# STUDIES OF NEOTROPICAL COMPOSITAE—XV. THE NEW GENUS CHAETACALIA, RETENTION OF AETHEOLAENA, CULCITIUM, HAPLOSTICHA, AND IOCENES, TWO NEW SPECIES OF SENECIO, AND LASIOCEPHALUS REVISITED AGAIN (SENECIONEAE: SENECIONINAE)

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#### **ABSTRACT**

New or noteworthy South American Compositae tribe Senecioneae subtribe Senecioninae include description of a new disciform penicillate-appendiculate-styled genus, retention of the genera Aetheolaena, Culcitium, Haplosticha, Iocenes, and Lasiocephalus, and description of two new species of Senecio. Five new combinations in Aetheolaena, two new combinations in Lasiocephalus, three new combinations in Haplosticha, and one new combination in each Chaetacalia, Humbertacalia, Iocenes, and Lomanthus are made. Nomenclatural innovations are these: Chaetacalia Pruski, gen. nov., Chaetacalia stylotricha (Cabrera) Pruski, comb. nov., Aetheolaena alatopetiolata (J. Calvo, E. Freire & Sklenář) Pruski, comb. nov., Aetheolaena betonicifolia (DC.) Pruski, comb. nov., Aetheolaena gargantana (Cuatr.) Pruski, comb. nov., Aetheolaena josei (Sklenář) Pruski, comb. nov., Aetheolaena piedrahitae (J. Calvo & F. Ávila) Pruski, comb. nov., Haplosticha arnicoides (Hook. & Arn.) Pruski, comb. nov., Haplosticha trifurcata (G. Forst.) Pruski, comb. nov., Haplosticha zosterifolia (Hook. & Arn.) Pruski, comb. nov., Humbertacalia leucopappa (DC.) Pruski, comb. nov., Iocenes virens (Phil.) Pruski, comb. nov., Lasiocephalus peruvianus (Klatt) Pruski, comb. nov., Lasiocephalus superparamensis (Sklenář) Pruski, comb. nov., Lomanthus coscayanus (Ricardi & Martic.) Pruski, comb. nov., Senecio perezioides Pruski, sp. nov., and Senecio vasquezii Pruski & R. Ortiz, sp. nov. Bolivian Chaetacalia is described as monotypic and diagnosed by perennial herbaceous non-scandent habit, short-caudate anthers, balusterform filament collars, 2-banded penicillate disk style branches that are also dense-papillose distally on the abaxial surfaces, and erect, ecalyculate, heterogamous, disciform capitula. *Chaetacalia* is keyed, and by erect disciform capitula is not considered by me to be a member of the Aetheolaena-Lasiocephalus generic group. Aetheolaena, Iocenes, and Lasiocephalus are each penicillate-appendiculate-styled and recognized formally with abbreviated synonymy given. Culcitium by nutant discoid capitula is similar to Aetheolaena and Lasiocephalus, and Haplosticha by white ray corollas is similar to Iocenes, but Culcitium and Haplosticha differ by their truncate exappendiculate styles. The first-described species of Haplosticha was by George Forster in a 1788 preprint, the GOET holding of which is shown to be 64 pages, but that copy seen is without the eight unpaginated plates found in the 1789 journal version. The two new species of Senecio described and keyed are perennial subrosulate herbs with radiate capitula. Peruvian Senecio vasquezii is recognized by its discolorous leaves, bracteate capitula, and fimbriate-scaled clinanthia and Bolivian Senecio perezioides by concolorous pinnatilobed leaves and glandular-hirsute indument. Lomanthus is a new generic record for Chile, and Haplosticha is a new generic record for Argentina.

Until the 1950s, Senecio L. (Compositae: Senecioneae), Astragalus L. (Leguminosae), and Drosophila (fruit fly), each thought to contain about 2,000–3,000 species, were taken as among the world's largest genera (Gray 1884; Solbrig 1963; Koyama 1967). Senecio and Drosophila, however, were not monophyletic, and generic restructuring has reduced their sizes, with species numbers of Senecio reduced from thousands, to hundreds, and ultimately perhaps phylogenetically to only a few dozen. Senecio, "a dangerous plant for man and beast" (Johnson et al. 1989), prior to the 1950s was a loose conglomerate of species mostly having alternate leaves, exappendiculate disk style branches that are not papillose abaxially (viz figs. 1A, 2A–B), ecaudate anthers (viz fig. 1B), calyculate involucres with uniseriate subequal free appressed phyllaries (Fig. 3C–F), and 10-nerved cypselae. Macromorphological mavericks with deeply lobed white (vs. Senecio's usual shallow-lobed yellow) disk corollas and/or opposite leaves, now placed in subtribe Tussilagininae, once often passed casually as Senecio. A waning Senecio has altered not, however, the numbers of tribe Senecioneae Cass., which still contains about 1% of all Angiosperm species; Senecioneae is a member of the GASCA group of tribes of Asteroideae, the largest subfamily of Compositae, and is largest tribe of Compositae, which is the largest family of Angiosperms (Pruski 2018; Pruski and Robinson 2018).

Microcharacters now known to help define subtribe Senecioninae include balusterform filament collars with inflated proximal cells (Figs. 7B, 8B here; Koyama 1967, fig. 3D–F; Wetter 1983, figs. 24–25, 27–28; Vincent and Getliffe 1992, fig. 3 + character 110 diagrams 1–3, 9; Pruski 1996, fig. 1G; Lapp et al. 2015, figs. 5-8; Pruski 2018, figs. 1, 35A, 36B, 37A, 50A); radial endothecial tissue (never polarized) (Robinson and Brettell 1973, fig. 2; Nordenstam 1978, fig. 2; Wetter 1983, figs. 30-31; Jeffrey and Chen 1984, pls. 2-3; Vincent and Getliffe 1988, fig. 1; Pruski 2018, figs. 35B, 37B); and disk style branches (stigmatophores) with adaxial (ventromarginal) paired/2-banded stigmatic surfaces (Figs. 2A–C, 7, 8D here; Nordenstam 1978, figs. 24E, 25E, 35; Wetter 1983, figs. 7–9; Pruski 2012b, fig. 2; Pruski 2018, figs. 2, 29B, 31A–B, 36C). Although, for example, Baillon (1886: 57) gave anther bases of tribe Senecioneae as ecaudate ("san prolongements") and styles apices as usually truncate with an abaxial-lateral apical semicircle of short-papillae ("tronquées, légèrement dilatée et finement pénicillée") as found in Senecio, many Senecioninae are not so characterized. Senecioninae characters discouraging inclusion in Senecio are obviously appendiculate disk styles (Fig. 2C–D here; Nordenstam 1978, figs. 25–27, 30F, 34F, 35; Jeffrey and Chen 1984, pl. 6E, J; Jeffrey 1986, figs. 1–2; Pruski 1996, fig. 1G; Nordenstam 2007, fig. 53; Pruski 2012b, fig. 2; Salomón et al. 2016, fig. 1B–D; Pruski 2018, fig. 2A, E), **caudate anthers** (Figs. 7B, 8B here; Nordenstam 1978, fig. 16K–L; Jeffrey and Chen 1984, pl. 4; Pruski 1991, fig. 1F; Pruski 2012b, fig. 1B; Lapp et al. 2015, figs. 5–8; Pruski 2018, figs. 35A, 36B, 50A), and/or ecalyculate capitula (Fig. 3A-B), and indeed since the 1950s plants with such characters have often been excluded from Senecio. While many macromorphologically delineated genera of Senecioneae in the Americas have long been recognized—e.g., dioecious Chersodoma Wedd., functionally staminate-disked Tussilago L., and connate-phyllaried Werneria Kunth—and several Senecioninae have been removed recently or resurrected from Senecio—e.g., Aetheolaena Cass., Iocenes B. Nord., Lasiocephalus Willd. ex Schltdl., Monticalia C. Jeffrey, Ortizacalia Pruski, Pentacalia Cass., Pseudogynoxys (Greenm.) Cabrera—in Andean South America plants of many faciès remain among the residuum called Senecio.

Bain and Jansen (1995), Kadereit et al. (1995), Knox and Palmer (1995), Sang et al. (1995), Kadereit and Jeffrey (1996), Swenson and Bremer (1999), Comes and Abbott (2001), Pelser et al. (2002, 2004, 2006, 2007, 2010a, 2010b), Wagstaff and Breitwieser (2004), Panero (2005), Dušková et al. (2010, 2017), Jones et al. (2014), Ozerova et al. (2017), Gichira et al. (2019), and Salomón et al. (2019) provided phylogenies for parts of Senecioneae studied here. Pelser et al. (2007) in parsimony analysis of their ITS dataset 1 recovered with low support (BS < 50%, PP 95) the *S. pubiger-S. sisymbriifolius* clade and the "*Faujasia-Oldfetia* clade" (Pelser et al. 2007: 1F, expanded cladogram in figs. 1G–1I). The later clade includes many American Senecioninae, some lineages with higher support values, e.g., *Pentacalia* (Fig. 2A here), *Pseudogynoxys* (Fig. 3E–F here), and *Graphistylis* B. Nord. (Fig. 13C here).

The expanded cladogram (Pelser et al. 2007: fig. 1G) shows the *S. pubiger-S. sisymbriifolius* clade, and variously supported clades within, includes weakly supported sister lineages (BS < 50%, PP 82; the abbreviation BS is bootstrap support, Bayesian posterior probability is PP) "New World *Senecio* clade 1" (here abbreviated **NWS clade 1**) and *S. achilleifolius-S. sisymbriifolius* clade (BS < 50%, PP < 50). Various small clades that vary individually in support are shown within *S. achilleifolius-S. sisymbriifolius* clade, among these the *S. spanomerus-S. donianus* clade (BS 57%, PP 95). The **NWS clade 1** includes *Aetheolaena*, *Culcitium* Bonpl., *Hasteola* Raf., *Iocenes*, *Lasiocephalus*, and a largely monophyletic *Robinsonia* DC. interspersed among various taxa called *Senecio* (Pelser et al. 2007). Support for relationships within NWS clade 1 are mostly low, e.g., *Robinsonia* +*Aetheolaena involucrata-A. patens* clade (BS < 50%, PP < 50), *Hasteola-Senecio triangularis* clade (BS < 50%, PP < 50), and *Iocenes-Senecio fistulosus* clade (BS < 50%, alternative topology) (Pelser et al. 2007: fig. 1H). The *S. spanomerus-S. donianus* clade (Pelser et al. 2007: fig. 1I) includes a weakly supported sister relationship of "New World *Senecio* Clade 2" and *S. nevadensis-S. viscosus* clade, deep within the later a well-supported (BS 87%, PP 100) Old World-centered *S. vernalis-S. viscosus* clade which includes the generitype *S. vulgaris* L.

In a previous study, Pelser et al. (2002) noted that although the *Emilia-Packera-Pseudogynoxys* clade was recovered as sister to *Senecio* sect. *Jacobaea* (Thunb.) DC., the relationship was "not conclusive" and "lacks strong bootstrap support" (BS < 50%). Similar low support in Pelser et al. (2007; fig. 1G) was given for relationships among NWS clade 1 and *S. achilleifolius-S.* 

sisymbriifolius clade, but Pelser et al. (2007) suggested reduction of all component genera of both clades into Senecio. While species of Aetheolaena, Culcitium, Hasteola, Iocenes, Lasiocephalus, and Robinsonia are indeed found alongside so-called Senecio species in NSW clade 1, the bootstrap support is weak for a sister relationship between NWS clade 1 and S. achilleifolius-S. sisymbriifolius clade. Thus, it may be equally premature to accept reduction of all NWS clade 1 genera to Senecio and/or to describe new genera to house potential unplaced "Senecios" of S. achilleifolius-S. sisymbriifolius clade and/or NWS clade 1.

The field characters that I have seen in US Gulf Coast wetlands and lower-Mississippi-Atchafalaya basin Senecios (now Packeras) and Andean Senecios, e.g., *S. formosus* HBK that I saw near Laguna de Mucubají (Venezuela), prompted me as a student in the 1970s to comment about the French Quarter weed *Senecio vulgaris* "I wonder why this plant is called *Senecio*." American Senecios in aspect simply do not appear to closely resemble Eurasian *Senecio*, which I learned later is typified by Old World native *S. vulgaris*. Therefore, it is not beyond the bounds of possibility to envision monophyly, in the strict sense, by accepting as *Senecio* only the few dozen obviously similar species of the Old World-centered monophyletic *S. vernalis-S. viscosus* clade of Pelser et al. (2007: fig. 1I), within which is the even-less-inclusive *S. vernalis-S. vulgaris* clade (BS 99, PP 100). *Senecio* in the strictest sense could ultimately be composed of only Old World-centered *Senecio* sect. *Senecio* (but not those of sect. *Jacobaea*) as treated by Alexander (1979), Nordenstam and Rechinger (1989), Kadereit et al. (1995), Comes and Abbott (2001), and Ebadi and Eftekharian (2021), with the genera of the NWS clade 1 and *Senecio* thus being unlikely congeners.

Chater and Walters (1976) recognized each Senecio sect. Senecio and Senecio sect. Jacobaea, whereas Alexander (1979) reduced Senecio sect. Jacobaea in synonymy of Senecio sect. Senecio. Alexander (1979) said it is "unrealistic to maintain" Senecio sect. Jacobaea as sectionally distinct. Alexander (1979) noted "problems" in identification, stated that taxonomy of some species is "difficult," and that some groups are "extremely confused." Pelser et al. (2004) recognized *Senecio* sect. Jacobaea, and said in Senecioneae "most [floral] characters are not suitable for identifying clades containing more than just a few closely related species." Bednorz and Podsiedlik (2013) studied cypsela characters of *Jacobaea*, noting most species have papillose cypselae, as given by Chater and Walters (1976). Pelser et al. (2006, 2007) resurrected *Jacobaea* at the generic rank, and noted it falls in a distant clade with Packera, Pentacalia, and Pseudogynoxys. Although Pelser et al. (2004, 2007) said no "clear morphological synapomorphies" in *Jacobaea* were found, these authors noted many of the two dozen or so species of Jacobaea have T-shaped trichomes and all species have an equal number of rays and phyllaries. Senecioneae trichome characters have been noted as being of systematic value for genera and species (e.g., Drury and Watson 1965; Drury 1966, 1973; Nordenstam 1978, 2007; Sahu 1983; Jeffrey 1987; Pruski 2018), and (as given above) style and anther characters have been used to distinguish between subtribes. Another character, the strongcostate disk corolla tubes I have seen in herbarium material of Jacobaea but not Senecio, may possibly distinguish them, but instead may be only an artifact of drying. Characters delineating Lasiocephalus and allies are known, and Cabrera (1949) keyed and described 21 sections of Senecio s.lat. in Chile. However, as in the case of *Jacobaea*, synapomorphic characters of clades (some of which may correspond to Cabrera sections or reinstated genera) appear not to be well worked out yet.

Because I recognize only species of the *S. achilleifolius-S. sisymbriifolius* clade of Pelser et al. (2007: fig. 1G, expanded cladogram in fig. 1I) as *Senecio*, **NWS clade 1** members appear to be generically distinct from *Senecio*, as provisionally defined here. Also, under this circumscription the two new species described herein are allowed within *Senecio*. Nordenstam (2007: 230, 232, 234, 235) recognized NWS clade 1 genera *Aetheolaena*, *Culcitium*, *Hasteola*, *Iocenes*, *Lasiocephalus*, and *Robinsonia*. At present, based on morphology as in Nordenstam (2007) I take the six aforementioned appendiculate-styled and associated genera centering about *Lasiocephalus* (and now a seventh, *Haplosticha*) of **NWS clade 1** as distinct generically from *Senecio*, basically returning to the generic framework used by Cuatrecasas (1978), Nordenstam (1977, 1978, 2007), and Bremer (1994). These seven genera appear to group within the *S. roseus-S. lastarianus* clade of a polytomy in Pelser et al. (2010a: fig. 2, ITS/ETS data set) and with moderate support (PP 98) (Pelser et al. 2010a: fig. 3, combined plastid-ITS/ETS data set) the *S. nemorensis-S. lastarrianus* clade. Elsewhere within NWS clade 1 (Pelser et al. 2007: fig. 1H), a few dozen species allied to those sampled by the authors fall among current *Senecio* synonyms *Brachypappus* Sch. Bip., *Rhetinodendron* Meisner, *Senecio* 

sections *Amplectentes* Greenm., *Hualtatini* Cabrera, and *Mulgedifolii* Greenm., and have valid names only in *Senecio*. These so-called Senecios may appear to be unplaced generically, but nevertheless it seems practical, by default, to refer to them as *Senecio*. Generic status and relationships of the sections and unplaced members of these clades is under study by the author. Within the NWS clade 1, *Aetheolaena* and *Lasiocephalus* as recognized here correspond, respectively, to the "forest clade" and the "páramo clade" in the phylogeny of Dušková et al. (2010, 2017). However, Dušková et al. (2010, 2017) did not find *Culcitium* to be monophyletic. Thus, *Culcitium* could be taken phylogenetically as monotypic, although morphologically several species seem to be core-species. Bremer (1994) and Nordenstam (2007) each accepted about "15 species" in *Culcitium*.

Walter et al. (2020) illustrated 18 species of *Senecio* that highlight its diverse morphology. Although Heath (1997, 1999), Barkley et al. (2006), Funston (2008), and Pruski and Robinson (2018) excluded three of the 18 species [i.e., *Curio rowleyanus* (H. Jacobsen) P.V. Heath, *Delairea odorata* Lem. (syn. *Senecio scandens* Buch.-Ham. ex D. Don), and *Roldana petasitis* (Sims) H. Rob. & Brettell] from the genus, *Senecio* s.lat. remains highly diverse. The Senecioneae appears ripe for the morphological and phylogenomic studies as Walter et al. (2020) suggested. Such studies could target study of generic status of members of **NWS clade 1** and/or to address whether or not *Senecio* should include species of only the *S. achilleifolius-S. sisymbriifolius* clade, the *S. elegans-S. polygaloides* clade (Pelser et al. 2010a; fig. 2), or even of only the narrow *S. vernalis-S. viscosus* clade. My morphology-based studies retain the generic framework used by Cuatrecasas (1978) and Nordenstam (1978, 2007), allowing information associated with *Lasiocephalus* et al. to stand apart from that of *Senecio*. In a somewhat parallel situation, Jeffrey (1986) noted for east African Senecioneae, that if segregate genera were not used the only way to achieve monophyly "would be to include the whole of African Senecioneae within *Senecio* itself" which could "cause complete loss of considerable information associated with ... segregates accepted here."

A broadly defined *Senecio* is cosmopolitan, but few of its species are cosmopolitan weeds. In the Neotropics, nearly all native species called *Senecio* are at some level regional. elevational and high Andes contain several similar-in-gestalt regional so-called Senecios which are Senecioninae, but have been excluded from Senecio by macromorphological, anther, and/or stylar distinctions. Not treated by me in this paper here are some onetime Senecios removed further afield to subtribe Tussilagininae, a subtribe distinguished by cacalioid microcharacters of cylindrical filament collars with equal-sized cells (Koyama 1967, fig. 3A-C; Nordenstam 1978, fig. 4; Wetter 1983, figs. 23, 26; Vincent 1996, figs. 4, 6; Pruski 2012a, fig. 1A-B; Pruski 2018, fig. 4A, 4C, 4E) and entire-continuous stigmatic surfaces (Wetter 1983, figs. 1–3; Pruski 2018, figs. 4F, 9B). Tussilagininae are mostly extra Neotropical and taxa with polarized endothecial tissue (viz Robinson and Brettell 1973, fig. 1; Nordenstam 1978, fig. 1; Wetter 1983, fig. 29; Pruski 2018, fig. 4B) are nearly always referable to Tussilagininae. Not all Tussilagininae, however, have polarized endothecial tissue. For example, Pruski (2012a) and Pruski and Robinson (2018) placed Mesoamerican Robinsonecio T.M. Barkley & Janovec and Barkleyanthus H. Rob. & Brettell in Tussilagininae, but described them as having radial endothecial tissue (viz Pruski 2012a, fig. 1C). The radial endothecial tissue of these two genera of Tussilagininae recalls the endothecium of subtribe Senecioninae, bringing to mind Bremer's (1994) suggestion that possible reticulate evolution across the two main Senecioneae subtribes may result in shuffled characters and a "disturbed picture." Hasteola seems cacalioid in its moderately long-lobed white disk corollas and deltate-hastate leaves, but has balusterform filament collars and is Senecioninae. Hasteola too seems to mix characters of the two largest subtribes of tribe Senecioneae.

In older classifications Andean *Senecio* has often been subdivided into manageable-sized groups marked by various macromorphological character combinations, including those of habit (lianas, subshrubs, or trees vs. herbs), leaves (size, shape, and vestiture), capitulescences (pluricephalous paniculate or corymbiform vs. paucicephalous cymose or even monocephalous), and capitula (radiate vs. discoid or disciform). These informal artificial groupings within Andean *Senecio* sometimes have been placed taxonomically in formal infragenera—sections, subsections, series, or subseries—based on these character suites. On occasion, however, some infragenera were said to be artificial—e.g., Nordenstam (1978) noted that *Senecio* sect. *Reflexus* Cuatr. contained members that "belong to at least three genera"—nevertheless, infrageneric groupings by default remain the basis for taxonomy of *Senecio* in the Andes.

From the outliers of 'Senecio' found in the Andes, several infragenera of Senecio are now recognized as genera. For example, the three non-typical sections of Senecio used by Cabrera (1985; Cabrera et al. 1999) are now taken as distinct generically: Senecio sect. Acanthifolium Cabrera is treated here as Iocenes; Old World native Senecio sect. Delairea (Lem.) Benth. & Hook. f. as Delairea Lem. (Pruski and Robinson 2018); and Senecio sect. Streptothamni Greenm. as Pentacalia (Pruski 2018). Even within the typical section a series—Senecio sect. Senecio ser. Myriocephi (Cabrera) Cabrera—is recognized currently as the genus Dendrophorbium (Cuatr.) C. Jeffrey (Jeffrey 1992; Pruski 2018).

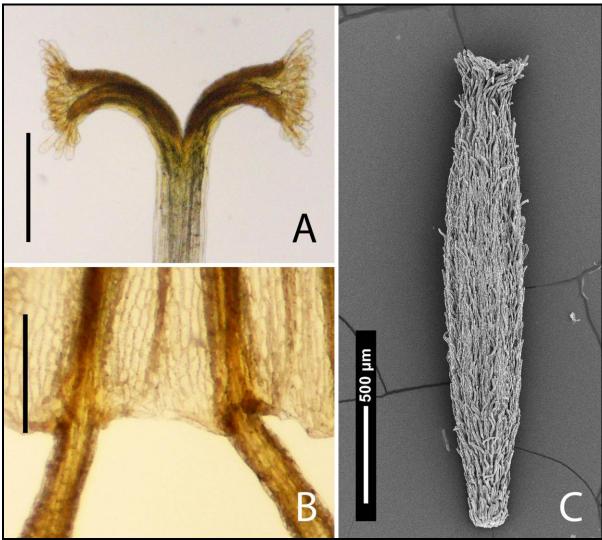


Figure 1. Style, anthers, and cypsela of select members of the GASCA tribes of Asteroideae. *Chaetacalia* has appendiculate disk style branches, short-caudate anthers, and glabrous cypselae, contrasting with those seen here in *Matricaria*, *Astranthium*, and *Senecio*. A. Disk style branches of *Matricaria chamomilla* L. (Anthemideae) showing the archetypical anthemoid-senecioid exappendiculate truncate-tipped style characteristic of Anthemideae and of much of Senecioneae subtr. Senecioninae. Such branches have paired stigmatic surfaces distinct throughout (i.e., not confluent apically). There are, however, at least 15 distinct style types (Vincent 1996) in tribe Senecioneae. B. *Astranthium purpurascens* (B.L. Rob.) Larsen (Astereae), adaxial view of two obviously ecaudate truncate-based anthers and distal portions of the filament collars. C. Cypsela of *Senecio vulgaris* L., although the genus *Senecio* is so named for its abundant white pappus bristles, the pappus bristles have been intentionally removed here; the dense covering of papillae mostly obscures the ten costae; the papillae when wetted emit threads much longer than the dry papillae. (A *Pruski 4606*, MO; B *Croat 66156*, MO; C *Khan et al. 985*, MO). Scale bars A 0.2 mm, B 0.1 mm.

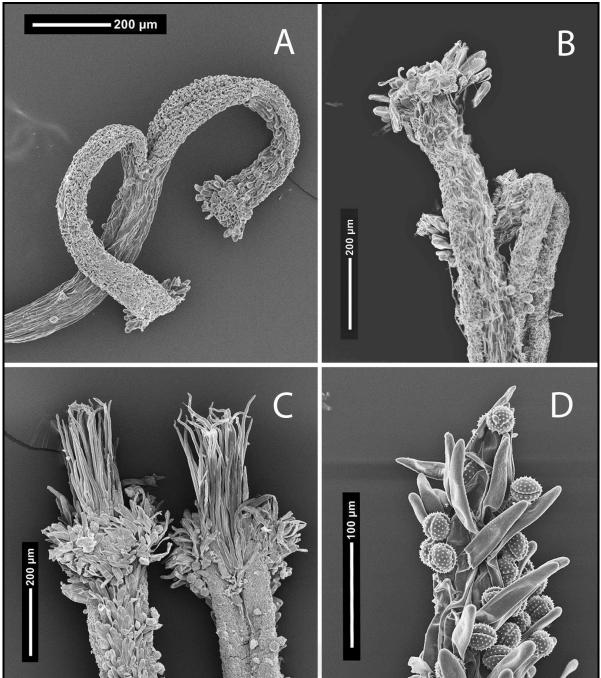


Figure 2. Style branches in disk florets of select Senecioneae subtr. Senecioninae. A–B archetypical exappendiculate *Anthemis-Senecio* type branches (A–B) with those on the right showing stigmatic surfaces 2-banded to apex and (C–D) two types of appendiculate branches. A. *Pentacalia phanerandra* (Cufod.) R. & C., recurved branches showing truncate apices with a semicircular crown of papillae and non-papillose abaxial branch surface. B. *Senecio callosus* Sch. Bip., branch on left showing truncate apex with a semicircular crown of papillae and non-papillose abaxial branch surface. C. *Ortizacalia austin-smithii* (Standl.) Pruski, heteromorphic-papillose-comose appendiculate branches, apical comae composed of linear free papillae; branch on left shows the papillose abaxial (outer) distal branch surface, branch on right shows the adaxial sigmatic lines free to apex and the lateral margins of apical semicircular crown. D. *Pseudogynoxys haenkei* (DC.) Cabrera, long-triangular-conical cellar-appendiculate branch apex with scattered pollen grains and papillae. (A *van der Werff* 7236, MO; B *Véliz* 8327, MO; C *Haber* & *Zuchowski* 9847, MO; D *Pruski et al.* 4195, MO).

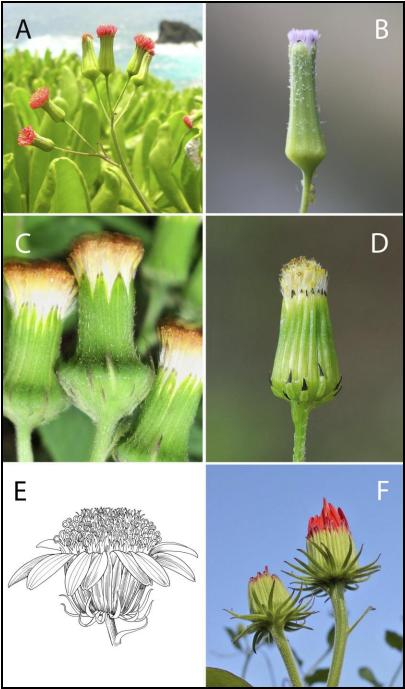


Figure 3. Involucres of capitula of select Senecioneae subtr. Senecioninae. A–B. Ecalyculate involucres, capitula discoid. A. *Emilia fosbergii* Nicolson. B. *Emilia sonchifolia* (L). DC. C–D. Unequally-irregularly calyculate capitula, bracteoles appressed, capitula discoid. C. *Crassocephalum crepidioides* (Benth.) S. Moore. D. *Senecio vulgaris* L., the generitype. E–F. Subequally-regularly calyculate capitula, bracteoles elongate spreading, capitula radiate. E. *Pseudogynoxys lobata* Pruski. F. *Pseudogynoxys benthamii* Cabrera; this is the commonly cultivated "hairy flame vine," reported as *P. cummingii* (Benth.) H. Rob. & Cuatr. by Pruski (1996), but redetermined as *P. benthamii* by Pruski and Robinson (2018). Various combinations of intermediate conditions are known in other Senecioninae. (A Hawaii, photograph by Forest Starr, unvouchered; B Tarapoto, *Pruski & Ortiz 4740*; C Honduras, *Pruski et al. 4531*; D Missouri, *Turner 13-013*, photograph by *Steve Turner*; E Pruski 1996: 102, fig. 1B, protologue figure; F Algiers, New Orleans, *Pruski & Ortiz 4007*).



Figure 4. *Centropappus brunonis* Hook. f., representative specimen, endemic to Tasmania. Monecious *Centropappus* in general aspect resembles superficially newly resurrect dioecious *Robinsonia*, but differs by its long-lobed, yellow disk corollas, cylindrical filament collars, and style branches with continuous stigmatic surfaces. (*Ratkowsky & Ratkowsky 227*, MO).

Recognition of the non-typical Bolivian and Argentinian sections of *Senecio* s.lat. in Cabrera (1985; Cabrera et al. 1999) as segregate genera raises effectively by a hierarchical rank *Senecio* sect.

Senecio, and in turn informally raises by one rank the remaining infragenera within this section that were recognized by Cabrera (1985; Cabrera et al. 1999). This returns Senecio sectional classification nearer to the scheme of Cabrera (1949), although some sections used by Cabrera were recovered by Pelser et al. (2007) in NWS clade 1. Jeffrey (1992) recognized 18 sections of Senecio subg. Senecio, but Kadereit and Jeffrey (1996) noted that the typical subgenus was not monophyletic. Several groups, which are otherwise nameless, are nevertheless by default called sections within Senecio.

