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COMPOSITAE OF CENTRAL AMERICA-VII. *DIGITACALIA, DRESSLEROTHAMNUS, PENTACALIA, ZEMISIA,* THEIR MICROCHARACTERS, AND SOME OTHER SENECIONEAE

JOHN F. PRUSKI
Missouri Botanical Garden
4344 Shaw Blvd.
St. Louis, Missouri 63110

ABSTRACT

In Central America tribe Senecioneae are represented by subtribes Senecioninae and Tussilagininae. Here, the southern Central America-centered genus *Dresslerothamnus* (subtribe Senecioninae) is monographed. Five species are recognized, including the new **Dresslerothamnus hammelii** Pruski, **sp. nov.**, from Panama. The Central American species of **Pentacalia** (subtribe Senecioninae) are revised with twelve regional species recognized. Lectotypes are designated for *Senecio calyculatus* Greenm. and *Senecio deppeanus* Hemsl., and an epitype is designated for *Senecio thomasii* Klatt. Former Jamaican endemic *Zemisia* is monographed and the new combination **Zemisia thomasii** (Klatt) Pruski, **comb. nov.**, is made. *Zemisia* is a new generic record for Mexico and Central America. A key to genera centering about *Pentacalia* is given. Mexican-centered *Digitacalia* (subtribe Tussilagininae) is monographed and its distribution expanded into Central America with **Digitacalia stevensii** Pruski, **sp. nov.**, from Honduras and Nicaragua newly described. Microscopic floral details of *Telanthophora steyermarkii* (Greenm.) Pruski are included, supporting its recent placement in Tussilagininae. Seven new combinations for associated South American Senecioninae are these: **Dendrophorbium castaneifolium** (DC.) Pruski, **comb. nov.**, **Dendrophorbium elatum** (Kunth) Pruski, **comb. nov**., **Dendrophorbium gritense** (Lapp, T. Ruíz & Torrec.) Pruski, **comb. nov.**, **Dendrophorbium huasense** (Cuatr.) Pruski, **comb. nov.**, **Dendrophorbium munchiquense** (S. Díaz & Cuatr.) Pruski, **comb. nov.**, **Dendrophorbium vallecaucanum** (Cuatr.) Pruski, **comb. nov.**, and **Monticalia barbourii** (M.O. Dillon & Sagást.) Pruski, **comb. nov.** SEM micrographs and LM photographs of microcharacters in *Aequatorium*, *Dendrophorbium*, *Digitacalia*, *Dresslerothamnus*, *Elekmania*, *Monticalia*, *Nordenstamia*, *Ortizacalia*, *Pentacalia*, *Pseudogynoxys*, *Robinsonecio*, *Scrobicaria*, *Senecio*, *Telanthophora*, and *Zemisia* are given, and subtribes Senecioninae and Tussilagininae are distinguished by floral microcharacters.

The cosmopolitan Compositae tribe Senecioneae Cass. contains about 3500 species, about 1% of all Angiosperms, and is the largest tribe of Compositae, the largest family of Angiosperms (Pruski & Robinson 2018). Senecioneae are recognized by having some or all of the following: uniseriate, subequal phyllaries, epaleate clinanthia, 4-nerved ray corolla limbs, truncate style branches, and non-carbonized, terete cypselae with a pappus of many capillary bristles (Cassini 1819a, 1819b, 1821, 1827; Nordenstam 1977, 1978, 2007; Cuatrecasas 1986; Bremer 1994; Nordenstam et al. 2009). Senecioneae often have a secondary chemistry characterized in most genera by presence of toxic pyrrolizidine alkaloids and the sesquiterpene lactone furanoeremophilane, and absence polyacetylenes (Hegnauer 1977; Mabry & Bohlmann 1977; Jeffrey 1979a; Nordenstam 2007; Langel et al. 2011), differing from other Compositae. For nearly a century *Senecio* L., the type of the tribe, often was circumscribed broadly following Bentham and Hooker (1873), who treated several genera of different subtribes (e.g., *Cacalia*) in synonymy of *Senecio*.

Four subtribes are now recognized in Senecioneae, and although cacalioids and senecioids have long been distinguished as informal groups (e.g., Koyama 1967; Pippen 1968; King & Robinson 1977; Nordenstam 1977, 1978), the numbers of recognized subtribes has varied. For example, Jeffrey and Chen (1984) recognized subtribes Senecioninae, Tussilagininae, and Tephroseridinae, with these three subtribes basically mirroring the informal groups of *Senecio* s.l. recognized by Jeffrey et al.

(1977) and Jeffrey (1979a). Nordenstam (1977) and Jeffrey (1992a) recognized only two subtribes: Senecioninae and Blennospermatinae. Bremer (1994) and Barkley et al. (1996) recognized three subtribes, Blennospermatinae (which included *Abrotanella* Cass.), Senecioninae, and Tussilagininae. Most recently, Pelser et al. (2007) and Nordenstam et al. (2009) recognized four subtribes: Abrotanellinae, Othonninae, Senecioninae, and Tussilagininae (including *Blennosperma* Less. and *Tephroseris* (Rchb.) Rchb.). Brachyglottidinae, Chersodominae, and perhaps Doronicinae (the only Senecioneae with polyacetylenes) may also merit recognition (Pelser et al. 2007; Nordenstam et al. 2009). Of the four recognized subtribes, only Senecioninae (senecioids) and Tussilagininae (cacalioids/tussilaginoids) are speciose and common.

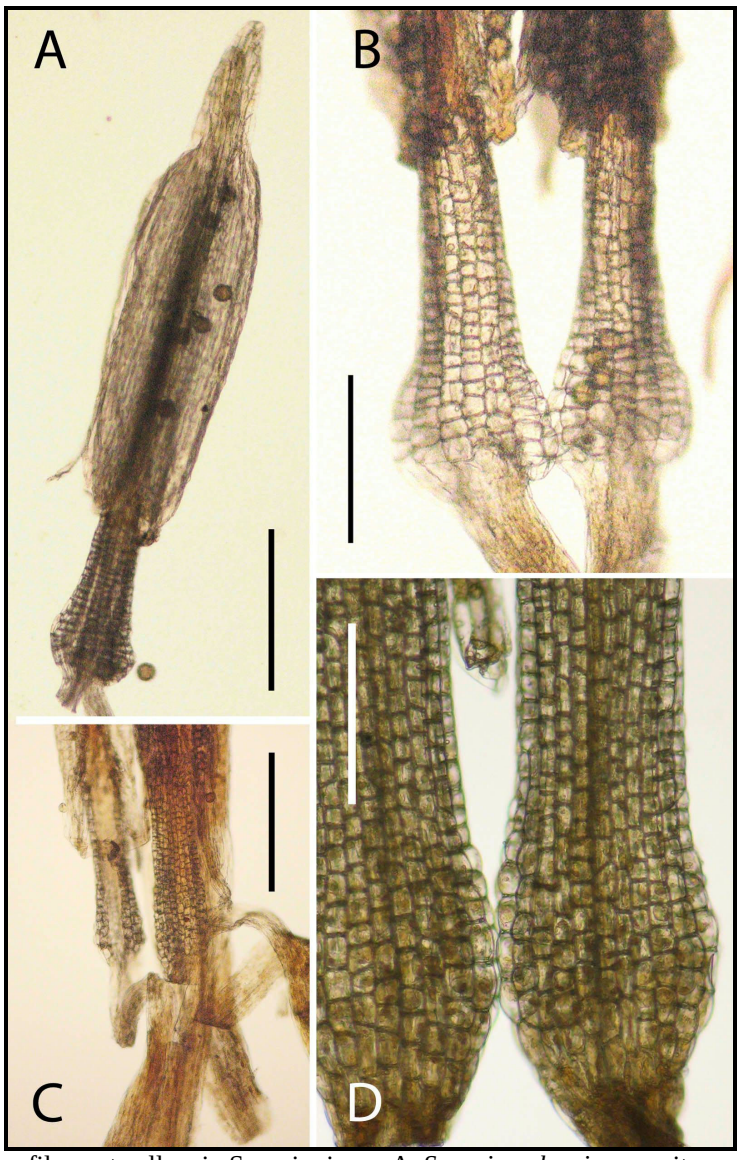

Figure 1. Balusterform filament collars in Senecioninae. A. *Senecio vulgaris*, generitype, two superimposed anthers showing collars, ecaudate thecae, a few pollen grains, and terminal appendages. B. *Senecio costaricensis*, close-up of two collars. C. *Scrobicaria ilicifolia*, generitype, the anther on the left is seen in adaxial view and shows the adaxial groove and caudate theca. D. *Pentacalia tonduzii*, collars of two caudate anthers showing (top center) tip of an anther tail. The collars in C and D (*Scrobicaria ilicifolia* and *Pentacalia tonduzii*) are only moderately broadened, but in each the basal cells are obviously enlarged. (A *Pruski & Ortiz 4561*, MO; B *Pruski et al. 3875*, MO; C *Gentry et al. 8931*, MO; D *Alfaro 1546*, MO). [Scale bars: A 0.15 mm, B 0.09 mm, C 0.14 mm, D 0.05 mm].

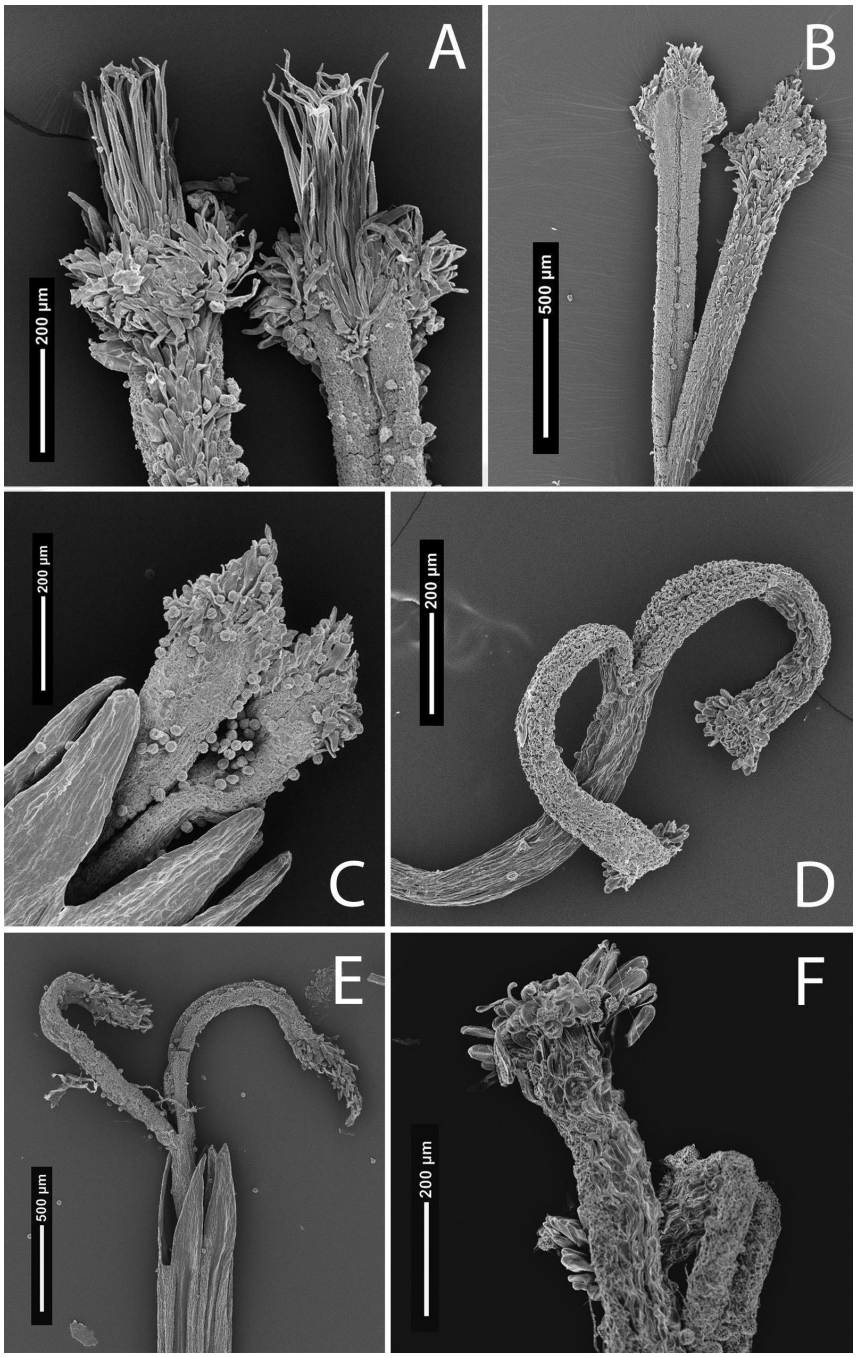

Figure 2. Styles in disk florets of Senecioninae, showing 2-banded stigmatic surfaces, and variously appendiculate (A–C, E) or truncate-exappendiculate (D, F) branch apices. A. *Ortizacalia austin-smithii*, generitype, branches with abaxial-outer (left) and adaxial-inner (right) surfaces showing heteromorphic papillae, apical comae composed of long thin papillae, and distal papillae between stigmatic bands (branch on right). B. *Pentacalia brenesii*, branches with adaxial (left) and abaxial (right) faces showing triangular appendages and isomorphic papillae, no distal adaxial papillae arising between stigmatic bands. C. *Dresslerothamnus angustiradiatus*, generitype, triangular-tipped branch emerging from anther cylinder. D. *Pentacalia phanerandra*, recurved branches showing truncate apices. E. *Pseudogynoxys haenkei*, branches emerging from anther cylinder and showing long-triangular cellar appendages. F. *Senecio callosus*, showing truncate branch apices. (A *Haber & Zuchowski 9847*, MO; B *Herrera & Schik 3830*, MO; C *McPherson 12334*, MO; D *van der Werff 7236*, MO; E *Pruski et al. 4195*, MO; F *Véliz 8327*, MO).

In Tropical American *Senecio*, Jesse Greenman (1901, 1902, 1915, 1916, 1918, 1923, 1926, 1938, 1950), Angel Cabrera (1949, 1950, 1954, 1957, 1985; Cabrera & Zardini 1980), and José Cuatrecasas (1950, 1951, 1953) were influential early workers who mostly followed the broad Benthamian circumscription of the genus. They each delineated sections and species groups within *Senecio* that were subsequently treated as genera. More recently, two large, long-recognized generic alliances marked by suites of unconventional floral microcharacters (i.e., senecioids and cacalioids/tussilaginoids) have come to be recognized as subtribe Senecioninae and Tussilagininae, and many satellite genera have been resurrected or segregated from *Senecio* (viz Rydberg 1924a, 1924b, 1927; Cuatrecasas 1955, 1960 1978, 1981, 1986, 1994; Koyama 1967; Pippen 1968; Robinson & Brettell 1973a, 1973b, 1974; Jeffrey et al. 1977; Nordenstam 1977, 1978, 2006, 2007; Robinson & Cuatrecasas 1977, 1978, 1993, 1994; Robinson 1978, 1989; Barkley 1985a, 1990; Wetter 1983; Jeffrey & Chen 1984; Jeffrey 1986, 1987, 1992a; Vincent & Getliffe 1988, 1992; Pruski 1991, 1996, 1997, 2010, 2012a, 2012b; Bremer 1994; Nordenstam & Pruski 1995; Barkley et al. 1996; Vincent 1996; Janovec & Robinson 1997; Díaz-Piedrahita & Cuatrecasas 1999; Dillon et al. 2001; Dillon 2005; Lundin 2006; Pelser et al. 2007; Nordenstam et al. 2009; Torrecilla & Lapp 2010; Lapp et al. 2015; Pruski & Robinson 2018).

In Central America, Senecioneae are represented basically only by members of subtribes Senecioninae and Tussilagininae, with much restructuring of regional species done or highlighted by José Cuatrecasas, Charles Jeffrey, Ted Barkley, Harold Robinson, and the author. [One species of *Euryops* (subtribe Othonninae) is grown ornamentally in Mesoamerica, but rarely escapes]. Some of the microcharacters used by them (e.g., stigmatic surface characters and shape and cellular features of the filament collar— sometimes called anther collar or antheropodium, and described by Drury 1966: 36 as "a downward extension of the connective" onto the filament—were used by Cassini, but endothecial tissue characters in Compositae were noted only later (e.g., Kuhn 1908 fig. 37) and mainstreamed much later by Dormer (1962), Robinson and Brettell (1973b), Nordenstam (1978), Wetter (1983), Thiele (1988), and Vincent and Getliffe (1988 fig. 3; viz also the *Dracaena* drawing in Manning 1996 fig. 2). Members of subtribe Senecioninae are characterized by **senecioid microcharacters** of balusterform filament collars dilated basally and with enlarged basal cells (Figs. 1, 35A, 36B, 37A, 50A; "en la forme de balustre" Cassini 1827: 454; Hoffmann 1894 fig. 65M; anglicized in Drury 1973b: 741), typically by 2-banded stigmatic surfaces (Fig. 2), a radial (sometimes transitional with thickenings both radial and polar) endothecial tissue pattern (Figs. 3A, 3C, 35B, 37B, 50B), and $x = 10$ basic chromosome number. Those of subtribe Tussilagininae, on the other hand, are distinguished by **cacalioid microcharacters** of cylindrical filament collars with more or less equal-sized cells throughout (Fig. 4A, 4C, 4E), entire-continuous stigmatic surfaces (Figs. 4F, 9B), and sometimes a polarized endothecial tissue pattern (Fig. 4B), $x = 30$ basic chromosome number, but the correlation of these characters is not absolute.

As noted by Wetter (1983), filament collar characters are the most consistently diagnostic ones distinguishing Senecioninae and Tussilagininae. Further distinguishing characters in Central American plants, however, include 2-banded styles, which are seen only in Senecioninae, and a sometimes polarized endothecial tissue pattern, seen solely in Tussilagininae. Although, Wetter (1983 figs. 4–5) characterized *Telanthophora* styles as cleft, this character was found by Bremer (1994: 488) as "difficult to uphold," and the term has fallen from common usage. Here, *Dresslerothamnus* H. Rob. (Senecioninae), *Pentacalia* Cass. (Senecioninae), *Zemisia* B. Nord. (Senecioninae), and *Digitacalia* Pippen (Tussilagininae) are revised, their respective subtribes characterized mostly by floral microcharacters, with supporting images included. Following the introduction, the taxonomic treatments within are grouped into three segments, with the Mexican and Central American treatments I and II placed first first: I. **Senecioninae**; II. **Tussilagininae**; and III. **New combinations in South American Dendrophorbium and Monticalia (Senecioninae)**. Within each chapter, the taxa treated are arranged alphabetically.

ANATOMICAL AND SEM METHODS

The wet slide mounts were viewed on an Olympus compound microscope and photographed with a 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.

I. SENECIONINAE Dumort., Fl. Belg. 65. 1827. **TYPE**: *Senecio* L.

Recognition of subtribes of Senecioneae, as mentioned above, has been slowed due to the influence of Bentham and Hooker's (1873) inclusive concept of *Senecio*. For example, Jeffrey et al. (1977) included members of several subtribes within the genus *Senecio*, but more recently (Jeffrey 1992a) recognized several genera from within his earlier broad concept of *Senecio*. Similarly, Nordenstam (1977, 2007) and Jeffrey (1992a) treated the cacalioid genera within subtribe Senecioninae, but now Tussilagininae (which includes the cacalioid genera) are generally taken as subtribally distinct from Senecioninae (Pelser et al. 2007; Nordenstam et al. 2009; Pruski & Robinson 2018). Nevertheless, some taxa still appear intermediate with others (Nordenstam 1977, 2007; Barkley 1985b), and some characters seem to show continuous variation (Jeffrey et al. 1977; Pelser et al. 2004), complicating generic and subtribal limits. In Central America, however, only the two common well-defined subtribes are native, with Senecioninae recognized by its senecioid microcharacters.

Not only are subtribe Tussilagininae accepted as segregated from Senecioninae, and in Chapter II the Tussilagininae genera *Digitacalia* and *Telanthophora* accepted as segregates of *Senecio*, but the caudate-anthered genera of subtribe Senecioninae revised here—*Dresslerothamnus*, *Pentacalia*, and *Zemisia*—are similarly accepted as distinct, well-diagnosed segregates of onetime monolithic *Senecio*. There has been a pushback of sorts, however, by Pelser et al. (2007 fig. 1H), wherein *Senecio* was again inflated by inclusion of several American ecaudate-anthered genera of "New World *Senecio* clade 1." But, the large New World *Senecio* clade 1 is sister to *Senecio* s. str. (which includes Australian clades 2 and 3, New World clade 2, etc.), rather than nested cladistically within it (Pelser et al. 2007 fig. IG, 1I). Although New World *Senecio* clade 1 has weak support (bootstrap support values of < 50%) and the relationships within are not resolved, the *Aetheolaena* subclade members (e.g., *Aetheolaena* Cass., *Culcitium* Bonpl., monotypic *Lasiocephalus* Willd. ex Schltdl., and monotypic *Iocenes* B. Nord.), for example, appear apt to being grouped into recognizable subunits (genera). Within the genera of the *Aetheolaena* subclade, *Culcitium* has priority and *Aetheolaena* includes all but one species referred formerly to *Lasiocephalus*. These genera have been treated variously by Blake (1937), Nordenstam (1978), and Cuatrecasas (1950, 1978), but do not appear to be congeneric with *Senecio vulgaris* L. The inclusive concept in Pelser et al. (2007) increases character diversity in *Senecio* s. lat., and in turn lessens character predictability. For example, *Culcitium* is recognized by its distinctive habit, as is the monotype *Lasiocephalus ovatus* Schltdl. *Aetheolaena*, presumably distinct from *Culcitium*, is characterized by nutant discoid capitula, and usually penicellate style apices (Nordenstam 1978; Cuatrecasas 1978, as *Lasiocephalus*), but was referred to *Senecio* s. lat. by Pelser et al. (2007). Salomón et al. (2016) called the group *Senecio* sect. *Aetheolaena*, and suggested the distinguishing style characters are "taxonomically uninformative." However, *Aetheolaena* is basically accepted here as circumscribed by Nordenstam (1978). In addition to penicellate style apices, the styles in the odd genus *Aetheolaena* often have adaxial (inner) surface distal papillae emerging between stigmatophores. The style branch characters of *Aetheolaena* roughly parallel the appendiculate styles of *Graphistylis* B. Nord., *Jessea* H. Rob. & Cuatr., and *Ortizacalia* Pruski, each of which are similarly maintained (viz Nordenstam 1978; Pruski & Robinson 2018). Forty years ago, Cuatrecasas (1978) stated that penicellate-tipped styles are "generically significant," Jeffrey (1979a) commented that in tropical America some groups have "well marked" penicellate styles, the first figure in Nordenstam (2007) is

of style branches inferring utility of the character, and Pruski (2012b) stated "style branch characters … generally seem to be" reliable taxonomically.

Neotropical *Dresslerothamnus* H. Rob. and *Pentacalia* Cass., two poorly collected epiphytic vining caudate-anthered segregates of *Senecio*, are treated here, as is caudate-anthered, woody *Zemisia*. Each *Dresslerothamnus* and *Pentacalia* contains species that reach high into the forest canopy, and when flowering are weak-stemmed and strongly dangling-pendent (Fig. 5B). Other species of each genus are fairly branched, scrambling plants (e.g., *Dresslerothamnus hammelii* and *Pentacalia wilburii*) of montane dwarf forests, the flowering stems of these scramblers are consequently more or less arching, rather than long-pendent. Thus, growth form is not a distinguishing character separating *Dresslerothamnus* and *Pentacalia*.

The capitulescence positions (Fig. 5) may vary from species to species, are useful in species-level taxonomies, but are not diagnostic of either *Dresslerothamnus* or *Pentacalia*. Most species of both *Dresslerothamnus* and *Pentacalia* have heterogamous—radiate or disciform—capitula, and although *Pentacalia* sometimes has strictly homogamous (discoid) species, capitula and florets types (Fig. 6) are often not diagnostic generically in Senecioneae. Similarly, the characters of the styles, crested clinanthia, and pappus tip cell shape of both *Dresslerothamnus* and *Pentacalia* overlap in morphology. *Dresslerothamnus* tends to show obtuse to triangular style tips often with a few papillae in an apiculum or tuft, whereas the style tips of *Pentacalia* tend to be mostly truncate or obtuse without a notable central tuft. But, *P. brenesii* (Fig. 2B) has a *Dresslerothamnus*-like style (Fig. 2C), and conversely those of *D. schizotrichus* are *Pentacalia*-like (Fig. 2D). Although most species of the two genera, as well as most Senecioneae, have pointed pappus bristle tips (Fig. 3D), species of each *Dresslerothamnus* and *Pentacalia* may have obtuse-tipped terminal cells, albeit not as pronounced as those seen, for example, in *Monticalia firmipes* (Greenm.) C. Jeffrey (Fig. 3E). *Dresslerothamnus*, *Ortizacalia*, and *Pentacalia* have similar habit and floral characters, and were considered close by Robinson (1978, 1989), Pruski (2012b), and Pruski and Robinson (2018).

Dresslerothamnus is monographed herein, characterized in part by vining habit, heterogamous capitula, 8–10-striate cypselae (Fig. 7) (vs. 5-costate ones in *Pentacalia*, Fig. 8A), and variously-modified multistoried pseudostellate-to-T-shaped trichomes (Figs. 11–12, 17, 20; trichome terminology is that of Robinson 1989). Five species are recognized in *Dresslerothamnus*, four of these in Central America (Costa Rica and Panama; three endemic) and two species present in Colombia with one endemic there. The generitype *D. angustiradiatus* is found from Limon, Costa Rica south to the Bajo Calima region in Valle del Cauca, Colombia. The modified trichomes of *Dresslerothamnus* may resemble those of other tribes (viz species of Old World *Andryala* and *Olearia*, in both Solereder 1908 and Metcalfe and Chalk 1979). But, branched trichomes in other Neotropical Senecioneae—e.g., *Aequatorium*, *Nordenstamia*, and some Monticalias (Figs. 9–10; Nordenstam 1978; Lundin 2006; Lapp et al. 2013 fig. 3B)—do not have the pluricellular stipe as in *Dresslerothamnus*, and trichome type helps distinguish American genera. Robinson (1978, 1989) noted a stylar apiculum in the generitype of *Dresslerothamnus*, but further collections show that an apiculum is less pronounced in other species.

Pentacalia in Central America is treated, with 12 species recognized. The genus is Neotropical and is most speciose in Andean South America, where more than 100 species are known. *Pentacalia* was resurrected from synonymy of *Senecio* by Robinson and Cuatrecasas (1978), and Cuatrecasas (1981) recognized two subgenera. Cuatrecasas (1981) basically took the generitype as intermediate with *Pentacalia* subgen. *Microchaete* Cuatr., influencing him to recognize as congeneric the shrubby elements as a second subgenus. More recently, shrubby, often ericoid *Pentacalia* subgen. *Microchaete* Cuatr. was excluded and recognized at the generic rank as *Monticalia* C. Jeffrey (≡ *Microchaete* Benth. 1845, non Nutt. 1841) (Jeffrey 1992a), which in addition to its shrubby habit is characterized by large carpopodia (Fig. 8B). In each *Pentacalia* and *Monticalia*, several species

groups are known (the Monticalias corresponding in part to *Senecio* sects. *Abietoides* Cuatr., *Arbutoides* Cuatr., *Ericoides* Cuatr., *Ledifolium* Cuatr., *Triana* Cuatr., and *Vacccinioides* Cuatr., each typified by species of *Monticalia* and available for infrageneric use there), are perhaps distinct from parent genera, and their generic limits are under continued study by the author. At present, the genera are circumscribed more or less as in Jeffrey (1992a) and Nordenstam (2007). For example, it seems some Monticalias although alternate-leaved are close to opposite-leaved *Scrobicaria* Cass. (Robinson et al. 1997; Pruski 1997). But, in gestalt, opposite-holly-leaved *Scrobicaria* does not resemble *Monticalia*, even though Cuatrecasas (1994) remarked "the opposite leaves … cannot be considered a reliable basis for separation" and reduced *Scrobicaria* to synonymy of *Pentacalia*. Shortly thereafter, Díaz-Piedrahita and Cuatrecasas (1999) reinstated *Scrobicaria*. Nordenstam (2007) and Pruski and Robinson (2018) treated *Monticalia* and *Scrobicaria* as distinct.

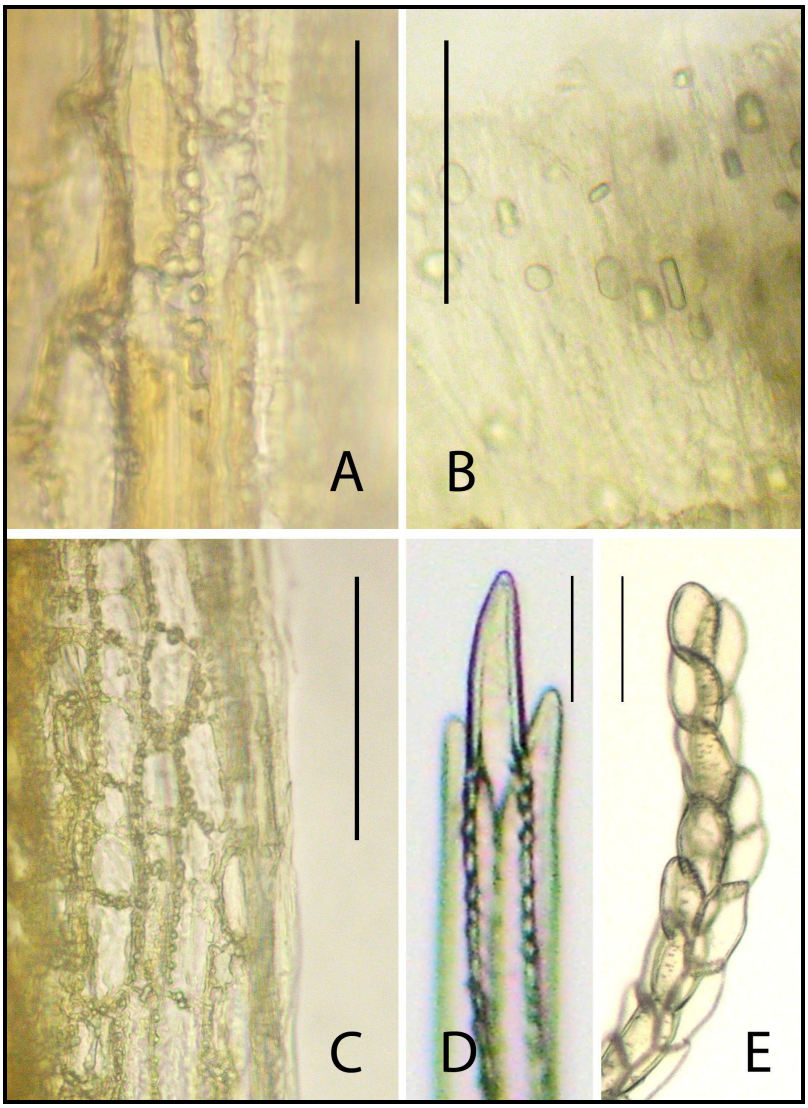

Figure 3. Floral microcharacters in Senecioninae. A. *Dresslerothamnus schizotrichus*, radial (approaching transitional) endothecial tissue. B. *Pentacalia arborea*, generitype, rectangular and hexagonal crystals of immature cypselae epidermis, representative of many Senecioninae. C. *Pentacalia tonduzii*, radial (approaching transitional) endothecial tissue. D. *Pentacalia tonduzii*, pointed tips of a pappus bristle. E. *Monticalia firmipes*, rounded terminal and distal cells of a pappus bristle. (A *Skutch 2502*, MO, holotype; B *King et al.10136*, MO; C–D *Alfaro 1546*, MO; E *Wilbur & Teeri 13937*, MO). [Scale bars: A 25 µm, B 50 µm, C 50 µm, D 30 µm, E 50 µm].

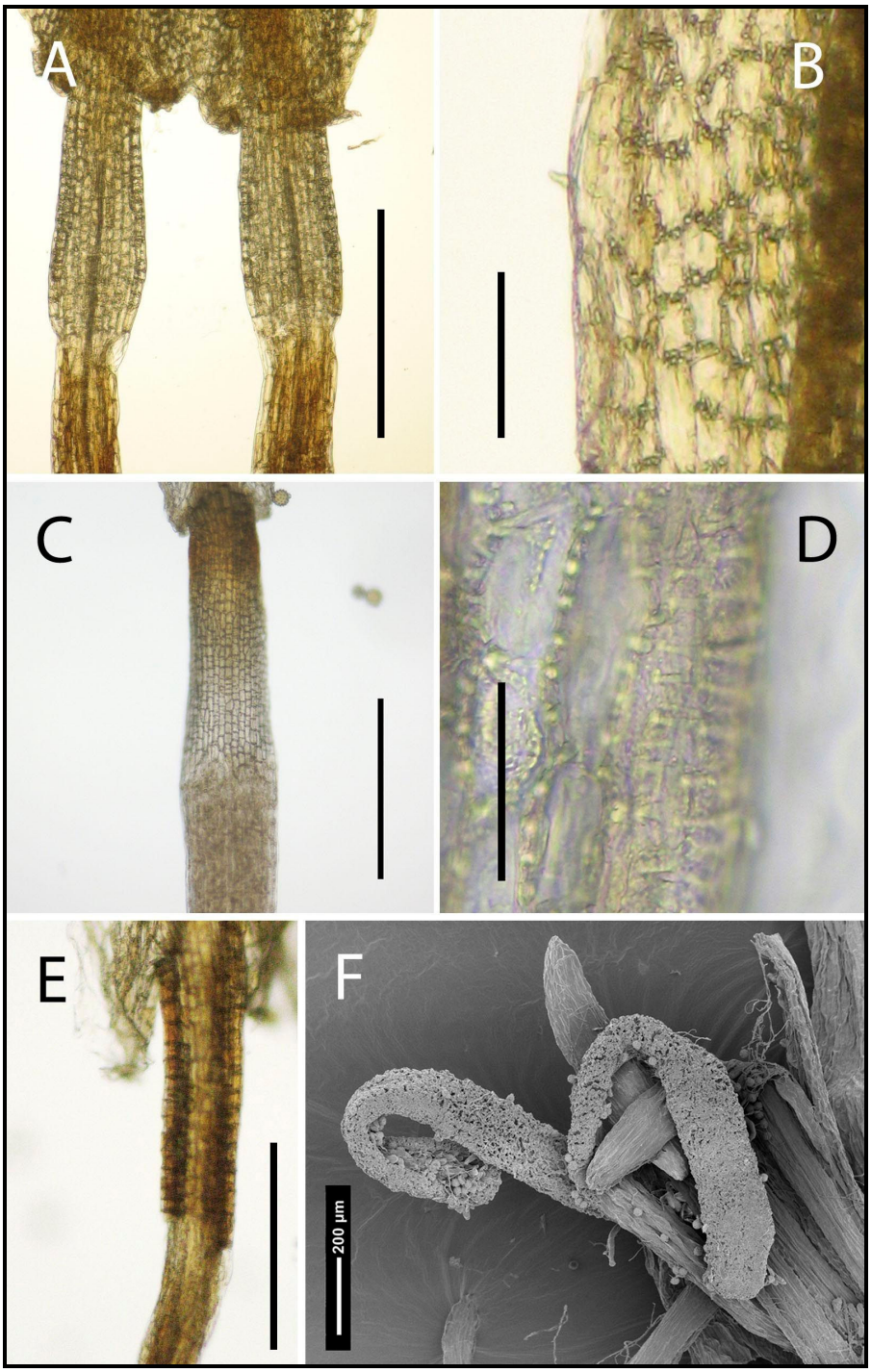

Figure 4. Tussilagininae (cacalioid) floral microcharacters. A. *Digitacalia stevensii*, cylindrical filament collars. B. *Digitacalia stevensii*, polarized endothecial tissue with thickenings on polar walls; C-shaped thickenings were not seen. C. *Robinsonecio gerberifolius,* cylindrical filament collar. D. *Robinsonecio gerberifolius*, radial endothecial tissue, showing (on left) radial cell walls and vertical columns of C-shaped thickening ends, and (on right) several horizontally oriented C-shaped thickenings. E. *Telanthophora steyermarkii*, cylindrical filament collar, adaxial view showing groove. F. *Telanthophora steyermarkii*, recurved disk floret style branches (left-center foreground) with continuous stigmatic surfaces, the anther cylinder is towards the lower right. (A–B *Stevens & Montiel 37259,* MO, holotype; C–D *Pruski & Ortiz 4163,* MO); E–F *Steyermark 49556*, MO, holotype). [Scale bars: A 0.4 mm, B 60 µm, C 0.25 mm, D 30 µm, E 0.2 mm].

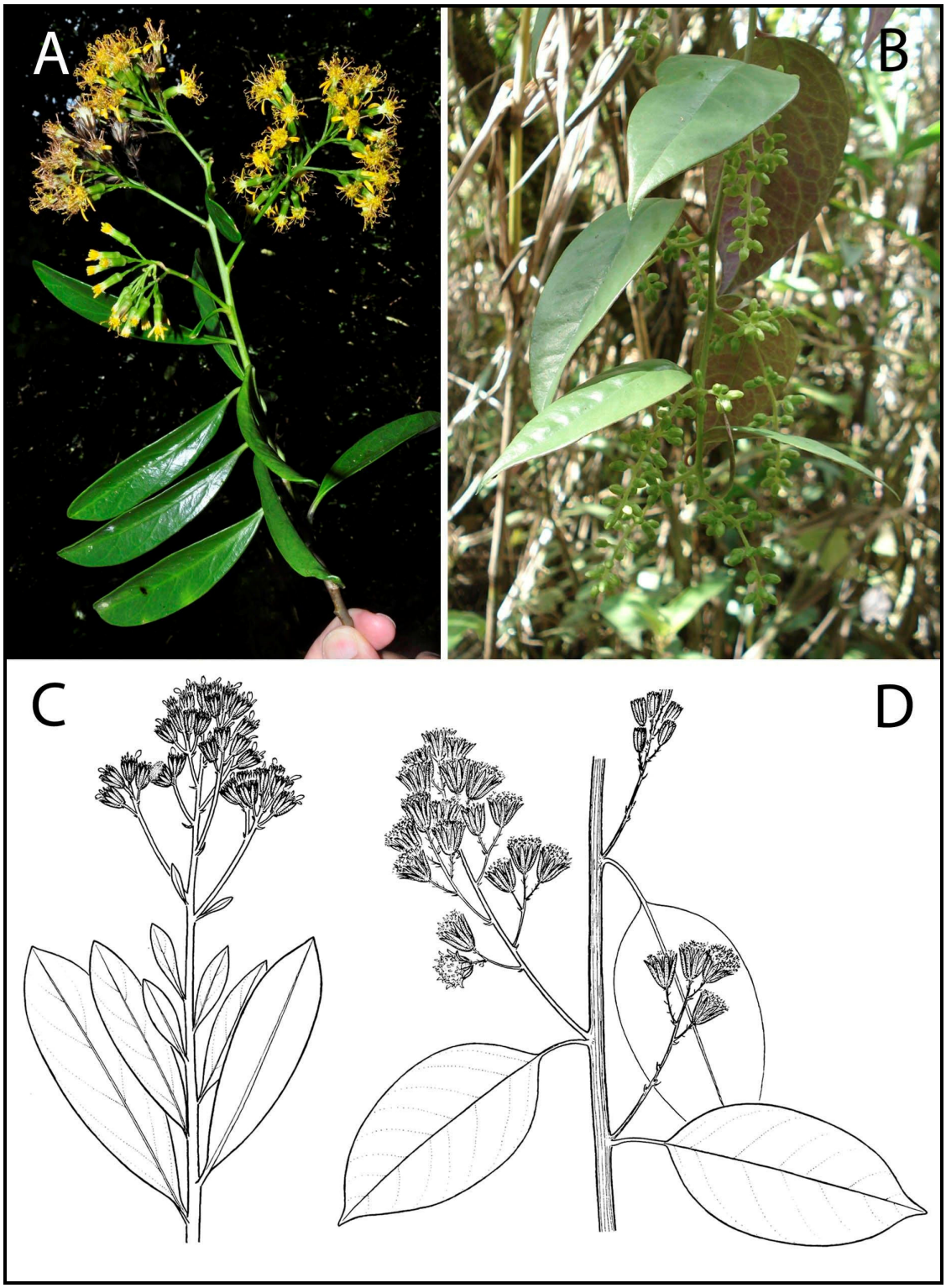

Figure 5. Capitulescence positions in Neotropical vining Senecioninae. A. Terminal capitulescence of *Ortizacalia austin-smithii*, generitype. B. Hanging flowering branch of a Peruvian species of *Pentacalia*, showing axillary capitulescences with budding capitula held within the subtending leaves. C. Terminal capitulescence of *Pentacalia phelpsiae*. D. Axillary capitulescences of *Pentacalia freemanii*. (A *Cascante-Marin & Trehos 2564*, photograph by Alfredo Cascante; B *Pruski et al. 4386*; C–D Drawn by Bruno Manara, modified from Pruski 1997 figures 286–287).

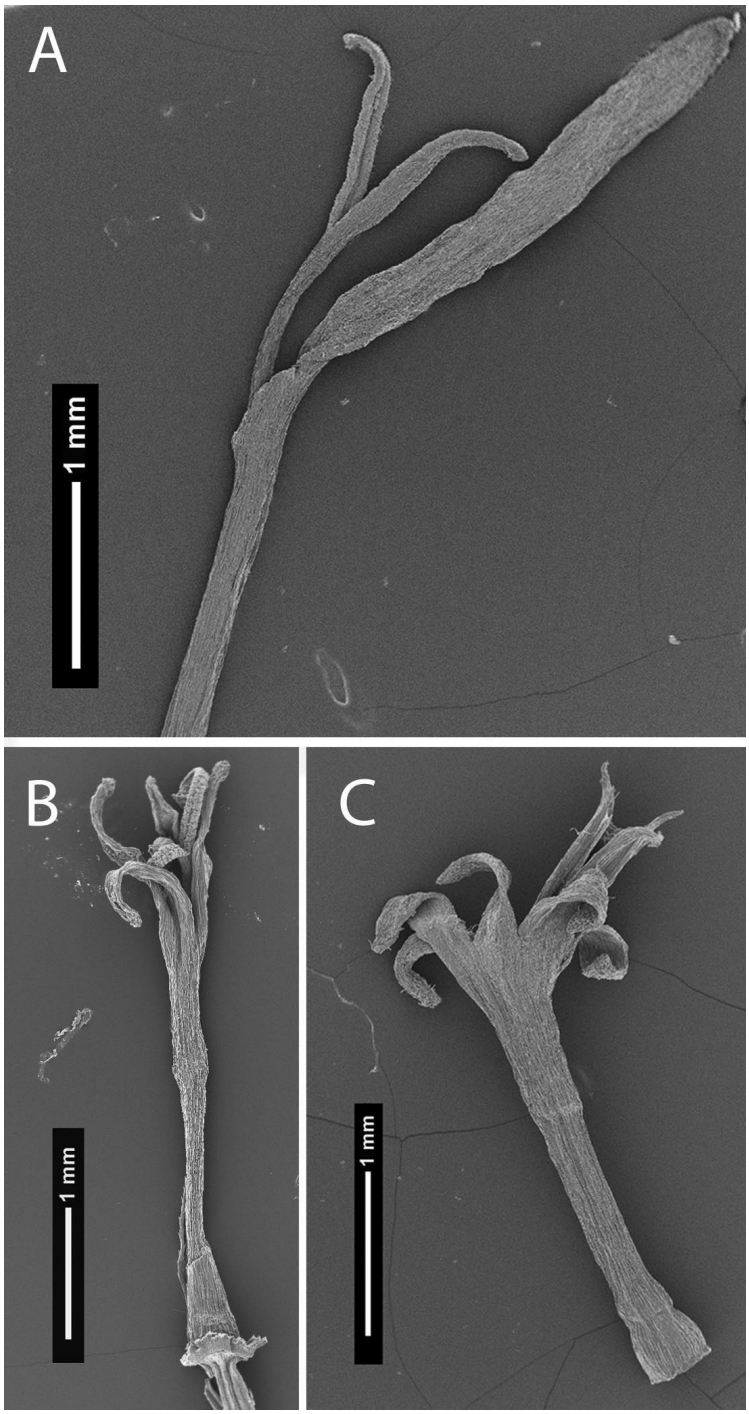

Figure 6. Floret and corolla types in *Dresslerothamnus* and *Pentacalia*; pappus bristles removed, A and C ovaries removed; florets in A–B are pistillate, C is bisexual. A. *Pentacalia tonduzii*, pistillate ray floret from heterogamous-radiate capitulum, corolla limb on upper right, bifid style on top center, adaxial view of style branch showing a 2-banded stigmatic surface, top center-left. B. *Dresslerothamnus hammelii*, pistillate marginal floret with tubular corolla from heterogamous-disciform capitulum. The two style branches are about as wide as the narrow corolla lobes. Disciform florets of heterogamous-disciform capitula are often overlooked, and the capitulum often incorrectly called homogamous-discoid. C. *Pentacalia phanerandra*, bisexual disk floret with funnelform corolla from disciform capitulum, anther cylinder on upper right, style removed. (A *Alfaro 1546*, MO; B *Kirkbride & Duke 977*, MO, holotype; C *van der Werff 7236*, MO).

Similarly, some yellowed-flowered, fleshy-leaved Pentacalias may perhaps belong to *Ortizacalia*, but the distal papillae between stigmatic bands, dimorphic stylar papillae, and stoutly long-comose stylar appendage characters (Fig. 2A) that help diagnose *Ortizacalia* are not seen in the yellow-flowered Pentacalias. Neither do the yellow-flowered vining Pentacalias seem congeneric with any of the West Indian vining segregates of *Senecio*. Nordenstam (2006, 2007) distinguished the West Indian vining genera from *Pentacalia* as follows: *Ekmaniopappus* Borhidi and *Odontocline* B. Nord. by 8–10-striate cypselae; *Herodotia* Urb. & Ekman and *Nesampelos* B. Nord. by ecaudate anthers; *Jacmaia* B. Nord. by its *Arbelaezaster-Garcibarrigoa-Pseudogynoxys*-like, cellular-triangular style branch appendage (Nordenstam 1978 fig. 30; Nordenstam 2007 fig. 53); and *Leonis* B. Nord. and *Mattfeldia* Urb. by trinerved leaves. Among these, *Ekmaniopappus* and *Herodotia* further differ from *Pentacalia* by their often opposite leaves. The yellow-flowered Pentacalias and the typical white-flowered elements of *Pentacalia* are treated here as congeneric.

The characters in *Pentacalia* of vining habit, herbage with simple trichomes, and 5-costate cypselae, albeit none of these characters unique in Senecioneae, are in combination useful in circumscribing *Pentacalia* (Jeffrey 1992a). The genera of the *Pentacalia* group (see generic key below) are mutually similar by their caudate anthers and solid clinanthia (Pruski 2012b fig. 3A), and by these characters genera of the group are obviously distinct from *Senecio* (Robinson 1989; Jeffrey 1992a: 62; Pruski 2012a; Pruski & Robinson 2018). Among neotropical genera, *Pentacalia* seems most similar to *Dresslerothamnus* by roughly similar habits, florets, and styles (Figs. 2, 5–6); and to *Monticalia* and *Ortizacalia* by pentagonal cypselae (Fig. 8). The genera in the following key, and their component species, were treated within *Senecio* prior to Robinson and Cuatrecasas (1978), Cuatrecasas (1981), Nordenstam (1978, 2006, 2007), Jeffrey (1992a), and Pruski (2012b).

Also revised here is *Zemisia* B. Nord., a genus of shrubs or trees that is reported as new to continental America. Continued work on the Trees of Mexico project has resulted in an acceptable generic placement of *Senecio thomasii* Klatt, the only generically unplaced Senecioneae in Pruski and Robinson (2018). A decade ago, I presumed this woody, caudate-anthered, yellow-rayed species with elongate, narrowly funnelform disk corollas was a *Monticalia*, but its (8–)10-costate, pubescent cypselae discouraged inclusion there. No American genus as currently circumscribed can house *S. thomasii*, although by woody habit, discolorous leaves, and similar (8–)10-costate, pubescent cypselae West Indian *Elekmania* B. Nord. and *Zemisia* B. Nord. do not seem very different. *Elekmania* differs from *S. thomasii*, however, by relatively short campanulate disk corollas with a short tube and ecaudate anthers. *Zemisia* as circumscribed by Nordenstam (2007) is white-flowered, thereby differing from both *Senecio thomasii* and *Elekmania*. In critical features other than flower color, however, *Senecio thomasii* Klatt matches *Zemisia* B. Nord., a formerly monotypic West Indian endemic described in 2006. *Zemisia* is monographed here, expanded here to include this second species—*Senecio thomasii*—resulting in a new generic record for continental America. The generic description of *Zemisia* is emended to reflect that it now contains both white-rayed and yellow-rayed plants.

A generic key that places *Dresslerothamnus*, *Pentacalia*, and *Zemisia*—each revised herein—into context follows. *Pentacalia*, and *Zemisia* were keyed by Nordenstam (2007: 213) following lead 136B "anthers basally obtuse to sagittate," but were described a few pages later by Nordenstam (2007: 227, 233) as including caudate-anthered species. *Dresslerothamnus*, keyed by Nordenstam (2007: 210) following trichome-based lead 23A, is also caudate-anthered.

Key to genera centering about Pentacalia

1. Vines or lianas.

    2. Style branch papillae obviously dimorphic, distally papillose between stigmatic bands, branch apex densely long-comose with 15–20 stiffly erect penicellate papillae about twice as long as branch diam.; trichomes simple; leaves carnose, with arching pinnate venation; corollas yellow; (1 sp.; Costa Rica) ..... **Ortizacalia** Pruski
    2. Style branch papillae isomorphic or nearly so, not distally papillose between stigmatic bands, branch apex papillose usually as a crescent-shaped fringe or sometimes as an apiculum but then apical papillae only to about as long as branch diam., apex not long-comose; trichomes simple to compound (variously modified multistoried pseudostellate-to-T-shaped); leaves chartaceous to carnose, venation pinnate to trinerved; corollas white, yellow, or reddish.

        3. Herbage with variously-modified multistoried pseudostellate-to-T-shaped trichomes; ray corollas (when present) filiform, reddish or yellow; cypselae 8–10-striate; (5 spp.; Colombia, Panama, Costa Rica) ..... **Dresslerothamnus** H. Rob.
        3. Herbage with simple trichomes; ray corollas (when present) lanceolate to elliptic-lanceolate, seldom narrowly linear-lanceolate, yellow; cypselae 5-costate; (100+ spp.; South America, less common northwards into Mexico)..... **Pentacalia** Cass.

1. Shrubby herbs, pachycaul trees, shrubs, or trees.

    4. Leaves opposite, blade margins holly-like; (3 spp.; Andean Colombia, Andean Venezuela) ..... **Scrobicaria** Cass.
    4. Leaves alternate, blade margins usually entire to weakly dentate or serrate.

        5. Cypselae 5-costate, glabrous; (50+ spp.; Andes, Panama, Costa Rica). ..... **Monticalia** C. Jeffrey
        5. Cypselae 8–10-striate-costate, glabrous or setose.

