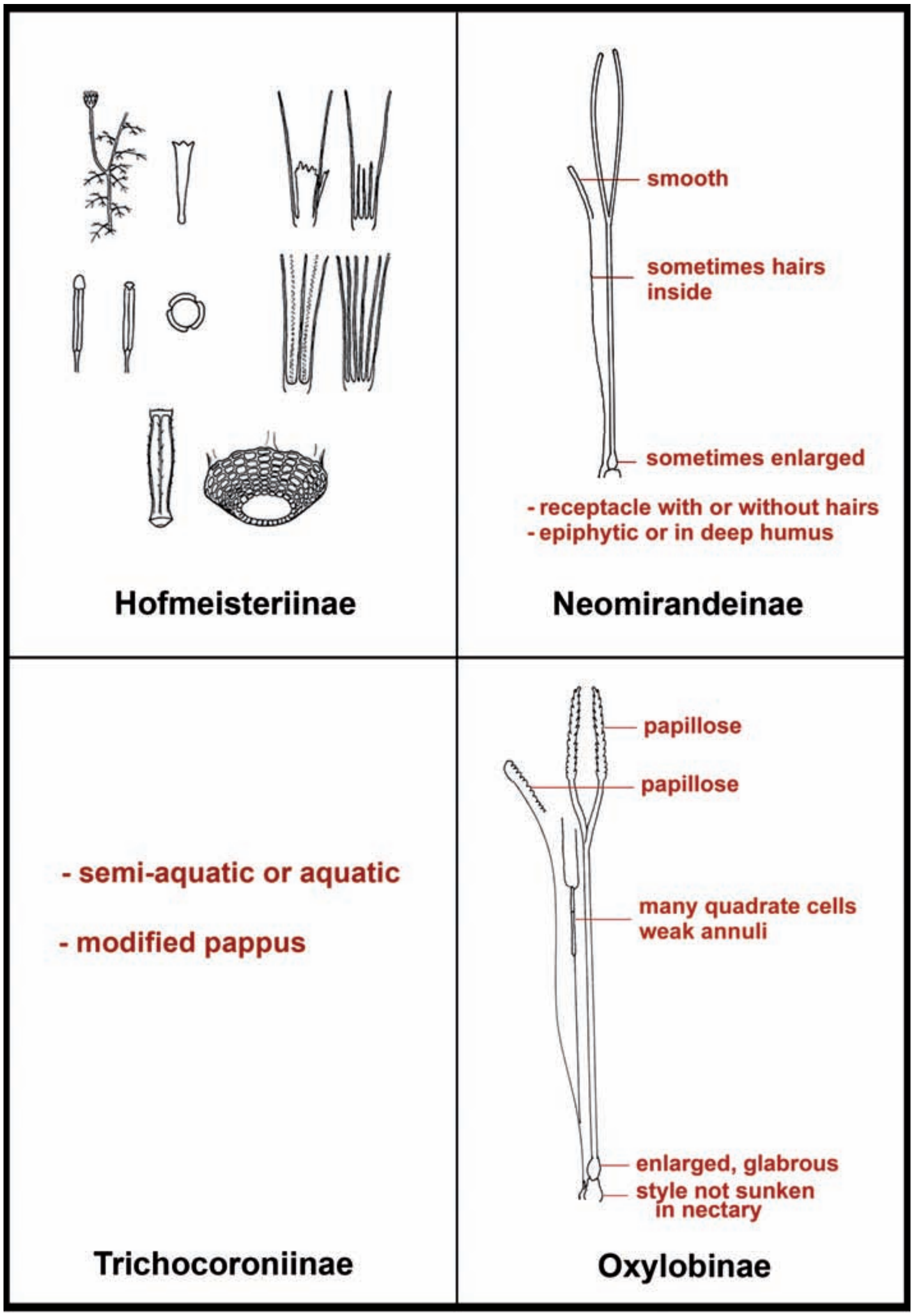

Fig. 43.6. Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Hofmeisteriinae, Neomirandeinae, Trichocoroninae, Oxylobinae.

to *Mikania* Willd. Nevertheless, structure suggests that *Piqueria* and *Stevia* are closely related to each other, and more complete DNA results are expected to confirm that. Existing data using different sites, is not regarded as sufficient basis for contrary conclusions. Probably closely related are *Microspermum* Lag. and *Iltisia* S.F. Blake that have more florets in the heads. They also have a chromosome number of $x = 12$.

These genera were placed by King and Robinson (1987) in the subtribe Ageratinae with *Ageratum* L. on the basis of the usually papillose corolla lobes, modified apical anther appendages, modified or absent pappus, and mostly non-Brazilian distribution. The present more restricted group is mostly Mexican and Central American with *Stevia* extending northward into the United States and southward into South America. A number of species of *Stevia* consist of both apomictic and non-apomictic populations (King and Robinson 1967). Some species of *Stevia* and most of the *Microspermum* group have zygomorphic peripheral corollas.

Mikaniinae. — (Fig. 43.7). $x = 16, 17, 18, 19, 20$. DNA sequences place the subtribe variously basal to everything

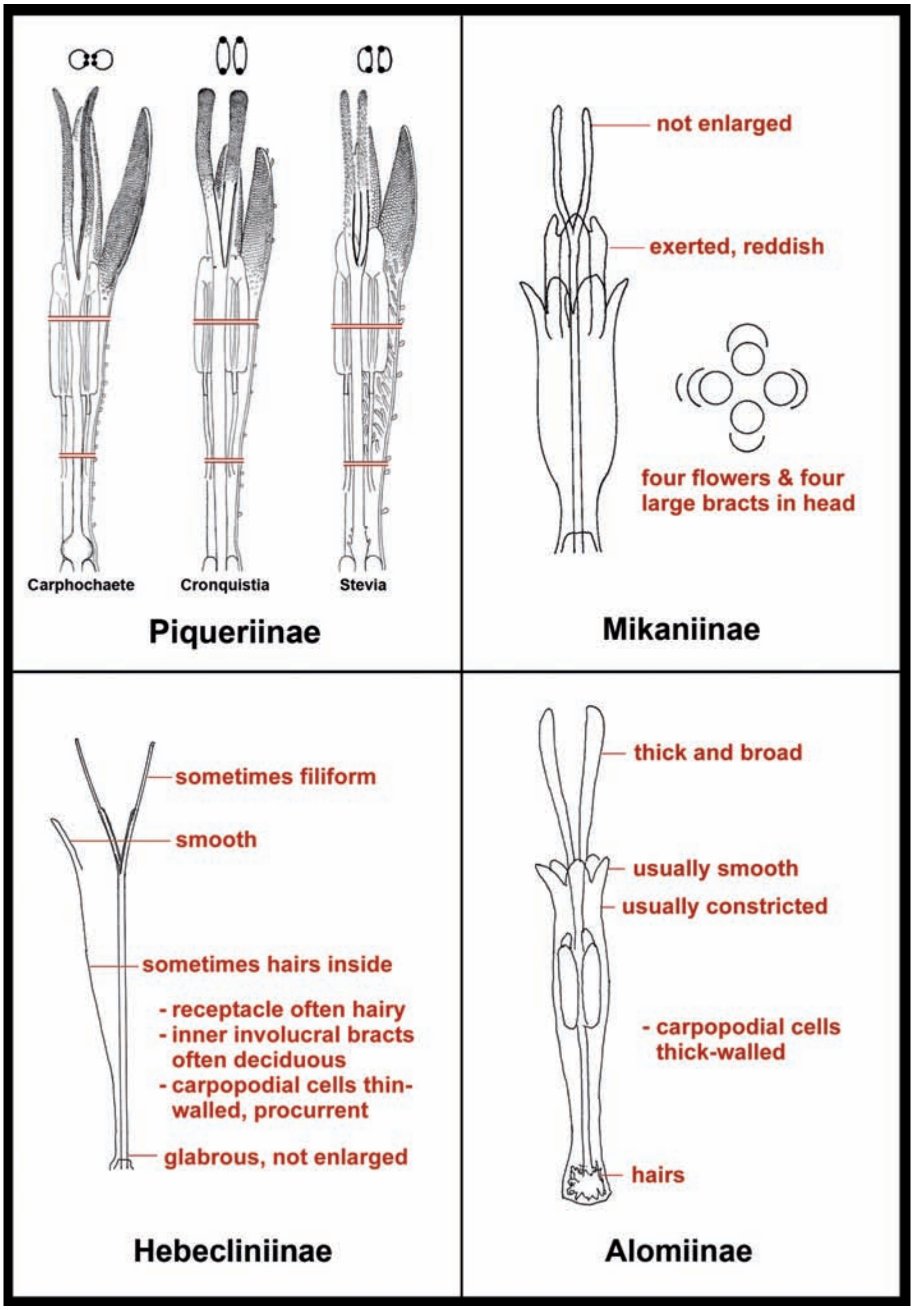

Fig. 43.7. Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Piqueriinae, Mikaniinae, Hebecliniinae, Alomiinae.

in the tribe above Hofmeisteriinae or basal to everything above the Oxylobinae/Neomirandeinae/Trichocoroninae group. The high chromosome number, the distinctive heads with four involucral bracts and four florets, exserted stamens, and an often pubescent style shaft of the single genus suggest a comparatively isolated position. *Mikania* Willd., with ca. 450 species, can be easily recognized, and does not seem closely related to any other. Species of *Litothamnus* R.M. King & H. Rob., in maritime Brazil, and a few species of *Ophryosporus* Meyen, with short apical anther appendages and usually broadened style tips, are only superficially similar to *Mikania*, but without close relationship. The distribution of the genus is throughout the moist temperate and tropical parts of America with one element that is pantropical. Most, but not all of the species are vines, and they occur frequently in forested areas such as the Amazon basin where other Eupatorieae are rare.

If further analysis of the DNA data corroborate present reports, and Mikaniinae and Piqueriinae are close, it would mean that the genera with number of involucral bracts characteristically equaling the number of florets are all rather closely related.

Hebecliniinae. — (Fig. 43.7). $x = 10$, 16. No DNA sequences are available, and the position assigned here is in serious doubt. Relationship was considered close to Critoniinae by King and Robinson (1987). Specializations include the usually domed receptacle, often with many prominent hairs, procurrent carpopodial extensions on the lower ribs of the achenes, very deciduous inner bracts of the involucres, and sometimes extremely filiform appendages of the style branches. The $x = 10$ chromosome numbers in the subtribe suggest a more Critoniine relation, and, if so, the $x = 16$ chromosome numbers of the more typical genera may be derived within the subtribe. The genera are concentrated in Central America with extensions into South America. One genus, *Guayania* R.M. King & H. Rob., is concentrated in the Guayana Highlands.

Alomiinae. — (Fig. 43.7). $x = 9$, 10. The three elements for which DNA has been sequenced, *Brickellia* Elliot, nom. cons., *Kuhnia* L. (which is part of *Brickellia*), and *Carminatia* Mocino ex DC. were all treated as members of Alomiinae in King and Robinson (1987). Included are representatives of *Brickellia* and its relatives with upwardly constricted corollas, style branches expanded in both width and thickness, flattened outer surfaces of the pappus bristles, and densely pubescent style bases, and *Carminatia* with less constricted corollas, narrow style branches, scarcely flattened outer surfaces of the pappus bristles, and glabrous style bases. Plumose pappus bristles have evolved twice in the subtribe, in the *Kuhnia* element of *Brickellia* and in *Carminatia*. A unique form of papillosity is found on the corolla lobes and style appendages in one genus, *Phanerostylus* (A. Gray) R.M. King & H. Rob. On the basis of structure, this mostly western North American and Mexican subtribe has many relatives in the eastern parts of South America and a few relatives in the Andes, the southernmost being *Helogyne* Nutt., but the latter relationships need confirmation from DNA analysis.

DNA indicates that at least one genus, *Steviopsis* R.M. King & H. Rob., placed in Alomiinae by King and Robinson (1987), is of questionable position in that subtribe. In the "Big Tree" based on ITS sampling of a more limited selection of genera (Fig. 43.4), *Steviopsis* is separated from Alomiinae with an intervening Fleischmanniinae/Ageratinae clade. In the more complete phylogeny using ITS and information from cpDNA (Fig. 43.5), *Steviopsis* falls directly between Alomiinae and closely related Ayapaninae in a clinal series. The Fleischmanniinae/Ageratinae clade and other subtribes are further derived in the same cline. The latter phylogeny, placing Alomiinae, *Steviopsis* and Ayapaninae next to each other, seems closer to the truth, but structure would suggest that the three would be together on a side-clade, not in a cline leading to other subtribes. For structural evidence see below under Ayapaninae.

Ayapaninae. — (Fig. 43.8). $x = 10$. Available DNA sequences place the subtribe somewhat apart from Alomiinae. However, the persistent subimbricate bracts of the involucre, the cells of the corolla lobes not differentiated from those of the throat, the thick cell walls of the carpopodium, the usually enlarged pubescent base of the style, and the sometimes both broadened and thickened branches of the style indicate Alomiinae and Ayapaninae are very close. Carpopodia of Ayapaninae are sometimes very specialized in having a very enlarged basal row of cells. The subtribe is mostly South American with extensions north into Central America as far as Mexico. A few members are very small ephemerals, similar in size and habit to some of the better known small, annuals or short-lived perennial genera in the *Ageratum* group, but the latter tend to have differentiated and often papillose cells in the corolla lobes.

Adenostemmatinae. — (Fig. 43.8). $x = 10$. No DNA sequences are available, and no structural feature shows particularly close resemblance to other members of the tribe. The placement here is based on the chromosome number, the $x = 10$ that is essentially consistent for the remainder of the tribe. Distinctive features are the uniquely unsclerified interstices of the receptacle, which allows for changes of shape during maturation, and the pappus in the form of glanduliferous and often sticky knobs in two of the three genera, *Adenostemma* J.R. & G. Forster, and *Sciadocephala* Mattf. The presumed effective distribution mechanism of the sticky knobs has resulted in a pantropical distribution for *Adenostemma*.

Critoniinae. — (Fig. 43.8). $x = 10$. Available DNA results place *Critonia* P. Br. basal to the *Fleischmannia/Ageratum* branch of the tribe. As delimited by King and

Robinson (1987), the subtribe Critoniinae is a large, mostly Central American, West Indian, and northern South American group. Structure is of limited help since the group mostly lacks specializations such as cells of the corolla lobes shaped differently from those of the throat, ornate anther collars, or pubescence on the style, and few have highly reduced anther appendages. The cells of the carpopodia tend to have thick walls and the inner bracts of the involucre are often deciduous. As such, the subtribe may be highly artificial. It is *Critonia* for which the DNA data are available, and the subtribe is listed here on that basis. Other genera that have been placed in the subtribe may or may not be closely related, sharing a lack of specialized characteristics, and having a generally tropical aspect. Some of the features used to define the subtribe in King and Robinson (1987) are those shared by members of Neomirandeinae, Hebecliniinae, and Praxelinae, to which some of the genera may prove to be related.

Fleischmanniinae. — (Fig. 43.8). $x = 4$, 10. DNA sequences place this almost monogeneric subtribe close to *Ageratum* L. to which it bears no particularly close resemblance. It is difficult to see close relationship for

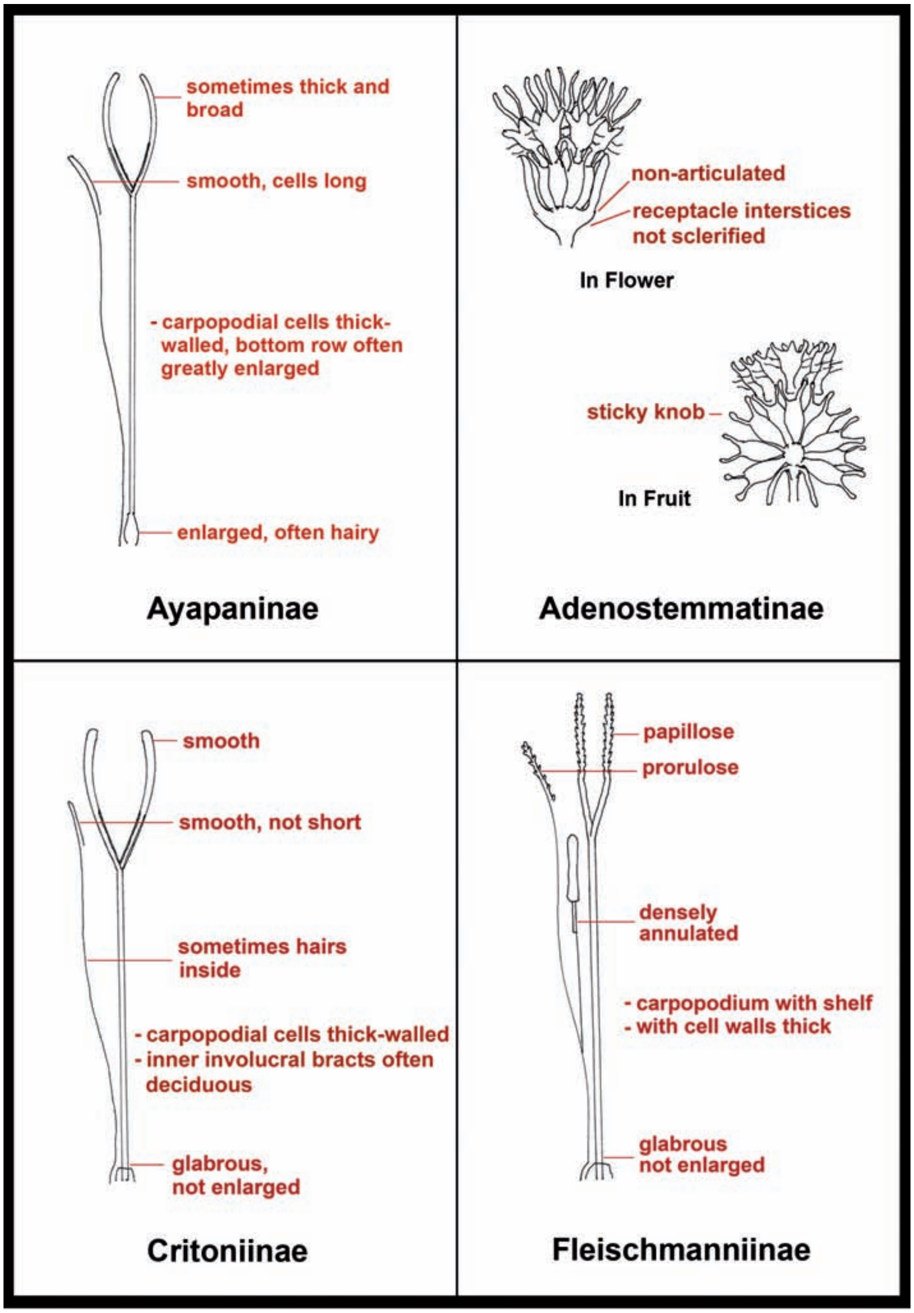

Fig. 43.8. Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Ayapaninae, Adenostemmatinae, Critoniinae, Fleischmanniinae.

Fleischmanniinae with thick-walled cells in the carpopodia to *Ageratum* and *Conoclinium* DC. and their closest relatives, which have thin-walled cells in their carpopodia. There may be some superficial resemblance between the genera in the field, since many *Fleischmannia* specimens have been labeled in the field as *Ageratum*. Distinctions of Fleischmanninae include the uniquely prorulose cells of both surfaces of the corolla lobes, the slender anther collars with cell walls obscured by annular thickenings, and carpopodia with projecting upper rims in addition to their thick-walled cells. The style shafts are simple and glabrous except in the monotypic *Sartorina* R.M. King & H. Rob. The pappus is capillary, usually with many bristles, sometimes with only five or ten. The $n = 4$ chromosome number in *Fleischmannia microstemon* Cass. (Baker 1967) is the result of dysploidy. The subtribe is primarily Mexican and Andean in South America, the Mexican part of the distribution overlapping closely with that of most species of *Ageratum*.

Ageratinae. — (Fig. 43.9). $x = 10, 15$. DNA sequences link the mostly Mexican *Ageratum* L. with the North American and Mexican *Conoclinium* DC., both with conical receptacles. Conical receptacles are also found in such genera as *Barrosoa* R.M. King & H. Rob., *Dasycondylus* R.M. King & H. Rob., and *Campuloclinium* DC. placed in Gyptidinae by King and Robinson (1987). DNA is available for *Campuloclinium*, which shows it is remote from Ageratinae. *Ageratum* is known mostly from highly weedy *A. conyzoides* L. and the widely planted *A. houstonianum* Mill., which have a pappus of five awns, but most of the species have no pappus or a coroniform pappus. The genus is concentrated in Mexico and Central America. *Conoclinium* of the United States and Mexico was placed in Gyptidinae by King and Robinson (1987). It differs from *Ageratum* by its pappus of numerous capillary bristles. The similarity between *Ageratum* and *Conoclinium* in their ITS DNA sequences includes both the alignments of nucleotides that are present and an almost identical large gap where nucleotides are missing.

Structural evidence seems to conflict with the DNA evidence for both the distance of Ageratinae from Gyptidinae and the closeness to Fleischmanninae.

A close relative of *Ageratum* is *Phania* DC. of the West Indies, which has pappus squamae with sinuous cell walls. Some other South American genera placed in the subtribe by King and Robinson (1987) such as *Phalacraea* DC. are probably related. It remains to be seen whether *Piqueriopsis* R.M. King, *Ferreyrella* S.F. Blake, *Guevaria* R.M. King & H. Rob., and *Ellenbergia* Cuatrec., among various small, mostly rather ephemeral Eupatorieae, that usually have many-flowered heads, should be retained in Ageratinae or placed elsewhere.

Excluded here are Piqueriinae (*Stevia*/*Piqueria* group (see above) on the basis of the higher chromosome numbers and the reduced number of florets in the heads with matching numbers of florets and involucral bracts. Ageratinae have carpopodia with thin or beaded cell walls, sometimes reduced anther appendages, and anther collars with annular thickenings. The thickenings of the anther collars are not as dense as in Fleischmanniinae and do not obscure the cellular structure.

Gyptidinae. — (Fig. 43.9). $x = 10$. The tribe is notable for a variety of habits, from large shrubs such as *Litothamnus* R.M. King & H. Rob., and *Bahianthus* R.M. King & H. Rob. to rosulate herbs such as *Bishopiella* R.M. King & H. Rob. Limits of the subtribe seem to be in need of revision. DNA sequences show close relationship between *Trichogonia* (DC.) Gardn. and *Campuloclinium* DC., which have been placed in the subtribe by King and Robinson (1987), but DNA also puts into the group two genera from other subtribes, *Acritopappus* R.M. King & H. Rob. from Ageratinae with a reduced pappus, and *Stomatanthes* from Eupatoriinae. The latter adds to the genera already known in the subtribe with hairs on the base or shaft of the style. All four sequenced genera are concentrated in Brazil, and relationship to each other is easily acceptable. Excluded according to DNA is the North American and Mexican *Conoclinium*, discussed above under Ageratinae.

Gyptidinae are notable for the differentiated cells of the corolla lobes, the usually thin-walled cells of the carpopodium, and the usually large number of florets in the heads. Trends within the diverse subtribe include many genera with stipitate bases on the achenes and another series of genera with closely spirally inserted alternate leaves. Two genera reaching the Andes are *Neocuatrecasia* R.M. King & H. Rob. of Bolivia and Peru, which is most certainly a member of the subtribe, and *Lourteigia* R.M. King & H. Rob. of Colombia and Venezuela, which has a unique deep constriction in the callus under the pappus that causes the pappus and callus to come off as a unit. This is not the kind of dehiscence from the achenial body that is characteristic of *Symphyopappus* Turcz. in Disynaphiinae. Sequencing of *Lourteigia* would be particularly helpful.

Disynaphiinae. — (Fig. 43.9). $x = 10$. No DNA sequences are available. The placement here is based on some possibly superficial resemblance to Eupatoriinae. The two subtribes share a tendency toward reduced numbers of florets in the heads, undifferentiated cells in the corolla lobes, and thin-walled cells in the carpopodium when the carpopodium is not vestigial. In Disynaphiinae, the floret number is five in all but one species (Robinson 2006a). Disynaphiinae differ from Eupatoriinae by being basically woody, having simple and glabrous style shafts, and having pitting of the phytomelanin in the achene walls in regular transverse rows. The leaves of *Disynaphia* Hook. & Arn. are spirally inserted, whereas most other genera have opposite leaves. The leaves of *Campovassouria*

R.M. King & H. Rob. are alternate or opposite. The unity of the members of Disynaphiinae is not considered to be in question. All but one species have a well-developed capillary pappus and persistent involucral bracts. The group is almost entirely Brazilian with a few species reaching as far as Peru.

Liatrinae. — (Fig. 43.9). $x = 10$. DNA sequencing places this almost exclusively eastern United States group of genera close to Eupatoriinae. Both subtribes are strongly North American, but do not seem particularly close on the basis of structure. Liatrinae have glabrous style bases and at least the young leaves are in a rosette. The spiciform cymes of most species of *Liatris* Gaertn. ex Schreb. seem unique in Asteraceae.

Praxelinae. — (Fig. 43.10). $x = 10$, 20, polyploids. DNA confirms close relationship between *Chromolaena* DC. and *Praxelis* Cass. The sequences also place the subtribe close to the subtribe Gyptidinae. The most notable character is the totally deciduous involucre, usually leaving a bare receptacle after anthesis. Characteristically the bracts do not spread as they mature or dry, they dehisce. The subtribe extends mostly from the Gulf Coast of the United States south to Argentina, but the concentration of genera and species is in Brazil the same as Gyptidinae.

Members of the subtribe include the extremely weedy *Chromolaena odorata* (L.) R.M. King & H. Rob. and potential weeds such as *Praxelis clematidea* R.M. King & H. Rob. The most exceptional member of the subtribe is

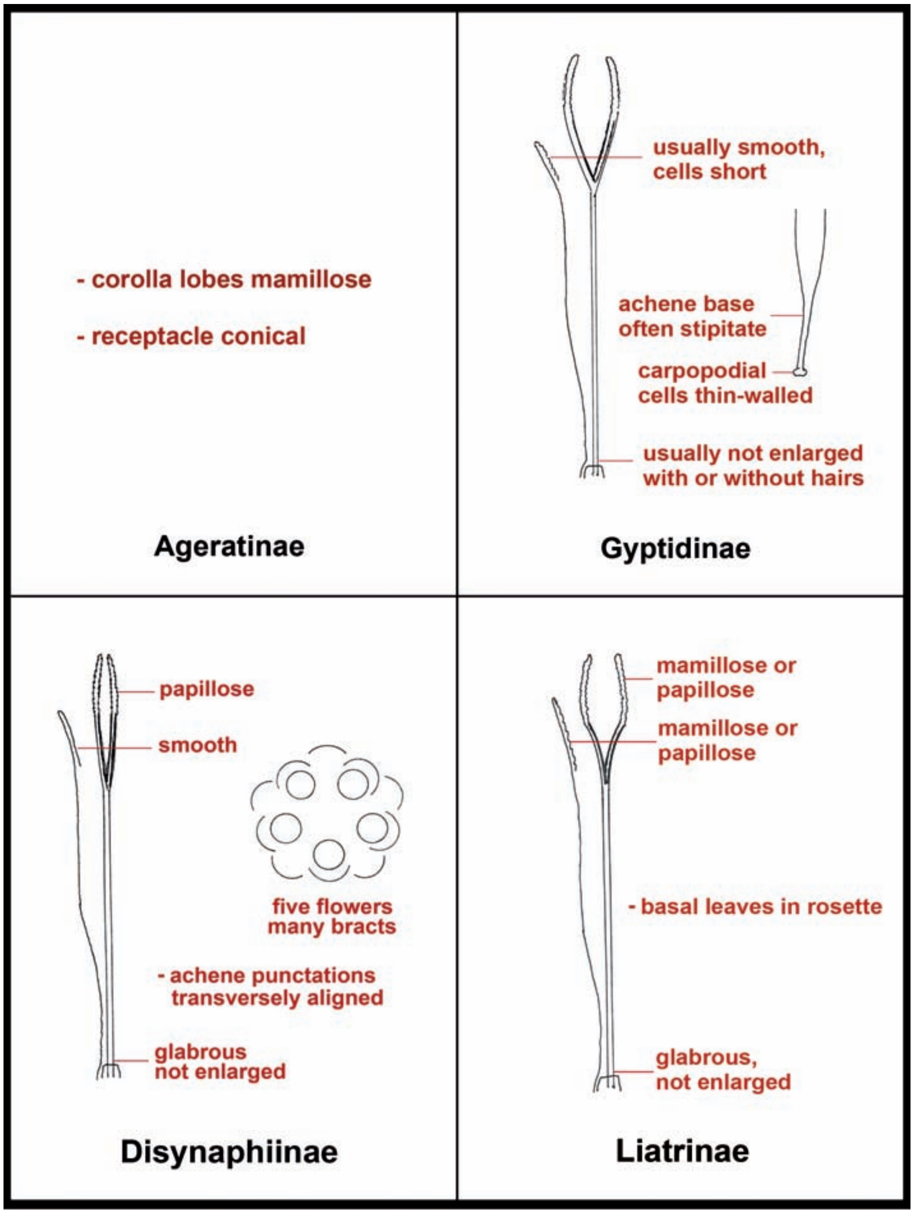

Fig. 43.9. Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in the text: Ageratinae, Gyptidinae, Disynaphiinae, Liatrinae.

Praxeliopsis G.M. Barroso, which was seemingly rare and occurring sparsely, but apparently occurs instead in large turfs as seen in Bolivian collections. It has the anthers mounted at the mouth of the zygomorphic corollas, and the style base is unique in the subtribe by being enlarged. Polyploidy and apomixis seem common in the subtribe, the best example being *Praxelis capillaris* (DC.) Sch.Bip.

The subtribe contains the only genera in the tribe with tangentially spreading style branches, most notably *Praxelis* Cass., *Eitenia* R.M. King & H. Rob. and *Eupatoriopsis* Hieron. (Robinson 1984). Corollas of the subtribe also sometimes have prominent colored resin ducts along the veins of the throat.

In the West Indies are found members of Eupatorieae that show unquestionable traits of Praxelinae combined with unquestionable traits of *Koanophyllon* Arruda de Camara of Critoniinae. This apparent intersubtribal hybridization seems to have produced many healthy offspring and should be examined more carefully (King & Robinson 1987, example *Osmiopsis* R.M. King & H. Rob.).

Eupatoriinae. — (Fig. 43.10). $x = 10$. This is one of the most completely studied subtribes of the tribe Eupatorieae, distributed as it is mostly in the north temperate zone. DNA sequences are available for *Eupatorium* L. and the subgroup of *Eupatorium* that has been known as *Eupatoriadelphus* R.M. King & H. Rob. or *Eutrochium* Raf. The genera have a north temperate distribution concentrated in North America.

The structurally related *Austroeupatorium* R.M. King & H. Rob. is mostly South American and a weedy introduction to the paleotropics. The bases of the styles are characteristically hairy, and relationship with the northern Eupatoriinae seems close on the basis of structure. On the basis of nuclear DNA sequences, Ito et al. (2000a) place the genus closer to *Eupatorium* than *Fleischmannia* or *Chromolaena*, but outside of the *Eupatorium*/*Eupatorium* sect. *Traganthes*/*Eutrochium* group. The present reworked tree based on GenBank data places *Austroeupatorium* even more remote, within Gyptidinae with *Stomatanthes*.

One of the genera placed here by King and Robinson (1987), *Stomatanthes* R.M. King & H. Rob. of eastern South America and sub-Saharan Africa, has been placed by DNA sequencing in Gyptidinae, which is also mostly eastern South American. The most notable distinguishing features of the latter were the densely setuliferous achenes and the usually enlarged tips of the style branches, and such placement is not unreasonable. It remains to be seen where *Hatschbachiella* R.M. King & H. Rob. will fall, since it, too, is eastern South American and has setulae on the achenes.

EVOLUTION

Hybridization seems to occur in a number of elements of Asteraceae. At the species level, as an obvious example, hybridization is seen in the Helianthean genus *Encelia* Adans. (Funk 1985), where its extent may be underestimated. Hybridization at higher levels may be rare, but could have marked effects, as in Coreopsideae (Panero 2007). On the basis of structural study, intersubtribal

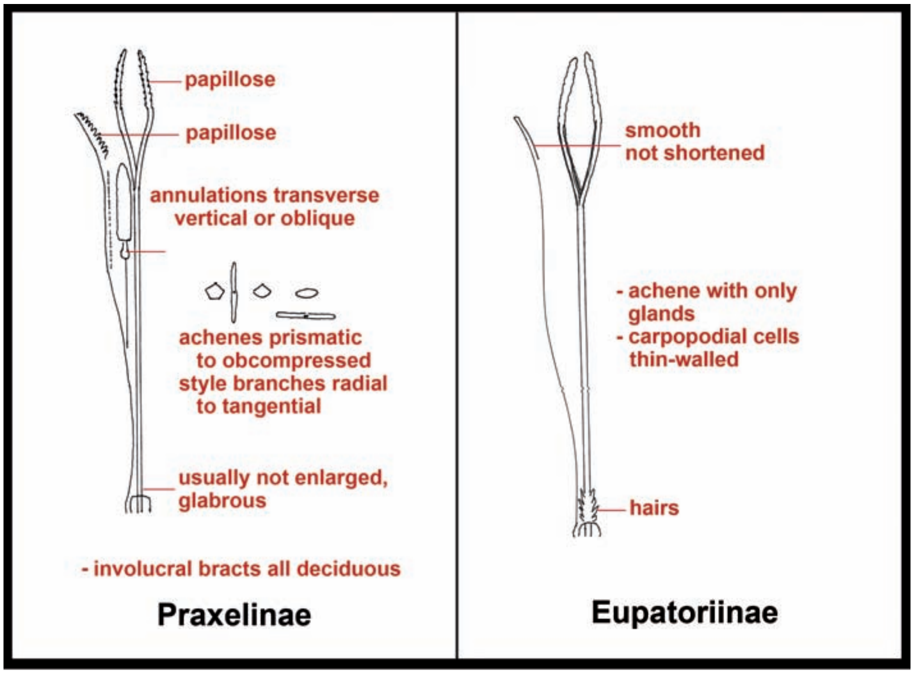

Fig. 43.10. Simplified analyses of the subtribes of Eupatorieae in the order in which they appear in text: Praxelinae, Eupatoriinae.

hybridization is particularly evident in Eupatorieae between Praxelinae and elements that have been placed by King and Robinson (1987) in Critoniinae. Notably, the areas of likely intersubtribal hybridization in Eupatorieae are between subtribes having a chromosome base of $x = 10$. These are also now seen to be the more recently evolved members of the tribe. Many of the more isolated and sharply defined genera of the tribe are ones with higher or lower chromosome base numbers. Previously, such higher numbers might have been considered a primary isolating mechanism for these latter genera, but the phylogeny based on DNA sequences might mean that these genera and subtribes are more isolated and resistant to hybridization primarily because of their greater evolutionary distance from each other.

CONCLUSION

Further DNA sequences in Eupatorian genera will fill in many gaps. Sequences of Adenostemmatinae, *Critonia* P. Browne, *Hebeclinium* DC., and Disynaphiinae are particularly desirable. Positions of many individual genera from some of the more crudely circumscribed groups will also be helpful, for example *Ferreyrella* S.F. Blake, *Guevaria* R.M. King & H. Rob., *Radlkoferotoma* Kuntze, and *Scherya* R.M. King & H. Rob., the latter having some aspects of both Gyptidinae and Ageratinae. Nevertheless, it seems unlikely that further changes as great as those shown above will be necessary. It is very reassuring that none of the changes suggested by known DNA sequences alter any of the groups circumscribed with certainty in King and Robinson (1987) having unique and well-defined characters.

The primary problem seen in the present study is the conflict between the sharp delimitation of the internally strongly cohesive Eupatorieae on the basis of non-DNA characters versus the DNA evidence of a position buried amidst a series of structurally very different and unlikely subtribes or tribes of the supertribe Helianthodae.

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Section IV

Conclusion

Chapter 44

Compositae metatrees: the next generation

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INTRODUCTION

Constructing a large combined tree of Compositae, a 'metatree' (also called 'meta-supertree' by Funk and Specht 2007 and 'megatree' by R. Ree, pers. comm.) allows one to examine the overall phylogenetic and biogeographic patterns of the family. The first modern attempts to understand the family were by the authors in Heywood et al. (1977) plus the paper by Cronquist (1977), which was initially intended to be in the Heywood publication. Literature prior to 1977 has been discussed in detail in other chapters (for the early literature, see Chapter 1). In Cronquist's 1977 paper he reaffirmed his agreement with Bentham's 13-tribe classification of the family and the concept that Heliantheae s.l. were the primitive members (Cronquist 1955; Bentham 1973a, b). Cronquist (1977) pointed out that the Heywood et al. volumes listed the tribes mostly in the order of Bentham 1873a rather than beginning with Heliantheae, which Bentham thought was most primitive (Bentham 1873b). The papers in the 1977 volumes did accept some changes such as the recognition of Liabeae and the conclusion that Helenieae were not a 'good' group, both more or less accepted by Cronquist in 1977. However, most proposed changes such as the new tribe Coreopsideae, etc. were not accepted by the synantherological community.

Cronquist (1977) believed that the primitive characters of the family were as follows (slightly modified): shrubby; leaves opposite; inflorescence cymose; heads few, each with many florets; involucre leafy, several-seriate; receptacle chaffy; ray florets present and fertile; disk florets perfect and fertile; lobes of the disk corollas with well developed mid-vein; pappus chaffy, of five members; and anthers connate, not tailed. Cronquist stated that the presence of ray florets may have predated the origin of Compositae, so that even discoid tribes might have had a radiate ancestry.

The acceptance of the modified Bentham system was not universal. There were at least two papers in the Heywood et al. volumes (Jeffrey 1977; Skvarla 1977) and two individuals who published elsewhere (Carlquist 1966, 1976; Robinson 1981) who had reservations about the concept of "13 tribes rooted in the Heliantheae". All of these dissenting authors observed that the data they were generating did not support all of the above-listed characteristics as primitive in the family. However, for the most part, the synantherological community continued to use the Bentham classification.

Not too long after 1977, opinions began to change with the advent of cladistic methodology and molecular data. Jansen and Bremer and their collaborators (Bremer 1987, 1992, 1994; Jansen and Palmer 1987, 1988; Hansen 1991a, b; Jansen et al. 1991a, b; Bremer and Jansen 1992; Jansen and Kim 1996; Bremer and Gustafsson 1997) reordered Compositae by placing Barnadesiinae as the sister group of the family and placing Heliantheae (including Eupatorieae) highly nested in the phylogeny of the family.

Bremer's cladistic analysis (1994) was the first revision of the whole family based on morphology since Bentham, and he recognized many of the problem areas in the cladograms of the family and tribes, but the morphology did not generate enough data to resolve many of the issues. Over ten years later Kadereit and Jeffrey (2007) reordered the genera, tribes, and subfamilies within the family based on morphology and molecular results, and this work is now the standard reference for descriptions of the tribes and genera of the family.

This chapter seeks to link the most recent molecular trees together in a metatree framework (Funk and Specht 2007) and to use that tree to provide a basis for understanding the systematics, evolution, and biogeography of the family.

MATERIALS AND METHODS

Construction of the metatree

The metatree for Compositae was developed using a compilation of trees. The name metatree was adopted for this type of tree because it is a "tree of trees", one that is based on a fixed 'base tree' topology (Funk and Specht 2007). This type of tree has also been called a meta-supertree or megatree (R. Ree, pers. comm.), and some authors refer to it as a supertree. It is, however, neither a tree produced by a combined analysis of coded cladograms obtained from individual datasets (classic 'supertrees') nor is it the result of analyzing a dataset in which data from multiple datasets have been combined ('supermatrix' trees). There has been some discussion on the pros and cons of the 'supertree' and 'supermatrix' methods (Steel et al. 2000; Gatesy et al. 2002; Bininda-Emonds et al. 2003), and both methods are compared with the metatree approach by Funk and Specht (2007). The metatree for this analysis was constructed in the following manner:

1. A 'base tree' was formed from the phylogeny of Panero and Funk (2008) with a few alterations. The most important change was the addition of taxa from the Heliantheae Alliance. The Heliantheae Alliance section of the Panero and Funk tree (which had only a few taxa) was replaced with the branching pattern of the Heliantheae Alliance from Baldwin (Baldwin et al. 2002; Chapter 41). Also, some refinements were made using the work of Ortiz (Chapters 18 and 19) and Ortiz et al. (Chapter 17) for Carduoideae, and Funk and Chan (Chapter 23) for Cichorioideae. The base tree was reduced to a matrix using Brooks Parsimony Analysis (BPA; Brooks 1982; Brooks and McLennan 2002), wherein any branching diagram can be reduced to a series of zeros and ones in a data matrix. We used MacClade to generate the data matrix (Maddison and Maddison 2001). The data matrix was run in a tree program (PAUP 4.0b10; Swofford 2002) to check for errors. All trees have been "ladderized to the right" for consistency, although anyone familiar with cladistics will understand that the tree can be "rotated" at any node. This feature is amply demonstrated by comparing the rooted tree (Fig. 44.1) and the unrooted tree (Fig. 44.2).
2. The most recent (and available) tree for each clade (see below) was reduced to a matrix (as above) and these matrices were added to the original matrix. Each time a new clade tree was added, the overall analysis was re-run to insure an accurate replication of the newly added tree, as well as to confirm that the addition did not result in topological changes elsewhere in the metatree. It should be noted that when a phylogeny for a tribe contained many taxa from the same area in a monophyletic group or a grade, these were often pruned to decrease the size of the tree without subtracting any biogeographical information. For instance, the phylogeny of Gnaphalieae contained a clade of 58 terminal taxa all endemic to Australia; this clade was reduced to 25 taxa.
3. A summary tree (Fig. 44.1) was produced in which each major clade was reduced to a single branch. This tree also shows the phylogenetic position of critically placed taxa and is displayed as an unrooted tree in Fig. 44.2.

See the section on optimization for an explanation of the biogeographic areas and how they were assigned.

Sources of the trees

General references for this study were Bremer (1994), Heywood (1993), Heywood et al., (1977), Hind (1996), and Kadereit and Jeffrey (2007). Below, the origin of each phylogeny on the metatree is discussed.

Outgroups

Lundberg (Chapter 10) examined the relationships among the families now contained in Asterales, including Compositae. His work indicated that Calyceraceae were the sister group of Compositae (1st outgroup) and that Goodeniaceae (2nd outgroup) were the sister group of the Calyceraceae + Compositae clade. The next most closely related family is Menyanthaceae, and it is followed by a clade containing Stylidiaceae, Alseuosmiaceae, Phellinaceae, and Argophyllaceae. The distribution of these eight families (Fig. 44.1) shows that the Compositae + Calyceraceae clade is nested in a grade of Australasian taxa (Australia, New Guinea, New Caledonia, and New Zealand). Each of these families is discussed below (listed in reverse order of relatedness to Compositae).

Argophyllaceae. — Two genera with ca. twenty species that are distributed on Australia, Lord Howe Island, New Caledonia, New Zealand, and Rapa Island.

Phellinaceae. — One genus with eleven species, all of which are found on New Caledonia.

Alseuosmiaceae. — Five genera and ten species all located on Australia, New Caledonia, New Guinea, and New Zealand.

Stylidiaceae. — Six genera with 245 species found in Australia and New Zealand with a few species in East Asia and South America.

Menyanthaceae. — Five genera with sixty species having an almost cosmopolitan distribution; however, four of the five genera are found in Australia, and because the closely related taxa are found in the Australia–New Zealand–New Guinea–New Caledonia area, this family is treated as having an Australasian distribution at its base.

Goodeniaceae. — The second outgroup of Compositae is a moderate-sized family of herbs and some shrubs: Goodeniaceae (fourteen genera, over 400 species). The family is largely confined to Australia, particularly western Australia, with only a few species extending elsewhere, mostly in the Pacific area (Gustafsson et al. 1996, 1997). A recent study (Howarth et al. 2003) has shown that the base of the phylogeny of Goodeniaceae is in Australia with dispersals by members of *Scaevola* into the Pacific area, coastal areas in southern Asia and Africa, and the east coast of the Americas.

Calyceraceae. — The first outgroup of Compositae, and therefore its sister group, is Calyceraceae, a small family (six genera, ca. sixty species) of annual and perennial herbs. The family is entirely South American, being most abundant in the Andes south from Bolivia, extending eastwards through Paraguay to Uruguay and southern Brazil and down through Argentina to southern Patagonia (Heywood 1993).

Cassini, in his famous 1816 diagram (Chapter 41: Fig. 41.1), showed Calyceraceae and Campanulaceae to be closely related to Compositae. Even though he did not have it in the diagram, he also thought Goodeniaceae were close (see Chapter 1).

Compositae

The base tree. — The basic structure of the tree was taken from Panero and Funk (2002, 2008) and Baldwin (Baldwin et al. 2002; Chapter 41); see above for details. The trees in Panero and Funk (2008) contained extensive sampling from the base of the tree, Mutisieae (sensu Cabrera), three to ten genera representing all other tribes (including the Heliantheae Alliance), and many taxa that had been "hard to place" in previous studies (including *Hecastocleis*, *Gymnarrhena*, and *Corymbium*). The Panero and Funk phylogeny was based on data from ten chloroplast gene regions (*ndhF*, *trnL-trnF*, *matK*, *ndhD*, *rbcL*, *rpoB*, *rpoC1*, *exon1*, *23S-trnI*, and *ndhI*). Relationships within tribes of the Heliantheae Alliance were taken from Baldwin et al. (2002) and Chapter 41 and were based on data from the ITS region of rDNA. Modifications were made in Cichorioideae (based on Chapter 23) and in Carduoideae (based on Ortiz, Chapters 18 and 19; and Ortiz et al. (Chapter 17).

Mutisieae s.l. sensu Cabrera (Chapter 12). **—** The tribe Mutisieae (sensu Cabrera) has 84 genera and ca. 900 species. The paraphyly of Mutisieae (sensu Cabrera) was suggested by morphological studies (Cabrera 1977; Hansen 1991b) as well as the first molecular studies of the family. The subtribe Barnadesiinae was recognized as being the sister group to the rest of the family (Jansen and Palmer 1987, 1988; Bremer 1994; Kim and Jansen 1995). Kim et al. (2002) showed that the remainder of the tribe (sensu Cabrera) could not be supported as a monophyletic group. Most recently, Panero and Funk (2002, 2008) published phylogenies based on molecular data from ten chloroplast regions that *(1)* confirmed that Mutisieae (sensu Cabrera) were paraphyletic, *(2)* identified additional clades, and *(3)* elevated several groups to tribal and subfamily levels. Except for Barnadesieae, the phylogeny of Panero and Funk (2008) formed the base tree for Mutisieae (sensu Cabrera) with a few additions from Kim et al. (2002) and Katinas et al. (2007).

Barnadesieae (Chapter 13)**. —** The subfamily Barnadesioideae (nine genera; 91 species) has one tribe, and it is the sister group for the rest of Compositae. This has been known since the seminal papers by Jansen and Palmer (1987, 1988) established the presence of a chloroplast DNA inversion shared by the rest of the family, but not by Barnadesieae or other flowering plants. The

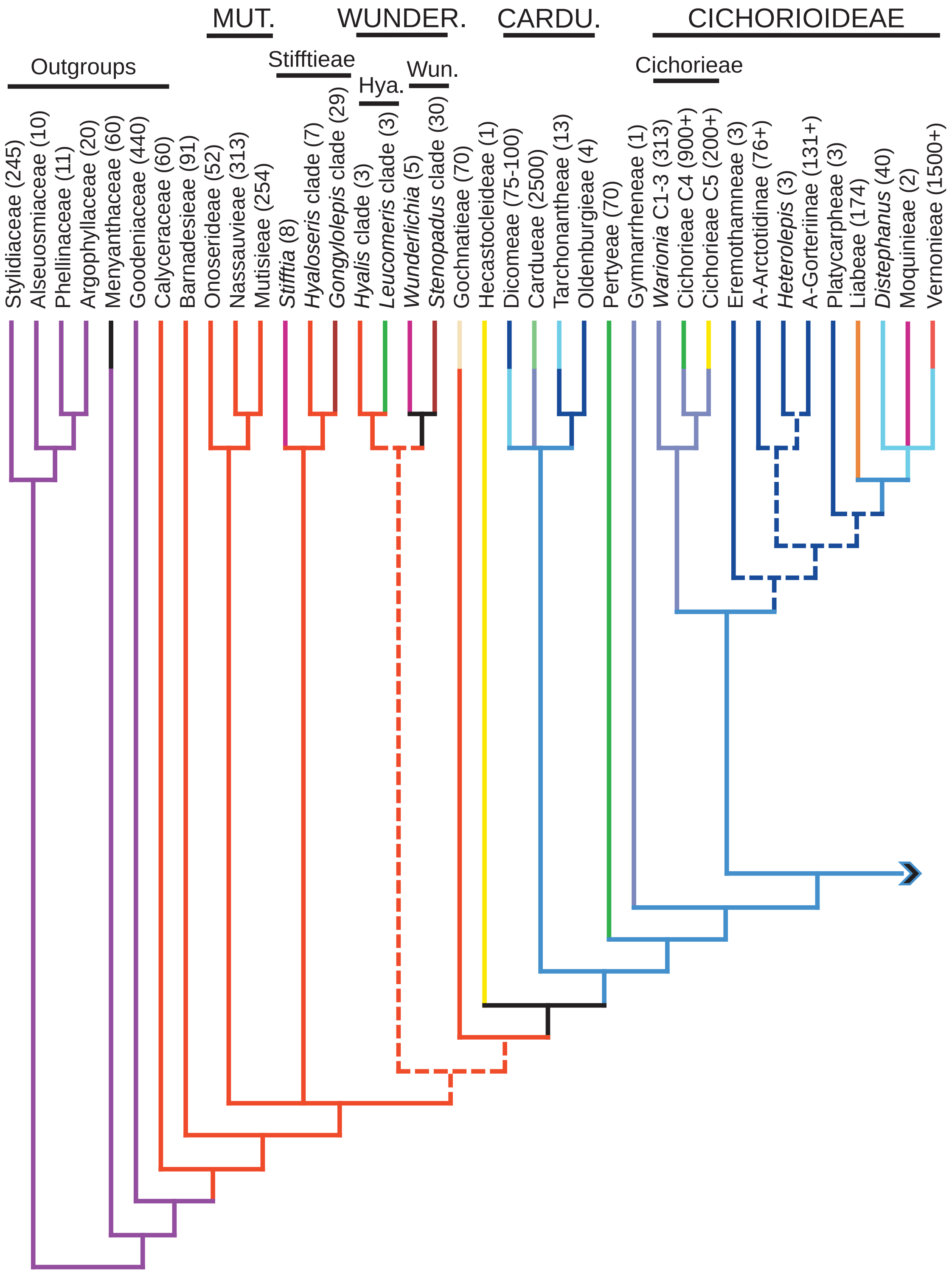
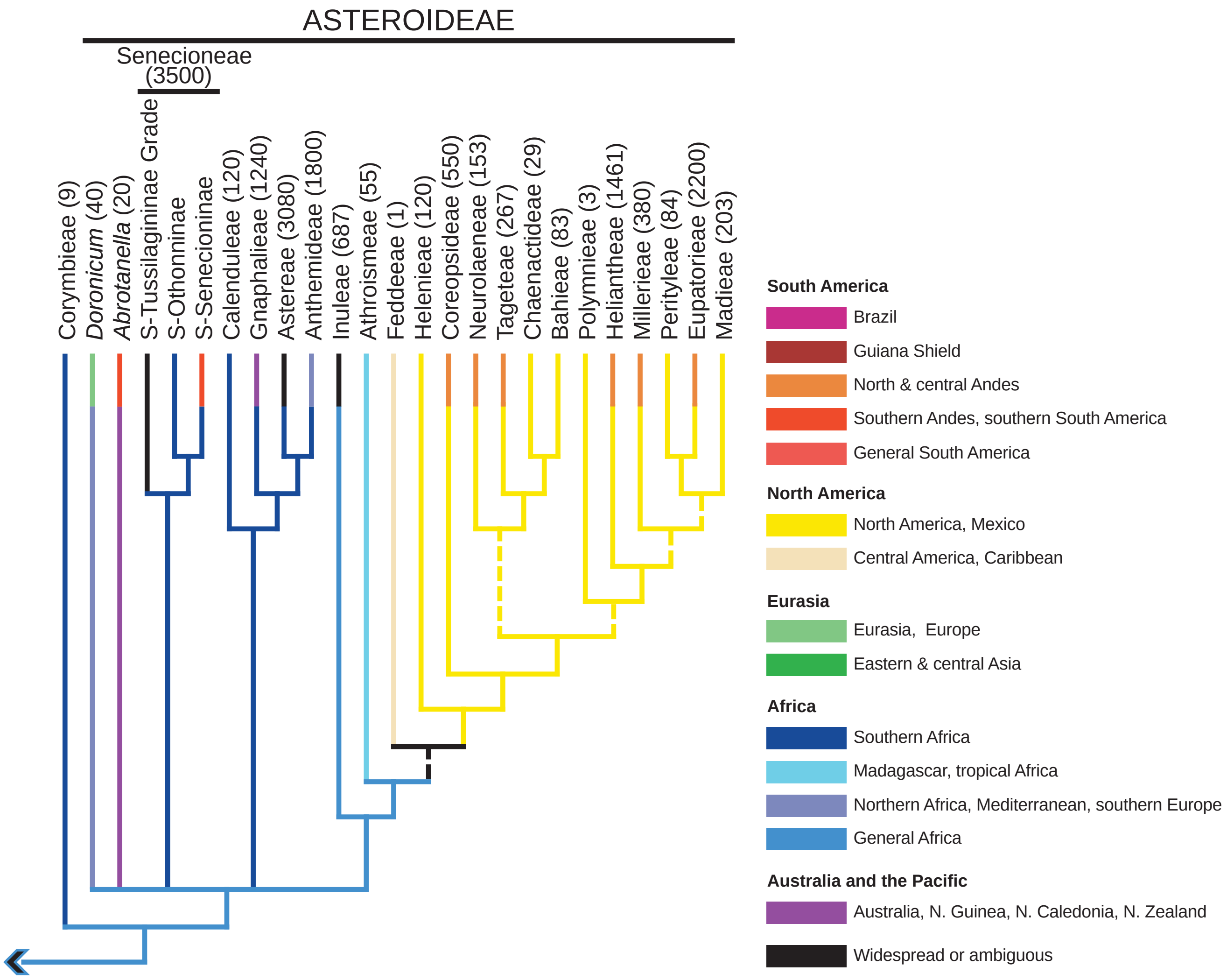


Fig. 44.1. A summary tree based on the metatree (Figs. 44.3–44.7). The tribes or clades have been represented by one to four-branches. The branches and internodes were colored according to the distribution of the taxon or the optimization of those distributions. The numbers by the terminal taxa reflect the number of species in that clade. Note that some areas have been combined (e.g., Mexico and North America) and that the red color in Vernonieae represents Tropical America. Subfamilies that have more than one tribe are indicated on the summary tree in capital letters (see Chapter 11 for details). A = Arctotideae; CARDU. = Carduoideae; Hya. = Hyalideae; MUT. = Mutisioideae; S = Senecioneae; Wun. = Wunderlichieae; WUNDER. = Wunderlichioideae.



first phylogeny of this tribe was done by Gustafsson et al. (2001), but it was not completely resolved. The phylogeny for the tribe was taken from Gruenstaeudl et al. (2009). It was based on DNA sequence data of nine chloroplast gene regions (*atpI-atpH* IGS, *matK*, *psbA-trnH* IGS, *rbcL*, partial *rpoC1* gene + intron, *rps16-trnK* IGS, partial *trnK* intron, *trnL* intron, *trnL-trnF* IGS), the nuclear ribosomal ITS region (ITS1, 5.8S, ITS2), recoded DNA insertions/deletions, and selected morphological characters from previous investigations. In their analysis all genera were monophyletic except for *Dasyphyllum*, which fell into two groups reflecting the subgenera and their respective distributions "east of the Andes" and "west of the Andes". There are two possible positions for *Schlechtendalia*, one of which is basal for the tribe, and the other is more highly nested. The ambiguity of the position of *Schlechtendalia* does not affect the biogeographic hypothesis for this tribe.