With no assertion of completeness, nor based on dissection of all South American species that is beyond the scope of the present study, I treat the nominant section here at the generic rank as *Senecio*. Accordingly, a few series names in Cabrera (1985) are informally here called sections. For example, series that may better be taken at the higher hierarchically sectional rank include *Senecio* sect. *Senecio* ser. *Corymbosi* (Cabrera) Cabrera, *Senecio* sect. *Senecio* ser. *Crassicephali* (Cabrera) Cabrera, *Senecio* sect. *Senecio* ser. *Otopteri* (Cabrera) Cabrera, which here are loosely called, respectively, *Senecio* sect. *Corymbosi* Cabrera, *Senecio* sect. *Crassicephali* Cabrera, *Senecio* sect. *Hualtatini* Cabrera, and *Senecio* sect. *Otopteri* Cabrera. On the other hand, NWS clade 1 member *Senecio* sect. *Senecio* ser. *Culcitium* (Bonpl.) Cuatr. ex Cabrera in Cabrera (1985) is treated by me at the generic rank as *Culcitium*.

The accurate treatment of Senecio by Weddell (1855) treated many of the more widespread and better-known Andean Senecios. In the past century for South America, the excellent floras of Senecio in Argentina (Cabrera 1941, 1974, 1978; Cabrera and Zardini 1980; Cabrera et al. 1999; Ariza Espinar and Freire 2013; Freire et al. 2014; except for the 2014 work, each with usable userfriendly indented keys); Chile (Cabrera 1949); Brazil, Paraguay, and Uruguay (Cabrera 1957); Venezuela (Aristeguieta 1964); and Bolivia (Cabrera 1985) have been provided. A revision of tribe Senecioneae—28 genera and 94 species—in the seven countries of Central American and in southeastern-most Mexico in the Flora Mesoamericana series was published recently (Pruski and Robinson 2018). Greenman (1902, 1923, 1938), Cabrera (1934, 1939, 1944, 1950a, 1952, 1953, 1954, 1955, 1966), Cuatrecasas (1942, 1944, 1950, 1951, 1953a 1953b, 1955), and Díaz-Piedrahita and Cuatrecasas (1999) are among the many references that provided us with detailed preliminary treatments of parts of Senecio s.lat. in the central and northwestern Andes. Recent checklists, departmental florals, species group treatments with keys or character tables for Senecio in parts of the central and northern Andes include useful works by Beltrán and Galán de Mera (1996), Vision and Dillon (1996), Montesinos Tubée (2014), Beltrán and Roque (2015), Pruski (2018), Salomón et al. (2018), Calvo et al. (2019), Calvo and Moreira-Muñoz (2020), and Aguilar-Cano and Hind (2020).

Among plants familiar to me that have been treated variously—as Aetheolaena, Culcitium, Lasiocephalus, Senecio sect. Aetheolaena (Cass.) O. Hoffm., or Senecio sect. Reflexus by Blake (1937), Cuatrecasas (1950, 1951, 1978, 1990, 1994), Nordenstam (1978, 1997, 2007), Cabrera (1985), Jeffrey (1992), and Bremer (1994)—Bolivian Chaetacalia Pruski is described. Chaetacalia is diagnosed by perennial herbaceous non-scandent habit, short-caudate anthers, balusterform filament collars, 2-banded penicillate disk style branches that are dense-papillose distally on the abaxial (outer) surface, and erect, basically ecalyculate, heterogamous, disciform capitula. I agree with Pruski (2018) who noted that NWS clade 1 genera "Aetheolaena Cass., Culcitium Bonpl. ... Lasiocephalus Willd. ex Schltdl., and ... Iocenes B. Nord." were deserving of recognition. Chaetacalia by floral features may perhaps prove to belong to the "Faujasia-Oldfetia clade" rather than to NWS clade 1. Chaetacalia is not considered by me to be near the Aetheolaena-Lasiocephalus group.

Accordingly, South American penicillate-appendiculate-styled *Aetheolaena* (Figs. 12C, 13D, 14–17A), *Iocenes* (Figs. 23–24), and *Lasiocephalus* (Figs. 11–12A, 17B–20) are each revisited and recognized again. None of these three NWS clade 1 genera have style branches dense-papillose distally on the abaxial (outer) surface, as characteristic of *Chaetacalia*. Also retained are North American *Hasteola* and three South American truncate-styled genera of NWS clade 1: *Culcitium* (Fig. 12B), *Haplosticha* (Figs. 21–22), and *Robinsonia* (viz fig. 4). South American *Culcitium* contains the truncate-styled, griseous-lanate-tomentose species of NWS clade 1 having discoid nutant capitula, but no new combinations are proposed within the genus.

I also recognize the remarkable dioecious radiate-capitulate rosette tree *Robinsonia* [syn. *Rhetinodendron* Meisner 1839 = *Balbisia* DC. 1833, non *Balbisia* Cav. 1804, nom. cons.,

Geraniaceae s.l.] of the Juan Fernández Islands. Robinsonia contains eight species, those in Sanders et al. (1987), plus one more described recently. The NWS clade 1 and the S. achilleifolius-S. sisymbriifolius clade (which includes the generitype S. vulgaris), with low support (BS < 50%, PP 82) were shown as sister, thus Robinsonia is perhaps not "deeply nested within Senecio" although stated as such in Pelser et al. (2010b).

Candolle (1833: 333-334) in their protologues said each Balbisia DC. and Robinsonia was "voisin des Senecons." The next year, Decaisne (1834) treated Rhetinodendron (as Balbisia DC.) and Robinsonia as distinct from each other and from Senecio. The shared characters given by Sanders et al. (1987) as noteworthy in each Senecio and the very odd Robinsonia—n = 20, truncate styles, and ornamented endothecium—are basically characters of many American genera of Senecioninae. The plant aspect, especially the distally-clustered narrow leaves and resinous stems, seen in dioecious Robinsonia recall monotypic Tasmanian Centropappus Hook. f. (Fig. 4) which is monecious and is a member of the very different Brachyglottis generic group. The similarity of these two Pacific Rim genera is noteworthy, however, perhaps more so than are similarities of either of the two with Mexico and Central American Telanthophora H. Rob. & Brettell (Tussilagininae), which Pruski and Robinson (2018) gave as also resinous-stemmed and often with apically-clustered narrow leaves. Centropappus (Nordenstam 1978; Orchard 2004; Thompson and Orchard 2015) is characterized by its cacalioid microcharacters and brush-tipped pappus, unlike senecioid Robinsonia.

Radiate-capitulate white-ray-flowered southern South American Haplosticha and Iocenes are reinstated. Haplosticha and Iocenes are not members of the discoid-capitulate clade containing the Aetheolaena-Culcitium-Lasiocephalus group, or is either similar to Chaetacalia or dioecious Robinsonia. Rather, in Pelser et al. (2007) Haplosticha and Iocenes are members of the partly unresolved NWS clade 1 that contains among its members the widely used isolated eastern North American Hasteola (viz Spellenberg and Zucker 2019; Wunderlin et al. 2020). Cabrera (1949; Cabrera et al. 1999) treated four subrosulate perennial species within *Senecio* sect. *Haplosticha* (Phil.) Cabrera, and of these I recognize three in *Haplosticha*: H. zosterifolia (Hook. & Arn.) Pruski (that includes in synonymy the generitype H. stolonifera Phil.), H. arnicoides (Hook. & Arn.) Pruski, and H. trifurcata (G. Forst.) Pruski. *Iocenes* is taken as monotypic following Nordenstam (1978, 2007) and contains only *Iocenes virens* (Phil.) Pruski.

Lastly, described here in Senecio are two Andean species new to science (one in collaboration with Rosa Ortiz). Senecio vasquezii Pruski & R. Ortiz (Figs. 25–29) and Senecio perezioides Pruski (Figs. 34–36) are Senecioninae having truncate exappendiculate archetypical anthemoid-senecioid styles (Figs. 1A, 2A-B)—characteristic of Anthemideae and much of Senecioneae—and thus fall morphologically within or near a broadly defined Senecio. The newly described Senecios are further similar to each other by their subrosulate habit and large yellow-flowered radiate capitula. Similarly, anthemoid-senecioid styles typical of Senecio s.lat. are found, for example, in Packera Á. Löve & D. Löve and Pericallis D. Don (Senecioninae), which each differ from Senecio by the extreme microcharacter of helianthoid pollen ultrastructure (columellae with internal foramina; Skvarla and Turner 1966; Nordenstam 1977; Bain and Walker 1995; Bain et al. 1997). However, freeing of stranded truncate-styled groups of Senecioninae from Senecio based on conventional microcharacters remains unfinished.

### ANATOMICAL AND SEM METHODS

The wet slide mounts were viewed on an Olympus compound microscope and photographed with an ocular-mount Nikon E5700 camera using a MM99 adapter S/N: 1815 (Martin Microscope Company, Easley, South Carolina) or with a top-mount Canon A640 camera. Lower magnification images were viewed in a dissection microscope, and were photographed with either a hand-held Sony Cyber-shot DSC W-50 with its 15 mm diameter lens positioned over the 25 mm diameter ocular, an ocular-mount Nikon E5700 camera using a MM99 adapter, or a top-mount Canon A640 camera. SEM mounts were sputter-coated with Au/Pd on a Denton Desk V Cold Sputter Coater operating at 35 mAmps for 120 seconds. The sputtered coated mounts were then micrographed on a JEOL NeoScope CM-5000 scanning electron microscope using 10 kV accelerating voltage, and operating under high vacuum. These are basically the same methods I used in Cariaga et al. (2008) and Pruski (2012a, 2012b, 2018).

# 1. CHAETACALIA Pruski, gen. nov. TYPE: Senecio stylotrichus Cabrera [≡ Chaetacalia stylotricha (Cabrera) Pruski]. Figures 5–10.

Herbae perennes 0.4-1.5 m altae, caules erecti striati glabrati; folia simplicia alterna sessilia, lamina (4-)6-13(-16) × (2-)3-6 cm, elliptico-lanceolata chartacea vel subcarnosa pinnatim venosa auriculata amplexicaula margine subintegra vel serrulata acuta vel attenuata concolorata glabra; capitulescentia usque 20 × 20 cm 4–13-capitulata laxe cymosa paucibracteolata, pedunculi 1.5–5 cm longi glabri; capitula heterogama disciformia erecta (9–)11–15  $\times$  6–10 mm ecalyculata; involucrum 8.5–10  $\times$  6– 10 mm campanulatum; phyllaria 8–10 subaequalia 8.5–10 × 2–3.5 mm lanceolata vel late lanceolata glabrata; clinanthium epaleaceum 3-3.5 mm latum glabratum; flosculi marginales pistillati 6-8 1-seriati, corolla 6.5-7.6 mm longa tubulosa ochroleucra glabrata; flosculi disci hermaphroditi 33-40, corolla 8-10.5(-11) mm longa tuboloso-infundibuliforma luteola glabrata quinquelobata, tubus 3.3-4.6 mm longus, lobi 1.2-1.8 mm longi lanceolati, antherae caudatae 2.5-2.8 mm longae collum basi dilatatum, styli rami circiter 1.1 mm longi distaliter penicillati extus valde papillati areis stigmaticis discretis; cypselae (3–)3.2– 4.5 mm longae oblongo-cylindricae bruneae glabratae; setae pappo vel 10 mm longae.

**Glabrous perennial herbs** 0.4–1.5 m tall; stems erect, subterete, exalate, 6+-striate, glabrous, sometimes deflected at nodes, leafy into capitulescence, few-branched distally, internodes mostly shorter than leaves, pith solid; neither caudex nor roots seen. Leaves simple, alternate, sessile; blade (4–)6–13(–16) × (2–)3–6 cm, elliptic-lanceolate, chartaceous to subcarnose, venation pinnate, secondary veins immersed, not prominent, sometimes reticulations slightly visible, base auriculateamplexicaule, each auricle broadly rounded (viz fig. 5), margins subentire to serrulate with up to 9 teeth per side, apex acute or attenuate, surfaces concolorous, glabrous, eglandular, abaxial surface sometimes purplish. Capitulescence (secondary arrangement of capitula) to 20 cm tall and broad, of few(-several) 4-13-capitulate open cymes terminal on main axis or terminal on branchlets from the distal nodes, branchlets (much) longer than subtending leaves, ascending, glabrous, proximal and mid-capitulescence branchlets typically subtended by subsessile, ovate glabrous, leafy bracts mostly 1–2 cm long, distal branchlets few-bracteolate; peduncles 1.5–5 cm long, longer than the capitula, glabrous, minutely few-bracteolate, bracteoles 1.5-2.5 × 0.2-0.3 mm, linear-lanceolate, sessile, glabrous, ascending, well-spaced but becoming spaced more closely distally. Capitula (primary inflorescence) heterogamous, disciform (subdiscoid), erect,  $(9-)11-15 \times 6-10$  mm, usually 39-45(-48)-flowered, ecalyculate; involucre  $8.5-10 \times 6-10$  mm, campanulate, peduncles bracteolate distally; phyllaries 8–10, 1-seriate, subequal, similar,  $8.5-10 \times 2-3.5$  mm, lanceolate to broadly so, free, flat, glabrous, herbaceous with pale scarious margins, weakly 4-9-nerved, nerves equally indistinct, phyllaries not carinate, apex acute, fringed, midzone green throughout or sometimes violet where overlapped laterally, margins narrowly scarious, 0-1 mm diam., sometimes about as wide as green midzone; clinanthium ("receptacle" of primary inflorescence) epaleate, 3-3.5 mm diam., flat, glabrous, solid. Marginal florets pistillate, 6–8, 1-seriate, maturation delayed, initially obscure and becoming visible only tardily after onset of disk floret anthesis; corolla 6.5–7.6 mm long, tubular, ochroleucous, glabrous, shortly few-lobed at apex, lobes ca. 1 mm long, erect; style weakly exserted from corolla. **Disk florets** bisexual, 33–40; corolla 8–10.5(–11) mm long, slightly exserted, tubularfunnelform, yellow with tube usually drying darker, glabrous, 5-lobed, tube 3.3–4.6 mm long, nearly as long as limb, broadened basally around stylopodium, limb narrow-ampliate, throat 3.5-4.1 mm long, lobes 1.2–1.8 mm long, lanceolate, shorter than throat, spreading to reflexed, abaxial (outer) apical epidermal cells slightly rounded-mamillose, medial resin canals in lobes not seen, margins and submarginal nerves dark-drying; anthers short-caudate, 2.5–2.8 mm long, pale brown, filament collars (anther collars) balusterform (dilated), 0.5–0.6 mm long, tan, tails non-polleniferous, 0.3–0.4 mm long, shorter than collar, endothecial tissue radial never polarized, apical appendage 0.4–0.5 mm long, lanceolate-ovate, longer than broad, apically broadly ovate to rounded, appendage nearly as wide as theca (seemingly more similar to those in Jeffrey 1987: 207, figs. 5b, 5d than to either of those depicted in figs. 5a, 5c) and never clearly apiculate, filaments about as long as or longer than anther thecae; style 9-12 mm long, penicillate-appendiculate and dense-papillose abaxially toward apex, stigmatic surface 2-banded, distinct throughout and not confluent apically, stylopodium (swollen style base) 0.4–0.6 mm long, broadened, free, held above nectary and not immersed, style branches ca. 1.1 mm long, spreading to reflexed, apex rounded to truncate, apical appendage a penicillate tuft of elongate papillae 0.15-0.2 mm long, relatively narrow and about as long as the disk style branch is wide, lateral apical crown semicircular, of papillae shorter but broader than those of apical tuft (as seen in dried herbarium material), the distal 2/3 of abaxial (outer) surface of branch with cells bulbous becoming densely papillose with papillae longer than broad, surface gradually becoming smooth in

proximal 1/3 and style shaft smooth below bifurcation, abaxial (outer) surface papillae shorter but broader than those of apical tuft (disk style branches nearly matching those drawn in Vincent 1996: 600, fig. 6 under the "peripheral Senecios"). Cypselae (achenes) of marginal pistillate florets and bisexual disks similar, (3–)3.2–4.5 mm long, oblong-cylindrical, subterete, brown, ca. 8–10-costate but with 5-8 ribs sometimes a bit thicker and lighter colored than the others (as seen on occasion in other genera, e.g., *Crassocephalum*), glabrous, ribs usually not obviously procurrent onto carpopodium, carpopodium 0.1–0.2 mm long, 10+ cells tall, tan, not obviously stopper-shaped but with a slight distal rim; ovary/pericarp cellular crystals ca. 20 µm long, hexagonal ("intermediate hexagonal" type, with length/width ratio between 1.5-6, as defined in Drury and Watson 1965; similar to those illustrated in Nordenstam 1978: fig. 9D, F-G), nearly homomorphic; pappus of marginal pistillate florets and bisexual disks similar, of numerous fine subequal scabridulous white bristles, to ca. 10 mm long, about as long as disk corollas, ca. 5 cells thick towards base and tapering ultimately to 2 cells thickness distally, apical cell tips pointed. Chromosome number unknown.

Etymology. The Latin generic name Chaetacalia is derived from the feminine Greek noun chaete—in reference (as is the epithet) to the apical papillae of the penicillate disk style branchesand the common-in-Senecioneae suffix calia.



Figure 5. Chaetacalia stylotricha (Cabrera) Pruski, close-up of a main stem distal node, showing auriculate-amplexicaule leaf base. (Molina 306, MO).



Figure 6. *Chaetacalia stylotricha* (Cabrera) Pruski, representative specimen, showing distal portion of stem and capitulescence with erect ecalyculate disciform capitula. *Humbertacalia amplexifolia* (Humbert) C. Jeffrey is remarkably similar in general aspect to *Chaetacalia stylotricha*. (Villarroel et al. 157, MO).

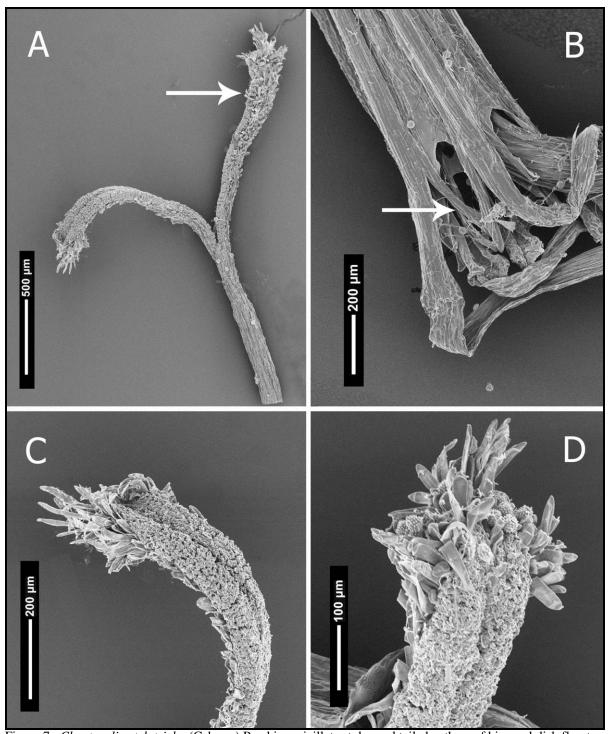


Figure 7. Chaetacalia stylotricha (Cabrera) Pruski, penicillate styles and tailed anthers of bisexual disk florets. The apical penicillate style appendage is a tuft of elongate papillae 0.15–0.2 mm long, whence the generic name, as seen in A, C–D. A. Bifid style, arrow pointing towards papillose distal abaxial (outer or dorsal) surface of branch on right. B. Proximal portion of anther cylinder with sterile tails (arrow) and balusterform collars; three narrower filaments and a thick style trunk are curved to the right. C–D. Distal abaxial surface of penicillate disk style branches, apical tuft longer than apical lateral semicircular crown and longer than the abaxial distal surface papillae that are visible on the left of each branch; the paired stigmatic lines are not fused distally and remain separated throughout their lengths by a sterile medial groove. (Villarroel et al. 157, MO).

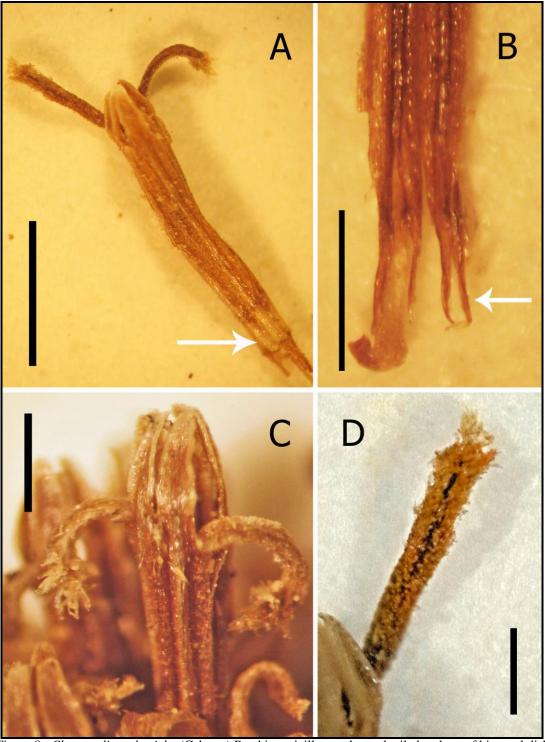
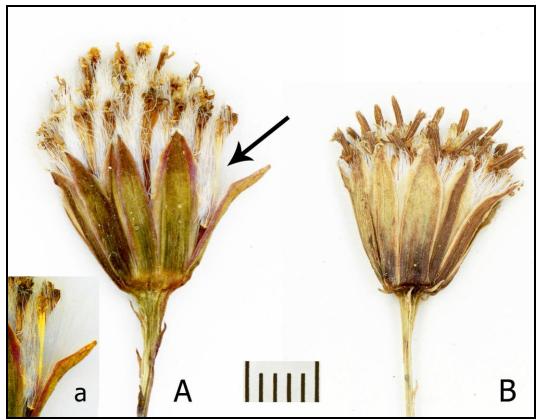


Figure 8. Chaetacalia stylotricha (Cabrera) Pruski, penicillate styles and tailed anthers of bisexual disk florets. A. Anthers and disk style branches; arrowing pointing towards the balusterform filament collars (lower right) of three anthers; the filaments are largely out of view. B. Adaxial view of two anthers; that on the left has intact collar; two obviously sterile non-polleniferous tails are seen on right (arrow) near the balusterform collar that is immediately to the left. C. Close up of abaxial distal portion of anther cylinder showing anther appendages longer than wide; exserted reflexed disk style branches are seen to both the right and left of cylinder. D. Disk style branch adaxial surface showing paired stigmatic lines separate to apex by a dark sterile medial groove. (*Villarroel et al. 157*, MO). Scale bars A 1.5 mm, B–D 0.5 mm.



Chaetacalia stylotricha (Cabrera) Pruski, representative heterogamous disciform ecalyculate capitula. A. Capitulum at late anthesis with the bisexual disk florets exserted; arrow pointing to a late-maturing pistillate marginal floret; the inset image lower left (a) is a close-up in high contrast highlighting the tubular corolla of this pistillate floret. B. Capitulum at anthesis, prior to disk style emergence. (Villarroel et al. 157, MO). The scale is 5 mm.

CHAETACALIA STYLOTRICHA (Cabrera) Pruski, comb. nov. Senecio stylotrichus Cabrera, Notas Mus. La Plata, Bot. 15(75): 107, f. 15. 1950. Lasiocephalus stylotrichus (Cabrera) Cuatr., Phytologia 76: 404. 1994. **TYPE**: **BOLIVIA**. Santa Cruz. Cerro Hosanna, 1300 m, 11 Aug 1917, *J. Steinbach 3363* (holotype: LIL; isotypes: A, US). (As "Cerro Hosana" in protologue; as "Cerro Hosane" at 17° 42' S, 64° 02' W in Paynter 1992: 62). Figures 5–10.

**Distribution and ecology.** Chaetacalia stylotricha (Cabrera) Pruski, the sole species of the genus Chaetacalia Pruski, is known only from south-central Bolivia in the department of Santa Cruz. where it occurs in openings in semideciduous forests from 525–1500 m elevation, and flowers from June-August. The type locality is about 100 km W of Santa Cruz de la Sierra, and three collections in the 2000s were made from 30–70 km SW of Santa Cruz de la Sierra.

Additional material examined. BOLIVIA. Santa Cruz. Florida, Comunidad de Bella Vista, Sendero El Cañadon, 18° 16' 24" S, 63° 40' 29" W, 1200–1500 m, 15 June 2006, *L. Arroyo et al.* 3363 (LP, MO, NY, USZ); Andrés Ibáñez, Monumento Natural Espejillos, en el bolson, siguiendo la ribera del río, 17° 54' 07" S, 63° 25' 56" W, 525 m, 23 July 2007, *A. Molina 306* (MO, US, USZ); Florida, Samaipata Bella Vista, Sendero Ecologico el Cañadon, 18' 11' 48" S, 63' 42' 23" W, 1487 m, 9 Aug 2005, D. Villarroel et al. 157 (MO-2, USZ; an incorrect label on the second MO sheet gives coordinates as near about 42° S, 79° W).

**Notes on specimens and collection numbers.** Chaetacalia stylotricha is known to me from four collections; two of these (Steinbach 3363 and Arroyo et al. 3363) are numbered "3363." Two differently labeled sheets of Villarroel et al. 157 are mounted at MO, one with unusually large leaves and a second sheet with a very broad capitulescence.

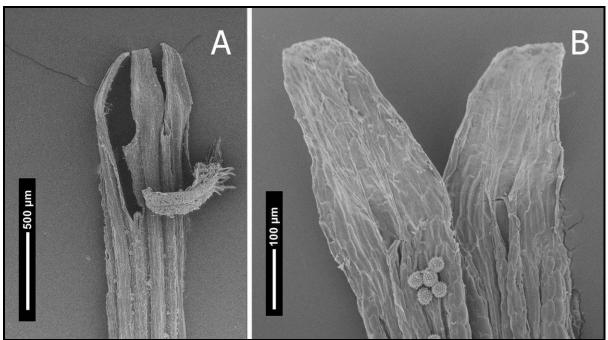


Figure 10. Chaetacalia stylotricha (Cabrera) Pruski, distal portions of anthers and anther appendages. The appendages are not noticeably narrower than the thecae, are longer than wide, and broadly obtuse to rounded apically. A. Three anthers, abaxial (outer) surface and (on right) a disk style branch exserted laterally. B. Close-up of two anther appendages, adaxial (inner) surface, five pollen grains are adherent. (Villarroel et al. 157, MO).

Cabrera (1950a) stated that leafy-stemmed *Chaetacalia stylotricha* is "muy diferente de todas las epecies de Senecio conocidas para Bolivia and Peru." Cabrera (1950a) continued and said it seemed premature to "separar ... [Chaetacalia stylotricha] ... como una nueva sección o género antes de hallar nuevos materiales." Three decades later Senecio stylotrichus was again suggested (Cabrera 1985) as perhaps representing either an undescribed section of *Senecio* or an undescribed genus. Cabrera (1985) said S. stylotrichus was known only from the type, and once again said it seemed wise to await collection of further material before addressing the affinities of S. stylotrichus.

Chaetacalia stylotricha (as S. stylotrichus) is one of three Bolivian species that Cabrera (1985) treated in Senecio sect. Aetheolaena. Senecio stylotrichus was placed intentionally first numerically (species 1 of 114) in Cabrera's (1985) treatment of Bolivian Senecios. In the same vein, the first of 90 species in Cabrera (1957) was S. argyrotrichus Dusén, one of six original species of Graphistylis B. Nord. (1978). Senecio acanthifolius, now Iocenes virens (Phil.) Pruski, was first of 270 species in the non-alphabetical Chilean flora by Cabrera (1949). Angel Cabrera (1949, 1957, 1985) placed at the vanguard these species that would become members of *Chaetacalia*, *Graphistylis*, and *Iocenes*. Cabrera tended to position aberrant species first in non-alphabetical floras, such as he did with *S. stylotrichus*.

Cuatrecasas (1994) treated subsequently the plant in Lasiocephalus, coining the name Lasiocephalus stylotrichus (Cabrera) Cuatr. for it. More recently, Salomón et al. (2018) treated the genera Aetheolaena and Lasiocephalus in synonymy with their concept of Senecio ser. Culcitium. Although Salomón et al. (2018) retained S. stylotrichus within Senecio, the authors excluded the species from Senecio ser. Culcitium. I have now seen and dissected sufficient new materials allowing comment on the uniqueness of *Chaetacalia stylotricha*, which is far more distinctive than recognized previously.

The capitula of *Chaetacalia* are ecalyculate (viz fig. 9A–B vs. fig. 3E–F). The description by Cabrera (1950a, 1985) of the capitula as discoid and of all florets as bisexual (Cabrera 1985: 83: 'capítulos discoides ... flores... isomorfas, hermafroditas") is mistaken. This was due seemingly to tardy maturation that is documented here in the short marginal pistillate florets (Fig. 9Aa). Similar delayed non-acropetal maturation of outer florets was reported by Harris (1995), widely in Anthemideae (e.g., Ren and Guo 2015), and by Pruski (2018: e.g., p. 78) elsewhere in Senecioneae. The capitula condition is emended here from "capítulos discoides" to capitula disciform with pistillate marginal florets with tubular corollas and bisexual disk florets (e.g., viz Pruski 2018: fig. 6B-C). This technical capitular character distinction excludes heterogamous disciform-capitulate Chaetacalia from the homogamous discoid-capitulate Aetheolaena-Lasiocephalus group. Elsewhere, Cabrera (1985) distinguished routinely between discoid and disciform capitula. For example, he keyed disciform-capitula S. subglomerosus Greenm. as "subdiscoides" and described it as having "flores The capitula of Chaetacalia are held erect (Figs. 6, 9), whereas the Aetheolaena-Lasiocephalus group members have nutant capitula (Fig. 12). Patagonian Iocenes (Figs. 23-24) of NWS clade 1 similarly has erect, ecalyculate capitula and glabrous cypselae, but in technical features differs from Chaetacalia by its white-rayed capitula (Fig. 24), ecaudate anthers, and styles that have the abaxial (outer) surface mamillose-lined towards the apex.

