Pruski, J.F. 2023. The new genera *Laceanthos*, *Podocalea, Tepuipappus*, the resurrected genera *Lemmatium*, *Meyeria*, *Tonalanthus*, and other novelties in the *Calea* Alliance I. Phytoneuron 2023-42: 1–171. Published 6 November 2023. ISSN 2153 733X

THE NEW GENERA *LACEANTHOS*, *PODOCALEA*, *TEPUIPAPPUS*, THE RESURRECTED GENERA *LEMMATIUM*, *MEYERIA*, *TONALANTHUS*, AND OTHER NOVELTIES IN THE *CALEA* ALLIANCE I.

JOHN F. PRUSKI
Missouri Botanical Garden
4344 Shaw Blvd.
St. Louis, Missouri 63110
john.pruski@mobot.org
orcid 0000-0001-8419-1438

ABSTRACT

From among genera long-time synonymous with typical and/or non-typical sections of *Calea* (Neurolaeneae), Mexican *Tonalanthus* Brandegee and the Brazil-centered genera *Lemmatium* DC. and *Meyeria* DC. are resurrected. **Laceanthos** Pruski, **gen. nov**. and **Podocalea** Pruski, **gen. nov.** are described as new genera and house 26 species formerly recognized in synonymous Brazil-centered *Calea* sect. *Haplocalea* and *Calea* sect. *Monanthocalea*, respectively. *Laceanthos* contains eight species, has fleshy fibrous roots, is often whorled leaved, has cymose-umbelliform capitulescences, short broad conduplicate paleae, disk corollas with reddish-orange to orange resin within ducts, and cypselar twin trichome terminal cell apices slightly divergent. *Lemmatium* houses 16 species and has stipitate cypselae with multicellular irregularly knotted twin trichomes. *Meyeria* contains 18 species, has short-pappose quadrangular cypselae with weakly asymmetric carpopodia, and x = 18 as a base chromosome number. *Podocalea* is newly described and includes 18 species that are most often relatively large-capitulate monocephalous scapose xylopodial plants with x = 16 as a base chromosome number, have clinanthia with linear non-conduplicate paleae, disk corolla throats with orangish resin within the single throat duct along each vein, and cypselar twin trichome terminal cell apices noticeably divergent. *Tonalanthus* is monotypic, has biconvex-compressed cypselae with unevenly developed short broad twin trichomes, and slender ascending style branches. *Laceanthos*, *Lemmatium*, and *Podocalea* each contain both radiate-capitulate and discoid-capitulate species, whereas *Meyeria* and *Tonalanthus* are strictly radiate-capitulate. Each of these five newly recognized genera are treated at least provisionally as members of tribe Neurolaeneae, but each differs in critical features from *Calea*. **Tepuipappus** Pruski, **gen. nov**. is newly described, placed in Heliantheae subtr. Verbesininae, and houses six species from the Duida Supergroup of tepui summits in the Lost World of the Guayana Highland. *Tepuipappus* is treated within the present paper in an internal paper titled "Compositae of the Guayana Highland–XV. The new genus *Tepuipappus* (Heliantheae subtr. Verbesininae) from Venezuela." The species of *Tepuipappus* are characterized by radiate capitula, quadrangular cypselae, weakly asymmetric carpopodia, and typically a pappus of 4 longer pappus scales on the edges of the cypselae with occasional intermediate scales or squamellae. Sixty three new combinations are proposed for the 67 species recognized in the three newly described and three newly resurrected genera treated here. The eight new combinations in *Laceanthos*, 15 new combinations in *Lemmatium*, 15 new combinations in *Meyeria*, 18 new combinations in *Podocalea*, six new combinations in *Tepuipappus*, and that in monotypic *Tonalanthus* are: **Laceanthos acaulis** (Baker) Pruski, **comb. nov.**, **Laceanthos chapadensis** (Malme) Pruski, **comb. nov.**, **Laceanthos crenatus** (Chodat) Pruski, **comb. nov.**, **Laceanthos cymosus** (Less.) Pruski, **comb. nov.**, **Laceanthos hasslerianus** (Chodat) Pruski, **comb. nov.**, **Laceanthos mediterraneus** (Vell.) Pruski, **comb. nov.**, **Laceanthos reticulatus** (Gardner) Pruski, **comb. nov.**, **Laceanthos rhombifolius** (S.F. Blake) Pruski, **comb. nov.**, **Lemmatium arachnoideum** (G.A.R. Silva & J.N. Nakaj.) Pruski, **comb. nov.**, **Lemmatium brittonianum** (Pruski) Pruski, **comb. nov.**, **Lemmatium clematideum** (Baker) Pruski, **comb. nov.**, **Lemmatium diamantinense** (G.A. Reis-Silva & J.N. Nakaj.) Pruski, **comb. nov.**, **Lemmatium divergens** (Sch. Bip. ex Baker) Pruski, **comb. nov.**, **Lemmatium fruticosum** (Gardner) Pruski, **comb. nov.**, **Lemmatium grazielae** (J.U. Santos) Pruski, **comb. nov.**, **Lemmatium intermedium** (Pruski & Urbatsch) Pruski, **comb. nov.**, **Lemmatium irwinii** (G.M. Barroso) Pruski, **comb. nov.**, **Lemmatium lemmatioides** (Sch. Bip. ex Baker) Pruski, **comb. nov.**, **Lemmatium morii** (H. Rob.) Pruski, **comb. nov.**, **Lemmatium nitidum** (Less.) Pruski, **comb. nov.**, **Lemmatium oxylepis** (Baker) Pruski, **comb. nov.**, **Lemmatium sickii** (G.M. Barroso)

Pruski, **comb. nov.**, **Lemmatium wedelioides** (Baker) Pruski, **comb. nov.**, **Meyeria aldamoides** (G.H.L. da Silva et al.) Pruski, **comb. nov.**, **Meyeria chodatii** (Hassler) Pruski, **comb. nov.**, **Meyeria funkiana** (V.R. Bueno & G. Heiden) Pruski, **comb. nov.**, **Meyeria heteropappa** (Pruski & Urbatsch) Pruski, **comb. nov.**, **Meyeria ilienii** (Malme) Pruski, **comb. nov.**, **Meyeria kristiniae** (Pruski) Pruski, **comb. nov.**, **Meyeria monocephala** (Dusén) Pruski, **comb. nov.**, **Meyeria nervosa** (G.M. Barroso) Pruski, **comb. nov.**, **Meyeria phyllolepis** (Baker) Pruski, **comb. nov.**, **Meyeria pruskiana** (V.R. Bueno & G. Heiden) Pruski, **comb. nov.**, **Meyeria quadrifolia** (Pruski & Urbatsch) Pruski, **comb. nov.**, **Meyeria semirii** (Pruski & D.J.N. Hind) Pruski, **comb. nov.**, **Meyeria sessilifolia** (V.R. Bueno & G. Heiden) Pruski, **comb. nov.**, **Meyeria subintegerrima** (Malme) Pruski, **comb. nov.**, **Meyeria triantha (**Vell.) Pruski, **comb. nov.**, **Podocalea abbreviata** (Pruski & Urbatsch) Pruski, **comb. nov.**, **Podocalea angustifolia** (Gardner) Pruski, **comb. nov.**, **Podocalea asclepiifolia** (Hassler) Pruski, **comb. nov.**, **Podocalea bakeriana** (Chodat) Pruski, **comb. nov.**, **Podocalea cabrerae** (Pruski) Pruski, **comb. nov.**, **Podocalea camporum** (Krasch.) Pruski, **comb. nov.**, **Podocalea catalaonensis** (Krasch.) Pruski, **comb. nov.**, **Podocalea cuneifolia** (DC.) Pruski, **comb. nov.**, **Podocalea formosa** (Chodat) Pruski, **comb. nov.**, **Podocalea multiplinervia** (Less.) Pruski, **comb. nov.**, **Podocalea oligocephala** (DC.) Pruski, **comb. nov.**, **Podocalea paraguayensis** (Kuntze) Pruski, **comb. nov.**, **Podocalea pedunculosa** (DC.) Pruski, **comb. nov.**, **Podocalea pohliana** (Sch Bip. ex Baker) Pruski, **comb. nov.**, **Podocalea rupicola** (Chodat) Pruski, **comb. nov.**, **Podocalea tomentosa** (Gardner) Pruski, **comb. nov.**, **Podocalea uniflora** (Less.) Pruski, **comb. nov.**, **Podocalea verticillata** (Klatt) Pruski, **comb. nov., Tepuipappus camani** (Maguire & K.D. Phelps) Pruski, **comb. nov.**, **Tepuipappus esposi** (Maguire & K.D. Phelps) Pruski, **comb. nov.**, **Tepuipappus kunhardtii** (Maguire) Pruski, **comb. nov.**, **Tepuipappus orbiculatus** (Maguire & Aristeg.) Pruski, **comb. nov.**, **Tepuipappus phelpsiae** (Lasser & Maguire) Pruski, **comb. nov.**, **Tepuipappus punctatus** (Maguire & Wurdack) Pruski, **comb. nov.**, and **Tonalanthus megacephalus** (B.L. Rob. & Greenm.) Pruski, **comb. nov.** **Calea juninensis** Pruski, **sp. nov.** from Junín, Peru and **Calea santanderensis** Pruski, **sp. nov.** from Santander, Colombia are newly described and compared to close congeners. *Calea juninensis* is distinctive among Peruvian species by its short-radiate mid-sized capitula, distally setose cypselae, and is the second species known from Junín and Pasco. Radiate relatively small-capitulate *Calea santanderensis* has abaxially glandular stiff-chartaceous leaves that are usually obtuse-round-based, and is unlike other northern Andean species. Alfred R. Wallace's Serras de Cababurís is possibly an earlier name for Sierra de la Neblina.

Calea L. (Compositae tribe Neurolaeneae Rydb.) is a widespread tropical and subtropical American genus of the Heliantheae Alliance (sensu Panero 2007) native to Mexico, Central America, the West Indies, and South America. One species, *Calea urticifolia* (Mill) DC., is introduced in Congo and Zaire (e.g., *Breyne 313*, MO; Lawalrée 1982; Pruski and Robinson 2018: 410, 416). *Calea* generally has opposite leaves and yellow corollas, like many Helianthoids, but differs from most by non-setose corollas, pale anthers, and a radial pappus of scales. The five genera of tribe Neurolaeneae recognized by Panero (2007), Turner (2014), and Pruski and Robinson (2018) are *Calea*, paucispeciose pantropical *Enydra* Lour., monotypic Mexican *Greenmaniella* W.M. Sharp, paucispeciose Cuban *Heptanthus* W.M. Sharp (viz Britton 1916), and the approximately dozen species of tropical American *Neurolaena* R. Br. Pruski and Robinson (2018) gave the genus *Calea* as containing about 150 species, but here my revisionary efforts cut that number nearly in half by formally exclusion to three new genera and three resurrected genera of 67 former-*Calea* species.

Calea was described by Linnaeus (1763, 1764) to house three American species that he had earlier (Linnaeus, Syst. Nat., ed. 10: 1207. 1759) described in *Santolina* L., an epappose Old World genus of tribe Anthemideae. These original three species of Linnaeus (1763) are *Calea jamaicensis* (L.) L. (the generitype), *Calea amellus* (L.) L. (now treated in synonymy with *Salmea scandens* (L.) DC.), and *Calea oppositifolia* (L.) L. (now *Isocarpha oppositifolia* (L.) Cass., a paleate member of tribe Eupatorieae). Although these three species were described in *Calea* in 1763, ICBN 2006: 28 Art. 13.4 allows for the generic description of *Calea* (Linnaeus, Gen. Pl., ed. 6, 2: 416. 1764) to be "associated" with the three species of *Calea* in Linnaeus (Sp. Pl. 1763). The Linnaean generic description of *Calea* (Linnaeus 1764) partly reads "*Pappus* pilosus, longitudine calycis" and "*Paleis* calyce paulo longioribus." Here in this report that is part of the *Latin American Compositae Initiative* (LACI) and an intermediate step in the revision of the *Calea* Alliance, my intention is to bring the taxonomic placement and circumscription of *Calea* into sharper focus, but this is still a work in progress.

Willdenow (1803) recognized eight species in *Calea*: the three original Linnaean species and five others. A decade later, Brown (1817) stated "it would not be difficult to point out a much greater number of species improperly united [than in] the genus *Calea*" and that its "structure and limits seem to be imperfectly understood." Brown (1817) lectotypified *Calea* by *Santolina jamaicensis* L., and stated "The first species, *Calea jamaicensis*, is the only [original element] that even seems to agree with the generic character…" Indeed, *Calea jamaicensis* has pappus and paleae about as long as the involucre, a Linnaean (1764) generic feature of *Calea*, whereas neither *Isocarpha* nor *Salmea* have this feature. *Calea jamaicensis* was subsequently lectotypified by Moore (1936: 260) upon LINN 984.1. Brown (1817) also noted that none of the five further species listed in Willdenow (1803) matched the Linnaean generic characters of *Calea* either, and indeed they are now referred to five different genera: *Baccharis* L., *Cassinia* R. Br., *Melanthera* Rohr., *Neurolaena* R. Br., and *Ozothamnus* R. Br.

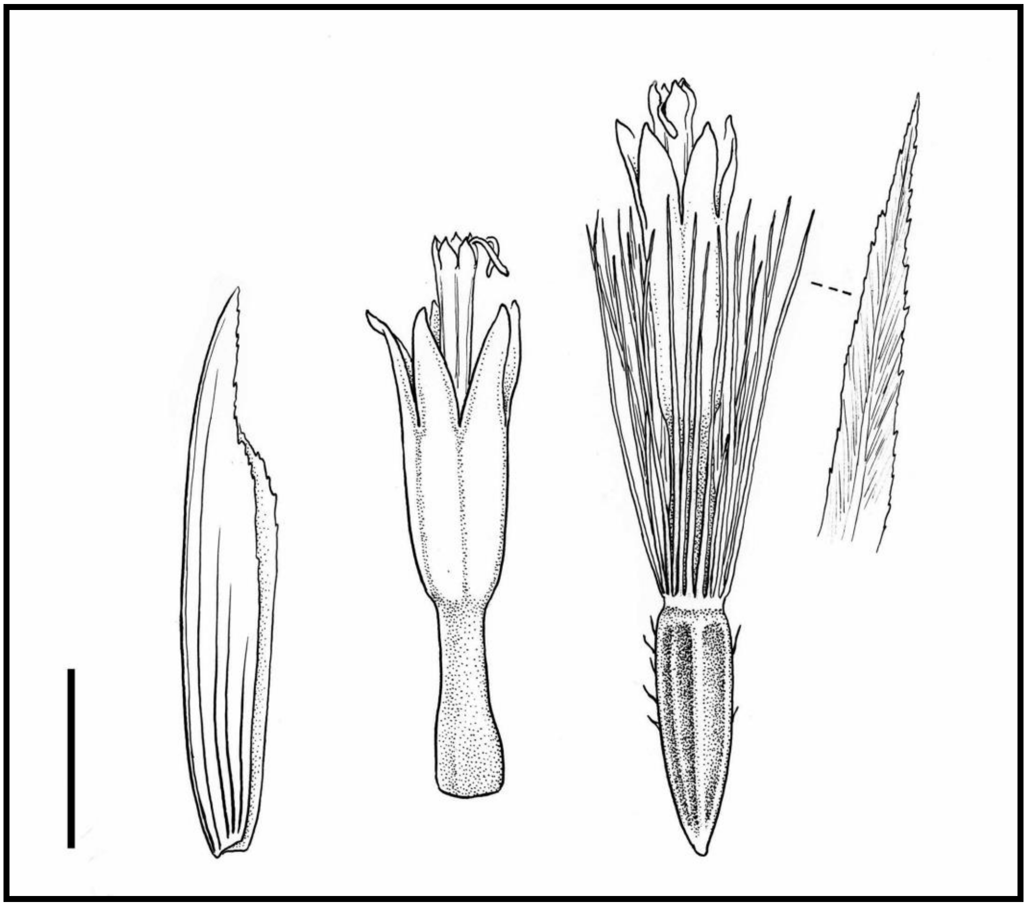


Figure 1. *Calea lutea* Pruski & Urbatsch, showing (left to right) salient generic features of a conduplicate palea, disk floret (cypsela removed) with non-setose corolla, and a bisexual disk floret with a radially symmetric pappus of scales, close-up (far right) of an individual flat pappus scale. (Drawn by Bobbi Angel from *Silva et al 76*, NY, isotype, modified from Pruski and Urbatsch 1988). Scale bar 2 mm.

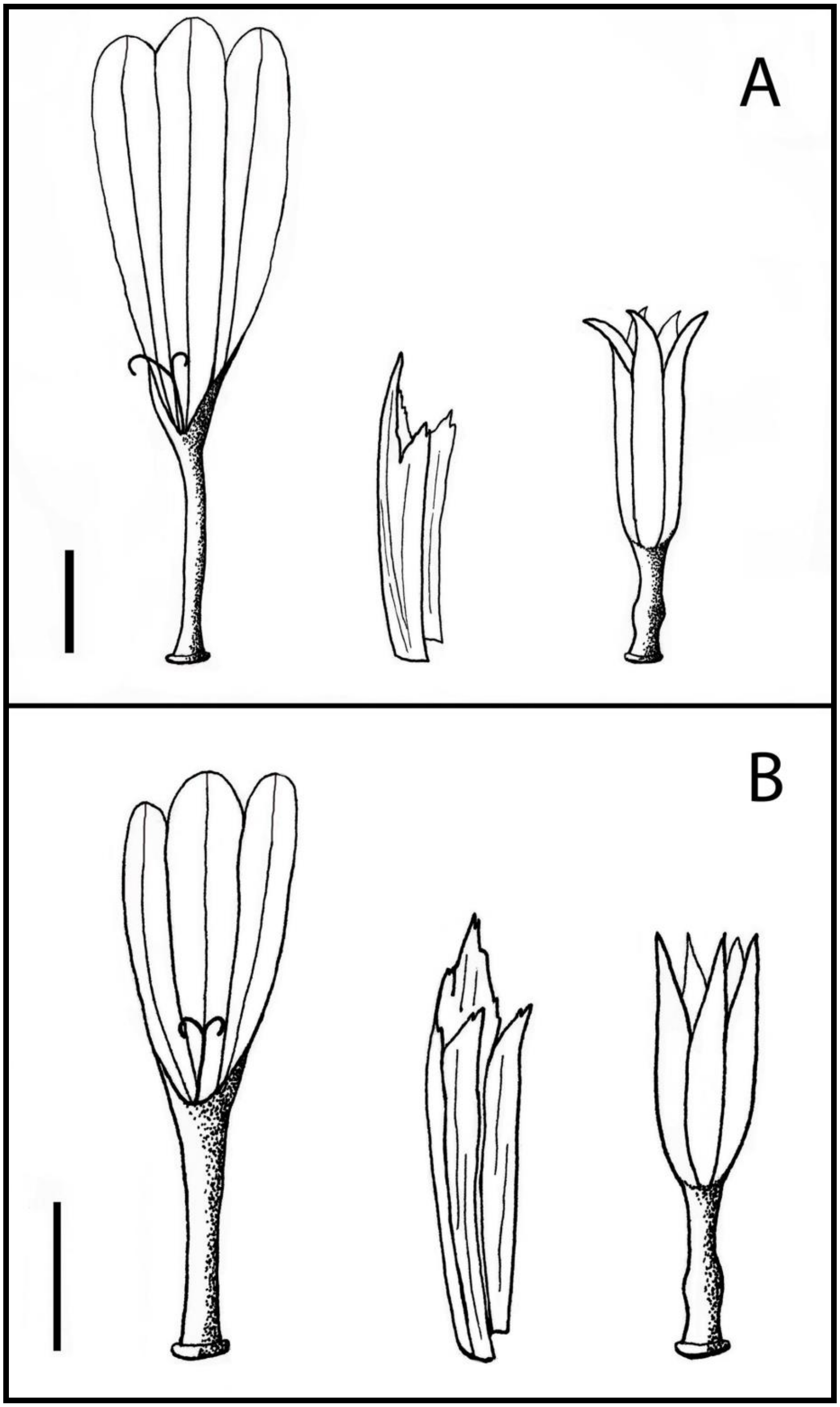


Figure 2. Representative florets and corollas of *Calea* L. The ray florets (cypselae removed) when present are pistillate having non-setose corollas with limbs with closed venation (left in each), paleae are conduplicate (center), and disk corollas are similarly non-setose (right). A. *Calea subcordata* S.F. Blake. B. *Calea gargantae* Cuatr. (Drawn by Kristin Malin, modified from Pruski 1982; A *Urbatsch & Pruski 3427A1311*, NY; B *Garganta 838*, F, holotype). Scale bars 2 mm.

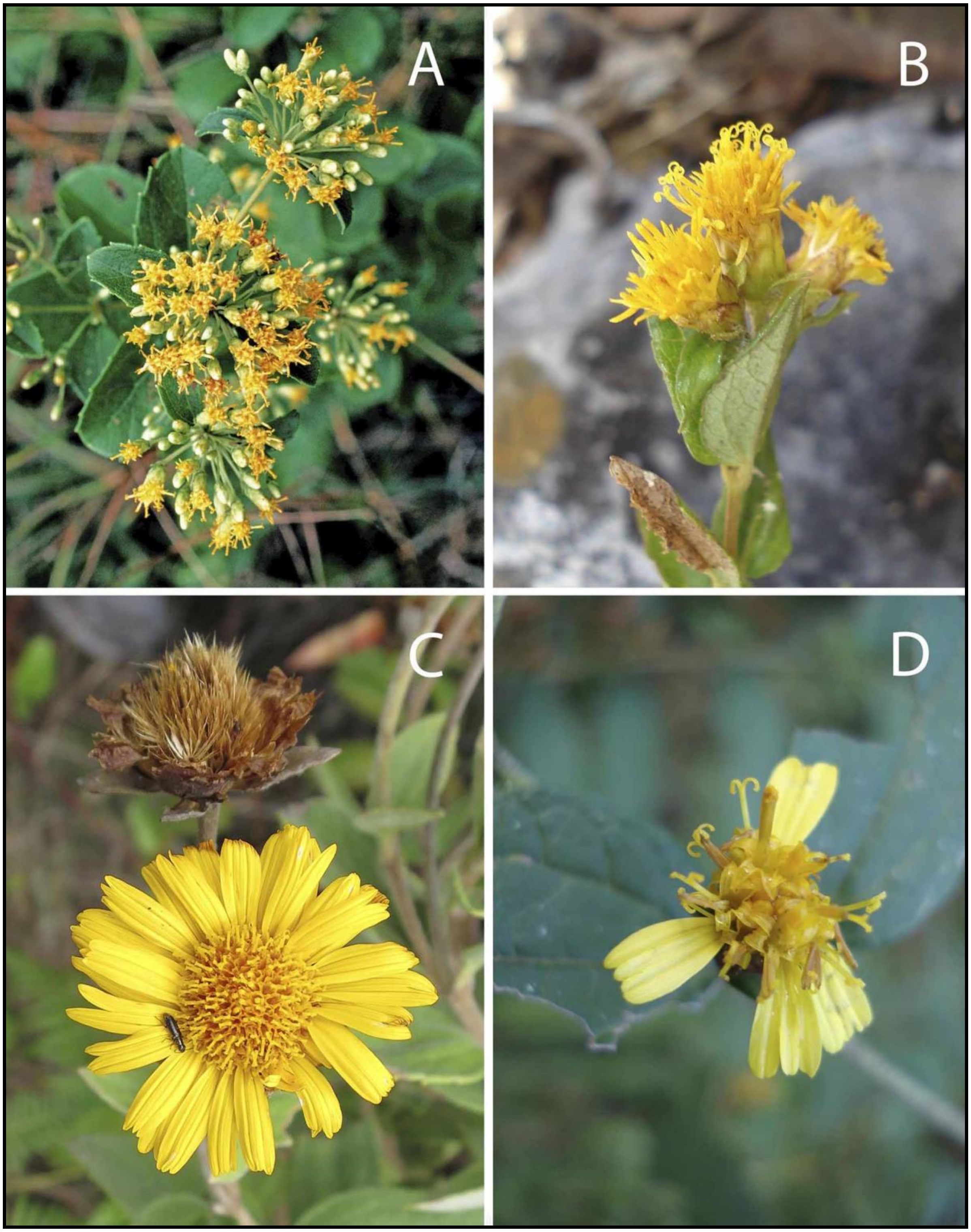


Figure 3. Capitula of representative species of *Calea* L., showing the yellowish anthers. A–B. Discoid capitula. C–D. Radiate capitula. A. *Calea prunifolia* Kunth, photographed in Trujillo, Venezuela. B. *Calea trichotoma* Donn. Sm., Chiapas, Mexico. C. *Calea peruviana* (Kunth) Benth. ex S.F. Blake, Boyacá, Colombia. D. *Calea urticifolia* (Mill.) DC., Veracruz, Mexico. (A *Urbatsch & Pruski 3407A1290*, B *Pruski et al. 4186*, C *Pruski & Ortiz 4810*, D *Pruski & Ortiz 4143*).

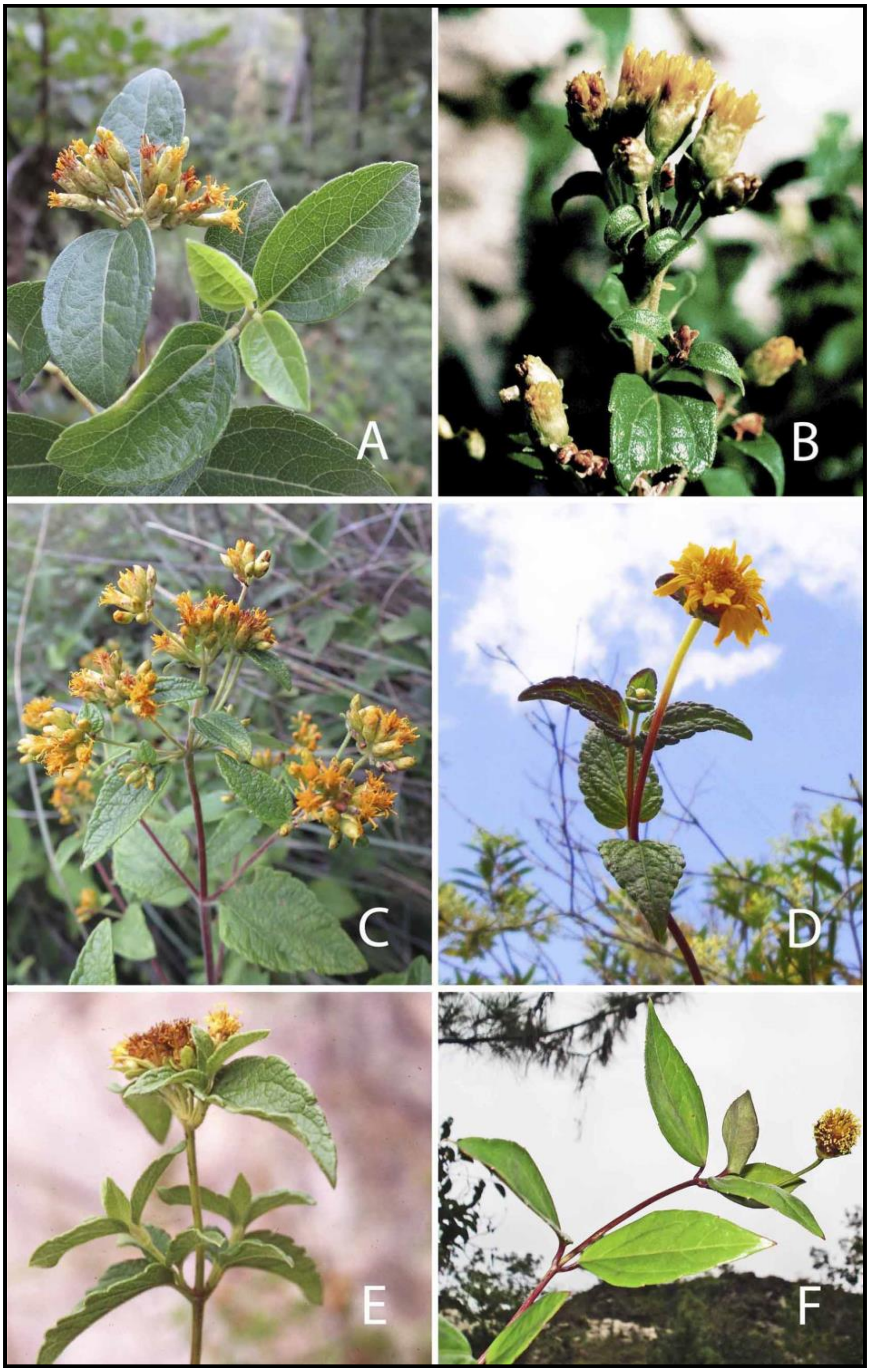


Figure 4. Opposite 3-nerved leaves of representative species of *Calea* L., infrequently individuals may be ternate-whorled-leaved. A. *Calea prunifolia* Kunth, photographed in Valle de Cauca, Colombia. B. *Calea jamaicensis* (L.) L., generitype, Jamaica, topotype. C. *Calea umbellulata* Hochr., Chachapoyas, Amazonas, Peru, topotype. D. *Calea montana* Klatt, Moyobamba, San Martín, Peru, topotype. E. *Calea berteriana* DC., Mérida, Venezuela. F. *Calea longipedicellata* B.L. Rob & Greenm., Guatemala. (A *Pruski et al. 4903*; B *Urbatsch & Pruski 3401A1284;* C *Pruski & Ortiz 4898*; D *Pruski & Ortiz 4643*; E *Urbatsch & Pruski 3455A1339*; F *Pruski et al. 4545*).

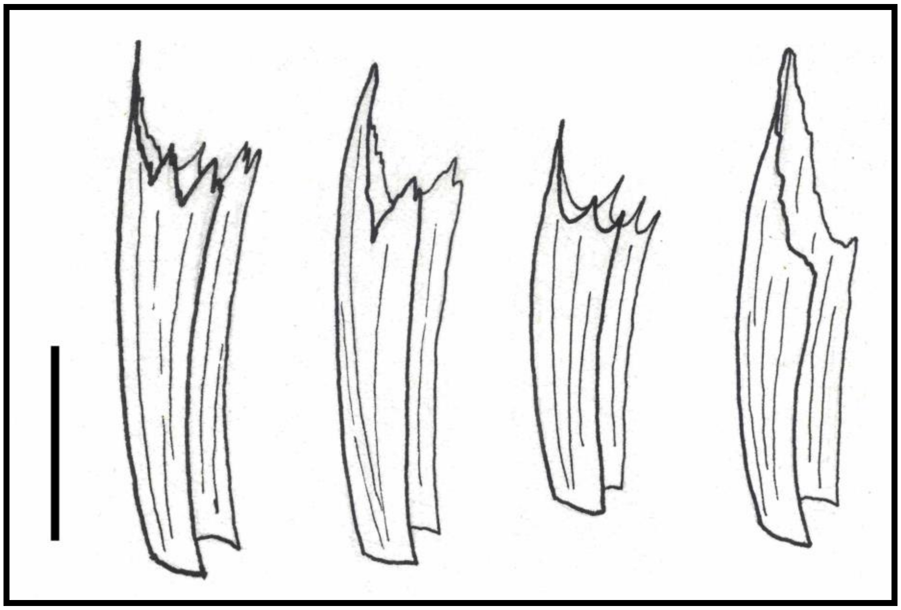


Figure 5. Representative paleae of *Calea* L., thin-chartaceous, conduplicate, usually reaching at least to the disk corollas throats, (left to right) *Calea peruviana* (Kunth) Benth. ex S.F. Blake, (*Goudot s.n.*, P), *Calea subcordata* S.F. Blake (*Urbatsch & Pruski 3427A1311*, NY), *Calea solidaginea* Kunth var. *solidaginea* (*Killip & Smith 14987*, NY), and *Calea prunifolia* Kunth (*Pruski 442*, LSU). [The paleae of *Laceanthos* Pruski (Fig. 36) are similar but reach only to the base of the disk corolla tubes]. (Drawn by Kristin Malin, modified from Pruski 1982). Scale bar 2 mm.

Several distinct South American subgenera of *Calea*—i.e., the two Brazil-centered ones first named by Lessing (1832: 241–242), who treated newly combined Andean *Calea* subgen. *Leontophthalmum* (Willd.) Less. 1832: 241 as distinct from those subgenera in Brazil—and several distinct Neotropical genera (e.g., those of Candolle 1836) were among the nine sections Bentham and Hooker (1873) recognized in *Calea*. To sectional rank within *Calea*, Bentham and Hooker (1873) also reduced Mexico-centered *Oteiza* La Llave, Mexico-centered *Tetrachyron* Schltdl., and *Allocarpus* Kunth. *Allocarpus* included montane neotropics-centered *Alloispermum* Willd.; each of these two generic names is Greek-derived and refers to the pappus condition of the rays cypselae vs. that of the disk cypselae. A decade later, Baker (1884) recognized three subgenera in Brazil, but not *Calea* sect. *Lemmatium* (DC.) Benth. & Hook. f., and at about the same time in another fine regional treatment Robinson and Greenman (1896, 1901) recognized five subgenera of *Calea* in Mexico. Baillon (1886) provided a summary of Compositae, listed synonymous genera, but did not focus on infragenera. Baillon (1886) aligned *Calea* with *Galinsoga*, as initially done by Candolle (1836: 499, 668) and later by Bentham and Hooker (1873: 198). Hoffmann (1894) recognized four sections of *Calea*, a genus he formally treated as one of nine genera in Heliantheae subtr. Galinsoginae Benth. & Hook. f. Shortly thereafter, Löfgren (1897) too recognized *Calea* as having three subgenera in Brazil.

The Benthamian sectional framework, however, for the next century became the standard infrageneric concept used for *Calea*. But over the past several decades, Lowell Urbatsch, Harold Robinson, and collaborators expelled several disparate Mexico and Central America-centered elements from *Calea*. For example, after a century-long synonymy with *Calea*, each *Alloispermum* (Robinson 1978a) and *Tetrachyron* (Wussow and Urbatsch 1979) were resurrected. Wussow and Urbatsch (1979) noted that *Tetrachyron* is characterized by its quadrangular stipitate cypselae and a pappus of four equal scales often with intermediate shorter squamellae (Fig. 16C–D). These same features were used in Strother (1999), Rzedowski et al. (2011), Turner (2016a), and Pruski and Robinson (2018) to help diagnose *Tetrachyron*. Pruski (1982), Strother (1999), Robinson (2006), and Pruski and Robinson (2018) noted *Alloispermum* differs from *Calea* by its setose corollas and epappose ray florets (Fig. 17).

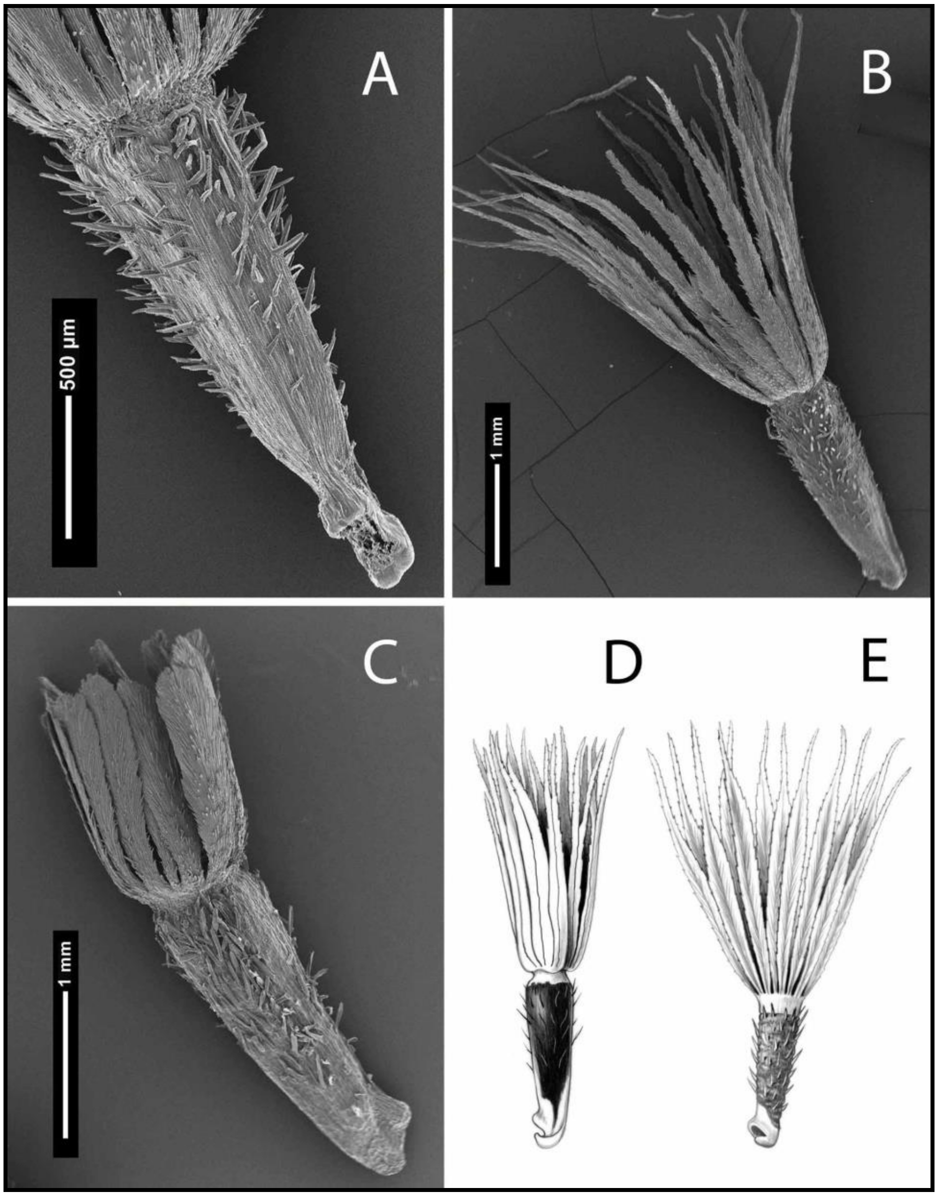


Figure 6. Cypselae and pappus scales representative of *Calea* L. The pappus scales have thickened midribs and are free at base; the carpopodia are strongly asymmetric; the twin trichomes are smooth, few-celled, and have elongate subequal laterally connate paired terminal cells with apices non-divergent (i.e., simple twin trichomes). A–B. *Calea prunifolia* Kunth, showing surfaces with simple twin trichomes, and pappus scales longer than the cypselae. C. *Calea ternifolia* Kunth, showing the simple twin trichomes and pappus scales shorter than the cypselae. D. *Calea jamaicensis* (L.) L., the generitype. E. *Calea huigrensis* S.F. Blake. (A–B *Urbatsch & Pruski 3407A1290*, NY; C C*lara 212*, MO; D × 12, drawn by Alice Tangerini, reproduced from Robinson 1981: fig. 139; E body 2.5 mm, drawn by Alice Tangerini from *Rose 22283*, US, reproduced from Robinson 2006: fig. 3J).

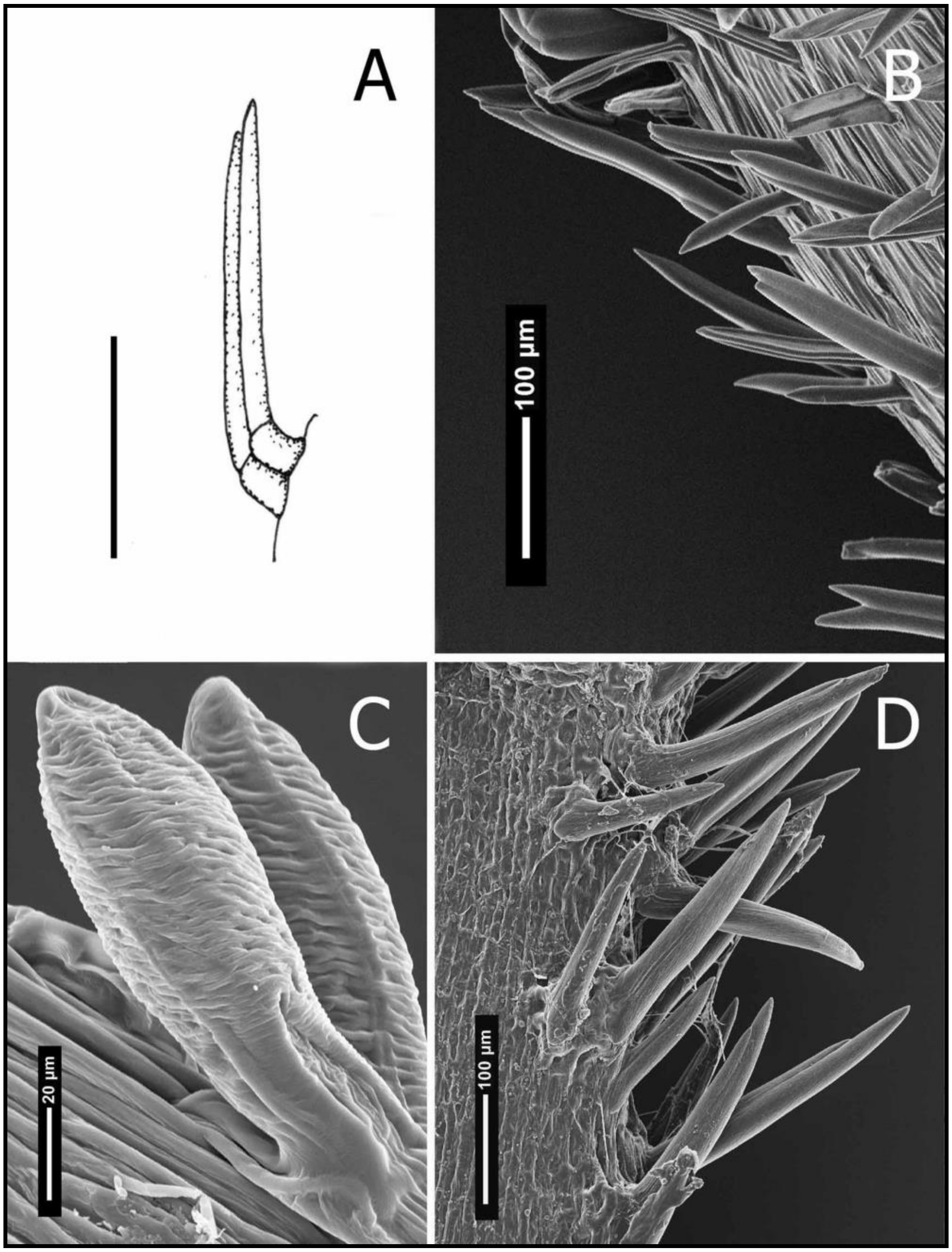


Figure 7. Select twin trichomes (also called Zwillingshaare, twin hairs, or duplex trichomes) of Compositae cypselae, showing those with pairs of elongate longitudinally connate terminal cells with tips appressed. A. *Laennecia araneosa* (Urb.) G. Sancho & Pruski, Astereae. B. *Calea prunifolia* Kunth, twin trichomes in *Calea* have no discernible cuticular pattern, Neurolaeneae. C. *Gerbera linnaei* Cass., Mutisieae, showing a distinct spiral cuticular pattern. D. *Bidens oerstediana* (Benth.) Sherff, Coreopsideae; the twin trichomes of this and other Coreopsids often extend upwards onto the pappus awns, showing that twin trichomes are not restricted to cypsela (see also Sancho and Katinas 2002) and that pappus structures are not homologous across Compositae; similarly, in *Perymenium*, Pruski (2016: fig. 3) showed several (true) annular pappus awns and on the same cypsela showed wings terminating into (false) pappus-like appendages. (A drawn by Gisela Sancho from *Ekman 13566*, US, modified from Sancho and Pruski 2004; B *Urbatsch & Pruski 3407A1290*, NY; C *Rodin 3100*, MO; D *Grayum et al. 12233*, MO). Scale bar A 50 µm.

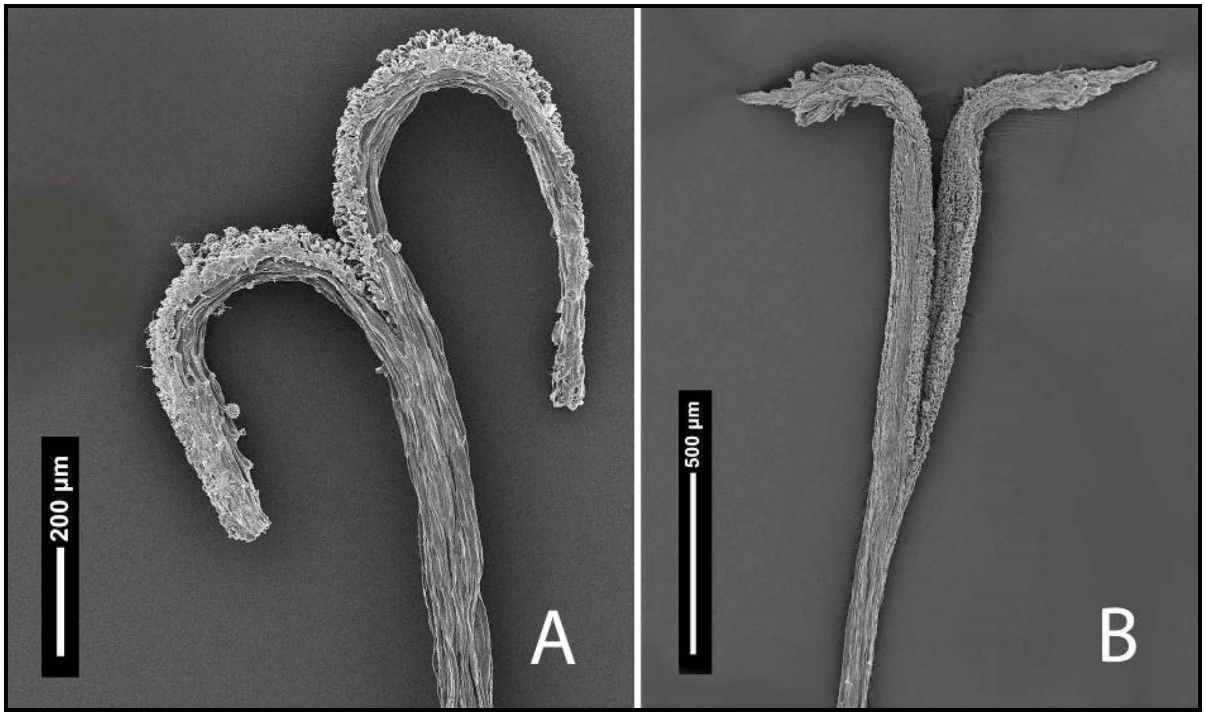


Figure 8. Disk floret style branch apex variation in *Calea* L.; disk floret style branches are the comparative standard across Compositae, except when not possible to be so, such as in our few dioecious genera, Cichorieae, and several Mutisioids. A. *Calea jamaicensis* (L.) L., branches at anthesis, recurved, apices obtuse. B. *Calea trichotoma* Donn. Sm., early anthesis, branches beginning to recurve, apices pointed. The style branch apices of *Calea* are typically obtuse and papillose, the distal portions of the abaxial surface are also papillose (the *Calea*-style morphotype), but the apex may be pointed in some species, a feature used by Pruski and Robinson (2018) to resurrect pointed-styled *C. trichotoma* from synonymy of obtuse-styled *C. jamaicensis*, the generitype. (A *Urbatsch & Pruski 3401A1284*, NY; B *Saunders 497*, MO).

Mexican-Guatemalan endemic *Calea insignis* S.F. Blake was earlier excluded from *Calea* by Fay (1975), who placed the species in the newly restored *Oteiza*. Subsequently, Panero et al. (1993) described two new species of *Oteiza*. Panero et al. (1993), Turner (2016b,) and Pruski and Robinson (2018) recognized *Oteiza* as containing four species, and treated *C. insignis* in synonymy with *Oteiza ruacophila* (Donn. Sm.) J.J. Fay; geographically, *Oteiza* jumps from Oaxaca, Mexico to Guatemala; e.g., the genus was not given by either Strother (1999) or Pruski and Robinson (2018) as known from intermediate Chiapas, Mexico. And still elsewhere in Mexico and Central America, *Calea skutchii* S.F. Blake was excluded from *Calea* (and placed in *Podachaenium* Benth., Fig. 89A–B) by Robinson (1978b). Shortly thereafter the species was treated as the sole species of the newly described genus *Squamopappus* R.K. Jansen, N.A. Harriman & Urbatsch (Fig. 89C; Jansen et al. 1982). *Calea standleyi* Steyerm. was excluded from *Calea* and treated within *Verbesina* by Nash (1975) and Wussow and Urbatsch (1978), but was placed within *Podachaenium* by Jansen et al. (1982), Turner and Panero (1992), Pruski (2016), and Pruski and Robinson (2018).

Alloispermum, *Oteiza*, *Podachaenium*, *Squamopappus*, and *Tetrachyron* were recognized as distinct from *Calea* also by Panero et al. (1993), Strother (1999), Panero (2007), Rzedowski and Calderón de Rzedowski (2008), Rzedowski et al. (2011), Pruski (2016), Turner (2016a, 2016b), and Pruski and Robinson (2018). Panero (2007), followed by Turner (2016a, 2016b) and Pruski and Robinson (2018), treated *Podachaenium*, *Squamopappus*, and *Tetrachyron* in Heliantheae subtr. Verbesininae, but placed *Alloispermum*, *Oteiza*, and *Galinsoga* in tribe Millerieae (syn. subtr. Galinsoginae). Here, following a suggestion by Turner (2008), biconvex-compressed-fruited

Mexican *Tonalanthus* Brandegee (Figs. 96–98), yet another long-time synonym, is reinstated from synonym of *Calea,* where it placed by Rzedowski (1968), Wussow et al. (1985), Turner (2014), and Pruski and Robinson (2018). I place *Tonalanthus* in Neurolaeneae.

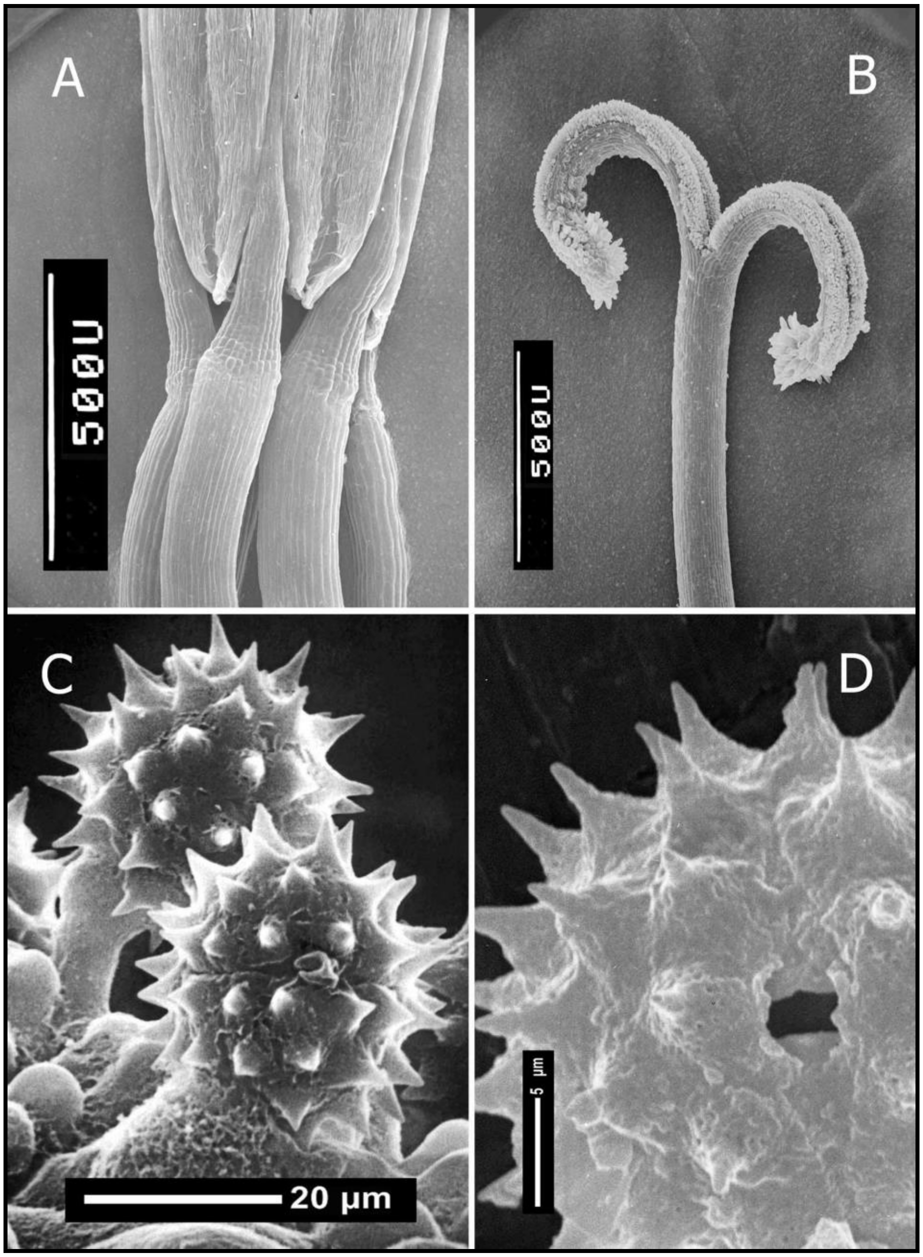


Figure 9. Anthers, style, and pollen characters of three north Andean species of *Calea* L. A. Anthers of *Calea prunifolia* Kunth, showing shortly sagittate thecae bases. B. Style of *Calea solidaginea* Kunth, showing recurved branches each with adaxial 2-banded stigmatic surfaces fertile and discrete nearly to the obtuse apex, which is papillose, as are the distal portions of the abaxial surface, the *Calea*-style morphotype. C–D. Echinate tricolporate pollen of *Calea septuplinervia* Hieron., C showing pollen tubes, D is a close-up of an aperture. (A *Urbatsch & Pruski 3407A1290*, NY; B modified from Pruski 1982, *Urbatsch & Pruski 3420A1304*, NY; C reproduced from Pruski 1980b, D modified from Pruski 1982, C–D *Urbatsch & Pruski 3457A1344*, NY).

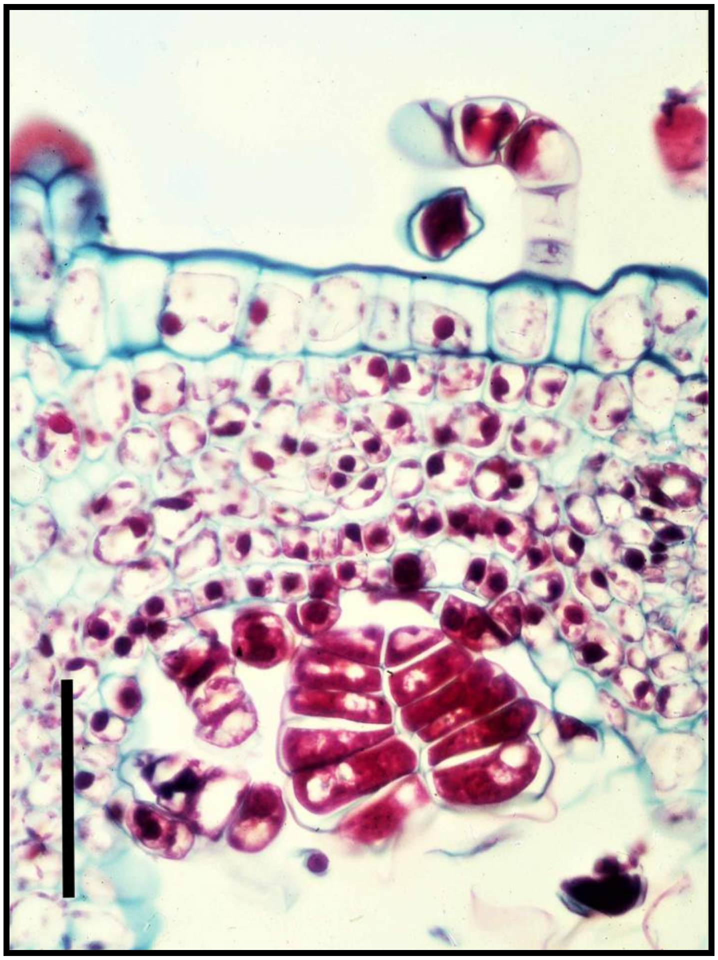


Figure 10. Transverse section though a leaf blade and foliar secretory trichomes of *Calea subcordata* S.F. Blake, leaves stained in safranin-toluidine blue, showing a 7-celled moniliform trichome on adaxial leaf surface (upper right, the penultimate cell is out of field of view) and a subsessile pluricellular biseriate glandular trichome on the abaxial leaf blade surface, septations visible within and between the two tiers of cells (lower center). Among pubescent species of *Calea* with these trichome types, generally moniliform trichomes are found on adaxial leaf blade surfaces and biseriate glands on abaxial leaf blade surfaces, as seen in this image. (*Urbatsch & Pruski 3427A1311*, NY, Táchira, Venezuela). Scale bar A 50 µm.

Field, herbarium, laboratory, and monographic studies of the genus *Calea* (Compositae: Heliantheae s.l.) in the Neotropics lead Pruski (1998a) to recognize five sections within *Calea* L. [i.e., *Calea* sect. *Calea*, *Calea* sect. *Haplocalea* (Less.) Pruski, *Calea* sect. *Lemmatium* (DC.) Benth. & Hook. f., *Calea* sect. *Meyeria* (DC.) Benth. & Hook. f., and *Calea* sect. *Monanthocalea* (Less.) Pruski]. Wussow et al. (1985) lectotypified two of these five, i.e., *Calea* sect. *Monanthocalea* (Less.) Pruski and *Meyeria* DC. It has been become increasingly apparent over the past few decades, however, that further Mexican and now some South American genera synonymized at various points in the last century and a half with *Calea* (viz, e.g., Bentham and Hooker 1873; Baker 1884; Hoffmann 1894; Löfgren 1897; Pruski 1982, 1984, 1997, 1998a, 2005, 2013; Pruski and Urbatsch 1983, 1987, 1988; Silva et al. 2016; Pruski and Robinson 2018; and Silva and Teles 2018) are significantly distinct generically and stand apart from *Calea*.

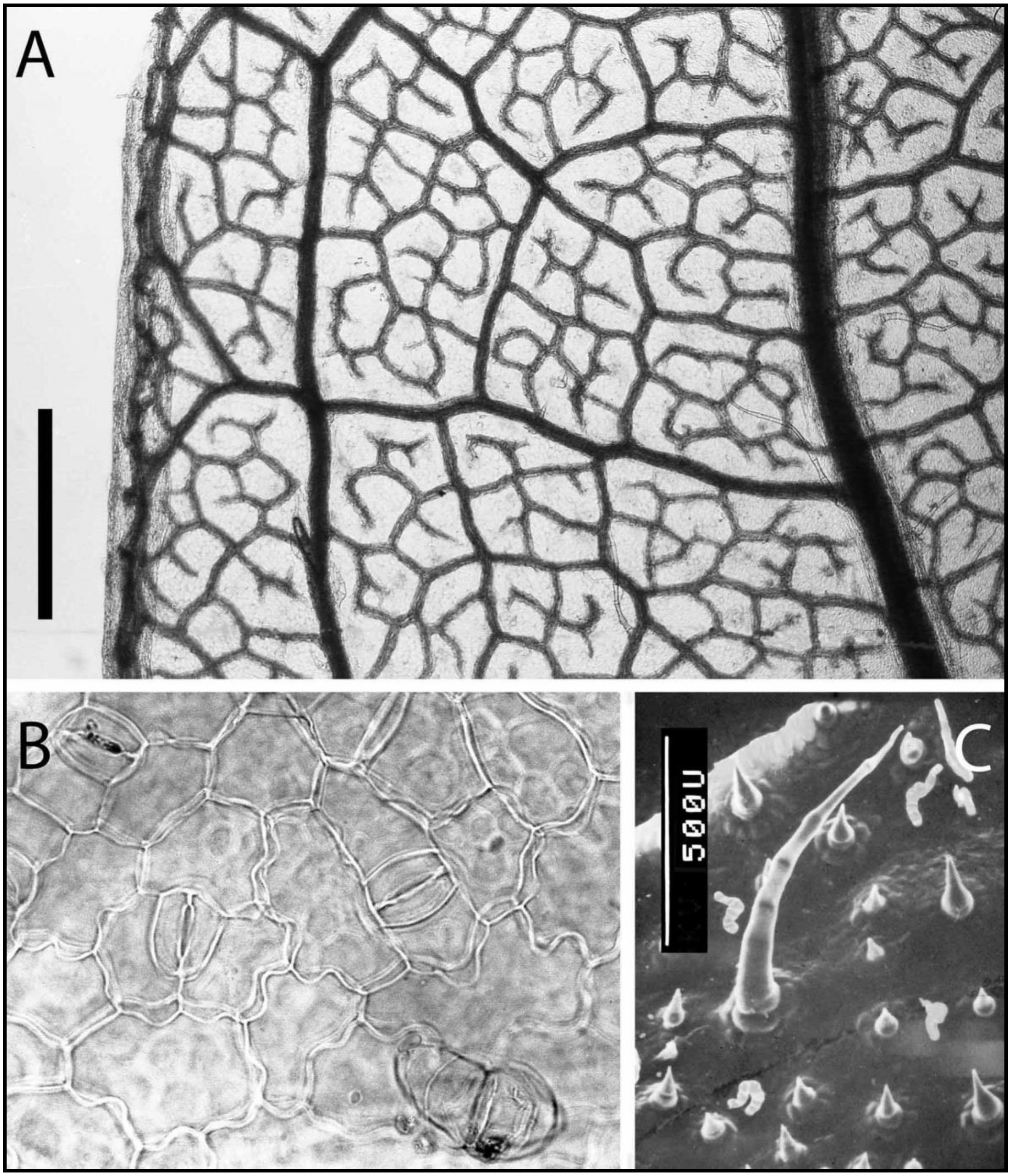


Figure 11. Leaf features of representative Colombian and Venezuelan species of *Calea* L. A. *Calea septuplinervia* Hieron., cleared blade, adaxial surface, showing veinlets with free endings within areoles. B. *Calea prunifolia* Kunth, cleared blade, abaxial surface, in high-contrast showing anomocytic stomatal pattern typical of *Calea*. C. *Calea prunifolia*, adaxial blade surface, in high-contrast showing an elongate uniseriate multicellular apically tapered simple trichome with septations visible, and scattered shorter few-celled conical simple trichomes. (A modified from Pruski 1980a and 1982, *Urbatsch & Pruski 3457A1344*, NY; B × 400, modified from Pruski 1980a, Pruski 1982: fig. 25, *Urbatsch & Pruski 3407A1290*, NY; C reproduced from Pruski 1980b, *Urbatsch & Pruski 3407A1290*, NY). Scale bar A 2.5 mm.

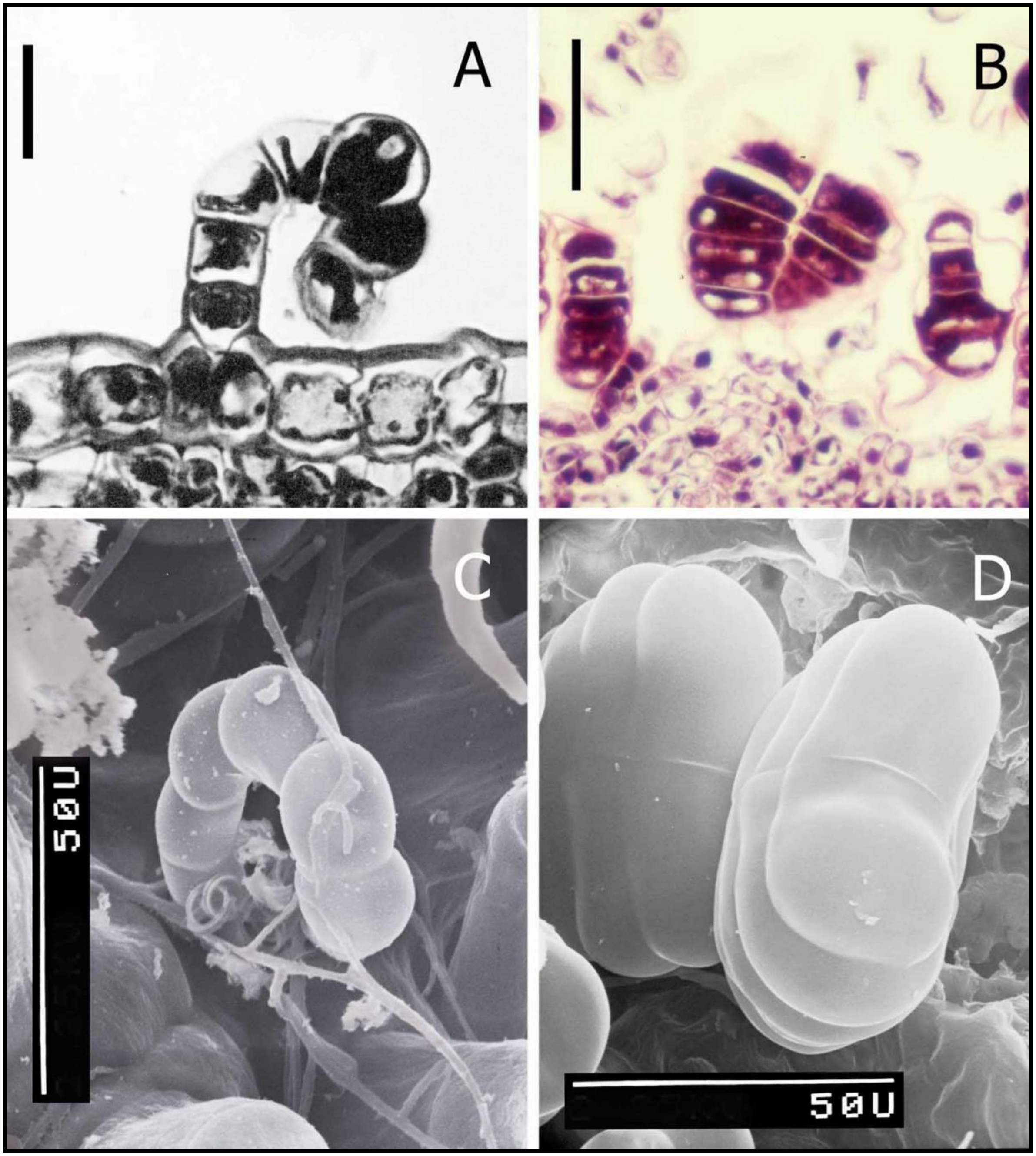


Figure 12. Foliar secretory trichomes of *Calea subcordata* S.F. Blake; A adaxial surface, B–D abaxial surfaces; A–B are longitudinal sections through trichomes, leaves are stained in safranin-toluidine blue, C–D material was critical-point-dried. A, C. Uniseriate 6–7-celled (cells same-sized) moniliform trichomes of the adaxial leaf blade surfaces, septations visible, C also shows scattered fungal hyphae. B, D. Subsessile pluricellular biseriate glandular trichomes of the abaxial leaf blade surface, septations visible within and between the two tiers of cells; this material was critical-point-dried. B. Tangential section, abaxial surface facing upwards, showing (center) both series of cells of a biseriate glandular trichome, partial sections of other glands are seen on the right and the left. D. Two biseriate glandular trichomes, abaxial surface. The typical biseriate glandular trichomes of helianthoids contain volatile sesquiterpene lactones (Hegnauer 1977); but Pruski (2011, 2013) noted that when specimens are field-pressed in EtOH the glands collapse and even their presence is obscured. (Modified from Pruski 1980b and 1982, *Urbatsch & Pruski 3427A1311*, NY, Táchira, Venezuela). Scale bars A 20 µm, B 50 µm.

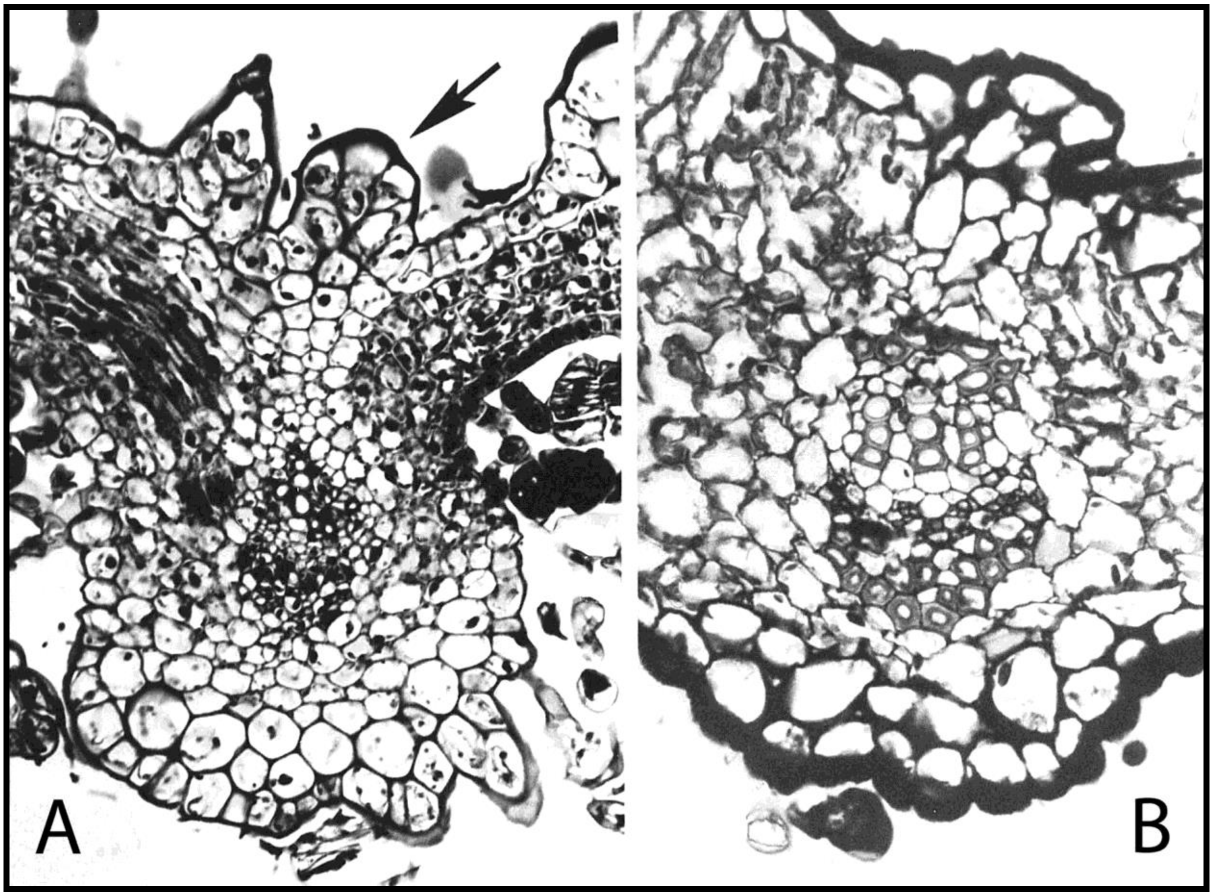


Figure 13. Transverse sections though leaf blade midribs of representative north Andean species of *Calea* L. The two species seen here each have parenchymatous bundle sheaths surrounding the xylem and phloem, and collenchymatous bundle sheath extensions. A. *Calea subcordata* S.F. Blake, showing a very large bundle sheath extension and basal subsidiary cells of an adaxial short conical trichome (arrow); no resin ducts were found associated with the vascular bundles. B. *Calea prunifolia* Kunth, showing a vascular bundles with a moderately large sheath extension with the associated adaxial resin ducts surrounded by regularly arranged parenchyma cells. The bifacial mesophyll of this species is divided into distinct palisade parenchyma and spongy parenchyma layers. (Modified from Pruski 1982; A × 250, *Urbatsch & Pruski 3427A1311*, NY; B × 400, *Urbatsch & Pruski 3407A1290*, NY).

Here, the four non-typical sections of Pruski (1998a) are recognized as the South American endemic genera **Laceanthos** Pruski, **gen. nov.**, *Lemmatium* DC., *Meyeria* DC., and **Podocalea** Pruski, **gen. nov**. The genera *Laceanthos* and *Podocalea* and the two Lessing infragenera—originally described as subgenera by Lessing in 1832—are each heterotypic, and the Lessing subgenera are treated by me simply within taxonomic synonymy. These two new genera—*Laceanthos* and *Podocalea*—are delineated following the Pruski (1998a) circumscriptions of *Calea* sections *Haplocalea* and *Monanthocalea*, respectively, albeit *Podocalea* is less inclusive than was Pruski's earlier more speciose *Calea* sect. *Monanthocalea*. The two resurrected genera—*Lemmatium* and *Meyeria*—more or less include the same species, with only minor additions, that Pruski and Urbatsch (1988) keyed as *Calea* sect. *Lemmatium* and that Pruski (2005) keyed as the *Calea myrtifoli*a group of *Calea* sect. *Meyeria*. Although two more species of *Calea* are newly described here, 67 species are removed from *Calea* reducing by nearly 50% (Pruski and Robinson 2018 recognized about "150" species) and to about 80 the number of species today remaining within the confines of *Calea*.

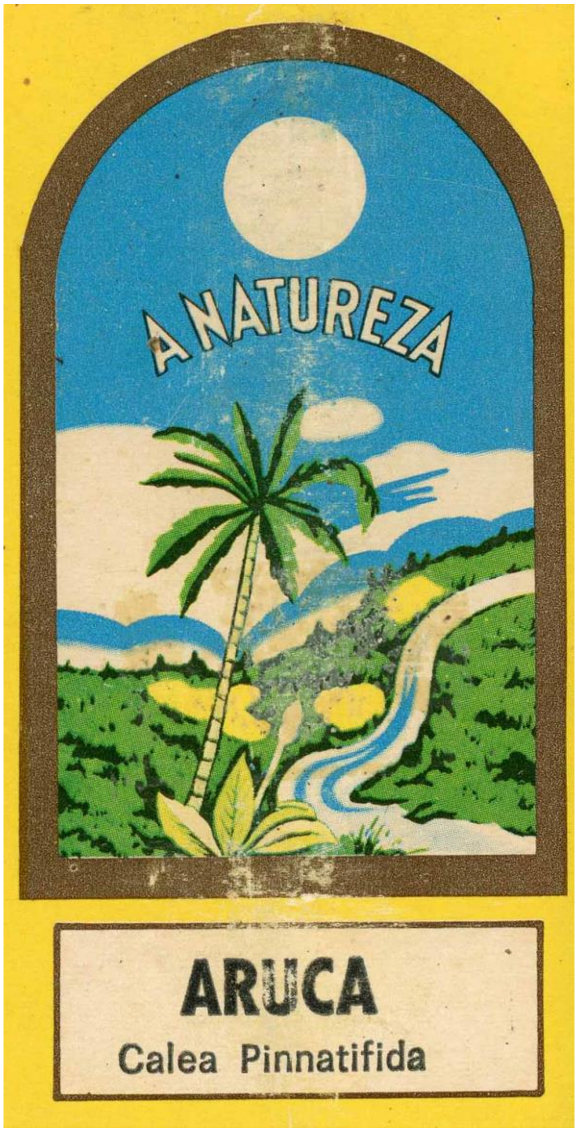


Figure 14. Front of a box that contained a 100 cc bottle of liquid extract of *Calea pinnatifida* (R Br.) Less. (a species called 'aruca'). This aruca extract was purchased in São Paulo, Brazil in 1987, and was sold as a medicinal. *Calea pinnatifida* matches typical elements of *Calea*, except in its often deeply pinnatifid leaves.

Each of the four newly recognized genera, despite some reticulate evolution, approaches monophyly, and I treat each genus as a member of the tribe Neurolaeneae. The Mexican endemic genus *Tonalanthus* is restored, and likewise retained within Neurolaeneae, raising to ten the number of genera I recognize in tribe Neurolaeneae. Additionally, Venezuelan (Pruski 1997) **Tepuipappus** Pruski, **gen. nov.** is newly described from among species earlier loosely referred to what has been called *Calea* sect. *Calea*. *Tepuipappus*, however, does not belong to tribe Neurolaeneae. Rather, *Tepuipappus* is placed in Heliantheae subtr. Verbesininae, where it is most similar to Mexican and Central American *Squamopappus* and *Tetrachyron*. The mostly South American genera here removed from *Calea*, *Tonalanthus* and the mostly Mexican and Central American genera removed by Urbatsch and others, and additional taxa near or once placed in the genus *Calea*, comprise what is called the *Calea* Alliance. This alliance, however, is an informal and loosely knit group of taxa with members now residing in one of three tribes: Heliantheae s. str., Millerieae, or Neurolaeneae). The core of the *Calea* Alliance are the six genera (*Calea*, *Laceanthos*, *Lemmatium*, *Meyeria*, *Podocalea*, and *Tonalanthus*) treated here and positioned in tribe Neurolaeneae.

As circumscribed here, the combined features allowing for recognition of species as *Calea* are being perennials with a chromosome base number of $x = 19$ (Pruski and Urbatsch 1984; Wussow et al. 1985), opposite 3-nerved leaves with an anomocytic stomatal pattern and surfaces often with elongate uniseriate multicellular simple trichomes, moniliform trichomes, and/or biseriate glandular trichomes, paleate clinanthia, conduplicate paleae, ray florets (when present) uniseriate and pistillate, bisexual disk florets, yellow non-setose corollas, single resin ducts with reddish resin along the veins of the disk corolla throats, yellowish anthers, glabrous style trunks, recurved style branches with 2-banded ventro-marginal (adaxial) stigmatic surfaces fertile and discrete to near the apices, usually obtuse style branch apices are papillose, papillose distal portions of the abaxial surfaces of style branches—the *Calea*-style morphological structure; a character similar to that used by Pruski (2021) to define *Chaetacalia* Pruski—isomorphic narrowly obconic-prismatic black cypselae that are not microstriate, asymmetric carpopodia, cypselae (when setose) with twin trichomes (Zwillingshaare of Hess 1938; also known as twin hairs or duplex trichomes) having a parallel pair of elongate subequal longitudinally connate terminal cells appressed to near apices, and a radially arranged pappus of subequal isomorphic basally broadened scales (Figs. 1–13, 20–24, 26–34). Further characteristic features of *Calea*, and also typical of most helianthoids, are anther thecae with shortly sagittate bases usually not surpassing the narrow collars (Figs. 9A, 21C, 23A); anthers with polarized endothecial tissue (Fig. 23C; the most prevalent state in Compositae, Cariaga et al. 2008); spheroidal tricolporate echinate helianthoid pollen (Fig. 9C–D), and blackened cypselae (Fig. 6D–E). The reports of Pruski (1980b, 1982) and Stanski et al. (2013) also show the tricolporate echinate spherical pollen of *Calea*. The helianthoid pollen and carbonized cypselae in *Calea* are especially typical of the tribes of the Heliantheae Alliance, which contains about 1% of the Angiosperms.

Pruski (1980a, 1980b, 1982) reported and provided images of two types of secretory trichomes (for terminology see Fahn 1979 and Ramayya 1962) in *Calea*: similar-cell-sized (cells isodiametric) moniliform trichomes (Figs. 10, 12A, 12C) and multicellular biseriate glandular trichomes (Figs. 10, 12B, 12D). Pruski (1980a, 1980b, 1982) and Camilotti et al. (2014) showed that other foliar trichomes seen in *Calea* include elongate multicellular uniseriate non-glandular apically tapered trichomes (Fig. 11C) and few-celled non-glandular shorter conical trichomes (their presence is basically reflected by many authors describing adaxial leaf blade surfaces as scabrous (Figs. 11C, 13A). These trichomes are similar to some of the trichomes seen in *Encelia* (Ehleringer and Cook 1987).

Cleared leaf blades of *Calea* have veinlets with free endings within areoles and abaxially mostly an anomocytic stomatal pattern (Fig. 11A–B; Pruski 1980a, 1982; Camilotti et al. 2014). Leaf cross-sections show the plants have a uniseriate adaxial epidermis, biconvex midribs, mostly parenchymatous bundle sheaths surrounding the xylem and phloem, and collenchymatous bundle sheath extensions (Figs. 10, 12–13; Pruski 1980a, 1982). Camilotti et al. (2014), Galvan et al. (2005), and Martarello et al. (2015) also reported on the leaf anatomy of *Calea* and Alliance members, but with only the excellent Camilotti et al. (2014) providing images. The report by Martarello et al. (2015) mentioned the leaf anatomy of *Calea hypoleuca* B.L. Rob. & Greenm. from Brazil, where it does not occur; their results are consequently hard to apply. Pruski and Robinson (2018) noted that *C. hypoleuca* is endemic to Mexico. Jana and Mukherjee (2015) studied cypselar anatomy of *Laceanthos cymosus*.

Most of the Caleas reported as medicinals over the years remain positioned taxonomically in *Calea*. For example, *C. zacatechichi* Schltdl. (viz Pruski and Urbatsch 1980) (a taxonomic synonym of *C. ternifolia* Kunth) has long been reported as a component of a mixture that has been reported

(Schultes 1976; Díaz 1979; Emboden 1979; Schultes and Hofmann 1979, 1980) as an auditory hallucinogen. The plant is also used medicinally in Mexico, as is *C. hypoleuca* B.L. Rob. & Greenm. *Calea urticifolia* DC. (Fig. 3D) was cited by Gupta et al. (sin dat.) as used medicinally in Mexico and Panama. *Calea berteriana* DC. (Fig. 4E) and *C. peruviana* (Kunth) Benth. ex S.F. Blake (Figs. 3C, 5 left, 28, 33A–B) have been reported by Pérez-Arbeláez (1956, 1975) and Pruski (1982) as used medicinally in Colombia, as has *C. prunifolia*. Gómez and Gil (2011) studied anti-inflammatory properties of widespread *C. prunifolia* in Colombia. Correa and Bernal (1992) listed *C. glomerata* as a medicinal used in Colombia. Pruski (1997) reported that, in the Lost World of the Guayana Highland, infusions of leaves of *C. divaricata* Benth. are used by Arekuna Amerindians as a cold remedy. Each of the aforementioned species were maintained in *Calea* s. str. by Pruski (1982, 1997) and/or Pruski and Robinson (2018). *Calea montana* (Fig. 4D) was reported by Valadeau et al. (2009) as used medicinally in east-central Peru. *Calea pinnatifida* (R Br.) Less. (Fig. 14; Lima et al. 2015) and *C. serrata* Less. (Camilotti et al. 2014) both remain positioned within *Calea* and are both used medicinally in southern Brazil. *Podocalea uniflora* (Figs. 81–82) is used medicinally in southeastern Brazil, where is known as *arnica* (Ramos et al. 2016), and before today had always been placed in *Calea*. Ferraz et al. (2009), however, said the plant "is not used in popular medicine." Reviews of some Caleas used as medicinals, and especially of the many phytochemical studies published for plants under the generic name *Calea* are found in Seaman (1982), Amaral et al. (2017), and Lima et al. (2018).

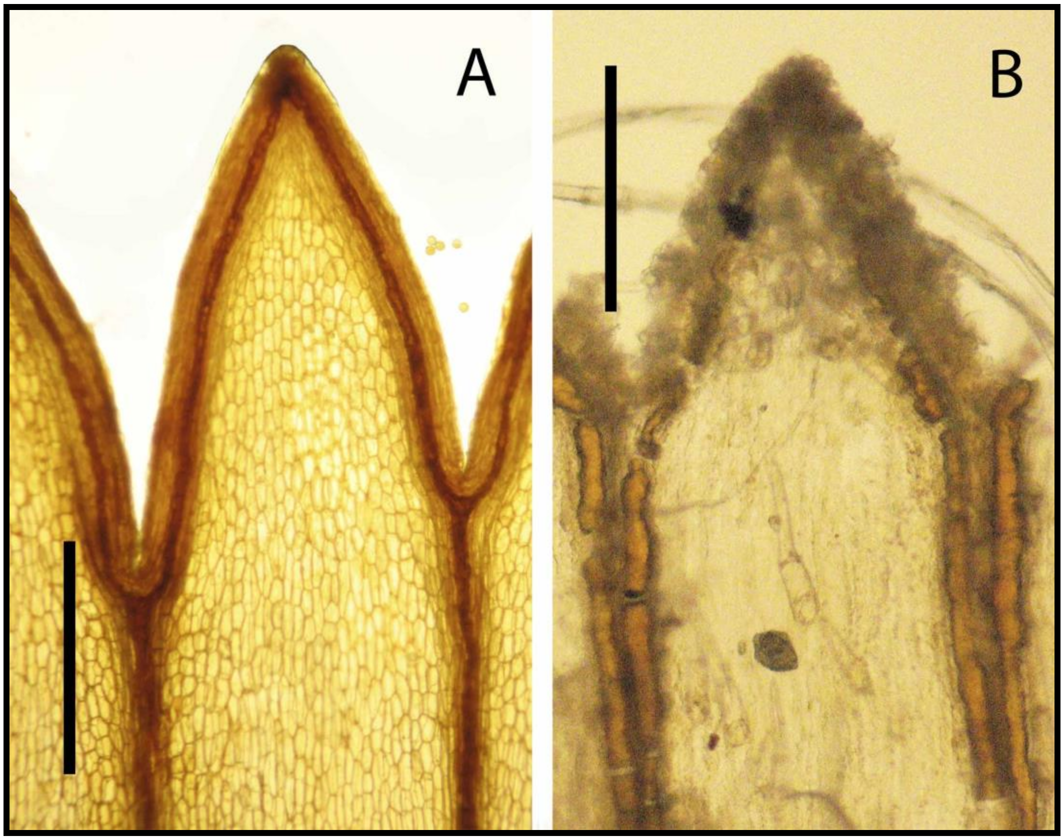


Figure 15. Resin ducts of helianthoid disk corolla lobes and throats, longitudinally section, abaxial view, lobes with submarginal ducts, and throats with two of the five main veins and associated resin ducts. A. *Podocalea cuneifolia* (DC.) Pruski (Neurolaeneae), showing single reddish-brown resin duct along the veins of disk corolla throat. B. *Galinsoga quadriradiata* R. & P. (Millerieae), showing pairs of brownish-yellow resin ducts bordering each vein in the disk corolla throat. (A *Hatschbach 44346*, MBM; B *Pruski & Ortiz 4757*, MO). Scale bars A 0.5 mm, B 0.2 mm.

