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Cover: *Benzingia elvirae* Pupulin.
(See page 295, Fig. 3.) Drawing by Franco Pupulin and Sara Poltronieri.

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The Journal of the Arnold Arboretum

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(Continued from page i)

ECHINOPS SHAKROKII (ASTERACEAE), A NEW SPECIES FROM KURDISTAN, IRAQ

SAMAN A. AHMAD[1]

Abstract. *Echinops shakrokii* is described and illustrated, and its relationship to the southwestern Asian species of *Echinops* is discussed. From the southwestern Asian species, *E. shakrokii* is easily distinguished by its smaller heads, 1.5–2.5 cm in diam., and capitula with 27–33 phyllaries.

Keywords: Asteraceae, *Echinops*, Kurdistan, Qara Dagh Mountains, Southwest Asia

During the past four years, I have been involved in the preparation of a checklist and field guide of the vascular plants of the Qara Dagh Mountains in Kurdistan, Iraq. This mountain range has been poorly explored botanically because of the lack of roads and because it was closed for military reasons. Presently, however, it has become possible to reach even some of the remote sites, resulting in many rare, poorly known, and new species being found there during this project. Among them is a new species of *Echinops* L., described below.

Echinops is a taxonomically difficult genus of ca. 120 species distributed in Europe, Africa, and Asia but centered in SW Asia (Mabberley, 2008: 296). Boissier (1875) and Rechinger (1979) recognized 42 and 76 species, respectively, and Hedge (1975) indicated that 16 species grow in Turkey, of which only *E. heterophyllus* Davis also grows in Iraq. Four years later Rechinger (1979) treated 15 species from Iraq, of which five were listed as endemic. The status of some of those species, however, remains problematic, even after Townsend (1988) evaluated some of them and described one as new. An additional new species is described here.

Echinops shakrokii S.A. Ahmad *sp. nov*. TYPE: IRAQ. Kurdistan Region: Sulaimani Province, Qara Dagh Mts., Qallay Darband Spi, mountainside dominated by *Quercus aegilops*, *Acer monspessulanum*, and a creeping species of *Prunus*, sandy soil on a steep slope, 1737 m, 35°17'36"N, 45°17'55"E, 18 September 2016, *S. A. Ahmad 16-4088, with A. Hama, K. Faraidun & S. R. Fayaq*. (Holotype: KBFH; Isotypes: KBFH, MO, SUFH). Fig. 1–2.

Echinops shakrokii is readily separated from the other Southwest Asian species of the genus by having smaller compound heads 1.5–2.5 cm in diam. with some 100 small capitulae collectively subtended by 27–33 phyllaries that are not plumose.

Herbs, perennial, 20–35 cm tall; caudex woody, several branched, to 1 cm in diam. *Stems* slender, obscurely sulcate, densely woolly and sparsely glandular-puberulent, with several short branches in inflorescence. *Basal leaves* and lowermost cauline leaves pinnatisect, 8–17 cm long; petiole 2–5 mm long, lanate; blade 2–7 mm wide, abaxially densely white lanate, adaxially greenish, sparsely pubescent and moderately to sparsely glandular-puberulent; lateral lobes 8–11, lanceolate, reduced in size apically, margin with few divisions terminated in a spine, 5–10 mm long; middle and upper cauline leaves sessile, pinnatisect, lanceolate, base auriculate, semiamplexicaul, auricles with dense spines, indumentum of both surfaces as in basal and lowermost cauline leaves. *Heads* compound, with ca. 100, 1-flowered capitulae, noncornigerous, 1.5–2.5 cm in diam.; peduncle 0.5–1 cm long; receptacle oblong-ovoid, 2.5–3.0 mm wide; bracts of common involucre reflexed, dentate, spiny. *Capitulum* compound, 13–15 mm long in flower; with few connate bristles at base; phyllaries 27–33; outer ones ca. 6–9, spatulate, 2.5–5.5 mm long, base attenuate, margin bristly, apex lacerate; middle phyllaries ca. 21, increasing in length inward, 5.5–12.0 mm long, lanceolate, margin bristly-ciliate, apex acuminate into a slender spine; innermost phyllaries 3, free, narrowly oblong, ca. 11 mm long, margin entire, apex lacerate. *Corolla* 11–12 mm long, pale blue, tube ca. 5 mm long, sparsely puberulent below apex. *Cypsellae* (including pappus) ca. 7 mm long; pappus barbellate bristly, ca. 2 mm long, about twice as long as apical hairs of achene.

Distribution: Iraq, Kurdistan, Qara Dagh Mts.; thus far known only from type locality.

Etymology: the specific epithet, *shakrokii***,** is from *shakroka*, the Kurdish word for sugar**.** The plant has a history of use as a delicacy; the sweet-tasting fresh receptacle is eaten raw. The plant is attractive to Lepidoptera, which gather in the leaf axils to suck the sap; they also make a round, white shell from the plant exudate in which they pupate. The shell, which has a mild, sweet taste, is collected and eaten.

Echinops shakrokii is easily distinguished from other southwest Asian species of *Echinops* by its smaller compound heads, 1.5–2.5 cm in diam., with ca. 100 flowering capitulae subtended by 27–33 phyllaries. It belongs to section *Echinops*, which is distinguished from other sections by having distinct inner phyllaries and nonplumose outer and middle ones. None of the southwest Asian species of section

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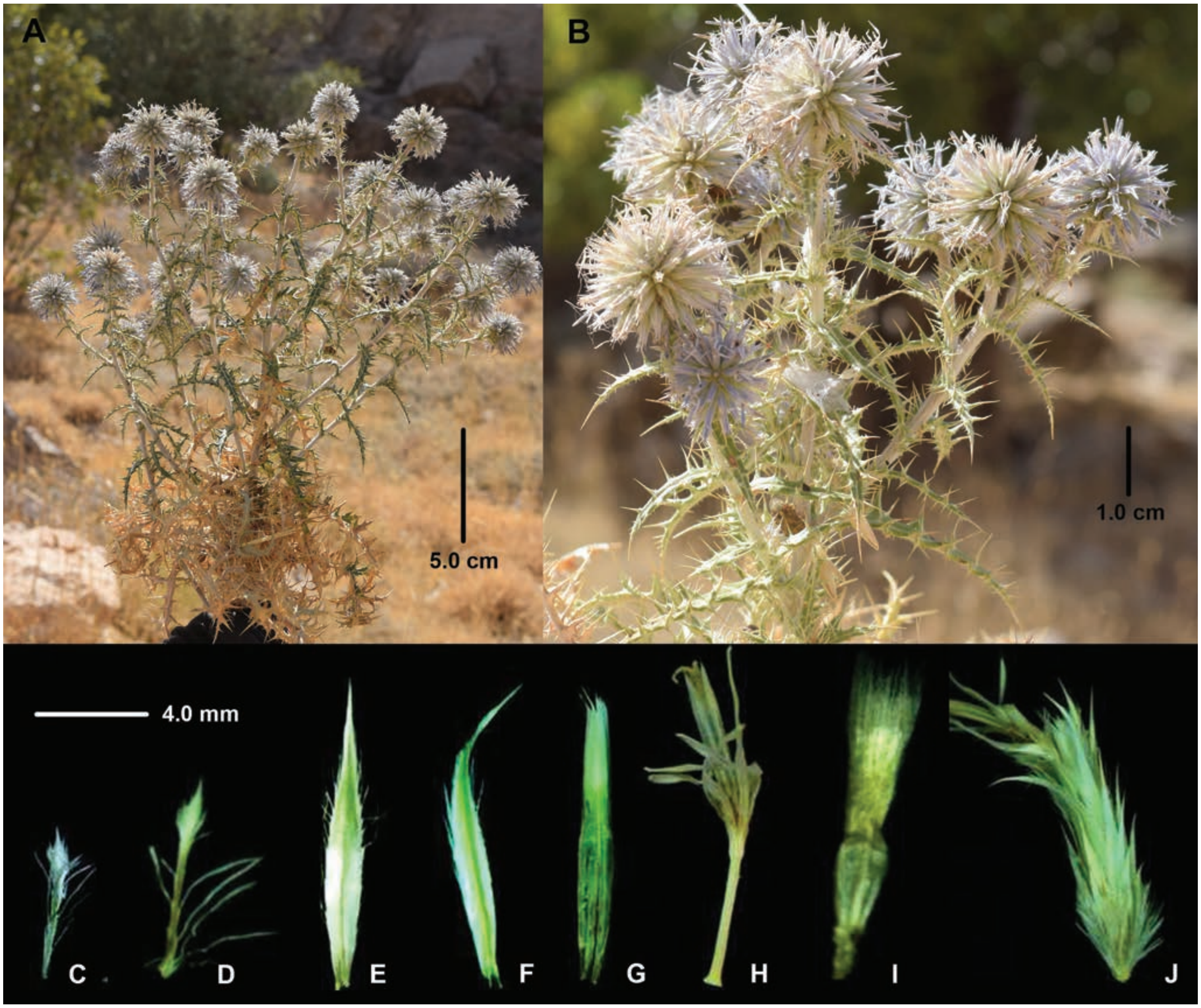

FIGURE 1. *Echinops shakrokii* S.A. Ahmad. **A,** plant habit; **B**, capitulum: **C** and **D**, outer phyllaries; **E**, **F,** and **G,** middle phyllaries; **H**, corolla; **I**, achenes; **J**, flower.

Echinops have small heads as in *E. shakrokii*, although both *E. ritro* L. of Turkmenistan and *E. freitagii* Rech.f. of northeastern Iran and Afghanistan have heads 2–4 and to 3 cm in diam., respectively. In addition to the remarkable geographical disjunction between the QaraDagh plants and those two species, *E. shakrokii* differs from *E. ritro* by being glandular (vs. non-glandular) and by having 27–33 (vs. 20–22) phyllaries. Although *E. freitagii* is glandular, it differs from *E. shakrokii* by having pinnatipartite (vs. pinnatisect) basal and lowermost cauline leaves as well as by having 18–23 (vs. 27–33) phyllaries.

A third species with small heads is *Echinops parviflorus* Boiss. & Buhse. It was reported by Rechinger (1979) from Karaj, Tehran, and Kermanshah (Iran) and doubtfully from Piramagrun (Iraq). The Iranian plants are non-glandular, whereas the Iraqi material is glandular. The plants of both countries have small corollas, 7–8 mm long, and 12–15 phyllaries per capitulum. By contrast, *E. shakrokii* has corollas 11–12 mm long and 27–33 phyllaries per capitulum. Therefore, *E. shakrokii* is remarkably different morphologically from all members of section *Echinops* with small heads to 3 cm long.

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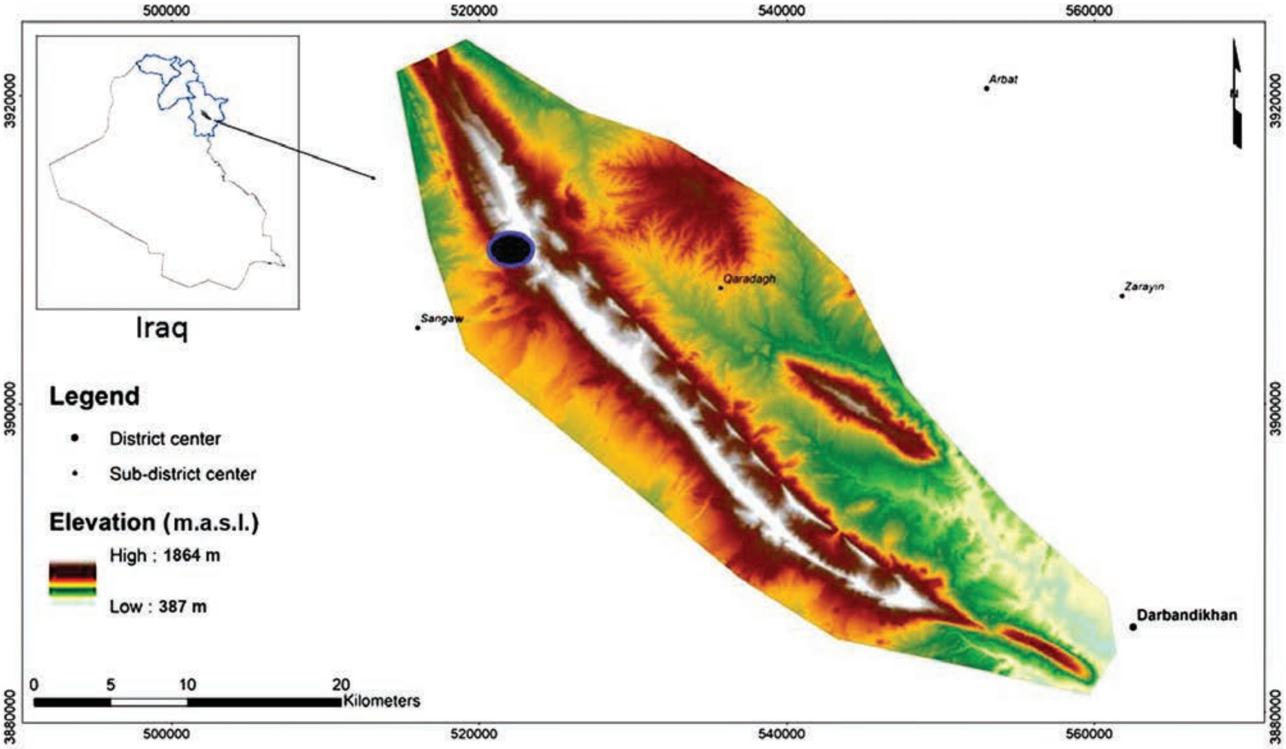

FIGURE 2. Map of Qara Dagh Mountains showing distribution of *Echinops shakrokii* S.A. Ahmad.

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THE DELIMITATION OF THE SOUTH AFRICAN *HELIOPHILA BRACHYCARPA* AND TWO RELATED SPECIES (BRASSICACEAE)

Ihsan A. Al-Shehbaz[1]

Abstract. Typification of *Heliophila brachycarpa, H. florulenta, H. glauca,* and *H. sclerophylla* is established. The second species has been erroneously synonymized with the first for the past 50 years, and the first three are recognized as distinct, whereas the last is reduced to synonymy of the third.

Keywords: Brassicaceae, Cruciferae, *Heliophila*, Lesotho, Namibia, South Africa, Swaziland.

The genus *Heliophila* L. (Brassicaceae or Cruciferae) includes 81 species (BrassiBase, 2019) all of which are native to South Africa (65 spp. endemic), with 16 species also native to Namibia (12 spp.), Lesotho (5 spp.), and Swaziland (1 sp.; author's compilation). In his excellent account of the genus for the floras of these countries, Marais (1970) recognized 71 species in *Heliophila*, two each in *Cycloptychis* E. Mey. ex Sond. and *Thlaspeocarpa* C.A. Sm., and one each in *Brachycarpaea* DC., *Schlechteria* Bolus, and *Silicularia* Compton. Based on molecular phylogenetic studies on this complex of six genera by Mummenhoff et al. (2005), the last five genera were united by Al-Shehbaz et al. (2005) into a more inclusive *Heliophila* s.l.

The present author has been involved in the past decade in monographing *Heliophila* s.l. in its entire range. As a result of examining well over 10,000 specimens on loan, many novelties are discovered and a large number of nomenclatural adjustments are needed. These will be published in separate papers. However, the present article deals with resolving the circumscription of four closely related species described in the nineteenth century. The first (*H. glauca* Burch. ex DC.) was described by de Candolle (1821), the next two (*H. sarcophylla* Meisn. and *H. brachycarpa* Meisn.) by Meisner (1842), and the last (*H. florulenta* Sond.) by Sonder (1846). Some duplicates of the type collections of all four species and their varieties were not examined, but their digital images were carefully checked in JSTOR (2019). Marais (1970) examined only the type collections at K, PRE, and SAM and did not study those of the two species described by Meisner (1842). As a result, the delimitations two of the three species below differ significantly from the conclusions reached by Marais. Meisner's types were not identified prior to the present study, and their images (Fig. 1–2) are shown here for the first time. Because the limits of *H. florulenta* and *H. brachycarpa* have been confused since the account of Marais some fifty years ago, detailed descriptions and examined specimens are given below for the three species recognized.

1. *Heliophila glauca* Burch. ex DC., Syst. Nat. 2: 690. 1821. TYPE: SOUTH AFRICA. Eastern Cape: Nelson Mandela Bay, Uitenhage, between Galgebos and Melk River, 17 February 1814, *W. J. Burchell 4782* (holotype: K [000230569]; isotype: G [00207088].

Homotypic synonym: *Heliophila glauca* var. *candida* DC., Syst. Nat. 2: 690. 1821.

Heterotypic synonyms: *Heliophila glauca* var. *purpurascens* DC., Syst. Nat. 2: 690. 1821. TYPE: SOUTH AFRICA. Western Cape: Garden Route, George, Uniondale, 14 March 1814, *W. J. Burchell 4969* (holotype: K [000230571]; isotypes: G [00207088], PRE [0408604-0, image seen].

Heliophila sarcophylla Meisn., London J. Bot. 1: 463. 1842. TYPE: SOUTH AFRICA. Western Cape: Garden Route, George, Langkloof, 1 March 1839, *C. F. F. Von Krauss 1245* (holotype: NY [03468226]; isotypes: BAS [image seen], FI [005684, image seen], M [0108058], TUB [000635, 000636, images seen], W [0009170]. Fig. 1.

Plants subshrubs or shrubs, glaucous. *Trichomes* absent. *Stems* woody at least along lower parts, 40–200 cm tall, smooth, terete, erect to ascending, virgate, simple or branched, glabrous. *Leaves* cauline, fleshy; petiole absent; blade simple, oblong to narrowly lanceolate, 0.8–1.5 cm × 1.5–4.0 mm, entire, unsegmented, minutely auriculate at base, without a pair stipule-like glands at node, glabrous, base articulate, not decurrent. *Racemes* terminal, lax, 15–35-flowered, elongated in fruit, not secund; rachis straight, glabrous; fruiting pedicels without a pair of basal bract-like glands, articulate at base, glabrous, slender, erect and subappressed to rachis, straight, persistent, lowermost 5–11(–14) mm long; buds oblong. *Sepals* ascending, oblong, 4.0–6.5 mm long, glabrous, caducous, lateral strongly saccate at base, median not saccate, all cucullate. *Petals* purple, mauve, or white, obovate, 7–12(–14) × (3–)4–6(–8) mm, ascending, rounded at apex, unappendaged, not papillate; claw 0.5–1.0 mm long. *Stamens* tetradynamous; filaments 2.5–7.0 mm long, glabrous, unappendaged; anthers oblong, 1.5–2.0 mm long, not apiculate at apex. *Nectar glands* lateral, lunar, median glands absent. *Ovary* glabrous; ovules 4–10 per ovary. *Fruit* dehiscent silique, capsular, narrowly oblong or subelliptic, (0.9–)1.5–2.8(–3.5) cm × 3.5–5.0 mm, latiseptate, glabrous, not moniliform, straight along replum, smooth, erect and appressed to rachis; valves

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I am grateful to the directors, curators, and collection managers of the herbaria cited herein.

[1] Missouri Botanical Garden, 4344 Shaw Boulevard, St. Louis, Missouri 63110, U.S.A.

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FIGURE 1. Holotype of *Heliophila sarcophylla* Meisn. (*C. F. F. Von Krauss 1245*, NY).

papery, coarsely reticulate veined, midvein distinct, margin not thickened; gynophore 0.2–1.0 mm long; style in fruit 2–6 mm long, cylindric tapering to apex, stout, glabrous; stigma entire. *Seeds* uniseriate, suborbicular, flattened, margined, 2.5–4.0 mm in diam.

Phenology: flowering August–April.

Habitat: well-drained clay stony grounds, rocky ridges, fynbos vegetation; 450–1590 m.

Distribution: South Africa, Western Cape (Cape Winelands, Central Karoo, and Garden Route districts) and Eastern Cape (Nelson Mandela Bay and Sarah Baartman districts).

Additional specimens examined: SOUTH AFRICA. Western Cape: Cape Winelands, Langeberg, Witberg, E of Robinson Pass, *G. C. Matthews 1236* (PRE). Garden Route, Kannaland [Calitzdrop], Rooiberg Pass, *J. P. H. Acocks 20391* (BM, K, M, PRE, W), *J. M. Wurts 1635* (NBG); N side of Rooiberg Mts., *Mauve et al. 42* (MO, NBG, W); Klein Swartberg, *J. M. Wurts 1514* (NBG); Rooiberg, *J. M. Wurts 1306* (NBG), *H. C. Taylor 9627* (NBG); Rooiberg, Bailey Peak, *J. J. Meyer 437* (PRE), *J. Volk 1786* (NBG), *E. G. H. Oliver 5454* (K, NBG), *M. F. Thompson 3352* (PRE); Touwsberg, *D. J. McDonald 2369, 2448* (NBG), *J. M. Wurts 1356* (NBG); Gamke Mt. Reserve, slopes of Paddafluitjieskloof, *Erasmus 131* (NBG); N slope of Gamka Mts, *A. F. Boshoff P174* (NBG); Klein Karoo, Gamka Mt. Reserve, *P. & J. Cattell 43* (BOL), *R. Allarice 1698* (NBG). Hessequa [Riversdale], Muiskraal, *E. E. Galpin 3742* (PRE); Little Karoo, N slopes of Touwsberg, above farm Miskraal, *G. A. Verboom 7* (BOL). George [Uniondale], Uniondale: 4 miles NW of Joubertina, *J. P. H. Acocks 20023* (PRE); Misgund hills, *E. Esterhuysen 6942* (BOL, K, NBG), *H. G. Fourcade 4241* (K). Oudtshoorn: Roodeberg, *Bond 222* (NBG); N side of Outeniqua Mts. near Moeras River, *E. Esterhuysen 19459* (BOL). Central Karoo, Laingsburg, Anysberg, *E. Esterhuysen 32859* (BOL, MO). Eastern Cape: Nelson Mandela Bay [Uitenhage], Loeri- and Camtoursrivier, *C. F. Ecklon & C. L. P. Zeyher 102* (B, C, K, M, MO). Sarah Baartman, Dr Beyers Naudé [Willowmore], Antoniesberg, *P. A. Bean & J. H. T. Volk 2045* (BOL); Kouga Mountains, Willowmore, *H. C. Taylor 898* (NBG). Kouga [Humansdrop]: Witelsbos, *H. G. Fourcade 2106* (PRE); Bo-Kouga, off Long Kloof, *R. D. A. Bayliss 7124* (G, M, MO, NY, UC); Patensie Hills, *W. F. Barker 7901* (NBG); Kouga Mts., above Geelhoutboskloof, *P. A. Bean 1090* (B, MO, NBG); Kouga Mts. near Enselandkop, *J. Volk 948* (MO).

The holotype of *Heliophila sarcophylla* consists or two branches on the left of sheet with a small label in the middle handwritten by Krauss and a fully detailed label on the left hand written by Meisner. The FI and M sheets of the type collection lack the collection number, but all of the other gathering data are identical to that of the holotype and, therefore, they are recognized here as isotypes.

As indicated by Stafleu and Cowan (1981), Meisner's herbarium is housed in NY, not BAS where he worked most of his life. His label of the species reads: "Heliophila (Lanceolaria) sarcophylla nob[is] in Hook. Lond. Journ. 1: p. 463. Differt a H. macrosperma seminibus angusta membranaceo-marginatis, etc. Non differt a H. glauca Burch DC.! Sonder in Litt. D. 7 Febr. 1845."

A controversial specimen of Krauss in the Bernhardi Herbarium, MO [1925794], has a label that reads "N. 1245. *Heliophila sarcophylla* n.sp. Meiss. In Landekloof, George, Mart." The label is identical to that of the holotype the above, but the plant definitely belongs to *H. florulenta*. Clearly, there is a mix-up of the label and the plant, and the specimen is not a type material of any taxon. It has the characteristic gland pairs at the bases of leaves and pedicels that *H. glauca* (including *H. sarcophylla*) lacks.

Heliophila glauca is easily distinguished among the shrubby members by having articulate leaves and fruiting pedicels lacking the basal pair of glands, minutely auriculate leaves, fruit and fruiting pedicels appressed to rachis, and narrowly oblong to subelliptic fruit.

2. *Heliophila florulenta* Sond., Abh. Naturwiss. Verein Hamburg 1: 263. 1846. TYPE: SOUTH AFRICA. Eastern Cape: Zwartkopsrivier, 1829, *C. F. Ecklon* (lectotype designated by Nordenstam (1980: 262): S [G8767]; isolectotypes: B [100153871, 100299439], C, GOET [002608, image seen], K, M [0108069], MO [925695], P [00739548], PRC [451618], PRE, SAM [0028064-0], UPS, W [0009167, 18890303895]).

Heterotypic synonym: *Heliophila florulenta* var. *obliqua* E.Mey. ex Sond., Abh. Naturwiss. Verein Hamburg 1: 263. 1846. TYPE: SOUTH AFRICA. Eastern Cape: Witpoortberg, *J. F. Drège s.n.* (lectotype designated by Nordenstam (1980: 262): S [G8766]; isolectotypes: B [100153870], P [05445366, 00739545], PRE [0408614-0, 0408615-0, images seen], W [0009168]).

Plants shrubs or small trees, glaucous. *Trichomes* papillate on stamens and petal claws, absent elsewhere. *Stems* woody, 0.5–2.2 m tall, striate, ridged and with contiguous papilla-like tubercles, erect to ascending, branched above, glabrous. *Leaves* cauline, fleshy; petiole undifferentiated; blade simple, linear to oblanceolate, 1.5–5.0 cm × 1–4 mm, entire, not auriculate at base, with a pair stipule-like subulate glands at node, glabrous, base decurrent, apex attenuate into pointed apicula. *Racemes* terminal on lateral branches, corymbose, 5–30-flowered, elongated slightly and remaining subcorymbose in fruit, not secund; rachis straight, papillate or smooth; fruiting pedicels with a pair of basal bract-like glands, not articulate at base, glabrous, slender or slightly stout, much expanded at receptacle, ascending to divaricate, straight, persistent, lowermost 5–10(–15) mm long; buds oblong. *Sepals* erect to ascending, oblong, 3–5 mm long, glabrous, caducous, lateral pair strongly saccate at base, median not saccate, all not cucullate. *Petals* white to creamy white, obovate-spatulate, 6–8 × 1.0–2.5 mm, ascending, rounded at apex, unappendaged; claw 2–4 mm long, strongly differentiated from blade, papillate. *Stamens* subequal; filaments 3.5–5.0 mm long, densely papillate at least along proximal half or third, unappendaged; anthers oblong, 0.6–0.8 mm long, not apiculate at apex. *Nectar glands* lateral, lunar; median glands absent. *Ovary* glabrous; ovules 4–6 per ovary. *Fruit* dehiscent silique, capsular, elliptic-lanceolate, 2.0–3.7 cm × (3.0–)4.5–6.0 mm, latiseptate, glabrous, not moniliform, straight along replum, smooth, ascending to divaricate; valves papery, midvein and lateral veins prominent, forming a reticulum, margin not thickened, apex attenuate into style; gynophore (0.5–)1.0–3.0 mm long; style in fruit (0.7–)1.0–2.0(–2.7) mm long, attenuate, glabrous; stigma entire. *Seeds* uniseriate, suborbicular, flattened, minutely reticulate, wingless, not margined, 2.5–4.0 mm in diam.

Phenology: flowering in July through August, rarely as early as May or as late as December.

Habitat: barren mountain slopes, scrubland, sandy soil on rocky ridge, rocky loams soil in arid fynbos; 50–1200 m.

Distribution: South Africa, Western Cape (Garden Route District) and Eastern Cape (Nelson Mandela Bay and Sarah Baartman disricts).

Additional specimens examined: SOUTH AFRICA. Western Cape: Garden Route, Mossel Bay, Hounslow Farm, ridge after Brakriver, *T. Dold & A. D. Booi 380* (GRA, NGB). Eastern Cape: Nelson Mandela Bay, Port Elizabeth, *J. F. Drège 9283* (PRE), *J. F. Drège 1711* (SAM), *R. Marloth 1703* (E); New Brighton, near Port Elizabeth, *E. West 312* (BOL). Sarah Baartman, Dr Beyers Naudé, Steytlerville, 10 miles from Steytlerville on Mt. Steaward Rd, *R. Storey 2490* (PRE); 25 miles E of Willowmore, *R. H. Compton 19649* (BOL, NBG). Makana, Coombes Valley, *R. D. A. Bayliss 4314* (NBG, UC). Kouga [Humansdrop], Lower Papiesfontein, *R. M. Cowling 776* (GRA); W bank of Gamloos River, near Hankey, *H. G. Fourcade 2272* (K).

Sonder (1846) listed two collections by Ecklon and Zeyher from Zwartkopsrivier and Bethelsdrop. However, as indicated by Nordenstam (1980), both collections were distributed mixed in all isolectotype sheets as *Ecklon & Zeyher 101*, and it is impossible to tell which specimen on a given sheet belongs to which locality.

Sonder (1846) had an isotype of *Heliophila brachycarpa* in his herbarium and recognized the species as distinct from the material he described in the same work as *H. florulenta*. Indeed, he placed the two species in different sections and indicated in the species descriptions that former has short-clawed, oblong-spatulate petals 2 lines wide, whereas the latter has puberulent long claws and ovate [actually obovate] petal blades 1 line wide. In that, Sonder's description of *H. brachycarpa* was more detailed than and fully in agreement with original of Meisner (1842). Despite these very significant differences in petal morphology, Marais (1970), who did not examine any specimen in Sonder's herbarium or authentic material of *H. brachycarpa,* reduced *H. florulenta* to synonymy of the earlier-published former species. Unfortunately, this misinterpretation by Marais continues for the past 50 years, and one still finds the two distinct species united in all herbaria of the world.

The entire species description of *Heliophila brachycarpa* in Marais (1970) is a perfect fit for *H. florulenta,* and his description of the floral and fruit morphology do not apply to the type collection of the former, which he never studied. Both Meisner (1842) and Sonder (1846) did not describe the mature fruit of *H. brachycarpa,* and that may have misled Marais to overlook the fact that the two species have very different fruit morphology, as evidenced from his 1 March 1962 annotation and his (Marais, 1970: 68) citation of the isolectotype sheet of *H. florulenta* (K) as *H. brachycarpa*. This sheet consists of a flowering branch of the isolectotype on the right and a fruiting branch near its base, and it is a mixed collection with *MacOwan 845* that includes two large flowering branches of *H. florulenta* (one on the left and the other in the center center) and a smaller fruiting branch of *H. brachycarpa*. I have not examined all of the specimens cited by Marais under his *H. brachycarpa*, but for at least two collections, *Compton 19649* (BOL, NBG) and *Fourcade 2272* (K), the plants definitely belong to *H. florulenta*. He cited *Compton 11216* (perhaps in NBG) from Whitehill that I did not examine. However, from the same locality he annotated on 8 Oct. 1963 *Compton 10880* (NBG), but this one has glabrous filaments and petal claws and definitely belongs to *H. brachycarpa* (sensu this author, not Marias; see below). Therefore, in order to avoid any future confusion, all material of the two species examined for this study are cited below. MacOwan's collection is a good indication that the two species grow sympatrically, at least for part of their ranges.

Heliophila florulenta is easily distinguished from *H. brachycarpa* in flower, fruit, and young sterile stems. It has white to creamy white, spatulate-obovate petals 6–8 × 1.0–2.5 mm, papillate petal claws strongly differentiated from blade and 2–4 mm long, densely papillate filaments along at least proximal half or third, anthers 0.6–0.8 mm long, elliptic-lanceolate fruit (3.0–)4.5–6.0 mm wide, and gradually attenuate styles (0.7–)1–2(–2.7) mm long (Fig. 3A, B, C). By contrast, *H. brachycarpa* has pale mauve to pink, oblanceolate petals 9–14 × (2.5–)3.0–5.0 mm, glabrous petal claws 1–2 mm long and hardly differentiated from blade, glabrous filaments, anthers 1.2–1.5 mm long, ovate-lanceolate fruit (6–)7–9 mm wide, and cylindrical style (4–)5–10 mm long, abruptly terminating fruit apex (Fig. 3D, E, F). When lacking both flower and fruit, plants *H. florulenta* are distinguished by having young stems with contiguous, minute, papilla-like tubercles that *H. brachycarpa* lacks.

3. *Heliophila brachycarpa* Meisn., London J. Bot. 1: 465. 1842. TYPE: SOUTH AFRICA. Eastern Cape: Nelson Mandela Bay, Uitenhage, *C. F. F. Von Krauss 1254* (holotype: NY [03468302]; isotypes: M [0152274], MO [1925731], S [1216058], TUB [000630, 000631, images seen]). Fig. 2.

Plants small trees or scrambling shrubs, not glaucous. *Trichomes* absent. *Stems* woody, 1–2 m tall, slightly striate, ridged, without papilla-like tubercles, erect to ascending, many branched, glabrous throughout. *Leaves* cauline, not fleshy; blade simple, linear to linear-oblanceolate, (1.3–)2.5–6.0 cm × 1–2 mm, attenuate to petiole-like base, margin entire, not auriculate at base, with a pair of stipule-like glands at node, glabrous, base not articulate, somewhat decurrent. *Racemes* terminal and lateral, not intercalary,

FIGURE 2. Holotype of *Heliophila brachycarpa* Meisn. (*C. F. F. Von Krauss 1254*, NY).

corymbose, 4–23-flowered, elongated in fruit, not secund; rachis straight, glabrous; fruiting pedicels with a pair of basal bract-like glands, not articulate at base, glabrous, slightly stout, divaricate-ascending to divaricate, straight or slightly curved, persistent, lowermost (6–)10–25 mm long; buds oblong-ovate. *Sepals* ascending, oblong, 5–6 mm long, glabrous, caducous, lateral pair not cucullate at apex, saccate at base, median pair slightly cucullate, not saccate. *Petals* pale mauve to pink, oblanceolate, 9–14 × (2.5–)3.0–5.0 mm, ascending, rounded at apex, unappendaged, not papillate; claw 1–2 mm long, hardly differentiated from blade. *Stamens* tetradynamous; filaments 3.5–6.0 mm long, glabrous at base, unappendaged; anthers oblong, 1.2–1.5 mm long, not apiculate at apex. *Nectar glands* lateral, median glands absent. *Ovary* glabrous; ovules 6–8 per ovary. *Fruit* dehiscent silique, capsular, ovate-lanceolate, 2.2–3.0 cm × (6–)7–9 mm, latiseptate, glabrous, not moniliform, straight along replum, not torulose, apex abruptly ending in style, ascending to suberect; valves thick papery, midvein and lateral veins prominent, margin not thickened; gynophore 1–2 mm long; style in fruit (4–)5–10 mm long, cylindric, stout, glabrous; stigma entire. *Seeds* uniseriate, ovate, flattened, wingless, not margined, 4.0–4.5 × 3.0–3.5 mm; sinus shallow, wide.

Phenology: flowering March, July–Aug; fruiting September into October.

Habitat: arid areas in shale, rocky places, flats at foot of mountains; ca. 600 m.

Distribution: South Africa, Western Cape (Central Karoo District) and Eastern Cape (Nelson Mandela Bay and Sarah Baartman districts).

Additional specimens examined: SOUTH AFRICA. Western Cape: Central Karoo, Laingsburg, Karoo Garden, Whitehill, *R. H. Compton 10880* (NBG). Eastern Cape: Sarah Baartman, Dr Beyers Naudé, Ganna Leegte, *M. R. Levyns 6468* (BOL). Makana: 27 miles on East London road from Grahamstown [=Mokhanda], *E. Brink 188* (GRA); near Trumpeters Drift, Albany, *L. L. Britten 7045* (GRA, PRE); Fish River Pass, *R. D. A. Bayliss 2257 (*A, G, MO, NBG, NY, UC).

Meisner's annotation on the label of the holotype of *Heliophila brachycarpa* reads "H. (Carpopodium) brachycarpa~~m~~, nob[is]. M[ihi. Hook. Lond. Journ. 1 p. 465." The above isotypes at M and the Bernhardi Herbarium (MO) have the exact locality data as that of the holotype but without the collection number.

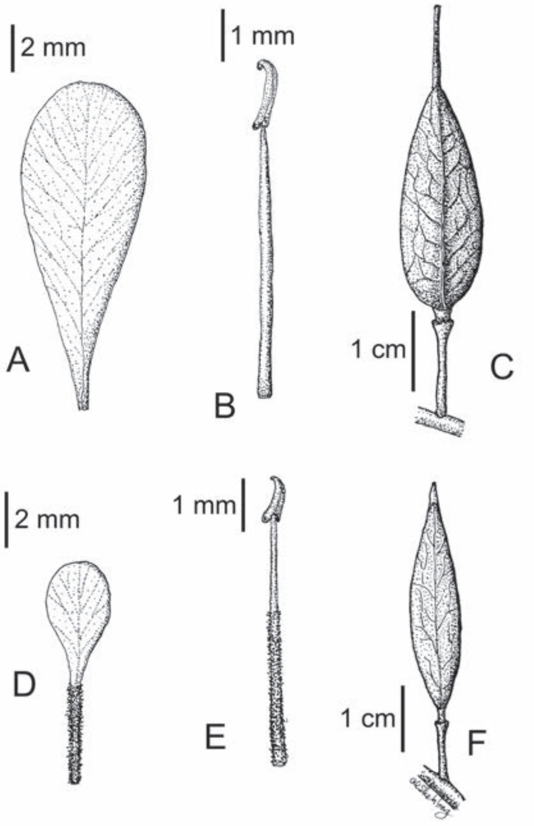

FIGURE 3. *Heliophila brachycarpa* Meisn. (**A–C**) and *H. florulenta* Sond. (**D–F**). **A**, **D**, Petals; **B**, **E**, Median stamens; **C**, **F**, Fruit and fruiting pedicel. Drawn by Al-Shehbaz: **A–C** from *R. D. A. Bayliss 2257* (MO [2007181]); **D**, **E** from *R. H. Compton 19649* (NBG); **F**, from *R. D. A. Bayliss 4314* (UC).

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APPENDIX
INDEX TO NUMBERED COLLECTIONS

J. P. H. Acocks 20023 (**1**); *20391* (**1**).

R. Allarice 1698 (**1**).

W. F. Barker 7901 (**1**).

R. D. A. Bayliss 2257 (**3**); *4314* (**2**); *7124* (**1**).

P. A. Bean 1090 (**1**).

P. A. Bean & J. H. T. Volk 2045 (**1**).

P. Bond 222 (**1**).

A. F. Boshoff P174 (**1**).

E. Brink 188 (**3**).

L. L. Britten 7045 (**3**).

W. J. Burchell 4782(**1**); *4969* (**1**).

P. Cattell & J. Cattell 43 (**1**).

R. H. Compton 10880 (**3**); *19649* (**2**).

R. M. Cowling 776 (**2**).

T. Dold & A. D. Booi 380 (**2**).

J. F. Drège 1711 (**2**); *Drège 9283* (**2**); *s.n.* [no date] (**2**).

C. F. Ecklon s.n. [no date] (**2**).

C. F. Ecklon & C. L. P. Zeyher 102 (**1**).

[*?*] *Erasmus 131* (**1**).

E. Esterhuysen 6942 (**1**); *19459* (**1**); *32859* (**1**).

H. G. Fourcade 2106 (**1**); *2272* (**2**); *4241* (**1**).

E. E. Galpin 3742 (**1**).

C. F. F. Von Krauss 1245 (**1**); *1254* (**3**).

M. R. Levyns 6468 (**3**).

R. Marloth 1703 (**2**).

G. C. Matthews 1236 (**1**).

A. Mauve et al. 42 (**1**).

D. J. McDonald 2369 (**1**); *2448* (**1**).

J. J. Meyer 437 (**1**).

E. G. H. Oliver 5454 (**1**).

R. Storey 2490 (**2**).

H. C. Taylor 898 (**1**); *9627* (**1**).

M. F. Thompson 3352 (**1**).

G. A. Verboom 7 (**1**).

J. Volk 948 (**1**); *1786* (**1**).

E. West 312 (**2**).

J. M. Wurts 1306 (**1**); *1356* (**1**); *1514* (**1**); *1635* (**1**).

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THE FIRST BOTANICAL EXPLORATION TO THE UPPER CUIARÍ (CUYARÍ) AND ISANA RIVERS, UPPER RÍO NEGRO BASIN, GUAINÍA DEPARTMENT, COLOMBIA

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Abstract. This account reports a journey of ca. 500 km from the city of Inírida to the Colombian basins of the Cuiarí and Isana Rivers (Guianía department) in April–May 2014, the first botanical expedition to this region. This area exemplifies one of the last innermost and botanically unexplored regions of the northwestern corner of the Amazon basin (the upper Río Negro basin), aside from the fieldwork started some 234 years ago with the exploration of the middle and lower portion of the Isana basin in Brazil (where it is called Içana) by the Portuguese naturalist Alexandre Rodrigues Ferreira. On our expedition we collected 1301 botanical numbers, which resulted in eight new species (two already published), two new families, and 24 species new to the Flora of Colombia. Another noteworthy feature is the high diversity of the forests in the upper Isana River, represented by between 108 and 162 spp. with a diameters ≥ 2.5 cm in different 40 x 40 m plots (1600 m^2). The Isana River is a white-water basin (with high levels of sediments), with large areas covered by the vegetation typical of black-water rivers (Amazon Caatinga forests, lower forests, savannas and sclerophyllous shrubby vegetation over white-sand soils). This feature results from the influence of several black-water rivers, the headwaters of which drain from Precambrian Guiana shield outcrops. This account of the first botanical exploration in the Colombian portion of the Cuiarí and Isana Rivers is yet another example of the need for continued floristic studies in regions where there are large geographic gaps in the knowledge of Amazonian flora. Advances in documentation of this flora can be achieved through institutional and private partnerships, improved training, and continued fieldwork in collaboration with local inhabitants. A discussion of demarcation issues regarding the frontier between Brazil and Colombia in this northwestern corner of the Amazon basin, its physical and biological environments, and its ancestral and current inhabitants is presented.

Keywords: Amazonia, botanical exploration, upper Río Negro basin, Cuiarí and Isana Rivers, Colombia

Resumen. La presente crónica describe el recorrido de aproximadamente 500 km desde la ciudad de Inírida hasta los sectores colombianos de las cuencas de los ríos Cuiarí e Isana (departamento del Guianía) en abril–mayo de 2014, actividad que representa la primera exploración botánica a esta region. Esta es una de las últimas regiones del Noroeste de la Cuenca Amazónica (alto Río Negro) que no se había explorado botánicamente, a pesar de la gran cantidad de trabajos de campo realizados en el alto Río Negro, las cuales comenzaron hace 234 años, con la exploración de las cuencas media y baja del río Isana en Brasil (donde es llamado Içana) por el naturalista portugués Alexandre Rodrigues Ferreira. Durante el viaje se colectaron 1301 números botánicos, de estos, se identificaron ocho especies nuevas para ciencia (dos ya publicadas), igualmente dos familias y veintecuatro nuevos registros para la Flora de Colombia. Otro aspecto biológicamente importante es la alta diversidad de los bosques del alto río Isana, donde se midieron entre 108 y 162 spp. (DAP ≥ 2.5 cm) en parcelas de 40 x 40 m (1600 m^2). La cuenca del rìo Isana es de aguas claras, con extensas áreas de vegetación propias de los sistemas de aguas negras (i.e. bosques de Caatinga Amazónica, extensas sabanas y arbustales esclerófilos sobre suelos de arena blanca). Esta situación es debido a los numerosos caños y ríos que desembocan en los sectores medios y bajos de la cuenca, provenientes de los afloramientos precámbricos del escudo guayanés. El presente registro de la primera exploración botánica en la parte colombiana de los ríos Cuiarí e Isana demuestra la necesidad de continuar con los estudios florísticos en sectores poco estudiados. Sin embargo, avances en documentar la flora y vegetación serán logrados a través de las alianzas institucionales y privadas, a través de entrenamientos en trabajos de campo y en el incremento de nuevas expediciones con la colaboración de los habitantes locales. Se incluye información acerca de la historia de la delimitación de la frontera entre Brasil y Colombia, aspectos físicos y biológicos de la cuenca del río Isana, sus habitantes antiguos y actuales, y reseñas de la exploración botánica del noroeste de la cuenca Amazónica.

Yaakuti iipenaa. (Abstract in Kuripako). Jlieje yaakutida likadaa wajnee, likaitepe jnete lidana najnikarun inakuapana wadeepedali 500 km iyapika likuñueta Inirida jnete liukawa Iniali jnete kuwialisre Colombiakawani (departamento del Guainía), katsa idejnikjeti ikuñuetakada nanakuaapana jnaja yajnikape ikapa awakada nesre. Katsa nene piketenkawa Noroeste Cuenca Amazonía (Padzawidza jiwidaan) karukawa nakanantakawa awakada inakuapana; nentsatja manupeka jnaja idejnikape pia nesre, 234 años nakuñuetakadzamina, nakapa pia jlieje lipamudzuaka jnete linumanaa jlieje Iniali Brazil kawani (najne nesreni Iniali) lima jlieje kaakunadali ipedzukada awakada Portugués Alexandre Rodrigues Ferreira. Najnikadanaku nesre naniwa 1301 jaikulima, nanakjite naaketa ochona jaiko waliperi karuperitsa nakapaali (Dzamada nanakjite upina nadana nanaku), jnetetsakja, dzamapuku jaikulima nadzawaka jnete veinticuatro waliperi jaiko karuperi pia paaketa Colombia liko. Pada kaakunadali linakjite jlieje nadejnikale, naaketakapuaka manupe nadzawaka jnaja awakadalima Isana jiwidansre, nawaa 108 jnete 162 nadzawaka jnaja jaiko (namakaneka ≥5 cm) jnete pakuraratanda awakada limakaiteka 40 x 40 m (1600 m^2). Jlieje Isana uni jalekjai, isrokada manupe awakadalima pakapampe nerikuda jnaja uni itakjaipe (i.e. bosques de Caatinga Amazónica, extensas sabanas y arbustales esclerófilos sobre suelos de arena blanca). Kadzuni, lima jlieje lisroka manupe iñaupukjape inukape linakjite jlieje jidzapa najnenda escudo guayanés jnete naaketakawa iniali yapidza. Jlieje wadananda pandza linakuapana jlieje idejnikjeti wadzekatali inali jnete kuwiali Colombia kawani, likananta fa wasrokatsa wakanantakapjaka awakada inaku karukawatua naaka nesre. Metsa, wataitakaru wadzekatakani nasrotsa nadejnika napidzawaka jnaja gobierno idzarupe jnete jnaja yakajleperitsa liudza, nakanantaka matsiawa jnete namanupeta jnaja idejnikjeti awakadaliku naapidza jnaja naiki liminanai. Lirikuda tsakja jlieje nenwatsa wakaite kuame piaka jneraka jnenana jnaja Colombia jnete Brazil, kjalekawaka lidzena jnete awakadalima inakuapana, jnaja liminanai upiperi jnete pandzaperi, jnete kuame najnikarun jnewa nakapa kadzuliaja Noroeste Cuenca Amazónica liko.

We gratefully acknowledge the support provided by Compensation International Progress S.A.–Greenlife (Ciprogress–Greenlife) and the Kuripaco indigenous alliance for our botanical expedition to the Cuyarí and Isana Rivers. The trip was sponsored by the Flor de Inírida REDD+ Project of the Guayana–Amazonian Transition Region, which made this undertaking possible. We also thank Martha Rivera, Claudia Restrepo, and María C. Montilla for logistic support, and Fredy Gómez, Jorge L. Contreras, Carolina Villegas, Jahir Bedoya, Orlando Cordubí, and Lino Flores for their field assistance. We are indebted to the Kuripaco people of the communities of Sejal, Amanadona, and Campo Alegre (Cuiarí River) for their help during different stages of the expedition, especially their effort carrying hundreds of kilograms of equipment and food along ancestral trails between the “Caño” Naquén and Cuiarí River, and the “raudal” Yuruparí along the Cuiarí River. Finally we thank Gustavo A. Romero (AMES) for his help finding literature and his comments on early versions of this text. — *Footnotes continued on next page.*

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The lowland rainforests of the Amazon basin harbor the highest tree diversity in the world, not found in any other terrestrial ecosystem (Gentry, 1992; ter Steege et al., 2013, 2016; Dexter et al., 2017; Antonelli et al., 2018; Dick and Pennington, 2019). According to current research on its vegetation (mainly referring to rainforest), it is botanically poorly known (Hopkins, 2007; Schulman et al., 2007; Cardoso et al., 2017). Cardoso et al. (2017) assert that "the Amazon is renowned for holding an unprecedented, yet poorly known or unexplored plant diversity," a statement we would dispute. These authors also point out that many regions inside the basin remain unrepresented by even a single collection, perhaps implying that many species distributions are still inadequately known, not well understood, or both (ter Steege et al., 2011, 2016, 2019). We argue that several of the innermost areas of the basin (e.g., the Río Negro basin, Manaus, and, the Guayana Shield *sensu lato*) have been relatively well explored and studied; information about the explorations are summarized in Aymard et al. (2016a,b) and ter Steege et al. (2016).

Currently, it is well-understood that the turnover or replacement of terrestrial taxa across rivers are driven by biogeographic patterns in the Amazon basin and its major tributaries (Ribas et al., 2012; Pirani et al., 2019). This pattern was first pointed out by Wallace (1852), and it has since been documented for other terrestrial organisms at multiple geographic scales (Naka and Brumfield, 2018). However, in this immense basin, western Amazonia (the area between the Andes and the Amazon River) is so far the place with the highest plant diversity (Valencia et al., 2004; Tuomisto et al., 2016; Draper et al., 2019), perhaps due to its remarkable geographic history during the Cenozoic (e.g., formation of the Amazon River and the uplift of the northern Andes), events that profoundly influenced climate, speciation, and biotic interchange, generating the highest diversity of habitats (Hoorn et al., 2010, 2017; Antonelli et al., 2018). Nonetheless, the accurate connection of these events with biotic diversification often is doubtful (Baker et al., 2014).

Although Amazonian forests have been shown to be diverse, some tree species are consistently more abundant than would be expected from chance alone, a feature initially pointed out by Black et al. (1950), Ducke and Black (1953), and Pires et al. (1953), and later corroborated by ter Steege et al. (2013) and Zizka et al. (2018). An estimated 11,676 tree species, belonging to 1225 genera and 140 families, make up Amazonian forests (ter Steege et al., 2016). However, a recently revised assessment places the number of Amazonian tree species at 10,071 (ter Steege et al. 2019), with over half the stems belonging to just 227 species. These disproportionately common trees have been dubbed the "hyperdominants" (ter Steege et al., 2013). Rare species also contribute to this diversity (Wills et al., 2006), but their spatial distribution remains unsatisfactorily understood (Zizka et al., 2018).

The Colombian portion of the Cuyarí (or Cuiarí) and upper Isana Rivers represents a prime example of the situation described above—a region located in the upper Río Negro (Guianía) that had been a complete botanical blank. In addition, that area (e.g., Papunaua River) had an important role in the Amazon rubber boom of 1860–1930, as a result of constant human movement between the upper Río Negro and the middle Orinoco River (Rivera, 1924). The cruel treatment to which rubber tappers were subjected for six to eight months of the year was called the "Putumayo scandals" (García-Jordán, 2001). These frightful events symbolized a dark chapter of human history characterized by exceptional exploitation of and cruelty toward Amerindian populations (for a review, see Coomes and Barham, 1994; Kraus, 2018).

The present account reports the first botanical exploration of the Colombian portion of the Cuyarí o Cuiarí and upper Isana Rivers (Fig. 1). Interest in studying these basins has been motivated by a project that would protect more than 4,000,000 ha of diverse vegetation, thus improving the quality of life of communities that live in the watersheds of several rivers (i.e., Cuyarí, Guianía, and Isana) that are part of the upper Río Negro basin. With its strategic location and well-conserved habitats, this region, which had been isolated from researchers and thus completely unknown biologically, is a potentially important site for biological exploration.

MATERIALS AND METHODS

We conducted a review of data from ca. 33,000 collection sites stored in digital biodiversity databases, and consulted bibliography sources available by April–May 2014. These tools allowed us to assemble data on the occurrence of species from various sources, such as herbaria and museums, as well as data from the literature. An updated database of botanical collections from the Isana (in Colombia) or Içana (in Brazil) River basins and surrounding areas in Brazil and Colombia was compiled from records in Tropicos (www.Tropicos.org), the speciesLink Network (http://www.splink.org.br), *Lista de espécies da Flora do Brasil* (http://inct.florabrasil.net/category/lista-de-especies-da-flora-do-brasil/), Jabot (http://www.jbrj.gov.br/jabot), and Global Biodiversity Information Facility (https://www.gbif.org/). We also reviewed the collections of herbaria at A, COAH, COL, GH, and NY (acronyms according to Thiers, 2012), and the most recent bibliographical analysis of Colombian Amazonian plants (Infante-Betancour and Rangel-Ch., 2018a,b). In order to indicate the route from the city of Inírida to the Colombian portion of the Cuiarí and the upper Isana Rivers, we marked all the points mentioned in our journey in a digital image of this region, which is available in the following link: https://drive.google.com/file/d/1VrvnOfMOY9R5bIk3TQEsVP1hQedecq-b/view

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Footnotes continued

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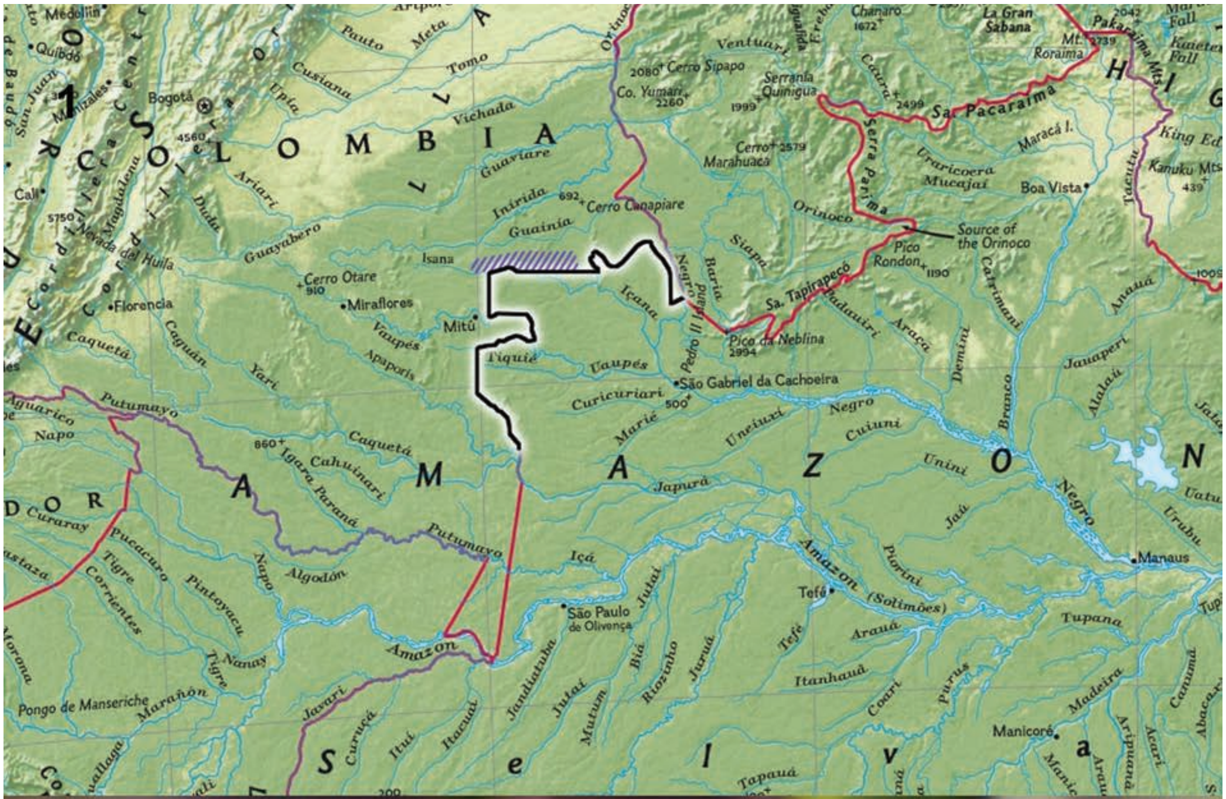

FIGURES 1–2. **1**. Map of Brazil and Colombia showing the border (double bold) according to the agreement known as the Treaty of Bogotá, or the treaty of Vázquez Cobo-Martins, signed in Bogotá in 1907. The area marked with diagonal lines represents the region of the first botanical exploration in the Colombian basins of the Cuiarí and Isana Rivers. Compiled by C. Méndez. **2**. Flower of *Asteranthos brasiliensis* Desf. (Lecythidaceae). Photograph courtesy of Hans ter Steege.

Results

The Río Negro Context: the Cuiarí and Isana River basins

The Cuiarí and Isana Rivers are found in the upper Río Negro basin, the largest black-water river in the world (Marengo et al., 2012). The latter has its headwaters in the sources of the Guianía River (Colombia), located in the northwestern corner of the Amazon basin, and it communicates with the Orinoco River basin through the Casiquiare Channel (Stokes et al., 2018). The basin of the Río Negro (the name that this river takes at the confluence of the Guianía River and the Casiquiare Channel) and its main tributaries (e.g., Río Branco and the Curicuriarí, Isana, Vaupés, and Xié Rivers) occupy a surface area of ca. 750,652 km^2 and have a combined length of ca. 1600 km. The Río Negro originates at the headwaters of the Guianía River and flows south in northwestern Brazil, turning eastward above the town of São Gabriel da Cachoeira. There the Río Negro is joined by the Içana River and then by the Vaupés, the latter flowing eastward from the confluence of the Itilla and Unilla Rivers, located south of Guayabero River, Colombia. The Río Negro continues flowing toward Manaus, where it meets the Solimões to form the main body of the Amazon River (Santos et al., 1984; Lleras, 1997; Epps and Stenzel, 2013). The name "Río Negro" (in Spanish; "Rio Negro" in Portuguese) means "black river," in reference to the dark waters of this river, due to their high tannin content, that create a stark contrast where they merge with the muddier waters (or "white waters") of the Solimões (Sioli, 1968; Leenheer and Santos, 1980). The sandy, acidic soils and low levels of nutrients in clear- and black-water river systems render them far less productive than the white-water systems found elsewhere in Amazonia (Ríos-Villamizar et al., 2014). However, the region sustains a complex system of vegetation, rivers, inhabitants, languages, and unique cultural practices (Márquez and Pérez, 1983; Kraus et al., 2018).

In general, this sector is characterized by elevations of 50–300 m, and has large surfaces of "terra firme" forests, flooded forests (Igapó and Varzéa), and sclerophyllous forests on oligotrophic soils known as "Caatinga Amazónica" or forested Campinarana, as well as shrublands (Banas, or low Campinas) and extensive and continuous white-sand savannas (Prance, 1989, 1996, 2001; Huber, 1995a,b; Lleras, 1997), the latter two of particular interest to those concerned with the conservation of the region's unique ecosystems and their natural resources.

As mentioned above, the Isana and Cuyari Rivers drain into the Río Negro basin; geographically, their basins are nested between the Xié (to the north) and the Vaupés (to the south) river basins. Politically, the upper portion of the Isana River is located in Colombia, the middle and lower portions in Brazil. The entire basin has a surface area of ca. 17,000 km^2 (of which ca. 60% is located in Brazil and 40% in Colombia), and the river is ca. 500 km long, extending across the Brazil-Colombia border up to its confluence with the right bank of the Río Negro, near São Gabriel da Cachoeira (Amazonas state, Brazil). The Cuiarí River has its headwaters on the east side of the "Serranía de Caranacoa" in Colombia. It has a surface area of ca. 4,000 km^2 (ca. 30% in Brazil and 70% in Colombia), and a length of ca. 200 km. The Cuiarí flows from Colombia to Brazil along the right side of the "Serranía de Naquén," until its confluence with the left bank of the Içana River, near Vista Alegre (Amazonas state, Brazil).

The Brazilian, Colombian, and Venezuelan Boundaries

The arrangement of the political borders of Brazil, Colombia, and Venezuela has always involved complex negotiations, because since the time of the arrival of explorers from the Iberian peninsula to the Amazon basin the frontiers between colonial territories of Portuguese and Spanish empires were not "sufficiently clear" (USDS, 1985). The Treaty of Madrid, signed in 1750, was a mechanism that expanded the territories of the Portuguese empire to reach almost the current area of Brazil (Ferreira-Reis, 1993): the extend this territory later was rectified in part by "La Comisión de límites del Orinoco" and other explorations that took place between 1754 and 1761 (Lucena Giraldo and de Pedro, 1992). The upper Rio Negro territory was thoroughly disputed, mainly by competing for hegemony over navigation between the Amazon and Orinoco basins through the Casiquiare Channel (Brito, 2014). This region was well known since the 17th century from maps elaborated by Jesuit missionaries (i.e., S. F. Gilij, M. de Tapia, and M. Román), and the Portuguese slavery networks (Donis-Ríos, 1989; Cabrera-Becerra, 2010). At the time they became independent, the Brazilian empire and new Republics (Colombia and Venezuela) inherited this situation (USDS, 1985), and frontier negotiations were complex because of two conflicting juridical principles. The Portuguese crown applied the principle of *uti possidetis facto*, which considers the position of their land through the factual exercise of sovereignty, whereas the Spanish crown utilized *uti possidetis jure*, by which they defended their rights to territory awarded to Spain and their colonies as long ago as the first European explorations in the New World (Ramírez, 2006). In 1826, more attempts were made to solve the border problems, which included the fact that Colombia's border with Brazil was also affected by the status of its disputes with Venezuela in the Río Negro district (García, 1942). In addition, Portugal claimed at this time that the precise location of New Granada Viceroyalty boundaries were uncertain (USDS, 1985). The latter was not true at all, because many maps published from 1798 to 1865 showed that the northwestern corner of the Amazon basin (the Rio Negro basin), and the middle Orinoco River belonged to the Viceroyalty of Nueva Granada, and the Captaincy General of Venezuela (see: http://babel.banrepcultural.org/cdm/singleitem/collection/p17054coll13/id/656/rec/32). An agreement was reached in 1907, known as the "Treaty of Bogotá" (or "El Tratado Vázquez Cobo-Martins"). However, this treaty considered only the northern section between the frontiers of Brazil and Colombia with Venezuela (USDS, 1985; López-Garcés, 2014). Therefore, through this instrument Colombia accepted as frontier a line ca. 300 km between the mouth of Apaporis River and "Uarirambá," a place where both banks of the upper Isana River start to belong to Brazil. From this landmark, the line goes 184 km straits to the East to the headwater of Memachí River. From the latter point the line up and down 50 km to North and South to get the "Cerro El Mono" located in South of "Serranía de Naquén." Finally, the line goes ca. 120 km to East, and turn ca. 120 km to South to reach "Piedra de Cocuy" on the Rio Negro (Fig. 1). After this moment to the present time, the lower and middle Içana and the lower Cuiari River basins became part of Brazil territory. The Brazilians were able to take advantage of the situation perhaps because they were more familiar with key locations and the courses of many rivers proposed as dividing landmarks.

The Inhabitants

It is now well known that the region comprising the upper Río Negro and the Orinoco River was traveled and inhabited for several millenia by ancestral groups such as the Makú-Puinave, the Arawak, and the Tucano as well (Franky-Calvo, 2006; Zucchi, 2006). These migrations came from the Central Amazon region approximately 4500–4000 B.P. (Meggers, 1979, 1994), as a result of devastating droughts (van der Hammen, 2006; Olivares et al., 2015). Therefore, the present-day indigenous peoples of northwestern Amazonia form part of a complex, hierarchical, pluriethnic, and multilingual social system shared among Brazil, Colombia, and Venezuela, involving over 24 ethnic groups (Stenzel, 2017).

Traditionally, the inhabitants of the upper Isana and Cuiarí Rivers, the Guianía, and some parts of the upper Inírida are the Kuripacos; the Baniwa groups occupy the lower and middle Içana, Cuiarí, and Ayarí (or Aiari) Rivers as well (Journet, 1980–1981). Two nations that belong to the Arawak language family have also lived for centuries in this area (Cabrera-Becerra, 2010). The headwaters of the Isana River are considered sacred by these cultures, who believe that the center of the world ("umbilicus"), where all human races began, is found in the pristine region known as "raudal" Uaipui or Wapui, located in the Ayarí (Aiari) River, a tributary of the middle Içana River in Brazil (Romero, 1993). Because large peneplains and residual plains separate the rivers, these indigenous groups built a unique network of trails to connect the rivers, making travel by foot possible. These trails are known as Kuwe or Kuwai (the name of a powerful cultural hero among the Arawak of the northwestern Amazon), and as "varaderos," "varadeiros," or "trochas" (portages) by the "Yalanai nai" (non-indigenous people). This trail network was used to reach sacred places, and for political, religious, and migratory purposes. They also were part of a long-term strategy for resisting incursions into their ancestral territories and for surviving exploitation and deprivation resulting from the rubber boom (Vidal and Zucchi, 1996; Vidal, 2000).

One topic that is impossible to avoid when discussing the basin of the Isana or Içana River is the evangelization of the native population by Sophie Muller, an American Protestant missionary affiliated with the New Tribes Mission. This evangelical crusade started in 1948, when she came from the Guianía River, funded numerous churches, and promoted values and practices under the influence of several other Protestant missionaries (Wright, 1999; Capredon, 2018). In less than five years, she converted most of the Baniwa people who lived in the middle and lower Isana or Içana River basin to Protestantism (Pollock, 1993; Boyer, 2008). This evangelic proselytism generated dramatic cultural changes (e.g., she convinced the Baniwa people to no longer use tobacco, or drink "caxiri," a fermented drink made with cassaba). In addition, she stamped out their ancestral shamanism practices known as "pajelança," and the initiation and exchange ceremonies called "podáali" as well (Wright, 1999). For centuries, shamans in the overall Amazon basin have made use of hallucinogenic snuffs (e.g., *Virola* ssp., Myristicaceae; *Anadenanthera peregrina* (L.) Speg., Fabaceae), psychoactive plants (e.g., *Banisteriopsis caapi* (Spruce ex Griseb.) C.V. Morton, Malpighiaceae; *Psychotria viridis* Ruiz & Pav., Rubiaceae), rock pieces (e.g., quartz stones), animal parts (e.g., feathers, jaguar canines and other animal teeth, and snakes' heads) to enter the spirit world, and achieve a trance and transform themselves into diverse kinds of animals and spirit beings (Wright and Hill, 1992; Wright, 1998, 2013). Currently, we estimate that about 80% of the native population is willing to continue with the values and practices imposed by Protestant missionaries and they no longer are interested at all in shamanism practices. However, they still are motivated to preserve several aspects of their ancestral cultures such as the use of Curare, *Strychnos* spp., an arrow poison, as well as the use of other plants for food and medicine.

Exploration

The Río Negro basin was relatively well explored and studied by the earliest inhabitants of the region, who were able to classify vegetation types and its most important species before Europeans arrived (Abraão et al., 2008). The first Iberian journeys down the Amazon River, from the Andes to the Atlantic Ocean, were undertaken by Francisco de Orellana (1541–1542) and Pedro de Ursúa (1560–1561), the latter accompanied by, among others, the infamous Lope de Aguirre. Chronicles of these travels (written by Fray G. de Carvajal in the case of Orellana's saga, and by F. Vázquez, P. de Almesto, and others in the case of Ursúa's, in many versions in the literature, e.g., Mampel González and Escandell Tur, 1981; Pastor and Callau, 2011) spoke of large areas of forest along the Amazon River; numerous, well-populated native villages; and a large river with black water that came from "El Poniente," the Río Negro (Carvajal, 1848; Simón, 1861). Subsequently, many outstanding researchers collected plants and studied the vegetation of this amazing river. Charles de la Condamine, who navigated the river in 1743, wrote the first biological report (La Condamine, 1745); his expedition is considered the beginning of the great era of Amazonian travel by European scientists (ter Steege et al., 2016). He remarked on numerous plant products such as curare, the arrow poison, *Strychnos* spp. (Loganiaceae); the quinine tree, *Cinchona officinalis* L. (Rubiaceae); and the rubber tree, *Hevea* spp. (Euphorbiaceae) (La Condamine, 1745).

Alexandre Rodrigues Ferreira made the first known large collection of Amazonian plants during his voyage of 1783–1792 (Wurdack, 1971). He explored the Amazon River and its main tributaries, including the Río Negro, where his itinerary notably included the Içana River (Rodrigues-Ferreira, 2008). His group collected and drew numerous plants and animals during this trip. *Asteranthos brasiliensis* Desf. (Lecytidaceae), with showy yellow, fused petals, and an actinomorphic androecia, is perhaps one of the most extraordinary plants they documented (Mori et al. 2017; see Fig. 2).

As we report here, botanical explorations in the Colombian portion of the Cuiarí and Isana Rivers had been limited before our journey. The only reference that we found was a note about the presence of *Brownea grandiceps* Jacq. in the upper Içana and Papunaua Rivers (Ducke, 1939, 1949). This record, nonetheless, is vague, since no specimen was cited: vouchers are crucial in authenticating the taxonomy of an organism, as a tool for identifying its procedence and distribution, and for additional taxonomic, genetic, ecological, and/or environmental research (Culley, 2013). In fact, Ducke based this information on "reliable informants" ("segundo informantes fidedignos"; see Ducke, 1939: 66, 1949: 95–96), and he never was in the Içana River basin (see Egler, 1963, and our database). Ducke did collect this species in São Gabriel da Cachoeira (*Ducke 23735*, US) in 1932, then a village (currently a city) located downstream of the confluence of the Içana River with the Rio Negro.

The present-day Amazonian Colombian territory was firstly botanical explored by C. F. P. von Martius, in "Montis Arara-Coara" (Araracuara), Caquetá River (Japurà or Yapurà in Brazil) in January–February 1820 (Martius, 1847). Remarkable of this trip were the collections of *Schoenocephalium arthrophyllum* Seub. (currently, *Monotrema arthrophyllum* (Seub.) Maguire) and *S. martianum* Seub. (Rapateaceae), the latter so far an endemic species of the Amazonian Colombian region (Berry, 2016). Almost a century later, the most legendary individual in the Amazon basin, the botanist and entomologist W. A. Ducke (Archer, 1962; dos Santos, 2016) collected near "La Pedrera," Caquetá River, in 1912 (Ducke, 1915; Dugand, 1948). The upper Río Negro River was explored by the famous naturalists F. H. A. von Humboldt and A. J. A. Bonpland (in 1800), A. R. Wallace (in 1851), and R. Spruce (in 1849–1854), at a time when biologists were preoccupied with a fascination for nature, and before modern scientific investigations of ecology and evolutionary biology (Ricklefs, 2012). Also, the explorers H. A. Rice and P. P. Bauer in 1912–1913 traveled in this region (Rice, 1914), and the middle and lower Içana were surveyed by T. Koch-Grünberg (with O. Schmidt) in 1903 (Kraus, 2004), and by C. Nimuendajú in 1927 (Nimuendajú, 1950).

After the Treaty of Bogotá between Colombia and Brazil was signed in 1907, the Brazilian government started a program of exploration inside the Río Negro basin in 1928–1929, under the charge of Marshall Boaberges Lopes de Sousa. The botanist on this expedition, F. von Luetzelburg (Lopes de Sousa, 1959), made significant annotations about the Içana's types of vegetation, observing the "Caatingas Amazon forests" in the lower part of the basin and terra firme forests mixed with Piaçava palm communities (*Leopoldinia piassaba* Mart.) in the middle (Lopes de Sousa, 1955). Later, R. de Lemos Fróes traveled for nine years (1941–1952) from the Içana River's mouth to the Cerro Tunuhí(y); about this time other explorers also were in this basin, among them B. A. Krukoff in 1942 and J. T. Baldwin, Jr., in 1944. Exploration of this river continued with the work of R. E. Schultes with J. Murça Pires, G. A. Black, and F. López in 1947, 1948, and 1952. On the 1947 trip, they reached the Serra de Tunuhí (Tunuí or Tunuhy; 1.4704187 N -68.1522703 W), a place that Schultes recorded as the Içana's headwaters (Davis, 1996), although they were still ca. 300 km away.

Alvaro Fernández-Pérez, a Colombian botanist, arrived in February 1953 at the Papunaua River (a tributary of the upper Inirida River), a river connected to the upper Isana by a 25 km long ancestral trail over a land isthmus (Bauer, 1919). This area was referred to in the famous novel *La Vorágine* as a place used as an indigenous refuge from the rubber barons (Rivera, 1924). Another noteworthy figure is M. U. Mee, the famous British botanical artist, who traveled to this river in 1965 and collected *Neoregelia margaretae* L.B. Sm. (Bromeliaceae), a species previously thought to be endemic to Brazil but recently found near the Vaupés River in Colombia (J. Aguirre-Santoro, pers. comm. 2019). However, the most significant botanical explorer of the Brazilian portion of the Içana River was the tireless Ricardo de Lemos Fróes (Brazil, Maranhão, 1891–1960). He participated in expeditions to the Amazon basin conducted by B. A. Krukoff between 1923 and 1950 (Landrum, 1986). However, he felt a special connection to the Içana River, making significant botanical collections in this area from 1941 to 1952. As a result, he collected several new species (e.g., *Anaxagorea angustifolia* Timm., Annonaceae; *Dichapetalum froesii* Pires, Dichapetalaceae; *Swartzia froesii* Cowan, *Clitoria tunuhiensis* Fantz, and *Dicymbe froesii* Ducke, Fabaceae). The two latter taxa, hitherto known only by his original collections from "Serra de Tunuhy" in November 1945 and May 1947, respectively. Since these earlier explorations, numerous botanists, anthropologists, and ecologists (the majority from Brazil) have visited the Brazilian portion of the Içana River to study the flora, vegetation, ethnography, and inhabitants (Aikhenvald, 1999; Ramírez, 2001; Abraão et al. 2008, 2009; Stropp et al., 2011; Epps and Stenzel, 2013; Iubel, 2015; Moraes-F. et al. 2019).

The Journey

The trip started on 10 April 2014, in Villavicencio city (Meta department), where we took a plane to Puerto Inírida (currently Inírida), the capital of the Colombian department of Guainía. As the airplane circled before landing in Inírida, we could see the amazing forest, swampy areas with palms, the low vegetation of scrubby vegetation, white-sand savannas, and the riverine forest along the Atabapo, Inírida, and Guaviare Rivers. Puerto Inírida was founded in 1963 in a place called Obando. Today it is a very active small city and can be reached by air from Bogotá and Villavicencio and by small-to-medium boats (called "bongos") from the upper Guaviare River, or from the confluence of the Atabapo, Guaviare, and Orinoco Rivers in Venezuela.

For the next five days we stayed in Inírida and made final arrangements for supplies, food, and personnel. On 15 April, we hired two "bongos" to take us to Huesito, a point located on the lower Inírida River, where we transferred our gear to two agricultural tractors with wagons; we then drove 170 km from Huesito to Puerto Caribe (Fig. 3) to reach the Guianía River through "Caño" Guamirza. The landscape in this area consists of an array of sclerophyllous forests ("Caatinga Amazónica") and swampy, white-sand shrubby communities, mixed with extensive and continuous areas of savanna dominated by "flor de Inírida" (*Guacamaya superba* Maguire; Rapateaceae) and numerous species of Cyperaceae, Eriocaulaceae , Rapateaceae, and Xyridaceae as well. In the showy inflorescences of "flor de Inírida" (Fig. 4), flowers open briefly to expose the tips of the petals; they are visited by hummingbirds seeking the nectar produced near the base of the petals. The inflorescences of this species are collected locally in Venezuela and Colombia, either fresh or dry (Berry, 2004), to make floral arrangements. These trips were made at night because of the high temperatures during the day: we departed from Huesito at 7 pm and it took all night because the speed was limited to ca. 20 km per hour and because one of the tractors had trouble with its tires. At midnight we arrived at Pato (after traveling 70 km), located on the middle Guasacavi River. It is a beautiful black-water river, whose confluence with Caño Temi and the Atacavi River forms the Atabapo River. The 12-hour trip was difficult because of the constant bouncing of the wagons, which made sleep impossible. However, we finally arrived at 6 am at Caño Guamirza (Fig. 5), a small black-water stream that has its headwaters in Colombia and then crosses into Venezuela, where it joins the Guianía River near Tonina. We took two bongos and navigated the Guamirza for ca. six hours until we reached Tonina. The vegetation of this small river consists of periodically flooded forests on black water called "Igapó" dominated by *Licania lanceolata* Prance (Chrisobalanaceae), *Aldina latifolia* Spruce ex Benth., *Macrosamanea pubiramea* (Steud.) Bar. & Grimes, and *Macrolobium angustifolium* (Benth.) R.S. Cowan (Fabaceae). Also, the river-banks and forest understories are mixed with a herbaceous matrix of dense colonies of *Thurnia polycephala* Schnee (Thurniaceae), *Spathanthus bicolor* Ducke (Rapateaceae), *Steyermarkochloa angustifolia* (Spreng.) Judz.(Poaceae), and *Lagenocarpus* spp. (Cyperaceae). In Tonina we drew up guidelines to set up our first plot in a place named Puerto Caribe on April 17, in a tall terra firme forest on a hill with clay soils. This community was dominated by *Monopteryx uaucu* Spruce ex Benth. (Fabaceae), a species locally known as "Awiñaa" (Kuripako).

The next day, we took a 12-hour trip up the Guiania River to San José del Guianía, which included navigating the rapids of Guarivén, Venado, Oso, and Sapo (Fig. 6). We stayed in San José del Guianía for two days, making preparations for the trip to the upper Guianía River (Fig. 7) and to explore the black-water river called "Caño" Naquén (Fig. 8). On 21 April, we reached Caño Naquén and made a one-day trip to the entrance of the "varador" (portage) of Naquén, an ancestral trail ca. 28 km long that links Caño Naquén with the Cuiarí River. We slept there, and at sunrise the next day the team and six Kuripacos (who carried an astonishing load of hundreds of kilograms of equipment and food) started walking on the trail. It took the team 12 hours to arrive, completely exhausted, at our destination, near the abandoned town of Miraflores, overlooking the Cuiarí River (Fig. 9). Along the way, we were able to classify more than 14 different types of vegetation; particularly noteworthy was a forest dominated by *Parkia panurensis* Benth. *ex* H.C. Hopkins (Fabaceae). We stayed in Miraflores for four days, waiting for the helpers to arrive with the rest of the equipment, gasoline, and food. While there, we set up a second plot on 25 April in a medium terra firme forest dominated by *Micrandra spruceana* (Baill.) R.E. Schult. (Euphorbiaceae) on a hill with sandy soils. In this forest, we documented a tree of *Peridiscus lucidus* Benth. (Peridiscaceae), the first report of Periscaceae in the vascular flora of Colombia (Aymard and Arellano, 2018). During the fieldwork on this plot, a large, the dangerous ant "Veinticuatro" or "Yanábe" (in Colombia and Venezuela; in English "bullet ant"; *Paraponera clavata* Fabricius, Formicidae) stung Adela Lozano's finger. This caused concern because "Veinticuatro" refers to the 24 hours of pain that follow the sting. Nonetheless, Orlando Cordubi, our local consultant, found nearby a species of a liana of the genus *Peritassa* (Celastraceae), made a string with the bark, and tied it around Adela's finger. Luckily the pain went down and she was able to continue working in the field. On 26 April we left Miraflores and continued up the Cuiarí River. The "bongos" use small engines called "rabetas" or "pequepeques," which are designed in Brazil and use a technology that reduces fuel consumption up to 30% as compared with conventional outboard engines. We reached the town of Sejal, where we stayed for three days. Then we passed through the towns of Barranquilla, Cucurital, and Amanadona, reaching the rapids and waterfall of Yuruparí on 30 April (Fig. 10). This part of the Cuiarí River is not navigable, so we walked a short "varador" of ca. 8 km to get above the falls (Fig. 11). Another group of Kuripacos was waiting for us there and helped us to get to the town of Campo Alegre. We stayed there for a week doing fieldwork; in "Caño" Guaviarito we collected a second arborescent species of *Ampelozizyphus* (*A. kuripacorum* Aymard & Castro-L. Rhamnaceae; see Fig. 12). Until the early 21st century, the genus was characterized by a lianoid habit (Aymard and Castro-Lima, 2015). Later, we explored the base of the "Serranía de Caranacoa" (Fig. 13) and found *Rhabdodendron amazonicum* (Spruce ex Benth) Huber (Rhabdodendronaceae; Fig. 14); this collection represented the first record of this family in the vascular flora of Colombia and the upper Río Negro basin (Aymard et al., 2016). This new locality extends considerably the northwesterly distribution of this taxon inside the Amazon

Figures 3–4. **3**. Road from Huesito to Puerto Caribe, on our way to the Guianía river via Caño Guamirza. Photograph by Adela Lozano. ©Ciprogress Greenlife. **4**. Inflorescence of *Guacamaya superba* Maguire (Rapateaceae). Photograph ©Ciprogress Greenlife.

FIGURES 5–6. **5**. Caño Guamirza, a small black-water stream that has its headwaters in Colombia and then flows into Venezuela, where it flows into the Guianía River, near Tonina. Photograph by Adela Lozano. © Ciprogress Greenlife. **6**. Oso rapids in the Guianía River. Photograph by Adela Lozano. © Ciprogress Greenlife.

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FIGURES 7–8. **7**. Guianía River, near the town of San José del Guianía. Photograph by Adela Lozano. ©Ciprogress Greenlife. **8**. Confluence of the Caño Naquén with the Guianía River. Photograph by María C. Montilla. ©Ciprogress Greenlife.

Figure 9. Upper Cuiarí River. Photograph by Jorge L. Contreras. © Ciprogress Greenlife.

Figures 10–11. **10**. Yuruparí rapids in the Cuiarí River. Photograph by Freddy Gómez. ©Ciprogress Greenlife. **11**. End portion of the "Varador (portage) de Raudal Yuruparí" at the Cuiarí River. Photograph by Freddy Gómez. ©Ciprogress Greenlife.

basin. The habitat of *R. amazonicum* is a tall Amazonian caatinga forest with a closed canopy, which lets little light filter to the understory. At this site, the primary dominant species were *Hevea rigidifolia* (Spruce ex Benth.) M. Arg. (Euphorbiaceae), *Mezilaurus caatingae* van der Werff (Lauraceae), *Caraipa longipedicellata* Steyerm. (Calophyllaceae), and *Micropholis maguirei* Aubrév. (Sapotaceae).

At Campo Alegre on 8 May, the team was divided in two groups, one going directly to Camanaos-Punta de Tigre, towns on the upper Isana River (Fig. 15). The other group continued up the Cuiarí River and passed through the towns of Berrocal de Cuiarí and Sabanita-Caño Yarí to reach the entrance of the "varador" of Puerto Canada (Fig. 16). They walked this trail for ca. 12 hours to arrive at Venado, located on the Colombian left bank of the Isana River. Across the river from Venado are the Brazilian towns of Uarirambá and Bethel; one km along both banks of the Isana River belongs to Brazil. The trip continued one more day up the Isana River until we reached Camanaos–Punta de Tigre. There we stayed a week, studying the surrounding forests and setting up three plots. We found that the terra firme forests of the upper Isana are richer in species: in a single plot 40 × 40 m (1600 m^2) we measured and identified 152 species. We continued exploring the upper Isana River and collected several new records for the Flora of Colombia. However, the most remarkable finding was a new species of the genus *Rapatea* (*R. isanae* Aymard & Arellano-P. - Rapateaceae), which is only the second species with white petals in a genus that otherwise has only yellow petals (Fig. 17; Aymard and Arellano-P., 2016). On 18 May, one group flew to Mitú, and the noteworthy aspect of this part of the trip was that A. Calero Cayopare's team returned to Inírida following the same route used to reach Punta de Tigre 33 days earlier.

FIGURES 12–13. **12**. *Ampelozizyphus kuripacorum* Aymard & Castro-Lima (Rhamnaceae). **A**, apex of a vegetative shoot, showing domatia on the lower surface of several leaves and a flower; notice the indument on leaf sheaths and petioles; **B**, side view of flower; **C**, flower viewed from above; **D–E**, two views of the fruits. Photographs by Francisco Castro-Lima. © Ciprogress Greenlife. **13**. Portion of Varador (portage) Campo Alegre to Serranía Caranacoa at the Cuiarí River. Photograph by Freddy Gómez. ©Ciprogress Greenlife.

FINAL REMARKS

Here, we describe and illustrate a journey of ca. 500 km from Inírida to the Colombian basins of the Cuiarí and Isana Rivers, the first botanical exploration of this particular portion of the Colombian Amazon, in the innermost corner of the northwestern Amazon basin (the upper Río Negro basin). This was one of the last regions of the planet botanically unexplored, in the particular case of the Rio Negro, aside from the collections in the lower basin, some 234 years ago, by Alexandre Rodrigues Ferreira and his group. Since then, thousands of new plant collections have

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FIGURES 14–15. **14**. *Rhabdodendron amazonicum* (Spruce ex Benth.) Huber (Rhabdodendraceae). Close-up of the immature fruits. Photograph by Francisco Castro-Lima. ©Ciprogress Greenlife. **15**. View of the upper Isana River near the town of Punta de Tigre. Photograph by Freddy Gómez. ©Ciprogress Greenlife.

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FIGURES 16–17. **16**. Entrance of the Varador (portage) of Puerto Canadá at the Cuiarí River. Photograph by Jorge L. Contreras. ©Ciprogress Greenlife. **17**. *Rapatea isanae* Aymard & Arellano-P. (Rapateaceae). Close-up of the inflorescences showing the petals. Photograph by Gerardo A. Aymard C. ©Ciprogress Greenlife.

been gathered, and currently we have a good understanding of the structure and floristic composition of the upper Río Negro (Dezzeo et al., 2000; Clark et al., 2000; Córdoba and Etter, 2001; Boubli, 2002; Aymard et al., 2009; Medina and Cuevas, 2011; Stropp et al., 2011; Pombo de Souza, 2012; Cárdenas-López et al., 2014).

In our case, we collected 1301 botanical numbers and identified 726 species, which yielded 8 new species (2 already published), 2 families, and 24 species new to the Flora of Colombia. Perhaps one of the most important features of this project was that it showed the value of fieldwork conducted through alliances between private initiatives and the Kuripaco nation.

Another noteworthy feature of this region is that it has a unique drainage system created by several black-water rivers flowing east into the upper Río Negro in Brazil. These rivers are separated by large peneplains and residual plains (sometimes interrupted by "Serranías" and numerous granitic outcrops), occupied by a unique array of plant communities. The Isana is a white-water river that has particular features in its physical and biological environments: it has its headwaters on hills with clay soils, dominated by tall terra firme forests located between the Papunaua and Querarí Rivers. After the waters of the Caño Suruí (Koliriarí) enter the river, the Isana flows for ca. 120 km, defining the border between Colombia and Brazil and then entering Brazilian territory near the town of Uarirambá-Bethel. In Camanaos, the tall terra firme forests of the headwaters region change to a medium forest mixed with palm communities; in the vicinity of the Wapuí waterfall and the Santaré and Venado rapids, the vegetation becomes a mosaic of Amazon Caatinga forests, Piaçava palm communities (*Leopoldinia piassaba* Mart., Arecaceae), and lower forests, savannas, and shrubby vegetation, over large areas of white-sand (podzols soils). These abrupt changes are due to the influence of the several black-water rivers, whose headwaters drain from Precambrian Guiana shield outcrops.

The terra firme forests located in the upper Isana region are plant communities with high species diversity. We measured between 108 and 162 spp., in three plots of 40 × 40 m (1600 m^2), with diameters ≥ 5 cm. In comparison, western Amazonia is so far the place with the highest plant diversity (Valencia et al., 2004; Draper et al., 2019). Valencia et al. (2004) reported between 473 and 644 ssp. (with diameters ≥1 cm) in 1 ha (10,000 m^2) in a plot located in Cuyabeno, Ecuador; Gentry (1988) measured more than 300 spp. in Iquitos in 1-ha plots (Perú).

The upper Río Negro region is reportedly not a region rich in plant species (Dezzeo et al., 2000; Boubli, 2002; Aymard et al., 2009). However, the higher diversity we found in this area could be attributed to the combination of white-water river (waters with sediments) vegetation (a feature of the upper Isana River) with larger areas covered by the vegetation typical of the black-water rivers.

This report of the first botanical exploration of the Colombian portion of the Cuiarí and Isana Rivers is yet another example demonstrating the need for continued floristic studies in regions where there are large geographic gaps in the knowledge of Amazonian flora, so that there can be adequate planning for conservation and sustainable use of regional biota. Advances in the documentation of the upper Río Negro flora will be achieved only through institutional and private partnerships, improvements in training, and continued fieldwork—mounting new expeditions with many researchers working in collaboration with the local people.

Finally, the Río Negro basin has outstanding global conservation significance due to its extraordinary biodiversity and the potential for long-term conservation, due to its large size and still-pristine nature, and the probability of its maintaining wet rainforest conditions while anticipated climate change–induced drought intensifies in the Western Amazon. Nonetheless, mining for precious and other minerals, selective logging, fires, and new road developments will continue to threaten its yet-to-be-determined conservation status.

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AQUATIC AND PALUSTRINE ANGIOSPERMS OF VIRUÁ NATIONAL PARK, BRAZILIAN AMAZON—NYMPHAEALES, ALISMATALES, DIOSCOREALES, AND ARECALES

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Abstract. The Viruá National Park (VNP) with its different plant formations (rainforest, white-sand savannas—“campinaranas,” and “buritizais”) is located in a region still lacking in botanical studies (Guiana Shield and Brazilian Amazon). Aiming to improve the knowledge of the region’s flora, collections were conducted in VNP from 2010 to 2015. The present work provides a taxonomic treatment of the aquatic and palustrine members of Nymphaeales, Alismatales, Dioscoreales, and Arecales. It includes identification keys to species, as well as descriptions, illustrations, and comments on taxonomy, ecology and geographical distribution. A dichotomous key to all families with at least one aquatic or palustrine species found in VNP is also provided.

Keywords: Flora, Igapó; Guiana Shield, Macrophytes, Taxonomy

Resumo. O Parque Nacional do Viruá (VNP), com suas diferentes formações vegetais (floresta tropical, savanas de areia branca — campinaranas, e buritizais), está localizado em uma região ainda carente de estudos botânicos (Escudo das Guianas e Amazônia Brasileira). Com o objetivo de aprimorar o conhecimento sobre a flora da região, foram realizadas coletas no VNP de 2010 a 2015. O presente trabalho prove o tratamento taxonômico dos membros aquáticos e palustres de Nymphaeales, Alismatales, Dioscoreales e Arecales. São apresentadas chaves de identificação para espécies, bem como, descrições, ilustrações e comentários sobre taxonomia, ecologia e distribuição geográfica. Uma chave dicotômica para todas as famílias com pelo menos um representante aquático ou palustre encontrado no VNP também é apresentada.

Palavras-chave: Flora, Igapó, Escudo das Guianas, Macrófitas, Taxonomia

The Amazon covers about 7.590.000 km^2 distributed among eight countries of the northern region of South America. The Amazon Depression comprises the basins of the Amazon and Tocantins Rivers in the more central portion and on its borders comprises sub-Andean areas and Guiana and Brazilian Shields. (Eva et al., 2005).

The Guiana Shield has a varied topology, which includes sandstone tepuis, granite inselbergs, white sands, seasonally flooded tropical savannas, lowlands with numerous rivers, isolated mountain ranges, and coastal swamps, each supporting a characteristic vegetation (Huber, 1995; Huber et al., 1995). This variety accounts for a great deal of the high diversity and endemicity of the Shield’s biota (Funk and Hollowell, 2007).

Located in the Brazilian portion of the Guiana Shield, the Viruá National Park (VNP) was object of a floristic survey, in which, we listed 207 species (distributed in 85 genera and in 37 families) of herbaceous and subshrubby aquatic and palustrine angiosperms (Costa et al., 2016).

The present work is the first of several other works to be published providing taxonomic treatments to the aquatic and palustrine taxa found in VNP. Here the families belonging to Nymphaeales (Cabombaceae and Nymphaeaceae), Alismatales (Alismataceae, Araceae and Hydrocharitaceae), Dioscoreales (Burmanniaceae) and Arecales (Arecaceae) are treated. We also provide a dichotomous key to all families in which at least one aquatic or palustrine species was found in VNP.

MATERIALS AND METHODS

Study Area

The Viruá National Park is located in the Caracaraí district, Roraima state, northern Brazil (01°19'11"N, 61°7'17"W DMS). The climate in the region is equatorial with the rainy season intercalated by a more or less short dry season, between October and March. This Conservation Unit presents igneous volcanic or metamorphic rocks in the hills and sandy soil of fluvial, aeolian or weathering sedimentary origin in the plains (Schaefer et al., 2009).

The VNP contains in its 227.011 ha different plant formations distributed in a mosaic (rainforest, white-sand savannas—“campinaranas,” and “buritizais”—flooded areas dominated by *Mauritia* L. f. palms) (Gribel et al., 2009). The conservation unit has its western boundary at the Branco River, a line drawn a few kilometers from an abandoned fragment of the BR-174 road (known as “Estrada Perdida”) as the northern and the eastern boundaries, and by the Anauá River in the southern limit (Schaefer et al., 2009).

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Collecting and Analyzing Data

We conducted expeditions in the Viruá National Park between February 2010 and January 2015. All plant formations in the VNP were sampled. The process of collecting and herborization followed Fidalgo and Bononi (1989); and only fertile individuals were sampled.

The collected materials are deposited in INPA herbarium. Duplicates were sent to UEC, UFP and UFRR (acronyms according to the Index Herbariorum: Thiers, continuously updated).

We identified the specimens through observation in nature; comparison with specimens deposited in K, INPA, MIRR, UEC and UFRR; consultation to original descriptions, revisions, regional floras and others specialized literature; whenever possible specialists were also consulted. We analyzed digital images of specimens deposited in K, F, MO, NY, P, and others *herbaria*, always taking into account the reliability of the identifications; with preference given to types, historical collections and specimens identified by specialists.

The families' classification followed APG IV (2016). We adapted the family and genera descriptions from specialized literature. Species descriptions and illustrations are based, predominantly, on the materials collected in VNP. When species' organ(s) was(were) not observed in VNP, its(their) description was(were) taken from literature and referenced. We based information on geographic distribution and species' authors on specialized literature, TROPICOS platform (last access june/2019) and Flora do Brasil 2020 (under construction). Comments on taxonomy and ecology considered field observations and specialized literature.

Results

Key to Aquatic and Palustrine Families of VNP

1a. Flowers achlamydeous, monochlamydeous or dichlamydeous and homochlamydeous 2

1b. Flowers dichlamydeous and heterochlamydous 10

2a. Perigone showy 3

2b. Perigone (when present) inconspicuous 7

3a. Leaves without sheath 4

3b. Leaves with sheath 5

4a. Amphibian herbs . . . . Molluginaceae

4b. Submerged or floating herbs . . . . Cabombaceae

5a. Palms . . . . Arecaceae

5b. Herbs 6

6a. Floating or emergent herbs; leaves not equitant . . . . Pontederiaceae

6b. Amphibian herbs; leaves equitant . . . . Haemodoraceae

7a. Inflorescences of the spadix type . . . . Araceae

7b. Inflorescences of another type 8

8a. Flowers grouped in heads . . . . Eriocaulaceae

8b. Flowers grouped in spikelets 9

9a. Stems generally triangular; leaves spirally arranged, with a generally closed sheath . . . . Cyperaceae

9b. Stems generally cylindrical or flattened; leaves distichous or rarely spirally arranged, with a generally open sheath . . . . Poaceae

10a. Perianth 3-merous; leaves with sheath 11

10b. Perianth usually 4–5-merous (sometimes with less or more pieces); leaves without sheath 20

11a. Palms . . . . Arecaceae

11b. Herbs 12

12a. Inflorescences capituliform 13

12b. Inflorescences of another type 15

13a. Anthers generally poricidal; base of leaves and inflorescences with mucilage . . . . Rapateaceae

13b. Anthers dehiscing by slits; base of leaves and inflorescences without mucilage 14

14a. Heads generally whitish, rarely black; flowers with white or brown corollas . . . . Eriocaulaceae

14b. Heads generally brown; flowers with yellow corolla . . . . Xyridaceae

15a. Gynoecium dialycarpous . . . . Alismataceae

15b. Gynoecium syncarpous 16

16a. Ovary superior 17

16b. Ovary inferior 18

17a. Leaves with conspicuously spiny margins . . . . Bromeliaceae

17b. Leaves with non-spiny margins . . . . Mayacaceae

18a. Androecium attached to the gynoecium forming a column . . . . Orchidaceae

18b. Androecium and gynoecium free among themselves 19

19a. Submerged, floating or partially emerged herbs; leaves well developed, palmate or parallel veined . . . . Hydrocharitaceae

19b. Palustrine herbs; leaves inconspicuous, 1-veined (rarely parallel veined), often scamiform . . . . Burmanniaceae

20a. Flowers dialypetalous 21

20b. Flowers synpetalous 30
21a. Petals numerous, gradually becoming similar to stamens .... Nymphaeaceae
21b. Petals 4–6, quite distinct from the stamens 22
22a. Flowers unisexual .... Euphorbiaceae
22b. Flowers bisexual 23
23a. Ovary inferior 24
23b. Ovary superior 25
24a. Venation pinnate .... Onagraceae
24b. Venation acrodromous .... Melastomataceae
25a. Leaves compound .... Fabaceae
25b. Leaves simple 26
26a. Stamens connate .... Polygalaceae
26b. Stamens free 27
27a. Herbs with leaf indument formed by many glandular and sticky trichomes; insectivorous .... Droseraceae
27b. Herbs, sub-shrubs or shrubs with leaf indument formed by non-glandular trichomes (if glandular, then non-sticky) or leaves glabrous; non-insectivorous 28
28a. Venation generally acrodromous; anthers falcate .... Melastomataceae
28b. Venation pinnate; anthers other than falcate 29
29a. Leaves decussate or 3(4-)-whorled, rare partially alternate .... Lythraceae
29b. Leaves alternate .... Ochnaceae
30a. Unisexual flowers .... Euphorbiaceae
30b. Bisexual flowers 31
31a. Plants with latex; stamens and stigmas fused (gynostegium) .... Apocynaceae
31b. Plants without latex; stamens and stigmas free 32
32a. Flowers grouped in heads or glomerules 33
32b. Flowers grouped in racemes, spikes, panicles, etc 34
33a. Stipules interpeciolar, rarely absent or reduced to a line between leaves of the same node; fruit: capsule, schizocarp, or pyrene .... Rubiaceae
33b. Stipules intrapeciolar; fruit: achene (cypsela) .... Asteraceae
34a. Leaves compound .... Fabaceae
34b. Leaves simple 35
35a. Ovary inferior .... Rubiaceae
35b. Ovary superior 36
36a. Corolla bilabiate 37
36b. Corolla regular 40
37a. Herbs bearing utricles, or if utricles absent then leaves viscous .... Lentibulariaceae
37b. Herbs without utricles and non-viscous leaves 38
38a. Inflorescences terminal, spiciform .... Verbenaceae
38b. Inflorescences cymose, racemose or flowers solitary 39
39a. Stigma “thick”, bilobate .... Plantaginaceae
39b. Stigma indistinct .... Linderniaceae
40a. Petals’ lobes fimbriate .... Menyanthaceae
40b. Petals’ lobes entire (not fimbriate) 41
41a. Aestivation contort .... Gentianaceae
41b. Aestivation imbricate 42
42a. Stamens 3 .... Plantaginaceae
42b. Stamens 4 .... Linderniaceae

1. CABOMBACEAE Rich. ex A. Rich. (Nymphaeales)

Aquatic *herbs* with creeping rhizomes rooting in substrate, and elongate, submerged, distally floating. *Submerged leaves* (*Cabomba* Aubl. only) opposite or whorled, short-petiolate, palmatisect. *Floating leaves*, alternate, sometimes opposite, short- to long-petiolate, simple, narrowly to broadly elliptic, peltate or occasionally with a basal sinus, entire. *Flowers* solitary, axillary, from distal nodes, long-pedicellate, floating in water or emerged (occasionally submerged), bisexual, actinomorphic; sepals (2–)3, free or connate only at the base; petals (2–)3, free, with nectariferous auricles near base; stamens 3–6 (*Cabomba*) or 12–36 rarely more (*Brasenia* Schreb.); carpels 1–4 (*Cabomba*) or 4–18 (*Brasenia*), free; ovary superior, each tapering toward a short style, stigma spherical and terminal (*Cabomba*), elongate, decurrent (*Brasenia*); ovules 1–5, placentation laminar. *Fruits* indehiscent, similar to achene or follicle. *Seeds* operculate (adapted from Ørgaard, 1991; Wiersema, 1997).

Cabombaceae are practically cosmopolitan, with two genera and six species (Wiersema, 1997). In Brazil, the family is represented only by *Cabomba*, with five species (Pellegrini, 2020). In VNP two species were found.

KEY TO CABOMBACEAE SPECIES

1a. Flowers yellow; floating leaves elliptic to ovate . . . . *Cabomba schwartzii*

1b. Flowers pink; floating leaves ensiform . . . . *Cabomba furcata*

1.a. *Cabomba* Aubl.

Perennial, submerged or floating. *Rhizome* branched or not. *Submerged leaves* decussate or ternate; dissected di- or trichotomically into filiform segments. *Floating leaves* alternate, peltate; blade oval, elliptic, linear to sagittate, margin entire. *Flowers* usually axillary; sepals imbricate, persistent, petaloid, obtuse-obovate to oblong; petals imbricate, persistent, of the same colour as the sepals, unguiculate, obtuse, base auriculate, nectaries 2, yellow, inserted in auricles; stamens 3–6, anthers yellow, longitudinally dehiscing; carpels 1–4, ovules 1–5; style short, stigma capitate. *Fruits* ovoid with elongated apex. *Seeds* ellipsoid-globose to oval (adapted from Ørgaard 1991; Wiersema, 1997).

Cabomba occurs from the eastern United States to northern Argentina; five species are registered (Wiersema, 1997). In Brazil, the genus is distributed throughout the national territory and counts on five species (Pellegrini, 2020).

1.a.1. *Cabomba furcata* Schult. & Schult. f., Syst. Veg., ed. 15 bis [Roemer & Schultes] 7(2): 1379. 1830. Fig. 1A–C.

Herbs with length varying according to the height of water level. *Submerged leaves* green, reddish when young; blade sparsely to densely setose, reniform to circular in outline, 31.5–37.0 × 17.0–34.0 mm, 3–5-splitted at base, with linear segments, 2–3-splitted, the first divisions often trifurcated and three-dimensional, the terminal ones bifurcated, two-dimensional, segments 3.7–7.7 mm long, 2–4 mucronate; petiole 6.5–20.0 mm length. *Floating leaves* ensiform, slightly involute, 14.5–15.0 × 0.5–0.8 mm, green, margins vinaceous, adaxial surface glabrous, abaxial surface sparsely setulose, punctate-glandulose; petiole 22.5–25.5 mm long. *Flowers* 6.3 mm length; peduncle 40.5 mm long, reddish, setulose; petals and sepals punctate-glandulose, lilac to pinkish with yellow base; sepals 3, 6.5–7.0 × 2.5–3.0 mm, apex obtuse; petals 3, ca. 6.0 × 2.5 mm, apex obtuse; stamens 6, filaments 2.5–3.0 mm length, anthers ca. 1.0 mm length; pistils 3, botuliform, punctate-glandulose, ca. 3.0 mm, style ca. 1/4 of the length of the pistil, ovary unilocular, ovules 3–5, some may be aborted, stigma whitish, ciliate. *Fruits* thin walled. *Seeds* globose to ellipsoid, ca. 1.5 mm length, echinate.

The flowers of *C. furcata* emerge from water around 10:00 a.m. and submerge around 4:00 p.m. During this time, they were seen being visited by bees and flies. *Cabomba furcata* co-occurs with populations of *C. schwartzii* in VNP. The species forms dense population aggregates, although these are smaller than those of *C. schwartzii*.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, Parque Nacional do Viruá, 01°24'03"N, 60°59'10"W, 25 January 2011, *S. M. Costa 763 & K. G. Cangani* (INPA, UEC); idem, 01°24'51"N, 60°59'12"W, 20 July 2010, *T. D. M. Barbosa 1201 & S. M. Costa* (INPA, UEC); idem, 01°24'00"N, 60°59'08"W, 22 July 2010, *T. D. M. Barbosa 1269 & S. M. Costa* (INPA, UEC); idem, Estrada perdida próximo a 1ª bueira, 16 September 2010, *S. M. Costa et al. 766* (INPA, UEC).

Additional specimens examined: BRAZIL. "Piauhy," July 1839, *Gardner 2478* (Isolectotype of *Cabomba piauhyensis* Gardner: [K000220408]).

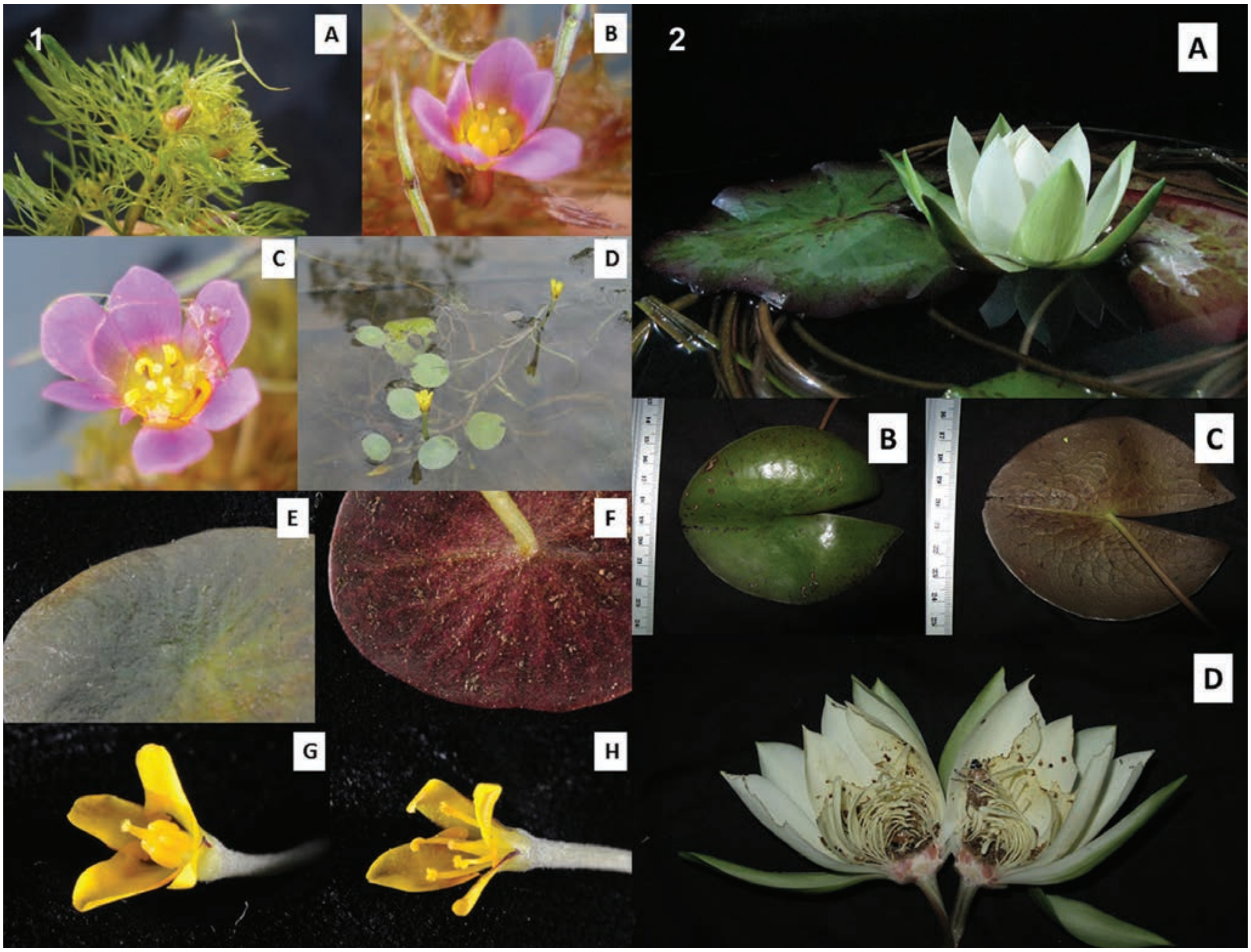
Geographical distribution and ecology: Herbs predominantly submerged; occur in ditches, lagoons, streams and along riverbanks, 50–400 m; Venezuela, Costa Rica, Cuba, eastern Colombia, Trinidad, Guyana, Suriname, French Guiana, Peru, Brazil and northern Bolivia (Wiersema, 1997). In Brazil, the species is found in the North (Amazonas, Pará, Rondônia, Roraima and Tocantins), Northeast (Bahia, Maranhão, Paraíba, Pernambuco and Piauí), Central-West (Distrito Federal, Goiás, Mato Grosso do Sul and Mato Grosso), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo) and South (Paraná, Rio Grande do Sul and Santa Catarina) regions (Pellegrini, 2020).

1.a.2. *Cabomba schwartzii* Rataj, Acta Amazon. 7: 143. 1977. Fig. 1D–H.

Herbs with length varying according to the height of water level. *Submerged leaves* green to reddish; blade sparsely to densely setose, reniform to circular, 53.0 × 50.5 mm, 3–5-splitted at the base, with linear segments, di-trichotomically splitted, the first divisions often trifurcated, three-dimensional, the terminal ones bifurcated, two-dimensional, segments 4.5–7.0 mm, 2–4 mucronate; petiole 9.0–12.5 mm long. *Floating leaves* broadly elliptic to oval, punctate-glandulose, 19.5–32.0 × 13.5–21.0 mm, adaxial surface olive green, sparsely tomentulose to glabrous, abaxial surface vinaceous, sparsely tomentulose, margin hyaline; petiole 23.0–30.0 mm length, hirsute. *Flowers* ca. 8.0 mm length; peduncle 30.5–37.0 mm long, hirsute; petals and sepals yellow; sepals 2, 6.5–7.5 × 2.5–3.0 mm, adaxial surface sparsely tomentose, sparsely punctate-glandulose, abaxial surface glabrous, not punctutate-glandulose, apex truncate, slightly obtuse, or retuse; petals 2, 6.5–7.5 × 2.5–3.0 mm, apex obtuse or retuse, adaxial surface sparsely tomentose, sparsely punctate-glandulose, abaxial surface glabrous, not punctate-glandulose, stamens 4, filaments ca. 4.0 mm length, anthers ca. 1.3 mm length; pistil 1, botuliform, tomentelous, sparsely punctate-glandulose, 6.0–6.5 mm length, style ca. 1/4 of the length of the pistil, glabrous, ovary unilocular, ovules 1–2, some may be aborted, stigma whitish, short ciliated. *Fruits* thin walled. *Seeds* ovoid, ellipsoid, 1.5–2.1 × ± 1.0 mm, verrucose.

The flowers of *Cabomba schwartzii* emerge from water around 10:00 a.m. and submerge around 4:00 p.m., during this time they are visited by bees and flies. The species occurs in large patches dominating the landscape.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, Parque Nacional do Viruá, 01°27'30"N, 60°58'26"W, 07 March 2010, *T. D. M. Barbosa et al. 1096*



FIGURES 1–2. **1.** Cabombaceae – *Cabomba furcata* Schult. & Schult. f. **A**, submerged and floating leaves (peltate narrowly lanceolate at the apex of the shoot); **B**, flower (first day); **C**, flower (second day). *Cabomba schwartzii* Rataj. **D**, habit; **E**, floating leaf (adaxial surface); **F**, floating leaf (abaxial surface); **G**, flower (first day); **H**, flower (second day). **2.** Nymphaeaceae – *Nymphaea gardneriana* Planch. **A**, habit; **B**, leaf (adaxial surface); **C**, leaf (abaxial surface); **D**, flower (longitudinal section).

(INPA, UEC); idem, 01˚24'44"W, 60˚13'00"W, 20 June 2010, *T. D. M. Barbosa 1230 & S. M. Costa* (INPA, UEC); idem, 01˚24'03"N, 60˚59'10"W, 25 January 2011, *S. M. Costa 894 & K. G. Cangani* (INPA, UEC); idem, Estrada perdida próxima a 1ª bueira, 16 September 2011, *S. M. Costa et al. 763,* (INPA, UEC).

Additional specimens examined: BRAZIL. Amazonas: Rio Negro, rio Itu, igarapé do Aduja, *Schwartz s/n* (Holotype [INPA53905]).

Geographical distribution and ecology: Submerged herbs; occur in ditches, lagoons, streams and along riverbanks. Species known only to the states of Amazonas and Roraima in the Brazilian North region (Barbosa et al., 2018).