The anther bases of Chaetacalia stylotricha were described by Cabrera (1950a, 1985) as "sagitadas," and the protologue illustration (Cabrera 1950a: fig. 15d) depicts them as polleniferouscalcarate. Cabrera (1985) characterized the two other Bolivian species he treated as section Aetheolaena as having "semisagitadas" (i.e., ecaudate) anther bases, thereby distinguishing them from Chaetacalia stylotricha. Recent dissections, however, show Chaetacalia anthers as short-caudate with distinctly non-polleniferous tails (Figs. 7B, 8B), albeit the tail lengths proportional to thecae of Chaetacalia are not much greater than those of, for example, Scrobicaria Cass. (Nordenstam 1978: fig. 4j; Pruski 2018: fig. 1C), Zemisia B Nord. (Pruski 2018: figs. 35A & 36B), or Odontocline glabra (DC.) B. Nord. (Nordenstam 1978: fig. 5c). Nordenstam (1977, 1978) noted that in Senecioneae caudate anthers "developed independently several times" in "distantly related groups," and may vary within an individual genus. For example, in the *Brachyglottis* generic group Nordenstam (1978: fig. 15S) noted anther tails in *Brachyglottis laxifolia* (Buchanan) B. Nord. [misreported in Nordenstam 1977 as B. greyi (Hook. f.) B. Nord., and redetermined in Nordenstam 1978], but merely sagittate tails in other species of Brachyglottis J.R. Forst. & G. Forst. Similarly, in the Faujasia-Oldfetia clade Dendrophorbium silvani (Cuatr.) C. Jeffrey, the generitype, was shown by Díaz-Piedrahita and Cuatrecasas (1999: fig. 4G) to have anthers with calcarate auriculate bases, but Pruski (2018: fig. 50A) noted distinctly long-caudate anthers in *D. multinerve* (Sch. Bip. ex Klatt) C. Jeffrey.

Elsewhere in the Faujasia-Oldfetia clade, Pruski (2018) and Pruski and Robinson (2018) gave the species of Monticalia, Ortizacalia, Pentacalia, and Zemisia as caudate-anthered, and in these four genera the caudate anther character does not seem to vary. Caudate-anthered *Chaetacalia*, by style characters and cypselae ca. 8-10-costate, however, is immediately set apart from *Monticalia*, Ortizacalia, Pentacalia, and Zemisia. Throughout much of the Faujasia-Oldfetia clade caudateanthered genera occur, whereas NWS clade 1 contains a fair proportion of appendiculate-styled genera, but these correlations of clades and floral characters are not absolute and departures are known. For example, several Faujasia-Oldfetia clade genera including Graphistylis (Fig. 13C) and Jessea H. Rob. & Cuatr. are appendiculate-styled. Nonetheless, I believe the caudate-anther character (Figs. 7B, 8B) seen suggests placement of Chaetacalia in the Faujasia-Oldfetia clade, but this supposition I am able not to verify. As noted by Bremer (1994), the anther base "distinction is sometimes difficult to make." I find in floral dissections that begin to dry, the thecae tend to curve inward, and thus the presence or absence of anther tails is thus generally best observed in adaxial view. The caudate anther character is not useful in supergeneric schemes in the tribe, but is better used with "caution" (Nordenstam 1977) at the genus level, as done here by taking caudate anthers as merely one of a syndrome of characters helping to define *Chaetacalia*.

The disk style branch character of the new genus Chaetacalia are noteworthy, were wellillustrated in the protologue (Cabrera 1950a: 108, fig. 16F), and Cabrera's epithet stylotrichus alludes to their unusual nature. Chaetacalia has gradually papillose-appendiculate disk style branch apices (Figs. 7–8) that distinguish it from truncate-styled *Senecio* (Fig. 2B), where it was placed by Cabrera (1950a, 1985) and Salomón et al. (2018). The disk style branch apices of *Chaetacalia* are moderately similar to those of the Aetheolaena-Lasiocephalus group, where they are abruptly (vs. gradually) papillose-appendiculate. Moreover, the gradually papillose-appendiculate disk style branches of Chaetacalia have prominent abaxial stylar papillae distally (Figs. 7–8), and are very different from styles in the Aetheolaena-Lasiocephalus group, where the disk style branches lack prominent abaxial papillae. Other Neotropical Senecioninae genera, e.g., Hoehnephytum Cabrera (Cabrera 1950b: fig. 1A-B; Hind 1993, 1994) and Ortizacalia (Pruski 2012b, 2018), have disk style branches with abaxial stylar papillae distally but otherwise do not resemble Chaetacalia in combined habit, leaf, and capitular-floral features. Among neotropical Tussilagininae, Cuatrecasas (1955: figs. 1-2) showed Gynoxys Cass. and Paragynoxys Cuatr. as also having disk style branches with abaxial stylar papillae distally. Another microfeature given by Nordenstam (1978) as useful in taxonomy of radiatecapitulate Senecioneae, but unavailable in disciform Chaetacalia of subtribe Senecioninae is adaxial ligule cellular patterns. Pandemic laboratory closures prevent comparative study of a further potentially useful microcharacter—crystal form in the ovary-pericarp cell walls in the Aetheolaena-Lasiocephalus group—which was not given in Nordenstam (1978), Calvo and Freire (2016), or Salomón et al. (2016, 2018). In Chaetacalia, the crystals seen here in immature cypselae are intermediate hexagonal (length/width ratio between 1.5-6, as defined in Drury and Watson 1965) and are nearly homomorphic.

The present study shows the combined characters of erect ecalyculate disciform capitula, caudate anthers, and gradually penicillate-appendiculate disk style branches with prominent abaxial papillae distally (Figs. 7–10) render *Chaetacalia* unmatched even within a liberal and broadly defined Senecio. Each of these characters alone is noteworthy, and as combined the syndrome of characters distinguishing Chaetacalia from Senecio and the Aetheolaena-Lasiocephalus group is actually quite startling. The plant may be safely excluded from Aetheolaena, Lasiocephalus, and Senecio. Among other regional NWS clade 1 members, Chaetacalia is somewhat similar to herbaceous, often caudateanthered Dendrophorbium. In Dendrophorbium, the disk style branches are exappendiculate (vs. appendiculate in *Chaetacalia*) and generally smooth (vs. prominently papillate) abaxially. Although on occasion in some species of *Dendrophorbium* the style branch abaxial surfaces are weakly mamillose, the style branch abaxial surfaces of *Dendrophorbium* genus are never prominently papillate distally, as they are in appendiculate-styled *Chaetacalia*. Among possible NWS clade 1 regional members, Brazilian Hoehnephytum moderately resembles Bolivian Chaetacalia by disk style branches with abaxial stylar papillae distally, but Hoehnephytum differs from Chaetacalia by discoid (vs. disciform) capitula, sagittate-based calcarate (narrow-pointed-caudate) anthers with polleniferous basal auricles (vs. non-polleniferous tails), disk corolla lobes with (vs. without) obvious supernumerary medial resin ducts, round-tipped exappendiculate (vs. penicillate-appendiculate) disk style branches, and setose faces (vs. glabrous throughout) of the cypselae.

Chaetacalia stylotricha, however, in leaf size, shape but not margins, positioning on flowering stems (i.e., internode length) does instantly recall Humbertacalia amplexifolia (Humbert) C. Jeffrey. Humbertacalia C. Jeffrey (Senecioninae) is Madagascar-centered, but typified by H. tomentosa (Lam.) C. Jeffrey from Réunion (not also found in Brazil as stated by Lamarck 1786-1788) (viz Jeffrey 1986, 1992; Humbert 1962, as Senecio group XIII; Hind et al. 1993). Humbertacalia is a vine, typically prehensile-petioled, caudate-anthered, and usually penicillatestyled. Humbertacalia was placed in the Synotoid group by Jeffrey (1986) and Pelser et al. (2010a), and H. leucopappa adjacent to Synotoid Senecio sect. Cissampelopsis [now Cissampelopsis (DC.) Miq.] by Candolle (1837). The styles of discoid-capitulate *Humbertacalia* are smooth abaxially, and very different from disciform Chaetacalia that is characterized by its styles dense-papillose abaxially distally. Moreover, Chaetacalia is not Synotoid, and differs from Humbertacalia in most vegetative characters. During routine curations I noted that an intended transfer of an 8-short-phyllaried, sessilesmall-capitulate vine by Jeffrey (1992) did not cite a basionym and is thus invalid (viz ICBN Art. 33.4 = ICN Art. 41.5): Jeffrey cited inadvertently as basionym an invalid pro. syn. The oversight is corrected here as: Humbertacalia leucopappa (DC.) Pruski, comb. nov. (Basionym: Cacalia leucopappa DC., Prodr. 6: 330. 1837 [1838]. Type: MADAGASCAR. Bojer s.n., holotype: G-DC).

Four described recently or resurrected (post Cabrera 1985) leafy-stemmed central Andean genera of Senecioninae are radiate-capitulate, thereby differing from Chaetacalia. Among the four, narrowly endemic Peruvian Caxamarca M.O. Dillon & Sagást. (Dillon and Sagástegui Alva 1999) is not penicillate-styled. The three other newer or resurrected genera, Dorobaea Cass., Lomanthus B. Nord. & Pelser, and Talamancalia H. Rob. & Cuatr., are more widespread and often have disk styles shortly penicillate. None of the three has disk style branches with prominent abaxial stylar papillae distally, however, as seen in *Chaetacalia*.

Angeldiazia M.O. Dillon & Zapata (Senecioninae), described by Dillon and Zapata Cruz (2010) from Lambayeque, Peru, resembles Chaetacalia by disciform capitula, but differs from it by being an annual with stem leaves deep-pinnatisect and by truncate-tipped disk style branches. Chaetacalia is found here to be singular, as stated by Cabrera (1950a, 1985). This Bolivian plant is without an apparent match elsewhere in Senecioneae and the new genus Chaetacalia is erected to house it. Monotypic Chaetacalia is diagnosed by perennial herbaceous non-scandent habit, shortcaudate anthers, balusterform filament collars, 2-banded penicillate-appendiculate disk style branches that are also dense-papillose distally on the abaxial surfaces, and erect, ecalyculate, heterogamous, disciform capitula.

## Key to Chaetacalia, Aetheolaena, Culcitium, and Lasiocephalus

- 1. Capitula erect, heterogamous, disciform; disk floret style branches penicillate apically, dense-1. Capitula nutant, homogamous, discoid; disk floret style branches penicillate apically or truncate, more or less smooth abaxially, apex not dense-papillose abaxially; anthers ecaudate.
  - 2. Disk floret style branches typically truncate apically, rarely penicillate and then plants 2. Disk floret style branches penicillate apically (sometimes only minutely so); plants scandent, subshrubs, or subscapose herbs.
    - 3. Plants scandent with leaves well-spaced, or plants erect and loosely leafy, if imbricate only moderately so; capitulescences (2-capitulate-)pluricephalous, capitula pedunculate on loosely to moderately leafy stems; phyllaries mostly  $\leq 21$ ; corollas 3. Usually densely imbricate-leaved erect subshrubs, when leaves inserted loosely the main stem then sometimes with a few distal branchlets each subtended by a reduced leaf and terminated by a single short-pedunculate capitulum; capitulescences usually monocephalous, capitula sessile, some mature leaves usually closely subtending capitulum; phyllaries mostly  $\geq 21$ ; corollas yellow; leaves mostly

#### 2-6. The reinstated genera Culcitium, Aetheolaena, Lasiocephalus, Haplosticha, and Iocenes.

I use stylar features in tandem with macromorphology to characterize, and to formally retain or resurrect—from a slumber near or nominally within Senecio—the NWS clade 1 genera Culcitium Bonpl. (genus 2, page 24), Aetheolaena Cass. (genus 3, page 26), Lasiocephalus Willd. ex Schltdl. (genus 4, page 34), Haplosticha Phil. (genus 5, page 40), and Iocenes B. Nord. (genus 6, page 48). The style characters of three of these genera match basically those in plants that Vincent (1996: 600) tagged as "peripheral Senecios." Recognition herein the appendiculate-styled and associated genera Aetheolaena, Ĉulcitium, Haplosticha, Hasteola, Iocenes, Lasiocephalus, and Robinsonia does not strongly conflict with the phylogeny of Pelser et al. (2007), which showed low support (BS < 50%, PP < 50) for a sister relationship of NWS clade 1 and S. achilleifolius-S. sisymbriifolius clade. Although Pelser et al. (2007) suggested that NWS clade 1 be included within Senecio, this suggested reduction of all component genera was perhaps premature and is not adopted here. Each Dušková et al. (2010), Silva-Moure et al. (2013), and Ávila et al. (2016) used Lasiocephalus, and each post-date Pelser et al. (2007). Dušková et al. (2017) gave moderate support (PP 99, BS 58%) a polytomy that includes the forest clade (Aetheolaena) and páramo clade (Lasiocephalus), and moderate values (PP 98 and PP 98, respectively), supporting the two clades, each of which included more than 20 accessions.

Aetheolaena (Cassini 1827) and Lasiocephalus (Schlechtendal 1818) are junior members of the broader Culcitium (Bonpland 1809) group, which is characterized by nutant discoid capitula and mostly flagelliform trichomes (viz Drury 1966: fig. 1b; Jeffrey 1987: fig. 3d). Nutant-discoidcapitulate species are found elsewhere among species allied with NWS clade 1 taxa sampled (viz Pelser et al. 2007), including North American Senecio bigelovii A. Gray of Senecio sect. Amplectentes (Greenman 1902; viz also Cronquist et al. 1978, Barkley et al. 2006) and S. callosus Sch. Bip. and S. rhyacophilus Greenm. of Senecio sect. Mulgedifolii (Pruski and Robinson 2018).

Although the nutant capitular character is not diagnostic generically, it proves useful taxonomically in some groups, and is found in several lineages of NWS clade 1.

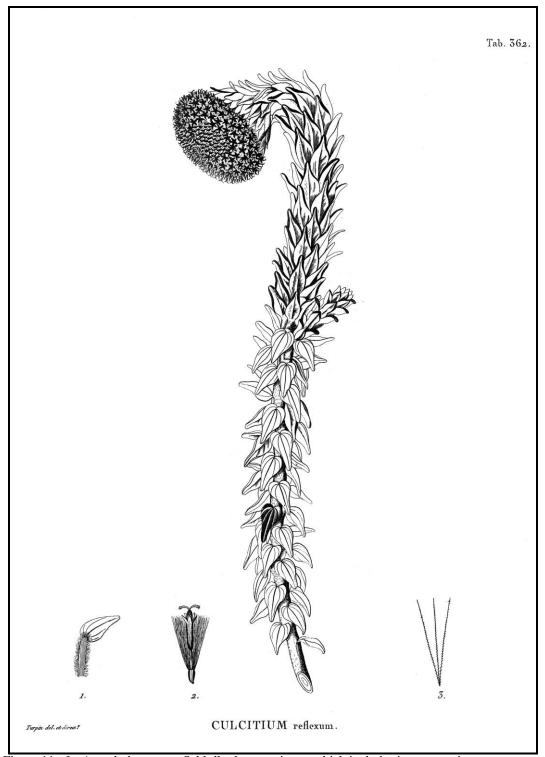


Figure 11. Lasiocephalus ovatus Schltdl., the generitype, which includes in taxonomic synonymy Culcitium reflexum Kunth. Lasiocephalus ovatus in aspect loosely resembles sympatric Chuquiraga jussieui J.F. Gmel. of tribe Barnadesieae. (From Kunth, Nova Genera et Species Plantarum (folio ed.), vol. 4, plate 362. 1820 [1818]).

Morphologically, Aetheolaena, Iocenes, and Lasiocephalus each have papillose-penicillate styles (the apical tuft is mostly on the adaxial apex opposite the semicircular abaxial crown) and stick out like sore thumbs from both Senecio and Culcitium. No members of Lasiocephalus or associated genera occur in Brazil (viz Cabrera 1957), Guayana (viz Pruski 1997), or Central America (viz Pruski and Robinson 2018). The five genera adopted here formally are South American endemics: Aetheolaena, Culcitium, and Lasiocephalus are central and northern Andean-centered, and Haplosticha and Iocenes are southern South American. The recognition of these genera, coupled with species limits modified from those used by Nordenstam (1978, 1997, 2007), Cuatrecasas (1950, 1951, 1978, 1990, 1994), Cabrera (1949, 1985), Cabrera and Zardini (1980), Silva-Moure et al. (2013), Calvo and Freire (2016), and Salomón et al. (2018), allows the new combinations in Aetheolaena, Haplosticha, Iocenes, and Lasiocephalus to be proposed here. Also resurrected here, but not otherwise treated, are the noteworthy North American genus Hasteola, and dioecious Robinsonia, the later endemic to the Juan Fernández Islands off the western coast of Chile and which in aspect and resinous stems recalls Tasmanian Centropappus (Fig. 4).

The three genera Aetheolaena, Culcitium, and Lasiocephalus were described in the early 1800s, and since have been in and out of circulation. These genera are noteworthy by the shared character of usually nutant discoid capitula (viz figs. 11-12, 14-16, 18-20), a trend towards welldeveloped medial disk corolla lobe resin ducts, and in the smaller capitulate species of Aetheolaena and Lasiocephalus a trend towards disk corollas having abruptly narrow-campanulate limbs (Fig. 17). The large-capitulate species of the group—e.g., Culcitium, Aetheolaena gargantana, and Lasiocephalus ovatus—tend to have numerous florets in each capitulum, and thereby limited physical space correspondingly for broadened corolla limbs. The abruptly campanulate disk corolla limbs seen in several Aetheolaena and Lasiocephalus species (Cuatrecasas 1978: 308; Díaz-Piedrahita and Cuatrecasas 1999: 7) are similar to those seen elsewhere in South American Senecioninae (e.g., S. websteri Hook. f., viz Cabrera 1971: 252, fig. 257d). Most Senecioninae, including S. vulgaris—the generitype—and Dorobaea Cass., have narrower tubular-funnelform disk corollas of a different form that are dissected longitudinally more easily while preparing microscope slide mounts. Similar variation in disk corolla form and resin duct expressions (e.g., *S. digitatus* Phil., viz Cabrera 1978: 514, fig. 216e) are known within Senecio, but nonetheless these traits help characterize Aetheolaena and Lasiocephalus.

Lessing (1832) recognized Culcitium and listed Aetheolaena as known poorly, but did not treat Lasiocephalus. Candolle (1837 [1838]) followed by Weddell (1855) treated Culcitium (Fig. 12B) with Lasiocephalus (Figs 11–12A) in synonymy, and Senecio as including Aetheolaena, albeit with de Candolle only provisionally (viz his "484. S? involucratus") reducing Aetheolaena. Bentham and Hooker (1873) and Hoffmann (1894) treated Culcitium as including Lasiocephalus, and listed Aetheolaena as a synonym of Senecio, mirroring de Candolle. Greenman (1923) treated the generitype Aetheolaena involucrata (Fig. 12C) within Senecio, and Cuatrecasas (1950) treated Culcitium as Senecio. Additional treatments by noted specialists include those by Blake (1937), Tinajero (1965), and Nordenstam (1977, 1978), who each recognized the genus Culcitium and treated Lasiocephalus as a synonym.

It was not until a century after Bentham that Aetheolaena and Lasiocephalus were noted as discordant elements of Senecio, resurrected as genera, and recognized as natural groups. Nordenstam (1978) reinstated Aetheolaena, but soon thereafter Cuatrecasas (1978) resurrected an expanded Lasiocephalus, within which in synonymy he included Aetheolaena and Senecio sect. Reflexus Cuatr. Following the taxonomy of Cuatrecasas (1978), each Jeffrey (1992), Gentry (1993), Funk et al. (1995), Díaz-Piedrahita and Cuatrecasas (1999), Dillon and Sagástegui Alva (2001), Sklenář (2001), and Dillon (2005) recognized Lasiocephalus as distinct with Aetheolaena therein mostly an indirect synonym. Dillon and Sagástegui-Alva (1996: 588) and Vision and Dillon (1996: 44, 45) used both Aetheolaena and Lasiocephalus, but neither recognized Culcitium. Robinson et al. (1997) recognized Culcitium and Lasiocephalus as distinct, and treated Aetheolaena in synonymy of Lasiocephalus. Nordenstam (1997), on the other hand, accepted Aetheolaena. Bremer (1994) and Nordenstam (2007) recognized each Aetheolaena, Culcitium, Lasiocephalus, and Iocenes. Silva-Moure et al. (2013) accepted *Lasiocephalus* in their fine revision of the genus in Venezuela, Dušková et al. (2010) recognized Lasiocephalus, Ávila et al. (2016) listed Lasiocephalus in the checklist of Colombia, but Rivero-Guerra (2020) gave these species as Senecios. Dušková et al. (2017) and Salomón et al.

(2018, 2019) treated Aetheolaena and Lasiocephalus within Senecio. In this study of the group, I recognize each Aetheolaena, Culcitium, and Lasiocephalus as distinct from Senecio.

There has been little fluctuation in species numbers of the Aetheolaena-Culcitium-Lasiocephalus group in the past seven decades. Cuatrecasas (1950, 1951) treated 40+ Andean species in Senecio sections Culcitium, Reflexus, and Hypsobates. Salomón et al. (2018) recognized these 43 species within Senecio ser. Culcitium. I treat these species as spread among Aetheolaena (15 spp.), Culcitium (Bremer 1994 and Nordenstam 2007 recognized ca. 15 spp.; albeit perhaps the genus is best treated phylogenetically as monotypic), Lasiocephalus (syn. Senecio sect. Reflexus Cuatr.; 4 spp.), and Senecio sect. Crassicephali (syn. Senecio sect. Hypsobates Cuatr.; Cabrera recognized ca. 10 spp.).

Koyama (1967), Nordenstam (1977), Solbrig (1977), Jeffrey (1992), Robinson et al. (1997), Pelser et al. (2007), and Pruski (2018) gave the base chromosome number of tribe Senecioneae as x =10, and 2n = 20 as characteristic of species "largely restricted to Europe and Africa," albeit Old World native S. vulgaris, 2n = 40, is perhaps an autotetraploid (Kadereit 1984). Nordenstam (1977) noted that "the majority of the cacalioid genera" have x = 30 as a base number. Jeffrey (1992), Cabrera (1999), and Nordenstam (2007) gave n = 20 as the haploid chromosome number or 2n = 40 as the diploid chromosome number of Iocenes virens (I. acanthifolius, S. acanthifolius), and Nordenstam (2007) gave n = 20 as the haploid chromosome number of *Robinsonia*. Robinson et al. (1997) reported diploid chromosome numbers of 2n = 40 in *Culcitium* and in four species treated here in Aetheolaena (reported as species of Lasiocephalus), which corresponds roughly to the counts the authors reported in high-elevational species of American Monticalia and Dendrophorbium. Highelevation Andean Compositae have elsewhere been noted as of polyploid origin (e.g., Nordenstam 1977; Solbrig 1977; Robinson et al. 1981; Pruski and Urbatsch 1983; Cuatrecasas 2013). The counts of 2n = 40 in our plants are not at all unexpected for American Senecioneae.

Salomón et al. (2016, 2018) suggested that stylar distinctions are "controversial" and insignificant in generic circumscription of *Senecio*, although taxonomy in Compositae is based largely on style and anther microcharacters. Although, I recognize *Lasiocephalus* et al. as distinct from Senecio, in part based on stylar morphology, I do so acknowledging that hybridizations between the two main subtribes of Senecioneae are possible (Bremer 1994) making distinct lineages seem indistinct. Moreover, hybrids are found in "many Senecioneae genera" (Pelser et al. 2010a); polyploids and past hybridizations between clades are frequent among high-Andean Senecioninae (Dušková et al. 2017); and hybridization events throughout Angiosperms may bring into question strict monophyly and may limit some plastid phylogenies, which are thereby not always a priori set in stone (viz Stevens 2001).

Each Dušková et al. (2017) and Salomón et al. (2019) recovered clades the authors treated within Senecio, and Dušková et al. (2010, 2017) called them the "páramo clade" and the "forest The "páramo clade" included six species, four of which are mostly drab, griseous or canescent, erect-stemmed, large-capitulate, monocephalous, evenly-leafy sticks (Figs. 11-12A) treated by me as *Lasiocephalus* s.str. The "forest clade" is made of a few erect, but of mostly scandent, small-capitulate species (Fig. 12C) that I recognize as *Aetheolaena*. The Dušková et al. (2010) study was similar to that of 2017, but recognized the two groups within the genus Lasiocephalus. Dušková et al. (2010, 2017) and Salomón et al. (2019) showed Culcitium species in different clades, but the generitype C. canescens is part of an unresolved polytomy that did group with either Aetheolaena (the forest clade) or Lasiocephalus (the paramo clade). Perhaps some of these plants are reticulated and involve hybridizations with other groups. Here, I take Senecio again as truncate-styled, and the genus is thus defined more readily micromorphologically by the exclusion of these appendiculate-styled, nutant-capitulate genera. Solbrig (1963) admitted that *Senecio* was then defined "largely on vegetative characters" and exclusion herewith of these penicillate-styled genera distances us from earlier artificial circumscriptions.

Genera defined by floral microcharacters are digested more easily when paralleled by habit differences, such as those given by Dušková et al. (2010, 2017) for these genera that were accepted subsequently by Pruski (2018). Following Pruski (2018), each Aetheolaena, Culcitium, Iocenes, and Lasiocephalus are reinstated formally as distinct genera. Also reinstated is truncate-styled Haplosticha, not mentioned by Pruski (2018). The species treated here in Aetheolaena were recognized mostly by Cuatrecasas (1978, 1990, 1994) as Lasiocephalus s.lat. The resurrections here of Aetheolaena, Haplosticha, Iocenes, and Lasiocephalus results in only five, three, one, and two nomenclatural innovations in each genus, respectively, but reassessment of *Culcitium* could result in further name changes and generic resurrections. The generic-level taxonomy proposed here combines parts of Cabrera (1949, 1950a, 1985), Cuatrecasas (1950, 1978, 1990, 1994), Nordenstam (1977, 1978, 1997, 2007), and Pruski (2018) to define as distinct genera morphologically a few satellites that I suggest are distinct generically from Senecio. I try basically to approach, not achieve, a monophyletic classification of the moderately evolutionarily recent, high elevational Andean nutantcapitulate, penicillate-styled Aetheolaena-Lasiocephalus group, and of Patagonian-centered whiterayed Haplosticha and Iocenes.

Variation of penicillate disk style branch characters has been noted by Cuatrecasas (1978) and Salomón et al. (2018) within individual genera and sometimes within individual species. Culcitium cocuyanum Cuatr. falls into the narrower concept of Culcitium used here, albeit having typically weakly penicillate styles (Barclay & Juajibioy 10398, MO; Salomón et al. 2018: 13, fig. 7Ĝ), unlike the dozen or so other species in the group. In addition, by stylar features I recognize as genera various plants associated loosely with Aetheolaena, Chaetacalia, and Lasiocephalus, namely Graphistylis (Nordenstam 1978) of the Faujasia-Oldfetia clade, Garcibarrigoa Cuatr. (Cuatrecasas 1986), and other appendiculate-styled genera seen in Figure 13. Another reliable generic marker is the caudate anther microcharacter, which other than in Dendrophorbium and Brachyglottis does not seem to vary within genera. The species of the Aetheolaena-Culcitium-Lasiocephalus group all have ecaudate anthers, as do Haplosticha and Iocenes.

Elsewhere in Senecio nutant-capitulate species are known (e.g., disciform S. tenuisagittatus, fig. 33A) that do not belong to the Aetheolaena-Culcitium-Lasiocephalus group. Conversely, some Andean discoid species with weakly nutant capitula not placed in Senecio ser. Culcitium by Salomón et al. (2018) are reminiscent of the Aetheolaena-Culcitium-Lasiocephalus group. Such Andean species not treated by Salomón et al. (2018) include S. arachnolomus Wedd., S. calvus Cuatr., S. diplostephioides Cuatr., S. ellenbergii Cuatr. from southern Cajamarca, Peru (and the described subsequently, recognized provisionally, hairier, but otherwise near-identical S. roseoandinus Montesinos & R. Zárate from northern Huánuco, Peru), S. mitonis Cuatr., and described recently S. phlomidifolius H. Beltrán; but of these only truncate-styled S. arachnolomus has campanulate corollas and seems Aetheolaena-Lasiocephalus-like. Another Aetheolaena-like species is Senecio tingoensis Cabrera & Zardini, which has erect radiate capitula, truncate styles, and ecaudate anthers.

2. CULCITIUM Bonpl., Pl. Aequinoct. 2: 1. 1809 [1808]. TYPE: Culcitium canescens Bonpl. Figure 12B.

Senecio sect. Culcitium (Bonpl.) Cuatr., Senecio sect. Senecio ser. Culcitium (Bonpl.) Cuatr. ex Cabrera.

Generitype (and abbreviated synonymy). Culcitium canescens Bonpl. (syn.: Culcitium boyacense Cuatr., Culcitium rufescens Bonpl., Culcitium rufescens var. canescens (Bonpl.) Benoist. Further possible core species (and abbreviated synonymy). Culcitium cocuyanum Cuatr. (syn.: Culcitium santanderense Cuatr., Senecio cocuyanus (Cuatr.) Cuatr.); Culcitium humile DC. (syn.: Culcitium glaciale Meyen & Walp., Senecio candollei Wedd., Senecio mandonianus Wedd., Senecio modestus Wedd.); Culcitium nivale Kunth (syn.: Culcitium haenkei Wedd., Culcitium neaei (DC.) Sch. Bip. ex Wedd., Culcitium nivale var. neaei DC.; Culcitium oligocephalum Cabrera (syn.: Culcitium albifolium Zöllner, Senecio keshua Cabrera, Senecio zoellneri Martic. & Quezada). Excluded species include discolorous-leaved Senecio comosus Sch. Bip. and Senecio culcitioides Wedd. which were placed in Senecio sect. Culcitioides Cuatr., albeit in different subsections, by Cuatrecasas (1951).

Culcitium, the senior member of the Aetheolaena-Culcitium-Lasiocephalus group is recognized, again. Although it may be best adopted as monotypic, in the broader sense members of the genus are recognized generally by their perennial herbaceous subrosulate stout habit, densely griseous-lanate-tomentose herbage, and large nutant discoid capitula (viz Fig. 12B). The genus has capitula similar to those in Aetheolaena and Lasiocephalus, but Culcitium differs from them by its typically exappendiculate disk style branches. The generitype Culcitium canescens is from Cajamarca, Peru, more or less in the center of distribution of the genus. Cabrera (1966) treated a few species of Culcitium within Senecio sect. Brachypappus (Sch. Bip.) Benth. & Hook. f., which is typified by *Brachypappus candicans* (J. Vahl) Sch. Bip. that has discolorous leaves, erect capitula.