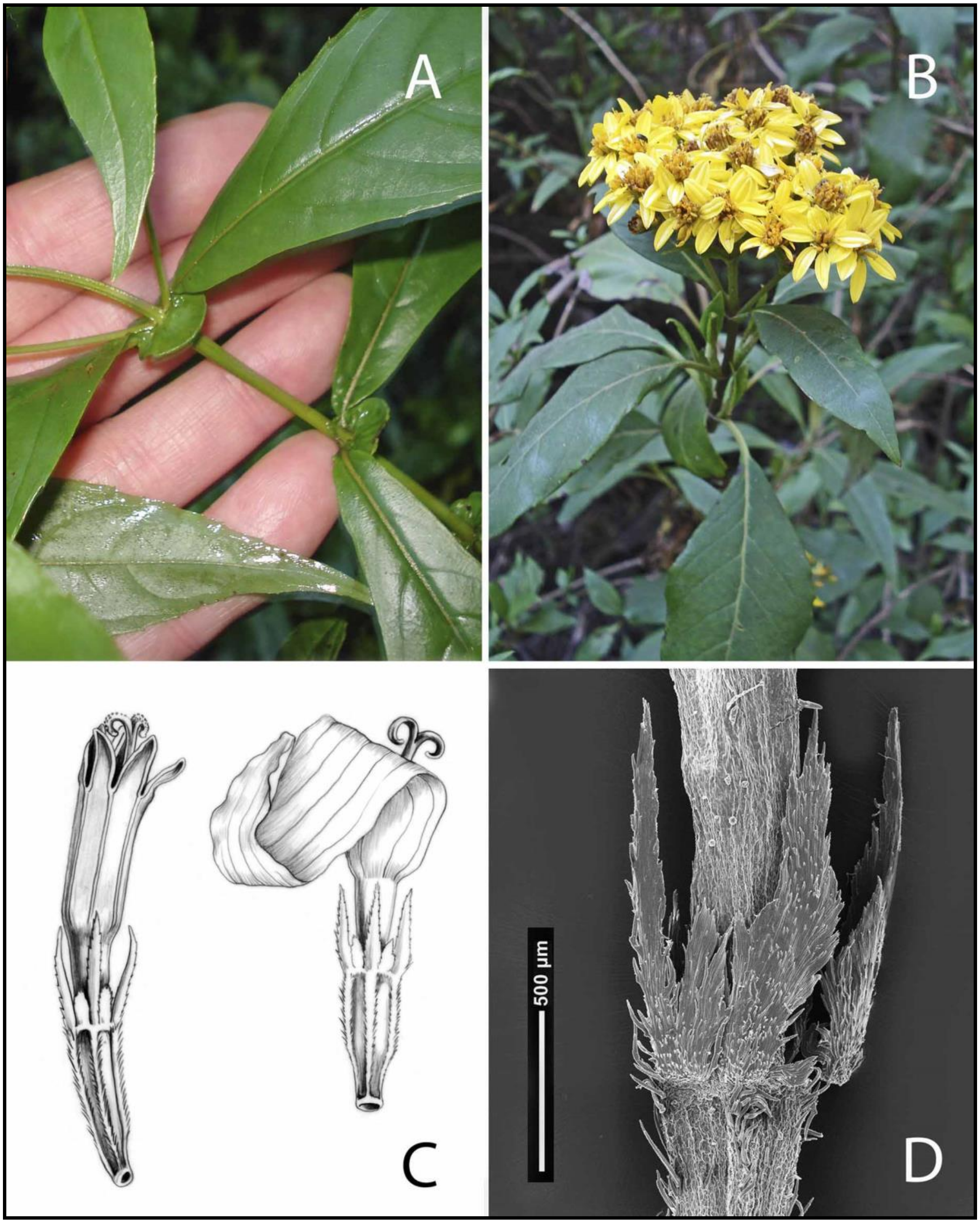


Figure 16. Features of *Tetrachyron* Schltdl. (a former synonym of *Calea*), Heliantheae subtr. Verbesininae. A. *Tetrachyron manicatum* Schltdl., generitype, close-up of stem with opposite pseudostipulate leaves. B. *Tetrachyron orizabense* (Klatt) Wussow & Urbatsch, flowering stem. C. *Tetrachyron orizabense*, disk floret (left) and ray floret (right). D. *Tetrachyron orizabense*, close-up of disk cypsela pappus of four subequal scales on angles and intermediate shorter squamellae. (A *Pruski et al. 4109*, Veracruz, Mexico; B *Pruski & Ortiz 4265*, Todos Santos, Guatemala; C × 12, drawn by Alice Tangerini, reproduced from Robinson 1981: figs. 142–143; D *Molina 14533*, NY).

Figure 17. Feature of *Alloispermum* Willd. (a former synonym of *Calea*), tribe Millerieae. A. *Alloispermum integrifolium* (DC.) H. Rob., flowering stem showing opposite leaves and white ray corollas; this a white-radiate-capitulate sprawling weak-stemmed plant typical of the genus, and is the most common *Alloispermum* species in Mesoamerica. B. *Alloispermum caracasanum* (Kunth) H. Rob., epappose ray floret with setose corolla tube (left), disk cypsela with a pappus of scales (right). C. *Alloispermum integrifolium* (DC.) H. Rob., disk cypsela showing pappus scales and carpopodium moderately asymmetric. (A, C *Pruski et al. 4210*, MO, Chiapas, Mexico; B × 12, drawn by Alice Tangerini, reproduced from Robinson 1981: figs. 148–149).

In their landmark treatment, Bentham and Hooker (1873) lumped many genera to synonymy of *Calea*, *Eupatorium*, and *Vernonia*. However, in the Neotropics in the past few decades both *Eupatorium* and *Vernonia* have been more narrowly delimited (e.g., King and Robinson 1987; Robinson 1999) and many species and species groups have been removed from them and placed in new or resurrected segregate genera. Elsewhere, in Brazil-centered plants several species groups have also been treated within segregate genera—e.g., from works most familiar to me, in Astereae by Nesom (1994a, 1994b, 1994c), and Sancho et al. (2006, 2010); and in Mutisioids by Pruski (1991) and Katinas et al. (2008).

Figure 18. *Galinsoga quadriradiata* R. & P., tribe Millerieae. A. Distal portion of stem showing opposite leaves, capitulum in mature fruit showing pappus of scales (center, above). B. Cypsela showing microstriate carbonized surface and pappus of scales. (A *Pruski & Ortiz 4757*; B × 12, drawn by Alice Tangerini, reproduced from Robinson 1981: fig. 145).

In some Brazil-centered helianthoids, however, some noteworthy recent lumping has been proposed: for example, Schilling and Panero (2011) placed most of *Viguiera* Kunth sensu Blake into *Aldama* La Llave, and Turner (1992) referred sterile-rayed *Aspilia* Thouars to fertile-rayed *Wedelia* Jacq. The transfers of the Central American *Zexmenias* (except for two) to *Wedelia* by Strother (1991) is followed. However, reduction of *Aspilia* to *Wedelia* and wholesale species transfers by Turner (1992) of Aspilias to *Wedelia* is not followed.

For example, from among plants treated mostly as *Wedelia* s. lat. by Turner (1992), the sterile-rayed Aspilioid segregate genera *Elaphandra* Strother and *Tuberculocarpus* Pruski were described by Strother (1991) and Pruski (1996), respectively. *Elaphandra* and *Tuberculocarpus* were maintained by Robinson (1992, 2006), Panero (2007), Pruski (1997, 2001, 2002), and Pruski and Robinson (2018). Additionally, a narrower concept of *Wedelia* used by Strother (1991) and Pruski (1996), who recognized pantropical plants in fertile-rayed *Sphagneticola* as generically distinct from *Wedelia*, for example, has also been adopted. As an aside, I should mention that the common name of *Sphagneticola trilobata* (L.) Pruski remains Wedelia and the plant has the dubious distinction of being listed by the International Union for Conservation of Nature (IUCN, iucngisd.org/gisd/pdf/100English.pdf) as one of the 100 World's Worst Invasive Alien Plant and Animal Species). In any event, Dra. Graziela Barroso (pers. comm. 1987) told me that *Aspilia*, *Calea*, and *Wedelia* are helianthoids equally widespread in Brazil, but a quick glance at the black anthers, aristate pappus, and often setose corollas of *Aspilia* and *Wedelia* helps distinguish them from *Calea*, which has non-setose corollas, yellowish-anthers, and radially symmetric pappus of scales. Here, certain elements are removed from *Calea* based on differences in base chromosome number, habit, capitulescence characters, palea shape and relative lengths, cypselae characters, carpopodial shape, pappus characters, and/or twin trichomes characters, but nevertheless most *Calea* Alliance members remain characterized as in Barroso (1986). However, *Podocalea* becomes the name of the group of former Caleas hat have been most frequently confused with *Aspilia*.

Not only have the component species of *Calea* varied, but the suprageneric placement of *Calea* has also varied widely. *Calea* was treated as a member of Heliantheae subtr. Galinsoginae by Bentham and Hooker (1873), Baker (1884), Hoffmann (1894), and Stuessy (1977), but by Robinson (1981) within Heliantheae subtr. Neurolaeninae Stuessy, B.L. Turner & A.M. Powell. *Alloispermum* and *Galinsoga* (Figs. 17–18) were each treated as members of Heliantheae subtr. Galinsoginae by Robinson (1981), and indeed the pappus of scales of these two genera are superficially *Calea*-like. In the same paper, however, Robinson (1981) noted that cypselae of *Calea* lack microstriatulations ("interruptions in the carbonized layer" to quote Robinson), whereas *Alloispermum* and *Galinsoga* differ from *Calea* by having cypselae microstriate (Fig. 18B). Also, Robinson (1981) noted in *Calea* only a single reddish resin duct associated with each corolla throat vein (Fig. 15A), differing from *Alloispermum* and *Galinsoga*, which have distinctly paired brownish-yellow resin ducts along each of the five veins of the disk corolla throats (Fig. 15B). Based on these microcharacters, Robinson (1981) excluded *Calea* from subtr. Galinsoginae, and placed the genus alongside *Neurolaena* in Heliantheae subtr. Neurolaeninae. *Neurolaena* is *Calea*-like by having only a single resin ducts superimposed over each disk corolla throat vein, and also by lacking microstriatulations in their cypselae. I follow Panero (2007), who placed *Calea* in tribe Neurolaeneae and simultaneously treated *Alloispermum*, *Galinsoga*, *Schistocarpha*, and allies in the resurrected tribe Millerieae.

It should be noted, however, that limits of, and elements treated as either tribe Neurolaeneae or subtribe Neurolaeninae have varied; and that in gross morphology none the five genera of Neurolaeneae sensu Panero (2007) actually closely resemble one another (viz, the alternate leaves of *Neurolaena* in Fig. 19A, D and the pluriseriate rays in Fig. 19E of the strange aquatic *Enydra*). Rydberg (1927) described Neurolaeneae as containing only *Neurolaena* (Fig. 19A–D) and *Schistocarpha*, but not *Calea*. Stuessy (1977) validated subtr. Neurolaeninae and included nine genera, but not *Calea*. Robinson (1981) excluded from subtr. Neurolaeninae seven of Stuessy's nine component genera, and placed *Calea* and *Tetrachyron* (Fig. 16) within Heliantheae subtr. Neurolaeninae. Panero (2007) treated *Tetrachyron* within Heliantheae subtr. Verbesininae and placed five genera total within Neurolaeneae. The five genera Jose Panero treated as comprising Neurolaeneae were American *Calea*, *Enydra* (Fig. 19E), *Greenmaniella*, *Heptanthus*, and of course neotropical *Neurolaena* (Fig. 19A–D), but earlier Baker (1884) placed *Enydra* in Heliantheae subtr. Verbesininae as (Verbesineae).

Generic placement of nearly all non-typical elements called *Calea* in South America has previously not been addressed. Pruski (1984, 1998a, 2005, 2013) and Urbatsch et al. (1986) recognized *Calea* sect. *Lemmatium* (DC.) Benth. & Hook. f. and *Calea* sect. *Meyeria* (DC.) Benth. & Hook. f. Pruski (1997) treated *Lemmatium* DC. and *Meyeria* DC. in synonymy of *Calea*, whereas Pruski and Robinson (2018) specifically removed the two genera from synonymy of *Calea*. Here, as in Pruski and Robinson (2018), each Brazil-centered *Lemmatium* and *Meyeria* are excluded from synonymy of *Calea*, being restored and recognized as generically distinct from each other and from *Calea*. The genus *Meyeria*, however, is at present circumscribed as including only the 18 species (albeit some of these are clearly segregates) centering about *C. myrtifolia* (DC.) Baker that were largely keyed by Pruski (2005). Additionally, *Laceanthos*, *Podocalea*, and *Tepuipappus* are recognized here as new genera and include more than two dozen species excluded from *Calea*. The structure of the present paper is similar to that of the seven genera of Senecioneae as treated by Pruski (2021): the seven generic portions of this helianthoid manuscript each could be dissected into independent papers, but most taxa treated here have a common bond as former Caleas, and it seems most pragmatic for them to be treated jointly, as done herewith.

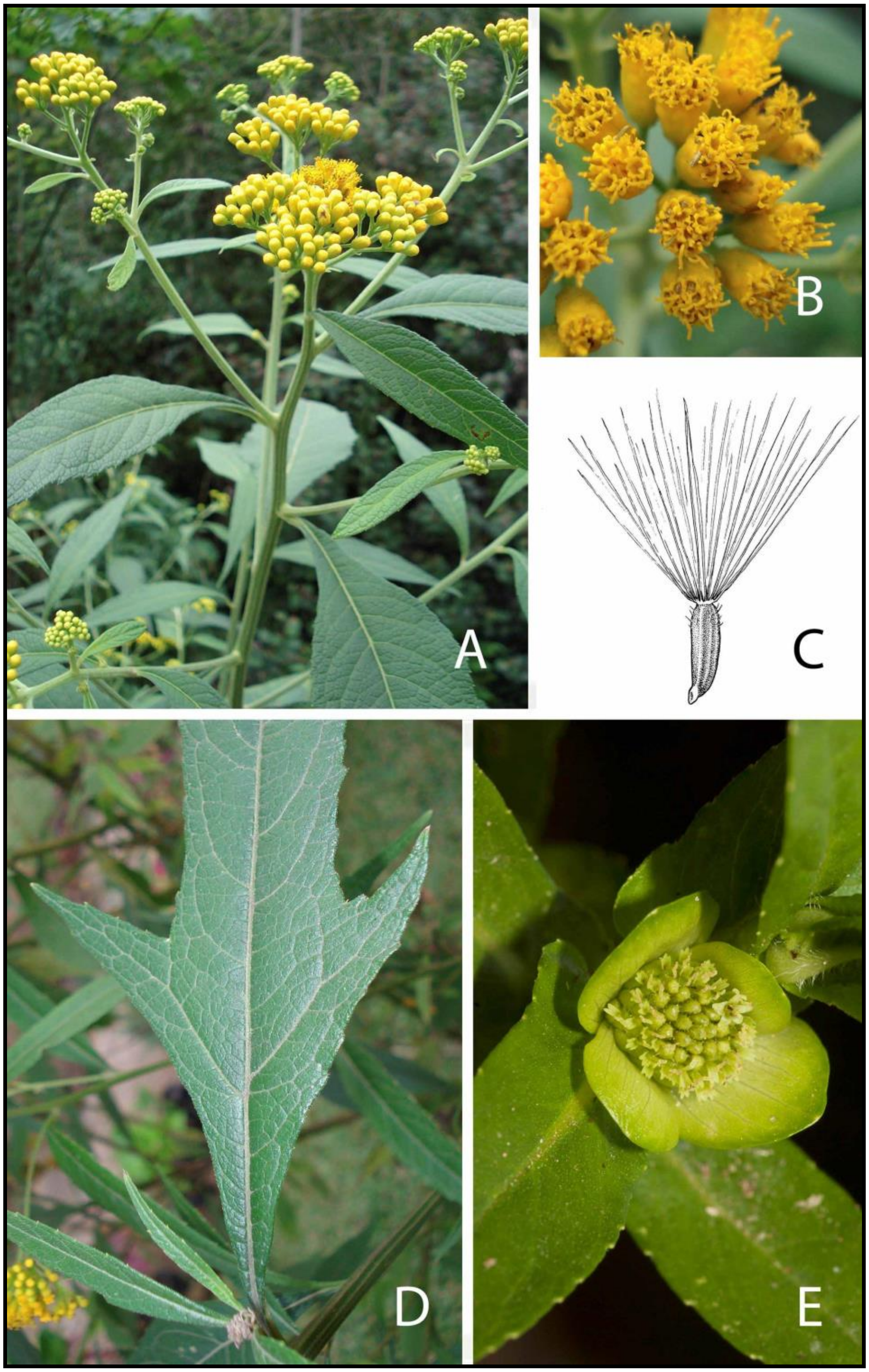


Figure 19. Representatives of tribe Neurolaeneae. A–D. *Neurolaena lobata* (L.) Cass. A. Flowering branch showing the alternate leaves. B. Close-up of the discoid capitula at anthesis. C. Cypsela, showing the slightly asymmetric carpopodium and pappus of many bristles. D. Lobed mid-stem leaf blade. E. *Enydra fluctuans* Lour., indistinctly radiate capitulum showing the 2-3-seriate ray florets and the mostly budding disk florets. (A–B, D *Pruski & Vega 4479.1*; C body 1.5 mm long, drawn by Bobbi Angell, reproduced from Funk and Pruski 1996: fig. 40E; E *Nee 57329*).

The specific-level nomenclatural innovations included in the six new or restored genera recognized here are validated preliminary to keyed synopses of each of them, and more immediately so that these new names may be used in my microcharacter paper that addresses generic and tribal affinities of *Calea* s. lat. The taxonomy of remaining species that Pruski (1998a) treated as *Calea* sect. *Meyeria* are to be given in a following companion paper by the author. Additionally, two new Andean species of *Calea*, **Calea juninensis** Pruski, **sp. nov.** and **Calea santanderensis** Pruski, **sp. nov.**, are described herein preliminary to my treatment of the Andean and northern South America species, and the characters of these two new species highlight salient features then and now used to circumscribe *Calea* in the strict sense.

ANATOMICAL AND SEM METHODS

The wet slide mounts were viewed on an Olympus compound microscope and photographed with an ocular-mount Nikon E5700 camera using a MM99 adapter S/N: 1815 (Martin Microscope Company, Easley, South Carolina) or with a top-mount Canon A640 camera. Lower magnification images were viewed in a dissection microscope, and were photographed with either a hand-held Sony Cyber-shot DSC W-50 with its 15 mm diameter lens positioned over the 25 mm diameter ocular, an ocular-mount Nikon E5700 camera using a MM99 adapter, or a top-mount Canon A640 camera. Leaf clearings and leaf sections were prepared and photographed as in Pruski (1980a, 1982), first materials were dehydrated in acidified "DMP" (2,2-dimethoxypropane), following procedures employed by Muller and Jacks (1975), and Postek and Tucker (1976). Some specimens were embedded in "Paraplast Plus" (Sherwood Medical Industries, St. Louis, Missouri), cut with a Spencer 820 rotary microtome to 7 µm thick, and stained in either hematoxylin, toluidine blue or safranin-fast green. Other specimens were embedded in "JB-4" methacrylate resin or in Araldite-Epon epoxy resin. Sections 2-4 µm thick were cut with a Sorvall JB-4 rotary microtome equipped with a glass knife and stained in toluidine blue (Sakai 1973). Dried leaves were cleared in 5–10% NaOH and in chloral hydrate (Shobe and Lersten 1967). Photomicrographs of sections were taken with a Leitz Orthoplan microscope and Orthomat camera.

SEM mounts were in large measure micrographed in one of two labs, in Baton Rouge on the Hitachi or in St. Louis on a JEOL. Scanning Electron Microscope observations on the Hitachi followed methods outlined in Pruski (1980b, 1982), and were made on fixed material and from dried or rehydrated herbarium specimens. Cypselae were air dried. Pollen was obtained from unopened anthers, acetolysed using the method of Erdtman (1960), and air dried. All other materials were critical point dried with a Denton pop-1 Critical Point Drier. All materials were mounted on aluminum stubs and sputter-coated with ca. 200 Å of AuPd in a Hummer Sputter Coater. The micrographs were taken on a Hitachi S-500 operating at 25 kV accelerating voltage. The micrographs taken on the JEOL SEM were first sputter-coated with Au/Pd on a Denton Desk V Cold Sputter Coater. The sputtered coated mounts were then micrographed on a JEOL NeoScope CM-5000 scanning electron microscope using a low-resolution 10 kV accelerating voltage. These methods used for the JEOL SEM are basically the same methods I used in Cariaga et al. (2008) and Pruski (2012a, 2012b).

1. TWO NEW SPECIES OF *CALEA*.

Field, herbarium, laboratory, and monographic studies have resulted in the detection of two new species of *Calea* (Neurolaeneae) described herein. Each new species is relatively small-capitulate, has recurved style branches, clinanthia with conduplicate paleae, obconic-prismatic cypselae with twin trichome apices appressed, asymmetric carpopodia, a pappus of many radially arranged subequal isomorphic basally broadened scales elongate scales, and each of the two new species match typical elements of *Calea*. In turn, the two new species contrast with characters of the mostly Mexican previously excluded genera and the six genera newly recognized herein.

CALEA JUNINENSIS Pruski, **sp. nov. TYPE. PERU. Junín.** Distr Tarma, near Catarata de San Pedro, about 2.5 km SW of Huacapistana in Río Palca valley, steep dry hillsides above road near bee hives, ca. 34.4 km NW of Plaza de Armas de Tarma on road to San Ramón, about 11° 14' 38" S, 75° 31' 27" W, 1950–2150 m, 7 Jul 2008, *John Pruski, Rosa Ortiz, Gino Castillo & Rigoberto Rivera 4433* (holotype: MO-6406819; isotypes: F, K (to be sent), NY, HOXA, UC, US, USM). Figures 20–26.

Fruticosa 0.4–1.5(–3) m alta; caules hirsutuli vel piloso-tomentosi; folia simplicia opposita brevipetiolata, lamina (1–)2–7.5 × (0.8–)1.5–5.5 cm ovato-lanceolata vel late ovata chartacea triplinervia basi saepius obtusa subtus leviter tomentosa vel tomentosa necnon glandulosa, petiolo 0.2–0.9 cm longo; capitulescentia terminalis cymosa vel corymbiformis; pedunculi 0.7–2.1 cm longi; capitula brevi-radiata 13–20 mm longa; involucrum 9–15 × 7–15 mm campanulatum vel turbinatum; phyllaria saepius 20–22 imbricata graduata 4–7-seriata, externa triangulari-lanceolata (oblonga) herbacea, interna 8–10 × 2–3.5 mm lanceolato-ovata scariosa; clinanthium paleaceum 3–5(–10) × 1–2.4(–4) mm conico-clavatum; paleae 4.5–7.5 × 1.3–3 mm lanceolatae vel elliptico-lanceolatae; flosculi radii 3–5(–7) pistillati, corollis 4.5–8 mm longis luteolis glabris, limbo 3.5–4.5 mm longo; flosculi disci 30–85 hermaphroditi, corollis (3.5–)5.5–8.3 mm longis infundibuliformo-campanulatis luteolis glabris; cypselae (2–)–2.5–3 mm longae setosae; pappi squamae 18–23, 4–6 mm longae lineari-lanceolatae.

Shrubs 0.4–1.5(–3) m tall, uncommon, moderately opposite-branched distally; stems erect to ascending or arching, loosely to moderately leafy distally, hexagonal-striate in distal few internodes, becoming weakly so in proximal internodes, drying brown, hirsutulous to pilose-tomentose, trichomes mostly 0.2–0.6+ mm long, distal leaves often slightly longer than internodes. **Leaves** simple, opposite, short-petiolate; blade (1–)2–7.5 × (0.8–)1.5–5.5 cm, mostly ovate-lanceolate to broadly ovate or sometimes triangular-ovate, broadest in basal third, stiff-chartaceous, moderately 3-nerved from above base but with a more-proximal thinner arching secondary vein usually present on each side, usually with about 4–7 main secondary veins on each side of the midrib, secondaries narrowing distally and looping submarginally, secondary and tertiary veins pale brown, base usually obtuse (broadly acute to nearly rounded), margins few-serrulate-crenulate, often slightly revolute especially when dried, apex broadly acute to obtuse, surfaces somewhat discolorous, adaxial surface nearly smooth to weakly rugulose, antrorse-scabrous, trichomes mostly 0.2–0.3 mm long, uniseriate, abaxial surface loosely tomentose to tomentose but secondary veins not obscured by tomentum, trichomes mostly 0.3–0.5+ mm long, uniseriate, also subsessile-biseriate-glandular abaxially, glands visible or sometimes obscured by tomentum; petiole 0.2–0.9 cm long, hirsute but the flat adaxial surface usually less so or with trichomes nearly appressed. **Capitulescence** terminal, cymose to corymbiform, mostly 9–20+-capitulate, on several distal branchlets, flowering branchlet tips each usually 3–5-capitulate, capitula pedunculate; peduncles 0.7–2.1 cm long, hirsutulous to pilose-tomentose. **Capitula** short-radiate (appearing disciform or discoid), 13–20 mm long, campanulate often pressing turbinate, mostly 34–90-flowered; florets not well-exserted from involucre; involucre 9–15 × 7–15 mm, campanulate often pressing turbinate; phyllaries mostly 20–22, imbricate, graduate (rarely weekly so), 4–7-seriate, appressed; outer few phyllaries 3–3.5(–9) × ca. 1.5(–4.5) mm, triangular-lanceolate (rarely oblong), mostly herbaceous or at least herbaceously tipped, venation not apparent, hirsutulous to pilose-tomentose, usually noticeably shorter than the inner, quickly but evenly graduating into the middle and inner phyllaries, outer few phyllaries rarely longer than next inner series; mid-phyllaries broadly ovate, much broader than innermost series; inner phyllaries 8–10 × 2–3.5 mm, lanceolate-ovate, scarious, somewhat hyaline-membranous distally, yellowish or sometimes purple-tinged, several-striate, glabrous, apex mostly obtuse becoming lacerate; clinanthium paleate, 3–5(–10) × 1–2.4(–4) mm, conical-clavate, the inner phyllaries inserted near the mid-point of the clinanthium and ca. 2(–6) mm distal to the outer phyllary insertion zone; paleae conduplicate, 4.5–7.5 × 1.3–3 mm, lanceolate to elliptic-lanceolate, scarious, pale yellow, ca. 5-striate, distally usually trifid. **Ray florets** 3–5(–7), pistillate (sometimes with a single staminode ca. 1

mm long consisting of a pale-colored apically tapered filament and no theca), often maturing after onset of anthesis of disk florets and thereby often overlooked (similar delayed non-acropetal maturation of outer florets is characteristic of *Chaetacalia* Pruski, as mentioned by Pruski 2021); corolla weakly exserted from involucre, 4.5–8 mm long, yellow, glabrous, often collected when limb is in-rolled (and thereby corolla moderately resembling a longitudinally sectioned disk corolla), tube 1.5–3.5 mm long, limb (lamina and lobes) 3–4.5 mm long, narrowly oblong, 3-lobed, limb adaxial surface cells flat but sinuous-walled, no cuticular pattern seen, lobes 0.5–1.8 mm long, limb lamina 4(–7)-nerved, the central two nerves of lamina diverging at base of each side of medial lobe with each lobe thus having paired submarginal main nerves, lamina also often with three smaller intercalary resin ducts visible into the middle of each lobe to near apex, each lobe thus appearing 2–3-nerved, limb abaxial surface eglandular and glabrous; ovary long-pappose; ray style ca. 4–5 mm long, about as long as limb of immature corolla and about half as long as fully elongated limb, style not at all well-exserted, branches ca. 1 mm long. **Disk florets** mostly 30–85, bisexual; corolla (3.5–)5.5–8.3 mm long, funnelform-campanulate, yellow, glabrous, tube (1–)2–3 mm long, basally enlarged where surrounding stylopodium and nectary, usually slightly shorter than limb, throat (1.5–)2.5–4 mm long, abruptly broader than tube, lobes 1–1.3 mm long, lanceolate, sometimes unequal, shorter than the throat, ascending; anthers 1.5–2.5 mm long, only slightly exserted with distal parts of filaments held well within throat, endothecial tissue polarized, appendage typically glandular, basal spur shorter than collar; stylopodium 0.4–0.5 mm long, broadened, free from the annular nectary on short stipe, style branches recurved, 0.9–1.2 mm long, apex rounded; nectary ca. 0.3 mm long, annular. **Cypselae** (2–)–2.5–3 mm long, narrowly obconic-subprismatic, black, distally setose to weakly so, eglandular, twin trichomes 0.1–0.15 mm long, never approaching width of cypsela body, the twin elongate subequal terminal cells apices appressed, carpopodium asymmetric; pappus scales 18–23, elongate, 4–6 mm long, linear-lanceolate, scabridulous, about twice as long as cypselae, about 2/3 as long as to nearly as long as disk corollas, usually reaching to about middle of corolla lobes, apex long-attenuate. Chromosome number unknown.

Paratypes. **PERU.** **Junín.** Prov. Jauja, Monobamba, [ca. 11° 25' 18" S, 75° 15' 04" W"], 1575 m, 1 May 2009 *Beltrán 6561* (USM); Along road between Tarma and San Ramón, 34.3 km NE of main plaza in Tarma, rocky slopes above road, 11° 13' 30" S, 75° 35' 00" W, 2400 m, 31 Mar 1984, *Croat 57689* (F, MO, NY, US); Prov. Tarma, Chuquischunca, 2 km arriba de Huacapistana, entre Tarma y San Ramón, selva subtropical, 2000–2400 m, 24 Jan 1946, *Ferreyra 455* (MO, NY, USM); in decliv. angust. fl. Chanchamayo, inter Huacapistana et Matichacra, s. elev., 21 Jan 1927, *Juzepczuk 10299* (LE-2); Huacapistana, thickets and open woods, 1800–2400 m, 5–8 Jun 1929, *Killip & Smith 24215* (F, GH, NY, US); Steep dry hillside above Huacapistana in Río Palca valley, ca. 36 km NE of the Plaza de Armas de Tarma on road to San Ramón, about 11° 14' S, 75° 31' W, 1900–2100 m, 7 Jul 2008, *Pruski, Ortiz, Castillo & Rivera 4434* (HOXA, USM; in the third week of June 2022 my manuscript and typification notes were compromised and became unsorted for me by someone after-hours, forestalling the present reconstructed text, also even though marked *Pruski, sp. nov. ined.* duplicates of *Pruski et al. 4434* were compromised and intermingled with an unmounted duplicate of *Pruski et al. 4433*, I have yet to correctly resort these sheets, thus a duplicate of *4434* has yet be deposited and mounted for MO, and similarly intended exchange sheets cannot yet be distributed); Prov. Jauja, Monobamba, 11° 23' 33" S, 75° 19' 59" W, 1678 m, 18 May 2021, *Vásquez, Rojas & Pinche 45720* (HOXA, MO, USM); Prov. Jauja, valle del río de Comas, monte bajo, compuesto de arbustos, 2500 m, 21 Apr 1913, *Weberbauer 6606* (MO, MOL-3, US-2; this collection has unusually large capitula with elongated clinanthia); Utcuyacu, sin. elev., 1948, *Woytkowski 468* (herbario del Colegio Salesiano n.v., US; this collection numbered *468* from Utcuyacu may be a differently numbered duplicate of *35468*, or may be an entirely different collection from similarly numbered and similarly early-flowering *35468* from nearby Agua Dulce); Prov. Tarma, Agua Dulce, 2400 m, 14 Mar 1948, *Woytkowski 35468* (F, G, MO, USM). **Pasco**. Distr. Oxapampa, Tsachopen, sector Gramazú, Cerro Picaflor, bordando el camino, 10° 31' S, 75° 27' W, 1726 m, "06/03" 2007, *Valadeau CV109* (USM; I cannot confirm the locality of this collection; Céline Valadeau is known from work in both Pasco and Junín, e.g., Valadeau et al. 2009, and Bull. Inst. Français Étud. Andines 47: 313–333. 2018, her collection is labeled, and the given coordinates plot, as from near the *Vasquez et al. 49697* locality in Oxapampa, Pasco, albeit I am familiar only with the Cerro Picaflor that is about 60 kms SW of Oxapampa and in the Department of Junín); Distr. Chontabamba, ecolodge Ulcumano, bosque achaparrado muy húmedo y en borde de quebrada, suelo de roca de arenisca, 10° 38' 08" S, 75° 25' 37" W, 2244 m, 15 May 2021, *Vásquez, Rojas & Pinche 45697* (HOXA).

Figure 20. Type collection of *Calea juninensis* Pruski. (*Pruski et al. 4433*, photograph taken by Gina Castillo).

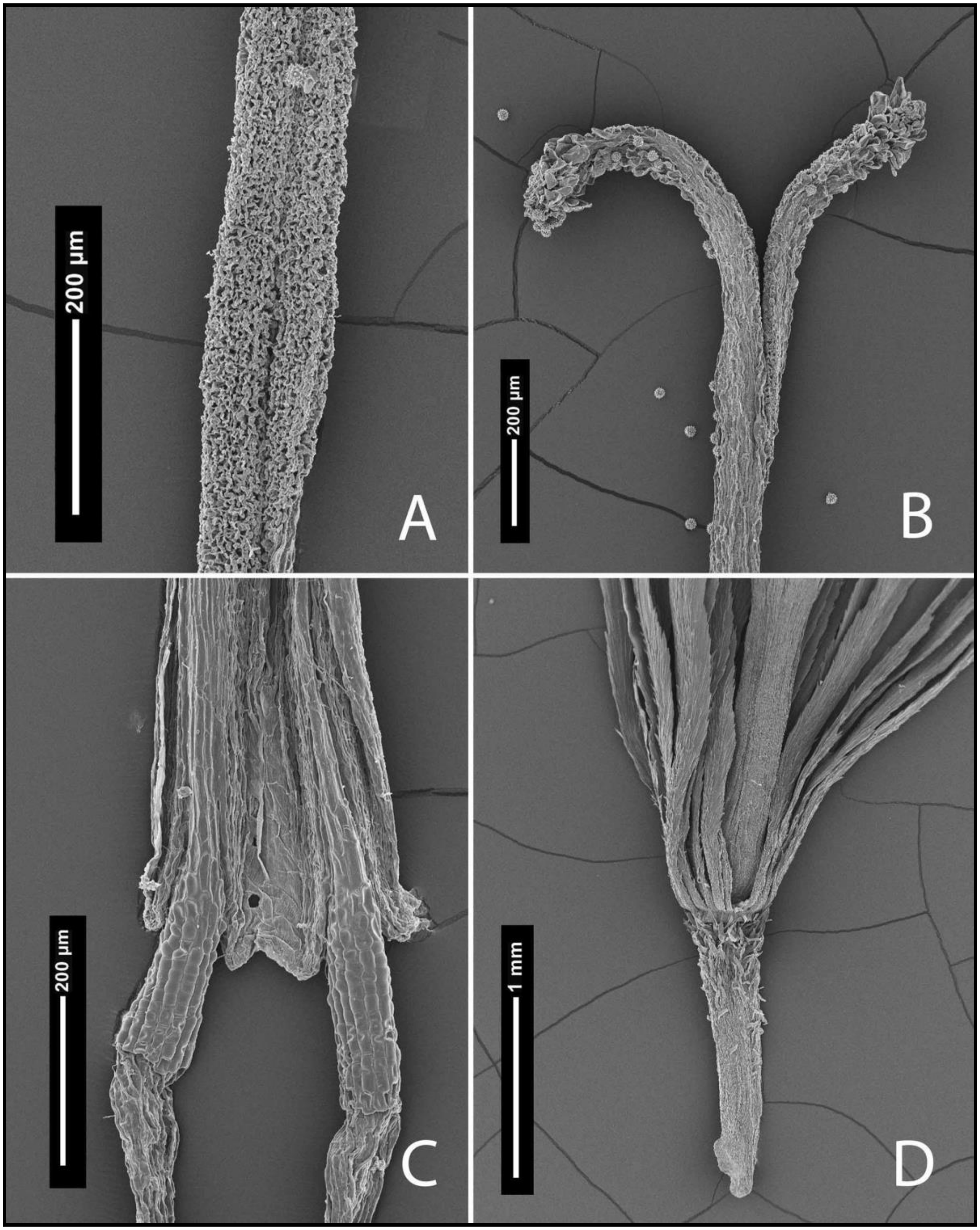


Figure 21. *Calea juninensis* Pruski. A. Style branch, close-up of mid-branch adaxial surface, showing sterile medial groove. B. Bifid style with obtuse apex, which is papillose, as are the distal portions of the abaxial branch surface, the *Calea*-style structural type, the style trunk is glabrous, lateral view. C. Abaxial surfaces of two post-anthesis dithecous anthers, showing theca bases not surpassing the collars. D. Disk cypsela, lateral view, showing asymmetric-based carpopodium and about a dozen of the broad-based flat pappus scales with scabrid margins; two central pappus scales have been removed to show non-setose glabrous tubular base of the corolla (center, directed towards the upper right). (*Juzepczuk 10299*, LE, paratype).

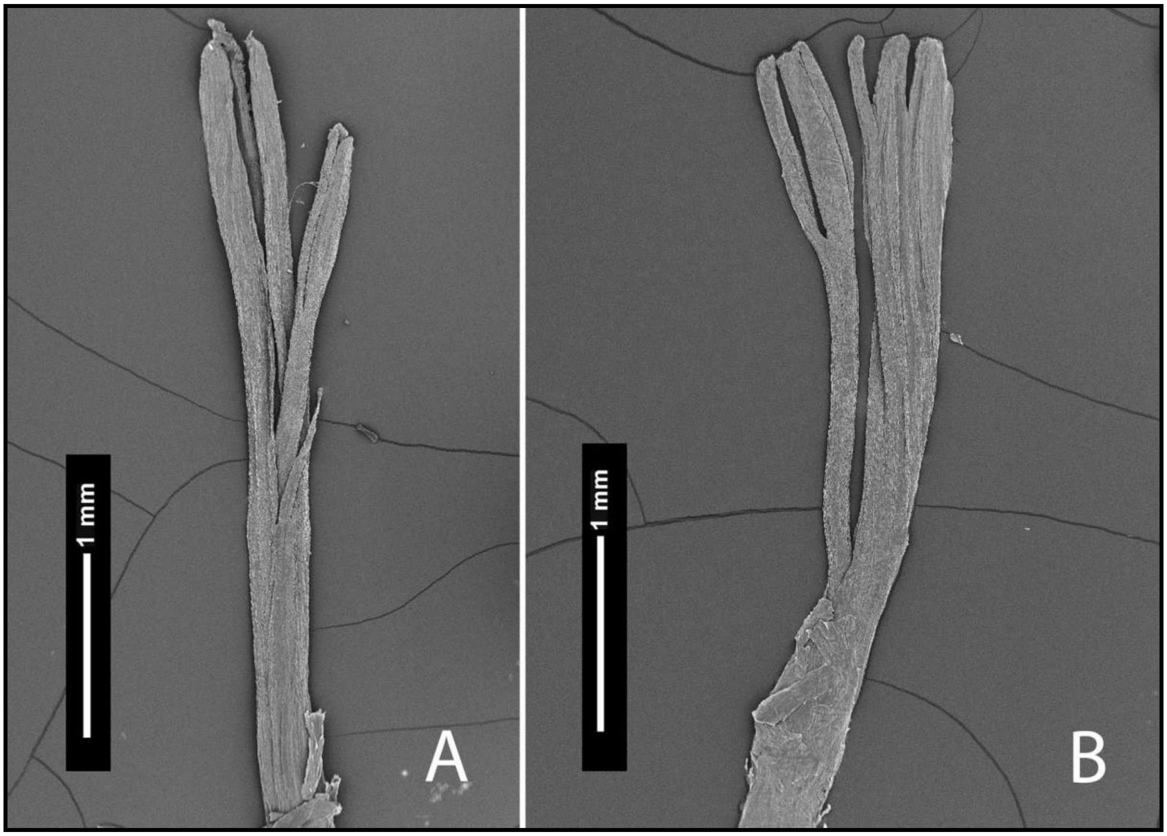


Figure 22. *Calea juninensis* Pruski, immature ray florets. A. Corolla limb in-rolled (left), style branches appressed (right). B. Corolla limb in-rolled (right), style (left) showing branches separate but still held erect and yet to recurved, style trunk glabrous. (*Croat 57689*, MO, paratype).

Etymology, Ecology, and Distribution. *Calea juninensis* is centered in northern Dept. Junín, Peru, whence the epithet, but is also know from adjacent southern Pasco. This new species occurs mostly in relatively dry shrubby vegetation (Fig. 25) on the eastern slopes of the Andes from about 1575–2500 meters elevation and flowers mostly from January to July. *Calea juninensis* was first collected on the east side of the Rio Palca (sometimes now called Rio Tarma) near Huacapistana, a well-known locality along the main road between low-elevational San Ramón and high-elevational Tarma, Junín. *Calea juninensis* is indeed typified from materials collected near Huacapistana, and the type collection was photographed there by Gina Castillo (Fig. 20). The Beltrán, Weberbauer, Woytkowski, and one of the two Vásquez collections, however, were made further east of San Ramón in the Rio Tutumayo drainage, Junín. The species was known to me for a few decades from only a few collections made in northern Junín, but two collections in nearby southern Pasco have recently been seen. One Pasco collection is labeled 'Cerro Picaflor' (i.e., the paratype *Valadeau CV109* cited above), but the Cerro Picaflor known to me is in Junín. In any event, the epithet 'juninensis' has been long-used and is retained.

Calea juninensis (Figs. 20–24, 26) may be recognized by its combination of trinerved leaves, yellow-flowered short-radiate (albeit sometimes appearing or mistaken as discoid, due to delayed non-acropetal maturation of pistillate florets) mid-sized capitula, often turbinate-pressed involucres, abaxially eglandular ray corolla limbs, and distally (weakly-)setose cypselae. Among Peruvian species of *Calea*, by its radiate capitula *C. juninensis* is reminiscent of *C. coriacea* DC. (Fig. 29), *C. jelskii* Hieron., *C. montana* Klatt (Fig. 4D), and *C. szyszylowiczii* Hieron. (Fig. 27). It is the abaxially eglandular short ray corolla limbs of *C. juninensis* that distinguish it from the four other radiate species found in Peru. Two of these four species are centered in northern Peru (but unknown near Cenepa viz Pruski 2010), and include small-capitulate subglabrous-ovaried *C. jelskii* and large-capitulate long-rayed *C. szyszylowiczii* (Fig. 27), but floral features distinguished them from allopatric southern *C. juninensis*. The two other previously described radiate Peruvian species are *C. montana* Klatt (syn. *C. ulei* Hieron.) (Fig. 4D), which is AndeAzon-centered (eastern Andean foothills and bordering lowlands-centered), often whorled-leaved, orange-ray-flowered, and nearly monocephalous; and Bolivia-centered *C. coriacea* (Fig. 29), which has leaves pinnately veined, but *C. juninensis* matches neither. *Calea juninensis* also recalls discoid-capitulate *C. umbellulata* Hochr. (Fig. 4C). *Calea juninensis* has occasionally been annotated as much smaller-capitulate *C. jelskii*.

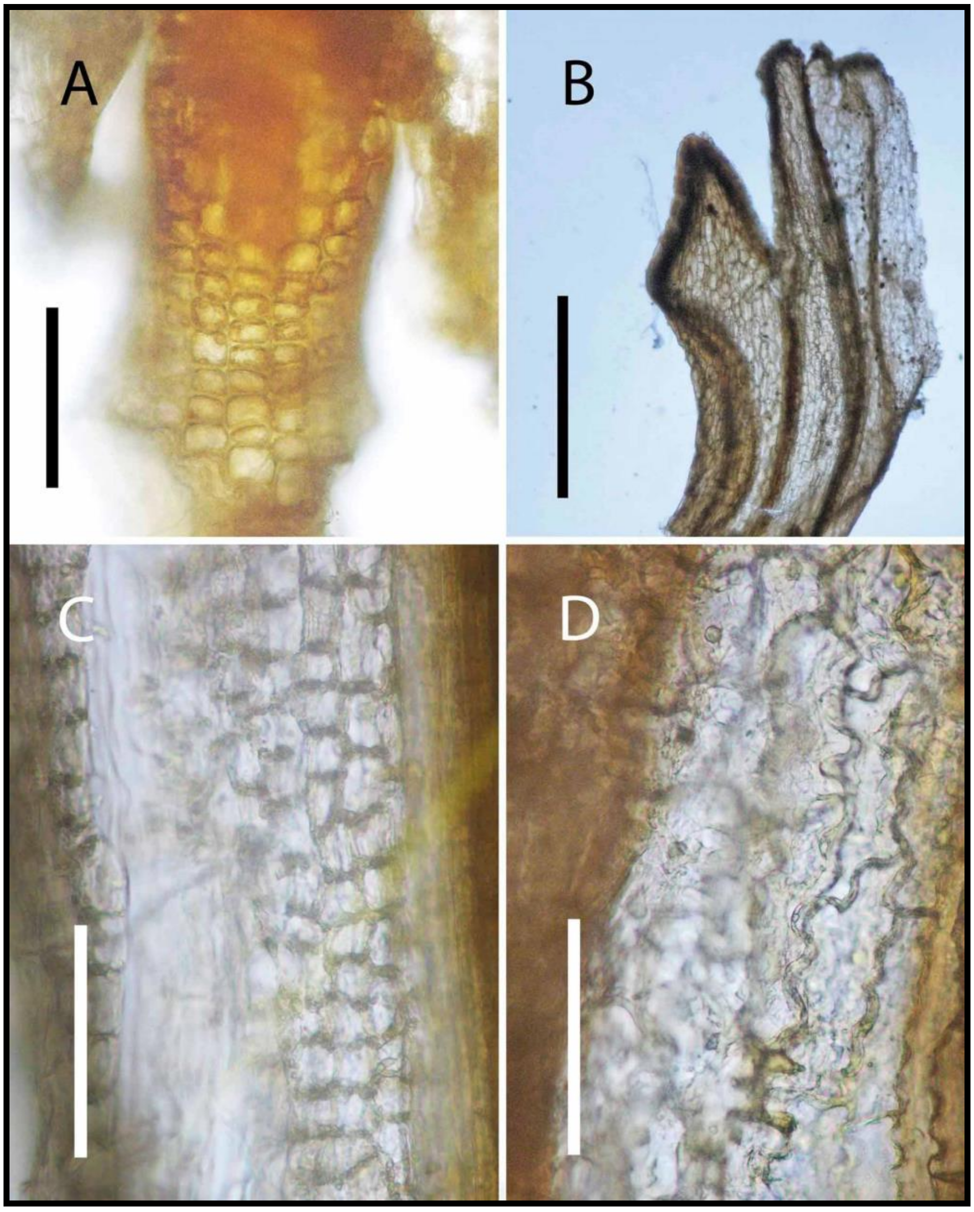


Figure 23. *Calea juninensis* Pruski. A. Anther collar showing thecae not surpassing it, abaxial view. B. Ray corolla limb, abaxial view. C. Endothecium showing polarized tissue, the pattern typical of most Compositae. D. Adaxial cells of proximal portion of a ray corolla limb. (*Pruski et al. 4434*, unmounted paratype). Scale bars A 80 µm, B 0.5 mm, C 100 µm, D 50 µm.

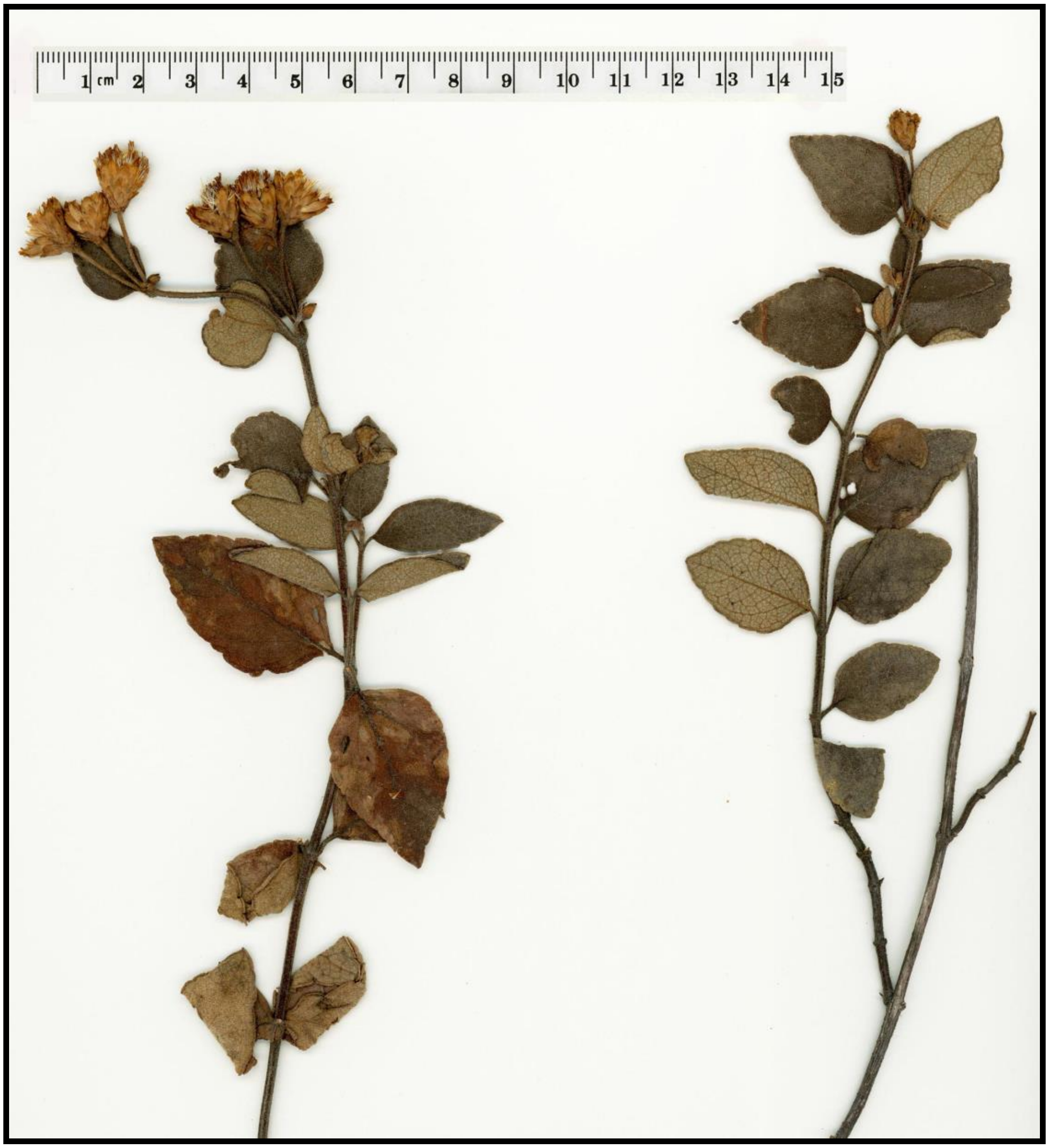


Figure 24. *Calea juninensis* Pruski, from the holotype, the two branch tips are upside down on the mounted sheet. (*Pruski et al. 4433* MO, right-hand half of sheet).

Another radiate-capitulate species of special interest and to be distinguished from *C. juninensis* is *C. peruviana* (Figs. 28, 33A–B), based on Humboldt and Bonpland material and described as from Peru, but instead endemic to Colombia (Pruski 1982). *Calea peruviana* in gestalt, however, seems more similar to north Peruvian endemic *C. szyszylowiczii* (Fig. 27), which differs by shorter peduncles and leaves less pubescent leaves, than to *C. juninensis*. Because *C. peruviana*, however, suspiciously recalls *C. szyszylowiczii*, one cannot help but wonder whether Humboldt and Bonpland collected each, but perhaps due to their moderate similarity, the locality information of the two were somehow confused, complicating the picture. It is well known that Humboldt and Bonpland collected in Cajamarca (Sandwith 1926, 1968) within the known distributional range of *C. szyszylowiczii*, but I do not know of a Humboldt and Bonpland collection of *C. szyszylowiczii*, or of anyone having publishing, based on Humboldt and Bonpland material, an earlier name for *C. szyszylowiczii*.

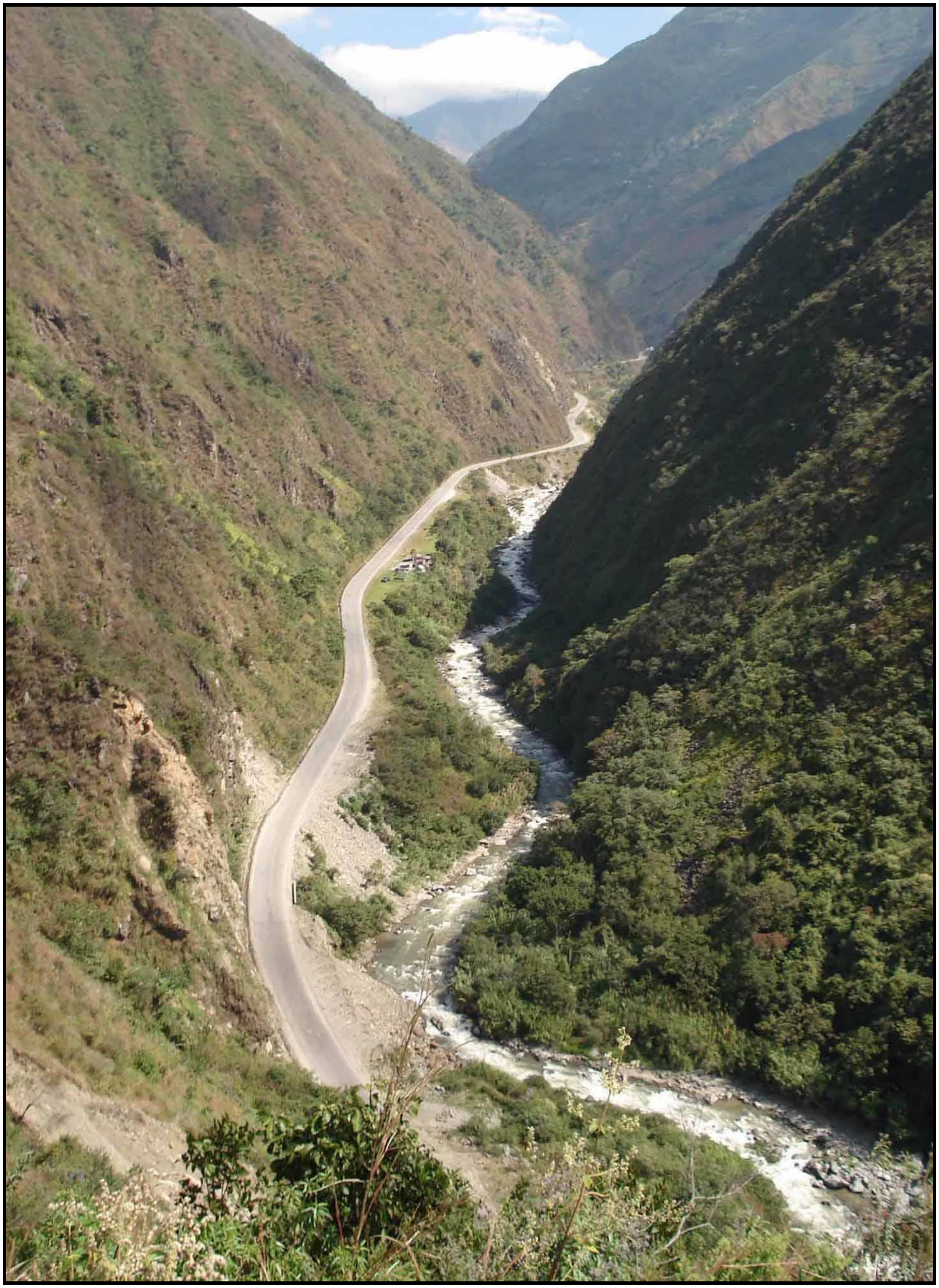


Figure 25. Type locality of *Calea juninensis* Pruski, view upriver, towards the southwest, of the río Palca and the San Ramón-Tarma highway paralleling it to the east (left). Open shrubby hillsides are a typical habitat of *Calea*.

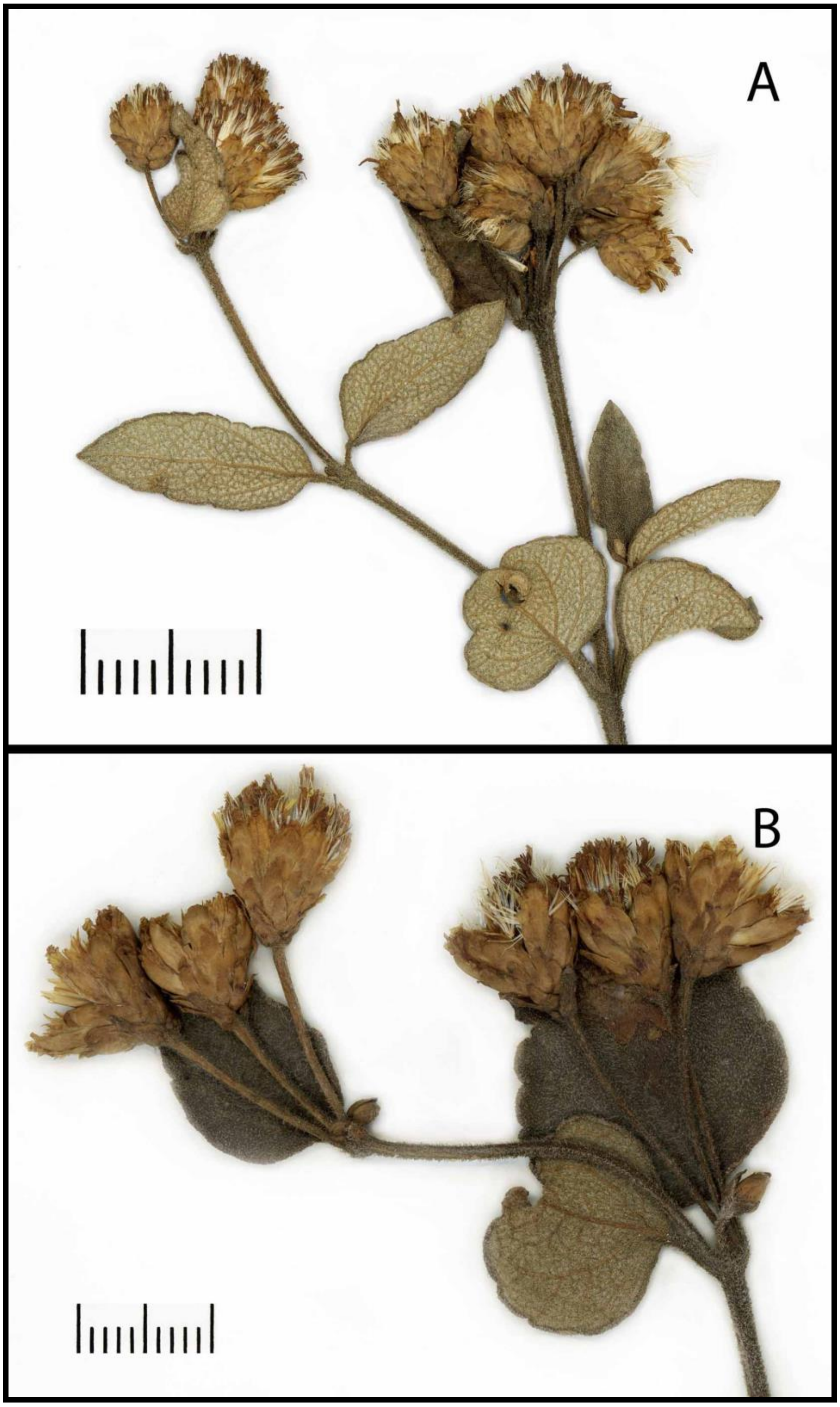


Figure 26. Capitulescences of *Calea juninensis* Pruski, showing the indistinctly short-radiate capitula with campanulate involucres that often press turbinate. (A *Pruski 4433*, unmounted isotype; B *Pruski 4433*, MO, holotype). A ten mm ruler is towards lower left of each image.

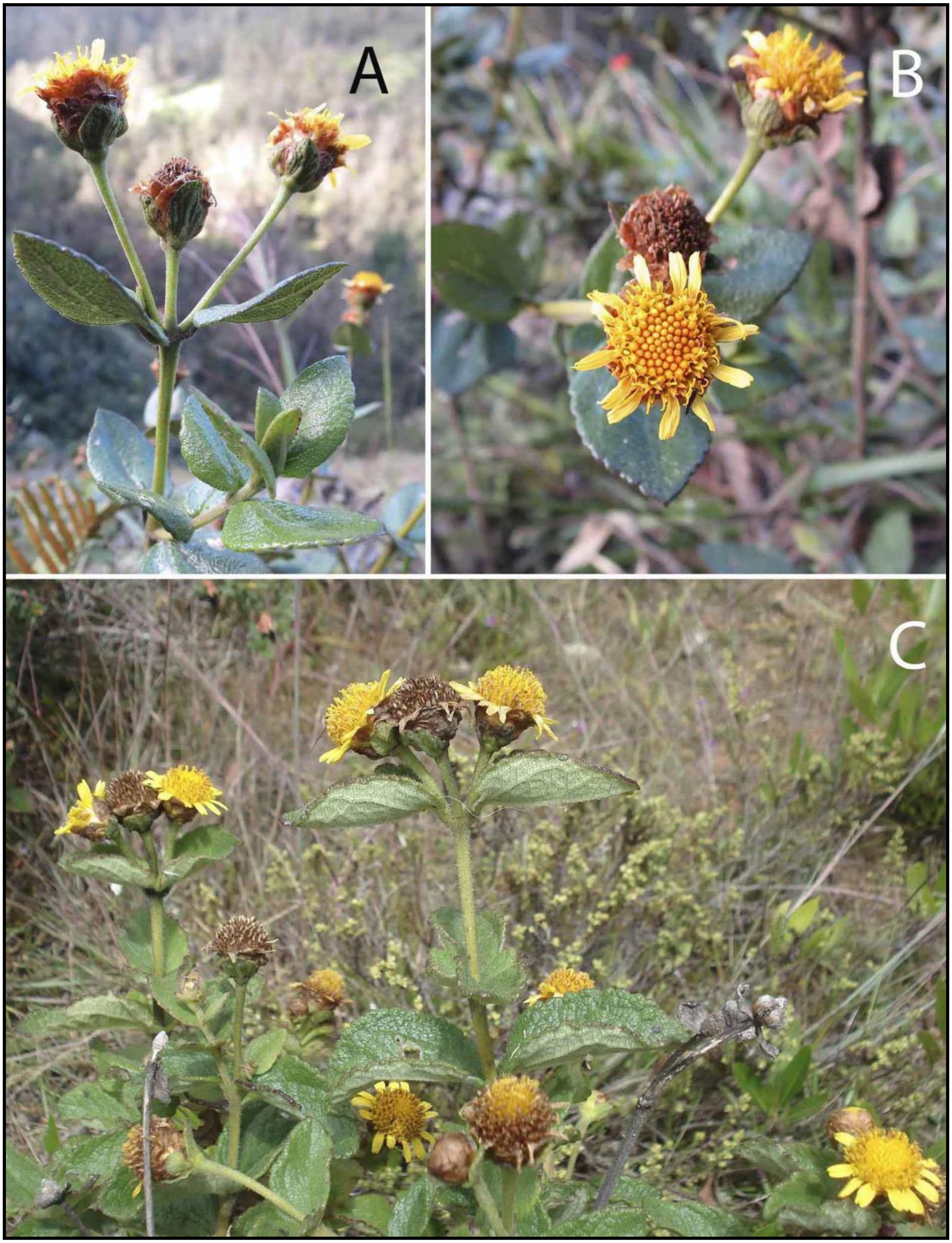


Figure 27. *Calea szyszylowiczii* Hieron., a north Peruvian endemic, showing the relatively large campanulate obviously radiate capitula in (determinate) open cymes. (A–B *Pruski & Ortiz 4888*, Karajia, Amazonas, Peru; C *Pruski & Ortiz 4987*, Huancas, Amazonas, Peru).

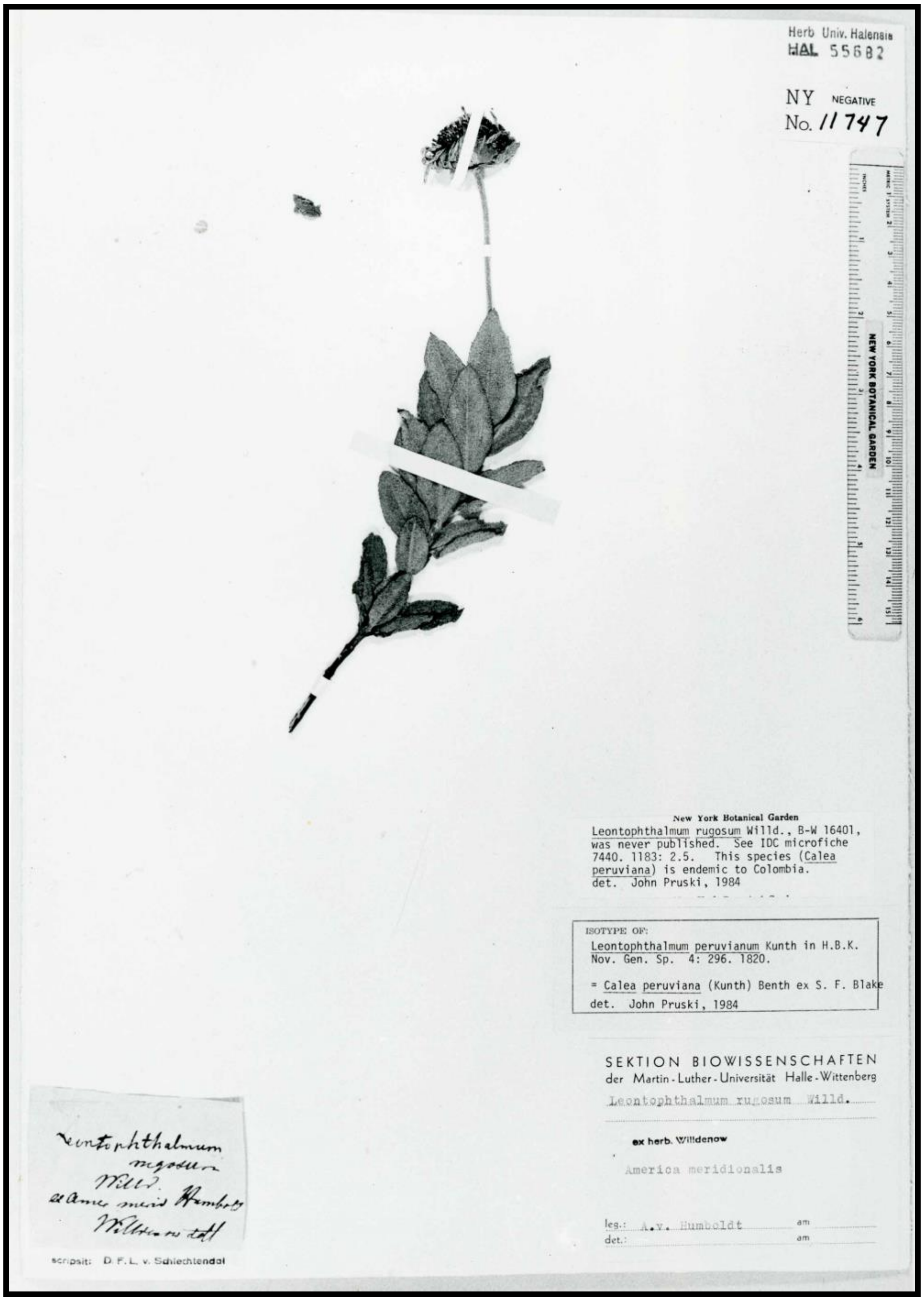


Figure 28. Isotype of *Leontophthalmum peruvianum* Kunth [≡ *Calea peruviana* (Kunth) Benth. ex S.F. Blake], showing a leafy-bracteate long-pedunculate large capitulum characteristic of this Colombian endemic. The binomial *Leontophthalmum rugosum* Willd. was never published. Willdenow travelled to Paris in 1810 during the Napoleonic Wars to continue Bonpland's study of the Humboldt and Bonpland collections, took sick in Paris, and died in Berlin in 1812. Willdenow's student Kunth completed the study of the Humboldt and Bonpland collections in Paris, but Kunth was not granted access to the Willdenow herbarium and in turn presumably did not see the material in the above image (viz Hiepko 2006; Lack 2004). (*Humboldt & Bonpland s.n.,* HAL; this is a duplicate of B-W 16401, presumably transferred from B to HAL after Schlechtendal assumed directorship of the Botanical Garden at Halle in 1833).

Figure 29. Representative specimen of Bolivia-centered *Calea coriacea* DC., showing its radiate campanulate relatively few capitula and pinnately-veined leaves that serve to distinguish it from *Calea juninensis*. (*Solomon 10795*, MO).

Country-level locality mix-ups, other than of *C. peruviana*, are known among Humboldt and Bonpland *Calea* collections. For example, Blake (1930) noted the then-unrecognized *C. sessiliflora* Less. (non Stokes)—an illegitimate later homonym that Pruski and Funston (2011) referred to *C. glomerata* Klatt—was published by Lessing (1830) as Mexican and based Humboldt and Bonpland material in B-W ("W. hrb. 15241. Mexico Humb."), but instead is a Colombia-endemic. I have examined two Paris isotype sheets of *C. sessiliflora* Less., and agree with Blake (1930) that *C.*

sessiliflora is typified by Colombian material. Conversely, Kunth published *C. ternifolia* as Colombian, but Pruski (1982) without question noted this was erroneous and instead gave Mexico as the type locality, simultaneously treating the long-used common-in-Mexico *Calea zacatechichi* Schltdl. as a taxonomic synonym. Here, we have a one-to-one match in Humboldt and Bonpland *Calea* type locality mix-ups: *C. ternifolia* labeled as Colombian is actually from Mexico, and conversely the moderately similar *C. sessiliflora* labeled as from Mexico is instead from Colombia.

This lends credence to the locality mix-up conjecture of type data of Colombia-endemic *C. peruviana* (Fig. 28) at some point perhaps having been mixed with an as-of-yet unrecognized perhaps-extant Humboldt and Bonpland collection of the loosely-similar Peruvian endemic *C. szyszylowiczii* (Fig. 27) hypothetically mislabeled as though from Colombia. Elsewhere, for example, Wurdack (1971), Robinson (1976), and Pruski and Robinson (2018) gave similar examples of 1700s and 1800s type locality errors. In any event, although Colombian *C. peruviana* and Peruvian *C. szyszylowiczii* are somewhat similar by each being obviously radiate-capitulate, *C. juninensis*, by its indistinctly radiate smaller-capitula, is clearly distinct and allopatric from these two other species.

Instead of being near *C. peruviana*, more similar to *C. juninensis* are five Peruvian taxa: the four others with radiate-capitula and discoid-capitulate *C. umbellulata* Hochr. (Fig. 4C). Trinerved-leaved indistinctly radiate-capitulate *C. juninensis* may be envisioned loosely as combining features of several: the short yellow ray corollas and leaf size and venation features of *C. jelskii*, leaves of discoid small-capitulate *C. umbellulata* Hochr., and nearly the capitula size of larger-capitulate *C. coriacea*, *C. montana*, and *C. szyszylowiczii*, but matching none of them. *Calea jelskii* and *C. szyszylowiczii* (Fig. 27) are endemic to northern Peru, *C. umbellulata* is centered in northern Peru (viz Robinson 2006), and none reach as far south as Pasco or Junín. Bolivia-centered *C. coriacea* spreads northwards only as far Puno and Cusco, Peru, but not reaching north to Junín.

The geography of widespread *C. montana* is as follows. *Calea montana* is common in San Martín near Tarapoto, Moyobamba, and granite-domed Morro de Calzada, and is now reported south to Pasco (*Rojas et al. 2913*, NY) and Junín (*Smith 6538*, MO), Peru. *Calea montana* is also of note by occurring to the northeast in Colombia, from collections only on or near Cerro Mitú, Vaupés, Colombia (but not reported in either Brazil or Venezuela by Pruski 1997). *Calea montana* was first reported in Colombia in 1984 by determination of material collected on Cerro Mitú by Bassett Maguire (*Maguire et al. 44101*, COL, MO, NY, US), but *Schultes & Cabrera 13905* (COL, US) from Cerro Mitú is an earlier, and apparently the first, collection of the plant made in Colombia. Cerro Mitú is an isolated mountain near the Rio Vaupes less than 50 kms from the frontier with Brazil. *Calea montana* should be looked for at similar elevations eastwards across the Brazilian border, perhaps between Rios Uaupés and Içana in the extreme northwestern corner of Brazil: less than 50 km due east of this border there are a series of 300–400 meter hills mapped by Kroonenberg et al. (2016: fig. 2) as "High-grade Mitú." Presumably, however, *C. montana* is not found 250 km east of Mitú on sandstone-topped Serra Tunuí (ca. 700 m), Brazil. Most reports attributing *C. montana* to Colombia, specifically to Guaviare, Meta, and Vichada—e.g., Cárdenas et al. (2008: 74) based on *Cárdenas 6512*, COAH; Lasso et al. (2010: 559) based on Cárdenas et al. (2008); Barona-Colmenares et al. (2018: 99) based on *Barona et al. 4221*, COAH and *Barona et al. 4282*, COAH; *Callejas & Marulanda 6966*, COAH, COL, HUA, MO; *Cárdenas 42516*, COAH; *Carvajal et al. 195*, UDBC—however, are based mostly on misdetermined materials of allopatric *Oyedaea cuatrecasasii* Pruski. In any event, *C. montana* is very different from *C. juninensis*. *Calea juninensis* and *C. montana* are the only two species of *Calea* in Pasco and Junín, but I know the very different *C. montana* from only a single collection in each of these two departments. The description of *C. juninensis* and present discussion serve to distinguish it from nearly sympatric *C. coriacea* and *C. montana*, and from the aforementioned species in northern Peru.

CALEA SANTANDERENSIS Pruski, **sp. nov.** **TYPE: COLOMBIA.** **Santander.** Municipio Suaita, inspección de San José de Suaita, vía San José de Suaita a Guadalupe, trayecto vereda El Placer-San José de Suaita, 6° 09' N, 73° 21' W, sin. elev. [ca. 1500 m], 7 Apr 2003, *J.L. Fernández-Alonso, L.A. Triana, V. Rico, E. Contreras, G. Hernández, M. Rojas et al. 20374* (holotype: HUA-159730; isotypes: COL n.v., MA-851191, a second unmounted isotype is at MA. I was unable to find the COL isotype during my visits to COL in 2018 and 2019, but José Luis Fernández-Alonso (pers. comm.) said that a duplicate was deposited in COL. HUA is in hand and is the sole sheet examined, i.e., it is the holotype. Figures 30–32.

Fruticosa 2–3 m alta; caules dense hirsutuli vel ferruginosa; folia simplicia opposita brevipetiolata, lamina 2–6 × 1–2.5 cm elliptico-ovata chartacea triplinervia basi obtusa vel rotundata subtus pilosa vel piloso-tomentosa necnon glandulosa, petiolo 0.2–0.7 cm longo; capitulescentia plerumque terminalis umbellato-corymbiformis longe-pedunculata interdum subsessilia-ternata; pedunculi (0.1–)1.5–3.5 cm longi dense hirsutuli vel piloso-tomentosi; capitula radiata 8–12 mm longa; involucrum 7.5–10 × 4–8(–11) mm campanulatum; phyllaria imbricata graduata 3–6-seriata, externa triangulari-lanceolata vel ovata herbacea, interna 7–9 × 2.4–3 mm lanceolato-ovata vel ovata scariosa; clinanthium paleaceum 1–2 × 1.2–2.5 mm; paleae 5–6.4 mm lanceolatae; flosculi radii 5–7 pistillati, corollis 8.5–12 mm longis luteolis, limbo 5.5–8 mm longo oblongo subtus glanduloso; flosculi disci 15–24(–30) hermaphroditi, corollis 5–6.8 mm longis infundibuliformis luteolis glabris; cypselae 1.8–2.5 mm longae inferme setosae vel setosae; pappi squamae ca. 20, 4.5–5.7 mm longae lineari-lanceolatae.

Arching shrubs to tree-like shrubs 2–3 m tall, opposite-branched; stems erect or arching, leafy, subterete-striate, drying brown, dense-hirsutulous to ferruginous, trichomes mostly 0.3–1 mm long, leaves usually longer than internodes. **Leaves** simple, opposite, short-petiolate; blade 2–6 × 1–2.5 cm, elliptic-ovate, broadest from basal third to mid-blade, stiff-chartaceous, moderately 3-nerved from above base but often with 1–2 pairs of more-proximal thin arching secondary veins usually present on each side, usually with about 2–6+ main secondary veins on each side of the midrib, secondaries closed-looping, tertiary veins visible, base obtuse or sometimes rounded, margins crenulate to serrulate, apex acute to obtuse, surfaces nearly concolorous, adaxial surface smooth, antrorse-scabrous, trichomes 0.2–0.3 mm long, uniseriate, abaxial surface moderately crisped pilose to pilose-tomentose, also subsessile-biseriate-glandular abaxially, secondary veins pubescent but raised and visible, trichomes mostly 0.5+ mm long, uniseriate; petiole 0.2–0.7 cm long, dense-hirsutulous to pilose-tomentose. **Capitulescence** terminal or infrequently proximal nodes with 3 capitula in axils, mostly umbelliform-corymbiform, mostly 7–28-capitulate, on several distal branchlets, individual flowering branchlet tips each usually 3–9-capitulate, capitula mostly long-pedunculate, occasionally branchlet tips with capitula subsessile and ternate; peduncles (0.1–)1.5–3.5 cm long and often several times longer than capitula, capitula sometimes subsessile, dense-hirsutulous to pilose-tomentose, also glandular. **Capitula** radiate, 8–12 mm long, 20–31(–37)-flowered, campanulate, not leafy-bracted; florets moderately exserted from involucre; involucre 7.5–10 × 4–8(–11) mm but pressing much wider, campanulate; phyllaries imbricate, graduate, 3–6-seriate, appressed; outer few phyllaries 1.5–6 × 1.5–4 mm, triangular-lanceolate to ovate, mostly herbaceous or at least herbaceously tipped, venation not apparent, both surfaces dense-hirsutulous to pilose-tomentose, also glandular, often noticeably shorter than the inner but occasionally nearly half as long as the inner, often evenly graduating into the middle and inner phyllaries; inner phyllaries 7–9 × 2.4–3 mm, lanceolate-ovate to ovate, scarious, stramineous, striate, glabrous, distal margins and apex hyaline, apex acute to obtuse; clinanthium paleate, 1–2 × 1.2–2.5 mm, convex-conical, the inner phyllaries inserted 0.5–0.8 mm distal to the outer phyllary insertion zone; paleae conduplicate, 5–6.4 mm long, lanceolate, scarious, stramineous, often becoming trifid, lobes acuminate-attenuate, central lobe and subapical lateral lobes. **Ray florets** 5–7, pistillate; corolla 8.5–12 mm long, exserted from involucre, yellow, tube 3–4 mm long, glabrous, limb 5.5–8 mm long, oblong, 5–8(–9)-nerved, denticulate, abaxial surface glandular; ovary long-pappose; ray style often exserted to about middle of fully elongated limb. **Disk florets** 15–24(–30), bisexual; corolla 5–6.8 mm long, funnelform, yellow, glabrous, tube 1.8–2.3 mm long, basally enlarged where surrounding stylopodium and nectary, usually slightly shorter than limb and about same length as throat, throat 2.2–3 mm long, somewhat broader than tube, lobes 1–1.5 mm long, narrowly lanceolate, shorter than the throat, slightly spreading; anthers 2–2.5 mm long, only slightly exserted with distal parts of filaments held well within throat, endothecial tissue polarized, appendage slightly glandular; stylopodium ca. 0.3 mm long, style branches recurved, ca. 1 mm long, apex rounded, nectary ca. 0.2 mm long, annular. **Cypselae** (immature) 1.8–2.5 mm long, obconic-subprismatic, black, weakly setulose distally to setulose nearly throughout, eglandular, twin trichomes 0.1–0.2 mm long, never approaching width of cypsela body, the twin elongate subequal terminal cell apices appressed, carpopodium asymmetric; pappus scales about 20, elongate, 4.5–5.7 mm long, linear-lanceolate, scabridulous, about twice as long as cypselae albeit only immature cypselae seen, about 2/3 as long as to nearly as long as disk corollas, usually reaching past middle of corolla lobes, apex long-attenuate. Chromosome number unknown.

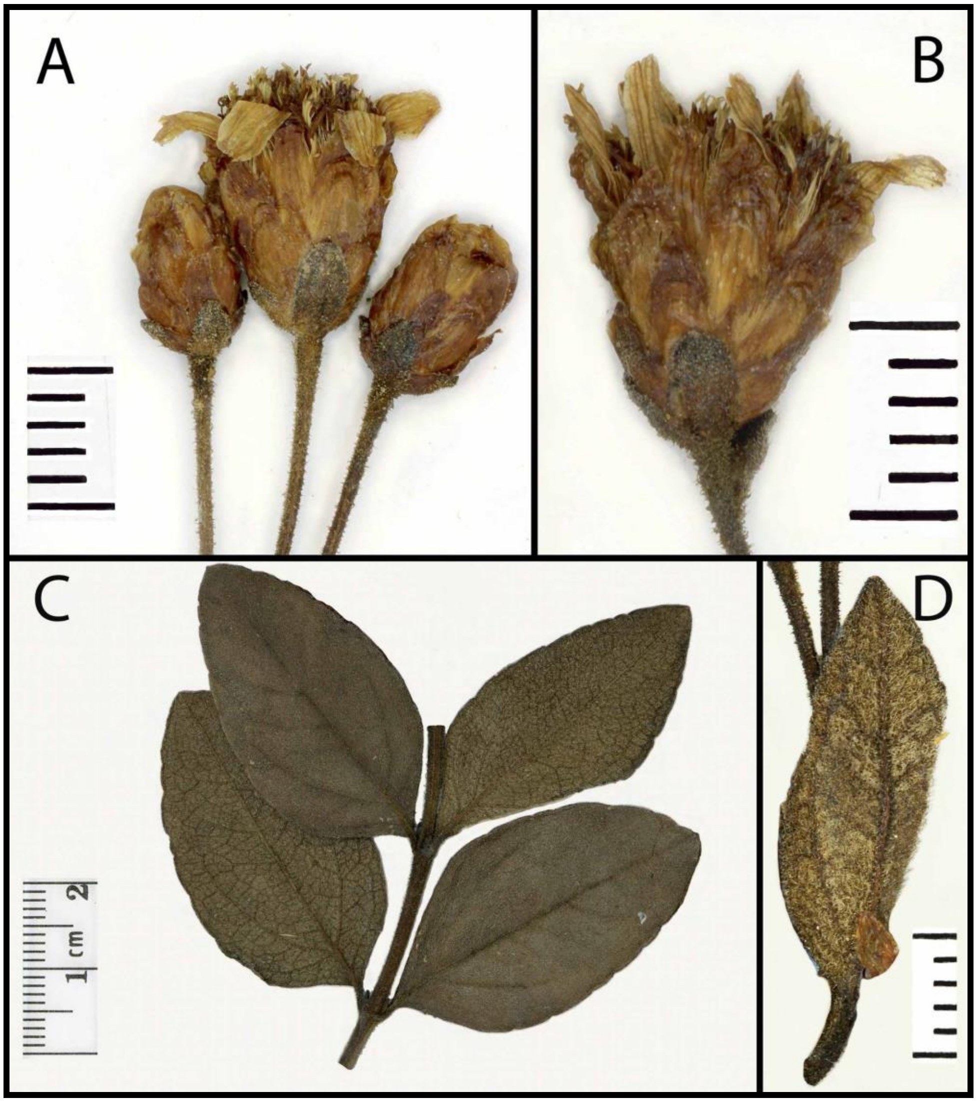


Figure 30. *Calea santanderensis* Pruski, holotype, close-ups of capitula and leaves. A–B. Capitula showing ray florets moderately exserted from graduated involucres. C. Portion of stem showing two pairs of leaves. D. Leaf, adaxial surface, in high contrast to show indument. There is a 5 mm ruler in A–B and D. (*Fernández-Alonso et al. 20374*, HUA).

20374 - Holotype (HUA·159730)

HERBARIO NACIONAL COLOMBIANO – COL

Calea santanderensis Pruski, sp. nov.

Determinó: John Pruski VIII-2018

HERBARIO NACIONAL COLOMBIANO

ASTERACEAE

Calea
Det: J.L. Fernández/2003

COLOMBIA. SANTANDER. Municipio de Suaita, Inspección de San José de Suaita, 6° 9' N – 73° 21' W. Vía San José de Suaita a Guadalupe, trayecto vereda El Placer-San José de Suaita.
7-IV-2003
Arbolito 2-3 m, lígulas amarillas.

N°. 20374 J. L. Fernández-Alonso, L. A. Triana, V. Rico, E. Contreras, G. Hernández, M. Rojas & al.

Figure 31. Holotype of *Calea santanderensis* Pruski, on the branch towards the upper left two capitula are subsessile clustered. (*Fernández-Alonso et al. 20374*, HUA).

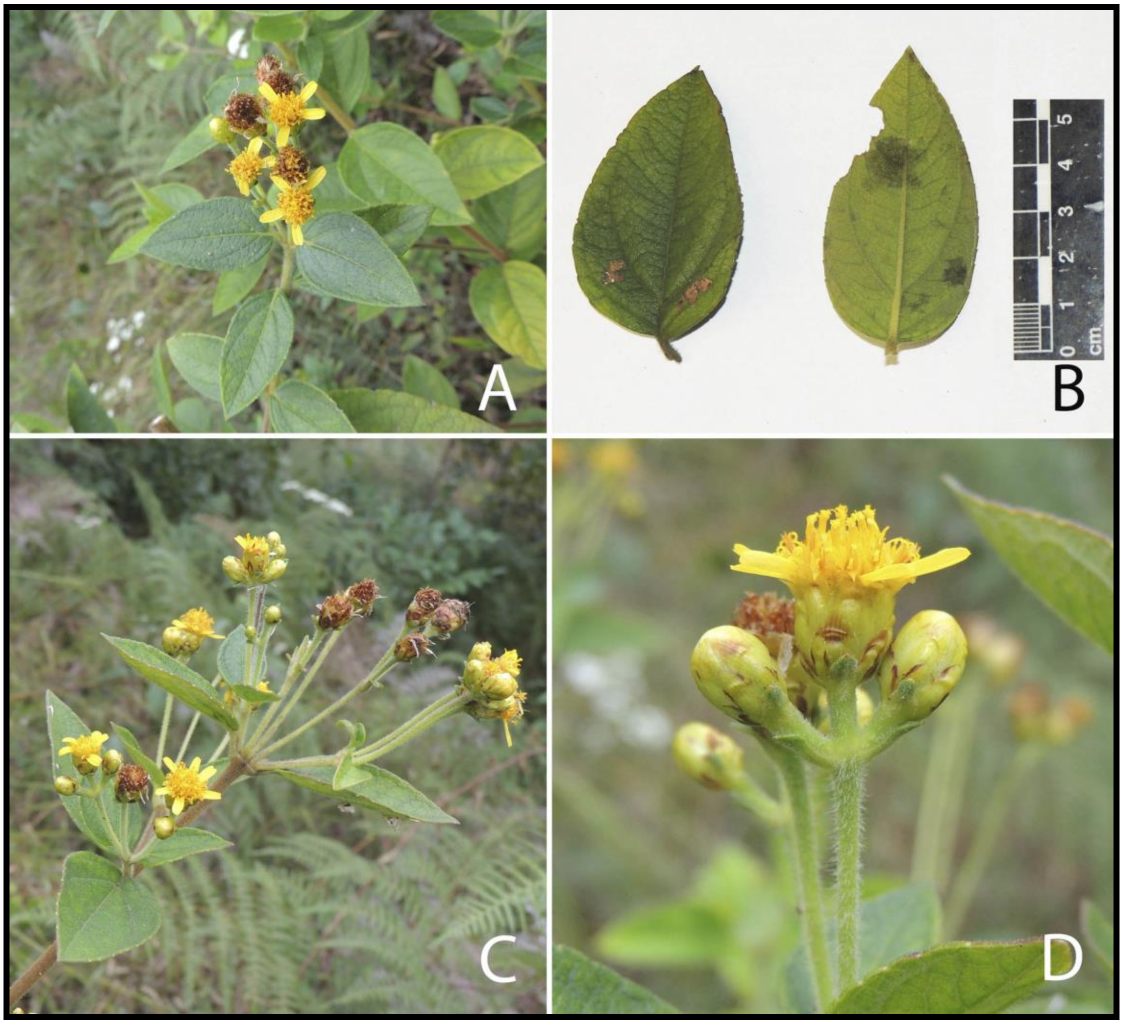


Figure 32. *Calea santanderensis* Pruski, paratype. A. Habit from above, showing the capitula with yellow ray corolla limbs. B. Leaves, left adaxial surface, right abaxial surface. C. Lateral view of capitulescence. D. Lateral view of branchlet apex, showing determinate maturation of the mid-sized capitula. (*Díaz-R. 2139*, Santander, Colombia, plate arranged by the writer from photographs taken by Daniel Díaz).

