

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

“Aureoid *Senecio*” classification history

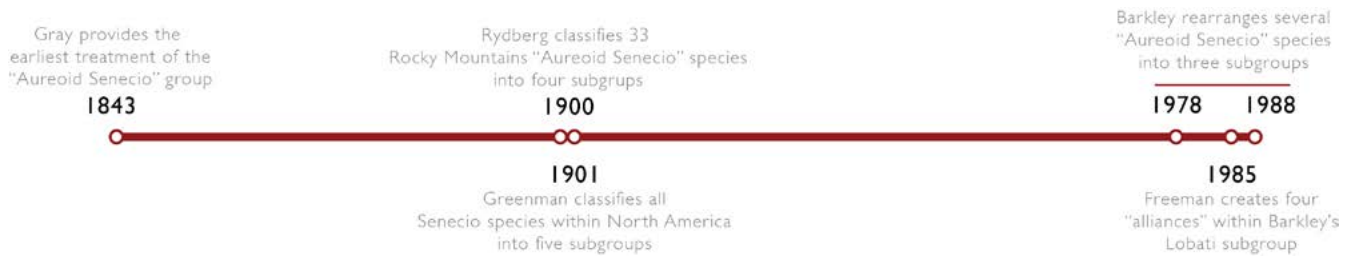


Figure 1. A timeline of “aureoid *Senecio*” subgroups classification over the last two centuries

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

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

Senecio subgroup assigned by each author on table

Author did not assign group
 Aurei
 Lobati
 Tomentosi

Informal group as currently circumscribed	Species	Gray 1843	Rydberg 1900	Greenman 1901	Barkley 1978	Barkley 1988
Tomentosi	<i>Packera antennariifolia</i> (Britton) W.A.Weber & Á.Löve					
	<i>Packera bellidifolia</i> (Kunth) W.A.Weber & Á.Löve					
	<i>Packera bernardina</i> (Greene) W.A.Weber & Á.Löve					
	<i>Packera cana</i> (Hook.) W.A.Weber & Á.Löve					
	<i>Packera candidissima</i> (Greene) W.A.Weber & Á.Löve					
	<i>Packera cynthioides</i> (Greene) W.A.Weber & Á.Löve					
	<i>Packera dubia</i> (Spreng.) Trock & Mabb.					
	<i>Packera fendleri</i> (A.Gray) W.A.Weber & Á.Löve					
	<i>Packera greenei</i> (A.Gray) W.A.Weber & Á.Löve					
	<i>Packera hesperia</i> (Greene) W.A.Weber & Á.Löve					
	<i>Packera ionophylla</i> (Greene) W.A.Weber & Á.Löve					
	<i>Packera laratifolia</i> (Greenm.) W.A.Weber & Á.Löve					
	<i>Packera macounii</i> (Greene) W.A.Weber & Á.Löve					
	<i>Packera mancosana</i> Yeatts, B.Schneid. & Al Schneid.					
	<i>Packera moranii</i> (T.M.Barkley) C.Jeffrey					
	<i>Packera neomexicana</i> (A.Gray) W.A.Weber & Á.Löve					
	<i>Packera umbraculifera</i> (S.Watson) W.A.Weber & Á.Löve					
<i>Packera wernerifolia</i> (A.Gray) W.A.Weber & Á.Löve ex Trock						
Lugentes	<i>Packera actinella</i> (Greene) W.A.Weber & Á.Löve					
	<i>Packera taluccana</i> (DC.) W.A.Weber & Á.Löve					
Not assigned to a group	<i>Packera castoreus</i> (S.L.Welsh) Kartesz					
	<i>Packera contermina</i> (Greenm.) J.F.Bain					
	<i>Packera crawfordii</i> (Britton) A.M.Mahoney & R.R.Kowal					
	<i>Packera heterophylla</i> (Fisch.) E.Wiebe					
	<i>Packera insulae-regalis</i> R.R.Kowal					
	<i>Packera malmstenii</i> (S.F.Blake ex Tidestr.) Kartesz					
	<i>Packera musiniensis</i> (S.L.Welsh) Trock					
	<i>Packera ogotarukensis</i> (Packer) Á.Löve & D.Löve					
	<i>Packera serpenticola</i> Boufford, Kartesz, S.H.Shi & R.Zhou					
<i>Packera spellenbergii</i> (T.M.Barkley) C.Jeffrey						
<i>Packera texensis</i> 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; Pelsner 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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