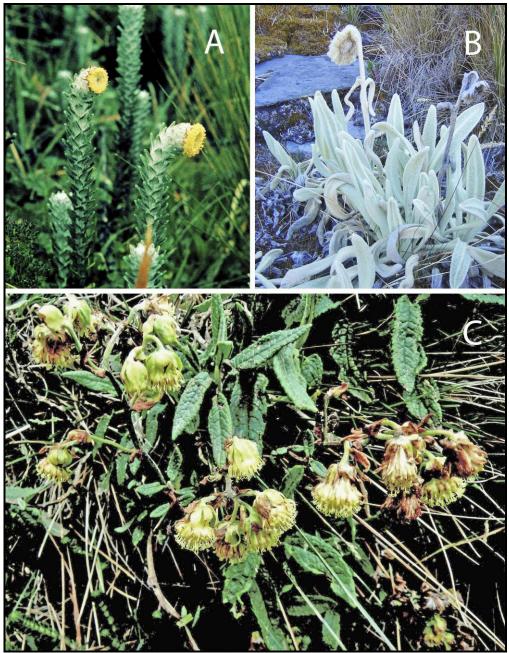


Figure 12. Habit images of generitypes of Aetheolaena, Culcitium, and Lasiocephalus. Each genus is characterized by discoid nodding capitula. A. Erect-stemmed *Lasiocephalus ovatus* Schltdl., the generitype, member of the "páramo clade." B. *Culcitium canescens* Bonpl., the generitype. C. Scandent *Aetheolaena involucrata* (Kunth) B. Nord., the generitype, member of the "forest clade," unusual in *Aetheolaena* by its cupular broadbracted calyculus, which is the double involucre character of Cassini. (A Photograph by Gunnar Harling, unvouchered; B Fuentes 9962, photograph by Alfredo Fuentes; C Croat et al. 104341, photograph by Thomas Croat).

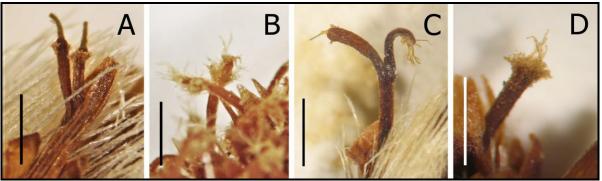


Figure 13. Appendiculate disk styles of select South American Senecioninae, hand-held camera images of herbarium material approximating magnification as seen through a hand lens. A. Cellular appendages; B-D. Penicillate appendages. A. Arbelaezaster ellsworthii (Cuatr.) Cuatr., the generitype. Crassocephalum is another genus characterized by a cellular appendage. B. Garcibarrigoa telembina (Cuatr.) Cuatr., the generitype, the appendage is penicillate and papillose crowned, but otherwise resemble roughly those of Pseudogynoxys. C. Graphistylis argyrotricha (Dusén) B. Nord., style branches penicillate and sparse-papillose abaxially, a Brazilian plant with discolorous serrate leaves, radiate-capitula, and ecaudate anthers. Graphistylis was treated as Senecio sect. Dichroa Cabrera by Cabrera (1950b, 1957). D. Aetheolaena longipenicillata (Sch. Bip. ex Sandwith) B. Nord., representative of Aetheolaena and Lasiocephalus. The epithet is spelled longipenicillata (viz Cuatrecasas 1980; Silva-Moure et al. 2013): the prefix is derived from longus, a group A adjective, hence longi; the prefix is not derived from the adverb longe. (A Benítez 5659, MO; B Eriksson 287, MO; C Hoehne 16966, MO; D Barclay 9655, MO). Scale bars A, C 0.7 mm, B 0.5 mm, D 0.4 mm.

Cuatrecasas (1950) noted Culcitium as then delineated was heterogeneous, sunk it into Senecio, which in turn resulted in a further heterogeneous Senecio. Cuatrecasas (1950) placed both Culcitium canescens Bonpl. and Senecio serratifolius (Meyen & Walp.) Cuatr. in Senecio sect. Culcitium (Bonpl.) Cuatr., whereas Cabrera (1985) positioned them in Senecio sect. Culcitium and Senecio sect. Crassicephali, respectively. The unresolved polytomy (pentatomy) in NWS clade 1 found by Dušková et al. (2010, 2017) and Salomón et al. (2019, a hexatomy) recovered Culcitium canescens Bonpl. and S. serratifolius in different branches, agreeing with Cuatrecasas's view of a heteromorphic Culcitium and with Cabrera's disassociation of the two species. I agree with Cabrera (1985), and distinguish *Culcitium* from *Senecio* sect. *Crassicephali* by differences in indument.

Lessing (1832), Candolle (1837), Weddell (1855), Bentham and Hooker (1873), Hoffmann (1894), Blake (1937), Tinajero (1965), Nordenstam (1977, 1978), and Robinson and Funk (1997) each recognized Culcitium. Cuatrecasas (1950, 1951), Jeffrey (1992), Vision and Dillon (1996), and Salomón et al. (2018), on the other hand, took *Culcitium* as a synonym of *Senecio*. Jeffrey (1992) placed both Culcitium canescens Bonpl., the generitype, and radiate Senecio comosus within Senecio ser. Culcitium, whereas I exclude Senecio comosus from the series (genus) as did Salomón et al. (2018). South American endemic high Andes-centered Culcitium is nevertheless well known and a genus recognized widely. However, because many high-elevational Andean groups may have evolved moderately recently and may possibly hybridize (e.g., viz Senecio rubrilacunae Cuatr. 1950: 35 described as a hybrid) and because its taxa were recovered in distinct clades of a polytomy, the taxonomy of *Culcitium* appears unsettled as stated by Nordenstam (1978) and shown by Dušková et al. (2017). Nordenstam (1977) noted the polyploid nature of some Culcitiums. Species numbers are not estimated here but rather listed are only a few core species that are together grouped traditionally and that correspond admirably to Culcitium. The lower-end species count in Bremer (1994: 499) and Nordenstam (2007: 235) of ca. "15 species" (vs. 43 species) is used provisionally here, although phylogenetically, perhaps *Culcitium* should be recognized as monotypic.

3. AETHEOLAENA Cass., Dict. Sci. Nat. (ed. 2) 48: 447, 453. 1827. Type: Cacalia involucrata Kunth [≡ *Aetheolaena involucrata* (Kunth) Cass.]. Figures 12C, 13D, 14–17A.

Senecio sect. Aetheolaena (Cass.) O. Hoffm.

**Species.** 15 species are recognized in *Aetheolaena* as given below in Table 1.

Nordenstam (1978) resurrected Aetheolaena from within Senecio recognizing 19 species, but treated Lasiocephalus in synonymy of Culcitium. Shortly thereafter, however, from Culcitium Cuatrecasas (1978) resurrected Lasiocephalus, recognized 21 species, and in synonymy placed Aetheolaena and Senecio sect. Reflexus Cuatr. Jeffrey (1992) recognized 23 species in Lasiocephalus. Nordenstam (2007 [2006]) recognized 17–18 species in the Lasiocephalus group: "circa 15 species" in Aetheolaena and "two or three" other species in Lasiocephalus. The species of Aetheolaena and Lasiocephalus were given in a nomenclator of 21 species by Calvo and Freire (2016) as "Senecio group Lasiocephalus" and Salomón et al. (2018) provided a synopsis-revision with very useful keys, maps, and illustrations of these plants under the name Senecio ser. Culcitium. I follow the generic circumscriptions of Nordenstam (2007) and Pruski (2018), and recognize explicitly the nutant-discoid-capitulate Aetheolaena, Culcitium, and Lasiocephalus from a decade-long trance near or nominally under Senecio. I place 19 species in the Aetheolaena-Lasiocephalus group, four of which I give as *Lasiocephalus*. The remaining 15 species are those of forest clade of Dušková et al. (2010, 2017) adopted here as Aetheolaena, a genus native to South America in mostly montane forest and subpáramo-jalca-puna regions of the central and northern Andes.

The treatment by Salomón et al. (2018) recognized 43 species in a defined broadly Senecio ser. Culcitium, within which they included Aetheolaena and Lasiocephalus. Aetheolaena is characterized by the combination of abrupt-penicillate disk style branches (Fig. 13D), mostly scandent (sometimes erect) habit, mostly petiolate proximal leaves, relatively small nutant discoid (short-)pedunculate capitula, and usually campanulate ochroleucous corollas. However, Cassini (1827) instead emphasized only the double involucre in the generitype A. involucrata (Fig. 12C), which in most other species of the genus is of variable size and often not at all obvious (Cuatrecasas 1978). Salomón et al. (2016) described five species of "Senecio sect. Aetheolaena" as having a "tuft of longer hairs" as in figure 13D above. Scandent plants of Aetheolaena often have petiolate asymmetric-based leaves proximally, and often distally have leaves becoming subsessile, rarely pandurate (i.e., A. otophora). The species are variously long-pubescent, but A. cuencana (Hieron.) B. Nord., A. mojandensis (Hieron.) B. Nord., and A. subinvolucrata (Cuatr.) B. Nord. are subglabrous.

Several names were applied differently by Nordenstam (1978, 1997), Cuatrecasas (1978), Calvo and Freire (2016), and Salomón et al. (2018). Moreover, some earlier names are available here for use in Aetheolaena, were blocked nomenclaturally in Senecio by earlier legitimate homonyms, and name applications therefore may not always appear straightforward. For example, Nordenstam (1978) coined the name Aetheolaena mochensis (Hieron.) B. Nord., Cuatrecasas (1978) used Lasiocephalus mochensis (Hieron.) Cuatr., Calvo and Freire (2016) used S. mochensis Hieron., but Salomón et al. (2018) used the resurrected name S. pindilicensis for the plant, and placed S. mochensis in synonymy of it. I use the name Aetheolaena heterophylla (Turcz.) B. Nord., following essentially name applications in Nordenstam (1978) and Cuatrecasas (1978) for this scandent species, and treat each S. mochensis and S. pindilicensis in synonymy. Another example: Nordenstam (1978) made the new combination Aetheolaena campanulata for a common scandent species. Cuatrecasas (1978) used the name Lasiocephalus campanulatus (Sch. Bip. ex Klatt) Cuatr. for the same plant, Calvo and Freire (2016) used resurrected S. betonicifolia DC. placing S. campanulatus in synonymy of it, and Salomón et al. (2018) used both S. betonicifolia DC. and S. campanulatus Sch. Bip. ex Klatt, basically as did Cabrera (1985). I follow the species synonymy of Calvo and Freire (2016), coin Aetheolaena betonicifolia (DC.) Pruski, and treat A. campanulata as a synonym. I follow basically Nordenstam's (1978, 2007) generic circumscriptions, but with species taxonomies modified from other taxonomies.

The specific taxonomy of Senecio senecioides (Kunth) Kuntze (syn.: Senecio rosanus Cuatr., S. assuayensis DC.) was given by Calvo (2016), who is followed here. Nordenstam (1978) recognized S. senecioides within Aetheolaena, and Cuatrecasas (1978) treated the plant as Lasiocephalus. Hind and Jeffrey (2001) suggested the plant was a synonym of Monticalia pulchella (Kunth) C. Jeffrey. Calvo and Freire (2016) included *S. senecioides* as a member of "Senecio group Lasiocephalus." Salomón et al. (2018) listed the species as of "dubious identity." I find that *S.* senecioides has neither the nutant capitula nor the penicillate styles seen in Aetheolaena and Lasiocephalus, exclude S. senecioides from each genus, and thus 15 remains the number of species recognized by me within Aetheolaena (Table I).

Cuatrecasas (1978) placed erect-stemmed large-capitulate species within typical Lasiocephalus, and within Lasiocephalus subg. Aetheolaena nom. provis. included a group of mostly "climbers" with smaller capitula. The two species groups discussed by Cuatrecasas (1978) were four decades later more or less borne out by the main groups recovered by Dušková et al. (2010, 2017): a montane forest clade taken here as Aetheolaena and a páramo-jalca-puna clade that I refer mostly to Lasiocephalus. The synonymy adopted here is mostly from the work of Jose Cuatrecasas (1960, 1978, undated). I worked for several years with Don Jose Cuatrecasas, of course knew of his "School for Style Branches" (Robinson et al. 1996), and have difficulty unlearning the Aetheolaena-Lasiocephalus group. Nevertheless, the Lasiocephalus group's peculiar characters call out for recognition as separate genera. That Bertil Nordenstam (1978, 1997, 2007) also recognized the group as distinct generically from Senecio is the taxonomic equivalent of a touchdown. The five new combinations in Aetheolaena that I propose are the following.

Table I. The 15 recognized species of Aetheolaena.

Aetheolaena alatopetiolata (J. Calvo, E. Freire & Sklenář) Pruski
Aetheolaena betonicifolia (DC.) Pruski
Aetheolaena cuencana (Hieron.) B. Nord.
Aetheolaena doryphylla (Cuatr.) B. Nord.
Aetheolaena gargantana (Cuatr.) Pruski
Aetheolaena heterophylla (Turcz.) B. Nord.
Aetheolaena involucrata (Kunth) B. Nord.
Aetheolaena josei (Sklenář) Pruski
Aetheolaena longipenicillata (Schultz-Bip. ex Sandw.) B. Nord.
Aetheolaena mojandensis (Hieron.) B. Nord.
Aetheolaena otophora (Wedd.) B. Nord.
Aetheolaena patens (Kunth) B. Nord.
Aetheolaena piedrahitae (J. Calvo & F. Ávila) Pruski
Aetheolaena puracensis (Cuatr.) B. Nord.
Aetheolaena subinvolucrata (Cuatr.) B. Nord.

AETHEOLAENA ALATOPETIOLATA (J. Calvo, E. Freire & Sklenář) Pruski, comb. nov. Senecio alatopetiolatus J. Calvo, E. Freire & Sklenář, Phytotaxa 243(2): 177, f. 1. 2016. Type: ECUADOR. Tungurahua: Cerro Hermoso, 3 Dec 2010, Sklenář 13100 (holotype: PRC; isotype: [cited in protologue but not found in backlog at MO] MO).

The scandent species is placed in Aetheolaena by virtue of its habit, nutant discoid capitula, and penicillate styles. The voucher cited by Dušková et al. (2017) placing Aetheolaena alatopetiolata in their forest clade is Sklenář 13100, the type. Aetheolaena alatopetiolata (J. Calvo, E. Freire & Sklenář) Pruski may be recognized by its elongate entire broad-based leaves, seen on occasion elsewhere in the genus, e.g., A. mojandensis (Hieron.) B. Nord. Its habit is that diagramed in Salomón et al. (2018, fig. 1B). Aetheolaena alatopetiolata has fewer and larger capitula than most other scandent species of Aetheolaena. Moreover, the leaves of A. alatopetiolata have nearly concolorous surfaces with a glandular-hirsute indument not seen elsewhere in the genus. Aetheolaena alatopetiolata occurs from southern Colombia to central Ecuador above 3000 m elevation (Calvo and Ávila 2021).

AETHEOLAENA BETONICIFOLIA (DC.) Pruski, comb. nov. Senecio betonicifolius DC., Prodr. 6: 422. 1837 [1838] (as "betonicaefolius"). Type: presumably PERU. [as "Peruv. seu Bogot.?"], sin. loc., [1790s–1810s], Haenke s.n. (holotype: PR; isotype: PRC). Figure 14.

[As stated in the protologue, the name was based on the holotype in PR (viz ICBN 8.1, ICN 8.1): "v. s. in h. Haenke à cl. de Sternberg miss." Lanjouw and Stafleu (1957) cited "PR (15.000, orig.)," Holmgren et al. (1990) listed Haenke material in PR but not in PRC, and the first set is taken traditionally as housed in PR (e.g., Pruski 2018). Indeed, the PRC sheet has a black and white photocopy label, and although the sheet contains a complete branch, it is presumably a fragment of the holotype. The PRC sheet is an isotype. There is no need to lectotypify this name as a holotype is extant, and its identity taxonomically is not in doubt.].



Figure 14. Aetheolaena betonicifolia (DC.) Pruski, representative specimen, showing the scandent habit and nutant discoid capitula. This specimen represents the less pubescent phase of the species. (Ferreyra 9462, MO).

Aetheolaena campanulata (Sch. Bip. ex Klatt) B. Nord., Aetheolaena decipiens (Benoist) B. Nord., Aetheolaena loeseneri (Hieron.) B. Nord., Lasiocephalus campanulatus (Klatt) Cuatr., Lasiocephalus decipiens (Benoist) Cuatr., Lasiocephalus loeseneri (Hieron.) Cuatr., Senecio campanulatus Sch. Bip. ex Klatt, Senecio decipiens Benoist, Senecio loeseneri Hieron.

Aetheolaena betonicifolia (DC.) Pruski was given by Candolle (1837) as Senecio #483 in his "discoidei, herbacei" group, preceding species #484-486 and adjacent to plants now referred to Its scandent growth form was diagramed in Salomón et al. (2018, fig. 1B). Aetheolaena campanulata (Sch. Bip. ex Klatt) B. Nord. is listed here as a synonym, following Calvo and Freire (2016). Cabrera (1985) recognized (in Senecio) both S. campanulatus and S. loeseneri, keying S. loeseneri as differing from S. campanulatus by its 5-6 (vs. 8-9) mm long involucres. Cabrera (1985: 85, fig. 1) provided a fine illustration (as S. campanulatus) of the species.

Salomón et al. (2018) recognized as distinct species both S. betonicifolius DC. and S. campanulatus, with S. betonicifolia distinguished from S. campanulatus by tomentose (vs. glabrous or subglabrous) stems, conflicting with Cabrera's (1985) characterization of S. campanulatus having "ramas ...tomentulosas." From the specimens in front of me, I find each of the four possible character combinations involving capitula size and stem indument, seeming to vary randomly, and thus follow provisionally the species synonymy of Calvo and Freire (2016). betonicifolia is a relative-widespread scandent broad-leaved plant centered in Peru, and is known also in Bolivia and Ecuador. The species occurs usually from 2000–4000 m elevation.

AETHEOLAENA GARGANTANA (Cuatr.) Pruski, comb. nov. Culcitium gargantanum Cuatr., Revista Acad. Colomb. Ci. Exact. 5(17): 29, f. 16. 1942. Senecio gargantanus (Cuatr.) Cuatr., Fieldiana, Bot. 27(1): 44. 1950. *Lasiocephalus gargantanus* (Cuatr.) Cuatr., Phytologia 40: 310. 1978. **Type: COLOMBIA. Nariño.** Volcán Galeras, 5 Jan 1941, *Garganta 205* (holotype: COL-19258; isotypes: COL-122780, F). It is unquestionable that the protologue figure was drawn from the holotype, whereas the isotype in COL is a later addition to that herbarium. The Revista web page indexes erroneously this as 1943. Figure 15.

Culcitium karstenii Sch. Bip. ex Benoist 1948.

Aetheolaena gargantana (Cuatr.) Pruski is an erect, griseous-pubescent, remote-leaved, monocephalous to paucicephalous perennial with penicillate disk style branches, and is thus here transferred to Aetheolaena. The type sheets, the type of the synonym, and most sheets in front of me have both single-capitulate and paucicapitulate plants mounted together. Aetheolaena gargantana was described by Cuatrecasas (1942) in *Culcitium*, and not long afterward was placed by Cuatrecasas (1950, 1951) within Senecio sect. Reflexus.

The voucher cited by Dušková et al. (2017) that placed Aetheolaena gargantana in their forest clade (as population 5C) is Sklenář & Dušková 12391 (from Volcán Galeras, just west of Pasto in Nariño, Colombia), a topotype that matches the type. Neither Dušková et al. (2010) nor Salomón et al. (2019) sampled Aetheolaena gargantana. An excellent illustration is found in the protologue, and a fine unvouchered line drawing of Aetheolaena gargantana (as Senecio) is found in Salomón et al. (2018: 16, fig. 9). Aetheolaena gargantana is one of the non-scandent members of the genus, and its growth form was diagramed in Salomón et al. (2018: 3, fig. 11). Aetheolaena gargantana is similar to Aetheolaena puracensis (Cuatr.) B. Nord., from which it differs (Cuatrecasas 1942, 1944) by distal leaves attenuate-tipped (vs. leaves elliptic-oblong). The holotype of the similar-in-gestalt Lasiocephalus superparamensis was determined originally as L. gargantana. I follow Cuatrecasas (1950, 1951, 1978, undated) in recognizing Aetheolaena gargantana as a member of the *Aetheolaena-Lasiocephalus* group.

This short-penicillate-styled species was not included by Nordenstam (1978) and since first described it has been without an available name in Aetheolaena. Aetheolaena gargantana was described from southern Colombia, but has since also been reported from Volcán Chiles, Carchi in extreme northern Ecuador along the border with Colombia (Marhold and Sklenář 2013). The Volcán Chiles plants (Holm-Nielsen et al. 5893, Sklenář & Kosteckova 1404) were cited earlier cited by Sklenář (2001) as Lasiocephalus sordiroi of the páramo clade. I know the more southern Culcitium ledifolium from only photographs of the degraded types (Cuatrecasas 1950: 47) that resemble A. gargantana, but C. ledifolium is referred to L. lingulata of the páramo clade as in Cuatrecasas (1960, 1978). Aetheolaena gargantana occurs usually above 3500 m elevation.

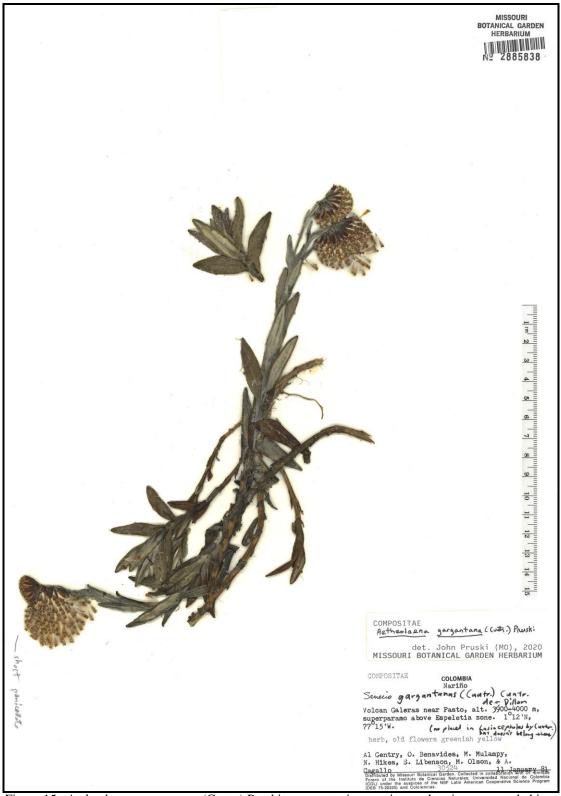


Figure 15. Aetheolaena gargantana (Cuatr.) Pruski, representative specimen, showing an erect habit and culcitioid demeanor. The original species determination by Michael Dillon naturally seems spot on. Rosa Ortiz tells me that other than for the word Senecio, the handwriting on the original collection label is that of Al Gentry. (Gentry et al. 30524, MO).

**AETHEOLAENA JOSEI** (Sklenář) Pruski, **comb. nov.** *Senecio josei* Sklenář, Nordic J. Bot. 30(4): 394, f. 1. 2012. **Type: ECUADOR. Loja**. Cordillera las Lagunillas, 16 Jun 2009, *Sklenář et al.* 12027 (holotype: PRC). Figures 16–17A.



Figure 16. Aetheolaena josei (Sklenář) Pruski, representative specimen, showing its erect habit, leaves broadest above base, and open branched capitulescence of few nutant capitula. (Ulloa & Minga 1399, MO).



Figure 17. Representative campanulate corollas of disk florets in Aetheolaena and Lasiocephalus. Cypselae removed from two florets towards the right in A; pappus bristle mostly removed from remaining florets. A. Aetheolaena josei. B. Lasiocephalus lingulatus. (A Ulloa & Minga 1399, MO; B Fernández et al. 1740, MO).

Aetheolaena josei (Sklenář) Pruski is transferred to Aetheolaena on the basis of its penicillate styles, habit, and open branching capitulescence with several nutant discoid capitula. The voucher cited by Dušková et al. (2017) that placed Aetheolaena josei in their forest clade (as population 28) is the type, Sklenář et al. 12027. It is one of the non-scandent narrow-leaved species of Aetheolaena. Its growth form is similar to that of A. gargantana (viz fig. 15), and was diagramed in Salomón et al.

(2018: 3, fig. 11). As noted in its protologue, Aetheolaena josei is nearly the southernmost erect species of the genus. I have seen only two collections of Aetheolaena josei not cited in the protologue, one of which (Fig. 16) may be the voucher of the field photograph by Danila Minga (Flora del Páramo del Cajas 2016: page 208). Aetheolaena josei is known only from central and southern Ecuador (Parque Nacional Cajas, Azuay and Cordillera las Lagunillas, Loja), where it occurs above 3300 m elevation. The type locality Cordillera las Lagunillas is within five kms of the frontier with Piura, Peru, and is very near the border of Zamora-Chinchipe, Ecuador. The species may reasonably be expected to occur in Peru, as well as between the documented localities in Ecuador.

Aetheolaena josei recalls the more northerly Lasiocephalus lingulatus Schltdl., also diagramed with the same habit (Salomón et al. 2018: 3, fig. 1I). In its protologue, Aetheolaena josei was compared to similarly erect-stemmed Lasiocephalus sodiroi (Hieron.) Cuatr., but that is a densely leafy, even narrower leaved, short-pedunculate species I treat as Lasiocephalus peruvianus (Klatt) Pruski) (viz fig. 19). By linear, lanate, revolute-margined leaves and discoid heads with ca. 21 lanate phyllaries, Monticalia angustifolia (Kunth) B. Nord. and Monticalia rosmarinifolia (Benth.) C. Jeffrey recall Aetheolaena josei, but differ by tubular-funnelform (vs. broad-campanulate) corollas with ca. 0.6 (vs. ca. 1) mm long lobes, caudate (vs. ecaudate) anthers, and by truncate (vs. penicillate) disk style branches.

AETHEOLAENA PIEDRAHITAE (J. Calvo & F. Ávila) Pruski, comb. nov. Senecio piedrahitae J. Calvo & F. Ávila, Phytotaxa 283(1): 92, f. 1. 2016. TYPE: COLOMBIA. Tolima. Cordillera Central, camino del paso de la Quebrada del África, 7 Feb 1980, Díaz-Piedrahita & Jaramillo 1914 (holotype: COL).

Aetheolaena piedrahitae (J. Calvo & F. Ávila) Pruski is characterized by its scandent habit, narrow asymmetric-based petiolate (at mid-stem) leaves, nutant discoid capitula, and penicillate styles. Salomón et al. (2018: 3, fig. 1B) provided a diagram of the general habit of it and other scandent species. It is similar clearly to the relatively common A. patens (Kunth) B. Nord. and A. subinvolucrata (Cuatr.) B. Nord., but differs from them by 21 (vs. 9–14) phyllaries. It also resembles A. longipenicillata (Schultz-Bip. ex Sandw.) B. Nord. as noted in the protologue, but differs by its mid-stem leaves asymmetrical-attenuate strongly at base. Aetheolaena piedrahitae is endemic to Colombia, where it has been found in the Cordillera Central above 4000 m elevation.

4. LASIOCEPHALUS Willd. ex Schltdl., Mag. Neuesten Entdeck. Gesammten Naturk. Ges. Naturf. Freunde Berlin 8: 308. (not dated to month) 1818. Type: Lasiocephalus ovatus Schltdl. Figures 11–12A, 17B, 18–20.

Senecio sect. Reflexus Cuatr.

Species recognized (4 species; each illustrated here as indicated below, abbreviated synonymy also follows). (1) Lasiocephalus lingulatus Schltdl. 1818 (Figs. 17B–18) (syn.: Aetheolaena ledifolia (Kunth) B. Nord., Aetheolaena lingulata (Schltdl.) B. Nord., Aetheolaena pichinchensis (Cuatr.) B. Nord., Cacalia arenaria Kunth 26 Oct 1818, Cacalia cinerioides Kunth 26 Oct 1818, Culcitium adscendens Benth., Culcitium hypoleucum Turcz., Culcitium ledifolium Kunth 26 Oct 1818, Culcitium lingulatum (Schltdl.) S.F. Blake, Culcitium pichinchense Cuatr., Lasiocephalus hypoleucus (Turcz.) C. Jeffrey, Lasiocephalus ledifolius (Kunth) C. Jeffrey, Lasiocephalus pichinchensis (Cuatr., Senecio lingulatus (Schltdl.) Cuatr., Senecio neoascendens Cuatr., Senecio pichinchensis (Cuatr.) Cuatr., Senecio quitensis Cuatr., Senecio sabulosus DC.); (2) Lasiocephalus ovatus Schltdl. 1818 (Figs. 11–12A) (syn.: Culcitium ovatum (Schltdl.) S.F. Blake, Culcitium reflexum Kunth 26 Oct 1818, Culcitium uniflorum Hieron. [intended as a new comb. based on the illegitimate Lamarck 1788 binomial], Gnaphalium uniflorum Lam. 1788—viz Steudel, Nomencl. Bot. 1: 696. 1840—non Miller 1768, Senecio reflexus (Kunth) Cuatr. 1950 non Kunth 1818, Senecio superandinus Cuatr.); (3) Lasiocephalus peruvianus (Klatt) Pruski (Fig. 19) (syn.: Culcitium peruvianum Klatt, Culcitium sodiroi Hieron., Lasiocephalus sodiroi (Hieron.) Cuatr., Senecio culciklattii Cuatr., Senecio imbaburensis Sklenář & Marhold, Senecio sodiroi (Hieron.) Cuatr. 1950 non Hieron. 1900); (4) Lasiocephalus superparamensis (Sklenář) Pruski (Fig. 20) (syn.: Senecio superparamensis Sklenář).