            6. Shrubby herbs or pachycaul trees; cypselae glabrous; (90+ spp.; South America) ..... **Dendrophorbium** (Cuatr.) C. Jeffrey
            6. Shrubs; cypselae setose.

                7. Leaf blade adaxial surfaces glutinous-nitidous, abaxial surfaces with secondary veins indistinct, yellow-tomentose; peduncles with few appressed bracteoles; styles sometimes with continuous stigmatic surfaces; (17 spp.; Cuba) ..... **Antillanthus** B. Nord.
                7. Leaf blade adaxial surfaces dull-green, abaxial surfaces with obvious secondary veins, white-tomentose; peduncles with several spreading bracteoles; styles with 2-banded stigmatic surfaces.

                    8. Capitula radiate or discoid; corollas yellow; disk corollas narrowly campanulate, tube shorter than limb; anthers auriculate-based; (9 spp.; Hispaniola) ..... **Elekmania** B. Nord.
                    8. Capitula radiate; corollas white or yellow; disk corollas narrowly funnelform, tube as long as or longer than limb; anthers caudate; (2 spp.; Jamaica, Mexico, Central America) ..... **Zemisia** B. Nord.

DRESSLEROTHAMNUS H. Rob., Phytologia 40: 494. 1978. **TYPE:** *Senecio angustiradiatus* T.M. Barkley (≡ *Dresslerothamnus angustiradiatus* (T.M. Barkley) H. Rob.).

Vines or lianas, flowering branches often completely pendent for 1–2+ m from tops of supporting trees; stems striate; herbage with variously-modified (T-shaped, pseudostellate, or schizotrichoid) multistoried trichomes with a many annular-celled, uniseriate stipe and multistoried unicellular cap cells equally (and appearing centric) or unequally (and appearing excentric) very elongated transversely (appearing branched), these cap cell arms (when viewed from above) may be fully superimposed and in a single plane or they may be arranged decussately and only superimposed at the stipe, arms each single-celled, often drying flat and slightly curved in four species but they are terete and straight in *D. angustiradiatus*, often fragile between stipe and cap cells with arms breaking off and the naked stipe imparting a hispid aspect to the indument. **Leaves** simple, alternate, petiolate; blade broad, often somewhat fleshy, venation pinnate, secondary veins forward-directed, often prominent, third order veins indistinct, margins entire, surfaces more or less concolorous. **Capitulescence** axillary from distal few-several distal nodes, pluricapitulate, variously paniculate, main lateral branches unbranched in proximal half, distal branchlets bracteolate, ultimate clusters of capitula subracemose to subumbellate; bracteoles linear-lanceolate. **Capitula** heterogamous, radiate or disciform; involucre 1-seriate, irregularly few-calyculate, calycular bracteoles and peduncular bracteoles similar, ascending; disk florets exserted about 2–5 mm from involucre; phyllaries commonly 5–8(–11), subequal, free, green to sometimes tinted reddish or purplish, the broader with tan-scarious margins; clinanthium solid, flat or weakly convex, epaleate, often enate-setose or setulose to aristate-squamellose; calycular bracteoles linear-lanceolate, resembling peduncular bracteoles. **Ray florets** 5 or 8, pistillate, rarely with staminodia; corolla glabrous, limb filiform, exserted but down-curved, visible surface reddish (color presumably in reference to the abaxial surface as seen when margins involute), perhaps obscured adaxial surface yellow, margins involute. **Marginal pistillate florets** 0 or 5–6; corolla actinomorphic, tubular-funnelform, yellow, tube longer than lobes. **Disk florets** 5–19, bisexual, 5-merous; corolla funnelform, 5-lobed, yellow, glabrous, tube elongate, gradually dilated at base, about as long as limb, thus throat shorter than tube, lobes lanceolate; anther thecae caudate, pale, tails straight, narrow, seemingly smooth, filament collar balusterform (basally broadened-bulbous and with enlarged basal cells) or sometimes somewhat indistinctly so with base very bulbous, endothecial tissue with cell wall thickenings radial(-transitional also with polar thickenings), apical appendage lanceolate to lanceolate-ovate, narrow apically or sometimes obtuse; style usually triangular-appendiculate, sometimes exappendiculate, base gradually dilated, branches recurved becoming once-coiled, stigmatic surfaces narrowly 2-banded, without distal papillae between stigmatic bands, apex subtruncate to triangular, never long-comose, often moderately papillose as subapical fringe or apiculum, papillae then isomorphic, free, and slightly shorter than to sometimes about as long as branch diameter, apex acute (infrequently rounded), the abaxial-lateral papillae gradually grading into sometimes longer terminal papillae. **Cypselae** tardily maturing, cylindrical or narrowly obconic, finely 8–10-striate, glabrous, brown, carpopodium annular, tan; pappus of many slender stramineous scabridulous capillary bristles, distal-most cells often acute-pointed and spreading, but obtuse (especially pre-anthesis) in two species.

Dresslerothamnus H. Rob. is a vining genus with senecioid microcharacters (Figs. 2C, 3A; balusterform filament collars, radial(-transitional) endothecial tissue, and 2-banded disk style branches). The genus was originally proposed as monotypic by Robinson (1978), who diagnosed it by the character combination of pseudostellate trichomes (Figs. 11A, 12; called 'stipitate-stellate' in Barkley 1975) and filiform ray corolla limbs (Fig. 19B). A decade later Robinson (1989) revised the genus and described two additional filiform-rayed species. The two newer species, however, have multistoried-T-shaped or schizotrichoid trichomes (Figs. 11B–C, 17, 20; trichome names derived from Greenman's *Senecio schizotrichus*; these called 'complex stelliform' by Jeffrey 1992a). The pseudostellate trichomes character once used to diagnose the genus became a species trait, and *Dresslerothamnus* was diagnosed then only by its filiform rays. The vining habit, tailed anthers, and

solid clinanthia of *Dresslerothamnus* were used by Robinson (1978, 1989), Pruski (2012b), and Pruski and Robinson (2018) to ally it with *Ortizacalia* and *Pentacalia*.

Jeffrey (1992a) expanded *Dresslerothamnus* to include a fourth species, disciform-capitulate *D. schizotrichus* (Greenm.) C. Jeffrey from Costa Rica, which has schizotrichoid trichomes (Fig. 20) similar to those of Robinson's *D. gentryi*. However, the Greenman species is odd and disciform-capitulate, whereas by filiform-rays *D. gentryi* is comfortably at home in *Dresslerothamnus* sensu Robinson (1989). The circumscription by Jeffrey (1992a) is supported by the discovery of *D. hammelii*, a second disciform species (Fig. 15) and a connecting link of sorts, having T-shaped trichomes (Fig. 17) as in filiform-radiate *D. peperomioides* combined with the disciform capitula character of *D. schizotrichus*. The T-shaped trichome caps of the two newer disciform species, however, are often broken with the remnant stipe mimicking simple trichomes, and these two species continue to be confused with *Pentacalia*.

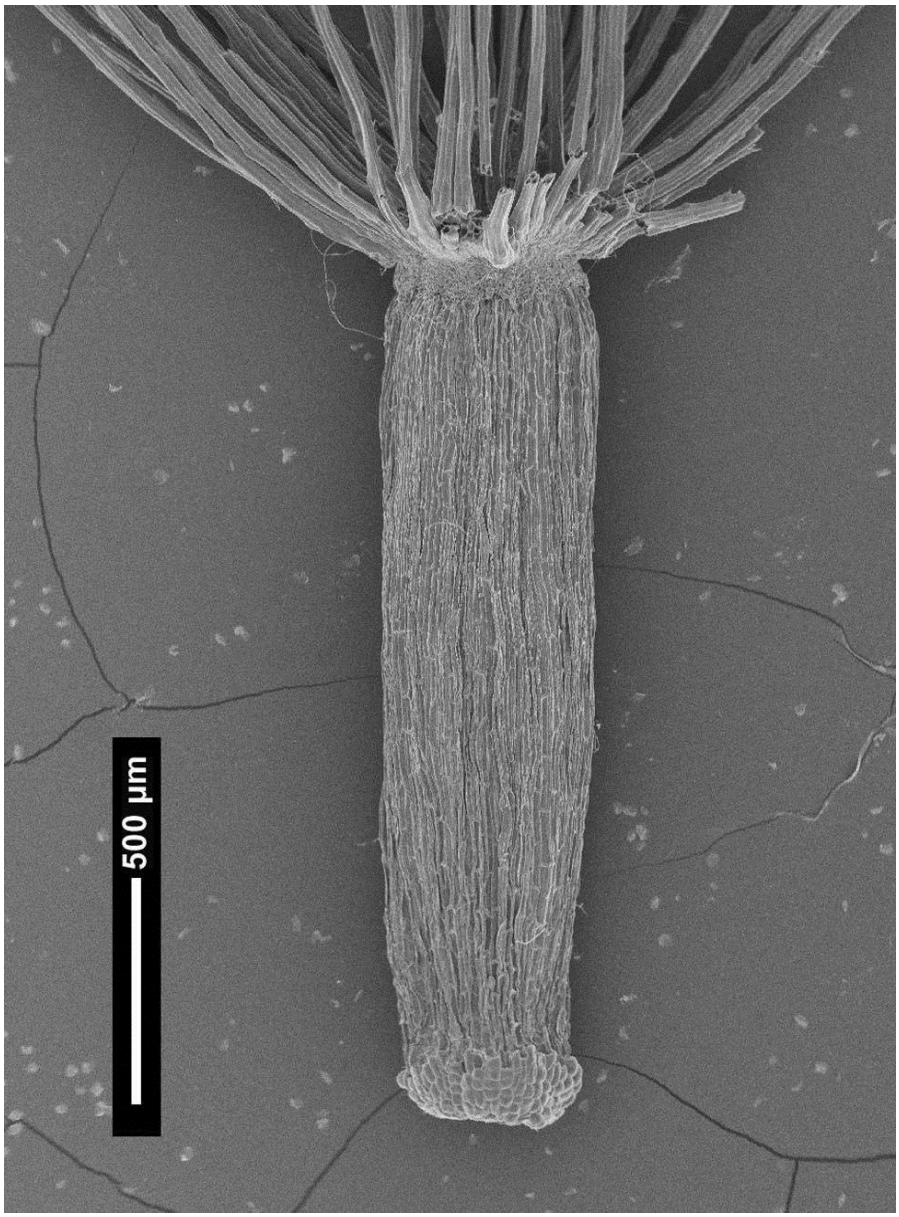

Figure 7. Pluristriate cypsela of *Dresslerothamnus angustiradiatus*, generitype. (*Croat 50008*, MO).

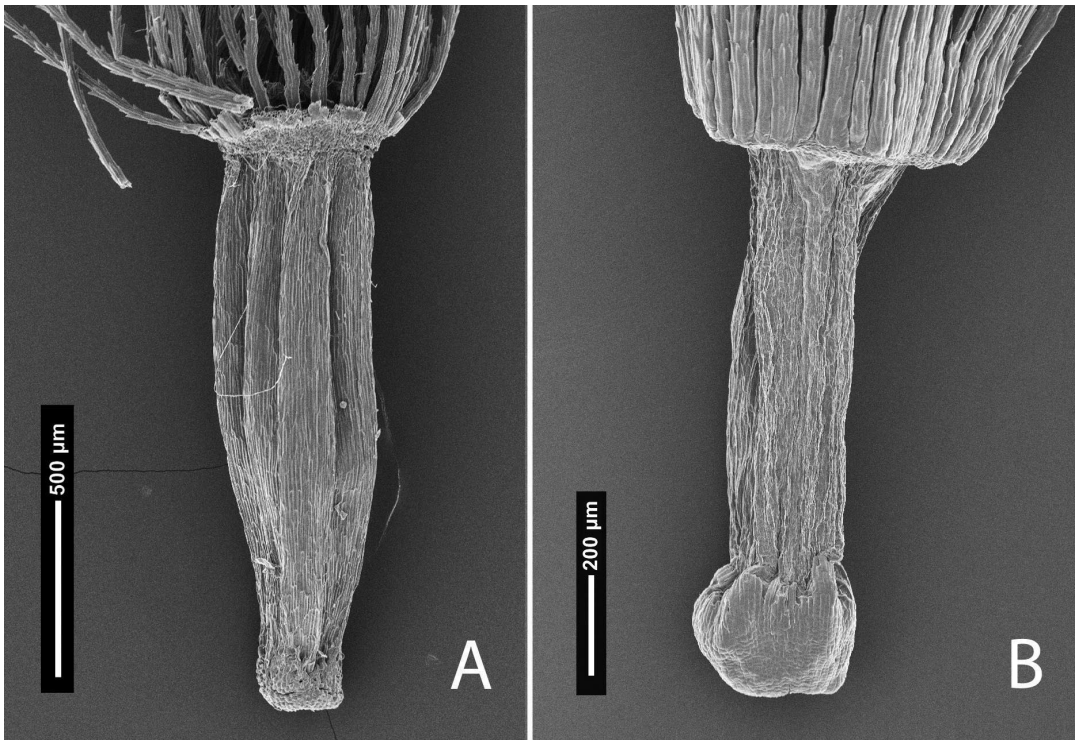

Figure 8. Cypselae in *Pentacalia* and *Monticalia*. A. *Pentacalia arborea*, generitype, mature 5-costate cypsela with a mid-sized annular carpopodium. B. *Monticalia pulchella*, generitype, immature cypsela showing large bulbous carpopodium, and two incipient costae apically. (A *King et al. 10136*, MO; B *Barclay 10427*, MO).

In Compositae, T-shaped or ramified trichomes are not peculiar to *Dresslerothamnus*. For example, pseudostellate trichomes sometimes occur in Cichorieae (e.g., Solereder 1908; Stebbins 1953; Metcalfe and Chalk 1979 fig. 5.4I) and *Olearia* Moench of Astereae (Solereder 1908 fig. 103D; Metcalfe and Chalk 1979 fig. 5.4G–H). Also in Cichorieae, Solereder (1908) notes that both pseudostellate and 'candelabra' trichomes occur in *Andryala* L. Dendroid trichomes were illustrated in *Artemisia* L. by Ling (1995). Holmes and Pruski (2000 fig. 2) reported *Mikania wurdackii* Pruski & W.C. Holmes as the sole Eupatorieae with dendroid trichomes. T-shaped (two-armed) trichomes have been found in Anthemideae (e.g., Solereder 1908; Ramayya 1962; Bremer and Humphries 1993; Ling 1995; Pruski and Robinson 2018), *Baccharis* L. (Müller 2006), mutisioids (Cabrera 1971; Freire et al. 2014; Padin et al. 2015), *Parthenium* L. (Ramayya 1962), and Vernonieae (e.g., Ramayya 1962; Faust & Jones 1973; Isawumi 1996; Robinson 2009; Redonda-Martínez et al. 2012; Wagner et al. 2014; Pruski 2016). Also in Vernonieae, stellate trichomes are found in some species of *Piptocarpha* R. Br. (Smith & Coile 2007; Pruski & Ortiz 2017), irregularly branched trichomes in *Critoniopsis* Sch. Bip. (Haro-Carrión & Robinson 2008; Robinson & Keeley 2015), and bladder-stellate trichomes in a few Brazilian and Andean genera (Wagner et al. 2014; Pruski 2016). The above examples suggest that in Compositae the T-shaped or ramified trichome characters are not tribally diagnostic, but are instead most useful in distinguishing genera and species (Sasikala & Narayanan 1998; Pruski 2016). Among American Senecioneae, however, the trichomes of *Dresslerothamnus* help circumscribe the genus.

In tribe Senecioneae, multistoried T-shaped trichomes were noted in *Brachyglottis* J.R. Forst. & G. Forst. and *Urostemon* B. Nord. (placed by Pelser et al. 2007 in provisional subtribe Brachyglottidinae) by Drury (1973a fig. 1G), Jeffrey et al. (1977), and Nordenstam (1978 fig. 16). Sahu (1983) reported stellate trichomes with 6–8 equal arms (and a short 6–8-celled stipe appearing embedded in the epidermis) in leaves of *Senecio nudicaulis* Buch.-Ham. ex D. Don (≡ *Jacobaea nudicaulis* (Buch.-Ham. ex D. Don) B. Nord.) and Pelser et al. (2004 fig. 4) showed single-cap-celled

T-shaped trichomes in several species of the *Incani* group of *Senecio* sect. *Jacobaea* (now *Jacobaea* Mill.). Nordenstam (2006) described 'much-branched' trichomes in monotypic West Indian *Herreranthus* B. Nord. (Senecioninae). On occasion, *Monticalia* (Senecioninae) has basic T-shaped trichomes with a single cap cell (Fig. 10B; Jeffrey 1987 fig. 3E–F; Jeffrey 1992a; Lapp et al. 2013 fig. 3B), which further distinguish some of its species from vining *Pentacalia*. Stipitate stellate-dendroid trichomes are found in the shrubby Andean genera *Nordenstamia* (Fig. 9C–D) and *Aequatorium*, with *Aequatorium* also having an underlayer of short-stipitate stellate-lepidote trichomes (Fig. 9A; Nordenstam 1978; Lundin 2006); each genus lacks the pluricellular stipe typical of *Dresslerothamnus*. The continuous stigmatic surfaces (Fig. 9B) of *Aequatorium* and *Nordenstamia*, however, position them in subtribe Tussilagininae (Nordenstam 1978; Lundin 2006). Moreover, the aforementioned American genera—except *Jacobaea*—are basically shrubs or trees, and none seem closely related to *Dresslerothamnus*, despite each group having faintly similar T-shaped or ramified trichomes.

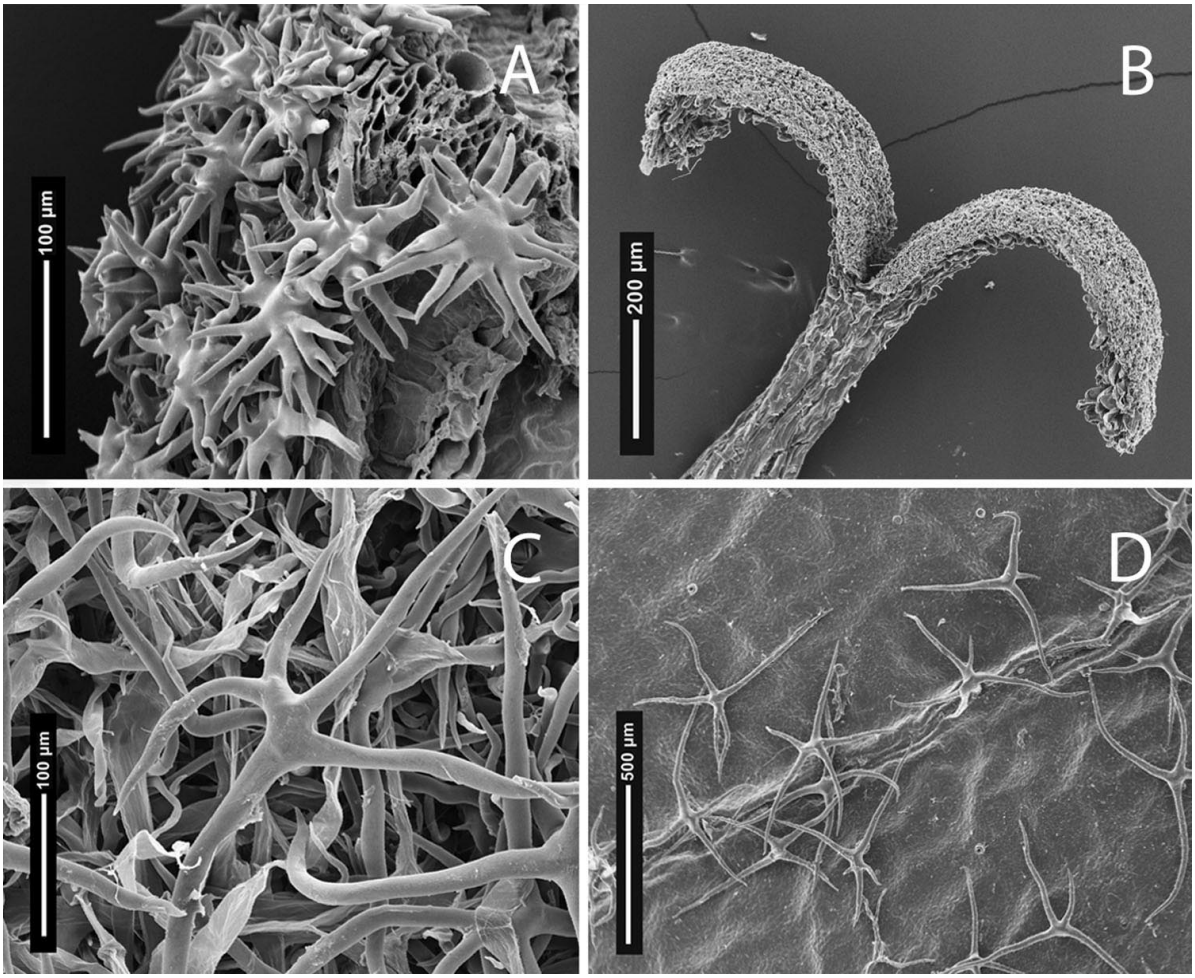

Figure 9. Branched trichomes and style branch of *Aequatorium* and *Nordenstamia* (subtribe Tussilagininae). A. Short-stipitate stellate-peltate-lepidote trichomes of the lower layer of tomentum on phyllary of *Aequatorium asterotrichum*, generitype. B. *Aequatorium asterotrichum*, generitype, style showing two branches with continuous stigmatic surfaces and obtuse branch tips. C. Long-stipitate stellate-dendroid trichomes on abaxial leaf blade surface of *Nordenstamia tovarii*. D. Moderately short-stipitate stellate-dendroid trichomes on adaxial leaf blade surface of *Nordenstamia tovarii*. The trichome arms in *Nordenstamia* are unequal, irregularly branched, and the trichomes are not truly stellate. (A–B *Cuamacás & Gudiño 459*, MO; C–D *Pruski et al. 4360*, MO).

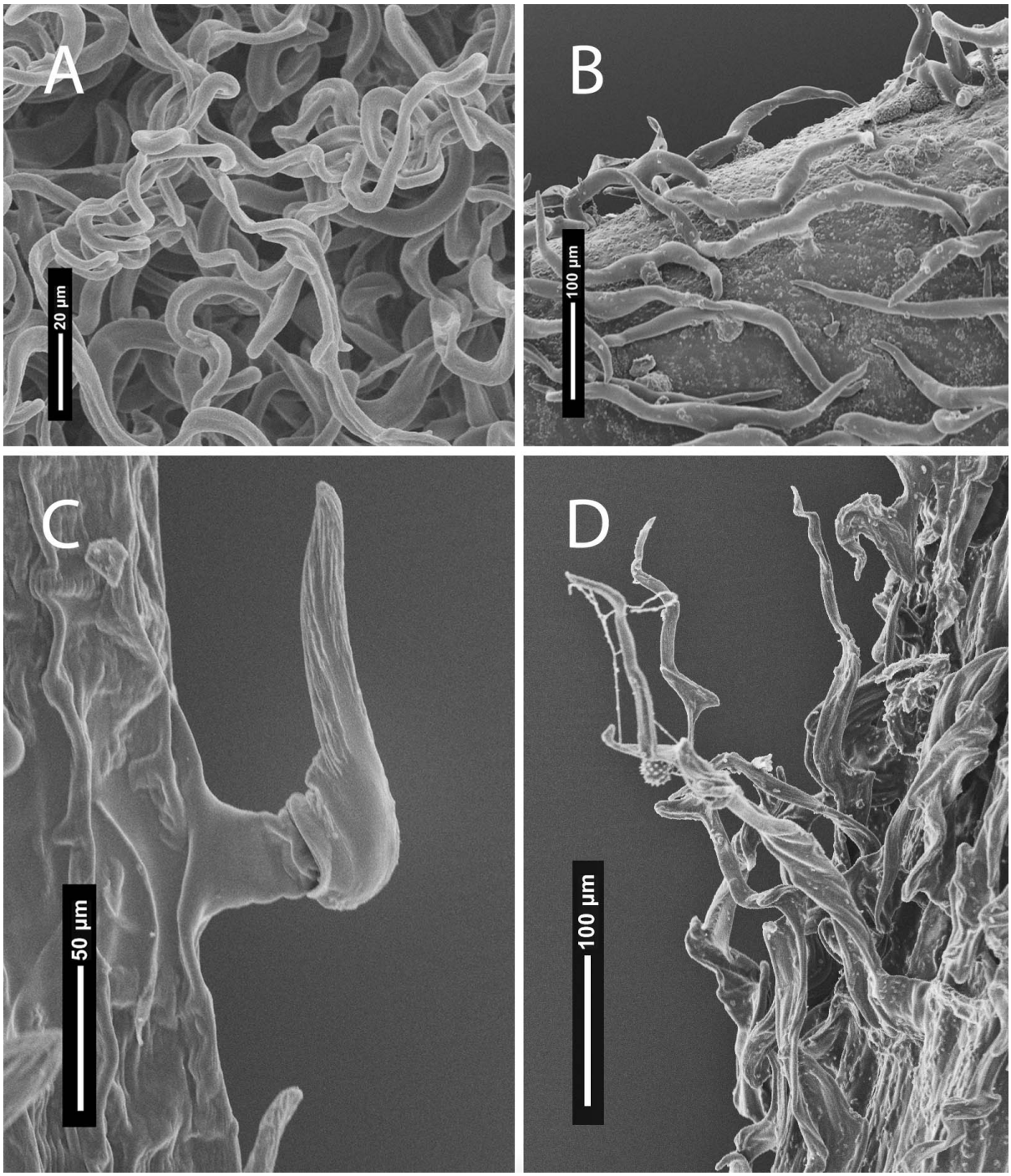

Figure 10. Trichomes in *Monticalia* and *Pentacalia* (subtribe Senecioninae). A. *Monticalia andicola*, simple, curled trichomes (similar to those in Drury and Watson 1965 fig. 5; and Jeffrey 1987 trichome type 3D) on abaxial leaf blade surface. B. *Monticalia ruiteranii*, short-stipitate, basic T-shaped trichomes with a single cap cell (similar to those in Jeffrey 1987 trichome type 3E) on adaxial leaf blade surface. C. *Pentacalia tonduzii*, collapsed, bent simple trichome on stem, the trichomes are often broken and mimic trichome stipes of *Dresslerothamnus*. D. *Pentacalia candelariae*, simple crisped-curled thin trichomes (similar to those in Jeffrey 1987 trichome type 3D). (A *Pruski et al. 3886*, MO; B *Duno et al. 1570*, MO; C *Hammel 7476*, MO; D *Wilbur 14351*, MO).

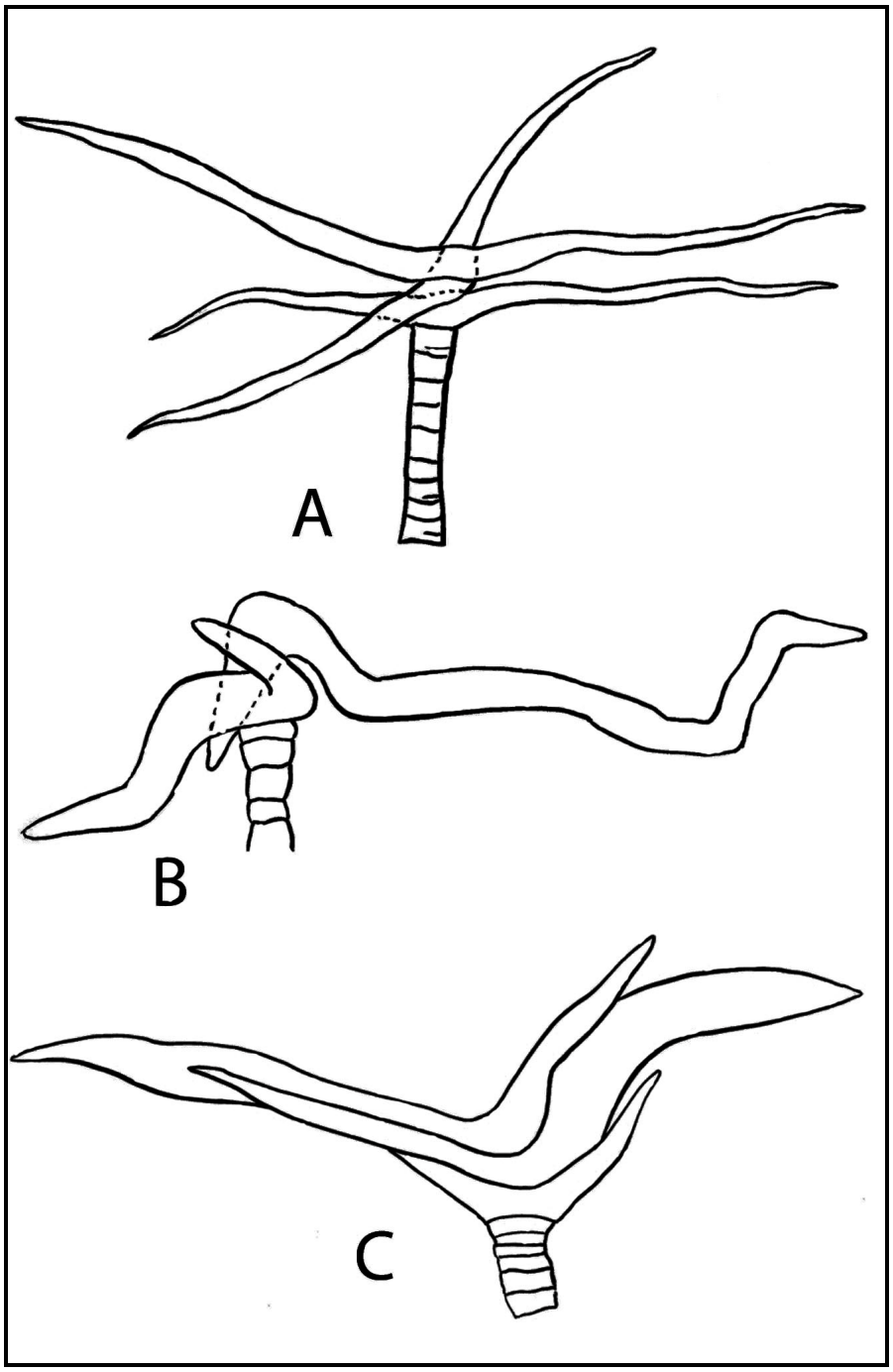

Figure 11. The three basic multistoried pseudostellate-to-T-shaped trichome type modifications in *Dresslerothamnus*. All trichomes are uniseriate, stipes pluricellular, and cap cells laterally elongated with two arms centric or excentric, equal or unequal, and decussate to superimposed. Tiers of cap cells vary from 2–5+. A. *Dresslerothamnus angustiradiatus*, generitype, "pseudostellate." Cap 3-storied, arms centric, equal, decussate. The stipe varies from shorter than to about as long as arms. B. *Dresslerothamnus gentryi*, "schizotrichoid." Cap 2-storied, arms as drawn here very excentric, unequal, irregular and sometimes curved, only partly superimposed, i.e., not in same plane when viewed from above. The same basic trichome type occurs in *D. schizotrichus.* C. *Dresslerothamnus peperomioides*, T-shaped, arms somewhat excentric, somewhat unequal, completely superimposed and in single plane when viewed from above. The same basic trichome type occurs in *D. hammelii* and the genus *Urostemon.* (Drawn by Alice Tangerini, modified from Robinson 1989).

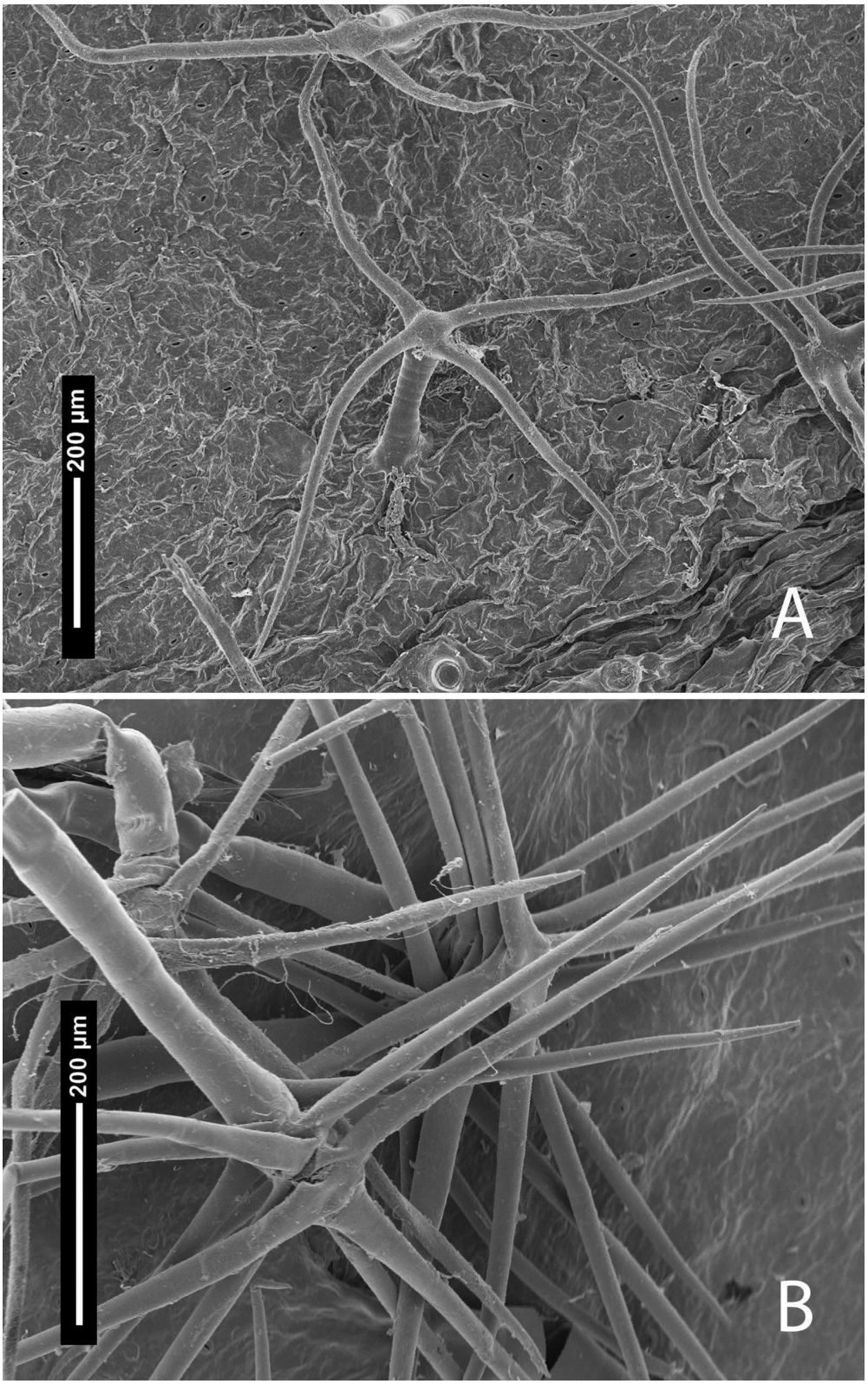

Figure 12. Variation in pseudostellate trichomes of *Dresslerothamnus angustiradiatus*, generitype. T-shaped or schizotrichoid trichomes infrequently co-occur with pseudostellate trichomes. A. Side view of trichome with pluricelled stipe and two cap cells with equal arms. B. View from above showing 5+ decussate cap cells. (A *McPherson 6990*, MO; B *Cogollo & Ramírez 3162*, MO).

Dresslerothamnus displays three basic types of pluricellular-stipitate multistoried trichomes (Figs. 11–12, 17, 20): pseudostellate, schizotrichoid, and T-shaped (Robinson 1989). Solereder (1908) stated T-shaped trichomes and pseudostellate trichomes in *Olearia* are "closely related," and also that transitional stages between these two trichome types occur in *Santolina* L. Similarly, in *Dresslerothamnus* intermediates may be found, both between species, within individual species, and within single individuals. For example, the schizotrichoid trichomes of *D. schizotrichus* seem intermediate between T-shaped and pseudostellate trichomes of other species. *Dresslerothamnus gentryi* contains both schizotrichoid and T-shaped trichomes, sometimes on the same leaf. *Dresslerothamnus angustiradiatus* typically has trichomes all pseudostellate, but both schizotrichoid and T-shaped trichomes may comingle with the pseudostellate trichomes on an individual leaf.

In *Dresslerothamnus*, the trichome cells are uniseriate, but variously pseudostellate-to-T-shaped by cap cell rotations and bilateral arm elongations. The 2(–several) apical cap cells are 'attached' directly above the obviously uniseriate stipe, with each cap cell having two arms. "What is not obvious is that the apical part is also uniseriate, but the cells are so elongated transversely as to obscure totally the fact" (quoted from Robinson 1989). The arms are equally or very unequally elongated, thereby appearing centrically or excentrically attached. The arms may be completely superimposed or superimposed only directly above stipe where 'attached.' In the herbarium, the cap cells of each type are sometimes fragile or damaged, and falling onto and littering the herbarium sheet. In these specimens the naked stipe may resemble a simple trichome, but their nature is revealed by the stipe's component annular cells, stoutness, and non-tapered apex.

The first multistoried pseudostellate-to-T-shaped trichome subtype in *Dresslerothamnus* is (1) that of the generitype *D. angustiradiatus*, for which Robinson used the term pseudostellate (viz Figs. 11A, 12; Robinson 1989 fig. 1B). These pseudostellate trichomes have 2-several cap cells with the radiating arms decussately arranged. The cap cells are superimposed only above attachment point with the stipe. Infrequently, intermediate stages of T-shaped or schizotrichoid trichomes seem to co-occur with pseudostellate trichomes. This pseudostellate trichome type (1) resembles those of *Olearia* and African *Andryala*. The pluricelled stipe in *D. angustiradiatus* appears, however, to be much stouter than those found in either *Olearia* or *Andryala*. The second trichome type (2) has cap cells excentric, arms unequal and only partly superimposed (irregularly T-shaped), curved, and flattened when dry. This trichome type modification is termed schizotrichoid (viz the *D. schizotrichus* protologue). In some Costa Rican material trichomes are often damaged and identification of imperfect material as either *Dresslerothamnus* or *Pentacalia* is problematic. The third trichome type (3) in *Dresslerothamnus* is T-shaped, with multistoried cap cell arms completely superimposed and oriented transversely in a single plane. This third type has a short several-celled stipe, with cap cell arms relatively broad and sometimes even some ranging to bulbous or inflated in appearance. Confusingly, *P. tonduzii* has collapsed, bent-broken simple trichomes (Fig. 10C), mimicking damaged T-shaped trichome type 3 of *Dresslerothamnus*. In any event, the multitiered pseudostellate type 1 trichome appears linked, by cap cell rotation, to T-shaped trichome type 3. The schizotrichoid type 2 appears to represent an intermediate stage (as suggested in other genera by Solereder 1908) of cap cell rotation.

Noteworthy unidentified collections of *Dresslerothamnus* or *Pentacalia* that do not conform include *Haber & Zuchowski 10384* from Monteverde, which is imperfect, has very thick leaves, and densely pubescent stems. The trichome type is not well seen but could be T-shaped or schizotrichoid, thus it could be a *Dresslerothamnus*, hence a western range extension. On the other hand, *Rodríguez et al. 7145* (INB) from 3200 meters elevation on Cerro Jaboncillo was originally determined and displayed on the Tropicos webpage as *Senecio angustiradiatus*, i.e., *Dresslerothamnus angustiradiatus*. The specimen of *Rodríguez et al. 7145* (MO) in front of me is imperfect, but it is likely a collection of radiate *P. tonduzii*, especially in light of the locality and elevation. Lastly,

imperfect material that I am unable to identify includes the Coclé specimens mentioned under *D. hammelii* and some Costa Rican material mostly from volcanoes mentioned under *D. schizotrichus*.

Dresslerothamnus is monographed here, and Panamanian *D. hammelii* is newly described. *Dresslerothamnus* is consequently enlarged to five species, one species endemic to Valle de Cauca, Colombia and four species centered in Costa Rica and Panama, albeit with *D. angustiradiatus* also trickling into Colombia.

Key to species of Dresslerothamnus

1. Capitula disciform.

    2. Leaf blades 2–5 cm long, evidently subcarnose; capitula with 5–6 bisexual disk florets; herbage with multistoried T-shaped trichomes with arms superimposed; (Panama) ..... **3. Dresslerothamnus hammelii** Pruski
    2. Leaf blades 3.5–9.5 cm long, drying as though chartaceous, sometimes becoming brittle and fragmenting; capitula with ca. 19 bisexual disk florets; herbage with schizotrichoid trichomes; (Costa Rica) ..... **5. Dresslerothamnus schizotrichus** (Greenm.) C. Jeffrey

1. Capitula filiform-radiate.

    3. Leaves blades 7–16 × 3.5–10 cm; herbage mostly with pseudostellate trichomes; capitulescence usually racemiform-cylindrical-paniculate and columnar in aspect; longer pappus bristles at post-anthesis with distal-most cells acute-pointed, spreading; (Costa Rica, Panama, Colombia) ..... **1. Dresslerothamnus angustiradiatus** (T.M. Barkley) H. Rob.
    3. Leaves blades 1.5–6.5 × 1–3.8 cm; herbage with T-shaped or schizotrichoid trichomes; capitulescence subumbellate-paniculate with rounded ultimate clusters of capitula; pappus bristles terminal cells mostly appressed, obtuse to rounded

        4. Leaf blade 3–6.5 × 1.8–3.8 cm, apex apiculate; ray florets ca. 8; disk florets ca. 15; phyllaries greenish; anther tails slightly irregular-contorted distally; trichomes schizotrichoid or multistoried T-shaped trichomes with arms superimposed; (Bajo Calima, Colombia) ..... **2. Dresslerothamnus gentryi** H. Rob.
        4. Leaf blade 1.5–4(–5) × 1–2.5(–3) cm, apex broadly obtuse to rounded; ray florets ca. 5; disk florets 5–8; phyllary mid-zone purplish-reddish; anther tails straight; trichomes multistoried T-shaped with arms superimposed; (Panama) ..... **4. Dresslerothamnus peperomioides** H. Rob.

1. DRESSLEROTHAMNUS ANGUSTIRADIATUS (T.M. Barkley) H. Rob., Phytologia 40: 494. 1978. *Senecio angustiradiatus* T.M. Barkley, Ann. Missouri Bot. Gard. 62: 1263. 1975 [1976]. **TYPE: PANAMA.** El Llano–Carti highway, ca. 10–12 km N of El Llano, 2 Mar 1974, *Dressler 4616* (holotype: MO; isotypes: MO, NY, US). Figures 2C, 7, 11A, 12–13.

Liana; stems hirsute-villous, brown, larger stems often fistulous; herbage mostly with pseudostellate brownish-red trichomes (seldom with each schizotrichoid and T-shaped types also on an individual leaf), trichome stipe stiff, mostly 1–1.5 mm long and 8–15 annular-celled, trichome cap cells multistoried in a decussate arrangement, arms mostly 3–6 mm long, radiating laterally, trichomes of stems much longer than those on the phyllaries, when cap cells of longer trichomes damaged, herbage may appear heterotrichous by the hispid appearance of these elongate naked stout trichome stipes. **Leaves** relatively short-petiolate; blade 5–16 × 3–10 cm, elliptic to ovate, subcarnose, lateral veins usually 4 or 5 per side, forward directed, base rounded, apex obtuse to acuminate, adaxial surface sparsely hirsute-villous to more commonly subglabrous, abaxial surface (densely) hirsute-villous to sparsely so; petiole 0.7–2.5 cm long, stout. **Capitulescence** lateral,

branches leafless, 4–28 cm long, usually racemiform-cylindrical-paniculate and columnar in aspect but sometimes becoming rounded corymbiform-paniculate, shorter than to much longer than the subtending leaf, secondary lateral branchlets few, 2–9 cm long, main axis unbranched proximally and usually longer than the 4–20-capitulate few-branched flowering portion, ultimate groups of few capitula subracemose when main axis elongated and pluricapitulate, or corymbiform in early flower, distal branchlets bracteolate, peduncles 7–10 mm long, hirsute-villous, 1(–4)-bracteolate; distal bracteoles ca. 3 mm long. **Capitula** (8–)10–13 mm long, filiform-radiate, (15–)18–23-flowered; involucre (4–)5–8 mm diam., about 2/3 as long as the fruiting disks, (cylindrical–)campanulate; phyllaries (5–)8–11, 6.5–8 × 1.5–2.5 mm, slightly reddish or purplish, strigose-villous (trichomes often short-stipitate), the broader phyllaries with margins narrower than colored mid-zone; calycular bracteoles 2–3(–5) mm long; clinanthium setose, setae 0.5–1 mm long. **Ray florets** (5–)8; corolla tube 4.5–6 mm long, limb 7–12 mm long. **Disk florets** 10–15; corolla 7–9 mm long, tube ca. 5 mm long, lobes 1–1.5(–2) mm long, moderately bulbous-papillose; anthers ca. 2.5 mm long, thecae ca. 1.5 mm long, tails ca. 0.5 mm long, smooth, filament collar ca. 0.5 mm long, appendage ca. 0.5 mm long, longer than wide; style branches 1–1.4 mm long, apex obtuse to broadly triangular, often irregularly tufted-papillose with a few papillae, papillae 0.1–0.25 mm long, the apical often the longest, but shorter than branch diam. **Cypselae** 1–2 mm long; pappus bristles 7–7.5 mm long, longer bristles at post-anthesis with distal-most cells acute-pointed, spreading.

Distribution and ecology. *Dresslerothamnus angustiradiatus*, the generitype, is the most common and widely distributed species. It was long-considered endemic to Panama, but has since been collected in Costa Rica (Pruski and Robinson 2018), and is here newly reported in Colombia, where it has been collected in Antioquia and Valle del Cauca. *Dresslerothamnus angustiradiatus* occurs from 300–1500 meters elevation, and flowers from February to June. The Costa Rican collection is from 300 meters and marks the lowest known elevation and the most northern locality. *Hampshire & Whitefoord 156* at 1500 m near Fortuna dam is the highest elevational voucher, and the collection from Valle de Cauca marks the southern limit of the species.

Representative collections. **COLOMBIA. Antioquia.** P.N. Las Orquideas, Calles, 1280–1320 m, 2 Jun 1988, *Cogollo & Ramírez 3162* (JUAM, MO). **Valle del Cauca.** Buenaventura, R.N. del Río Escalerete, 500 m, (in bud), 14 Apr 1993, *Devia et al. 3986* (F, MO; trichomes pseudostellate to short-stipitate and nearly T-shaped). **COSTA RICA**. **Limón**. 300 m, 10 Feb 1990, *Grayum et al. 9648* (CR, MO, TEX). **PANAMA**. *Croat 50008* (MO); *Hampshire & Whitefoord 156* (BM, MO, PMA); *Liesner 789* (MO); *McPherson 6990* (COL, F, MO); *McPherson 7015* (MO, NY); *McPherson 12334* (MO, US); *Valdespino et al. 645* (MO, PMA, US); *van der Werff & van Hardeveld 6537* (GH, MO, S); Cerro Pate Macho, *van der Werff & van Hardeveld 6551* (MO, NY, USM; labeled as orange-rayed).

Dresslerothamnus angustiradiatus has long-enjoyed nominal status as a Panamanian endemic, but is now documented in both Costa Rica and Colombia. The localities in Panama are basically oriented in an east-west line (as is the country) and the presence of the plant in Limon, Costa Rican collection extends the distribution only slightly further to the west. The Antioquia collection of *D. angustiradiatus* was made in Las Orquideas National Park in the northwestern Cordillera occidental, and is an expected range extension. The Las Orquideas collection is only about 240 SE of the Panamanian locality of *McPherson 7015*, which is near Cerro Pirre and about 50 km from the border with Choco, Colombia. The Valle del Cauca collection (*Devia et al. 3986*) is the southernmost of the species, but is in the Chocó biogeographic province as are plants from southern Panama. This marks the first report of the species in both Antioquia (viz Pruski & Funston 2011) and Valle de Cauca, Colombia, a is new continental record of the species, and a new generic record for Antioquia.

Figure 13. Isotype of *Senecio angustiradiatus* T.M. Barkley (≡ *Dresslerothamnus angustiradiatus*), generitype of *Dresslerothamnus*. (*Dressler 4616*, NY).

The species is generally recognized by its large leaves with long-stipitate pseudostellate trichomes. The trichomes are the largest in the genus. But, on occasion leaves of a single individual may have trichomes mostly short-stipitate T-shaped, with fewer pseudostellate and T-shaped ones, but otherwise (in capitulescence shape, leaf size, and pappus distal cell shape) match the species. Some atypical plants (e.g., *Valdespino et al. 645*, *van der Werff & C. van Hardeveld 6537*) have shorter, few-capitulate capitulescences, cylindrical involucres, on average fewer phyllaries (a character often used elsewhere as a species marker) and disk florets, 5 rays, shorter (7–8 mm long) ray corolla limbs, as compared to the more typical 8-rayed plants. The typical plants have longer pluricapitulate capitulescences and broader more-flowered capitula, but intermediates occur on these same specimens. Also very striking is the very dense pubescence of *van der Werff & C. van Hardeveld 6551*, collected at the same locality a day later than *6537*. In some Senecioneae genera such differences in indument density, number of phyllaries, and ray florets number are taken as species characters, but the plants in front of the author are all very similar in aspect and technical characters, and are taken here as conspecific. All but three collections known to me are from Panama, so basically the variation seen is not taken as geographically significant, and instead could be responses to micro-environmental conditions.

2. DRESSLEROTHAMNUS GENTRYI H. Rob., Syst. Bot. 14: 384. 1989. **TYPE: COLOMBIA. Valle del Cauca.** Bajo Calima, Juanchao Palmeras area, mature pluvial forest, 3º 55' N, 77º 02' W, 50 m, 29 Aug 1986, *Gentry & Monsalve 55603* (holotype: US; isotype: MO). Figure 11B.

Scandent vines; stems moderately hirsute-pilose; herbage with T-shaped to schizotrichoid trichomes, stipe 2–4-celled, cap cells somewhat excentrically and sometimes only partly superimposed with ends free. **Leaves** petiolate; blade 3–6.5 × 1.8–3.8 cm, ovate, subcarnose, lateral veins 2–3 per side, base broadly acute to obtuse, apex apiculate, surfaces hirsute-pilose; petiole 0.7–1.5 cm long. **Capitulescence** subumbellate-paniculate with rounded ultimate clusters of capitula, ultimate groups of (3–)5–6 capitula, subumbellate; peduncles 3–7 mm long, somewhat dense hirsute-villous, 1bracteolate; bracteoles linear. **Capitula** 11–12 mm long, filiform-radiate, ca. 23-flowered, pedunculate, weakly calyculate; involucre 5–7 mm diam., narrow-campanulate; phyllaries 8, ca. 9 × 1.5–2.5 mm, lanceolate to lance-ovate, glabrous or base weakly hirsute-pilose, mostly greenish, apex acute; clinanthium not setose. **Ray florets** ca. 8; corolla tube ca. 7 mm long, limb ca. 11 mm long, sometimes with staminodia. **Disk florets** ca. 15; corolla 9–10 mm long, tube 4–6 mm long, lobes ca. 2 mm long, shorter than throat; anthers 2–2.5 mm long, tails slightly irregular-contorted; style branch apex obtuse or triangular, evenly low-papillose or sometimes with 1–few longer somewhat tufted papillae. **Cypselae** (immature) ca. 1.5 mm long; pappus bristles ca. 8 mm long, terminal cells mostly appressed, obtuse to rounded, but not at all obviously bulbous.

