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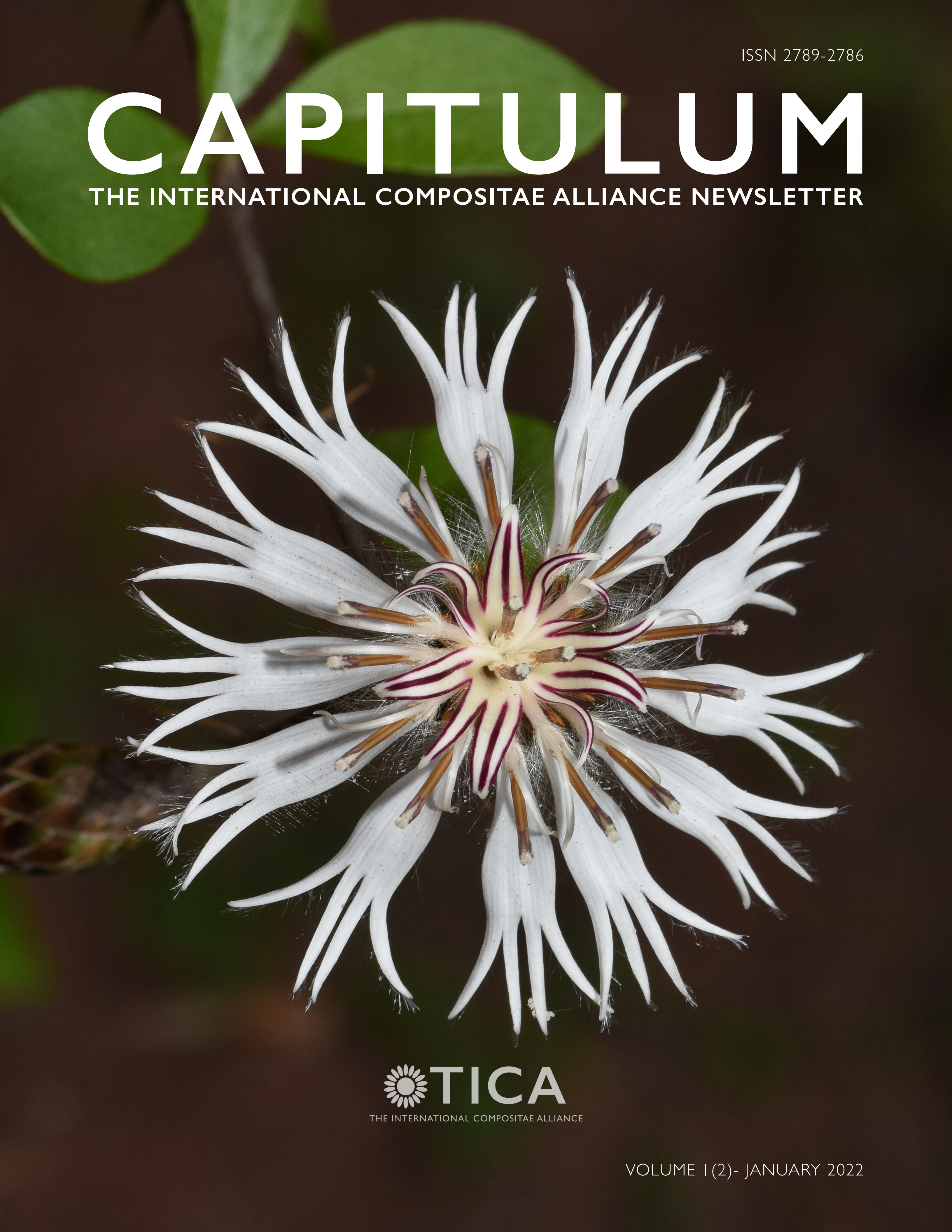
CAPITULUM

THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER



TICA

THE INTERNATIONAL COMPOSITAE ALLIANCE

VOLUME 1(2)- JANUARY 2022

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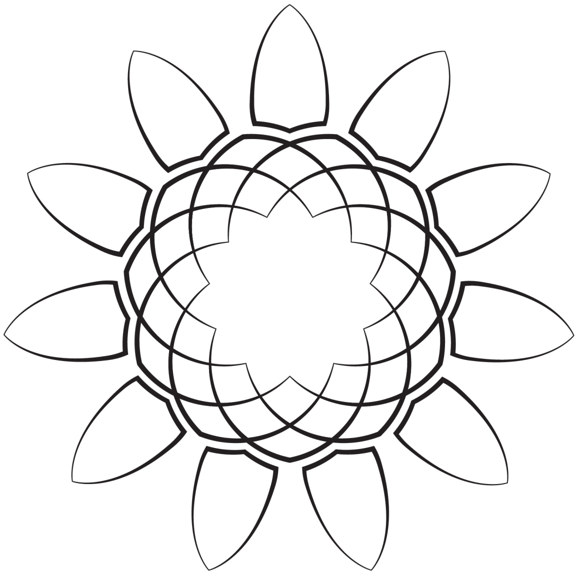

CAPITULUM

For the community & by the community.

TICA

THE INTERNATIONAL COMPOSITAE ALLIANCE

CAPITULUM
THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

CAPITULUM

CAPITULUM is the Newsletter of The International Compositae Alliance and is meant to be a venue for all things Compositae and welcomes all kinds of diversity in both its contributions and contributors. ISSN 2789-2786.

EDITORIAL BOARD

SUBMISSIONS

Manuscripts or photos intended for publication in CAPITULUM are to be submitted at www.compositae.org

A NOTE FROM THE EDITORIAL BOARD

on the new series of the TICA Newsletter

Thank you for joining us in this latest–actually just our second–issue of the reboot of the Compositae Newsletter, CAPITULUM. We made it! Issue 1 was a beautiful compilation of articles and images that we shared via email to The International Compositae Alliance (TICA) list, Twitter, colleagues, friends, and beyond.

In this second round, we've made some changes, notably we welcome six new members to the team of Associate Editors: Ilse Breitweiser (New Zealand), Luis Palazzesi (Argentina), Gisela Sancho (Argentina), Ed Schilling (USA), Alexander Schmidt-Lebuhn (Australia), Alfonso Susanna (Spain).

CAPITULUM now has an ISSN: 2789-2786, and we have made some changes to the way we handle manuscripts with an eye toward setting up an online manuscript submission portal in 2022 (let's see!). In particular, each manuscript in Issue 2 was assigned a Handling/Associate Editor and has been peer reviewed by at least two referees. We believe this will ensure high-quality articles are published in CAPITULUM and encourage a diverse set of submissions and submitters from the community.

In this second issue, we bring to you three 'Head Topics' articles: Alexander Schmidt-Lebuhn shares with us a review of taxonomy and phylogenetics of native Australian Asteraceae in "Daisies Down Under". Next, Ilse Breitwieser and J.M. Ward take us on a journey through the New Zealand indigenous Gnaphalieae, and finally Jennifer Ackerfield describes two new species of alpine thistles from the southern Rocky Mountains–one of which she names in memory of our late friend and colleague Vicki Funk. This issue hosts two articles in 'Brevia' one from Cristina Trujillo, María Victoria Valtierra, and Eduardo Marchesi describing a new record of *Dasyphyllum* (Barnadesieae) from Uruguay and another from Robert McKenzie, Kenneth Oberlander, and Nigel Barker on the *Arctotis* annual clade in a semi-arid region of southern Africa. In 'Handlens', from Robb Eastman-Densem and Peter Pelser we learn about the complexity of New Zealand's *Brachyglottis rotundifolia* species complex (Senecioneae). Curious about the plants of the past? Abigail Moore brings us an exploration of the American West by exploring an herbarium sheet of *Grindelia ciliata* with two specimens, one collected by Thomas Nuttall and the other collected by Samuel Woodhouse about 30 years apart, yet mounted on the same sheet. In this issue's 'Pipet and the Press' Teng Zhang and Paula Elomaa describe methods and approaches for understanding capitulum development using Gerbera hybrida inflorescence meristem as an experimental system. Finally, view the stunning images from four contributors to 'Style': Behnaz Balmaki, Phil Garnock-Jones, Oriane Hidalgo, and Jaume Pellicer.

Once again, we hope you enjoy reading our second issue of CAPITULUM.
Please share the newsletter broadly with friends and colleagues and consider sharing broadly.

J. Mauricio Bonifacino

Ilse Breitwieser
Ilse Breitwieser

Benoit Loeuille

Jennifer Mandel
Jennifer R. Mandel

Abigail J. Moore
Abigail Moore

Erika Moore
Erika R. Moore

Luis Palazzesi

Elizabeth Roeble
Lizzie Roeble

Gisela Sancho

Alexander Schmidt-Lebuhn

Ed Schilling

Alfonso Susanna

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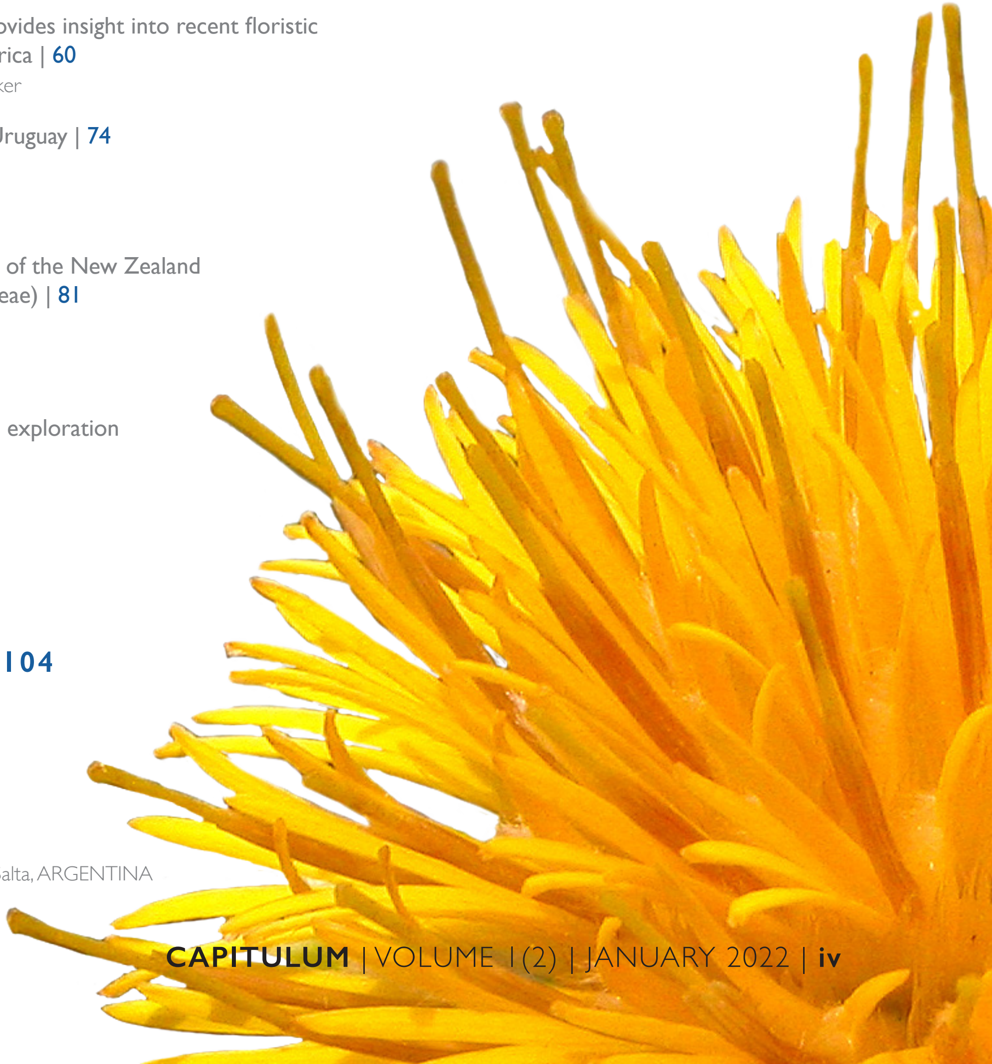

Cover photo: *Barnadesia odorata* Griseb. (Barnadesieae), Salta, ARGENTINA
Photo by M. Bonifacino

Hiding in plain sight:

Two new species of alpine thistles, *Cirsium culebraensis* and *C. funkiae* (Cardueae) from the southern Rocky Mountains (United States)

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ABSTRACT

The circumscription of the *Cirsium eatonii* varietal complex of North American alpine thistles has changed significantly given recent molecular phylogenetic studies demonstrating that the complex was not monophyletic. To improve their taxonomy, all varieties within the *C. eatonii* complex were recognized as distinct species. However, three remaining unique evolutionary lineages corresponded to undescribed phenotypic variation. Two of these lineages from the southern Rocky Mountains in the United States are described and illustrated here as *Cirsium culebraensis* sp. nov. and *Cirsium funkiae* sp. nov. A combination of molecular, morphological, and geographical evidence, as well as, a bit of historical detective work was used to sort out the *C. eatonii* varietal complex taxonomy. A key to the recognized species is provided.

Keywords: *Funk's thistle, Sangre de Cristo Mountains, Culebra Range*

INTRODUCTION

When we think of new species discoveries, we often picture exotic places like the Amazon rainforest, the crater of an extinct volcano, or an underexplored, inaccessible island. However, new species discoveries don't just occur in these locations, but in relatively well-explored regions such as the southern Rocky Mountains (Nazaire & Hufford, 2012; Reznicek & Murray, 2013; Alexander et al., 2015; Wolfe et al., 2021). For some recently speciated groups within these regions, morphological distinction among taxa may be slight, given the short amount of geologic time for differences to accrue. Thus, undescribed species may hide in plain sight, assumed to be species already named to science simply exhibiting morphological variation across their geographic range.

Cirsium Mill. is comprised of approximately 100 species distributed across North America (Keil, 2006). Within *Cirsium*, one of the most difficult species to delimit has been the morphologically polymorphic *C. eatonii* B.L.Rob. ("mountaintop thistle") varietal complex. This complex was treated as seven varieties by Keil (2006) in the treatment for *Flora of North America*: *C. eatonii* var. *clokeyi* (S.F. Blake) D.J. Keil, *C. eatonii* var. *eatonii*, *C. eatonii* var. *eriocephalum* (A. Gray) D.J. Keil, *C. eatonii* var. *hesperium* (Eastw.) D.J. Keil, *C. eatonii* var. *murdockii* S.L. Welsh, *peckii* (L.F. Hend.) D.J. Keil, and *C. eatonii* var. *viperinum* D.J. Keil. The common name "mountaintop thistle" was derived from the distribution of these varieties on mountaintops throughout the southern Rocky Mountains and adjacent Intermountain Region in the United States.

Molecular phylogenetic inferences utilizing both Sanger and hybridization sequencing (Hyb-Seq) data to test the monophyly of this varietal complex demonstrated that *C. eatonii*, as circumscribed by Keil (2006), was polyphyletic. Each variety in turn corresponded to a unique evolutionary lineage exhibiting a distinct phenotype and geographic range (Ackerfield et al., 2020; Siniscalchi & Ackerfield, unpublished data). To resolve this polyphyly, varieties within the *C. eatonii* complex were separated out as distinct species. Previously described *C. clokeyi*

S.F.Blake, *C. murdockii* (S.L.Welsh) Cronquist, *C. peckii* L.F.Hend., and *C. tweedyi* (Rydb.) Petr. were reinstated, and two new combinations were made – *C. harrisonii* (S.L.Welsh) Ackerfield & D.J.Keil and *C. viperinum* (D.J.Keil) Ackerfield & D.J.Keil (Ackerfield et al., 2020; Siniscalchi & Ackerfield, unpublished data).

Not only was *C. eatonii* resolved as polyphyletic, but *C. eatonii* var. *eriocephalum* and *C. eatonii* var. *hesperium* were resolved as polyphyletic as well (Ackerfield et al., 2020; Siniscalchi & Ackerfield, unpublished data). Three unique evolutionary lineages were recovered for *C. eatonii* var. *eriocephalum*, each corresponding to a unique phenotype (pale purple style branches with heads in a nodding cluster, yellow style branches with heads in a nodding cluster, and whitish-pink style branches with heads in a spiciform arrangement; Figure 1). Plants exhibiting heads arranged in a spiciform arrangement were endemic to the La Sal Mountains of Utah, and clearly represented an undescribed species. We are currently working with members of the Ute Mountain Ute tribe to find a name for this species that acknowledges their legacy of use of these mountains. Thus, this new species will be described in a future manuscript.

The binomial *Cirsium scopulorum* Cockerell then had to be applied to one of the remaining two lineages, as this was the only species previously described corresponding to *C. eatonii* var. *eriocephalum*. Before this could be done, two confounding lines of evidence had to be evaluated. The original description of *C. scopulorum* by Gray (1863) stated that the corolla color was yellow. However, the most accurate location on one type specimen indicated that the collection made by Charles Parry was within the geographic boundary of the pale purple phenotype. Upon closer inspection of additional type specimens, a handwritten note was found which stated "This is the high alpine nodding-headed yellow-flowered thistle but too young. Perhaps Parry got in better shape." This indicated that the type specimens were actually too immature to see the corolla color, and that Gray used the information in this handwritten note for the original description. Therefore, the best line of evidence was the geographic location of Parry's type specimen. The name *C. scopulorum* was thus applied to the pale purple phenotype, leaving the yellow phenotype as another undescribed species.

The final new species came from *C. eatonii* var. *hesperium*, also resolved as polyphyletic. While one lineage from the San Juan Mountains of southwestern Colorado corresponded to the already named *C. hesperium* Rydb., the other lineage represented undescribed variation (Figure 2).

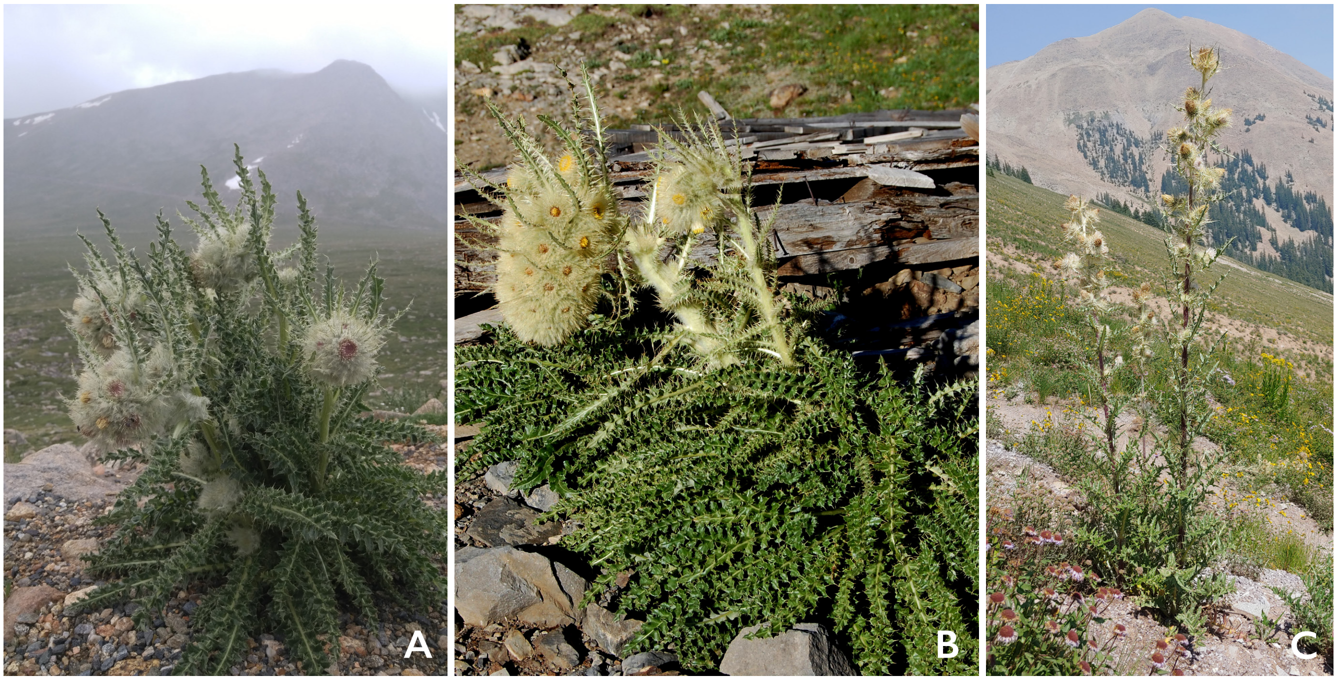

Figure 1. A. *Cirsium scopulorum* (Greene) Cockerell. **B.** *Cirsium funkiae* Ackerf. **C.** *Cirsium* **sp. nov.** 'La Sal Mts.' Photos: J. Ackerfield.

MATERIALS AND METHODS

Herbarium loans were obtained from CS, KHD, RM, and UNM. Additionally, herbarium specimens from COLO and HU were viewed online (acronyms from Thiers, 2020). All taxonomic measurements were taken from pressed specimens. iNaturalist observations were used to document the style tip color, which fades on herbarium specimens, of each species across their geographic range.

Species delimitation was performed based on morphology and phylogenetic inference. The general lineage species concept (De Queiroz, 2007) was used, which defines a species as a unique evolutionary lineage. This concept was used in conjunction with the phylogenetic concept (Nixon & Wheeler, 1990) in which a species is the smallest system of related populations with a uniquely diagnosable set of morphological character states.

RESULTS AND DISCUSSION

Style branch coloration (white, yellow, pink, or purple), corolla color, and position of the heads (erect or nodding) are the best characters to delimit among the alpine thistles of the southern Rocky Mountains (Table 1). While often labeled as corolla color on herbarium labels, the more visible coloration of the disk flowers is actually that of the anther tube and style branches. Corollas are often

Figure 2. A. *Cirsium hesperium* (Eastw.) Petr. **B.** *Cirsium culebraensis* Ackerf. Photos: J. Ackerfield.

The mountain thistle

Cirsium scopulorum, or mountain thistle, was long thought to be the only species of thistle occurring in the alpine tundra. Molecular, morphological, and geographical evidence now support the recognition of five species of thistles in the alpine tundra of the southern Rocky Mountains. Two of these species are new to science - *Cirsium culebraensis* and *C. funkiae*.

Circium scopulorum, near the top of Mt. Evans, Clear Creek Co., Colorado. Elevation 4175 m a.s.l.
Photo by J. Ackerfield

Table 1. Comparison of the alpine thistles of the southern Rocky Mountains.

TAXA	CHARACTERS			
	Style branch color	**Corolla color**	**Anther tube color**	**Head arrangements**
C. culebraensis	Pale pink	Pale pink	Pale pink with darker pink stripes	Erect terminal cluster, sometimes a few axillary
C. funkiae	Yellow	Pale yellow or brownish (in age)	White or pale yellow with brown stripes	Nodding, terminal cluster
C. griseum var. **osterhoutii**	White	White	White with purple stripes	Erect, terminal cluster or axillary
C. hesperium	Purple	Lavender	Pale purple with purple stripes	Erect, terminal cluster, sometimes a few axillary
C. scopulorum	White, pale pink, or pale purple	Pale pink or pale purple	Pale pink to pale purple with purple stripes	Nodding to spreading, sometimes a few axillary, or axillary and densely packed along the stem nearly to the ground

not readily visible, as they barely surpass the involucral bracts. The style branches are the most readily visible feature of the flowers, as they extend well past the involucral bracts and corollas. The flowers of *Cirsium* often fade to brown shortly after collecting, and thus coloration is often not discernable from herbarium specimens. Therefore, iNaturalist observations were valuable in correlating style tip coloration with geographic distribution, as each observation is a photograph of an individual plant at that exact locality. iNaturalist observations of the plants in situ were also useful at documenting the range of each phenotype, and determining if phenotypes overlapped in geographic range.

Taxonomic confusion surrounding the delimitation of the alpine thistles in the southern Rocky Mountains is the result of several factors. First, *C. scopulorum*, *C. eatonii*, and *C. hesperium* were the only alpine thistles included in dichotomous keys for Colorado thistles (Harrington, 1954; Weber & Wittmann, 2011). However, *C. eatonii* was erroneously reported as present in the southern Rocky Mountains (Weber & Wittmann, 2011). Subsequently, specimens corresponding to *C. griseum* var. *osterhoutii* were identified as *C. eatonii*, or sometimes *C. hesperium* or *C. scopulorum* simply because of their alpine habitat. Because *C. griseum* var. *osterhoutii* can co-occur with *C. funkiae* or *C. scopulorum*, this confused the taxonomy even further (Figure 3). The majority of the alpine thistle specimens assigned to *C. eatonii* from the southern Rocky Mountains have since been annotated to *C. griseum* var. *osterhoutii* by the author.

Second, the original description for the alpine thistle *Cirsium scopulorum* erroneously stated that the corolla color was yellow, despite the lack of visible, mature corollas on type specimens (Gray, 1863). Third, in the dichotomous key to *Cirsium* for Colorado, Weber & Wittmann (2011) inadvertently switched the distribution of the two phenotypes of *C. scopulorum*, stating that the yellow phenotype was distributed in the northern counties and the pale purple phenotype in the southern counties. Fourth, most alpine thistles eventually turn brown on herbarium sheets, making accurate determination of the corolla color nearly impossible. Lastly, undescribed phenotypic variation (i.e., *C. culebraensis*) confused the taxonomy further, with no clear binomial to assign to these specimens. The taxonomic treatment here resolves these issues by describing two new species – *C. culebraensis* and *C. funkiae*. A key to the alpine thistles of the southern Rocky Mountains is provided. A comparison of the morphology of the alpine thistles is also presented for additional taxonomic clarification (Figure 4).

The Culebra thistle

The Culebra thistle is endemic to the Culebra Range of the Sangre de Cristo Mountains in southern Colorado and northern New Mexico, where it rises tall against a landscape of tiny alpine plants. Type specimens were made from this very thistle by the author and fellow botanist Lori Brummer.

Circium culebraensis, Trinchera Peak, Huerfano County, Colorado, elevation ca. 3960 m a.s.l.
Photo by J. Ackerfield

KEY TO THE ALPINE THISTLES OF THE SOUTHERN ROCKY MOUNTAINS

1. Heads in nodding to spreading arrays
  2. Style branches yellow.......... **Cirsium funkiae**
  2. Style branches white, pale pink, or pale purple.......... **Cirsium scopulorum**
1. Heads in erect arrays
    3. Corollas white; style branches white to pale pink; stems usually dark maroon.......... **Cirsium griseum** var. **osterhoutii**
    3. Corollas pale pink to purple; style branches purple, pale pink, or white; stems green or dark maroon
      4. Style branches purple.......... **Cirsium hesperium**
      4. Style branches pale pink .... **Cirsium culebraensis**

TAXONOMIC TREATMENT

Cirsium culebraensis Ackerf., **sp. nov.**

Diagnosis: similar to *Cirsium scopulorum*, but differs in that the heads are in an erect, terminal cluster versus in a nodding, terminal cluster.

TYPE: U.S.A., Colorado: Huerfano Co.: Culebra Range, below summit of Trinchera Peak ca. 50 miles west of Trinidad, 12,800 ft., 8 Aug 2018, *J.Ackerfield 6540* (holotype: KHD!)

Perennial, caulescent herbs, stems 1–few, erect, 1.5–5.2 dm tall, simple or sparingly branched, tomentose. **Leaves** oblong to narrowly elliptic, undulate and pinnatifid with 8–15 pairs of lobes, or occasionally flat and nearly entire but spinose, 8.5–17 cm long and 1–3 cm wide (including lobes), midribs 5–10 mm wide, lobes 3–11 mm long and 3–6 mm apart, main spines 3–6 mm long, adaxial surfaces glabrate to villous or arachnoid-tomentose, abaxial surfaces tomentose, cauline leaves well-distributed, sessile and sometimes clasping but not decurrent on the stem, distal closely subtending heads. **Heads** 5–25, sessile or shortly-pedunculate, in a dense, erect, terminal cluster, closely subtended by reduced leaves, or often also with heads arising from the proximal 2/3 of leaf axils on the stem. **Involucres** green, broadly ovoid to broadly campanulate, 1.7–2.5 × 1.7–3.1 cm, densely tomentose. Phyllaries in 4–5 series, subequal, with entire margins, tapering to spines 6–10 mm long, apices straight. **Corollas** pale pink, 15–20 mm long, tubes 5–8 mm long, throats 4–6 mm long, lobes 3–5 mm long. **Anther** tubes pale pink with darker pink stripes, 5–7 mm long. **Style** branches pale pink, 3–4 mm long, conspicuously exserted beyond the corolla lobes. **Cypselae** dark brown, 4–6 mm long. **Pappus** 10–15 mm long. (Figure 5).

Phenology: This species flowers from late July to mid-August, and fruits from mid-August to early September.

Distribution: This species is endemic to the Culebra Range of the Sangre de Cristo Mountains, where it is primarily found on mountaintops above tree line (Figure 3). The Culebra Range runs north to south, with the northern limit at La Veta Pass in Colorado and the southern limit at Costilla Creek just south of Big Costilla Peak in New Mexico.

Habitat: This species occurs in high elevation spruce-fir forests and alpine tundra. It is primarily found on rocky scree slopes, in boulder fields, and alpine meadows. This species occurs principally with *Picea engelmannii* Parry ex Engelm. var. *engelmannii*, *Polemonium pulcherrimum* Hook. subsp. *delicatum* (Rydb.) Brand, and *Carex rossii* F.Boott at its lower elevational limits. Above treeline, in the alpine tundra, this species occurs primarily with *Geum rossii* (R.Br.) Ser. var. *turbinatum* (Rydb.) C.L.Hitchc., *Trifolium attenuatum* Greene, *Salix nivalis* Hook., and *Dasiphora fruticosa* (L.) Rydb.