African Mutisieae (Chapters 17–19). — With the exception of *Gerbera* and the closely related and sometimes congeneric *Perdicium*, which are found in Africa and to a lesser extent in Asia, all Mutisieae (sensu Cabrera) from Africa are no longer part of Mutisioideae (sensu Panero and Funk) and are now in Carduoideae. Using ITS and *ndhF* sequence data, Ortiz and his collaborators (Chapters 17–19) have shown that these segregate African Mutisieae form three (or four) distinct groups that are separated by striking morphological as well as molecular differences. Currently, there are three tribes: Dicomeae, Oldenburgieae, and Tarchonantheae. However, it is possible, but not yet certain, that the tribe Dicomeae may fall into two distinct groups that are not sister taxa. In addition, there is still some ambiguity as to the relationships among some of the tribes.

The tribe Dicomeae contains seven African genera (ca. 75–100 species) occurring in tropical and southern Africa and Madagascar with a minor presence in the Arabian Peninsula, India, and Pakistan. The tribe Tarchonantheae contains two African genera (13 species) occurring

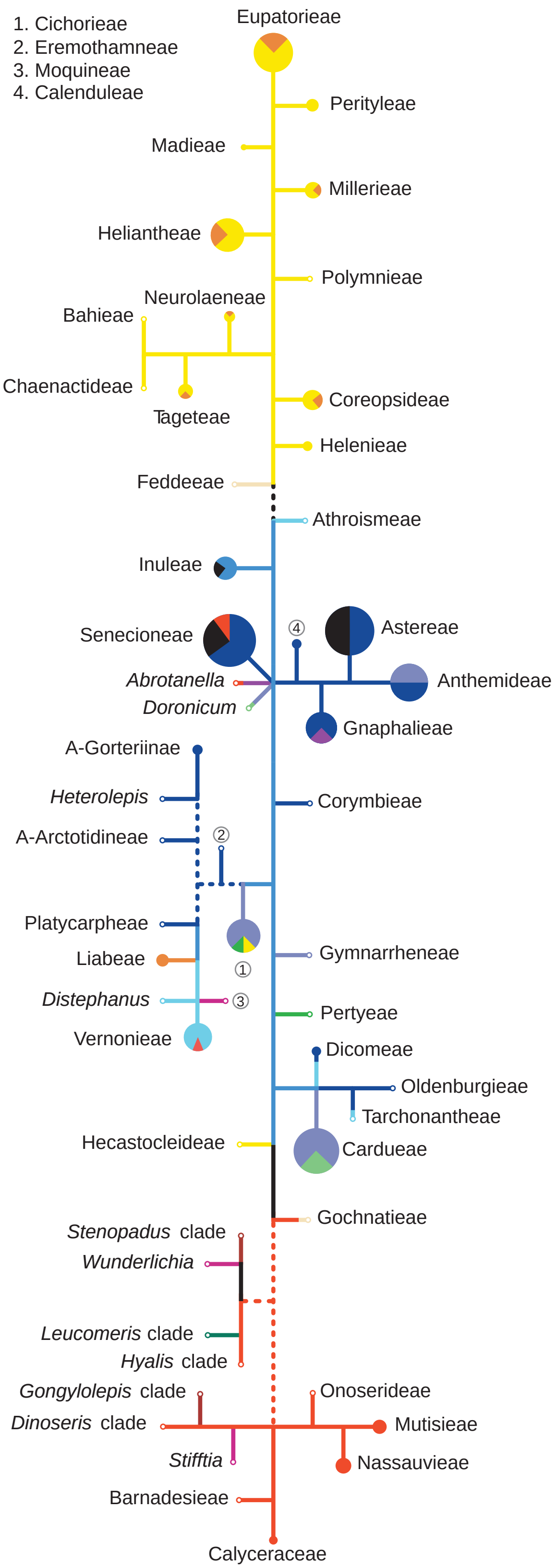


Fig. 44.2. An unrooted representation of the summary tree. The size of the circle indicates the number of species found in that clade. Colors are the same as in Fig. 44.1.

mainly in tropical and southern Africa, and Madagascar, but it is also present on the Arabian Peninsula. The tribe Oldenburgieae has only the genus *Oldenburgia* (4 species), which is endemic to the Cape Floristic Region of South Africa.

Cardueae (Chapter 20). — Cardueae (thistles; 73 genera, ca. 2500 species) are now known to be nested within a paraphyletic Mutisieae (sensu Cabrera). This tribe is the sister group of the African Mutisieae clades. The tribes Cardueae, Tarchonantheae, Oldenburgieae, and Dicomeae form a monophyletic group that is now the subfamily Carduoideae. The Cardueae tree used for the metatree is based on *matK*, *trnL-F*, and ITS sequence data (Susanna et al. 2006).

Cichorieae (Lactuceae; Chapter 24). — The phylogeny of the mainly north temperate dandelion tribe Cichorieae (Lactuceae) has long been problematic. It has 93 genera arranged in eleven subtribes, but the number of species varies depending on one's species concept. If one excludes the problematic genera *Hieracium*, *Pilosella*, and *Taraxacum*, there are about 1400 species (Kilian et al., Chapter 24). The Cichorieae tree used in this study was provided by Gemeinholzer and her collaborators based on recent molecular analyses of a large ITS dataset (428 taxa of 83 genera; Gemeinholzer and Bachmann 2003; Kilian et al., Chapter 24; Gemeinholzer et al., unpub.). The analyses revealed the existence of five major clades, with a total of eleven subclades, within the tribe.

The position of *Gundelia* (Gundelieae) as basal within Cichorieae was suggested by Karis et al. (2001) based on *ndhF* data, and this was supported by Panero and Funk (2008), who also found *Warionia* to be at the base. However, the current studies of Gemeinholzer and her collaborators comprising more basally branching taxa place the Northern African genus *Warionia* at the base of Cichorieae with the Mediterranean *Gundelia* slightly more highly nested. Since both are from the same biogeographic area, the two different placements of *Gundelia* and *Warionia* do not affect the biogeographic analysis.

Arctotideae, Eremothamneae, Platycarpheae, and Heterolepis (Chapters 25, 26, 29, 31). — The tribe Arctotideae (African Daisies) is a diverse and interesting group (18 genera, 215 species). Recent molecular studies are ambiguous as to the monophyly of this tribe, and some former members have been moved out of the tribe based on morphology and/or molecular data. The positions of *Heterolepis* (Funk and Karis, Chapter 31) and the tribe Eremothamneae (2 genera, 3 species; Robinson and Funk, Chapter 26) vary depending on the data used in the analysis, and the new tribe Platycarpheae (2 genera and 3 species) is most likely closely related to the Liabeae + Vernonieae clade (Funk et al., Chapter 29). Although Arctotideae cannot be unambiguously diagnosed, the two core subtribes are distinctive based on morphology as well as molecular data (Funk et al. 2004; Karis et al., Chapter 25). Recently published phylogenies using both chloroplast and nuclear DNA and representing all of the genera (some with many species) provided the structure for the trees (Funk and Chan 2008; McKenzie and Barker 2008) and the relationships among the clades was taken from Funk et al. 2004 and Funk and Chan, Chapter 23).

Liabeae (Chapter 27). — Liabeae are a monophyletic Neotropical tribe containing approximately 174 species distributed in 17 genera and occupying a wide variety of habitats throughout Mexico, Central America, the West Indies, and the Andes. The greatest diversity in the tribe is found in Peru, where no fewer than 14 genera and over 70 species are represented. After a long history of moving from tribe to tribe, the current members were brought together by Robinson (1983). A previous morphological analysis resolved a northwestern Andean origin (Funk et al. 1996). The tree for our study was based on Dillon et al. (Chapter 27) and contains all the genera of the tribe except the monotypic *Bishopanthus*, which is only known from the type. Although the type was relatively recently collected, it is just a small piece of the original collection, most of which was destroyed by one of the collectors.

Vernonieae and Moquinieae (Chapters 28, 30). — The tribe Vernonieae with 126 genera and 1500 species has until recently had most of its species placed in the large and complicated genus *Vernonia* (ca. 1000; Jones 1977; Keeley and Robinson, Chapter 28). The tribe is widely distributed with centers of diversity in tropical Africa and Madagascar, Brazil, and North America. However, it has been the subject of recent revisions that concentrated on recognizing monophyletic genera from within the 1000 species of the core genus *Vernonia* s.l. (e.g., Robinson 1999), first in the Americas and more recently in Africa and Asia. Vernonieae have recently been examined by Keeley et al. (2007; Keeley and Robinson, Chapter 28) based on *ndhF*, *trnL-trnF*, and ITS sequence data. Their work supports the monophyly of the tribe and the non-monophyly of *Vernonia*. However, in the analysis of the subfamily Cichorioideae (Funk and Chan, Chapter 23), *Distephanus* had alternative placements: as the sister group to the rest of Vernonieae, or unresolved at the base with the tribe Moquinieae (Robinson, Chapter 30).

Senecioneae (Chapter 34). — Senecioneae are the largest tribe with over 150 genera containing 3500 species (Nordenstam 2007a) and they have a global distribution. Pelser et al. (2007), recently published a phylogenetic analysis of the tribe based on ITS data that, while unresolved at the base, showed several well supported clades. The genus *Senecio*, which contained the majority of the species of the tribe, was shown to be non-monophyletic, and the authors indicated that revisions of the generic boundaries that are needed to achieve monophyletic groups are completed or in progress.

The relationship of Senecioneae to other clades is uncertain. The tribe is variously positioned as *(1)* the sister group to the rest of Asteroideae, *(2)* the sister group to the Calenduleae + Gnaphalieae + Astereae + Anthemideae clade, or, in the least likely scenario, *(3)* the sister group to the Inuleae + Athroismeae + Heliantheae Alliance clade. The support for its inclusion is strongest for option 1, but the relatively short branches make its placement there tentative (see Pelser and Watson, Chapter 33). This ambiguity will not be resolved until more taxa and characters from both plastid and nuclear markers are included in a tribal-level study of the subfamily. At this time we are following the resolution favored by Panero and Funk (2008), which shows the Senecioneae in a polytomy with the clade formed by the Inuleae + Athroismeae + Heliantheae Alliance and the clade containing Calenduleae + Gnaphalieae + Astereae + Anthemideae. *Doronicum* and *Abrotanella*, the two additional taxa in this polytomy, are Senecioneae genera that have been hard to place and may have to be excluded from the tribe (Pelser et al. 2007).

Calenduleae (Chapter 35). — The placement of Calenduleae as the sister taxon to the Gnaphalieae + Anthemideae + Astereae clade is based on the Panero and Funk (2008) analysis as well as those by Kim and Jansen (1995) and Eldenäs et al. (1999). The sister group relationship of Calenduleae to the other three tribes is strongly supported in the Panero and Funk (2008) study, even though the number of taxa sampled is small. The tribe Calenduleae has 12 genera with 120 species (Nordenstam 2007b), and most genera have distinct centers of distribution in southern Africa; most of the species occur in the Cape Floristic Region. However, one genus, *Calendula*, is found in northern Africa and the Mediterranean north to Central Europe and east into Turkey, Iraq, and Iran; but it is nested in the higher portion of the tree and so does not affect the biogeographic pattern.

Gnaphalieae (Chapter 36). — Gnaphalieae are a moderately large tribe whose members were traditionally included in the tribe Inuleae. It has only been recently that the tribe has been shown to be isolated from the remainder of "old" Inuleae (Anderberg 1989, 1991). The approximately 180–190 genera and ca. 1240 species of Gnaphalieae are most numerous in the southern hemisphere, with strong centers of diversity in southern Africa, Australia, and South America (Anderberg 1991; Bayer et al. 2007). The tree for this study was provided by Bayer and his collaborators (Ward et al., Chapter 36) and it is based on chloroplast DNA sequences for *matK*, the *trnL* intron, and the *trnL-trnF* intergenic spacer. The principal improvement of this tree over previously published DNA sequence phylogenies for Gnaphalieae is that it includes a broad sampling of genera from Africa and Australasia together with some from other continents.

Astereae (Chapter 37). — With 170 genera, ca. 3000 species, and a worldwide distribution, Astereae are the second largest tribe after Senecioneae. It has centers of diversity in southwestern North America, the Andes, South Africa, Australia, and New Zealand. The tree presented in this book (Brouillet et al., Chapter 37) is the first global, molecular phylogenetic analysis of the tribe. It is based on ITS sequence data and shows that interrelationships among genera are better reflected by geographic origin than by the current classification.

Anthemideae (Chapter 38). — The tribe Anthemideae is composed of 111 genera and ca. 1800 species with main concentrations of species in southern Africa, the Mediterranean region, and Central Asia. The phylogeny for the metatree was generated using data from two recent publications that used *ndhF* (Watson et al. 2000; Himmelreich et al. 2008) and one that used ITS (Oberprieler et al. 2007).

Inuleae and Plucheeae (Chapter 39). — Plucheeae are now known to be nested within Inuleae, and so they are recognized as a single tribe with about 66 genera and ca. 700 species (Anderberg and Eldenäs 2007). The tree for this study was provided by Anderberg and his collaborators (Anderberg et al. 2005) based on *ndhF* data. Inuleae are a mainly Eurasian and east and southern African tribe, but some genera (e.g., *Pluchea*) have a worldwide distribution.

Athroismeae (Chapter 40). — The tribe Athroismeae is the sister group to the rest of the large and diverse clade that is the Heliantheae Alliance. The five genera (only two were included in Panero and Funk 2008) and 55 species in Athroismeae are centered in eastern tropical Africa and were in Inuleae until moved to Heliantheae s.l. (Eriksson 1991).

Heliantheae Alliance (including Eupatorieae) (Chapters 41–43). — The tribe Eupatorieae is nested in the Heliantheae Alliance, and former Heliantheae s.l. have been reorganized into twelve tribes (Baldwin et al. 2002; Panero and Funk 2002; Cariaga et al. 2008). Bremer (1994) divided this part of the family into three groups, Helenieae (including Athroismeae), Heliantheae, and Eupatorieae, but recognized that the groups would need to be re-arranged once additional information was available. The studies of both Baldwin et al. (2002) and Panero and Funk (2002) showed Helenieae and Heliantheae of Bremer to be non-monophyletic, and they described additional tribes where needed. More recently, Cariaga et al. (2008) published a treatment of the problem genus *Feddea* based on *ndhF* sequence data. As part of their study the genus was placed in a new tribe by itself, Feddeeae, located as the sister group of the "rest" of the Heliantheae Alliance (minus Athroismeae). The inclusion of the tribes Feddeeae and Eupatorieae in the Heliantheae Alliance brings the total number of tribes in the Alliance to 13.

The tree for this clade in the metatree was formed by using the Baldwin treatment of the Heliantheae Alliance (Chapter 41), the Coreopsideae treatment of Crawford et al. (Chapter 42), and the Funk et al. paper (2005). The branching within Eupatorieae was taken from Robinson et al. (Chapter 43).

The tree for the Heliantheae Alliance section of the family contains 160 out of ca. 460 genera and so represents about 35% of the generic diversity of this clade. This is the lowest percentage for any clade on the metatree, however the poor representation is found primarily in three tribes, Eupatorieae (the tree has 25 genera represented out of a total of 182; there are 2200 species), Heliantheae (6 out of 113 genera were represented; there are 1461 species), and Millerieae (3 genera out of 36 were represented; there are 380 species). When totaled together, these three tribes are represented by only about 10% of the generic diversity within them. The other ten tribes in the Alliance are much better represented, some at or close to 100% (see below). Because the members of former Helenieae form the basal grade, the under-representation of three of the more highly nested groups does not present an obstacle to the biogeographic analysis, although it does give an under-estimate of the importance of the northern and central Andes.

The tribe Heliantheae s.l. was broken up by Baldwin et al. (2002) and by Panero and Funk (2002) when Eupatorieae were found to be nested within what is now referred to as the Heliantheae Alliance (Fig. 44.1). Most of the new tribes, however, were actually not new and had been described previously by others but not picked up by the synantherological community. In fact, only three of the tribes recognized by Baldwin needed to be described as new (Baldwin et al. 2002): Bahieae (17 out of 20 genera were represented in the analysis; there are 83 species), Chaenactideae (all 3 genera were represented; 29 species), and Perityleae (4 out of 7 genera were represented; 84 species) (see Funk et al., Chapter 11). Other tribes in the Heliantheae Alliance (not mentioned above) include: Coreopsideae (21 genera out of 30 were represented; 550 species), Helenieae (all 13 genera were represented; 120 species), Madieae (35 genera were represented out of 36; 203 species), Neurolaeneae (1 out of 5 genera was represented; 153 species), Polymnieae (the only genus was represented; 3 species), and Tageteae (17 out of 32 genera were represented; 267 species).

Area optimization analysis using parsimony

The terminal branches of the metatree were colored based on the distribution of each terminal taxon; taxa that span more than one area have multiple colors (Figs. 44.1–44.7). The internode distributions were mapped onto the metatree using the Farris double pass method (1970). The results of the mapping were checked using the PAUP 'Acctran' option (Swofford 2002). These techniques provided the hypothesized distributions at deep branches and nodes.

Following the theory that bold hypotheses are better than weak ones (courtesy of Popper), equivocal situations were resolved when possible to present the most predictive estimate of the biogeographic history. In a few instances there were equivocal resolutions which were left black, or if the two areas were contained in a single continent, they were coded for that continent (e.g., general Africa). In essence, we created an 'area metatree' as opposed to an 'area cladogram'. In the summary tree and unrooted tree (Figs. 44.1, 44.2), some of the biogeographic areas were combined (e.g., North America was combined with Mexico).

RESULTS AND DISCUSSION

The first supertree (=metatree) for Compositae was published in 2005 (Funk et al.), and since then there has been considerable progress in the reconstruction of evolutionary relationships in many clades. In fact, we now have robust phylogenies for most of the clades in the family. Descriptions and diagnostic characters for all of the tribes and critical clades are found in Chapter 11. Without a doubt the most substantial progress has been made in the large and complicated Astereae, Cichorieae, Senecioneae, and Vernonieae tribes, all of which were problematic in the 2005 publication (Funk et al. 2005) but now have their first comprehensive molecular phylogenetic hypotheses (Keeley et al. 2007; Pelser et al. 2007; Brouillet et al., Chapter 37; Kilian et al., Chapter 24; and other references in the corresponding chapters). For the first time within these tribes we have a fairly good idea of what the basal groups are and where different clades are found, and we know that the large genera with global distributions are not monophyletic.

Considering the entire metatree, most of the traditional thirteen tribes were found to be monophyletic or could easily be made monophyletic with only a few rearrangements. The big exceptions to this are Mutisieae (sensu Cabrera) and the Heliantheae Alliance, both were broken up into many groups. The genera that were once placed in Mutisieae by Cabrera or others are now in fourteen tribes, Helenieae are in seven, and Heliantheae are in six (including Feddeeae).

For such a large and interesting family, relatively little has been published on its geographic origin and diversification since Bentham (1873b). Bentham (1873b), Small (1919), Raven and Axelrod (1974), and Turner (1977) all believed that Compositae had their origin in the northwest portion of South America, in the Andes. Rzedowski (1972) and Hu (1958) pointed out the high diversity of the family in montane areas. More recently, Bremer (1992, 1994) developed a method he called 'Ancestral Areas Analysis' and came to the conclusion that the family originated in "South America and the Pacific". DeVore and Stuessy (1995) suggested that the family originated in southern South America, which was re-emphasized by Bremer and Gustafsson (1997). Graham (1996) summarized the fossils for the family but had wide estimates of the age of some of the pollen. Other than these efforts, little attention has been paid to this topic. Perhaps the size of the family, its global distribution, the lack of macrofossils and paucity of discriminating characters in fossil pollen, and the lack of an agreed upon phylogeny have restricted attempts to understand its history.

The meta showing the overall phylogeny of Compositae allows us to use information from the most recent available molecular phylogenies to look at the family as a whole and to try to discern its origin and history. It is also an excellent method for determining critical areas of the tree for future work (Funk and Specht 2007).

The metatree and its sections

In order to more easily discuss the tree it has been broken into sections. Section 1 (Fig. 44.3) covers the Basal Grade, from the outgroups through monotypic Gymnarrheneae. Section 2 (Fig. 44.4) covers the large subfamily Cichorioideae. Section 3 (Fig. 44.5) covers Corymbieae, Senecioneae, Calenduleae, and Gnaphalieae; Section 4 (Fig. 44.6) Anthemideae and Astereae; and finally, Section 5 (Fig. 44.7) Inuleae, Athroismeae, and the Heliantheae Alliance (including the Eupatorieae). Figure 44.8 has some of the proposed ages of the clades and Figs. 44.9 and 44.10 show some of the morphological variation.

Since we have no macrofossil data, the following discussion is based on extant taxa.

Section 1, Basal Grade (Figs. 44.3, 44.9A–D). — Except for Calyceraceae (the sister group of Compositae), the most closely related families to Compositae are found in Australia, New Zealand, New Guinea, and New Caledonia (purple lines; Fig. 44.3). The members of Calyceraceae are from southern South America.

The first split within Compositae is between the subfamily Barnadesioideae and the remainder of the family (Fig. 44.3). Gustafsson et al. (2001) and Stuessy et al. (Chapter 13) examined the biogeography and concluded that the Barnadesioideae clade has its origin in southern South America; this is confirmed by our analysis. In the sister group of Barnadesioideae the relationships among the basal groups are largely unresolved and are shown as a trichotomy (Fig. 44.3). However, this part of the tree could have been shown as a polytomy containing four or even five clades because support for monophyly of the subfamily Wunderlichioideae is not consistently strong, nor is its phylogenetic position; this ambiguity is

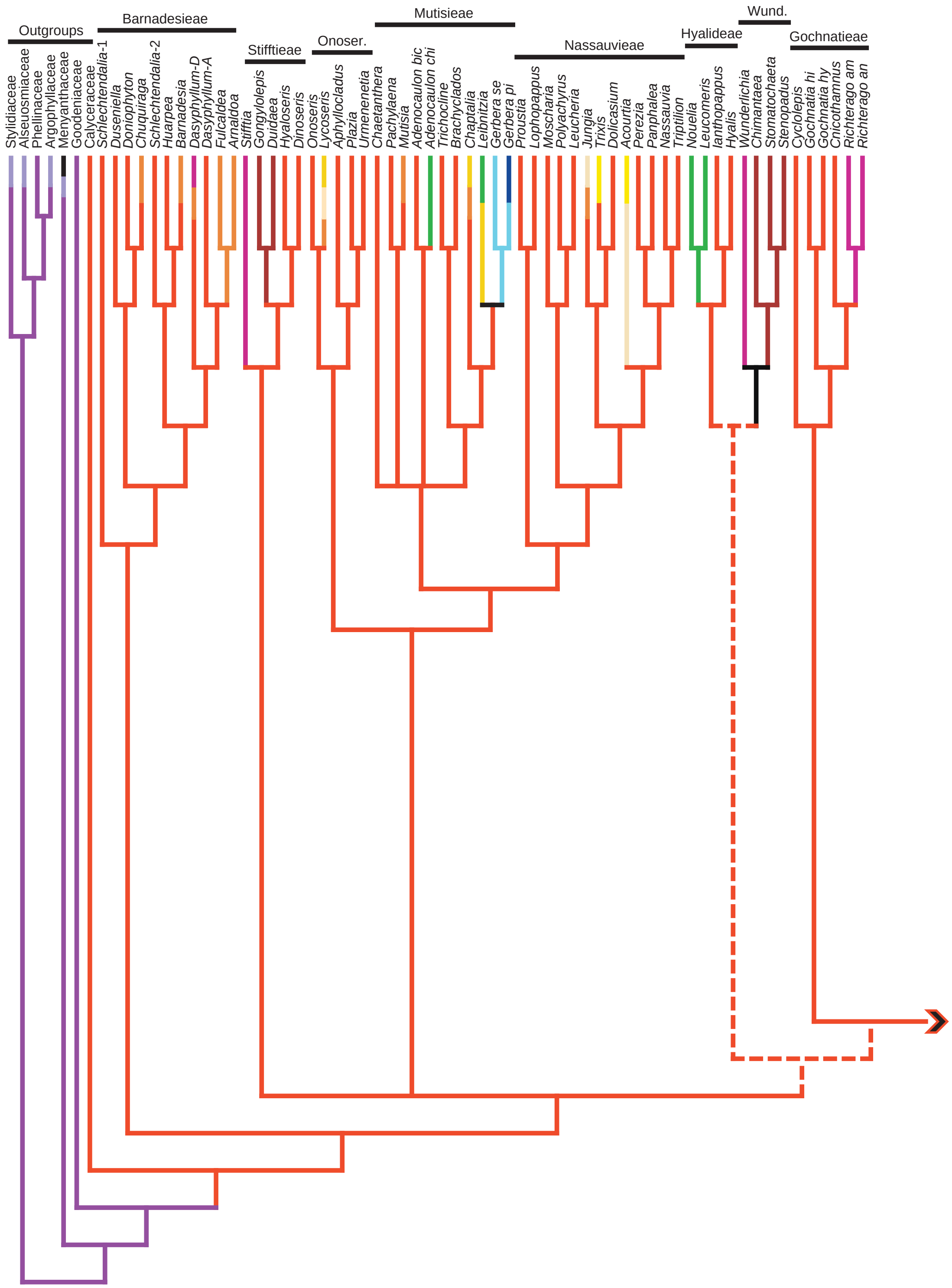
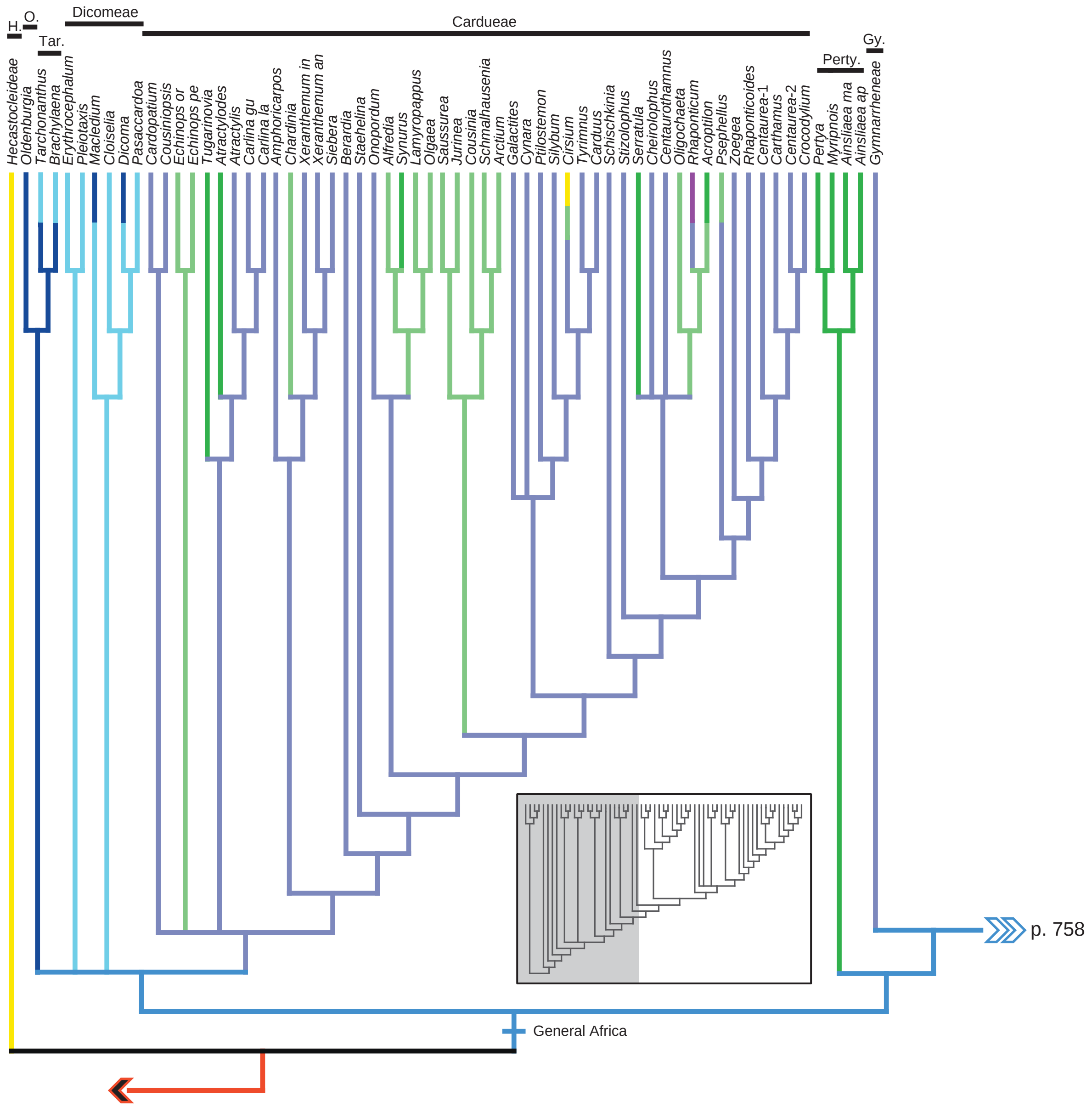


Fig. 44.3. The metatree of Compositae has been broken up into five figures with two to three parts for each figure. The original trees are from the various chapters in this volume, but some taxa with redundant distributions have been pruned from the tree to save space. Figure 44.3 covers the Basal Grade of the family and includes the outgroups through Gymnarrheneae, including thistles (some of the internodes have been compressed). All outgroups except for the sister group are Australasian. The extant taxa from the sister group of the family, Calyceraceae, along with those from the basal grade of Compositae have a southern South American origin. For subfamily groups see Chapter 11, for color chart see Fig. 44.7. Gy. = Gymnarrheneae; H. = Hecastocleideae; O. = Oldenburgieae; Onoser. = Onoserideae; Perty. = Pertyeae; Tar. = Tarchonantheae; Wund. = Wunderlichieae.



indicated in Fig. 44.3 by a dotted line. However, many of the main clades basal to the clade formed by *Hecastocleis* and its sister group are consistently resolved as having a southern South American origin, with the exception of the tribe Wunderlichieae whose members are found in the Guiana Shield and Brazil. The large Mutisioideae clade (composed of the tribes Mutisieae, Nassauvieae, and Onoserideae) contains mostly southern South American taxa, but it also contains *Gerbera* from tropical and southern Africa and Asia, North America taxa (e.g., *Acourtia*), and *Leibnitzia* from Asia and Mexico. Hyalideae have two clades, one from Asia and one from southern South America. Gochnatieae contain genera mainly from southern South America and Brazil, but there is also a radiation in Cuba. It is clear from the optimization that the extant taxa at the base of the Compositae metatree have their origin in southern South America.

The internode between the southern South American grade and the beginning of the African radiation (labeled "General Africa" in Fig. 44.3) is left unresolved as to origin because there are no areas shared among the three (South American base, African radiation, and the North American genus *Hecastocleis*). A species level analysis of the tribe Gochnatieae (4–5 genera) is underway (Sancho et al., pers. comm.) and its relationships to *Hecastocleis* may provide some insight into the problem, because one of the genera (*Gochnatia*) is found in South America, the West Indies, and North America.

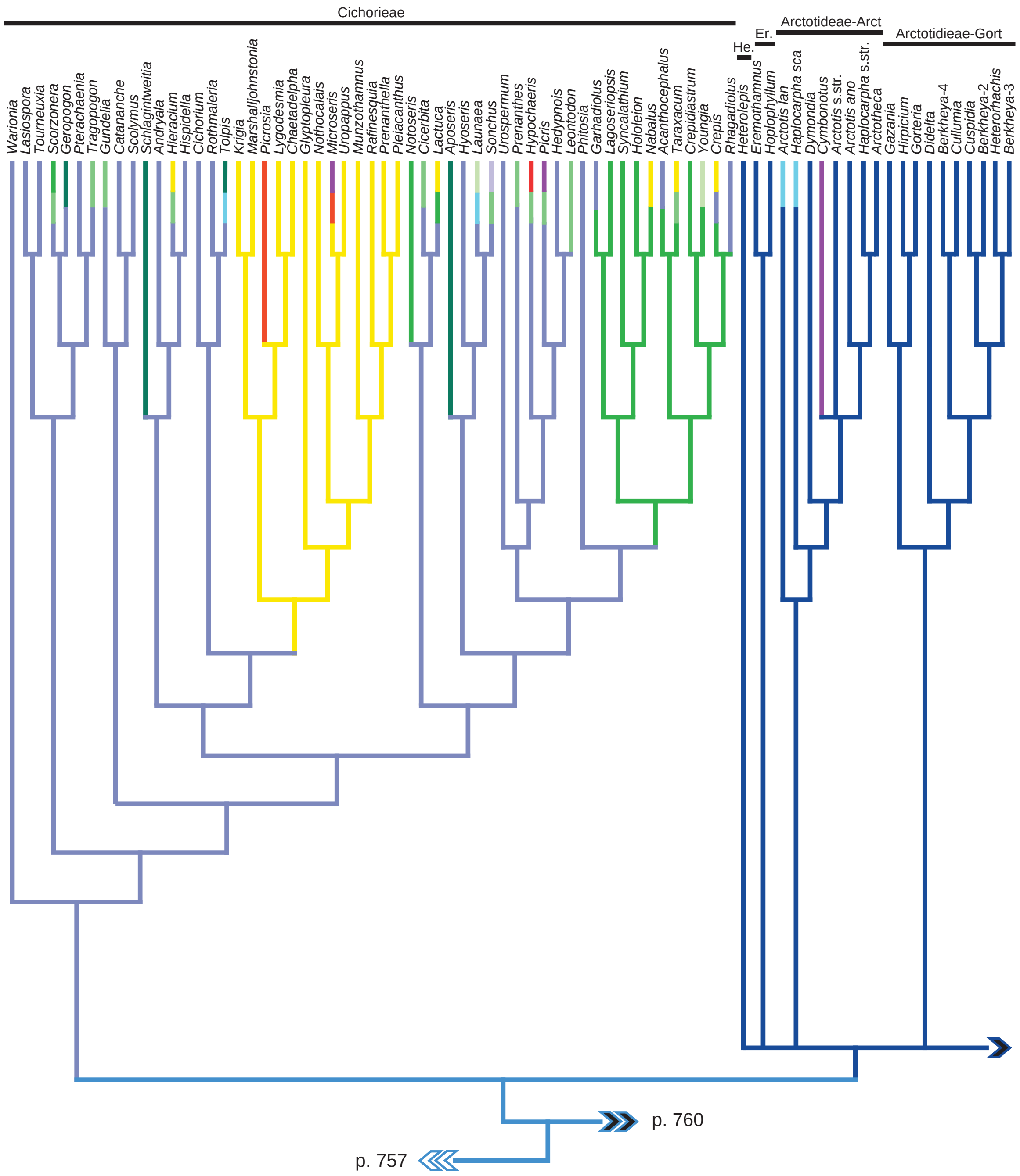
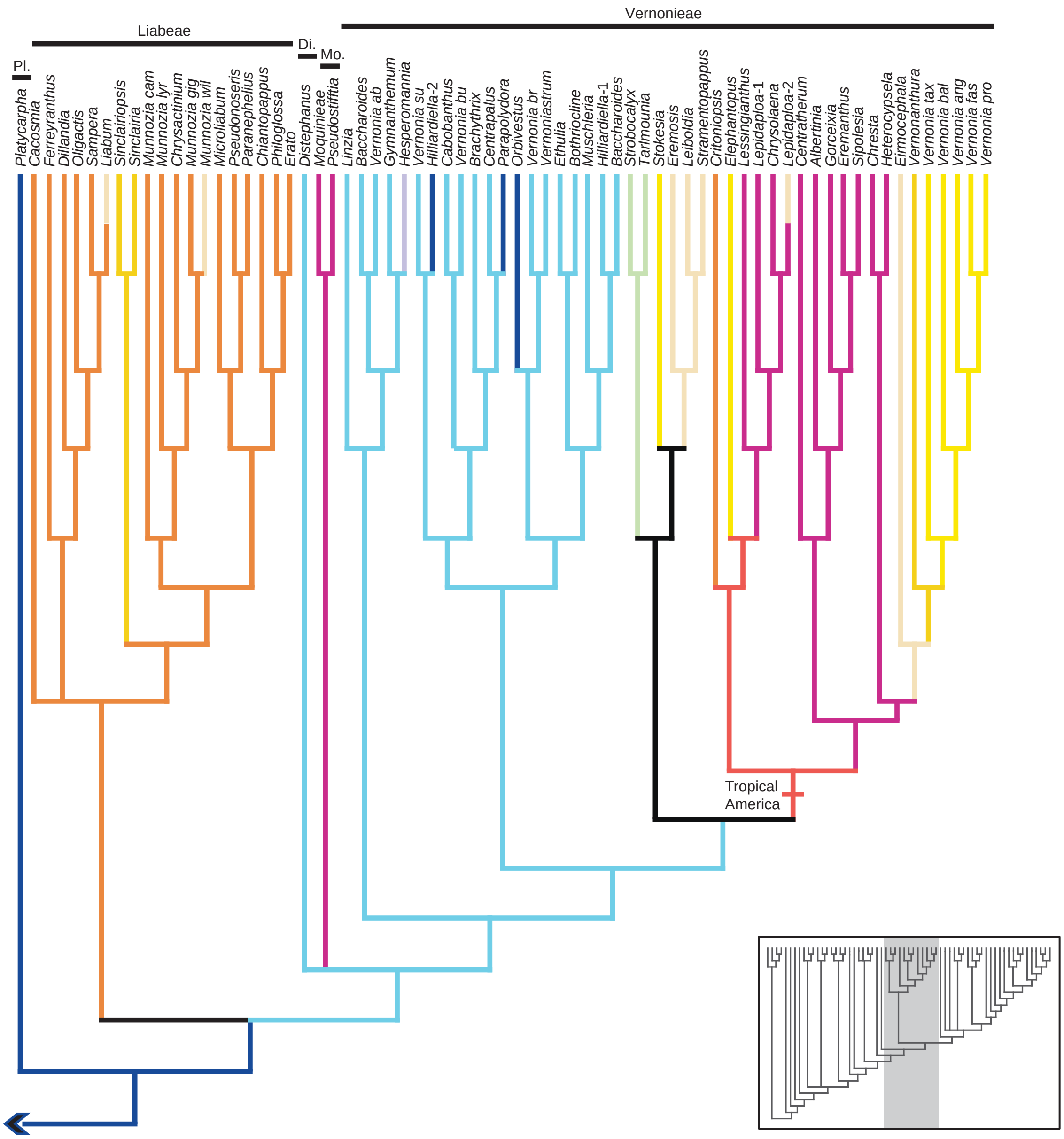


Fig. 44.4. Monotypic Cichorioideae (internodes have been compressed). For subfamily groups see Chapter 11, for color chart see Fig. 44.7. Di. = *Distephanus*; Er. = Eremothamneae; He. = *Hecastocleis*; Mo. = Moquinieae; Pl. = Platycarpheae.

The largest clade of the basal grade contains the subfamily Carduoideae (Tarchonantheae, Oldenburgieae, Dicomeae, Cardueae; Fig. 44.3); this is followed on the metatree by the Pertyeae (Asia) and Gymnarrheneae (northern Africa). At the base of Carduoideae are several former members of Mutisieae from southern and tropical Africa (African Mutisieae). The relationships of these clades to one another are unresolved at this time, except for the sister group relationship between Oldenburgieae and Tarchonantheae. The thistles (Cardueae) are monophyletic and show a Mediterranean–northern African radiation with numerous incursions into Eurasia and Asia. The combination of the Mediterranean–northern African base of the thistles and the tropical and southern African Tarchonantheae, Oldenburgieae, and Dicomeae give a 'general Africa' base to this clade.



The sister group of Carduoideae is the remainder of the family (Pertyeae, Gymnarrheneae, Cichorioideae, Corymbieae, and Asteroideae) all of which, except for Pertyeae (Asia), presumably originated in Africa. The first group to split off is Pertyeae followed by Gymnarrheneae (Northern Africa) followed by Cichorioideae.

Section 2, subfamily Cichorioideae (Figs. 44.4, 44.9E, F). — This large clade contains six tribes: Cichorieae (Fig. 44.4; also referred to as Lactuceae) is the sister group to the remainder. This tribe has a Mediterranean–northern African base with independent radiations in North America and Asia. Interestingly, the main North American clade of Cichorieae is not nested within the Asian radiation as was predicted (Funk et al. 2005). In that paper, it was thought that the biogeographic pathways of Cichorioideae would lead from the Mediterranean via Eurasia to Asia and across to North America but it seems that the Asian and North American taxa are separately derived from Mediterranean clades.

At the base of the rest of the subfamily Cichorioideae there are five clades containing members of the former Arctotideae: two are subtribes of that tribe (Arctotidinae and Gorteriinae), two are now recognized at the tribal level (Eremothamneae and Platycarpheae), and one is an unplaced genus (*Heterolepis*). All are from southern Africa (Fig. 44.4) and are prominent members of the Cape Floral Region, which is the subject of intense conservation interest. Because all of the basal taxa in each subtribe are in

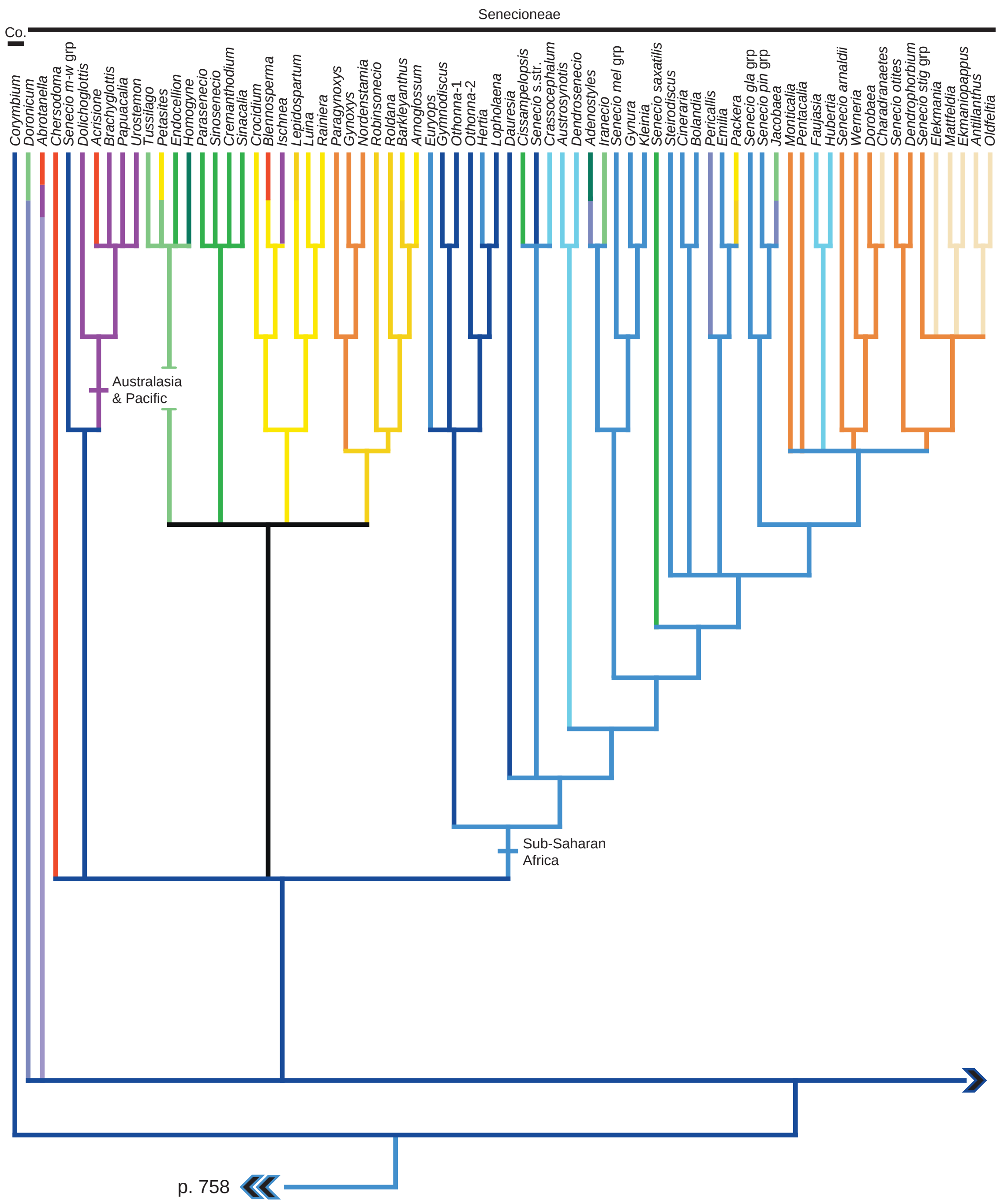
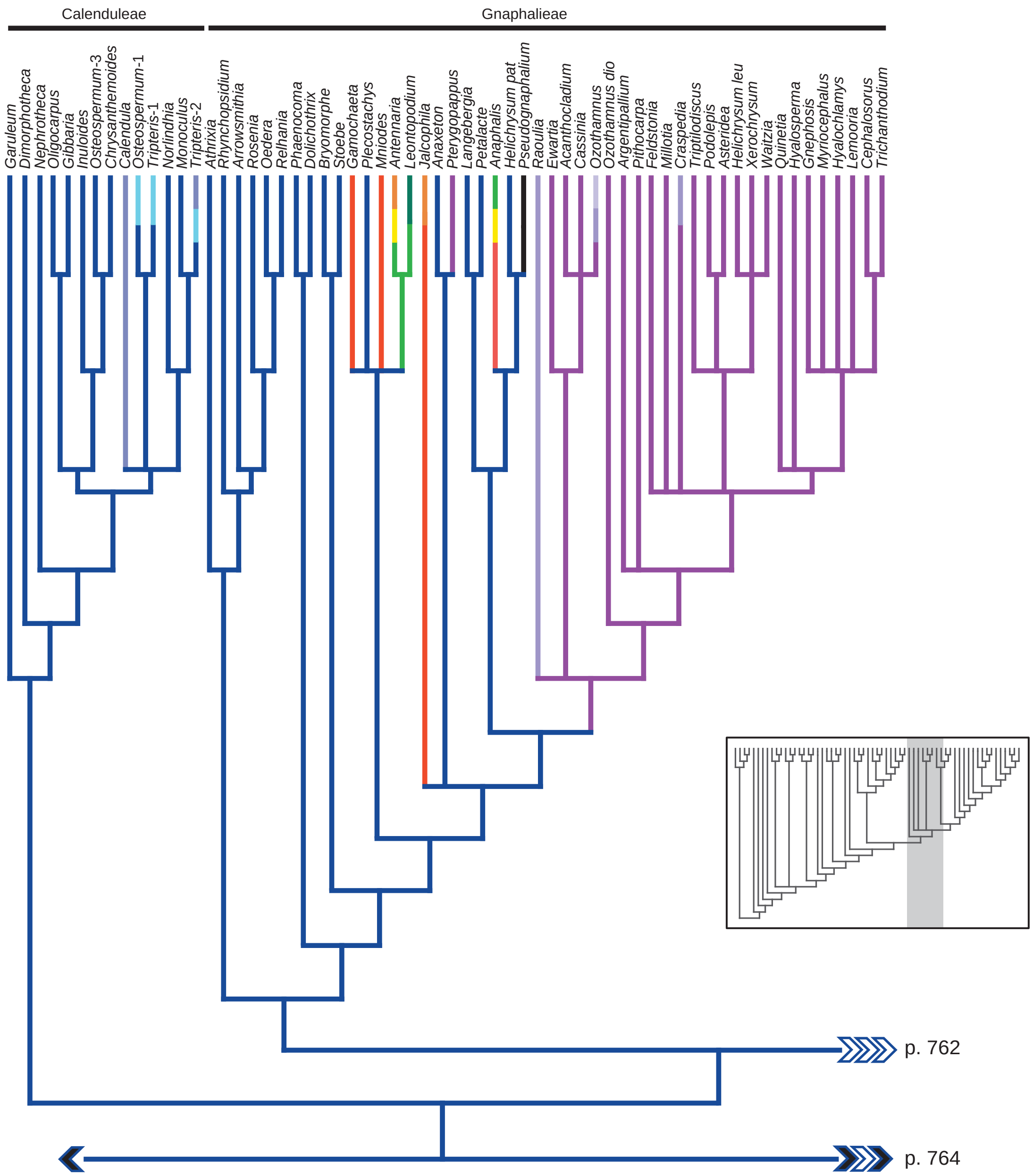


Fig. 44.5. Corymbieae, Senecioneae, Calenduleae, and Gnaphalieae. For subfamily groups see Chapter 11, for color chart see Fig. 44.7. Co. = Corymbieae.

southern Africa, the lack of evidence for the monophyly of Arctotideae does not affect the biogeographic hypotheses produced in this study.

The tribe Platycarpheae (southern Africa) is the sister taxon of the Liabeae + Vernonieae clade (including *Distephanus* and Moquinieae) but without strong support. This clade is nested in a grade formed by the southern African clades (Fig. 44.4). Liabeae are predominantly central Andean and the tribe is believed to have originated in northern Peru and southern Ecuador with small incursions into Central America and radiations in Mexico (*Sinclairia*) and the Caribbean (*Liabum*). The basal branches of Vernonieae are from the area we have designated as 'tropical Africa and Madagascar'. New to the analysis is



the small Brazilian tribe Moquinieae (*Pseudostifftia* and *Moquinia*). In some of the analyses the inclusion of this tribe results in *Distephanus* changing position from being the sister group of the rest of the tribe to being ambiguous at the base of the Vernonieae-Moquinieae clade (Keeley and Robinson, Chapter 28; Funk and Chan, Chapter 23). More highly nested members of Vernonieae are from Brazil and North America. In Vernonieae, the unusual North American genera *Stokesia* and *Elephantopus* are not in the main North American clade but rather represent two independent lineages (Fig. 44.4). With the exception of Liabeae, every tribe or subtribe in Cichorioideae s.str. has its origins in Africa, either north, tropical or southern, in effect covering the whole continent. As a result the final biogeographic resolution of the subfamily is listed as 'General Africa'.

Sections 3–5 (Figs. 44.5–44.7) cover Corymbieae (Corymbioideae) and its sister group Asteroideae.

Section 3, tribes Corymbieae, Senecioneae, Calenduleae and Gnaphalieae (Figs. 44.5, 44.10). — The tribe Corymbieae (Corymbioideae) consists of only one genus, *Corymbium*, and this distinctive group is restricted to southern South Africa (Nordenstam 2007c; Fig. 44.5).