Paratypes. COLOMBIA. Santander. Mun. Zapoteca, vereda La Cacica, Reserva Natural La Montaña Mágica-El Poleo, en la parte alta, 6° 50' 08" N, 73° 08' 28" W, 2000–2300 m, 13 Nov 2019, *D. Diaz-R. 2139*; also at the same locality: *Diaz-R. 2213* (seen unmounted, duplicates of each collection to be deposited at MEDEL).

Etymology, Ecology, and Distribution. *Calea santanderensis* Pruski is endemic to the northeastern Colombian Andes in Santander, whence the epithet. This new species has been collected from about 1500–2300 meters elevation, and flowering in April and November. The paratype locality is about 15 kms east of Zapoteca, and about 85 kms NNE of the type locality that is just outside of Suaita. Suaita is about 15 kms north of the border with Boyacá, Colombia, and the new species could reasonably be expected to be found in adjacent Boyacá. It seems possible that *Camargo & Huertas 7805* (COL) from 2700 meters elevations near Santa Rosa de Viterbo, Boyacá may represent the new species. Dr. Jose Cuatrecasas kindly showed me his loans in the 1990s, which included this sheet from COL, but the material could not be dissected, and the identity of this collection remains unknown.

Figure 33. Representative radiate-capitulate northern Andean species of *Calea* L. A–B. *Calea peruviana* (Kunth) Benth. ex S.F. Blake, an endemic to Colombia (Pruski 1982). C–D. *Calea subcordata* S.F. Blake, a long-lived shrub. (A–B *Pruski & Ortiz 4810*, Boyacá, Colombia, photographs taken by Rosa Ortiz, C–D *Urbatsch & Pruski 3427A1311*, Táchira, Venezuela, photograph of the author taken by Lowell Urbatsch, the locality is along the river forming the border with Norte de Santander, Colombia and is within one kilometer of Herrán, Colombia, seen in the background).

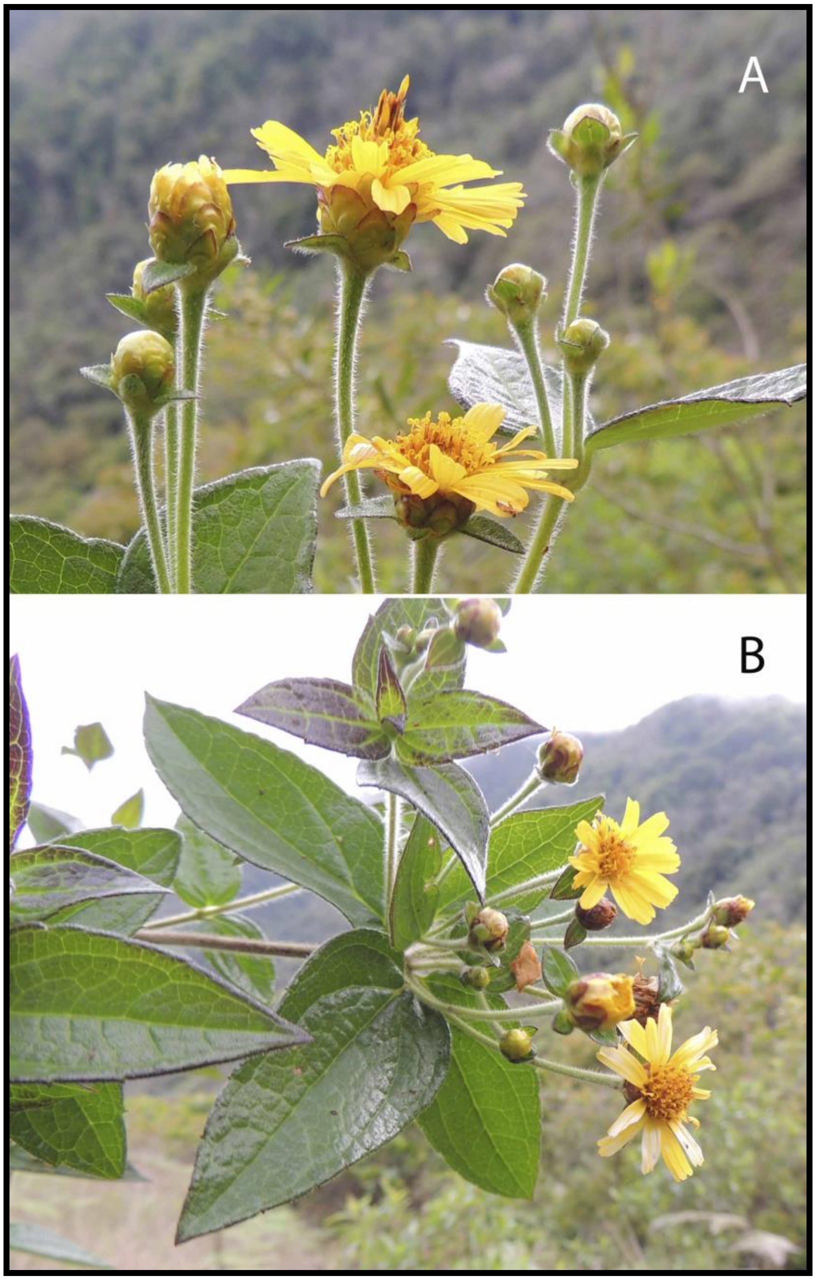


Figure 34. *Calea bucaramangensis* Pruski & Urbatsch, a radiate-capitulate species sympatric with *Calea santanderensis*. Photographed by Daniel Díaz in Zapoteca, Santander Colombia.

Calea santanderensis is known only from three collections, and some variation occurs, but is not taxonomically significant. Variation seen in specimens of *C. santanderensis* includes the longer more narrowly lanceolate corolla lobes seen in the type than in the paratypes and the more densely setulose cypselae of the type. The paratypes, however, have longer stem pubescence than does the type collection, and also several subsessile-ternate clustered capitula, whereas the holotype only one subsessile cluster was seen. Subsessile-ternate capitula are seen occasionally in several typically pedunculate species in Central America and in South America, and is not used as a taxonomic marker in material of *C. santanderensis*. The variation in the uniseriate non-glandular trichome length seen in stems of *C. bucaramangensis* is similar to that seen in *C. bucaramangensis,* and is typical of ecotypes. The unmounted MA isotype and one branch of *Díaz-R. 2213* are very unusually stiffly erect. *Calea bucaramangensis* has a distribution similar to that of *C. santanderensis*, extending from near Bucaramanga and Zapoteca to its southernmost known station, documented here as near Suaita, Santander, Colombia (*Fernández-Alonso et al. 21460*, COL).

Among shrubby radiate-capitulate regional Andean *Calea* species, radiate *C. santanderensis* is recognized by its abaxially glandular stiff-chartaceous obtuse-round-based leaves, relatively small capitula, narrowly lanceolate disk corolla lobes, and setose cypselae. Andean Colombian *C. trianae*, by its leaf characters, and *C. gargantae*, by relatively small capitula, are the two species that seem most similar to *C. santanderensis*. *Calea trianae* occurs from Tolima north to Santander, whereas the once-collected allopatric *C. gargantae* is endemic to North de Santander. *Calea santanderensis* differs from *C. trianae* by smaller more numerous non-leafy-bracted capitula. The new species differs from monotype *C. gargantae* by leaves with obtuse-round (vs. subcordate) bases and cymose-corymbiform (vs. few-capitulate cymose) capitulescences. *Calea santanderensis* seems to combine the leaf characters of *C. trianae* with the relatively small capitula of *C. gargantae*, but matches neither. Other regional radiate-capitulate species similar to *C. santanderensis* include sympatric C. *bucaramangensis* Pruski & Urbatsch (Fig. 34) from Santander, Colombia and Andean Venezuelan *C. trujilloi* V.M. Badillo. However, their round-based to subcordate-based merely moderately chartaceous leaves that are eglandular abaxially and their glabrous cypselae distinguishes each of these two species from *C. santanderensis*. *Calea santanderensis* and the other known regional radiate species have abaxially glandular leaves.

Also moderately similar to the new species is subcoriaceous-leaved *C. subcordata* S.F. Blake (Fig. 33C–D). *Calea subcordata* is distinct in its long-radiate capitula, cordate leaves, and in general aspect it is much different from *C. santanderensis*. *Calea peruviana* (Figs. 3C, 28, 33A–B), endemic to Colombia (Pruski 1982), is distinct from *C. santanderensis* by being typically stoutly long-pedunculate, obviously radiate-capitulate, and having cuneate-obtuse-based leaves. *Calea peruviana* differs further from *C. santanderensis* by having canescent-villous-tomentose vegetative indument of trichomes to 2 mm long, few large capitula often with lobed ray floret corolla limbs, and leafy outer bracts. Although moderate trichome length variation is seen in *C. santanderensis*, the trichome differences between *C. peruviana* and *C. trianae* are much more striking and are especially noteworthy.

Calea peruviana is the generitype of *Leontophthalmum* Willd., and was treated by Pruski (1982) as characterized by being adapted vegetatively to high elevations, yet with cypsela characters typical of those of *Calea* sect. *Calea*. Pruski (1982) recognized as distinct species *C. gargantae*, *C. peruviana*, and *C. subcordata*, but treated *C. trianae* as a variety of *C. peruviana*. Indeed, *C. peruviana* and *C. trianae* are mostly sympatric and usually similarly large-bracteate, but differ in gestalt and by indument characters. The two species are now recognized by me as specifically distinct from one another. The characters seen in *C. gargantae*, *C. subcordata*, and *C. trianae* serve to further link *C. peruviana* to mainstream Caleas.

Calea bucaramangensis, *C. peruviana*, *C. subcordata*, and *C. trianae* are among the more frequently encountered of these aforementioned radiate-capitulate northern Andean Caleas. In general, the geographically-narrowly-distributed shrubby radiate-capitulate species from the northern Colombian Andes do not seem to vary much in leaf shapes, but elsewhere notable leaf shape (linear-lanceolate to broadly ovate) variations are seen in usually low-elevational northwestern South American *C. tolimana* Hieron. Other regional radiate species are *C. montana*, *C. perijaensis* Cuatr., *C. saxatilis* Cuatr., and the aforementioned subcoriaceous-leaved *C. tolimana*, but none of them seem very similar to *C. santanderensis*, which is described herein as a species new to science.

2–7. The new or resurrected *Calea* Alliance genera *Laceanthos*, *Lemmatium*, *Meyeria*, *Podocalea*, *Tepuipappus*, and *Tonalanthus*.

Bentham and Hooker (1873) used broad tribal and broad generic concepts in the landmark *Genera Plantarum*, which has long been a standard reference. They treated (1873: 198) *Calea* as a member of Heliantheae subtr. Galinsoginae (as Tribe V Helianthoideae subtr. 9 Galinsogeae), whereas they placed *Neurolaena* (1873: 207) within Senecioneae subtr. Liabinae (as Tribe VIII Senecionideae subtr. 1 Liabeae). Baillon (1886) grouped *Calea*, *Galinsoga*, and three other genera in "une petit sous-série *Caléées*" and maintained *Neurolaena* in the "petit groupe (*Liabéés*)." In the deservedly influential *Pflanzenfamilien*, Hoffmann (1894: 245) treated *Calea* in Heliantheae subtr. Galinsoginae, whereas *Neurolaena* (Hoffmann 1894: 286) was placed in Senecioneae subtr. Senecioninae. Rydberg (1927) described Neurolaeneae as containing only *Neurolaena* (Fig. 19A–D) and *Schistocarpha*, but not *Calea*. Robinson (1981) in his comprehensive review of helianthoids was the first to directly align *Calea* and *Neurolaena*, doing so within Heliantheae subtr. Neurolaeninae. More than a century after *Genera Plantarum* and *Pflanzenfamilien*, Panero (2007), Turner (2014), and Pruski and Robinson (2018) treated *Calea* and *Neurolaena* together within tribe Neurolaeneae.

At the generic level, Mexico-centered *Oteiza* La Llave, Mexico-centered *Tetrachyron* Schltdl., montane neotropics-centered *Alloispermum* Willd., Brazil-centered *Lemmatium* DC., and Brazil-centered *Meyeria* DC. were among several genera that Bentham and Hooker (1873) reduced to synonymy of *Calea*. Several of these genera were recognized by Bentham and Hooker (1873) at the sectional rank in *Calea*, a genus within which they recognized a total of nine sections. The Benthamian sectional framework over the next century or so became the standard infrageneric concept used for *Calea*. After a century-long synonymy, however, *Oteiza*, *Alloispermum*, and *Tetrachyron* were resurrected from synonymy with *Calea* by Fay (1975), Robinson (1978a), Wussow and Urbatsch (1979), respectively. From among the residue, Pruski (1984, 1987, 1997, 1998a, 2005, 2013) recognized *Calea* has containing five sections, four somewhat-monophyletic non-typical sections, and a broadly circumscribed *Calea* sect. *Calea*, itself also somewhat heterogeneous. The four non-typical sections of *Calea* that Pruski recognized are *Calea* sect. *Haplocalea* (Less.) Pruski, *Calea* sect. *Lemmatium* (DC.) Benth. & Hook. f., *Calea* sect. *Meyeria* (DC.) Benth. & Hook. f., and *Calea* sect. *Monanthocalea* (Less.) Pruski.

Earlier, some of these sections of *Calea* were described, however, as subgenera of *Calea* by Lessing (1832), and by others as independent genera by Candolle (1836), e.g., *Lemmatium* DC. and *Meyeria* DC. For facility sake, the writer earlier characterized these four atypical sections by the easily observed, but basically artificial, character of relative pappus scale to cypsela lengths. Pappus features have been used traditionally to characterize genera of the *Calea* alliance, which have a pappus of scales, but members of other groups also may have a pappus of scales, and the character is not apomorphic. For example, Robinson and Greenman (1896), Wussow et al. (1985), Strother (1999), and Pruski and Robinson (2018) accepted *Calea* sect. *Calea* within Mesoamerican as containing species of various pappus lengths relative to cypsela lengths (viz Fig. 6B vs. Fig. 6D). Pruski (1997), Pruski and Urbatsch (1988), and Pruski and Hind (1998) recognized a few individual species of *Calea* as having isomorphic yet unequal uniseriate scales characteristic of a heteropappose condition. However, with the present acknowledgment of *Lemmatium*, *Meyeria,* and *Tepuipappus* as distinct genera, *Calea* in the strictest of senses now basically contains only species with cypsela pappus scales uniseriate, isomorphic, and subequal in length.

Several emendments proposed here involve restructuring of the infrageneric grouping of *Calea* used in Baker (1884) and Löfgren (1897), who recognized three subgenera in *Calea*: subgen. *Eucalea*, subgen. *Meyeria* (DC.) Baker, and subgen. *Leontophthalmum* (Willd.) Less. The typical subgenus was characterized as narrow-capitulate and by densely corymbiform-paniculate capitulescences (Baker 1884; Löfgren 1897), and they included *C. lantanoides* among the five species of *Eucalea* they recognized in Brazil. Of these, I retain only *C. lantanoides* within *Calea* (*Eucalea*), where it is most similar to Bolivian *C. brevifolia* and northern South American *C. berteriana*. *Calea lantanoides* and *C. berteriana*, through their connecting link of Mesoamerican of *C. trichotoma*, are ultimately considered to be centered near the generitype *C. jamaicensis*. Four of the five other Brazilian species treated by Baker and Löfgren in *Eucalea* are treated by me with restored *Lemmatium*, and have dense capitulescences. Two other species of *Lemmatium* known to Baker and Löfgren (e.g., *C. clematidea*, *C. divergens*) by their campanulate capitula, however, were placed by them in *Calea* subgen. *Meyeria* (taken here as generically distinct). Indeed, my concept of *Lemmatium* includes species that are either open-cymose-flowered or campanulate-capitulate, non-typical traits, yet found in about half of the 16 species of *Lemmatium*.

Candolle (1836), and Krascheninnikov (1923) each recognized a large-capitulate *Calea* sect. *Leontophthalmum* (Willd.) DC. and Baker (1884), Robinson and Greenman (1896), and Löfgren (1897) each recognized more or less the same large-capitulate group, albeit at the subgeneric rank as *Calea* subgen. *Leontophthalmum*. (Willd.) Less. Robinson and Greenman (1896) considered their newly described Mexican endemic C. *megacephala* as a member of *Calea* subgen. *Leontophthalmum*. Because I defer to the scheme and ranks used by Bentham and Hooker (1873), I'll mostly use the names and ranks *Calea* sect. *Leontophthalmum*, *Calea* sect. *Meyeria*, etc. Here, I exclude the Robinson and Greenman species from *Calea* sect. *Leontophthalmum* sensu auct., and treat it in resurrected monotypic Mexican *Tonalanthus*. *Tonalanthus* is characterized by its unusually slender and ascending (not recurved) disk floret style branches and by its biconvex-compressed cypselae (Fig. 96) with broad unevenly developed adjacent twin trichomes (Figs. 96D, 98B–C). The high-elevational north Andean Colombian endemic (Pruski 1982) *Calea peruviana* (Fig. 28), the generitype of *Calea* synonym *Leontophthalmum*, proves to be just one of several large-capitulate radiate species of *Calea* sect. *Calea* that newly described *C. santanderensis* centers about. Similarly, the protologue of *C. ulei* Hieron., a synonym of *C. montana* Klatt, related it to *Calea* sect. *Leontophthalmum* sensu auct., from which that species must be excluded as well. Pruski (1998) placed into *Calea* sect. *Monanthocalea* the linear-paleate large-capitulate xylopodial plants centered in Brazil that had earlier passed as members of *Calea* sect. *Leontophthalmum*, and disassociated (as did Lessing 1832) these Brazil-centered species from the aforementioned Andean ones. Here, Andean *Calea* sect. *Leontophthalmum* is treated within *Calea* s. str.

From among genera long-time synonymous with typical and/or non-typical sections of *Calea*, the genera *Lemmatium* DC., and *Meyeria* DC. are resurrected. **Laceanthos** Pruski, **gen. nov**. and **Podocalea** Pruski, **gen. nov.** are described as new genera endemic to southern South America. *Laceanthos* contains 8 species, *Lemmatium* 16 species, *Meyeria* 18 species, and *Podocalea* 18 species. The species recognized in *Lemmatium* include most of those recognized and keyed by Pruski and Urbatsch (1988), and those in *Meyeria* include most of those recognized and keyed by Pruski (2005). *Podocalea* and *Laceanthos* house most of the two dozen or so relatively large-capitulate often radiate species that Pruski (1998a) placed in either *Calea* sect. *Haplocalea* or *Calea* sect. *Monanthocalea*.

No members of either of these two Pruski sections, however, have ever received generic recognition in recent useful regional treatments (e.g., Krascheninnikov 1923; Malme 1933; Cabrera 1937, 1974; Barroso 1986; Pruski 1984, 1997, 1998a, 2005, 2013; Pruski and Urbatsch 1988; Pruski and Hind 1998; Soria et al. 1998; Nakajima 2000; Nakajima et al. 2001; Basualdo and Soria 2002; Bringel and Cavalcanti 2009; Gutiérrez et al. 2015; Silva et al. 2016; Silva and Teles 2018). The species of *Podocalea* and *Laceanthos* are basically those, or at least most of the same Brazil-centered component species that earlier Baker (1884), Löfgren (1897), and Krascheninnikov (1923) treated as *Calea* sect. *Leontophthalmum* sensu auct. The species are indeed mostly radiate and relatively large-capitulate, but these characters are neither apomorphic nor belying of any monogamous long-lasting relationships. Thus, each non-typical *Calea* section—sections *Lemmatium*, *Meyeria*, *Haplocalea* and *Monanthocalea*—recognized by Pruski (1984, 1997, 1998a, 2005, 2013), Silva et al. (2016), and Silva and Telles (2018) are treated here as belonging to one of four distinct newly described or reinstated genera, and all component species are endemic to southern South America. Also, from within the inferred *Calea* sect. *Calea* of Pruski (1997, 1998a), Mexican *Tonalanthus* Brandegee is reinstated from synonymy, and **Tepuipappus** Pruski, **gen. nov**. is newly established. *Tonalanthus* is a Mexican monotype, and *Tepuipappus* contains 6 species endemic to tepuis in Venezuela.

The six genera of the *Calea* Alliance newly recognized here—*Laceanthos* Pruski, *Lemmatium* DC., *Meyeria* DC., *Podocalea* Pruski, *Tepuipappus* Pruski, and *Tonalanthus* Brandegee––like *Calea* s. lat., are characterized by their combined features of mostly opposite leaves, (Figs. 20, 24, 26–34, 49, 53, 55–56, 62-68, 97) and paleate clinanthia (Figs. 1A, 2, 5, 36, 42, 48, 58–59, 72). *Calea* Alliance characteristic flora features include ray florets (when present) pistillate (Figs. 2, 22, 46B, 46D, 48, 54A, 55, 56E, 58–59, 60A), non-setose disk corollas (Figs. 1A, 2, 36C, 37A, 46, 48, 58–59, 66C, 76A–B, 77B) with throats having single reddish-brown-orange resin duct superimposed over the veins (Figs. 15A, 37B), pale or at least never-blackened anthers (Figs. 3, 32–34, 36B, 40, 52B, 63, 75A), polarized endothecial tissue (Figs. 23C, 37C, 98A), style branches with paired stigmatic lines and papillose distal-abaxial surfaces (Figs. 9B, 21A–B, 54A, 61), and free stylopodia (Fig. 76C). Important fruiting characters in *Calea* Alliance members include carbonized non-microstriatulate cypselae (Fig. 6D) and the very characteristic radially arranged pappus of flat mostly isomorphic usually subequal scales (Figs. 1A, 6, 21D, 35, 36, 48, 55–60, 62, 65–67, 76B, 76D, 96B). Nevertheless critical features, e.g., habit, capitulescence characters, chromosome number, cypsela structure and indument, carpopodial structure, and cypselar twin trichomes structure, are also stressed here as of significance in delimiting genera of the *Calea* Alliance. In short, when I dissect opposite-leaved helianthoids, I first look for (useful although not even diagnostic to tribe) features of pale anthers, non-setose corollas, and a pappus of scales, to see whether or not that specimen appears to be a *Calea* Alliance member, then depending on the state of individual specimens, hopefully the aforementioned characters microcharacters may variously reveal themselves.

[As an aside, it is noted the term *paleaceum* is a Latin adjective (paleate in English) used by Humboldt, Kunth, de Candolle, Lessing, Bentham, and Baker. Similarly, the fully Latin term *epaleate* (the Latin stem with the Latin prefix "e") is also widely used. Descriptive epithets for leaves include, for example, the compounds such as Latin-derived *latifolia* and Greek-derived *platyphylla*, but not the malformed *latiphylla*. Bueno et al. (2021) proposed the new words *holopaleaceous* and *oligopaleaceous* (use of the Greek prefixes *holo* and *oligo* with Latin *paleaceum* result in linguistic hybrid terms) for "paleate" and the simple and commonly used "partly paleate," respectively. However, the potential adoption of the Greek-Latin linguistic hybrid term *holopaleaceous* in Compositae, about 10% of the Angiosperms, conflicts with accepted usages of Candolle, Bentham, and Baker. Thus, uses of the traditional terms paleate, epaleate, and partly paleate are retained here].

Each of the six newly recognized genera thus differ in critical features from *Calea*. In paleae features, for example, the new genera stand apart from *Calea*, which has strongly conduplicate paleae usually reaching to about the top of the disk corolla throat. *Podocalea*, on the other hand, has flat linear paleae, *Tepuipappus* has indurate paleae, and *Laceanthos* has short merely moderately conduplicate paleae. These and other distinguishing characters, arranged by genus, briefly follow. *Laceanthos* has fleshy fibrous roots, cymose-umbelliform capitulescences, proportionally short paleae not reaching to the disk lobes, and plump cypselae. *Lemmatium* has stipitate cypselae with multicellular knotted twin trichomes. *Meyeria* has marginally callose leaves, quadrangular cypselae with weakly asymmetric carpopodia, and a pappus of reduced scales. *Podocalea* species are usually relatively large-capitulate monocephalous scapose xylopodial plants, have flat linear paleae nearly as long as and often confusable with the pappus scales, apically divergent tips of the paired terminal cells of the twin trichomes of the cypselae, and have $x = 16$ as a chromosome base number. *Tepuipappus* houses six species from table top tepui summits in the Lost World (Steyermark 1955; Pruski 1991, 1997) of the Guayana Highland, that are characterized by indurate paleae and quadrangular cypselae with heteromorphic pappus scales. *Tonalanthus* has slender ascending (rather than recurved) style branches and biconvex-compressed cypselae with broad unevenly developed adjacent twin trichomes in its cypselae.

The species of these six new or reinstated genera, however, may seem macromorphologically hard to grasp, as are many groups among the Compositae, again 10% of the Angiosperms. For example, the species of *Lemmatium* with open capitulescences of few relatively large capitula, seen for example in *L. grazielae L. irwinii*, and *L. wedelioides*, on the surface seem so different than those species—e.g., *L. nitidum*, *L. oxylepis*, and *L. rotundifolium*—with densely corymbiform-paniculate capitulescences of many small capitula. However, it is the microcharacters that unite the species considered here as *Lemmatium*, viz for example the multicellular irregularly knotted twin trichomes in open and discoid capitulate *L. irwinii* that are so similar to those of the densely-radiate-capitulate generitype *L. rotundifolium*. The few large capitula and their arrangement in *L. irwinii* that seem much different than typical densely pluricapitulate species, recall similar swings in these obvious, but non-critical, characters seen in the related genera *Calea* s. str., *Meyeria*, and *Podocalea*. In *Meyeria*, the long-pedunculate large-capitulate *M. ilienii* and in *Podocalea* the relatively small capitulate *P. verticillata* Klatt seem like misfits, until examined microscopically. On the other hand, the cymose-umbelliform capitulescences of *Laceanthos* and the large radiate capitula seen in the *Tonalanthus* and *Tepuipappus* nevertheless prove to be useful guides in generic recognitions, but in each of these instances it is actually the somewhat obtuse microcharacters that prove to be of a defining nature.

Indeed, as stated two centuries ago by Brown (1817), *Calea* is one of several genera where the "structure and limits seem to be imperfectly understood." Karis (1993) stated the characters—opposite leaves, etc.—"mentioned by Pruski (1984) are not unique to *Calea*, and there are obviously no synapomorphies" for *Calea*. The genus in the strict sense is brought into sharper focus here by excluding these six anomalous elements, and its limits will be further refined by the author in forthcoming companion papers.

2. LACEANTHOS Pruski, **gen. nov. TYPE:** *Calea reticulata* Gardner [≡ *Laceanthos reticulatus* (Gardner) Pruski].

Calea subgen. *Haplocalea* Less., Syn. Gen. Compos. 241. 1832. *Calea* sect. *Haplocalea* (Less.) Pruski, Kew Bull. 53: 683. 1998. **TYPE:** *Calea cymosa* Less. [≡ *Laceanthos cymosus* (Less.) Pruski].

Plantae herbaceae perennes; caules stricta vel adscendens; folia simplicia paucijuga opposita vel verticillata sessilia vel brevipetiolata, lamina chartacea plerumque plinervia; capitulescentia terminalis umbelliformes vel cymosa, capitula pedunculata discoidea vel radiata, involucrum campanulatum vel hemisphaericum, phyllaria pauciseriata, clinanthium paleaceum subglobosum vel conicum; paleae breves olbongae conduplicatae; flosculi radii (0–)5–9 pistillati; flosculi disci hermaphroditi, corollae anguste infundibuliformae aliquando salverformes glabrae vel aliquando pauciglandulosae; antherae palidae; styli rami recurvati, areis stigmaticis discretis; cypselae obconicae nigrae, setosae eglandulosae; pappi squamae 20–28 subaequales lanceolatae.

Herbaceous perennials with fleshy roots, stems simple, strict or ascending, single–few from caudex, stems commonly sparsely leafy in proximal half with few regularly spaced nodes, infrequently leaves all basal in compacted nodes, caudex sometimes moderately enlarged but not greatly expanded into large xylopodium contrary to my incorrect 2005: 2024 characterization; herbage glabrous to tomentose with uniseriate multicellular trichomes, often also with sessile-glandular trichomes. **Leaves** simple, simple, in few pairs-whorls, opposite or whorled, sessile to short-petiolate; blade lanceolate or ovate to obovate or nearly suborbicular, chartaceous, smooth to strongly reticulate, usually trinerved from base or from proximal portion of blade, margins entire to serrate or dentate, apex narrowly acute to obtuse or nearly rounded, surfaces often concolorous but sometimes strongly discolorous, glabrous, sessile-glandular, and/or becoming pilose or villous-tomentose. **Capitulescence** terminal, held well-above leaves, umbelliform or sometimes merely cymose, on occasion a secondary pseudoumbel is borne within and exserted above the primary umbelliform group, few–several(–many)-capitulate, scape usually bracteate at node subtending the much shorter peduncles, capitula pedunculate, mostly seemingly equally mature when umbelliform, but when cymose sometimes more clearly various-aged and with variously elongated peduncles. **Capitula** radiate or discoid, several–many-flowered, mid-sized; involucre broadly campanulate or hemispherical; phyllaries weakly graduate to subequal, weakly dimorphic, usually with outer few phyllaries subherbaceous or subherbaceous-tipped, inner series of phyllaries few-seriate, chartaceous, appressed at anthesis, entire, mostly stramineous or yellowish, few-striate; clinanthium paleate, dome-shaped or conical; paleae slightly longer than the cypselae not reaching to the disk lobes, proportionally much shorter than most Alliance members, mostly oblong, moderately conduplicate, pale-colored, few-striate laterally short-trifid or usually margins entire, apex sometimes lacerate. **Ray florets** pistillate, uniseriate, ca. (0–)5–9, exserted from involucre; corolla often yellow but sometimes ochroleucous-white-rayed (in two species), limb 5+-nerved, often abaxially lightly glandular, apex few-crenulate; style branches slightly exserted and slightly recurved. **Disk florets** bisexual, several to many; corolla narrow-funnelform to sometimes campanulate or even salverform, mostly glabrous or rarely few-glandular, sometimes with trichome-like tissue at tube-throat juncture, yellow or pale yellow, tube expanded at base around stylopodium, throat typically much longer than lobes but throat in *L. hasslerianus* minute, lobes 5 usually triangular-lanceolate to infrequently long-lanceolate and cut nearly to base of throat, erect to spreading, resin ducts submarginal; anthers pale yellow, endothecial tissue polarized, appendage few-glandular; pollen tricolporate, echinate; style trunk glabrous, stylopodium dilated, free from the annular nectary, branches recurved, 2-banded from base to apex, apex convex to triangular, distal-abaxial papillae covering about half the length of the branches. **Cypselae** isomorphic, broadly turbinate-obconical, plump, carbonized, dark**,** body slightly incurved basally, always setulose–setose and eglandular, twin trichomes with elongate terminal cells longitudinally connate throughout or weakly divergent at very apex, base somewhat rounded with carpopodium moderately asymmetric and moderately developed as shield-plate; pappus radially symmetric, of about 20–28 subequal scales, lanceolate with distinct midrib and broad lacerate-serrate margins, apex acuminate to attenuate, longer than the cypsela body, mostly stramineous-pale but sometimes pinkish, midzone thicker than margins. Chromosome number unknown.

Etymology. The name *Laceanthos* is formed in an arbitrary manner. The generic name is treated in Latin as a masculine noun. Although formed arbitrarily, the name *Laceanthos* may be thought of as a compound name using as a prefix an anagram of *Calea* (a name of unknown derivation) and the Greek *anthos* for flower as a suffix, the Greek word element being transliterated into Roman characters. Similarly, a Greek prefix was used by Lessing (1832) who coined each *Calea* subgen. *Haplocalea* and *Calea* subgen. *Monanthocalea*. Stearn (1983: 260) wrote "Greek is a rich flexible language in which pleasing compounds are readily made" and in the present case the elements of the name *Laceanthos* have long been hiding in plain sight.

Geographic Distribution. The species of *Laceanthos* are restricted to southern South America, where they occur in Argentina, Bolivia, Brazil, Paraguay and Uruguay. One species, widespread *L. cymosus* (Less.) Pruski, occurs in Uruguay. *Laceanthos rhombifolius* (S.F. Blake) Pruski is the only species known in Bolivia, and is newly reported in adjacent Brazil. Two discoid species are endemic to Brazil, whereas no species are endemic to Argentina, Bolivia, Paraguay, or Uruguay.

Figure 35. *Laceanthos chapadensis* (Malme) Pruski, holotype, a whorled-leaved discoid-capitulate plant; collected in 1902; the determination year "1901" [sic] is erroneous. (*Malme 2122*, S).

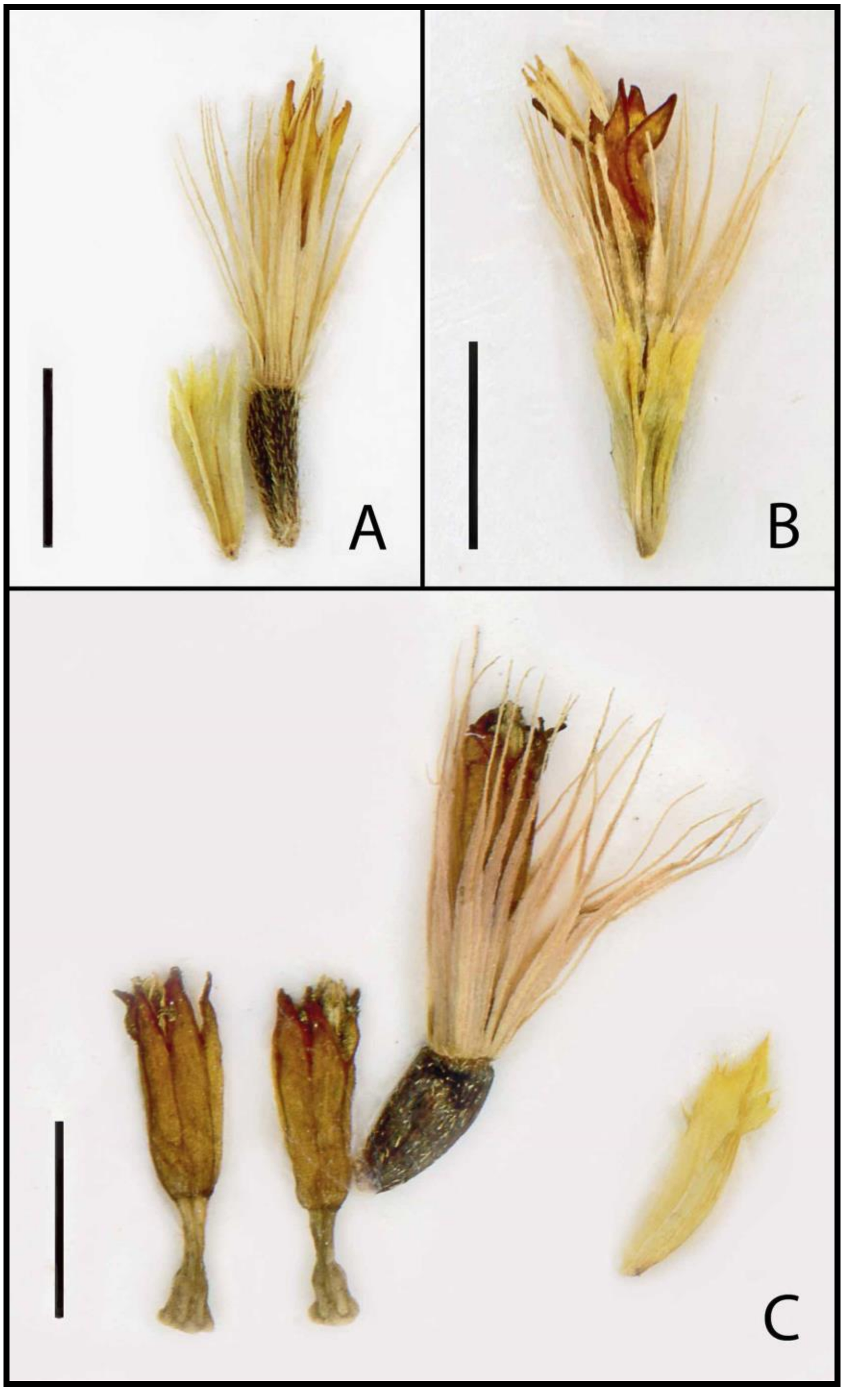


Figure 36. *Laceanthos* Pruski, representative post-anthesis disk florets and paleae; the palea are short (vs. long in *Calea* s. str., figs. 2, 5), broad, and stramineous, the pappus scales somewhat pinkish. A–B. *Laceanthos* sp.: A showing on left adaxial (inner) face of palea; B showing abaxial (outer) face of apically-lacerate medially-torn palea covering associated cypsela, and above the distal portions of the floret with pale anthers, the palea and pappus scales are nearly concolorous. C. *Laceanthos acaulis* (Baker) Pruski, showing (left and second to left) two disk florets with narrowly funnelform short-lobed glabrous corollas, the cypselae and pappus have been removed; second from right shows a disk floret with carbonized plump cypsela and pinkish pappus scales; on far right is a palea showing adaxial (inner) face. (A–B *Maciel in herb. Macedo 1364*, MO; C *Wollston 1023*, U). Scale bars 3 mm.

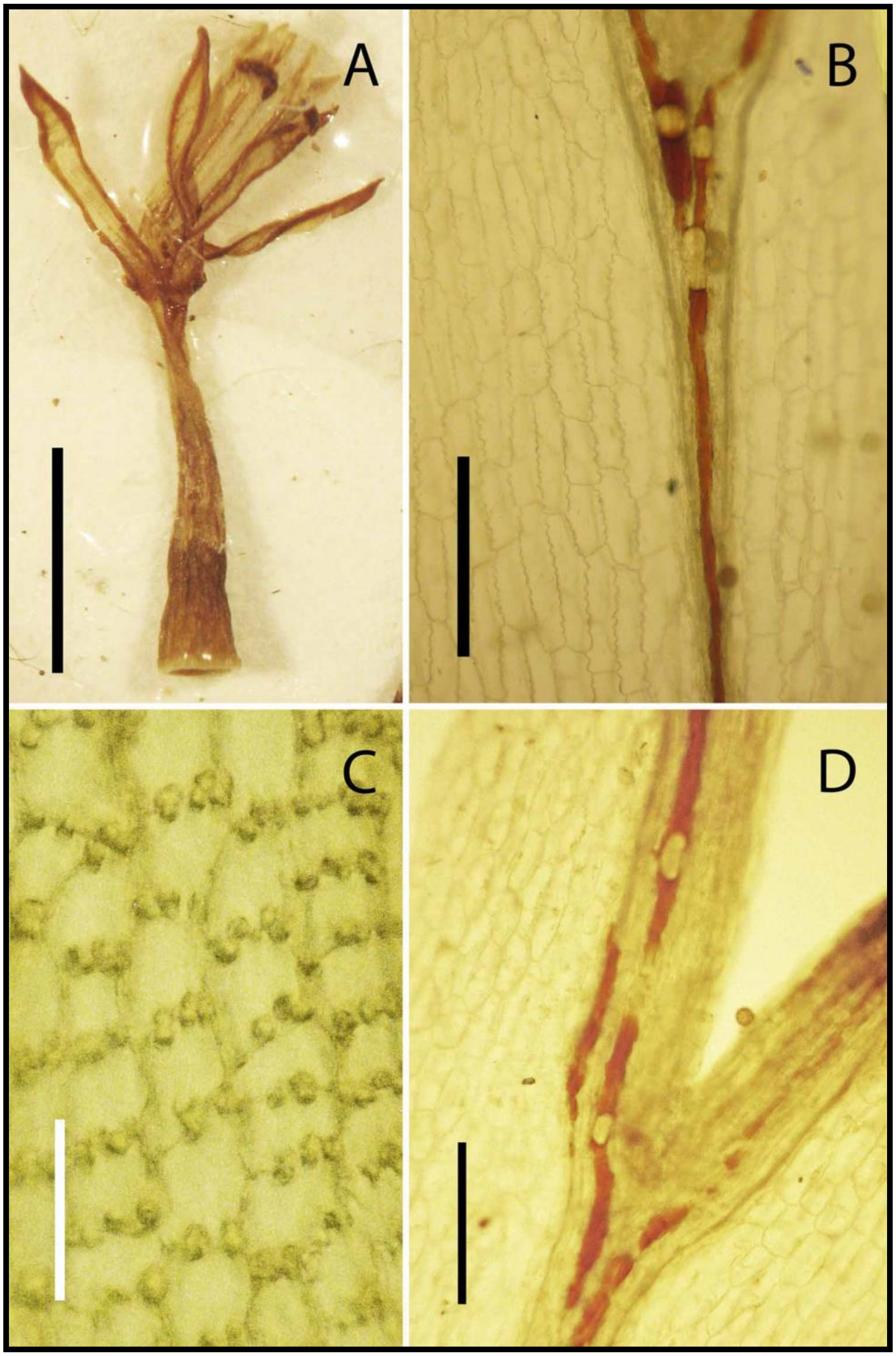


Figure 37. *Laceanthos* Pruski, floral features. A. *Laceanthos hasslerianus* (Chodat) Pruski, disk floret (cypsela removed), showing salverform corolla, unusual in the genus, with elongate spreading corolla lobes and anther and filaments fully exposed above the very short throat. B–D. *Laceanthos acaulis* (Baker) Pruski. B. Resin ducts in corolla lobes (upper) merging in the throat (lower) into single reddish-orange resin duct. C. Endothecial tissue, polarized pattern. D. Corolla showing orange resin within resin ducts, showing lobe (upper center) with abnormal development two parallel resin ducts, and (bottom center) resin ducts that diverged from the single resin duct (out of field of view) of the disk corolla throat. (A *Zardini & Gamarra 51949*, MO; B–D *Dusén 15613*, S). Scale bars A 1.5 mm, B 0.2 mm, C 40 µm, D 0.1 mm.

The genus *Laceanthos* (Compositae tribe Neurolaeneae) is newly described for eight southern South American *Calea* Alliance helianthoid species that are open-cymose or umbelliform-capitulate opposite-whorled-leaved low herbs with basically equally spaced internodes (except for *L. acaulis*) and caudices with thick fleshy roots. The capitulescences are commonly well-exserted from the uppermost leafy nodes. *Laceanthos* is further characterized by moderately conduplicate broad paleae (Fig. 42B) reaching only to the disk corolla tubes (Fig. 36A–B) and never to the tips of the disk pappus, glabrous disk corollas (Figs. 36C, 37A) with reddish-orange to orange resin within ducts (Fig. 37B, 37D), ducts single along veins in disk corolla throat (Fig. 37B), pale anthers (Fig. 36B) with a polarized endothecium (Fig. 37C), often pinkish pappus scales (viz the non-published description of the genus "*Pyrrhocarpha* Mart." on a BR specimen: photograph 10.13) that are longer than the plump, always setulose–setose and eglandular cypselae (Fig. 36) that have twin trichome terminal cell apices connate or slightly divergent. Strangely, the disk corollas of *Laceanthos* on occasion have lobes with paired resin ducts (Fig. 37D) and/or trichome-like tissue at the throat-tube juncture. The trichome-like tissue sometimes seen in *Laceanthos* flowers near the disk corolla tube-throat juncture may be in association with some sort of damage, but no similar tissue has be seen in damaged corollas of other *Calea* Alliance members.

The species that are the basis of *Laceanthos* are often yellow-flowered and whorled-leaved, but *C. cymosus* is ochroleucous-white-flowered (Fig. 40) and a second species is often ochroleucous-white-flowered. *Laceanthos* contains five radiate-capitulate species: *L. acaulis* (Baker) Pruski, *L. crenatus* (Chodat) Pruski, *L. cymosus* (Less.) Pruski, *L. mediterraneus* (Vell.) Pruski, and *L. rhombifolius* (S.F. Blake) Pruski. In radiate species of *Laceanthos*, the disk corolla lobes are usually triangular-lanceolate and shorter than the disk corolla throats (Fig. 36), the typical condition of most helianthoids. Three of the radiate species are primarily opposite-leaved (Figs. 39, 41) (*L. cymosus* is fairly variable in this regard, however), *L. acaulis* is basal-leaved and scapose-acaulescent (Fig. 38), and *L. mediterraneus* is whorled-leaved (Fig. 44). The three discoid-capitulate species—*L. chapadensis* (Malme) Pruski, *L. hasslerianus* (Chodat) Pruski, and *L. reticulatus* (Gardner) Pruski—are each whorled-leaved (Figs. 35, 43, 45). Among the discoid species, the common and broadly delimited *L. hasslerianus* is many-flowered and moderately large-capitulate; otherwise similar, but smaller-capitulate, *L. chapadensis* and *L. reticulatus* are more narrowly distributed and more narrowly circumscribed. *Laceanthos* is typified by whorled-leaved yellow-flowered discoid-capitulate moderately-long-disk-lobed *L. reticulatus*, which is a typical element of this admittedly variable-in-non-technical-features genus. *Laceanthos reticulatus* has disk corolla lobes about twice as long as the throat, thus when compared to radiate species of the genus, the generitype may be said to be moderately-long-disk-lobed, but when compared to *L. hasslerianus* (Fig. 37A), however, is relatively short-disk-lobed. Brazilian *Laceanthos chapadensis* and *L. reticulatus* are infrequently collected, then often only in bud, and field work seems needed to satisfactorily delineate the provisionally recognized tomentose-leaved *L. chapadensis* that basically centers about *L. reticulatus*. These two discoid Brazilian species are in part circumscribed with a geographic element in mind, as are the similarly weakly distinguished radiate species pair of *L. crenatu*s and *L. rhombifolius*.

The nine species of *Laceanthos* were earlier referred by Pruski (1998a, 2005) to now defunct *Calea* sect. *Haplocalea*, which was originally described by Lessing (1832) as a subgenus typified by ochroleucous-white-flowered radiate-capitulate *C. cymosa* Less. Here, the new genus *Laceanthos* is described and typified by yellow-flowered discoid-capitulate material, yet includes *L. cymosus* in taxonomic synonymy. *Laceanthos* is basically delineated following the Pruski (1998a, 2005) circumscription of *Calea* sect. *Haplocalea*, an infragenus which until now has never been accorded generic stature. Phylogenetically, the mostly opposite-leaved fewer-capitulate open-cymose radiate-capitulate species—e.g., *L. crenatus* and *L. cymosus*—seem early divergent, albeit perhaps *L. cymosus* less so by derived ray corolla color. Several elements of *Laceanthos* are whorled-leaved and have relatively short disk corolla lobes, be they radiate capitulate, e.g., *L. mediterraneus*, or discoid-capitulate, e.g., *L. reticulatus*. Overall, however, the whorled-leaved condition is unusual in *Calea* Alliance members and in other helianthoids. Whorled-leaved discoid-capitulate salverform extremely long-disk-lobed (Fig. 37A) *L. hasslerianus* is considered a late-divergent *Laceanthos*, and the extremely long-lobed salverform disk corolla condition too, is anomalous in most helianthoids.

Pruski (1998a) recognized only seven species in *Calea* sect. *Haplocalea*, and mistakenly placed discoid *L. hasslerianus* in synonymy with radiate *L. mediterraneus*. Here, *L. hasslerianus* is recognized following Pruski (2005), and eight species are recognized in *Laceanthos*. The character of opposite vs. whorled leaves is neither stable nor monolithic, however: for example, mostly opposite-leaved *L. cymosus* is typified by suite of Sellow sheets that include some ternate-leaved individuals. Although leaf and stem pubescence may vary within species and within individuals, the range seen in the genus is illustrated by comparing the following two species. The common *L. cymosus* has characteristic asperous-hirtellous-scabridulous herbage and appears weak-pubescent, whereas in contrast the uncommon generitype *L. reticulatus* is characteristically abaxially white-tomentose-leaved. The abaxially densely white-tomentose leaves of *L. chapadensis* are atypical in the *Calea* Alliance and as well as atypical among helianthoids, albeit this character may be at least in part influenced environmentally. *Laceanthos mediterraneus* and *L. hasslerianus* seem effectively heterotrichous by their densely asperous-hirtellous-scabridulous underlayer of herbage—recalling *L. cymosus*—but are overtopped by few scattered much longer uniseriate non-glandular trichomes. Several species (e.g., the aforementioned *L. hasslerianus* and *L. mediterraneus*) occasionally have six or more leaves per stem node, and pluribracteolate pseudoumbels. Here, it seems as though three compact nodes without associated internodes are present, but this reasoning cannot apply to the common occurrence of ternate-leaved (i.e., with three leaves per node) individuals in the genus. The umbel-like groups too sometimes seems compacted and thus umbelliform, as evidenced by several leafy bracts at what, perhaps incorrectly so, I (loosely) call a single terminal node. For example, often in *L. cymosus* the node subtending the capitula in 3-capitulate plants is opposite-bracted, but often the subtending node of 5-capitulate plants is 4-bracted. Several species are pluricapitulate and umbelliform, whereas others have open cymose capitulescences. *Laceanthos acaulis* most often has two compacted basal nodes, is 4-leaved, and seems scapose-acaulescent, the only such species of *Laceanthos*. The wide swings in indument characters, leaf arrangement, capitula type, and capitulescence forms are features, however, that are variously combined among the eight species of *Laceanthos*.

This group thus displays a traditional character labyrinth, and is nearly monophyletic with some variation the result of hybridization and reticulate evolution. Microcharacter apomorphies are given in a companion paper, and the plants of this lineage are described as the new genus *Laceanthos* for use in microcharacter studies, floras, and checklists. The eight species treated in *Laceanthos* follow.

LACEANTHOS ACAULIS (Baker) Pruski, **comb. nov.** *Calea acaulis* Baker, in Martius, Fl. Bras. 6(3): 266. 1884. **LECTOTYPE** (designated by Urbatsch et al., 1986): **PARAGUAY**. Itapé, 9 Sep 1874, *Balansa 807* (lectotype: K, photograph 12.0 and kodochrome 83.16, barcode K000323159; isolectotypes: F, G negative 11740 Herb. Candolle, P, US). US is a fragment of K. The second syntype collection was collected nearly two years after the first; I have seen two Paris sheets of the syntype *807a* collected 1 Apr 1876 at Caaguazú, and Berlin had a sheet of 807a, now destroyed; the *807* series (i.e., *807*, *807a*, etc.) is obviously a taxon number series. Figures 36C, 37B–D, 38.

Calea bipontinii Krasch., Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 4: 50. 1923. **TYPE: BRAZIL.** [**Mato Grosso do Sul**]. Rio Pardo, Sep 1826, *Riedel 512* (holotype: LE, photograph 9.28 and negative 11776). *Calea rotundifolia* Sch. Bip. ex Krasch., pro syn.

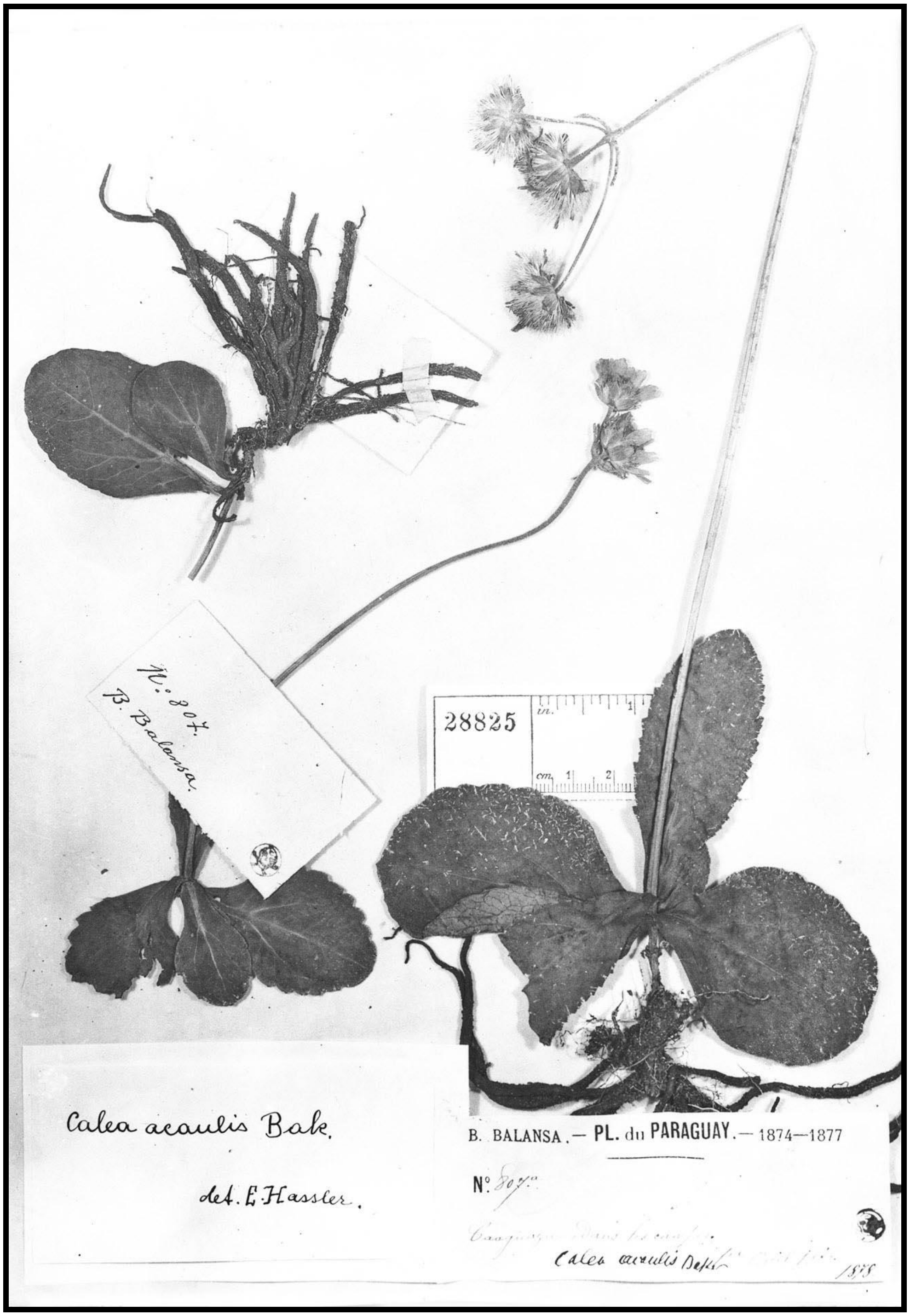


Figure 38. *Laceanthos acaulis* (Baker) Pruski, destroyed syntype. (*Balansa 807a*, B†, Macbride neg. 28825).

Laceanthos acaulis (Baker) Pruski is known from Paraguay and Brazil. In Brazil it is centered in São Paulo and Paraná, with the holotype of synonymous *C. bipontinii* is labeled as along Rio Pardo in adjacent Mato Grosso do Sul (viz Urban 1906: 91; Krascheninnikov 1923: 50). *Laceanthos acaulis* is the only scapose-acaulescent species in the genus and is typically open-cymose albeit sometimes monocephalous (Krascheninnikov 1923, viz holotype of *C. bipontinii* Krasch.). Most plants have only two pairs of leaves, which are nearly superimposed and thereby clearly decussate, an arrangement typical of members of the *Calea* Alliance. This radiate species is yellow-flowered, and a very distinctive element among the five radiate-capitulate species of *Laceanthos*.

LACEANTHOS CHAPADENSIS (Malme) Pruski, **comb. nov.** *Calea chapadensis* Malme, Ark. Bot. 24A, no. 8: 51. 1932. **TYPE: BRAZIL. Mato Grosso**. Santa Anna da Chapada, 28 Jul 1902, *Malme II. 2123* (holotype: S numbered S-R-862, photograph 3.35, ektachrome 84.20, and negative 11772; isotype: S photograph 3.34). The volume part number 8 is needed in the citation as each part number is paginated from page 1 onward. The holotype is annotated on a second label in Malme's hand as "Typus!" whereas the isotype is marked only with the binomial on the collection label. Santa Anna da Chapada is alternatively called Chapada dos Guimarães, and is just NE of Cuiaba. Figure 35.

Laceanthos chapadensis (Malme) Pruski is endemic to Brazil, and odd in its abaxially white-tomentose whorled leaves. The morphology is consistent, however, in topotypes (e.g., *Saddi et al. 3225*, RB), material from adjacent Goiás (e.g., *Irwin & Soderstrom 8448a*, NY, RB, US, etc. from Serra do Caiapó), and plants further-to-the-northeast (e.g., *Harley & Souza 10954*, P, from Geraldo Dao). Discoid-capitulate *L. chapadensis* seems most similar to *L. hasslerianus*, and perhaps less similar to the far-less-pubescent *L. reticulatus*. The disk lobes of *L. chapadensis* are about twice as long as the throat, but relatively short when compared to those of discoid *L. hasslerianus*, the latter having salverform corollas and lobes cut to near base of throat. *Laceanthos chapadensis* has a distinct disk throat within which the filaments are held, rather than being fully visible, as in *L. hasslerianus*. Nonetheless, these two species by their whorled leaves, yellow corollas, and umbelliform capitulescences are taken as typical mainstream members of *Laceanthos*.

LACEANTHOS CRENATUS (Chodat) Pruski, **comb. nov.** *Calea crenata* Chodat, Bull. Herb. Boissier, sér. 2, 3(8): 726. 1903; (see also extract in Chodat, Pl. Hassl. II: 154. 1903). **LECTOTYPE**, designated here, chosen from among three syntype collections: **PARAGUAY**. Apa, Dec 1901/2, *Hassler 8303* (lectotype sheet, designated here: G-Hass, photograph 11.22, barcode 00195695, the "Herbier Emil Hassler" label was attached after 1984, when this annotated loan sheet was returned to G; isolectotypes: BM negative 11620, NY). Figure 39.

Chodat cited three syntype collections, and here *Hassler 8303* is designated as the lectotype collection. However, I find no sheet in the Chodat personal herbarium, and the G-Hassler herbarium lectotype sheet was not annotated with the binomial until 1983. Although a Chodat herbarium sheet may exist and may be found, I have studied the lectotype designated here, which I found to match the protologue in essential details. One syntype, *Hassler 8303a*, is robust and has a large plant with 5 variously mature capitula, is known to me from only a single sheet, thus is not used as lectotype. Rather, *Hassler 8303* is designated as the lectotype collection to fix application of the name, is the collection in best flower, has duplicates in two other major herbaria, and two specimens in the lectotype suite each have several individuals. The BM isolectotype is databased on the web as the lectotype.

Laceanthos crenatus (Chodat) Pruski is phylogenetically an early divergent member of *Laceanthos* as seen by its morphology of an open-cymose capitulescence, yellow-flowers, and radiate capitula. *Laceanthos crenatus* also has phyllaries glandular and pilose, and has mostly opposite leaves trinerved from above the base. In these regards, it is very similar to Bolivia-centered *L. rhombifolius*. *Laceanthos crenatus* was described from Paraguay, and is known also in Mato Grosso, Brazil. *Calea crenata* Sch. Bip. nom. illeg. pro syn. (viz Baker 1884) is a different genus and species. *Podocalea oligocephala* DC., atypical in *Podocalea* by its distal second capitulum and differing by its broader outer phyllaries, nevertheless recalls *L. crenatus*.

Figure 39. *Laceanthos crenatus* (Chodat) Pruski, isolectotype. (*Hassler 8303*, NY).

Figure 40. *Laceanthos cymosus* (DC.) Pruski, the cymose capitula in this species have ochroleucous ray corollas, yellow disk corollas, and pale yellowish anthers and styles. (Photograph by Mauricio Bonifacino, sent for use in Pruski 2004a, voucher not seen).

LACEANTHOS CYMOSUS (Less.) Pruski, **comb. nov.** *Calea cymosa* Less., Linnaea 5: 158. 1830. **TYPE**: **BRAZIL or URUGUAY**. Locality not clearly readable on the Berlin holotype (Fig. 41), Feb 1823, *Sellow s.n.* (holotype: B† Macbride neg. 15364, one plantlet opposite-leaved, the second whorled-leaved; lectotype, designated by Gutiérrez et al. 2015, 178: HAL, annotated in Lessing's hand, whorled-leaved, photograph 1.31 and ektachrome 84.14; possible isotypes: BR binomial in Lessing's hand as *3326* photograph 3.28 and ektachrome 84.7, G-DC as IDC microfiche 800. 976.I.7, K-2 both p.p. distributed from Berlin in 1859 photograph 12.8 + kodachrome 83.19 and second sheet distributed from B in 1863 [sic] photograph 12.28, LE photograph 9.17, LY as *3940* and dated 1818 (unmounted Gandoger Herbarium) photograph 3.29 and ektachrome 84.6, P distributed from Berlin in 1861, W photograph 9.16). Figures 40–41.

The Sellow holotype locality is possibly Queguay, the locality in the Urban (1906) itinerary––compiled from select families—seemingly most closely matching localities Urban gave for Jan–Mar 1823. The Sellow locality is also possibly Chapicuy, Uruguay (Fig. 41 shows label at the bottom), however this is a locality not in the Urban (1906) listings of February 1823 Sellow collection localities. B and HAL are indeed possibly of a single gathering, or at least the whorled-leaved (3 leaves per node) stems are seemingly of the same gathering, or were treated by Lessing as of the same gathering.

The Sellow sheets cited here are all certainly conspecific and the application of the name is not in doubt. Although the collection numbers and localities of these sheets are unknown, it seems fine taxonomically to consider the HAL sheet the lectotype sheet, and the others as possibly isotypes. I use isotypes here, because Dan Nicolson (pers. comm.) once told me that in cases involving destroyed Berlin holotypes, that the isotypes (if any) (should) continue to be called isotypes, and that the only isotype that changes nominal status is the lectotype sheet. Indeed, in 1984 I annotated as isotype the HAL sheet, the then-undesignated lectotype. The same method of using the word/concept of isotype is favored by me elsewhere on occasion, for example, in treating Chodat names with a single type numbered collection but with multiple (Hassler) sheets in G from various formerly personal herbaria.

The destroyed holotype had a right hand branch with midstem node with ternate mature leaves, also has the node subtending umbelliform groups has ternate large leaves, not seen on the possible isotypes. Sellow's cousin crossed-out the "w" from the name Sellow on the Berlin sheet (né Sello, Sellow added the "w" to his name while living in Brazil), but did not do so on the HAL sheet. The handwriting of the binomial and of *Brasilia* on B and HAL is that of Lessing, but the 's' in the words *cymosa* and *Brasilia*, for example, on the K and P sheets are not typical of Lessing's hand. The blue-inked label on each K and on P is of the same hand, and these material was distributed decades after the death of Sellow. Some stem nodes on each G, K, LE, P, and W seem to be 4-leaved. These aforementioned sheets are unnumbered, i.e., *Sellow s.n.* Much Macbride-photographed B materials in Compositae do not show label data and many Sellow B sheets must be taken as *Sellow s.n.*, yet the photographed materials nonetheless influence our typifications. On occasion, Baker (1884) cited more than a single Sellow number under individual species, the citations hard to reconcile with single B sheets photographed by Macbride. Even though the phototype of the B sheet of *L. cymosus* shows the locality information, I remain uncertain of specific localities of the several sheets that I call possible isotypes.

It is not clear to me whether the numbers on the BR and LY sheets are collection numbers or herbarium-distribution numbers. Although this species is common and thus possibly/presumably collected more than once by Sellow, although BR is numbered *3326* and LY is dated 1818 and numbered *3940*—Urban 1906: 110 gives 4300 numbers collected on trips II and III including collections from 1818, and trips consecutively numbered the LY 3940 could be from among the 4300 numbers of /near 1818—all the Sellow materials seen are taken by me as very provisionally possibly of a single gathering: they are certainly conspecific. It is less common in Compositae to see Sellow sheets numbered, yet the BR and LY sheets are numbered. *3326* and *3940* may be collections numbers, however, from either pre-1823 trips or from post-1823 trips, rather than herbarium numbers, and thus B, BR, and LY each may be from different gatherings, but this is unknown. On the other hand, because some possible isotypes were distributed decades after the death of Sellow, some label information given is understandably minimal. Many collections distributed from the Olfers handled materials well after the death of Sellow in 1831 are collections without numbers and without specific localities or with the country incorrect. For example, although Uruguay separated from Brazil before the death of Sellow, some material from Uruguay was nevertheless labeled Brasilia. The date 1830 on G-DC may be an accession date, rather than date of collection. Rupert Barneby (pers. comm.) once told me that when blue or red colored ink is used on Sellow sheets and labels that the ink color may indicate that particular collection is from Sellow trip 6 1829–1831, but *L. cymosus* may not have been collected on that trip. I give this digression to stress that here in the case of *Laceanthos cymosus*, as well as in other unnumbered Sellow sheets seen, I often cannot tell (from my notes, which sheets are of the same flowering stage, or how individual specimens dried) which sheets may be of same gathering. Therefore, I often annotate Sellow duplicates as "possibly" type material.

Laceanthos cymosus (Less.) Pruski is widely distributed and known from Argentina, Brazil, Paraguay, and Uruguay. Along with *L. hasslerianus* and *L. mediterraneus*, it among the most common species of the genus. The common species—the type of *Calea* sect. *Haplocalea* (Less.) Pruski—is somewhat atypical of *Laceanthos*, however, being characterized by cream-white ray floret corolla limbs, finely and densely asperous-hirtellous-scabridulous herbage, opposite or whorled leaves trinerved (the main 3-5 veins are sometimes very pale colored) from their bases, and by relatively large ovate green thin outer phyllaries. Jana and Mukherjee (2015: fig. 4) illustrated well the cross-sectional anatomy of cypselae of *L. cymosus*.

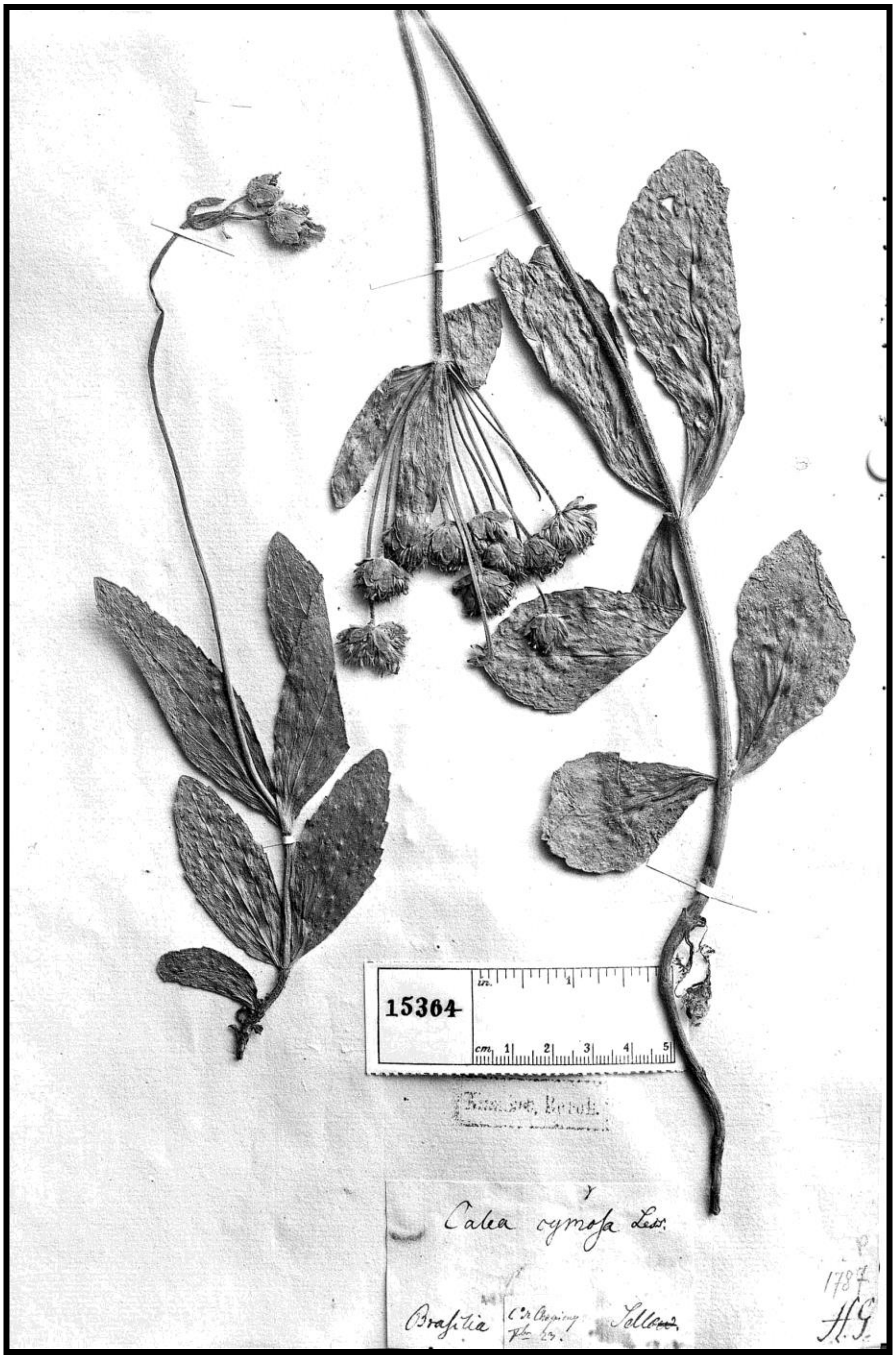


Figure 41. *Laceanthos cymosus* (Less.) Pruski, destroyed holotype. The large leaves subtending the cyme of the plant on the right-hand side of the sheet are among the largest bracteate leaves seen in the species and in the entire genus. (*Sellow s.n.*, B†, Macbride neg. 15364).

The ochroleucous ray flowers in *Laceanthos cymosus* superficially recall the sometimes white bracts of the totally unrelated *Calea lutea* Pruski & Urbatsch, a discoid species so named to highlight the yellow flowers of that plant occurring near austro-Amazonia, a zone awash with mauve Vernonieae and Eupatorieae that are more commonly encountered than are yellow-flowered helianthoids. There is a fine line drawing of *L. cymosus* in Cabrera (1974: 394, fig. 230).

LACEANTHOS HASSLERIANUS (Chodat) Pruski, **comb. nov.** *Calea hassleriana* Chodat, Bull. Herb. Boissier, sér. 2, 3(8): 727. 1903. nom. nov. (see also extract in Chodat, Pl. Hassl. II: 155. 1903). The basionym is: *Calea platylepis* var. *mollis* Chodat, Bull. Herb. Boissier, sér. 2, 2(4): 395. 1902; (see also extract in Chodat, Pl. Hassl. I: 166. 1902). **TYPE**: **PARAGUAY**. Apépu, (Tapiraguay), Aug 1900, *Hassler 4349* (lectotype, sheet designated here: G-Chod, sheet 1 of 2 in Herb. Chodat, now barcoded G00195684; isotypes: BM p.p. photograph 5.31, G-Chod sheet 2 of 2 in Herb. Chodat not barcoded, G-Hass photograph 5.32 + ektachrome 84.10 incorrectly annotated by me in 1984 as holotype and now barcoded G00092720, G-BOIS-2 sheets the top sheet of which is now barcoded G00092719 and the second sheet stamped as loan sheet 000317, K, LY, MO, NY, P-2, S, UC, US, W photograph 5.30). The US sheet is a fragment of one of the two sheets in the Chodat herbarium then at University of Geneva. Figures 37A, 42–43.

[*Calea hassleriana* forma *mollis* Chodat is illeg. with the correct name nomenclaturally for the typical forma being *Calea hassleriana* forma *hassleriana*, an autonym establish by simultaneous published heterotypic *Calea hassleriana* forma *rigida* Chodat; taxonomically, however, no infraspecies of *L. hasslerianus* are accepted by me].

In 1984, I annotated the herbarium Hassler sheet (G00092720) as holotype—presumably at one time seen by Chodat: it is marked Chodat-style with the "d"—but since I have seen the Chodat Herbarium material. The Chodat herbarium material was without question studied by Chodat, and sheet 1 of 2 is designated as lectotype sheet, fixing application of the name. This lectotype sheet is marked with both the Chodat 1902 trinomial and 1903 binomial, each name followed by *nob*., and with the 1902 trinomial in parentheses. The lectotype sheet has a secondary umbel, is very ample, and is discoid-capitulate as specifically mentioned in the expanded description in Hassler (1903: 727). The second of two sheets in the G-Chod lectotype folder of the lectotype seems authentic, has pencil lines drawings, but is not marked in Chodat's hand and is taken by me as an isotype. Given my (mis)annotation of the herbarium Hassler sheet as holotype, it seem best to designate a lectotype sheet. Moreover, because there is but a single protologue collection cited, all remaining sheets are following tradition called isotypes, albeit the ICN (the much modified ICBN) would like to have us do otherwise.

Calea cymosa var. *trichophylla* Baker, Mart. Fl. Bras. 6(3): 267. 1884. **TYPE**: **PARAGUAY**. Caaguazú, 1 Aug 1875, *Balansa 806c* (holotype: K, photograph 12.9; isotypes: G-Cand-2 sheets photographs 3.32–33 and the first as Macbride neg. 28829, P).

[806c is also a syntype collection of *Calea platylepis* var. *scabra* Chodat]. Caaguazú is equidistant between Asunción and Foz do Iguazu. The Kew holotype is whorled-leaved, discoid-capitulate, and has disk corollas deeply-lobed, hence my synonymy; more recently, I studied the two isotypes in Candolle herbarium at G; this is the earliest published name for this species.

Calea platylepis var. *scabra* Chodat, Bull. Herb. Boissier, sér. 2, 2(4): 395. 1902; (see also extract in Chodat, Pl. Hassl. I: 166. 1902). **LECTOTYPE**, designated here, chosen from among two syntype collections: **PARAGUAY**. Caaguazú, Nov 1874, *Balansa 806* (lectotype sheet, designated here: G-Cand, Herb. Candolle now barcode G00195686; isolectotypes: G-BOIS-2 sheets, P).

Hassler annotated the lectotype sheet as Baker's var. *trichophylla* and Chodat annotated the lectotype sheet directly on the Balansa label with the *scabra* trinomial and "nob." Neither isolectotype sheet is annotated by either Chodat or Hassler. The lectotype sheet is in old flower, labeled as "fleures jaunes" albeit without rays. In 1984 I annotated the budding discoid isolectotype as *Calea platylepis*, this when I considered discoid *L. hasslerianus* and radiate *Laceanthos mediterraneus* to be synonymous. The second cited syntype of *Calea platylepis* var. *scabra* Chodat is the conspecific *Balansa 806c*, an isotype of *Calea cymosa* var. *trichophylla*.

Calea hassleriana fo. *rigida* Chodat, Bull. Herb. Boissier, sér. 2, 3(8): 728. 1903; (see also extract in Chodat, Pl. Hassl. II: 156. 1903). **TYPE**: **PARAGUAY**. Prope Valenzuela, in valle fluminis Y-aca, Dec 1900, *Hassler 6789* (holotype: G; isotypes: B† as Macbride neg. 15370, BM p.p., K, MO, NY, P, S photograph 3.30, UC, US). The US isotype is a fragment of G-DEL. GH has a photograph of G. This collection is noteworthy in both its broad leaves and secondary pseudoumbels.

Laceanthos hasslerianus (Chodat) Pruski is fairly common in Argentina and Paraguay, and by far is the most common and larger capitulate of the three discoid species of *Laceanthos*. *Laceanthos hasslerianus* is the only discoid species (it was described as "flores omnes … tubulosi") not endemic to Brazil. The disk corollas are salverform, the throat extremely short, and the corolla lobes very elongate with the pale anthers thereby fully exserted. I mistook the anthers for ray corollas, perhaps furthering my confusion and cementing in my mind the one-time synonymy (viz, my uncritical synonymy in Pruski 1998: 684 of this discoid plant with radiate *L. mediterraneus*; a synonymy reversed subsequently by Pruski 2005: 2024). The corolla lobe-to-throat length ratio in this species is proportionally the greatest found in the genus. Some material of *L. hasslerianus* has leaves nearly as tomentose abaxially as are those of *L. chapadensis*.

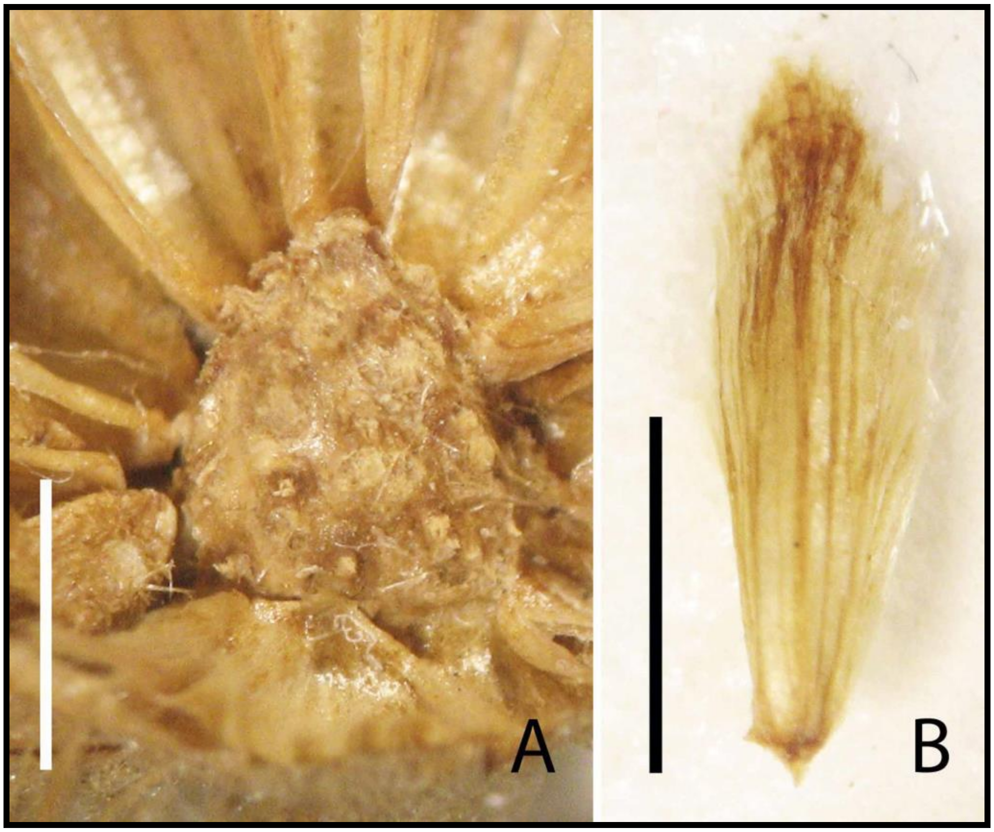


Figure 42. *Laceanthos hasslerianus* (Chodat) Pruski, select capitular features. A. Dome-shaped paleate clinanthium, some paleae removed. B. Moderately conduplicate broad palea, abaxial view, showing the striations and oblong outline; the palea are never obviously trifid as in *Calea* s. str. in figure 2 herein. (*Zardini & Gamarra 51949*, MO). Scale bars 2 mm.

Figure 43. Isotype of *Calea platylepis* var. *mollis* Chodat [≡ *Laceanthos hasslerianus* (Chodat) Pruski]. (*Hassler 4349*, MO).

Baker (1884), Chodat (1902, 1903), and Pruski (1998, 2005) each treated *L. hasslerianus* and *L. mediterraneus* variously. Baker (1884) treated *L. hasslerianus* as a different species than *C. platylepis*, albeit as a variety of *P. cymosa*. Chodat (1902) recognized a single species, but treated *L. hasslerianus* as a variety of *C. platylepis*. Pruski (1998) synonymized the two species and recognized them as *C. platylepis*; whereas Chodat (1903) and then a century later Pruski (2005) recognized them.

The filaments of *L. hasslerianus* are also usually fully visible, and the throat extremely short. The infraspecies described under *C. hassleriana* will be treated in a companion paper.

LACEANTHOS MEDITERRANEUS (Vell.) Pruski, **comb. nov.** *Buphthalmum mediterraneum* Vell., Fl. Flumin. Icon. 8: t. 135. 1827[1831]. *Calea mediterranea* (Vell.) Pruski, Sida 21: 2024, f. 1. 2005. **LECTOTYPE** (designated by Pruski, Sida 21: 2024. 2005): Velloso, Fl. Flumin. (Icones) 8: t. 135 (1827) 1831. Figure 44.

Calea platylepis Sch. Bip. ex Baker, in Martius, Fl. Bras. 6(3): 267. 1884. **LECTOTYPE**, chosen from among ten syntype collections: **BRAZIL**. **Minas Gerais**. Caldas, 1845, *Widgren 162* (lectotype, here designated: BR, annotated by Baker, photograph 11.14 and ektachrome 84.22; isolectotypes: C photograph 11.13, LD photograph 5.14, R fide Martins and Esteves BMN n.s. 111: 8. 2000, S-2 photographs 11.7–8, UPS-3 photographs 11.10–12 and one as ektachrome 84.1 each of the three annotated by Sch. Bip. as both *C. platylepis* and *C. verticillata*). The LD and UPS sheets are not numbered *162*.

In 1984, Pruski (en sched.) annotated the BR sheet of *Widgren 162* as lectotype of *Calea platylepis*. Indeed, *Widgren 162* is cited in the protologue, radiate-capitulate, and matches the protologue of *Calea platylepis*. Pruski (2005) deferred formalizing lectotypification at that time because syntype *Balansa 806a* is discoid-capitulate, referable to *L. hasslerianus*, and further study seemed appropriate. The Baker-cited reference of "*Calea verticillata Mart. herb*." is in reference to the herbarium name "*Calea verticillata* Sch.- Bip." used on sheets in P, UPS, W, and in the Martius herbarium in Bruxelles; it is not in reference to a collection made by Martius. In the interim, an attempted lectotypification of *Calea platylepis* by Gutiérrez et al. (2015: 179) was proposed, but cannot be followed because that specimen, *Martius s.n.* (K-Hook), because is neither cited syntype collection nor determined as *Calea verticillata*. A specimen in BR-Herbarium-Martii includes a five line hand-written Latin description of the non-published new genus "*Pyrrhocarpha* Mart." Here, I designate radiate-capitulate *Widgren 162* in BR as lectotype, fixing usage of the name as synonymous with L. *mediterraneus*.

Calea platylepis var. *reticulata* Chodat, Bull. Herb. Boissier, sér. 2, 3(8): 727. 1903; (see also extract in Chodat, Pl. Hassl. II: 155. 1903). **LECTOTYPE**, designated here, chosen from among three syntype collections: **PARAGUAY**. Region fluminis Apa, Feb 1901–1902, *Hassler 8490* (lectotype, sheet designated here: G-Chod, photograph 5.29, now barcoded G00092721; isolectotypes: BM p.p., G-BOISS, G-Hass, MO, NY, S, UC, US).

Laceanthos mediterraneus (Vell.) Pruski is one of the most common species of the genus, and is moderately frequent in Argentina, Brazil, and Paraguay (Pruski 2005). It was known as *Calea platylepis* Sch. Bip. ex Baker for more than a century. Pruski (2005) deferred lectotypification. Study of all available material allows for lectotypification herein, which agrees with the lectotypification of Pruski (en sched BR 1984). Much material of synonymous *C. platylepis* was originally marked as non-published *Calea verticillata* Sch. Bip. (non *Podocalea verticillata*). However, I have not seen the Prince Maximilianus (Princeps Neovidensis) syntype, and it is possible that not all syntype materials made during the life of Schultz Bipontinus (1805-1867) were seen or determined by him, but some perhaps later and only by Baker. I know of three descriptive names for synonymous *Calea platylepis*: *Pyrrhocarpha* alludes to the reddish pappus scales, *verticillata* is in reference to the leaf arrangement, and *platylepis* describes the broad phyllaries found in some (but fewer than half) collections in front of me. *Balansa 806a*, a syntype collected after the death of Schultz Bipontinus, is discoid-capitulate and determined by me as *L. hasslerianus*.

Figure 44. *Laceanthos mediterraneus* (Vell.) Pruski, lectotype. (Reproduced from Velloso, Fl. Flumin. (Icones) 8: t. 135 (1827) 1831; also reproduced by Pruski 2005: fig. 1).

Figure 45. *Laceanthos reticulatus* (Gardner) Pruski, holotype, generitype; the leaves of the BM holotype are obtuse-tipped and less deeply toothed than are those, for example, of the destroyed B isotype seen in Macbride neg. 15388. (*Gardner 3292*, BM).

Although by its whorled leaves *L. mediterraneus* is perhaps the quintessential *Laceanthos*, the name is typified by a drawing and is unavailable as generitype. Pruski (1998: 684) mistakenly treated discoid-capitulate *C. hassleriana* in synonymy of radiate-capitulate *C. platylepis*. In turn, all of my ca. 1984 annotations of materials as *Calea platylepis* are doubly incorrect: incorrect to genus and incorrect to species.

Pruski (2005: 2024) resurrected discoid *C. hassleriana* from synonymy, and also placed radiate *C. platylepis* into synonymy with *C. mediterranea*. Here, I follow the species-level taxonomy and synonymy of Pruski (2005), albeit now I treat these plants as members of *Laceanthos*. The small proximal-most whorl of leaves seen in the Velloso illustration (Fig. 44) are also typical of other species of *Laceanthos*, *Podocalea*, *Aspilia*, and a host of other southern South American helianthoids.

