Packed with *Packera* Á. Löve & D. Löve:

Brief history of the "aureoid *Senecio*" subgroup in Senecioneae

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ABSTRACT

Senecioneae within Compositae is a very large and complicated tribe. Once considered a tribe composed of many species in the mega-genus *Senecio* and a few smaller genera, it is now delimited to many genera with two-thirds of *Senecio* separated into newly named, smaller genera. These genera typically follow subgroup classifications originally created by taxonomists over a century ago. One of those segregate genera is *Packera*, previously known as the Aureoids or "aureoid *Senecio*" subgroup. *Packera* is a somewhat recently described genus with an estimated 64 species and varieties found exclusively in North America. Members of this group have continuously been grouped together given shared morphological and ecological characteristics. Here, we describe the history of *Packera*'s subgroup classifications as the "aureoid *Senecio*" group over the last century, how this group differs from *Senecio*, and our current understanding of this complicated genus.

Keywords: chromosome counts, classification, hybridization, pollen.

INTRODUCTION

Senecioneae, the largest tribe in Compositae, contains roughly 150 genera and 3,500 species (Mandel et al., 2019). Members of Senecioneae can be found almost everywhere in the world, with centers of diversity in temperate and subtropical arid or montane regions (Funk et al., 2009). The classic view of the tribe has been of a mega-genus *Senecio* L., along with other genera that vary in their level of distinctiveness (Barkley, 1985). Circumscription and delimitation within the tribe have been challenging because of its large size, lack of intergeneric relationship understanding, presence of conflicting morphological characters, and absence of a precise delimitation or circumscription of genus *Senecio* (Pelser et al., 2007).

Senecio is a very large (ca. 1,000 taxa) and complicated genus with a worldwide distribution. Evolutionary relationships within the group are consistently recovered as polyphyletic (i.e., Pelser et al., 2007, 2010; Panero & Funk, 2008; Funk et al., 2009; Fu et al., 2016; Mandel et al., 2019), leading some to suggest that *Senecio* could be further split into additional genera. Initially, species were lumped into the genus for convenience (ca. 3,000 taxa), though taxonomists have tried to break *Senecio* into smaller and more tractable segregate genera, or informal subgroups, for over a century (i.e., Rydberg, 1900; Greenman, 1902; Packer, 1972; Nordenstam, 1977, 1978). For example, North American *Senecio* members were organized into 22 informal subgroups by Jesse M. Greenman in 1901 (Greenman, 1902), one of those subgroups being

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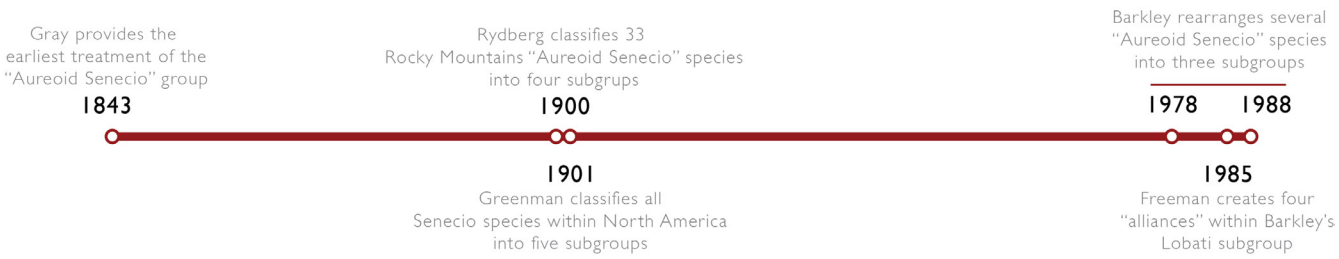

Figure 1. A timeline of "aureoid *Senecio*" subgroups classification over the last two centuries

the "aureoid *Senecios*", later segregated into *Packera* Á. Löve & D. Löve. In this article, we summarize the history of subgroup classification in *Packera* from 1843 to present. Additionally, we discuss our current understandings of this genus and the various ways it differs from *Senecio*.