Asteroideae encompass the remainder of the family phylogeny, and it is the largest subfamily. It was recognized by Cassini (1816) and Bentham (1873a) due to the

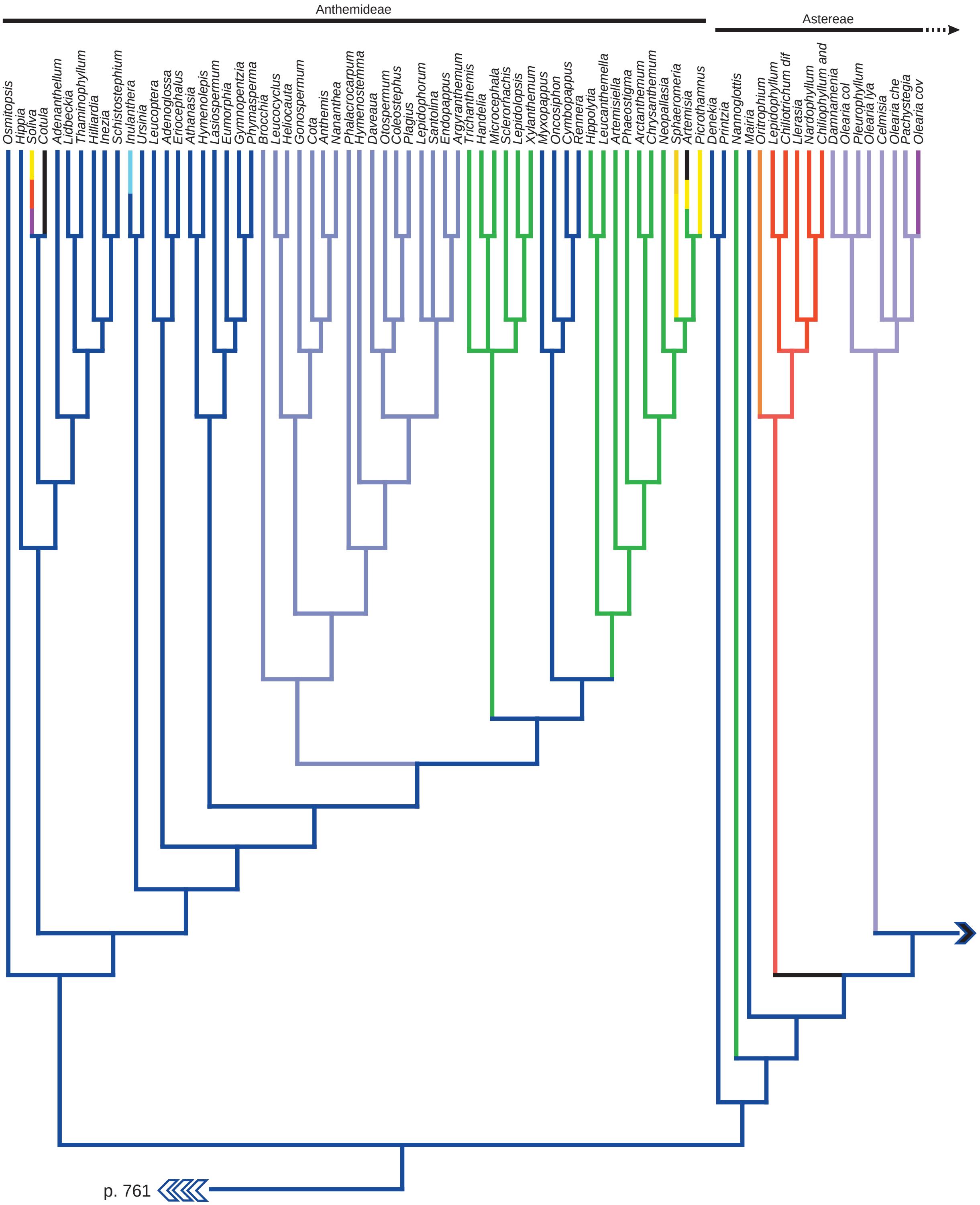
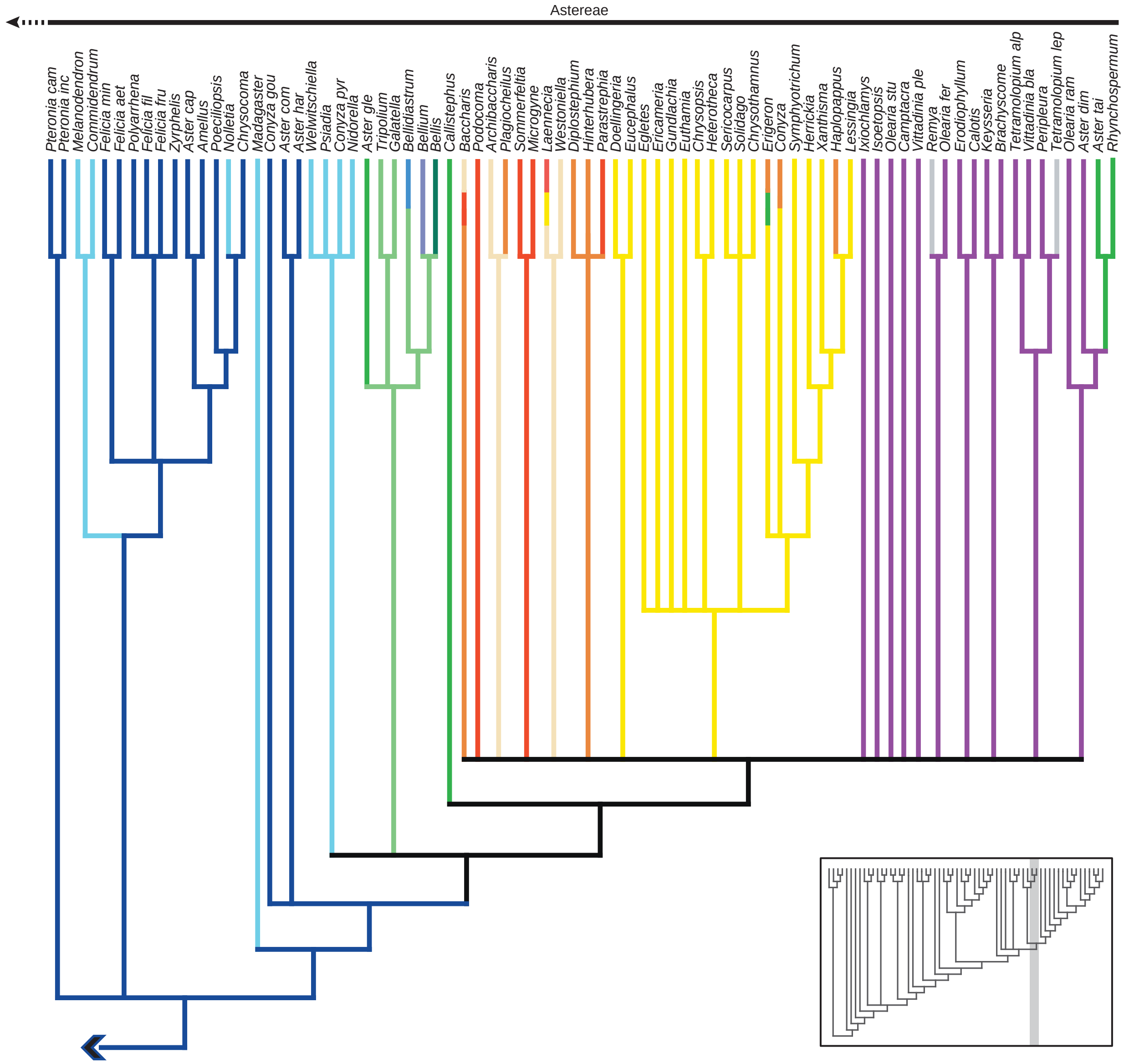


Fig. 44.6. Anthemideae and Astereae. All taxa are in the subfamily Asteroideae; see Fig. 44.7 for the color chart.



combination of its capillary pappus, true rays, and a receptive area in two lines on the inside of the style branches.

Senecioneae have long been one of the largest and most difficult groups to understand; they are truly a global tribe with major radiations in sub-Saharan Africa, West and East Asia, Andean South America, and Mexico. Because of uncertainty about the phylogenetic positions of the core of Senecioneae and two of the genera usually assigned to this tribe, relationships among these taxa and the clade formed by the other Asteroideae tribes are presently unresolved.

Two genera of Senecioneae, *Doronicum* (Eurasia and northern Africa) and *Abrotanella* (Australasia and southern South America), “fall out” of monophyletic Senecioneae. Since there is a general problem of tribal relationships among Senecioneae and its potential sister groups, there are not enough data to determine whether or not these two genera should stay in the tribe as subtribes or be moved to tribes of their own. The authors of the Senecioneae Chapter (Nordenstam et al., Chapter 34) have reserved final judgment on this matter until they have more information.

Within the core Senecioneae clade there are four clades that form a polytomy. One represents the bulk of the species, which are found in two monophyletic subtribes that are sister taxa (Othonninae + Senecioninae). This major clade has a sub-Saharan African base with highly nested groups of species from South America and Central America–Caribbean basin. The second clade, the core of subtribe Tussilagininae, has clades in Asia, Eurasia, North

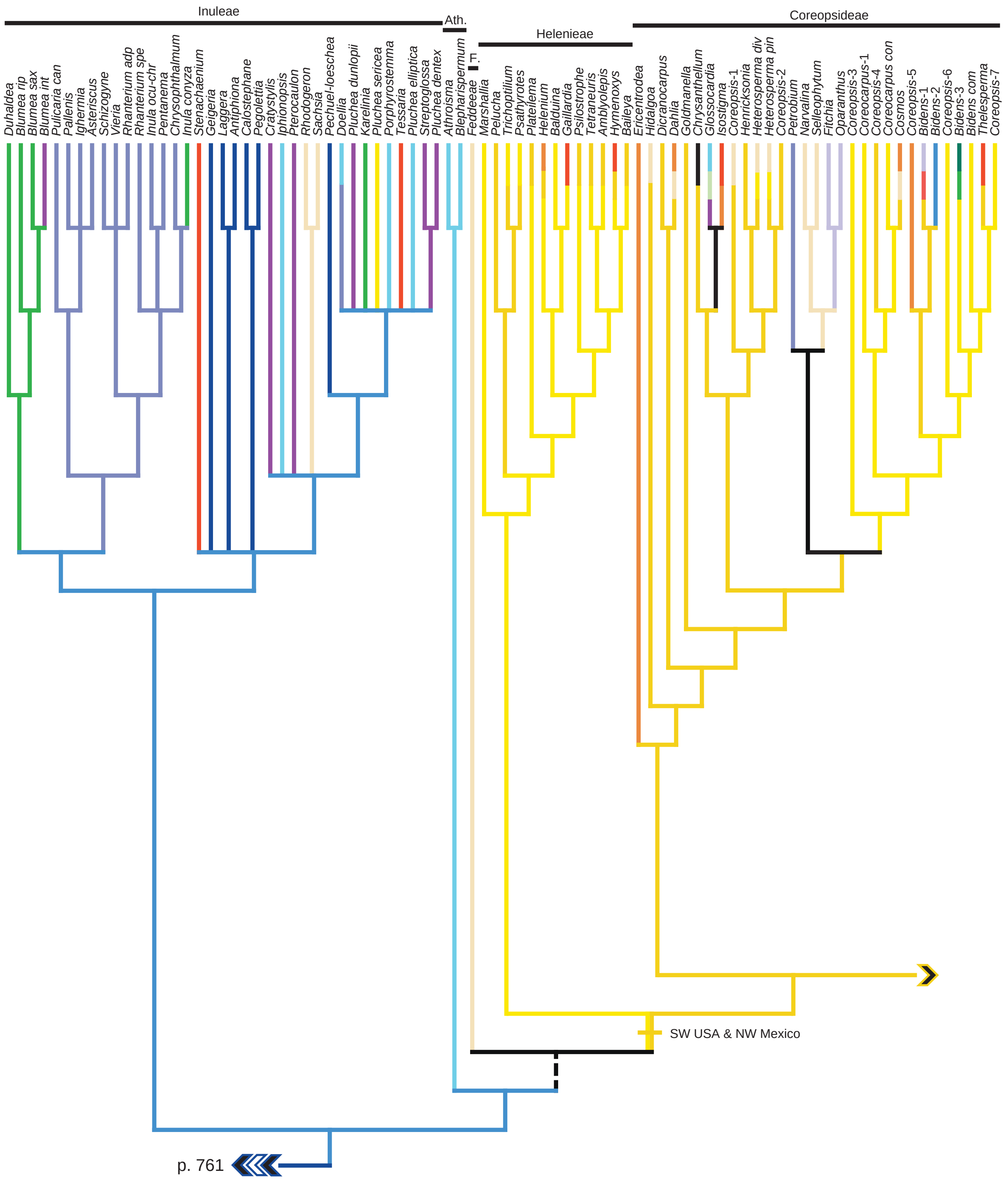
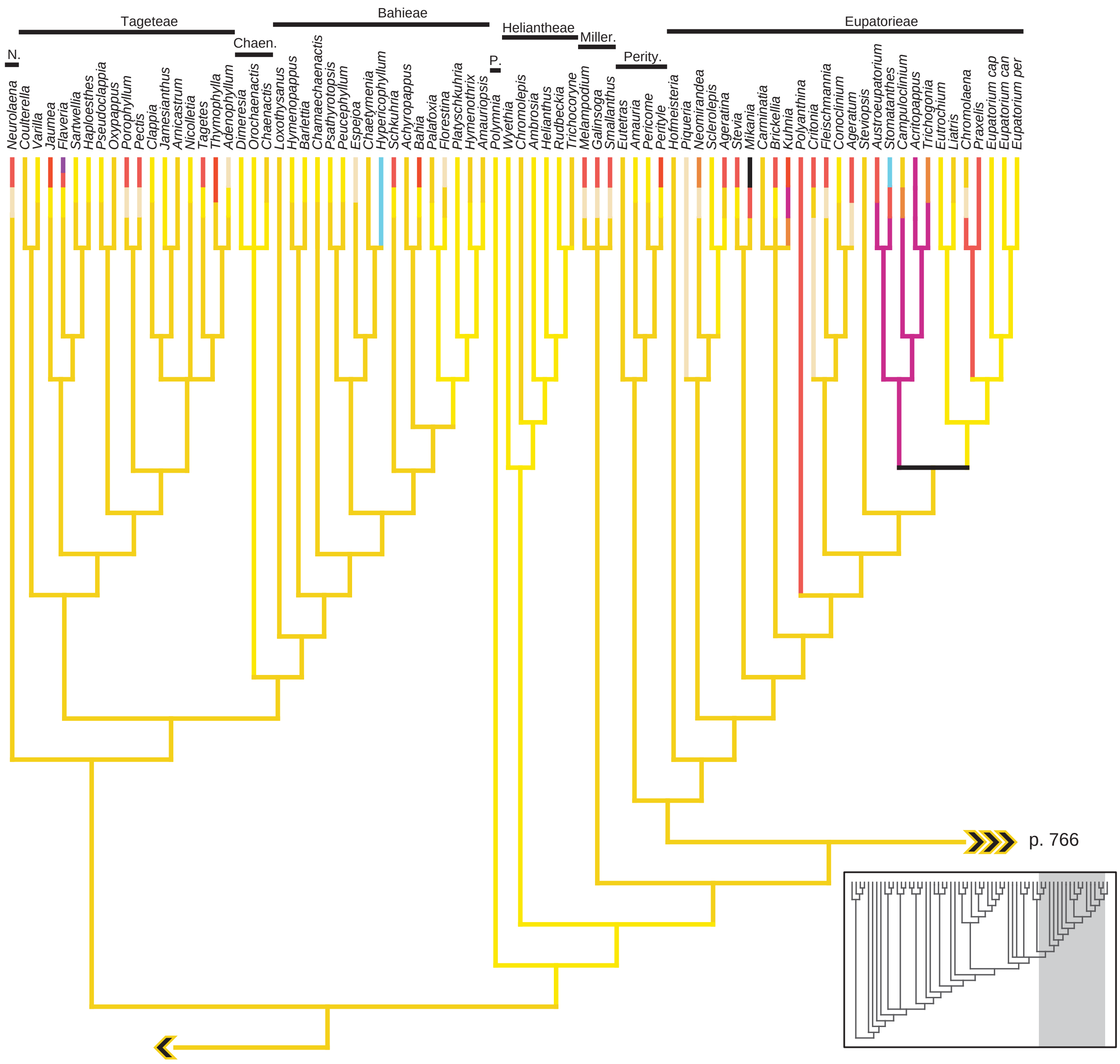


Fig. 44.7. Inuleae, Athroismeae, and the Heliantheae Alliance. All taxa are in the subfamily Asteroideae. See p. 766 for color chart. Chaen. = Chaenactideae; F. = Feddeeae; Miller. = Millerieae; N. = Neurolaeneae; P. = Polymnieae; Perity. = Perityleae.

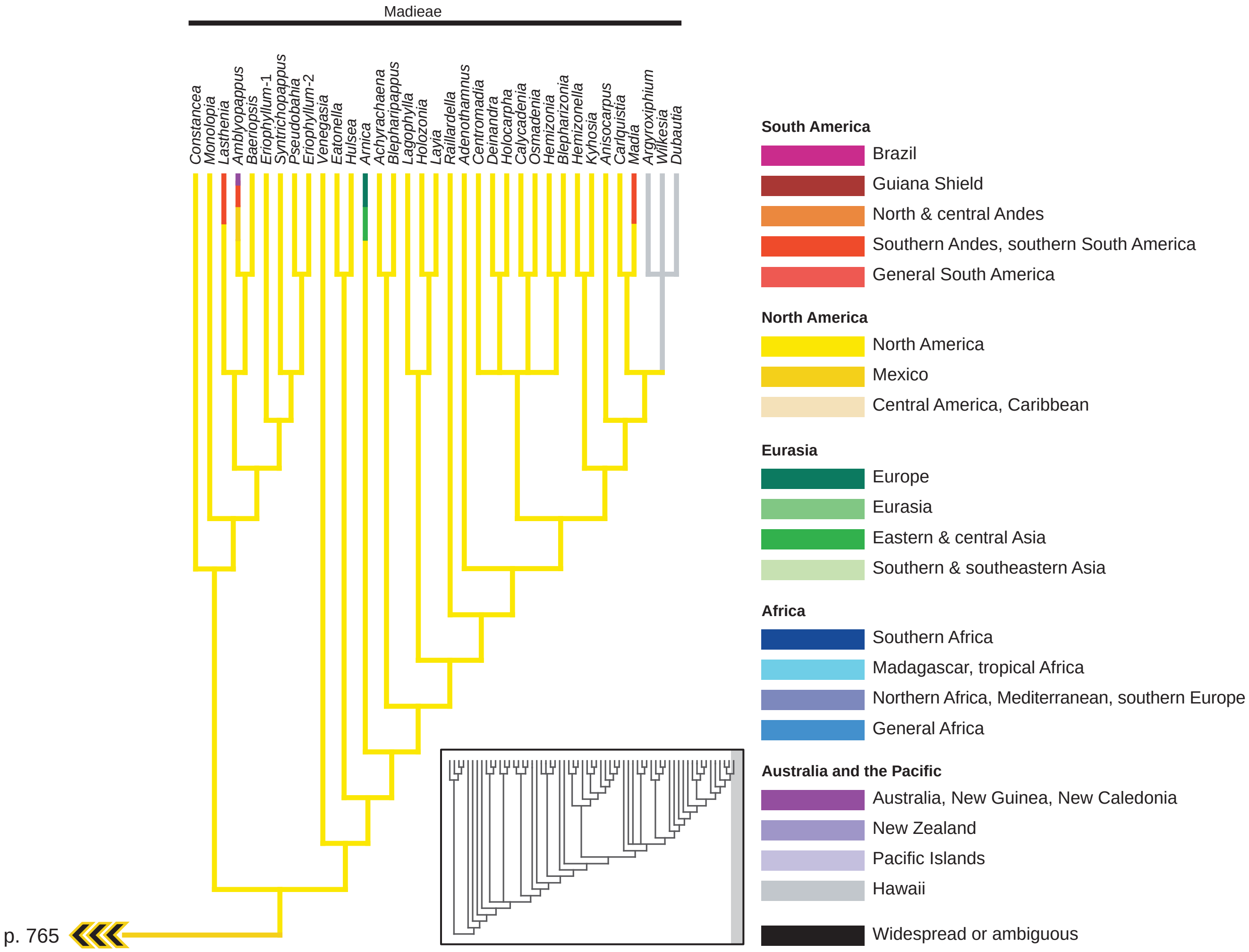


America, Mexico, and South America, but the relationships among these clades are not resolved. Two small clades complete Senecioneae. One is the South American genus *Chersodoma*, and the other is a clade composed of two groups: *(1)* an Australasian-Pacific subclade of nine genera, and *(2)* a subclade composed of a few succulent species from sub-Saharan Africa that were historically included in *Senecio* (*Senecio* m-w group, Fig. 44.5).

On the basis of the biogeographic patterns observed in the metatree, one can certainly propose a sub-Saharan origin for the Othonninae + Senecioninae clade and possibly a southern African origin for the tribe with radiations into other areas. The southern African origin is reinforced by the fact that the most closely related clades in more basal and derived positions in the metatree have a southern African origin (i.e., Corymbieae and the clade made up by Calenduleae + Gnaphalieae + Astereae + Anthemideae).

The small tribe Calenduleae is found almost exclusively in Africa with its greatest diversity in southern Africa; the tropical and northern African groups are nested high in the tree. It is the sister taxon of Gnaphalieae + Anthemideae + Astereae clade (Figs. 44.5, 44.6).

The extant members of the Gnaphalieae had a major radiation in southern Africa early in their history with large radiations into Australia and New Zealand.



Although not reflected in this figure, this tribe also has large highly nested groups of taxa in South America and Asia indicating dispersal to these regions as well (Ward et al., Chapter 36).

Section 4, tribes Anthemideae and Astereae (Fig. 44.6, pp. 762, 763; Fig. 44.10C). — Sister to Gnaphalieae is the clade consisting of Anthemideae + Astereae (Fig. 44.6). The tribe Anthemideae has a southern African grade at the base followed by a Mediterranean–northern African clade as well as one or two Asian clades (Oberprieler et al. 2009, Chapter 38).

The phylogeny of the tribe Astereae (Fig. 44.6) is not as clearly based in southern Africa as are the other tribes in this clade: Calenduleae, Gnaphalieae, and Anthemideae. Nevertheless, this origin is the most parsimonious explanation for the basal grade of this tree. Although the tribe is nested among clades with a southern African origin, there are several taxa from other regions that are found in basal positions in the Astereae clade (e.g., *Nannoglottis* from south-central China, a clade from South America, and one from New Zealand). More highly nested in the tribe are some tropical African and Asian groups as well a clade with representatives in South America, North America, and Australia, although their relationships to one another are somewhat unresolved.

The extant members of the large clade consisting of Calenduleae + Gnaphalieae + Anthemideae + Astereae, has an African origin, most likely sub-Saharan or southern Africa. As mentioned earlier it is possible that the Senecioneae are the sister group of this clade.

Section 5, tribes Inuleae, Athroismeae and the Heliantheae alliance (Fig. 44.7, pp. 764–766; Fig. 44.10D–F). — The next clade on the metatree (Fig. 44.7) contains Inuleae (including Plucheeae). The tribe is divided into two subtribes, Plucheinae and Inulinae (Anderberg et al., Chapter 39). The Inulinae clade has a split between a Mediterranean–northern African clade and an Asian clade. The Plucheinae clade has a southern African basal polytomy (except for *Stenachaenium*) with a pantropical clade nested within (including southern Africa, tropical

Africa, and northern Africa). Given that one subtribe has the potential for being rooted in the Mediterranean–northern African area and the other in southern Africa and that the clades basal to Inuleae as well as Athroismeae are most likely rooted in sub-Saharan Africa or southern Africa, it seems likely that Inuleae have an African origin, and it is shown as 'General Africa' in origin in Fig. 44.7.

The tribe Athroismeae is the sister group of the Heliantheae Alliance and includes five genera from Africa, mostly from the tropical eastern region (Fig. 44.7). This clade marks the end of the African influence on the family and signals a dramatic shift to the Americas, most notably southwestern United States (SW USA) and northwestern Mexico (NW Mexico).

The recently described tribe Feddeeae is endemic to Cuba and is supported as being part of the Heliantheae Alliance (Cariaga et al. 2008). However, it may be the sister group to the rest of the Alliance, grouped near the base, or related to Athroismeae. For now it sits with some ambiguity at the base (Fig. 44.7).

The core Heliantheae Alliance begins with the tribe Helenieae and its sister group (Fig. 44.7). This clade has strong support. Many of the clades within the core Heliantheae Alliance are ambiguous as to whether they are rooted in Mexico or North America (north of Mexico). This is the result of the somewhat artificial political categories selected for the biogeographic portion of this analysis. Some of the clades of the Heliantheae Alliance are from both SW USA and NW Mexico and frequently switch from one location to the other or inhabit both. Other clades are more firmly affiliated with either Mexico or North America (north of Mexico). For instance, the tribe Madieae (Fig. 44.7) is almost totally in North America (north of Mexico) while Helenieae (Fig. 44.7A), Coreopsideae (Fig. 44.7), Tageteae (Fig. 44.7), and Bahieae (Fig. 44.7), are frequently found in both areas. For tribes such as Heliantheae (Fig. 44.7) and Millerieae (Fig. 44.7), there are too few taxa sampled to make a decision on the origin of these clades. These sampling concerns are minor since the root of the entire radiation is clearly in NW Mexico and the SW USA, with repeated incursions into Central America, the Andes, and back to North America. This agrees with Baldwin et al. (2002) who said, "the most recent common ancestor of taxa referable to Helenieae s.l. (and to Heliantheae s.l. + Eupatorieae) … probably occurred in southwestern North America (including northern Mexico)." Baldwin et al. (2002) also pointed out that the endemic Californian diversity in the Heliantheae Alliance is mostly confined to one clade, Madieae.

Nested within the Heliantheae Alliance is the large and distinctive tribe Eupatorieae (Fig. 44.7), a large New World tribe with its base in Mexico and repeated dispersals to Brazil, South America, and North America.

What happened in the history of Compositae between the radiations in Africa and the Heliantheae Alliance in North America? Previously, Funk et al. (2005) speculated that since the base of the Heliantheae Alliance was in the SW USA and NW Mexico, the path from Africa to North America and Mexico might have been via Asia. However, if *Feddea* (Cuba) is the sister taxon of the core Heliantheae Alliance, then that proposition seems less likely. One possibility might be something like a peri-Tethyan dispersal, but these dates (late Triassic 6–2 Ma) would make the clade much younger than previously thought. Much depends on whether or not *Feddea* is ultimately supported as the sister group of the core Alliance.

The summary trees for the family (Figs. 44.1, 44.2) show the results of the parsimony mapping of the distributions. In this condensed tree it is even more evident that extant Compositae had a South American base with an African diversification and radiation into Asia, Eurasia, Europe, Australia, etc. followed by the burst of diversification in North America. The unrooted diagram provided greater clarity as to the biogeographic patterns of the phylogeny (Fig. 44.2).

Odd genera

Throughout the history of the classification of Compositae there have been a number of difficult-to-place genera. Funk et al. (2005) and Panero and Funk (2008) discussed how important these genera were to resolving biogeographic hypotheses for the family. These problem genera were traditionally grouped with taxa that they were "less different from" rather than groups with which they shared characters. It is interesting to note that many of these taxa have secondary or tertiary heads, with primary heads reduced to one or a few florets and then re-aggregated onto a common receptacle. As a result they usually lack ray florets and do not have the common involucral and receptacular characters, adding to the difficulty of assigning them to tribe.

The advent of molecular data has allowed us to determine the relationships of many of these odd genera. Some that have relevance to the biogeography of the family are discussed here. Their positions have turned out to be among the more interesting aspects of this study because they are frequently relatively species-poor sister groups of large radiations: *Cratystylis*, in Plucheinae, Athroismeae, or even *Feddea*, as the sister group to the Heliantheae Alliance, *Corymbium* as the sister group to Asteroideae, *Platycarpha* as the sister group to the Vernonieae + Liabeae clade, *Gymnarrhena* as the sister group of Cichorioideae + Asteroideae, African Mutisieae at the base of the thistles, and *Hecastocleis* as the sister group to the major radiation of the family. All of these have important phylogenetic positions for the biogeographic analysis and illustrate the fact that odd taxa should always be included in analyses at all levels (Funk et al. 2005; Funk and Chan, 2008; Panero and Funk 2008). Although, some of these taxa are on long branches and their position may be affected by 'long branch attraction'.

Age of origin

Considering the size and importance of Compositae, surprisingly little has been published about the possible area of its origin or its age since Bentham (1873a, b). As mentioned before, one reason may be because of the absence of any reliable macrofossils from the early diversificaiton of the family. A few individuals have guessed at a possible age. Turner (1977) thought that the family originated in the mid-late Cretaceous (ca. 100 Ma), possibly near the time of the first upheaval of the Andes (ca. 90 Ma). Other recent estimates include 60 Ma (Zavada and de Villiers 2000), 53–43 Ma from DeVore and Stuessy (1995), and 38 Ma from Bremer and Gustafsson (1997). In the 2005 supertree paper (Funk et al.), an examination of the relationship of Compositae to its two most closely related families was used to suggest an age of around 50 Myr for the separation of Compositae + Calyceraceae (southern South America) from Goodeniaceae (Australia).

Lundberg's study (Chapter 10) included the whole of the order Asterales. In addition to Goodeniaceae, the other families of the order that are closely related to Compositae are all found in Australia, New Guinea, New Caledonia, and/or New Zealand (Fig. 44.3). As a result of these distribution patterns, one can hypothesize that the ancestor of these eight families of Asterales had a Gondwanan distribution, and that the split between the ancestor of Goodeniaceae and the ancestor of Calyceraceae + Compositae took place with the formation of the Drake Passage that separated South America and Australia from Antarctica. Estimations of when that passage was formed range from middle Eocene to Oligocene to early Miocene but recent evidence narrows it to 50–41 Ma (Ghiglione et al. 2008 and references cited therein). The earlier date reflects a spreading with low incursions of water and the younger time period reflects a deeper water passage. The question then becomes how deep and wide did the Drake Passage have to be to prevent easy dispersal of pollen and seeds? Other factors to consider include the fact that the oldest part of the Andes Mountains is the southern section, and the uplift of this area began ca. 90 Ma and lasted until ca. 50 Ma. The mountains were high enough to cause a drying effect only late in this time period; in fact, pollen records show that 53 Ma southern South America was forested. So, the earliest time of separation between the continents coincides with the final uplift of the southern mountains. Geological, climatic, and ecological considerations, therefore, can be used to suggest an origin of the Calyceraceae-Compositae clade at some time after 50 Ma (perhaps as recent as 41 Ma), with the base of Compositae radiating as the Andes developed. Since Africa drifted away from Gondwana some time before South America and Australia each drifted away from Antarctica, it appears unlikely that the movement of the African continent had any influence on the base of the cladogram.

Within the family, most authorities agree that, based on pollen data (Germeraad et al. 1968; Muller 1970), most of the current tribes were in existence by the end of the Oligocene (25–22 Ma; Muller 1981). An older date is given by Graham (1996) who dates the earliest pollen from Mutisieae as Eocene to middle Oligocene (50–25 Ma), pollen from the Astereae-Heliantheae-Helenieae group as Eocene (50–35 Ma), and pollen of the *Ambrosia*-type (Heliantheae) from latest Eocene/early Oligocene (35–25 Ma). Given the phylogenetic position of taxa with the *Ambrosia*-type pollen, we can use the date of 35–25 Ma for the base of the Heliantheae Alliance (Fig. 44.8). There are four Hawaiian taxa estimated to have diverged 7–5 Ma nested high in the metatree. A radiation in the northern Andes (Espeletiinae), with an age of approximately 2 Myr, is in line with the occurrence of the sub-páramo habitat. The tribe Liabeae is a north-central Andean clade that can be dated 15–5 Ma when the central Andes were uplifted. Finally, there are taxa from the basal grade that are found on the Guiana and Brazilian Shields; these plants inhabit areas where the rock is older than the family. For instance, in the Guiana Shield area, the final uplift was probably in the Cretaceous (Gibbs and Barron 1993), and so predates the origin of Compositae and is of no help in determining the ages of those clades.

The authors of some of the chapters in this book have speculated as to the age of origin of their clades. The Barnadesieae clade, which is the sister group to the rest of the family, is estimated to be at least 23 Myr old (Stuessy et al., Chapter 13). A minimum age of 23–28 Myr (Late Oligocene) for fossil pollen related to the extant genera of Gochnatieae, and a minimum of 20–23 Myr (Early Miocene) for fossil pollen of Nassauvieae and Barnadesieae were reported (Katinas et al. 2007). On the basis of ITS divergence, Wang et al. (2007) suggested a date of 29–24 Ma for the separation of Cardueae from the African (former Mutisieae) tribes; and in Chapter 20, Susanna and Garcia-Jacas stated that Cardueae originated as part of the Tertiary flora and benefited extensively from the new habitats that were open during the deep climatic and geological changes during the Miocene (24–5 Ma), based on data from Cox and Moore (2004). In Cichorieae, Kilian et al. (Chapter 24) point out that the fossil record shows three different types of echinolophate pollen, i.e., the *Cichorium intybus* L. type (age 22–28.4 Myr; Hochuli 1978), the *Scorzonera hispanica* L. type (minimum age 3.4 Myr; Blackmore et al. 1986), and the *Sonchus oleraceus* type (minimum age 5.4 Myr; Blackmore et al. 1986),

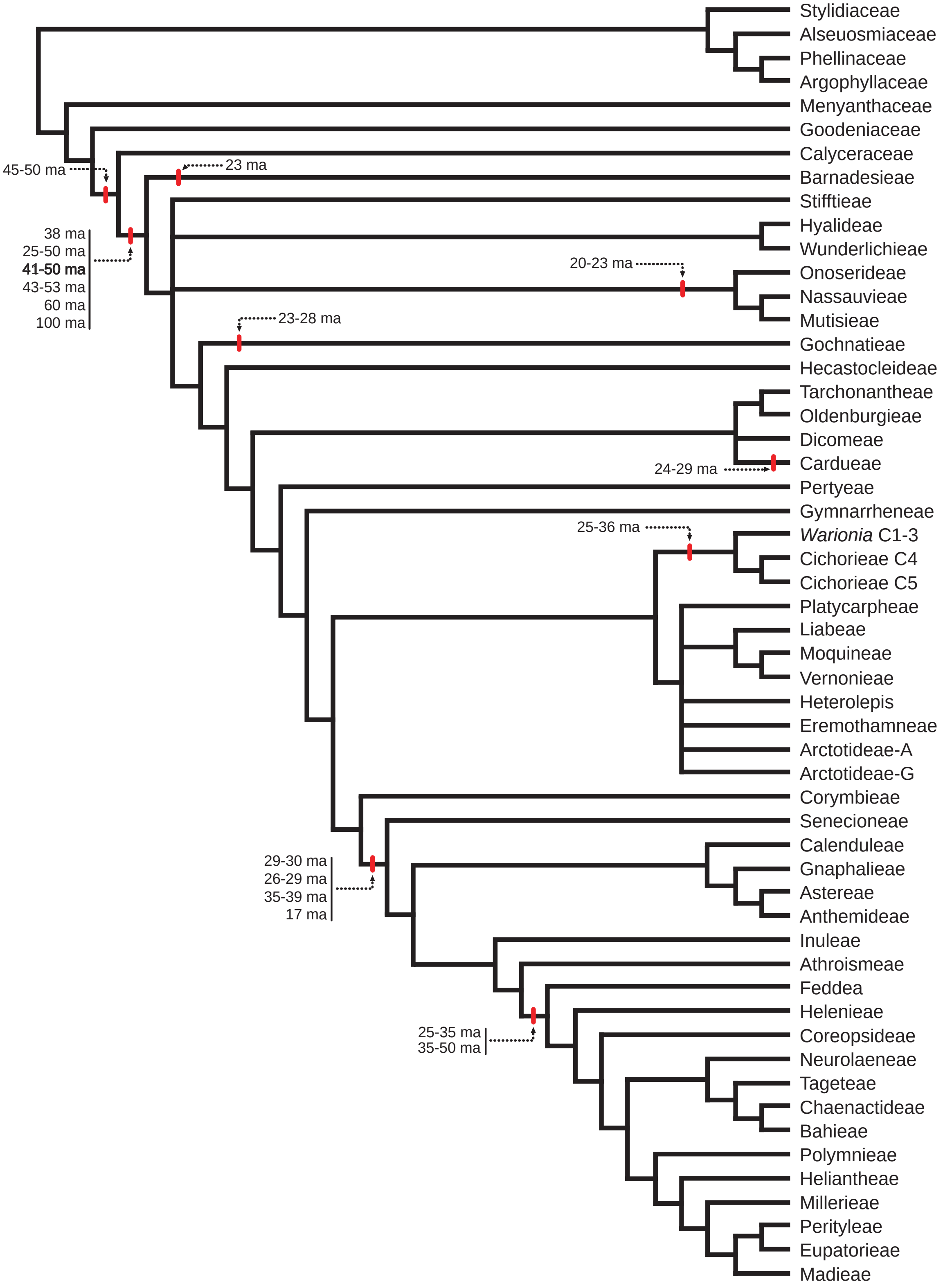


Fig. 44.8. There are few dates that can be placed on the phylogeny of Compositae with any certainty. The separation of the outgroup lineages from that of Calyceraceae-Compositae may be placed at a time when Australia separated from Antarctica–South America (the flora is believed to have separated about 50–41 Ma), and the radiation at the base of Compositae may be linked to uplift of the southern Andes.

that were used to calibrate the phylogenetic tree; and estimates were calculated by using an uncorrelated relaxed molecular clock approach (Drummond et al. 2006). The results indicated a most probable origin of the tribe in the Late Eocene or Oligocene (36.2–25.8 Ma; Tremetsberger et al., unpub. data) in North Africa.

Pelser and Watson (Chapter 33) discussed the age of the subfamily Asteroideae on the basis of age estimates in the recent literature. Hershkovitz et al. (2006) estimated the crown age of Asteroideae to be ca. 29–30 Myr. Kim et al. (2005) used nonparametric rate smoothing in their molecular dating study of *ndhF* data and *Cornus* as an internal calibration point and arrived at an estimate for the subfamily of 26–29 Myr. Their age estimate for Asteroideae derived from average synonymous nucleotide substitutions using the same dataset and substitution rates for Poaceae and Oleaceae was 35–39 Myr (Kim et al. 2005). These studies and unpublished data for Senecioneae (Pelser et al., in prep.) further indicate that the Heliantheae Alliance and all Asteroideae tribes outside of it are 17 Myr old or older and were the result of a family-wide, rapid Oligocene–Early Miocene diversification. These results are roughly in line with other molecular dating studies in Compositae (e.g., Wikström et al. 2001; Wagstaff et al. 2006) and with paleo-palynological data (e.g., Katinas et al. 2008), although the latter source of data generally results in somewhat lower age estimates for Asteraceae lineages.

Most of the dates discussed above are displayed on Fig. 44.8 and if we eliminate some of the outliers, we find that all of the tribes are proposed to have, more or less, the same age, around 25–35 Myr, and the age of the family seems to be 41–50 Myr. Initiation of all of the known major radiations of Compositae 35–25 Ma places their origins within the Oligocene, which is often considered an important time of transition, a link between "[the] archaic world of the tropical Eocene and the more modern ecosystems of the Miocene" (Scotese 2008). It makes ecological sense that a rapid expansion of the number of taxa in many groups of Compositae would have coincided with the regression of tropical broad-leaf forests to the equatorial belt and the expansion of open, drier areas.

The comparatively recent origin and great diversity of Compositae are likely indicative of the ecological success and evolutionary lability of the family (as is evidenced by their diverse appearance in Figs. 44.9 and 44.10), especially in drier environments. Turner (1977) felt that the family's "rich secondary metabolite chemistry, often short life cycle, facultative pollination, and freedom from many co-evolutionary restraints may be responsible for this success." It seems likely that the high seed set, dispersal ability, and ability to radiate into new habitats have helped as well.

Barker et al. (2008) examined gene duplication and retention in Compositae and found that there were at least three ancient whole genome duplications in the family resulting from paleopolyploidization events: at the base of the family just prior to its radiation, and near the base of tribes Mutisieae and the large Heliantheae Alliance. As one explanation for Compositae's evolutionary success, they suggest that retention of the resulting duplicates of *CYCLOIDEA* genes, which code for transcription factors associated with floral symmetry and branching patterns, were likely significant in the evolution of Compositae, because Chapman et al. (2008) observed that some copies have experienced positive selection and that the expression of *CYC* genes is subfunctionalized among the disk and ray florets of the composite inflorescence. Thus, ancient polyploidization may be, in part, responsible for the evolutionary success of the family.

CONCLUSIONS

The Calyceraceae-Compositae clade (as we know it today) may have originated in southern South America ca. 50–41 Ma, and the diversification of the family started in the same area. The diversification of Calyceraceae was modest by comparison with that of Compositae, which have traveled the globe. In Compositae, following the southern South American radiation, there was an African explosion. Of the 1600–1700 genera in Compositae today, about two-thirds are in clades with the basal branches in Africa, many in southern Africa. In fact, with the exception of the Mutisieae (sensu Cabrera) grade at the base and the highly nested Heliantheae Alliance, all of the major clades in the family appear to have an African origin or a major African presence near the base of their phylogenies. From this African origin came numerous movements into Asia, Eurasia, Europe, Australia, etc., many of which have spawned substantial radiations (e.g., Cardueae, Vernonieae, Anthemideae). The clade formed by the core Heliantheae Alliance has a North American (including NW Mexico) origin beginning by 35–22 Ma, which coincides with a land bridge connection from Asia. Previously (Funk et al. 2005) it was suggested that, because the sister clade to the Heliantheae Alliance is found in tropical eastern Africa, the ancestor of the Heliantheae Alliance could have come over the land bridge from Asia into western North America and down into Mexico. However, the position of the Cuban *Feddea* at the base of the American clade of the Heliantheae Alliance does not reinforce a land-bridge hypothesis. Given the success of a diversity of young lineages in the Heliantheae Alliance and long-distance dispersal to remote oceanic islands and between continents (see Baldwin 2009, Chapter 41), the possibility of a direct Old World to New World dispersal

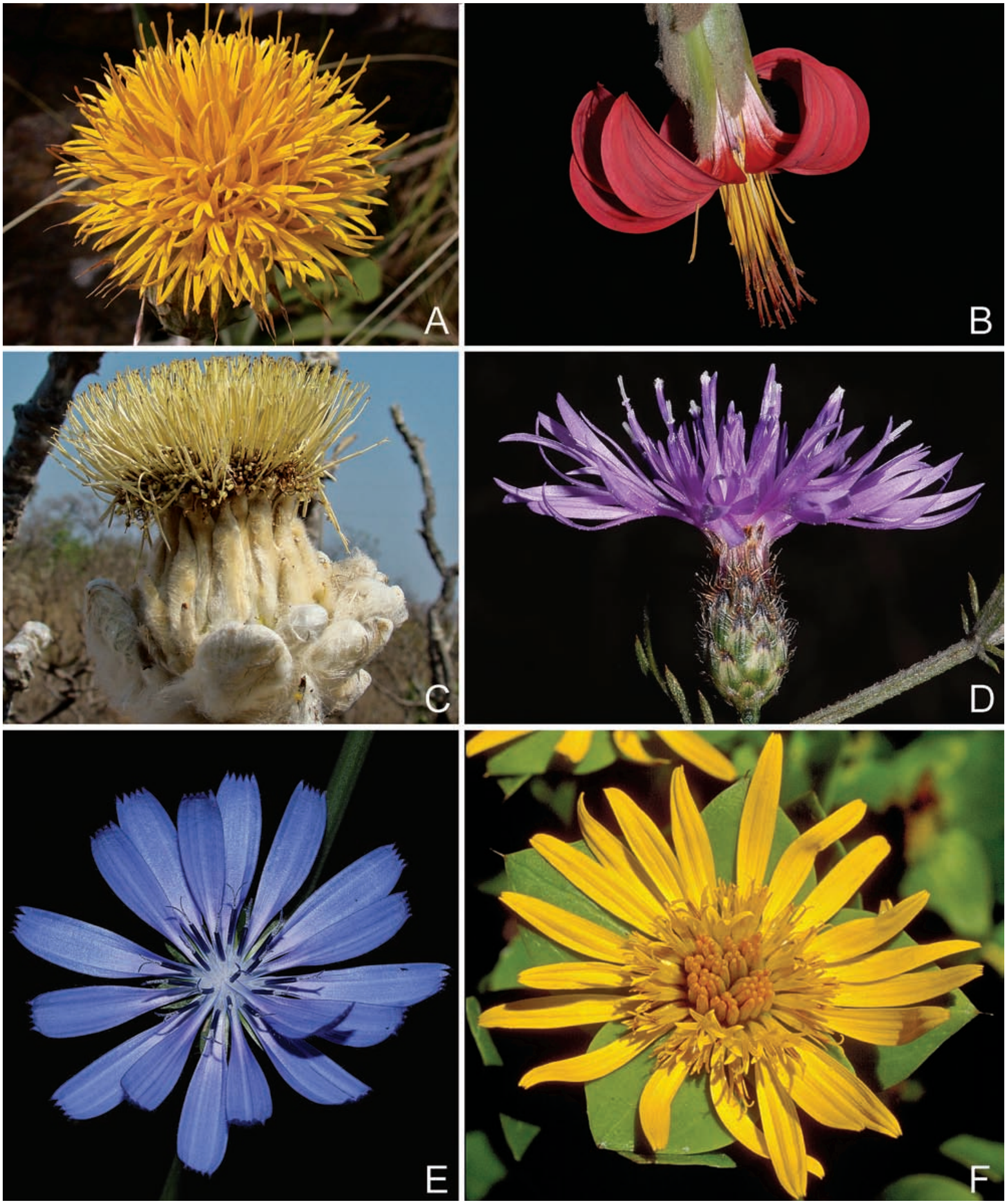


Fig. 44.9. Members of Compositae, subfamilies Barnadesioideae through Cichorioideae. **A** *Schlechtendalia luzulaefolia* Less. (Barnadesieae from Uruguay: Maldonado, Piriápolis, Cerro San Antonio); **B** *Mutisia clematis* L. (Mutisieae from Colombia: Cundinamarca, Finca "El Cerro"); **C** *Wunderlichia mirabilis* Riedel (Wunderlichieae from Brazil: Minas Gerais, Cerra do Cipó; *Roque 1622*); **D** *Centaurea stoebe* L. (Cardueae from USA: Virginia, Shenandoah National Park); **E** *Cichorium intybus* L. (Cichorieae from Uruguay: Montevideo); **F** *Didelta spinosa* Ait. (Arctotideae from South Africa, Northern Cape: *Funk and Koekemoer 12641*). [Photographs: A, B, D, E, J.M. Bonifacino; C, N. Roque; F, V.A. Funk]

Fig. 44.10. Members of Compositae subfamily Asteroideae. **A** *Senecio ceratophylloides* Griseb. (Senecioneae from Uruguay: Canelones); **B** *Dimorphotheca sinuata* DC. (Namibia); **C** *Bellis perennis* L. (Astereae from Argentina: Tierra del Fuego, close to Paso Garibaldi); **D** *Stenachaenium megapotamicum* (Spreng.) Baker in Mart. (Inuleae from Uruguay: Maldonado, Sierra de las Animas); **E** *Helianthus annuus* L. (Heliantheae s.str. from Uruguay: Río Negro, close to Fray Bentos); **F** *Gyptis pinnatifida* Cass. (Eupatorieae from Uruguay: Rivera, Arroyo Lunarejo). [Photographs: B, C.A. Mannheimer; A, C–F, J.M. Bonifacino.]

of the ancestor of the American clade of the Heliantheae Alliance must be taken seriously.

What about *Hecastocleis*? This monotypic North American genus from the mountains of Nevada and the Death Valley area sits between the southern South American basal radiation and the African diversification. In Funk et al. (2005) two possible scenarios were proposed (apart from errors and misidentifications). First, there could have been two events of long distance dispersal, one from South America to North America and one from North America to Africa. The second possibility is that Compositae moved into North America from South America, then over to Europe and down into northern Africa followed by extensive extinction in the northern hemisphere (Panero and Funk 2008). There are, no doubt, other explanations; however, we do not have sufficient data to favor one hypothesis over another. One key group, Gochnatieae, is located just below *Hecastocleis* on the metatree, and it is being studied at the species level using both molecular and morphological data in the hope of providing a better estimation of the early biogeographic history of Compositae (Sancho et al., pers. comm.).

Prior to the development of molecular techniques, most workers in the family followed the traditional concept of the family laid down by Bentham and elaborated upon in Cronquist (1955, 1977). Cronquist had detailed ideas about the characteristics of ancestral Compositae. He believed that the tribe Heliantheae, and more specifically core Heliantheae, were the cauldron out of which the rest of the tribes evolved. He thought that the ancestor might have been something like *Viguiera* (Heliantheae s.l.), but he pointed out that it was still "not exact" because the genus has neutral ray florets and only two principal pappus members (Cronquist 1977). Several scientists disagreed with Cronquist. Skvarla (1977) and Jeffrey (1977) pointed out that the characters were not consistent with the position that Heliantheae s.l. was the primitive group of the family. In publications outside the 1977 Heywood et al. volumes, Carlquist (1966, 1976) and Robinson (1981) tried to add additional tribes and to point out that the proposed direction of evolution did not make sense. These synantherologists thought that the pollen, anatomy, and morphology of Mutisieae were more like that of the related families, and that Heliantheae and other tribes had derived characters.

Acknowledging that extant lineages of Barnadesieae have been around for as long as the most highly nested branches of the family, it is wise to not put too much emphasis on the characteristics that are found in this basally diverging group but rather on characteristics that are shared by all early diverging branches and the outgroups. Many characters of Barnadesieae and Mutisioideae are variable (e.g., corolla morphology), but a few common characteristics can probably be determined: the pollen was probably psilate (Skvarla 1977; Zao et al. 2006; Blackmore et al., Chapter 7); the basal chromosome number for the closely related families is $x = 9$ and that number has been proposed for Compositae with $x = 10$ as the apparent basal number for tribes of South African origin (Semple and Watanabe, Chapter 4); and secondary chemical compounds have developed from a small number of relatively simple flavonoids, polyacetylenes, coumarins, and triterpenes to a large number of complex compounds from many different chemical classes (Calabria et al., Chapter 5).

Bremer (1994) started the process of updating the characters attributed to a hypothetical ancestor and Lundberg (Chapter 11) has added to the list. Here we have refined some of the characters and added a few more. Here we offer a list of potential plesiomorphic characters for the extant members of Compositae (⋆ indicates that the character defines a larger clade than the Calyceraceae + Compositae clade; bold indicates a potential character unique to the ancestral members of Compositae):

- ⋆Shrubs or subshrubs; ⋆no internal secretory systems.
- **Inflorescence cyme-like.**
- ⋆Leaves alternate and spirally inserted.
- **Heads indeterminate;** few heads per plant, each with many flowers.
- **Involucral bracts in several series, imbricate without hyaline or scabrous margins.**
- **Receptacle naked.**
- Florets perfect and fertile, arranged in a head; ⋆parts in 5's; mostly one type of flower, **some differentiation in floral morphology in peripheral florets possible** but without true rays.
- Corolla white or possibly pink, yellow or blue; ⋆probably 5-lobed, lobes deeply divided and with much variation.
- ⋆Stamens alternate with the corolla lobes; **anthers fully connate at the margins with the filaments free** with upper part of filaments forming a filament collar; **thecae spurred (calcerate) and possibly tailed (caudate);** possibly without apical appendage; ⋆dehisce by longitudinal slits; pollen kit present.
- **Pollen grains 3-celled,** ⋆pollen prolate and psilate.

- Styles slender, shortly bifid, without hairs; **solid band of stigmatic surface on inside of style branches; ovary consistently inferior with ovule in a basal position.**
- **Pappus of capillary bristles.**
- Fruit an indehiscent achene; ribbed.
- *Base chromosome number: *x* = 9.
- Secondary chemistry simple and characterized by a small number of flavonoids, polyacetylenes, coumarins, and triterpenes.
- Southern South American in distribution; probably growing in open dry habitats.

Finally, looking to the future, advances in genomics are changing the way we do research in systematics. Phylogenomics, the use of whole genomes for phylogenetic studies, is already occurring in many plant and animal groups and at ever increasing speeds (see brief overview in Pennisi 2008) and will no doubt become the standard of the future in Compositae systematics as costs decrease and technology becomes more widely available. Whole chloroplast genomes have already been sequenced for many plant groups and used in phylogenetic studies, particularly for establishing the position of basal angiosperms (Goremykin et al. 2004; Soltis et al. 2004). Phylogenomic studies in Compositae lag considerably behind those of the Angiosperm Phylogeny Group (APG) and that of many animals groups as well. Although the genomes of a number of Cichorioideae taxa are currently under study (Rieseberg, pers. comm.) only two economically important taxa, *Helianthus annuus* L. and *Lactuca sativa* L., are the subject of a coordinated, large scale effort. The Compositae Genome Project (CGP), headquartered at the UC Davis Genome Center, has a wide range of objectives for its studies of lettuce and sunflower (and presumably others in the future). The goal as given on the home page (http://compgenomics.ucdavis.edu/index.php) is to "integrate information at the genetic, physiological and population/evolutionary levels for a broad range of genes involved in evolution of cultivated plants and weeds, evaluate the relative importance of changes in gene sequence versus gene expression in phenotypic evolution, determine the genotypic consequences of parallel phenotypic evolution, and provide a basis for future functional analyses." For most systematists, however, the focus of whole genome sequencing will be on more accurately reconstructing the evolutionary history of a particular group of plants, most of which are not cultivated and for which the vast funding required to map genes and determine their functions will likely never be available.

As in all molecular studies, a cautionary note has been sounded relative to the resolving power of genomics for phylogenetic study (Soltis et al. 2004; Pennisi 2008). Data analysis of huge numbers of sequences is daunting and will probably still require collaboration with mathematicians and bioinformaticists. Another issue is lack of congruence, particularly with existing trees. Hervé Philippe (University of Montreal; cited in Pennisi 2008) stresses that datasets will have to be reanalyzed with different methods in order to determine the best tree. The latter is not necessarily guaranteed by more data. Additionally, taxon sampling will remain an issue. Lots of information from only a few taxa does not guarantee a sound phylogeny no matter how cutting-edge the sequencing or the analyses. Still, we can expect that genomes will be increasingly common tools in future phylogenetic studies. Hopefully, as the data accumulate there will be better resolution of taxonomic placements, particularly in the location of Senecioneae and at the base of the Compositae family tree where the position of some mutisioids and some enigmatic genera remain unclear.

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Section V

Appendices

Appendix **A**

Illustrated glossary of Compositae

Nádia Roque, David J. Keil and Alfonso Susanna

Abaxial lip
Portion of the corolla limb of a bilabiate or pseudobilabiate corolla that is oriented away from the center of the head (Figs. 1A, 54A); the lamina of a ray corolla (Fig. 2) is homologous with the abaxial lip of a bilabiate or pseudobilabiate corolla. See **Adaxial lip.**

Achene
A single-seeded indehiscent dry fruit with the seed free from the pericarp except at the placenta; the fruit in almost all Compositae. Generally breaks free from the receptacle at maturity and often falls together with pappus elements, which are borne at distal end of the achene (Figs. 3–21, 32–35). Achenes may be pappose (bearing pappus elements; Fig. 3) or epappose (without a pappus) (Figs. 4, 5). Achenes in cross section may be terete (Fig. 6), prismatic (Fig. 7), compressed (laterally flattened; Fig. 8), or obcompressed (dorsiventrally flattened; Fig. 11), and may bear ribs (Fig. 9) or wings (Figs. 8, 10, 11). Longitudinally they range from narrowly cylindrical (Fig. 101) to fusiform (Figs. 12, 13), obovoid (Fig. 14), or globose (Fig. 5), and may be straight to strongly arcuate (e.g., *Calendula*). Surfaces may be glabrous, papillose, variously hairy (often with twin hairs, sometimes glandular), or may bear tubercles or prickles. Taxonomically important variations include the number of ribs or angles (Figs. 4, 7, 9); presence or absence or degree of development of basal attenuation (Fig. 16) or stipe (Figs. 17, 18) or of apical attenuation (beaked achene; Fig. 19); type of indument; differences in form of the abscission zone or carpopodium (Figs. 20, 21); and presence or absence of apical nectaries or basal elaiosomes. In Eupatorieae, Heliantheae and Tageteae, achenes are usually blackened (carbonized) by phytomelanin deposits (Figs. 32–34); in most Cardueae, some layers accumulate phytomelanins. The achenes of Compositae, derived from inferior ovaries, are often termed cypselas. See **Cypsela, Pappus.**

Achene complex
Unit of dispersal in which one or more achenes are dispersed together with adherent phyllaries and/or paleas and sometimes with non-fruiting florets. In some Compositae each ray achene falls together with a subtending phyllary. Spine-like appendages (e.g., *Acanthospermum*; Fig. 15) or glandular trichomes or appendages (e.g., many Madieae) on the phyllary may aid in epizoochory. In *Berlandiera* the achene complex comprises a ray achene that is dispersed together with a subtending phyllary, two paleas and two staminate disk florets. In *Pectis prostrata* Cav. the basally coherent phyllaries and all the enclosed achenes break free from the receptacle and are dispersed together. In *Ambrosia* and *Xanthium* all of the paleas are fused into a spiny, knobby, or winged bur containing one or two achenes. The flattened fruiting head of *Delilia biflora* (L.) Kuntze (Figs. 50, 51) falls as an anemochorously dispersed unit enclosing a solitary ray achene.

Actinomorphic
See **Radial symmetry.**

Adaxial lip
Portion of the corolla limb of a bilabiate or pseudobilabiate corolla that is oriented toward the center of the head (Figs. 1B, 54B). See **Abaxial lip.**

Aggregate heads
Heads tightly grouped without losing their individual identities (Fig. 22).

Alveolate receptacle
Receptacle surface more or less deeply pitted, with alveoles (cavities) partially or totally enclosing the achenes.

Androecium

Collective of all the stamens in a flower; the third whorl of parts of a complete flower. In Compositae the androecium comprises (3–)5 stamens alternating with corolla lobes, with their filaments inserted at junction of corolla tube and throat (Fig. 23).

Angled achene

Achene polygonal in cross section (Fig. 7). See **Prismatic achene, Ribbed achene.**

Anthemoid style

Style with a brush-like tuft of sweeping hairs at the tip of each style branch (Fig. 24).