LACEANTHOS RETICULATUS (Gardner) Pruski, **comb. nov.** *Calea reticulata* Gardner, London J. Bot. 7: 416. 1848. **TYPE: BRAZIL. Goias.** Mission of Douro [as "Duro"], Oct 1839, *Gardner 3292* (holotype: BM, photograph 4.9, ektachrome 84.18, and negative 11736; isotypes: B† Macbride neg. 15388, K-Benth photograph 11.32, K-Hook, OXF photograph 5.5, P-2, US. The US sheet is a fragment of the Kew Hooker sheet. The types mostly have 3 leaves per node and stems 3-5 leafy nodes. Figure 45.

Ichthyothere ternifolia Baker, in Martius, Fl. Bras. 6(3): 267. 1884. **TYPE**: **BRAZIL. Minas Gerais.** Lagoa Santa, *Warming s.n.* (lectotype sheet, designated here: C, as Macbride neg. 22566). This collection is possibly a unicate.

Laceanthos reticulatus (Gardner) Pruski, the generitype, is endemic to Brazil and characterized by usually ternate-leaved nodes, and by its discoid capitula appears similar to the more southern whorled-leaved *L. hasslerianus*. The capitula of *L. reticulatus*, however, are about half of the size of those of *L. hasslerianus*. The budding lectotype of *Ichthyothere ternifolia* Baker is a good match for *L. reticulatus*. Transfer of the synonymous Baker name to *Calea* was never considered, and is blocked by the earlier *C. ternifolia* Kunth from Mexico.

The report of *L. reticulatus* in Uruguay (Arechavaleta 1907–1908: 354-355, pl. 76) is based on a misidentification of *L. cymosus*. *Laceanthos chapadensis* is a narrow segregate recognized for more northwestern tomentose-leaved populations, and it and *L. reticulatus* are represented by much imperfect material. Turner et al. (1979) reported a chromosome base number of x = 18 in *C. reticulata* but this count is based on a misdetermination of a future paratype of *Meyeria quadrifolia* (Pruski & Urbatsch) Pruski (*Turner 9143*, LL). The chromosome base number of *Meyeria* is thus taken as x = 18. True species as *Calea* have chromosome base number of x = 19 (Pruski and Urbatsch 1984; Wussow et al. 1985).

LACEANTHOS RHOMBIFOLIUS (S.F. Blake) Pruski, **comb. nov.** *Calea rhombifolia* S.F. Blake, Proc. Biol. Soc. Wash. 36: 53. 1923. **TYPE: BOLIVIA. Beni.** Distr. Yacuma, open pampa at Lake Rogagua, Oct 1921, *Rusby 2164* (holotype: US; isotypes: F, LE photograph 9.18, MICH, NY-2, UC).

Laceanthos rhombifolius (S.F. Blake) Pruski a long-time Bolivian endemic, it reported here as new to Brazil (Brazil. Mato Grosso. Serra da Pedro (Serra Aguapei), 11 Aug 1978, *Pires & Silva 16593*, NY) from along the Bolivian border, and about 350 kms WSW of Cuiabá. *Laceanthos rhombifolius* is the sole *Laceanthos* known in Bolivia. The species is yellow-flowered, radiate-capitulate, and is mostly opposite-leaved, recalling *L. crenatus*. The proximal leaves are trinerved from the very base of blade, whereas the more distal leaves are trinerved from above the blade base. *Laceanthos rhombifolius* is the only species of *Laceanthos* not illustrated here, but is a usually a narrower leaved plant than is *L. crenatus* (Fig. 39).

3. LEMMATIUM DC., Prodr. 5: 669. 1836. *Caleacte* Less., Linnaea 5: 158. 1830; Syn. Gen. Compos. 248. 1832 as "*Caleacte* Linnaea V. 158 nec R. Br." [non *Caleacte* R. Br., lectotype, from among two Robert Brown names, designated by Pfeiffer, Nom. Bot., ed. 1: 530. 1873: *Caleacte urticifolia* (Mill.) R. Br. ≡ *Calea urticifolia* (Mill.) DC.]. *Calea* sect. *Lemmatium* (DC.) Benth. & Hook. f., Gen. Pl. 2: 390. 1873. **TYPE:** *Caleacte rotundifolia* Less. [≡ *Lemmatium rotundifolium* (Less.) DC.]. *Lemmatium*, whether considered a replacement name for illegitimate later homonym *Caleacte* Less. 1830, 1832 or as newly described, was treated by Candolle as monotypic, and is typified by *Lemmatium rotundifolium* (Less.) DC.

Brasilia G.M. Barroso, Arch. Jard. Bot. Rio de Janeiro 17: 19, + unnumbered figure on page 20. 1959–1961 [1962–1963]. [ING gives (incorrectly so) the journal as "Arq. Inst. Biol. Veg.," which seems only to have four volumes published, those from 1934-1938, during the decade-long hiatus between Arch. Jard. Bot. Rio de Janeiro volume 6 (1933) and volume 7 (1947); the title page of Arch. Jard. Bot. Rio de Janeiro volume 17 has the printed date of 1959–1961, but the effective date of publication is not clear to me, ING gives 1962, whereas the Gray Cards and the bound Gray Herbarium Index vol. 2 (Atro–Chad): 281. 1968 dated the Barroso genus as 1963]. **TYPE:** *Brasilia sickii* G.M. Barroso [≡ *Lemmatium sickii* (G.M. Barroso) Pruski].

The southern Brazil-centered mostly tropical genus *Lemmatium* DC. (Compositae: tribe Neurolaeneae) was originally defined (Lessing 1830; Candolle 1836) by radiate capitula having florets with proximally connate pappus scales (Figs. 46, 47A, 54). Delessert (1839, 4: tab. 44), Dietrich (1847: 1579), Endlicher (1836–1840: 425), Meisner (1836–1843, 1: 207), Spach (1841: 18), and Walpers (1843: 629) are among those who treated *Lemmatium* at the generic rank. More than a century ago, however, *Lemmatium* was recast as *Calea* sect. *Lemmatium* (DC.) Benth. & Hook. f. by Bentham and Hooker (1873), who simultaneously added three other species to the group, none of which had the formerly generically diagnostic character of proximally connate pappus scales. *Lemmatium* was further demoted by Baker (1884; and Löfgren 1897) who treated it within *Calea* subgen. *Eucalea*. More recently, its species were placed into *Calea* sect. *Lemmatium* (e.g., Hoffmann 1894: 246; Urbatsch et al. 1986; Pruski and Urbatsch 1988). *Lemmatium* remains a genus of the *Calea* Alliance—marked by opposite leaves (Figs. 49, 53, 55–56), non-setose often glandular corollas (Figs. 46, 48), ray florets (when present) pistillate (Figs. 46B, 46D, 48, 54A, 55), pale anthers (Fig. 52B), distal style branches abaxially papillose (Figs. 48, 54A)—and is a typical member of tribe Neurolaeneae by its pappus scales in most species usually completely free from one another (Figs. 48, 51).

The stipitate quadrangular pilose cypselae is a key feature uniting the species of *Lemmatium*, and the irregularly knotted pluricelled longitudinally connate twin trichomes of the cypselae body are also particularly noteworthy (Figs. 46–48, 51A), suggesting an associated and uniformity of these distinctive characters in the genus. On average, there are up to about a dozen pappus scales per cypsela in *Lemmatium*, and the scales are usually nearly as long as the cypsela (Figs. 46–48, 51A). The form and length of pappus scales is a useful marker, but varies greatly in the genus, although it is more or less stable within individual species. For example, the scales of *L. diamantinense* are noticeably longer than the cypselae and the pappus scales of *L. clematideum* are very nearly laterally barbellate (Fig. 51), so much so that at times in poor material the pappus scales seem nearly blend into extremely strange cypselar twin trichomes of that species (viz also Barroso 1959–1961: 20c).

The distinctions between the conditions of radiate vs. discoid capitula are useful at the species level, but provide no basis for generic rank separations. Urbatsch et al. (1986) reduced *Brasilia* G.M. Barroso to *Calea* sect. *Lemmatium* and although generitype *Brasilia sickii* (now *Lemmatium sickii*) is discoid-capitulate, it had proximally connate pappus scales matching those of radiate-capitulate *L.*

rotundifolium, the type of *Calea* sect. *Lemmatium*, i.e. *Lemmatium*. Expression of the knotting in the twin trichomes of the cypselae in *Lemmatium* also varies from weakly so in *L. sickii*, to moderately so in *L. rotundifolium* (Fig. 47), to especially strongly so (Fig. 51) in *L. clematideum*.

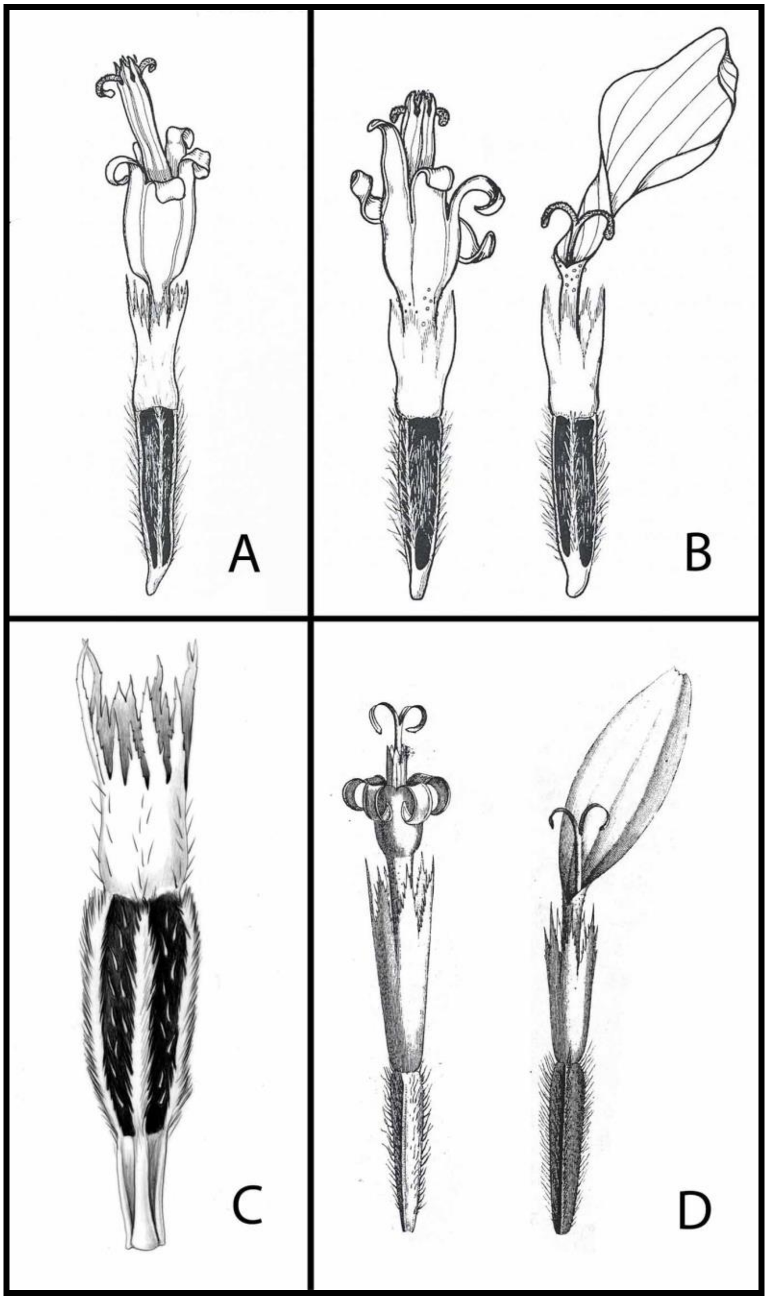


Figure 46. Cypselae and florets of *Lemmatium* DC. The stipitate cypselae are representative of the genus, whereas proximally connate unequal pappus scales are known only in the two species shown here, the generitypes of *Lemmatium* and synonymous *Brasilia* G.M. Barroso. A, C. *Lemmatium sickii* (G.M. Barroso) Pruski, a discoid-capitulate species that is the generitype of *Brasilia*. B, D. *Lemmatium rotundifolium* (Less.) DC., generitype, radiate-capitulate with rays pistillate. (A–B Drawn by Amy Zlotsky, modified from Urbatsch et al. 1986; C Drawn by Alice Tangerini, reproduced from Robinson 1981: fig. 141 as *Brasilia sickii*; D modified from Delessert, Compositae-Senecionideae, Icon. Sel. Pl. 4: tab 44. 1839).

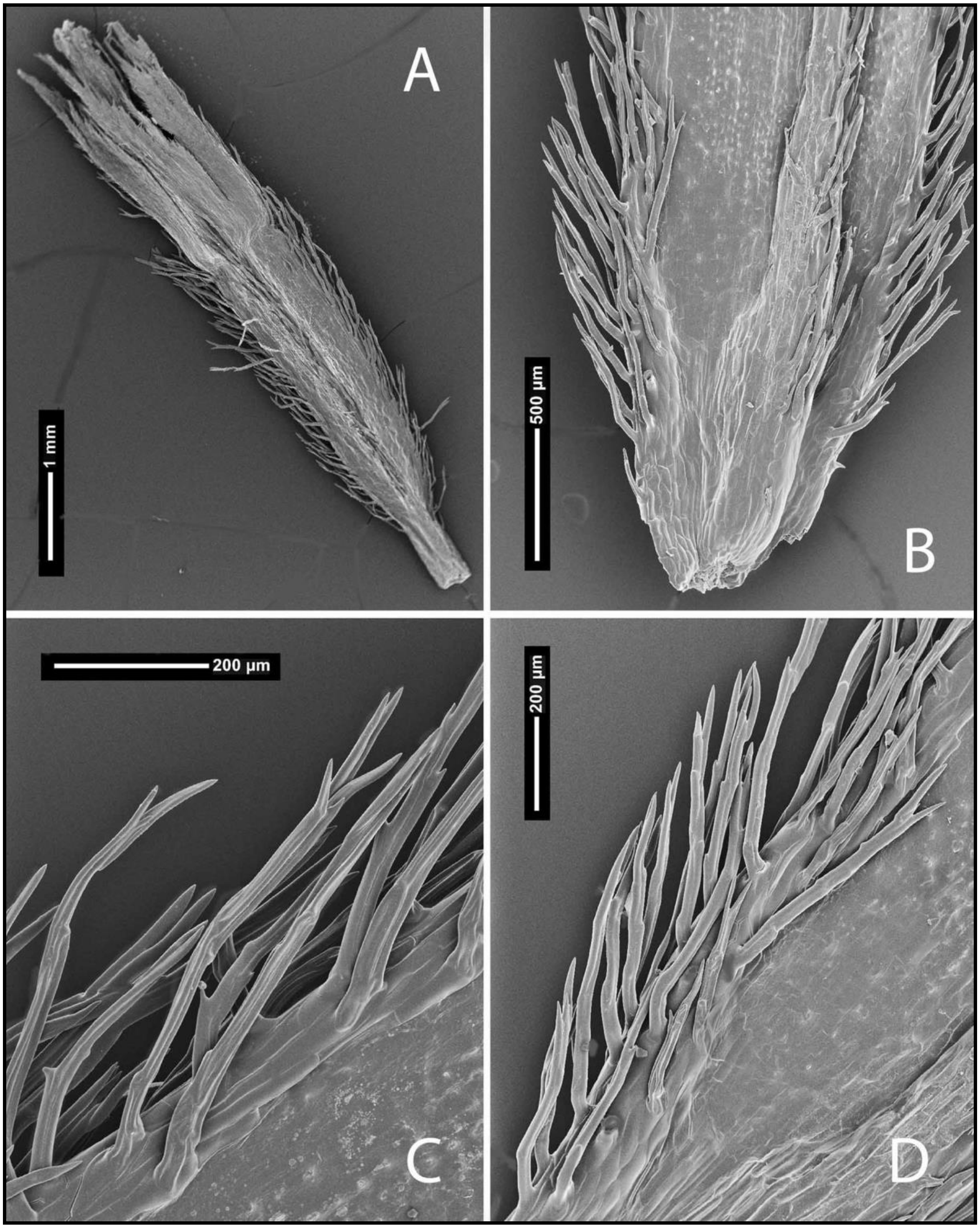


Figure 47. *Lemmatium rotundifolium* (Less.) DC., the generitype, cypselae and multicellular knotted twin trichomes. A. Cypsela showing angled body, stipitate carpopodium, and proximally connate unequal pappus scales nearly as long as cypsela body. B. Close-up of the nearly symmetric stipitate carpopodium and proximal twin trichomes. C–D. Close-ups of the knotted twin trichomes with free-diverging terminal cells; extremes in twin trichome knotting in *Lemmatium* range from weakly so with merely slightly divergent apical cells in *L. sickii* to strongly so with even the mid trichome cells with tips diverging laterally in *L. clematideum*. (*Anderson 9007*, MO).

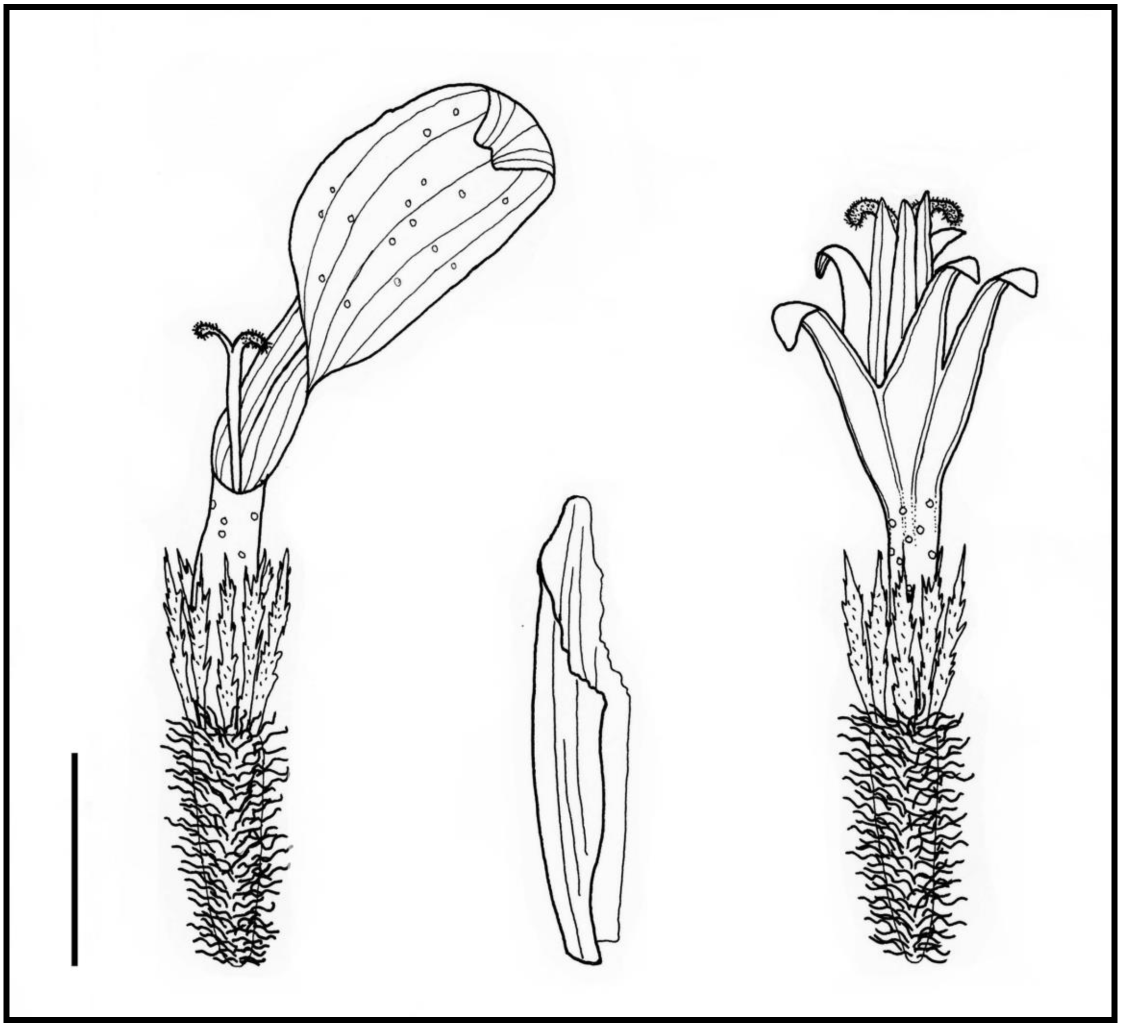


Figure 48. *Lemmatium brittoniaum* (Pruski) Pruski, showing (left to right) ray floret, palea, disk floret. The pappus scales are free throughout, the cypselae are densel-setose with irregularly knotted twin trichomes. (Drawn by Kristin Malin from *Saint-Hilaire Catal. C1, 357*, P, the holotype; modified from Pruski 1984). Scale bar 3 mm.

Species placed in *Lemmatium* here largely follow the species grouping or sectional placements and boundaries of Baker (1884), Urbatsch et al. (1986), and Pruski and Urbatsch (1988). Pruski and Urbatsch (1988) keyed the 12 species recognized by them within the group, which they recognized at the sectional level within *Calea*. Here, *Calea arachnoidea*, *C. clematidea*, *C. diamantinensi*s, and long-ignored *C. divergens* are each newly aligned and treated within *Lemmatium*. As delimited here, *Lemmatium* contains 16 South American species, and is centered in Brazil. The base chromosome of x = 19 reported by Wulff et al. (1996) for *L. clematideum* is refreshingly congruent with the present placement of *Lemmatium* in tribe Neurolaeneae adjacent to *Calea* s. str., which Pruski and Urbatsch (1984) gave $x = 19$ as the chromosome base number.

Of the 16 species recognized by me within *Lemmatium*, eight are discoid-capitulate and the eight others are radiate-capitulate. The eight discoid species of *Lemmatium* are *L. diamantinense*, *L. divergens*, *L. fruticosum*, *L. grazielae*, *L. intermedium*, *L. irwinii*, *L. morii*, and *L. sickii*. The eight radiate species of *Lemmatium* are *L. arachnoideum*, *L. brittonianum*, *L. clematideum*, *L. lemmatioides*, *L. nitidum*, *L. oxylepis*, *L. rotundifolium*, and *L. wedelioides*.

There is no pattern of strict sister radiate-discoid species pair relationships in the genus. For example, it appears the discoid pair *L. diamantinense* and *L. intermedium* are each other's most similar congener. On the other hand, discoid *L. fruticosa* and once-synonymous *L. morii* are similar, but similar too is radiate capitulate *L. rotundifolium*. Although radiate *L. rotundifolium* and discoid *L. sickii* are the only two species of *Lemmatium* with connate pappus bristles (Figs. 46, 47A), their capitulescence structure is much different, and they do not appear to be sister species. The capitulescences in *Lemmatium* vary from small-capitulate, pluricephalous and broadly corymbiform (Figs. 52A, 55) in some species to relatively large-capitulate, paucicephalous, and open-cymose (Figs. 49, 56) in other species. Discoid-capitulate *L. grazielae* (Fig. 53) and radiate-capitulate *L. wedelioides* are large-capitulate yet compact-cymose. The capitulescence form varies independent of the discoid vs. radiate capitular condition. The sixteen species recognized in *Lemmatium* are as follows.

LEMMATIUM ARACHNOIDEUM (G.A.R. Silva & J.N. Nakaj.) Pruski, **comb. nov.** *Calea arachnoidea* G.A.R. Silva & J.N. Nakaj., Phytotaxa 494: 130. 2021. **TYPE: BRAZIL**. **Minas Gerais**. Rio Preto, Vilarejo do Funil, 4 Nov 2017, *Reis-Silva et al. 299* (holotype: VIC; isotypes: K n.v., MO n.v.). [The first author of the species abbreviates his name "G.A. Reis-Silva"].

Calea saint-hilaireana Pruski & Urbatsch, Pruski (en sched.), V-1987. **TYPE: BRAZIL**. **Minas Gerais**. Sin. loc., [1821–1822], *Saint-Hilaire Catal. D 79 (1298)* (en sched Paris, now bar-coded P02412543). Dwyer (1955) gave the collection date as 1821–1822.

Lemmatium arachnoideum (G.A.R. Silva & J.N. Nakaj.) Pruski is a recently described as a pinnately-veined relatively large radiate-capitulate species from extreme southeastern Minas Gerais, Brazil, endemic to the region of Rio Preto. *Lemmatium arachnoideum* is placed in *Lemmatium* by its hairy cypselae with free nearly subequal linear-lanceolate pappus scales, even though I have not seen material with mature obviously stipitate fruits. The cypsela bases in immature *L. arachnoideum* resemble those at similar stages of development in *L. brittonianum* (Fig. 48), which also has pinnate leaf venation. *Lemmatium arachnoideum* was described as having unequal pappus scales, but the scales seem nearly subequal. Nevertheless, unequal pappus scales are well-known elsewhere in *Lemmatium*, and are especially manifest (Figs. 46, 47A) in the two species with proximally connate pappus scales. *Lemmatium arachnoideum* was described as heteropappose, and near the *Meyeria heteropappa* species group.

By its pinnate leaf venation and few relatively large cymose capitula, however, *L. arachnoideum* most closely recalls *Lemmatium wedelioides*, which Urbatsch et. al. (1986) map as found within 100 kms of Rio Preto, and as endemic to adjacent Rio de Janeiro, Brazil. Urbatsch et. al. (1986) describe the poorly collected *L. wedelioides*, has having relatively large capitula, these about 30–40-flowered. The protologue of *L. arachnoideum* gave the plant as capitula as about 35–50-flowered, and as having leaves glossy adaxially. Other species of *Lemmatium* with similar strongly nitidous leaves adaxially include *L. oxylepis* and especially *L. nitidum*. *Lemmatium arachnoideum* was first recognized by the author more than three decades ago (in May, 1987) as undescribed, and annotated as *Calea saint-hilaireana* Pruski & Urbatsch, based upon *Saint-Hilaire D, 79*, taxon *1298* (P, now barcoded P02412543). The material in Paris, however, was not in good flowering condition and it was deemed prudent to await better material before description. Generally speaking, because material of this species seen is often poor and past flower one cannot help but suspect that a short flowering period is a species trait. Another species trait appears to be (as in the related sticky-when-pressed *L. intermedium* and *L. oxylepis*) presence of arachnoid-like artifacts on the leaves especially when pressed in EtOH: I cannot confirm the nature of these arachnoid-like features on leaves *L. arachnoideum*.

Lemmatium brittonianum (Pruski) Pruski

det. John Pruski (MO), 2019
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Universidade de São Paulo – Herbário SPF

Compositae

Calea brittoniana Pruski
det. John Pruski, 2009

Brasil. Minas Gerais. São Roque de Minas. Parque Nacional da Serra da Canastra. Estrada que liga São Roque a Sacramento 20°15′28′′S, 46°25′15,8′′W. Altitude 1351 m.a.m. Afloramento rochoso ao lado de córrego.

Arbusto ca. 1,2 m. Folhas discolores. Capítulos amarelos.

M. Magenta 567, J.E. Magenta Neto, A. Pontes e M. A. Farinaccio 16.03.2003

Figure 49. Representative specimen of *Lemmatium brittonianum* (Pruski) Pruski, leaf blade surfaces are discolorous and the capitula are radiate. (*Magenta et al. 567*, MO).

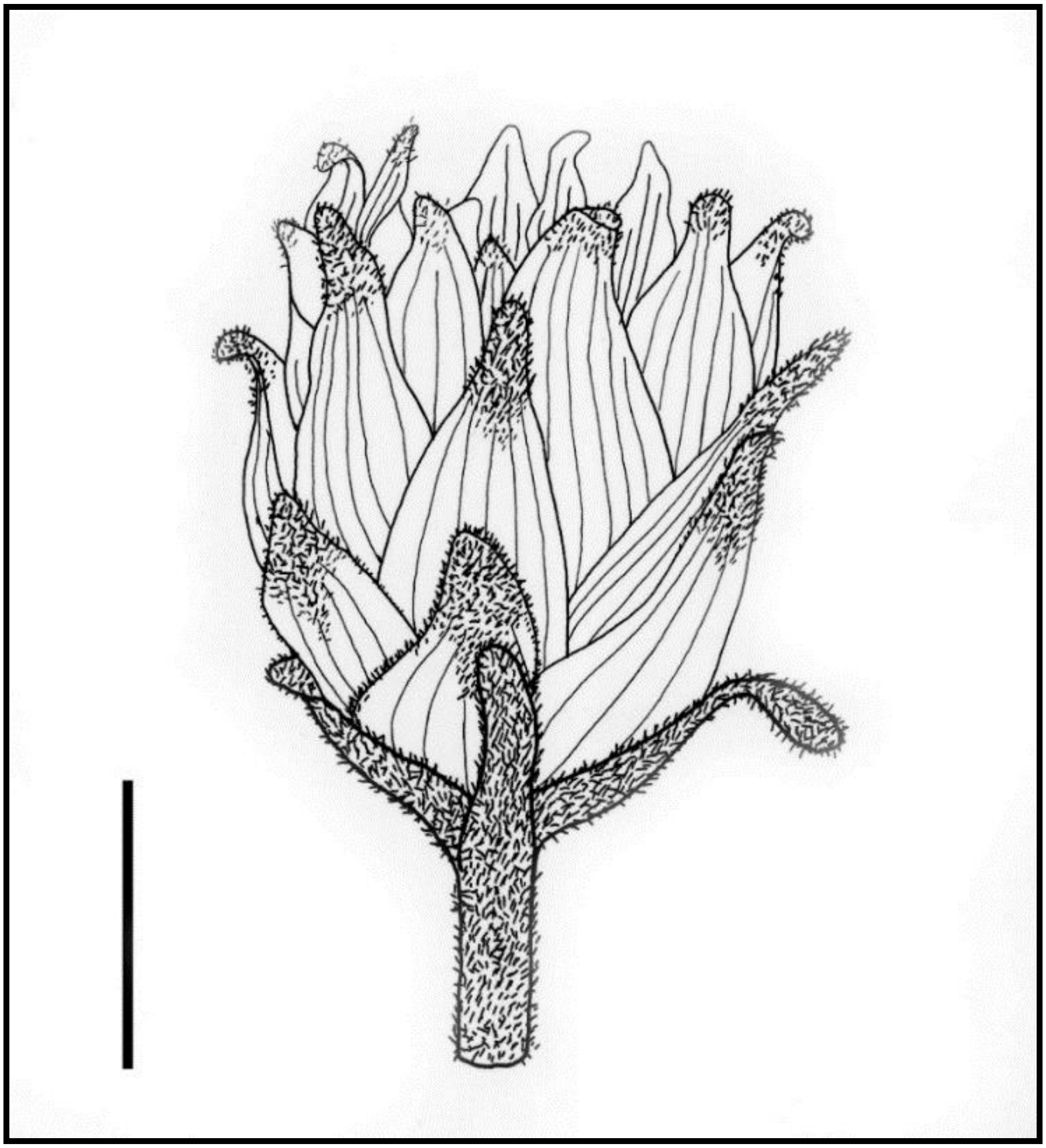


Figure 50. Capitulum of *Lemmatium brittonianum* (Pruski) Pruski, showing the hairy and herbaceous outer phyllaries. (Drawn by Kristin Malin from *Saint-Hilaire Catal. C1, 357*, P, the holotype; modified from Pruski 1984). Scale bar 5 mm.

LEMMATIUM BRITTONIANUM (Pruski) Pruski, **comb. nov.** *Calea brittoniana* Pruski, Brittonia 36: 98. 1984. **TYPE: BRAZIL**. **Minas Gerais.** Serra da Canastra, 9–16 Apr 1819, *Saint-Hilaire Catal. C1*, *357* (taxon 1309) (holotype: P, photographs 1.8 + 4.21 and ektachromes 84.17 + 84.31; isotypes: P-2). Figure 48–50.

Lemmatium brittonianum (Pruski) Pruski is recognized by its abaxially dense-rust-tomentose discolorous leaves with pinnate venation, green outer phyllaries, and mid-sized radiate capitula in open cymes (Figs. 48–50). *Lemmatium brittonianum* is known from only near Serra da Canastra in Minas Gerais, Brazil, but should be expected in adjacent São Paulo. The plant was first collected by Auguste Saint-Hilaire (viz Dwyer 1955), long-remained known from only this single collection, and went undescribed for more than a century. In the past few decades, however, the plant has been collected a few times, but still appears to be a narrow endemic.

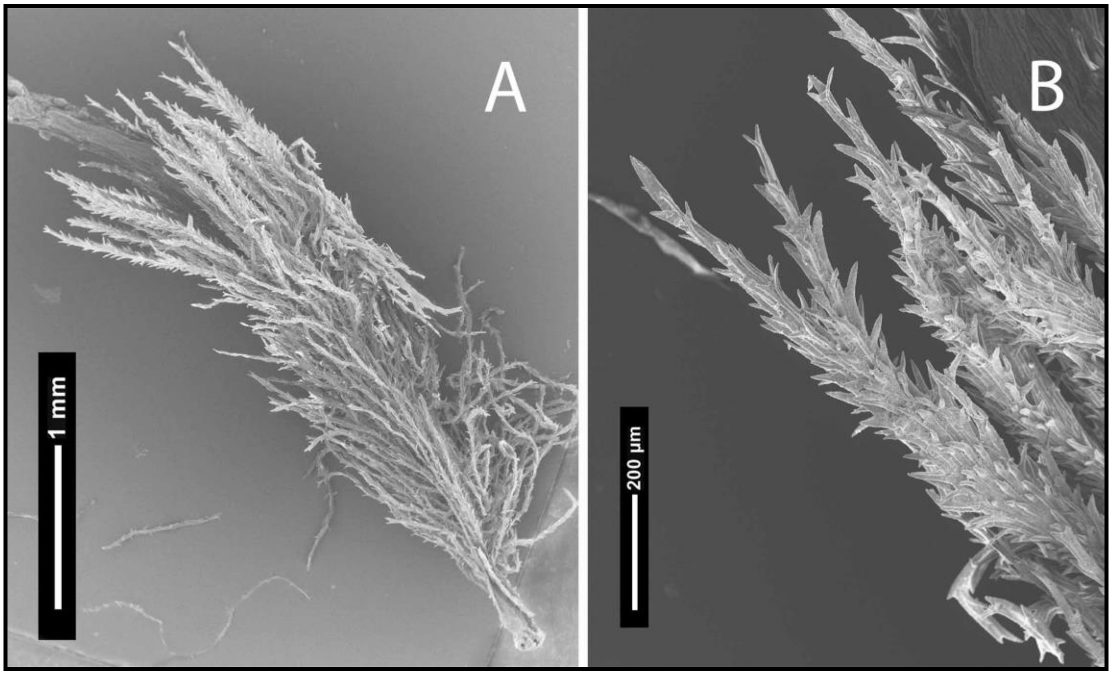


Figure 51. Cypselae of *Lemmatium clematideum* (Baker) Pruski, showing the irregularly knotted long twin trichomes overlapping with the very nearly laterally barbellate pappus scales. In poor material, these strange pappus scales seem to blend proximally into the equally strange cypselar twin trichomes. A. Cypsela (lower right) with free pappus scales (upper left). B. Close-up of pappus scales. (*Pérez 543,* MO).

LEMMATIUM CLEMATIDEUM (Baker) Pruski, **comb. nov.** *Calea clematidea* Baker, in Martius, Fl. Bras. 6(3): 262. 1884. **TYPE: PARAGUAY**. Asunción [as Assomption], Aug 1874, *Balansa 845* (holotype: K, photograph 12.6 and kodachrome 83.18, the binomial in Baker's hand is below the collection label on the upper left of the sheet, now barcoded K000323195; isotypes: BM, BR-2 one as photograph 2.25, F, G-3, LD, LE, P-3, S photograph 2.26). The holotype is marked as rec'd at Kew in 1/1878, was distributed to K as *C. serrata* Less., and is annotated by Baker with his binomial. Figure 51, 52B.

Calea rojasiana Chodat, Bull. Herb. Boissier, sér. 2, 3(8): 728. 1903; (see also extract in Chodat, Pl. Hassl. II: 156. 1903). **TYPE: PARAGUAY.** Concepcion, Sep 1901/2, *Hassler 7390* (lectotype, designated here: G-Chod sheet 1 with binomial in Chodat's hand, now barcoded G00092754; isotypes: BM p.p., F, G-BOIS 3 sheets barcode G00092652, G-Cand-2 sheets barcode G00092753, G-Chod sheet 2 not barcoded, G-Hass barcode G00092651, GH-A, K-2, LIL, LY, MICH, MO, NY, P-3, RB, S, UC, US-2, W). One US sheet is a fragment of the Chodat Univ. of Geneva sheet. Although Pruski (en sched 1983) annotated the Hassler herb. as "holotype," sheet 1 of 2 in the Chodat herbarium is designated here as the lectotype sheet. There appear to be eight isotypes in G, including the sheet I (mis)annotated in 1983 as holotype. I have seen more than 20 sheets of the type number.

Lemmatium clematideum (Baker) Pruski is among the most common species of *Lemmatium*, being known in Argentina, Brazil, Paraguay, and Uruguay. Arechavaleta (1907–1908) and Cabrera (1937), respectively, documented this species in Uruguay and Argentina. Extremes in severe pappus serrations and in knotting of the twin trichomes seen in *Lemmatium* are simultaneously reached in *L. clematideum* (Fig. 51), the southernmost species of the genus. Ferraz et al. (2009) evaluated *L. clematideum* pharmacologically. *Magenta et al. 599* gives the plants as "15 m" high, which seems to have been intended as 1.5 m tall.

Figure 52. A. *Lemmatium fruticosum* (Gardner) Pruski, habit of plants in late fruit showing the pluricapitulate flat-topped corymbiform capitulescence and the capitula with dried brown phyllaries. B. *Lemmatium clematideum* (Baker) Pruski, showing yellow-radiate capitula with exserted yellow anthers. (A Distrito Federal, Brazil, *Eiten & Pruski 16007A3534*, photograph of the writer behind waist-high plants, by George Eiten; B photograph by Mauricio Bonifacino, voucher not seen).

LEMMATIUM DIAMANTINENSE (G.A.R. Silva & J.N. Nakaj.) Pruski, **comb. nov.** *Calea diamantinensis* G.A.R. Silva & J.N. Nakaj., Phytotaxa 432: 200. 2020. **TYPE: BRASIL. Minas Gerais.** Diamantina, estrada Diamantina a Conselheiro Mata, 11 Oct 2017, *Reis-Silva et al. 289* (holotype: VIC; isotype: MO n.v.).

Lemmatium diamantinense (G.A. Reis-Silva & J.N. Nakaj.) Pruski is discoid-capitulate and a rare recently described endemic of Minas Gerais, Brazil. The sericeous cypselae with the carpopodium decurrent onto the ribs, are characters used by me best align provisionally non-dissected *L. diamantinense* with other species of *Lemmatium*. Indeed, *L. diamantinense* is nearly a dead-ringer in gestalt to *L. intermedium*, albeit the pappus scales are much longer than otherwise found in *Lemmatium*, the twin trichomes of the cypselae are only weakly-knotted, and the glands on the cypselae are also very odd for *Lemmatium*. The glandular disk corollas, however, render it in this regard as similar to the species of *Lemmatium*, e.g., *L. brittonianum*, *L. fruticosum*, *L. grazielae*, *L. irwinii*, *L. lemmatioides*, *L. nitidum*, *L. oxylepis*, *L. rotundifolium*, *L. sickii*, and *L. wedelioides*. *Lemmatium diamantinense* in involucres and floret numbers especially recalls *L. fruticosum* and *L. oxylepis*.

LEMMATIUM DIVERGENS (Sch. Bip. ex Baker) Pruski, **comb. nov.** *Calea divergens* Sch. Bip. ex Baker, in Martius, Fl. Bras. 6(3): 262. 1884. **TYPE: BRAZIL.** Engenho do Capit. Pires, [ca. 1819 ex itinerary], *Pohl diar. 446 (1792)* (lectotype, designated here: K-Hook, barcoded K000323386; isotypes: B† as Macbride neg. 15365 and labeled as var. *patens,* K-Benth, NY, P-Sch-Bip gives 446 but also gives 249 HRB …VINDOB, W-2 photographs 2.19–2.20). Although in 1982 I annotated the Hooker herbarium in Kew sheet as holotype, it now seem best to designated this as the lectotype sheet. Both Kew sheets of diar. number 446 are ample, both have Baker's handwriting and each were apparently examined by Baker, albeit perhaps seen, studied, and marked at different times. Following the old traditional code (ICBN) and Dan Nicolson's advice, the non-lectotype sheets of the single type gathering are called isotypes, although some (ICN) may quibble they should be called isolectotypes, however, that usage historically implies that there is more than a single type gathering, which in this case there is not. The Schultz-Bipontinus herbarium sheet in Paris-Cosson gives the Diar number but also "249" which seems to be a Vienna exchange number of some sorts rather than a Pohl number, a marking similar to that on the Paris sheet of var. *patens*.

Calea divergens var. *patens* Sch. Bip. ex Baker, in Martius, Fl. Bras. 6(3): 263. 1884. **TYPE: BRAZIL.** Bonfin, S. Cruz, Alvez d Caldas, [ca. 1820 ex itinerary], *Pohl diar. 443 (2686)* (lectotype, designated here; K-Benth; isotypes: F, K-Hook, NY-2 both ex W, P, P-Sch-Bip gives 443 but also gives 248 HRB …VINDOB, US, W photograph 2.21). The Bentham herbarium sheet in Kew has Baker's handwriting, whereas the Hooker sheet does not. The US isotype is a fragment of a P sheet.

Lemmatium divergens (Sch. Bip. ex Baker) Pruski is discoid-capitulate and known in Distrito Federal, Goiás, Minas Gerais, Brazil, albeit seemingly never common. The non-typical variety was described as having serrate leaf blades, but this distinction is not accepted in this species as taxonomically significant. In Baker (1884) an infraspecies of the basionym was given as "var. CALEA PATENS Schultz Bip." rather than clearly as the trinomial *Calea divergens* var. *patens*. In 1984 I incorrectly considered the name invalid, but shortly thereafter Rupert Barneby (pers. comm.) said that Baker's intent was obvious and the variety should be taken as valid. In any event, when I thought the infrataxon was invalid I incorrectly annotated the W specimen of *Pohl Diar 443 (2686)* (W) Diar 443 as a paratype of *C. divergens* typica, but it is an isotype of the variety. On November 10, 1997 Pruski noted (en sched. *Fonseca et al. 1032*, US) that the species belongs to *Calea* sect. *Lemmatium*.

LEMMATIUM FRUTICOSUM (Gardner) Pruski, **comb. nov.** *Amphicalea fruticosa* Gardner, London J. Bot. 7: 412. 1848. *Calea fruticosa* (Gardner) Urbatsch, Zlotsky & Pruski, Syst. Bot. 11: 506. 1986. **TYPE: BRAZIL. Minas Gerais.** On the confines of the province of Minas Gerais with that of Goias, Serra das Araras, Jun 1840, *Gardner 4925* (holotype: BM, photograph 1.12, ektachrome 84.25, and negative 11579; isotypes: K-Benth, K-Hook photograph 13.6]. Figure 52A.

Calea belemii H. Rob., Phytologia 44: 436. 1979. **TYPE: BRAZIL. Minas Gerais.** Mata Cipó, 27 Jun 1968, *Belem 3763* (holotype: US; isotypes: F, K, NY, RB, S photograph 1.30).

Calea heringeri H. Rob., Phytologia 47: 261. 1980. **TYPE: BRAZIL. Distrito Federal.** Brasilia, Bacia do Rio São Bartolomeu, 15 Apr 1980, *Heringer et al. 4383* (holotype: IBGE, kodachrome 87N12.26; isotypes: NY, US). (p. 261 as *herlingeri*, corrected on p. 263).

Lemmatium fruticosum (Gardner) Pruski, referred without combination to *Calea* by Bentham and Hooker (1873) and to synonymy with *L. rotundifolium* by Jackson (1893), is discoid-capitulate and relatively widespread in Distrito Federal, Goiás, and Minas Gerais, Brazil. The species was treated by Baker (1884) as synonymous with radiate-capitulate *L. rotundifolium*, but was resurrected from a century-long synonymy by Urbatsch et al. (1986). In turn, three similarly discoid-capitulate plants were treated in synonymy with *L. fruticosum* by Urbatsch et al. (1986), but soon thereafter one of these, *L. morii*, was reinstated by Pruski and Urbatsch (1988). The report by Urbatsch et al. (1986) of *L. fruticosum* in Bahia was based on material that Pruski and Urbatsch (1988) later referred to L. *morii*. *Lemmatium fruticosum* may thus be excluded from Bahia, Brazil.

Figure 53. *Lemmatium grazielae* (J.U. Santos) Pruski, topotype, identified in 1963 by Dra. Graziela Barroso as a new species, and appropriately dedicated in 1980 to her by Ubiratan Santos. (*Maguire et al. 49018*, NY).

LEMMATIUM GRAZIELAE (J.U. Santos) Pruski, **comb. nov.** *Calea grazielae* J.U. Santos, Bradea 3(16): 119. 1980. **TYPE: BRAZIL. Minas Gerais.** Jaboticatubas, Serra do Cipó, Km 114 da rodovia Lagoa Santa-Conceição do Mato Dentro, 5 Jun 1970, *Joly et al. CFSC 45* (holotype: UEC kodochrome 87N12.1, negative 12517; isotype: SP photograph 1.27). Figure 53.

Lemmatium grazielae (J.U. Santos) Pruski is discoid-capitulate and narrowly endemic to Minas Gerais, Brazil. It is known to me from fewer than ten collections, mostly along the road from Jaboticatubas to the summit of Serra do Cipó. This odd species was dedicated by good friend and *Aspilia* expert João Ubiratan Santos to the late Dra. Graziela Barroso (Pruski 2003, 2004b), who in her lifetime the world authority of Brazilian Compositae, and also Ubiratan's major professor. *Lemmatium grazielae* is most distinctive in its discolorous cordate leaves and bracteate large discoid capitula. It was first placed in the *Lemmatium* group and keyed by Pruski and Urbatsch (1988), but earlier was overlooked by them (Urbatsch et al. 1986) in their sectional revision of the group.

LEMMATIUM INTERMEDIUM (Pruski & Urbatsch) Pruski, **comb. nov.** *Calea intermedia* Pruski & Urbatsch, Brittonia 40. 351. 1988. **TYPE: BRAZIL. Minas Gerais.** Mun. de Varzea da Palma, Serra do Cabral, estrada que liga este Mun. ao de Joaquim Felício, 17° 35' S, 44° 58' W, 1000 m, 24 May 1982, *Bautista 638* (holotype: RB, negative 12529; isotype: MG). The branches (and negative annotation label) on the RB holotype were repositioned in RB post-description (the left-hand branch is now on the right and vice versa).

Lemmatium intermedium (Pruski & Urbatsch) Pruski is discoid-capitulate and was described from Minas Gerais, Brazil, where it remains a narrow endemic, but among its congeners is *intermediate* geographically. *Lemmatium intermedium* is similar in gestalt to *L. diamantinense* but differs from it by undulate-crenulate-serrulate (vs. entire) leaves with glandular and sparely pubescent (vs. glandular, otherwise glabrous) surfaces; nearly obgraduate (vs. graduate) involucre with phyllaries acute to rounded (vs. obtuse) at apex; 16–18 (vs. 7–9) disk florets; and by fewer, 1.5–2.5 (vs. 4–5) mm long pappus scales shorter (vs. longer) than eglandular (vs. glandular) cypselae.

LEMMATIUM IRWINII (G.M. Barroso) Pruski, **comb. nov.** *Calea irwinii* G.M. Barroso, Sellowia 26: 108. 1975. **TYPE: BRAZIL**. **Goiás.** Chapada dos Veadeiros, ca. 10 km W of Alto do Paraíso (formerly Veadeiros), 24 Mar 1969, *Irwin et al. 25002* (holotype: UB; isotypes: C photograph 8.17A, F, K, MO, NY, RB-3 kodachromes 87.03–05, US). In the protologue Barroso cited "Holotypus … UB, RB, NY" and based on the non-alphabetic citation of herbaria, the original "*Calea irwinii*" card version of the Gray Cards (not reproduced in the bound E.A. Shaw, Gray Herbarium Index, first supplement, vol. 1 A–J: 145. 1978) clearly cited UB as the holotype, as did Urbatsch et al. (1986). Either or both the individual *Calea irwinii* Gray card or Urbatsch et al. (1986) can be taken as effective lectotypification. The Irwin field collections books that I worked with at NYBG give the distribution of duplicates of *25002* as: "NY, UB, F, US…" However, I did not see the UB holotype during a 1987 visit to the UB herbarium, but I did see the RB material a few weeks later, helped kindly in Rio de Janeiro by Dra. Graziela Barroso. One of the three RB sheets is a good match for the protologue illustration and in lieu of an UB sheet, at least this RB sheet may be considered authentic. Nevertheless, all type material seen represents the same taxon, and lectotypification is unneeded taxonomically to fix application of the name.

Lemmatium irwinii (G.M. Barroso) Pruski, narrowly endemic to Goiás, Brazil, is characterized by its relatively few large discoid capitula held in stiff upright open-cymose capitulescences. The leaves have thick-callous margins, recalling those seen in Meyerias, but the stipitate cypselae of *L. irwinii* have irregularly twin trichomes typical of *Lemmatium*.

LEMMATIUM LEMMATIOIDES (Sch. Bip. ex Baker) Pruski, **comb. nov.** *Calea lemmatioides* Sch. Bip. ex Baker, in Martius, Fl. Bras. 6(3): 252. 1884. **LECTOTYPE**, chosen from among syntype collections by Urbatsch et al. 1986: **BRAZIL**. **Minas Gerais.** Serra do Caraça, Jan 1824–1825, *Riedel 1437* (lectotype, sheet designated by Urbatsch et al. 1986: LE, photograph 2.5 and ektachrome 84.3, the sheet with the hand-written *Riedel 1437* label, obviously examined by Baker—viz the protologue *in sched. Riedel*.—when *L. oxylepis* was seen; isolectotypes: G**,** K, LE-2 photographs 2.3–2.4 without number and both seemingly dated Jan 1825, P-Sch-Bip). The Riedel LE lectotype type is more robust than the K isolectotype; the two Pohl lectoparatype sheets in Kew, one as photograph 13.14, were annotated by Baker. A Paris ex Glaziou ex LE Riedel sheet is unnumbered and a possible type.

Lemmatium lemmatioides (Sch. Bip. ex Baker) Pruski is radiate-capitulate and an uncommon endemic in Minas Gerais, Brazil. This species is characterized by its relatively few large capitula that are not well-exserted from the crowded distal-most leaves.

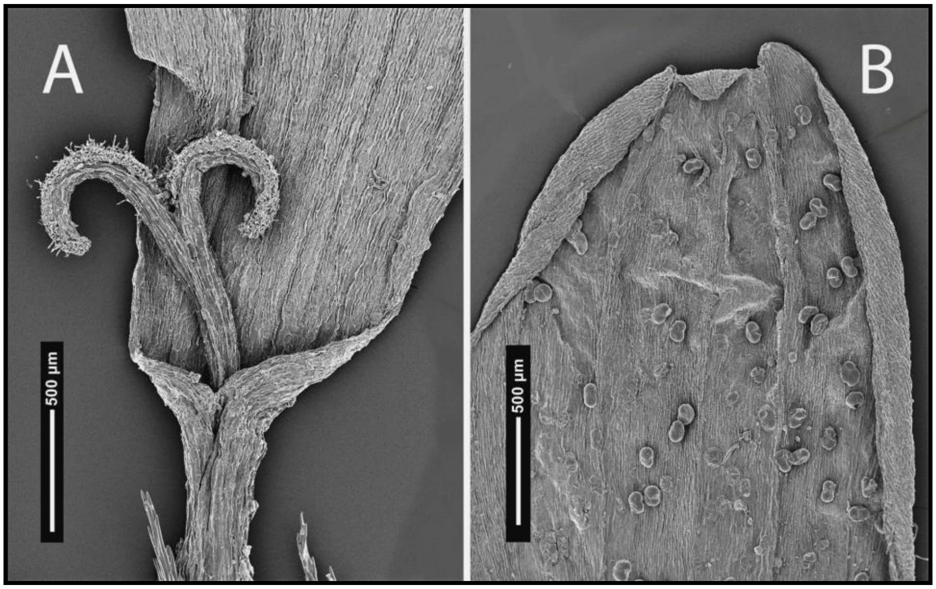


Figure 54. *Lemmatium rotundifolium* (Less.) DC., ray corolla and style. A. Style and proximal adaxial portion of corolla, adaxial stigmatic lines infected with fungal hyphae, distal portions of style branch abaxially papillose. B. Distal abaxial portion of the same corolla limb as in A, showing glands and equally thickened nerves. (*Anderson 9007,* MO).

LEMMATIUM MORII (H. Rob.) Pruski, **comb. nov.** *Calea morii* H. Rob., Phytologia 44: 437. 1979. **TYPE: BRAZIL. Bahia.** Municipio do Rio de Contas, base de Pico das Almas, a 18 km ao NW de Rio de Contas, 1300 m, 22 Jul 1979, *King, Mori, Santos & Hage 8097* (holotype: RB; isotypes: CEPEC, K, M, MO, US).

Lemmatium morii (H. Rob.) Pruski is discoid-capitulate and endemic to Bahia, Brazil. This densely pubescent plant was treated in synonymy of *L. fruticosum* by Urbatsch et al. (1986), but was reinstated by Pruski and Urbatsch (1988), who excluded *L. fruticosum* from Bahia.

LEMMATIUM NITIDUM (Less.) Pruski, **comb. nov.** *Calea nitida* Less., Linnaea 5: 158. 1830 (non *Calea nitida* Chodat 1902). **TYPE: BRAZIL**. **Minas Gerais.** Serra do Caraça, s.d., *Sellow 865.1102* (lectotype, designated by Urbatsch et al. 1986: K, photograph 13.10 and kodochrome 83.38, now barcoded K000323178; isolectotype or perhaps holotype: B† (as 865, Macbride neg. 15380). Baker (1884) cited *Sellow 865* and *Sellow 1102*; the photograph and destroyed B sheet may have been *Sellow 865/1102*, and indeed some Sellow collections of other taxa are double-numbered; the Kew lectotype has two labels, the lower left reads *Sello*, and the upper right gives *865.1102*, but also has a sideways *610* on the same label. It is unclear whether there were ever two or more collections in Berlin, and whether the Berlin and Kew sheets are of the same gathering, but available evidence implies they are.

Calea floribunda Baker, Bull. Misc. Inform. 79: 157. 1893. **TYPE: BRAZIL. Minas Gerais.** Biribiry, Diamantina, Mar-Apr, *Glaziou 19543* (holotype: K photograph 13.11; isotypes: C photograph 2.32 and Macbride neg. 22502, G, LE photograph 2.0A, P-3, US (frag.).

Lemmatium nitidum (Less.) Pruski is radiate-capitulate and endemic to Minas Gerais, Brazil. The species is most similar to *L. oxylepis,* both species being characterized by their many small few-flowered capitula held in a well-exserted broadly corymbiform capitulescence.

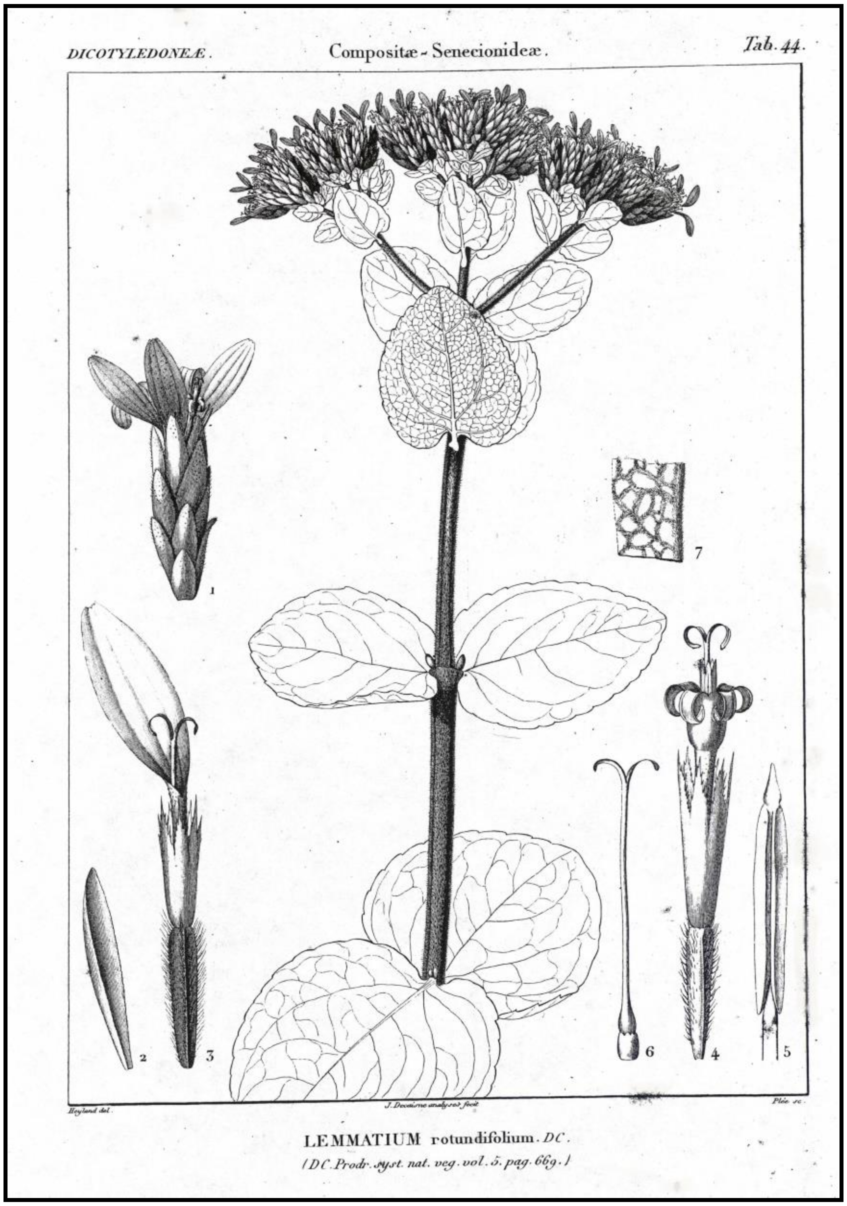


Figure 55. *Lemmatium rotundifolium* (Less.) DC., the generitype, showing the many small capitula in a flat-topped corymbiform capitulescence (top), and below ray and disk florets (lower right, lower left) with connate pappus scales. (Reproduced from Delessert, Icones Selectae Plantarum 4: tab. 44. 1839).

LEMMATIUM OXYLEPIS (Baker) Pruski, **comb. nov.** *Calea oxylepis* Baker, in Martius, Fl. Bras. 6(3): 254. 1884. **TYPE: BRAZIL**. **Minas Gerais.** Serra da Lapa, 1824, *Riedel 1106* (lectotype, annotated by me in 1983 as isotype, but designated as lectotype by Urbatsch et al. 1986: LE, photograph 9.36, with full Riedel label, determined in Baker's hand; isotypes: F, G photograph 5.36**,** K-Hook photograph 13.12, LE p.p. photograph 9.37 mixed with *L. rotundifolium*, P-Sch-Bip as Macbride neg. 38065, US). The F and US sheets are fragments of P. Some lectotype materials are whorled-leaved. The Sch. Bip. binomial in *Amphicalea* on the lectotype was listed but not validated by Baker; rather Baker described the plant in *Calea*, explaining why Baker annotated this Riedel sheet with his new binomial, but not other LE sheets, e.g., *Calea lemmatioides*, where Baker used the Sch. Bip. binomial.

Lemmatium sickii (G.M. Barroso) Pruski
det. John Pruski (MO), 2019
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Calea sickii (G.M. Barroso) Urb.,
Zlot. & Pruski
det. John Pruski (MO), 2008
MISSOURI BOTANICAL GARDEN HERBARIUM

280(5)

FUNDAÇÃO INSTITUTO BRASILEIRO DE GEOGRAFIA E ESTATÍSTICA.
HERBÁRIO DA RESERVA ECOLÓGICA DO IBGE
Brasília - DF Brasil
Brasilia sickii
det: E. P. Heringer 1980
Compositae
(Asteraceae)

Brasília DF, morro à margem direita do córrego Cabeça do Viado.
Artusto; capítulos amarelos; folhas duras e ásperas; exalando cheiro agradável; cerrado limpo sobre morro.

4264 08-IV-1980

LEG: E. P. HERINGER, T. S. FIGUEIRAS, R. C. MENDONÇA, B. A. S. PEREIRA, A. E. HERINGER SALLES & F. CHAGAS E SILVA.

Figure 56. Representative specimen of *Lemmatium sickii* (G.M. Barroso) Pruski, leaf blade surfaces are concolorous and the capitula are discoid. (*Heringer et al. 4264*, MO).

Lemmatium oxylepis (Baker) Pruski is radiate-capitulate and endemic to Minas Gerais, Brazil. The species is characterized by its glandular otherwise subglabrous leaves. *Lemmatium nitidum* and *L. oxylepis* are similarly occasional, restricted to Minas Gerais, but differ clearly in leaf morphology. Jackson (1893: 383) gave the *Calea oxylepis* protologue page number as 354.

LEMMATIUM ROTUNDIFOLIUM (Less.) DC., Prodr. 5: 669. 1836. *Caleacte rotundifolia* Less., Linnaea 5: 158. 1830; Syn. Gen. Compos. 248. 1832. *Calea rotundifolia* (Less.) Baker, in Martius, Fl. Bras. 6(3): 253. 1884. **TYPE: BRAZIL**. Brasilia aeqinoctiales, s.d., *Sellow 866/1103* (holotype: B† as Macbride neg. 15390; lectotype, designated by Urbatsch et al. 1986: HAL, photograph 1.33 and ektachrome 84.12; possible isolectotypes: LE photograph 9.28 and ektachrome 84.4, LY photographs 1.15–16 (unmounted, both sides imaged, Gandoger Herbarium) and ektachrome 84.3, P-Rich photograph 13.15 and kodachrome 83.37). It is not at all clear if the sheets cited by me are of a single gathering. Figures 46B, 46D, 47, 54–55.

Lemmatium rotundifolium (Less.) DC., the generitype, is radiate-capitulate and endemic to Minas Gerais. Brazil. It is the only radiate species of *Lemmatium* having proximally connate pappus bristles. Discoid-capitulate *L. fruticosum* was treated by Baker (1884) as synonymous with *L. rotundifolium*, but was resurrected from a century-long synonymy by Urbatsch et al. (1986).

LEMMATIUM SICKII (G.M. Barroso) Pruski, **comb. nov.** *Brasilia sickii* G.M. Barroso, Arch. Jard. Bot. Rio de Janeiro 17: 19, + unnumbered figure on page 20. 1959–1961 [1962–1963]. *Calea sickii* (G.M. Barroso) Urbatsch, Zlotsky & Pruski, Syst. Bot. 11: 504. 1986. **TYPE: BRAZIL. Distrito Federal** [as Goias]. Brasilia, May 1957, *H. Sick s.n.* (Herb. Pabst 4472) (holotype: HB). Figure 46A, 46C, 56.

[Protologue pages 19 and 20 are unnumbered, but page numbers are inferred from numbered pages in preceding and following papers; the TOC gives this two page Barroso paper as beginning on page 19].

Lemmatium sickii (G.M. Barroso) Pruski, endemic to Distrito Federal and Goiás, Brazil, is the generitype of synonymous *Brasilia* G.M. Barroso. The plant should be looked for in adjacent Minas Gerais. The anatomy of *L. sickii* has been studied by Paviani (e.g., 1977, 1987). *Lemmatium sickii* is the only discoid-capitulate *Lemmatium* with proximally connate pappus scales. The size, shape, and open arrangement of capitula in *L. sickii* are very characteristic (Fig. 56), recalling Japanese *Macroclinidium rigidulum* (Miq) Makino.

LEMMATIUM WEDELIOIDES (Baker) Pruski, **comb. nov.** *Viguiera wedelioides* Baker, J. Bot. 20: 226. 1882. *Calea wedelioides* (Baker) S.F. Blake, Contr. Gray Herb., n. ser. 54: 189. 1918. **TYPE: BRAZIL**. Pedra do Conego, a Novo Friburgo, environs de Rio Janiero, Mar 1882, *Glaziou 12845* (holotype: K, photograph 13.5, now barcoded K000323173; isotypes: G, P-3 one as Macbride neg. 37816, US). Urbatsch et al. (1986: 512) listed an isotype once in B, which may have been in error for the photographed P sheet.

Lemmatium wedelioides (Baker) Pruski, described in 1882 as having a "Wedelioid habit" and not included in Baker (1884), is a shrubby, pinnately-veined, radiate-capitulate, rare endemic from Rio de Janeiro, Brazil, albeit given in *Index Herbariorum* as from Madagascar. The invalid name *Calea petropolitana* Glaziou, Mem. Soc. Bot. France 57, 3e: 415. 1910 was used (based on *Glaziou 13986*, *17101*, and *18317*) by Glaziou's daughter after his death, was without diagnosis, and was not accepted in the paper: it is a nom. nud. The leaves are typically villous, but otherwise the plant and its distribution recalls *Lemmatium arachnoideum*.

4. MEYERIA DC., Prodr. 5: 670. 1836, nom. cons. prop. *Calea* sect. *Meyeria* (DC.) Benth. & Hook. f., Gen. Pl. 2: 391. 1873. *Calea* subgen. *Meyeria* (DC.) Baker, in Martius, Fl. Bras. 6(3): 252. 1884. [non *Meyera* Adans., Fam. Pl. 2: 257. 1763, nom. illeg. superfl. (for *Holosteum* L., Sp. Pl. 1: 88. 1753, Caryophyllaceae); nec *Meyera* Schreb., Gen. Pl. 570. 1791, hom. illeg. (a taxonomic synonym of *Enydra* Lour.). *Meyeria* DC. is in use, is not dedicated to the same Meyer as either *Meyera* Adans. or *Meyera* Schreb., and neither illegitimate name has ever been confused with *Meyeria* DC. Nevertheless, elsewhere I am proposing *Meyeria* DC. for conservation over both earlier never-used—except in passing by Cassini—illegitimate generic names to avoid any possible future confusion]. **LECTOTYPE** (designated by Wussow et al. 1986): *Meyeria myrtifolia* DC.

Meyeria sect. *Gluphiphyllaea* DC., Prodr. 5: 671. 1836. **LECTOTYPE**, designated here: *Meyeria myrtifolia* DC. This section by lectotypification becomes a nomenclatural and homotypic synonym of *Meyeria* sect. *Meyeria*.

Meyeria sect. *Holophyllaea* DC., Prodr. 5: 670. 1836. **TYPE:** *Meyeria hispida* DC. [= *Meyeria triantha* **(**Vell.) Pruski].

The genus *Meyeria* DC. (Compositae: tribe Neurolaeneae), is herein reinstated from synonymy of *Calea*, under which for a century it rested at the sectional rank as *Calea* sect. *Meyeria* (DC.) Benth. & Hook. f. (Bentham and Hooker 1873; Pruski 1984, 1998a, 2005, 2013; Pruski and Urbatsch 1988; Pruski and Hind 1998; Bueno et al. 2021; Bueno and Heiden 2022). Baker (1884) and Löfgren (1897) recognized the group as *Calea* subgen. *Meyeria* (DC.) Baker, but here I defer to sectional classification of Bentham and Hooker (1873). Delessert (1839, 4: tab. 46), Dietrich (1847: 1580), Endlicher (1836–1840: 425), Meisner (1836–1843, 1: 207), Spach (1841: 18), Walpers (1843: 629; 1851–1852: 878), Gardner (1847), and Pfeiffer (1874, 2(1): 298) are among those who treated *Meyeria* at the generic rank. Hoffmann (1894), on the other hand, is a noteworthy reference not recognizing *Meyeria* as a genus or infragenus, instead placing *Meyeria* within *Calea* sect. *Eucalea*.

Thus, the name *Meyeria*, at one taxonomic hierarchical rank or another—either the generic or sectional rank—has for nearly two centuries been in near continuous use for a group of Brazilian-centered shrubs and subshrubs. Candolle (1836) noted that *Meyeria* DC. (1836) is a near parahomonym of two valid but illegitimate earlier names, *Meyera* Adans. (1763) and *Meyera* Schreb. (1791). Neither of the two near parahomonym Meyeras is a strict homonym of *Meyeria* DC., nor were either taken by Candolle (1836) as strict homonyms. Candolle mentioned that neither of the two Meyeras had ever been used subsequent to when first proposed. *Meyera* Adans., Fam. Pl. 2: 257. 1763 is an illegitimate and superfluous renaming of *Holosteum* L., Sp. Pl. 1: 88. 1753 (Caryophyllaceae). The illegitimate *Meyera* Schreb., Gen. Pl. 570. 1791 hom. illeg., is an exactly spelled later homonym of *Meyera* Adans. (1763). *Meyera* Schreb. was given by Candolle (1836: 636) in taxonomic synonymy of *Enydra* Lour. (Compositae). *Meyera* Schreb. was named for Johann Meyer (Candolle 1836), "the etymology of *Meyera* Adanson (1763) is not explained by Adanson," and *Meyeria* DC. was dedicated by Candolle to Carl Anton von Meyer "and to four of his namesakes" (quotes from Stafleu and Cowan TL-II, vol. 3: 445. 1981), i.e., neither earlier *Meyera* nor the later *Meyeria* were named for or dedicated to the same individual named Meyer, and in this regard neither *Meyera* is confusable with *Meyeria* DC. Although neither earlier *Meyera* is in current use, nor significantly overlaps geographically with *Meyeria*, and although neither earlier *Meyera* is spelled exactly the same as *Meyeria*, these two Meyeras could conceivably be confused with the near parahomonym *Meyeria* by someone at some time in the near or distant future.

Thus, because *Meyeria* DC. is a near parahomonym of two earlier names and because it is a name that has been in near continuous use for nearly two centuries, the name *Meyeria* DC. is being proposed by me for conservation over both the earlier orthographically similar and potentially confusable names *Meyera* Adans. and *Meyera* Schreb. Similarly, in the vein of homonymy, it seems appropriate to mention that *Calia* Terán & Berland. (1832), a longtime synonym of *Sophora* L. (Leguminosae), was voted recently to be a name confusable with the earlier *Calea* L. (viz Taxon 60: 231–232. 2011), albeit neither name is spelled exactly the same. At one point, when cornered, I considered the new replacement name *Meyeriopsis* Pruski for *Meyeria* DC., but taking this option, i.e., proposing a name change for a name that has never fallen out of use, is undesirable. The name *Meyeria* DC. is thus retained and used here.

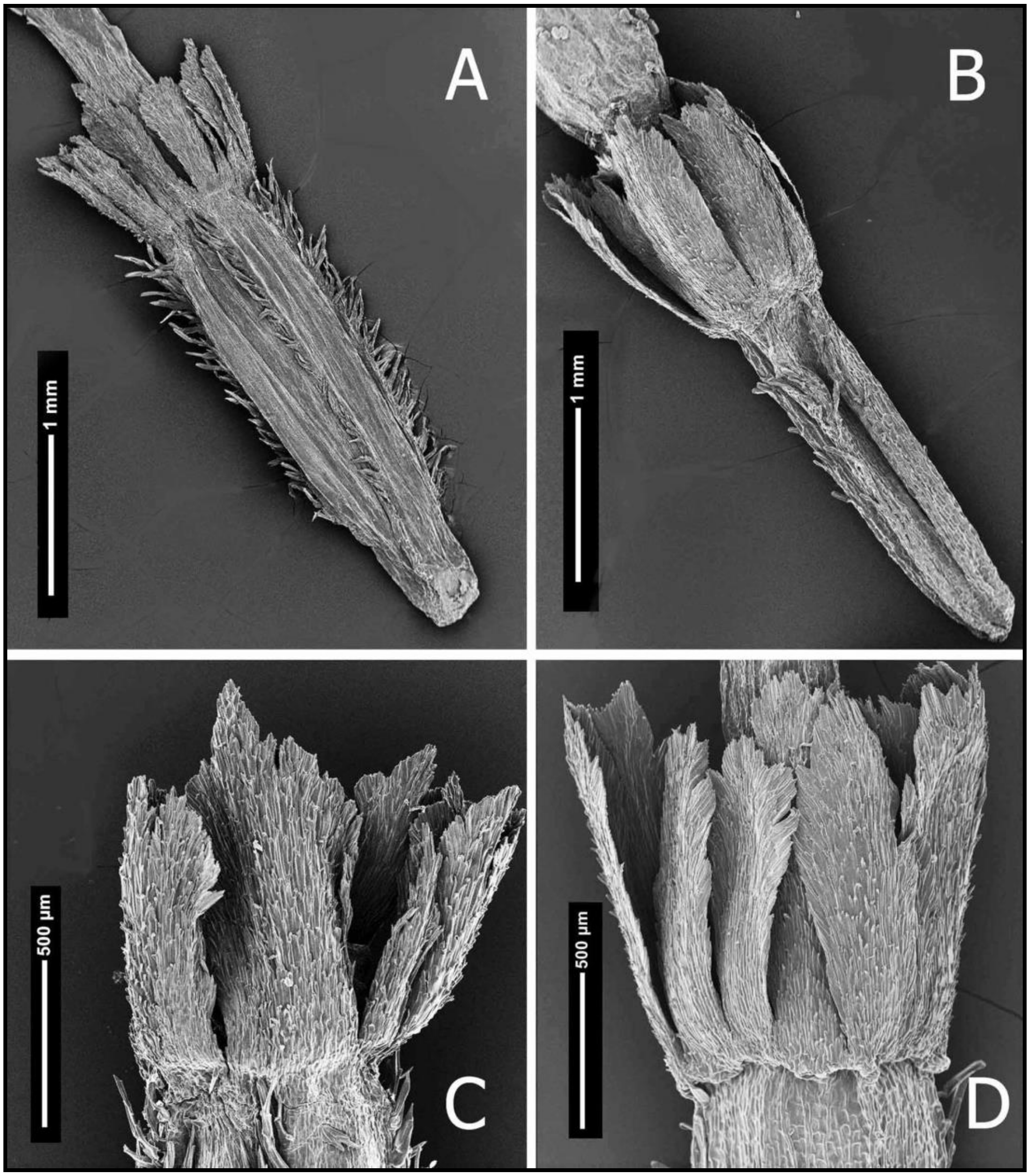


Figure 57. Disk cypselae and pappus of two of the four original species of *Meyeria* DC. A & C. *Meyeria myrtifolia* DC., generitype. B & D. *Meyeria parvifolia* DC. A. *Meyeria myrtifolia*, cypsela showing base with slightly asymmetric carpopodium. B. *Meyeria parvifolia*, cypsela showing base with slightly asymmetric carpopodium. C. *Meyeria myrtifolia*, close-up of pappus scales. D. *Meyeria parvifolia*, close-up of pappus scales. (A & C *Irwin et al. 21807*, NY; B *Hatschbach & Cordeiro 52829*, NY; D *Swallen 8696*, US).

Figure 58. *Meyeria myrtifolia* DC., generitype. (Reproduced from Delessert, Icones Selectae Plantarum 4: tab. 46. 1839).

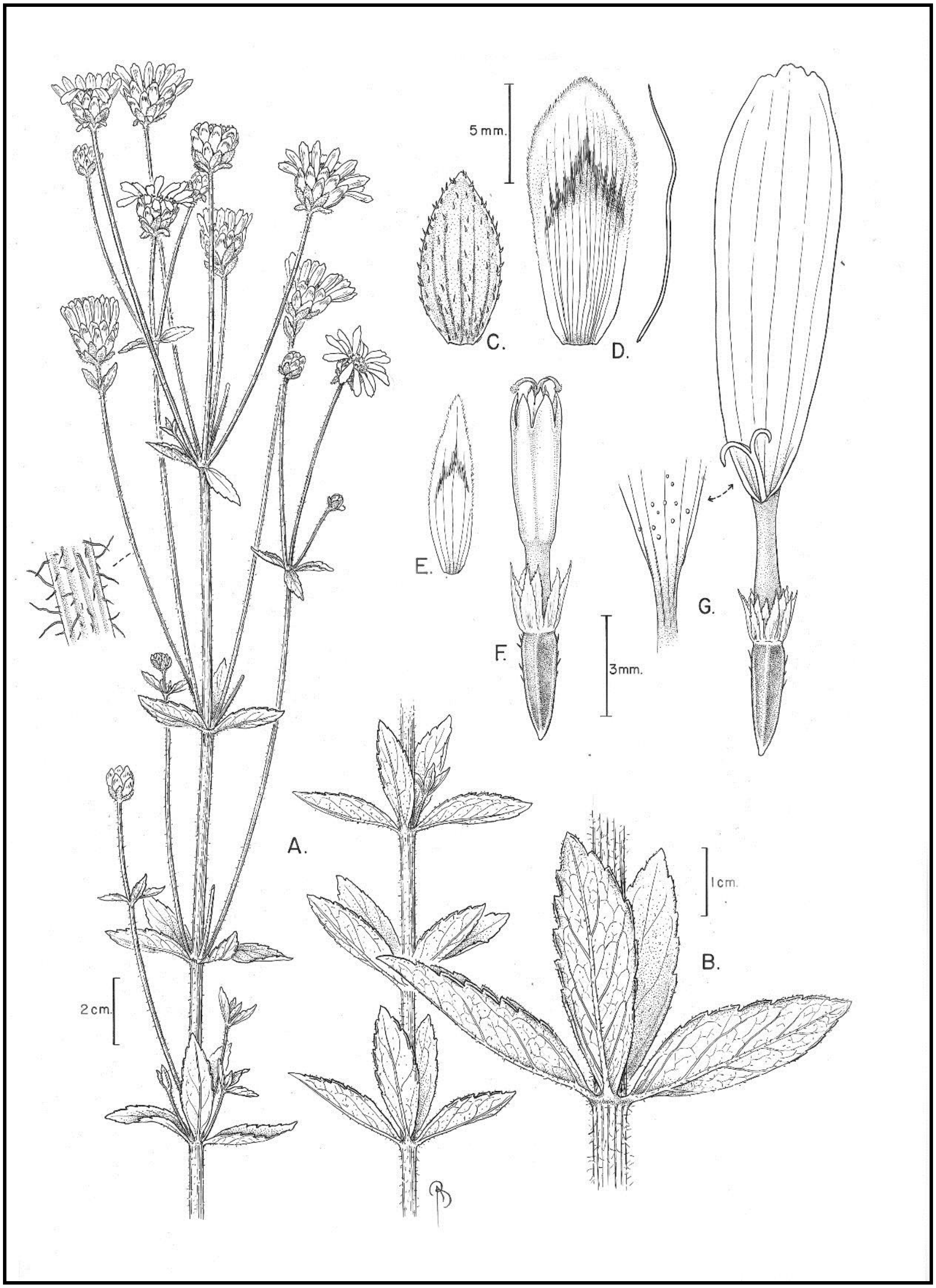


Figure 59. *Meyeria quadrifolia* (Pruski & Urbatsch) Pruski. A. Habit, more proximal portion of stem (bottom center) shows three whorled-leaved nodes. B. Close-up of node showing whorled leaves. C. Outer phyllary. D. Inner phyllary with (on right) profile. E. Palea. F. Disk floret. G. Ray floret, pistillate, and adaxial face of corolla; to the left note glands on abaxial surface of the corolla limb. (Drawn by Bobbi Angel from *Hatschbach et al. 32636*, NY, an isotype; also used in Pruski and Urbatsch 1988, the protologue).

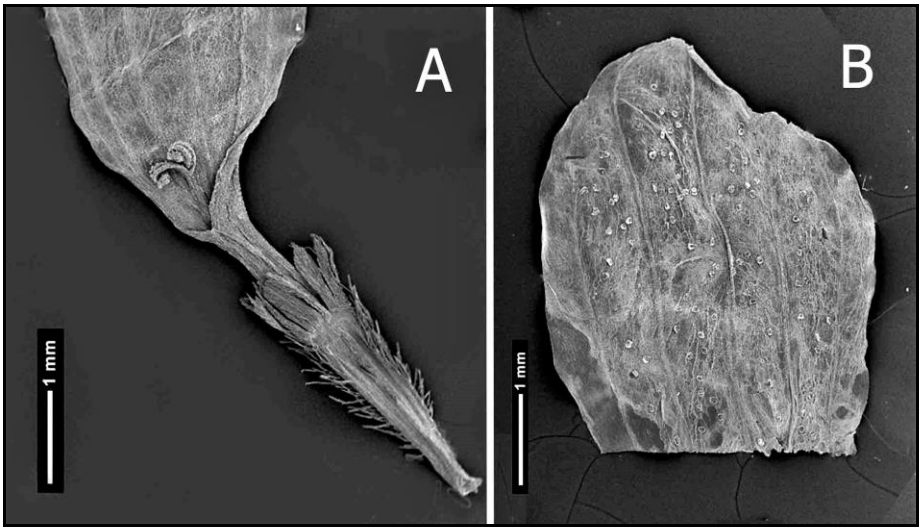


Figure 60. *Meyeria subintegerrima* (Malme) Pruski, ray floret, pistillate. A. Triquetrous cypsela, style, and proximal adaxial portion of corolla. B. Distal abaxial portion of the same corolla, showing glands and equally thickened nerves that are closed (looping) apically. (*Smith et al. 14522*, NY).

Key morphological features (some are generalized *Calea* Alliance features) characterizing the newly reinstated *Meyeria* are often callose-margined leaves and/or phyllaries (Figs. 64–65, 67), always radiate capitula (Figs. 58–59, 60A, 63–64, 66, 68), pistillate rays florets (Figs. 58, 59G, 60A, 66E), broad paleae (Figs. 59E, 66D), often pointed disk style branch apices (Fig. 61), quadrangular disk cypselae with weakly asymmetric carpopodia (Figs. 57A–B, 60A, 62B) (the rays are triquetrous, Figs. 58–59, 60A, 62A), non-descript twin trichomes (Figs. 57A, 60A; as in *Calea* s. str., e.g., Fig. 7B), and the relatively short reduced flat scales of the pappus (Figs. 57–60, 62, 65–67). Turner et al. (1979) reported a chromosome number of $x = 18$ ($2n = 36$) in *C. reticulata*, but their voucher, *Turner 9143* (LL) was later identified as a paratype of *M. quadrifolia*. Because Turner et al (1979) and Pruski and Urbatsch (1988) then took a broad view of *Calea*, they suggested (basically assumed) this $x = 18$ Turner et al. (1979) report was probably a miscount, especially given that Pruski and Urbatsch (1984) gave $x = 19$ as the chromosome base number across true *Calea*. However, the Turner et al. (1979) report of $x = 18$ for *Turner 9143* (LL)—a voucher now treated as a species of *Meyeria*—cannot be disproven, and until shown otherwise, the chromosome base number of the genus *Meyeria* must be taken as $x = 18$.

Meyeria is recognized by me at present as housing 18 species, the 13 species of the *Calea myrtifolia* (DC.) Baker group discussed and keyed by Pruski (1984, 1998, 2005), Pruski and Urbatsch (1988), and Pruski and Hind (1998) plus five further species. The *Calea myrtifolia* group was so called by Pruski (1998: 692) and Pruski and Hind (1998: 699) because *M. myrtifolia* is the generitype of *Meyeria*. Additionally, all species of the *Calea myrtifolia* group, now recognized at the generic rank as *Meyeria*, are accepted as congeneric, albeit perhaps not fully monophyletic with a subset of species being whorled-leaved (e.g., *M. quadrifolia*, *M. heteropappa* and, *M. semirii*) and/or consistently having a pappus of unequal scales (e.g., *M. heteropappa*, *M. semirii*, and a few other related species). Sometimes Meyerias have a periderm that may be readily torn away, this has been seen in other groups, and thus may not be phylogenetically significant. Similarly, also retained in *Meyeria* is *M. nervosa*, although it sometimes differs from most Meyerias by sometimes being corky-fruited. Elsewhere in Compositae corky fruits are often an environmental response seen in wet area plants, and the presence of this modified corky periderm type is not always an indicator of relationships.

Meyeria remains a member of the *Calea* Alliance, a generic group characterized by mostly opposite leaves (Figs. 58, 64–68), non-setose corollas (Figs. 58–60, 66), pale anthers (Fig. 63), style branches with paired stigmatic lines and papillose distal-abaxial branch surfaces (Fig. 61), a pappus of scales (Figs. 57–60, 62, 65–67), and paleate clinanthia (Figs. 58, 59E, 66D). The protologue trait of opposite leaf arrangement is not a constant in *Meyeria*, however, as several species are characterized by being consistently either ternate-leaved or whorled-leaved (Figs. 59, 63). Leaf arrangement within individual species too may vary, for example, the type collection of *M. phyllolepis* is mostly ternate-leaved, whereas otherwise the species is mostly opposite-leaved. Other mostly opposite-leaved *Calea* Alliance member genera (e.g., *Calea*, *Podocalea*, *Tepuipappus*) on occasion too have plants ternate-leaved, and *Calea* Alliance member *Laceanthos* contains equal numbers of species with opposite and with whorled leaf arrangements. Leaf arrangement, the most basic of characters, thus, is not always a distinguishing intergeneric marker in the *Calea* Alliance, or is it always an infrageneric marker. Martarello et al. (2015) mentioned leaf anatomy, but provided no images, of *Meyeria ilienii* (Malme) Pruski and *Meyeria monocephala* (Dusén) Pruski.

Similarly, most *Calea* Alliance members have isomorphic subequal pappus scales, usually a reliable barometer, but Pruski and Urbatsch (1988), Pruski and Hind (1998), Bueno and Heiden (2022) respectively, noted that *Meyeria heteropappa* (Pruski & Urbatsch) Pruski (Fig. 62), *M. semirii* (Pruski & D.J.N. Hind) Pruski (Pruski and Hind 1998: fig. 2F, 2K), and *M. sessilifolia* (V.R. Bueno & G. Heiden) Pruski each break the mold by being heteropappose. Similarly, Pruski and Hind (1998: 701) reported that *M. triantha* (Vell.) Pruski is heteropappose and has some collections with 1–2 long-caudate pappus scales emerging from among its otherwise mostly subequal smaller scales (e.g., *Hatschbach 18347*, UEC). Bueno and Heiden (2022) erred by saying unequal scales characteristic of heteropappose condition are a "characteristic exclusive of a few species belonging to the *C. myrtifolia* complex," because they overlooked that six decades earlier Maguire and Aristeguieta (in Maguire and Wurdack 1957: 372) gave the pappus scales as "inaequaliter" in the protologue of *Tepuipappus orbiculatus* (Maguire & Aristeg.) Pruski; three decades ago Urbatsch et al. (1986: fig. 1) showed unequal scales in *Calea* sect. *Lemmatium*; two decades ago Pruski (1997) gave "pappus scales 4–12, obviously unequal in length" as a prime lead in the tepui flora key to species of the *Calea kunhardtii* group; and unequal pappus scales of species placed here in *Tepuipappus*, but described in *Calea*, were illustrated by Maguire and Phelps (1951–1952: fig. 2D) and Pruski (1997: fig. 183). Mesoamerican *Squamopappus* and *Tetrachyron*—largely based on one-time Caleas—are also heteropappose, a morphology infrequently also seen also in *Podocalea*.