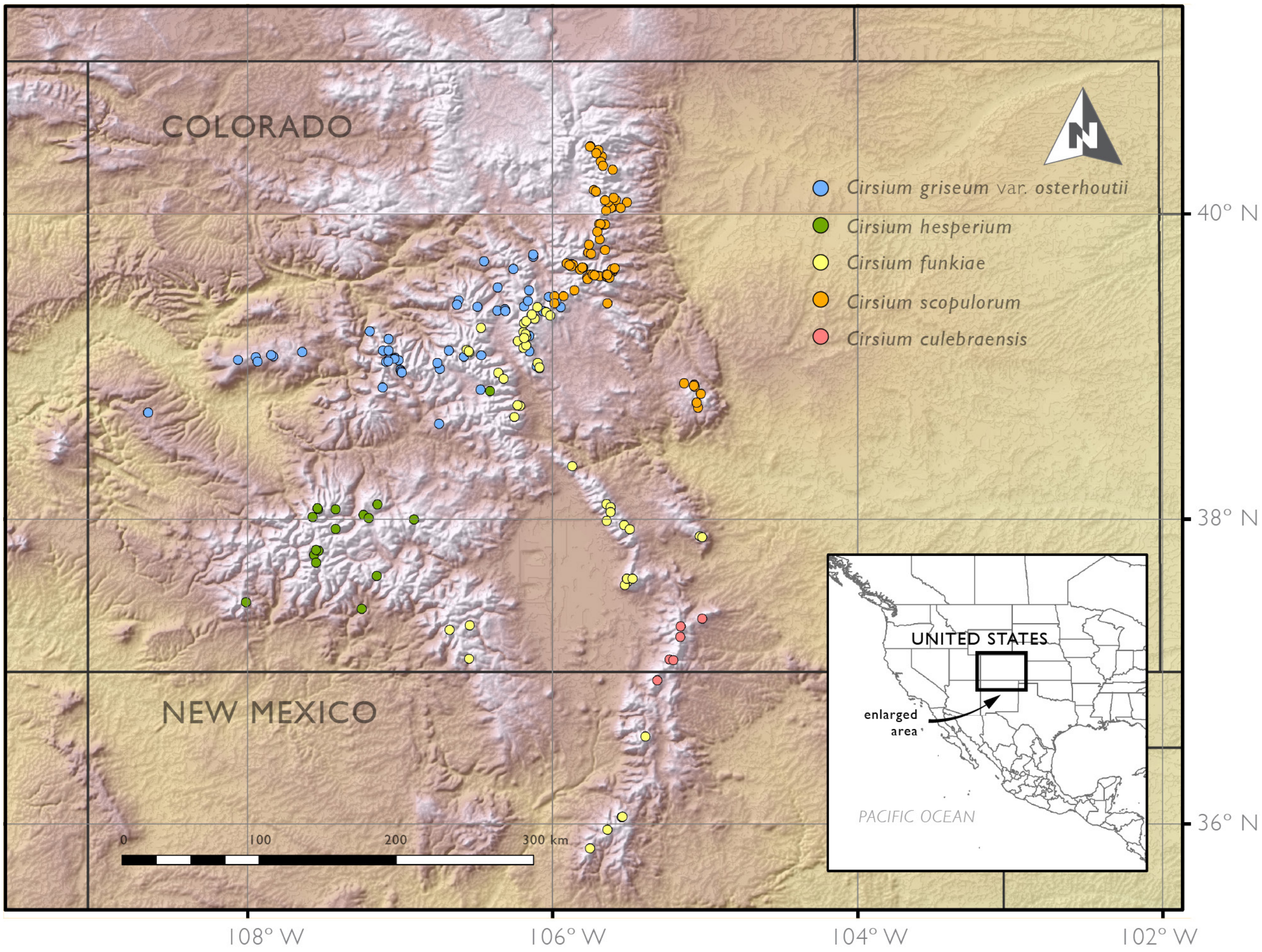

Figure 3. Distribution map of the alpine thistle species in the southern Rocky Mountains.

Conservation: This species is found primarily in the alpine zone on difficult to access mountaintops. In conjunction with inaccessibility, it occurs primarily on federally-owned land, both of which offer it protection. Although it occupies a narrow geographic range, populations appear to be stable.

Etymology: *Cirsium culebraensis* is named for the Culebra Range, to which it is endemic. The Culebra Range is part of the Sangre de Cristo Mountains.

Additional specimens examined: United States. Colorado: Costilla Co.: Upper slope of saddle at head of N Fk Whiskey Ck, Culebra Range, 16 Aug 1987, *B.Neely 4673* (CS); Costilla Co.: Culebra Range 40 air mi W of Trinidad, 7 Aug 2014, *T.Hogan 5424* (COLO); Huerfano Co.: Below summit of Trinchera Peak, 8 Aug 2018, *J.Ackerfield 6545* (CS); Huerfano Co.: Below summit of Trinchera Peak, approx. 2 mi SW of Bear Lake Campground, 8 Aug 2018, *J.Ackerfield 6551* (CS); Huerfano Co.: Approx. 3000 ft. west of Cordova Pass off of FR415, 7 Aug 2018, *J.Ackerfield 6529* (CS). **New Mexico:** Taos Co.: Sangre de Cristo Mts, 4.9 air mi SW of Angostura, 31 Jul 2013, *R.Sivinski & R.Culp 8592* (UNM); Taos Co.: Vermejo Park Ranch, Culebra Range, on E-facing slope 1.75 air mi NE of Big Costilla Peak, 25 Jul 2009, *B.Legler 11537* (RM).

Cirsium funkiae Ackerf., sp. nov.

Diagnosis: similar to *Cirsium scopulorum* in having heads in a nodding, terminal array, but differs in that the style branches are yellow instead of white, pale pink, or pale purple.

TYPE: U.S.A., Colorado: Park Co., Pike National Forest, near the base of Mt. Sherman near the beginning of the trailhead to the summit, ca 13 mi. west of Fairplay, scattered on scree slopes, 12,100 ft., 2 Sep 2020, *J.Ackerfield* et al. 8003 (holotype: KHD!).

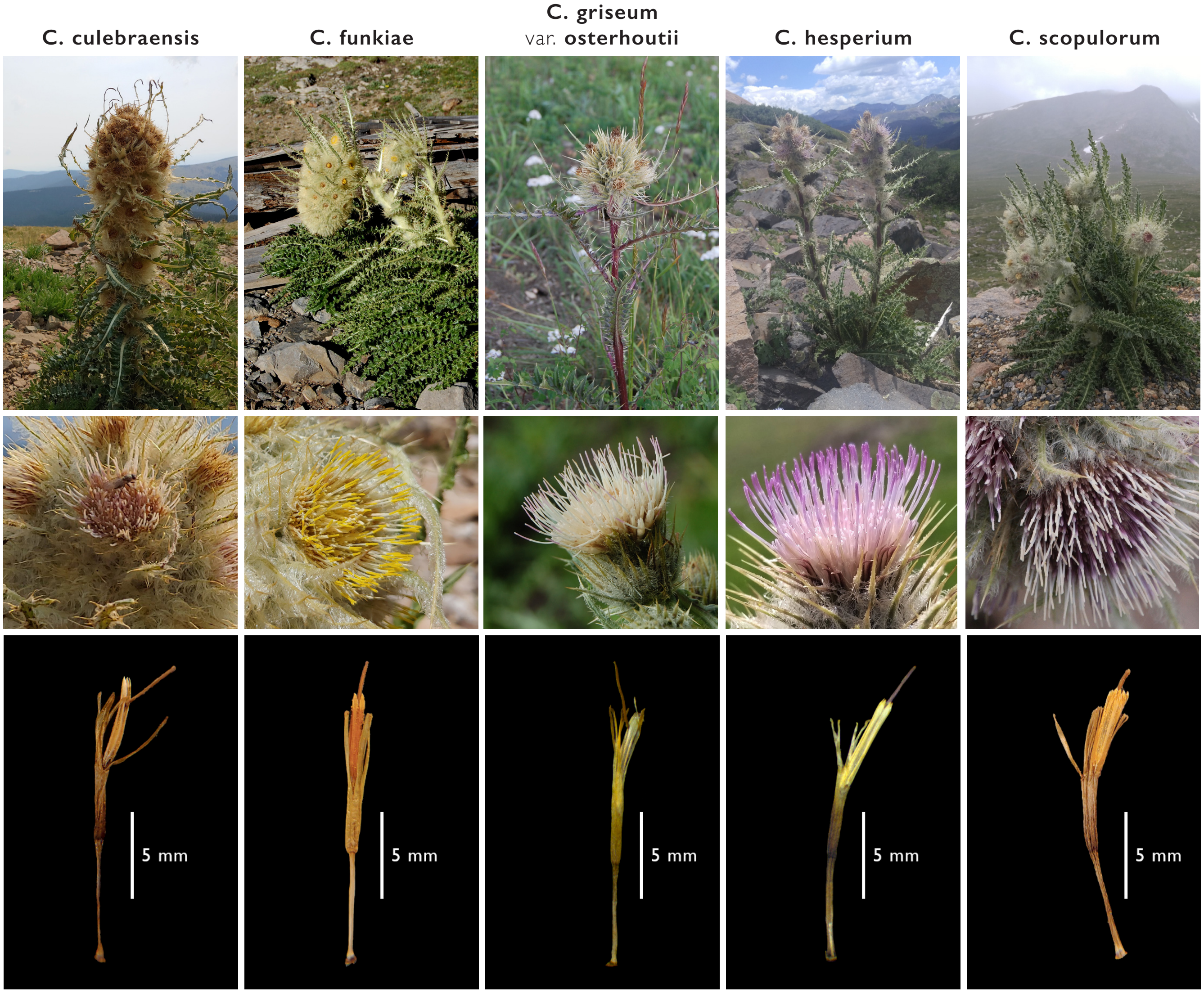

Figure 4. Morphological comparison of the alpine thistles of the southern Rocky Mountains. From top to bottom: Overall plant, close up of one head, one individual disk floret (ovary and pappus removed). Photos: J. Ackerfield.

Perennial, caulescent herbs, stems 1–few, erect, 2–7 (–12) dm tall, simple or sparingly branched, tomentose. **Leaves** oblong to narrowly elliptic, undulate, pinnatifid with 8–18 pairs of lobes, 8–25 cm long and 1.5–3.5 cm wide (including lobes), midribs 5–18 mm wide, lobes 7–11 mm long and 3–10 mm apart, main spines 3–11 mm long, adaxial surfaces glabrate to villous or arachnoid-tomentose, abaxial surfaces tomentose, cauline leaves well-distributed, sessile and sometimes clasping but not decurrent on the stem, distal closely subtending heads. **Heads** 9–35, sessile or shortly-pedunculate, in a dense, nodding, terminal cluster, closely subtended by reduced leaves, usually also with heads arising from leaf axils on the stem. **Involucres** green, broadly ovoid to broadly campanulate, 1.5–3.5 × 1.7–3 cm, densely tomentose. Phyllaries in 4–5 series, subequal, with entire margins, tapering to spines 5–17 mm long, apices straight. **Corollas** pale yellow, or brownish in age, 15–19 mm long, tubes 6–8 mm long, throats 4–5 mm long, lobes 4–5 mm long. **Anther** tubes white or pale yellow with brown stripes, 5–7 mm long. **Style** branches yellow, 2–4 mm long, conspicuously exserted beyond the corolla lobes. **Cypselae** dark brown or grayish-brown, 4–6 mm long. **Pappus** 10–17 mm long. (Figure 6).

Phenology: Flowers from mid-July to late August, and fruits from mid-August to early September.

Distribution: This species is found on mountaintops in the Sangre de Cristo, Mosquito, and Tenmile Ranges. Its northernmost distribution is south of Breckenridge, CO near Hoosier Pass and its southernmost distribution is near Santa Fe, NM (Figure 3).

Habitat: Occurs in high elevation spruce-fir forests and alpine tundra. It is primarily found on rocky scree slopes, in boulder fields, and alpine meadows. When found at its lower elevational limits, this species is found with *Picea engelmannii* Parry ex Engelm. var. *engelmannii*, *Potentilla pulcherrima* Lehm., *Bistorta bistortoides* (Pursh) Small, and *Sibbaldia procumbens* L. When found in rocky alpine slopes and meadows, this species occurs with *Cirsium griseum* (Rydb.) K.Schum. var. *osterhoutii* (Rydb.) Ackerfield & D.J.Keil, *Carex scopulorum* Holm, *Castilleja miniata* Douglas ex Hook., *Castilleja occidentalis* Torr., *Senecio atratus* Greene, *Geum rossii* (R.Br.) Ser. var. *turbinatum* (Rydb.) C.L.Hitchc., *Trifolium dasyphyllum* Torr. & A.Gray, *Claytonia megarhiza* (A.Gray) Parry ex S.Watson, *Polemonium confertum* A.Gray, and *Senecio fremontii* Torr. & A.Gray var. *blitoides* (Greene) Cronq. When found on scree slopes at its highest elevation limits, this is often the only species found, or occasionally it grows in association with *Senecio soldanella* A.Gray.

Conservation: This species is found primarily in the alpine zone on difficult to access mountaintops. In conjunction with inaccessibility, it occurs primarily on federally-owned land, both of which offer it protection. Populations appear to be stable. However, when encountered by members of the public with preconceived notions that all thistles are invasive weeds, it is often pulled up and left along the side of trails.

Etymology: *Cirsium funkiae* is named in honor of my mentor, Dr. Vicki Funk, Senior Curator of Compositae at the Smithsonian Institution, who provided invaluable leadership and was a world leader in Compositae research. Although the correct common name is technically "Funk's thistle," I like to think of this thistle as "the funky thistle." *Cirsium funkiae*, with its dense mass of woolly, nodding heads, is funky indeed.

Additional specimens examined: United States. Colorado: Costilla Co.: Wet Mts, S of Purgatorie Peak on Peak 11929, 20 Aug 1999, *B.Elliott 11357* (CS); Fremont Co.: Wet Mts, around Bushnell Lakes, 31 Jul 1998, *B.Elliott 4691* (CS); Park Co.: E slope of Wheeler Mt. above the summit of Hoosier Pass, 9 Sep 1942, *J.Ewan 14689* (COLO); Park Co.: Mosquito Range, about 1/8 mi SW of Peak 12615, 2 Aug 1998, *R.Orthner 704* (KHD); Park Co.: Horseshoe cirque, 4 Aug 1987, *P.Bichier & N.Shelton sn* (KHD); Park Co.: Mt Sherman, 9 Aug 2015, *J.Ackerfield 15-127* (CS); Summit Co.: State Hwy 9, 0.7 mi N of Hoosier Pass, 2 Aug 1972, *S.Nelson 1091* (CS); Summit Co.: Blue Lakes SW of Breckenridge, 21 Jul 2007, *J.Ackerfield 2958* (CS); Teller Co.: Vicinity of Gillett, 30 Jul 1967, *D.Denham 1719* (CS). **New Mexico:** Mora Co.: Santa Fe National Forest and vicinity, Sangre de Cristo Mountains, Pecos Wilderness, 3 air mi NE of Pecos Falls, 10 Aug 2004, *B.Reif 10339* (RM); Santa Fe Co.: Lake Peak, 12 Aug 1926, *Bro.G.Arsene & Bro.A.Benedict 17248* (UNM).

Note: This species has been hiding in plain sight under the binomial *C. scopulorum* because of an erroneous original species description which stated that the corolla color was yellow (Gray, 1863). However, examination of the type material collected by Charles Parry and Elijah Hall helped sort out the taxonomy. In particular, a brief history of Parry's collection trips helped elucidate which phenotype (yellow or pale purple) to designate as *C. scopulorum*.

Charles Parry first visited the mountains of central Colorado in 1861, collecting alpine and subalpine plants for Asa Gray from what he labeled the "headwaters of Clear Creek and the alpine ridges lying east of Middle Park, Colorado Territory." Parry returned to Colorado in 1862 with Hall and Harbour. The collection locality listed for all specimens from the 1862 expedition is much less informative: "Colorado Territory, lat. 39°–41°, alpine and subalpine." However, through Parry's correspondences to Gray, more accurate descriptions of their 1862 collection destinations are recorded (Parry & Gray, 1861). Thanks to Parry's notes, we can infer that the 1862 expedition began at the upper waters of the Platte near South Park (Park Co.). From there, the party returned to Denver by way of Pike's Peak (El Paso Co.), ascending the mountain peak on July 1st, 1862. From Denver, the expedition returned to Parry's original collection site at the headwaters of Clear Creek (Clear Creek Co.) to determine the altitude of Torrey's, Gray's, and Engelmann peaks. They finished the expedition in the vicinity of Long's Peak (Boulder Co.). These collections were made within the geographic boundary of the pale purple phenotype.

The designation of the corolla color as yellow by Gray (1863) came from a single, hand-written note affixed to one of Hall & Harbour's specimens [U.S.A., CO Territory: Rocky Mountain Flora Lat 39°–41°, Hall & Harbour s.n. (HU)], which described the high alpine thistle as "dense, many headed yellow flowered species but too young perhaps Parry got it in [a] better state." This note indicates that these plants were in fact too immature to see any corollas, much less to determine that they were yellow. Although Gray (1863: 69) described *Cirsium eriocephalum* (name invalid, referencing *C. scopulorum*) as having "heads of yellow flowers […] crowded into a capitate cluster as large as a man's fist," the only record from Parry or Hall of the yellow corolla color is Hall's handwritten note on an immature specimen lacking visible corollas. The corolla color was therefore erroneously reported as yellow by Hall and then incorporated into the original species description by Gray. Therefore, the best line of evidence to support the pale purple phenotype as *C. scopulorum* is geographic range,

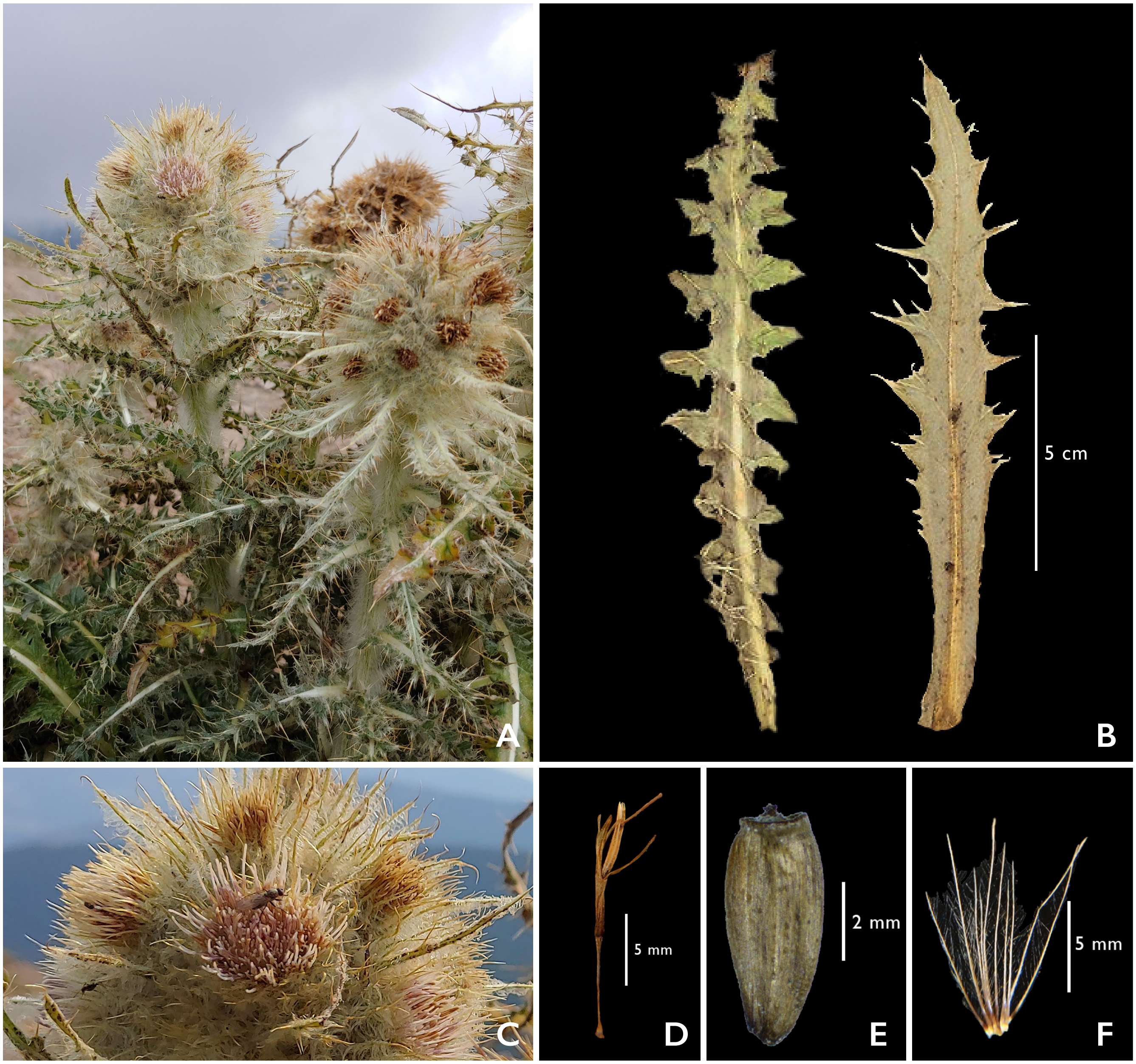

Figure 5. *Cirsium culebraensis* Ackerf. **A.** Habit. **B.** Leaves. **C.** Close-up of heads. **D.** Disk floret (ovary and pappus removed). **E.** Cypsela. **F.** Pappus fragment. Photos: J. Ackerfield.

Vicki's thistle

In September 2020, the author was joined by representatives from the U.S. Forest Service, Denver Botanic Gardens, and Colorado State University to make type collections of *Cirsium funkiae* on Mt. Sherman. Pictured here is CSU Master's student, Austin Rosén, holding one of the type specimens.

Circium funkiae, Mt. Sherman, Park County, Colorado, elevation ca. 4000 m a.s.l.
Photo by J. Ackerfield

Funky thistle

Vicki Funk had a special tune she sang when collecting thistles because of sharp spines - "*Ooh Eeh Ooh Ah Aah Ting Tang Walla Walla Bing Bang.*" I will never forget the first time I met Vicki, after describing my thistle research, she broke into this song almost immediately! Vicki was a not only a leader in Compositae research, but also my mentor and friend. I can think of no better way to commemorate her memory than by naming the funkiest of all new thistles, *Cirsium* funkiae, in her honor. I hope that anyone who ever collects this thistle for scientific research also sings Vicki's little thistle song too.

Close up of *Circium funkiae*, Mt. Sherman, Park County, Colorado, ca. 4000 m a.s.l.
Photo by J. Ackerfield

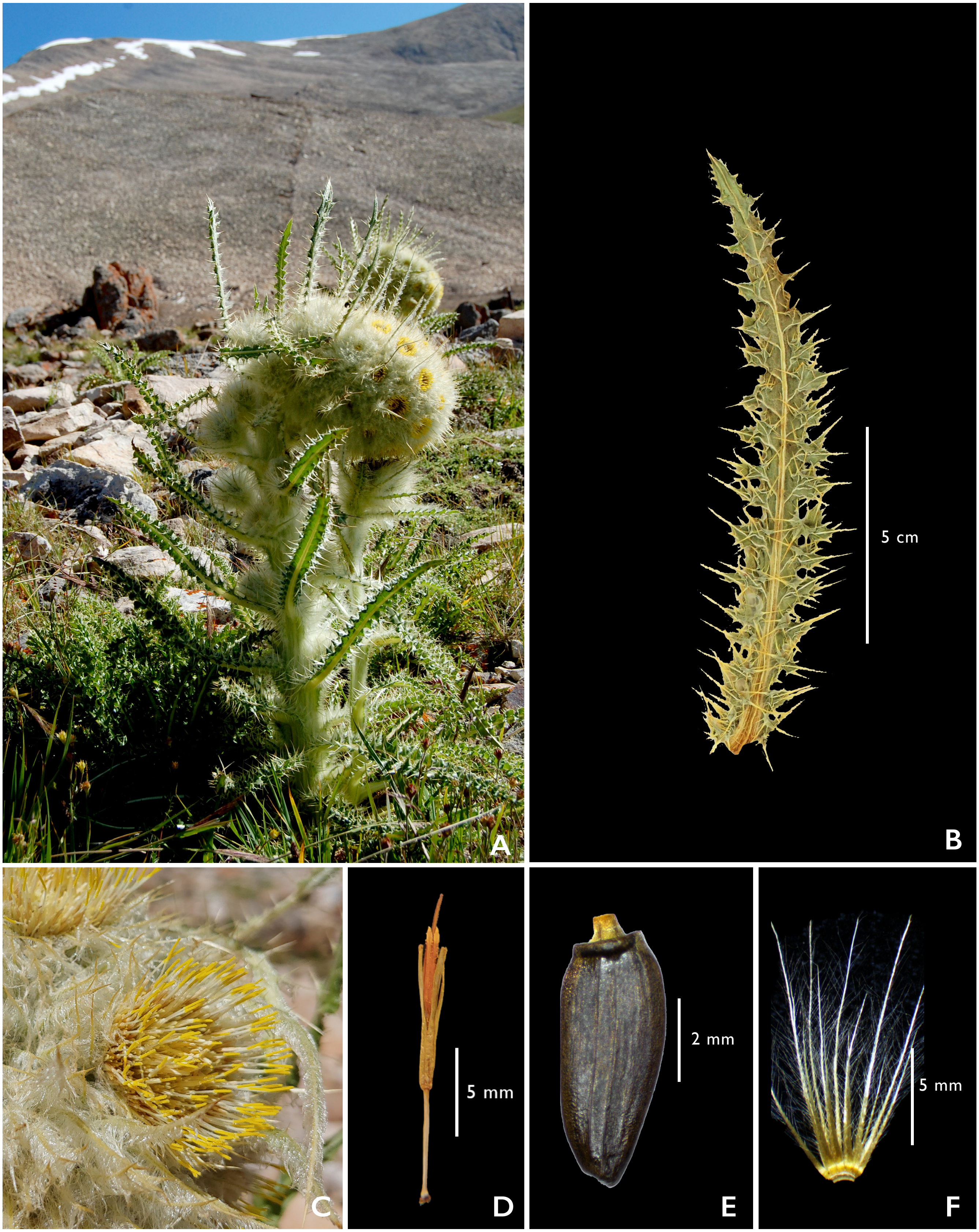

Figure 6. *Cirsium funkiae* Ackerf. **A.** Habit. **B.** Leaf. **C.** Close-up of head. **D.** Disk floret (ovary and pappus removed). **E.** Cypsela. **F.** Pappus fragment. Photos: J. Ackerfield.

as all of Parry's and Hall & Harbour's collections were made within the geographic boundary of this phenotype (Figure 3).

It has been noted by the author that American pika (*Ochotona princeps*) forage on *C. funkiae*, and are often seen running around with bundles of thistle leaves in their mouths during August and September. Additionally, the author has noted that *C. funkiae* is frequently visited by bumble bees (*Bombus* sp.), which also overnight for warmth within the densely tomentose heads.

ACKNOWLEDGEMENTS

I thank Christina Alba, Richie Hum, Alissa Iverson, Sheila Lamb, Steve Olson, Austin Rosén, and Jedediah Smith for joining me to collect type specimens of *C. funkiae* on Mt. Sherman. I also thank Lori Brummer for joining me to collect type specimens of *C. culebraensis* on Trinchera Peak. Lastly, I thank Anthony Meluso for making the distribution map.

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Diversity in New Zealand Gnaphalieae

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ABSTRACT

New Zealand indigenous Gnaphalieae are examined for endemism, ecological and morphological diversity, hybridism and taxonomic difficulty. The *Raoulia* alliance, an almost endemic clade, is shown to be remarkably diverse in morphology but with some interconnections within this diversity. Similarities between *Leucogenes* and *Leontopodium*, *Anaphalioides* and *Anaphalis*, *Raoulia* and *Mniodes*, and *Ewartiothamnus* and *Ewartia* are hypothesized to be due to the independent acquisition of remarkably similar morphological adaptations.

Keywords: convergent evolution, endemism, hybridism, morphology, *Raoulia* alliance

OVERVIEW

Compositae/Asteraceae tribe Gnaphalieae Cass. ex Lecoq & Juill. comprises about 2,100 species in 178 genera (Smissen et al., 2020), of which 65 species in 11 genera are indigenous to New Zealand (Schönberger et al., 2020). Only species that have been formally described are included in this number and in the following account. Many species await description, particularly in *Craspedia* G.Forst. and *Raoulia* Hook.f. The New Zealand Gnaphalieae flora is noteworthy for its degree of endemism, ecological and morphological diversity, propensity for hybridization and taxonomic intractability.

The New Zealand seed plant flora as a whole has a remarkable degree of endemism, with 82% of its species not occurring elsewhere (Breitwieser et al., 2012). Gnaphalieae exceed even this figure, with 56 of the 65 species endemic (Schönberger et al., 2020). Four genera are endemic (*Ewartiothamnus* Anderb., *Leucogenes* Beauverd, *Rachelia* J.M.Ward & Breitw., and *Raoulia*), and this number is expected to rise when current revision work is published.

A wide range of ecological tolerance is apparent in New Zealand Gnaphalieae, with species found from seashore to mountain top and from bog to semi-desert. They inhabit coastal sands, braided river flood-plains, low tussock grasslands, rocky cliffs, scrub, forest margins, wet banks, arid grasslands, tall tussock grasslands, alpine rock faces, herbfield, fellfield, alpine bogs, snow hollows and mobile screes.

They are morphologically diverse, with forms ranging from tall shrubs (e.g., *Ozothamnus* R.Br.) through smaller shrubs (whipcord *Helichrysum* Mill., Figure 1), cushion shrubs (pulvinate *Raoulia*, Figure 2), and one liane (*Helichrysum dimorphum* Cockayne), to upright, decumbent or prostrate, often woody-based perennial herbs (e.g., *Ewartiothamnus*) and perennial mat-forming (mat-forming *Raoulia*, Figure 3) and rosette herbs (e.g., *Euchiton* Cass.), with or without stolons. Leaves range in length from less than 2 mm to more than 200 mm and may be petiolate, sessile, or with the lower part broad but non-photosynthetic and partly sheathing the stem. One species, *Helichrysum dimorphum*, even has two morphologically and anatomically different leaf types

Mountains Gandalf!

The country where Tolkien characters came to life harbors amazing scenary and otherworldy daisies. This blanket bog near the remote Lake Monk in Fiordland National Park is the habitat of an undescribed *Craspedia.*

Lake Monk in Fiordland National Park, South Island
Photo by Rainer Vogt

Figure 1. The small shrub *Helichrysum coralloides* (Hook.f.) Benth. & Hook.f. has an unusual whipcord growth form; Molesworth, South Island. Photo: R.W. Vogt.