The páramo clade of Dušková et al. (2010, 2017), in large measure, is recognized here at the generic rank as newly resurrected Lasiocephalus. Blake (1937) treated both original species L. *lingulatus* and generitype *L. ovatus* as members of *Culcitium*, but a decade later Cuatrecasas (1951) placed these two original species in Senecio sect. Reflexus Cuatr. Nordenstam (1978), based on characters of habit, nutant discoid capitula, corolla form, and penicillate styles, reinstated Aetheolaena from a century-long synonymy under Senecio. The fine line drawing of L. lingulatus in Nordenstam (1978: fig. 25A-F) shows clearly the penicillate styles, and a SEM image of the penicillate style of L. lingulatus was also given in Salomón et al. (2018: 8, fig. 3C). Nordenstam (1978) transferred L. lingulatus to Aetheolaena, but he retained L. ovatus within Culcitium. Soon thereafter, Cuatrecasas (1978) recognized 21 species in newly resurrected Lasiocephalus—in synonymy previously for more than one and a half centuries—and reduced Aetheolaena and Senecio sect. Reflexus Cuatr., to synonymy with Lasiocephalus.

Nordenstam (2007 [2006]) recognized "circa 15 species" in Aetheolaena, but within Lasiocephalus only "two or three species [in the] Andes of Peru, Ecuador, [and] Colombia." In Dušková et al. (2010, 2017), all vouchers referred to species of Lasiocephalus grouped together in their páramo clade, except for parts of a single mixed voucher from Volcán Chiles of population 88 (Sklenář et al. 11509) that in the 2017 phylogeny was called S. aff. quitensis (a synonym of L. lingulatus) and fell into both the páramo clade and the forest clade. Within the páramo clade, exsiccatae of Culcitium nivale were recovered as sister to Lasiocephalus in the analyses of each Dušková et al. (2010) and Salomón et al. (2019), but Dušková et al. (2017) recovered Culcitium nivale+Lasiocephalus superparamensis and the three other species of Lasiocephalus as sister clades. Here, following the lead of Pruski (2018), Aetheolaena, Culcitium, and Lasiocephalus are each recognized as distinct, again. I retain C. nivale in Culcitium, and thus treat Culcitium as containing more than a single species, as has been done traditionally. The generic concepts I adopt parallel those of Nordenstam (2007), and I find four species that answer to the characters of Lasiocephalus. The two original species of Lasiocephalus (Schlechtendal 1818) and the two new combinations proposed herein, are the four species I recognize in Lasiocephalus.

As circumscribed here, Lasiocephalus is centered in páramos in Colombia and Ecuador. Two of its four species have been reported, however, as also found in jalca and puna vegetation in Peru (Klatt 1894; Sylvester et al. 2017). Lasiocephalus peruvianus is typified by a historical specimen from Peru presumably on or near the border with Ecuador, but the species is otherwise known only from Ecuador. Sylvester et al. (2017: fig. 1a) reported a determination by Nicholas Hind of otherwise Ecuadorian endemic L. lingulatus in Cusco, Peru as vouchered by Sylvester 1880 (K, LPB, Z, not seen by me). The generitype L. ovatus appears to be endemic to Colombia and Ecuador. I am unaware of any modern vouchers documenting the generitype as occurring in Peru. MA-816339 from the Ruiz and Pavón herbarium is L. ovatus, but this specimen is presumably not a Ruiz & Pavón collection, and is presumably not from Peru.

Lasiocephalus ovatus Schltdl. (published in 1818, but undated and perhaps not datable to month), the generitype, includes in taxonomic synonymy the above illustrated (Fig. 11) Culcitium reflexum Kunth (a name dated as 26 October 1818). Lasiocephalus ovatus (Schlechtendal 1818) has been taken traditionally as having priority over Culcitium reflexum (Kunth 1820), which has been long taken as published in 1820 as dated on its title page, but now is known to have also been published effectively 26 October 1818. It seems reasonable to accept priority of the name Lasiocephalus ovatus over Culcitium reflexum (Fig. 11), although formal conservation technically may be desired. Similarly, Lasiocephalus lingulatus (Schlechtendal 1818) has been understood historically to have priority over Cacalia arenaria Kunth (26 Oct 1818) and Culcitium ledifolium Kunth (26 Oct 1818), and it seems reasonably to take newly synonymous Cacalia cinerioides Kunth (26 Oct 1818) (Fig. 18B) as a later name as well.

Lasiocephalus is commonly stiffly erect and simple-stemmed, but a fair number of herbarium specimens of L. ovatus are branched. Branching stems may also be found infrequently in L. lingulata (e.g., Jameson 172, P, an isotype of Culcitium hypoleucum Turcz.; Fernández et al. 1740, MO, which matches the type of Cacalia cinerioides Kunth) and in L. peruvianus (e.g., Cerón & Mena 1214, MO, US). Lasiocephalus peruvianus has linear-lanceolate, strongly discolorous, adaxially glabrous leaves (Fig. 19), but is similar moderately to narrow leaved material of *L. lingulatus*, which has adaxially lanate, weakly discolorous leaves (Fig. 18). Both L. peruvianus and L. lingulatus are relatively smallcapitulate, whereas L. ovatus and L. superparamensis are each large-capitulate. The three more typical species (L. ovatus, L. peruvianus, and L. superparamensis) (Figs. 11-12A, 19-20) are densely leafy, but L. lingulatus is often clearly loosely leaved (Fig. 18A). Indeed, the habit of L. lingulatus was diagramed in Salomón et al. (2018: 3, fig. 11) with an open capitulescence of relatively small capitula (more or less as in Aetheolaena josei, fig. 16). However, in material of L. lingulatus in front of me the vegetative stems are few-branched apically/distally with each axillary branchlet subtended by a (reduced) leaf, and the capitula thereby are solitary technically and terminating the branchlets, as in the three more densely leaved species of the genus. Nevertheless, the habit of L. lingulatus is seemingly as given in Salomón et al. (2018: 3, fig. 11). I follow the synonymy of Cuatrecasas (1978) for L. lingulatus, which seems to be the most broadly defined species of the genus. The habits of the three larger capitulate, usually monocephalous, densely leafy species of Lasiocephalus are as diagramed in Salomón et al. (2018: 3, fig. 1G).

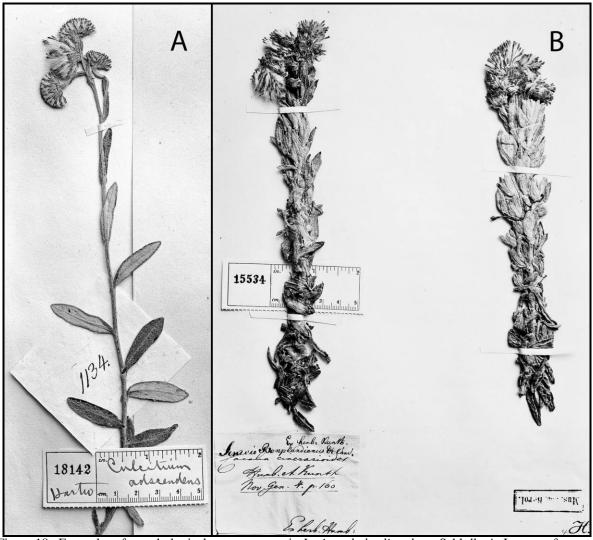


Figure 18. Examples of morphological extremes seen in *Lasiocephalus lingulatus* Schltdl. A. Isotype of synonymous *Culcitium adscendens* Benth.; this is the most sparsely leaved isotype seen of the Bentham name; relatively sparsely leaved plants with open capitulescences are the more commonly collected forms of Lasiocephalus lingulatus. B. Isotype of Cacalia cinerioides Kunth; this name joins a half dozen synonyms of the broadly defined Lasiocephalus lingulatus, and is its leafiest and most robust form. Such plants are the less common growth form of Lasiocephalus lingulatus, albeit resembling more closely the type of Lasiocephalus lingulatus than do the less leafy plants. (A Hartweg 1134, B†, Macbride negative 18142; B Humboldt & Bonpland s.n., B†, Macbride negative 15534).

Two collections from Volcán Chiles, Ecuador on the border with Colombia (Holm-Nielsen et al. 5893, Sklenář & Kosteckova 1404) were cited by Sklenář (2001) as L. sordiroi (here taken as a syn. of L. peruvianus). Sklenář (2012) cited a collection from Volcán Chiles (Sklenář et al. 11510), which I have not seen, as a paratype of Senecio superparamensis. Sklenář (2012) suggested that Lasiocephalus superparamensis, which occurs in part on Volcán Chiles, is of hybrid origin with Culcitium nivale and Lasiocephalus ovatus as "likely parent taxa." Marhold and Sklenář (2013) referred "the population" from Volcán Chiles to Aetheolaena gargantana, but did not mention a presumed second population from Volcán Chiles was a paratype of Senecio superparamensis (Sklenář 2012). Salomón et al. (2018) cited *Holm-Nielsen et al.* 5893 from Volcán Chiles again as S. imbaburensis (also a syn. of L. peruvianus). Salomón et al. (2019) cited DNA voucher Sklenář et al. 11511 from Volcán Chiles both as S. sodiroi and S. imbaburensis, each of which I treat in synonymy with L. peruvianus. In the phylogeny Dušková et al. (2017 and electronic supporting information) the DNA voucher Sklenář et al. 12391 from Nariño, Colombia fell in to the forest clade and was cited as Aetheolaena gargantana. In Dušková et al. (2017) and Salomón et al. (2019), Sklenář et al. 11509 and Sklenář et al. 11511 fell largely into the páramo clade (here adopted as Lasiocephalus), albeit the two vouchers are associated variously with six species names in three genera and with Sklenář et al. 11509 being mixed and falling into both the paramo and the forest clades. Thus, materials from Volcán Chiles once thought to represent a single taxon (Sklenář 2001), have been referred by Petr Sklenář at various times in cited literature to Aetheolaena gargantana, Lasiocephalus lingulatus, Lasiocephalus peruvianus (as L. sodiroi), and the described more recently Lasiocephalus superparamensis. As with many high elevational, recently evolved species or incipient species, anatomical leaf features are similar (e.g., Silva-Moure et al. 2014) and there is often no great separation in either morphology or in phylogenies. Indeed, individual herbarium specimens of the Aetheolaena-Lasiocephalus group do not always pigeonhole well, with those from Volcán Chiles being among the more notorious.

LASIOCEPHALUS PERUVIANUS (Klatt) Pruski, comb. nov. Culcitium peruvianum Klatt, Ann. K. K. Naturhist. Hofmus. 9(3-4): 363. 1894. Senecio culciklattii Cuatr., Fieldiana, Bot. 27(1): 43. 1950. TYPE: PERU. [? Ecuador]. Sin. loc., Anon. s.n. (holotype: W, Macbride negative 33310). [Given the documented distribution of the species, the plant was collected presumably near the Peru-Ecuador border, perhaps within Ecuador]. Figure 19.

Culcitium sodiroi Hieron. 1900: 63, Lasiocephalus sodiroi (Hieron.) Cuatr., Senecio imbaburensis Sklenář & Marhold, Senecio sodiroi (Hieron.) Cuatr. 1950 non Hieron. 1900: 73.

Lasiocephalus peruvianus (Klatt) Pruski, based on Culcitium peruvianum (holotype as fig. 19A), is the earliest name known to me for the monocephalous or occasionally paucicephalous plant known variously as Culcitium peruvianum (Cuatrecasas 1942), Lasiocephalus sodiroi (Cuatrecasas 1990; Sklenář 2001), or Senecio culciklattii (Cuatrecasas 1950). The homotypic (with Lasiocephalus peruvianus) new name Senecio culciklattii was provided by Cuatrecasas (1950), while reducing Culcitium to synonymy of Senecio. In the genus Senecio, a new name was desired because Senecio peruvianus Pers. blocked transfer of Culcitium peruvianum Klatt to Senecio. Subsequently, Cuatrecasas (1990) resurrected the similar Lasiocephalus sodiroi, which is treated here as Lasiocephalus peruvianus. More recently, the blocking Persoon name has been noted by Jeffrey (1992) and Pruski (2018) as the very different shrubby Monticalia peruviana (Pers.) C. Jeffrey. Surprisingly similar to Lasiocephalus peruvianus in gestalt, however, is regional Andean Monticalia rosmarinifolia (Benth.) C. Jeffrey. Lasiocephalus peruvianus in gestalt recalls also S. hypsobates Wedd. (of Senecio sect. Crassicephali), which differs by being subrosulate, branched openly in the capitulescence, having florets with narrow corollas, and by truncate-tipped styles.

Lasiocephalus peruvianus is characterized by its flexuous to stiffly erect densely leafy stems, linear-lanceolate discolorous leaves, discoid short-pedunculate capitula, its monocephalous to less commonly paucicephalous capitulescences, campanulate disk corollas (Fig. 19B, upper left), and penicillate styles. Salomón and Freire (2014) and Salomón et al. (2018) listed Lasiocephalus peruvianus in Senecio under the homotypic synonym Senecio culciklattii, and as of "dubious identity." Salomón and Freire (2014) and Salomón et al. (2018) stated they did not know in which herbarium the holotype of *C. peruvianum* was deposited, but the title of the Klatt protologue paper (Klatt 1894) noted that W houses the holotype. Neither *Culcitium peruvianum* nor *Senecio* culciklattii Cuatr. (both homotypic synonyms of Lasiocephalus peruvianus) were mentioned in the

'group Lasiocephalus' paper by Calvo and Freire (2016). One of the páramo clade vouchers cited by Dušková et al. (2017) under names I place in synonymy with L. peruvianus was Sklenář et al. 11511, which seems similar to L. superparamensis. Similarly, other vouchers of names I treat as L. peruvianus were, along with L. lingulatus, recovered by Dušková et al. (2017) in differing parts of the páramo clade. A fine unvouchered line drawing of Lasiocephalus peruvianus (as S. imbaburensis) is found in Salomón et al. (2018: 20, fig. 12), and the identity of the species seems clear. Salomón et al. (2018: 3, fig. 1G) diagramed (as S. imbaburensis) its uniformly leafy growth form.

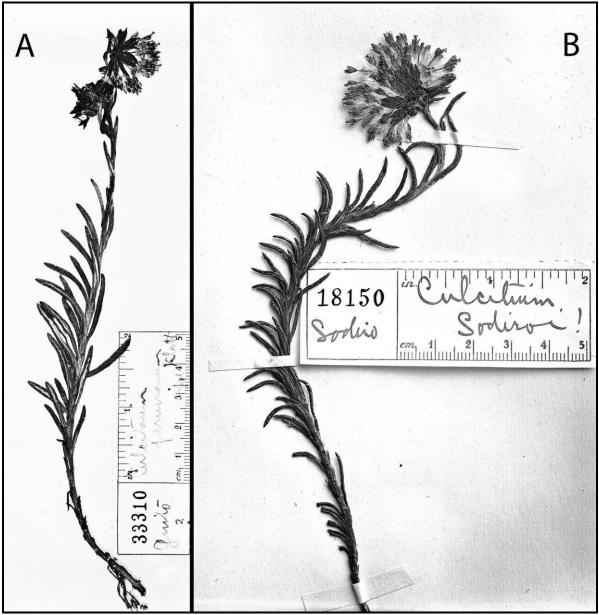


Figure 19. Photographs of holotypes of linear-lanceolate-leaved Lasiocephalus peruvianus (Klatt) Pruski and synonymous Lasiocephalus sodiroi (Hieron.) Cuatr. A. Holotype of Culcitium peruvianum Klatt (≡ Lasiocephalus peruvianus (Klatt) Pruski). The title of the Klatt protologue paper (Klatt 1894) indicated the holotype as in the W herbarium. The paucicephalous capitulescence of this leafy-stemmed plant occurs in about one out of ten specimens, whereas the monocephalous condition dominates. B. Holotype of Culcitium sodiroi Hieron. (= Lasiocephalus sodiroi (Hieron.) Cuatr.; = Lasiocephalus peruvianus (Klatt) Pruski) showing the monocephalous capitulescence and its campanulate disk corollas. (A Anonymous s.n., W, Macbride negative 33310, described in the protologue as "Hab.: Peru, legit?"; B Sodiro s.n., B†, Macbride negative 18150).



Figure 20. Representative specimen of *Lasiocephalus superparamensis* (Sklenář) Pruski. (*Sklenář & Sklenarova 3303*, US, paratype).

Culcitium sodiroi was treated in Senecio by Cuatrecasas (1950), was not mentioned in either Nordenstam (1978) or Cuatrecasas (1978), but was given as Lasiocephalus sodiroi by Cuatrecasas (1990) and Sklenář (2001). Lasiocephalus peruvianus is similar in aspect to Lasiocephalus ovatus, which has larger sessile capitula and densely imbricate leaves. Lasiocephalus peruvianus is centered in Ecuador where it occurs above 3800 m elevation, but the type was collected possibly in [northern] Peru as labeled. Should Lasiocephalus peruvianus prove endemic to Ecuador, it would be similar in geographic epithet and extra-Peruvian distribution to Calea peruviana (Kunth) Benth. ex S.F. Blake, which Pruski (1982) gave as endemic to Colombia. Geographic errors are occasional in historic Andean plants, and a similar locality error was noted by Cuatrecasas (2013): Colombian endemic Espeletiopsis corymbosa (Bonpl.) Cuatr. was published by Bonpland (1809) as "Peruviae frigidis, juxta urbem Almaguer."

LASIOCEPHALUS SUPERPARAMENSIS (Sklenář) Pruski, comb. nov. Senecio superparamensis Sklenář, Nordic J. Bot. 30(4): 396, f. 2. 2012. Type: ECUADOR. Napo. Antisana, 1 Nov 2007, Sklenář & Rejzkova 10701 (holotype: PRC). Figure 20.

Lasiocephalus superparamensis (Sklenář) Pruski is a monocephalous plant with densely inserted griseous leaves and weakly penicillate styles. Dušková et al. (2010) cited as "Lasiocephalus sp. 4 (cf. ledifolius)" the type and several paratypes of L. superparamensis. The species differs from the generitype by its elliptical-lanceolate (vs. ovate) leaves. The uniformly densely leafy habit of Lasiocephalus superparamensis was diagramed in Salomón et al. (2018: 3, fig. 1G). Senecio superparamensis was cited by Calvo and Freire (2016) as having (no or) very minute penicillateappendiculate style appendages, and excluded from "Senecio group Lasiocephalus." Salomón et al. (2018) included Lasiocephalus superparamensis in Senecio ser. Culcitium. The corollas are narrower than the average corollas of the related genus Aetheolaena, but match the corolla form of the generitype *L. ovatus*.

Dušková et al. (2017) recovered in their páramo clade Lasiocephalus superparamensis and Culcitium nivale in the same polytomy, but the generitype of Culcitium—Culcitium canescens—was not recovered in that branch. Nevertheless, Culcitium nivale is retained in Culcitium as is tradition. Sklenář & Karbulkova 11121 was cited as L. superparamensis by Salomón et al. (2018), but instead is L. lingulatus as cited in Dušková et al. (2017). Sklenář & Sklenarova 3303 (US) (Fig. 20) was determined originally as Aetheolaena (Lasiocephalus) gargantana, and was described subsequently as Senecio superparamensis Sklenář (3303 is a paratype). The plants are still treated in separate genera, but they are very similar in gestalt. The Lasiocephalus has subsessile, solitary capitula, whereas the Aetheolaena has campanulate corollas. Although a paratype of L. superparamensis is from Volcán Chiles on the border with Colombia, the species is endemic seemingly to Ecuador, where it occurs at elevations above 4000 meters.

**5.** HAPLOSTICHA Phil., Linnaea 30: 193. 1859. TYPE: Haplosticha stolonifera Phil. [= Haplosticha zosterifolia (Hook. & Arn.) Pruski]. Figures 21–22.

Senecio sect. Haplosticha (Phil.) Cabrera (as Haplostichia), Senecio ser. Haplostichi (Phil.) Cabrera & S.E. Freire.

Haplosticha, resurrected here from Senecio, is a genus containing three subrosulate whiteray-flowered exappendiculate-obtuse-truncate-styled extra-tropical species, as keyed below. Two of the three species are monocephalous, ecalyculate or nearly so, glabrous-fruited, and centered in Patagonia. A third species, H. arnicoides (Hook. & Arn.) Pruski, has a paucicephalous corymbiform capitulescence, weakly calyculate capitula, setose fruits, and is endemic to central Chile. The combination of characters found in *Haplosticha* render it unmatched among other Pacific rim genera.

These three perennial herbs were grouped together by Hooker and Arnott (1841) as species 2044–2046, and as species of Senecio. Soon thereafter in the Captain Ross Antarctic voyage report, Hooker (1847) provided a fine, albeit too yellow, illustration of *H. trifurcata* (reproduced here as figure 21) that was described originally by Forster (1788, 1789) based on materials collected on the second Captain Cook voyage. Willdenow (1803: 1965) and Persoon (1807: 455) each recognized Tussilago trifurcata, Cassini (1825: 191) said the Forster description was too insufficient for study of the generic placement of Tussilago trifurcata, and Sprengel (1826: 551) treated the species as Cineraria trifurcata (G. Forst.) Spreng. Of this species, Hooker (1847) said "the very pale colour of the ray ... seems to have deceived the older authors" and that "in this respect it differs from the majority of Seneciones."

White ray corollas such as those found in Haplosticha and Senecio smithii DC. [syn.: Brachypappus smithii (DC.) Sch. Bip.; described from, and naturalized in, the British Isles] are indeed infrequent in Senecioninae, among Andean chain Senecioninae white-rayed comps most familiar to collectors are species of Werneria, which are caespitose plants with connate phyllaries being much different from Haplosticha. Brachypappus Sch. Bip. 1855, typified by Cacalia candicans Vahl, is a large-leaved discoid-capitulate pluricapitulate genus. *Iocenes* is also reinstated, southern South American, and white-rayed, but differs from Haplosticha by its leafy caulescent habit, many smaller capitula, and appendiculate disk style branches.

Haplosticha was described as monotypic and typified H. stolonifera Phil. by Philippi (1859). Philippi characterized his new genus by its glabrous fruits and its generitype by monocephalous capitulescences, which its generic name referenced. Bentham and Hooker (1873), however, reduced Haplosticha to synonymy with Senecio, where it remained until now, and synonymized H. stolonifera with Senecio zosterifolius Hook. & Arn.

Klatt (1888) and Jackson (1893) also recognized Senecio zosterifolius Hook. & Arn. as including the H. stolonifera, but spelled the generic name "Haplostichia." Kanchi Gandhi (pers. comm. 2021) agreed that the original Philippi spelling of Haplosticha need not be corrected [viz ICBN 60.1, ICN 60.1], and the spelling of the genus name *Haplosticha* is retained. Reiche (1905) keyed together the two Patagonia-centered species as Senecio group 1A.1 by their white ray corollas and monocephalous capitulescences. Reiche (1905) keyed as Senecio group 1B.1 H. arnicoides, as the only white-radiate, paucicephalous, setose-fruited Chilean so-called Senecio, albeit using the name Senecio plantagineus Bertero ex Colla.

Cabrera (1949) treated the three species recognized here in *Haplosticha* as *Senecio* sect. Haplosticha. These are the species numbered 2044-2046 and aligned adjacently in Hooker and Arnott (1841). Subsequently, Cabrera (1954) described white-flowered Senecio infimus Cabrera, from Jujuy in northern Argentina, and four decades thereafter (Cabrera et al. 1999: 32) treated it as the fourth species of the group. Although Senecio infimus is paucicephalous and setose-fruited as is H. arnicoides, the excluded S. infimus is not subrosulate and lacks basal rosette leaves at anthesis. I have seen no material of S. infimus, and thus do not include the plant in Haplosticha.

Although, H. arnicoides is paucicephalous and has setose cypselae, it matches otherwise the two typical Patagonian-centered species by subrosulate habit and white ray corollas. Haplosticha arnicoides is accepted as the third species of Haplosticha, following the alignments in Hooker and Arnott (1841) and Cabrera (1949). Pelser et al. (2010b: figs 1A, 1B, 2) recovered Haplosticha arnicoides and Haplosticha trifurcata (as Senecio) as sister in their bayesian consensus trees. Senecio infimus and Senecio smithii are not placed here. The three recognized species of Haplosticha are endemic to southern South America, ecaudate-anthered, and truncate-styled, much unlike Chaetacalia. My taxonomy merges concepts of Philippi (1859), Bentham and Hooker (1841), and Cabrera (1949).

## **Key to species of Haplosticha (modified from Cabrera 1949)**

- 1. Capitulescences paucicephalous corymbiform; capitula weakly calyculate; peduncles and leaves sometimes glandular-hirsute; leaves ovate or oblanceolate; cypselae setose; 1. Capitulescences monocephalous; capitula ecalyculate or nearly so; peduncles and leaves mostly glabrous and not glandular-hirsute; leaves linear or cuneate; cypselae glabrous; (centered in Patagonian Argentina and Chile).

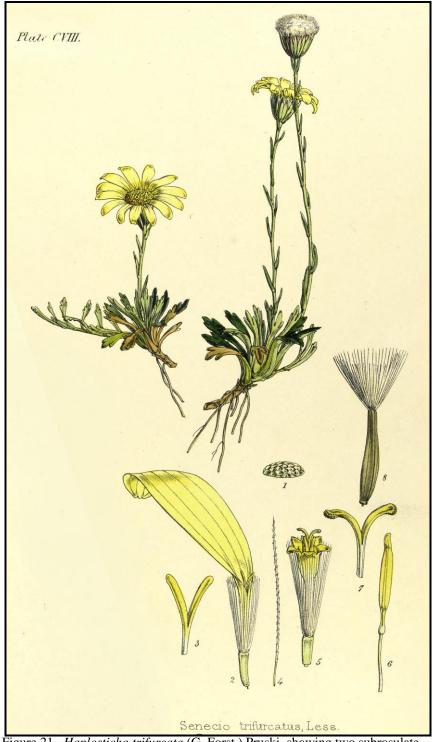


Figure 21. Haplosticha trifurcata (G. Forst.) Pruski, showing two subrosulate plants topped by their monocephalous capitulescences, and floral details, including broadly-obtuse-tipped style branches each with a 2-banded stigmatic surface (3, 7), and anthers with a balusterform filament collar (6), and a glabrous cypsela (8). The ray corollas are white, not yellow as seen here. [Modified from J.D. Hooker, Bot. Antarctic Voy., vol. 1, part 2 (i.e., Fl. Antarct.) tab. 108 right, 1846; the left-hand side of Fl. Antarct. tab. 108 was reproduced by Pruski (2017) in the Talamancaster Pruski protologue paper].

HAPLOSTICHA ARNICOIDES (Hook. & Arn.) Pruski, comb. nov. Senecio arnicoides Hook. & Arn., Bot. Beechey Voy. 32. 1830. TYPE: CHILE. [Bío-bío.] Concepción, [Oct 1825], Beechey Voyage s.n. (holotype: K herb. Hooker, presumably plant to left of barcode 527540, presumably plant second from the left margin of the sheet in the sheet with five plants and four barcodes, 527539–527542).

Senecio plantagineus Bertero ex Colla, 1833.

The title of Hooker and Arnott (1830-1841) report gives collectors as "Lay and Collie, and other officers of the expedition." The preface in Hooker and Arnott (1830–1841: ii) reads "collections were made by Mr. Lay the Naturalist, and by the officers of the ship generally; but in particular by Mr. Collie, who, during the temporary absence of Mr. Lay, zealously undertook..." A collection simply as "Beechey" was cited subsequently by Hooker and Arnott (1841: 341). Hooker and Arnott (1835: 30) in the introduction of the first installment of their journal series said "the whole of the species here enumerated, one or two only excepted, are in our herbaria." It seems reasonable therefore that nearly all authentic specimens of the contemporaneous Beechey enumeration are similarly in either E and/or K. Henry Noltie (2010: 168), of specimens of S. arnicoides said, "none found at E or K," and he gave the type as collected by "Lay and Collie." I find only one plant on a Kew Herbarium Hooker sheet (and no E ex GL Arnott herbarium sheet) that is presumably the unicate holotype of Senecio arnicoides.

On the Kew Hooker herbarium sheet there are five individual plants, each apparently of a different gathering, though the sheet in 2021 has only four (not five) barcodes, 527539–527542. The plants on the Kew sheet clockwise from small central plant have two (Bridges?), two (Beechey?), five (Cuming 516), six subumbellate (Capt. King s.n., the upside-down glued plant), and four (two broken) (Matthews 243) capitula, respectively. None of the five plants on this Kew Hooker herbarium sheet matches exactly the protologue description of "corymbo subtrifloro," simply because apparently one capitulum of the "subtrifloro" plant was dissected for the protologue description. It is the second plant from the left on the Kew sheet (the taller of the 2-capitulate plants), more than the four others, that seems to match closely the protologue "foliis radicalibus lanceolatis angulatodentatis ... longe petiolatus" phrase, and is considered by me as likely the unicate holotype.

Haplosticha arnicoides (Hook. & Arn.) Pruski is endemic to temperate central Chile, from Valparaíso south to Valdivia in Los Lagos (Cabrera 1949).