Anther

The pollen-bearing portion of a stamen, borne at the distal tip of a filament. In Compositae each anther comprises four microsporangia that mature as two pollen sacs (thecas) united by a connective with a usually membranous distal appendage. The connective generally extends proximally of the attachment of the anther sacs as a cylindrical anther collar (Fig. 25). Anther bases can be rounded (Fig. 25), truncate, sagittate (Fig. 26) or cordate, or pollen-bearing basal lobes of the anther sacs may extend proximal to the insertion of the anther collar (calcarate anthers; Fig. 26). The bases of the anther sacs may bear tail-like sterile appendages (caudate anthers; Figs. 27, 28). Variations in the form of anther tip appendages and anther base appendages are very important characters in the taxonomy of the family. Compositae anthers are generally accrescent, laterally cohering by their margins (synanthery) into a tube that envelops the style and the stigma (Fig. 23). Anthers are distinct in some wind-pollinated genera (e.g., *Ambrosia*, *Xanthium*). In many Heliantheae, anthers are diagnostically darkly pigmented. See **Filament, Stamens, Theca.**

Anther base appendages

Basal lobes or sterile appendages of the anther thecas. Pollen-bearing portions of the anther sac bases often are prolonged as lobes proximal to the insertion of the anther collar (calcarate anthers; Fig. 26) or bear sterile appendages (caudate anthers; Figs. 27, 28). Anther base appendages can be important for the taxonomy of tribes and genera. See **Calcarate anther base, Caudate anther base, Ecalcarate anther base, Ecaudate anther base.**

Anther collar

A proximal extension of the anther connective in Compositae borne at distal tip of filament (Fig. 25). The collar has abaxial epidermal cells enlarged and lignified and adaxial cells smaller and unlignified. In Mutisieae and Barnadesioideae, this region is imperceptible. Among Eupatorieae, the anther collar shows more variation than in any other tribe. Basal cells are usually short and the uppermost ones are elongated.

Anther tip appendage

More or less membranous sterile appendage that represents a distal prolongation of the anther connective. It can be wider than long, as long as wide, much longer than wide (Fig. 28), toothed (Fig. 26), apiculate (Fig. 27), acute (Fig. 29), retuse (Fig. 25), or obtuse. Anther tip appendages are important for the taxonomy of tribes and genera.

Anther tube

Hollow tube formed by side-to-side connation of anthers (Fig. 30) with introrse dehiscence; not formed in a few genera (e.g., *Ambrosia*). Pollen released into anther tube is generally expressed by elongation of style (Fig. 31).

Apetalous floret

See **Naked floret.**

Arctotoid style

Style with a ring of sweeping hairs borne on the shaft of the style proximal to the style branches. Differs from the Carduoid style in the swollen articulation below branches of the latter.

Aristate pappus

A pappus composed of one or more awns of variable length and diameter (Figs. 32–34).

Aristate scale

A membranous pappus element bearing a terminal bristle or awn (Fig. 35).

Astylous ray floret

A neuter ray floret without a style (Fig. 36). See **Neuter ray floret, Styliferous ray floret.**

Awn

A generally straight, stiff pappus element, varying from stiffly bristle-like to hard and needle-like (e.g., *Bidens*; Figs. 12, 13). Awns may be smooth (Fig. 101), retrorsely (Fig. 32) or antrorsely (Fig. 33, 34) barbed, or plumose (Fig. 7).

Barbellate bristle

A slender, more or less hair-like pappus element with minute, but noticeable lateral projections (Fig. 37).

Beak

A short to elongated, more or less cylindrical, distal seedless part of the achene in some Compositae (Fig. 19). A beak may be erect or more or less bent. Pappus elements are often borne at distal tip of the beak (e.g., *Taraxacum*, *Chaptalia*).

Bi- to multiseriate pappus

Pappus with elements disposed in two or more series (Figs. 38, 39).

Bilabiate corolla

Bilaterally symmetric corolla characterized by a 2-lobed adaxial lip and a 3-lobed abaxial lip (Figs. 1, 68). The abaxial lip may be enlarged, resembling the lamina of a ray floret (e.g., *Acourtia*, *Trixis*) or may be weakly differentiated and erect or nearly so (e.g., central florets of head of *Onoseris*).

Bilateral symmetry

Descriptive of corolla with petals or lobes unequal in size and shape and arranged in such a way that only one line of symmetry can divide the corolla into mirror images. Bilabiate, pseudobilabiate, ray, and ligulate floret corollas are bilateral. See **Radial symmetry.**

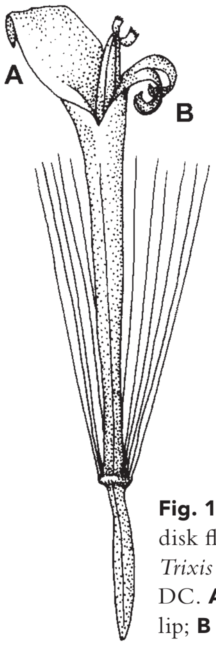


Fig. 1. Bilabiate disk floret of *Trixis vauthieri* DC. **A** abaxial lip; **B** adaxial lip.

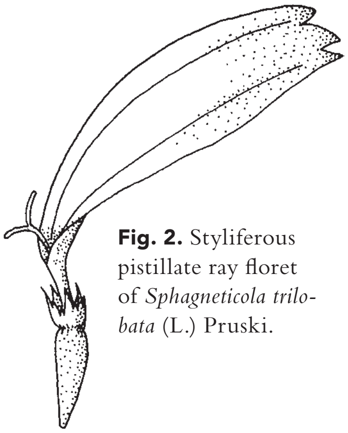


Fig. 2. Styliferous pistillate ray floret of *Sphagneticola trilobata* (L.) Pruski.

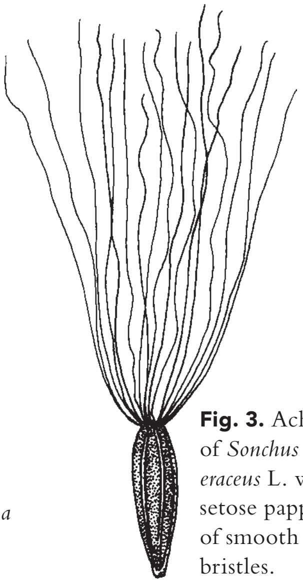


Fig. 3. Achene of *Sonchus oleraceus* L. with setose pappus of smooth bristles.

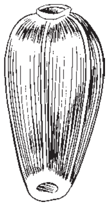


Fig. 4. Epappose ribbed achene of *Aphanactis jamesoniana* Wedd.

Fig. 5. Epappose achene of *Smallanthus riparius* (Kunth) H. Rob.

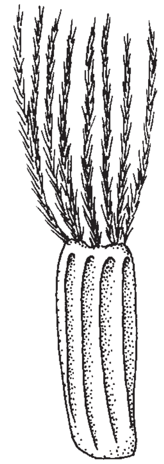


Fig. 6. Ribbed achene of *Centratherum punctatum* DC. with setose pappus of plumose bristles.

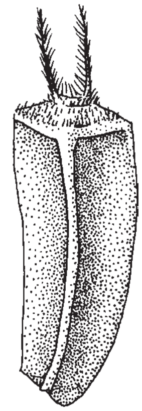


Fig. 7. Four-sided prismatic achene of *Blainvillea rhomboidea* Cass. with aristate pappus of two short plumose awns.

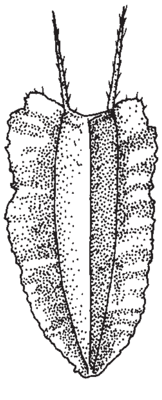


Fig. 8. Compressed, winged achene of *Verbesina diversifolia* DC. with aristate pappus of two narrow awns.

Fig. 9. Epappose ribbed achene of *Sigesbeckia jorullensis* Kunth.

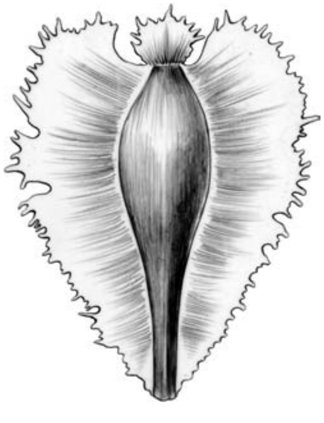


Fig. 10. Winged, obcompressed achene of *Cyathomone sodiroi* S.F. Blake. Pappus of fringed scales.

Biseriate involucre
With phyllaries in two series; phyllaries in the abaxial and adaxial series may be similar or different.

Bisexual floret
See **Perfect floret.**

Bisexual palea
Receptacular bracts (e.g., in some Gnaphalieae) that individually or collectively subtend central perfect florets within head.

Bracts
Modified leaves associated with flowers or flower clusters. Bracts in Compositae include peduncular bracts (Fig. 40), units of a calyculus (Figs. 41, 42), phyllaries (primary involucral bracts; Figs. 43–45), secondary involucral bracts (Fig. 46), and paleas (receptacular bracts; Figs. 47, 48).

Branches of the stigma
See **Style.**

Bristly receptacle
Receptacle bearing soft to stiff hair-like projections or slender, setiform scales that are not homologous with paleas (receptacular bracts; e.g., *Centaurea*, *Cirsium*).

Bur
A unit of dispersal containing one or more achenes, characterized by spine-tipped, knob-like, or winged bracts (e.g., *Ambrosia*, *Arctium*).

Calcarate anther base
Bases of anther thecas with pollen-containing portion prolonged below the insertion of the anther collar as spur-like projections (Fig. 26). See **Ecalcarate anther base.**

Calycle
See **Calyculus.**

Calyculate involucre
Involucre subtended by a calyculus (Fig. 41, 42).

Calyculus
Structure formed by an outer row of differentiated bracts immediately subtending the true involucral bracts. Sometimes described as an outer involucre. It is frequent and characteristic of some tribes: Senecioneae, Helenieae and Heliantheae (Fig. 41, 42). Synonym: epicalyx. See **Involucral bracts, Involucre, Phyllary.**

Calyx
Collective term for the sepals of a flower; the outermost whorl of parts of a complete flower; sepals in most families are more or less herbaceous and are commonly green or otherwise pigmented. In Compositae the calyx is modified as a pappus of dry scales, bristles, and/or awns; individual units of the pappus correspond very rarely to sepals. See **Pappus.**

Capillary bristle
Very slender, hair-like pappus element. See **Pappus bristle.**

Capitulescence
Secondary inflorescence in which the floral units are heads; the clustering of heads in Compositae. See **Secondary inflorescence.**

Capitulum
See **Head.**

Carbonized layer
A hardened, dark brown to black phytomelanin deposit in the pericarp of achenes in some Compositae tribes (Figs. 32–34). See **Phytomelanins.**

Carduoid style
Style with a ring of sweeping hairs borne on the shaft of the style below the style branches. With few exceptions, the style is distinctly swollen proximal to the articulation of the style branches (Fig. 49).

Carpopodium
Basal abscission zone of the fruit, formed by one or more rows of cells generally different from the ones in the achene wall, more or less hardened. The carpopodium is the anchor point of the inferior ovary of the floret to the inflorescence or head. It also constitutes the abscission zone of the achene and can be symmetrical in a ring (Fig. 18), asymmetrical (Fig. 35) or decurrent along the ribs (Fig. 21), among other modifications (see also Figs. 20, 38).

Caudate anther base
Bases of anther thecas flanking anther collar bearing tail-like basal appendages composed of sterile cells. Appendages can be laciniate, plumose (Fig. 27), ciliate, smooth (Fig. 28) or absent. See **Ecaudate anther base.**

Chaff scale
See **Paleas.**

Chaffy receptacle
See **Paleate receptacle, Scaly receptacle.**

Collar of the filament
See **Anther collar.**

Columnar receptacle
See **Cylindric receptacle.**

Compressed achene
Flattened laterally, parallel to a radius of the head (Fig. 8). See **Obcompressed achene.**

Compressed involucre
Flattened involucre formed by 2–8 foliaceous involucral bracts (Figs. 50, 51).

Concave receptacle
Receptacle shallowly depressed in center.

Conical receptacle
Receptacle narrowing from periphery to center with shape of a cone (e.g., *Matricaria prostrata*, *Rudbeckia hirta*) (Fig. 52).

Fig. 11. Winged, obcompressed, tuberculate ray achene of *Rensonia salvadorica* S.F. Blake.

Fig. 12. Narrowly fusiform ribbed achene of *Bidens pilosa* L. with aristate pappus of retrorsely barbed awns.

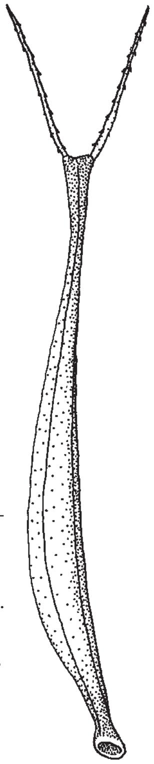


Fig. 13. Narrowly fusiform achene of *Bidens sulphurea* Sch.Bip. with beak and aristate pappus of retrorsely barbed awns.

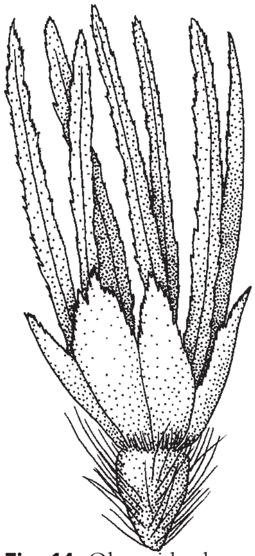


Fig. 14. Obovoid achene of *Stilpnopappus semirianus* R.L. Esteves with biseriate paleaceous pappus of ovate (outer) and linear (inner) scales.

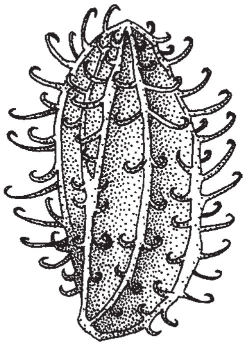


Fig. 15. Epappose ray achene of *Acanthospermum australe* (Loeft.) Kuntze closely enveloped by hardened inner phyllary armed with uncinate prickles.

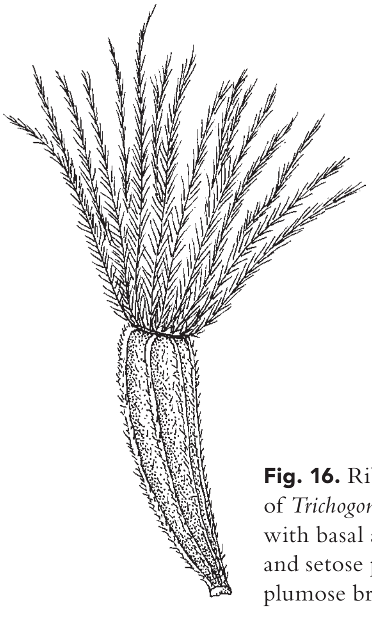


Fig. 16. Ribbed achene of *Trichogonia santosii* with basal attenuation and setose pappus of plumose bristles.

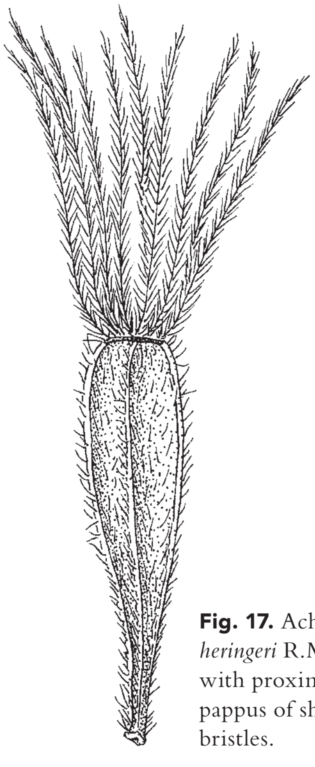


Fig. 17. Achene of *Trichogonia heringeri* R.M. King & H. Rob. with proximal stipe and setose pappus of short barbellate bristles.

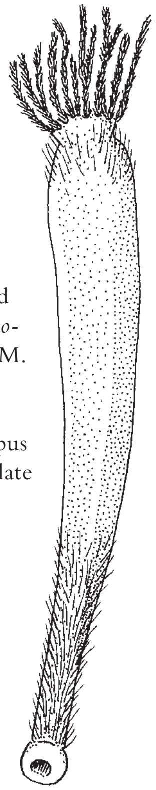


Fig. 18. Ribbed achene of *Trichogonia prancii* G.M. Barroso with proximal stipe and setose pappus of short barbellate bristles.

Connective

Portion of the anther axis (filament tip) to which the anther sacs are laterally connected (Figs. 25–30). The anther collar is a proximal extension of the anther connective below the anther sac attachment. The apical anther appendage is a distal membranous prolongation of the connective beyond the anther sacs. See **Anther, Anther collar, Anther tip appendage.**

Convex receptacle

Receptacle elevated in the center forming a smooth curve (Fig. 53).

Cordate anther base

Shallowly notched, ecalcarate or shortly calcarate bases of anther thecas flanking anther collar.

Corolla

Collective term for the petals of a flower; the second whorl of parts of a complete flower. The corolla of a Compositae floret generally comprises five proximally connate petals and has radial (Fig. 48) or bilateral (Fig. 1) symmetry. Number of petals is reduced to four or rarely three in some disk florets, and two corolla lobes corresponding to an adaxial lip are generally wholly suppressed in ray florets (Figs. 2, 36). Corollas in Compositae are generally deciduous from mature achenes, but ray corollas persist and fall with achenes in a few genera (e.g., *Baileya*, *Zinnia*).

Corolla limb

In a disk floret or ligulate floret the portion of the corolla distal to insertion of anthers, composed of corolla throat and lobes; in a ray floret the more or less expanded distal portion, including the lamina.

Corolla lip

One of the two halves of the limb of a bilaterally symmetric, sympetalous corolla; sinuses separating lips are generally deeper than those separating lobes of a lip though the sinuses between lobes of the adaxial lip may be deeply incised (e.g., Trixis; Figs. 1, 68). Bilabiate florets have a 2-lobed adaxial lip and a 3-lobed abaxial lip (Figs. 1A, 68); pseudobilabiate florets have a 4-lobed lip and a 1-lobed lip (Fig. 54). The lamina of a ray floret (Figs. 2, 36) is usually homologous with the abaxial lip of a bilabiate floret or rarely with the 4-lobed lip of a pseudobilabiate floret.

Corolla lobe

Distal, distinct petal tips of sympetalous corolla. The limb of a disk floret generally has five (less frequently four or three) equal corolla lobes (Figs. 48C, 55A). Lobes vary in shape from shortly triangular to elongated and linear. Bilabiate florets have a 2-lobed adaxial lip and a 3-lobed abaxial lip (Figs. 1, 68); pseudobilabiate florets have a 4-lobed lip and a 1-lobed lip (Fig. 54). The ligule of a ligulate floret is tipped by five lobes (Fig. 56). The lamina of a ray floret most typically has three lobes (Fig. 1) though these may be vestigial or absent in some cases (Fig. 36) or further divided in others. The ray lamina in some Arctoteae is 4-lobed.

Corolla throat

Cylindric to variously dilated portion of disk corolla distal to corolla tube (Figs. 23, 48B) where the anthers are localized.

Corolla tube

Generally cylindric portion of a floret's corolla, in disk (Figs. 23, 48A) and ligulate florets the portion proximal to insertion of filaments. The corolla tube is obsolete in ray florets of some genera.

Coroniform pappus

A pappus composed of very short, distinct or connate elements that collectively form a crown-like ring. Individual elements of a crown may be distinguishable as short bristles or scales, or may be more or less completely connate into a lobed or unlobed crown (Figs. 48, 55).

Corymbiform

A more or less flat-topped simple or compound secondary inflorescence in which the distal, central, most mature heads are borne on shorter peduncles than outer, proximal, less mature heads (Figs. 57, 71).

Corymb-like

See **Corymbiform.**

Corymbose

See **Corymbiform.**

Cylindric receptacle

Elongated receptacle with diameter unchanged from base toward apex (e.g., *Ratibida columnifera*).

Cyme-like

See **Cymiform.**

Cymiform

A simple or compound secondary inflorescence that develops in the pattern of a simple or compound cyme. Usually restricted in Compositae descriptions to secondary inflorescences that develop in a distinctly cymose pattern, though most Compositae secondary inflorescences are technically cymiform because they are wholly or in part determinate in their pattern of development.

Cymose

See **Cymiform.**

Cynarioid style

See **Carduoid style.**

Cypsela

Indehiscent, syncarpic, unilocular and monospermic dry fruit originated from an inferior ovary (Spjut 1994; Stearn 2004). For Marzinek et al. (2008), cypsela is a complex fruit with the pericarp sensu lato formed by the real pericarp (cells from the ovarian wall) and extracarpelar tissues from the receptacle, and hence the fruit of Compositae is a cypsela. In this book, however, we will follow Wagenitz (1976) and Jeffrey (2007) who consider that the more widespread term *achene* is preferable. See **Achene.**

Deciduous paleas

Paleas that break free from the receptacle at maturity of the head. Deciduous paleas sometimes fall together with achenes as part of an achene complex. See **Achene complex, Persistent paleas.**

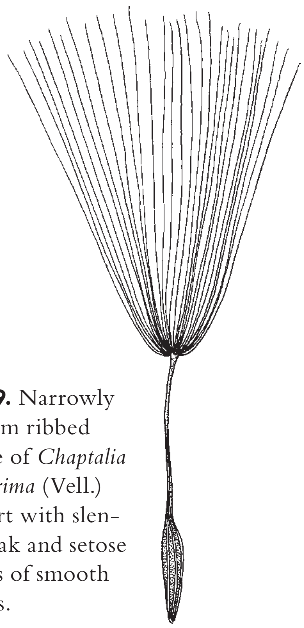


Fig. 19. Narrowly fusiform ribbed achene of *Chaptalia integerrima* (Vell.) Burkart with slender beak and setose pappus of smooth bristles.

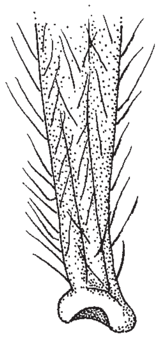


Fig. 20. Proximal portion of stipitate achene of *Trichogonia heringeri* R.M. King & H. Rob. with carpopodium.

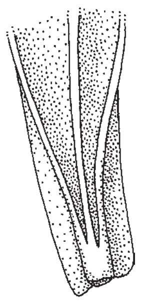


Fig. 21. Proximal portion of achene of *Trichogonia cinerea* (Gardner) R.M. King & H. Rob. with decurrent carpopodium.

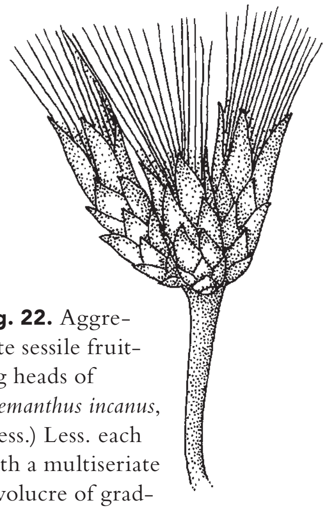


Fig. 22. Aggregate sessile fruiting heads of *Eremanthus incanus*, (Less.) Less. each with a multiseriate involucre of graduated phyllaries.

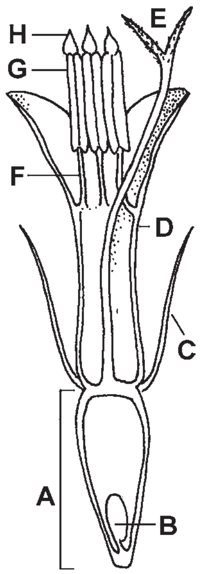


Fig. 23. Diagrammatic longitudinal section of disk floret. **A** inferior ovary; **B** basal ovule; **C** pappus element; **D** corolla; **E** style, style branches; **F** filament; **G** connate anthers; **H** anther tip appendage (based on Pruski and Sancho 2004).

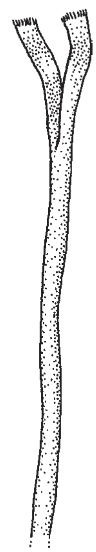


Fig. 24. Anthemoid style of *Trixis vauthieri* DC. with tufts of sweeping hairs terminating style branches.

Fig. 25. Stamen of *Trichogonia prancii* G.M. Barroso with anther collar, rounded, ecalcarate anther base and retuse anther tip appendage.

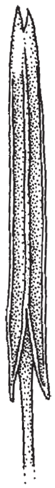


Fig. 26. Distal portion of stamen of *Dasyphyllum sprengelianum* (Gardner) Cabrera with calcarate, sagittate anther base and toothed anther tip appendage.

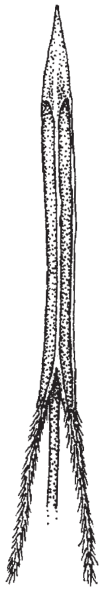


Fig. 27. Distal portion of stamen of *Richterago discoidea* (Less.) Kuntze with plumose, caudate and calcarate anther base, and narrowly apiculate anther tip appendage.

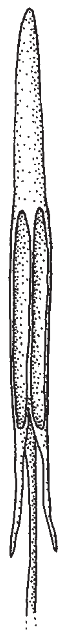


Fig. 28. Distal portion of stamen of *Trixis vauthieri* DC. with caudate anther base, and linear-oblong anther tip appendage.

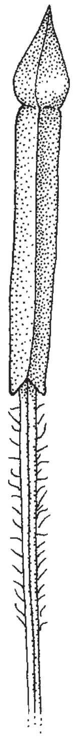


Fig. 29. Distal portion of stamen of *Bidens sulphurea* Sch. Bip. with puberulent anther collar, ecalcarate, shortly sagittate anther base, and ovate-acute anther tip appendage.

Deciduous phyllaries
Phyllaries that break free from the receptacle at maturity of the head. Deciduous phyllaries sometimes fall together with subtended achenes as part of an achene complex. See **Achene complex, Persistent phyllaries.**

Dioecious
A plant in which all flowers are imperfect, and staminate and pistillate flowers are produced on different individuals (e.g., *Baccharis*). See **Monoecious, Polygamous, Synoecious.**

Disciform head
Type of heterogamous head bearing perfect or functionally staminate disk florets in the center and peripheral filiform florets (e.g., *Pluchea*, *Pseudognaphalium*; Fig. 58), naked florets (e.g., *Cotula coronopifolia*) or functionally neutral florets with reduced corollas (some *Centaurea*); or a homogamous head consisting solely of filiform florets as in the pistillate head of *Baccharis* or naked florets as in pistillate head of *Ambrosia*. Staminate heads of *Baccharis* and *Ambrosia* are discoid. A disciform head superficially resembles a discoid head in lacking ray florets. See **Discoid head, Liguliflorous head, Radiant head, Radiate head.**

Discoid head
Homogamous head that contains only disk florets (Figs. 59, 60). Corollas may be tubulose, pseudobilabiate, or bilabiate. Ray florets are always absent. In most discoid heads all florets are perfect. In dioecious or monoecious Compositae with separate staminate and pistillate heads (e.g., *Baccharis*, *Ambrosia*) the staminate heads are discoid, composed of staminate disk florets; pistillate heads of these taxa are disciform, composed of filiform florets with tubulose corollas (*Baccharis*) or naked florets (*Ambrosia*). See **Disciform head, Liguliflorous head, Radiant head, Radiate head.**

Disk
The more or less flat-topped to strongly convex aggregate of the disk florets of a radiate or discoid head, or of all the florets of a disciform head. The diameter of the disk is often included in descriptions of heads.

Disk achene
Achene formed by a fertile disk floret.

Disk floret
A perfect, or less commonly functionally staminate, or rarely sterile, floret with a more or less tubulose, (3–4)5-lobed, radial corolla limb (Fig. 48); less commonly the limb is bilabiate (Fig. 1) or pseudobilabate. Disk florets are the only floret types in discoid heads (Fig. 59, 60), and are the centrally located florets in disciform (Fig. 58), radiate (Fig. 61), and radiant heads. Disk florets collectively form the disk of a radiate or discoid head. See **Filiform floret, Ligulate floret, Naked floret, Ray floret.**

Distal
The portion of a structure farthest from its developmental origin; apical. **See Proximal.**

Double hairs
See **Twin hairs.**

Double pappus
Pappus with elements in two series that usually are different in length, in texture, or both (Figs. 14, 62, 63).

Drupe
A fleshy, usually one-seeded indehiscent fruit with the pericarp differentiated into an exocarp, a fleshy mesocarp, and a stony endocarp that contains the seed. A rare fruit type in Compositae (e.g., *Chrysanthemoides*, *Tilesia*; Fig. 64).

Ecalcarate anther base
Bases of anther thecas not extending proximal to insertion of anther collar as spur-like projections (Figs. 25, 29). See **Calcarate anther base.**

Ecalyculate involucre
Involucre not subtended by a calyculus (Fig. 44).

Ecaudate anther base
Bases of anther thecas flanking anther collar without tail-like basal appendages composed of sterile cells (Figs. 25, 29). See **Caudate anther base.**

Endothecial tissue
Inner cell layer of anther theca with cells generally elongated parallel to anther axis. Patterns of thickenings in radial, horizontal, and outer tangential cell walls of endothecial cells are variable within Compositae and may be taxonomically useful microcharacters.

Epaleate receptacle
Receptacle without paleas (receptacular bracts; Fig. 59). See **Paleate receptacle.**

Epappose achene
Achene without a pappus (Figs. 4, 5, 9). See **Pappose achene.**

Epicalyx
See **Calyculus.**

Equal phyllaries
In one or more series of the same length (Fig. 52).

Eupatorioid style
Style branches bearing elongated, cylindrical to flattened, often distally clavate appendages (Fig. 65). Discrete stigmatic lines, often separated by glands, are restricted to the proximal half of the style branches.

Female floret
See **Pistillate floret.**

Fertile disk floret
A disk floret with an ovary that matures as an achene, the most commonly encountered type of disk floret.

Fertile ray floret
A ray floret with an ovary that matures as an achene, the most commonly encountered type of ray floret (Fig. 2).

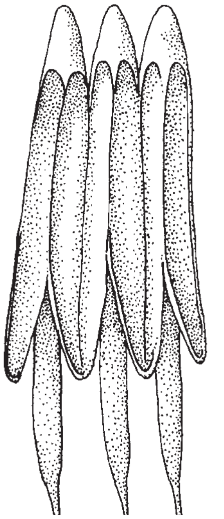


Fig. 30. Stamens of *Chresta amplexifolia* Dematt., Roque & Miranda Gonç. with distally enlarged filaments, calcarate anther bases, and obtuse anther tip appendages.

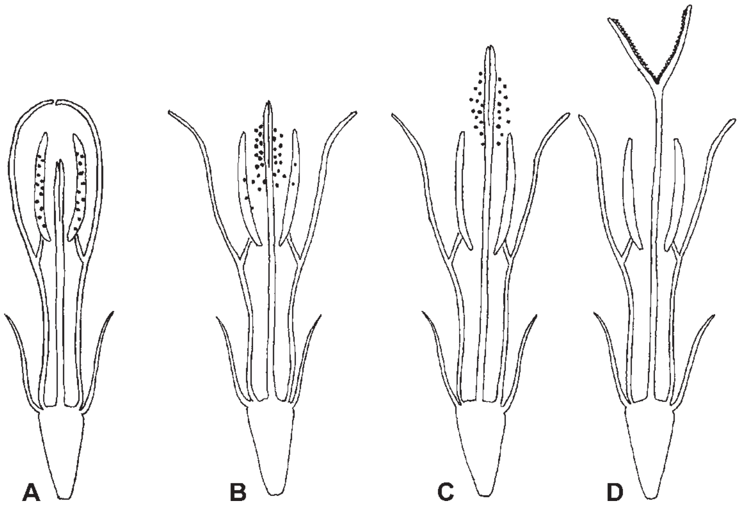


Fig. 31. Pollen presentation in Compositae. **A** Style within anther tube prior to anthesis. **B** Introrse dehiscence of anthers and elongation of style. **C** Continued elongation of style removes pollen from anther tube. **D** Style branches separate, exposing stigmas.

Fig. 32. Obcompressed achene of *Bidens* sp. bearing marginal prickles and aristate pappus of two retrorsely barbed awns. Pericarp carbonized by phytomelanin deposits.

Fig. 33. Narrowly winged obcompressed achene of *Calyptocarpus vialis* Less. with aristate pappus of two antrorsely barbed awns. Pericarp carbonized by phytomelanin deposits.

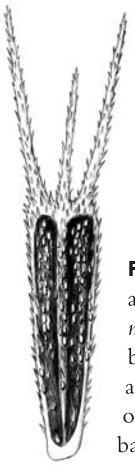


Fig. 34. Ribbed achene of *Synedrella nodiflora* Gaertn. bearing prickles and aristate pappus of three antrorsely barbed awns. Pericarp carbonized by phytomelanin deposits.

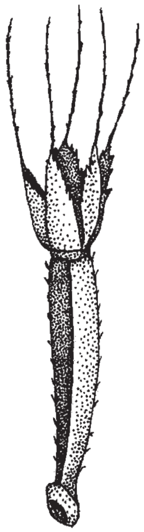


Fig. 35. Prismatic 5-angled achene of *Ageratum conyzoides* L. with a paleaceous pappus of five awn-tipped scales.

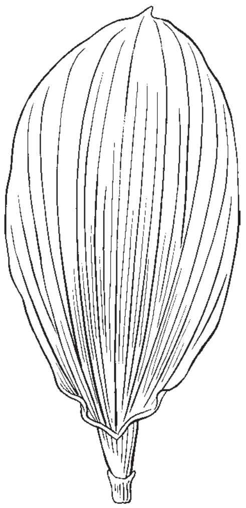


Fig. 36. Astylous ray floret of *Dahlia pinnata* Cav. with unlobed lamina.

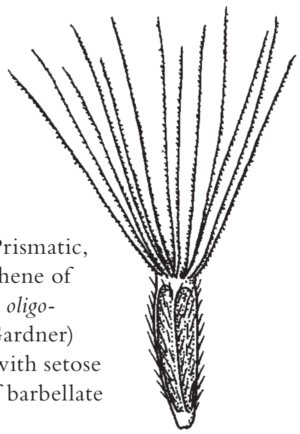


Fig. 37. Prismatic, ribbed achene of *Gochnatia oligocephala* (Gardner) Cabrera with setose pappus of barbellate bristles.

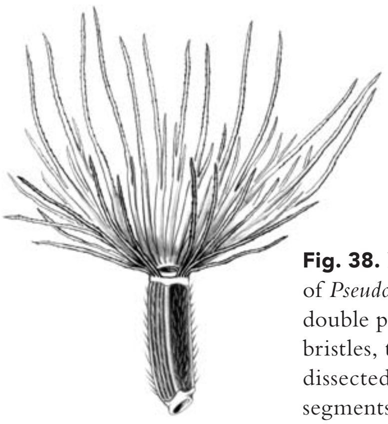


Fig. 38. Prismatic, ribbed achene of *Pseudoclappia arenaria* Rydb. with double pappus, the outer of barbellate bristles, the inner of setiform scales dissected into barbellate, bristle-like segments.

Filament

Stalk-like base of a stamen. In most Compositae the filaments are distinct and individually inserted at the junction of corolla tube and throat (Fig. 23); in a few genera they are connate into a filament tube. In many genera of Cardueae, filaments are contractile in response to touch, resulting in pollen exposure as anthers are pulled back. Except in Barnadesioideae and Mutisieae, the distal end of the filament is separated from the body of the anther by an anther collar. See **Anther, Stamen.**

Filament tube

Narrowly tubular structure formed by fusion of filaments of the stamens of a floret (e.g., *Dicoria*, *Xanthium*); rare in Compositae.

Filiform floret

Pistillate floret characterized by a narrowly tubulose corolla (Fig. 68), sometimes with an unlobed limb or with vestigial lobes (Fig. 66). Filiform florets are located peripheral to central disk florets in disciform heads (e.g., *Pseudognaphalium*) or in separate pistillate heads (e.g., *Baccharis*). Rarely they occur in a head that also contains both disk florets and ray florets (Fig. 67). See **Disk floret, Ligulate floret, Naked floret, Ray floret.**

Flat receptacle

Receptacle planar over surface (Fig. 90).

Floral unit

See **Primary inflorescence, Secondary inflorescence.**

Floret

The small flower characteristic of Compositae (synonym: floscule; Fig. 23). The highly modified calyx (sometimes much reduced or absent) is a pappus of bristles, scales, and/or awns and is adnate to the distal end of the inferior ovary/fruit. The corolla is (3–)5-merous, sympetalous, diversely tubulose, radial or variously bilateral. The androecium comprises (3–)5 equal stamens with (usually) distinct, epipetalous filaments and (usually) connate anthers forming a tube with introrse dehiscence. The gynoecium comprises 2 connate carpels with a distally 2-branched style and a unilocular inferior ovary containing 1 erect, basal ovule; the ovary matures as an achene. Compositae have several types of florets that differ in corolla symmetry and sexual condition (Fig. 68). Disk, bilabiate, pseudobilabiate and ligulate florets are usually perfect (bisexual). Ray and filiform florets are usually pistillate, less frequently neuter. Heads may contain a single floret type or two or more kinds that may or may not differ in sexual disposition. See **Disk floret, Filiform floret, Ligulate floret, Naked floret, Ray floret.**

Floscule

See **Floret.**

Foveolate receptacle

Receptacle surface minutely pitted.

Gamopetalous

See **Sympetalous.**

Glomerules

Small, compact, irregular clusters of heads.

Graduated phyllaries

In several series with the outer shortest, the inner longest, and a gradual transition through series of intermediate length between (Figs. 69, 70).

Gynoecium

Collective term for the carpels of a flower; the centermost whorl of parts of a complete flower. In Compositae the gynoecium comprises two connate carpels with an inferior, 1-loculed compound ovary containing a single erect ovule, a slender style with two distal style branches, and two stigmas borne on the adaxial faces of the style branches (Fig. 23). The ovary in Compositae generally matures as an achene, rarely as a drupe.

Head

A short, dense indeterminate inflorescence of sessile flowers attached to a common receptacle. Heads are the primary inflorescence type characteristic of Compositae (Fig. 47), generally with an involucre of distinct or connate phyllaries, a receptacle with or without paleas, and one to many florets of one or more kinds. Discoid heads (Figs. 40, 41, 43, 59, 60) contain only disk florets. Radiate heads (Figs. 47, 61, 71) contain peripheral ray florets and central disk florets. Disciform heads (Fig. 58) contain peripheral filiform florets and central disk florets or only filiform florets. Liguliflorous heads contain only ligulate florets (Fig. 72). Rarely a head contains three or more floret types (Fig. 67). The sequence of floral initiation and maturation in Compositae heads is indeterminate. Heads may be solitary or in various types of usually determinate secondary inflorescences. The family name Compositae derives from the superficial resemblance of a head to the individual flowers of some other families; the head is a flower-like composite of many smaller flowers (florets). Synonym: capitulum. See **Disciform head, Discoid head, Liguliflorous head, Radiant head, Radiate head.**

Hermaphroditic floret

See **Perfect floret.**

Heterocarpous

Condition of a head in which achenes of two or more morphologies are present (e.g., ray achenes of *Leptosyne calliopsidea* are epappose, glabrous, and winged; the disk achenes have a pappus of lanceolate scales, are adaxially hairy, long-ciliate, and wingless).

Heterogamous head

Head that encloses florets with different sexual disposition, usually pistillate and bisexual (Figs. 47, 67). Radiate heads and most disciform heads are heterogamous (Fig. 58, 61). Radiant heads may be homogamous or heterogamous. See **Homogamous head.**

Heteromorphic pappus

Condition in which some florets in a head have a different type of pappus than others. For example: in *Barnadesia caryophylla* (Vell.) S.F. Blake the peripheral ray-like pseudobilabiate florets have a pappus of plumose bristles (Fig. 54), and the disk florets have a pappus of smooth setiform scales (Fig. 73). **See Isomorphic pappus.**

Homogamous head

Head that encloses florets with the same sexual disposition,

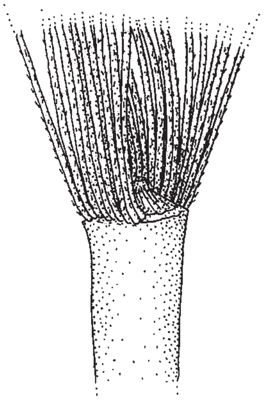


Fig. 39. Distal end of achene of *Gochnatia paniculata* (Less.) Cabrera illustrating biseriate setose pappus with outer and inner series both composed of barbellate bristles.

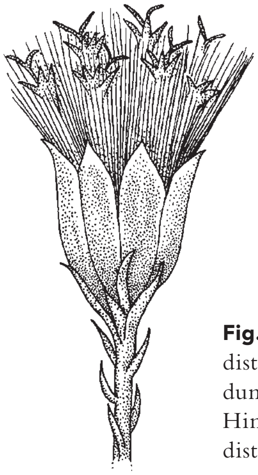


Fig. 40. Discoid head and distal portion of bracted peduncle of *Senecio harleyi* D.J.N. Hind. Uniseriate involucre of distinct phyllaries.

Fig. 41. Discoid head and distal bractless portion of peduncle of *Erechtites valerianifolius* (Wolf) DC. Uniseriate involucre of distinct phyllaries subtended by calyculus of narrow bracts.

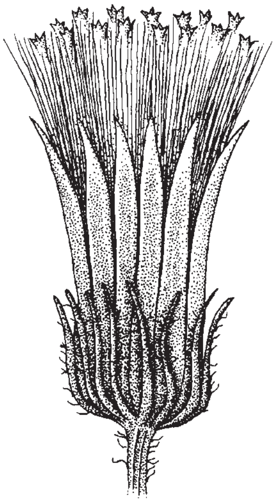


Fig. 42. Radiate head and distal portion of bracted peduncle of *Pseudogynoxys lobata* Pruski. Uniseriate involucre of distinct phyllaries subtended by calyculus of narrow bracts.

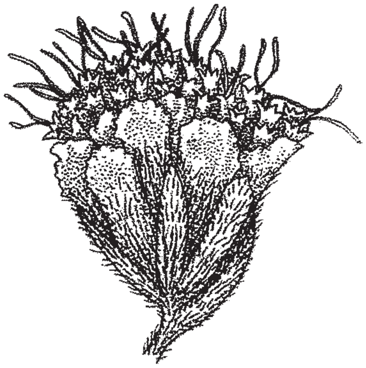


Fig. 43. Discoid head and tip of peduncle of *Scherya bahiensis* R.M. King & H. Rob. Distalmost peduncular bract resembling outer phyllaries of pluriseriate involucre of subequal phyllaries.

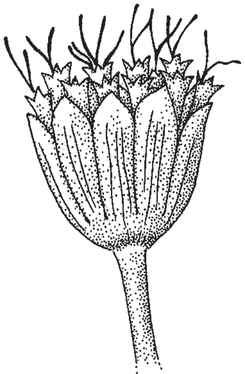


Fig. 44. Discoid head and distal tip of bractless peduncle of *Adenostemma brasilianum* (Pers.) Cass. Uniseriate involucre of proximally connate phyllaries.

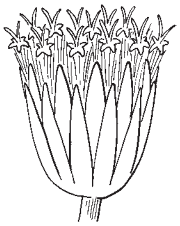


Fig. 45. Involucre with subequal phyllaries in two series.

Fig. 46. Peduncled secondary head of *Paralychnophora atkinsiae* D.J.N. Hind subtended by secondary involucre of subulate bracts. Primary discoid heads each with pluriseriate involucre of graduated phyllaries.

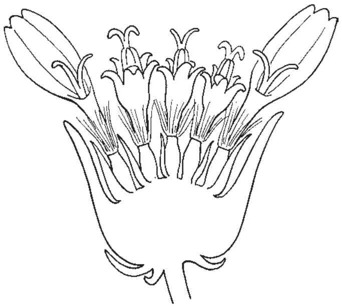


Fig. 47. Diagrammatic longitudinal section of radiate head with calyculus subtending phyllaries, convex paleate receptacle, peripheral ray florets, and central disk florets.

usually all perfect (bisexual) and fertile (Fig. 59). Discoid heads and liguliflorous heads are homogamous (Fig. 60, 72). See **Heterogamous head.**

Honey-combed receptacle
See **Alveolate receptacle.**

Imbricated phyllaries
Phyllaries of unequal length in several series, overlapping each other like shingles on a roof (Figs. 69, 70).

Imperfect floret
A floret in which the androecium, or gynoecium, or both are nonfunctional (Fig. 68). See **Neuter floret, Pistillate floret, Staminate disk floret.**

Inflorescence
The grouping of flowers into clusters (primary inflorescences or floral units; e.g., heads in Compositae) or the grouping of floral units into clusters (secondary inflorescence; e.g., clustering of heads in Compositae).

Inner pappus
Collective term for adaxial elements of a double pappus (Figs. 14, 62, 63). See **Outer pappus.**

Introrse dehiscence
Anthers that open on the adaxial side. The connate anthers in Compositae release pollen into the interior of the anther tube where it is brushed or pushed out by sweeping hairs in conjunction with elongation of style or contraction of filaments (Fig. 31).

Involucral bracts
Modified leaves or scales grouped in a ring or cup enclosing or closely subtending an inflorescence, differing from ordinary foliage leaves in size, shape, color or texture. The bracts act functionally as sepals, protecting the young inflorescence during its development. Phyllaries are the involucral bracts of Compositae that surround or enclose individual heads. Syncephalous secondary and tertiary heads found in some Compositae often are enclosed by secondary or tertiary involucral bracts (Figs. 46, 74–76). See **Phyllary.**

Involucre
A disk-like to cup-shaped, ovoid, or cylindric group of bracts in one or more series that collectively subtend or surround the florets of a head (primary involucre; Figs. 40, 45). Involucres are absent in a few genera (e.g., *Psilocarphus*, *Xanthium*), and secondary and tertiary involucres may subtend syncephalous aggregations of heads in other genera (Fig. 46, 74–76). Primary involucres of some Compositae are subtended by a calyculus (Figs. 41, 42) that is sometimes described as an outer involucre. See **Calyculus, Involucral bracts, Phyllary.**

Isomorphic pappus
All the florets in the head have morphologically similar pappus (Figs. 47, 59). **See Heteromorphic pappus.**

Lamina
The distal, more or less flat, strap-shaped, generally 0–4-lobed abaxial lip of the corolla of a ray floret (Figs. 2, 36). See **Bilabiate corolla, Ligule.**

Ligulate floret
A perfect floret with a proximal tube and a distal, more or less flat, strap-shaped, 5-lobed, bilateral corolla limb (ligule). Ligulate florets are the only floret types in liguliflorous heads (Fig. 56, 68). See **Disk floret, Filiform floret, Naked floret, Ray floret.**

Ligulate head
See **Liguliflorous head.**

Ligule
The distal, more or less flat, strap-shaped, 5-lobed portion of the corolla limb of a ligulate floret. Used in some references for the lamina of a ray floret (Fig. 56, 68). See **Lamina.**

Liguliflorous head
Type of homogamous head bearing only ligulate florets (e.g., *Taraxacum*, *Lactuca*; Fig. 72). See **Disciform head, Discoid head, Radiant head, Radiate head.**

Male floret
See **Staminate disk floret.**

Mixed pappus
Pappus composed of two or more types of pappus elements (e.g., an outer series of narrow scales and an inner series of barbellate bristles) (Figs. 14, 62, 63).

Monoecious
A plant in which all flowers are imperfect, and staminate and pistillate flowers are produced on the same individual. Staminate and pistillate flowers may be produced in the same head (e.g., *Blennosperma* and *Delilia* with pistillate ray florets and staminate disk florets; Fig. 51) or in different staminate and pistillate heads (e.g., *Xanthium*). See **Dioecious, Polygamous, Synoecious.**

Multiseriate involucre
Involucral bracts arranged in many series (Figs. 69, 70).

Naked floret
Pistillate floret that lacks a corolla. Naked florets may be located peripheral to central disk florets in disciform heads (e.g., *Dicoria*, some *Cotula*) or in separate pistillate heads (e.g., *Ambrosia*, *Xanthium*) (Fig. 68). See **Disk floret, Filiform floret, Ligulate floret, Ray floret.**

Naked receptacle
See **Epaleate receptacle.**

Nectary
Secretory structure that produces nectar as pollinator reward, in Compositae borne within corolla as enlarged base of style (stylopodium; Fig. 78).

Neuter disk floret
An unusual type of disk floret that has both non-functional

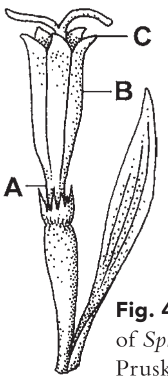


Fig. 48. Palea and disk floret of *Sphagneticola trilobata* (L.) Pruski with coroniform pappus of connate scales and a radially symmetric, 5-lobed corolla. **A** corolla tube; **B** corolla throat; **C** corolla lobe.

Fig. 49. Distal portion of Carduoid style of *Cirsium vulgare* (Sav.) Ten. with subterminal swelling bearing sweeping hairs and linear style branches with stigmatic surfaces evenly distributed on the adaxial faces of the branches.

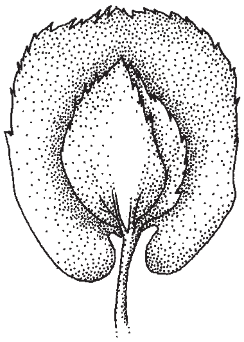


Fig. 50. Flattened involucre of *Delilia biflora* (L.) Kuntze composed of three unequal phyllaries, the largest much exceeding the others.

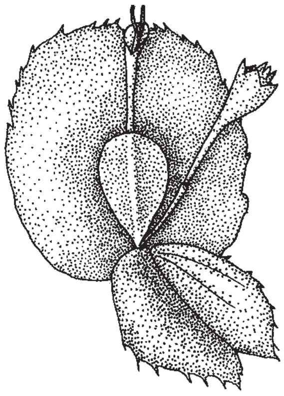


Fig. 51. Flattened involucre of *Delilia biflora* (L.) Kuntze composed of three unequal phyllaries enclosing a single ray floret with a vestigial lamina and a single staminate disk floret.

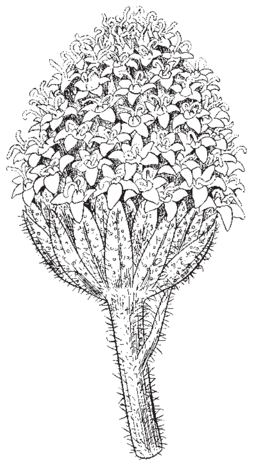


Fig. 52. Discoid head and distal portion of bracted peduncle of *Isocarpha microcephala* S.F. Blake. Biseriate involucre of subequal distinct phyllaries. Florets borne on convex receptacle.

Fig. 53. Distal portion of peduncle and convex epaleate receptacle of *Trichogonia cinerea* (Gardner) R.M. King & H. Rob.

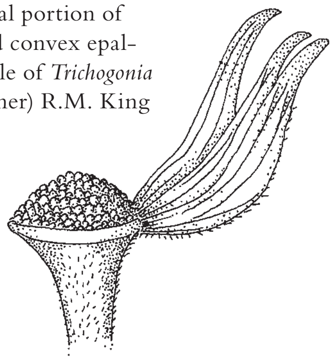


Fig. 54. Ray-like pseudobilabiate peripheral floret of *Barnadesia caryophylla* (Vell.) S.F. Blake with setose pappus of distally plumose bristles. **A** abaxial lip; **B** adaxial lip.

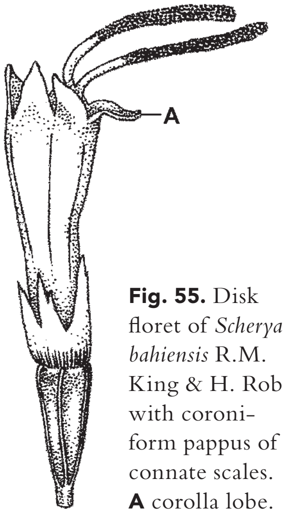


Fig. 55. Disk floret of *Scherya bahiensis* R.M. King & H. Rob. with coroniform pappus of connate scales. **A** corolla lobe.

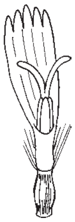


Fig. 56. Ligulate floret. The ligule is tipped by five lobes.

Fig. 57. Corymbiform secondary inflorescence of radiate heads of *Erato costaricensis* E. Moran & V.A. Funk.

stamens and a non-functional ovary (e.g., peripheral florets of many *Centaurea*) (Fig. 68).

Neuter floret

A floret in which the gynoecium is non-functional, ranging from vestigial to full-sized, but not producing a functional ovule, and the androecium is absent or non-functional and does not produce pollen grains (Fig. 36, 68). Some ray florets (e.g., *Helianthus*) and the peripheral florets of radiant heads in some genera (e.g., *Centaurea*) are neuter. See **Perfect floret, Pistillate floret, Staminate disk floret.**

Neuter ray floret

A ray floret in which the gynoecium is non-functional, failing to form an achene (Fig. 68). An ovary is always present though sometimes much reduced. A style may be present (styliferous ray floret) or absent (astylous ray floret, Figs. 36, 68). The lamina of a neuter ray floret is often well developed (Fig. 36), functioning as a pollinator attractant. See **Astylous ray floret, Fertile ray floret, Styliferous ray floret.**

Obcompressed achene

Dorsiventrally flattened in cross section, perpendicular to a radius of the head (Figs. 10, 11, 33). See **Compressed achene.**

Outer pappus

Collective term for abaxial elements of a double pappus (Figs. 14, 62, 63). See **Inner pappus.**

Ovary

Ovule-containing part of a pistil, attached to the receptacle. In Compositae the ovary is inferior with one locule and one basal ovule (Fig. 23). It matures as an achene in most Compositae, rarely as a drupe. Pappus elements and corolla are inserted on the distal end of the ovary. Ovaries of functionally staminate or neuter florets may be much reduced (Fig. 51) or of normal proportions.

Paleaceous pappus

A pappus composed of one or more flat, more or less membranous scales of variable shape and length (Figs. 79, 80). Scales may be entire, toothed, or variably dissected.

Paleas

Small bracts borne on the receptacle subtending all or some of the florets of a head (Figs. 47, 48); paleas may be similar in size and/or texture to phyllaries or more commonly smaller and of membranous to chartaceous texture. They are a constant character in Heliantheae (with only a few exceptions), in some Anthemideae and Eupatorieae, and in Hypochaeris (Lactuceae). Paleas have been interpreted as rudimentary bracts at the base of each floret or as involucral bracts (Stuessy and Spooner 1988) placed among the florets (Fig. 47). In some genera, each palea is associated with a floret, and if the palea is removed from the head the floret is also removed. In *Ambrosia* and *Xanthium* all of the paleas of pistillate heads are fused into a spiny, knobby, or winged bur containing one or two achenes. Receptacles in some genera, e.g., *Carlina*, *Xeranthemum*, and allies (Cardueae), bear scales that are not homologous with paleas.