Distribution and ecology. *Dresslerothamnus gentryi*, named by Harold Robinson of the Smithsonian Institutions and dedicated to Al Gentry, was the initial *Dresslerothamnus* reported in Colombia. *Dresslerothamnus gentryi* is at present known from only two collections and is a narrow endemic in the Chocó forest region at Bajo Calima, where it was collected in flower in August. One of the two Colombian collections that newly documents former Panamanian endemic *D. angustiradiatus* in Colombia is from the Bajo Calima region, the second is to the north in Antioquia. In turn, *D. gentryi* could reasonably be expected to occur also between Bajo Calima (perhaps in Choco or Antioquia) and the Panamanian frontier.

Additional collection. **COLOMBIA. Valle del Cauca.** Bajo Calima, along road between Buenaventura and Málaga, 40–65 m, 28 Feb 1990 (post fruit), *Croat 71030* (MO, US).

The trichomes of *Dresslerothamnus gentryi* (Fig. 11B) are similar to those of disciform-capitulate *D. schizotrichus*. In leaf size and filiform-radiate capitula, *D. gentryi* is similar to *D. peperomioides*.

3. DRESSLEROTHAMNUS HAMMELII Pruski, **sp. nov. TYPE: PANAMA. Bocas del Toro-Chiriquí** border. Elfin forest at divide on Chiriquicito-Calderas trail, sin. elev., 20 Apr 1968, *Kirkbride & Duke 977* (holotype: MO). [*977* was cited in Barkley (1975: 1272) and Wetter (1983: 21) as *Senecio parasiticus*, and was one of two floral microcharacter vouchers cited by Wetter as *Pentacalia*]. Figures 6B, 14–18.

Suffrutex volubilis; caules glabri vel distale valde puberuli; folia simplicia alterna petiolata, lamina 2–5 × 0.7–2 cm elliptico-ovata subcarnosa concolora pinnatim venosa glabrata vel puberula basi cuneata margine integra vel crenulata concolorata, petiolo 0.7–1.4 cm longo; capitulescentia 4–7 × 6–9 cm terminalis late corymbiformis; pedunculi 1–8 mm longi; capitula heterogama disciformia 9–10 mm alta; involucrum 2–3 mm diam. cylindricum; phyllaria 5–6, 6.5–7.5 × circiter 1 mm lanceolata glabra; flosculi pistillati circiter 5, corolla 5–6.5 mm longa tubulosa luteola lobis 4–5 circiter 1.5–2 mm longis lanceolatis; flosculi disci 5–6, corolla 6–7 mm longa infundibuliforma luteola glabra, tubo et limbo subaequalia lobis 5, 1.5–2 mm longis lanceolatis; antherae 2.2–2.5 longae caudatae, collum basi anguste dilatatum appendicibus apicalibus anguste lanceolatis; styli rami 1.2–1.5 mm longi breviter appendiculati papillae 0.1–0.2 mm longae, areis stigmaticis discretis; cypselae 1.3–2.2 mm longae circiter 5-costatae glabrae; setae pappo 5–5.5 mm longo.

Scandent vines; stems glabrous to puberulent distally, apparently solid, flowering stems leafy to near apex; herbage with brownish, multistoried, 2-armed T-shaped trichomes with cap cells sometimes variously shaped, stipe of each type 5–6 annular-celled, shorter than arms, cap cells usually 2, centric to somewhat excentric, arms superimposed throughout, ranging from relatively thick, either bulbous-inflated and reflexed thereby partly obscuring stipe to more commonly cap cells thinner and laterally spreading often parallel to leaf or stem epidermis, arms infrequently minute (or broken) and the naked trichome stipe falsely resembling simple trichomes or stipitate glands. **Leaves** petiolate; blade 2–5 × 0.7–2 cm, elliptic-ovate, subcarnose, venation pinnate, lateral secondary veins 2–4 per side, forward-directed, tertiary venation indistinct, base cuneate, margins subentire to paucicrenulate, apex acute(obtuse), surfaces more or less concolorous, glabrous to sparsely puberulent; petiole 0.7–1.4 cm long, moderately slender. **Capitulescence** 4–7 × 6–9 cm, broadly corymbiform, 15–30+capitulate, somewhat open, rounded on top with lateral branches ascending and nearly over-topping central axis, leafless, held above stem leaves, main lateral branches to 6 cm long, much longer than the subtending bracteate leaves, distal branches and branchlets drying terete; peduncles 1–8 mm long, puberulent. **Capitula** disciform, 9–10 mm long, 10–11-flowered; involucre 2–3 mm diam., cylindrical; phyllaries 5–6, 6.5–7.5 × ca. 1 mm, glabrous; clinanthium ca. 0.7 mm diam., enate, enations 0.1–0.2 mm long. **Ray florets** absent. **Marginal florets** ca. 5; corolla 5–6.5 mm long, actinomorphic, tubular, yellow, lobes 4–5, 1.5–2 mm long. **Disk florets** 5–6; corolla 6–7 mm long, funnelform, yellow, glabrous, tube 3.5–4 mm long, throat ca. 1 mm long, lobes 1.5–2 mm long, lanceolate, longer than throat; anthers 2.2–2.5 mm long, narrowly balusterform, with enlarged basal cells; style branches 1.2–1.5 mm long, stigmatic lines separated by a very narrow groove, apex obtuse to broad triangular, short-appendiculate, papillae 0.1–0.2 mm long. **Cypselae** 1.3–2.2 mm long, ca. 5-costate, glabrous; pappus bristles 5–5.5 mm long, many, distal-most cells acute-pointed, somewhat spreading.

Distribution and ecology. *Dresslerothamnus hammelii* is endemic to western Panama, and known from only three sympatric collections (Fig. 16). It occurs in elfin and dwarf cloud forests near Cerro Pate Macho (Cerro Pata de Macho), near the Bocas del Toro-Chiriquí borders. The localities are about 40 km east of Volcán Chiriquí (Volcán Barú). The type locality is near Fortuna Dam, and the two paratypes from Cerro Pate Macho were collected only about 15 km to the west of the type locality. *Dresslerothamnus hammelii* has been collected at (1646–)2164 meters elevation, and flowers from November to April.

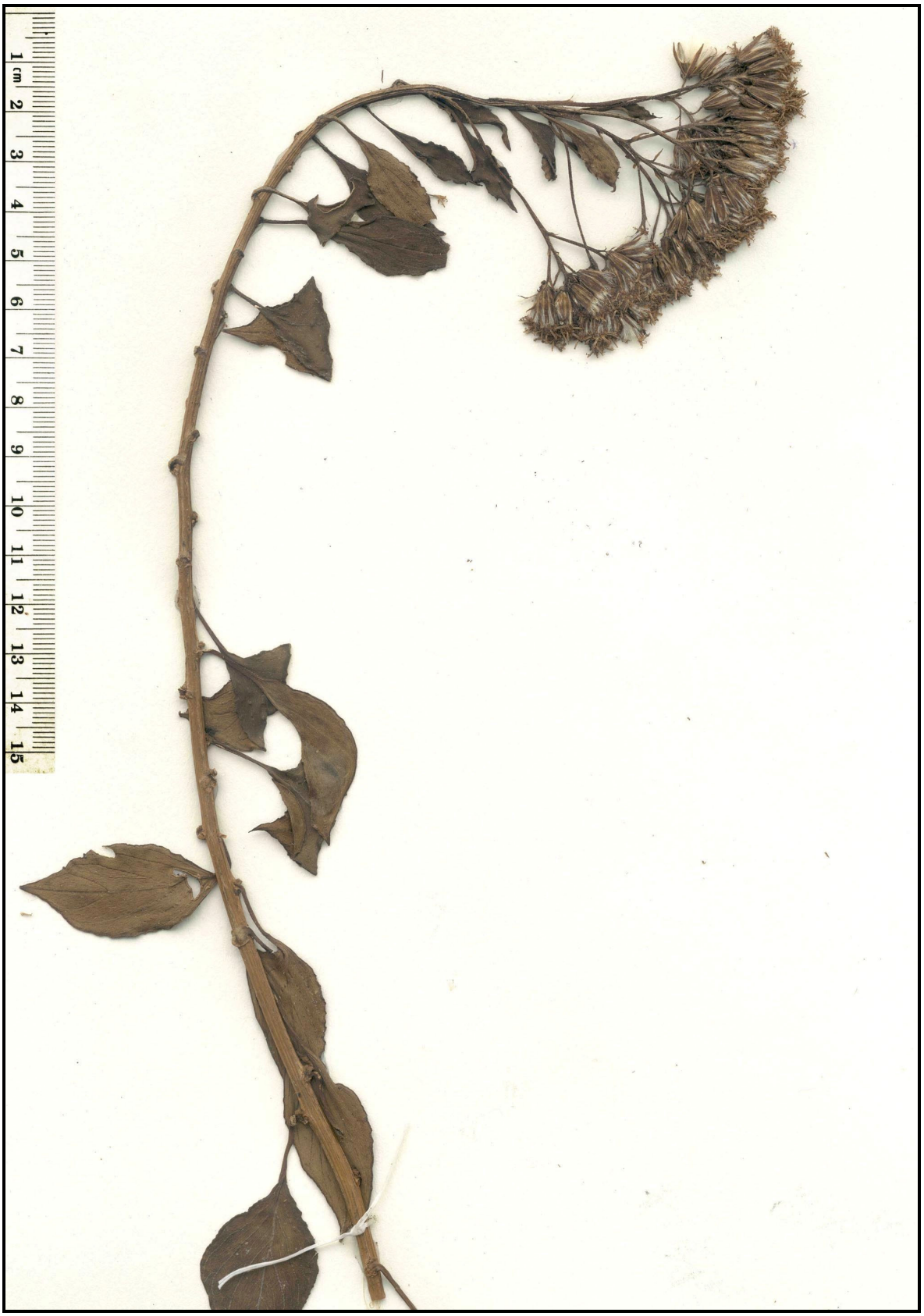

Figure 14. Paratype of *Dresslerothamnus hammelii* Pruski. (*D'Arcy et al. 12637*, MO).

Figure 15. Paratype of *Dresslerothamnus hammelii* Pruski, disciform capitula with narrow involucre of five phyllaries. (*D'Arcy et al. 12637*, MO).

Paratypes. PANAMA. Bocas del Toro-Chiriquí border. Forest along trail from end of Río Palo Alto road, near peak of Cerro Pate Macho, 7100 ft [2164 m], 20 Nov 1978, *Hammel 5778* (MO). **Chiriquí.** Between Palo Alto and top of ridge (divide) near Cerro Pate Macho, above Río Palo Alto, NE of Boquete, 5400–7100 ft. [1646–2164 m], 18 Mar 1979, *D'Arcy, Hammel & Averett 12637* (MO; voucher of photographs used).

Eponymy. The epithet of *Dresslerothamnus hammelii* honors Barry E. Hammel, collector of the two paratypes. Barry Hammel is well-known for his taxonomic work in Clusiaceae and as co-editor of the "Manual de Plantas de Costa Rica."

Dresslerothamnus hammelii is an elfin forest species collected at about (1646–)2164 meters elevation. It is characterized by disciform capitula (Fig. 15), 5–6 phyllaries, and multistoried T-shaped trichomes with cap cell arms fully superimposed throughout. The lateral flowering branches of *D. hammelii* are elongate, ascending, nearly overtop the central axis, and the relatively small capitulescence is overall moderately open and round-topped. The leaves are weakly pubescent, but the stems appear nearly heterotrichous with extreme forms of a few scattered trichomes that are large and thick-armed (Fig. 17A) to many smaller and thin-armed trichomes (Fig. 17B), but with intermediate forms linking these extremes. I do not know if the extremes in trichome morphologies are ontological, in response to damage or environmental conditions, or because material was pressed in EtOH. Often, the nature of the trichomes in *D. hammelii* are difficult to discern, and as alluded to

below it seem likely that material of this species may pass at times as *Pentacalia*. Indeed, both Barkley (1975) and Wetter (1983) cite the holotype as *S. parasiticus* (now *Pentacalia parasitica*), which I exclude from Panama. In any event, *D. hammelii* becomes the fifth species attributed to *Dresslerothamnus*.

Dresslerothamnus hammelii is similar to Costa Rican *D. schizotrichus* by similar-sized disciform capitula, but differs by geography and T-shaped (vs. schizotrichoid) trichomes. *Dresslerothamnus hammelii* has leaves similar-sized (although obtuse to round-tipped) to Panamanian *D. peperomioides*, but the Robinson species differs obviously by radiate capitula. The two other species of *Dresslerothamnus*, *D. angustifolia* and *D. gentryi*, seem only moderately similar to *D. hammelii*.

By the similar-sized disciform capitula and similar size-leaves, I have also mistaken the new species for the similar-in-gestalt and partly sympatric *P. candelariae*. For example, the imperfect *Hammel 6290* was cited in haste by Pruski and Robinson (2018) as *D. hammelii*, but this collection fits better within the broadly defined *P. candelariae*. *Dresslerothamnus hammelii* differs from *P. candelariae* by having 5–6 (vs. 7–8) phyllaries and by T-shaped (Fig. 17) (vs. simple merely slightly curled-coiled, viz Fig. 10D) trichomes, albeit the trichomes are often not well-preserved in herbarium material. Also, in *P. candelariae* the distal flowering branches tend to be very flattened as in the imperfect material. The trichomes in *P. candelariae* are simple, crisped, darker, and much thinner (Fig. 10D) than in the new species, but in the imperfect material the trichomes are mostly damaged, and generic disposition unresolved. Nevertheless, imperfect material (*D'Arcy 11343*; *Folsom & Robinson 2398*; *Hammel 6290*) from 800–1066 meters elevation in cloud forests flowering in March and April in Coclé, some 200 km to the east of *D. hammelii* localities, appears to be disciform and recalls *D. hammelii*. Although many trichomes in the Coclé plants seem damaged, others seem crisped, and imperfect materials from Coclé are provisionally referred to in *P. candelariae*.

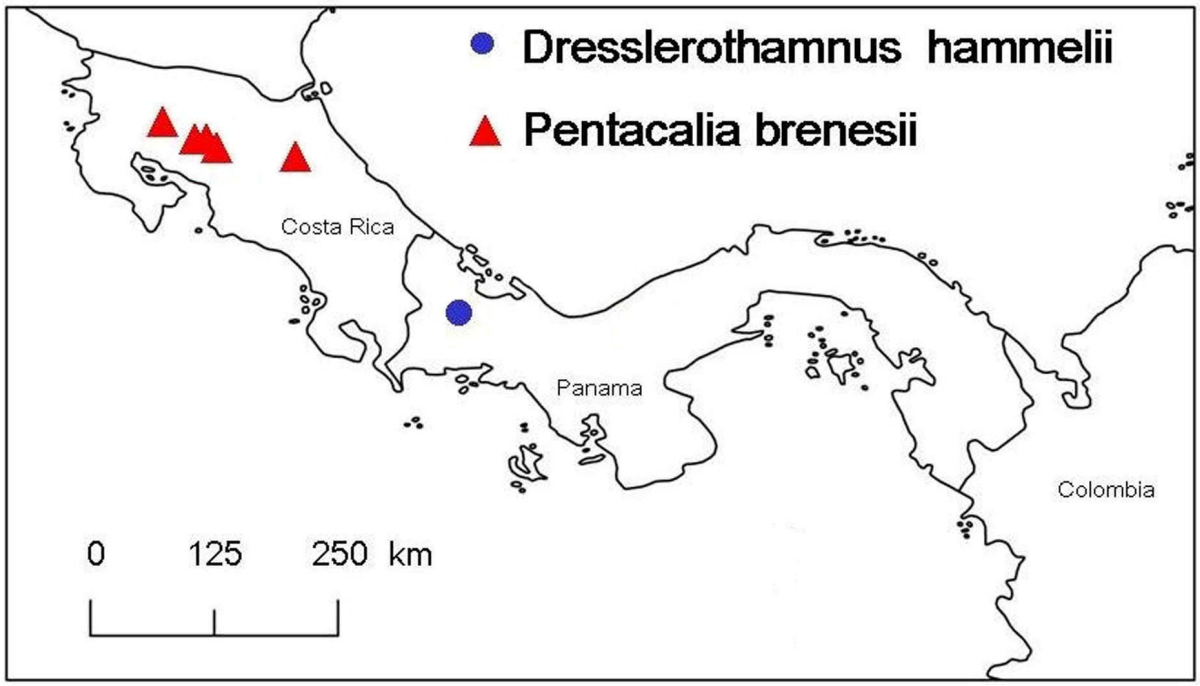

Figure 16. Distributions of *Dresslerothamnus hammelii* and *Pentacalia brenesii*.

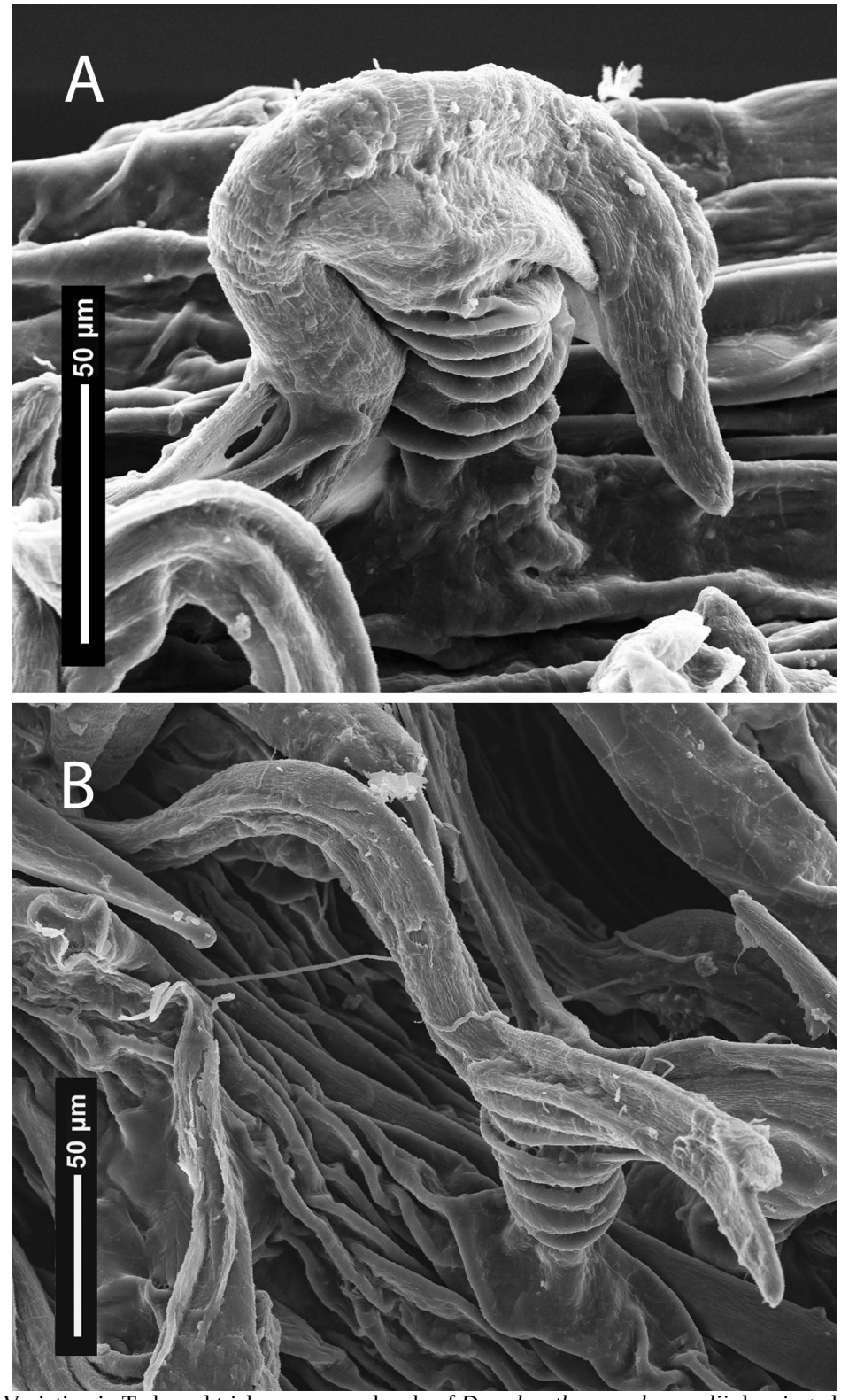

Figure 17. Variation in T-shaped trichomes on peduncle of *Dresslerothamnus hammelii* showing pluricelled stipes and 2-celled caps with arms superimposed. A. Cap cells centric and arms down-turned; under the dissection scope this relatively uncommon trichome type appears as a dark bump. B. Cap cell arms excentric and directed laterally; trichomes very abundant and light-colored. (From the holotype, *Kirkbride & Duke 977*, MO).

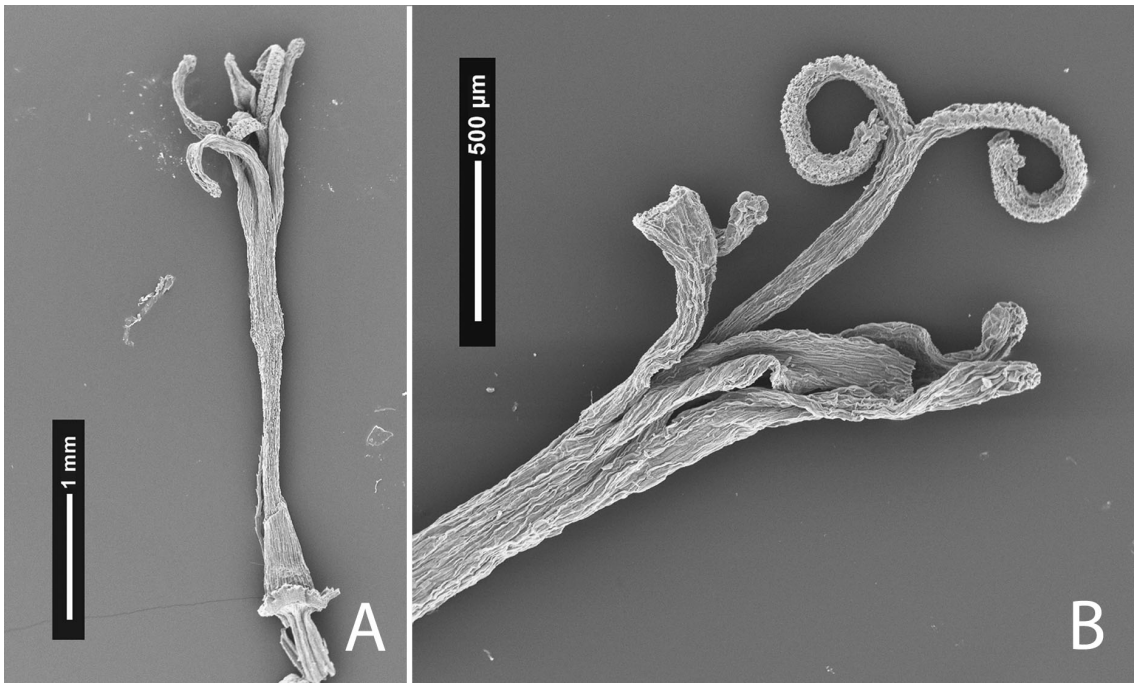

Figure 18. Marginal pistillate florets of *Dresslerothamnus hammelii*. The corollas are tubular but slightly asymmetric. (From the holotype, *Kirkbride & Duke 977*, MO).

4. DRESSLEROTHAMNUS PEPEROMIOIDES H. Rob., Syst. Bot. 14: 386. 1989. **TYPE: PANAMA. Chiriquí.** Fortuna Dam watershed, above Rio Hornito, 8° 45' N, 82° 15' W, 1250 m, 1 Jul 1987, *McPherson 11160* (holotype: MO). Figures 11C, 19.

Scandent vines; stems hirsute-pilose with T-shaped trichome arms mostly upturned, brown, herbarium specimens mostly of leafy-bracteate lateral flowering branches that are thin and seem to have a solid pith, sometimes leafless larger stems also present on specimens; herbage with brownish trichomes with cap cells superimposed and in a single plane to sometimes slightly oblique-spirally oriented as seen from above and with ends free, arms mostly to ca. 5 mm long with shorter ca. 1 mm long stipes, but stems of *Sullivan 361* with many trichomes with stout stipes to 7 mm long, stem trichomes 2(–4)-armed, cap cells often excentric, superimposed and in single plane or sometimes oblique, cap cell arms commonly upturned (at least in dried material) and trichomes in turn Y-shaped, leaf trichomes very short-stipitate, mostly 2-armed, cap cells centric, in a single plane, often close to surface, T-shaped trichomes, and indument appearing strigose. **Leaves** petiolate; blade 1.5–4(–5) × 1–2.5(–3) cm, ovate to suborbicular, subcarnose, lateral veins 1–2 per side, base obtuse to subtruncate, apex broadly obtuse to rounded, surfaces strigose to sparsely pilosulose; petiole 0.6–2.5 cm long. **Capitulescence** (narrowly) subumbellate-paniculate with rounded ultimate clusters of capitula, main lateral branches 15–30 cm long, bracteate-leafy proximally, 20–30-capitulate, branches and branchlets brown, straight; secondary lateral branchlets 2–4 cm long, ultimate groups of 4–8 capitula subumbellate with proximal peduncles noticeably elongate but not over-topping distal peduncles; peduncles 3–9 mm long, hirsute-villous, ca. 3-bracteolate; distal bracteoles ca. 2 mm long. **Capitula** 9–12 mm long, filiform-radiate, 10–13-flowered, pedunculate; involucre 2.5–3.5(–4) mm diam., nearly as long as the disk florets, cylindrical, base sparsely pilosulose; phyllaries usually 8, (6.5–)7–8.5 × 1–1.6(–2.1) mm, lanceolate, glabrous for most of their length, the broader phyllaries with margins subequal in diam. (infrequently much narrower) to purplish-reddish colored mid-zone, apex acute to acuminate; clinanthium somewhat setose-squamellose, setae-squamellae ca. 0.5 mm long, bordering alveolate; calycular bracteoles ca. 2 mm long, linear to linear-lanceolate. **Ray florets** 5; corolla tube 3.5–4 mm long, limb 4–7 mm long, often damaged. **Disk florets** 5–8; corolla 7.5–8

mm long, tube ca. 4 mm long, lobes 1.3–1.9 mm long, shorter than throat, weakly papillose, often spreading post-anthesis and exposing half or more of the anther, but anthers not fully exserted and collar not visible; anthers yellow, 2.5–3 mm long, tails straight; style branch apex broadly obtuse, with short semicircle or crown of few papillae 0.1–0.2 mm long. **Cypselae** 1.2–2.5 mm long, carpopodium sometimes to 0.2 mm long; pappus bristles 5–7.5 mm long, longer bristle terminal cells mostly appressed, obtuse (sometimes obviously bulbous in budding capitula).

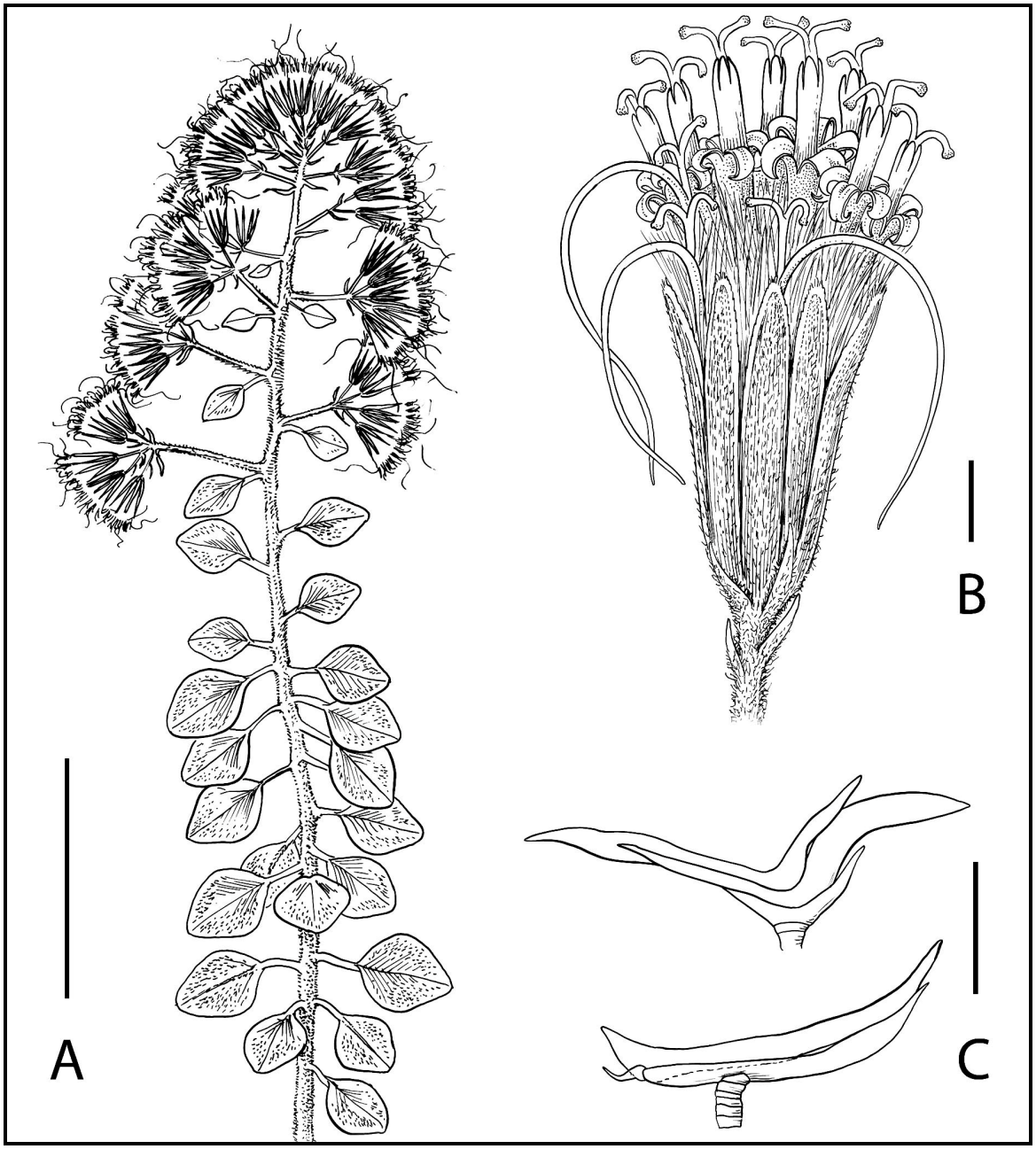

Figure 19. Drawing of holotype of *Dresslerothamnus peperomioides*. A. Leafy lateral flowering branch with subumbellate capitula. B. Capitulum showing subequal phyllaries, filiform ray corolla limbs, and anther cylinders and styles exserted from disk florets. C. Multistoried T-shaped foliar trichomes with arms superimposed, stipe many annular-celled, cap cells unicellular, excentric, arms in a single plane. (*McPherson 11160*, MO; drawn by Alice Tangerini, modified from Robinson 1989 fig. 2). [Scale bars: A 5 cm, B 2 mm, C 0.2 mm].

Distribution and ecology. *Dresslerothamnus peperomioides* is endemic to Panama (Chiriquí and Darién). The species was described by Robinson (1989) as then known from only the type, but is now known to me from seven collections. Several collections are from near Fortuna Dam (the type locality), but the initial collections of the species appear to be the two collections made on 15 July 1976 on Cerro Colorado, some 60 km to ESE of the Fortuna site. The recent Flores collection was made on Cerro Chucanti, in Darién very near the border with Panama; it extends the known range of the species 400+ km to the east. *Dresslerothamnus peperomioides* is found from 900–1600 meters elevation, and flowers from March to September.

Collections examined. **PANAMA**. **Chiriquí.** *Correa et al. 2241* (MO, PMA); *Croat 37239* (MO, US); *Folsom et al. 5356* (MO); *McPherson 12848* (F, K, KSC, MO, US); *Sullivan 361* (MO). **Darién.** *Flores & Morales 577* (MO).

Most collections known to me of this small-leaved species date from the 1970s and 1980s, with two of these collections originally determined as *P. streptothamna*, a species very similar in gestalt. Further regional plants with similar aspects are *P. candelariae*, *D. hammelii*, and *D. schizotrichus*. *D'Arcy et al. 12637*, a paratype of similar-sized-leaved but disciform *Dresslerothamnus hammelii* Pruski, for example, was initially misdetermined by the author as *D. peperomioides*. These four near look-alike but different plants mostly differ from filiform-radiate *D. peperomioides* by disciform capitula, or in the case of *P. streptothamna* by broader ray corolla limbs. Other distinctions include the simple trichomes in the Pentacalias and the sessile ultimate capitula and pointed terminal pappus cells in *D. schizotrichus*.

Dresslerothamnus peperomioides is similar to Colombian *D. gentryi* H. Rob. by gestalt, filiform rays, and appressed obtuse or rounded apical pappus cells, albeit these almost bulbous in *D. gentryi*. *Dresslerothamnus peperomioides* differs from *D. gentryi* by 1–4(–5) cm long round-tipped (vs. 3–7 cm long acute-tipped) leaf blades, purplish-reddish (vs. green) phyllaries, and five (vs. eight) ray and 5–7 (vs. 10–15) disk flowers per capitulum.

5. DRESSLEROTHAMNUS SCHIZOTRICHUS (Greenm.) C. Jeffrey, Kew Bull. 47: 64. 1992. *Senecio schizotrichus* Greenm., in Standley, Flora of Costa Rica, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1518. 1938. **TYPE: COSTA RICA. San José.** Vicinity of El General, 975 m, Jan 1936, *Skutch 2502* (holotype: MO; isotypes: K, MICH, NY, US). [The Compositae introduction in Standley (1938: 1419) stated that Greenman supplied three new species descriptions]. Figures 3A, 20–21.

High climbing liana; stems densely villous-strigose, grayish-brown, fistulose, sometimes nodally deflected distally; herbage grayish with schizotrichoid trichomes, trichomes short-stipitate multistoried 4–8-armed trichomes (often damaged or poorly preserving), cap cells 2–4, unequally elongated (excentric), only partially superimposed as seen from above and with ends free, cap cell arms sometimes curved, often parallel to stems and leaf epidermis but sometimes upturned or ascending. **Leaves** moderately petiolate; blade 3.5–9.5 × 1.5–5.5 cm, elliptic-lanceolate to elliptic, subcarnose but drying as though chartaceous (herbarium material sometimes becoming brittle and fragmenting), lateral secondary veins 5–7 per side, third order veins slightly visible as well, base cuneate to obtuse, margins sometimes drying crenulate or at least when damaged appearing crenulate, apex acute(obtuse), surfaces hirsute-villous to sparsely so; petiole 0.7–1.2 cm long, moderately slender. **Capitulescence** corymbiform-paniculate, subcylindrical or narrow-pyramidal, distal few nodes of main axis deflected at nodes or straight, main lateral branches 4–14 cm long, slightly longer than the main axis subtending leaves, 10–40+capitulate, lateral branches leafless but branchlets each subtended by axially linear-lanceolate bracteoles, branches and branchlets griseous-villosulous; secondary lateral branchlets ≤ 2 cm long, columnar in aspect, ultimate three capitula sometimes in subsessile clusters, but irregularly ternate or short-pedunculate and racemiform; peduncles 1–4 mm

long, hirsute-villous, 1–3-bracteolate; distal bracteoles 2.5–7 mm long. **Capitula** (in early anthesis) disciform, 9–12 mm long, 22–25-flowered; involucre 3.5–4 mm diam., cylindrical-turbinate; phyllaries usually 8, 6.5–8 × 1.5–1.8 mm, rarely a few connate to near apex, puberulent, the broader phyllaries with margins slightly narrower than colored mid-zone; clinanthium enate-setulose, enations-setulae 0.1–0.2 mm long; calycular bracteoles 2.5–4 mm long, narrowly linear-lanceolate. **Ray florets** absent. **Marginal florets** 5–6; corolla 4–6 mm long, actinomorphic, tubular-funnelform, yellow, tube 3–5 mm long, lobes 4–5, ca. 1 mm long. **Disk florets** 17–19; corolla (4–)5–6(–7.5) mm long, tube 2–3.8 mm long, lobes 1–1.4 mm long, weakly papillose; anthers ca. 1.5 mm long, collar ca. 0.5 mm long, tails ca. 0.2 mm long, less than half as long as the collar, appendage narrowly lanceolate, apex obtuse; style branches 1–1.4 mm long, apex nearly truncate, with only a few spreading distal papillae ca. 0.1 mm long in an abaxial semicircle, no central tuft seen. **Cypselae** (immature) ca. 1 mm long; pappus bristles (3.5–)4.5–6(–6.5) mm long, longer bristle distal-most few cells very slightly spreading and not as long as bristle width, broadly acute-pointed.

Distribution and ecology. *Dresslerothamnus schizotrichus* is endemic to Costa Rica, where it flowers in January and February from 975–1500 meters elevation. I know the species with certainty from only the two collections cited here.

Additional collection. **COSTA RICA**. **Cartago.** Between 2–4 km SW of Muñeco on steep slopes of remnant forest and pasture above Río Sombrero, 1500 m, 25 Feb 1978, *Utley 5858* (MO).

The schizotrichoid trichomes of *Dresslerothamnus schizotrichus* have 2–4 variously superimposed cap cells, thereby showing up to eight radiating arm tips. When dry, the arms may shrivel irregularly, curve, become variously directed, and as distorted they may appear to be slightly stellate, serrate, or divided. The trichomes of *D. schizotrichus* thus are very different in aspect from those of the common *D. angustiradiatus*, which has arms free and decussate. Instead, the trichomes of *D. schizotrichus* are more similar to those occasionally seen in Colombian *D. gentryi* (Fig. 11B; Robinson 1989 fig. 2B) and *Urostemon kirkii* (Hook. f. ex Kirk) B. Nord. (viz Drury 1973a fig. 1G; Nordenstam 1978 fig. 16N), the latter from New Zealand.

This species was described in the protologue as discoid, and was long known from only the type. An additional collection from Costa Rica (*Utley 5858*) distributed as *Senecio candelariae*, however, in SEM study (Fig. 20C) proves to be *D. schizotrichus.* The two known localities are in central Costa Rica and about 50 km apart. Another collection (*Salas et al. 185* n.v.) in the Tropicos database may be this species (as determined by Alex Rodríguez in 2015) or the similar *P. candelariae*. Among the type specimens of *D. schizotrichus*, some have the stem apex nodally deflected (zig-zag), whereas in *Utley 5858* and some type material the stems are straight.

Dresslerothamnus schizotrichus further differs from *D. gentryi* by its smaller disciform (vs. filiform–radiate) capitula and by pointed (vs. obtuse to rounded) apical pappus cells. The similarity in trichome types of filiform-radiate *D. gentryi* and disciform *D. schizotrichus*, supports Jeffrey's (1992a) inclusion of *D. schizotrichus* in the genus. The broader circumscription of *Dresslerothamnus* by Jeffrey (1992a) is further supported here by discovery of disciform *D. hammelii*, which has T-shaped trichomes, and serves to link the two disciform species to three radiate *Dresslerothamnus* sensu Robinson (1989).

The two cited collections of *Dresslerothamnus schizotrichus* have abaxial leaf blade trichomes with moderately long stipes, and the schizotrichoid nature of the trichomes apparent in SEM studies (Fig. 20). It seems possible that further collections are similarly filed in herbaria as either *Pentacalia* or *Senecio*, as was the Utley collection. Moderately similar-in-leaf-size Costa Rican material mostly from volcanoes of disciform-capitulate *P. candelariae* with damaged trichomes resembles *D. schizotrichus*, but the *Dresslerothamnus* differs by petioles and abaxial leaf blade

surfaces that are denser pubescent and by non-fascicled capitula. In general, the trichomes of Pentacalias are often thin, elongate terminal cells, whereas the trichome arms in species of *Dresslerothamnus* are thicker, relatively short, thereby helping distinguish the genera.

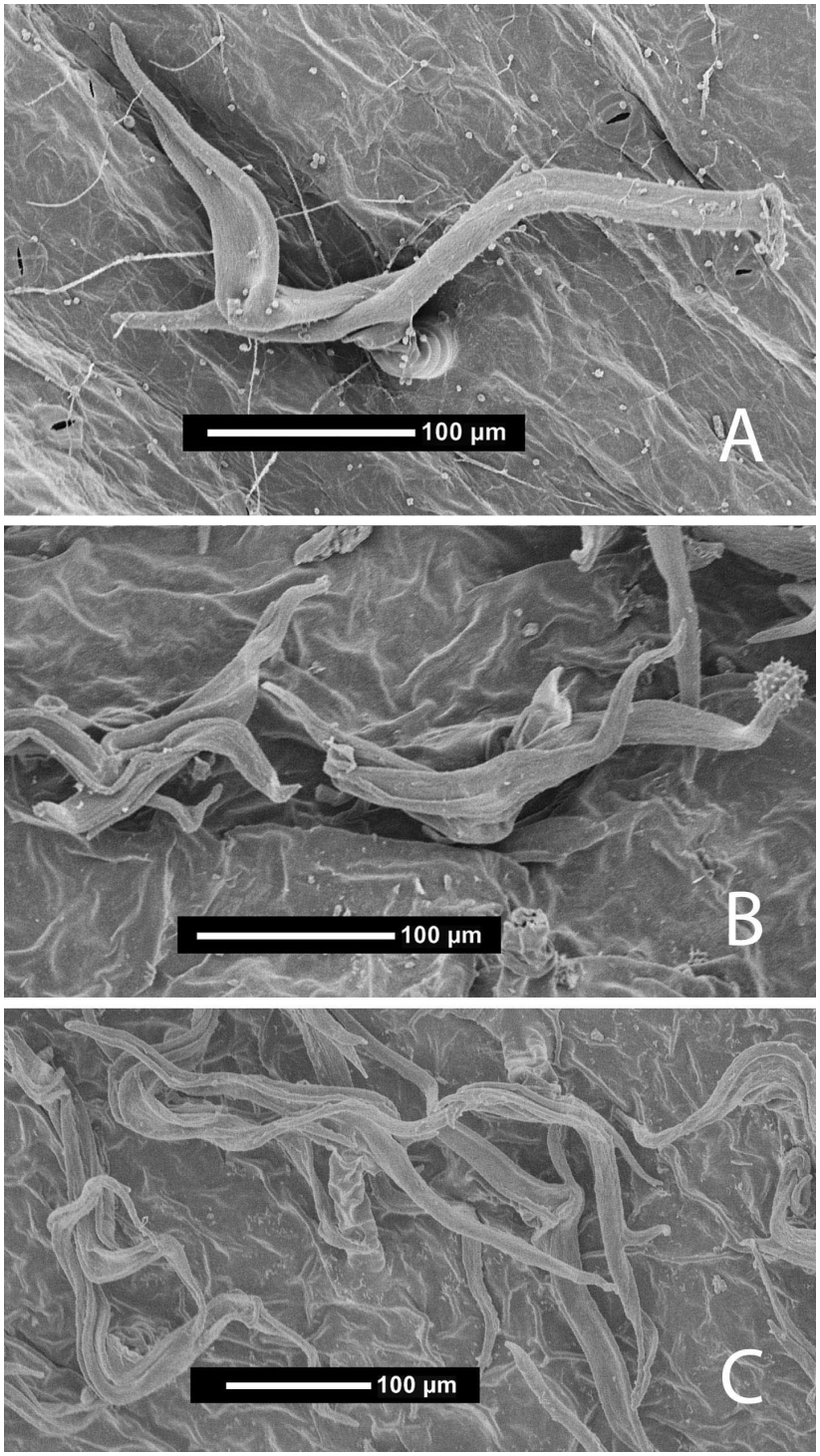

Figure 20. Schizotrichoid trichomes of abaxial leaf surfaces of *Dresslerothamnus schizotrichus.* The 2–3 cap cells are excentric, unequal, and only partly superimposed. The stipes are relatively short and few-celled. The trichome in A is moderately well-preserved; trichomes in B–C are poorly preserved, and grotesquely disfigured. (A–B from the holotype, *Skutch 2502,* MO; C *Utley 5858*, MO).

Figure 21. Holotype of *Senecio schizotrichus* Greenm. (≡ *Dresslerothamnus schizotrichus*), showing stems deflected at distal nodes. (*Skutch 2502*, MO).

PENTACALIA Cass. in F. Cuvier (ed.), Dict. Sci. Nat. (ed. 2) 48: 449, 461, 466. 1827. **TYPE:** *Cacalia arborea* Kunth (≡ *Pentacalia arborea* (Kunth) H. Rob. & Cuatr.).

Senecio sect. *Streptothamni* Greenm., *Senecio* sect. *Triana* Cuatr.

Scandent to climbing woody vines, often with long hanging-pendent flowering branches with the leaves upside-down or upturned; stems subterete, pubescent or glabrous, leaves mostly in distal half but often not greatly decrescent, distal internodes often shorter than leaves; herbage with simple trichomes when pubescent, sometimes obliquely appendaged but appendage thin-walled. **Leaves** simple, alternate or rarely opposite, petiolate or rarely sessile; blade generally elliptic to ovate, sometimes oblanceolate or obovate, subcarnose to less commonly chartaceous or coriaceous, venation typically pinnate with secondary veins forward-directed, infrequently (the generitype group) secondaries at nearly right angles to midrib, margins usually entire or when serrate the serrations regular, our eglandular. **Capitulescence** terminal (on main axis or on elongated branches much longer than main stem leaves) or less commonly axillary on branches shorter than subtending leaves, pluricapitulate to less frequently paucicapitulate, generally corymbiform-paniculate, often pyramidal to rounded or flat-topped, less commonly cylindrical, not usually leafy with specialized large primary bracts. **Capitula** nearly always heterogamous (radiate or disciform), some South American species consistently homogamous-discoid, usually (5–)11–64-flowered, not nutant, subsessile or more commonly pedunculate; involucre 1-seriate, typically calyculate; phyllaries commonly 5–13, subequal, free, rarely strongly connivent to near apex, usually stiff, median abaxial surface with nerves well-embedded, without evident nerves or costae, often with narrowly scarious (outer) ones alternating with broadly scarious-margined (inner) ones, slightly to moderately spreading in fruit; calycular bracteoles usually small and subglabrous, typically less than half the length of involucre (rarely obviously calyculate with calycular bracts as long as involucre or even white-lanate-tomentose calycular bracts and then about half as long as involucre); clinanthium solid, flat, epaleate, often shortly cristate. **Ray florets** (when present) usually (1–)4–14, pistillate, corolla sometimes quickly deciduous; corolla commonly yellow, glabrous, tube and limb often subequal, limb weakly to moderately exserted, usually lanceolate or elliptic-lanceolate to oblong or obovate, usually 4(+)-nerved and about as wide as phyllaries, infrequently linear-lanceolate, 2-nerved, and obviously narrower than phyllaries. **Pistillate marginal florets** (when disciform) usually 1–8, often shorter than and held within involucre; corolla tubular-funnelform; shortly symmetrically 3–5-lobed, flattened radiating limb absent, or very rarely corollas pseudobilabiate and florets with staminodia. **Disk florets** usually (4–)7–50, bisexual, 5-merous; corolla campanulate or more commonly funnelform and often much-elongated at maturity, commonly yellow, glabrous, tube base usually dilated around stylopodium at maturity, lobes longer than wide, sometimes with a medial resin duct; anthers stramineous, filament collar balusterform (swollen), with enlarged basal cells, thecae caudate (not rounded), tails usually shorter than collar, apical appendage oblong and sometimes thick-margined; style exappendiculate or seldom somewhat appendiculate, base nodular, held above basal nectary on stipe, branches with paired stigmatic lines, papillae isomorphic, adaxially without distal papillae arising between stigmatic bands, abaxially with gradually diminishing collecting papillae, apices mostly truncate or obtuse, sometimes triangular, smooth to slightly papillose with short apical tuft or peripheral semicircular fringes of relatively small papillae shorter than branch diam., apices never long-comose. **Cypselae** obconic, subterete, tardily maturing and in capitula of herbarium specimens, often more or less collapsed, 5-costate at maturity (but mature fruits infrequently seen), pericarp with rectangular and hexagonal crystals (Fig. 3B), ribs sometimes decurrent onto carpopodium, glabrous or rarely long-pilose near base; carpopodium symmetric-annular, moderate-sized, broader than cypsela base, with a narrow distal rim; pappus bristles of rays and disks similar, many, 1(–2)-seriate, white to stramineous (rarely pinkish), scabridulous to barbellate, about as long as the disk corollas, apex usually evenly narrowed. $x = 20, 40$ (viz Robinson et al. 1997; higher counts reported by them as *Pentacalia* prove instead to be for species of *Dendrophorbium*).