2. NYMPHAEACEAE Salisb. (**Nymphaeales**)

Herbs, rhizomatous, perennial, rooted in substrate. *Leaves* arising directly from the rhizome, simple, alternate, long-petiolate; blade ovate-lanceolate to orbicular, cordate to peltate. *Flowers* emerged, occasionally submerged, solitary, axillary, or extra-axillary, pedicel long, originating from the rhizome, bisexual, actinomorphic; sepals 4–6(–14), free or adnate to ovary; petals 4–70, free, spirally arranged or the external ones arranged in whorls of 4, hypogynous to perigynous, often transitional to stamens or staminodes; stamens 14–700, spirally arranged, usually grading from outer laminar forms to inner forms with more distinctive filament and anther, anthers 2-thecae, introrse, longitudinally dehiscing; ovary superior to inferior, carpels 3–50, 3–many locules and 2–many ovules per locule, totally or partially united, stigma sessile 3–50, in numbers equal to the carpels, ovules pendulous, laminar placentation. *Fruits* coriaceous, berry-like or capsule-like, with irregular dehiscence, usually retracted beneath the water surface. *Seeds* arillate or not, ovoid to globose, operculate, seed coat glabrous to pilose (adapted from Feres and Amaral, 2003; Wiersema, 2003).

Broad distribution in temperate and tropical zones, lakes and bays, from fresh to little brackish waters. The family consists of six genera; the largest of them, *Nymphaea* L., is cosmopolitan, with about 70 species, as well as several hybrids and varieties (Feres and Amaral, 2003). In Brazil, the family is found throughout the national territory with two genera (*Nymphaea* and *Victoria* Lindl.) and 23 species (Flora do Brasil, 2019d). In VNP only *Nymphaea* was found with two species.

KEY TO NYMPHAEACEAE SPECIES

1a. Margins of leaf irregularly toothed; sepals reddish-green. . . . .*Nymphaea rudgeana*

1b. Margins of leaf repand; sepals green (never reddish) . . . . *Nymphaea gardneriana*

2.a. *Nymphaea* L.

Rhizome erect or horizontal. *Leaves* usually floating; blade elliptic-ovate to orbicular, base cordate to sagittate, apex rounded to acute, margin entire to sinuous-toothed, venation palmate with a prominent central vein. *Flowers* with pedicels mostly stouter than petioles; sepals usually 4, hypogynous, imbricate, free, oblong to lanceolate; petals 7–40, showy, imbricate, free, hypogynous to perigynous, oblong to lanceolate, inserted in several series, transition from petals to stamens gradual or abrupt; stamens 20–700, multiseriate, peryginous to epigynous, free, the external ones petaloid, the internal ones filiform, connective with or without terminal appendage; ovary semi-inferior, syncarpous or apocarpous, carpels 5–50; stigmatic tissue radial terminated by triangular, linear, lingulate or clavate carpellary appendage. *Capsule* ripening under water, dehiscence irregular. *Seeds* with a floating membranous aril, often with ridges or hair-like papillae on outer surface (adapted from Feres and Amaral, 2003; Wiersema, 2003).

Distributed in tropical to temperate habitats on all continents except Antarctica, with ca. 45–50 species (Wiersema, 2003). In Brazil, *Nymphaea* is found throughout the national territory, with 21 species (Flora do Brasil, 2019d). The genus occurs in stagnant waters or waters with little movement (Feres and Amaral, 2003). In VNP two species were found.

2.a.1. *Nymphaea gardneriana* Planch., Fl. Serres Jard. Eur. 8: 120. 1853. Fig. 2A–D.

Leaves with greenish petiole, glabrescent, without ring of trichomes at apex, blade chartaceous, elliptic to suborbicular, apex round to mucronate, margin repand, adaxial surface green or reddish, with longitudinal striae caused by the acicular sclereids of the mesophill, abaxial surface green or reddish, with spider web-like veins, central and major veins sulcate, 7.2–11.2 × 4.5–8.7 cm. *Flowers* with greenish pedicel, ca. 6.1 mm diam.; sepals 4, cymbiform, base white, other parts green, white longitudinal striae, ca. 60.0 × 20.0 mm, narrow-elliptic, oblanceolate, apex cucullate, acute or rounded; petals 17, cymbiform, whitish, the outermost narrowly elliptical, 55.2 × 21.7 mm, the inner most narrowly elliptic to oblanceolate, 44.4 × 14.5 mm; gradual transition to stamens, apex mucronate; stamens 79, white, the most external ones ca. 36.3 × 4.7 mm, the most internal ca. 16.3 × 2.0 mm; external and internal apical extensions absent; external anthers ca. 20.1 × 3.1 mm, the innermost 9.6 × 2.1 cm; carpels 24, carpellary appendages 14.3 × 1.8 mm, white, fusiform. *Fruits* not seen.

According to Wiersema (2003) most of the species of *Nymphaea* of Venezuela are nocturnal species apparently exclusively pollinated by beetles *Cyclocephala* Latreille. In Viruá, we also found beetles pollinating the flowers of *N. gardneriana*, and they probably belong to *Cyclocephala* as well. *Nymphaea gardneriana* is very common in the area; its flowers begin the anthesis in the late afternoon exuding a scent that dominates the environment. The species was seen mostly in open areas, but it was also collected in flooded areas in the interior of forest, where it is less frequent.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, 20 July 2010, 01°24'44"N, 60°13'00"W, *T. D. M. Barbosa 1229 & S. M. Costa* (INPA, UEC); idem, grade PPBio L1/N6, 12 September 2010, *S. M. Costa 694 & T. D. M. Barbosa* (INPA, UEC).

Additional specimens examined: BRAZIL. "in prov. Piauhy," Jul-Sep, 1839, *Gardner 2476* (Isolectotype [K000220394]); Goiás, 1840, *Gardner 3568* (Isolectotype of *Nymphaea stenaspidota* [K000220395]).

Geographic distribution and ecology: Venezuela, Guyana, Brazil, eastern Bolivia, Paraguay, northeastern Argentina (Wiersema, 2003). In Brazil, the species is found in the North (Acre, Pará, Roraima and Tocantins), Northeast (Paraíba and Piauí), Central-West (Distrito Federal, Goiás, Mato Grosso do Sul and Mato Grosso), Southeast (Minas Gerais and São Paulo) and South (Paraná) regions (Flora do Brasil, 2019d).

2.a.2. *Nymphaea rudgeana* G. Mey., Prim. Fl. Esseq. 198. 1818. Figure in *Flora Brasiliensis*. Vol. IV, Part II. Fasc. 77, plate 35. 1878.

Leaves with reddish petiole, glabrescent, without ring of trichomes at apex, blade subcoriaceous, broadly elliptic, apex truncate to rounded, margin irregularly toothed with repand apex, adaxial surface green or reddish, abaxial surface green or red, pleated, with central and main veins strongly prominent, radial, other veins irregularly reticulated, 25.0–31.2 × 28.0–32.0 cm. *Flowers* with reddish pedicel, ca. 7.0 mm diam.; sepals 4, cymbiform, reddish-green or pinkish, sometimes with reddish spots, 4.5–5.7 × 1.9–2.2 cm, elliptic, apex cucullate, acute or rounded; petals 17, cymbiform, white to pinkish, the outermost elliptic, 4.8 × 2.1 cm, the most internal ones narrowly elliptic, 3.8–4.1 × 1.2–1.4 cm; gradual transition to stamens, apex rounded; stamens 50–54, the most external ones ca. 3.5 × 1.2 cm, the most internal ca. 1.7 × 2.8 cm; filaments white, apical extensions yellowish-white, the outermost ca. 1.0 mm length, the most internal absent; anthers yellowish-white, the outermost ca. 1.2 × 0.4 cm, the innermost 8.2 × 2.6 cm; carpels 16, carpellary appendages 1.0 × 0.2 cm, yellowish-white, clavate, pink. *Fruits* 2.5–4 × 3.2–5.3 cm. *Seeds* oval, 1.4–2.0 × 1.0–1.5 mm, seed coat smooth, with trichomes arranged in longitudinal rows.

Flowers with nocturnal anthesis, flower buds emerge and close during the day. Among the strictly aquatic plants from Viruá it can be easily recognized by its large leaves, with irregularly toothed margin and repand apex.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, 20 January 2011, 01°24'50"N, 60°59'17"W, *M. C. E. Amaral 2011/33 & C. F. Silva* (INPA, UEC); idem, 21 September 2010, 01°16'46"N, 60°59'20"W, *S. M. Costa et al. 815* (INPA, UEC).

Additional specimens examined: BRAZIL. Pará, December, 1849, *Spruce 479* (Lectotype of *Nymphaea sinuata* Salzman ex Lehmann [K000220402]).

Geographic distribution and ecology: Venezuela, Cuba, Jamaica, Guadaloupe, Martinique, northeastern Colombia, Trinidad, Guyana, Suriname, French Guiana, Brazil (Wiersema, 2003). In Brazil, the species is found in the North (Amazonas, Amapá, Pará, Rondônia, Roraima and Tocantins), Northeast (Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo) and South (Paraná) regions (Flora do Brasil, 2019d).

3. ALISMATACEAE Vent. (**Alismatales**)

Herbs rooted in substrate, annual or perennial, cormose, stoloniferous, often rhizomatous. *Leaves* emerged, submerged or floating, basal, sessile or petiolate; petioles cylindrical to trigonal, with open and non-auriculate sheaths; blades linear, lanceolate, sagittate, ovate to rhomboid, sometimes marked by pellucid dots or lines, venation acrodromous. *Inflorescences* erect, rarely floating, scapose, racemose, paniculate, rarely umbellate, spathe absent; bracts whorled, linear, entire. *Flowers* hypogynous, actinomorphic, bisexual or unisexual (hermaphroditic, monoecious, or rarely dioecious plants), subsessile to long-pedicellate; sepals 3, green, persistent in fruit; petals 3, white (yellow base in *Sagittaria* Rupp. ex L.); stamens 6, 9 or many, free, yellow; anthers 2-thecae, basifixed or versatile, longitudinal dehiscence, extrorse; pistils 6–many, free, yellow, 1 whorled or spiraled, 1-locular, each with 1(2) ovules, placentation basal; styles terminal or lateral, persistent; stigma linear. *Fruits* usually achenes compressed or cylindrical, often winged, with longitudinal ribs or ribs absent, glands present or absent (adapted from Haynes and Holm-Nielsen, 1995).

Cosmopolitan family, with ten genera and about 80 species (Haynes and Holm-Nielsen, 1995). In Brazil, Alismataceae are recorded in all regions and states, with five genera and 37 species (Matias, 2019). In VNP two genera and three species were found.

Key to Alismataceae Species

1a. Flowers bisexual; fruits almost cylindrical, predominantly ribbed . . . . *Helanthium tenellum*
1b. Flowers, at least the most basal, unisexual; fruits conspicuously compressed, not ribbed 2
2a. Leaves floating, sagittate . . . . *Sagittaria guayanensis*
2b. Leaves emerged, linear, ovate-lanceolate or elliptic . . . . *Sagittaria rhombifolia*

3.a. ***Helanthium*** (Benth. & Hook. f.) Engelm. ex J.G. Sm.

Scapose *herbs*, pseudostoloniferous. *Emerged leaves* petiolate, blades narrow to elliptic, 1–5-veined, pellucid marks absent or present in the form of lines; submerged leaves sessile, blade linear. *Inflorescences* umbellate or racemose composed of 2–3-whorls of flowers; bracts ovoid. *Flowers* bisexual, pedicellate; sepals ovate; petals unguiculate; stamens (6–)9; anthers globulose; pistils 10–20. *Fruits* turgid, obovate, 3–4-ribbed, not carinate, beak erect (adapted from Lehtonen and Myllys, 2008).

Helanthium is a genus with broad phenotypic plasticity. According to Haynes and Holm-Nielsen (1994), the genus has two species and is distributed from the northeastern United States of America to southern Brazil and Argentina.

3.a.1. ***Helanthium tenellum*** (Mart. ex Schult. f.) Britton, Man. Fl. N. States [Britton], ed, 2. 54. 1905. Fig. 3A–B.

Herbs palustrine or submerged, up to 25 cm, stoloniferous. *Emerged leaves* lanceolate, apex acute, base acute to attenuate, 3–5 veins, pellucid marks absent; submerged leaves oblanceolate, ca. 30.0 × 1.8 mm, apex acute, base attenuate, 1–3 veins. *Inflorescences* umbellate, with 1 whorl, or racemose with 2 whorls; scape erect, cylindrical, glabrous, ca. 52.0 × 0.55 mm, whorls 5-flowered; peduncle ca. 31.5 mm length; bracts smaller than the pedicel, connate till ca. 1/2 of the length, 2.20 × 1.40 mm, conduplicate, apex acute; pedicel ca. 11.0 × 0.2 mm. *Flowers* ca. 4.2 mm diam.; sepals ca. 1.80 × 1.40 mm, appressed to patent, 4-veined, veins without papillae; petals ca. 3.6 × 2.6 mm, apex rounded to emarginate; stamens 9–10; pistils 15–20. *Fruits* ca. 1.0 × 0.7 mm.

No emergent leaves were seen (description according to Amaral et al., 2008). The specimens were collected in campinaranas, in floodplain areas, preferably in sunny locations. Species found in abundance where it occurs.

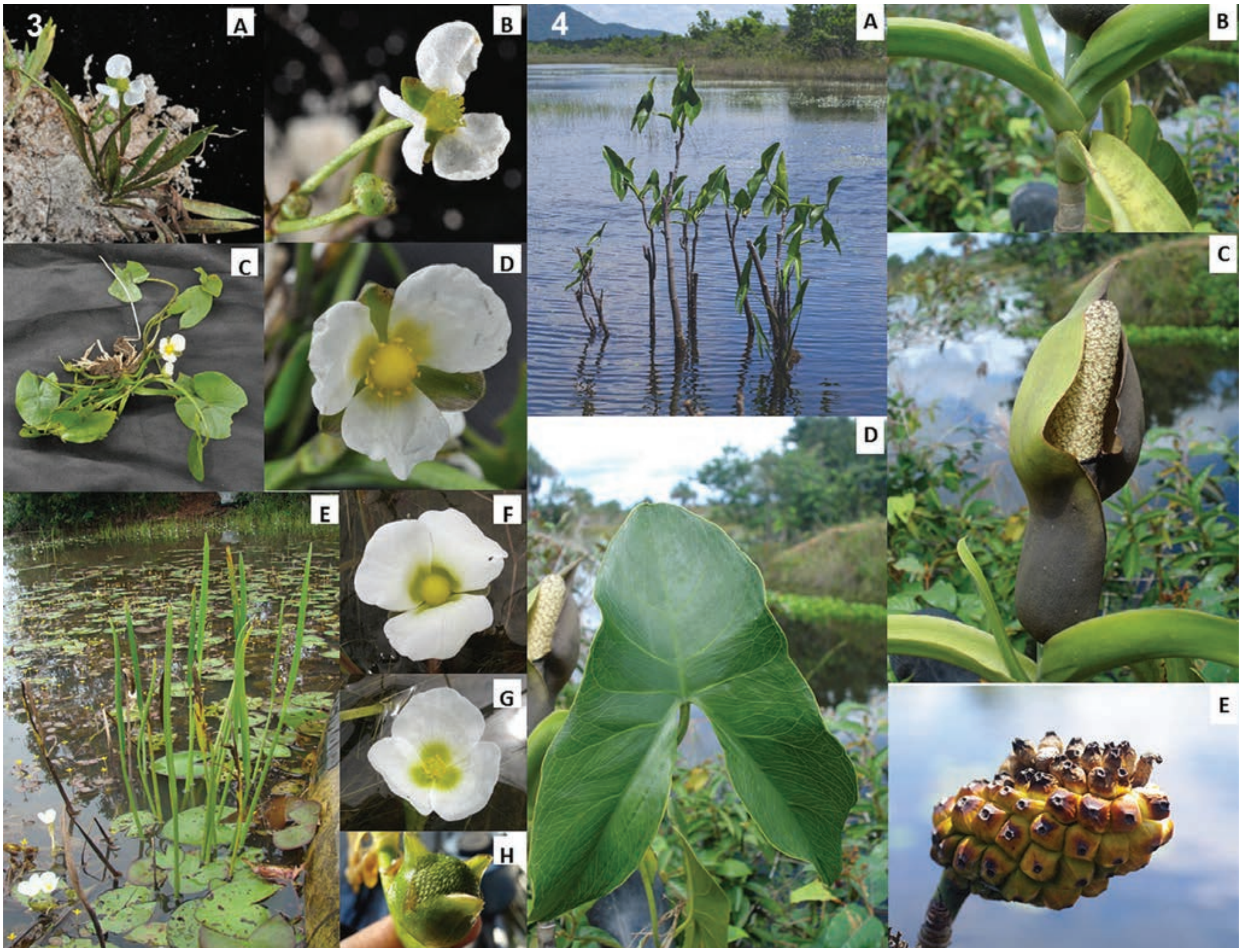
Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, 07 March 2010, 01°25'15"N, 60°59'08"W, *T. D. M. Barbosa et al. 1094* (INPA, UEC); idem, Estrada Perdida, 16 September 2010, *S. M. Costa et al. 754* (INPA, UEC).

Additional specimens examined: BOLIVIA. Reyes, 25 October 1921, *White 1540* (Isolectotype of *Helanthium bolivianum* (Rusby) Lehtonen & Myllys [K000061663]).

Geographical distribution and ecology: In sandy and soaked soils. From the Northeastern United States, to Mexico, Nicaragua, Cuba, Jamaica, Dominican Republic, Colombia, Guyana, Bolivia, Argentina and Brazil (Haynes and Holm-Nielsen, 1995). In Brazil, the species is found in all regions and states (except Acre) (Matias, 2019).

3.b. ***Sagittaria*** Rupp. ex L.

Rhizomatous *herbs*, the rhizomes occasionally terminated by tubers, or cormose. *Emerged* or *floating leaves* petiolate, blades sagittate, rhombiform to linear; submerged leaves sessile, blades linear. *Inflorescences* usually a raceme or



FIGURES 3–4. **3.** Alismataceae – *Helanthium tenellum* (Mart. ex Schult. f.) Britton. **A**, habit; **B**, flower and flower bud. *Sagittaria guayanensis* Kunth. **C**, habit; **D**, flower. *Sagittaria rhombifolia* Cham.. **E**, habit; **F**, pistillate flower; **G**, staminate flower; **H**, fruit. **4.** Araceae – *Montrichardia arborescens* (L.) Schott. **A**, habit; **B**, leaves' basis; **C**, inflorescence; **D**, leaf (adaxial surface); **E**, infructescence.

panicle, whorls 1–17 with 2 or 3 flowers; bracts obtuse to acute. *Flowers* at least the lower ones unisexual; pedicellate; sepals elliptic (staminate flowers) or ovate to almost deltoids (pistillate flowers); petals obovate; staminate flowers with 7–numerous stamens, anthers linear to sagittate, pistillode rarely present; pistillate flowers with numerous pistils, arranged spirally, surrounded by a whorl of staminodes (sometimes absent). *Fruits* laterally compressed, usually with thin and curved margin, winged, with apical or lateral keel (adapted from Haynes and Holm-Nielsen, 1995; Pansarin and Amaral, 2005).

Genus with approximately 30 species distributed in temperate and tropical regions of the globe, from the temperate north to tropical America, extending to Patagonia. Of these species, 14 occur in the neotropics, six occur in Brazil (Haynes and Holm-Nielsen, 1994; Matias, 2019; Pansarin and Amaral, 2005).

3.b.1. ***Sagittaria guayanensis*** Kunth, Nov. Gen. Sp. (quarto ed.) 1: 250. 1815[1816]. Fig. 3C–D.

Emerged or floating-fixed *herbs*, cormose, up to ca. 15 cm tall. *Emerged* or *floating leaves* sagittate, ca. 30.0–45.0 × 25.0–36.5 mm, apex acute-rounded, base sagittate to cordate, venation actinodromous, 10–11-veined. *Submerged leaves* linear, apex rounded to obtuse, 3–5-veined, base acute to attenuate. *Inflorescences* scape with 1–7 whorls, ca. 56.0 × 1.55 mm; bracts of staminate and pistillate flowers ovate. *Staminate flowers* with pedicel 19.5 × 0.5 mm, glabrous; sepals ca. 6.0 × 3.0 mm; petals ca. 6.5 × 5.0 mm; stamens 7, pistillodes ca. 40; *pistillate flowers* with ring of staminodes; pedicel ca. 9.75 × 0.80 mm, pubescent; sepals erect in flowers and fruits. *Fruits* ca. 2.0 × 1.5 mm, with lateral keel horizontal to ascending, face tuberculate.

No submerged leaves were observed in VNP (description according to Amaral et al., 2008). The species was collected in a shallow lake, with clay soil, in a sunny area.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, 01°27'30"N, 60°58'26"W, 07 March 2010, *T. D. M. Barbosa et al. 1097* (INPA, UEC).

Geographic distribution and ecology: In lakes, canals and flooded areas. From the southeastern United States, passing through Jamaica, the Dominican Republic, and Mexico, Central America and South America to Paraguay and northern Argentina (Amaral et al., 2008; Haynes and

Holm-Nielsen, 1994). In Brazil, the species is found in the North (Acre, Amazonas, Pará, Roraima and Tocantins), Northeast (Alagoas, Bahia, Ceará, Maranhão, Pernambuco, Piauí, Rio Grande do Norte, Sergipe), Central-West (Goiás, Mato Grosso do Sul and Mato Grosso) and Southeast (Minas Gerais) reagions (Matias, 2019).

3.b.2. *Sagittaria rhombifolia* Cham., Linnaea 10: 219. 1835. Fig. 3E–H.

Emerged *herbs*, rhizomatous or cormose, up to 1.0 m tall. *Emerged leaves* linear, lanceolate-ovate, less often narrow-elliptic, often conduplicate, 12.0–15.0 × 1.0–2.0 cm, apex and base acute, parallel-bowed venation, 5–8-veined. *Submerged leaves* linear, apex rounded to acute, 1–3-veined. *Inflorescences* scape with 1–12 whorls, ca. 100.0 × 0.5 cm; bracts of staminate flowers ovate to deltoid; bracts of the pistillate flowers deltoid. *Staminate flowers* with pedicel 24.0 × 1.5 mm, glabrous; sepals ca. 11.75 × 7.0 mm; petals ca. 21.0 × 20.5 mm; stamens 9–12, pistillodes ca. 20; *pistillate flowers* with or without staminodes ring; pedicel 11.5 × 3.0 mm, glabrous; sepals appressed on flowers and fruits. *Fruits* ca. 4.0 × 1.5 mm, with lateral or horizontal keel, face non-tuberculate.

The inflorescence can be found both above and below the water. In both cases, the flowers open around 11:00 a.m. Apparently in cases where the axis is below the water only the flowers' pedicel rises causing the flowers to emerge. Bees and flies were seen visiting *S. rhombifolia* flowers in VNP.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, Estrada Perdida, 19 September 2010, *S. M. Costa et al. 770b* (INPA, UEC); idem, 14 October 2011, *C. T. Pedrollo et al. 140* (INPA, UEC); idem, 01°25'15"N, 60°59'06"W, 16 July 2010, *T. D. M. Barbosa 1110 & S. M. Costa* (INPA, UEC).

Additional specimens examined: BRAZIL. *s.d.*, *Sellow s.n.* (Isolectotype [K000587167]); idem, August 1839, *Gardner 2737* (Lectotype of *Sagittaria pugioniformis* var. *platyphylla* Micheli [K000587168]); idem, 1841, *Gardner 2737* (Isolectotype of *Sagittaria pugioniformis* var. *platyphylla* Micheli [K000587169]).

Geographic distribution and ecology: In palustrine and shallow lagoon environments (Amaral et al., 2008). From Costa Rica to Argentina (Haynes and Holm-Nielsen, 1994). In Brazil, it is found in the North (Acre, Pará, Rondônia, Roraima and Tocantins), Northeast (Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí and Sergipe), Central-West (Goiás, Mato Grosso do Sul and Mato Grosso), Southeast (Minas Gerais and São Paulo) and South (Paraná, Rio Grande do Sul and Santa Catarina) regions (Matias, 2019).

4. ARACEAE Juss. (Alismatales)

Herbs sometimes latisciferous. *Stems* subterranean and rhizomatous or cormose, or aerial and erect, creeping or climbing. *Leaves* alternate, sometimes distichous, basal or cauline; petiole with a sheath, often geniculate; blade usually simple, entire or variously dissected, primary lateral veins often radiate or pinnate. *Inflorescences* spadix subtended by a free spathe or partially adnate to it. *Spathe* patent, reflexed, or convolute, sometimes differentiated into a basal tube and an apical limb. *Spadix* generally cylindrical. *Flowers* sessile, ebracteate, bisexual or unisexual (monoecious plants, rarely dioecious), often the most basal flowers pistillate and the most apical flowers staminate; perianth absent or generally with 4–6 tepals (monochlamydeous flowers), usually free; stamens 2–6(–9), free or synandria, anthers often subsessile, extrorse, longitudinal, or poricidal, when sterile then the staminodes free or synandrodia; pistils generally free; ovary usually superior, 1–many loculate, each with 1–many ovules, placentation parietal, axillary or apical; style usually absent or short; stigma rounded to linear. *Fruits* usually an infructescence composed of separate indehiscent berries with 1–many seeds (adapted from Buntig, 1995).

Family with approximately 110 genera and about 3500 species. Araceae are distributed throughout the world except for polar regions and drier deserts, mainly in tropical and subtropical regions (Li et al., 2010). In Brazil Araceae are found in all regions and states, 511 species are registered in 38 genera (Flora do Brasil, 2019a). In VNP two genera and two species were found.

KEY TO ARACEAE SPECIES

1a. Free floating plants; leaves arranged in rosette . . . . *Pistia stratiotes*
1b. Emergent plants, rooted in the substrate; leaves alternate. . . . . *Montrichardia arborescens*

4.a. *Montrichardia* Crueg.

Herbs erect. *Stems* unbranched, spiny or not. *Leaves* mostly terminal, apparently resupinate with posterior lobes held toward the ground and the adaxial surface outward; petioles sheathed up to middle or beyond, wings ending in a ligule; blades sagittate or ovate, posterior lobes of approximately the same length as the anterior lobe, primary lateral veins confluent into a collective vein close to margin, veins of higher orders reticulate. *Inflorescences* with solitary and short peduncles. *Spathe* slightly convolute and constrict, entirely deciduous, limb partially opening. *Spadix* shorter than spathe, pistillate portion 2–3 times shorter than staminate portion and contiguous to it. *Flowers* unisexual, achlamydeous; *staminate flowers* with 3–6 stamens, free, prismatic, thecae oblong, lateral and dehiscent by an apical slit; *pistillate flowers* with 1-loculate ovary, 1–2 ovules, placentation basal; apical portion of the style subtruncate with a central concavity; stigma discoid. *Infructescences* ellipsoid or ovoid. *Fruits* bacaceous, spongy, 1-seeded (adapted from Bunting, 1995).

Genus distributed in the neotropics, with two species: *M. arborescens* and *M. linifera* (Arruda) Schott (Bunting, 1995). In Brazil, the genus is distributed in the North (Acre, Amazonas, Amapá, Pará, Rondônia and Roraima), Northeast (Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe), Central-West (Mato Grosso) and Southeast (Espírito Santo, Minas Gerais and Rio de Janeiro) regions (Mayo and Andrade, 2019). In VNP one species was found.

4.a.1. ***Montrichardia arborescens*** (L.) Schott, Arac. Betreff. 1: 4. 1854. Fig. 4A–E.

Herbs emerged, amphibians, ca. 2.0 m tall. *Stems* with internodes ca. 4.0–5.0 × 6.5–9.0 mm. *Leaves* with petiolate sheath 89.0 × 10.5 mm; petiole 45.5 × 2.0 mm; not geniculate; blade chartaceous, discolor, sagittate, 15.5–18.5 × 8.5–10.0 cm, apex obtuse, margin wavy; venation colocasioid, 3 primary lateral veins, 2 acroscopic, 0–1 basiscopic, slightly prominent on both surfaces. *Inflorescences* 1 per leaf axil; peduncle 23.0–35.0 × 3.5–5.0 mm, green. *Spathe* 10.0 × 18.0 mm, green externally, internally white with red base. *Spadix* ca. 83.5 × 33.5 mm, stipite 1.5 mm length, cream, pistillate area 26.5 mm, staminate area 56.5 mm. *Infructescences* erect, ellipsoid, ca. 10.0 × 6.0 cm. *Fruits* green, or brown, apex convex, 2–3 cm long, 1-seeded. *Seeds* up to 1.5 cm long.

Herbs with whitish latex turning reddish over time. Species collected in grassy campinaranas, occurring more or less isolated, or in forested areas (mainly in the forest edges of the Iruá river), where it occurs in dense populations.

According to Bunting (1995), the distinction between *M. arborescens* and *M. linifera*, both occurring in the Brazilian Amazon, is difficult. Many plants have intermediate characteristics between them, making it difficult to identify, particularly in the Amazon. One of the characteristics that distinguish the two species is that in *M. arborescens* the primary lateral veins are in number of 3 or 4, whereas in *M. linifera* the veins are 5 to 7. The specimens collected in Viruá present 3 primary veins and were thus identified as *M. arborescens*.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, Estrada Perdida, 16 September 2010, *S. M. Costa et al. 768* (INPA, UEC).

Additional specimens examined: PANAMA. February, 1850, *Fendler 432* (Type of *Montrichardia fendleri* Schott [K000434763] - image), idem, February 1850, *Fendler 433* (Type of *Montrichardia fendleri* Schott [K000434764] - image).

Geographic distribution and ecology: occurs in river banks, lagoons and in forests with seasonal flooding. Often forming large colonies in sunny or partially shaded areas. Species widely distributed in Central America, Puerto Rico, the Caribbean, Trinidad and Tobago and South America (Bunting, 1995). In Brazil, the species is found in the North (Acre, Amazonas, Pará, Rondônia and Roraima), Central-West (Mato Grosso) and Southeast (Minas Gerais) regions (adapted from Mayo and Andrade, 2019).

4.b. *Pistia* L.

The genus is monotypic, so the descriptions is as follows.

4.b.1. ***Pistia stratiotes*** L., Sp. Pl. 2: 963. 1753. Figure in *Flora Brasiliensis*. Vol. III, Part II, Fasc. 76, plate 52. 1878.

Floating aquatic *herbs*, perennial, stoloniferous, acaulescent, with feathery roots. *Leaves* rosulate, densely pubescent; petiole ca. 2.5 mm long, externally pilose, internally glabrous; sheath ligulate, ca. 4.5 mm long, scarious, punctate-glandulose, surrounding the petiole, apex irregular; blade ca. 19.5 × 19.0 mm, obovate-cuneate to obovate-oblong, slightly spongy, apex rounded, truncate to retuse, cuneate towards the base, veins 5, subparallel, emerging from the base, slightly divergent and approaching the margins near apex, strongly prominent abaxially, venation of higher orders reticulate. *Inflorescences* solitary, ca. 1.0 cm length; peduncle pubescent. *Spathe* white, slightly constricted in the middle, pubescent externally, glabrous internally, proximal margins connate and adnate to the ovary's wall forming a tube, the free margins between the tube and lamina folded forming a partition between a staminate distal chamber and a pistillate proximal chamber. *Spadix* mostly adnate to spathe, shorter than this, only the staminate apical portion free, pistillate zone with a single gynoecium at the base. *Flowers* unisexual, glabrous; *staminate flowers* a synandrium, consisting of 2 connate stamens, dehiscing by an apical slit; *pistillate flowers* with gynoecium adnate to the axis of the spadix, ovary ovoid, 1-loculate, ovules numerous, placentation apparently parietal, style region attenuate, bending towards the staminate flowers, stigma discoid, subcapitate. *Fruits* thin walled, utricular, many-seeded, berry ellipsoid, marcescent. *Seeds* ellipsoid, seed coat reticulate-alveolate.

Collected floating in white water (igarapé do Cobra), among dense populations of *Eichhornia* Kunth.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, 00°57'53"N, 61°21'30"W, 26 March 2011, *T. D. M. Barbosa 1403 & S. M. Costa* (INPA, UEC).

Geographic distribution and ecology: Pantropical species occuring in river banks and lagoons. It is widely distributed in the tropics and subtropics (Amaral et al., 2008). In Brazil, the species is recorded in all regions and states (except Rondônia and Tocantins) (adapted from Mayo and Andrade, 2019).

5. HYDROCHARITACEAE Juss. (Alismatales)

Annual or perennial *herbs*, submerged, floating, or emerged, usually glabrous. *Stems* rhizomatous or erect. *Leaves* basal or caulinar, alternate, opposite, or whorled, entire or serrate, sessile or petiolate, 1–many-veined; stipules when present forming a tubular sheath around the stem; parallel-veined. *Inflorescences* axillary, terminal, or scapose, solitary or cymose, 1–multi-flowered, subtended by a bifid bract or a pair of opposite, sessile or pedunculate bracts. *Flowers* unisexual or bisexual (monoecious, dioecious or hermaphroditic plants), usually actinomorphic and dichlamydeous; sepals free, valvate; petals free, imbricate or convolute; stamens absent or 2–many in 1–more whorls, the inner often staminodal, free or connate, anthers basifixed, 2-thecae, dehiscing via short slits; carpels absent or 2–5, connate; ovary inferior, 1-locular, placentation parietal or laminar; ovules numerous; style 2–5; stigma usually bifid. *Fruits* capsule similar to berry. *Seeds* fusiform, ellipsoid, ovoid, or globose (adapted from Haynes and Holm-Nielsen, 1999).

Native mainly to tropical and subtropical waters of the world, but also in temperate areas. Hydrocharitaceae has

16 genera and ca. 100 species (Haynes and Holm-Nielsen, 1999). In Brazil, 14 species are recorded in seven genera. The family is found in all regions and states (except Acre) (Lourenço and Bove, 2019). In VNP one species was found.

5.a. *Elodea* Michx.

Herbs submerged, perennial, glabrous, dioecious or hermaphrodite. *Stems* erect, branched or not. *Leaves* simple, sessile, linear to narrow-elliptical, in whorls of 3–7, or rarely opposite, 1-veined, serrate, vein without dorsal prickle. *Inflorescences* solitary, axillary; spathes sessile, usually narrowed towards the base, cylindrical to elliptic-spatulate, 1-flowered. *Flowers* bisexual or unisexual, usually projected to water's surface by the elongating hypanthium base; sepals 3, herbaceous, green; petals 3, membranaceous, white to pale blue, free, elliptic, unguiculate; stamens 3–9, or reduced to 3 staminodes, anthers oblong to ellipsoid, filaments subulate to lanceolate, free or the 3 inner connate halfway to apex; carpels 3, 1-locular, placentation parietal; styles 3, stigmas 3, bifid. *Fruits* ovoid to lanceolate-ellipsoid, corniculate. *Seeds* 3–8, cylindrical to fusiform (adapted from Haynes and Holm-Nielsen, 1999).

Genus distributed in the western hemisphere. *Elodea* has six species (Haynes and Holm-Nielsen, 1999), only one in VNP. The six species of *Elodea* are separated into two subgenera: *Elodea* and *Apalanthe* Planch. The subgenera can be separated into subgenus *Elodea* with five species, with unisexual flowers, staminate flowers with 6–9 stamens and some filaments connate; and subgenus *Apalanthae* with *Elodea granatensis* only, with bisexual flowers, with 3 free stamens and filaments (adapted from Haynes and Holm-Nielsen, 1999).

Due to such discrepant features commonly the subgenus *Apalanthe* has been treated as a genus apart from *Elodea*. In this case, the only species belonging to this taxon would be *Apalanthe granatensis* (Humb. & Bonpl.) Planch. (Haynes and Holm-Nielsen, 1999).

5.a.1. *Elodea granatensis* Bonpl. in Humb. & Bonpl., Pl. Aequinoct. 2(16): 150. 1809 [1813]. Figure in Hall and Gil (2016) under the name *Apalanthe granatensis* (Humb. & Bonpl.) Planch.

Stems irregularly branched. *Prophylls* paired, oblique, almost triangular, gradually attenuated to an acute apex, ca. 1.9 × 0.4 mm. *Leaves* 5–6-whorled, imbricate, linear to narrowly elliptic, 6.7–7.8 × 1.6–1.8 mm, apex acute, margins serrate. *Spathe* tubular, ca. 8.25 × 2.40 mm, apex bifid. *Flowers* bisexual, sessile; hypanthium ca. 40.0 × 1.5 mm, cylindrical; sepals oblong to narrowly oblong, ca. 1.70 × 0.60 mm, reflexed, apex rounded; petals patent, oblong, ca. 4.0 × 1.0 mm; stamens 3, antisepalous, yellow or white, filaments ca. 1.2 mm, anthers ca. 0.5 × 0.4 mm; styles antipetalous, ca. 2.0 mm, slightly flattened, irregularly divided into 3 lobes, divisions almost to the base, stigmatic lobes white, flat, papillose, base of styles thickened. *Fruits* thin walled, irregularly dehiscent, botuliform, ca. 5.6 × 2.0 mm, bearing remnants of the hypanthium. *Seeds* 6–7 per fruit, fusiform, 2–3 × 0.4–0.5 mm, bearing a persistent micropylar projection ca. 0.4 mm length, seed coat covered by trichomes, ca. 0.6 mm, straight, ascending.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, Estrada Perdida, 20 January 2011, *M. C. E. Amaral 2011/34 & C. F. Silva* (INPA, UEC); idem, 16 September 2010, *S. M. Costa et al. 762* (INPA, UEC).

Additional specimens examined: BRAZIL. *Spruce 1991* (Type of *Elodea guyannensis* var. *dicranioides* Spruce ex Caspary [K000587176] - image).

Geographical distribution and ecology: Venezuela, Colombia, Guyana, Suriname, Brazil and Bolivia. It is found mainly in low altitude areas, however it is recorded up to 1500 m in Colombia (Cook, 1985). In Brazil, the species is found in the North (Amazonas, Pará, Roraima and Tocantins), Northeast (Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe), Central-West (Goiás, Mato Grosso do Sul and Mato Grosso) and Southeast (Minas Gerais, Rio de Janeiro and São Paulo) regions (Lourenço and Bove, 2019).

6. BURMANNIACEAE Blume (Discoreales)

Herbs annual or perennial, saprophytic or autotrophic, glabrous, usually rhizomatous. *Stems* usually not branched. *Leaves* alternate, often rosulate, simple, entire, sessile, without stipules. *Inflorescences* usually terminal cyme, bearing bracts, often bifurcate, 1–many-flowered. *Flowers* usually pedicellate, bisexual, syntepalous; floral tube usually persistent, sometimes provided with longitudinal wings or ribs; tepals 6, the three outer ones often much larger than the inner ones, usually valvate to induplicate; stamens 3 or 6, inserted in the floral tube, anthers 2-thecae, introrse, transversely dehiscent, connective dilated, and generally with basal and/or apical appendages; ovary inferior, 3-carpelar, 1- or 3-locular, placentation parietal or axillary, often with septal nectaries or with nectaries on top of the ovary, ovules numerous; style 3-branched at the apex, each branch with 3-apical stigma, sometimes provided with appendages, or stigma capitate. *Fruits* capsules, dehiscing longitudinally or transversely through slits or valves, or irregularly dehiscing. *Seeds* usually fusiform to subglobose (adapted from Kamer and Maas, 2003; Maas and Maas, 1997).

Family with about 150 species, distributed in 15 genera that occur in all tropical and subtropical regions of the old and new world; some outside the tropics (Kamer and Maas, 2003; Maas and Maas, 1997). In Brazil, the family is distributed throughout all the national territory, with 26 species distributed in eight genera (Flora do Brasil, 2019c). In VNP one genus with two species was found.

Key to Burmanniaceae Species

1a. Inflorescences 1–6 flowered; flowers blue-purplish with yellow tepals . . . . *Burmannia bicolor*
1b. Inflorescences multi-flowered; flowers white to yellowish-white, sometimes green or purplish . . . . *Burmannia capitata*

6.a. *Burmannia* L.

Herbs erect, usually autotrophic. *Rhizome* absent. *Stems* branched or not. *Leaves* spirally arranged, small and scale-like, sometimes relatively large especially near the base of the stem, sometimes rosulate. *Inflorescences* a terminal cyme, bifurcate, lax to capitate, or just a single terminal flower; bracts sometimes imbricate. *Flowers* sessile to short pedicelate; inner tepals smaller than external ones; floral tube cylindrical to trigonous, wings absent to largely 3-winged, wings running from the top of the floral tube down to the ovary, sometimes continuing as a crest over the outer tepals; anthers 3, sessile, inserted just below the inner tepals, connective with 2 apical and 1 basal appendage; ovary 3-locular, placentation axillary, septal nectaries 3; style 3-branched at apex, each branch with a bilabiate stigma, upper lip erect and usually clavate, lower lip flat and patent. *Capsules* crowned by persistent perianth, transversely dehiscent by several slits in the membranous wall, or irregularly dehiscent through the membranous and marcescent wall between the ribs. *Seeds* usually ellipsoid (adapted from Kamer and Maas, 2003; Maas and Maas, 1997).

Pantropical genus with about 60 species (Maas and Maas, 1997). About 20 Neotropical species, distributed from the southern United States, Mexico, Central America and the Antilles, to Peru, Paraguay, Argentina and Brazil (Maas et al., 1986). In Brazil, the genus is represented by 12 species, of which four are endemic to the country. It occurs in all regions and all states (Flora do Brasil, 2019c). In VNP two species were found.

6.a.1. ***Burmannia bicolor*** Mart., Nov. Gen. Sp. Pl. (Martius) 1(1): 10, t. 5. 1824. Fig. 5A–C.

Amphibian *herbs*, up to ca. 35 cm tall, glabrous. *Stems* angular, ca. 0.5 mm diam., green, sometimes the apical part purplish, predominantly unbranched. *Leaves* green, narrowly triangular-ovate to subulate, 4.0–13.0 × 1.0–2.0 mm, parallel-veined, apex acuminate, basal leaves rosulate. *Inflorescences* generally a single terminal flower, less often a bifurcate cincinnus, 2–6-flowered, each cincinnus ca. 8.0 mm length; bracts narrowly ovate, elliptic to subulate, 2.5–3.0 × 0.4–0.5 mm, apex acute to acuminate. *Flowers* blue-purplish with yellow tepals, ca. 13.0 mm length; outer tepals oval-triangular, ca. 2.0 × 1.5 mm, margins involute, 1-ribbed; inner tepals narrowly triangular to narrowly elliptic, almost columnar, 1.0 × 0.5 mm, sometimes margins involute; floral tube ca. 5.5 × 2.0 mm; wings semi-elliptic, 10.5 × 3.0 mm; style ca. 5.0 mm length; branches 1.0 mm length; ovary largely ovoid to obconical, 4.0 × 1.5 mm. *Capsules* purple, obovate to obconical, sometimes narrow, 2.5–5.5 × 1.5–3.0 mm. *Seeds* 0.2–0.7 × 0.1–0.2 mm.

The capsules were not seen in the specimens collected in Viruá—description from Maas et al. (1986). In VNP, the species is found in waterlogged areas, both in the grassy campinaranas of "Estrada Perdida" and in the "spots" of campinaranas encrusted in the forested areas of the PPBio grid.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, PARNA Viruá, 15 September 2010, *S. M. Costa et al. 742* (INPA, UEC); idem, 01°28'56"N, 61°01'13"W, 24 January 2011, *S. M. Costa 870 & K. G. Cangani* (INPA, UEC).

Additional specimens examined: BRAZIL. Minas Gerais, *s.d.*, *Martius 1196 p.p* (probable Isotype [K000524564] - image).

Geographic distribution and ecology: Cuba and South America except in the Andean parts; predominantly in sandy savannas or swamps, and in gallery forests; predominantly at low altitudes, but up to 1500 m (Maas et al., 1986). In Brazil, the species is found in the North (Amazonas, Amapá, Pará, Rondônia and Roraima), Northeast (Bahia and Maranhão), Central-West (Distrito Federal, Goiás and Mato Grosso), Southeast (Minas Gerais, Rio de Janeiro and São Paulo) and South (Paraná) regions (Flora do Brasil, 2019c).

6.a.2. ***Burmannia capitata*** (Walter ex J.F. Gmelin) Mart., Nov. Gen. Sp. Pl. (Martius) 1(1): 12. 1824. Figure in Giulietti (2016).

Amphibian *herbs*, up to ca. 14.0 cm tall, glabrous. *Stems* almost cylindrical, ca. 0.5 mm diam., yellowish or greenish, predominantly unbranched. *Leaves* subulate to narrowly ovate, 2.5–8.5 × ± 1.0 mm, parallel-veined, apex acute to predominantly acuminate, basal leaves rosulate. *Inflorescences* multi-flowered, capitate, consisting of 2 contracted and recurved cincinnus, or cincinnus less contracted and facing upward, 6.0 × 9.0 mm; bracts ovate to elliptic, imbricate, 2.0–2.5 × 1.0–1.5 mm, apex acute. *Flowers* white to yellowish-white, sometimes purple to greenish, ca. 3.5 × 1.0 mm; external tepals deltoid, 0.45 × 0.40 mm, margins involute; inner tepals ovate to triangular, 0.1 × 0.1 mm, sometimes absent; floral tube 1.5 × 1.0 mm; wings reduced to ribs; style 0.75 mm length; branches 0.2 mm length; ovary obovoid to ellipsoid, 2.0 × 1.0 mm. *Capsules* white to yellow, obovoid to ellipsoid, sometimes globose, 1.3–2.9 × 0.9–2.0 mm. *Seeds* 0.2–0.4 × 0.1 mm.

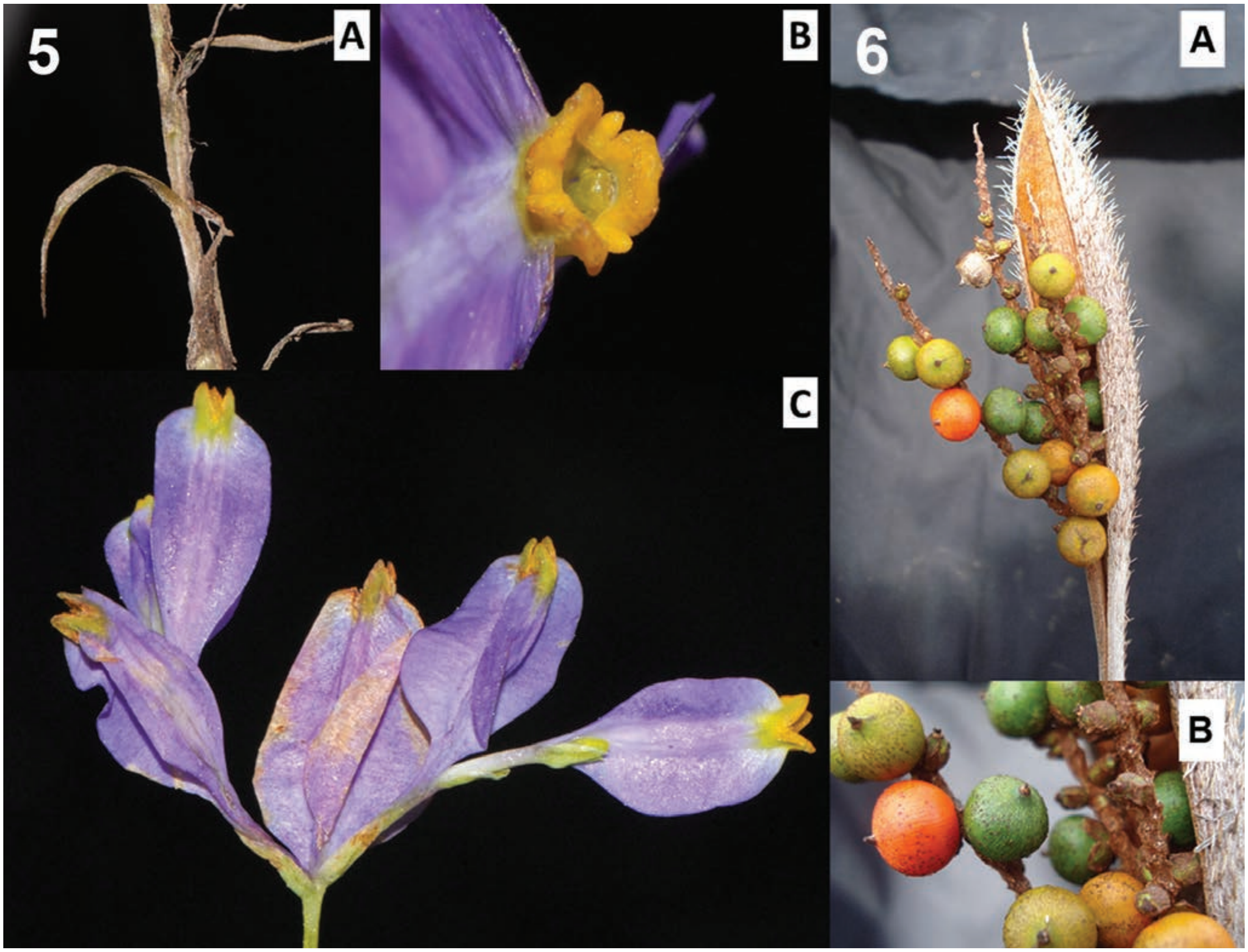
The capsules were not seen in the materials collected in Viruá—description from Maas et al. (1986).

Specimens examined from VNP: BRAZIL. Roraima: PARNA Viruá, 01°16'46"N, 60°59'20"W, 20 September 2010, *S. M. Costa et al. 792* (INPA, UEC).

Geographic distribution and ecology: from the south of the United States and Caribbean to northern Argentina, Paraguay and southern Brazil in the south; in savannas or swamps, in sandy or clayey soils (Maas et al., 1986). In Brazil, the species is found in all regions and states (except Acre) (Flora do Brasil, 2019c).

7. ARECACEAE Bercht. & J. Presl (Arecales)

Palm trees solitary or cespitose, spiny or not. *Stems* woody, aerial or subterranean. *Leaves* spirally or distichously arranged, palmate, costapalmate, pinnate, or entire with pinnate venation; usually petiolate; rachis conspicuous or very small; sheaths open or closed. *Inflorescences* inter or intrafoliar, usually solitary, spicate or branched; peduncle usually bearing a prophyll and 1–many bracts. *Flowers* usually 3-merous, heterochlamydeous, bisexual or unisexual (monoecious plants), sessile or pedicellate, often solitary or in triads, dyads or forming small fascicles;



FIGURES 5–6. **5.** Burmanniaceae – *Burmannia bicolor* Mart. **A**, leaves; **B**, flower (apex); **C**, inflorescence. **6.** Arecaceae – *Bactris campestris* Poepp. **A**, infructescence; **B**, fruit.

sepals generally 3, free or connate; petals generally 3, free or connate; stamens (3–)6–many, free or connate or adnate to the corolla base, staminodes present or absent; anthers basifixed or dorsifixed, 2-thecae; gynoecium apocarpous (1–)3(4) carpels or variously syncarpous generally 3-locular, or with 1 fertile locule, pistillode rudimentary or absent; style generally absent or short; stigma 3; ovule 1 per locule. *Fruits* more or less subtended by the persistent perianth, dry or drupaceous, sometimes covered by overlapping scales. *Seeds* generally one (adapted from Henderson, 1997).

Arecaceae are distributed in the tropics and subtropics of the world, few species occur in warmer temperate areas. The family has approximately 200 genera and about 2,000 species (Henderson, 1997). In the neotropics, palms are found in a wide variety of environments, from semi-deserts to savannas, mangroves, and lowland or mountain forests (Henderson, 1990). In Brazil, 37 genera and 300 species are recorded in all regions and states (Flora do Brasil, 2019b).

In this article, we chose to describe only *Bactris campestris* Poepp., because it is frequently encountered in the campinaranas of the VNP alongside other aquatic and palustrine herbs, subshrubs and shrubs. Nevertheless, it is worth mentioning that *Mauritia* sp. also occurs in VNP.

7.a. ***Bactris*** Jacq. ex Scop.

Monoecious *palm trees*, spiny. *Stems* solitary or cespitose. *Leaves* pinnate, entire with pinnate venation; sheaths open or close; pinnae regularly spaced or clustered, in 1 to several planes, or ± fused and then leaves entire, 1-veined. *Inflorescences* one order branched or spiciform, interfoliar; peduncles short; bract 1, much larger than the prophyll; rachillae glabrous or tomentose. *Flowers* unisexual, in triads; *staminate flowers* with (3–)6(–12) stamens, anthers linear, basifixed, pistillode minute or absent; *pistillate flowers* with varied calyx, corolla larger than the calyx or of the same length; staminodes absent or small, fused into a staminodal ring; gynoecium 3-locular and 3-ovulate, stigmas 3, sessile. *Fruits* globose to ovoid, or oblong, with apical stigmatic remnant, 1-seeded. *Seeds* with homogeneous endosperm, coriaceous (adapted from Henderson, 1997, 2000).

Bactris has a neotropical distribution and has about 100 species (Henderson, 1997). In Brazil, there are 45 species in all regions and all states (except Ceará, Rio Grande do Norte and Paraíba in Northeast region) (Flora do Brasil, 2019b). In VNP one species was found.

7.a.1. ***Bactris campestris*** Poepp., ex Mart., Hist. Nat. Palm. 2: 146. 1837. Fig. 6A–B.

Amphibious, cespitose, 1.0–2.0 m tall. *Stems* 2.5 cm diam.; spines at the base of the leaf flattened and black, ca. 20.0 × 1.0 mm. *Leaves* densely villose, trichomes whitish-gray, pinnas spirally arranged, ensiform, ca. 22.5–29.0 × 1.0–1.5 cm, both surfaces glabrous, abaxial surface slightly lighter; peduncle 16.0 × 5.0 cm, grayish; rachilla 14.5 × 0.5 cm, densely rusty. *Fruits* depressed-globose, 6.0 × 7.0 mm, green when unripe, yellow or red when ripe.

In VNP, *Bactris campestris* is found in woody-grassy campinaranas where it occurs very frequently.

Specimens examined from VNP: BRAZIL. Roraima: Caracaraí, Parque Nacional do Viruá, N1-N2/L3, 22 January 2011, *S. M. Costa 840* (INPA, UEC); idem, 01°24'09"N, 60°59'11"W, 25 July 2010, *T. D. M. Barbosa 1343 & S. M. Costa* (INPA, UEC).

Additional specimens examined: GUYANA. January 1880, *E.F. im Thurm* (probable type of *Bactris leptocarpa* Trail ex im Thurm [K000584792] - image).

Geographic distribution and ecology: Colombian Amazon, Trinidad, Guyana, Suriname, French Guiana, Brazilian Amazon [in the North (Amazonas, Amapá, Pará and Roraima) and Northeast (Maranhão) regions] (Flora do Brasil, 2019b; Henderson, 1997).

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Appendix

Index to Numbered Collections

Amaral, M.C.E. 2011/33 & Silva, C.F. (**2.a.2**); *2011/34* (**5.a.1**)

Barbosa, T.D.M. 1201 & Costa S.M. (**1.a.1**); *1269* (**1.a.1**); *1230* (**1.a.2**); *1229* (**2.a.1**); *1110* (**3.b.2**); *1403* (**4.b.1**); *1343* (**7.a.1**)

Barbosa, T.D.M. et al. 1096 (**1.a.2**); *1094* (**3.a.1**); *1097* (**3.b.1**)

Costa, S.M. 840 (**7.a.1**)

Costa, S.M. 694 & Barbosa, T.D.M. (**2.a.1**)

Costa, S.M. 763 & Cangani, K.G. (**1.a.1**); *894* (**1.a.2**); *870* (**6.a.1**)

Costa, S.M. et al. 766 (**1.a.1**); *763* (**1.a.2**); *815* (**2.a.2**); *754* (**3.a.1**); *770b* (**3.b.2**); *768* (**4.a.1**); *762* (**5.a.1**); *742* (**6.a.1**); *792* (**6.a.2**)

Pedrollo, C.T. et al. 140 (**3.b.2**)

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CLARIFYING THE IDENTITY OF THE ENIGMATIC MISTLETOE *CLADOCOLEA BIFLORA* (LORANTHACEAE)

Marcos A. Caraballo-Ortiz[1, 2] and Pedro Acevedo-Rodríguez[1]

Abstract. Since its description almost 40 years ago, the mistletoe *Cladocolea biflora* (Loranthaceae) has been considered an extraordinary species due to its combinations of unique morphological characters, which made it difficult to confidently assign it to any of the extant genera of Neotropical Loranthaceae. In this contribution, we propose that the specimen from which *C. biflora* was described does not represent a mistletoe but instead the hemiparasitic tree *Schoepfia schreberi* (Schoepfiaceae). Morphological characters evaluated to justify this decision and taxonomic implications are discussed, and a synonymization of *C. biflora* under *S. schreberi* is proposed.

Resumen. Desde su descripción hace casi 40 años, el muérdago *Cladocolea biflora* (Loranthaceae) ha sido considerado una especie extraordinaria por su combinación de caracteres morfológicos únicos, los cuales han hecho difícil el posicionarlo con certeza dentro de uno de los géneros actuales de Lorantáceas neotropicales. En este trabajo, proponemos que el espécimen bajo el cual *C. biflora* se describió no representa un muérdago, sino el árbol hemiparasítico *Schoepfia schreberi* (Schoepfiaceae). Se discuten los caracteres morfológicos evaluados para justificar esta decisión y sus implicaciones taxonómicas, y se propone una sinonimización de *C. biflora* bajo *S. schreberi*.

Keywords: Mexico, parasitic plants, Santalales, *Schoepfia*, Schoepfiaceae

Almost 40 years ago, an intriguing mistletoe from Mexico showing an array of unusual characters was described as *Cladocolea biflora* Kuijt (Loranthaceae). In its original publication, Kuijt (1980) recognized the extraordinary nature of this species and placed it tentatively as a member of *Cladocolea* Tiegh. Since then, *C. biflora* has been highlighted as enigmatic, mainly due to its atypical floral morphology, and was considered the sole example of a Neotropical mistletoe with a gamopetalous corolla (Kuijt, 2009a,b; Kuijt and Hansen, 2015). In fact, the unique features shown by *C. biflora* led Kuijt (2013) to believe that the new species perhaps belonged in a new genus of Loranthaceae, but because of the lack of adequate material he never described it. Thereafter, the taxonomic status of *C. biflora* remained unsolved, awaiting additional material (Kuijt, 2013).

While studying Neotropical Loranthaceae, we noticed that the protologue of *Cladocolea biflora* contains a series of features that otherwise correspond with *Schoepfia* Schreb. (Schoepfiaceae), a member of hemiparasitic Santalales. The most evident characters are the presence of alternate leaves with plicate-falcate blades and angled cream or grayish stems, characters that are rare on Loranthaceous mistletoes but common in at least some *Schoepfia*, hence justifying the common name "graytwig" for species such as *S. schreberi* J.F. Gmel. (Wunderlin et al., 2017). Reproductive characters also suggest a better fit for *C. biflora* in *Schoepfia* than *Cladocolea*. These include fasciculate 2-flowered inflorescences, large cupules from the connation of bracts and bracteoles, gamopetalous corolla with monomorphic epipetalous, sessile anthers in the middle of the monomorphic corolla lobes, a conspicuous tuft of bristles inside the corolla tube directly behind the anthers, and a thick nectariferous disk (Sleumer, 1984; Kuijt and Hansen, 2015). Detailed drawings of the abovementioned features from the type specimen of *C. biflora* are presented in Kuijt (1980).

A possible reason behind the misidentification of this specimen of *Schoepfia* is its phenological status, which does not present flowers in full anthesis but mostly immature flower buds. The fragmented status of the type (*F. M. Liebmann 3147*, C) could have further masked its recognition, and its original identification as "*Loranthus*" seems to have misled identification efforts by assuming that it was a mistletoe. It is unfortunate that Frederick M. Liebmann did not provided any further description of the plant nor its locality within Mexico, although Standley (1927) points out that Liebmann's specimens were collected in the southern part of the country where *S. schreberi* has been reported (Sleumer, 1984). Efforts to locate the field notes of Liebmann or duplicates of the type specimen of *C. biflora* have been unsuccessful. Although Loranthaceae and Schoepfiaceae are not very distantly related families within Santalales (Su et al., 2015), specimens of *Schoepfia* in herbaria have been rarely misidentified as mistletoes. In a second case detected recently, Raymond M. Harley identified a specimen of *S. brasiliensis* A. DC. as an unknown species of *Struthanthus* Mart., describing it as "hemiparasitic in small tree" (*Harvey 21248*, US barcode 01335267). As far as we know, members of Schoepfiaceae comprise trees and shrubs that are exclusively root parasites and have never been suspected or confirmed to be aerial mistletoes.

Regarding the identity of the species of *Schoepfia*, the key provided by Sleumer (1984) in his taxonomic treatment of Olacaceae sensu lato led to two possible species:

We thank Emmanuel Martínez-Ambriz for initial discussions on possible identities of *Cladocolea biflora*. We are grateful to the curators and staff from the C, GH, MO, NY, and US herbaria for making their collections available either physically or through online resources. MACO was financially supported by the Peter Buck Postdoctoral Fellowship from the Smithsonian Institution.

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S. schreberi (corolla to 5 mm long) and *S. vacciniiflora* Planch. ex Hemsley (corolla 7–8 mm long). The holotype of *Cladocolea biflora* (examined and measured through JSTOR Global Plants: https://plants.jstor.org/ (accessed September 3, 2019, 07:30 GMT)) shows a few well-developed flower buds that do not exceed 3 mm long. Thus, we propose that the correct name for the type should be *S. schreberi*, rendering *C. biflora* a synonym of it. All of the other morphological characters observed in the holotype of *C. biflora* fit within the range of variation of *S. schreberi* described by Sleumer (1984), supporting our determination. A comprehensive taxonomic summary with synonyms of *S. schreberi* can be found in Sleumer (1984), and a representative illustration for the species can be found in Sagra (1850, t. 54) as the type of *S. chrysophylloides* (A. Rich.) Planch. (available at http://plantillustrations.org/illustration.php?id_illustration=48710 (accessed September 3, 2019, 07:30 GMT)).

Schoepfia schreberi J. F. Gmel. Syst. 2: 376. 1791. TYPE: SANTA LUCIA (LESSER ANTILLES). Collected before 1810, *J. W. von Crudy s.n.* (Holotype: M [Schreber Herbarium, not seen]; Isotypes: BR [BR0000005942473, image], S [S07-9719, image]).

Heterotypic synonym: *Cladocolea biflora* Kuijt, Brittonia 32: 519–521, f. 1–6, 1980. TYPE: MEXICO. Collected 1841–1843, *F. M. Liebmann 3147* (Holotype: C [C10014032, image]), *syn. nov.*

By recognizing *Cladocolea biflora* as a member of Schoepfiaceae, the taxonomy of the small-flowered Neotropical mistletoes is less convoluted by excluding the occurrence of gamopetaly and other features inconsistent with their typical traits. Now, diagnostic characters for *Cladocolea* are more refined, although the genus as currently defined still shows a broad variability and will require further taxonomic efforts to test boundaries and clarify relationships with other close groups such as *Struthanthus*.

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PENTAGONIA BAUMANNII AND *P. CARNIFLORA* (RUBIACEAE: CONDAMINEEAE): TWO NEW SPECIES WITH ORNAMENTAL POTENTIAL FROM COLOMBIA AND ECUADOR

Xavier Cornejo[1,2] and Johan Rova[3]

Abstract. Two new species of Rubiaceae (Condamineeae) are here described and illustrated. *Pentagonia baumannii* is a shrub endemic to the lowlands of northwestern Ecuador. The second novelty is *P. carniflora*, an unbranched to few-branched pachycaule tree restricted to the eastern lowlands of the Departments of Antioquia and Caldas in northwestern Colombia. The relations of both species with their closest relatives are discussed.

Keywords: Colombia, Ecuador, endemics, *Pentagonia*, Rubiaceae

Resumen. Dos nuevas especies de Rubiaceae (Condamineeae) son descritas e ilustradas. *Pentagonia baumannii* es un arbusto endémico de las tierras bajas del noroccidente de Ecuador. La segunda novedad es *P. carniflora*, un árbol paquicaule no ramificado o con escasas ramas restringido a las tierras bajas del este de los departamentos de Antioquia y Caldas, en el noroccidente de Colombia. Se discute las relaciones de ambas especies con las más cercanas.

Palabras claves: Colombia, Ecuador, endémicas, *Pentagonia*, Rubiaceae

Pentagonia Bentham (Rubiaceae: Condamineeae) is a Neotropical genus that comprises about 50 species of understory low-to-medium-size trees and shrubs, inhabiting wet to pluvial forests from Guatemala to Peru and Brazil, from sea level to 1600 (–1800) m (Cornejo 2009, 2010). According to our data base of herbaria collections, the highest concentrations of species in the genus are found in Colombia (22 spp.) and Ecuador (18 spp.). Both countries encompass a preliminary total of 32 species of *Pentagonia* (Andersson and Rova, 2004; Delprete and Cortés-B., 2015; Rova et al., in prep.), and new species in the genus are still expected to be found in that region. Half of the generic diversity (about 25 spp.) occur in the Chocoan–Panamanian forests, and 16 local or regional endemics are found only in the Choco region. As compared with Mesoamerica, which harbors a total of 18 species, of which 12 are locally or regionally endemic (Taylor, 2012; Hammel, 2015), this high concentration of species together with the relative high endemism suggest that the Choco bioregion is the main center of diversity of *Pentagonia*. In South America, the Andean cordillera is an effective orographic barrier that makes a clear separation between Chocoan and Amazonian species in the genus. The distinctive allopatric pattern of distribution allows the recognition of one group of species that occur in the Pacific lowlands and the westernmost slopes of the Andes in Ecuador and Colombia, and another group of species that is restricted to the Amazonian rainforests from Colombia to Peru and Brazil. Recently, molecular studies (Rova et al., in prep.) have brought to light new insights into the genus and the discovery of two new species from the Equatorial Choco and the Magdalena Valley. These new species, both decorated with showy inflorescences and of ornamental potential, are formally described and presented here.

TAXONOMY

Pentagonia baumannii Cornejo & Rova, *sp. nov.* TYPE: ECUADOR. Esmeraldas: Santa Teresa environs, finca Julio, sector Mono, 0°43'51"N, 79°49'27"W, 65 m, 15 October 2014 (fl), *X. Cornejo & B. Baumann 8635* (Holotype: GUAY; Isotype: GB). Fig. 1.

Pentagonia baumannii is closely related to *P. sprucei* Standl. but differs from the latter by having subsessile leaves, lobed leaf blades, well-developed reddish bracts, and reddish calyces and corollas. It is also similar to *P. subsessilis* L. Andersson & Rova, from which it differs by having lobed leaf blades and flowers with greenish stigma lobes.

Few-branched *shrub* to 3 m tall. *Stipules* light-green, 5–8 × 1.7–2.3 cm, lanceolate, acuminate, chartaceous, abaxially densely strigose, adaxially glabrous. *Leaves* simple; subsessile to shortly petiolate, to 2 cm long; blade 90–110 × 50–60 cm, oblanceolate to spatulate, basally attenuate, coriaceous, dull on both surfaces, densely and minutely strigose on main and secondary nerves abaxially, loosely

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Thanks are due to Bruno Baumann for hosting the senior author and helping to collect the type of *Pentagonia baumannii* in northwestern Ecuador. Philip Silverstone-Sopkin,† former Director of CUVC, shared his field and herbarium images of the type of *P. carniflora* with the senior author; Andrés Bohórquez Osorio (FAUC) and Claes Persson (GB) made available herbarium and field images of the paratypes of *P. carniflora*. Boris Villanueva Tamayo is acknowledged for kindly providing field images of *P. magnifica*.

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FIGURE 1. *Pentagonia baumannii* Cornejo & Rova. **A**, terminal branches holding mature leaves; **B**, close-up of new lobed leaf blades; **C**, stipule; **D–E**, inflorescences; **F**, close-up of open calyx, note the centered nectary cup and colleters clustered around sinuses within. Photographs of the holotype, *X. Cornejo & B. Baumann 8635* (GUAY).

strigulose on main nerves adaxially, lobed to strongly dentate (1/3–1/4 the way to the midrib), and with 17–18 secondary veins per side, intersecondaries present, the lobes 4 to 6 per side, 3–8 × 3.5–6.5 cm, the sinus 10–20 cm from the midrib. *Inflorescences* congested cymose panicles; peduncle to 30 mm; bracts light green to reddish, 15–20 × 10–13 mm, ovate to shortly lanceolate, abaxially strigose; flowers up to 20, subsessile or with pedicel to 5 mm, densely strigose. *Calyx* tube pink or greenish, ca. 5 mm, ± funnelform, coriaceous, densely strigose; calyx lobes 5, the lobes pink, imbricate, ± obovate to oblong, 9–12 × 3–6 mm, with colleters clustered around sinuses within, apically obtuse to rounded; a fleshy nectary cup present at inner base. *Corolla* light coral to salmon, subcylindric, ca. 20–25 × 3–4 mm (dried), the tube densely strigose without, glabrous within, the lobes deltoid, 5–6 × ca. 3 mm (dried), 6–8 × 5–6 mm (in vivo), widely divergent at anthesis; stamens with the filament ca. 14 mm when dried, ca. 20 mm in vivo, inserted at ca. 6 mm above the base of the tube, basally swollen and densely hyaline-tomentose, the anthers ca. 4 mm; style ca. 17–20 mm when dry, ca. 25 mm in vivo, stigma lobes 3 mm, greenish. *Berries* not seen.

Etymology: the epithet of this taxonomic novelty honors Bruno Baumann, a Swiss collector of native species of ornamental potential for cultivation in Ecuador and co-collector of the type; he was aware of this interesting novelty and led the senior author to find the species in the field.

Habitat, distribution, conservation status, and phenology: *Pentagonia baumannii* is known only from the type locality, a disturbed remnant wet forest located in the lowlands of the Esmeraldas province, northwestern Ecuador; this is the southernmost area of Choco, one of the main centers of diversity for the genus in South America. Because deforestation, fragmentation, and extinction of small patches of native vegetation are steadily ongoing in northwestern Ecuador, and because *P. baumannii* has not been recorded in any protected area of the country, the conservation status Endangered (EN B1ab[iii]) (IUCN, 2012) is suggested for this new species. *Pentagonia baumannii* flowers in October.

Propagation: *Pentagonia baumannii* can be vegetatively propagated by cuttings, for example, to be planted as an ornamental shrub (X. Cornejo, pers. obs.).

On the basis of ITS and rps16 sequences, this new species is related to *Pentagonia sprucei* Standl. and *P. subsessilis* L. Andersson & Rova (Rova et al., in prep.). and *Pentagonia baumannii* differs from *P. sprucei*, which is endemic to western Ecuador, by having subsessile leaves with attenuate leaf bases and lobed leaf blades (vs. petiolate leaves with acute to subcordate leaf bases and entire margin), the presence (vs. absence) of numerous conspicuous bracts, pink (vs. green) calyx lobes, and salmon to light coral (vs. white to pale green, or sometimes distally pinkish) corollas. *Pentagonia baumannii* also resembles *P. subsessilis*, a species restricted to NW Ecuador and SW Colombia, but differs morphologically by lobed (vs. entire) leaf blades, pale greenish-pinkish (vs. pink to reddish) bracts, and flowers with stigmas greenish (vs. white). It should be noted that young individuals of *P. baumannii* present entire leaf blades, and during this stage it can easily be confused with *P. subsessilis* or some other species with subsessile to shortly petiolate leaves in the genus. This form of heteropylly has been observed also in young stages of several other species of *Pentagonia* that eventually bear lobed leaf blades [e.g., *P. gymnopoda* (Standley) Standley, *P. lanciloba,* and *P. tinajita*] (Rova et al., in prep, pers. obs.); therefore, mature individuals are needed for a reliable identification.

Pentagonia carniflora Cornejo & Rova, *sp. nov.* TYPE: COLOMBIA. Caldas: Mpio. Norcasia, reserva Río Manso, valle medio del Río Magdalena, a 40 km por carretera al norte de La Dorada, cerca de quebrada Tostada, bosque húmedo tropical, 5°40'N, 74°46'W, 192 m, 1 Nov 2014 (fl), *P. Silvertone-Sopkin, A. F. Bohórquez, M. E. Cardona et al. 11931* (Holotype: CUVC). Fig. 2.

Pentagonia carniflora mostly resembles the Amazonian *P. gigantifolia* Ducke, *P. subauriculata* Standl., and *P. williamsii* Standl., but the new species differs from the other three by having ebracteate to minutely linear-bracteate flowers, the bracts green (vs. red), the calyx, and corollas with crimsom red limb (vs. corollas yellow or white to pinkish). *Pentagonia carniflora* differs from *P. magnifica* K. Krause by having green and spathaceous (vs. red and 5-lobed) calyx and greenish-white (vs. red) corolla tube.

Unbranched to few-branched pachycaule *tree* to 12 m tall and to 42 cm dbh. *Stipules* light-green turning brown, ca. 5–7 × 2 cm, narrowly-lanceolate, acuminate, chartaceous, adaxially densely strigose. *Leaves* simple; subsessile; blade 90–122 × 50–70 cm, obovate to obovate-elliptic, basally broadly obtuse to subcordate, coriaceous, dull on both surfaces, densely strigose on main and secondary nerves abaxially, strigulose on main nerves and glabrescent adaxially**,** the margin entire, laterally somewhat undulate, and with ca. 18–21 secondary veins per side, intersecondaries sometimes present. *Inflorescences* congested cymose panicles; peduncle to 30 mm; ebracteate, otherwise bracts light green, 3–4 × 1 mm, linear, abaxially strigose (*Bohórquez et al. 1259*); *flowers* up to 30, the terminal subsessile, the lateral with pedicel to 7 mm, densely strigose. Hypanthium turbinate, ca. 5 × 3(–4) mm, densely strigose; *calyx limb* spathaceous, somewhat laterally compressed at apex in bud, laterally splitting for upper third to half of its length, greenish throughout (*Idarraga et al. 5319*), otherwise greenish at lower half, turning to cream or greenish-white with 5 weak longitudinally brownish-red stripes (the type) at distal half, ca. 17–23 mm, membranaceous, densely strigose; a fleshy nectary cup present at inner base. *Corolla* funnelform, ca. 35–38 × 15–20 mm (dried), ca. 60 × 35–50 mm (fresh, *fide* the type), the limb dark-red to bright-red, the tube subcylindric, greenish-white, glabrous on both sides, the lobes deltoid, ca. 12 × 7–10 mm (dried), patent to reflexed at anthesis; stamens with the filament ca. 20–26 mm (dried), inserted at ca. 6 mm above the base of the tube, basally swollen and densely hyaline-tomentose, the anthers ca. 4 mm; style 25–33 mm (dried), stigma lobes green. *Berries* not seen.

Additional specimens examined: COLOMBIA. Antioquia: municipio de Puerto Berrío, vía Puerto Berrrío-Yondó, finca San Juan de Bedout, 06°36'06.2"N,

FIGURE 2. *Pentagonia carniflora* Cornejo & Rova. **A**, leaf blade, partial view of abaxial side; **B**, auriculate, sessile leaf base and part of detached stem; **C**, stipule; **D–E**, inflorescences; **F**, spathaceous calyces and a 5-costate flower bud. Photos A–C and E–F courtesy of Claes Persson; photo D, courtesy of Philip Silverstone-Sopkin.

74°26'40.2"W, 159–190 m, 20 April 2013 (fl), *A. Idarraga, C. Persson & C. Sánchez 5319* (HUA). Caldas: Mpio. Norcasia, vereda Quebrada de San Roque, reserva Río Manso, 5°39'54.1"N, 74°46'54.8"W, 204 m, 1 November 2014 (fl), *A. F. Bohórquez, P. A. Silvertone-Sopkin, J. A. Orozco, O. A. Bedoya & estudiantes de Botánica y Sistemática, Universidad del Valle 1259* (JAUM).

Etymology: the epithet of this taxonomic novelty refers to the bright red color of the corolla limb that resembles the color of flesh.

Habitat, distribution, conservation status, and phenology: *Pentagonia carniflora* is known only from the Magdalena Valley in the lowlands of the northeast of departments Antioquia and Caldas in northwestern Colombia. It occurs between 160 and 200 m in wet forests with 3500 mm average annual rainfall. As forests in eastern Antioquia and Caldas are disturbed by selective cutting, clearing, and fragmentation, the conservation status Endangered (EN B1ab[iii]) (IUCN, 2012) is suggested for this new species. *Pentagonia carniflora* flowers from April to October and November.

Pentagonia carniflora appears to be closely related to the Mesoamerican *P. donnell-smithii* (Standl.) Standl. and *P. tinajita* Seem. (Rova et al., in prep.), for example, but the new species mainly differs from the two latter (and all Mesoamerican species with subsessile, entire leaves) by the spathaceous (vs. 5-lobed) calyx and bright red (vs. cream to yellow) corolla limb. Furthermore, *P. carniflora* has leaf blades entire and sessile (vs. deeply lobed in *P. tinajita* and distinctively petiolate in *P. donnell-smithii*). Because of the large sessile leaves and spathaceous calyx, *P. carniflora* resembles the Amazonian *P. gigantifolia* Ducke, *P. subauriculata* Standl., and *P. williamsii* Standl., but differs from them mainly by having corollas with red limb (vs. white to cream or yellow), the calyx green (vs. red), and floral bracts that are absent or barely shortly linear (vs. well developed and laterally expanded). By its large, subsessile leaves and red corollas, *Pentagonia carniflora* also resembles *P. bonifaziana* Cornejo from NW Ecuador, but the new species sharply differs from the latter by the pubescence strigose (vs. conspicuously hirsute) throughout, the calyx spathaceous (vs. 5-lobed), and the stipules narrowly lanceolate (vs. elliptic). It is also similar to the Chocoan *P. magnifica* K. Krause, but it differs by having green and spathaceous (vs. red and regularly 5-lobed) calyx and a white (vs. red) corolla tube. *Pentagonia magnifica* also possesses well-developed bracts, in contrast to *P. carniflora*. It should be noted that the B holotype of *P. magnifica* only exists as a photo and small bud fragments at F, and calyx lobation is not easily interpreted on that material or the isotypes. However, the description clearly states that the calyx of *P. magnifica* is 5-lobed, and this is also obvious from photos of recently collected fresh material of *P. magnifica* (B. Villanueva Tamayo, pers. obs.).

It is interesting to note that, on the basis of molecular results (Rova et al., in prep.), *Pentagonia carniflora* has a Mesomerican origin and that the strong resemblance to the discussed South American conspecifics could be a case of evolutionary convergence.

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A NEW COMBINATION IN *GARCINIA* (CLUSIACEAE) BASED ON *RHEEDIA MARTINII*, A TREE SPECIES FROM SURINAME

Lucas C. Marinho[1]

Abstract. Several new combinations were recently proposed to merge species of *Rheedia* into *Garcinia*. Because some species were not part of larger taxonomic treatments, revisions, or local floras, new combinations for them were not proposed. *Garcinia martinii* is a new combination based on the basionym *Rheedia martinii*, an Amazonian tree species from the high mountains of Suriname, in South America.

Keywords: Amazon Forest, nomenclature, *Rheedia*, South America, taxonomy

Garcinia L. (ca. 250 spp.) is the second largest genus of Clusiaceae (Sweeney, 2008). Members of the genus are widely distributed across the Paleotropics, with about 95% species in the Old World and only 5% in the Neotropics (Medellín-Zabala, 2015). American species usually have white to greenish flowers with free stamens. Few floral morphological differences in *Garcinia* species have placed greater taxonomic significance on the leaves and the fruits in this genus. The leaves of *Garcinia* are strongly marked by prominent secondary veins and prominent exudate channels, which are variable across the genus; the fruits are edible, and characters such as shape, size, color, and texture of the epicarp are relevant for species delineation.

Rheedia L. has recently been treated as synonym of *Garcinia* on phylogenetic and morphological grounds (Sweeney, 2008). To accommodate this change, several combinations and new names were proposed to allocate *Rheedia* species within *Garcinia*. Much of this taxonomic work has been gradually accomplished in taxonomic treatments, revisions, and local floras (*e.g*. Sweeney and Rogers, 2008; Rogers *et al*., 2011), especially in Africa. New names and combinations have also been proposed for the American species (*e.g*. Adams, 1970; Bohridi, 1982; Lioger, 1986; Hammel, 1989; Bernal *et al*., 2015), particularly those from Brazil (*e.g*. Zappi, 1993; Cabral *et al*., 2017; Bittrich and Marinho, 2018). However, there still exist species that were never included in formal studies and remain in *Rheedia*.

Marinho (2017) identified 50 type specimens during a herbarium research trip that aimed to identify and listed types belonging to *Garcinia* and related genera housed in the W herbarium (acronym according to Thiers, 2019). The author also provided information about new combinations, new names and synonyms for all species housed in W, except *Rheedia martinii* Maguire, which has never been validly published as a combination in *Garcinia*. Here, *Garcinia martinii* is presented as a new combination based on *Rheedia martinii*, an Amazonian tree from the high mountains of Suriname, in South America.

Garcinia martinii (Maguire) L. Marinho, *comb. nov.* Basionym: *Rheedia martinii* Maguire, Bull. Torrey Bot. Club 75: 437. 1948. TYPE: SURINAME. "Sipaliwini District", Tafelberg, south rim Arrowhead Basin, tree 12 m. high, 15 cm. diameter, yellow latex copious, flowers whitish, petals reflexed, 20 August 1944, *B. Maguire 24427* (Holotype: NY [NY00076031]; Isotypes: A [A00067867], BR [BR0000006808006, not seen], F [F0054519F, not seen], K [K000488551], P [P01901274], U [U0002431, not seen], UC [UC794029], US [US00114325, not seen], VEN [VEN27221, not seen], W [no. W-1956-0014782], WTU [WTU-V-000698, not seen]). Fig. 1.

Iconography: Maguire (1948, Fig. 21, p. 427): abaxial leaf surface, staminate flower, petal, stamen, and anther.

Distribution: *Garcinia martinii* is only known from Tafelberg (in the Tafelberg Nature Reserve), one of the highest mountains in Suriname, reaching up to 1,020 m.s.l. This region is formally included in the Amazonia (sensu Eva and Huber, 2005).

Garcinia martinii is known only from the type collection. Since only a staminate specimen has been examined, Maguire (1948) did not include the species in any of the sectional divisions proposed at that time, which were based on epicarp texture (smooth *vs*. tuberculate). Although the author does not know the fruits of the species, Maguire (1948) suggested that leaves of *G. martinii* were similar to three species that are now treated under the synonymy of *Garcinia madruno* (Kunth) Hammel, which presents a tuberculate epicarp. *Garcinia martinii* can be distinguished from *G. madruno* by vegetative characters: leaf base (rounded *vs*. decurrent in *G. madruno*) and texture (coriaceous *vs*. chartaceous in *G. madruno*). Additionally, in the herbarium material, leaves of *G. martinii* are very close to each other and grouped at the apex of the branches, a characteristic that does not occur in *G. madruno*. However, this difference can only be certified when new specimens have been collected.

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New York Botanical Garden Tropical Expedition - 1944
Plants of Tafelberg (Table Mountain), Surinam
No. 24427 TYPE
Rheedia Martinii Maguire

Tree 12 m. high, 15 cm. diam., copious yellow latex; flowers whitish, petals reflexed; high bush, rim of Arrowhead Basin.

Bassett Maguire August 20, 1944

Expedition financed in part by aid from the American Philosophical Society, the John Simon Guggenheim Memorial Foundation and Mr. Pierre Jay

FIGURE 1. Holotype of *Rheedia martinii* Maguire. Image courtesy of the C. V. Starr Virtual Herbarium, New York Botanical Garden (http://bluegum.nybg.org/science/vh/).

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A TAXONOMIC REVISION OF *ESPELETIA* (ASTERACEAE). THE VENEZUELAN RADIATION

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Abstract. Subtribe Espeletiinae (Asteraceae) represents the best example of morphological and ecological diversification in the Northern Andes high-elevation ecosystem known as *páramo*. These plants, formerly considered as belonging to a single genus, *Espeletia*, were later referred to eight genera defined mainly according to their habit, branching pattern, and inflorescence position and structure. However, several molecular phylogenetic analyses have shown that this classification system is artificial since the larger genera, regrouping ca. 85% of the species, are polyphyletic. Here, a return to the previous classification system of the subtribe at the generic level is proposed, adopting the view that only *Espeletia* should be recognized, with the other seven genera considered as (heterotypic) synonyms. At the species level, a taxonomic revision is made of the nomenclature, morphology, and distribution of the taxa in the Venezuelan clade of *Espeletia*, one of the two major clades that compose the genus. Fifty-four species are accepted, 48 entirely endemic to the Venezuelan Cordillera de Mérida, 2 broadly distributed in this range and nearby areas in Colombia and Venezuela, and 4 endemic to the northern section of the Colombian Cordillera Oriental and Sierra de Perijá. Distribution maps for all species are proposed, along with brief morphological descriptions and lists of diagnostic features that facilitate their identification against similar species. Thirteen hybrid taxa and their putative parental species are also given, eight of them proposed here for the first time.

Keywords: Andes, Asteraceae, caulescent rosette, Cordillera de Mérida, *Espeletia*, páramo, Venezuela

The plants in subtribe Espeletiinae (Asteraceae) represent perhaps the best example of taxonomic, morphological, and ecological diversification among tropical high-elevation taxa (Diazgranados, 2012; Cuatrecasas, 2013; Diazgranados and Barber, 2017; Pouchon et al., 2018). The ca. 140 species in the group are distributed in the high Andes of Venezuela, Colombia, and Northern Ecuador, with two important diversity centers in the Colombian Cordillera Oriental (ca. 76 species, Fig. 1A) and the Venezuelan Cordillera de Mérida (ca. 50 species, Fig. 1B). These plants originated from a single ancestor about 2.5 mya (Pouchon et al., 2018), after the final uplift of the Northern Andes, which facilitated environmental conditions for the rise of the tropical high-elevation grassland ecosystem known as *páramo* to which the subtribe is endemic (Hooghiemstra et al., 2006; Torres et al., 2013). The diversification of Espeletiinae occurred very rapidly indeed, particularly during the intensification of climatic variability after the middle Pleistocene transition, 1.25–0.70 mya (Clark et al., 2006), and it is now considered one of the fastest-evolving plant groups in the world (Madriñán et al., 2013; Pouchon et al., 2018). In this short time Espeletiinae generated a notable degree of ecological diversity with regard to (1) elevation, ranging from montane cloud forests at about 2000 m.a.s.l. to the very edge of glaciers at 4800 m.a.s.l.; (2) humidity, from wet páramo bogs to xeric periglacial talus slopes and rocky outcrops; and (3) solar irradiation, from gaps in the montane forest to open vegetation such as páramo grasslands. However, what has attracted the greatest attention to these plants is their large disparity in morphological types, which includes profusely branched, dichotomous, and unbranched trees; shrubs; short-branched rosettes; sessile rosettes; and, notably, giant caulescent rosettes. The latter is a growth form that produces an erect and unbranched stem usually tightly covered by the bases of old and dead leaves and crowned by a rosette of green young leaves around the apical bud (Fig. 1B). The group also exhibits diversity in reproductive strategies, with polycarpic species that reproduce repeatedly across adult life and monocarpic species that reproduce only once before death (Smith, 1981; Cuatrecasas, 2013), and in pollination syndromes, with entomophilous and anemophilous species (Berry and Calvo, 1989).

Given the diversity and ecological dominance of Espeletiinae in the páramos, particularly in Colombia and Venezuela, it is not surprising that they have been the subject of many scientific studies, mainly in population and community ecology, eco-physiology, and, of course, taxonomy. Taxonomic research in particular started more than two centuries ago with the formal publication of *Espeletia* Mutis ex Bonpl. and descriptions of three Colombian species in Humboldt and Bonpland (1809: 10). *Espeletia* was attributed by the authors to José Celestino Mutis, director of the "Expedición Botánica del Nuevo Reino de Granada," who first named the genus at the end of the 18th century (see the detailed chronological account of systematic studies in Cuatrecasas, 2013). In 1814 Bonpland

This work is dedicated to two friends: Angel Fernández, director of the Instituto Venezolano de Investigaciones Científicas herbarium (IVIC), who provided invaluable assistance in the field while allowing innumerable trips to the páramos of Venezuela, and Serge Aubert (1966–2015), director of Station Alpine Joseph Fourier (France), a colleague and a tireless traveling companion in the páramos who, unfortunately, passed away too soon to see this work finished. I am very grateful for the help provided during fieldwork by Benito Briceño, Gilberto Morillo, John Parra, Luis "Kicke" Gámez, Reina Gonto, Sébastien Lavergne, Susana González, and Thibaud Syre, and for logistic support provided by the Centro de Investigaciones de Astronomía (CIDA), Dirección Regional Inparques Mérida, and Teleférico Mukumbarí. I am also very grateful to the staff in herbaria IVIC, MERF, and MY for the support provided for this work. Université Grenoble Alpes and the CNRS provided funding (PEPS and OSUG grants).

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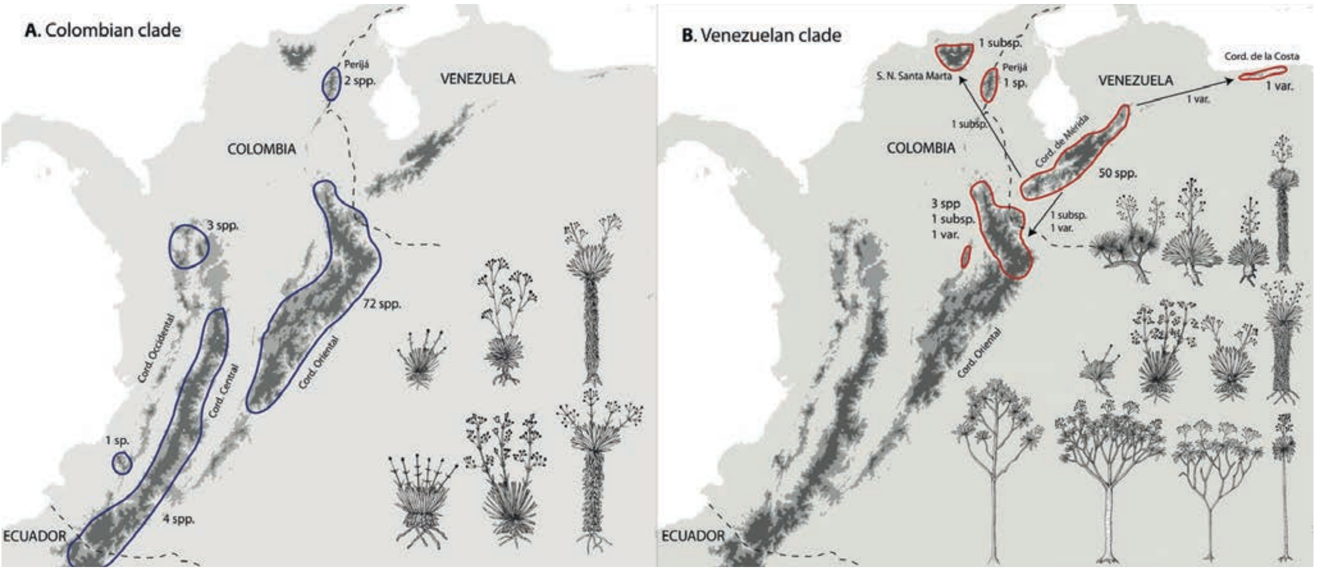

FIGURE 1. **A**, species diversity and distribution in the Colombian clade of Espeletiinae. Plants: upper row—examples of polycarpic rosette plants with monochasial inflorescences; lower row—examples of polycarpic rosette plants with dichasial inflorescences. **B**, species diversity and distribution in the Venezuelan clade of Espeletiinae. Arrows give the number of shared taxa between geographic sections. Plants: upper row—examples of monocarpic rosette plants with monochasial inflorescences; middle row—examples of polycarpic rosette plants with inflorescences monocephalous (left), dichasial (2nd) or monochasial (3rd, right); lower row—examples of trees with branched and unbranched stems.

described a new species with arborescent habit collected by him and Humboldt in La Silla de Caracas, Venezuela, as *Trixis neriifolia* Bonpl. ex Humb. The same species was renamed as *Baillieria? neriifolia* (Bonpl. ex Humb.) Kunth (Humboldt et al., 1820), and later as *Clibadium? neriifolium* (Bonpl. ex Humb.) DC. According to Weddell (1855: 68), Schultz Bipontinus was the first to notice that this species with branched stems belonged to *Espeletia* and renamed it as *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. The genus remained undivided in almost all subsequent taxonomic treatments of the group: 11 species in Weddell (1855), 17 species in Standley (1915), 30 species (18 from Venezuela, 12 from Colombia) in Smith and Koch (1935), 71 species (26 from Venezuela, 42 from Colombia with 1 reaching Ecuador, 3 in Venezuela and Colombia) in Cuatrecasas (1949), and 45 species from Venezuela in Aristeguieta (1964). The only exception to this single genus system came from Ernst (1870), who, probably unaware of Weddell's work, placed *E. neriifolia* in a new genus as *Libanothamnus neriifolius* (Bonpl. ex Humb.) Ernst. In 1976 the 124 species known at the time were raised to subtribe Espeletiinae and split into seven genera in Cuatrecasas (1976, 1986b), after which an additional genus was added in Cuatrecasas (1995). The eight-genera system has been used in recent treatments of the group; 141 species in Diazgranados (2012) and 126 species in Cuatrecasas (2013). The latter work, unfortunately published posthumously in an unfinished state (one genus and ca. 20 species missing), represents an impressive monographic masterpiece of the subtribe. Therein, among many other topics, Cuatrecasas fully developed the classification and nomenclature system of this group sketched in his 1976 and 1986 works, which defined the genera mainly according to the plant habitus and the position and structure of the inflorescence, summarized here:

A. Rosette plants: a compact crown of green leaves arranged spirally around the apical meristem, each leaf possessing a flat sheath tightly imbricated under and over the sheaths of nearby leaves. Stem with a large central pith surrounded by secondary vascular tissues, entirely covered in its apical part by the sheaths of the green leaves. The stem is usually unique and unbranched, but some species can be slightly branched near ground level, each branch producing a terminal crown of rosette leaves.

A.1. *Coespeletia* Cuatrec. Unbranched stem. Lateral inflorescences with monochasial structure: botryoid, botryoid-paniculate, or monocephalous. Endemic to Cordillera de Mérida.

A.2. *Espeletia* Mutis ex. Bonpl. Unbranched stem. Lateral inflorescences with dichasial structure: thyrsoid, oligocephalous, or monocephalous. Cordillera de Mérida, Sierra de Perijá, Colombian Andes, and Northern Ecuador (1 sp. shared with Colombia).

A.3. *Espeletiopsis* Cuatrec. Unbranched stem (some occasionally branched). Lateral inflorescences with monochasial structure: corymboid or corymboid-paniculate, rarely monocephalous. Cordillera de Mérida and Colombian Cordillera Oriental.

A.4. *Paramiflos* Cuatrec. Unbranched stem. Lateral inflorescences with monochasial structure: corymboid. Involucre with sharp separation between outer and inner phyllaries. Monotypic. Endemic to Colombian Cordillera Oriental.

A.5. *Ruilopezia* Cuatrec. Unbranched stem (one species frequently branched, some occasionally branched). Terminal inflorescences with monochasial structure: corymboid or corymboid-paniculate. All species but one endemic to

Cordillera de Mérida, the exception is endemic to Páramo de Tamá in Colombian Cordillera Oriental.

B. Trees: have a distinct woody trunk with a small or no pith in comparison with the surrounding wood. Branched at a considerable distance from the ground (one species unbranched). Little or no overlapping of consecutive leaf sheaths, although some leaf crowding is frequent at the ends of the branches. Leaf sheaths are either curved with free margins and embracing most of the branch, or tubular and encircling the branch entirely (one species with open and flat sheaths).

B.1. *Carramboa* Cuatrec. Monopodial branching. Lateral inflorescences with primary structure dichasial: corymboid. Endemic to Cordillera de Mérida.

B.2. *Libanothamnus* Ernst. Main branching monopodial, peripheral branching sympodial (one species unbranched). Terminal inflorescences with monochasial structure: corymboid. Most species endemic to Cordillera de Mérida, some occurring as well in nearby areas in Colombia, and two endemic to either the Tamá region or Sierra de Perijá.

B.3. *Tamania* Cuatrec. Main branching sympodial. Open and flat leaf sheaths. Terminal inflorescences with monochasial structure: corymboid. Monotypic. Endemic to Páramo de Tamá and nearby areas in Colombian Cordillera Oriental.

At the generic level, all six nonmonotypic genera are found in Cordillera de Mérida in Venezuela, two of them entirely endemic to this range (*Carramboa* and *Coespeletia*) and two others nearly so (*Ruilopezia* and *Libanothamnus*). This observation motivated the hypothesis of a center of origin and diversification for the group in Venezuela (Smith and Koch, 1935; Cuatrecasas, 1986b), with multiple subsequent dispersal events towards the Colombian Andes in *Espeletia*, *Espeletiopsis*, *Libanothamnus*, *Ruilopezia*, and *Tamania*.

Molecular Phylogenetic Studies in the Subtribe Espeletiinae

The subtribe Espeletiinae has become the subject of a certain number of recent molecular studies aiming to understand its closest relatives and positioning within the tribe Heliantheae (Panero et al., 1999; Rauscher, 2002), internal phylogenetic relationships (Sánchez-Andrade, 2005; Diazgranados and Barber, 2017; Pouchon et al., 2018), diversification dynamics (Madriñán et al., 2013; Pouchon et al., 2018), and the metabolic similarities among its taxa (Padilla-González et al., 2017). These studies have provided unequivocal evidence for several phylogenetic relationships in Espeletiinae, some of them supporting previous hypotheses for the evolution of this group, such as its monophyly, recent origin, and close affinities with Melampodiinae and Milleriinae, while others are novel and somehow in contradiction with previous ideas (see examples in Diazgranados and Barber, 2017; Pouchon et al., 2018). Two important results in the second category, particularly relevant to the theme of this work, are the following:

(1) There have been two geographically delimited and mostly disconnected radiations in the Venezuelan and Colombian Andes, respectively, instead of an initial radiation in Venezuela followed by multiple colonizations of Colombia, as proposed by Smith and Koch (1935) and Cuatrecasas (1986b, 2013). The "Venezuelan Espeletiinae clade" comprises all species living in the Venezuelan Cordillera de Mérida, plus a few lineages that colonized the Tamá region and nearby areas in the Colombian Cordillera Oriental, Sierra de Perijá, and Sierra Nevada de Santa Marta. The "Colombian Espeletiinae clade" comprises all remaining species in the subtribe living in the Colombian Andes, Sierra de Perijá, and Northern Ecuador.

(2) As currently circumscribed, most genera in Cuatrecasas's classification system of Espeletiinae are poly- or paraphyletic (Fig. 2). For instance, the phylogenomic analysis by Pouchon et al. (2018), based on whole plastomes and 1877 fragments covering about a million bp of the nuclear genome, has shown that the three largest genera in the subtribe—*Espeletia*, *Espeletiopsis*, and *Ruilopezia*—representing ca. 85% of the species, are clearly polyphyletic. Each of the former two genera comprises at least two distantly related clades, one in Venezuela and one in Colombia, a number that could increase on analysis of more taxa from the latter country. The polyphyly of *Ruilopezia* is even greater, since it embraces at least three unrelated clades in Venezuela. *Coespeletia* is paraphyletic with regard to *Espeletia semiglobulata* Cuatrec., while the monotypic *Tamania* and *Paramiflos* are nested within one clade of *Ruilopezia* and the Colombian *Espeletiopsis*, respectively. Only *Carramboa* and *Libanothamnus* appeared to be monophyletic. This pattern of extensive polyphyly/paraphyly among Espeletiinae genera could be even worse, as suggested by Diazgranados and Barber (2017), whose phylogenetic analysis of a larger taxonomic sample of the subtribe indicates that the clade of Colombian *Espeletia* could be nested within the Colombian *Espeletiopsis*.

The Need for a New Classification System of the Subtribe Espeletiinae

The classification system with eight genera of Espeletiinae (Cuatrecasas, 1976, 2013) is therefore largely artificial and must be modified. One such modification, following a "splitter approach," could include (1) preserving the seemingly monophyletic genera *Carramboa* and *Libanothamnus*, (2) modifying the definition of *Coespeletia* so that it can accept *Espeletia semiglobulata*, (3) creating a new genus for the Venezuelan *Espeletiopsis*, (4) creating a new genus for the Venezuelan *Espeletia*, (5) deciding whether *Tamania* is preserved or merged into *Ruilopezia*, (6) splitting *Ruilopezia* into three or four genera depending on the decision made in (5), (7) deciding whether *Paramiflos* is preserved or merged into *Espeletiopsis*, and (8) splitting the Colombian *Espeletiopsis* into two or more genera depending on the decision made in (7). The number of genera in the subtribe would thus increase to 10–15, according to the actions taken. The problem with this approach is that it would require a considerable amount of time and effort to identify the synapomorphies that define the new genera, as well as the creation of many new name combinations.

A more workable and stable solution is proposed here, adopting the view that only the genus *Espeletia* should be recognized in the subtribe, with the other seven genera considered as (heterotypic) synonyms. In this case, the

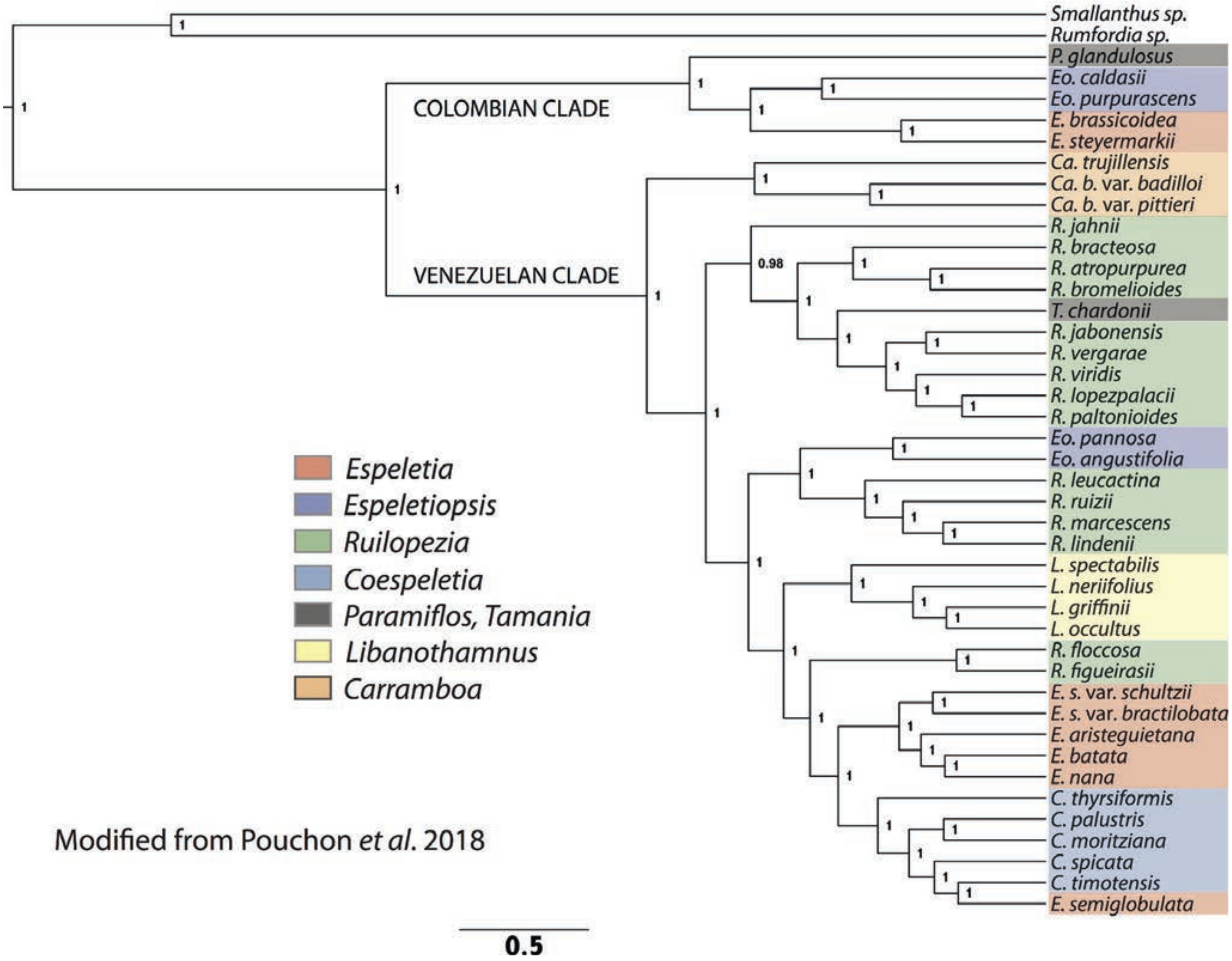

FIGURE 2. Molecular phylogeny of Espeletiinae genera sensu Cuatrecasas (1976, 2013), based on a maximum-likelihood (ML) analysis of nuclear data. Numbers on nodes give ML support values. Modified from Pouchon et al. (2018).

genus *Espeletia* would recover its original definition, currently employed for the subtribe Espeletiinae, without the need for additional morphological definitions for new groupings. Another advantage of this solution is that since the majority of the species in the subtribe were originally described under the genus *Espeletia* (ca. 130 species), the proposed change implies essentially the restoration of species names discarded by Cuatrecasas (1976, 1996, 2013) and 12 new combinations for some species described after 1976: 2 in *Coespeletia* (Cuatrecasas, 2013; Diazgranados and Morillo, 2013), 5 in *Espeletiopsis* (Diaz-Piedrahita and Obando, 2004; Diaz-Piedrahita et al., 2006; Diaz-Piedrahita and Rodríguez-Cabeza, 2008, 2010; Diazgranados and Sánchez, 2013), 2 in *Libanothamnus* (Cuatrecasas, 1980b), and 3 in *Ruilopezia* (Cuatrecasas, 1986a).

In this work, the proposed changes in the nomenclature are applied to the ensemble of the Venezuelan clade of Espeletiinae. Six species found within Venezuela's political borders but belonging to the clade of Colombian Espeletiinae will not be treated here but in a taxonomic revision of that clade to be published in the near future. A succinct but diagnostic description is also given for each species, together with distribution maps, most of them provided here for the first time.

MATERIALS AND METHODS

A total of 2264 samples were analyzed for this study: 1450 samples deposited in herbaria B, BC, BR, COL, F, G, GH, HAL, IVIC, K, LD, MER, MERF, MO, MY, NY, P, S, U, US, and W (according to Thiers, 2019), and 814 plants identified during fieldwork by the author and some colleagues (250 of which are now deposited at herbarium IVIC) (see Supplementary Material). Several diagnostic morphological traits were measured in the fresh samples, with an emphasis on traits of the leaf, inflorescence, and capitulum, which can also be measured nondestructively in dry specimens, either directly on sheets or on high-quality photographs. However, to avoid possible biases due to differences between fresh and dry material, comparisons between capitula from different species were done for traits measured only on dry samples from herbarium sheets (IVIC, MERF, MY) and new field-dried specimens. The majority of traits used are visible to the naked eye and can be measured without the need for sophisticated equipment; however, for some minute details such as disc corolla's tube length or the presence of glands, a small optical magnification device was necessary. It should be mentioned that the purpose of these morphological descriptions is not to provide a complete portrayal of the taxa but to facilitate their identifications in the field. Readers interested in more-detailed morphological accounts of these taxa should consult their original descriptions and other appropriate works.

Plant samples collected in this study were geo-referenced with a GPS during fieldwork, whereas for herbarium sheets this information was either retrieved directly from labels when inferred from the descriptions of collection sites and 1:25,000 maps of Colombia and Venezuela. The geographic coordinates were used to produce distribution maps of each species using R package raster v2.3-33.

The ensemble of the information gathered for each taxon was summarized as follows:

Valid name, followed by the appropriate reference or *status*. Taxa below the rank of species are also given; subspecies (subsp.), variety (var.), and forma (f.), even if the validity of most of these secondary ranks remains to be verified. Autonyms are provided as well, for databasing purposes. TYPE information: whenever possible, given as COUNTRY. State. Locality, elevation, collection date, *collection number* (herbaria acronyms).

List of all names associated with the taxon. Information about the TYPE is provided for basionyms and heterotypic synonyms.

A brief and standardized morphological description is provided for (1) Growth form: *habitus*, type of stem branching, size; (2) *Leaf* shape, pseudopetiole length, type and degree of adaxial pubescence, leaf length, leaf width, length-to-width ratio, shape and distribution of secondary nerves; (3) *Inflorescence* position, structure (simple or compound), branchlet organization (monochasial or dichasial; Fig. 3), inflorescence length, number and distribution of bracts; (4) *Capitulum* shape, diameters of capitulum, ligular circle and disc, color of ray ligules. The key morphological characteristics that allow the identification of the taxon with respect to similar taxa are also provided.

Information on distribution is provided as confirmed presence of the taxon on the major geographic units of páramo traditionally considered for Venezuela and Eastern Colombia (Fig. 4). Recorded minimum and maximum elevations are also given, together with a description of the main habitat types in which the taxon is found: (1) the páramo proper, located between ca. 3500 and ca. 4200 m.a.s.l., composed mostly of small sclerophyllous shrubs, herbs, grasses, and rosette plants; (2) an upper transition zone, the superpáramo, from ca. 4200 m.a.s.l. to the limits of glaciers, characterized by a mixture of bare soil, low-height vegetation (mostly grasses, herbs), and some caulescent rosette plants; and (3) a lower transition zone, the subpáramo, from the upper Andean forest to ca. 3500 m.a.s.l., characterized mainly by a shrubby vegetation mixed with patches of meadows and small trees that are usually isolated or in thickets (Hooghiemstra et al., 2006).

A list of some representative samples of each taxon is given, with an emphasis on exsiccata that include both vegetative and reproductive material, and that are available in online herbarium databases.

A list of interspecific hybrid taxa in Venezuelan Espeletiinae is provided at the end of the Taxonomy section. The status of some of these taxa had already been proposed or at least conjectured (Morillo and Briceño, 2007; Diazgranados, 2012; Cuatrecasas, 2013), while others are proposed here for the first time. Inferences about the hybrid nature of these taxa are mostly based on the study of living plants, which allows the analysis of the evidence for hybridization on important diagnostic traits that are usually unavailable in dried specimens, such as habit, size, branching structure, pubescence organization, and different instances of color. Furthermore, inferences of hybridization based on living plants also permit the gathering of important morphological and ecological data from the sympatric putative parental species. Parents in hybrid formulae are provided in alphabetical order.

Both Diazgranados (2012) and Cuatrecasas (2013) provided lists of Spanish names that appear on the labels of herbarium samples and that are supposedly attributed to some Espeletiinae species. However, it is unclear to what extent those names represent common uses by local populations or attempts by scientists to socialize the knowledge about these plants. To explore this issue, adult people living near collection sites were asked to provide the names they give to the plants, directly in the field whenever possible, or using good quality photographs or fresh samples.

RESULTS

Taxonomic Changes

The type of *Espeletia pannosa* Standl. contains a mixture of that species and *Espeletia floccosa* Standl. A lectotype is designated here for the part that corresponds most with the original description of *E. pannosa*. Seven new combinations are proposed for taxa at the species level, and 10 for taxa below species. New status is proposed for eight taxa now considered to be interspecific hybrids. Changes in the spelling of four epithets are proposed in accordance with rules of the International Code of Nomenclature for algae, fungi, and plants, hereafter ICN (Turland et al., 2018).