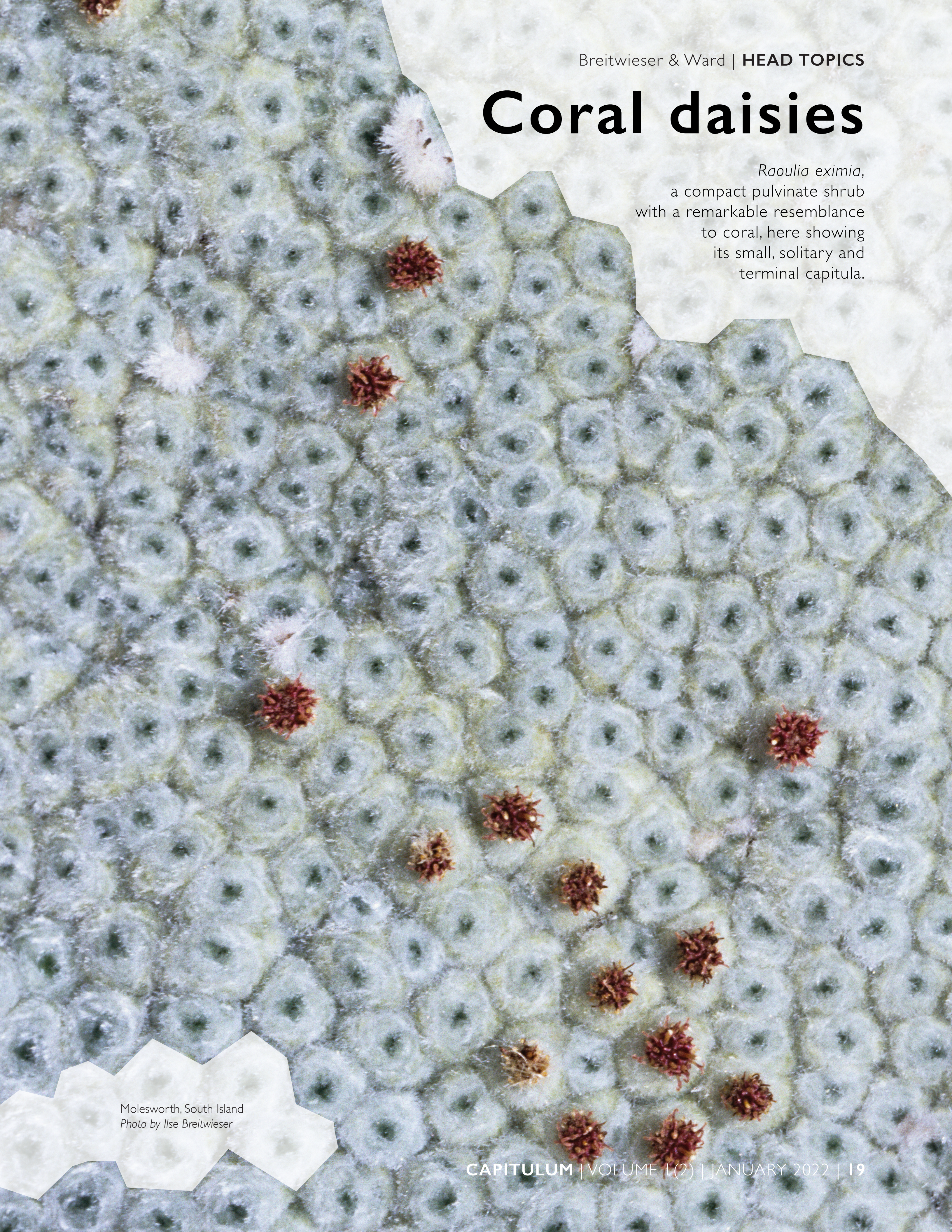
alternating in bands up the stem. Capitula are borne in lax to dense panicles (*Ewartiothamnus*, Figure 4A), in lax [e.g., *Anaphalioides* (Benth.) Kirp., Figure 4B] to very dense corymbs (*Leucogenes*, Figure 4C), in loose glomerules [*Helichrysum lanceolatum* (Buchanan) Kirk] or in densely glomerular secondary heads (*Craspedia*, Figure 5); frequently they are solitary, and then they may be terminal (e.g., *Raoulia*, Figure 3C) or lateral and sessile or scapose, or sessile at flowering and scapose at fruiting. Capitula range from homogamous to almost entirely female. Corollas may be white, yellow, red, greenish or colourless, opaque or translucent. Pappus is variable, ranging from a few broad, persistent hairs in a ring to several hundred very fine caducous hairs in several series. Inner involucral bracts may be shorter than the florets or more than twice their length, and range in colour from white through cream to yellow, and from pale translucent brown to almost black. Fruits vary in size, shape, epidermal cell configuration and twin hair type.

Interspecific hybrids are common in New Zealand (Cockayne & Allan, 1934; Connor, 1985), possibly reflecting the youth of much of the flora and the disturbed nature of the landscape, so the frequency of such hybrids in Gnaphalieae is not particularly surprising. More surprising and noteworthy are the hybrids that occur sporadically in the wild between species in different genera of Gnaphalieae (Allan, 1939, 1961; Ward, 1997).

Asteraceae in general and Gnaphalieae in particular are renowned for being taxonomically difficult. In New Zealand Gnaphalieae taxonomic problems occur at several levels. In *Craspedia* and *Ozothamnus* R.Br., for example, generic delimitation is clear but species delimitation is problematic, whereas

Coral daisies

Raoulia eximia,
a compact pulvinate shrub
with a remarkable resemblance
to coral, here showing
its small, solitary and
terminal capitula.



Molesworth, South Island
Photo by Ilse Breitwieser

Figure 2. Cushion shrub, *Raoulia rubra*, Round Lake, Kahurangi National Park, South Island. **A.** Habit. **B.** Close up of heads. Photos: K.A. Ford.

in *Raoulia*, species are clear-cut but the genus has defied satisfactory delimitation for over 150 years. A group of genera, including *Raoulia*, *Leucogenes*, *Anaphalioides*, *Ewartiothamnus*, *Rachelia*, and those species not yet transferred from *Helichrysum*, exhibits reticulate character distribution, in which one species may show features characteristic of several different genera. One result of this has been a great deal of horizontal reshuffling, with several species having been assigned at different times to three or four different genera.

SUBTRIBES AND CLADES OF GNAPHALIEAE

In view of their degree of morphological diversity it is perhaps to be expected that the indigenous New Zealand Gnaphalieae will be taxonomically diverse. This appears to be borne out by the comprehensive classification of Gnaphalieae (Anderberg, 1991, 1994), in which they were distributed through four of the five subtribes (the fifth being almost endemic to Africa). However, based on recent advances in our understanding of their phylogenetics and evolution, a revised subtribal classification (Smissen et al., 2020) showed that, with the exception of *Pseudognaphalium* Kirp., all New Zealand Gnaphalieae belong to the "Australasian clade" within subtribe Gnaphaliinae Dumort. Schmidt-Lebuhn and Bovill's (2021) study of Australian Gnaphalieae, which included only those New Zealand genera also occurring in Australia, placed *Craspedia* in their "Angianthus clade", *Ozothamnus* in their "Cassinia clade", and *Euchiton* Cass. and *Argyrotegium* J.M.Ward & Breitw. in their "Euchiton clade", all falling within their "Australian clade".

The remaining six New Zealand genera (*Anaphalioides*, *Ewartiothamnus*, *Leucogenes*, *Rachelia*, *Raoulia*, and the species not yet transferred from *Helichrysum*) comprise the Raoulia alliance (e.g., Smissen et al., 2006). With 42 currently recognized species, the Raoulia alliance is endemic to New Zealand except for two species of *Anaphalioides* that are endemic to New Guinea. It has also been referred to as the New Zealand endemic clade (e.g. Breitwieser et al., 1999; Smissen et al., 2004). Data from natural and artificial hybridization suggest a close relationship among *Anaphalioides*, *Ewartiothamnus*, *Leucogenes*, *Raoulia*,

Vegetable Sheep

Some of the cushion species of *Raoulia* look, from the distance, like woolly sheep and have misled botanists and farmers alike.

Mt Hutt, South Island
Photo by Ilse Breitwieser

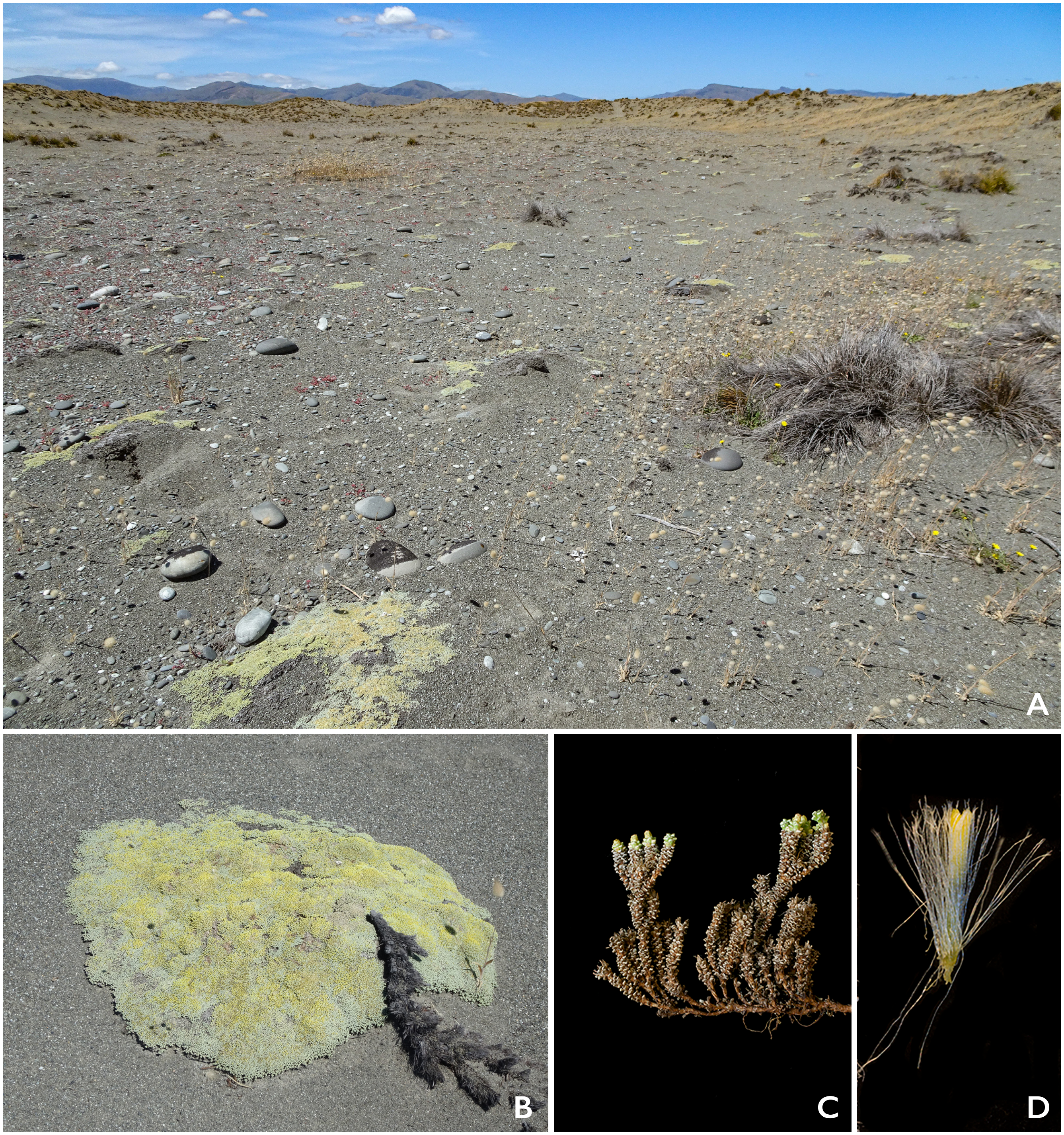


Figure 3. Mat-forming *Raoulia australis* Hook.f. ex Raoul at Kaitōrete Spit, near Christchurch, South Island. **A.** Habitat. **B.** Habit. **C.** Close up of branches, notice long and short shoots. **D.** Floret. Photos: A-B, R.W. Vogt; C-D, K.A. Ford.

and the species not yet transferred from *Helichrysum*. This is supported by morphological, anatomical, palynological and molecular data, which also support the inclusion of *Rachelia*. An ITS sequence analysis of a selection of Australasian Gnaphalieae (Breitwieser et al., 1999) retrieved a strongly supported clade comprising these six genera.

INTERGENERIC HYBRIDS IN THE RAOULIA ALLIANCE

Crosses between species in different genera are well known in the Raoulia alliance (e.g., Allan, 1961), but only some are well documented. Generally, they occur as isolated individuals, occasionally as very

Figure 4. A. *Ewartiothamnus sinclairii* Anderb. has capitula in lax to dense panicles; it is found only in Molesworth, South Island **B.** *Anaphalioides trinervis* (G.Forst.) Anderb. has a lax corymb; Arthur's Pass National Park, South Island. **C.** *Leucogenes grandiceps* (Hook.f.) Beauverd has a dense corymb; it grows here in a rock face in Molesworth, South Island. Photos: A-B, R.W. Vogt; C, J.D. Lovis.

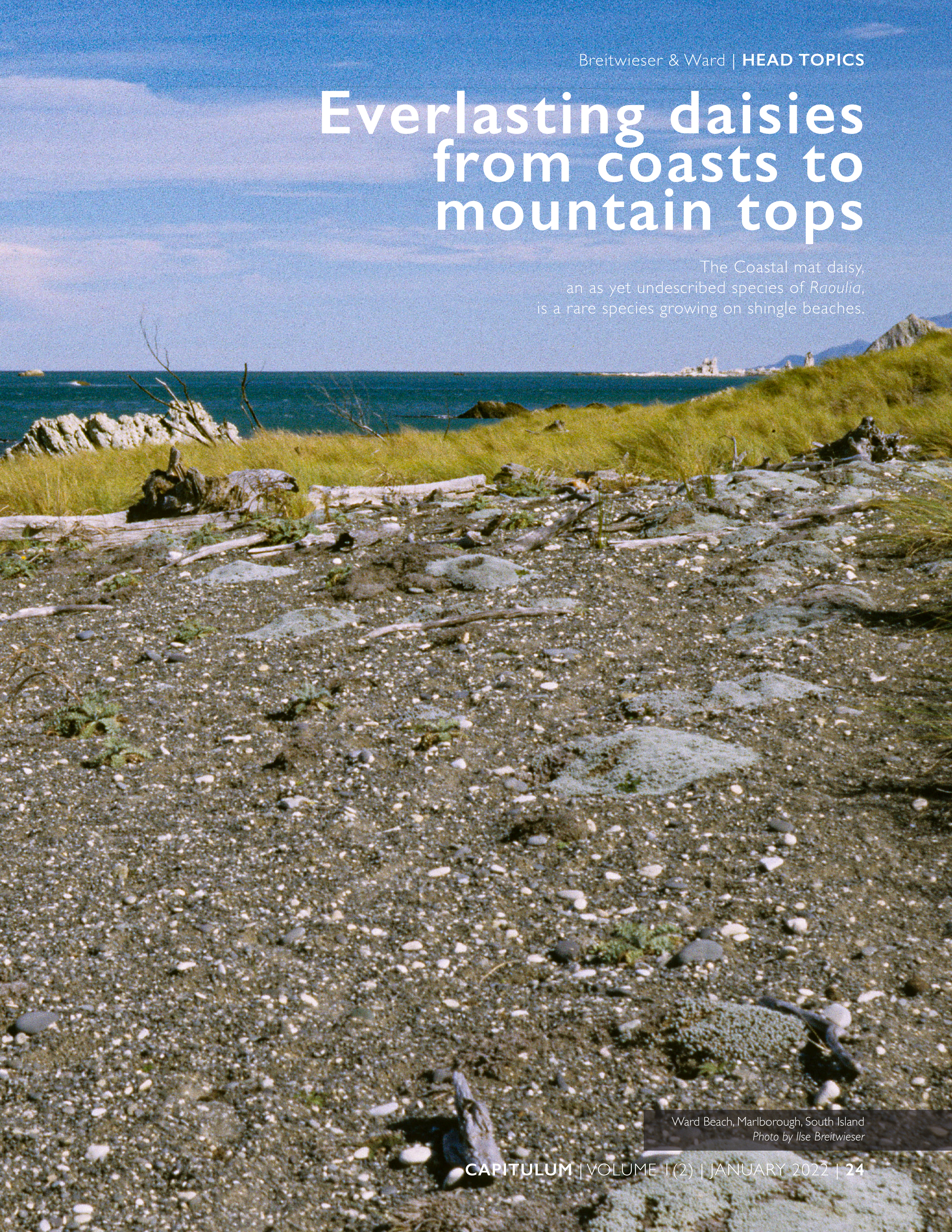
small populations, intermediate in form between the putative parents (Figure 6A) and usually in close proximity to one or both (Figure 6B). Within the Raoulia alliance five of the six genera are linked by wild hybrids to at least two of the other genera. The exception is *Rachelia*, which is monotypic, with a very limited distribution and a specialized alpine habitat on fine scree containing argillite. It does not grow in proximity to any other Gnaphalieae except *Raoulia bryoides* Hook.f., a cushion shrub that is adapted to a disparate alpine habitat on rock outcrops. Survival of offspring is rare even for these species, so would be very unlikely for hybrids.

Detailed study of hybrids between *Anaphalioides bellidioides* (G.Forst.) Glenny and *Ewartiothamnus sinclairii* (Hook.f.) Anderb. (McKenzie et al., 2004, 2008) has demonstrated fertility in the F1 generation and successful production of plants from seed of wild and artificial hybrids, with evidence of back-crossing to *A. bellidioides* and possible advanced-generation hybrids. By far the most commonly reported generic combination is between *Leucogenes* and the pulvinate shrub species of *Raoulia* subg. *Psychrophyton* Beauverd (e.g. Allan, 1939, 1961). This may be due in part to the ease of recognizing hybrids between two such morphologically different genera. There is no doubt the hybrids are common in the wild and found in most geographically feasible species combinations. Experimental crosses by McKenzie (2001) generally followed the wild hybrid pattern, except that the autogamous genus *Euchiton* was crossed successfully with *Anaphalioides*, *Ewartiothamnus*, *Helichrysum*, *Leucogenes* and *Raoulia* (but not *Ozothamnus* or *Pseudognaphalium*). Attempted crosses between *Leucogenes* and the similar looking but distantly related Eurasian *Leontopodium* were unsuccessful.

More recently we used DNA sequencing to confirm intergeneric hybridization between *Helichrysum lanceolatum* and *Anaphalioides bellidioides* (Smissen et al., 2007). Using DNA fingerprinting we found some evidence of reduced seed set in hybrids. Two wild back-crosses to *H. lanceolatum* were identified using AFLP profiles. Subsequent generations have been produced in the glasshouse, and some come close to recovering the morphology of *H. lanceolatum* (Smissen, unpubl.). However, F1 hybrids were far more common than second and later generation hybrids in nature, and introgression between the parental populations was not detected. Glasshouse-grown backcrosses to *A. bellidioides* show marked morphological variation, as would be expected in recombinant generations descended from a cross between two morphologically distinct species.

Everlasting daisies from coasts to mountain tops

The Coastal mat daisy,
an as yet undescribed species of *Raoulia*,
is a rare species growing on shingle beaches.



Ward Beach, Marlborough, South Island
Photo by Ilse Breitwieser

Figure 5. *Craspedia lanata* (Hook. f.) Allan from the Pisa Range, South Island. A. Habit. B. Close up of densely glomerular secondary head. Photos: R.W. Vogt.

With the help of analyses of nuclear rDNA ITS sequences and plastid *trn*K intron, we also confirmed that wild intergeneric hybrids occur between *Argyrotegium mackayi* (Buchanan) J.M.Ward & Breitw. and *Leucogenes leontopodium* (Hook.f.) Beauverd (Smissen et al., 2015). This is the only known instance of wild hybrids between species inside and outside the Raoulia alliance.

MORPHOLOGICAL DIVERSITY AND EVOLUTION OF THE RAOULIA ALLIANCE

The Raoulia alliance embraces most of the remarkable morphological and ecological variation described above for New Zealand Gnaphalieae, apart from conventional shrubs and rosette herbs. A close relationship among taxa with such diverse morphology may seem unlikely, but some connections between very different forms can be demonstrated. The distinctive condensed corymb of *Leucogenes* (Figure 7A), with its ring of showy, white-tomentose bracts, found elsewhere in the tribe only in *Leontopodium* (Pers.) R.Br. *ex* Cass., is very different from the small, solitary, terminal capitula nested among the uppermost leaves of a pulvinate *Raoulia* (Figure 7B). Yet a possible linking form can be seen in *Rachelia* (Figure 7C), in which the capitula are terminal and lateral in the axils of the uppermost leaves. These leaves are large, white-tomentose and very close-set, giving the appearance of a rosette. It would require only minor morphological adjustments to convert this to the inflorescence of a *Leucogenes*. Alternatively, loss of lateral capitula would result in the solitary, sessile, terminal capitulum of *Raoulia*. Isolated plants with solitary capitula, but otherwise conforming in all aspects to other plants in the population, have been observed at least twice in *Leucogenes* (Figure 7C), demonstrating that this transition is developmentally feasible.

The leaves of the whipcord species of *Helichrysum* (Figure 8 A-B) are scale-like, imbricate, appressed and abaxially glabrous, very different from the spreading, densely tomentose leaves found in other genera. However, the whipcord species are heteroblastic and their juvenile leaves are spreading and densely tomentose (Figure 8C).

Braided rivers

New Zealand's South Island is a braided river hot-spot. The distinctive flora of these vast braided river floodplains includes a range of everlasting daisies.

Waimakariri River, South Island
Photo by Rainer Vogt

Figure 6. Intergeneric hybrid between *Raoulia* and *Leucogenes* at Mt Hutt, South Island. **A.** *Raoulia exima* surrounded by *Leucogenes grandiceps* with one plant of *Leucogenes* growing in the *Raoulia* cushion. **B.** Close up of putative hybrid. Photos: R.W.Vogt.

Figure 7. A. The distinctive condensed corymb of *Leucogenes*. **B.** Inflorescence of *Rachelia*, characterized by capitula that are terminal and lateral in the axils of the uppermost leaves. **C.** *Leucogenes* showing a solitary capitulum. Photos: A, C: R.W. Vogt; B: I. Breitwieser.

Hybrids are a well-documented source of intermediate and novel characters. We have shown (Smissen et al., 2004) that chloroplast lineages in the Raoulia alliance do not correspond to taxonomic units, with groups suggested by analysis of morphological characters, or with groups indicated by nuclear rDNA ITS sequences. This suggests complex inter-relationships among extant species and past reticulation among diverging populations. Hybridization may have played a significant role in producing the present-day diversity seen in the Raoulia alliance (see Smissen et al., 2011), as well as the reticulate character distribution that makes it so taxonomically intractable. The Raoulia alliance has radiated into a wide array of forms to colonize the myriad new habitats formed by Pliocene/Pleistocene mountain building and glacial/interglacial climate cycles (e.g., Breitwieser et al., 1999; Smissen et al., 2004).

GENERIC PARALLELISMS WITHIN GNAPHALIEAE

Evidence from hybridization and analyses from sequences of nrDNA spacers, cpDNA and low-copy nuclear markers support the existence of a morphologically and ecologically diverse mainly New Zealand lineage, the Raoulia alliance (Breitwieser et al., 1999; Smissen et al., 2011), and do not support Anderberg's (1991) classification based on phylogenetic analyses of morphological data and the purported close relationship between *Leucogenes* and *Leontopodium*, *Anaphalioides* and *Anaphalis* DC., or the cushion-forming species of *Raoulia* and other Gnaphalieae such as *Mniodes* (A.Gray) Cuatrec.; nor do they support the pairing of *Ewartiothamnus* with the Australian genus *Ewartia* Beauverd. This is surprising, because, with the possible exception of

Aotearoa Edelweiss

The common name of *Leucogenes* refers to the similarity to the European edelweiss. This similarity is hypothesized to be due to the independent acquisition of remarkably similar morphological adaptations.

Leucogenes grandiceps, Mt Hutt, South Island
Photo by Rainer Vogt

Leucogenes and *Leontopodium*, which have not been compared in detail, these pairs of genera show much more than superficial similarity. *Ewartiothamnus* and *Ewartia* (Ward, 1993), as well as *Anaphalioides* and *Anaphalis* (Breitwieser & Ward, 2003), show high levels of overall similarity. *Raoulia* and *Mniodes* have not been fully compared reproductively, although it is known that *Raoulia* is gynomonoecious to functionally monoecious and *Mniodes* is dioecious. However, the habit (Figure 9) and the unusual leaves of *Raoulia eximia* Hook. f. and *Mniodes andina* (A.Gray) Cautrec. are almost identical down to the smallest detail. This leads one to speculate how many cases exist where a true genetic relationship has been obscured by the independent acquisition of such remarkably similar adaptations.

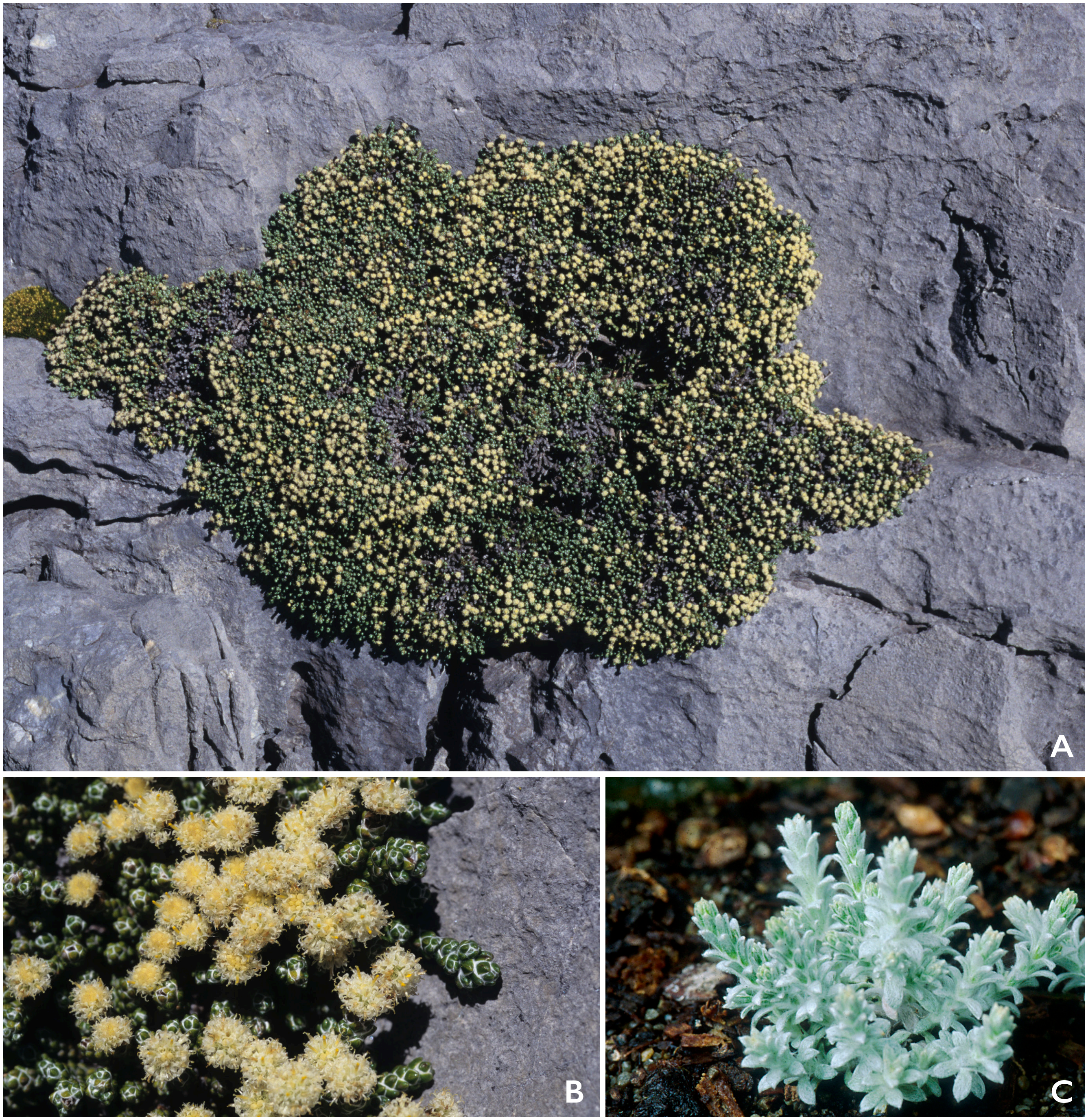


Figure 8. A. Adult form of *Helichrysum intermedium* G. Simpson has scale-like, imbricate, appressed and abaxially glabrous leaves **B.** Close up of heads and leaves. **C.** Juvenile form showing leaves spreading and densely tomentose. Photos: A-B: R.W. Vogt; C: J.M. Ward).

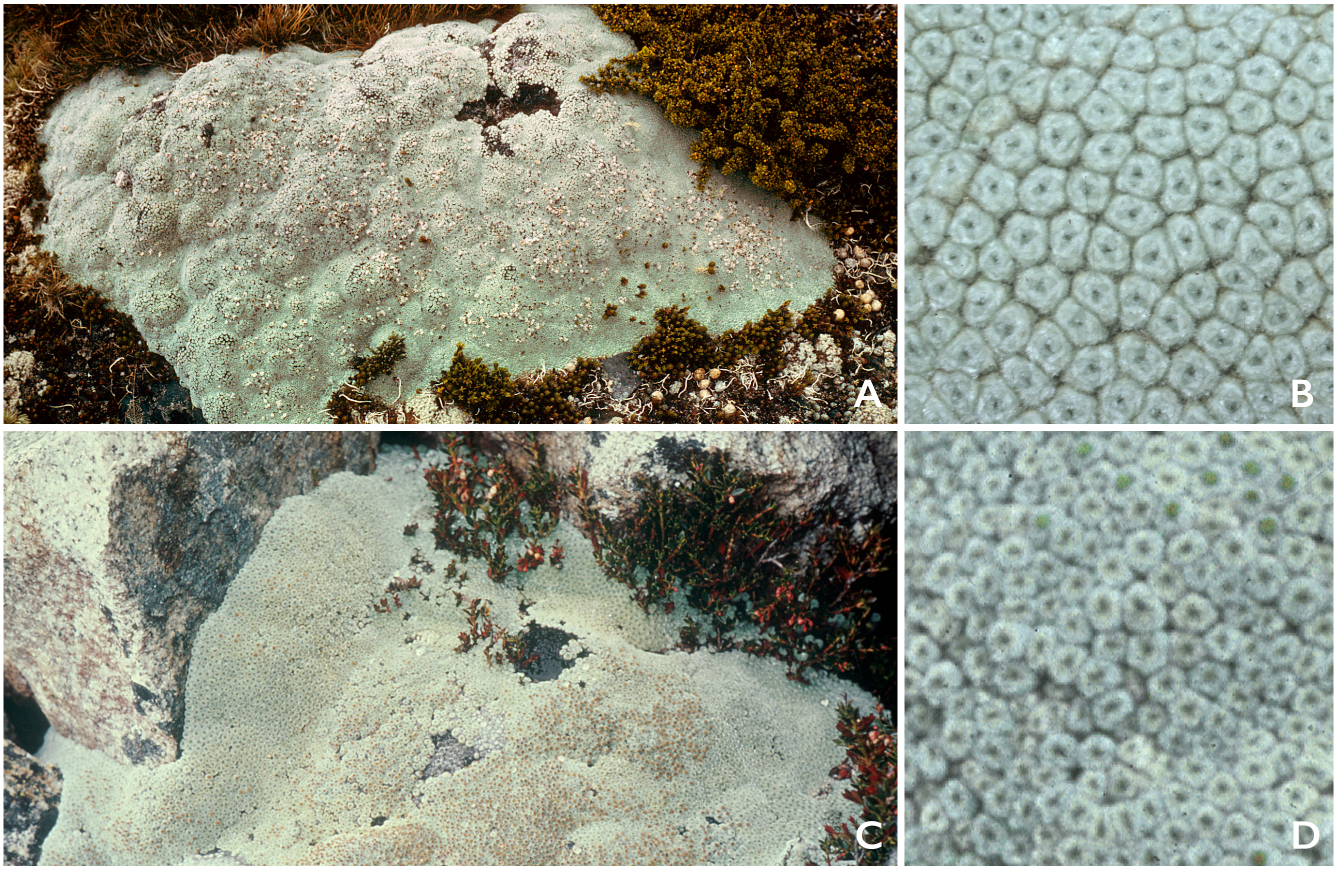


Figure 9. Startling morphological similarities in not closely related taxa. **A-B** *Raoulia eximia* (New Zealand). **C-D.** *Mniodes andina* (Peru). Photos: A-B: J.M. Ward; C-D: H. Wilson.