THE AUREOIDS

Packera was previously included in the genus *Senecio* as the informal group known as the "aureoid *Senecios*" (or Aureoids) first recognized by Asa Gray (Gray & Torrey, 1843; Gray, 1886; Mahoney, 2000). Gray provided the earliest treatments of the group by recognizing that distinct members share most of these characters: perennial herbs arising from creeping rootstocks or a stout caudex; basal leaves well developed, cauline leaves progressively reduced upwards, leaf margins without callose denticles; roots fibrous, thin and branching; and haploid chromosome numbers of 22 or 23 (Barkley, 1988). Asa Gray, along with John Torrey, classified most of the eastern species, later known as the 'Aurei' subgroup by Theodore M. Barkley and Greenman (Greenman, 1918; Barkley, 1968), as varieties of *Senecio aureus* L. (≡*Packera aurea* (L.) Á. Löve & D. Löve; Gray and Torrey, 1843; Gray, 1886), which is also the type species of the group (Löve and Löve, 1975). These taxa consisted of *S. aureus* (with five varieties), *S. tomentosus* Michx. (=*P. dubia* (Spreng.) Trock & Mabb.), *S. canus* Hook. (≡*P. cana* (Hook.) W.A.Weber & Á.Löve), and *S. elliottii* Torr. & A.Gray (=*P. obovata* (Willd.) W.A.Weber & Á.Löve).

Subgroups of these "aureoid *Senecios*" were later proposed by P.A. Rydberg in 1900, who classified 33 of the "aureoid *Senecio*" species into four groups: 'Aureus' (=Aurei [18 species]), 'Tomentosus' (=Tomentosi [9 species]), 'Lobatus' (=Lobati [5 species]), and 'Subnudus' (=Subnudi [1 species]; Figure 1, Table 1; Rydberg, 1900). Within a year of his work, Rydberg discovered that Greenman was also working on classifying *Senecios* in North America into subgroups. Therefore, Greenman and Rydberg reached an agreement that Rydberg would only classify Rocky Mountain *Senecios* and Greenman would classify all *Senecios* within North America (Rydberg, 1900). Greenman recognized the 'Aurei' [51 species], 'Tomentosi' [30 species] and 'Lobati' [14 species] subgroups defined by Rydberg, but added two more sections: 'Bolanderi' [3 species] and 'Sanguisorboidei' [13 species] (Figure 1, Table 1; Trock, 1999).

Later, Barkley followed Greenman and others by recognizing a greater number of species (59 taxa; Rydberg, 1900; Greenman, 1918), better reflecting our current understanding of the Aureoids (Barkley, 1962, 1988). Additionally, Barkley adopted the informal species groups of Rydberg, but followed Greenman in combining the 'Subnudi' with the 'Aurei'. He also combined the 'Bolanderi' and 'Sanguisorboidei' of Greenman with the 'Lobati' and rearranged a number of species within these informal groups; resulting in three subgroups that are currently recognized today: 'Aurei' [27 species], 'Tomentosi' [15 species], and 'Lobati' [18 species] (Figure 1, Table 1; Greenman, 1902; Barkley, 1978, 1988; Freeman, 1985; Trock, 1999). Later, Freeman

The first of many

Packera aurea (L.) Á. Löve & D. Löve, one of the 64 currently recognized species of *Packera* Á. Löve & D. Löve., has a widespread distribution along the east coast of North America. Not only is it the type species of the genus, *P. aurea* is also the "type" for the 'Aurei' subgroup originally defined by Asa Gray in 1843.

Packera aurea (L.) Á. Löve & D. Löve in LaPorte County, Indiana, USA
Photo by Cassi Saari

Figure 2. Species of *Packera* in North America. **A.** *P. debilis* (Nutt.) W.A.Weber & Á.Löve. **B.** *P. thurberi* (A.Gray) B.L.Turner **C.** *P. glabella* (Poir.) C.Jeffrey **D.** *P. antennariifolia* (Britton) W.A.Weber & Á.Löve **E.** *P. cana* (Hook.) W.A.Weber & Á.Löve. *Photos: A-B, E, Robert Lagier; C, Cassi Saari; D, Vida Svahnström.*

(1985) investigated members of Barkley's 'Lobati' subgroup within Mexico and created four additional groups (or 'alliances') within 'Lobati' based on morphology, ecological preferences, and distribution: 'Multilobatus', 'Millelobatus', 'Sanguisorbae', and 'Bolanderi'. A full list of the "aureoid *Senecio*" species associated with each subgroup can be found in Supplemental Table 1 on FigShare (https://figshare.com/projects/Packed_with_Packera_Brief_history_of_the_aureoid_Senecio_subgroup_in_Senecioneae/153780).