Diversity

The analysis of morphological data in both herbarium samples and living plants formerly considered to belong to the Venezuelan *Espeletia* clade revealed that this group is composed of 54 species, which, together with the 6 other species found within Venezuela's political borders but phylogenetically affiliated with the clade of Colombian *Espeletia*, elevate the total diversity of the genus in Venezuela to 60 species The remaining 13 species were found to represent the product of interspecific hybridization; 4 between rosette parents, 3 between tree parents, and 6

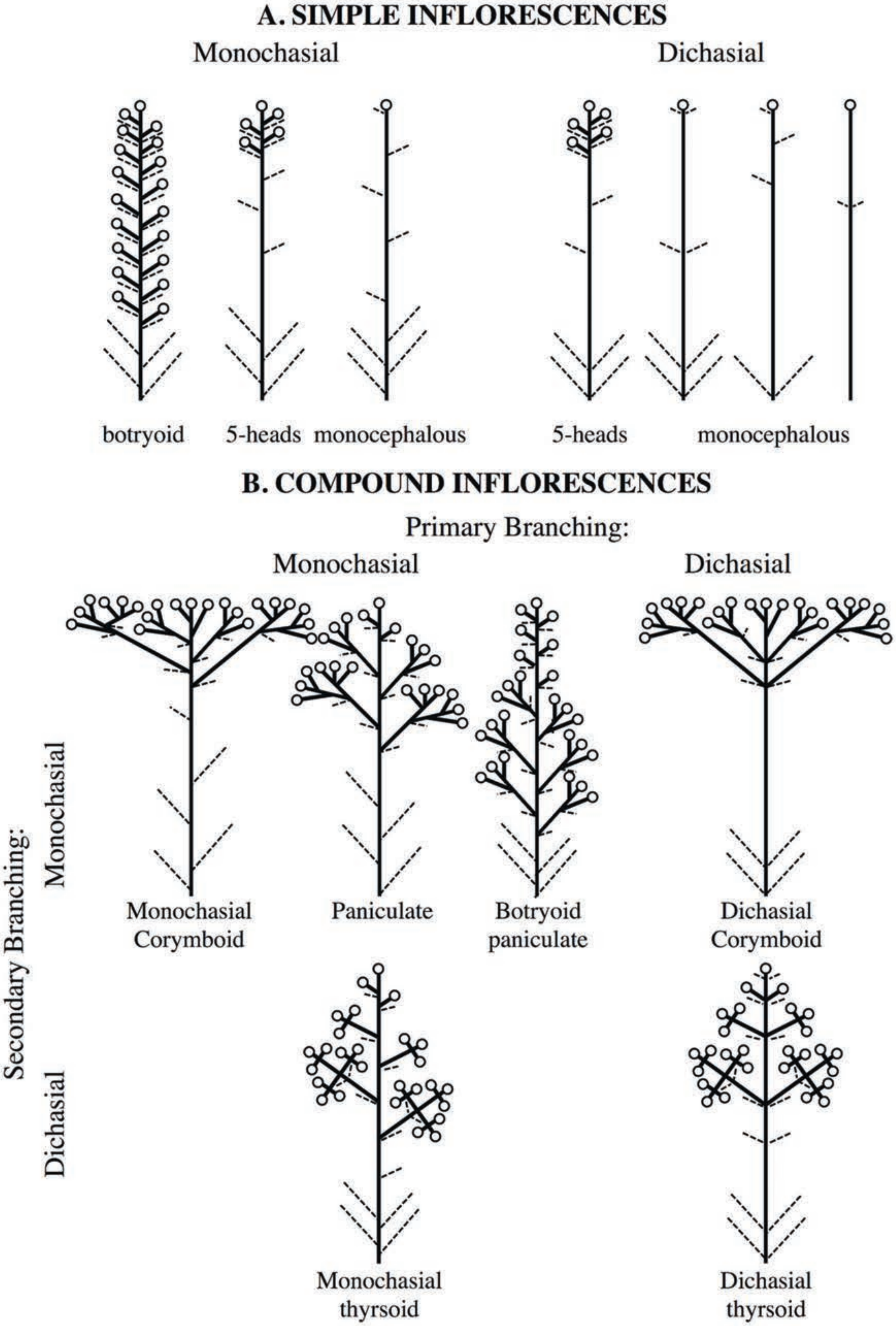

FIGURE 3. Schematic representation of main types of inflorescence structure in the Venezuelan clade of *Espeletia* Mutis ex Bonpl.

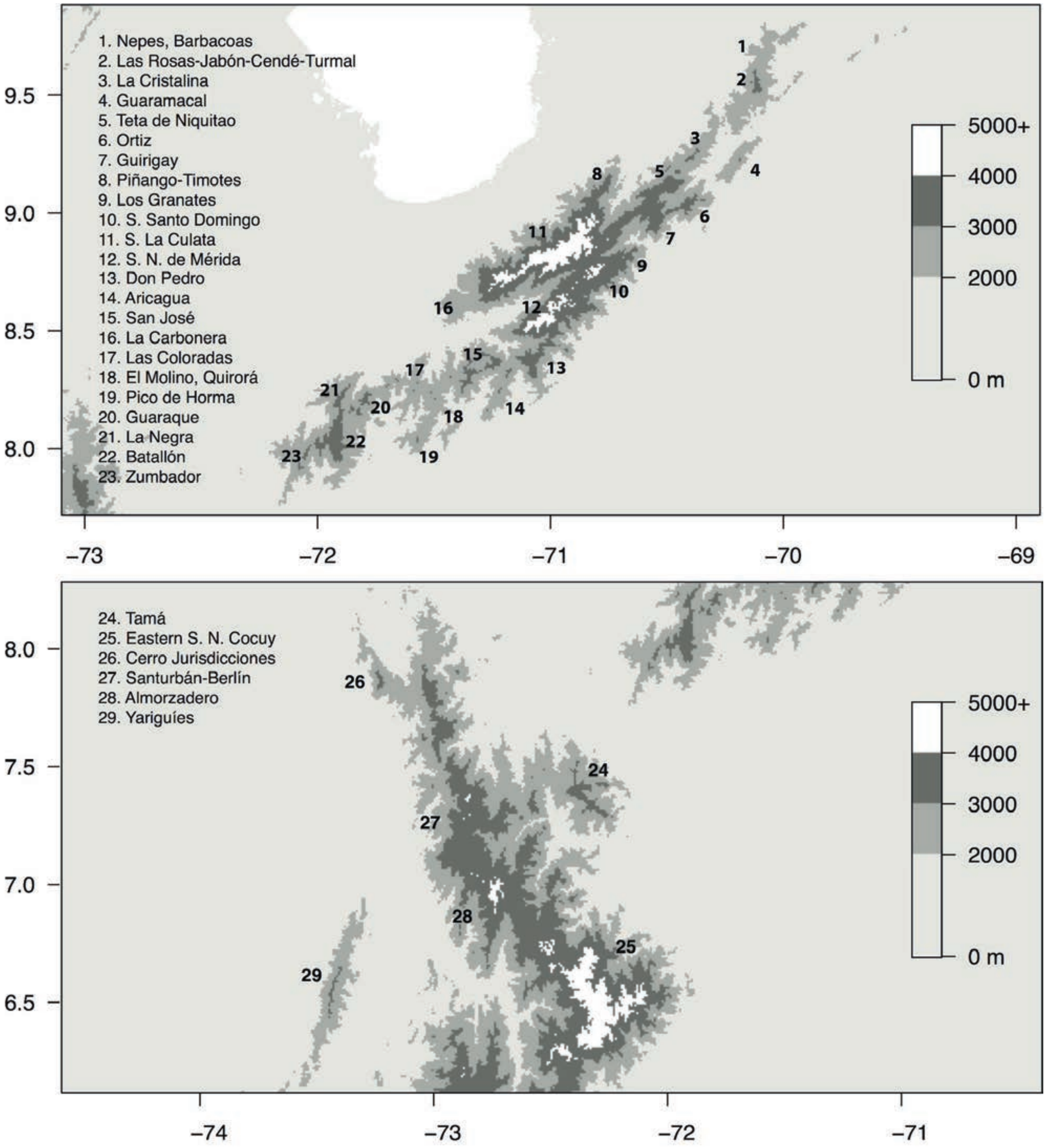

FIGURE 4. Maps of the Venezuelan Cordillera de Mérida (upper panel) and northern section of the Colombian Cordillera Oriental (lower panel) with locations of main páramo areas.

between a rosette and a tree parent (see Fig. 5 and Hybrid Taxa section). Eight of these hybrid taxa are proposed here for the first time.

Distribution

Of the 54 species in the Venezuelan *Espeletia* clade, (1) 48 are endemic to Cordillera de Mérida, (2) two are broadly distributed in this range, in nearby areas in the Colombian Cordillera Oriental and even out of the Andes: *E. neriifolia* and *E. occulta* S.F. Blake, and (3) four are distributed outside Cordillera de Mérida: *E. cardonae* Cuatrec., *E. chardonii* A.C. Sm., and *E. tamana* Cuatrec. in the eastern extreme of the Colombian Cordillera Oriental, and *E. divisoriensis* (Cuatrec.) Mavárez in Sierra de Perijá. It is worth noting that five out the six species nonendemic to Cordillera de Mérida are trees, which implies higher dispersal ability in this growth form, probably as a consequence of their preference for lower elevation habitats.

Of the 48 species endemic to Cordillera de Mérida, 30 are found in the central core, composed of Sierra de la Culata, Sierra Nevada de Mérida, Sierra de Santo Domingo, and mountains around Guirigay and Teta de Niquitao. Despite its comparatively smaller area, the northern section of Cordillera de Mérida (i.e., Guaramacal and the complex Las Rosas-Jabón-Cendé-Turmal) harbor 12 species, 8 of them endemic to these páramos and 4 shared with the central core. Sixteen species are found in the southern section of Cordillera de Mérida (i.e., Aricagua, San José, Las Coloradas, El Molino-Quirorá, Guaraque, and the complex Batallón-la Negra-Zumbador), 10 of them endemic to these páramos and 4 shared with the central core. None of the endemic species to Cordillera de Mérida is found in all three geographic sections, but *Espeletia schultzii* Wedd. is found all over the central core, to the south in Páramo de San José and to the north in Páramo de la Teta de Niquitao and Páramo de la Cristalina.

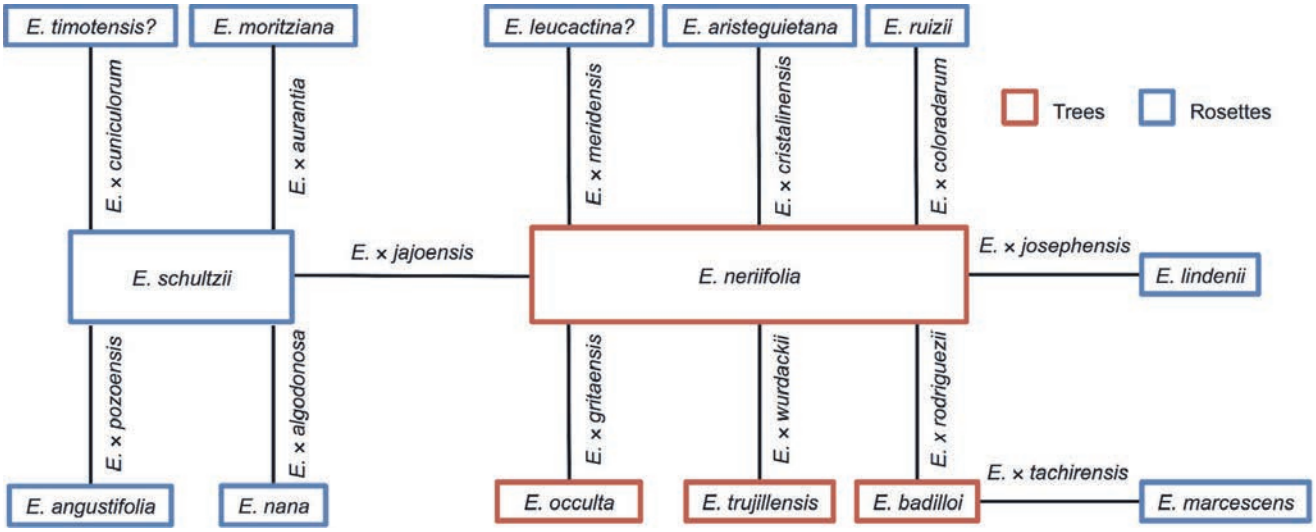

FIGURE 5. Hybrid taxa and their parental combinations in the Venezuelan clade of *Espeletia* Mutis ex Bonpl.

Microendemism and Conservation

According to the IUCN guidelines, most if not all species endemic to the Cordillera de Mérida must be considered at least in the "Endangered" category because they forcibly occupy an area smaller than 5000 km^2 (the total area of páramo in this range is ca. 3000 km^2; Josse et al., 2009) with a significant projected decline in the extent of their suitable habitat due to climate change (Mavárez et al., 2018). However, about a third of the species inhabit single páramo units in the north or south sections, or relatively isolated areas within the central core, which probably makes them qualify for the "Critically Endangered" category. For instance, three endemics to the highest elevations in Páramo de Cendé—*Espeletia liscanoana* Cuatrec., *E. parvula* (Cuatrec.) Mavárez, and specially *E. ulotricha* Cuatrec.—are known from single populations covering an area probably smaller than 10 km^2, and that will certainly disappear or be deeply modified by global warming in the near future. The same extinction risk is likely faced as well by the two endemics to Páramo de Guaramacal, *E. griffinii* Ruiz-Terán & López-Fig. and *E. lopezpalacii* Ruiz-Terán & López-Fig., and by some of the endemics to the low-elevation páramos in the south sections, such as *E. bromelioides* Cuatrec. and *E. ruizii* Cuatrec. Whatever the appropriate threat category for these taxa, it is clear that some urgent measures are required to guarantee their conservation.

Morphology

Growth form (Fig. 6A). There are 14 trees and 40 rosette plants in the Venezuelan *Espeletia* clade. On average, rosette plants tend to occupy higher elevations than trees, notably above 3900 m.a.s.l., which appears to be the upper elevation limit to the tree growth form in this group. On the other hand, the rosette plants are not exclusively associated with the higher elevations, since about half of species with this growth form have been found below 3000 m.a.s.l. and five have not been collected above this elevation.

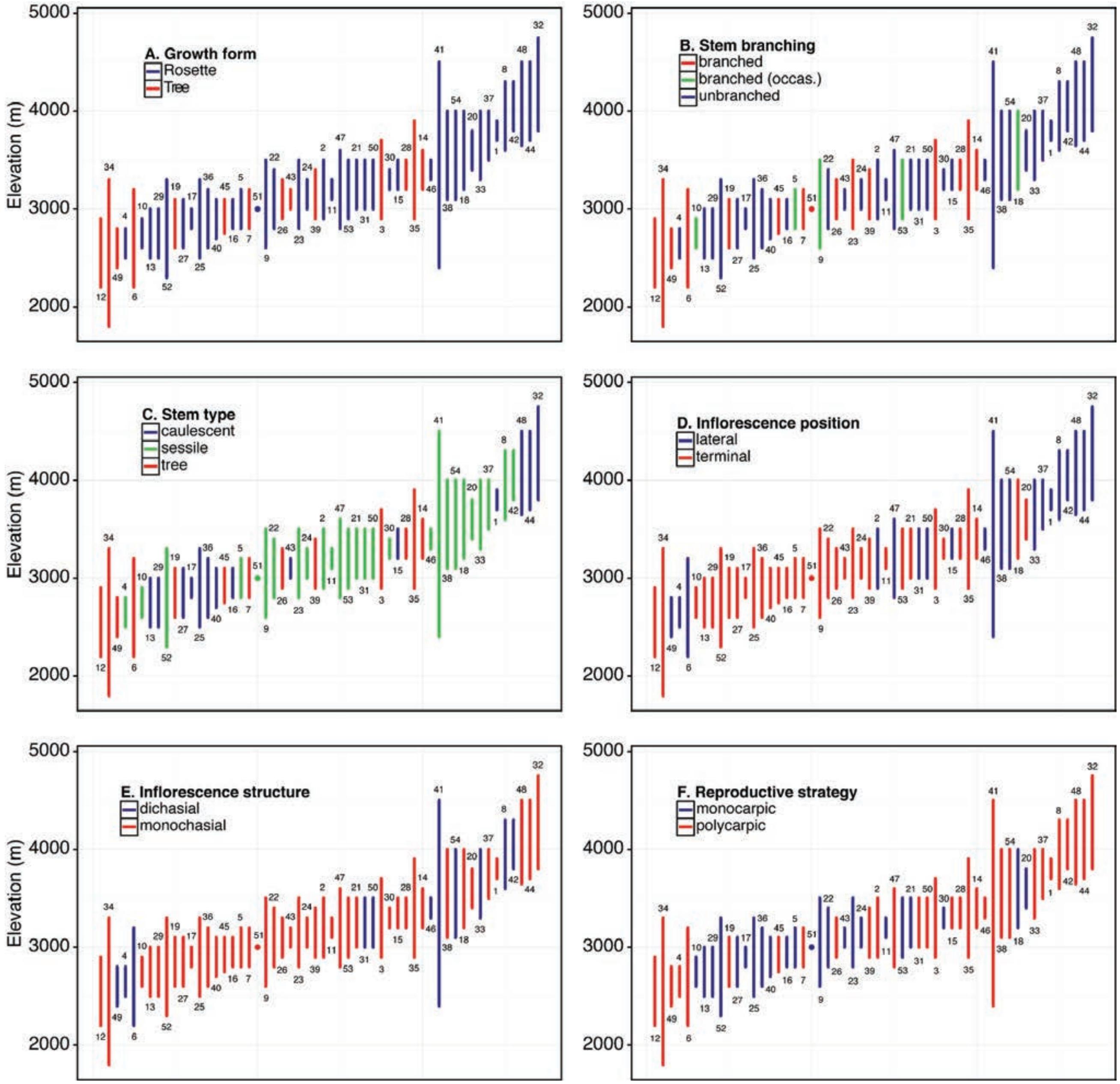

Figure 6. Minimum and maximum elevation limits of the 54 species in the Venezuelan clade of *Espeletia* Mutis ex Bonpl., organized according to: **A**, growth form; **B**, stem branching; **C**, stem type; **D**, inflorescence position; **E**, inflorescence structure; and **F**, reproductive strategy. Species labels: 1. *E. albarregensis* (Cuatrec.) Mavárez. 2. *E. angustifolia* Cuatrec. 3. *E. arborea* Aristeg. 4. *E. aristeguietana* Cuatrec. 5. *E. atropurpurea* A.C. Sm. 6. *E. badilloi* Cuatrec. 7. *E. banksiifolia* Sch. Bip. & Ettingsh. ex Wedd. 8. *E. batata* Cuatrec. 9. *E. bracteosa* Standl. 10. *E. bromelioides* Cuatrec. 11. *E. cardonae* Cuatrec. 12. *E. chardonii* A.C. Sm. 13. *E. cuatrecasasii* Ruiz-Terán & López-Fig. 14. *E. divisoriensis* (Cuatrec.) Mavárez. 15. *E. elongata* A.C. Sm. 16. *E. emmanuelis* (Cuatrec.) Mavárez. 17. *E. figueirasii* Cuatrec. 18. *E. floccosa* Standl. 19. *E. griffinii* Ruiz-Terán & López-Fi 20. *E. grisea* Standl. 21. *E. hanburyana* Cuatrec. 22. *E. jabonensis* Cuatrec. 23. *E. jahnii* Standl. 24. *E. leucactina* Cuatrec. 25. *E. lindenii* Sch. Bip. ex Wedd. 26. *E. liscanoana* Cuatrec. 27. *E. lopezpalacii* Ruiz-Terán & López-Fig. 28. *E. lucida* Aristeg. 29. *E. marcescens* S.F. Blake. 30. *E. margarita* Cuatrec. 31. *E. marthae* Cuatrec. 32. *E. moritziana* Sch. Bip. & Ettingsh. ex Wedd. 33. *E. nana* Cuatrec. 34. *E. neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. 35. *E. occulta* S.F. Blake. 36. *E. paltonioides* Standl. 37. *E. palustris* (Diazgr. & Morillo) Mavárez. 38. *E. pannosa* Standl. 39. *E. parvula* (Cuatrec.) Mavárez. 40. *E. ruizii* Cuatrec. 41. *E. schultzii* Wedd. 42. *E. semiglobulata* Cuatrec. 43. *E. spectabilis* Cuatrec. 44. *E. spicata* Sch. Bip. ex Wedd. 45. *E. tamana* Cuatrec. 46. *E. tenorae* Aristeg. 47. *E. thyrsiformis* A.C. Sm. 48. *E. timotensis* Cuatrec. 49. *E. trujillensis* Cuatrec. 50. *E. ulotricha* Cuatrec. 51. *E. usubillagae* (Cuatrec.) Mavárez. 52. *E. vergarae* (Cuatrec. & López-Fig.) Mavárez. 53. *E. viridis* Aristeg. 54. *E. weddellii* Sch. Bip. ex Wedd.

Stem branching (Fig. 6B). Among trees, 13 species are branched and one is unbranched (*Espeletia spectabilis* Cuatrec.). Among rosette plants, seven species are branched: one frequently, *E. jahnii* Standl.; five occasionally; and one known only from the type collection, *E. usubillagae* (Cuatrec.) Mavárez. The remaining 33 rosette species are almost invariably unbranched, although some rare branched individuals have been observed in some species, most likely resulting from accidental division of the apical bud.

Stem type (Fig. 6C). There are about two orders of magnitude of variation in stem height among rosette plants, from ca. 15 cm to ca. 15 m. Most sessile and short-stemmed rosette plants (< 1 m) live in páramo habitats between 3000 and 4000 m.a.s.l., some in relatively humid areas within superpáramos, such as *Espeletia batata* Cuatrec. and *E. semiglobulata*, and some in open places in subpáramos, such as *E. aristeguietana* Cuatrec. and *E. bromelioides*. On the other hand, caulescent rosette plants (> 1 m) occupy two very different habitat types: either the coldest and more exposed areas in páramos and superpáramos, such as *E. moritziana* Sch. Bip. ex Wedd., *E. spicata* Sch. Bip. ex Wedd., and *E. timotensis* Cuatrec.; or the relatively warmer and shrubby subpáramos, such as *E. cuatrecasasii* Ruiz-Terán & López-Fig., *E. paltonioides* Standl., and *E. spectabilis*. The giant stems in the Venezuelan *Espeletia* clade could therefore be the response to two rather different selective pressures imposed by the habitats in which these species live: the positioning of the apical bud as far as possible from the ground, where the temperatures are lowest in the superpáramos; and the competition for light, pollinators, or both in the structurally more complex habitat of the subpáramos.

Inflorescence position (Fig. 6D). Twelve tree species have terminal inflorescences, whereas they are placed in lateral position in the remaining two, *Espeletia badilloi* Cuatrec. and *E. trujillensis* Cuatrec. Among rosette plants the proportion is more equilibrated, with terminal inflorescences in 22 species and lateral in 18 species. Rosette plants with lateral inflorescences clearly tend to occupy higher elevations than those with terminal inflorescences, with an important exception to this pattern in *E. aristeguietana*.

Inflorescence structure (Fig. 6E). Among trees, 12 species have inflorescences with monochasial and alternate structure, whereas they are dichasial and opposite in the remaining 2, *Espeletia badilloi* and *E. trujillensis*. The same trend is observed among rosette plants, with monochasial and alternate inflorescences in 31 species, and dichasial and opposite in 9 species. However, if the 7 rosette species with monocephalous inflorescences are excluded, the proportion of monochasial/alternate to dichasial/opposite becomes 29 to 4. It is worth mentioning that the opposite trend is observed among the Colombian *Espeletia* clade, in which taxa with dichasial/opposite inflorescence structure are much more diverse than those with monochasial/alternate inflorescence structure (Cuatrecasas, 2013).

Monocarpy/polycarpy (Fig. 6F). Strict monocarpy—death of the plant after the single reproduction event—is found among *Espeletia* in unbranched plants with terminal inflorescences. This combination of morphological features is observed in 1 tree, *E. spectabilis*, and 16 rosette species. However, monocarpy is also observed frequently among rosette plants with branching capacity, either by lack of branching after reproduction in individuals with single stems or as the simultaneous reproduction of all rosettes in multibranched individuals. Interestingly, the latter phenomenon has also been observed in some trees (e.g., *E. neriifolia*).

Spanish Names

After more than 10 years of extensive fieldwork in the Venezuelan Andes and interviewing about 100 people with regard to Spanish names, I have noticed that these plants, notably the rosette plants with dense indumentum on leaves, are indeed collectively known as *frailejón* (plural, *frailejones*), a name that nonetheless is also applied to some species of *Senecio* and *Orithrophium*. Branched forms are simply known as *árbol*, and I have rarely or never seen the use of the supposedly common names *incienso*, *anime*, or *carrambo*. Those names must therefore today be very rare or extremely localized. As noted by Diazgranados (2012) and Cuatrecasas (2013), there are some Spanish names that appear relatively more specific, particularly among rosette plants, but none is used bi-univocally. For instance, *frailejón (f.) amarillo* is used indistinctly for *Espeletia moritziana* (also known as *f. dorado*) and *E. schultzii* (also known as *f. de octubre*). The six dwarf *Espeletia* species are known as *f. pata de burro, f. batato*, or *f. chijí*, while *f. plateado* is used for all species with silvery indumentum: *E. jabonensis* Cuatrec., *E. floccosa, E. pannosa* (also known as *f. lanoso* and *f. chirique*) and *E. angustifolia* Cuatrec. (also known as *f. chirique*). Spanish names therefore seem to be rare or inconsistent in this plant group and, contrary to the practice promoted by Diazgranados (2012) and Cuatrecasas (2013), they will not be provided in this work. New Spanish names will not be proposed either. I share the view expressed in Diazgranados (2012) that giving common names helps in "socializing the knowledge of these species and instilling a feeling of responsibility among local inhabitants to protect these resources," but I also believe that these names would have a greater chance of being accepted and used if chosen by or in agreement with local communities.

TAXONOMY

Espeletia Mutis ex Bonpl., Plant. Aeq. 2: 10. 1809.

Type species: *Espeletia grandiflora* Bonpl., Plant. Aeq. 2: 11. 1809. COLOMBIA. Santa Fe de Bogotá i Quindio, *Herbier de l'Amérique équatoriale, donné par M. A. Bonpland, s.n.* (Holotype: P [MNHN-P-P00320272]; Isotypes: P [MNHN-P-P00320273, MNHN-P-P00307378, MNHN-P-P00680447]).

Synonyms: *Carramboa* Cuatrec., Phytologia 35: 54. 1976.

Type species: *Espeletia pittieri* Cuatrec., Ciencia (México) 6: 262. 1945. VENEZUELA. Mérida: forest between El Molino and ridge above San Isidro Alto, 2430–2895 m.a.s.l., 14 May 1944, *J. Steyermark 56532* (Holotype: VEN [not seen]; Isotypes: F, NY, US).

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FIGURES 7–8. *Espeletia albarrengensis* (Cuatrec.) Mavárez. Laguna Albarregas, Mérida, Venezuela. **7**. Photograph by S. Aubert. **8**. Photograph by L. Gámez.

Coespeletia Cuatrec., Phytologia 35: 56. 1976. Type species: *Espeletia spicata* Sch. Bip. ex Wedd., Chlor. Andina: 65. 1855. VENEZUELA. Mérida: Sierra Nevada de Mérida, 14,000 pieds, August 1842, *J. Linden 400* (Holotype: P; Isotypes: F, FI [not seen], K, P).

Espeletiopsis Cuatrec., Phytologia 35: 54. 1976. Type species: *Espeletia jimenezquesadae* Cuatrec., Rev. Acad. Col. Ci. Exact. 3: 247. 1940a. COLOMBIA. Boyacá: Cordillera Oriental, Nevado del Cocuy, hacia la Cueva, en la Zanja, 3700 m.a.s.l., 13 Septiembre 1938, *J. Cuatrecasas & H. García-Barriga 1635* (Holotype: COL; Isotype: US).

Libanothamnus Ernst, Vargasia 7: 186. 1870. Type species: *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd., Chlor. Andina: 67. 1855. VENEZUELA. Caracas: Silla de Caracas, 3 Janvier 1800, *Herbier donné par M. Bonpland en 1833 N° 652* (Lectotype: P [MNHN-P-P04086343]; Isolectotype: P [MNHN-P-P04086342]).

Ruilopezia Cuatrec., Phytologia 35: 51. 1976. Type species: *Espeletia figueirasii* Cuatrec., Phytologia 20: 475. 1971. VENEZUELA. Mérida: Sierra Nevada de Santo Domingo, Páramo de los Granates, Loma de Paja, las Escaleras, 3240 m.a.s.l., 11 October 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28068* (Holotype: US; Isotypes: F, IVIC, MERF, U, US).

Paramiflos Cuatrec., Proc. Biol. Soc. Wash. 108: 748. 1995. Type species: *Espeletia glandulosa* Cuatrec., Rev. Acad. Col. Ci. Exact.: 434. 1940b. COLOMBIA. Boyacá: Cordillera Oriental, Alto de Canutos, Páramo de Guantiva, vertiente sur, 3200–3400 m.a.s.l., *J. Cuatrecasas 10360* (Holotype: COL; Isotypes: COL, F, P, US).

Tamania Cuatrec., Phytologia 35: 53. 1976. Type species: *Espeletia chardonii* A.C. Sm., Bol. Soc. Ven. Ci. Nat. 7: 237. 1942. VENEZUELA. Táchira: Páramo de Tamá, El Paramito, 2550 m.a.s.l., 15 August 1939, *C. E. Chardon 78* (Holotype: US; Isotypes: NY, VEN [not seen]).

1. Espeletia albarregensis (Cuatrec.) Mavárez, *comb. nov.* Basionym: *Coespeletia albarregensis* Cuatrec., Mem. New York Bot. Gard. 107: 588. 2013. TYPE: VENEZUELA. Mérida: Laguna Albarregas, Páramo de los Conejos, Sierra de la Culata, 3850 m.a.s.l., 27 March 1972, *L. Ruiz-Terán 7050* (Holotype: US; Isotype: MERF). Fig. 7–9.

Rosette polycarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially densely pubescent, lanuginose, length 30–45 cm, width 2.8–5.0 cm, ratio 9–10:1, secondary nerves parallel, 5–10 mm apart. *Inflorescence* lateral, simple, monochasial, botryoid, axes 60–80 cm, 9–11 monocephalous peduncles, vegetative part usually with 4–6 alternate bracts. *Capitulum* diam. 35–55 mm, ligular circle equal or slightly shorter than the involucre, disc 20–25 mm, ray ligules yellow. *Espeletia albarregensis* can be distinguished from other Venezuelan rosette plants for its botryoid inflorescences with large capitula (diam. > 35 mm). It resembles *E. timotensis*, from which it can be distinguished for its smaller stem

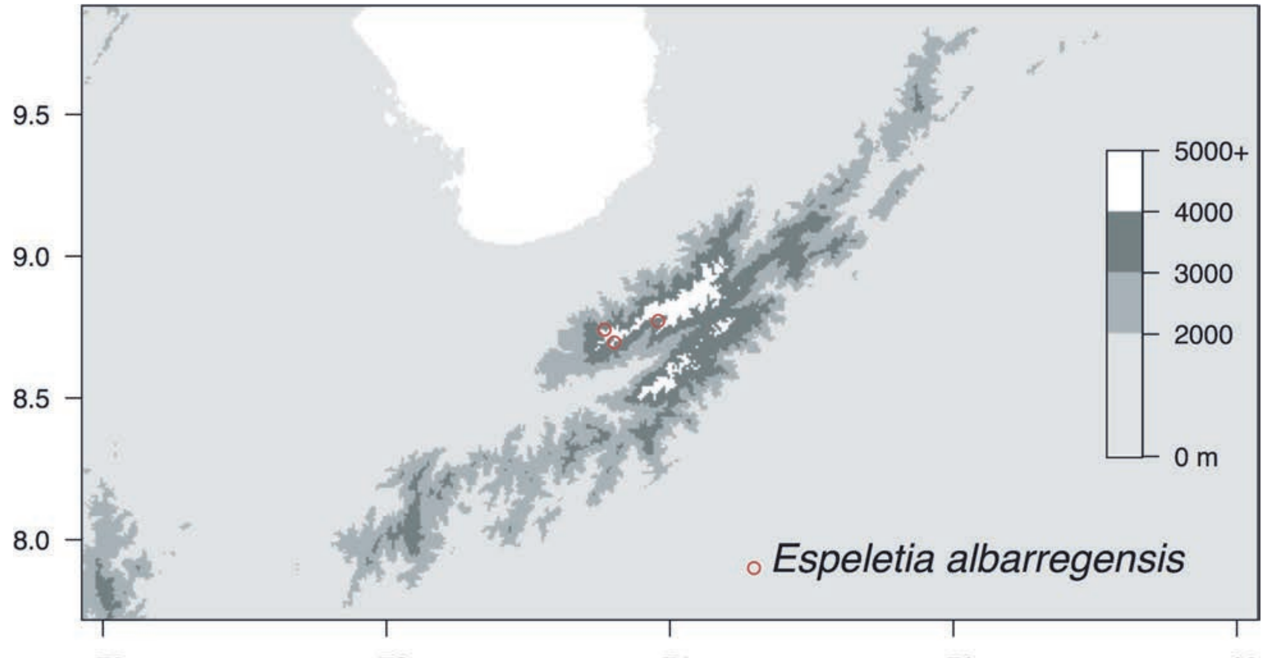

FIGURE 9. Distribution of *Espeletia albarregensis* (Cuatrec.) Mavárez.

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FIGURES 10–11. *Espeletia angustifolia* Cuatrec. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

(< 1.0 m vs. > 1.0 m), smaller length-to-width leaf ratio (< 10:1 vs. > 10:1), shorter inflorescences (< 80 cm vs. > 85 cm), fewer capitula (9–11 vs. 8–15). and longer ray corollas (> 11.0 mm vs. < 9.0 mm).

Distribution: VENEZUELA. Mérida: originally known only from the type locality. However, I have recently found a few isolated individuals 3 km NW of the town of la Culata (8˚46'19.1"N 71˚02'30.9"W), about 20 km NW of the type locality. 3700–3900 m.a.s.l., on steep and rocky páramo slopes, and down to the lakeshore in the type locality (Fig. 9).

Additional specimens examined (selection): *L. Ruiz-Terán 7050* (US), *L. Ruiz-Terán 7051* (US), *López-Figueiras 30545* (US). *P. Berry 3852* (US) is probably a hybrid: *E. albarregensis* × *E. schultzii* or *E. schultzii* × *E. timotensis*.

2. *Espeletia angustifolia* Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 80. 1956a. TYPE: VENEZUELA. Mérida: Páramo de Mijará, 3300 m.a.s.l., 18 March 1922, *A. Jahn 973* (Holotype: US; Isotypes: G, NY). Fig. 10–12.

Homotypic synonym: *Espeletiopsis angustifolia* (Cuatrec.) Cuatrec., Phytologia 35: 55. 1976.

Rosette polycarpic, sessile. *Leaf* open sheath, sessile, adaxially densely pubescent, lanuginose, length 15–30 cm, width 0.7–1.5 cm, ratio 20–25:1, secondary nerves obsolete or thin, 1–3 mm apart when visible. *Inflorescence* lateral, compound, primary branching monochasial, corymboid, length 50–70 cm, vegetative part with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle 25–35(40) mm, disc 12–15 mm, ray ligules white. *Espeletia angustifolia* differs from other species for its sessile polycarpic rosette habit and its capitulum with white ray ligules. It resembles *E. pannosa*, from which it can be distinguished for its leaves with smaller ratios (< 25:1 vs. > 30:1) and lanuginose indumentum on both sides (vs. silvery/sericeous adaxially).

Distribution: VENEZUELA. Mérida: Páramo de Mijará, de San José, and de la Veguilla. 2900–3500 m.a.s.l., in open grass páramos and well-drained slopes (Fig. 12).

Additional specimens examined (selection): *A. Jahn 973* (US, G, NY), *C. Sobrevila & M. Guariguata 1534* (US), *P. Berry*, *C. Sobrevila & C. Estrada 4291* (US), *P. Berry & R. Calvo 4396* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28098* (US).

J. Steyermark 56279 in F is not an isotype but a paratype.

3. *Espeletia arborea* Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 286. 1959. TYPE: VENEZUELA. Trujillo: Guirigay, hacia Peña Blanca, 3200 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3635* (Holotype: VEN [not seen]; Isotypes: NY, US). Fig. 13–15.

Homotypic synonym: *Libanothamnus arboreus* (Aristeg.) Cuatrec., Phytologia 35: 50. 1976.

Tree profusely branched, height up to 5 m. *Leaf* tubular sheath, pseudopetiolate (length 1.5–2.5 cm), leaf length 15–25 cm, width 3.0–7.0 cm, ratio 3.0–4.0:1, secondary nerves parallel, 1–2(3) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at about the same level as the surrounding leaves, length 15–30 cm, branched near the base. *Capitulum* diam. 12–18 mm, ligular circle 24–30 mm, disc 14–18 mm, ray ligules cream or greenish. *Espeletia arborea* differs from other tree

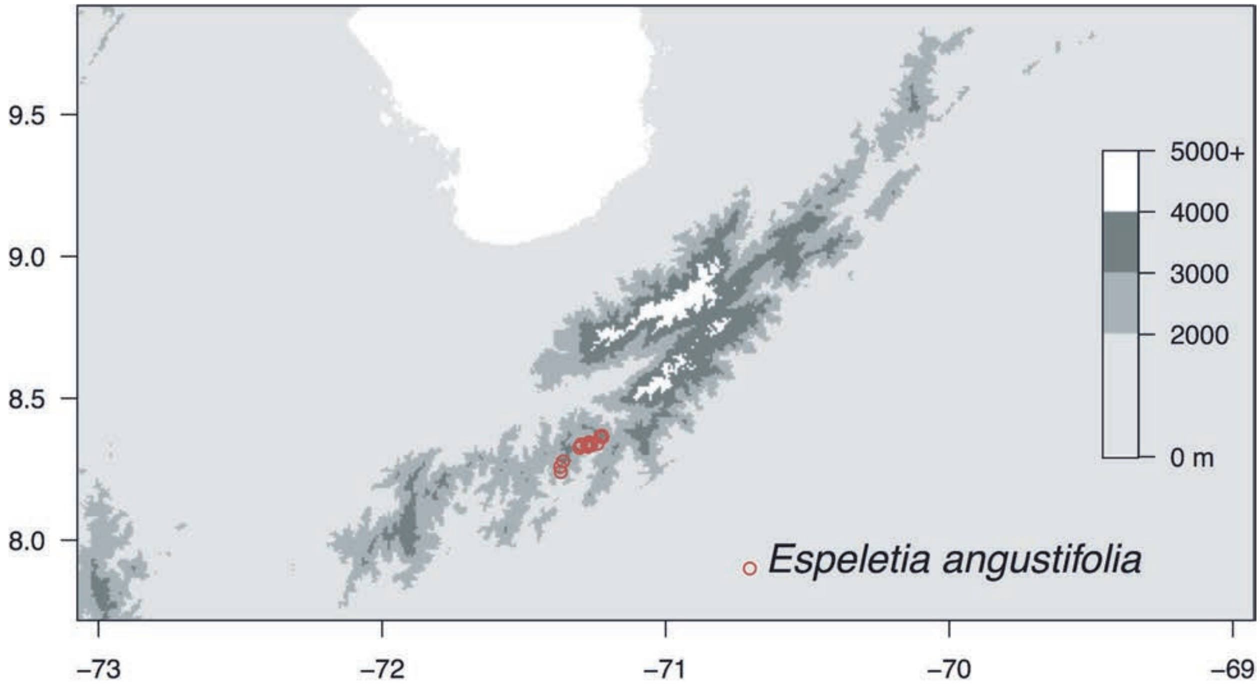

FIGURE 12. Distribution of *Espeletia angustifolia* Cuatrec.

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FIGURES 13–14. *Espeletia arborea* Aristeg. Laguna de Santo Cristo, Mérida, Venezuela (Photographs by S. Aubert).

species for its pseudopetiolate leaves with sheaths adaxially glabrous, closely packed parallel secondary nerves (< 3 mm apart), and its ligulate capitulum with diam. > 12 mm.

Distribution: VENEZUELA. Trujillo: Páramo de Guirigay, in the upper basins of rivers Aracay and Burate. Mérida-Barinas border: Páramo de los Granates, de Gavidia, and around Laguna de Santo Cristo in Sierra Nevada de Mérida. Northern populations (var. *arborea*) found 2900–3200 m.a.s.l. in the upper level of the Andean forest below the timberline, whereas southern populations (var. *lancifolia*) found 3300–3700 m.a.s.l., usually in subpáramo habitats above the timberline, as well as in humid páramos near rivers and lakes (Fig. 15).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3635* (US, NY), *L. Ruiz-Terán & López-Figueiras 13081* (US), *R. Riina*, *R. Duno*, *R. Ghinaglia & R. Gonto 635* (US), *López-Figueiras & H. Rodríguez 8823* (US), *López-Figueiras 14520* (US).

Only "L. Aristeguieta" (E. Medina missing) appears as collector in the labels of the isotypes at NY and US.

3.1. *Espeletia arborea* Aristeg. var. *arborea*

Distribution: Venezuela. Trujillo: Páramo de Guirigay, in the upper basins of rivers Aracay and Burate. 2900–3200 m.a.s.l., found in the upper level of Andean forest below the timberline, as well as in low-elevation shrubby subpáramo habitats.

3.2. Espeletia arborea Aristeg. var. *lancifolia* (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus arboreus* (Aristeg.) Cuatrec. var. *lancifolius* Cuatrec., Mem. New York Bot. Gard. 107: 438. 2013. TYPE: VENEZUELA. Mérida-Barinas border: Laguna Azul o del Corazón, arriba de Loma de Paja, Páramo de los Granates, unos 18 km al E. de Sierra Nevada de Santo Domingo, 3350 m.a.s.l., 17 September 1971, *L. Ruiz-Terán 6348* (Holotype: US; Isotype: MERF).

Differs from *Espeletia arborea* var. *arborea* for its acutely lanceolate leaves and its involucre completely covered by the last row of outer phyllaries (*vs*. with several imbricated levels).

Distribution: VENEZUELA. Mérida-Barinas border: Páramo de Los Granates, de Gavidia, and Laguna de Santo Cristo in Sierra Nevada de Mérida. 3300–3700 m.a.s.l., found in subpáramo habitats above the timberline, as well as in humid páramos near rivers and lakes.

Additional specimens examined (selection): *L. Ruiz-Terán 6348* (US), *L. Ruiz-Terán 8462* (US), *L. Dorr & L. Barnett 5632* (US).

Collection date given as "17 October 1971" in Cuatrecasas (2013: 438).

4. *Espeletia aristeguietana* Cuatrec., Phytologia 27: 174. 1973b. TYPE: VENEZUELA. Trujillo: la Cañada, Páramo de la Cristalina, 2500–2600 m.a.s.l., 30 October 1969. *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28194* (Holotype: US; Isotype: US). Fig. 16–18.

Rosette polycarpic, sessile. *Leaf* open sheath, sessile, adaxially densely pubescent, tomentose-velvety, greenish, length 40–55 cm, width 7.5–14.0 cm, ratio 4.0–5.7:1, bases of secondary nerves parallel, unevenly distributed, 8–20 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, thyrsoid, length 70–90 cm, vegetative part with 2 pairs of opposite bracts. *Capitulum* diam. 10–14 mm, ligular circle 24–28 mm, disc 10–11 mm, ray ligules yellow.

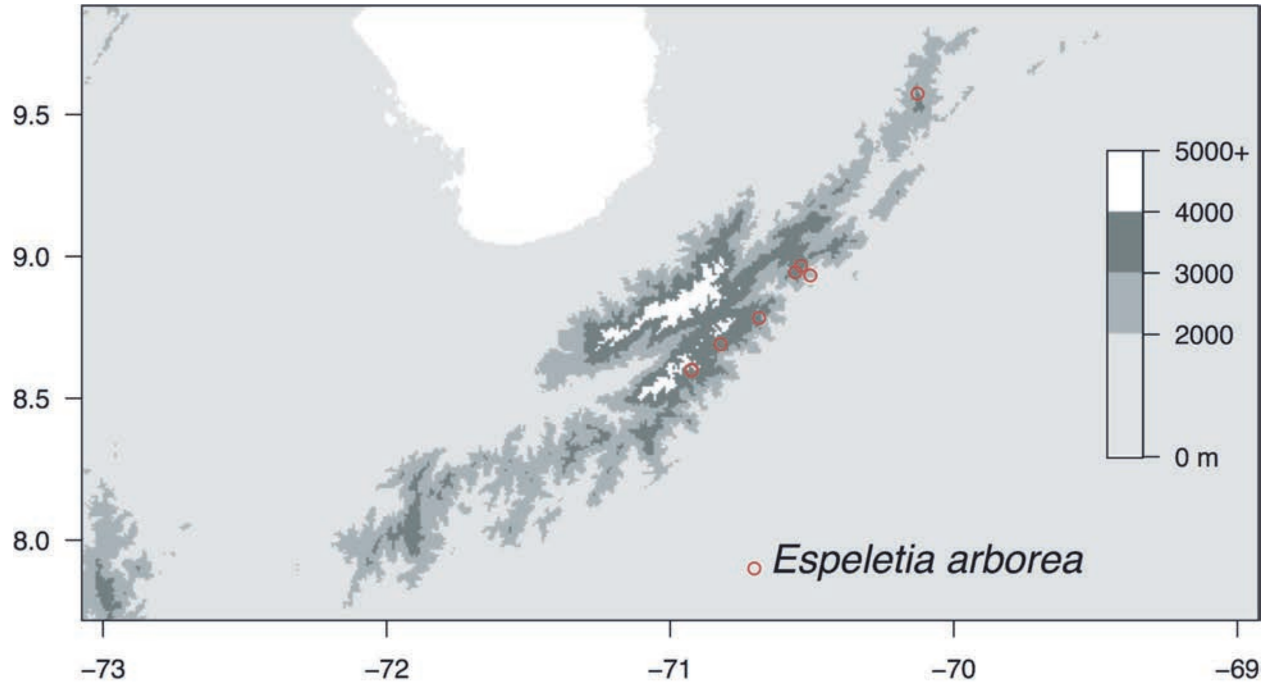

FIGURE 15. Distribution of *Espeletia arborea* Aristeg.

FIGURES 16–17. *Espeletia aristeguietana* Cuatrec. Páramo de la Cristalina, Trujillo, Venezuela (Photographs by S. Aubert).

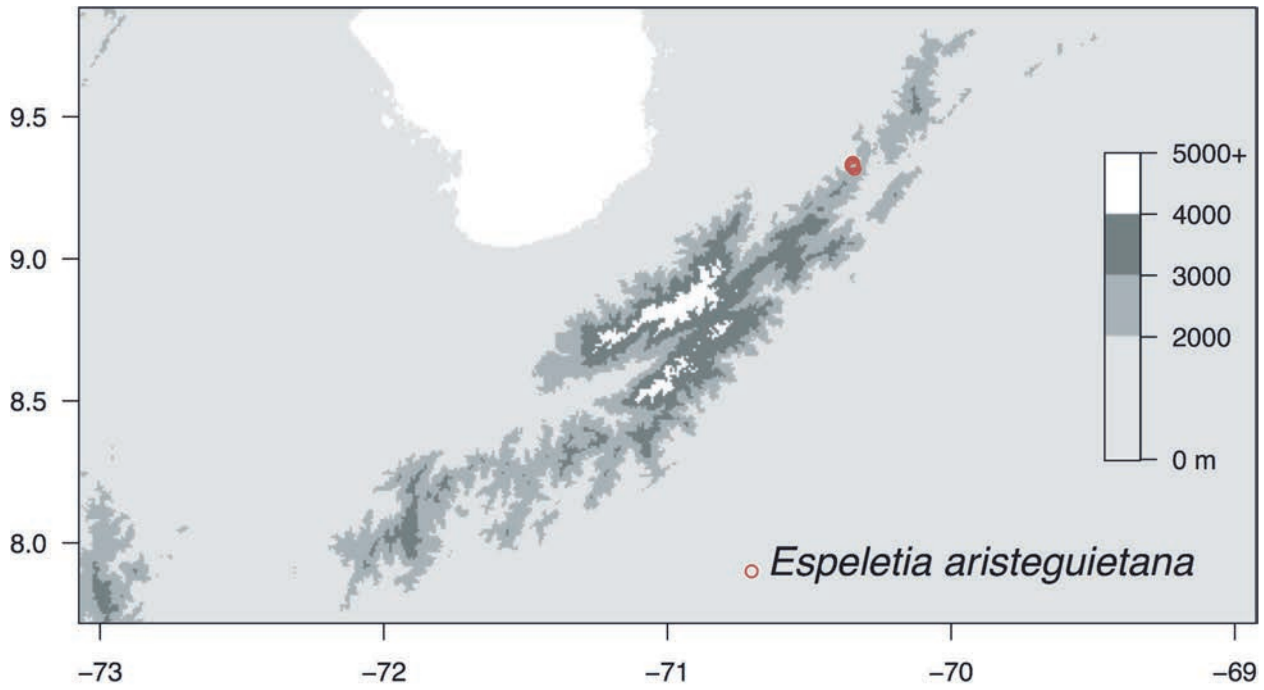

FIGURE 18. Distribution of *Espeletia aristeguietana* Cuatrec.

Espeletia aristeguietana can be easily distinguished from other species with dichasial thyrsoid inflorescences for its unique tomentose, velvety indumentum on both sides of leaves and for its small capitulum (diam. < 15 mm).

Distribution: VENEZUELA. Trujillo: known only from the type locality. 2500–2800 m.a.s.l., found in open locations within a relatively low-elevation subpáramo habitat, and in clearings in the highly degraded upper level of the Andean forest (Fig. 18).

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28194* (US); *id. 28559* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28560* (US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28994* (US), *L. Ruiz-Terán & M. López-Figueiras 2258* (US).

5. ***Espeletia atropurpurea*** A.C. Sm., Brittonia 1: 508. 1935. TYPE: VENEZUELA. Mérida: Páramo de Quirorá, 3200 m.a.s.l., 8 October 1971, *A. Jahn 731* (Holotype: US; Isotypes: F, G, GH, NY, US, VEN [not seen]). Fig. 19–21.

Homotypic synonym: *Ruilopezia atropurpurea* (A.C. Sm.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes with smaller rosettes budding at the base of the main rosette, sessile. *Leaf* open sheath, strongly pseudopetiolate (length 5–25 cm), adaxially glabrous, glossy green, length 20–45 cm, width 4.0–9.0 cm, ratio 4–8(11):1, margins sometimes dentate, teeth 4–10 mm apart, secondary nerves filiform, parallel, 3–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, paniculate, length 100–200 cm, usually branched from near the base, although rather loosely. *Capitulum* diam. 10–14 mm, up to 20 mm when dry, eligulate. *Espeletia atropurpurea* can be easily distinguished from other species for its sessile monocarpic rosette habit, strongly pseudopetiolate and oblong leaves glabrous on the adaxial side, and eligulate ray corollas.

Distribution: VENEZUELA. Mérida: widespread in the southern páramos of Sierra Nevada de Mérida (e.g., Don Pedro, Aricagua, San José, Quirorá), and of Sierra de la Culata (e.g., los Conejos). Also found in the western slopes of Pico Bolívar, between cable car stations La Aguada and Loma Redonda. Border Mérida-Táchira: Páramo de Guaraque, hills above El Portachuelo and Las Porqueras (above La Grita) and Páramo de la Negra. Táchira: Páramo del Batallón. Usually 2800–3200 m.a.s.l., but the population west of Pico Bolívar can reach 3700 m.a.s.l. Found in shrubby subpáramo habitats and in forest clearings near the timberline (Fig. 21).

Additional specimens examined (selection): *A. Jahn 731* (F, G, GH, NY, US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2702* (US), *C. Sobrevila*, *A. Weitzman & D. Solbrig 1560* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28013* (F, U, US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28001* (F, U, US).

6. ***Espeletia badilloi*** Cuatrec., Ciencia (México) 6: 261. 1945. TYPE: VENEZUELA. Mérida: Páramo de Don Pedro, 2900 m.a.s.l., 18 July 1944, *V. Badillo 991* (Holotype: VEN). Fig. 22–25.

Homotypic synonym: *Carramboa badilloi* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Heterotypic synonyms: *Espeletia littlei* Aristeg., Fl. Venez. 10(1): 434. 1964. TYPE: VENEZUELA. Mérida: La Carbonera, 2700 m.a.s.l., October 1953, *Little 15592* (Holotype: VEN).

Carramboa littlei (Aristeg.) Cuatrec., Phytologia 35: 54. 1976.

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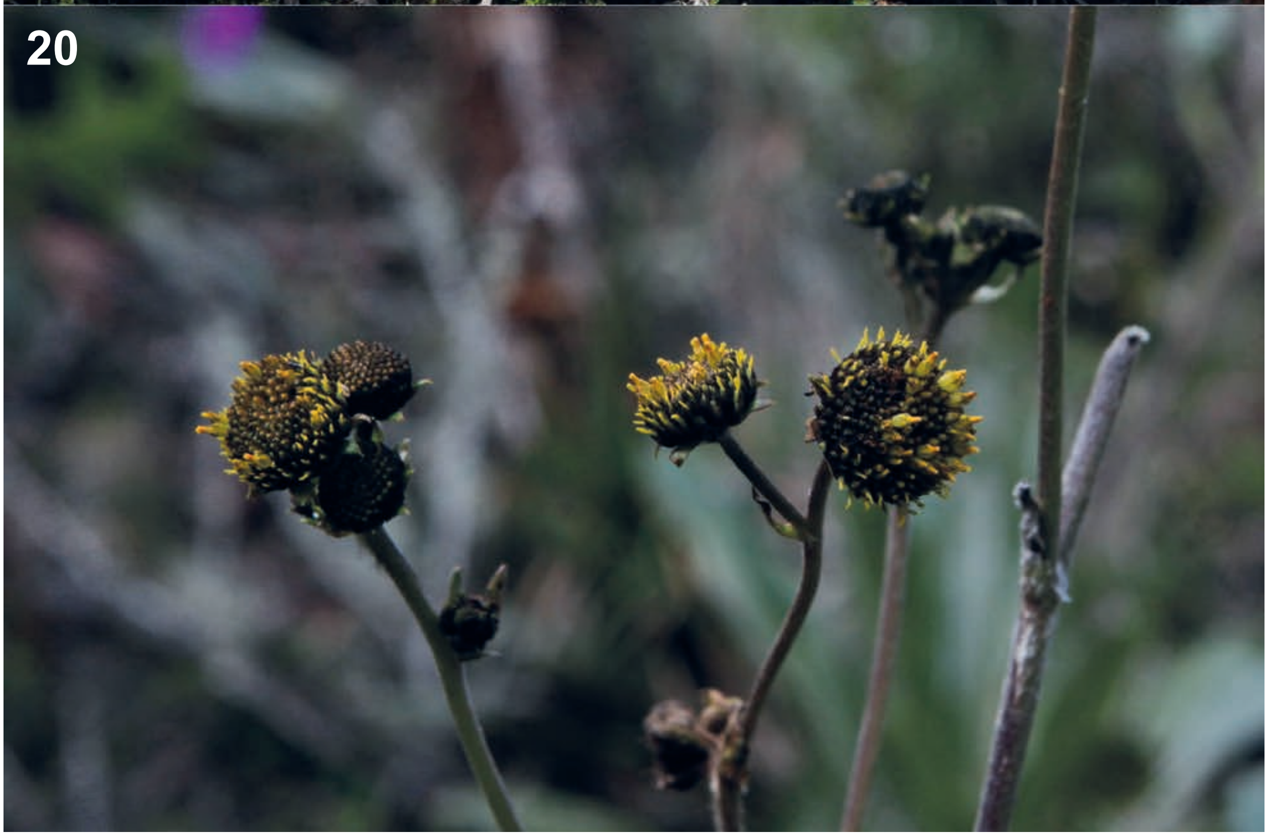

Figures 19–20. *Espeletia atropurpurea* A.C. Sm. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

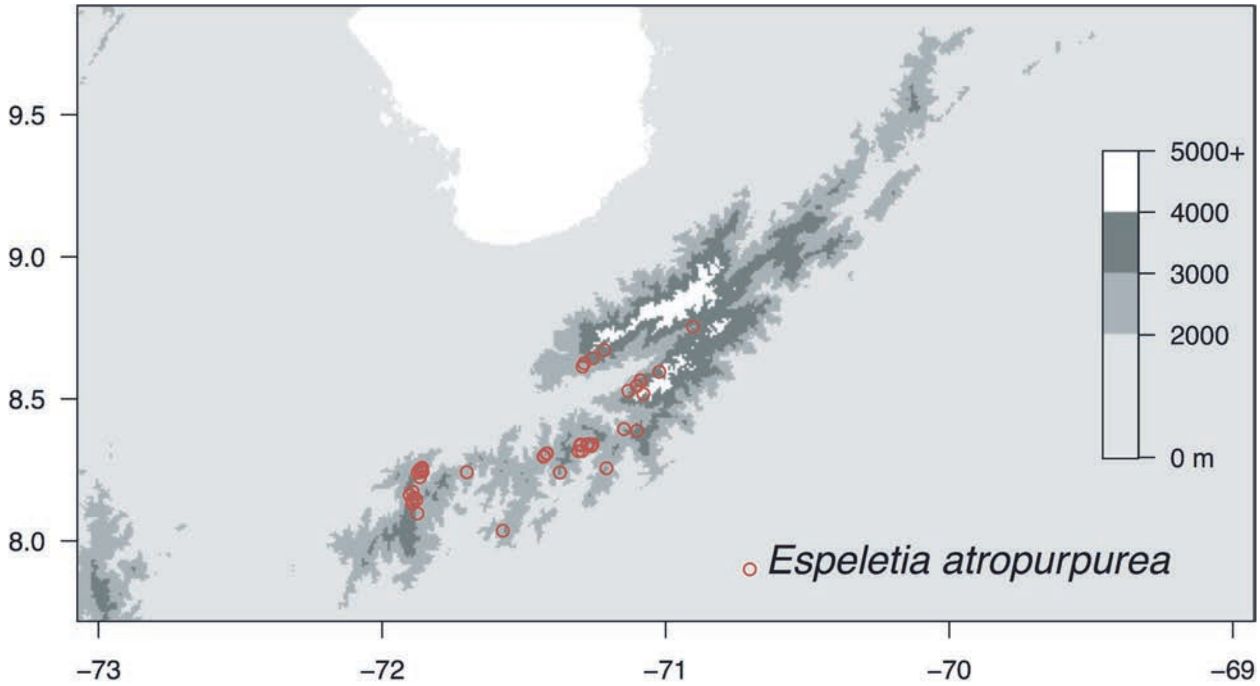

FIGURE 21. Distribution of *Espeletia atropurpurea* A.C. Sm.

Tree profusely ramified, height up to 20 m. *Leaf* tubular sheath, pseudopetiolate (length 2.5–9.0 cm), adaxially glabrous or loosely short-hirsute, dark green, length 25–60 cm, width 15–35 cm, ratio 1.3–2.2:1, bases of secondary nerves parallel, unevenly distributed, 10–40 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, corymboid, length 20–70 cm, at the same level or slightly surpassing the surrounding leaves, vegetative part leafless, about half of total length. *Capitulum* diam. 6–9 mm, ligular circle 12–22 mm, disc 5–8 mm, ray ligules yellow. *Espeletia badilloi* can be distinguished from other tree species for its profusely ramified habit, pseudopetiolate leaves with low length-to-width ratio (< 2.2:1), and dichasial corymboid inflorescences with vegetative part aphyllous.

Distribution: VENEZUELA. Border Barinas-Trujillo: forested hills in Páramo de Guirigay and de Ortiz. Mérida: forested areas in the southern slopes of Sierra Nevada de Mérida, toward Páramo de Don Pedro and the hills above Aricagua, Páramo de las Coloradas (above El Molino), de Quirorá, de Guaraque, and Pico de Horma. Southern slopes of Sierra de la Culata in the valley of Río Capaz and slopes of Pico Campanario. Mérida-Táchira: forested hills above Pregonero, El Portachuelo, and Las Porqueras (la Grita) and below Páramo de la Negra and del Batallón. 2400–3200 m.a.s.l., locally down to 2200 m.a.s.l., usually found in gregarious populations in forests clearings and along trails/roads (Fig. 25).

Additional specimens examined (selection): *M. López-Figueiras*, *R. Ovando & F. Ricardi 14120* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28149* (F, U, US), *M. López-Figueiras & L. Ruiz-Terán 14013* (US).

6.1. *Espeletia badilloi* Cuatrec. var. ***badilloi***

Distribution: VENEZUELA. Border Barinas-Trujillo: forested hills in Páramo de Guirigay and de Ortiz. Mérida: forested areas in the southern slopes of Sierra Nevada de Mérida, towards Páramo de Don Pedro and the hills above Aricagua. Southern slopes of Sierra de la Culata in the valley of Río Capaz and slopes of Pico Campanario. Between 2400 and 3200 m.a.s.l., sometimes down to 2200 m.a.s.l., usually found in gregarious populations in forest clearings and along trails/roads.

6.2. Espeletia badilloi Cuatrec. var. ***pittieri*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Espeletia pittieri* Cuatrec., Ciencia (México) 6: 262. 1945. TYPE: VENEZUELA. Mérida: forest between El Molino and ridge above San Isidro Alto, 2430–2895 m.a.s.l., 14 may 1944, *J. A. Steyermark 56532* (Holotype: VEN [not seen]; Isotypes: F, NY, US).

Homotypic synonyms: *Carramboa pittieri* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Carramboa badilloi (Cuatrec.) Cuatrec. var. *pittieri* Cuatrec., Mem. New York Bot. Gard. 107: 396. 2013.

According to Cuatrecasas (2013: 396), *Espeletia badilloi* var. *pittieri* can be distinguished from *E. badilloi* var. *badilloi* for its rigidly coriaceous leaves (vs. chartaceous), scarcely pilose adaxially and rough to the touch (vs. softly hirsute), with shorter pseudopetioles (1.5–5.5 cm vs. 2.5–9.0 cm) and with many conspicuous transverse nerves near the base (vs. none or few). However, these differences are subtle and depend largely on subjective criteria, making

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FIGURES 22–24. *Espeletia badilloi* Cuatrec. Páramo de Don Pedro, Mérida, Venezuela (Photographs by S. Aubert).

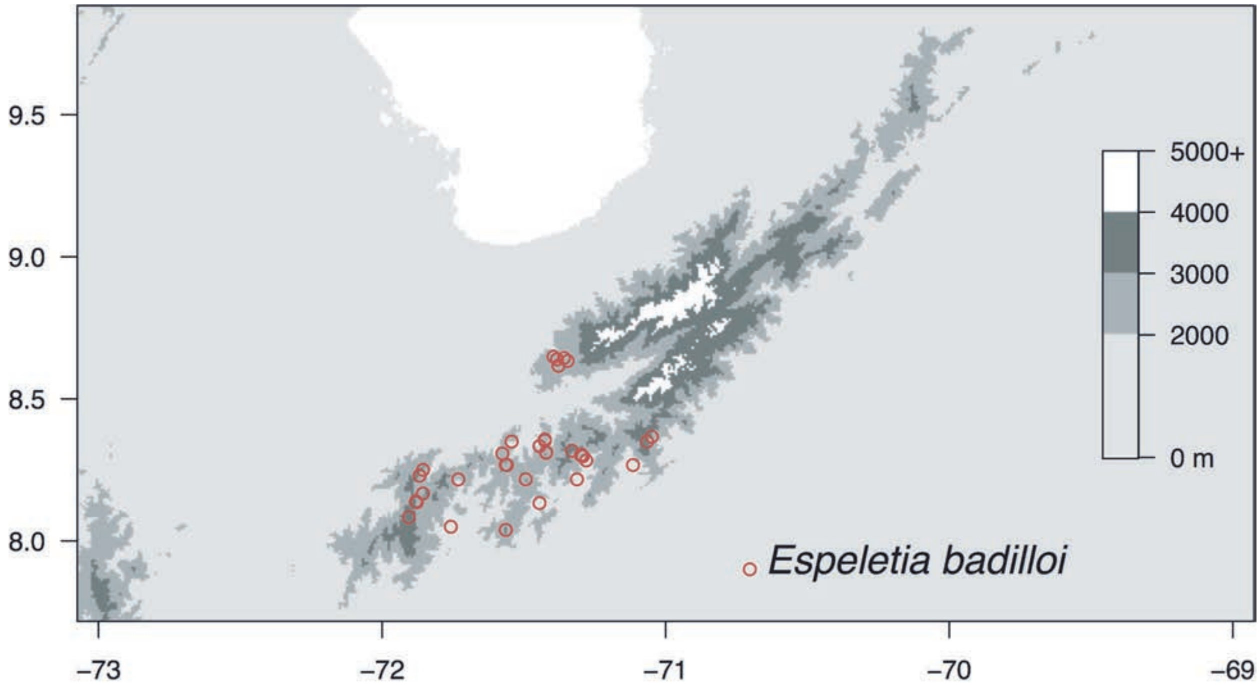

FIGURE 25. Distribution of *Espeletia badilloi* Cuatrec.

the identification of *E. badilloi* var. *pittieri* quite difficult. Besides, individuals with intermediate or mosaic characters are relatively common. More studies will be necessary to determine the validity of this taxon.

Distribution: VENEZUELA. Mérida-Táchira: forested hills in the southern end of Sierra Nevada de Mérida, in Páramo de las Coloradas (between Santa Cruz de Mora and El Molino), de Quirorá, de Guaraque, de la Negra, and del Batallón; Pico de Horma; hills above Pregonero; and El Portachuelo (La Grita). 2400–3200 m.a.s.l., usually found in gregarious populations in forest clearings and along trails/roads.

Additional specimens examined (selection): *J. Steyermark 56532* (F, NY, US), *L. Ruiz-Terán & M. López-Figueiras 9320* (US), *L. Ruiz-Terán & M. López-Figueiras 1468* (US), *L. Ruiz-Terán & M. López-Figueiras 541* (U, US).

7. *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd., Chlor. Andina: 67. 1855. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 10,000 pieds, Juin 1847, *N. Funck & L. J. Schlim 1550* (Holotype: P; Isotypes: BR, F, G, GH, LD, P). Fig. 26, 27.

Homotypic synonym: *Libanothamnus banksiifolius* (Sch. Bip. & Ettingsh. ex Wedd.) Cuatrec., Phytologia 35: 50. 1976.

The final epithet of this species was originally spelled “*banksiaefolia*.” According to ICN Art. 60.10, the correct spelling is “*banksiifolia*.” Also, collectors are given as “*V. A. Funck & L. J. Schlim*” in Diazgranados (2012: 35).

7.1. *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd. subsp. ***banksiifolia***

Tree size and architecture unknown. *Leaf* tubular sheath, pseudopetiolate (length 2.5–5.0 cm), adaxially glabrous, green, length 15–30 cm, width 4.5–6.5 cm, ratio 3.5–5.0:1, margins clearly dentate, teeth 0.5–1.0 mm long, 2–5 mm apart, secondary nerves parallel, 1–2 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, barely surpassing the surrounding leaves, length 18–30 cm, branched near the base. *Capitulum* diam. 18–22 mm, ligular circle 25–35 mm, disc 13–18 mm, ray ligules white. *Espeletia banksiifolia* can be distinguished from other tree species for its oblong leaves with dentate margins and sheaths adaxially barbate. Other trees occasionally show some teeth in their leaves, but with lower density and smaller size, and not as a consistent feature of the species.

Distribution: VENEZUELA. Mérida-Barinas: known only from the type collection, without precise locality.

Specimens examined: *N. Funck & L. J. Schlim 1550* (P, BR, F, G, GH, LD).

7.2. Espeletia banksiifolia Sch. Bip. & Ettingsh. ex Wedd. subsp. ***granatesiana*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Espeletia granatesiana* Cuatrec., Phytologia 27: 44. 1973a. TYPE: VENEZUELA. Mérida: Sierra de Santo Domingo, Páramo de Los Granates, Loma de Paja, 3100 m.a.s.l., 11 October 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28063* (Holotype: US; Isotypes: COL, F, MERF, U, US).

Homotypic synonyms: *Libanothamnus granatesianus* (Cuatrec.) Cuatrec., Phytologia 35: 50. 1976.

Libanothamnus banksiifolius Sch. Bip. & Ettingsh. ex Wedd. subsp. *granatesianus* Cuatrec., Mem. New York Bot. Gard. 107: 443. 2013.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, pseudopetiolate (length 2.5–6.0 cm), adaxially

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FIGURES 26–27. *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd. Páramo de los Granates, Mérida, Venezuela (Photographs by S. Aubert).

glabrous, green, length 20–40 cm, width 7.0–15.0 cm, ratio 2.0–3.5:1 (young individuals may have bigger leaves), margins clearly dentate, teeth 0.5–1.0 mm long, 2–6 mm apart, secondary nerves parallel, 1.5–3.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, surpassing the surrounding leaves, length 25–60 cm, width 15–30 cm, vegetative part with several alternate bracts, about half of total length. *Capitulum* diam. 10–12 mm, ligular circle 15–25 mm, disc 8–12 mm, ray ligules white or greenish-creamy. *Espeletia banksiifolia* subsp. *granatesiana* can be distinguished from other tree species for its leaves with dentate margins. It differs from the *E. banksiifolia* subsp. *banksiifolia* in its broader leaves (width > 7.0 cm) and its much smaller capitulum (diam. < 12 mm).

Distribution (Fig. 28): VENEZUELA. Mérida-Barinas: all along the eastern slopes of Sierra Nevada de Mérida, in Páramo de Don Pedro, Filo la Vagabunda (between El Morro and Aricagua), Las Lajas (Mucutuy), Los Aranguren, and Minungú (approx. 10 km E. of Tabay). Also found in Páramo de Los Granates in Sierra de Santo Domingo, and in Páramo de Guirigay. 2800–3200 m.a.s.l., in humid locations in the upper levels of the Andean forest below the timberline.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28063* (US, F, U), *M. López-Figueiras 21973* (U, US), *L. Ruiz-Terán & M. López-Figueiras 9393* (US), *L. Ruiz-Terán & M. López-Figueiras 9394* (US).

Cuatrecasas, *Ruiz-Terán & López-Figueiras 28063* in F should be labelled as isotype.

8. *Espeletia batata* Cuatrec., Phytologia 40: 27. 1978. TYPE: VENEZUELA. Mérida: Alto del Morato, Páramo de los Granates, Sierra Nevada de Santo Domingo, 3600 m.a.s.l., 10 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28058* (Holotype: US; Isotypes: F, MERF, US). Fig. 29–31.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate-lanuginose, white-cinereous, length 6.5–14.5 cm, width 0.8–2.0 cm, ratio 5–15:1, bases of secondary nerves parallel, 2–4 mm apart. *Inflorescence* lateral, simple, dichasial, monocephalous, length 25–55 cm, with 2–3 pairs of opposite bracts. *Capitulum* diam. 18–24 mm, ligular circle 30–40 mm, disc 12–15 mm, yellow ligules. *Espeletia batata* can be distinguished from other Venezuelan rosette plants with monocephalous inflorescences by its leaf sheaths densely barbate abaxially and its inflorescences with 2–3 pairs of opposite bracts (vs. 1, rarely 2 opposite basal pairs and 5–12 alternate in *E. ulotricha*). *Espeletia batata* also resembles some uncommon individuals of *E. weddellii* with monocephalous inflorescences, from which it can be distinguished by its broader leaves (0.8–2.0 cm vs. 0.3–1.0 cm), with oblong or spatulate shape (vs. linear) and covered by a lanate indumentum on both sides (vs. villous and subappressed adaxially).

Distribution: VENEZUELA. Mérida: Sierra de la Culata, Sierra Nevada de Mérida and Sierra de Santo Domingo. 3600–4300 m.a.s.l., in humid locations close to swamps and streams, also in seasonally humid places where some water can be retained within apparently dry rocky areas (Fig. 31).

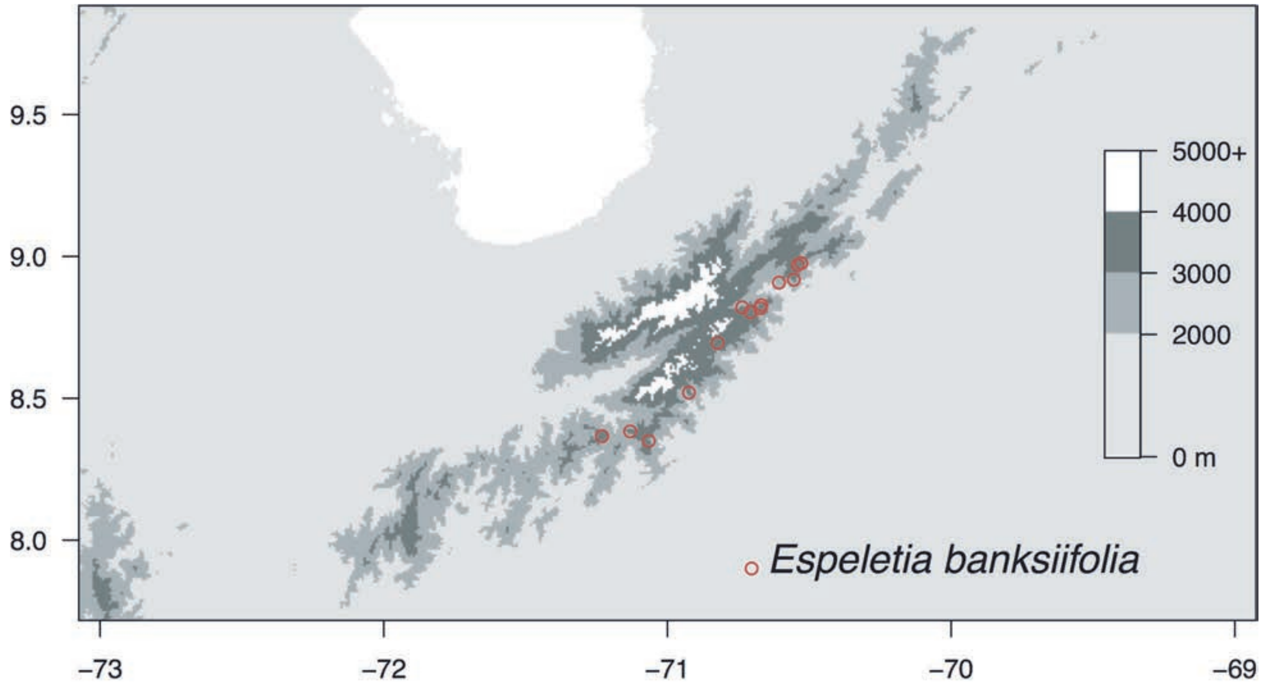
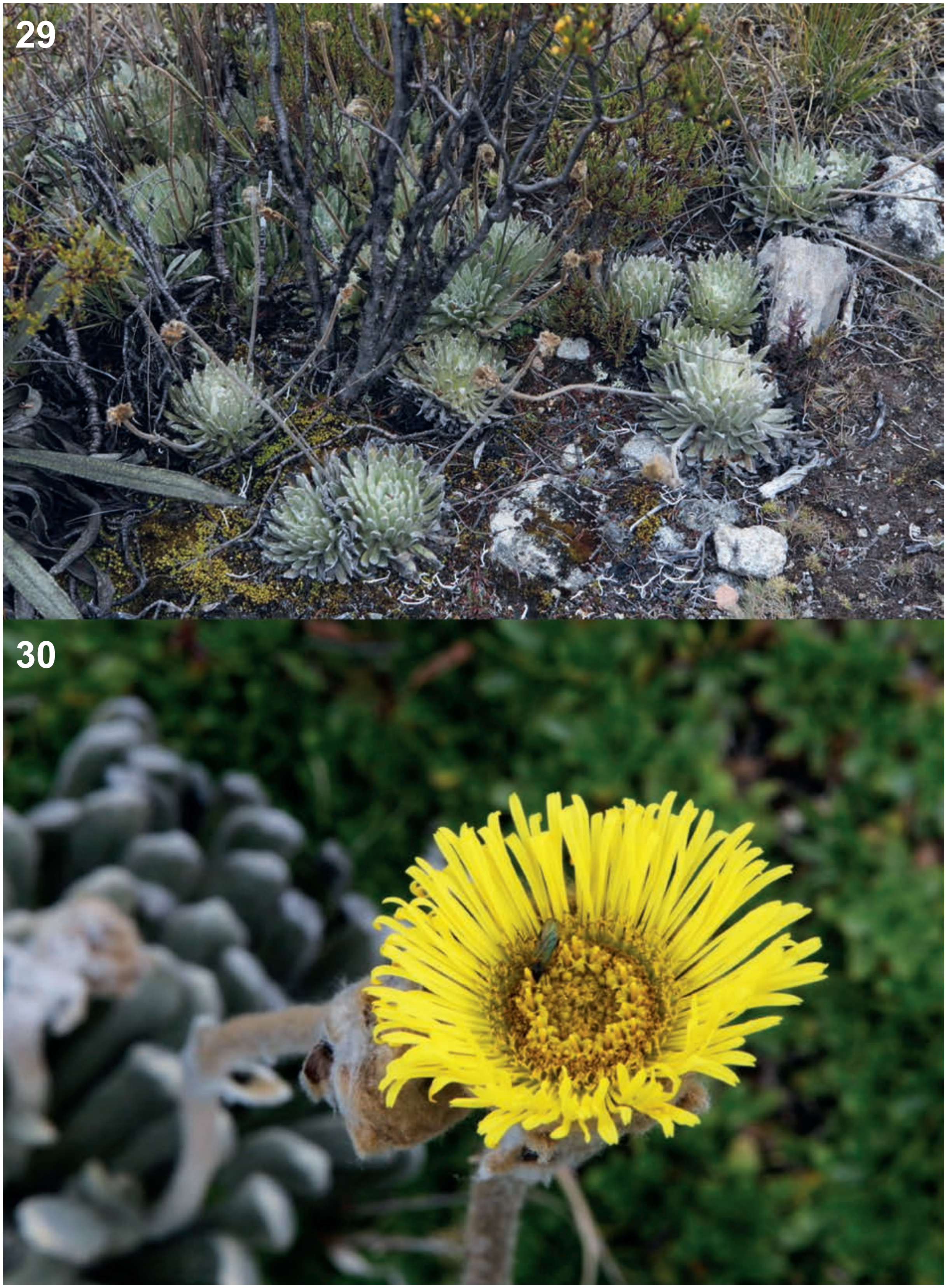


FIGURE 28. Distribution of *Espeletia banksiifolia* Sch. Bip. & Ettingsh. ex Wedd.



FIGURES 29–30. *Espeletia batata* Cuatrec. Páramo de Piedras Blancas, Mérida, Venezuela (Photographs by S. Aubert).

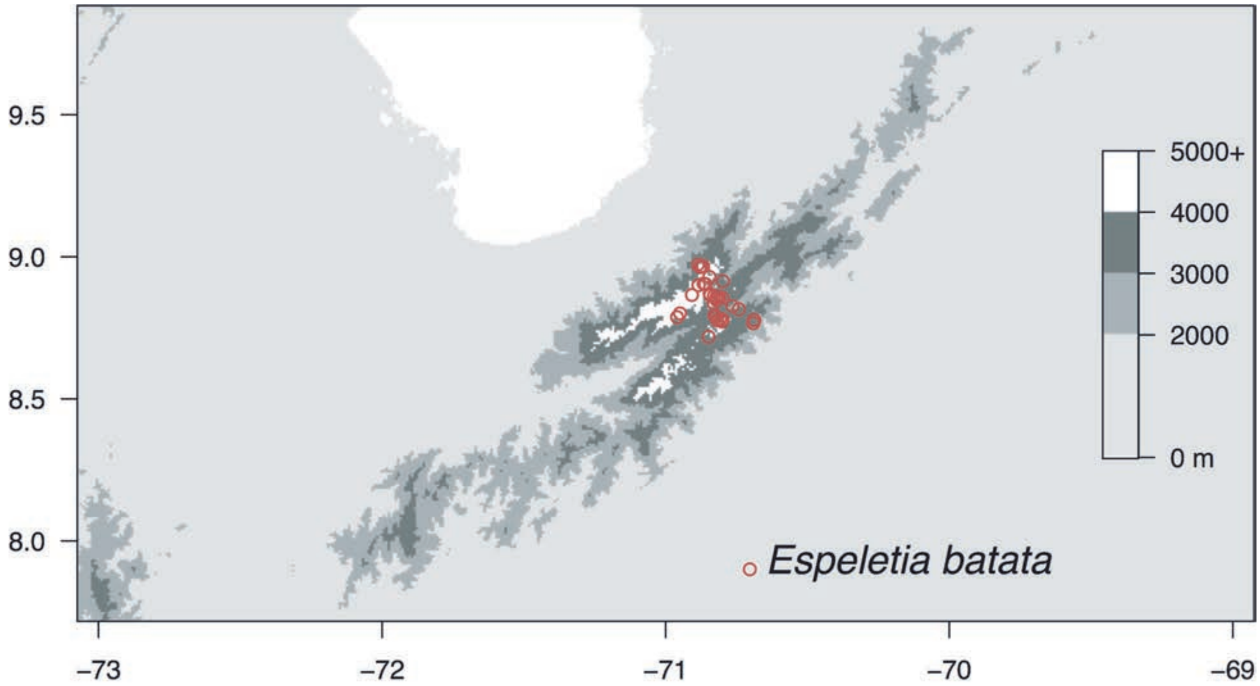


FIGURE 31. Distribution of *Espeletia batata* Cuatrec.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28058* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28081* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras*. *28036* (F, U, US), *P. Berry 3860* (US), *L. Ruiz-Terán & M. López-Figueiras 1071* (US).

Cuatrecasas, *Ruiz-Terán & López-Figueiras 28058* in F should be labelled as an isotype.

9. ***Espeletia bracteosa*** Standl., Amer. J. Bot. 2: 484. 1915. TYPE: VENEZUELA. Trujillo: Páramo de la Cristalina, 2900 m.a.s.l., 20 December 1910, *A. Jahn 156* (Holotype: US; Isotype: VEN [not seen]). Fig. 32–34.

Homotypic synonym: *Ruilopezia bracteosa* (Standl.) Cuatrec., Phytologia 35: 52. 1976.

Heterotypic synonyms: *Espeletia frailejonota* Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 284. 1959. TYPE: VENEZUELA. Trujillo: Páramo de Guirigay, hacia Laguna la Parida, 3400 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3576* (Holotype: VEN [not seen]; Isotypes: NY, US).

Ruilopezia frailejonota (Aristeg.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes branched at the base, sessile. *Leaf* open sheath, strongly pseudopetiolate (length 3–10 cm), adaxially glabrous, length 20–75 cm, width 2.0–10.0 cm, ratio 7–15:1, secondary nerves parallel, 4–12 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–200 cm, vegetative part copiously bracteate, about half of total length. *Capitulum* diam. 12–15 mm, ligular circle 20–30(35), disc 10–14 mm, ray ligules yellow. *Espeletia bracteosa* can be easily distinguished from other species by its monocarpic sessile rosette habit, strongly pseudopetiolate obate-elliptic leaves, and capitulum with yellow ray ligules.

Distribution: VENEZUELA. Trujillo: Páramo de la Cristalina, Filo la Cañada (4.5 km SW of Burbusay), and Páramo de Guirigay. Border Trujillo-Barinas: Páramo de Ortiz. Border Mérida-Trujillo: Páramo del Arenal (between Pueblo Llano and Tuñame). Usually 3000–3500 m.a.s.l., locally down to 2600 m.a.s.l., found in páramo habitat and relatively open subpáramos (Fig. 34).

Additional specimens examined (selection): *A. Jahn 156* (NY, US), *B. Stergios*, *L. Dorr & K. Wurdack 20582* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28173* (F, U, US), *López-Figueiras 13948* (US), *López-Figueiras & H. Rodríguez 8835* (US).

10. ***Espeletia bromelioides*** Cuatrec., Phytologia 29: 369. 1975. TYPE: VENEZUELA. Mérida: Potreros de San Rafael, Páramo de las Coloradas, Distrito Sucre, 2600 m.a.s.l., 18–20 July 1974, *M. López-Figueiras & H. Rodríguez 9054* (Holotype: US; Isotypes: F, MERF). Fig. 35–37.

Homotypic synonym: *Ruilopezia bromelioides* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes branched at the base, sessile. *Leaf* open sheath, sessile, adaxially glabrous, green, length 20–30 cm, width 1.2–2.5 cm, ratio 10–15:1, with 3–4 secondary basal nerves parallel to the costa. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–80 cm, vegetative part copiously bracteate, about half of total length. *Capitulum* diam. 7–13 mm, ligular circle shorter than the involucre,

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FIGURES 32–33. *Espeletia bracteosa* Standl. Páramo de Ortiz, Barinas-Trujillo, Venezuela (Photographs by S. Aubert).

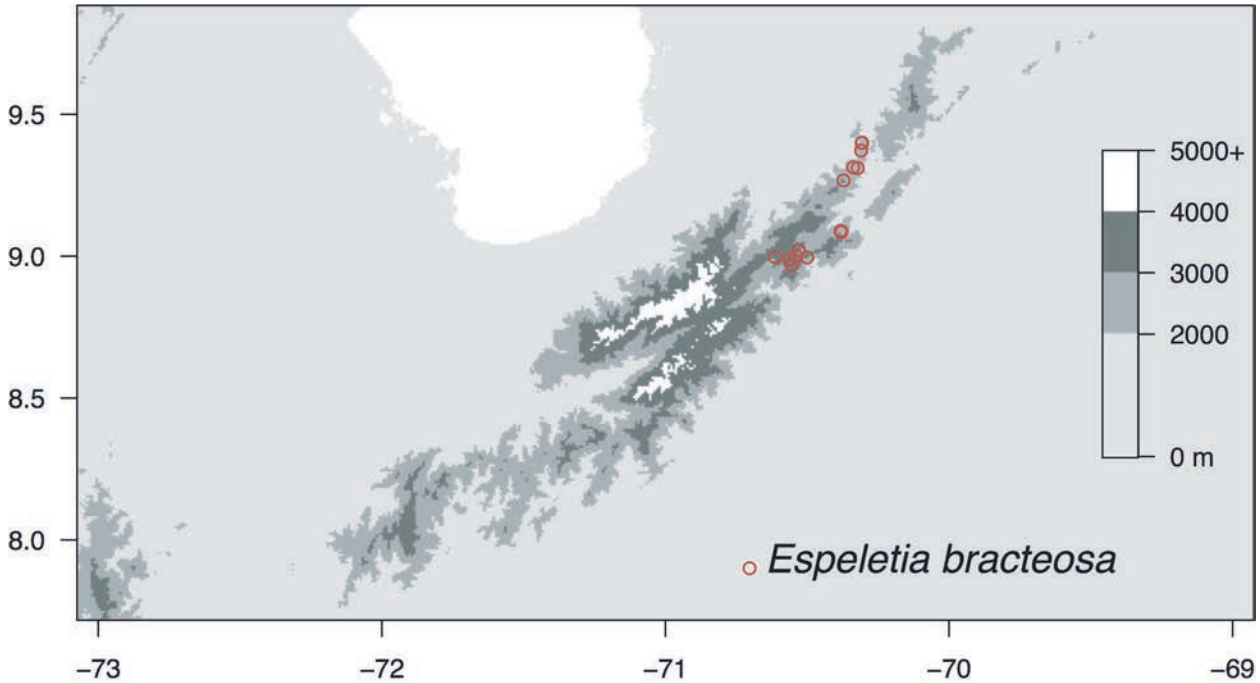

FIGURE 34. Distribution of *Espeletia bracteosa* Standl.

disc 5–10 mm, frequently eligulate or with very small yellowish/greenish ray ligules. *Espeletia bromelioides* can be easily distinguished from other species by its monocarpic short-branched sessile rosette habit, its linear-cuneate green leaves exhibiting longitudinally parallel basal nerves, its inflorescences with axis almost entirely covered by many erect bracts, and its eligulate or shortly-radiate capitulum.

Distribution: VENEZUELA. Mérida: known only from Páramo de las Coloradas, between Santa Cruz de Mora and El Molino. 2600–2900 m.a.s.l., in well drained and rather dry/rocky open subpáramo habitats (Fig. 37).

Additional specimens examined (selection): *M. López-Figueiras & H. Rodríguez 9054* (F, US), *M. López-Figueiras & H. Rodríguez 9042* (US), *M. López-Figueiras & H. Rodríguez 9044* (US), *M. López-Figueiras & L. Ruiz-Terán 14017* (US), *López-Figueiras & M. Keogh 9106* (US).

FIGURE 35. *Espeletia bromelioides* Cuatrec. Páramo de las Coloradas, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 36. *Espeletia bromelioides* Cuatrec. Páramo de las Coloradas, Mérida, Venezuela (Photograph by S. Aubert).

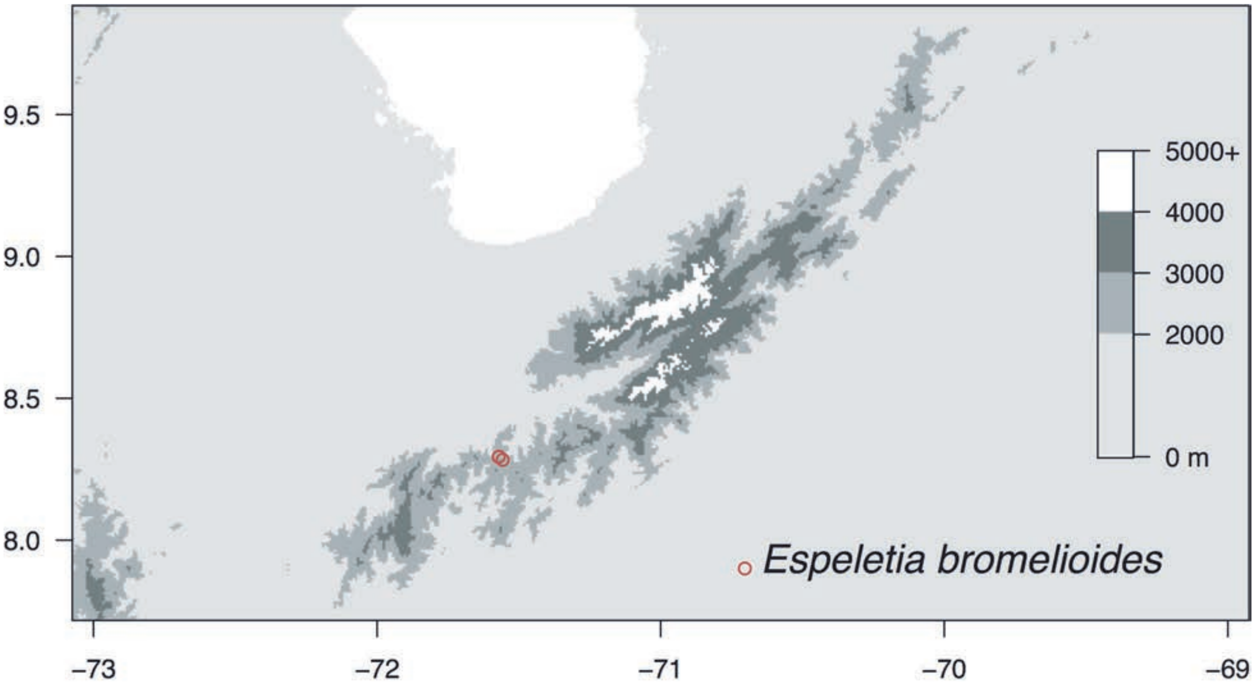

FIGURE 37. Distribution of *Espeletia bromelioides* Cuatrec.

11. *Espeletia cardonae* Cuatrec., Rev. Acad. Col. Ci. Exact. 5: 20. 1942. TYPE: VENEZUELA. Táchira: Páramo de Tamá, cabeceras del Río Oirá, 3100–3300 m.a.s.l., July 1939, *F. Cardona 304* (Holotype: VEN [not seen]; Isotypes: COL [fragment], F, US). Fig. 38–39.

Homotypic synonym: *Ruilopezia cardonae* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height usually up to 0.5 m, rarely up to 1.0 m, entirely covered by marcescent leaves and sheaths. *Leaf* open sheath, pseudopetiolate

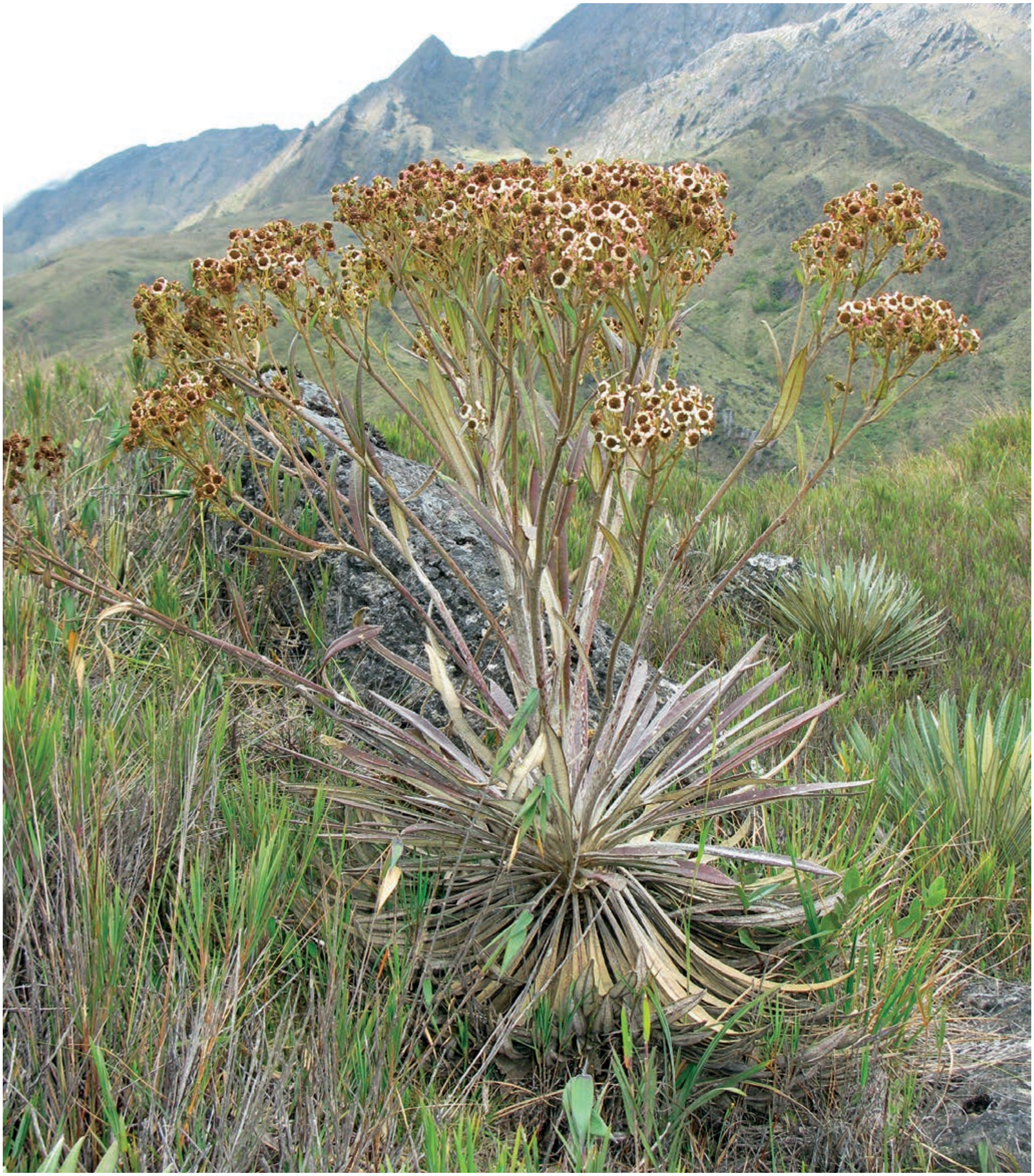

FIGURE 38. *Espeletia cardonae* Cuatrec. Páramo de Tamá, Norte de Santander, Colombia (Photograph by M. Diazgranados).

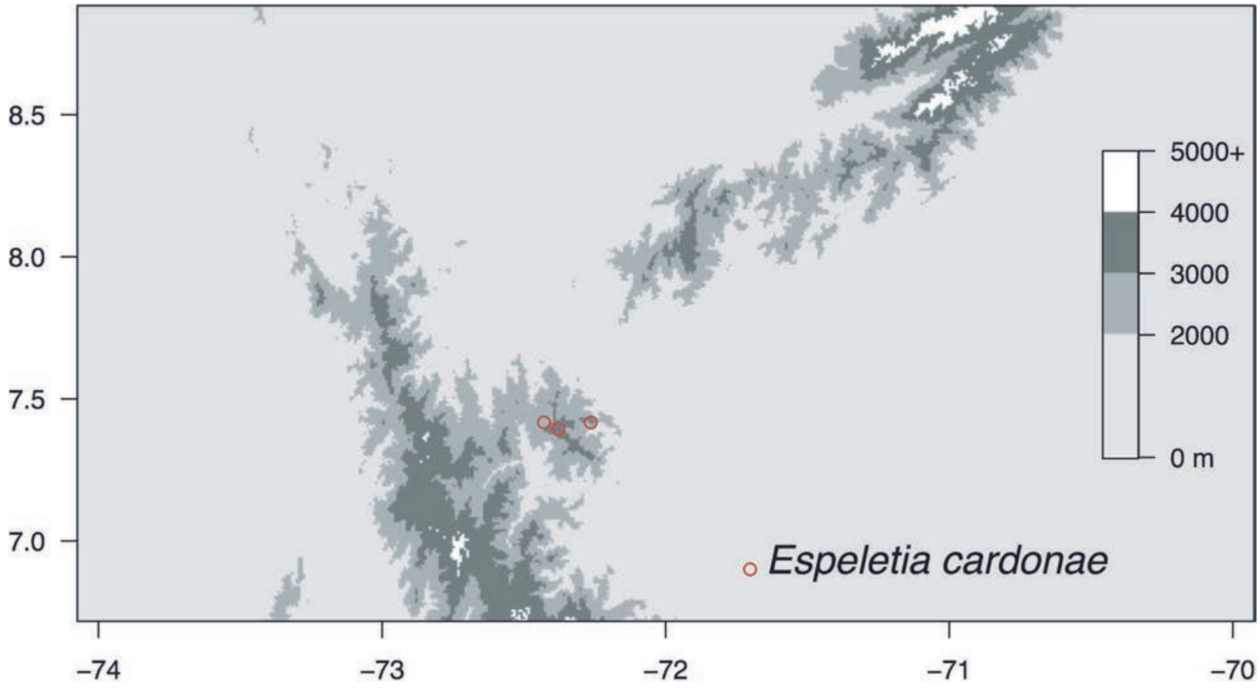

FIGURE 39. Distribution of *Espeletia cardonae* Cuatrec.

(length 5–8 cm), adaxially glabrous, green, length 25–50 cm, width 1.5–3.0 cm, ratio 15–20:1, secondary nerves parallel, 1.5–2.5 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–100 cm, branched near the base. *Capitulum* diam. 10–12 mm, ligular circle 20–25 mm, disc 8–11 mm, ray ligules white, turning pinkish/purplish with age according to Diazgranados (2012). *Espeletia cardonae* can be distinguished from other species by its unbranched caulescent monocarpic rosette habit, adaxially glabrous pseudopetiolate leaves, and capitulum with white ray ligules.

Distribution: VENEZUELA. Táchira: Páramo de Tamá, in the headwaters of Río Oirá, extending locally across the border with Colombia in Norte de Santander (Diazgranados, 2012: 46). 3100–3300 m.a.s.l., on well-drained slopes in subpáramo and grassy páramo habitats (Fig. 39).

Additional specimens examined (selection): *F. Cardona 304* (F, US), *Ruiz-Terán & M. López-Figueiras 8820* (US), *Ruiz-Terán & M. López-Figueiras 8820A* (US), *M. López-Figueiras 30238* (US).

12. *Espeletia chardonii* A.C. Sm., Bol. Soc. Ven. Ci. Nat. 7: 237. 1942. TYPE: VENEZUELA. Táchira: Páramo de Tamá, El Paramito, 2550 m.a.s.l., 15 August 1939, *C. E. Chardon 78* (Holotype: US; Isotypes: NY, VEN [not seen]). Fig. 40–42.

Homotypic synonym: *Tamania chardonii* (A.C. Sm.) Cuatrec., Phytologia 35: 53. 1976.

Heterotypic synonym: *Espeletia leporina* Cuatrec., Rev. Acad. Col. Ci. Exact. 5: 17. 1942. TYPE: COLOMBIA. Norte de Santander: Alto del Venado, between Samaria and Toledo, 2300–2400 m.a.s.l., 31 October 1941, *J. Cuatrecasas, R. E. Schultes & E. Smith 12813* (Holotype: COL; Isotypes: COL, F, GH, U, US).

Tree sparingly branched, sympodial branching giving pseudodichotomous aspect, height up to 10 m. *Leaf* open sheath, pseudopetiolate (length 1.0–4.0 cm), adaxially glabrous, green, length 12–30 cm, width 4.0–12.0 cm, ratio 3.2–5.2:1, bases of secondary nerves parallel, 4–6(8) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, largely surpassing the surrounding leaves, length 30–80 cm, vegetative part about half of total length, usually with 1–3 bracts. *Capitulum* diam. 7–10(11) mm, ligular circle 12–18 mm, disc 6–8 mm, ray ligules yellow, turning orange or reddish when old. *Espeletia chardonii* is a unique species that can be easily distinguished by its pseudodichotomous tree habit and leaves with open sheaths.

Distribution: VENEZUELA. Táchira: Páramo de Tamá. COLOMBIA. Norte de Santander: Southern slopes of Páramo de Tama around Margua valley. Santander: Cordillera (or Cuchilla) de Los Cobardes, area known as El Picacho, near Galán. 2200–3000 m.a.s.l., in the upper level of the Andean forest, particularly in climatically wet areas (Fig. 42).

Additional specimens examined (selection): *C. E. Chardon 78* (NY, US), *J. Cuatrecasas, R. E. Schultes & E. Smith 12813* (COL, F, GH, U, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28375* (F, US), *J. Cuatrecasas, L. Ruiz-Terán & J. Araque-Molina 28247* (F, U, US), *S. Díaz-Piedrahita 89* (US), *S. Díaz-Piedrahita 95* (US).

Isotype at NY labelled as "A. Escalona (Chardon 78), Aug. 25, 1939."

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Figures 40–41. *Espeletia chardonii* A.C. Sm. Páramo de Tamá, Táchira, Venezuela (Photographs by S. Aubert).

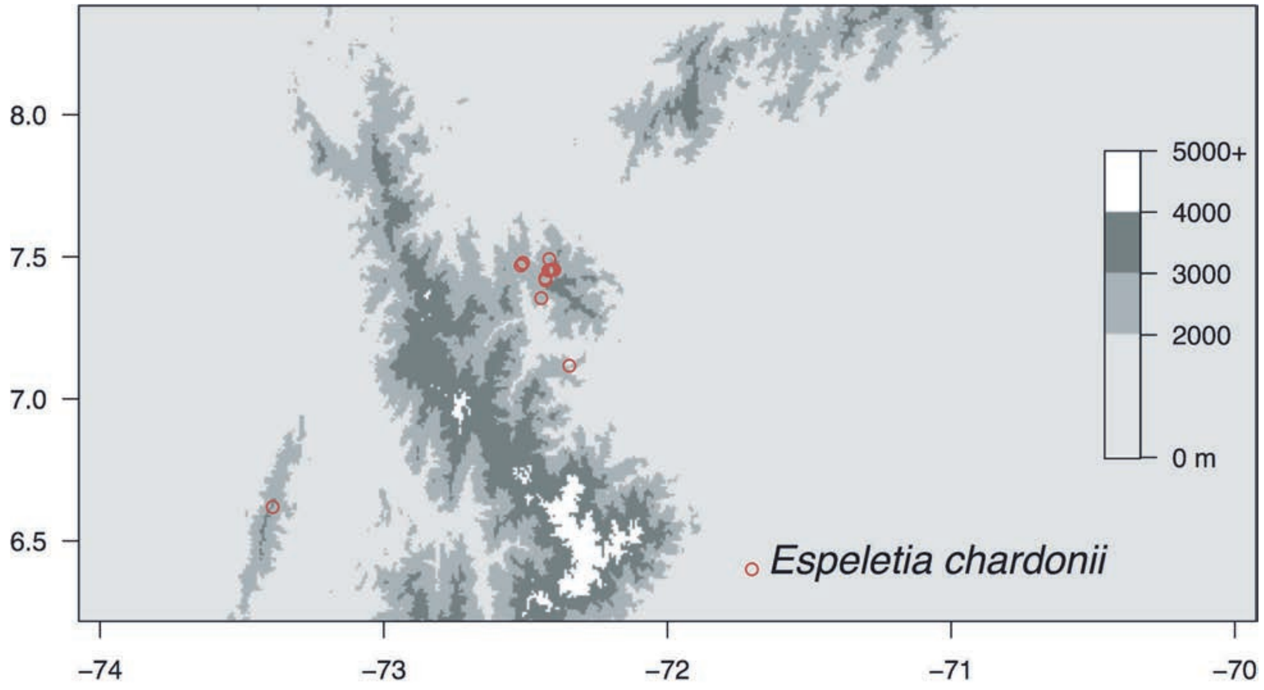

FIGURE 42. Distribution of *Espeletia chardonii* A.C. Sm.

13. *Espeletia cuatrecasasii* Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes. 14: 5. 1974. TYPE: VENEZUELA. Mérida: Laguna Tapada, antes del Portachuelo, junto a la carretera entre El Morro y Aricagua, Distrito Libertador, 2630 m.a.s.l., 9 June 1973, *L. Ruiz-Terán & M. López-Figueiras 8738* (Holotype: MERF; Isotype: US). Fig. 43–45. Homotypic synonym: *Ruilopezia cuatrecasasii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 8 m, mostly naked, with marcescent leaves only below the rosette. *Leaf* open sheath, sessile, usually auriculate-amplectant above sheaths, adaxially glabrous or loosely hirsute, green, length 25–60 cm, width 4.5–10.0 cm, ratio 5–6:1, margins dentate, teeth 3–6 mm apart, bases of secondary nerves parallel, 3–8 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 35–70 cm, branched near the base, branches and sheaths of bracts reddish-purplish. *Capitulum* outer phyllaries herbaceous, diam. 12–18 mm, ligular circle 24–35 mm, disc 11–13 mm, rose, reddish or purplish ray ligules. *Espeletia cuatrecasasii* can be distinguished from other species for its tall caulescent monocarpic rosette habit, sessile green leaves with small length-to-width ratio (< 7:1) and capitula with herbaceous outer phyllaries and rose, reddish, purplish ray ligules. *Espeletia cuatrecasasii* resembles *E. marcescens*, but besides the numerous color differences, *E. cuatrecasasii* has leaf bases more prominently auriculate, lower density of secondary nerves (4–8 mm vs. 2–5 mm apart), smaller deviation angles (60–65° vs. 70–90°), smaller capitulum diam. (< 18 mm vs. > 20 mm), and shorter ray corollas (7–9 mm vs. 12–17 mm).

Distribution: VENEZUELA. Mérida: known only from Páramo de Aricagua and the western slopes of Páramo de Don Pedro. 2500–3000 m.a.s.l., found in very humid clearings and stream margins in the upper level of the Andean forest (Fig. 45).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 8738* (US), *M. López-Figueiras & C. Torres 13926* (U), *M. López-Figueiras 12581* (US), *V. M. Badillo 6538* (US).

14. Espeletia divisoriensis (Cuatrec.) Mavárez, *comb. nov.* Basionym: *Libanothamnus divisoriensis* Cuatrec., Phytologia 47: 1. 1980b. TYPE: VENEZUELA. Zulia: Environs of "Campamento Frontera II" (10°00'13"N, 72°58'25"W), mesa below international boundary on main ridge, headwaters of Río Negro, Sierra de Perijá, Serranía de los Motilones, 3000 m.a.s.l., 27 June to 5 July 1974, *S. Tillett & W. Hönig 746–746* (Holotype: US; Isotypes: MY, US, VEN [not seen]). Fig. 46–47.

Tree profusely branched, height up to 5 m. *Leaf* tubular sheath, pseudopetiolate (length 1.0–3.0 cm), adaxially glabrous, green, length 20–35 cm, width 5.0–8.0 cm, ratio 3.5–5.0:1, secondary nerves parallel, 2–4 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, surpassing the surrounding leaves, length 30–50 cm, branched near the base. *Capitulum* diam. 8–11 mm, ligular circle 14–21 mm, disc 8–10 mm, ray ligules white or cream. *Espeletia divisoriensis* can be distinguished from other tree species for its pseudopetiolate leaves with sheaths adaxially glabrous, densely packed secondary nerves (< 4 mm apart) and small capitula (diam. < 12 mm).

Distribution: VENEZUELA-COLOMBIA border. Sierra de Perijá. 3200–3600 m.a.s.l., at the timberline or right below in the upper level of the Andean forest (Fig. 47).

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FIGURES 43–44. *Espeletia cuatrecasasii* Ruiz-Terán & López-Fig. Páramo de Don Pedro, Mérida, Venezuela (Photographs by S. Aubert).

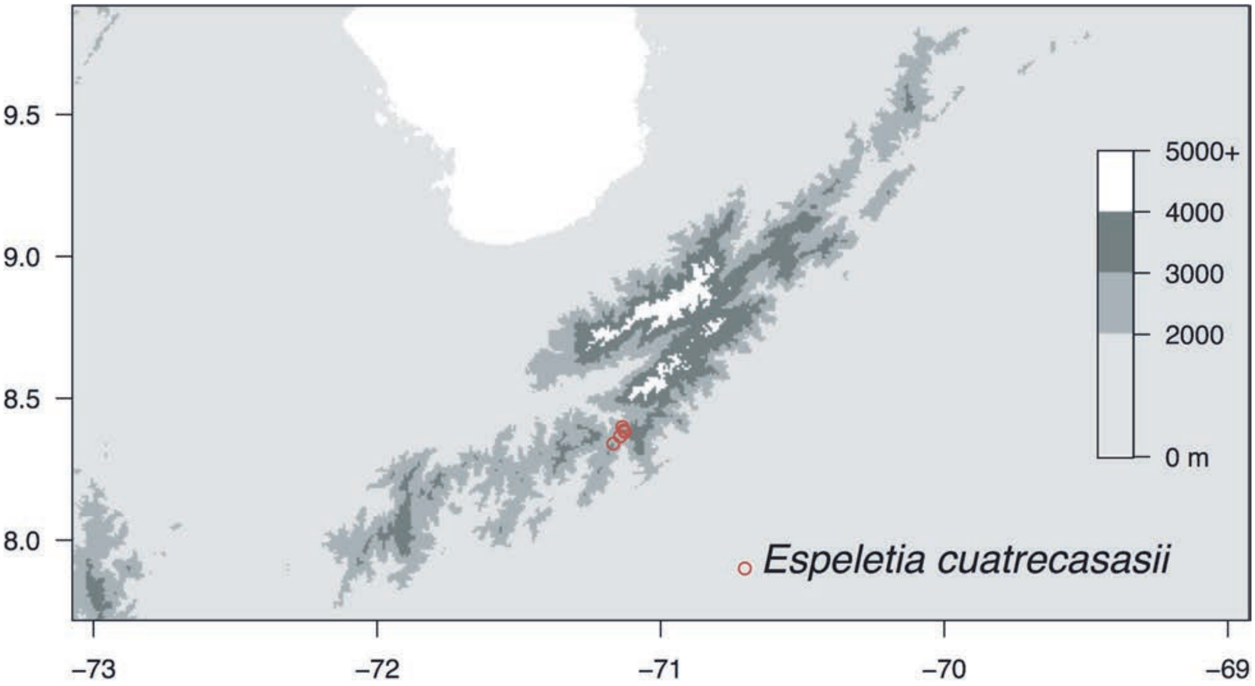

FIGURE 45. Distribution of *Espeletia cuatrecasasii* Ruiz-Terán & López-Fig.

FIGURE 46. *Espeletia divisoriensis* (Cuatrec.) Mavárez. Páramo de Sabana Rubia, Cesar, Colombia (Photograph by J. O. Rangel).

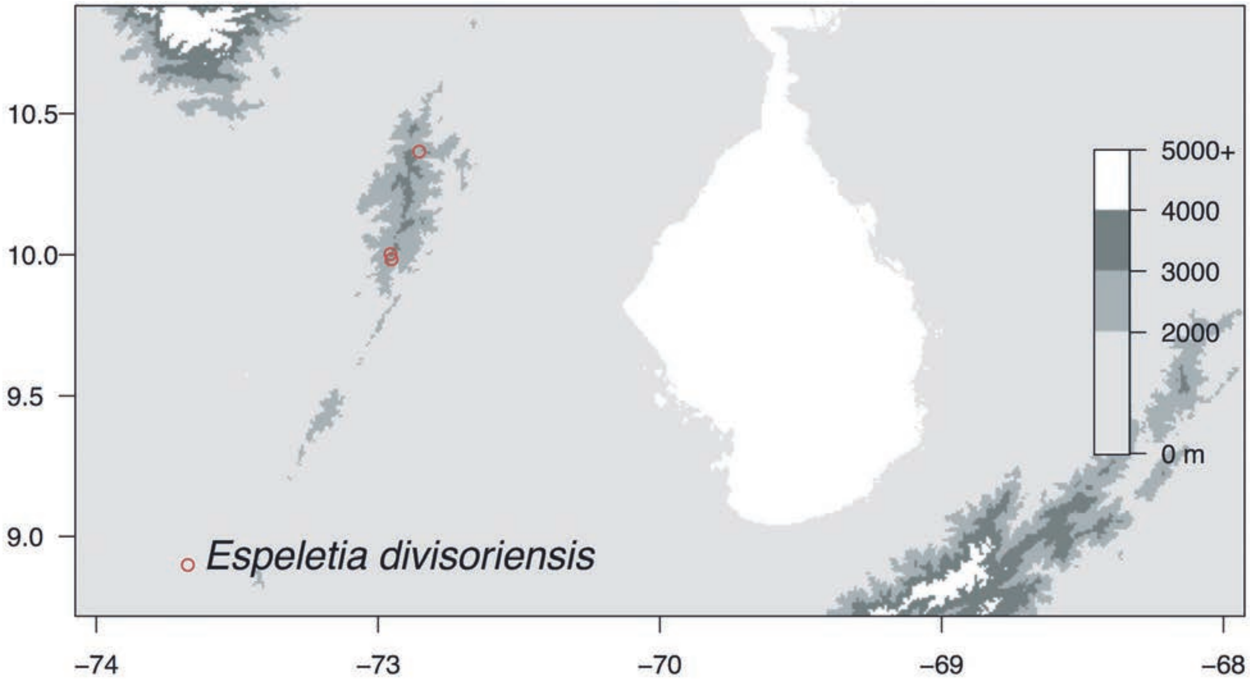

FIGURE 47. Distribution of *Espeletia divisoriensis* (Cuatrec.) Mavárez.