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Daisies Down Under:

Review of the state of taxonomy and phylogenetics of native Australian Asteraceae

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ABSTRACT

Because of the long history of isolation of Australia, the continent is home to a unique diversity of Asteraceae. The native daisy flora of *ca.* 1,105 species is dominated by Gnaphalieae, Astereae, Senecioneae, and Inuleae, whereas other globally diverse tribes such as Cardueae, Cichorieae, or Heliantheae are poorly represented. The last *ca.* forty years have seen taxonomic revisions of most major genera of Australian Asteraceae with the notable exceptions of *Olearia* and *Ozothamnus*. Despite this, current genus-level classification is often based on few morphological characters traditionally considered important (e.g., presence of pappus or capitulum scales). It is therefore likely that many genera are non-monophyletic in their current circumscriptions, as recently confirmed (e.g., for *Coronidium*, *Olearia*, and *Ozothamnus*). As of writing, phylogenetic studies of several other taxa are being conducted or under review. Once phylogenetic relationships have been resolved, the research focus will shift to understanding the evolution of the continental Asteraceae flora in time and space and the impact of Australia's aridification and key evolutionary and biogeographic events on patterns of diversification.

Keywords: Australia, phylogenetics, taxonomy, review

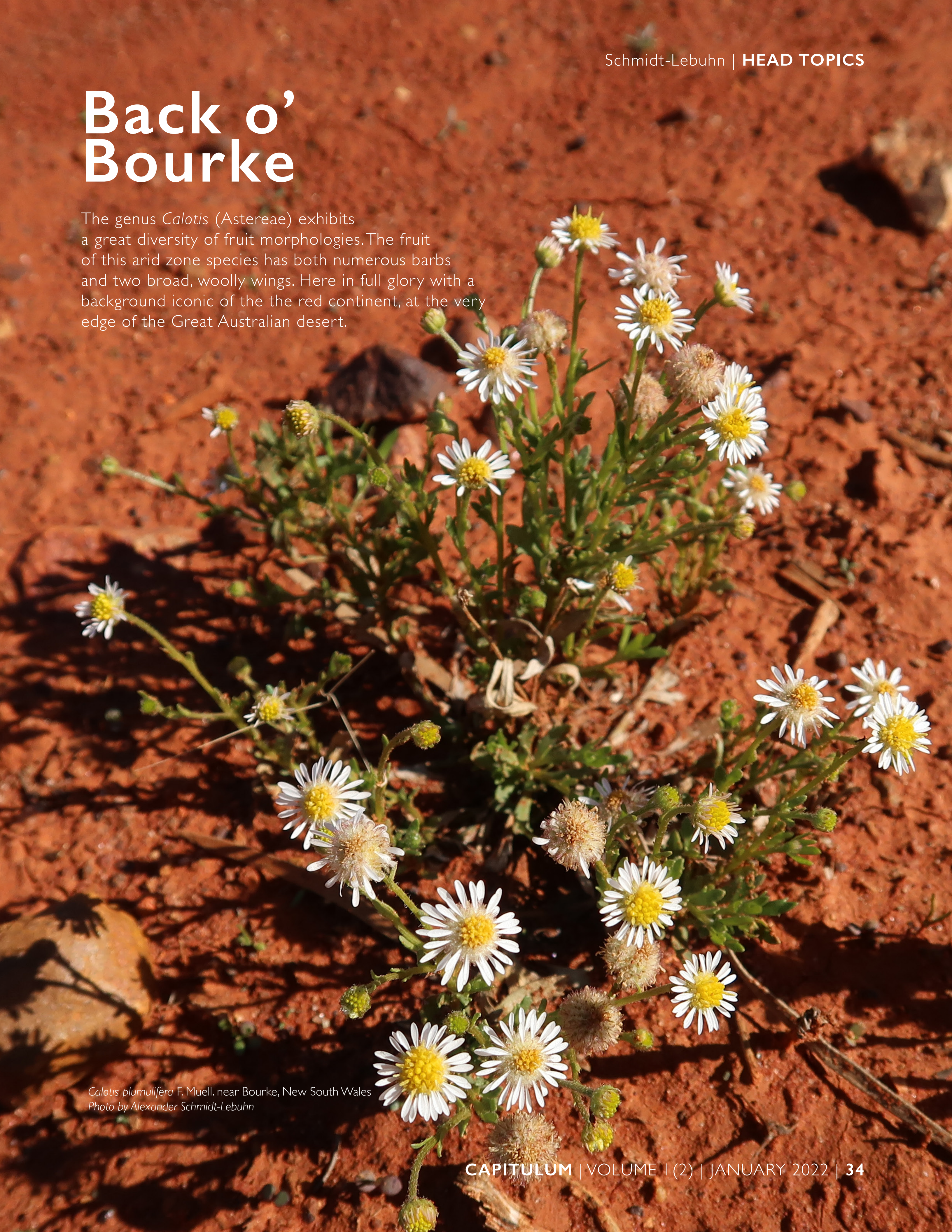
INTRODUCTION

The Australian Asteraceae comprise *ca.* 1,105 formally described native species, plus *ca.* 354 introduced species (Australian Plant Census, https://biodiversity.org.au/nsl/services/search/taxonomy, accessed June 2021). The continent is dominated by only four of the more than 40 tribes of the family (Figure 1). The vast majority of the native Asteraceae flora belongs to tribes Gnaphalieae Cass. ex Lecoq & Juillet (510 spp., Figure 2), Astereae Cass. (334 spp., Figure 5), Senecioneae Cass. (103 spp.), and Inuleae Cass. (65 spp., incl. Plucheae (Cass. ex Dum.) A.Anderb.), whereas the other globally diverse tribes Cardueae Cass., Vernonieae Cass., Cichorieae Lam. & DC., Anthemideae Cass., Eupatorieae Cass., and Heliantheae Cass. are represented with only few species (e.g., Heliantheae, 25 spp; Cichorieae, 23 spp.). All tribes except the two largest have been treated in the Flora of Australia series (Wilson, 2015), meaning, conversely, that *ca.* 80% of the diversity are yet to be included in a flora treatment at the national level. Although the Australian Plant Census and Australian Plant Name Index (https://biodiversity.org.au/nsl/services/search/names) provide up-to-date taxonomic and nomenclatural information, other details such as descriptions and keys are consequently scattered across an enormous number of papers in journals published predominantly by state herbaria and state floras of varying age.

The present review summarizes the state of knowledge of taxonomy, molecular phylogenetics, and biogeography of Australian Asteraceae with a focus on the most important publications of the last *ca.* forty years, i.e., to the exclusion of some papers

Back o' Bourke

The genus *Calotis* (Astereae) exhibits a great diversity of fruit morphologies. The fruit of this arid zone species has both numerous barbs and two broad, woolly wings. Here in full glory with a background iconic of the the red continent, at the very edge of the Great Australian desert.



Calotis plumulifera F. Muell. near Bourke, New South Wales
Photo by Alexander Schmidt-Lebuhn

presenting only new species and combinations or revisions of very small genera. Its purpose is to (1) serve as a guide to the existing literature, and (2) identify gaps for future research.

GNAPHALIEAE

Gnaphalieae are the largest tribe of Asteraceae in Australia. Their centres of diversity are in the southwest and the southeast of the continent, including the southeastern mountain ranges and Tasmania. They comprise significant parts of the vegetation in the subalpine and alpine zones and, transiently, in the arid zone of the continent, where carpets of ephemeral species appear after strong rainfall events (Figure 2A).

Over the last *ca.* forty years, the genus level classification of Australian Gnaphalieae has changed considerably. The changes were prompted to a great degree by the realization that the genera *Helipterum* DC. and *Helichrysum* Mill., to which many of the species previously belonged, were polyphyletic (Anderberg, 1991).

Species formerly classified as *Helichrysum* were accommodated in the newly described or reinstated genera *Argentipallium* Paul G.Wilson and *Anemocarpa* Paul G.Wilson (Wilson, 1992c), *Coronidium* Paul G.Wilson (Wilson, 2008), *Leiocarpa* Paul G.Wilson (Wilson, 2001), *Ozothamnus* R.Br. (Anderberg, 1991), and *Xerochrysum* Tzvelev (Bayer, 2001), supplemented by later additions of species (e.g., Walsh, 2014; Wilson, 2017; Schmidt-Lebuhn et al., 2018). Those formerly in *Helipterum* have been accomodated in the genera *Hyalosperma* Steetz (Wilson, 1989), *Leucochrysum* (A.Cunn. ex DC.) Paul G.Wilson (Wilson, 1992b), and *Rhodanthe* Lindl. (Wilson, 1992a).

Concurrently, most large and medium-sized genera underwent taxonomic revisions, or at least saw the publication of synopses including identification keys. They include *Angianthus* J.C.Wendl. and relatives (Short, 1983; Keighery, 2004; Lyons & Keighery, 2015), *Chthonocephalus* Steetz (Short, 1990), *Cassinia* R.Br. and its satellite genera (Orchard, 2004d, 2004c, 2004b, 2004a, 2006; Orchard & Orchard, 2005, 2009), *Calocephalus* R.Br. and *Gnephosis* Cass. (Short, 2015), *Chrysocephalum* Walp. in part (Wilson, 2016), *Millotia* Cass. (Short, 1995), *Myriocephalus* Benth. (Short, 2000), *Podolepis* Labill. (Jeanes, 2015, 2020), *Rutidosis* DC. (Holland, 1994, 1999), and *Waitzia* J.C.Wendl. (Wilson, 1992d). *Craspedia* G.Forst., a genus of rosette plants with a centre of diversity in alpine areas, has received significant taxonomic attention (Everett & Doust, 1992a; Everett & Thompson, 1992; McDougall & Walsh, 2008; Rozefelds et al., 2011; Schmidt-Lebuhn, 2013), including the reinstatement of its previously synonymized sister group *Pycnosorus* Benth. (Everett & Doust, 1992b).

Apart from Anderberg's cladistic analyses of morphological data (Anderberg, 1990, 1991; Short & Anderberg, 1995), and excepting a limited number of studies on the delimitation of species, i.e. below the genus level (Dennis & Walsh, 2010; Ohlsen et al., 2010; Salas & Schmidt-Lebuhn, 2018), none of these changes were supported by formal analysis or explicit consideration of natural groups and synapomorphies. Many generic concepts are consequently based on single character states, e.g. absence or presence of pappus or receptacle scales, suggesting that they may represent apomorphic segregates.

Molecular phylogenies allowing the testing of these concepts remain sparse. The first molecular phylogeny at the tribal level was published by Bayer et al. (2002). More recently, a study using sequence capture data resolved four major lineages, the predominantly annual and arid zone-centred Angianthus clade (Fig. 2A), the shrubby Cassinia clade (Figure 2B; see page 43), the Euchiton clade (Figure 2C; Figure 3) largely of cudweed-like and cushion plants, and the predominantly perennial and eastern-temperate Waitzia clade (Schmidt-Lebuhn & Bovill, 2021; see page 40). Neither study, however, sampled densely enough to address genus boundaries. Conversely, a molecular phylogeny of *Podolepis* (Konishi et al., 2000) did not include sufficient potential relatives to test monophyly.

Where studies were designed to test genus boundaries, they generally confirmed the problems described above. All genera of the Cassinia clade, including the large genus *Cassinia* itself, are nested in *Ozothamnus* (Schmidt-Lebuhn & Constable, 2013); *Haeckeria* F.Muell. and *Odixia* Orchard are epappose *Cassinia* and *Ozothamnus*, respectively, and *Cassinia* is *Ozothamnus* with receptacle scales.

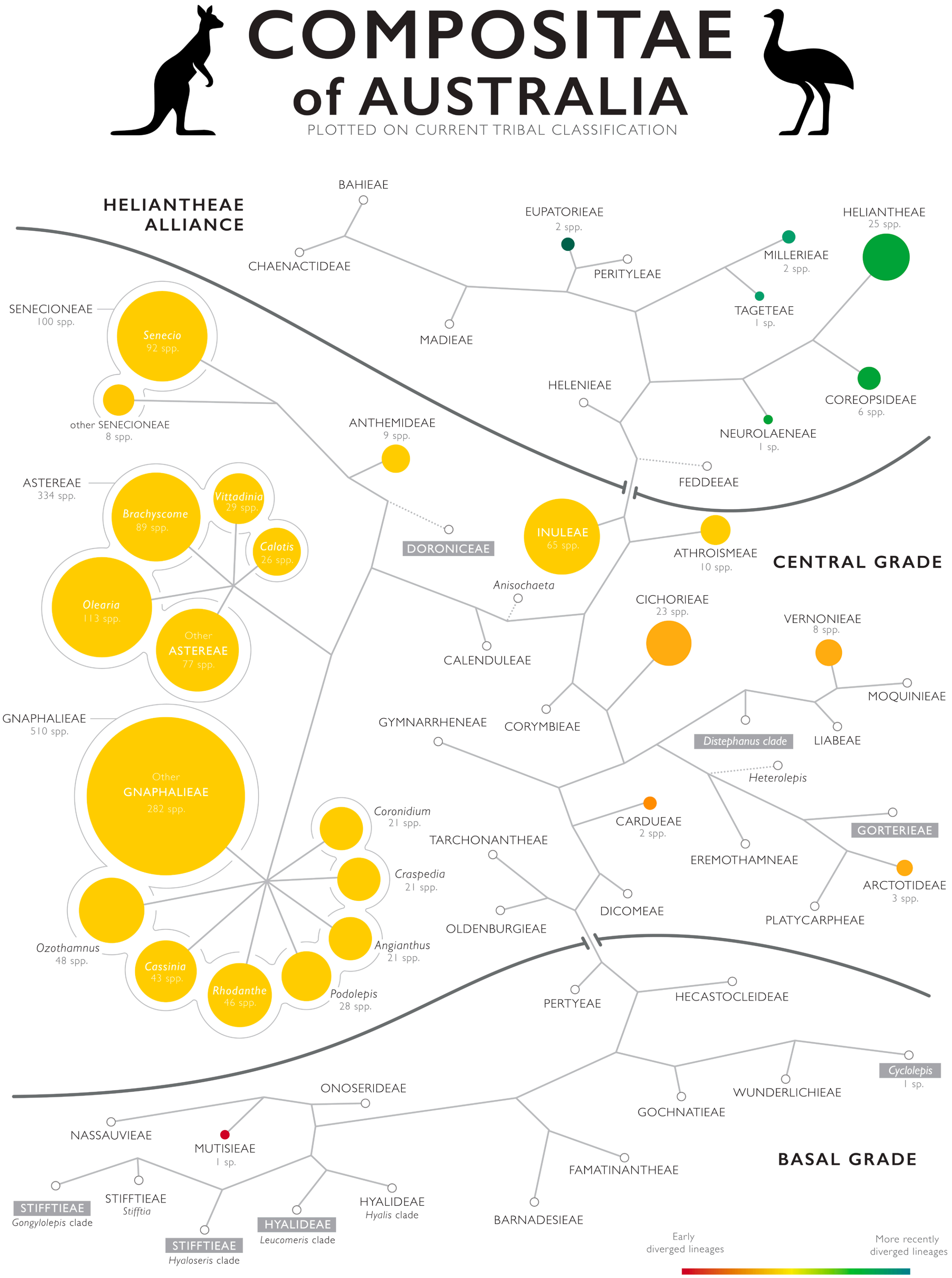


Figure 1. Diversity of native Australian Compositae (Asteraceae) plotted on current classification (Susanna et al., 2020). Circle size is indicative of species number; empty circles indicate taxa absent as natives in the continent; only genera with at least twenty native species are shown.

Of the three species groups of *Coronidium*, two are paraphyletic to *Xerochrysum*, and the third is unrelated (Schmidt-Lebuhn et al., 2015). Comprehensive taxonomic revisions and phylogenetic analyses of the two genera have recently been completed (Tim Collins, ms. in prep.; Figure 4), but the affinities of the Coronidium scorpioides group are still unclear. One species of *Leucochrysum* was found to be sister to *Waitzia*, which was not recognized previously because *Watzia* had been defined by the beak of the cypsela (Weber & Schmidt-Lebuhn, 2015). It is to be expected that similar results will be obtained from phylogenetic analyses of other genera. Current work focuses on the Angianthus and Euchiton clades, which have so far received the least attention (Schmidt-Lebuhn, unpubl. data).

An interesting aspect of some arid zone taxa in the Angianthus clade is the impact of breeding systems on species concepts. There are several pairs of otherwise indistinguishable populations differing only in their outcrossing versus asexual reproduction, in the latter case diagnosable by smaller anthers with an order of magnitude fewer pollen grains. Often the asexual forms occupy much larger ranges, presumably because they need only a single seed to establish a new population. The pairs have been recognized as separate species (Short, 1985, 1986), but the species concept underlying this taxonomy was not made explicit.

ASTEREAE

Australian Astereae show a wide diversity of morphologies ranging from minuscule ephemeral herbs to treelets prized by woodworkers (*Olearia argophylla* (Labill.) F. Muell. ex Benth.). Their centre of diversity is in the temperate southeast of the continent, but they are found across most major ecological zones.

Although considerable revisionary work has been conducted over recent decades, the tribe has seen much less dramatic taxonomic changes than the Gnaphalieae. The large herbaceous genus *Brachyscome* Cass. (Figure 5C) has recently been revised, and another segregate, *Roebuckiella* P.S.Short, was created (Short, 2014a, 2014b), adding to the growing number of small satellite genera including *Allittia* P.S.Short, *Hullsia* P.S.Short, and *Pembertonia* P.S.Short. The widespread southern hemisphere genus *Lagenophora* Cass. likewise has an up-to-date treatment (Wang & Bean, 2019), although the status of potentially phylogenetically nested *Solenogyne* Cass. remains unclear, as has *Camptacra* N.T.Burb. (Bean, 2020b).

Older but still comparatively recent taxonomic revisions are available for *Minuria* DC. (Lander & Barry, 1980) and *Vittadinia* A.Rich. (Burbidge, 1982). *Calotis* R.Br. (see page 34), which is of interest for its diverse pappus morphologies ranging from standard bristles to barbed spines, has not been reviewed since Davis (1952).

Comprehensive treatments are lacking for other medium-sized genera, although *Celmisia* Cass. (Figure 5D), which in Australia constitutes an important part of the alpine vegetation, saw the addition of three new species and one new combination (Gray & Given, 1999), and a group of mostly alpine species previously classified as *Erigeron* L. has been segregated as *Pappochroma* Raf. (Nesom, 1998) (Figure 5B).

In its current circumscription, *Olearia* Moench. (Figure 5A) is with *ca.* 113 species the largest genus of Asteraceae in Australia, but, perhaps because of its size, no monographic treatment is available. Various new species have been described in recent years (Walsh, 2004; Bean & Mathieson, 2015; Messina & Walsh, 2019; Bean, 2020a). The most detailed work was conducted on *Olearia* section *Asterotriche* Benth. using both morphological (Messina et al., 2013) and molecular data (Messina et al., 2014).

Although several of the smaller genera of Australian Astereae are very likely natural units, the largest of them, *Olearia* and *Brachyscome*, are more problematic. Molecular phylogenetic studies of *Olearia* and relatives suggested that the genus is non-monophyletic (Cross et al., 2002; Wagstaff et al., 2011). A recent Ph.D. project in New Zealand on the Celmisia group confirmed this and also found *Celmisia* to be non-monophyletic, which may have implications for the Australian members of that genus (Patricio Rodrigo Saldivia Pérez, unpubl. data). Recently the splitting of *Olearia* into ten new genera was suggested (Nesom, 2020) with reference to the phylogeny of Cross et al. (2002), but this new taxonomy has not yet found widespread acceptance and may at any rate have to be reconsidered in the light of Saldivia Pérez' results.

Figure 2. Australian Gnaphalieae. **A.** *Cephalipterum drummondii* A.Gray mass-flowering in Western Australia in spring. **B.** *Cassinia longifolia* R.Br., a representative of the woody Cassinia group. **C.** *Euchiton sphaericus* (Willd.) Holub in the Australian Capital Territory. Photos: A.N. Schmidt-Lebuhn.

Figure 3. The Euchiton clade of Australian Gnaphalieae contains several alpine cushion plants, such as this *Ewartia*. *Ewartia nubigena* (F. Muell.) Beauverd in Kosciuszko National Park, New South Wales. Photo: A.N. Schmidt-Lebuhn.

A molecular phylogeny of *Brachyscome* has long been available (Denda et al., 1999). Although its sampling was limited compared to the size of the genus, the results already demonstrated that *Allittia*, *Pembertonia*, and *Roebuckiella* are deeply nested in *Brachyscome* and constitute apomorphic segregates, even before they were in fact segregated. A more broadly sampled phylogenetic study of *Brachyscome* has recently been completed (Megan Hirst, unpubl. data.).

Phylogenies of the remaining genera, where they exist, provide little evidence on generic delimitation. A phylogeny of the Vittadinia group suggested that *Minuria* may be non-monophyletic and was unable to resolve *Vittadinia* and *Tetramolopium* Nees as entirely reciprocally monophyletic, but the results had limited resolution and support (Lowrey et al., 2001). A study of *Calotis* showed little resolution at the base of the genus and included only two outgroup samples (Watanabe et al., 2006).

SENECIONEAE

The vast majority of Australian Senecioneae species belong to *Senecio* L. *sens.str.* (Figure 6A), which is most diverse in the temperate southeast of the continent. The most recent, very thorough revision of the genus in Australia led to the description of several new species and recognised seven species groups (Thompson, 2004c, 2004a, 2004b, 2005a, 2005b, 2006).

Few of the species groups, however, were resolved as natural groups in subsequent molecular phylogenies. Ribosomal and chloroplast trees both resolved three clades but showed marked incongruence, suggesting some reticulate evolution and the existence of four Australasian species groups partly defined by chromosome numbers (Liew et al., 2018). Subsequently, several Australian species previously treated as *Senecio* were found to be only distantly related to that genus, leading to the description of

Habitat specialists

Leucochrysum (Gnaphalieae) is only a small genus, but its five species have adapted to very diverse habitats. This adaptive radiation must have been very recent, because four of the species can still be crossed with each other. The species depicted here is alpine; the others occur, respectively, on red sand in the western part of the arid zone, on heavy soils in the eastern part of the arid zone, in temperate areas along the mountain ranges of eastern Australia, and only on ironstone-sandstone rock pagodas in a small area near the Blue Mountains.

Leucochrysum alpinum (F. Muell.) R.J. Dennis & N.G. Walsh in Kosciuszko National Park, New South Wales
Photo by Alexander Schmidt-Lebuhn

Figure 4. The genus *Xerochrysum*, commonly called the golden everlastings, is the horticulturally most important group of Australian native Asteraceae. Colorful hybrid variants are cultivated globally as cut-flowers. *Xerochrysum viscosum* (Sieber ex DC.) R.J. Bayer, mass-flowering in the Australian Capital Territory.

a new genus of alpine rosette plants, *Scapisenecio* Schmidt-Leb., and the expansion of previously monotypic *Lordhowea* B.Nord. (Schmidt-Lebuhn et al., 2020).

OTHER TRIBES

Recent taxonomic treatments exist for most of the larger genera representing other tribes in Australia. Molecular phylogenies are available and well-sampled for some important taxa but entirely absent for others.

In contrast to the top three, the regionally fourth largest tribe, Inuleae, is most diverse in the northern half of the continent. Several genera have been taxonomically revised in recent years, including *Pluchea* Cass. (Hunger, 1996, 1997; King-Jones, 2001; Bean, 2011b, 2013b), *Pterocaulon* Elliott sect. *Monenteles* (Labill.) Kuntze (Bean, 2011a), *Streptoglossa* Steetz (Dunlop, 1981), and *Sphaeromorphaea* DC. and *Ethuliopsis* F.Muell. (Bean, 2013a). Australian *Blumea* DC. was last reviewed in the Flora of Australia (Dunlop & Orchard, 2015), not in a dedicated monograph. No phylogenetic studies have been published with a focus on diversification in Australia.

Genus limits have been redrawn in Heliantheae, in particular with the segregation of *Apowollastonia* Orchard (seven Australian species) from *Wedelia* Jacq. (Orchard, 2013). This new taxonomy was subsequently supported by phylogenetic analysis (Edwards et al., 2018). *Pentalepis* F.Muell., with six Australian species, was revised twice in recent decades (Karis et al., 1993; Orchard & Cross, 2012).

Apart from a variety of introduced weeds, two genera of Cichorieae are significant in Australia. The regionally largest is *Picris* L. with *ca.* ten species, all which had for several decades been considered to represent introduced *P. hieracioides* L., which, however, had never established after an early incursion (Holzapfel, 1994). Species delimitation in Australian *Microseris* D.Don. (Figure 6D) is traditionally controversial, but it is currently considered to comprise three species (Walsh, 2016). The root tubers of the genus, commonly known as murnong or yam daisy, were an important food source for indigenous people (Gott, 1983).

Anthemideae are represented with only nine species of *Cotula* L. and *Leptinella* Cass., part of a southern hemisphere clade of the tribe. *Cotula alpina* (Hook.f.) Hook.f. (Figure 6B) is nested in *Leptinella* Cass. (Himmelreich et al., 2012), as morphologically

Figure 5. Australian Astereae. **A.** *Olearia tomentosa* (J.C.Wendl.) DC., coastal New South Wales. **B.** *Pappochroma setosum* (Benth.) G.L.Nesom. **C.** *Brachyscome stolonifera* G.L.Davis. **D.** *Celimisa* sp. in the alpine zone of Kosciuszko National Park, New South Wales, where Asteraceae constitute *ca.* 20% of the vascular flora. Photos: A.N. Schmidt-Lebuhn.

Amaranth Daisy

Most species of the predominantly woody Cassinia clade belong to the large, shrubby genera *Cassinia* and *Ozothamnus*. Of the smaller genera, some are apomorphic segregates very similar to the former, but some are highly unusual. Monotypic *Calomeria* ("incense plant") is a woody biennial up to 2 m tall with rich pyramidal capitulescences and tiny capitula of only 2-4 florets.

Calomeria amaranthoides Vent. (Gnaphalieae) in the Blue Mountains, New South Wales
Photo by Alexander Schmidt-Lebuhn

Figure 6. A. *Senecio gunnii* (Hook. f.) Belcher (Senecioneae). **B.** *Cotula alpina* (Hook. f.) Hook. f. (Anthemideae), Kosciuszko National Park, New South Wales. **C.** *Cymbonotus* sp. (Arctotideae), Australian Capital Territory. **D.** *Microseris lanceolata* (Walp.) Sch.Bip. (Cichorieae), New South Wales. **E.** Fruits of *Picris angustifolia* DC. (Cichorieae), Namadgi National Park, Australian Capital Territory. Photos: A.N. Schmidt-Lebuhn.

suggested by its stoloniferous habit, but the species has not yet been transferred.

Centipeda Lour. (Athroismeae) has been studied taxonomically (Walsh, 2001), and phylogenetically (Nylinder et al., 2013). The only Australian genus of Arctotideae, *Cymbonotus* Cass. (Figure 6C), has been expanded to three species (Holland & Funk, 2006).

BIOGEOGRAPHY OF AUSTRALIAN ASTERACEAE

There is no general pattern of biogeographic history across the Australian Asteraceae, as already suggested by the large number of tribes that are present and their enormous differences in species numbers. Despite the long isolation of the continent, numerous natural introductions must have occurred, in some cases across large distances.

With few exceptions in *Gnaphalium* L. and *Pseudognaphalium* Kirp., the Australian Gnaphalieae are all part of a single clade, the Australasian clade (Smissen et al., 2020). This informal clade name contrasts with the other clade names in the tribe, which are derived from genus names. This is a consequence of its species richness and splitting into many genera in combination with narrow occurrence in that biogeographic region, whereas the other clades are either small (and thus comfortably named after a single core genus) or widespread. It is likely that the clade is derived from a single dispersal event from southern Africa, perhaps as recent as *ca.* 15 MYA (Bergh & Linder, 2009; Nie et al., 2016).

Even in Australasia, and even accounting for over-splitting, few genera of Gnaphalieae are widespread, suggesting that dispersal capability is limited. The Euchiton group (Schmidt-Lebuhn & Bovill, 2021) is the most mobile, ranging across Australia, New Zealand, New Guinea, and into the Pacific area. *Craspedia* originated in Australia and dispersed into New Zealand, radiating there into a bewildering array of forms awaiting taxonomic resolution (Ford et al., 2007). *Ozothamnus* follows the same pattern, with the New Zealand species presumably related to the Tasmanian *O. ledifolius* (A.Cunn. ex DC.) Hook.f. complex (Breitwieser & Ward, 1997). *Xerochrysum*, finally, is found in both Australia and New Guinea; all other genera are endemic.

Senecioneae, in contrast, appear to be highly mobile. Some genera have dispersed to Australia but did not diversify (*Arrhenechthites* Mattfeld, *Gynura* Cass.), but, more importantly, the Australasian ribosomal and chloroplast clades of *Senecio* are nested between various non-Australasian clades (Liew et al., 2018), suggesting repeated dispersals from different directions followed by diversification. The small woody genera *Bedfordia* DC. and *Centropappus* Hook.f. are nested within New Zealand *Brachyglottis* J.R.Forst. & G.Forst. (Wagstaff & Breitwieser, 2004), suggesting they are derived from a trans-Tasman dispersal. The alpine cushion plants of the genus *Abrotanella* Cass. have what appears to be a classic Gondwanan distribution, including in southeastern Australia, but clade ages in the genus are too young to be explained by vicariance (Swenson et al., 2012).

The recent expansion of *Lordhowea* to include mainland species resolved the puzzle of the origin of previously isolated *Lordhowea insularis* (Benth.) B.Nord. (Schmidt-Lebuhn et al., 2020). In doing this, however, the puzzle was shifted to a deeper phylogenetic level, because *Lordhowea* and the new genus *Scapisenecio* appear to form two lineages seemingly on a grade below the northern hemisphere Adenostylinae Benth. & Hook.f. It is possible that this unexpected pattern is the result of relatively ancient dispersal events and extinctions. A well-sampled, time-calibrated backbone phylogeny of the tribe will be required to infer the most probable scenario.

The Celmisia group in Astereae shows biogeographic connections to New Zealand and subantarctic islands (Wagstaff et al., 2011). The Vittadinia group likewise ranges across Australia and New Zealand but also the Pacific, with *Tetramolopium* most speciose in New Guinea and Hawai'i .The most thoroughly studied case in the tribe may, however, be *Lagenophora* (Sancho et al., 2015), which parallels *Abrotanella* in both its Gondwanan pattern and the absence of a pappus that would facilitate wind dispersal.