Paleate receptacle

Receptacle with paleas subtending some or all of the florets (Fig. 47). See **Epaleate receptacle.**

Panicle-like

See **Paniculiform.**

Paniculate

See **Paniculiform.**

Paniculiform

A more or less pyramidal compound secondary inflorescence with a central rachis and shorter side branches; sequence of head initiation and maturation is determinate.

Pappose achene

Achene bearing one or more pappus elements. See **Epappose achene.**

Pappus

Modified calyx consisting of bristles, dry scales, and/or awns, characteristic of Compositae, some Dipsacaceae and some Valerianaceae. Individual units of the pappus may or may not correspond to sepals. The pappus is one of the most important structures in the classification of Compositae. A setose pappus is composed of one or more series of slender, flexible to stiff, bristle-like pappus elements of uniform or variable length and diameter that may be smooth or nearly so (Figs. 3, 81), barbellate (Fig. 37), or plumose (Figs. 16, 82), depending on the divergence and length of the cells that form the bristles. There is a continuum in thickness and stiffness from very fine, hair-like, capillary bristles (Fig. 3) to stiffer, thicker bristles to awns. Bristles may be slender to the base or proximally dilated and may be distinct or proximally connate; bristles grade along a continuum into setiform scales. A paleaceous pappus (Figs. 14, 79, 80) is composed of flat, more or less membranous scales of variable shape and length. Scales may be entire, toothed, or variably dissected into slender lobes or bristle-like segments (e.g., *Adenophyllum*), the latter sometimes treated as bristles connate in groups. Aristate scales (Fig. 35) taper to or are abruptly tipped by bristles or awns. An aristate pappus is composed of one or more awns of variable length and diameter (Figs. 32–34). Awns may be smooth (Fig. 101), antrorsely (Figs. 33, 34), or retrorsely barbed (Figs. 12, 13, 32), or plumose, and vary from erect to sharply divaricate (Fig. 101). Awn-like structures in some genera traditionally interpreted as pappus elements may be outgrowths of the pericarp. A coroniform pappus (Figs. 2, 55) is composed of very short, distinct or connate pappus elements that collectively form a crown-like ring. Individual elements of a crown may be distinguishable as short bristles, scales, or awns, or may be more or less completely connate into a lobed or unlobed crown. A mixed pappus (Figs. 62, 63) comprises two or more types of pappus elements (e.g., a series of scales and a series of awns or bristles). The pappus may be reduced or entirely absent (Figs. 4, 5, 9). Pappus elements may be diversely deciduous (individually or as a single unit, as in many Cardueae and *Wunderlichia mirabilis*), persistent, or some elements persistent and others deciduous.

The pappus has a dual function (Stuessy and Garver 1996): it is a defensive structure against predators of the head, blocking the

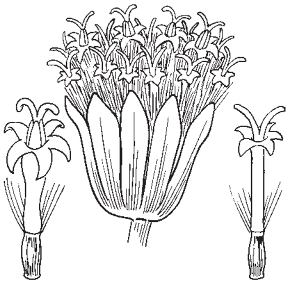


Fig. 58. Disciform head composed of peripheral filiform florets and central disk florets (in detail).

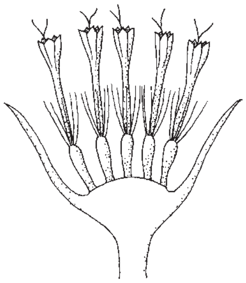


Fig. 59. Diagrammatic longitudinal section of discoid head with convex, epaleate receptacle.

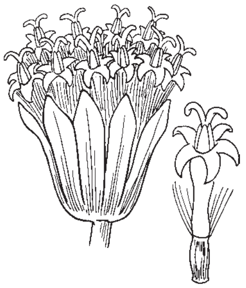


Fig. 60. Discoid head composed of only disk florets (in detail).

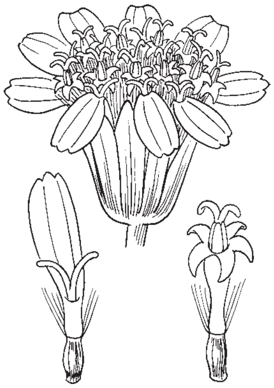


Fig. 61. Radiate head composed of peripheral ray florets and central disk florets (in detail).

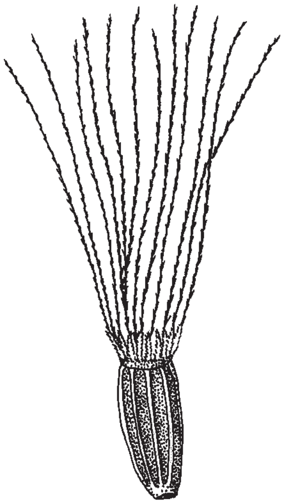


Fig. 62. Ribbed achene of *Cyrtocymura harleyi* (H. Rob.) H. Rob. with biseriate pappus, the outer of short bristle-like scales and the inner of barbellate bristles.

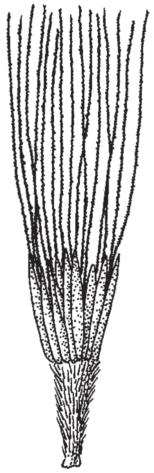


Fig. 63. Obconic achene of *Lessingianthus santosii* (H. Rob.) H. Rob. with biseriate pappus, the outer of narrow scales and the inner of barbellate bristles.

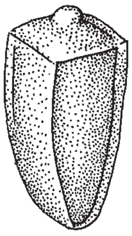


Fig. 64. Four-sided endocarp of drupe of *Tilesia baccata* (L.) Pruski.

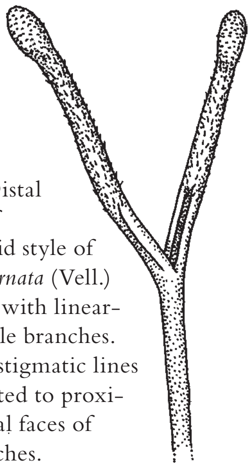


Fig. 65. Distal portion of Eupatorioid style of *Mikania ternata* (Vell.) B.L. Rob. with linear-clavate style branches. Marginal stigmatic lines are restricted to proximal adaxial faces of style branches.

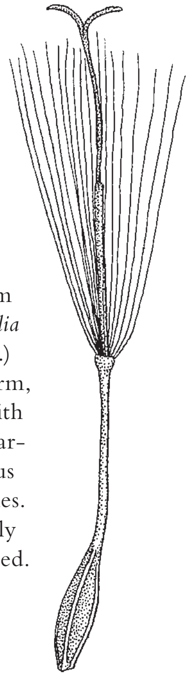


Fig. 66. Filiform floret of *Chaptalia integerrima* (Vell.) Burkart. Fusiform, ribbed ovary with slender beak bearing setose pappus of smooth bristles. Corolla narrowly tubulose, unlobed.

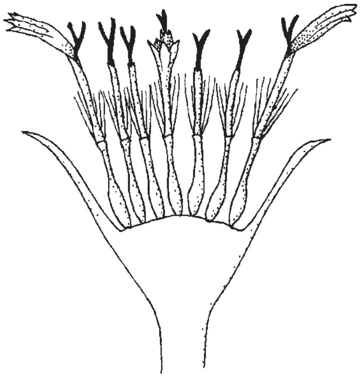


Fig. 67. Diagrammatic longitudinal section of radiate head of *Chaptalia* with epaleate receptacle bearing peripheral ray florets, intermediate filiform florets, and central, functionally staminate disk floret.

space between florets; and it facilitates dispersal of the achenes. Pappus elements may serve in epizoochory through attachment to fur or feathers and in anemochorous dispersal of the achenes by increasing the resistance between the air and the achene and hence prolonging the time of fall. According to Sheldon and Burrows (1973), effectiveness of the pappus in disseminating achenes by anemochory is determined not only by the shape and size of the pappus, but also by the size of the achenes and ecological factors.

Pappus bristle

Flexible to stiff, more or less hair-like pappus element. There is a continuum in thickness and stiffness from very fine, hair-like capillary bristles (Fig. 19) to stiffer, thicker bristles to awns. Bristles may be slender to the base or proximally dilated; bristles grade along a continuum into setiform scales. The surface may be smooth, barbellate, or plumose. See **Capillary bristle.**

Pappus elements

The individual bristles, scales, awns, or other units of the pappus of an achene.

Pauciseriate involucre

Involucral bracts arranged in few series (Figs. 43–45).

Peduncle

The stalk on which a head is borne; it may be weakly to clearly differentiated from vegetative stems (Figs. 40, 71, 83).

Peduncular bract

Bracts borne on the peduncle, separated by long to very short internodes from each other or from the head (Figs. 40, 83).

Pellucid glands

Schizogenous cavities formed beneath epidermis of leaves, phyllaries, and sometimes corollas in most genera of Tageteae (Figs. 100, 101). The glandular contents are often highly scented mixtures of monoterpenes and other oil-like substances. Gland contents are non-scented or very weakly scented in some species of *Pectis*. The chemicals apparently serve as deterrents to herbivory.

Perfect floret

Floret with a functional androecium that forms pollen and a functional gynoecium that matures as a seed-bearing fruit (bisexual floret) (Figs. 23, 68, 84). Fertile disk florets and ligulate florets are perfect. Sometimes apparently bisexual florets are functionally staminate, the style being not receptive, and produce only pollen grains. See **Neuter floret, Pistillate floret, Staminate disk floret.**

Persistent paleas

Paleas that remain attached to the receptacle at maturity of the head. See **Deciduous paleas.**

Persistent phyllaries

Phyllaries that remain attached to the receptacle at maturity of the head. Persistent phyllaries may retain their original position in the head when dry or may spread or reflex in age. See **Deciduous phyllaries.**

Phyllary

One of bracts that forms the primary involucre in Compositae (Fig. 85). The form and arrangement of phyllaries are of great taxonomic value in Compositae. Phyllaries are usually distinct (Fig. 43), but in some groups they are connate. In *Adenostemma* (Eupatorieae), phyllaries are distinct almost to the base, where they are connate (Fig. 44). Phyllaries are arrayed in one to many series and range from equal (Fig. 77) or subequal in length (Fig. 52, 85) to strongly graduated (Figs. 69, 70). At maturity of the head they may be deciduous or persistent and may spread or reflex when dry. Phyllaries may function in protection (of the ovaries and achenes against predators), may serve a role in dispersal (e.g., by epizoochory as in *Arctium* and some Madieae), may play a role in pollination (sometimes the bracts are colored increasing the visual appearance of the head as in *Carlina* or *Xeranthemum*) and, in some cases, provide protection to achenes during germination (in species in which the whole head constitutes the disseminating unit). See **Calyculus, Involucral bract, Involucre.**

Phyllary appendage

Distal portion of phyllary that is differentiated from proximal portion in texture, shape, margin, or other features.

Phyllary body

Medial region of a phyllary that is differentiated by texture from phyllary margin and/or apex.

Phyllary lamina

Ascending to widely spreading foliaceous blade of a phyllary.

Phyllary series

A set of phyllaries inserted at the same level around the receptacle (Fig. 85). The involucre may comprise only one or two series (uniseriate or biseriate) or may have several to many series of phyllaries (pluriseriate or multiseriate).

Phytomelanins

Hardened, blackish organic polymers (resinoids) deposited in cell walls and intercellular spaces of the pericarp of achenes in some Compositae (especially Eupatorieae, Heliantheae, Tageteae; Fig. 32–34). Phytomelanins are chemically inert, resistant to both acids and bases, and may serve as a defense against seed predators.

Pistil

Visual unit of the gynoecium (Figs. 23, 78), in Compositae comprising an inferior, one-loculed compound ovary containing a single erect, basal ovule, a slender style with two distal style branches, and two stigmas borne on the adaxial faces of the style branches.

Pistillate floret

An imperfect floret with a functional gynoecium that matures as a seed-bearing fruit. Pistillate florets in Compositae usually lack stamens altogether, but staminodes are sometimes present. Filiform florets (Figs. 66, 68) and many ray florets (Figs. 2, 68) are pistillate. See **Neuter floret, Perfect floret, Staminate disk floret.**

Pistillate head

A type of homogamous head containing only pistillate florets (e.g., *Baccharis*, *Xanthium*).

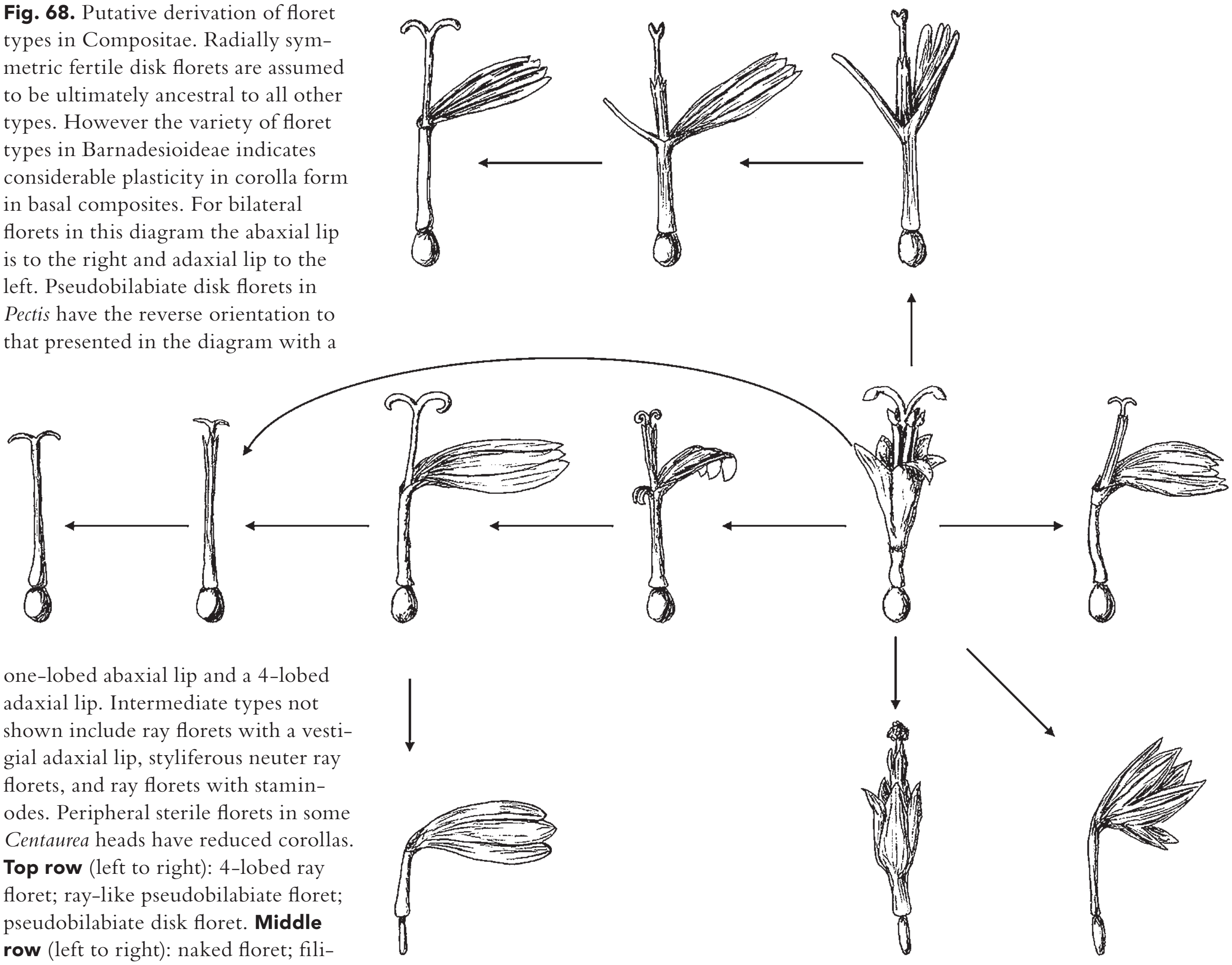


Fig. 68. Putative derivation of floret types in Compositae. Radially symmetric fertile disk florets are assumed to be ultimately ancestral to all other types. However the variety of floret types in Barnadesioideae indicates considerable plasticity in corolla form in basal composites. For bilateral florets in this diagram the abaxial lip is to the right and adaxial lip to the left. Pseudobilabiate disk florets in *Pectis* have the reverse orientation to that presented in the diagram with a one-lobed abaxial lip and a 4-lobed adaxial lip. Intermediate types not shown include ray florets with a vestigial adaxial lip, styliferous neuter ray florets, and ray florets with staminodes. Peripheral sterile florets in some *Centaurea* heads have reduced corollas. **Top row** (left to right): 4-lobed ray floret; ray-like pseudobilabiate floret; pseudobilabiate disk floret. **Middle row** (left to right): naked floret; filiform floret; 3-lobed ray floret; bilabiate disk floret; radial disk floret; ligulate floret. **Bottom row** (left to right): astylous neuter ray floret; staminate disk floret; ray-like neuter disk floret. [Drawing by Michaela Keil.]

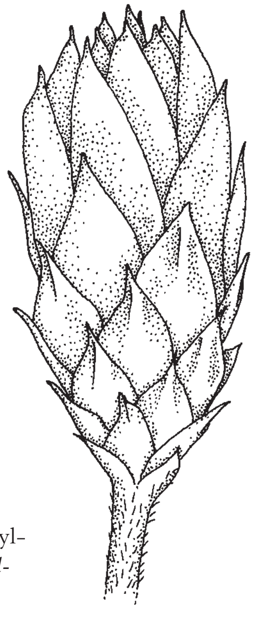


Fig. 69. Distal portion of peduncle and multiseriate involucre of graduated phyllaries of *Dasyphyllum brasiliense* (Spreng.) Gardner.

Fig. 70. Multiseriate involucre of graduated phyllaries of *Chresta amplexifolia* Dematt., Roque & Miranda Gonç.

Pistillate paleas

Receptacular bracts (e.g., in some Gnaphalieae) that individually subtend pistillate florets within head.

Plumose

Branched like a feather, with a central shaft and slender, hair-like lateral projections (Figs. 16, 82, 86), descriptive of pappus elements (e.g., bristles of *Helminthotheca*, awns of *Tragopogon*, setiform scales of *Cirsium*) and basal appendages of caudate anthers (e.g., *Richterago*; Fig. 27).

Pluriseriate involucre

With phyllaries in several series (Figs. 69, 70).

Polarized endothecial tissue

Characterized by endothecial wall thickenings restricted to horizontal walls.

Pollen grains

Usually tricolporate, porate, regular to large in size, often echinate (spinose), lophate, or psilate. Compositae show an interesting and elaborate secondary pollen presentation mechanism. The style is prolonged within the anther-tube, brushing the pollen grains to the exterior of the tube when the branches are still closed protecting the stigmatic area, making the floret protandrous. The stigmatic areas of the style are always placed on the adaxial faces of the branches and are exposed only after the passage of the style through the anther-tube. The morphology of the style is associated with this pollen presentation mechanism (Fig. 31) and offers some fine examples of coevolution (see Chapter 20).

Polygamous

Plants producing both perfect and imperfect flowers, on the same or different individuals. Plants with radiate heads and disciform heads are generally polygamous. See **Dioecious, Monoecious, Synoecious.**

Primary inflorescence

Grouping of flowers into clusters or floral units; heads are the primary inflorescences in Compositae. See **Head, Inflorescence.**

Prismatic achene

Achene polygonal in a cross section with three or more longitudinal angles and planar faces (Figs. 7, 35–38). See **Angled achene.**

Proximal

The portion of a structure nearest to its developmental origin; basal. See **Distal.**

Pseudanth

A generic noun for a condensed inflorescence in which many small flowers are grouped in such a way that the cluster simulates a single flower (Weberling 1989). The most frequent are the head (e.g., Compositae), the sycon (Moraceae) and the cyathium (Euphorbiaceae). The family name Compositae derives from the superficial resemblance of a head to the individual flowers of some other families; the head is a flower-like composite of many smaller flowers (florets).

Pseudobilabiate corolla

Bilaterally symmetric corolla characterized by a (3)4-lobed adaxial lip and a 1-lobed abaxial lip (e.g., most *Pectis*) or a 1-lobed adaxial lip and a 4-lobed abaxial lip as in some Barnadesioideae (Figs. 54, 68). See **Bilabiate corolla.**

Raceme-like

See **Racemiform.**

Racemiform

A more or less cylindrical secondary inflorescence with a central rachis and heads borne on generally unbranched peduncles. Sequence of inflorescence development is usually determinate with distal heads maturing before proximal heads, but in a few Compositae (e.g., some *Ambrosia* species) the sequence appears to be indeterminate.

Racemose

See **Racemiform.**

Radial endothecial tissue

Characterized by wall thickenings more or less evenly distributed around endothecial cells.

Radial symmetry

Descriptive of corolla with petals or lobes equal in size and shape; the corolla may be divided into mirror images along any radius that bisects a corolla lobe. Corollas of disk florets are usually radial (Fig. 48). See **Bilateral symmetry.**

Radiant head

Type of heterogamous or homogamous head bearing ordinary disk florets in the center and peripheral florets with more or less dilated, radial to strongly bilateral corollas. The peripheral florets may be perfect and fertile (e.g., *Chaenactis*, *Lessingia*), pistillate, or neuter (many *Centaurea*; Fig. 68). See **Disciform head, Discoid head, Liguliflorous head, Radiate head.**

Radiate head

Type of heterogamous head bearing disk florets in the center and peripheral ray florets (e.g., *Leucanthemum*, *Helianthus*; Fig. 61). See **Disciform head, Discoid head, Liguliflorous head, Radiant head.**

Ray

See **Lamina, Ray floret.**

Ray achene

Achene formed by a ray floret.

Ray floret

Bilaterally symmetric floret with a (2–)3(–4)-lobed (or sometimes unlobed) limb and generally no adaxial lobes. This is the most widespread type of peripheral florets in the family (Figs. 2, 68, 87). Ray florets usually lack an adaxial corolla lip, but an inconspicuous adaxial lip is sometimes present (e.g., *Monolopia*, *Onoseris*, *Sigesbeckia*). Ray florets are usually pistillate or neuter; neuter ray florets have an ovary (sometimes much reduced) and may or may not have a style (Fig. 36). Rarely staminodes or

Fig. 71. Corymbiform secondary inflorescence of radiate heads of *Richterago polyphylla* (Baker) Ferreyra.

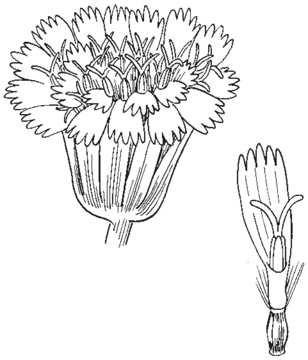


Fig. 72. Liguliflorous head composed of only ligulate florets (in detail).

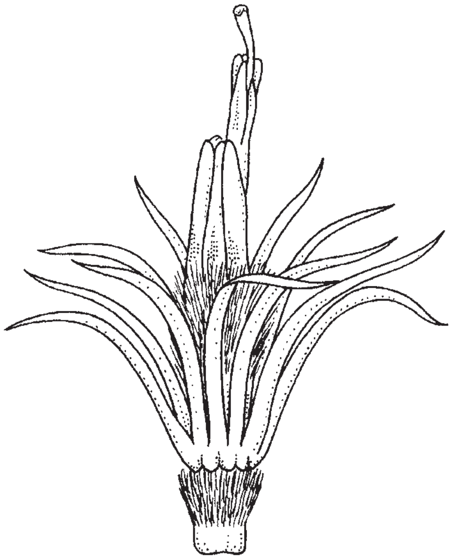


Fig. 73. Disk floret of *Barnadesia caryophylla* (Vell.) S.F. Blake with broadly cylindric ovary bearing pappus of basally connate, smooth setiform scales and proximally pubescent pseudobilabiate corolla with exserted anther tube and shortly bilobed style tip.

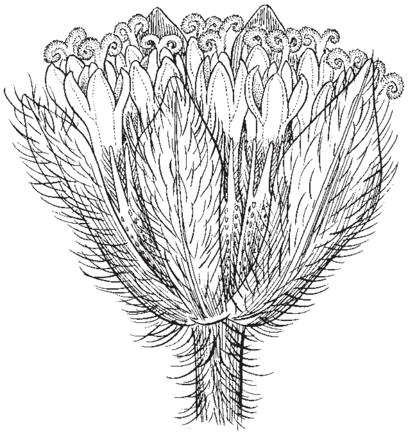


Fig. 74. Peduncled secondary head of *Lagascea mollis* Cav. composed of one-flowered primary heads, each with an involucre of five connate, acute-tipped phyllaries. Bracts subtending the secondary head compose a secondary involucre.

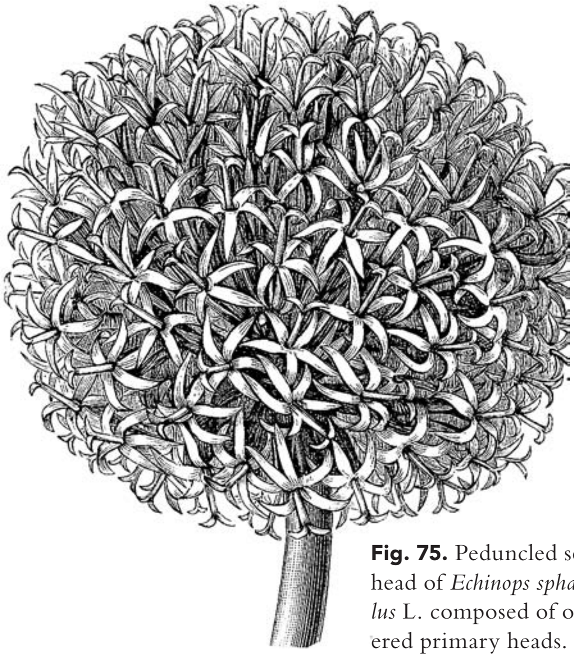


Fig. 75. Peduncled secondary head of *Echinops sphaerocephalus* L. composed of one-flowered primary heads.

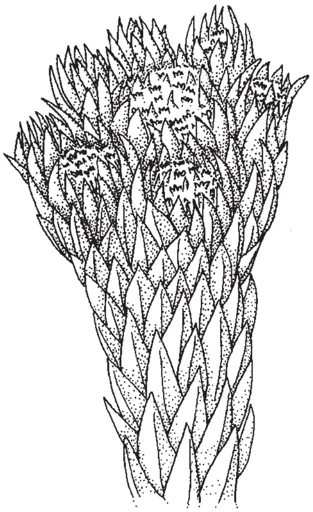


Fig. 76. Secondary head of *Catolesia* sp. nov. with one central head surrounded by seven peripheral heads.

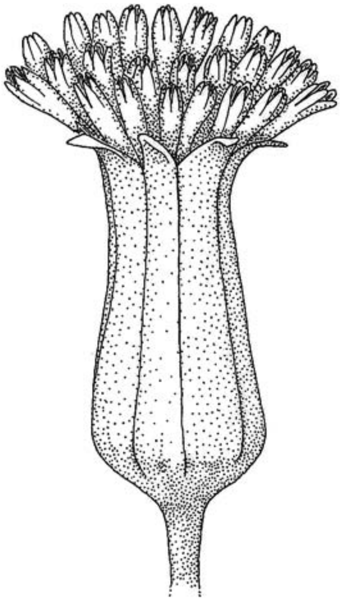


Fig. 77. Discoid head and distal portion of bractless peduncle of *Emilia fosbergii* Nicolson. Uniseriate involucre of distinct phyllaries with coherent, interlocking margins.

functional stamens are present. Ray florets are located peripheral to central disk florets in radiate heads (Figs. 47, 61). See **Disk floret, Filiform floret, Ligulate floret, Naked floret.**

Receptacle

Basal part of the head onto which are inserted phyllaries, florets, and often paleas (Figs. 53, 88, 90). Receptacle shape varies from weakly concave to flat (Fig. 90), convex (Fig. 53), conical (Fig. 52), or cylindric. The surface may be paleate (e.g., most Heliantheae; Fig. 47) or epaleate (Fig. 59), smooth, foveolate or shallowly to deeply alveolate, glabrous, scaly or variously pubescent (*Lasiolaena*), bristly, or scaly (*Baccharis*; Figs. 88, 89).

Receptacular bract

See **Paleas.**

Ribbed achene

Bearing raised, longitudinal ridges (Figs. 4, 9, 82).

Rostrum

See **Beak.**

Rounded anther base

Ecalcarate bases of anther thecas flanking anther collar forming a smooth curve.

Sagittate anther base

Ecalcarate (Fig. 29) or shortly calcarate (Fig. 26) bases of anther thecas flanking anther collar with short, projecting lobes.

Scabrid bristle

See **Barbellate bristle.**

Scale

A flat, membranous pappus element (Figs. 14, 79) or receptacular appendage (Fig. 89).

Scaly receptacle

Receptacle bearing membranous scales that are not homologous with paleas (Figs. 88, 89).

Scapose head

Solitary head borne at tip of a leafless, essentially naked peduncle that arises directly from a caudex, rhizome, or stolon at or below ground level (e.g., *Taraxacum*, Chaptalia; Fig. 83).

Secondary head

A compact secondary inflorescence in which two or more heads are grouped together onto a common receptacle. Each primary head usually has its own involucre, and the secondary head is often enclosed by a secondary involucre (e.g., *Lagascea*, *Echinops*; Figs. 46, 74–76). See **Syncephaly, Tertiary head.**

Secondary inflorescence

The grouping of floral units into a cluster (synflorescence). The same terminology employed for families in which the basic inflorescence unit is a single flower has often been used for the clustering of the heads in Compositae: e.g., cyme, umbel, spike, corymb, panicle, thyrse, raceme, or head. Some of these primary inflorescences are indeterminate, others are determinate. With the aim of making the descriptions simpler, Bremer (1994) suggested that the disposition of the heads should be described as "corymbose heads" rather than "heads arranged in corymbs" or even "corymbose capitulescence". Because the sequence of head initiation and maturation in Compositae secondary inflorescences (capitulescences) is almost always determinate, the application of terms such as corymbose, spicate, paniculate, racemose, etc. that apply to indeterminate clusters is inaccurate. Use of descriptors such as corymbiform (Figs. 57, 71), spiciform, paniculiform, and racemiform alludes to the superficial resemblance of the clustering of heads to such inflorescences while acknowledging that they do not follow the same pattern of development. See **Capitulescence.**

Senecioid style

See **Anthemoid style.**

Sessile

Stalkless.

Setiform scale

A long, narrow, flattened pappus element or receptacular appendage that resembles a bristle and may taper to a hair-like tip (e.g., *Cirsium*), sometimes described as a flattened bristle (Figs. 38, 73).

Setose pappus

A pappus composed of one or more smooth (Figs. 3, 81), barbellate (Fig. 37), or plumose (Figs. 6, 82) bristles.

Setose receptacle

See **Bristly receptacle.**

Simple pappus

A pappus in which the elements are equal (Fig. 82).

Smooth bristle

A slender, hair-like pappus element without evident lateral projections (Fig. 3, 81).

Smooth receptacle

An unappendaged receptacle surface without depressions or with very shallow depressions (Fig. 85).

Solitary head

Head borne in a position on the plant in which it is not clustered with others in a secondary inflorescence (Fig. 83).

Spicate

See **Spiciform.**

Spiciform

A more or less cylindrical secondary inflorescence with a central rachis and sessile or subsessile heads. The sequence of inflorescence development is usually determinate with distal heads maturing before proximal heads (e.g., *Liatris*).

Spike-like

See **Spiciform.**

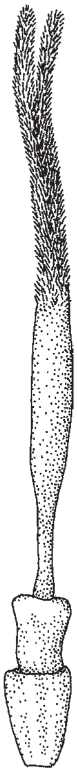


Fig. 78. Pistil of *Chresta amplexifolia* Dematt., Roque & Miranda Gonç. with Vernonioid style surrounded at base by nectary, distally enlarged style with sweeping hairs extending proximally to bifurcation, and long branches.

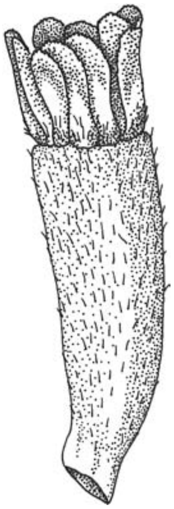
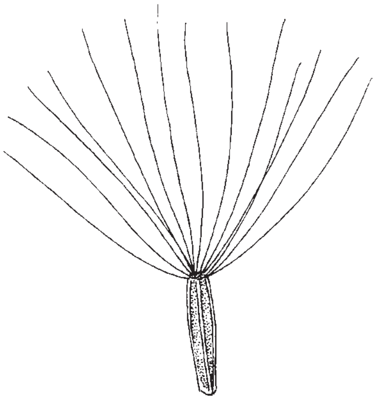


Fig. 79. Terete achene of *Calea pilosa* Baker bearing pappus of short, obtuse scales.

Fig. 80. Terete achene of *Calea huigrensis* S.F. Blake bearing pappus of linear-acuminate scales.

Fig. 81. Prismatic, 5-ribbed achene of *Emilia fosbergii* bearing setose pappus of smooth bristles.



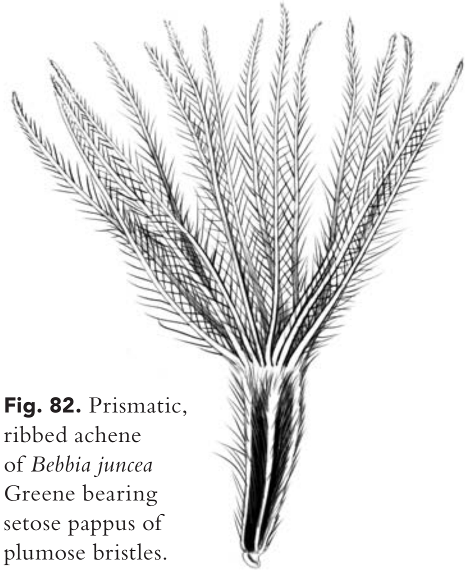


Fig. 82. Prismatic, ribbed achene of *Bebbia juncea* Greene bearing setose pappus of plumose bristles.

Fig. 83. Plant of *Richterago conduplicata* Roque with scapose, radiate head borne on bracted peduncle.

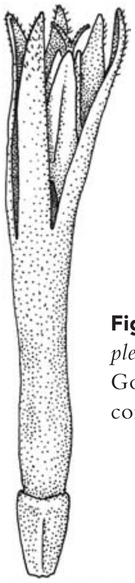


Fig. 84. Disk floret of *Chresta amplexifolia* Dematt., Roque & Miranda Gonç. with tubulose, deeply 5-lobed corolla and epappose ovary.

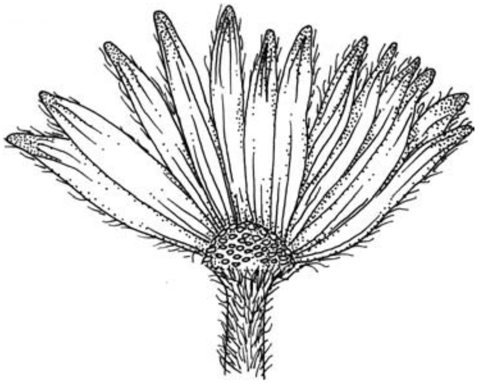


Fig. 85. Distal portion of peduncle and convex epaleate receptacle of *Trichogonia prancii* G.M. Barroso with subequal distinct phyllaries.

Squamella
See **Scale.**

Stamens
Perfect and functionally staminate Compositae flowers have 5 (rarely 3–4) epipetalous stamens with distinct filaments and introrse anthers that are connate into a tube. The filaments are proximally adnate to the corolla, generally at the junction of the corolla tube and throat (Fig. 23). In some groups (especially in Cardueae) filaments are papillose or bear trichomes in association with a more elaborate pollen presentation mechanism. See **Anther, Filament.**

Staminate disk floret
A disk floret that has functional, pollen-producing anthers and an ovary that fails to mature as an achene (Figs. 51, 68); the ovary may be of normal size or more or less reduced (e.g., *Ambrosia*). Staminate disk florets may be centrally located in the same heads as ray florets (e.g., *Blennosperma*), filiform florets (*Pseudognaphalium*), or apetalous florets (e.g., some *Cotula*), or they may be in separate heads on the same individual (e.g., *Ambrosia*) or different plants (e.g., *Baccharis*). See **Neuter floret, Perfect floret, Pistillate floret.**

Staminate head
A type of homogamous head containing only staminate disk florets (e.g., *Baccharis*, *Xanthium*).

Staminate palea
Receptacular bracts (e.g., in some Gnaphalieae) that individually or collectively subtend central staminate disk florets within a head.

Stereome
Thickened, herbaceous to cartilaginous divided or undivided phyllary body in many Gnaphalieae that is differentiated from hyaline or scarious margin and apex.

Sterile disk floret
See **Neuter disk floret;** sometimes inappropriately used for a staminate disk floret.

Sterile floret
See **Neuter floret.**

Sterile ray floret
See **Neuter ray floret.**

Stigma
Pollen-receptive structure of gynoecium (arrays of papillae), usually borne at or near tip of style or style branch; in Compositae presented as stigmatic lines along the adaxial faces of style branches (Fig. 92). Compositae style branches often bear non-stigmatic sterile distal appendages. See **Style, Style appendage, Style branches.**

Stigmatic line
Linear stigmatic arrays of papillae borne along adaxial faces of style branches (Figs. 65, 91, 92).

Stipe
A short to elongated, more or less cylindrical, stalk-like proximal seedless part of the achene in some Compositae (Fig. 18).

Style
Morphology of the style is critical for the tribal classification of Compositae (Jeffrey 2007). The basal part of the style is often dilated and usually glabrous, with the exception of some Eupatorieae and a few Heliantheae. It is often surrounded or partially surrounded at the base by a nectary (Fig. 78). The style is apically divided into two branches that can be short, as in Cardueae, Mutisieae and Barnadesioideae (Fig. 93) or elongated as in Vernonieae (Fig. 78) and Eupatorieae (Fig. 94). Stigmas or stigmatic areas are borne on the adaxial faces of the style branches and may be evenly distributed on the faces of the branches as in Barnadesioideae, Mutisioideae, Carduoideae and Cichorioideae (Fig. 49) or separated in two parallel marginal lines as in the other subfamilies (Fig. 65). Styles vary according to their thickness, grade of bifurcation, disposition and pattern of trichomes and papillae, organization of papillae within the stigmatic areas and morphology of the base of the branches of the style. All these important characters are observed only in the bisexual florets. Styles of ray florets and filiform florets are less ornamented than those of disk florets of the same species, without sweeping hairs and often with more openly displayed stigmatic surfaces (Fig. 2). The disposition of pollen-collecting trichomes or papillae is also a critical character. The collecting brush can be papillose (Figs. 94, 95) or pilose (Fig. 78). Some styles bear trichomes on the abaxial surfaces of the branches sometimes reaching below the bifurcation, as in Vernonieae (Figs. 78, 96), Cichorieae, Plucheeae, and occasionally in members of other tribes (Figs. 91, 98). In Cardueae, the styles have a ring of collecting trichomes just below the bifurcation of the branches, usually on a more or less marked thickening (Fig. 49). In some cases (many Asteroideae and in Nassauviinae), the penicillate collecting trichomes are concentrated on the apex of the truncate branches of the style (Figs. 24, 92). Some tribes (Eupatorieae, Astereae, many Heliantheae and some Senecioneae) have style branches provided with sterile appendages prolonged above the stigmatic areas (Fig. 91). Style branches in Astereae often cling together at the tip. Style branches of functionally staminate disk flowers often fail to separate at anthesis and are reduced to an undivided tack-shaped structure in *Ambrosia*. See **Stigma, Style appendage, Style branches.**

Style appendage
Distal, non-stigmatic tip of style branch of disk floret, sometimes bearing sweeping hairs (Fig. 91), variable in shape and size.

Style branches
The result of incomplete fusion of the distalmost portion of connate carpels of a compound pistil in which the carpel tips are distinct. Compositae styles generally bear two short to elongated branches, each of which is often tipped with an appendage. See **Stigma, Style, Style appendage.**

Styliferous ray floret
A pistillate or neuter ray floret with a style (Figs. 2, 68). See **Astylous ray floret, Fertile ray floret, Neuter ray floret.**

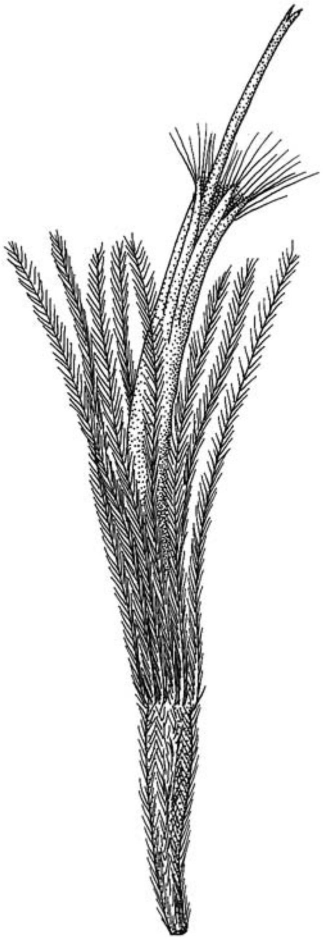


Fig. 86. Floret of *Dasyphyllum candolleanum* (Gardner) Cabrera with setose pappus of plumose bristles, pseudobilabiate corolla with distally pilose lobes, and style with short lobes.

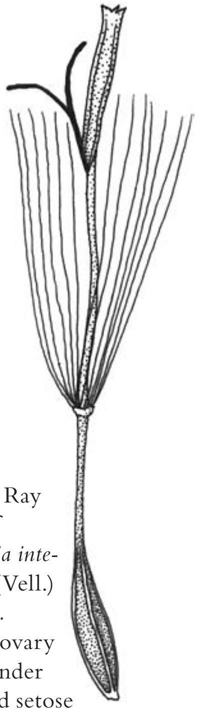


Fig. 87. Ray floret of *Chaptalia integerrima* (Vell.) Burkart. Ribbed ovary with slender beak and setose pappus of smooth bristles.

Fig. 88. Distal portion of peduncle and convex epaleate receptacle of *Baccharis dracunculifolia* DC. with distinct phyllaries.

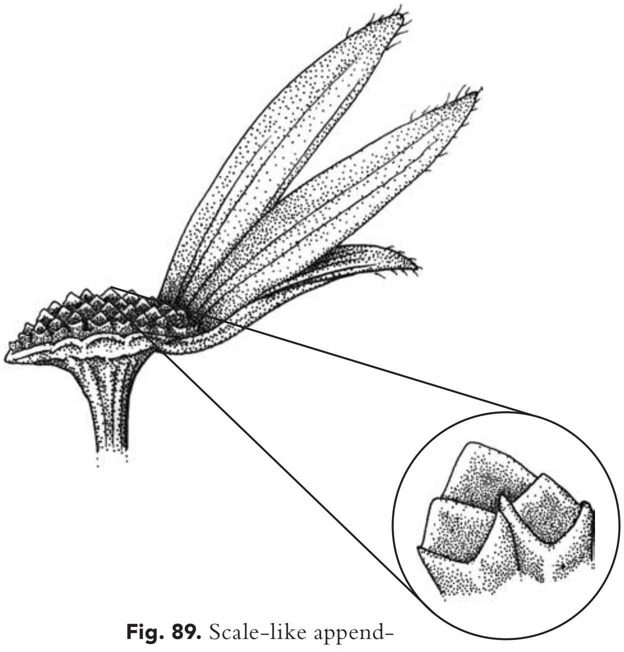


Fig. 89. Scale-like appendages on epaleate receptacle of *Baccharis dracunculifolia* DC.

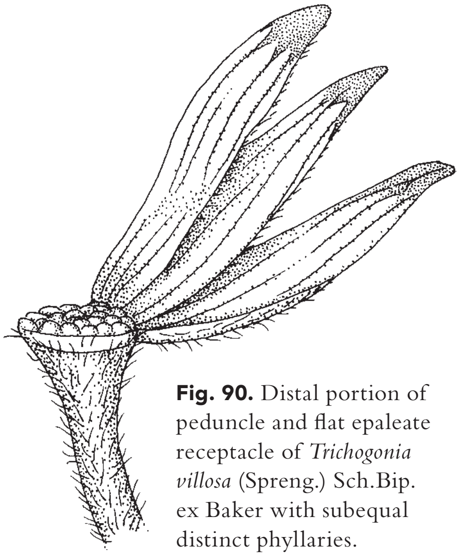


Fig. 90. Distal portion of peduncle and flat epaleate receptacle of *Trichogonia villosa* (Spreng.) Sch.Bip. ex Baker with subequal distinct phyllaries.

Fig. 91. Distal portion of Eupatorioid style of *Stylotrichium corymbosum* (DC.) Mattf. bearing sweeping hairs below the bifurcation, and linear-clavate style branches that are densely papillose proximal to the tips. Marginal stigmatic lines are restricted to proximal adaxial faces of style branches.

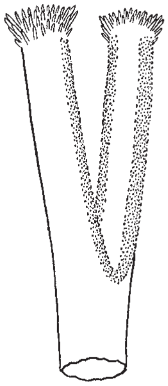


Fig. 92. Distal portion of anthemoid style of *Pentacalia elatoides* (Wedd.) Cuatrec. with marginal stigmatic lines and tufts of sweeping hairs terminating style branches.

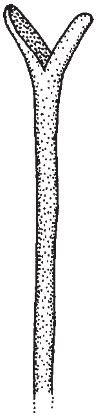


Fig. 93. Distal portion of glabrous style of *Gochnatia paniculata* (Less.) Cabrera with stigmatic surfaces covering adaxial faces of short style branches.

Stylopodium

Structure formed by the basal portion of the style associated with a nectary located at the apex of the ovary (Matzenbacher 1998). The basal part of the style can be totally enclosed in the nectary (Fig. 78), which is then annular (Cardueae, Eupatorieae, Vernonieae), partially inserted (Heliantheae) or placed at the top of the nectary (Astereae and Senecioneae). In Eupatorieae, nectaries have stomas that probably act as secretory pores.

Subequal phyllaries

In two or more series of approximately the same length (Figs. 52, 85).

Sweeping hairs

Hairs borne on distal portion of style and at style tip that brush pollen grains from within anther tube as style elongates or filaments contract (Figs. 24, 78, 95, 96).

Sympetalous

A corolla of connate petals, as in all Compositae corollas.

Synanthery

Anthers laterally connate and introrse, forming a tube that encloses the style and the stigma.

Syncephaly

Combination of several heads into a new morphological entity resembling a single head (Weberling 1989; Figs. 74–76). Individual heads can be free or fused, and they are often subtended by second-order involucral bracts (Figs. 46, 74). See **Secondary head, Tertiary head.**

Synflorescence

See **Secondary inflorescence, Capitulescence.**

Synoecious

Plants in which all flowers are perfect. Compositae with discoid heads and ligulate heads are generally synoecious. See **Dioecious, Monoecious, Polygamous.**

Tailed anther base

See **Caudate anther base.**

Terete achene

Round in cross section (Fig. 79).

Tertiary head

A congested secondary inflorescence in which sessile small heads are grouped together onto a common receptacle, and these sessile secondary clusters are in turn further clustered (e.g., *Gundelia*); each primary and secondary head may have its own involucre, and the tertiary head may be subtended or enclosed by a tertiary involucre. See **Head, Secondary head, Syncephaly.**

Theca

Pollen sac of an anther (syn. anther sac); each anther has two thecas, separated by their lengthwise attachment to the anther connective (Figs. 25, 26, 28). Variation in the shape and appendages of anther theca bases can be taxonomically useful. Patterns of cell wall thickenings in the inner cell walls of anther thecae are also useful characters. Thecas of adjacent anthers in a floret are coherent, collectively forming an anther tube and are adaxially dehiscent, releasing pollen into the anther tube. See **Calcarate anther base, Caudate anther base, Ecalcarate anther base, Ecaudate anther base, Endothecial tissue, Introrse dehiscence.**

Thyrsoid-paniculate

See **Paniculiform.**

Truncate anther base

Ecalcarate bases of anther thecas squared off on either side of anther collar.

Tubular corolla

See **Tubulose corolla, Tubulose-filiform corolla.**

Tubulose corolla

Generally radially symmetric corolla usually divided into a tube and a limb (Figs. 48, 97), the latter enclosing the anther tube in disk florets. Florets with tubulose corollas are arranged in the center of radiate heads; in disciform and discoid heads, they are distributed throughout the head.

Tubulose-filiform corolla

Tubulose corolla of the pistillate florets of disciform heads (Fig. 58), sometimes with an unlobed limb or with vestigial lobes (Fig. 66). They are usually narrowly cylindrical (Fig. 68), a shape associated with the absence of stamens. See **Filiform floret.**

Twin hairs

Two-celled trichomes characteristic of the achenes of many Compositae.

Unequal phyllaries

Phyllaries in one or more series of differing lengths (Figs. 69, 70).

Uniseriate involucre

Involucral bracts arranged in a single series (Figs. 40, 44, 77).

Uniseriate pappus

Pappus with elements arranged in a single series (Fig. 99)

Unisexual floret

See **Pistillate floret, Staminate disk floret.**

Vernonioid style

Style with sweeping hairs borne on abaxial surfaces of style branches and extending below the style branches onto the shaft of the style (Figs. 78, 96).

Winged achene

Bearing flattened, longitudinal membranous appendages (Figs. 8, 10, 11).

Zygomorphic

See **Bilateral symmetry.**

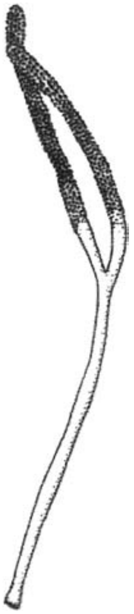


Fig. 94. Distal portion of Eupatorioid style of *Scherya bahiensis* R.M. King & H. Rob. with linear, distally papillose style branches. Marginal stigmatic lines are restricted to proximal adaxial faces of style branches.

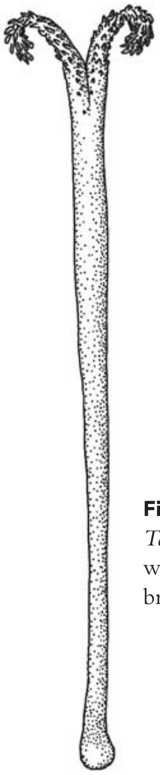


Fig. 95. Style of *Tagetes minuta* L. with papillose style branches.

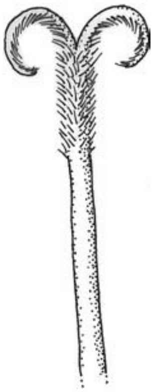


Fig. 96. Distal portion of Vernonioid style of *Centratherum punctatum* DC. with sweeping hairs extending proximally to bifurcation and long branches.

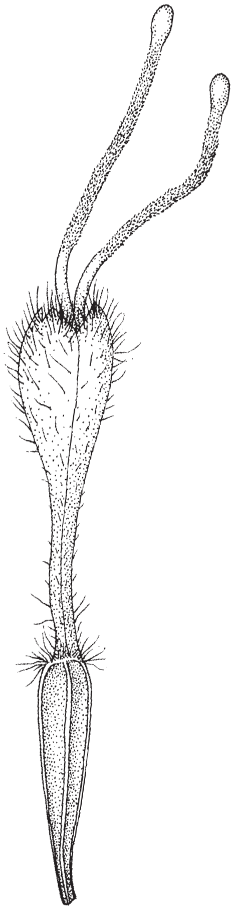


Fig. 97. Disk floret of *Trichogonia cinerea* (Gardner) R.M. King & H. Rob. with epappose, 5-ribbed, prismatic ovary, tubulose, short-lobed corolla with included stamens, and long-exserted Eupatorioid style.

Fig. 98. Densely puberulent style tip of *Pectis brevipedunculata* (Gardner) Sch.Bip. with stigmatic surfaces covering adaxial faces of very short style branches.

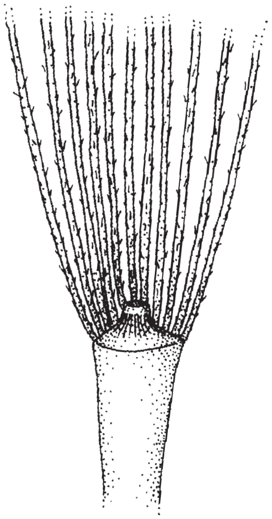


Fig. 99. Distal end of achene of *Richterago discoidea* (Less.) Kuntze illustrating uniseriate setose pappus composed of barbellate bristles.

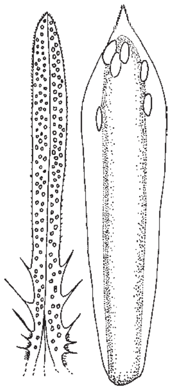


Fig. 100. Abaxial surfaces of leaf and phyllary of *Pectis* ×*floridana* with pellucid glands.

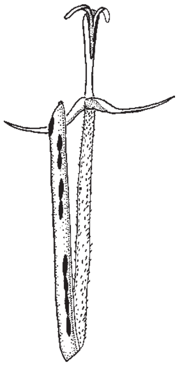


Fig. 101. Phyllary and ray floret of *Pectis linifolia* L. Phyllary dotted with pellucid glands. Ovary is inserted on base of subtending phyllary and matures as a cylindrical, terete achene with an aristate pappus of divaricate smooth awns.

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Stuessy, T.F. & Spooner, D.M. 1988. The adaptive and phylogenetic significance of receptacular bracts in the Compositae. *Taxon* 37: 114–126.

Wagenitz, G. 1976. Was ist eine Achäne: zur Geschichte eines karpologischen Begriffs. *Candollea* 31: 79–85.

Weberling, F. 1989. *Morphology of Flowers and Inflorescences.* Cambridge University Press, Cambridge, Massachusetts.