Additional specimens examined (selection): *S. Tillett & W. Hönig 746–746* (US), *S. Tillett & W. Hönig 747-921* (US), *M. L. Grant 10965* (US), *O. Rangel-Ch. 13706* (US), *O. Rangel-Ch 13616* (US).

15. *Espeletia elongata* A.C. Sm., Amer. J. Bot. 27: 546. 1940. TYPE: VENEZUELA. Mérida: Páramo de los Conejos, 13,000 ft, 10 September 1938, *J. Hanbury-Tracy 83* (Holotype: NY; Isotype: K). Fig. 48–50.
Homotypic synonym: *Coespeletia elongata* (A.C. Sm.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, caulescent, stem height up to 2.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, pseudopetiolate (length 5–10 cm), adaxially densely pubescent, lanate-lanuginose, length 50–70 cm, width 3.5–5.0 cm, ratio 9–18:1, secondary nerves parallel, 5–7 mm apart. *Inflorescence* lateral, compound, primary branching monochasial, botryoid-paniculate, axes 75–110 cm, 30–60 peduncles, proximal polycephalous (3–5 capitula), vegetative part with 3–5 alternate bracts. *Capitulum* diam. 15–25 mm, ligular circle about the same size or slightly shorter than the involucre, disc 14–15 mm, ray ligules bright yellow. *Espeletia elongata* can be distinguished from all other Venezuelan rosette plants for its caulescent and entirely marcescent polycarpic rosette habit, its pseudopetiolate leaves, and its botryoid-paniculate inflorescences with large number of peduncles (30–60), the proximal ones polycephalous.

Distribution: VENEZUELA. Mérida: páramos in Sierra de la Culata. Between 3200–3500 m.a.s.l., especially in humid locations (Fig. 50).

Additional specimens examined (selection): *J. Hanbury-Tracy 83* (K, NY), *P. Berry & R. Calvo 4395* (US), *López-Figueiras 23698* (US), *López-Figueiras 23699* (US), *L. Ruiz-Terán & J. Dugarte 12418* (US).

Collection year given as “1983” in Diazgranados (2012: 7) and Cuatrecasas (2013: 603).

16. Espeletia emmanuelis (Cuatrec.) Mavárez, *comb. nov.*
Basionym: *Ruilopezia emmanuelis* Cuatrec., Phytologia 61: 56. 1986a. TYPE: VENEZUELA. Trujillo: Páramo de las Rosas, en las lajas de Barro Amarillo, 2900–3000 m.a.s.l., 8 March 1985, *M. López-Figueiras & D. Griffin 32405* (Holotype: US; Isotypes: F, G, K, MERF, NY, US). Fig. 51–52.

Rosette monocarpic, caulescent, stem height up to 1.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, pseudopetiolate (length 1–4 cm), adaxially pubescent, villous-velvety, length 35–50 cm, width 3.5–5.5 cm, ratio 9–10:1, secondary nerves parallel, 5–8 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–70 cm, branched near the base. *Capitulum* diam. 10–12 mm, ligular circle 20–25 mm, disc 9–10 mm, ray ligules yellow. *Espeletia emmanuelis* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit with pseudopetiolate leaves and its capitulum with yellow ray ligules.

Distribution: VENEZUELA. Border Lara-Trujillo: páramos in the northern end of the Cordillera de Mérida: Páramo de Los Nepes, de la Nariz, de las Rosas, de Cendé, and del Turmal. 2800–3100 m.a.s.l., usually in flat and rather humid locations within subpáramo habitats (Fig. 52).

Additional specimens examined (selection): *M. López-Figueiras & D. Griffin 32405* (F, G, K, NY, US), *M. López-Figueiras & H. Rodríguez 26234* (US), *M. López-Figueiras 32490* (US), *R. Riina*, *R. Duno*, *R. Ghinaglia & R. Gonto 729* (US).

Distribution given as on the border Trujillo-Barinas in Cuatrecasas (2013: 555).

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FIGURES 48–49. *Espeletia elongata* A.C. Sm. Páramo de la Culata, Mérida, Venezuela (Photographs by S. Aubert).

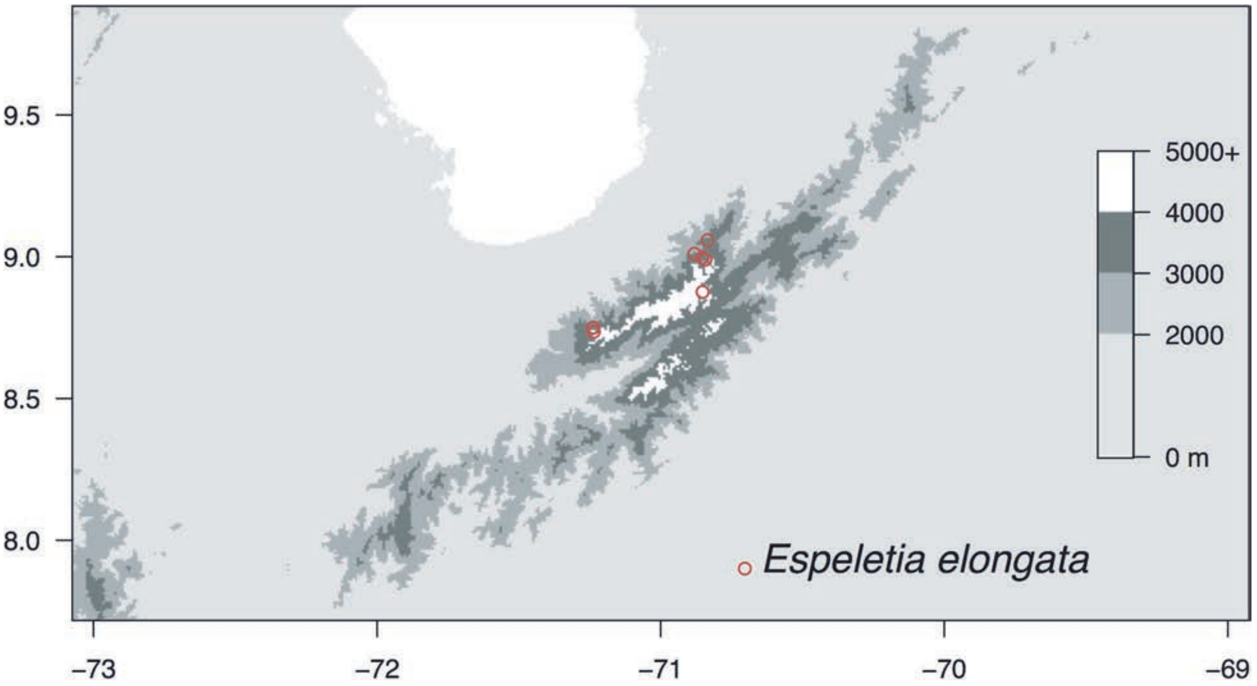

FIGURE 50. Distribution of *Espeletia elongata* A.C. Sm.

FIGURE 51. *Espeletia emmanuelis* (Cuatrec.) Mavárez. Páramo de los Nepes, Lara-Trujillo, Venezuela (Photograph by M. Quiroga).

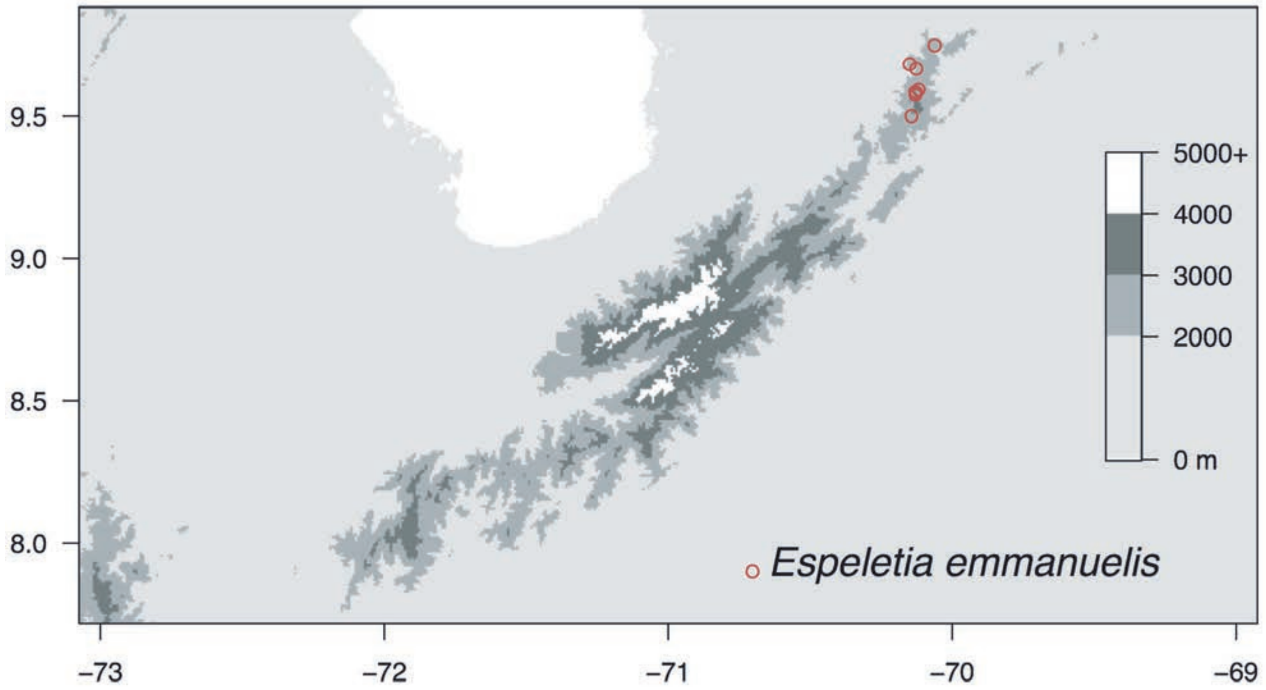

FIGURE 52. Distribution of *Espeletia emmanuelis* (Cuatrec.) Mavárez.

17. ***Espeletia figueirasii*** Cuatrec., Phytologia 20: 475. 1971. TYPE: VENEZUELA. Mérida: Sierra Nevada de Santo Domingo, Páramo de los Granates, Loma de Paja, las Escaleras, 3240 m.a.s.l., 11 October 1969, *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28068* (Holotype: US; Isotypes: F, IVIC, MERF, U, US). Fig. 53–56.

Homotypic synonym: *Ruilopezia figueirasii* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 2.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially glabrous, green, length 25–40 cm, width 0.7–2.5 cm, ratio 20–30:1, apex with a sharp teeth, 1.0–2.0 mm long, secondary nerves obsolete. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 100–250 cm, vegetative part profusely bracteate, about a third of total length. *Capitulum* diam. 12–22 mm, eligulate. *Espeletia figueirasii* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit with long, sessile, flexible, green leaves and its eligulate semiglobose capitulum.

Distribution: VENEZUELA. Mérida: slopes of Sierra Nevada de Santo Domingo, Páramo de Los Granates and Páramo de Guirigay, Sierra de la Culata in the slopes above Piñango, Páramo de la Sal, and Páramo de Palmira. 2800–3000 m.a.s.l., in the upper level of the Andean forest below the timberline (Fig. 56).

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28068* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28619* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28620* (F, U, US), *L. Dorr & L. Barnett 5597* (US), *L. Ruiz-Terán 6449* (F, U, US).

18. ***Espeletia floccosa*** Standl., Amer. J. Bot. 2: 481. 1915. TYPE: VENEZUELA. Mérida: Páramo de Timotes, 3300–4000 m.a.s.l., and Sierra Nevada de Mérida, 4000 m.a.s.l., October 1910, *A. Jahn 154* (Holotype: US). Fig. 57–59.

Homotypic synonym: *Ruilopezia floccosa* (Standl.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sometimes branched at the base, sessile. *Leaf* open sheath, sessile, adaxially pubescent, silvery-sericeous, length 25–30 cm, width 1.5–2.5 cm, ratio 15–20:1, secondary nerves almost obsolete, 2–4 mm apart when present. *Inflorescence* terminal, compound, primary branching monochasial, multiple branches spreading radially from the base, each one botryoid-paniculate or corymboid-paniculate with length 50–120 cm, proximal part about half of the branch's total length, with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle 40–50 mm, disc 13–17 mm, ray ligules yellow. *Espeletia floccosa* can be distinguished from other species for its sessile monocarpic rosette habit with densely pubescent silvery-sericeous leaves, its inflorescences with extremely short or no central axis, and its large yellow-rayed capitulum.

Distribution: VENEZUELA. Mérida: widespread in páramos of Sierra de la Culata (e.g., Mucuchíes, Piedras Blancas, Piñango, Timotes), and through the Nudo de Apartaderos to the páramos in the Sierra Nevada de Santo Domingo (e.g., Gavidia, Laguna de Mucubají, Laguna Negra, and Laguna Victoria). Trujillo: Páramo de Teta de Niquitao, de Cabimbú, and de Tuñame. 3200–4000 m.a.s.l., in open and humid páramos (Fig. 59).

Additional specimens examined (selection): *A. Jahn 154* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28110* (F, U, US), *L. Ruiz-Terán & M. López-*

FIGURES 53–55. *Espeletia figueirasii* Cuatrec. **53**. Piñango, Mérida, Venezuela (Photograph by S. Aubert). **54–55**. Páramo de los Granates, Mérida, Venezuela (Photographs by S. Aubert).

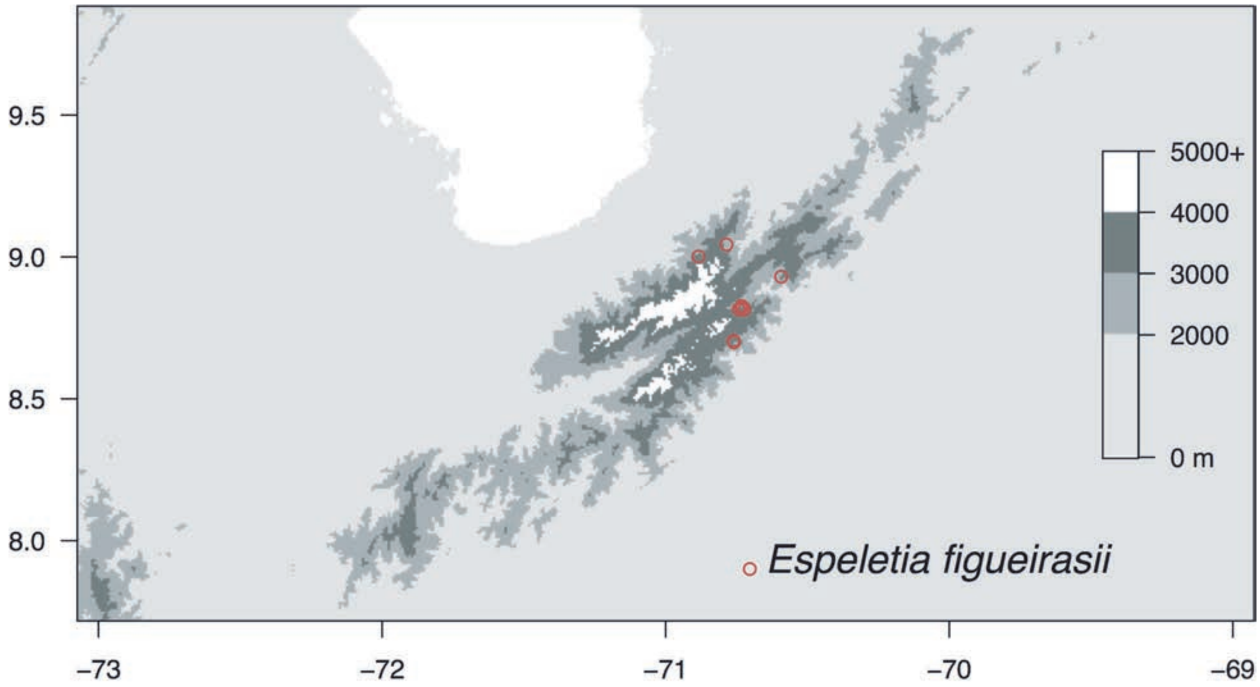

FIGURE 56. Distribution of *Espeletia figueirasii* Cuatrec.

FIGURES 57. *Espeletia floccosa* Standl. Laguna de Mucubají, Mérida, Venezuela (Photograph by S. Aubert).

FIGURES 58. *Espeletia floccosa* Standl. Laguna de Mucubají, Mérida, Venezuela (Photograph by S. Aubert).

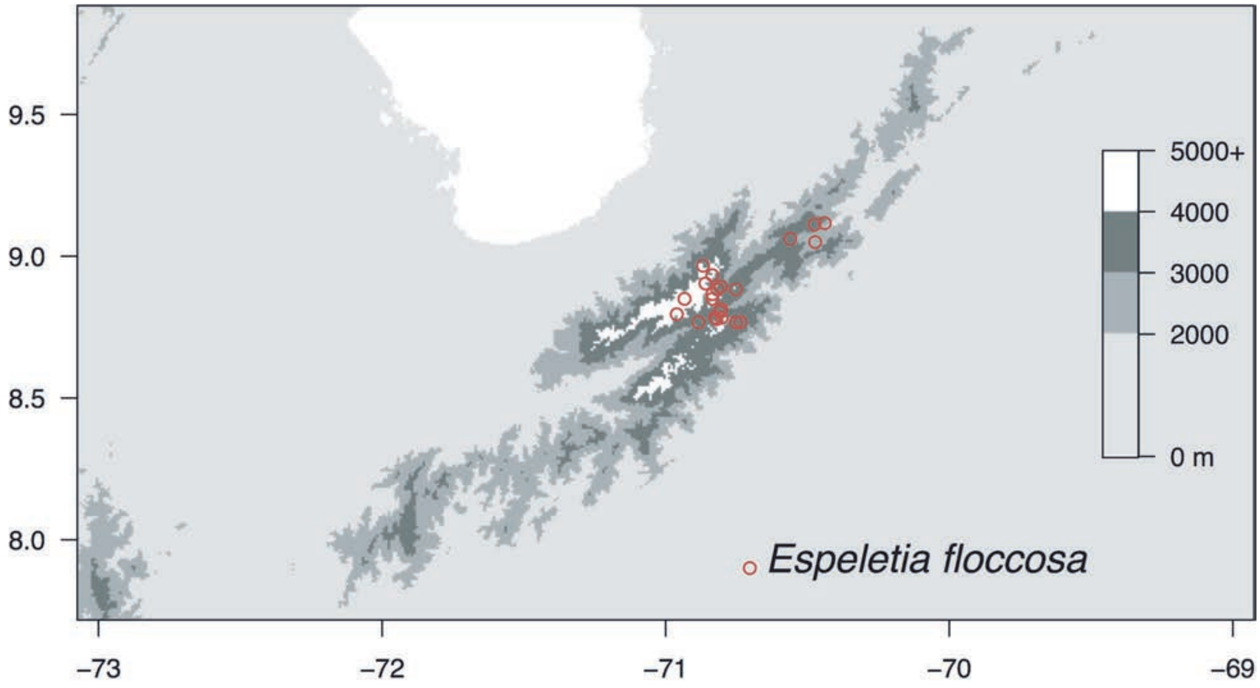

FIGURE 59. Distribution of *Espeletia floccosa* Standl.

FIGURES 60–61. *Espeletia griffinii* Ruiz-Terán & López-Fig. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

Figueiras 371 (US), *L. Ruiz-Terán & M. López-Figueiras 184* (U, US), *L. Ruiz-Terán & M. López-Figueiras 2218* (US).

As noted by Cuatrecasas (2013: 565), the locality "Páramo del Jabón" and the description "white flowers" in *Jahn 154* are certainly confusions with *E. jabonensis* and *E. pannosa*, two species that also have sessile rosette habit and long linear leaves covered with silvery-sericeous indumentum. The type locality of *E. floccosa* should be Páramo de Timotes and Sierra Nevada de Mérida.

19. ***Espeletia griffinii*** Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes 17: 27. 1976. TYPE: VENEZUELA. Trujillo: Páramo de Guaramacal, aprox. 15 km E. de Boconó, 2600 m.a.s.l., 9 August 1975, *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12606* (Holotype: MERF; Isotype: US). Fig. 60–62.

Homotypic synonym: *Libanothamnus griffinii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 50. 1976.

Shrub or *small tree* profusely branched, height up to 4 m. *Leaf* tubular sheath, pseudopetiolate (length 1.0–3.0 cm), adaxially glabrous, green, length 7–15 cm, width 2.5–4.5 cm, ratio 2.5–3.5:1, secondary nerves parallel, 1–2(3) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, largely surpassing the surrounding leaves, length 10–20 cm, branched near the base. *Capitulum* diam. 10–12(13) mm, ligular circle 15–20 mm, disc 8–12 mm, ray ligules white or cream. *Espeletia griffinii* can be distinguished from other tree species by its distinctly pseudopetiolate small leaves (< 15 cm). Only two other tree taxa have leaves with somewhat similar lengths, but they have either a sessile outline (*E. parvula*) or short pseudopetioles < 1 cm long and a capitulum diam. < 10 mm (*E. neriifolia* var. *cristamontis*).

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal. 2600–3100 m.a.s.l., above the timberline in shrubby subpáramo habitat (Fig. 62).

Additional specimens examined (selection): *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12606* (US), *H. Werff & F. Ortega 6081* (US), *J. Cuatrecasas & L. Ruiz-Terán 28811* (F, U, US), *L. Ruiz-Terán & J. Dugarte 12771* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2643* (US).

Collectors and date given as "*L. Ruiz-Terán*, *M. López-Figueiras & D. Griffin*" (*N. Griffin* missing) and "3 August 1975" in Diazgranados (2012: 35) and Cuatrecasas (2013: 446).

20. ***Espeletia grisea*** Standl., Amer. J. Bot. 2: 477. 1915. TYPE: VENEZUELA. Mérida: Chorro Blanco, Sierra Nevada de Mérida, 3000–4000 m.a.s.l., January 1911, *A. Jahn 157* (Holotype: US). Fig. 63–65.

Homotypic synonym: *Ruilopezia grisea* (Standl.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially loosely hirsute, green aspect, length 20–35 cm, width 1.0–2.5 cm, ratio 12–15:1, secondary nerves parallel, 1.5–3.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–120 cm, branched near the base. *Capitulum* diam. 12–15 mm, ligular circle 15–22 mm, disc 11–14 mm, ray ligules short and white. *Espeletia grisea* can be distinguished from other species for its caulescent-marcescent monocarpic rosette habit, its sessile

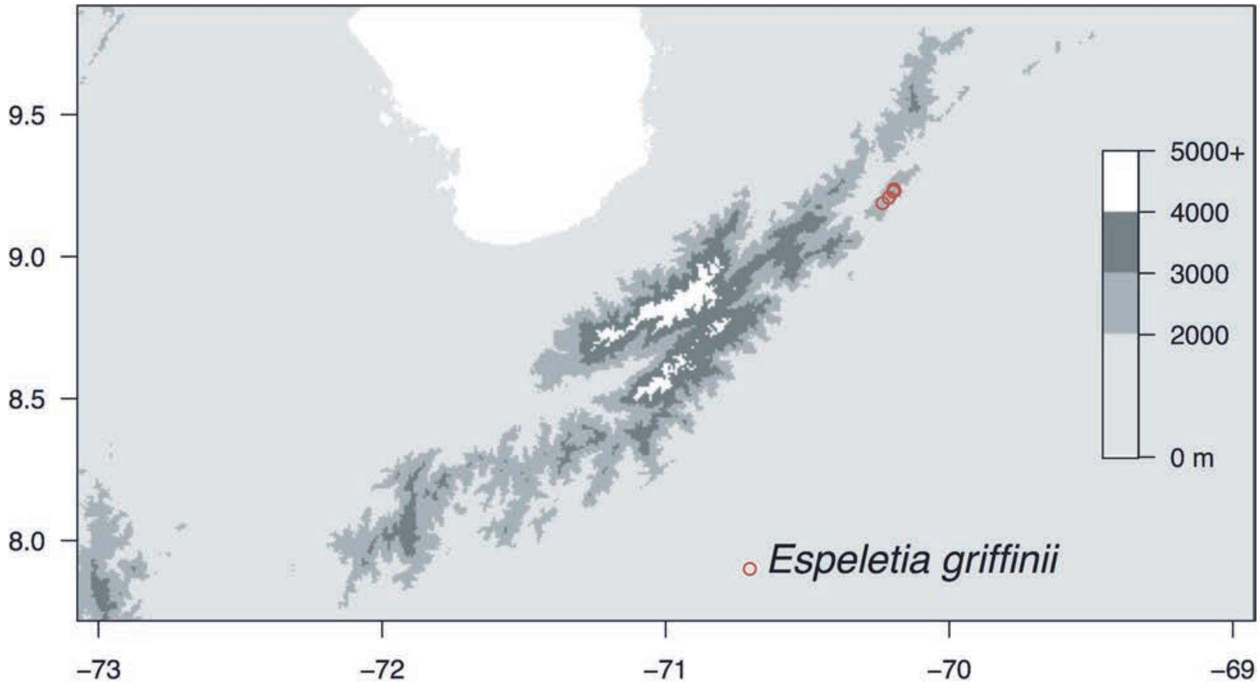

FIGURE 62. Distribution of *Espeletia griffinii* Ruiz-Terán & López-Fig.

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FIGURES 63–64. *Espeletia grisea* Standl. Páramo de los Nevados, Mérida, Venezuela (Photographs by S. Aubert).

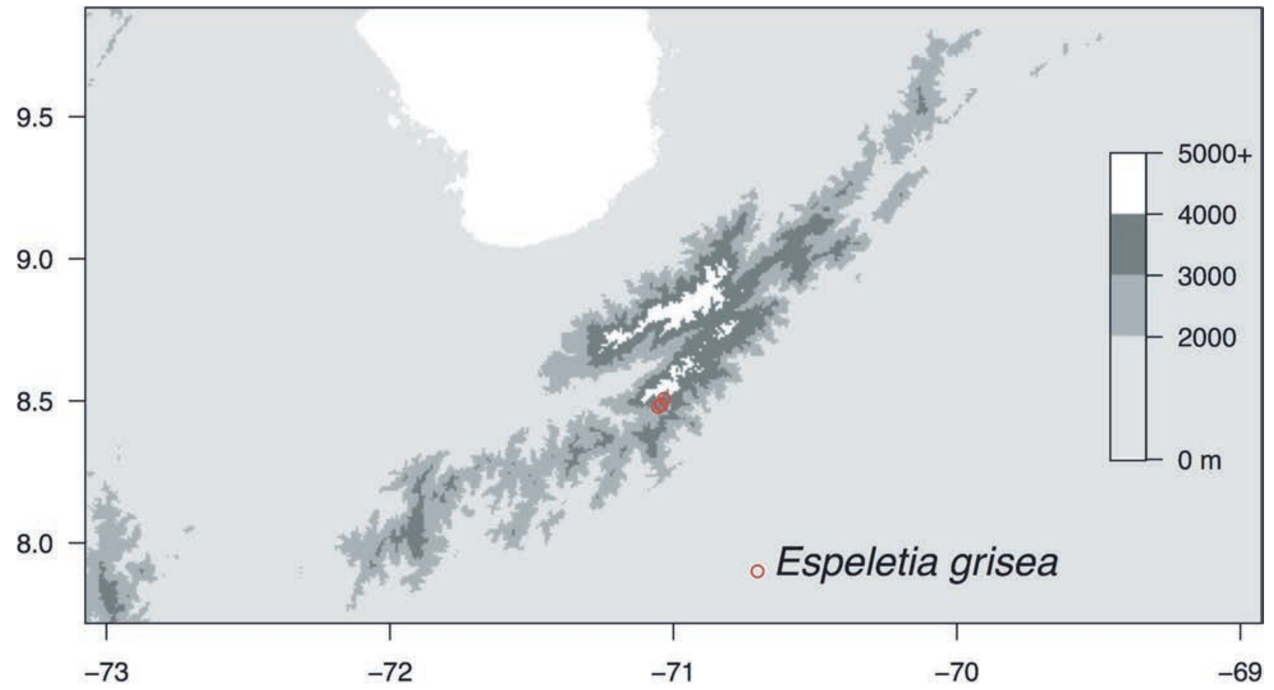

FIGURE 65. Distribution of *Espeletia grisea* Standl.

thinly hirsute leaves, secondary nerves < 3 mm apart with deviation angles > 50°, and its subglobose capitulum with short white ray ligules (corolla length < 7 mm).

Distribution: VENEZUELA. Mérida: known only from the southern slopes of Sierra Nevada de Mérida to the N of town Los Nevados. Between 3400–3800 m.a.s.l., in humid páramos along streams and ravines (Fig. 65).

Additional specimens examined (selection): *A. Jahn 157* (US), *L. Ruiz-Terán 6809* (US); *id. 6745* (US).

21. ***Espeletia hanburyana*** Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 86. 1956a. TYPE: VENEZUELA. Mérida: Páramo de Acequias, 12,000 ft, 18 October 1938, *J. Hanbury-Tracy 130* (Holotype: K; Isotypes: NY, US). Fig. 66–67.

Homotypic synonym: *Ruilopezia hanburyana* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves, densely leafy rosette. *Leaf* open sheath, sessile, adaxially glabrous, green, length 20–45 cm, width 1.2–2.2 cm, ratio 14–23:1, secondary nerves parallel, 1.5–2.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–60 cm, branched near the base. *Capitulum* diam. 15–20 mm, ligular circle 32–42 mm, disc 14–17 mm, ray ligules white. *Espeletia hanburyana* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit with a large number of straight and narrow green leaves, which gives a globose aspect to the rosette, and for its capitulum with long white ray ligules. The species resembles caulescent individuals of *E. lindenii*, but it has adaxially glabrous and slender leaves (ratio > 14:1 vs. < 12:1) and narrower sterile phyllaries (width 3–5 mm vs. 5–12 mm) with membranaceous texture and without glands (vs. foliaceous and copiously glanduliferous).

Distribution: VENEZUELA. Mérida: known only from the region Pueblos del Sur in the southern end of the Sierra Nevada de Mérida (e.g., Páramo de Acequias, de San José, and de Aricagua). 3000–3500 m.a.s.l., in humid subpáramos near depressions, streams, and lakes (Fig. 67).

Additional specimens examined (selection): *J. Hanbury-Tracy 130* (K, NY, US), *M. López-Figueiras*, *H. Rodríguez*, *J. Wurdack & M. Wurdack 8937* (US), *M. López-Figueiras 30158* (US), *M. López-Figueiras 30159* (US).

This taxon honors N. F. J. Hanbury-Tracy (Cuatrecasas, 2013: 550). According to ICN Art. 60.8, the correct spelling for the derived substantival epithet is "*hanburyana*" (not "*hanburiana*").

22. ***Espeletia jabonensis*** Cuatrec., Phytologia 23: 360. 1972. TYPE: VENEZUELA. Trujillo: Tres Pozos, un sector del Páramo del Turmal, unos 14,4 km al E. de la población de Carache, distrito Carache, 2800–2850 m.a.s.l., 8 June 1971, *L. Ruiz-Terán & M. López-Figueiras 1995* (Holotype: US; Isotypes: MERF, NY, US). Fig. 68–70.

Homotypic synonym: *Ruilopezia jabonensis* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, sessile, densely leafy rosette. *Leaf* open sheath, sessile, rigid, linear, adaxially pubescent, shiny silvery-sericeous, length 10–30 cm, width 0.3–0.8 cm, ratio 30–40:1, secondary nerves obsolete. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 40–80 cm, branched near the base, vegetative part profusely bracteate. *Capitulum* diam. 12–16

FIGURE 66. *Espeletia hanburyana* Cuatrec. Páramo de Acequias, Mérida, Venezuela (Photograph by S. Aubert).

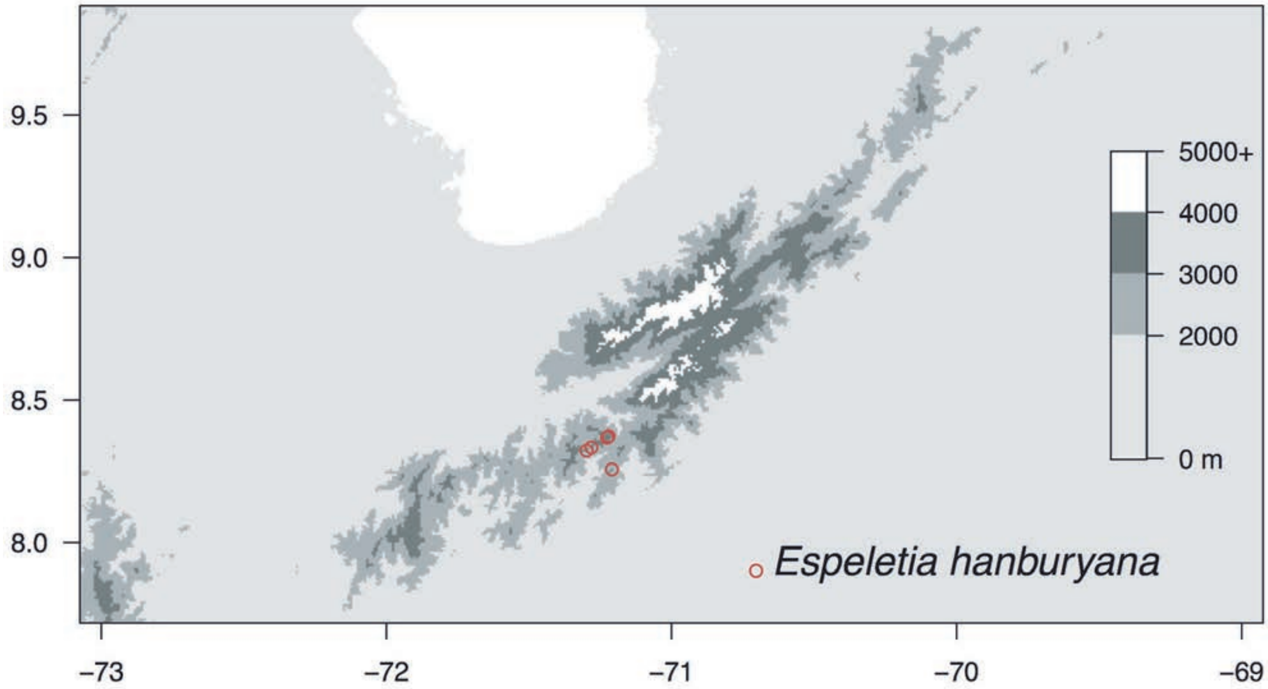

FIGURE 67. Distribution of *Espeletia hanburyana* Cuatrec.

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FIGURES 68–69. *Espeletia jabonensis* Cuatrec. **68**. Páramo de Guaramacal, Trujillo, Venezuela (Photograph by S. Aubert). **69**. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

mm, ligular circle 25–35 mm, disc 10–15 mm, yellow ray ligules. *Espeletia jabonensis* can be distinguished from other species for its sessile monocarpic rosette habit with a large number of straight and narrow silvery-shiny leaves, and its axial inflorescence with yellow-ligulate capitula. Flowering individuals are however relatively rare, suggesting some form of reproductive synchrony, so the identification of *E. jabonensis* must frequently be achieved using vegetative characters alone. The species can be distinguished from other taxa with silvery-sericeous indumentum by its strictly linear leaves with small rectangular sheaths (2.0–2.5 cm × 0.5–0.8 cm).

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal. Border Trujillo-Lara: Páramo de Cendé, del Jabón, and del Turmal. 2800–3400 m.a.s.l., in open subpáramos and páramos, particularly in exposed and windy slopes, summits, and crests (Fig. 70).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 1995* (NY, US), *L. Ruiz-Terán & M. López-Figueiras 2101* (US), *G. Aymard*, *F. Ortega & R. Morán 2924* (US), *M. López-Figueiras 13940* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28541* (F, US).

23. *Espeletia jahnii* Standl., Amer. J. Bot. 2: 479. 1915. TYPE: VENEZUELA. Táchira: Páramo del Batallón, 3000 m.a.s.l., March 1911, *A. Jahn 155* (Holotype: US; Isotype: VEN [not seen]). Fig. 71–74.

Homotypic synonym: *Ruilopezia jahnii* (Standl.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, the axis frequently divided into prostrate branches, each one entirely covered with marcescent leaves or sheaths and ending with a densely leafy rosette. *Leaf* open sheath, sessile, linear, adaxially glabrous, green, length 15–35 cm, width 0.2–0.4 cm, ratio 50–100:1, secondary nerves obsolete. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 50–80 cm, vegetative part profusely bracteate, about half of total length. *Capitulum* diam. 12–18 mm, eligulate. *Espeletia jahnii* can be distinguished from other species by its multibranched monocarpic rosette habit with a large number of straight and linear green leaves, and its inflorescence with eligulate capitula.

Distribution: VENEZUELA. Táchira: Páramo del Batallón and del Zumbador. 2800–3500 m.a.s.l., in open and exposed páramo slopes, summits, and crests (Fig. 74).

Additional specimens examined (selection): *A. Jahn 155* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2705* (US), *P. Berry & R. Calvo 4415* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28414* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & L. Marcano-Berti 27992* (F, U, US).

24. *Espeletia leucactina* Cuatrec., Phytologia 29: 377. 1975. TYPE: VENEZUELA. Táchira: Páramo del Batallón, 3000 m.a.s.l., 13 August 1974, *M. López-Figueiras 9151* (Holotype: US; Isotypes: MY, MERF, US). Fig. 75–77.

Homotypic synonym: *Ruilopezia leucactina* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Rosette monocarpic, mostly sessile, rarely with a stem up to 0.3 m. *Leaf* open sheath, sessile, adaxially pubescent, densely appressed, cinereous-ashy, length 35–45 cm, width 2.0–3.3 cm, ratio 15–30:1, secondary nerves parallel, 1.5–4.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–100 cm, branched near the base. *Capitulum* diam. 15–16 mm,

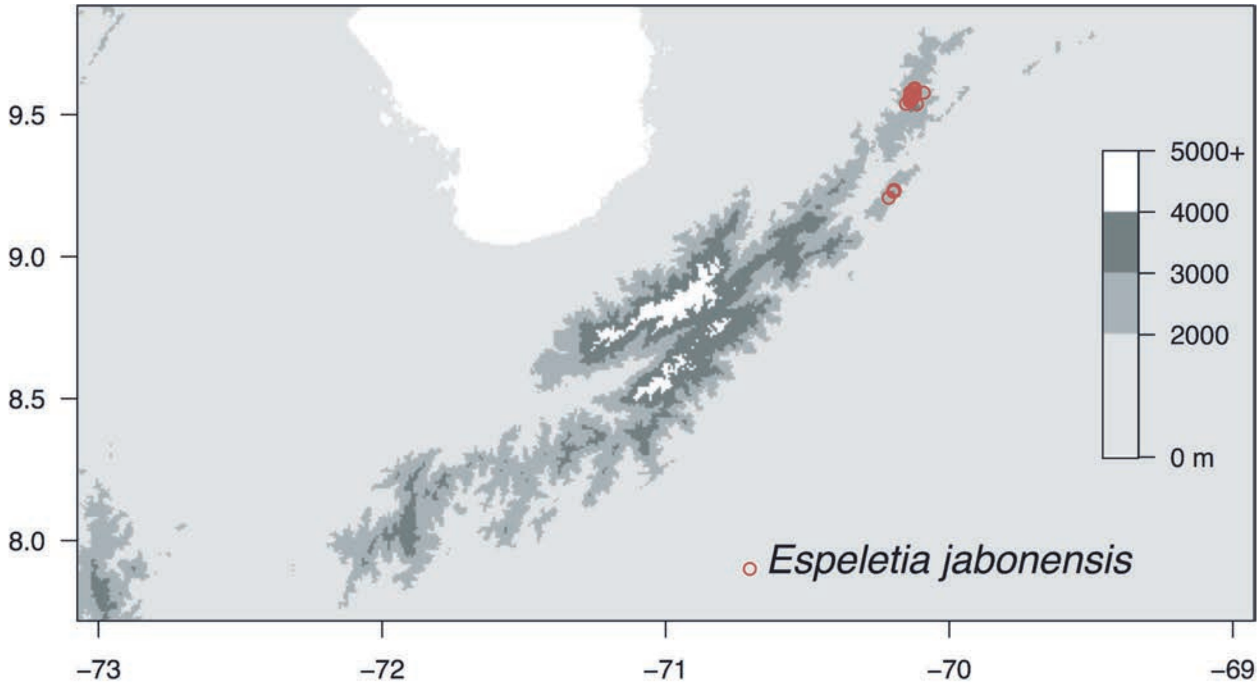
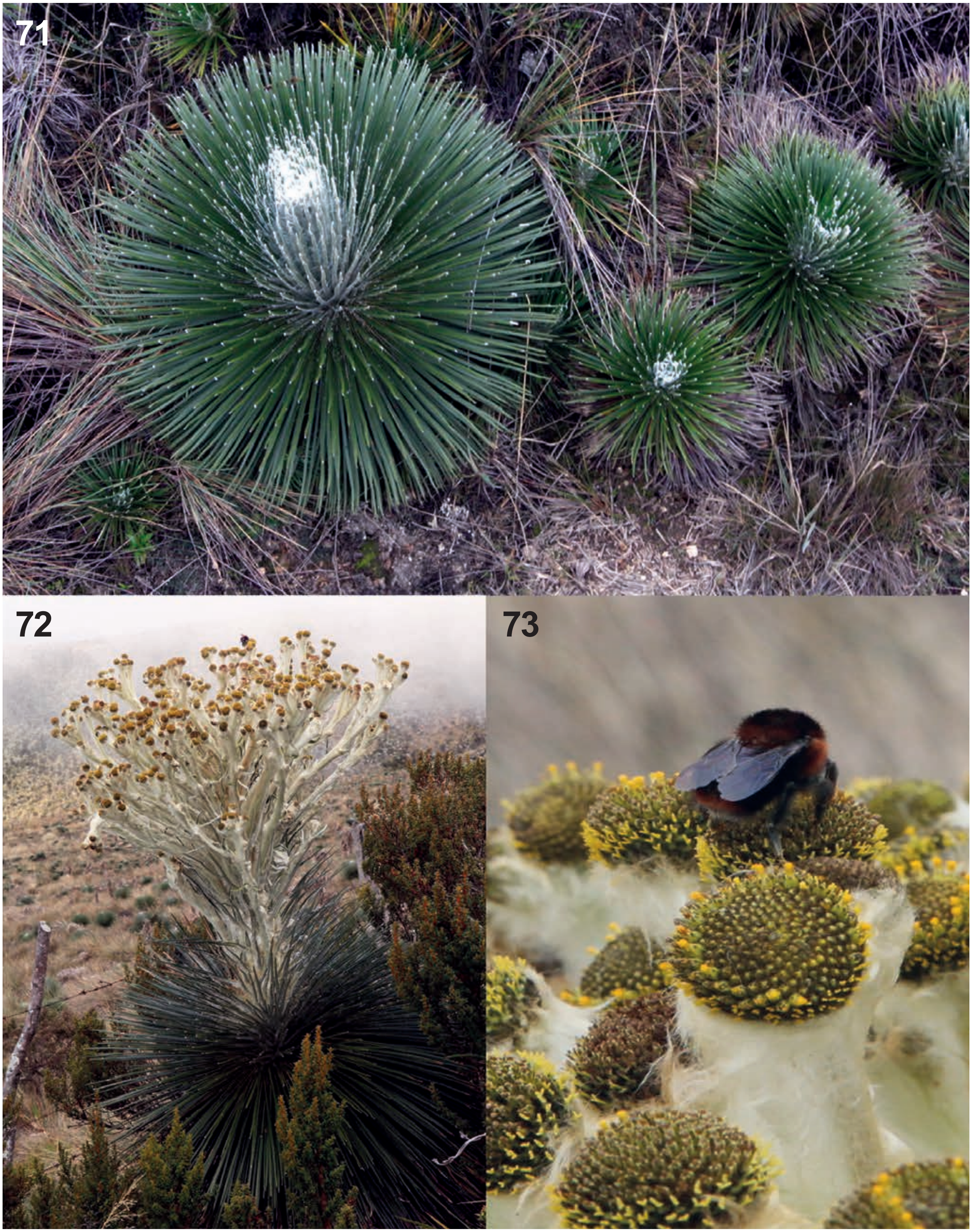


FIGURE 70. Distribution of *Espeletia jabonensis* Cuatrec.



FIGURES 71–73. *Espeletia jahnii* Standl. Páramo del Batallón, Táchira, Venezuela (Photographs by S. Aubert).

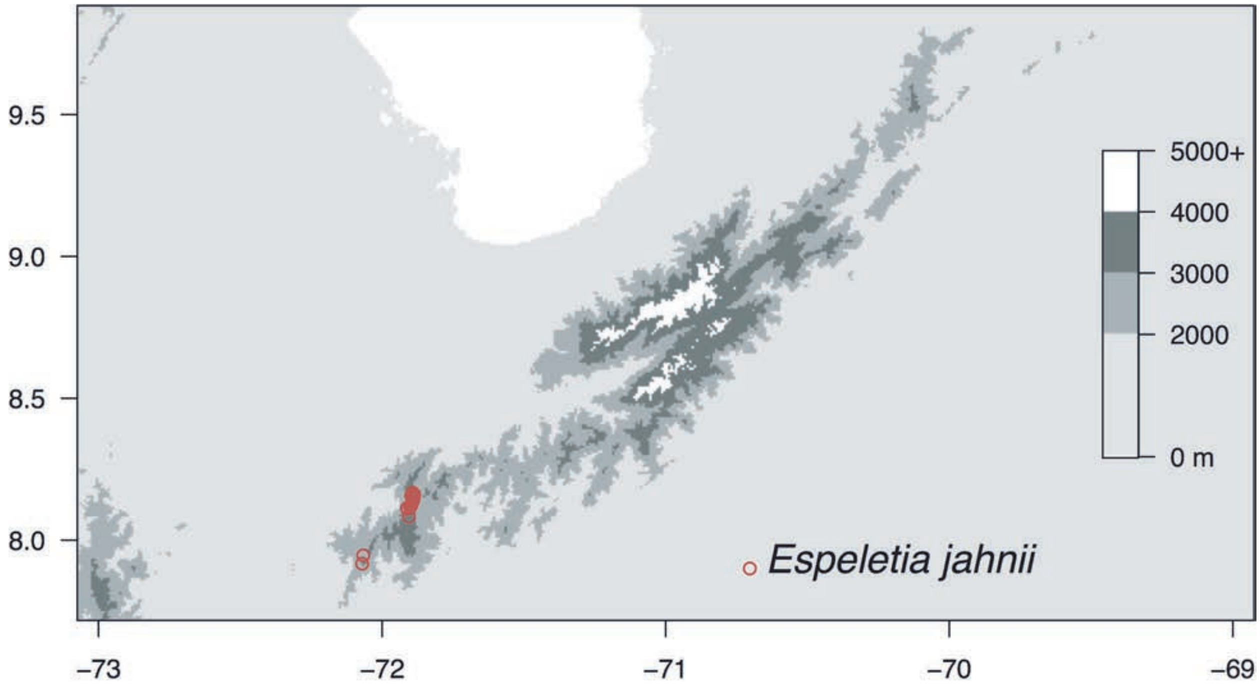


FIGURE 74. Distribution of *Espeletia jahnii* Standl.

FIGURE 75. *Espeletia leucactina* Cuatrec. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

FIGURE 76. *Espeletia leucactina* Cuatrec. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

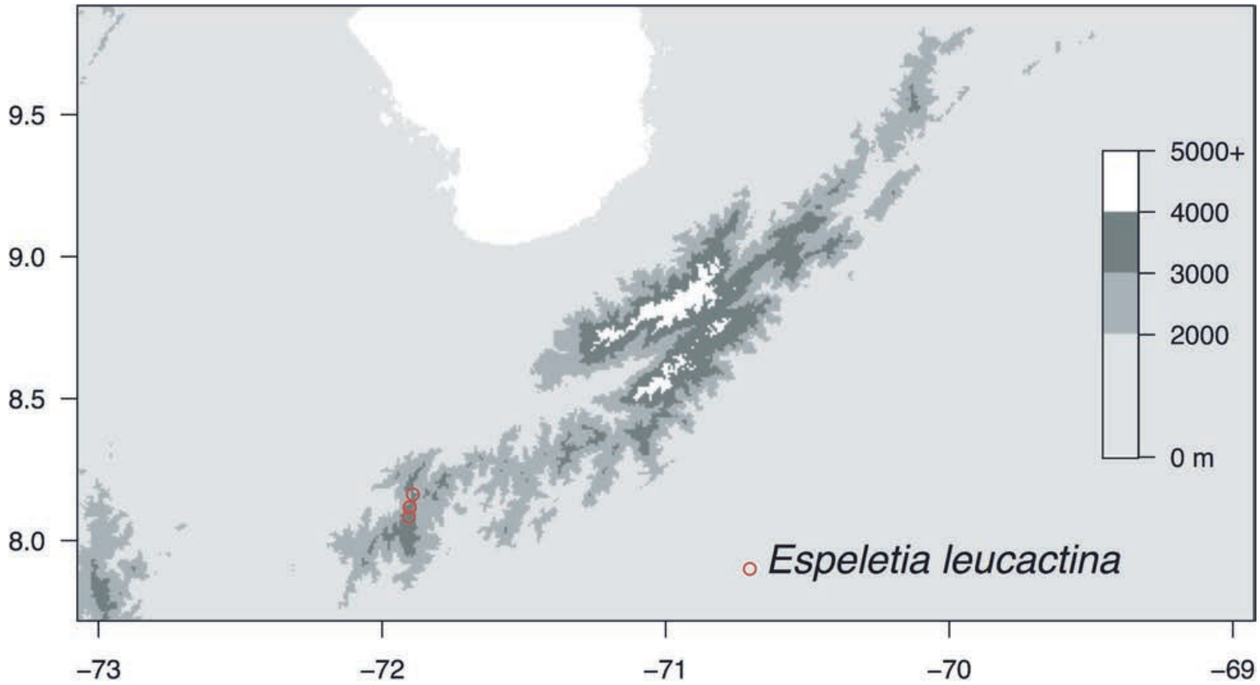


FIGURE 77. Distribution of *Espeletia leucactina* Cuatrec.

ligular circle 22–25 mm, disc 11–12 mm, ray ligules white. *Espeletia leucactina* can be distinguished from other species by its large sessile monocarpic rosette habit with long adaxially pubescent leaves, and its capitulum with white ray ligules. The species resembles *E. margarita* Cuatrec., from which it can be distinguished by its broader leaves (width 2.0–3.3 cm vs. 0.8–1.4 cm), secondary nerves with much larger deviation angle (60˚–80˚ vs. 20˚–25˚ when present), and its shorter ray corollas (8–10 mm vs. 13–17 mm).

Distribution: VENEZUELA. Táchira: Páramo del Batallón and del Portachuelo (between La Grita and Bailadores). 3000–3300 m.a.s.l., in open páramo, particularly in humid depressions and along streams (Fig. 77).

Additional specimens examined (selection): *M. López-Figueiras 9151* (US), *M. López-Figueiras 9152* (US), *M. López-Figueiras*, *H. Rodríguez & B. Rock 24651* (US), *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12594* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28408* (F, US).

25. ***Espeletia lindenii*** Sch. Bip. ex Wedd., Chlor. Andina: 66. 1855. TYPE: VENEZUELA. Mérida: Province de Mérida, 10,000 pieds, July 1843, *J. Linden 1414* (Holotype: P; Isotypes: BR, F, FI [not seen], G, K, P). Fig. 78–80.

Homotypic synonym: *Ruilopezia lindenii* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, sessile in Sierra Nevada de Mérida, caulescent with a stem height up to 2.0 m and entirely covered by marcescent leaves in Páramo El Tambor. *Leaf* open sheath, sessile, adaxially thinly villous-sericeous, green-grey aspect, length 15–30 cm, width 1.5–4.0 cm, ratio 7–9:1 (in Páramo El Tambor: leaf length up to 50 cm, width up to 5 cm, ratio up to 11.5:1), secondary nerves parallel, 1.5–4.0 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–80 cm (up to 240 cm in Páramo El Tambor), vegetative part profusely bracteate, about half of total length. *Capitulum* outer phyllaries foliaceous, diam. 18–25 mm, ligular circle 20–30(35) mm, disc 10–17 mm, ray ligules white, cream, or pale green. *Espeletia lindenii* from south of Sierra Nevada de Mérida can be distinguished from other species by its sessile monocarpic rosette habit, sessile adaxially green lanceolate leaves with ratio 7–9:1, and capitula with rather large herbaceous outer phyllaries and creamy/greenish ligules. The population from south of Sierra de la Culata differs for its tall caulescent and marcescent monocarpic rosette habit with longer leaves and inflorescences.

Distribution: VENEZUELA. Mérida: páramos in the southern ends of both Sierra Nevada de Mérida (e.g., Aricagua, Quirorá, San José, Las Coloradas) and Sierra de la Culata (e.g., Páramo El Tambor at the SW of La

FIGURE 78. *Espeletia lindenii* Sch. Bip. ex Wedd. Páramo de San José, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 79. *Espeletia lindenii* Sch. Bip. ex Wedd. Páramo de San José, Mérida, Venezuela (Photograph by S. Aubert).

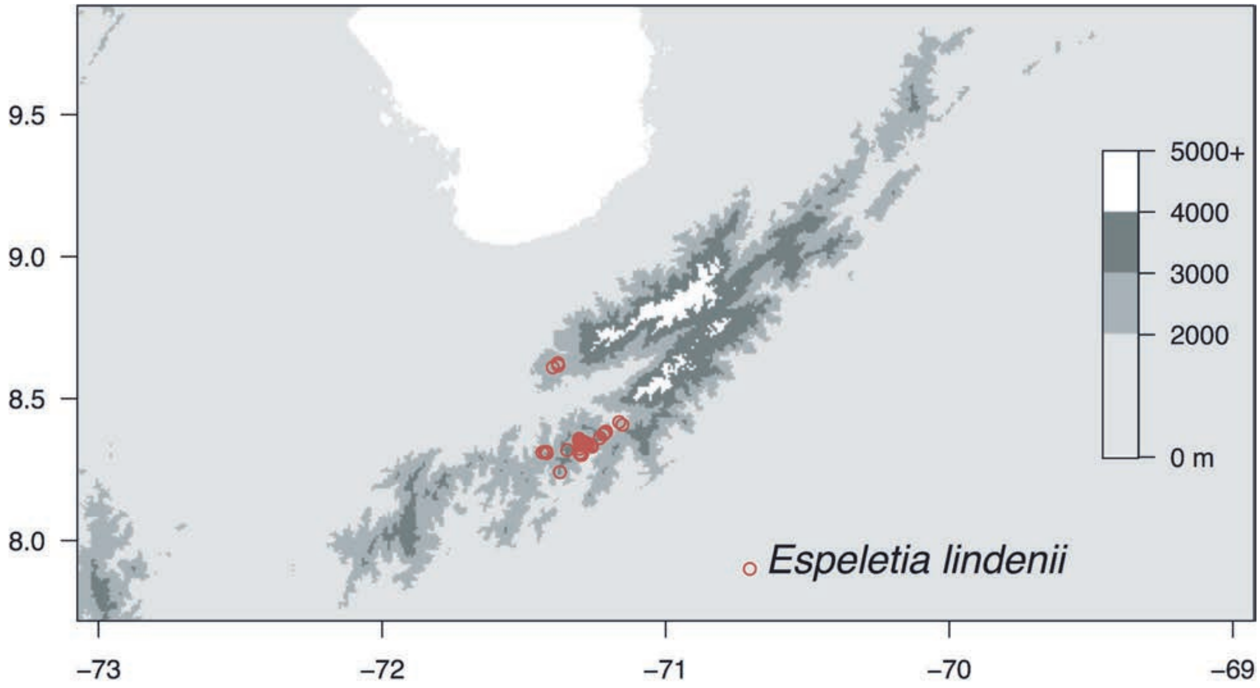


FIGURE 80. Distribution of *Espeletia lindenii* Sch. Bip. ex Wedd.

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Figures 81–82. *Espeletia liscanoana* Cuatrec. Páramo del Jabón, Lara-Trujillo, Venezuela (Photographs by S. Aubert).

Carbonera). The two allopatric populations of this species grow in rather different habitats: 2600–2800 m.a.s.l., in flat and rather humid subpáramo habitat in Páramo el Tambor, and 2500–3300 m.a.s.l., in open subpáramo slopes with dry/rocky soils in Sierra Nevada de Mérida (Fig. 80).

Additional specimens examined (selection): *J. Linden 1414* (BR, F, G, K, P), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28477* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28478* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28479* (U, US). Páramo el Tambor: *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28157* (F, U, US).

26. ***Espeletia liscanoana*** Cuatrec., Phytologia 27: 41. 1973a. TYPE: VENEZUELA. Lara: Páramo del Jabón, vertiente oriental, 3100–3400 m.a.s.l., 2 November 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28206* (Holotype: US; Isotypes: MERF, US). Fig. 81–83.

Homotypic synonym: *Libanothamnus liscanoanus* (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length 15–30 cm, width 3.5–9.0 cm, ratio 3.2–5.5:1 (young individuals may have bigger leaves), secondary nerves parallel, (4)5–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at the same level or slightly surpassing the surrounding leaves, length 20–35 cm, branched near the base. *Capitulum* diam. 15–20 mm, ligular circle 25–30 mm, disc 10–15 mm, ray ligules cream, greenish, or pale-yellow. *Espeletia liscanoana* can be easily distinguished from other tree species by its sessile leaves with loosely packed secondary nerves (> 4 mm apart).

Distribution: VENEZUELA. Border Lara-Trujillo: Páramo del Jabón, de Cendé, and del Turmal. 2900–3300 m.a.s.l., in humid locations in the upper level of the Andean forests usually below the timberline. Also found in subpáramo habitats, in places locally protected from winds, such as stands of tall trees, big rocks, and along ravines (Fig. 83).

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28206* (US), *R. Duno & R. Riina 765* (US), *Monasterio 3525* (US), *R. Riina*, *R. Duno*, *R. Ghinaglia & R. Gonto 634* (US), *L. Ruiz-Terán & M. López-Figueiras 957* (US).

27. ***Espeletia lopezpalacii*** Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes 17: 13. 1976. TYPE: VENEZUELA. Trujillo: Páramo de Guaramacal, unos 15 km al E. de Boconó, distrito Boconó, 2600 m.a.s.l., 9 August 1975, *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12619* (Holotype: MERF; Isotype: US). Fig. 84–86.

Homotypic synonym: *Ruilopezia lopezpalacii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 1.0 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, usually narrowed toward the base in an apparent pseudopetiole (length 1–4 cm), adaxially pubescent, appressed-sericeous, greenish-ashy aspect, length 25–38 cm width 1.5–2.3 cm, ratio 14–23:1, secondary nerves parallel, irregular length, long ones 4–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 120–180 cm, vegetative part

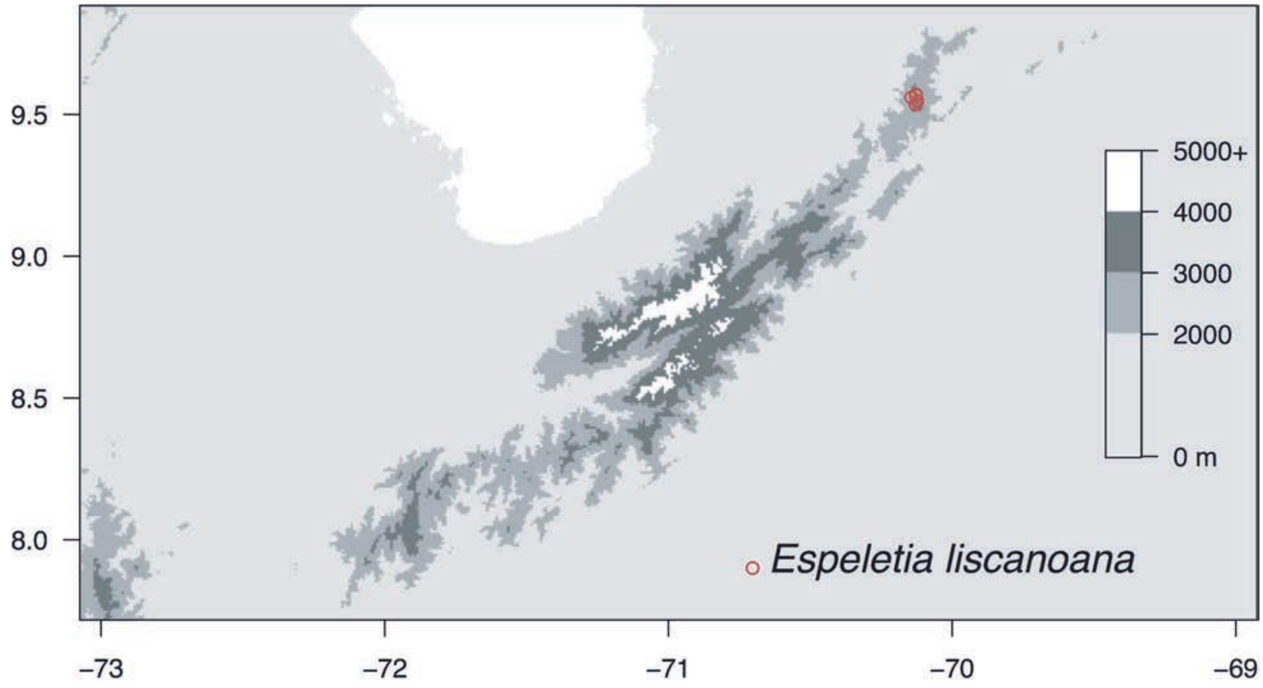

FIGURE 83. Distribution of *Espeletia liscanoana* Cuatrec.

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FIGURES 84–85. *Espeletia lopezpalacii* Ruiz-Terán & López-Fig. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

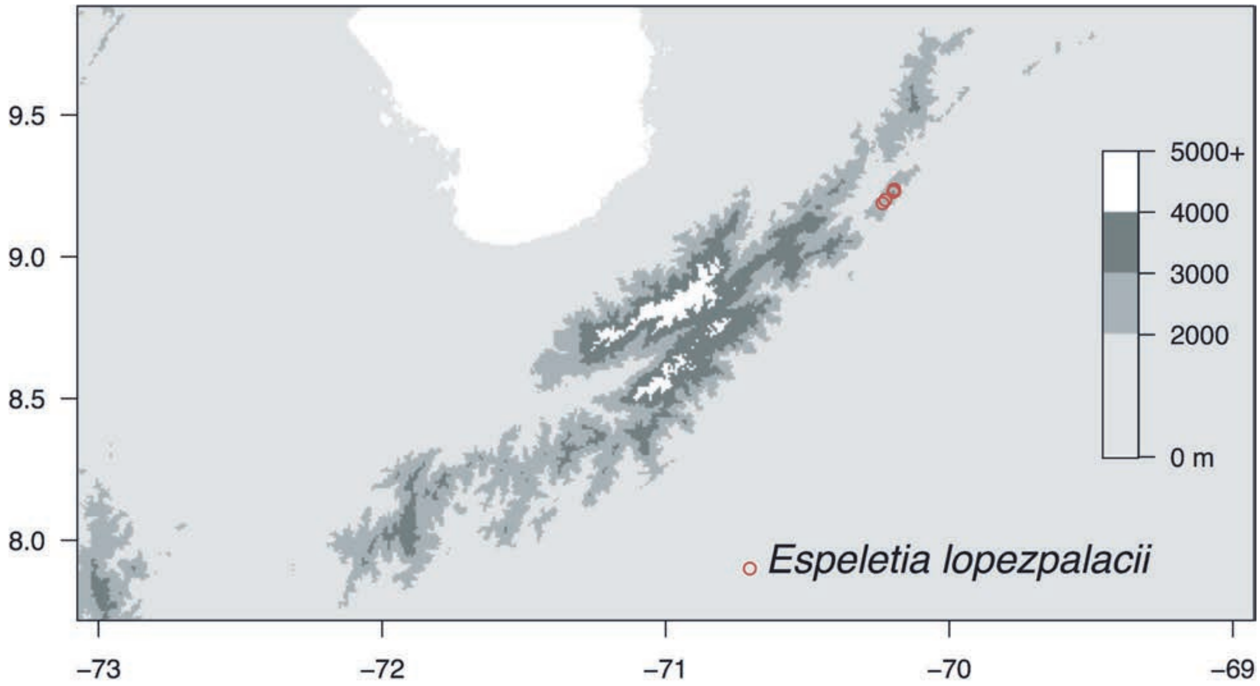

FIGURE 86. Distribution of *Espeletia lopezpalacii* Ruiz-Terán & López-Fig.

bracteate, about a third of total length. *Capitulum* diam. 7–10 mm, ligular circle 12–15 mm, disc 6–9 mm, ray ligules white. *Espeletia lopezpalacii* can be distinguished from other species by its caulescent-marcescent monocarpic rosette habit, lanceolate and pubescent leaves, secondary nerves > 4 mm apart with deviation angles < 40° and long inflorescence with rather small white-ligulate capitula.

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal. Between 2600–3100 m.a.s.l., in humid locations within shrubby subpáramo habitats (Fig. 86).

Additional specimens examined (selection): *L. Ruiz-Terán*, *M. López-Figueiras*, *D. Griffin & N. Griffin 12619* (US), *J. Cuatrecasas & L. Ruiz-Terán 28812* (F, US), *J. Cuatrecasas & L. Ruiz-Terán 28813* (US), *M. López-Figueiras 13941* (US), *G. Aymard*, *F. Ortega & R. Morán 2920* (US).

This taxon honors S. López Palacios (Cuatrecasas, 2013: 531). According to ICN Art. 60.11, the correct spelling for the derived substantival epithet is "*lopezpalacii*" (not "*lopez-palacii*"). Also, collectors given as "*L. Ruiz-Terán*, *M. López-Figueiras & D. Griffin*" (*N. Griffin* missing) in Diazgranados (2012: 41) and Cuatrecasas (2013: 529).

28. ***Espeletia lucida*** Aristeg., Fl. Venez. 10(1): 420. 1964. TYPE: VENEZUELA. Mérida: Camino al Pico Bolívar, 3800 m.a.s.l., 9 April 1951, *ULA-1001* (Holotype: VEN [not seen]; Isotype: MER). Fig. 87–89.

Homotypic synonym: *Libanothamnus lucidus* (Aristeg.) Cuatrec., Phytologia 35: 51. 1976.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, pseudopetiolate (length 10–25 cm), adaxially glabrous, lucid green, length 15–30 cm, width 3.5–5.0 cm, ratio 4.0–5.5:1, secondary nerves parallel, (1.5)2–3(4) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at the same level or slightly surpassing the surrounding leaves, length 20–30 cm, branched near the base. *Capitulum* diam. 9–12 mm, eligulate. *Espeletia lucida* can be easily distinguished from other tree species by its eligulate ray corollas.

Distribution: VENEZUELA. Mérida: restricted to a limited area in the western slopes of the Sierra Nevada de Mérida, between la Aguada cable-car station and lagunas la Coromoto and Verde to the SE of Tabay. 3200–3500 m.a.s.l., in the upper level of the Andean forest near the timberline and in secondarily open or disturbed vegetation (Fig. 89).

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28591* (US), *M. López-Figueiras & S. López-Palacios 8692* (US), *L. Ruiz-Terán & S. López-Palacios 1674* (US), *H. Barclay & P. Juajibioy 9945* (US).

29. ***Espeletia marcescens*** S.F. Blake, Contr. U.S. Nat. Herb. 20: 536. 1924. TYPE: VENEZUELA. Mérida: Southern slopes of Páramo de Quirorá, 2950 m.a.s.l., 24 February 1922, *A. Jahn 875* (Holotype: US; Isotypes: G, GH, K, NY, US, VEN [not seen]). Fig. 90–93.

Homotypic synonym: *Ruilopezia marcescens* (S.F. Blake) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 10 m, usually covered by marcescent leaves in the distal half, sometimes only below the rosette. *Leaf* open sheath, sessile, usually with small folding at the base, adaxially glabrous, bright green, length 20–50 cm, width 3.5–8.0 cm, ratio 5.5–6.2:1, margins dentate, teeth 1–5 mm apart, bases of

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FIGURES 87–88. *Espeletia lucida* Aristeg. Estación la Aguada, Mérida, Venezuela (Photographs by S. Aubert).

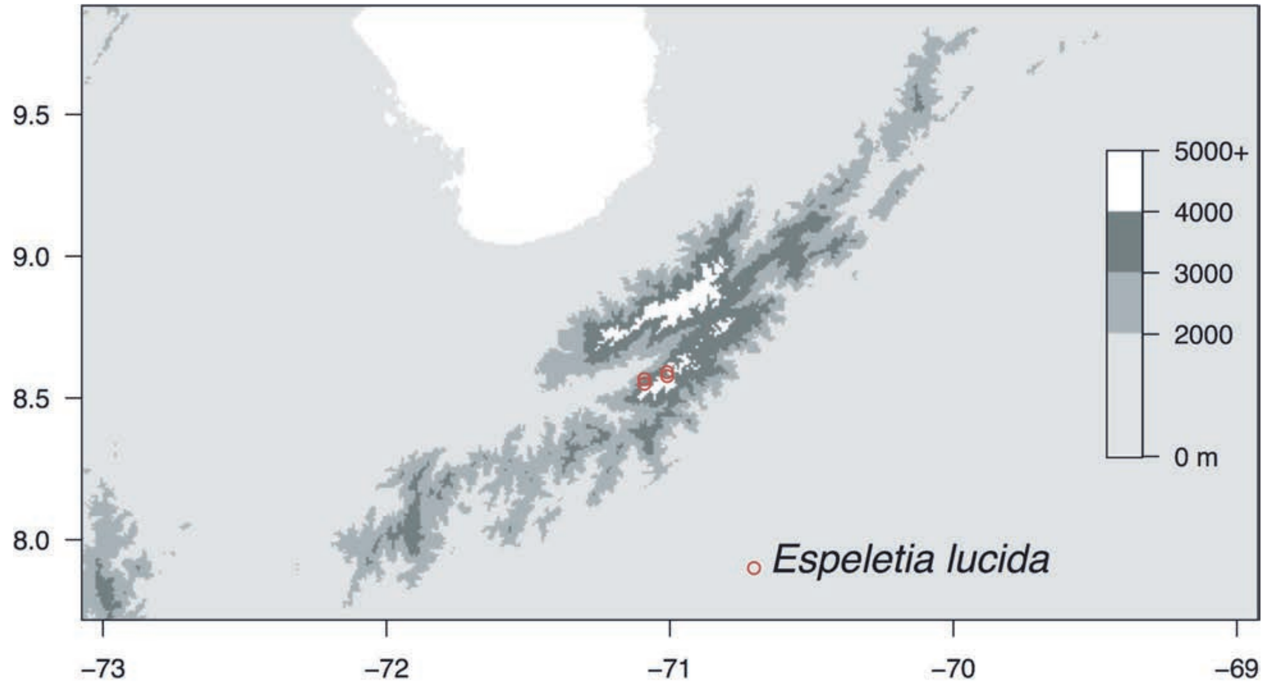

FIGURE 89. Distribution of *Espeletia lucida* Aristeg.

secondary nerves parallel, unevenly distributed, 2–5 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 40–80 cm, branched near the base, branches and sheaths of bracts pale green. *Capitulum* outer phyllaries herbaceous, diam. 20–25 mm, ligular circle 30–45 mm, disc 15–20 mm, ray ligules white, cream, or pale green. *Espeletia marcescens* can be distinguished from other species by its tall caulescent monocarpic rosette habit, sessile green leaves with small length-to-width ratio (< 7:1), and capitula with herbaceous outer phyllaries and creamy/greenish ligules. *Espeletia marcescens* resembles *E. cuatrecasasii*, but in addition to numerous color differences, *E. marcescens* has leaves with less prominent auriculate bases, greater density of secondary nerves (2–5 mm vs. 4–8 mm apart), greater deviation angles (70–90˚ vs. 60–65˚), larger capitulum diam. (> 20 mm vs. < 18 mm), and longer ray corollas (12–17 mm vs. 7–9 mm).

Distribution: VENEZUELA. Mérida: páramos in the southern end of Sierra Nevada de Mérida (e.g., Aricagua, Quirorá, San José, Las Coloradas) toward the border with Táchira state (e.g., Portachuelo, La Grita). Táchira: Páramo de la Negra and Páramo del Batallón. 2500–3000 m.a.s.l., found in humid clearings and margins of the upper level of the Andean forest below the timberline (Fig. 93).

Additional specimens examined (selection): *A. Jahn 875* (G, GH, K, NY, US), *M. López-Figueiras 12579* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2699* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28398* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28500* (F, US), *M. López-Figueiras*, *H. A. Rodríguez & J. Wurdack & M. Wurdack 8916* (US).

30. ***Espeletia margarita*** Cuatrec., Phytologia 27: 49. 1973a. TYPE: VENEZUELA. Mérida: Alrededores inmediatos de la Laguna Brava, Páramo de Los Granates, Sierra Nevada de Santo Domingo, 3300 m.a.s.l., 20 May 1971, *M. López-Figueiras 8720* (Holotype: US; Isotypes: BC, F, K, MERF, NY, U, US, VEN [not seen]). Fig. 94–96.

Homotypic synonym: *Ruilopezia margarita* (Cuatrec.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, sessile. *Leaf* open sheath, sessile, linear, adaxially pubescent, villous-sericeous, green-ashy aspect, length 25–40 cm, width 0.8–1.4 cm, ratio 20–40:1, secondary nerves frequently obsolete, distributed unevenly when visible. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 50–100 cm, branched near the base. *Capitulum* diam. 15–18 mm, ligular circle 30–40, disc 12–15, ray ligules white. *Espeletia margarita* can be distinguished from other species by its sessile monocarpic rosette habit with long-linear adaxially pubescent leaves, and its capitulum with white ray ligules. The species resembles *E. leucactina*, from which it can be distinguished by its thinner leaves (width 0.8–1.4 cm vs. 2.0–3.3 cm), scarcity of secondary nerves with smaller deviation angles when visible (20˚–25˚ vs. 60˚–80˚), and its capitulum with longer ray corollas (13–17 mm vs. 8–10 mm).

Distribution: VENEZUELA. Mérida: Páramo de Los Granates in Sierra Nevada de Santo Domingo. 3200–3400 m.a.s.l., in open páramo near lakes (Fig. 96).

Additional specimens examined (selection): *M. López-Figueiras 8720* (F, K, NY, U, US), *B. Vergara 1* (US), *B. Vergara 1A* (US), *L. Ruiz-Terán 6346* (US).

FIGURES 90–92. *Espeletia marcescens* S.F. Blake. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

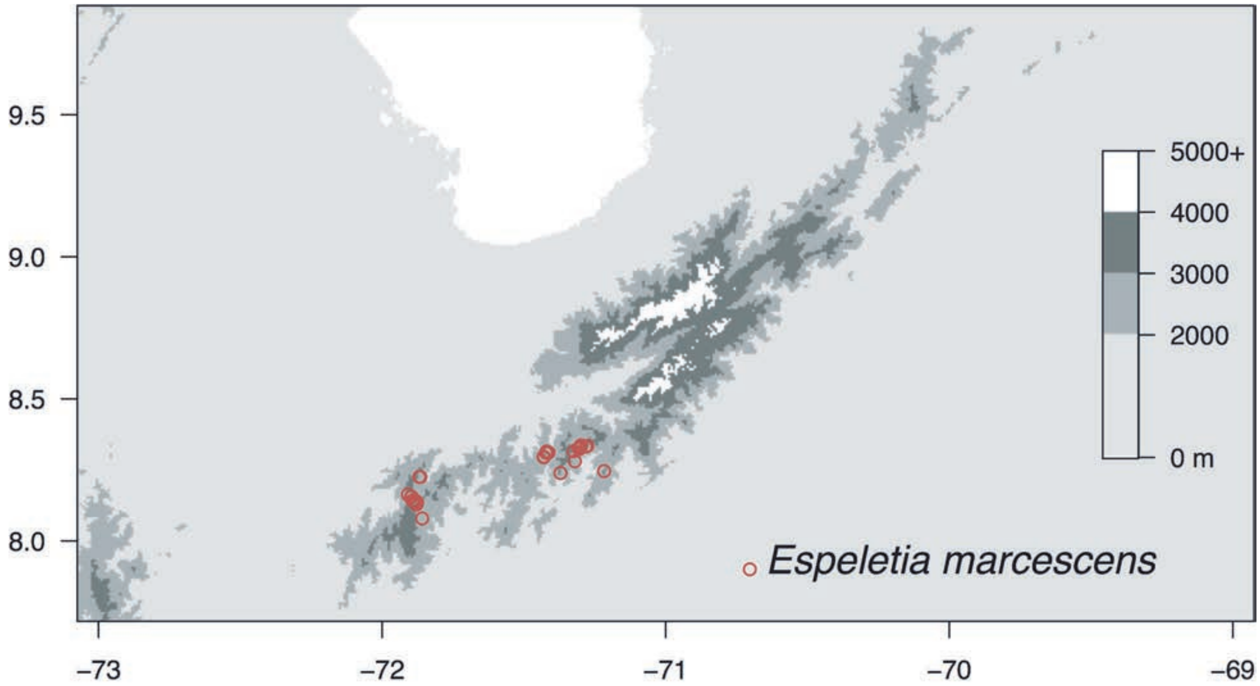

FIGURE 93. Distribution of *Espeletia marcescens* S.F. Blake.

FIGURE 94. *Espeletia margarita* Cuatrec. Páramo de Ortiz, Barinas-Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 95. *Espeletia margarita* Cuatrec. Páramo de Ortiz, Barinas-Trujillo, Venezuela (Photograph by S. Aubert).

31. *Espeletia marthae* Cuatrec., Phytologia 36: 20. 1977. TYPE: VENEZUELA. Mérida: Llano Corredor, Páramo de Guirigay, 3300 m.a.s.l., 25 October 1969. *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28162* (Holotype: US; Isotypes: F, MERF). Fig. 97–99.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially pubescent, silvery-sericeous, length 4.0–6.5 cm, width 0.4–0.5 cm, ratio 10–14:1, secondary nerves reticulate. *Inflorescence* lateral, simple, dichasial, monocephalous, length 25–40 cm, with 3–5 pairs of opposite bracts. *Capitulum* diam. 19–21 mm, ligular circle 30–35 mm, disc 9–12 mm, yellow ray ligules. *Espeletia marthae* can be distinguished from all other Venezuelan dwarf rosette plants with monocephalous inflorescences by its leaf sheaths glabrous on both sides and its inflorescences with 3–5 pairs of basal opposite bracts plus one or more solitary, alternate leaves. The species resembles *E. nana*, but it has smaller leaves covered with silvery-sericeous indumentum (vs. villous-lanate) and a smaller capitulum disc (< 12 mm and < 125 flowers).

Distribution: VENEZUELA. Border Mérida-Trujillo: Páramo de Guirigay. 3000–3500 m.a.s.l., in swampy areas, very humid depressions, and ponds (Fig. 99).

Additional specimens examined (selection): *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28162* (F, US), *L. Ruiz-Terán & M. López-Figueiras 12979* (US), *M. López-Figueiras & H. Rodríguez 8873* (US), *M. López-Figueiras & H. Rodríguez 8879* (US), *L. Aristeguieta 3571* (US).

Cuatrecasas, *López-Figueiras & Marcano-Berti 28162* in F should be labelled as isotype.

32. *Espeletia moritziana* Sch. Bip. ex Wedd., Chlor. Andina: 65. 1855. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 13,000 à 14,000 pieds, August 1842, *J. Linden 399* (Syntype: P [MNHN-P-P04086194]; Isosyntypes: P [leaves in MNHN-P-P02441522]). Mérida: Sierra Nevada de Mérida, 1852, *J. W. K. Moritz 1416* (Syntype: B destroyed [photo 15156 in F]). Fig. 100–102.

Homotypic synonym: *Coespeletia moritziana* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, usually sessile, occasionally caulescent with stem height up to 1.0 m and entirely covered by marcescent leaves. *Leaf* open sheath, sessile, linear, adaxially densely pubescent, lanate-lanuginose, yellowish-greenish aspect, length 25–50 cm, width 0.5–1.5 cm, ratio 20–40:1, secondary nerves parallel, (2.0)2.5–4.0 mm apart. *Inflorescence* lateral, simple, monochasial, monocephalous, axes 60–80 cm, with several alternate bracts. *Capitulum* diam. 40–60(–80) mm, ligular circle shorter than the involucre, disc 27–37(–40) mm, ray ligules bright yellow, orange, reddish. *Espeletia moritziana* can be easily recognized by its polycarpic rosette habit, long linear leaves, and monocephalous inflorescences with very large capitula (the largest in the subtribe). It resembles *E. palustris*, from which it can be distinguished by its yellowish–greenish indumentum (vs. whitish), smaller sheaths (5.0–7.0 cm × 0.9–2.2 cm vs. 7.0–10.0 cm × 2.2–2.5 cm), bracteate inflorescences (vs. aphyllous), sterile phyllaries with orderly pubescence (vs. dishevelled), and capitula with higher number of both disc (600–860 vs. 215–280) and ray (400–740 vs. 95–200) flowers.

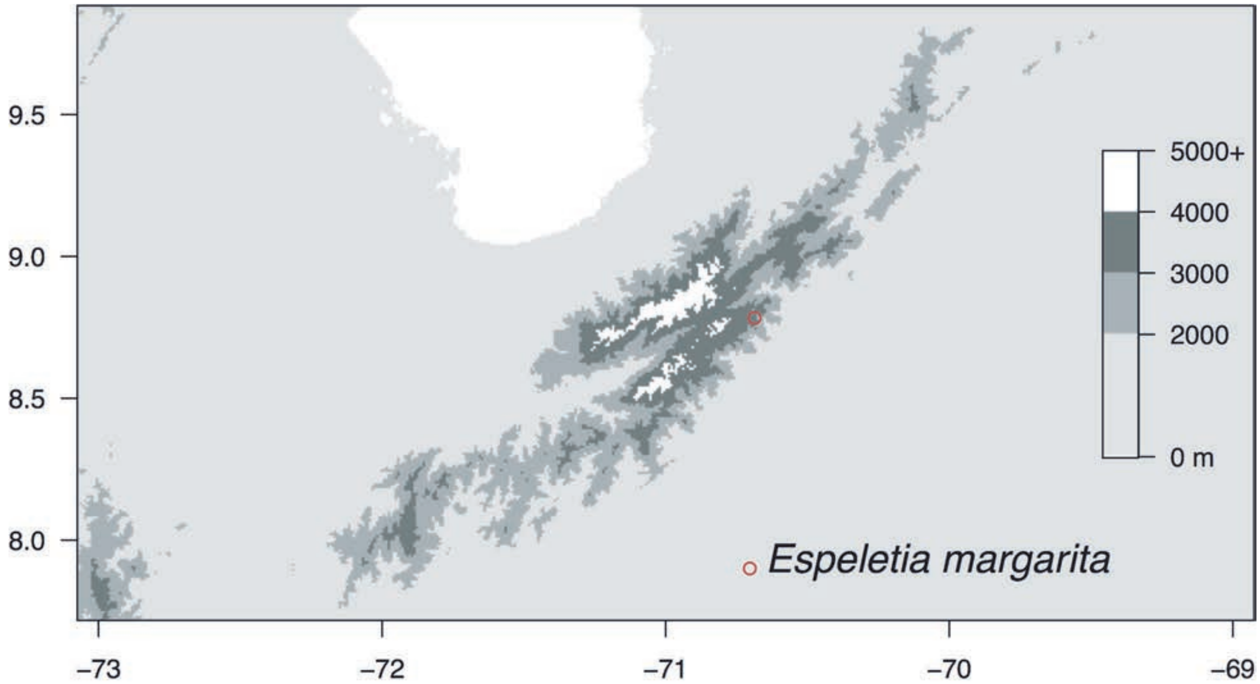

FIGURE 96. Distribution of *Espeletia margarita* Cuatrec.

FIGURE 97. *Espeletia marthae* Cuatrec. Páramo de Guirigay, Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 98. *Espeletia marthae* Cuatrec. Páramo de Guirigay, Trujillo, Venezuela (Photograph by S. Aubert).

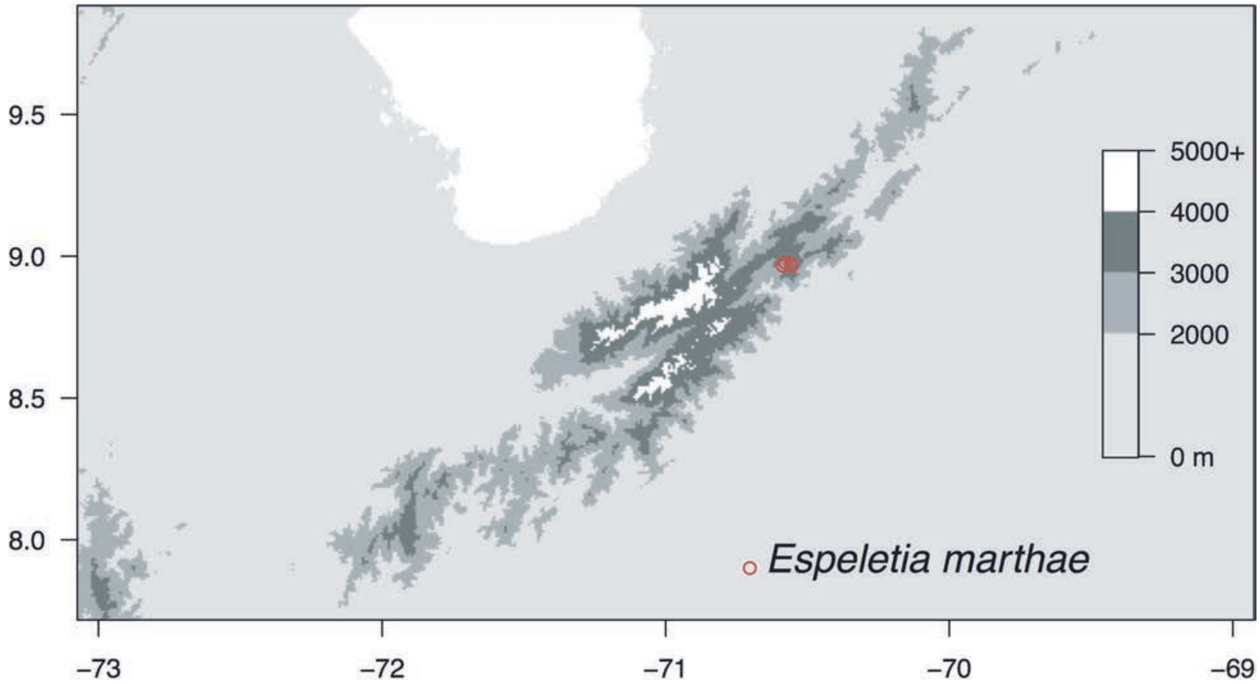

FIGURE 99. Distribution of *Espeletia marthae* Cuatrec.

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FIGURES 100–101. *Espeletia moritziana* Sch. Bip. ex Wedd. Sierra de la Culata, Mérida, Venezuela (Photographs by L. Gámez).

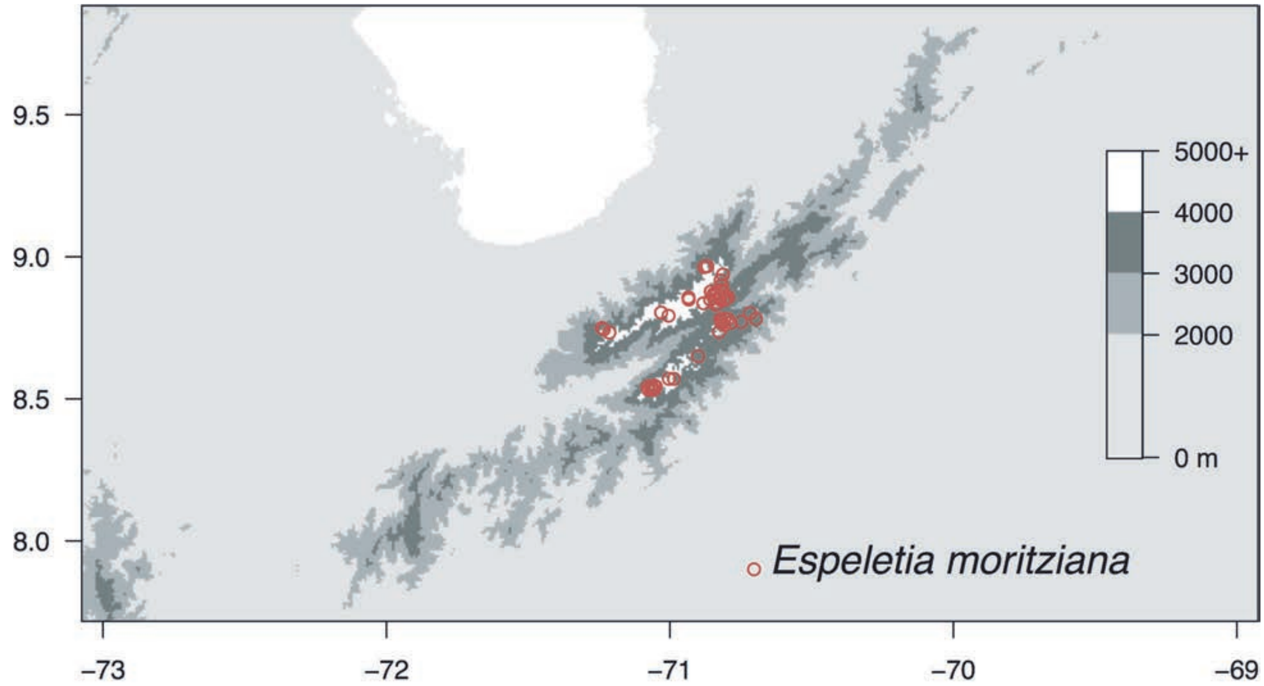

FIGURE 102. Distribution of *Espeletia moritziana* Sch. Bip. ex Wedd.

Distribution: VENEZUELA. Mérida: Sierra de la Culata and Sierra Nevada de Mérida. Usually 3800–4500 m.a.s.l., occasionally up to 4750 m.a.s.l. below Pico Espejo and Pico Bolívar, higher than any other Espeletiinae. Found in cold and windy superpáramos, usually on rocky crests (Fig. 102).

Additional specimens examined (selection): *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2669* (US), *Barclay & P. Juajibioy 10043* (US), *L. Ruiz-Terán & M. López-Figueiras 369* (US), *L. Ruiz-Terán 6882* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28031* (F, U, US).

Weddell (1855: 65) mentioned two specimens in the protologue of *E. moritziana*: *J. Linden 399* and *Moritz 1416*. However, both Weddell (1855: 63) and Cuatrecasas (2013: 579) noticed that some confusion took place in the labelling of the Linden collections, with some numbers including a mixture of *Espeletia moritziana* and *E. semiglobulata*. I revised the Linden collections in P and noticed that *Linden 399* (MNHN-P-P04086194) contains only *E. moritziana* and should be considered as a syntype, whereas *Linden 399* (MNHN-P-P02441522) is a mixture of *E. moritziana* leaves and *E. semiglobulata* inflorescences, and therefore only the leaves should be considered as an isosyntype. Cuatrecasas (2013: 579) also suggested that *Linden 368* and *Linden 398* probably are duplicates of *Linden 399*. I revised these collections and noticed that *Linden 368* (MNHN-P-P04086193 in P), *Linden 398* (MNHN-P-P02441483 in P), and *Linden 398* (catalogue number 1473203 in US) contain only *E. moritziana*, but *Linden 398* (MNHN-P-P04086312 in P) is a mixture of *E. moritziana* leaves and *E. semiglobulata* inflorescences. If Cuatrecasas's suggestion is correct, all the material in the former three, but only the leaves in the last one, could be considered as isosyntypes.

33. *Espeletia nana* Cuatrec., Phytologia 40: 29. 1978. TYPE: VENEZUELA. Trujillo: Distrito Urdaneta, la Morita, cresta arriba de la capilla, entre el caserío de Tuñame y la población de Jajó, 3000 m.a.s.l., 13 July 1971, *L. Ruiz-Terán & M. López-Figueiras 2204* (Holotype: US; Isotype: MERF). Fig. 103–105.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially pubescent, lanate-lanuginose, length 4–13 cm, width 0.4–1.1 cm, ratio 8–14:1, secondary nerves obsolete or unevenly distributed when visible. *Inflorescence* lateral, simple, dichasial, monocephalous, length 25–45 cm, usually with 2 pairs of opposite basal bracts, plus 1–5 alternate bracts along the axis. *Capitulum* diam. 20–26 mm, ligular circle 24–35 mm, disc 12–16 mm, ray ligules yellow. *Espeletia nana* can be recognized from other dwarf rosette plants by its leaf sheaths glabrous on both sides and its monocephalous inflorescences with 2 pairs of basal opposite bracts. *Espeletia nana* resembles *E. marthae*, but it has bigger leaves covered with villous-lanate indumentum (vs. silvery-sericeous) and larger capitulum discs (> 12 mm and > 125 flowers).

Distribution: VENEZUELA. Trujillo: Páramo de Tuñame, de Cabimbú, de Guirigay, de Ortiz, de Niquitao, and de la Cristalina. 3300–4000 m.a.s.l., frequently found in humid and swampy locations, but also in dryer ridges and slopes (Fig. 105).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 2204* (US), *L. Ruiz-Terán & M. López-Figueiras 2221* (US), *M. López-Figueiras 11885* (US), *L. Ruiz-Terán & M. López-Figueiras 11886* (US), *L. Ruiz-Terán 8996* (US).

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Figures 103–104. *Espeletia nana* Cuatrec. Páramo del Arenal, Mérida, Venezuela (Photographs by S. Aubert).

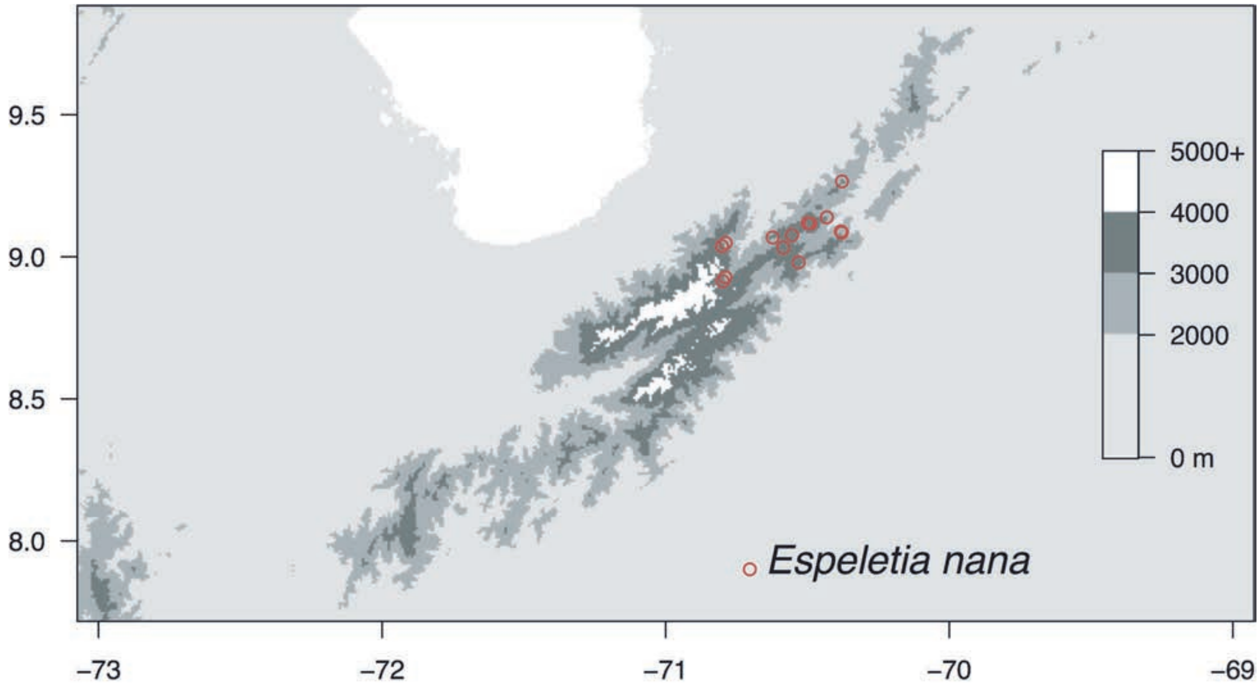

FIGURE 105. Distribution of *Espeletia nana* Cuatrec.

34. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd., Chlor. Andina: 67. 1855. TYPE: VENEZUELA. Caracas: Silla de Caracas, [3] January 1800, *Herbier donné par M. Bonpland en 1833 N° 652* (Lectotype: P [MNHN-P-P04086343]; Isolectotype: P [MNHN-P-P04086342]). Fig. 106–108.

Homotypic synonyms: *Trixis neriifolia* Bonpl. ex Humb., Voy. Reg. Aeq. Rel. Hist. 1: 605. 1814.

Baillieria neriifolia (Bonpl. ex Humb.) Kunth, Nov. Gen. Sp. 4: 289. 1820.

Clibadium neriifolium (Bonpl. ex Humb.) DC., Prodr: 507. 1836.

Libanothamnus neriifolius (Bonpl. ex Humb.) Ernst, Vargasia 7: 186. 1870.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, pseudopetiolate (length 1.0–3.0[4.0] cm), adaxially glabrous, green, length 15–30(40) cm, width 4.0–8.0 cm, ratio 4.0–6.5:1 (young individuals may have bigger leaves), margins frequently entire, sometimes with teeth up to 0.5 mm long and 3–10 mm apart, secondary nerves parallel, (3)4–10 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, frequently longer than surrounding leaves, length 15–25 cm, branched near the base. *Capitulum* diam. 7–10 mm, ligular circle 14–20 mm, disc 6–10 mm, ray ligules white or cream. *Espeletia neriifolia* can be distinguished from other tree species by its distinctly pseudopetiolate leaves with loosely packed parallel secondary nerves (> 4[3] mm apart).

Distribution: VENEZUELA. Widespread: all over the Cordillera de Mérida, from hills south of Páramo de las Rosas (Táchira) to Sierra de Barbacoas (Lara). Also found in the highest elevations in Cordillera de la Costa (Aragua, Distrito Federal, and Miranda). Border Colombia-Venezuela: Páramo de Tamá. Colombia. Norte de Santander: Páramos de Pamplona and de Ocaña. Frequently 2200–3000 m.a.s.l., but can also be found down to 1800 m.a.s.l. or as high as 3300 m.a.s.l. *Espeletia neriifolia* is a very common tree in the uppermost level of the Andean forest and can even be the dominant element in the timberline. It is also found naturally in more exposed places such as shrubby subpáramos and dry/windy mountaintops and crests, and is an aggressive colonizer of upper Andean forests recently opened by fire or deforestation (Fig. 108).

Additional specimens examined (selection): *Williams 10903* (US), *H. Pittier 6240* (US), *M. López-Figueiras 25148* (US).

The lectotype of *Espeletia neriifolia* was designated by Smith and Koch (1935: 503) as "Venezuela. Federal District: Silla de Caracas, *Bonpland* (P, type)" for material collected by Aimé Bonpland and Alexander von Humboldt and described as *Trixis neriifolia*. Two herbarium samples in P match this description (MNHN-P-P04086343 and MNHN-P-P04086342), holding labels "lecto-holotypus" and "lecto-isotypus," respectively, added by José Cuatrecasas. The herbarium samples in B (B -W 16672) and HAL (HAL0113153, HAL0112801) are not lectotypes, as stated in Diazgranados (2012: 36) and Cuatrecasas (2013: 419).

Neither *Moritz 372* nor *Cuatrecasas*, *Schultes & Smith 12721* are types of *L. neriifolius* or *E. neriifolia* as stated in Diazgranados (2012: 35). *Moritz 372* was not collected in Colombia as stated in Diazgranados (2012: 35) but in Venezuela.

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FIGURES 106–107. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. Páramo de los Conejos, Mérida, Venezuela (Photographs by S. Aubert).

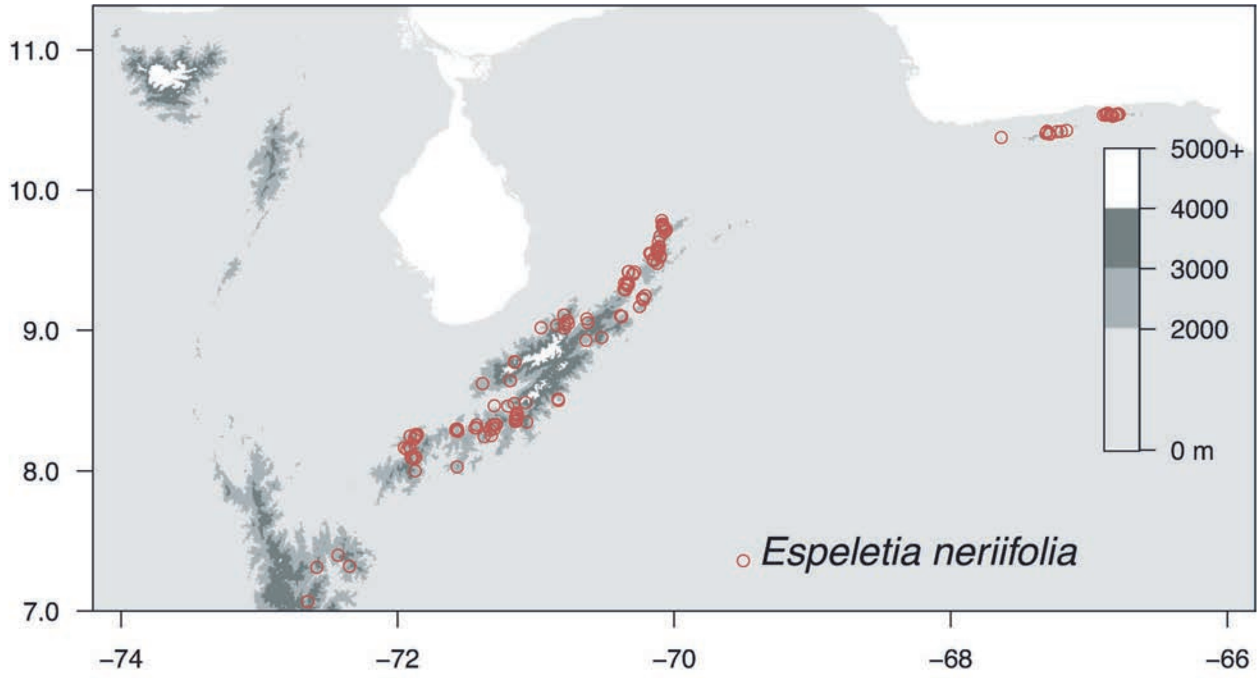

FIGURE 108. Distribution of *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd.

Over its broad geographic distribution *E. neriifolia* has been found to hybridize with *E. angustifolia*, *E. aristeguietana*, *E. badilloi*, *E. bromelioides*, *E. lindenii*, *E. marcescens*, *E. occulta*, *E. ruizii*, *E. schultzii*, *E. vegarae*, *E. thyrsiformis*, and *E. trujillensis* (see Hybrid Taxa section).

34.1. ***Espeletia neriifolia*** (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***neriifolia***.

Distribution: VENEZUELA. Distrito Federal: along the crest that connects Lagunazo and Pico Naiguatá. Aragua: Pico Codazzi and nearby areas around Colonia Tovar. Usually found above 2200 m in dry and windy locations on mountaintops and crests, occasionally down to 1800–2000 m.a.s.l., in the upper level of the Andean forest below the timberline.

34.2. ***Espeletia neriifolia*** (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***columbica*** Cuatrec., Rev. Acad. Col. Ci. Exact. 5: 19. 1942. TYPE: COLOMBIA. Norte de Santander: Páramo de Tamá, vertiente hacia Samaria, 2600–2900 m.a.s.l., 29 October 1941, *J. Cuatrecasas*, *R. E. Schultes & E. Smith 12721* (Holotype: COL; Isotypes: BC, COL, F, GH, MO, NY, U, US).

Homotypic synonyms: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *columbicus* Cuatrec., Mem. New York Bot. Gard. 107: 429. 2013.

According to Cuatrecasas (1942, 2013: 428), *E. neriifolia* var. *columbica* can be distinguished from any other variety by its more prominent secondary nerves in the abaxial side of leaves and, particularly, its longer tubes of disc corollas (0.5–1.2 mm vs. 0.3–0.5 mm).

Distribution: VENEZUELA. Widespread: found in all mountains in the Andes, from Páramo de Tamá (Táchira) to de Timotes (Trujillo) and de Los Granates (Mérida-Barinas). COLOMBIA. Norte de Santander: Páramo de Tamá and de Pamplona. 2500–3000 m.a.s.l., occasionally as low as 2200 m.a.s.l., in the upper level of the Andean forest, in the timberline, and in shrubby subpáramos.

Additional specimens examined (selection): *J. Cuatrecasas*, *R. E. Schultes & E. Smith 12721* (F, GH, MO, NY, U, US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2669* (US), *C. Sobrevila & A. Weitzman 1349* (US).

34.3. Espeletia neriifolia (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***cristamontis*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *cristamontis* Cuatrec., Mem. New York Bot. Gard. 107: 428. 2013. TYPE: VENEZUELA. Trujillo: Entre el Alto y los Pocitos, en la fila o cresta del cerro paralela al camino hacia Humocaro Alto, divisoria entre los estados Lara y Trujillo, a 15 km al E. de Carache, 3150 m.a.s.l., 5 October 1970, *L. Ruiz-Terán & M. López-Figueiras 1034a* (Holotype: US; Isotypes: MERF, US).

Homotypic synonym: *Libanothamnus cristamontis* Cuatrec., Phytologia 47: 5. 1980b.

Espeletia neriifolia var. *cristamontis* can be distinguished from other varieties of *E. neriifolia* by its inflorescences covered with thick indumentum and its small leaves (length 10–15 cm, width 3.0–4.0 cm), very short pseudopetioles (length 0.1–0.8 cm), and relatively denser secondary nerve packing (2–4 mm apart). Individuals with very small leaves can look superficially similar to sympatric *E. parvula*, from which they differ by the lower density of secondary nerves (2–4 mm vs. 1–2 mm apart), smaller deviation angles (70–75° vs. 75–90°), and smaller sterile phyllaries (3.5–4.0 mm × 2.3–2.8 mm vs. 4.5–5.5 mm × 4.0–5.5 mm). The morphological ressemblance and sympatry between *E. neriifolia* var. *cristamontis* and *E. parvula* suggests that the former might be the results of hybridization between lower elevation *E. neriifolia* and higher elevation *E. parvula*.

Distribution: VENEZUELA. Border Lara-Trujillo: along the mountain crest that connects the summits Cajingo, El Jabón, Cendé, and El Turmal. 3000–3200 m.a.s.l., at the timberline, in dry and windy locations on mountaintops and crests.

Additional specimens examined: *L. Ruiz-Terán & M. López-Figueiras 1034a* (US).

The other two varieties of *Espeletia neriifolia* described by Cuatrecasas (1980b: 6–7) are morphologically very close to each other and to *E. neriifolia* var. *columbica*. Furthermore, their identification can be difficult because some of the supposedly distinctive traits in the keys and descriptions provided in Cuatrecasas (2013: 428) can be rather subjective, hard to measure in the wild with the required precision, or show overlapping values among taxa. The two varieties will nonetheless be listed below, but their status must remain uncertain until more comprehensive studies are performed.

34.4. Espeletia neriifolia (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***boconensis*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *boconensis* Cuatrec., Phytologia 47: 6. 1980b. TYPE: VENEZUELA. Trujillo: Páramo de la Cristalina, 2250–2300 m.a.s.l., 30 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28190* (Holotype: US; Isotypes: F, MERF, U, US).

Morphologically close to *E. neriifolia* var. *columbica*, but with secondary nerves abaxially less prominent and with shorter tubes of disc corollas (0.3–0.5 mm vs. 0.5–1.2 mm). Also very similar to *E. nerifolia* var. *turmalensis*, from which it can be distinguished by its larger leaves (15–30 × 3.5–7.5 cm vs. 12–18 cm × 2.5–4.5 cm).

Distribution: VENEZUELA. Lara: Páramo de los Nepes and Alto del Filo (near Agua de Obispo) in Sierra de Barbacoas. Trujillo: Páramo de Tuñame, de Teta de Niquitao, de Cabimbú, de Guaramacal, de la Morita (above Jajó), de las Siete Lagunas (above Monte Carmelo), and de la Cristalina. Trujillo-Barinas border: Páramo de Guirigay and de Ortiz. 2200–3000 m.a.s.l., in the upper level of the Andean forest and small forest stands below the timberline, occasionally in subpáramo habitat in association with other large shrubs and trees.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28190* (F, U, US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28972* (US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28976* (US).

34.5. *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. var. ***turmalensis*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Libanothamnus neriifolius* (Bonpl. ex Humb) Ernst var. *turmalensis* Cuatrec., Phytologia 47: 7. 1980b. TYPE: VENEZUELA. Trujillo: Páramo del Turmal, hacia el Páramo del Jabón y Páramo de las Rosas (vertiente occidental), hoya del Río Turmal, al E. de Carache, 2800–2900 m.a.s.l., 3 November 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28239* (Holotype: US; Isotypes: F, MERF, U, US).

Morphologically close to *E. neriifolia* var. *columbica*, but with secondary nerves less prominent abaxially and with shorter tubes of disc corollas (0.3–0.5 mm vs. 0.5–1.2 mm). Also very similar to *E. nerifolia* var. *boconensis*, from which it can be distinguished by its smaller leaves (12–18 cm × 2.5–4.5 cm vs. 15–30 × 3.5–7.5 cm).

Distribution: VENEZUELA. Lara: Páramo de Los Nepes and Alto del Filo (near Agua de Obispo) in Sierra de Barbacoas. Border Trujillo-Lara: Páramo de las Rosas, del Jabón, de Cendé, and del Turmal. 2100–3300 m, in the upper level of the Andean forest and in subpáramo habitats above the timberline, occasionally in relatively open and exposed páramo hills.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28239* (F, U, US), *M. López-Figueiras 32304* (US), *M. López-Figueiras & H. Rodríguez 26231* (US).

35. *Espeletia occulta* S.F. Blake, Contr, U.S. Nat. Herb. 20: 537. 1924. TYPE: VENEZUELA. Mérida: Páramo de Quirorá, 3000 m.a.s.l., 8 October 1921, *A. Jahn 730* (Holotype: US; Isotypes: MERF, US). Fig. 109–111.

Homotypic synonym: *Libanothamnus occultus* (S.F. Blake) Cuatrec., Phytologia 35: 51. 1976.

Libanothamnus occultus (S.F. Blake) Cuatrec. var. *salomonii* Cuatrec. & López-Fig., Phytologia 61: 51. 1986a. TYPE: VENEZUELA. Táchira: Laderas occidentales alrededor de Pico de Horma, 7.5 km SE. de Mesa de Quintero, 3100 m.a.s.l., 11 January 1985, *M. López-Figueiras*, *H. Rodríguez & N. Rengifo 31344* (Holotype: US; Isotypes: F, MERF, NY, US).

Tree profusely branched, height up to 15 m. *Leaf* tubular sheath, sessile, rarely with short pseudopetiole (length < 0.3 cm), adaxially glabrous, green, length 18–40 cm, width 4.5–10.0 cm, ratio (2.5)3.0–4.5:1 (young individuals may have bigger leaves), margins frequently entire, occasionally with teeth up to 0.5 mm long and 5–10 mm apart, secondary nerves parallel, 2.5–4(5) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at about the same level as or slightly surpassing surrounding leaves, length 20–40 cm, branched near the base. *Capitulum* diam. 14–22 mm, ligular circle 20–30(35) mm, disc 9–15 mm, ray ligules white, cream, or yellowish. *Espeletia occulta* can be distinguished from other tree species by its large sessile leaves (> 18 cm), with sheaths barbate only in the abaxial side and with densely packed secondary nerves (< 5 mm apart).