All species of *Meyeria* have radiate capitula, and like *Calea* Alliance members, when present the ray florets are pistillate (Figs. 59G, 60A, 66E) and have corolla limbs with equally thickened nerves (Figs. 59G, 60B, 66E). The pointed disk floret style branch apices of *Meyeria* (Fig. 61) and *Laceanthos* differ in shape from the obtuse-rounded apices typical of many species of *Calea* (e.g., Figs. 9B, 21B). However, this obvious different character state may perhaps not be overly significant generic marker in the *Calea* Alliance because, for example, the long-time synonymous (viz Wussow et al. 1986; Strother 1999) difficult-to-distinguish species pair *Calea jamaicensis*-*Calea trichotoma* similarly differ in their disk floret style branch apex shape (viz Fig. 8A vs. Fig. 8B), supporting the Pruski and Robinson (2018) reinstatement of *C. trichotoma*. Elsewhere in helianthoids, however, style apex shape is generally a good indicator of relationships. For example, *Viguiera porteri* (A. Gray) S.F. Blake was recognized by Cronquist (1980), but Pruski (1998b) noted that the then-recognized genus *Viguiera* Kunth has disk floret style branch apices acute to obtuse. *Viguiera porteri* (A. Gray) S.F. Blake was taken by Pruski (1998b) as out of place in *Viguiera* by its long-appendiculate disk floret style branches, which instead is a character typical of *Helianthus* L. (Robinson 1981; Pruski 1998b), and the plant—the Stone Mountain Daisy—has since been treated as *H. porteri* (A. Gray) Pruski.

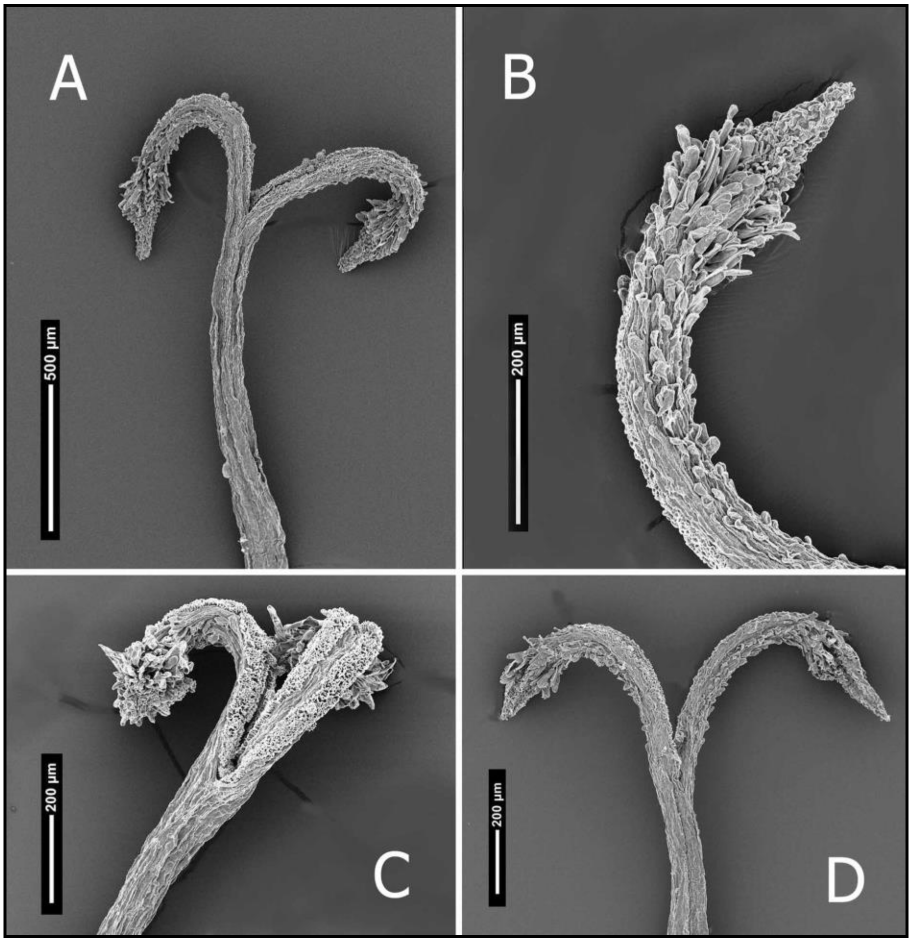


Figure 61. Disk floret style branches in two of the four original species of *Meyeria* DC., showing pointed-tipped 2-banded styles with papillose abaxial surfaces. A–B, D. *Meyeria myrtifolia* DC., generitype. C. *Meyeria parvifolia* DC. (A–B, D *Irwin et al. 21807*, NY; C *Hatschbach & Cordeiro 52829*, NY).

A synopsis of *Meyeria*, i.e., what I had earlier called the *Calea myrtifolia* group as within *Calea* sect. *Meyeria*, is anticipated and in progress for publication. The remaining species that Pruski (1984, 1998a, 2005, 2013), Pruski and Hind (1998), Pruski and Urbatsch (1988) treated as distinct species groups within *Calea* sect. *Meyeria*, i.e., the *Calea pilosa* group and the *Calea teucriifolia* group, are at present not transferred by me today to *Meyeria*, but are being treated by me in a companion paper. I have seen no material of *Calea repanda* Bueno et al. (2022) (the protologue illustration shows a pair of terminal capitula, but the protologue text implies misleadingly that the species too has terminal paired capitula, rather than the presumed terminal 3-capitulate clusters), which in gestalt recalls *Meyeria*, but is unplaced by me. The SEM micrographs of styles, cypselae, and pappus scales included here serve to illustrate some distinguishing characters of *Meyeria*. The 15 required new combinations for the 18 species I now recognized in *Meyeria* follow.

MEYERIA ALDAMOIDES (G.H.L. da Silva, Bringel & A.M. Teles) Pruski, **comb. nov**. *Calea aldamoides* G.H.L. da Silva, Bringel & A.M. Teles, Phytotaxa 265: 280. 2016. **TYPE: BRAZIL**. **Goiás.** Cavalcante, estrada para a Estação Ecológica Córrego Branco, 1 Feb 2015, *Bringel 1188* (holotype: CEN; isotype: MO n.v.). The 2016 protologue-cited MO sheet has not been received at MO.

Meyeria aldamoides (G.H.L. da Silva et al.) Pruski is narrow endemic and known only from the type collected in Goiás, Brazil, just south of the border with Tocantins and about 60 km NW of Chapada dos Veadeiros. By its monocephalous capitula, *M. aldamoides* was described as near *Calea* sect. *Monanthocalea* (Less.) Pruski, a taxonomic synonym of *Podocalea* Pruski, but lacks the linear paleae of *Podocalea*. Instead, *M. aldamoides* has the oblong paleae typical of *Meyeria*. *Meyeria aldamoides* is accepted here, apparently is most closely related to *M. nervosa*, and is envisioned basically a monocephalous variant of *M. nervosa*. *Meyeria nervosa* is centered in the Chapada dos Veadeiros, just SW of the type locality of *M. aldamoides*.

MEYERIA CHODATII (Hassler) Pruski, **comb. nov.** *Calea chodatii* Hassler, Repert. Spec. Nov. Regni Veg. 14: 174. 1915 as "chodati", nom. nov. for *Calea nitida* Chodat, Bull. Herb. Boissier, sér. 2, 2(4): 396. 1902 nom. illeg.; (see also extract in Chodat, Pl. Hassl. I: 167. 1902), non *C. nitida* Less., 1830. **LECTOTYPE**, collection designated here, chosen from among two syntype collections: **PARAGUAY**. Itapé, 9 Sep 1874, *Hassler 4314* (lectotype sheet, designated here: G Herb. Hassler, photograph 3.9 and ektachrome 84.18, now G00092645; isolectotypes: BM p.p. photograph 3.7, F, G-BOIS, G-Cand photograph 3.8 and as Macbride neg. 28828, G-Chod-2, K, LY, NY, P-2, US, W, Z. The F and US sheet are fragments of Geneva sheets.

In 1983, I annotated this Hassler herbarium sheet of *Hassler 4314* (G-00092645) as lectotype. Material of *Hassler 4314* is more robust and more widely distributed than material of *Hassler 3279*, the second of two cited syntype collections. The herbarium Hassler sheet is chosen as the lectotype sheet because it is marked "*Calea nitida* Chod" in Chodat's hand, has more than ten good flowering capitula, and generally speaking is more robust than the herbarium Chodat material. The lectotype sheet is also marked "*Calea chodatiana* Hassler" in Hassler's hand. The herbarium Chodat contains two sheets with a single label, which is marked "*Calea nitida* nob" in Chodat's hand, and is obviously authentic material too, but is less robust.

Meyeria chodatii (Hassler) Pruski is endemic to Paraguay. The Hassler infraspecies will be treated at a later date.

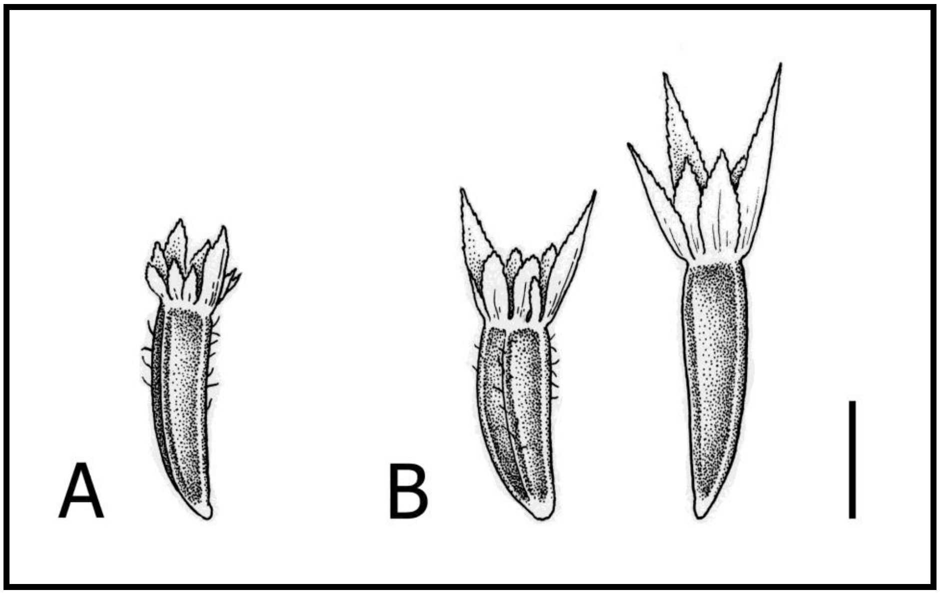


Figure 62. *Meyeria heteropappa* (Pruski & Urbatsch) Pruski, heteropappose costate cypselae, i.e., with pappus scales of unequal lengths. A. Ray cypsela, triquetrous. B. Two disk cypselae, quadrangular. (Drawn by Bobbi Angel from *Duarte 2618*, RB, the holotype sheet 2 of 3; also used in Pruski and Urbatsch 1988, the protologue). Scale bar 2 mm.

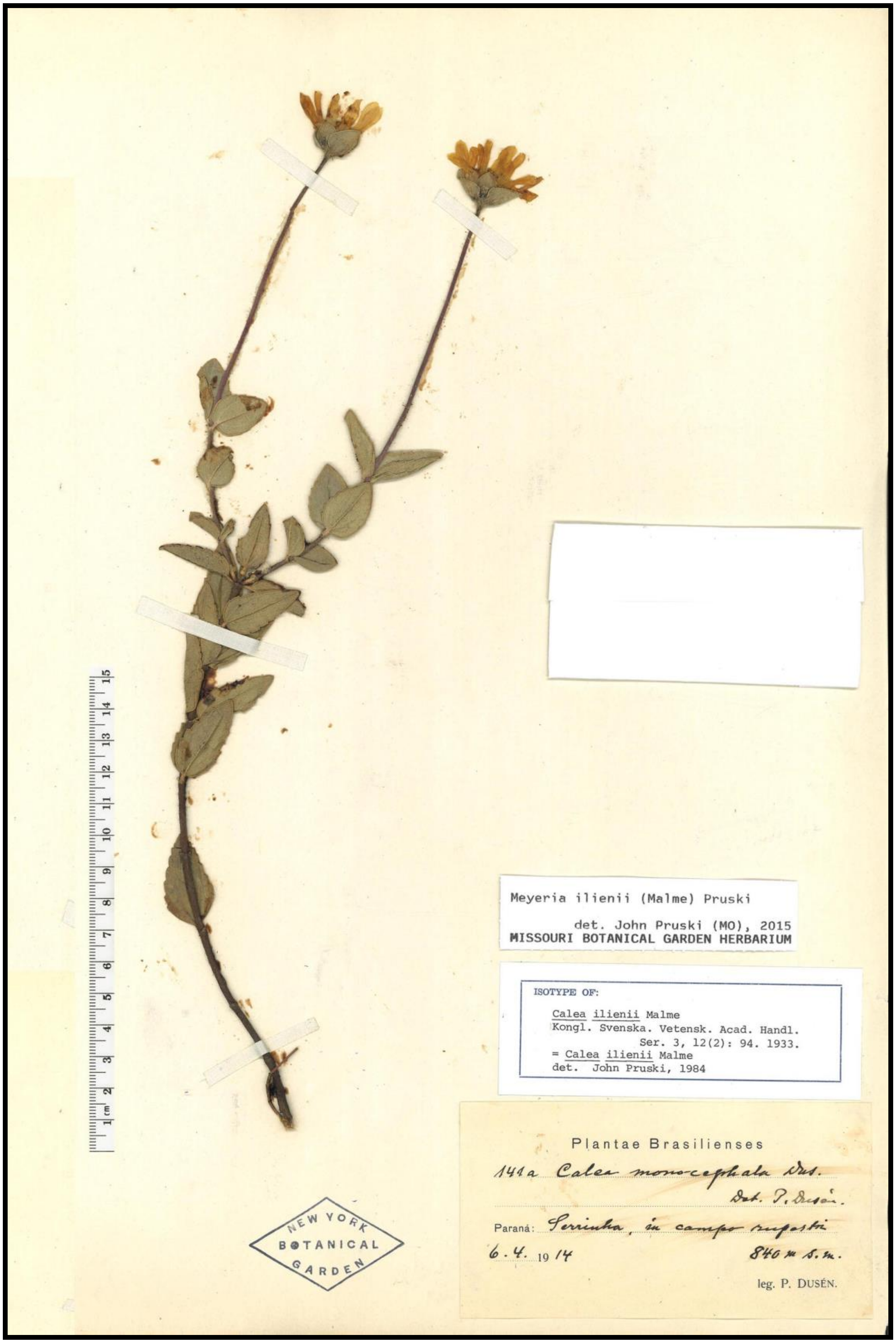
Figure 63. *Meyeria heteropappa* (Pruski & Urbatsch) Pruski, topotype. (Photographs on Serra do Cipó by Benoît Loeuille, who kindly sent these images to the writer; voucher not seen).

MEYERIA FUNKIANA (V.R. Bueno & G. Heiden) Pruski, **comb. nov.** *Calea funkiana* V.R. Bueno & G. Heiden, Syst. Bot. 46: 470. 2021. **TYPE: BRAZIL. Minas Gerais.** Serra do Cipó, 28 Feb 1991, *Mayo et al. CFSC7026* (holotype: SPF; isotypes: SP, UEC).

Meyeria funkiana (V.R. Bueno & G. Heiden) Pruski is endemic to Minas Gerais, Brazil. These plants were treated by Pruski (2005) as *M. triantha*, but are accepted here as a more strongly pubescent, but otherwise somewhat narrowly defined, segregate of *M. triantha*.

MEYERIA HETEROPAPPA (Pruski & Urbatsch) Pruski, **comb. nov.** *Calea heteropappa* Pruski & Urbatsch, Brittonia 40: 346. 1988. **TYPE: BRAZIL. Minas Gerais.** Serra do Cipó, km 129 e 131, 1100–1260 m, 18 Apr 1950, *Duarte 2618* (holotype: RB-70584, 3 sheets, each sheet is stamped 70584, but only the first sheet has a collection label, the protologue drawing is from sheet 2, the sheet with the packet; isotype: F). Figures 62–63.

Meyeria heteropappa (Pruski & Urbatsch) Pruski is endemic to Minas Gerais, Brazil (Pruski and Urbatsch 1988; Pruski and Hind 1998; Pruski 2005). It was the first described consistently heteropappose ternate-leaved *Meyeria.*



Meyeria ilienii (Malme) Pruski

det. John Pruski (MO), 2015
MISSOURI BOTANICAL GARDEN HERBARIUM

ISOTYPE OF:

Calea ilienii Malme
Kongl. Svenska. Vetensk. Acad. Handl.
Ser. 3, 12(2): 94. 1933.
= Calea ilienii Malme
det. John Pruski, 1984

Plantae Brasilienses
141a Calea mono-cephala Dus.
Det. P. Dusén.
Paraná: Serrinha, in campo rupestri
6.4. 1914 840 m s.m.
leg. P. DUSÉN.

Figure 64. Isotype of *Meyeria ilienii* (Malme) Pruski. (*Dusén 141a*, NY).

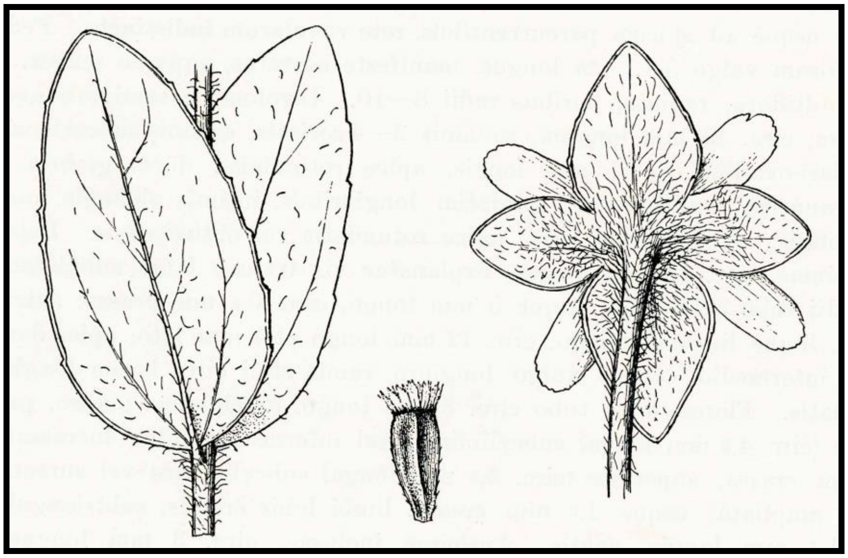


Figure 65. *Meyeria ilienii* (Malme) Pruski, showing (left to right) leaf pair, callose-margined; quadrangular disk cypsela; involucre from below showing the hairy-leafy callose-margined decussate outer four bracteate-phyllaries. (Reproduced from protologue in Malme 1933: fig. 17).

MEYERIA ILIENII (Malme) Pruski, **comb. nov**. *Calea ilienii* Malme, Kongl. Svenska Vetensk. Acad. Handl., ser. 3, 12(2): 94, fig. 17. 1933. (as Kungl. …Akad. … Tredje Serien; viz BPH-2: 1: 686). **TYPE: BRAZIL. Paraná.** Serrinha, in campo rupestri, 6 Apr 1914, *Dusén 141a* (holotype: S photograph 3.10; isotypes: F, G, K, MO, NY, PH photograph 5.9, US). Figures 64–65.

The part number is needed in the literature citation as it begins on page 1, and is confusable with other parts of the series, each of which begins on a page 1. My reprint of Malme is from S.F. Blake, has a green cover, and reads "Kungl. …Akad. … Tredje Serien."

Meyeria ilienii (Malme) Pruski is endemic to Paraná and Santa Catarina, Brazil. *Meyeria ilienii* is a less-leafy long-pedunculate congener of the earlier *M. monocephala*, but differs by its hairy, glandular, and toothed leafy outer four callose-margined bracteate phyllaries (Fig. 64).

MEYERIA KRISTINIAE (Pruski) Pruski, **comb. nov.** *Calea kristiniae* Pruski, Brittonia 36: 100. 1984. **TYPE: BRAZIL. Rio Grande do Sul**. Vila Manresa, prope Porto Alegre, 1 Oct 1948, *Rambo 37768* (holotype: S, photograph 4.20 and ektachromes 84.16 + 84.32; isotypes: B, PACA kodachromes 87.30–87.31). The collection date on the holotype label is "1.10.1948" and was published in error by Pruski (1984) as "10 Jan 1948, i.e. misread as written as 10-I-1948. The correct transliteration is 1-X-1948, i.e., 1 Oct 1948 as written in botanical exsiccatae, pointing out that the utility of the traditional convention in science of using Roman numerals for months. Figure 66.

Meyeria kristiniae (Pruski) Pruski was described from Rio Grande do Sul, and is also known along the border just into Uruguay (Uruguay, Livramento, Sep 1935, *Herter 9 5863, Pl. Ur. 1963*, F, US, det. Pruski en sched. 29 Apr 1987). This species is one of only two Meyerias not endemic to Brazil, and it occurrence in Uruguay is the southernmost known station of *Meyeria*. The species is distinctly subtropical, being as far south of the equator as New Orleans is north of it. The species was dedicated to Kristin Malin, who in the 1980s illustrated many species then placed in *Calea*.

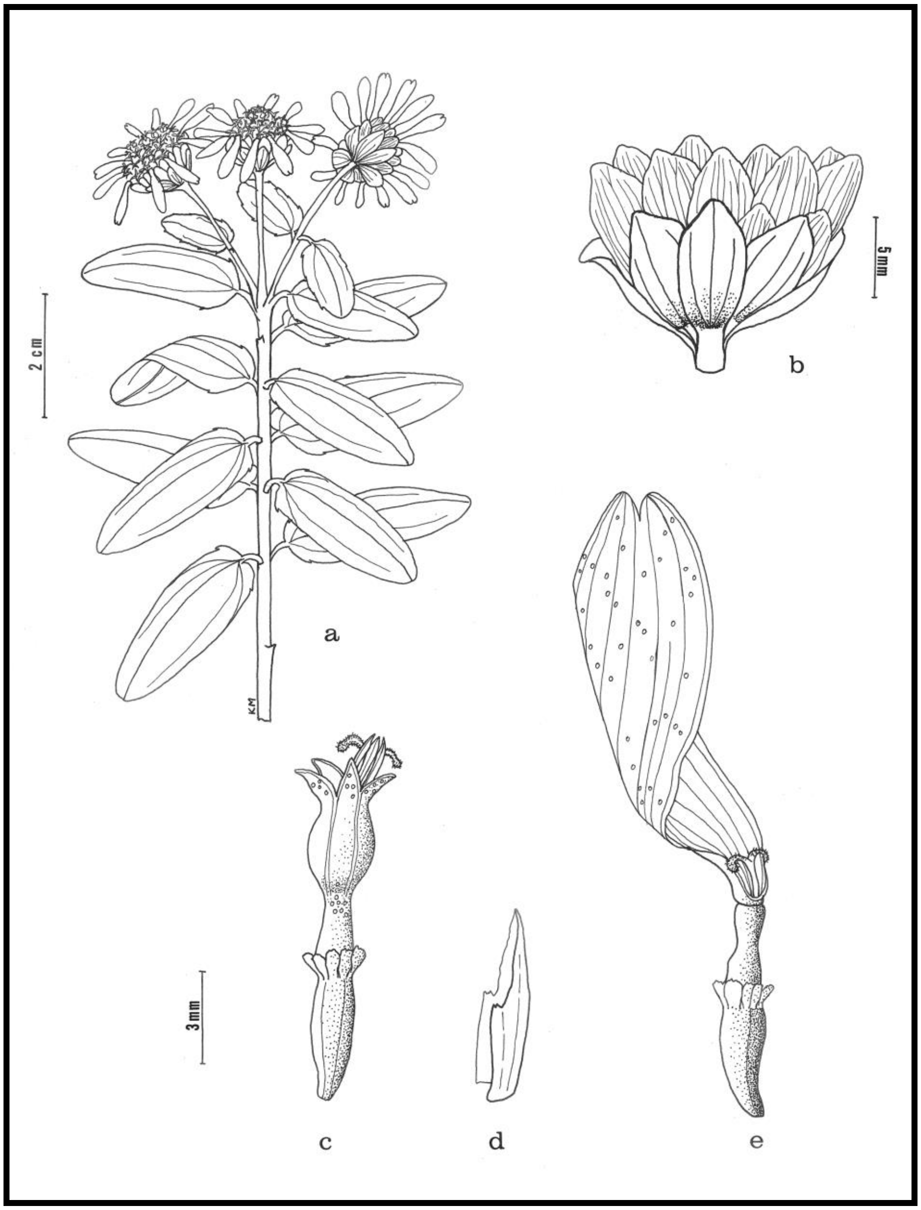


Figure 66. *Meyeria kristiniae* (Pruski) Pruski. A. Flowering branch. B. Involucre of fruiting capitulum. C. Disk floret. D. Palea. E. Ray floret. (Drawn by Kristin Malin from *Rambo 37768*, S, the holotype; also used in Pruski 1984, the protologue).

MEYERIA LONGIFOLIA DC., Prodr. 5: 671. 1836. *Calea longifolia* (DC.) Baker, in Martius, Fl. Bras. 6(3): 260 1884, nom. illeg. (non *Calea longifolia* Gardner, 1848). *Calea marginata* S.F. Blake, J. Wash. Acad. Sci. 27: 387. 1937 nom. nov. *Calea barrosoana* H. Rob., Phytologia 44: 274. 1979, nom. nov. illeg. **TYPE: BRAZIL.** Prov. São Paulo, 1833, *Herb. Imp. Bras. 407* (holotype: P, photograph 12.15 and kodachrome 83.25, as Macbride neg. 38063, barcode P02140741; isotypes: F, G-DC as IDC microfiche 800. 975.III.I; it seems possible that there could be an unrecognized isotype in R). The Paris holotype was specifically cited by Candolle as "v. s. in h. reg. Par. ex h. Mus. imp. Bras. sub n. 407" and is labeled with a red "TYPE" annotation just above the Paris label. Both the F and G-DC isotypes are fragments of the Paris holotype. The type is without collector, but may be a Sellow via Gaudichaud collection. Figure 67 left.

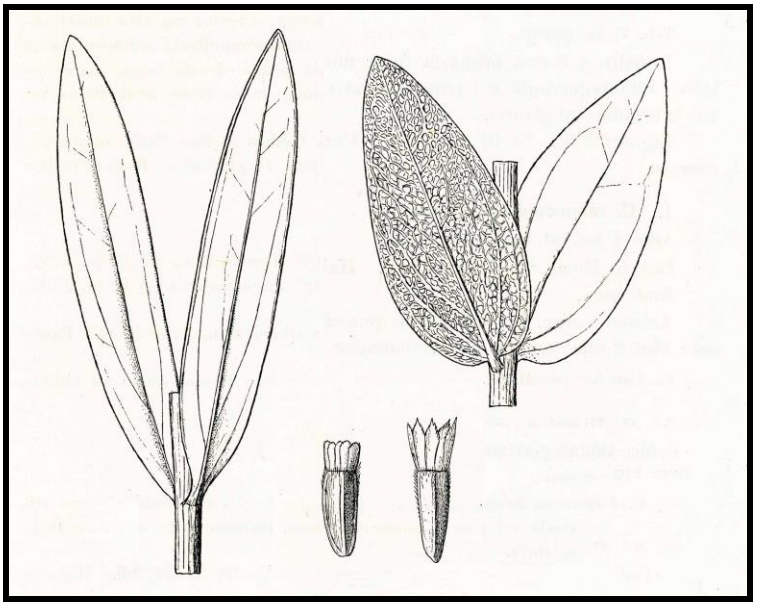


Figure 67. Leaf pairs and quadrangular disk cypselae in two of the four original species of *Meyeria* DC. Left: *Meyeria longifolia* DC. Right: *Meyeria parvifolia* DC. (Modified from Malme 1933: fig. 16).

Meyeria longifolia DC. is known in Paraná and São Paulo, Brazil. Pruski (2005) reported this distribution using the name *Calea marginata* S.F. Blake, a name used when the species is treated within *Calea*. Both *C. marginata* S.F. Blake and *Calea barrosoana* H. Rob. were proposed as replacement names, the two are homotypic, but the latter is illegitimate.

MEYERIA MONOCEPHALA (Dusén) Pruski, **comb. nov.** *Calea monocephala* Dusén, Ark. Bot. 9(15): 32. 1910. **LECTOTYPE**, selected here from among possibly more than one collection, no number coted in protologue: **BRAZIL. Paraná.** Desvio Ribas, 20 Jan 1909, *Dusén 7599* (lectotype, sheet selected here: S, photograph 10.22 and ektachrome 84.28, numbered S-R-882; isolectotypes: B† as Macbride neg. 15378, BM, E, GH, K, M, NY, US). There is a photograph of K in GH. No specimens were cited in the protologue, however, the only available authentic material is *Dusén* 7599. The S sheet is photograph number 10:10, the M sheet is photograph number 8:34. The journal part number is needed in the literature citation as it begins on page 1, confusable with other parts of the series.

Meyeria monocephala (Dusén) Pruski is endemic to Paraná, Brazil, and is a xylopodial plant similar to the later described long-pedunculate *Meyeria ilienii* (Malme) Pruski. *Meyeria monocephala* has robust stems densely leafy with the single capitulum relatively short-pedunculate and subglabrous-bracteate. Although shorter-stemmed, less-leafy differently-bracteate *M. ilienii* may be an ecological variant, both species are accepted as distinct.

MEYERIA MYRTIFOLIA DC., Prod. 5: 670. 1836. *Calea myrtifolia* (DC.) Baker, in Martius, Fl. Bras. 6(3): 260. 1884. **TYPE: BRAZIL**. **Minas Gerais.** prope Diamantina (sub "Tejuco"), 1833, *Vauthier 320* (holotype: G-DC, as IDC microfiche 800. 975.II.7; isotypes: F, G photograph 10.26, GH-2, NY, P-3 herb. Richard as photograph 12.20 and kodachrome 83.29, W photograph 10.25). The protologue gives the collection number as 370, the holotype and all other available specimens are numbered 320. The protologue number is a simple typographical error. A third sheet in GH, this from the Klatt herbarium and potentially a type, is labelled "Tejuco, Minas Geraës, *Vauthier 320*, Lagoa Santa, Claussen." Figures 57A, 57C, 58, 61A–B, 61D.

Calea myrtifolia (BC.) Baker, in Martius var. *paucidentata* Sch. Bip. ex Baker, in Martius, Fl. Bras. 6(3): 260. 1884 [as "Var. CALEA PAUCIDENTATA *Schultz Bip. in sched. Riedel*"]. **LECTOTYPE**, designated here from among two cited collections: **BRAZIL. Minas Gerais.** Serra do Caraça, Jan 1827, *Riedel 1427 (1483)* (lectotype, sheet designated here: LE photograph 2.1; isolectotypes: G, K as s.n. but with trinomial in Baker's hand, NY ex LE-Hrb. Fischer). The lectotype collection is chosen because a Riedel collection was explicitly cited by Baker, at least the cited LE and NY sheets are numbered, and the LE lectotype is marked "*Meyeria paucidentata* Sch. Bip." in the hand of Schultz Bipontinus in faint ink just above the four-line dark-ink handwritten locality label at the bottom of the sheet. In 1983 I annotated this LE sheet as photograph 2.1 has ample material consisting of six branchlets as *M. myrtifolia*, but at that time I incorrectly thought that the Sch. Bip binomial is "invalid." Since, Rupert Barneby (pers. comm.) has said Baker's intent is clear and that the trinomial is valid.

I similarly mistakenly annotated sheets several herbaria, e.g., W, saying *Calea paucidentata* is invalid, although being valid at the varietal rank using a trinomial. *Claussen 48* and *Claussen 668* in Paris-Sch-Bip, etc. may be different collections and in Paris some material is also numbered as species number 1269. Although I may have been correct in 1981 in marking the K-Hook sheet that has the Baker trinomial as probably *Claussen 48*, Baker may not have seen the Paris material, and thus the bulk of Claussen materials perhaps cannot be numbered with certainty. Riedel appears to have collected the variety a single time, the *Riedel s.n.* sheets thus be numbered *Riedel 1427 (1483)* being from the known locality of Serra do Caraça, and this ample lectotype sheet in LE is the most complete of originally identified material, hence its selection herewith.

Meyeria myrtifolia DC., the generitype, is known in Minas Gerais, Paraná, and São Paulo, Brazil. Pruski and Urbatsch (1988) and Pruski (2005) gave the distribution as "Minas Gerais south to Rio Grande do Sul" but the material from Rio Grande do Sul (e.g., *Rambo 108*, LP, PACA) has been redetermined as *M. phyllolepis*.

MEYERIA NERVOSA (G.M. Barroso) Pruski, **comb. nov.** *Calea nervosa* G.M. Barroso, Sellowia 26: 109. 1975. **TYPE: BRAZIL**. **Goias.** Cerra Geral do Paraná, gallery forest and adjacent cerrado, 3 km S São Joao da Alianca, near riacho, 850 m, 15 Mar 1971, *Irwin, Harley & Smith 31796* (holotype: UB; isotypes: C, COL, F, K, LIL, MO, NY, RB-166206, US). Barroso in her protologue cited "Holotypus … UB, RJ, NY" and based on the non-alphabetic citation of herbaria the original card version of Gray Cards (as reproduced in E.A. Shaw, Gray Herbarium Index, first supplement, vol. 1 A–J: 145. 1978) clearly cited UB as the holotype, which could be considered to effect lectotypification if desired, albeit subsequently Pozo and Hind (Kew Bull. 68: 4. 2013) took the view that "no distinction was made" between the cited sheets. Barroso's citation of RJ is not in reference to R (the National Museum, where an isotype sheet was not found by R. Estevez pers. comm.), but rather "RJ" more likely refers to RB-166206, an isotype which Pozo and Hind (Kew Bull. 68: 4. 2013) took as the lectotype. Although the UB holotype sheet is not reproduced in jstor, I examined the holotype (as cited by Barroso and the Gray Cards) on 23–X–1987 with George Eiten during my visit to UB.

Meyeria nervosa (G.M. Barroso) Pruski seems to have been first collected as *Glaziou 21551 bis* (P) in 1894, but remained undescribed for 80 years. It is a striking plant that is a narrow endemic centered in the Chapada dos Veadeiros, Goiás, Brazil. *Meyeria nervosa* is most similar in gestalt to

M. aldamoides, recently described from about 60 km NW of Chapada dos Veadeiros. *Meyeria nervosa* is on occasion characterized by a somewhat corky epidermis in its fruits, which is not taken here as taxonomically significant, but rather appears to be a microclimate-influenced feature resembling the epidermal corky fruit layer found in several unrelated helianthoids of moist habitats.

MEYERIA PARVIFOLIA DC., Prodr. 5: 670. 1836. *Calea parvifolia* (DC.) Baker, Fl. Bras. 6(3): 259. 1884. **TYPE: BRAZIL**. Prov. São Paulo, s.d., *Herb. Imp. Bras. 406* (holotype: P, as Macbride neg. 38066, barcode P02140753; isotype: G-DC, as IDC microfiche 800. 975.II.8; it seems possible that there could be an unrecognized isotype in R). This Paris sheet was specifically cited by Candolle as "v. s. in h. Mus. reg. Par. ex h. Mus. imp. Bras. sub n. 406" but is labeled with a red "ISOTYPE" annotation on the Paris label. The type is without collector, but may be a Sellow via Gaudichaud collection. Figures 57B, 57D, 61C, 67 right.

Herb. Imp. Bras. 406 is also the cited type number of *Calea gentianoides* DC., but because the number on the label on that Paris sheet was modified perhaps to *416* at one point it seems best to cite that as *Herb. Imp. Bras. 406 bis?/416?*.

Meyeria parvifolia DC. is among the more common species of *Meyeria*, and Pruski and Urbatsch (1988) and Pruski (2005) reported the species as known in Paraná and São Paulo, Brazil.

MEYERIA PHYLLOLEPIS (Baker) Pruski, **comb. nov.** *Calea phyllolepis* Baker, in Martius, Fl. Bras. 6(3): 260. 1884. **LECTOTYPE**, collection designation here, from among three possibly different collections of Sello: **BRAZIL**. Prov. São Paulo, s.d., *Sellow s.n.* (lectotype, sheet designation here: K, as photograph 12.12, now barcoded K000323167; presumed isotypes: B† as Macbride neg. 15384, US). Baker cites several Sellow collections (*1044*, *2534*, *3140*). It is not clear to me what the collection number is on either the Kew lectotype or the Berlin sheet. The Macbride-photographed Berlin sheet is possibly *Sellow 2534*, as labeled in the Field Museum database. The material in Berlin was destroyed in March 1943 in a WWII bombing and fire. The lectotype appears to have the specific name written on it in Baker's hand (albeit on a label rather than directly on the sheet as I have seen for most of Baker's annotations). US is a fragment of the Kew lectotype.

Meyeria phyllolepis (Baker) Pruski is centered in Rio Grande do Sul and Santa Catarina, Brazil, but Pruski (2005) also reported the species from "coastal São Paulo." Some material in Rio Grande do Sul had been determined previously as *M. myrtifolia* and *M. triantha*. *Meyeria phyllolepis* is one of several species of *Meyeria* that may have ternate leaves, and while this is seen in the type collection, it is found only occasionally among other collections. Amy Zlotsky (en sched. 1982) annotated the Kew type as syntype, which in 1987 I updated (onto her label) in red ink as "Lecto!" (i.e., lectotype).

MEYERIA PRUSKIANA (V.R. Bueno & G. Heiden) Pruski, **comb. nov.** *Calea pruskiana* V.R. Bueno & G. Heiden, Syst. Bot. 47: 576. 2022. **TYPE: BRAZIL. São Paulo.** Trilha do Rio Sapucai, Parque Estadual de Campos do Jordão, 4 Feb 1988, *Robim & Carvalho 530* (holotype: UEC; isotype: SPSF).

Meyeria pruskiana (V.R. Bueno & G. Heiden) Pruski is found in extreme southeastern Minas Gerais and immediately adjacent São Paulo, Brazil. These plants were treated by Pruski (2005) as *M. triantha*, but are accepted here as a very narrowly defined segregate of *M. triantha* and differing by usually variable traits of slightly longer rays corolla limbs and few-branched stems.

MEYERIA QUADRIFOLIA (Pruski & Urbatsch) Pruski, **comb. nov.** *Calea quadrifolia* Pruski & Urbatsch, Brittonia 40: 341. 1988. **TYPE: BRAZIL**. **Distrito Federal.** Chapada da Contagem, 17 Feb 1975, *Hatschbach, Anderson, Barneby & Gates 36236* (holotype: MBM, negative 12533; isotypes: C, K, LP, LSU, NY, US). Figure 59.

Meyeria quadrifolia (Pruski & Urbatsch) Pruski was described from material in Distrito Federal and Goiás, Brazil (Pruski and Urbatsch 1988), but more recently material from Minas Gerais has been seen. This common *Meyeria* was noted to have whorled leaves (usually 4 leaves per node), but had frequently been misidentified as discoid *Laceanthos reticulata*. This material was described as *M. quadrifolia*, was described simultaneously with *M. heteropappa*, and these two species proved to be the first described species of *Meyeria* having consistently whorled leaves. A paratype of M. *quadrifolia* is the voucher for the chromosome report of x = 18 by Turner et al. 1979.

MEYERIA SEMIRII (Pruski & D.J.N. Hind) Pruski, **comb. nov.** *Calea semirii* Pruski & D.J.N. Hind, Kew Bull. 53: 698. 1998. **TYPE: BRAZIL**. **Minas Gerais**. Mun. Grão Mogol, Vale do Ribeirao dos Bois, 22 May 1987, *Mello-Silva & Pirani CFCR 10804* (holotype: SPF; isotypes: NY, UEC).

Meyeria semirii (Pruski & D.J.N. Hind) Pruski is endemic to Minas Gerais, Brazil (Pruski and Hind 1998; Pruski 2005).

MEYERIA SESSILIFOLIA (V.R. Bueno & G. Heiden) Pruski, **comb. nov.** *Calea sessilifolia* V.R. Bueno & G. Heiden, Syst. Bot. 47: 587. 2022. **TYPE: BRAZIL. Minas Gerais.** Serra do Espinhaço, ca. 12 km SW of Diamantina, 23 Jan 1969, *Irwin et al. 22491* (holotype: RB; isotypes: NY, US).

Meyeria sessilifolia (V.R. Bueno & G. Heiden) Pruski was given in the protologue as herbaceous and endemic to Minas Gerais, Brazil; it is surely a perennial.

MEYERIA SUBINTEGERRIMA (Malme) Pruski, **comb. nov.** *Calea hispida* fo. *subintegerrima* Malme, Kongl. Svenska Vetensk. Acad. Handl., ser. 3, 12(2): 94, plate V-sinistra-left. 1933. (as Kungl. … Akad. … Tredje Serien; viz BPH-2: 1: 686). *Calea subintegerrima* (Malme) V.R. Bueno & G. Heiden, Syst. Bot. 47: 577. 2022, comb. inval. (basionym literature reference incorrect). **LECTOTYPE**, designated here, chosen from among two syntype collections: **BRAZIL. Paraná.** Jaguariahyba [now Jaguariaíva], 5 Feb 1910, *Dusén 9187* (lectotype, sheet and lectotype branchlets designated here: S, photograph 5.11 and ektachrome 84.32b, numbered S-R-875, top three hispid-hirsute-stemmed branchlets with subentire leaves; isolectotypes: G photograph 5.10, GH, US). Figure 60.

The middle of the three lectotype branchlets is that branchlet of which the reverse face was reproduced in protologue plate V-left hand side (sinistra); the lower left larger branchlet has stems hirtellous-hirsutulous and toothed leaves. Because the top middle hispid-hirsute subentire-leaved branchlet on *Dusén 9187* is that photographed in the plate accompanying the protologue and is most representative of the taxon as envisioned by Dusén (viz the epithet: *subintegerrima*), it and the adjacent two branchlets are chosen as the lectotype over *Dusén 11296*. *Dusén 9187* (S: S-R-875) was in 1984 (en sched.) annotated by me as the lectotype, remains the lectotype, and the top three hispid-hirsute subentire-leaved branchlets match the protologue (epithet, description, and accompanying plate), more so than the lower S branchlet and the G, GH, and US isolectotypes, which have stems hirtellous-hirsutulous. The branchlet pubescence and leaf margin variation, however, is seen as micro environmental, and both phases have fertile pollen. The published collection number "9189" is in error and the available sheets are "9187." The citation by Bueno and Heiden (2022) cited of *Dusén 9189* (GH) as lectotype is not accepted as this collection number is a different taxon. The Geneva sheet is from the Delessert Herbarium and was stamped as loan 5944 sheet 165. The part number is needed in the literature citation as it begins on page 1, and is confusable with other parts of the series, each of which begins on a page 1. My reprint of Malme is from S.F. Blake, has a green cover, and reads "Kungl. …Akad. … Tredje Serien."

Segregate *Meyeria subintegerrima* (Malme) Pruski occurs in Paraná and Santa Catarina, Brazil.

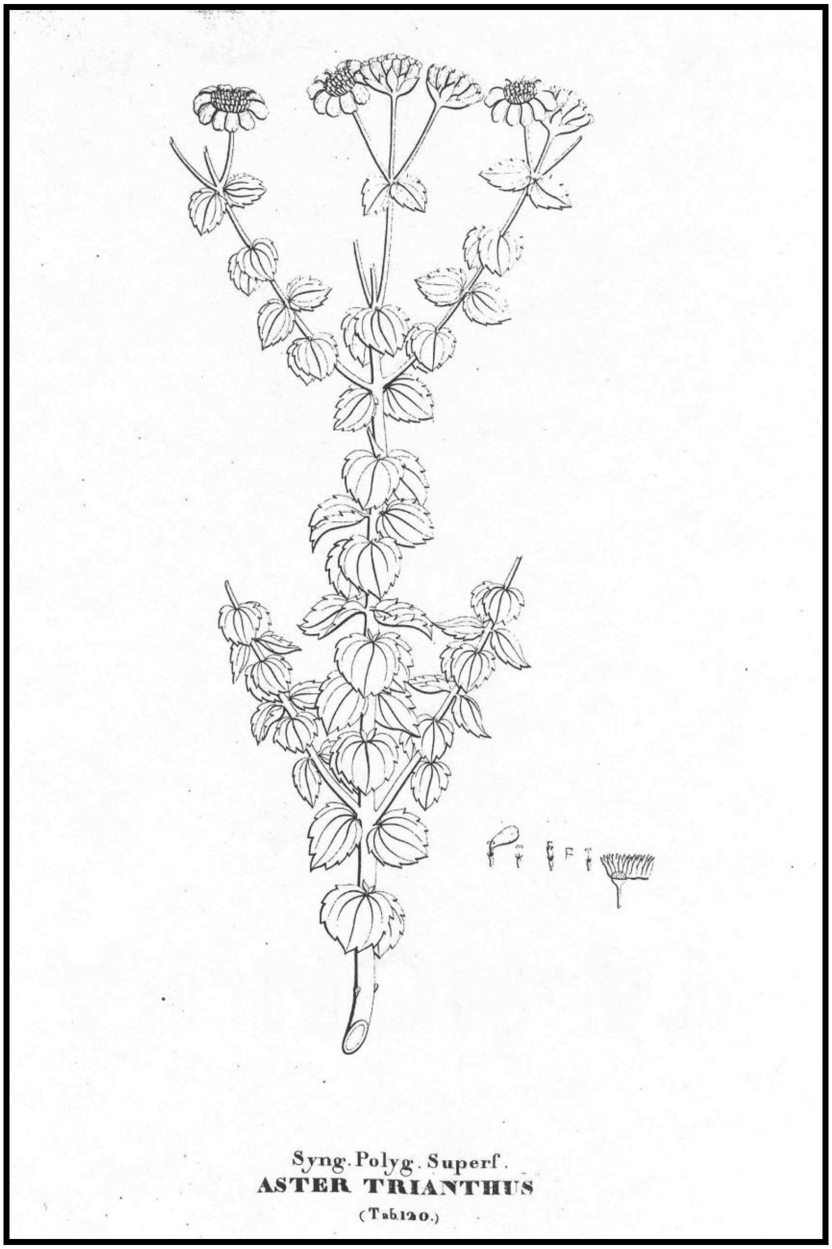


Figure 68. Lectotype of *Aster trianthus* Vell. [≡ Meyeria *triantha* (Vell.) Pruski]. (Reproduced from Velloso, Fl. Flumin. (Icones) 8: tab. 120. 1827 [1831]; also reproduced by Pruski 2005: fig. 2).

MEYERIA TRIANTHA (Vell.) Pruski, **comb. nov.** *Aster trianthus* Vell., Fl. Flumin. (Icones) 8: t. 120. 1827 [1831]. *Calea triantha* (Vell.) Pruski, Sida 21: 2027. 2005. **LECTOTYPE** (designated by Pruski, 2005: 2027): tab. 120, Vell., Fl. Flumin. (Icones) 8. 1827 [1831]. Figure 68.

Meyeria hispida DC., Prod. 5: 671. 1836. *Calea hispida* (DC.) Baker, in Martius, Fl. Bras. 6(3): 261. 1884. **LECTOTYPE**, designated by Pruski, 2005: 2027: **BRAZIL.** Prov. São Paulo, campis editis, Nov. 1833, *Lund 866* (lectotype: G-DC, as IDC microfiche 800. 975.III.2 large branch on left; isolectotypes: C-4 as photographs 2.33–2.36, S, W).
The G-DC lectotype also has a small twig of *H. Imp. Bras. 405* (possibly a Sellow via Gaudichaud plant mounted to the lower right of the Lund collection).
[Lectoparatype: *Herb. Imp. Bras 405* (possibly Sellow via Gaudichaud): F (fragment of a sheet from P), G-DC (fragment of a sheet from P), P-2 one as photograph 12.12 and kodachrome 83.23; it seems possible that there could be an unrecognized isotype in R].

[*Meyeria regnellii* Sch. Bip., nom. proviso inval., Linnaea 22: 570. 1849, cited voucher is *Regnell I. 192*; *M. regnellii* post-dates *M. hispida*, to which it is not linked nomenclaturally. Schultz Bipontinus (1859–1860: 181) subsequently redetermined his earlier cited voucher—*Regnell I. 192*—as *M.* (*Calea*) *hispida* DC., linking bibliographically *M. regnellii* and *M. hispida*].

Meyeria triantha **(**Vell.) Pruski, long known as either *Meyeria hispida* DC. or *Calea hispida* (DC.) Baker (e.g., Candolle 1836; Schultz Bipontinus 1859–1860; Baker 1884; Malme 1933; Pruski and Hind 1998), is the most common species of *Meyeria*. Schultz Bipontinus (1849: 570, 1859–1860: 181) reported *Regnell I. 192* as the common but now synonymous *M. hispida*. *Meyeria triantha* was given by Pruski and Urbatsch (1988) and Pruski (2005) as occurring from "Minas Gerais south to Santa Catarina" (i.e., Minas Gerais, Paraná, Santa Catarina, and São Paulo), Brazil.

Material from Cerro Corá, Paraguay determined as *Calea hispida*, proves instead to be *Podocalea*. The common hairier variant of *M. triantha* frequent near Serra do Cipó of the Espinhaço mountains in Minas Gerais is recognized as the segregate *M. funkiana* (V.R. Bueno & G. Heiden) Pruski. Other segregates of *M. triantha* are *M. pruskiana* (V.R. Bueno & G. Heiden) Pruski and *M. subintegerrima* (Malme) Pruski, and all three species were among materials that Pruski (2005) determined as *M. triantha*. Occasionally, *M. triantha* is weakly heteropappose (e.g., *Hatschbach 18347*, UEC; Pruski and Hind 1998: 701).

Names in *Meyeria* for species not recognized here. (i.e., *Meyeria* species peripheral to the *Meyeria myrtifolia* DC. group; each of the below six species is a Brazilian endemic near the *Meyeria teucriifolia* Gardner group, and under revision by the writer):

Meyeria angustifolia Gardner, London J. Bot. 7: 414. 1848.

Meyeria candolleana Gardner, London J. Bot. 7: 414. 1848.

Meyeria elongata Gardner, London J. Bot. 7: 415. 1848.

Meyeria hypericifolia Gardner, London J. Bot. 7: 413. 1848.

Meyeria microphylla Gardner, London J. Bot. 7: 413. 1848.

Meyeria teucriifolia Gardner, London J. Bot. 7: 412. 1848.

5. PODOCALEA Pruski, **gen. nov. TYPE:** *Calea cuneifolia* DC. [≡ *Podocalea cuneifolia* (DC.) Pruski].

Calea subgen. *Monanthocalea* Less., Syn. Gen. Compos. 242. 1832. *Calea* sect. *Monanthocalea* (Less.) Pruski, Kew Bull. 53: 684. 1998. **LECTOTYPE** (chosen by Wussow et al. 1985): *Calea uniflora* Less. [≡ *Podocalea uniflora* (Less.) Pruski].

Plantae herbaceae perennes vel suffruticosae, xylopodio magni; caules stricta; folia simplicia opposita aliquando ternata lamina chartacea vel subcarnosa plinervia; capitulescentia terminalis monocephala aliquando cymosa; capitula radiata vel aliquando discoidea, involucrum campanulatum vel hemisphaericum, phyllaria plerumque dimorpha; clinanthium paleaceum; paleae planae lineares; flosculi radii (0–)5–20 pistillati; flosculi disci hermaphroditi, corollae anguste infundibuliformae vel campanulatae glabrae vel glandulosae; antherae palidae; styli rami recurvati, areis stigmaticis discretis; cypselae obconicae nigrae; pappi squamae 10–18 subaequales.

Xylopodial herbaceous-stemmed scapose monocephalous perennial herbs or cymose-capitulate subshrubs, usually several-stemmed from caudex or xylopodium, stems 1–several from subterranean xylopodium, xylopodium small but in many herbarium specimens collected they are commonly golf-ball-sized or larger, sometimes collected above the xylopodium, stems strict or ascending, usually simple, sometimes few-branched near base just above ground-level, infrequently subshrubby and stems moderately branched nearly throughout, individual stems subterete or subhexagonal, wider stems striate, glabrous to hispid or pilose, commonly sparsely leafy in proximal half with 2–several pairs of leaves, plants infrequently moderately leafy nearly throughout; herbage glabrous to pilose with sessile-glandular trichomes and/or with simple subappressed or more typically ascending multicellular trichomes. **Leaves** simple, opposite or very infrequently ternate, sessile to short-petiolate; blade narrowly lanceolate to ovate or obovate, rarely suborbicular, stiffly chartaceous to subcarnose, usually 3–5-plinerved from base or from near base, base neither strongly cordate nor strongly clasping, margins entire to serrate or dentate, apex long-acuminate to obtuse or rounded, surfaces concolorous, glabrous, sessile-glandular, and/or becoming pilose or villous-tomentose. **Capitulescence** terminal, usually often scapose-monocephalous and held well-above leaves, usually long-pedunculate, sometimes short-pedunculate or even open cymose; peduncle ebracteate. **Capitula** radiate or infrequently discoid, many-flowered, often moderately large; involucre campanulate to hemispherical, phyllaries evenly graduated or as with outer 2–4 herbaceous or herbaceous-tipped and nearly half as long as capitulum; phyllaries few-seriate, subequal to graduate, usually at least somewhat dimorphic, outer phyllaries usually at least herbaceous-tipped, triangular to oblong or pyriform, often hirtellous, inner series of phyllaries glabrous and quickly transitioning from outer few, appressed at anthesis, entire, broadly triangular or often long-ovate or obovate, flat or concave, chartaceous-scarious-membranous or becoming hyaline distally, mostly stramineous or yellowish but often becoming purplish distally, pluristriate, nerves often darkish, innermost series of phyllaries usually much narrower than mid-series phyllaries; clinanthium convex to dome-shaped, paleate; paleae usually long-persistent, longer than the cypselae, generally linear, flat but with base slightly broadened and incurved, apex narrowed and often bent inward before cypsela maturation, 1-nerved, midrib brown, pale-colored along the usually entire margins. **Ray florets** pistillate (when present), uniseriate, usually about (0–)5–20, exserted from involucre; corolla yellow or infrequently white, limb 5+-nerved, abaxially glabrous or glandular, apex few-denticulate; style branches only slightly recurved. **Disk florets** several to many, bisexual; corolla narrow-funnelform to campanulate, glabrous or glandular, usually yellow, tube slightly dilated at base, throat typically longer than lobes, lobes 5 usually triangular-lanceolate, erect to spreading, resin ducts submarginal; anthers pale yellow, endothecial tissue polarized; pollen tricolporate, echinate; style trunk with two nerves, stylopodium slightly dilated, free and held above the annular nectary, branches recurved, 2-banded from base to apex, apex convex, distal-abaxial papillae shorter than convex apex. **Cypselae** isomorphic, turbinate-obconical, carbonized, dark**,** body slightly incurved basally, glabrous to setulose, twin trichomes with elongate terminal cells longitudinally connate for part of their lengths but with apices free and divergent, carpopodium oblique-annular and not well-developed, infrequently of greatly inflated cells; pappus radially symmetric, of about 10–18 subequal scales, rarely heteropappose, these narrowly linear-lanceolate with broad lacerate-serrate margins, apex acuminate to attenuate, pappus scales usually longer than the cypsela body, or less commonly oblong with apex obtuse to rounded, much shorter than the cypsela body, mostly stramineous-pale but sometimes pinkish, midzone thicker than margins, margins in palea longer than cypselae are sometimes broad near the middle. Chromosome number $2n = 32$.

Etymology. The prefix of the arbitrary formed generic name *Podocalea* is from the Greek noun *podos* for foot (Brown 1956: 620), and I use this prefix here in reference to the superficial caudex or underground xylopodium, found in most species. Many generic names have the prefix of either *poda* (e.g., *Podachaenium* Benth. viz Pruski 2016) or the equally grammatically correct *podo* (e.g., *Podocarpus* L'Hér. ex Pers., *Podocoma* Cass. viz Sancho et al. 2010, *Podophyllum* L., *Podostemum* Michx.), and the spelling *Podocalea* used here is somewhat mellifluous. The generic name *Calea* is of unknown derivation (Robinson and Greenman 1896) and I combine the generic name with a Greek prefix as done by Lessing who coined *Calea* subgen. *Haplocalea* and *Calea* subgen. *Monanthocalea*, each infragenus similarly used a Greek noun as the basis of its prefix.

Geographic Distribution. The species of *Podocalea* are restricted to tropical and subtropical southern South America, where they occur in Argentina, Bolivia, Brazil, Paraguay, and Uruguay. Many populations of *Podocalea* occurs in the southward-flowing drainage systems of rios Paraguai or Paranaiba, but a few occur in the Rio Tocantins drainage. The northwestern-most collection of *P. rupicola* seems to be in drainage system of either the rios Madeira, Tapajós, or Tocantins that flow northwards and ultimately into the Rio Amazonas.

The new genus *Podocalea* Pruski—typified by *P. cuneifolia*—(Compositae tribe Neurolaeneae) from southern South American is established for a series of former Caleas that are usually few-stemmed low xylopodial herbs with proximally disposed opposite leaves and large, often scapose monocephalous capitula (Figs. 69–70, 74, 78–82). In most species of *Podocalea*, one or more stems arise from a superficial caudex or subterranean xylopodium (Fig. 69; viz also Rawitscher and Rachid 1946; Eiten 1972; Vilhalva and Appezzato-da-Glória 2006; Appezzato-da-Glória et al. 2008), and the plants are usually less that waist-high (Fig. 70). The species of *Podocalea* are indeed mostly radiate and relatively large-capitulate (Figs. 70, 74A, 75B, 79–82), but these characters are neither apomorphic nor belying of any monogamous long-lasting relationships. More significant at the genus level are the important capitular features defining *Podocalea* and distinguishing it from *Calea*: flat linear non-conduplicate (vs. broad conduplicate) paleae (Figs. 71–72, 76D) nearly as long as (vs. shorter than) and often confusable with the pappus scales and the divergent (vs. appressed) terminal cell tips of the cypselar twin trichomes (Fig. 73). That these important capitular features are partly obscured and held with within the broad involucres and not easy evident without dissection does not negate their worthiness. A further technical distinction may be found in the base chromosome number of *Podocalea*, which is $x = 16$, whereas that of *Calea* is $x = 19$.

Baker (1884) and Löfgren (1897) recognized *Calea* subgen. *Leontophthalmum* (Willd.) Less. and Krascheninnikov (1923) recognized *Calea* sect. *Leontophthalmum* (Willd.) DC. (here I defer to sectional scheme of Bentham and Hooker 1873) and treated most species of *Podocalea* within large-capitulate *Calea* sect. *Leontophthalmum*, but *Leontophthalmum* is typified by shorter-broader-conduplicate-paled (Fig. 5) Andean material from Colombia, and species of *Podocalea* were excluded from that Andean group by Lessing (1832) and Pruski (1998). Instead, Pruski (1998, 2005, 2013), Silva et al. (2016), and Silva and Teles (2018) treated those southern South American species of then-undescribed *Podocalea* as *Calea* sect. *Monanthocalea* (Less.) Pruski, typified by *Podocalea uniflora* (Less.) Pruski. Although Mexican *Tonalanthus megacephalus* (B.L. Rob. & Greenm.) Pruski was allied to *Podocalea uniflora* by Wussow et al. (1985), *Tonalanthus* has conduplicate-broad paleae (Cockerell 1915: 71, fig. C as "disc bracts"), unusually slender ascending disk floret style branches, biconvex-compressed cypselae with adjacent twin trichomes (some elongated, some incipient) length differences (Figs. 96, 98C), and is placed in newly reinstated *Tonalanthus*. *Podocalea* has paleate clinanthia (Fig. 72), mid-series phyllaries with colored longitudinally-parallel resin ducts (Figs. 72A, 75B, 77A), non-setose corollas (Figs. 76A–B, 77B) with throats with a single reddish-brown resin duct along the veins (Fig. 15A), pale anthers (Fig. 75A), polarized endothecial tissue, free stylopodia (Fig. 76C), distal portions of the style branches papillose abaxially, and a radially arranged pappus of either short (Fig. 76B) or elongate (Fig. 76D) scales, typical of *Calea* Alliance members.

The combined morphological, anatomical, and cytological features seen in *Podocalea* are all suggestive of a status related to but outside of the confines of the genus *Calea*. The new genus *Podocalea* is thus established and is typified by *P. cuneifolia* (DC.) Pruski, a species which was fully described and has an extant holotype (Fig. 80A). *Podocalea uniflora* is the type of heterotypic synonym *Calea* sect. *Monanthocalea* (Less.) Pruski, a species validated by the four word description *involucri foliolis extimis obtusis*, and whose holotype in Berlin (Fig. 82) was destroyed in March 1943 in a fire resulting from WWII allied bombing. Thus, *Podocalea uniflora* would not be an ideal choice as the type of *Podocalea*, whereas the writer has collected *P. cuneifolia* (Fig. 70), described it in the Fontes do Ipiranga, São Paulo flora (Pruski in Nakajima et al. 2001), it is without doubt representative of *Podocalea*, and thus is designated as the generitype. *Podocalea* is less inclusive, however, than was Pruski's (1998, 2005, 2013) earlier more speciose *Calea* sect. *Monanthocalea*.

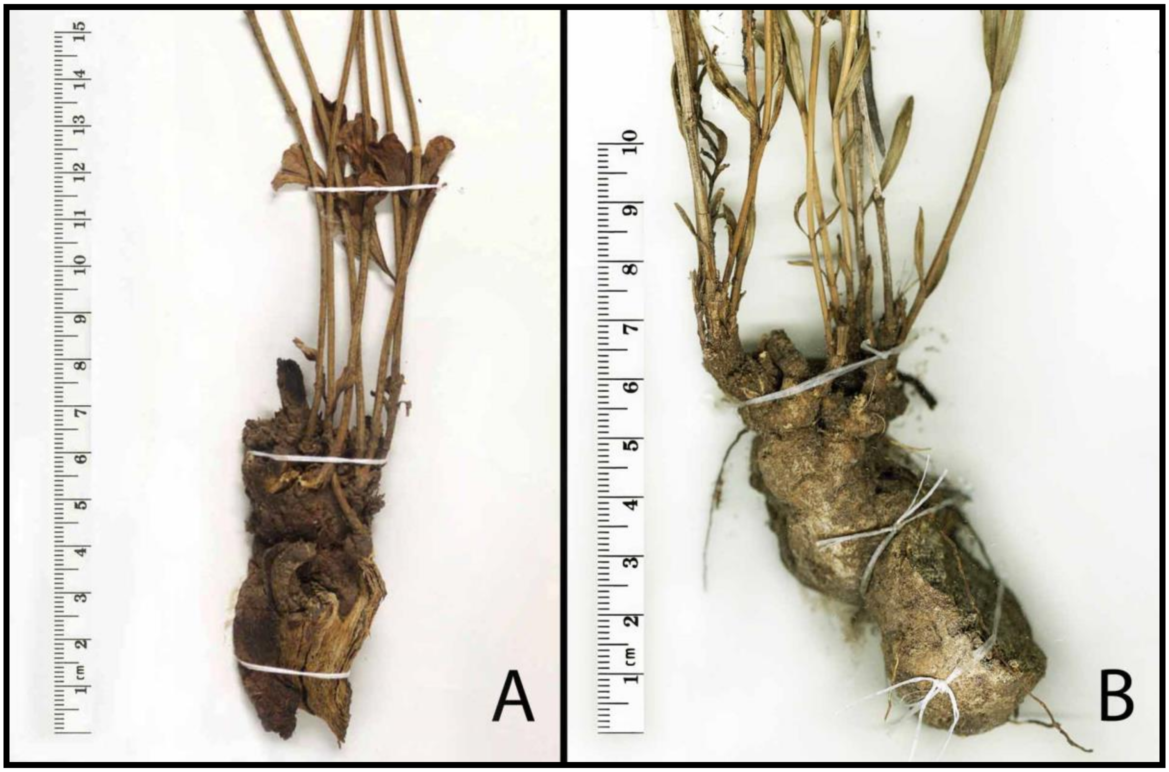


Figure 69. Xylopodia of representative species of *Podocalea* Pruski, whence the prefix of the generic name. A. *Podocalea cuneifolia* (DC.) Pruski, generitype. B. *Podocalea cabrerae* (Pruski) Pruski. (A *Pruski & Pirani 3536*, US, photographed by Susan B. Hunter; B *Zardini & Ramírez 51247*, MO, holotype, photographed by Stephanie Keil).

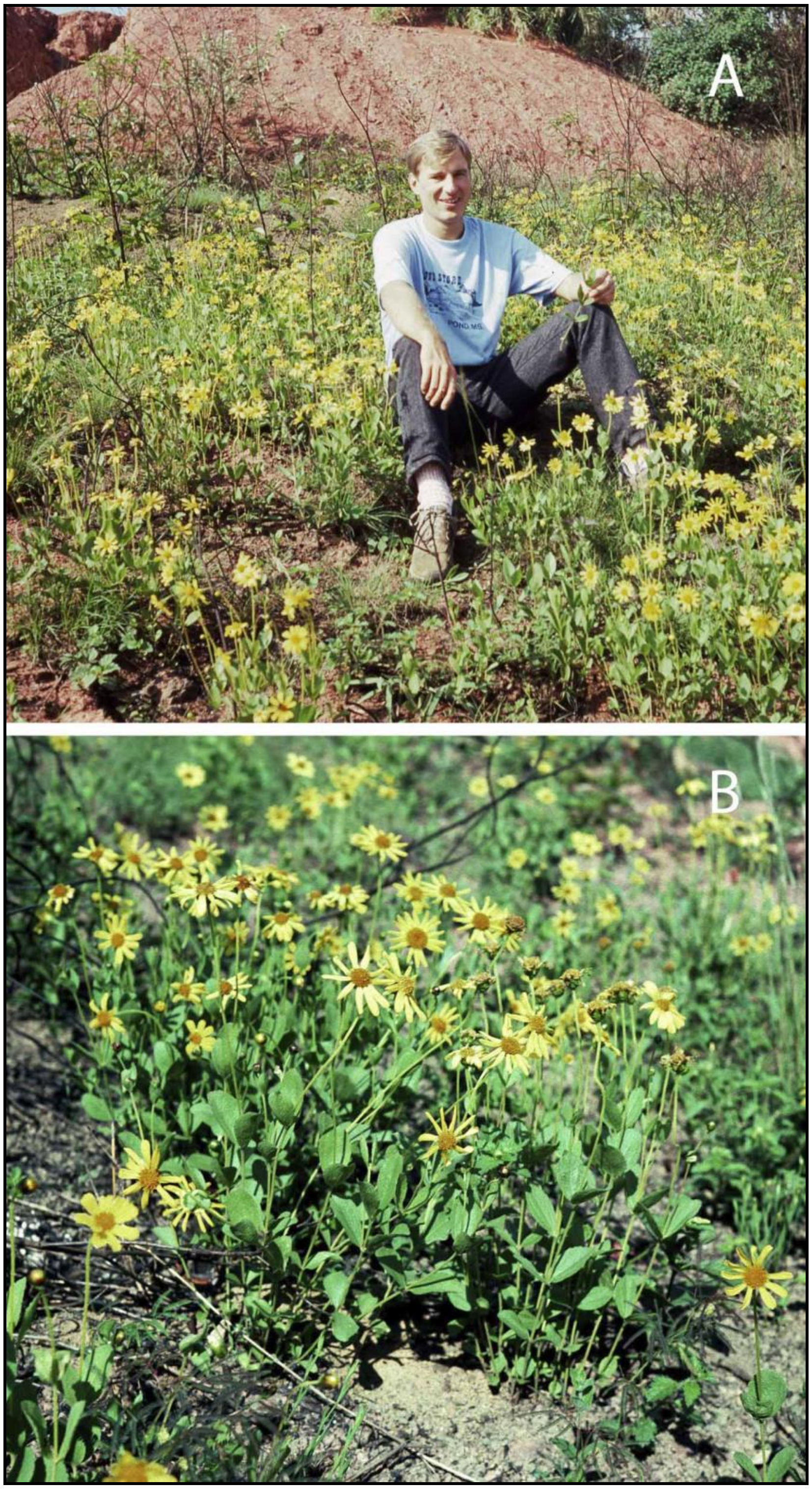


Figure 70. *Podocalea cuneifolia* (DC.) Pruski, generitype, habit, the yellow-flowered monocephalous radiate-capitula seen here are typical of the genus. A. Colony, showing several clustered stems per xylopodium; the plants are shorter than the writer's knees. B. Close-up, showing the simple monocephalous stems, yellow-flowered radiate-capitula, and opposite or occasionally ternate-whorled leaves. (*Pruski & Pirani 3536*, in 1987 this large colony was behind the USP herbarium building in São Paulo, Brazil; A photographed by Jose Pirani).

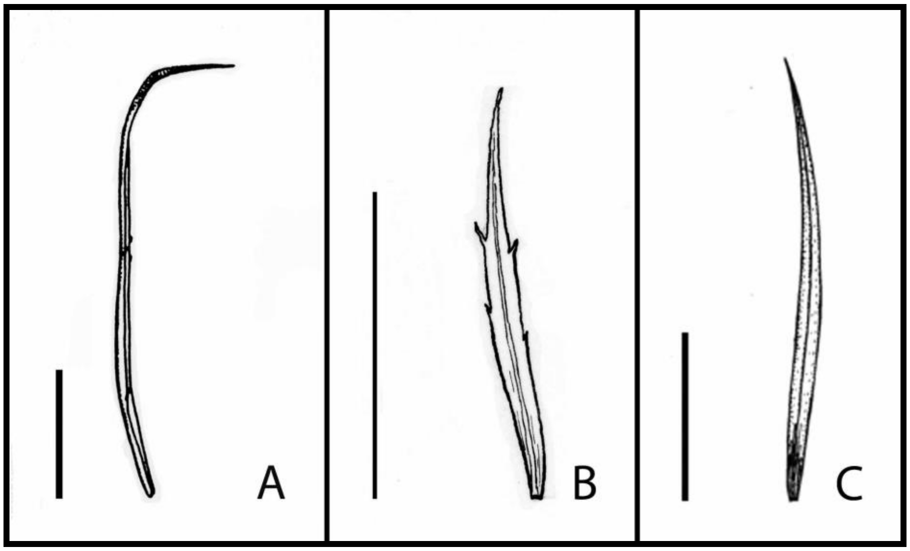


Figure 71. Paleae of *Podocalea* Pruski. A. *Podocalea verticillata* (Klatt) Pruski, showing bent apex. B. *Podocalea abbreviata* (Pruski & Urbatsch) Pruski. C. *Podocalea cabrerae* (Pruski) Pruski. (A *Silva Ribeiro 130*, HRCB, drawn by the collector, also used in Pruski 1998a: fig. 2; B Drawn by Bobbi Angel, from *Irwin et al. 9285*, NY, the holotype, also used in protologue; C Drawn by Gisela Sancho from *Zardini & Ramírez 51247*, unmounted isotype, also used in the protologue). Scale bars 3 mm.

Although most species of *Podocalea* are yellow-flowered large-capitulate low erect monocephalous xylopodial herbs stems with proximally disposed leaves (Figs. 70, 74, 78–82), a few species or *Podocalea* are relatively small-capitulate (e.g., *P. abbreviata*, *P. rupicola*) (Figs. 74B, 75A, 78), discoid-capitulate (i.e., *P. pedunculosa*) (Fig. 76D), white-ray-flowered (i.e., *P. paraguayensis*), sprawling-stemmed (e.g., synonymous *C. bakeriana var. volubilis*), robust leafy stemmed branched subshrubs that may have open cymose capitula (e.g., *P. rupicola*, *P. verticillata*) (Figs. 83–84), and even on occasion may have some nodes ternate-leaved (e.g., *P. angustifolia*, *P. cuneifolia*, *P. formosa*, *P. verticillata*) (Fig. 83).

The caudices and xylopodia in branched-stemmed *P. rupicola* and *P. verticillata* are relatively small, as are those of the reduced herb *P. abbreviata* (Fig. 74B, 78) that sometimes merely has a superficial caudex, but in most species—including *Podocalea cuneifolia*, the generitype—xylopodia are often well-developed and relatively large (Fig. 69). Elsewhere in the *Calea* Alliance, occasionally species (e.g., *Meyeria monocephala*) have similar-sized xylopodia, and thus the observable trend towards well-developed xylopodia in *Podocalea* is not a distinguishing character. In Compositae the underground storage organs of crop species are known to respond to artificial selection (Dempewolf et al. 2008), so similarly the xylopodia of *Podocalea* may principally be a response to environment and only secondarily an indicator or relationships. Presence of xylopodia in *Podocalea* (Fig. 69) recalls similar ecological adaptations found in plants of dry or fire-prone cerrados and savannas (Eiten 1972; Vilhalva and Appezzato-da-Glória 2006; Appezzato-da-Glória et al. 2008), albeit *P. abbreviata* sometimes, for example, seems ecologically adapted to waterlogged soils. The xylopodia in *Podocalea* mostly enlarge asymmetrically after stems die back to ground level. The caudex and xylopodia in branched-stemmed characters of branching stems in most plants of *P. rupicola* and *P. verticillata*, smaller capitula in *P. abbreviata* and *P. rupicola*, and the white ray corollas of *P. paraguayensis* are each noteworthy at the species rank, but are not generic indicators. The lack of well-developed xylopodia in *P. rupicola* and *P. verticillata* basically seems to a functional character of their wetter habits, and does not seem to be driven primarily by phylogenetic factors.

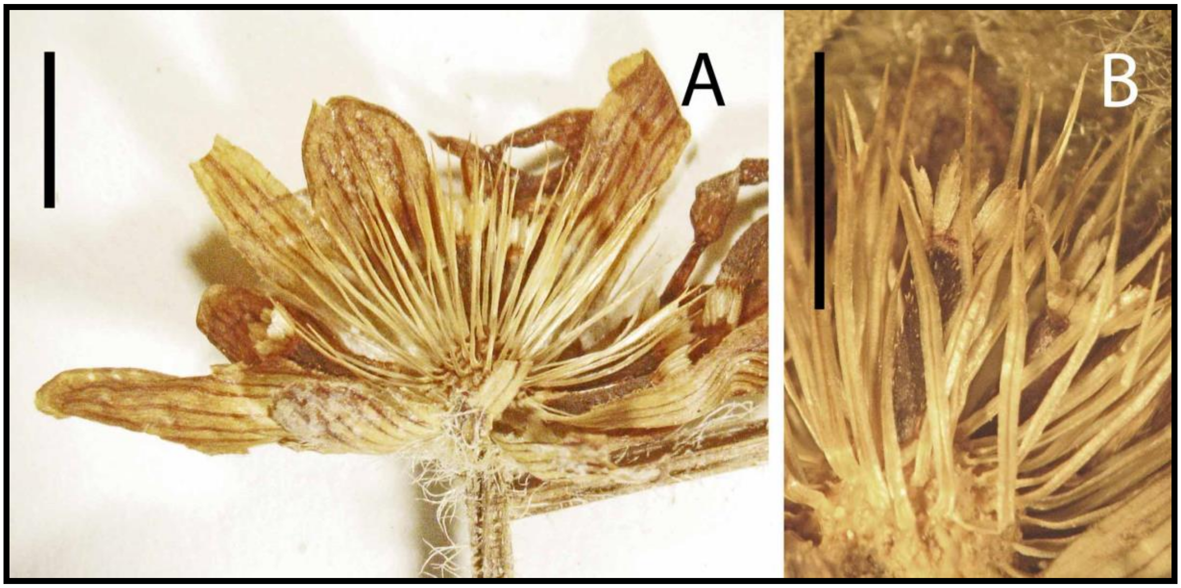


Figure 72. Paleae of *Podocalea rupicola* (Chodat) Pruski. A. Dissected old fruiting capitulum showing the convex clinanthium and the linear paleae. B. Close-up showing the tips of the paleae reaching above the short broad pappus scales. Many species of Podocalea differ by elongate narrow-tipped pappus scales (viz Fig. 76D). (*Zardini & Espinoza 53725*, MO). Scale bars 3 mm.

Indeed, while species of *Podocalea* may often be recognized by their gestalt, it is instead technical morphological, anatomical, and cytological features—clinanthia with flat linear non-conduplicate paleae that surpass and curve over the budding disk florets (Klatt 1889) (Figs. 72, 76D), floral microcharacters (e.g., the divergent apex of the elongate terminal pair of cells of the twin trichomes of the ovary and cypsela) (Fig. 73), and base chromosome number of x = 16 (Coleman 1968; Molero et al. 2006; Aguilera et al. 2012)—that define *Podocalea*. The x = 16 chromosome reports by Coleman (1968), Molero et al. (2006), and Aguilera et al. (2012) are from subshrubby pluricapitulate *P. verticillata* as well as from herbaceous-stemmed monocephalous *P. uniflora*, and do not conflict with my congeneric conjecture that the two differing —scapose and subshrubby— morphotypes are equally at home within *Podocalea*.

The linear paleae of *Podocalea* (Fig. 71) bring to mind those seen in *Eclipta* L. (Heliantheae: Ecliptinae). Traits of the paleae in the Heliantheae Alliance (sensu Panero 2007) are usually useful and reliable taxonomic marker, for example, as applied in taxonomy of *Eclipta*. A well-known exception to this generalization is seen in *Melanthera nivea* (L.) L. as circumscribed by Pruski (1997) and Pruski and Robinson (2018). In *M. nivea*, notoriously variable in habit and leaf morphology, the notoriously variable palea range from apically rounded to apiculate, rendering them an unreliable taxonomic marker. The traits of paleae are constant in *Podocalea*, however, and I feel they may safely be applied here in circumscription of the genus.

Likewise, the divergent apices of the otherwise laterally connate paired terminal cells of the twin trichomes of the cypsela (Fig. 73) is an example of one of the microcharacters used in characterizing *Podocalea*. Although apices of the paired terminal cells of the of twin trichomes of species of *Calea* s. str. on occasion may be slightly spreading, they are never as extremely divergent as are those of *Podocalea*. Pruski and Urbatsch (1988) and Pruski (2005) aligned *C. coronopifolia* Sch. Bip. ex Krasch., *C. graminifolia* Sch. Bip. ex Krasch., *C. kirkbridei* H. Rob., and *C. tridactylita* Sch. Bip. ex Krasch. with species now placed in *Podocalea*, but their affinities are under further study by me, and at present I do not place them in *Podocalea*. The following 18 species are recognized in *Podocalea*.

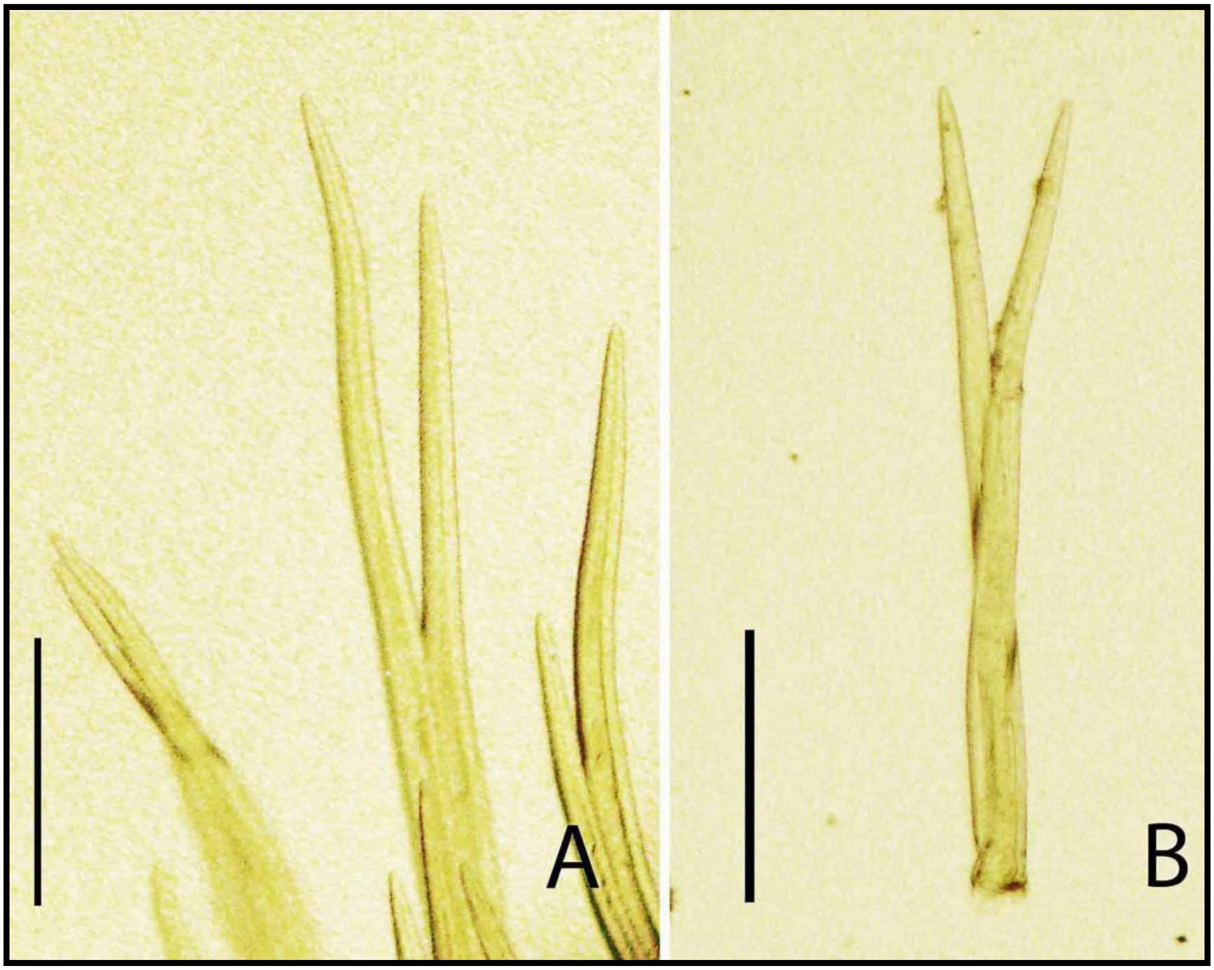


Figure 73. Twin trichomes of cypselae of *Podocalea cuneifolia* (DC.) Pruski, showing cells laterally connate below the divergent tips. A Close-up of distal portions. B. Paired terminal cells, longitudinally connate proximally, free distally; broken near cross walls of basal cells. (*Hatschbach 44346*, MO). Scale bars A 80 µm, B 100 µm.

PODOCALEA ABBREVIATA (Pruski & Urbatsch) Pruski, **comb. nov**. *Calea abbreviata* Pruski & Urbatsch, Brittonia 40: 348. 1988. **TYPE. BRAZIL. Goiás.** Chapada dos Veadeiros, ca. 12 km NW of Veadeiros, 1200 m, 19 Oct 1965, *Irwin et al. 9285* (holotype: NY, negative 12523; isotype: US). Materials of Irwin's 9200 series once deposited in UB, including an isotype of *C. abbreviata*, were insect damaged and discarded before 1988, fide G. Eiten (pers. comm.). Figures 71B, 74B, 76B, 78.

Podocalea abbreviata (Pruski & Urbatsch) Pruski is endemic to Goiás, Brazil and should be looked for in adjacent Minas Gerais. *Podocalea abbreviata* was treated in the region works by Bringel and Cavalcanti (2009) and Silva and Teles (2018). *Podocalea abbreviata* is typical of the genus in its basally disposed leaves and radiate-capitulate monocephalous stems, but has a relatively small caudex from which its few stems arise (Figs. 74B, 78). Many species of *Podocalea* are fire-adapted and have well-developed xylopodia, but *P. abbreviata* sometimes is found in wet areas.

Podocalea abbreviata is the smallest leaved *Podocalea*, has relatively small capitula, a pappus of short scales, merely herbaceous-tipped outer phyllaries, and subglabrous cypselae. Pruski and Urbatsch (1988) allied it with strict-stemmed xylopodial *P. multiplinervia*—then including *P. angustifolia*—and with usually branched-spreading-stemmed *P. rupicola*. *Podocalea abbreviata* more closely recalls partly sympatric *P. angustifolia*, resurrected from synonymy by Pruski (20013), which differs by its longer leaves, setose cypselae, and by elongate pappus scales about as long as the cypselae and about as long as the disk corollas.

Figure 74. Representative monocephalous species of *Podocalea* Pruski. A. *Podocalea cabrerae* (Pruski) Pruski. B. *Podocalea abbreviata* (Pruski & Urbatsch) Pruski. (A Drawn by Gisela Sancho from *Zardini & Ramírez 51247*, unmounted isotype, also used in the protologue; B Drawn by Bobbi Angell from *Irwin et al. 9285*, NY, holotype, also used in the protologue). Scale bars A 5 cm, B 3 cm.