Appendix **B**

Bibliography of pollen literature in Compositae

Alexandra H. Wortley, Stephen Blackmore and John J. Skvarla

INTRODUCTION

The idea of a bibliography of pollen literature is not new. From 1927 to 1957, Erdtman published 14 volumes of "Literature on Palynology" (*Forhandlingar Geologiska Foreningen i Stockholm* 49–79). Following this, in 1959 Madame Van Campo published the first of a yearly series of pollen bibliographies as supplements to the journal *Pollen et Spores* (Van Campo, M. 1959. References Bibliographiques. *Supplement à Pollen et Spores* 1: 9–144), containing 763 references. The final supplement was in 1986 (Van Campo, M. 1986. Palynologie 1986–1987. *Supplement à Pollen et Spores* 28: 1–147) and contained 23,340 references, indicating the vast amount of palynological work conducted during the intervening years. In addition, in 1974, Hans Tralau compiled a 358-page *Bibliography and Index to Palaeobotany and Palynology, 1950–1970* (Hans Tralau, Stockholm), plus a 261-page index, with a primary focus on fossil pollen, and between 1991 and 1997 Bustillo and co-workers published a number of bibliographies of palynological studies relating to Spain (Lain, C.S. and Bustillo, M.G. 1991. Bibliografiá palinológica española (1932–1988). *Lazaroa* 12: 69–119; Bustillo, M.G. 1994. Bibliografía palinológica española. Años 1988–92 y adiciones. *Lazaroa* 14: 139–165; Bustillo, M.G. and Pérez, E.O. 1997. Bibliografiá palinológica española. Años 1993–1996 y adiciones. *Lazaroa* 18: 189–232). A listing of regional pollen atlases has also been compiled by Hooghiemstra and Van Geel (1998), with the aim of facilitating identification in Quaternary palynological studies (Hooghiemstra & Van Geel. 1998. World list of Quaternary pollen and spore atlases. *Review of Palaeobotany and Palynology* 104: 157–182). The first full "Index *Bibliographique* sur la Morphologie des Pollens d'Angiosperms" was published in 1972 by Ganapathi Thanikaimoni, and this index continues to be updated through supplements produced by him and, following his untimely death, his colleagues at the Institut Français de Pondichéry, India (Thanikaimoni, G. 1972. Index bibliographique sur la morphologie des pollens d'angiospermes. *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry* XII(1): 1–337; Thanikaimoni, G. 1973. Index bibliographique sur la morphologie des pollens d'angiospermes. Supplément – 1. *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry* XII(2): 1–164; Thanikaimoni, G. 1976. Index bibliographique sur la morphologie des pollens d'angiospermes. Supplément – 2. *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry* XIII: 1–386; Thanikaimoni, G. 1980. Quatrieme index bibliographique sur la morphologie des pollens d'angiospermes. *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry* XVII: 1–336; Thanikaimoni, G. 1986. Cinquième index bibliographique sur la morphologie des pollens d'angiospermes. *Travaux de la Section Scientifique et Technique, Institut Français*

Dedication. This bibliography is dedicated to Ganapathi Thanikaimoni (1938–1986).

de Pondichéry XXII: 1–293; Tissot, C. 1990. Sixième index bibliographique sur la morphologie des pollens d'angiospermes. *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry* XXVII: 1–304; Tissot, C. and Van der Ham, R.W.J.M. 1994. Septième index bibliographique sur la morphologie des pollens d'angiospermes. *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry* XXXVI: 1–342; Thanikaimoni, K. and Van der Ham, R.W.J.M. 1999. Huitième index bibliographique sur la morphologie des pollens d'angiospermes. *Travaux de la Section Scientifique et Technique, Institut Français de Pondichéry* XXXIX: 1–346). In 1977, in the proceedings of the Reading (UK) conference on *The Biology and Chemistry of the Compositae*, Thanikaimoni produced a more specialist list on Compositae work (Thanikaimoni, G. 1977. Appendix: Principal works on the pollen morphology of the Compositae. Pp. 249–265 in: Heywood, V.H., Harborne, J.B. and Turner, B.L. (eds.), *The Biology and Chemistry of the Compositae*. Academic Press, London). This source proved invaluable in researching the pollen of the Compositae for Chapter 7, and inspired us to generate an updated list, which is presented here.

The bibliography comprises 1269 references and is presented in two parts. The first part of the bibliography is arranged taxonomically, and covers only references relating to the genera in the recent Compositae supertree (=metatree; Funk, V.A., Bayer, R.J., Keeley, S., Chan, R., Watson, L., Gemeinholzer, B., Schilling, E., Panero, J.L., Baldwin, B.G., Garcia-Jacas, N., Susanna, A. and Jansen, R.K. 2005. Everywhere but Antarctica: using a supertree to understand the diversity and distribution of the Compositae. *Biologiske Skrifter* 55: 343–374). These genera are arranged alphabetically within tribes (or tribal-level groups), as presented in the supertree. The citations listed for each genus refer to the subsequent full bibliography. The second part is a typical bibliography, arranged alphabetically by author. Where possible, following each entry is a list of Compositae genera whose pollen is mentioned therein. Not all of these references have been seen by the authors—204 (16%) have not been seen, and these are marked with an ⋆. Genus names are taken from Kadereit and Jeffrey (Kadereit, J.W. and Jeffrey, C. (eds.). 2007. *The Families and Genera of Vascular Plants*, vol. 8, *Flowering Plants. Eudicots. Asterales*. Springer, Berlin, Heidelberg, New York). The only exceptions are a few very recently described or resurrected genera. Taxa known only from fossils are not included.

Following the bibliography is a list of generic "synonyms"—alternative generic names, along with the name under which they are treated in this paper and in Kadereit and Jeffrey (2007). These are not all synonyms in the strict sense of the word—some are later homonyms, illegitimate names, orthographic variants, or infrageneric names that may have been confused with genera. It does not cover species which have been treated under different genera. This list is included to aid searching for references to a genus which may have been known by a different name at different times in the literature. We hope it might make the bibliography more useful and easier to navigate. This listing is not complete—rather it includes those names we came across during compiling the bibliography. Thus there may still be instances in the following list where a paper is cited erroneously as providing information on a genus that it does not contain, or contains a genus which is not listed under its currently accepted name. We hope such instances will be rare, but for this reason we suggest that the generic lists, particularly for older papers, be taken only as a guide to the genera that are to be found therein.

Despite the huge amount of work that has been done on Compositae pollen, some taxa have apparently not been studied in recent years, perhaps since the advent of the scanning electron microscopy. Examples include *Othonna* L., last studied by Tarnavschi and Mitriou (1959), *Aaronsohnia* Warburg & Eig, by Skvarla and Turner (1966a) and *Euryops* Cass. (Nordenstam 1968). Most of these understudied genera seem to lie in Asteroideae, perhaps reflecting the relatively homogeneous nature of pollen morphology in this group. It is also important to note the huge contribution made by early palynologists, in providing detailed accounts of the pollen morphology of large numbers of genera that are still useful today. Such works include Mohl (1835), with 61 genera, Fischer (1890), with over 100, and R.P. Wodehouse's large number of works published between 1926 and 1935.

This bibliography in no way claims to be comprehensive and we are aware that certain sets of literature are poorly represented. There is a deliberate focus on papers containing pollen images—TEM, SEM, light micrographs and drawings—or detailed descriptions of pollen morphology and ultrastructure, primarily of extant species. We also had limited success in obtaining references from outside the western world. Particularly underrepresented, therefore, are works from Chinese and Russian institutions, as well as the wealth of literature devoted to the more applied aspects of palynology: airborne pollen, bee and honey palynology and allergy studies as well as palaeobotanical work. However, we hope it will prove a useful starting point for those attempting to access the wealth of knowledge available on Compositae pollen morphology.

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TAXONOMIC LISTING OF SUPERTREE GENERA WITH REFERENCES

Barnadesioideae

BARNADESIEAE

Arnaldoa; Hansen 1991a, b; Stuessy & al. 1996; Urtubey & Tellería 1998; Zhao 1999; Zhao & al. 2000; Stuessy & Urtubey 2007.

Barnadesia; Edgeworth 1877; Wodehouse 1928a, b, 1929b, 1934, 1935, 1945; Erdtman 1952; Cabrera 1959; Ueno 1972; Robinson 1975, 1987a; Gamerro 1985; Blackmore 1986; Hansen 1991a, b; Stuessy & al. 1996; Urtubey 1997, 1999; Urtubey & Tellería 1998; Zhao 1999; Zhao & al. 2000; Gustafsson & al. 2001; Urtubey & Stuessy 2001; Stuessy & Urtubey 2007; Blackmore & al. 2009 (Chapter 7).

Chuquiraga; Wodehouse 1928a, b, 1929b; Cabrera 1959; Parra & Marticorena 1972; Marticorena & Parra 1975; Markgraf & D'Antoni 1978; Robinson 1987a; Skvarla & al. 1988; Hansen 1991a, b; Gustafsson & al. 1996, 1997, 2001; Stuessy & al. 1996; Urtubey & Tellería 1998; Zhao 1999; Torres 2000; Zhao & al. 2000; Urtubey & Stuessy 2001; Andrada & Tellería 2002, 2005; Tellería & Forcone 2002; Meier-Melikyan & al. 2004; Tellería & Katinas 2005; Katinas & al. 2007; Stuessy & Urtubey 2007; Blackmore & al. 2009 (Chapter 7).

Dasyphyllum; Cabrera 1959; Moreira 1969; Parra & Marticorena 1972; DeVore & al. 1986; Robinson 1987a; Skvarla & al. 1988; Hansen 1991a, b; Gustafsson & al. 1996, 1997; Stuessy & al. 1996; Urtubey & Tellería 1998; Zhao 1999; Zhao & al. 2000; Urtubey & Stuessy 2001; Tellería & Katinas 2005; Cancelli & al. 2007; Stuessy & Urtubey 2007; DeVore & Skvarla, 2008; Blackmore & al. 2009 (Chapter 7).

Doniophyton; Parra & Marticorena 1972; Marticorena & Parra 1975; Bolick 1978b, 1980; Markgraf & D'Antoni 1978; DeVore & al. 1986; Hansen 1991a, b; Stuessy & al. 1996; Urtubey & Tellería 1998; Zhao 1999; Zhao & al. 2000; Gustafsson & al. 2001; Urtubey & Stuessy 2001; Stuessy & Urtubey 2007; Blackmore & al., in press.

Fulcaldea; Cabrera 1959; Hansen 1991b; Stuessy & al. 1996; Urtubey & Tellería 1998; Zhao 1999; Zhao & al. 2000; Gustafsson & al. 2001; Urtubey & Stuessy 2001; Stuessy & Urtubey 2007.

Huarpea; Gamerro 1985; Hansen 1991b; Stuessy & al. 1996; Urtubey & Tellería 1998; Zhao 1999; Zhao & al. 2000; Gustafsson & al. 2001; Urtubey & Stuessy 2001; Stuessy & Urtubey 2007.

Schlechtendalia; Wodehouse 1928b, 1929b; Robinson 1981b; DeVore & al. 1986; Hansen 1991a, b; Stuessy & al. 1996; Urtubey & Tellería 1998; Zhao 1999; Zhao & al. 2000; Urtubey & Stuessy 2001; Tellería & Katinas 2005; Stuessy & Urtubey 2007; DeVore & Skvarla, 2008.

STENOPADUS CLADE

Chimantaea; Carlquist 1957a; Hansen 1991a, b; Zhao 1999; Rull 2003; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Tellería, 2008.

Hyalis; Hansen 1991a, b; Torres 2000; Tellería & Forcone 2002; Tellería & Katinas 2004; Katinas & al, 2008a.

Ianthopappus; Roque & Silvestre Capelato 2001; Katinas & al, 2008a.

Leucomeris; Marticorena & Parra 1975; Nair & Lawrence 1985; Hansen 1991b; Ling 1993.

Nouelia; Hansen 1991a, b; Ying & al. 1993; Zhao 1999; Lin & al. 2005; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Stenopadus; Carlquist 1957a; Barroso & Maguire 1973; Marticorena & Parra 1975; Hansen 1991a, b; Zhao 1999; Rull 2003; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Tellería 2008; Blackmore & al. 2009 (Chapter 7).

Stomatochaeta; Carlquist 1957a; Hansen 1991a, b; Zhao 1999; Zhao & al. 2006; Katinas & al, 2008a; Tellería, 2008.

Wunderlichia; Wodehouse 1929b; Carlquist 1957a; Moreira 1969; Barroso & Maguire 1973; Marticorena & Parra 1975; Moreira & al. 1981; Hansen 1991a, b; Zhao 1999; Tellería & al. 2003; Rodriguez & al. 2004; Zhao & al. 2006; Katinas & al, 2008a; Tellería 2008; Blackmore & al. 2009 (Chapter 7).

STIFFTIA CLADE

Duidaea; Carlquist 1957a; Hansen 1991a, b; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Tellería 2008.

Gongylolepis; Carlquist 1957a; Maguire 1967; Barroso & Maguire 1973; Marticorena & Parra 1975; Hansen 1991a, b; Rodriguez & al. 2004; Katinas & al, 2008a; Tellería 2008; Blackmore & al. (2009, Chapter 7).

Hyaloseris; Hansen 1991a, b; Zhao 1999; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Stifftia; Carlquist 1957a; Barroso & Maguire 1973; Marticorena & Parra 1975; Robinson & Kahn 1985a; Pastana 1989; Hansen 1991a, b; Robinson 1991; Zhao 1999; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Tellería 2008; Blackmore & al. 2009 (Chapter 7).

Mutisioideae

MUTISIEAE s.str.

Acourtia; Reveal & King 1973; Crisci 1974a; Hansen 1991a, b; Zhao 1999; Cabrera & Dieringer 2003; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Adenocaulon; Erdtman 1952; Ikuse 1956; Ornduff & al. 1967; Leins 1968b; Wittenbach 1970; Heusser 1971; Wagenitz 1976; Skvarla & al. 1977; Bittmann 1990; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Jansen & Ki-Joong 1996; Zhao 1999; Kim & al. 2002; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7), and in press.

Aphylloclados; Parra & Marticorena 1972; Hansen 1991b; Zhao 1999; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a.

Brachyclados; Parra & Marticorena 1972; Hansen 1991a, b; Andrada & Tellería 2002; Tellería & Katinas 2004; Katinas & al, 2008a.

Chaetanthera; Wodehouse 1929b; Parra & Marticorena 1972; Markgraf & D'Antoni 1978; Wingenroth & Heusser 1983; Hansen 1991a, b; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Chaptalia; Wodehouse 1929b; Moreira 1969; Parra & Marticorena 1972; Salgado-Labouriau 1982b, 1983; Gandi & Thomas 1989; Pastana 1989; Hansen 1990, 1991b; Roubik & Moreno 1991; Torres 2000; Tellería & Katinas 2004, 2005; Zhao & al. 2006; Katinas & al, 2008a.

Dolichlasium; Crisci 1974a; Hansen 1991a, b; Katinas & al, 2008a.

Gerbera; Wodehouse 1929b; Maheswari Devi 1957; Chaubal & Deodikar 1965; Southworth 1966, 1969a, 1971, 1973, 1974, 1983a, b, 1990a, b; Ueno 1971; Rowley & Dahl 1977; Payne 1981; Nair & Lawrence 1985; Provoost & al. 1988; Southworth & Knox 1988, 1989; Hansen 1990, 1991a, b; Fuhsiung & al. 1995; Reille 1995; Chen & al. 2004; Tellería & Katinas 2004;

Lin & al. 2005; Meo 2005; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Jungia; Wodehouse 1929a; Crisci 1971a, 1974a; Pastana 1989; Hansen 1991a, b; Reille 1998; Zhao 1999; Zhao & al. 2006; Barrea & al. 2008.

Leibnitzia; Ikuse 1956; Hansen 1991a, b; Nagamitsu & Nagamasu 1994; Zhao 1999; Tellería & Katinas 2004; Lin & al. 2005; Zhao & al. 2006; Katinas & al, 2008a.

Leucheria; Wodehouse 1929a; Crisci 1971a, b, 1974a, b, 1976; Parra & Marticorena 1972; Markgraf & D'Antoni 1978; Wingenroth & Heusser 1983; Hansen 1991a, b; Zhao 1999; Meier-Melikyan & al. 2004; Zhao & al. 2006; Katinas & al. 2008a, b.

Lophopappus; Parra & Marticorena 1972; Crisci 1974a; Cabrera 1977; Hansen 1991a, b; Zhao 1999; Tellería & al. 2003; Zhao & al. 2006; Katinas & al, 2008a.

Lycoseris; Wodehouse 1929b; Egerod & Stahl 1969; Hansen 1991a, b; Tellería & Katinas 2004; Tellería & Katinas 2005; Katinas & al, 2008a.

Mutisia; Wodehouse 1929b; Zander 1935; Erdtman 1952, 1964; Stix 1960; Skvarla & Turner 1966b; Southworth 1966; Heusser 1971; Parra & Marticorena 1972; Markgraf & D'Antoni 1978; Pastana 1989; Hansen 1991a, b; Graham 1996; Zhao 1999; Torres 2000; Tellería & Forcone 2002; Tellería & al. 2003; Tellería & Katinas 2004; Cancelli & al. 2005b; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Nassauvia; Wodehouse 1929a; Parra & Marticorena 1972; Crisci 1974a; Markgraf & D'Antoni 1978; Cabrera 1982; Wingenroth & Heusser 1983; Crisci & Freire 1986; Hansen 1991a, b; Zhao 1999; Tellería & al. 2003; Meier-Melikyan & al. 2004; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Onoseris; Wodehouse 1929b; Stix 1960; Crisci 1974a; Skvarla & al. 1977; Hansen 1991a, b; Zhao 1999; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. in press.

Pachylaena; Wodehouse 1929b; Parra & Marticorena 1972; Markgraf & D'Antoni 1978; Hansen 1991a, b; Zhao 1999; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a.

Perezia; Fischer 1890; Wodehouse 1929a; Hernandez 1966; Martin & Drew 1969; Simpson Vuilleumier 1970; Parra & Marticorena 1972; Crisci 1974a; Marticorena & Parra 1974; Skvarla & al. 1977; Crisci & Marticorena 1978; Markgraf & D'Antoni 1978; Wingenroth & Heusser 1983; Hansen 1991a, b; Zhao 1999; Meier-Melikyan & al. 2004; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7), and in press.

Plazia; Wodehouse 1929b; Parra & Marticorena 1972; Robinson 1980a; Hansen 1991a, b; Zhao 1999; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Proustia; Wodehouse 1929a; Heusser 1971; Parra & Marticorena 1972; Crisci 1974a; Cabrera 1977; Markgraf & D'Antoni 1978; Hansen 1991a, b; Zhao 1999; Cabrera & Dieringer 2003; Tellería & al. 2003; Zhao & al. 2006; Katinas & al. 2007, 2008a; Barreda & al. 2008.

Trichocline; Wodehouse 1929a; Parra & Marticorena 1972; Zardini 1975; Cabrera 1977; Markgraf & D'Antoni 1978; Robinson 1988b; Hansen 1990, 1991a; Zhao 1999; Torres 2000; Andrada & Tellería 2002; Tellería & Katinas 2004; Zhao & al. 2006; Cancelli & al. 2007; Katinas & al, 2008a.

Triptilion; Wodehouse 1929a; Parra & Marticorena 1972; Crisci 1974a; Crisci & Freire 1986; Hansen 1991a, b; Zhao 1999; Zhao & al. 2006; Katinas & al, 2008a.

Trixis; Wodehouse 1929a; Stix 1960; Erdtman 1964; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Martin & Drew 1969; Moreira 1969; Anderson 1972; Parra & Marticorena 1972; Skvarla & al. 1977; Crisci & Marticorena 1978; Robinson 1978d, 1979b, k, 1981b, 1988c; Gonçalves-Esteves & Esteves 1986; Pastana 1989; Hansen 1991a, b; Jones & al. 1995; Katinas 1996; Zhao 1999; Torres 2000; Cabrera & Dieringer 2003; Tellería & al. 2003; Cancelli & al. 2006a; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7). and in press.

Gochnatioideae

GOCHNATIEAE

Cnicothamnus; Hansen 1991a, b; Zhao 1999; Tellería & Katinas 2004; Zhao & al. 2006; Katinas & al. 2007, 2008a; Blackmore & al. 2009 (Chapter 7).

Cyclolepis; Wodehouse 1929b; Hansen 1991a, b; Tellería & Forcone 2002; Katinas & al, 2008a.

Gochnatia; Wodehouse 1929b; Moreira 1969; Parra & Marticorena 1972; Crisci 1974a; Marticorena & Parra 1974, 1975; Cabrera 1977; Markgraf & D'Antoni 1978; Moreira & al. 1981; Pastana 1989; Hansen 1991a, b; Zhao 1999; Ortiz 2000; Roque & Pirani 2001; Roque & Silvestre-Capelato 2001; Tellería & Katinas 2004, 2005; Lin & al. 2005; Sancho & al. 2005; Zhao & al. 2006; Cancelli & al. 2007; Modro & al. 2007; Katinas & al, 2008a.

Richterago; Wodehouse 1929b; Moreira & al. 1981; Hansen 1991a, b; Zhao 1999; Roque & Pirani 2001; Roque & Silvestre-Capelato 2001.

Hecastocleioideae

HECASTOCLEIDEAE

Hecastocleis; Wodehouse 1929b; Hansen 1991a, b; Tellería & Katinas 2004, 2005; Wortley & al. 2007; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Carduoideae

DICOMEAE

Dicoma; Wodehouse 1929b; Stix 1960; Parveen & Bhandari 1981; Nair & Lawrence 1985; Qaid 1990; Hansen 1991a, b; Perveen & al. 1994; Jeffrey 1995; Perveen 1999; Zhao 1999; Ortiz 2000; Netnou 2001; Tellería & al. 2003; Zhao & al. 2006; Blackmore & al. 2009 (Chapter 7), and in press.

Macledium; Netnou 2001.

Pasacardoa; Hansen 1991a, b; Chissoe & al. 1994; Zhao 1999; Ortiz 2000; Zhao & al. 2006.

OLDENBURGIEAE

Oldenburgia; Hansen 1991a, b; Zhao 1999; Ortiz 2000; Zhao & al. 2006; Blackmore & al. 2009 (Chapter 7).

TARCHONANTHEAE

Brachylaena; Wittenbach 1970; Leins 1971; Wagenitz 1976; Cilliers 1991; Hansen 1991b; Keeley & Jansen 1991; Jeffrey 1995; Jansen & Ki-Joong 1996; Zhao 1999; Kim & al. 2002; Zhao & al. 2006; Blackmore & al. in press.

Tarchonanthus; Erdtman 1952; Wittenbach 1970; Leins 1971; Wagenitz 1976; Skvarla & al. 1977; Hansen 1991a; Keeley & Jansen 1991; Jeffrey 1995; Jansen & Ki-Joong 1996; Zhao 1999; Kim & al. 2002; Zhao & al. 2006; Wortley & al. 2007; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

CARDUEAE

Acantholepis; Qaid 1990; Petit & al. 1996; Tomsovic 1997; Reille

1998; Meo 2005; Garnatje & Martín 2007; Blackmore & al. 2009 (Chapter 7).

Acroptilon; Wagenitz 1955; Carlquist 1958; Avetisian 1964; Dittrich 1977; Gandi & Thomas 1989; Javeid 1991; Fuhsiung & al. 1995; Meier-Melikyan & al. 2004; Meo 2005.

Alfredia; Fischer 1890; Schtepa 1977; Reille 1998; Meier-Melikyan & al. 2004; Blackmore & al. 2009 (Chapter 7).

Arctium; Mohl 1835; Zander 1935; Wodehouse 1945; Ikuse 1956; Tarnavschi & Mitroiu 1959; Schtepa 1966, 1973b, 1977; Kuprianova & Alyoshina 1972; Dittrich 1977; Kuprianova & Cherneva 1982; Nair & Lawrence 1985; Díez 1987; Valdés & al. 1987; Faegri & Iversen 1989; Gandi & Thomas 1989; Qaid 1990; Tormo & Ubera 1990b, 1995; Javeid 1991; Ling 1993; Fuhsiung & al. 1995; Reille 1995; Tellería 1995; Petit & al. 1996; Chester & Raine 2001; Meier-Melikyan & al. 2004; Meo 2005; Jafari & Ghanbarian 2007; Blackmore & al. 2009 (Chapter 7), and in press; Punt & Hoen, in press.

Atractylis; Dimon 1971a, b; Dimon-Cathary 1973; Tormo & al. 1984, 1986; Díez 1987; Qaid 1990; Tormo & Ubera 1990b, c, 1995; Reille 1995; Chung & al. 2003.

Atractylodes; Ikuse 1956; Ma 1980; Ling 1993; Fuhsiung & al. 1995; Anon., 2000; Kim & Chung 2000; Chung & al. 2003; Blackmore & al. 2009 (Chapter 7).

Berardia; Stix 1960; Marticorena & Parra 1975; Cabrera 1977; Zhao 1999; Zhao & al. 2006.

Callicephalus; Wagenitz 1955; Carlquist 1958; Jeffrey 1968; Avetisian & Tonyan 1975; Dittrich 1977; Hidalgo & al. 2008.

Cardopatium; Qaid 1990; Petit & al. 1996.

Carduus; Mohl 1835; Edgeworth 1877; Fischer 1890; Avebury 1912; Zander 1935; Erdtman 1952, 1964; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Pla Dalmau 1961; Schtepa 1962, 1977; Jeffrey 1968; Dimon 1971b; Visset 1974; Dittrich 1977; Inceoglu & Karamustafa 1977; Moore & Web 1978; Devesa 1979; Devesa & Talavera 1981; Nair & Lawrence 1985; Díez 1987; Valdés & al. 1987; Tormo & Ubera 1988b, 1990b, 1995; Gandi & Thomas 1989; Qaid 1990; Javeid 1991; Ying & al. 1993; Fuhsiung & al. 1995; Lunau 1995; Reille 1995, 1998; Tellería 1995; Coutinho 1996; Kapp & al. 2000; Torres 2000; Beug 2001; Andrada & Tellería 2002, 2005; von Gaisberg & Wagenitz 2002.; Meo & Khan 2003b; Meier-Melikyan & al. 2004; Meo 2005; Jafari & Ghanbarian 2007; Blackmore & al. 2009 (Chapter 7); Punt & Hoen, in press.

Carlina; Fischer 1890; Zander 1935; Stix 1960; Dimon 1971a, b; Dittrich 1977; Ma 1980; Tormo & al. 1984, 1986; Díez 1987; Valdés & al. 1987; Faegri & Iversen 1989; Qaid 1990; Tormo & Ubera 1990b, 1995; Reille 1995, 1998; Tarnavschi & Mitriou 1959; Petit & al. 1996; La-Serna & al. 1999, 2002; Beug 2001; Chester & Raine 2001; Meier-Melikyan & al. 2004; La-Serna & Gómez Ferreras 2006; Punt & Hoen, in press.

Centaurea; Mohl 1835; Edgeworth 1877; Smith 1877; Fischer 1890; Avebury 1912; Wodehouse 1930; Zander 1935; Erdtman 1952, 1969; Wagenitz 1955, 1963, 1996; Carlquist 1958; El Hadidy 1958; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Pla Dalmau 1961; Ikuse 1962; Maurizio & Louveaux 1963; Avetisian 1964; Chaubal & Deodikar 1965; Assemien 1966; Jeffrey 1968; Parra 1969–1970; Dimon 1971a, b; Heusser 1971; Greuter 1973a; Solomon & al. 1973; Guinet & Maley 1974; Visset 1974; Avetisian & Tonyan 1975; Tonyan & Mekhakyan 1975; Dittrich 1977; Inceoglu & Karamustafa 1977; Nilsson & al. 1977; Nordenstam & El Ghazaly 1977; Bolick 1978a, b, 1980; Lee 1978; Blanca & Rosúa 1979; Georgiadis 1980, 1987; Van Helvoort 1980; Blanca 1981a, b; Payne 1981; Cusma Velari 1982, 1984; Cusma Velari & Vuerich 1982; Kuprianova & Cherneva 1982; Blackmore & al. 1984; De Leonardis & al. 1984; Kaya 1985; Nair & Lawrence 1985; Siljak-Yakovlev 1986; Bremer 1987; Díez 1987; Valdés & al. 1987; Skvarla & al. 1988; Tormo & Ubera 1988c, 1990b, c, 1995; Faegri & Iversen 1989; Gandi & Thomas 1989; Qaid 1990; Javeid 1991; Moore & al. 1991; Trigo & al. 1991; Garcia-Jacas 1992; Lietava 1992; Chissoe & al. 1994; Pehlivan 1994, 1995a, b, 1996; Gabrielian 1995; Jeffrey 1995; Kaya & al. 1995; Lunau 1995; Reille 1995, 1998; Tellería 1995; Petit & al. 1996, 2001; Pinar & Inceoglu 1996; Kapp & al. 2000; Martín & Garcia-Jacas 2000; Torres 2000; Beug 2001; Chester & Raine 2001; Garcia-Jacas & al. 2001; Vilatersana & al. 2001; Andrada & Tellería 2002, 2005; Bancheva & Raimondo 2003; Binka 2003; Meier-Melikyan & al. 2004; Meo & Khan 2004b; Celik & al. 2005; Meo 2005; Uysal & al. 2005; Sa-Otero & al. 2006; Cancelli & al. 2007; Jafari & Ghanbarian 2007; Hidalgo & al. 2008; Raimondo & Spadaro 2008; Uysal & al. 2008; Punt & Hoen, in press.

Chardinia; Qaid 1990; Petit & al. 1996; Meo 205; Garnatje & Martín 2007; Blackmore & al. 2009 (Chapter 7).

Cirsium; Mohl 1835; Fischer 1890; Zander 1935; Wodehouse 1945; Harris & Filmer 1948; Erdtman 1952, 1964, 1969; Ikuse 1956, 1962; Schtepa 1958, 1962, 1965, 1977; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Pla Dalmau 1961; Maurizio & Louveaux 1963; Moore & Frankton 1964; Nair 1965; Jeffrey 1968; Martin & Drew 1969, 1970; Dimon 1971a, b; Heusser 1971; Huang 1972; Kuprianova & Alyoshina 1972; Dimon-Cathary 1973; Greuter 1973; Greuter & Dittrich 1973; Visset 1974; Moore 1975; Talavera & Valdés 1976; Cabrera 1977; Dittrich 1977; Inceoglu & Karamustafa 1977; Skvarla & al. 1977; Moore & Webb 1978; Van Helvoort 1980; Bir & Sidhu 1982; Nair & Lawrence 1985; Díez 1987; Valdés & al. 1987; Tormo & Ubera 1988b, 1990b, c, 1995; Faegri & Iversen 1989; Gandi & Thomas 1989; Qaid 1990; Hansen 1991b; Javeid 1991; Moore & al. 1991; Ling 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Jones & al. 1995; Lunau 1995; Reille 1995, 1998; Kapp & al. 2000; Martín & Garcia-Jacas 2000; Beug 2001; Chester & Raine 2001; Andrada & Tellería 2002; Kesseler & Harley 2004; Meier-Melikyan & al. 2004; Willard & al. 2004; Meo 2005; Jafari & Ghanbarian 2007; Punt & Hoen, in press.

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Echinops; Mohl 1835; Fischer 1890; Zander 1935; Wodehouse 1945; Erdtman 1952, 1969; Tarnavschi & Mitriou 1959; Stix 1960, 1964, 1970; Pla Dalmau 1961; Ikuse 1962; Chaubal & Deodikar 1965; Jeffrey 1968; Dakshini & Singh 1970; Dimon 1971a, b; Kuprianova & Alyoshina 1972; Payne 1972; Wagenitz 1976; Dittrich 1977; Rowley & Dahl 1977; Tomsovic 1977; Bolick 1981; Parveen & Bhandari 1981; Nair & Lawrence 1985; Bremer 1987; Díez 1987; Tormo & Ubera 1988a, 1990b, 1995; Faegri & Iversen 1989; Blackmore 1990; Blackmore & Barnes 1990b; Qaid 1990; Javeid 1991; Ling 1993; Perveen & al. 1994; Fuhsiung & al. 1995; Lunau 1995; Reille 1995, 1998; Petit & al. 1996; Perveen 1999; Beug 2001; Chester

& Raine 2001; Gabarayeva & al. 2003; Meo & Khan 2003b; Meier-Melikyan & al. 2004; Garnatje & Martín 2007; Jafari & Ghanbarian 2007; Punt & Hoen, in press.

Galactites; Fischer 1890; Pla Dalmau 1961; Dimon 1971a, b; Dittrich 1977; Díez 1987; Qaid 1990; Tormo & Ubera 1990b, 1995; Reille 1995; La-Serna & al. 1999, 2002; La-Serna & Gómez Ferreras 2006; Blackmore & al. 2009 (Chapter 7).

Jurinea; Fischer 1890; Tarnavschi & Mitroiu 1959; Stix 1960; Ikuse 1962; Nair 1965; Dimon 1971a, b; Kuprianova & Alyoshina 1972; Schtepa 1973a, 1977; Dittrich 1977; Inceoglu & Karamustafa 1977; Nair & Lawrence 1985; Siljak-Yakovlev 1986; Qaid 1990; Tormo & Ubera 1990b, 1995; Javeid 1991; Ying & al. 1993; Fuhsiung & al. 1995; Petit & al. 1996, 2001; Reille 1998; Beug 2001; Chester & Raine 2001; Meier-Melikyan & al. 2004; Meo 2005; Garnatje & Martín 2007; Jafari & Ghanbarian 2007; Blackmore & al. 2009 (Chapter 7); Punt & Hoen, in press.

Notobasis; Fischer 1890; Schtepa 1962; Greuter 1973; Greuter & Dittrich 1973; Qaid 1990; Tormo & Ubera 1990b, 1995; Reille 1995; Blackmore & al. 2009 (Chapter 7), and in press.

Onopordum; Fischer 1890; Zander 1935; Tarnavschi & Mitriou 1959; Ikuse 1962; Dimon 1971a, b; Dimon-Cathary 1973; Dittrich 1977; Schtepa 1977; Al Sarraf 1979; Díez 1987; Valdés & al. 1987; Skvarla & al. 1988; Faegri & Iversen 1989; Qaid 1990; Tormo & Ubera 1990b, c, 1995; Javeid 1991; Reille 1995, 1998; Tellería 1995; Petit & al. 1996; Beug 2001; Andrada & Tellería 2002, 2005; Meier-Melikyan & al. 2004; Meo 2005; Punt & Hoen, in press.

Picnomon; Schtepa 1962, 1977; Díez 1987; Qaid 1990; Tormo & Ubera 1990b, 1995; Reille 1995; Chester & Raine 2001.

Ptilostemon; Greuter 1973; Greuter & Dittrich 1973; Schtepa 1977; Díez 1987; Qaid 1990; Tormo & Ubera 1990b, 1995; Reille 1995.

Serratula; Mohl 1835; Fischer 1890; Avebury 1912; Zander 1935; Wagenitz 1955; Ikuse 1956; Carlquist 1958; Tarnavschi & Mitroiu 1959; Stix 1960; Jeffrey 1968; Kuprianova & Alyoshina 1972; Visset 1974; Avetisian & Tonyan 1975; Tonyan & Mekhakyan 1975; Dittrich 1977; Cantó 1985, 1987, 1988; Nair & Lawrence 1985; Faegri & Iversen 1989; Qaid 1990; Tormo & Ubera 1990b, 1995; Javeid 1991; Moore & al. 1991; Pehlivan 1995b; Reille 1995, 1998; Petit & al. 1996, 2001; Martín & Garcia-Jacas 2000; Beug 2001; Garcia-Jacas & al. 2001; Meier-Melikyan & al. 2004; Meo 2005; Hidalgo & al. 2008; Punt & Hoen, in press.

Silybum; Fischer 1890; Zander 1935; Ikuse 1956; Pla Dalmau 1961; Schtepa 1962, 1977; Nair & Lawrence 1985; Jeffrey 1968; Dimon 1971a, b; Dimon-Cathary 1973; Dittrich 1977; Díez 1987; Qaid 1990; Tormo & Ubera 1990b, 1995; Javeid 1991; Meo 2005; Blackmore & al. 2009 (Chapter 7).

Synurus; Ikuse 1956; Dittrich 1977; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995.

Tyrimnus; Díez 1987; Qaid 1990; Tormo & Ubera 1990b, 1995; Blackmore & al. 2009 (Chapter 7).

Xeranthemum; Mohl 1835; Fischer 1890; Tarnavschi & Mitriou 1959; Ikuse 1962; Dimon 1971a, b; Dimon-Cathary 1973; Inceoglu & Karamustafa 1977; Tormo & al. 1986; Díez 1987; Valdés & al. 1987; Qaid 1990; Tormo & Ubera 1990b, 1995; Reille 1995, 1998; Petit & al. 1996; Beug 2001; Meier-Melikyan & al. 2004; Garnatje & Martín 2007; Punt & Hoen, in press.

Zoegea; Mohl 1835; Wagenitz 1955; Jeffrey 1968; Dittrich 1977; Martín & Garcia-Jacas 2000; Garcia-Jacas & al. 2001; Meo & Khan 2003b; Meier-Melikyan & al. 2004; Meo 2005; Jafari & Ghanbarian 2007; Blackmore & al. 2009 (Chapter 7).

Pertyoideae

PERTYEAE

Ainsliaea; Wodehouse 1929b; Ikuse 1956; Stix 1960; Kapil & Sethi 1962; Huang 1972; Marticorena & Parra 1975; Nair & Lawrence 1985; Hansen 1991a, b; Ling 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Pacini 1996; Zhao 1999; Tellería & al. 2003; Lin & al. 2005; Meo 2005; Tellería & Katinas 2005; Zhao & al. 2006; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Pertya; Wodehouse 1929a; Ikuse 1956; Ikuse 1962; Marticorena & Parra 1975; Hansen 1991a, b; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Zhao 1999; Lin & al. 2005; Zhao & al. 2006; Katinas & al, 2008a.

Gymnarrhenoideae

GYMNARRHENEAE

Gymnarrhena; Wittenbach 1970; Leins 1973; Dimon 1971a, b; Skvarla & al. 1977; Anderberg 1991; Reille 1995; Zhao 1999; Anderberg & al. 2005; Zhao & al. 2006; Panero & Funk 2007; Wortley & al. 2007; Blackmore & al. 2009 (Chapter 7).

Cichorioideae s.str.

GUNDELIEAE

Gundelia; Stix 1960; Wagenitz 1976; Robinson 1994d; Jafari & Ghanbarian 2007; Jeffrey 2007; Wortley & al. 2007; Katinas & al, 2008a; Blackmore & al. 2009 (Chapter 7).

Warionia; Dimon 1971a, b; Marticorena & Parra 1975; Dittrich 1977; Qaid 1990; Hansen 1991a, b; Jeffrey 1995; Reille 1995; Petit & al. 1996; Zhao 1999; Zhao & al. 2006; Wortley & al. 2007; Katinas & al, 2008a, c; Blackmore & al. 2009 (Chapter 7).

CICHORIEAE

Arnoseris; Pausinger-Frankenburg 1951; Erdtman & al. 1961; Askerova 1970a, 1987; Blackmore 1976, 1981, 1984a; Blackmore & Barnes 1984b; Laparra 1990.

Chondrilla; Fischer 1890; Pausinger-Frankenburg 1951; Tarnavschi & Mitroiu 1959; Ikuse 1962; Blackmore 1976, 2000; Inceoglu & Karamustafa 1977; Nair & Lawrence 1985; Askerova 1987; Díez 1987; Chanda & Pal 1990–1991; Reille 1998; Koscinska Pajak 2000; Pozhidaev 2000; Meier-Melikyan & al. 2004; Meo 2005; Blackmore & al. in press.

Cichorium; Mohl 1835; Fischer 1890; Wodehouse 1928c, 1929c, 1935; Zander 1935; Pausinger-Frankenburg 1951; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Pla Dalmau 1961; Nair 1965; Askerova 1970a, 1982, 1987; Blackmore 1976, 1981, 1982a–c, 1984a, b, 1986; Inceoglu & Karamustafa 1977; Lee 1978; Muller 1980; Longly 1981, 1984; Haque & Godward 1983; Blackmore & Barnes 1984b, 1990b; Blackmore & Claugher 1984; Evrard & al. 1984; Nair & Lawrence 1985; Barnes & Blackmore 1986a; McDonald 1986; Díez 1987; Gibbs & Ferguson 1987; Gandi & Thomas 1989; Pacini & Keijzer 1989; Stainier & al. 1989; Chanda & Pal 1990–1991; Laparra 1990; Moore & al. 1991; Punt & al. 1994; Jeffrey 1995; Lunau 1995; Reille 1995, 1998; Tellería 1995; Pacini 1996; Varotto & al. 1996; Kapp & al. 2000; Kiers 2000; Chester & Raine 2001; Erbar & Enghofer 2001; Meier-Melikyan & al. 2001a, 2003, 2004; Andrada & Tellería 2002; Meo & Khan 2004a; Meo 2005; Osman 2006b; Jafari & Ghanbarian 2007.

Hyoseris; Askerova 1970a, 1987; Tomb 1975; Blackmore 1976, 1981, 2000; Reille 1995; Osman 2006b.

Lapsana; Mohl 1835; Fischer 1890; Zander 1935; Pausinger-Frankenburg 1951; Ikuse 1956; Tarnavschi & Mitriou 1959;

Erdtman & al. 1961; Blackmore 1976, 1984a; Askerova 1987; Inceoglu & Karamustafa 1977; Nair & Lawrence 1985; Díez 1987; Chanda & Pal 1990–1991; Nagamitsu & Nagamasu 1994; Chester & Raine 2001; Meier-Melikyan & al. 2004; Meo 2005.

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Microseris; Cranwell 1942; Heusser 1971; Feuer 1974a, b; Blackmore 1976; Feuer & Tomb 1977; Askerova 1987; Anon., 1988; Jansen & al. 1991; Moar 1993.

Picris; Cranwell 1942; Pausinger-Frankenburg 1951; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Huang 1972; Blackmore 1976, 1984a; Lack & Leuenberger 1979; El Ghazaly 1980; Nair & Lawrence 1985; Askerova 1987; Díez 1987; Moore & al. 1991; Moar 1993; Nagamitsu & Nagamasu 1994; Reille 1995, 1998; Tellería 1995; Chester & Raine 2001; Meier-Melikyan & al. 2004; Meo 2005; Osman 2006b; Jafari & Ghanbarian 2007; Lack, s.d.

Rhagadiolus; Fischer 1890; Tomb 1975; Blackmore 1976; El Ghazaly 1980; Askerova 1987; Díez 1987; Chanda & Pal 1990–1991; Osman 2006b; Lack, s.d.

Scolymus; Mohl 1835; Fischer 1890; Wodehouse 1928c, 1929c, 1935; Pausinger-Frankenburg 1951; Tarnavschi & Mitroiu 1959; Ueno 1972; Askerova 1982, 1987; Tomb 1975; Blackmore 1976, 1981, 1982a, 1984c, 1986, 1992, 2000; Inceoglu & Karamustafa 1977; El Ghazaly 1980; Bremer 1987; Díez 1987; Blackmore & Barnes 1990a, b; Jeffrey 1995; Reille 1995; Chester & Raine 2001; Osman 2006b; Blackmore & al. 2009 (Chapter 7).

Scorzonera; Mohl 1835; Fischer 1890; Wodehouse 1935; Zander 1935; Pausinger-Frankenburg 1951; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Ikuse 1962; Askerova 1969, 1970b, 1971, 1982, 1987; Gustafsson & Snogerup 1972; Ueno 1972; Tomb 1975; Blackmore 1976, 1982a–c, 1984a, b, 1986, 2000; Inceoglu & Karamustafa 1977; Díaz & Blanca 1983; Blackmore & Barnes 1984a, 1990a, b; Blackmore & Claugher 1984, 1987; Blanca & Díaz de la Guardia 1985; Díaz de la Guardia & Blanca 1985, 1986, 1988a; Nair & Lawrence 1985; Barnes & Blackmore 1986b; Moinet 1986; Díez 1987; Blackmore & Crane 1988; Chanda & Pal 1990–1991; Laparra 1990; Stuessy 1990; Fuhsiung & al. 1995; Jeffrey 1995; Reille 1995, 1998; Chester & Raine 2001; Duran 2002; Gabarayeva & al. 2003; Meo & Khan 2004a, c; Meier-Melikyan & al. 2004; Meo 2005; Blackmore & al. 2007, 2009 (Chapter 7), and in press; Osman 2006b; Jafari & Ghanbarian 2007; Qureshi & al. 2008b.

Sonchus; Mohl 1835; Smith 1877; Fischer 1890; Wodehouse 1935; Zander 1935; Batalla 1940; Cranwell 1942; Pausinger-Frankenburg 1951; Erdtman 1952; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Saad 1961; Chaubal & Deodikar 1965; Nair 1965; Skvarla & Turner 1966b; Boulos 1972a–c, 1973a, b, 1974; Huang 1972; Pons & Boulos 1972; Ueno 1972; Askerova 1987; Aldridge 1976; Blackmore 1976, 1984a, 1986, 2000; De Paz 1976; Kozar & Aaron 1976; Lander 1976; Perez de Pax 1976; Parveen & Bhandari 1981; Bir & Sidhu 1982; Nair & Lawrence 1985; McDonald 1986; Díez 1987; Blackmore & Crane 1988; Gandi & Thomas 1989; Chanda & Pal 1990–1991; Laparra 1990; Mejias 1990; Moore & al. 1991; Mejias & Díez 1993; Moar 1993; Perveen & al. 1994; Punt & al. 1994; Fuhsiung & al. 1995; Jones & al. 1995; Reille 1995; Tellería 1995; Pacini 1996; Chen & Wang 1999; Díez & al. 1999; La-Serna & al. 1999; Perveen 1999; Torres 2000; Chester & Raine 2001; Andrada & Tellería 2002; Qureshi & al. 2002b, 2008a, b; Meier-Melikyan & al. 2004; Willard & al. 2004; Meo 2005; Kandemir & al. 2006; La-Serna & Gómez Ferreras 2006; Osman 2006b; Modro & al. 2007; Blackmore & al. 2009 (Chapter 7); Lack, s.d.

Tragopogon; Mohl 1835; Edgeworth 1877; Fischer 1890; Wodehouse 1935; Zander 1935; Pausinger-Frankenburg 1951; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Pla Dalmau 1961; Askerova 1970b, 1971, 1982, 1987; Knox & Heslop-Harrison 1970; Ueno 1972; Tomb 1975; Blackmore 1976, 1982a–c, 1984a, b, 1986, 1992, 2000; Inceoglu & Karamustafa 1977; Blackmore & Dickinson 1981; Díaz & Blanca 1983; Nair & Lawrence 1985; McDonald 1986; Blackmore & Barnes 1987b, 1990a, b; Blackmore & Claugher 1987; Díez 1987; Díaz de la Guardia & Blanca 1988b, c, 2004; Gandi & Thomas 1989; Chanda & Pal 1990–1991; Laparra 1990; Moore & al. 1991; Punt & al. 1994; Reille 1995, 1998; Pacini 1996; Chester & Raine 2001; Qureshi & al. 2002c, 2008c; Meier-Melikyan & al. 2004; Meo 2005; Osman 2006b; Blackmore & al. 2007, 2009 (Chapter 7).

Urospermum; Fischer 1890; Erdtman & al. 1961; Pla Dalmau 1961; Dimon 1971a; Visset 1974; Blackmore 1976; Inceoglu & Karamustafa 1977; Lack & Leuenberger 1979; El Ghazaly 1980; Chiguryaeva & Tereshkova 1983; Askerova 1987; Díez 1987; Reille 1998; Osman 2006b; Lack, s.d.

Youngia; Ikuse 1956; Huang 1972; Kaul 1973; Blackmore 1976; Askerova 1987; Gandi & Thomas 1989; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Meier-Melikyan & al. 2004; Willard & al. 2004; Meo 2005.

ARCTOTIDEAE

Arctotheca; Edgeworth 1877; Skvarla & al. 1977; Ahlstrand 1979; Díez 1987; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Arctotis; Mohl 1834, 1835; Wodehouse 1935; Erdtman 1952, 1964; Ikuse 1956; Stix 1960; Skvarla & Turner 1966b; Besold 1971; Norlindh 1977a; Skvarla & al. 1977, 1988; Ahlstrand 1979; Nair & Lawrence 1985; Hansen 1991b; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Berkheya; Wodehouse 1935; Stix 1960; Erdtman 1963, 1969; Leins 1970; Leins & Thyret 1971; Ueno 1972; Chaubal 1976; Norlindh 1977a; Skvarla & al. 1977; Blackmore 1986; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Cymbonotus; Skvarla & al. 1977; Ahlstrand 1979; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Didelta; Stix 1960; Skvarla & Turner 1966b; Leins & Thyret 1971; Norlindh 1977a; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Eremothamnus; Leins 1970; Robinson 1973b, 1992e; Robinson & Brettell 1973d; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Gazania; Stix 1960; Pla Dalmau 1961; Dimon 1971a; Leins & Thyret 1971; Ueno 1972, 1978; Norlindh 1977a; Blackmore 1986; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Gorteria; Erdtman 1952, 1964, 1969; Stix 1960; Leins & Thyret 1971; Chaubal 1976; Norlindh 1977a; Blackmore 1986; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Haplocarpha; Stix 1960; Besold 1971; Ahlstrand 1979; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

Hirpicium; Stix 1960; Skvarla & Turner 1966b; Leins & Thyret 1971; Norlindh 1977a; Blackmore 1986; Wortley & al. 2008; Blackmore & al. 2009 (Chapter 7).

LIABEAE

Chrysactinium; Robinson 1978a, 1983a; Robinson & Marticorena 1986; Moran & Funk 2006; Funk & Dillon 2007; Funk & al. 2007.

Erato; Robinson 1978a, 1983a; Robinson & Marticorena 1986; Moran & Funk 2006; Funk & Dillon 2007.

Liabum; Stix 1960; Skvarla & Turner 1966b; Marticorena & Parra 1974; Robinson & Brettell 1974; Robinson 1976c, e, 1977d, 1978a, 1980n, 1983a, d; Bolick 1983; Robinson & Marticorena 1986; Liu 2000; Funk & Dillon 2007; Blackmore & al. 2009 (Chapter 7).

Munnozia; Robinson 1976d, e, 1977b, d, 1978a, f, 1983a, 1984g, 1987e, 1994c, d, 1999a; Robinson & Marticorena 1986; Moran & Funk 2006; Funk & Dillon 2007; Funk & al. 2007.

Oligactis; Robinson 1977b, 1978a, 1980n, 1983a; Robinson & Marticorena 1986; Funk & Dillon 2007.

Paranephelius; Robinson & Brettell 1974; Robinson 1977c, 1978a, 1983a, 1999a; Robinson & Marticorena 1986; Funk & al. 1996; Funk & Dillon 2007; Blackmore & al. 2009 (Chapter 7).

Philoglossa; Robinson 1976b, 1978a, 1983a; Robinson & Marticorena 1986; Funk & al. 1996; Moran & Funk 2006; Funk & Dillon 2007.

Sinclairia; Skvarla & Turner 1966a, b; Robinson & Brettell 1974; Nordenstam 1977; Robinson 1983a; Robinson & Marticorena 1986; Liu 2000; Funk & Dillon 2007.

VERNONIEAE

Albertinia; King & Robinson 1970e; Robinson & al. 1980; Mendonça & al. 2005d; Pecanha & al. 2005; Robinson 2007; Blackmore & al. 2009 (Chapter 7).

Baccharoides; Smith 1969; Robinson & al. 1980; Robinson 1988b, 1990a, b, 1999b, 2007; Isawumi 1995a; Isawumi & al. 1996; Blackmore & al. 2009 (Chapter 7).

Bolanosa; Bolick 1978a, 1981, 1983; Robinson 1999a, 2007.

Bothriocline; Kingham 1976; Bolick 1978a; Jeffrey 1987; Robinson 1999b, 2007.

Cabobanthus; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Centauropsis; Kingham 1976; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Centrapalus; Guinet & Maley 1974; Jones 1981; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Chresta; Robinson 1980g, 1983b, 1992d, 1996, 1999a, 2007; Robinson & al. 1980; MacLeish 1984, 1985.

Chrysolaena; Robinson 1988e, 1990b, 1992g, 2007; Mendonça & al. 2005e; Dematteis 2007.

Critoniopsis; Robinson 1980f, 1993a, 1999a, 2007.

Cyanthillium; Robinson & al. 1980; Robinson & Kahn 1986; Robinson 1990a, b, 1992f, 1999a, b, 2007.

Distephanus; Robinson & Kahn 1986; Robinson 1996, 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Elephantopus; Cabrera 1944; Stix 1960; Chaubal & Deodikar 1965; Huang 1972; Bolick 1978a, 1981; Nair & Lawrence 1985; Vasanthy 1985; Robinson & Kahn 1986; Jeffrey 1987; Gandi & Thomas 1989; Roubik & Moreno 1991; Robinson 1992f, 1996, 1999a, 2007; Ling 1993; Fuhsiung & al. 1995; Pozhidaev 2000; Skvarla & al. 2005; Modro & al. 2007; Bunwong & Chantaranothai 2008; Blackmore & al. 2009 (Chapter 7), and in press.

Ethulia; Mohl 1835; King & Robinson 1970e; Dimon 1971a; Kingham 1976; Bolick 1978a, 1978a, b, 1980; Nair & Lawrence 1985; Bremer 1987; Jeffrey 1987; Jansen & Ki-Joong 1996; Robinson 1999b, 2007.

Gutenbergia; Stix 1960; Kingham 1976; Bolick 1978a; Jeffrey 1987; Robinson 1999b, 2007.

Gymnanthemum; Robinson & al. 1980; Robinson & Kahn 1986; Robinson 1999b, 2007; Robinson & Skvarla 2006; Blackmore & al. 2009 (Chapter 7).

Hilliardiella; Jones 1981; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Hololepis; Robinson & al. 1980; Robinson 2007.

Lepidaploa; Wodehouse 1928c; Keeley & Jones 1977; Robinson 1987b–d, 1988d, 1990b, 1992c, f, g, 1996, 1999a, 2007; Mendonça & Esteves 2000a; Mendonça & al. 2005d, 2007.

Lepidonia; Robinson & Funk 1987; Robinson 2007.

Lessingianthus; Robinson 1988d, 1990b, 1996, 1999a, 2007; Mendonça & al. 2005c; Dematteis 2006; Borges & Dematteis 2008; Blackmore & al. 2009 (Chapter 7).

Linzia; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Muschleria; Kingham 1976; Bolick 1978a; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Orbivestus; Jones 1981; Robinson 1999b, 2007.

Polydora; Guinet & Maley 1974; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Sipolisia; Robinson 1996, 1999a, 2007.

Stokesia; Fischer 1890; Wodehouse 1928c, 1934; Ikuse 1956; Ueno 1972; Bolick 1978a, 1981; Robinson & al. 1980; Blackmore 1986; Robinson & Kahn 1986; Gandi & Thomas 1989; Robinson 1996, 1999a, c, 2007.

Stramentopappus; Robinson & Funk 1987; Robinson 2007.

Vernonanthura; Smith 1969; Robinson 1992a, 1994b, 1996, 2007; Mendonça & al. 2005b.

Vernonia; Mohl 1835; Fischer 1890; Avebury 1912; Wodehouse 1928c, 1935; Cabrera 1944; Ikuse 1956; Stix 1960; Chaubal & Deodikar 1965; Nair 1965; Skvarla & Turner 1966b; Arachi 1968; Moreira 1969; Smith 1969, 1971; Dakshini & Dadlani 1970, 1978; Jones 1970, 1973, 1979, 1981; King & Robinson 1970e; Dimon 1971a; Huang 1972; Ueno 1972; Dimon-Cathary 1973; Robinson & Reed 1973; Sowunmi 1973; Kingham 1976; Robinson 1976a, 1979c, d, 1980b, c, e, 1981a, d, 1983e, 1988a, d, e, 1990a, b, 1992d, 1994b, 1996, 1999b, 2007, 2008; Vasanthy 1976, 1978, 1985; Keeley & Jones 1977, 1979; Tomb & Zeleznak 1977; Turner & Powell 1977; Bolick 1978a, 1981; Bonnefille & Riollet 1980; Robinson & al. 1980; Esteves 1981, 1983–1985; Parveen & Bhandari 1981; Stutts 1981; Bir & Sidhu 1982; Lane 1985; Nair & Lawrence 1985; Robinson & Kahn 1985b; Blackmore 1986; Pocock & Vasanthy 1986; Robinson & Marticorena 1986; Jeffrey 1987, 1988; Robinson & Funk 1987; Skvarla & al. 1988, 2005; Anderberg 1989; Gandi & Thomas 1989; Keeley & Turner 1990; Roubik & Moreno 1991; Ling 1993; Saxena 1993; Vasanthy & al. 1993; Bolick & Keeley 1994; Perveen & al. 1994; Tissot & al. 1994; Fuhsiung & al. 1995; Isawumi 1995b, 1996; Book 1996; Isawumi & al. 1996; Torres 1998, 2000; Perveen 1999; Hind 2000; Kapp & al. 2000; Mendonça & Esteves 2000a; Dematteis & Salgado 2001; Pecanha & al. 2001; Takeda & al. 2001; Dematteis 2003; Cancelli & al. 2005b, 2006, 2007; Esteves & al. 2005; Mendonça & al. 2005a; Hind & al. 2006; Robinson & Skvarla 2006; Modro & al. 2007; Sodré Gda & al. 2007; Bunwong & Chantaranothai 2008; Blackmore & al. 2009 (Chapter 7), and in press.