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FIGURES 109–110. *Espeletia occulta* S.F. Blake. Páramo del Batallón, Táchira, Venezuela (Photographs by S. Aubert).

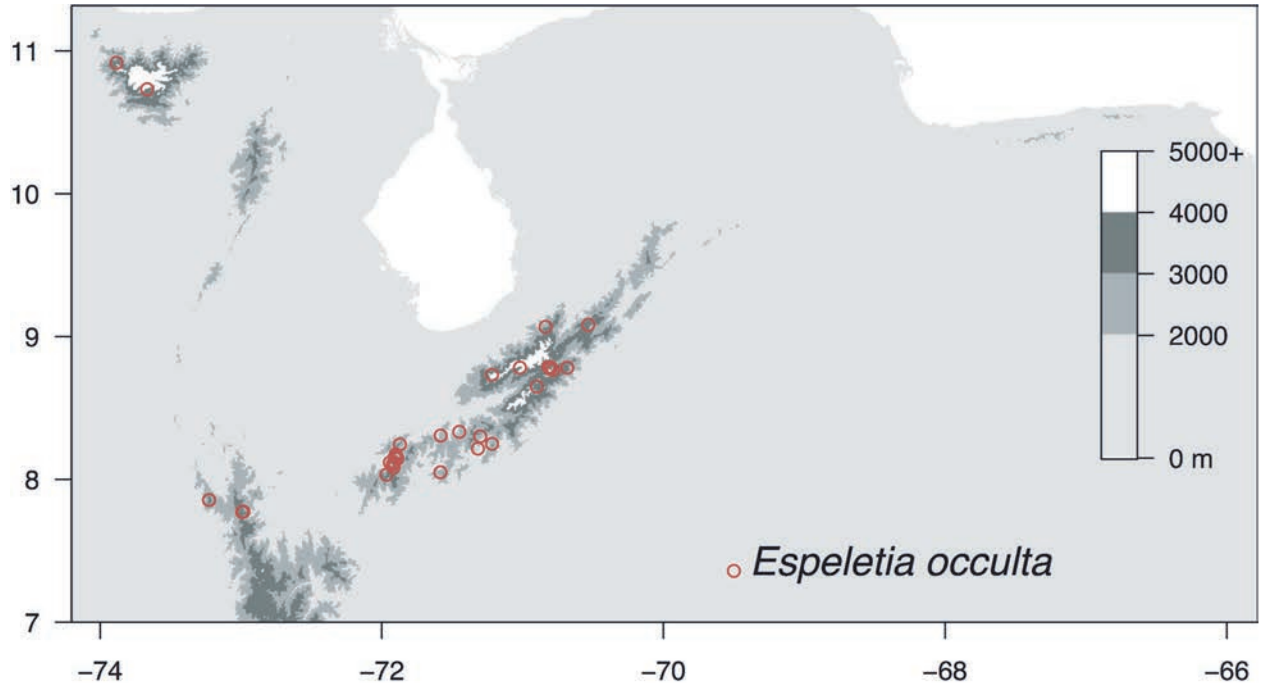

FIGURE 111. Distribution of *Espeletia occulta* S.F. Blake.

Distribution: VENEZUELA. Mérida: mountains in the southern end of the Sierra Nevada de Mérida: Aricagua, Chacantá, El Molino, and the area known as "Pueblos del Sur" (subsp. *occulta*). Páramos along the central and north sections of the Sierra Nevada de Mérida, Sierra de Santo Domingo and Páramo de Los Granates. Sierra de la Culata, from Páramo de los Conejos to the páramos between Piñango and Timotes (subsp. *humbertii*). Táchira: Pico de Horma, mountains nearby La Grita, Las Porqueras, Páramo del Batallón, and Páramo de las Rosas. Trujillo: El Paramito, between Jajó and Tuñame (subsp. *occulta*). COLOMBIA. Magdalena: Sierra Nevada de Santa Marta (subsp. *glossophylla*). Norte de Santander-Cesar: Las Jurisdicciones, Cerro de Oroque (subsp. *oroquensis*). 2900–3800 m.a.s.l., from the uppermost level of the Andean forest just below the timberline to shrubby subpáramo, extensions of forest growing at higher elevations along streams and some relatively humid and protected locations within open páramo habitat (Fig. 111).

35.1. *Espeletia occulta* S.F. Blake subsp. *occulta*

Distribution: VENEZUELA. Mérida: mountains in the southern end of the Sierra Nevada de Mérida: Aricagua, Chacantá, El Molino, and the area known as "Pueblos del Sur." Táchira: Pico de Horma, mountains nearby La Grita, Las Porqueras, Páramo del Batallón, and Páramo de las Rosas. Trujillo: El Paramito, between Jajó and Tuñame. 2900–3400 m.a.s.l., from the uppermost level of the Andean forest just below the timberline to shrubby subpáramo, also in extensions of forest growing at higher elevations along streams within otherwise open páramo habitat.

Additional specimens examined (selection): *A. Jahn 730* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2701* (US), *C. Sobrevila & A. Weitzman 1542* (US), *M. López-Figueiras 13992* (US).

35.2. Espeletia occulta S.F. Blake subsp. *glossophylla* (Mattf.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus occultus* (S.F. Blake) Cuatrec. subsp. *glossophyllus* (Mattf.) Cuatrec., Mem. New York Bot. Gard. 107: 465. 2013. TYPE: COLOMBIA. Magdalena: Mamancanaca valley, Sierra Nevada de Santa Marta, 3450 m.a.s.l., 8 March 1928, *A. Schultze 1300* (Holotype: B [destroyed], photo 15153 in F).

Homotypic synonyms: *Espeletia glossophylla* Mattf., Notizbl. Bot. Gart. Berlin-Dahlem 10: 702. 1929.

Libanothamnus glossophyllus (Mattf.) Cuatrec., Phytologia 35: 50. 1976.

Heterotypic synonyms: *Espeletia subneriifolia* Cuatrec., Mutisia 16: 3. 1953. TYPE: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta, about 30 km inland from Dibulla, 3850 m.a.s.l., July 1932, *W. Seifriz 440* (Holotype: US; Isotype: COL).

Libanothamnus subneriifolius (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Espeletia occulta subsp. *glossophylla* can be distinguished from other subspecies by its leaves with large length-to-width ratios (> [6]8:1), smaller disc corollas (< 5.0 mm), and copiously glanduliferous fertile phyllaries and pales (Cuatrecasas, 2013: 456).

Distribution: COLOMBIA. Magdalena: Sierra Nevada de Santa Marta. 3400–3800 m.a.s.l., in open páramo. According to Cuatrecasas (2013: 470), this taxon can also be found as low as 2550 m.a.s.l., in shrubby subpáramo habitat (although probably not anymore due to habitat destruction), and as high as 4000 m.a.s.l. along streams.

Additional specimens examined (selection): *W. Seifriz 440* (US), *H. Cuadros & A. Gentry 2729* (US), *S. White & W. Alverson 622* (US), *J. Hanbury-Tracy 312* (US).

35.3. Espeletia occulta S.F. Blake subsp. ***humbertii*** (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus occultus* (S.F. Blake) Cuatrec. subsp. *humbertii* Cuatrec., Mem. New York Bot. Gard. 107: 461. 2013. TYPE: VENEZUELA. Mérida: Sierra Nevada de Santo Domingo, versant NW, Laguna Negra, 3600 m.a.s.l., 21 September 1952, *H. Humbert 26441* (Holotype: P; Isotypes: COL, F, P, US, VEN [not seen]).

Homotypic synonyms: *Espeletia humbertii* Cuatrec., Notul. Syst. 15: 233. 1956b.

Libanothamnus humbertii (Cuatrec.) Cuatrec., Phytologia 35: 50. 1976.

Tree profusely branched, height up to 10 m. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length 18–35 cm, width 3.5–6.0 cm, ratio (4.0)4.5–6.0(7.0):1 (young individuals may have bigger leaves), margins frequently dentate, teeth 0.2–0.4 mm long and 2–5 mm apart, secondary nerves parallel, 1.0–2.5(3.0) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, usually not exceeding the surrounding leaves, length 15–30 cm, branched near the base. *Capitulum* diam. 13–16 mm, ligular circle 22–30 mm, disc 12–15 mm, ray ligules white, cream, greenish, or yellowish. *Espeletia occulta* subsp. *humbertii* can be distinguished from subsp. *occulta* for its larger length-to-width leaf ratios, smaller capitulum diam. (13–16 mm vs. 14–22 mm), and slender sterile phyllaries (8–13 mm × 5.0–6.5 mm vs. 12–20 mm × 6.0–9.0 mm).

Distribution: VENEZUELA. Mérida: páramos along the central and north sections of the Sierra Nevada de Mérida, Sierra de Santo Domingo, and Páramo de Los Granates. Sierra de la Culata, from Páramo de Los Conejos to the páramos between Piñango and Timotes. 3300–3800 m.a.s.l., from the uppermost level of the Andean forest just below the timberline to shrubby subpáramo, extensions of forest growing at higher elevations along streams, and some relatively humid and protected locations within open páramo habitat.

Additional specimens examined (selection): *H. Humbert 26441* (F, P, US), *M. López-Figueiras 8741* (US), *L. Ruiz-Terán 6276* (US), *L. Ruiz-Terán 7008* (US).

35.4. Espeletia occulta S.F. Blake subsp. ***oroquensis*** (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus occultus* (S.F. Blake) Cuatrec. subsp. *oroquensis* Cuatrec., Mem. New York Bot. Gard. 107: 471. 2013. TYPE: COLOMBIA. Norte de Santander-Cesar: Las Jurisdicciones, Cerro de Oroque, 20 km al S. de Abrego, 3700–3900 m.a.s.l., 22–27 July 1974, *H. García-Barriga & R. Jaramillo-Mejía 20600* (Holotype: US; Isotypes: COL, U, US).

Espeletia occulta subsp. *oroquensis* is morphologically very close to subsp. *occulta*, from which it can be distinguished by its larger receptacle diam. (8–9 mm vs. 5–6 mm) and the presence of numerous glands on the surface of its fertile phyllaries and pales (Cuatrecasas, 2013: 471). These differences are nonetheless rather subtle and based on the inspection of a few samples. Further studies will be necessary before the status of *E. occulta* subsp. *oroquensis* can be firmly validated.

Distribution: COLOMBIA. Norte de Santander-Cesar: known only from the type locality. According to Cuatrecasas (2013: 471), this taxon can be found at 3700–3900 m.a.s.l., growing close to the locally high-elevation limit between the upper Andean forest and the subpáramo habitat in sandstone hills.

Additional specimens examined (selection): *H. García-Barriga & R. Jaramillo-Mejía 20600* (U, US), *H. García-Barriga & R. Jaramillo-Mejía 20601, H. García-Barriga & R. Jaramillo-Mejía 19731* (U, US), *19771* (U, US).

36. *Espeletia paltonioides* Standl., Amer. J. Bot. 2: 482. 1915. TYPE: VENEZUELA. Trujillo: Páramo de las Rosas, 3200 m.a.s.l., October 1912, *A. Jahn 159* (Holotype: US; Isotype: VEN [not seen]). Fig. 112–115.

Homotypic synonym: *Ruilopezia paltonioides* (Standl.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 10 m, mostly leafless, occasionally with marcescent leaves below the rosette. *Leaf* open sheath, sessile (but strongly attenuated at the base), adaxially with short pubescence, strigose, greenish-greyish aspect, length 30–45 cm, width 1.4–3.0 cm, ratio 12–20:1, secondary nerves frequently obsolete or thin, 6–8 mm apart when visible. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 30–50 cm, branched near the base. *Capitulum* diam. 8–12 mm, ligular circle 14–15 mm, disc 7–10 mm, short ray ligules pale green or pale yellow. *Espeletia paltonioides* can be distinguished from other species by its tall leafless monocarpic rosette habit, its greenish leaves strongly attenuated at the base and with large length-to-width ratio (> 12:1), and its shortly radiated capitulum with yellowish/greenish ligules.

Distribution: VENEZUELA. Trujillo: Páramo de Guaramacal, de la Cristalina, and de Cabimbú. Border Trujillo-Lara: Páramo de las Rosas, de Cendé, and del Turmal. Border Trujillo-Barinas-Mérida: Páramo de Guirigay. Mérida: Páramo de Los Granates in Sierra Nevada de Santo Domingo and Páramo de Palmira (NE of Piñango). 2600–3200 m.a.s.l., in the upper level of the Andean forest below the timberline (Fig. 115).

Additional specimens examined (selection): *A. Jahn 159* (US), *M. López-Figueiras & J. Dugarte 29413* (US), *H. Werff & F. Ortega 6085* (US), *M. López-Figueiras 13943* (US), *L. Ruiz-Terán & J. Dugarte 12419* (US).

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FIGURES 112–113. *Espeletia paltonioides* Standl. **112**. Páramo de Guaramacal, Trujillo, Venezuela (Photograph by S. Aubert). **113**. *Espeletia paltonioides,* Páramo de Cendé, Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 114. *Espeletia paltonioides* Standl. Páramo de Cendé, Trujillo, Venezuela (Photograph by S. Aubert).

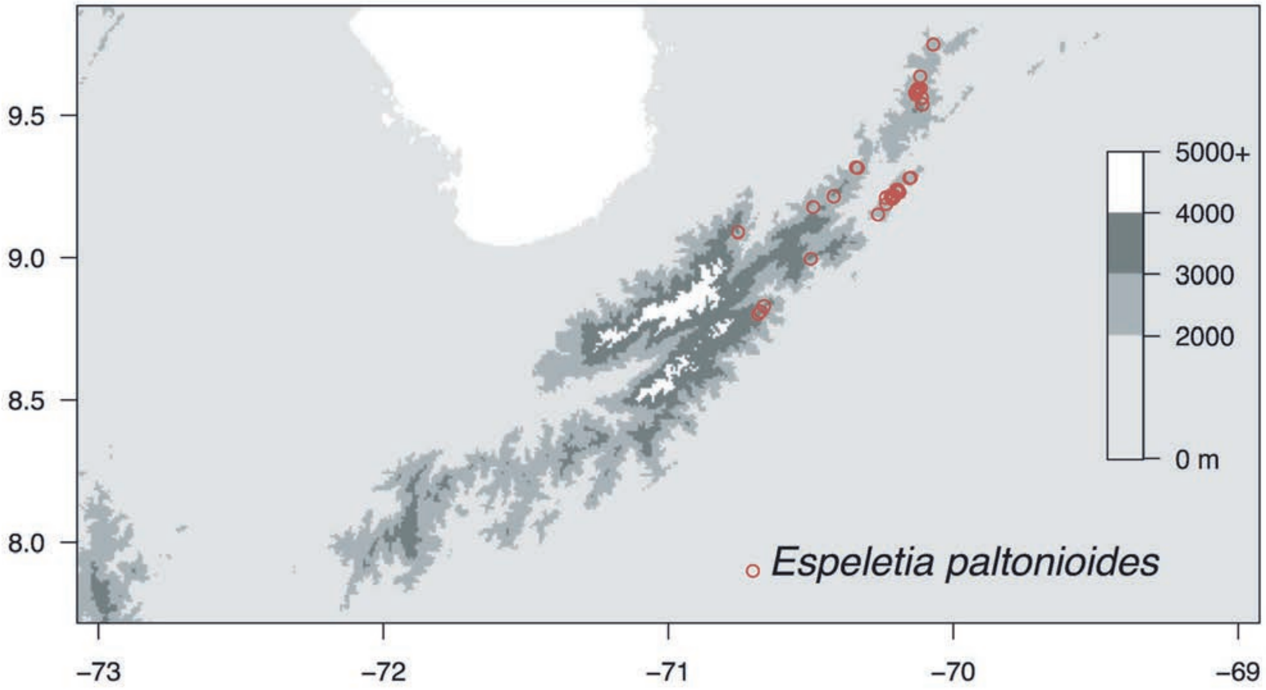

FIGURE 115. Distribution of *Espeletia paltonioides* Standl.

37. Espeletia palustris (Diazgr. & Morillo) Mavárez, *comb. nov.*

Basionym: *Coespeletia palustris* Diazgr. & Morillo, Phytokeys 28: 9. 2013. TYPE: VENEZUELA. Mérida: Páramo de Santo Domingo, alrededores de laguna de los Patos, en zona de turbera, 3729 m, 8.77522 N, -70.80349 E, 29 September 2011, *G. Morillo*, *M. Diazgranados*, *L. Gámez*, *S. Rodríguez & J. Parra 14155* (Holotype: MER; Isotype: VEN [not seen]). Fig. 116–118.

Rosette polycarpic, usually sessile, rarely with a short stem up to 0.2 m. *Leaf* open sheath, pseudopetiolate (length 2 cm), adaxially densely pubescent, lanuginose, whitish-grayish aspect, length 28–38 cm, width 0.7–1.3 cm, ratio 28–35:1, secondary nerves parallel, (2.0)2.5–4.0 mm apart. *Inflorescence* lateral, simple, monocephalous, axes 60–80 cm, aphyllous. *Capitulum* diam. 45–65 mm, ligular circle about the same size as the involucre, disc 22–24 mm, ligules bright yellow, becoming brownish/reddish toward the apex. *Espeletia palustris* can be easily recognized by its polycarpic rosette habit with long linear leaves and monocephalous inflorescences with large capitula. It resembles *E. moritziana*, from which it can be distinguished for its whitish indumentum (vs. yellowish–greenish), bigger sheaths (7.0–10.0 cm × 2.2–2.5 cm vs. 5.0–7.0 cm × 0.9–2.2 cm), aphyllous inflorescences (vs. bracteate), sterile phyllaries with dishevelled pubescence (vs. relatively ordered), and capitula with smaller number of both disc (215–280 vs. 600–860) and ray (95–200 vs. 400–740) flowers.

Distribution: VENEZUELA. Mérida: Páramo de Santo Domingo, de Los Granates, and de Gavidia in Sierra Nevada de Mérida, and Páramo El Banco in Sierra de la Culata. 3500–4000 m.a.s.l., in swampy and wet locations nearby marshes, lakes, and streams (Fig. 118).

Additional specimens examined (selection): *H. Barclay & P. Juajibioy 9741* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28055* (F, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28057* (F, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28584* (US), *L. Aristeguieta 2445* (US).

FIGURE 116. *Espeletia palustris* (Diazgr. & Morillo) Mavárez. Páramo el Banco, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 117. *Espeletia palustris* (Diazgr. & Morillo) Mavárez. Laguna de los Patos, Mérida, Venezuela (Photograph by L. Gámez).

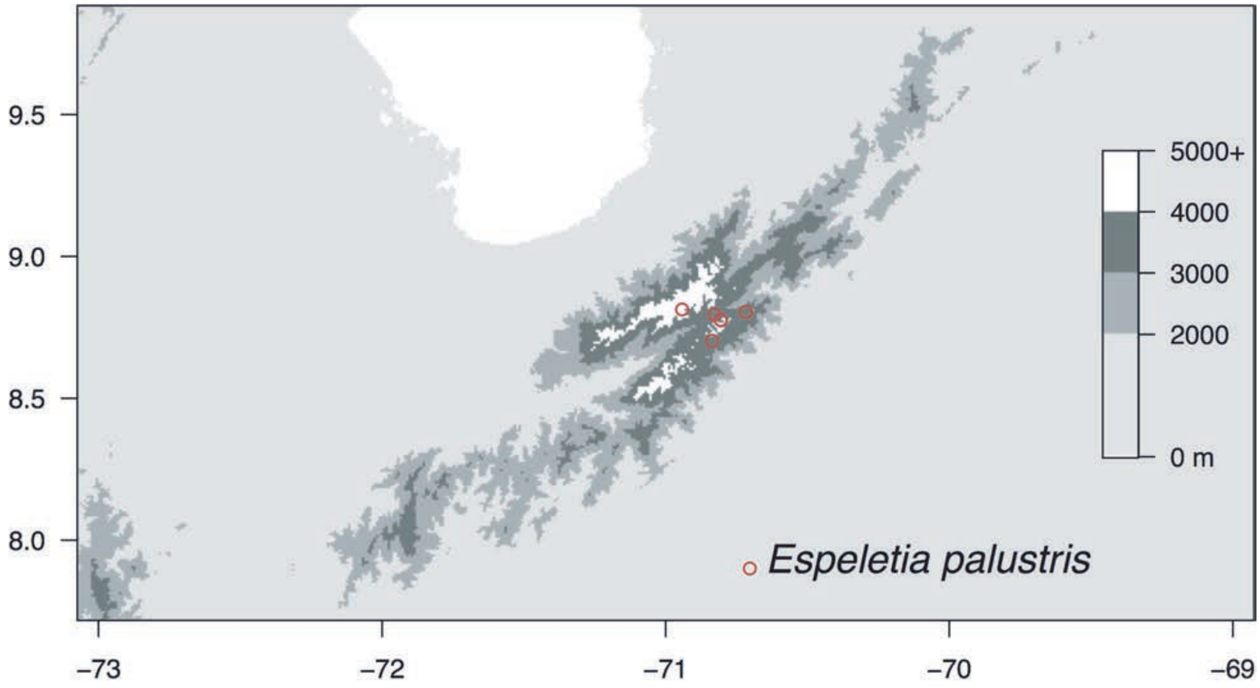

FIGURE 118. Distribution of *Espeletia palustris* (Diazgr. & Morillo) Mavárez.

38. ***Espeletia pannosa*** Standl., Amer. J. Bot. 2: 480. 1915. TYPE: VENEZUELA. Trujillo: Páramo del Jabón, 3000–3200 m.a.s.l., October 1910, *A. Jahn 165* (Lectotype: US, designated here). Fig. 119–121.

Homotypic synonym: *Espeletiopsis pannosa* (Standl.) Cuatrec., Phytologia 35: 56. 1976.

Heterotypic synonym: *Espeletia sericea* Cuatrec., Ciencia (México) 6: 263. 1945. TYPE: VENEZUELA. Mérida: Mucurubá, 3500–4000 m.a.s.l., 18 July 1930, *W. Gehriger 342* (Holotype: VEN [not seen]; Isotypes: F, G, MO, US).

Rosette polycarpic, sessile. *Leaf* open sheath, sessile, adaxially pubescent, appressed silvery-sericeous, length 25–45 cm, width 0.4–1.0 cm, ratio 30–40:1, secondary nerves obsolete or very thin, 1–3 mm apart when visible. *Inflorescence* lateral, compound, primary branching monochasial, corymboid, 45–60 cm, vegetative part about half the total length, with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle 25–30 mm, disc 12–15 mm, ray ligules white. *Espeletia pannosa* can be distinguished from all other species for its polycarpic rosette habit, leaves adaxially covered with shiny silvery-sericeous indumentum and capitula with white ligules. It closely resembles *E. angustifolia*, from which it differs in its more slender leaves (ratio 30–40:1 vs. 20–25:1), adaxially covered with silvery/sericeous indumentum (*vs*. lanuginose).

Distribution: VENEZUELA. Mérida: widespread in páramos of Sierra de la Culata and Sierra Nevada de Mérida. 3100–4000 m.a.s.l., in open páramo meadows and well-drained slopes (Fig. 121).

Additional specimens examined (selection): *A. Jahn 165* (US), *C. Sobrevila*, *A. Weitzman & D. Solbrig 1551* (US), *M. López-Figueiras 23689* (US), *L. Ruiz-Terán 7914* (US), *L. Ruiz-Terán & M. López-Figueiras 1607* (US) .

The original type of *Espeletia pannosa* Standl. is *A. Jahn 165*, from Páramo del Jabón, 3000–3200 m.a.s.l., Trujillo, Venezuela, October 1910 (US). However, *A. Jahn 165* is a mixture of two taxa, *E. pannosa* Standl. and *E. floccosa* Standl. José Cuatrecasas noticed the mixing in *A. Jahn 165* and added a handwritten note to the specimen, designating part of it as the holotype of *Espeletiopsis pannosa* (Standl.) Cuatrec. According to Art. 9.14 of the ICN, when a type contains parts that belong to more than one taxon, a lectotype must be designated for the part that corresponds most with the original description or diagnosis.

39. Espeletia parvula (Cuatrec.) Mavárez, *comb. nov.*

Basionym: *Libanothamnus parvulus* Cuatrec., Phytologia 47: 3. 1980b. TYPE: VENEZUELA. Border Lara-Trujillo: Laja del Díctamo, un sector de la vertiente oriental del Páramo de Cendé, 2900 m.a.s.l., 10 June 1971, *L. Ruiz-Terán & M. López-Figueiras 2036* (Holotype: US; Isotype: MERF). Fig. 122–124.

Shrub or *small tree* profusely branched, height up to 1 m. *Leaf* tubular sheath, sessile or with short pseudopetiole (length < 0.1 cm), adaxially glabrous, green, length 6–10(15) cm, width 2.5–4.5 cm, ratio 2.2–4.0(4.5):1, margins entire, secondary nerves parallel, 1.0–1.5(2.0) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, at the same level or slightly surpassing the surrounding leaves, length 5–10 cm, branched near base. *Capitulum* diam. 10–11(12) mm, ligular circle 15–21 mm, disc 9–10 mm, ray ligules white. *Espeletia parvula* can be distinguished from other species by its shrubby/tree habit with small size and its small sessile leaves (< 10(15) cm). It can look superficially similar to some small individuals of *E. neriifolia* var. *cristamontis*, but *E. parvula* has higher density of secondary nerves (1–2 mm vs. 2–4 mm apart), larger deviation angle (75–90˚ vs. 70–75˚), and larger sterile phyllaries (4.5–5.5 mm × 4.0–5.5 mm vs. 3.5–4.0 mm × 2.3–2.8 mm).

Distribution: VENEZUELA. Border Lara-Trujillo. Páramo de las Rosas, del Jabón, and de Cendé. 2900–3400 m.a.s.l., above the timberline, in the subpáramo habitat located in the eastern slopes of hills and crests exposed to the strong winds that predominate in the region (Fig. 124).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 2036* (US), *L. Dorr*, *L. Barnett*, *R. Rivero & W. Díaz 5323* (US), *M. López-Figueiras 32306* (US, this sample has leaves with pseudopetioles).

40. ***Espeletia ruizii*** Cuatrec., Phytologia 23: 362. 1972. TYPE: VENEZUELA. Mérida: Loma de la Libertad, Páramo de las Coloradas, unos 500 m después del Portachuelo (el Ramal) entre las poblaciones de Santa Cruz de Mora and el Molino, 2750–2800 m.a.s.l., 16 January 1971, *L. Ruiz-Terán & M. López-Figueiras 1457* (Holotype: US; Isotypes: MERF, NY, US). Fig. 125–127.

Homotypic synonym: *Ruilopezia ruizii* (Cuatrec.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, caulescent, stem height up to 1.5 m, most individuals with the upper half of the stem covered by marcescent leaves, some entirely marcescent, a few entirely naked. *Leaf* open sheath, sessile, linear, adaxially glabrescent, glossy green aspect, length 15–40 cm, width 0.5–1.8 cm, ratio 20–45:1, secondary nerves parallel, 1.5–2.5 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 30–80 cm, branched from the base. *Capitulum* diam. 15–18 mm (densely cottony), ligular circle 16–22 mm, covered by the tips of the sterile phyllaries, disc 8–12 mm, young ray ligules white, turning pink or reddish when old. *Espeletia ruizii* can be distinguished from other species by its caulescent monocarpic rosette habit, its sessile, linear, glossy green leaves, and its capitulum with long cottony sterile phyllaries conspicuously surpassing the ligular circle and pinkish/reddish old ray ligules.

Distribution: VENEZUELA. Mérida: Páramo de las Coloradas, in the southern end of Sierra Nevada de Mérida. Between 2700–3100 m.a.s.l., in dry and exposed rocky slopes within subpáramo habitat (Fig. 127).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 1457* (NY, US), *P. Berry*, *R. Calvo & S. Beaujon 4374* (US), *M. López-Figueiras & H. Rodríguez 9045* (US), *L. Ruiz-Terán & S. López-Palacios 1869* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28510* (F, US).

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FIGURES 119–120. *Espeletia pannosa* Standl. Estación la Aguada, Mérida, Venezuela (Photographs by S. Aubert).

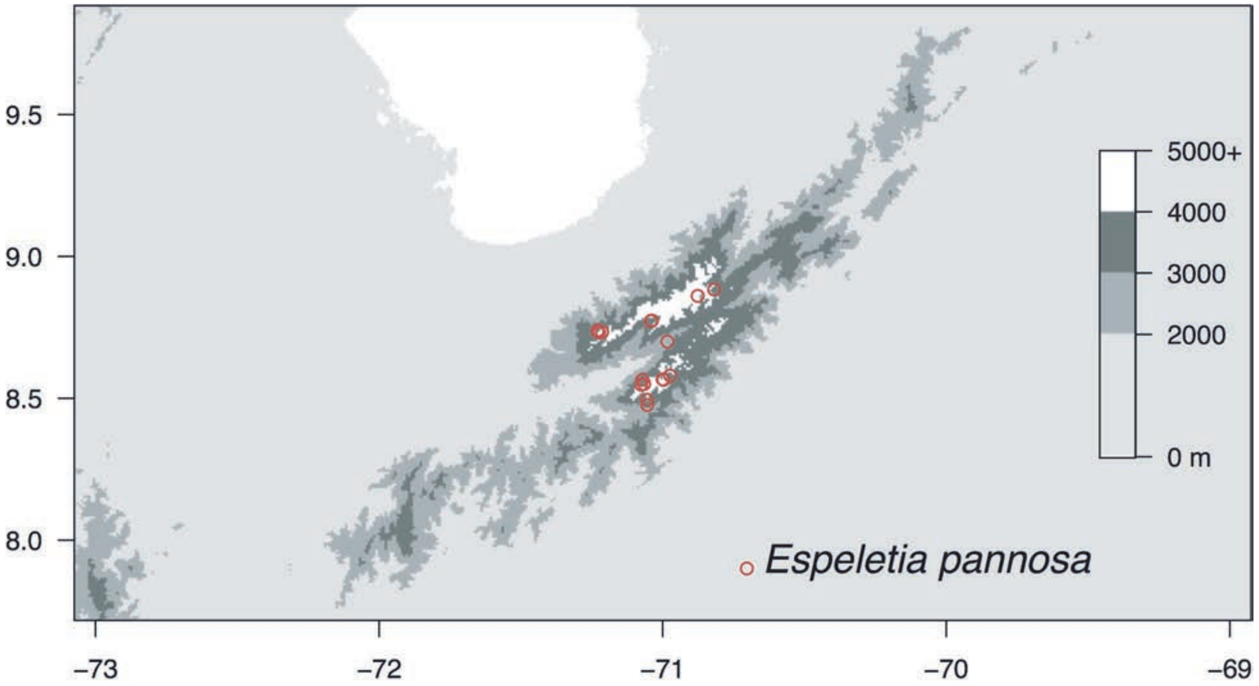


FIGURE 121. Distribution of *Espeletia pannosa* Standl.

FIGURE 122. *Espeletia parvula* (Cuatrec.) Mavárez. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

FIGURE 123. *Espeletia parvula* (Cuatrec.) Mavárez. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

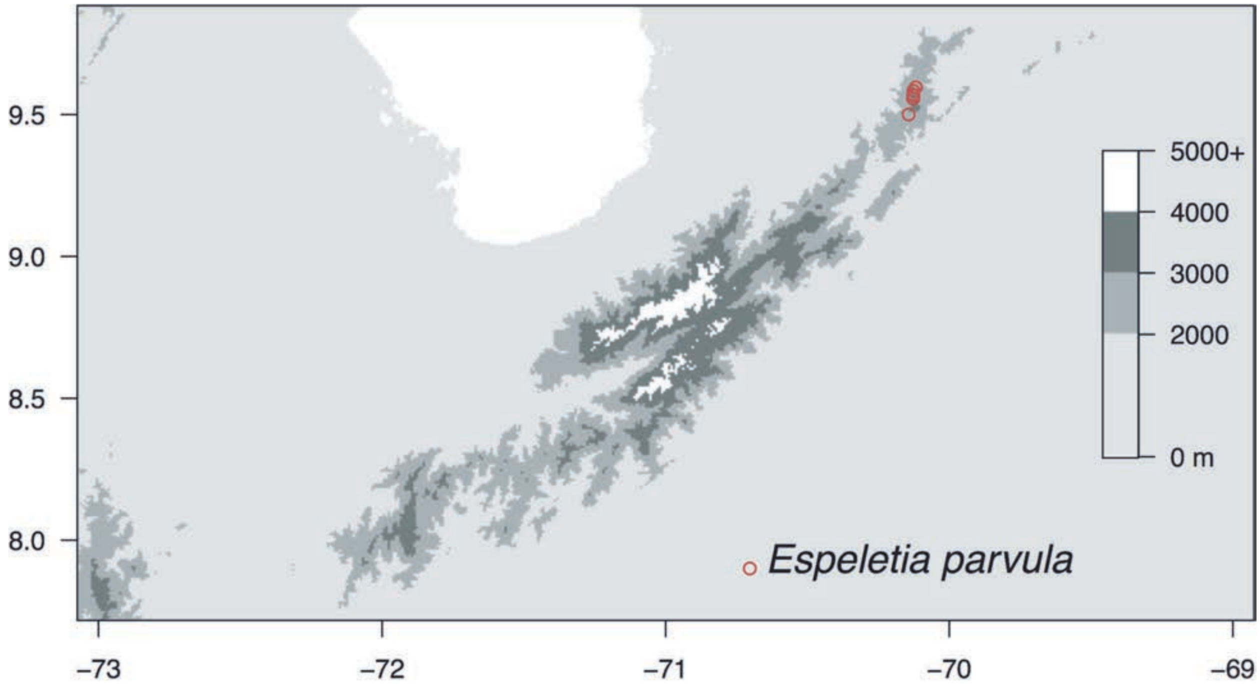
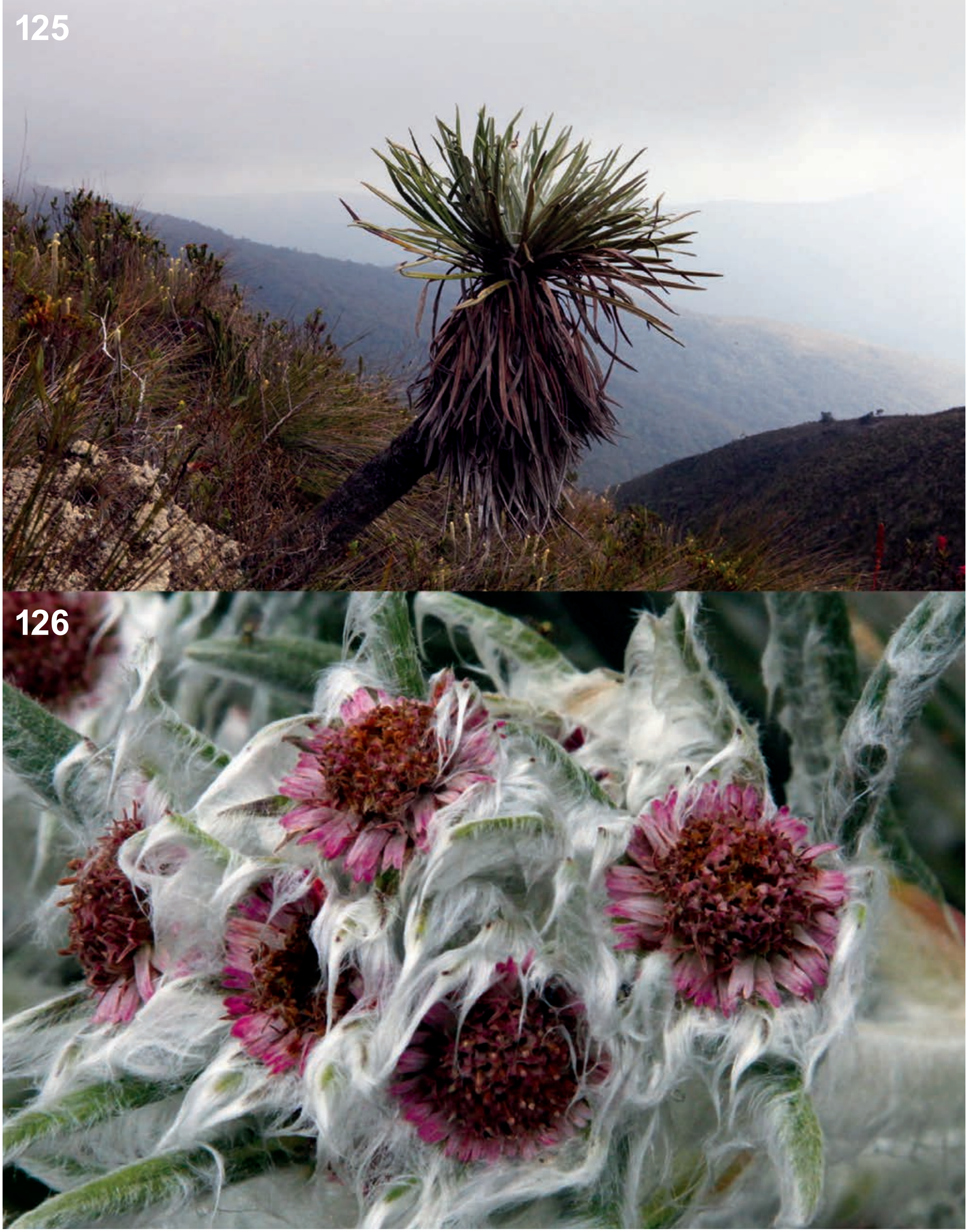


FIGURE 124. Distribution of *Espeletia parvula* (Cuatrec.) Mavárez.



FIGURES 125–126. *Espeletia ruizii* Cuatrec. Páramo las Coloradas, Mérida, Venezuela (Photographs by S. Aubert).

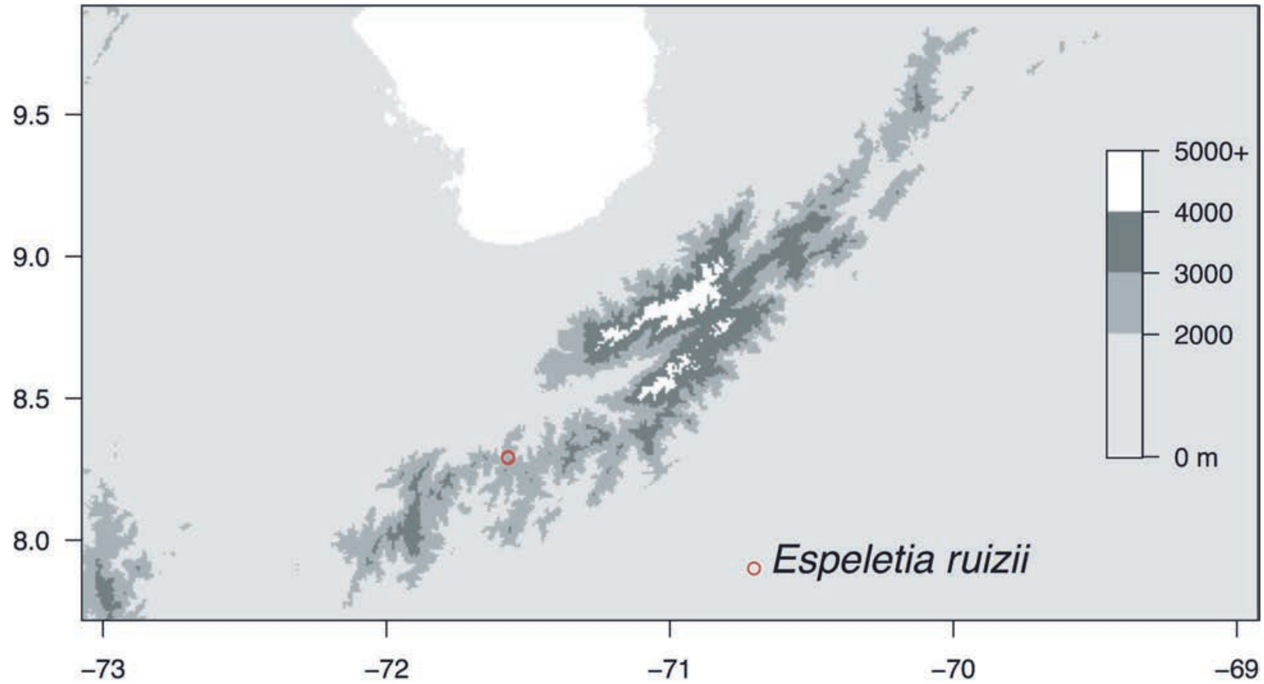


FIGURE 127. Distribution of *Espeletia ruizii* Cuatrec.

41. *Espeletia schultzii* Wedd., Chlor. Andina: 63. 1855. TYPE: VENEZUELA. Mérida: Páramos dans la province de Mérida, 10.000 à 11.000 pieds, Juin 1842(1843), *J. Linden 370* (Syntype: P; Isosyntypes: BR, F, FI [not seen], G, P, US, W), *Moritz 1419* (Syntype: P; Isosyntypes: BR, G, K, P, W). Fig. 128–130.

Rosette polycarpic, usually sessile, occasionally caulescent with a stem height up to 1.0 m, entirely covered by marcescent leafs. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate-lanuginose, whitish-grayish aspect, length 25–50 cm, width 3.0–8.0 cm, ratio 4.7–12.0:1, bases of secondary nerves parallel, unevenly distributed, 4–12 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, thyrsoid, length 70–180 cm, vegetative part usually with 2–3 pairs of opposite bracts. *Capitulum* diam. (12)20–30 mm, ligular circle (22)30–50 mm, disc (9)12–18 mm, ray ligules yellow. *Espeletia schultzii* is easily recognizable by its polycarpic rosette habit, sessile leaves and dichasial thyrsoid inflorescences. It superficially resembles *E. aristeguietana*, from which it can be distinguished by its larger capitulum and leaves with whitish/grayish lanuginose indumentum (vs. greenish tomentose-velvety).

Distribution: VENEZUELA. Mérida: widespread in Sierra Nevada de Mérida, Sierra de la Culata, Sierra de Santo Domingo, and southward to Páramo de San José and Páramo de Mijará. Trujillo: Páramo de Tuñame, de Teta de Niquitao, de Cabimbú, and de la Cristalina. Border Trujillo-Barinas: Páramo de Guirigay and de Ortiz. *Espeletia schultzii* has the broadest elevation span of any Espeletiinae, ca. 2400–4500 m.a.s.l. (Fig. 6), and the second largest geographic distribution among rosette plants (after Colombian *E. hartwegiana* Cuatrec.) The species is found near the upper limit of the Andean forest, in shrubby subpáramo, in proper páramo, and in protected spots in the superpáramo. It thrives particularly well in the undisturbed open páramos, but also in more disturbed locations such as recent forest clearings, road margins, and abandoned agricultural fields. In fact, *E. schultzii* is only absent from the extremely cold and dry superpáramo locations and the very humid areas around swamps, ponds, and streams (Fig. 130).

Additional specimens examined (selection): *J. Linden 370* (BR, F, G, P, US, W), *P. Berry 4621* (US), *P. Berry 4411* (US), *M. López-Figueiras 30155* (US), *L. Dorr*, *L. Barnett & B. Stergios 9283* (US).

Weddell (1855: 64) cited two specimens in the protologue of *E. schultzii*: *Linden 370* and *Moritz 1419*, without designation of either as the nomenclatural type. According to the ICN (Art. 9.5), these specimens must be considered as syntypes; however, most herbaria treat *Linden 370* as the holotype and *Moritz 1419* as a paratype. This should be corrected wherever necessary.

Espeletia schultzii has been found to hybridize with *E. angustifolia*, *E. banksiifolia*, *E. batata*, *E. floccosa*, *E. grisea*, *E. lindenii*, *E. margarita*, *E. moritziana*, *E. nana*, *E. neriifolia*, *E. occulta*, *E. pannosa*, *E. spectabilis*, *E. spicata*, *E. tenorae*, *E. timotensis*, and *E. weddellii*.

As do other Espeletiinae with broad distributions, *Espeletia schultzii* exhibits large morphological diversity, particularly with regard to leaf shape, inflorescence size and architecture, and capitulum size. Cuatrecasas (2013: 345–347) examined this variation and concluded that it is best described as representing four varieties within a single species: a widespread nominal variety (*E. schultzii* var. *schultzii*), plus three varieties with somehow restricted geographic distributions: *E. schultzii* var. *bractilobata*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FIGURES 128–129. *Espeletia schultzii* Wedd. Páramo de Piedras Blancas, Mérida, Venezuela (Photographs by S. Aubert).

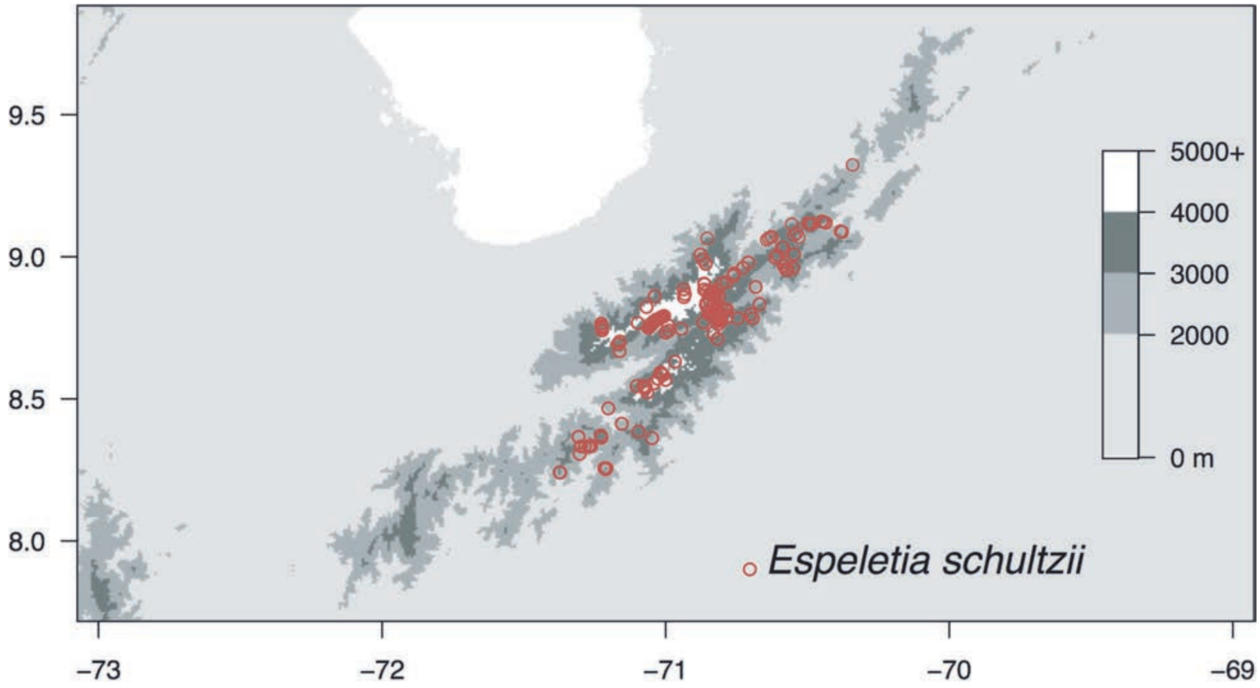

FIGURE 130. Distribution of *Espeletia schultzii* Wedd.

Cuatrec. (subpáramo between Jajó and Tuñame in Trujillo), *E. schultzii* var. *mucurubana* Cuatrec. (subpáramo above Mucurubá in Sierra de la Culata), and *E. schultzii* var. *subparamuna* Cuatrec. (subpáramos de la Cristalina in Trujillo and San José/la Veguilla in Mérida). I believe that some of the taxa represent in fact the extremes of morphological variation distributed continuously along elevational gradients. For instance, individuals from lower elevations frequently show the broader leaves, longer inflorescences, and larger capitula characteristic of *E. schultzii* var. *subparamuna*. On the other hand, over its broad distribution area, *E. schultzii* coexists in sympatry with more than 30 other *Espeletia*, hybridizing with at least 17 of them, which certainly contributes to the variation observed in this species (see note below). Thus, in places where hybridization is frequent between *E. schultzii* and other species with monochasial inflorescences and smaller capitula (e.g., *E. floccosa*), certain hybrids have the rosette appearance and leaf shapes of *E. schultzii* but exhibit inflorescence structures and capitulum sizes intermediate between the two parental species, looking very similar to *E. schultzii* var. *mucurubana*.

41.1 ***Espeletia schultzii*** Wedd. var. ***schultzii***.

41.2 ***Espeletia schultzii*** Wedd. var. ***bractilobata*** Cuatrec., Phytologia 45: 27. 1980a. TYPE: VENEZUELA. Trujillo: Paramillo above Jajó via Tuñame, 3100 m.a.s.l., 29 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28189* (Holotype: US; Isotypes: F, MERF, U).

Vegetative part of the inflorescence with some 2- or 3-lobed bracts.

Distribution: VENEZUELA. Trujillo: the type locality in the Morita-Paramito region between Jajó and Tuñame. Mérida: area between Los Frailes and Santo Domingo.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28189* (F, U, US), *C. Sobrevila 1513* (US), *L. Ruiz-Terán 2141* (US).

41.3 ***Espeletia schultzii*** Wedd. var. ***mucurubana*** Cuatrec., Phytologia 45: 28. 1980a. TYPE: VENEZUELA. Mérida: Páramo de Mucurubá, 3250 m.a.s.l., 20 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28148* (Holotype: US; Isotypes: F, MERF, U).

Inflorescences with predominant monochasial branching and smaller capitula (diam. 12–20 mm, ligular circle 22–28 mm, disc 9–13 mm).

Distribution: VENEZUELA. Widespread between 3000 and 3500 m.a.s.l., but relatively rare.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28148* (F, U, US), *M. López-Figueiras* 23696 (US), *C. Sobrevila*, *A. Weitzman & C. Estrada 1569* (US).

41.4 ***Espeletia schultzii*** Wedd. var. ***subparamuna*** Cuatrec., Phytologia 45: 29. 1980a. TYPE: VENEZUELA. Trujillo: Páramo de la Cristalina, 2500–2600 m.a.s.l., 17 February 1973, *J. Cuatrecasas*, *L. Ruiz-Terán*, *M. López-Figueiras 28557* (Holotype: US; Isotypes: BC, F, G, NY, MERF, US).

With broad leaves (ratio 4.7–6.5:1), a large number of flowers (ray: 100–170, disc: 150–340), and outer phyllaries abruptly acuminate.

Distribution: VENEZUELA. Widespread at the lower elevation ranges of the species, 2400–3200 m.a.s.l.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán*, *M. López-Figueiras 28557* (F, G, NY, US), *L. Ruiz-Terán & J. Dugarte 12248* (US), *L. Ruiz-Terán 9141* (US).

42. *Espeletia semiglobulata* Cuatrec., Ciencia (México) 6: 264. 1945. TYPE: VENEZUELA. Mérida: Páramo de Piedras Blancas, 3800 m.a.s.l., 17 May 1944, *V. M. Badillo 821* (Holotype: VEN [not seen]; Isotype: VEN [not seen]). Fig. 131–132.

Heterotypic synonym: *Espeletia rufescens* Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 88. 1956a. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 12,000 pieds, August 1842, *J. J. Linden 398* (Holotype: P [inflorescences in MNHN-P-P04086312]; Isotype: NY [inflorescences in barcode number 579543]).

Rosette polycarpic, usually sessile, sometimes caulescent, stem height up to 0.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, pseudopetiolate (length 15–25 cm), adaxially densely pubescent, appressed lanate, whitish-cinereous, length 35–50 cm, width 2.0–4.5 cm, ratio 10–20:1, secondary nerves parallel, 2–4 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, thyrsoid, length 1.5–2.0 m, vegetative part with 4–5 pairs of opposite bracts. *Capitulum* diam. 15–20 mm, ligular circle not exceeding the involucre (14–18 mm), disc 10–14 mm, ray ligules yellow. *Espeletia semiglobulata* can easily be distinguished from the other Venezuelan species with dichasial thyrsoid inflorescences by its long and thin pseudopetiolate leaves and its short-radiate capitula.

Distribution: VENEZUELA. Mérida: Sierra Nevada de Mérida, Sierra de Santo Domingo and Sierra de la Culata. 3800–4300 m.a.s.l., in very humid locations such as wet depressions and along the margins of streams, ponds, and small lakes (Fig. 132).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 272* (US), *L. Ruiz-Terán & M. López-Figueiras 351* (US); *id. 370* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28583* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28598* (F, U, US).

Other samples of *Linden 398* (MNHN-P-P02441483 in P, catalog number 1473203 in US) contain only material belonging to *E. moritziana* and should be considered as isosyntypes of that species (see notes on *E. moritziana*).

43. *Espeletia spectabilis* Cuatrec., Phytologia 27: 46. 1973a. TYPE: VENEZUELA. Mérida: Páramo de San José, Zanjón del Cupís, orillas de la carretera San José-Mucutuy, a 7 km de San José, 3100 m.a.s.l., 18–21 November 1972,

FIGURE 131. *Espeletia semiglobulata* Cuatrec. Páramo de Piedras Blancas, Mérida, Venezuela (Photograph by S. Aubert).

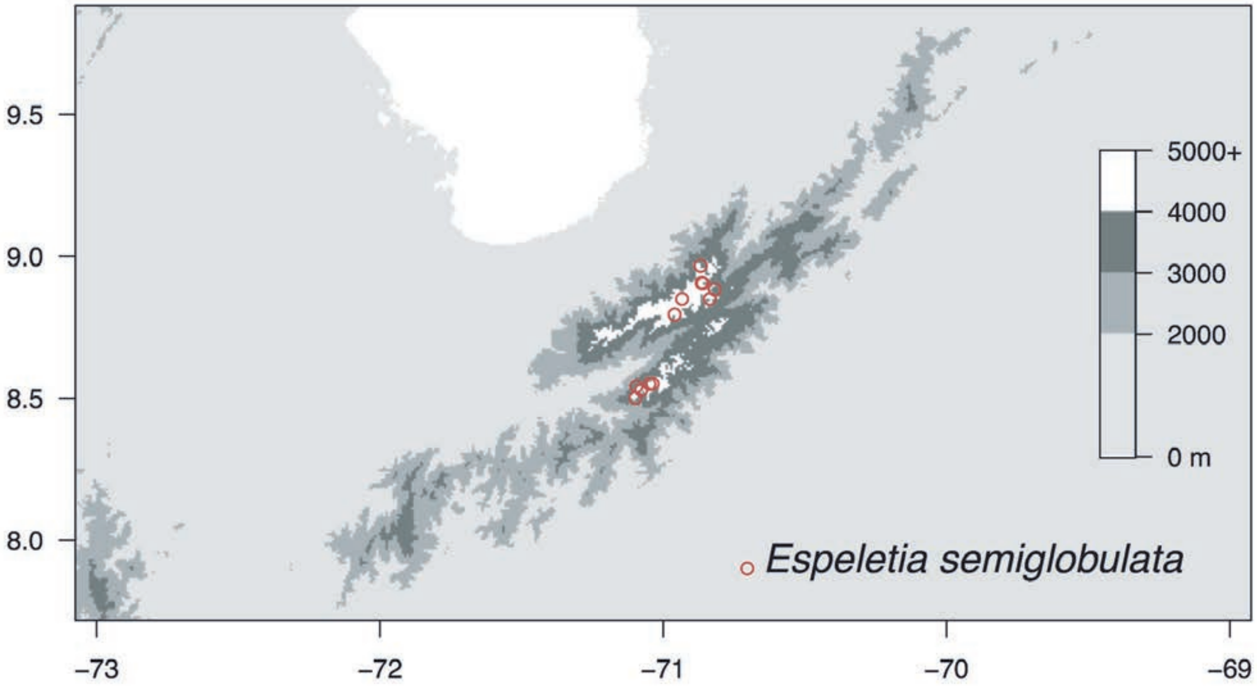

FIGURE 132. Distribution of *Espeletia semiglobulata* Cuatrec.

M. López-Figueiras, H. A. Rodríguez, J. Wurdack & M. Wurdack 8912 (Holotype: US; Isotypes: BC, F, G, K, MERF, MO, NY, US). Fig. 133–136.

Homotypic synonym: *Libanothamnus spectabilis* (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Tree monocarpic, unbranched stem, stem height up to 10 m, mostly leafless, marcescent leaves only below the apical rosette of green leaves. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length (25)40–65 cm, width 7.5–15.0 cm, ratio (3.5)4.0–5.0(6.5):1, margins frequently entire, sometimes with small teeth up to 1.0 mm long, secondary nerves parallel, 1.5–3.0(4.0) mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, largely surpassing the surrounding leaves, length 40–60 cm, branched near the base. *Capitulum* diam. 15–20 mm, ligular circle (25)30–35 mm, disc (12)14–18 mm, ray ligules cream or yellowish. *Espeletia spectabilis* is a truly exceptional species that can be easily distinguished from any other by its unique combination of tall monocarpic caulescent rosette habit and leaves with tubular sheaths. More generally, *E. spectabilis* exhibits a mixture of several ecological and morphological features characteristic of both trees and rosette plants, which suggests that this taxon could be the result of a hybrid speciation event involving branched and unbranched parental species (Pouchon et al. 2018).

Distribution: VENEZUELA. Mérida: Apparently restricted to the Páramo de San Jose and some nearby areas in the south of Sierra Nevada de Mérida. 3000–3200 m.a.s.l., limited to the belt within the uppermost level of the Andean forest and the subpáramo habitat (Fig. 136).

Additional specimens examined (selection): *M. López-Figueiras, H. Rodríguez & J. Wurdack & M. Wurdack 8912* (F, G, K, MO, NY, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28457* (US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28458* (F, U, US), *J. Cuatrecasas, L. Ruiz-Terán & M. López-Figueiras 28458A* (U, US), *L. Ruiz-Terán & S. López-Palacios 6651* (US).

44. *Espeletia spicata* Sch. Bip. ex Wedd., Chlor. Andina: 65. 1855. TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 14,000 pieds, August 1842, *J. Linden 400* (Holotype: P; Isotypes: F, FI [not seen], K, P). Fig. 137–139.

Homotypic synonym: *Coespeletia spicata* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35: 57. 1976.

Heterotypic synonyms: *Espeletia alba* A.C. Sm., Brittonia 1: 512, 1935. TYPE: VENEZUELA. Mérida: Páramo de Mucurubá, cabeceras de la quebrada del pueblo (El Rincón, El Colorado, Fila de Estití), Sierra Nevada de Mérida, 3900 m.a.s.l., April 1930, *W. Gehriger 125* (Holotype: G; Isotypes: F, MO, PH [not seen], NY, VEN [not seen]).

Coespeletia alba (A.C. Sm.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, caulescent, stem height up to 2.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate, whitish-cinereous, length 35–50 cm, width 1.2–2.0 cm, ratio 20–35:1, secondary nerves parallel, 4–6 mm apart. *Inflorescence* lateral, simple, monochasial, botryoid, axes 75–130 cm, (14)20–38 monocephalous peduncles, vegetative part with several alternate bracts. *Capitulum* diam. 15–25 mm, ligular circle shorter than the involucre, ray ligules yellow. *Espeletia spicata* can be easily distinguished from other species with strictly botryoid inflorescences by its leaves

FIGURES 133–135. *Espeletia spectabilis* Cuatrec. Páramo de San José, Mérida, Venezuela (Photographs by S. Aubert).

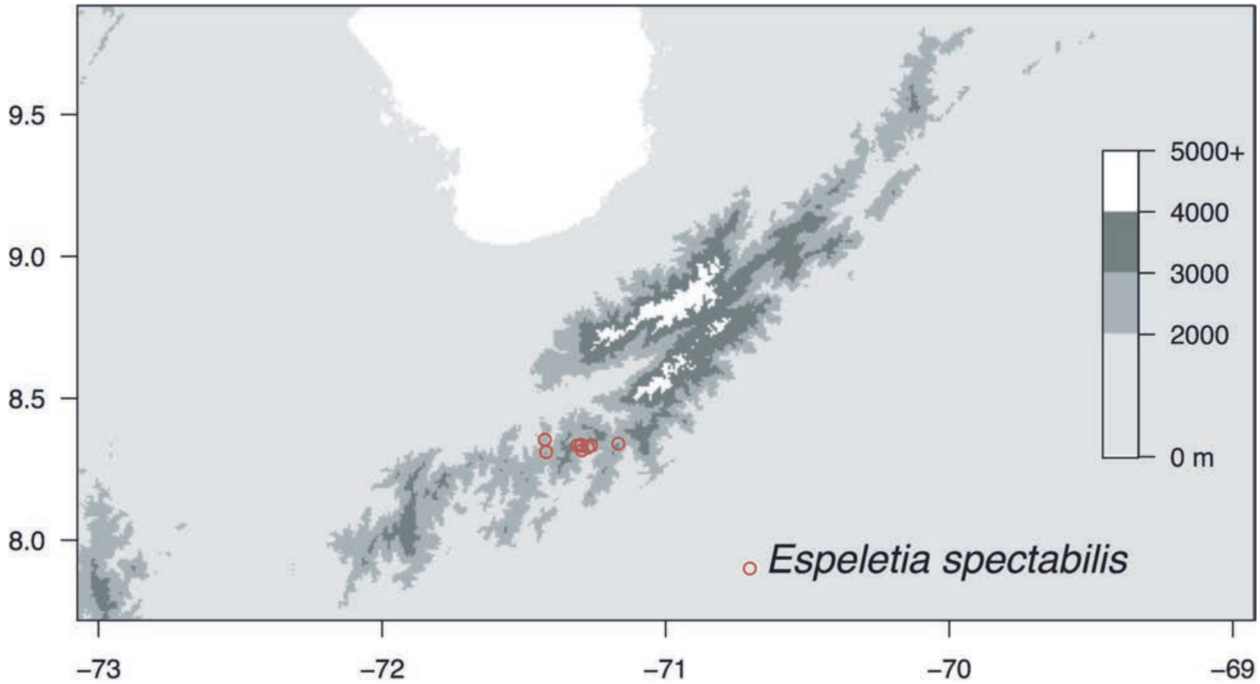

FIGURE 136. Distribution of *Espeletia spectabilis* Cuatrec.

FIGURE 137. *Espeletia spicata* Sch. Bip. ex Wedd. Páramo de Piedras Blancas, Mérida, Venezuela (Photograph by S. Aubert).

FIGURE 138. *Espeletia spicata* Sch. Bip. ex Wedd. Páramo de Piedras Blancas, Mérida, Venezuela (Photograph by S. Aubert).

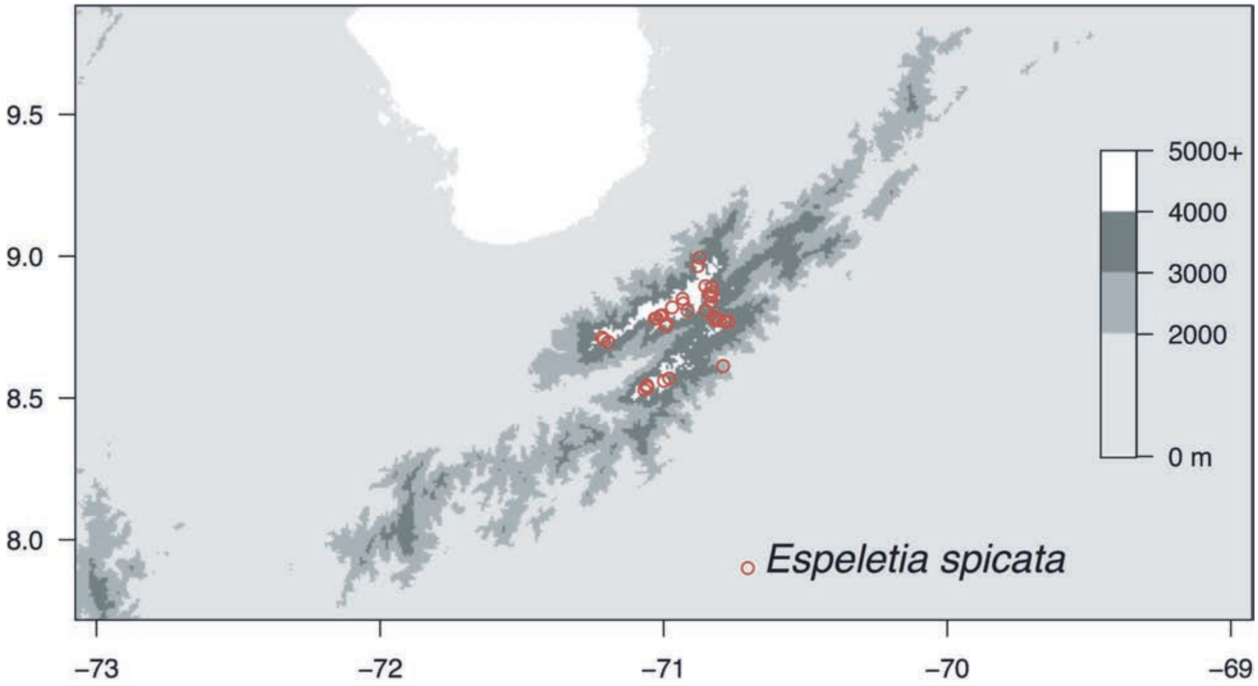

FIGURE 139. Distribution of *Espeletia spicata* Sch. Bip. ex Wedd.

with large length-to-width ratios (> 20:1), large number of peduncles (>[14]20), and small capitulum diam. (< 25 mm).

Distribution: VENEZUELA. Mérida: Sierra de la Culata and Sierra Nevada de Mérida. Superpáramos 3800–4300 m.a.s.l., locally reaching 4500 m.a.s.l. Frequently associated with *E. timotensis*, with *E. spicata* usually occupying the lower and more humid sections of the slopes (Fig. 139).

Additional specimens examined (selection): *J. Linden 400* (F, K, P), *L. Ruiz-Terán & M. López-Figueiras 203* (U, US), *L. Ruiz-Terán 6976* (US), *L. Ruiz-Terán 7770* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28117* (F, U, US).

Linden 400 in F labelled as from "Colombia."

45. ***Espeletia tamana*** Cuatrec., Phytologia 27: 171. 1973b. TYPE: VENEZUELA. Táchira: Cabeceras semiboscosas de la Quebrada El Reposo, 6–7 km N de Villa Páez, en el Páramo de Tamá, 2800 m.a.s.l., 28 June 1973, *L. Ruiz-Terán & M. López-Figueiras 8915* (Holotype: US; Isotype: MERF). Fig. 140–142.

Homotypic synonyms: *Libanothamnus tamanus* (Cuatrec.) Cuatrec., Phytologia 35: 51. 1976.

Tree moderately branched, height up to 5 m. *Leaf* tubular sheath, sessile or with short pseudopetiole (length 2.0–4.0 cm), adaxially glabrous, green, length 25–50 cm, width 3.0–6.5 cm, ratio 6–9:1, margins entire or with small teeth concealed under the indumentum, secondary nerves parallel, 1–2 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, surpassing the surrounding leaves, length 40–80 cm, vegetative part profusely bracteate, about a quarter of the total length. *Capitulum* diam. 10–12 mm, ligular circle 20–25 mm, disc 8–10 mm, ray ligules white. *Espeletia tamana* can be distinguished from other tree species for its pseudopetiolate leaves with lanceolate outline and sheaths barbate adaxially. *Espeletia tamana* can look similar to *E. banksiifolia*, but it has slender leaves (ratio > 6:1 vs. < 5:1) and shorter disc corollas (< 4 mm vs. > 4 mm).

Distribution: VENEZUELA. Táchira: Páramo de Tamá (extending towards Norte de Santander, Colombia). COLOMBIA. Arauca: headwaters of Río Casanare, on the eastern slopes of Sierra Nevada del Cocuy. 2700–3100 m.a.s.l., in the upper level of the Andean forest, below the timberline (Fig. 142).

Additional specimens examined (selection): *L. Ruiz-Terán & M. López-Figueiras 8915* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28322* (U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28353* (F, U, US), *M. López-Figueiras & M. E. Hale 9255* (US), *L. Ruiz-Terán, M. López-Figueiras & D. Griffin 12571* (US).

Collection date given as "2 June 1973" in Diazgranados (2012: 37) and Cuatrecasas (2013: 444).

FIGURE 140. *Espeletia tamana* Cuatrec. Páramo de Tamá, Táchira, Venezuela (Photograph by S. Aubert).

FIGURE 141. *Espeletia tamana* Cuatrec. Páramo de Tamá, Táchira, Venezuela (Photograph by S. Aubert).

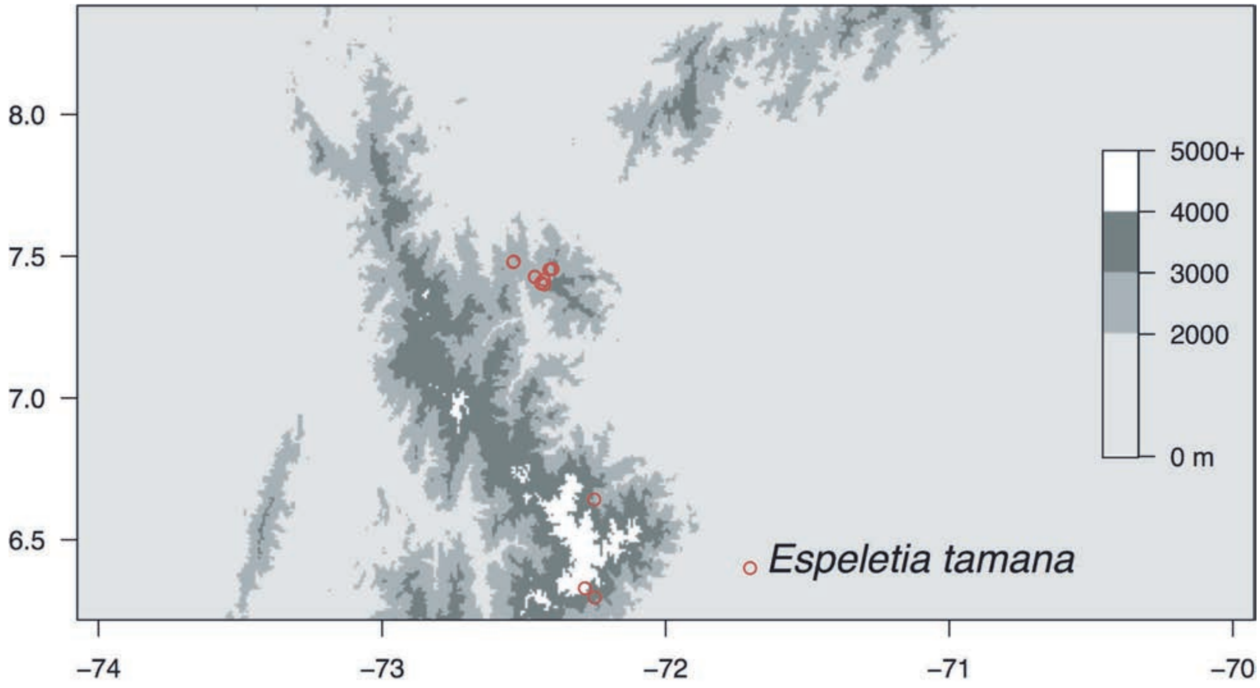

FIGURE 142. Distribution of *Espeletia tamana* Cuatrec.

46. ***Espeletia tenorae*** Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 275. 1959. TYPE: VENEZUELA. Trujillo: Páramo del Guirigay, hacia Laguna la Parida, 3500 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3572* (Holotype: VEN [not seen]; Isotypes: NY, US). Fig. 143–145.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate, whitish-cinereous, length 4–7 cm, width 0.4–0.7 cm, ratio 10–14:1, secondary nerves reticulate. *Inflorescence* lateral, simple, monocephalous, length 25–50 cm, usually without bracts, sometimes with 1–2 opposite or alternate bracts near the distal part. *Capitulum* diam. 40–50 mm (densely cottony), ligular circle shorter than the floccose involucre (20–30 mm), disc 16–18 mm, ray ligules yellow. *Espeletia tenorae* can be distinguished from all other Venezuelan dwarf rosette plants with monocephalous inflorescences by its leaf sheaths glabrous on both sides and its inflorescences usually aphyllous or with 1–2 distal bracts. *Espeletia tenorae* is also the Venezuelan dwarf rosette with the largest proportion of ray flowers (53%–57%).

Distribution: VENEZUELA. Border Mérida and Trujillo: known only from the type locality and nearby areas in Páramo de Guirigay. 3300–3500 m.a.s.l., in swampy areas, humid depressions, and ponds (Fig. 145).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3572* (NY, US), *B. Stergios*, *L. Dorr & K. Wurdack 20327* (US), *L. Ruiz-Terán & M. López-Figueiras 13127* (US), *L. Ruiz-Terán & M. López-Figueiras 13128* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28167* (F, U, US).

47. ***Espeletia thyrsiformis*** A.C. Sm., Brittonia 1: 513. 1935. TYPE: VENEZUELA. Mérida: Páramo de Mucuchíes, December 1927, *R. Gutzwiller 36* (Holotype: US; Isotypes: G, NY). Fig. 146–148.

Homotypic synonym: *Coespeletia thyrsiformis* (A.C. Sm.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, usually sessile, sometimes caulescent, stem height up to 0.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile, adaxially densely pubescent, lanate, whitish-cinereous, length 25–50 cm, width 4.5–8.0 cm, ratio 4–10:1, bases of secondary nerves parallel, 5–10 mm apart. *Inflorescence* lateral, compound, monochasial, botryoid-paniculate, axes 70–130 cm, 17–35 peduncles, proximal polycephalous (3–7 capitula), proximal part with several alternate bracts. *Capitulum* diam. 15–20 mm, ligular circle about the same size or slightly shorter than the involucre, disc 10–12 mm, ray ligules yellow. *Espeletia thyrsiformis* can be distinguished from all other Venezuelan species for its sessile or subsessile leaves with low length/width ratio (4–10:1) and botryoid-paniculate inflorescences with a moderate number of peduncles (17–33).

Distribution: VENEZUELA. Northern Táchira and nearby Mérida: south-western end of the Cordillera de Mérida in Páramo del Batallón, de la Negra, del Rosal and del Zumbador. Between 2800–3600 m.a.s.l., in grassy and dry páramos with rocky soils, but also in some humid depressions (Fig. 148).

Additional specimens examined (selection): *R. Gutzwiller 36* (G, NY, US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28002* (F, U, US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28017* (F, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28430* (F, U, US), *M. López-Figueiras 13993* (US).

The type locality "Páramo de Mucuchíes" in *Gutzwiller 36* is certainly a mistake. The species is endemic to the region around Páramo del Batallón, de la Negra, and del Zumbador, more than 70 km to the south of Páramo de Mucuchíes. Other numbers in R. Gutzwiller collections suggest that the correct type locality for the type of *E. thyrsiformis* should be "Páramo de la Negra, Mérida, Venezuela" (e.g., *R. Gutzwiller 34*). Also, Gutzwiller spelled "Gutzviller" in Diazgranados (2012: 8) and Cuatrecasas (2013: 597).

47.1. ***Espeletia thyrsiformis*** A.C. Sm. f. ***thyrsiformis***

47.2. Espeletia thyrsiformis A.C. Sm. f. ***marcanoana*** (Cuatrec.) Mavárez, *comb. nov*.

Basionym: *Coespeletia thyrsiformis* (A.C. Sm.) Cuatrec. f. *marcanoana* Cuatrec., Mem. New York Bot. Gard. 107: 603. 2013. TYPE: VENEZUELA. Táchira: Páramo del Colorado, continuación del Páramo del Zumbador, 3100–3200 m.a.s.l., 1 October 1969, *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 27993* (Holotype: US; Isotypes: F, MERF, U, US).

Homotypic synonyms: *Espeletia marcanoana* Cuatrec., Phytologia 20: 476. 1971.

Coespeletia marcanoana (Cuatrec.) Cuatrec., Phytologia 35: 57. 1976.

Heterotypic synonyms: *Espeletia racemosa* Cuatrec., Ciencia (México) 6: 266. 1945. TYPE: VENEZUELA. Mérida: Páramos de Apartaderos, *Fortanier s.n.* (Holotype: VEN [not seen]).

Espeletia thyrsiformis f. *marcanoana* resembles the nominal form but shows no polycephalous peduncles, or only a few restricted to the most basal section of the inflorescence.

Distribution: VENEZUELA. Northern Táchira and nearby Mérida: Páramo del Zumbador and del Batallón.

Additional specimens examined (selection): *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 27993* (F, U, US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28376* (US), *L. Ruiz-Terán & M. López-Figueiras 8297* (US).

This taxon was dedicated to Luis Marcano (Cuatrecasas, 2013: 603). According to ICN Art. 60.8, the correct spelling for the derived adjectival epithet is "*marcanoana*" (not "*marcana*").

48. ***Espeletia timotensis*** Cuatrec., Bol. Soc. Ven. Ci. Nat. 17: 84. 1956a. TYPE: VENEZUELA. Mérida: Páramo de Piñango-Timotes, Sierra Nevada de Mérida, 4000 m.a.s.l., 9 December 1938, *J. Hanbury-Tracy 193* (Holotype: K; Isotypes: K, NY). Fig. 149–151.

Homotypic synonym: *Coespeletia timotensis* (Cuatrec.) Cuatrec., Phytologia 35: 57. 1976.

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FIGURES 143–144. *Espeletia tenorae* Aristeg. Páramo de Guirigay, Trujillo, Venezuela (Photographs by S. Aubert).

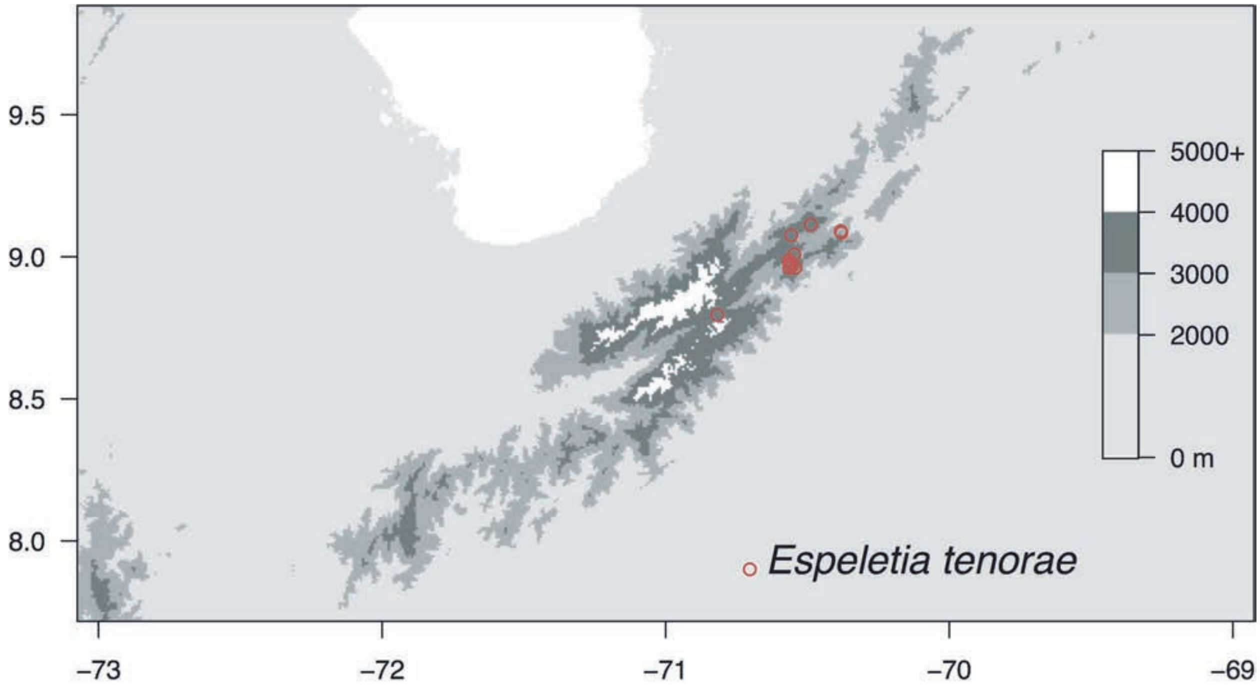

FIGURE 145. Distribution of *Espeletia tenorae* Aristeg.

FIGURE 146. *Espeletia thyrsiformis* A.C. Sm. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

FIGURE 147. *Espeletia thyrsiformis* A.C. Sm. Páramo del Batallón, Táchira, Venezuela (Photograph by S. Aubert).

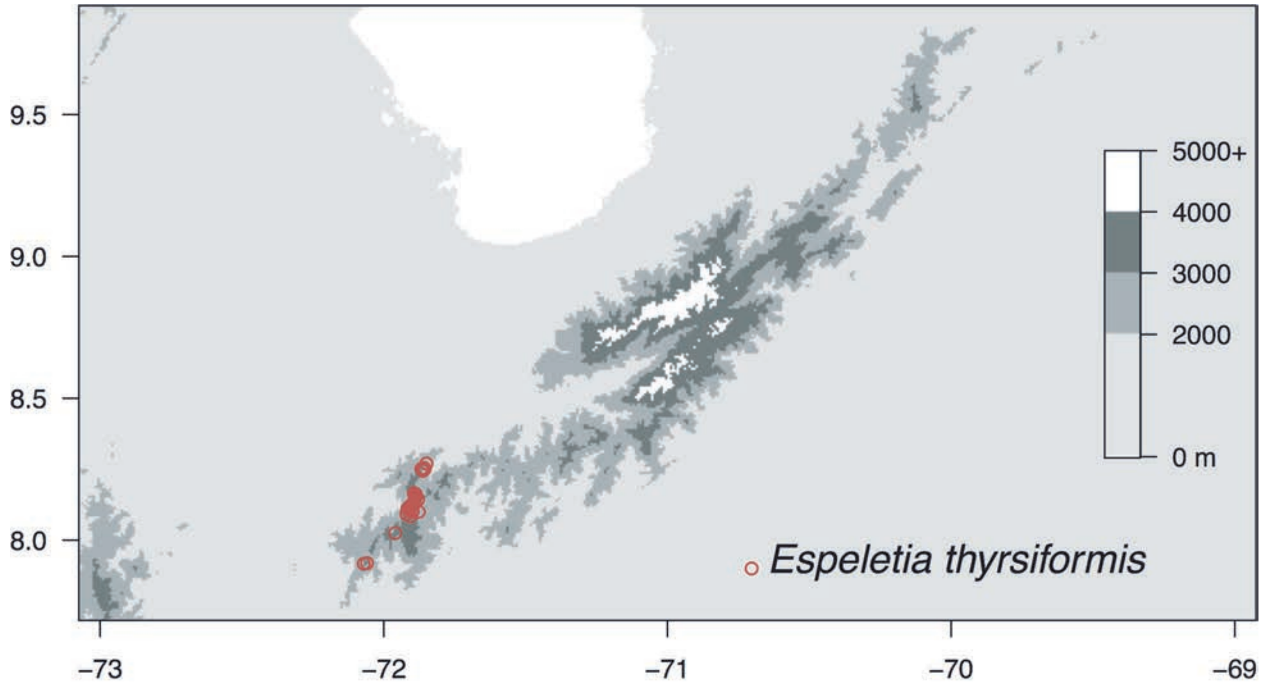

FIGURE 148. Distribution of *Espeletia thyrsiformis* A.C. Sm.

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FIGURES 149–150. *Espeletia timotensis* Cuatrec. Páramo el Banco, Mérida, Venezuela (Photographs by S. Aubert).

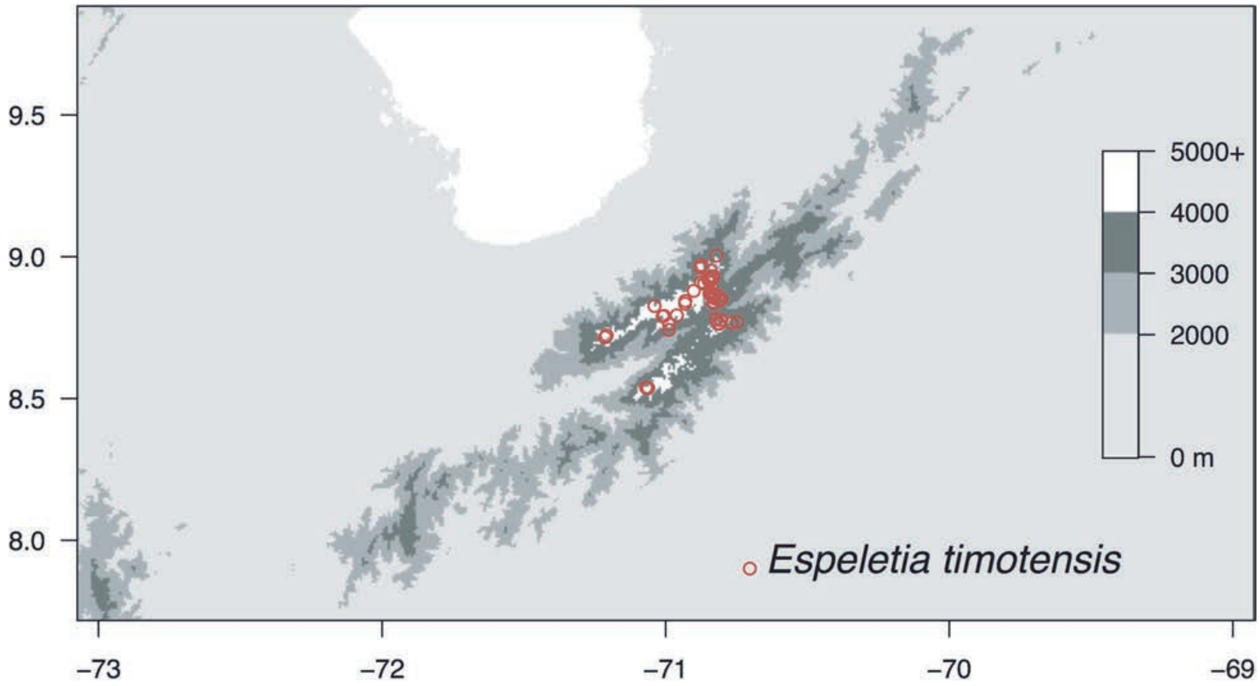

FIGURE 151. Distribution of *Espeletia timotensis* Cuatrec.

Heterotypic synonym: *Espeletia lutescens* Cuatrec. & Aristeg., Fl. Venez. 10(1): 443. 1964. TYPE: VENEZUELA. Mérida: Páramo de Timotes, 3000–3500 m.a.s.l. [4000 m on added tag], December 1910, *A. Jahn 149* (Holotype: US; Isotypes: G, VEN [not seen]).

Coespeletia lutescens (Cuatrec. & Aristeg.) Cuatrec., Phytologia 35: 57. 1976.

Rosette polycarpic, caulescent, stem height up to 3.5 m, entirely covered by marcescent leaves. *Leaf* open sheath, sessile or with short pseudopetiole (length 2–6 cm), adaxially densely pubescent, lanate, white-cinereous, length 40–55 cm, width 2.5–4.0 cm, ratio 10–18:1, bases of secondary nerves parallel, 4–6 mm apart. *Inflorescence* lateral, simple, monochasial, botryoid, axes 85–150 cm, 8–15 monocephalous peduncles, vegetative part with several alternate bracts. *Capitulum* diam. 35–55 mm, ligular circle shorter than the involucre (30–38 mm), disc 23–30 mm, ray ligules bright yellow or orange, turning brownish with age. *Espeletia timotensis* can be distinguished from other Venezuelan rosette plants by its botryoid inflorescences with large capitula (diam. > 35 mm). It closely resembles *E. albarregensis*, but *E. timotensis* has taller stems (1.0–3.5 m vs. 0.5–1.0 m), longer inflorescences (85–150 cm vs. 60–80 cm), and larger number of capitula (8–15 vs. 9–11).

Distribution: VENEZUELA. Mérida: Sierra de la Culata and Sierra Nevada de Mérida. 4000–4500 m.a.s.l., locally down to 3650 m.a.s.l., in dry superpáramos (Fig. 151).

Additional specimens examined (selection): *J. Hanbury-Tracy 193* (K, NY), *A. Jahn 149* (G, US), *L. Ruiz-Terán 227* (US), *P. Berry 4213* (US), *M. López-Figueiras & A. Usubillaga 14022* (US), *L. Ruiz-Terán & M. López-Figueiras 1128* (US).

49. *Espeletia trujillensis* Cuatrec., Mutisia 16: 5. 1953. TYPE: VENEZUELA. Trujillo: Quebrada del Cortijo, above Humocaro Bajo, 2600–2800 m.a.s.l., 6 February 1944, *J. Steyermark 55341* (Holotype: F; Isotype: F). Fig. 152–154.

Homotypic synonym: *Carramboa trujillensis* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Tree profusely ramified, up to 20 m. *Leaf* tubular sheath, sessile, adaxially glabrous, green, length 30–60 cm, width 12–25 cm, ratio 2.3–3.5:1, bases of secondary nerves parallel, unevenly distributed, 10–30 mm apart. *Inflorescence* lateral, compound, primary branching dichasial, corymboid, length 35–60 cm, vegetative part about half of total length, with 1–2 pairs of opposite bracts. *Capitulum* diam. 6–9 mm, ligular circle 16–21 mm, disc 6–9 mm, ray ligules yellow. *Espeletia trujillensis* can be distinguished from all other species by its profusely ramified tree habit, sessile leaves with low length-to-width ratio (2.3–3.5:1), and primarily dichasial corymboid inflorescences with proximal part bracteate.

Distribution: VENEZUELA. Trujillo: forested hills in Páramo de la Cristalina and Guaramacal. Lara: forested hills around Humocaro Bajo. 2400–2800 m.a.s.l., found in rather humid locations and along forest streams (Fig. 154).

Additional specimens examined (selection): *J. Steyermark 55341* (F), *L. Ruiz-Terán 9214* (US), *L. Ruiz-Terán 9215* (US), *M. López-Figueiras 12956* (US), *J. Cuatrecasas, M. López-Figueiras & H. Rodríguez 28979* (US).

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FIGURES 152–153. *Espeletia trujillensis* Cuatrec. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

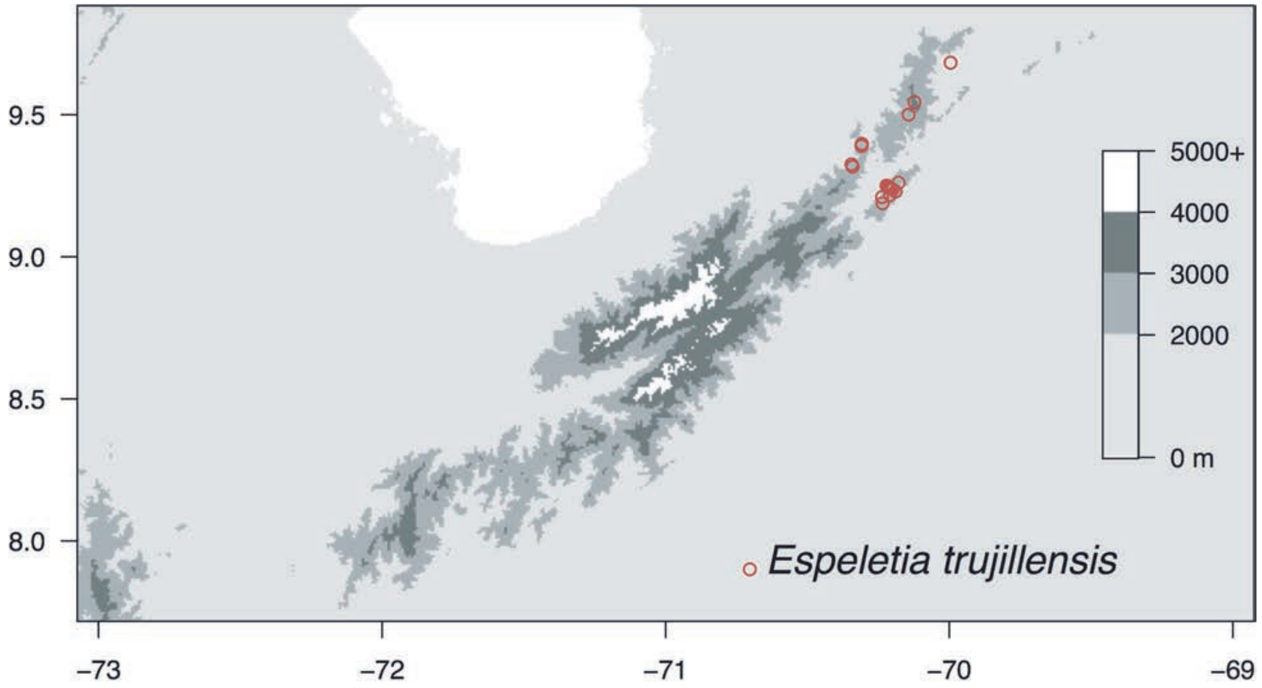

FIGURE 154. Distribution of *Espeletia trujillensis* Cuatrec.

50. *Espeletia ulotricha* Cuatrec., Phytologia 23: 364. 1972. TYPE: VENEZUELA. Lara: Páramo del Jabón, vertiente oriental, 3100–3400 m.a.s.l., 2 November 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28220* (Holotype: US; Isotypes: F, MERF, US). Fig. 155–156.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, crispy lanate, whitish-cinereous, length 10–25 cm, width 0.7–1.2 cm, ratio 15–28:1, secondary nerves filiform, parallel, 3–6 mm apart. *Inflorescence* lateral, simple, dichasial, monocephalous, rarely with 2 or 3 capitula, length 30–70 cm, with 1 pair (rarely 2) of opposite bracts near the base and 5–12 alternate along the inflorescence. *Capitulum* diam. 24–32 mm, ligular circle 40–45 mm, disc 20–25 mm, ray ligules yellow. *Espeletia ulotricha* can be distinguished from all other Venezuelan dwarf rosette plants with monocephalous inflorescences by its leaf sheaths barbate abaxially, lamina with cylindrical outline and thick crispy-lanate indumentum, and inflorescences with 5–12 alternate bracts.

Distribution: VENEZUELA. Border Lara-Trujillo: Páramo del Jabón, de Cendé, and del Turmal. 3000–3500 m.a.s.l., in open and windy páramos on top of hills and rocky ridges (Fig. 156).

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28220* (F, US), *M. López-Figueiras & H. Rodríguez 26235* (US), *L. Ruiz-Terán & M. López-Figueiras 929* (US), *L. Ruiz-Terán & M. López-Figueiras 2055* (US), *Monasterio 3518* (US).

51. Espeletia usubillagae (Cuatrec.) Mavárez, *comb. nov.* Basionym: *Ruilopezia usubillagae* Cuatrec., Phytologia 61: 53. 1986a. TYPE: VENEZUELA. Mérida: Páramo de Aricagua, 3000 m.a.s.l., 31 March 1922, *A. Jahn 1021* (Holotype: US; Isotypes: US, VEN [not seen]). Fig. 157.

Rosette stem divided, each branch short, erect, ending with a leafy rosette. *Leaf* open sheath, subsessile, or with a short "winged" pseudopetiole, oblong, adaxially glabrous, green, length 12–20 cm, width 3.0–3.3 cm, ratio 4–6:1, secondary nerves parallel, 2–4 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 56 cm, vegetative part profusely bracteate, about half of the total length. *Capitulum* diam. 15–18 mm, ligular circle 25 mm, disc 12–14 mm, ray ligules white, with purplish blotches. *Espeletia usubillagae* can be distinguished from other species by its multibranched rosette habit, oblong subsessile leaves, and radiate capitula with white ray ligules.

Distribution: VENEZUELA. Mérida: known only from the type collection. Given the locality and elevation, the habitat probably corresponds to a shrubby subpáramo (Fig. 157).

Additional specimen examined: *A. Jahn 1021* (US).

Collection date given as "3 November 1922" in Diazgranados (2012: 42) and Cuatrecasas (2013: 494).

A handful of Espeletiinae rosette plants exhibit branched stems, with the best example of this growth form found in *Espeletia jahnii*, and to a lesser extent in a few related species (e.g., *E. bracteosa*, *E. bromelioides*, or *E. viridis*), which frequently produce multiple sessile or prostrate rosette plants connected through a common stem. Multi-branched rosette plants with erect branches or stems, such

FIGURE 155. *Espeletia ulotricha* Cuatrec. amid *E. jabonensis* Cuatrec. Páramo del Jabón, Lara-Trujillo, Venezuela (Photograph by S. Aubert).

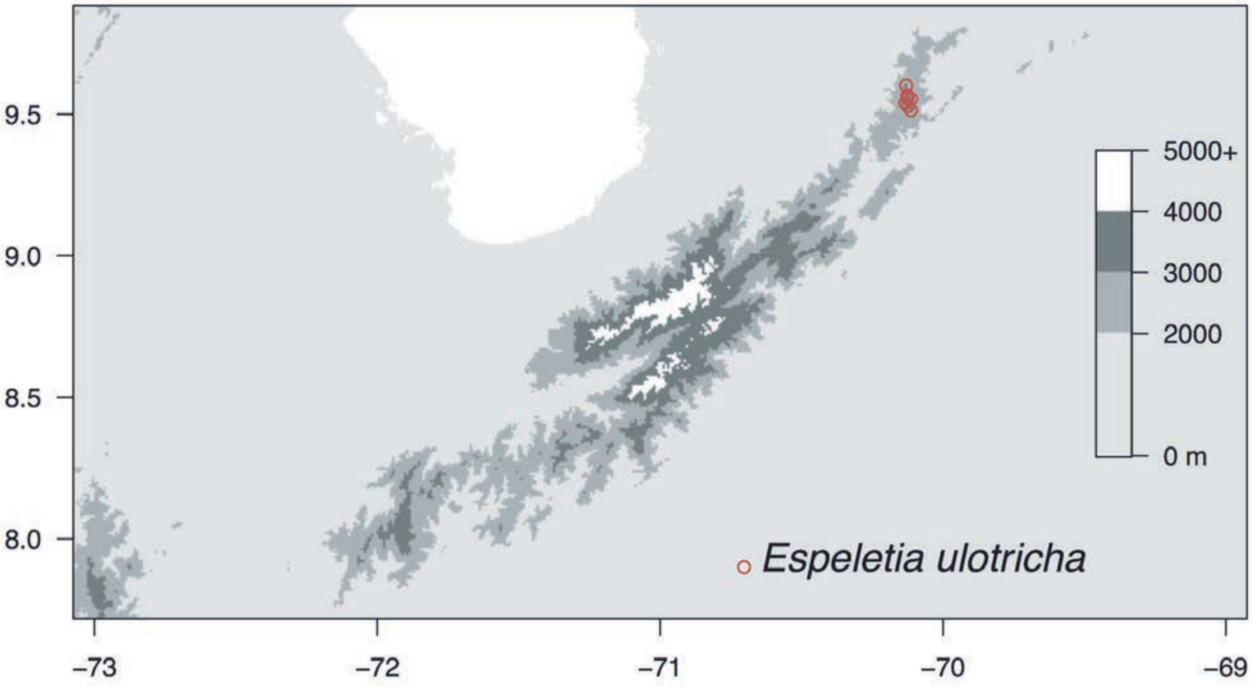

FIGURE 156. Distribution of *Espeletia ulotricha* Cuatrec.

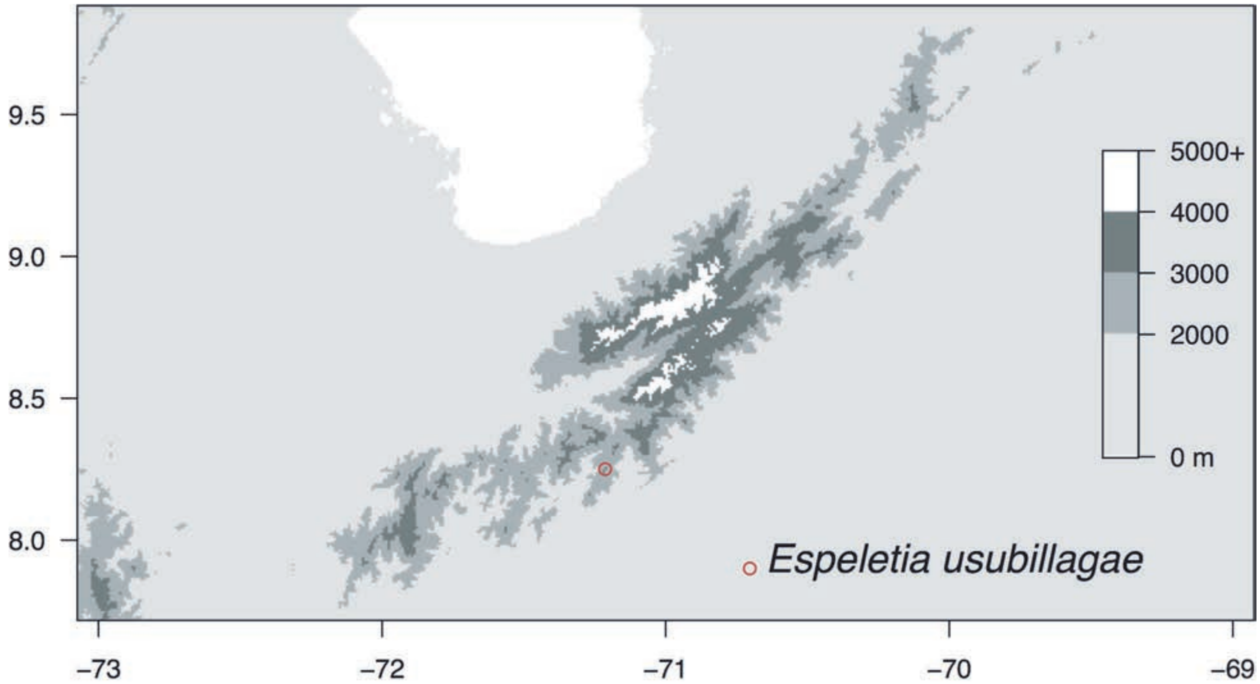

FIGURE 157. Distribution of *Espeletia usubillagae* (Cuatrec.) Mavárez.

as *E. usubillagae*, have also been observed but much more rarely, and with all examples representing cases of interspecific hybridization between rosette and tree species (e.g., *E. cristalinensis* and *E. meridensis*; see below). The type of branching in *E. usubillagae* and its extreme scarcity suggest that this taxon probably represents an interspecific hybrid instead of a good species with a primitive growth form, but more studies will be necessary before a conclusion can be reached in this regard.

52. Espeletia vergarae (Cuatrec. & López-Fig.) Mavárez, *comb. nov*.

Basionym: *Ruilopezia vergarae* Cuatrec. & López-Fig., Phytologia 61: 58. 1986a. TYPE: VENEZUELA. Trujillo: la Palma [Las Palmas], 10–15 km [NE] de Carache, en la carretera hacia Agua de Obispo, 2390 m.a.s.l., 4 April 1976, *M. López-Figueiras 12960* (Holotype: US; Isotypes: F, K, MA [not seen], MERF, NY, U, US, VEN [not seen]). Fig. 158–160.

Rosette monocarpic, sessile. *Leaf* open sheath, sessile, adaxially densely pubescent, appressed sericeous, whitish-cinereous, length 20–40 cm, width 1.1–3.0 cm, ratio 10–20:1, secondary nerves parallel, 10–15 mm apart. *Inflorescence* terminal, compound, primary branching monochasial, corymboid-paniculate, length 80–100 cm, branched near the base. *Capitulum* diam. 12–17 mm, ligular circle 25–35 mm, disc 10–16 mm, ray ligules yellow. *Espeletia vergarae* can be distinguished from other species for its sessile monocarpic rosette, leaves adaxially appressed-sericeous, and capitula with bright-yellow ray ligules. The species resembles sympatric *E. jabonensis*, from which it can be distinguished by its appressed-sericeous leaves (vs. shiny-silvery), with smaller length-to-width ratio (10–20:1 vs. 30–40:1), visible secondary nerves (vs. obsolete), and ovate sheaths 2.5–3.0 cm × 3.5–4.0 cm (vs. rectangular sheaths 2.0–2.5 cm × 0.5–0.8 cm).

Distribution: VENEZUELA. Border Trujillo-Lara: páramos in the northern end of the Cordillera de Mérida, Sierra de Barbacoas, Los Nepes, and the complex Las Rosas-Jabón-Cendé-Turmal. 2300–3300 m.a.s.l., in open subpáramo and páramo slopes, also in deforested spots in former upper Andean forest (Fig. 160).

Additional specimens examined (selection): *M. López-Figueiras 12960* (F, K, NY, U, US), *M. López-Figueiras 12951* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28547* (US), *L. Ruiz-Terán & M. López-Figueiras 1029* (US), *L. Ruiz-Terán & M. López-Figueiras 1997* (US), *L. Ruiz-Terán & M. López-Figueiras 2058* (US).

53. ***Espeletia viridis*** Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 278. 1959. TYPE: VENEZUELA. Trujillo: Páramo de Guirigay, hacia Laguna la Parida, 3500 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3570* (Holotype: VEN [not seen]; Isotypes: NY, US, VEN [not seen]). Fig. 161–163.

Homotypic synonym: *Ruilopezia viridis* (Aristeg.) Cuatrec., Phytologia 35: 53. 1976.

Rosette monocarpic, frequently short-branched at the base, sessile. *Leaf* open sheath, sessile, adaxially glabrous, glossy green, length 25–45 cm, width 0.7–2.0 cm, ratio 15–50:1, minimum width located in the proximal half above the base, apex with a sharp teeth, 1.0–1.5 mm long, secondary nerves obsolete or fused into a reticulum. *Inflorescence* terminal, compound, primary branching monochasial, corymboid, length 100–150 cm, vegetative part profusely bracteate,

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FIGURES 158–159. *Espeletia vergarae* (Cuatrec. & López-Fig.) Mavárez. Páramo de Cendé, Trujillo, Venezuela (Photographs by S. Aubert).

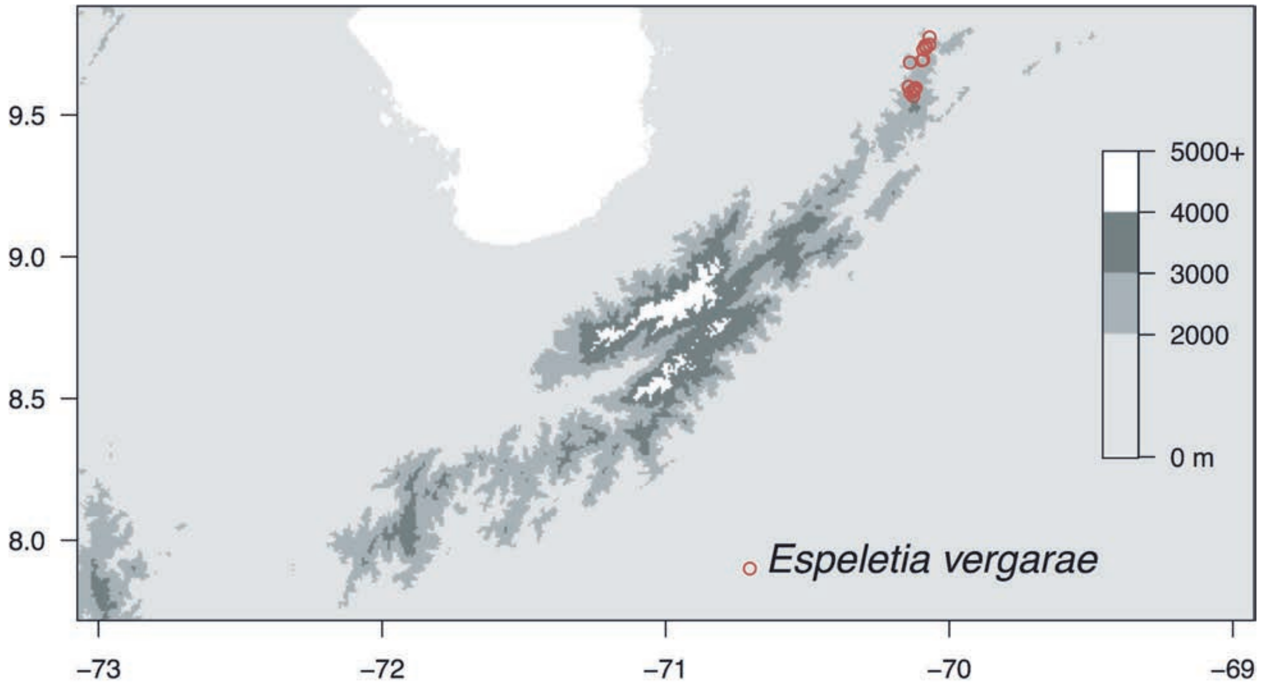

FIGURE 160. Distribution of *Espeletia vergarae* (Cuatrec. & López-Fig.) Mavárez.

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FIGURES 161–162. *Espeletia viridis* Aristeg. Páramo de Guaramacal, Trujillo, Venezuela (Photographs by S. Aubert).

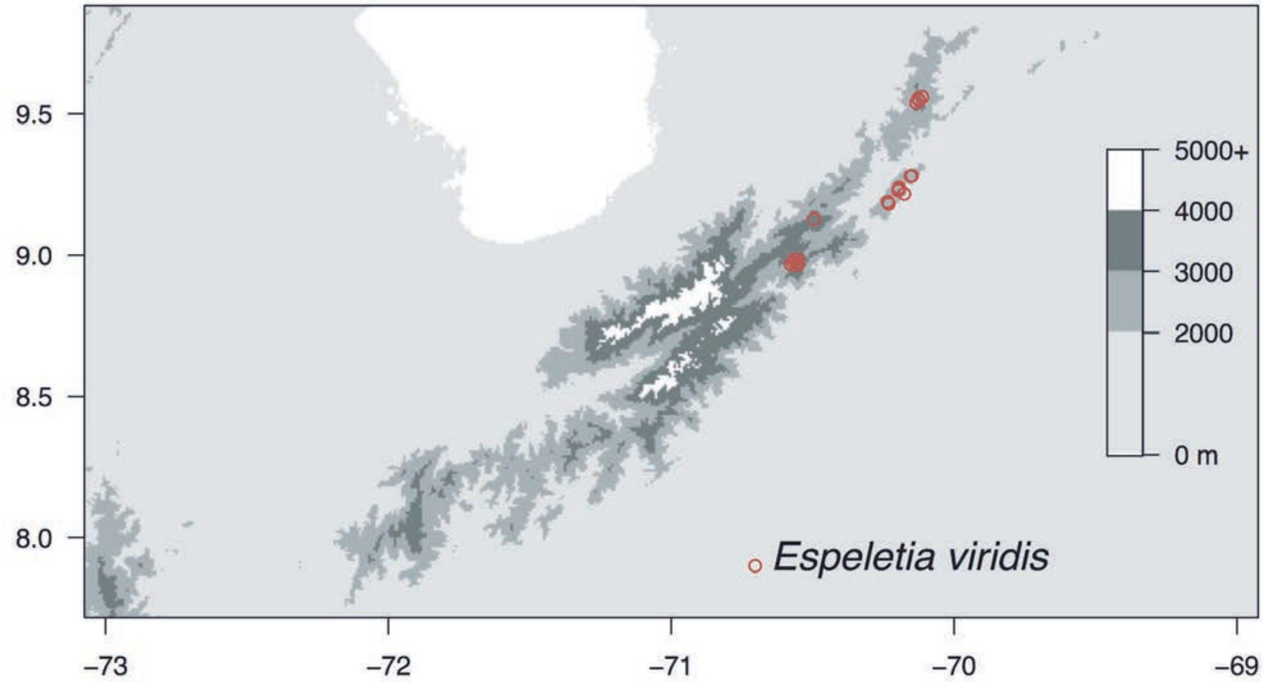

FIGURE 163. Distribution of *Espeletia viridis* Aristeg.

about half of total length. *Capitulum* diam. 14–17 mm, ligular circle 22–35 mm, disc 12–16 mm, bright yellow ray ligules. *Espeletia viridis* can be distinguished from other species by its sessile monocarpic rosette habit with long, sessile, flexible, green leaves, and its capitulum with yellow ray ligules.

Distribution: VENEZUELA. Border Trujillo-Lara: Páramo de Cendé, Páramo del Jabón, and Páramo del Turmal. Trujillo: Páramo de Guaramacal. Border Trujillo-Barinas-Mérida: Páramo de Guirigay. 2900–3500 m.a.s.l., found in humid locations within open subpáramo and páramo habitats (Fig. 163).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3570* (NY, US), *J. Cuatrecasas & L. Ruiz-Terán 28814* (F, US), *M. López-Figueiras & H. Rodríguez 8803* (US), *B. Stergios*, *L. Dorr & K. Wurdack 20436* (US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28168* (F, U, US).

54. *Espeletia weddellii* Sch. Bip. ex Wedd., Chlor. Andina: 66. 1855. TYPE: VENEZUELA. Trujillo: Páramo de Niquitao, 12,500 pieds, July 1843, *Linden 1443* (Holotype: P; Isotypes: BR, F, G, K, P, US, W). Fig. 164–166.