Originally, many taxonomists treated the various subgroups as formal sections (e.g., Rydberg, 1900; Greenman, 1901); however, it is best to treat them as "groups-of-convenience" since species boundaries are imprecise and are subject to re-interpretation (Barkley, 1988). In addition, phylogenetic studies of *Packera* show that the molecular data does not support the subgroupings or the hypotheses behind the groupings (Bain & Jansen, 1995; Bain & Golden, 2000). For example, Barkley (1988) predicted that the 'Aurei' subgroup would be considered

Table 1. A table summarizing "aureoid *Senecio*" subgroup classifications and their corresponding taxa from 1843 to present. All currently recognized *Packera* species, excluding varieties and hybrid taxa, are listed in the first column. Columns to the right of the species list represent a publication detailing which "aureoid *Senecio*" species were included in specified subgroups given that author and year. Subgroups are colored accordingly; if a species was considered as belonging to more than one subgroup, the block is split diagonally and contain both subgroup colors. No block in a column indicates that the species is not present in the publication. *Packera* taxa not assigned to a subgroup contain no blocks. A complete list of the "aureoid *Senecio*" taxa associated with each subgroup can be found in Supplemental Table 1 on FigShare (https://figshare.com/projects/Packed_with_Packera_Brief_history_of_the_aureoid_Senecio_subgroup_in_Senecioneae/153780).

Senecio subgroup asigned by each author on table

Author did not asign group | Subnudus | Bolanderi | Sanguisorboidei | Aurei | Lobati | Tomentosi

Informal group as currently circunscribed	Species	Gray 1843	Rydberg 1900	Greenman 1901	Barkley 1978	Barkley 1988
Aurei	*Packera anonyma* (Alph.Wood) W.A.Weber & Á.Löve		Aurei	Aurei	Aurei	Aurei
	Packera aurea (L.) Á.Löve & D.Löve	Author did not asign group		Aurei	Aurei	Aurei
	Packera cardamine (Greene) W.A.Weber & Á.Löve			Aurei	Aurei	Aurei
	Packera clevelandii (Greene) W.A.Weber & Á.Löve				Aurei	Aurei
	Packera crocata (Rydb.) W.A.Weber & Á.Löve		Aurei	Aurei	Aurei	Aurei
	Packera cymbalaria (Pursh) W.A.Weber & Á.Löve			Aurei	Aurei	Aurei
	Packera debilis (Nutt.) W.A.Weber & Á.Löve		Aurei	Aurei	Aurei	Aurei
	Packera dimorphophylla (Greene) W.A.Weber & Á.Löve			Aurei	Aurei	Aurei
	Packera ganderi (T.M.Barkley & R.M.Beauch.) W.A.Weber & Á.Löve				Aurei	Aurei
	Packera hartiana (A.Heller) W.A.Weber & Á.Löve			Aurei	Aurei	Aurei
	Packera hintoniorum (B.L.Turner) C.Jeffrey					Aurei
	Packera hyperborealis (Greenm.) Á.Löve & D.Löve			Aurei	Aurei	Aurei
	Packera indecora (Greene) Á.Löve & D.Löve		Aurei	Aurei	Aurei	Aurei
	Packera layneae (Greene) W.A.Weber & Á.Löve				Aurei	Aurei
	Packera obovata (Willd.) W.A.Weber & Á.Löve	Author did not asign group		Aurei	Aurei	Aurei
	Packera pauciflora (Pursh) Á.Löve & D.Löve		Aurei	Aurei	Aurei	Aurei
	Packera paupercula (Michx.) Á.Löve & D.Löve		Aurei	Aurei	Aurei	Aurei
	Packera plattensis (Nutt.) W.A.Weber & Á.Löve		Tomentosi	Aurei	Aurei	Aurei
	Packera porteri (Greene) C.Jeffrey			Aurei	Aurei	Aurei
	Packera pseudaurea (Rydb.) W.A.Weber & Á.Löve		Aurei / Tomentosi	Aurei	Aurei	Aurei
	Packera quebradensis (Greenm.) W.A.Weber & Á.Löve					Aurei
	Packera schweinitziana (Nutt.) W.A.Weber & Á.Löve			Aurei	Aurei	Aurei
	Packera streptanthifolia (Greene) W.A.Weber & Á.Löve		Aurei	Aurei	Aurei	Aurei
	Packera subnuda (DC.) Trock & T.M.Barkley		Subnudus	Aurei	Aurei	Aurei
	Packera thurberi (Rydb.) W.A.Weber & Á.Löve		Aurei	Aurei	Aurei	Aurei
Lobati	*Packera bolanderi* (A.Gray) W.A.Weber & Á.Löve			Bolanderi	Lobati	Lobati
	Packera brewerii (Burtt Davy) W.A.Weber & Á.Löve			Lobati	Lobati	Lobati
	Packera coahuilensis (Greenm.) C.Jeffrey			Sanguisorboidei		Lobati
	Packera eurycephala (Torr. & A.Gray) W.A.Weber & Á.Löve			Lobati	Lobati	Lobati
	Packera flettii (Wiegand) W.A.Weber & Á.Löve			Bolanderi		Lobati
	Packera franciscana (Greene) W.A.Weber & Á.Löve			Lobati	Lobati	Lobati
	Packera glabella (Poir.) C.Jeffrey			Sanguisorboidei	Lobati	Lobati
	Packera millefolium (Torr. & A.Gray) W.A.Weber & Á.Löve			Sanguisorboidei		Lobati
	Packera millelobata (Rydb.) W.A.Weber & Á.Löve		Lobati	Lobati	Lobati	Lobati
	Packera montereyana (S.Watson) C.Jeffrey			Sanguisorboidei	Lobati	Lobati
	Packera multilobata (Torr. & A.Gray) W.A.Weber & Á.Löve		Lobati / Tomentosi	Lobati		Lobati
	Packera quercetorum (Greene) C.Jeffrey			Tomentosi	Lobati	Lobati
	Packera rosei (Greenm.) W.A.Weber & Á.Löve			Aurei	Lobati	Aurei / Lobati
	Packera sanguisorbae (DC.) C.Jeffrey			Sanguisorboidei		Lobati
	Packera sanguisorboides (Rydb.) W.A.Weber & Á.Löve		Lobati	Sanguisorboidei		Lobati
	Packera scalaris var. scalaris (Greene) C.Jeffrey				Lobati	Lobati
	Packera tampicana (DC.) C.Jeffrey		Lobati	Sanguisorboidei		Lobati
	Packera zimapanica (Hemsl.) C.C.Freeman & T.M.Barkley			Sanguisorboidei		Lobati