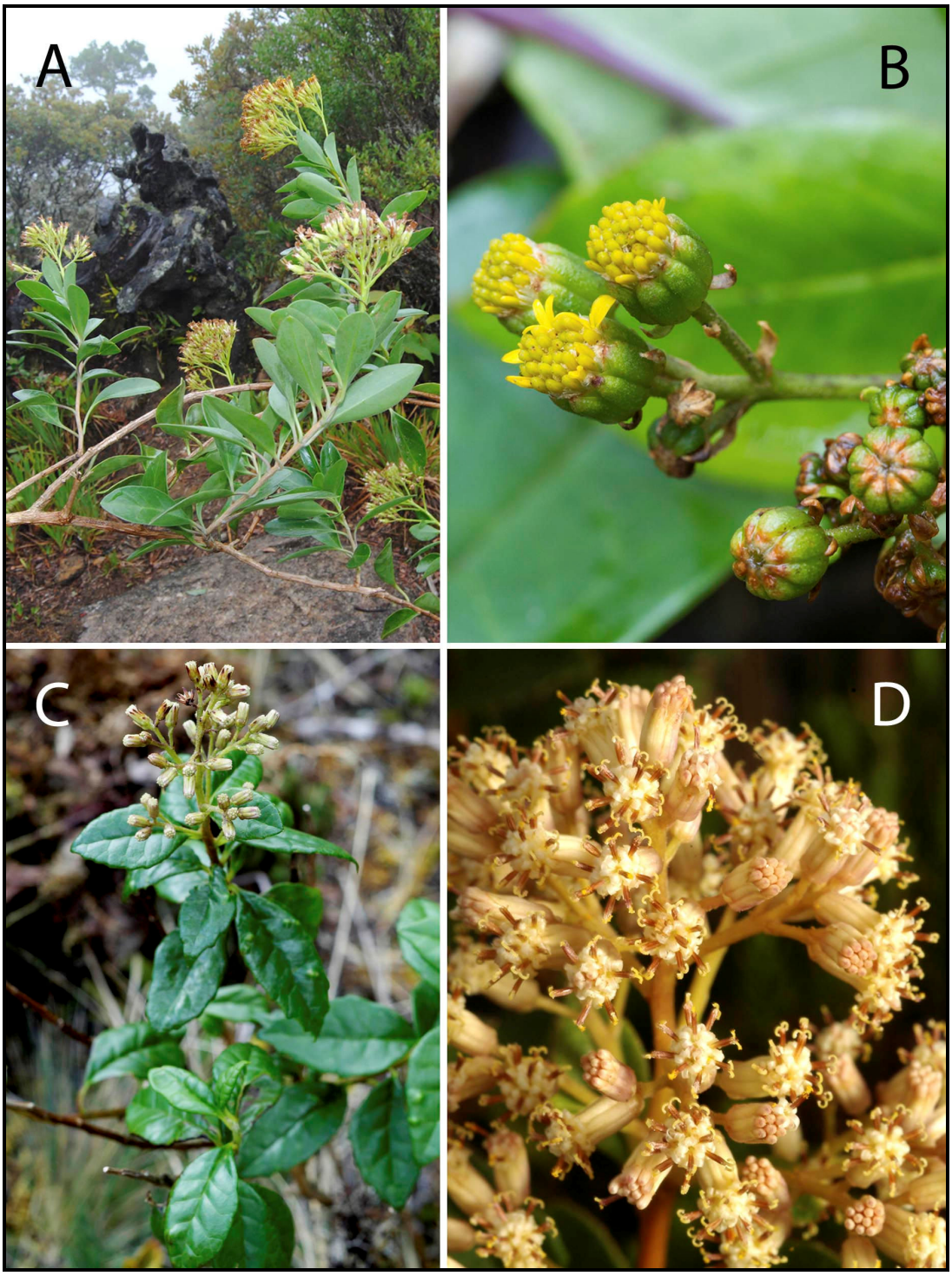

Figure 22. Habit, leaves, terminal capitulescences, and corolla colors in *Pentacalia*. A. *Pentacalia wilburii*, showing vining habit, subcoriaceous, entire-margined leaves with immersed, arching secondary veins, and post-anthesis capitulescences with cylindrical capitula. B. *Pentacalia morazensis*, capitulescence showing short-radiate, broadly campanulate capitula with eight phyllaries and yellow corollas. C. *Pentacalia phanerandra*, pre-anthesis flowering branch showing the chartaceous, pinnately veined, denticulate leaves. D. *Pentacalia phanerandra*, capitulescence showing disciform, broadly cylindrical capitula with white corollas. (A *Santamaría & Monro 8848*, photograph by Alex Monro; B *Stevens et al. 32812*, photograph by Olga Martha Montiel; C–D *Monro & Knapp 5175*, photographs by Alex Monro).

Pentacalia is a speciose (about 130 species) neotropical segregate of *Senecio*, distinguished from *Senecio* by its vining habit (Figs. 5B, 22A, 22C), typically subcarnose leaf blades with arching-pinnate or immersed secondary venation (Figs. 5B–D, 22A, 32), caudate anthers (Fig. 1D), and 5-costate glabrous cypselae (Fig. 8A). However, in herbarium material of *Pentacalia* the cypselae are nearly always immature and not clearly 5-costate (viz Barkley 1990). The usually immature cypselae of *Pentacalia*, consequently, slow determinations and limit pericarp surface detail studies. *Pentacalia* resembles *Senecio* by its herbage with simple trichomes (Figs. 10D, 24) and typically truncate exappendiculate styles (Fig. 2D). Most Pentacalias are South American forest-dwellers with long-pendent flowering branches and yellow flowers. The generitype and a small species group are characterized as often vining shrubs with hanging vine-like branches and having discoid capitula with white corollas (Figs. 22C–D, 23). Here the 12 Mesoamerican species are treated, with microscopic images and specimen photographs supplementing the treatment. Four species of *Pentacalia* occur in Mexico (Villaseñor 2016), two of these, *P. guerrerensis* (T.M. Barkley) C. Jeffrey and *P. venturae* (T.M. Barkley) C. Jeffrey, are extra-Mesoamerican (not present in Chiapas or the Yucatan) and not treated here.

The vining habit and gestalt are basically as useful in recognizing *Pentacalia* as are floral microcharacters. For example, truncate to short triangular style branches, caudate anthers, and solid clinanthia are each useful in helping circumscribe *Pentacalia*, but none are diagnostic. In Mesoamerica, *Pentacalia* ranges from mostly having truncate style branches (Fig. 2D) typical of *Senecio* (Fig. 2F), to triangular style branches (Fig. 2B) more typical of *Dresslerothamnus* (Fig. 2C). Nevertheless, *Pentacalia* is maintained as generically distinct from them. The triangular moderately papillose style branch apex seen in *P. brenesii* (Fig. 2B) and in some South American species recalls *Lasiocephalus*, *Ortizacalia* (Fig. 2A), and *Dresslerothamnus* (Fig. 2C), but Pentacalias never have style apices with dimorphic papillae, stout-comose appendages longer than the branch width, nor do they have distal papillae between the stigmatic bands. Most Pentacalias have anther tails shorter than the filament collar (Fig. 1D), but on occasion (e.g., *P. wilburii*) the tails are obviously longer than the filament collars. Similar variation in anther tail relative length is found in West Indian *Odontocline* B. Nord., and Nordenstam (1978: 23) concluded tail lengths are "generally of poor diagnostic value within the tribe."

Characters, the key to species, and species delimitation. Because Mesoamerican Pentacalias are basically always heterogamous (radiate or disciform), I do not use a heterogamous vs. homogamous lead in the first key couplet. Instead, the initial couplet uses a radiate-obviously zygomorphic vs. disciform-actinomorphic or subradiate lead. Specifically, because *Pentacalia matagalpensis* and *P. phorodendroides* capitula are indistinctly short-radiate, termed here subradiate (i.e., with ray corolla limbs shorter than tube and only about as long as anther cylinders of disk florets), I key them together with disciform species in lead 1A. Each of our five primarily heterogamous disciform-capitulate *Pentacalia* species (as well as *Dresslerothamnus schizotrichus*) were original described in their protologues as homogamous-discoid-capitulate, but nevertheless correctly key via the actinomorphic first couplet. *Pentacalia matagalpensis* has disk floret anther cylinders about half as long as ray limbs, sometimes obscuring them, and thus keys better following lead 1A. In *P. phorodendroides*, on occasion, typical disciform capitula are sometimes very short-radiate, and the species as circumscribed by the author is plastic. It seems possible that favorable garden conditions favored the elongation of normally actinomorphic marginal floret corolla limbs in *P. phorodendroides* into the subradiate corollas seen in the type of the synonymous described-from-cultivation *P. horickii*. In this case, the disciform and subradiate conditions seem linked. Moreover, *P. phorodendroides* appears plastic in involucre characters, with its often eight phyllaries tending to coalesce into as few as five phyllaries. The moderate-exserted radiate condition of species that follow the second half of the first key couplet do not seem as flexible as the aforementioned species, and seem best keyed this way. But, in some radiate species ray corollas may break or fall, and keying becomes difficult.

Within this context, we should note that although the ray corollas of radiate species do not deviate much, other mostly vegetative characters—capitulescence branch bract sizes, peduncle lengths, phyllary number, pappus bristles cell tip shapes—in radiate species may vary more than seen in disciform species. The best marked key characters in the Central America species are the chartaceous leaves with lateral-spread prominent secondary veins (viz Figs. 22C, 23) and white flowers of *Pentacalia phanerandra* (Fig. 22C–D), our only confirmed white-flowered species; the white-lanate-tomentose indument of the calyculus in *P. calyculata* (Fig. 25B, vs. typical subglabrous ones in Figs. 22B, 25A, 25C, 31C); moderately prominent secondary veins in leaf blades of *P. epidendra*; and the discolorous leaves of *P. brenesii* (Fig. 26). Each of these is a clearly marked species.

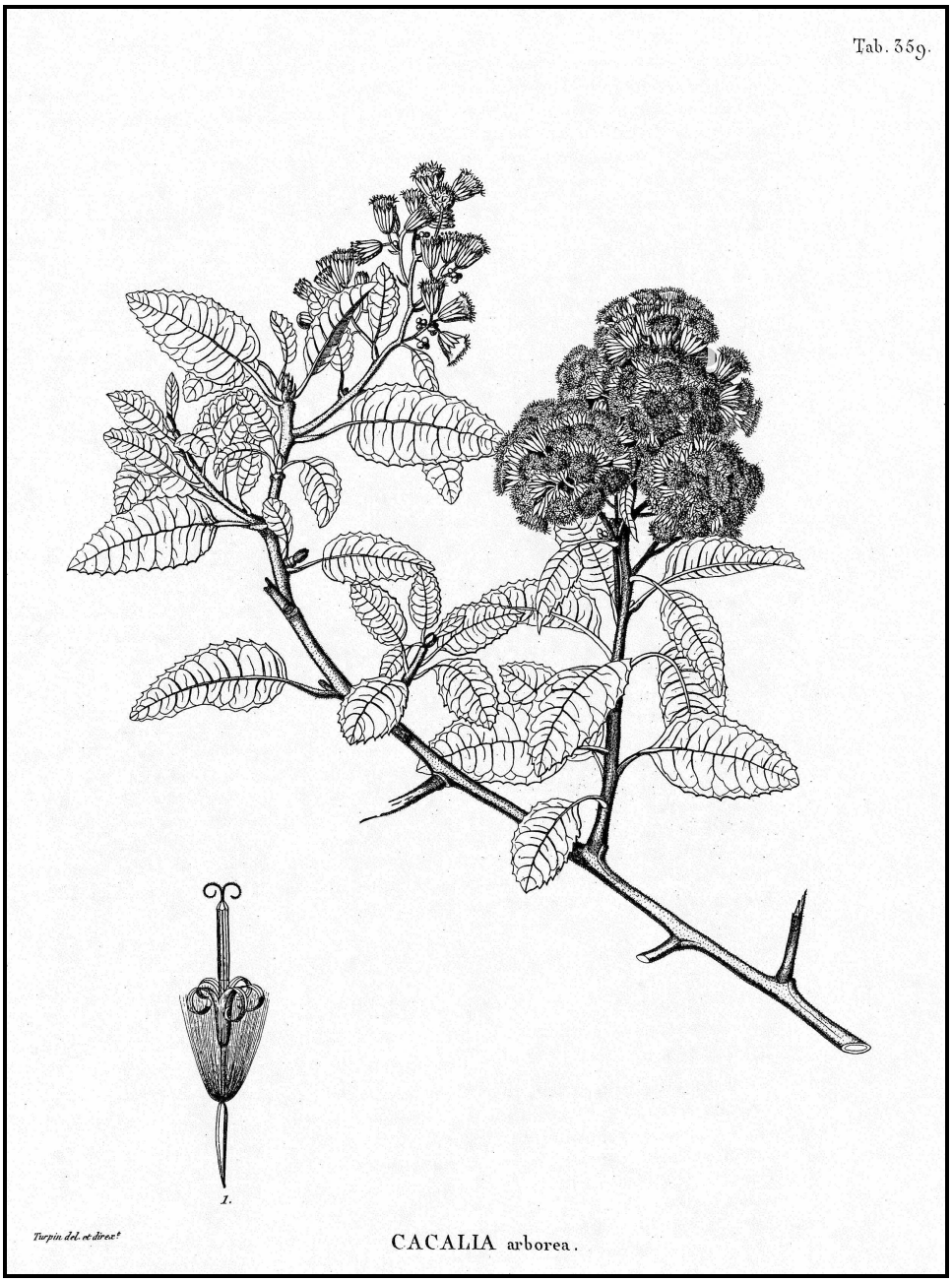

Figure 23. Protologue illustration of *Cacalia arborea* Kunth (≡ *Pentacalia arborea*), generitype of *Pentacalia*. (From Kunth, Nov. Gen. Sp. Pl., folio ed. 4 figure 359. 1818).

The remaining species are less well-marked taxa, and I have taken a broad species concept, opting to be conservative given the paucity and poor state of materials at hand. Although much variation has been seen, this variation is mostly in trivial or flexible characters, and it is routine for me to conceptualize intermediate character states in yet-to-be-collected plants. For example, it seems reasonable to allow a fair amount of variation in usually disciform *Pentacalia phorodendroides* (syn.: *P. horickii* H. Rob.), as well as in radiate *P. morazensis* (syn.: *P. magistrate), P. streptothamna*, and *P. tonduzii*. On the other hand, two narrow endemics, *P. matagalpensis* and *P. wilburii*, are circumscribed nearly as narrowly as in Robinson and Cuatrecasas (1978); both are usually recognized by relatively few-flowered capitula usually with five phyllaries. The corollas of *P. matagalpensis* have been called white, which seems odd. Also, some imperfect materials with eight phyllaries are provisionally referred to otherwise narrowly circumscribed *P. wilburii*, highlighting the need for fieldwork observation of character variation in populations in western Panama, basically where I have seen the least material and where I feel least confident with the material in front of me.

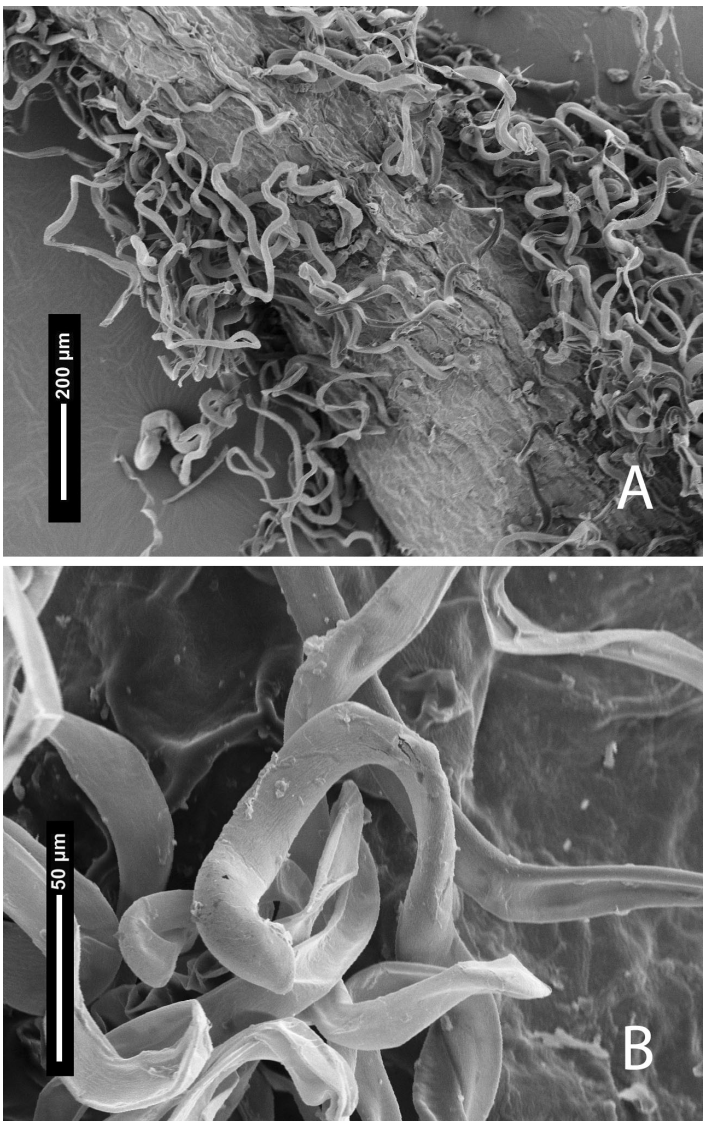

Figure 24. Simple trichomes of *Pentacalia brenesii*, the trichomes have terminal cell curved-coiled. These trichomes are similar to those illustrated in Drury and Watson (1965 fig. 5) and Jeffrey (1987, trichome type 3D), common in *Pentacalia*, and much of Neotropical Senecioneae. A. Phyllary. B. Adaxial leaf blade surface. (From isotype, *Brenes 5342*, NY).

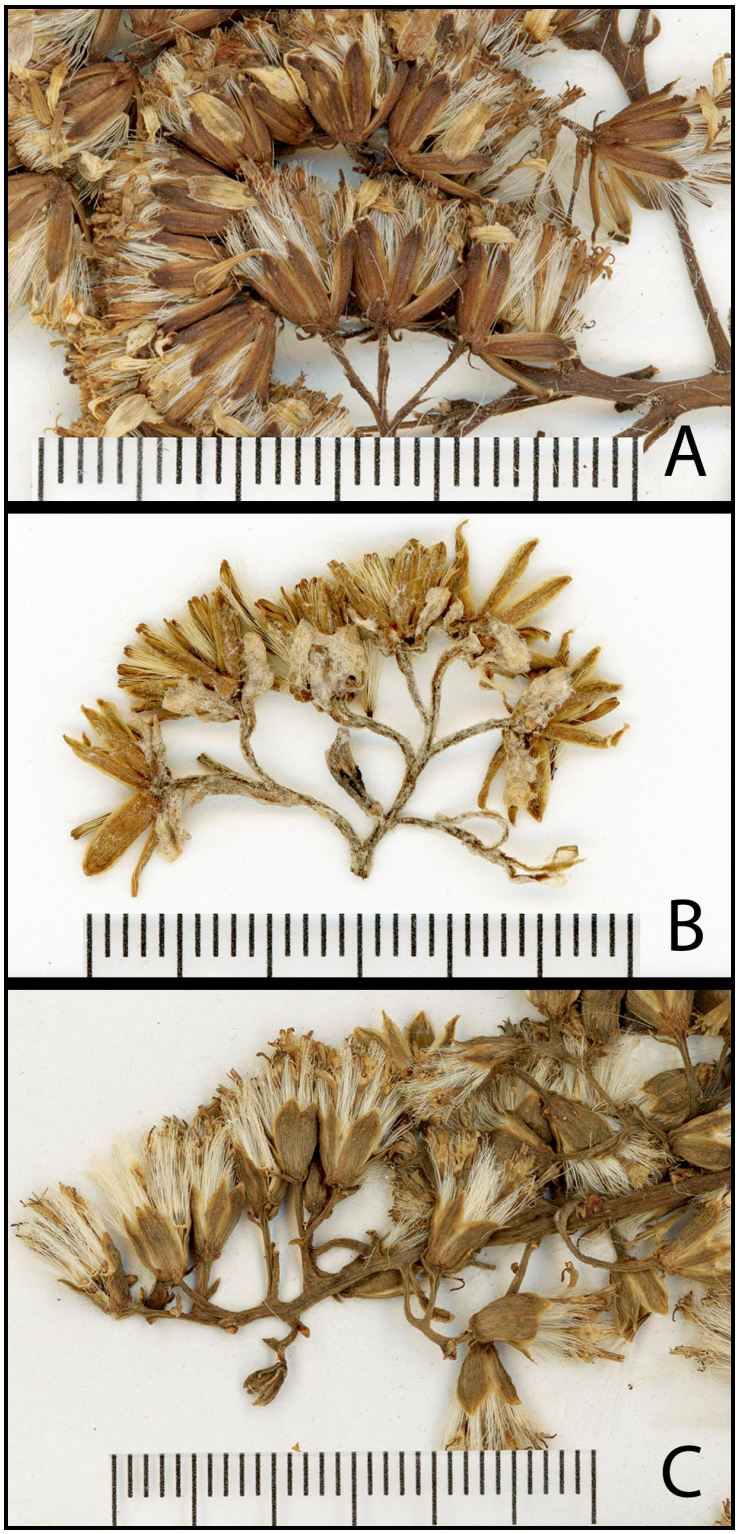

Figure 25. Capitula of *Pentacalia* showing florets, involucres, phyllaries, and calycular bracts. A. *Pentacalia streptothamna*, short-radiate capitula, weakly calyculate, the calycular bracts are small and subglabrous, typical of the genus. B. *Pentacalia calyculata*, post-anthesis capitula, obviously calyculate, showing densely white-lanate-tomentose indument covering the large outer calycular bracts. C. *Pentacalia phorodendroides*, disciform capitula, weakly calyculate, adjacent phyllaries often connate and broad. (A *Haber et al. 11029*, MO; B *Pittier 7503* / *13242*, MO, isotype of *Senecio calyculatus*; C *Standley 85080*, MO).

Geography, authors, and history. The Central American Pentacalias have been treated by Greenman (1901, 1902, 1950), Standley (1938), Robinson and Cuatrecasas (1978), and Williams (1976, 1984). Barkley (1990) provisionally assigned two Chiapas collections to *Pentacalia venturae* (T.M. Barkley) C. Jeffrey, a taxon which he compared to *P. magistri*, *P morazensis*, *P. parasitica*, and *P. phorodendroides*. Here, these collections from Chiapas are referred to *P. epidendra*, but because I have not seen the type material from Veracruz of the very similar *P. venturae*, Barkley's species is placed adjacent to, rather than treated in synonymy of *P. epidendra*. *Pentacalia parasitica* may be safely excluded from Panama, and it proves to be a more northerly species. No Pentacalias are known in Belize or in Mexican Yucatan, but both *P. parasitica* and *P. phorodendroides* should be looked for in Tabasco and Campeche. None of the twelve species treated here occur in South America, but because similar species abound it is obvious that Central American Pentacalias are "merely an appendage on the Andean group" (Barkley 1990).

Four species of Central American *Pentacalia* are more or less historically recognized: *P. candelariae* (Benth.) H. Rob. & Cuatr., *P. calyculata* (Greenm.) H. Rob. & Cuatr., *P. parasitica* (Hemsl.) H. Rob. & Cuatr., and *P. phanerandra* (Cufod.) H. Rob. & Cuatr. The next four species were described in the mid-1900s by Dr. Jesse More Greenman (1867–1951), long-time curator at the Missouri Botanical Garden and admired *Senecio* specialist, whose bulk determinations, herbarium curation, and publications are the foundation of this revision. The regional species, all Central America endemics, described by Greenman that postdate his *P. calyculata* are: *P. brenesii* (Greenm. & Standl.) Pruski, *P. morazensis* (Greenm.) H. Rob. & Cuatr., *P. streptothamna* (Greenm.) H. Rob. & Cuatr., and *P. tonduzii* (Greenm.) H. Rob. & Cuatr., with *S. morazensis* Greenm. described in Dr. Greenman's final publication. Four more recently named regional species are recognized, of these four species two were described by each Louis O. Williams and Harold Robinson. Two proposed species, one each by Robinson and Williams, are treated here in synonymy.

Key to species of Pentacalia in Mesoamerica

1. Capitula disciform or infrequently discoid, sometimes inconspicuously subradiate with ray corolla limb shorter than tube, included or nearly so within involucre, limb about as long as disk anthers and somewhat falsely resembling them.

    2. Disk corollas white and leaf blades chartaceous, secondary veins spreading at nearly right angles to midrib, margins usually denticulate or dentate; (Costa Rica, Panama) ..... **8. Pentacalia phanerandra** (Cufod.) H. Rob. & Cuatr.
    2. Disk corollas yellow or pale yellow, rarely reportedly white in *P. matagalpensis* but then never with leaves chartaceous nor with secondary veins spreading at nearly right angles to midrib; leaf blades mostly subcarnose, secondary veins moderately forward directed, margins entire.

        3. Leaf blade surfaces strongly discolorous, abaxial surfaces densely lanate-tomentose; (Costa Rica) ..... **1. Pentacalia brenesii** (Greenm. & Standl.) Pruski
        3. Leaf blade surfaces concolorous, surfaces glabrous to sparsely crisped-puberulent.

            4. Capitula 6–8.5 mm long, ultimate capitula typically subfasciculate; stems or peduncles often crisped-pubescent, hispidulous, villosulous to sometimes subglabrous.

                5. Capitula disciform; phyllaries usually 8; disk corollas (yellow), lobes 1.3–2 mm long, spreading with anthers exserted and collars sometimes visible, filaments included in corolla; (Costa Rica, Panama) ..... **3. Pentacalia candelariae** (Benth.) H. Rob. & Cuatr.

5. Capitula indistinctly subradiate; phyllaries 5; disk corollas (reportedly white), lobes 1.5–2.5 mm long, spreading to recurved with anthers, collars, and filaments visible; (Nicaragua)
..... **5. Pentacalia matagalpensis** H. Rob.

4. Capitula 7.5–10.5 mm long, ultimate capitula pedunculate and usually well-spaced; stems glabrous or subglabrous.

6. Capitulescences terminal or when mostly axillary the branches much longer than the subtending leaves (e.g., Fig. 5A, 5C); phyllaries 8, typically nearly as long as disk florets and free; (Mexico, Guatemala, ?Honduras)
..... **7. Pentacalia parasitica** (Hemsl.) H. Rob. & Cuatr.

6. Capitulescences of mostly axillary branchlets shorter than to slightly longer than the subtending leaves (e.g., Fig. 5B, 5D); phyllaries 5–8, typically shorter than disk florets, several capitula per branch with some phyllaries connate to near apex; (Chiapas, Guatemala, El Salvador)
.. **9. Pentacalia phorodendroides** (L.O. Williams) H. Rob. & Cuatr.

1. Capitula radiate with ray corolla limb usually moderately exserted from involucre, ray limb usually about as long as tube.

7. Capitula obviously calyculate, calycular bracts completely covered with dense white-lanate-tomentose indument, bracteoles usually about half as long as involucre; (Costa Rica)
..... **2. Pentacalia calyculata** (Greenm.) H. Rob. & Cuatr.

7. Capitula usually slightly to moderately calyculate, but not with white-lanate-tomentose calycular bracteoles, bracteoles typically less than half as long as involucre.

8. Capitula broadly campanulate.

9. Stems moderately to densely villosulous, peduncles moderately puberulent or villosulous; leaf blades 6–14 cm long, secondary veins moderately prominent; disk corollas lobes 1–1.5 mm long, usually shorter than throats; (Chiapas, Guatemala, Nicaragua)
..... **4. Pentacalia epidendra** (L.O. Williams) H. Rob. & Cuatr.

9. Stems glabrous, peduncles sparsely puberulent; leaf blades 4–7(–8) cm long, secondary mostly immersed; disk corollas lobes 1.5–2 mm long, about as long as throat; (Honduras, El Salvador, Nicaragua)
..... **6. Pentacalia morazensis** (Greenm.) H. Rob. & Cuatr.

8. Capitula cylindrical to narrowly campanulate or turbinate-campanulate.

10. Capitulescences leafy-bracteate with specialized large elliptic to ovate primary bracts; stems puberulent with collapsed bent simple trichomes; ray corolla limbs often linear-lanceolate; (Costa Rica, Panama)
..... **11. Pentacalia tonduzii** (Greenm.) H. Rob. & Cuatr.

10. Capitulescences not leafy-bracteate, without specialized large primary bracts; stems glabrous, or when pubescent trichomes not bent; ray corolla limbs elliptic-oblong.

11. Stems puberulent to glabrate; phyllaries 8; capitula 10–15-flowered; disk corolla lobes about as long as throat; pappus bristles usually reaching to about the middle of the disk corolla lobes; (Nicaragua, Costa Rica, Panama)
..... **10. Pentacalia streptothamna** (Greenm.) H. Rob. & Cuatr.

11. Stems glabrous; phyllaries 5(–8); capitula 7–11(–14)-flowered; disk corolla lobes shorter than throat; pappus bristles at maturity usually reaching to only about base of the disk corolla lobes; (Costa Rica, Panama) ..... **12. Pentacalia wilburii** H. Rob.

Figure 26. Isotype of *Senecio brenesii* Greenm. & Standl. (≡ *Pentacalia brenesii*). (*Brenes 5342*, NY).

1. PENTACALIA BRENESII (Greenm. & Standl.) Pruski, Flora Mesoamericana vol. 5, parte 2: 444. 2018. *Senecio brenesii* Greenm. & Standl., in Standley, Flora of Costa Rica, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1513. 1938. **TYPE: COSTA RICA. Alajuela.** La Palma de San Ramón, 1100 m, 16 Jan 1927, *Brenes 5342* (holotype: F; isotype: NY). Figures 2B, 24, 26.

Climbing vines, flowering branches pendent; stems few-several branched distally, brownish-gray lanate-tomentose distally, glabrate proximally, pith solid; herbage with simple trichomes with long and curved terminal cell appendages. **Leaves** petiolate; blade 5–9 × 1.7–4 cm, elliptic to elliptic-ovate, subcarnose, pinnately veined, 2–4 arching secondaries per side, these forward directed, surfaces strongly discolorous, adaxial surface glabrous, abaxial surface yellowish-brown, densely lanate-tomentose, midrib visible, secondary veins thin and obscured by indument, base broadly cuneate to rounded, margins entire, often pressing revolute, apex acuminate; petiole 0.7–2.5 cm long. **Capitulescence** 10–23 × 5–10 cm, openly corymbiform-paniculate to sometimes columnar in aspect, terminal and exserted from distal leaves, often also axillary on lateral branchlets 2–5 cm long, from distal few nodes, branchlets subequal to slightly longer than subtending stem leaf, ultimately in subumbellate cluster of 3–7(–13) capitula; peduncles 3–9 mm long, lanate-tomentose. **Capitula** 10–14 mm long, disciform(discoid); 15–25-flowered; involucre 5–6 mm diam., campanulate or narrowly so, disk florets moderately exserted (or in fruit sometimes rarely well-exserted by ca. 5 mm); phyllaries ca. 8, 7.5–9.5 × 1–2 mm, lanceolate, laxly tomentose to glabrate, bases often quickly indurate; clinanthial setae to ca. 0.5 mm long. **Ray florets** absent. **Marginal florets** (0–)1–2; corolla slightly exserted from involucre. **Disk florets** 15–23; corolla 8–10 mm long, campanulate, yellow, glabrous, tube 5–6 mm long, much longer than limb, lobes 1.5–2.5 mm long, shorter than to about as long as the throat; anthers 2.2–2.4 mm long, collar ca. 0.5 mm long, filament collar balusterform, with enlarged basal cells, tails about 1/2 as long as thecae, appendage 0.3–0.4 mm long, lanceolate-ovate, apex obtuse; style base gradually dilated in basal ca. 0.7 mm, branches 1.6–1.9 mm long and often well-exserted from anther cylinder, stigmatic surfaces 2-banded and reaching to the apex, without papillae arising between the stigmatic surfaces, apex tufted-papillose (papillae varying from short to long but more or less isomorphic), triangular in outline, abaxially papillose in distal 1/4 with papillae smaller but otherwise similar to apical papillae, composed of cellular material, laterally and apically papillose, papillae 0.1–0.2 mm long, isomorphic, subequal to usually shorter than branch diam. **Cypselae** 1–1.5 mm long, glabrous; pappus bristles 8–10 mm long, usually reaching to about the middle of the disk corolla lobes, barbellate distally.

Distribution and ecology. *Pentacalia brenesii* is a Costa Rican endemic (Fig. 16) known from 800–1100 meters elevation, and flowers in January and February.

Collections examined. **COSTA RICA**. *Bello 1917* (CR, MO); *Herrera & Chacón 492* (MO); *Herrera & Schik 3830* (CR, MO, UC); *Herrera et al. 4925* (CR, INB, MO, UC)**.**

By the character combination of discolorous abaxially-tomentose leaves and at maturity large capitula (Fig. 26), *Pentacalia brenesii* is remarkable and unequaled in Central America. In these characters it closely matches Colombian *P. popayanensis* (Hieron.) Cuatr., which is a different radiate-capitulate species. Similarly, other large-capitulate species, e.g., Peruvian *P. carpishensis* (Cuatr.) Cuatr., Bolivian *P. dictyophlebia* (Greenm.) Cuatr., Mesoamerican *P. epidendra*, Bolivian *P. epiphytica* (Kuntze) Cuatr., and Mesoamerican *P. morazensis*, also differ from *P. brenesii* by radiate capitula; moreover, each is concolorous-leaved.

The style branches of *Pentacalia brenesii* often have a central papillose apiculum Fig. 2B), recalling both *Dresslerothamnus* and *Ortizacalia,* never have distal papillae between stigmatic lines, as in *Ortizacalia*. The style branch apex of *P. brenesii* is sometimes triangular in outline (Fig. 2B), as often occurs in *Dresslerothamnus* too, but herbage trichome characters distinguish the two genera. In species of the Peruvian-Bolivian *P. oronocensis* (DC.) Cuatr. group, we find the apiculate-stylar

condition loosely associated with discolorous leaves, but the species of this group are relatively small-capitulate as compared to *P. brenesii*.

2. PENTACALIA CALYCULATA (Greenm.) H. Rob. & Cuatr., Phytologia 40: 41. 1978. *Senecio calyculatus* Greenm., Bot. Gaz. 37: 419. 1904. **TYPE: COSTA RICA. Cartago.** Volcán Turrialba, 2700 m, Jan 1899, *Pittier 7503* / *13242* (lectotype, designated here: US-1404140 ex J.D. Smith herb.; isolectotypes: G-3, MO, US-2). Both numbers are cited in the protologue. It seems as though 7503 is Smith exsiccatae distribution number, and that 13242 is the Pittier collection number. The US lectotype and US isolectotype each include both numbers. None of the sheets seen by the author include a hand-written determination in the hand of Greenman. Figure 25B.

Woody vines to 10 m tall; stems closely arachnoid-tomentose to quickly puberulent or glabrate, pith solid. **Leaves** petiolate; blade 2.5–6 × 1.3–4 cm, elliptic to ovate, subcarnose, pinnately veined, usually with 2–5 pairs of partly immersed arching secondaries per side, tertiary venation indistinct, surfaces concolorous, glabrous or midrib adaxially arachnoid-puberulent, base cuneate to sometimes obtuse, margins entire, apex acute(–acuminate) to sometimes obtuse; petiole 1–2 cm long. **Capitulescence** terminal, broadly corymbose-paniculate, moderately dense, without specialized large primary bracts, few-bracteolate, branchlets arachnoid-tomentose, ultimate clusters with capitula not fasciculate, bracteoles to 10 mm long, lanceolate; peduncles 1–7 mm long, arachnoid-puberulent, often 1–2-bracteolate, bracteoles usually arachnoid-pubescent or white-lanate-tomentose. **Capitula** radiate, 8–11 mm long, 8–12-flowered, obviously calyculate; involucre 3–4 mm diam., narrowly campanulate, at anthesis slightly shorter than disk florets, in fruit the persistent disk corolla sometimes exserted 3–4 mm from involucre; phyllaries 5–6(–7) × 1.2–2.5 mm, broadly lanceolate to ovate, sparsely arachnoid-puberulent to glabrate, apex acute to obtuse, often fimbriate-papillose; calycular bracts 2–3(–4), 3–4.5 mm long, usually about half as long as involucre, elliptic to obovate, completely covered with dense white-lanate-tomentose indument. **Ray florets** 2–5; ray corolla yellow, glabrous, limb 3–4 mm long, about as long as to slightly shorter than tube, elliptic-lanceolate. **Disk florets** 6–7; corolla 5.5–7 mm long, narrowly funnelform, yellow, glabrous, lobes ca. 1.5 mm long, triangular-lanceolate, slightly shorter to about as long as throat. **Cypselae** 1–2 mm long, glabrous; pappus bristles 4–6 mm long, usually reaching to about the middle of the disk corolla lobes.

Distribution and ecology. *Pentacalia calyculata* is a local endemic known only from montane areas (e.g., Volcán Irazú, Volcán de Turrialba, Cordillera de Talamanca) of Costa Rica. It occurs from 2000–3300 meters elevation, and flowers from (August–)November–February.

Representative collections. **COSTA RICA**. *Garwood et al. 344* (BM, MO-2); *Jiménez 2649* (MO, NY); *Pittier 16985* (US); *Standley 35206* (US); *Wilbur & Teeri 13745* (MO, US); *Williams et al. 24444* (NY, US).

This species was cited in the protologue as discoid, and as sessile-capitulate in Standley (1938), but instead is radiate and short-pedunculate.

3. PENTACALIA CANDELARIAE (Benth.) H. Rob. & Cuatr., Phytologia 40: 41. 1978. *Senecio candelariae* Benth., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 108. 1853. **TYPE: COSTA RICA. San José/Cartago.** Candelaria, 6000 ft, 1851, *Oersted 148* (holotype: K). [An isotype in C was not found in IDC microfiche 2204]. Figure 10D.

Climbing vines; stems often densely crisped-pubescent (Fig. 10D; these crisped trichomes have been loosely described elsewhere as torulose or loriform), villosulous to subglabrous, larger stems sometimes narrowly fistulose; herbage (when pubescent) with crisped trichomes. **Leaves** petiolate; blade 6–9 × 2–4.5 cm, lanceolate to elliptic or less commonly elliptic-ovate, subcarnose, thinly pinnate-veined or sometimes indistinctly pinnate with secondary veins sometimes immersed,

typically with 3–6 visible secondary veins per side, these moderately forward directed, tertiary venation immersed or slightly visible and forming a very loose reticulum with areolae 2–5+ mm diam., surfaces sparsely crisped-puberulent to glabrous, base cuneate to obtuse or less commonly rounded, margins entire, apex acute to attenuate; petiole 0.5–2 cm long. **Capitulescence** mostly terminal, sometimes on axillary branches but then often about 1.5 times as long as the often large subtending leaves of main stem, pyramidally corymbiform-paniculate, each branchlet subtended by a linear-lanceolate bracteole 2–4 mm long, branches and branchlets usually crisped-puberulent or villosulous, ultimate branchlets mostly racemose with ultimate capitula mostly subsessile and in subfasciculate clusters, 3–7-capitulate, infrequently capitula always pedunculate, branchlets in herbarium material often dries flattened; peduncles 0–2(–6) mm long, crisped-puberulent or villosulous, sometimes few-bracteolate, bracteoles 1–2 mm long, usually much shorter than 1/2 as long as the phyllaries, lanceolate to elliptic. **Capitula** 6–8 mm long, disciform, 8–14-flowered; involucre 3–4.3 mm diam., broadly cylindrical, disk florets only slightly exserted to well-exserted, basal disk sometimes broadened and indurate, phyllaries usually 8, 3.5–6 × ca. 1.1 mm, lanceolate to lanceolate-ovate, typically free or rarely a few connate to near apex, glabrous or sparsely crisped-puberulent, apex usually acute, sometimes ciliate-fimbrillate; calycular bracteoles ca. 1 mm long, lanceolate, subglabrous. **Ray florets** absent. **Pistillate marginal florets** 1–3, noticeably smaller than disk florets, corolla sometimes quickly deciduous; corolla 4–4.5 mm long, usually yellow or pale yellow, lobes 1–1.2 mm long. **Disk florets** 7–11; corolla 4.8–5.6 mm long, usually yellow or pale yellow, glabrous, lobes 1.3–2 mm long, about as long as throat, spreading with anthers exserted and collars sometimes visible, filaments included in corolla, lobes with faint medial nerve sometimes visible. **Cypselae** 1–2 mm long, glabrous; pappus bristles 4–5.3 mm long, mostly 1-seriate, usually reaching to about the middle of the disk corolla lobes, distal-most few cells slightly more scabrid with spreading tips nearly as long as bristle width.

Distribution and ecology. *Pentacalia candelariae* is a common regional endemic known only from Costa Rica and Panama. It occurs from 800–2000 meters elevation, and flowers mostly from February to May.

Representative collections. **COSTA RICA**. *Fletes 4* (INB, MO, NY; weak-puberulent, pedunculate-capitulate); *Gómez 20075* (K, MO, NY, TEX, USM); *Gómez et al. 21066* (CR, MO, TEX); *Haber & Zuchowski 10521* (F, MO, UC); *Herrera 3767* (CR, MO, UC); *Herrera 6012* (INB, MO; weak-puberulent, pedunculate-capitulate; cited in Monro 2017: 161 as *Pentacalia* "*parasiticus*" [sic]); *Standley & Torres 51132* (MO); *Wilbur 14351* (MO, NY, US). **PANAMA**. *Churchill et al. 4573* (MO, US); *Hammel 6290* (KSC, MO-2; cited in haste by Pruski and Robinson 2018 as *D. hammelii*, but subsequent slower-paced SEM study showed the trichomes to be simple); *Sytsma and D'Arcy 3633* (MO); *van der Werff & Herrera 7228* (MO, US).

Standley (1938) mentioned that "considerable variation" in *P. candelariae,* that Greenman used a non-published name for some specimens, and that the many specimens may "represent as many as three entities." The species generally has flowering branches crisped-pubescent and ultimate capitula subfasciculate, but some collections have peduncles weak-puberulent, and non-fasciculate capitula as in *P. parasitica* and *P. phorodendroides*, but the capitula in *P. candelariae* are smaller and the species is more southerly distributed. Some material determined as disciform *P. candelariae* by Standley (in sched.), is instead radiate *P. streptothamna*. Also, it seems possible that some variation noted by Standley, is instead in reference to low-elevational material of *P. phanerandra* or to near look-alike *D. schizotrichus*. It seems Standley may have been referencing variation based on both subglabrous plants and radiate plants of other species. Although Panamanian *D. hammelii* in gestalt is similar (viz the Pruski and Robinson 2018 misdetermination of *Hammel 6290* cited as *D. hammelii*), it seems unlikely that Standley was referencing the plants from Panama.

4. PENTACALIA EPIDENDRA (L.O. Williams) H. Rob. & Cuatr., Phytologia 40: 41. 1978. *Senecio epidendrus* L.O. Williams, Phytologia 31: 440. 1975. **TYPE: MEXICO. Chiapas.** Near crest of ridge on road from San Cristobal de las Casas to Tenejapa, Chamula paraje of Las Ollas, 8300 ft (= 2530 m), 19 Feb 1965, *Breedlove 9053* (holotype: MICH; isotypes: CAS-3, ENCB, F, NY, TEX, WIS).

Woody vines; stems moderately to densely villosulous, often fistulous, those on herbarium sheets relatively thick. **Leaves** petiolate; blade 6–14 × 4.5–9 cm, ovate, subcarnose, pinnately veined with 4–8 moderately prominent forward-directed secondaries per side, surfaces concolorous, adaxial surface subglabrous or midrib sparsely villosulous, adaxially sparsely villosulous, base cuneate to obtuse, sometimes obliquely so, margins entire, apex acute to obtuse but mucronate; petiole 1.5–3 cm long. **Capitulescence** corymbiform-paniculate, terminal or on spreading axillary branches to (5–)30 cm long, much longer than subtending leaves, main branches bracteolate but without specialized large primary bracts; peduncles 5–15 mm long, moderately puberulent or villosulous, often indistinctly 1–few-bracteolate. **Capitula** 9–13 mm long, radiate, 20–30-flowered, loosely few-calyculate; involucre 4–9 mm diam., broadly campanulate at anthesis, disk florets well-exserted with most of limb fully visible; phyllaries 8, 4.5–8 × 1.5–2 mm, noticeably shorter than disk florets, narrowly oblong to ovate, usually puberulent; calycular bracteoles 1–few, 1–2.5 mm long, usually arising from base of subinvolucre; clinanthium crest evident. **Ray florets** ca. 5; corolla yellow, glabrous, limb 5–6 × 1–1.5 mm, about as long as tube, oblanceolate, 4–7-nerved. **Disk florets** 15–25; corolla 7–8.5 mm long, funnelform, yellow, glabrous, lobes 1–1.5 mm long, usually shorter than throat; anthers 2.5–3 mm long, connective often resinous. **Cypselae** 1–2 mm long, glabrous; pappus bristles usually 5–7 mm long, nearly as long as disks and reaching to about the middle of the disk corolla lobes, apical cells pointed or a few bristles with cells sometime bulbous-obtuse.

Distribution and ecology. *Pentacalia epidendra* is an infrequent regional endemic described from Chiapas and Guatemala, and extending southeastwards into Nicaragua, where it is rare. Nicaragua material was determined by Neil Harriman (in Dillon et al. 2001), and is relatively low-elevational. The Guatemalan paratype is immature, as noted by Williams (1976: 410), but the species has more recently been collected flowering on Sierra de las Minas. The species is known to me from only half a dozen collections, two of these imperfect. *Pentacalia epidendra* occurs from (1100–)1500–2700 meters elevation, and flowers from January to March.

Collections examined. **GUATEMALA.** *Peña-Chocarro et al. 2920* (BM, MO); *Steyermark 42889* (F, MO). **MEXICO. Chiapas.** *Breedlove 9053* (type as cited above); ?*Breedlove 31764* (CAS n.v., web shows and imperfect sheet, referred by Barkley 1990 to extra-Mesoamerican *P. venturae*); *Breedlove 49771* (CAS, MO); *Breedlove & Almeda 58095* (CAS, US). **NICARAGUA.** *Williams et al. 23508* (F, NY; in bud, but stems villosulous and secondary leaf veins prominent).

Among Central American species, *P. epidendra* may be recognized by its radiate capitula with campanulate involucres, villosulous herbage, and large fleshy leaves with prominent arching secondary veins. Barkley (1990) provisionally referred *Breedlove 31764* to *P. venturae* (T.M. Barkley) C. Jeffrey, a plastic-capitulate species originally described as radiate, but which sometime has marginal florets with staminodia and pseudobilabiate corollas. I find *Breedlove 31764* to have typical radiate capitula and thus this collection fits comfortably within either *P. morazensis* or more likely *P. epidendra.*

5. PENTACALIA MATAGALPENSIS H. Rob., Phytologia 40: 43. 1978. **TYPE: NICARAGUA. Matagalpa.** Near Sta. Maria de Ostuma, between Matagalpa and Jinotega, 1500 m, 20–24 Feb 1963, *Williams et al. 25036* (holotype: US; isotypes: F-2, NY). Figure 27.

Climbing vines; stems much-branched, pale brown, distally hispidulous to subglabrous, internodes often elongate, at least some trichomes obliquely appendaged. **Leaves** petiolate; blade

Figure 27. Holotype of *Pentacalia matagalpensis* H. Rob. (*Williams et al. 25036*, US).

2.5–6 × 1–2.3 cm, elliptic, subcarnose, thinly pinnately veined, usually with 2–4 visible arching secondary veins per side, surfaces concolorous, glabrous, base cuneate, margins entire, apex acuminate; petiole 0.5–1 cm long. **Capitulescence** mostly axillary, branches longer than subtending leaves (position typically apparent on herbarium specimens), mostly 10–20 cm long, each pyramidal and moderately longer than subtending leaf, ultimate capitula subfasciculate; peduncles 1–4 mm long, densely crisped-hirsutulous, usually 1–4-bracteolate or capitula 1–2-calyculate, peduncular or calycular bracteoles 1–1.5(–2) mm long, sessile, elliptic-ovate, chartaceous. **Capitula** inconspicuously subradiate, 6.5–8.5 mm long, 5–7-flowered; involucre 2–2.5 mm diam., cylindrical, moderately shorter than florets; phyllaries 5, 5–6 × 1–1.5 mm, lanceolate to elliptic-lanceolate, glabrous, margins very narrowly scarious, apex acute to obtuse. **Ray florets** indistinct, 1–2; corolla reportedly white (but this perhaps in reference instead to exserted anther thecae), glabrous, tube 3–4 mm long, limb 2–2.5 × ca. 0.5 mm, shorter than tube, elliptic-lanceolate, limb about as long as disk anther cylinders and somewhat falsely resembling them. **Disk florets** 4–5; corolla ca. 6 mm long, reportedly white, glabrous, lobes 1.5–2.5 mm long, lanceolate, sometimes longer than the throat, lobes spreading to recurved with anthers, collars, and filaments visible; anthers ca. 2 mm long; style branch distally abaxially and marginally papillose, papillae 0.1–0.2 mm long. **Cypselae** 1–2 mm long, glabrous; pappus bristles ca. 5 mm long, bristle apical cells pointed.

Distribution and ecology. *Pentacalia matagalpensis* is an uncommon regional endemic known only from Nicaragua. It occurs from 900–1500 meters elevation, and flowers in February and March. It has been collected in fruit in April.

Representative collections. NICARAGUA. *Pipoly 6076* (MO); *Rueda et al. 13363* (MO); *Rueda et al. 13431* (MO); *Rueda et al. 15947* (MO).

Pentacalia matagalpensis is the only *Pentacalia* typified by material from Nicaragua. The type of *P. matagalpensis* H. Rob. was distributed as *Senecio candelariae*, which occurs in Costa Rica and Panama, and differs by its disciform capitula with eight phyllaries. By its five phyllaries P. *matagalpensis* is similar to *P. wilburii*, and by its long axillary capitulescences is similar to *P. phorodendroides*.

Pentacalia matagalpensis is keyed here as inconspicuously subradiate following lead 1A, and its corollas have been called white, which seems odd. Nordenstam (1978) stated the adaxial surfaces of the ray corolla limbs of white-rayed Senecioneae are generally papillose, but at low magnifications those of *P. matagalpensis* seem neither obviously papillose, nor oblong-tabular celled. The corolla color of *P. matagalpensis* needs further observation.

6. PENTACALIA MORAZENSIS (Greenm.) H. Rob. & Cuatr., Phytologia 40: 44. 1978. *Senecio morazensis* Greenm., Ceiba 1: 122. 1950. **TYPE: HONDURAS. Francisco Morazán.** Mountains above San Juancito, 2000 m, 25 Mar 1948, *Williams & Molina 13976* (holotype: MO; isotypes: EAP, F, MO). The sheet in F is a fragment. Figures 22B, 28.

Pentacalia magistri (Standl. & L.O. Williams) H. Rob. & Cuatr., *Senecio magistri* Standl. & L.O. Williams.

Climbing vines, 1–3+ m tall; stems glabrous to infrequently sparsely tomentose, often fistulous. **Leaves** petiolate; blade 4–8 × (1.5–)2–3 cm, elliptic-lanceolate to sometimes ovate, subcarnose, pinnately thin-veined, 4–5 mostly immersed arching secondary veins per side, surfaces concolorous, glabrous, base broadly cuneate to obtuse, margins entire, apex acuminate to acute; petiole 1–1.5 cm long. **Capitulescence** corymbiform-paniculate, terminal or on spreading axillary branches longer than subtending leaves, sometimes with relatively large bracts subtending branchlets; peduncles 5–15 mm long, typically sparsely villosulous especially immediately below involucre, infrequently glabrate, often 1–3-bracteolate, bracteoles 3–5 mm long, sessile, linear-lanceolate, thin-

chartaceous. **Capitula** radiate to (on poor soils) rarely seemingly disciform, 10–14 mm long, 22–38-flowered; involucre 5–8 mm diam., broadly campanulate at anthesis, disk florets well-exserted; phyllaries 8–13 (often on a single plant), 6–7 × 2–3(–4) mm, linear-lanceolate to oblong, glabrous except at the ciliate-fimbriate apex, some phyllaries partly connate, apex acute to obtuse; calycular bracts 1–few, 3–6 mm long, usually linear or very narrowly oblanceolate, often arising from base of subinvolucre, often half as long to as long as involucre, slightly spreading, sometimes drying much paler in color than phyllaries. **Ray florets** 5–8; corolla yellow, glabrous, tube 3–3.5 mm long, limb 4–7 × 1–2.5 mm, elliptic to oblong, usually about as long as tube, rarely some per plant deeply bilobed to near tube, with lobules 1–2 mm long and thus these few capitula seemingly disciform. **Disk florets** 17–30; corolla 5.5–6.5 mm long, yellow, glabrous, lobes 1.5–2 mm long, about as long as throat. **Cypselae** (immature) 1–1.8 mm long, glabrous; pappus bristles 7–8 mm long, usually reaching to about the middle of the disk corolla lobes, apical cells pointed, pre-anthesis bristles sometimes clavate distally.

Distribution and ecology. *Pentacalia morazensis* is an occasional regional endemic long-known only in Honduras, but more recently collected in both El Salvador and Nicaragua, where it seems less frequent. It was not reported in Nicaragua by Harriman (in Dillon et al. 2001). *Pentacalia morazensis* occurs from 2000–2600(–2800) meters elevation, and flowers mostly from January–March(–April).