Rosette polycarpic, sessile, dwarf. *Leaf* open sheath, sessile, adaxially densely pubescent, appressed villous-lanate, whitish-cinereous, length 5–15 cm, width 0.3–1.0 cm, ratio 10–25:1, secondary nerves obsolete or filiform, irregularly fused into a reticulum. *Inflorescence* lateral, simple, botryoid, with 2–5 alternate monocephalous peduncles, rarely a single one, length 15–70 cm, with 2 pairs (rarely 1 or 3) of opposite bracts near the base and 1–3 alternate along the inflorescence. *Capitulum* diam. 15–25 mm, ligular circle 20–30 mm, disc 10–15 mm, yellow ray ligules. *Espeletia weddellii* can be distinguished from all other Venezuelan dwarf rosette plants by its polycephalous inflorescences. Some atypical individuals of *E. weddellii* with monocephalous inflorescences look similar to *E. batata*, but they can be recognized by their slender leaves (width 0.3–1.0 cm vs. 0.8–2.0 cm), with rather linear shape (vs. oblong or spatulate) and covered adaxially by a subappressed-villous indumentum (vs. lanuginose).

Distribution: VENEZUELA. Mérida: Páramo de Los Granates in Sierra de Santo Domingo. Trujillo: Páramo de Tuñame, de Cabimbú, de Guirigay, de Ortiz, and de Niquitao. 3100–4000 m.a.s.l., in páramo meadows and relatively open places within subpáramo habitats (Fig. 166).

Additional specimens examined (selection): *Linden 1443* (BR, F, G, K, P, US, W), *B. Stergios 19884* (US), *L. Dorr & L. Barnett 9182* (US), *M. López-Figueiras 8716* (US), *M. López-Figueiras & H. Rodríguez 8877* (US).

Hybrid Taxa

H1. *Espeletia* × *algodonosa* Aristeg., Bol. Soc. Ven. Ci. Nat. 20: 282. 1959. (= *E. nana* × *E. schultzii*), hybrid status in Cuatrecasas (2013: 349). TYPE: VENEZUELA. Trujillo: El Paramito, hacia Tuñame, vía Jajó-la Morita, ca. 3000 m.a.s.l., August 1958, *L. Aristeguieta & E. Medina 3453* (Holotype: VEN [not seen]; Isotypes: NY, US).

Distribution: VENEZUELA. Trujillo: in areas where *E. schultzii* and *E. nana* occur in syntopy (i.e., Cabimbú, Guirigay, Tuñame).

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3453* (NY, US), *L. Ruiz-Terán & M. López-Figueiras 2223* (US), *M. López-Figueiras & H. Rodríguez 8868* (US), *M. López-Figueiras 11895* (US).

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Figures 164–165. *Espeletia weddellii* Sch. Bip. ex Wedd. Páramo de Guirigay, Trujillo, Venezuela (Photographs by S. Aubert).

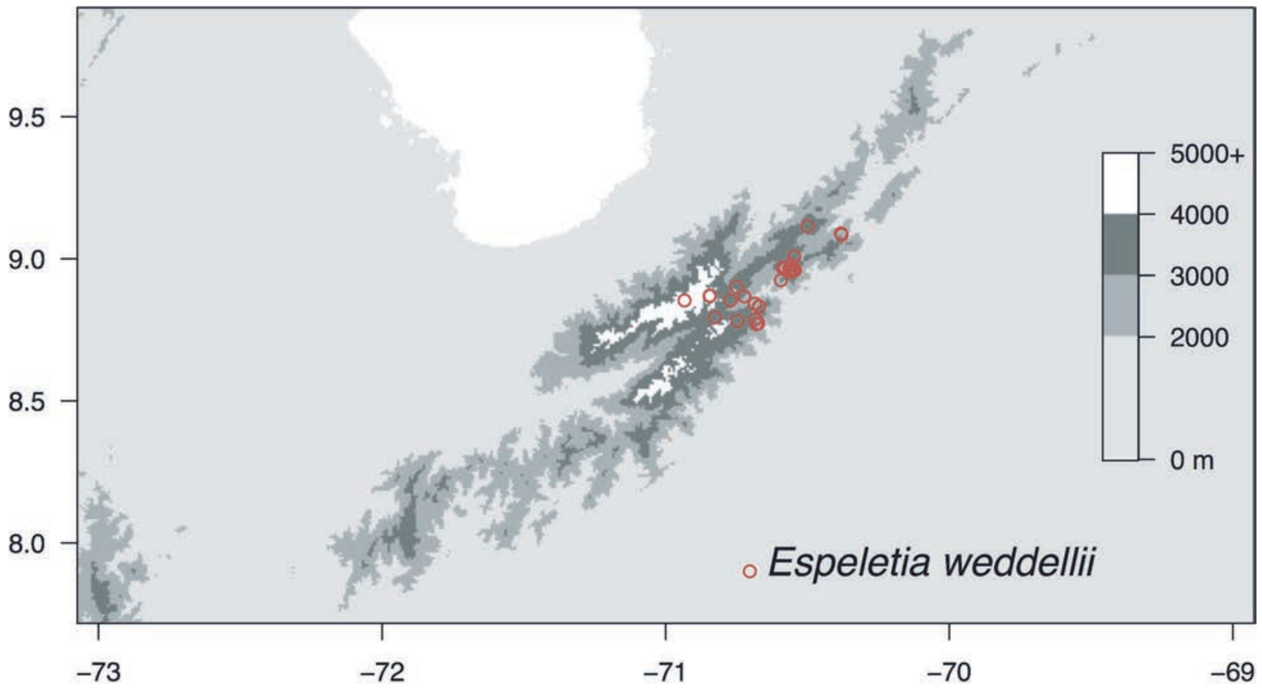

FIGURE 166. Distribution of *Espeletia weddellii* Sch. Bip. ex Wedd.

H2. ***Espeletia*** **×** ***aurantia*** Aristeg., Fl. Venez. 10(1): 448. 1964. (= *E. moritziana* × *E. schultzii*), hybrid status in Cuatrecasas (2013: 579). TYPE: VENEZUELA. Mérida: Laguna Verde, 4100 m.a.s.l., 1 October 1956, *L. Aristeguieta 2613* (Holotype: VEN [not seen]; Isotypes: GOET [not seen], K, US).

Distribution: VENEZUELA. Mérida: a relatively common hybrid found in areas where *E. schultzii* and *E. moritziana* occur in sympatry.

Additional specimens examined (selection): *L. Aristeguieta 2613* (K, US), *P. Berry 4188* (US), *P. Berry 4189* (US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2670* (US).

H3. ***Espeletia*** **×** ***coloradarum*** Cuatrec., Phytologia 29: 372. 1975. (= *E. neriifolia* × *E. ruizii*). TYPE: VENEZUELA. Mérida: potrero de San Rafael, Páramo de las Coloradas, 2700 m.a.s.l., 3 July 1974, *M. López-Figueiras & M. Keogh 9108* (Holotype: US; Isotypes: F, MERF, NY, US).

Homotypic synonym: *Ruilopezia coloradarum* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Espeletia × *coloradarum* represents an interspecific hybrid between an *E. neriifolia* tree and an *E. ruizii* monocarpic rosette. All known specimens of this taxon have been collected exclusively in a restricted area within Páramo de las Coloradas, in which I have observed that hybridization between *E. neriifolia* and *E. ruizii* is very active. The leaves of *E.* × *coloradarum* are clearly intermediate between its putative parental species with regard to size, shape, color, nerve structure, and pubescence. Its inflorescences are also rather intermediate in size and structure, although the long subtending bracts and small capitula are closer to *E. neriifolia*. The hybrid nature of *E.* × *coloradarum* is even more evident when studied directly in the *E. neriifolia*/*E. ruizii* hybrid zone at Las Coloradas, where several individuals in the morphological continuum from *neriifolia*-like to *ruizii*-like can usually be compared at once.

Distribution: VENEZUELA. Mérida: known only from the type locality.

Additional specimens examined (selection): *M. López-Figueiras & M. Keogh 9108* (F, NY, US), *J. L. Panero*, *C. E. Benítez & V. M. Badillo 2694* (US), *M. López-Figueiras & H. Rodríguez 9046* (US), *M. López-Figueiras & H. Rodríguez 9047* (US).

H4. ***Espeletia*** **×** ***cristalinensis*** Cuatrec., Phytologia 27: 169. 1973b. (= *E. aristeguietana* × *E. neriifolia*), hybrid status in Diazgranados (2012: 38). TYPE: VENEZUELA. Trujillo: Distrito Boconó, Páramo de la Cristalina, 2500–2600 m.a.s.l., 17 February 1973, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28556* (Holotype: US; Isotypes: MERF, U, US).

Homotypic synonym: *Espeletiopsis cristalinensis* (Cuatrec.) Cuatrec., Phytologia 35: 55. 1976.

This taxon exhibits a mixture of vegetative and reproductive traits that strongly suggest it represents a case of hybridization between *Espeletia aristeguietana* rosette plants and *E. neriifolia* trees. For instance, *E.* × *cristalinensis* are frequently branched, but their open leaf sheaths are characteristic of rosette plants. Their foliose, alternate and corymboid inflorescences structurally resemble *E. neriifolia*, but their large size and dense pubescence is similar to *E. aristeguietana*. Their capitula are also, in many ways, intermediate between the two parental species. Finally, individuals of this taxon are scarce, morphologically variable, and found only in close syntopy with *E. aristeguietana* and *E. neriifolia*.

Distribution: VENEZUELA. Trujillo: known only from Páramo de la Cristalina, in syntopy with *E. aristeguietana* and *E. neriifolia*.

Additional specimens examined (selection): *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28556* (U, US), *M. López-Figueiras 13949* (US), *M. López-Figueiras 13950* (US), *L. Ruiz-Terán & M. López-Figueiras 2257* (US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28993* (US).

H5. ***Espeletia* × *cuniculorum*** Cuatrec., Phytologia 40: 25. 1978. (= *E. schultzii* × *E. timotensis*). TYPE: VENEZUELA. Mérida: Páramo de los Conejos, Cañada de los Puentes, Sierra de la Culata, 3350 m.a.s.l., 19 October 1972, *L. Ruiz-Terán 7722* (Holotype: US; Isotypes: MERF, MY, US).

Espeletia × *cuniculorum* represents an interspecific hybrid between *E. schultzii* and another rosette species with lanceolate leaves from Sierra de la Culata, most likely *E. timotensis*, or perhaps *E. albarregensis*. This taxon not only exhibits a series of morphologic traits that appear intermediate with regard to those taxa, but that also match the variation observed in interspecific hybrids between the aforementioned taxa. For instance, the long lanceolate leaves with white/shiny pubescence of *E.* × *cuniculorum* are quite similar to *E. timotensis*. Its relatively small ligular circle in comparison with a rather large capitulum is also reminiscent of this species. On the other hand, the dichasial inflorescence of *E.* × *cuniculorum* is structurally similar to *E. schultzii*, although a possible influence of *E. timotensis* is found in the number of capitula per branch (3 in the proximal, 2 in the middle, and 1 in the terminal), as well as in the copiously hirsute receptacles (Cuatrecasas, 2013: 351). Besides, *E.* × *cuniculorum* is still known only from the type collection despite the many visits I and other researchers have made to the type locality and nearby areas. Demographic scarcity is a predominant feature of several interspecific hybrids that were initially described as species in *Espeletia* (e.g., *E.* × *cristalinensis*).

Distribution: VENEZUELA. Mérida: known only from the type collection.

Additional specimens examined (selection): *L. Ruiz-Terán 7722* (US). Specimen *P. Berry 3852* (US) looks similar to *E.* × *cuniculorum*. This sample was initially considered by Paul Berry to be a hybrid, *E. schultzii* × *E. timotensis*, and later identified by José Cuatrecasas as *E. albarregensis*.

H6. Espeletia × gritaensis (Cuatrec.) Mavárez, *comb. nov.* (= *E. neriifolia* var. *columbica* × *E. occulta*), hybrid status in Cuatrecasas (1980b: 7).

Basionym: *Libanothamnus* × *gritaensis* Cuatrec., Phytologia 47: 7. 1980b. TYPE: VENEZUELA. Táchira: Llano de Campoalegre, cercanías de La Grita, hacia Páramo del Batallón, 2520 m.a.s.l., 2 October 1969, *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 27999* (Holotype: US; Isotypes: F, MERF, U, US).

Distribution: the taxon has been known only from the type locality. However, hybrids between *E. neriifolia* var. *columbica* and *E. occulta* are frequently found wherever the two species coexist in sympatry.

Specimens examined (selection): *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 27999* (F, U, US).

H7. ***Espeletia* × *jajoensis*** Aristeg., Fl. Venez. 10(1): 424. 1964. (= *E. neriifolia* × *E. schultzii*). TYPE: VENEZUELA. Trujillo: el Paramito, hacia Tuñame, vía Jajó-la Morita, 3000 m.a.s.l., Aug. 1958, *L. Aristeguieta & E. Medina 3452* (Holotype: VEN [not seen]; Isotypes: NY, US).

Homotypic synonym: *Espeletiopsis jajoensis* (Aristeg.) Cuatrec., Phytologia 35: 56. 1976.

The combination of morphological traits in this taxon is so unique that Cuatrecasas (2013: 375) created a new group within *Espeletia* just for it, with the revealing name "Group Aberrantes." Indeed, *E.* × *jajoensis* is the only polycarpic rosette species in the subtribe whose inflorescences exhibit monochasial (alternate) primary branching but with secondary branching frequently dichasial (opposite). Cuatrecasas was visibly puzzled by this architecture, which explains why he moved this taxon from *Espeletia* to *Espeletiopsis* (Cuatrecasas, 1976: 56) and then back to *Espeletia* (Cuatrecasas, 1996: 377). Cuatrecasas also noted an unusual leaf polymorphism in this taxon; with most individuals exhibiting sessile leaves with rather parallel and dense secondary nerves, while others have clearly pseudopetiolate leaves with bent and more loosely packed secondary nerves. He proposed that "these variations indicate instability and a probably hybrid origin (…) the result of a cross pollination probably between *Espeletia schultzii* and *Espeletiopsis cristalinensis*." Cuatrecasas's final insight in this sense was partially correct, since *E.* × *jajoensis* is the product of hybridization between *E. neriifolia* and *E. schultzii*, where it represents the fraction of the morphological spectrum of the hybrids closest to the rosette plants, probably as a consequence of backcrossing toward *E. schultzii*.

Distribution: VENEZUELA. Trujillo: páramos in the Jajó-Tuñame and Timotes-Piñango areas. Mérida: found sporadically in most páramos Sierra Nevada de Santo Domingo, Sierra de la Culata, and Sierra Nevada de Mérida, where *E. neriifolia* and *E. schultzii* coexist in sympatry.

Additional specimens examined (selection): *L. Aristeguieta & E. Medina 3452* (NY, US), *M. López-Figueiras & B. Vergara 14514* (US), *M. López-Figueiras & B. Vergara 14515* (US); *14516* (US), *L. Ruiz-Terán*, *M. López-Figueiras & M. Hale 10436* (US).

Aristeguieta (1964: 424) used the suffix *-ense* (neuter) in the original spelling of the epithet of this taxon. Cuatrecasas (1976: 56) changed the suffix to *-ensis* (masc./fem.) to match the epithet with the feminine gender of both *Espeletia* and *Espeletiopsis*.

H8. ***Espeletia* × *josephensis*** Cuatrec., Phytologia 29: 374. 1975. (= *E. lindenii* × *E. neriifolia*). TYPE: VENEZUELA. Mérida: Páramo de San José de Acequias, arriba de Veguilla, distrito Arzobispo Chacón, 2600 m.a.s.l., 18–20 June 1974, *M. López-Figueiras & H. A. Rodríguez 9073* (Holotype: US; Isotypes: F, MERF, MY, US).

Homotypic synonym: *Ruilopezia josephensis* (Cuatrec.) Cuatrec., Phytologia 35: 52. 1976.

Espeletia × *josephensis* represents an interspecific hybrid between an *E. lindenii* monocarpic rosette and an *E. neriifolia* tree. All known specimens of this taxon have been collected in two restricted areas in Sierra Nevada de Mérida (Páramo de San José and Páramo de Acequias) and Sierra de la Culata (Páramo el Tambor), in which I have observed that hybridization between *E. lindenii* and *E. neriifolia* is very active. Most vegetative and reproductive traits in this taxon are indeed intermediate between its putative parental species, including growth form, since there are branched and unbranched individuals in *E.* × *josephensis*. The latter fact is particularly suggestive of an origin from hybridization and backcrossing toward both tree and rosette parental species.

Distribution: known until recently only from the type locality and nearby areas in the S. of Sierra Nevada de Mérida, I have found a few isolated individuals in Páramo el Tambor in the S. end of Sierra de la Culata.

Additional specimens examined (selection): *M. López-Figueiras & H. A. Rodríguez 9073* (F, US), *M. López-Figueiras & J. Dugarte 29536* (US), *M. López-Figueiras & J. Dugarte 29537* (US), *M. López-Figueiras & J. Dugarte 29538* (US), *M. López-Figueiras & J. Dugarte 29541* (US).

Correct spelling of the epithet is "*josephensis*," not "*joséphensis*" as in Diazgranados (2012: 41). Collection date given as "18–20 July" in Diazgranados (2012: 41) and Cuatrecasas (2013: 551).

Although the habit of the typus of *E.* × *josephensis* was described as "Arbolito de 2–2,5 m de alto" (i.e., small tree 2.0–2.5 m tall) in Cuatrecasas (1975: 377), the species was characterized as "Caulirosula" in the original description provided in the same work (p374). In his last treatment of this taxon, Cuatrecasas maintained the categorization as caulirosula (Cuatrecasas, 2013: 551), but he changed the description of the habit of the typus to "Caulirosula 2.0–2.5 m" (p660), without further explanations. This change appears unjustified since the labels in the holotype and isotypes clearly say "Arbolito."

H9. *Espeletia* × *meridensis* Cuatrec., Mutisia 16: 4. 1953. (= *E. leucactina* × *E. neriifolia*). TYPE: VENEZUELA. Mérida: Carretera Andina, Páramo de la Negra, 3000 m.a.s.l., 26 November 1948, *H. García-Barriga 13297* (Holotype: US; Isotypes: COL, MEDEL [not seen], NY, VEN [not seen]).

Homotypic synonym: *Espeletiopsis meridensis* (Cuatrec.) Cuatrec., Phytologia 35: 56. 1976.

Espeletia × *meridensis* is undoubtedly the result of interspecific hybridization between a tree and a rosette species. The tree parent is most likely *E. neriifolia*, an abundant species in the distribution area of *E.* × *meridensis* and whose contribution to this taxon is clearly noticeable in the shape and structure of both its leaves and inflorescences. Indeed, the similarities between *E.* × *meridensis* and *E. neriifolia* are so important that Cuatrecasas considered the reassignment of the former to *Libanothamnus* (Cuatrecasas, 2013: 434). The rosette parent of *E.* × *meridensis* is relatively harder to identify, as individuals arising from more than one interspecific hybrid combination have probably been included in this taxon. Thus, some specimens have corymboid-paniculate inflorescences with white/cream ray ligules, while others have racemiform inflorescences with pale-yellow ray ligules. One good candidate parent for the former hybrid type is *E. leucactina*, the only local rosette species with corymboid-paniculate inflorescences and white ray ligules, frequently found in close sympatry with *E. neriifolia*. Several diagnostic traits in *E.* × *meridensis* are intermediate between *E. leucactina* and *E. neriifolia*, such as leaf size and shape, capitulum size, ray corollas length and color, and outer phyllaries shape and size. For the second hybrid type, the best parent candidate is *E. thyrsiformis*, the only rosette species in the area with botryoid-paniculate inflorescences and yellow ray ligules.

Distribution: VENEZUELA. Mérida and Táchira: Páramos de la Negra, del Batallón and del Rosal.

Additional specimens examined (selection): corymboid-paniculate inflorescences with white/cream ray ligules: *H. García-Barriga 13297* (NY, US), *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28018* (US). Racemiform inflorescences with pale yellow ray ligules: *J. Cuatrecasas*, *M. López-Figueiras & L. Marcano-Berti 28006* (US), *C. Smith & R. Jorgensen 3533* (US).

According to Art. H.4 of the ICN, hybrid names should be circumscribed so as to include only one particular hybrid formula. In this case, the typus of *E.* × *meridensis* probably represents an *E. leucactina* × *E. neriifolia* cross. If this turns to be correct and the name *E.* × *meridensis* is conserved, another hybrid name would be needed for the hybrid combination *E. neriifolia* × *E. thyrsiformis*.

H10. *Espeletia* × *pozoensis* Cuatrec., Ciencia (México) 6: 266. 1945. (= *E. angustifolia* × *E. schultzii*). TYPE: VENEZUELA. Mérida: Páramo de Pozo Negro, entre San José and Beguilla [la Veguilla], 2950–3220 m.a.s.l., 3 May 1944, *J. A. Steyermark 56278* (Holotype: VEN [not seen]; Isotypes: F, NY).

Homotypic synonym: *Espeletiopsis pozoensis* (Cuatrec.) Cuatrec., Phytologia 35: 56. 1976.

Espeletia × *pozoensis* represents an interspecific hybrid between two polycarpic rosette plants, *E. angustifolia* and *E. schultzii*. All known specimens of this taxon have been collected in the páramos in the "Pueblos del Sur" region in which both parental species coexist in sympatry and hybridize rather frequently. As for other hybrids in *Espeletia*, quantitative traits in this taxon are clearly intermediate between *E. angustifolia* and *E. schultzii*, most notably with regard to the size, shape, and structure of leaves, which differ greatly in the parental species. The branching of the inflorescence, as in other crossings between species with alternate and opposite architectures, is alternate in *Espeletia* × *pozoensis*. Flowering individuals of this taxon can also be easily recognized by their pale-yellow ray ligules, a color quite intermediate between white in *E. angustifolia* and bright yellow in *E. schultzii*.

Distribution: VENEZUELA. Mérida: Páramos de Mijará, de San José and de la Veguilla.

Additional specimens examined (selection): *J. A. Steyermark 56278* (F, NY), *M. López-Figueiras 30160* (US), *L. Ruiz-Terán & S. López-Palacios 6562* (US), *C. Sobrevila & M. Guariguata 1533* (US), *P. Berry & R. Calvo 4387* (US). Several specimens identified as *Espeletia* × *pozoensis* appear instead to be the morphologically similar hybrid *E. pannosa* × *E. schultzii* (e.g., *L. Ruiz-Terán 7723* US).

H11. ***Espeletia*** **×** ***rodriguezii*** Cuatrec., Phytologia 29: 379. 1975. (= *Espeletia badilloi* × *E. neriifolia*). TYPE: VENEZUELA. Mérida: Betania, entre el Páramo de las Coloradas y el Molino, 2400 m.a.s.l., 18–20 June 1974, *M. López-Figueiras & H. Rodríguez 9050* (Holotype: US; Isotypes: F, MERF, US).

Homotypic synonym: *Carramboa rodriguezii* (Cuatrec.) Cuatrec., Phytologia 35: 54. 1976.

Espeletia × *rodriguezii* represents an interspecific hybrid between two trees with very different leaves and inflorescences, *E. badilloi* and *E. neriifolia*. *Espeletia* × *rodriguezii* leaves are somehow closer to *E. neriifolia*, since they tend to be clustered at the end of branches, have similar length-to-width ratios, and have secondary nerves relatively straight, parallel, and evenly distributed. The opposite trend can be observed in the inflorescences of *E.* × *rodriguezii*, much closer to *E. badilloi* given their lateral positioning, dichasial (opposite) organisation of sterile bracts and main branches, and capitula with yellow ray ligules.

Distribution: VENEZUELA. Mérida: found in all páramos in the S. end of Cordillera de Mérida where *E. badilloi* and *E. neriifolia* coexist in sympatry, particularly in Páramo de San José and Páramo de las Coloradas. *Espeletia* × *rodriguezii* is a relatively common hybrid, particularly in degraded areas of former upper Andean forest that have been aggressively colonized by *E. neriifolia*, such as in the “Pueblos del Sur” region, where flowering individuals of *E.* × *rodriguezii* can be recognized by their resemblance to an *E. neriifolia* tree with yellow capitula.

Additional specimens examined (selection): *M. López-Figueiras & H. Rodríguez 9050* (F, US), *M. López-Figueiras & H. Rodríguez 9049* (US), *P. Berry 4367* (US), *P. Berry 4368* (US), *P. Berry & R. Calvo 4560* (US).

H12. ***Espeletia*** **×** ***tachirensis*** Aristeg., Fl. Venez. 10(1): 427. 1964. (= *E. badilloi* var. *pittieri* × *E. marcescens*), hybrid status in Morillo and Briceño (2007). TYPE: VENEZUELA. Táchira: Páramo del Batallón, hacia Pregonero, 2800 m.a.s.l., 26 Sept 1956, *L. Aristeguieta 2533* (Holotype: VEN [not seen]; Isotype: US).

Homotypic synonyms: *Espeletiopsis tachirensis* (Aristeg.) Cuatrec., Phytologia 35: 56. 1976.

Carramboa tachirensis (Aristeg.) Cuatrec., Phytologia 52: 158. 1982.

Distribution: VENEZUELA. Mérida: páramos in the southern end of Sierra Nevada de Mérida (e.g., Aricagua, Quirorá, San José, Las Coloradas) toward the border with Táchira state (e.g., Portachuelo, La Grita). Táchira: Páramo de la Negra and Páramo del Batallón.

Additional specimens examined (selection): *L. Aristeguieta 2533* (US), *M. López-Figueiras 13988* (US), *V. Badillo 5271* (US), *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28418* (US).

H13. ***Espeletia*** **×** ***wurdackii*** Ruiz-Terán & López-Fig., Rev. Fac. Farm. Univ. Andes 17: 1. 1976. (= *Espeletia neriifolia* × *E. trujillensis*). TYPE: VENEZUELA. Trujillo: Finca Florencia, Páramo del Turmal, cercanías de Carache, ca. 2450 m.a.s.l., 3 April 1976, *M. López-Figueiras 12957* (Holotype: MERF; Isotypes: NY, US).

Homotypic synonyms: *Libanothamnus wurdackii* (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 35: 51. 1976.

Carramboa wurdackii (Ruiz-Terán & López-Fig.) Cuatrec., Phytologia 52: 158. 1982.

Espeletia × *wurdackii* represents another example of interspecific hybridization between two trees with very different leaves and inflorescences, *E. neriifolia* and *E. trujillensis*. *Espeletia* × *wurdackii* leaves are very close to *E. neriifolia*, since they tend to be clustered at the end of branches, are pseudopetiolate, have a lanceolate outline with similar length-to-width ratios, and have secondary nerves straight, parallel, and 5–10 mm apart. In fact, the only obvious contributions of *E. trujillensis* to *E.* × *wurdackii* leaves are found in their relatively large size (compared to *E. neriifolia*) and their velvety-felty abaxial indumentum. On the other hand, an important contribution of *E. trujillensis* to *E.* × *wurdackii* is evident in the lateral position of the inflorescences, as well as in the dichasial (opposite) organization of some sterile bracts and main branches, and the yellow ray ligules. The inflorescences of *E.* × *wurdackii* are nonetheless variable, particularly with regard to their structure, with some specimens exhibiting predominant alternate branching. These combinations of vegetative and reproductive characteristics make it difficult to fully fit *E.* × *wurdackii* into any of the tree genera proposed by Cuatrecasas, which explains why he first classified this taxon as a *Libanothamnus* (Cuatrecasas, 1976: 51) and latter as a *Carramboa* (Cuatrecasas, 1982: 158).

Distribution: VENEZUELA. Trujillo: known only from the type locality and nearby areas below Páramo del Turmal.

Additional specimens examined (selection): *M. López-Figueiras 12957* (NY, US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28980* (F, US), *J. Cuatrecasas*, *M. López-Figueiras & H. Rodríguez 28983* (US).

SUPPLEMENTARY MATERIAL

An Excel file with information on Taxon, Sample type, Collectors, Collection number, Herbarium, Country, Province, Locality, Latitude, Longitude, and Elevation of all plants examined is available at: https://www.researchgate.net/publication/336369055_Mavarez_Espeletia_I_Appendix.

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NEW COMBINATIONS IN *MYRIOPUS* (HELIOTROPIACEAE)

José Iranildo Miranda de Melo[1]

Abstract. Three new combinations in *Myriopus* (Heliotropiaceae) endemics from Brazil are proposed in this paper: *Myriopus gardnerianus*, *M. membranaceus* and *M. salicifolius*.

Resumen. En este trabajo se proponen tres nuevas combinaciones en *Myriopus* (Heliotropiaceae) endémicas de Brasil: *Myriopus gardnerianus*, *M. membranaceus* y *M. salicifolius*.

Keywords: Boraginales, flora, nomenclature, South America

The genus *Myriopus* (Heliotropiaceae) was proposed by Small (1933: 1131) and according to recommendations of Diane et al. (2003), encompasses all the species incorporated into *Tournefortia* sect. *Cyphocyema* I.M. Johnst. (Johnston 1930), a Neotropical group presenting approximately 25 species (Melo pers. obs.) and the majority of them occurs in Brazil where various are endemics from this country.

Myriopus representatives are lianas or subscandent shrubs with supporting branches. The leaves are alternate to pseudo-opposite, elliptic, and lanceolate to ovate or obovate. Inflorescences are axillar or terminate, generally secundiflorous, many-flowered, all them ebracteose. The fruit are fleshy 4-lobed with embryo curved (Diane et al., 2016), the latter consisting of one of the main morphological characteristics for the recognition of its species.

According to The Plant List (2018) *Myriopus* currently it has 18 names being necessary to proceed various new combinations. For this reason, based on the current morphological characterization of *Myriopus*, here three representatives of *Tournefortia* endemics from Brazil are transfer to the genus *Myriopus* (Heliotropiaceae *sensu* BWG, 2016; Diane et al., 2016).

Myriopus gardnerianus (A. DC.) J.I.M. Melo, *comb. nov.*
Basionym: *Tournefortia gardneri* A. DC., Prodr. 9: 526. 1845. TYPE: BRASIL. Rio de Janeiro: In a road, Botafogo Bay, September 1836, *G. Gardner 175* (Holotype: not located; Isotype: K [000583440]).

Distribution: Brazil.

Myriopus membranaceus (A. DC.) J.I.M. Melo, *comb. nov.*
Basionym: *Tournefortia membranacea* A. DC., Prodr. 9: 530. 1845. TYPE: BRASIL. Rio de Janeiro: Morro do Flamengo, September 1836, *G. Gardner 82* (Holotype: MO [1606071]; Isotypes: P [03864425, 03864426]).

Distribution: Brazil.

Myriopus salicifolius (Gardner) J.I.M. Melo, *comb. nov.*
Basionym: *Messerschmidia salicifolia* Gardner, London J. Bot. 1: 181. 1842. TYPE: BRÉSIL. Rio de Janeiro, 1836, *G. Gardner 81* (Holotype: not located; Isotypes: FI [005005], K [000583437, 000583438], P [04037958, 04037960]).

Distribution: Brazil.

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NEW COMBINATIONS IN *EUPLOCA* (HELIOTROPIACEAE) FROM FRENCH POLYNESIA

José Iranildo Miranda de Melo[1] and Márcio Gleisson Medeiros Gonçalves[2]

Abstract. Two new combinations in *Euploca* (Heliotropiaceae) from Marquesas Islands, endemic from French Polynesia, are proposed in this paper: *Euploca marchionica* and *Euploca perlmanii*.

Resumen. En este trabajo se proponen dos nuevas combinaciones en *Euploca* (Heliotropiaceae) de las Islas Marquesas, endémicas de la Polinesia Francesa: *Euploca marchionica* y *Euploca perlmanii*.

Keywords: Boraginales, nomenclature, Pacific Ocean

In the last two decades, the collections of the main South American, North American and European herbaria have been studied including all the type specimens and other material especially the historical collections belonging to Boraginaceae subfamily Heliotropioideae (= Heliotropiaceae). Based on the publication of Diane et al. (2003), currently all the genera subordinated to the subfamily Heliotropioideae (Boraginaceae) are relegated to Heliotropiaceae (Boraginales) represented by four genera: *Euploca* Nutt., *Heliotropium* L., *Ixhorea* Fenzl (endemic from Argentina) and *Myriopus* Small (BWG, 2016).

The genus *Euploca* was reestablished by Diane et al. (2003) to accommodate the species belonging to *Heliotropium* sect. *Orthostachys* R.Br. and the representatives of the genera *Hilgeria* Förther and *Schleidenia* Endl., being one of the most of the family encompassing approximately 100 species, several of them endemic to South America and Mexico, the latter one of the main centers of diversification of the genus. New combinations were proceeded in American representatives of *Euploca* (Feuillet, 2016; Feuillet and Hasle, 2016; 2017; Luebert and Frohlich, 2016; Melo 2017a, b; Melo 2019; Melo and Gonçalves, 2018; Melo and Fernández-Alonso, 2015); nonetheless, several taxa from other regions of the world still require nomenclatural updates.

Based on the current morphological circumscription of *Euploca* associated with knowledge still incipient of its representation in the Pacific Ocean region, two species originally described under *Heliotropium*, endemic from Marquesas Islands, French Polynesia, are here transfer to *Euploca* (Heliotropiaceae *sensu* BWG, 2016; Diane et al., 2016). JSTOR (Journal Storage) – the Global Plants Platform also was consulted in order to complement the information about type specimens. The acronyms of the herbaria follow Thiers (continuously updated).

Euploca marchionica (Decne.) J.I.M. Melo, *comb. nov.*
Basionym: *Heliotropium marchionicum* Decne., Voy. Venus, Bot. [Atl.]: 21. 1864. TYPE: FRENCH POLYNESIA. Iles Marquises [Marquesas Islands], Noukahiva [Nuku Hiva], "toutemanou," pl. herbacee sur le sommet du montagne, Le Bastard 76 (Holotype P00610129, digital image!; Isotype fragment A00097761, digital image!).

Distribution: Marquesas Islands (French Polynesia).

Euploca perlmanii (Lorence & W.L. Wagner) J.I.M. Melo, *comb. nov.*
Basionym: *Heliotropium perlmanii* Lorence & W.L. Wagner, Phytoneuron 47: 51. 2015. TYPE: FRENCH POLYNESIA. Marquesas Islands: Eiao, north side of large valley which is south of Vaittuha Valley, Opituha Valley. Sea cliffs, with *Heliotropium*, *Dodonaea*, *Cordia lutea*. Shrubs 1-2 ft. tall; flower; leaves smaller than Nuku Hiva plants; not silvery, 1050 ft [320 m], 7 Jul 1988, S. Perlman & J. Florence 10052 (Holotype PTBG 009229; Isotypes BISH, F, MO, P, PAP, US01195929, digital image!).

Distribution: Marquesas Islands (French Polynesia).

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TWO NEW SPECIES OF LAURACEAE FROM ESPÍRITO SANTO, BRAZIL

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Abstract. Two new species from the Brazilian Atlantic rainforest of Espírito Santo State, *Licaria spiritusanctensis* and *Ocotea teresae*, are described and illustrated. Their putative relationships within the respective genera are discussed. We also provide illustrations and comments on micromorphological and anatomical features of leaves of these new species, comparing them to those of congenerics and showing that they can be useful for recognition of different taxa.

Keywords: leaf cuticle, leaf vascular bundle, *Licaria*, *Ocotea*, taxonomy

In this study, two new species are described respectively for *Licaria* Aubl. and *Ocotea* Aubl. The work is a by-product of the treatment of the Lauraceae for the Flora of Espírito Santo, Brazil. The descriptions and illustrations of the new species are presented below, as well as a discussion on their possible relationships with congenerics.

Licaria is a Neotropical genus of about 65 species (Trofimov and Rohwer, 2018 [although 77 names are currently in use by different authors]), distributed from southern Florida and Mexico to southern Brazil and Bolivia (Kurz, 2000; Moraes, 2018; Moraes and Vergne, 2018; Trofimov and Rohwer, 2018; van der Werff, 2009b). The latest revision of *Licaria* was carried out by Kurz (1983), in his Ph.D. dissertation, which was only published years later (Kurz, 2000), at which time the author updated it with the addition to some taxa of some new synonyms and a few newly examined specimens. Kurz (2000) also described three subgenera of *Licaria* on the basis of stamen characters, particularly on the manner of opening of the locelli: subgen. *Licaria*, subgen. *Canella* H.W. Kurz, and subgen. *Armeniaca* H.W. Kurz. A detailed account of those three subgenera can be found in van der Werff (2009b). The genus is characterized by the combination of flowers with two-celled anthers, a well-developed cupule, often double-rimmed, and alternate or opposite leaves (Moraes, 2018; Moraes and Vergne, 2018; Rohwer, 1993; van der Werff, 2009b).

Ocotea is the largest genus among the Neotropical Lauraceae, estimated to have ca. 400 recognized species in the Americas (Trofimov et al., 2019; van der Werff, 2011). However, since 2011, another 74 species have been published and one transferred to the genus (see Moraes, 2018; Moraes and Vergne, 2019; van der Werff, 2018a,b), which make such estimates somewhat obsolete. As pointed out by Moraes and Vergne (2019), the last revision of *Ocotea* sensu Kostermans (1957), including *Nectandra* Rol. ex Rottb. and *Pleurothyrium* Nees, dates back to the *Lauraceae americanae* of Mez (1889). Rohwer (1986) published a synopsis of the genus, proposing its subdivision into smaller informal entities, which encompassed 29 groups of species sharing morphological affinities, and 54 species treated singly. No subsequent monographic treatments of these groups have been published, except for the study of the *Ocotea indecora* (Schott) Mez group (Assis and Mello-Silva, 2010). A synopsis of the Central American species was published by van der Werff (2002), but the South American species are still less well known (Moraes and van der Werff, 2011; van der Werff, 2011). Several studies have shown that *Ocotea* is polyphyletic, or paraphyletic with respect to other Neotropical genera of Lauraceae (Chanderbali, 2004; Chanderbali et al., 2001; Rohde et al., 2017; Trofimov et al., 2016, 2019) and in need of a revision. Its large size, however, makes the revision of the genus difficult to accomplish (Rohwer, 1993), being beyond the scope of most botanists (van der Werff, 2014). Recently, Trofimov et al. (2019) have reinstated the genus *Mespilodaphne* Nees & Mart. as a first step toward a phylogenetic classification, therefore transferring to *Mespilodaphne* eight species that had been positioned in *Ocotea*.

Ocotea is characterized by having paniculate-cymose inflorescences with the lateral flowers of the terminal cymes strictly opposite, flowers with six equal tepals, nine four-celled stamens with the locelli arranged in two superposed pairs, staminodes of fourth whorl, when present, stipitiform, and the fruits seated in a more or less well-developed cupule (van der Werff, 2009a, 2011, 2013). As currently circumscribed, both species with unisexual and bisexual flowers have been placed in *Ocotea* (van der Werff, 2011, 2013). Although the combination of characters listed above is unique to *Ocotea*, each is individually present in other genera of Lauraceae and there are no features known to be exclusive for *Ocotea* (van der Werff, 2013). For these reasons, the genus is regarded as a "dustbin" for species that do not fit into better-defined genera of the tribe Perseeae Nees (Rohwer, 1993).

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MATERIAL AND METHODS

This study was based on literature review and morphological analysis of specimens deposited in the following herbaria: BHCB, BR, CEPEC, COL, CVRD, ESAL, F, G, G-DC, GZU, HBG, HBR, HRCB, HUEFS, IAN, INPA, K, KIEL, L, LE, M, MBM, MBML, MG, MO, NY, OXF, P, R, RB, RFA, SPSF, U, UEC, UPCB, US, VEN, and VIES (acronyms according to Thiers, continuously updated).

Photographs of floral structures of the new species of *Licaria* were obtained with a stereomicroscope (Leica MZ125) equipped with a camera (Leica DFC290). Photographs of other morphological characters, particularly the indument, and of floral structures of the new species of *Ocotea* were acquired by a stereomicroscope (Leica M80) equipped with a camera (Leica IC80 HD), using the software LAS (Leica Application Suite) version 4.3.0. Photographs of specimens analyzed at the Kew Gardens were obtained with a stereomicroscope (Leica MZ12) equipped with a camera (ToupCam XCam Full HD). Electron micrographs of floral parts and leaf cuticles were acquired using a Hitachi (TM3000) scanning electron microscope. Prior to observation in the SEM, the specimens were coated with gold in a BAL-TEC SCD 050 sputter coater for 180 s at 50 mA, depositing 10 nm of gold on the material surface.

In order to compare the new species of *Licaria* with congenerics from the Amazon region and the Atlantic rainforest, the following species have also been analyzed in more detail: *L. armeniaca* (Nees) Kosterm. (Kostermans, 1936: 732, 1937: 584), *L. bahiana* H.W. Kurz (Kurz, 2000: 146), *L. debilis* (Mez) Kosterm. (Kostermans, 1936: 737, 1937: 596), and *L. subbullata* Kosterm. (Kostermans, 1962: 286). The specimens examined and used in the micromorphological and anatomical analyses are listed after the paratypes of the new species.

For the study of leaf cuticles, leaf samples of 1 cm^2, taken from the median region of mature leaves of herbarium specimens of each species, were boiled in a water bath until the material felt pliable (usually for 5–10 min). After that, the samples were macerated in Jeffrey's solution (Jeffrey, 1917; we slightly modified it to be equal parts 20% chromic and bench concentrated nitric acids; Johansen, 1940; Stace, 1965), for about 16 hr, in order to isolate the cuticular membrane. After maceration, cuticles were thoroughly (three times) rinsed with distilled water, then dehydrated in alcohol series before staining them in 1% safranin in 50% ethanol for 5–10 min. For the anatomical analysis of cross sections of blade midribs and petioles, leaf samples of herbarium specimens were boiled in a water bath for about 10 min. Freehand transverse sections were made at the median region of the blade and of the petiole, and the sections were partially decolorized with household bleach (20%), then thoroughly (three times) washed with distilled water. Dehydration of the cleared samples was done in alcohol series before staining them with safranin and Astra Blue (Safrablau) (Bukatsch, 1972, modified by Kraus and Arduin, 1997). All preparations were mounted on microscope slides in Entellan.® Photomicrographs were obtained with a photomicroscope (Leica DM500) coupled with a camera (Leica ICC50) and the software LAS EZ v.3.0.0.

Descriptive terminology of leaf cuticles follows Barthlott and Ehler (1977), Wilkinson (1979), Faggetter (1985, 1987), and Trofimov and Rohwer (2018). Terminology of leaf venation follows Hickey (1973, 1979), Coe-Teixeira (1980), Christophel and Rowett (1996), and Ellis et al. (2009). Terminology of the vascular bundle arrangement in midribs and petioles follows Howard (1979), Santos and Oliveira (1988, 1995), Nishida and Christophel (1999), and Vaz et al. (2019). Abbreviations used in the text are as follows: fl. = flower; fr. = fruit; immat. fr. = immature fruit; l. = left; r. = right.

TAXONOMY

Licaria spiritusanctensis P.L.R. Moraes & T.D.M. Barbosa, *sp. nov*.

TYPE: BRAZIL. Espírito Santo: Santa Teresa, terreno do Boza, 26 October 1999, bud, fl., *V. Demuner, E. Bausen & W. Pizziolo 173* (Holotype: MBML [11290]; Isotypes: HRCB, RB, UEC). Fig. 1.

Licaria spiritusanctensis can be recognized by the combination of leaves glabrous above, glabrous to glabrescent below, trichomes short, straight, appressed, sparse trichomes mainly on midrib, often somewhat bullate above, inflorescences pubescent to dense pubescent, flowers glabrescent to sparse pubescent, floral tube glabrous to sparse pubescent inside, tepals subequal, stamens free, elongate, apical-extrorse, staminal valves large, locelli opening away from the center of the flower, the flaps laterally swinging toward the center of anthers, filaments as wide as or narrower than the anthers, with two large basal glands, elongate, almost as long as the filament, appressed, sagittate, sessile, staminodes of fourth whorl in irregular numbers, 1 to 3 or wanting, pistils glabrous, and fruits seated on a distinctly swollen and turbinate pedicel that gradually merges into a shallow cupule, conspicuously double-rimmed.

Small *trees* up to 10 m tall. Cortex slightly aromatic. *Terminal buds* ovoid to elongate, densely covered with short, straight, appressed-to-ascending trichomes. Young *branchlets* angular, glabrous or with short, straight, appressed, whitish trichomes, moderately sparse to dense immediately below terminal bud, and slowly glabrescent on older parts of the twig; twigs in living material glossy, gray-bluish. *Petioles* 1.0–1.8 cm long, glabrous to glabrescent, densely pubescent in young leaves, indument ± as on twigs, (±) roundish below, canaliculate above, flat, or irregularly ridged. *Leaves* alternate, evenly distributed along branchlets, mostly elliptic to lanceolate, varying toward (sub)oblong or obovate, 5.4–27.0 × 1.7–8.5 cm, subcoriaceous to chartaceous, glabrous above, glabrous to glabrescent below, with short, straight, appressed, sparse trichomes mainly on midrib, papillate (but the papillae are not well developed; outer periclinal walls

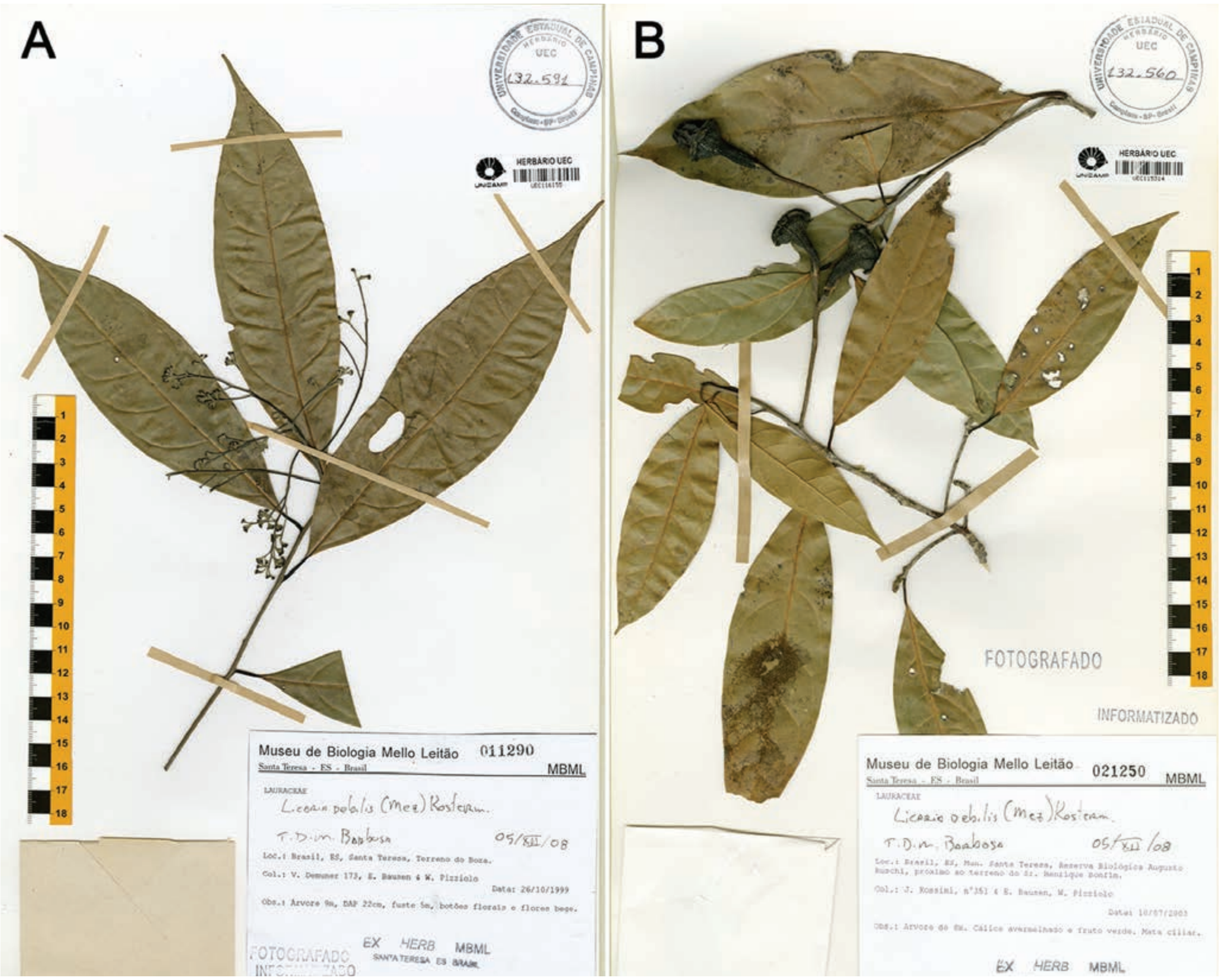


FIGURE 1. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A**, isotype (*Demuner 173*, UEC); **B**, paratype (*Rossini 351*, UEC).

variously convex, low domed), glossy above, paler below, tip often long acuminate to cuspidate, base attenuate, cuneate or subrounded (mostly obtuse), mostly symetrical, margin sclerified, flat to minutely revolute; upper surface somewhat bullate in several specimens; venation pinnate, eucamptodromous to brochidodromous, reticulation imperfect, areoles randomly arranged (not oriented), irregular, veinlets linear to branched once, or absent; midrib above usually prominulous to slightly prominent in a distinct impression, sometimes flat to level toward the base, (very) prominent below, secondary veins above usually convex in an often slight impression to flat to level, prominulous to prominent below, 6–11 on each side of the midrib, reticulation flat to level to immersed above, prominulous below. *Inflorescences* paniculate, 1.25–9.70 cm long, in the axils of foliage leaves as well as in the axils of cataphylls at the base of the new growth, below the terminal bud, or on axillary brachyblasts, few-flowered to (sub)many-flowered, much shorter than leaves, pubescent to densely pubescent, trichomes grayish to whitish, short, appressed to ascending. *Pedicels* 2.7–3.2 mm long, 0.29–1.10 mm thick, indument denser than peduncles. *Flowers* yellow in living material (but also recorded as white, beige, orange, green, green-yellowish, or yellow-greenish), blackish in dried material, 2.3–2.8 × 1.9–2.7 mm, glabrescent to sparse pubescent, trichomes short, appressed, floral tube relatively shallow, ca. 0.6–0.9 mm deep, infundibuliform, glabrous to sparse pubescent inside, trichomes whitish, short, appressed; tepals 6, subequal, inner ones slightly longer than outer ones, erect to spreading at anthesis, 0.80–1.96 × 0.9–1.7 mm, ovate to depressed ovate, mainly glabrous to sparsely pubescent, trichomes short, appressed; staminodes of first and second whorl foliaceous, almost panduriform to rectangular, narrowed toward the base, apex obtuse to truncate, glabrous at the base, first whorl 0.8–1.1 × 0.5–0.6 mm, second whorl 0.8–1.2 × 0.5 mm; stamens of third whorl free, elongate, 0.79–1.40 × 0.39–0.70 mm, apical-(sub)extrorse, staminal valves relatively large (in proportion to stamen size), the locelli opening away from the center of the flower, with the flaps laterally swinging toward the center of anthers, from the borders of the septum separating the locelli, filaments as wide as or narrower than the anthers, pilose, with two basal glands, large, 0.44–1.00 mm long, elongate, almost as long as the filament, appressed, sagittate, (sub)sessile; staminodes of fourth whorl 1 to 3 when present, 0.54–0.88 mm long, liguliform to conic, pilose; pistil glabrous, 1.5–1.9 mm long, ovary ellipsoid, 0.64–0.80 mm long, style relatively stout, 0.7–1.1 mm long, stigma minute, ovule ellipsoid, 0.48–0.64 mm long. *Fruits* 1.9–2.8 × 1.1–1.9 cm, ellipsoid, smooth, seated on a distinctly swollen and turbinate pedicel that gradually merges into a shallow cupule; cupules red in living material, 0.4–1.6 × 1.48–2.30 cm, hemispheric to infundibuliform, verrucose, double-rimmed, margin 4.0–8.0 mm thick, pedicels 1.3–1.9 cm long. Fig. 2–4, 5A–D.

Phenology: flowers collected from June to January. Immature fruits collected from September to July.

Etymology: the species name refers to the Brazilian state of Espírito Santo, where the species has been collected so far.

Distribution and habitat: *Licaria spiritusanctensis* is known only from two municipalities of the state of Espírito Santo, Águia Branca and Santa Teresa, in the Atlantic rainforest domain. However, in the region of Santa Teresa, which has been thoroughly surveyed for many years, the species seems to be relatively frequent in the understory of the Montane Atlantic rainforest. Evidence of that are the 43 specimens collected in that region, a number that is notably higher than the average of collections of the other Lauraceae recorded there (see Barbosa et al., 2012). (Fig. 4).

Additional specimens examined [*Licaria spiritusanctensis*]: BRAZIL. Espírito Santo: Águia Branca, Córrego Jabuticaba, propr. Rosangela Fausti, 19°01'22"S, 40°38'52"W, 190–550 m, 30 November 2006, immat. fr., *L. F. S. Magnago et al. 1659* (MBML); Santa Teresa, Alto São Lourenço, sítio da Cachoeira (Lídio), 25 October 2000, fl., *V. Demuner et al. 1489* (HRCB, MBML, RB, UEC); idem, Sítio L. Bringhenti, 19°58'22"S, 40°35'36.1"W, 819 m, 10 September 2011, immat. fr., *P. L. R. de Moraes et al. 3228* (HBG, HRCB); idem, Estação Biológica de Santa Lúcia, divisa à direita depois da trilha Bonita, 750 m, 25 November 1998, fl., *L. Kollmann et al. 1109* (HRCB, MBML, RB, UEC); idem, Estação Biológica de Santa Lúcia, trilha do Tapinoã, 30 December 1999, fl., *V. Demuner et al. 434* (HRCB, MBML, RB, UEC); idem, Estação Biológica de Santa Lúcia, 1 October 2004, *F. A. G. Guilherme 373* (ESAL, MBML, RFA); idem, Estação Biológica de Santa Lúcia, 11 October 2004, bud, *F.A.G.Guilherme 388* (MBML, RFA); idem, Estação Biológica de Santa Lúcia, 19°58'05.4"S, 40°31'57.4"W, 623 m, 20 December 2012, fl., *P. L. R. de Moraes 3555* (HBG, HRCB); idem, Mata da Prefeitura, 8 December 1999, fl., *V.Demuner & E.Bausen 284* (MBML, RB, SPSF); idem, São Lourenço, terreno de Clério Loss, 750 m, 28 October 1998, fl., *L. Kollmann et al. 830* (MBML, RB, SPSF); idem, Mata Fria, terreno de Clério Loss, lado direito do asfalto, 9 December 1999, fl., *V. Demuner & E. Bausen 316* (HRCB, MBML, RB, UEC); idem, Nova Lombardia, Reserva Biológica Augusto Ruschi, 800 m, 16 October 2001, fl., *L. Kollmann & E. Bausen 4835* (HRCB, MBML, RB, UEC); idem, beira da estrada, 800 m, 6 November 2001, fl., *L. Kollmann & E. Bausen 4946* (HRCB, MBM, MBML, RB, UEC); idem, estrada para Goiapaba-Açu, 850 m, 11 December 2001, fl., *L. Kollmann et al. 5177* (ESAL, MBML, RB, UEC); idem, 11 December 2001, fl., *L. Kollmann et al. 5181* (MBM, MBML, RB, UEC); idem, estrada de Nova Lombardia, 850 m, 9 January 2002, fl., *L. Kollmann et al. 5229* (MBML, RB, UEC); idem, estrada para João Neiva, 24 September 2002, fl., *R. R. Vervloet et al. 1060* (BHCB, MBM, MBML, RB, UEC); idem, estrada para Goiapaba-Açu, parte final, 800 m, 24 October 2002, fl., *R. R. Vervloet et al. 1265* (MBML, RB, UEC); idem, Goiapaba-Açu (marcos 78, 77, 76), 850 m, 29 October 2002, fl., *R. R. Vervloet et al. 1317* (BHCB, MBML, RB, UEC); idem, Nova Lombardia, Reserva Biológica Augusto Ruschi, trilha da Tronqueira, 800 m, 30 October 2001, fl., *L. Kollmann et al. 4939* (MBML, RB, UEC); idem, valão à direita da sede velha, 800 m, 29 November 2001, fl., *L. Kollmann et al. 5102* (BHCB, MBML, RB, UEC); idem, 775 m, 5 November 2002, fl., *R.R.Vervloet et al. 1341* (MBML, RB, UEC); idem, trilha da Preguiça, 810 m, 3 December 2002, fl., *R. R. Vervloet & E. Bausen 1396* (MBML, RB, UEC); idem, trilha da Cachoeira, partindo da sede, 790 m, 4 December 2002, fl., *R. R. Vervloet & E. Bausen 1430* (ESAL, MBML, RB, UEC); idem, linha de divisa, marco 108, 825 m, 10 December 2002, fl., *R. R. Vervloet et al. 1451* (BHCB, MBML, RB, UEC); idem, trilha da Cachoeira, partindo da nova sede, 11 March 2003, immat. fr., *R. R. Vervloet & E. Bausen 1967* (MBML, RB, UEC); idem, próximo ao terreno do Sr. Henrique Bonfim, 10 July 2003, immat. fr., *J. Rossini et al. 351* (HRCB, MBML, RB, UEC); idem, trilha da Roda d'Água até área aberta, 19°54'39"S, 40°33'15.3"W, 787 m, 10 December 2012, fl., *J. A. Lombardi et al. 9822* (HRCB, UPCB); idem, São Lourenço, estrada do Caravage, Reserva da Prefeitura (Estação Biológica da Caixa D'Água), 750 m, 27 October 1998, fl., *L. Kollmann et al. 809* (MBML, UEC); idem, estrada do Caravagem (Caravaggio), 850 m, 18 November 1998, fl., *L. Kollmann et al. 1045* (MBML, RB, SPSF); idem, Mata da Prefeitura, estrada do Caravaggio, 19°55'05"S, 40°36'50.1"W, 780 m, 11 September 2011, immat. fr., *P. L. R.de Moraes et al. 3238* (HBG, HRCB); idem, Rio Saltinho, 13 May 2005, immat. fr., *L. Kollmann & A. P. Fontana 7787* (MBML); idem, Santo Antônio, terreno do Boza, 750 m, 7 October 1998, bud, *L. Kollmann et al. 734* (MBML, RB, SPSF, UEC); idem, 7 October 1998, fl., *L. Kollmann et al. 739* (MBML, RB, UEC); idem, 750 m, 29 October 1998, fl., *L. Kollmann et al. 854* (MBML, RB, SPSF); idem, 29 October 1998, fl., *L. Kollmann et al. 855* (MBML, RB, SPSF); idem, 850 m, 17 November 1998, fl., *L. Kollmann et al. 1034* (MBML, RB, SPSF, UEC); idem, 29 October 1999, fl., *V. Demuner et al. 154* (MBML, RB, SPSF); idem, 24 October 2000, fl., *V. Demuner et al. 1454* (MBML, RB, UEC); idem, 19°54'37"S, 40°35'41"W, 800 m, 8 June 2012, immat. fr., *F. Z. Saiter et al. 472* (MBML); idem, São Lourenço, Caixa d'Água, 30 November 1999, fl., *V. Demuner & W. Pizziolo 276* (MBML, RB, SPSF); idem, Vale do Canaã, 18 June 1985, fl., *J. M. Vimercat 283* (MBML, MO, SPSF); idem, estrada para Santa Maria de Jetibá, 19°56'12"S, 40°41'17.7"W, 828 m, 11 September 2011, bud, immat. fr., *P. L. R. de Moraes et al. 3245* (HBG, HRCB).

FIGURE 2. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A–B**, **D–J**, **O**. Flowers from *Kollmann 5181* (UEC). **C**, **K–N**, **P–Q**. Flowers from *Vervloet 1396* (UEC). **R**. Flower from *Vervloet 1060* (UEC). **A**, flower with erect tepals; **B**, flower with two tepals and two staminodes removed; **C**, anomalous flower, tetramerous, with spreading tepals; **D**, outer tepal and staminode of first whorl, adaxial surface; **E**, inner tepal and staminode of second whorl, adaxial surface; **F**, outer tepals, adaxial (l.) and abaxial (r.) surfaces; **G**, inner tepals, adaxial (l.) and abaxial (r.) surfaces; **H**, staminodes of first whorl, abaxial (l.) and adaxial (r.) surfaces; **I**, staminodes of second whorl, abaxial (l.) and adaxial (r.) surfaces; **J–L**, stamens of third whorl with glands, abaxial (l.) and adaxial (r.) surfaces; **M–N**, staminodes of fourth whorl; **O–P**, pistils; **Q–R**, pistils showing the ovule. Bars = 2 mm (A, B, C); 1 mm (D, E, F, G); 0.5 mm (H, I, J, K, L, M, N, O, P, Q, R).

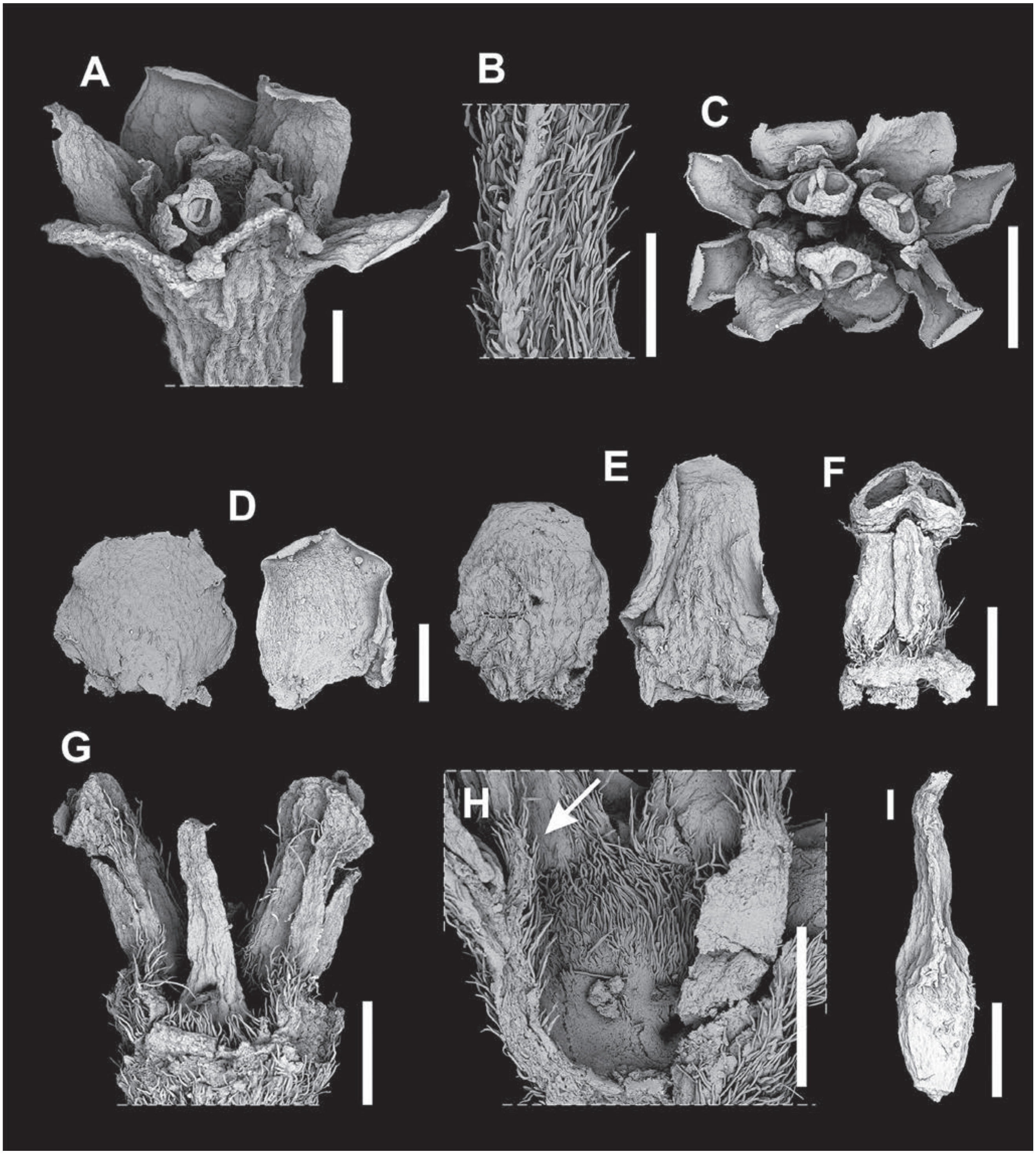


FIGURE 3. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A**, **E**. Flowers from *Kollmann 5229* (UEC). **B**. Flower from *Demuner 173* (UEC). **C**, **F–I**. Flowers from *Vervloet 1396* (UEC). **D**. Flower from *Lombardi 9822* (HRCB). **A**, flower with patent tepals; **B**, detail of pedicel; **C**, anomalous tetramerous flower, top view; **D**, outer tepals, abaxial (l.) and adaxial (r.) surfaces; **E**, inner tepals, abaxial (l.) and adaxial (r.) surfaces; **F**, stamen of third whorl with glands; **G**, side view of stamens of third whorl and pistil; **H**, view of floral tube inside and staminode of fourth whorl (arrow); **I**, pistil. Bars = 1 mm (B); 0.5 mm (A, D, E, F, G, H, I); 0.3 mm (C).

FIGURE 4. Geographic distribution of *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **A**, South America; **B**, Brazil; **C**, State of Espírito Santo.

Additional specimens examined [*Licaria armeniaca* (Nees) Kosterm.]: BRAZIL. Amazonas. Borba, BR 230, estrada Transamazônica, 1–5 km upstream from Sucunduri, along margin of river, 06°50'S, 59°00'W, 9 May 1985, *A. Henderson et al. 407* (HRCB, INPA, MO), *A. Henderson et al. 429* (F, HRCB, INPA, MBM, MO); near mouth of Rio Embira, 7°30'S, 70°15'W, 5 July 1933, *B. A. Krukoff 5185* (LE, MO, NY, US); Humaitá, near Três Casas, 14 September–11 October 1934, *B. A. Krukoff 6155* (LE, MO, NY). Paraná. Adrianópolis, Tatupeba, estrada para João Surrá, 24°42'01"S, 48°45'26"W, 130 m, 30 November 2016, *J. M. Silva et al. 9661* (HRCB, HUEFS, MBM). Rio Grande do Sul. Morrinhos do Sul, Perdida, 6 October 2016, *P. L. R. de Moraes et al. 5385* (HRCB). Rio de Janeiro. "in umbr. sylvaticis R. Jan.," June–July 1832, *L. Riedel 478* (LE, Lectotype of *Mespilodaphne parviflora* Meisn.; Isolectotypes: G, K—3 sheets, NY, US); idem, Serra dos Órgãos, April 1833, *B. Luschnath s.n.* (BR, KIEL, LE; syntype of *M. parviflora* Meisn.). Santa Catarina. Sombrio, Garapuvu, Vista Alegre, 19 March 1960, *R. Reitz & R. M. Klein 9593* (RB, holotype of *Licaria reitzkleiniana* Vattimo-Gil; isotype: HBR). São Paulo. Sete Barras, Parque Estadual Intervales, Saibadela, May 2002, *F. A. G. Guilherme 341* (HRCB). COLOMBIA. Amazonas-Vaupés. Río Apaporis, Soratama, entre el Río Pacoa y el Río Kananari, 1 August 1951, *R. E. Schultes & I. Cabrera 13237* (P). PERU. "Maynas circa oppidum Tocache ad fl. Huallagan," June 1831, *E. F. Poeppig 1787* (W [not seen], lectotype of *Evonymodaphne armeniaca* Nees; isolectotypes: B†, F, G, GZU, L, LE—2 sheets, M, NY, OXF, P—2 sheets); "Tocache," 1830/1831, *E. F. Poeppig 1861 ex parte* (B, F, GZU—2 sheets, NY, P, US; syntype of *E. armeniaca* Nees).

Additional specimens examined [*Licaria bahiana* H.W. Kurz]: BRAZIL. Bahia. km 25 da rod. Guaratinga/São Paulinho, 2 April 1973, *R. S. Pinheiro 2085* (HBG-509810, Holotype; CEPEC [9182], RB00133993, Isotype). Pedras Pretas, 29 May 1918, *H. M. Curran 364* (NY; paratype). Porto Seguro, Reserva Biológica do Pau-Brasil, 11 December 1971, *A. Eupunino 83* (CEPEC, HBG, RB; paratype); idem, RPPN Estação Veracel, 30 November 2014, *P. L. R. de Moraes et al. 4267* (HRCB). Prado, Rod. BA 284, trecho Prado/Itamaraju, ca. 65 km a NW de Prado, 18 September 1978, *S. A. Mori et al. 10638* (CEPEC, HBG, NY, RB; paratype), *S. A. Mori et al. 10671* (CEPEC, HBG, K, NY, RB; paratype); idem, km 31 da Rod. Prado/Itamaraju, (Rod. BA 284), 17°12'S, 39°24'W, 31 October 1979, *L. A. Mattos Silva & H. S. Brito 699* (CEPEC, HBG; paratype). Santa Cruz de Cabrália, arredores da Est. Ecológica do Pau-Brasil, 18 October 1978, *S. A. Mori et al. 10783* (HBG, NY, RB; paratype); idem, antiga rodovia que liga a Estação Ecológica Pau-Brasil à Sta. Cruz de Cabrália, 28 November 1979, *S. A. Mori et al. 13041* (CEPEC, HBG; paratype). Una, ca. 35 km S of Itabuna, 27 September 1979, *K. Kubitzki & H.-H. Poppendieck 79-259* (HBG, NY; paratype). Uruçuca, Lagoa Encantada, 4 June 1971, *R. S. Pinheiro 1286* (BHCB, CEPEC, HBG; paratype). Espírito Santo. Linhares, Reserva Natural Vale, 6 September 2011, *P. L.R. de Moraes et al. 3166* (CVRD, HRCB, MBM).

Additional specimens examined [*Licaria debilis* (Mez) Kosterm.]: BRAZIL. Pará. Bragança, 24 October 1926, *A.Ducke s.n.* (HBG, RB00128046, U [1359273]); Breves, Rio Tajapuru in aestuario amazonico loco Antonio Lemos, 8 July 1923, *A. Ducke s.n.* (RB00129178, U [1359288]); plantation de Paricatuba, route de Belém-Mosqueiro, 13 March 1968, *C. Sastre & F. Sastre 157* (P); Capitão Poço, Colônia S. José, 12 August 1966, *J.E.dePaula 289* (MG). FRENCH GUIANA. Cayenne, *J. B. Patris 53* (G00368864, holotype of *Acrodiclidium debile* Mez; isotype: F [1023382]); Fleuve Kourou, sur la crique Couy, 19 September 1967, *R. A. A. Oldeman B-1326* (P, U); idem, 21 September 1967, *R. A. A. Oldeman B-1354* (K). GUYANA. Kangaruma-Potaro landing, 25–27 June, 1921, *H. A. Gleason 230* (K, NY, US); Kanaku Mountains, near Nappi Creek, Pirara River, ca. 200 m, 8 October 1931, *Davis in Forest Department 2218*

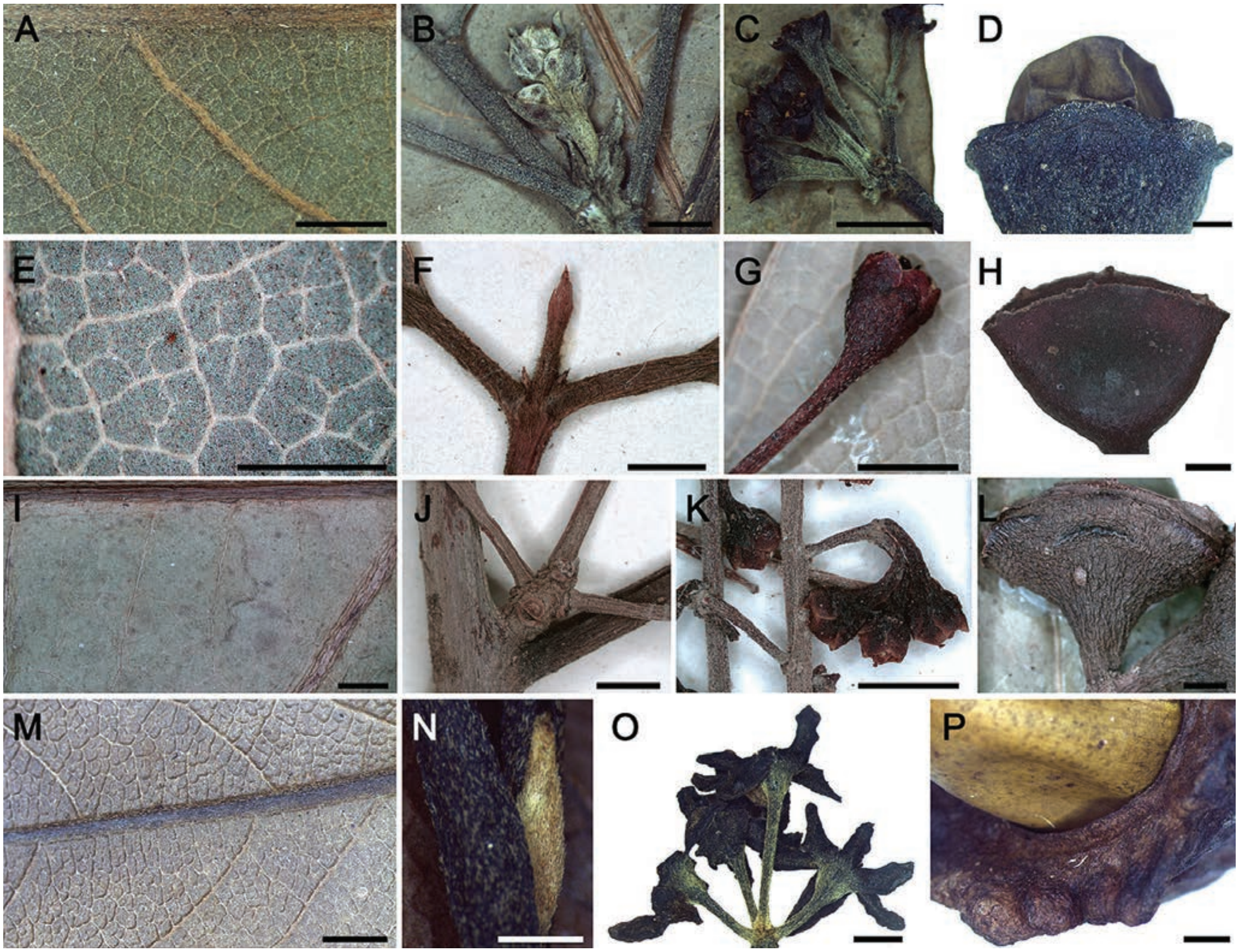


FIGURE 5. **A–D**. *Licaria spiritusanctensis* P.L.R. Moraes & T.D.M. Barbosa. **E–H**. *L. debilis* (Mez) Kosterm. **I–L**. *L. subbullata* Kosterm. **M–P**. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A**, leaf abaxial surface (*Demuner 316*, UEC); **B**, detail of peduncles and buds (*Kollmann 739*, UEC); **C**, detail of flowers (*Demuner 173*, UEC); **D**, detail of cupule and young fruit (*Vervloet 1967*, UEC); **E**, leaf abaxial surface (*Gleason 230*, K); **F**, petioles and bud (*Gleason 230*, K); **G**, flower (*Lindeman 285*, K); **H**, detail of cupule (*Gleason 230*, K); **I**, leaf abaxial surface (*Forest Department 5595*, K); **J**, detail of peduncles and petiole (*Forest Department 5595*, K); **K**, detail of peduncle and flowers (*Forest Department 5595*, K); **L**, detail of cupule (*Mori 8454*, K); **M**, leaf abaxial surface (*Kollmann 1171*, UEC); **N**, detail of petioles and bud (*Kollmann 2557*, UEC); **O**, flowers (*Demuner 334*, UEC); **P**, detail of margin of cupule (*Kollmann 2557*). Bars = 2.5 mm (A, B, C, D, E, F, G, H, I, J, K, L, M, O, P); 1.25 mm (N).

(K); Puruhi River, 1 April 1953, *Forest Department 7748* (K, NY); Kanaku Mountains, slope of Nappi Mountains, Camp 2, 03˚20'N, 59˚34'W, 450 m, 12 November 1987, *M. J. Jansen-Jacobs et al. 902* (K, U); Barima-Waini Region, Barima River Head, 7˚38'N, 60˚07'W, 1 m, 2 August 1986, *J. J. Pipoly III & H. Lall 8187* (F, MO); Kamoa River, Toucan Mountain, 01˚33'N, 58˚50'W, 260–360 m, 22 September 1989, *M. J. Jansen-Jacobs et al. 1741* (K, MO, U); Cuyuni-Mazaruni region, Aurora, 06˚47'30"N, 59˚44'30"W, 4 October 1989, *L. J. Gillespie & S. Tiwari 2090* (MO, U, US); U. Takutu-U. Essequibo region, Maparri River, 03˚20'N, 59˚15'W, 8 June 1996, *D. Clarke & T. McPherson 2062* (MO, U, US); idem, Sipu River, 01˚24'N, 58˚57'W, 245 m, 23 August 1998, *D. Clarke et al. 7087* (MO, U, US); idem, Acarai Mountains, 8 km S of Sipu River, 01˚21'N, 58˚57'W, 610 m, 3 September 1998, *D. Clarke et al. 7406* (MO, U, US). SURINAME. Brownsberg, 12 September 1924, *B.W. 6653* (U—2 sheets); Lely Mountains, 24 September 1975, *J. C. Lindeman et al. 285* (F, K, P, U); Jodensavanne-Mapane kreek area (Suriname River), 13 June 1953, *J. C. Lindeman 4054* (F, K, NY, U), 15 June 1953, *J. C. Lindeman 4086* (INPA, NY, U). VENEZUELA. Territorio Delta Amacuro, Rio Amacuro, Venezuela-Guyana frontier, Sierra Imataca, 65–80 m, 1 November 1960, *J. A. Steyermark 87206* (F, NY, U, US, VEN). Fig. 5E–H.

Additional specimens examined [*Licaria subbullata* Kosterm.]: BRAZIL. Amazonas. Manaus, Distrito Agropecuário, Reserva 1501 (km 41) da WWF/INPA Projeto da Dinâmica Biológica dos Fragmentos Florestais, 2˚24'26"S–2˚25'31"S, 59˚43'50"W, 50–150 m, 28 September 1989, *N. M. Lepschda Cunha & E. C. Pereira 400* (INPA, MO, NY, U); idem, Reserva Florestal Ducke, 02˚53'S, 59˚58'W, 12 July 1994, *A. Vicentini & P. A .C. L. Assunção 595* (INPA, K, MG, MO, NY, RB, U); idem, 17 January 1995, *P. A. C. L.*

Assunção 150 (INPA, K, MG, MO, NY, RB, U, UEC); Maués, Rio Parauari, entre os lugares Laranjal e Vila Darcy ao longo do rio, 17 July 1983, *C. A. Cid Ferreira 4199* (INPA, K, MO, NY, RB, US). Pará. Peixe Boi, 30 August 1949, *N.T.Silva 334* (IAN, U); BR 163, km 1305, vicinity of Igarapé José Preto, 23 November 1977, *G. T. Prance et al. 25679* (F, HBG, MG, U); Parauapebas [Marabá], Serra Norte, clareira à direita da estrada para o acampamento Azul, N1, 29 May 1982, *R. S. Secco et al. 381* (F, K, MG, MO, NY, RB, US); Serra Norte, 3 km southeast of AMZA mining camp 3-Alfa and west along secondary logging road, 5°49'S, 50°32'W, 225–250 m, 15 June 1982, *C. R. Sperling et al. 6190* (MG, MO, NY, US). FRENCH GUIANA. Saül, Monts La Fumée, 3°37'N, 53°12'W, 200–400 m, 8 September 1982, *S. A. Mori et al. 14887* (NY, P); idem, La Fumée Mountain Trail, vicinity of Antenne Nord, 28 July 1987, *S. A. Mori 18593* (K, MG, MO, NY, P). GUYANA. 75 miles Bootica-Potaro Road, Wallaba forest on white sand, 21 November 1947, *Forest Department 5595* (K000602008, holotype); Rupununi District, between Kuyuwini Landing and Kassikaityu River, 21 October 1992, *M. J. Jansen-Jacobs et al. 3032* (F, K, P); slopes of Mountain Makarapan, along Makarapan Creek, 3°59'N, 58°57'W, 250 m, *P. J. M. Maas et al. 7523* (K). SURINAME. Wilhelmina Gebergte, lower slopes of Frederik Top, 2 km southeast of Juliana Top, 325 m, 7 August 1963, *H. S. Irwin et al. 54585* (K, NY; paratype of *L. wilhelminensis* C.K. Allen); idem, ca. 3 km S of Juliana top, 12 km N of Lucie River, 3°39'N, 56°32'W, 500 m, 24 August 1963, *H. S. Irwin et al. 55018* (COL, F, K, NY; paratype of *L. wilhelminensis* C.K. Allen); idem, 325 m, 23 August 1963, *H.S. Irwin et al. 55028* (NY, holotype of *L. wilhelminensis* C.K. Allen; isotypes: F, K, U, US, VEN); idem, 3.5 km SSE of Juliana Top, 11.5 km north of Lucie River, 450 m, 8 August 1963, *H. S. Irwin et al. 54590* (COL, F, K, NY; paratype of *L. wilhelminensis* C.K. Allen); idem, West Rivier, 4 km south of Juliana Top, 450–700 m, 1 September 1963, *H. S. Irwin et al. 55307* (K, NY; paratype of *L. wilhelminensis* C.K. Allen); Lely Mountains, SW plateaus covered by ferrobauxite, 550–710 m, 20 September 1975, *J. C. Lindeman et al. 99* (F, K, U); idem, 175 km SSE of Paramaribo, 500–700 m, 12 October 1976, *S. A. Mori & A. Bolten 8454* (K, HBG). Fig. 5I–L.

In the revision of *Licaria* by Kurz (2000), a collection of 1985 from Santa Teresa, ES, *J. M. Vimercat 283* (MBML, MO, SPSF), was listed under *L. debilis*, therefore representing a disjunct distribution between the Amazon and the Atlantic rainforest domains. The known distribution of *L. debilis* is concentrated in the Guiana Highlands (in the three Guianas) and also recorded in Venezuela and the Brazilian state of Pará, being found in the understory of the Terra Firme forest, preferably on the border with flood forest, but also on white sand and in high savannah vegetation. Particularly related to Vimercat's collection, Kurz pointed out that it "has some characteristics that are related to *L. bahiana*" (but he did not specify them). In Barbosa et al. (2012), the authors have accepted Kurz's circumscription of *L. debilis*, thus including the specimens from Santa Teresa as belonging to that species. Nevertheless, after the analyses of specimens of *L. debilis* from the Guiana Highlands and the Brazilian Amazon, it has become clear to us that the specimens from Espírito Santo belong to a different taxon that had not been described so far.

Based on Kurz's (2000) key to subgenera, *Licaria spiritusanctensis* will key to subgen. *Armeniaca*, since it has stamens with anthers with valvate dehiscence, ovary glabrous, twigs glabrous or pubescent, apical-extrorse anther cells with flaps opening away from the stigma (i.e., the center of the flower), tepals often spreading, and staminodes 6 or 9. Nevertheless, in his key to the species of subgen. *Armeniaca*, the characters of *L. spiritusanctensis* fit up to the couplet 4, "stamens free. Staminodes of fourth whorl lacking or present," which then leads to couplet 5 and forward, where the characters of the former species do not fit at all. The couplet 5a leads to couplets 6, which encompass *L. macrophylla* (A.C. Sm.) Kosterm. and *L. subbullata*, whereas couplet 5b leads to couplets 7, encompassing *L. bahiana* and *L. debilis*. Taking the former four species for comparison with *L. spiritusanctensis*, *L. macrophylla* has stamens clearly forming a shield around the stigma, with very small valves (whereas *L. spiritusanctensis* does not have such stamens and the valves are relatively large), stalked glands (vs. sessile glands), floral tube inside with silky, rusty-brown trichomes (vs. glabrous to sparse pubescent, trichomes whitish), leaves 15–40 cm long (vs. 5.4–27.0 cm long), shortly narrowed at the base (vs. base attenuate, cuneate, or subrounded), clustered at the end of branchlets (vs. evenly distributed), and petioles 2–5 cm long (vs. 1.0–1.8 cm).

In terms of general morphological appearance of dried specimens and some flower features, *Licaria subbullata* has a combination of morphological characters that best resemble those found in *L. spiritusanctensis*: both species are small trees (up to 15 m height vs. 10 m height), with leaves alternate, evenly distributed, glabrous, with almost similar shapes and sizes (13.0–21.0 × 5.0–10.0 cm vs. 5.4–27.0 × 1.7–8.5 cm), tip cuspidate to acuminate, upper surface somewhat bullate, similar number of secondary veins on each side of the midrib (7–11 vs. 6–11), petioles of similar size (1.0–2.0 cm long vs. 1.0–1.8 cm), floral tube glabrous inside (vs. glabrous to sparse pubescent), stamens of third whorl free, elongate, with extrorse anthers, two large basal glands, elongate, almost as long as the filament, staminodes of fourth whorl present, and pistil glabrous. However, in spite of these similarities, *L. subbullata* differs from *L. spiritusanctensis* by leaves often asymmetrical at the base (vs. mostly symmetrical), with secondary veins strongly sunken on the upper surface, reticulation incomplete (vs. imperfect), coarse (vs. relatively fine), veinlets multibranched (vs. linear to branched once), flowers smaller (ca. 2.0 mm long vs. 2.3–2.8 mm long), glabrous (vs. glabrescent to sparse pubescent), staminal valves medium (vs. relatively large in proportion to stamen size), fruits smaller, 1.2–1.8 × 0.8 cm (vs. 1.9–2.8 × 1.1–1.9 cm), cupules 1.0 × 0.8–1.5 cm (vs. 0.4–1.6 × 1.48–2.30 cm), and pedicels short, slightly obscure (vs. 1.3–1.9 cm long). It is worth mentioning that Richter (1985) says that *L. subbullata* is "the literally most 'outstanding' species of the entire genus." According to him, its wood and bark features are incongruous with all other species of *Licaria*, which puts in doubt its position in the genus, or raises doubts regarding the present circumscription of the genus based on floral and vegetative morphology.

As for *Licaria bahiana*, whose distribution is also in the Atlantic rainforest domain and is sympatric in the region of Santa Teresa with *L. spiritusanctensis*, this species has been recently illustrated by Moraes and Vergne (2018). Both species can be easily distinguished, since *L. bahiana* is usually taller, reaching up to 22 m height, with flowers glabrous, pedicels relatively long, 3.6–4.0 mm long (vs. 2.7–3.2 mm long), stamens without basal glands, staminodes of fourth whorl wanting, pistil 2.2–2.4 mm long (vs. 1.5–1.9 mm long), fruits larger, 2.5–4.0 × 1.5–3.0 cm (vs. 1.9–2.8 × 1.1–1.9 cm), and cupules larger, 2.0–4.0 × 2.0–4.0 cm (vs. 0.4–1.6 × 1.48–2.30 cm).

Licaria debilis appears similar to *L. spiritusanctensis* at first glance because of the general morphological appearance of dried specimens of both species, which resemble each other. However, in *L. debilis*, the indument of buds, branchlets, petioles, and inflorescences consist of rusty trichomes of different sizes (vs. only short, grayish-to-whitish trichomes), the leaves on average are smaller, 6.0–16.0 × 2.0–5.5 cm (vs. 5.4–27.0 × 1.7–8.5 cm), often opposite to subopposite (vs. alternate), glabrescent on both sides, with long-persistent trichomes (longer than 0.5 mm) on midrib (vs. glabrous to glabrescent below, short trichomes), petioles slender, 0.3–1.0 cm long (vs. 1.0–1.8 cm long), inflorescences reddish in dried material (vs. blackish), flowers glabrous or nearly so (vs. glabrescent to sparsely pubescent), 1.0–2.0 mm long (vs. 2.3–2.8 mm long), pedicels thin, 2.0–5.0 mm long (vs. 2.7–3.2 mm long), stamens rather thick, ca. 1.0 mm long (vs. 0.79–1.40 mm long), filaments not distinct (vs. filaments as wide as or narrower than the anthers, therefore distinct), staminal valves medium (vs. staminal valves relatively large), basal glands in irregular numbers, 2–6 (vs. always 6), minute (vs. large, elongate), pin-shaped (vs. sagittate), located far to the side of the filaments (vs. along the abaxial surface of filaments), staminodes of fourth whorl wanting (vs. present), floral tube densely sericeous inside, with brown-yellowish trichomes (vs. glabrous to sparsely pubescent, trichomes whitish), fruits smaller, 2.0 × 1.0 cm (vs. 1.9–2.8 × 1.1–1.9 cm), cupules in average smaller, 0.8–1.2 × 0.8–1.5 cm (vs. 0.4–1.6 × 1.48–2.3 cm), scarcely recognizable with double margins (margin 1.0–2.0 mm thick; vs. conspicuously double-rimmed, margin 4.0–8.0 mm thick), reddish in dried material (vs. blackish), pedicels ca. 1.0 cm long (vs. 0.4–1.6 cm long).

In addition to the species compared above with *Licaria spiritusanctensis*, *L. armeniaca* is another species with distribution in the Atlantic rainforest domain that could be confused with the former by the seeming vegetative resemblance. However, *L. armeniaca* can be distinguished by the leaves on average usually smaller and narrower, 8.0–18.0 × 2.5–6.0 cm (vs. 5.4–27.0 × 1.7–8.5 cm), lower number of secondary veins on each side of the midrib, 5–9 (vs. 6–11), petioles slender, smaller, 0.3–1.5 cm long (vs. 1.0–1.8 cm long), inflorescences larger, 2.0–13.0 cm long (vs. 1.25–9.70 cm long), glabrous to sparsely pubescent (vs. pubescent to densely pubescent), flowers smaller, 1.0–2.0 mm long (vs. 2.3–2.8 mm long), glabrous (vs. glabrescent to sparsely pubescent), pedicels thin, long, (3.0–)8.0–15.0 mm long (vs. 2.7–3.2 mm long), floral tube sericeous inside (vs. glabrous to sparsely pubescent), tepals unequal, inner ones conspicuously larger than outer ones (vs. subequal, inner ones slightly longer than outer ones), stamens with apical-introrse valves, the locelli always opening outward from the center of the flower, and the flaps swinging toward the tip of the anthers (vs. apical-(sub)extrorse, the locelli opening away from the center of the flower, and the flaps laterally swinging toward the center of anthers), staminodes of fourth whorl wanting (vs. wanting to present, then 1 to 3), fruits relatively smaller, 1.5–2.5 × 0.8–1.5 cm (vs. 1.9–2.8 × 1.1–1.9 cm), cupules smaller, 0.4–1.5 × 0.6–1.5 cm (vs. 0.4–1.6 × 1.48–2.3 cm), pedicels up to 2.5 cm long (vs. 1.3–1.9 cm long).

Ocotea teresae P.L.R. Moraes & T.D.M. Barbosa, *sp. nov*. TYPE: BRAZIL. Espírito Santo: Santa Teresa, São Lourenço, Country Club, 16 December 1999, fl., *V. Demuner, E. Bausen & W. Pizziolo 334* (Holotype: MBML [11393]; Isotypes: HRCB, RB, UEC). Fig. 6.

Ocotea teresae can be recognized by the combination of leaves alternate to subopposite, evenly distributed along branchlets, without domatia, flowers large, densely pubescent, floral tube pubescent inside, tepals patent, spreading at anthesis, subequal, sparsely papillate outside, moderately papillate inside, stamens papillate, with short, pilose filaments, pistil glabrous, and relatively large fruits seated on large, hemispheric, hexalobed, double-rimmed cupules.

Small *trees* up to 12 m tall. *Terminal buds* elongate, densely covered with short, straight, appressed to ascending, yellow trichomes. *Branchlets* subangular, pubescent, trichomes short, straight, mostly appressed, yellowish, dense immediately below terminal bud, and slowly glabrescent on older parts of the twig. *Petioles* 0.5–1.1 cm long, blackish, glabrous to sparsely pubescent, densely pubescent in young leaves, indument ± as on twigs, (±) roundish below, canaliculate above. *Leaves* alternate to subopposite, evenly distributed along branchlets, elliptic, varying towards suboblong or obovate, 6.4–13.0 × 2.5–4.1 cm, subcoriaceous to coriaceous, glabrous above, sparsely pubescent below, with short, straight, mostly appressed trichomes mainly on midrib, glossy on both surfaces, paler below, tip obtuse, long acuminate to acuminate, base acute to cuneate, margin sclerified, flat; venation pinnate, eucamptodromous to brochidodromous, reticulation perfect to imperfect, areoles randomly arranged (not oriented), irregular, veinlets branched once, or absent; midrib prominent on both surfaces, secondary veins prominulous on both surfaces, 7–10 on each side of the midrib, without domatia, reticulation subdense, prominulous on both surfaces, conspicuous. *Inflorescences* racemose to paniculate, in the axils of foliage leaves and subterminal apical buds, or lateral, few-flowered, shorter than leaves, pubescent, trichomes yellowish, short, mostly appressed, peduncles angular, 1.8–4.5 cm long. *Flowers* bisexual, white in living material, blackish in dried material, large,

FIGURE 6. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A**, isotype (*Demuner 334*, UEC); **B**, paratype (*Kollmann 2557*, UEC).

ca. 6.0–8.0 × 5.0–6.0 mm at anthesis, densely pubescent, trichomes short, straight, mostly appressed, floral tube suburceolate, relatively shallow, ca. 1.0 mm deep, pubescent inside, trichomes grayish, relatively long (ca. 0.4 mm long), mostly appressed; tepals patent at pre-anthesis, spreading at anthesis, subequal, outer ones slightly larger than inner ones, ca. 2.2–4.1 × 1.1–2.0 mm, narrow ovate to suboblong, sparse pubescent to glabrescent, trichomes short, straight, appressed, sparse papillate outside, moderately papillate inside; stamens of first and second whorl almost of same size and shape, 0.7–1.0 mm long, upper pair of locelli introrse, lower pair lateral-introrse, anthers almost orbicular to roundish-trapeziform to trapeziform, glabrous, connective papillate, mainly on apex, the latter obtuse to truncate, filaments very short, ca. 0.15–0.3 mm long, shorter than anthers, pilose; stamens of third whorl 0.7–1.0 mm long, anthers subrectangular, glabrous, papillate, apex truncate, upper locelli lateral-extrorse, lower ones extrorse, filaments slightly shorter than anthers, pilose, with two basal glands, large, 0.48–0.70 × 0.57–0.67 mm, globose, short stalked; staminodes of fourth whorl stipitiform to subsagittate, pilose; pistil glabrous, 1.6–2.4 mm long, ovary ovoid, 0.9–1.4 mm long, style stout, 0.7–0.9 mm long, stigma robust, discoid, trilobed. *Fruits* 2.0–5.0 × 1.0–3.0 cm, ellipsoid, smooth, cupules 1.5–4.0 × 1.5–5.0 cm, hemispheric, hexalobed, double-rimmed, margin 4.0–8.0 mm thick, pedicels short. Fig. 5M–P, 7–8.

Phenology: flowers collected in November and December. Unripe fruits collected in January and June.

Etymology: the species name refers to the municipality of Santa Teresa, where the species has been collected so far.

Distribution and habitat: *Ocotea teresae* is known only from five specimens collected in the municipality of Santa Teresa, Espírito Santo, in the Atlantic rainforest domain; the localities are virtually the same as those shown in Fig. 4 for *Licaria spiritusanctensis*.

Additional specimens examined: BRAZIL. Espírito Santo: Santa Teresa, Reserva Biológica da Caixa D'água, alt. 700 m, 24 November 1998, bud, fl., *L. Kollmann et al. 1070* (HRCB, MBML, RB, SPSF, UEC); Santa Teresa, São

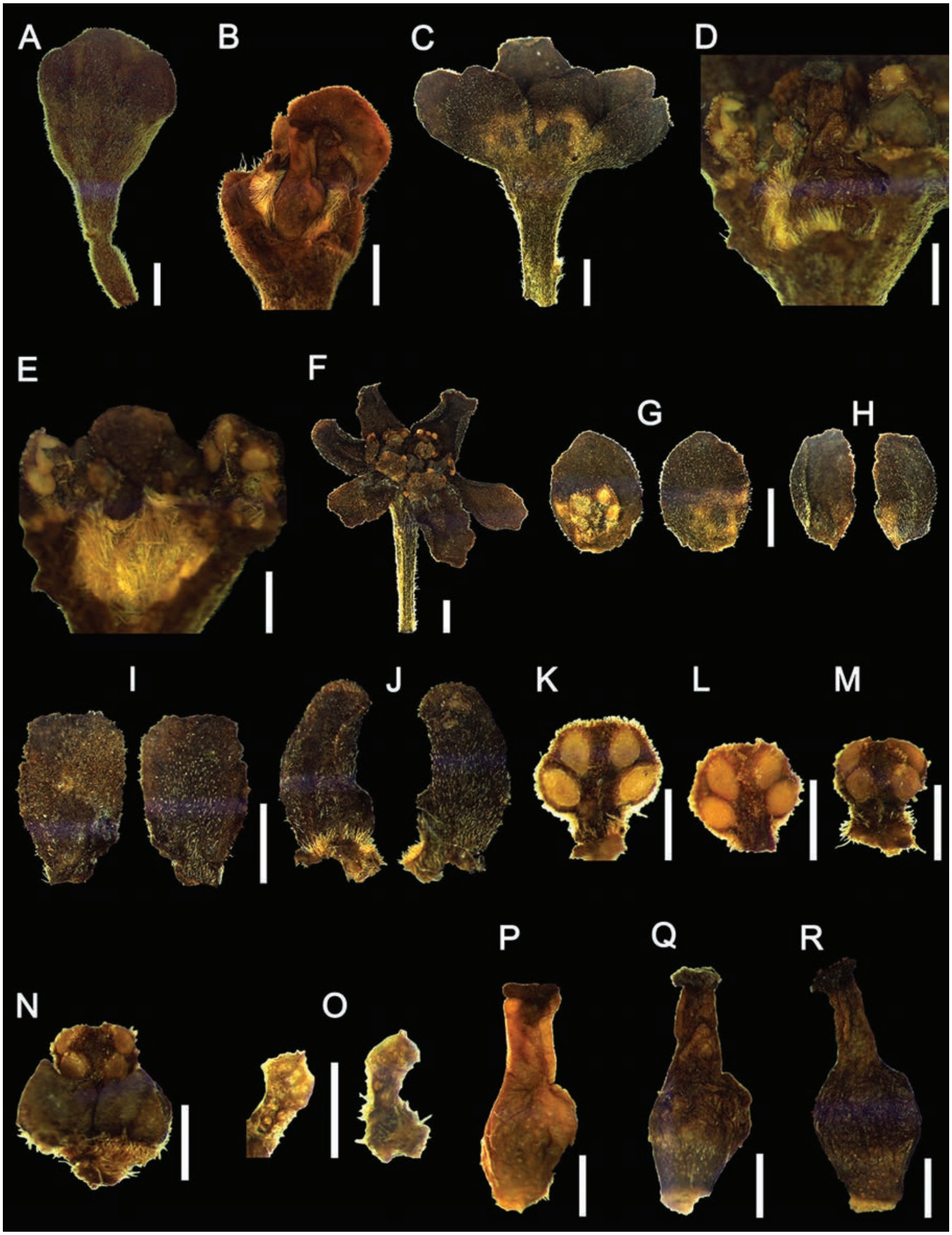


FIGURE 7. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A–B**, **P**. Flower buds from *Kollmann 1070* (UEC). **C–O**, **Q–R**. Flowers at pre-anthesis and post-anthesis from *Kollmann 1171* (UEC). **A**, bud; **B**, detail of pistil insertion in the floral tube from the previous bud; **C**, flower at pre-anthesis with patent tepals; **D**, detail of pistil insertion in the floral tube from the previous flower; **E**, detail of floral tube inside; **F**, flower at post-anthesis with spreading tepals; **G**, outer tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in C; **H**, inner tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in C; **I**, outer tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in F; **J**, inner tepals, adaxial (l.) and abaxial (r.) surfaces, from the flower in F; **K**, stamen of first whorl from flower at pre-anthesis; **L**, stamen of second whorl from flower at pre-anthesis; **M**, stamen of third whorl from flower at pre-anthesis; **N**, stamen of third whorl with basal glands from flower at pre-anthesis; **O**, staminodes of fourth whorl from flower at pre-anthesis; **P**, pistil from flower bud; **Q**, pistil from flower at pre-anthesis; **R**, pistil from flower at post-anthesis. Bars = 1 mm (A, B, C, F, G, H, I, J); 0.5 mm (D, E, K, L, M, N, O, P, Q, R).

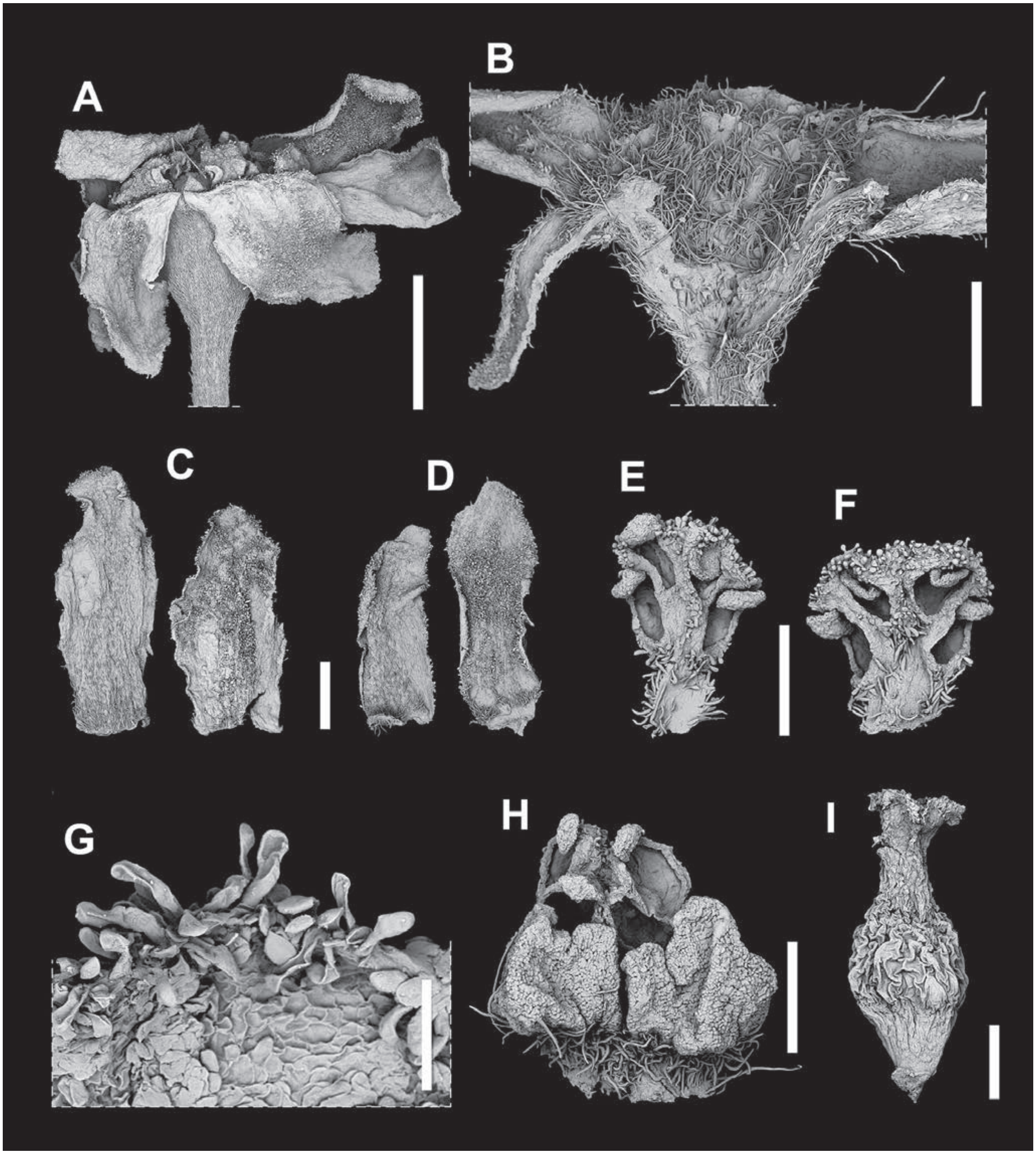


FIGURE 8. *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. Flowers at post-anthesis from *Demuner 334* (UEC). **A**, sideview; **B**, sideview showing floral tube inside; **C**, outer tepals, abaxial (l.) and adaxial (r.) surfaces; **D**, inner tepals, abaxial (l.) and adaxial (r.) surfaces; **E**, stamen of second whorl; **F**, stamen of first whorl; **G**, detail of papillae on surface of anther apex; **H**, stamen of third whorl with basal glands; **I**, pistil. Bars = 2 mm (A); 1 mm (B, C, D); 0.5 mm (E, F, H, I); 0.1 mm (G).

Lourenço, Mata Fria, terreno de Clério Loss, valão à direita do asfalto, alt. 750 m, 2 December 1998, fl., *L. Kollmann et al. 1171* (HRCB, MBML, RB, UEC); Santa Teresa, Santo Antônio, terreno do Boza, alt. 750 m, 14 January 1999, immat. fr., *L. Kollmann & E. Bausen 1557* (ESAL, MBML, UEC); idem, alt. 850 m, 15 June 1999, immat. fr., *L. Kollmann et al. 2557* (MBML, RB, UEC).

From the combination of morphological characters found in *Ocotea teresae*, its placement in the informal groups of species proposed by Rohwer (1986) must be among those with bisexual flowers. It seems to fit best in the *O. indecora* group, which encompasses species with stamens with distinct, pubescent filaments, anthers usually somewhat papillate, staminodes present, floral tube usually deeply tubular; cupule in most species for most of its development hemispherical to almost spherical, sometimes double-rimmed. Nevertheless, it does not appear to present rhythmic growth of the branchlets, showing growth units starting with a long internode, and leaves and branches often more or less crowded, which are characteristic of this group. In the general morphological aspect, *O. teresae* resembles *O. complicata* (Meisn.) Mez and *O. elegans* Mez, but differs from them by the flowers larger, ca. 8.0 × 6.0 mm (vs. 4.0–6.0 × 3.0–6.0 mm and 2.3–5.0 × 1.3–5.0 mm, respectively) and cupules double-rimmed. Several species of the *O. indecora* group develop double-rimmed cupules, like *O. calliscypha* L.C.S. Assis & Mello-Silva, *O. marcescens* L.C.S. Assis & Mello-Silva, *O. mosenii* Mez, *O. oppositifolia* S. Yasuda, *O. pumila* L.C.S. Assis & Mello-Silva, and *O. virgultosa* (Nees) Mez (= *O. lobbii* (Meisn.) Rohwer). However, none of them has cupules similar to those of *O. teresae*, which are different in shape, larger, thicker, with margins fairly conspicuous, resembling those of *Licaria bahiana*. *Ocotea teresae* is also vegetatively similar to *O. catharinensis* Mez and *O. oppositifolia* S. Yasuda, but both species have domatia in the leaves, which are not found in the former. The large flowers of *O. teresae*, with papillate tepals, are also found in species of *Nectandra*. However, both tepals and stamens of the former are less papillate than those usually found in *Nectandra*, besides other differences.

MICROMORPHOLOGICAL AND ANATOMICAL NOTES

Further characters for the description of *Licaria spiritusanctensis* are provided here on the basis of investigation of its leaf cuticle and vascular bundles of midrib and petioles as compared with those of selected congenerics. Similarly, these characters are presented for *Ocotea teresae*, for both flowering and fruiting specimens, in order to verify their matching. No effort has been made here for a complete and detailed description of all epidermal features that could be analyzed in a more comprehensive study.

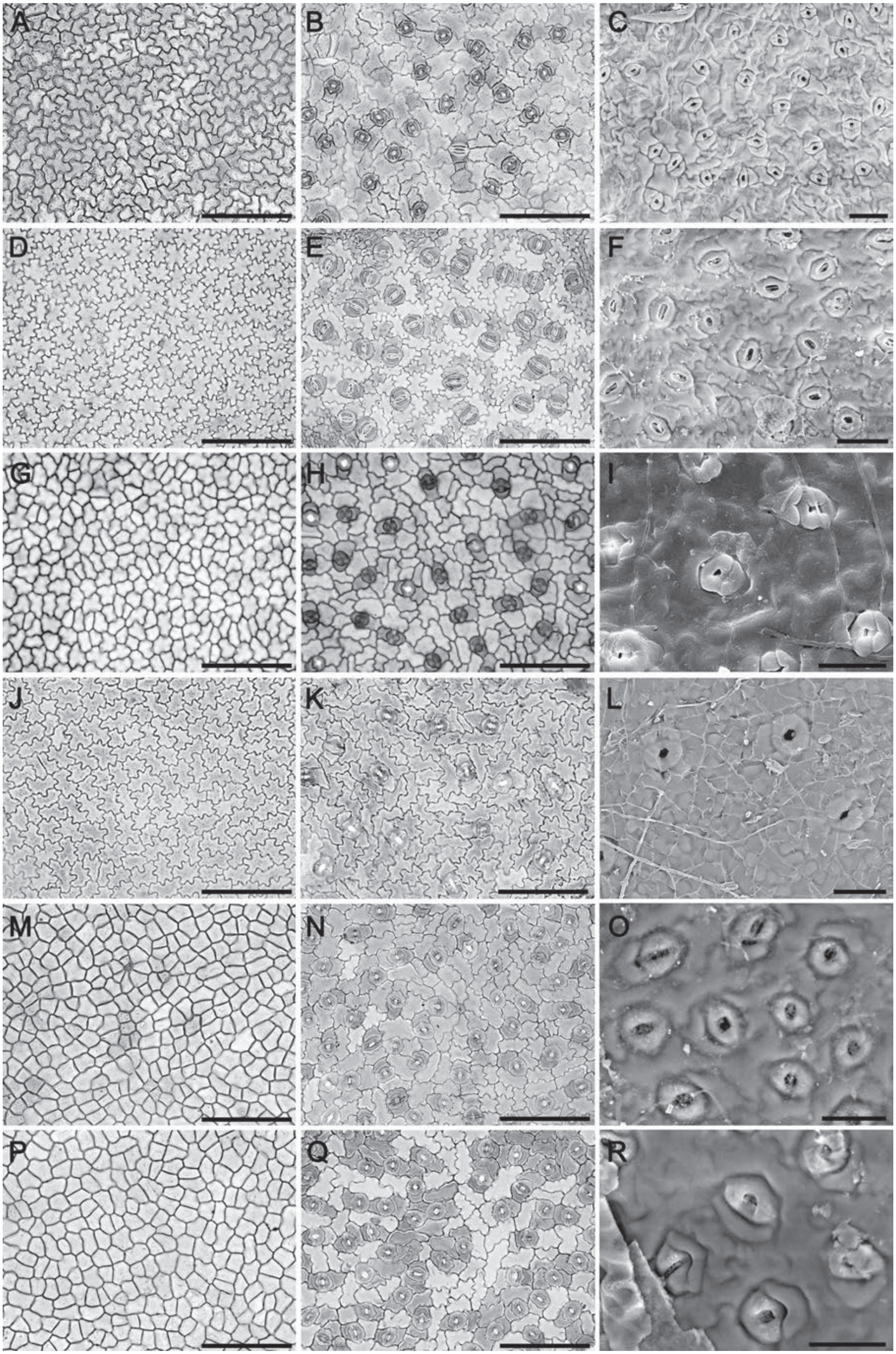
Leaf cuticles: Figure 9 shows the straightness of the epidermal anticlinal walls, in frontal view, for both adaxial and abaxial sides, as well as the overall shape of the stomatal complex. For the adaxial side of the epidermis, the epidermal anticlinal walls of *Licaria spiritusanctensis* are sinuate (Fig. 9A), whereas they are Ω-shaped in *L. armeniaca* and *L. subbullata* (Fig. 9D and J, respectively), and undulate to sinuate in *L. bahiana* (Fig. 9G). For *Ocotea teresae*, the anticlinal walls are curved and the cells are of the same size in both the flowering and fruiting specimens examined (Fig. 9M and P, respectively). On the abaxial side, *L. spiritusanctensis* shows cells slightly larger than those of the adaxial side, with sinuate to almost Ω-shaped walls (Fig. 9B), whereas in the other species the cells are of the same size and the anticlinal walls are as straight as on the adaxial side, that is, Ω-shaped in *L. armeniaca* and *L. subbullata* (Fig. 9E and K, respectively), and undulate to sinuate in *L. bahiana* (Fig. 9H). In *O. teresae*, the cells of both specimens examined are slightly larger than those on the adaxial side, and the anticlinal walls are sinuate to almost Ω-shaped (Fig. 9N and Q, respectively).