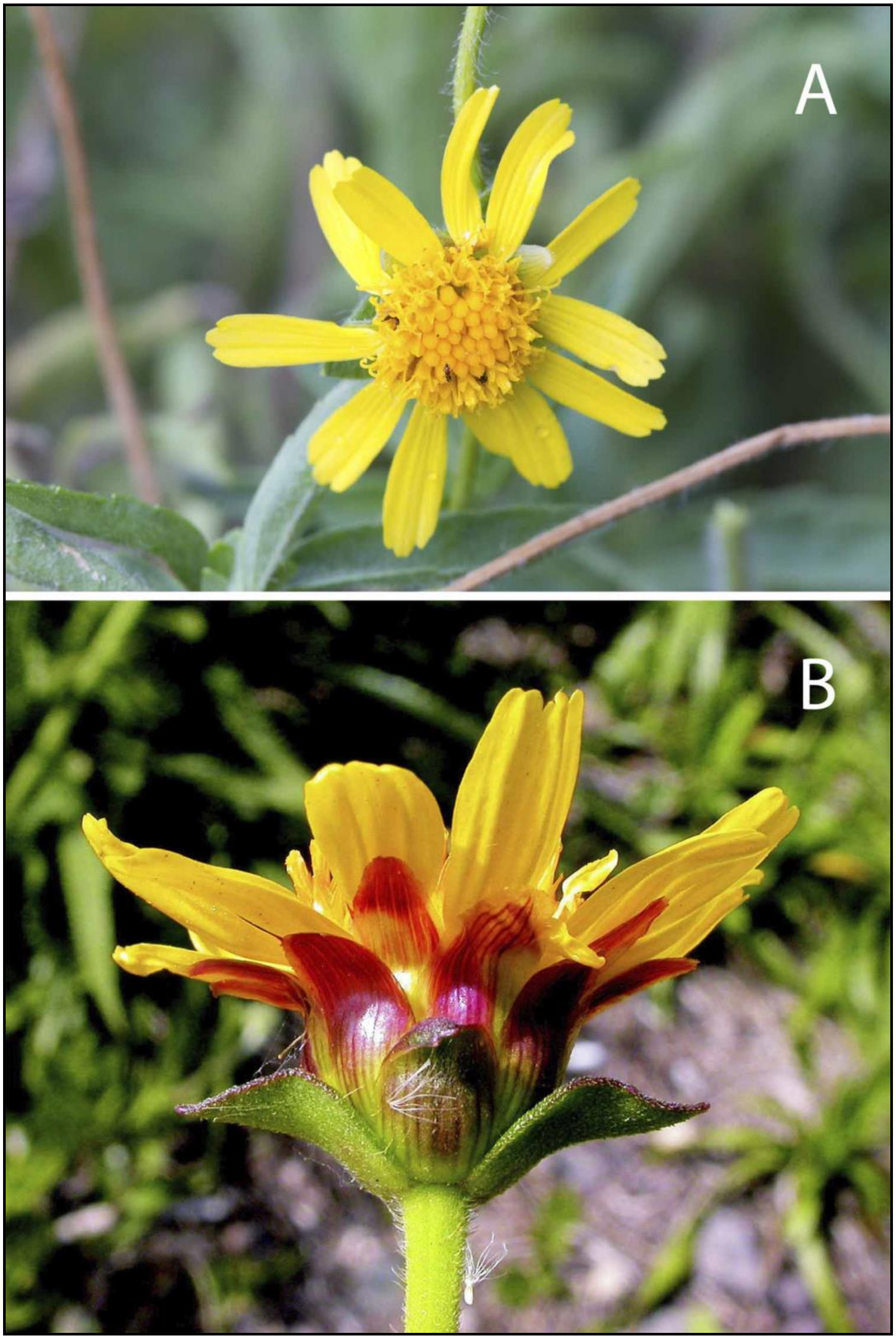


Figure 75. Representative radiate capitula of *Podocalea* Pruski; most species are radiate-capitulate, but discoid-capitulate or white-rayed species are also known. A. *Podocalea rupicola* (Chodat) Pruski, showing one capitulum of the open cyme. B. *Podocalea uniflora* (Less.) Pruski, showing a pair of herbaceous outer phyllaries and the striate mid and inner series of phyllaries. (A *Stevens et al. 31323*, photograph by Olga Martha Montiel, B photograph by Mauricio Bonifacino, voucher not seen).

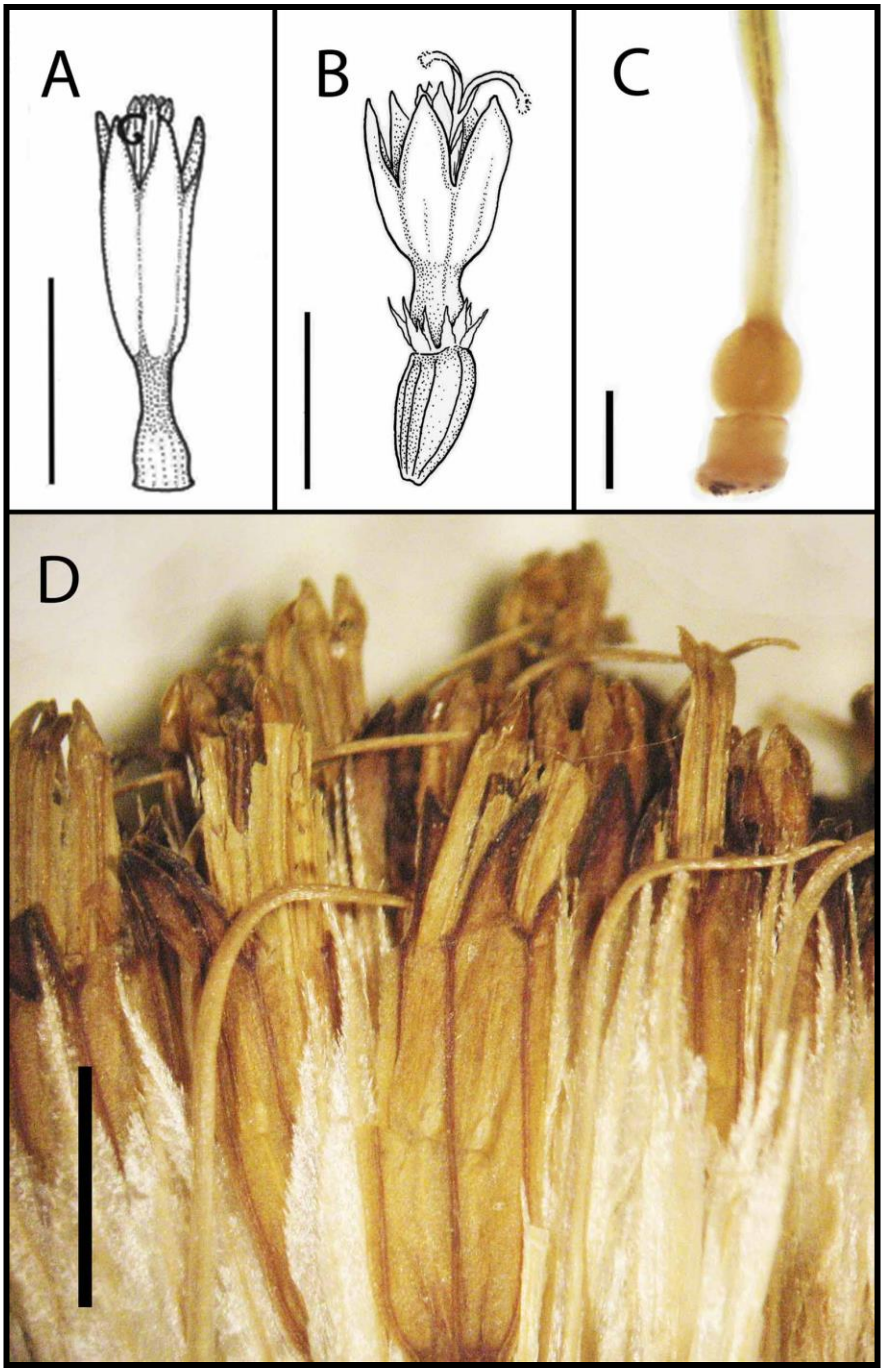


Figure 76. Floral features of *Podocalea* Pruski. A. *Podocalea cabrerae* (Pruski) Pruski, showing a non-setose disk corolla. B. *Podocalea abbreviata* (Pruski & Urbatsch) Pruski, disk floret showing non-setose corolla, subglabrous cypsela, short pappus scales, and exserted style branches. C. *Podocalea angustifolia* (Gardner) Pruski, free stylopodium held above the annular nectary. D. *Podocalea pedunculosa* (DC.) Pruski, portion of capitulum showing bent tips of pale brown paleae and associated disk florets showing in high contrast (bottom right and left) the elongate light-colored pappus scales. (A *Zardini & Ramírez 51247*, unmounted isotype, also used in protologue; B *Irwin et al. 9285*, NY, holotype, also used in protologue; C *Irwin et al. 8036*, NY; D *Zardini & Guerrero 46641*, MO). Scale bars A–B 3 mm, C 0.2 mm, D 2 mm.

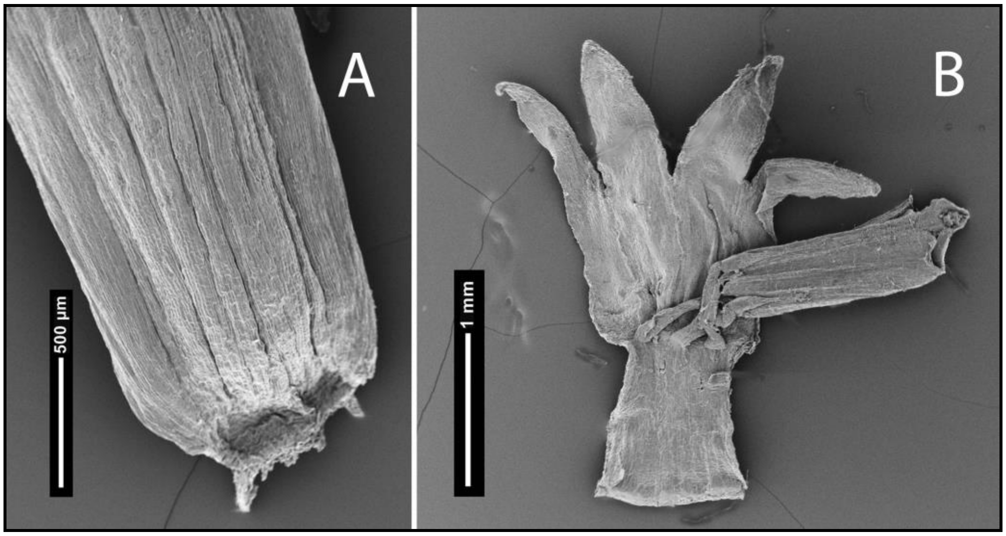


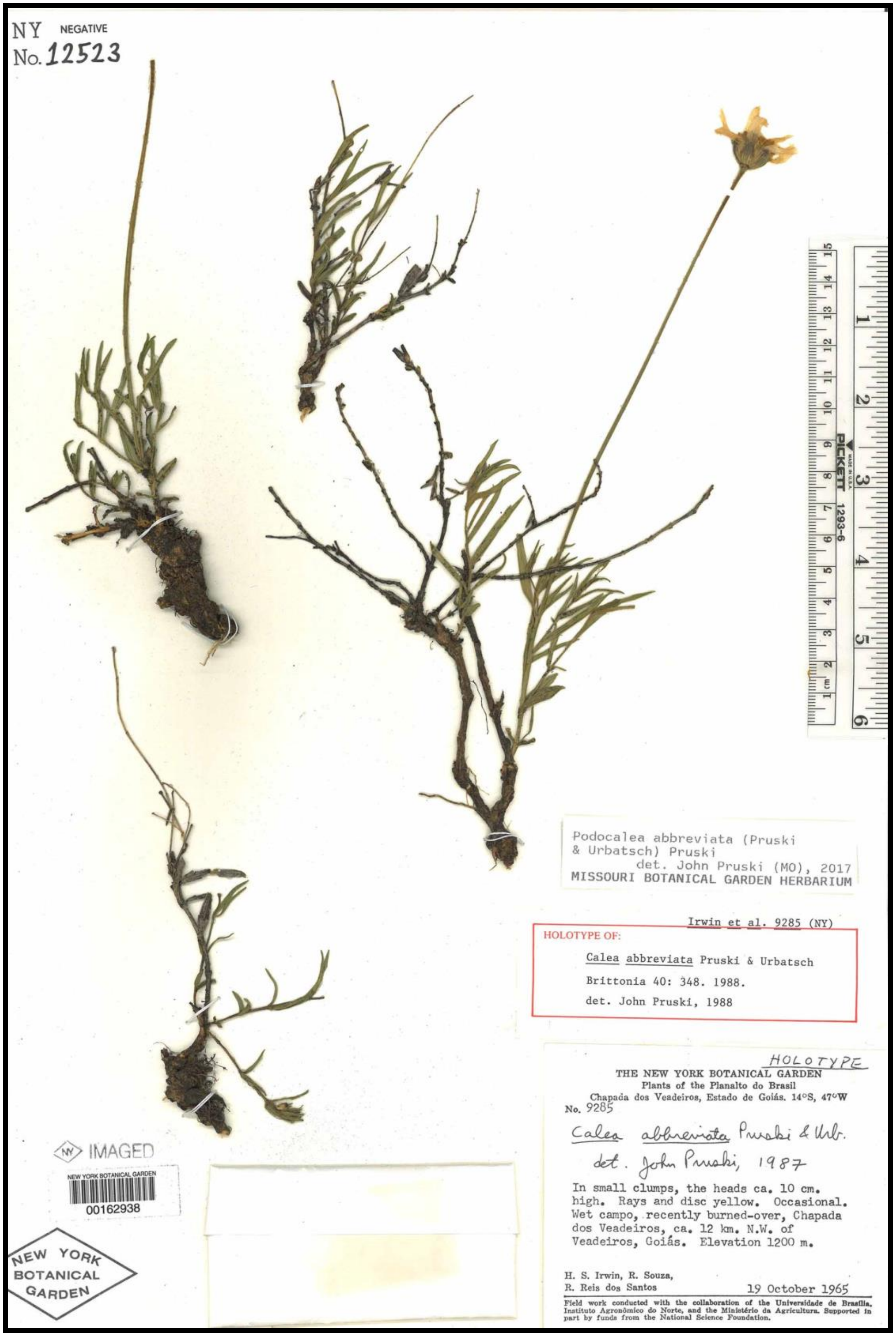
Figure 77. *Podocalea multiplinervia* (Less.) Pruski. A. Abaxial base of mid-series phyllary, showing the parallel indurate costae; in fresh material the colored resin ducts run parallel along border the costae. B. Disk corolla opened longitudinally, inner-adaxial view showing four corolla lobes (upper), the short filaments (center) of the attached anthers (center right; abaxial surface is non-setose). (*Irwin 8036*, MO).

PODOCALEA ANGUSTIFOLIA (Gardner) Pruski, **comb. nov**. *Calea angustifolia* Gardner, London J. Bot. 7: 417. 1848. *Calea multiplinervia* var. *angustifolia* (Gardner) Baker, in Martius, Fl. Bras. 6(3): 264. 1884. **TYPE: BRAZIL. Tocantins** (as "Goyaz"). Villa de Arraias (as "Arrayas"), May 1840 (May on holotype, in protologue as "Apr 1840"), *Gardner 3859* (holotype: BM, photograph 10.8, ektachrome 84.34, and negative 11745; isotypes: K-Benth n.v., K-Hook photograph 12.19 and kodachrome 83.28, OXF photograph 10.11 and negative 11759, W). Figure 76C.

In 1981 I annotated *Podocalea angustifolia* (Gardner) Pruski in the Kew Hooker herbarium isotype as "type" and treated the plant as *Calea multiplinervia* var. *angustifolia*, but in 1984 when I annotated the BM holotype I simply treated *C. angustifolia* as a synonym of *P. multiplinervia*. Indeed, *P. angustifolia* for more than a century was considered to be a variety of or a synonym of *P. multiplinervia*, but this narrow-leaved western Brazilian endemic was reinstated from synonymy without hesitation by Pruski (2013). The holotype of *Podocalea angustifolia* in BM has both of its distal nodes ternate-leaved. Recent collections of *P. angustifolia* (e.g., *Cavalcanti et al. 3507*, CEN; *Fonseca et al. 584*, US; etc.) are narrower leaved than is the type collection, but match the species by mid-length pappus scales about as long as the cypselae and nearly as long as the disk corollas.

PODOCALEA ASCLEPIIFOLIA (Hassler) Pruski, **comb. nov**. *Calea asclepiifolia* Hassler, Repert. Spec. Nov. Regni Veg. 14: 173. 1915, as *asclepiaefolia*. **TYPE. PARAGUAY.** In campis combustis Esperanza, Sierra de Amambay, flor. mens. Sep 1907/1908, *Hassler 10626* (holotype: G-Hass-2 sheets, photographs 3.23–24, ektachromes 84.34–35, and negatives 11755–11756, stamped loan 5944 sheets 13–14, the first Hassler herbarium sheet has the binomial in Hassler's hand, the second is on jstor and without barcode; isotypes: B† as Macbride neg. 15359, BM photograph 3.25 and negative 11767).

Calea glabrata Sch. Bip. ex Krasch., Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 4: 52. 1923. **TYPE: BRAZIL.** [**Mato Grosso do Sul**]. Rio Pardo, Sep 1826, *Riedel 566* (holotype: LE, photograph 2.10, ektachrome 84.9, negative 11730; isotypes: OXF photograph 8.7A, P-Sch-Bip.).



Podocalea abbreviata (Pruski
& Urbatsch) Pruski
det. John Pruski (MO), 2017
MISSOURI BOTANICAL GARDEN HERBARIUM

Irwin et al. 9285 (NY)

HOLOTYPE OF:
Calea abbreviata Pruski & Urbatsch
Brittonia 40: 348. 1988.
det. John Pruski, 1988

HOLOTYPE
THE NEW YORK BOTANICAL GARDEN
Plants of the Planalto do Brasil
Chapada dos Veadeiros, Estado de Goiás. 14°S, 47°W
No. 9285
Calea abbreviata Pruski & Urb.
det. John Pruski, 1987

In small clumps, the heads ca. 10 cm. high. Rays and disc yellow. Occasional. Wet campo, recently burned-over, Chapada dos Veadeiros, ca. 12 km. N.W. of Veadeiros, Goiás. Elevation 1200 m.

H. S. Irwin, R. Souza,
R. Reis dos Santos 19 October 1965

Field work conducted with the collaboration of the Universidade de Brasília, Instituto Agronômico do Norte, and the Ministério da Agricultura. Supported in part by funds from the National Science Foundation.

Figure 78. *Podocalea abbreviata* (Pruski & Urbatsch) Pruski, holotype, showing the basally disposed leaves of radiate-capitulate monocephalous stems. (*Irwin et al. 9285*, NY).

Podocalea asclepiifolia (Hassler) Pruski occurs in Argentina, Brazil, and Paraguay. The holotype is on two sheets in a single folder at G: sheet one is stamped loan 5944-013 and has a locality annotated by Hassler, and sheet 2 is stamped loan 5944-14 and has an unannotated preprinted data label. The species is very distinctive in its leafy stems having well-spaced large subglabrous entire-margined leaves.

PODOCALEA BAKERIANA (Chodat) Pruski, **comb. nov.** *Calea bakeriana* Chodat, Bull. Herb. Boissier, sér. 2, 2(4): 395. 1902 nom. nov. sp. rank; (see also extract in Chodat, Pl. Hassl. I: 166. 1902). Based on: *Calea cuneifolia* var. *paraguariensis* Baker, in Martius, Fl. Bras. 6(3): 266. 1884. **TYPE: PARAGUAY.** Caaguazu, 11 Nov 1874, *Balansa 813* (holotype: K, photograph 12.7, now bar-coded K000323165; isotypes: BR photograph 11.36 and ektachrome 84.2, G-3 two as photographs 4.2–4.3 the first of these as Macbride neg. 28827, GOET, LE, P).

Podocalea bakeriana (Chodat) Pruski is centered in Paraguay, is merely moderately pubescent, and is a large-leaved moderately tall and stout (proximal stems ca. 5 mm diam. in herbaria) segregate of *P. cuneifolia*, which has proximal stems ca. 3 mm diam. *Podocalea bakeriana* was described by Baker (1884) as a variety of *P. cuneifolia* and as having leaves *rigidioribus* and the leaves are strongly raised-reticulate abaxially and sometimes even so adaxially. *Podocalea bakeriana* may be envisioned too as a few-glandular-leaved similar southern congener of obtuse-leaved *P. pohliana* and tomentose-leaved *P. camporum*. *Podocalea bakeriana*, *P. camporum*, *P. cuneifolia*, and *P. pohliana* are yellow-flowered, whereas white-flowered *P. paraguayensis* (Kuntze) Pruski, a sympatric congener, is white-ray-flowered. *Podocalea bakeriana* has previously commonly been misapplied to white-ray-flowered weak-stemmed *P. paraguayensis*. Each aforementioned species has a tendency towards being leafy stemmed, but each is taken as differing slightly in details. The two infraspecies described under *P. bakeriana* will be treated in a companion paper.

PODOCALEA CABRERAE (Pruski) Pruski, **comb. nov.** *Calea cabrerae* Pruski, Phytoneuron 2013–72: 1. 2013**. TYPE: PARAGUAY. Canindeyú.** Mbaracayú Natural Reserve, Aguará Ñú, cerrado scrub on red sandy soil, 24° 11' 01" S, 55° 16' 48" W, [ca. 225 m], 23 Sep 1999, *E. Zardini & S. Ramírez 51247* (holotype: MO; isotypes: AS, G-2, K, LP, NY, RB, US). Figures 69B, 71C, 74A, 76A.

Podocalea cabrerae **(**Pruski) Pruski is endemic to Paraguay, and known only from the type collection close to the border with Brazil, where this species may reasonably be expected to occur. *Podocalea cabrerae* is the most recently described species of *Podocalea* with short-scaled cypselae.

PODOCALEA CAMPORUM (Krasch.) Pruski, **comb. nov**. *Calea camporum* Krasch., Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 4: 51. 1923. **TYPE: BRAZIL.** [**Mato Grosso do Sul**]. Salto do Curán, Rio Pardo, Oct 1826, *Riedel 575* (holotype: LE, photograph 2.15 and negative 11775). (Spelled Salto do *Curau* in protologue). An invalid name (pro syn.) is *Calea riedelii*, as listed by Krascheninnikov (1923). The type locality Salto do Curán along the Rio Pardo is Mato Grosso do Sul (viz Urban 1906: 91; Krascheninnikov 1923: 51). Figure 79.

Podocalea camporum (Krasch.) Pruski is a stiffly erect stemmed plant with several well-spaced pairs of sharp-serrate tomentose leaves, and is centered in Brazil. *Podocalea camporum* is similar by its dense pubescence to less leafy *P. formosa* and *P. tomentosa*. *Podocalea camporum* also recalls *P. bakeriana* that has less-pubescent smooth-toothed leaves and *P. pohliana* that differs by leaves broadest above the middle. Material of *P. camporum* is often misidentified as *Calea clausseniana*, a synonym of *P. tomentosa*.

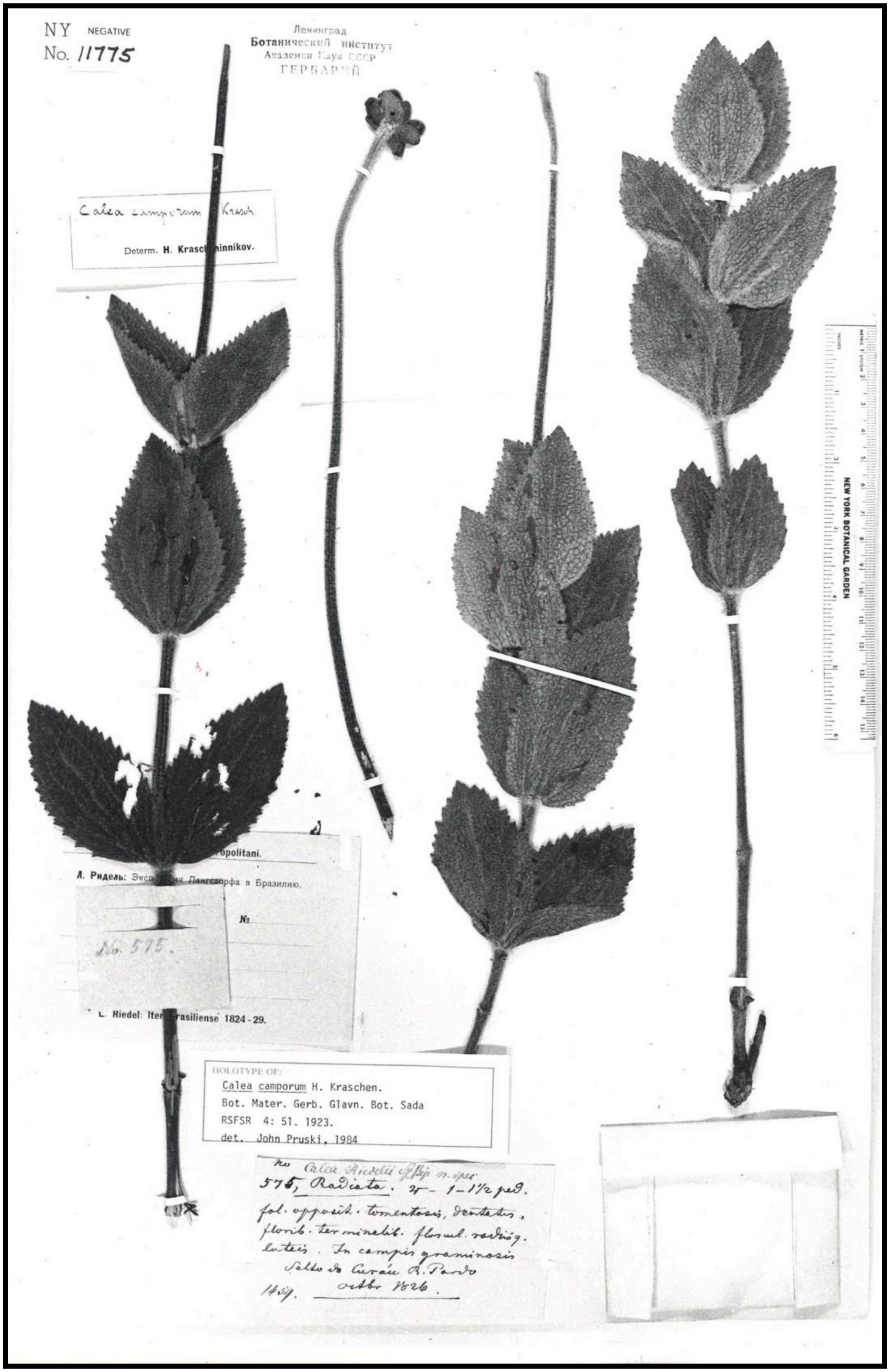


Figure 79. Holotype of *Podocalea camporum* (Krasch.) Pruski, showing the stout stems evenly leafy with several pairs of serrate tomentose leaves. (*Riedel 575*, LE).

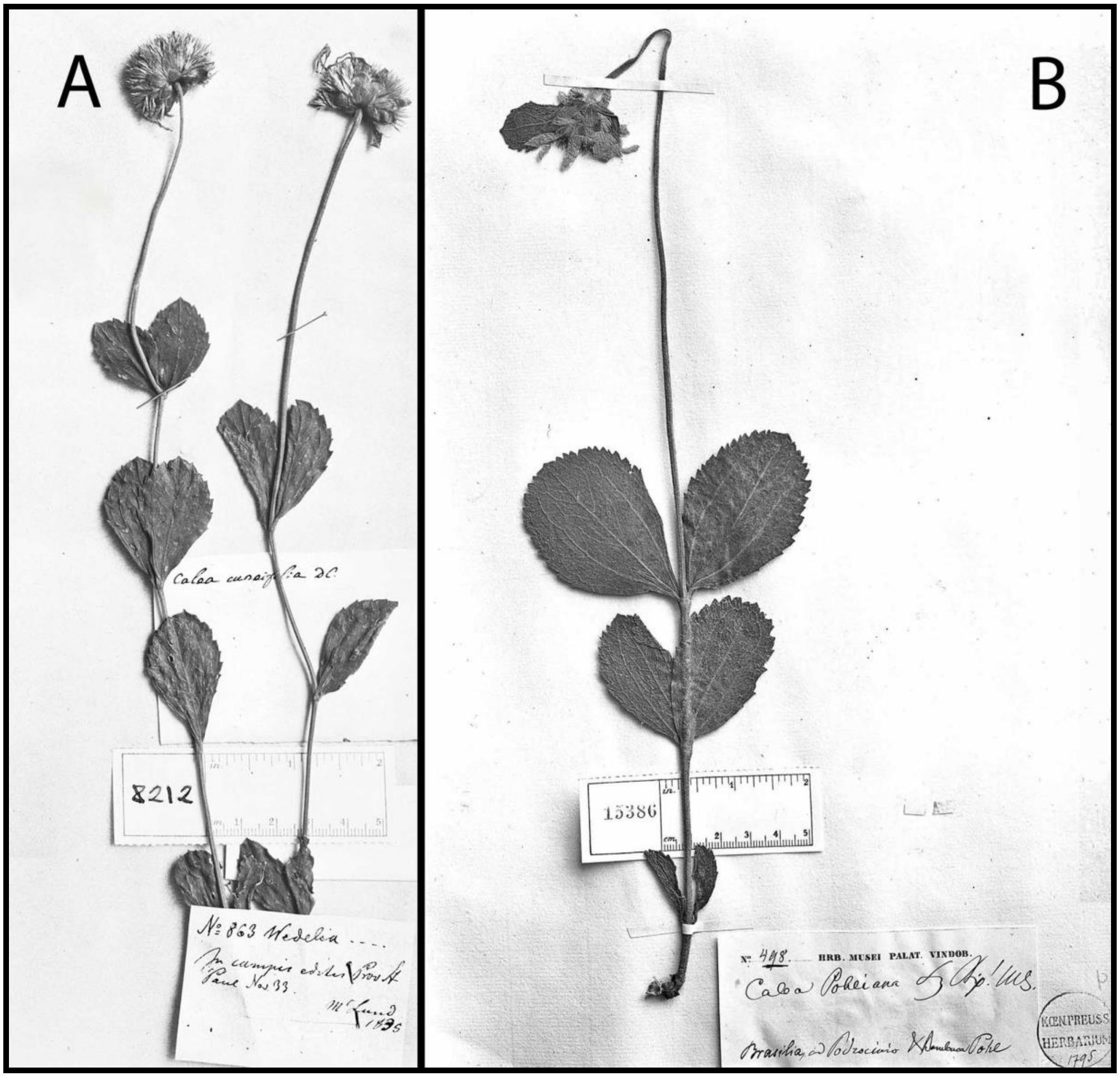


Figure 80. Radiate-capitulate monocephalous leafy-stemmed species of *Podocalea* Pruski with few pairs of leaves that are broadest above the middle. A. *Podocalea cuneifolia* (DC.) Pruski, holotype, generitype. B. *Podocalea pohliana* (Sch Bip. ex Baker) Pruski. (A *Lund 863* G-DC, Macbride neg. 8212; B *Pohl 498* B†, Macbride neg. 15386).

PODOCALEA CATALAONENSIS (Krasch.) Pruski, **comb. nov.** *Calea catalaonensis* Krasch., Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 4: 51. 1923. **TYPE: BRAZIL. Goias**. Catalaô, Aug-Oct 1834, *Riedel 2976 p.p*. (lectotype, sheet designated here: LE, photograph 2.14; isolectotype: LE p.p., photograph 2.13).

The lectotype sheet is not mixed, whereas the isolectotype sheet is mixed with an alternate-leaved helianthoid (right-center on sheet), hence the desire to lectotypify the name. The lectotype is annotated *Calea asperifolia* Sch. Bip., and the isolectotype sheet is annotated as *Meyeria myrtifolia*. The isolectotype appears to be marked as either species number 795 or 798 [sic] on the annotation label by the monumentally influential Carl Heinrich Schultz Bipontinus, who first recognized about a dozen and a half mostly Brazilian new species in the *Calea* alliance (viz Baker 1884 and Krascheninnikov 1923).

Brazilian *Podocalea catalaonensis* (Krasch.) Pruski was reduced to synonymy of *Calea verticillata* (Klatt) Pruski by Pruski (1998a) and Gutiérrez et al. (2015), but is restored here to contain xylopodial weakly asperous-leaved plants. The type locality is slightly more than 200 km to the south of the Distrito Federal, and not far north of the Paranaíba River.

PODOCALEA CUNEIFOLIA (DC.) Pruski, **comb. nov**. *Calea cuneifolia* DC., Prodr. 5: 674. 1836. **TYPE. BRAZIL.** São Paulo, Nov 1833, *Lund 863* (holotype: G-DC, as IDC microfiche 800 976.II.1, as Macbride neg. 8212). Materials of *Riedel and Lund 793-1736* (e.g., LE-2, NY, P-3, etc.) collected in November 1833 at the type locality are surely authentic, but were incorrectly and to loosely annotated by me as isotypes. The Lund sheet in G-DC is simple-stemmed (I did not find a Lund isotype in C), whereas several Riedel duplicates have pairs of branchlets at some stem nodes. Figures 15A, 69A, 70, 73, 80A.

Podocalea cuneifolia (DC.) Pruski is the generitype, and occurs in Brazil and Paraguay (Pruski in Nakajima et al. 2001). *Podocalea pohliana* (Baker) Pruski was earlier considered by me as synonymous, but differs by its longer pair of more pubescent outer herbaceous phyllaries.

PODOCALEA FORMOSA (Chodat) Pruski, **comb. nov**. *Calea formosa* Chodat, Bull. Herb. Boissier, sér. 2, 2(4): 396. 1902; (see also extract in Chodat, Pl. Hassl. I: 167. 1902). **TYPE. PARAGUAY.** Ipé hú, Oct 1898–1899, *Hassler 4943* (lectotype, sheet designated here: G photograph 4.1, Herb. Chodat, barcode 00092705; isotypes: BM, G-2 [G-Bois photograph 11.37, G-Hass], K, LY, NY, P-2, S, UC, W). There are photographs of K and of one G sheet in GH.

The lectotype was annotated by me as holotype in 1983, is from the Chodat herbarium, and annotated by Chodat as "Calea sp. nova!" and "Calea formosa Chod."

Podocalea formosa (Chodat) Pruski is a very stout tomentose monocephalous plant centered in Paraguay. The few pairs of stem leaves are broadest below the middle; very infrequently the leaves may be whorled. *Podocalea formosa* is obviously similar to *P. camporum*, but is distinct morphologically and geographically yet both are in need of field studies study their morphologies.

PODOCALEA MULTIPLINERVIA (Less.) Pruski, **comb. nov**. *Calea multiplinervia* Less., Linnaea 5: 159. 1830. **TYPE(S): BRAZIL.** [**Minas Gerais** fide Urban]: Fazenda da Roma [fide Baker 1884 in Martius], [Nov-Dec 1818], Sellow s.n., possibly either or both *Sellow 862* and *Sellow 1099* [as cited by Baker 1884 in Martius] (type(s): B†). It is not clear if the two Sellow numbers cited by Baker (1884) are type material, but they presumably were, although now presumably destroyed. The species is so common that I for some times I did not check my notes on types, but I apparently have seen no Sellow collections, and thereby to fix name applications, I choose the type of synonymous *Calea longifolia* Gardner as the neotype of *Calea multiplinervia* Less. **NEOTYPE**, designated here: **BRAZIL. Tocantins** (as "Goyaz"). Dry campos near Villa de Natividade, Nov 1839 (in protologue as "Dec 1839"), *Gardner 3289* (neotype: BM, photograph 8.21, ektachrome 84.27, and negative 11733; isoneotypes: F, K-Benth n.v., K-Hook p.p. photograph 12.14 and kodachrome 83.24, OXF, P-3, W photograph 10.28 and Macbride neg. 33358). Figure 77.

Although Lessing's protologue lists no specimens, this name is most likely based on collections of Sello, two of which are the only collections listed by Baker (1884) that pre-date the protologue. Baker listed *Sellow 862* and *Sellow 1099* and thus it seems likely that this name is based on two collections, although none were photographed by McBride. If indeed based on two collections, it seems likely that a duplicate of at least one may ultimately be uncovered and be suitable to serve as lectotype. The application of this name by Baker is inferred from his synonymy and determinations, and in lieu of a type in hand it seems useful to select as epitype a collection from near Fazenda da Roma, to accompany the geographically more distant synonymous Gardner neotype. **Epitype** (designated here): **BRAZIL. Goiás.** Catalão, BR-050, km 234 da rodovia Cristalina-Catalão, 22 Nov 2005, *Cavalcante et al. 3653* (MO).

Calea longifolia Gardner, London J. Bot. 7: 418. 1848, non *Calea longifolia* (DC.) Baker (1884). **TYPE: BRAZIL. Tocantins** (as "Goyaz"). Dry campos near Villa de Natividade, Nov 1839 (in protologue as "Dec 1839"), *Gardner 3289* (holotype: BM, photograph 8.21, ektachrome 84.27, and negative 11733; isotypes: F, K-Benth n.v., K-Hook p.p. photograph 12.14 and kodachrome 83.24, OXF, P-3, W photograph 10.28 and Macbride neg. 33358). NY has mounted photographs of BM and OXF; F has a mounted photograph of K.

Podocalea multiplinervia (Less.) Pruski, a Brazilian endemic, is a distinctive element in the genus recognized by its strongly 3-5-plinerved narrow basally proximally disposed leaves. *Podocalea multiplinervia* (Less.) Pruski, *P. uniflora* (Less.) Pruski, and *P. verticillata* (Vell.) Pruski were among the earliest described species of the genus.

PODOCALEA OLIGOCEPHALA (DC.**)** Pruski, **comb. nov**. *Calea oligocephala* DC., Prodr. 5: 675. 1836. **TYPE: BRAZIL. Minas Gerais.** Serra do Frio, 1833, *Vauthier 318* (holotype: G-DC, as IDC microfiche 800 976.II.3; possible isotypes: P as Macbride neg. 38064, P-Sch-Bip photograph 12.22 and kodachrome 83.30). The Schultz-Bipontinus herbarium sheet is without number but is oligocephalous (few-capitulate) and marked by LEU & JP 1987 as an isotype.

There is another sheet labeled *C. oligocephala* that has been seen. This is a monocephalous third Paris sheet (P-Rich-Drake) labeled Serra do Frio, which seems to be closer to *P. tomentosa* s. str. than to *P. oligocephala*.

Podocalea oligocephala (DC.) Pruski is known from scanty cymose-flowered material, but as noted by Pruski (en sched. 1984) may prove to be the earliest name for monocephalous *P. tomentosa*. Indeed, the respective type localities of *P. oligocephala*, *P. tomentosa*, and synonymous *Calea clausseniana* are very near Belo Horizonte. The stems of the type gathering of Vauthier seem to have been broken at the base above the xylopodium. The Paris isotype (now barcoded P02140707) has only two capitula, so I did not dissect a capitulum in the 1980s when I had the specimen in front of me, preferring to await further collections of the morphotype suitable for dissection. Baker (1884: 266) treated the plant is synonymy with *P. cuneifolia*; and Pruski and Urbatsch (1988) and Pruski (2005) as a *Podocalea* near *P. cuneifolia*; these are not fully satisfying dispositions.

PODOCALEA PARAGUAYENSIS (Kuntze) Pruski, **comb. nov**. *Tridax paraguayensis* Kuntze, Revis. Gen. Pl. 3(3): 182. 1898. [Part 1 is the Roman numeral part; the forward in the first of two English parts gives it as III II]. *Calea paraguayensis* (Kuntze) Deble, Balduinia 29: 5. 2011. **TYPE: PARAGUAY**. Süd-Paraguay, Sep 1892, *Kuntze s.n.* (holotype: NY).

Podocalea paraguayensis (Kuntze) Pruski is a Paraguay-centered white-flowered former synonym of *P. uniflora*. *Podocalea paraguayensis* was initially resurrected from synonymy of *P. uniflora* (I annotated the holotype as *C. uniflora*) by Leonardo Deble, who provided a wonderful, account as well as a fine line drawing (Balduinia 29: 6, fig. 2. 2011). The white ray corollas of P. *paraguayensis* are unusual in *Podocalea*, and as a taxonomic character are used cautiously here at the specific level. The species of *Podocalea* are typically yellow-flowered. Plants of the common *P. paraguayensi*s are often identified as the yellow-flowered, but otherwise very similar, *P. uniflora*.

PODOCALEA PEDUNCULOSA (DC.) Pruski, **comb. nov**. *Calea pedunculosa* DC., Prodr. 5: 673. 1836. *Calea uniflora* var. *discoidea* Baker, in Martius, Fl. Bras. 6(3): 265. 1884, a later homotypic infraspecific name for the Candolle plant. **TYPE: BRAZIL.** "Prov. Rio Grande" [1833 seems to be the date Gaudichaud deposited this in P, not collection date], *Herb. Imp. Bras. 1050* (? *Sellow 880*) (holotype: P, annotated by me in red ink as holotype, photograph 12.23 and kodochrome 83.31, now barcode P02140741, the branch on right-hand side of sheet was photographed as Macbride neg. 38067, the branch on the left is slightly thicker stemmed and labeled *880*, which may be an original Sellow label; possible or presumed isotypes: BR photograph 9.8 accession 590040 stamped loan number 3315/83 105—originally labeled as *uniflora* and *Sellow* but annotated by me in 1984 as questionably *C. uniflora*—thick stemmed as branch of left of holotype of *C. pedunculosa*, G-DC as IDC microfiche 800. 975.III.8). Figure 76D.

Candolle specifically cited the Paris holotype, doing so as "v.s. in h. Mus. reg. Par. ex h. Mus. imp. Bras. sub n. 1050 miss.", and the printed label of Paris sheet gives *Gaudichaud 1833*; above the Paris label is a red TYPE annotation label/sticker. The F Macbride web site gives collection date as 30 Nov 1832, but this is after the 1831 death of Sellow, so the F date is questioned. I take the two branchlets on P to be of the same Sellow gathering and mounted at the same time; although the provenance of the two P plants, the G-DC branchlet, and the BR 2-capitulate plant are not clear, it seems as though the four branchlets are of a single gathering, and I give them here as of the same gathering; the four branchlets are certainly conspecific. Although I saw these BR and P sheets in the 1980s, I obviously did not dissect any of the four capitula, preferring to await further collections, which I have since dissected.

Discoid *Podocalea pedunculosa* (DC.) Pruski, here broadly defined to house discoid elements, is known in Argentina, Brazil, and Paraguay. The type and the material in Argentina—Cabrera 1974: 397 called this plant *Calea uniflora* var. *discoidea* Baker— have lightly pubescent leaves with glands visible on the abaxial leaf blade surface. Also accepted as *P. pedunculosa* are more recent discoid materials from Paraguay that have fairly pubescent leaf blades without obvious glands abaxially. While it is possible that the modern collections from Paraguay were pressed in EtOH and any potential glands thereby destroyed, the Paraguay plants are more densely pubescent-leaved than are materials from Brazil and Argentina.

PODOCALEA POHLIANA (Sch Bip. ex Baker) Pruski, **comb. nov**. *Calea pohliana* Sch Bip. ex Baker, in Martius, Fl. Bras. 6(3): 266. 1884. **TYPE: BRAZIL. Goias.** Ad Padrocinio et Bambuca, s.d. [distributed to Bentham in 1837], *Pohl 498 (669)* (lectotype, designated here, from among sheets of type collection: K-Benth, photograph 11.29 and kodachrome 83.34; isotypes: B† Macbride neg. 15386, K-Hook, P as 669, W photograph 9.20). Both K sheets have the binomial in Baker's hand, with the lectotype selected being the more robust of the two. The lectotype sheet "*498*" appears to be a distribution/species number, and that *669* is the collection number. Figure 80B.

Calea pohliana var. *burchelliana* Baker, in Martius, Fl. Bras. 6(3): 266. 1884. **TYPE: BRAZIL.** [Goias] s.d., *Burchell 5030* (holotype: K p.p. photograph 11.30). The holotype with trinomial in Baker's hand is on the left side of this sheet, which is mixed with Burchell *5887*.

Podocalea pohliana (Sch Bip. ex Baker) Pruski is accepted as a narrow segregate of widespread *P. cuneifolia*, but the quintajugate variety is treated in synonymy. At one point I usually determined materials of this more northwestern species as being included in the broad concept of *Podocalea cuneifolia*—e.g., viz my 1996 determination of *Hatschbach 63600* MBM, US, etc. and

Graziela Barroso's determination of *Prance et al. 19265* K, RB, S, etc. both from Chapada dos Guimarães near Cuiaba, as *P. cuneifolia*—but I follow the Pruski (1998) restored of *Podocalea pohliana* from synonymy. *Podocalea pohliana* is characterized by its two very large outermost phyllaries, whereas *P. cuneifolia* has smaller outer phyllaries and a graduated involucre. The plants of these two species have very few pairs of stem leaves and are taken by me as distinct from leafy stemmed relatives (e.g., *P. bakeriana*, *P. camporum*, *P. formosa*), that for the most part occur nearly 500 kms to the southwest. *Hatschbach 63600* has some plants with ternate nodes, a condition found occasionally in typically opposite-leaved Podocaleas including in *P. angustifolia*, *P. cuneifolia*, *P. verticillata*, etc.

PODOCALEA RUPICOLA (Chodat) Pruski, **comb. nov**. *Calea rupicola* Chodat, Bull. Herb. Boissier, sér. 2, 3(8): 726. 1903 (see also extract in Chodat, Pl. Hassl. II: 154. 1903). **LECTOTYPE** (designated here from among three syntype collections): **PARAGUAY. Cordillera.** Tobaty, Mar 1898-99, *Hassler 4041* (lectotype, sheet designated here: G-Hass, ektachrome 84.30, now barcoded G00092724; isolectotypes: B† as Macbride neg. 15391, BM p.p., F, G-BOIS now barcoded G00092725, G-Cand-2 first sheet now barcoded G00092732, G-Chod now barcoded G00195679, GH, LY, NY, P-2, US, W photograph 4.19). Figures 72, 75A.

The lectotype collection is in good flower, but none of the 5 G sheets seem to be annotated in Chodat's hand. Of the G sheets seen, only the Hassler and the Chodat herbarium sheets have the printed label reading 1898-99. The G-Chod sheet is without binomial, whereas the selected G-Hass lectotype sheet has the binomial. The G-Hass lectotype is in better flower that the G-Chod sheet, and I have no hesitation in designating it as lectotype, as annotated by me in 1984. The G-Chod sheets of the two other syntype collections (*6137* and *8457*) similarly are not marked with the binomial in Chodat's hand, whereas often for other binomials the G-Chod herbarium sheets on Chodat names based on Hassler Paraguay collections are marked with binomials and "nob." in Chodat's hand. The US sheet is a fragment and photograph of the G Herb. Barb-Boiss. sheet but with plants arranged differently than when I saw the G sheet.

Representative specimens examined. ARGENTINA. Expected (*Zardini & Ojeda 55725* from near Yabebiry, Paraguay was collected within 20 km of Argentina). **BOLIVIA**. **Santa Cruz**. W. lado de Cerro Mutún, 334 m, 28 Feb 2014, *Nee 60821* (MO) [about 50 W km of Serra do Urucum and Corumbá, where collected earlier as *Hatschbach 29520*]. **BRAZIL** (reported as new to Brazil by Pruski 2013). **Mato Grosso do Sul.** Mun. Corumbá, Serra do Urucum, 15 Apr 1972, *Hatschbach 29520* (LP, MBM); Mun. Porto Murtinho, Corrego Capivara, 17 Mar 1985, *Hatschbach & Zelma* 49212 (MBM, NY); Mun. Miranda, Fazenda 23 de Marco, 13 Oct 2003, *Hatschbach et al 76292* (MBM, MO, US). [**Rondônia?]**. Cataqueama (as Cataqui-iaman), campo do Urupás, [illegible] do Cautário, Dec 1918, *Kuhlmann 2367* (RB-8934, annotated by me on 26 August 1990 as *Calea matogrossensis* Pruski, which is unpublished and is instead a strict-stemmed form of *P. rupicola;* Paynter and Traylor, Orn. Gaz. Brazil 2: 661. 1991 gave campos do Urupás as "not located". **PARAGUAY.** Common in Paraguay, and typified by *Hassler 4041* from Tobaty, Paraguay.

Podocalea rupicola (Chodat) Pruski, known in Bolivia, Brazil, and Paraguay, is on the periphery of *Podocalea* (Pruski 2013), is low branched subshrub, and typically has a single relatively small capitulum terminating each of the several branches. On occasion, some plants are dwarf with much smaller than-average-sized-leaves. Even less frequently (e.g., *Calea annua* ined., *Hassler 12632*, from Ypacaray/Ypacaraí, Paraguay; *C. matogrossensis* ined., *Kuhlmann 2367*, from Mato Grosso-Rondônia, Brazil) and in wet (not dry rocky) areas, young plants are robust, unbranched below, large-leaved, larger-capitulate (10 mm vs. 8 mm tall), and openly cymose with three capitula per branch tip. By gestalt and distribution, *Kuhlmann 2367* is somewhat reminiscent of and presumably even further to the NW of Bolivian *Calea huanchacana* Pruski, but both it and *Hassler 12632* are *Podocalea* as seen by their linear paleae, even though their pales are shorter than in many plants, only reaching to the disk corolla lobe bases. However, I was unable to dissect the Kuhlmann material, so my determination is unverified.

I am uncertain of the locality of *Kuhlmann 2367*, however, which seems to be from Campo do Urupás, which is NW of Cuiabá and perhaps near the Serra dos Parecis Mato Grosso-Rondônia, Brazil, and in turn perhaps is in the drainage systems of either the rios Madeira, Tapajós, or Tocantins that ultimately flow into the Rio Amazonas. *Kuhlmann 2367*, labelled as from Mato Grosso, may thus be in modern Rondônia. Kuhlmann was possibly working with the telegraph line survey between Mato Grosso and Amazonia, I have seen Kuhlmann Acre collections, so the collection data on this northwestern-most collection of *P. rupicola* is presumably correct.

PODOCALEA TOMENTOSA (Gardner) Pruski, **comb. nov**. *Calea tomentosa* Gardner, London J. Bot. 7: 418. 1848. **TYPE: BRAZIL. Minas Gerais.** Serra de Curral del Rey, Sep 1840, *Gardner 4926 bis* (holotype: BM, photograph 11.35 and ektachrome 84.21). This species was not treated by Baker, in Martius, Fl. Bras. 6(3). 1884.

Calea clausseniana Baker, in Martius, Fl. Bras. 6(3): 265. 1884. **LECTOTYPE**, chosen from among syntype collections: **BRAZIL. Minas Gerais.** Cachoeira do Campo, Apr-Aug 1840, *Claussen s.n.* (*481A*) (lectotype, here chosen: K-Benth, photograph 12.4 and kodachrome 83.17, now barcoded K000323147; (possible) isolectotypes; BM p.p. photograph 11.31, BR-2 photographs 11.28 and 11.32, LE, NY as s.n., US). The US isolectotype is a fragment of the lectotype. Baker cited unnumbered Claussen and Warming specimens, which seem to be equally complete; the lectotype at K has "*clausseniana* Baker" written in Baker's own hand upon the collection label, which is without number but is presumably 481A. Also, sheets in BR and LE are unnumbered. BM photograph 11.31, BR photograph 11.29, and P-Sch-Bip have sheets or parts of sheets of syntype *Claussen 657*. BM also has a sheet as *Claussen 168*.

Podocalea tomentosa (Gardner) Pruski was overlooked in Flora Brasil by Baker, and is usually a monocephalous plant with very-proximally disposed leaves. *Podocalea tomentosa* includes in synonymy *Calea clausseniana*: indeed the respective type localities are only about 60 km apart and very near to Belo Horizonte, Minas Gerais. Specifically, Serra de Curral del Rey is immediately south of Belo Horizonte, and Cachoeira do Campo is slightly further to the southwest. I have dissected much material of this moderately well-collected plant. While basically scapose, *P. tomentosa* is on rare occasions three-capitulate and open-cymose, very nearly matching the slightly less-pubescent earlier-described *P. oligocephala* (Gardner 1848), which is also based on material from Belo Horizonte.

Podocalea oligocephala is maintained as distinct, however, as four decades ago I deemed the type material of it too scant to warrant dissection before I could do adequate field population studies in the environs of Belo Horizonte in order to study variation. Leafy stemmed *P. camporum* and *P. formosa* are also tomentose plants, but are taken by me as distinct relatives. The typology of the three infraspecies described under *P. clausseniana* will be treated in a companion paper.

PODOCALEA UNIFLORA (Less.) Pruski, **comb. nov**. *Calea uniflora* Less., Linnaea 5: 159. 1830. **TYPE**: **BRAZIL**. Brasilia meridionalis, *Sellow s.n.* (holotype: B† Macbride neg. 15400; lectotype, designated by Gutiérrez et al. 2015, 181: HAL, annotated in Lessing's hand, photograph 1.32 and ektachrome 84.13; possible isotypes: G-DC rec'd from Berlin in 1830 as IDC microfiche 800 976.II.2, GH as 3324 photograph 13.2, K-Hook-2 each p.p. one as photograph 13.1 and kodachrome 83.36, LE-4 two are p.p. photographs 9.9 and 9.11–13, LY as 3324 dated 1818 (unmounted Gandoger Herbarium) photograph 5.18 and ektachrome 84.5, NY, P *Herb. Imp. Bras. 1014* barcoded as P02469822 may be a Sellow collection, UPS photograph 5.17 and ektachrome 84.4, W p.p. photograph 9.10). Figures 75B, 81–82.

Figure 81. *Podocalea uniflora* (Less.) Pruski, habit showing few pairs of proximal leaves on yellow-flowered radiate-capitulate monocephalous stems. (Photograph by Mauricio Bonifacino, voucher not seen).

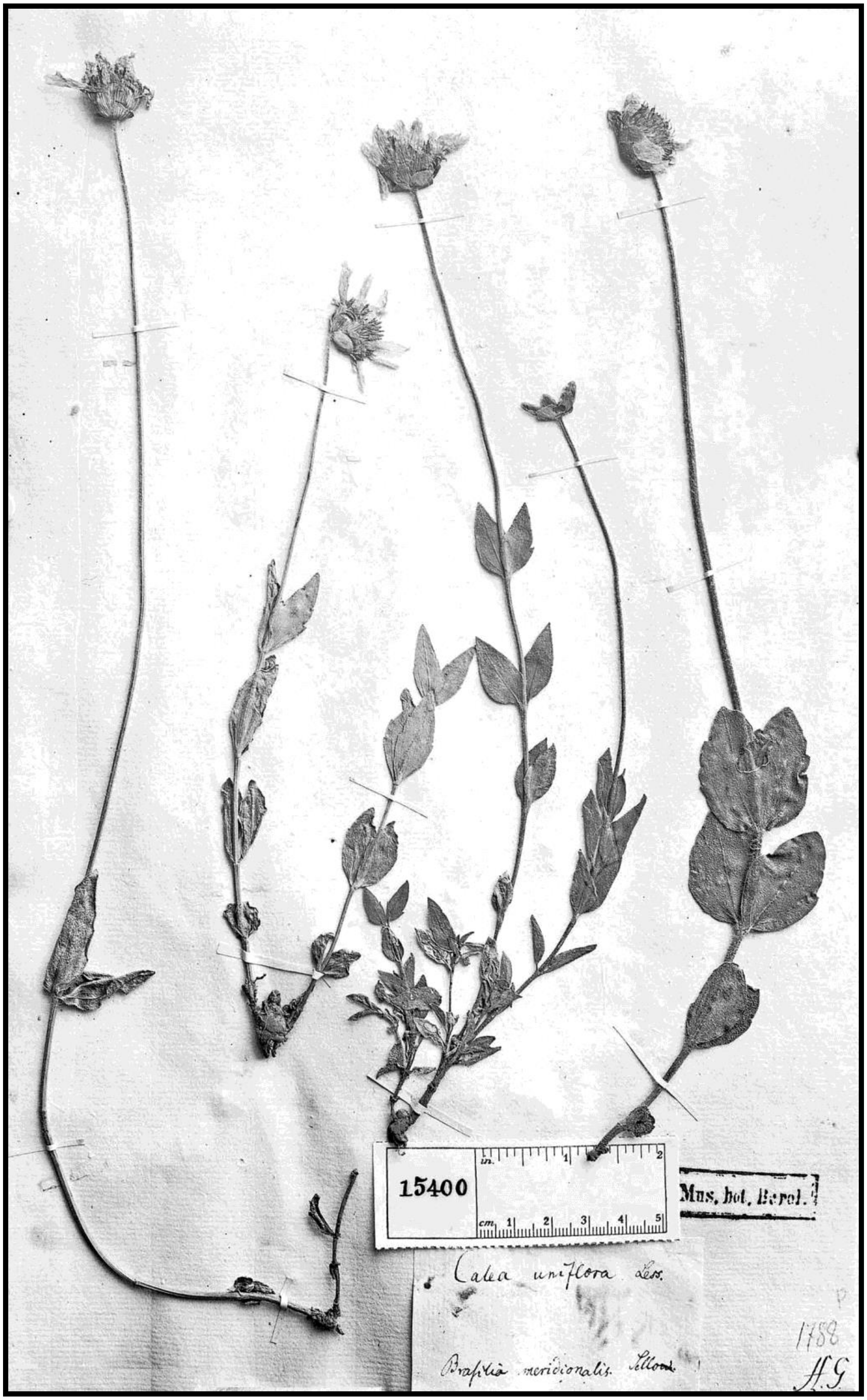


Figure 82. *Podocalea uniflora* (Less.) Pruski, destroyed holotype, showing few pairs of proximal leaves on radiate-capitulate monocephalous stems. (*Sellow s.n.* B†, Macbride neg. 15400).

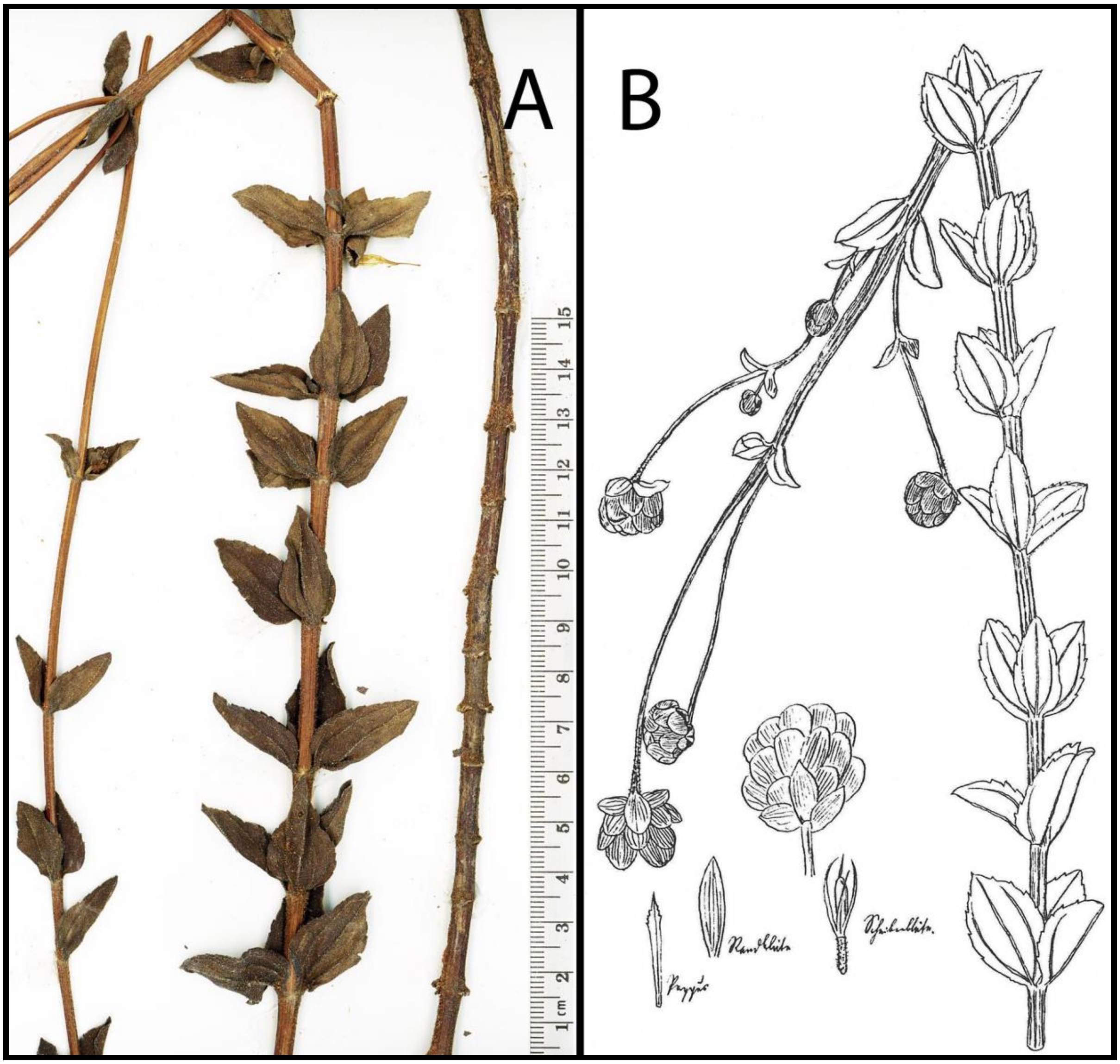


Figure 83. *Podocalea verticillata* (Klatt) Pruski, stems with seven three-leaved nodes subtending a few open-cymose capitula, these two sheets (B now destroyed) are the only two imaged with verticillate leaves from among the more than a score of basically opposite-leaved specimens seen by me. The species is taller than most Podocaleas, as evidenced in many herbarium specimens by stems too long to be pressed without bending to fit into newspapers. A. Three-leaved nodes of rarely seen branch, center. B. Drawing by Friedrich Wilhelm Klatt, in GH, of the destroyed Berlin holotype. The epithet *verticillata* references the ternate leaves of the holotype; evenly graduated involucre shown in lower center. (A *Zardini & Acosta 56122*, unmounted duplicate; B *Sellow s.n.*).

The are two Sellow sheets of *Podocalea uniflora* in Hooker herbarium, each mixed with other collections but each may be considered as possible duplicates of the types; one of the mixed LE sheets and the W sheet are mixed with a *Sellow s.n.* collection of *P. cuneifolia*, other sheets label as Sellow *P. uniflora* are completely *P. cuneifolia* and not a mixture (e.g., UPS loan 83 photograph 5.16; if the GH and LY sheet number *3324* is a collection number, it is interesting to note that a sheet of the equally common *Laceanthos cymosus* in BR is numbered *3326*.

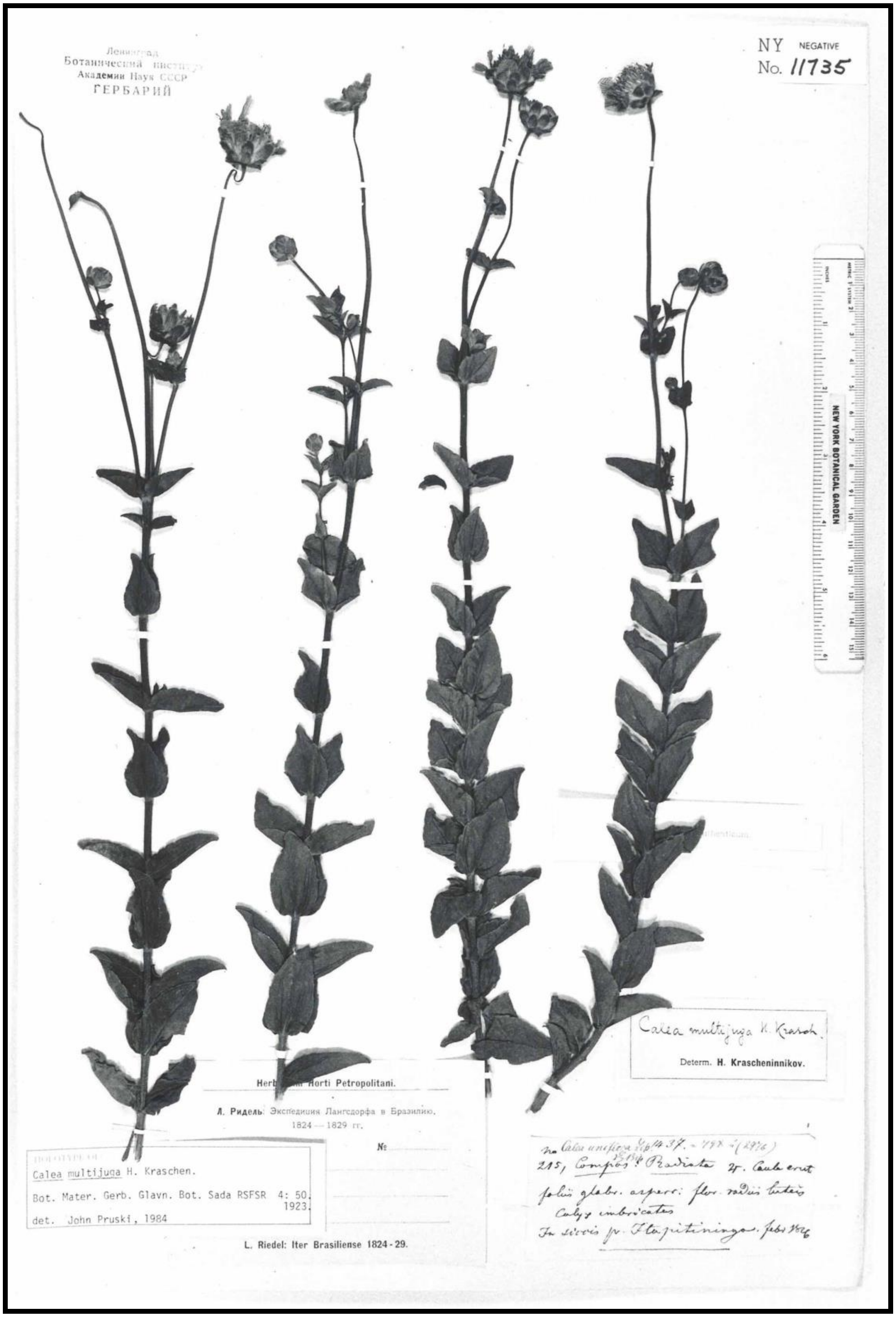


Figure 84. Holotype of *Calea multijuga* Krasch., showing the many paired leaves indicated by the epithet, designated in 1998 as neotype of *Podocalea verticillata* (Klatt) Pruski. This is the common form of the species and has stems with several pairs of opposite leaves. (*Riedel 215*, LE).

Podocalea uniflora (Less.) Pruski is a moderately common plant in Argentina, Brazil, Paraguay, and Uruguay from which several segregates have been extracted, including robust *P. bakeriana* (Chodat) Pruski, white-rayed *P. paraguayensis* (Kuntze) Pruski, and discoid-capitulate *P. pedunculosa*, (DC.) Pruski. Herbarium specimens of *P. uniflora* often dry with adaxial leaf blade surface veins raised, which may be a consequence of drying. In 1981, I mis-annotated a King collection in K-Benth as a possible type.

Ferraz et al. (2009) and Ramos et al. (2016) listed *P. uniflora* as used medicinally. There are two fine line drawing of *P. uniflora* in Cabrera (1974: 396–397, figs. 231–232).

PODOCALEA VERTICILLATA (Klatt) Pruski, **comb. nov**. *Tridax verticillata* Klatt, Leopoldina 25: 107. 1889. *Calea verticillata* (Klatt) Pruski, Kew Bull. 53: 689 1998. **TYPE: BRAZIL.** sine loc., s.d., *Sellow s.n.* (holotype: B†, presumably source material for the drawing in GH (Fig. 83B), there is a photograph of the GH drawing in US). **NEOTYPE** (designated by Pruski 1998): **BRAZIL. São Paulo.** In campis graminosis prope Itapetininga, Feb 1826, *Riedel 215* (neotype: LE, photograph 2.2A, ektachrome 84.11, and negative 11735; isoneotype: OXF, photograph 8.5A). The neotype is the type of *C. multijuga*, which by the Pruski (1998) typification became a nomenclatural synonym. **EPITYPE** (designated here): **PARAGUAY. Amambay**. Around Cerro Corá, 22° 39' 53" S, 55° 59' 18" W, 27 Feb 2001, *Zardini & Acosta 56122* (epitype: MO-6438502). Figures 71A, 83–84.

It seems possible there could be unidentified duplicates Sellow sheets of the s.n. now-destroyed Berlin type of *Tridax verticillata* Klatt in either the national museum in Rio de Janeiro or in European herbaria. The species seems not to be rare, but the verticillate leaf arrangement (Fig. 83) in herbarium material of it is exceptionally rare. Sellow was a prolific collector, but no further authentic Sellow materials of this verticillate-leaved plant were seen by the writer, and Pruski (1998) designated an opposite-leaved neotype in LE (Fig. 84) to fix application of the Klatt (1889) name. Here, the MO sheet of a collection with some verticillate-leaves is designated as epitype, this epitype surely conspecific with the neotype.

Calea multijuga Krasch., Bot. Mater. Gerb. Glavn. Bot. Sada RSFSR 4: 50. 1923. **TYPE: BRAZIL. São Paulo**. Prope Itapetininga, Feb 1826, *Riedel 215* (holotype: LE, photograph 2.2A, ektachrome 84.11, and negative 11735; isotype: OXF, photograph 8.5A). Figure 84.

The itinerary of Urban (1906: 91) gave the state of Itapetininga as São Paulo.

Riedel and Sellow were apparently among the first naturalists to collect the fairly common-in- Brazil-and-Paraguay *Podocalea verticillata* (Klatt) Pruski, the epithet *verticillata* referencing the verticillate-ternate leaves of the holotype. Synonymous *C. multijuga* was named descriptively also, its epithet being in reference to the several—many pairs of leaves on the leafy stem (Fig. 84). Pruski (1998) synonymized the two species, and because no extant type material of *Tridax verticillata* Klatt (1889) is known, he designated the type material of *Calea multijuga* as the neotype of the Klatt name.

The majority of Podocaleas, however, have few-pairs of basally opposite disposed leaves, whereas the present species is leafy-stemmed, fairly densely so with opposite or on occasion whorled leaves. *Podocalea verticillata* is usually opposite-leaved (viz Basualdo and Soria 2002: 51, fig. 19; voucher *Soria 7890*, vidi). Ternate-leaved individuals have been collected in both Brazil (the destroyed holotype) and Paraguay (some duplicates of *Zardini & Acosta 56122*) (Fig. 83), and the whorled-leaved individuals from these two countries are basically indistinguishable from the vastly more commonly opposite-leaved materials represented by the neotype (Fig. 84) of Pruski (1998).

Compositae of the Guayana Highland–XV. The new genus *Tepuipappus* (Heliantheae subtr. Verbesininae) from Venezuela. John F. Pruski, Phytoneuron 2023-42: 127–149. 2023.

The Guayana Highland in northern South America is the vast region footed by the Precambrian igneous-metamorphic bedrock basement of the Guayana Shield, and is topped by an once-continuous, but now dissected, sedimentary cover of scattered tepuis (Figs. 85–86, 93), for which it is best known (Pinson et al. 1962; Maguire 1979; Schubert and Huber 1989; Pruski 1991, 1997; Huber 1995; Santos et al. 2003; Kroonenberg et al. 2016; Reis et al. 2017; Huber et al. 2018; Kroonenberg 2019; Ibañez–Mejia 2020; Ibañez-Mejia and Cordani 2020; Bonilla et al. 2023). The often horizontally-layered (Fig. 85C) superimposed sedimentary and conglomerate tunica of the Guayana Shield too is Precambrian but is not homogenous, instead originating from fluvial sediment deposition "in two separate but overlapping basins" during at least two geologic pulses (Maguire 1979; Schubert and Huber 1989; Huber 1995; Santos et al. 2003; Kroonenberg et al. 2016; Reis et al. 2017; Huber et al. 2018; Kroonenberg 2019; Ibañez-Mejia and Cordani 2020). The minimum age of these fossil-poor sandstones have been dated by the characters of younger intrusions (Santos et al. 2003; Reis et al. 2017).

The present-day Guayana Highland is centered in southern Venezuela and is now spectacularly eroded, having 50-plus steep-sided flat-topped remnant sandstone tepuis. The region is mostly contained between the ríos Guaviare-lower-Orinoco and the more southern Amazonas-Japurá-Caquetá basins (Maguire 1979). The Amazon river fills the great chasm between the Guayana Shield and southern the Brazilian Shield. Santos et al. (2003), Huber et al. (2018: fig. 23.3), and Kroonenberg (2019: fig. 3.38) recognized four main basement age groups for the residual (meta)sandstone summits—roughly from ENE to WSW these are the Roraima, Duida (as "Neblina"), Tunuí (now seemingly including Neblina), and Chiribiquete Supergroups of tepuis.

The Guayana Highland extends eastwards from its epicenter in Venezuela to Tafelberg in Suriname (Maguire 1944, 1945, 1970; Kroonenberg et al. 2016) and to the west to cerros on both sides of the Río Vaupés upstream from Mitú, Colombia (Wallace 1853a; Schultes 1944; Sánchez et al. 1990). In the Gran Sabana of the eastern Guayana Highland, both tepuis and the inter-tepui moderate-elevation valleys (of savannas) are part of the superimposed sedimentary cover, having only moderate elevational relief (Fig. 85A). Conversely, in Amazonas, Venezuela we find many towering tepuis, vestiges of the once-continuous superimposed sedimentary cover, with the low-elevational inter-tepui valleys often eroded fully through the former-sandstone-cover to near the bedrock basement and harboring vast forest, and having great elevational relief from valleys to summits (Fig. 93B). The erosion of much of the original ancient sandstone cover of the onetime-extensive plateau continues, and has left the remnant tepuis subtended by massive amounts of nutrient-poor sediments, albeit much of these sediments have been carried away by the region's great rivers (Kubitzki 1990). Along the periphery of the Guayana Highland—to the west in Colombia, to the east in Suriname, and to south along the Amazon River—the once continuous sandstone cover is often completely eroded down to near its bedrock basement with only a few low tepuis with only moderate relief remaining (Maguire 1979; Huber 1995; Mykle 1998; Kroonenberg et al. 2016; Kroonenberg 2019; Ibañez–Mejia 2020; Mora et al. 2000).

Otto Huber (1995) noted that although the Pemón Amerindians used the word "tepui" for only sandstone mesas that dot the eastern Gran Sabana, the term now applies to all sandstone table-top plateaus atop the Guayana Shield. The diagrams in Steyermark (1966: 32, figs. 1–2; 1986: 319, fig. 13–2) and Huber (1992: 67, fig. 4.3) illustrate stylized tepuis and show their three main elements: the table-top summit subtended by sheer vertical escarpments, below which are talus slopes that often support magnificent forest. The term "pantepui" used, for example, by Mayr and Phelps (1967), Steyermark (1979, 1982), and Huber (1987, 1988a), refers collectively to the areas of the Guayana

Highland mostly above 1300 meters elevation, i.e., the entire assemblage of ca. 1300+ meters-elevational flat-topped sandstone tepuis.

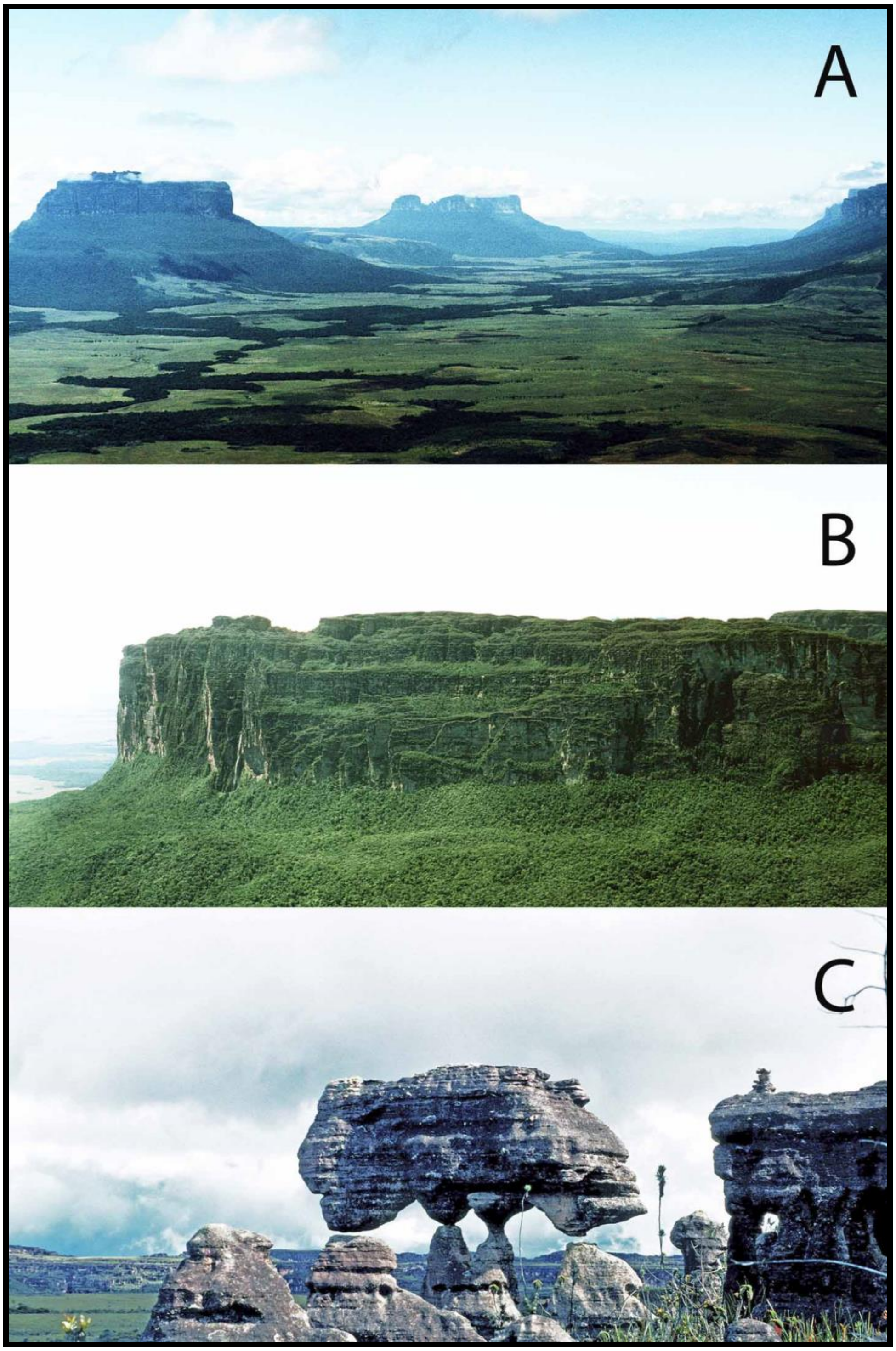


Figure 85. A. Two Guayana Highland tepuis, Upuigma-tepui at 2100 meters elevation (left) and double-topped Angasima-tepui at 2250 meters (background center). B. Acopán-tepui showing block-eroded vertical cliffs and forested talus slopes. C. Eroded double-pedestal rock on the Chimantá Massif, showing horizontal strata (see also Huber 1992: 120, foto 44). (Photographs by the writer).

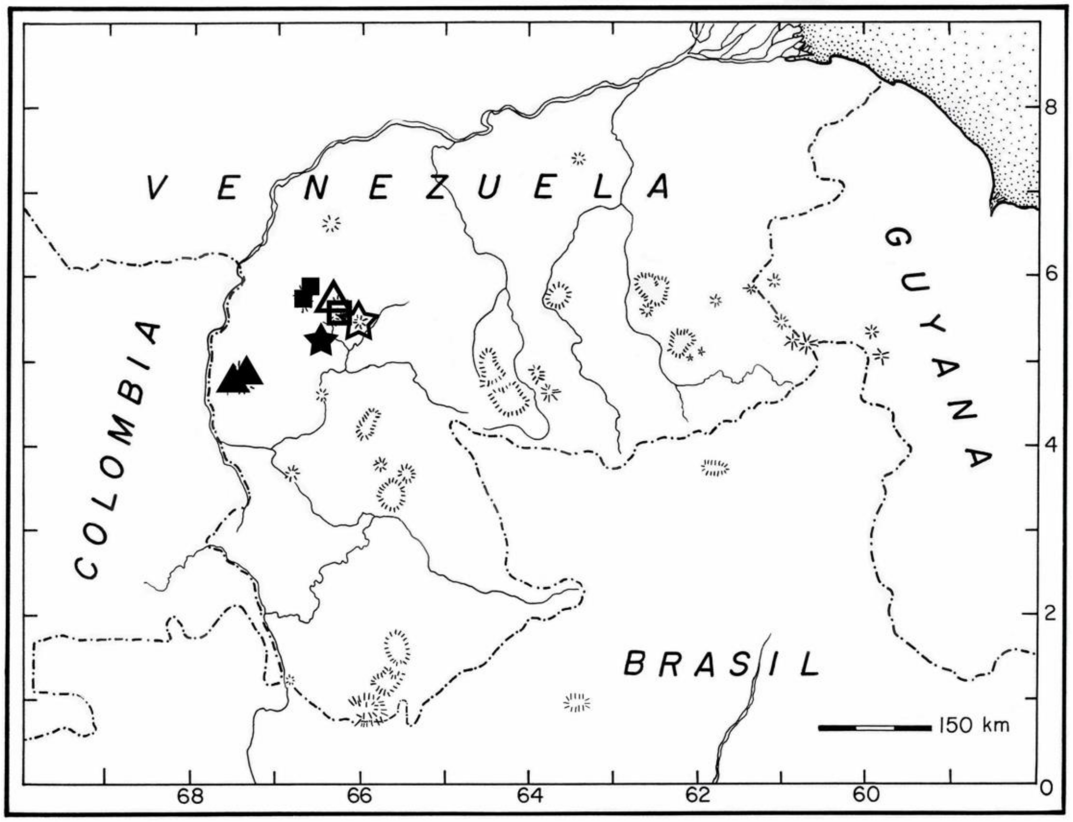


Figure 86. The central Guayana Highland showing distribution of *Tepuipappus* Pruski. Abaxially tomentose-leaved species are represented by solid symbols. Solid star, *Tepuipappus camani*, generitype (Cerro Camani). Solid triangles, *Tepuipappus kunhardtii* (Cerros Sipapo, Autana, and Cuao). Solid squares, *Tepuipappus esposi* (Cerro Guanay). Open symbols represent species with leaves abaxially either weakly pubescent or glandular. Open star, *Tepuipappus phelpsiae* (Cerro Yaví). Open triangle, *Tepuipappus orbiculatus* (Cerros Yutajé and Coro Coro). Open square, *Tepuipappus punctatus* (Cerro Yutajé). (Base map, modified from that drawn by Bobbi Angel, shows select lajas, major rivers, and stylized major sandstone tepuis of the Roraima and Duida Supergroups, with the two southernmost drawn here being Neblina and Aracá of the Tunuí Supergroup).

The Pantepui measures only about 6000–7000 of the total 1,000,000–1,135,000 square kilometers of the Guayana Highland, only about half of one percent of the total area of Guayana (viz Maguire 1970; Huber 1997; Santos et al. 2003; Huber et al. 2018). The "Guayana Highland" of Maguire (Botany of the Guayana Highland, I–XIII, 1953–1989), Steyermark and Dunsterville (1980), Pruski (Compositae of the Guayana Highland, I–XV, 1989–2023), Valdespino (1992), and Steyermark et al. (Flora of The Venezuelan Guayana, volumes 1–9, 1995–2005) is used in the singular. Sometimes the English spelling Guiana (for Guayana) is used.

Sir Walter Raleigh (1596) was a noted very early explorer of Guayana. Two centuries later, in 1800, while travelling south from the Venezuela coast to the Rio Orinoco, naturalists Humboldt and Bonpland saw Cerro Duida and neighboring tepuis (Amazonas, Venezuela). Alexander von Humboldt (1833: 275) wrote of this tepui "the summit of Duida is so steep that no person has ever ascended it." Decades later, the now well-known Mount Roraima, which is more than 400 kms ENE of Duida, was "discovered" by Robert Schomburgk. Schomburgk (1841b, 1841c) similarly reported being unable to summit Roraima, then crossed westward over Sierra Parima to Duida, which he too was unable to climb. Wallace (1853a: 204) travelling from the Atlantic entered the Rio Negro and as he continued upstream saw yet another spectacular mountain, of which he said Brazilian "Curicuriarí

… Serras" that are situated south of the Río Negro near São Gabriel da Cachoeira are the "finest mountains [he] had yet seen." Wallace (1853a: 205) estimated the granitic Serras de Curicuriarí to be "three thousand feet high." Each of these early explorers had approached Pantepui from differing directions.

Robert Schomburgk (in 1839; 1841c), Alfred R. Wallace (in 1851; 1853a, 1853b), and Richard Spruce (1853; 1908) (Spruce and Wallace met twice during their voyages), were perhaps (among) the first western naturalists to see what has become modern Sierra de la Neblina, which they saw from either or both Piedra-del-Cocuy [Piedra de Cucuy] and Marabitanas along the Río Negro, and which they called variously "Serras de Cababurís," "Serrania Pirá-pukú," and "Imei." Robert Schomburgk (1841c: 252) possibly saw Neblina from along the Rio Negro between Cocuy [Cucuy] and Marabitanas and what he saw he called "the Pirabuku chain of mountains." Similarly, Spruce (1908, 1: 354, 361) described the high mountains seen from along the Orinoco near Marabitanas, Brazil and 35 km to the north from Piedra-del-Cocuy as "Serrania Pirá-pukú or The Long Fish, whose base is laved by the Cauaborís" (i.e., near the Río Cauaburi) and that "those who have ascended the river Cauaboris describe it as very picturesque and possessing a peculiar vegetation." Later, from Cerro Tururtmeri and Laja Catipán along Rio Pacimoni Spruce again saw *Neblina* and said he "was astonished at the magnificent scene that burst upon [him and saw] all of the mountains … especially Imei in its entire length" (Spruce 1908: 434). Schomburgk, Wallace, and Spruce also each mapped differently the mountains they saw from various vantage points along the Río Negro.

Wallace (1853b: 215) said in height the "Serras de Cababurís, near the sources of the river Cababurís are perhaps nearly equal to them [i.e., Serras de Curicuriarí]." Wallace (1853a: 232–233) said he saw his *Serras de Cababurís* (Neblina) from Marabitanas. The mouth of the river Cababurís is near Paranari, Brazil, and Wallace mapped the lower rio Cababuris correctly as coming from the northwest and upriver leading to his Serras de Cababurís, basically in direction of the ca. 3000 m tall Neblina. Although, Wallace mapped the Serras de Cababurís southwest of Marabitanas (Neblina instead is about 75 kms east of Marabitanas) and said that his map (1853b: 217) "does not pretend to any minute accuracy in general positions," Wallace surely did not confuse his Serras de Cababurís with the long-known Serra Imeri (which is about another 80 kms further east of Neblina). Spruce (1908, 1: 354) clearly was describing Wallace's "Serras de Cababurís" saying that on a clear day from Marabitanas looking to the east: "with my telescope I could distinguish steep escarpments [of] this lofty ridge … their highest part–an abrupt truncated peak," truncated as are tepuis. It seems most likely that from the lay of the land and from Wallace's height comparison of "Serras de Curicuriarí" (south of but near São Gabriel) to the distant "Serras de Cababurís" seen from Marabitanas that he (Wallace 1853b: 215) was applying the name "Serras de Cababurís" to modern Sierra de la Neblina, located about 40 miles (about 60 kms) east of Marabitanas.

Maguire (1955) said these early citings and namings were each in reference to the same mountain, which a century later he called (renamed) Sierra de la Neblina, the highest of all tepuis, the watershed between Brazil and Venezuela (viz the 1859 "Tratado de límites y navegación fluvial entre Venezuela y el Brasil"). Maguire (1955) said Spruce's "Imei" applied instead to the ca. 80 kms east-of-Neblina Serra Imeri, which long been the name of the 500 ca. lower-elevational range near the frontier. Further to the east of Serra Imeri and forming another part of the watershed between Venezuela and Brazil is the long-known even-more-distant Sierra Tapirapecó. Maguire (1955: 31, 44–45) seemed to name Neblina because in 1854 from along the Río Pasimoni (Pacimoni) Spruce (1908: 423-434) for a second time saw Neblina, but Spruce did realize it was the same as Wallace's Serras de Cababurís or the same he had earlier seen from Marabitanas with his "telescope." Of another regional mountain, Rice (1921: 325) said "these hills … are constantly undergoing a confusing change of names. In Spruce's time they were called Serra da Gama; previous to that, Urucú-iuitéra …" A early 1900s name for the Sierra de la Neblina-Serrania Pirá-pukú-Serra Imeri complex may be "Cerro Palo Yuca" as mapped by Razetti (1937), and even earlier names may be in the Yanomami anthropological literature. More recently, Pirapukú was applied by Ort (1965: 200) and Brewer-Carías (1988: 11, fig. 7) to a single mountaintop (not at all on *Peakery*—a mountain climbers web site—recalling Spruce's Long Fish) in front of (southwest) and 1,000 meters lower in elevation than Sierra de la Neblina, and just to the northeast of Canal Maturacá. In naming Neblina, Maguire (1955) discussed Robert Schomburgk's (1841c) Pirabuku and Spruce's (1908) Imei, but did not mention Wallace's (1853a, 1853b) and Spruce's (1908) earlier identifications and namings of "Serras de Cababurís," which may possibly be an earlier name for Sierra de la Neblina. Application of Wallace's Serras de Cababurís seemingly has remained unexplained until now. However, because there is a Brazilian "Parque Nacional do Pico da Neblina" and a Venezuelan "Parque Nacional Serranía La Neblina," it seems as though the earlier sightings and apparent namings of Sierra de la Neblina may continue to be obscured by the "Mountain of the Mists" mystique.