Representative collections. EL SALVADOR. *Martinez 874* (B, EAP, LAGU, MO); *Tucker 1028* (US). **HONDURAS**. *Dario 347* (EAP, KSC, MO); *Evans 1473* (K, MO, NY); *Evans 1524* (EAP, KSC, MO, TEFH); *Kelly et al. 16122* (MO, TRIN); *Molina 5050* (F, US; type collection of synonymous *Senecio magistri;* stems sparsely tomentose); *Molina 13752* (NY, US); *Molina 17423* (NY, US); *Molina 23397* (NY, US); *Molina 23404* (NY, US); *Molina et al. 31318* (MO); *Williams & Molina 13705* (MO); *Williams & Molina 17104* (EAP, MO; paratype). **NICARAGUA**. *Stevens et al. 32812* (MO; voucher of photograph used here as Fig. 22B); *Stevens & Montiel 34283* (MO).

Williams (1984) gave *Pentacalia morazensis* as the only regional "forest inhabiting, fleshy-leaved vine." By radiate capitula with broad involucres (Figs. 22B, 28), *P. morazensis* is among Central American species similar to *P. epidendra*, but in Honduras may be mistaken for *P. parasitica* as well. Robinson and Cuatrecasas (1978) recognized as distinct *P. morazensis* by clavate pappus bristles and *P. magistri* by apically narrowed pappus bristles, whereas Williams (1984) and Pruski and Robinson (2018) treated *P. magistri* in synonymy of *P. morazensis*. The pappus bristles in this species seem more typically clavate in young flower, but post-anthesis are often apically narrowed. While the clavate pappus bristle condition (not as extreme as seen in *Monticalia firmipes*, Fig. 3E) was used by Robinson and Cuatrecasas (1978) to distinguish *P. magistri*, its type (*Molina 5050*) is otherwise a good match for *P. morazensis*. A few imperfect Honduran plants, perhaps a poor soil ecotype, resemble *P. morazensis* and have somewhat clavate pappus bristles, but appear disciform. These imperfect Honduran plants may be the same that Nelson (2008) called *P. parasitica*. In Oaxaca, *Breedlove & Sigg 65897* was determined by B.L. Turner (in sched.) as *P. morazensis*, but is referred here to *P. parasitica*.

Barkley (1990) provisionally assigned two Chiapas collections (including *Breedlove 31764*) to *Pentacalia venturae* (T.M. Barkley) C. Jeffrey, a taxon that he compared to *P. magistri*, *P morazensis*, *P. parasitica*, and *P. phorodendroides*. Here, these collections from Chiapas are referred to *P. epidendra*, but because I have not seen the type material from Veracruz of the very similar *P. venturae*, it is placed adjacent to, rather than in synonymy of *P. epidendra*.

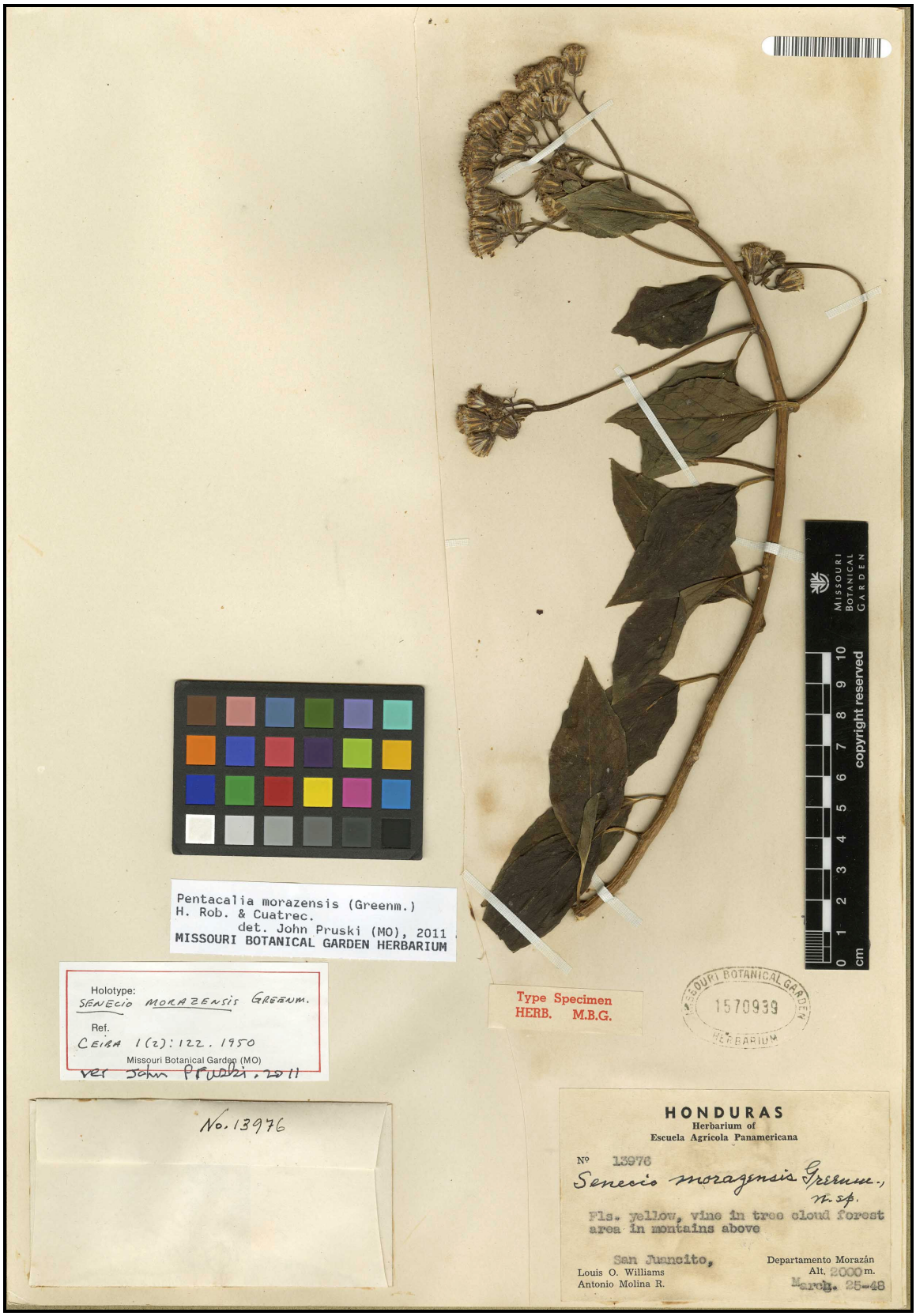

Figure 28. Holotype of *Senecio morazensis* Greenm. (≡ *Pentacalia morazensis*). (*Williams & Molina 13976*, MO).

7. PENTACALIA PARASITICA (Hemsl.) H. Rob. & Cuatr., Phytologia 40: 44. 1978. *Senecio parasiticus* Hemsl., Biol. Cent.-Amer., Bot. 2: 244. 1881. *Cacalia parasitica* (Hemsl.) Sch. Bip. ex A. Gray, Proc. Amer. Acad. Arts 19: 53. 1883. **SYNTYPES: MEXICO. Veracruz**. Orizaba, Mar 1855, *Botteri 1087* (G, K-HOOK). **MEXICO. Veracruz**. Vallée de Cordova, 24 Feb 1866, *Bourgeau 1926* (BR, K, MPU, P, US). **MEXICO. Veracruz**. Mirador, 1842, *Liebmann 165 (8873)* (C-2, GH, K, P; the two sheets in C of *Liebmann 165 (8873)* are on IDC microfiche 2204 set, 192.I.1–192.I.2; the sheet in GH is a fragment and drawing of sheet 1 in C, the sheet with a single large branch; *8873* may be the collection number, but *165* is the number in the protologue, albeit perhaps a species number).

[Lectotypification is neither nomenclaturally nor taxonomically needed, and I simply follow traditional application of the name using the circumscription method. Study in NY, US, and MO over the years hints that each of the three syntypes of *P. parasitica* represents the same disciform taxon, and it seems unlikely that any K syntype sheets are instead radiate *P. venturae*. Nevertheless, lectotypification will be proposed only when each K syntype is in hand, critical details of the florets of each are studied simultaneously, and can be confirmed to represent a single taxon.]

Climbing vines; stems glabrous or subglabrous; herbage glabrous or subglabrous. **Leaves** petiolate; blade 4–9 × 1.4–3 cm, elliptic-ovate to ovate, subcarnose, pinnate-veined with 2–4 visible or immersed arching secondary veins per side, tertiary venation usually not visible, when visible tertiary venation forming an extremely loose reticulum with areolae ca. 5+ mm diam., surfaces concolorous, glabrous, base cuneate to obtuse, margins entire, apex acuminate to attenuate; petiole 0.4–1.2 cm long. **Capitulescence** to 20+ × 15+ cm, mostly terminal, pyramidally racemose or cymose-paniculate, leafless, proximal lateral branches to 10+ cm long, ultimate 2–4 capitula pedunculate, usually well-spaced (sometimes closely spaced); peduncles 1–5(–7) mm long, puberulent or subglabrous, sometimes weakly 1–2-bracteolate or capitula 1–2-subcalyculate, bracteoles ca. 1–1.5 mm long, sessile, lanceolate, chartaceous. **Capitula** disciform (?sometimes discoid), 8–10.5 mm long, (15–)19–23-flowered; involucre 2.5–4 mm diam., broadly cylindrical, florets usually only slightly exserted to rarely post-fruit well-exserted; phyllaries usually 8, (5–)6.5–9 × 1–1.5 mm, about as long as disk florets, lanceolate to elliptic-lanceolate, typically free, glabrous or rarely apex ciliate-fimbrillate, apex acute to obtuse; calycular bracteoles usually 1–4 and 1–3.5 mm long. **Ray florets** absent. **Marginal pistillate florets** usually (4–)5, sometimes loosely associated with an individual phyllary and not much exserted from it; corolla 5–6 mm long, yellow, lobes ca. 1 mm long. **Disk florets** (11–)14–18; corolla 6–7.5 mm long, yellow, glabrous, tube longer than or subequal to limb, lobes 1–1.5 mm long, usually shorter than to about as long as throat; anthers ca. 2 mm long, tails ca. 0.2–0.3 mm long, shorter than to about half as long as collar. **Cypselae** 1–2 mm long, glabrous; pappus bristles 5–7 mm long, 1(–2)-seriate, usually reaching to about the middle of the disk corolla lobes, apices sometimes obtuse.

Distribution and ecology. *Pentacalia parasitica* is an infrequent regional Atlantic slope endemic known only from Mexico and Guatemala. It may also occur in Honduras. The species flowers mostly from October to April, and occurs from (700–)1000–2300(–2700) meters elevation.

Representative collections. **GUATEMALA**. *Contreras 9451* (MO, TEX, US; with budding disciform capitula, elongate phyllaries, and mostly short terminal capitulescences). [?**HONDURAS**. *House 1132* n.v., cited by Nelson 2008, but neither seen nor verified by the author, may perhaps be the *P. morazensis*-like imperfect plants with somewhat clavate pappus bristles seen by the author]. **MEXICO. Chiapas**. Cited by Redonda-Martínez and Villaseñor-Ríos (2011) and Villaseñor (2016). **Oaxaca**. *Breedlove & Sigg 65897* (CAS, MO, TEX; distributed as *P. morazensis*); *García 157* (MEXU n.v., cited by Redonda-Martínez and Villaseñor-Ríos 2011); *Lorence et al. 4342* (MO, NY); *Torres & Martinez 4831* (MO; from Cerro Baul within a few km of the border with Chiapas, appears

to be a short involucral variant of *P. parasitica*). **Puebla**. Cited by Villaseñor (2016: 93). **Veracruz**. *Purpus 8160* (MO, US); *Schaffner 358* (P).

Pentacalia parasitica is recognized by its terminal capitulescence of disciform capitula (given as discoid in the protologue) with an involucre of eight free phyllaries nearly as long as the florets. *Pentacalia parasitica* is, among regional species, similar to both Mexican *P. guerrerensis* (T.M. Barkley) C. Jeffrey and Pacific-slope Mesoamerican *P. phorodendroides*, both of which differ from *P. parasitica* by their relatively short involucres, with P. *phorodendroides* differing further by its axillary flowering and its adjacent phyllaries often connate.

Material of *Pentacalia parasitica* from Oaxaca may have involucres much shorter than the disk florets as typical of *P. guerrerensis*, but otherwise, especially in lacking the large calycular bract of *P. guerrerensis*, the Oaxacan material seems to match *P. parasitica*. *Torres & Martinez 4831* (MO) from Oaxaca, on the western foot of Cerro Baul within a few km of the border with Chiapas, appears to be another unusually short involucral disciform variant of *P. parasitica*. Some collections from Guatemala and Chiapas formerly referred to *P. parasitica* have axillary capitulescences and are now referred to *P. phorodendroides*.

Breedlove (1986: 54) cited *Matuda 5461* from Chiapas as *Pentacalia parasitica*, but instead this collection is a paratype of *P. phorodendoides*. Barkley (1975: 1272) referred material from Panama to *Senecio parasiticus*, but *Kirkbride & Duke 977* cited by Barkley as *Senecio parasiticus*, is instead the type of *Dresslerothamnus hammelii*. Of material of the three collections (two imperfect) cited in the Flora of Panama, Barkley (1975) says they possibly represent "more than one entity." Robinson and Cuatrecasas (1978) and Pruski and Robinson (2018) excluded this species from Panama, and instead give its distribution as only Mexico, Guatemala, and possibly Honduras.

8. PENTACALIA PHANERANDRA (Cufod.) H. Rob. & Cuatr., Phytologia 40: 44. 1978. *Senecio phanerandrus* Cufod., Arch. Bot. (Forlì) 9: 203 (as "103"). 1933. **TYPE: COSTA RICA. Alajuela.** Volcán Poás, 2400 m, 25 Apr 1930, *Cufodontis 544* (holotype: W; isotypes: F, MO). Figures 2D, 6C, 22C–D, 29.

Sprawling shrub with hanging branches to climbing vines 1–5 m tall; stems much-branched, often at nearly right angles, pluristriate, hirsutulous-puberulent at least in axils to sometimes subglabrous, pith solid, trichomes uniseriate, several-celled, patent. **Leaves** petiolate; blade 2.5–8 × 1–2.8 cm, lanceolate to elliptic, chartaceous to stiffly so, pinnately veined, secondary veins not immersed, 6–13 per side, spreading at nearly right angles to midrib, tertiary venation visible and forming reticulum, surfaces concolorous, glabrous, base cuneate to obtuse, margins usually denticulate or dentate with 10–17 teeth per side or less frequently subentire, apex usually acute to acuminate; petiole 0.5–1.4 cm long. **Capitulescence** terminally corymbiform-paniculate on the many elongate (10–25 cm long) distal axillary laterally spreading branches, branches much longer than subtending leaves, ultimate capitula 3–10 in 1–2 cm diam. clusters; peduncles 2–5 mm long, crisped-puberulent, often 1–2-bracteolate; bracteoles ca. 1 mm long, sessile, elliptic-lanceolate, thin-chartaceous. **Capitula** disciform or sometimes discoid, 5–7 mm long, 10–14-flowered; involucre usually ca. 2(–2.5) mm diam., shorter than florets, broadly cylindrical, usually loosely 2–5-calyculate, calycular bracteoles 1–3 mm long, elliptic-lanceolate; phyllaries 8, 3.8–4.2 × 0.8–1.2 mm, linear-lanceolate, typically free, often 3-costate proximally, glabrous or apex sometimes fimbrillate, base often gibbous, usually narrow-margined, apex acute to obtuse. **Ray florets** absent. **Marginal florets** (0–)1–2; corolla 4–5-lobed. **Disk florets** 10–12; corolla 3.5–4.5 mm long, white, glabrous, lobes 1.2–1.7 mm long, usually much longer than the throat, often recurved, central resin duct often visible; anthers usually well-exserted, sometimes pale violet; styles often directed outward, margins distally papillose, apex sometimes also papillose. **Cypselae** 1–1.5 mm long, glabrous, pappus bristles 3–3.5 mm long, 2-seriate with some bristles distinctly inserted within outer series.

Distribution and ecology. *Pentacalia phanerandra* is a locally common regional endemic known only from Costa Rica and Panama, most often on volcanoes and the Cordillera de Talamanca. It occurs from (1300–)1500–3300 meters elevation, and flowers mostly from January–May(–July).

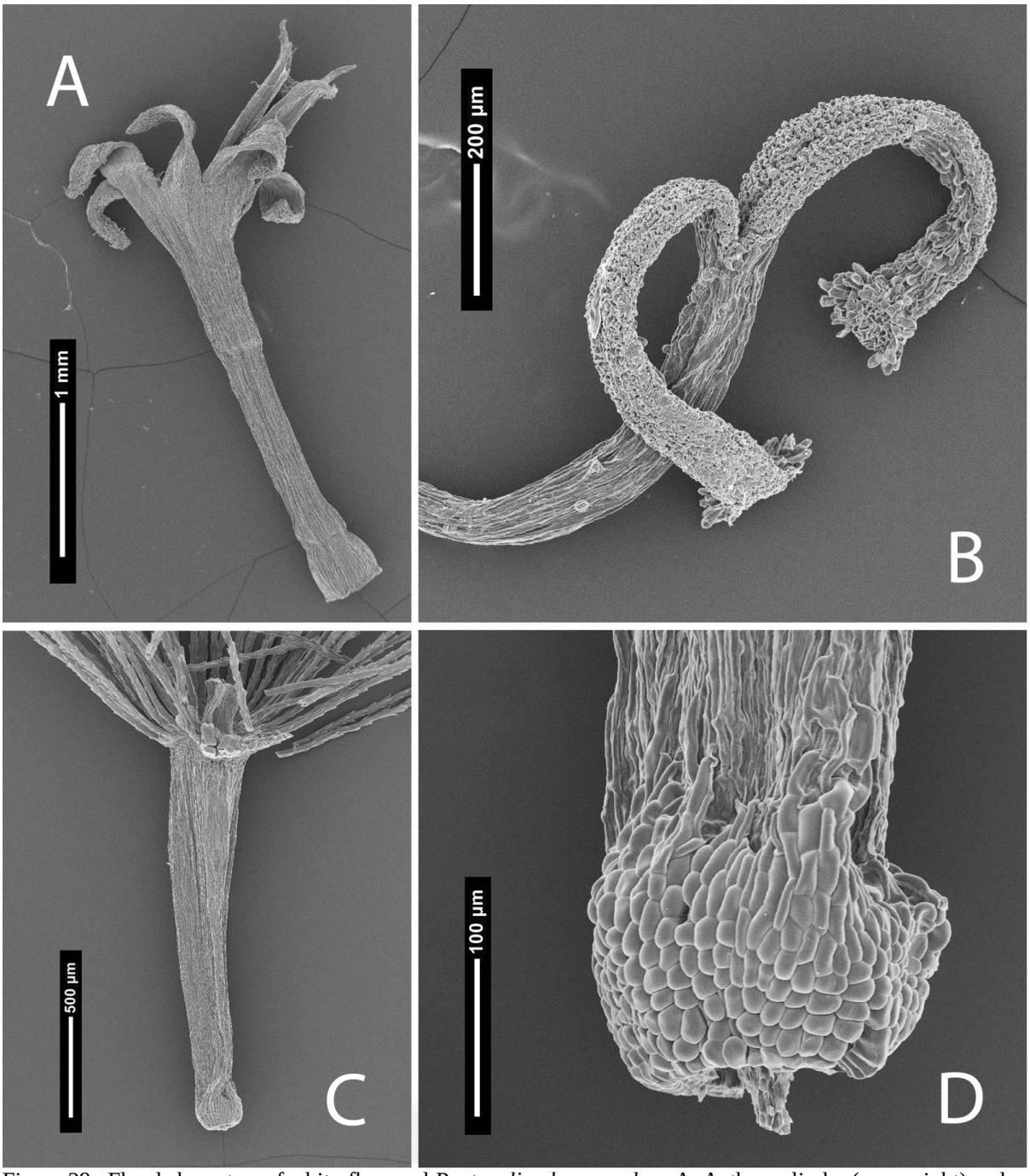

Figure 29. Floral characters of white-flowered *Pentacalia phanerandra*. A. Anther cylinder (upper right) and disk corolla. B. Bifid style, with branch on right showing the 2-banded adaxial stigmatic surface. C. Obconic, glabrous, immature cypsela. D. Immature cypsela base showing symmetrical mid-sized carpopodium and several rows of carpopodial cells. (From *van der Werff & Herrera 7236*, MO).

Representative collections. **COSTA RICA.** *Almeda & Nakai 3806* (US); *Grayum & Quesada 7433* (MO, TEX); *Greenman & Greenman 5392* (MO); *Hammel et al. 19484* (CR, MO); *King 6436* (MO, NY, US); *King & Castro 10005* (MO, US); *Morales 7533* (MO); *Pittier 2050* (US); *Rodríguez et al. 10662* (INB, MO); *Standley & Valerio 50544* (MO, US); *Tonduz 1894* (US): *Williams 16280* (MO). **PANAMA.** *Davidse et al. 25466* (MO); *Gómez et al. 22667* (MO, US); *Hammel 7384* (MO, US); *Klitgaard et al. 835* (BM, MO, PMA; in PMA web database as *P. wilburii*); *Monro & Knapp 5175* (BM, INB, MEXU, MO, PMA; voucher of photographs used here in as Fig. 22C–D); *van der Werff & Herrera 7236* (MO, US).

By its leaves that are chartaceous, pinnately veined, often ovate and dentate and by its white or ochroleucous corollas (Fig. 22C–D), *Pentacalia phanerandra* is obviously similar to a group of otherwise South American species centering about *P. arborea*, the generitype (Figs. 3B, 8A, 23). *Pentacalia phanerandra* is the only Central American member of this tightly knit species group. *Pentacalia phanerandra* is endemic to Central America and was named for its well-exserted anthers. The species is now known from both Costa Rica and Panama, but was long-known from only Costa Rica (viz Greenman 1950; Robinson and Cuatrecasas 1978). Barkley (1975) did not report the species in Panama, but *P. phanerandra* is now known from several Panamanian collections.

As an aside, one noteworthy range extension of a related species is recorded here. Colombian *Pentacalia chaquiroensis* (Greenm.) Cuatr. is the *P. arborea* group member geographically nearest to Central America. *Pentacalia chaquiroensis* was long-known from only the type (Díaz-Piedrahita and Cuatrecasas 1999) collected near Páramo de Chaquiro about 200 km SW of Panama. The type is labeled as Bolívar, but instead is in Córdoba along the northern frontier with Antioquia. The species was not listed in Antioquia, Colombia by Pruski and Funston (2011), but is documented here as new to Antioquia, where it is known to the author from eight collections in páramos and montane forests. The voucher information is: **Pentacalia chaquiroensis** [Colombia. Córdoba (*Pennell 4290*, holotype NY, isotype MO); **Antioquia** (*Alzate et al. 4523*, *4716*, *4830*; *Atehortúa et al. 1253*; *Callejas & Uribe 12305*; *Fonnegra et al. 4369*; *Pipoly et al. 18555*, *18558*; specimens of each at MO)]. *Pentacalia chaquiroensis* occurs from 2200–3400 meters elevation, and should be looked for in Panama along the Colombian border on Serranía del Darién (Cerro Tacarcuna, 1875 m), Alturas de Nique (1700 m), and on Serranía de Pirre (ca. 1450 m). These peaks in Panama, however, are several hundred meters lower in elevation than the lowest recorded elevation for *P. chaquiroensis* in Colombia.

Standley (1938) noted that "tuberculate-scabrous" indument characterized *Pentacalia phanerandra*, in reference to the stiff trichomes of the dense-pubescent stemmed plants, although weaker pubescent plants often have merely crisped trichomes and then mostly in the inflorescence. Basically, the stems are more pubescent than the often subglabrous or glabrous leaves. Standley (1938) noted that some plants have distinctly narrow leaves that are subentire, thus atypical for the species. From material in front of me it appears that such variation is environmental, and the entire lanceolate leaves plants are generally from the lower elevation than are the typical ovate dentate leaved plants.

9. PENTACALIA PHORODENDROIDES (L.O. Williams) H. Rob. & Cuatr., Phytologia 40: 44. 1978. *Senecio phorodendroides* L.O. Williams, Phytologia 31: 445. 1975. **TYPE: GUATEMALA. Escuintla.** Finca Monterrey, south slope of Volcán de Fuego, 1140–1260 m, 5 Feb 1939, *Standley 64554* (holotype: F). Figure 25C.

Pentacalia horickii H. Rob.

Large climbing vines; stems subglabrous, internodes much shorter than the relatively narrow leaves. **Leaves** petiolate; blade 4.5–10 × 1–4 cm, lanceolate to elliptic or oblong, subcarnose, indistinctly pinnately veined, surfaces concolorous, glabrous, base narrowly cuneate, margins entire,

apex acuminate or attenuate to infrequently obtuse; petiole 0.7–1.5 cm long. **Capitulescence** of mostly axillary (position distinctive even on fragmentary herbarium specimens) branchlets from the distal 5–10+ nodes, corymbiform or corymbiform-paniculate, more or less cylindrical in shape, branches 3.5–10 cm long and shorter than to slightly longer than subtending leaves, ultimate capitula pedunculate and usually well-spaced; peduncles 1.5–13 mm long, puberulent, often 1–3-bracteolate, bracteoles 1–2 mm long, sessile, lanceolate, chartaceous. **Capitula** disciform or sometimes obscurely very short-subradiate with limb or limb-like spreading throat-lobes of marginal florets held within involucre (sometimes both conditions on single individuals), 7.5–9.5 mm long, 10–18-flowered; involucre 2–3.5 mm diam., narrowly campanulate, disk florets well-exserted, not obviously calyculate to sometimes loosely few-calyculate; phyllaries 5–8 (i.e., 8 coalescing into as few as 5), 4–6 × 1.2–2.5 mm, typically shorter than disk florets, lanceolate to ovate, glabrous, apex acuminate to obtuse, several capitula per branch with some phyllaries connate to near apex. **Ray florets** characteristically absent, but sometimes pistillate showing a very reduced to minute limb; they are described below as marginal florets, where they are termed subradiate. **Pistillate marginal florets** 2–3, actinomorphic and narrowly tubular or sometimes slightly zygomorphic and subradiate; corolla yellow, glabrous, tube (3–)4–5 mm long, longer than limb, limb 1–2 × ca. 0.5 mm and slightly zygomorphic (then limb about as long as disk anthers and somewhat falsely resembling them) or 1–2.5 mm and actinomorphically 3–5-lobed, when zygomorphic sometimes loosely enclosing style trunk. **Disk florets** 8–15; corolla 6–7 mm long, yellow, glabrous, lobes (1–)1.5–2.2 mm long, about as long as throat; style branch distal abaxial surface and margins relatively short-papillose, papillae to ca. 0.1 mm long. **Cypselae** 1.4–2.4 mm long, glabrous; pappus bristles 5–6.5 mm long, usually reaching to about the middle of the disk corolla lobes.

Distribution and ecology. *Pentacalia phorodendroides* is an uncommon regional endemic known from mostly Pacific slopes in Chiapas, Guatemala, and El Salvador. It occurs in forests from 1100–2800 meters elevation, and flowers mostly from December–February.

Representative collections. **EL SALVADOR.** *Villacorta 528* (LAGU, MO). **GUATEMALA**. *Horich /Blydenstein 57.247-1* (US; of Guatemalan stock, but grown in California); *Kellerman 6805* (US); *Standley 85080* (MO; voucher of photograph of involucres with connate phyllaries used here). **MEXICO. Chiapas**. *Breedlove & Almeda 58149* (CAS, US); *Breedlove & Thorne 31042* (CAS, MO); *Matuda 5461* (CAS, MEXU, TEX).

Pentacalia phorodendroides is somewhat morphologically plastic in that the adjacent phyllaries are sometimes connate (Fig. 25C), and its capitula may be either disciform or obscurely very short-subradiate. *Pentacalia phorodendroides* is unusual among disciform species by its proximal nodes often with an axillary capitulescence, this characteristically shorter than the subtending leaves. This axillary flowering character occurs elsewhere in Central American species, e.g., *P. matagalpensis*, which is consistently (short) radiate and has disk corolla lobes much longer than throat. The involucre characters of its eight phyllaries sometimes fused into as few as five overly broad phyllaries is noteworthy. The connate phyllary character diagnoses the species among Central American species, but occasional fusion of phyllaries occurs sporadically elsewhere in the genus. In *P. phorodendroides* the involucre often much shorter than the florets, but nevertheless the species is similar to disciform *P. parasitica*, a species that occurs in the Gulf-Atlantic slope forests and has free phyllaries about as long as the disk florets and terminal capitulescences.

Pentacalia phorodendroides was described by Williams (1975, 1976) as "discoid." The paratypes *Standley 85080* from San Martín Chile Verde and *Matuda 5461* from Chiapas were cited by Williams (1975), respectively, as *"58080*" and "*15461*". *Matuda 5461* is from an elevation of 2585 meters, but was cited by Williams as from "258" meters elevation.

10. PENTACALIA STREPTOTHAMNA (Greenm.) H. Rob. & Cuatr., Phytologia 40: 44. 1978. *Senecio streptothamnus* Greenm., in Standley, Flora of Costa Rica, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1518. 1938. **TYPE: COSTA RICA.** Las Vueltas, Tucurrique, 635–700 m, Mar 1889, *Tonduz 13275* (holotype: GH; isotypes: B† (as Macbride negative 15756), K, MO, P-2, US). Figures 25A, 30.

Figure 30. Isotype of *Senecio streptothamnus* Greenm. (≡ *Pentacalia streptothamna*). The species is radiate, but nevertheless similar in gestalt to *P. candelariae*. (*Tonduz 13275*, B†).

Woody vines to 15 m tall; stems puberulent to glabrate, sometimes fistulose, trichomes not bent. **Leaves** petiolate; blade (2.5–)4–7 × 1.5–2.5(–3.5) cm, elliptic to ovate or oblanceolate, subcarnose, with 3–5 mostly immersed arching secondaries per side, tertiary venation somewhat distinct, surfaces concolorous, glabrous, base cuneate to attenuate, margins entire, apex acuminate to obtuse; petiole 0.5–1(–2) cm long. **Capitulescence** terminal on larger stems and held above leaves, corymbiform-paniculate, not leafy-bracteate, without specialized large primary bracts, moderately dense, larger branchlets crisped-puberulent, subtended by a thin-chartaceous lanceolate to ovate bracteole 5–20 mm long; peduncles 2–20 mm long, few-bracteolate, crisped-puberulent, bracteoles 2–4 mm long, linear-lanceolate, often spreading. **Capitula** radiate, (6–)7–10 mm long, 10–15-flowered; involucre 3–5 mm diam., narrowly campanulate, disk florets slightly to moderately exserted; phyllaries 8, 5–6.5(–7) mm long, lanceolate, typically glabrous (infrequently puberulent) with apex usually ciliate-fimbriate; calycular bracteoles 1–3 mm long, lanceolate to elliptic. **Ray florets** 2–5; corolla yellow, glabrous, tube ca. 3.5 mm long, limb 2.5–5 × 1–1.5 mm, elliptic-oblong, 4-nerved. **Disk florets** 8–10; corolla (4.5–)5.5–7 mm long, narrowly funnelform, yellow, glabrous, lobes 1.5–2 mm long, about as long as throat; style branch papillae to ca. 0.15 mm long. **Cypselae** 1–2 mm long, glabrous or subglabrous; pappus bristles 5–6 mm long, usually reaching to about the middle of the disk corolla lobes.

Distribution and ecology. *Pentacalia streptothamna* is one of the most common regional endemic Pentacalias, and is known from Nicaragua southeast to Panama. It occurs from 500–2600 meters elevation, and flowers mostly from February–July.

Representative collections. COSTA RICA. *Burger & Gentry 8644* (F, MO, US); *Grayum 9685* (K, MO, NY, USJ, TEX, US); *Haber et al. 11029* (INB, MO, TEX); *Herrera 5859* (CR, MO, TEX); *King 6834* (MO, US); *Skutch 3440* (MO, NY, US). **NICARAGUA.** *Wright s.n.* (NY, US; the budding NY sheet is presumably the same collection as flowering US sheet). **PANAMA.** *Croat 37239* (MO, US); *Croat 66596* (MO); *van der Werff & Herrera 7103* (KSC, MO).

Among Central American Pentacalias, *Pentacalia streptothamna* is obviously similar to *P. tonduzii*, but the two are readily distinguished by technical characters. *Senecio streptothamnus* (*P. streptothamna*) is the type of synonymous *Senecio* sect. S*treptothamni* Greenm. Although the author citation of *Senecio streptothamnus*, the basionym, is sometimes given as 'Greenm. ex Standl.', Standley (1938: 1419) in his introduction to the Compositae treatment for Flora of Costa Rica, credits 'Dr. J. M. Greenman' who "supplied descriptions of several new species" (i.e., *S. brenesii* Greenm. & Standl., *S. schizotrichus* Greenm., *S. streptothamnus* Greenm., and *S. tonduzii* Greenm.). The author citations attributions used by Standley are followed here.

11. PENTACALIA TONDUZII (Greenm.) H. Rob. & Cuatr., Phytologia 40: 44. 1978. *Senecio tonduzii* Greenm., in Standley, Flora of Costa Rica, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1519. 1938. **TYPE: COSTA RICA.** La Palma, 1459 m, 8 Sep 1898 [as 'August' in protologue], *Tonduz 12542* (holotype: US; isotypes: B† (as Macbride negative 15770), BM, G, GH, K). Figures 1D, 6A, 10C, 31–33.

Scrambling vines; stems puberulent with collapsed bent simple trichomes, falsely appearing oblique-appendiculate, pith solid or sometimes narrowly fistulous. **Main stem leaves** petiolate; blade 6–12(–17) × 3.5–9.5 cm, ovate, subcarnose, with 3–5 partly immersed arching secondaries per side, surfaces concolorous, glabrous or subglabrous, base cuneate, margins entire, apex acuminate or acute to broadly ovate or rounded acute; petiole 1–2.5 cm long. **Capitulescence** terminal on main axis or on lateral branches and moderately longer than subtending leaves, openly corymbiform to corymbiform-paniculate, leafy-bracteate with specialized large elliptic to ovate, subsessile primary bracts to ca. 4 cm long; peduncles 10–30 mm long, paucibracteolate, puberulent. **Capitula** radiate, 9–10 mm long, 17–21(–24)-flowered; involucre 5–7 mm diam., turbinate-campanulate, disk florets

slightly to moderately exserted; phyllaries 8, 6–8 mm long, lanceolate, glabrous with apex ciliate-fimbriate; short-calyculate. **Ray florets** ca. 5(–8); corolla yellow, glabrous, tube 2.7–5 mm long, limb 3.7–5 mm long, often linear-lanceolate and 2-nerved to oblong and 4-nerved. **Disk florets** 12–16; corolla 7.2–8 mm long, narrowly funnelform, yellow, glabrous, lobes 1.5–2 mm long, about as long as throat; anthers 2–2.2 mm long, collar ca. 0.5 mm long; style branch papillae to ca. 0.1 mm long. **Cypselae** (immature) ca. 1 mm long, glabrous; pappus bristles 4–5.5 mm long, reaching only to about the base of the disk corolla lobes.

Figure 31. Florets and capitula of *Pentacalia tonduzii*. A. Distal portion of ray floret showing bifid style on left and corolla limb on right. The ray corolla limb of *P. tonduzii* is often 2-nerved, linear-lanceolate, and about the same width as a disk floret anther cylinder. B. Close up of ray floret style branches showing on left the 2-banded adaxial stigmatic surface. C. Capitula showing the uniseriate involucre of 8 subequal glabrous phyllaries, short calyculus, and short ray corolla limbs reaching to about the same height as the disk floret anther cylinders. (From *Alfaro 1546*, MO).

Figure 32. *Pentacalia tonduzii*, showing subcarnose leaves with arching pinnate venation and lateral bracteate capitulescences. (*Alfaro 1546*, MO).

Distribution and ecology. *Pentacalia tonduzii* is an infrequent regional endemic known only from Costa Rica and Panama. It occurs from 1500–2200(–2500) meters elevation, and has been collected in flower mostly in May, July, and September.

Figure 33. Post-anthesis isotype of *Senecio tonduzii* Greenm. (≡ *Pentacalia tonduzii*). (*Tonduz 12542*, B†).

Representative collections. COSTA RICA. *Alfaro 1546* (INB, MO); *Burger & Burger 7556* (F, MO, US); *Burger & Burger 7951* (NY); *Lankaster K146* (K; paratype); *Morales 6205* (INB, MO); *Wilbur & Almeda 16780* (US). **PANAMA.** *Correa et al. 2208* (MO, PMA); *Hammel 7476* (K, KSC, MO, NY, US; material is very robust, but the plant has the narrow ray limbs and large primary bracts, typical of the species).

Variation in ray limb size in *Pentacalia tonduzii* is noteworthy. The typical form has a short and narrow, 2-nerved ray corolla limb, but in some materials the limbs are larger and 4-nerved. At one point I considered using the epithet *leptopetala* for material with narrow ray corolla limbs, but I find no significant differences in other critical characters, and it seems best to simply circumscribe *P. tonduzii* broadly. Field studies are needed to study the range of variation in ray corolla limb lengths in this species, with the variation perhaps indicative of a relatively genetically flexible taxon.

Pentacalia tonduzii is notorious for having in many herbarium specimens collapsed, bent, simple trichomes. These bent trichomes are 0.15–0.3 mm long, curving, distal portion that is sometimes whitish and flattened (Fig. 10C), thereby superficially resembling pseudostellate-to-T-shaped trichomes of *Dresslerothamnus*. A very few trichomes appear nearly arachnoid with wispy apices. Nevertheless, in all specimens the trichomes are simple and the plants prove to be *Pentacalia*. Although the bent or broken trichome may hide its generic affinities, the trichomes as seen on much dried herbarium material nevertheless are basically diagnostic of the species.

Trichomes aside, *Pentacalia tonduzii* may be recognized most readily by large subsessile flowering bracts, corymbiform-paniculate capitulescences, and narrow ray corolla limbs, albeit overall the species is very similar to *P. streptothamna*. Although most specimens of *P. tonduzii* have moderate-sized, broad-tipped leaves, *Hammel 7476* seems different by its relatively long, narrower tipped leaves and corymbiform capitulescences. The subsessile-bracteate capitulescences and narrow ray corolla limbs of *Hammel 7476*, however, otherwise matches *P. tonduzii*. Costa Rican *Burger & Burger 7556* is intermediate in morphology between *Hammel 7476* and the more broad-tipped more typical leaf form of *P. tonduzii*. Several collections of *P. tonduzii* have linear-lanceolate ray corolla limbs (e.g., *Alfaro 1546*, Fig. 31A), somewhat atypical of *Pentacalia*, but never approaching the morphology of filiform-rayed *Dresslerothamnus*. On one hand, *P. tonduzii* seems like an overly narrowly circumscribed (simultaneously named) segregate of *P. streptothamna*, whereas at other times it seems atypical of *Pentacalia*. In technical characters, however, the species is shown to be both distinct from *P. streptothamna* and well-placed in *Pentacalia*.

12. PENTACALIA WILBURII H. Rob., Phytologia 40: 44. 1978. **TYPE: PANAMA. Chiriquí.** Above Cerro Punta towards Bajo Grande, about 6500 ft, 14 Jan 1970, *Wilbur et al. 10919* (holotype: DUKE; isotype: US). Figure 22A.

Woody vines; stems glabrous, sometimes with indurate ivory-white epidermal cells distally. **Leaves** petiolate; blade 3–6.5 × 1.5–3.3 cm, elliptic to obovate, carnose, with 2–3 fully immersed weakly visible ascending secondaries per side, without visible tertiary venation, surfaces concolorous, glabrous, base cuneate to somewhat attenuate, margins entire, apex acute; petiole 1–1.7 cm long. **Capitulescence** terminal on larger stems and held above leaves, broadly rounded corymbose-paniculate, without specialized large primary bracts, moderately dense, larger branchlets subtended by a small thin-chartaceous linear-oblanceolate bracteole to 10 mm long; peduncles 3–10 mm long, sparsely crisped puberulent, trichomes oblique-flagelliform, few-bracteolate, bracteoles 3–4 mm long, linear, spreading, glabrous or subglabrous, often nearly half as long as the phyllaries. **Capitula** radiate, 7–11(–14)-flowered, 8–10 mm long; involucre 3–4 mm diam., cylindrical to narrowly campanulate, disk florets slightly exserted; phyllaries 5(–8), 5–7 × 1–2 mm, linear-lanceolate to oblong, glabrous with apex ciliate-fimbriate; calycular bracteoles 3–4 mm long, linear. **Ray florets** 2–3; corolla yellow, glabrous, tube ca. 3.5 mm long, limb 3.5–4 × ca. 1.5 mm, elliptic-oblong, 3–6-nerved. **Disk florets** 5–8(–11); corolla 6.8–8.2 mm long, narrowly funnelform, yellow, glabrous, tube 3.5–4 mm long, lobes 1.3–1.7 mm long, much shorter than throat; anthers 2.5–3 mm long, tail longer (Robinson and Cuatrecasas 1978) or shorter (pers. obs.) than filament collar; style branch papillae to ca. 0.1 mm long. **Cypselae** 1.5–2 mm long, glabrous; pappus bristles 4–6 mm long, at maturity usually reaching to only about base of the disk corolla lobes.

Distribution and ecology. *Pentacalia wilburii* is an uncommon regional endemic known only from Costa Rica and adjacent western Panama. It occurs from 1900–3100 meters elevation, and flowers mostly from January to April.

Representative collections. COSTA RICA. *Alfaro 1582* (INB, MO); *Davidse & Pohl 1643* (US); *Davidse et al. 26141* (MO); *Santamaría & Monro 8848* (voucher of field photographs used in Fig. 22A, herbarium material not seen, and determination thus provisional; capitula radiate, pappus relatively short, and peduncular bracteoles relatively long as in *P. wilburii*). **PANAMA**. *Hammel et al. 6447* (MO); *Klitgaard et al. 734* (BM, MO, PMA).

Pentacalia wilburii may be recognized by its usually small leaves, peduncles with spreading linear-bracteoles, and radiate narrow capitula, typically with only five phyllaries, but which on occasion have eight phyllaries.

Excluded species

Pentacalia andicola (Turcz.) Cuatr., Phytologia 49: 252. 1981. ≡ **Monticalia andicola** (Turcz.) C. Jeffrey, Kew Bull. 47: 69. 1992.

Pentacalia firmipes (Greenm.) Cuatr., Phytologia 49: 254. 1981. ≡ **Monticalia firmipes** (Greenm.) C. Jeffrey, Kew Bull. 47: 70. 1992.

ZEMISIA B. Nord., Compositae Newslett. 44: 71. 2006. **TYPE:** *Cineraria discolor* Sw., Prodr. 114. 1788. (≡ *Zemisia discolor* (Sw.) B. Nord.).

Shrubs to trees; stems branched, subterete to weakly angled, costate-striate but not strongly angled, evenly and loosely leafy distally but never with leaves clustered distally in aerial rosettes, petiole base persistent; pith to 4+ mm diam., solid, not chambered; herbage (when pubescent) white-tomentose with simple eglandular trichomes without clear basal cells and with greatly elongated sinuous terminal cell (similar to Drury and Watson 1965 trichomes type 5 and Jeffrey 1987 trichome type 3d, but some seemingly longitudinally grooved as in Drury and Watson 1965 trichomes type 1). **Leaves** simple, alternate, petiolate or distal ones subsessile; blade stiffly chartaceous, midrib prominent abaxially, venation pinnate but secondaries forward arching, main secondaries 5–10 per side, tertiary reticulum occasionally prominent, surfaces obviously discolorous, eglandular, adaxial surface relatively dull-green, abaxial surface persistently white-tomentose, margins entire to denticulate, often slightly revolute. **Capitulescence** terminal, pluricapitulate and generally corymbiform to corymbiform-paniculate, rounded on top, individual capitula short-pedunculate; peduncle pluribracteolate; bracteoles linear, spreading. **Capitula** radiate, very loosely few-calyculate, sometimes fragrant; involucre narrowly campanulate, 1-seriate, subinvolucre obturbinate, often broad and sometimes inflated and indurate in fruit, with the few calycular bracteoles mostly proximal toward peduncle and resembling the peduncular-bracteoles; phyllaries (11–)12–13(–15), subequal, lanceolate, free or sometimes 1–2 pairs of adjacent phyllaries connate, margins stramineous-hyaline and relatively broad, midzone darkened, midnerve slightly resinous to obviously orange-resinous, at least some with margins usually scarious; calycular bracteoles linear-subulate; clinanthium solid, epaleate, convex, alveolate. **Ray florets** pistillate, uniseriate (3–)5–8; corolla white or yellow, glabrous, tube about as long as to shorter than limb. **Disk florets** bisexual; corolla narrowly funnelform, white or yellow, glabrous, shortly 5-lobed, resin ducts 10, tube dilated basally, as long as or longer than limb, lobes triangular, shorter than throat, 3-nerved, the medial resin duct sometimes obviously darkened, apical abaxial cells bulbous-thickened; anthers yellow, caudate, filament collar balusterform, basal cells slightly enlarged, endothecial tissue radial, tails of thecae narrow and elongate-pointed; style basically exappendiculate, stylopodium dilated, branches abaxially minute-papillose distally, stigmatic surfaces moderately discrete and 2-banded, abaxial collecting papillae short, sometimes a subapical abaxial crescent of a few slightly longer papillae present, apices convex. **Cypselae** oblong, terete in cross-section, (8–)10-costate, furrows scattered papillose-setose with

myxogenic duplex trichomes, carpopodium distinct, annular, apical rim supporting pappus tan, ribs not decurrent onto carpopodium; pappus of many elongate, persistent but very fragile in dissected material, white, scabridulous bristles usually nearly as long as disk corollas.

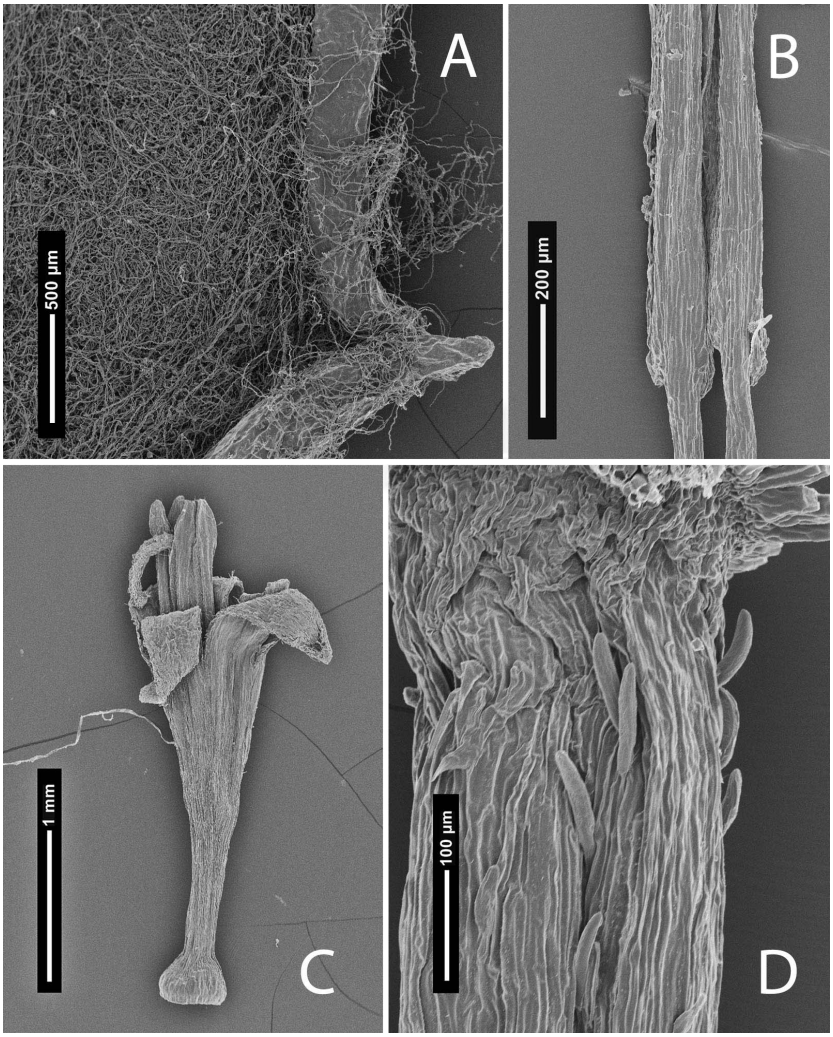

Figure 34. *Elekmania barahonensis* (Urb.) B. Nord., generitype. A. Abaxial leaf blade surface showing loose arachnoid-villous tomentum and marginal tooth. B. Anthers showing ecaudate thecae. C. Narrowly campanulate disk corolla showing relatively short tube. D. Cypsela showing papillose-setose surface with myxogenic duplex trichomes. From *Pruski & Ortiz 4068*, MO.

Senecio thomasii Klatt (syn. *S. deppeanus* Hemsl.), an arborescent Mexican and Central American plant with strongly discolorous leaves, was placed in *Senecio* sect. *Fruticosi* Greenm. by Greenman (1901, 1902, 1926) and Barkley (1985a), but was removed from *Senecio* by Pruski and Robinson (2018). Its balusterform filament collars (Figs. 36B, 37A) mark *S. thomasii* as a member of subtribe Senecioninae, but its caudate anther thecae (Fig. 36B) and convex-tipped (vs. truncate) style branches (Figs. 36C, 38A–C) are at odds with *Senecio* (Fig. 2F). *Senecio thomasii*, by woody habit, discolorous leaves, and caudate anthers, resembled continental *Monticalia*, but differed by (8–)10-costate, papillose-setose (vs. 5-costate, glabrous) cypselae with myxogenic duplex trichomes. Furthermore, *Senecio thomasii* never has ericoid-leaved habit nor holly-like leaves, thus differing from both *Monticalia* and *Scrobicaria*. In its myxogenic duplex trichomes (Fig. 36D), the cypselae of *S. thomasii* are similar to those of *Senecio* s. str., rather than to glabrous-fruited *Monticalia* (Fig. 8B). Pruski and Robinson (2018) though excluding it from *Senecio*, refrained from including the Klatt

species in *Monticalia*, treating *S. thomasii* instead as "Género **A** sp. A," the only generically unplaced Mesoamerican Compositae. Because *Senecio thomasii* is unmatched in Mesoamerica, a home for it among the several endemic West Indian genera of Senecioneae was considered.