HAPLOSTICHA TRIFURCATA (G. Forst.) Pruski, comb. nov. Tussilago trifurcata G. Forst., De Plantis Magellanicis et Atlanticis Commentationes p. 28. 1788 [April–May 1788]; Commentat. Soc. Regiae Sci. Gott. 9: 38. 1789 [before 23 May 1789]. The citation of the two references is allowed in the Code (viz ICBN 33.7 = ICN 41.8). Cineraria trifurcata (G. Forst.) Spreng., Syst. Veg. 3: 551. 1826, basionym epithet as "3furcata." Senecio trifurcatus (G. Forst.) Less. ex DC., Prodr. 6: 435. 1837 [1838]. LECTOTYPE (basionym reference incorrect in Freire et al. 2014, and thus designated here): [CHILE]. [Western] Tierra del Fuego [as "Terram Ignis" in Forster (1788, 1789)], [Christmas Sound], collibus aridioribus [as "Habitat cum praecedente" in Forster (1788, 1789)], [ca. 21–27 Dec 1774, the second Captain Cook voyage from 1772–1775, eastward aboard the Resolution], Forster s.n. (lectotype: K barcode 527538 ex LIV 1885; possible the same collector(s) and of same gathering, thus isolectotypes, given by Nicolson and Fosberg (2004: 326–327) and/or seen on the web include: BM-Pallas #2-left, BM-Lambert #1-right, estate set 1 #178, P-Sprengel Herb. 1384-Sch.Bip.-Cosson, P-Buffon n.v. (given to Buffon in 1777, as Terre de feu, Forster 151), S-Montin #189, UPS-Thunberg 19523 IDC microfiche 1036. 814.II.4, W-Jacquin-51164). The lectotype designated herein agrees with all significant and diagnostic features given in the protologue description. The data and handwriting on most Forster sheets is that "later owners or curators" (Fosberg 1993), and numbers on the sheets are basically either estate sale numbers, catalogue numbers, or herbarium numbers, rather than Forster collection numbers. The basionym in each Forster text (which have the same content) was given as species #24 that read "Habitat cum praecedente." A BM sheet of species #23 [Perezia magellanica (L.f.) Less.] gives the collection data as "Christmas Sound Harbour ... 27 Dec 1774" (Nicolson and Forster 2004: 319); one of the Forster sheets of Perezia

magellanica is labeled as Christmas Sound; and Forster drawings in BM of both Haplosticha trifurcata and Perezia magellanica are dated "27 December" which Cook (1777, 1821) gave as at Christmas Sound. The Resolution departed in the morning of 28 December 1774 (Cook 1777: 188, 1821: 173) and although several George Forster illustrations are dated 27 December, they were perhaps drawn over a several-day period ending on 27 December. Indeed, most species treated in Forster (1788, 1789) are from Christmas Sound. The type locality of Tussilago trifurcata G. Forst. thus is in western Tierra del Fuego, Chile. This is confirmed by the coordinates of "latitude 55° 27' S., longitude 70° 16' W." for the entrance of Christmas Sound [as "portu Natiuiltatis Christi" in Forster (1788, 1789)], near the presumed type locality, given by Captain James Cook (1777: 185, 1821: 170). Figure 21.

Possible syntypes or original elements fide Nicolson and Fosberg (2004: 326–327) and/or on the web. The Captain Cook second circumnavigation voyage 1772-1775, eastward aboard the Resolution: [CHILE]. [Western] Tierra del Fuego, Christmas Harbour, Anderson s.n. (BM n.v.); Sketch done in Tierra del Fuego, [seemingly labeled faintly] in pencil as "Tussilago magellanica 25 Dec [1774], George Forster drawing 214 (BM; labeled subsequently in ink as "Tussilago trifurcata Pl. Magell. in Commentat. Soc. Regiae Sci. Gotting. 9 p. 38. n. 24;" the date "25 Dec [1774]" is given by Nicolson and Fosberg 2004: 327, the date "27/12/1774" is given on the web). Captain Cook first voyage 1768–1771, westward aboard the Endeavour: [ARGENTINA/CHILE]. Tierra del Fuego, [Jan 1769], Banks & Solander s.n. (BM n.v.); Sydney Parkinson watercolor 44 dated 1769 as "Aster trifurcatus" (BM, two figures, the first is a color watercolor, a second is the image in reverse which is apparently the engraving proof). The published Forster epithet, the epithet of "Senecio 3furcata Banks" in the Paris Forster manuscript, and the Aster trifurcatus Banks epithet on the Parkinson watercolor are the same, indicative of the close contact between Banks and the Forsters, and it seems possible that Banks allowed, or even encouraged, the Forsters to examine the earlier Banks collection and the Parkinson illustration.

Senecio pentadactylus Phil., Senecio trifurcatus var. pentadactylus (Phil.) Speg., Senecio trifurcatus var. pisensis Sch. Bip. ex Wedd.

Haplosticha trifurcata (G. Forst.) Pruski basionym reference notes (the journal vs. the independently paginated preprint(s) and IPNI; see also Forster 1788 in the literature cited). The Tussilago trifurcata-containing G. Forster (Forster 1788) independently paginated 64-page preprint title is De Plantis Magellanicis et Atlanticis Commentationes (Stafleu and Cowan 1976 TL-2/1824). The preprint has been dated as between April–May 1788 (Nicolson and Fosberg 2004; see also discussion in Forster 1788 in the Literature Cited below). The reference of the Tussilago trifurcata-containing paper in the journal is Fasciculus Plantarum Magellanicarum, Commentat. Soc. Regiae Sci. Gott. 9: 13-45 + pl. 1-8. 1789 [before 23 May 1789] (Forster 1789). The preprint is independently paginated, and is the earlier of the two printings of Forster text (Stafleu and Cowan 1976). I have examined the journal version in the rare book room in the MO library and several online copies. Gretchen Wade (Harvard Library) and Linda Oestry (MO library) sent me a pdf copy of GOET holding of the original 64-page preprint, which is undated and appears to lack the eight unpaginated plates. [A hypothetical 62-page preprint citation (that was so cited by Nicolson and Fosberg 2004: 65) with the extrapolated page citation of the binomial may be G. Forster, Fasciculus Plantarum Magellanicarum p. 26. 1788; however, I presume this 62-page preprint citation in Nicolson and Fosberg (2004: 65) is erroneous, and instead that it is actually in reference to the 64-page preprint; indeed, Nicolson and Fosberg (2004: 326) cited the basionym as page "28" of the preprint, i.e., of the 64-page preprint.] Christian Heyne, who was associated with the Commentationes Societatis Regiae Scientiarum Gottingensis and Forster's father-in-law—George Forster and Therese Heyne were married in 1785—could have helped expedite printing of the separate. In validating Haplosticha trifurcata (G. Forster) Pruski above, I use the basionym citation from both the 1788 preprint, as well as from the 1789 journal version that is available more widely, as is permissible in the Code [viz ICBN 33.7 = ICN 41.8].

The paper following immediately Forster (1789) in volume 9 of Commentationes Societatis Regiae Scientiarum Gottingensis is George Forster's "Plantae Atlanticae ..." Commentat. Soc. Regiae Sci. Gott. 9: 46–74. 1789, which has no accompanying plates. Combined, the two journal papers by

George Forster are 62 printed pages plus 8 unpaginated plates. The journal title page is dated 1789. The entire volume 9 was reviewed in Gottingische Anzeigen 1789 (83): 833. 23 May 1789 (Moore 1971), thus the two included George Forster papers are dated as earlier than 23 May 1789.

Nicolson and Fosberg (2004: 57, 65), however, cited this as a 62-page preprint, doing so seemingly as two separately presented publications: pages 1–33 the "Fasciculus Plantarum Magellanicarum," and pages 34–62 as "Plantae Atlanticae ..." Page 34 of the second George Forster segment of the hypothetical 62-page preprint is presumably the verso of page 33, so the parts of the preprint are presumably not wholly independent papers. A 62-page preprint would shift forward by two pages all binomial page citations as opposed to those in the '64-page TL-2/1824 preprint.' I do not adopt the abbreviation "Fasc. pl. magell." suggested by Stafleu and Cowan (1976) for the Tussilago trifurcata-containing preprint. This is because Tussilago trifurcata is on page 38 of volume 9 of the journal, on page 28 of a 64-page preprint, and presumably on page 26 of a hypothetical 62-preprint. The prior listings of the two (or three) variants of the paper each abbreviated "Fasc. pl. magell." is not acceptable bibliographically. Pritzel (1851: item 3285; 1872: item 2977) on the other hand, gave the preprint as "64 p." but more or less used the title spelled-out as cited by Nicolson and Fosberg (2004: 65) for the hypothetical 62-page preprint. The Stafleu and Cowan (1976) citation of "MO" having this item in its library holdings may have been in error. I was unable to locate an independently paginated preprint at MO (including the William Trelease collection) and the only copy seen by me is a pdf of the GOET holding. I avoid not the arguably dull subjects of nomenclatural priority, signatures, and chain lines [see also discussion in the Forster 1788 citation in my Literature Cited] because of the historic significance attached to most things Captain James Cook-related.

IPNI in 2021, except in three cases, seems to index G. Forster names in the Commentationes-De Plantis-Fasciculus-Plantae Atlanticae journal-preprint as appearing in the journal, i.e., Commentat. Soc. Regiae Sci. Gott. volume 9. Today, IPNI has two entries for Tussilago trifurcata, one is "Fasc. Pl. Magell. 9: 28" and the other "Commentat. Soc. Regiae Sci. Gott. 9: 39 (1789)." Tussilago trifurcata is on page 38 of the journal (as given correctly by Cabrera 1949), not on page 39 as in IPNI today and as in Jackson (1895). The two other instances where I find IPNI citations using Fasciculus Plantarum Magellanicarum are for "Borago tristis G.Forst., Fasc. Pl. Magell. 51 (1788)" and "Teucrium canescens G.Forst., Fasc. Pl. Magell. 58 (1788)." The Borago tristis and Teucrium canescens citations merge incorrectly one of the two suggested titles of the independently paginated preprint and the journal paginations. In the independently paginated '64-page TL-2/1824 preprint' the correct citations are instead pages 41 and 48, but in the hypothetical 62-page preprint pages 39 and 46, respectively. Examination of the 64-page TL-2/1824 preprint titled "De plantis"... "in hand with the journal version in hand seems to show that in 2021 IPNI is inconsistent in citation of the G. Forster names. The citation of "Fasc. Pl. Magell. 9: 28" is certainly erroneous, as the preprint of the paper does not have 9 volumes.

Haplosticha trifurcata (G. Forst.) Pruski type collection notes. In the type series of Tussilago trifurcata, Nicolson and Fosberg (2004) cited five specimens: BM-Pallas, BM-Lambert [these two BM specimens are mounted on a single sheet], P-Buffon, UPS-Thunberg, and W-Jacquin. Freire et al. (2014) cited the non-existent "Fasc. Pl. Magell. 9: 28" that is not linked directly to Tussilago trifurcata, and specimens in K and P. It appears that P-Sprengel is a different sheet than P-Buffon, and that the sheets cited by Freire et al. (2014) were not among the five specimens on four sheets in the type series cited by Nicolson and Fosberg (2004). I now see an eighth specimen, a S sheet from the Montin herbarium, raising to eight specimens on seven sheets the numbers listed in my typology above. Because in just the past two decades, numbers of specimens have increased from five to seven and now to eight, it seems possible that further authentic plants may exist; nevertheless, I designated a lectotype collection and sheet herein, although the identity of the species is clear. The Forsters had apparently several plants of *Tussilago trifurcata* unmounted in a folder, and for this and other species gave away apparently individual plants at several times both while in England (on two occasions Joseph Banks was given sets of duplicates) and at times when they visited and/or lived in continental Europe. Nicolson and Fosberg (2004) mention that in 1780, George Forster's "books and herbarium had been lost in a shipwreck," but that by 1872 Joseph Banks had returned some duplicates to George Forster. As such, other than for where plants are shown to be unicates, there is often no clear holotype of Forster names (Fosberg 1993; Nicolson and Fosberg 2004).

The Kew lectotype sheet of *Tussilago trifurcata* is by far the most ample of the few sheets known to me. Nicolson and Fosberg (2004) point out that Forster materials are cited as "Forster." I take the Forster material of Tussilago trifurcata as of a single gathering, even though dates of 25 December 1774 and 27 December 1774 have at times been given. Another original element is a George Forster unpublished drawing from fresh material, which is hard to match to any of the 14 individual pressed plants known to me from the lectotype collection series. The Anderson s.n. (BM) sheet was collected basically at the same time and seen possibly by the Forsters in the field. When the species was described more than a dozen years after collected, the Anderson plant was not in front of George Forster, who by then had already been 'encouraged' by the Admiralty and circumstances to leave England, and was living in Germany. The Anderson plant, while from the Captain Cook second voyage materials, and listed by Nicolson and Fosberg (2004), never was a prime candidate for lectotype. William Anderson, who later bequeathed whatever collections he made to Joseph Banks, was a surgeon's mate, Johann Reinhold Forster (the father) the naturalist, and Forster's 17-year-old (at the time of departure) son George Forster the biological illustrator on Captain Cook's second voyage (Nicolson and Fosberg 2004). A general account of the Forster collections was given by Britten (1885), and the very thorough Nicolson and Fosberg (2004) is a name-by-name study of the James Cook voyage Forster specimens. Further aspects of these collections and herbaria holding Forster specimens are given in Lambert (1811), Merrill (1954), Marshall (1979), and Fosberg (1993).

The Kew lectotype was presumably intended by Freire et al. (2014) to be linked to Tussilago trifurcata, but their citation appears to not include a direct basionym reference. Rather their citation is the same as the one of the two IPNI literature citations, which itself is seemingly incorrect. Freire et al. (2014) and IPNI cited "Fasc. Pl. Magell. 9: 28, no. 24 1787," which combines elements apparently from two/three references: (1) the title of the first paper using the suggested TL-2/1824 abbreviation, but not the "special" title of the 64-page preprint, (2) the volume of the journal but not the journal title, and (3) page 28 of the 64-page preprint pagination, whereas the journal volume 9 page is 38. Freire et al. (2014), Jackson (1895), and IPNI listed "Senecio trifurcatus (G. Forst.) Less., Syn. Gen. Compos. 392. 1832" for the species, where the inferred binomial combination in Senecio does not actually appear. Freire et al. (2014) treated the plant as S. trifurcatus Less., but include neither a correct nor direct reference to that name either. The combination Senecio trifurcatus instead first appeared in Candolle (1837), and was attributed as such by Hooker and Arnott (1841: 341).

The rosette leaves of the monocephalous Haplosticha trifurcata (G. Forst.) Pruski are cuneate and 3-5-lobed distally and the peduncular bracts usually linear, although on rare occasions they too may be cuneately trifid. Hooker (1847: fig. 108, right; reproduced here as figure 21) provided a fine illustration, said the plant was "abundant," and collected by "Banks and Solander, and all succeeding voyagers." Hoffmann et al. (1998) gave the common name of "senecio blanco" for Haplosticha trifurcata, and provided a fine color illustration by Andres Jullian of the plant. Field images labeled Senecio trifurcatus are in several Patagonian field guides, and Haplosticha trifurcata is moderately well-represented in major herbaria. Dusén (1900), Macloskie (1905–1906: 859, fig. 102), Cabrera (1949, 1971, Cabrera et al. 1999), and Moore (1983) treated the plant as Senecio trifurcatus (G. Forst.) Less. ex DC. Haplosticha trifurcata is endemic to southern Argentina and southern Chile from Neuquén and Río Negro Argentina and La Araucanía Chile at about 38° South latitude, south to the Tierra del Fuego archipelago at the extreme southern tip of the continent of South America.

HAPLOSTICHA ZOSTERIFOLIA (Hook. & Arn.) Pruski, comb. nov. Senecio zosterifolius Hook. & Arn., J. Bot. (Hooker) 3: 342. 1841 (as zosteraefolius). Type: CHILE. Margins of the laguna de Ranco near Valdivia, s.d., Bridges 632 (holotype: K barcode 527546; isotypes: E, E ex GL the Arnott sheet but without binomial, M). [The holotype is the only sheet with both the binomial and the full locality data of the protologue, and appears to be the sole element used in the protologue description; the E ex GL isotype appears to be the Arnott herbarium sheet, but does not bear an annotation with the binomial]. Figure 22.

Haplosticha stolonifera Phil., Senecio cotuloides Reiche, Senecio graminifolius Sch. Bip. ex Phil., Senecio potamogetonifolius Sch. Bip., Senecio uliginosus Phil.

Philippi (1859: 193) treated what I call Haplosticha zosterifolia (Hook. & Arn.) Pruski as Haplosticha stolonifera, the generitype of his Haplosticha. Remy (1849: 203), Bentham and Hooker (1873), Klatt (1888), Reiche (1905: 153, and also on page 155 as Senecio cotuloides Reiche, a

synonym), Cabrera (1949: 333), and Cabrera (1971: 232) each treated Haplosticha zosterifolia within Senecio. Perezia lactucoides (Vahl) Less. (tribe Nassauvieae) is fairly similar to Haplosticha zosterifolia in general aspect. Haplosticha zosterifolia is endemic to Argentina and Chile, being known only from Neuquén and Río Negro, Argentina and Valparaíso south to Valdivia in Los Lagos, Chile (Cabrera 1949, 1971; Cabrera et al. 1999). As such, Haplosticha zosterifolia does not apparently extend to the tip of the continent in Tierra del Fuego (viz Dusén 1900; Macloskie 1905-1906; Cabrera 1971; Moore 1983).



Figure 22. Representative specimen showing the monocephalous capitulescences and linear leaves of Haplosticha zosterifolia (Hook. & Arn.) Pruski, which includes in synonymy the generitype, *Ĥaplosticha stolonifera* Phil. (Seijo 2206, MO).

6. IOCENES B. Nord., Opera Bot. 44: 58. 1978. Type: Senecio acanthifolius Hombr. & Jacquinot 1845 non (Rchb.) Kostel. 1833. [= *Iocenes virens* (Phil.) Pruski]. Figures 23–24.

Senecio sect. Acanthifolium Cabrera.

Species. Monotypic, contains only *Iocenes virens* (Phil.) Pruski.

Iocenes (Figs. 23–24) is a perennial leafy-stemmed herb, has lobed leaves, uniseriate conical trichomes (type 2d, 2f in Jeffrey 1987; Jeffrey 1992), and is pluricapitulate with relatively small erect ecalyculate white-rayed capitula with linear subcalycular bracts (viz Nordenstam 1978: fig. 27; Cabrera 1949: fig. 1; Cabrera 1971: fig. 256). Further distinguishing floral features of *Iocenes* include semisagittate-based (auriculate, ecaudate) anthers, white ray corollas (Fig. 24), yellow disk corollas, appressed-fused-penicillate-appendiculate disk styles that have abaxially a single central, short, mamillose line distally (Nordenstam 1978: fig. 27; Salomón et al. 2016: fig. 1b), and glabrous 10-ribbed cypselae. The excellent line drawing in Cabrera (1949) is reproduced by Freire et al. (2014), but Cabrera (1971) also provided a second, different, fine line drawing for this remarkable plant. Similarly, newly resurrected *Haplosticha* is also white-radiate-capitulate.

Cabrera (1949, 1979), Freire et al. (2014), and Rodríguez et al. (2018) each used the name Senecio acanthifolius for what is called here Iocenes virens (Phil.) Pruski. The single species of *Iocenes* has a diploid chromosome number of 2n = 40 (Jeffrey 1992: 76; Cabrera 1999: 57). I agree with Pruski (2018) and resurrect formally Nordenstam's monotypic *Iocenes*.

Iocenes has erect, radiate capitula and is not a member of discoid, nutant-capitulate Aetheolaena-Culcitium-Lasiocephalus generic group. Cabrera (1949) treated the species as the sole species of monotypic Senecio sect. Acanthifolium, a section treated by Nordenstam (1978, 2007) at the generic rank as monotypic Iocenes. Iocenes virens (as Senecio acanthifolius) is the first of 208 species Cabrera (1949) revised in Chile, and it is common knowledge that Cabrera often treated the most extreme-aberrant species first in non-alphabetical floras.

IOCENES VIRENS (Phil.) Pruski, comb. nov. Senecio virens Phil., Anales Univ. Chile 88: 259. 1894 [species #78]. Iocenes acanthifolius subsp. virens (Phil.) B. Nord., Opera Bot. 44: 59. 1978. Senecio acanthifolius subsp. (Phil.) virens Cabrera & Zardini, Darwiniana 22: 453. 1980. TYPE: CHILE. Valle del río Palena, Jan-Feb 1887, Delfin s.n. (holotype: SGO). Figures 23-24.

Iocenes acanthifolius B. Nord. 1978 [intended as a new comb. based on the illegitimate 1845 binomial], Senecio acanthifolius Hombr. & Jacquinot 1845 nom. illeg. non (Rchb.) Kostel. 1833, Senecio auriculatus Albov 1896 non Burm. f. 1768, Senecio ombrophyllus Skottsb. 1906.

Iocenes virens (Phil.) Pruski is endemic to Patagonian Argentina and Chile, where it is found from 200-1500 m elevation (Cabrera 1949, 1971; Nordenstam 1978; Cabrera et al. 1999; Rodríguez et al. 2018). Remy (1849: 198), Dusén (1900: 109), Macloskie (1905-1906: 837), Macloskie and Dusén (1914: 267), Cabrera (1949), and Moore (1983: 251) treated the plant as Senecio acanthifolius. Senecio acanthifolius (species 9) and S. auriculatus (species 12) were by their glabrous fruits keyed closely by Reiche (1905) as members of his herbaceous white-radiate group I, whereas S. virens (species 37) was placed in his radiate pinnatilobe-leaved group V but without ray corolla color stated by Reiche. Macloskie and Dusén (1914: 278) also recognized S. virens.

The synonymy more or less followed here is that of Angel Cabrera (1949; Cabrera and Zardini 1980; Cabrera et al. 1999) and Nordenstam (1978), except that Cabrera and Nordenstam recognized two infraspecies, the atypical one being called S. acanthifolius subsp. (Phil.) virens and Iocenes acanthifolius subsp. virens (Phil.) B. Nord., respectively. Rodríguez et al. (2018: 180) did not recognize infraspecies, and listed S. acanthifolius as including in synonymy S. virens and its homotypic nomenclatural synonyms S. acanthifolius subsp. virens and Iocenes acanthifolius subsp. virens. Calvo and Morales-Fierro (2021) noted correctly that S. acanthifolius Hombr. & Jacquinot (used in Reiche 1905; Cabrera 1949; Cabrera et al. 1999) is an illegitimate later homonym antedated by the Kosteletzky name. Nordenstam (1978) intended to make a new combination, but *Iocenes* acanthifolius B. Nord. is a nom. nov. (replacement name) having 1978 as a starting date for its

priority. The nomenclaturally correct name in *locenes*, given my acceptance of the species synonymy in Cabrera (1949; Cabrera and Zardini 1980; Cabrera et al. 1999) and Nordenstam (1978), is *Iocenes* virens based on the senior available taxonomic synonym.

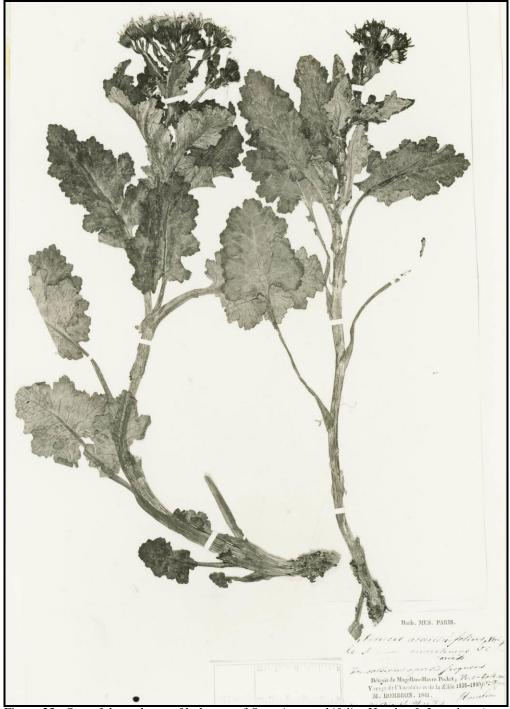


Figure 23. One of three sheets of holotype of Senecio acanthifolius Hombr. & Jacquinot (= Indice 25. One of three sheets of holotype of senects deduning that Ironiof. & sacquinot (= Iocenes virens (Phil.) Pruski). This is the most robust of the three type sheets, is now bar-coded as 2296163, and is now (mis)marked with a generic Paris "isotype" sticker. The full label seen in this image was glued subsequently onto the P sheet bar-coded recently 2296161, an incomplete sheet that is now marked with generic Paris "type" sticker. (MO phototype of Field image 37897 of Hombron s.n., P).



Figure 24. *Iocenes virens* (Phil.) Pruski showing the white ray corollas. (Chile, Magallanes, *Solomon & Solomon 4678*, photograph by James Solomon).

TYPE: PERU. Pasco. Oxapampa. Dist. SENECIO VASQUEZII Pruski & R. Ortiz, sp. nov. Huancabamba, P.N. Yanachaga-Chemillen, Sector Santa Barbara, bosque montano con abundante Chusquea, 10° 20' 06" S, 75° 38' 42" W, 3340 m, 11 Mar 2004, R. Vásquez & A. Monteagudo 30000 (holotype: MO-6956060; isotypes: AMAZ, F, OXA, US, USM). Figures

Herbae perennes subrosulatae 0.6-1.2 m altae, caules erecti simplices pauce costati lanatoarachnoidei ad basem dense foliosi; folia simplicia alterna petiolata vel distale subsessilia; folia basilaria et inferiora 15-40 × 1-2.8 cm (lamina et petiola) lamina anguste oblanceolata, subcarnosa vel crasse chartacea pinnatim venosa basi longe attenuata margine integra vel pauce serrulata apice anguste acuta vel acuminata discolorata supra glabrata virida laevis subtus dense niveo-lanato-tomentulosa, nervo medio conspicuo glabrato, petiolo usque 10 cm longo; folia caulinaria simillima sed subsessilia pauca  $2-10 \times 1-2$ cm lanceolata vel ovata basi late amplectentia serrulata apice anguste attenuata parce floccoso-arachnoidea vel glabrata; capitulescentia cymosa vel laxe pauce corymbiforma 3–16-capitulata 10–15 cm lata bracteata, pedunculi 1.5–6.5(–10) cm longi parce floccoso-arachnoidei, bracteolis 0–2; capitula heterogama radiata usque circiter 17 mm longa magni calyculata; involucrum 12-15 × 10-15 mm, late campanulatum; phyllaria 17-21 subaequalia 14-15 × 1.5-2 mm lanceolata basi parce floccosoarachnoidea margine integra apice acuminata vel attenuata; bracteolae calyculi  $\leq 11$ ,  $1\hat{1}-17 \times 3-7$  mm ovato-pyriformae vel ovato-lanceolatae margine serrato-dentatae apice cuspidato-attenuatae; clinanthium epaleaceum 4-6 mm latum valde fimbriato-alveolatum, squamae 1-1.7 mm longae; flosculi radiati pistillati 17–20, corolla 20–26 mm longa luteola glabrata tubo 5–6 mm longo, limbo 15–20 × 3–4 mm 7– 9-nervio; flosculi disci hermaphroditi 84–138, corolla 7.9–9.5 mm longa tuboloso-infundibuliforma luteola glabrata quinquelobata, tubus 3.5-4.2 mm longus, lobi 0.9-1.1 mm longi longe triangulares, antherae ecaudatae 2.5–2.7 mm longae collum basi dilatatum, styli rami 1–1.2 mm longi truncati areis stigmaticis discretis; cypselae 1–1.5 mm longae glabratae; setae pappo 8.5–9.5 mm longae.

**Perennial subrosulate rhizomatous herbs** 0.6–1.2 m tall; stems 1–few from rhizome, erect, simple and only becoming few-branched in capitulescence, 0.4–0.9+ cm diam. proximally, sheathed by overlapping rosette leaf bases, exalate, few-costate, loosely lanate-arachnoid pubescent, purplish proximally grading to pale green distally, several rosette leaves present at anthesis and not withered, stem leaves few, quickly reduced distally towards capitulescence; rhizome thick, ca.  $6 \times 2$  cm, roots fibrous; trichomes of herbage simple, uniseriate, multicellular with elongate terminal cells (approaching those of Jeffrey 1987: 207, fig. 3d), the arachnoid indument on occasion spreading laterally to 3+ mm long near leaf axils. Leaves simple, basal or alternate, long-petiolate proximally to subsessile distally, usually much longer than internodes. Basal-radical and proximal leaves several-many, ascending but often spreading-reflexed at curved petiole, 15-40 × 1-2.8 cm (blade and petiole), blade longer than petiole, narrowly oblanceolate, subcarnose or thick-chartaceous, venation pinnate, secondary veins 5–10+ per side becoming closely spaced distally, sometimes obscure, arching towards apex, base clasping stem, base long-attenuate, margins entire or very weakly few-serrulate, sometimes weakly revolute, apex narrowly acute to acuminate, discolorous, adaxial surface green and glabrous, smooth, abaxial surface (except midrib) closely white-lanate-tomentulose, midrib 1–2 mm diam., purplish and glabrous; petiole to 10 cm long, purplish, 0.5–0.7 cm diam. at mid petiole but broadened to sheathing pluri-parallel-nerved, base ca. 1+ cm diam. Midstem and distal bracteate leaves progressively fewer and increasingly more well-spaced, ascending, subsessile, mostly  $2-10 \times 1-2$  cm, lanceolate to ovate, broadest in proximal 1/4, chartaceous to thickchartaceous, green or loosely floccose-arachnoid, venation of 9-14 subparallel, strongly ascending thin secondary veins from base with midrib slightly thicker than secondaries, sometimes tertiary reticulations visible, base somewhat broad and clasping, distinctly few-several-serrulate proximally, otherwise entire, teeth spreading or ascending, mostly 0.5–1 mm long, apex narrowly attenuate, surfaces slightly discolorous to concolorous, adaxial surface green and glabrous throughout or loosely floccose-arachnoid at apex, abaxial surface paler and loosely floccose-arachnoid to glabrate. **Capitulescence** terminal, cymose or laxly corymbiform, 3–16-capitulate, broadly rounded, mostly 10-15 cm broad, branches and branchlets striate-costate, loosely floccose-arachnoid, bracteate with a single bracteate leaf subtending each branch and branchlet, sometimes also 1-2-bracteate at midpeduncle, capitula erect; peduncles 1.5–6.5(-10) cm long, striate-costate, loosely floccose-arachnoid becoming more densely so distally, 0–2-bracteate, bracts mostly ca.  $2 \times 0.7$  cm, glabrous or surfaces loosely arachnoid-pubescent proximally. Capitula heterogamous, radiate, to ca. 17 mm long, relatively large, > 100-150-flowered, long-calyculate, central disk convex or dome-shaped, disk florets not well exserted; involucre  $12-15 \times 10-15$  mm, broadly campanulate; phyllaries 17–21, subequal, 14–15 × 1.5–2 mm, lanceolate, loosely floccose-arachnoid at base just adaxial to calycular bract bases, otherwise basically glabrous except at the crisped-setulose apex and along the ciliolatefimbriate margins, margins otherwise entire, the green mid-zone often with 3 prominent resin ducts, mid-zone about as broad as or broader than hyaline stramineous margins, apex acuminate to attenuate, concolorous with green midzone, not blackened apically; calyculus spreading-cupular but pressing as though appressed; calycular bracts  $\leq 11$ , in 1–2 loosely overlapping series,  $11-17 \times 3-7$ mm, the outer ones ovate-pyriform and inner ones ovate-lanceolate, all chartaceous, ultimately glabrate throughout but initial very loosely floccose-arachnoid, venation of 7–13 subparallel veins from the relatively broad base, margins serrate-dentate, teeth 6–10 per margin, 0.1–0.5 mm long, apex cuspidate-attenuate; clinanthium epaleate, 4-6 mm diam., convex, surface glabrous, fimbriatealveolate especially peripherally, enations 1–1.7 mm long, linear to linear-lanceolate; phoranthium solid (non-fistulose) but not densely so. **Ray florets** pistillate, 17–20; corolla 20–26 mm long, lemon-yellow, glabrous, limb well-exserted, tube 5–6 mm long, limb 15–20 × 3–4 mm, oblanceolate, 7–9-nerved, apex narrowed with minute denticulations, not at all obviously denticulate. **Disk florets** bisexual, 84-138; corolla 7.9-9.5 mm long, tubular-funnelform, only weakly ampliate above tube, yellow, glabrous, 5-lobed, tube 3.5–4.2 mm long, slightly shorter than limb, tube and throat nearly subequal, limb 5-veined but medial resin ducts visible in lobes, throat 3.5–4.2 mm long, lobes 5, 0.9– 1.1 mm long, long-triangular, margins minutely papillose; anthers ecaudate, 2.5–2.7 mm long, filament collar balusterform, 0.3-0.4 mm long, endothecial tissue radial, apical appendage 0.3-0.5 mm long, narrow-lanceolate; style base gradually dilated, free from nectary, stylopodium (swollen style base) ca. 0.2 mm long, style branches exappendiculate, 1–1.2 mm long, stigmatic surface 2banded, apex truncate, abaxially with an apical semicircle of short-papillae; nectary small. Cypselae (immature) 1–1.5 mm long, terete, brownish, ca. 10-striate, glabrous; pappus bristles numerous, 8.5– 9.5 mm long, white. Chromosome number unknown.