The overall shape of the stomatal complex is elliptic in *Licaria spiritusanctensis* and *L. bahiana* (Fig. 9C and I, respectively), and elliptic to broadly circular in *L. armeniaca* and *L. subbullata* (Fig. 9F and L, respectively). In *Ocotea teresae*, both specimens show the overall shape mostly elliptic to almost broadly circular (Fig. 9O and R, respectively).

According to Nishida and van der Werff (2011), an increasing number of studies on cuticular characters of extant Lauraceae have been conducted after the report of their usefulness for the family by Christophel et al. (1996). Nevertheless, there are few studies on these characters involving species of *Licaria* (e.g., Faggetter, 1985; Kostermans and Baas, 1976; Nishida and van der Werff, 2011; Petzold, 1907; Trofimov and Rohwer, 2018).

Petzold (1907) was the first to report general information on the anatomy of leaves of the American Lauraceae, on the basis of collections housed at the Berlin-Dahlem herbarium (B), following the taxonomic treatment undertaken by Mez (1889). Petzold presented anatomical descriptions for 15 species of *Licaria*, which were classified by Mez under *Acrodiclidium* Nees or *Misanteca* Cham. & Schltdl. Particularly referring to the straightness of the epidermal anticlinal walls, for both adaxial and abaxial sides, he discriminated only between straight and undulate walls, remarking when the undulation was more pronounced on one of the sides but not providing any illustration. Following this criterion, Petzold reported that *Acrodiclidium brasiliense* Nees (≡ *Licaria brasiliensis* (Nees) Kosterm.) shows anticlinal walls undulate on the adaxial side and straight on the abaxial, an exception to his observations that

FIGURE 9. (Shown on next page.) Leaf cuticles and stomata complex of *Licaria* species and *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa. **A–C**. *L. spiritusanctensis* (*Kollmann 4946*, UEC). **D–F**. *L. armeniaca* (*Henderson 407*, HRCB). **G–I**. *L. bahiana* (*Moraes 4267*, HRCB). **J–L**. *L. subbullata* (*Secco 381*, MG). **M–O**. *O. teresae* (*Demuner 334*, UEC). **P–R**. *O. teresae* (*Kollmann 2557*, UEC). **A–B**, **D–E**, **G–H**, **J–K**, **M–N**, **P–Q**, adaxial and abaxial surfaces, respectively, by optical microscopy; **C**, **F**, **I**, **L**, **O**, **R**, stomatal complex by SEM. Bars = 100 µm (A–B, D–E, G–H, J–K, M–N, P–Q); 25 µm (C, F, I, L, O, R).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the species usually have cells with anticlinal walls more undulate on the abaxial side, as he has pointed out for *A. guianense* Nees (= *Licaria polyphylla* (Nees) Kosterm.) and *A. parviflorum* (Meisn.) Mez (= *Licaria armeniaca*). Under *Misanteca*, *M. capitata* Cham. & Schltdl. (≡ *Licaria capitata* (Cham. & Schltdl.) Kosterm.) and *M. pittieri* Mez (= *Licaria triandra* (Sw.) Kosterm.) were indicated with anticlinal walls undulate only on the abaxial side, whereas in *M. jurgensenii* Mez (= *L. triandra*) and *M. triandra* (Sw.) Mez (≡ *L. triandra*) the anticlinal walls were undulate on both sides. As for *L. armeniaca*, our results partially agree with Petzold, from the specimens examined for leaf cuticles (*Guilherme 341*, *Henderson 407*, *Moraes 5385*, and *Silva 9661*), since their epidermal anticlinal walls were shown to be Ω-shaped on both sides, without any pronounced difference between them. A similar result has been found by Trofimov and Rohwer (2018). Regarding *L. capitata*, photographs of epidermal anticlinal walls of both sides are available at the Cuticle Database Project (http://cuticledb.eesi.psu.edu/; former Leaf Cuticle Database Project; Barclay et al., 2007), from a sample of *E. Keber 410* (F), Mexico, prepared by David Dilcher (Contributor specimen no. 00169). The images show anticlinal walls curved adaxially, and curved to undulate to sinuate abaxially, therefore agreeing with Petzold. For *L. triandra*, Nishida and van der Werff (2011) examined a sample from *Vasquez 25139* (MO), Peru, which shows anticlinal walls "with tight U-shaped curves" (equivalent to sinuate and/or Ω-shaped walls, as used by Trofimov and Rohwer, 2018, and here) on both surfaces, agreeing with Petzold's findings for *M. jurgensenii* and *M. triandra*, but not for *M. pittieri*. In Vaz et al. (2019), *L. triandra* is said to have anticlinal walls straight adaxially and curved abaxially (but no voucher is reported for the sample used). In the protologue of *M. pittieri*, Mez (1903) cited only the fruiting specimen of "*Tonduz in herb. inst. phys.-geogr. Costar. 11612*," in "Herb. Berol., Mez," (duplicates in BM, BR, G, GH, K, NY, P, US), which most likely was the specimen analyzed by Petzold. This species was placed in the synonymy of *Licaria limbosa* (Ruiz & Pav.) Kosterm. by Kostermans (1937), which was not accepted by Allen (1945), who positioned it in *Licaria*, combining it as *L. pittieri* (Mez) C.K. Allen. Nevertheless, Kurz (1983, 2000) synonymized both *L. limbosa* and *L. pittieri* under *L. triandra*, thus widening the circumscription of the latter. Burger and van der Werff (1990) accepted the synonymy of *L. pittieri* in *L. triandra* but commented that the Costa Rican larger-leaved highland collections, which are well matched by the description and type of *L. pittieri*, contrasting with smaller-leaved lowland collections, would be worthy of subspecific rank. Despite the different opinions of taxonomists about the delimitation of *L. triandra*, it is worth mentioning that "the anticlinal walls of epidermal cells vary so much in the extent to which they are straight, curved, or undulating that the use of the surface view appearance of cells in taxonomic studies is severely limited" (Metcalfe, 1979) and should be used with caution (see Moraes and Paoli, 1999; Vaz et al., 2019).

Kostermans and Baas (1976) described the leaf anatomy of the type of *Licaria guianensis* Aubl. (*J. B. C. F. Aublet s.n.*, French Guiana; P00128471, P00128472). According to them, the unspecialized epidermal cells show strongly undulating (anticlinal) walls of about equal size adaxially and abaxially, but those on the abaxial side with very lowly dome-shaped, lignified, outer periclinal walls (in transverse section). In Nishida and van der Werff (2011), photographs of the epidermal anticlinal walls of both surfaces and the overall shape of the stomatal complex are presented from the collection of *Sabatier 3645* (MO), French Guiana.

The Ph.D. dissertation of Faggetter (1985) was a detailed study of the leaf cuticle in selected Laurales. She included two species of *Licaria* sampled from specimens deposited at Kew. The first was *A. J. G. H. Kostermans 15018*, from Trinidad (duplicates also in B, BO, L, NY, P, RB, U, and others), which was identified by Kostermans as *L. guianensis*, the name used by Faggetter. Later, in 1992, it was identified as *L. subbullata* by Henk van der Werff and confirmed by Holger Kurz in 2000 in the specimen housed at Utrecht. The second specimen was *J. de J Jiménez 1395*, from the Dominican Republic (duplicate in US), correctly identified as *L. triandra*. From Kostermans's specimen, she described epidermal anticlinal walls as straight, which does not agree with our results from the specimens *Secco 381* and *Sperling 6190,* which showed anticlinal walls Ω-shaped on both sides. As for *Jiménez 1395*, Faggetter reported curved anticlinal walls.

In the study by Nishida and van der Werff (2011), four species of *Licaria* were included: *L. cannella* (Meisn.) Kosterm. (correct name: *L. crassifolia* (Poir.) P.L.R. Moraes), *L. guianensis*, *L. martiniana* (Mez) Kosterm., and *L. triandra*. According to the authors, all of them presented epidermal anticlinal walls "with tight U-shaped curves" (ca. sinuate and/or Ω-shaped walls) on both surfaces. These species appear to form a clade in the phylogeny inferred by Chanderbali et al. (2001), which was supported by the cuticular characters analyzed by Nishida and van der Werff (2011), since they did not vary within the group. However, those cuticular characters were be incongruent with the subgenera proposed by Kurz on the basis of stamen characters, since *L. cannella* belongs to subgen. *Canella* and the other three species belong to subgen. *Licaria*.

Trofimov and Rohwer (2018) have examined and illustrated the leaf cuticle and stomatal complex in 85 species of the *Ocotea* complex by optical and scanning electron microscopy. They included samples of four species of *Licaria* subgen. *Armeniaca*: *L. armeniaca* (*Kvist & Ruiz 1052* (AAU), from Loreto, Peru), *L. bahiana* (*Moraes 3166* (HRCB), from Linhares, Espírito Santo, Brazil), *L. pachycarpa* (Meisn.) Kosterm. (*Henkel 3021* (HBG), from U. Takutu-U. Essequibo, Guyana), and *L. rodriguesii* H.W. Kurz (*Silva 1960* (HBG), from Pará, Brazil). Results from these samples showed epidermal anticlinal walls Ω-shaped on both sides for *L. armeniaca*, whereas they were sinuate on both sides for *L. bahiana* and *L. rodriguesii*, and undulate adaxially and sinuate abaxially for *L. pachycarpa*. For the overall shape of the stomatal complex and the surface appearance of epidermal periclinal walls, *L. armeniaca* showed stomata circular with a circular and protruding surface appearance of periclinal walls forming a symmetric

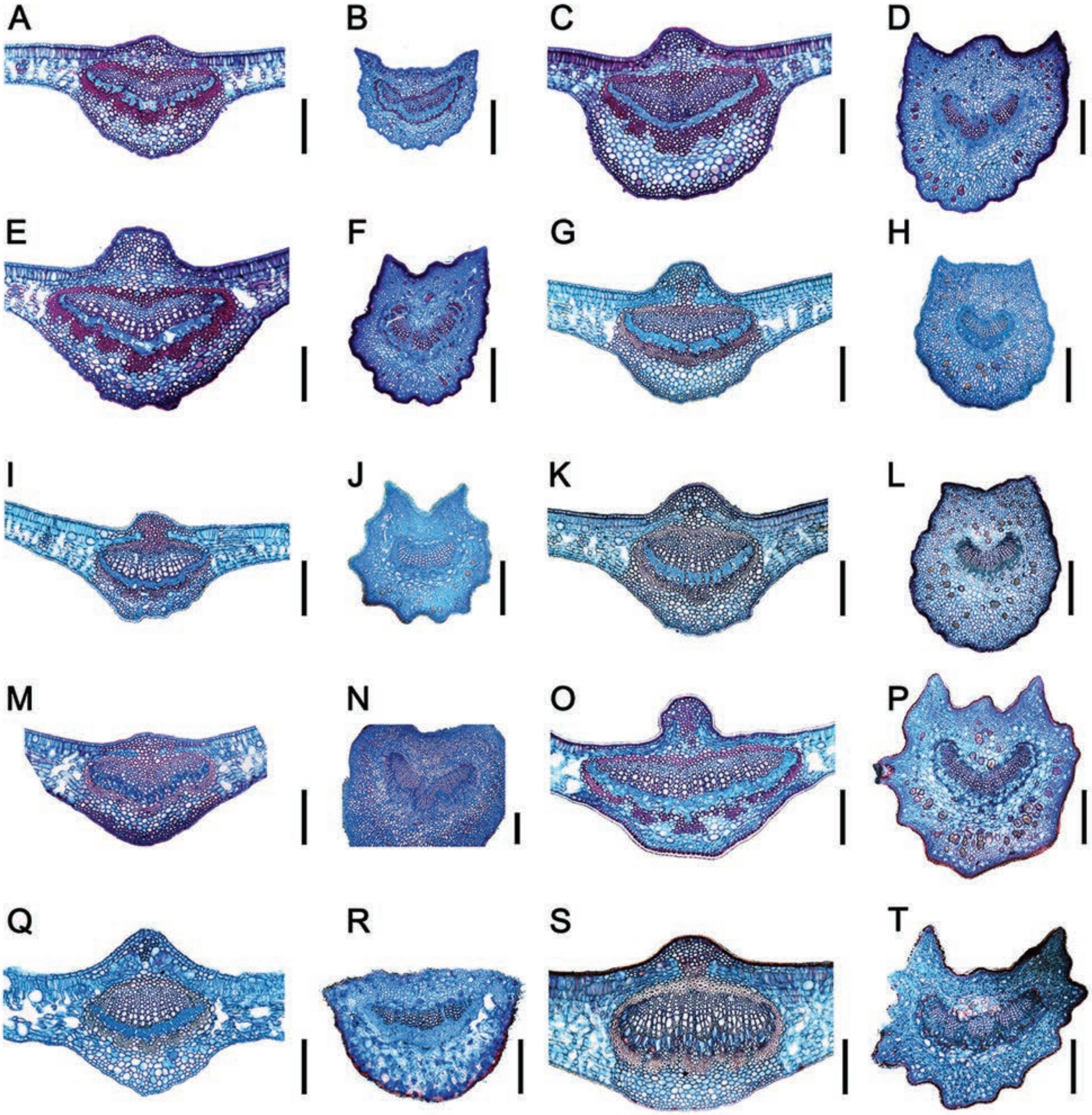

FIGURE 10. Leaf cross sections of *Licaria* species and *Ocotea teresae* P.L.R. Moraes & T.D.M. Barbosa through blade midribs and petioles. **A–B**. *L. spiritusanctensis* (*Kollmann 4946*, UEC). **C–D**. *L. spiritusanctensis* (*Moraes 3238*, HRCB). **E–F**. *L. spiritusanctensis* (*Moraes 3245*, HRCB). **G–H**. *L. armeniaca* (*Guilherme 341*, HRCB). **I–J**. *L. armeniaca* (*Henderson 407*, HRCB). **K–L**. *L. armeniaca* (*Moraes 5385*, HRCB). **M–N**. *L. bahiana* (*Moraes 3166*, HRCB). **O–P**. *L. subbullata* (*Secco 381*, MG). **Q–R**. *O. teresae* (*Demuner 334*, UEC). **S–T**. *O. teresae* (*Kollmann 2557*, UEC). **A**, **C**, **E**, **G**, **I**, **K**, **M**, **O**, **Q**, **S**, blade midrib; **B**, **D**, **F**, **H**, **J**, **L**, **N**, **P**, **R**, **T**, petiole. Abbreviations: ph, phloem; sc, sclerenchyma; se, sheath extension; xy, xylem. Bars = 250 µm (A, C, E, G, I, K, M, O, Q, S); 500 µm (B, D, F, H, J, L, N, P, R, T).

circle, whereas in the other species they were elliptic with a surface appearance narrowly circular, protruding, with evenly wide margin. Our results from samples of *L. armeniaca* showed that stomata can vary between elliptic to circular in almost equal proportions, making it difficult to select the most frequent type as typical for the specimen or species.

Regarding *Licaria debilis*, Kurz (2000) has pointed out that it is one of the few species in the genus that could be safely recognized vegetatively. Under a reflected light microscope, or even under a magnifying glass with a 50-fold magnification, it is possible to see that the epidermal anticlinal walls are strongly wavy (ca. sinuate to Ω-shaped) and shine more brightly than their surroundings. Although we had no sample at hand to illustrate this feature, we have observed it in specimens at Kew, through a stereomicroscope. Unfortunately, we did not succeed in obtaining pictures of high enough quality to include here.

As pointed out by van der Werff (2009b), fruiting specimens of *Licaria* can often be identified only by matching them with flowering ones from the same area. This is also often true in *Ocotea*, and the leaf epidermal features have been useful for confirming the identity of our samples of *O. teresae*.

Leaf vascular bundles: Figure 10 shows leaf cross sections through blade midribs and petioles. All *Licaria* species presented midribs and petioles supplied with single collateral vascular bundles, with xylem adaxially and phloem abaxially. Midrib bundles are arranged in flattened arches and are sheathed by a continuous sclerenchyma (somewhat discontinuous close to phloem in *L. subbullata*); bundle sheath extensions touch only the adaxial surface (Fig. 10A, C, E, G, I, K, M, O). The various specimens of *L. spiritusanctensis* (Fig. 10A, C, E) and *L. armeniaca* (Fig. 10G,I,K) show a closer anatomical similarity within each species, as would be expected, despite the overall similarity among them and in comparison with the specimens of *L. bahiana* (Fig. 10M) and *L. subbullata* (Fig. 10O). However, among their differences, *L. armeniaca* and *L. bahiana* have the presence of two palisade layers, whereas *L. spiritusanctensis* and *L. subbbullata* have an uniseriate palisade layer; and *L. armeniaca* shows a relatively narrower midrib bundle, whereas *L. subbullata* presents the widest one in comparison to the others. As for the petioles, the vascular bundles are crescent-shaped or in arch (ca. U- or V-shaped) in all species of *Licaria* (Fig. 10B, D, F, H, J, L, N, P). The presence of a sclerenchymatic sheath surrounding the bundle varied among the specimens of *L. spiritusanctensis* and *L. armeniaca*, and was clearly perivascular only in the sample of *Kollmann 4946* (Fig. 10B), whereas it was adaxially absent or discontinuous in the other specimens. All species presented large sclereids isolated and dispersed in the cortex.

In the specimens of *Ocotea teresae*, midribs (Fig. 10Q, S) and petioles (Fig. 10R, T) have a single collateral vascular bundle, with xylem adaxially and phloem abaxially. Midrib bundles are semicircular to arch with a perivascular sclerenchymatic sheath that can be discontinuous close to the phloem. The petioles also varied between the samples, with the bundle arranged in a flattened arch in *Demuner 334*, and crescentic in *Kollmann 2557*.

The anatomy of the leaf midrib and the petiole in Lauraceae has been studied in only a few genera and species, for example: several Philippine species of *Cinnamomum* Schaeff. by Santos (1930); *Umbellularia californica* (Hook. & Arn.) Nutt. and *Laurus nobilis* L. by Kasapligil (1951); several species of *Aniba* Aubl. by Vattimo (1968a,b,c,d, 1969a,b,c); three species of *Nectandra* Rol. ex Rottb. by Gonzalez et al. (1997); *Beilschmiedia* Nees by Nishida and Christophel (1999); several species of *Ocotea* by Santos and Oliveira (1988, 1995), Farago et al. (2005), and Coutinho et al. (2006a,b); one species of *Cryptocarya* R. Br. by Moraes and Castro (2007); and species of the *Mezilaurus* Kuntze ex Taub. clade by Vaz et al. (2019). Vaz et al. (2019) pointed out that *Licaria triandra* shows a midrib bundle arranged in arch, similar to what we have shown for the examined species.

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UNA NUEVA ESPECIE DE *HEDYOSMUM* (CHLORANTHACEAE) PARA LOS ANDES DE VENEZUELA

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Abstract. *Hedyosmum guaramacalense*, found in montane forest (1600–2600 m) on the south slope of Guaramacal National Park, Trujillo state, Venezuela, is described and illustrated. The new species belongs to *H.* subgenus *Tafalla* section *Microcarpa* and is similar to *H. goudotianum* var. *goudotianum*, but can be distinguished by its elliptic or narrowly elliptic, coriaceous or chartaceous leaves, scabrous above and below, with 5–8 lateral nerves; strigose or floccose petiolar sheaths with fimbriate appendages either restricted to two patches or evenly distributed along the apical margin; and staminate inflorescences in a cyme with 2–3 spikes, each spike 1–5 cm long. A key to the species of *Hedyosmum* currently known in the Venezuelan Andes also is provided.

Keywords: *Hedyosmum*, Chloranthaceae, Andes, Venezuela

Resumen. Se describe y se ilustra *Hedyosmum guaramacalense* de bosque de altas montañas (1600–2600 m.s.n.m.) en la vertiente sur del Parque Nacional Guaramacal, estado Trujillo, Venezuela. La nueva especie pertenece al subgénero *Tafalla* sección *Microcarpa* y es similar a *H. goudotianum* var. *goudotianum* pero se puede distinguir por sus hojas elípticas o estrechamente elípticas, coriáceas o cartáceas, áspera por ambas caras, con nervios laterales 5–8; vainas peciolares ásperas o flocosas, con apéndices fimbriados, restringidos a dos parches o uniformemente distribuidos a lo largo del margen apical; inflorescencias estaminadas en una cima con 2–3 espigas, cada espiga de 1–5 cm de largo. También se presenta una clave con las especies de *Hedyosmum* hasta ahora conocidas en los Andes de Venezuela.

Palabras claves: *Hedyosmum*, Chloranthaceae, Andes, Venezuela

Hedyosmum Sw. (Chloranthaceae) es un género pantropical con ca. 45 especies, de las cuales 44 se encuentran en el Neotrópico y una (*H. orientale* Merr. & Chun) en el Sudeste Asiático (Todzia, 1988, 2010). En Venezuela se reconocen 12 especies; 9 de ellas se encuentran en la región andina. El género se distingue por sus hojas opuestas con los márgenes dentados o crenados, vainas peciolares presentes, nudos prominentes, las inflorescencias estaminadas ebrácteadas y con numerosos estambres solitarios, las inflorescencias pistiladas subtendidas por una bráctea y por el agradable olor que difunden todas las partes de la planta (Every, 2019; Todzia, 1988, 2010). De acuerdo con el tratamiento monográfico realizado por Todzia (1988) para el Neotrópico, *Hedyosmum* está dividido en dos subgéneros: *Hedyosmum* (secciones *Hedyosmum* y *Orientale* Todzia) y *Tafalla* Solms [secciones *Artocarpoides* (Solms) Todzia, *Macrocarpa* Solms y *Microcarpa* Solms]. Posterior a la monografía de Todzia (1988), cuatro especies del género han sido descritas de los Andes (Colombia y Ecuador) y de las regiones montañosas del escudo Guayanés, respectivamente (Todzia, 1993). Sin embargo, las numerosas exploraciones botánicas de las últimas cuatro décadas y los estudios fitosociológicos de la vegetación en el ramal de Guaramacal ubicado entre los estados Portuguesa y Trujillo en los Andes de Venezuela (Cuello, 1997; Cuello y Cleef, 2009a,b,c, 2011; Cuello et al., 2010) han permitido obtener material de *H. guaramacalense* S.M. Niño & Dorr. Esta nueva especie pertenece al subgenus *Tafalla* sección *Microcarpa* (Todzia, 1988).

Hedyosmum guaramacalense S.M. Niño & Dorr, *sp. nov.* TYPE: VENEZUELA. Trujillo: Municipio Boconó, Parque Nacional Guaramacal, selvas nubladas de la vertiente sur, Parcela de estudio fitosociológico No. 9, 09°13'N, 070°07'W, 2100 m, 20–22 Enero 1996, *A.Licata, J.Farreras, R.González & C.Oraá 685* (♀) (Holotipo: PORT; Isotipos: MO, TEX, US [00513874]). Fig. 1, 2A.

Differs from *Hedyosmum goudotianum* Solms var. *goudotianum* (Fig. 2, Table 1) in having elliptic or narrowly elliptic (vs. ovate or obovate, rarely elliptic or narrowly elliptic), coriaceous or chartaceous (vs. subcoriaceous or coriaceous) leaves that are scabrous above and below (vs. scabrous above and smooth or slightly scabrous below); leaf or petiolar sheaths that are 0.4–0.7 cm wide at the apex (vs. 0.6–1.8 cm wide), strigose or floccose (vs. glabrous to strigose) and with either 2 fimbriate stipular appendages or fimbriae distributed along the entire apical margin (vs. only 2 fimbriate stipular appendages); and staminate inflorescences composed of 2–3 spikes, spikes 1–5 cm long (vs. 3–5 spikes, spikes 2.8–8.3 cm long).

Árbol dioico de 2–10 m de altura, tallo leñoso con diámetro entre 2.5 y 10 cm, las partes jóvenes fragantes, las ramas cuadrangulares, pubescentes, con vestigios de la vaina peciolar en la madurez, entrenudos de 2–14 cm de separación. Hojas elípticas o estrechamente elípticas, dentadas o ligeramente crenadas, basalmente sin dientes, separación entre dientes 0.5–2.0 mm y altura 0.3–0.6 mm; láminas ásperas, 2–14 × 1.5–6.0 cm; ápice acuminado,

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Los autores agradecen a Alice Tangerini (US) por la elaboración de la ilustración, a Lauren Peters (MO) y George Yatskievych (TEX) por la ayuda a verificar la presencia de especímenes de la nueva especie en las colecciones de los herbarios MO y TEX, respectivamente, y a dos revisores anónimos que hicieran sugerencias para mejorar el manuscrito.

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FIGURA 1. *Hedyosmum guaramacalense* S.M. Niño & Dorr. **A**, planta con inflorescencias estaminadas; **B**, espiga estaminada; **C–E**, estaminadas con conectivos agudos; **F**, planta con inflorescencias pistiladas; **G**, vaina peciolar pubescente; **H**, inflorescencia pistilada; **I**, címula pistilada; **J**, flore pistilada con dos ventanas. A–E, *Licata & al. 684* (PORT); F–J, *Licata & al. 685* (US [00513874]). Dibujo de A. R. Tangerini.

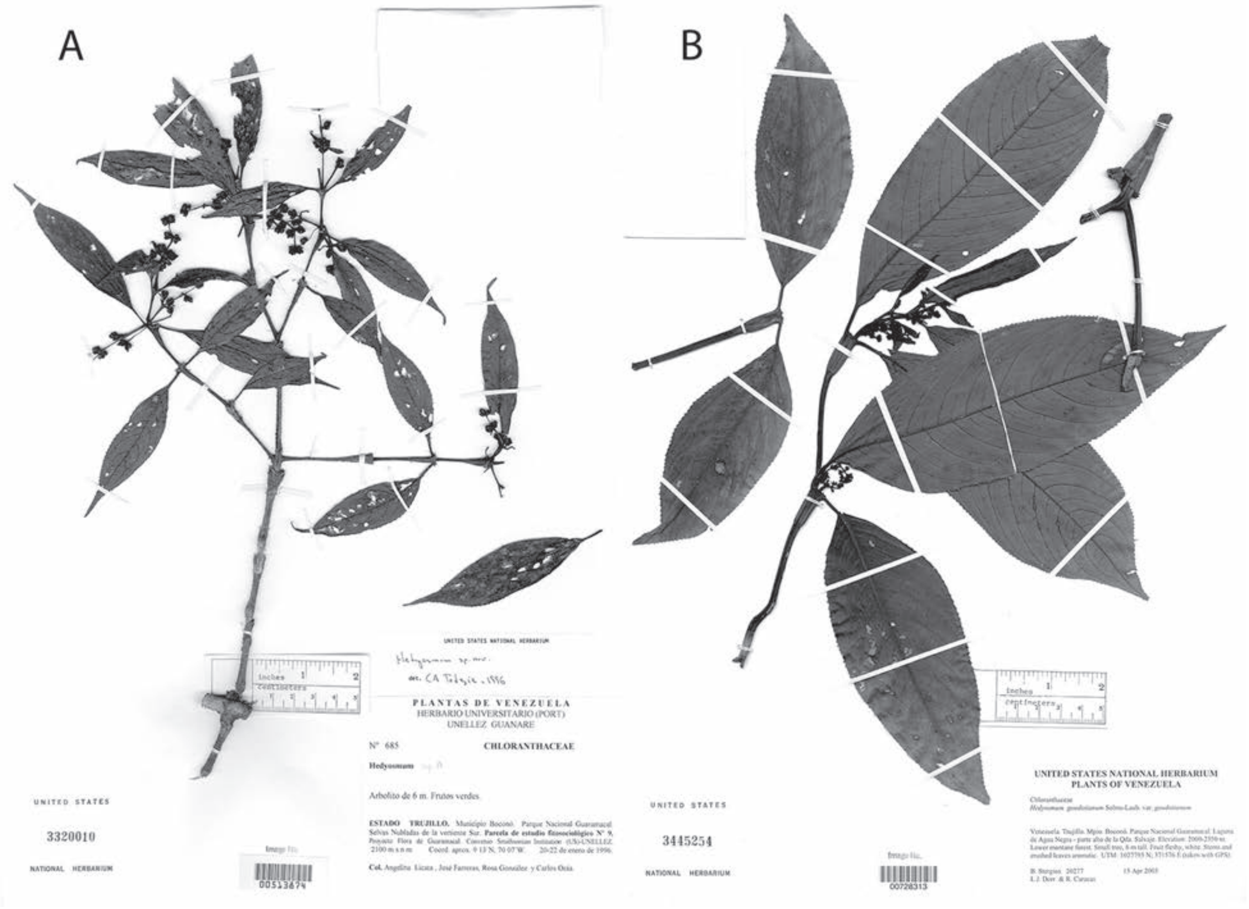

FIGURA 2. **A,** *Hedyosmum guaramacalense* S.M. Niño & Dorr; **B**, *H. goudotianum* Solms var. *goudotianum*. A, *Licata & al. 685* (US [00513874]); B, *Stergios & al. 20277* (US [00728313]).

TABLA 1. Comparación morfológica entre *Hedyosmum guaramacalense* y *H. goudotianum* var. *goudotianum*.

	***H. guaramacalense* S.M. Niño & Dorr**	***H. goudotianum* Solms var. *goudotianum***
Lámina de hojas secas	Elíptica o estrechamente elíptica, coriácea o cartácea, áspera por ambas caras, nervios laterales 5–8.	Ovada u obovada, a veces elíptica o estrechamente elíptica, subcoriácea o coriácea, áspera por el envés y suave o ligeramente áspera por el haz, nervios laterales 6–14.
Vaina	Estrigosa o flocosa, ápice inflado de 0.4–0.7 cm de ancho, con apéndices estipulares fimbriados divididos en dos mechones, o distribuidos por todo el margen.	Glabra o estrigosa, ápice inflado de 0.6–1.8 cm de ancho, casi siempre con dos apéndices estipulares fimbriados.
Inflorescencia estaminada	Posee 2–3 espigas que nacen en nudos terminales, cada espiga de 1–5 cm de largo.	Posee 3–5 espigas, con 1–2 pares de espigas opuestas en 1–2 nudos, cada espiga de 2.8–8.3 cm de largo.
Inflorescencia pistilada	2–5 cm de largo, címulas con 2–6 flores.	3.0–8.5 cm de largo, címulas con 3–8 flores.

agudo de 0.5–2.0 cm de largo, dentado; nervio central de la lámina prominente, pubescente; nervios laterales en pares de 5–8, ascendentes, glabros o con pubescencia dispersa, opuestos o ligeramente alternos, separados entre sí 0.5–1.5 cm; parte libre del peciolo acanalado, 0.4–1.5 cm de largo, casi siempre pubescente; vaina peciolar pubescente, cubierta por numerosas escamas, a veces glabra, áspera al tacto, de 1.0–2.5 cm de largo, ápice inflado de 0.4–0.7 cm de ancho, persistente, con apéndices estipulares laterales de 1.0–1.5 mm, fimbriados, divididos en dos o enteros. Inflorescencias estaminadas compuestas por 1–2 cimas de espigas terminales o axilares, cada una con raquis recto de 1.5–2.0 cm de largo, en cuyo ápice nacen 2–3 espigas, sésiles, 1–5 cm de largo, subtendidas por dos brácteas lanceoladas o elípticas, dentadas, similar a las hojas pero de menor tamaño de 1.0–1.5 × 0.4–0.6 cm, sésiles o con un corto peciolo de 1–3 mm; flores estaminadas compuestas de 80–120 anteras por espiga, triangulares, de 0.9–2.0 × 0.5–1.0 mm; aberturas laterales 2, ovoides; conectivo agudo, algunas veces truncado, extendido de 0.2–0.4 mm. Inflorescencias pistiladas axilares o terminales; racimos de 2–5 cm, subtendidos por brácteas similares a hojas, dentadas y pequeñas de 0.4–2.5 cm de largo; pedúnculo 0.5–2.1 cm de largo, liso o indumento esparcido en la base; címulas 2–8 por nudo fértil, erectas, algunas veces con ramificación secundaria en la base de la inflorescencia, sésiles o con pedicelos cortos de 0.5–2.0 mm de largo; flores 2–6 por címula, trígonas 3–4 × 1.5–2.5 mm, lóbulos 3, muy cortos; ventanas 2, laterales, circulares a ovoides, casi siempre en la parte media del ovario; estilo curvo, base lisa, 1.2–1.7 mm de largo; estigma papilado, caduco. Fruto blanco, globoso; semilla blanca o translucida, triangular, de 1.0–1.5 mm de largo.

Etimología: el epíteto hace referencia al Parque Nacional Guaramacal, lugar donde ubicaron las primeras poblaciones de la especie.

Distribución, hábitat, y aspectos fenológicos: hasta el presente solo conocida de colecciones del Parque Nacional Guaramacal, y evidentemente es endémica de Venezuela, donde se encuentra formando comunidades en bosque nublado de mediana altura (10–18 m). *Hedyosmum guaramacalense* es una especie característica de la Subasociación miconietosum suaveolentis de la Asociación Schefflero ferrugineae–Cybianthetum laurifolii, descritas por Cuello y Cleef (2009a). Es parte del bosque donde los biotipos comunes son *Critoniopsis paradoxa* (Sch. Bip.) V.M. Badillo, *Hieronyma scabrida* (Tul.) Müll. Arg., *Miconia suaveolens* Wurdack, *Clusia alata* Planch. & Triana, *Cyathea pauciflora* (Kuhn) Lellinger, *Weinmannia lechleriana* Engl., y *Meliosma venezuelensis* Steyerm. & A.H. Gentry (Cuello y Cleef, 2011).

También se establece con facilidad a orillas de carreteras y sitios abiertos muy húmedos. Es abundante y frecuente en bosque de la vertiente sur del parque entre 2100 y 2600 m.s.n.m. (Cuello y Cleef, 2009a), llegando a tener su mayor valor de importancia en comunidades a 2300 m.s.n.m., donde son frecuentes los deslizamientos de tierra debido a altas precipitaciones de lluvia (Cuello, 1997). Regularmente se observa en el sotobosque, establecida en el segundo estrato o formando parte de dosel. Las plantas presentan flores y frutos entre Noviembre y Abril, que corresponde a la temporada menos lluviosa de la región.

La nueva especie es morfológicamente intermedia entre *Hedyosmum goudotianum* var. *goudotianum* y *H. translucidum* Cuatrec., pues mantiene poblaciones en pisos altitudinales y condiciones climáticas similares. Sin embargo, la mayor cercanía parece ser con *H. goudotianum* var. *goudotianum* al compartir pubescencia e indumento escabroso en la vaina peciolar y hojas, junto con inflorescencias femeninas con pocas flores por címulas (2–8) y espigas de flores masculinas de 1–5 cm de largo. Difieren en el mayor tamaño de casi todas las estructuras de *H. goudotianum* var. *goudotianum*: hojas con lámina de 5–20 × 3.0–8.5 cm, vaina de 0.5–3.0 × 0.4–1.5 cm, e inflorescencias de 1.3–8.5 cm de largo. Mejor detalle de sus diferencias se puede apreciar en la Tabla 1.

Especímenes adicionales examinados: VENEZUELA. Trujillo: Municipio Boconó, Parque Nacional Guaramacal, vertiente sur, Parcela de estudio fitosociológico No. 6, 2400 m, 09°13'32"N, 070°10'01"W, 13–15 Diciembre 1995, *N.Cuello, C.Oraá, A.González y E.Cavallaro 1232* (estéril) (MO, PORT, US [00513877]); Parque Nacional Guaramacal, vertiente sur, Parcela de estudio fitosociológico No. 7, 1950 m, 09°12'28"N, 070°09'41"W, 19–22 Diciembre 1995, *N.Cuello, R.González, A.González y O.León 1296* (estéril) (MO, PORT, US [00513880]); Parque Nacional Guaramacal, vertiente sur, Parcela de estudio fitosociológico No. 7, 1950 m, 09°12'28"N, 070°09'41"W, 19–22 Diciembre 1995, *N.Cuello, R.González, A.González y O.León 1311* (♀) (MO, NY, PORT, TEX, US [00513878]); Parque Nacional Guaramacal, vertiente sur, Parcela de estudio fitosociológico No. 8, 2300 m, 09°12'45"N, 070°09'51"W, 3–5 Enero 1996, *N.Cuello, R.González, C.Oraá y A.González 1323* (♀) (F, MO, PORT, TEX, US [00513881]); Parque Nacional Guaramacal, vertiente sur, 2100 m, 21 Abril 1998, *N.Cuello, A.Licata y P.Marvez 1425* (♀) (PORT, US [00628149]); Parque Nacional Guaramacal, road from Boconó to Guaramacal, SE of Boconó, ca. 15 km from the post of the park guards, 09°13'N, 070°12'W, 2 November 1998, *L.J.Dorr, E.Briceño, G.Briceño and R.Caracas 8421* (♀) (PORT, TEX, US [00603131]); Parque Nacional Guaramacal, road from Boconó to Guaramacal, SE of Boconó, ca. 15 km from the post of the park guards, 09°13'N, 070°12'W, 3 November 1998, *L.J.Dorr, E.Briceño, G.Briceño and R.Caracas 8474* (♀) (K, MO, PORT, TEX, US [00603139]); Parque Nacional Guaramacal, vertiente sur, Parcela de estudio fitosociológico No. 9, 2100 m, ca. 09°13'N, 070°07'W, 20–22 Enero 1996, *A.Licata, J.Farreras, R.González y C.Oraá 665* (estéril) (MO, PORT, US [00513875]); Parque Nacional Guaramacal, vertiente sur, Parcela de estudio fitosociológico No. 9, 2100 m, 09°13'N, 070°07'W, 20–22 Enero 1996, *A.Licata, J.Farreras, R.Gonzalez y C.Oraá 684* (♂) (PORT); 12 km E of Boconó, 1 km N to 4 km NNE of Guaramacal, 1600–1900 m, 09°12'–09°13'N, 070°09'W, 15 March 1982, *R.Liesner, A.González, B.Stergios and G.Aymard 12958* (♀) (MO, PORT); Parque Nacional Guaramacal, Sector trocha Laguna Negra-quebrada del Salvaje, 1850–2100 m, 15 Junio 2002, *B.Stergios y R.Caracas 19669* (♀) (GH, PORT, US [00772513]); Parque Nacional Guaramacal, Laguna de Agua Negra—parte alta de la Qda. Salvaje, 2000–2350 m, UTM 1027793 N 371576 E, 15 Abril 2003, *B.Stergios, L.J.Dorr y R.Caracas 20279* (♀) (K, P, PORT, US [00728311]).

Clave para las Especies de *Hedyosmum* Encontradas en los Andes de Venezuela

1a. Tallo, hojas, y vainas peciolares glabras 2

1b. Tallo, hojas, y vainas peciolares, o sólo algunas de ellas, pubescentes o con vestiduras diminutas o densas 4

2a. Vainas peciolares verrugosas; apéndices estipulares faltantes; nódos fértiles con 1–3 címulas . . . . *H. cuatrecazanum*

2b. Vainas peciolares lisas o ligeramente ásperas; apéndices estipulares 2–4, caducos; nodos fértiles con 2–10 cimulas 3

3a. Hojas planas 6–16 × 3–6 cm, 11–16 venas laterales; inflorescencias pistiladas 3–12 cm de largo, 2–3 flores por címula . . . . *H. gentryi*

3b. Hojas generalmente revolutas, 3–6 × 1.5–2.5 cm, 7–10 venas laterales; inflorescencias pistiladas 1–2 cm de largo, 1(2) flor por címula . . . . *H. pseudoandromeda*

4a. Vainas peciolares ligeramente tomentosas (en ocasiones glabras), lisas al tacto; láminas de la hoja lisas 5

4b. Vainas peciolares tomentosas y casi siempre escabrosas al tacto; láminas de la hoja escabrosas debajo 7

5a. Nodos fértiles con 1–3 inflorescencias pistiladas, cada una con 1 címula . . . . *H. parvifolium*

5b. Nodos fértiles con 3–muchas inflorescencias pistiladas, cada una con 4–30 címulas 6

6a. Margen de la hoja crenulado; inflorescencias pistiladas compuestas de 4–12 címulas, cada címula 1- a 4-floreadas; inflorescencias estaminadas compuestas de 1–2 pares de espigas opuestas que terminan en una espiga simple, pedúnculos 4–10 mm de largo . . . . *H. crenatum*

6b. Margen de la hoja dentado o ligeramente crenulado; inflorescencias pistiladas compuestas de 5–30 címulas, cada címula 2- a 8-floreadas; inflorescencias estaminadas compuestas de 1–3 espigas por nodo, sésiles o poco pedunculadas (1–4 mm de largo) . . . . *H. racemosum*

7a. Tricomas de hojas abundantes en la nervadura central y nervios secundarios; inflorescencias de 1–5 cm de largo . . . . *H. guaramacalense*

7b. Tricomas de hojas dispersos en la nervadura central y venas secundarias; inflorescencias 1.3–12.5 cm de largo 8

8a. Láminas foliares hasta 20 × 8 cm; estípulas con 2 apéndices fimbriados; inflorescencias estaminadas compuestas de 1–2 pares de espigas opuestas; inflorescencias pistiladas compuestas de 4–16 címulas, cada címula 2- a 4-floreadas . . . . *H. goudotianum*

8b. Láminas foliares hasta 14.5 × 5.5 cm; estípulas con 2–4 apéndices fimbriados, caducas; inflorescencias estaminadas compuestas de 1–3 pares de espigas opuestas; inflorescencias pistiladas compuestas de 5–12 címulas, cada címula 4- a 7-floreadas . . . . *H. translucidum*

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NEOTROPICAL ORCHID MISCELLANEA 2

Paul Ormerod[1]

Abstract. Literature and herbarium studies of various orchid taxa that occur in the New World lead to the recognition of two new species and five new synonyms, and the transfer of two names. Thus two transfers are proposed, *Bifrenaria parthonii* and *Ida insolita*, and two new species are proposed, *Microchilus croatii* and *M. topoensis*.

Keywords: Neotropics, orchids, *Bifrenaria, Ida, Microchilus*

This paper is a continuation of previous research (Ormerod, 2016) that deals with various problems that the author encountered during studies of Neotropical orchids.

Bifrenaria Lindl., Gen. Sp. Orch. Pl.: 152. 1832.
Type species: *Maxillaria atropurpurea* Lindl.

A genus of 18–20 species mostly confined to Brazil, with a few outliers reaching north to Venezuela, and south to Argentina. The genus was effectively revised by Koehler and Amaral (2004) with a seemingly sound taxonomic approach, but curiously they omitted several synonyms and quoted incorrect types for a number of names.

Bifrenaria parthonii (Dumort.) Ormerod, *comb. nov.*
Basionym: *Maxillaria parthonii* Dumort., Hort. Belg. 2: 245. 1834.
TYPE: BRAZIL. Without locality, *cult. L.B.vanHoutte s.n.* (Holotype: lost).
Heterotypic synonyms: *Bifrenaria clavigera* Rchb.f., Hamb. Gartenz. 21: 296. 1865 *syn. nov.*
TYPE: BRAZIL. Without locality, *cult. Blunt for H.Low s.n.* (Syntype: W-R, not seen); 1864, *cult. J.Stone for J.Day s.n.* (Syntype: W-R 42636, image seen).

Stenocoryne clavigera (Rchb.f.) Kraenzl., Xenia Orch. 3: 142. 1896.

Adipe clavigera (Rchb.f.) M. Wolff, Orchidee (Hamb.) 41, 2: 36. 1990.

Stenocoryne wendlandiana Kraenzl., Xenia Orch. 3: 154. 1896.

TYPE: BRAZIL. Without locality, *cult. H.Wendland s.n.* (Holotype: lost). Lectotype (Koehler and Amaral 2004: 325): t. 289, in Xenia Orch. 3, 1896.

Bifrenaria wendlandiana (Kraenzl.) Cogn., in Martius, Fl. Bras. 3, 5: 489. 1902.

Adipe wendlandiana (Kraenzl.) M. Wolff, Orchidee (Hamb.) 41, 2: 37. 1990.

Distribution: Brazil.

After analysis of the protologue of *Maxillaria parthonii* I conclude it is the earlier name for *Bifrenaria clavigera*. Dumortier notes the compressed, unifoliate pseudobulbs, multiflorous inflorescence, rose-gray petals, lateral sepals forming a mentum, unlobed labellum with denticulate margins, inside with carmine points, and a medial citron yellow spot. A good image exemplifying these characters has been published by Chiron and Bolsanello (2014) as *B. clavigera*.

Ida A. Ryan & Oakley, Orch. Digest 67, 1: 9. 2003.
Type species: *Lycaste locusta* Rchb.f.

A genus of 40–45 large-flowered species occurring in the Caribbean and South America. It has until recently been known as *Sudamerlycaste* Archila until Pupulin and Karremans (2017) showed that *Ida* was the oldest name, and that the publication dates of the former were erroneous. In a recent treatment (Ormerod, 2018) of *Xylobium* Lindl., an excluded species (*X. insolitum*) was transferred to the younger name; this is here corrected.

Ida insolita (Szlach. & Kolan.) Ormerod, *comb. nov.*
Basionym: *Xylobium insolitum* Szlach. & Kolan., Phyton (Horn) 54, 1: 73. 2014.
TYPE: COLOMBIA. Norte de Santander: Municipio de Playa de Belen, Quebrada la Teneria, Area Natural Unica los Estoraques, 1600 m, 14 April 2002, *R.Galindo-Tarazone 805* (Holotype: COL; Isotype: UIS, images seen).
Homotypic synonym: *Sudamerlycaste insolita* (Szlach. & Kolan.) Ormerod, Harvard Pap. Bot. 23, 1: 74. 2018.

Distribution: Colombia.

Microchilus Presl, Reliq. Haenk. 1, 2: 94. 1827.
Lectotype species (Ormerod 2002: 214): *Microchilus minor* Presl

A genus of Goodyerinae with about 145–150 species confined to the New World, distributed from Mexico and the Caribbean to Argentina and Paraguay. It is particularly well represented in the Andes of Colombia, where about half the species occur. Apart from the two new species described here, it is necessary to propose some new synonymy.

Microchilus capitatus Ormerod, Harvard Pap. Bot. 9, 2: 400. 2005.
TYPE: PERU. Cuzco: Prov. Urubamba, ruins of Machu Pichu, 2100 m, 28 July 1966, *C.Vargas C. 17638* (Holotype:

I wish to thank herbarium and library staff at the Harvard University Herbaria (A, AMES, GH) and Kew (K) for their help and hospitality during my visits. DUKE, F, MO, NY, SEL, and US kindly loaned material for study.

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AMES; Isotype: CUZ [photograph seen], NY).

Heterotypic synonym: *Microchilus peruvianus* Szlach. & Kolan., Phyton (Horn) 56, 2: 257. 2016 *syn. nov.*

TYPE: PERU. Cuzco: Prov. La Convencion, Distrito Quellouno, road to Lacco, 1000–2100 m, 27 August 2007, *L.Valenzuela, A.Carazas, B.Rado & S.Flores 10223* (Holotype: MO).

Distribution: Peru.

Additional specimen examined: PERU. Cuzco: Prov. Urubamba, Machu Pichu, 500 m N of Sayacmarca and Ayobamba Rivers, 2405 m, 12 October 1982, *B.Peyton & S.TilneyPeyton 1481* (MO).

Examination of the holotype of *Microchilus peruvianus* reveals no characters that distinguish this entity from *M. capitatus*. Critical characters such as the densely congested rachis, smallish flowers (sepals 4.2–5.2 mm long), truncate-subbilobulate petals, apically clawed hypochile, obliquely spathulate-cuneate epichile lobules, and short column (2.0–2.4 mm long) are all found in the material at hand.

Microchilus croatii Ormerod, *sp. nov.*

TYPE: ECUADOR. Zamora-Chinchipe: along road between Zumba and Vilcabamba, 74.5 km N of Zumba, 44.3 km S of Yangana, 1233 m, 28 July 2004, *T.B.Croat 92514* (Holotype: SEL; Isotype: MO, not seen). Fig. 1.

Similar to *Microchilus viridissimus* Ormerod but the flowers with a lunate-anchoriform (vs. transversely oblong) labellum epichile, and a stouter (vs. slender) column.

Terrestrial *herb,* to 62.5 cm tall in flower. *Rhizome* not seen. *Stem* with lower part decumbent, upper part erect, terete, sublaxly 4- to 5-leaved, 15.2 × 0.4-0.6 cm; internodes 3.35–6.30 cm long. *Leaves* mostly damaged in the type, only intact one obliquely elliptic, subacuminate, 11.0 × 4.8 cm; petiole and sheath 3.0–4.8 cm long. *Inflorescence* pubescent, 47.3 cm long; peduncle 34.3 cm long; sheathing bracts lax, 7, 1.45–2.60 cm long; rachis subsecundly and subdensely many-flowered, ca. 13 cm long; floral bracts ovate-lanceolate, subacuminate, to 1.1 cm long. *Flowers* white, externally laxly pubescent. *Pedicel with ovary* fusiform, laxly pubescent, 5–6 mm long. *Dorsal sepal* oblong-lanceolate, obtuse, forming with the petals a galea, 4.0 × 1.6 mm. *Lateral sepals* obliquely oblong, obtuse, 4.7–5.0 × 1.3–1.4 mm. *Petals* obliquely ligulate-oblanceolate, apex shallowly bilobed-obtuse, lower apical margin minutely dentate to ciliate, 4.0–4.2 × 1.1–1.2 mm. *Labellum* spurred, trilobed, joined to the column for 1 mm; spur oblongoid-ellipsoid, obtuse, 1.8 mm long, 1.0–1.1 mm wide laterally; hypochile oblong, 2.8 × 1.6 mm; epichile lunate-anchoriform, shortly and broadly apiculate, papillose-pubescent, ca. 0.9 × 4.0 mm (2.8 mm unspread); lobules oblong, obtuse, subfalcate, ca. 1.4 × 0.4 mm. *Column* stout, 2.7 mm long.

Distribution: Ecuador.

Etymology: named after Thomas B. Croat (1938–), specialist in Aroids, and collector of the type.

This taxon appears similar to its Ecuadorian congener *Microchilus viridissimus* Ormerod, having flowers about the same size; however, it differs in having a lunate-anchoriform (vs. transversely oblong) labellum epichile with half as wide (0.4 vs. 0.9 mm) lobules, and a much stouter column.

Microchilus maasii Ormerod, Harvard Pap. Bot. 11, 2: 161. 2007.

TYPE: COSTA RICA. Cartago: Rio Atirro, La Esperanza, 800 m, 8 October 1974, *P.J.M.Maas 1171* (Holotype: F; Isotype: MO).

Heterotypic synonyms: *Microchilus campanensis* Kolan., Pol. Bot. J. 59, 2: 185. 2014 *nom. illeg., syn. nov.* (*non* Ormerod 2009).

TYPE: PANAMA. Prov. de Panama: Distrito de Capira, Cerro Campana, 700–1000 m, 12 January 1995, *C.Galdames 1877 & C.Guerrera* (Holotype: PMA, image seen).

Microchilus dressleri Kolan., Phytotaxa 208, 2: 182. 2015.

Distribution: Costa Rica; Panama.

Specimens from Panama tend to have flowers at the lower end of floral size (sepals ca. 6 mm long) but otherwise do not differ from Costa Rican plants. In this regard I find no characters that justify the separation of *Microchilus campanensis* Kolan., which agrees in all features with the numerous examples already studied (see Ormerod, 2007, for specimen citation).

Microchilus nigrescens (Schltr.) Ormerod, Lindleyana 17, 4: 219. 2002.

Basionym: *Physurus nigrescens* Schltr., Beih. Bot. Centralbl. 36: 380. 1918.

TYPE: COSTA RICA. Without locality, *F.C.Lehmann s.n.* (Holotype: B, destroyed; drawing AMES).

Homotypic synonym: *Erythrodes nigrescens* (Schltr.) Ames, Orch. 7: 74. 1922.

Heterotypic synonyms: *Erythrodes killipii* Ames, Proc. Biol. Soc. Wash. 34: 150. 1921.

TYPE: PANAMA. Chiriqui: Valley of the Rio Caldero, from El Boquete to the Cordillera, 1400–1600 m, 1 February 1918, *E.P.Killip 3561* (Holotype: AMES; Isotypes: GH; BH, NY, images seen).

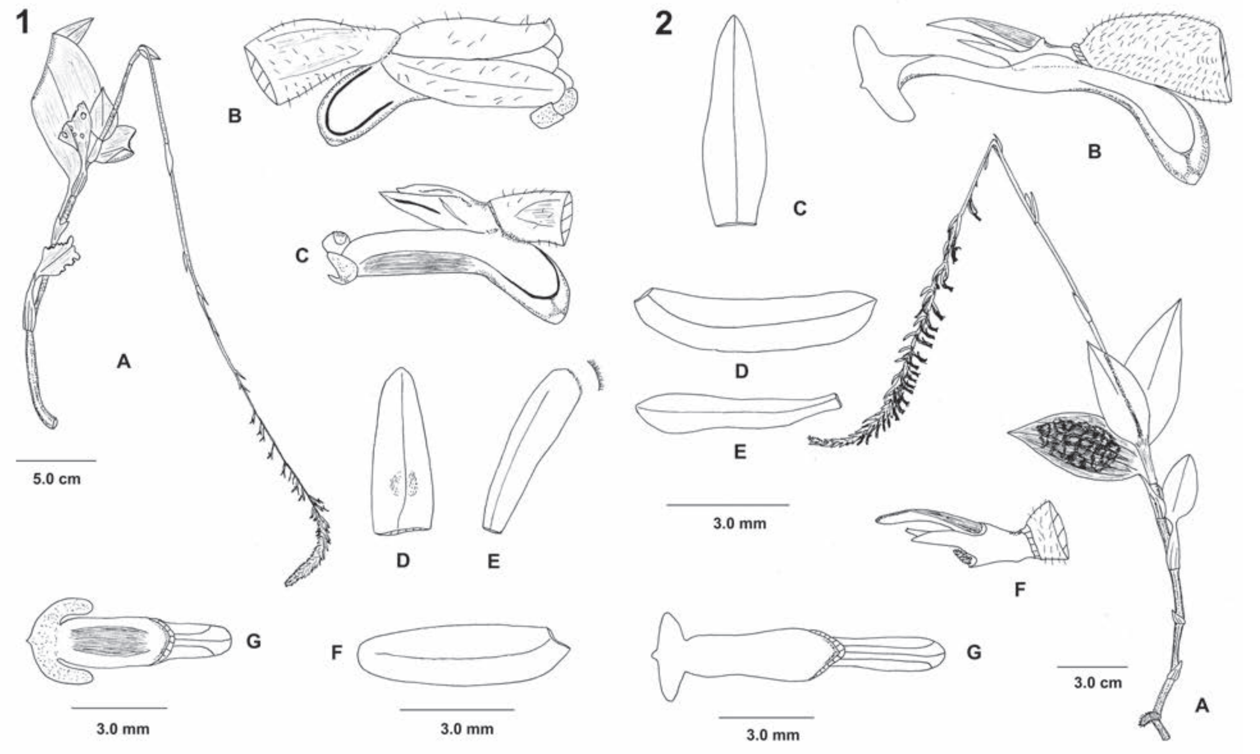
Microchilus killipii (Ames) Ormerod, Lindleyana 17, 4: 217. 2002.

Microchilus atwoodii Szlach. & Kolan., Phyton (Horn) 56, 2: 261. 2016 *syn. nov.*

TYPE: COSTA RICA. Puntarenas: Monteverde, in cloud forest owned by Campbell family, 1575 m, 2 March 1989, *J.T.Atwood 89-10* (Holotype: MO; Isotypes: F, GH, K, 2 sheets).

Distribution: Costa Rica; Panama.

Additional specimens examined: COSTA RICA. Cartago: Cerro de La Carpintera, 1500–1850 m, February 1924, *P.C.Standley 35677* (US); same data, *P.C.Standley 35614* (US); same data, *P.C.Standley 35581* (US); Carpintera Mountains, 1800 m, *leg. C.Horich s.n., Univ. Calif. Berkeley 59.319* (US); same data, *Univ. Calif. Berkeley 59.319-1* (MO); Eastward trail into mountains from road into Tapanti Reserve, ca. 1 km S of junction of Quebrada Salto and Rio Grande de Orosi, 1500–1800 m, 1 February 1986, *M.H.Grayum, P.Sleeper, J.Dickie,*



FIGURES 1–2. 1. *Microchilus croatii* Ormerod. **A,** plant; **B,** flower; **C,** flower minus tepals; **D,** dorsal sepal; **E,** petal; **F,** lateral sepal; **G,** labellum and spur. Drawn from holotype. 2. *Microchilus topoensis* Ormerod. **A,** plant; **B,** flower minus tepals; **C,** dorsal sepal; **D,** lateral sepal; **E,** petal; **F,** column; **G,** labellum and spur. Drawn from holotype.

A.R.Smith & T.Beliz 6282 (MO); Hacienda Queveri, Rio Mache de Paraiso, along road leading to Rio Blanco, 1630 m, 15 July 1984, *M.H.Grayum 3491* (MO); Estrella to Santa Maria road, 2135 m, 21 April 1928, *H.E.Stork 1508* (MO). Guanacaste: Canton de Abangares, 5 km N of Monteverde at the Rio Negro on road to Finca San Bosco, Atlantic slope, 1300 m, 2 February 1989, *W.Haber 9086 & W.Zuchowski* (MO). Puntarenas: near Monteverde, in Cordillera de Tilaran, 1500 m, 8 May 1971, *F.Almeda & J.Utley 679* (DUKE); ca. 2 km SE of Monteverde, 1500–1550 m, 18–21 March 1973, *W.C.Burger & J.L.Gentry Jr. 8543* (F, MO). Cascajal, [received at K July 1919], *C.H.Lankester 57* (K); Varablanca, April 1925, *C.H.Lankester 1482* (K); San Luis de Zarcero, 1310 m, 15 February 1938, *A.Smith H 335* (F). PANAMA. Prov. Chiriqui: above Boquete on trail to Bocas del Toro, along Rio Caldera, 1550 m, 8 February 1986, *G.McPherson & M.Morello 8348* (MO); upper Caldera River, near Camp I, Holcomb's Trail, above El Boquete, 1450–1650 m, 22–24 March 1911, *W.R.Maxon 5570* (US); Bajo Chono, 1830 m, 24 February 1938, *M.E.Davidson 317* (F, US).

For a long time, most herbarium material of relatively robust Central American *Microchilus* bore the name *Erythrodes killipii*. Nonetheless, a critical examination of the specimens showed that three species were actually confounded, the other two being *M. maasii* and *M. panamanicus*. Furthermore, study of a sketch of the type of *Physurus nigrescens* in AMES revealed this entity to be the older name for *Erythrodes killipii*. From the other two taxa (*M. maasii* and *M. panamanicus*) one can recognize *M. nigrescens* by its smaller (sepals to 6.5 mm long), more ovoid (vs. tubular, campanulate) flowers, shorter spur (3 mm long), and very stout column. There are no characters to separate *M. atwoodii*, though the rachis is somewhat laxer in the holotype than most in specimens, but the isotypes have subdensely flowered inflorescences just like the other material.

Microchilus panamanicus Ormerod, Harvard Pap. Bot. 9, 2: 414. 2005.

TYPE: PANAMA. Prov. de Panama: Cerro Trinidad, 800–1000 m, 20 October 1946, *P.H.Allen 3768* (Holotype: AMES; Isotype: F).

Microchilus folsomii Szlach. & Kolan., Phyton (Horn) 56, 2: 262. 2016 *syn. nov.*

TYPE: PANAMA. Prov. Darien: Cerro Pirre, ridgetop and slope from Rancho Frio to Rancho Plastico, 800–1200 m, 10–20 July 1977, *J.P.Folsom 4199* (Holotype: MO 2622087, MO 3493352).

Distribution: Panama.

Additional specimens examined: PANAMA. Prov. Chiriqui: E of the Fortuna Dam main campsite, 1200–1600 m, 12 September 1977, *J.P.Folsom & R.Dressler 5287* (MO); Campamento de Fortuna, site of the dam of Trocha 3 de November, between Santa Maria and Pinola, 1000–1200 m, 26 September 1976, *M.D.Correa, R.Dressler, N.Salazar, J.Mendieta, C.Garibaldi, F.Farnum & T.Beliz 2933* (MO). Prov. de Panama: high ridges of the Serrania de Maje, S of Ipeti Village, ca. 5 hours walk from village, 650–800 m, 31 March 1982, *M.Huft, S.Knapp, R.Foster & J.Mallett 1676* (MO). Prov. Darien: Rancho Frio (500 m) to summit of Cerro Pirre (1140 m), 30 March 1985, *W.G.D'Arcy & G.McPherson 16189* (MO); summit of Cerro Pirre, 1000–1400 m, 29 December 1972, *A.Gentry & A.Clewell 7083* (MO); Cerro Pirre, valley between Cerro Pirre and next most southerly peak, 10–20 July 1977, *J.P.Folsom 4453* (MO, 2 sheets); Cerro Pirre, 11 April 1967, *N.Bristan 609* (MO); N slope of Cerro Pirre, 700–950 m, 7 April 1975, *S.Mori & J.Kallunki 5495* (MO); NE slope of Cerro Sapo summit, approach from Garachine, 975 m, 8 May 1979, *B.Hammel 7241* (MO); Comarca de San Blas, Cerro Brewster, 800–850 m, 20 November 1985, *G.deNevers, A.Henderson, H.Herrera, G.McPherson & L.Brako 6296* (MO).

Examination of the type material of *Microchilus folsomii* reveals no characters distinguishing this entity from *M. panamanicus*. Re-examination of the original flowers used in the description of *M. panamanicus* shows that the fleshy labellum hypochile has split in the example used for the illustration in the protologue. Thus the hypochile is shown to be too broad in the lower half. The labellum hypochile varies from oblong-lanceolate to oblong-rectangular to oblong-oblanceolate. The latter shape is most apparent when one cannot flatten down the rigid sides of the hypochile, which is fleshiest in the lower half.

Microchilus panamanicus is a member of the *M. major* Presl complex, recognizable by the robust plants, paleaceous floral bracts, and large labellar spur (ca. 4–5 mm long).

Microchilus topoensis Ormerod, *sp. nov.*
TYPE: ECUADOR. Tungurahua: 2 km E of Rio Topo, 31 km E of Banos on road to Puyo, 1250–1450 m, 4 June 1985, *B.A.Stein 2983* (Holotype: MO). Fig. 2.

Usage synonym: *Erythrodes anchorifera* auct. non (Schltr.) Garay: Dodson, Icon. Pl. Trop. s. 2: t. 494. 1989; Dodson, Nat. Ecuad. Orch. 2: 305, fig. 622. 2001.

Similar to *Microchilus anchorifer* (Schltr.) Ormerod but the flowers with narrower (1.00 vs. 1.50–2.15 mm) petals, longer (3.2 vs. 1.9–2.0 mm) spur, and a longer (2.9 vs. 2.0–2.2 mm) column.

Terrestrial *herb,* to 43 cm tall in flower. *Rhizome* not seen. *Stem* erect, terete, 4-leaved in upper half, 10.5 × 0.25–0.30 cm. *Leaves* obliquely ovate-lanceolate to ovate-elliptic, acute to subacuminate, transversely mottled dark green, 2.90–7.00 × 1.45–2.65 cm; petiole and sheath 1.7–2.1 cm long. *Inflorescence* pubescent, to 33.1 cm long; peduncles 19.1 cm long; sheathing bracts 7, lax, 1.1–1.9 cm long; rachis subdensely and subsecundly many-flowered, 14 cm long; floral bracts ovate-lanceolate, acute, to 9.0 × 2.5 mm. *Flowers* white, green basally, externally pubescent. *Pedicel with ovary* clavate, pubescent, 7 mm long. *Dorsal sepal* oblong-lanceolate, acute, 4.9 × 1.5–1.6 mm. *Lateral sepals* obliquely oblong-ligulate, subacute, 5.9–6.0 × 1.3–1.5 mm. *Petals* obliquely ligulate-oblanceolate, obtuse, 4.9 × 1.0 mm. *Labellum* spurred, joined to column for 1.0–1.2 mm; spur obliquely clavate, obtuse, 3.2 mm long; hypochile narrowly cuneate-oblong, ca. 3.8 mm long, base 1.6 mm wide, subapical area 1.3 mm wide; epichile transversely oblong-rhombic, 0.9–1.0 × 2.9 mm, lobules ovate, obtuse, 0.7–0.8 mm wide. *Column* 2.9 mm long to tips of brachia, 3.5–3.6 mm long to tip of anther cap.

Distribution: Ecuador.

Habitat and ecology: slightly disturbed wet montane forest, 1250–1450 m.

Etymology: named after the Rio Topo, which is near the type locality.

This species is superficially similar to *Microchilus anchorifer* (Schltr.) Ormerod in having leaves with dark green markings, but the petals are narrower, the spur longer, and the column longer.

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NOTES ON THE IDENTITIES OF THREE MALESIAN *DENDROBIUM* (ORCHIDACEAE: DENDROBIINAE)

PAUL ORMEROD[1, 2] AND HUBERT KURZWEIL[3]

Abstract. Three Malesian species of *Dendrobium* are discussed regarding their typification and identity. Thus *D. curvum* is found to be based on a mixture and after lectotypification is proposed as the earlier name for *D. rappardii*; the previously obscure *D. dactyliferum* is found to be an earlier name for *D. pandaneti*; and *D. triflorum* is found to be a commonly misapplied name, which after typification is proposed as a synonym of *D. geminatum*.

Keywords: Malesia, *Dendrobium*, synonymy, typification

The genus *Dendrobium* Swartz is now recognized as the sole member of Subtribe Dendrobiinae. It is believed to have about 1600–1800 species, distributed from Sri Lanka to Tahiti. The plants are usually to be found as epiphytes, but a few species are exclusively terrestrial (e.g., *D. metrium* Kraenzl.). There is great diversity in the habit of the plants, ranging from those with tiny pea-shaped pseudobulbs, 5-m-long canes, to pendulous chandeliers of terete leaves.

During research on Indonesian *Dendrobium*, some problems were encountered while trying to locate type material of three species. The proposed resolutions are dealt with below.

Dendrobium curvum Ridl., J. Fed. Mal. St. Mus. 8, 4: 91. 1917.
TYPE: INDONESIA. Sumatra, W side of Barisan Range, Barong Bharu, Tapan, 1220 m, 10 June 1914, *H.C.Robinson & C.B.Kloss 179* (Lectotype here designated: BM 000038209, image seen).
Homotypic synonym: *Eurycaulis curvus* (Ridl.) M.A. Clem., Telopea 10, 1: 286. 2003.
Heterotypic synonyms: *Dendrobium rappardii* J.J. Sm., Blumea 5: 308. 1943 *syn. nov.*
TYPE: INDONESIA. Sumatra, Bengkulu, Air Sablat Lebong, 650 m, 8 September 1938, *F.W.Rappard 172* (Holotype: L 0059462, image seen).

Eurycaulis rappardii (J.J. Sm.) M.A. Clem., Telopea 10, 1: 287. 2003.

Distribution: Indonesia (Sumatra).

Ridley (1917) cited two collections when establishing *Dendrobium curvum,* one from Sumatra and another found by John Hewitt in Quop, Sarawak, Malaysia. Neither collection could be located in BM or Kew, where the collections that are the basis for Ridley's 1917 paper are generally stored. However, Ridley occasionally did not update annotations on specimens he studied when he had a late change of mind about the status of a plant he studied (e.g., *Dendrobium korinchense* Ridl. found under the manuscript name "*Eria striatella*," and *Eria sordida* Ridl. found under the manuscript name "*Eria ovatibracteata*"). A check of all Sumatran *Dendrobium* at BM finally revealed one of the sought-after collections, which had been named as *D. crabro* Ridl. by Ridley and later determined correctly by Jeff Wood of Kew as *D. rappardii*. This specimen completely matches the protologue of *D. curvum* in leaf size, 5-cm-long inflorescence peduncle, laxly flowered 5-cm-long rachis, and large flowers with a broad curved mentum. Thus, we propose the Sumatran specimen (*Robinson & Kloss 179*) as lectotype, with the result that the later *D. rappardii* must be treated as a synonym of *D. curvum*.

The other collection (*J.Hewitt s.n.*) mentioned by Ridley from Sarawak we found at K (again not annotated with the name *D. curvum* but with a manuscript name "*D. uncinulatum*"), where it had been found by Jeff Wood to be an isotype of *D. multiflorum* Ridl. 1908 *nom. illeg.* (non Par. & Rchb.f. 1874), a taxon since renamed *D. sarawakense* Ames. This entity, like *D. crabro* mentioned above, is endemic to Borneo (Wood, 2014). All three taxa have in common a prominent curved mentum and belong to section *Pedilonum* Blume.

Dendrobium dactyliferum Rchb.f., Gard. Chron. n.s. 21: 638. 1884.
TYPE: WITHOUT KNOWN ORIGIN. *I.F.Foerstermann s.n.* (Holotype: W-R 21025, image seen).
Heterotypic synonyms: *Dendrobium pandaneti* Ridl., J. Linn. Soc., Bot. 32: 257. 1896 *syn. nov.*
TYPE: SINGAPORE. Bukit Mandai, 1893, *H.N.Ridley 5029* (Lectotype [Seidenf. 1985: 173 as type]: BM, image seen; Isolectotype: SING); MALAYSIA. Johor: Pulau Kukub, 25 January 1890, *W.Nanson s.n.* (Syntype: SING); Johor Strait, Tanjong Kopang, 1894, *H.N.Ridley s.n.* (Syntype: SING).

Distichorchis pandaneti (Ridl.) M.A. Clem., Telopea 10, 1: 282. 2003.

Distribution: Thailand, Malaysia, Singapore, Indonesia (Lingga Archipelago, Sumatra, Java, Kalimantan).

This species is well known and aptly named *Dendrobium pandaneti,* since it has a long, creeping rhizome adapted to

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growing on *Pandanus* and palms, usually in lowland forests. However, while checking the description (and subsequently images) of the obscure *D. dactyliferum*, it became apparent that this entity is the older name for *D. pandaneti,* thus leading to the proposed synonymy above. The species is a member of section *Distichophyllae* J.D. Hook., a group well represented in Sumatra and Borneo.

Dendrobium geminatum (Blume) Lindl., Gen. Sp. Orch. Pl.: 77. 1830.

TYPE: INDONESIA. Java: Mt. Gede and Mt. Salak, *C.L.Blume 2028* (Lectotype here designated: L 0059933, image seen; possible Isolectotype: W-R 34323, image seen).

Basionym: *Desmotrichum geminatum* Blume, Bijdr.: 332. 1825.

Homotypic synonyms: *Callista geminata* (Blume) Kuntze, Rev. Gen. Pl. 2: 654. 1891.

Sarcopodium geminatum (Blume) Rolfe, Orch. Review 18: 238. 1910.

Katherinea geminata (Blume) A.D. Hawkes, Lloydia 19: 96. 1956.

Epigeneium geminatum (Blume) Summerh., Kew Bull. 12, 2: 262. 1957.

Heterotypic synonyms: *Desmotrichum triflorum* Blume, Bijdr.: 331. 1825 *syn. nov.*

TYPE: INDONESIA. Java: Mt. Salak, *C.L.Blume 1897* (Lectotype here designated: L 0059934, image seen; possible Isolectotype: P 00368880, image seen).

Dendrobium triflorum (Blume) Lindl., Gen. Sp. Orch. Pl.: 77. 1830.

Callista triflora (Blume) Kuntze, Rev. Gen. Pl. 2: 655. 1891.

Sarcopodium triflorum (Blume) Rolfe, Orch. Review 18: 239. 1910.

Epigeneium triflorum (Blume) Summerh., Kew Bull. 12, 2: 262. 1957.

Distribution: Malaysia; Indonesia (Sumatra, Java).

Dendrobium geminatum is distinctive among the Javanese species of section *Sarcopodium* Benth. in flowering on immature growths and bearing geminate pseudoterminal inflorescences. Comber (1990) recognized three species of *Epigeneium* Gagn. (= *Dendrobium* section *Sarcopodium*) in Java, namely, *E. geminatum*, *E. triflorum* (with *Desmotrichum elongatum* Blume reduced to a variety), and *E. cymbidioides* (Blume) Summerh. However, this treatment does not stand scrutiny because there may be up to 10 species in Java but only 4 available names at specific level. Another complicating factor is that type material of *Desmotrichum elongatum* has not been located, and application of the name is currently uncertain. Furthermore, the names *D. cymbidioides* (Blume) Lindl. and *D. triflorum* are evidently misapplied in the herbarium and literature.

In an attempt to resolve the problems with the Javanese species of section *Sarcopodium,* an effort was made to locate the types of the relevant names. At first there seemed to be no type material of *Desmotrichum triflorum* until it was noticed that one of the supposed syntypes (*Blume 1897*) of *Desmotrichum geminatum* bore original labels of the former annotated by Blume. The enigmatic, brief diagnosis of *D. triflorum* is congruent with this material, mentioning that the pseudobulbs are ovate, compressed, but that the older ones are tetragonous (i.e., implying the plant flowers from the younger bulbs), and the leaves oval-lanceolate. The leaves of all other section *Sarcopodium* species described by Blume are ligulate to ligulate-oblong, but only exposed plants of *Dendrobium geminatum* have short, ovate-lanceolate leaves. We speculate that Blume later realized that *Desmotrichum geminatum* and *D. triflorum* were conspecific, and thus merged the material of the two, fortunately keeping the original labels.

In treating *Dendrobium geminatum* and *D. triflorum* as conspecific, we choose the name *D. geminatum* since its use is stable and uncontroversial. The material misnamed *D. triflorum* requires revision, as do all Javanese specimens of section *Sarcopodium*.

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NOTES ON SOME MALESIAN ORCHIDACEAE

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Abstract. Herbarium and literature studies of various orchids from the Malesian floristic zone reveal some new species, synonymy, and the need for a few nomenclatural proposals. Thus, the synonymy of *Cestichis halconensis* is elaborated; *Cymboglossum* is found to be the older name for *Ascidieria,* requiring 8 transfers; *Dendrobium appendiculoides* is reduced to *D. zamboangense*; *Dendrobium philippinense* is reduced to *D. gerlandianum*; *Epidendrum subulatum* is reduced to *Thrixspermum filiforme*; *Eria* section *Polyura* is transferred to *Pinalia*; *Eria villosissima* is transferred to *Mycaranthes*; and *Myrmechis philippinensis* is renamed *Odontochilus marivelensis*. Six new species are proposed, namely, *Dendrobium rubroflavum, Pinalia edanoana, P. kitangladensis, P. pentalopha, P. sanguinea,* and *P. tonglonensis*.

Keywords: *Cymboglossum, Dendrobium, Pinalia,* Malesia, synonymy, new species

This paper is a collaborative venture on Malesian orchids, with a bias toward Philippine taxa (the specialty area of the second and third authors). The basic Malesian area extends from the Malaysian peninsula to the Solomon Islands, north to the Philippines. Our studies frequently overlap, and we thought it best to deal with a number of taxonomic and nomenclatural issues in one place. Since Malesia mostly consists of mountainous tropical islands, many once clad in various types of rainforest, it is particularly rich in orchid species. It is fairly evident that there is a high endemism rate (e.g., about 87% in New Guinea) on the larger islands, but this doesn't preclude the fact that there are taxa with broader distributions than previously realized. Indeed ,as with most tropical floras, a true picture of their composition is yet to emerge due to their diversity and lack of systematic, thorough collecting.

Cestichis Pfitz., Entwurf Anordn. Orch.: 56, 101. 1887.
Type species: *Epidendrum cespitosum* Lam.

A genus of primarily epiphytic plants of subtribe Malaxideae, distributed from Africa and Madagascar, through India and Southeast Asia, Malesia, to Tahiti. Formerly all the species were included in *Liparis* L.C. Rich. In the broad sense it would contain about 150 species, but molecular studies by Tang et al. (2015) indicate that further division may be necessary. Fortunately, the species discussed below belongs to the core group of species, and it is one of few that were first proposed in the genus.

Cestichis halconensis Ames, Philipp. J. Sci. 2, C: 321. 1907.
TYPE: PHILIPPINES. Mindoro: Mt. Halcon, 365–670 m, 8 November 1906, *E.D.Merrill 5799* (Holotype: AMES; Isotype: K, images seen).
Homotypic synonym: *Liparis halconensis* (Ames) Ames, Orch. 5: 80. 1915.
Heterotypic synonyms: *Liparis viridicallus* Holtt., Gard. Bull. Singap. 14: 4. 1953, *syn. nov.*
TYPE: MALAYSIA. Pahang: Fraser's Hill, 1220 m, January 1953, *R.E.Holttum 39465* (Holotype: K, image seen).
Stichorkis viridicallus (Holtt.) Marg., Szlach. & Kulak, Acta Soc. Bot. Polon. 77, 1: 39. 2008.
Liparis terrestris J.B. Comber, Orch. Sumatra: 156. 2001.
TYPE: INDONESIA. Java: Puncak, 1500 m, 29 August 1986, *J.B.Comber 1687* (Holotype: K, image seen).
Usage synonyms: *Liparis forbesii* auct. non Ridl.: J.J. Sm., Orch. Java: 268. 1905.
Liparis bootanensis auct. non Griff.: J.B. Comber, Orchids Java: 135. 1990.

Distribution: Indonesia (Sumatra, Java); Malaysia; Philippines.

Additional specimens examined: INDONESIA. Sumatra: Asahan, headwaters of Aek Liang (region between Dolok Si Manoek-manoek and Tor Matoetoeng), 1300 m, 15 October to 11 November 1936, *R.Si Boeea 10589* (AMES); Asahan, Adian Rindang, vicinity of Hoeta Tomoean Dolok, 17 November to 10 December 1935, *R.Si Boeea 8538* (AMES); Toba, vicinity of Toloen na Oeli (E of Dolok Si Manoek-manoek, near headwaters of Aek Mandosi), 1–12 December 1936, *R.Si Boeea 11201* (A); Toba, vicinity of Aek Mandosi (vicinity of Taloen na Oeli, near Toba to Asahan boundary), 29 September to 5 December 1936, *R.Si Boeea 11025* (A). MALAYSIA. Sabah: Mt. Kinabalu, Penibukan, 1525 m, 11 November 1933, *J.Clemens & M.S.Clemens 51317* (BM); Mt. Kinabalu, Penibukan, ridge above Pina Taki River, 1220 m, 16 January 1933, *J.Clemens & M.S.Clemens 31044* (BM); Mt. Kinabalu, Ulu Dahobang, 1095 m, 8 March 1933, *C.E.Carr SFN 26466* (AMES). PHILIPPINES. Luzon: Rizal Prov., without precise locality, September 1909, *A.Loher 14710* (AMES).

Ames (1908) published an illustration of *Cestichis halconensis* that is rather misleading as it appears to show that the inflorescence peduncle is bracteate. The figure is

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based on the righthand specimen on the type sheet in AMES. That specimen consists of a sterile plant with a broken-off inflorescence mounted between the leaves. *Cestichis halconensis* is one of the few terrestrial species of *Cestichis*; it is further characterized by its bifoliate pseudobulbs being clothed by about four 3- to 5-cm-long distichous sheaths, and a shortly clawed lip with a broad, emarginate callus. The shape of the lip blade is rather variable, varying from broadly elliptic to almost transversely elliptic-suborbicular.

Cymboglossum (Schltr.) Rauschert, Rep. Sp. Nov. Regni Veg. 94: 446. 1983

Basionym: *Eria* Lindl. section *Cymboglossum* Schltr., Bot. Jahrb. Syst. 45, Beibl. 104: 40. 1911.

Type species: *Eria cymbiformis* J.J. Sm.

Heterotypic synonym: *Ascidieria* Seidenf., Nord. J. Bot. 4, 1: 44. 1984.

Type species: *Eria longifolia* J.D. Hook.

Rauschert (1983) pointed out that *Cymboglossum* Brieger was invalid due to the citation of an incorrect and incomplete basionym. Rauschert therefore corrected Brieger's mistake and validated the generic name *Cymboglossum*. Seidenfaden (1984) was aware of Rauschert's paper but maintained *Ascidieria* as a separate genus on account of its flowers having a very short, seemingly absent column foot, and deeply saccate lip (vs. a distinct column foot, and nonsaccate lip). However, molecular analyses of the Tribe Podochileae published by Ng et al. (2018) showed that it is impractical to keep the two genera separate and that they should be merged. These authors overlooked the priority of *Cymboglossum*, so we make the requisite combinations here. We are also aware that a number of varieties have been proposed for some of the taxa treated here, but we prefer not to transfer them until their status can be better understood.

Cymboglossum caricifolium (J.J. Wood) Ormerod & Cootes, *comb. nov.*

Basionym: *Eria caricifolia* J.J. Wood, Lindleyana 5, 2: 93. 1995.

TYPE: MALAYSIA. Sarawak: Gunung Temabok, Upper Baram Valley, 1200 m, 5 November 1920, *J.C.Moulton 6673* (Holotype: K; Isotype: SING, images seen).

Homotypic synonym: *Ascidieria caricifolia* (J.J. Wood) J.J. Wood, Males. Orch. J. 5: 87. 2010.

Distribution: Malaysia (Sarawak, Sabah).

Cymboglossum cymbidiifolium (Ridl.) Ormerod & Cootes, *comb. nov.*

Basionym: *Eria cymbidiifolia* Ridl., J. Bot. (Lond.) 38: 212. 1898.

TYPE: INDONESIA. Kalimantan: Pontianak, *cult. Singapore Bot. Gard. s.n.* (Holotype: SING, image seen).

Homotypic synonym: *Ascidieria cymbidiifolia* (Ridl.) W. Suarez & Cootes, Orchideen J. 16, 2: 71. 2009.

Distribution: Malaysia (Sarawak, Sabah); Indonesia (Sumatra, Kalimantan); Philippines.

Cymboglossum grande (Ridl.) Ormerod & Cootes, *comb. nov.*

Basionym: *Eria grandis* Ridl., Trans. Linn. Soc. s.2, Bot. 4: 237. 1894.

TYPE: MALAYSIA. Sabah: Mt. Kinabalu, *G.D.Haviland 1157* (Holotype: SING; Isotypes: K, images seen; SAR, not seen).

Homotypic synonym: *Ascidieria grandis* (Ridl.) J.J. Wood, Orch. Mt. Kinabalu 2: 51. 2011.

Distribution: Malaysia (Sabah).

Cymboglossum maculiflorum (J.J. Wood) Ormerod & Cootes, *comb. nov.*

Basionym: *Ascidieria maculiflora* J.J. Wood, Males. Orch. J. 1: 105. 2008.

TYPE: MALAYSIA. Sabah: Sipitang District, Ulu Padas, *c.* 8 km NW of Long Pa Sia, 1400 m, 24 October 1985, *J.J.Wood 644* (Holotype: K, spirit and pressed, image seen of latter).

Distribution: Malaysia (Sarawak, Sabah).

Cymboglossum maculosum (Cabactulan, Cootes, M. Leon & R.B. Pimentel) Ormerod & Cootes, *comb. nov.*

Basionym: *Ascidieria maculosa* Cabactulan, Cootes, M. Leon & R.B. Pimentel, Orchideen J. (Internet) 6, 2: 4. 2018.

TYPE: PHILIPPINES. Mindanao: Bukidnon Prov., 1200 m, 3 March 2018, *M.D.Leon MDL1803002* (Holotype: CAHUP).

Distribution: Philippines.

Cymboglossum palawanense (Ames) Ormerod & Cootes, *comb. nov.*

Basionym: *Eria palawanensis* Ames, Philipp. Leafl. Bot. 5: 1578. 1912.

TYPE: PHILIPPINES. Palawan: Puerto Princesa (Mt. Pulgar), May 1911, *A.D.E.Elmer 13209* (Holotype: AMES, image seen).

Homotypic synonym: *Ascidieria palawanensis* (Ames) W. Suarez & Cootes, Orchideen J. 16, 2: 71. 2009.

Distribution: Philippines.

Cymboglossum pseudocymbiforme (J.J. Wood) Ormerod & Cootes, *comb. nov.*

Basionym: *Eria pseudocymbiformis* J.J. Wood, Kew Bull. 39, 1: 84. 1984.

TYPE: MALAYSIA. Sarawak: Gunung Mulu National Park, Gunung Api, below Pinnacle Camp, 800–1000 m, 24 February 1978, *I.Nielsen 486* (Holotype: AAU, image seen; Isotype: K, spirit, not seen).

Homotypic synonym: *Ascidieria pseudocymbiformis* (J.J. Wood) J.J. Wood, Orch. Mt. Kinabalu 2: 53. 2011.

Distribution: Malaysia (Sarawak, Sabah); Brunei.

Cymboglossum zamboangense (Ames) Ormerod & Cootes, *comb. nov.*

Basionym: *Eria zamboangensis* Ames, Orch. 5: 160. 1915.

TYPE: PHILIPPINES. Mindanao: Zamboanga District, Sax River Mountain, 1100 m, November to December 1911, *E.D.Merrill 8143* (Holotype: AMES, image seen).

Homotypic synonym: *Ascidieria zamboangensis* (Ames) W. Suarez & Cootes, Orchideen J. 16, 2: 71. 2009.

Distribution: Philippines.

Dendrobium Swartz, Nova Acta Regiae Soc. Sci. Upsal. ser. 2, 6: 82. 1799 *nom. cons.*

Type species: *Dendrobium moniliforme* (L.) Swartz *typ. cons.*

A genus of 1600–1800 species distributed from Sri Lanka and India to Tahiti. We discuss here three species from the Philippines and one from the Mariana Islands. *Dendrobium gerlandianum, D. oblongimentum,* and *D. rubroflavum* belong to section *Crumenata* Pfitz., a species-rich group with tender, ephemeral flowers. They have a characteristic habit whereby the lower 2–3 internodes of the stem are variously swollen, but the rest of the stem is slender.

Dendrobium gerlandianum Kraenzl., Rep. Sp. Nov. Regni Veg. 6: 317. 1909.

TYPE: PHILIPPINES. Luzon: Manila, *leg. A. Loher,* fl. in cult. January 1909, *hort. Bot. Gard. Erlangen s.n.* (Holotype: B, destroyed; drawing of type AMES). Epitype (here designated): Philippines, Luzon, Manila, *leg. A. Loher,* fl. in cult. 1910, *hort. Bot. Gard. Erlangen s.n.* (Isoepitype: M, image seen). Fig. 1.

Homotypic synonym: *Ceraia gerlandiana* (Kraenzl.) M.A. Clem., Telopea 10, 1: 291. 2003.

Heterotypic synonyms: *Dendrobium philippinense* Ames, Philipp. J. Sci., C, Bot. 8: 424. 1914.

TYPE: PHILIPPINES. Leyte: Dagami, 20 November 1912, *C.A.Wenzel 6* (Holotype: AMES; Isotypes: GH; K, image seen).

Ceraia philippinensis (Ames) M.A. Clem., Telopea 10, 1: 293. 2003.

Distribution: Philippines.

Additional specimens examined: PHILIPPINES. Luzon: sine loc., fl. in cult. Manila, 9 July 1905, *A.Loher 6022* (AMES); sine loc., 180 m, June 1908, *W.S.Lyon O" (=67)* (AMES); central Luzon, May 1947, *R.S.Davis 5* (AMES). Laguna Prov., sine loc., 24 June 1912, *J.Reillo 37* (AMES); sine loc., July and December 1909, *L.E.Griffin BS 5641* (AMES); Mayjayjay, 300 m, fl. 15 September and 12 January [no year], *cult. I. McCrory in E.H.Taylor 365* (AMES); Mt. Banajao, *leg. Mrs. Hombstet, cult. Bureau Sci. Orch. House,* 11 November 1929, *E. Quisumbing 5448 (=BS 78833)* (AMES); Lignaum, 28 September 1946, *R.S.Davis 3 (=PNH 5407)* (AMES). Rizal Prov., sine loc., 60–305 m, August 1948, *R.S.Davis 9-7-48* (AMES). Tayabas Prov., Umiray, 2 June 1917, *M.Ramos & G.Edano BS 29031* (AMES); Guinayangan, March/April 1913, *L.Escritor BS 20684* (AMES). Polillo Island: Anibawan, 0 m, 9 January 1949, *R.B.Fox 276 (=PNH 9152)* (AMES). Panay Island: Capiz Prov., October/November 1925, *G.Edano BS 46100* (AMES). Leyte Island: Dagami, Panda, 60 m, 4 February 1913, *C.A.Wenzel 142* (AMES, GH); Panda, 60 m, 31 January 1913, *C.A.Wenzel 77* (AMES, GH). Samar Island: Cagmanabo, 2 March 1916, *A.Plores s.n.* (AMES). Mindoro Island: Gusay, Naujan, 150 m, 13 October 1947, *M.Celestino & A.Castro 140 (=PNH 2259)* (AMES); sine loc., cult. in Manila, September 1911, *E.D.Merrill BS 5658* (AMES). Palawan Island: SE Mt. Victoria, Panacan, bank of Karaniogan River, 120 m, 12 May 1950, *M.D.Sulit 3790 (=PNH 12677)* (AMES).

Ames, when proposing *Dendrobium philippinense*, suspected it might be conspecific with the earlier *D. gerlandianum*. Later Ames obtained a tracing of the type of *D. gerlandianum* from Rudolf Schlechter in Berlin. Schlechter also sent Ames a floral analysis of a plant flowering in Berlin in June 1918. Analysis of the protologue of *D. gerlandianum* and the sketches supplied by Schlechter confirms the suspicions of Ames that his *D. philippinense* is indeed a synonym. We have chosen as epitype a collection apparently derived from the original consignment sent by Loher. *Dendrobium gerlandianum* is a rather commonly collected lowland Philippine species. It is characterized by slender stems with the lower few centimeters modestly swollen with alternating, subulate leaves above this. The flowers emerge from chaffy bracts, are thin in texture, usually pale greenish, ageing to a deep yellow. The lip is quite simple, somewhat elliptic, adorned above with two lamellate keels that converge apically. The collection from Palawan has no flowers, so its identity is not certain. It could be *D. rubroflavum,* which as speculated below may be from the Calamian Group, just north of Palawan.

Stone (1970) recorded *Dendrobium philippinense* from Guam on the basis of a collection by G. C. Moore. Examination of the AMES duplicate of *Moore 271* shows this is referrable to *D. oblongimentum* Hosokawa & Fukuyama. The latter taxon has much larger (mentum 10 vs. 4–6 mm) white flowers with more closely parallel keels that converge lower down on the lip.

Dendrobium oblongimentum Hosokawa & Fukuyama, Trans. Nat. Hist. Soc. Formos. 32: 12. 1942.

TYPE: MARIANA ISLANDS. Rota Island, *leg. Y. Aoki,* cult. on Saipan, *T.Hosokawa 7627-a* (Holotype: TI, not seen).

Usage synonym: *Dendrobium philippinense auct. non* Ames: B.C. Stone, Micronesiaca 6: 156. 1970.

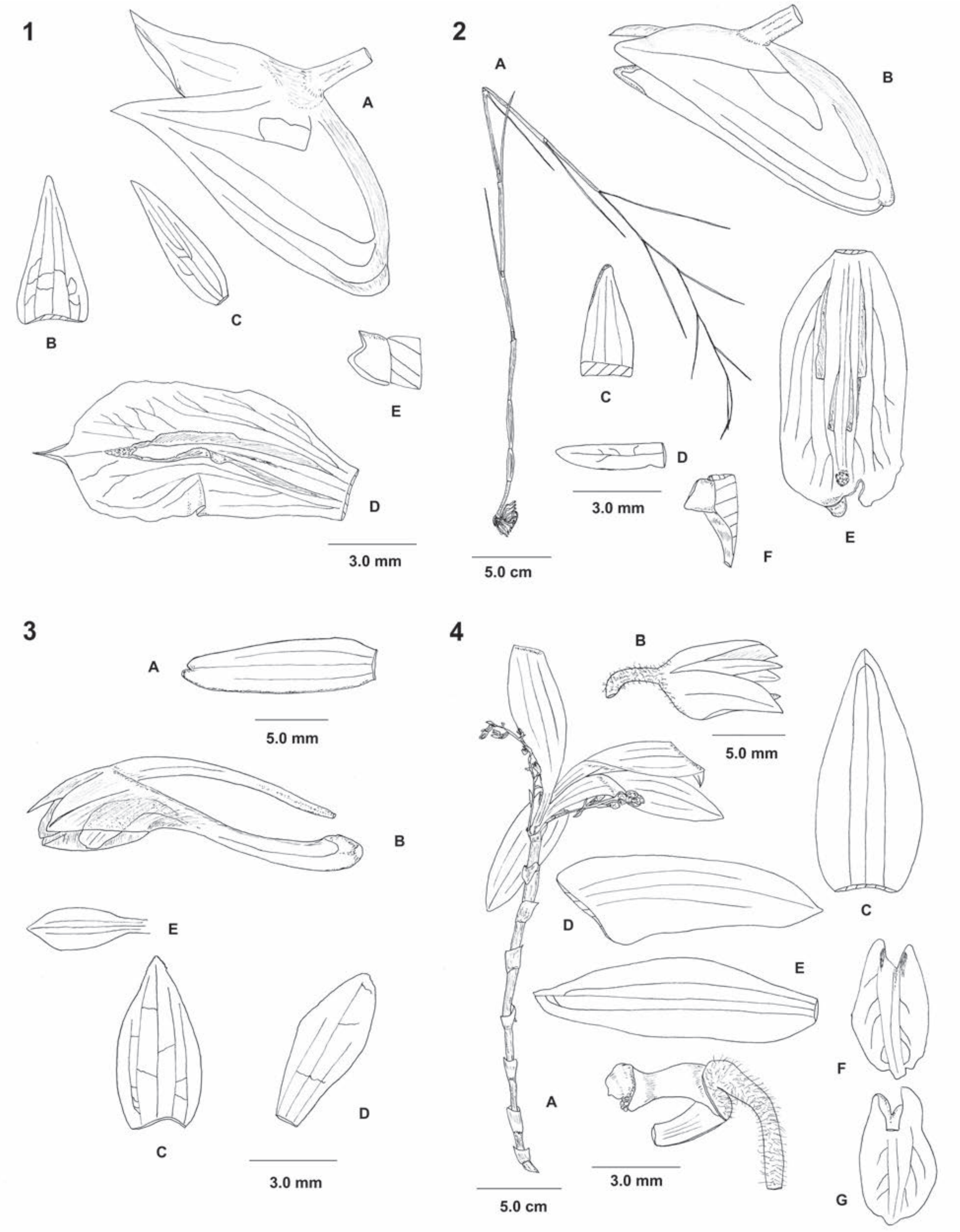
Distribution: Mariana Islands (Rota, Guam).

Additional specimen examined: MARIANA ISLANDS. Guam, E coast, 3.2 km E of Yigo, 3 February 1946, *G.C.Moore 271* (AMES; US, not seen).

Study of the specimen cited by Stone (1970) shows that it is not *Dendrobium philippinense* but rather *D. oblongimentum*, which differs in its larger white flowers as noted above.

Dendrobium rubroflavum Ormerod & Naive, *sp. nov.*

TYPE: PHILIPPINES. Luzon: sine loc., *ex Mr. Brown's garden, cult. Bureau Sci. Orch. House,* Manila, 5 June 1930, *E.Quisumbing 6092 (=BS 79073)* (Holotype: AMES). Fig. 2.



FIGURES 1–4. 1. *Dendrobium gerlandianum* Kraenzl. **A,** flower; **B,** dorsal sepal; **C,** petal; **D,** labellum; **E,** column (no scale). Drawn from *C.A.Wenzel 77* (AMES). 2. *Dendrobium rubroflavum* Ormerod & Naïve. **A,** plant; **B,** flower; **C,** dorsal sepal; **D,** petal; **E,** labellum; **F,** column (no scale). Drawn from holotype. 3. *Dendrobium zamboangense* Ames. **A,** leaf; **B,** flower; **C,** dorsal sepal; **D,** petal; **E,** labellum (no scale). Drawn from *G.E.Edano 1029* (AMES). 4. *Pinalia edanoana* Ormerod & Naïve. **A,** plant; **B,** flower; **C,** dorsal sepal; **D,** lateral sepal; **E,** petal; **F,** labellum (above and below); **G,** column. Drawn from holotype.

Related to *Dendrobium gerlandianum* Kraenzl. but the flowers red-yellow (vs. greenish), and the labellum with the two outer keels truncate, terminating in lower half (vs. keels apically convergent in upper half).

Presumably epiphytic *herb*. *Roots* slender, terete, several, 0.4–1.0 mm thick. *Stems* caespitose, simple to branching above (branches to 18 cm long), laxly leafy in upper part, basal two internodes slender, these 0.7–1.2 cm long, next two internodes swollen, quadrangular to hexangular in section, these 2.0–3.5 cm long (in total swollen part 4.2–6.8 cm long) upper internodes terete, 3.6–5.7 cm long, with an apical exposed portion not covered by leaf sheaths 0.1–0.4 cm long, in total to 52 cm long, slender parts 0.05–0.15 cm thick, swollen parts 0.15–0.30 cm thick. *Leaves* subulate, acute, obliquely erect, 2.9–10.0 cm long, 0.08 cm wide; leaf sheaths tubular, tightly amplectant, 2.8–5.2 cm long. *Inflorescences* consisting of 1–2 groups of chaffy bracts (2–4 mm long) emerging from the upper nodes of both leafy and leafless stems, very short. *Flowers* red-yellow. *Pedicel with ovary* clavate, ca. 8.5 mm long. *Dorsal sepal* ovate-lanceolate, obtuse, 3-veined, 3.6 × 1.7 mm. *Lateral sepals* ovate with lower side elliptically dilatate, obtuse, 3- to 4-veined, 3.7 mm long, 7.5 mm wide, forming with the column foot an ellipsoid, obtuse, 6.2-mm-long mentum. *Petals* ligulate-lanceolate, obtuse, vein 1, branching, 3.5 × 0.8 mm. *Labellum* elliptic, obtuse, 8.2 × 4.0 mm; outer 2 lamellae widely parallel, truncate, terminating midway on lip, the veins the lamellae lie on converging below the apex of the lip in a rough excrescence; above termination of lateral lamellae is a kind of rectangular, thickened medial area, itself with low flanking truncate lamellae. *Column* very short, stout, 0.5 mm long.

Distribution: Philippines.

Etymology: from the Latin *rubens,* red, and *flavus,* yellow, in reference to the flower color.

This species is externally identical to *Dendrobium gerlandianum* and was found misidentified under the synonym *D. philippinense*. It however differs in having red-yellow flowers and shorter, truncate keels on the lip. The type is a plant cultivated in Manila, originating from the garden of a Mr. Brown, its precise place of origin not known. However, Mr. Brown is likely Dr. William H. Brown (1884–1939), who was Director of the Bureau of Science, Manila, from 1924 to 1933. He visited Curon Island (Calamian Group, at the northern tip of Palawan), bringing back some live plants, among which was *Dendrobium modestum* Rchb.f., also a subulate-leaved, lowland species of section *Crumenata* (Ames and Quisumbing, 1932). It is possible that he collected *D. rubroflavum* on Curon Island, or on nearby Culion Island (where he visited the Leper Colony).

Dendrobium zamboangense Ames, Orch. 5: 145. 1915.

TYPE: PHILIPPINES. Mindanao: Zamboanga District, November to December 1911, *E.D.Merrill 8174* (Holotype: AMES). Fig. 3.

Homotypic synonym: *Eurycaulis zamboangensis* (Ames) M.A. Clem., Telopea 10, 1: 288. 2003.

Heterotypic synonyms: *Dendrobium appendiculoides* Ames, Orch. 7: 93. 1922 *nom. illeg., syn. nov.,* (non J.J. Sm. 1913).

TYPE: PHILIPPINES. Mindanao: Bukidnon Subprov., Mt. Bunuan, 1525 m, 27 June 1920, *M.Ramos & G.E.Edano BS 38940* (Holotype: AMES).

Dendrobium bunuanense Ames, Sched. Orch. 9: 53. 1925.

Eurycaulis appendiculoides M.A. Clem., Telopea 10, 1: 285. 2003 *nom. illeg.*

Distribution: Philippines (Mindanao).

Additional specimens examined: PHILIPPINES. Mindanao: Agusan Prov., Cabadbaran (Mt. Urdaneta), September 1912, *A.D.E.Elmer 13697* (AMES). Davao Prov., Mt. McKinley, 14 September 1946, *G.E.Edano 1029 (= PNH 1247)* (AMES).

Among the Philippine species of section *Pedilonum* Blume, this taxon may be recognized by its small (about 12–13 mm long), shortly, evenly bilobed leaves, and pink flowers with a 15-mm-long, narrowly clavate mentum. Study of the type of *Dendrobium appendiculoides* Ames showed it to not differ in critical characters from *D. zamboangense,* and therefore we find them conspecific.

Another very similar taxon is *Dendrobium stricticalcarum* W. Suarez & Cootes from Luzon. It also has rather short leaves, pink flowers, and a long, narrow mentum. It differs from *D. zamboangense* in having obliquely bilobed leaves, narrower (1.3 vs. 2.1 mm), ligulate (vs. rhombic) petals, and an undilated mentum.

Mycaranthes Blume, Bijdr.: 352. 1825.

Type species: *Mycaranthes latifolia* Blume

This is a genus of Eriinae with about 40 species distributed from Nepal to Papua New Guinea. Most of the taxa are found in the Malesian region. They are epiphytic, caulescent plants with generally terminal inflorescences. The flowers are relatively small (sepals ca. 3–5 mm long), often yellowish and marked with red, the lip with one or farinose calli and some lesser lateral keels, and the column bearing eight pollinia. One species requires transfer to the genus; it has had a rather convoluted history.

Mycaranthes villosissima (Rolfe) Ormerod, *comb. nov.*

Basionym: *Eria villosissima* Rolfe, J. Linn. Soc., Bot. 42: 150. 1914.

TYPE: MALAYSIA. Sabah: Mt. Kinabalu, Marai Parai, 1675–2135 m, February 1910, *L.S.Gibbs 4090* (Holotype: K, image seen; Isotype: BM, image seen).

Heterotypic synonyms: *Eria major* Rolfe, J. Linn. Soc., Bot. 42: 150. 1914 *nom. illeg.* (non Ridl. 1896).

TYPE: MALAYSIA. Sabah: Mt. Kinabalu, 1830 m, *G.D.Haviland 1250* (Holotype: K, image seen).

Mycaranthes major J.J. Wood, Orch. Mt. Kinabalu 2: 414. 2011 *nom. inval.*

BASIS FOR NAME: MALAYSIA. Sabah: Mt. Kinabalu, 1830 m, *G.D.Haviland 1250* (K, image seen).

Distribution: Malaysia (Sabah).

The history of this entity starts when Ridley (in Stapf, 1894) recorded from Mount Kinabalu, Borneo, a plant (*Haviland 1250*) he identified as *Eria kingii* J.D. Hook., a species based on material from the Malay Peninsula. Stapf realized that the name *E. kingii* J.D. Hook. was a homonym of *E. kingii* F. Muell., described from the Solomon Islands in 1882. So Stapf proposed a replacement name, *E. scortechinii,* listing in synonymy also an "*Eria major* Ridl." But *Eria scortechinii* Stapf was also a homonym, the name having been used by Joseph Hooker in 1890 for a different Malayan plant. Realizing his mistake, Stapf withdrew his *E. scortechinii* in the index of the "Transactions" (1896: 525), and substituted *E. major.* Thus the name *E. major* is a replacement name for *E. kingii* J.D. Hook.; at no stage was a new species proposed. Ridley (1896: 288–289) explained that originally he had intended to propose a "*Eria kingii* var. *major*" for the Kinabalu plant, since it is somewhat more robust than the Malayan plant.

Rolfe (1914) superfluously proposed that the Malayan plant be called *Eria ridleyi,* reserving the name *E. major* for the Kinabalu plant, contrary to its type, and thus creating a homonym. Rolfe was the first to definitively separate the Malayan and Bornean entities. Tang and Wang (1951) tried to explain the confusing situation that had arisen; unfortunately they followed Rolfe's use of the name *E. major* (but accredited it to Ridley), and accepted *E. ridleyi* as the correct name for the illegitimate *E. kingii* J.D. Hook. In transferring *Eria major* to *Mycaranthes,* Wood et al. (2011) cited as basionym the appearance of the name *Eria major* where it was a *nomen nudum* and a synonym of *Eria scortechinii* Stapf. Consequently the name *Mycaranthes major* is also invalid.

To sum it all up, *Eria major* Ridl. is the correct replacement name for *E. kingii* J.D. Hook., whereas *E. scortechinii* Stapf and *E. ridleyi* Rolfe are nomenclatural synonyms. Eventually Seidenfaden and Wood (1992) placed them all in synonymy of *Eria oblitterata* (Blume) Rchb.f., now *Mycaranthes oblitterata* Blume. Whereas *Eria major* Rolfe is a homonym and is a taxonomic synonym of *E. villosissima,* the latter is here transferred to *Mycaranthes.*

Odontochilus Blume, Coll. Orch. Arch. Ind.: 79. 1858; Fl. Javae Ins. Adj. n.s. 1: 66. 1858.
Type species: *Anoectochilus flavescens* Blume

A genus of Goodyerinae with 55–60 species, distributed from India to Samoa, and north to Hawai'i, now construed to include the former genera *Cystopus* Blume, *Evrardia* Gagnep., *Evrardianthe* Rauschert, *Myrmechis* (Lindl.) Blume, *Pristiglottis* Cretz. & J.J. Sm., *Tubilabium* J.J. Sm., and *Vexillabium* F. Maekawa. They are tender terrestrial herbs found mostly in undisturbed montane forests. One new name is required for a Philippine species previously referred to *Myrmechis.*

Odontochilus marivelensis Ormerod & Cootes, *nom. nov.*
Basionym: *Myrmechis philippinensis* Ames, Orch. 2: 64. 1908.
TYPE: PHILIPPINES. Luzon: Bataan Prov., Mt. Mariveles, 800 m, 20 July 1904, *J.B.Leiberg s.n.* (Holotype: AMES).
Homotypic synonym: *Odontochilus philippinensis* (Ames) T. Yukawa, Bull. Natl. Mus. Nat. Sci., Ser. B, 42, 3: 108. 22 Aug. 2016 *nom. illeg.* [*non* (Ames) J.M.H. Shaw, Jun. 2016].

Distribution: Philippines.

Additional specimens examined: PHILIPPINES. Palawan: Mt. Gantung, May 1929, *G.E.Edano BS 77629* (AMES); Brooke's Point, Mt. Balabag, Mantalingahan Range, 1855 m, 13 May 1947, *G.E.Edano PNH 403* (AMES); Mt. Matalingahan, 1660 m, 13 May 1947, *G.E.Edano PNH 642* (AMES).

Etymology: named after the type locality, Mt. Mariveles.

It is necessary to provide a new epithet for this plant in *Odontochilus* because the name is already occupied for a different species, *O. philippinensis* (Ames) J.M.H. Shaw (Basionym: *Cystopus philippinensis* Ames. Synonym: *Odontochilus luzonensis* T. Yukawa *nom. superfl.*).

Pinalia Lindl., Orch. Scelet.: 14, 21, 23, t. 71. 1826.
Lectotype species (here designated): *Pinalia alba* Buch.-Ham. ex Lindl., Orch. Scelet. (App.): sub t. 41B. 1826 [= *P. spicata* (D. Don) S.C. Chen & J.J. Wood].

A genus of Eriinae with about 210 species distributed from India and Sri Lanka to Tahiti, with the most species in Indonesia. They were formerly included in a broad concept of *Eria* Lindl. The four species described here belong to section *Polyura* (here transferred from *Eria*).

Pinalia section **Polyura** (Schltr.) Ormerod & Naive, *comb. nov.*
Basionym: *Eria* Lindl. section *Polyura* Schltr., Rep. Sp. Nov. Regni Veg. 9: 106. 1911.
Type species: *Eria polyura* Lindl.

This section contains about 40 species (new taxa included) distributed from Indochina (Cambodia, Laos, Vietnam) to Tahiti. There are two centers of speciation, one in the Philippines, and one in New Guinea. The section is characterized by the flowers having a relatively simple lip, which is often much smaller than the sepals; it is usually adorned with a pair of semilunate to deltate fleshy, purple calli. The taxonomy of the group is often frustrated by the delicate flowers, which preserve poorly and are difficult to rehydrate and study (the floral parts often sticking together). Two growth forms are present in the section, one is the traditional sympodial format and another is basally sympodial plants with superposed pseudobulbs above (giving the appearance of branched plant).

Pinalia edanoana Ormerod & Naive, *sp. nov.*
TYPE: PHILIPPINES. Mindanao: Mount Apo, N slope, Lake Linau, 2300 m, 30 October 1936, *G.E.Edano 1250 (= PNH 2309)* (Holotype: AMES). Fig. 4.

Related to *Pinalia formosana* (Rolfe) Ormerod but with broader (2.20–3.10 vs. 1.20–2.15 cm wide) leaves, an ovate-lanceolate (vs. oblong-lanceolate) dorsal sepal, and an elliptic (vs. ovate-elliptic) lip lamina.

Epiphytic *herb. Roots* slender, terete. *Pseudobulbs* superposed, terete-subclavate, 5-leaved apically, below which laxly and loosely 7-sheathed (these 15–25 mm long), part preserved 22.0 × 0.35–0.50 cm; internodes 2.5–3.5 cm long. *Leaves* oblong to oblong-lanceolate, acute to obtuse, papyraceous, 9.0–10.0 × 2.2–3.1 cm. *Inflorescence* pubescent, 7–9 cm long; peduncle ca. 1 cm long; rachis laxly 20–25 flowered, 6–8 cm long; floral bracts ovate-oblong, acute, 5–7 mm long. *Flowers* white, externally sparsely pubescent on bases of sepals. *Pedicel with ovary* weakly clavate, densely pubescent, 5.0–6.5 mm long. Dorsal sepal ovate-lanceolate, subacute, 3-veined, 7.0–8.0 × 3.0–3.2 mm. Lateral sepals obliquely oblong-lanceolate, acute, 7-8 × 3 mm, forming with the column foot an obliquely forward-pointing, 3.3-mm-long mentum. *Petals* oblong, acute, 3-veined, 7.2–8.5 × 2.5 mm. *Labellum* elliptic from a decurved base, apex weakly lobulate, obtuse, 3-veined, basal sides with a low semi-discoid callus each side, 4.2 × 2.2 mm. *Column* semiterete, 2.5 mm long; column foot ca. 2.5 mm long.

Distribution: Philippines.

Habitat: on a tree trunk in mossy montane forest, 2300 m.

Etymology: named after Gregorio Edano (d. 1960), prodigious collector of Philippine plants and many orchids.

This species is quite similar to *Pinalia formosana* (Rolfe) Ormerod from Taiwan, but it has somewhat broader leaves, a broader (3.0–3.2 vs. 2.2 mm), ovate-lanceolate (vs. oblong-lanceolate) dorsal sepal, a shortly clawed (vs. sessile) lip with an elliptic (vs. ovate-elliptic) lamina.

Pinalia kitangladensis Ormerod & Naive, *sp. nov.*
TYPE: PHILIPPINES. Mindanao: Bukidnon Prov., Mt. Katanglad, summit of middle peak, 2350 m, 14 April 1949, *M.D.Sulit 3477 (= PNH 10193)* (Holotype: AMES; Isotype: PNH, not seen). Fig. 5.

Related to *Pinalia jimcootesii* Naïve & Ormerod but with larger (sepals 8.5–10.0 vs. 5.2–6.5 mm long) flowers, and a larger (5.0 x 2.5 vs. 3.0–3.5 x 2.2–2.5 mm), shortly clawed (vs. sessile) lip.

Presumably epiphytic *herb*. *Roots* slender, terete, pubescent, to 1 mm thick. *Stems* terete or very weakly clavate apically, 5- to 6-leaved, clothed by laxly spaced (30–35 mm apart), inflated, tubular sheaths (these 25–40 mm long), 39.50 × 0.45–0.60 cm; internodes 5.0–6.5 cm long. *Leaves* linear-ligulate, apex obliquely subacutely bilobed, 17.2–21.0 × 0.85–1.80 cm wide. *Inflorescences* 2, pubescent, 13.5–14.5 cm long; peduncle 1.5–2.0 cm long; rachis densely many-flowered, 12.0–12.5 cm long; floral bracts oblong-lanceolate, acute, reflexed, 5–6 × 2 mm. *Flowers* creamy white, externally laxly pubescent on basal third of sepals, nonresupinate. *Pedicel with ovary* terete-subclavate, pubescent, 8 mm long. *Dorsal sepal* oblong-oblanceolate, obtuse, 5-nerved, 10 × 3 mm. *Lateral sepals* obliquely oblong-lanceolate, apiculate, 4-nerved, 8.5 × 3.5 mm, forming with the column foot a 1.5- to 2.0-mm-long mentum. *Petals* oblong, obtuse, 3-nerved, 9 × 3 mm. *Labellum* ovate-lanceolate, subacuminate, shortly clawed, 3-nerved, above base 2 very obscure, small calli, 5.0 × 2.5 mm. *Column* semiterete, 2.2 mm long (minus anther cap); column foot 1.5–1.9 mm long.