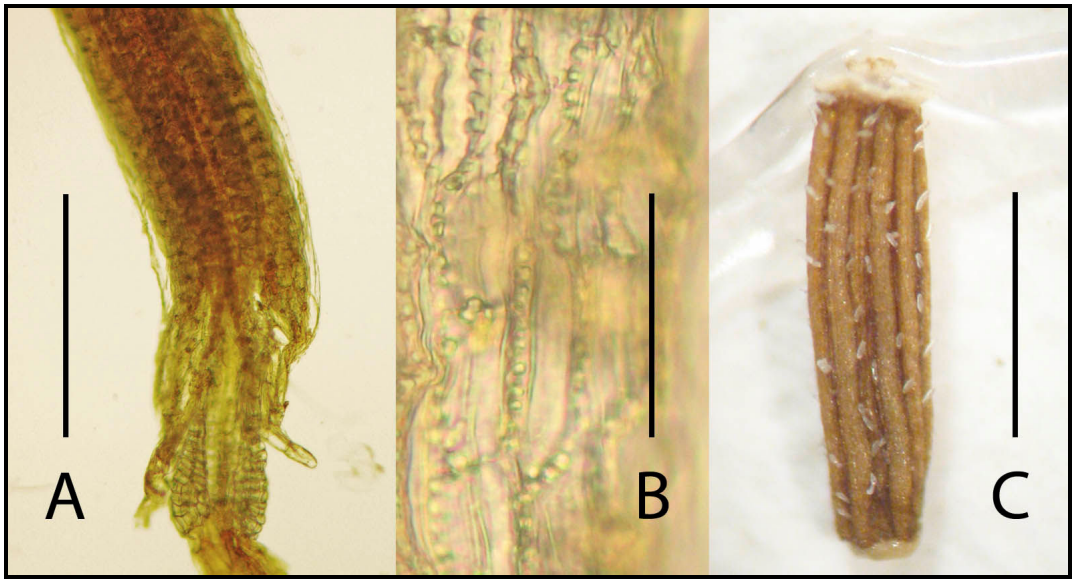

Figure 35. *Zemisia discolor*, generitype. A. Caudate stamen with balusterform filament collar, adaxial view. B. Radial endothecial tissue. C. Pluricostate papillose-setose cypsela showing myxogenic duplex trichomes. From *Gentry & Kapos 28324*, MO. [Scale bars: A 0.3 mm; B 20 μm; C 1 mm].

Nordenstam (2006) described seven new genera of West Indian Senecioneae. Six of these seven genera were sampled by Pelser et al. (2007 fig. 1K), and were recovered in a weakly supported clade (< 50% bootstrap support values) that mostly included other West Indian taxa. Two of these Nordenstam genera are exclusively vining, but several are shrubs to small trees. Included among the shrubs and small trees are three that are discolorous-leaved: *Antillanthus* B. Nord., *Elekmania* B. Nord. (Fig. 34), and *Zemisia* B. Nord. These three similar genera were initially presumed by the author to be *Monticalia*-like, but each has cypselae similar to those of *Senecio thomasii*, thereby differing from *Monticalia*. *Zemisia* is the only one of the three genera that is obviously caudate-anthered (Fig. 35A), but by its white-radiate capitula (Fig. 39) did not immediately match the so-called '*Senecio*' *thomasii* Klatt of Mexican and Central America.

Flower color aside, however, *Senecio thomasii* (Fig. 41) is nearly a dead ringer for *Zemisia discolor* (Fig. 39). Cypsela trichome characters are often significant generically in Senecioneae, but are not always so. For example, three species of Central American *Jessea* H. Rob. & Cuatr. (Senecioninae) have glabrous cypselae, but the fourth, *J. cooperi* (Greenm.) H. Rob. & Cuatr., has setose cypselae (Pruski and Robinson 2018). Koyama (1967) noted that in *Emilia* Cass. and *Gynura* Cass., cypsela pubescence characters are "of significance only at the specific level." Nevertheless, in the case of *Senecio thomasii*, cypsela characters are accepted as generic markers, precluding *Monticalia* from absorbing *Senecio thomasii*. *Senecio thomasii* (Figs. 36–37, 38A, 38C), by balusterform anthers, characteristic cypselae, and convex style branch tips, keys in Nordenstam's (2007) Senecioneae generic key to leads 177B and 181A. But, in the penultimate couplet (182) of the key, by yellow rays *S. thomasii* keys to Hispaniolan *Elekmania* B. Nord., rather than to white-rayed *Zemisia*. *Elekmania* (Fig. 34), however, has disk corollas narrowly campanulate with the tube shorter than limb, auriculate-based anthers, smaller dentate-serrate leaves, a different gestalt, and thus stands apart from *Zemisia*. All other woody continental and West Indian genera of Senecioneae with caudate anthers are distinct from *S. thomasii* and *Zemisia* in the stylar microcharacters of either

continuous stigmatic surfaces, branch apices truncate or narrowed, stylar collecting papillae characters, or by lacking longitudinally grooved pubescent trichomes.

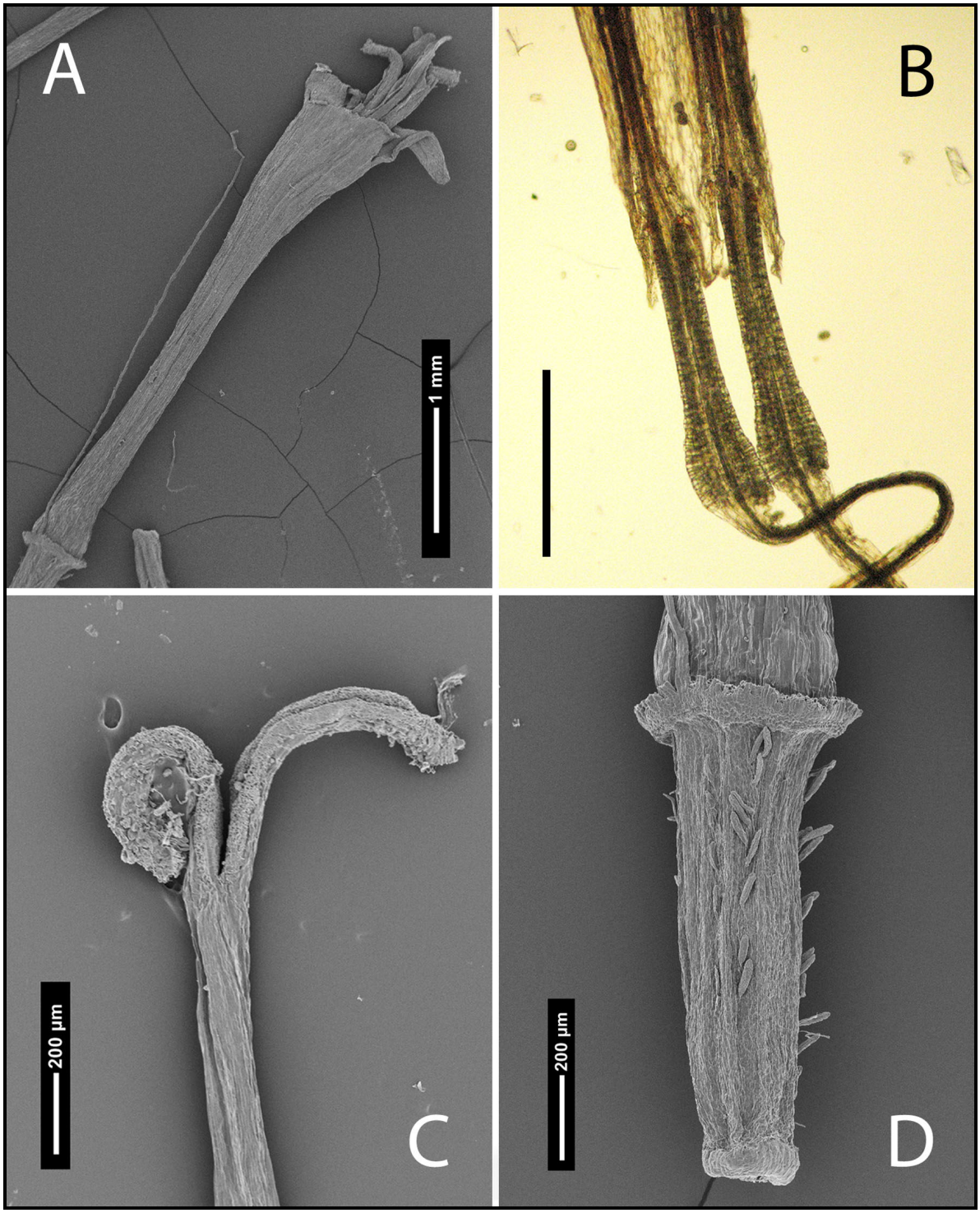

Figure 36. Floral morphology of *Zemisia thomasii*. A. Disk floret with narrowly funnelform corolla, one pappus bristle (on left) intact. B. Two stamens showing anther tails and balusterform filament collars. C. Disk floret style showing the two branches, each with a 2-banded stigmatic surface and convex branch apex. D. Immature cypsela showing papillose-setose surface with myxogenic duplex trichomes. (A, D *Breedlove 24567*, MO; B *Villacorta & Lara 2540*, MO; C *Monterrosa & Carballo 508*, MO). [Scale bar: B 0.25 mm].

Although white flowers are often associated with the Cacalioid Syndrome (Pippen 1968), they are not exclusive to subtribe Tussilagininae; conversely not all Tussilagininae are exclusively white-flowered. Nordenstam (1978, 2007) noted that *Brachyglottis* J.R. Forst. & G. Forst. (Tussilagininae in Bremer 1994) from New Zealand includes a handful of white-radiate species, but that most species are yellow-flowered. Bertil Nordenstam (1978) suggested that the white rays in these species may in part reflect the Insular Syndrome (Carlquist 1974). The Insular Syndrome which in part correlates white flowers and lack of fragrance, however, does not seem to apply to sweet-scented (Moore 1936) *Zemisia discolor* (Senecioninae). However, given the variation in flower color in *Brachyglottis* accepted by Nordenstam (1978, 2007), the yellow flowers of continental *Senecio thomasii* do not discourage its inclusion in formerly monotypic, formerly white-flowered, formerly West Indian endemic *Zemisia*. The similar gestalt, large discolorous leaves, caudate anthers, convex styles, disk corolla morphologies, and pubescent pluricostate cypselae suggest that *Senecio thomasii* is a second species of *Zemisia*.

Here, *Senecio thomasii* is treated as congeneric with formerly monotypic *Zemisia* B. Nord., typified by Jamaican *Z. discolor* (Sw.) B. Nord. *Zemisia* is monographed, the new combination *Zemisia thomasii* (Klatt) Pruski made, the genus boundaries are broadened, and the generic description is emended to reflect that both white-rayed and yellow-rayed plants are now included in *Zemisia*. Although most Senecioninae are yellow-flowered, by its balusterform filament collar (Fig. 35A) white-flowered *Zemisia discolor* is obviously Senecioninae. Robinson (in Proctor 1982) treated the generitype of then-unpublished *Zemisia* as *Pentacalia discolor* (Sw.) H. Rob., but I follow Jeffrey (1992a) and Nordenstam (2006, 2007) and recognize (8–)10-costate-fruited, woody American elements as distinct from pentagonal-fruited *Pentacalia* and *Monticalia*. *Zemisia* seems most similar to simultaneously validated *Elekmania*, but as mentioned above disk corolla and anther characters distinguish them. *Zemisia* is a new generic record for Mexico and Central America and is revised in conjunction with the Trees of Mexico project.

The penultimate lead in the key to genera of Senecioneae in Nordenstam (2007) may thus be modified as follows:

182. Capitula radiate; corollas white or yellow; disk corollas narrowly funnelform, tube as long as or longer than limb; anthers caudate; (2 spp.; Jamaica, Mexico, Central America) ..... **477. Zemisia**

182. Capitula radiate or discoid; corollas yellow; disk corollas narrowly campanulate, tube shorter than limb; anthers auriculate-based; (9 spp.; Hispaniola) ..... **479. Elekmania**

As treated here the two species of *Zemisia* each have equal-sized, strongly discolorous leaves. The leaves of *Z. discolor* are more broad-based, whereas the secondary venation is more prominent in *S. thomasii*. *Zemisia discolor* has much denser phyllary pubescence, and *Zemisia thomasii* has a prominent central resin duct abaxially in its phyllaries. Conversely, the phyllaries of *Zemisia thomasii* are loosely arachnoid at base, and in post fruiting involucres of *Zemisia discolor* a resin duct is apparent adaxially. Shrubby *Senecio cinerarioides* Kunth has a prominent central resin duct abaxially in its phyllaries similar to those of *Zemisia thomasii*, but the *Senecio* is not congeneric with *Zemisia*. In these two cases, the author does not take the value of this resin duct character as generically significant. Although vining Cuban *Leonis* B. Nord. has phyllaries with noticeable resin ducts, these resinous lines are thin, darkly staining, do not recall other genera, and in this example perhaps are generic significant. Many technical characters of disk corolla shapes and apical cells characters (less pronounced than those in *Scrobicaria*), anthers, style branches, and cypselae unit the two species of *Zemisia*, although the two differ so obviously in flower color and in turn presumably in pollinators. *Zemisia* is montane and mid elevational, as are many woody Neotropical tribe Senecioneae. The bulbous-thickened disk corolla lobe character of *Zemisia* is found also in several other woody Neotropical subtribe Senecioninae (e.g., *Monticalia* and *Scrobicaria*).

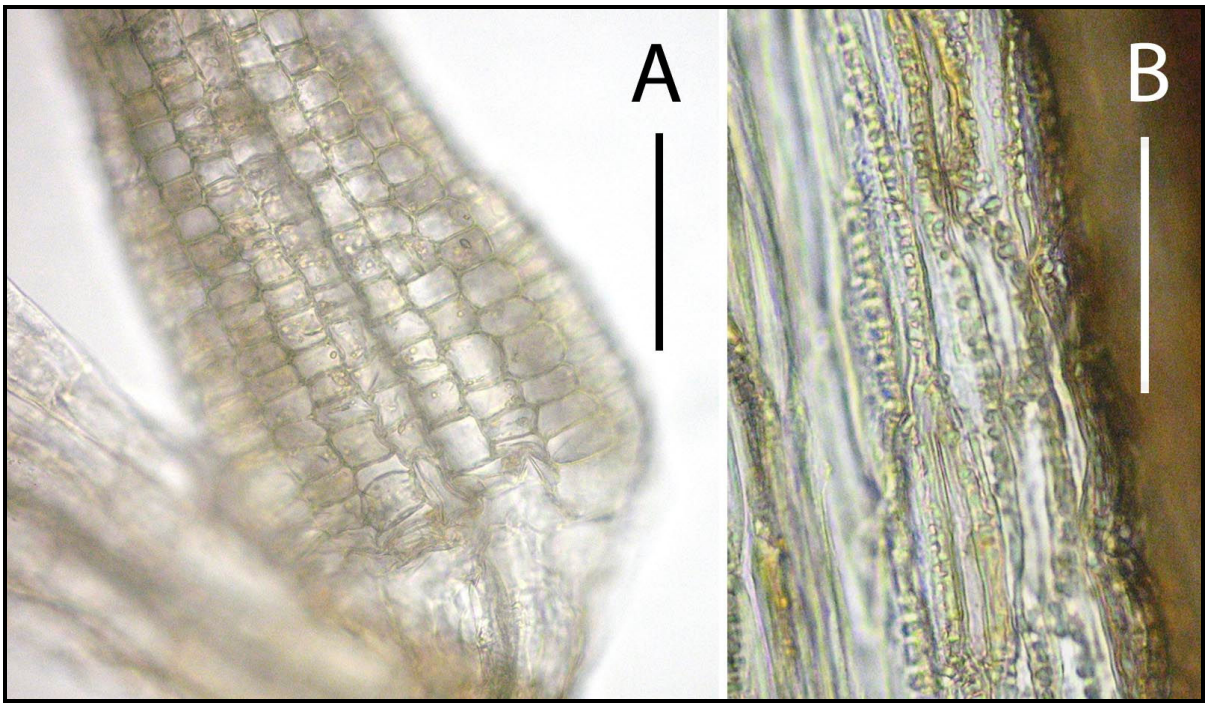

Figure 37. Floral microcharacters of *Zemisia thomasii*. A. Close-up of balusterform filament collar showing enlarged basal cells. B. Radial endothecial tissue showing the irregular thickenings arranged vertically. From *Villacorta & Lara 2540*, MO. [Scale bars: A 0.08 mm; B 15 µm].

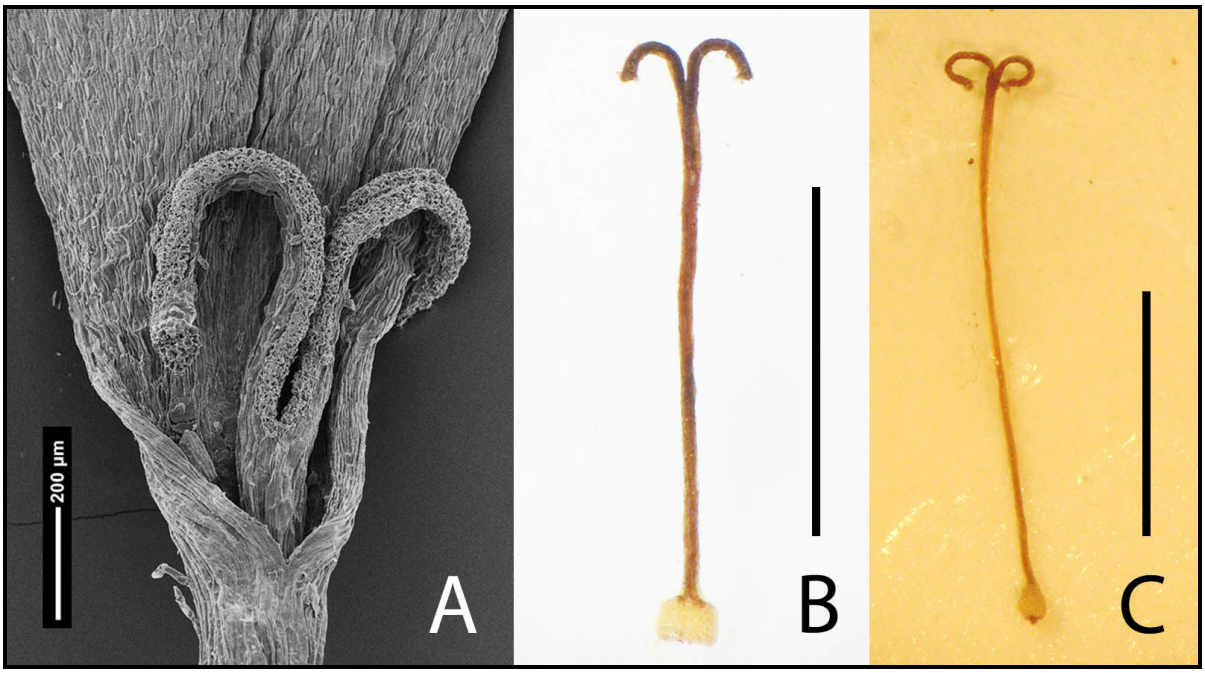

Figure 38. Ray floret and disk styles of *Zemisia*. The style branch apices are convex and the stylopodium enlarged. A. *Zemisia thomasii*, ray floret showing bifid style. The adaxial ligule epidermal cells are quadrangular, typical of yellow ray florets of Senecioneae. B. *Zemisia discolor*, disk style. C. *Zemisia thomasii*, disk style. (A *Breedlove 24567*, MO; B *Gentry & Kapos 28324*, MO; C *Villacorta & Lara 2540*, MO). [Scale bars: B 2.2 mm; C 3 mm].

Key to species of Zemisia

1. Ray corollas white; leaf blade base broadly obtuse to truncate or subcordate; peduncles mostly densely white arachnoid-tomentose; phyllaries densely white arachnoid-tomentose with glabrous tips, without obvious broad central resin duct abaxially; disk corollas 3–4 mm long; (Jamaica) ..... **1. Zemisia discolor** (Sw.) B. Nord.

1. Ray corollas yellow; leaf blade base cuneate to narrowly obtuse; peduncles very loosely lanate to glabrous; phyllaries mostly glabrous or sometimes lingering arachnoid-villous, with a broad orange central resin duct abaxially; disk corollas 4.5–6.5 mm long; (Mexico, Guatemala, Honduras, El Salvador) ..... **2. Zemisia thomasii** (Klatt) Pruski

1. ZEMISIA DISCOLOR (Sw.) B. Nord., Compositae Newslett. 44: 72. 2006. *Cineraria discolor* Sw., Prodr. 114. 1788. *Senecio discolor* (Sw.) DC., Prodr. 6: 412. 1837 [1838], non Desf. 1804. *Pentacalia discolor* (Sw.) H. Rob., J. Arnold Arbor. 63: 311. 1982. **TYPE: JAMAICA**. *Swartz s.n.* (lectotype, designated by Nordenstam 2006: S; isolectotype: S). Figures 35, 38B, 39.

Erect to scrambling shrubs 1–4 m tall; stems straight or sometimes deflected at the distal nodes, white-arachnoid-tomentose distally to glabrate. **Leaves** petiolate; blade (3–)5–13(–15) × (1–)1.5–4.5 cm, lanceolate or sometimes oblanceolate, adaxial surface (drying) finely reticulate otherwise nearly smooth, adaxial surface of immature leaves gray-arachnoid (infrequently densely so), adaxial surface of nearly mature leaves sometimes with midrib arachnoid, adaxial surface of mature leaves soon completely glabrous throughout, abaxial surface densely white-tomentose, base broadly obtuse to truncate or subcordate, margins typically denticulate or sometimes entire, apex nearly obtuse to more commonly narrowly acute to mucronate; petiole (0.5–)1–2(–2.5) cm long. **Capitulescence** to 20 cm diam., broad and slightly rounded on top with lateral branchlets nearly overtopping central axis; peduncles 1–4(–7) mm long, mostly densely white arachnoid-tomentose (infrequently glabrate in patches), several-bracteolate, bracteoles usually 1–2 mm long, linear, loosely lanate to often glabrous distally, the darker bracteoles often strongly contrasting in color with the peduncle. **Capitula** 5–8 mm long, sweet-scented (fide Moore 1936); involucre 3–3.5(–4) mm diam.; phyllaries (11–)13, adjacent ones occasionally fused, 3–4 × 0.6–1 mm, densely white arachnoid-tomentose but glabrate in patches and with glabrous tips, laterally spread phyllaries of post-fruiting capitula without obvious broad central resin duct abaxially, instead midzone dark green with an embedded dark resin duct (best seen adaxially), apex acuminate; calycular bracteoles 1–2 mm long; clinanthium ca. 1 mm diam. **Ray florets** (3–)5, short-exserted; corolla white, tube 2–2.5 mm long, limb 2–3.5 × 1–1.5 mm, oblong or obovate to infrequently nearly orbicular, 3–4(–6)-nerved, epidermal cells of adaxial surface weakly papillose. **Disk florets** (10–)12–13(–15); corolla 3–4 mm long, narrowly funnelform, supernumerary resin ducts mostly visible in lobes not in throat, tube 2–2.5 mm long, about as long as limb, lobes ca. 0.6 mm long; anthers ca. 1 mm long, tails of thecae half to nearly as long as filament collar, appendage ovate-lanceolate; style 3.5–4.5 mm long, branches 0.7–0.8 mm long. **Cypselae** 1.2–2.2 mm long, (8–)10-costate, papillose-setose**;** pappus bristles 3–4 mm long, very fragile.

Distribution and representative collections. Jamaica. *Alexander (Prior) s.n.* 25 Mar 1850 (GH, K, NY-2); *Anonymous s.n.* (perhaps Bertero) (MO-52609, fertile); *Anonymous s.n.* (perhaps Browne or Sloane) (LINN 1309.23); *Anonymous s.n.* (LD-2, one as Thunberg, who did not visit Jamaica); *Bertero s.n.* (P, sterile); *Bretting J-362* (IJ, MO, NY); *Britton 3129* (NY, US); *Clute 16* (MO, NY, P, US); *Eggers 3492* (C, MO, P, US); *Gentry & Kapos 28324* (MO); *Gillis 14974* (MO); *Harris 11068* (NY, US); *Harris 12854* (NY-2); *Houstoun s.n.* (BM n.v.); *Maxon & Killip 399* (GH, NY, US); *Maxon & Killip 1200* (GH, P, US); *Norman 72* (BM, MO, NY); *Oersted 8852* (C, MO); *Proctor 21901* (IJ, NY, US); *Purdie 416* (TCD); *Wunderlin & Gustafson 8868* (MO, UMO).

Figure 39. Color drawing of *Zemisia discolor*, generitype, showing white ray corollas and discolorous leaves. (Reproduced from Sims, Curtis's Bot. Mag. 53: Plate 2647. 1826 as *Cineraria discolor*).

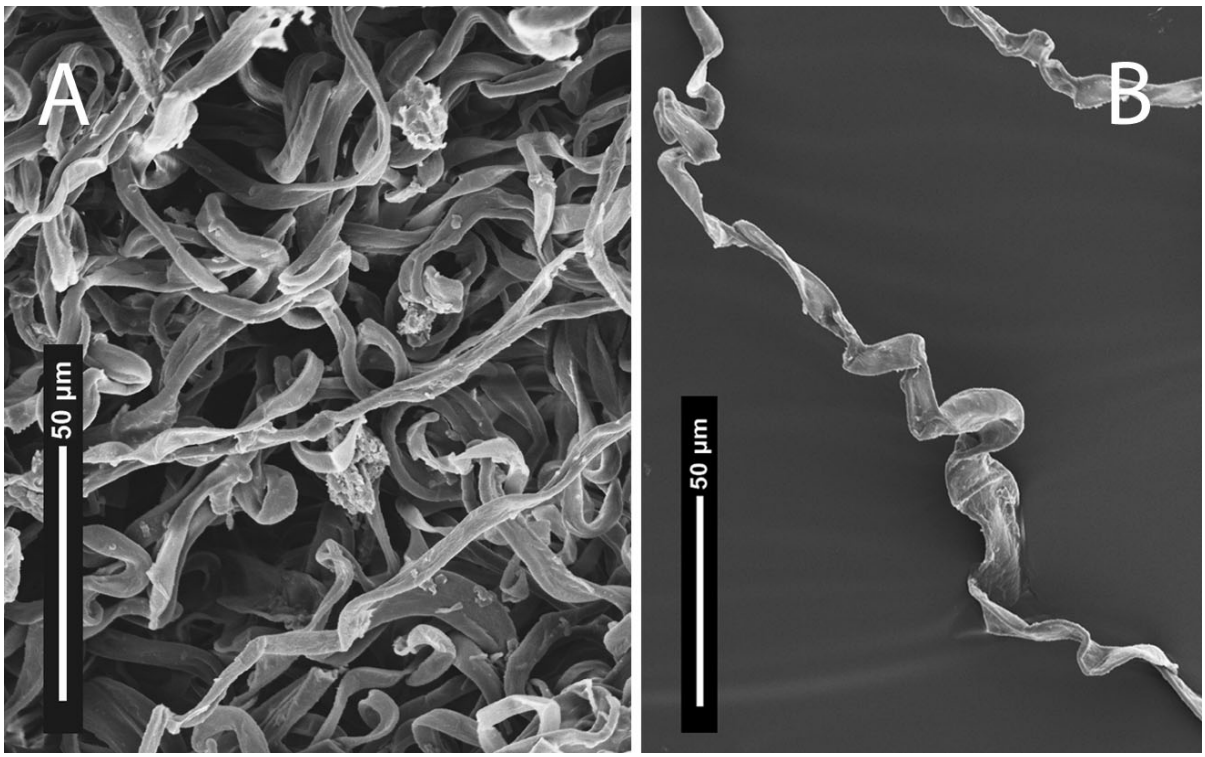

Figure 40. *Zemisia thomasii*, simple eglandular leaf trichomes with elongated sinuous terminal cells. A. Abaxial blade surface. B. Individual trichome. From *King & Renner 7134*, MO.

The protologue is four lines long and the description in Willdenow (1803) is the same as in the protologue, but more complete descriptions were given in Swartz (1806), Sims (1826), Candolle (1837), Grisebach (1864), Moore (1936), Adams (1972), and naturally in Nordenstam (2006). *Zemisia discolor* in its discolorous-leaves and tomentose phyllaries is superficially very similar to *Pentacalia subdiscolor* H. Rob. (Robinson in Proctor 1982). The two species, however, are not conspecific, despite my 1985 (in sched.) "looks same as discolor" annotation on *Proctor 35585* (NY), a paratype of the Robinson name. Recent study confirms this *Pentacalia* differs by dull-tomentose leaves, sometimes axillary (vs. always terminal) capitulescence, disciform (vs. radiate) capitula, 8 (vs. 13) phyllaries, and pentagonal, glabrous (vs. mostly (8–)10-costate, papillose-setose) cypselae, as noted by Robinson (in Proctor 1982). *Pentacalia subdiscolor* in generic features thereby is at odds with *Zemisia discolor*. Proctor (1982) cited *Zemisia discolor* as similar to *Antillanthus discolor* (Griseb.) J.-S. Girard, a different heterotypic plant from Cuba (Girard and Pruski 2012).

2. ZEMISIA THOMASII (Klatt) Pruski, **comb. nov.** *Senecio thomasii* Klatt, Abh. Naturf. Ges. Halle 15(2): 332. November 1881; Neue Compositen, in dem Herbar des Herrn Francaville p. 12. November 1881. [The simultaneous citation of the journal vol. 15 part 2 and of the preprint in Nat. Novit. 3(23): 185, 188. November 1881 established the date of effective publication. TL-2 item 3711 listing of the Klatt preprint stated "to be cited from the journal"]. **TYPE**: **MEXICO**. **Veracruz.** Orizaba, 1864, *Thomas s.n.* (holotype: herb. "Francaville," now P-Drake, Lanjouw and Stafleu 1957: 207; isotype: GH n.v., cited by Klatt 1888 as 'Herb. Klatt'). **EPITYPE (designated here)**: **MEXICO. Veracruz.** Bluffs of barrancas near Jalapa, 3000 ft, 24 Apr 1899, *Pringle 8121* (epitype: MO-3171798; isoepitypes: GH, MEXU, NY, P, US). Figures 36–37, 38A, 38C, 40–41.

Senecio deppeanus Hemsl., Biol. Cent.-Amer., Bot. 2(10): 239. December 1881. **LECTOTYPE**: (chosen here from among four syntype collections): **MEXICO. Veracruz.** Malpays de

Naulingo, Apr 1829, *Schiede & Deppe 243* (lectotype: K-Benth-497695, specimen on right; isolectotypes: B†, MO-3171769). [The collector names Schiede and Deppe were added to the original ticket of the K lectotype specimen of *Senecio deppeanus*, which apparently was distributed without a determination. The original label of Bernhardi herbarium specimen in MO gives only "243 *Senecio scytophyllus*," i.e., without collector and locality. Although lectotypification of taxonomic synonyms is usually not needed taxonomically, in this instance a lectotype is designated from among the four syntype collections because the lectotype collection is clearly radiate, matching the protologue, whereas at least some other authentic material is imperfect. The locality of *Schiede & Deppe 243* was given as Malpays de Naulingo, under the name *Senecio scytophyllus* Kunth by Schlechtendal (1835)].

Ascending to erect shrubs to trees 1–3(–5) m tall; stems densely white-tomentose, leaf base persistent. **Leaves** petiolate or distal-most leaves sometimes subsessile; blade 6–19 × 1–6 cm, usually lanceolate or elliptic-lanceolate, rarely linear-lanceolate, adaxial surface green, smooth to often rugulose, midrib appressed tomentulose, surface otherwise sparsely arachnoid to more commonly glabrous, abaxial surface densely white-tomentose, base cuneate to narrowly obtuse, margin entire to sinuous-denticulate, apex narrowly acute to acuminate; petiole (0–)1–2.5 cm long. **Capitulescence** 5–20+ cm diam., rounded on top with lateral branchlets not overtopping central axis; peduncles 3–11(–15) mm long, very loosely lanate to glabrous, several-bracteolate, bracteoles usually 2–7 mm long, very loosely lanate to glabrous. **Capitula** 7–9 mm long; involucre 3.5–5 mm diam., loosely arachnoid-pubescent basally; phyllaries 12–13(–15), 5.5–6 × 0.8–1.1 mm, mostly glabrous or sometimes lingering arachnoid-villous, with a broad orange central resin duct abaxially, sometimes two thin resinous lateral nerves present, apex acuminate; calycular bracteoles 2–4 mm long; clinanthium ca. 2 mm diam. **Ray florets** 6–8, short-exserted; corolla yellow, elongation sometimes delayed and later than disk corolla anther cylinder emergence, tube 3.5–4.5 mm long, limb (2.5–)3.6–5 × 1.2–2.2 mm, oblong, 4–8-nerved (broader rays tend to have more nerves), epidermal cells of adaxial surface indistinctly quadrangular, in early fruiting plants limb often destroyed but tube intact. **Disk florets** (13–)21–25; corolla 4.5–6.5 mm long, narrowly funnelform, yellow, supernumerary resin ducts visible in lobes and throat, tube 2.5–3.5 mm long, longer than limb, lobes ca. 0.7 mm long; anthers ca. 2 mm long, filament collar ca. 0.5 mm long, basal cells slightly enlarged, tails of thecae about 1/3 as long as collar, appendage lanceolate; style 5–7 mm long, branches 0.8–1 mm long, abaxially papillose in ca. distal 1/3; nectary low-cylindrical, ca. 0.2 mm long. **Cypselae** 1.2–2.4 mm long (8–)10-costate, papillose-setose**;** pappus bristles 4.5–6 mm long, very fragile.

Distribution and representative collections. EL SALVADOR. *Martínez 587* (B, EAP, K, LAGU, MO); *Monterrosa & Carballo 508* (B, LAGU, MO); *Rodriguez et al. 1278* (LAGU, MO); *Sandoval s.n.* 25 Apr 1998 (B, EAP, K, LAGU, MO); *Villacorta & Lara 2540* (B, K, LAGU, MO). **GUATEMALA.** *Fosberg 27236* (MO, US); *Greenman & Greenman 5911* (MO); *Heyde & Lux 3410* (MO, US); *Kellerman 4996* (MEXU, US); *King & Renner 7135* (MO, US); *Pittier 145* (US); *Ramírez & Cobar 614* (BIGU, MO); *Rojas 300* (MO, US); *Standley 62893* (MO, US); *Tuerckheim 1183* (P, US); *Tuerckheim II 2147* (MO, US). **HONDURAS.** *Blackmore & Chorley 4078* (BM, MO); *Clewell 3779* (MO, US); *Daniel & Molina 9257* (CAS, MO); *Elvir 139* (MO); *A. Molina 11695* (US); *D. Molina 156* (MO); *Nelson 4002* (MO); *Nelson & Vargas 2597* (MO-2); *Renfrow & Renfrow 62* (MO, UC); *Standley 56345* (US); *Williams & Molina 14014* (MO-2, US). **MEXICO. Chiapas**. *Breedlove 24567* (CAS, MO); *Breedlove 50145* (CAS, MEXU, MO); *Breedlove 50350* (CAS, MO); *Croat 47677* (KSC, MO, NO-LSU); *Linden 430* (GENT, K; syntype of *Senecio deppeanus*); *Morales 7* (HEM, MO); *Ton 5624* (MEXU, MO, US, XAL); *Ton 5631* (MO, TEX, XAL); *Ton 5866* (MEXU, MO, XAL); *Ventura & López 4469* (IEB, MEXU, MO). **Guerrero**. *Rico et al. 440bis* (MEXU, MO). **Oaxaca**. *Calzada 20868* (MEXU, MO, NY); *Liebmann 173/8862* (C; as *S. lindenii* Sch. Bip, as Macbride negative 22625); *Nelson 2569* (US; on web as 2589); *Quedensley et al. 7062* (MEXU, NY); *Rzedowski 34929* (ENCB, MEXU, MO); *Tenorio et al. 11128* (MEXU, MO). **Veracruz**. *Bilimek 559* (K, P-2, US); *Botteri 1120* (K; syntype of *Senecio deppeanus*); *Dorantes 558* (MEXU,

MO); *Purpus 2368* (MO, UC, US); *Purpus 11600* (MO, UC); *Ventura 5277* (ASU, UNM); *Ventura 18330* (MEXU, MO). Without locality. *Jurgensen s.n.* (K n.v.; syntype of *Senecio deppeanus*). The citation of the plant in Costa Rica as Género A sp. A by Pruski and Robinson (2018: 473) was a clerical error. *Zemisia discolor* is unknown in Costa Rica.

Notes on the type of Senecio thomasii. The title of the Klatt (1881a, 1881b) protologue paper of *Zemisia thomasii* (Klatt) Pruski gives the type as herb. Francaville, i.e., herb. Albert comte de Franqueville, listed by Lanjouw and Stafleu (1957) as "P (herb. Drake)." Materials of these 1881 Klatt names that I have seen annotated by Klatt are, in each case, in P and labeled 'Herbier E. Drake,' in agreement with Lanjouw and Stafleu (1957). Material in P was not found on JSTOR for some 1881 Klatt names, including *Senecio thomasii*.

Type citations of some other 1881 Klatt names include: Díaz-Piedrahita and Cuatrecasas (1999: 51, 107) cited the lectotype of *Senecio semidentatus* Klatt and the holotype of *Senecio trianae* Klatt as in P, but holotypes of *Eupatorium exsertovenosum* Klatt and *Senecio polymerus* Klatt, each described in the same Klatt paper, were listed by Robinson (Eupatorieae, Fl. Ecuador 83: 25. 2007) and Díaz-Piedrahita and Cuatrecasas (1999: 192), respectively, as in W. A sheet of *Senecio caracasanus* Klatt in P not annotated by Klatt is marked as holotype (Cuatrecasas in sched., albeit thereafter marked 'isotype' in a red-typeface Paris annotation label), but an annotated-by-Klatt Drake herbarium holotype sheet (P-1816866) exists. Because Klatt (1881a, 1881b) clearly stated that his names are based on material in herb. Franqueville (i.e., P-Drake), holotypes or syntypes of each name should be expected in P-Drake.

Date and priority notes. Dating priority of *Senecio thomasii* Klatt over conspecific *S. deppeanus* by Greenman (1926) is followed here. The effective date of publication of *S. thomasii* as November 1881 was established by simultaneous citation of both the journal and of the preprint versions in Nat. Novit. 3(23): 185, 188. November 1881. The pagination of the preprint begins on page 1 (typical of preprints, whereas offprints and reprints use the journal paginations), and although preprints typically antedate journals, TL-2 item 3711 dated each as November 1881. The versions are basically identical, differing mainly in the preprint being signatures 1–2, and the journal version signatures 42–43. Indirect evidence that the preprint may antedate the journal version is that the 1881 literature review in Just's Bot. Jahresber. 9(2): 115. 1884 listed the preprint as item 393, whereas a full year later the initial listing of Abh. Naturf. Ges. Halle 15(2), as item 379, appeared (Just's Bot. Jahresber. 10(2): 100. 1885). Dating to month effective publication is drudgery and typically merely a bibliographic triviality, but in this case because the junior name was validated the same year, dating publications to month was needed and allows for the combination *Zemisia discolor* to be made.

The date of effective publication of taxonomic synonym *Senecio deppeanus* Hemsl., published in Flora Biol. Cent.-Amer., Bot. 2 part 10, is that given TL-2 item 2627, i.e., December 1881, one month after the date established for the Klatt name. The journal part 15(2) of Abh. Naturf. Ges. Halle—which includes the Klatt paper—has the printed date as 1881, but is sometimes miscited as 1882. This (incorrect) dating may be because the final part of Abh. Naturf. Ges. Halle 15(3–4) is dated 1882, as is vol. 15 title page. This perhaps explains the citation in the Royal Society of London (1894: 408) catalogue of Klatt's paper as published in 1882. The next year, Jackson (1895: 882) in Index Kewensis dated *S. thomasii* as 1882. A century thereafter, Clewell (1975) Williams (1976), and Barkley (1985a) recognized *S. deppeanus*, with *S. thomasii* dated 1882 and placed in synonymy. Redonda-Martínez and Villaseñor-Ríos (2011) gave the Klatt name as validated in Leopoldina in 1888, where no description is given. In addition to Nat. Novit. 3(23) and TL-2 dating the Klatt paper as 1881, thus having priority over *S. deppeanus*, the Klatt preprint was also listed in the “Neue Litteratur” listings in Bot. Zeitung (Berlin) 39(52): 868. 30 December 1881 as published in 1881.

Figure 41. Isolectotype of *Senecio deppeanus* Hemsl. (= *Zemisia thomasii*). (*Schiede & Deppe 243*, MO).

Species circumscription. Klatt (November 1881a, November 1881b) described *Senecio thomasii* as discoid and as having glabrous cypselae. The type material seen and described by Klatt as discoid is apparently imperfect. Hemsley (December 1881b) described *Senecio deppeanus* as radiate and as with puberulent cypselae. Seven years later, Klatt (1888) cited the following as *Senecio thomasii*: *Sartorius s.n.*, *Linden 430*, *Schiede & Deppe 243* (B), *Liebmann 173* (C), and "Thomas 1864 Herb. Klatt." The Linden and Schiede materials are syntype collections of *S. deppeanus*. The *Schiede & Deppe 243* sheet in front of me is radiate and has faintly papillose-setose cypselae. The citation of this collection—*Schiede & Deppe 243—as Senecio thomasii* serves to emend Klatt's protologue description of this species, described as discoid, but known instead to be radiate. Basically it appears most material seen by Klatt and Hemsley is imperfect as are many modern sheets that have ray corolla limbs damaged, but *Schiede & Deppe 243* is clearly radiate-capitulate. Moreover, *Zemisia thomasii* has delayed ray limb elongation (seen in many Senecioneae, but infrequent elsewhere in Compositae), and is thereby sometimes mistakenly characterized as discoid. Thus, *Schiede & Deppe 243* (K) is designated here as the lectotype of *Senecio deppeanus* Hemsley. A sheet from Veracruz that is obviously conspecific, similarly radiate-capitulate, widely distributed in herbaria, from a nearby locality from the same Mexican state, and annotated as *Senecio thomasii* by Jesse Greenman—i.e., *Pringle 8121* (MO)—is designated here to serve as the interpretive epitype of *Senecio thomasii* Klatt. *Senecio thomasii* Klatt is recognized as in Greenman (1926) in Standley's Trees and Shrubs of Mexico, i.e., with *S. deppeanus* Hemsl. in synonymy. *Zemisia thomasii* occurs from Mexico south to El Salvador and Honduras, and flowers from November to June from about 500 to 2200 meters elevation.

Each of the four collections of taxonomically synonymous *Senecio deppeanus* cited by Hemsley (1881b) is Mexican, and other than the lectotype the protologue cited syntype collection include: *Botteri 1120* (K) from Orizaba; *Linden 430* (K) from Cacaté and Ciudad Real (Chiapas); and *Jurgensen s.n.* (K) without specific locality. *Schiede & Deppe 243* was cited by Schlechtendal (1835: 591) as *Senecio scytophyllus* Kunth (now *Dendrophorbium scytophyllum* (Kunth) C. Jeffrey), a South American plant. The number *Schiede & Deppe 243* was also used by Schlechtendal and Chamisso (Linnaea 5: 121. 1830) for *Crescentia alata* Kunth (Bignoniaceae), and I do not know which usage of the number 243 is in reference to a taxon number and which is to the collection number. Hemsley (1887: 64) included *S. thomasii* in the supplement to Biol. Cent.-Amer., Bot., but listed no collections other than the Thomas type, and did not relate it to *S. deppeanus*.

Taxonomically, it seems clear that the now epitypified *Zemisia thomasii* and the now lectotypified *S. deppeanus* represent the same taxon. Clewell (1975), Williams (1976, 1984), and Berendsohn et al. (2009) each recognized *S. thomasii* as the only Central American shrubby *Senecio* with discolorous lanceolate leaves. Greenman (1926) gave the only two discolorous-narrow-leaved species of *Senecio* sect. *Fruticosi* Greenm. in Mexico as northern *Senecio cinerarioides* Kunth and southern *Zemisia thomasii*. Both species are radiate-capitulate and have pubescent cypselae; neither is discoid with glabrous cypselae as in Klatt's protologue of *S. thomasii*. These two species comingle on Orizaba, the type locality of *S. thomasii*, but although Klatt appears to have misdiagnosed *S. thomasii*, it seems unlikely that Klatt confused these two very different-leaved woody plants. *Senecio cinerarioides* has larger, persistently radiate capitula with more phyllaries and more flowers than Klatt described for *S. thomasii*. Moreover, the subsessile linear leaves (< 1.5 cm wide) of *Senecio cinerarioides* conflict with the protologue of *S. thomasii*. Shrubby discolorous lanceolate-leaved ecaudate-anthered *Senecio cinerarioides* Kunth remains in *Senecio* s. lat., and as such is not congeneric with *Zemisia thomasii*. Thus, the sole Compositae not placed generically by Pruski and Robinson (2018), i.e., Género **A** sp. A, is by all indications the second species of *Zemisia*. It is recognized here as *Zemisia thomasii* and epitypified by *Pringle 8121* (MO).

II. TUSSILAGININAE Dumort., Fl. Belg. 64. 1827. **TYPE**: *Tussilago* L.

Members of subtribe Tussilagininae have long been called cacalioids and have cacalioid/tussilaginoid microcharacters (e.g., Koyama 1967; Robinson & Brettell 1973a, 1973b, 1974; Nordenstam 1978, 2007; Wetter 1983; Jeffrey & Chen 1984; Jeffrey 1986; Bremer 1994; Nordenstam et al. 2009; Pruski 2012a; Pruski & Robinson 2018). The genus *Cacalia*, however, has been rejected nomenclaturally, and *Tussilago* is atypical of Tussilagininae in its functionally staminate disk florets. Nevertheless, the correct name for this cacalioid group is subtribe Tussilagininae, which includes in synonymy subtribes Blennospermatinae and Tephroseridinae (Bremer 1994; Pelser et al. 2007; Nordenstam et al. 2009).

Traditional characters associated with the group (discoid capitula with relatively deeply lobed white corollas) are readily seen, but the floral microcharacters that technically characterize the group require dissection to be seen. The cylindrical filament collar usually about the same diameter as the filament without enlarged basal cells character is one of the most consistent in the group (Figs. 4A, 4C, 4E, 48A; Jeffrey et al. 1977; Wetter 1983; Jeffrey 1992a). On occasion, the filament collars of Tussilagininae are somewhat wider than the filaments, but the basal cells are always relatively small. The second consistent character of Tussilagininae is found in essentially entire-continuous stigmatic surface (Figs. 4F, 9B). A large number of Tussilagininae, especially those of the Old World or temperate regions of the New World, have the presence together of palmate leaf venation, discoid capitula, white, deeply lobed corollas, and polarized endothecial tissue, but there are many exceptions to this character combination, and many yellow-radiate plants (e.g., *Telanthophora*, *Nordenstamia*) are cacalioid.

Treated here are two noteworthy Central American Tussilagininae: *Digitacalia*, a stereotypical white-flowered discoid-capitula genus of Tussilagininae, and the yellow-flowered radiate-capitulate *Telanthophora steyermarkii*, the placement of which is supported by floral microcharacters.

DIGITACALIA Pippen, Contr. U.S. Natl. Herb. 34: 378. 1968. **TYPE:** *Cacalia jatrophoides* Kunth (≡ *Digitacalia jatrophoides* (Kunth) Pippen).

Stiffly erect perennial leafy-stemmed herbs to 4 m; stems annual, lacking basal rosette at maturity, otherwise evenly leafy proximal to the capitulescence, subterete to less commonly angled; herbage bearing simple trichomes, eglandular. **Leaves** alternate, petiolate; blade usually 3–9-lobed, in *D. chiapensis* and *D. stevensii* about 2/3 distance to midrib, in other species sometimes more deeply so, pinnately or subpalmately lobed and veined, chartaceous, lobe margins entire to serrulate. **Capitulescence** large, often at least 30 cm tall and broad, terminal or terminating axillary branches, many capitulate, infrequently (only *D. stevensii*) with pyramidal thyrsoid-panicles, most species corymbiform-paniculate and broadly rounded to nearly flat-topped, lateral branches of the corymbiform-panicles sometimes overtopping central axis, branches generally subtended by bracteate leaves; peduncles minute-bracteolate. **Capitula** small, discoid, calyculate; involucre 1-seriate, turbinate to narrowly campanulate, only slightly longer than mature fruits, the often persistent corollas and pappus then nearly fully exserted; phyllaries 5–8, subequal, free; calycular bracts or bracteoles (1–)3–7, usually shorter than phyllaries; clinanthium +/- flat, foveolate, not fleshy-crested. **Ray florets** absent. **Disk florets** bisexual, 5-merous; corolla salverform, white or ochroleucous, never yellow, persistent on maturing fruits, glabrous, deeply 5-lobed nearly to tube, tube narrowly cylindrical to base, about as long as limb, throat nearly absent or short, lobes elongate, 3-nerved; anthers exserted, theca base obtuse, filament collar cylindrical, without enlarged basal cells, endothecial tissue pattern polarized, apical appendage lanceolate; style cylindrical to base, stylopodium without swollen basal node, branches each with a continuous stigmatic surface, but abaxially with dark-staining line, spreading to recurved, apex exappendiculate, truncate to obtuse,

sometimes with lateral round-tipped papillae. **Cypselae** narrowly cylindrical to oblong, 8–12-costate, ribs broad and well-defined, glabrous or setulose when young, wider than the intermediate furrows; pappus bristles many, mostly about as long as corollas, white, capillary, scabrid, distal cell tips pointed. $x = 30$.

Leafy-stemmed *Digitacalia* (Tussilagininae) was described by Pippen (1968), who included five Mexican endemics, mostly from among species Rydberg (1924a, 1924b, 1927) treated within predominantly rosulate *Odontotrichum* Zucc. Prior to Rydberg, these five species were placed in either *Cacalia* (Candolle 1837; Gray 1883) and/or *Senecio* (Schultz-Bipontinus 1845; Bentham and Hooker 1873; Hemsley 1881a). Although the influential Benthamian synonymy and consequential broad definition of *Senecio* to include *Cacalia* in synonymy trivialized some subtribal and generic distinctions in Senecioneae, *Digitacalia* may nevertheless be considered a segregate of *Cacalia* L. Rydberg (1924a) and Pippen (1968) noted that the discoid-capitula with relatively deeply lobed white corollas—the "cacalioid condition" of Pippen (Figs. 42, 43A)—help distinguish the often ambiguous *Cacalia*. To better appreciate *Digitacalia* and cacalioids/tussilaginoids, we should understand why Rydberg (1924a) asked "to which group should the name *Cacalia* L. be applied?"

The name *Cacalia* is pre-Linnaean, and historically the name has been applied variously, with each of its three one-time proposed lectotypes affecting application of the name. Linnaeus (1753) included ten species in *Cacalia*, but at times each was excluded, and segregate genera from Eurasia, southern Africa, eastern Asia, and the Americas proposed. The ten Linnaean names of *Cacalia* are now recognized as belonging to nine genera in two families, Crassulaceae and Compositae. Rydberg (1924a) proposed *Cacalia alpina* L. (now *Adenostyles* Cass.) as the first generitype of *Cacalia*. Moreover, Rydberg (1924a, 1924b, 1927) took 4-merous, eupatorioid-styled, Eurasian *Cacalia alpina* as generically distinct from American so-called Cacalias, prompting him to exclude *Cacalia* from the Americas. Following Greene (1897), Rydberg and adopted *Mesadenia* (now *Arnoglossum*) for our familiar North American plants, albeit these on occasion still called *Cacalia* (e.g., Pippen 1978; Cronquist 1980; Antonio & Masi 2001). In tropical America Rydberg (1924a, 1924b, 1927) resurrected *Psacalium* Cass. and *Odontotrichum* for a group of rosulate cacalioids/tussilaginoids. Elsewhere in the Neotropics, more than a dozen cacalioid segregates have since been recognized (viz Cuatrecasas 1955, 1960, 1986; Pippen 1968; Robinson & Brettell 1973a, 1973b, 1974; Robinson & Cuatrecasas 1978, 1993; Nordenstam 1978, 2006, 2007; Barkley 1985a; McVaugh 1984; Turner 1990; Barkley et al. 1996; Clark 1996; Nordenstam 2007; Nordenstam et al. 2009; Pruski 2012a; Pruski & Robinson 2018).