Several other tribes show striking disjunctions of Australian species from their areas of origin, again with divergence dates too recent for vicariance to be feasible. A single species of Mutisieae Cass., *Trichocline spathulata* (A.Cunn. ex DC.) J.H.Willis, occurs in southwestern Western Australia. Despite

A model of evolution

The *Senecio pinnatifolius* A. Rich. (formerly *S. lautus* auct. non G.Forst. ex Willd.) complex comprises several varieties ranging in ecological adaptation from coastal dunes to the alpine zone. It is used as a model system for the study of evolution and speciation by the lab of Daniel Ortiz-Barrientos at the University of Queensland.

Senecio pinnatifolius var. *alpinus* (Ali) I. Thomps. in Kosciuszko National Park, New South Wales. *Photo by Alexander Schmidt-Lebuhn* the diversity of Cardueae on other continents, only two potentially native species are found in Australia, *Hemisteptia lyrata* (Bunge) Fisch. & C.A.Mey and *Rhaponthicum australe* (Gaudich.) Sojak. *Cymbonotus* is deeply nested inside otherwise southern African Arctotideae Cass. (Funk et al., 2007). In Cichorieae, *Microseris* (Figure 6D) is North American and Australasian (Vijverberg et al., 1999). A comprehensive biogeographic study on the ancestral range evolution of *Picris* (Figure 6E) inferred its dispersal to Australia from Asia (Slovák et al., 2018). Several genera of the Heliantheae alliance occur with few species in Australia, often in the northern half of the continent.

THE WAY FORWARD

Although it can be assumed that the vast majority of Asteraceae have already been discovered, remote parts of Australia remain insufficiently explored. Most herbarium specimens were collected close to major cities, whereas the eastern half of the largest state, Western Australia, is so poorly sampled that it is difficult to even estimate the local species numbers (Schmidt-Lebuhn et al., 2012). As the Australian taxonomic community enacts it Decadal Plan (www.taxonomyaustralia.org.au/decadal-plan), targeted collecting in under-collected areas will be critical to complete the inventory of continental biodiversity.

As of the writing of this manuscript, the Australian Plant Census accepted 48 phrase name species in Asteraceae. These are are placeholder names following the format "*Rhodanthe* sp. Point Lookout (J.J.Bruhl 2078) NE Herbarium" and are used to enable the conservation of and communication about species while their formal scientific publication is in preparation (Barker, 2005). Unfortunately, it can often take a decade or more before a phrase name species is validated. It is possible that this is partly due to the taxonomic impediment, i.e. lack of taxonomists. It is also possible, however, that the custom of using phrase names actually discourages their validation, as taxonomists might be worried either about 'scooping' the person who registered the phrase name or about being scooped themselves if they invested the time, because that person may already have a manuscript under review. Whatever the cause, it would be desirable to accelerate the description of new species that are already known to exist.

A greater gap than species discovery are, however, genus-level studies. Several important genera have not been comprehensively revised, including some of the largest, *Olearia* and *Ozothamnus*. Even genera recently having seen taxonomic changes and additions of species are frequently lacking identification keys covering all their species (e.g., *Pycnosorus*). Many existing keys are outdated, and with the exception of the Cassinia group (keys.lucidcentral.org/keys/v3/cassinia/), interactive identification tools using terminology accessible to non-taxonomists are all but non-existent. Collections technicians, researchers, conservation managers, biosecurity practitioners, and the general public therefore find it difficult to reliably identify Asteraceae specimens and would benefit from the publication of additional modern, electronic identification tools and field guides.

On the other hand, phylogenetic studies have been produced at an increasing rate in recent years. Publications of well-sampled phylogenies covering major groups of interest such as *Olearia* and *Celmisia*, *Brachyscome*, and *Coronidium* and *Xerochrysum* are currently in preparation. The Australian Angiosperm Tree of Life (AAToL) initiative in the Genomics for Australian Plants consortium (GAP, www.genomicsforaustralianplants.com) has produced sequence capture data for one species of each genus. In this case, the over-splitting of Gnaphalieae genera means that a very densely sampled backbone phylogeny will soon be available to guide future research.

Significant gaps in our knowledge of phylogenetic relationships will be filled in the next few years. In Gnaphalieae, a particular focus will be the Angianthus clade, where major changes in the circumscription of genera can be expected due to the large number of potential apomorphic segregates. Genomic data will be required to resolve conflicting ribosomal and chloroplast signals in Senecioneae.

Once species-level data have become available for all major groups, attention can turn towards evolutionary questions, ideally in the context of time-calibrated phylogenies: How was the Australian Asteraceae flora assembled in time and space? What was the impact of the aridification of the continent on patterns of diversification? What are key innovations that drove adaptive radiations into arid and alpine areas?

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Understanding capitulum development:

Gerbera hybrida inflorescence meristem as an experimental system

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ABSTRACT

Inflorescences, the flower-bearing structures in plants, show enormous diversity in nature. Their architecture, in terms of number and arrangement (phyllotaxis) of flowers, play a central role in reproductive success and adaptation of plants, as well as yield in crops. We apply Compositae capitula, or flower heads, as our model system to study inflorescence development. The unique architecture of capitula, often composed of morphologically and functionally distinct types of flowers, is considered the key innovation for the evolutionary success of this largest family of flowering plants. Moreover, the arrangement of individual flowers in intersecting spirals in capitula represent an iconic example of the geometric regularity found in nature. Our aim is to explore the gene regulatory networks that control patterning of the Compositae inflorescence meristems and their subsequent development. In this brief review, we summarize the recent technological developments and tools that allow us to explore and follow meristem patterning early on – already before we can see any visual changes in them. These include visualization of capitulum development by X-ray micro-computed tomography (micro-CT), live-imaging of dissected meristems on tissue culture media, and application of laser ablation to disrupt meristem organization and to follow its re-patterning. We anticipate that these methods are applicable to distinct species to promote comparative studies and understanding of developmental diversity of capitula within Compositae.

Keywords: laser ablation, live-imaging, meristem, micro-CT

INTRODUCTION

Gerbera (*Gerbera* × *hybrida* Hort.) is a highly popular ornamental crop. Our group has explored this species since the late 1980's, first developing an *Agrobacterium*-mediated genetic transformation method in collaboration with a Finnish company motivated by the extreme hype in plant biotechnology at that time. At the beginning, we focused on understanding the regulation of anthocyanin pigmentation patterns. Only later we, as molecular biologists, fully realized the uniqueness of the system. With advanced imaging technologies combined with genomics and molecular tools, gerbera has emerged as a model for plant developmental studies expanding them beyond the conventional models (Figure 1).

Most recently, our focus has turned to meristems, the small growing points that give rise to different types of organs in plants such as leaves and flowers. Exploring meristem patterning has proven to be most informative to understand capitulum development. The gerbera inflorescence meristems (IM) initiate hundreds of florets in an iconic phyllotactic pattern forming regular left- and right-curving spirals (Zhang et al., 2021a). Intriguingly, the spiral numbers represent two consecutive numbers of the Fibonacci series. We have visualized the plant hormone auxin in transgenic gerbera using the *DR5rev*::3XVENUS-N7 reporter (Heisler et al., 2005), and shown how auxin defines the positions of future florets (see the fluorescent signals on IMs visualized by confocal and light-sheet microscopy in Figure 1) – this happens before we see the bulging florets by conventional

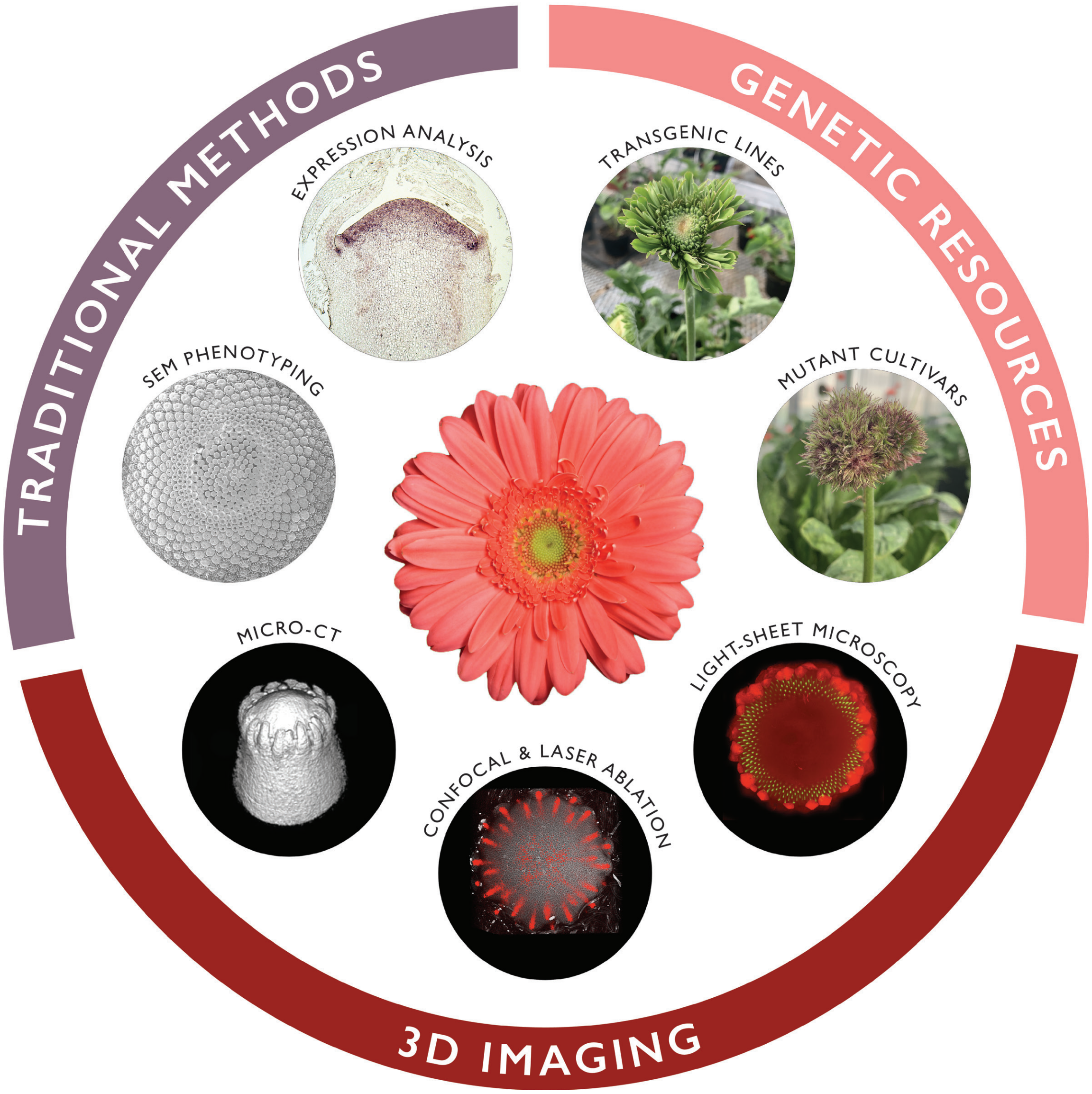

Figure 1. Available research methods and resources for studying *Gerbera* capitulum development. 3D imaging methods including micro-CT, confocal and light-sheet microscopy were recently optimized and integrated among the more conventional methods.

scanning electron microscopy (SEM). Combining the *in vivo* microscopic data with X-ray micro-computed tomography (micro-CT) based growth analysis, a 3D computational model for capitulum phyllotaxis was established in collaboration with Prof. Prusinkiewicz's team at the University of Calgary (Zhang et al., 2021a). Our recent molecular data shows that many genes regulating flower development have been recruited to regulate IM development in gerbera (Zhao et al., 2016; Zhang et al., 2017; Zhao et al., 2020). Altogether the data supports the botanical hypotheses suggesting that the capitulum may have evolved from a single, determinate meristem (Classen-Bockhoff & Bull-Hereñu, 2013). Based on these data, we propose that the giant gerbera IM provides a useful model to understand meristem patterning beyond the conventional model species.

Here, our aim is to introduce selected experimental approaches that facilitate our aims to understand capitulum development, and that potentially can be applied in other species to explore the developmental diversity in Compositae.

Gerbera: a model system

Gerbera, a well-known ornamental crop, has turned out to be a working model for plant developmental studies. The vegetatively propagated plants are easy to grow in greenhouses. They flower continuously and produce material for sampling. Genetic modification provides a key tool to discover functions of genes of interest.

Gerbera hybrida cultivar 'Terra Regina', Greenhouse at the Viikki Campus, University of Helsinki
Photo by Teng Zhang

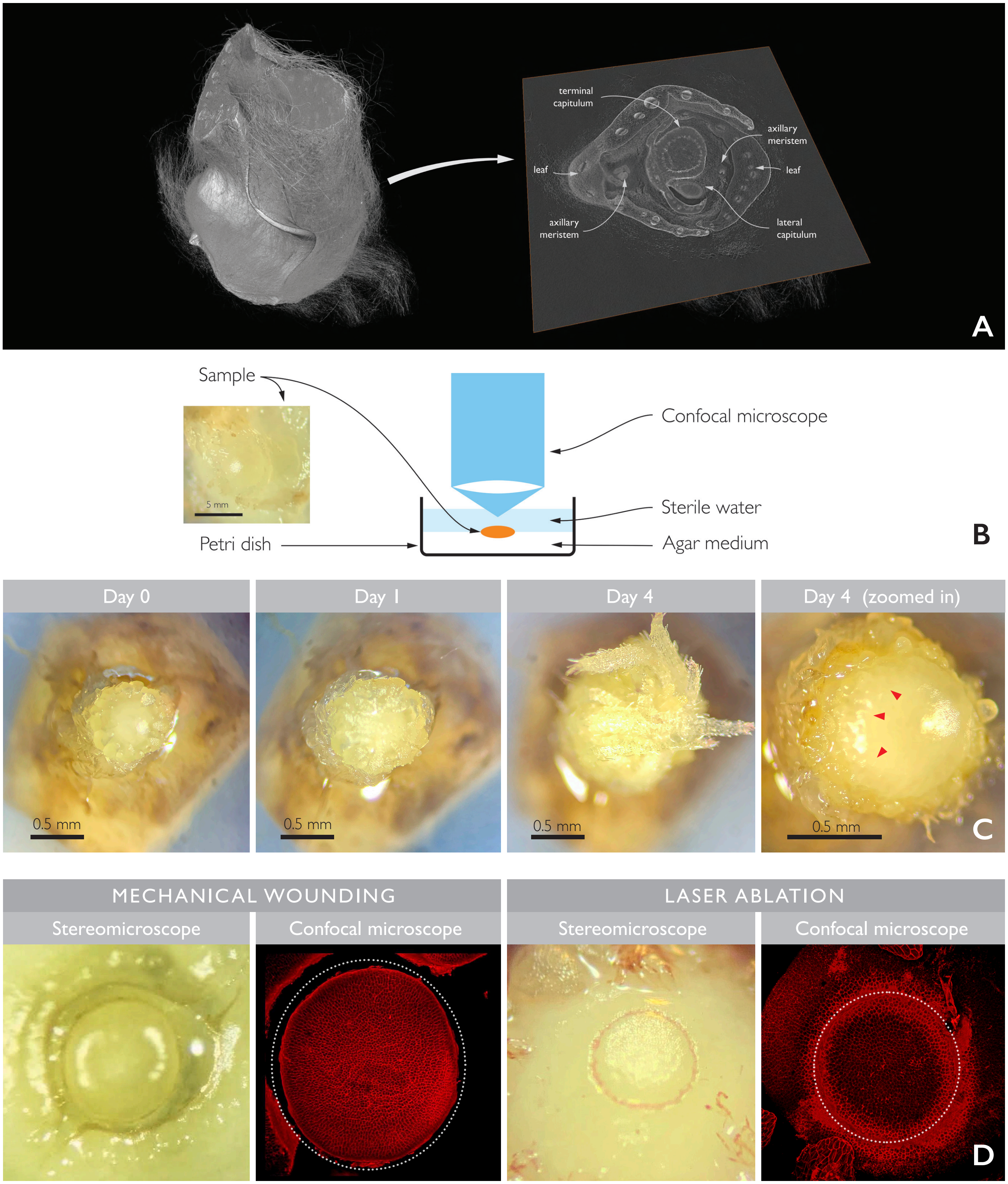

Figure 2. Micro-CT, live-imaging and wounding experiments conducted on developing capitula. **A.** Micro-CT segmentation helps to locate the developing gerbera IMs in the rosette. **B.** Sample setup for confocal microscopic imaging. The image on the left shows a sample sector that contains the shiny, dome-shaped meristem. **C.** Stereomicroscope images showing a growing *Gerbera* IM explant *in vitro*. The IM at 4-day timepoint is covered by involucral bracts and the zoom-in image shows initiating floret primordia (red arrows). **D.** Side-by-side stereomicroscope and confocal microscope images from the wounding experiments performed by mechanical wounding and by laser ablation. Cylindrical cuts are marked by the dashed line in the confocal microscope images.

TOWARDS 4D PHENOTYPING OF GERBERA CAPITULUM DEVELOPMENT

To understand the phyllotactic patterning of the gerbera capitulum, we had to first determine how to properly find and dissect the IM samples. At the earliest developmental stage, the diameter of the IM is about 300-500 μm. The IMs are hidden within the rosette leaves, below the soil, and they are covered by protective hairs (Figure 2A). We applied micro-CT scanning to follow the early capitulum growth. For micro-CT, sample fixation is done as for the regular SEM but most importantly, the structures can be targeted by X-rays without very accurate dissection of the surrounding tissues. These scans were very informative as we learned from the 3D reconstructed images to precisely locate the meristems (Figure 2A), and later to expose them under the stereomicroscope (Figure 2B) and to dissect them apart from the hairy leaf axils. Based on our experience, micro-CT scans are valuable for creating detailed 3D phenotypic data and could easily be applied to any species of interest.

Live-imaging is another key method that allows visualization of developmental events with the addition of the time component, i.e., 4D. This methodology has been widely applied to analyze the dynamic growth of the *Arabidopsis thaliana* (L.) Heynh. shoot apical meristem (Heisler & Ohno, 2014), as well as organs such as leaves (Kierzkowski et al., 2019) and stamens (Silveira et al., 2021). Live-imaging of capitula requires that they are separated from the leaf rosettes and grown on tissue culture media. For this purpose, we dissected the rosette sectors (3 × 3 mm in size) containing an intact IM (Figure 2B, C). Since the sectors were collected from the greenhouse, Plant Preservative Mixture treatment (PPM™, a kind suggestion from Dr. Siobhan Braybrook) was used to eliminate contamination during culturing. Using a modified gerbera multiplication medium, we were able to follow the growth of the IM explants *in vitro* up to two weeks (Zhang et al., 2021a). This allowed us to capture confocal microscopic stacks from the same IM explant in multiple time points, and thus the development could be rendered with cellular resolution. The live-imaging method allowed us to follow the propagation of the DR5 auxin signals from cell-to-cell during meristem growth. We discovered that the DR5 signal (representing the emerging bract initia) moves not only radially but also laterally through the cells between its two neighboring maxima in the expanding meristem. This movement was found to be the key for the emergence of Fibonacci numbers of auxin maxima during the early stages of meristem patterning (Zhang et al., 2021a).

REVISITING THE CLASSIC EXPERIMENTS ON CAPITULUM WITH NEW TECHNIQUES

We have always been fascinated by the pioneering experiments in sunflower in the 1980s to manipulate capitulum development. Among these, mechanical wounding of the capitulum resulted in *de novo* patterning from the wound margins, i.e., initiation of new bracts, ray and disc florets (Palmer & Marc, 1982; Hernandez & Palmer, 1988). After optimizing the live-imaging method for gerbera, we revisited these experiments. We conducted cylindrical cuts using a modified syringe tip and further adopted laser ablation to achieve more precise wounding of gerbera IMs (Figure 2D). By wounding of the IMs of the DR5 auxin reporter lines (Zhang et al., 2021b), our results faithfully recapitulated the wound responses previously observed in sunflower and showed conserved changes at the cellular level similar to those observed in the *Arabidopsis* IM (Caggiano et al., 2017). Besides wounding, exogenous application of hormones such as cytokinin (Hernandez, 1996) or physical compression (Hernandez & Green, 1993) can also alter capitulum development. Revisiting these experiments with modern techniques, combined with molecular level studies, could provide new insights into mechanisms of *de novo* patterning.

Despite its complexity, the large IM of gerbera provides an additional model to understand spatio-temporal patterning of meristems beyond the traditional models like Arabidopsis and tomato. The major challenge is to understand how changes in the functions of key developmental genes and their regulatory networks have led to the enormous morphological diversity of flowering plants. This requires comparative studies across multiple species – hopefully including new models of Compositae in the future.

Capitula diversity: gerbera and more

Compositae is the largest among the flowering plant families. Understanding evolution of the huge morphological diversity within this family waits for comparative genomic and molecular level studies. Such knowledge facilitates crop breeding and helps to sustain global biodiversity.

Gerbera hybrida cultivar 'Terra Regina', Greenhouse at the Viikki Campus, University of Helsinki
Photo by Paula Elomaa

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Monarchs in the veld:

The Arctotis Annual Clade provides insight into recent floristic diversification in a semi-arid region of southern Africa

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ABSTRACT

A revision of the main clade of annual species of *Arctotis* L. recognises eight species. All but one taxa are distributed in the winter and/or year-round rainfall regions of southern Africa, with the highest species diversity in semi-arid areas. Altitude and several temperature and precipitation parameters best explain latitudinal and longitudinal gradients in the distribution of taxa. Cypsela and pappus morphology suggest adaptation for reduced dispersibility in a semi-arid environment during diversification. Phylogenetic analyses of ITS and noncoding cpDNA sequence data resolve strongly supported basal nodes and a haplotype network suggests a degree of taxonomic structure to cpDNA diversity. Further research to resolve a genetically diverse "*A. fastuosa* species complex" is required. Diversification of the clade is not explainable solely by a simple vicariance model with parapatric speciation. A biogeographic hypothesis for diversification of the clade is formulated for future testing.

Keywords: biogeography, Namaqualand, Namibia, South Africa, taxonomy

South Africa hosts a rich temperate vascular plant flora (Raimondo et al., 2013), of which the Asteraceae constitutes almost one-tenth (~250 genera and 2250 species; Koekemoer, 1996). Endemism in the Greater Cape Floristic Region, which roughly corresponds to the winter rainfall region of South Africa, is estimated to be 77.9% of the ~11,000 seed plant species (Snijman, 2013). The northern part of this region is a mild, semi-arid area, colloquially known as Namaqualand, which is a magnet for wildflower enthusiasts and photographers. The Namaqualand flora is renowned in part for spectacular flowering displays by annual species in winter and spring.

A conspicuous component of the Namaqualand annuals flora is a clade of showy annual species of the genus *Arctotis* L. (tribe Arctotideae Cass.), informally designated the '*Arctotis* Annual Clade' (McKenzie & Barker, 2008). Several clade members are common in cultivation, of which *A. fastuosa* Jacq. is often sold under the name 'Monarch of the Veld' by commercial seed companies. Although a popular ornamental, *Arctotis* has long been synonymous with taxonomic chaos. An ongoing revision of the genus aims to instill taxonomic order. A revised taxonomy for the *Arctotis* Annual Clade (McKenzie & Barker in press) recognises eight species (Figure 1 and Figure 2) primarily distinguishable by cypsela and pappus morphology (Table 1). The updated taxonomy includes two previously unrecognised species (*A.* "chrysantha" and *A.* "namibiensis"). A putative cline between *A. fastuosa* and *A.* "namibiensis", to which the name *A. macrocephala* (DC.) Beauverd is applicable and is treated as a nothospecies. The taxa are distributed in western and central southern

Figure 1. Species in the *Arctotis* Annual Clade. **A-B.** *Arctotis venusta* Norl. **C.** *Arctotis* "chrysantha". **D.** *Arctotis leiocarpa* Harv. **E-F.** *Arctotis flaccida* Jacq. Photos: R.J. McKenzie.

Figure 2. Species in the *Arctotis* Annual Clade. **A-B.** *Arctotis hirsuta* (Harv.) Beauverd. **C-D.** *Arctotis fastuosa* Jacq. **E.** *Arctotis "namibiensis"*. **F.** *Arctotis subacaulis* (DC.) Beauverd. Photos: A, D. Gwynne-Evans; B-D, F, R.J. McKenzie; E, C.A. Mannheimer.

Table 1. Character states useful to discriminate taxa in the *Arctotis* Annual Clade.

TAXA	**CHARACTERS**														
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**
A. **sp. nov. *"chrysantha"***	a	a	a	b	a	b	a,b	b	a	d	a	c	a	a,b	b
A. fastuosa	a,b	a,b	a	a	a	a	b	a	b	b	NA	a	NA	NA	NA
A. flaccida	b	b	b	b	a	b	b	b	b	b,c	NA	b	b	b	a
A. hirsuta	b	b	b	b	a	b	a	b	b	b	NA	b	b	b	a
A. leiocarpa	a,b	a,b	a	b	b	b	a,b	b	a	a,d	b	c	a	c	c
A. "macrocephala"	b	b	b	b	a,b	a	a,b	a	b	b,c	NA	a,b	b	b	a
A. **sp. nov. *"namibiensis"***	b	b	b	b	b	a	b	a	b	c	NA	b	b	b	a
A. subacaulis	b	b	b	b	a	a	b	a	a,b	a,b	NA	a,b	b	b	a
A. venusta	a	a	b	b	a	b	a,b	b	a	d	b	c	a	a,b	c

Characters: 1, Leaf pubescence: a, lanate; b, pilose. **2**, Outer involucral bract pubescence: a, lanate; b, pilose. **3**, Cypsela shape: a, obconical; b, obovoid. **4**, Cypsela symmetry: a, bilaterally flattened in tangential plane; b, not bilaterally flattened. **5**, Shape of cypsela base: a, subtruncate to tapering; b, abruptly narrowed above base. **6**, Number of abaxial wings on cypsela: a, two; b, three. **7**, Margin of cypsela wings: a, entire; b, undulate to dentate. **8**, Number of abaxial 'cavities' on cypsela: a, one; b, two. **9**, Cypsela surface: a, smooth; b, rugose. **10**, Pubescence on cypsela surface: a, glabrous; b, papillate to clavate; c, pilose; d, lanate. **11**, Length of basal whorl of twin hairs relative to cypsela length: a, shorter to ±equal length; b, distinctly longer. **12**, Number of whorls of pappus scales: a, zero; b, uniseriate; c, biseriate. **13**, Shape of pappus scales in inner whorl: a, obovate; b, suborbicular. **14**, Apex of pappus scales in inner whorl: a, obtuse; b, rounded; c, subtruncate. **15**, Length of pappus scales of inner whorl relative to cypsela length: a, shorter; b, ±equal length; c, distinctly longer. NA, Not applicable.

Africa (Figure 3). Dissection of relationships within this clade is providing fascinating insights into factors that contributed to recent floristic diversification in semi-arid southern Africa.

The only molecular data currently available for phylogenetic reconstruction of the clade are nucleotide sequences for non-coding nrDNA (ITS) and cpDNA (*trnT–trnF* and *trnH–psbA*) regions (McKenzie & Barker, 2008). Bayesian inference consistently resolves a previously unrecognised species, *A.* "chrysantha", restricted to coastal red aeolian sediments of the Kalahari Group, as an early divergence (Figure 4). The monophyly of *A. venusta* Norl. and *A. leiocarpa* Harv., from the year-round and summer rainfall regions (Figure 3), is supported but the sequence of divergence events varies depending on the dataset. The remaining taxa form a poorly resolved "*A. fastuosa* species complex".

A cpDNA haplotype network, constructed using the TCS statistical parsimony algorithm (Templeton et al., 1992), suggests there is a degree of taxonomic structure to cpDNA haplotype diversity (Figure 5). *Arctotis venusta* and *A.* "chrysantha" harbour taxon-specific haplotype lineages, and a group of haplotypes is predominantly detected in *A. subacaulis* (DC.) Beauverd (group D, Figure 5). Notably, *A. fastuosa* includes haplotypes from at least four independent lineages and harbours the greatest haplotype diversity. Resolution of an "*A. fastuosa* species complex" is not supported.

The species exhibit limited vegetative diversification: initially rosulate, caulescent upon flowering, and usually lyrate-pinnatisect or pinnatisect, relatively thin to fleshy, glandular leaves with thin woolly or pilose pubescence (Figure 1 and Figure 2). The involucre exhibits subtle differences among the taxa, with the outer involucral bracts bearing a leafy apical appendage that varies in length, width and shape, and clothed with cobwebby or pilose pubescence (Figure 6). In contrast, the cypsela and pappus have undergone notable evolution (Figure 4, Table 1), putatively concomitant with geographic expansion and taxonomic diversification.

Land of extremes

The Desert biome is the most arid region of South Africa, hugging the lower Gariep River to the Atlantic coast. This is a region of extremes: the lowest amount and highest variability in rainfall, among the highest temperatures recorded, and the highest incidence of coastal fog.

Near the eastern limit of the Desert biome, north of Pofadder, Northern Cape
Photo by Robert McKenzie

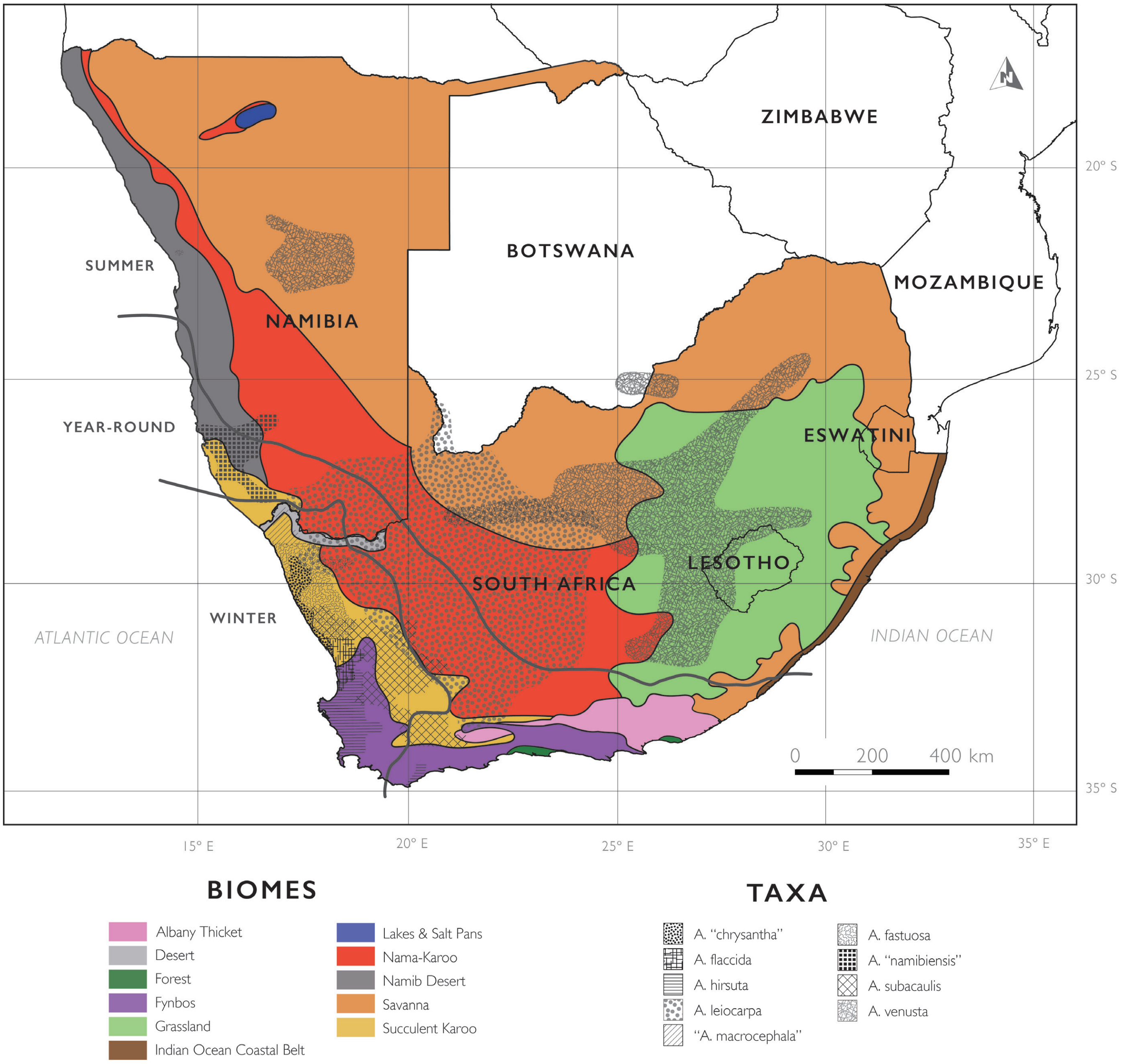


Figure 3. Known distribution in southern Africa of the taxa recognised in the *Arctotis* Annual Clade by McKenzie & Barker (in press) in relation to recognised biomes. The biomes for Namibia and South Africa are as delineated by Mendelsohn et al. (2002) and SANBI (2018), respectively. The boundaries of the regions in which greater than 66% of the annual precipitation falls in either the winter or summer months, with a transitionary region that receives rainfall all year round (based on Chase & Meadows, 2007), are indicated. Biome areas have been simplified and Azonal Vegetation is not shown.