Figure 25. Capitula of Senecio vasquezii Pruski & R. Ortiz, showing the cupular calycular bracts spreading of capitula at bottom on image, the upper capitulum showing the yellow ray corolla limbs. (Vásquez & Monteagudo 30000, photograph of the type population by Rodolfo Vásquez and Abel Monteagudo).



Figure 26. Close-up of the cymose capitulescence of holotype of Senecio vasquezii Pruski & R. Ortiz. (Vásquez & Monteagudo 30000, MO).

Paratype. PERU. Huánuco. Tambo de Vaca, wet slopes, 3960 m (as 13000 ft), 10–24 Jun 1923, Macbride 4429 (MO). Macbride 4429 (MO) was determined in schedula by Greenman as Senecio comosus Sch. Bip. (Figs. 31-32) and by Cabrera as Senecio comosus var. blancus Cuatr. Typical S. comosus is known from Tambo de Vaca (e.g., Macbride 4353, MO), but Macbride 4429 has bracteate-capitula (Fig. 29A) with lacerate-alveolate clinanthia, and is thus referred to S. vasquezii.

**Eponymy.** Rosa Ortiz and I are pleased to dedicate the striking *Senecio vasquezii* to Rodolfo Vásquez, our friend, colleague, and professor. Rodolfo Vásquez has made more than 44000 collections in Peru, including the type of Senecio vasquezii, and it is altogether fitting and proper for us to dedicate this undescribed species to him. One of us (RO) has known Rodolfo for nearly four decades: in the 1980s when Rosa Ortiz was an undergraduate student at UNAP in Iquitos, Rodolfo Vásquez was one of her botany instructors. Rodolfo Vásquez also illustrated the late Al Gentry's northwestern South America Field Guide (Gentry 1993). Rodolfo Vásquez is well known for his Flórula de las reservas biológicas de Iquitos, Perú (Monogr. Syst. Bot. MBG volume 63: 1-1046. 1997). More recently, Rodolfo Vásquez was first author on Flora del Río Cenepa, Amazonas, Perú (Monogr. Syst. Bot. Missouri Bot. Gard. volume 114. 2010). While in Lima in 2018 visiting with Rocío and Rosa, I commented to Rodolfo that upon collection he must have realized Senecio vasquezii was a species new-to-science; and in the next breath I asked why did he number the collection 30000? Rodolfo smiled slyly, and replied because it was after 29999.



Figure 27. Holotype of *Senecio vasquezii* Pruski & R. Ortiz, the specimen is now mounted with this side face-down. (*Vásquez & Monteagudo 30000*, MO).



Figure 28. *Senecio vasquezii* Pruski & R. Ortiz, showing its subrosulate habit. (*Vásquez & Monteagudo 30000*, photograph of the type population by Rodolfo Vásquez and Abel Monteagudo).

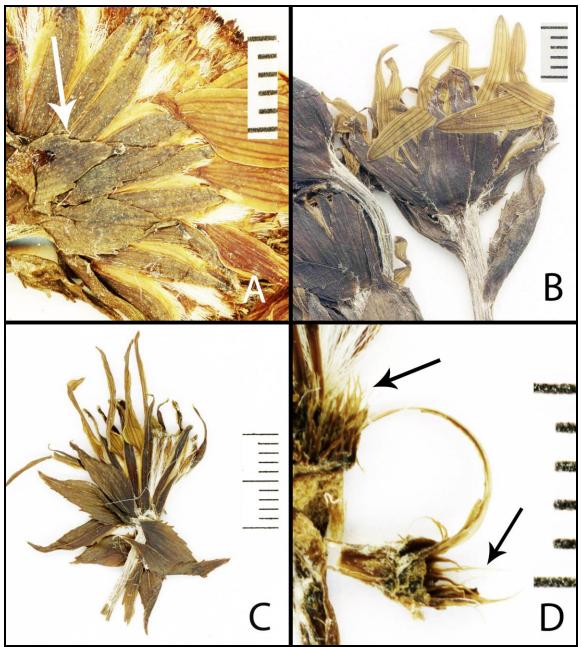


Figure 29. Bracteate capitula of Senecio vasquezii Pruski & R. Ortiz, showing the serrulate bracts and the 6-9-nerved ray corolla limbs. A. Capitulum pressed with calycular bracts (arrow) folded and directed towards the right. B. Capitula with calycular bracts pressed flat and partly obscuring phyllaries. C. Part of a dissected capitulum, rehydrated and repressed by me to show the spread-laterally ovate-pyriform calycular bracts. D. Fimbriate-alveolate clinanthium showing (arrows) the elongate squammose enations. (A Macbride 4429, MO, paratype; B-D Vásquez & Monteagudo 30000, MO, holotype). A metric scale is on the right of each image.

Distribution and ecology. Senecio vasquezii is known only from two high-elevational localities on the eastern slopes of the Andes in Central Peru on both sides of the Huánuco-Pasco frontier. The northern station in Huánuco is about 50 km east of the city of Huánuco, and the southern locality in Pasco is about 40 kms northwest of Oxapampa. These two known stations are about 35 kms apart. The plant was collected from 3340-3400 m elevation and grows in open areas on wet slopes of the bosque montano zone.



Figure 30. Habit of discolorous-leaved Costa Rican Senecio hansweberi Cuatr., one of two Central American species that Cuatrecasas placed in Senecio sect. Culcitiopsis "subsect. Radiati." Senecio hansweberi is characterized by its 13 (vs. 17–20) ray florets per capitulum and setulose (vs. glabrous) cypselae, thereby differing from Senecio vasquezii. (Cerro Chirripó, 3500 m, Pruski et al. 3912).

Key to Senecio vasquezii and similar regional Andean taxa of Senecio sect. Culcitiopsis subsect. Radiati Cuatr. hom. illeg. (1951: 74, non Senecio ser. Radiati Benth. 1867: 662, nec Senecio subsect. Radiati Cabrera 1949: 174)

- 1. Leaves usually discolorous; herbage not glabrate.
  - 2. Capitula with an obvious spreading-cupular calyculus, calycular bracts ovate-pyriform to ovate-lanceolate; clinanthia lacerate-alveolate, enations to 1.7 mm long
  - 2. Capitula without distinct cupular calyculus, calycular bracts lanceolate to less commonly
  - ovate-lanceolate; clinanthia weakly alveolate, enations usually < 1.2 mm long.
    - 3. Leaves consistently serrate ...... Senecio comosus var. blancus Cuatr.
    - 3. Leaves entire or sometimes serrulate or irregularly serrate.
      - 4. Leaves usually linear-lanceolate ...... Senecio comosus Sch. Bip.
      - 4. Leaves usually linear ...... Senecio coymolachensis Cabrera

Senecio vasquezii is placed among the six species and one non-typical variety (Cuatrecasas 1951, 1982) recognized within *Senecio* sect. *Culcitiopsis* "subsect. *Radiati* Cuatr.", which was described erroneously as "capitulis discoideis" by Cuatrecasas (1951: 74). The Cuatrecasas subsection is an illeg. homonym of at least both Senecio ser. Radiati Benth., Fl. Austral. 3: 662. 1867 and Senecio subsect. Radiati Cabrera (1949: 174) (viz ICBN 53.4, ICN 53.4); it seems possible that elsewhere another heterotypic infragenus of Senecio also used the epithet Radiati. In any event, the seven taxa of Cuatrecasas's "subsect. Radiati" are mostly South American, but S. hansweberi Cuatr. (Fig. 30) and S. kuhbieri Cuatr. are endemic to páramos on Cerro Chirripó, the tallest mountain in

Costa Rica. The Central American species each differ from S. vasquezii by their smaller stature, relatively small capitula with narrow calycular bracteoles, weakly alveolate clinanthia, longer pluribracteolate peduncles, and 12-14 ray florets per capitulum. From Senecio vasquezii, S. hansweberi is further distinguished by sparsely setulose cypselae and S. kuhbieri by flexuous stems. Members of this subsection were treated as Senecio ser. Culcitium in Cabrera (1985). Senecio comosus was treated as Senecio sect. Culcitium by Jeffrey (1992), but differs from Culcitium as now defined by always being subrosulate and with radiate capitula. Pelser et al. (2007) recovered with low support (BŠ < 50%) S. comosus and S. hansweberi in NWS clade 1, but not as sister taxa. Instead, Pelser et al. (2007) recovered radiate S. comosus and discoid S. culcitioides Sch. Bip. as sister, and both species are similar by their elongate discolorous leaves and subrosulate habit. In any event, because S. comosus, S. vasquezii, and similar species are truncate-styled, I follow precedent and recognize them as Senecio, and treat them in the subsection containing radiate species only as circumscribed originally by Cuatrecasas (1951). A key to South American members of Senecio sect. Culcitiopsis "subsect. Radiati" is given above.

The four South American species and one variety of Cuatrecasas's Senecio sect. Culcitiopsis "subsect. Radiati" include the relatively common and widespread Peruvian and Bolivian S. comosus Sch. Bip. (Figs. 31–32), and four uncommon Peruvian endemics: S. comosus var. blancus Cuatr., S. coymolachensis Cabrera, S. soukupii Cuatr., and now S. vasquezii Pruski & R. Ortiz. The adaxial leaf surfaces in young leaves are sometimes tomentose, but for the most part the leaves of these taxa are discolorous. Senecio vasquezii differs from the four other Andean taxa of Senecio sect. Culcitiopsis "subsect. Radiati" by its combination of discolorous, narrowly oblanceolate entire-margined proximal leaves (Figs. 27-28), loosely lanate-arachnoid stems, capitula with an obvious spreading-cupular calyculus of long and broad bracts (Figs. 25–26, 29), and lacerate-alveolate clinanthia with enations to 1.7 mm long (Fig. 29D). Cuatrecasas (1950) suggested in Senecioneae that a cupular calyculus functions effectively "as a multiseriate involucre," and Cuatrecasas (1978) noted that with increasing elevation the number and length of calycular bracts of some Senecioneae might increase. Nowhere else in Senecio sect. Culcitiopsis "subsect. Radiati," however, have such large cupular calycular bracts been seen, and although possibly under some environmental influence, they remain unmatched. Because alveolate clinanthia with short enations occur in disparate groups elsewhere in Senecioneae (e.g., Culcitium) the character is thus not apparently a priori of generic-level significance, but the extreme clinanthial enation development in S. vasquezii nevertheless appears to be useful in characterizing the species. Senecio vasquezii also has about equal numbers of phyllaries and rays.

Senecio comosus var. blancus is recognized as a distinct taxon, albeit treated in synonymy with S. comosus by Salomón et al. (2018). On the other hand, the synonymy of S. comosus var. debilis Cuatr. with S. comosus given in Salomón et al. (2018) is followed. Salomón et al. (2016: 12, fig. 2b; 2018) gave S. comosus as having a cylindrical filament collar, but instead it appears that the anther structure was misinterpreted and seen in adaxial (vs. abaxial) view from degraded material. The filament collars of S. comosus (viz Cabrera 1985: fig. 10f) and the other members of Senecio sect. Culcitiopsis "subsect. Radiati" are always balusterform, typical of subtribe Senecioninae.

Senecio vasquezii in stem and leaf character seems to resemble most closely S. comosus, placed by Cuatrecasas (1951, 1982) and Cabrera (1953) in Senecio sect. Culcitiopsis "subsect. Radiati." Senecio comosus differs technically from S. vasquezii by its merely moderately narrowly calyculate (non-cupular calyculate) capitula and its weakly alveolate clinanthia, which have not been seen to be as lacerate as in the new species. North-Peruvian S. coymolachensis is a plant of small stature, has linear leaves, and narrow calycular bracts, thus differing from S. vasquezii. Although in Leymebamba, Amazonas and adjacent La Libertad, Peru a very few plants seem intermediate between S. coymolachensis, S. comosus, and S. vasquezii, all three species are taken by me as distinct.

The protologue of S. coymolachensis (Cabrera 1953) noted it as similar to S. comosus, thus aligning it indirectly with the other taxa of Cuatrecasas's subsection. Radiate Senecio coymolachensis, however, also seems very similar to discoid Senecio bolivarianus Cuatr. A second radiate-discoid species pair is the aforementioned radiate S. comosus and discoid S. culcitioides pair; herbarium material of the two species are often misdetermined as each other. Senecio sect. Culcitiopsis "subsect. Radiati" defined in part by radiate (never discoid) capitula, thus may prove to be delineated artificially. Indeed, Jeffrey (1992) and Beltrán and Galán de Mera (1996) placed both

discoid Culcitium canescens Bonpl., the generitype of Culcitium, and radiate Senecio comosus within Senecio ser. Culcitium, further downplaying the radiate vs discoid distinction. Nevertheless, Senecio sect. Culcitiopsis "subsect. Radiati" is treated here as in Cuatrecasas (1951), and Senecio vasquezii finds it most similar congeners among the species treated by Cuatrecasas in this subsection.



Figure 31. Isotype of Senecio comosus Sch. Bip., an entire-margined discolorous-leaved radiate-capitulate species treated by Jose Cuatrecasas (1951) in *Senecio* sect. *Culcitiopsis* "subsect. *Radiati*." (*Lechler 2051*, NY).



Figure 32. *Senecio comosus* Sch. Bip. of *Senecio* sect. *Culcitiopsis* "subsect. *Radiati*." This field image is from material collected in Junín, Peru at 4200 m elevation, and shows the discolorous entire leaves and non-bracteate yellow-flowered radiate capitula. (Peru, Junín, 4200 m, *Valenzuela* 28883, photograph by Luis Valenzuela).

Regional endemic (centered in Cusco and Junín, Peru) S. soukupii is also similar to S. vasquezii, but S. soukupii differs by glabrate herbage and main stem leaves mostly concolorous and serrulate. The general aspect of S. soukupii approaches that of S. comosus. Other than in S. soukupii s.str., deciduous floccose indument has been seen by me in material of the subsection only in the strange collections of nearly concolorous-leaved relatively small-capitulate Ochoa 2006 from Junín and discolorous-leaved very large-capitulate Valenzuela et al. 6368 from Cusco, both with reservation determined by me as S. aff. soukupii, although they seem to be different from it and from each other.

Among the other South American taxa of Senecio sect. Culcitiopsis "subsect. Radiati," herbage with deciduous floccose indument is rare, and only S. comosus var. blancus has consistently serrate leaves. I do not have the type of S. comosus var. blancus in front of me at present, however, and judgments on identities of two aberrant collections of the subsection, Ochoa 2006 and Valenzuela et al. 6368, are withheld. By its serrate discolorous leaves, S. comosus var. blancus seems to differ from both S. comosus and S. soukupii, albeit simultaneously seemingly intermediate with them. The serrate leaves and narrow calycular bracts that serve to distinguish S. comosus var. blancus conflict with those of the newly described S. vasquezii. Ochoa 2006 has moderately discolorous serrate leaves, seems intermediate between S. comosus and S. soukupii, but differs by unusually leafy stems with two distal nodes each with three nearly opposite bracteate leaves. Valenzuela et al. 6368 has floccose adaxial leaf surfaces, minutely serrulate leaf margins, relatively broad calycular bracts, and a nearly monocephalous capitulescence with capitula twice as large as seen normally in the subsection: it seems intermediate between S. comosus var. blancus and S. soukupii.

Senecio comosus var. blancus, S. coymolachensis, S. soukupii, and the paratype of S. vasquezii, have at times each been taken as S. comosus or as intermediate with it. The recognition of these five South American taxa, coupled with recognition of Costa Rican S. hansweberi (Fig. 30) and S. kuhbieri, tighten the limits of S. comosus. The plant stature and pubescence help to define the above earlier described three species, but these features are at times influenced environmentally. Senecio comosus var. blancus, S. coymolachensis, and S. soukupii, are recognizable generally, but on occasion intermediate plants with abortive pollen have been seen. I have not studied pollen fertility in either Ochoa 2006 or Valenzuela et al. 6368, which may prove to be hybrids. The newly described S. vasquezii differs from the four other South American taxa of Senecio sect. Culcitiopsis "subsect. Radiati" in capitular features, which are taken as reliable species markers. Senecio sect. Culcitiopsis "subsect. Radiati" is thus expanded and now includes seven taxa, five of these South American, albeit the status of *S. comosus* var. *blancus* appears to be unsettled.

Regional Andean radiate species resembling loosely S. vasquezii include the more northern Peruvian S. radiatus Cuatr., Colombian S. latiflorus Wedd., and Colombian S. niveoaureus Cuatr., which were placed by Cuatrecasas (1950) in Senecio sect. Latiflorus Cuatr. These three species have concolorous griseous-lanate-tomentose leaves throughout, thereby differing from discolorous-leaved S. vasquezii, and have an aspect similar to regional Andean species of Culcitium. Senecio romeroi Cuatr. from Sierra Nevada de Santa Marta, Colombia is radiate-capitulate, discolorous-leaved plant similar to S. vasquezii. Senecio romeroi, unplaced seemingly to section, is a somewhat leafystemmed plant with serrulate leaves, thereby differing from S. vasquezii.

Thus, the close relatives of S. vasquezii are relatively few, and in the central Andes, they are partly over-shadowed the many often-nodding discoid-capitulate and disciform-capitulate species. For example, the widespread (Colombia south to Bolivia) subrosulate perennial herb, discoid S. culcitioides has narrowly elongate discolorous leaves, as mentioned above is very similar in gestalt to and misdetermined sometimes as radiate S. comosus. Greenman (1923) distinguished by capitula types discoid-capitulate S. culcitioides from radiate-capitulate S. comosus. In turn, from a distance discoid S. culcitioides appears similar to radiate S. vasquezii. Two other plants very similar to S. culcitioides are S. subculcitioides Cuatr. and S. summus Cuatr., which each may prove synonymous with S. culcitioides. Senecio calvus Cuatr. of the same alliance is nearly a dead ringer of S. culcitioides, except that is a glabrous plant, implying that pubescence traits may be fleeting. These discoid-capitulate species were treated by Cuatrecasas (1951) as Senecio sect. Culcitiopsis subsect. Discoidei Cuatr.

Cabrera (1985) recognized S. culcitioides as S. comosus var. culcitioides (Sch. Bip) Cabrera and placed it within Senecio sect. Senecio ser. Culcitium. Senecio culcitioides is treated as Senecio sect. Culcitium ser. Culcitiopsis in Jeffrey (1992). Not only is the indument variable and the capitular morphology interpreted variously, but the large size of Senecio as well as the artificial nature of the infragenera, may be inferred from this single taxon being treated as two different species and placed in three different infragenera by three (Cabrera, Cuatrecasas, and Jeffrey) prominent specialists.

Two regional Andean subrosulate species even less similar to radiate S. vasquezii are disciform-capitulate S. tenuisagittatus Cuatr. (Fig. 33A) and discoid-capitulate, S. tephrosioides Turcz. (Fig. 33B), both concolorous-leaved. Cabrera treated S. tephrosioides in Senecio sect. Crassicephali (syn., fide Cabrera 1985, Senecio sect. Hypsobates Cuatr.), and other than for its disciform capitula S. tenuisagittatus seems near S. ellenbergii of Senecio sect. Crassicephali. Each of the two aforementioned species further differs from S. vasquezii by their nodding capitula. Senecio tephrosioides is not known to me from Pasco, but is very similar to S. burkartii Cabrera, a leafystemmed, concolorous-leaved, discoid-capitulate species sympatric partly with S. vasquezii. Most of these discoid species in the above-mentioned groups are more widespread than S. vasquezii, and none resembles it closely.

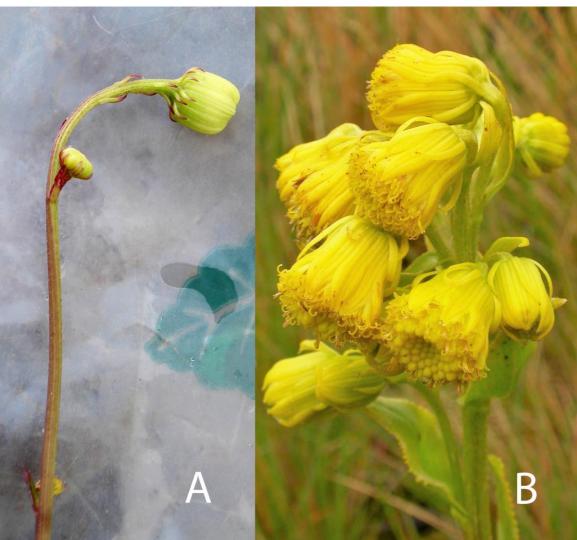


Figure 33. Select Andean subrosulate eradiate Senecios. These two species are nearly concolorous-leaved and have narrow calycular bracteoles. At a glance, they are distinct from cupular-calyculate, radiatecapitulate Senecio vasquezii. A. Senecio tenuisagittatus Cuatr. This disciform-capitulate species is almost sympatric wholly with S. vasquezii. B. Widespread Senecio tephrosioides Turcz. (A Peru, Pasco, 2700– 2800 m, Pruski, Ortiz, Vásquez, Castillo & Rivera 4358; B Bolivia, La Paz, 3900 m, Fuentes et al. 9817, photograph by Moises Mendoza).

SENECIO PEREZIOIDES Pruski, sp. nov. TYPE: BOLIVIA. La Paz. Parque Nacional Madidi, Queara, Lampayani alto, pajonal de yungas en ceja de monte superior pluvial, 4190 m, 14° 40' 43" S, 69° 06 '30" W, 14 Apr 2008, A. Fuentes, P. Paco & R. Canaza 12528B (holotype: MO-6284883; isotype: LPB n.v.). Figures 34–36.

Herbae perennes subrosulatae 0.3–0.35 m altae, caules erecti simplices pauce glanuloso-hirsuti ad basem foliosi; folia simplicia alterna pinnatilobata anguste alato-petiolata vel distale sessilia; folia basilaria et inferiora 8–14 × 1.2–2.5 cm (lamina et petiola) lamina oblanceolata, chartacea pinnatim venosa margine 4–7 lobata apice acuta concolorata glanuloso-hirsuta; folia caulinaria 2–4, 4–7 × 1–1.5 cm simillima sed sessilia; capitulescentia cymosa 3-7-capitulata, pedunculi 1.5-4.5 cm longi; capitula heterogama radiata 10-15 mm longa calyculata; involucrum 9-11 × 10-15 mm late campanulatum; phyllaria circiter 21 subaequalia 9-11 × 1.5-2.9 mm lanceolata pauce glanuloso-hirsuta margine integra apice acuminata; bracteolae calyculi 8–11, 8–10  $\times$  2.5–4 mm pinnatilobatae margine 1–4 lobatae; clinanthium epaleaceum 3–5 mm latum; flosculi radiati pistillati 12–13, corolla 12.5–15.7 mm longa luteola glabrata, tubus 2.5–3.7 mm longus, limbo  $10-12 \times 2-3$  mm (3–)5-nervio; flosculi disci hermaphroditi circiter 132, corolla circiter 6.5 mm longa tuboloso-infundibuliforma luteola glabrata quinquelobata, tubus circiter 2 mm longus, lobi circiter 0.5 mm longi longe triangulares, antherae ecaudatae circiter 2 mm longae collum basi dilatatum; styli rami 1.5–2 mm longi truncati areis stigmaticis discretis; cypselae circiter 1.2 mm longae circiter 10striatae glabratae; setae pappo 6–6.5 mm longae.

**Perennial subrosulate herbs** 0.3–0.35 m tall; stems 1, erect, simple in proximal 2/3, fewbranched in capitulescence, to ca. 0.5 cm diam. proximally, exalate, ca. 8 costate, loosely glandularhirsute, several rosette leaves present at anthesis and not withered, the few stem leaves quickly reduced distally towards capitulescence, roots fibrous; herbage loosely glandular-hirsute, trichomes of herbage (approaching those of Cabrera 1985: 121, fig. 11b; Jeffrey 1987: 207, fig. 4a), 0.5-1 mm long, those of abaxial leaf midrib often the longest, multicellular, minutely gland-tipped, uniseriate stipe cells equal sized from base to apex. Leaves simple, basal or alternate, sessile or narrowly winged-petiolate, pinnatilobed about halfway to midrib, the distal leaves few shorter than internodes, the glandular-hirsute indument on the adaxial blade surfaces and on the midrib abaxially 0.5-1 mm long, trichomes shorter elsewhere on abaxial surface. Basal-radical and proximal leaves several, ascending, 8-14 × 1.2-2.5 cm (blade and petiole), oblanceolate in outline, chartaceous, venation pinnate, base 3-5-parallel-nerved and broadened or weakly clasping stem, margins mostly with 4-7 lobes per side, sometimes 1-dentate between lobes, lobes 0.3–1.5 cm long, forward directed, lobe margins entire to secondarily 2-5-lobed-dentate, apex acute, surfaces concolorous, glandular-hirsute, also sometimes weakly glandular-hirsute marginally; winged-petiolar base to 4 cm long. **Distal stem leaves** 2–4, ascending, sessile, mostly  $4-7 \times 1-1.5$  cm, otherwise resembling proximal leaves. Capitulescence terminal, open-cymose, 3-7-capitulate, branches and branchlets striate, loosely glandular-hirsute, few-leafy-bracteate, 1 leafy bract at each branch and branchlet base, 0-3-bracteate from branch base to capitulum, bracts 1.5–3.5 cm long, sessile, somewhat clasping, resembling stem leaves in shape, lobing, and indument, capitula erect; peduncles 1.5–4.5 cm long. heterogamous, radiate, 10-15 mm tall and broad, relatively large, > 140-flowered, calyculate, central disk convex, disk florets not well exserted; involucre 9-11 × 10-15 mm, broadly campanulate; phyllaries ca. 21, subequal,  $9-11 \times 1.5-2.9$  mm, lanceolate, the inner ones laterally overlapped and broader than outer, loosely glandular-hirsute, the green mid-zone 1-nerved with pinnately-arranged lateral nervelets visible adaxially in dried material, mid-zone narrower than to slightly broader than hyaline stramineous margins, apex mostly acuminate, somewhat papillose-setose, the green midzone narrow distally, not obviously blackened; calyculus ascending, bracts 8–11, ca. 1-seriate, 8–10 × 2.5– 4 mm, pinnatilobed-dentate with 1-4 lobes-teeth per margin, chartaceous, reticulate-nerved, loosely glandular-hirsute, marginal lobes 0.4–1.5 mm long, apex acute; clinanthium epaleate, 3–5 mm diam., flat, surface glabrous, low-alveolate. **Ray florets** pistillate, 12–13; corolla 12.5–15.7 mm long, lemon-yellow, glabrous, limb well-exserted, tube 2.5-3.7 mm long, limb  $10-12 \times 2-3$  mm, oblanceolate, (3–)5-nerved, apex narrowed, bidenticulate or even emarginate. **Disk florets** bisexual, ca. 132; corolla ca. 6.5 mm long, tubular-funnelform, only weakly ampliate above tube, yellow, glabrous, 5-lobed, tube ca. 2 mm long, much shorter than throat, throat ca. 4 mm long, 5-veined, lobes 5, ca. 0.5 mm long, triangular, no medial resin ducts visible in lobes, margins minutely papillose; anthers ecaudate, ca. 2 mm long, filament collar abruptly balusterform at very base, to ca. 1 mm long, the distal portion of collar much longer than swollen base, endothecial tissue radial, apical appendage 0.2-0.3 mm long, lanceolate; style base gradually dilated, free from nectary, stylopodium (swollen style base) 0.2–0.3 mm long, style branches exappendiculate, 1.5–2 mm long, stigmatic surface 2banded, apex truncate, with a few papillae in a semicircle. Cypselae (immature) ca. 1.2 mm long, terete, ca. 10-striate, glabrous; pappus bristles numerous, 6-6.5 mm long, white. Chromosome number unknown.