After Rydberg's typification, from among the residue of the original Linnaean names, North American *Cacalia atriplicifolia* L. (now *Arnoglossum*) and Asian *C. hastata* (now *Parasenecio* W.W. Sm. & J. Small) were proposed as the second and third lectotype of the *Cacalia* (viz Gray 1883, 1884; Greene 1897; Hitchcock & Green 1929; Kitamura 1938, 1942; Shinners 1950; Cuatrecasas 1955, 1960; Pojarkova 1960, 2000; Vuilleumier & Wood 1969; Robinson & Brettell 1973b; Pippen 1968, 1978; Jeffrey 1979b, 1992b; Wetter 1983). Adoption as lectotype of any of the three Linnaean names could disrupt then current usage (Jeffrey 1992b; Wagenitz 1995), and Wagenitz formally proposed nomenclatural rejection of *Cacalia* L., which was subsequently finalized in the ICN. Even though *Cacalia* L. is nomenclaturally rejected, white-flowered discoid-capitulate genera and their allies (some yellow-flowered and radiate) are commonly still referred to as cacalioids (sometimes as tussilaginoids), albeit these genera treated in subtribe Tussilagininae by Pelser et al. (2007) and Nordenstam et al. (2009).

The species of *Digitacalia* are strict, leafy-stemmed, herbaceous perennials, discoid-capitulate, and most notably have deeply-lobed white corollas. *Digitacalia* by its cacalioid condition (viz Figs. 4A, 48A; Pippen 1968) and especially by its polarized endothecial tissue (Fig. 4B) fits comfortably in subtribe Tussilagininae. North American *Arnoglossum* (Fig. 42) resembles

Digitacalia by its leafy flowering stems without basal rosettes, discoid capitula with white corollas, and sometimes medially scarious-keeled phyllaries, but differs by its weakly calyculate capitula with convex, fleshy-crested (vs. flat, foveolate) clinanthia (Pippen 1968: 375 sub *Cacalia* sect. *Conophora* DC. 1837: 329; viz also Hooker 1829–1834: 332), a radial (vs. polarized) endothecial tissue pattern (Fig. 4B; Robinson and Brettell 1973b figs. 1–2; Wetter 1983 figs. 29, 31–32; Nordenstam 2007), and disk corolla lobes incised only partly (vs. nearly completely) to the corolla tube.

Among Mexican cacalioids/tussilaginoids, Pippen (1968) compared *Digitacalia* to leafy-stemmed, radiate-capitulate, pale-yellow-flowered short-lobed *Pericalia* Cass. (now *Roldana*), and to acaulescent, discoid, white-flowered, elongate-lobed *Psacalium* Cass. (and the now synonymous *Odontotrichum* Zucc.). From them, Pippen (1968) distinguished *Digitacalia* by its character combination of leafy stems, rhizomes lacking tubercules, and absence of a basal rosette at maturity. Robinson and Brettell (1974) summarized *Cacalia* segregates that were newly named or recognized subsequent to the Pippen (1968) treatment and segregated further genera. *Digitacalia* is the sole leafy-stemmed, discoid-capitulate Mexican and Central American cacalioid with deeply-lobed white corollas (Barkley et al. 1996; Pruski & Robinson 2018).

In Mesoamerica, *Digitacalia* is most similar to *Psacalium* by white deeply-lobed corollas. *Psacalium*, however is an acaulescent plant and as noted by Rydberg (1924a) often has filiform so-called Vernonioid style branches. *Digitacalia*, on the other hand, is leafy-stemmed (Figs. 44, 46–47) and has short obtuse-tipped style branches (Fig. 48B). Other regional acaulescent cacalioids/tussilaginoids include non-monophyletic *Psacaliopsis*, *Robinsonecio*, and on occasion *Roldana* (e.g., the species treated as *Pericalia* by Pippen 1968), but each differs from *Digitacalia* by their generally yellow flowers and generally radial endothecial tissue, with *Psacaliopsis* further differing by peltate leaves *and Robinsonecio* by small stature. Peltate leaves (excentrically so) also are frequent in *Roldana*, which however is generally leafy stemmed. Other caulescent-leaved Mesoamerican cacalioid genera differ from *Digitacalia* by yellow flowers and/or moderately short disk corolla lobes. Among caulescent cacalioid genera in Mesoamerica, *Pittocaulon* is the only pachycaulous seasonally leafless shrub, thus further distinguished from *Digitacalia*. Few South American cacalioids/tussilaginoids have discoid capitula with deeply-lobed white corollas in combination with a polarized endothecial pattern, and among them shrubby, branched-stemmed *Cacalia* segregate *Paracalia* Cuatr., except in habit, is somewhat reminiscent of *Digitacalia*.

In *Digitacalia*, Pippen (1968) noted four species central to his concept. However, he took *D. heteroidea* (Klatt) Pippen as anomalous and intermediate with *Pericalia* (now *Roldana*). The transfer of *D. heteroidea* to typically yellow-flowered *Roldana* La Llave (syn.: *Pericalia* Cass). by Robinson and Brettell (1974) effectively reduced to four, the number of species recognized in *Digitacalia*. Turner (1990) raised again to five, the species total in *Digitacalia* by proposing two new Mexican species, and by simultaneously sinking 8-phyllaried *D. tridactylitis* into 5-phyllaried *D. napeifolia*. However, neither of Turner's proposed new species is taken here as distinct; *D. tridactylitis* is here resurrected from synonymy; and the four Mexican species I recognize in *Digitacalia* are the four of Robinson and Brettell (1974), each of the four circumscribed here basically as by Pippen (1968).

Hitherto, *Digitacalia* was known as a genus endemic to Mexico. Three Mexican species occur in Oaxaca and further to the northwest, and two of them, *D. napeifolia* and *D. tridactylitis*, are typified by material from the Sierra San Felipe area of Oaxaca. None of these three species are known to occur east of the Isthmus of Tehuantepec. *Digitacalia chiapensis* is known presently from only Chiapas, Mexico and is the only Mexican species east of the Isthmus of Tehuantepec. It should be looked for in nearby Guatemala. The only Central American species of *Digitacalia* is *D. stevensii*, which is newly described from Honduras and nearby Nicaragua. As such, *Digitacalia* can no longer be taken as endemic to Mexico, and recognition of Central American endemic *D. stevensii* serves to extend to the southeast by more than 500 km the known distribution of the genus. The species are

mostly mid-elevational or montane plants occurring from (540–)1400–2800 meters elevation in oak savannas, pine forests, and mixed forests, mostly on the Pacific watershed (Pippen 1968 map 1; Turner 1990 fig. 1).

Here, the genus *Digitacalia* is revised, and Central American *D. stevensii* Pruski is described as new. The five species I recognize in *Digitacalia* are a slightly different complement than either the five of Pippen (1968) or the five of Turner (1990). Specimen photographs and illustrations, and maps for a few species were given in Pippen (1968), McVaugh (1984), Turner (1990), and Redonda-Martínez & Villaseñor-Ríos (2011). Now, with the included specimen photographs (Figs. 44, 46–47), images of each of the five species are available. Among the five *Digitacalia* species, *D. chiapensis* has the smallest flowers, *D. napeifolia* is the only species typically with five phyllaries, and *D. stevensii* is the only species with a pyramidally thyrsoid-paniculate capitulescences. *Digitacalia jatrophoides*, *D. napeifolia*, and *D. tridactylitis* are each relatively widespread in Mexico.

Key to the species (and former species) of Digitacalia

1. Capitula ≥ 15 mm tall; florets 40+; corollas pale yellow, tube much longer than limb, lobes relatively short; (Mexico: Oaxaca); (syn.: *Digitacalia heteroidea* (Klatt) Pippen) ..... **Roldana heteroidea** (Klatt) H. Rob. & Brettell

1. Capitula ≤ 15 mm tall; florets ≤ 13; corollas white to ochroleucous, tube and limb subequal or tube only slightly longer than limb, lobes relatively long.

2. Phyllaries 5(–6), flat, except towards subsucculent base, margins narrowly scarious; florets 5(–6); (Mexico: Guerrero, Jalisco, Michoacán, Oaxaca, Puebla); (syn.: *Digitacalia hintoniorum* B.L. Turner) ..... **3. Digitacalia napeifolia** (DC.) Pippen

2. Phyllaries 7–8, at least the inner phyllaries usually finely or narrowly keeled in proximal half and with scarious margins broader than mid-zone; florets (7–)8–10.

3. Capitula 5–6.5 mm long; corollas 3–4.5 mm long; cypselae glabrous or very sparsely setulose; pappus bristles 3–4 mm long; (Mexico: Chiapas) ..... **1. Digitacalia chiapensis** (Hemsl.) Pippen

3. Capitula 7–15 mm long; corollas 4–8 mm long; cypselae glabrous; pappus bristles (3.5–)4–7 mm long.

4. Leaf blades deeply 5–7-subpalmately lobed, margins subentire; (Mexico: Guanajuato, Jalisco, Michoacán, Oaxaca, and possibly Zacatecas); (syn.: *Digitacalia jatrophoides* var. *pentaloba* B.L. Turner) ..... **2. Digitacalia jatrophoides** (Kunth) Pippen

4. Leaf blades trilobed or pinnately 5(–7)-lobed, margins subentire to infrequently coarsely serrate.

5. Leaf blades pinnately 5(–7)-lobed; capitulescences pyramidally thyrsoid-paniculate, lateral branches not overtopping the central axis; (Honduras, Nicaragua) ..... **4. Digitacalia stevensii** Pruski

5. Leaf blades trilobed; capitulescences rounded corymbiform-paniculate, lateral branches nearly overtopping the central axis; (Mexico: Guerrero, México, Morelos, Oaxaca); (syn.: *Digitacalia crypta* B.L. Turner) ..... **5. Digitacalia tridactylitis** (B.L. Rob. & Greenm.) Pippen

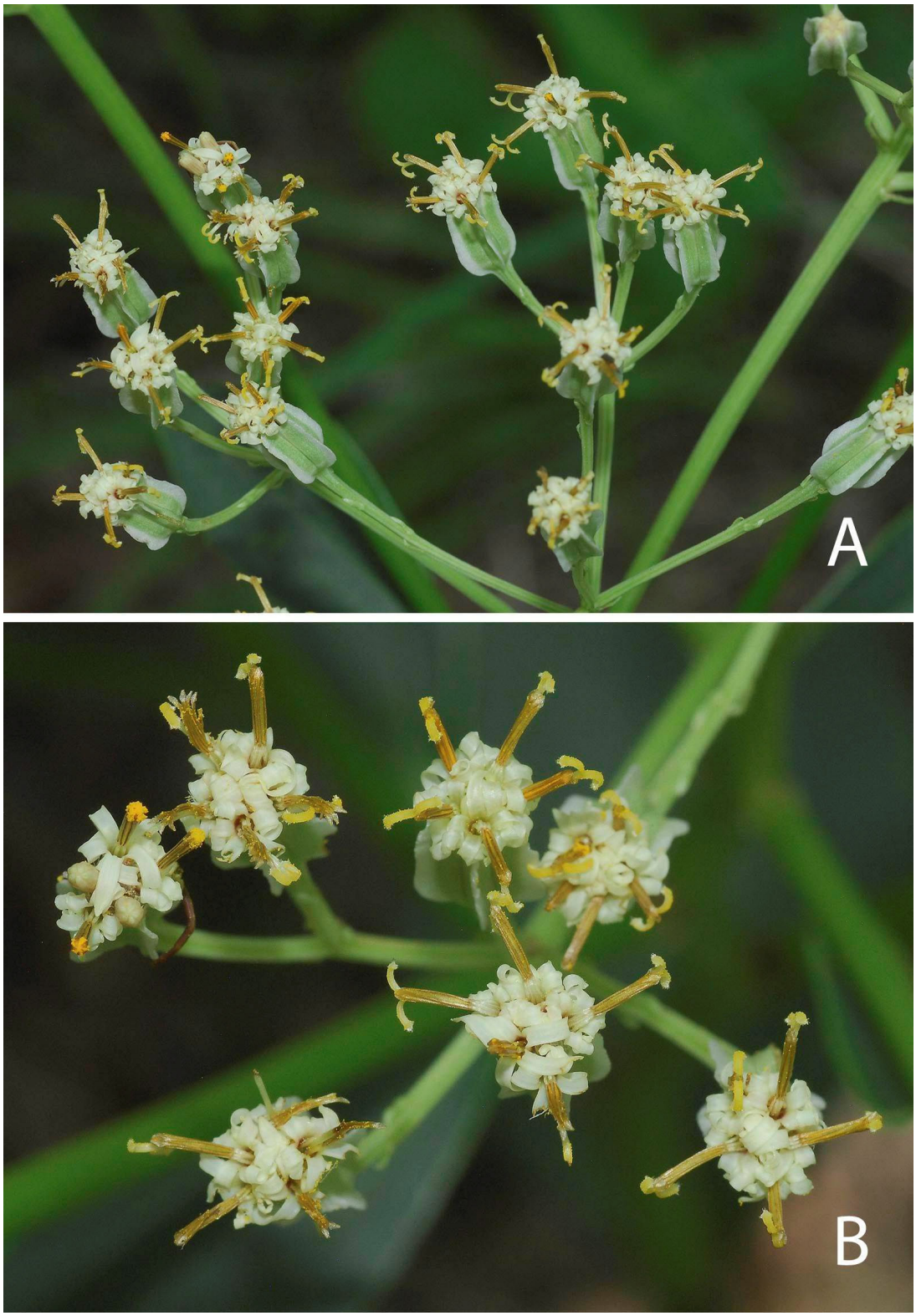

Figure 42. Capitulescences of cacalioid *Arnoglossum plantagineum*, generitype of North American *Arnoglossum*. A. Lateral view of involucres showing subequal, obviously-keeled phyllaries. B. View of capitula from above showing white disk corollas with relatively short recurved lobes and well-exserted anthers. [*Digitacalia* has similar white-flowered discoid capitula, but differs by its long-lobed corollas and crested clinanthia]. (*S. Turner 14-123*, photographs by Steve R. Turner).

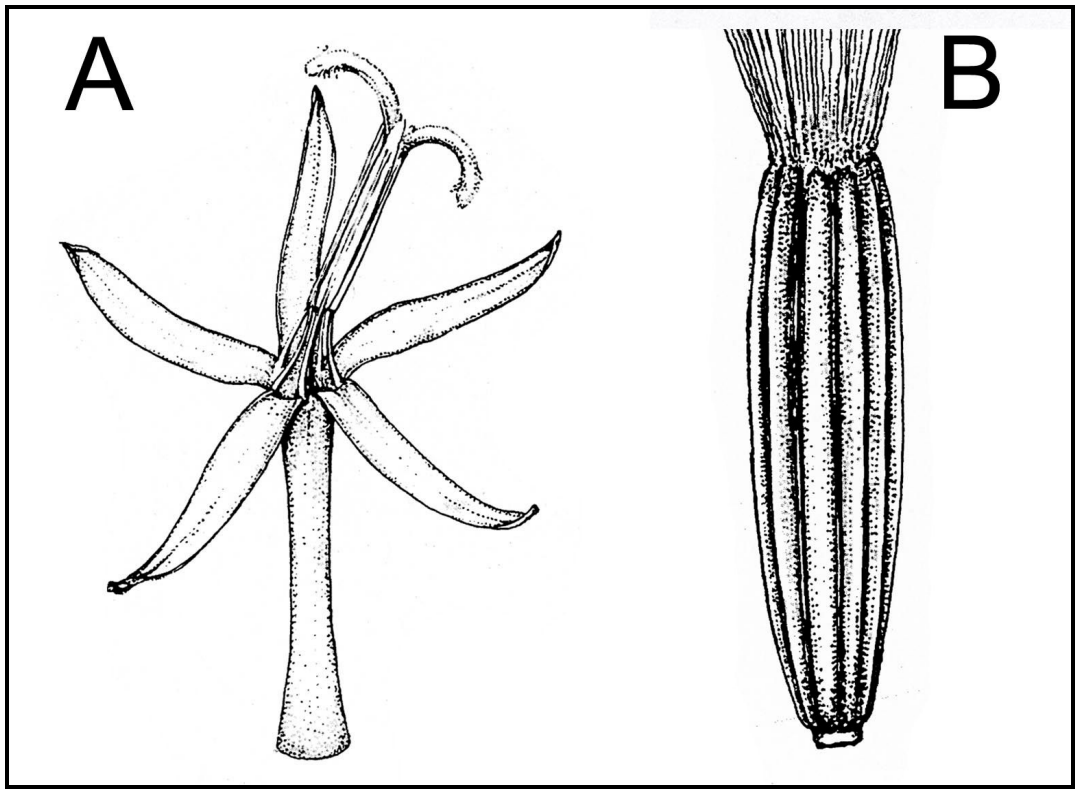

Figure 43. *Digitacalia jatrophoides*, generitype. A. Floret with corolla lobes cut to top of corolla tube and anthers fully exserted. B. Cypsela showing the prominent costae. (Modified from McVaugh 1984 figure 46).

1. DIGITACALIA CHIAPENSIS (Hemsl.) Pippen, Contr. U.S. Natl. Herb. 34: 379. 1968. *Senecio chiapensis* Hemsl., Biol. Cent.-Amer., Bot. 2: 238. 1881. *Cacalia chiapensis* (Hemsl.) A. Gray, Proc. Amer. Acad. Arts 19: 53. 1883. *Odontotrichum chiapense* (Hemsl.) Rydb., Bull. Torrey Bot. Club 51: 418. 1924. **TYPE: MEXICO. Chiapas.** Austro-Mexico, Chiapas etc., 1864–1870, *Ghiesbreght 537* (holotype: K; isotypes: GH-2, MO, NY, YU). [Gray (in sched.) referred the plant to *Cacalia*, and used the epithet "*ghiesbreghtii*" on each of the five cited full/complete sheets, these distributed prior to being described by Hemsley in *Senecio*; the Klatt herbarium sheet in GH is a drawing of the K holotype and an included fragment packet]. Figure 44.

Herbs to 3 m tall; stems striate, fistulose; herbage glabrous or nearly so. **Leaves** pinnately lobed to young leaves few-angulate, glabrous or abaxial face of larger veins puberulent; main stems leaves long-petiolate; blade (6–)10–15 × (4–)9–15 cm, pinnately 5-lobed about 2/3 distance to midrib, base cordate to truncate, sometimes slightly decurrent onto petiole, proximal pair of lobes sometimes each with a proximal lobule, lobes elliptic-ovate, 3–7 × 1.5–4 cm, margins entire or subentire, apex acute to acuminate, sinuses broadly rounded, narrower than to about as broad as lobes, capitulescence leaves abruptly reduced, short-petiolate, pinnately few-angulate, 2–5 × 1–3 cm, ovate to rhomboidal, base truncate to broadly obtuse, entire or subentire, apex acute to acuminate; petiole (1–)5–7 cm long. **Capitulescence** to 30 × 25 cm, corymbiform-paniculate, branches small-leaved, lateral branches not overtopping central axis; peduncles 5–8 mm long, slender, few-costate-sulcate, 1–4-bracteolate; bracteoles ca. 1 mm long, lanceolate. **Capitula** 5.5–7.5 mm long; involucre 3–4 mm diam.; phyllaries (6–)8, 4–5 × to ca. 1.5 mm, elliptic-ovate to oblong basally subgibbous, the narrow mid-zone green, margins stramineous, about as wide as mid-zone, acute, glabrous; calycular bracteoles ca. 3, 1–1.5 mm long, linear-lanceolate; clinanthium ca. 1 mm diam. **Disk florets** 7–11; corolla 3.5–5 mm long, tube 1.7–2.5 mm long, throat 0.2–0.5 mm long, more or less indistinct, lobes 1.5–2 mm

long, lanceolate, spreading or recurved, nerves submarginal, rarely also with a medial resinous nerve; anthers ca. 1.4 mm long, theca apex abruptly appendaged, appendage elliptic-lanceolate; style branches ca. 0.8 mm long, recurved. **Cypselae** (immature) 1.2–1.4 mm long, setulose; pappus 3–4 mm long. $2n = 60$ (Strother 1983).

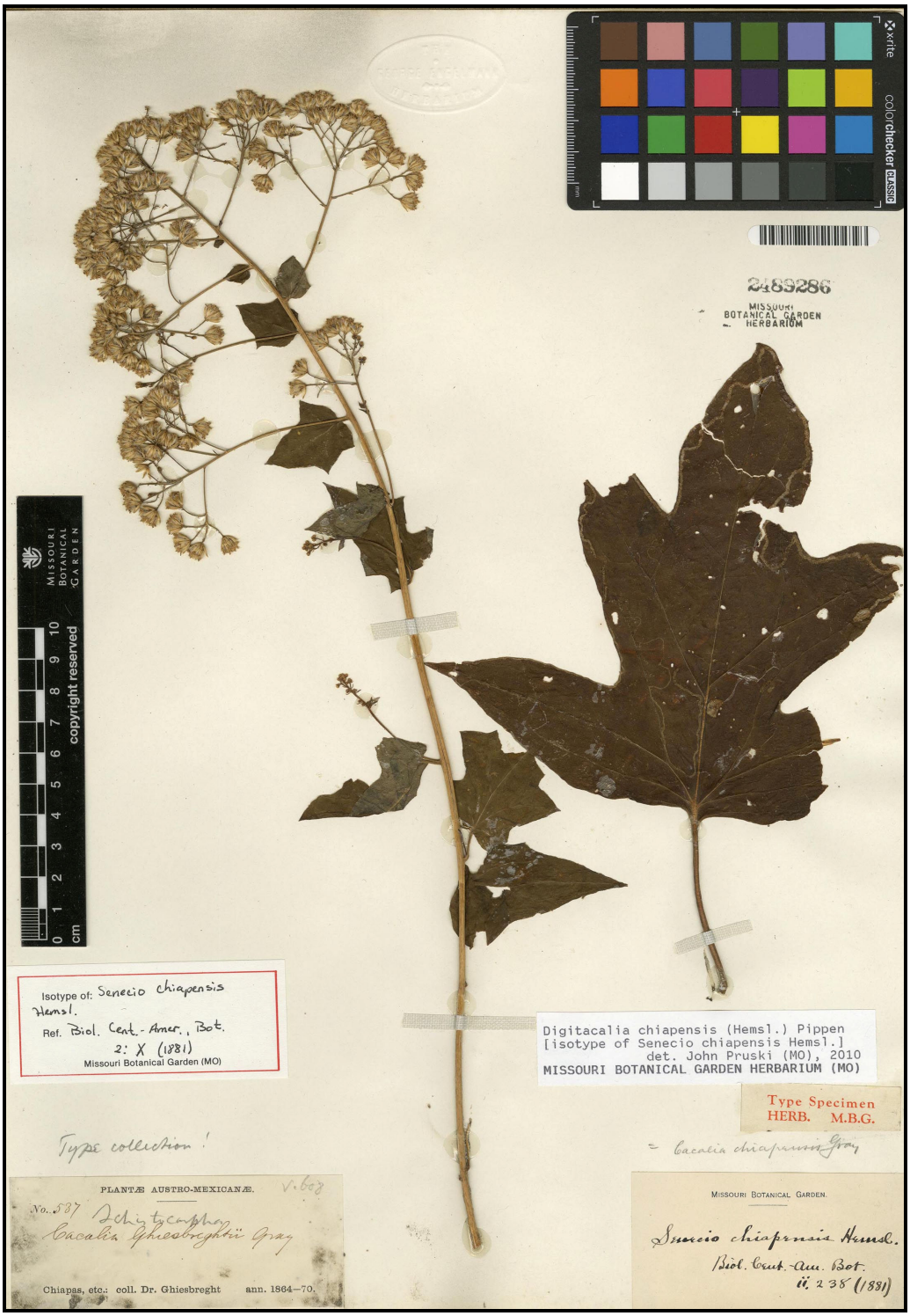

Figure 44. Isotype of *Senecio chiapensis* Hemsl. (≡ *Digitacalia chiapensis*). (*Ghiesbreght 537*, MO; the annotation label on the lower right is in the hand of Jesse Greenman).

Distribution and representative collections. **Mexico** (endemic to Chiapas): *Breedlove 23342* (CAS, MO, NY, TEX, US); *Breedlove 41140* (CAS, MO, TEX); *Breedlove 47010* (CAS n.v., cited by Strother 1983); *Laughlin 1932* (CAS, F); *Nelson 3467* (GH, US); *Raven & Breedlove 19954* (US); *Ton 1493* (CAS, F, NY).

Gray (1883), in his treatment of tussilaginoid species from Mexico, noted the uniqueness of this "singular species." The four other species of the genus differ from *Digitacalia chiapensis* by their taller capitula and longer pappus bristles. The Klatt herbarium sheet in GH has a faithfully rendered drawing of the holotype, as well as a fragment packet.

2. DIGITACALIA JATROPHOIDES (Kunth) Pippen, Contr. U.S. Natl. Herb. 34: 381. 1968. *Cacalia jatrophoides* Kunth, Nov. Gen. Sp. (folio ed.) 4: 132. 1818 [also quarto ed. 4: 169. 1820]. *Senecio jatrophoides* (Kunth) Sch. Bip., Flora 28: 498. 1845. (the Hemsley 1881a: 242 isonym is invalid). *Odontotrichum jatrophoides* (Kunth) Rydb., Bull. Torrey Bot. Club 51: 419. 1924. **TYPE: MEXICO. Michoacán.** "Prope lacum Cuiseo et montem Andaracuas, 900 hex, Sep" [1803], *Humboldt & Bonpland 4298* (holotype: P-HBK, as Macbride negative 37869, as IDC microfiche 6209 104.III.6; isotype: B-W 15074, as IDC microfiche 7400 1086.I.7). [The locality on the holotype is Cuiseo (i.e., Lake Cuitzeo); the Humboldt itineraries by Sprague (1924: 23; 1968: 97) give the protologue localities are numbers 106 and 108, and the date of collection as September 1803]. Figure 43.

Cacalia digitata Sessé & Moc., *Digitacalia jatrophoides* var. *pentaloba* B.L. Turner

Herbs to 3 m tall; stems fistulose, glabrous to tomentulose in the capitulescence. **Leaves** very deeply subpalmatilobed to subpalmatifid with 5–7 lobes or segments (central segment the longest), long-petiolate; blade 4–16 × 4–21 cm, nearly orbicular in outline, divided or lobed to midrib or nearly so, never decurrent onto petiole, surfaces sparsely pubescent along larger veins and margins, lobes or segments 3–12 × 0.8–1.8 cm, lanceolate, flat or sometimes conduplicate, margins subentire, apex attenuate; petiole 3–16 cm long. **Capitulescence** to 30 × 30 cm, corymbiform-paniculate, lateral branches not overtopping central axis, tomentulose to finely tomentulose; peduncles mostly 2–8 mm long, tomentulose. **Capitula** mostly 10–14 mm long; involucre 4–5 mm diam.; phyllaries 7–8, 4–5.5 × 1–1.5 mm, a few sometimes keeled, glabrous; calycular bracteoles 3–7, 2–5 mm long, subulate. **Disk florets** (5–)7–10; corolla 6–9 mm long, throat minute, lobes ca. 3 mm long; anthers ca. 2 mm long; style branches ca. 1 mm long. **Cypselae** 4–5 mm long, glabrous; pappus 5–7 mm long, sometimes becoming tawny when mature.

Distribution and representative collections. **Mexico** (Guanajuato, Jalisco, Michoacán, Oaxaca, and possibly Zacatecas): *Breedlove & Almeda 59818* (CAS, TEX; type of synonymous *Digitacalia jatrophoides* var. *pentaloba* B.L. Turner); *Koch & Fryxell 8963* (US); *McVaugh 17160* (MICH); *Pringle 4262* (GH, MO, NY, US); *Sessé & Mociño 2826* (MA-2; type of synonymous *Cacalia digitata* Sessé & Moc.); *Smith 388* (MO, NY, US); *Soule & Brunner 2464* (MO, TEX).

Digitacalia jatrophoides was illustrated in both McVaugh (1984) and Redonda-Martínez and Villaseñor-Ríos (2011) as synonymous *D. jatrophoides* var. *pentaloba*. Villaseñor (2016) cited this species as occurring in several other states (basically broadening its range from Sinaloa east to San Luis Potosí and southward), but I have not seen specimens or photographs from those localities. Among species that are at least partly sympatric with it, *Digitacalia jatrophoides* most closely resembles *D. tridactylitis*, differing from it by its subpalmatilobed-subpalmatifid leaves with blade not decurrent onto petiole.

3. DIGITACALIA NAPEIFOLIA (DC.) Pippen, Contr. U.S. Natl. Herb. 34: 382. 1968. *Cacalia napeifolia* DC., Prodr. 6: 328. 1837 [1838] (as "*napeaefolia*"). *Senecio napeifolius* (DC.) Sch. Bip., Flora 28: 498. 1845 (the Hemsley 1881a: 244 isonym is invalid). *Odontotrichum*

napeifolium (DC.) Rydb., Bull. Torrey Bot. Club 51: 418. 1924. **TYPE: MEXICO. Oaxaca.** Summo monte San Felipe ad glaciei, (April)July 1834, *Andrieux Pl. mexic. exsic. 280* (holotype: G-DC, as Macbride negative 33809, as IDC microfiche 800 1100.III.2; isotypes K-2). [The protologue, holotype, and one isotype gives the month of collection as July, whereas a second Kew isotype reads July on one label, but gives April on another label].

Digitacalia hintoniorum B.L. Turner

Herbs to 3 m tall; stems becoming fistulose; herbage subglabrous. **Leaves** deeply subpinnately 5–7-lobed, long-petiolate; blade mostly 6–15 × 7–24 cm, broadly ovate to orbicular in outline, lobes typically divided 2/3+ to midrib, lobes in proximal half or 1/3 of blade, base often truncate or sagittate, never decurrent onto petiole, adaxial surface green, glabrous, abaxial surface pale green, persistently puberulent to tomentulose (sometimes nearly glabrate), lobes 3.5–12 × 1–5 cm, lanceolate or rhomboid, margins serrulate to distinctly serrate, apex attenuate, basal two lobes lateral (each sometimes with a small proximal lobule), the distal 2–4 forward-directed lobes and terminal lobe arising from well above basal lobes; petiole 3–10 cm long. **Capitulescence** to 45 × 45 cm, corymbiform-paniculate, lateral branches not overtopping central axis, tomentulose; peduncles mostly 2–10 mm long, tomentulose. **Capitula** mostly 8–13 mm long; involucre mostly 3–4 mm diam.; phyllaries 5(–6), 4–5 mm long, flat except towards subsucculent base, glabrous or sparsely ciliate, margins narrowly scarious; calycular bracteoles 1.5–3 mm long, subulate. **Disk florets** 5(–6); corolla 6–8 mm long, throat minute, lobes 3–4 mm long; anthers 2–3 mm long; style branches 1–2 mm long. **Cypselae** 4–5 mm long, glabrous; pappus 5–7 mm long, sometimes becoming tawny when mature.

Distribution and representative collections. Mexico (Guerrero, Michoacán, Oaxaca, Puebla, and possibly Jalisco): *Calzada 20479* (MEXU, MO, NY); *Davidse & Davidse 9768* (MO); *Galeotti 2082* (K, n.v., cited by Hemsley 1881a: 244); *Gentry et al. 20392* (US; a flowering branch with single bracteate leaf, mixed with a species of *Verbesina*); *Gentry et al. 20435* (US); *Hinton 12572* (GH, MICH, NY, TEX, US; type of synonymous *Digitacalia hintoniorum* B.L. Turner); *Lorence et al. 3650* (CAS, MEXU, MO); *Nelson 1133* (GH, US); *Pringle 4778* (GH, MO, NY, US).

Digitacalia napeifolia is unique in the genus by its typically five (vs. eight) phyllaries. An illustration of *D. napeifolia* was provided by Turner (1990) under the name of *D. hintoniorum*. The Hinton collection cited above is the type of the synonymous *D. hintoniorum*, but was cited as *D. napeifolia* by Pippen (1968: 383) and McVaugh (1984: 298), who are followed here. My notes from the 1990s give *Rose 3040* (US) as having about five phyllaries, which if correct would imply the sheet would thereby match *D. napeifolia*, and apparently would be the sole voucher of the species from what seems to be Jalisco, albeit labeled as Zacatecas. *Rose 3040* was cited by Rydberg (1924b: 429) as *Odontotrichum jatrophoides* and by Pippen (1968: 382) as *D. jatrophoides*.

4. DIGITACALIA STEVENSII Pruski, **sp. nov. TYPE: NICARAGUA. Nueva Segovia.** 2 NW of Ocotal–Jalapa highway at km 269.5, along road into mountains, 13° 47' 11" N, 86° 13' 6" W, 621 m, 12 Mar 2016 (in flower), *Stevens & Montiel 37259* (holotype: MO; isotype: HULE). Figures 4A–B, 45–48.

Plantae herbaceae perennes 1–3 m altae, caule erecta foliata villosula vel arachnoidea a glabrata fistulosa; folia alterna petiolata, lamina (5–)9–19 × (3.5–)7–15 cm ovato-rhomboidea 5(–7)-pinnatilobata chartacea basi obtusa vel truncata; capitulescentia usque 25 × 13 cm dense thyrsoidea-paniculata pyramidalis pluricapitulata (20–50+ capitula), pedunculi 5–8 mm longi; capitula discoidea 7–8 mm alta, involucrum 4.5–5.5 mm latum, phyllaria 8 uniseriata 4.5–5.5 × 1–1.8 mm pallida glabra, clinanthium epaleaceum 0.5–1 mm latum; flosculi disci hermaphroditi 9–10, corolla 4.5–5.5 mm longa profunde quinquelobata alba glabra; cellulae endotheciales oblongo-hexagonales nodulis polaribus; lineae stigmaticae connatae; cypselae 1.6–2.3 mm longae; pappi setae numerosae 4–5 mm longae.

Erect, monopodial, leafy-stemmed herbs 1–3 m tall, presumably perennial based with annual stems, these evenly leafy throughout, but lacking basal rosette at maturity, rhizomes presumably without tubercules; stem striate-costate, subterete to less commonly somewhat angled, fistulose, sparsely villosulous grading distally to capitulescence branches moderately villosulous to villosulous-arachnoid; herbage bearing simple eglandular trichomes. **Leaves** alternate, pinnately 5(–7)-lobed, petiolate, with marginal petiole, never peltate; blade (5–)9–19 × (3.5–)7–15 cm, ovate-rhomboid in outline, marginally lobed about half to 2/3 distance to midrib, chartaceous, larger secondary veins about 3–5 per side, each with 1–2 faint ascending tertiary veinlets, lobes evenly spaced, forward-directed, the sinuses broadly rounded, about as wide as the lobes, surfaces more or less concolorous, sparsely villosulous-arachnoid to subglabrous, base obtuse to truncate, sometimes slightly decurrent onto petiole, the four primary marginal lobes subequal, proximal pair of lobes sometimes each with a lobule very near blade base, lobe margins few-denticulate or few-dentate with teeth 0.1–0.5 mm long, lobes 1–6 × 1–5 cm, triangular to elliptic-ovate, apex acute to obtuse, capitulescence leaves subtending lateral branches abruptly reduced; petiole (2–)5–7 cm long. **Capitulescence** large and moderately dense, pyramidally thyrsoid-paniculate, terminal or terminating axillary branches, elongate with the spreading, lateral branches not overtopping the central axis, to 25 × 13 cm, many-capitulate (20–50+ capitula), few-bracteolate; peduncles slender, 5–8 mm long, villosulous to villosulous-arachnoid, 0–2+-bracteolate; bracteoles ca. 1 mm long, lanceolate, ascending. **Capitula** discoid, 7–8 mm long, 9–10-flowered, weakly subcalyculate; involucre 4.5–5.5 mm diam., turbinate to narrow-campanulate, green at very base; phyllaries 8, free, 4.5–5.5 × 1–1.8 mm, nearly scarious and estriate except for narrowly herbaceous midrib and occasional pair of lateral veinlets, glabrous or nearly so, sometimes slightly medially narrow-keeled proximally, mostly whitish with a narrow green midrib-keel and pale hyaline margins, midrib continuing to the acute apex, the inner four phyllaries broader with broader margins; subcalycular bracteoles 1–3, loosely inserted, 1–2 mm long, much shorter than phyllaries, linear-lanceolate, green; clinanthium epaleate, 0.5–1 mm broad, flat and foveolate, neither convex nor obviously fleshy-crested. **Ray florets** none. **Disk florets** bisexual, 9–10, in early anthesis with corolla partly exserted from involucre, in mature fruit corolla presumably mostly exserted form involucre; corolla 4.5–5.5 mm long, deeply 5-lobed nearly to tube, salverform, white (ochroleucous), glabrous, tube 2.7–3.2 mm long, slightly longer than limb, weakly dilated or narrowly cylindrical to base, throat indistinct, ca. 0.2 mm long, lobes 1.6–2.1 mm long, linear-lanceolate, recurved, nerves submarginal, medial resin duct typically present; anthers exserted from throat, ca. 1.5 mm long (excluding collar), abruptly appendaged, collar ca. 0.4 mm long, cylindrical, about same diameter as filament, without enlarged basal cells, about as long as anther appendage and about as long as the short filament, thecae bases tapered to slightly sagittate, endothecial tissue pattern polarized, cells oblong-hexagonal, apical appendage 0.4–0.5 mm long, lanceolate, sometimes fragile-based and breaking; style exappendiculate, ca. 5.5 mm long, nearly cylindrical to base, without obvious swollen basal node, branches recurved, ca. 1 mm long, with a continuous stigmatic surface, apex obtuse, with a few round-tipped papillae. **Cypselae** (immature) 1.6–2.3 mm long, narrowly oblong in outline, dark brown, glabrous, 9–12-costate, ribs broad and well-defined, (presumably pale at maturity), carpopodium symmetrical, 0.2–0.3 mm long, stramineous; pappus bristles many, 4–5 mm long, white, capillary, scabrid, apical cells pointed.

Distribution and ecology. *Digitacalia stevensii* is known from three collections in north-central Honduras and Nicaragua along the western border with Honduras (Fig. 45). The Nicaraguan type locality is about 10 km southeast of the border with Honduras, and the paratype locality only about 3 km south of the border with Honduras. The type locality in Nicaragua is about 50 km east of the Nicaraguan paratype locality. *Digitacalia stevensii* is the only species of the genus not known from Mexico. It has been collected in bud in December and February, and flowering in March. The label of the holotype—*Stevens & Montiel 37259*, MO—reads "fleshy monopodial herb, 1–3 m tall, heads dull yellow." The pre-anthesis anthers appear to be yellow, and the corollas are white (ochroleucous). Although the yellow anthers make the capitula seem yellowish, the corollas are not

yellow, as are the corollas in the somewhat similar genus *Roldana*. In any event, the new species is presumed to be pollinated by small insects. *Digitacalia stevensii* occurs between 540–974 meters elevation, and has been found along roadsides, in pine-oak forests, and in dry forests along rocky streams. It is by far the lowest elevational species. Doug Stevens (pers. comm.) has said the type locality is on weathered granite soil. The species was not relocated at either Nicaraguan locality by Doug Stevens in April 2018.

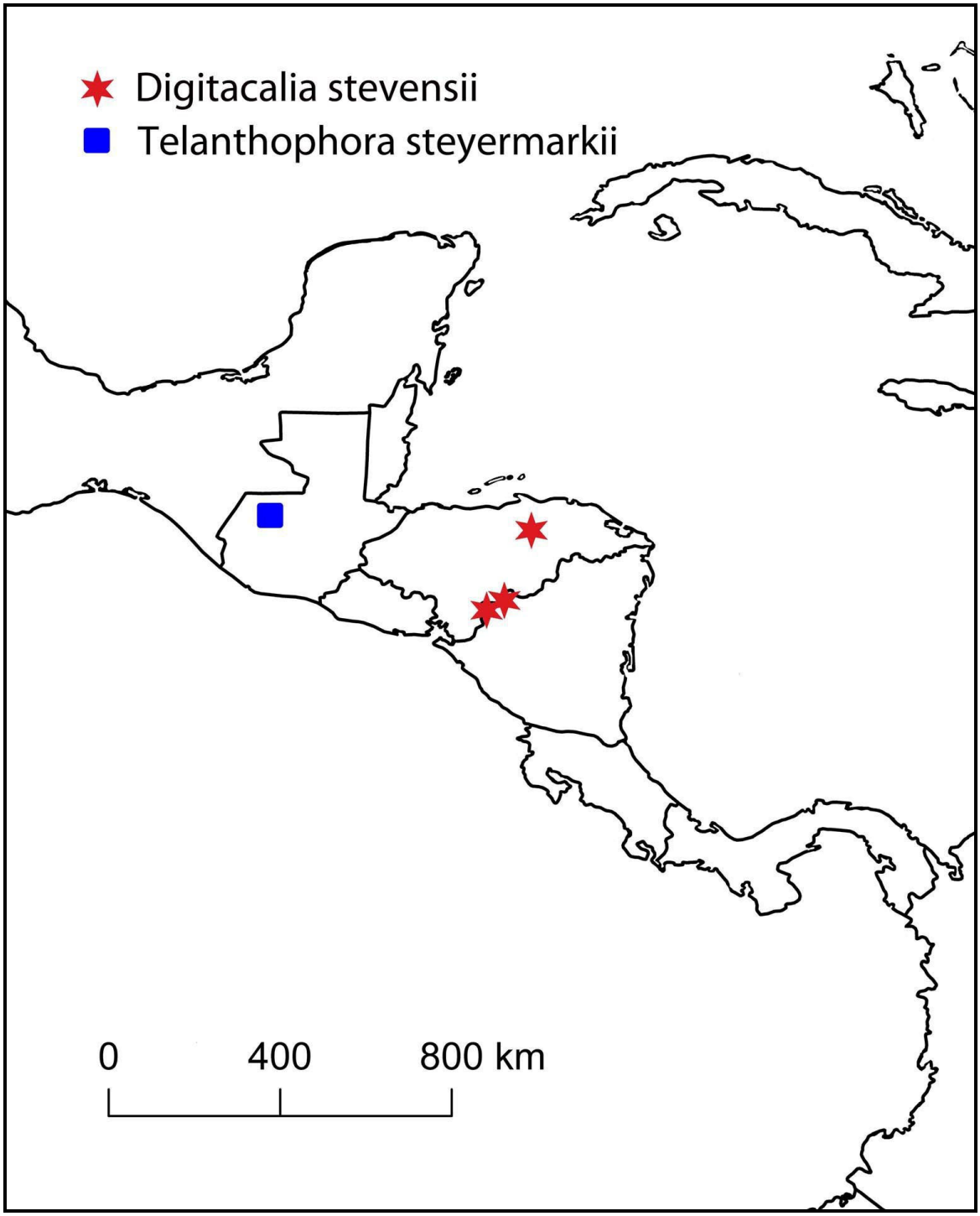

Figure 45. Distributions of *Digitacalia stevensii* and *Telanthophora steyermarkii*.

Figure 46. Holotype of *Digitacalia stevensii* Pruski. (*Stevens & Montiel 37259*, MO).

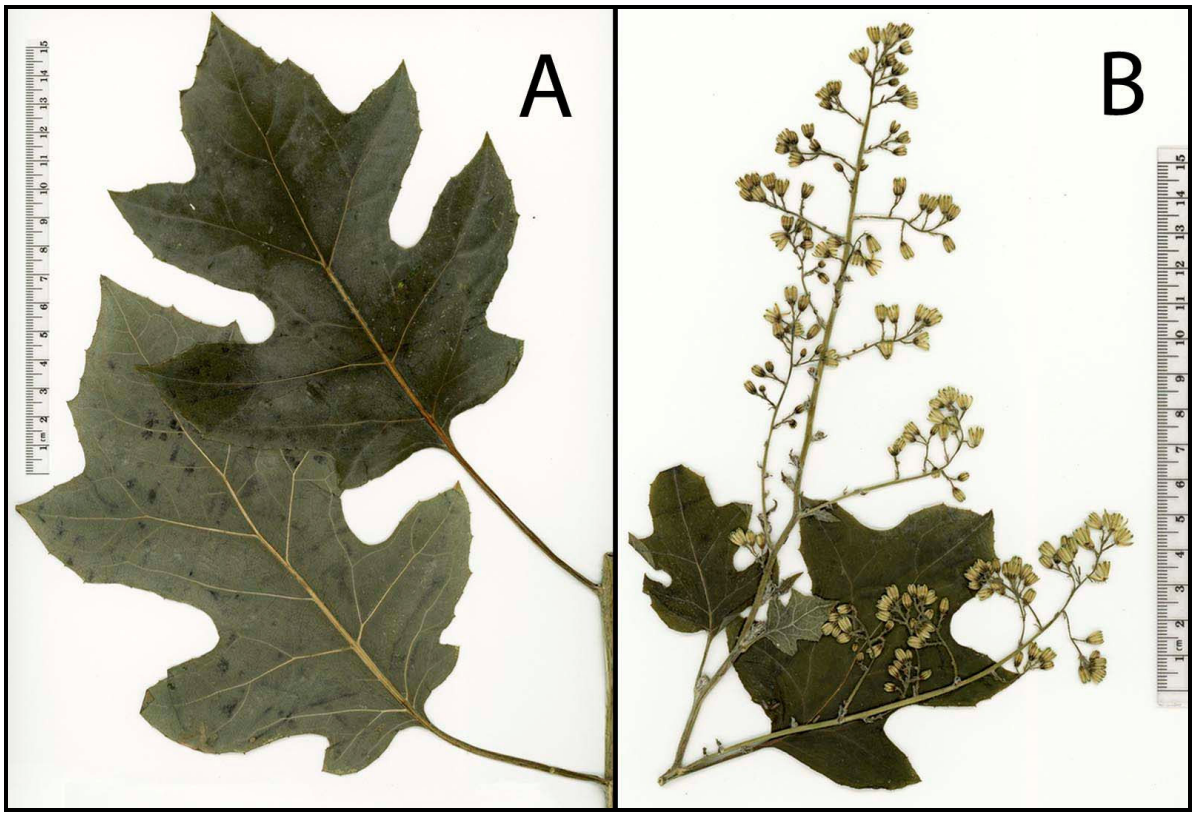

Figure 47. Paratype of *Digitacalia stevensii* Pruski. (*Stevens & Montiel 38871*, MO).

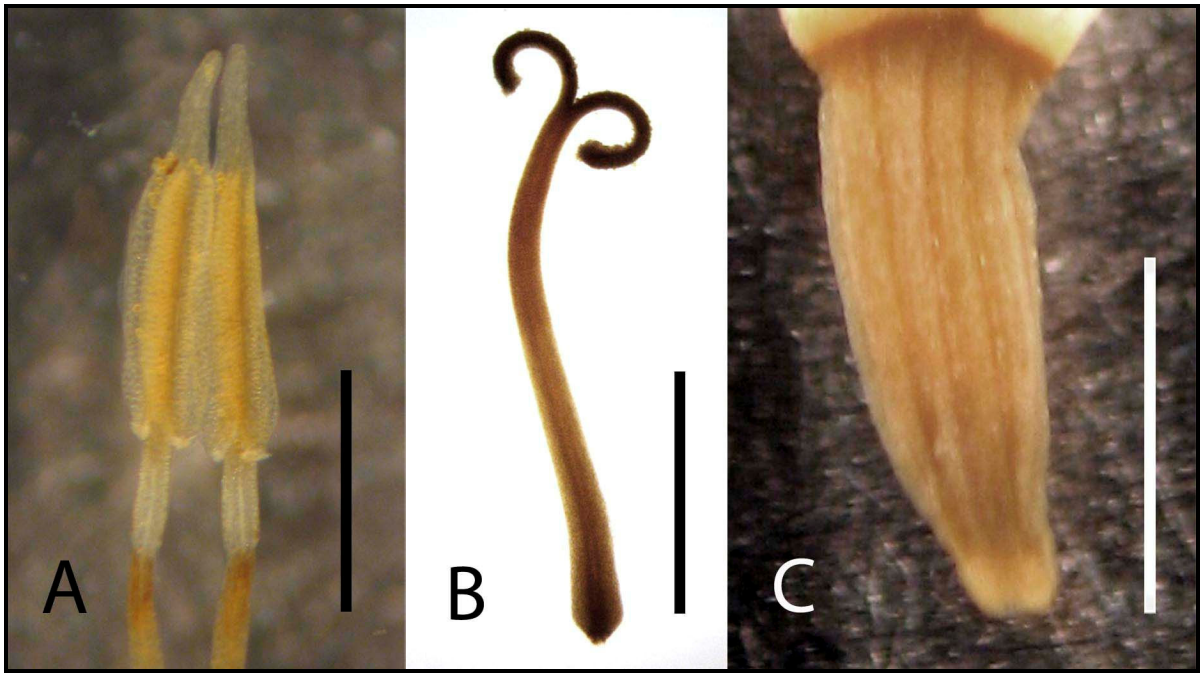

Figure 48. Floral microcharacters of *Digitacalia stevensii*. A. Two anthers, showing cylindrical filament collars and lanceolate apical appendages. B. Bifid style with short, obtuse-tipped branches. C. Immature cypsela showing several broad costae. (From the holotype, *Stevens & Montiel 37259*, MO). [Scale bars: A 0.9 mm, B 2 mm, C 1.5 mm].

Paratypes. **HONDURAS**. **Olancho.** Along Río Olancho, on road between Gualaco and San Bonito Oriental, 7.4 miles NE of San Estéban, 15° 20' N, 85° 42' W, 540 m, 7 Feb 1987 (in bud), *Croat & Hannon 64339* (MO, US; originally determined by Harold Robinson in 1987 as "*Roldana* ?"). **NICARAGUA. Nueva Segovia.** 10.8 km NW of Ococona along road to Santa María, 13° 45' 02" N, 86° 39' 48" W, 974 m, 30 Dec 2016 (in bud), *Stevens & Montiel 38871* (HULE, MO).

Eponymy. *Digitacalia stevensii* is named for Warren D. Stevens, collector of the type material and world authority of the flora of Nicaragua. Doug Stevens is the lead author of the three volume series "Flora de Nicaragua," published in 2001, and a specialist of Asclepiadoideae taxonomy.

Among the four previously recognized species, each a Mexican endemic, *Digitacalia stevensii* may be distinguished at a glance from *D. jatrophoides* and *D. napeifolia*, which differ by deeply-lobed leaves. Instead, *D. stevensii* is more similar to pinnatilobed *D. chiapensis* and trifid-leaved *D. tridactylitis*. *Digitacalia stevensii* seems to combine characters of the two, having the leaves of *D. chiapensis* and capitulum and floret sizes of *D. tridactylitis*. The elongate, narrow-pyramidal, thyrsoid-paniculate capitulescence of *D. stevensii*, however, serves to distinguish it from both species, and is unique in the genus. By geography, it is tempting to equate the new species with *D. chiapensis*, but *D. stevensii* differs from *D. chiapensis* by a more southerly distribution, moderately villosulous (vs. glabrous) stems, moderately dense, thyrsoidal-paniculate (vs. open, corymbiform) capitulescences, capitula 7–8 (vs. 5.5–7.5) mm long, corollas 4.5–5.5 (vs. 3–5) mm long, glabrous (vs. sometimes setulose) cypselae, and pappus bristles 4–5 (vs. 3–4) mm long.