Although incompletely resolved, the phylogenies enable formulation of a hypothesis of cypsela and pappus evolution in the clade. *Arctotis* is characterised by cypselae with three woody, abaxial wings that are fused at each end to create two 'cavities' (McKenzie et al., 2005). The earliest-diverging extant lineages in the Annual Clade (*A.* "chrysantha", *A. venusta* and *A. leiocarpa*) have relatively large cypselae with three well-developed abaxial wings, forming two 'cavities', and a biseriate pappus of scales with the inner whorl longer than the cypsela (Figure 4). The *A. fastuosa* complex exhibits reduction in size of the cypsela, abaxial wings and pappus scales, with loss of the medial abaxial wing and pappus in *A. fastuosa* and *A. subacaulis*. These taxa are distributed in the most arid areas (average annual rainfall as low as ~50 mm). The latter cypsela phenotypes are consistent with adaptation for reduced dispersibility in a semi-arid, desert-like environment.

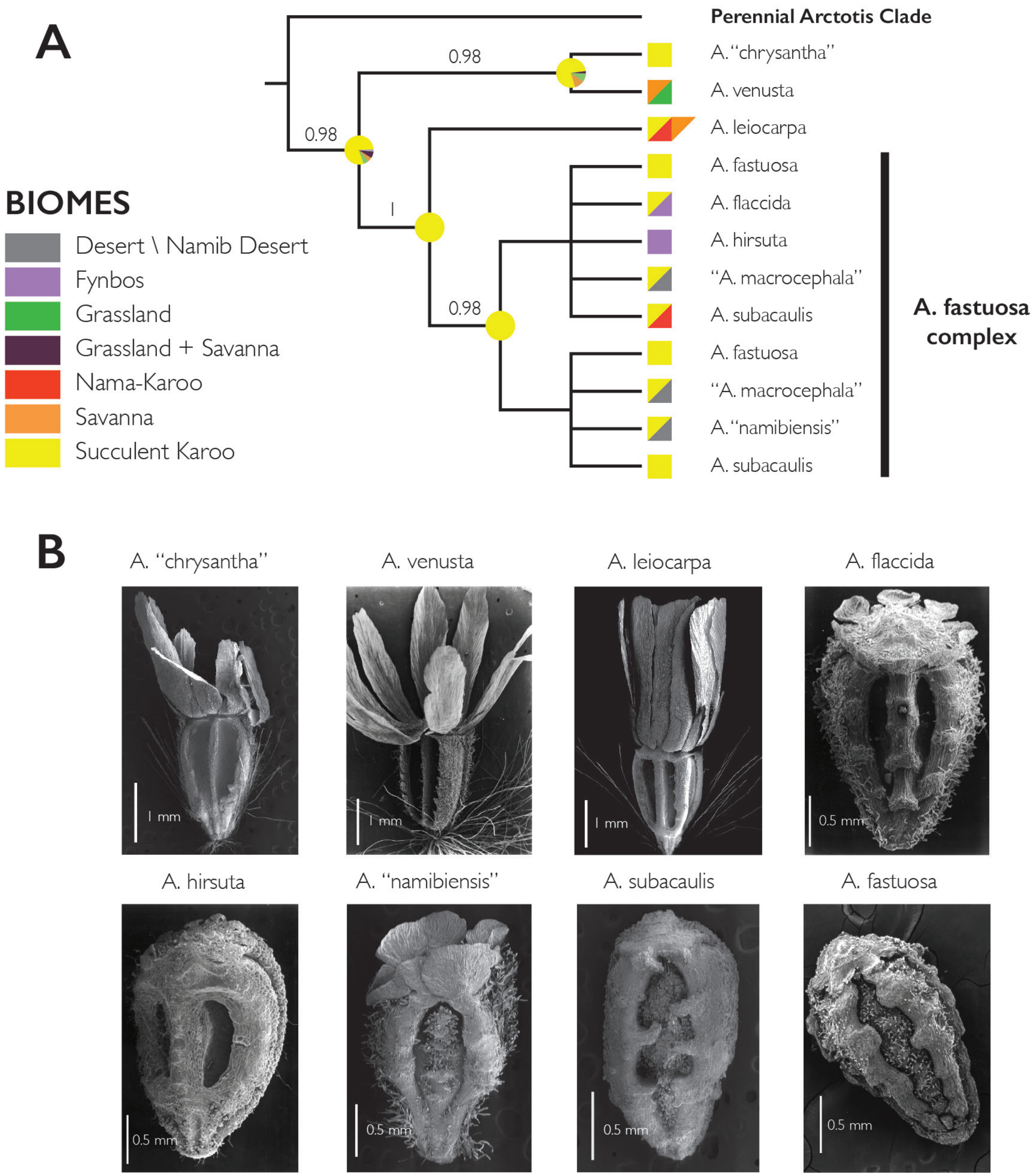


Figure 4. A. Simplified Bayesian inference phylogeny of the *Arctotis* Annual Clade reconstructed from nrDNA ITS sequences and cypselae of the recognised taxa. Support values at nodes are posterior probabilities. Pie charts at nodes indicate ancestral ranges estimated using the dispersal–extinction–cladogenesis model, including the *j* parameter to allow for founder-event speciation, maximum of six areas, and conservative root date of 9.1 Mya, as implemented in BioGeoBEARS (Matzke, 2018). Boxes beside species names indicate present-day biome distributions. **B.** SEM photos of *Arctotis* annual clade. The fruit of *A. "chrysantha"*, *A. leiocarpa* and *A. venusta* are typical for *Arctotis* as a whole: the abaxial vascular ribs of the cypsela are elaborated into either three woody wings, which create two abaxial 'cavities'; the pappus comprises two unequal whorls of papery scales; and a persistent whorl of long twin trichomes is attached to the cypsela base (mostly removed in the depicted fruit). The *A. fastuosa* complex exhibits reduction of these structures to varying degrees and loss of the whorl of twin trichomes.

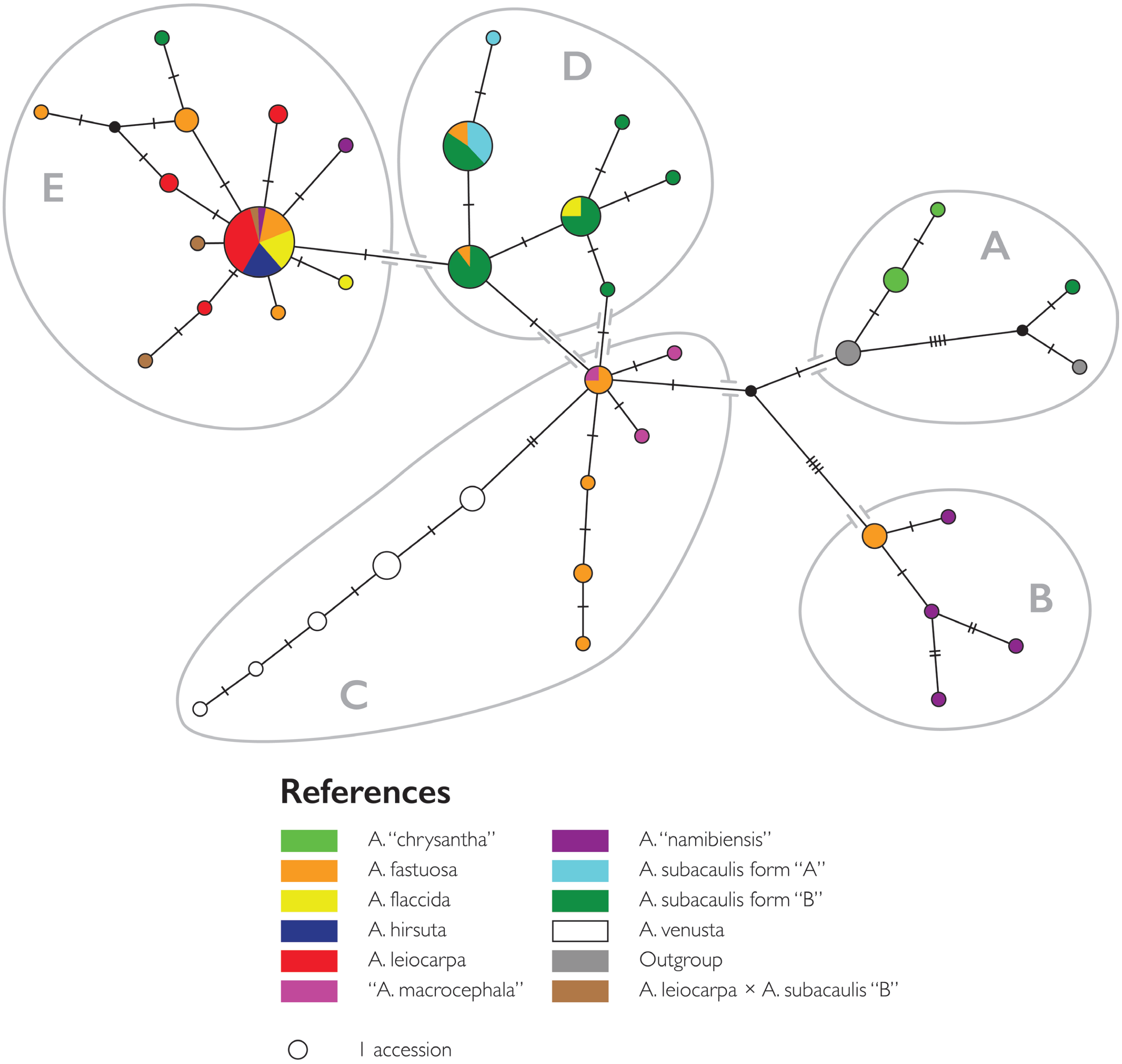


Figure 5. Chloroplast DNA haplotype network constructed from concatenated sequences for the *trnT–trnF* and *trnH–psbA* regions using the TCS statistical parsimony method.

An early attempt at estimating the timing of divergence of the *Arctotis* Annual Clade, using published ITS mutation rates for other Asteraceae groups and a relaxed molecular clock with branch substitution rates drawn from a lognormal distribution (McKenzie & Barker, 2008), yielded 95% highest posterior density intervals ranging from 1.5 to 9.1 Mya (Late Miocene to Early Pleistocene). While imprecise, this range coincides with the trend for increasing seasonal aridity in the northwestern Cape, especially during the past ~3.2 My (Marlow et al., 2000). A possible Late Pliocene/Early Pleistocene origin of the clade is comparable with estimates for development of annualness in southern African *Nemesia* (Datson et al., 2008).

Here, we present results from preliminary bioclimatic and historical biogeographic analyses of the clade. An exploratory DIVA-GIS analysis of the relationships of altitude and 19 bioclimatic variables (WorldClim

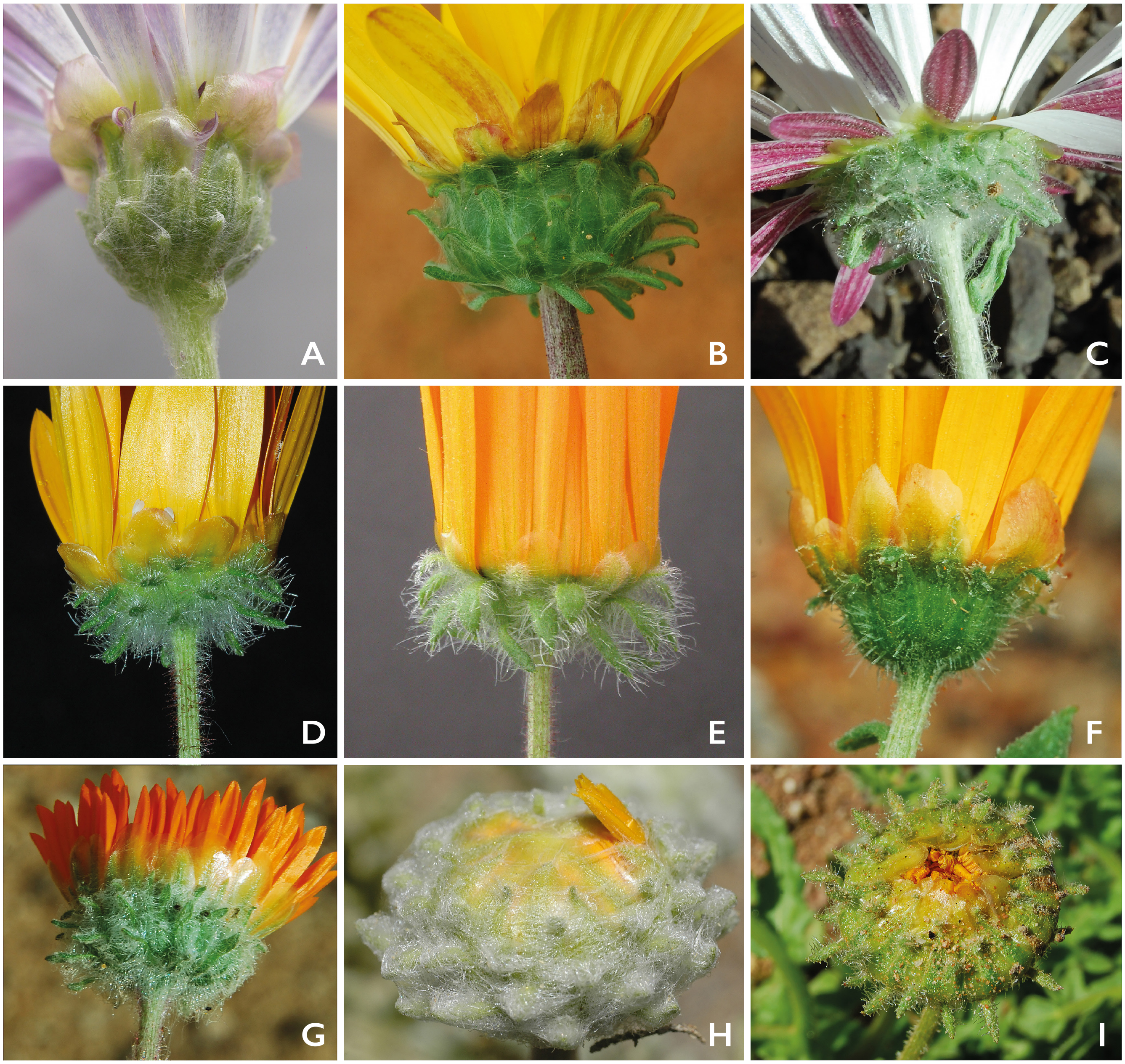


Figure 6. Involucre of species in the *Arctotis* Annual Clade. **A.** *Arctotis venusta* Norl. **B.** *Arctotis "chrysantha"*. **C.** *Arctotis leiocarpa* Harv. **D.** *Arctotis flaccida* Jacq. **E.** *Arctotis hirsuta* (Harv.) Beauverd. **F.** *Arctotis subacaulis* (DC.) Beauverd. **G-H.** *Arctotis fastuosa* Jacq. **I.** *Arctotis macrocephala* (DC.) Beauverd. Photos: A–G, I, R.J. McKenzie; H, D. Gwynne-Evans.

database; https://www.worldclim.org/data/bioclim.html) and the provenance of the 118 sequenced accessions suggests that altitude and several temperature and precipitation parameters may have contributed to the adaptive radiation (Figure 7). Further analysis to eliminate autocorrelated variables and incorporate geomorphic (e.g., edaphic) factors with an expanded dataset incorporating authenticated herbarium accessions will be undertaken.

The extant species distributions suggest a relationship with biomes in Namibia and South Africa (Figure 3). Model-building methods and statistical testing in historical biogeography continue to evolve and various technical challenges remain. Methods in current use each have advantages and drawbacks (Ree & Sanmartín, 2018; Schram, 2019). We acknowledge that resolution of relationships within the *A. fastuosa* complex is crucial to enable

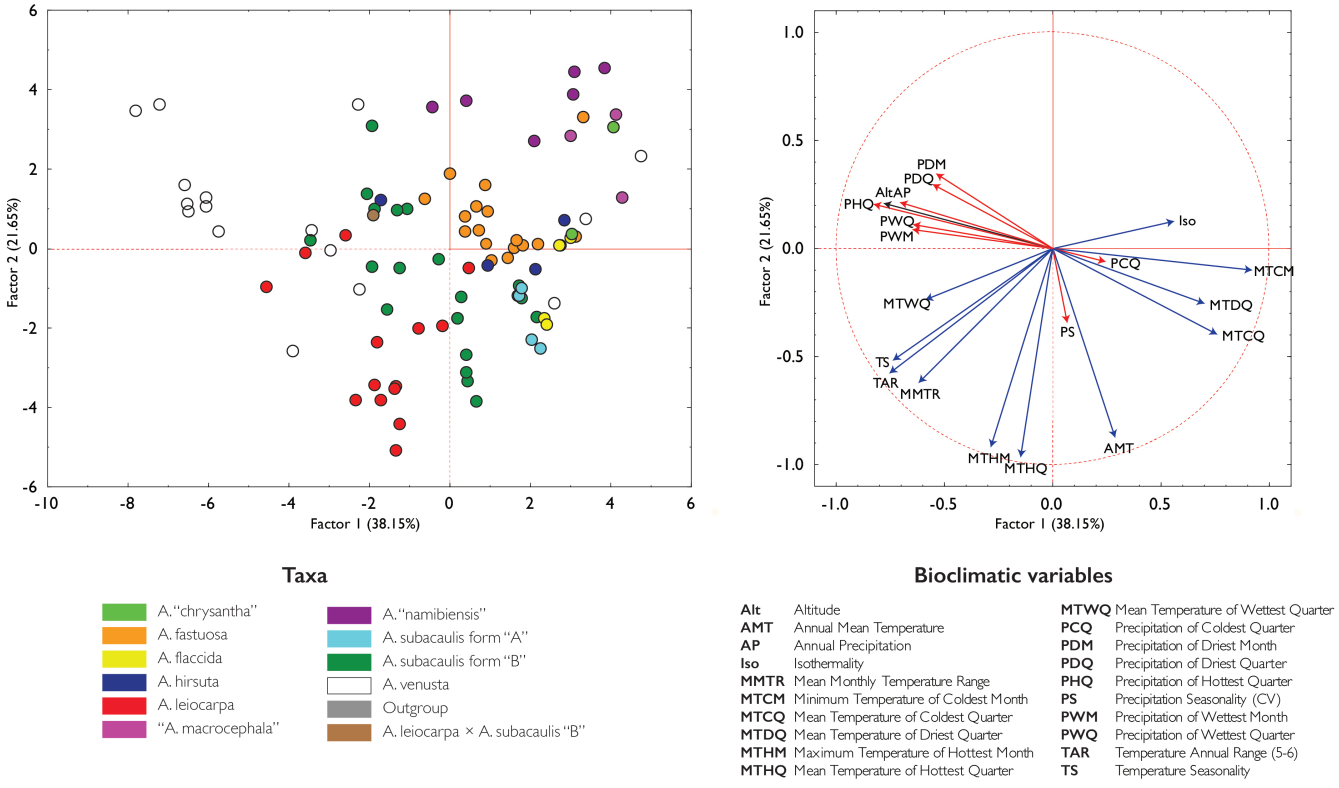


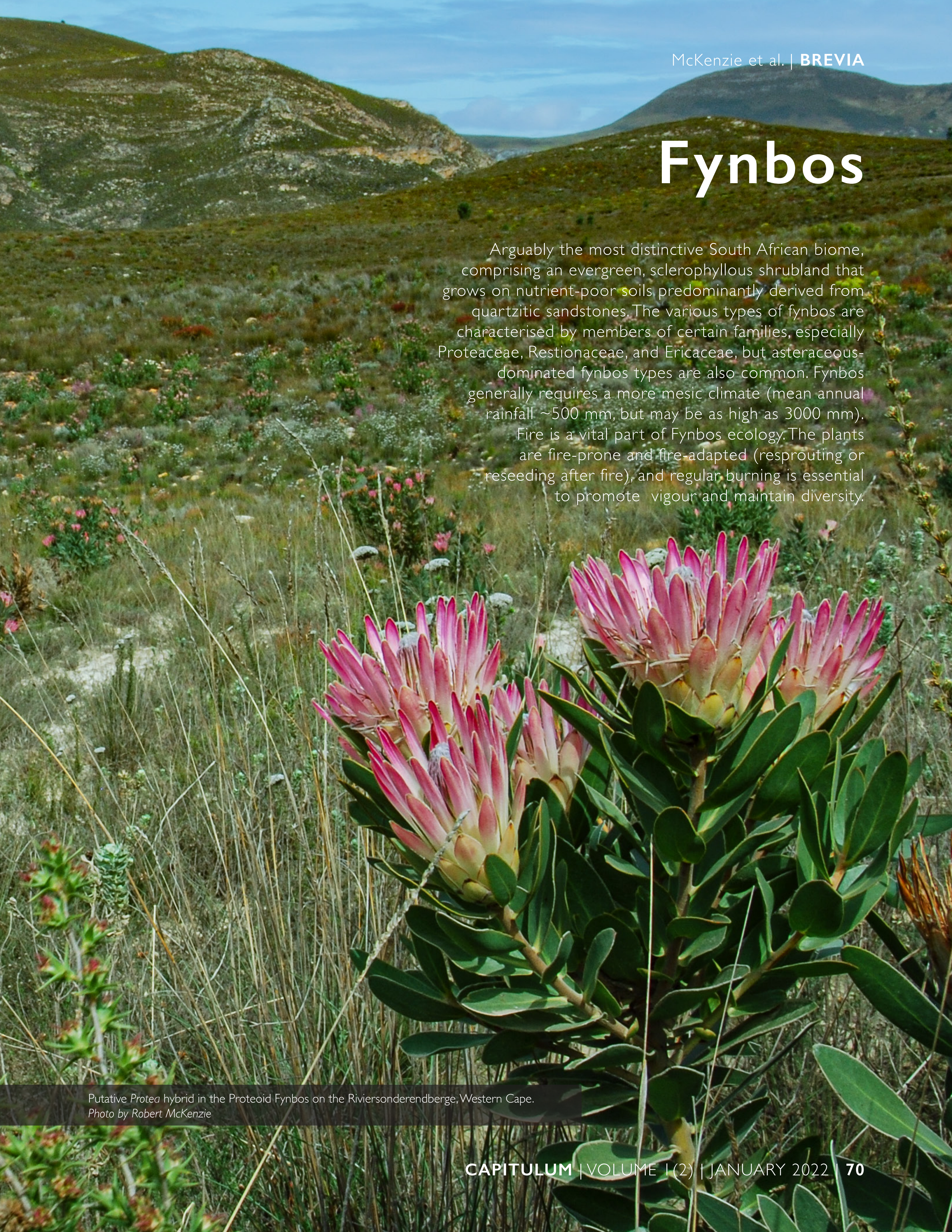
Figure 7. DIVA-GIS analysis of the geographic distribution of the 115 sequenced accessions and 20 bioclimatic variables. The loadings of precipitation- and temperature-related variables to the first two factors are represented by red and blue vectors, respectively.

rigorous testing of biogeographic hypotheses. Keeping this limitation in mind, we conducted an exploratory estimation of biome-scale ancestral ranges with the R package 'BioGeoBEARS' (Matzke, 2018). A chronogram was generated from the majority-rule consensus Bayesian inference tree, using a relaxed molecular clock and the aforementioned minimum and maximum posterior densities from McKenzie and Barker (2008) to date the root, with the function 'chronos' in the R package 'ape' (Paradis et al., 2021). Six models were compared: dispersal–extinction–cladogenesis (DEC; Ree & Smith, 2008), dispersal–vicariance analysis-like (DIVA-LIKE; Yu et al., 2010) and BAYAREA-LIKE (Landis et al., 2013), each with or without the 'jump dispersal' (*j*; founder event) parameter. The DEC + *j* model showed the best fit in all analyses based on corrected Akaike information criterion values. Ancestral range estimations with all models that included the *j* parameter were highly consistent. Maximum range size (4 or 6 areas) and pruning of terminals (28% of the total number, removing multiple accessions from the same biome of a taxon within a clade) had negligible impact on range and parameter estimates but the latter improved model fit. The analyses suggested that diversification within the clade is not explainable solely by a simple vicariance model with parapatric speciation.

Formulation of a biogeographic hypothesis for future testing, with emphasis on the basal nodes, is feasible. The clade ancestor likely diverged in a region of low, erratic or aseasonal rainfall, possibly in present-day southwestern Namibia or northwestern South Africa (Figure 8). Southwestern Africa has a long history of aridity dating to the Middle Miocene (~16–17 Mya; Senut et al., 2009). Populations of annual *Arctotis* species in southwestern Namibia and northern Namaqualand harbour the highest present-day cpDNA haplotype diversity. Populations in this region harbour derivatives of hypothetically early-evolving cpDNA haplotypes.

Fynbos

Arguably the most distinctive South African biome, comprising an evergreen, sclerophyllous shrubland that grows on nutrient-poor soils predominantly derived from quartzitic sandstones. The various types of fynbos are characterised by members of certain families, especially Proteaceae, Restionaceae, and Ericaceae, but asteraceous-dominated fynbos types are also common. Fynbos generally requires a more mesic climate (mean annual rainfall ~500 mm, but may be as high as 3000 mm). Fire is a vital part of Fynbos ecology. The plants are fire-prone and fire-adapted (resprouting or reseeding after fire), and regular burning is essential to promote vigour and maintain diversity.



Putative *Protea* hybrid in the Proteoid Fynbos on the Riviersonderendberge, Western Cape.
Photo by Robert McKenzie

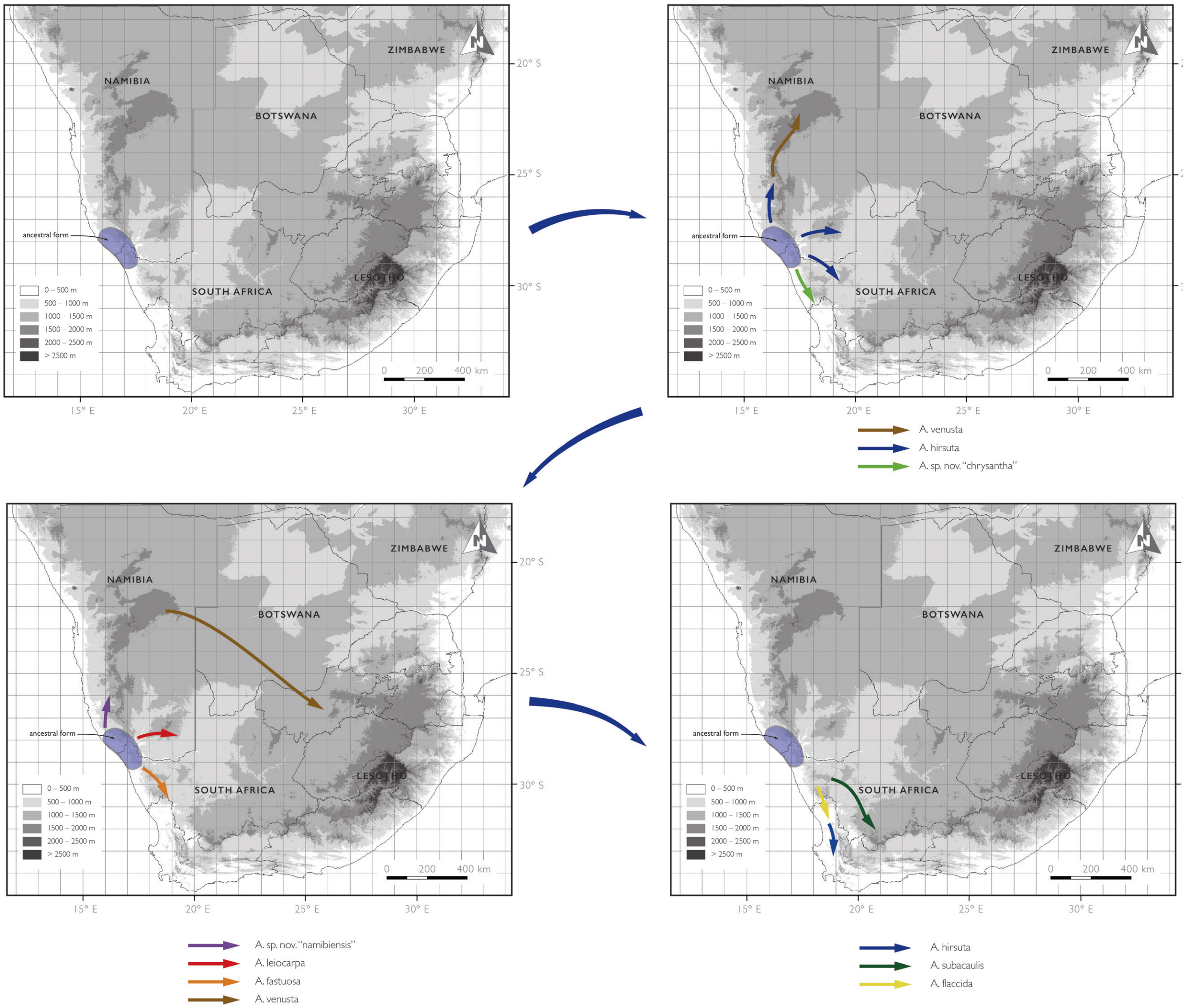


Figure 8. Biogeographic hypothesis of the possible ancestral area and taxonomic diversification of the *Arctotis* Annual Clade.