In any event, in 1884, Mount Roraima sitting mostly in Bolívar, Venezuela became the first tepui successfully climbed to its summit. Roraima was "discovered" and charted in 1838 by Robert Schomburgk, who collected on its slopes (Schomburgk 1841b). Whitely (1884: 462) stated that in 1883 he had seen a gradual near-continuous ledge on the southwest face of Roraima. In December 1884 this now-famous oblique ledge was used by Everard Im Thurn (1885) to summit Roraima. Soon thereafter, the "Lost World" moniker (Doyle 1912) used informally for the region was hatched. It was more than a century after Humboldt saw Cerro Duida and adjacent tepuis, and four decades after Thurn climbed Mount Roraima to its cumbre, before Cerro Duida became, in 1928, the second tepui summited, having been climbed by George Tate of the American Museum of Natural History as part of the Tyler-Duida expedition. More than a dozen other tepuis, including Auyán-tepui, Chimantá-tepui, Cerro Sipapo, Cerro Yaví, and Cerro Yutajé, were climbed by December 1953 (see Maguire et al. 1953; Huber 1990, 1995), when Sierra de la Neblina was first documented as being climbed. We now know, however, that although the Guayana Highland may seem to be a remote region, and several individual tepuis are relatively isolated and hard to access, the Guayana Highland flora did not originate in total isolation.

Humboldt (1852–1853, 3: 20) wrote of the vegetation on either side of the Maigualida-Parima line and stated "the Paragua [and] the Cordillera of Pacaraimo [are] full of fine savannahs [that are] no way resembling [those of the] upper Orinoco" (i.e., fide Huber 1982 those near the Raudal de Atures and Raudal de Maipures). Huber et al. (1984) and Huber (1995) noted the Guayana Highland is intersected into eastern and western halves by the exposed granitic north-south oriented Maigualida complex and Sierra Parima, the later both of a more rounded nature. Pruski (1991, 1997) stated this another way, noting in Pantepui that the Roraima region of eastern Guayana Highland has concentrations of endemic actinomorphic-flowered genera (e.g., *Chimantaea* Maguire, Steyerm., & Wurdack, *Quelchia* N.E. Br., *Stenopadus* S.F. Blake, and *Stomatochaeta* Maguire & Wurdack) of the former Mutisieae, and took the Roraima region as the easternmost (first) tepui Mutisieae floristic zone in Guayana. To the west of Huber's Maigualida-Parima divide, on the other hand, Pruski (1991, 1997) gives the Duida region of western Venezuelan Guayana Highland as having concentrations of endemic zygomorphic-flowered genera (e.g., *Duidaea* S.F. Blake, *Glossarion* Maguire & Wurdack, *Gongylolepis* R.H. Schomb., and *Neblinaea* Maguire & Wurdack) of the former Mutisieae.

The Duida region was taken by Pruski (1991, 1997) as the second tepui Mutisieae floristic zone in Guayana. The regions and their floras are not mutually exclusive, however, and for example Pruski (1991, 1997, 1998c, 2019) and Pruski and Beltrán (2003) noted that the otherwise-Guayana-Highland-endemic genera *Stenopadus* of the Roraima Mutisieae zone and *Gongylolepis* of the Duida Mutisieae Floristic Zone each contain a single Andean species. West of the rios Orinoco-Negro, the flora of Colombian Guayana and northwestern Brazil are conceptualized by me as belonging to a low-tepui third floristic zone, composed of plants of the Tunuí Supergroup and the Chiribiquete

Supergroup. The Tunuí-Chiribiquete Mutisieae zone seems more natural, however, once Neblina and Aracá are excluded.

These three Mutisieae floristic zones partly match the tepui supergroup regions of Santos et al. (2003), Huber et al. (2018), and Kroonenberg (2019), but again excepting the floras of Neblina and Aracá that align more closely with that of the Duida tepuis rather than with the floras of the lower elevational Tunuí and Chiribiquete Supergroups of tepuis. Maguire (1979) noted the river drainage patterns in the Guayana Highland define the area west of the Río Coroní, that includes Cerros Guaiquinima and Jaua, as a distinctive zone. Humboldt (1852–1853, 3: 19–20) noted the nearby, but slightly further to the west, Río Paragua as a natural divide.

Near the western edge of the Venezuelan pantepui along the Rio Orinoco, upstream and downstream from Puerto Ayacucho, the area is characterized by a crescent of scores of intrusive granitic lajas (Kroonenberg 2019), as are parts of Colombian Guayana. Similarly, east of Tafelberg are granitic inselbergs (lajas) scattered eastward into French Guiana. Along the Amazon downriver from Santarém I saw the tepui-like hills near Monte Alegre, Brazil (mapped by Kroonenberg et al. 2016: fig. 2 as near the "undifferentiated Tumucumaque basement").

Although Davis et al. (2017) gave some artifacts found at the Caverna da Pedra Pintada near Monte Alegre as made of sandstone, its Compositae flora is not at all overtly tepuian, and Monte Alegre may simply be a "Roraima-like outlier" (viz Santos et al. 2003). Monte Alegre is about 750 kms south of Tafelberg, Suriname and although near the Amazon River basically seems to be the farthest southeastern isolate of the "poorly studied" (Kroonenberg et al. 2016) Tumuc Humac Mountains (Serra do Tumucumaque) along the borders of Suriname, French Guiana, and Amapá-Pará, Brazil. Otto Huber (1988b) used the term "Guayana Lowland" to apply to a broad spectrum of areas and vegetations, including for example the peripheral lajas, and various low-elevational forests and savannas between many tepui bases and on the periphery of the Guayana Shield.

The Guayana Highland in Colombia was called Colombian Amazonia by Schultes (1988; the Amacayacu-Leticia region of Colombia, and to the north between the rios Putumayo and Caquetá, however, are indeed Amazonian) and by others is sometimes called Orinoquia. North of the Orinoco River the great Llanos region is found, and to the south the great Amazon River and adjacent Amazonian Hylaea border Guayana. Colombian Serranía de Macarena is near the westernmost edge of the Guayana Shield in the upper Río Guaviare basin (Pinson et al. 1962; Ibañez-Mejia and Cordani 2020).

The more or less north-south oriented Macarena was called an "outlier of the Eastern Cordillera" (Kroonenberg 2019: 170), yet is in part Guayanan with its eastern face marked by two areas containing sandstones of the Araracuara-Chiribiquete Formation (Kroonenberg 2019: fig. 3.38; Ibañez-Mejia and Cordani 2020: fig. 2; viz also Bonilla et al. 2023: fig. 2). On the other hand, although parts of the Cordillera Cóndor (Ecuador-Peru) are sandstone, is home to *Stenopadus andicola* (a species of a former Mutisieae genus otherwise endemic to Guayana), and its parts have been called tepuis, geologically the Cordillera Cóndor is not subtended by the Guayana Shield and is not a tepui. Rather the Cordillera Cóndor has been associated with the Andean "forelands" (Kroonenberg 2019; Ibañez–Mejia 2020; Ibañez-Mejia and Cordani 2020). Similarly, the sole *Gongylolepis* (former Mutisieae) outside of Guayana extends from Mérida, Venezuela to the western Andean Cordillera in Antioquia, Colombia, which is not a tepui.

Beginning with the work of Basset Maguire (often in company with John Wurdack, William Phelps, Jr., and Kathleen Deery Phelps) and Julian Steyermark in the mid-1940s, a newer era of Guayana Highland botany and exploration began. [Otto Huber 1990 similarly distinguished two phases of botanical exploration in Guayana: the historical phase and then beginning in 1884 a "mountain phase"]. Since the 1940s, the amount of Guayana Highland materials have grown exponentially, especially due to the collecting efforts of Maguire, Steyermark, Huber, Richard Schultes, Felix Cardona and the Herbario Nacional de Venezuela staff, Projeto Flora Amazônica, the 1980s Neblina expeditions, the Guianas project, Dairon Cárdenas and the COAH staff, and MBG expedition personnel such as Gerrit Davidse, Ron Liesner, and Bruce Holst. Maguire (e.g., 1944, 1945, 1955, 1956, 1957, 1964, 1970, 1979), Schultes (1944, 1988), Hitchcock (1947), Lasser and Maguire (1950), Maguire and Phelps (1951, 1951–1952), Maguire et al. (1953), Steyermark (e.g., 1955, 1966, 1967, 1968, 1974, 1975, 1979, 1982, 1986; and Steyermark and Collaborators 1951, 1952, 1953, 1957, 1989), Maguire and Wurdack (1957, 1959, 1960), Huber (e.g., 1982, 1987, 1988a, 1988b, 1989, 1990, 1992, 1995 1997, 2005), Pruski (1982, 1989, 1991, 1992, 1996a, 1996b, 1996c, 1997, 1998c, 1998d, 2001, 2002, 2005, 2011, 2019, 2023), Huber and Wurdack (1984), Huber et al. (1984), Brewer-Carías (1987, 1988), Huber and Frame (1989), Ek (1990), De Granville (1991), Prance and Johnson (1992), Cortés-B. et al. (1998), Arbeláez and Callejas (1999), Ter Steege (2000), Cárdenas et al. (2008), Barbosa-Silva et al. (2016), Barona-Colmenares et al. (2018), and Huber et al. (2018) are noteworthy newer Guayana Highland bio-references. For Guayana Highland Compositae, the series Botany of the Guayana Highland I–XIII (Maguire et al. between 1953–1989), Compositae of the Guayana Highland I–XV (Pruski between 1989–2023), Flora of the Venezuelan Guayana volumes 1–9 (Steyermark et al. between 1995–2005), Aristeguieta (1964), and Badillo (1994) continue to be useful references.

I first became aware of the Guayana Highland in the early 1970s from an episode of *American Sportsman* that showed footage from Angel Falls to the Yanomami, and since BBC (Skydive to Autana 1985; the broken leg video), National Geographic, and PBS (The Lost World: Venezuela's ancient tepuis, 2003) filmed or broadcasted tepui films. I have seen the VHS video tape compiled from Maguire's 16 mm silent movies, various film clips of the 1980s Neblina trips, and the web as well holds various tepui videos. Wonderful coffee-table-books on the Guayana Highland include those of Brewer-Carías and Steyermark (1976), Weidmann et al. (1986), Brewer-Carías (1987), George (1988, which is very detailed), Michelangeli et al. (1988), Schultes (1988), Schubert and Huber (1989), Huber (1992, 1995, which are definitive references), and McPherson (2008).

Popular Guayana Highland overview papers at hand that are often chocked full of fantastic photographs include those by Holt (1931), Begley (1984), Blonston (1985), NYBG (1985), Gentry (1986), Michelangeli and Michelangeli (1986), Conover (1987), Rachowiecki (1988), George (1989), Stolzenburg (1993), and Smith (2010). Further accounts dating from the 1800s to the mid-1900s of various parts of the Guayana Highland—especially Mount Roraima and high tepuis—have given much background information, floristic summaries, tepui maps, and the like (e.g., Bentham 1838–1839, 1840; Whitely 1884; Perkins 1885; Thurn 1885; Thurn and Oliver 1887; United States Commission 1897; Brown 1901; Rice 1921; Tate 1930a, 1930b; Tate and Hitchcock 1930; Gleason 1929, 1931; Hitchcock 1931; Tate 1938; Gleason and Killip 1939; Smith 1940; Williams 1942).

The United States Commission (1897, 3: 383-506), for example, gave a 100+ page listing by Marcus Baker of "Schomburgk Line" regional maps then produced. Maguire et al. (1953), Huber and Wurdack (1984), and Huber (1995) gave thorough accounts of Guayana Highland botanical history, but the Alexander von Humboldt, Robert H. Schomburgk (1836 etc.), M. Richard Schomburgk (1847–1848, 1876), Alfred R. Wallace, and Richard Spruce accounts of the rios Orinoco-Negro and the Guayana Highland remain landmarks. Some of these areas of Guayana I have seen firsthand.

Santos et al. (2003) and Kroonenberg (2019) using Zircon U–Pb geochronology (Uranium–Lead) dated the basement of the Guayana Shield and gave the first tepui supergroup in the Guayana Highland, the classical Roraima Supergroup (Fig. 85), as centered in southeastern Bolívar, Venezuela, basically east of Huber's Maigualida-Parima divide. The Roraima Supergroup includes many of the best-known of all tepuis: Mount Roraima (Whitely 1884; Thurn 1885; Tate 1930a, 1930b), Auyán-tepui (Tate 1938; Gleason and Killip 1939; Steyermark 1967), the Chimantá Massif (Huber 1992; Pruski 1997), the tepuis of the Gran Sabana (Schubert and Huber 1989), Mounts Ayanganna and Wokomung (Pruski 1990, 1991) in Guyana, and extends to the remnant outlier Tafelberg (Maguire 1944, 1945) in Suriname. The Roraima Supergroup in this geologic concept (viz Santos et al. 2003: fig. 1; Kroonenberg 2019: fig. 3.38) include Cerros Guaiquinima and Jaua, both plateaus being west Maguire's Río Coroní drainage line yet east of Huber's Maigualida-Parima line. Tate (1930a) noted the horizontal strata (viz fig. 85C) of Mount Roraima and that its relief from base to summit was noticeable less than that of Cerro Duida, which Tate noted has some strata that are "intensely folded."

The second tepui supergroup characterized by Santos et al. (2003), Huber et al. (2018), and Kroonenberg (2019) as we move from east to west, is the Duida Supergroup of tepuis that are west of the Huber's Maigualida-Parima line. The tepuis of the Duida Supergroup include most of the plateaus in Amazonas, Venezuela and some of the best-known tepuis of western Pantepui such as Cerros Aracamuni and Avispa (Spruce 1908; Steyermark et al. 1989), Cerro Sipapo, Cerro Yaví (Hitchcock 1947; Lasser and Maguire 1950), Cerro Yutajé (Maguire and Phelps 1951, 1951–1952), Cerro Marahuaca (Michelangeli et al. 1988), Cerro Autana (Steyermark 1974, 1975), and the first tepui seen by naturalists, Cerro Duida (Humboldt 1833: 275; Tate and Hitchcock 1930). Santos et al. (2003) summarized by Huber et al. (2018) used Zircon U–Pb (Uranium–Lead) geochronology to align Duida and Neblina similarly, as members of the second tepui supergroup, the so-called "Neblina Supergroup of tepuis." However, the Kroonenberg (2019, viz fig. 3.38) Zircon U–Pb (Uranium–Lead) geochronology dated Sierra de la Neblina differently (than did Santos), dating it within the Tunuí Supergroup of tepuis, thus disassociating Neblina from the "Neblina" Supergroup of tepuis. Here, the once-so-called "Neblina Supergroup of tepuis" (sensu Santos et al. 2003 and Huber et al. 2018), geologically may or may not include Neblina, and this tepui supergroup is provisionally called the "Duida Supergroup of tepuis." Santos et al. (2003) and Kroonenberg (2019) dated Cerro Moriche differently as well: Santos et al. (2003) placed Moriche with the third supergroup (the Tunuí Supergroup), whereas Kroonenberg (2019) aligned Moriche with the Duida Supergroup.

Centered further to the south and west of the second supergroup, and for the most part downstream from Mitú on both sides of the lower Vaupes-Uaupés River in Brazil and Colombia is the Tunuí Supergroup of tepuis, the third supergroup (Paiva 1928; Santos et al. 2003; Huber et al. 2018; Kroonenberg 2019; Bonilla et al. 2023). The Tunuí Supergroup formation is very distinct geologically, containing "folded and/or metamorphosed sandstone units" (Santos et al. 2003). Its tepuis are mostly low-elevational, with the notable exception in Kroonenberg (2019), who considered the Tunuí Supergroup to include Sierra de la Neblina (i.e., Wallace's 1853a, 1853b "Serras de Curicuriarí"), which is the highest of all tepuis and the highest mountain in Brazil (Maguire 1955; Maguire and Wurdack 1959, 1960; Ort 1965; Brewer-Carías 1988).

The fourth supergroup of cerros in the Guayana Highland, still further west and upstream from Mitú, is the Chiribiquete Supergroup (Santos et al. 2003; Huber et al. 2018; Kroonenberg (2019). The Chiribiquete Supergroup of tepuis is found only in Colombia, and includes the north-south oriented Cerros Chiribiquete (Vaupés) and Araracuara (along the Río Caquetá on the border of Amazonas and Caquetá) (Galvis et al. 1979; Huber et al. 2018; Bonilla et al. 2023). The Chiribiquete Supergroup has a relatively young bedrock basement dating from the Paleozoic (Galvis et al. 1979; Huber et al. 2018; Kroonenberg 2019). Kroonenberg et al. (2016) called the "western part" of the Guayana the "Rio Negro belt" which they said is "the youngest belt." Serranía de Macarena, near the western edge of this supergroup, also contains Ordovician sedimentary rock (Moreno-Sánchez et al. 2020: fig. 1). The Tunuí and Chiribiquete tepui supergroups are mostly composed of low-elevational sandstone plateaus (excepting Neblina and Aracá that are part of Pantepui), with broad inter-tepui valleys that are eroded down to the bedrock basement (Kroonenberg 2019). The four tepui supergroups are thus of decreasing ages as we move from east to west (Galvis et al. 1979; Santos et al. 2003; Kroonenberg et al. 2016).

Here, I describe **Tepuipappus** Pruski, **gen. nov.**, endemic to northern tepuis of the Duida Supergroup of tepuis in northern Amazonas and adjacent western Bolívar, Venezuela (Fig. 86). *Tepuipappus* is a member of Heliantheae tribe Verbesininae. In the Guayana Highland, the six upland radiate-capitulate helianthoid species treated here as comprising *Tepuipappus* are true super-endemics. These species are endemic (Pruski 1997) to eight individual tepuis or tepui clusters of the western-Pantepui Sipapo-Yutajé-Complex in northern Amazonas and adjacent western Bolívar, Venezuela (Fig. 86; viz also Huber 1995; Maguire 1979: fig. 1 as region V; Santos et al. 2003), and their distributions are as follows.

Four of these species occur on Cerros Coro-Coro, Guanay, Yaví, and Yutajé in northern Amazonas, Venezuela, but the distribution of *T. esposi* on Cerro Guanay is at least in part north and across the border in western Bolívar, Venezuela. *Tepuipappus esposi* is the sole species of *Tepuipappus* known from Edo. Bolívar, and although labeled by Maguire and Phelps (1951, 1951–1952) as Amazonas, Venezuela, most of Cerro Guanay actually lies within Edo. Bolívar. A fifth species of *Tepuipappus* is endemic to nearby Cerro Camani, northern Amazonas, Venezuela, that is only 30 kms (Maguire and Phelps 1951, 1951–1952) to the south of Guanay, Yaví, and Yutajé. The final species—*T. kunhardtii*, the most common species of the genus—occurs 140+ kms to the southwest of Cerro Camani on granite-spotted Cerro Sipapo, northern Amazonas, Venezuela. *Tepuipappus kunhardtii* has less commonly also been collected on adjacent Cerro Autana (Fig. 93B) only 18 kms to the SW and on Cerro Cuao. Huber (1995) says the Cuao-Sipapo massif is massive and consists of "many separate mountain ranges," and thus perhaps *T. kunhardtii* may eventually be found on other nearby peaks.

6. TEPUIPAPPUS Pruski, **gen. nov. TYPE:** *Calea camani* Maguire & K.D. Phelps [≡ *Tepuipappus camani* (Maguire & K.D. Phelps) Pruski].

Fruticosa; folia simplicia opposita aliquando ternata petiolata lamina chartacea vel coriacea triplinervia vel pinnatim venosa; capitulescentia terminalis monocephala vel cymosa; capitula omnis radiata, involucrum campanulatum vel hemisphaericum, phyllaria plerumque dimorpha, imbricata, 3+-serrata; clinanthium paleaceum; paleae lanceolatae induratae; flosculi radii 12–30 pistillati, corolla luteolis; flosculi disci hermaphroditi numerosi, corolla anguste infundibuliforme luteolis glabrate; antherae palidae; styli rami brevi, areis stigmaticis discretis; cypselae quadrature heteropappose nigrae; pappi squamae circiter 4–6 inaequales.

Shrubs 0.3–3 m tall; stems moderately branched or infrequently simple, hexagonal to proximally subterete, leafy distally, subglabrous to densely pannose-tomentose. **Leaves** simple, opposite or infrequently whorled, sessile to short-petiolate; blade elliptic to orbicular, never clasping, stiffly chartaceous to more characteristically subcoriaceous or coriaceous, venation pinnate to trinerved from near base, margins crenate or serrulate to serrate or dentate, apex acute to obtuse, surfaces concolorous or nearly so to infrequently strongly discolorous, the adaxial surface glabrous or glandular (glands biseriate) to tomentulose, the abaxial surface weakly glandular or substrigose to hirtellous or extremely densely buff-pannose-tomentose. **Capitulescence** terminal, monocephalous to paucicephalous and cymose, nearly included to slightly exserted, usually short-pedunculate; peduncle sometimes few bracteate. **Capitula** always radiate, many-flowered, usually moderately large; involucre campanulate to hemispherical; phyllaries typically strongly dimorphic, 3+-seriate; usually with 2–6 decussate herbaceous-subfoliaceous (in two species merely stiff-chartaceous), other series imbricate, outer phyllaries about half as long to as long as capitulum, sometimes weakly reticulate veined and/or crenulate, margins usually entire or weakly few-serrulate, abaxial (outer) surface often tomentose, sometimes merely glandular or even subglabrous; inner series of phyllaries in the typical elements quickly transitioning from outer few, spiral-alternate, graduate, appressed at anthesis, stiff, entire; clinanthium paleate, convex to dome-shaped; paleae generally lanceolate, weakly navicular, rigid, longer than the cypselae, pale-colored, margins usually entire. **Ray florets** pistillate, uniseriate, 12–30, exserted from involucre; corolla yellow, limb 5+-nerved, nerves equally thin, i.e., without a pair of prominent so-called calyx nerves, apex sometime bilobed, abaxially glandular, very rarely also glandular adaxially; style branches slightly recurved. **Disk florets** bisexual, many; corolla narrow-funnelform, yellow, glabrous, tube slightly dilated at base, throat elongate, not at all greatly ampliate, much longer than lobes, lobes 5, triangular-lanceolate, erect; anthers pale yellow, appendage triangular, usually glandular, endothecial tissue polarized; pollen tricolporate, echinate; stylopodium slightly dilated, relatively narrow, free from the annular nectary, branches relatively thin, recurved, stigmatic surface 2-banded from base to the broad apex, abaxial surface smooth or sometimes with a few very small papillae. **Cypselae** quadrangular, broad-based, heteropappose, carbonized, dark, glabrous to setulose, carpopodium weakly asymmetric, oblique-annular, small and not well-developed; pappus not at all obviously radially symmetric, mostly of 4–6 unequal scales from edges and margin, scales evenly thickened and without strong midnerve, unequal and sometimes unequally manifest within an individual capitulum, sometimes very reduced but usually reaching to about apex of disk corolla tubes and the longer two–few often about as long as mature cypselae, occasionally with smaller intermediate scales or squamellae, stramineous. Chromosome number unknown.

Etymology. The name *Tepuipappus* is an arbitrarily formed generic name that uses the prefix *tepui* (that ends in a vowel) connected to the suffix *pappus*, albeit the quadrangular cypselae of the genus are as distinctive as is the strange non-*Calea*-like pappus (Figs. 87–88). *Tepuia* Camp (Ericaceae) and *Tepuianthus* Maguire & Steyerm. (Thymelaeaceae) are two other similarly named Guayana Highland endemic genera.

Geographic Distribution. *Tepuipappus* is endemic to Guayana Highland tepuis in the Sipapo-Yutajé-Complex, specifically occurring on Cerros Autana, Camani, Coro-Coro, Cuao, Guanay, Sipapo, Yaví, and Serrania Yutajé in northern Amazonas and adjacent western Bolívar, Venezuela (Fig. 86). These tepuis were mapped by Kathleen Phelps (Maguire and Phelps, 1951, 1951–1952) and Huber (1995: figs. 1-31 and 1-32). Parts of six of these tepuis (but not Cerros Autana and Cuao) are in the Rio Ventuari (Huber 1996: plate 9) drainage, which thence flows southwestwards into the Río Orinoco. Three species are known from elevations of 1700 meters elevation or greater, but the low-end elevations of *T. kunhardtii*, *T. orbiculatus*, and *T. punctatus* are notable, ranging from 1200–1250 meters elevation. *Tepuipappus punctatus* is endemic to Cerro Yutajé and the consistently the lowest elevational species of the genus, known only from about 1250–1400 meters elevation. *Tepuipappus orbiculatus* was also described from relatively low elevational material on Cerros Coro Coro and Yutajé, but has since been collected at 1800 meters. The only two sympatric species are *T. orbiculatus* and *T. punctatus*, both occurring on Cerro Yutajé. Four of the six species of *Tepuipappus* have been recollected since they were discovered, but *T. punctatus* and *T. camani* have not been rediscovered. Distinctly trinerved *T. punctatus* is known only from the four original protologue-cited collections, and the generitype *T. camani* remains known only from the type collection series.

These six species were described in the 1950s by Bassett Maguire and colleagues as *Calea*, but have long-been known as anomalous. In 1989 we designated these species as members of *Calea* sect. "*Tepuiopappus* Pruski & Maguire" nom. provis. inval. (Amer. J. Bot. 76-6: 278. 1989, in Urbatsch and Pruski 1989), but did not formally name or publish the section. Pruski (1997) called these six species the "*Calea kunhardtii* group" (now redefined and excluding *C. politii*) and keyed them in a prime lead by their peculiar pappus characters. These six species are extracted from *Calea* and placed in newly described ***Tepuipappus*** Pruski, **gen. nov. (**Compositae Heliantheae subtr. Verbesininae). *Tepuipappus* becomes the fifth genus of subtribe Verbesininae, and the only one of the five genera endemic to South America.

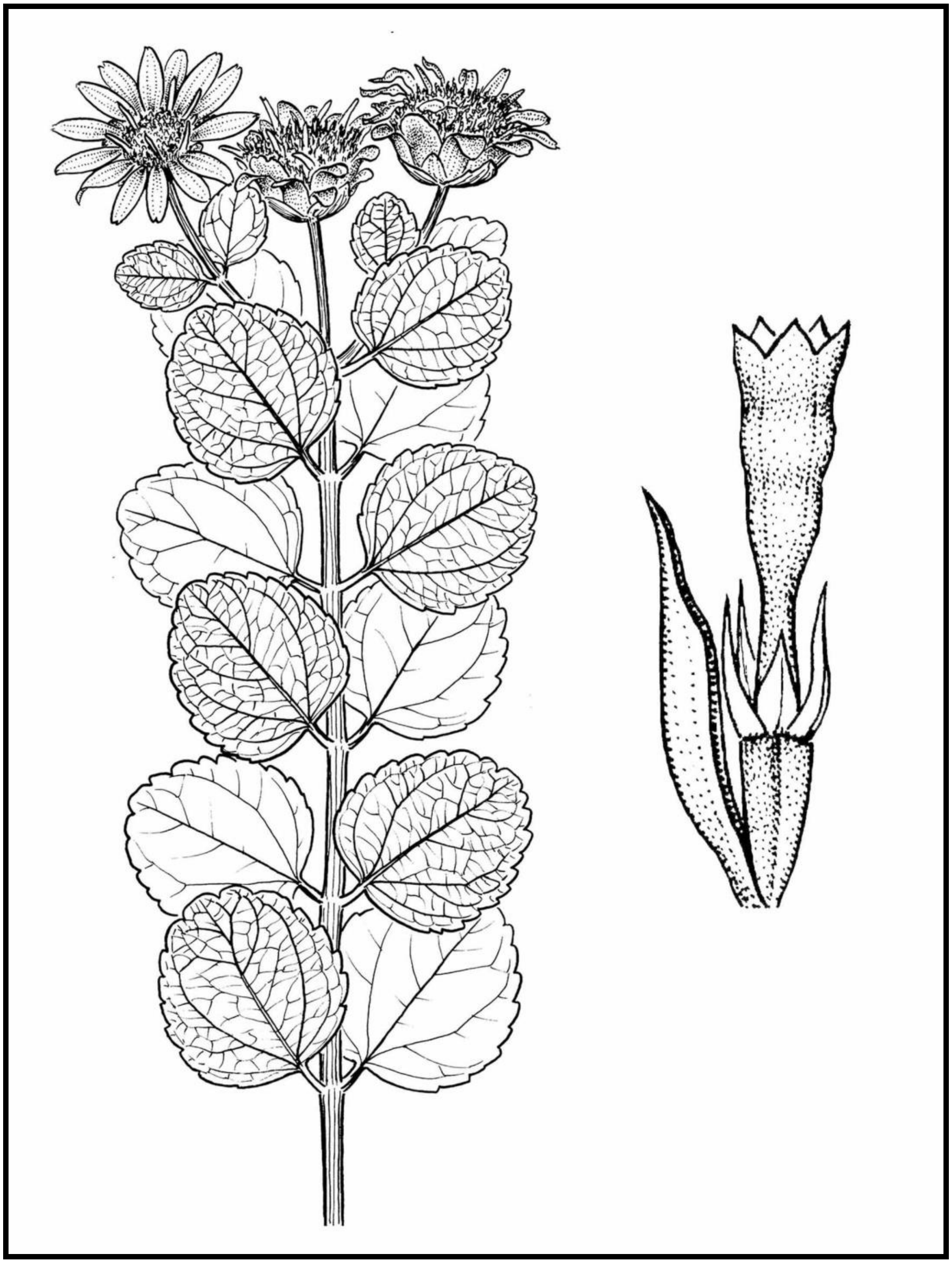


Figure 87. *Tepuipappus punctatus* (Maguire & Wurdack) Pruski. Flowering stem (left) showing the relatively short-pedunculate radiate large capitula and the opposite trinerved strongly reticulate subcoriaceous petiolate leaves. The close-up (right) shows a disk floret and the subtending clinanthial palea; the few uniseriate pappus scales are unequal, defined by Pruski and Urbatsch (1988) as the heteropappose condition. (Drawn by Bruno Manara and partly based on the protologue illustration, modified from Pruski 1997).

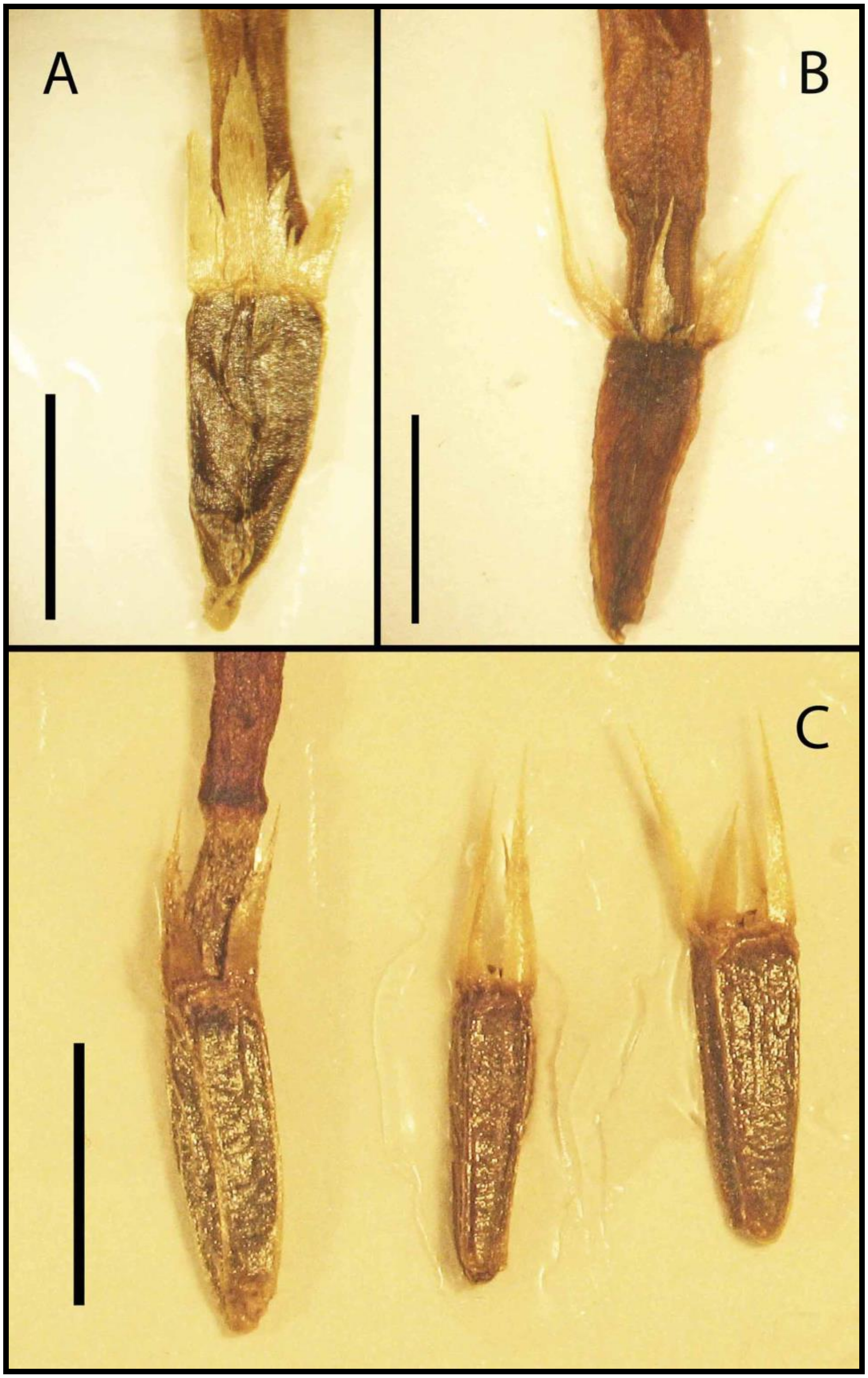


Figure 88. Representative species of *Tepuipappus* Pruski, round-based cypselae carbonized and the heteromorphic pappus (heteropappose) with unequal broad uniseriate pappus scales. A. *Tepuipappus orbiculatus* (Maguire & Aristeg.) Pruski, carbonized immature disk cypsela. B–C. *Tepuipappus camani* (Maguire & K.D. Phelps) Pruski, immature (B) disk cypsela and mature quadrangular (C) disk cypselae. (A *Maguire & Maguire 35197*, NY, holotype; B–C *Maguire 31829*, NY, holotype, generitype). Scale bars A–B 2 mm, C 3 mm.

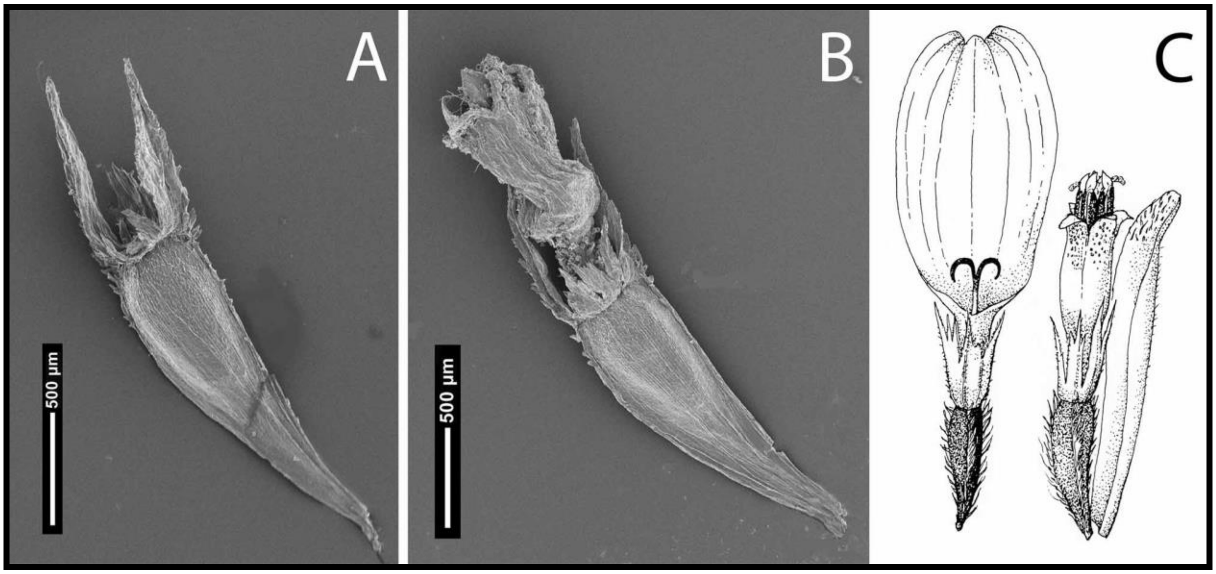


Figure 89. Florets and heteropappose biconvex stipitate-tapered cypselae of white-rayed *Podachaenium* Benth. and yellow-rayed *Squamopappus* R.K. Jansen et al. of Heliantheae subtribe Verbesininae. In each genus the longer scale tips narrow and become awn-like. A–B. *Podachaenium eminens* (Lag.) Sch. Bip., showing cypselae that are long-awned on edges and have intermediate fimbriate-lacerate squamellae on each side. C. *Squamopappus skutchii* (S.F. Blake) R.K. Jansen et al., either one or both angles of the biconvex disk cypselae are long-awned and the intermediate fimbriate-lacerate squamellae are subequal and about half as long. (A–B *Pena 1032,* MO; C reproduced from Nash and Williams 1976: fig. 56).

Recalling percentages of endemicity in Guayanan former-Mutisieae, the six species in the *Tepuipappus* are wholly endemic to the Pantepui of the Guayana Highland. *Tepuipappus* becomes the ninth largest genus of Compositae now recognized in the Venezuelan Guayana. Maguire (1956) suggested that the Guayanan mutisioids likely evolved locally and migrated centrifugally outwards. However, because *Tepuipappus* recalls several Mexican and Central American Verbesininae it seems that either the reverse migrational direction after formation of the geologically recent Panama land bridge may have occurred in these Verbesininae or perhaps simply that *Tepuipappus* and Mesoamerican Verbesininae have undergone convergence. I know of no extant genera similar to these Mesoamerican Verbesininae or *Tepuipappus* from any geographically intermediate regions between Sipapo-Yutajé-Complex and Mesoamerica, thus the origins of these groups are unknown.

Maguire (1956) discussed the regional genera of Mutisieae and *Calea* as the groups of Guayanan Compositae with the highest endemicity. Among regional Mutisieae, Pruski (1991) gave 91% of the species and 75% of these genera as Guayana endemics. Pruski (1991, 1998c, 2019) gave Guayana-centered *Stenopadus* and *Gongylolepis* (each now a former-Mutisieae genus) as alike in that both genera are largely restricted to the Guayana Shield, except for a single species in each genus—*Gongylolepis colombiana* (Cuatr.) Cuatr. of the three main Cordilleras in Colombia and Venezuela northern and *Stenopadus andicola* Pruski in the Condor (Pruski 1998c, 2019)—occurring in the Andes. Pruski (1997) gave the two largest genera of Compositae in the Venezuelan Guayana as *Mikania* and *Calea*, each with 27 species, *Calea* having 24 of 27 species as Guayana Highland endemics. Pruski (2011) reduced the number of regional species in *Calea* to 26 by reappraisal of the once-collected dense-glandular-narrow-leaved fungus-infected "*Calea* sp. A" from Cerro Jaua-Sarisariñama, now determined again as *C. lucidivenia* var. *punctata* Maguire & Wurdack (viz Brewer-Carías and Steyermark 1976: 224, 402). The restructured *Calea*, now after the extrication of *Tepuipappus* and its six component species, becomes the second largest genus of Compositae in the Venezuelan Guayana Highland, containing 20 species, 17 of which are endemic to the Guayana Highland.

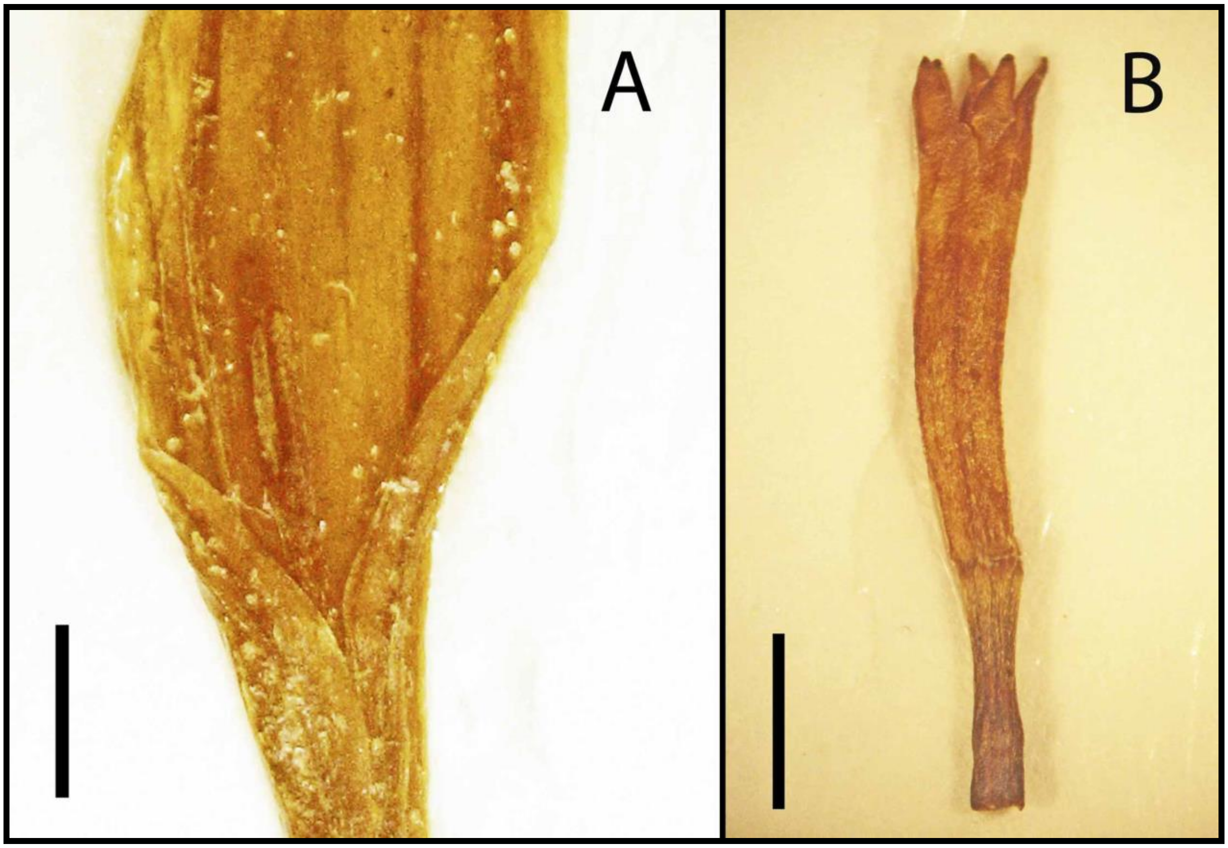


Figure 90. Corolla features of *Tepuipappus* Pruski. A. *Tepuipappus camani* (Maguire & K.D. Phelps) Pruski, close up of immature ray floret corolla limb in high contrast showing unusually positioned glandular trichomes on the adaxial surface (center), also seen (bottom left) are glandular trichomes of the abaxial surface; the style branches (left-center) are erect and weakly elongated and the nerves of the limb are equally thin, i.e., without a pair of prominent so-called calyx nerves). B. *Tepuipappus orbiculatus* (Maguire & Aristeg.) Pruski, tubular-funnelform disk corolla, showing tube with only a slight stylopodial bulge. (A *Maguire et al. 31829*, NY, holotype, generitype; B *Maguire & Maguire 35197*, NY, holotype). Scale bars A 1 mm, B 2 mm.

Although Santos (2003) said Precambrian paleocurrent data suggest "a dominantly western source for most sandstones in the tepuis of the Neblina Basin," the main uplift of the Guayana Highland, and subsequent erosion that formed the tepuis began in the Miocene. This uplift and proto-tepui formation thus happened well after the Compositae diverged from their southern South American ancestor shared with the sister Calyceraceae. The geological data sheds little light on the origins of *Tepuipappus*, but the geological data does not conflict my assumption that the Mesoamerican Verbesininae and *Tepuipappus* may share a common recent ancestor, especially now knowing that the tepui flora did not develop in total isolation. It is perhaps less compelling to suggest the Mesoamerica-centered *Calea*-segregate genera now placed in Verbesininae are the direct progeny of Guayanan ancestors. Of course, widespread speciose *Verbesina* is the genus geographically nearest to lands inhabited by *Tepuipappus*, actually *Verbesina ligulata* (Maguire & Wurdack) Pruski partly occurs on Cerro Yutajé and is sympatric with both *T. orbiculatus* and *T. punctatus*, but it is perhaps equally uncompelling to suggest quadrangular-fruited *Tepuipappus* and compressed-fruited *Verbesina* share a recent direct common ancestor.

Studies of Colombian pollen deposits reveal Pleistocene Epoch floristic shifts, with dry glacial maxima lowering sea levels and causing downslope "displacement of vegetation" and conversely warmer wetter interglacial periods prompting upslope displacement of vegetational zones

(Simpson Vuilleumier 1971; van der Hammen 1974; Pruski 2019). Pre-Pleistocene glacial and interglacial periods are also known to have occurred several times over the past two million years in the Colombian Andes shifting vegetational zones by as much as 1000–1500 meters (Simpson Vuilleumier 1971; van der Hammen 1974). Lowered amounts of vertical displacement has also been proposed and documented in eastern Guayana (Steyermark and Dunsterville 1980; Schubert et al. 1994; Rull 2004).

Schubert et al. (1994) noted that Pleistocene downslope displacements on Chimantá may have altered vegetational zones by several hundred meters, which during Glacial Maxima in the eastern Pantepui Roraima Supergroup tepuis could have brought adjacent tepui floras into contact in the lower elevational inter-tepui valleys. In the Guayana Highland, such displacements could be used to explain, for example, the distribution of *Chimantaea*, a Chimantá-centered genus of nine species (Pruski 1997), two of which are known, respectively, on nearby Auyán-tepui and Murisipán-tepui. Conversely, Steyermark and Dunsterville (1980) suggested "easy access for centripetal invasion" may have accentuated colonization from lowlands to the gently sloping 700–1680 meters in elevation summit of Cerro Guaiquinima "during one of the warmer interglacial stages of the Pleistocene Epoch." Similarly, Rull (2004) documented interglacial upslope Pleistocene migration of *Stegolepis* (Rapateaceae) into *Chimantaea* meadows.

Thus, vegetation zone flux in eastern Guayana has been proposed to have resulted from effects of both Pleistocene Glacial Maxima and Glacial Minima. Such drastic Pleistocene interglacial upslope or glacial downslope vertical displacements (> 1000 m) of vegetation in western Guayana have not been documented. However, such displacements in theory may have brought now isolated upland floras of the high-relief Western Pantepui Duida Supergroup into contact with each other in inter-tepui connecting valleys, and perhaps even somehow brought them into contact with elements of the Mesoamerican flora. Pre-Pleistocene climatic oscillations affecting ancestors of *Tepuipappus*, or Pleistocene climatic events affecting the now-isolated species of *Tepuipappus*, however, remains unproven conjecture. Such theoretical mixing of *Tepuipappus* species and populations at lower elevations than known at present, perhaps once brought them into relatively close contact, where they could have hybridized. The species of *Tepuipappus*, while perhaps at some level immigrants to tepuis, nowhere seem common nor overly successful adapted to tepui summits. But quite naturally, if tepui summits are the only available open sunny regional habitats, then sunflowers (helianthoids) may perhaps occur there, whether well-adapted or not to high elevations. There certainly are morphologically mainstream species of *Tepuipappus*, whereas sometimes individual specimens of *T. kunhardtii* and *T. phelpsiae* display some noted morphological variation, on occasion exhibiting having fewer or more and shorter or longer pappus scales than typical. Perhaps such species are ill-suited to their habitats, or are simply pliable as far as expression of morphological traits that could affect seed dispersibility.

Tepuipappus is characterized by its shrubby habit, usually opposite leaves, radiate capitula, narrowly tubular-funnelform glabrous disk corollas, which at the level of the stylopodium have only slight stylopodial bulges in their corolla tubes (Figs. 88, 90B), relatively narrow stylopodia, and quadrangular heteropappose cypselae (Figs. 87–88). The strange cypselae of *Tepuipappus* typically have 4–6 unequal pappus scales on the edges and margins, occasionally have intermediate scales or squamellae, have broad-based bodies, and have small weakly asymmetric carpopodia. It is also the very un-*Calea*-like disk corolla shape that technically further distinguishes *Tepuipappus* from the more ampliate disk-flowered *Calea*. Also similar to *Tepuipappus* are alternate-leaved Duida-endemic *Tyleropappus* Greenm. and the weak-stemmed equally pappose *Geissopappus* Benth. The biseriate glandular trichomes of *Tepuipappus* (Fig. 91) are mainstream, however, and resemble those of *Calea* and *Encelia*.

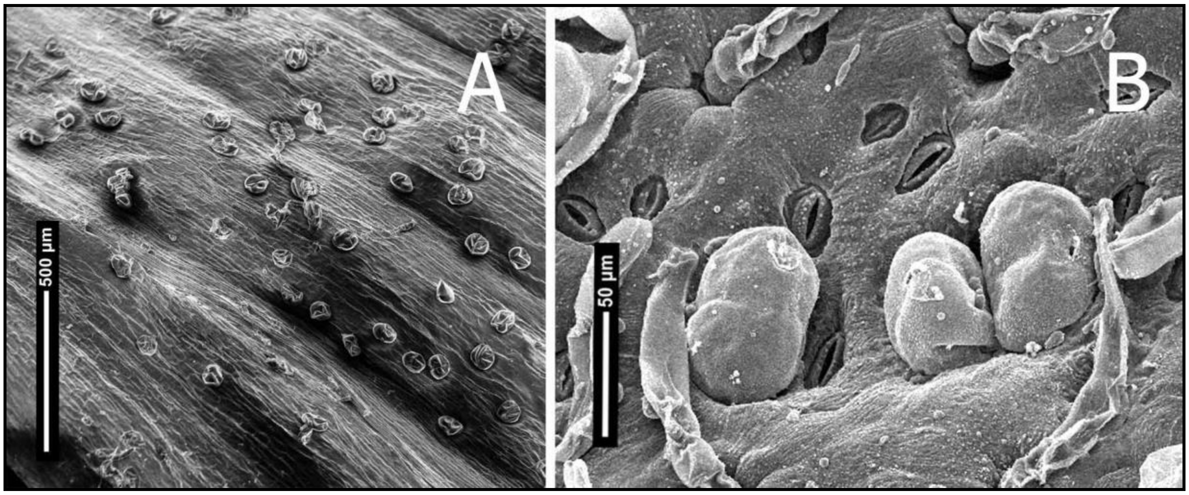


Figure 91. Secretory biseriate glandular trichomes of *Tepuipappus* Pruski. A. *Tepuipappus orbiculatus* (Maguire & Aristeg.) Pruski, ray corolla limb, abaxial surface. B. *Tepuipappus punctatus* (Maguire & Wurdack) Pruski, leaf blade, abaxial surface showing cross-septum of three glands, also showing collapsed elongate uniseriate trichomes, micrographed in 2001 by Gisela Sancho. (A *Holst & Liesner 3322*, MO; B *Maguire & Maguire 35067*, NY, paratype).

The whorled leaves occasionally seen in *Tepuipappus esposi* recalls similar variation in typically opposite-leaved *Chromolaena*, *Mikania*, *Aspilia*, and *Wedelia*. These whorled leaves also recall *Calea heteropappa* and *C. semirii* of the *Calea myrtifolia* group (sensu Pruski 2005, both herein placed in *Meyeria*) as does the heteropappose nature of the species stressed in the key to regional *Calea* species by Pruski (1997). Pruski and Urbatsch (1988) characterized the heteropappose condition as having pappus elements uniseriate, irregularly fimbriate-lacerate, and unequal, and named *Calea heteropappa* Pruski & Urbatsch. Unequal pappus scales have also been noted elsewhere in *Calea* in a different species group by Barroso (1959–1961, 1986, albeit under *Brasilia sickii*, which Urbatsch et al. 1986 treated as *Calea sickii* within *Calea* sect. *Lemmatium*).

Another pappus term, double-pappus, has long-been used for the distinctly unequal distinct biseriate pappus seen in some tribe Astereae (e.g., Blake 1922), but perhaps the most striking and well-known examples of double pappus are in Vernonieae (Pruski and Sancho 2004: fig. 17; Mukherjee and Nordenstam 2008). In any event, the heteropappose condition in *Calea* was said by Bueno and Heiden (2022: 590) to be "exclusive of a few species belonging to the *C. myrtifolia* complex" although two decades earlier the heteropappose condition was a prime lead in the *Calea* key of Pruski (1997), and is known as well in *Calea* sect. *Lemmatium* (Figs. 46, 47A; see also Urbatsch et al. 1986). Two heteropappose species endemic to Mesoamerica (Pruski and Robinson 2018)—*Calea skutchii* S.F. Blake (generitype of *Squamopappus*) and *Calea standleyi* Steyerm. (now placed in *Podachaenium*)—and sometimes heteropappose *Tetrachyron* were removed from *Calea* in the late 1900s.

The Verbesininae are a subtribe of Heliantheae with a checkered past. Although Robinson (1981) recognized Ecliptinae as including *Verbesina* and Bremer (1994) recognized Verbesininae but treated *Eclipta* L. as incertae sedis, I follow Panero (2007), Pruski (2016), Turner (2016), and Pruski and Robinson (2018), who recognized each subtribe Ecliptinae and Verbesininae as distinct. Among previously described genera known to me, *Tepuipappus* seems to be more similar to three Mexican and Central American genera of Verbesininae, rather than to *Verbesina* itself. I place *Tepuipappus* next to *Podachaenium*, *Squamopappus*, and *Tetrachyron* (Figs. 16, 89), its apparent generic allies within Heliantheae subtr. Verbesininae. Each Panero (2007), Pruski (2016), Turner (2016), and Pruski and Robinson (2018) provided keys to the then-known four genera comprising subtribe

Verbesininae. The six species of *Tepuipappus* and most recognized species of *Podachaenium* (excepting *P. eminens*), *Squamopappus*, and *Tetrachyron* similarly were placed historically in *Calea* (Heliantheae s.l., now Neurolaeneae).

Among these five genera, *Tepuipappus* differs from *Calea* by its heteropappose quadrangular cypselae (Figs. 87–88) and by its narrowly tubular-funnelform disk corollas with only a small stylopodial bulge in the tube (Figs. 88B–C, 90B). Within subtribe Verbesininae, *Tepuipappus* differs by round-based cypselae (Fig. 88C) from each Mexico and Central American-centered *Podachaenium, Squamopappus,* and *Tetrachyron* that usually have stipitate-tapered cypsela bases (Figs. 16C, 89). The previously known genera of subtribe Verbesininae have biconvex or compressed cypselae, except for *Tetrachyron* which has quadrate cypselae as does *Tepuipappus*. *Tepuipappus* and *Tetrachyron* by their angled cypsela are thus similar to each other, perhaps more so than either of the two are to *Podachaenium* or *Squamopappus* (Fig. 89). The cypselae of *Tetrachyron* differ from those of *Tepuipappus* by being long-stipitate (vs. round-based), and typically subequally pappose only on the angles (Fig. 16C–D). The typical element of *Podachaenium* is characterized by having two equally long radial pappus bristles (Fig. 89A–B), in this regard recalling *Verbesina*, but *Podachaenium* often also has intermediate shorter fragile squamellae, unlike *Verbesina*. Each of the five non typical species of *Podachaenium* seem more closely allied to each other by their cuneate-based cypselae rather than to the generitype, *P. eminens* (Pruski 2016), which has long tapered cypselae bases (Fig. 89A–B). On occasion, the cypsela characters of the five non-typical species of *Podachaenium* (viz Pruski 2016: Fig. 9C–D) seem superficially *Tepuipappus*-*Tetrachyron*-like, but all of the six species of *Podachaenium* are consistently white ray-flowered, thereby at a glance distinct from *Squamopappus*, *Tepuipappus*, and *Tetrachyron*. *Squamopappus* does have a resemblance to *Tepuipappus* by its dimorphic pappus, but in addition to its long-stipitate biconvex (vs. quadrate) cypselae, *Squamopappus* differs from the typical elements of *Tepuipappus* by its involucre with moderately graduated phyllaries, the outer series are which are mostly stiff-scarious and subherbaceous only distally.

It deserves mention that similar-in-gestalt *C. venosa* Pruski from Cerro Coro-Coro is not a *Tepuipappus*, and I agree with Pruski (2011) that the affinities of *C. venosa* are likely with *Calea lucida* Maguire & Wurdack that was described from Ilú tepui in Bolívar, Venezuela. *Calea politii* Maguire was described from a unicate holotype collected on Cerro Sipapo, and as having herbage granular-arachnoid and 10–12 pappus scales 2–3.5 mm long. Because of the character of slightly unequal pappus scales, I believe I was mistaken when I aligned (Pruski 1997) *C. politii* with members of section "*Tepuiopappus* Pruski & Maguire" (viz Amer. J. Bot. 76-6: 278. 1989, nom. inval.). However, I now agree with Maguire's protologue in Maguire and Wurdack (1957) that *C. politii* "is not immediately related to *Calea kunhardtii*." Instead, the outer phyllaries in *C. politii* are 5-nerved, subglabrous, and elliptic, recalling those of *C. nana* Maguire, also described from Cerro Sipapo. *Calea nana* is now known from both Cerro Cuao and Cerro Sipapo, there sympatric with *T. kunhardtii*, but *C. nana* has long-tubed ampliate disk corollas, asymmetric carpopodia, oblong-prismatic cypselae, and pappus scales typical of *Calea*, where it is maintained. The six species I place in *Tepuipappus* are as follows.

TEPUIPAPPUS CAMANI (Maguire & K.D. Phelps) Pruski, **comb. nov**. *Calea camani* Maguire & K.D. Phelps, Bol. Soc. Venez. Ci. Nat. 14: 16. 1951–1952 (Bot. Exped. Phelps Guayana Ven. 12. 1951; the full journal version of the volume is dated 1951 on page 1, but the cover is dated 1952; it is not clear to me whether the repaginated separate in hand is a preprint or a reprint, and consequently which version was the first to be distributed). **TYPE: VENEZUELA. Amazonas.** Cerro Camani, occasional in exposed rocky places on cumbre, 1800 m (erroneously as 2200 m), 17 Feb 1951, *Maguire, Phelps, Hitchcock & Budowski 31829* (holotype: NY; isotypes: US, VEN). Figures 88B–C, 90A.

Distribution and ecology. *Tepuipappus camani* (Maguire & K.D. Phelps) Pruski is endemic to the tepui summit of Cerro Camani in northern Amazonas, Venezuela (Fig. 86), where it has been collected at about 1800 meters elevation. *Tepuipappus camani* is the generitype of *Tepuipappus,* and the species occurring nearest to the distributional epicenter of the genus.

Tepuipappus camani, its epithet a noun in apposition, remains known only from the type collection. Huber and Wurdack (1984) and Huber (1990) reported that the only expedition to the summit of Cerro Camani was that of Maguire and Phelps in 1951. In 1979, Otto Huber collected at the base and lower slopes of Cerro Camani, and apparently did not recollect *T. camani*. The holotype of *T. camani* has mature quadrangular heteropappose cypselae (Fig. TEPUI 3C), and it is because of this, as well as its centric distribution, the name is designated as the generitype of *Tepuipappus*.

Tepuipappus camani is characterized by its peduncles that are densely tomentose and by tomentose subfoliaceous outer phyllaries. The species has obovate-orbicular obtuse-based leaf blades with arching pinnate-venation and its margins are serrate-dentate. The leaf blades are prominent-reticulate even when viewed abaxially, and the abaxial surfaces are abaxially densely tomentose. In addition to the un-*Calea*-like pinnate leaf venation and its strange cypsela characters, the crenulate-undulate-margined reticulate-veined outer phyllaries are noteworthy. In the phyllaries, the veins are less pubescent than the areoles, hence the visible reticulations, and this is basically similar to the vein-areole pubescence differences seen in the leaves. The leaf blades are seemingly glandular-punctate adaxially, but not clearly so, and it seems possible that the plants were pressed in EtOH. The sometimes-lobed ray corolla limbs seen in *T. camani* are odd, perhaps just quirks rather than what B.L. Robinson called "disconcerting exceptions," and have been seen on occasion elsewhere in well-collected plants such as *Calea lucidivenia* and *Calea peruviana*, or in well-studied plants such as *Calea venosa* and *Bishopanthus werffii* Pruski and R. Ortiz (Pruski et al. 2019: fig. 7A).

TEPUIPAPPUS ESPOSI (Maguire & K.D. Phelps) Pruski, **comb. nov**. *Calea esposi* Maguire & K.D. Phelps, Bol. Soc. Venez. Ci. Nat. 14: 16. 1951–1952 (Bot. Exped. Phelps Guayana Ven. 12. 1951; the full journal version of the volume is dated 1951 on page 1, but the cover is dated 1952; it is not clear to me whether the repaginated separate in hand is a preprint or a reprint, and consequently which version was the first to be distributed). **TYPE: VENEZUELA. Amazonas**. Summit of Cerro Guanay, open rock habitats, 2000 m, 3 Jan 1951, *Maguire, Phelps, Hitchcock & Budowski 31700* (holotype: NY; isotypes: US, VEN). The species was dedicated by Kathleen Phelps to her husband, ornithologist William H. Phelps, Jr.; *espos* is treated as Latinized and thus the genitive termination with a single "i" is used (see Stern 1983: 296), as explained to me by Jose Cuatrecasas about this particular instance, as well as for his use of the genitive in *Schistocarpha sinforosi* Cuatr. Figure 92A.

Distribution and ecology. *Tepuipappus esposi* (Maguire & K.D. Phelps) Pruski is endemic to the tepui summit of Cerro Guanay in northern Amazonas and northwards across the border into western Bolívar, Venezuela (Fig. 86), and it has been collected from about 1700–2000 meters elevation. Cerro Guanay is mostly in Edo. Bolívar, and it seems at least possible that the type locality is actually in Edo. Bolívar, albeit published by Maguire and Phelps (1951, 1951–1952) as Edo. Amazonas.

Tepuipappus esposi is characterized by its densely pannose-tomentose stems, densely tomentose peduncles, and densely pannose-tomentose leafy outer phyllaries. The species is seen to have persistently discolorous leaves with blade surfaces adaxially tomentulose-glabrescent but perhaps eglandular, and abaxially densely buff-pannose-tomentose. The leaf blades of *T. esposi* are ovate-orbicular, the margins crenate-dentate, and the venation is arching pinnate (Fig. 92A). *Tepuipappus esposi* is known only from four collections. *Tepuipappus esposi* recalls *T. camani*, but the leaves in *T. esposi* are smaller and much more tomentose. Three original collections were cited in the protologue, but Otto Huber visited the summit of Cerro Guanay three decades after the 1951 Maguire trip and recollected *T. esposi*. In 1995, Fabián Michelangeli collected on nearby lajas at 1150 meters elevation, but did not collect *Tepuipappus*. Huber and Wurdack (1984) and Huber (1990) listed the Maguire and Huber trips, but do not list any other visits to the summit of Cerro Guanay.

TEPUIPAPPUS KUNHARDTII (Maguire) Pruski, **comb. nov**. *Calea kunhardtii* Maguire, Mem. New York Bot. Gard. 8: 146. 1953. **TYPE: VENEZUELA. Amazonas.** Cerro Sipapo (Paráque), lower Caño Grande (label; in protologue as lower Caño Negro), 1400 m, 25 Dec 1948, *Maguire & Politi 27900* (holotype: NY; isotypes: US, VEN). Figure 92B.

Distribution and ecology. *Tepuipappus kunhardtii* **(**Maguire) Pruski is endemic to the relatively closely spaced tepui complex (Fig. 86) of Cerro Autana (Fig. 93B; Steyermark 1974: fig. 1; George 1988: 158; Huber 1995: plates 11, 16, 65), Cerro Cuao, and Cerro Sipapo (Huber 1995: plate 46) in northwestern Amazonas, Venezuela, where it has been collected from about 1230–2000 meters elevation.

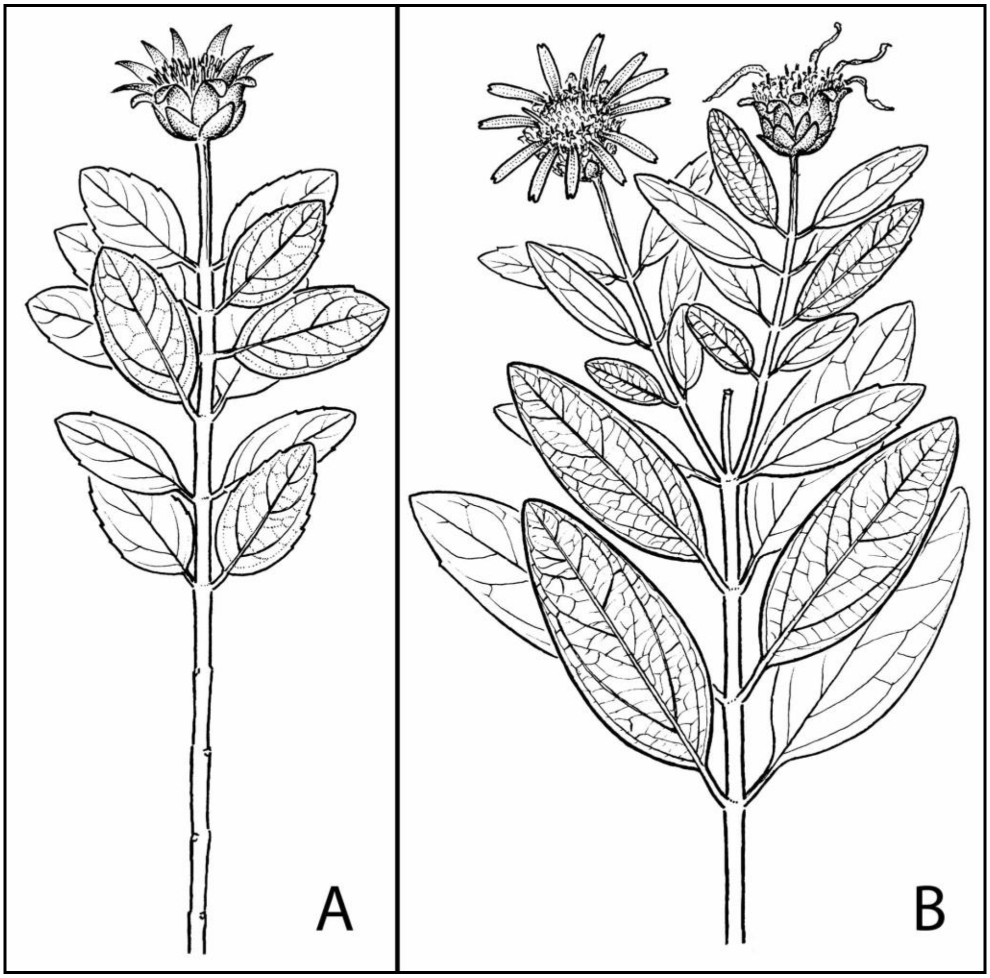


Figure 92. A. *Tepuipappus esposi* (Maguire & K.D. Phelps) Pruski, on occasion the leaves may be broader with more closely spaced prominent secondary veins directed outwards towards the more-deeply toothed margins. B. *Tepuipappus kunhardtii* (Maguire) Pruski, a weakly trinerved specimen. (Drawn by Bruno Manara, modified from Pruski 1997).

Figure 93. Select tepuis in the Venezuelan Guayana Highland. A. Clustered tepuis of the Chimantá Massif, view at about 1950 meters elevation from the summit of Acopán-tepui towards the 2400 meters elevation summit (center and background right) of neighboring Churi-tepui. B. Cerro Autana, an isolated tepui, albeit only a few kms from the Sipapo Massif proper, is one of the three summits in the Sipapo-Yutajé-Complex of the Duida Supergroup of tepuis on which *Tepuipappus kunhardtii* (Maguire) Pruski occurs. (A photograph by the writer, B from Inparques.gob.ve, the Instituto Nacional de Parques).

Tepuipappus kunhardtii is known from at least eleven collections. It seems to be the only moderately well-collected species of the genus, having been collected at least six times after description. The Fernández and the Sanoja collections are from Cerro Cuao, and were made on the same day at the same elevation. *Steyermark 105116* (cited by Steyermark 1975) is from the spectacular isolated Cerro Autana (Fig. 93B), merely 18 kms from Cerro Sipapo (Steyermark 1974). This collection was made from 1230–1240 meters, and the maximum elevation of Cerro Autana is about 1300 meters, making this plateau elevationally on the low-end of the tepuis on which *Tepuipappus* is known.

Tepuipappus kunhardtii is characterized by its densely pubescent peduncles, tomentose foliar outer phyllaries, and leaves that are usually trinerved from above the base with major veins prominent adaxially (Fig. 92B). Also characteristic of the species are its elliptic leaf blades that are abaxially densely tomentose and margins that are serrulate to nearly entire. The leaves are short-petiolate, but are as distinctly petiolate as known in the genus, i.e., as distinctly petiolate as in *T. punctatus*. The leaf blade adaxial surface is seemingly glabrous, but in the herbarium specimens in front of me is dried as though densely minute-punctate, this perhaps merely reflecting that the areolae collapse whereas the finest veinlet reticulations do not. The pappus lengths of the examined collections of *T. kunhardtii* (as also noted in *T. phelpsiae*) display more variation that seen in most other species of *Tepuipappus.*

TEPUIPAPPUS ORBICULATUS (Maguire & Aristeg.) Pruski, **comb. nov**. *Calea orbiculata* Maguire & Aristeg., Mem. New York Bot. Gard. 9: 372. 1957. **TYPE: VENEZUELA. Amazonas.** Cerro Yutajé, left fork Cano Yutajé, scrub savanna in rocky places, 1350 m, 12 Feb 1953, *Maguire & Maguire 35197* (holotype: NY; isotype: VEN). Figures 88A, 90B, 91A, 94A.

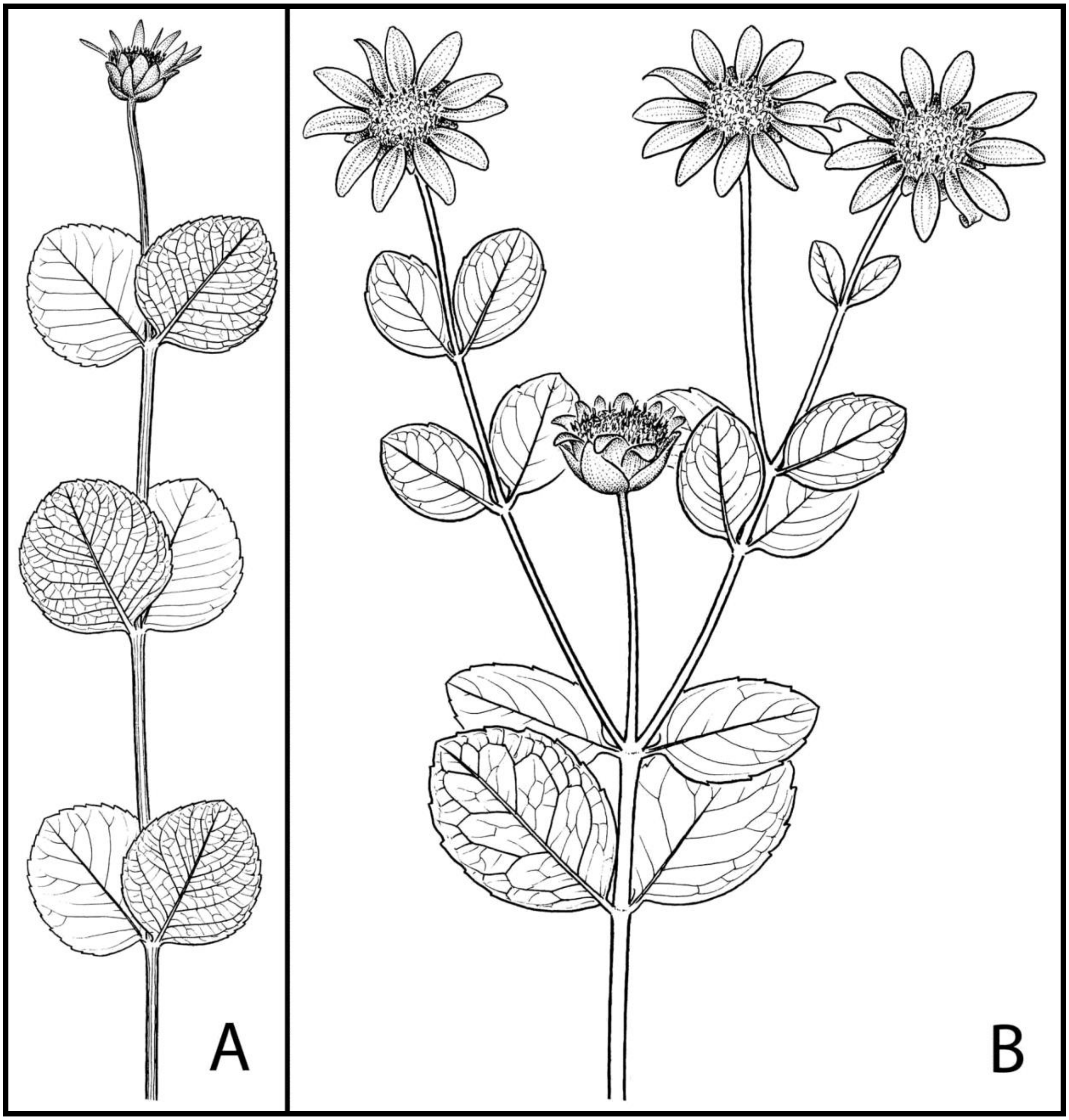


Figure 94. A. *Tepuipappus orbiculatus* (Maguire & Aristeg.) Pruski. B. *Tepuipappus phelpsiae* (Lasser & Maguire) Pruski. These two species are close congeners and are from adjacent tepuis. They are recognized here as distinct, their respective holotypes seem to be at opposite ends of the morphological spectrum, but the few newer collections sometimes seem intermediate between the two species. (Drawn by Bruno Manara, modified from Pruski 1997).

Distribution and ecology. *Tepuipappus orbiculatus* (Maguire & Aristeg.) Pruski is endemic to tepuis in northern Amazonas Venezuela, where it has been collected on adjacent Cerro Coro Coro and Cerro Yutajé (Fig. 86), the two protologue localities, from about 1200–1800 meters elevation. *Tepuipappus orbiculatus* is known from about a half dozen collections, three cited in the protologue, while the others collections are more recent, dating from 1987–1988.

Tepuipappus orbiculatus is characterized by its capitula subtended by weakly pubescent indurate subherbaceous cucullate-navicular outer few phyllaries, as are those of the similar and earlier

T. phelpsiae, which is known from a neighboring tepui. The never tomentose subglabrous leaves of *T. orbiculatus* are subsessile, vs. very short-petiolate in the otherwise similar *T. phelpsiae*. The 7–10 major lateral veins per side of the leaf blade midrib are spreading-pinnate-disposed being somewhat directed outward and closely spaced. The orbicular leaf blades of *T. orbiculatus* have weakly toothed margins, are eglandular adaxially, abaxially glandular, and otherwise subglabrous or proximally weakly tomentulose-glabrescent. It is obvious that *T. orbiculatus* and *T. phelpsiae* are very similar, as noted in the protologue of *T. orbiculatus* that gave it as "most closely related" to *T. phelpsiae*. Indeed, one paratype of *T. orbiculatus* was distributed as *Calea phelpsiae*, which was collected six years earlier and described seven years earlier than was *T. orbiculatus*.

Figure 95. *Tepuipappus phelpsiae* (Lasser & Maguire) Pruski showing exserted yellow ray corolla limbs and the arching-pinnate leaf blade venation, with the principal secondaries fewer and slightly more well-spaced than in otherwise very similar *T. orbiculatus*. (*Huber 11860*, unmounted duplicate).

TEPUIPAPPUS PHELPSIAE (Lasser & Maguire) Pruski, **comb. nov**. *Calea phelpsiae* Lasser & Maguire, Brittonia 7: 87. 1950. **TYPE: VENEZUELA. Amazonas.** Cerro Yaví, 2200–2300 m, 1–3 Mar 1947, *Phelps & Hitchcock 56* (holotype: NY; isotypes: US, VEN). The species was dedicated to the collector, Kathleen Phelps, a photograph of whom at the type locality on the Yaví summit camp was published by Hitchcock (1947: fig. 29). *Tepuipappus phelpsiae* was the first collected species of *Tepuipappus*, and was the first described species of *Tepuipappus*. *Tepuipappus esposi* along with *T. phelpsiae* are the first pair of closely related species in *Calea* (each now treated within *Tepuipappus*) described for a husband and wife. Figures 94B, 95.

Distribution and ecology. *Tepuipappus phelpsiae* (Lasser & Maguire) Pruski is endemic to the tepui summit of Cerro Yaví in northern Amazonas, Venezuela (Fig. 86), and has been collected from about 2100–2300 meters elevation.

Tepuipappus phelpsiae is characterized by its capitula being subtended by weakly pubescent indurate subherbaceous cucullate-navicular outer few phyllaries, recalling those of *T. orbiculatus*. The never tomentose leaves of *T. phelpsiae* are moderately reticulate-veined and distinctly very short-petiolate, vs. subsessile in its closest congener *T. orbiculatus*. The 7–8 major lateral veins per side of the leaf blade midrib are arching-pinnate-disposed, and seem to be more well-spaced and more apically directed than in the very similar *T. orbiculata*. *Tepuipappus phelpsiae* has elliptic to suborbicular leaf blades with weakly toothed margins. The leaf blades of *T. phelpsiae* are eglandular adaxially, whereas abaxially they are glandular and otherwise subglabrous or proximally weakly tomentulose-glabrescent. *Tepuipappus phelpsiae* may have several pappus scales that are elongate and longer than the cypselae. *Tepuipappus phelpsiae* was described from a single collection, but is now known to have been recollected at least once. The newer material seen by me is a topotype collected by Otto Huber in 1986. Huber and Wurdack (1984) and Huber (1990) listed the Phelps and Huber trips, but do not list any other visits to the summit of Cerro Yaví. Material of *Maguire & Maguire 35067* and *Maguire & Maguire 35448* were distributed as *Calea phelpsiae*, but are paratypes of *T. punctatus* and *T. orbiculatus*, respectively. *Tepuipappus phelpsiae* was the first described species of *Tepuipappus*, and is the name having priority, were *T. orbiculatus* be taken as conspecific with *T. phelpsiae.*

TEPUIPAPPUS PUNCTATUS (Maguire & Wurdack) Pruski, **comb. nov**. *Calea punctata* Maguire & Wurdack, Mem. New York Bot. Gard. 9: 373. 1957. **TYPE: VENEZUELA. Amazonas.** Cerro Yutajé, left fork Cano Yutajé, below south rim, scrub savanna, frequent on rocky places and in thickets, 1350 m, 12 Feb 1953, *Maguire & Maguire 35196* (holotype: NY; isotypes: F, GH, K, NY, S, US, VEN). The type number and that of *T. orbiculatus* are adjacent collection numbers from the same locality and day. Figures 87, 91B.

Distribution and ecology. *Tepuipappus punctatus* (Maguire & Wurdack) Pruski is endemic to savannas and scrub vegetation of Cerro Yutajé in northern Amazonas, Venezuela (Fig. 86), where it has been collected from about 1250–1600 meters elevation. Huber et al. (2018) gave the summit of Cerro Yutajé as more than 2100 meters elevation, but I know of no collections of *T. punctatus* made above 1600 meters elevation.

Tepuipappus punctatus remains known only from the four collections cited in the protologue, and apparently has never been recollected. *Tepuipappus punctatus* is characterized by its broad, plinerved to nearly trinerved from base, strongly reticulate-veined round-tipped leaves having crenate margins. The leaves are densely glandular on each surface, otherwise the adaxial surface is weakly hirtellous and the abaxial surface sparsely and laxly appressed sericeous. The outer phyllaries are foliar-herbaceous, subglabrous, and few-crenate margined.

7. TONALANTHUS Brandegee, Univ. Calif. Publ. Bot. 6: 75. 1914. **TYPE:** *Tonalanthus aurantiacus* Brandeg. [= *Tonalanthus megacephalus* (B.L. Rob. & Greenm.) Pruski].

Simple-stemmed perennial herbs, mostly simple-scapose but occasionally flowering from distal node, < 1 m tall, stems leafy basally or only proximally in 4–6(–9) usually closely spaced internodes, occasionally leafy to mid-stem, stems dying back to the soil; stems large-leaved, leafy basally or only proximally, occasionally leafy to mid-stem, erect, striate-sulcate and angulate, white-hirsute-pilose. **Leaves** simple, opposite, wing-based, subpetiolate; blade 5–12 × 1.5–9 cm above middle of the pseudopetiole, (elliptic-lanceolate-)deltate to rhombic-ovate, thin-chartaceous, prominently trinerved from basal acumination, surfaces eglandular, adaxial surface sparsely hirsute-scabridulous, abaxial surface hirsute-pilose to glabrate, trichomes multicellular with stout bases and elongate terminal cells, base cuneate to truncate then abruptly contracted and attenuate-decurrent onto pseudopetiole, sometimes with margins crenulate to coarsely crenate or sometimes irregularly dentate, apex of proximal leaves (acute-)obtuse to rounded grading to that of distal leaves acute; pseudopetiole usually about half as long as blade, nearly winged to base, the winged portion distally to 1+ cm diam., gradually narrowing proximally to ca. 0.2 cm diam. **Capitulescence** mostly terminal and monocephalous, sometimes also axillary from distal most nodes, capitula borne single on 1(–4) leafless peduncles; peduncles 16–55 cm long, hirsute-pilose to sparsely so proximally, trichomes 0.3–3 mm long. **Capitula** (12–)15–22 mm tall, radiate, the disk short-conical; involucre 12–20 mm diam., hemispherical; phyllaries 16–22, 3–4-seriate, subequal to weakly graduated, appressed, pluristriate, outer 2–6 phyllaries 7–17 × 3.5–4.5 mm, nearly as long as to about half as long as the inner, somewhat brownish-green herbaceous-tipped but becoming paler proximally, elliptic-ovate to oblong, hirsute-pilose, apex acute to rounded, inner phyllaries 11.5–20 × 4–5 mm, lanceolate-ovate, striate, stramineous but apex often purple-scarious, usually hirtellous or scabridulous, apex acute to rounded; clinanthium conical, paleate, to ca. 11 × 5 mm; paleae 6.5–10 × ca. 1 mm, lanceolate, conduplicate proximally, stramineous-yellowish, apex acuminate to attenuate, subentire to moderately or even sometimes deeply trifid. **Ray florets** 13–22, style well-exserted from tube; tube 5.5–8 mm, slender, glabrous, limb 8–15 × 4–6 mm, well-exserted, oblong, sometimes lateral tearing at base and appearing bilabiate, orange drying yellow, 11–13-nerved, all nerves equally thick, calyx nerves not prominent, adaxial surface papillose, apex unevenly lobed. **Disk florets** 35–60; corolla 9–11 mm long, narrowly funnelform, yellow or yellow-orange to sometimes reddish apically, glabrous, tube 3–4 mm long, throat longer than tube, lobes 2–3.5 mm long, triangular-lanceolate to lanceolate, erect; anthers not exserted, pale; style branches ascending and not strongly recurved, ca. 2.5 mm long, slender, sometimes long-papillose apically or abaxial-distally. **Cypselae** 4–5 mm long, when mature often nearly as long as the paleae, elongate-oblong, biconvex-compressed, carbonized, black or edges stramineous-indurate, the faces unevenly setose with short-broad twin trichomes with the pair of elongate terminal cells connate to near apex whereas adjacent trichomes may be underdeveloped and appearing as short-papillate but seeming instead are incipient twin trichomes; carpopodium strongly asymmetric, stramineous; pappus scales 12–20, 4.5–6 mm long, slightly longer than mature cypselae and reaching to about distal third of disk corolla throat, lanceolate, typically with midrib dark and thick especially proximally, margins and abaxial surface imbricate-scabridulous or fimbriate. $2n = 38$.

Tonalanthus Brandegee (Compositae tribe Neurolaeneae) is newly resurrected from synonymy of *Calea*, where it was treated by Wussow et al. (1985), Turner (2014), and Pruski and Robinson (2018). *Tonalanthus* is monotypic, and appears isolated among Mexican and Central American Compositae. *Tonalanthus megacephalus* was described by Robinson and Greenman (1896), who placed it within *Calea* subgen. *Leontophthalmum* (Willd.) Less., i.e., alongside nine South American species that Baker (1884) recognized within that subgenus and alongside five species Peruvian species that Bentham and Hooker (1873) recognized as *Calea* sect. *Leontophthalmum* (Willd.) DC. Pruski (1998) disassociated *Tonalanthus*, the five Peruvian species, and *Calea* subgen./sect. *Leontophthalmum* from those Brazilian-centered species (as did Lessing 1832), and placed the Brazilian-centered plants in *Calea* sect. *Monanthocalea* (Less.) Pruski, the latter recognized here as *Podocalea*.