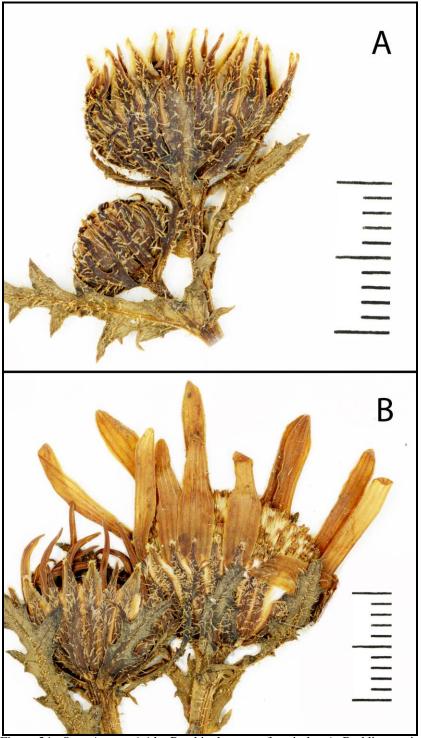


Figure 34. Senecio perezioides Pruski, close-up of capitula. A. Budding capitula showing glandular-hirsute indument of the leafy-bracts and phyllaries. B. Flowering capitula, that on right showing 11 exserted ray corollas. (*Fuentes et al. 12528B*, MO, holotype).

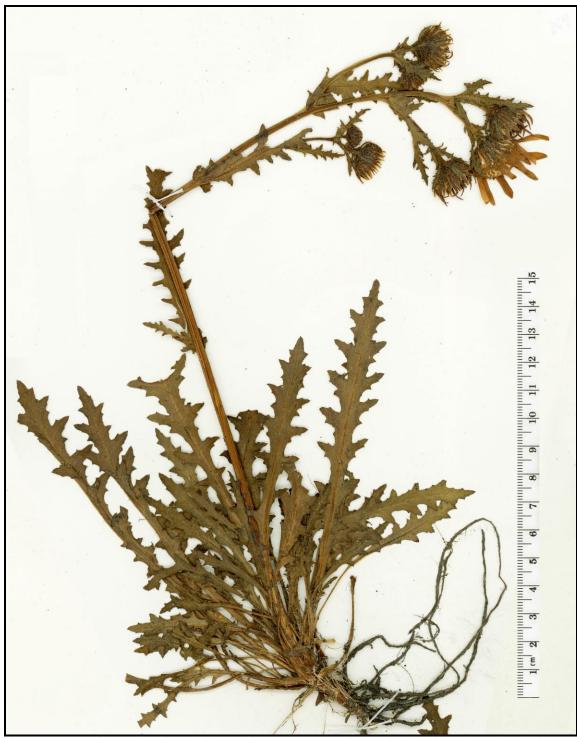


Figure 35. One of two plants from holotype of Senecio perezioides Pruski, showing subrosulate habit, pinnatilobed leaves, paucicapitulate capitulescence, and large radiate capitula. (Fuentes et al. 12528B, MO).

Etymology. The pinnatilobed leaves of Senecio perezioides recall those of some other South American Compositae (e.g., Perezia multiflora (H. & B.) Less. and Polyachyrus carduoides Phil. of tribe Nassauvieae), whence the epithet. Indeed, the holotype of Senecio perezioides, numbered by me as 12528B, was sent to MO mixed with, and labeled as, Perezia (Fuentes et al. 12528). I have not seen an isotype in LPB.



Figure 36. Senecio perezioides Pruski, a dissected capitulum with florets removed. This capitulum was rehydrated and repressed by me with phyllaries and pinnately lobed-dentate calycular bracts spread laterally. A. Abaxial (outer) surface of bracts and phyllaries. B. Clinanthium and adaxial (inner) face of phyllaries and their stramineous margins. (Fuentes et al. 12528B, MO, holotype).

**Distribution and ecology.** Senecio perezioides is known only from the type collection. The new species was discovered by Alfredo Fuentes in wet pajonal vegetation at 4190 m elevation, and flowers in April.

Glandular-hirsute indument, subrosulate habit, pinnatilobed leaves, radiate capitula, and glabrous cypselae (Figs. 34-36) characterize Senecio perezioides. These are nearly the same characters used by Lindley (1828) and Cabrera (1949) to characterize Chilean radiate-capitulate Senecio sect. Corymbocephalus subsect. Adenotrichi (Lindley) Cabrera (basionym Adenotrichia Lindley) (Fig. 37). It is near the ten species of this subsection, that species similar relatively to Senecio perezioides may be found. Senecio perezioides, however, differs clearly from the ten species of the subsection by its subrosulate habit.

Among the ten species of Senecio sect. Corymbocephalus subsect. Adenotrichi, Senecio perezioides would key in Cabrera (1949) to the three glabrous-fruited Chilean species (S. adenotrichius DC., S. murinus Phil., and S. rivularis J. Rémy) placed there by Cabrera (1949). Among these three species, Senecio perezioides seems most similar to S. adenotrichius DC. (given by Pelser et al. 2007: fig. 1I as in "New World Senecio Clade 2"), which is also a perennial herb with similar-sized capitula. Senecio adenotrichius, native to central Chile from Coquimbo south to Santiago, however, is a more leafy-stemmed plant with denser glandular-hirsute indument than S. perezioides. Senecio adenotrichius further differs from S. perezioides by capitula with 15–20 (vs. 12– 13) ray florets and by ca. 40 (vs. ca. 29–32; i.e., ca. 21 + 8-11) phyllaries and calycular bracts, the calycular bracts of which are entire-margined (vs. lobed, as seen in fig. 36). Seven species of the subsection, e.g., S. coquimbensis Phil. (Fig. 37), by setose cypselae differ from the three glabrousfruited species of the subsection, as well as from Senecio perezioides. A key distinguishing glabrousfruited Senecio perezioides from the three glabrous-fruited species of Cabrera's radiate-capitulate, glandular-hirsute subsection is given here, and is modified from that in Cabrera (1949: 380–381).



Figure 37. Glandular-hirsute phyllaries in capitula of *Senecio coquimbensis* Phil., a subshrubby glandular-hirsute species similar to subrosulate *Senecio perezioides*, and placed in *Senecio* sect. *Corymbocephalus* subsect. *Adenotrichi* by Cabrera (1949). *Senecio coquimbensis*, however, is one of about seven species of the subsection differing from *Senecio perezioides* by their setose cypselae. A. Capitula from above, showing phyllaries of immature capitula (just above the middle) and 13–15 ray florets per capitulum (left center). B. Capitula lateral view, showing entire-margined calycular bracteoles. (Chile, *Rosa Ortiz & Alina Freire 491*, photographs by Rosa Ortiz).

## Key to Senecio perezioides and Chilean species with glabrous cypselae recognized in Senecio sect. Corymbocephalus subsect. Adenotrichi (modified from Cabrera 1949)

- 1. Perennial subrosulate herbs, basal leaves present at anthesis, stem leaves 2–4; herbage loosely glandular-hirsute; (Bolivia at about 14° 40' South latitude and at about 4190 meters
- 1. Leafy-stemmed non-rosulate perennial herbs or subshrubs, basal leaves absent at anthesis, stem leaves several—many; herbage glabrous to densely glandular-hirsute.
  - 2. Phyllaries about 12–13; calyculus poorly developed. [homotypic syn.: Senecio rivularis J. Rémy 1847, non S. rivularis (Waldst. & Kit.) DC. 1837]; (centered Coquimbo, region IV, Chile, south of about 30° South latitude and between about 300–2500 m elevation)

  - 2. Phyllaries about 30–40; calyculus well-developed.
    - 3. Leaves lanceolate, marginal lobes acute-tipped; stem trichomes 2–3 mm long; (centered in Coquimbo and Valparaíso, regions IV–V, Chile, south of about 28° South latitude and between about 300–1200 m elevation)

    - 3. Leaves oblong, marginal lobes mostly obtuse-tipped; stem trichomes < 1 mm long; (centered in Antofagasta, Coquimbo, and Valparaíso, regions III-V, Chile, south of about 22° South latitude and between about 400–1400 m elevation) Senecio murinus Phil.

By its habit and combined characters, Senecio perezioides differs technically even further from remaining regional species of other infragenera. Nevertheless, among these more distant infragenera are several other glandular-hirsute, deeply serrate to pinnatilobed-leaved species in Argentina and Chile that somewhat recall S. perezioides. For example, radiate-capitulate S. grindeliifolius DC. of Chile and Argentina of Senecio sect. Andina Cabrera (Cabrera 1949) has glandular-hirsute indument, incised-pinnatilobed-leaves, and is radiate-capitulate, but all members of the section are much reduced subshrubs, unlike S. perezioides. Similarly, Chilean Senecio donianus Hook. & Arn. of Senecio sect. Leucanthemifolium Cabrera (Cabrera 1949) recalls S. perezioides in indument and leaf features, but all members of the section differ from the new Bolivian species by their leafy stems and discoid capitula. Among the many other regional Senecios, no species match the character suite found the new Bolivian species described herein.

The Peruvian and Bolivian Andes are awash with Senecios, and it is convenient to order them into groups, even though groupings may be based artificially on gestalt, habit, and flowers. Many common regional species (at least as seen in NY, MO, and US) tend to be those of such speciose artificial grouping, such as those species groups that are: caespitose (e.g., S. humillimus Sch. Bip., S. jarae Phil.); erect shrubby herbs with pinnately lobed leaves (e.g., S. leuceria Cabrera, S. pentapterus Cabrera, S. rudbeckiifolius Meyen & Walp.); shrubby herbs with elongate leaves (e.g., S. boliviensis Sch. Bip. ex Klatt, S. lopez-mirandae Cabrera, S. peruensis Cuatr.); or gnarly, narrowly-lobed or narrow-leaved shrublets (e.g., S. adenophyllus Meyen & Walp., S. neoviscosus Cuatr., S. pinnatilobatus Sch. Bip.). Occasional pinnatilobed or glandular-hirsute species are found within these groupings, but by gestalt and habit, such species are set apart from S. perezioides. Among the aforementioned species, the fine line drawing by Angel Cabrera of Senecio leuceria Cabrera (Cabrera 1952: fig. 2a-d, 1985: fig. 2A-D) of Senecio sect. Corymbosi, a low subshrub from Santa Cruz, Bolivia recalls unnervingly S. perezioides. Indeed, S. leuceria is very similar in aspect to S. perezioides, but S. leuceria is leafy throughout and not subrosulate, lacks hirsute-glandular-hirsute indument, has discolorous leaves that are tomentose abaxially, has relatively small radiate capitula, and has densely sericeous cypselae, thereby being distinguished from the new species.

Glandular-hirsute indument is relatively uncommon in Senecio, and this feature when found is useful in species comparisons. At the species level, this character is usually consistent and not pliable. Glandular-hirsute indument is scattered throughout different sections of regional Senecios, however, and is thus not always a true marker for infrageneric systematics. For example, in Senecio sect. Otopteri from Bolivia, Cabrera (1985) gives only S. herrerae Cabrera as glandular-hirsute among its seven Bolivian species. Senecio herrerae and the similar S. yunguyensis Cuatr. from adjacent Puno, Peru of section Otopteri are leafy-stemmed and small-radiate-capitulate, and although their leaves are marginally dentate-incised, both are easily seen as unlike S. perezioides. Yet another example of glandular indument being uncommon in Senecio is found within Senecio sect. Corymbosi, where only about a third of the nearly 30 Bolivian species are given by Cabrera (1985: 158) as glandular-hirsute. Thus, it seems useful to compare Senecio perezioides to other regional largeradiate-capitulate species that are similar to the new species in gestalt, and that are glandular-hirsute. Cabrera (1985) placed to infragenus all Bolivian Senecios, but a single reference placing all Peruvian Senecios to infragenus is lacking. Thus, here I refer mostly to Peruvian species without mention of infrageneric placement, even though Beltrán and Galán de Mera (1996) provided a very useful infrageneric framework of the species of *Senecio* that occur in Lima, Peru.

Within Senecio sect. Corymbosi in Bolivia, Senecio perezioides recalls glandular-hirsute radiate-capitulate moderately common S. agapatensis Sch. Bip., S. alniphilus Cabrera, and S. crepidifolius DC., each of which differs from the new species by a non-rosulate habit (as does the section) and smaller capitula. These three leafy-stemmed species seem more similar to each other, than to *Senecio perezioides*. Similarly, other regional taxa of *Senecio* sect. *Corymbosi* that are common and glandular-hirsute include S. hastatifolius Cabrera, S. pentlandianus DC., and S. rufescens DC., but these three leafy-stemmed species are each discoid-capitulate and thereby distinct from S. perezioides. Within Bolivian species of the section, S. perezioides may be most similar to Senecio leuceria, which as mentioned above, however, lacks glandular-hirsute indument.

Among other Bolivian species, Senecio perezioides by its glandular-hirsute indument and subrosulate habit with basal leaves present usually at flowering, recalls the herbaceous S. rhizomatus Rusby (syn. S. erosus Wedd. 1855, non L.f. 1782) (Figs. 38–39), the only glandular-hirsute Bolivian species treated by Cabrera (1985) in Senecio sect. Crassicephali. Similarly, in Lima, Peru, Beltrán and Roque (2015) key only S. rhizomatus (Figs. 38–39) and S. hyoseridifolius as glandular-hirsute. Senecio rhizomatus in subrosulate habit and glandular-hirsute indument is fairly similar to S. perezioides, but differs from it by its nutant, discoid/disciform, larger capitula. subrosulate, regional species of discoid-capitulate Senecio sect. Crassicephali also listed by Cabrera (1985) include S. burkartii Cabrera, S. calvus Cuatr., S. praeruptorum Sch. Bip. ex Klatt, S. serratifolius (Meyen & Walp.) Cuatr., and S. tephrosioides Turcz. (Fig. 33B), but each of these five species have eglandular herbage and are even less similar to S. perezioides than is S. rhizomatus.

Senecio rhizomatus extends from Bolivia into Peru, and by its discoid/disciform capitula and glandular-hirsute indument resembles S. hastatifolius Cabrera (of Bolivia and Peru), central to north-Peruvian S. hyoseridifolius Wedd., north-Peruvian S. sipoccruncus Cabrera & Zardini, and Ecuadorian S. eliseae J. Calvo. Senecio eliseae—resurrected here from synonymy with S. rhizomatus, where Salomón et al. (2018) placed it—is recognized as a narrow geographic segregate of S. hastatifolius. Senecio hyoseridifolius species number 44 in Weddell (1855) and S. rhizomatus were noted as mutually similar by Weddell: when described S. erosus (Fig. 39) was numbered "44 bis" in Weddell (1855: 228). Greenman (1938) recognized Senecio rhizomatus, gave S. erosus Wedd. as a later homonym of S. erosus L.f., and treated the illegitimate homonym S. erosus Wedd. in synonymy of the Rusby name. Senecio rhizomatus was treated by Cabrera (1985, at rank of series) as a member of Senecio sect. Crassicephali, whereas it was placed in Senecio ser. Culcitium by Salomón et al. (2018). These glandular-hirsute, more northerly species are subshrubby, leafy-stemmed, lack basal rosettes at anthesis, and are discoid-capitulate, thus each may be distinguished from radiate, subrosulate S. perezioides. Senecio klattii Greenm. is also similar, but eglandular.

As an aside, I must not forget to mention that the holotype of S. rhizomatus Rusby (1896, the third number of his Bang collection enumerations) is understood to be Bang 1050 NY-COLOMBIA-COLLEGE (the NY sheet with "Colombia College" purple-stamped, now bar-coded as 00259378). Rusby (1893) in the first number of his Bang collections enumeration stated "Set No. 1 Columbia College, New York City" and these and similar purple-stamped sheets have for a century been taken as the first set, as stated in 1893, in our case being the holotype of S. rhizomatus. The third set of Bang collections was the Mr. William M. Canby set, which included Bang 1050 collected in 1891. Bang 1050 was distributed as S. erosus Wedd., but not long after Mr. Canby, then 71 years of age, sold his entire herbarium to the College of Pharmacy. The NY-COLOMBIA-COLLEGE sheet of

Bang 1050 was cited as the type by Greenman (1938), the Canby-College of Pharmacy isotype then not housed in NY. Bang 1046 was in the protologue referred with doubt to S. rhizomatus, is not a paratype, and proves to be Senecio klattii Greenm. The NY-COLOMBIA-COLLEGE specimen original determination as S. erosus was in hand, this overwritten in the hand of Rusby and annotated as "rhizomatus Rusby sp. n.," i.e., it is the holotype. The Canby-College of Pharmacy sheet was annotated much later by Rusby, in handwriting matching that of Rusby in his *Descr. S. Amer. Pl.* 1920-era of his later years, simply as "*rhizomatus* Rusby." I was incorrect and too vague in 1983 when I annotated Bang 1050 of Set No. 3, the Canby-College of Pharmacy sheet (Fig. 38), as the "holo- or iso-" type of Senecio rhizomatus. Nearly four decades later, it seems clear that Canby-College of Pharmacy specimen was not the sheet in hand from which the protologue diagnosis was derived. The Canby-College of Pharmacy sheet of Bang 1050 is an isotype of S. rhizomatus Rusby. Ultimately, the College of Pharmacy herbarium was transferred to NY in 1948, eight years after the 1940 death of Henry Hurd Rusby and ten years after Greenman (1938) cited the NY-COLOMBIA-COLLEGE holotype. In the more than a decade that I was at NY, I noted the purple-stamped Bang sheets were the sheets from which descriptions of any given Rusby names were written, except in a single incident for a single name when a Canby-College of Pharmacy sheet was marked with binomial followed by "sp. n." in Rusby's hand, but the Columbia College sheet was not so marked. Both sheets of Bang 1050 now at NY are conspecific, and application of the name S. rhizomatus is not in doubt. Similarly, the holotype of Senecio psidiifolius Rusby is the NY sheet (now bar-coded as 00259371) with the purple "Colombia College" stamp, whereas the Canby-College of Pharmacy isotype sheet that I annotated in 1983 is a later (1948) addition to NY, albeit both with the same style printed label that included the printed binomial. I have taken the opportunity here of mentioning the typification of S. rhizomatus, because I am familiar with Bang materials of Rusby names, and because among Bolivian species treated by Cabrera (1985), S. rhizomatus (of Senecio sect. Crassicephali Cabrera), along with Senecio leuceria (of Senecio sect. Corymbosi Cabrera), are seemingly the species most similar to S. perezioides.

Senecio gracilipes A. Gray from Lima and Ancash, Peru (viz Beltrán and Roque 2015) resembles S. perezioides by its subrosulate habit, lobed leaves, and large capitula, but differs from the new species by hirsute (vs. glandular-hirsute) indument and discoid capitula. Radiate-capitulate glandular-hirsute S. allapajanus Cuatr. from Ayacucho, Peru is leafy-stemmed, has serrate leaves, 9 (vs. 12–13) ray florets, and setose (vs. glabrous) cypselae, and is not overly similar to S. perezioides. Radiate-capitulate glandular-hirsute S. chavanilloensis Cuatr. from central-northern Peru has leafy stems, relatively small pinnatilobed leaves, and small short-rayed capitula thereby differing from  $\dot{S}$ . perezioides. In northern Argentina, perennial herbaceous S. yalae Cabrera and subshrubby S. friesii Cabrera (of Senecio sect. Senecio ser. Corymbosi subser. Viscosi and subser. Brasilienses, respectively, in Cabrera et al. 1999) by their glandular-hirsute indument, incised-lobed leaves, and radiate capitula resemble superficially S. perezioides, but they differ from the new Bolivian species by leafy stems, more numerous and smaller capitula, and setose cypselae. Albeit eglandular and glabrous, radiate-capitulate spiny-pinnatilobed-leaved S. toroanus Cabrera from west-central Argentina recalls S. perezioides, but differs by its subshrubby habit and sericeous-setose cypselae. I find no pinnatilobed-leaved, glandular-hirsute (or eglandular), radiate (or discoid) regional species resembling closely S. perezioides, which I thus newly described herein.

Several species similar by pinnatilobed-leaves, large radiate capitula, and 5-nerved rays to S. perezioides that occur at least in part in relatively nearby Lima, Peru have recently (Nordenstam et al. 2009) been excluded from Senecio and referred to Lomanthus. Lomanthus differs from S. perezioides by mostly abaxially white-tomentose leaves, sometimes weakly penicillate disk styles, and papillose cypselae (Nordenstam et al. 2009). Lomanthus is a member of the "Faujasia-Oldfetia clade" (viz placement of S. arnaldii Cabrera in Pelser et al. 2007: 1090, fig. 1K). Lomanthus species found in Lima, Peru include Lomanthus arnaldii (Cabrera) B. Nord. & Pelser, L. calachaquensis (Cabrera) B. Nord. & Pelser, L. lomincola (Cabrera) B. Nord. & Pelser, L. subcandidus (A. Gray) B. Nord. & Pelser, L. tovari (Cabrera) B. Nord. & Pelser, and L. velardei (Cabrera) B. Nord. & Pelser (viz Beltrán and Galán de Mera 1996; Beltrán and Roque 2015). Similarly, Senecio perezioides by pinnatilobed-leaves, 5-nerved ray corolla limbs, and radiate capitula is in gestalt similar superficially to Chilean Lomanthus coscayanus (Ricardi & Martic.) Pruski, comb. nov. (Basionym: Senecio coscayanus Ricardi & Martic., Gayana, Bot. 11: 15, fig. 5. 1964. TYPE: CHILE. Tarapacá. Coscaya, 2 Apr 1961, Ricardi et al. 392, holotype: CONC). Lomanthus coscayanus differs from S.

perezioides by its leaves that are oblong, discolorous, and abaxially white-tomentose, and also by its papillose cypselae. Lomanthus coscayanus from Tarapacá, Chile, is relatively near geographically the type locality of Bolivian S. perezioides, and its recognition raises to 20 the number of species attributed to *Lomanthus*. No species of *Lomanthus* were reported in Chile by Cabrera (1949), Nordenstam et al. (2009), or in the checklists of Chile (Marticorena and Quezada 1985; Rodríguez et al. 2018). Thus, Lomanthus is a new generic record for Chile.



Figure 38. Isotype of subrosulate Senecio rhizomatus Rusby. (Bang 1050, NY-Canby-College of Pharmacy).



Figure 39. Isotype of *Senecio erosus* Wedd. 1855, non L.f. 1782, a taxonomic synonym of *Senecio rhizomatus* Rusby. (*Mandon 114*, NY).

Asa Gray in his last letter (see Zoe 4: 372. 1894) wrote to Nathaniel Lord Britton, in whom Gray was disappointed, "we look to you and to such as yourself, placed at well-furnished botanical centres, to do your share of conscientious work." It is without question that work in large museums includes the challenging responsibility of study of all relevant specimens and literature available in their collections. Also axiomatic is that the abundant material of speciose genera in large herbaria brings an inherent obligation for staff to curate large messy groups, and simultaneously to determine bulk staff expedition materials from core project areas, in my case at the Missouri Botanical Garden each in support of the Garden's mission. I have done so herein with *Senecio* and Senecioneae, which I find both large and messy. The novelties and adjustments proposed here, supplemented with field, herbarium, and laboratory images, are given to document some of my recent work in tribe Senecioneae, which comprises about 1% of the Angiosperms.

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2004: 57). Fosberg (1993) also cited this independently paginated paper with the same title, pagination, and also as with 8 plates, but dated erroneously both preprint (Forster 1788) and journal (Forster 1789) versions as "1778." Pritzel (1851: item 3285; 1872: item 2977) on the other hand, gave the preprint as "64 p." and without mention of plates, but more or less used the title as in 62-page preprint citation of Nicolson and Fosberg (2004: 65).].

[However, the pdf copy of the GOET holding of the original 64-page preprint that lacks the eight unpaginated plates was sent to me this year by Gretchen Wade (Harvard Library) and Linda Oestry (MO library) and is possibly the same as the original seen by Dr. Gerhard Wagenitz (GOET); other than for the missing plates it matches the title and pagination as given for TL-2/1824 by Stafleu and Cowan (1976). Above, my citation of this 1788 preprint does not cite plates and is thus modified slightly from that given in TL-2/1824. The plateless 64-page preprint copy in hand does, however, list plate numbers in the margins near the binomials of the eight taxa illustrated. The journal-version plates are numbered, unpaginated, and appear to be inserted individually in the bound copies of the journal versions that I have seen. The 64-page preprint (Forster 1788) is quarto, has the "special t.p." as mentioned in TL-2/1824 that is unpaginated, and the t.p. corresponds to pages [1-2]; the text begins on unnumbered page [3] as signature "A 2" and matches the content of the first page of text in the 1789 journal version, except the journal version text begins on page 13 and is signature "B 3." Page 4 is the first numbered page in the 64-page preprint, is the second page of text in the preprint, and matches page 14 of the journal version, which is the second page of the 1789 journal text. Page 61 of the preprint is signature H 3, page 63 corresponds to unmarked signature H 4, and verso page 64 is the last of the preprint.].

[The journal version of the paper as printed/bound is from more than a score of quarto sheets; each 8-page signature being twice-folded as are quartos by definition. The pages as bound in the journal are with horizontal chain lines in the paper. For example, in the 1789 journal Plantae Atlanticae portion, page 57 (with taxon 77, Euphorbia polygonifolia) is the first page of signature H, page 59 is H 2, page 61 is H 3, and the fourth was not indicated; the pattern

repeats with the 8 pages of signature I, the 8 pages of signature J, and so on, all pages with horizontal chain lines. Of course in the 1788 quarto preprint, page 57 (with taxon 135, Gnaphalium luteo-album) is the first page of signature H as well, but the preprint content page numbering is off by ten pages as compared to the numbering seen in the journal volume 9 (1789), where taxon 135, the *Gnaphalium luteo-album* text, occurs on page 67. Because the signatures of the independently paginated 1788 preprint differ from those of the 1789 journal publication, I suspect the respective printings may have been completed at slightly different times/days (viz Pruski 2018: 74). The first pages of the two Forster quarto journal articles (1789: 13 is B 3, and 46 is F 3-verso) are not the first pages of any 8-page signature, a vrai offprint thereby seemingly unlikely. The 64-page preprint of course is composed similarly of eight 8-page signatures, and as expected based on earlier examination of the 1789 journal signature markings, the 64-page preprint has the first page of the first signature and penultimate page of the last signature (A 1 and H 4, respectively) unmarked. It is a given that at one point the horizontal chain lines of the quarto journal will be compared to those of the 64-page quarto preprint, which I have only as a pdf.].

What is not perfectly clear, however, is whether or not there are two different 1788 preprint versions. I suspect there is but one. Nevertheless, there are literature citations of both a 64page and a 62-page version. The potential third variant of the paper, a 62-page preprint, is cited by Nicolson and Fosberg (2004: 57, 65) as "Fasciculus Plantarum Magellanicarum: 1-33, t. 1–8 [&] Plantae Atlanticae ... 34–62." Such a hypothetical 62-page preprint contains presumably only the 62 pages of the journal text, thus lacking a special title page. The text of the 64-page preprint begins on page 3, but a hypothetical 62-page preprint would have text beginning on page 1, the remaining pages repaginated as well. The second part of such a hypothetical 62-page preprint would have the 'Plantae Atlanticae' title of the second Forster journal text as a subtitle buried deep within on verso page 34. Thus a 62-page preprint would appear to be titled solely Fasciculus Plantarum Magellanicarum. In the 64-page TL-2/1824 preprint, pages 35–36 are back-to-back, and the second part of the text—Plantae Atlanticae begins deep within the preprint on verso page 36, but is indicated clearly on the special title page.].

[A hypothetical 62-page [1-62] preprint, however, does not fit well with my "eight 8-page signatures" count, whereas the 64-page preprint in hand is marked clearly as composed of signatures A–H, each signature of 8 pages. The journal versions seen have three of the eight plates positioned between signature [C, D, E] page 1 and page 2 opposite the text where cited. In the MO journal-version holding, plate 5 is larger than the other plates, and is folded. In the NY holding, the plates are placed after the text. In the plates of the journal version, we find the only place where "Commentat. Vol. IX" is given within either the preprint or journal texts. Nicolson and Fosberg (2004: 57) noted "extant letters from George Forster" written in 1788 mentioned "some copies of the offprints accidentally ... left behind in Frankfurt," and that [in the 1900s] "Prof. G. Wagenitz pers. comm." established the existence of this "**preprint**." [The boldface in the quotes is mine.] In the same paragraph of their bibliographic note 2, however, Nicolson and Fosberg (2004: 57) used both the words 'preprint' and 'offprint,' but eight pages later they list the 'preprint' as "not seen." Gretchen Wade (Harvard Library) and Linda Oestry (MO Library) have also verified that the independently paginated 64-page preprint exists, and have sent me a pdf copy of the GOET holding of it. Nicolson and Fosberg (2004) deduced that a version of preprints/offprints were "distributed by March or April 1788." I presume there is no 'Frankfurt-offprint'—a potential fourth variant of the paper—and that the 62-page preprint citation by Nicolson and Fosberg (2004) is instead in reference to the 64-page independently paginated plate-less preprint, more or less as cited in TL-2/1824. In any event, I take the distribution-effected date of the 64-page preprint of TL-2/1824 as March or April 1788, albeit this date is from third-hand indirect evidence.].

Back to the matter at hand, the protologue of *Tussilago trifurcata* G. Forst. is on page 28 of the 64-page TL-2/1824 preprint copy that I have in hand and page 38 of the journal volume 9 version, but would be presumably on page 26 of a hypothetical 62-page preprint. The journal version reference for *Tussilago trifurcata* is Commentat. Soc. Regiae Sci. Gott. 9: 38. 1789. What is clear is that TL-2/1824 64-page preprint is neither spread out over 9 volumes nor imprinted 'Vol. IX' on its first page. Clearly, a page citation of Tussilago trifurcata in a hypothetical 62-page preprint and a 62-page preprint title are to me known not. I presume,

- however, that the independently paginated 64-page preprint in hand and a hypothetical 62page independently paginated preprint—that was cited presumably erroneously by Nicolson and Fosberg (2004: 65) as "Fasciculus plantarum Magellanicarum: 1–33, t. 1–8. [&] Plantae Atlanticae ...: 34–62. [the boldface is their own]—will prove ultimately to be a single item.].
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[In much of the introductory text of this paper, I have adopted the format "1978, fig." for figures cited in 1978, i.e., having the year followed by comma, rather than the usual format of the year followed by a colon. The usual/standard format "1978: fig." is misread easily and is difficult to distinguish from "1978;" (that is year semicolon), especially when several references closely follow one another].