Strong climatic and edaphic gradients and habitat heterogeneity are likely to have been important drivers of diversification. *Arctotis* "chrysantha" may have arisen as an early adaptation to southwestern redistribution of Kalahari Group red aeolian sediments. The oldest Kalahari sand deposits are of Pliocene to Pleistocene age (Vainer et al., 2018), but the deposits on the Namaqualand coastal plain are of more recent origin (e.g., Philander & Rozendaal, 2015). Current molecular data provide conflicting signals on the timing of divergence of *A. venusta*, the only summer-rainfall endemic species. Namibian cpDNA haplotypes of *A. venusta* are indicated to be ancestral to South African haplotypes (Figure 5), suggesting *A. venusta* adapted to a summer-rainfall regime in central or southern Namibia. Eastward expansion through the summer-rainfall savanna and grassland of Botswana is more plausible than through the semi-arid, erratic-rainfall Nama-Karoo, which undoubtedly poses a severe biogeographic barrier to eastward migration of Namaqualand species. Nevertheless, *A. leiocarpa* adapted to the erratic, year-round transitional rainfall zone in eastern Karas and the Nama-Karoo and may have secondarily dispersed into the Succulent Karoo.

Diversification of the *A. fastuosa* complex in the winter-rainfall region may have coincided with reduction in cypsela size and dispersibility. Southward and eastward range expansion and parapatric speciation may account for the divergence of *A. flaccida* Jacq. and *A. hirsuta* (Harv.) Beauverd on the coastal plain, and *A. subacaulis* in drier inland regions. Expansion and contraction of the winter-rainfall zone in wetter glacial and drier interglacial periods, respectively, during the Pleistocene is implicated (Tankard & Rogers, 1978; Chase & Meadows, 2007). Such oscillations may have promoted allopatric speciation in refugia, while also contributing to introgression and genetic blurring between contiguous taxa in the *A. fastuosa* complex. Biogeographic exploration of the adaptation to extreme aridity by *A. "namibiensis"* requires resolution of the taxon's paraphyly in phylogenetic reconstructions.

Alternative data, such as polymorphic molecular markers or next-generation sequencing data, are needed to improve resolution of the *A. fastuosa* complex to test this biogeographic hypothesis. A target-enrichment sequencing methodology for Compositae (Mandel et al., 2014) has shown potential for resolving relationships within traditionally recalcitrant groups (Susanna, 2021), and offers a promising tool to resolve relationships within the Arctotidinae. Phylogenetic dating using additional recent fossil records for the family (see Mandel et al., 2019) may refine divergence and diversification estimates for the clade, and improve correlation with past geoclimatic changes.

ACKNOWLEDGMENTS

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New record of *Dasyphyllum* (Barnadesieae) from Uruguay

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ABSTRACT

Dasyphyllum spinescens (Barnadesioideae) is here reported for the flora of Uruguay. This new record redefines the geographic area for *Dasyphyllum* (containing *ca.* 31 spp.) by extending its southern limit. We provide a detailed morphological description with illustrative photographs and information on the distribution, habitat, and phenology of *D. spinescens*.

Keywords: Asteraceae, Barnadesioideae, geographic distribution
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INTRODUCTION

Dasyphyllum Kunth (Barnadesioideae) is exclusively distributed in South America, being recorded in the Andes from Venezuela to northwestern Argentina, and from Eastern Brazil, through Bolivia, Paraguay until northeastern Argentina (Cabrera, 1959; Stuessy et al., 2009; Urtubey, 2014; Ferreira et al., 2021). It occurs in a large number of environments ranging from dry areas such as the Puna and Cerrado to humid areas such as Atlantic forest (Cabrera, 1959; Stuessy et al., 2009; Saavedra et al., 2014, 2018; Ferreira et al., 2019, 2021). Species of *Dasyphyllum* generally present a shrubby habit, sometimes arboreal and lianas, the leaves have acrodromous venation, capitula are discoid with monoclinous or functionally pistillate florets (gynodioecy), corollas cream to white, and anthers show bilobed apical appendices (Stuessy et al., 2009; Ferreira et al., 2021).

Cabrera (1959) recognized 36 species of *Dasyphyllum* placed in two subgenera: *Dasyphyllum* subg. *Archidasyphyllum* Cabrera with two species and *Dasyphyllum* subg. *Dasyphyllum* Cabrera with 34 species. From early on, the monophyly of *Dasyphyllum* was questionable. The species of the subg. *Archidasyphyllum* had characteristics that set them apart from the rest of the *Dasyphyllum* species (Cabrera, 1959). Recent works that combine morphological and molecular analyzes confirm that *Dasyphyllum*, as it is traditionally known, is a paraphyletic group (Saavedra, 2011; Ferreira et al., 2019). Saavedra (2011) in her taxonomic review of the genus recognized 33 species. More recently, Ferreira et al. (2019) proposed a new circumscription of *Dasyphyllum* by raising the subg. *Archidasyphyllum* to generic rank. According to Ferreira et al. (2021), the genus includes 27 species and four species not yet described, which would render the total current

A brand new addition

The list of Barnadesieae for Uruguay adds now to monotypic *Schlechtendalia* Less., *Dasyphyllum spinescens* (Less.) Cabrera. The new record represents a new Compositae tree for the country, increasing the number to four, the others being *Baccharis longiattenuata* A.S.Oliveira (Astereae), *Moquiniastrum polymorphum* (Less.) G.Sancho (Gochnatieae) and *Tessaria integrifolia* Ruiz & Pav. (Inuleae).

Dasyphyllum spinecens, Sierra de Ríos, Cerro Largo, Uruguay.
Photo by Mauricio Bonifacino

Figure 1. *Dasyphyllum spinescens* (Less.) Cabrera. **A.** Habitat in Sierra de Ríos, Cerro Largo, Uruguay. **B.** Young branch, with spines; notice the distinctive acrodromous venetion (a generic distinctive feature). **C.** Rhytidome and characteristic fasciculate spines. **D.** Top view of the capitulum; arrow indicates bifid connectival appendage (a generic distinctive feature). **E.** Side view of capitulescence. Photos: M. Bonifacino.

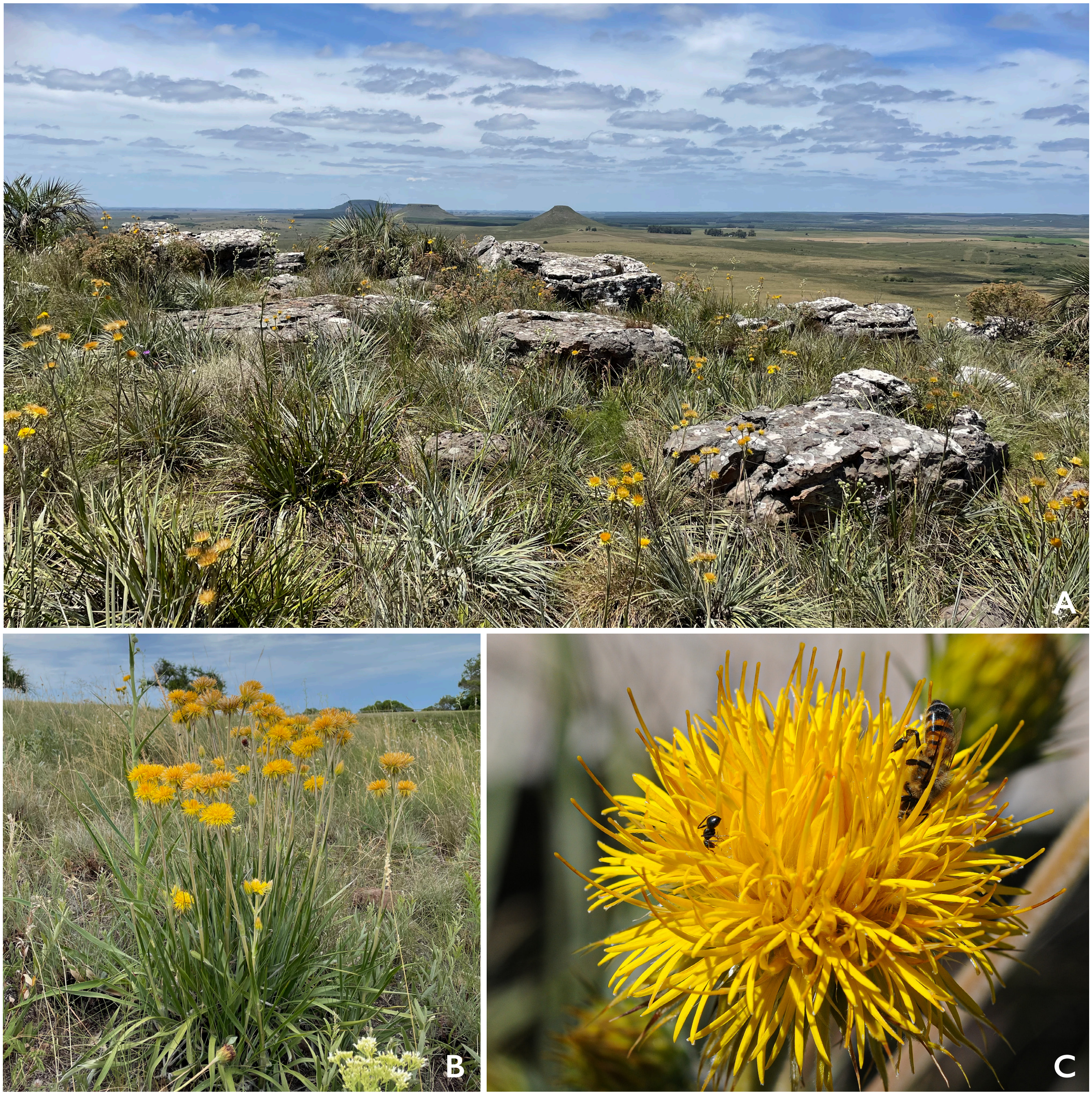

Figure 2. *Schlechtendalia luzulilfolia* Less., the other Barnadesieae species found in Uruguay. **A.** Habitat in Cerro Miriñaque (Rivera). **B.** Habit, notice grass like appearance. **C.** Close up of capitulum, notice pseudobilabiate corollas. Photos: M. Bonifacino.

figure to ca. 31 spp., still retaining its status as the largest genus of the tribe. The greatest diversity of the genus is in Brazil where 21 species are recognized (Stuessy et al., 2009; Saavedra, 2010).

As part of our ongoing project titled "Flora del Uruguay: Familia Compositae", we discovered *Dasyphyllum* (Figure 1), a second genus of Barnadesieae for Uruguay. Of those two genera, monotypic *Schlechtendalia* Less. (Figure 2) is widely distributed across the country, while *Dasyphyllum* is so far restricted to one locality in northern Uruguay.

After studying collected specimens and comparing them with the information provided in the literature and the study of the type materials, we conclude that the species found in Uruguay represents the southernmost distribution of *Dasyphyllum spinescens*

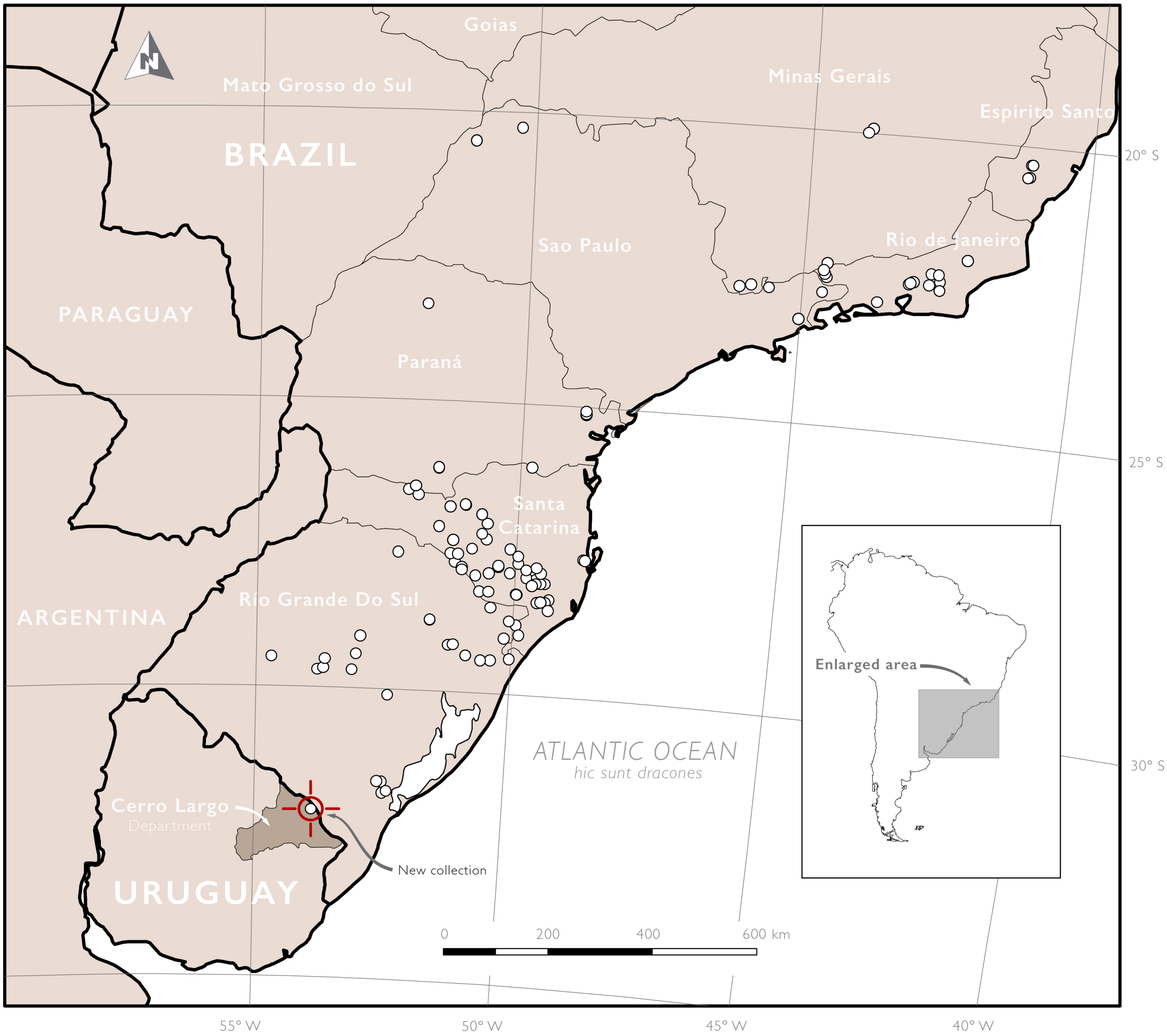

Figure 3. *Dasyphyllum spinescens* (Compositae: Barnadesieae) geographic distribution map.

(Less.) Cabrera, and therefore the southernmost distribution of *Dasyphyllum*. According to Cabrera (1959), *D. spinescens* is a tree characterized by light brown bark and fasciculate spines, by its upper leaves with very conspicuous spiny apex, sparsely pubescence, and capitulum with involucre campanulate.

The objective of this work is to report the presence of *Dasyphyllum spinescens* in Uruguay thus expanding the limits of the genus geographic distribution. We present a detailed morphological description, photographs, and a distribution map.

The images of the type specimens available on Jstor Global Plant (JSTOR, 2021) were analyzed, and the herbarium database (Reflora, 2021) was used to access the herbarium records from CEPEC, CRI, ECT, ESA, FLOR, FURB, HDCF, HEPH, HUEM, HUFU, LUSC, MBML, MG, NY, RB, RBR, US, VIES, acronyms according to Thiers (2017). For the maps, the geographical distribution was obtained from the records analyzed and plotted using QGIS version 3.4 (QGIS Development Team, 2019).

From the specimen deposited in MVFA and the fresh material collected, we made a detailed description.

The analysis of the reproductive morphology of *Dasyphyllum spinescens* was carried out with both pressed material and fresh cultivated material, from a specimen of the same accession as the individual found in the wild.

TAXONOMIC TREATMENT

Dasyphyllum spinescens (Less.) Cabrera, Revista Mus. La Plata, Secc. Bot. 9 (38): 57, 1959. *Flotovia spinescens* Less., Linnaea 5: 251, 1830. *Chuquiraga spinescens* (Less.) Baker, Fl. Bras. 6 (3): 362, 1884. Type: Brazil, Brasilia, *Sellow* s.n. (B†) Figure 1.

Trees, evergreen, ca. 6 m tall, stems erect, cylindrical to quadrangular, sericeous-pubescent with lenticels, adult branches with fasciculate spines. **Leaves** alternate, 3.5–6 × 0.85–1.5 cm, petioles 0.5–1 cm long, narrowly elliptic, base acute, apex acuminate to mucronate, adaxial and abaxial surfaces sericeous, acrodromous venation, herbaceous to coriaceous, discolor, margins entire. **Capitulescences** paniculiform, capitula 9 to 15, peduncles 0.8–2.5 cm long, sericeous-pubescent. **Involucres** 8–9 × 4–5 mm, campanulate; subinvolucral bracts 0 to 4, 3–6 × 1.5–2 mm, elliptic, apex acuminate to mucronate, herbaceous-coriaceous; phyllaries in 7 to 9 series, graduated in length, imbricate, dark brown, outer phyllaries 3–6 × 2–3 mm, ovate, base rounded to obtuse, apex acute, pubescent towards the margin, chartaceous, margin entire, inner phyllaries 6–7 × 2–2.3 mm, ovate, curved outwards, base acute to obtuse, apex acute, pubescent to puberulous on abaxial surface, puberulous at the apex on adaxial surface, chartaceous, margin entire. **Receptacles** flat, paleate, pilose. Paleae ca. 14, 10.5–11 × 0.5 mm, linear in the first two-thirds and elliptic towards the apex, base acute, apex acute, pubescent on abaxial surface and glabrous on adaxial surface, chartaceous, margins entire. **Florets** ca. 25, monoclinous, in 2 to 3 series, corollas tubulose, tube 4–4.2 mm long, lobes 5, 4–5 × 0.5–0.6 mm, elliptic, corollas light yellow to white-yellow, tube villous inside, lobes villous to tomentose towards the apex on abaxial surface and glabrous adaxially. **Anthers** slightly sagittate 4.2–4.3 mm long, basal appendages 0.3 mm long, connective appendix 0.3 × 0.3 mm, bilobed, lobes ovates, apex acute. **Style** 12 mm long, style branches 0.5 mm long, ovate, apex acute, glabrous. **Cypselae** 2.1–2.5 mm long, fusiform cylindrical, tomentose. **Pappus** 7–8.5 mm long, uniseriate, homomorphic, stramineous plumose bristles, persistent.

Distribution and habitat: Southeastern and southern Brazil, in the states of Minas Gerais, Espírito Santo, São Paulo, Rio de Janeiro, Paraná, Santa Catarina and Rio Grande do Sul (Cabrera, 1959; Saavedra, 2010). *Dasyphyllum spinescens* has only been reported for Uruguay in the department of Cerro Largo (Figure 3), where it grows in subtropical semideciduous submontane riverine forests (Figure 1A).

Phenology: Flowering from February to March.

Specimens examined: URUGUAY. CERRO LARGO: Sierra de Ríos, Cuchilla de Yaguarón, S 32°07'40.21" W 53°49'49.67", 13-III-2012, *Bonifacino & Speroni 4273* (MVFA).

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It's complicated:

A brief overview of the taxonomy of the New Zealand *Brachyglottis rotundifolia* species complex (Senecioneae)

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ABSTRACT

Brachyglottis J.R.Forst. & G.Forst. (Senecioneae Cass.; Asteraceae) is a mostly woody genus of *ca.* 24 species. It is endemic to New Zealand in classifications where *B. brunonis* (Hook.f.) B.Nord. from Tasmania is segregated as *Centropappus brunonis* Hook.f. As part of his undergraduate research project at University of Canterbury, Eastman-Densem performed an unpublished pilot study into patterns of morphological variation in a group of four discoid *Brachyglottis* species with unclear taxonomic boundaries (i.e., the *B. rotundifolia* species complex): *B. buchananii* (J.B.Armstr.) B.Nord., *B. cockaynei* (G.Simpson & J.S.Thomson) B.Nord., *B. elaeagnifolia* (Hook.f.) B.Nord., and *B. rotundifolia* J.R.Forst. & G.Forst. With the aim of supporting future studies focused on resolving this species complex, we here provide a brief overview of its current taxonomic treatment and synonymy (summarized in Table 1), with notes about its complicated taxonomic history. We conclude that although *Senecio bennettii* G.Simpson & J.S.Thomson is listed as a synonym of *B. buchananii* in recent publications and other works and treatments, this name should instead be considered as a synonym of *B. rotundifolia* if the current taxonomic delimitation of the complex is followed.

Keywords: Asteraceae, Compositae, nomenclature, *Senecio bennettii*, species delimitation

INTRODUCTION

The Brachyglottidinae (Senecioneae) are a mostly Australasian subtribe in which currently between seven and nine genera are recognised. Its center of diversity is in New Zealand, where all but three of its genera are found. *Brachyglottis* J.R.Forst. & G.Forst. is the largest of these. The relatively recent diversification of this genus, coupled with the varied topography and climate of New Zealand has contributed to impressive morphological diversity within *Brachyglottis* (Wagstaff & Breitwieser, 2004), as well as groups of species within which species boundaries are difficult to determine (i.e., Mennes et al., 2012; Millar et al., 2018). This is certainly the case for a group of four discoid *Brachyglottis* species (i.e., the *B. rotundifolia* J.R.Forst. & G.Forst. species complex; Figure 1). An overview of its taxonomic history of this *Brachyglottis* complex was prepared as part of a preliminary study aimed at resolving its species delimitation.

TAXONOMIC OVERVIEW

Brachyglottis rotundifolia J.R.Forst. & G.Forst., Char. Gen. Pl., ed. 2: 92 (1776) ≡ *Cineraria rotundifolia* (J.R.Forst. & G.Forst.) G.Forst., Fl. Ins. Austr. Prodr.: 56 (1786) ≡ *Senecio reinoldii* Endl., Ann. Wiener Mus. Naturgesch. 1: 169 (1836), nom. nov., non *Senecio rotundifolius* Stokes (1812), nec Lapeyr. (1813) ≡ *Senecio rotundifolius* (J.R.Forst. & G.Forst.) Hook.f., Bot. Antarct. Voy. II. (Fl. Nov.-Zel.). 1: 149 (1852), nom. illeg., auct non Stokes (1812), nec Lapeyr. (1813) ≡ *Senecio puffini* Allan ex Rehder, J. Arnold Arbor. 27: 174 (1946), nom. superfl. **Type:** Forster (K00844033*), Dusky Bay.

Senecio bennettii G.Simpson & J.S.Thomson, Trans. & Proc. Roy. Soc. N. Z. 72: 39 (1942). **Type:** G. Simpson (CHR29513!, syn), J.S. Thomson & G. Simpson (AK35247*, syn), Mt. Cargill, near Dunedin, upper forest margins, 600m.

Complex past

The *Brachyglottis rotundifolia* complex has a dynamic history of changes in its species delimitation. Close-up of the capitulescence, showing its flower heads.

Stewart Island, New Zealand
Photo by Ilse Breitwieser

This taxon was first described as *Brachyglottis rotundifolia* (Forster & Forster, 1776), and then transferred to *Cineraria* L. (i.e., *Cineraria rotundifolia* (J.R.Forst. & G.Forst.) G.Forst.; Forster, 1786). Endlicher (1836) subsequently moved it to *Senecio* L., creating the nomen novum *S. reinoldii* Endl., because the name *S. rotundifolius* was occupied by a northern hemisphere species (i.e., *S. rotundifolius* Stokes). Hooker (1852) seems to have overlooked this and made the illegitimate combination *S. rotundifolius* (J.R.Forst. & G.Forst.) Hook.f. Unfortunately, this combination continued to persist, appearing for example in Kirk (1899) and Cheeseman (1906a, 1925). Rehder (1946) finally recognised that this combination could not be used and, following correspondence with Allan, created the replacement name *S. puffini* Allan ex Rehder. However, this is a superfluous name, because *S. reinoldii* was already validly published before this new name was created. Allan (1961), apparently realized this, and used *S. reinoldii* in his Flora of New Zealand. This name was also used by Drury (1973).The original name, *Brachyglottis rotundifolia,* became the preferred name when Nordenstam (1978) transferred the species back to *Brachyglottis,* and it is used until this day.

In 1942, Simpson & Thomson described *Senecio bennettii* G.Simpson & J.S.Thomson for South Island and Stewart Island plants that were before that time considered *S. elaeagnifolius* Hook.f., but that the authors considered taxonomically distinct (Simpson & Thomson, 1942). In their publication they noted that they had not seen *S. elaeagnifolius* in the South Island and wrote that "...*S. bennettii* is in need of further study and must meanwhile be regarded as a composite of two or more closely-related forms." (Simpson & Thomson, 1942, p. 39). Allan (1961) accepted this somewhat tenuous species, giving a distribution from 40° 30' southwards (i.e., South Island and Stewart Island). Drury (1973) did not recognize *S. bennettii*. He included plants from the northern part of the distribution of *S. bennettii* in *S. elaeagnifolius* and those with a southern distribution in *S. reinoldii* (Drury, 1973; Haase 1986). Nordenstam (1978) listed *S. bennettii* as a synonym of *Brachyglottis buchananii* (J.B.Armstr.) B.Nord. and noted "As typified by Drury (1973 b p. 746) *S. buchananii* is synonymous to *S. bennettii* and takes priority" (Nordenstam, 1978, p. 29), but this seems incorrect, because Drury (1973) considered the type of *S. bennettii* to belong to *S. reinoldii* (*B. rotundifolia*) instead of *S. elaeagnifolius var. buchananii.* This is clear from the text in Drury's section about *S. reinoldii*: "Until the limits of the discoid species are resolved, it seems best to include here the southern portion of *S. bennettii* Simp. & Thoms. (the type specimen from Mt. Cargill, Dunedin, has 13 involucral bracts)" (Drury 1973, p. 752). The added note about the number of involucral bracts of the type of *S. bennettii* is important, because Drury's identification key indicates that he considered specimens with about 13 involucral bracts to belong to *S. reinoldii*, whereas those with 7–9 involucral bracts key to *S. elaeagnifolius.* Therefore, *S. bennettii* should be regarded a synonym of *B. rotundifolia* instead of *B. buchananii* in Nordenstam's (1978) classification.

Brachyglottis rotundifolia var. **ambigua** (Cheeseman) B.Nord., Opera Bot. 44: 29 (1978) ≡ *Senecio rotundifolius* var. *ambiguus* Cheeseman, Man. N. Zeal. Fl., ed. 2: 1026 (1925) ≡ *Senecio reinoldii* var. *ambiguus* (Cheeseman) Allan, Fl. New Zealand 1: 754 (1961). **Type:** H.J. Matthews (not found, syn), B.C. Aston (not found, syn), North-west Nelson – West Wanganui; W. Townson (AK10757*, syn), Cape Foulwind, near Westport; W. Townson (CHR331498!, syn), Cape Foulwind, Nelson; D. Petrie (AK10758*, AK10759*, syn), Cape Foulwind, near Westport, Feb-1913.

This taxon was first noted by Petrie (1913) as plants from Cape Foulwind (South Island) that were initially identified as *Senecio rotundifolius*. He suggested that they instead belong to *S. elaeagnifolius*. Cheeseman (1925), however, considered them taxonomically distinct and described the new variety *S. rotundifolius* var. *ambiguus,* acknowledging similarities between this taxon and *S. elaeagnifolius* in leaf shape. Allan (1961) transferred the variety to *S. reinoldii.* In the section of his publication about *S. reinoldii*, Drury wrote that *S. reinoldii* var. *ambiguus* "is sometimes placed under *S. reinoldii* and at other times under *S. elaeagnifolius*" (Drury, 1973, p.752), and refrained from giving it formal taxonomic recognition in either species. Nordenstam (1978) subsequently placed it in *Brachyglottis rotundifolia*.

Brachyglottis elaeagnifolia (Hook.f.) B.Nord., Opera Bot. 44: 29 (1978) ≡ *Senecio elaeagnifolius* Hook.f., Bot. Antarct. Voy. II. (Fl. Nov.-Zel.). 1: 150 (1852). **Type:** Colenso 39 (K000844032*, ?WELT SP024196/A (not seen), ?WELT SP024196/B (not seen), syn), Ruahine mountains, 1847.

This species was first described as *Senecio elaeagnifolius* by Hooker (1852) based on plants from the Ruahine Range (North Island), although he later regarded this taxon "probably only a form of *S. rotundifolius*" (Hooker, 1867, p. 734). Kirk (1899), however, accepted *S. elaeagnifolius* (incl. *Senecio elaeagnifolius* var. *buchananii* (J.B.Armstr.) Kirk, see below) as a distinct species with a distribution from the eastern part

Figure 1. Diversity within *Brachyglottis rotundifolia* species complex. **A.** Coastal specimen, Stewart Island. **B.** Plant in exposed open habitat, Mt. Aspiring National Park, South Island. **C.** Capitulum, Stewart Island. **D.** Inflorescence, Otira Valley, South Island. **E.** Abaxial view of leaf of plant in forest habitat, Mount Aspiring National Park, South Island. **F.** Abaxial view of leaf in exposed open habitat, Mount Aspiring National Park, South Island. Photos: A, C, M. Ford; B, D, F, G, P.B. Pelser; E, D. Lyttle.

Table 1. Key taxonomic treatments of the *Brachyglottis rotundifolia* species complex. For each treatment, the table shows the accepted name used for each basionym (and its homotypic synonyms). Most authors did not explicitly list autonyms at the level of variety and these were therefore inferred from information presented in the literature cited.