Table 1. (cont.) A table summarizing "aureoid *Senecio*" subgroup classifications and their corresponding taxa from 1843 to present.

Senecio subgroup asigned by each author on table

Author did not asign group | Aurei | Lobati | Tomentosi

Informal group as currently circunscribed	Species	Gray 1843	Rydberg 1900	Greenman 1901	Barkley 1978	Barkley 1988
Tomentosi	*Packera antennariifolia* (Britton) W.A.Weber & Á.Löve			Tomentosi		
	Packera bellidifolia (Kunth) W.A.Weber & Á.Löve			Tomentosi		
	Packera bernardina (Greene) W.A.Weber & Á.Löve			Tomentosi		
	Packera cana (Hook.) W.A.Weber & Á.Löve	Author did not asign group		Tomentosi		
	Packera candidissima (Greene) W.A.Weber & Á.Löve					
	Packera cynthioides (Greene) W.A.Weber & Á.Löve			Tomentosi		
	Packera dubia (Spreng.) Trock & Mabb.	Author did not asign group		Tomentosi	Tomentosi	Tomentosi
	Packera fendleri (A.Gray) W.A.Weber & Á.Löve		Lobati	Tomentosi		Tomentosi
	Packera greenei (A.Gray) W.A.Weber & Á.Löve			Aurei	Tomentosi	Tomentosi
	Packera hesperia (Greene) W.A.Weber & Á.Löve				Tomentosi	Tomentosi
	Packera ionophylla (Greene) W.A.Weber & Á.Löve			Lobati		Tomentosi
	Packera loratifolia (Greenm.) W.A.Weber & Á.Löve				Tomentosi	Tomentosi
	Packera macounii (Greene) W.A.Weber & Á.Löve			Tomentosi	Tomentosi	Tomentosi
	Packera mancosana Yeatts, B.Schneid. & Al Schneid.				Tomentosi	Tomentosi
	Packera moranii (T.M.Barkley) C.Jeffrey				Tomentosi	Tomentosi
	Packera neomexicana (A.Gray) W.A.Weber & Á.Löve		Tomentosi	Lobati	Tomentosi	Tomentosi
	Packera umbraculifera (S.Watson) W.A.Weber & Á.Löve			Tomentosi	Tomentosi	Tomentosi
	Packera werneriifolia (A.Gray) W.A.Weber & Á.Löve ex Trock			Aurei		
Lugentes	*Packera actinella* (Greene) W.A.Weber & Á.Löve			Tomentosi	Tomentosi	Tomentosi
	Packera toluccana (DC.) W.A.Weber & Á.Löve			Aurei		
Not asigned to a group	*Packera castoreus* (S.L.Welsh) Kartesz					Tomentosi
	Packera contermina (Greenm.) J.F.Bain				Tomentosi	Tomentosi
	Packera crawfordii (Britton) A.M.Mahoney & R.R.Kowal					
	Packera heterophylla (Fisch.) E.Wiebe				Tomentosi	Tomentosi
	Packera insulae-regalis R.R.Kowal				Tomentosi	
	Packera malmstenii (S.F.Blake ex Tidestr.) Kartesz					
	Packera musiniensis (S.L.Welsh) Trock					
	Packera ogotorukensis (Packer) Á.Löve & D.Löve					
	Packera serpenticola Boufford, Kartesz, S.H.Shi & R.Zhou					
	Packera spellenbergii (T.M.Barkley) C.Jeffrey					
	Packera texensis O'Kennon & Trock					