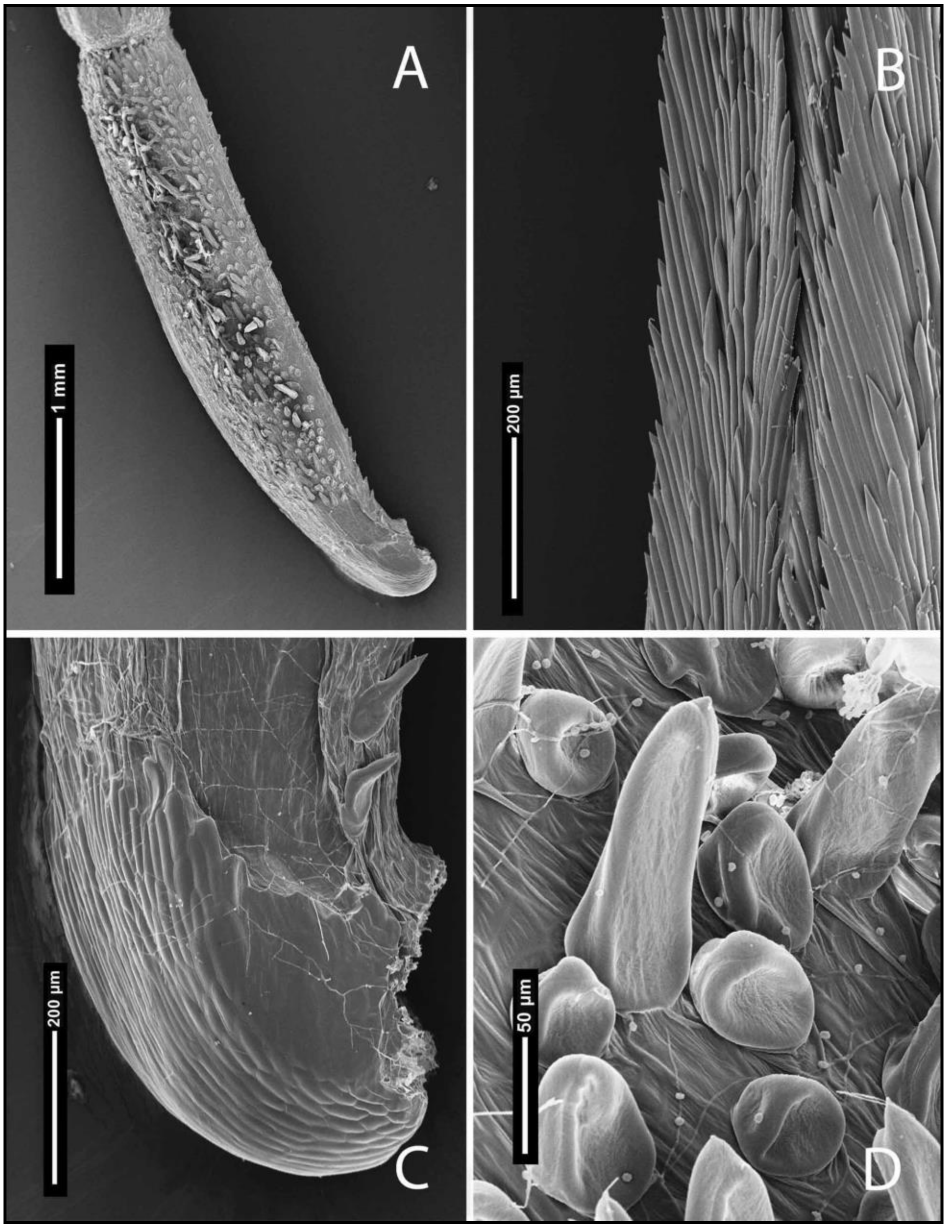


Figure 96. Select microcharacters features of cypselae in *Tonalanthus megacephalus* (B.L. Rob. & Greenm.) Pruski. A. Biconvex-compressed cypsela, side view showing unevenly developed adjacent broad twin trichomes, these differently elongated trichomes are structurally similar but their elongation expressed differentially, the short-papillose-appearing trichomes actually seem to be incipient twin trichomes; both extremes in trichome size as well as intermediate-sized ones are odd in that they often dry-collapse horizontally. B. Middle abaxial surface of two pappus scales. C. Carpopodium, strongly asymmetric. D. Unevenly developed adjacent twin trichomes of cypsela, these relatively short and broad trichomes with terminal cells connate nearly to apices are unevenly elongated over surface; adjacent twin trichomes in cypselae of *Calea* (viz Figs. 6, 7B, 12D) are more or less found at the same stage of development. (All from *Urbatsch & Wussow 3338*, MO).

Tonalanthus megacephalus (BL Rob. &
Greenm.) Pruski, comb. nov.
det. John Pruski (MO), 2015
MISSOURI BOTANICAL GARDEN HERBARIUM

Missouri Botanical Garden Herbarium 741807

7002

ISOTYPE OF:
Tonalanthus aurantiacus Brandegee
Univ. Calif. Publ. Bot. 6: 75. 1914.
ver. John Pruski (NY), 1991

gen. nov.
7002 PLANTÆ MEXICANÆ PURPUSIANÆ
CHIAPAS
Tonalanthus aurantiacus Brandg.
Sierra de Tonala
C. A. Purpus Sept. 1913

See
Brandegee in Univ. Calif. Pub.
Bot. 6: 75. 1914.

Place it temporarily
next to [illegible]

Figure 97. Generitype of *Tonalanthus* Brandegee; isotype of *Tonalanthus aurantiacus* Brandegee. [= *Tonalanthus megacephalus* (B.L. Rob. & Greenm.) Pruski]. (*Purpus 7002*, MO).

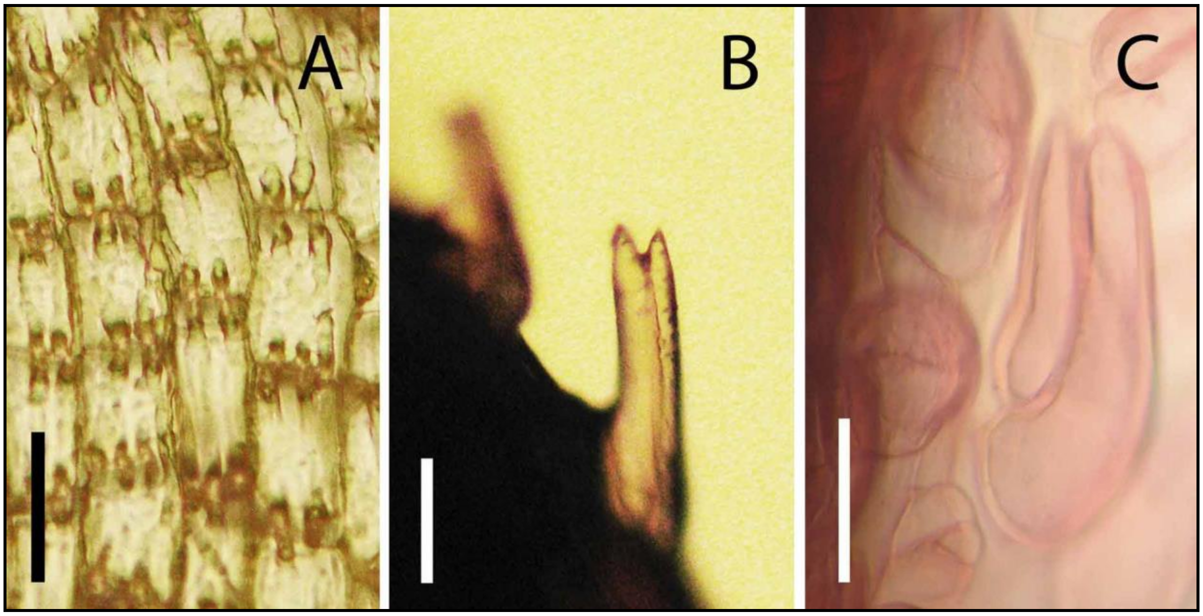


Figure 98. Select microcharacters of *Tonalanthus megacephalus* (B.L. Rob. & Greenm.) Pruski. A. Endothecial tissue, abaxial view, polarized as is typical of *Calea* Alliance genera and most helianthoids, with portions of the 2–3 longitudinal ribs per cell visible in upper right. B–C. Broad twin trichomes of cypselae showing nearly embedded basal pair of cells and pair of elongate terminal cells connate nearly to apices. (*Panero 4483*, NY). Scale bars A 30 µm, B–C 50 µm.

Strother (1983) was the first to report (as *x* = 19) the base chromosome number of *Tonalanthus*, this based on *Breedlove & Strother 46562*. Sundberg et al. (1986) and Wussow et al. (1985) each cited the base chromosome number of *Tonalanthus* as *x* = 19 and the type of then-undescribed synonymous *C. megacephala* var. *pachutlana* as *C. megacephala*. *Tonalanthus megacephalus* is one of the taxa in the GenBank (as *Calea*) aligned with *Neurolaena*, thus fixing its position as a member of tribe Neurolaeneae. Indeed, *Tonalanthus* albeit strange, remains a *Calea* Alliance as suggested by the combined features of opposite leaves (Fig. 97), paleate clinanthia, non-setose disk corollas with throats having a single reddish-orange resin duct (although unusually thin) superimposed over each of the five disk corolla throat veins, never-blackened anthers, polarized endothecial tissue (Fig. 98A), disk florets style branches although slender are with paired adaxial stigmatic lines and papillose distal-abaxial surfaces, free stylopodia, carbonized cypselae, and a radially symmetric pappus of many flat isomorphic usually subequal scales (Figs. 96B).

The cypselae of *Tonalanthus* are biconvex-compressed (Fig. 96A), unlike the subterete cypselae of *Calea* s. str. Each Wussow et al. (1985) and Pruski and Robinson (2018) described the cypselae of *Tonalanthus* as "densely strigose-hirsute as well as short-papillate." However, LM and SEM studies (Figs. 96, 98) appear to show only a single trichomes type on the cypselae of *Tonalanthus*. These trichomes appear to be structurally similar, however, their elongation is expressed differentially and this uneven development may be seen in adjacent twin trichomes (Figs. 96A, 96D, 98C). On any individual cypsela the trichomes appear to grade continuously in size from elongated (Figs. 96A, 98B–C) to the many that are short and papilloid-like (as described by Wussow et al. 1985; Pruski and Robinson 2018), the shorter ones being taken here as being incipient twin trichomes. This variously-sized cypselar indument of the single trichome type is very much more pronounced than ever seen in *Calea*, where only on occasion are some twin trichome size variations observed. Although these elongated trichomes in *Tonalanthus* are clearly twin trichomes—having a pair of longitudinally connate terminal cells (Fig. 98B–C)—they are broader than are twin trichomes of *Calea* s. str. Additionally, these unevenly developed broad twin trichomes of *Tonalanthus* often dry-collapse horizontally, a condition not observed in *Calea* s. str. The disk florets style branches of *Tonalanthus* are ascending and not strongly recurved, whereas *Calea* differs in its spreading to recurved disk style branches, a feature furthering the two genera from one another.

TONALANTHUS MEGACEPHALUS (B.L. Rob. & Greenm.) Pruski, **comb. nov.** *Calea megacephala* B.L. Rob. & Greenm., Proc. Amer. Acad. Arts 32: 21. 1896. **LECTOTYPE** (designated by Wussow et al., 1985): **MEXICO. Chiapas**. Tonalá, 1200–2500 ft, 10 Aug 1895, *Nelson 2884* (lectotype: GH-589116; isolectotypes: K, US-2). A second sheet in GH numbered 2884, but collected 18 Jul 1895 at Santa Efigenia, is better cited as 2844b. Figures 96–98.

Tonalanthus aurantiacus Brandegee, Univ. Calif. Publ. Bot. 6: 75. 1914. **TYPE: MEXICO. Chiapas.** Sierra de Tonalá, Sep 1913, *Purpus 7002* (holotype: UC; isotypes: F, GH, MO, NY, US).

Calea megacephala var. *pachutlana* B.L. Turner, Phytologia 90: 230. 2008. **TYPE: MEXICO. Oaxaca.** Distr. Pachutla, Mpio. Pluma Hidalgo, ca. 9 mi N of Pachutla, southern slopes of Cerro Espina, 23 Aug 1980, *Turner 80A-29* (holotype: TEX).

Distribution and ecology: *Tonalanthus megacephalus* (B.L. Rob. & Greenm.) Pruski is endemic to the Pacific watershed of Oaxaca and Chiapas in southern Mexico. The species was long-known only from Chiapas, but in the past few decades has been collected in immediately adjacent Oaxaca. *Tonalanthus megacephalus* is found mostly in pine-oak forests and seasonal evergreen forests from about 100–1100 meters elevation, and flowering occurs mostly between July and November.

Tonalanthus megacephalus was described by Robinson and Greenman (1896) as a member of the genus *Calea*. The fine account by Cockerell (1915) provided a more complete description of *T. megacephalus,* and also a figure of some of its distinguishing characters, including its conduplicate-broad paleae (Cockerell 1915: 71 fig. C as "disc bracts"). Only a year earlier, Brandegee (1914) described *Tonalanthus* based on *T. aurantiacus* Brandeg. (Fig. 98), which Rzedowski (1968) noted was conspecific with the plant then known as *C. megacephala*.

Turner (2008) described a second variety, but Pruski and Robinson (2018) reduced it to synonymy, not accepting leaf width ≤ 6 cm, peduncle lengths of ≤ 35 cm, or the shorter apical peduncular trichome lengths of ≤ 1 mm as distinguishing infrataxa. *Calea megacephala* var. *pachutlana*, however, is on average leafier stemmed than most Chiapan materials of *Tonalanthus megacephalus*, but proves to be synonymous. Turner (2008) suggested *T. megacephalus* was not conspecific with *Calea*, and although Pruski and Robinson (2018) retained the plant in *Calea*, *Tonalanthus* is formally reinstated here, requiring the single nomenclatural innovation that is proposed herein. In addition to its simple-stemmed herbaceous habit, distinct among Mesoamerican Caleas, monocephalous scapose capitulescence, orange ray corolla lobes, and slender ascending style branches, *Tonalanthus* differs from *Calea* s. str. by its biconvex-compressed cypselae with its strange compliment of broad twin trichomes, as discussed above.

ACKNOWLEDGEMENTS

Field work and herbarium studies in Mexico, Guatemala, Honduras, Costa Rica, Jamaica, Colombia, Venezuela, Peru, and Brazil were supported by the **Asociación Colombiana de Herbarios** (ACH), **CVG-EDELCA** (Venezuela), **National Science Foundation** (grant DEB78-04265), Julian Steyermark Fund, and Ghillean Prance coordinated **Projeto Flora Amazônica**. I would like to acknowledge the kind help received from the late Victor Badillo, Rupert Barneby, Graziela Barroso, Dairon Cárdenas, Arthur Cronquist, Jose Cuatrecasas, Santiago Díaz P., George Eiten, Gert

Hatschbach, Bernard Lowy, Bassett Maguire, Harold Robinson, João Semir, Phil Silverstone, and Julian Steyermark. Hamilton Beltrán, Gina Castillo, Otto Huber, Guy Nesom, Rosa Ortiz, Carlos Parra, Marcos Rios, Rocío Rojas, Basil Stergios, Shirley Tucker, Lowell Urbatsch, Rodolfo Vásquez, and Jorge Vélez are thanked for much help, sometimes commenting on parts of the manuscript. Funding from the Julian Steyermark Fund enabled me to study collections at F, GH, and TEX during the two decades I worked at NY and US. Mike Blomberg, Donald Black, Andrew Colligan, Susan B. Hunter, Stephanie Keil, and Daniel Tarazona are thanked for taking some or working on some of the specimen images included here, and Christine Niezgoda (F) is thanked for permission to reproduce the Macbride phototypes. Bobbi Angell, Kristin Malin, Bruno Manara, Gisela Sancho, Alice Tangerini, and Amy Zlotsky kindly provided their fine drawings used here. Gisela Sancho is thanked for use of her SEM micrograph of *Tepuipappus punctatus*. Mauricio Bonifacino, Gina Castillo, Daniel Díaz, George Eiten, Benoît Loeuille, Olga Martha Montiel, Mike Nee, Rosa Ortiz, Jose Pirani, and Lowell Urbatsch are thanked for sending me their field photographs used here. The plates were composed by the writer.

LITERATURE CITED

Aguilera, P.M., J.R. Daviña, and A.I. Honfi. 2012. Asteraceae. Pg. 889, in K. Marhold (ed.), APT/IOPB chromosome data 13. Taxon 61: 889–902.

Amaral, P.D.A., F.V. Costa, A.R. Antunes, J. Kautz, V. Citadini-Zanette, F. Lohézic-Le Dévéhat, J. Barlow, and S. DalBó. 2017. The genus *Calea* L.: A review of isolated compounds and biological activities. J. Med. Pl. Res. 11: 518–537.

Appezzato-da-Glória, B., G. Curry, M.K.M. Soares, R. Rocha, and A.H. Hayashi. 2008. Underground systems of Asteraceae species from the Brazilian cerrado. J. Torrey Bot. Soc. 135: 103–113.

Arbeláez, M.V. and R. Callejas. 1999. Florula de la meseta de arenisca de la comunidad de Monochoa (Región de Araracuara, Medio Caquetá). Florula of the sandstone plateau of the community of Monochoa (Araracuara region, middle Caquetá basin). Tropenbos, Bogotá.

Arechavaleta, J. 1907–1908. Flora Uruguaya, Tomo III. Compositae. Anales Mus. Nac. Montevideo 6, Entrega 2: 85–228, Entrega 3: 229–481.

Aristeguieta, L. 1964. Compositae. Pp. 1–941, in T. Lasser (ed.). Flora de Venezuela, vol. 10. Instituto Botánico, Ministerio de Agricultura y Cri, Caracas.

Badillo, V.M. 1994 [1995]. Enumeración de las Compuestas (Asteraceae) de Venezuela. Revista Fac. Agron. (Maracay) 45: 1–191.

Baillon, H.E. 1886 [1882]. Composées. Asteraceae. Histoire des Plantes 8: 1–316. Libraire Hachette & Co., Paris.

Baker, J.G. 1884. Compositae IV. Helianthoideae, Helenioideae, Anthemideae, Senecionideae, Cynaroideae, Ligulatae, Mutisiaceae. Pp. 135–442, t. 45–108, in C.F.P. de Martius and A.G. Eichler (eds.). Flora Brasiliensis, vol. 6(3) (fasc. XCIII). Fleischer, Monachii, Lipsiae.
[The part numbers need to be cited as each part begins on a page 1; the two columns on each page are numbered on the top in the running header, odd-numbered pages are flush-left and even-numbered pages are flush-right; the columns numbers are to be cited basically as though there are pages numbers. The new species described therein are cited by me as "Baker, in Martius, Fl. Bras."; although (1) Jackson (1893: 382–383) used "Baker, in Mart. Fl. Bras." and the t.p. of the individual parts is "Martii Flora Brasiliensis," (2) Martius died in 1868 and Baker's 1884 editors are Martius and Eichler, and (3) "Martius, Herbarium Florae Brasiliensis" exsiccatae series in Flora, and also as a repaginated book, is bibliographically similar].

Barbosa-Silva, R.G., P.H. Labiak, A.D.S.B. Gil, R. Goldenberg, F.A. Michelangeli, G. Martinelli, M.A.N. Coelho, D.C. Zappi, and R.C. Forzza. 2016. Over the hills and far away: new plant records for the Guayana Shield in Brazil. Brittonia 68: 397–408.

Barona-Colmenares, A., J. Contreras H., D. Cárdenas L., and C. Vriesendorp. 2018. Appendix 3. Plantas vasculares / Vascular plants. Pp. 198–210, in C. Vriesendorp et al. (eds.). Colombia: La Lindosa, Capricho, Cerritos. Rapid Inventories 29. Field Museum, Chicago.

Barroso, G.M. 1959–1961 [1962–1963]. Um novo gênero de Compositae. Arch. Jard. Bot. Rio de Janeiro 17: 19–20. [Neither the printed date of this (new genus *Brasilia* G.M. Barroso) publication nor its effective date of publication is clear to me; each page of this Barroso paper, 19 and 20, is unnumbered, but page numbers are inferred from numbered pages in preceding and following papers; the TOC gives this two page Barroso paper as beginning on page 19; the title page of Arch. Jard. Bot. Rio de Janeiro volume 17 has the printed date of 1959–1961; ING gives *Brasilia* G.M. Barroso as 1962, whereas the Gray Cards and the bound Gray Herbarium Index vol. 2 (Atro–Chad): 281. 1968 dated the Barroso genus as 1963; ING gives (incorrectly so) the journal as "Arq. Inst. Biol. Veg.," which seems only to have four volumes published, those from 1934–1938, during the decade-long hiatus between Arch. Jard. Bot. Rio de Janeiro volume 6 (1933) and volume 7 (1947)].

Barroso, G.M. 1986. Sistemática de Angiospermas do Brasil 3: v + 1–326. Univ. Federal de Viçosa. Viçosa, Brazil.

Basualdo, I. and N. Soria. 2002. 100 especies del cerrado en Paraguay. Departamento de Botánica, FCQ-UNA, San Lorenzo.

Begley, S. 1984. Journey to a lost world: new life is found on the "Mountain of the Mists." Newsweek 16 April 1984: 97–98.

Bentham, G. 1838–1839. Enumeration of plants collected by Mr. Schomburgk, British Guiana. Ann. Nat. Hist. 2: 105–111, 441–451.

Bentham, G. 1840. Enumeration of plants collected by Mr. Schomburgk, British Guiana. J. Bot. (Hook.) 2: 38–103.

Bentham, G. and J.D. Hooker. 1873. Compositae. Genera Plantarum 2: 163–533. Reeve, London.

Blake, S.F. 1922. Key to the genus *Diplostephium*, with descriptions of new species. Contr. U.S. Natl. Herb. 24: 65–86.

Blake, S.F. 1930. Notes on certain type specimens of American Asteraceae in European herbaria. Contr. U.S. Natl. Herb. 26: 227–263.

Blonston, G. 1985. Mountain of the mists. Science 85 (July/August): 61–69.

Bonilla, A., J.A. Franco V., T. Cramer, J. De Grave, S. Nachtergaele, N. Cogné, and A. Piraquive. 2023. The NW Amazonian Craton in Guainía and Vaupés departments, Colombia: Evidence of a Mesoproterozoic thermal event from apatite LA-ICP-MS U-Pb geochronology and its relation to continental rifting. Precambr. Res 395(107148): 1–15.

Brandegee, T.S. 1914. Plantas Mexicanas Purpusianae, VI. Univ. Calif. Publ. Bot. 6: 51–77.

Bremer, K. 1994. Asteraceae: Cladistics and Classification. Timber Press, Portland.

Brewer-Carías, C. 1987. The lost world of Venezuela and its vegetation. [Text written mostly by Julian Steyermark though not credited to him; English translation by Francois Beun and Elizabeth Tylor of Vegetacíon del mundo perdido]. Brewer-Carías, Caracas.

Brewer-Carías, C. (ed.). 1988. Cerro de la Neblina: resultados de la expedición 1983–1987. Fundación para el Desarrollo de las Ciencias Físicas Matemáticas y Naturales, Caracas.

Brewer-Carías, C. and J.A. Steyermark. 1976. Simas de Sarisariñama y su vegetación. Sociedad Venezolana de Ciencias Naturales, Caracas.

Bringel, J.B.d.A., Jr. and T.B. Cavalcanti. 2009. Heliantheae Asteraceae) na bacia do rio Paranã (Goiás, Tocantins), Brasil. Rodriguésia 60: 551–580.

Britton, N.L. 1916. Studies of West Indian plants–VIII. Bull. Torrey Bot. Club. 43: 441–469.

Brown, N.E. 1901. Report on two botanical collections made by Messrs. F.V. McConnell and J.J. Quelch at Mount Roraima in British Guiana. Trans Linn. Soc. London, n.s., 6: 1–107 + plates 1–14.

Brown, R. 1817 [1818]. Some observations on the natural family of plants called Compositae. Trans. Linn. Soc. London 12: 76–142.

Bueno, V.R. and G. Heiden. 2022. *Calea sessilifolia* (Asteraceae, Neurolaeneae), a new species from the Diamantina plateau, Minas Gerais, Brazil. Syst. Bot. 47: 586–592.

Bueno, V.R., M.R. Gostel, and G. Heiden. 2021. *Calea repanda* (Asteraceae: Neurolaeneae), a new species and novel characters for the taxonomy of the genus. Phytotaxa 544: 280–288.

Cabrera, A.L. 1937. Compuestas argentinas nuevas e interesantes. Notas Mus. La Plata, Bot. 2(16): 171–204.

Cabrera, A.L. 1974. Compositae, Compuestas. Flora Ilustrada de Entre Ríos (Argentina) 6(6): 106–538. Instituto Nacional de Tecnología Agropecuaria, Buenos Aires.

Camilotti, J.G., C.C. Biu, P.V. Farago, V.L.P. Santos, C.R.C. Franco, and J.M. Budel. 2014. Anatomical characters of leave [sic, i.e., leaf] and stem of *Calea serrata* Less., Asteraceae. Braz. Arch. Biol. Technol. 57: 867–873.

Candolle, A.P. de. 1836. Compositae (Compositarum Tribus Priodes). Prodromus Systematis Naturalis Regni Vegetabilis, vol. 5. Treuttel et Würtz, Paris.

Cárdenas L., D., N. Castaño A., M. Zubieta V., and M. Jaramillo E. 2008. Flora de las formaciones rocosas de la Serranía de La Lindosa. SINCHI, Bogotá.

Cariaga, K.A., J.F. Pruski, R. Oviedo, A.A. Anderberg, C.E. Lewis, and J. Francisco-Ortega. 2008. Phylogeny and systematic position of *Feddea* (Asteraceae: Feddeeae): a taxonomically enigmatic and critically endangered genus endemic to Cuba. Syst. Bot. 33: 193–202.

Cockerell, T.D.A. 1915. The Helianthoid genus *Tonalanthus*. Torreya 15: 70–71.

Coleman, J.R. 1968. Chromosome numbers in some Brazilian Compositae. Rhodora 70: 228–240.

Conover, A. 1987. Expedition to a 'lost' world. Internatl. Wildlife 17(3): 38–43.

Correa Q., J.E. and H. Bernal. 1992. Especies vegetales promisorias de los países del Convenio Andrés Bello Tomo VII. Guadalupe Ltda., Bogota, Colombia.

Cortés-B., R., P. Franco-R., and J.O. Rangel-C. 1998. La flora vascular de la Sierra de Chiribiquete, Colombia. Caldasia 20: 103–141.

Davis, C.S., A.C. Roosevelt, W. Barnett, and J.P. Brown. 2017. Paleoindian solar and stellar pictographic trail in the Monte Alegre hills of Brazil: Implications for Pioneering New Landscapes. J. Anthr. Arch. 5: 1–17.

De Granville, J.-J. 1991. Remarks on the montane flora and vegetation types of the Guianas. Willdenowia, bd. 21: 201–213.

Delessert, B. 1839. Icones Selectae Plantarum, vol. 4. Fortin, Masson & Sociorum, Paris.

Dempewolf, H., L.H. Rieseberg, and Q.C. Cronk. 2008. Crop domestication in the Compositae: A family-wide trait assessment. Genet. Resour. Crop Evol. 55: 1141–1157.

Díaz, J.L. 1979. Ethnopharmacology and taxonomy of Mexican psychodysleptic plants. J. Psychedelic Drugs 11: 71–101.

Dietrich, D. 1847. Synopsis Plantarum, vol. 4. Voigtii, Vimariae.

Doyle, A.C. 1912. The Lost World. Hodder & Stoughton, London.

Dwyer, J.D. 1955. The botanical catalogues of Auguste de St. Hilaire. Ann. Missouri Bot. Gard. 42: 153–170 + pl. 17–19.

Ehleringer, J.R. and C.S. Cook. 1987. Leaf hairs in *Encelia* (Asteraceae). Amer. J. Bot. 74: 1532–1540.

Eiten, G. 1972. The cerrado vegetation of Brazil. Bot. Rev. 38: 201–341.

Ek, R.C. 1990. Index of Guyana plant collectors. Flora of the Guianas, suppl. ser., fasc. 2: 1–97.

Emboden, W. 1979. Narcotic plants. Revised and enlarged. Macmillan, New York.

Endlicher, S. 1836–1840. Genera plantarum secundum ordines naturales disposita. Beck, Vindobonae.

Erdtman, C. 1960. The acetolysis method - a revised description. Svensk Botaniska Trdskr. 54: 561–564.

Fahn, A. 1979. Secretory tissues in plants. Academic Press, London.

Fay, J.J. 1975. New combinations in *Perymenium* and *Oteiza* (Asteraceae-Heliantheae). Phytologia 31: 16–17.

Ferraz, A.D.B.F., S.P. Pinheiro, P.A. de Oliveira, F.L. Lino, J.N. Picada, and P. Pereira. 2009. Pharmacological and genotoxic evaluation of *Calea clematidea* and *Calea uniflora*. Latin Amer. J. Pharm. 28: 858–862.

Funk, V.A. and J.F. Pruski. 1996. Asteraceae. Pp. 85–122, in P. Acevedo-Rodríguez and collaborators. Flora of St. John U.S. Virgin Islands. Mem. New York Bot. Gard. 78.

Galvan, J., B. Brasil, M.d.S. Vieira, C. Mondin, and E.D. Heuser. 2005. Caracterização histológica de folhas de *Calea kristiniae* Pruski (Compositae: Heliantheae). Resumos do 56º Congresso Nacional de Botânica 278.

Galvis, J., A. Huguett, and P. Ruge. 1979. Geologia de la Amazonia Colombiana. INIGM informe 1792. Bol. Geol. (Bogotá) 22(3): 1–86. [Part number needed in citation, part 3 begins numbering from page 1].

Gardner, G. 1848. Contribution towards a Flora of Brazil, being the distinctive characters of some new species of Compositae, belonging to the tribe Senecionideae. London J. Bot. 7: 395–425.

Gentry, A.H. 1986. Exploring the mountain of the mists. Science Year. The World Book of Science Annual 1986: 125–139.

George, U. 1988. Inseln in der Zeit. Venezuela expeditionen zu den letzten weißen Flecken der Erde. Gruner & Jahr, Hamburg.

George, U. 1989. Venezuela's islands in time. Nat. Geogr. 175(5): 526–561.

Gleason, H.A. 1929. Studies on the flora of northern South America–XIII. The Tate collection from Mount Roraima and vicinity. Bull. Torrey Bot. Club 56: 391–408.

Gleason, H.A. 1931. Botanical results of the Tyler–Duida Expedition. Bull. Torrey Bot. Club 58: 277–506 + map + plates 17–45.

Gleason, H.A. and E.P. Killip. 1939. The flora of Mount Auyán-Tepui, Venezuela. Brittonia 3: 141–204.

Gómez, M. and J.F. Gil. 2011. Topical anti-inflammatory activity of *Calea prunifolia* HBK (Asteraceae) in the TPA Model of mouse ear inflammation. J. Braz. Chem. Soc. 22: 2391–2395 + electronic supplement S1–S8.

Gupta, M.P., A.I. Santa, and A. Espinosa. sin. dat. Plantas medicinales de Panamá. www.scribd.com.

Gutiérrez, D.G., L. Ariza Espinar, and M.L. Stampacchio. 2015. *Calea*. Pp 176–183, in S.E. Freire (coord.) and F.O. Zuloaga et al. (eds.). Flora vascular de la República Argentina, vol. 7, tomo II: Dicotyledoneae. Asteraceae: Cichorieae, Helenieae a Mutisieae. Instituto de Botánica Darwinion, Buenos Aires.

Hegnauer, R. 1977. The chemistry of Compositae. Pp. 283–335, in V.H. Heywood et al. (eds.). The Biology and Chemistry of the Compositae, vol. 1. Academic Press, London.

Hess, R. 1938. Vergleichende Untersuchungen über die Zwillingshaare der Compositen. Bot. Jahrb. Syst. 68: 435–496.

Hiepko, P. 2006. Humboldt, his botanical mentor Willdenow, and the fate of the collections of Humboldt & Bonpland. Bot. Jahrb. 126: 509–516.

Hitchcock, C.B. 1931. Cerro Duida and the Guayana Highlands. Torrey Bot. Club. Bull. 58: 284–287.

Hitchcock, C.B. 1947. The Orinoco-Ventuari region, Venezuela. Geogr. Rev. 37: 525–566.

Hoffmann, O. 1894 [1890–1894]. Compositae. Pp. 87–402, in A. Engler and K. Prantl (eds.). Nat. Pflanzenfam. IV(5). Engelmann, Leipzig.

Holt, E.G. 1931. In Humboldt's wake. Natl. Geogr. 60(5): 621–644.

Huber, O. 1982. Significance of savanna vegetation in the Amazon Territory of Venezuela. Pp. 221–244, in G.T. Prance (ed.). Biological diversification in the tropics. Columbia University Press, New York.

Huber, O. 1987 (Marzo). Consideraciones sobre el concepto de Pantepui. Pantepui 1(2): 2–10. [Part number needed in citation, part 2 begins numbering from page 1].

Huber, O. 1988a. Vegetacion y flora de Pantepui, region Guayana. Acta Bot. Bras. (Suppl.) 1: 41–52.

Huber, O. 1988b. Guayana highlands versus Guayana lowlands, a reappraisal. Taxon 37: 595–614.

Huber, O. 1989. Shrublands of the Venezuelan Guayana. Pp. 271–285, in L.B. Holm-Nielsen et al. (eds.). Tropical Forests: Botanical Dynamics, Speciation and Diversity. Academic Press, London.

Huber, O. 1990. Estado actual de los conocimientos sobre la flora y vegetacion de la region Guayana, Venezuela. Pp. 337–386, in F.H. Weibezahn et al. (eds.). El Río Orinoco como ecosistema. Impresos Rubel, Caracas.

Huber, O. (ed.) 1992. El Macizo del Chimantá. Todtmann, Caracas.

Huber, O. 1995. Volume I: Introduction. Chapters 1–3, 5, and two separate maps (and Chapter 4: 161–191 by Paul Berry, Otto Huber, and Bruce K. Holst), in J.A. Steyermark et al. (eds.). Flora of the Venezuelan Guayana. Timber Press, Portland and Missouri Botanical Garden Press, St. Louis.

Huber, O. 1997. Pantepui region of Venezuela. CPD Site SA2, Pp. 312–315, in S.D. Davis, V.H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A.C. Hamilton (eds.). Centres of Plant Diversity–A Guide and Strategy for their Conservation, vol. 3. The Americas. WWF-IUCN, Oxford.

Huber, O. 2005. Diversity of vegetation types in the Guayana region: An overview. Biol. Skr. 55: 169–188.

Huber, O. and J.J. Wurdack. 1984. History of botanical exploration in Territorio Federal Amazonas, Venezuela. Smithsonian Contr. Bot. 56: 1–83 + map.

Huber, O. and D. Frame. 1989. Venezuela. Pp. 362–374, in D. Campbell and D. Hammond (eds.). Floristic inventory of tropical countries: The status of plant systematics, collections, and vegetation, plus recommendations for the future. Scientific Publications Department, New York Botanical Garden, Bronx.

Huber, O., J.A. Steyermark, G.T. Prance, and C. Alès. 1984. The vegetation of the Sierra Parima, Venezuela-Brazil: Some results of recent exploration. Brittonia 36: 104–139.

Huber, O., G.T. Prance, S.B. Kroonenberg, and A. Antonelli. 2018. The tepuis of the Guiana Highlands. Pp. 339–353, in C. Hoorn et al. (eds.). Mountains, climate and biodiversity. Wiley & Sons, Oxford.

Humboldt, A. von. 1833. The travels and researches of Alexander von Humboldt: being a condensed narrative of his journeys in the equinoctial regions of America, and in Asiatic Russia; together with analyses of his more important investigations. Edited by W. Macgillivray. Second Edition. Oliver & Boyd, Edinburgh.

Humboldt, A. von. 1852–1853. Personal narrative of travels to the equinoctial regions of America during the years 1799–1804, by Alexander von Humboldt and Aime Bonpland, with maps, plans, &c. Written in French by Alexander de Humboldt. Translated and edited by Thomasina Ross in three volumes. Routledge and Sons, London. [English translation of 'Voyage aux régions équinoxiales du nouveau continent, fait en 1799, 1800, 1801, 1802, 1803, et 1804'; an earlier English translation titled '…. equinoctial regions of the new continent …' is by Helen Maria Williams. Longman et al., London]. The Ross three volume translation is cited here.

Ibañez–Mejia, M. 2020. Chapter 6. The Putumayo orogen of Amazonia: A synthesis. Pp. 101–131, in J. Gómez and D. Mateus-Zabala (eds.). The Geology of Colombia, vol. 1. Proterozoic – Paleozoic. Servicio Geológico Colombiano, Publicaciones Geológicas Especiales 35, Bogotá.

Ibañez-Mejia, M. and U.G. Cordani. 2020. Chapter 4. Zircon U–Pb geochronology and Hf–Nd–O isotope geochemistry of the Paleo– to Mesoproterozoic basement in the westernmost Guiana Shield. Pp. 65–90, in J. Gómez and D. Mateus-Zabala (eds.). The Geology of Colombia, vol.

1. Proterozoic–Paleozoic. Servicio Geológico Colombiano, Publicaciones Geológicas Especiales 35, Bogotá.

Jackson, B.D. 1893. Index Kewensis 1: 1–1268. Clarendon Press, Oxford.

Jana, B.K. and S.K. Mukherjee. 2015. Cypselar morpho-anatomy of *Calea cymosa* - tribe Neurolaeneae (Compositae). Indian J. Applied & Pure Bio. 30: 27–32.

Jansen, R.K., N.A. Harriman, and L.E. Urbatsch. 1982. *Squamopappus* gen. nov. and redefinition of *Podachaenium* (Compositae: Heliantheae). Syst. Bot. 7: 476–483.

Karis, P.O. 1993. Heliantheae sensu lato (Asteraceae), clades and classification. Pl. Syst. Evol. 188: 139–195.

Katinas, L., J.F. Pruski, G. Sancho, and M.C. Tellería. 2008. The subfamily Mutisioideae (Asteraceae). Bot. Rev. (Lancaster) 74: 469–716.

Klatt, F.W. 1889. Beiträge zur Kenntniss der Compositen. Leopoldina 25: 104–109.

Krascheninnikov, H. 1923. Compositae austro-americanae novae. II. Bot. Mater. Gerb. Glavn. Bot. Sada R.S.F.S.R. 4: 49–54. 1923. [Sometimes abbreviated Notulae Syst. Herb. Hort. Petrop.; for journal information see BPH-2, vol. 1 A–M: 231. 2004].

Kroonenberg, S.B. 2019. Chapter 3. The Proterozoic basement of the western Guiana Shield and the northern Andes. Pp. 115–192, in F. Cediel and R.P. Shaw (eds.). Geology and Tectonics of Northwestern South America. Springer, Switzerland.

Kroonenberg, S.B., E.W.F. de Roever, L.M. Fraga, N.J. Reis, T. Faraco, J.-M. Lafon, U. Cordani, and T.E. Wong. 2016. Paleoproterozoic evolution of the Guiana Shield in Suriname: A revised model. Netherlands J. Geosci. 95: 491–522.

Kubitzki, K. 1990. The Psammophilous flora of northern South America. Mem. New York Bot. Gard. 64: 248–253.

Lack, H.W. 2004. The botanical field notes prepared by Humboldt and Bonpland in Tropical America. Taxon 53: 501–510.

Lasser, T. and B. Maguire. 1950. A report on the plants of the Phelps Cerro Yaví expedition of 1947. Brittonia 7: 75–90.

Lasso, C.A., J.S. Usma, F. Trujillo, and A. Rial (eds.). 2010. Biodiversidad de la cuenca del Orinoco. I.I.R.B. Alexander von Humboldt, WWF Colombia … Univ. Nac. Colombia, Bogotá.

Lawalrée, A.G.C. 1982. Une Asteracée américaine introduite au Zaïre: *Calea urticifolia* (Miller) DC. Bull. Jard. Bot. Natl. Belg. 52(1–2): 129–132.

Lessing, C.F. 1830. Synanthereae Rich. Cass. Pp. 128–164 + Tab. II, in D. Schlechtendal and A. Chamisso. Plantarum Mexicanarum a cel. viris Schiede et Deppe collectarum. Recensio brevis. Linnaea 5: 71–174. [plate I is to be cited with the Lessing Nassauvieae paper beginning on page 1, and plates III–IV are part of the Mutisieae paper beginning on page 237].

Lessing, C.F. 1832. Synopsis Generum Compositarum xi + 1–473. Sumtibus Dunckeri et Humblotii, Berlin.

Lima, T.C., A.D.C. Santos, D.T.M. Costa, R.J. Souza, A. Barison, M. Steindel, and M.W. Biavatti. 2015. Chromenes from leaves of *Calea pinnatifida* and evaluation of their leishmanicidal activity. Rev. Bras. Farmacogn. 25: 7–10.

Lima, T.C., R.J. Souza, F.D. Silva, and M.W. Biavatti. 2018. The genus *Calea* L.: A review on [sic] traditional uses, phytochemistry, and biological activities. Phytother. Res. 32: 769–795.

Linnaeus, C. von. 1759. Systema Naturae (ed. 10). Stockholm.

Linnaeus, C. von. 1763. Species Plantarum (ed. 2). Stockholm.

Linnaeus, C. von. 1764. Genera Plantarum (ed. 6). Stockholm.

Löfgren, A. 1897. Flora paulista I. Familia Compositae. Commissão Geographica e Geologica de São Paulo, Bol. 12: 1–496.

Maguire, B. 1944. Notes on the geology and geography of Tafelberg, Suriname. Geogr. Rev. 35: 563–579.

Maguire, B. 1945. The first botanical exploration of Table Mountain in Surinam. J. New York Bot. Gard. 46: 256–272, 277–287.

Maguire, B. 1955. Cerro de la Neblina, Amazonas, Venezuela: A newly discovered sandstone mountain. Geogr. Rev. 45: 27–51.

Maguire, B. 1956. Distribution, endemicity, and evolution patterns among Compositae of the Guayana Highland of Venezuela. Proc. Amer. Philos. Soc. 100: 467–475.

Maguire, B. 1957. Exploration. A.I.B.S. Bull. November 1957: 14–17.

Maguire, B. 1964. Two decades of exploration in the American tropics. Gard. Bull. July–August 1964: 124–134.

Maguire, B. 1970. On the flora of the Guayana Highland, Biotropica 2: 85–100.

Maguire, B. 1979. Guayana, region of Roraima sandstone formation. Pp. 224–238, in K. Larsen and L.B. Holm-Nielsen (eds.). Tropical Botany. Academic Press, London.

Maguire, M. and K.D. Phelps. 1951–1952. Botanica de las Expediciones Phelps en la Guayana Venezolana–I. Territorio Amazonas. Bol. Soc. Venez. Ci. Nat. 14(78): 5–19. [The first page of the journal volume is dated 1951, but the cover is dated 1952; Maguire et al. 1953: 92 cited this as "in press"].

Maguire, M. and K.D. Phelps. 1951. Botanica de las Expediciones Phelps en la Guayana Venezolana–I. Territorio Amazonas. 1–15. Caracas. [My copy was that of D.D. Keck, and has a green cover dated 1951, there is no date within from page 1–15, however; the green cover also reads "Extracto del" Bol. Soc. Venez. Ci. Nat. "Tomo XIV - No. 78 - Enero–Julio 1951 - páginas 5–19"; it is not clear to me whether this differently paginated 'extract' is a preprint or a reprint, and it seem best to cite both of the differently paginated versions, which are confusable].

Maguire, B. and J.J. Wurdack. 1957. The botany of the Guayana Highland–Part II. Mem. New York Bot. Gard. 9: 235–392.

Maguire, B. and J.J. Wurdack. 1959. The position of Cerro de la Neblina, Venezuela. Geogr. Rev. 49: 566–568.

Maguire, B. and J.J. Wurdack. 1960. La posicion del Cerro de la Neblina, Venezuela. Bol. Soc. Venez. Ci. Nat. 96: 234–239.

Maguire, B., R.S. Cowan, and J.J. Wurdack. 1953. The botany of the Guayana Highland. A report of the Kunhardt, the Phelps, and the New York Botanical Garden Venezuela expedition. Mem. New York Bot. Gard. 8: 87–160.

Malme, G.O. 1933. Compositae Paranensis Dusenianae. Kongl. Svenska Vetensk. Acad. Handl., n.s. 12(2): 1–122. + 6 plates.

Martarello, D.C.I., L.A. de Souza, J.H.G. de Oliveira, and L. da Silva Santos. 2015. Morfologia e anatomia de folhas de cinco espécies de Asteraceae ocorrentes no Parque Estadual de Vila Velha, Ponta Grossa, Paraná. Encontro Intern. de Produção Ci. IX EPCC (03 à 06 de Novembro de 2015): 4 pages (on web http item //rdu.unicesumar.edu.br/handle/123456789/2983).

Mayr, E. and W.H. Phelps, Jr. 1967. The origin of the bird fauna of South Venezuelan Highlands. Bull. Amer. Mus. Nat. His. 136: 269–327 + pl. 14–21. [there is not text on page 328].

McPherson, S. 2008. Lost worlds of the Guiana Highlands. Redfern Natural History Productions, Poole, Dorset, England.

Meisner, C.F. 1836–1843. Plantarum vascularium genera: secundum ordines naturales digesta eorumque differentiae et affinitates tabulis diagnostacis expositae, two volumes. Weidmannia, Lipsiae.

Michelangeli A., A., F. Michelangeli A., R.S. Borges, W. Smitter, A. Subero, and K. Jaffé. 1988. Marahuaka. Armitano, Caracas.

Michelangeli, F. and A. Michelangeli. 1986. De Canaima al Churún Merú. Montana Gráfica, Caracas.

Molero, J., J.R. Daviña, A.I. Honfi, and D. Franco. 2006. Chromosome studies on plants from Paraguay II. Candollea 61: 373–392.

Moore, S.L.M. 1936. Family CXXV. Compositae. Pp. 150–289, in W. Fawcett and A.B. Rendle (eds.). Flora of Jamaica, vol. 7. British Museum, London.

Mora, A., E. Tesón, J. Martínez, M. Parra, A. Lasso, B.K. Horton, R.A. Ketcham, A. Velásquez, and J.P. Arias–Martínez. 2020. Chapter 5. The Eastern Foothills of Colombia. Pp. 123–142, in J. Gómez and D. Mateus-Zabala (eds.). The Geology of Colombia, vol. 3. Paleogene – Neogene. Servicio Geológico Colombiano, Publicaciones Geológicas Especiales 37, Bogotá.

Moreno-Sánchez, M., A. Gómez-Cruz, and J. Buitrago-Hincapié. 2020. Paleozoic of Colombian Andes: New paleontological data and regional stratigraphic review. Pp. 167–203, in J. Gómez and D. Mateus-Zabala (eds.). The Geology of Colombia, vol. 1. Proterozoic – Paleozoic. Servicio Geológico Colombiano, Publicaciones Geológicas Especiales 35, Bogotá.

Mukherjee, S.K. and B. Nordenstam 2008. Diversity of pappus structures in some tribes of the Asteraceae. Phytotaxonomy 8: 32–46.

Mykle, R. 1998. Colombia's Sierra de la Macarena. [Online at https://www.planeta.com/sierra-de-la-macarena-mykle/].

Nakajima, J.N. 2000. A familia Asteraceae no Parque Nacional da Serra da Canastra, Minas Gerais, Brazil. Unpublished PhD. thesis, 2 vols. Universidad Estadual de Campinas.

Nakajima, J.N., R.L. Esteves, V. Gonçalves-Esteves, M.A.G. Magenta, R.S. Bianchini, J.F. Pruski, and D.J.N. Hind. 2001. Familia 159 - Asteraceae. Flora Fanerogâmica da Reserva do Parque Estadual das Fontes do Ipiranga (São Paulo, Brasil). Hoehnea 28(2): 111—181.

Nash, D.L. 1975. Studies in American plants, VII. Phytologia 31: 361–364.

Nash, D.L. and L.O. Williams. 1976. Flora of Guatemala–Part XII: Compositae. Fieldiana, Bot. 24(12): x + 1–603.

Nesom, G.L. 1994a. Comments on *Microgynella*, *Sommerfeltia*, and *Asteropsis* (Asteraceae: Astereae). Phytologia 76: 101–105.

Nesom, G.L. 1994b. *Apopyros* (Asteraceae: Astereae), a new genus from southern Brazil, Argentina and Paraguay. Phytologia 76: 176–184.

Nesom, G.L. 1994c [1995]. Review of the taxonomy of *Aster* sensu lato (Asteraceae: Astereae), emphasizing the New World species. Phytologia 77: 141–297.

NYBG. 1985. NYBG scientists participate in exceptional expedition. New York Bot. Gard. Inform. Bull. 18(4): 1–4.

Ort, P. 1965. The expedition of the Brazilian-Venezuelan Boundary Commission to Cerro de la Neblina. Gard. J. New York Bot. Gard. 15(5): 199–203.

Panero, J.L. 2007 [2006]. XVIII. Tribe Athroismeae; XIX. Tribe Helenieae; XX. Tribe Coreopsideae; XXI. Tribe Neurolaeneae; XXII. Tribe Tageteae; XXIII. Tribe Chaenactideae; XXIV. Tribe Bahieae; XXV. Tribe Polymnieae; XXVI. Tribe Heliantheae; XXVII. Tribe Millerieae; XXIX. Tribe Perityleae. Pp. 395–492, 507–510, in Kubitzki, K. (ed.). The Families and Genera of Vascular Plants, vol. 8. Springer, New York.

Panero, J.L., J.L. Villaseñor, and R. Medina. 1993. New species of Asteraceae-Heliantheae from Latin America. Contr. Univ. Michigan Herb. 19: 171–193.

Paiva, G. de. 1928. Reconhecimentos geolóogicos nas fronteriras do Brasil com Venezuela e Cólombia. Estado do Amazonas, Río de Janeiro.

Paviani, T.I. 1977. Estudo morfológico e anatômico de *Brasilia sickii* G.M. Barroso. II: Anatomia da raiz, do xilopódio e do caule. Rev. Bras. Biol. 37: 307–324.

Paviani, T.I. 1987. Anatomia do desenvolvimento do xilopódio de *Brasilia sickii* G.M. Barroso, estagio inicial. Cien. Cult. 39: 399–405.

Pérez-Arbeláez, E. 1956. Plantas útiles de Colombia. Sucesores de Rivadeneyra, Madrid. [The title page listed the name 'Pérez-Arbeláez' with a hyphen. Although the title page of the 1975 version of the original 1937 book does not use a hyphen, both the 1956 and 1975 citations here are given as by 'Pérez-Arbeláez' i.e., with a hyphen].

Pérez-Arbeláez, E. 1975. Plantas medicinales y venenosas de Colombia. Salazar, Medellín.

Perkins, H.I. 1885. Notes on a journey to Mount Roraima, British Guiana. Proc. Roy. Geogr. Soc., n.s., 7: 522–534; also see map, table of contents p. vii gives map as (opposite) page 560.

Pfeiffer, L. 1873. Nomenclator botanicus, pars priori. vol. 1, pars priori. [i.e., 1(1)]. Fischer, Kassel. [Pagination is continuous from pars priori into pars alterna].

Pfeiffer, L. 1874. Nomenclator botanicus, vol. 2, pars alterna. [i.e., 2(1)]. Fischer, Kassel. [Pagination is continuous from pars priori into pars alterna].

Pinson, W.H., Jr., P.M. Hurley, E. Mencher, and H.W. Fairbairn. 1962. K-Ar and Rb-Sr ages of biotites from Colombia, South America. Geol. Soc. Amer. Bull. 73: 907–910.

Postek, M.T. and S.C. Tucker. 1976. A new short chemical dehydration for light microscopy preparations of plant material. Canad. J. Bot. 54: 872–875.

Prance, G.T. and D.M. Johnson. 1992. Plant collections from the plateau of Serra do Aracá (Amazonas, Brazil) and their phytogeographic affinities. Kew Bull. 47: 1–24.

Pruski, J.F. 1980a. Leaf anatomy of three species of *Calea*. Department of Botany 4172: 5 pp. + 1 plate. Louisiana State University, Baton Rouge.

Pruski, J.F. 1980b. Scanning electron microscope studies of three species of *Calea* (Asteraceae: Heliantheae). Department of Botany 7703: 28 pp. including 20 figures. Louisiana State University, Baton Rouge.

Pruski, J.F. 1982. A systematic study of the Colombian species of the genus *Calea* (Compositae): x + 1–178. Unpublished M.S. thesis, Louisiana State University, Baton Rouge.

Pruski, J.F. 1989. Compositae of the Guayana Highland–II. Novelties in *Gongylolepis* and *Stenopadus* (Mutisieae). Ann. Missouri Bot. Gard. 76: 993–1003.

Pruski, J.F. 1991 [1993]. Compositae of the Guayana Highland–V. The Mutisieae of the Lost World of Brazil, Colombia, and Guyana. Bol. Mus. Paraense Emílio Goeldi, sér. Botânica 7: 335–392.

Pruski, J.F. 1992. Compositae of the Guayana Highland–VI. *Huberopappus maigualidae* (Vernonieae), a new genus and species from Venezuela. Novon 2: 19–25.

Pruski, J.F. 1996a. Compositae of the Guayana Highland–X. Reduction of *Pollalesta* to *Piptocoma* (Vernonieae: Piptocarphinae) and consequent nomenclatural adjustments. Novon 6: 96–102.

Pruski, J.F. 1996b. Compositae of the Guayana Highland–XI. *Tuberculocarpus* gen. nov. and some other Ecliptinae (Heliantheae). Novon 6: 404–418.

Pruski, J.F. 1996c. Compositae of the Guayana Highland–XII. *Siapaea liesneri* (Eupatorieae), a new genus and species from Amazonas, Venezuela. Brittonia 48: 188–191.

Pruski, J.F. 1997. Asteraceae. Pp. 177–393, in J.A. Steyermark et al. (eds.). Flora of the Venezuelan Guayana, vol. 3. Missouri Botanical Garden Press, St. Louis.

Pruski, J.F. 1998a. Novelties in *Calea* (Compositae: Heliantheae) from South America. Kew Bull. 53: 683–693.

Pruski, J.F. 1998b. *Helianthus porteri* (A. Gray) Pruski (Compositae), a new combination validated for the Confederate Daisy. Castanea 63: 74–75.

Pruski, J.F. 1998c. *Stenopadus andicola* sp. nov. (Asteraceae: Mutisieae), a new generic record for Ecuador. Novon 8: 67–69.

Pruski, J.F. 1998d. Compositae of the Guayana Highland–XIII. New combinations in *Conyza* (Astereae), *Praxelis* (Eupatorieae), and *Riencourtia* (Heliantheae) based on Richard names. Brittonia 50: 473–482.

Pruski, J.F. 2001. A new combination in *Elaphandra* and a new variety of *Eleutheranthera ruderalis* (Compositae: Heliantheae: Ecliptinae) from Andean South America. Revista Acad. Colomb. Ci. Exact. 25(96): 315–319.

Pruski, J.F. 2002. Asteraceae (Composite Family). Pp. 93–116 + pl. 21, in S.A. Mori, G. Cremers, C.A. Gracie, J.-J. de Granville, S.V. Heald, M. Hoff, and J.D. Mitchell. Guide to the vascular plants of central French Guiana. Part 2. Dicotyledons. Mem. New York Bot. Gard. 76(2).

Pruski, J.F. 2003. Compositae News: Graziela Maciel Barroso (1912–2003); James C. Parks (1942–2002); John Beaman Receives José Cuatrecasas Medal. Compositae Newslett. 40: 64–68.

Pruski, J.F. 2004a. Asteraceae (Compositae). Missouri Botanical Garden: Research. Missouri Botanical Garden, St. Louis.

Pruski, J.F. 2004b. Graziela Maciel Barroso (1912–2003). Taxon 53: 225–226.

Pruski, J.F. 2005. Studies of neotropical Compositae–I. Novelties in *Calea*, *Clibadium*, *Conyza*, *Llerasia*, and *Pluchea*. Sida 21: 2023–2037.

Pruski, J.F. 2010. Asteraceae Bercht. & J. Presl (Compositae Giseke, nom. alt. et cons.). Pp. 339–420, in R. Vasquez et al. (eds.). Flora del Río Cenepa, Amazonas – Perú. Monogr. Syst. Bot. Missouri Bot. Gard. 114.

Pruski, J.F. 2011. Compositae of the Guayana Highland–XIV. Four new species of *Calea* (Neurolaeneae) from tepui summits in Venezuela. Phytoneuron 2011–52: 1–9.

Pruski, J.F. 2012a. Compositae of Central America–I. The tussilaginoid genus *Robinsonecio* (Senecioneae), microcharacters, generic delimitation, and exclusion of senecioid *Senecio cuchumatanensis*. Phytoneuron 2012–38: 1–8.

Pruski, J.F. 2012b. Compositae of Central America–II. *Ortizacalia* (Senecioneae: Senecioninae), a new genus of lianas with comose style branches. Phytoneuron 2012–50: 1–8.

Pruski, J.F. 2013. Studies of Neotropical Compositae–IX. Four new species of *Calea* (Neurolaeneae) from Bolivia, Brazil and Paraguay. Phytoneuron 2013–72: 1–14.

Pruski, J.F. 2016. Compositae of Central America–VI. *Perymenium hondurense*, *Podachaenium salvadorense*, and *Verbesina monteverdensis*, three new woody species of Heliantheae. Phytoneuron 2016–83: 1–21.

Pruski, J.F. 2019. Studies of Neotropical Compositae–XIII. *Lagascea espinalii* (Heliantheae: Helianthinae), a new species from dry canyons in Antioquia, Colombia and two noteworthy range extensions. Phytoneuron 2019-57: 1–20.

Pruski, J.F. 2021. Studies of Neotropical Compositae–XV. The new genus *Chaetacalia*, retention of *Aetheolaena*, *Culcitium*, *Haplosticha*, and *Iocenes*, two new species of *Senecio*, and *Lasiocephalus* revisited again (Senecioneae: Senecioninae). Phytoneuron 2021-65: 1–83.

Pruski, J.F. 2023. Compositae of the Guayana Highland–XV. The new genus *Tepuipappus* (Heliantheae subtr. Verbesininae) from Venezuela. Phytoneuron 2023-42: 127–148.

Pruski, J.F. and H. Beltrán. 2003. *Stenopadus andicola* (Compositae: Mutisieae), a new generic record for Peru. Compositae Newslett. 39: 2–12.

Pruski, J.F. and A.M. Funston. 2011. Asteraceae. Pp. 308–340, in A. Idárraga P., R. del C. Ortiz, R. Callejas P., and M. Merello. (eds.). Flora de Antioquia, catálogo de las plantas vasculares, vol. 2, listado de las plantas vasculares del departamento de Antioquia. Univ. de Antioquia. Medellín.

Pruski, J.F. and D.J.N. Hind. 1998. Two new species of *Calea* (Compositae: Heliantheae) from Serra do Grão Mogol and the surrounding area, Minas Gerais, Brazil. Kew Bull. 53: 695–701.

Pruski, J.F. and H. Robinson. 2018. Asteraceae. Compositae, nom. alt. Pp. 1–608, in G. Davidse et al. (eds.). Flora Mesoamericana, vol. 5, parte 2. Missouri Botanical Garden Press, St. Louis.

Pruski, J.F. and G. Sancho. 2004. Asteraceae or Compositae (Aster or Sunflower Family). Pp. 33–39 + pl. 5, in N. Smith et al. (eds.). Flowering plants of the Neotropics. Princeton University Press, Princeton.

Pruski, J.F. and L.E. Urbatsch. 1980. A systematic study of the *Calea zacatechichi* Schlechtendal complex. Proc. Louisiana Acad. Sci. 43: 179.

Pruski, J.F. and L.E. Urbatsch. 1983. *Calea bucaramangensis* (Asteraceae), a new species from the Colombian Andes. Syst. Bot. 8: 93–95.

Pruski, J.F. and L.E. Urbatsch. 1984. Chromosome counts in *Calea* (Asteraceae-Heliantheae). Pl. Syst. Evol. 144: 151–153.

Pruski, J.F. and L.E. Urbatsch. 1987. *Calea dalyi* (Compositae: Heliantheae), a new species from the Serranía de Santiago, Bolivia. Brittonia 39: 201–204.

Pruski, J.F. and L.E. Urbatsch. 1988. Five new species of *Calea* (Compositae: Heliantheae) from Planaltine Brazil. Brittonia 40: 341–356.

Pruski. J.F., R.D.C. Ortiz, and C.A. Amasifuen Guerra. 2019. Studies of Neotropical Compositae–XIV. *Bishopanthus werffii* (Liabeae), a new species from Chachapoyas, Peru. Phytoneuron 2019-65: 1–14.

Rachowiecki, R. 1988. The Lost World of Venezuela. Americas 40(5): 44–49, 64–65. [Part number needed in citation, all parts begin numbering from page 1].

Raleigh, W. 1596. Discovery of the large, rich, and beautiful empire of Guiana.

Ramayya, N. 1962. Studies on the trichomes of some Compositae I. General Structure. Bull. Bot. Surv. India 4: 177–188.

Ramos, L.S., P.S. Cardoso, M.D. Freitas, R. Paghan, M.S. Borges, and V. Citadini-Zanette. 2016. Popular medicinal uses of *Calea uniflora* Less. (Asteraceae) and its contribution to the study of Brazilian medicinal plants. Anais Acad. Brasil. Ci. 84: 2319–2330.

Rawitscher, F. and M. Rachid. 1946. Troncos subterraneos de plantas brasileiras. Anais Acad. Brasil. Ci. 18: 261–280.

Razetti, R. 1937. Mapa fisico y politico de los estados unidos de Venezuela. Reimpresion de la edición de 1928. Comercio, Caracas.

Reis, N.J., S. Nadeau, LM. Fraga, L.M. Betiollo, M.T.L. Faraco, J. Reece, D. Lachhman, and R. Ault. 2017. Stratigraphy of the Roraima Supergroup along the Brazil‐Guyana border in the Guiana shield, Northern Amazonian Craton – results of the Brazil‐Guyana geology and geodiversity mapping project. Braz. J. Geol. 47: 43–57.

Rice, A.H. 1921. The Rio Negro, the Casiquiare canal, and the upper Orinoco, September 1919–April 1920. Geogr. J. 58: 321–343.

Robinson, B.L. and J.M. Greenman. 1896. Revision of the Mexican and Central American species of the genus *Calea*. Proc. Amer. Acad. Arts 32: 20–30. [dated 2 December 1896].

Robinson, B.L. and J.M. Greenman. 1901 [1899]. Supplementary notes upon *Calea*, *Tridax*, and *Mikania*. Proc. Boston Soc. Nat. Hist. 29: 105–108.

Robinson, H. 1976. Studies in the Liabeae (Asteraceae). III. Notes on the genus, *Cacosmia*. Phytologia 38: 46–52.

Robinson, H. 1978a. Studies in the Heliantheae (Asteraceae). IX. Restoration of the genus *Alloispermum*. Phytologia 38: 411–412.

Robinson, H. 1978b. Studies in the Heliantheae (Asteraceae). X. The relationship of *Calea skutchii*. Phytologia 38: 413–414.

Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). Smithsonian Contr. Bot. 51: iv + 1–102.

Robinson, H. 1992. New combinations in *Elaphandra* Strother (Ecliptinae-Heliantheae-Asteraceae). Phytologia 72: 144–151.

Robinson, H. 2006. 190(6). Compositae-Heliantheae Part I: Introduction, genera A–L. Flora of Ecuador 77(1): 1–230.

Royal Society of London (Compiled). 1871. Catalogue of scientific papers (1800–1863), vol. 5. Clay and sons, London.

Rull, V. 2004. An evaluation of the Lost World and vertical displacement hypotheses in the Chimantá Massif, Venezuelan Guayana. Global Ecol. Biogeogr. 13: 141–148.

Rydberg, P.A. 1927. (Carduales) Carduaceae: Tribe 13. Liabeae, Tribe 14. Neurolaeneae, Tribe 15. Senecioneae (part). North American Flora 34(4): 289–360. [22 June 1927].

Rzedowski, J. 1968. Nota sobre la identidad de los generos *Aiolotheca* DC. y *Tonalanthus* T.S. Brandegee (Compositae). Brittonia 20: 166–168.

Rzedowski, J. and G. Calderón de Rzedowski. 2008. Familia Compositae. Tribu Heliantheae I (géneros *Acmella–Jefea*). Fl. Bajío 157: 1–344.

Rzedowski, J., G. Calderón de Rzedowski, and P. Carrillo-Reyes. 2011. Familia Compositae, Tribu Heliantheae (géneros *Lagascea–Zinnia*). Fl. Bajío 172: 1–409.

Sakai, W.S. 1973. Simple method for differential staining of paraffin embedded plant material using toluidine-blue O. Stain Tech. 48: 247–249.

Sánchez P., H., J.I. Hernández C., J.V. Rodríguez M., and C. Castaño U. 1990. Nuevos parques nacionales Colombia. Instituto Nacional de los Recursos Naturales Renovables y del Ambiente - INDERENA, Bogotá.

Sancho, G. and L. Katinas. 2002. Are the trichomes in corollas of Mutisieae (Asteraceae) really twin hairs? Bot. J. Linn. Soc. 140: 427–433.

Sancho, G. and J.F. Pruski. 2004. *Laennecia araneosa* (Compositae: Astereae), a new combination for the West Indies. Novon 14: 486–488.

Sancho, G., J.M. Bonifacino, and J.F. Pruski. 2006. Revision of *Microgyne* (Asteraceae: Astereae), the correct name for *Microgynella*. Syst. Bot. 31: 851–861.

Sancho, G., D.J.N. Hind, and J.F. Pruski. 2010. Systematics of *Podocoma* (Asteraceae: Astereae): a generic reassessment. Bot. J. Linn. Soc. 163: 486–513.

Sandwith, N.Y. 1926 (also 1968). Humboldt and Bonpland's itinerary in Ecuador and Peru. Bull. Misc. Inform. 1926: 181–900. [Also, with different pagination, in 1968 in W.L. Stearn. Humboldt, Bonpland, Kunth and Tropical American Botany. Cramer, Stuttgart.

Santos, J.O.S., P.E. Potter, N.J. Reis, L.A. Hartmann, I.R. Fletcher, and N.J. McNaughton. 2003. Age, source, and regional stratigraphy of the Roraima Supergroup and Roraima-like outliers in northern South America based on U-Pb geochronology. Geol. Soc. Amer. Bull. 115: 331–348.

Schomburgk, Robert H. 1836. Report of an expedition into the interior of British Guayana, in 1835–6. J. Roy. Geogr. Soc. 6: 224–284 + map. [R.H. Schomburgk is Robert Schomburgk].

Schomburgk, R.H. 1837a. Diary of an ascent of the river Corentyn, in British Guayana, in October, 1836. J. Roy. Geogr. Soc. 7: 285–301. [the table of contents reads ' … in British Guayana, 1836.' i.e., omitting 'in October,'].

Schomburgk, R.H. 1837b. Diary of an ascent of the river Berbice, in British Guayana, in 1836–7. J. Roy. Geogr. Soc. 7: 302–350 + map. [viz List of illustrations to Vol. VII: to face page 350].

Schomburgk, R.H. 1838. Travels in British Guiana and discovery of *Victoria regia*. Ann. Nat. Hist. 1: 63–68. [this letter was in the *VII.–Information respecting Botanical Travellers.* column, but was indexed in the Catalogue of Scientific Papers compiled by the Royal Society of London 1871: 521 item 8 using the title 'Travels in British Guiana and discovery of *Victoria regia*'].

Schomburgk, R.H. 1840a. Expedition in Guiana. Ann. Nat. Hist. 4: 194–199, 262–266, 322–328, 429–434. [these writings were in the Travellers Information columns and were indexed in the Catalogue of Scientific Papers compiled by the Royal Society of London 1871: 521 item 13 using the title 'Expedition in Guiana'].

Schomburgk, R.H. 1840b. Expedition in Guiana. Ann. Nat. Hist. 5: 29–35, 282–288, 343–348, 399–405. [these writings were in the Travellers Information columns and were indexed in the Catalogue of Scientific Papers compiled by the Royal Society of London 1871: 521 item 13 using the title 'Expedition in Guiana'].

Schomburgk, R.H. 1840c. A description of British Guiana, geographical and statistical: exhibiting its resources and capabilities, together with the present and future conditions and prospects of the colony. Simpkin, Marshall, and Co., London.

Schomburgk, R.H. 1841a. Report of the third expedition into the interior of Guayana, comprising the journey to the sources of the Essequibo, to the Carumá Mountains, and to Fort San Joaquim, on the Rio Branco, in 1837–8. J. Roy. Geogr. Soc. 10: 159–190 + map. [viz List of illustrations to Vol. X: to face page 190]. [here I date volume 10 as 1841 because the title page of volume 10 is dated 1841 in Roman numerals and volume 10 was cited by van Dam 2002: 209 as 1841; some web listings, however, date volume 10 as 1840; I have not seen title pages of any possible individual parts of this volume, however].

Schomburgk, R.H. 1841b. Journey from Fort San Joaquim, on the Rio Branco, to Roraima, and thence by the rivers Parima and Merewari to Esmeralda, on the Orinoco, in 1838–9. J. Roy. Geogr. Soc. 10: 191–247.

Schomburgk, R.H. 1841c. Journey from Esmeralda, on the Orinoco, to San Carlos and Moura on the Rio Negro, and thence by Fort San Joaquim to Demerara, in the spring of 1839. J. Roy. Geogr. Soc. 10: 248–267. [the map to 1841a is not placed with that paper by jstor, but rather is misplaced by jstor here, i.e., in the pdf of 1841c].

Schomburgk, R.H. 1841d. Robert Hermann Schomburgk's Reisen in Guiana und am Orinoko während der Jahre 1835–1839. [German translation by Otto Schomburgk of 'Voyage in Guiana and upon the shores of the Orinoco during the years 1835–39']. Wigand, Leipzig.

Schomburgk, R.H. 1841e. Twelve views in the interior of Guiana. Ackermann and Co., London.

Schomburgk, R.H. 1842a. Expedition to the lower parts of the Barima and Guiania rivers, in British Guiana. J. Roy. Geogr. Soc. 12: 169–178 + map. [the journal table of contents p. vi listed an accompanying map, but did not say which page in which chapter the map should face; page 172, 176, 178-third line of the text imply the map is part of the present paper, i.e., 1842a].

Schomburgk, R.H. 1842b. Excursion up the Barima and Cuyuni rivers, in British Guiana, in 1841. J. Roy. Geogr. Soc. 12: 178–196.

Schomburgk, R.H. 1843. Visit to the sources of the Takutu, in British Guiana, in the year 1842. J. Roy. Geogr. Soc. 13: 18–75 + map.

Schomburgk, R.H. 1845. Journal of an expedition from Pirara to the upper Corentyne, and from thence to Demerara. J. Roy. Geogr. Soc. 15: 1–104 + map.

Schomburgk, M.R. 1847–1848. Reisen in British-Guiana in den Jahren 1840–1844. Three volumes. [1922 English translation of vols. 1–2 as 'Travels in British Guiana during the years 1840–1844' by W.E. Roth; volume three was not translated]. Weber, Leipzig. [M.R. Schomburgk is Richard Schomburgk].

Schomburgk, M.R. 1876. Botanical reminiscences in British Guiana. Cox, Adelaide.

Schubert, C. and O. Huber. 1989. The Gran Sabana. Panorama of a region. Lagoven, Caracas. [The year 1989 of the Spanish version is used here, but this English translation of the 1989 Spanish La Gran Sabana seems to be undated].

Schubert, C., P. Fritz, and R. Aravena. 1994. Late quaternary paleoenvironmental studies in the Gran Sabana (Venezuelan Guayana shield). Quaternary Intern. 21: 81–90.

Schultes, R.E. 1944. Notes on the ecology of some isolated sandstone hills of the Vaupés region. Pp. 124–130, in R.E. Schultes. Plantae Colombianae, IX. Caldasia 3: 121–130.

Schultes, R.E. 1976. Hallucinogenic Plants. A Golden Guide. [Illustrated by E.W. Smith]. Golden Press, New York.

Schultes, R.E. 1988. Where the gods reign. Plants and peoples of the Colombian Amazon. Synergetic Press, Oracle, Arizona.

Schultes, R.E. and A. Hofmann. 1979. Plants of the gods. Their sacred, healing and hallucinogenic powers. McGraw-Hill, New York.

Schultes, R.E. and A. Hofmann. 1980. The Botany and Chemistry of Hallucinogens (ed. 2). Charles C. Thomas, Springfield.

Schultz Bipontinus, C.H. 1849. Compositae. Pp. 569–573, in Anonymous (given only as "varii auctores" on page 511 of the introductory paragraph). Plantae Regnellianae. Linnaea 22: 511–583.

Schultz Bipontinus, C.H. 1859–1860 [?1861]. Cassiniaceae Regnellianae Brasilienses, editio secunda emendata. Linnaea 30: 179–184.

Seaman, F.C. 1982. Sesquiterpene lactones as taxonomic characters in the Asteraceae. Bot. Rev. (Lancaster) 48: 121–595.

Shobe, W.R. and N.R. Lersten. 1967. A technique for clearing and staining gymnosperm leaves. Bot. Gaz. 128: 150–152.

Silva, G.H.L. and A.M. Teles. 2018. *Calea* (Asteraceae, Neurolaeneae), no estado de Goiás, Brasil. Rodriguésia 69: 1851–1875.

Silva, G.H.L., J.B.A. Bringel, and A.M. Teles. 2016. A new species of *Calea* (Asteraceae–Neurolaeneae) from Goiás state, Brazil. Phytotaxa 265: 279–284.

Simpson Vuilleumier, B. 1971. Pleistocene changes in the flora and fauna South America. Science 173(3999): 771–780.

Smith, A.C. 1940. A collection of flowering plants from Mount Roraima and adjacent Venezuela, British Guiana, and Brazil. Bull. Torrey Bot. Club 67: 283–299.

Smith, A. 2010. A tour of the Gran Sabana and some of its tepuis. Associazione Italiana Piante Carnivore, Special Issue 2. AIPC, Mira, Italy.

Soria, N., I. Basualdo, and W.D. Stevens. 1998. Las Compuestas del Parque Nacional Cerro Corá - Paraguay. Rojasiana 4: 164–245.

Spach, E. 1841. Histoire naturelle des végétaux: Phanerogames, vol. 10. Librairie encyclopédique de Roret, Paris.

Spruce, R. 1908. Notes of a botanist on the Amazon and Andes. [edited and condensed from the journals of the Royal Geographical and Linnean Societies by A.R. Wallace]. Two volumes. Macmillan, London.

Stafleu, F.A. and R.S. Cowan. 1981. Taxonomic Literature: A selective guide to botanical publications and collections with dates, commentaries and types, 2nd ed., vol. III: Lh–O. Regnum Vegetabile, vol. 105. Bohn, Scheltema & Holkema, Utrecht.

Stanski, C., C.F.P. Luz, A. Nogueira, and M.K.F.d.S. Nogueira. 2013. Palynology of species in the Astereae and Heliantheae tribes occurring in the region of Campos Gerais, Paraná State, Brazil. Iheringia, Sér. Bot., Porto Alegre 68: 203–214.

Stearn, W.T. 1983. Botanical Latin. (third edition, revised). David & Charles, London.

Steyermark, J.A. 1955. Rare plants and animals discovered in 'Lost World.' Chicago Nat. Hist. Mus. Bull. 26(5): 2–3. [Part number needed in citation, part 5 begins numbering from page 1].

Steyermark, J.A. 1966. Contribuciones a la flora de Venezuela. Parte 5. Acta Bot. Venez. 1(3–4): 9–256.

Steyermark, J.A. 1967. Flora of Auyán–tepui. Acta Bot. Venez. 2 (5–8): 5–370.

Steyermark, J.A. 1968. Contribuciones a la flora de la Sierra de Imataca, altiplanicie de Nuria y region adyacente del Territorio Federal Delta Amacuro al sur del Rio Orinoco. Acta Bot. Venez. 3: 49–175.

Steyermark, J.A. 1974. The summit vegetation of Cerro Autana. Biotropica 6: 7–13. [as J. Steyermark]

Steyermark, J.A. 1975. Informe sobre la flora del Cerro Autana. Acta Bot. Ven. 10: 219–233.

Steyermark, J.A. 1979. Flora of the Guayana highland: endemicity of the generic flora of the summit of the Venezuela tepuis. Taxon 28, 45–54.

Steyermark, J.A. 1982. Relationships of some Venezuelan forest refuges with lowland tropical floras. Pp. 182–220, in G.T. Prance (ed.). Biological diversification in the tropics. Columbia University Press, New York.

Steyermark, J.A. 1986. Speciation and endemism in the flora of the Venezuelan tepuis. Pp. 317–373, in F. Vuilleumier and M. Monasterio (eds.). High altitude [sic elevation] tropical biogeography. Oxford University Press, New York.

Steyermark, J.A. and Collaborators. 1951. Contributions to the flora of Venezuela. Botanical exploration in Venezuela, I. Fieldiana Bot. 28: 1–242.

Steyermark, J.A. and Collaborators. 1952. Contributions to the flora of Venezuela. Botanical exploration in Venezuela, II. From Droseraceae through Umbelliferae. Fieldiana Bot. 28: 243–447.

Steyermark, J.A. and Collaborators. 1953. Contributions to the flora of Venezuela. Botanical exploration in Venezuela, III. From Ericaceae through Compositae. Fieldiana Bot. 28: 449–678.

Steyermark, J.A. and Collaborators. 1957. Contributions to the flora of Venezuela. Botanical exploration in Venezuela, IV. Fieldiana Bot. 28(4): 679–1190.

Steyermark, J.A. and G.C.K. Dunsterville. 1980. The lowland floral element on the summit of Cerro Guaiquinima and other cerros of the Guayana Highland of Venezuela. J. Biogeo. 7: 285–303.

Steyermark, J.A., B.K. Holst, and Collaborators. 1989. Flora of the Venezuelan Guayana–VII. Contributions to the flora of the Cerro Aracamuni, Venezuela. Ann. Missouri Bot. Gard. 76: 945–992.

Stolzenburg, W. 1993. Magic Mesas. Venezuela's tepuys. Nature Conservancy 43(4): 10–14. [Part number needed in citation, all parts begin numbering from page 1].

Strother, J.L. 1983. More chromosome studies in Compositae. Amer. J. Bot. 70: 1217–1224.

Strother, J.L. 1991. Taxonomy of *Complaya*, *Elaphandra*, *Iogeton*, *Jefea*, *Wamalchitamia*, *Wedelia*, *Zexmenia*, and *Zyzyxia* (Compositae–Heliantheae–Ecliptinae). Syst. Bot. Monogr. 33: 1–111.

Strother, J.L. 1999. Compositae–Heliantheae s.l. Pp. 1–232, in D.E. Breedlove (ed.). Flora of Chiapas, vol. 5. California Academy of Sciences, San Francisco.

Stuessy, T.F. 1977. Heliantheae-Systematic Review. Pp. 621–671, in V.H. Heywood et al. (eds.). The Biology and Chemistry of the Compositae. Academic Press, London.

Sundberg, S.D., C.P. Cowan, and B.L. Turner. 1986. Chromosome counts of Latin American Compositae. Amer. J. Bot. 73: 33–38, 86–87.

Tate, G.H.H. 1930a. Notes on the Mount Roraima region. Geogr. Rev. 20: 53–68 + map.

Tate, G.H.H. 1930b. Through Brazil to the summit of Mount Roraima. Natl. Geogr. 58(5): 585–606.

Tate, G.H.H. 1938. Auyantepui: Notes on the Phelps Venezuelan Expedition. Geogr. Rev. 28: 452–474.

Tate, G.H.H. and C.B. Hitchcock. 1930. The Cerro Duida region of Venezuela. Geogr. Rev. 20: 31–52.

Ter Steege, H. 2000. Chapter 10. Flora, vegetation, endemism and altitudinal gradients in the Guayana Highland area: a brief overview. Plant Diversity in Guyana, Tropenbos Ser. 18: 139–146.

Thurn, E.F. Im. 1885. The ascent of Mount Roraima. Proc. Roy. Geogr. Soc., n.s., 7: 497–521; also see map, table of contents p. vii gives map as (opposite) page 560. As Everard Im Thurn.

Thurn, E.F. Im and D. Oliver. 1887. The botany of the Roraima expedition of 1884: being notes on the plants observed, by Everard F. im Thurn; with a list of the species collected, and determination of those that are new, by Prof. Oliver, F.R.S., F.L.S., and others. Trans. Linn. Soc. London, Bot., ser. 2, 2(13): 249–300 + pl. 37–56.

Turner, B.L. 1992. New names and combinations in New World *Wedelia* (Asteraceae, Heliantheae). Phytologia 72: 389–395.

Turner, B.L. 2008. A new variety of *Calea megacephala* (Asteraceae: Heliantheae) from Oaxaca, Mexico. Phytologia 90: 230–232.

Turner, B.L. 2014. The Comps of Mexico. A systematic account of the family Asteraceae. Chapter 14, Tribe: Neurolaeneae. Tribe: Heliantheae; subtribes: Ambrosiinae, Chromolepidinae and Dugesiinae). Phytologia Mem. 19: 1–156.

Turner, B.L. 2016a. The Comps of Mexico. A systematic account of the family Asteraceae. Chapter 20, subtribes: Montanoinae (*Montanoa*); Rojasianthinae *(Rojasianthus*); Rudbeckiinae (*Ratibida*, *Rudbeckia*); Spilanthinae (*Acmella*, *Salmea*, *Spilanthus* [sic, i.e., *Spilanthes*]); Verbesininae [in part] (*Podachaenium*, *Squamopappus*, *Tetrachyron*, *Verbesina*). Phytologia Mem. 24a: 1–109.

Turner, B.L. 2016b. The Comps of Mexico. A systematic account of the family Asteraceae. Chapter 22, Tribe Millerieae Lindl., subtribe Desmanthodiinae: *Desmanthodium*; subtribe Dyscritothamninae: *Bebbia*, *Cymophora*, *Dyscritothamnus*, *Tetragonotheca*, *Tridax*; subtribe Galinsoginae: *Alepidocline*, *Alliospermum* [sic *Alloispermum*], *Aphanactis*, *Faxonia*, *Galinsoga*, *Oteiza*, *Schistocarpha*, *Selloa*, *Stenocarpha*. Phytologia Mem. 26a: 1–176.

Turner, B.L. and J. Panero. 1992. New species and combinations in *Podachaenium* (Asteraceae, Heliantheae. Phytologia 73: 143–148.

Turner, B.L., J. Bacon, L.E. Urbatsch, and B. Simpson. 1979. Chromosome numbers in South American Compositae. Amer. J. Bot. 66: 173–178.

United States Commission on Boundary Between Venezuela and British Guiana. 1897. Report and accompanying papers of the commission appointed by the President of the United States "to investigate and report upon the true divisional line between the Republic of Venezuela and British Guiana." vol. 3. Geographical. Government Printing Office, Washington. [the Title Page gives this as 'United States Commission …'; there are six reports bound together, the t.o.c. gives report 1 as by S. Mallet-Prevost, 2 as by J. Winsor, 3–4 as by L. Burr, and sections 5–6 being the bulk of the text and running from pages 219–506 as by M. Baker; the 'notes of the geography' is report 5, pages 219–381 and the 'partial list of maps' is report 6, pages 383–506].

Urban, I. 1906. Vitae itineraque collectorum botanicorum, notae collaboratorum biographicae, Flora Brasiliensis ratio edendi chronologica, systema, index familiarum. Pp. 1–268, in C.F.P. de Martius, A.G. Eichler, and I. Urban (eds.). Flora Brasiliensis, vol. 1(1). Oldenbourg, Monachii. [Tabulae of Martius is bound in 1(1) and can be cited as credited and numbered, i.e., by Martius and using Roman numerals [I–]–III–CX; the collectors index section by Urban in 1(1) is numbered in Arabic from [1–]3–154; collaborators and the remaining indices by Urban are numbered in Arabic as [155–]157–268].

Urbatsch, L.E., A. Zlotsky, and J.F. Pruski. 1986. Revision of *Calea* sect. *Lemmatium* (Asteraceae-Heliantheae) from Brazil. Syst. Bot. 11: 501–514.

Urbatsch, L.E. and J.F. Pruski. 1989. A sectional treatment for the genus *Calea* (Asteraceae, Heliantheae). Amer. J. Bot. 76(6, suppl.): 277–278. Abstracts 1989, Toronto, Canada.

Valadeau C., A. Pabon, E. Deharo, J. Albán–Castillo, Y. Estevez, F.A. Lores, R. Rojas, D. Gamboa, M. Sauvain, D. Castillo, and G. Bourdy. 2009. Medicinal plants from the Yanesha (Peru): Evaluation of the leishmanicidal and antimalarial activity of selected extracts. J. Ethnopharmac. 123: 413–422.

Valdespino, I.A. 1992. New Species of *Selaginella* (Selaginellaceae) from the Guayana Highland of Venezuela. Brittonia 44: 199–207.

Van Dam, J.A.C. 2002. The Guyanan plant collections of Robert and Richard Schomburgk. Flora of the Guianas, suppl. ser., fasc. 3: iii + 1–211.

Van der Hammen, T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. J. Biogeogr. 1: 3–26.

Vilhalva, D.A.A. and B. Appezzato-da-Glória. 2006. Morfo-anatomia do sistema subterrâneo de *Calea verticillata* (Klatt) Pruski e *Isostigma megapotamicum* (Spreng.) Sherff - Asteraceae. Revista Brasil. Bot. 29: 39–47.

Wallace, A.R. 1853a. A narrative of travels on the Amazon and Rio Negro, with an account of the native tribes, and observations on the climate, geology, and natural history of the Amazon valley. Reeve and Co., London.

Wallace, A.R. 1853b. On the Rio Negro. J. Roy. Geogr. Soc. 23: 212–217 + map.

Walpers, G.G. 1843. Repertorium botanices systematicae, vol. 2. Hofmeister, Lipsiae.

Walpers, G.G. 1851–1852 [1852]. Annales botanices systematicae, vol. 2. Hofmeister, Lipsiae.

Weidmann, K., M. Pérez V., and O. Huber. 1986. La 'Gran Sabana.' Todtmann, Caracas.

Whitely, H. 1884. Explorations in the neighbourhood of Mounts Roraima and Kukenam, in British Guiana. Proc. Roy. Geogr. Soc., n.s., 6: 452–463 + unpaginated map (positioned after page 488). [The British spelling "neighbourhood" is used].

Willdenow, C.L. 1803. Species Plantarum. Editio quarta 3(3): [1476]–2409. Nauk, Berolini.

Williams, L. 1942. Exploraciones botánicas en la Guayana Venezolana. Servicio botánico, Ministerio de agricultura y cría, Caracas.

Wulff, A.F., J.H. Hunziker, and A. Escobar. 1996. Estudios cariológicos en Compositae VII. Darwiniana 34: 213–231.

Wurdack, J.J. 1971. Geographic errors in Bonpland collections of Melastomataceae. Taxon 20: 591–593.

Wussow, J.R. and L.E. Urbatsch. 1978. A taxonomic study of the *Calea orizabensis* complex and its bearing on the nomenclature of *Verbesina standleyi* (Asteraceae). Brittonia 30: 477–482.

Wussow, J.R. and L.E. Urbatsch. 1979 [1980]. A systematic study of the genus *Tetrachyron* (Asteraceae: Heliantheae). Syst. Bot. 4: 297–318.

Wussow, J.R., L.E. Urbatsch, and G.A. Sullivan. 1985. *Calea* (Asteraceae) in Mexico, Central America, and Jamaica. Syst. Bot. 10: 241–267.