Basionym & *homotypic synonyms*	Current classification	Nordenstam 1978	Drury 1973	Allan 1961	Simpson & Thomson 1942	Cheeseman 1925	Kirk 1899
Senecio rotundifolius *var.* ***ambiguus*** Cheeseman. *Senecio reinoldii var. ambiguus* (Cheeseman) Allan, *Brachyglottis rotundifolia var. ambigua* (Cheeseman) B.Nord.	***B. rotundifolia*** *var.* ***ambigua***	*B. rotundifolia var. ambigua*	*S. elaeagnifolius* or *S. reinoldii*? (see text)	*S. reinoldii var. ambiguus*	*S. rotundifolius var. ambiguus*	*S. rotundifolius var. ambiguus*	
Brachyglottis rotundifolia J.R.Forst. & G.Forst. *Cineraria rotundifolia* (J.R.Forst. & G.Forst.) G.Forst. *Senecio reinoldii* Endl. *Senecio rotundifolius* (J.R.Forst. & G.Forst.) Hook.f. *Senecio puffini* Allan ex Rehder	***B. rotundifolia*** *var.* ***rotundifolia***	*B. rotundifolia var. rotundifolia*	*S. reinoldii*	*S. reinoldii var. reinoldii*	*S. rotundifolius var. rotundifolius*	*S. rotundifolius var. rotundifolius*	*S. rotundifolius*
Senecio bennettii G.Simpson & J.S.Thomson	***B. rotundifolia*** *var.* ***rotundifolia***	*B. buchananii*	*S. reinoldii*	*S. bennettii*	*S. bennettii*		
Senecio buchananii J.B.Armstr. *Senecio elaeagnifolius var. buchananii* (J.B.Armstr.) Kirk *B. buchananii* (J.B.Armstr.) B.Nord.	***B. buchananii***	*B. buchananii*	*S. elaeagnifolius* or *S. reinoldii*? (see text)	*S. bennettii*	*S. bennettii*	*S. elaeagnifolius var. buchananii*	*S. elaeagnifolius var. buchananii*
Senecio elaeagnifolius Hook.f. *Brachyglottis elaeagnifolia* (Hook.f.) B.Nord.	***B. elaeagnifolia***	*B. elaeagnifolia*	*S. elaeagnifolius*	*S. elaeagnifolius*	*S. elaeagnifolius*	*S. elaeagnifolius var. elaeagnifolius*	*S. elaeagnifolius var. elaeagnifolius*
Senecio cockaynei G.Simpson & J.S.Thomson *Brachyglottis cockaynei* (G.Simpson & J.S.Thomson) B.Nord.	***B. cockaynei***	*B. cockaynei*	*S. elaeagnifolius*	*S. cockaynei*	*S. cockaynei*		

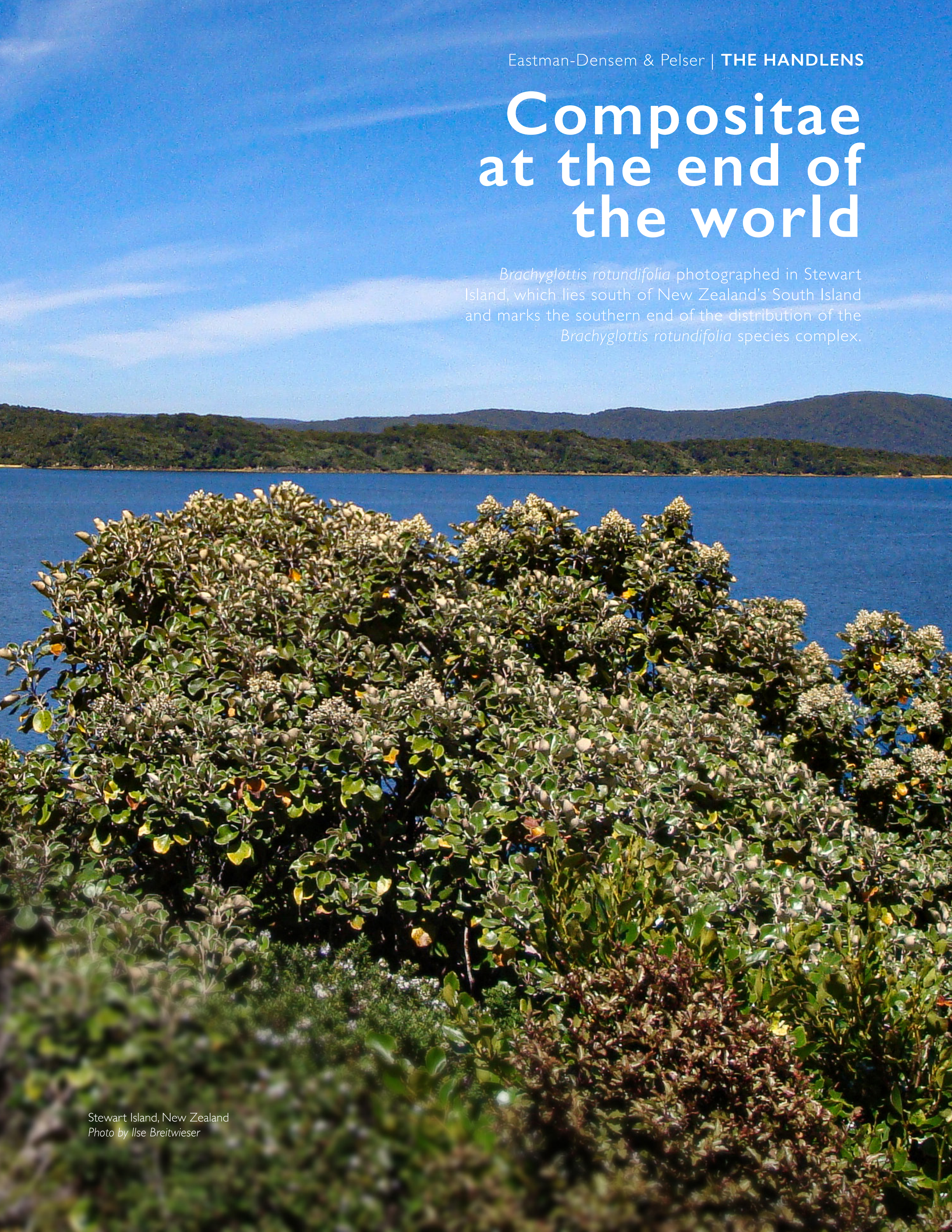
of the North Island (i.e., East Cape) south through the South Island and Stewart Island. Simpson & Thomson (1942) and Allan (1961) considered South Island and Stewart Island plants of Kirk's *S. elaeagnifolius* as better accommodated in *S. benettii* G.Simpson & J.S.Thomson or *S. cockaynei* G.Simpson & J.S.Thomson, reducing *S. elaeagnifolius* to a species endemic to the North Island. The delimitation of *S. elaeagnifolius* was again revised by Drury (1973), who suggested the inclusion of *S. cockaynei* and plants from the northern part of the distribution of *S. bennettii* (excl. the type, see previous discussion). Nordenstam (1978) made a new combination for *S. elaeagnifolius* in *Brachyglottis*, but recognized *S. cockaynei* (as *B. cockaynei* (G.Simpson & J.S.Thomson) B.Nord.) and *S. elaeagnifolius* var. *buchananii* (as *B. buchananii* and including *S. bennettii* as a synonym) as distinct at the species level.

Brachyglottis buchananii (J.B.Armstr.) B.Nord., Opera Bot. 44: 29 (1978) ≡ *Senecio buchananii* J.B.Armstr., New Zealand Country J. 3: 56 (1879) ≡ *Senecio elaeagnifolius* var. *buchananii* (J.B.Armstr.) Kirk, Stud. Fl. New Zealand: 349 (1899). **Type:** "Found on Arthur's Pass, and Mount Egmont. J.B. Armstrong and others". (See comments on the type material below)

Armstrong (1879) described this species from plants from Mt. Egmont (North Island) and Arthur's Pass (South Island), but he also mentioned Kaikoura and Otago (South Island) as part of its distribution in a later publication (Armstrong, 1881). Kirk (1899) reduced this taxon to a variety of *Senecio elaeagnifolius* and this classification was followed by Cheeseman (1906a, 1925). Interestingly, Allan (1961) did not mention the names *S. buchananii* and *S. elaeagnifolius* var. *buchananii* in his Flora of New Zealand. Drury (1973), however, mentioned that the only specimen in the Armstrong herbarium (CHR635537!) from one of the localities of the original material used for describing *S. buchananii* (i.e., Arthur's Pass) would be considered *S. bennettii* in the delimitation of that taxon used by Allan (1961). Although Drury (1973) concluded that this is the only material available for the lectotypification of the name *S. buchananii*, he did not lectotypify the name, nor did he detail whether he considered Armstrong's specimen to belong to *S. reinoldii* (*Brachyglottis rotundifolia*) or *S. elaeagnifolius* (*B. elaeagnifolia*). Drury (1973) did not explicitly recognise *S. elaeagnifolius* var. *buchananii* as a distinct taxon and stated that the Mt. Egmont plants that Armstrong (1879, 1881) placed in his *S. buchananii* "are properly treated with *S. elaeagnifolius*

Compositae at the end of the world

Brachyglottis rotundifolia photographed in Stewart Island, which lies south of New Zealand's South Island and marks the southern end of the distribution of the *Brachyglottis rotundifolia* species complex.



Stewart Island, New Zealand
Photo by Ilse Breitwieser

(cf. Kirk 1899, Cheeseman 1906a, 1925, and Allan 1961)." (Drury, 1973, p.747). In 1978, Nordenstam transferred *S. buchananii* to *Brachyglottis*. Until the name *S. buchananii* is lectotypified, it will remain unclear for what plants (if any) the name *B. buchananii* should be used.

Brachyglottis cockaynei (G.Simpson & J.S.Thomson) B.Nord., Opera Bot. 44: 29 (1978). ≡ *Senecio cockaynei* G.Simpson & J.S.Thomson, Trans. & Proc. Roy. Soc. N. Z. 72: 38 (1942). **Type:** G. Simpson (CHR29505!, holo), cultivated, Dunedin ex Westhaven, West Wanganui Inlet, Nelson.

Cheeseman (1906b) first noted the occurrence of plants that he identified as *Senecio rotundifolius* in the West Wanganui Inlet (northern South Island), mentioning that this find extended the known distribution range of this species. Cockayne (1918) commented that he received a specimen of this population and that he could not determine if it belonged to *S. elaeagnifolius* or *S. rotundifolius*, pointing out morphological differences with both taxa. Simpson & Thomson (1942) considered these differences significant enough to describe this taxon as *S. cockaynei,* and this view was adopted by Allan (1961). Drury (1973) recommended including *S. cockaynei* in *S. elaeagnifolius,* awaiting further studies into the delimitation of the species complex. Nordenstam (1978) transferred the name to *Brachyglottis*.

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Grindelia ciliata (Astereae), Thomas Nuttall, and the exploration of the American West

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ABSTRACT

Early herbarium specimens collected on exploring expeditions are of both historical and scientific importance. Even when the specimen labels have little information, records of the expeditions can put the specimens into context. This is explored with an herbarium sheet of *Grindelia ciliata* with two specimens, one collected by Thomas Nuttall and the other collected by Samuel Woodhouse.

Keywords: Arkansas Territory, colonialism, *Haplopappus*, *Wyethia*

INTRODUCTION

In addition to being of scientific importance, herbarium specimens are also historic documents. Many of the earliest specimens collected in the US were made during military or colonial expeditions, which were often aimed at claiming territory for European settlers or resettling the people that were displaced by these territory claims. A sheet of *Grindelia ciliata* (Nutt.) Spreng. (Astereae: PH 00025850/PH 00009642; Figure 1, see page 90) is a window into this period of American history.

This herbarium sheet is in the herbarium of the Academy of Natural Sciences of Philadelphia (PH), which is now part of Drexel University. The Academy of Natural Sciences is one of the oldest natural history institutions in the United States, founded in 1812, and houses important early collections from North America, including the famous Lewis and Clark herbarium and many type specimens for species collected across western North America (Lottinville, 1980; Mears, 1981).

The herbarium sheet includes two different collections of the same species, collected about 30 years apart and mounted on the same sheet, as was a common practice in herbaria at the time. Also, unfortunately common at the time, neither collection was dated, and the locality information was very approximate. However, we know more about these collections from their collectors' published writing and other information about the expeditions (Nuttall, 1821a, 1821b; Tomer & Brodhead, 1992).

Figure 1. Nuttall (PH 00025850) and Woodhouse (PH 00009642) specimens of *Donia ciliata* Nutt., now *Grindelia ciliata* (Nutt.) Spreng. Image copyright the Academy of Natural Sciences of Drexel University.

NUTTALL'S COLLECTION

The earlier collection, located on the right, was collected by Thomas Nuttall (Figure 2) and was part of the original material of *Donia ciliata* Nutt. Nuttall was a largely self-taught botanist and ornithologist who made several expeditions into the western territories of the United States between 1809 and 1836 (Graustein, 1967; Lottinville, 1980; Isely, 1994; Tyrl & Shryock, 2013). Nuttall travelled both with large parties, including Nathaniel Wyeth's expedition to the northwestern territories of the United States, and solo. During his travels, Nuttall was a copious collector. He would frequently collect plant material, including herbarium specimens and seed or bulbs to later sell, and a range of animal specimens, from birds to mollusks, all the while making notes on the local geology.

At the time that Nuttall went through present-day Oklahoma, he traveled with various people, including fur traders and people in the U.S. Army. From his description, it is clear that Nuttall saw *G. ciliata* in several places, although it is unclear where this collection was actually found. The species was mentioned once in his published diaries: "Amongst several other new plants, I found a very curious *Gaura*, an undescribed species of *Donia*, of *Eriogonum*, of *Achyranthes*, *Arundo*, and *Gentian*" (Sept. 8, 1819; Nuttall, 1821a: 230–232). This was on what he called the Great Salt River, and is now known as the Cimarron River, a tributary of the Arkansas River. It seems likely it was in present day Pawnee or Payne County (Lottinville, 1980: 222). This was land that, at the time, had been given by treaty to the Osage Nation (Nuttall, 1821a; Kappler, 1904). In his published diaries, Nuttall writes about his encounters with members of the Osage Nation, as well as their customs, history, and relations with the Cherokee and Pawnee Nations that are also in the area (Nuttall, 1821a).

Figure 2. Thomas Nuttall (1786–1859), Harvard University Portrait Collection, Gift of Professor Edward Tuckerman to Asa Gray for the University, 1865, Photo © President and Fellows of Harvard College, H185

Nuttall was one of the earliest people in the western territories to not only collect both plants and animals, but to also describe them. At the time, it was more common for expedition naturalists or leaders to collect specimens and to give them to specialists to describe, who were not themselves familiar with the plants and animals in the field and whose descriptions were entirely based on the specimens themselves and any notes taken by the collectors. For example, Nuttall described the plants from an earlier Wyeth expedition, naming what he presumably considered the nicest plant Wyeth collected after him, *Wyethia helianthoides* Nutt. (Heliantheae: Engelmanniinae; Figure 3, Figure 4) Nuttall, 1834).

In Nuttall's descriptions of the plants he collected himself, he was not limited to the information on the labels and from the specimens but could also draw on his observations of the plants in the field. This is fortunate, because often his labels only contain a brief mention of the place, but no date or year. (In this case, the collection is simply labeled "Arkansas", which probably served as a general locality for his entire expedition, since he was traveling in what was then known as Arkansas Territory, although it could have been somewhat more specific and referred to the Arkansas River.) He gives much more information in his formal description of the species: "On the alluvial banks of the Arkansa, and Great Salt River.—Flowering time, from August to October" (Nuttall, 1821b: 119).

Figure 3. Wyeth specimen of *Wyethia helianthoides* on right, specimen from another collector on left (GH 00014111). Image from the Gray Herbarium of Harvard University.

A unique kind of pappus

With a pappus of many bristles (instead of a few awns) and resin that is kept within the leaves, *Grindelia ciliata* is morphologically distinct from other members of the genus. It is currently found in disturbed, open habitats throughout Kansas, Oklahoma, Texas, and eastern New Mexico.

Grindelia ciliata from Martin County, Texas, USA.
Photo by Abigail Moore

Figure 4. *Wyethia helianthoides*, Yellowstone National Park. Photo: J. W. Frank, National Park System (USA).

Despite the locality information, it is not completely clear whether Nuttall's collection was actually from wild material or was grown from seed (or whether the two branches were even collected in the same place). The type locality is, "Cultivated in the garden of the University of Pennsylvania" (Nuttall, 1821b: 119). The specimen at Kew (K) is indeed labeled "Seeds from Arkansa. Nuttall", and it may be that Nuttall only collected seed, and not herbarium specimens, of *G. ciliata* on his travels in Arkansas Territory.

WOODHOUSE'S COLLECTION

The second collection on the sheet was by Samuel W. Woodhouse on the U.S. Army Corps of Topographical Engineers Sitgreaves Expedition, which took place from 1849 to 1851. Woodhouse was a surgeon and naturalist with the U.S. Army as well as a member of the Academy of Natural Sciences in Philadelphia (Tyrl & Shryock, 2013). Although Woodhouse himself was based in Philadelphia, he gave most of his plant specimens to John Torrey to describe, so they are now at the New York Botanical Garden (NY). Torrey wrote the account of the botany of the expedition (Torrey, 1853), although it does not include a full list of the plants collected or reference to this species. It is not clear who determined Woodhouse's specimen of *G. ciliata*, but the fact that it was called *Donia ciliata*, which was not the accepted name at the time, indicates that it was not determined by Torrey, who would have used the current name.

The locality of Woodhouse's collection is "Cherokee Nation". The objective of the first part of the Sitgreaves Expedition was to survey the boundary between lands given to the Muscogee (then called Creek) and Cherokee Nations. Two surveys of this boundary took place in July through October of 1849 and July through August of 1850 (Tomer & Brodhead, 1992). These areas were in the vicinity of Nuttall's localities along the Arkansas and Cimarron Rivers (then called the Red Fork of the Arkansas River). They had been taken away from the Osage Nation by treaty in 1825 (Kappler, 1904) and given to the Muscogee and Cherokee Nations after they were forcibly displaced from their ancestral homelands. Instead of following the rivers, as Nuttall did for that part of his expedition, the Sitgreaves Expedition traveled straight across country, along the boundary they were surveying. While Woodhouse's diary of the expedition is now published (Tomer & Brodhead, 1992), his natural history observations are largely confined to birds and other vertebrates, as these were his primary interest, and this species was not mentioned.

NOMENCLATURAL HISTORY

The herbarium sheet as a whole has three different names, none of which is the currently accepted name, *Grindelia ciliata*. Nuttall originally described the plant as *Donia ciliata* (Nuttall, 1821b). The genus *Donia* R. Br. was described in 1813 (Brown, 1813) for another species that is now also considered to be part of *Grindelia* Willd., *D. glutinosa* (Cav.) R. Br. (originally described as *Aster glutinosus* Cav., now called *G. glutinosa* (Cav.) Dunal). Once Dunal (1819) realized that *Grindelia* and *Donia* were synonyms,

A sanctuary for pollinators

Grindelia ciliata is important for pollinators such as this Euglossine bee, because it grows in disturbed areas where there are seldom any other good nectar plants.

Grindelia ciliata from Gray County, Texas, USA.
Photo by Abigail Moore

the name *Donia* gradually dropped from usage to be replaced by *Grindelia*, a change that was accepted by Nuttall for most of the species he originally placed in *Donia*, once he became aware of the name *Grindelia* (e.g., Nuttall, 1834, 1840).

Sprengel (1826) made the combination *Grindelia ciliata*. However, de Candolle (1836) instead put the species in *Aplopappus* Cass. (spelling later corrected to *Haplopappus* by Endlicher, 1837), commenting that *Aplopappus* was very similar in habit to *Grindelia* and was distinguished by pappus differences (with a pappus of numerous bristles instead of few awns; de Candolle, 1836). In Nuttall's later work, instead of putting this plant into *Grindelia* or *Aplopappus*, he placed it in a new monotypic genus, *Prionopsis* Nutt., but followed de Candolle by putting *Prionopsis* next to *Aplopappus* and distant from *Grindelia* (Nuttall, 1840).

The last annotation was presumably by Gray, for his *Synoptical Flora of North America* (Gray, 1884: 125). He put *G. ciliata* back into *Aplopappus*, but in its own section, section *Prionopsis*, and again commented that the species was similar vegetatively to *Grindelia*. Due to the pappus differences, *G. ciliata* continued to be accepted as part of either *Haplopappus* or *Prionopsis* for the next hundred years. However, micromorphological (Nesom et al., 1993) and molecular (Moore et al., 2012) data showed that it was clearly nested within *Grindelia*, and it is currently accepted as a member of that genus. In addition to being historical documents of the time they were collected, herbarium specimens continue to document the changes in scientific thought afterwards, through their annotation histories.

ACKNOWLEDGEMENTS

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STYLE

Where art and science converge

▲

THE TWILIGHT ZONE

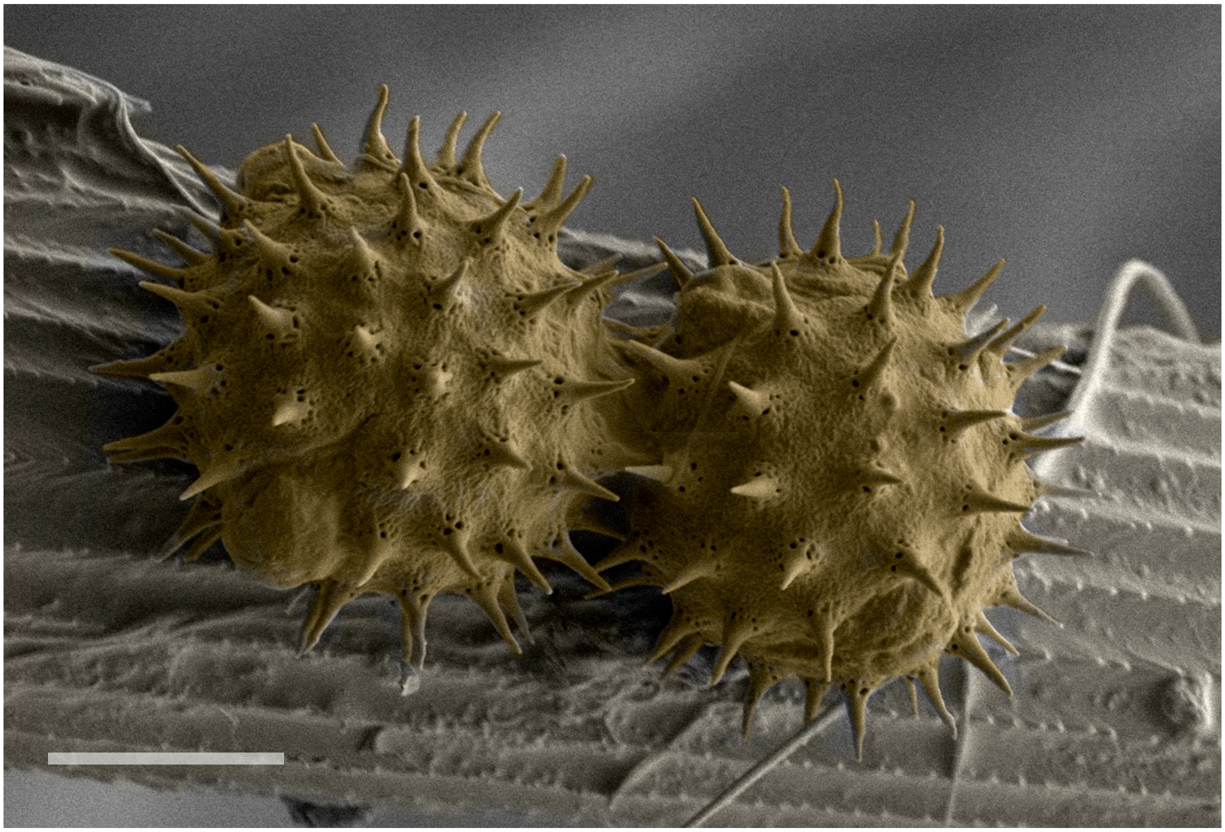
Corolla and pappus of *Craspedia robusta* var. *pedicellata* (Kirk) Allan (Gnaphalieae) from Stewart Island, New Zealand. The unusual growths emerging from the corolla tube appear to be perianth elements that are part pappus and part corolla. Perhaps a mis-timing of action of floral homeotic genes has led to some inner pappus elements fusing to the lower corolla tube and developing corolla-like expanded papillate apices. We'd welcome other interpretations or observations of similar structures. Scale bar: 1 mm

Phil Garnock-Jones

HYALOSERIS ▶

From a distance *Hyaloseris rubicunda* Griseb. looks like a dead bush, but as you get closer you can admire its delicate, deep red capitula. I saw this species in Salta (northwestern Argentina) during a fieldtrip with Luis Palazzesi and Iralys Ventosa.

Oriane Hidalgo



VOYAGERS

These are Asteraceae pollen grains covering the leg of a Nymphalid butterfly from the collections at the University of Nevada, Reno, Museum of Natural History. I am interested in understanding the interactions between plant and pollinator, pollinators' responses to past and future climate change, and how pollination webs are changing in response to anthropogenic disturbances. Scale bar: 10 µm

Behnaz Balmaki

LAND OF GIANTS

Archidasyphyllum diacanthoides (Less.) Ferreira, Saavedra & Groppo (Barnadesioideae) a relatively tall tree (up to 20 m) that grows in very humid regions along the Andean range in Patagonia (Chile and Argentina), where virtually no other daisies are found. This was the first time I saw so many capitula at the canopy level.

Jaume Pellicer

talks

TICA

THE INTERNATIONAL COMPOSITAE ALLIANCE

After a short break in July, the second half of 2021 brought us another stellar series of talks by Compositae experts from all over the world. We had a good balance of organismal talks targeting specific groups in the family, and process-focused talks.

In August we had Dr. Nádia Roque (Universidade Federal da Bahia, Brazil) and Dr. Morgan Gostel (Botanical Research Institute of Texas, USA) presenting the current panorama of systematics and taxonomy of the tribe Gochnatieae, including fresh-from-the-oven phylogenetic results that will be essential in explaining the incredible reproductive diversity found in this small tribe.

In September our attention was entirely dedicated to the mega-diverse genus *Baccharis* (Astereae). Dr. Gustavo Heiden (Embrapa Clima Temperado, Brazil) presented an overview of *Baccharis*, based on a recently published paper in Capitulum, with information about morphology, phylogeny, and distribution. The talk including the important taxonomic work being done to stabilize the infrageneric classification of this large genus and make it easier for everybody to identify them. Dr. Itziar Arnelas (Universidad Técnica Particular de Loja, Ecuador) impressed us with the diversity of *Baccharis* in southern Ecuador, where more than 20 species are found!

October brought us some of the complicated genomic processes involved in Compositae diversification. Dr. Oliver White (Royal Botanic Gardens, Kew, UK) gave a talk about his work to untangle the genomic processes of hybridization and speciation in the daisy-like genus Argyranthemum, including molecular and morphological evidence. Dr. José Cerca (Norwegian University of Science and Technology, Norway) showed us some of the unique challenges of working with Compositae genomes, which are widely recognized for being very complicated, by ways of his work with the Galapagos-endemic genus Scalesia.

Speakers at TICA TALKS. A. Nadia Roque (Universidade Federal da Bahia, Brazil). **B.** Morgan Gostel (Botanical Research Institute of Texas, USA). **C.** Itziar Arnelas (Universidad Técnica Particular de Loja, Ecuador). **D.** Gustavo Heiden (Embrapa Clima Temperado, Brazil). **E.** Geoffrey Finch (University of Arizona, USA). **F.** José Cerca (Norwegian University of Science and Technology, Norway). **G.**Oliver White (Royal Botanic Gardens, Kew, UK).

November brough us back to chromosome issues, this time in the subtribe Machaerantherinae (Astereae). PhD student Geoffrey Finch (University of Arizona, USA) showed us some of the challenges of modelling chromosome number evolution in Compositae.

To close the year celebrating this plant family that we love so much, we had the help of lots of folks around the world, who sent us photos of their favorite Compositae species. We were all touched by the beauty of these plants and the emotional connections we form with them. The photos and text are in the process of being compiled in a booklet that will be available on the TICA website.

We are still looking for speakers for 2022. Our seminars are attended by a mix of Compositae researchers, students and enthusiasts, providing a low-pressure environment where you can showcase your research, fieldwork finds and lab anecdotes. Please contact us at ticaseminarseries@gmail.com if you are interested in presenting a talk. Make sure to check past talks on our YouTube channel:https://www.youtube.com/channel/UCX0qRBdc7F85QQJ1lhBMovA/videos.

CAPITULUM
THE INTERNATIONAL COMPOSITAE ALLIANCE NEWSLETTER

GUIDELINES FOR AUTHORS

HEAD TOPICS

Section to showcase current research on Compositae. It could be a digest of a paper recently published or a description of a research project among other things. Length of articles could be up to 3000 words.

PIPET & PRESS

Articles about methods and techniques. Length of articles up to 1000 words.

BREVIA

Same scope as in HEAD TOPICS section but not as long. Length of articles could be up to 1500 words.

THE HANDLENS

A close up look to a given species or morphological structure.Length of article up to 1500 words

THE CABINET

A window to the stories behind ancient or recent herbarium samples and the botanists behind them. Length of articles up to 1500 words

FROM THE FIELD

The place where the bold and the adventurous share their latest finds in their eternal pursuit of the more recalcitrant comps. Length of articles up to 2000 words

STYLE

Where science and art converge, artistic photography, botanical illustration or creative infographics. All is welcome if it comes with style.

PREPARATION OF TEXT

Consult a recent issue of CAPITULUM and follow these instructions. Language for submission is English. Contributions are sent two external reviewers. Use Times New Roman/Arial typography. Provide a title and if needed, a subtitle. Include names of all authors and their professional affiliations and emails. Include a list of 5–6 keywords in alphabetical order. Provide an abstract of up to 250 words. There is no set structure on how to organize your text; however you may include the classic I-M&M-R-D or none of these, but you should include Acknowledgements and Literature Cited. Up to two subheading categories are accepted. Keep title and subheadings short and informative. All scientific names at the rank of tribe or inferior should include authorship the first time they appear in the text, following Brummitt & Powell, Authors of Plant Names (Kew, 1992; info included in the International Plant Names Index [IPNI]). In text, a single space must follow a period, colon, semi-colon, or comma. Tables must be prepared using MS Excel, please include different tables as different spreadsheets on the same file. Figures should be provided in either TIFF format (for photos) or as vector graphics such as AI or EPS for diagrams, illustrations, or phylogenetic trees. Maps should be provided as shape files when possible or as vector graphics. You may send the photos and other graphics ordered and arranged following your preference, but you are advised that we could edit them to adjust them to CAPITULUM style. All figures must be uploaded as individual original files. Photos should be at least 300 dpi in resolution. Literature citation: please check that all your references are cited and vice versa. For the style of references check a recent issue of CAPITULUM.

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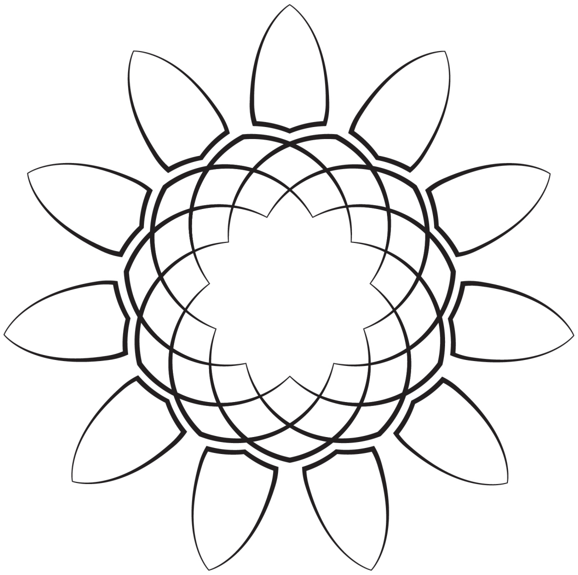

Magno amore in familiam Synantherearum captus
Lessing, 1829

TICA
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