the deepest branching lineage/subgroup, and that 'Lobati' and 'Tomentosi' arose from the Aurei during the late Tertiary period; however, Bain & Jansen (1995) or Bain & Golden (2000) have found no support for either hypothesis.

PACKERA

The Aureoids became fully recognized as a new genus by Áskell and Doris Löve in 1976 (Löve & Löve, 1976). Most of the species were not classified as *Packera* until 1981 by William A. Weber and Áskell Löve, largely based on differences in morphology and chromosome numbers (Weber & Löve, 1981; Jeffrey, 1992). Senecioneae specialists initially resisted the idea of separating the Aureoids into a different genus since morphologically, they are not that different from other North American *Senecios* (Barkley, 1988). However, the inclusion of molecular data (Bain & Jansen, 1995; Bain & Golden, 2000; Pelser et al., 2007, 2010; Schilling & Floden, 2015) and the discovery of various morphological characteristics (Barkley, 1988) support its distinctiveness, making the genus more accepted (Trock, 1999). *Packera* differs from *Senecio* with several traits: 1) *Packera* taxa have haploid chromosome numbers [n] of 22 or 23, or polyploids of these numbers, while *Senecio* has n of 20 or 30 (Barkley, 1988; Funk et al., 2009); 2) *Packera* has helianthoid pollen (fully or partially caveate with internal foramina) instead of senecioid pollen (fully or partially caveate without internal foramina), which is the most commonly found type within Senecioneae; and 3) receptacles within *Packera* tend to have extensive fistulosity, while *Senecio* has much less (Funk et al., 2009; Robinson, 2009; Bain & Walker, 1995).

Packera as currently circumscribed has ca. 64 species and varieties (55 species and nine varieties; Trock, 2006; Figure 2), though the number continuously changes with the description of new taxa (e.g., Kowal

et al., 2011; Yeatts et al., 2011; Boufford et al., 2014), or from splitting/lumping of already named taxa (e.g., Mohlenbrock, 2004; Mahoney & Kowal, 2008). Most species are endemic to North America, apart from *P. heterophylla* (Fisch.) E.Wiebe in Siberia, with a majority of taxa occurring in the western temperate regions of central to southern North America (Barkley, 1988). *Packera* occurs in multiple ecosystems, with some species abundant and widely distributed, while others are endemic or restricted to specialized or isolated habitats, placing some under conservation concern. *Packera* is taxonomically complex due to the species' ability to easily hybridize and roughly 40% of taxa presenting polyploidy, aneuploidy, and other cytological disturbances (Barkley, 1988; Trock, 2006). This complexity has historically made it difficult to reconstruct evolutionary relationships in this group (Bain & Jansen, 1995; Bain & Golden, 2000), though recent advancements in sequencing technologies (e.g., target-enrichment sequencing) may benefit our current understanding of *Packera* and how it has diversified over time. Given its taxonomic, ecological, and genetic complications, *Packera* is a great system to study complex groups within Compositae.

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