Vernoniastrum; Robinson 1999b, 2007; Blackmore & al. 2009 (Chapter 7).

Corymbioideae

CORYMBIEAE

Corymbium; Mohl 1835; Bolick 1978a, b, 1980; Bremer 1987; Jansen & Ki-Joong 1996; Robinson 1996; Funk 2007; Wortley & al. 2007; Blackmore & al. 2009 (Chapter 7).

Asteroideae

SENECIONEAE

Blennosperma; Skvarla & Turner 1966a, 1966b; Turner & Powell 1977; Stuessy 1979; Lane 1985; Karis 1993.

Cineraria; Mohl 1835; Cheshire 1880; Fischer 1890; Tarnavschi & Mitroiu 1959; Vincent & Getliffe-Norris 1989; Saxena 1993.

Euryops; Skvarla & Turner 1966b; Nordenstam 1968.

Gynoxys; Skvarla & Turner 1966b; Skvarla & al. 1977; Salgado -Labouriau 1982b, 1983; Robinson & Cuatrecasas 1984; Bain & al. 1997.

Gynura; Ikuse 1956; Skvarla & Turner 1966b; Huang 1972; Turner & Powell 1977; Davies 1981; Vincent & Getliffe Norris 1989; Fuhsiung & al. 1995.

Kleinia; Mohl 1835; Bonnefille & Riollet 1980; Robinson 1981b; Vincent & Getliffe Norris 1989; Reille 1998; La-Serna & al. 1999, 2002; La-Serna & Gómez Ferreras 2006.

Ligularia; Fischer 1890; Tarnavschi & Mitroiu 1959; Stix 1960; Huang 1972; Belkina 1975; Jintan & al. 1990; Ling 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Reille 1998; Liu 2000; Liu 2000; Beug 2001; Meier-Melikyan & al. 2004; Meo 2005; Punt & Hoen, in press.

Othonna; Tarnavschi & Mitroiu 1959.

Packera; Bain & Walker 1995; Bain & al. 1997; Bain & Golden 2000; Liu 2000; Nordenstam 2007.

Pericallis; Bain & Golden 2000; Liu 2000.

Petasites; Fischer 1890; Zander 1935; Ikuse 1956; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Toman & Stary 1965; Skvarla & Turner 1966b; Huang 1972; Kuprianova & Alyoshina 1972; Belkina 1975; Skvarla & al. 1977; Faegri & Iversen 1989; Nagamitsu & Nagamasu 1994; Reille 1995, 1998; Liu 2000; Beug 2001; Chester & Raine 2001; Meier-Melikyan & al. 2004; Punt & Hoen, in press.

Psacalium; Robinson 1978i; Bain & al. 1997.

Roldana; Bain & al. 1997.

Senecio; Mohl 1835; Fischer 1890; Zander 1935; Batalla 1940; Cranwell 1942; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Pla Dalmau 1961; Nair 1965; Hernandez 1966; Skvarla & Turner 1966a, 1966b; Martin & Drew 1969, 1970; Dimon 1971a, b; Heusser 1971; Huang 1972; Robinson & Brettell 1973a; Visset 1974; Belkina 1975; Vasanthy 1976, 1978; Inceoglu & Karamustafa 1977; Skvarla & al. 1977; Turner & Powell 1977; Markgraf & D'Antoni 1978; Bolick 1980; Robinson 1980o; Pacini & al. 1981; Payne 1981; Wingenroth & Heusser 1983; Tormo & al. 1985, 1986; Díez 1987; Valdés & al. 1987; Faegri & Iversen 1989; Gandi & Thomas 1989; Vincent & Getliffe Norris 1989; Blanca & al. 1991; Bolick & Vogel 1992; Lietava 1992; Otieno & Mesfin Tadesse 1992; Moar 1993; Saxena 1993; Nagamitsu & Nagamasu 1994; Abott & al. 1995; Bain & Walker 1995; Fuhsiung & al. 1995; Hodálová & Mártonfi 1995; Reille 1995, 1998; Barkley & al. 1996; Knox 1996; Lane 1996; Pacini 1996; Vincent 1996; Bain & al. 1997; Janovec & Robinson 1997; Colinvaux & al. 1999; Kapp & al. 2000; Liu 2000; Torres 2000; Beug 2001; Chester & Raine 2001; Fagundez 2001; Andrada & Tellería 2002; Hiscock & al. 2002, 2003; Pelser & al. 2002; Tellería & Forcone 2002; Coleman & al. 2003; Valencia-Barrera & al. 2003; Wei & al. 2003; Cancelli & al. 2005b, 2006, 2007; Meier-Melikyan & al. 2004; McInnes & al. 2005; Meo 2005; Luengo & al. 2007; Modro & al. 2007; Punt & Hoen, in press.

Tussilago; Mohl 1835; Fischer 1890; Zander 1935; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Visset 1974; Inceoglu & Karamustafa 1977; Faegri & Iversen 1989; Jintan & al. 1990; Ling 1993; Fuhsiung & al. 1995; Liu 2000; Beug 2001; Chester & Raine 2001; Kesseler & Harley 2004; Meier-Melikyan & al. 2004; Blackmore & al., in press; Punt & Hoen, in press.

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Calendula; Mohl 1835; Fischer 1890; Zander 1935; Ikuse 1956; Tarnavschi & Mitroiu 1959; Stix 1960; Pla Dalmau 1961; Erdtman 1964, 1969; Ibrahim 1965; Dakshini & Singh 1970; Dimon 1971a, b; Dimon-Cathary 1973; Visset 1974; Norlindh 1977b; Praglowski & Grafstrom 1980; Bolick & al. 1984; Ahlstrand 1985; Tormo & al. 1986; Díez 1987; Valdés & al. 1987; Faegri & Iversen 1989; Pacini & Keijzer 1989; Bolick & Vogel 1992; Ling 1993; Lunau 1995; Reille 1995; Linskens & Jorde 1997; Chester & Raine 2001; Meier-Melikyan & al. 2003, 2004; Wei & al. 2003; Noor & al. 2004; Meo 2005; Polevova 2006; Chengqi 2007; El-Garf & Osman 2007; Jafari & Ghanbarian 2007; Blackmore & al. 2009 (Chapter 7); Punt & Hoen, in press.

Chrysanthemoides; Heusser 1971; Skvarla & al. 1977; Praglowski & Grafstrom 1980; Bolick & al. 1984; Ahlstrand 1985.

Dimorphotheca; Fischer 1890; Ikuse 1956; Stix 1960; Skvarla & al. 1977, 1988; Praglowski & Grafstrom 1980; Bolick & al. 1984; Ahlstrand 1985; Meier-Melikyan & al. 2003, 2004; Blackmore & al., in press.

Osteospermum; Stix 1960; Heusser 1971; Skvarla & al. 1977; Praglowski & Grafstrom 1980; Bolick & al. 1984; Ahlstrand 1985; Meier-Melikyan & al. 2004; El-Garf & Osman 2007.

GNAPHALIEAE

Ammobium; Fischer 1890; Ikuse 1956; Davis 1962b; Leins 1968a; Leins 1971.

Anaphalis; Kirpichnikov & Kuprianova 1950; Ikuse 1956; Nair 1965; Skvarla & Turner 1966b; Drury 1970; Grierson 1972; Huang 1972; Vasanthy 1976; Pullaiah 1979; Anderberg 1991; Ling 1993; Moar 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Breitwieser & Sampson 1997a, b; Varma & Vijayavalli 1998; Breitwieser & Ward 2003; Meier-Melikyan & al. 2004; Meo & Khan 2004b; Meo 2005; Punt & Hoen, in press.

Anaxeton; Anderberg 1989, 1991.

Antennaria; Gattinger 1939; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Wittenbach 1970; Kuprianova & Alyoshina 1972; Belkina 1975; Faegri & Iversen 1989; Gandi & Thomas 1989; Chiemeleski & Chiiappa 1990; Anderberg 1991; Reille 1995, 1998; Beug 2001; Chester & Raine 2001; Meier-Melikyan & al. 2004; Punt & Hoen, in press.

Apalochlamys; Anderberg 1991.

Arrowsmithia; Anderberg 1991.

Athrixia; Wittenbach 1970; Besold 1971; Anderberg 1989, 1991.

Cassinia; Cranwell 1942; Besold 1971; Anderberg 1989, 1991; Moar 1993; Breitwieser & Sampson 1997a, b.

Craspedia; Cranwell 1942; Skvarla & Turner 1966b; Besold 1971; Anderberg 1991; Moar 1993.

Edmondia; Anderberg 1991.

Gamochaeta; Díez 1987; Anderberg 1991.

Helichrysum; Mohl 1835; Fischer 1890; Avebury 1912; Gattinger 1939; Cranwell 1942; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Erdtman & al. 1961; Pla Dalmau 1961; Wittenbach 1970; Dimon 1971a, b; Visset 1974; Inceoglu & Karamustafa 1977; Skvarla & al. 1977; Bonnefille & Riollet 1980; Díez 1987; Valdés & al. 1987; Villari 1987a, b; Anderberg 1989, 1991; Moar 1993; Reille 1995; Mesfin Tadesse & Reilly 1995; Breitwieser & Sampson 1997a, b; Varma & Vijayavalli 1998; Pinar & Oybak Donmez 2000; Chester & Raine 2001; Breitwieser & Ward 2003; Merti 2003; Meier-Melikyan & al. 2004; Blackmore & al. 2009 (Chapter 7); Punt & Hoen, in press.

Hyalosperma; Anderberg 1991.

Jalcophila; Anderberg 1991.
Langebergia; Anderberg 1991.
Leucophyta; Anderberg 1991.
Millotia; Wittenbach 1970; Anderberg 1991.
Myriocephalus; Wittenbach 1970; Anderberg 1991.
Oedera; Anderberg & Källersjö 1988; Anderberg 1991; Koekemoer 2002.
Ozothamnus; Anderberg 1991; Breitwieser & Sampson 1997a, b; Breitwieser & Ward 2003.
Petalacte; Wittenbach 1970; Anderberg 1991.
Phaenocoma; Anderberg 1989, 1991; Koekemoer 2002.
Plecostachys; Anderberg 1991.
Podolepis; Henderson 1969; Besold 1971; Anderberg 1991.
Pseudognaphalium; Kirpichnikov & Kuprianova 1950; Anderberg 1991; Moar 1993; Breitwieser & Sampson 1997a, b; Breitwieser & Ward 2003.
Pterygopappus; Anderberg 1991; Breitwieser & Ward 2003.
Rosenia; Anderberg 1991; Koekemoer 2002.
Stoebe; Wittenbach 1970; Besold 1971; Skvarla & al. 1977; Anderberg 1991; Koekemoer 2002; Blackmore & al. 2009 (Chapter 7).
Tenrhynea; Anderberg 1991.
Vellereophyton; Anderberg 1991; Blackmore & al. 2009 (Chapter 7).

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Amellus; Mohl 1835; Fischer 1890; Rommel 1977; Blackmore & al. 2009 (Chapter 7).
Brachyscome; Davis 1964; Nair & Lawrence 1985; Moar 1993.
Conyza; Mohl 1835; Stix 1960; Pla Dalmau 1961; Ikuse 1962; Nair 1965; Dakshini & Singh 1970; Huang 1972; Ogden & al. 1974; Pullaiah 1978; Bir & Sidhu 1982; Salgado-Labouriau 1982b, 1983; Nair & Lawrence 1985; Tormo & al. 1986; Díez 1987; Gandi & Thomas 1989; Robinson 1990a; Roubik & Moreno 1991; Perveen & al. 1994; Lunau 1995; Reille 1995; Perveen 1999; Chester & Raine 2001; Merti 2003; Cancelli & al. 2005b; Meo 2005; El-Garf & Osman 2007.
Diplostephium; Zander 1935; Salgado-Labouriau 1982a, b, 1983; Bolick & al. 1984; Blackmore & al. 2009 (Chapter 7).
Erigeron; Mohl 1835; Smith 1877; Fischer 1890; Wodehouse 1930, 1945; Zander 1935; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Solbrig 1960; Erdtman & al. 1961; Chaubal & Deodikar 1965; Nair 1965; Skvarla & Turner 1966b; Dakshini & Singh 1970; Wittenbach 1970; Huang 1972; Kuprianova & Alyoshina 1972; Markgraf & D'Antoni 1978; Salgado-Labouriau 1982b, 1983; Wingenroth & Heusser 1983; Nair & Lawrence 1985; Dobson 1988; Faegri & Iversen 1989; Gandi & Thomas 1989; Ling 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Reille 1995, 1998; Chester & Raine 2001; Meier-Melikyan & al. 2004; Meo 2005; Punt & Hoen, in press.
Grangea; Mitra 1947; Stix 1960; Dakshini & Singh 1970; Nair & Lawrence 1985; Meo 2005; El-Garf & Osman 2007.
Grindelia; Fischer 1890; Markgraf & D'Antoni 1978; Clark & al. 1980; Dobson 1988; Gandi & Thomas 1989; Torres 2000; Meier-Melikyan & al. 2004; Andrada & Tellería 2005.
Lagenifera; Cranwell 1942; Huang 1972; Salgado-Labouriau 1982b, 1983; Moar 1993.
Olearia; Cranwell 1942; Moar 1993.
Oritrophium; Salgado-Labouriau 1982a, 1983.
Solidago; Fischer 1890; Avebury 1912; Zander 1935; Wodehouse 1945; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Maurizio & Louveaux 1963; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Huang 1972; Kuprianova & Alyoshina 1972; Visset 1974; Saenz de Rivas 1976; Nilsson & al. 1977; Bassett & al. 1978; Markgraf & D'Antoni 1978; Pullaiah 1978; Melhem & al. 1979; Nair & Lawrence 1985; Gibbs & Ferguson 1987; Faegri & Iversen 1989; Gandi & Thomas 1989; Jintan & al. 1990; Rowley & El Ghazaly 1992; Ling 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Lunau 1995; Jones & al. 1995; Reille 1995, 1998; Kapp & al. 2000; Torres 2000; Beug 2001; Chester & Raine 2001; Fagundez 2001; Milne & al. 2005; Ogden & al. 1974; Pla Dalmau 1961; Meier-Melikyan & al. 2004; Willard & al. 2004; Meo 2005; Cancelli & al. 2006a; Palazzesi & al. 2007; Punt & Hoen, in press.
Vittadinia; Fischer 1890; Cranwell 1942; Moar 1993.

ANTHEMIDEAE

Achillea; Mohl 1835; Edgeworth 1877; Fischer 1890; Zander 1935; Ikuse 1956, 1962; El Hadidy 1958; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Pla Dalmau 1961; Nair 1965; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Oswiecimska & Gawlowska 1967; Dabrowska 1971; Dimon 1971a; Visset 1974; Hamalova 1976; Inceoglu & Karamustafa 1977; Nilsson & al. 1977; Chiguryaeva & Tereshkova 1983; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Faegri & Iversen 1989; Gandi & Thomas 1989; Harley & Ferguson 1990; Bolick & Vogel 1992; Lietava 1992; Pardo 1992; Ling 1993; Anon., 1994; Vezey & al. 1994; Fuhsiung & al. 1995; Lunau 1995; Reille 1995, 1998; Chester & Raine 2001; Yurukova Grancharova & al. 2002; Meier-Melikyan & al. 2004; Meo & Khan 2003c; Kesseler & Harley 2004; Meo 2005; Jafari & Ghanbarian 2007; Ramsey 2007; Punt & Hoen, in press.
Ajania; Jintan & al. 1990; Chen & Zhang 1991; Vezey & al. 1994; Reille 1998; Martin & al. 2001; Meier-Melikyan & al. 2004; Sanz & al. 2008.
Anacyclus; Fischer 1890; Pla Dalmau 1961; Dimon 1971a, b; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Federonchuk & Savitiskii 1988; Vezey & al. 1994; Reille 1995.
Anthemis; Fischer 1890; Wodehouse 1928a; Zander 1935; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Mitsuoka 1968; Dimon 1971a, b; Skvarla & Turner 1971; Visset 1974; Heywood & Humphries 1977; Inceoglu & Karamustafa 1977; Skvarla & al. 1977; Markgraf & D'Antoni 1978; Melhem & al. 1979; Chiguryaeva & Tereshkova 1983; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Benidi Gonzalez 1988; Federonchuk & Savitiskii 1988; Faegri & Iversen 1989; Gandi & Thomas 1989; Moore & al. 1991; Vezey & al. 1994; Reille 1995, 1998; Mori Secci & al. 1997; Nasreen & Khan 1998; Beug 2001; Qureshi & al. 2002g; Meier-Melikyan & al. 2004; Meo 2005; Sa-Otero & al. 2006; Jafari & Ghanbarian 2007; Punt & Hoen, in press.
Arctanthemum; Martin & al. 2003.
Aaronsohnia; Skvarla & Turner 1966a, 1966b.
Artemisia; Mohl 1835; Fischer 1890; Avebury 1912; Wodehouse 1926, 1928c, 1930, 1935, 1945; Zander 1935; Monoszon 1948, 1950a, b; Smolina 1950; von Lüdi 1950; Gorodkow 1952; Straka 1952; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Erdtman 1964; Nair 1965; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Southworth 1966, 1973, 1983a, 1990b; Erdtman 1969; Martin & Drew 1969, 1970; Singh & Joshi 1969; Dakshini & Singh 1970; Dimon 1971a, b; Heusser 1971; Nilsson 1971; Praglowski 1971; Southworth & Branton 1971; Huang 1972; Kuprianova & Alyoshina 1972; Dahl & Rowley 1974; Persson 1974; Ogden & al. 1974; Kozar & Aaron 1976; Rowley 1976, 1978, 1981; Saenz de Rivas 1976; Heywood & Humphries 1977; Inceoglu & Karamustafa 1977;

Nilsson & al. 1977; Rowley & Dahl 1977; Skvarla & al. 1977; Tomb 1977; Bassett & al. 1978; Bolick 1978b, 1987, 1990; Markgraf & D'Antoni 1978; Hesse 1979; Melhem & al. 1979; Muller 1980; Rowley & al. 1980, 1981a, b, 1999; Buchen & Sievers 1981; Nilsson & Palmberg-Gotthard 1982; Yeou-Ruenn 1985, 1995; Tormo & al. 1986; Vallès 1986; Blackmore & Claugher 1987; Díez 1987; Lecuona Neumann & al. 1987; Tormo & Ubera 1987; Valdés & al. 1987; Vallès & Seoane 1987; Vallès & al. 1987; Faegri & Iversen 1989; Gandi & Thomas 1989; Lodari & al. 1989; Jintan & al. 1990; Lahoz & al. 1990; Qaid 1990; Vallès & Oliva 1990; Blanca & al. 1991; Ling 1993; Saxena 1993; Caramiello & Fossa 1994; Nagamitsu & Nagamasu 1994; Punt & al. 1994; Vezey & al. 1994; Caramiello & al. 1995; Fuhsiung & al. 1995; Jeffrey 1995; Ouyahya 1995; Reille 1995, 1998; Graham 1996; Munuera & al. 1996; Pacini 1996; Gupta & Nautiyal 1997; Pinar & Adiguzel 1998; Torrell & al. 1999; Kapp & al. 2000; Mumtaz & al. 2000; Tellería 2000; Beug 2001; Chester & Raine 2001; Martin & al. 2001, 2003; Andrada & Tellería 2002; Watson & al. 2002; Yurukova Grancharova & al. 2002; Meier-Melikyan & al. 2004; Meo & Khan 2004b; Wang 2004; Meo 2005; La-Serna & Gómez Ferreras 2006; Arilla & al. 2007; D'Amato & al. 2007; Liu & al. 2008; Sanz & al. 2008; Blackmore & al. in press; Punt & Hoen, in press.

Athanasia; Vezey & al. 1994.

Chamaemelum; Dimon 1971a, b; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Lewis 1992; Vezey & al. 1994; Reille 1995, 1998.

Chrysanthemum; Mohl 1835; Fischer 1890; Avebury 1912; Zander 1935; Wodehouse 1945; Manum 1955; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Pla Dalmau 1961; Erdtman 1964; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Brewer 1970; Brewer & Henstra 1970, 1974; Nilsson 1971; Huang 1972; Payne 1972; Visset 1974; Belkina 1975; Nordenstam 1976; Heywood & Humphries 1977; Nilsson & al. 1977; Lee 1978; Markgraf & D'Antoni 1978; Melhem & al. 1979; Chiguryaeva & Tereshkova 1983; Newman 1984; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Iwanumi & al. 1988; Faegri & Iversen 1989; Gandi & Thomas 1989; Bolick 1990; Jintan & al. 1990; Saxena 1993; Vezey & al. 1994; Fuhsiung & al. 1995; Lunau 1995; Reille 1995, 1998; Hussain 2003; Martin & al. 2003; Wei & al. 2003; Meier-Melikyan & al. 2004; Noor & al. 2004; Meo 2005; Punt & Hoen, in press.

Cotula; Wodehouse 1928a; Cranwell 1942; El Hadidy 1958; Stix 1960; Erdtman & al. 1961; Davis 1962a; Ikuse 1962; Nair 1965; Skvarla & Turner 1966b; Heusser 1971; Skvarla & al. 1977; Markgraf & D'Antoni 1978; Parveen & Bhandari 1981; Bir & Sidhu 1982; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Gadek & al. 1989; Moar 1993; Vezey & al. 1994; Fuhsiung & al. 1995; Nasreen & Khan 1998; Qureshi & al. 2002g; Meo 2005; Punt & Hoen, in press.

Crossostephium; Wodehouse 1926, 1928c, 1935; Skvarla & Turner 1966b; Heywood & Humphries 1977; Vezey & al. 1994; Martin & al. 2003.

Cymbopappus; Nordenstam 1976.

Eriocephalus; Skvarla & al. 1977; Federonchuk & Savitiskii 1988; Reille 1995.

Glossopappus; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987.

Gonospermum; Vezey & al. 1994; Reille 1998.

Kaschgaria; Yeou-Ruenn 1985; Jintan & al. 1990; Chen & Zhang 1991; Martin & al. 2001; Watson & al. 2002; Martin & al. 2003; Sanz & al. 2008.

Lasiospermum; Federonchuk & Savitiskii 1988.

Leucanthemella; Chiguryaeva & Tereshkova 1983.

Leucanthemum; Fischer 1890; Wodehouse 1935; Pla Dalmau 1961; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Dimon 1971a, b; Visset 1974; Heywood & Humphries 1977; Chiguryaeva & Tereshkova 1983; Díez 1987; Tormo & Ubera 1987; Vezey & al. 1987; Blanca & al. 1991; Reille 1998; Chester & Raine 2001; Punt & Hoen, in press.

Lonas; Dimon 1971a, b.

Matricaria; Fischer 1890; Zander 1935; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Pla Dalmau 1961; Braga & al. 1962; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Mitsuoka 1968; Dimon 1971a, b; Visset 1974; Chiguryaeva & Tereshkova 1983; Díez 1987; Tormo & Ubera 1987; Faegri & Iversen 1989; Gandi & Thomas 1989; Vezey & al. 1994; Reille 1995, 1998; Tellería 1995; Pacini 1996; Harley & al. 1998; Nasreen & Khan 1998; Rowley & al. 1999; Chester & Raine 2001; Andrada & Tellería 2002; Qureshi & al. 2002g; Meier-Melikyan & al. 2004; Meo 2005; Jafari & Ghanbarian 2007; Punt & Hoen, in press.

Microcephala; Chiguryaeva & Tereshkova 1983; Meier-Melikyan & al. 2004.

Osmitopsis; Stix 1960; Leins 1968a; Wittenbach 1970; Bremer 1972; Reitbrecht 1974; Heywood & Humphries 1977; Skvarla & al. 1977; Vezey & al. 1994.

Pentzia; Dimon 1971a, b; Vezey & al. 1994.

Santolina; Fischer 1890; Pla Dalmau 1961; Dimon 1971a, b; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Federonchuk & Savitiskii 1988; Gandi & Thomas 1989; Blanca & al. 1991; Vezey & al. 1994; Reille 1995; Mori Secci & al. 1997; Mariotti & al. 1999; Chester & Raine 2001; Meier-Melikyan & al. 2004.

Seriphidium; Monoszon 1950b; Yeou-Ruenn 1985; Vallès 1986; Vallès & al. 1987; Jintan & al. 1990; Chen & Zhang 1991.

Soliva; Skvarla & al. 1977; Díez 1987; Gadek & al. 1989; Gandi & Thomas 1989; Cancelli & al. 2007; Blackmore & al. in press.

Tanacetum; Mohl 1835; Fischer 1890; Wodehouse 1926, 1928c, 1935; Pla Dalmau 1961; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Kuprianova & Alyoshina 1972; Inceoglu & Karamustafa 1977; Hesse 1979; Robinson 1981b; Chiguryaeva & Tereshkova 1983; Tormo & al. 1986; Díez 1987; Tormo & Ubera 1987; Gandi & Thomas 1989; Vezey & al. 1994; Reille 1995, 1998; Chester & Raine 2001; Martin & al. 2001; Meier-Melikyan & al. 2001a, 2004; Yurukova Grancharova & al. 2002; Meo 2005; Jafari & Ghanbarian 2007; Punt & Hoen, in press.

Tripleurospermum; Fischer 1890; Erdtman & al. 1961; Inceoglu & Karamustafa 1977; Chiguryaeva & Tereshkova 1983; Reille 1998.

Ursinia; Fischer 1890; Stix 1960; Robinson & Brettell 1973b; Heywood & Humphries 1977; Skvarla & al. 1977, 1988; Vezey & al. 1994.

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Blumea; Banerji 1942; Randeria 1960; Chaubal & Deodikar 1965; Dakshini & Singh 1970; Wittenbach 1970; Leins 1971; Huang 1972; Vasanthy 1976; Merxmüller & al. 1977; Skvarla & al. 1977; Pullaiah 1979; Parveen & Bhandari 1981; Bir & Sidhu 1982; Anderberg 1989; Ling 1993; Perveen & al. 1994; Fuhsiung & al. 1995; Reille 1995; Varma & Vijayavalli 1998; Perveen 1999; Pornpongrungrueng & Chantaranothai 2002; Meo 2005; El-Garf & Osman 2007.

Callilepis; Leins 1968b, 1971; Wittenbach 1970; Besold 1971; Skvarla & al. 1977; Anderberg 1991; Blackmore & al. 2009 (Chapter 7).

Cratystylis; Anderberg & al. 1992, 2005; Zhao 1999; Zhao & al. 2006; Blackmore & al. 2009 (Chapter 7).

Epaltes; Wittenbach 1970; Leins 1971; Huang 1972; Merxmüller & al. 1977; Ling 1993.

Inula; Mohl 1835; Fischer 1890; Wodehouse 1928c; Zander 1935; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Pla Dalmau 1961; Nair 1965; Skvarla & Turner 1966b; Wittenbach 1970; Leins 1968a, b, 1971; Dimon 1971a; Dimon-Cathary 1973; Visset 1974; Belkina 1975; Inceoglu & Karamustafa 1977; Skvarla & al. 1977; Tormo & al. 1986; Díez 1987; Valdés & al. 1987; Anderberg 1989; Faegri & Iversen 1989; Fuhsiung & al. 1995; Reille 1995, 1998; Beug 2001; Chester & Raine 2001; Dawar & al. 2002; Meier-Melikyan & al. 2004; Meo 2005; Osman 2006a; Coutinho & Dinis 2007; Blackmore & al. 2009 (Chapter 7); Punt & Hoen, in press.

Pegolettia; Stix 1960; Leins 1968b, 1971; Wittenbach 1970; Dimon 1971a, b; Parveen & Bhandari 1981; Anderberg 1989; Osman 2006a.

Pluchea; Dakshini & Singh 1970; Wittenbach 1970; Dimon 1971a, b; Dimon-Cathary 1973; Huang 1972; Merxmüller & al. 1977; Bonnefille & Riollet 1980; Parveen & Bhandari 1981; Anderberg 1989; Gandi & Thomas 1989; Keeley & Jansen 1991; Roubik & Moreno 1991; Karis 1993; Perveen & al. 1994; Perveen 1999; Mendonça & al. 2002; El Naggar & Abdel Hafez 2003; Willard & al. 2004; Meo 2005; Cancelli & al. 2006b; El-Garf & Osman 2007.

Streptoglossa; Merxmüller & al. 1977.

Zoutpansbergia; Wittenbach 1970; Besold 1971.

ATHROISMEAE

Athroisma; Wittenbach 1970; Besold 1971; Leins 1973; Merxmüller & al. 1977; Skvarla & al. 1977; Bremer 1987; Blackmore & al. 2009 (Chapter 7).

Blepharispermum; Wittenbach 1970; Leins 1973; Merxmüller & al. 1977; Skvarla & al. 1977; Bremer 1987.

HELENIEAE

Amblyolepis; Skvarla & al. 1977; Robinson 1981b; Jones & al. 1995.

Balduina; Robinson 1981b.

Baileya; Martin & Drew 1970; Skvarla & al. 1977; Turner & Powell 1977; Robinson 1981b; Dobson 1988.

Gaillardia; Fischer 1890; Zander 1935; Tarnavschi & Mitroiu 1959; Skvarla & Turner 1966b; Dakshini & Singh 1970; Solomon & al. 1973; Markgraf & D'Antoni 1978; Payne 1981; Robinson 1981b; Díez 1987; Gandi & Thomas 1989; Ling 1993; Jones & al. 1995; Torres 2000; Fagundez 2001; Andrada & Tellería 2002; Meo 2005.

Helenium; Fischer 1890; Avebury 1912; Zander 1935; Stix 1960; Robinson 1981b; Gandi & Thomas 1989; Jones & al. 1995; Torres 2000.

Hymenoxys; Robinson 1981b.

Marshallia; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Robinson 1978d, 1981b; Gandi & Thomas 1989; Karis 1993.

Pelucha; Skvarla & al. 1988.

Plateilema; Robinson 1981b.

Psathyrotes; Skvarla & Turner 1966b; Robinson 1981b.

Psilostrophe; Martin & Drew 1970; Turner & Powell 1977; Robinson 1981b.

Tetraneuris; Robinson 1981b.

Trichoptilium; Robinson 1981b.

COREOPSIDEAE

Bidens; Fischer 1890; Wodehouse 1928a; Zander 1935; Sheriff 1937; Batalla 1940; Cranwell 1942; Ikuse 1956, 1962; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Maheshwari Devi 1963; Felippe & Labouriau 1964; Chaubal & Deodikar 1965; Nair 1965; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Dakshini & Singh 1970; Dimon 1971a, b; Huang 1972; Guinet & Maley 1974; Lee 1978; Markgraf & D'Antoni 1978; Melhem 1978; Melhem & al. 1979; Parveen & Bhandari 1981; Robinson 1981b; Bir & Sidhu 1982; Salgado-Labouriau 1982a, b, 1983, 1984; Moncada & Salas 1983; Bolick & al. 1984; Mesfin Tadesse 1984; Tormo & al. 1986; Díez 1987; Sun & Ganders 1987; Valdés & al. 1987; Faegri & Iversen 1989; Gandi & Thomas 1989; Saxena 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Jones & al. 1995; Mesfin Tadesse & al. 1995; Reille 1995; Varma & Vijayavalli 1998; La-Serna & al. 1999, 2002; Torres 2000; Beug 2001; Chester & Raine 2001; Fagundez 2003; Wei & al. 2003; Meier-Melikyan & al. 2004; Cancelli & al. 2005b, 2007; Meo 2005; La-Serna & Gómez Ferreras 2006; Modro & al. 2007; Sodré Gda & al. 2007; Blackmore & al. 2009 (Chapter 7); Punt & Hoen, in press.

Coreopsis; Fischer 1890; Wodehouse 1928a; Zander 1935; Ikuse 1956; Skvarla & Turner 1966b; Huang 1972; Robinson 1981b; Dobson 1988; Gandi & Thomas 1989; Fuhsiung & al. 1995; Lunau 1995; Mesfin Tadesse & al. 1995; Meo 2005.

Cosmos; Mohl 1835; Wodehouse 1928a; Ikuse 1956; Tarnavschi & Mitroiu 1959; Maheshwari Devi 1963; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Heslop Harrison 1969a, b; Dakshini & Singh 1970; Knox & Heslop-Harrison 1970; Huang 1972; Howlett & al. 1973; Knox 1973; Dickinson 1976; Dickinson & Potter 1976; Buchen & Sievers 1981; Robinson 1981b; Guédès 1982; Bolick & al. 1984; Blackmore & Barnes 1985, 1986a, b, 1990b; Barnes & Blackmore 1986a, b; Iwanumi & al. 1988; Gandi & Thomas 1989; Pacini & Keijzer 1989; Saxena 1993; Pacini 1996; Varma & Vijayavalli 1998; Torres 2000; Ludlow-Wiechers & al. 2003; Meier-Melikyan & al. 2004; Cancelli & al. 2005b; Meo 2005; Blackmore & al. 2007.

NEUROLAENEAE

Neurolaena; Stix 1960; Robinson 1981b; Roubik & Moreno 1991; Liu 2000; Blackmore & al. 2009 (Chapter 7).

TAGETEAE

Adenophyllum; Robinson 1981b.

Arnicastrum; Robinson 1981b.

Clappia; Robinson 1981b.

Coulterella; Robinson 1978c, 1981b.

Flaveria; Mohl 1835; Misra 1957; Heusser 1971; Parveen & Bhandari 1981; Robinson 1981b; Skvarla & al. 1988; Tellería & Forcone 2002.

Haploësthes; Skvarla & Turner 1966b; Robinson 1981b.

Jamesianthus; Robinson 1981b.

Jaumea; Skvarla & Turner 1966b; Robinson 1981b.

Nicolletia; Robinson 1981b.

Oxypappus; Robinson 1981b.

Pectis; Robinson 1981b; Mendonça & al. 2002.

Porophyllum; Martin & Drew 1970; Torres 2000; Cancelli & al. 2006a, 2007.

Pseudoclappia; Skvarla & Turner 1966b; Robinson 1978c, 1981b.

Sartwellia; Skvarla & Turner 1966b; Robinson 1981b.

Tagetes; Mohl 1835; Fischer 1890; Zander 1935; Tarnavschi & Mitroiu 1959; Stix 1960; Heslop Harrison 1969a, c; Huang 1972; Robinson 1973a, 1981b; Robinson & Nicolson 1975; Muller 1980; Blackmore & Crane 1988; Iwanumi & al. 1988; Gandi & Thomas 1989; Blackmore & Barnes 1990a, b; Fuhsiung & al. 1995; Linskens & Jorde 1997; Torres 2000; Meier-Melikyan & al. 2004; Noor & al. 2004; Meo 2005.

Thymophylla; Robinson 1981b.

Varilla; Skvarla & Turner 1966b; Robinson 1978c.

CHAENACTIDEAE

Chaenactis; Martin & Drew 1969, 1970; Robinson 1981b; Blackmore & al., in press.

Dimeresia; Wittenbach 1970; Besold 1971; Skvarla & al. 1977; Robinson 1978d, 1981b.

Orochaenactis; Robinson 1981b.

BAHIEAE

Achyropappus; Robinson 1981b.

Amauriopsis; Robinson 1981b.

Bahia; Skvarla & Turner 1966b; Heusser 1971; Robinson 1981b.

Bartlettia; Skvarla & Turner 1966b; Robinson 1981b; Liu 2000.

Chamaechaenactis; Robinson 1981b.

Espejoa; Skvarla & Turner 1966b; Robinson 1981b.

Florestina; Robinson 1981b.

Hymenopappus; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Turner & Powell 1977; Robinson 1981b; Gandi & Thomas 1989; Karis 1993; Jones & al. 1995.

Hymenothrix; Robinson 1981b; Buchmann & Shipman 1996.

Hypericophyllum; Robinson 1981b.

Loxothysanus; Robinson 1981b.

Palafoxia; Skvarla & Turner 1966b; Robinson 1981b; Dobson 1988; Gandi & Thomas 1989.

Peucephyllum; Skvarla & Turner 1966b; Robinson 1981b.

Platyschkuhria; Robinson 1981b.

Psathyrotopsis; Robinson 1981b.

Schkuhria; Fischer 1890; Stix 1960; Robinson 1981b; Torres 2000.

Thymopsis; Robinson 1981b.

POLYMNIEAE

Polymnia; Mohl 1835; Wodehouse 1928a; Stix 1960; Fischer & Wells 1962; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Wells 1971; Robinson 1978d, 1981b; Gandi & Thomas 1989; Jones & al. 1995.

HELIANTHEAE

Ambrosia; Mohl 1835; Wodehouse 1928a, 1928c, 1930, 1945; Batalla 1940; Ikuse 1956; Tarnavschi & Mitroiu 1959; Larson & al. 1962; Harringto & Metzger 1963; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Heslop-Harrison 1969a; Martin & Drew 1969, 1970; Southworth 1969b, 1973, 1974, 1983b; Ueno 1969, 1971, 1972; Grashoff & Beaman 1970; Payne & Skvarla 1970; Heusser 1971; Knox & Heslop-Harrison 1971; Nilsson 1971; Payne 1972, 1981; Howlett & al. 1973; Knox 1973; Peterson & Payne 1973; Ogden & al. 1974; Kozar & Aaron 1976; Linskens & Jorde 1977; Tomb 1977; Tomb & Zeleznak 1977; Turner 1977a; Bassett & al. 1978; Bolick 1978b, 1980, 1985a, 1988, 1990; Knox 1979; Melhem & al. 1979; Robins & al. 1979; Robinson 1981b; Southworth 1983a, 1990b; Bolick & al. 1984; Newman 1984; Crane 1986; Gonçalves-Esteves & Esteves 1986; Díez 1987; Valdés & al. 1987; Iwanumi & al. 1988; Faegri & Iversen 1989; Gandi & Thomas 1989; Collinson 1990; Lester & Curtis 1990; Baraniuk & al. 1992; Ling 1993; Saxena 1993; Nagamitsu & Nagamasu 1994; Punt & al. 1994; Reille 1995; Tellería 1995; Buchmann & Shipman 1996; Dechamp 1996; Graham 1996; Lane 1996; Pacini 1996; Kapp & al. 2000; Andrada & Tellería 2002; Ludlow-Wiechers & al. 2003; Baum & al. 2004; Chupov 2004; Meier-Melikyan & al. 2004; Willard & al. 2004; Polevova 2006; D'Amato & al. 2007; Ghosh & al. 2008; Blackmore & al. 2009 (Chapter 7), and in press; Punt & Hoen, in press.

Chromolepis; Robinson 1981b.

Helianthus; Mohl 1835; Fischer 1890; Avebury 1912; Wodehouse 1928a, 1945; Zander 1935; Muhlethaler 1953; Ikuse 1956; Carlquist 1957b; Tarnavschi & Mitroiu 1959; Stix 1960; Maheshwari Devi 1963; Maurizio & Louveaux 1963; Chaubal & Deodikar 1965; Ibrahim 1965; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Dakshini & Singh 1970; Martin & Drew 1970; Cerceau-Larrival 1973; Nakashima & Hosokawa 1974; Ogden & al. 1974; Horner 1977; Linskens & Jorde 1977; Tomb & Zeleznak 1977; Melhem & al. 1979; Vithanage & Knox 1979; Buchen & Sievers 1981; Robinson 1981b; Blackmore & Barnes 1987a; Horner & Pearson 1978; Moncada & Salas 1983; Southworth 1983a; Barnes & Blackmore 1986a; Díez 1987; Gibbs & Ferguson 1987; Valdés & al. 1987; Chen & Wang 1988; Faegri & Iversen 1989; Gandi & Thomas 1989; Pacini & Keijzer 1989; Jintan & al. 1990; Toderich 1992; Ling 1993; Saxena 1993; Chissoe & al. 1994; Kini & al. 1994; Fuhsiung & al. 1995; Galan 1995; Jones & al. 1995; Lunau 1995; Tellería 1995, 2000; Garg 1996; Pacini 1996; Varma & Vijayavalli 1998; Kapp & al. 2000; Klimko & al. 2000; Beug 2001; Chester & Raine 2001; Yang 2001; Andrada & Tellería 2002; Agadi & Hegde 2003; Meric & al. 2003; Wei & al. 2003; Jovanka 2004; Meo & Khan 2004e; Meier-Melikyan & al. 2004; Gopfert & al. 2005; Meo 2005; Polevova 2006; Ghosh & al. 2008; Gotelli & al. 2008; Blackmore & al. 2009 (Chapter 7), and in press; Punt & Hoen, in press.

Rudbeckia; Mohl 1835; Fischer 1890; Wodehouse 1928a; Zander 1935; Ikuse 1956; Tarnavschi & Mitroiu 1959; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Movsesjan & Oganesjan 1969; Robinson 1978d, 1981b; Gandi & Thomas 1989; Beug 2001; Punt & Hoen, in press.

Trichocoryne; Robinson 1981b.

Wyethia; Carlquist 1957b; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Robinson 1981b; Dobson 1988.

MILLERIEAE

Galinsoga; Mohl 1835; Fischer 1890; Wodehouse 1928a; Zander 1935; Batalla 1940; Tarnavschi & Mitroiu 1959; Skvarla & Larson 1965a, b; Skvarla & Turner 1966b; Robinson 1979l, 1981b; Faegri & Iversen 1989; Gandi & Thomas 1989; Fuhsiung & al. 1995; Reille 1998; Varma & Vijayavalli 1998; Meier-Melikyan & al. 2004; Meo 2005; Cancelli & al. 2007; Punt & Hoen, in press.

Melampodium; Wodehouse 1928a; Skvarla & Larson 1965a; Skvarla & Turner 1966b; Gonçalves 1977; Robinson 1981b; Roubik & Moreno 1991; Varma & Vijayavalli 1998.

Smallanthus; Robinson 1981b.

MADIEAE

Achyrachaena; Carlquist 1959; Robinson 1981b.

Adenothamnus; Carlquist 1959; Robinson 1981b.

Amblyopappus; Skvarla & Turner 1966b; Turner & Powell 1977; Robinson 1981b.

Anisocarpus; Robinson 1981b.

Argyroxiphium; Skvarla & Larson 1965a, b; Carlquist 1959; Robinson 1981b.

Arnica; Fischer 1890; Zander 1935; Ikuse 1956; Tarnavschi & Mitroiu 1959; Stix 1960; Erdtman & al. 1961; Braga & al. 1962; Nordenstam 1977; Robinson 1981b; Karis 1993; Nagamitsu & Nagamasu 1994; Reille 1995; Punt & Hoen, in press.

Baeriopsis; Robinson 1981b.

Blepharipappus; Carlquist 1959; Robinson 1981b.

Blepharizonia; Carlquist 1959; Robinson 1981b.

Calycadenia; Carlquist 1959; Skvarla & Larson 1965a; Skvarla & Turner 1966b.; Robinson 1981b

Dubautia; Carlquist 1959; Robinson 1981b.

Eatonella; Robinson 1981b.

Eriophyllum; Martin & Drew 1970; Robinson 1981b; Dobson 1988.
Hemizonia; Wodehouse 1928a; Carlquist 1959; Skvarla & Larson 1965a; Skvarla & Turner 1966a, b; Robinson 1981b; Chissoe & al. 1995.
Holocarpha; Carlquist 1959; Robinson 1981b.
Holozonia; Carlquist 1959; Robinson 1981b.
Hulsea; Skvarla & Turner 1966b; Robinson 1981b.
Lagophylla; Carlquist 1959; Robinson 1981b.
Lasthenia; Fischer 1890; Skvarla & Turner 1966b; Robinson 1981b.
Layia; Carlquist 1959; Skvarla & Turner 1966b; Solomon & al. 1973; Robinson 1981b; Dobson 1988.
Madia; Mohl 1835; Fischer 1890; Wodehouse 1928a; Carlquist 1959; Heusser 1971; Robinson 1981b.
Monolopia; Skvarla & Turner 1966b; Robinson 1981b.
Pseudobahia; Robinson 1981b.
Raillardella; Carlquist 1959; Robinson 1981b; Liu 2000.
Syntrichopappus; Robinson 1981b.
Venegasia; Skvarla & Turner 1966b; Robinson 1981b.
Wilkesia; Carlquist 1959; Robinson 1981b.

PERITYLEAE
Amauria; Robinson 1981b.
Eutetras; Robinson 1981b.
Pericome; Skvarla & Turner 1966b; Robinson 1981b.
Perityle; Solomon & al. 1973; Robinson 1981b.

EUPATORIEAE
Acritopappus; King & Robinson 1972s, 1978b, 1980n, 1987.
Ageratina; King & Robinson 1972h, 1974j, 1975ia, b, 1977b, 1978b, 1983a, 1985, 1987; Jones & al. 1995; La-Serna & al. 1999, 2002; La-Serna & Gómez Ferreras 2006; Blackmore & al. 2009 (Chapter 7).
Ageratum; Fischer 1890; Mitra 1947; Tarnavschi & Mitroiu 1959; Stix 1960; Dimon 1971a; Huang 1972; King & Robinson 1972k, 1974a, 1975a, 1978a, 1987; Bonnefille & Riollet 1980; Mattozo dos Reis & Ferreira 1981a, b; Parveen & Bhandari 1981; Reis & Ferreira 1981; Bir & Sidhu 1982; Nair & Lawrence 1985; Gandi & Thomas 1989; Johnson 1989; Ling 1993; Fuhsiung & al. 1995; Garg 1996; Shaw 1999; Willard & al. 2004; Meo 2005; El-Garf & Osman 2007.
Brickellia; Stix 1960; Leite & da Silva 1977; King & Robinson 1987; Gandi & Thomas 1989; Blackmore & al., in press.
Campuloclinium; King & Robinson 1972t, 1980a, 1987.
Carminatia; King & Robinson 1987.
Chromolaena; King & Robinson 1975a, 1978a, 1980m, 1982c, 1987; Roubik & Moreno 1991.
Conoclinium; King & Robinson 1987; Willard & al. 2004.
Eupatorium; Mohl 1835; Fischer 1890; Zander 1935; Ikuse 1956; Tarnavschi & Mitroiu 1959; Stix 1960; Pla Dalmau 1961; Erdtman 1964; Moreira 1969; Smith 1969; Dakshini & Singh 1970; Grashoff & Beaman 1970; Dimon 1971a; Heusser 1971; Huang 1972; Kuprianova & Alyoshina 1972; King & Robinson 1974h, 1987; Visset 1974; Sullivan 1975, 1976; Inceoglu & Karamustafa 1977; Lee 1978; Mattozo dos Reis & Ferreira 1981a, b; Reis & Ferreira 1981; Nair & Lawrence 1985; Tormo & al. 1986; Díez 1987; Iwanumi & al. 1988; Gandi & Thomas 1989; Bolick 1990; Ling 1993; Nagamitsu & Nagamasu 1994; Fuhsiung & al. 1995; Jones & al. 1995; Lamont 1995; Reille 1995; Book 1996; Lane 1996; Thapa & Wongsiri 1997; Chen & Wang 1999; Colinvaux & al. 1999; Kapp & al. 2000; Schmidt & Schilling 2000; Torres 2000; Beug 2001; Chester & Raine 2001; Skvarla & al. 2001, 2003; Villanueva-Gutiérrez, 2002; Meier-Melikyan & al. 2004; Willard & al. 2004; Meo 2005; Cancelli & al. 2005b, 2007; Modro & al. 2007; Blackmore & al., in press; Punt & Hoen, in press.
Fleischmannia; King & Robinson 1972c, p, 1974a, d, 1975g, 1977b, 1978c, 1986, 1987; Roubik & Moreno 1991.
Hofmeisteria; King & Robinson 1966, 1970b, 1987; King 1967b; Robinson & King 1977; Blackmore & al. 2009 (Chapter 7).
Liatris; Fischer 1890; Zander 1935; Stix 1960; King & Robinson 1987; Gandi & Thomas 1989.
Praxelis; King & Robinson 1987.
Steviopsis; King & Robinson 1972e, 1987.
Stomatanthes; King & Robinson 1987.
Trichogonia; King & Robinson 1978i, 1980l, 1987.

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Anderberg, A.A. 1991. Taxonomy and phylogeny of the tribe Gnaphalieae (Asteraceae). *Opera Botanica* 104: 1–195. [*Acanthocladium*, *Achyrocline*, *Acomis*, *Actinobole*, *Alatoseta*, *Aliella*, *Amphiglossa*, *Anaphalis*, *Anaphaloides*, *Anaxeton*, *Ancistrocarphus*, *Angianthus*, *Anisochaeta*, *Anisopappus*, *Anisothrix*, *Antennaria*, *Antithrixia*, *Apalochlamys*, *Argyroglottis*, *Arrowsmithia*, *Artemisiopsis*, *Asteridea*, *Athrixia*, *Atrichantha*, *Basedowia*, *Bellida*, *Belloa*, *Berroa*, *Blennospora*, *Bombycilaena*, *Bryomorphe*, *Callilepis*, *Calocephalus*, *Calomeria*, *Calotesta*, *Cassinia*, *Catatia*, *Cephalipterum*, *Cephalosorus*, *Chamaepus*, *Chevreulia*, *Chiliocephalum*, *Chionolaena*, *Chrysocephalum*, *Chthonocephalus*, *Cladochaeta*, *Craspedia*, *Cuatrecasasiella*, *Cymbolaena*, *Decazesia*, *Denekia*, *Disparago*, *Dithyrostegia*, *Dolichothrix*, *Edmondia*, *Elytropappus*, *Epitriche*, *Eriochlamys*, *Erymophyllum*, *Euchiton*, *Evacidium*, *Ewartia*, *Ewartiothamnus*, *Facelis*, *Filago*, *Galeomma*, *Gamochaeta*, *Gilberta*, *Gilruthia*, *Gnaphaliothamnus*, *Gnaphalium*, *Gnephosis*, *Gratwickia*, *Haeckeria*, *Helichrysopsis*, *Helichrysum*, *Humeocline*, *Hyalochlamys*, *Hyalosperma*, *Hydroidea*, *Ifloga*, *Isoetopsis*, *Ixiolaena*, *Ixodia*, *Jalcophila*, *Lachnospermum*, *Langebergia*, *Lasiopogon*, *Lawrencella*, *Leontopodium*, *Lepidostephium*, *Leptorhynchos*, *Leptorhynchus*, *Leptotriche*, *Leucogenes*, *Leucophyta*, *Leysera*, *Logfia*, *Loricaria*, *Lucilia*, *Macowania*, *Metalasia*, *Micropsis*, *Micropus*, *Millotia*, *Mniodes*, *Myriocephalus*, *Neotysonia*, *Odixia*, *Oedera*, *Oreoleysera*, *Oxylaena*, *Ozothamnus*, *Parantennaria*, *Petalacte*, *Phaenocoma*, *Phagnalon*, *Pithocarpha*, *Planea*, *Plecostachys*, *Pleuropappus*, *Podolepis*, *Podotheca*, *Pogonolepis*, *Polycalymma*, *Printzia*, *Pseudognaphalium*, *Psilocarphus*, *Pterothrix*, *Pterygopappus*, *Quinetia*, *Quinqueremulus*, *Raoulia*, *Raouliopsis*, *Relhania*, *Rhodanthe*, *Rosenia*, *Rutidosis*, *Schoenia*, *Scyphocoronis*, *Siloxerus*, *Sinoleontopodium*, *Stenocline*, *Stenophalium*, *Stoebe*, *Stuartina*, *Stuckertiella*, *Stylocline*, *Syncarpha*, *Syncephalum*, *Tenrhynea*, *Thiseltonia*, *Toxanthes*, *Trichogyne*, *Triptilodiscus*, *Troglophyton*, *Vellereophyton*, *Waitzia*].