Before seeing field photographs showing the type plants of *Digitacalia stevensii* to be white-flowered, I naively thought the plant was yellow-flowered and probably a species of *Roldana*. Indeed, by gestalt and thyrsoidal capitulescences, *D. stevensii* recalls top-snatch specimens of *Roldana greenmanii* H. Rob. & Brettell, which differs by solid stems, pubescent pluristriate merely narrowly scarious-margined phyllaries, yellow short-lobed corollas with elongate throat, and proximal stem leaves palmatilobed, albeit on occasion with a few pinnatilobed distal leaves resembling those of *D. stevensii*.

5. DIGITACALIA TRIDACTYLITIS (B.L. Rob. & Greenm.) Pippen, Contr. U.S. Natl. Herb. 34: 383. 1968. *Cacalia tridactylitis* B.L. Rob. & Greenm., Amer. J. Sci. Arts, ser. 3: 50. 159. 1895. *Odontotrichum tridactylitis* (B.L. Rob. & Greenm.) Rydb., Bull. Torrey Bot. Club 51: 419. 1924. **TYPE: MEXICO. Oaxaca.** Sierra de San Felipe, 6000 ft., 19 Nov 1894, *Pringle 5841* (holotype: GH, as Beaman color slide 7221, also as Pippen 1968 plate 1; isotype: VT). [The VT isotype on JSTOR is incorrectly numbered 5840, which page 158 of the protologue publication gives instead as collected 17 November 1894 and as the type number of *Cacalia obtusiloba* B.L. Rob. & Greenm. (= *Psacalium megaphyllum*); the GH holotype was not found in JSTOR].

Digitacalia crypta B.L. Turner

Herbs to 3 m tall; stems puberulent. **Leaves** very deeply proximally trilobed (nearly digitate) or proximal stem leaves only moderately trilobed from near midblade, petiolate; blade mostly 6–20 × 4–13 cm, trullate, rhombic or hastiform, lobed nearly to midrib or proximal leaves only about halfway to midrib, base shortly decurrent onto petiole, adaxial surface sparsely pubescent, abaxial surfaces tomentulose, lobes lanceolate to triangular, margins usually subentire but the type is coarsely serrate, apex attenuate; petiole 1–4 cm long. **Capitulescence** to 30 × 25 cm, corymbiform-paniculate, broadly rounded to nearly flat-topped, lateral branches sometimes overtopping central axis, tomentulose; peduncles mostly 3–7 mm long, tomentulose. **Capitula** 7–10 mm long; involucre 3–4 mm diam.; phyllaries (7–)8, 3.5–4(–5) × 1–1.5 mm, a few sometimes keeled, glabrous; calycular bracteoles few–several, 1.5–3.5 mm long, subulate. **Disk florets** 8–10; corolla 5–6 mm long, throat

0.1–0.5 mm long, lobes 2–3 mm long; anthers 2–3 mm long; style branches 1–1.5 mm long. **Cypselae** 3–5 mm long, glabrous; pappus 4–5.5 mm long, sometimes becoming tawny when mature. 2*n* = 60 (Pippen 1968).

Distribution and representative collections. **Mexico** (Guerrero, México, Morelos, Oaxaca); *Barrie 722* (MEXU, TEX; type of synonymous *Digitacalia crypta* B.L. Turner); *Krause 1226* (MEXU, MO); *Martinez et al. 5734* (MEXU, MO); *McVaugh 21903* (MICH); *Nelson 2080* (US); *Pringle 6164* (CAS, CM, COLO, F, GH, MEXU, MO, NDG, NY, US); *Pringle 9877* (CAS, CM, F, GH, MO, NMC, NY, US); *Smith 380* (MICH, MO, NY).

The proximal leaves (often not present on herbarium specimens) of *Digitacalia tridactylitis* are very reminiscent of those of *Neurolaena lobata* (L.) Cass. The type collection has leaf margins coarsely serrate, but most material seen has subentire margins. The deeply digitate leaves of many collections are noteworthy, but on some plants they co-occur with moderately trilobed leaves. Robinson and Greenman (1895) described the species as having "about 7" phyllaries. Turner (1990) treated typically 8-phyllaried *D. tridactylitis* in synonymy of 5-phyllaried *D. napeifolia*. Although some individual Senecioninae as circumscribed here (e.g., *Dresslerothamnus angustiradiatus* and *Pentacalia wilburii*) may vary in phyllary number, individual cacalioid species are more consistent in phyllary number, and Turner's notion was considered but ultimately rejected here. The species is thereby interpreted broadly, more or less as by Pippen (1968).

An illustration of *Digitacalia tridactylitis* was provided by Turner (1990) under the name of *D. crypta*. The Pringle collections cited above are paratypes of the synonymous *D. crypta*, but were cited as *D. tridactylitis* by Pippen (1968: 383) and Wetter (1983: 21), who are followed here.

Excluded species.

Digitacalia heteroidea (Klatt) Pippen ≡ **Roldana heteroidea** (Klatt) H. Rob. & Brettell.

1. TELANTHOPHORA STEYERMARKII (Greenm.) Pruski, Flora Mesoamericana vol. 5, parte 2: 471. 2018. *Senecio steyermarkii* Greenm., Ceiba 1: 124. (1 April) 1950. [non *Senecio steyermarkii* Cuatr., Fieldiana, Bot. 27(1): 32 (8 June) 1950, hom. illeg.]. **TYPE: GUATEMALA. Huehuetenango**. Sierra de los Cuchumatanes, near cafetal of Finca Soledad, 5 km SE of Barillas, 1150 m, 26 Jul 1942, *Steyermark 49556* (holotype: MO; isotype: F). Figures 4E–F, 45, 49.

Pachycaulous shrubs 3–7 m tall; stems floccose-tomentose distally to irregularly subglabrate. **Leaves** petiolate; blade 10–22 × 4–10 cm, elliptic-ovate, stiffly chartaceous, venation pinnate with 10–12 secondary veins per side, surfaces obviously discolorous, adaxial surface green, sparsely arachnoid-tomentose along veins to glabrate, abaxial surface white-gray, densely and persistently arachnoid-tomentose throughout or sometimes glabrate in patches, never completely glabrate, base cuneate to obtuse, margins subentire to few-dentate (remotely and shallowly sinuous-lobulate), apex acuminate to obtuse; petiole 3–8 cm long. **Capitulescence** 6–15 cm diam., branches and peduncles tomentulose, bracteoles 3–5 mm long, linear-lanceolate. **Capitula** 6.5–8 mm long, short-radiate; involucre 3–4 mm diam., campanulate; phyllaries ca. 8, 4–5.5 mm long, tomentulose in the middle or only so basally; calycular bracteoles 1–2 mm long, linear-lanceolate. **Ray florets** 2–3; corolla limb ca. 3+ mm long, weakly exserted, 5–6-nerved. **Disk florets** 7–10; corolla ca. 5 mm long, tube shorter than limb, lobes 1.5–2 mm long, about as long as throat, long-lanceolate, with median resin duct; anthers short-caudate, collar 0.2–0.3 mm long, cylindrical, without enlarged basal cells, endothecial tissue radial; style branches 1.5–2 mm long, apex obtuse, stigmatic surfaces continuous. **Cypselae** (immature) 1–1.5 mm long; pappus bristles ca. 5 mm long.

Figure 49. Holotype of *Senecio steyermarkii* Greenm. (≡ *Telanthophora steyermarkii*). (*Steyermark 49556*, MO).

Distribution and ecology. *Telanthophora steyermarkii* is endemic to Guatemala (Fig. 45), where it was collected flowering in July at 1150 meters elevation. The species is known from only the type collection.

Microscopic study of floral details shows *Telanthophora steyermarkii* has cylindrical filament collars (Fig. 4E) and continuous stigmatic surfaces (Fig. 4F). By these characters it is thus a typical member of subtribe Tussilagininae. A question has arisen as to whether or not the species is distinct. Williams (1975) treated *Telanthophora* in synonymy of *Senecio*, recognized the species using the name *Senecio steyermarkii*, but did not mention subtribal placement. On the other hand, Clark (1996) recognized *Telanthophora* but treated *T. steyermarkii* in synonymy with *T. grandifolia*.

Among species in Mesoamerica, involucres of five phyllaries are characteristic of a group of four species that are sometimes discoid-capitulate: *Telanthophora cobanensis* (J.M. Coult.) R. & B., *T. molinae* R. & B., *T. sublaciniata* (Greenm.) B.L. Clark, and *T. uspantanensis* (J.M. Coult.) R. & B.. Involucres of eight phyllaries are found in *T. bartlettii* R. & B., *T. grandifolia* (Less.) R. & B., and *T. steyermarkii* (Greenm.) Pruski. In gestalt and oblong leaves, however, *T. bartlettii* otherwise resembles species of the first group. Thus by the process of elimination, *T. grandifolia* and *T. steyermarkii* may be close congeners, and indeed Clark (1996) treated *T. steyermarkii* in synonymy with *T. grandifolia*.

Telanthophora grandifolia, however, is typically pinnatilobed and concolorous-leaved, and does not match *T. steyermarkii*. *Telanthophora steyermarkii* was recently resurrected and is distinguished by its radiate capitula with eight phyllaries and by its leaf blade surfaces obviously discolorous, abaxially densely arachnoid-tomentose throughout or sometimes glabrate in patches, never completely glabrate. Nevertheless, *T. steyermarkii* is somewhat similar to *Senecio serraquitchensis* Greenm., which is loosely arachnoid-tomentose abaxially only along the midrib, and which proves to fit moderately comfortably in synonymy with *T. grandifolia*, which is widespread from Mexico to Costa Rica.

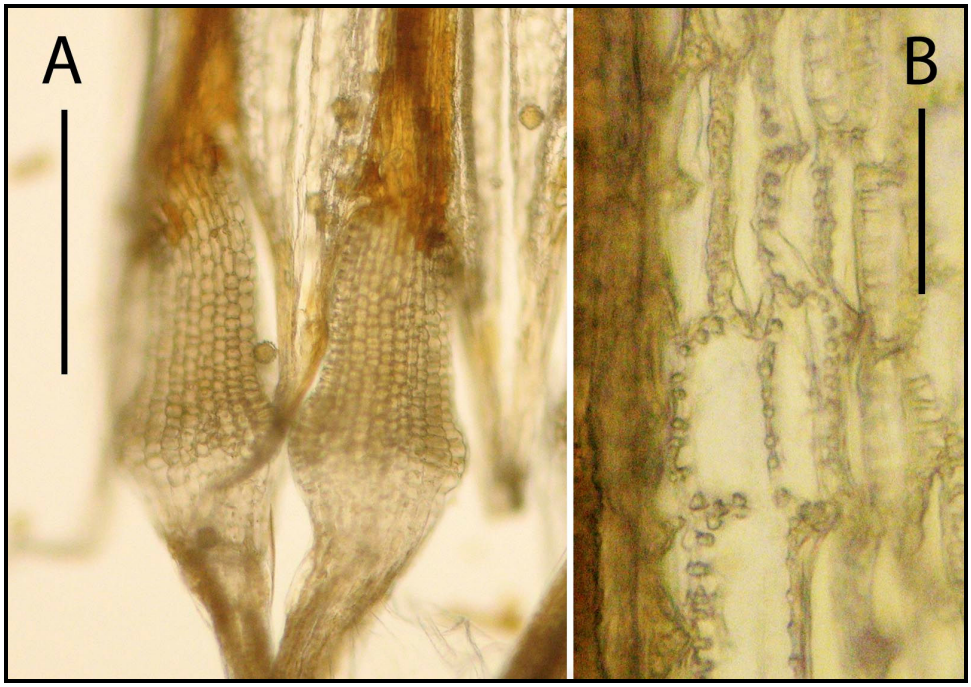

Figure 50. Floral microcharacters of *Dendrophorbium multinerve*. A. Balusterform filament collars and tails. B. Radial (approaching transitional) transitional endothecial tissue. (*Solomon 18723*, MO). [Scale bars: A 0.5 mm, B 30 μm].

III. NEW COMBINATIONS IN SOUTH AMERICAN DENDROPHORBIUM AND MONTICALIA (SENECIONINAE)

Dendrophorbium and *Monticalia* (Senecioninae) were segregated by Jeffrey (1992a) from *Senecio* and *Pentacalia*, respectively. These two segregates are recognized here more or less as circumscribed by Jeffrey (1992a) and Nordenstam (2007), and are distinguished by floral microfeatures and habit. The new combinations in South American *Dendrophorbium* and *Monticalia* proposed here are for names that mostly have been used informally for more than a decade. These names are validated here for further use in specimen determinations and various floristic projects, and those in *Dendrophorbium* are proposed preliminary to a revision of the Peruvian species underway by the author.

Dendrophorbium and *Monticalia* are centered in the Andes, but *Dendrophorbium lucidum* (Sw.) C. Jeffrey occurs in the Lesser Antilles, several species are known from Brazil, and two species of *Monticalia* were recognized in Central America by Pruski and Robinson (2018). *Dendrophorbium* (Fig. 50) and *Monticalia* each have moderately balusterform anther collars, exappendiculate style branches with 2-banded stigmatic surfaces, and radial(-transitional) endothecial patterns, typical of subtribe Senecioninae.

Dendrophorbium

The genus *Dendrophorbium* (keyed by the author with *Pentacalia* allies above) contains more than 90 species, these mostly Andean. *Dendrophorbium* was described by Cuatrecasas (1951) as a section of *Senecio*, and retained by Cuatrecasas (1981) in *Senecio*, which it resembles by 10-striate-costate cypselae. *Dendrophorbium* differs from *Senecio* in habit, however, being shrubby herbs or pachycaul trees. The leaves in *Dendrophorbium* may be relatively well-spaced along the distal half of the stem, but at other times are clustered apically. The species are mostly dentate-leaved (Figs. 51A, 52–55) and the capitulescence broadly corymbiform, but the plants may be entire-leaved and in several species the capitulescence is pyramidally thyrsoid-paniculate (Figs. 51B, 52). The genus is often characterized as having sagittate anthers, but the anthers in some species are caudate (viz Fig. 50A; Jeffrey 1992a). As is typical of subtribe Senecioninae, the endothecial tissue is typically radial (sometimes transitional with both radial and polar thickenings) (Fig. 50B).

Cuatrecasas (1951) gave leaf texture as a distinguishing feature between *Senecio* sect. *Dendrophorbium* Cuatr. and now synonymous *Senecio* sect. *Macbrideus* Cuatr. Cabrera (1985: 136) keyed Bolivian material under the name *Senecio* ser. *Myriocephali* (Cabrera) Cabrera, and gave *Senecio* sect. *Pluricephali* Cabrera in synonymy. These aforementioned *Senecio* infragenera are now treated as the genus *Dendrophorbium*.

Dendrophorbium was characterized by Jeffrey (1992a), Bremer (1994), and Díaz-Piedrahita and Cuatrecasas (1999) as having cypselae 5-costate, and *Senecio* ser. *Myriocephali* was said to be "generalmente pentcostados" by Cabrera (1985). Nordenstam (2007: 233) described the cypselae of *Dendrophorbium* as "5-ribbed," but keyed the genus (Nordenstam 2007: 214 lead 164b) by cypselae "8–10-ribbed." In the author's above key to genera centering about *Pentacalia*, the cypselae in *Dendrophorbium* are described as "8–10-striate-costate," supernumerary rib on each face initially less-pronounced than the costae on the angles, but at maturity the cypselae of *Dendrophorbium* become subterete and 8–10-striate-costate.

Figure 51. Habit (A) and close-up of capitulescence details (B) of typical member of the *Dendrophorbium reflexum* species group. The group is characterized by closely serrate leaf margins, rigid-chartaceous leaf blades, and narrowly pyramidal capitulescences. (Peru, San Martín, Tocache, entre Metal y Manan, 1900 m, 4 Jul 2014, *Pruski et al. 4687*).

Figure 52. Holotype of *Senecio castaneifolius* DC. (≡ *Dendrophorbium castaneifolium*). (*Haenke s.n.*, PR-377362).

1. DENDROPHORBIUM CASTANEIFOLIUM (DC.) Pruski, **comb. nov.** *Senecio castaneifolius* DC., Prodr. 6: 425. 1837 [1838], as "*castaneaefolius*." **TYPE:** presumably **Peru. [?Cusco].** "America meridionalis montibus Oronocensibus" in protologue, "Peruano montano oronocenses" [sic] on holotype label, [1790s–1810s], *Haenke s.n.* (holotype: PR; isotype: G, as Macbride negative 8255 labelled as in G-DEL, not seen in G-DC in IDC microfiche 800 card 1140). Figure 52.

[As stated in the protologue, the name was based on the holotype in PR: "v. s. in h. Haenke à cl. de Sternberg miss." The G sheet is merely a fragment of the PR holotype. Elsewhere in Prodromus, Candolle often indicated when Haenke material was given to him (now mostly G-DC) as "v. s. in h. Haenk. ab ill. de Sternberg comm.," which is not the case with *Senecio castaneifolius*, the holotype of which is in PR.].

Dendrophorbium castaneifolium (DC.) Pruski is characterized by thin-chartaceous elongate leaves with the many secondary veins closely spaced, narrow-pyramidal open axillary or terminal capitulescences of 15+ large radiate capitula closely subtended by several linear bracteoles, 7–8 mm tall involucres composed of 10–12 phyllaries, 12 ray florets, 25–30 disk florets, and slightly bulbous-tipped pappus bristles. The collector of the type—Thaddaeus Haenke—visited Lima, Arequipa, Cusco (Peru), and for 20 years used as a home base Cochabamba (Bolivia), where he died in 1816 or 1817 (Gicklhorn 1966, viz map 2). The type locality of *D. castaneifolium* thereby could be in either Bolivia or southern Peru.

The citation by Candolle (1837) of *Dendrophorbium castaneifolium* as from "Amer. meridionalis" differs from the locality of another regional plant collected by Haenke, i.e., *Senecio oronocensis* DC. (1837: 423), which was given by Candolle as "Amer. australis." Cabrera (1954: 595) suggested that Haenke material labeled as "Oronocensibusis" is likely from the Serranía de Orinoca, Oruro, Bolivia, west of Lago de Poopó, and at about 3000 meters elevation. Although Cabrera (1954) suggested the type of *S. oronocensis* may be from Oruro, Bolivia, Cabrera (1985: 103) listed no material of the species from Oruro, and instead gave it as known only from La Paz, Bolivia north to Huánuco, Peru. Similarly, *D. castaneifolium* is unknown in Oruro, which is very high-elevational, dry, and poor in *Dendrophorbium* species. All contemporary material of *D. castaneifolium* (e.g., *Boeke & Boeke 3246*, *Calatayud et al. 2039*, *Valenzuela et al. 487*, *Valenzuela et al. 7292*) in front of me is Peruvian, suggesting the type locality of the species is in Peru, perhaps in Cusco where the plant is centered and most frequently encountered between 900–2300 meters elevation.

Cabrera (1985) did not treat *D. castaneifolium* as Bolivian, but simply noted its similarity to *D. cabrerae* (Cuatr.) C. Jeffrey and *D. peregrinum* (Griseb.) C. Jeffrey, which are similarly thin-leaved but small-capitulate Bolivian species. Another Bolivian *Dendrophorbium* with similar leaves is *D. coroicense* (Rusby) C. Jeffrey, which also has smaller capitula than those of *D. castaneifolium.* Bolivian *D. medullosum* (Sch. Bip. ex Greenm.) C. Jeffrey and *D. yungasense* (Britton) C. Jeffrey are large-capitulate radiate-flowered species, but differ by their much fewer, well-spaced secondary leaf veins. Peruvian and Bolivian *D. biacuminatum* (Rusby) C. Jeffrey is similar to the Greenman and Britton species, and differs from them and *D. castaneifolium* by its winged-petiolate leaves. In its narrowly pyramidal capitulescences, *D. castaneifolium* is similar to the common northern *D. reflexum* (Peru to Venezuela), but differs by its thin-textured narrow leaves that are not prominently veined, more open capitulescences with long peduncles, and shorter and broader phyllaries. Another somewhat similar regional species is *D. vargasii* (Cabrera) H. Beltrán from Cusco, which differs in its oblong leaves and rounded capitulescences. The relatively uncommon *D. castaneifolium* basically combines the leaf texture character of the Bolivian species and the capitulescence form of the more northern species, and is accepted by me as endemic to Peru.

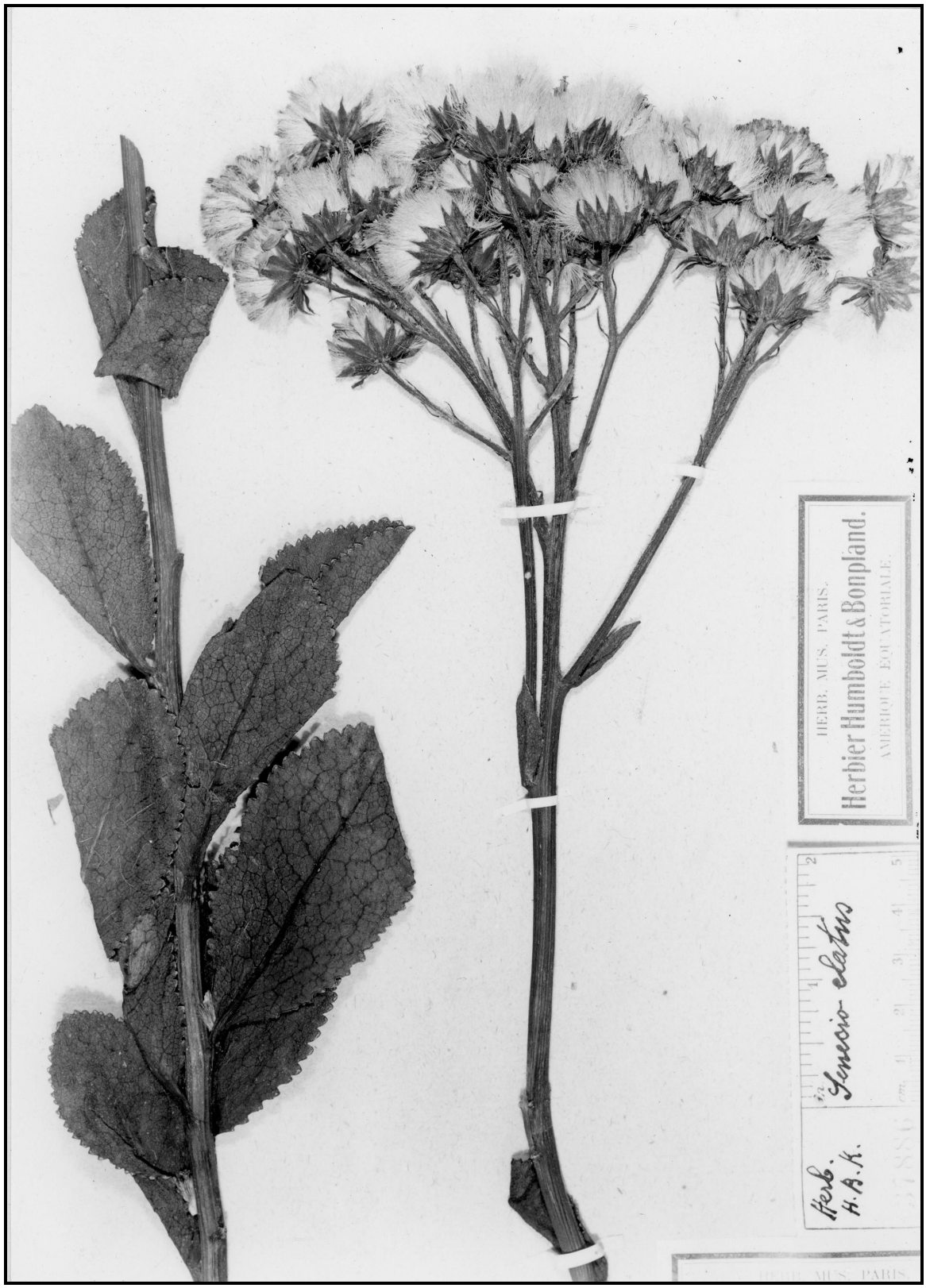

Figure 53. Holotype of *Senecio elatus* Kunth (≡ *Dendrophorbium elatum*). The MO photograph of the holotype is labeled as though it is a print from Macbride negative 37886 and this number is given as this species on the F web site, but that number is not seen in the photograph. (*Humboldt & Bonpland 3572*, P-HBK).

2. DENDROPHORBIUM ELATUM (Kunth) Pruski, **comb. nov.** *Senecio elatus* Kunth, Nov. Gen. Sp. (folio ed.) 4: 141. 1820 [1818] [also quarto ed. 4: 180. 1820]. **TYPE: PERU**. [?**Cajamarca**]. Páramo de Yamoca, inter Colasey et Chontaly, 2468 m [as 1350 hex], Aug [1802], *Humboldt & Bonpland 3572* (holotype: P-HBK, as Macbride negative 37886, as IDC microfiche 6209. 105.III.7). The binomial on the holotype does not seem to be in Kunth's handwriting. The Depto. for Páramo de Yamoca (Humboldt and Bonpland locality 194 in Sandwith 1968: 93) is not known with certainty to me, but is between Pomahuaca (locality 193) and Passo de Pucara (locality 197), both in Cajamarca southwest of Jaen. Figure 53.

Dendrophorbium elatum (Kunth) Pruski is a shrubby herb to 2 m tall occurring in Loja, Ecuador and northern Peru (Deptos. Amazonas, Ancash, Cajamarca, and La Libertad). The species was not previously reported in Ecuador. *Dendrophorbium elatum* has been collected above 2000 meters elevation. It flowers year-round with an apparent flowering peak from June to August. Contemporary collections (e.g., *Jorgensen et al. 733* from Ecuador; *Campos et al. 5021* from Peru) confirm that *D. elatum* is characterized by oblong leaf blades often with obtuse tips, broadly rounded capitulescences, pilosulose peduncles, few calycular bracts often only about half as long as the involucre, and (8–)10-costate glabrous cypselae. *Dendrophorbium elatum* is similar to north Peruvian *D. usgorense* (Cuatr.) C. Jeffrey, which differs by its acute-tipped leaf blades, nearly subglabrous peduncles, and calycular bracts nearly as long as the involucre. Another similar regional species is *D. vanillodorum* (Cabrera) H. Beltrán, which is a much denser pubescent plant.

3. DENDROPHORBIUM GRITENSE (Lapp, T. Ruíz & Torrec.) Pruski, **comb. nov.** *Pentacalia gritensis* Lapp, T. Ruíz & Torrec., Ernstia 23(1): 18. 2013. **TYPE: VENEZUELA. Táchira.** Páramo El Batallón, vía a la Laguna Grande, 3279 m, 24 Oct 2012, *Lapp et al. 616* (holotype: MY; isotype: VEN). Figures 54–55.

Shrubs 1–1.5 m tall, leafy only distally; stems sericeous to puberulent distally, leaf scars ca. 0.5 cm diam., prominent; distal internodes much shorter than the leaves. **Leaves** simple, alternate, subsessile; blade 5–10.5 × 1.7–3 cm, narrowly elliptic to oblong, subcoriaceous or stiffly chartaceous, pinnately veined usually with 8–10 secondary veins per side, arching strongly towards apex, tertiary veins immersed, surfaces glabrous or glabrate, base cuneate to attenuate and tapering into a petiolariform base, distal margins shallowly dentate-serrate, apex acute; petiolar base 0.5–1.5 × ca. 0.3 cm, stout. **Capitulescence** corymbiform, to 9 × 7 cm, nearly flat-topped, few-branched, bracteolate; peduncles 2.5–5 cm long, glabrous, few-bracteolate, bracteoles ca. 2 mm long, lanceolate, glabrous or weakly ciliolate. **Capitula** 11–13 mm tall, radiate; involucre 9.5–11 × 10–12 mm, campanulate, loosely calyculate; phyllaries ca. 13, subequal, persistent, 9.5–11 × 2–2.4 mm, lanceolate, broad-margined, apex acuminate, densely papillose at apex, otherwise glabrous, rarely sparingly arachnoid throughout; calycular bracteoles ca. 6, ca. 3.5 mm long, lanceolate, subherbaceous throughout, papillose at apex; clinanthium 4–6 mm diam., flat, ridged-areolate. **Ray florets** 11–13; corolla 17.3–19.3 mm long, yellow, glabrous, limb 5–7-nerved, 12–14.5 × 2–2.3 mm. **Disc florets** 45–50, bisexual; corolla 7.6–8.4 mm long, tubular-funnelform, shortly 5-lobed, yellow, glabrous; anthers ca. 3 mm long, short-caudate, endothecial tissue pattern radial; style 8.5–10 mm long, basal node ca. 0.5 mm tall, branches ca. 1.8 mm long, stigmatic surfaces 2-banded, apex obtuse, exappendiculate, weakly papillose. **Cypselae** ca. 2.6 mm long; obconic, (8–)10-costate, brown, glabrous, carpopodium symmetric, non-sculptured; pappus of 50+ bristles 6–7.2 mm long.

Additional collections examined. VENEZUELA. Trujillo (limité con Lara). Mun. Carache, P.N. Dinira, arriba de Mesa Arriba, cumbre del pico Cendé y laderas, 9° 32' N, 70° 07' W, 3330–3350 m, 2 Apr 1999, *R. Duno & Riina 796* (US; post-fruit); Mun. Carache, P.N. Dinira, arriba de Mesa Arriba, camino del páramo de Jabón al Pico Cendé, 9° 33' N, 70° 07' W, 3000 m, 30 Dec 1999, *R. Duno, Riina, & Meier 1132* (US, VEN).

For a more than a decade, *Dendrophorbium gritense* was in fertile condition known to me from only *Duno et al. 1132* (US), and in 2000 I annotated this sheet as *Pentacalia dunoi* mihi (Fig. 55). However, by (8–)10-costate cypselae (Fig. 54G) *Duno et al. 1132* proves to be a *Dendrophorbium*, as noted by Bertil Nordenstam (pers. comm. 2000). In 2013 the species was described as *Pentacalia gritensis*, and the needed new combination in *Dendrophorbium* is proposed here. Venezuelan *Monticalia greenmaniana* (Hieron.) C. Jeffrey has similar veined leaves but is a densely pubescent plant with pilose corollas and is retained provisionally in *Monticalia*. It seems likely that *D. gritense* occurs in páramos between the two known, moderately distant localities, which are nearly at opposite ends of the Venezuelan. The description provided shows that the Venezuelan materials are conspecific and that the plant is best placed in *Dendrophorbium*.

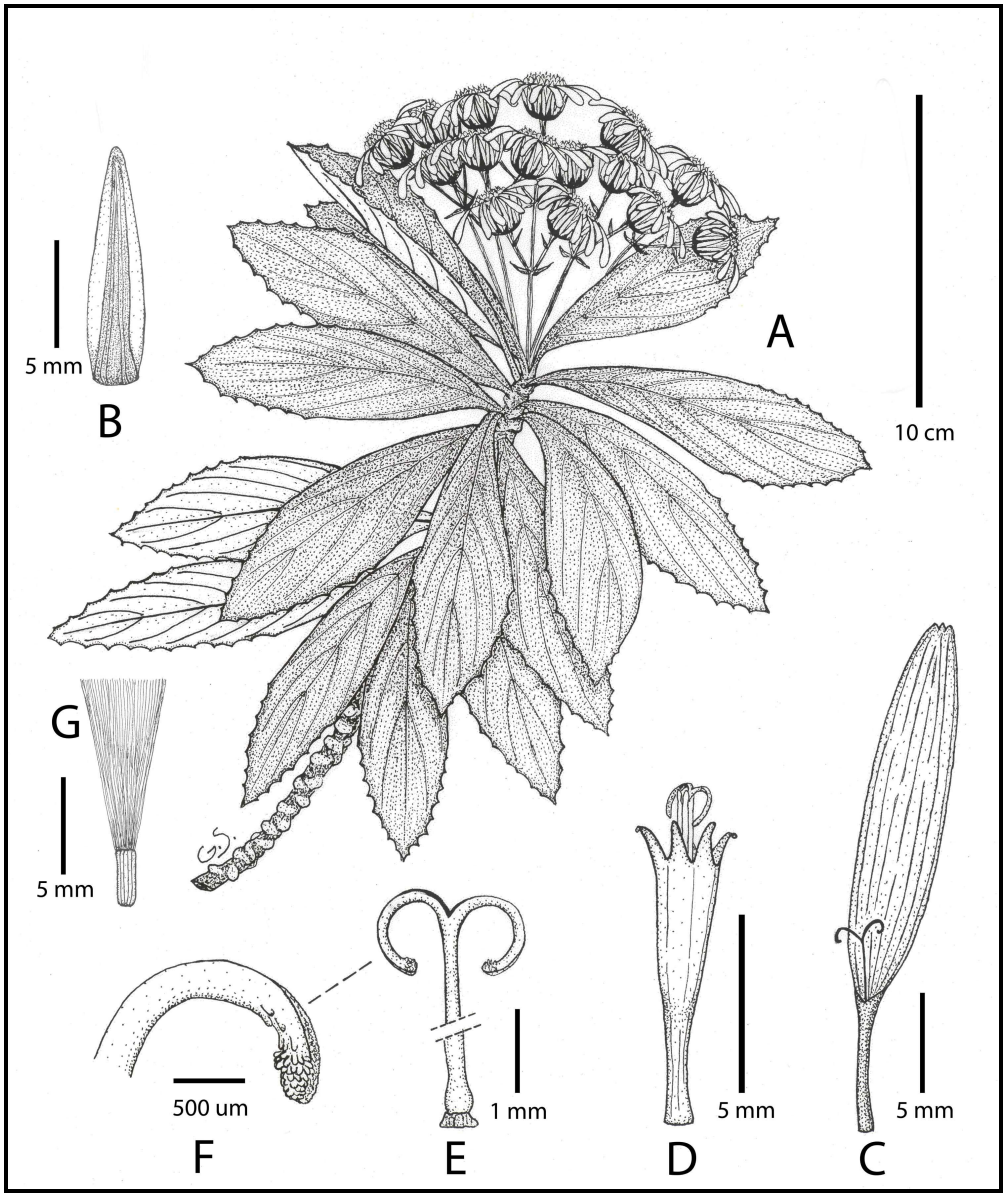

Figure 54. *Dendrophorbium gritense*. A. Flowering branch. B. Phyllary. C. Ray floret, ovary and pappus removed. D. Disk floret, ovary and pappus removed. E. Style from disk floret. F. Close-up of style branch from disk floret. G. Disk cypselae, showing several costae. (Drawn by Gisela Sancho from *Duno et al. 1132*, US).

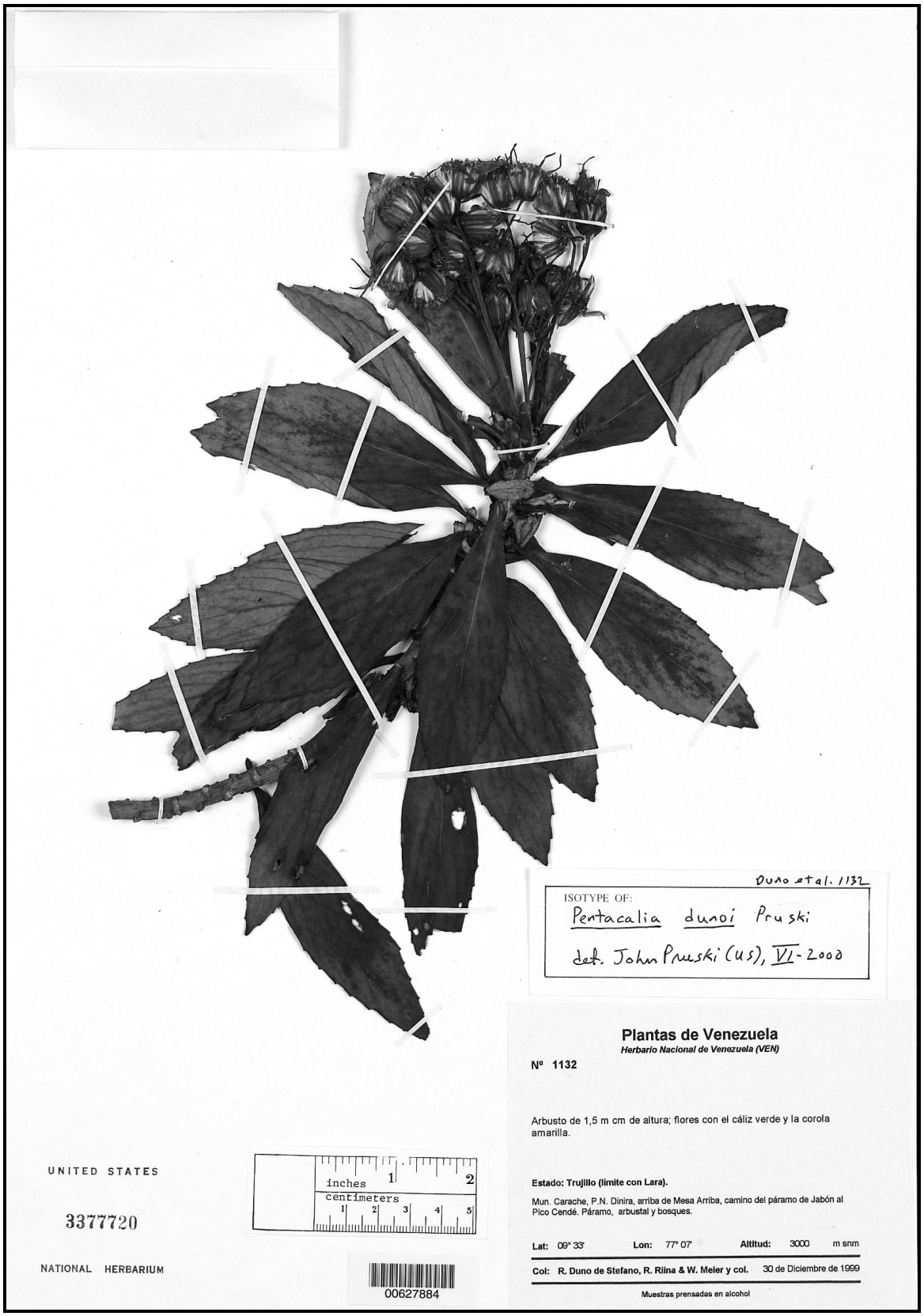

Figure 55. *Dendrophorbium gritense*. Photograph taken in 2000 of intended type of unpublished *P. dunoi*, a taxon subsequently validated in 2013 as *Pentacalia gritensis*. *Duno et al. 1132*, US.

4. DENDROPHORBIUM HUASENSE (Cuatr.) Pruski, **comb. nov.** *Senecio huasensis* Cuatr., Brittonia 8: 187. 1956. **TYPE: PERU. Junin.** Huasa Huasi, [1778–1784], *Dombey s.n.* (holotype: P).

Dendrophorbium huasense (Cuatr.) Pruski, endemic to Peru, is distinctive in its broad-based leaves, arachnoid-tomentulose abaxial leaf blade surfaces, and closely spaced small radiate capitula with 13 phyllaries.

5. DENDROPHORBIUM MUNCHIQUENSE (S. Díaz & Cuatr.) Pruski, **comb. nov.** *Pentacalia munchiquensis* S. Díaz & Cuatr., Revista Acad. Colomb. Ci. Exact. 19(72): 21. 1994. **TYPE: COLOMBIA. Cauca.** Parque Nacional Munchique, El Tambo, vereda La Romelia, La Gallera, 2000 m, 26 Jul 1993, *Ruiz et al. 309* (holotype: COL; isotype: COL, MA, US).

Dendrophorbium munchiquense (S. Díaz & Cuatr.) Pruski, known to me from only a few collections in Cauca, was by its caudate anthers treated by Díaz-Piedrahita and Cuatrecasas (1999) within *Pentacalia*. It is characterized by its long lanceolate entire glabrous leaves and radiate capitula with eight phyllaries. *Dendrophorbium moscopanum* (Cuatr.) C. Jeffrey, also from Cauca, Colombia, is somewhat similar to *D. munchiquense* but differs by its smaller, arachnoid-tomentulose dentate leaves.

6. DENDROPHORBIUM VALLECAUCANUM (Cuatr.) Pruski, **comb. nov.** *Senecio vallecaucanus* Cuatr., Fieldiana, Bot. 27(1): 23. 1950. **TYPE: COLOMBIA**. **Valle del Cauca.** Cordillera Occidental, Los Farallones, extremo N, vertiente oriental, Alto del Buey, 3300–3450 m, 13 Oct 1944, *Cuatrecasas 18062* (holotype: F; isotypes: COL-2, F, P, US).

Dendrophorbium vallecaucanum (Cuatr.) Pruski is characterized by its large strongly reticulate finely serrate leaves, narrow capitulescence, disciform (practically discoid Cuatrecasas 1950) capitula with eight phyllaries, and conical style appendage. It was keyed by Díaz-Piedrahita and Cuatrecasas (1999) as "claramente radiatos," but by its very small pistillate floret limbs it is disciform, as noted by Cuatrecasas (1950). It recalls several Colombian species, including the common *D. americanum* (L.f.) C. Jeffrey, which is obviously radiate-capitulate. Instead, it is similar to weakly-radiate to disciform *D. kleinioides* (Kunth) B. Nord., which differs by smaller serrulate leaves.

Monticalia

Shrubby often ericoid-leaved *Monticalia* was treated earlier as *Pentacalia* subgen. *Microchaete* (Benth.) Cuatr. by Cuatrecasas (1981) and Díaz-Piedrahita and Cuatrecasas (1999) but maintained at generic rank by Nordenstam (1999, 2007). *Monticalia* resembles *Pentacalia* in technical feature of caudate anthers and 5-costate cypselae, but differs in habit.

The new combination proposed here for Peruvian *Monticalia barbourii* (M.O. Dillon & Sagást.) Pruski (Senecioninae) reflects acceptance of the segregation (Jeffrey 1992a) of shrubby elements from *Pentacalia*, where they were treated by Cuatrecasas (1981). Pending further study, the genus is maintained as proposed by Jeffrey (1992a), although several distinct species groups (weakly supported lineages) are known in *Monticalia*.

1. MONTICALIA BARBOURII (M.O. Dillon & Sagást.) Pruski, **comb. nov.** *Pentacalia barbourii* M.O. Dillon & Sagást., Brittonia 40: 225. 1988. **TYPE: PERU. Amazonas.** Prov. Bagua, Cordillera Colán NE of La Peca, ca. 3290 m [as 10800 ft], 9 Sep 1978, *Barbour 3450* (holotype: F; isotypes: LSU, MO). Figure 56A.

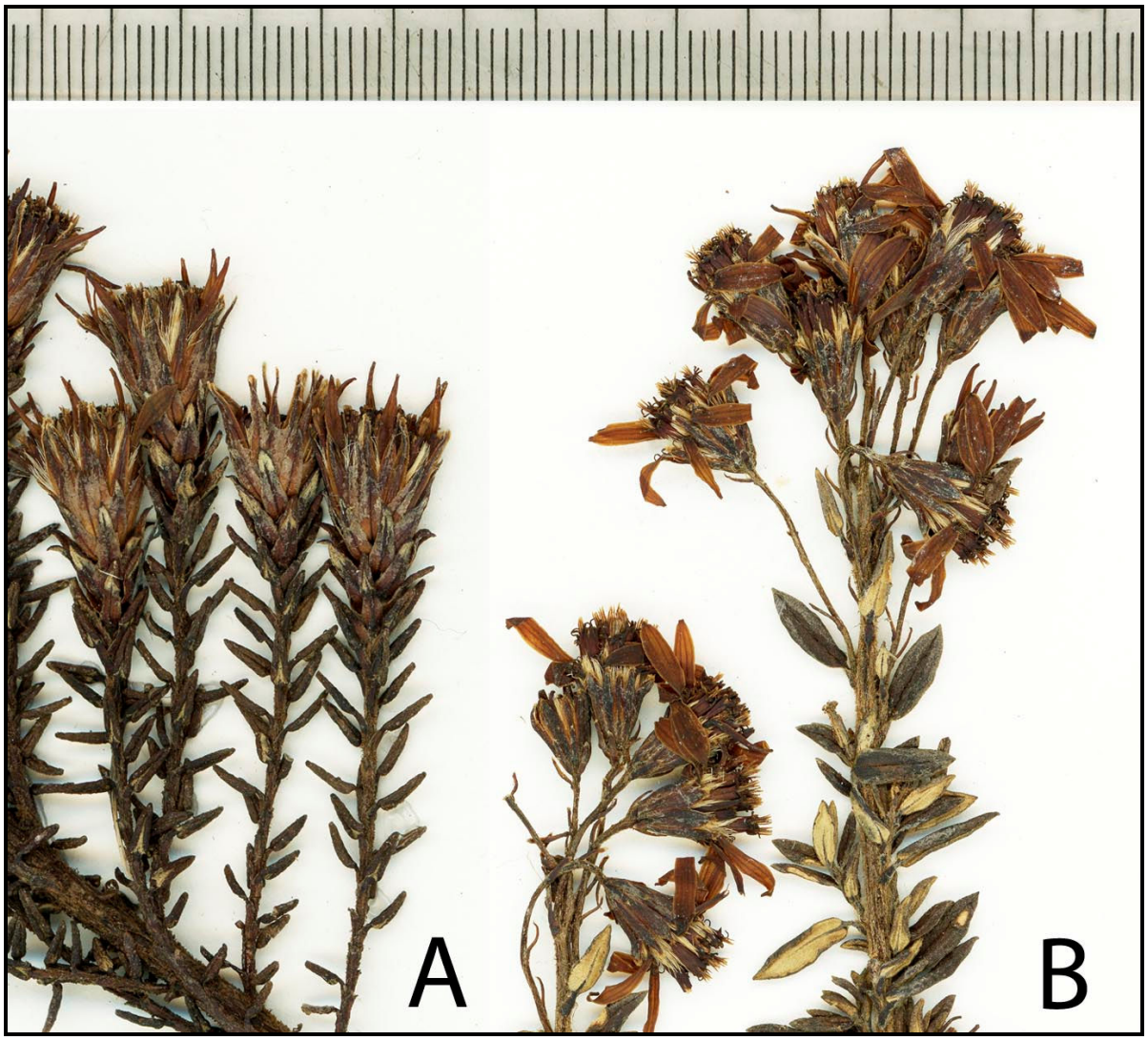

Figure 56. A. *Monticalia barbourii*, showing solitary subsessile capitula. B. *Monticalia verticillata*, showing cymose capitulescences with pedunculate capitula. (A *Vega et al. 288*, MO; B *Bussmann et al. 16624*, unmounted duplicate).

Distribution and ecology. *Monticalia barbourii* is a rare endemic of Andean north Peru (Deptos. Amazonas, La Libertad, and San Martín), where it has been collected flowering in May, September, and November from 3290–3550 meters elevation. The species was known previously from only the type collection, but two more recent collections have been seen, extending its range about 200 km to the south. The label coordinates of the two recent collections are in Depto. San Martín within two km of the border, but the departments cited in the exsiccatae below are those given on specimen labels. The recent collections are from near the corner of Amazonas, La Libertad, and San Martín, and the species may reasonably be expected to occur in each of these three departments.

Additional collections examined. PERU. Amazonas (border with San Martín)**.** Leimebamba, Tablacha, 6° 55' 52" S, 77° 43' 09" W, 3414 m, 23 May 2015, *Vega et al. 288* (HAO, MO). **La Libertad** (border with San Martín). Uchumarca, Chivane, subida a Conga de Yonan, 7° 04' 02" S, 77° 43' 35" W, 3550 m, 21 Nov 2013, *Paniagua et al. 8857* (MO).

Monticalia barbourii (M.O. Dillon & Sagást.) Pruski is a revolute-margined, discolorous-leaved, radiate-capitulate, much-branched microphyllous ericoid shrub (Fig. 56A). Dillon and Sagástegui (1988) related *M. barbourii* to *M. peruviana* (Pers.) C. Jeffrey, *M. vernicifolia* (Cuatr.) C. Jeffrey, *M. verticillata* (Klatt) C. Jeffrey, and Ecuadorean endemic *M. empetroides* (Cuatr.) C. Jeffrey. Each of these five species is a shrub with 5-costate cypselae and recognized by me in *Monticalia*. Small-leaved *M. myrsinites* (Turcz.) C. Jeffrey has similar hirsute stems but may be distinguished from the five former species by its flat leaves that are glabrous throughout. *Monticalia barbourii* is distinguished by its very small (3.5–4.5 mm long), lanceolate to triangular-ovate, truncate-cordate-based, adaxially subglabrous (sometimes sparsely lingering arachnoid adaxially near margins) leaves, subglabrous petioles, distal stems patent-pubescent hirsute, and solitary subsessile radiate capitula with 13 phyllaries. *Monticalia barbourii* occurs south and east of the Huancabamba deflection in the deep upper Río Marañón basin (Pruski 2012c). The type locality is about 100 km northwest of Chachapoyas, the two newer collections are about 100 km south of Chachapoyas, and the species should be expected at high elevations between the three known localities.

Monticalia barbourii resembles, by very small leaves, *M. empetroides*, which is centered near Cuenca, Azuay, Ecuador, about 200+ km north of Cordillera Colán. *Monticalia empetroides* differs by arachnoid-lanate stems lacking hirsute indument. Longer-leaved *M. peruviana* (syn. *Senecio ericifolius* Benth.) is from northern Peru, Ecuador, and southern Colombia, and typical (but not all) forms of this variable species similarly differ from *M. barbourii* in stem indument. Although *M. vernicifolia* is heterotrichous with a mixed hirsute and arachnoid-lanate stem indument partly resembling *M. barbourii*, it is geographically isolated from it and occurs west of the Río Marañón in Piura. Moreover, *M. vernicifolia* is relatively broad-leaved, ochraceous-pubescent, and characterized by capitula with eight phyllaries.

Monticalia barbourii appears most similar to *M. verticillata* (Fig. 56B) (Dillon & Sagástegui 1988), which it resembles in subglabrous petioles and usually patent-pubescent hirsute distal stems. *Monticalia verticillata* was described as glabrous-stemmed but provisionally includes in synonymy *Senecio verticillatus* var. *trichophorus* Greenm., based on material of the more common hirsute-stemmed morphotype of the species. *Monticalia verticillata* is a longer-broader-leaved plant having cuneate-obtuse leaf blade bases, gray-pubescent leaves, and on occasion nearly glabrous-stems (Greenman 1938); it has 8–13 (vs. 8) ray florets, cymose (Fig. 56B) (vs. monocephalous Fig. 56A) capitulescences with pedunculate (vs. subsessile) capitula, but nevertheless by discolorous leaves and hirsute stems it is similar to *M. barbourii*. *Monticalia verticillata* occurs in Amazonas and Cajamarca, Peru, and is slightly more widely distributed than is the narrowly endemic *M. barbourii*. Dillon and Sagástegui (1988 figure 3) provided a fine drawing of *Monticalia barbourii*.

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