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LIST OF GENERIC "SYNONYMS"

Abasoloa La Llave = *Eclipta* L.
Acanthambrosia Rydb. = *Ambrosia* L.
Acanthoxanthium Fourr. = *Xanthium* L.
Acarphaea Harv. & A. Gray ex. A. Gray = *Chaenactis* DC.
Achaenipodium Brandegee = *Verbesina* L.
Achaetogeron A. Gray = *Erigeron* L.
Achyrophorus Adans. = *Hypochoeris* L.
Achyrothalamus O. Hoffm. = *Erythrocephalum* Benth.
Aciphyllaea A. Gray = *Thymophylla* Lag.
Acoma Benth. = *Coreocarpus* Benth.
Acrolophus Cass. = *Centaurea* L.
Acroptilon Cass. = *Centaurea* L.
Actinea Juss. = *Helenium* L.
Actinella Pers. = *Helenium* L.
Actinomeris Nutt. = *Verbesina* L.
Actinoseris (Endl.) Cabrera = *Richterago* Kuntze
Actinospermum Elliott = *Balduina* Nutt.
Actites Lander = *Sonchus* L.
Adelmannia Rchb. = *Borrichia* Adans.
Adenanthemum B. Nord. = *Adenanthellum* B. Nord.
Adenolepis Less. = *Cosmos* Cav.
Adenopappus Benth. = *Tagetes* L.
Adenospermum Hook. & Arn. = *Chrysanthellum* Rich.
Adventina Raf. = *Galinsoga* Ruiz & Pav.
Aegialophila Boiss. & Heldr. = *Centaurea* L.
Aetheopappus Cass. = *Centaurea* L.
Aganippea DC. = *Jaegeria* Kunth
Agarista DC. = *Coreopsis* L.
Agassizia Gray & Engelm. = *Gaillardia* Foug.
Agiabampoa Rose = *Alvordia* Brandegee
Alarconia DC. = *Wyethia* Nutt.
Alcantara Glaz. = *Xerxes* J.R. Grant
Alcina Cav. = *Melampodium* L.
Alciope DC. = *Capelio* B. Nord.
Allocarpus Kunth = *Calea* L.
Altamirania Greenm. = *Podachaenium* Benth. ex Oerst.
Amblyopogon Fisch. & C.A. Mey. ex DC. = *Amberboa* (Pers.) Less.
Amida Nutt. = *Madia* Molina
Amphicalea Gardner = *Calea* L.
Amphoricarpos Vis. = *Jurinea* Cass.
Anacis Schrank = *Coreopsis* L.
Anaglypha DC. = *Gibbaria* Cass.
Anaitis DC. = *Sanvitalia* L.
Anastraphia D. Don = *Gochnatia* Kunth
Ancistrophora A. Gray = *Verbesina* L.
Andrieuxia DC. = *Heliopsis* Pers.
Angelphytum G.M. Barroso = *Dimerostemma* Cass.
Anomostephium DC. = *Wedelia* Jacq.
Antheropeas Rydb. = *Bahia* Lag.
Anvilleina Maire = *Anvillea* DC.
Apargia Scop. = *Leontodon* L.
Apargidium Torr. & A. Gray = *Haplopappus* Cass.
Aphanopappus Endl. = *Lipochaeta* DC.
Aplopappus Cass. = *Haplopappus* Cass.
Arachnospermum Berg = *Hypochaeris* L.
Arachnospermum F.W. Schmidt = *Scorzonera* L.
Argyrovernonia MacLeish = *Chresta* Vell. ex DC.
Armania Bert ex DC. = *Encelia* Adans.
Artemisiastrum Rydb. = *Artemisia* L.
Asaemia Harv. = *Athanasia* L.
Aspilia Thouars = *Wedelia* Jacq.
Aspiliopsis Greenm. = *Podachaenium* Benth. ex Oerst.
Astemma Less. = *Monactis* Kunth
Asteromoea Blume = *Aster* L.
Asteropterus Adans. = *Leysera* L.
Atalanthus D. Don = *Sonchus* L.
Austroliabum H. Rob. & Brettell = *Liabum* Adans.
Babcockia Boulos = *Sonchus* L.
Baccharidastrum Cabrera = *Baccharis* L.
Baeria Fisch. & C.A. Mey. = *Lasthenia* Cass.
Balbisia Willd. = *Tridax* L.
Baldwinia Nutt. = *Balduina* Nutt.
Ballieria Juss. = *Clibadium* L.
Balsamita Mill. = *Tanacetum* L.
Barattia A. Gray & Engelm. = *Encelia* Adans.
Barrattia A. Gray & Engelm. = *Simsia* Pers.
Bartolina Adans. = *Tridax* L.
Baziasa Steud. = *Sabazia* Cass.
Berkheyopsis O. Hoffm. = *Hirpicium* Cass.
Berthelotia DC. = *Pluchea* Cass.
Bikera Adans. = *Tetragonotheca* L.
Bipontia S.F. Blake = *Soaresia* Sch.Bip.
Boebera Willd. = *Dyssodia* Cav.
Bojeria DC. = *Inula* L.
Bolocephalus Hand.-Mazz. = *Dolomiaea* DC.
Bourdonia Greene = *Chaetopappa* DC.
Brachyactis Ledeb. = *Erigeron* L.
Brachycome Cass. = *Brachyscome* Cass.
Brachymeris DC. = *Phymaspermum* Less.
Bradburia Torr. & A. Gray = *Chrysopsis* Nutt.
Brasilia Torr. & A. Gray = *Calea* L.
Brassavola Adans. = *Helenium* L.
Brauneria Neck. = *Echinacea* Moench
Brotera Willd. = *Cardopatium* Juss.
Broteroa Kuntze = *Cardopatium* Juss.
Burrielia DC. = *Lasthenia* Cass.
Cacalia L. = *Emilia* Cass.
Caleacte R. Br. = *Calea* L.
Calebrachys Cass. = *Calea* L.
Calhounia A. Nels. = *Lagascea* Cav.
Calliachyris Torr. & A. Gray = *Layia* Hook. & Arn. ex. DC.
Callichroa Fisch. & C.A. Mey. = *Layia* Hook. & Arn. ex. DC.
Calliglossa Hook. & Arn. = *Layia* Hook. & Arn. ex. DC.
Calliopsis Rchb. = *Coreopsis* L.
Calopappus Meyen = *Nassauvia* Comm. ex Juss.
Calycocorsus F.W. Schmidt = *Willemetia* Neck.
Calydermos Lag. = *Calea* L.
Campylotheca Cass. = *Bidens* L.
Cardonaea Aristeg., Maguire & Steyerm. = *Gongylolepis* R.H. Schomb.
Cargilla Adans. = *Chrysogonum* L.
Carphostephium Cass. = *Tridax* L.
Carterothamnus R.M. King = *Hofmeisteria* Walp.
Castalis Cass. = *Calendula* L.
Centrospermum Kunth = *Acanthospermum* Schrank
Cephalobembix Rydb. = *Schkuhria* Roth
Cephalophora Cav. = *Helenium* L.
Cercostylos Less. = *Gaillardia* Foug.
Chaenocephalus Griseb. = *Verbesina* L.
Chamaeleon Cass. = *Carlina* L.
Chamaestephanum Willd. = *Schkuhria* Roth
Chamartemisia Rydb. = *Artemisia* L.
Chamissomenia Kuntze = *Schlechtendalia* Less.
Chamomilla Gray = *Santolina* L.

Charieis Cass. = *Felicia* Cass.
Chartolepis Cass. = *Centaurea* L.
Chatiakella Cass. = *Wulffia* Neck.
Cheilodiscus Triana = *Pectis* L.
Cheirolepis Boiss. = *Centaurea* L.
Chilodia R. Br. = *Wulffia* Neck.
Chlamydites J.R. Drumm. = *Linosyris* Aster L.
Chlamysperma Less. = *Villanova* Lag.
Chorisiva Rydb. = *Iva* L.
Chromopappus Boriss. = *Tragopogon* L.
Chrysanthellina Cass. = *Chrysanthellum* Rich.
Chrysomelea Tausch = *Coreopsis* L.
Chrysopappus Takht. = *Centaurea* L.
Chrysophania Kunth ex Less. = *Zaluzania* Pers.
Chrysostemma Less. = *Coreopsis* L.
Chthonia Cass. = *Pectis* L.
Chylodia Rich. ex Cass. = *Wulffia* Neck.
Clomenocoma Cass. = *Dyssodia* Cav.
Cnicus L. = *Cirsium* Mill.
Codonocephalum Fenzl = *Inula* L.
Coespeletia Cuatrec. = *Espeletia* Mutis
Coinogyne Less. = *Jaumea* Pers.
Collaea Spreng. = *Chrysanthellum* Rich.
Colobogyne Gagnep. = *Acmella* Rich. ex Pers.
Comptonanthus B. Nord. = *Ifloga* Cass.
Coreopsoides Moench = *Coreopsis* L.
Coronocarpus Schumach. & Thonn. = *Wedelia* Jacq.
Correllia A.M. Powell = *Perityle* Benth.
Cosmidium Nutt. = *Thelesperma* Less.
Cosmophyllum K. Koch = *Podachaenium* Benth.
Crassina Scepin = *Zinnia* L.
Crockeria Greene ex A. Gray = *Lasthenia* Cass.
Cryphiospermum P. Beauv. = *Enydra* Lour.
Cullumiopsis Drake = *Dicoma* Cass.
Cupularia Godr. & Gren. = *Inula* L.
Cyanopsis Cass. = *Volutaria* Cass.
Cyanus L. = *Centaurea* L.
Cyclachaena Fresen. = *Iva* L.
Cymbia Standl. = *Krigia* Schreb.
Cynthia D. Don = *Krigia* Schreb.
Delucia DC. = *Bidens* L.
Demidium DC. = *Gnaphalium* L.
Dendranthema (DC.) Des Moul. = *Chrysanthemum* L.
Desmocephalum Hook. f. = *Delilia* Spreng.
Dialesta Kunth = *Oliganthes* Cass.
Diaspananthus Miq. = *Ainsliaea* DC.
Dicalymma Lem. = *Podachaenium* Benth.
Dichaeta Nutt. = *Lasthenia* Cass.
Dichaeta Sch.Bip. = *Macvaughiella* R.M. King & H. Rob.
Diglossus Cass. = *Tagetes* L.
Dinoseris Griseb. = *Hyaloseris* Griseb.
Diodonta Nutt. = *Coreopsis* L.
Diomedea Bert. ex Colla = *Helianthus* L.
Diomedea Cass. = *Borrichia* Adans.
Diotis Desf. = *Otanthus* Hoffmanns. & Link
Diplazoptilon Y. Ling = *Jurinea* Cass.
Diplosastera Tausch = *Coreopsis* L.
Diplothrix DC. = *Zinnia* L.
Dipterotheca Sch.Bip. ex Hochst. = *Wedelia* Jacq.
Discomela Raf. = *Helianthus* L.
Dolichlasium Lag. = *Trixis* P. Browne
Dracopsis Cass. = *Rudbeckia* L.
Dracunculus Ledeb. = *Artemisia* L.
Dugaldia Cass. = *Hymenoxys* Cass.
Durandoa Pomel = *Carthamus* L.
Dysodium Rich. ex Pers. = *Melampodium* L.
Echinocephalum Gardner = *Melanthera* Rohr
Echinomeria Nutt. = *Helianthus* L.
Eisenmannia Sch.Bip. ex Hochst. = *Blainvillea* Cass.
Electra DC. = *Coreopsis* L.
Elvira Cass. = *Delilia* Spreng.
Embergeria Boulos = *Sonchus* L.
Enalcida Cass. = *Tagetes* L.
Epilepis Benth. = *Coreopsis* L.
Episcothamnus H. Rob. = *Lychnophoriopsis* Sch.Bip.
Eremiastrum A. Gray = *Monoptilon* Torr. & A. Gray
Eremopappus Takht. = *Centaurea* L.
Eremosis Gleason = *Vernonia* Schreb.
Ericentrodea S.F. Blake & Sherff = *Narvalina* Cass.
Eriocoma Kunth = *Montanoa* La Llave
Eriocoryne Wall. = *Saussurea* DC.
Eriopappus Arn. = *Layia* Hook. & Arn. ex DC.
Eriopappus Hort. ex Loudon = *Eupatorium* L.
Eriosphaera Less. = *Galeomma* Rauschert
Espeletiopsis Cuatrec. = *Espeletia* Mutis
Eupatoriastrum Greenm. = *Eupatorium* L.
Eupatoriophalacron Mill. = *Verbesina* L.
Euxenia Cham. = *Podanthus* Lag.
Evax Gaertn. = *Filago* L.
Faberia Hemsl. = *Prenanthes* L.
Feaea Spreng. = *Selloa* Kunth
Feaella S.F. Blake = *Selloa* Kunth
Ferdinanda Lag. = *Zaluzania* Pers.
Filaginella Opiz = *Gnaphalium* L.
Fingalia Schrank = *Eleutheranthera* Poit. ex Bosc
Fontquera Maire = *Perralderia* Coss.
Fornicaria Raf. = *Salmea* DC.
Fougeria Moench = *Baltimora* L.
Fougerouxia Cass. = *Baltimora* L.
Francoeuria Cass. = *Pulicaria* Gaertn. ex Schreb.
Franseria Cav. = *Ambrosia* L.
Fresenia DC. = *Felicia* Cass.? *Pegolettia* Cass?
Gaertneria Medik. = *Ambrosia* L.
Galophthalmum Nees & Mart. = *Blainvillea* Cass.
Gamolepis Less. = *Steirodiscus* Less.
Garcilassa Poepp. & Endl. = *Hymenostephium* Benth.
Georgina Willd. = *Dahlia* Cav.
Giflifa Chrtek & Holub = *Logfia* Cass.
Glaziovanthus G.M. Barroso = *Chresta* Vell. ex DC.
Glossogyne Cass. = *Glossocardia* Cass.
Gnaphalodes Mill. = *Micropus* L.
Goldmania Greenm. = *Goldmanella* Greenm.
Gongrothamnus Steetz = *Distephanus* Cass.
Gonotheca Raf. = *Tetragonotheca* L.
Graciela Rzed. = *Strotheria* B.L. Turner
Graemia Hook. = *Helenium* L.
Grantia Boiss. = *Iphiona* Cass.
Greenella A. Gray = *Gutierrezia* Lag.
Greenmania Hieron. = *Unxia* L. f.?
Grossheimia Sosn. & Takht. = *Centaurea* L.
Guaiacaia Maguire = *Glossarion* Maguire & Wurdack
Guenthera Regel = *Xanthocephalum* Willd.
Guerreroia Merr. = *Glossocardia* Cass.
Gymnolomia Kunth = *Wedelia* Jacq.
Gymnostyles Juss. = *Soliva* Ruiz & Pav.
Haarera Hutch. & E.A. Bruce = *Erlangea* Sch.Bip.
Haenselera Boiss. ex DC. = *Rothmaleria* Font Quer
Halea L. = *Eupatorium* L.

Hamulium Cass. = *Verbesina* L.
Haplocalymma S.F. Blake = *Viguiera* Kunth
Haplostephium Mart. ex DC. = *Lychnophora* Mart.
Harpaecarpus Nutt. = *Madia* Molina
Harpalium Cass. = *Helianthus* L.
Harpephora Endl. = *Wedelia* Jacq.
Harthamnus H. Rob. = *Plazia* Ruiz & Pav.
Hartmannia DC. = *Hemizonia* DC.
Hecubaea DC. = *Helenium* L.
Heleniastrum Fabr. = *Helenium* L.
Helepta Raf. = *Heliopsis* Pers.
Helianthopsis H. Rob. = *Pappobolus* S.F. Blake
Helichroa Raf. = *Echinacea* Moench
Helicta Cass. = *Borrichia* Adans.
Heliogenes Benth. = *Jaegeria* Kunth
Heliophthalmum Raf. = *Rudbeckia* L.
Helioreos Raf. = *Pectis* L.
Helipterum DC. = *Syncarpha* DC.
Helminthia Juss. = *Helminthotheca* Vaill. ex Zinn
Hemiambrosia Delpino = *Ambrosia* L.
Hemistepta Bunge = *Saussurea* DC.
Hemisteptia Bunge = *Cirsium* Mill.
Heteromma Benth. = *Chrysocoma* L.
Heywoodiella Svent. & Bramwell = *Hypochoeris* L.
Hingstonia Raf. = *Verbesina* L.
Hingtsha Roxb. = *Enydra* Lour.
Hirschia Baker = *Iphiona* Cass.
Hochstetteria DC. = *Dicoma* Cass.
Hoehnelia Schweinf. = *Ethulia* L. f.
Hoffmeisteria = *Pleurocoronis* R.M. King & H. Rob.
Hologymne Bartl. = *Lasthenia* Cass.
Homognaphalium Kirp. = *Gnaphalium* L.
Hopkirkia DC. = *Schkuhria* Roth.
Humea Sm. = *Humeocline* Anderb.
Hyalea Jaub. & Spach = *Centaurea* L.
Hymenatherum Cass. = *Dyssodia* Cav.
Hymenocephalus Jaub. & Spach = *Centaurea* L.
Hymenoclea Torr. & A. Gray = *Ambrosia* L.
Hypelichrysum Kirp. = *Gnaphalium* L.
Infantea Remy = *Amblyopappus* Hook. & Arn.
Jacea L. = *Centaurea* L.
Jurinella Jaub. & Spach = *Jurinea* Cass.
Kallias Cass. = *Heliopsis* Pers.
Kanimia Gardner = *Mikania* Willd.
Kaulfussia Nees = *Felicia* Cass.
Kegelia Sch.Bip. = *Eleutheranthera* Poit. ex Bosc
Kentrophyllum Neck. Ex DC. = *Carthamus* L.
Kerneria Moench = *Bidens* L.
Kuhnia L. = *Brickellia* Elliott
Lactucosonchus (Sch.Bip.) Svent. = *Sonchus* L.
Lagenophora Cass. = *Lagenifera* Cass.
Lagoseris M. Bieb. = *Crepis* L.
Lamottea Pomel = *Carduncellus* Adans.
Lamprachaenium Benth. = *Phyllocephalum* Blume
Lancisia Fabr. = *Cotula* L.
Laphamia A. Gray = *Perityle* Benth.
Lasallea Greene = *Aster* L.
Latreillea DC. = *Ichthyothere* Mart.
Laxmannia R. Br. = *Petrobium* R. Br.
Leachia Cass. = *Coreopsis* L.
Lebetina Cass. = *Adenophyllum* Pers.
Leiboldia Schltdl. ex Gleason = *Vernonia* Schreb.
Leighia Cass. = *Viguiera* Kunth
Leighia Scop. = *Ethulia* L. f.
Lembertia Greene = *Eatonella* A. Gray
Leontonyx Cass. = *Helichrysum* Mill.
Leontophthalmum Willd. = *Calea* L.
Lepachys Raf. = *Ratibida* Raf.
Lepia Hill = *Zinnia* L.
Lepidostephanus Bartl. = *Achyrachaena* Schauer
Leptopharynx Rydb. = *Perityle* Benth.
Leptophora Raf. = *Helenium* L.
Leptopoda Nutt. = *Helenium* L.
Leucampyx A. Gray = *Hymenopappus* L'Hér.
Leucelene Greene = *Chaetopappa* DC.
Leuceria Lag. = *Leucheria* Lag.
Leuciva Rydb. = *Iva* L.
Leucopholis Gardner = *Chionolaena* DC.
Leucophyton Less. = *Leucophyta* R. Br.
Leuzea DC. = *Centaurea* L.
Libanothamnus Ernst = *Espeletia* Mutis ex Humb. & Bonpl.
Limnogenneton Sch.Bip. = *Sigesbeckia* L.
Linosyris Cass. = *Aster* L.
Linsecomia Buckley = *Helianthus* L.
Lipotriche Less. = *Lipochaeta* DC.
Lipotriche R. Br. = *Melanthera* Rohr
Lopholoma Cass. = *Centaurea* L.
Lorentea Lag. = *Pectis* L.
Lorentea Ortega = *Sanvitalia* Lam.
Lowellia A. Gray = *Thymophylla* Lag.
Luciliopsis Wedd. = *Chaetanthera* Ruiz & Pav.
Lugoa DC. = *Anthemis* L.
Macdougalia A. Heller = *Hymenoxys* Cass.
Macella K. Koch = *Jaegeria* Kunth
Macledium Cass. = *Dicoma* Cass.
Macraea Hook. f. = *Lipochaeta* DC.
Macrocarphus Nutt. = *Chaenactis* DC.
Macronema Nutt. = *Ericameria* Nutt.
Madaria DC. = *Madia* Molina
Madorella Nutt. = *Madia* Molina
Mallotopus Franch. & Sav. = *Arnica* L.
Mandonia Wedd. = *Tridax* L.
Maruta (Cass.) Gray = *Anthemis* L.
Melarhiza Kellogg = *Wyethia* Nutt.
Mendezia DC. = *Spilanthes* L.
Menotriche Steetz = *Wedelia* Jacq.
Meratia Cass. = *Delilia* Spreng.
Mesodetra Raf. = *Helenium* L.
Micrelium Forssk. = *Eclipta* L.
Microchaeta Nutt. = *Lipochaeta* DC.
Micrococcia Hook. f. = *Delilia* Spreng.
Microdonta Nutt. = *Heterosperma* Cav.
Microlecana Sch.Bip. = *Bidens* L.
Microlecane Sch.Bip. = *Bidens* L.
Microlonchus Cass. = *Centaurea* L.
Microlophus Cass. = *Centaurea* L.
Microseris D. Don = *Haplopappus* Cass.
Microtrichia DC. = *Grangea* Adans.
Mieria La Llave = *Schkuhria* Roth.
Minyranthes Turcz. = *Sigesbeckia* L.
Mirasolia Sch.Bip. ex Benth. & Hook. f. = *Tithonia* Desf.
Mnesiteon Raf. = *Balduina* Nutt.
Mocinna Lag. = *Calea* L.
Modestia Kharadze & Tamamsch. = *Anacantha* (Iljin) Soják
Mollera O. Hoffm. = *Calostephane* Benth.
Monenteles Labill. = *Pterocaulon* Elliott
Monopholis S.F. Blake = *Monactis* Kunth
Monothrix Torr. = *Perityle* Benth.

Montagnaea DC. = *Montanoa* Cerv. in La Llave & Lex.
Mulgedium Cass. = *Lactuca* L.
Mycelis Cass. = *Prenanthes* L.
Nablonium Cass. = *Ammobium* R. Br.
Nardosmia Cass. = *Petasites* Mill.
Nauenbergia Willd. = *Flaveria* Juss.
Nauplius (Cass.) Cass. = *Asteriscus* Mill.
Needhamia Cass. = *Narvalina* Cass.
Neilreichia Fenzl = *Schistocarpha* Less.
Neothymopsis Britton & Millsp. = *Thymopsis* Benth.
Nesothamnus Rydb. = *Perityle* Benth.
Neuractis Cass. = *Chrysanthemum* Rich
Niebuhria Neck. = *Wedelia* Jacq.
Nitelium Cass. = *Dicoma* Cass.
Nocca Cav. = *Lagascea* Cav.
Nothocalais Greene = *Haplopappus* Cass.
Notonia DC. = *Kleinia* Mill.
Notoniopsis B. Nord. = *Kleinia* Mill.
Notoptera Urb. = *Otopappus* Benth.
Obeliscotheca Vaill. ex Adans. = *Rudbeckia* L.
Ochronelis Raf. = *Verbesina* L.
Odontoloma Kunth = *Oliganthes* Cass.
Odontospermum Neck. ex Sch.Bip. = *Asteriscus* Mill.
Ogiera Cass. = *Eleutheranthera* Poit. ex Bosc
Oligandra Less. = *Lucilia* Cass.
Oliganthemum F.Muell. = *Pluchea* Cass.
Omalotheca Cass. = *Gnaphalium* L.
Onobroma Gaertn. = *Carduncellus* Adans.
Orcya Vell. = *Acanthospermum* Schrank
Oreophila D. Don. = *Hypochaeris* L.
Ormenis Cass. = *Chamaemelum* Miller
Orsina Bertol. = *Inula* L.
Orsinia Bertol. ex DC. = *Clibadium* L.
Osmites L. = *Osmitopsis* Cass.
Oswalda Cass. = *Clibadium* L.
Oswaldia Less. = *Clibadium* L.
Othake Raf. = *Gaillardia* Foug.
Outreya Jaub. & Spach = *Jurinea* Cass.
Oxylepis Benth. = *Helenium* L.
Oxytenia Nutt. = *Iva* L.
Oxyura DC. = *Layia* Hook. & Arn.
Paleista Raf. = *Eclipta* L.
Paleolaria Cass. = *Palafoxia* Lag.
Panargyrum D. Don = *Nassauvia* Comm. ex Juss.
Pappothrix (A. Gray) Rydb. = *Perityle* Benth.
Paraixeris Nakai = *Crepidiastrum* Nakai
Paramicrorhynchus Kirp. = *Launaea* Cass.
Passacardoa Wild = *Pasaccardoa* Kuntze
Pectidium Less. = *Pectis* L.
Peramibus Raf. = *Coreopsis* L.
Perotriche Cass. = *Stoebe* L.
Perplexia Iljin = *Jurinea* Cass.
Persoonia Michx. = *Marshallia* Schreb.
Petalactella N.E. Br. = *Ifloga* Cass.
Petrollinia Chiov. = *Inula* L.
Peyrousea DC. = *Cotula* L.
Phacellothrix F. Muell. = *Helichrysum* Mill.
Phaecasium Cass. = *Crepis* L.
Phaeocephalus S. Moore = *Hymenolepis* Cass.
Phaeopappus Boiss. = *Centaurea* L.
Phaethusa Gaertn. = *Verbesina* L.
Phalacrachena Iljin = *Centaurea* L.
Phalolepis Cass. = *Centaurea* L.
Phileozera Buckley = *Hymenoxys* Cass.
Phyteumopsis Juss. ex Poir. = *Marshallia* Schreb.
Picradenia Hook. = *Helenium* L.
Picradeniopsis Rydb. = *Bahia* Lag.
Picridium Desf. = *Reichardia* Roth.
Piloselloides (Less.) C.Jeffrey ex Cufod. = *Gerbera* Cass.
Pilostemon Iljin = *Saussurea* DC.
Pionocarpus S.F. Blake = *Iostephane* Benth.
Platychaete Boiss. = *Pulicaria* Gaertn. ex Schreb.
Platypteris Kunth = *Verbesina* L.
Plummera A. Gray = *Hymenoxys* Cass.
Podospermum DC. in Lam. & A. DC. = *Scorzonera* L.
Pollalesta Kunth = *Piptocoma* Cass.
Polycline Oliv. = *Athroisma* DC.
Polymniastrum Lam. = *Polymnia* L.
Polymniastrum Small = *Smallanthus* Mack.
Polypteris Less. = *Gaillardia* Foug.
Pontesia Vell. = *Riencourtia* Cass.
Postia Boiss. & Blanche = *Rhanteriopsis* Rauschert
Prenanthella Rydb. = *Prenanthes* L.
Prionopsis Nutt. = *Grindelia* Willd.
Pronacron Cass. = *Melampodium* L.
Psathurochaeta DC. = *Melanthera* Rohr
Psectra (Endl.) Tomšovic = *Echinops* L.
Pseudactis S. Moore = *Emilia* Cass.
Pseudobartlettia Rydb. = *Psathyrotes* (Nutt.) A. Gray
Pseudokyrsteniopsis R.M. King & H. Rob. = *Eupatorium* L.
Psila Phil. = *Baccharis* L.
Psychrophyton Beauverd = *Raoulia* Hook. f.
Pterigeron (DC.) Benth. = *Streptoglossa* Steetz ex F. Muell.
Pterotheca Cass. = *Crepis* L.
Ptilomeris Nutt. = *Lasthenia* Cass.
Ptilostephium Kunth = *Tridax* L.
Punduana Steetz = *Vernonia* Schreb.
Pycnocephalum DC. = *Eremanthus* Less.
Pyrethrum Zinn = *Tanacetum* L.
Raillardia Spreng. = *Dubautia* Gaudich.
Ramtilla DC. = *Guizotia* Cass.
Rancagua Poepp. & Endl. = *Lasthenia* Cass.
Rhabdotheca Cass. = *Launaea* Cass.
Rhetinodendron Meisn. = *Robinsonia* DC.
Rhynea DC. = *Tenrhynea* Hilliard & B.L. Burtt
Ridan Adans. = *Verbesina* L.
Riddellia Nutt. = *Psilostrophe* DC.
Rodigia Spreng = *Crepis* L.
Rothia Lam. = *Hymenopappus* L'Hér.
Rothia Schreb. = *Andryala* L.
Ruilopezia Cuatrec. = *Espeletia* Mutis ex Humb. & Bonpl.
Rydbergia Greene = *Tetraneuris* Greene
Salmeopsis Benth. = *Salmea* DC.
Sanvitaliopsis Sch.Bip. ex Benth. & Hook. f. = *Zinnia* L.
Saubinetia Remy = *Verbesina* L.
Scariola F.W. Schmidt = *Lactuca* L.
Schizophyllum Nutt. = *Lipochaeta* DC.
Sclerostephane Chiov. = *Pulicaria* Gaertn. ex Schreb.
Scolospermum Less. = *Baltimora* L.
Scyphopappus B. Nord. = *Argyranthemum* Webb
Seala Adans. = *Pectis* L.
Sebastiana Benth. & Hook. f. = *Chrysanthellum* Rich.
Seridia Juss. = *Centaurea* L.
Seriola L. = *Hypochaeris* L.
Seris Less. = *Richterago* Kuntze
Seris Willd. = *Onoseris* DC.
Serpaea Gardner = *Oyedaea* DC.
Sogalgina Cass. = *Tridax* L.

Solenotheca Nutt. = *Tagetes* L.
Sosnovskya Takht. = *Centaurea* L.
Sparganophorus Boehm. = *Struchium* P.Browne
Spathipappus Tzvelev = *Tanacetum* L.
Sphaeroclinium (DC.) Sch.Bip. = *Matricaria* L.
Sphaeromorphaea DC. = *Epaltes* Cass.
Spitzelia Sch.Bip. = *Picris* L.
Stammarium Willd. ex DC. = *Pectis* L.
Stebbinsoseris K.L. Chambers = *Microseris* D. Don.
Stemmacantha Cass. = *Rhaponticum* Vaill.
Stemmatella Wedd. ex Benth. & Hook. f. = *Galinsoga* Ruiz & Pav.
Stemmodontia Cass. = *Wedelia* Jacq.
Stenactis Cass. = *Eigeron* L.
Stengelia Sch.Bip. = *Baccharoides* Moench
Stenocarpha S.F. Blake = *Galinsoga* Ruiz & Pav.
Stenotopsis Rydb. = *Ericameria* Nutt.
Stephanochilus Coss. & Durieu ex Benth. & Hook. f. = *Amberboa* (Pers.) Less.
Stephanolepis S. Moore = *Erlangea* Sch.Bip.
Stilpnophytum Less. = *Athanasia* L.
Strophopappus (DC.) DC. = *Stilpnopappus* Mart. ex DC.
Stylesia Nutt. = *Bahia* Lag.
Sventenia Font Quer = *Sonchus* L.
Symphyochaeta (DC.) Skottsb. = *Robinsonia* DC.
Syncephalantha Bartl. = *Dyssodia* Cav.
Synchaeta Kirp. = *Gnaphalium* L.
Synosma Raf. ex Britton = *Hasteola* Raf.
Taeckholmia Boulos = *Sonchus* L.
Tamania Cuatrec. = *Espeletia* Mutis
Telfordia = *Ozothamnus* R. Br.
Tepion Adans. = *Verbesina* L.
Tetracarpum Moench = *Schkuhria* Roth
Tetragonosperma Scheele = *Tetragonotheca* L.
Tetramorphaea DC. = *Centaurea* L.
Tetraotis Reinw. = *Enydra* Lour.
Tetrodus Cass. = *Helenium* L.
Thelechitonia Cuatrec. = *Wedelia* Jacq.
Thrincia Roth. = *Leontodon* L.
Tiarocarpus Rech. f. = *Cousinia* Cass.
Tolbonia Kuntze = *Calotis* R. Br.
Tollatia Endl. = *Layia* Hook. & Arn.
Tomanthea Coss. = *Centaurea* L.
Torrentia Vell. = *Ichthyothere* Mart.
Tragoceras Spreng. = *Isostigma* Less.
Tragoceros Kunth = *Zinnia* L.
Trattenikia Pers. = *Marshallia* Schreb.
Tricarpha Longpre = *Sabazia* Cass.
Trichostemma Cass. = *Wedelia* Jacq.
Trichostephium Cass. = *Wedelia* Jacq.
Trichostephus Cass. = *Wedelia* Jacq.
Trichymenia Rydb. = *Hymenothrix* A. Gray
Trimeranthes Cass. = *Sigesbeckia* L.
Trimetra Moc. ex DC. = *Borrichia* Adans.
Triplotaxis Hutch. = *Vernonia* Schreb.
Tulocarpus Hook. & Arn. = *Guardiola* Cerv.
Tursenia Cass. = *Baccharis* L.
Uhdea Kunth = *Montanoa* La Llave
Uropappus Nutt. = *Haplopappus* Cass.
Vanillosmopsis Sch.Bip. = *Eremanthus* Less.
Vargasia DC. = *Galinsoga* Ruiz & Pav.
Vasquesia Phil. = *Unxia* L. f.
Venidium Less. = *Arctotis* L.
Vermifuga Ruiz & Pav. = *Flaveria* Juss.
Vesicarpa Rydb. = *Sphaeromeria* Nutt.
Veslingia Vis. = *Guizotia* Cass.
Vicoa Cass. = *Pentanema* Cass.
Viereckia R.M. King & H. Rob. = *Eupatorium* L.
Vigolina Poir. = *Galinsoga* Ruiz & Pav.
Vilobia Strother = *Tagetes* L.
Virletia Sch.Bip. ex Benth. & Hook. f. = *Bahia* Lag.
Vladimiria Iljin = *Dolomiaea* DC.
Volkensia O. Hoffm. = *Bothriocline* Oliver ex Benth.
Volutarella Cass. = *Volutaria* Cass.
Wahlenbergia Schum. = *Enydra* Lour.
Waldheimia Kar. & Kir. = *Allardia* Decne.
Whitneya A. Gray = *Arnica* L.
Wiborgia Roth = *Galinsoga* Ruiz & Pav.
Wirtgenia Sch.Bip. = *Wedelia* Jacq.
Wootonella Standl. = *Verbesina* L.
Wuerschmittia Sch.Bip. ex Hochst. = *Melanthera* Rohr
Wulffia Neck. ex Cass. = *Tilesia* Mey.
Xantho Remy = *Lasthenia* Cass.
Ximenesia Cav. = *Verbesina* L.
Xyridopsis B. Nord. = *Emilia* Cass.
Yunquea Skottsb. = *Centaurodendron* Johow
Zacintha Mill. = *Crepis* L.
Zacyntha Adans. = *Crepis* L.
Zarabellia Cass. = *Melampodium* L.
Zarabellia Neck. = *Berkheya* Ehrh.
Zemisne O. Deg. & Sherff = *Scalesia* Arn.
Zoutpansbergia Hutch. = *Callilepis* DC.
Zycona Kuntze = *Schistocarpha* Less.

Appendix C

Original figure legends for plates in Chapter 1

Compiled by Vicki A. Funk and J. Mauricio Bonifacino

Fig. 1.3. Tabula 251 from Tournefort’s (1700) *Institutiones Rei Herbariae*, vol. 3 (cf. pages 438 and 467, vol. 1).

Flore Flosculoso. Flos Flosculosus **A** (ut jam diximus) componitur ex plurimis flosculis **B** dense positis, eodemque calyce **E E** comprehensis. Flosculi autem sunt petala fistulosa, tenuia, quórum suprema pars ampliatur, multifariam, sæpius tamen stellæ instar divisa, infidentque tenero plerumque fructui sive embryoni **C**, è quo prodit capillamentum **F** ultra vaginam **G** protensum, quinque fulcros **H** innixam. Embryones fundum **D** calycis occupant, quod Thalamus vocatur abeuntque in semen **I**, **M** pappis instructum **L**, **N** vel iisdem carens **O**, aut aculeatum **P Q**. Hujusmodi flores observantur in Santolina, Jacea, Carduis, cæterisve.

Flore Semiflosculoso. Flos Semiflosculosus **A B** (ut jam diximus) componitur ex plurimis semiflosculis in orbem vel unicum vel multiplicem positis, eodemque calyce **O P**, qui per maturitatem sæpe invertitur ⋆, comprehensis. Semiflosculi autem **C**, **D** sunt petala, infernâ parte fistulosa, mediâ verò & supremâ plana, ac velut in linguam producta, foliis intermediis **R** nonnunquam ab invicem sejuncta, insidentque tenero fructui sive embryoni **K N**, è quo prodit capillamentum. Embryones autem fundum **Q** calycis occupant, quod Thalamus vocatur, abeuntque in semen nunc pappis instructum **S T**, nunc papporum expers **V**, modò coronatum **X Z**, quandoque foliatum **&**.

Fig. 1.5. Tabula 20, taken from Vaillant’s (1721) *Établissement de Nouveaux Caractères de Trois Familles ou Classes de Plantes à Fleurs Composées; Sçavoir, des Cynarocéphales, des Corymbifères, et des Cichoracées*: 277–318.

Explication des Figures appartenantes aux Corymbiferes dont la fleur est ordinairement en disque. **1**. Fleur de la 5^{me}. espece de Seneçon. **2**. … de la 11^{me}. espece d’*Helichrysum*.

3. … de la 1^{re}. espece de *Cotula*. **4**. … de la 22^{me}. espece de *Conyza*. Cette fleur, de même que celle de la 6^{me}. espece de ce genre, est composée de fleurons hermaphrodites, entourés de fleurs effleurées. **5**. Fleur de la 1^{re}. espece d’*Ananthocyclus*. **6**. … de la 1^{re}. espece de *Filago* beaucoup plus grande que nature. **7**. Peloton de fleurs de la 1^{re}. espece de *Filago*. **8**. Fleur de la *Santolina*. **9**. Faisceau de fleurs de la 1^{re}. espece de *Gnaphalium*, plongé dans une fraise de feüilles a, a, a, a. **10**. Fleur *de la Bellis incana*, *Chrysanthemi Cretici folia. Bocc. Mus.* On donne ici cette fleur pour exemple d’une fleur radiée. **11**. Fleur de la 1^{re}. espece d’*Elephantopus*. **12**. Tête de la 3^{me}. espece de *Sphæranthos*. **13**. Exemple d’un fleuron hermaphrodite dont le pavillon *a* est régulier & découpé en étoile. *b* est l’ovaire. **14**. Exemple d’un fleuron hermaphrodite dont le pavillon *a* est régulier, & découpé en quatre quartiers qui forment une croix. b est l’ovaire dont la tête est chargée d’une couronne de poils. **15**. Fleuron de la couronne *a a Fig. 3.* Le pavillon *a* de ce fleuron est irrégulier, & découpé en quatre quartiers. *b* est l’ovaire. **16**. Fleuron femelle *a* de la 1^{re}. espece de *Tarchonanthos*, lequel est sans pavillon & sans découpures apparentes. *b* est l’ovaire. *c*, *c*, les cornes de la trompe qui enfile le fleuron. **17**. Est la même que la 16^{me}, à la trompe près que l’on a emportée pour mieux faire paroître l’embouchure du fleuron. **18**. Demi-fleuron femelle dont l’ovaire *b* est chargé d’une couronne de poils. **19**. Autre demi-fleuron femelle dont l’ovaire *b* est à tête nue. **20**. Exemple d’un fleuron mâle dont le pavillon *a* est régulier, & découpé en étoile. *b* est le faux germe. **21**. Calyce de la fleur Fig. 3. *a* est le placenta. **22**. Exemple d’un demi-fleuron neutre. *b* est le faux germe. **23**. Fleur effleurée dont l’ovaire *b* est à tête nuë. **24**. … faite d’aprés une de celles de la fleur Fig. 5. **25**. … faite sur une de celles de la fleur Fig. 4. *b* est l’ovaire dont la tête est couronnée de poils. **26**. Cette Figure & la suivante n°. **27**. appartiennent au genre de *Gnaphalodes I. R. Herb.439.* lequel doit être exclus d’entre les Plantes dont la fleur est composée de fleurons. **28**. Calyce de la. 1^{re}. espece de Seneçon. **29.** & **30**. Deux ovaires de differentes formes, faits d’aprés ceux de *Cotula* *flore luter radiato. I. R. Herb.* que nous rangerons sous le genre de *Camomille.* **31**. Ovaire de la 7^{me}. espece d'Armoise. **32**. Un brin de la 8^{me}. espece d'Absinthe, chargé de fleurs *a a a*. **33**. Ovaire de la 4^{me}. espece de *Tanacetum*.

34. … de Santolina. **35**. … de Sparganophoros. a est le diademe ou bandeau quarré. **36**. Un brin d'Armoise commune, garni de fleurs. **37**. & **38**. Ovaires à tête couronnée de poils. Tels sont les ovaires d'*Helichrysum*, de *Filago*, de *Conyza*, d'*Eupatorium*, de *Petasites*, de *Cacalia*, de Seneçon, &c. **39**. Ovaire de la 1^{re}. espece de *Porrophyllum*. *a* est la couronne de poils. **40**. Ovaire de *Ptephoros*, garni de sa couronne de plume. **41**. Ovaire de la 1^{re}. espece d'Elephantopus. **42**. Une feüille de la 2^{de}. espece de *Santolina*, un peu plus grande que nature. **43**. & **44**. Bales de differentes formes. **45**. Un brin de la 4^{me}. espece d'*Artemisia*, garni de fleurs.

Fig. 1.6. Tabula 4, taken from Berkhey's (1760) *Expositio Characteristica Structurae Florum qui Dicuntur Compositi.*

TABULAE QUARTAE. Explicatio. **Fig. 1.** Anthera Silphii 2. *Roy. Prod. pag.* 181. Magnitudine naturali. **Fig. 2.** Eadem, aft aucta, demonstrans decursum filamenti usque ad apices antherae. (a) Anthera ipsa, polline impleta. (b) Filamentum ipsam in duo vascula dividens. (c) Apex antherae bidentatus. **Fig. 3.** Limbus Silphii 2. per longitudinem scissus & reflexus, ut situs filamentorum appareat. (a) Limbus reflexus cum quinque suis laciniis, quicum flosculo ligulato comparatus indicat hujusmodi di flosculum nihil esse nisi *Limbum* quasi *perscissum*. (b) Collum limbi sive corollae propriae. (c) Tria filamenta ab antheris separata. (d) Duo filamenta totidem antheras sustinentia. (e) Stigma simple & stilus. **Fig. 4.** Anthera istius floris magnitudine naturali. **Fig. 5.** Eadem, verum major, denotans figuram ei esse triquetram. **Fig. 6.** Tres antherae, quae lateribus coalitae ostendunt cavitatem, qua stilus continetur. (a) Apices antherarum. (bb) Latera quibus antherae reliquis adhaerent. (c) Filamenta. (d) Basis antherae filamentis adnexa. **Fig. 7.** Quinque antheerarum circumscriptio lateribus separatis, unde pateat modus, quo latera se mutuo in cylindrum conjungunt. (a) Antherae. (b) Filamenta. (cccc) Apices sive denticuli antherarum. **Fig. 8.** Omnes proxima figura expositae antherae in cylindrum coaliate, aucta magnitudine. (a) Cylindrus antherarum. (b) Stigma. (c) Filamenta (dd) Collum corollae. **Fig. 9.** Limbus memorati Silphii per medium scissus, ut situs antherarum & stili naturali appareat magnitudine. (a) Limbi lacinia. (b) Initium tubi. (c) Decursus stili. (d) Antherae longitudine limbi. **Fig. 10.** Ejusdem flosculus hermaphroditus figura perfecta. (a) Limbus infundibiliformis. (b) Tubus. (c) Stigma. **Fig. 11.** Pistillum modo dicti flosculi e *Disco*, magnitudine naturali. (a) Germen. (b) Stilus. (c) Stigma simplex. **Fig. 12.** Stigma cum parte *stili* aucta, ad indicandum, ubi a stilo distinguatur. (a) Stigma hirsutum simplex. (b) Pars stili. **Fig. 13.** Pistillum flosculi feminei e *Radio* ejusdem floris Silphii. (a) Germen cordatum planum. (b) Stilus. (c) Stigma bifidum laciniis longissimis. **Fig. 14.** Pistillum floris hermaphroditi monopetali Helianthii. *Roy. Prod. pag.* 180. Stigmata revoluto. (a) Germen triquetrum. (b) Stilus. (c) Stigma revolutum. **Fig. 15.** Germen a stilo & calyculo proprio abruptum. **Fig. 16.** Calyculus proprius dyphyllus a germine separatus. **Fig. 17.** Idem germini adhaerens. (a) Germen. (b) Calyculus. **Fig. 18.** Pistillum flosculi hermaphroditi e *Disco* filiforme. Stigmate obtuso Centaureae 33. *Roy. Prod. pag.* 133. (a) Germen cum calyculo vel perianthio proprio. (b) Stilus filiformis incurvus. (c) Stigma obtusum bifidum. **Fig. 19**. Pistillum flosculi hermaphroditi e *Disco* stigmate rhomboideo Asteris 7. *Roy. Prod. pag.* 167. magnitudine naturali. **Fig. 20.** Idem ac prius sed majus. (a) Germen. (b) Stilus. (c) Stigma rhomboideum revolutioni paratum. (d) Pappus. **Fig. 21.** Germen longissimum Echinopi 1. *Roy. Prod. pag.* 144. pericarpio suo separatum, cum ipsius pericarpii ambitu. (a) Germen. (b) Receptaculum stili. (c) Stilus. (d) Circumscriptio pericarpii proprii. **Fig. 22.** Germen cum corona sua papposa Floris hermaphroditi Onopordi *Roy. Prod. pag.* 143. (a) Germen. (b) Corona pappola nondum extensa. **Fig. 23.** Stilus filiformis coronatus, a stigmare simplici separabilis. (a) Stilus. (b) Stigma simplex. (c) Finis stili, ubi inferitur stigma sive ejus corona vel stigma coronatum. **Fig. 24.** Stigma Echinopi compressum erectum, quod Tab. 3. fig 18. apparet clausum, naturali magnitudine. (a) Pars stili. (b) Stigma compressum bifidum. **Fig. 25.** Idem lentis ope visum. (a) Pars stili. (b) Stigma hirsutum polline obsitum. **Fig. 26.** Stilus cum stigmate Helianthi 1. *Roy. Prod. pag.* 180. flosculi hermaphroditi e *Disco*, ab antherarum cylindro separatus, ut ejus longitudo cum antheris comparari possit. (a) Basis antherae. (b) Stilus. (c) Antherae. (d) Stigma. **Fig. 27.** Antherarum cylindrus ejusdem flosculi explanatus, stylum in medio proponens, quo utriusque conferatur longitudo, naturali magnitudine. **Fig. 28.** Idem, sed explicationis gratia auctus. (a) Basis stili. (b) Stilus longitudine antherarum. (c) Filamenta antherarum. (d) Testiculi sive antherae. (e) Insertio filamentorum. (ff) Limbi lacinia. (gg) Stigma revolutum bipartitum. **Fig. 29.** Partes eaedem, figura & magnitudine graphice delineatae. **Fig. 30.** Majorem harum partium exhibet delineationem. (a) Tria filament antherarum paulum dilatata. (b) Antherae. (c) Tubus floris germini infertus. (d) Stigma revolutum, antherarum cylindro perforato. (e) Vestigia limbi. **Fig. 31.** Superioris pistilli stigma magis etiam auctum, ut liqueat quomodo revolvatur, & quam hirsutum ubique sit, ut pollen ibi adhaereat. (aa) Laciniae revolutae. **Fig. 32.** Tragopogonis flosculi hermaphroditi stigma filiforme laciniis reflex-patentibus. (aa) Stigmata. (b) Pars stili. **Fig. 33.** Iam annotatus flosculus hermaphroditus Helianthi e *Disco*, quo per schema ob oculos ponantur omnes partes, tubulosum flosculum construentes, & quidem per flosculum, tubo brevi. Sic omnia de genitalibus explicate elucent. (a) Germen. (bb) Calyculus proprius dyphyllus deciduus. (c) Tubus floris ei impositus in limbum abiens, per punctula stili decursum notans. (d) Collum corollulae filamenta recipiens e cylindro antherarum. (e) Limbus longitudinaliter scissus & explanatus. (f) Filamenta antherarum, ab iis pendula, & corolla collo inserta. (gg) Antherarum cylindrus. (b) Earum apices ieu denticuli, paulum reflexi. (i) Stigma bifidum. (kk) Istius lacinia hirsute vel serrata. (l) Longitudo pistilli a basi germinis usque ad summitatem stigmatis altius quam antherae non surgens. (m) Longitudo antherarum a collo corollulae usque ad earum apices, qui stigma tangunt. **Fig. 34.** Constructio flosculi hermaphroditi, limbo profunde in quinque lacinias diviso, ex Echinope *Roy Prod. pag.* 144. eodem delineate scopo, quo superior figura, quippe ut aliorum flosculorum configurationem ostendat. (a) Tota flosculi & pistilli longitudo. (b) Particula Disci globosi, cui pericarpium proprium cum germine est insertum. *Conf.* Tab. 7. (c) Stigma bifidum, apertum, compressum. (d) Stilus antherarum cylindrum perforans, cujus rei perspicuitas ut clarior fieret, antherarum filamenta quodammodo sunt dilatata. (e) Antherae cum suis filamentis. (f) Antherae proprie sic dictae, sive testiculi. (g) Filamenta capillaria antherararum magis extensa. (hh) Denticuli Antherum seu apices. (ii) Collum corollae propriae, quo usque laciniae limbi sunt incisae. (kkkk) Lacinia longa limbi revoluta, profunde incisa. (l) Tubus flosculi, in quem desinunt laciniae. (m) Stigma bifidum compressum, summitas pistilli. (n) Pericarpium hirsutum quo germen includitur. (o) Positio germinis. *Conf.* Fig. 21. **Fig. 35.** Tota structura flosculi hermaphroditi ligulari Hypochaeridis 2. *Roy. Prod. pag.* 125. (a) Germen parvum fere ovatum. (bbb) Margo flosculi tubo perscisso, vel limbus in ligulam extensus. (c) Decursus tubi flosculi. (dd) Quinque denticuli truncate, a quinque costis ligulam constituentibus producti. (ee) Stili decursus per filamenta fecundum flosculi figuram parum curvatus. (ff) Filamenta antherarum amplificata, collo ligulae inferta. (gg) Antherarum cylindrus. (h) Earum denticuli. (ii) Stigma filiforme bipartitum laciniis longis revolutis patentibus, quae per lentem examinatae parum ferratas fe oculis offerunt. (k) Decursus totius pistilli. (l) Decursus vel longitudo antherarum. **Fig. 36.** Constructio genitalium in flosculo perfecte tubuloso, seu fistuloso ONOPORDI *Roy. Prod. pag.* 134. eodem modo ac tres proxime antecedente figurae apparens. (a) Germen pentagonum, *coronatum* dictum. (bbbb) Stilus longus filiformis e germine usque ad antherarum cylindrum extensus. (c) Basis stili & tubi floris, ut & papposae coronae. (d) Apex stigmatis simplicis. (eeee) Tubulus floris cum stili decursu. (fffff) Perscissam denotat corolla monopetalam, seu tubum & limbum. (ggggg) Filamenta quinque a collo limbi extracta, & a suis antheris pendula. (h) Cylindrus antherarum paulum explanatus (ii) Denticuli earum sive apices. (kkkk) Laciniae limbi. (l) Limbus ventricosus erectus, explanatus. (m) Corona papposa. (n) Tota longitude pistilli. (o) Antherarum tota longitudo.

Fig. 1.8. Tabula taken from Cassini's (1826) *Opuscules Phytologiques*, vol. 1.

[Left part of figure 1.8:] **1**. Style et stigmate de Fleur hermaphrodite. **2**. Face intérieure d'une branche du style. **3**. Face extérieure. **4**. Style et stigmate de fleur femelle. **5**. Style de fleur mâle. **6**. Le même vu par le sommet. **7**. Etamines. **8**. Corolle de fleur hermaphrodite ou mâle. **9**. Ovaire. **10**. Nectaire.

[Right part of figure 1.8:] **1**. Style et stigmate de fleur hermaphoridite. **2**. Face intérieure d'une branche du style. **3**. Face extérieure. **4**. Etamines. **5**. Corolle de fleur hermaphrodite. **6**. Ovaire. **7**. Portion d'une double aigrette vue en dedans, pour rendre manifeste l'aigrette intérieure. **8**. Squamellule barbellée. **9**. Ovaire coupé transversalement. **10**. Ovaire coupé longitudinalement contenant l'ovule, et portent sur son areole apicilaire un plateau ceint d'un anneau duquel naissent les squamellules de l'aigrette, et sur le plateau, la corolla et le nectaire, qui porte luimême le style. **11**. Nectaire.

Fig. 1.10. Tabula taken from Lessing's (1832) *Synopsis Generum Compositarum Earumque Dispositionis Novae Tentamen Monographiis Multarum Capensium Interjectis.*

Explicatio tabulae. **1**. Stylus Floris hermaphroditi in *Carduo nivali* (Trib. Cynaroideae. Subtrib. Cynareae.). **2**. Id. in *Arctotheca repente* (Trib. Ead. Subtrib. Arctotideae.). **3**. Stylus floris masculi in *Hertia crassifolia* (Trib. ead. Subtrib. Othonneae). **4**. Id. in *Tripteride amplexicauli* (Trib. ead. Subtrib. Calenduleae.). **5**. Stylus floris hermaphroditi in *Chaetanthera spathulata* (Trib. Mutisiaceae. Subtrib. Mutisieae.). **6**. Id. in *Seride polymorpha* (Trib. id. Subtrib. Ead.). **7**. Id. in *Vernonia brasiliensi* (Trib. Vernoniaceae. Sbt. Vernonieae.). **8**. Id. in *Liabo Deppeano* (Trib. ead. Subtrib. Liabeae.). **9**. Id. in *Eupatorio altissimo* (Trib. Eupatoriaceae. Subtrib. Eupatorieae.). **10**. Stylus floris masculi in *Nardosmia angulata* (Trib. ead. Subt. Tussilagineae). **11**. Idem in *Tussilagine Farfara* (Trib. et Subtrib. eadem). **12**. Stylus floris hermaphroditi in *Bellio bellidioidi* (Trib. Astereideae. Subtrib. Astereae.). **13**. Stylus floris masculi in *Filagine pygmaea* (Trib. ead. Subtrib. Tarchonantheae.). **14**. Stylus floris hermaphroditi in *Palleni spinosa* (Trib. ead. Subtrib. Buphthalmeae.). **15**. Stylus floris disci in *Schistostephio flabelliformi* (Trib. Senecionideae. Subtrib. Chrysanthemeae.). **16**. Id. in *Brachystephio leucanthemoide* (Trib. ead. Subtrib. Senecioneae.). **17**. Idem in *Lessingia germanorum* (Trib. et Subrib. eadem.). **18**. Id. in *Balduina multiflora* (Trib. ead. Subtrib. Helenieae.). **19**. Idem in *Obeliscaria pinnatifida* (trib. eadem Subtrib. Heliantheae.). **20**. Idem in *Spilantho repente* (Trib. et Subtrib. ead.). **21**. Stylus floris masculi in *Blennospermate chilensi* (Trib. ead. Subtrib. Artemisieae.). **22**. Idem in *Tragocerate Schiedeano* (Trib. ead. Subt. Ambrosieae.). Omnes magis minusve aucti, magnitudine naturali, linea perpendiculari expressa, adposita.

Fig. 1.15. Figures 65(A) and 77(B) taken from Hoffmann's (1890–1894) "Compositae" in: Engler & Prantl's *Die natürlichen Pflanzenfamilien.*

Figure A. Stb., bei **B**, **L**, **M** nur der untere Teil der **A**. mit dem oberen Teil des Stf. in stärkerer Vergrößerung, um den Schwellkörper des Dtf. Zu zeigen. **A**, **B** *Vernonia fasciculate* Michx. **C** *Piptocarpha opaca* (Benth.) Baker. **D** *Eupatorium purpureum* L. **E–G** Pollenkörner von: **E** *Elephantopus scaber* L., **F** *Xanthium macrocarpum* DC, **G** *Helianthus annuus* L. **H–O** Stb. von: **H** *Pluchea odorata* Cass., **J** *Leuceria senecioides* H. A., **K** *Brachyclados lycioides* Gill., **L** *Melampodium divaricatum* (Rich.) DC, **M** *Cineraria lobata* L'Hér., **N** *Spilanthes repens* Michx., **O** *Tricholepis furcata* DC. **P** Bl. Von *Silybum Marianum* (L.) Grtn. Nach Entfernung des Blumenkronensaumes.

Figure B. **A** Kf. Und Bl. Von *Decachaeta Haenkeana* DC. **B–D** Kf., aufgeschlitzte Blkr. und Fr. Nebst Querschnitt von *Piqueria trinervia* Cav. **E–G** *Phania matricarioides* (Less.) Gris., **E** Kf., **F** Bl., **G** die zu einer Bl. Gehörigen Pappusschuppen. **H**, **J** Kf. Und Bl. Von *Ophryosporus Regnellii* Bak. **K** Fr. von *Gymnocoronis spilanthoides* DC. **L–O** *Adenostemma viscosum* Forst., **L** junge, **M** reife Fr. nebst Querschnitt, **N** blühendes, **O** fruchttragendes Kf. (**A** nach Delessert, **H**, **J** nach Baker, Flora Brasiliensis, sonst Original).

Appendix **D**

New names and combinations

Appendix E

Complete list of literature cited*

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Taxon index

Page numbers: *Italics*, name occurs in table; ***bold italics***, photograph or drawing of plant (or parts of plant); **bold**, other image type (map, tree, etc.; names in the trees are not indexed); ⋆, major treatment of taxon. For non-plants see end of the index.

Non-plants