Distribution: Philippines.

Etymology: named after Mt. Katanglad (modern spelling Kitanglad), the type locality.

This taxon appears to be related to its Philippine congener *Pinalia jimcootesii* Naive & Ormerod, sharing with it a simple, seemingly ecallose or barely callose lip. However, it has much (39.5 vs. 15.0–17.0 cm) longer stems, larger flowers, with a larger, shortly (vs. sessile) clawed lip.

Pinalia pentalopha Ormerod & Naive, *sp. nov.*
TYPE: PHILIPPINES. Luzon: Bontoc Subprov., without precise locality, 1700 m, 31 December 1912, *M. Vanoverbergh 2230* (Holotype: AMES). Fig. 6.

Similar to *Pinalia polyura* (Lindl.) Kuntze but the labellum with 5 thick (vs. 2 laminate) calli.

Presumably epiphytic *herb*. *Stem* fragment clavate, 7-leaved apically, 12.0 × 0.9 cm; internodes 1.6 cm long. *Leaves* ligulate-oblanceolate, acute, finely 13- to 15-veined, 12.8–20.0 × 2.2–2.8 cm. *Inflorescence* slender, minutely pubescent, to 14 cm long; peduncle ca. 1 cm long; rachis subdensely many-flowered, 13 cm long; floral bracts oblong, acute, margins minutely dentate toward apex, reflexed, 4.0–6.0 × 1.1–1.2 mm. *Flowers* white and pink, externally pubescent, nonresupinate. *Pedicel with ovary* terete-subclavate, pubescent, 4.5–5.5 mm long. *Dorsal sepal* oblong-oblanceolate, subacute, 3-veined, 7.5 x 2.1 mm. *Lateral sepals* obliquely ovate-triangular, subacute, subfalcate, 3-veined, top margin 6 mm long, lower margin 3 mm long, 3 mm wide, forming with the column foot a 2.5- to 3.0-mm-long mentum. *Petals* obliquely oblong-lanceolate, acute, 3-nerved, 7.2 × 2.1 mm. *Labellum* broadly ovate-cordate, apex subacuminate, fleshy, 3- to 5-veined, ca. 3.0 × 2.8–3.0 mm; calli 5, basal pair thick laminate, transverse, 1 each side at base of lip, in front of which (and perpendicular to) a parallel pair of thick laminate ridges, midridge thick, rounded. *Column* semiterete, arcuate, 2 mm long; column foot slightly incurved, 2 mm long.

Distribution: Philippines.

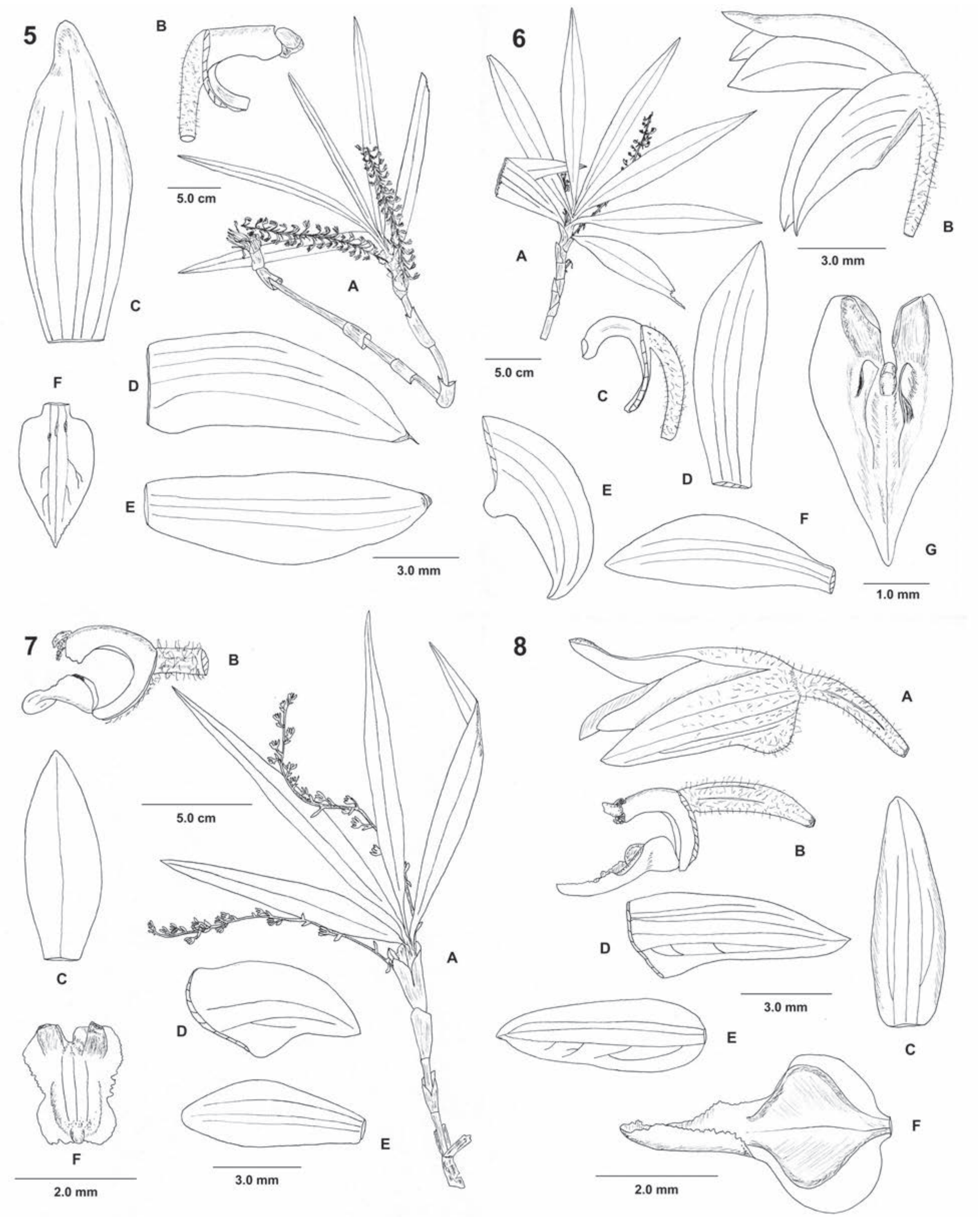
Etymology: from the Classical Greek prefix *penta,* meaning five, and *lophus,* meaning crest, in reference to the five calli on the lip.

This species is superficially identical to *Pinalia polyura* in habit, in that it produces superposed stems that impart a branching appearance. It clearly differs in its lip, which, though similar in shape, is thicker and has five thick calli (vs. two laminate, semilunate calli).

Pinalia sanguinea Ormerod & Naive, *sp. nov.*
TYPE: PHILIPPINES. Luzon: Bontoc Subprov., Mt. Pukis, 1860 m, 9 March 1920, *M.Ramos & G.E.Edano BS 37758* (Holotype: AMES). Fig. 7.

Distinguished from other Philippine taxa of section *Polyura* in having blood-red to reddish brown (vs. white, yellow, or pink) sepals, and a subpandurate lip that is erose-dentate (vs. entire) in the lateral sinuses.

Epiphytic *herb*. *Roots* terete, elongate. *Stems* narrowly clavate, superposed, new stems emerging 1.0–2.5 cm below leaves, each node with an infundibuliform, reddish-brown drying, papyraceous sheath, 4- to 5-leaved at apex, 12.2–14.0 × 0.3–0.4 cm; internodes 1.0–2.7 cm long. *Leaves* linear-ligulate, acute, thinly coriaceous, 9.0–15.6 × 0.9–1.7



FIGURES 5–8. 5. *Pinalia kitangladensis* Ormerod & Naïve. **A,** plant; **B,** column; **C,** dorsal sepal; **D,** lateral sepal; **E,** petal; **F,** labellum. Drawn from holotype. 6. *Pinalia pentalopha* Ormerod & Naïve. **A,** plant; **B,** flower; **C,** column; **D,** dorsal sepal; **E,** lateral sepal; **F,** petal; **G,** labellum. Drawn from holotype. 7. *Pinalia sanguinea* Ormerod & Naïve. **A,** plant; **B,** flower minus tepals; **C,** dorsal sepal; **D,** lateral sepal; **E,** petal; **F,** labellum. A–E from holotype; F from *M.Celestino 0565* (AMES). 8. *Pinalia tonglonensis* Ormerod & Naïve. **A,** flower; **B,** flower minus tepals; **C,** dorsal sepal; **D,** lateral sepal; **E,** petal; **F,** labellum. Drawn from holotype.

cm. *Inflorescences* usually 2 per stem, pubescent, emerging just below the leaves, 8–17 cm long; peduncle 1 cm long; rachis sublaxly many-flowered, 7–16 cm long; floral bracts oblong, acute, concave, ca. 4.0 × 1.3 mm. *Flowers* "reddish blood," or reddish-brown with yellow-green, externally pubescent. *Pedicel with ovary* narrowly clavate, pubescent, 4–5 mm long. *Dorsal sepal* oblong-lanceolate, subacute, 6.5 × 2.6 mm. *Lateral sepals* obliquely ovate, subacute, 2- to 3-veined, 5.7 × 3.0 mm, forming with the column foot a ca. 2.0- to 2.3-mm-long mentum. *Petals* oblong-rhombic, obtuse, 3-veined, 5.7 x 2.2 mm. *Labellum* subpandurate, lateral sinuses erose-dentate, ca. 2.2–2.5 × 1.5–1.7 mm, basal half each side with a fleshy, partly free, triangular, obtuse callus. *Column* weakly arcuate, 2.5 mm long; column foot forward-pointing, gently incurved, 2 mm long.

Distribution: Philippines.

Habitat and ecology: tree trunk in mossy, montane forest (type); on tree branches up western ridges in mossy, montane forest (*Celestino 0565*), 1860–2040 m.

Additional specimen examined: PHILIPPINES. Luzon: Mountain Prov., Ifugao, Mt. Polis, 2040 m, 16 May 1948, *M.Celestino 0565 (= PNH 5582)* (AMES).

Etymology: from the Latin *sanguineus,* of blood, or blood-red, in reference to the flower color.

This taxon is without close relatives. It may be recognized by its superposed stems (thus imparting a branching appearance), blood-red to reddish-brown flowers, and subpandurate lip with erose-dentate lateral margins. *Pinalia serrulata* Ormerod from Indonesian Papua has a similarly shaped lip with erose-dentate lateral margins, but its stems are not superposed, and the lip lacks prominent basal calli.

Pinalia tonglonensis Ormerod & Naive, *sp. nov.*
TYPE: PHILIPPINES. Luzon: Benguet Prov., Mt. Tonglon (Mt. Santo Tomas), December 1908, *M.Ramos BS 5391* (Holotype: AMES). Fig. 8.

Related to *Pinalia tomentosiflora* (Hayata) W. Suarez & Cootes but with larger flowers (sepals 6.8–7.1 vs. 4.0–4.5 mm long), and a longer (4.0 vs. 2.5 mm) lip with 2 large, triangular calli (vs. 4 thickened lines).

Presumably epiphytic *herb*. *Roots* terete, pubescent, 1–2 mm thick. *Stems* terete, superposed, new stems (usually 1, but sometimes 2) emerging at or below leaves in upper third of stem, each node with an infundibuliform, reddish-brown drying, papyraceous sheath, 6- to 7-leaved in apical quarter, 13.0–16.5 × 0.4–0.7 cm thick; internodes 2.0–2.3 cm long. *Leaves* ligulate, acute, 10.0–18.5 × 1.1–1.8 cm. Inflorescence to 10 cm long; peduncle 1 cm long; rachis sublaxly many-flowered, 9 cm long; floral bracts ovate-lanceolate, acute, 4 mm long. *Flower* color not known, externally laxly pubescent. *Pedicel with ovary* narrowly clavate, pubescent, 4 mm long. *Dorsal sepal* oblong-lanceolate, obtuse, 3- to 5-veined, 7.1 × 2.6 mm. *Lateral sepals* obliquely oblong-lanceolate, acute, 4- to 5-veined, 6.8 × 2.8 mm, forming with the column foot 2-mm-long mentum. *Petals* oblong-lanceolate, subacute, 3-veined, 6.7 × 2.2 mm. *Labellum* trilobed, 4.0 × 2.5 mm; hypochile suborbicular, ca. 1.8 × 2.5 mm, each side with a fleshy, partly free, broadly triangular, obtuse callus; epichile lanceolate-cymbiform, margins irregularly shallowly dentate, 2.2 × 1.0 mm. *Column* semiterete, weakly curved, 2 mm long; column foot weakly curved, 1.8 mm long.

Distribution: Philippines.

Etymology: named after Mt. Tonglon, the type locality.

This taxon is superficially identical to *Pinalia formosana* (Rolfe) Ormerod (Syn.: *Eria plicatilabella* Hayata; *Eria tomentosiflora* sensu T.P. Lin 1977, *non* Hayata) from Taiwan in habit (in that the terete, superposed stems impart a branching appearance). However, the floral details are quite different since the flowers have a trilobed lip with a suborbicular hypochile, and lanceolate-cymbiform epichile (vs. entire, ovate-elliptic). Another externally identical but much closer species is *Pinalia tomentosiflora* (Hayata) W. Suarez & Cootes, also from Taiwan. Illustrations labelled as this species (e.g., Lin 1977), are actually of *P. formosana*. The lip of the true *P. tomentosiflora* is trilobed with a suborbicular hypochile, and a lanceolate epichile. The new species differs in having larger flowers (sepals 6.8–7.1 vs. 4.0–4.5 mm), and a longer (4.0 vs. 2.5 mm) lip with two large, triangular calli (vs. four thickened lines).

Thrixspermum Lour., Fl. Cochinch. 2: 516, 519. 1790.
Type species: *Thrixspermum centipeda* Lour.

A genus of about 200 primarily epiphytic, monopodial orchids. They are distributed from India and Sri Lanka to Samoa. Species taxonomy in the genus is hampered by the ephemeral, poorly preserving flowers. Thus, it is often necessary to work from living plants, as herbarium material is in many cases flowerless. The species discussed here was formerly placed in the genus *Cordiglottis* J.J. Sm., a concept found through molecular studies to be nested in *Thrixspermum* (Kocyan and Schuiteman, 2014).

Thrixspermum filiforme (J.D. Hook.) Kuntze, Rev. Gen. Pl. 2: 682. 1891.
Basionym: *Sarcochilus filiformis* J.D. Hook., Fl. Brit. Ind. 6: 39. 1890.
TYPE: MALAYSIA. Perak: Larut, Goping, 90–150 m, April 1884, *G. King's coll. [prob. H.Kunstler] 5930* (Holotype: K, image seen).
Homotypic synonyms: *Dendrocolla filiformis* (J.D. Hook.) Ridl., J. Linn. Soc., Bot. 32: 382. 1896.

Cheirorchis filiformis (J.D. Hook.) C.E. Carr, Gard. Bull. Singap. 7: 46. 1932.

Cordiglottis filiformis (J.D. Hook.) Garay, Bot. Mus. Leafl. Harv. Uni. 23, 4: 176. 1972.

Heterotypic synonyms: *Epidendrum subulatum* J.G. Koen., in Retz, Observ. Bot. 6: 51. 1791 *nom. illeg., syn. nov.* (*non* Swartz 1788). TYPE: NOT CITED [THAILAND. Phuket, 9 June 1779]. *J.G.Koenig s.n.* (Holotype: lost).

Limodorum subulatum Willd., Sp. Pl. ed. 4, 4: 126. 1805.

Aerides subulata (Willd.) Schltr., Rep. Sp. Nov. Regni Veg. 19: 382. 1924 *nom. illeg.* [non (Blume) Lindl. 1833].

Papilionanthe subulata (Willd.) Garay, Bot. Mus. Leafl. Harv. Uni. 23, 10: 372. 1974.

Distribution: Thailand, Malaysia, Singapore, Philippines.

Ever since Lindley (1833) questionably associated *Epidendrum subulatum* J.G. Koen. with *Aerides cylindrica* Lindl. from India, the former name has been associated with members of what is now the genus *Papilionanthe* Schltr. In 1995 Seidenfaden realized that Koenig's species could not have come from India, but that it actually originated from Phuket, Thailand. Therefore he proposed *Papilionanthe cylindrica* (Lindl.) Seidenf. for the Indian plant and moved the well-known *P. teres* (Roxb.) Schltr. into the synonymy of *P. subulata* (Willd.) Garay. The problem with this position is that *P. teres* is not known from Phuket, which is an island on the western side of peninsular Thailand. Unfortunately not enough attention was paid to the protologue of *Epidendrum subulatum* by one of the major contributors (the first author of this paper) in the work by Seidenfaden (1995). Only after publication was it realized by the first author that *E. subulatum* could not be a *Papilionanthe*; however, its true identity remained elusive.

A recent analysis of Koenig's description of *Epidendrum subulatum* reveals several key characters that allow the name to be identified. Thus, the critical features Koenig describes are of a terete-leaved plant, the leaves about 19 cm long, with the rachis much shorter than the peduncle, the flowers white, the lip with yellow-orange sidelobes, and a yellow, pubescent midlobe. This can only be *Thrixspermum filiforme,* which is also known from Phuket. Even though the binomial *Limodorum subulatum* is the earliest available name, the epithet is pre-empted in *Thrixspermum* by *T. subulatum* (Blume) Rchb.f.

Thus, the name *Papilionanthe teres* (Roxb.) Schltr. should continue in use, and its south Indian and Sri Lankan relative should be called *P. cylindrica* (Lindl.) Seidenf.

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ZYGOPETALINAE NOVAE ET CRITICAE (ORCHIDACEAE)

Franco Pupulin[1]

Abstract. The new genus *Pridgeonia*, and eight new orchid species in the genera *Benzingia*, *Daiotyla*, *Dichaea*, *Ixyophora*, and *Pridgeonia*, all belonging to the subtribe Zygopetalinae, are described. Complete descriptions, with notes on etymology, habitat, and ecology, and discussion of phylogenetic affinities, are provided for each new taxon, supplemented with line drawings, photographs, digital composite plates, and distribution maps. New combinations and synonyms are proposed in the genera *Aetheorhyncha, Benzingia, Dichaea,* and *Ixyophora*. *Dichaea dressleri* and *Kefersteinia alata* are recorded and illustrated for the first time for the flora of Costa Rica. Keys for the genus *Benzingia* and the Costa Rican species of *Dichaea* are proposed.

Keywords: flora of Colombia, flora of Costa Rica, flora of Ecuador, flora of Nicaragua, new genus, new records, new species

The publication of the general treatment of subtribe Zygopetalinae (Orchidaceae) in *Genera Orchidacearum* (Pupulin et al., 2009), now 10 years ago, represented a unique opportunity to summarize our knowledge about this group of plants from the wet American tropics and to review in detail the circumscription of genera and the critical application of names of the over 400 species of this group as accepted today. Since then, new species and combinations have been proposed in the genera *Aganisia* Lindl. (Barros and Guimaraes, 2010), *Benzingia* Dodson ex Dodson (Romero-González and Dodson, 2010), *Dichaea* Lindl. (Bolsanello, 2010; Krahl et al., 2014; Valsko et al., 2014a,b; Archila Morales and Chiron, 2015; Campacci et al., 2015; Sambin and Chiron, 2015; Krahl et al., 2016; Archila Morales et al., 2017; Pupulin and Karremans, in press), *Huntleya* Bateman ex Lindl. (Ortiz Valdivieso, 2004), *Kefersteinia* Rchb.f. (Carnevali Fernández Concha et al., 2015), *Koellensteinia* Rchb.f. (Hall et al., 2015), *Promenaea* Lindl. (Barberena and Barros, 2015), and *Zygopetalum* Hook. (Castro-Neto and Campacci, 2000).

Over the past decade I have maintained my interest in this group of plants and have continued to work on the systematics of Zygopetalinae, in particular on the native groups of Costa Rica and the Ecuadorean Andes.

Below, I introduce the results of these studies, proposing a number of new taxa, new combinations, and new records in seven genera of Zygopetalinae, which I present in alphabetical order.

Aetheorhyncha Dressler

The monotypic genus *Aetheorhyncha* is superficially similar to *Chondroscaphe* (Dressler) Senghas & G. Gerlach in flower lip with a small, toothed callus in the center of the disc, but it lacks the distal callus that characterizes the latter. The flowers, held almost vertically, with a very narrow lip opening, the pubescent lamina of the lip with a strong median keel basal to the bilobed callus, and the narrow, truncate viscidium, distinguish the genus among other relatives in the *Chondrorhyncha* complex (Pupulin, 2009a) (Fig. 1, 6A, 30B).

1. ***Aetheorhyncha andreettae*** (Jenny) Dressler, Lankesteriana 5(2): 95. 2005.

Basionym: *Chondrorhyncha andreettae* Jenny, Orchidee (Hamburg) 40(3): 92. 1989.

TYPE: ECUADOR. Morona-Santiago: Cutucú, 900 m, 1987, *A. Andreetta s.n.* (Holotype: CH).

Heterotypic synonym: *Chondrorhyncha panguensis* Dodson ex Harding, Orquideología 25(2): 166–169, 175–177. 2008, *syn. nov*.

TYPE: ECUADOR. Morona Santiago, cerca de Panguí, 1500 m, *C. H. Dodson 16003* (Holotype: MO).

When Harding (2008) described *Chondrorhyncha panguensis*, she mixed up several collections, including the photograph of a plant grown at Ecuagenera, Ecuador, the drawing of *Chondrorhyncha andreettae* Jenny that appeared in one of Dodson and Marmol de Dodson's (1989) accounts on the orchids of Ecuador, and a dried specimen collected at El Pangui, in Amazonian Ecuador, now conserved in the herbarium of the Missouri Botanical Garden (*C. H. Dodson*

This paper, which took 10 long years to be completed, would have not been possible without the human and logistic support of my friend José "Pepe" Portilla, and the activity of the Andean Orchid Research Center (CIOA, for the acronym of its name in Spanish, Centro de Investigación en Orquídeas de los Andes) of the now-dissolved University Alfredo Pérez Guerrero of Quito, Ecuador. At the CIOA, the assistance of my colleagues Hugo Medina Troyani and Gilberto Merino was substantial for documenting and understanding the exceedingly rich and difficult flora of the Ecuadorian Andes and Amazonia. Their unselfish and open-minded cooperation in the systematic work carried out at the CIOA cannot be acknowledged enough. In Costa Rica, I deeply acknowledge my colleagues at the Lankester Botanical Garden for the fruitful discussions on the taxonomy of Zygopetalinae and the continuous help with the fieldwork required for this study. Among them, I particularly want to thank Diego Bogarín, Melissa Díaz-Morales, Melania Fernández, and Adam P. Karremans. I would also like to thank Sara Poltronieri, who became an accomplished botanical illustrator at our research center, for the beautiful illustrations she contributed to this paper. The Ministry of Environment and Energy (MINAE) of the Republic of Costa Rica, and its National System of Protetcted Areas (SINAC), are acknowledged for extending the required permits to import material for study and to collect plants in the field, particularly in national parks.

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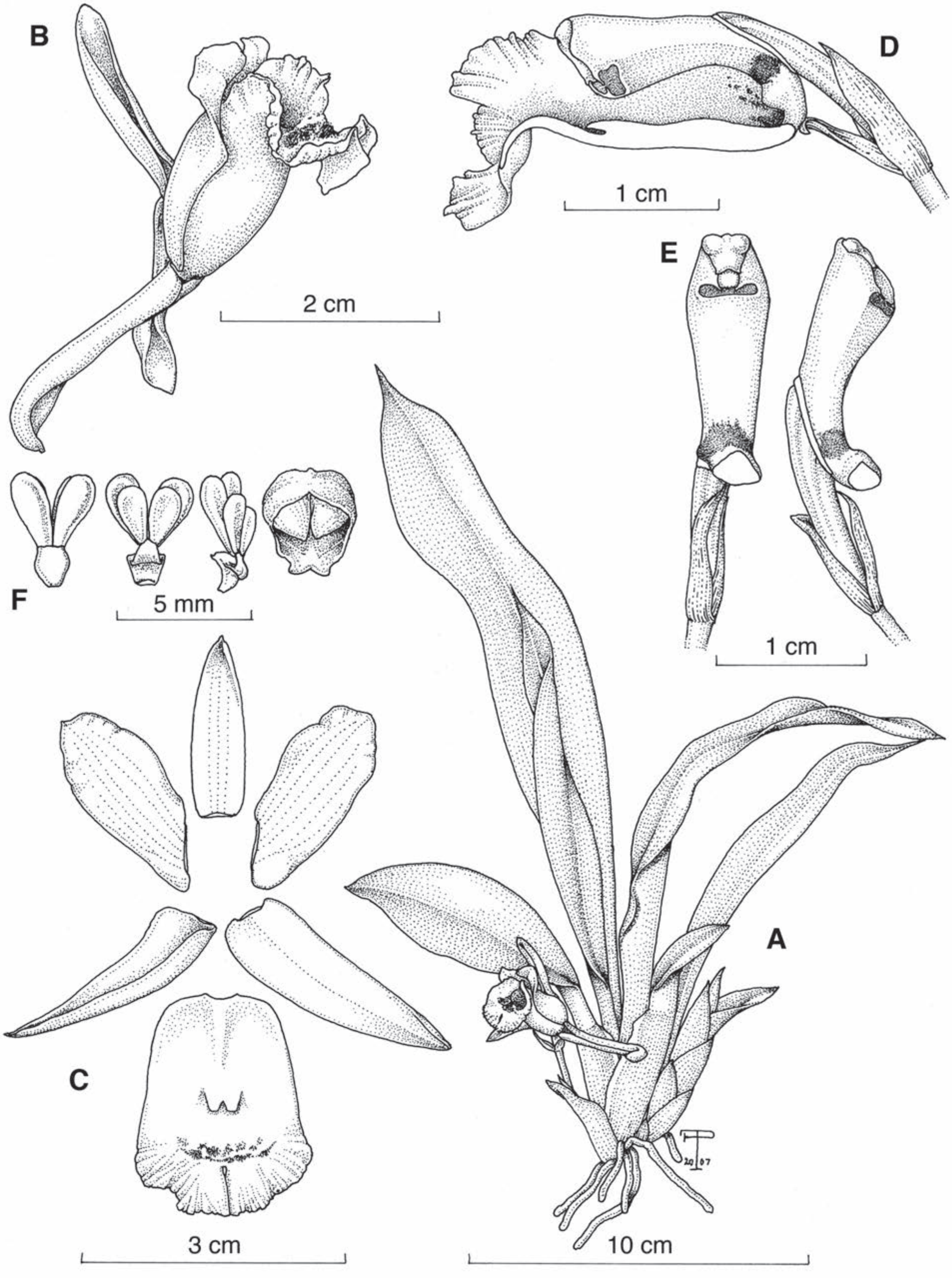

FIGURE 1. *Aetheorhyncha andreettae* (Jenny) Dressler. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, frontal and three-quarter views; **F**, pollinarium (three views) and anther cap. Drawn by F. Pupulin from *Pupulin 6560* (CIOA).

Chondrorhyncha andreettae Jenny & Dodson 1992

PLANTS OF ECUADOR

ORCHIDACEAE

Chondroryncha panguensis Dodson sp. nov.
Det. C. H. Dodson 1985

Plants cultivated at the Jardin Botanico de Uzphud near Paute by Father Angel Andreetta. Collected by A. Andreetta & M. Portillo.

Pangui, Prov. Morona-Santiago, alt. 1500 m.
Flower white; lip white with yellow throat, spotted heavily with red-brown.

C. H & P. M. Dodson 16003 22 Jul 1985
T. Dodson & A. Embree
Missouri Botanical Garden Herbarium (MO)

FIGURE 2. Holotype of *Chondrorhyncha panguensis* Dodson ex Harding (MO 3573348). Courtesy of the Herbarium, Missouri Botanical Garden.

16003) (Fig. 2). Harding (2008) compared *C. panguensis* with *C. velastigui* Dodson, from which it could supposedly be differentiated by the inrolled dorsal sepal (vs. concave), the relative lengths of the apical teeth of the callus, and the straplike shape of the leaves (vs. broad and "oval"). In describing the flower, Harding used characters from both the photograph of the plant cultivated at Ecuagenera and from Dodson's notes affixed to the herbarium specimen, whereas measurements are mostly taken from the herbarium sheet and from Dodson and Marmol de Dodson's (1989) description of *C. andreettae* in the *Icones Plantarum Tropicarum*. These measurements well correspond to those recorded for the holotype plant of *C. andreettae* (Jenny, 1989), whereas all the parts of the flowers in the species photographed at Ecuagenera are at least two times larger. As the plant photographed by Alex Portilla and the specimen collected by Dodson at El Pangui are quite obviously two different taxa, the final result of Harding's description is simply a chimaera. It is fortunate, however, that the author selected *Dodson 16003* as the holotype of *C. panguensis*, as this specimen belongs in fact to *Aetheorhyncha andreettae*, and the illusory organism described by Harding can be reduced into synonymy of the latter. The name, *C. panguensis*, as originally annotated in 1995 by Dodson on one of his specimens (i.e., *Dodson 16003*, MO), was an intended name for a species still undescribed at that time. After Jenny's (1989) description of the same taxon as *Chondrorhyncha andreettae*, Dodson himself corrected the label of the herbarium specimen with the latter name in 1992. As to the yellow-flowered plant grown at Ecuagenera, whose flowers are among largest in the *Chondrorhynhca* complex, it is described in the following pages as *Pridgeonia insignis*.

BENZINGIA DODSON EX DODSON

2. **Benzingia chocoensis** (Uribe-Velez & Sauleda) Pupulin, *comb. nov*.

Basionym: *Chondrorhyncha chocoensis* Uribe-Velez & Sauleda, New World Orch. Nomencl. Notes 46: 2. 2018.

Uribe-Velez and Sauleda (2018) found that some of the characters of their new taxon would best fit *Stenotyla* Dressler (e.g. the presence of rudimentary pseudobulbs), whereas the narrowly oblong, gray-green leaves were consistent with *Benzingia*. As the authors concluded that the circumscription of the genera of the *Chondrorhyncha* complex proposed by Whitten and collaborators (2005) "cannot resolve the taxonomy" of the group (Uribe-Velez and Sauleda, 2018), they eventually opted for describing this species under a broad concept of *Chondrorhyncha* Lindl.

Nevertheless, the "groups" recovered by the analysis carried out by Whitten et al. (2005) are not only based on a genetic rationale but also present quite a strong consistency from both morphological and phylogeographic points of view (Pupulin, 2019). The species of the more basal groups in the Zygopetalinae, both those with plicate leaves close to *Warrea* Lindl. and those with conduplicate leaves close to *Zygopetalum* Hook., are truly pseudobulbous, so that the presence of probably nonfunctional pseudobulbs in the derivate group of species of the *Huntleya* clade should not be surprising, considering that it represents the ancestral condition in the subtribe. The author has personally observed vestigial pseudobulbs not only in *Stenotyla* but occasionally also in *Chaubardiella* Garay and *Warczewiczella* Rchb.f.

On the other hand, the vegetative and floral characters of *Chondrorhyncha colombiana* are inseparable from the diagnostic features of *Benzingia*, in particular the long-petiolate, narrow, pendent grayish-green leaves; the swept-back, basally inrolled lateral sepals; and the funnel-shaped lip provided with a broad callus almost occupying the entire basal half of the labellum. As the phylogenetic framework recovered by the studies of Whitten and collaborators offers a consistent way to interpret the evolutive patterns in the subtribe and an acceptable model of morphologically diagnosable nomenclature, it is highly advisable not to have both a polyphyletic *Chondrorhyncha* and a paraphyletic *Benzingia* as a result of Uribe-Velez and Sauleda's proposed nomenclature.

3. **Benzingia elvirae** Pupulin, *sp. nov.*

TYPE: ECUADOR. Morona-Santiago: Santiago de Tiwintza, forest remnants along the Río Santiago, 3˚02'18"S, 78˚02'27"W, 400–500 m, 2002, flowered in cultivation in the collection of Ecuagenera at El Pangui, 3 November 2007, *F. Pupulin 6899* (Holotype: CIOA-spirit).[2] Fig. 3, 6B.

Species Benzingiae chocoensis (Uribe-Velez & Sauleda) Pupulin *similis, sed habito ebulboso labello flavo duabus striis et macula magna puniceis notato, callo labelli bilobato apice in duo latera quadridentato plerumque differt*; *a Benzingiae estradae* (Dodson) Dodson *floribus sepalis petalisque albis immaculatis et labello macula punicea notato, petalis rotundis vel truncatis, labello truncato-emarginato, callo labelli denticulato recedit*.

An epiphytic, fan-shaped, cespitose, suberect to pendent *herb* without pseudobulbs, to 20 cm tall. *Roots* flexuous, glabrous, ca. 1 mm in diam. *Stem* abbreviated, completely enclosed by the conduplicate, rectangular, somewhat loose, fibrous leaf sheaths; the sheaths provided with hyaline-scarious margins, to 3 cm long. *Leaves* 5–6, articulate with the sheaths, narrowly elliptic-oblong, subsessile or narrowing into a very short petiole, acuminate, subcoriaceous, matte green, the margins loosely wavy, the central vein strongly prominent abaxially, the upper ones progressively longer, 12–18 × 2.2–3.1 cm. *Inflorescence* lateral, 1 per shoot, an arched-pendent, 1-flowered raceme to 6 cm long; peduncle terete, to 3 cm long, provided with an ovate, subacute, glumaceous, tightly clasping bract ca. 7 × 5 mm. *Floral bract* double, glumaceous, loose; the outer bract broadly

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[2] Even though the Andean Orchid Research Center (Spanish acronym CIOA) formally ceased operations in 2012 with the dissolution of the University Alfredo Pérez Guerrero of Quito, to which it was ascribed, the Center's herbarium and liquid material are conserved in its operational headquarters in Gualaceo, Cuenca, Ecuador, where Ecuagenera keeps them accessible to the public on request. An agreement is pending to transfer the herbarium to the Universidad Técnica Particular of Loja, Ecuador (HUTPL), where the materials would eventually be deposited for permanent curation.

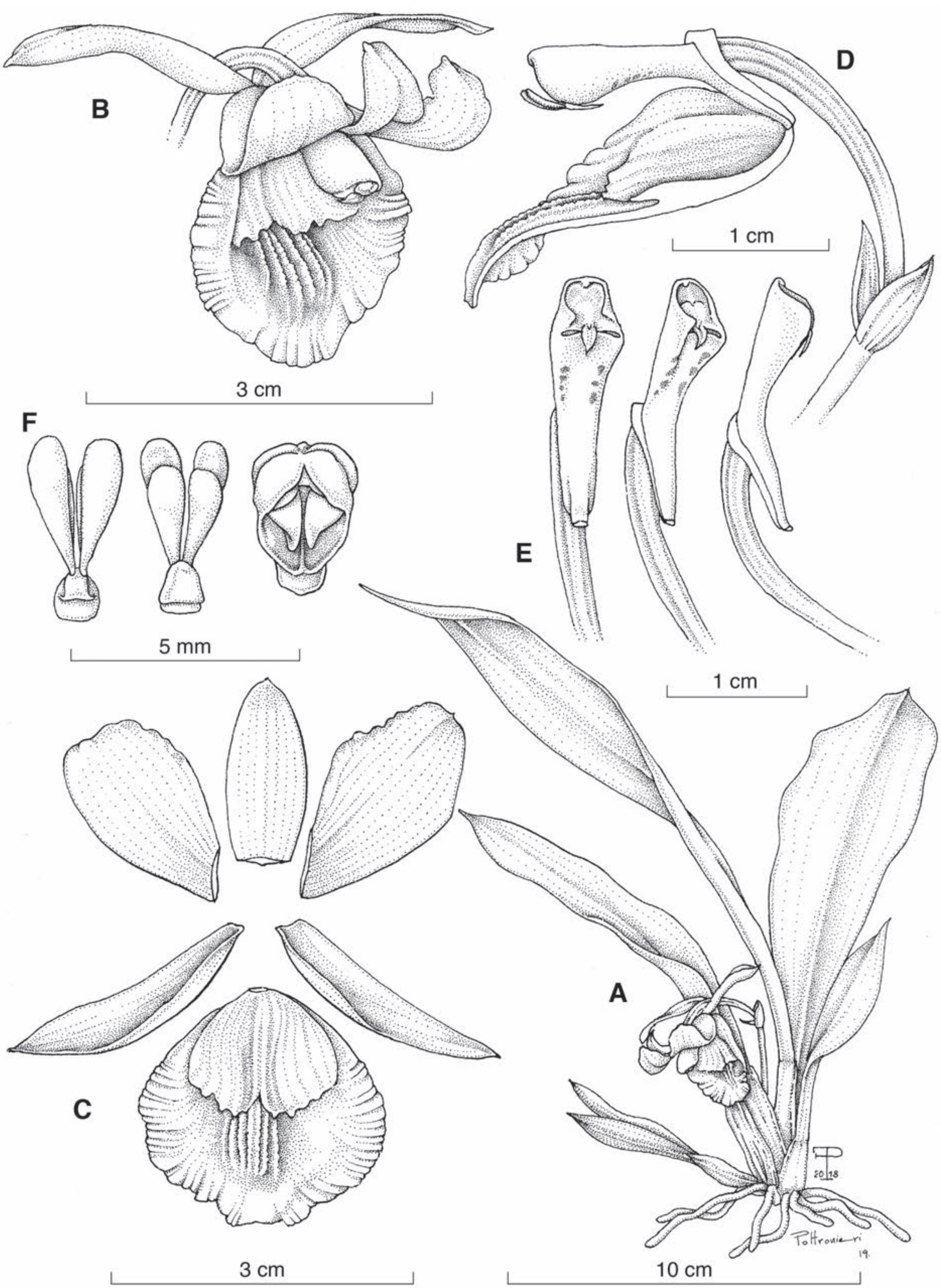


FIGURE 3. *Benzingia elvirae* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view (the lip longitudinally dissected) ; **E**, column, ventral, three-quarter, and lateral views; **F**, pollinarium (two views) and anther cap. Drawn by F. Pupulin and S. Poltronieri from the holotype.

ovate, cucullate, acute, 8 x 6 mm; the inner bractlet smaller, lanceolate, acute, concave, 7.0 × 3.5 mm. Pedicellate *ovary* beret-subclavate, gently arching, round in section, apically provided with rounded, low wings, 2 cm long including the pedicel. *Flowers* spreading, showy, with sepals and petals creamy white, the lip yellow, fading to pale yellow along the margins, the central portion of the disk boldly striped with red, the callus bright yellow faintly suffused with red, the column cream with ventral reddish brown spots. *Dorsal sepal* lanceolate-elliptic, obtuse-rounded, the apex gently reflexed in natural position, 7-veined, 17 × 9 mm. *Lateral sepals* narrowly lanceolate-elliptic, acute to minutely apiculate, spreading-subreflexed, the labellar margin convolute to form a deeply concave-funneled base, 7-veined, 28 × 6–7 mm. *Petals* obliquely obovate, truncate-rounded, subporrect, inserted along the column foot, the apex gently reflexed, the apical margins subundulate, the inner margin irregularly erose, 11- veined, 25 × 15 mm. *Lip* faintly 3-lobed, transversely elliptic-obovate, truncate, slightly convex at apex, concave at the base, 25 × 26 mm, the margins irregularly minutely dentate, undulate-ruffled; the lateral lobes elliptic, basally suberect, spreading at apex, 23–24 mm long; midlobe transversely subrectangular, short, slightly reflexed, ca. 3 mm long; disc with 7 low, irregular, tuberculate lamellae running from the callus to the insertion of the midlobe; callus laminar, subrheniform-rounded, bilobed, excised at the elevated apex, each half irregularly 4-dentate, decurring laterally on the body of the lateral lobes. *Column* semiterete, clavate, distinctly thickened at apex, 1.2 cm long, apically produced into massive, elliptic, parastygmatic wings; clinandrium low, subquadrate, with low rim; anther incumbent; stigma ventral, slit-like; rostellum obtrullate, apically acuminate, 2 mm long. *Pollinia* 4, lanceolate-pyriform, in 2 pairs dorsiventrally superposed, the ventral pair smaller, on a small trapezoidal stipe and a larger, obpeltate-triangular, hyaline visciidum.

Eponymy: the name of the species honors my wife, Elvira Salas Hidalgo, Ph.D., neurobiologist and biochemist, in recognition of her excellence as a scientist and of her patient support of my work.

Distribution: known only from the *locus typicus* in Amazonian Ecuador. To be expected in the adjacent regions of Peru (Map 1).

Habitat and ecology: lowland, tropical wet forest, epiphytic in secondary vegetation along pasture edges. Flowering has been recorded in November–December in cultivation.

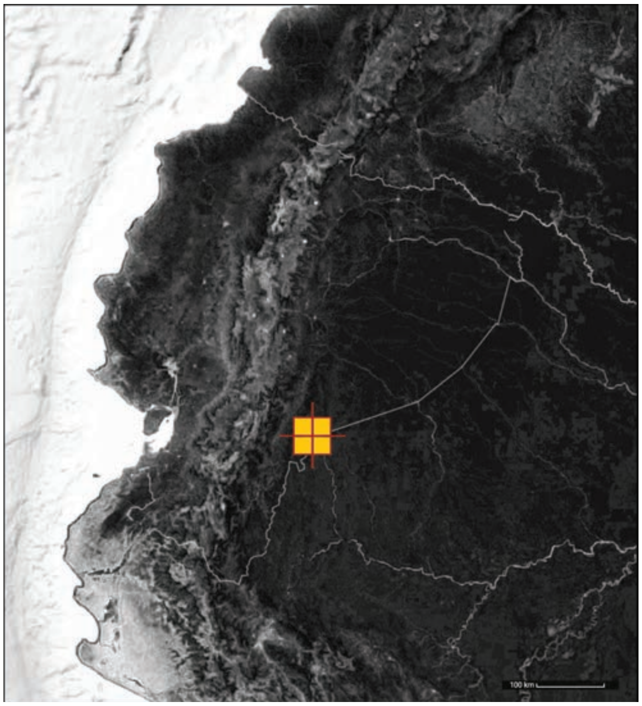
Species of *Benzingia* form a quite heterogenous group, from the point of view of both the vegetative habit and the morphology of flowers. Whereas the delicate-textured, matte, gray-green leaves, with the adaxial surface someway cellular-prismatic, are characteristic of most species, *B. estradae*, *B. hirtzii* Dodson (*typus generis*), and *B. thienii* (Dodson) P. A. Harding have grassy green, subcoriaceous, shiny leaves. Most species of *Benzingia* are truly pendent plants, with the leaves distinctly oblanceolate from a narrow and long petiole, but *B. estradae* and *B. hirtzii* have suberect to erect habit. The flowers of *Benzingia* are mostly resupinate, with the notable exception of *B. hirtzii*, which has nonresupinate flowers on short, erect inflorescences, somewhat reminiscent of those of *Chaubardiella* Garay.

Benzingia elvirae is most similar to *B. chocoensis*, from which it differs by the ebulbose plant (vs. provided with a rudimentary pseudobulb), the flower with a yellow lip (vs. white) marked with two red stripes in the callus area and a large red blotch in front of the callus (vs. suffused with yellow, white), and the bilobed callus with 4 teeth on each side (vs. a single tooth). In habit it resembles *B. estradae* and *B. hirtzii*, with suberect plants and matte green, but not grayish-green, leaves; florally, however, it is very different from both these taxa, and is most similar to *B. reichenbachiana* and, especially, to *B. chocoensis*.

I propose the following key to the species of the genus:

KEY TO THE SPECIES OF *BENZINGIA*

1a. Flower nonresupinate; margins of the lip finely fimbriate . . . . *B. hirtzii*
1b. Flower resupinate; margins of the lip entire to crenulate or serrulate 2
2a. Lip deeply saccate-calciform, held erect toward the column, the basal margins involving the column, the apex provided with a narrow ligule, pointing up 3
2b. Lip concave to shallowly saccate, the lateral lobes erect but not encircling the column, the apex bluntly obtuse to rounded, without terminal ligule, pointing down 5
3a. Mouth of the lip open, wide, broadly elliptic . . . . *B. palorae*
3b. Mouth of the lip narrow, circular 4
4a. The lip yellow, with 2 teeth next to the apical ligule . . . . *B. jarae*
4b. Lip white, without teeth next to the apical ligule . . . . *B. caudata*
5a. Flowers spreading; lateral sepals reflexed, inrolled at the base into a false nectary 6
5b. Flowers campanulate; lateral sepals spread but not reflexed, the basal margins not inrolled into a false nectary 9
6a. Lip cymbiform, the distal margin involute . . . . *B. thienii*
6b. Lip spreading, the distal margin flat to convex 7
7a. Lateral sepals inrolled at apex forming a hook . . . . *B. reichenbachiana*
7b. Lateral sepals reflexed but straight, not hook-shaped 8
8a. Lip subquadrate when spread, white, suffused with yellow in the callus area; apex of the bilobed callus with a single tooth on each side . . . . *B. chocoensis*
8b. Lip obovate-suborbicular when spread, yellow, suffused with 2 red stripes on the callus and with a red blotch in front of the callus; apex of the bilobed callus with 4 teeth on each side . . . . *B. elvirae*
9a. Lip provided at apex with a distinct, triangular, up-curved lobe . . . . *B. cornuta*
9b. Lip acute to blunt obtuse, without apical ligulate lobe 10
10a. Callus in the basal half of the lip, bilobed excised . . . . *B. estradae*
10b. Callus in the apical half of the lip, 4-toothed . . . . *B. hajekii*



Map 1. Distribution of *Benzingia elvirae* in Ecuador.

Daiotyla Dressler

Typified by *Chondrorhyncha albicans* Rolfe, *Daiotyla* is a genus of four to five species distributed from Costa Rica to Colombia, characterized by the broad, thick, fleshy, two-parted callus at the base of the lip, which extends to about the middle of the blade (Pupulin, 2006, 2009c). The generic name, from the Greek *daio*, divide, and *tyle*, knot, refers to the characteristic shape of the lip callus in *Daiotyla* species (Dressler in Whitten et al., 2005). The molecular analyses carried out by Whitten and collaborators (2005) strongly support *Daiotyla* as sister to *Stenia*, which it resembles in the oblong to oblanceolate, dark green leaves. The same clade also includes *Benzingia* and *Euryblema* Dressler, to which species of *Daiotyla* are similar in their wide, laminar callus. Species of *Daiotyla* occur as epiphytes in shady places in lowland to midmontane, evergreen wet forests at 250–1800 m elevation.

In my monograph of Zygopetalinae for *Flora Costaricensis* (Pupulin, 2010), I treated *Daiotyla albicans* as including two different states, the typical form with the callus tinged with pale yellow (Fig. 4A, 6C), and a form with the callus solidly blotched with purple-red (Fig. 4B, 6D), noting that the two morphs present minor but consistent differences in the shape of the callus and the size of the opening formed by the callus and the ventral surface of the column. As these differences seem to suggest that the flowers of the two morphs utilize a different color lure to attract pollinators and that the size of the lip mouth may effectively discriminate among the visiting insects able to remove the pollinarium (Fig. 4), it is advisable to give the two entities taxonomic recognition.

Daiotyla albicans is typified by a specimen flowered in the collection of Walter Rothschild, Tring Park, England, which was exhibited in 1896 at a meeting of the Royal Horticultural Society and presented as a species of *Batemania* from Costa Rica. Rolfe (1898) described the flowers as "white with a faint tinge of green in places," and the holotype at Kew (K79617) confirms that the callus is of a light color. I therefore propose to give specific recognition to populations with solid purple callus as follows:

4. **Daiotyla rhodotyla** Pupulin, *sp. nov.*
TYPE: COSTA RICA. Cartago: Turrialba, Río Pacuare, without specific locality, from the collection of W. Chacón at San Vito de Java, 14 November 2002, flowered in cultivation at the Lankester Botanical Garden, 19 May 2006, *F. Pupulin 4372* (Holotype: JBL). Fig. 4B, 5, 6D.

Species Daiotylae albicanti (Rolfe) Dressler *similis, floribus magis campanulatis, callo labelli obovato-subquadrato mayore maculis magnis puniceis notato, carina humilis pinguis in disco, faucium ingresso angustiore, columna tenuis alibus minoriibus duobus callis rotundatis in basi fornita, anterhae cucullo ovato apiculato recedit.*

An epiphytic, fan-shaped, cespitose, suberect *herb* without pseudobulbs, to 10 cm tall. *Stem* abbreviated, completely enclosed by the conduplicate, triangular to subrectangular, deeply conduplicate leaf sheaths, the upper 1–2 foliaceous; the sheaths provided with hyaline margins, to 2 cm long. *Leaf* shortly petiolate, conduplicate, obovate-oblong, broadly obtuse to rounded, dark green, with a distinctly protruding adaxial mid-vein, 3.5–7.5 × 2.3–3.0 cm. *Inflorescence* lateral, from the axil of the lower sheaths, 1-flowered; peduncle terete, arched-pendent, to 3 cm long, with a single, triangular, adpressed bract near the base. *Floral bract* double, glumacoeus, conduplicate, loose; the external one broadly ovate, 6 × 5 mm, the internal bractlet ligulate, 4 × 1 mm. *Ovary* to 2 cm long including the pedicel. *Flower* with sepals and petals white to pale cream, the disc suffused yellow, the callus of the lip tinged pale yellow with solid purple blotches. *Dorsal sepal* lanceolate, acute, conduplicate-folded and hooked at apex, 13 × 3 mm. *Lateral sepals* oblanceolate, acute, reflexed, strongly conduplicate-folded, hooked at apex, 21 × 9 mm. *Petals* obovate-elliptic, rounded, notched at apex, 17 × 11 mm. *Lip* obovate, obscurely 3-lobed, rounded-truncate, retuse, the apical margin finely crisped, the basal margins suberect, 23 × 20 mm; basal callus thickened, bilobed, obovate-subquadrate, apically deeply emarginate, ca. 8 × 13 mm; disc with a central, raised, rounded, cushionlike keel running from the apex of the callus to attachment of the midlobe. *Column* semiterete, straight, clavate, ca. 13 × 6 mm, with 2 raised calli at the base and a short foot ca. 2 mm long, produced toward the apex into a pair of triangular, massive stigmatic wings, the ventral surface flat to slightly concave, with transverse, slit-like narrow stigma; the anther incumbent, seated in a shallow clinandrium. *Anther cap* ovate, cucullate, 2-celled. *Pollinia* 4, in 2 pairs of different sizes, on a triangular, brownish, hyaline stipe, scarcely distinct from the ventral, elongate viscidium.

Additional specimens examined: COSTA RICA. Alajuela: San Ramón, Angeles, Cuenca del San Carlos, Zona Protectora Arenal-Monteverde, Río Peñas Blancas, sector Alemán, 900 m, 10.3-84.7500003, 1990-03-20 (flor blanca, labelo con una mancha púrpura en su interior), *E. Bello 2012*

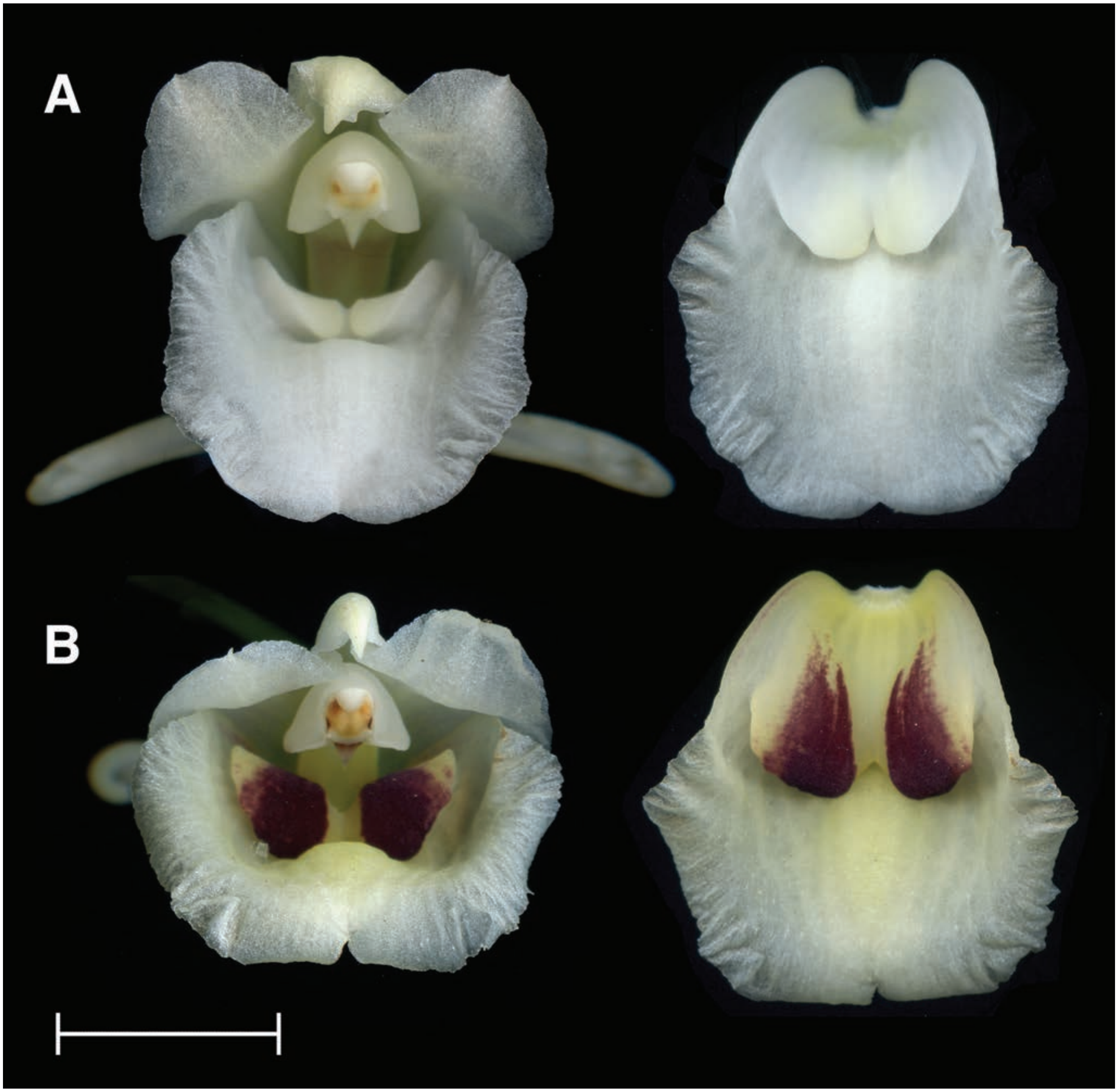


FIGURE 4. **A–B**. Comparison between *Daiotyla albicans* (**A**) and *D. rhodotyla* (**B**). Left, frontal view of the flowers. Right, lip partially spread. A, *Bogarín 6261*; B, *Pupulin 4372*. Scale bar = 1 cm. Photographs by F. Pupulin.

(CR); Alajuela: San Ramón, Peñas Blancas, Cuenca del San Carlos, Zona Protectora Arenal-Monteverde, Río Peñas Blancas, Sociedad IQPSA, Ston's., 800 m, 10.3166667-84.71666723, 1 Mar. 1990 (flor crema, centro del labelo púrpura), *E. Bello 1995* (CR).

Etymology: form the Greek *rhodos*, red, and *tylos*, knot or callus, in reference to the eminently red callus that easily characterizes the species.

Distribution: documented only from Costa Rica, where it is known from the Caribbean slopes of the Cordillera de Tilarán, south to to the medium basin of the Río Pacuare along the northeastern end of the Cordillera de Talamanca, at elevations between 700 and 1000 m (Map 2). The photograph taken in Panama by Arturo Carrillo and identified as *D. crassa* (Dressler) Dressler (in Pfahl, 2018) likely illustrates a specimen of *Daiotyla rhodotyla*, possibly extending the range of the species to the south of Costa Rican border.

Habitat and ecology: like other species in the genus, *Daiotyla rhodotyla* is an uncommon epiphyte, known from a few localities in Costa Rica and possibly Panama. In Costa Rica, it has been recorded from the temperate wet forests and tropical rain forest along the Caribbean watershed of the Tilaran and Talamanca mountain ranges, at elevations between 700 and 1000 m. *Daiotyla albicans*, its sister species, is known from the Central Volcanic Cordillera in Costa Rica

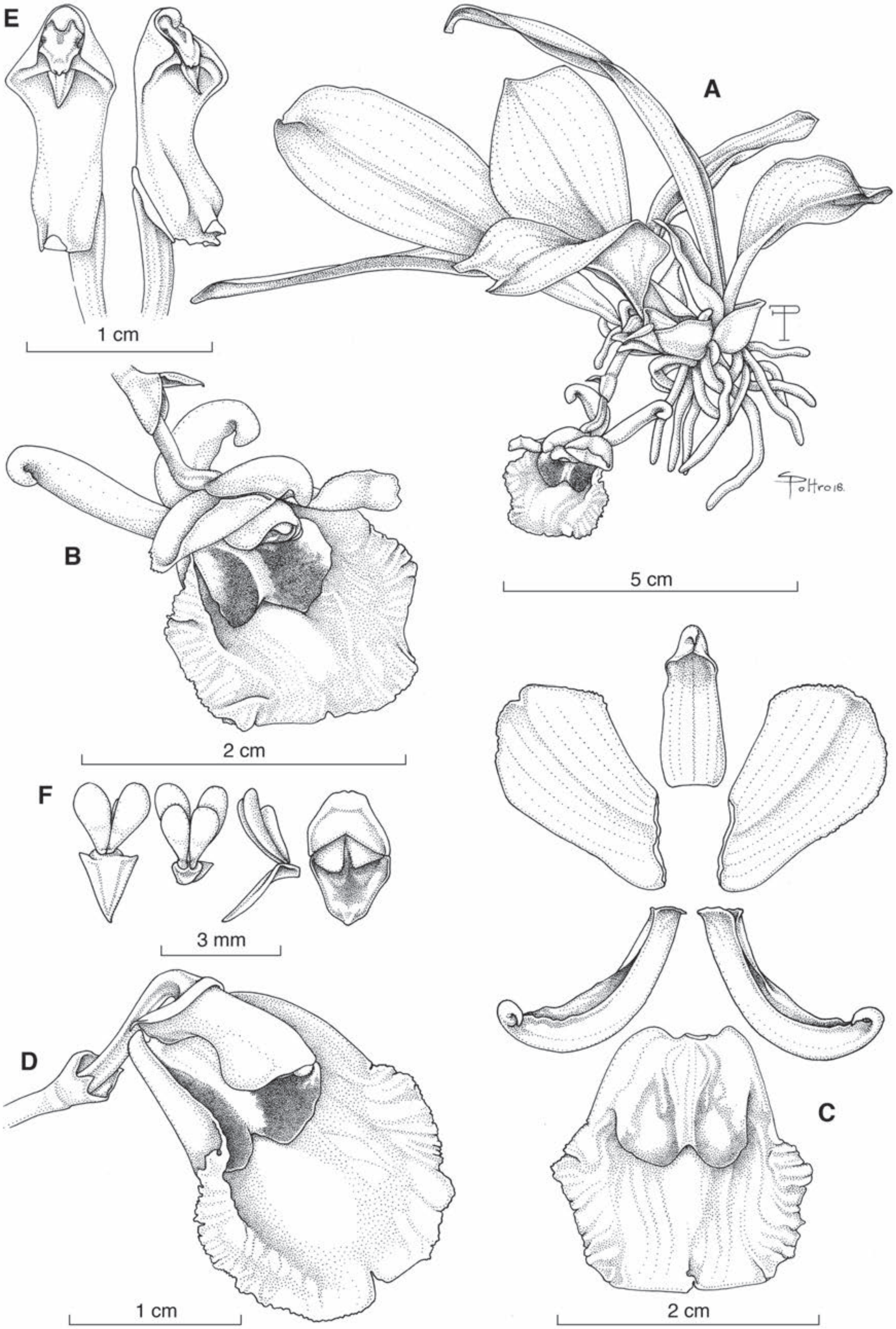


FIGURE 5. *Daiotyla rhodotyla* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, three-quarter view; **E**, column, ventral and three-quarter views; **F**, pollinarium (three views) and anther cap. Drawn by F. Pupulin and S. Poltronieri from the holotype.

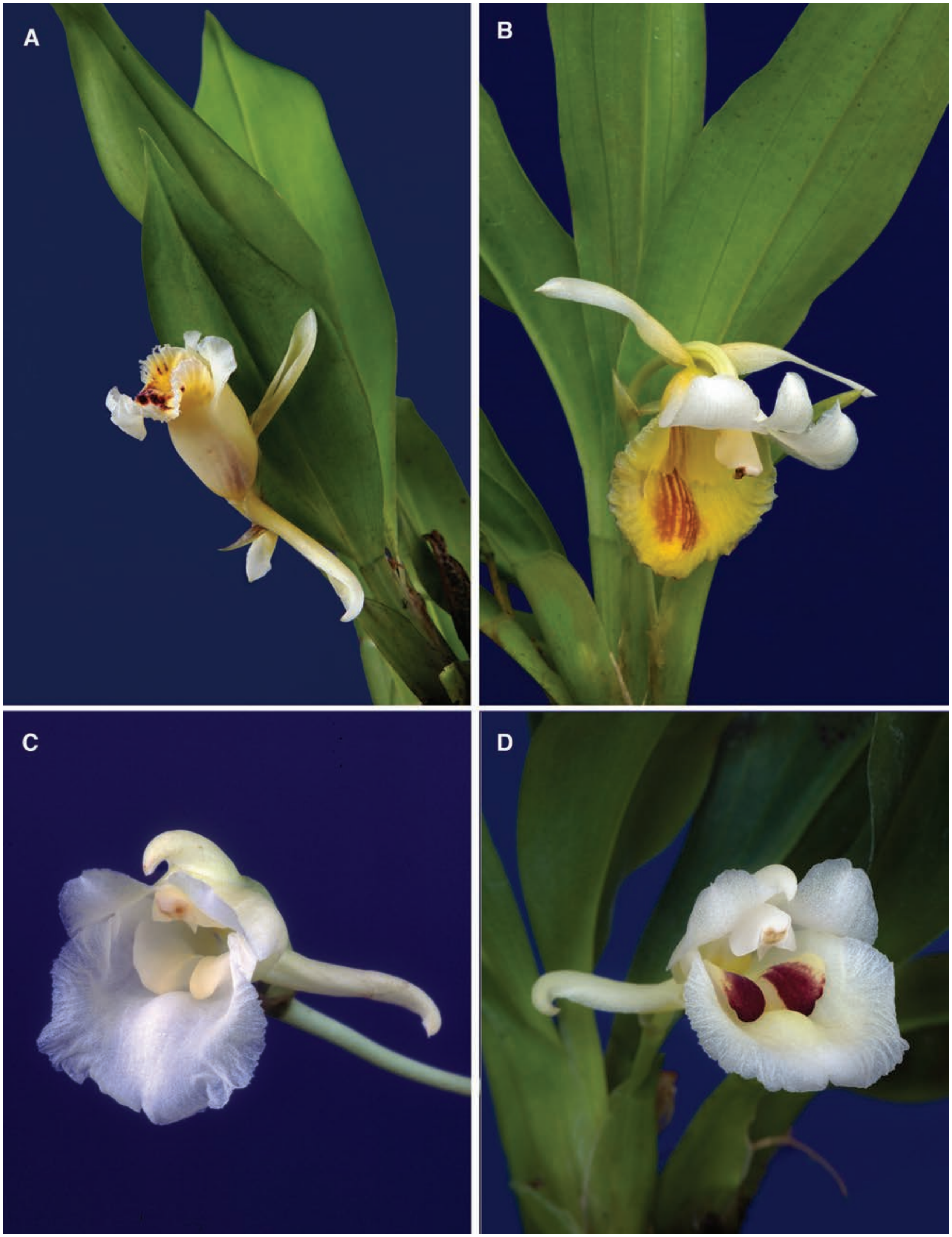


FIGURE 6. **A–D**. Flowers of Zygopetalinae species. **A**, *Aetheorhyncha andreettae* (*Pupulin 6560*); **B**, *Benzingia elvirae* (*Pupulin 6899*); **C**, *Daiotyla albicans* (*Pupulin 3510*); **D**, *D. rhodotyla* (*Pupulin 4372*). Photographs by F. Pupulin.

Map 2. Distribution of *Daiotyla rhodotyla* (squares) and *D. albicans* (circles).

southward to the Atlantic slopes of the Chiriquí massif in Panama (Map 2). In its native habitats, the flowering of the species has been recorded from March to September.

Daiotyla rhodotyla is a close relative of *D. albicans*, with which it shares the general morphology of plant and flower. However, the flower of *D. rhodotyla* is somewhat more "cupped," as the apical portion of the lip does not bend so distinctly as in *D. albicans* (Fig. 4A–B). Furthermore, the callus of the new species is obovate-subquadrate (vs. ovate), notably larger (9 × 11 vs. 7 × 9 mm), and its free portion almost twice as high (6 vs. 3 mm) (Fig. 4A–B). Together with the straighter shape of the lip and the distinctly raised median cushion of the disc, *D. rhodotyla* presents a much more reduced entrance to the "throat" of the flower, which lets us suppose that only smaller-sized bees can reach the chamber found beyond the callus. The callus lobes boldly blotched with solid purple (vs. white) may perhaps play a different role in the visual attraction of potential pollinators. The column of *D. rhodotyla* is notably more slender than that of *D. albicans*, with distinctly narrower stigmatic wings. It also has a pair of raised, round calli on the basal margins, which are absent in *D. albicans*. Finally, the shape of the anther cap is very different in the two species, being ovate and apiculate in *D. rhodotyla* and obovate, apically round, and retuse in *D. albicans* (Fig. 7).

Dichaea Lindl.

The genus *Dichaea*, with some 110 species distributed from Mexico through Central America and the West Indies to Bolivia and Argentina (Pupulin, 2009d), proved to be quite a difficult group for taxonomists. As a fairly common element of the shaded, understory forests all over the Neotropics, *Dichaea* species have been known to Western botanists since the end of the 18th century, when the first species were illustrated and described from French Guyana (Aublet, 1775), Jamaica (Swartz, 1788), and Peru (Ruiz and Pavón, 1798). However, due to the overall similarity of vegetative and floral morphology among the species, as well as a noteworthy plasticity in vegetative characters (Pupulin, 2005, 2007), modern authors have frequently opted for using a few, all-purpose old names in a very broad—and often incorrect—sense (Dressler and Folsom, 2005), or to simply ignore them, favoring the creation of new taxa with little discussion about evolutionary affinities. This situation still obscures the real diversity of the genus in Neotropical floras even in very recent treatments (see, for example, Szlachetko et al., 2012).

Furthermore, the flowers of *Dichaea* are, in general, ephemeral and do not conserve well in dried specimens, and in several species they present temporal activity during anthesis (which mostly endures three to four days) as a response to weather conditions and, probably, to the activity of their potential pollinators. When the climate is rainy, or simply cloudy, it is not rare that the single flower of a *Dichea* just partially opens in the early morning and closes within one or two hours, repeating this behavior until it eventually wilts. Actually, the chances to collect a plant of *Dichaea* in flower, and with a flower open for scrutiny, are quite reduced in the field. The relative abundance of individuals and the relative paucity of flowers explain the large numbers

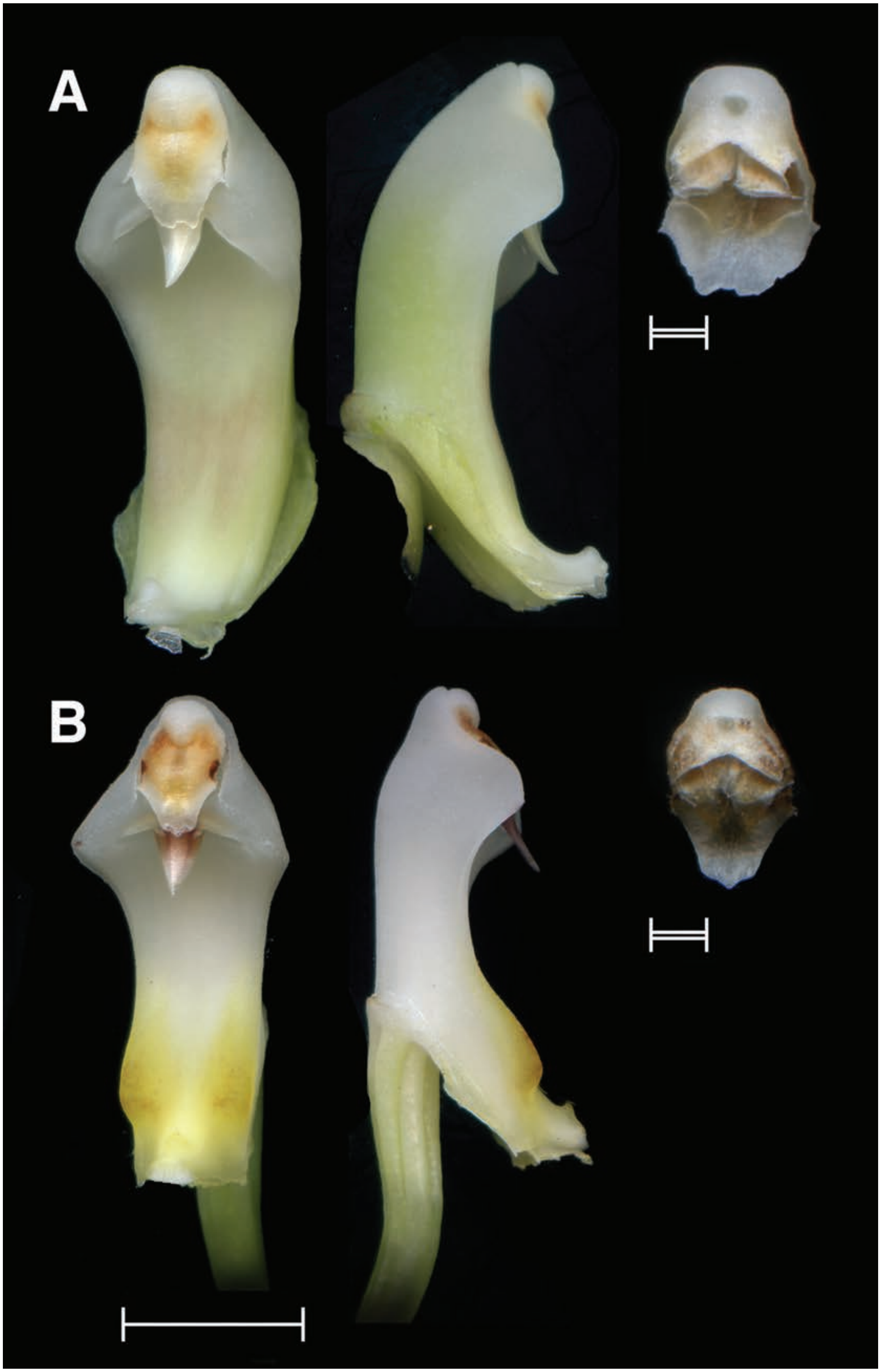


FIGURE 7. **A–B**. Comparison between the columns and the anther caps of *Daiotyla albicans* (**A**) and *D. rhodotyla* (**B**). **A**, *Bogarín 6261*; **B**, *Pupulin 4372*. Single bar = 1 cm; double bar = 1 mm. Photographs by F. Pupulin.

of sterile and undetermined plants of *Dichaea* found in any major herbarium, and perhaps the apparent "rarity" of some species as well.

During the last 10 years, scientists at the Lankester Botanical Garden, University of Costa Rica, have been engaged in a progressive evaluation of the taxonomic status and identity of *Dichaea* species in several American regions, with particular emphasis on the floras of Costa Rica and Ecuador. In the wake of this scrutiny, a number of the examined taxa remain to be fully understood by science or taxonomically clarified. Here I describe two new species of *Dichaea* sect. *Dichaea* from Costa Rica and Ecuador, and two new large species of sect. *Pseudodichaea* from the latter country. Furthermore, I discuss the identity of two other taxa of sect. *Pseudodichaea*; the South American *D. calyculata* Poepp. & Endl. (reducing *D. caveroi* into its synonymy); *D. dressleri* Folsom, previously known only from the original collection made in Panama, of which I present a new record and a complete botanical illustration based on a specimen from Costa Rica; and *D. fragrantissima* subsp. *eburnea*, which I propose here to treat at the specific rank.

DICHAEA SECT. *DICHAEA*

5. **Dichaea elvirae** Pupulin, *sp. nov.*

TYPE: COSTA RICA. Puntarenas: Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1"N, 82°44'30.9"W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 6 Junio 2010, *D. Bogarín & A. P. Karremans 7702* (Holotype: JBL). Fig. 8, 9A–B, 10.

Species ad sectionem Dichaeam pertinens, ab omnibus speciebus generis Dichaeae Lindl. *labello sessili callo magno totam basim replenti, hoc carina media humilis duabusque fossis lateralibus parvis vadis concavis notato distinguitur.*

Epiphytic, caespitose, pendent *herb*, suberect when young, up to 16 cm tall. *Roots* slender, flexuous, whitish, the apices green, ca. 1 mm in diam., produced from the short rhizome and the lower nodes of the stem. *Stem* terete (appearing strongly flattened by the shape of the sheaths), frequently branching, foliaceous, with 2 rows of alternate leaves, completely covered by the base of the leaf sheaths; sheaths subrectangular, conduplicate, ancipitous, somewhat loose, whitish green suffused with rose-purple, the veins neatly visible, marked pale purple, continuous with the leaf (non articulate). *Leaves* narrowly lanceolate, acute, minutely and finely apiculate abaxially, the midvein quite prominent on the underside, pale to medium green, sometimes suffused with pale purple on the lower surface, particularly on the midvein, the margins slightly convolute, minutely ciliate toward the apex, 2.0–3.2 × 4–6 mm, axially twisted to arrange dorsiventrally parallel to the stem, nonarticulate to the sheaths, so drying and rooting in place when old, eventually dissolving. *Inflorescence* single-flowered, produced singly or in groups of 2–3 flowers opening simultaneously or subsimultaneously, exerted from the axils of the leaves and flowering under the foliage, ca. 1 cm long; peduncle terete, provided with a minute, basal, triangular bract ca. 2 mm long. *Floral bract* double, glumaceous, the outer bract broadly ovate, subacuminate, cucullate, 4.6 × 3.3 mm, the inner bractlet narrowly lanceolate, 2.5 × 0.5 mm. Pedicellate *ovary* terete-subclavate, round in section, echinate, 2 mm long, completely covered by dense, long, soft, papillose hairs, becoming stiff from a rounded, cuspidate base during maturation of the fruit. *Flowers* small for the genus, not completely spreading, exhibiting temporal activity during the 3–4 days of anthesis, the sepals and petals pale greenish yellow, flushed with chestnut brown along the veins, abaxially longitudinally flushed with brown along the middle, the lip white, the proximal half bright yellow, the column white with purple bands on the sides of the stigmatic cavity, the anther white, blotched with red on the sides of the apical margin or completely red. *Dorsal sepal* ovate acute, abruptly subacuminate, concave, the margins irregularly and minutely ciliate, 5-veined, the midvein keeled and microscopically erose abaxially, 4.8–5.0 × 3.0–3.2 mm. *Lateral sepals* obliquely asymmetrically ovate, acute, concave, the margins irregularly and minutely ciliate, 7-veined, the midvein keeled and microscopically erose abaxially, 5.2–5.8 × 3.3–3.5 mm. *Petals* lanceolate, abruptly subacuminate, the margins minutely ciliate, 3-veined, 5.0 × 2.6–2.8 mm. *Lip* sessile, obscurely 3-lobed, the hypochile transversely elliptic, fleshy-thickened, 3.5 × 5.8 mm, the epichile broadly sagittate-anchoriform, concave, broadly rounded at the apex, provided with a short, obtuse apicule, 5.5 × 2.5 mm, the apical margin microscopically papillose-ciliate, the lateral lobes short, rounded; the basal callus cushionlike, occupying the whole hypochile, bright yellow, 2.7 × 1.0 mm, with a low central keel flanked by 2 rounded, shallowly concave depressions. *Column* hemiterete, short, stout, suberect, 3.2 mm long, provided with a short, triangular, minutely papillose substigmatic ligule ca. 1 mm long; the clinandrium subcucullate, shallow, with thickened walls; the stigma transversely elliptic, the anther incumbent. *Anther cap* transversely reniform, subcucullate, shallowly 2-celled. *Pollinia* 4, transversely elliptic-complanate, in 2 superposed pairs of different size, on a elliptic-pyriform stipe and a triangular, hyaline viscidium. *Fruit* echinate, subspherical, ca. 1 × 1 cm.

Additional specimens examined: COSTA RICA. Puntarenas: Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1"N, 82°44'30.9"W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 20 abril 2010, *A. P. Karremans & J. Gemmel 5359* (JBL); same locality and date, *A. P. Karremans & J. Gemmel 5360* (JBL).

Eponymy: named for my wife Elvira Salas Hidalgo, to recognize her extraordinary contribution improving all aspects of my life and my work.

Distribution: currently known only from the southern, Pacific slopes of the Talamanca mountain range in Costa Rica, where populations have been found at 1700–1800 m elevation (Map 3). Because of the close proximity of the *locus typicus* to the border with Panama, the species is surely to be found in this country as well.

Habitat and ecology: populations of *Dichaea elvirae*

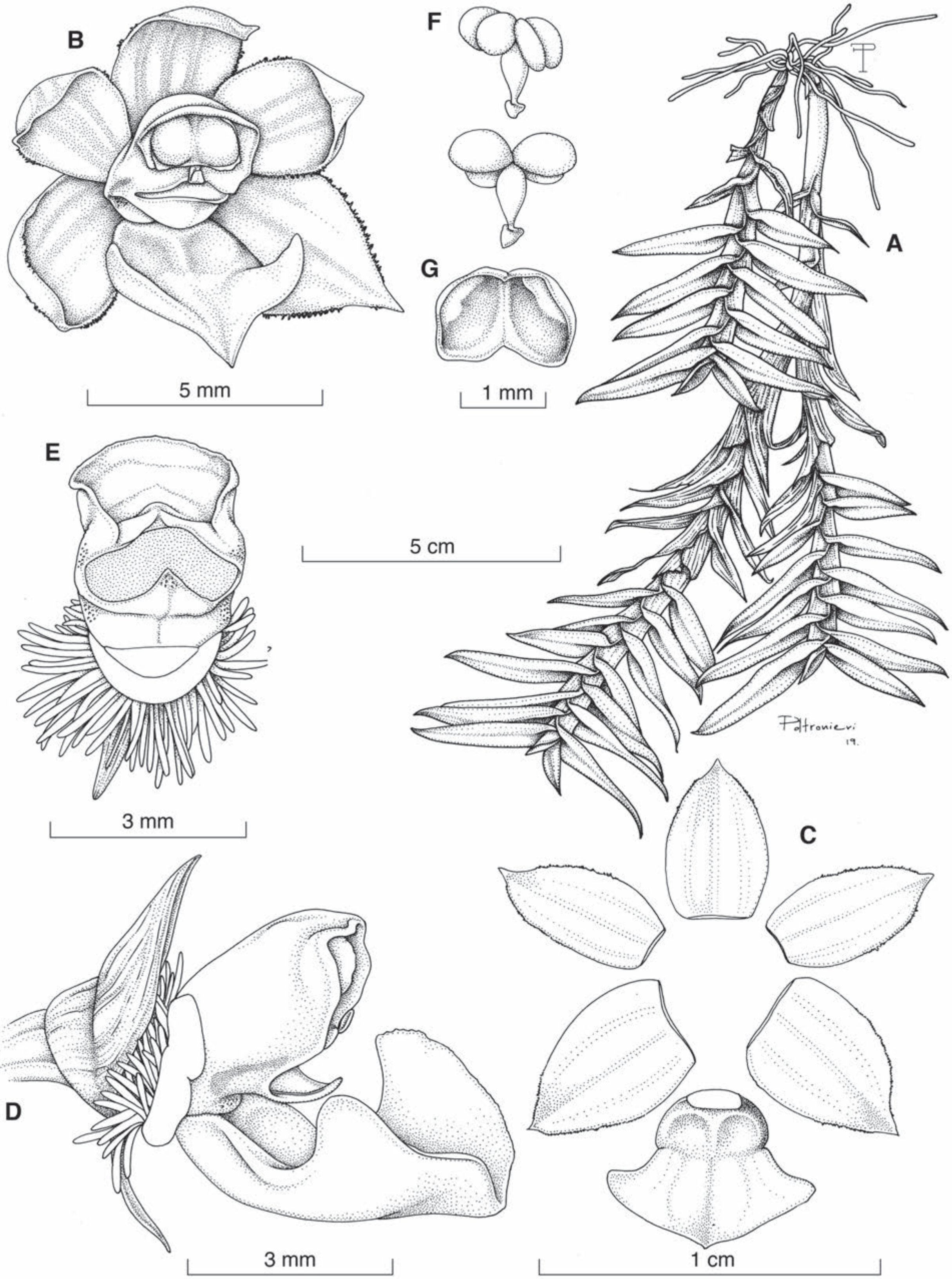
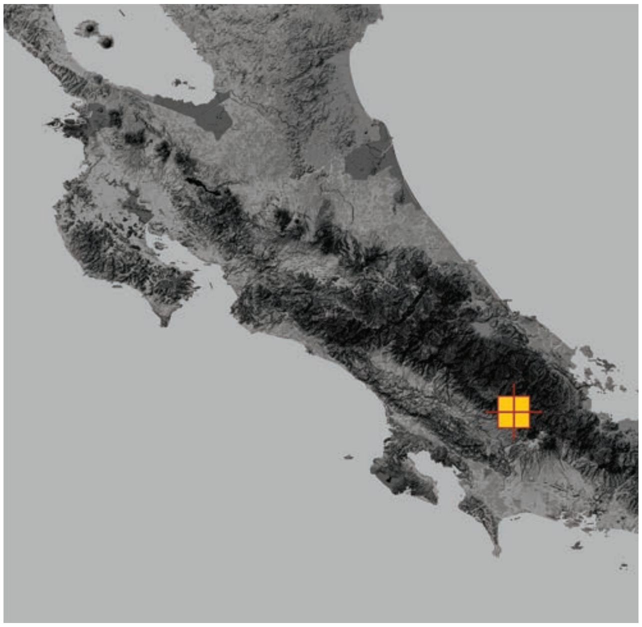


FIGURE 8. *Dichaea elvirae* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, pollinarium (two views); **G**, anther cap. Drawn by F. Pupulin and S. Poltronieri from the holotype.



Map 3. Distribution of *Dichaea elvirae*.

have been found growing epiphytically in shaded and partially exposed spots, in secondary mature vegetation and margins of primary woods, and in the lower mountain rainforest of the southern slopes of Talamanca mountain range in southern Costa Rica. Flowering has been recorded sporadically from August to December, with an apparent peak in August-September.

The flowers of *Dichaea elvirae* are most similar to those of a group of species close to the Jamaican *D. graminoides* (Sw.) Lindl, a species of sect. *Pseudodichaea* that has been traditionally treated as a widespread taxon ranging on the mainland at least from Mexico to the Guyanas and Colombia in South America. The species has never been documented from Costa Rica, and recent work on the "*Dichaea graminoides"* complex (Archila Morales and Chiron, 2015; Chiron et al., 2016) suggests that the species described by Swartz could be a strictly Antillean endemic, whereas several distinct taxa could be recognized in Central America as well as in northern South America. The combination of the habit with nonarticulate leaves (typical of sect. *Dichaea*), together with a lip provided with a large, cushionlike callus that occupies all of the proximal portion of the lip, made *D. elvirae* unique within the genus. The elevated callus presents two shallow, rounded cavities on the sides of a low, median keel that runs up to the callus front to merge into the lamina (Fig. 10). Whereas in most species of *Dichaea* the lip presents a distinct basal claw, which connects with the terminal, transversely triangular lamina, and may be quite long (as in *D. cogniauxiana* Schltr.), in a few taxa, it is distinctly sessile as in *D. elvirae* (i.e., *D. ancorelabia* C. Schweinf., *D. australis* Cogn., *D. campanulata* C. Schweinf., *D. graminoides, D. integrilabia* Valsko, Krahl & Chiron, *D. melunae* Archila & Chiron, *D. peruviensis* D.E.Benn. & Christenson, and *D. trichocarpa* (Sw.) Lindl.). Also, whereas the typical condition for the genus is that the hypochile is flat or slightly concave, a few species present a keel or thickening at the base, sometimes running to the midportion of the lip, where the keel merges with the blade (i.e., *D. camaridioides* Schltr., *D. graminoides* (Sw.) Lindl., *D. hystricina* Rchb.f., *D. longipedunculata* D.E.Benn. & Christenson, *D. morrisii*, *D. tenuifolia* Schltr., and *D. tuerckheimii* Schltr.). Nevertheless, only in *D. graminoides* (which belongs to another section of the genus) is the general morphology of the lip somewhat comparable to that of *D. elvirae*, but in the latter the cushionlike callus completely occupies the hypochile, whereas in *D. graminoides* it is reduced to a central, raised, quite-sharp keel, decurring laterally toward the edges of the lateral lobes.

In the photograph of a *Dichaea* species from Escobar and collaborators' series on Colombian orchids (Escobar, 1990), the lip looks quite similar to *D. elvirae* for the presence of a yellow basal callus on a flower produced by an apparently small-sized plant with nonarticulate leaves. The species was identified as *D. camaridioides* Schltr. (Escobar, 1990:115, upper photo; Morales *et al.,* 2015), but in this species, the hypochile is thin, not thickened, and only in the central part of the disc there is a low keel running to the insertion of the epichile (Mansfeld, 1929).

6. **Dichaea pseudohystricina** Pupulin & Neubig, *sp. nov.* TYPE: ECUADOR. Without collecting locality, flowered in cultivation in the collection of Ecuagenera at Gualaceo, accession *CIOA-000470* (Holotype: CIOA; Isotype: CIOA-spirit) Fig. 9C, 11.

Species sectionis Dichaeae, a Dichaea hystricina Rchb.f. *simillissima, sed caulibus plerumque ramosis, foliis axialiter semper tortis, inflorescentiis multo brevioribus, sepalis abaxialiter glabris, hypochilo multo latiore ecalloso, epichili lobulis lateralibus triangularibus brevis rotundatis.*

Epiphytic, caespitose *herb* forming a mass of suberect to pendent, branched stems, up to 15 cm tall. *Roots* slender, flexuous, whitish, the apices green, ca. 0.7 mm in diam., produced from the short rhizome and the lower nodes of the stem. *Stem* terete (appearing slightly flattened by the shape of the sheaths), frequently branching, foliaceous, with 2 rows of alternate leaves, completely covered by the base of the leaf sheaths; sheaths subrectangular, conduplicate, slightly dilated at apex, long-ciliate along the margins, pale green continuous with the leaf (nonarticulate). *Leaves* lanceolate-elliptic, acute, abaxially provided with a minute apicule, medium green, densely ciliate along the margins, 4.5–9.0 × 2.0–2.5 mm, axially twisted to arrange dorsiventrally parallel to the stem, nonarticulate to the sheaths, so drying and rooting in place when old, eventually dissolving. *Inflorescence* single-flowered, produced singly, exerted from the axils of the upper leaves and flowering under the foliage, 3–4 mm long; peduncle terete, provided with a basal, triangular, adpressed bract ca. 0.5 mm long. *Floral bract* double, glumaceous, the outer bract cumulate, transversely ovate, acute, 1.5 × 2.2 mm, the inner bractlet narrowly lanceolate, 2.0 × 0.5 mm. Pedicellate *ovary* terete-subclavate, round in section, echinate, 2.2 mm long, apically covered by dense, long, soft, papillose hairs. *Flowers* of average size for the genus, spreading, without temporal activity, the sepals and petals cream, transversely striped

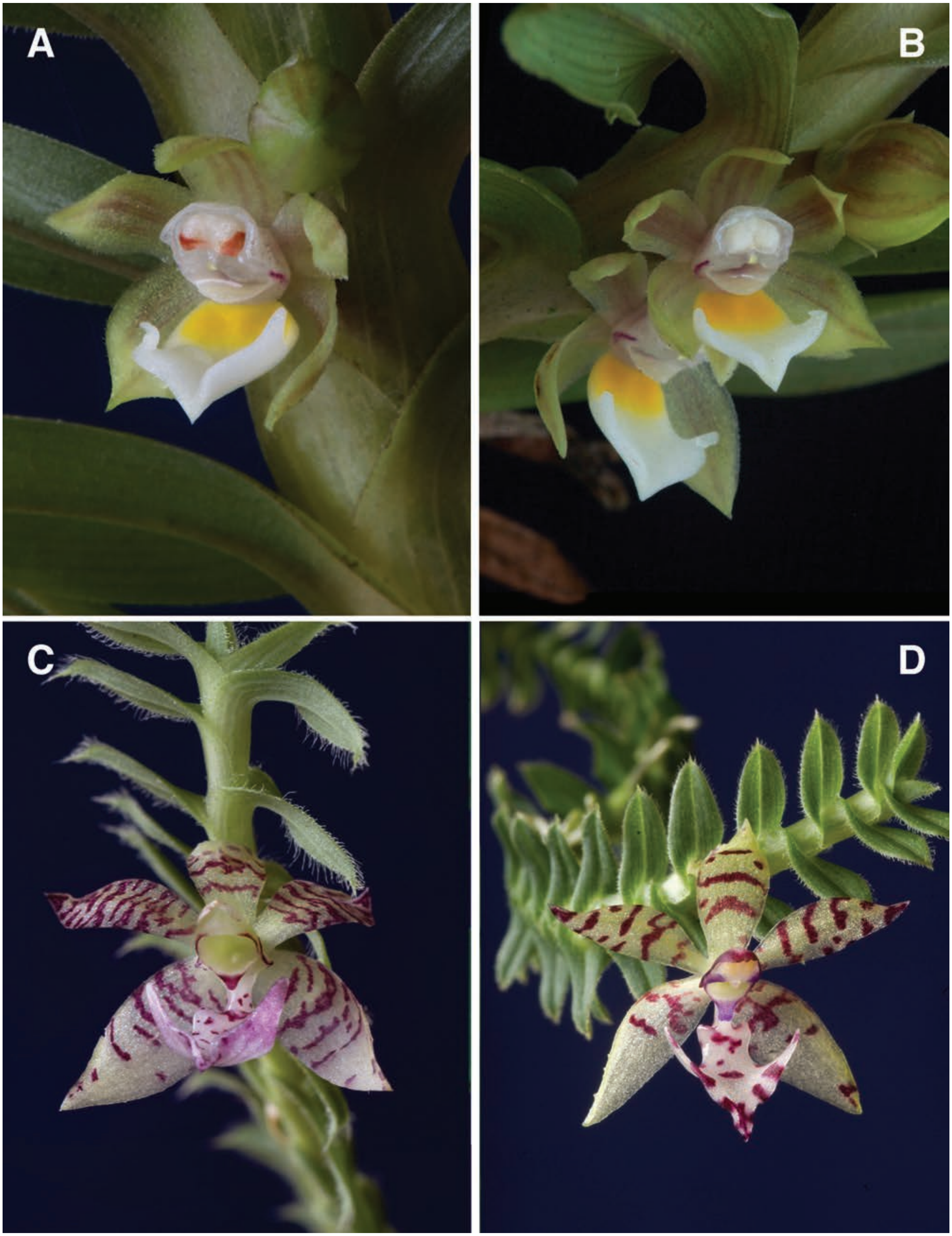


FIGURE 9. **A–D**. Species of *Dichaea* sect. *Dichaea*. **A–B**, *Dichaea elvirae* (*Bogarín 7702* and *Karremans 5359*); **C**, *D. pseudohystricina* (*CIOA-000470*); **D**, *D. hystricina* (*CIOA-000779*). Photographs by F. Pupulin.

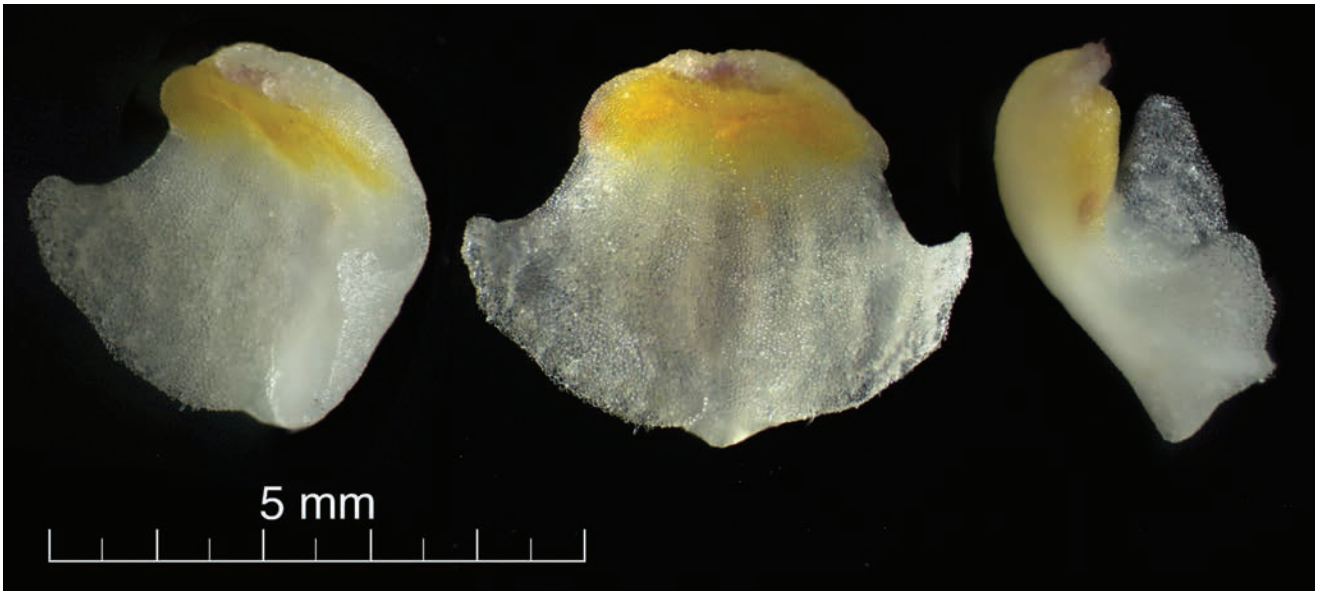


FIGURE 10. Lip of *Dichaea elvirae* in three-quarter, frontal, and lateral views. Microphotographs by F. Pupulin.

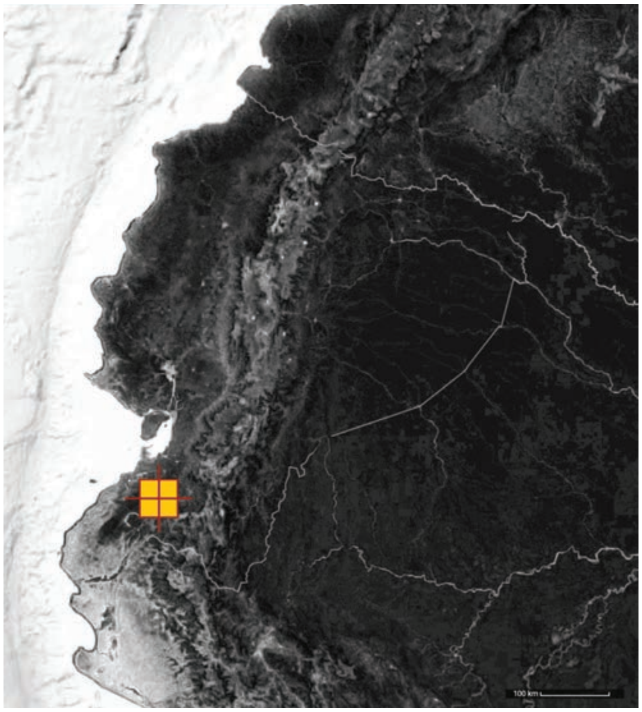
with purple-violet, the lip white, spotted and blotched with violet, particularly toward the ends of the midlobe extensions, the column greenish white, flushed with purple bands on the sides of the stigmatic cavity and the ligule, the anther white, becoming pale brown with age. *Dorsal sepal* narrowly elliptic, acute, concave, 3-veined, 15.0 × 3.0–3.5 mm. *Lateral sepals* obliquely asymmetrically elliptic, acute, concave, 5-veined, 15.0 × 5.5–6.0 mm. *Petals* oblanceolate from a short claw, acute to abruptly subacuminate, 3-veined, 10 × 4 mm. *Lip* shortly unguiculate, 3-lobed, 10 × 10 mm, the rectangular claw ca. 1 mm long, with a longitudinal, low, median keel, the hypochile subrectangular, humerate, thickened, the epichile sagittate-anchoriform, rounded, minutely apiculate, the lateral lobes narrowly triangular, rounded. *Column* hemiterete, suberect, broadest toward the base, 4.5 mm long, provided with a short, triangular, retrorse, minutely papillose substigmatic ligule ca. 0.7 mm long; the clinandrium subcucullate, shallow, with thin, irregularly denticulate walls; the stigma transversely elliptic, the anther incumbent. *Anther cap* transversely broadly elliptic, subcucullate, recuse, shallowly 2-celled. *Pollinia* 4, transversely ovate-complanate, in 2 superposed pairs of different size, on a narrowly ligulate stipe and a pelatet, hyaline viscidium. *Fruit* not seen.

Additional specimens examined: ECUADOR. El Oro: Around Villa Seca, 3˚49'52.54"S, 80˚01'25.28"W, 650 m, growing epiphytically, December 2016, grown in the collection of Ecuagenera at Gualaceo, *H. Medina 198* (CIOA).

Etymology: from the Greek *pseudo-*, "false, resembling," in reference to its deceptive similarity to *D. hystricina*.

Distribution and ecology: known only from the premontane, warm regions along the western slopes of the Andes in southern Ecuador, at about 600–700 m of elevation (Map 4). The species flowers in cultivation from December to March, but it is probable that new flowers can be produced year-round as the new shoots reach maturity.

The discovery of new, cryptic species through comparison of DNA sequences has been evoked as one of the potential by-products of molecular analyses of the Orchidaceae. Actually, the probability of revealing new taxa through a random sampling of individuals, both collected or cultivated, in any given orchid genus is quite low. Even in a genus like *Stelis* Sw., likely one of the most diverse genera in the family with 1282 valid species recognized today, 645 of which have been described in the last 16 years (Damián and Karremans, 2016; Karremans 2016; Luer 2106a,b,



MAP 4. Distribution of *Dichaea pseudohystricina* in Ecuador.

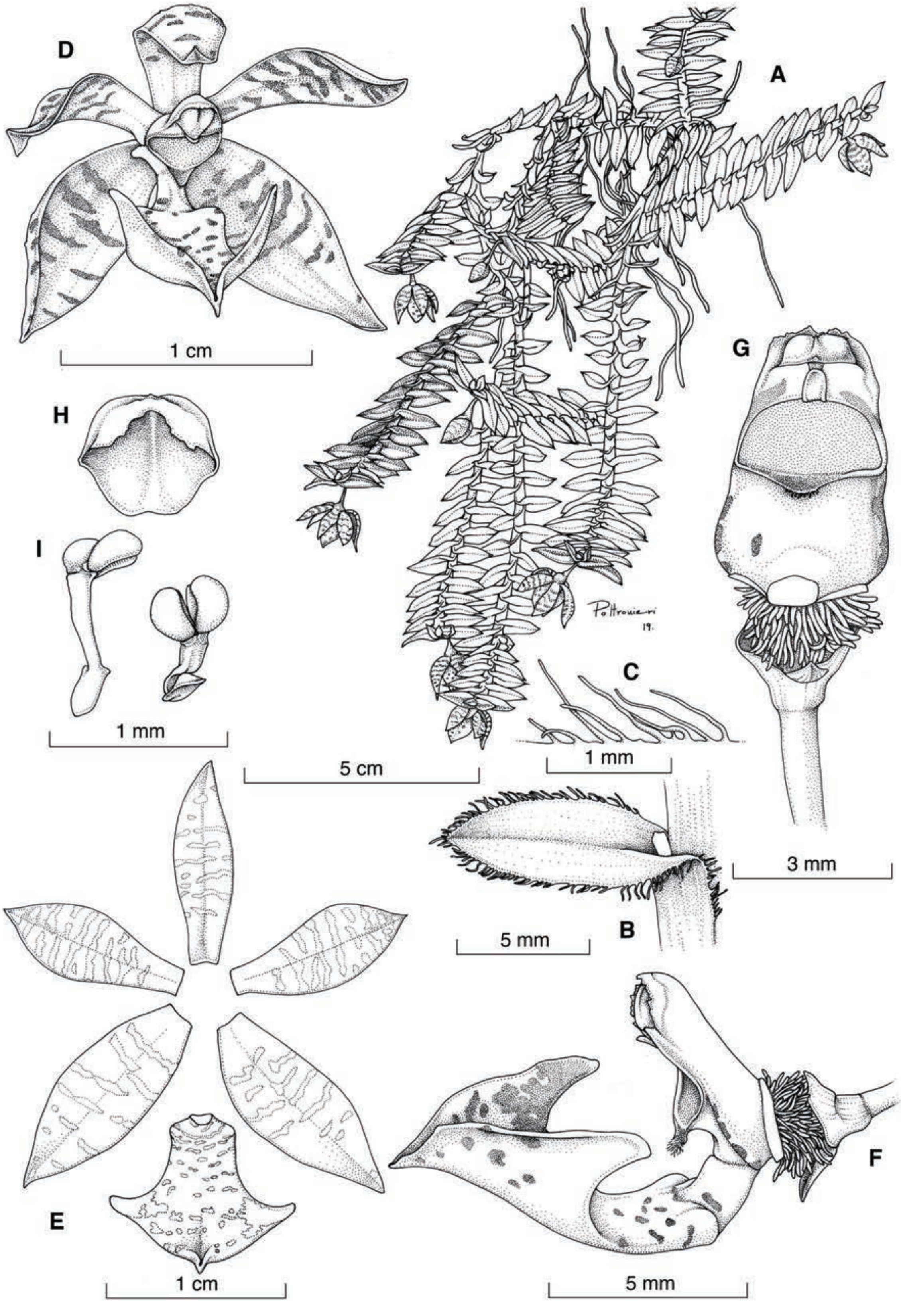


FIGURE 11. *Dichaea pseudohystricina* Pupulin & Neubig. **A**, habit; **B**, leaf; **C**, margin of the leaf; **D**, flower; **E**, perianth; **F**, column and lip, lateral view; **G**, column, ventral view; **H**, anther cap; **I**, pollinarium (two views). Drawn by F. Pupulin and S. Poltronieri from the holotype.

2107a,b, 2108a,b; Collantes et al., 2017; Karremans and Díaz-Morales, 2017), the astonishing number of individual plants would prevent any attempts at finding new species by chance through a blind sample of unassessed specimens. Pupulin et al. (1991) accounted for 295 individuals of *Stelis*, likely belonging to 5 morphospecies, on a single, medium-sized *Protium* sp. tree in the Reserva Forestal de San Ramón, Costa Rica (today Alberto M. Brenes Biological Reserve). Given the frequency per hectare of suitable phorophytes and the size of the Reserve (7800 ha), one may easily assume that this single protected area alone in Costa Rica can host more than 200 million plants of *Stelis*, certainly not a manageable size for any random trial. It was therefore rather surprising that a new, cryptic species of *Dichaea*, at first sight morphologically undistinguishable from the widespread and variable *D. hystricina* Rchb.f., could be effectively discovered thanks to the molecular analyses carried out by Kurt Neubig in the framework of his phylogenetic studies on the genus (Neubig et al., 2009). Whereas the three accessions of *D. hystricina* from Costa Rica grouped together in the phylogenetic tree, two specimens from Ecuador (*Neubig 6–2006* and *Whitten 2329*, both at FLAS) grouped together on a sister branch with high statistical support (as *D.* sp. nov. *1* and *D.* sp. nov. *2* in Neubig et al., 2009, fig. 2–3). I had the opportunity to study one of the plants that served as a voucher for the molecular analyses, and under a closer scrutiny *D. pseudohystricina* may be distinguished from its widespread relative by a set of morphologically diagnosable features. The stems of *D. pseudohystricina* are freely branching, contrasting with the mostly simple stems of *D. hystricina*; the leaves are always axially twisted, whereas in the latter species they are often spreading horizontally from the stem, so that is does not have a distinct “front”; the inflorescences are distinctly shorter (2.2 vs <10 mm); the sepals are glabrous, vs. abaxially covered with sparse warts; the hypochile is much broader, thickened but without the lateral knobs knobs characteristic of *D. hystricina*; and the lateral lobes of the epichile are triangular, rounded, vs. narrowly triangular-filiform, acuminate, and retrorse.

Populations of the true *Dichaea hystricina* also exist in Ecuador. In the collection of Ecuagenera at Gualaceo, I documented a specimen that vouchers the species for that country:

ECUADOR. Esmeraldas: El Cristal, *legit* L. Lapo, 2000, accession No. CIOA-000779, 17 June 2008, *F. Pupulin 7064* (CIOA) (Fig. 9D).

Dichaea sect. *Pseudodichaea*

The Swedish botanist Olof Peter Swartz (1760–1818) first described from Jamaica a stout plant of *Dichaea* with large, articulated leaves and large, fleshy flowers in 1799, as *Cymbidium muricatum* (Swartz, 1799, 1806). The relatively poor specimen conserved among the primary set of Swartz’s collections at the Swedish Museum of Natural History in Stockholm favored a general misunderstanding of his specific concept, and the name *Dichaea muricata* (Sw.) Lindl. was subsequently utilized in floristic treatments all over the Neotropics to refer to completely different species, belonging to a different section of the genus *Dichaea*. With the discovery of a perfect type specimen among the Swartzian collections kept in the Reichenbach Herbarium in Wien (Pupulin, 2008), it became obvious that the traditional interpretations of the identity of *Cymbidium muricatum* were untenable and that the name coined by Swartz was the first valid and legitimate name for the species known in taxonomic literature as *D. morrisii* Fawc. and Rendle (1910), whose type also come from Jamaica. In order to avoid the necessity of correcting the established nomenclature used in the floristics of the Neotropical region, as well as the hundreds of specimens of large *Dichaea* of sect. *Dichaeopsis* annotated in the herbaria around the world, the latter name was conserved against the original one proposed by Swartz (Dressler and Folsom, 2005). With a proper typfication of *Cymbidium muricatum* at hand, it became also clear that the diversity of *Dichaea* of sect. *Dichaeopsis*, relative to the identity of populations with tall plants and large flowers, had been grossly underestimated. In 2006, Robert Dressler and collaborators described two new Mesoamerican taxa of *Dichaea* with caducous leaves, *D. globosa* Dressler & Pupulin and *D. fragrantissima* subsp. *eburnea* Dressler & Pupulin (Dressler et al., 2006). The authors favored at that time the treatment of populations with immaculate flowers as a subspecies of *D. fragrantissima*, but the study of literally hundreds of individuals, and the documentation of a large number of them, without finding any evidence of intermediate forms blending into subsp. *fragrantissima* convinced me that the common taxon widespread on the Atlantic forest from Costa Rica to Panama deserves specific recognition. I am recognizing it here at the specific rank as follows:

7. **Dichaea eburnea** (Dressler & Pupulin) Endrés ex Pupulin, *comb. et stat. nov.*

Basionym: *Dichaea fragrantissima* subsp. *eburnea* Dressler & Pupulin, Novon 16(3): 340. 2006.

TYPE: COSTA RICA. Alajuela: San Ramón, Res. Biol. A. M. Brenes, fl. in cult. at Jard. Bot. Lankester, 13 June 2000, *M. Blanco 513* (Holotype: USJ). Fig. 12A.

Together with *Dichaea trulla* Rchb.f., this is the most common species of *Dichaea* sect. *Pseudodichaea* along the Caribbean drainage of the Costa Rican cordilleras, from where it ranges south to the Atlantic slopes of the Talamanca mountain range in Panama (Dressler et al., 2006; Bogarín et al., 2014). Both these species with large habit and flowers were beautifully illustrated from Costa Rica in Endrés’s early drawings (Pupulin et al., 2013). Endrés also proposed to his scientific mentor the name “Dichaea eburnea” and prepared a detailed botanical description of the new taxon, but Reichenbach never published it. In describing *D. fragrantissima* subsp. *eburnea*, Dressler et al. (2006) cited among the paratypes a Nicaraguan specimen (*Pipoly 5156*) from Cerro el Hormiguero. At that time, I had not seen the actual specimen at MO, but I realized that this same specimen was illustrated by Hamer in his treatment of the orchids of Nicaragua for *Icones Plantarum Tropicarum* (Hamer, 1982: pl. 654). The drawing by Hamer unequivocally shows a specimen of *D. morrisii*, with flowers marked with violet stripes and the lateral lobes of the lip reflexed. In his chapter

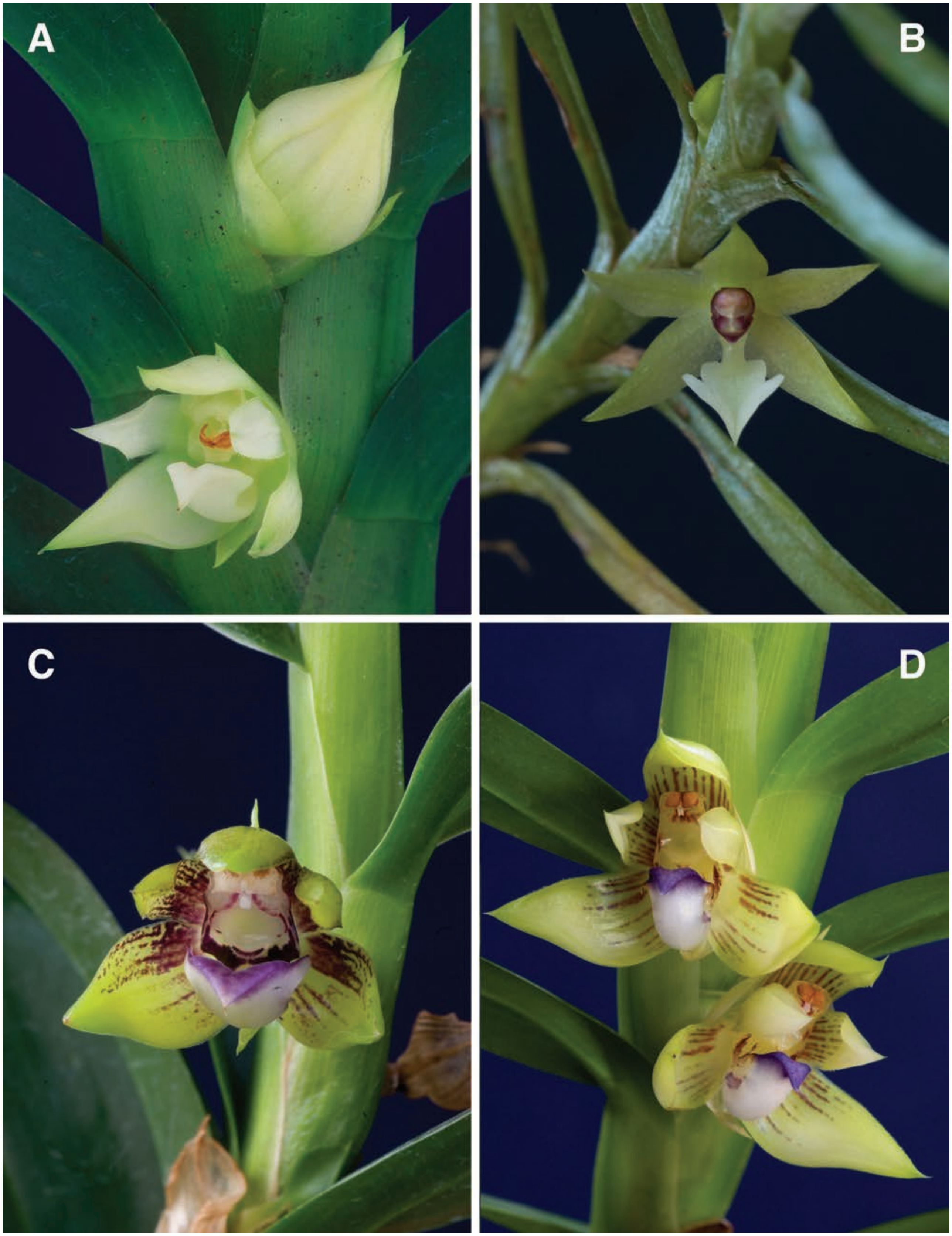
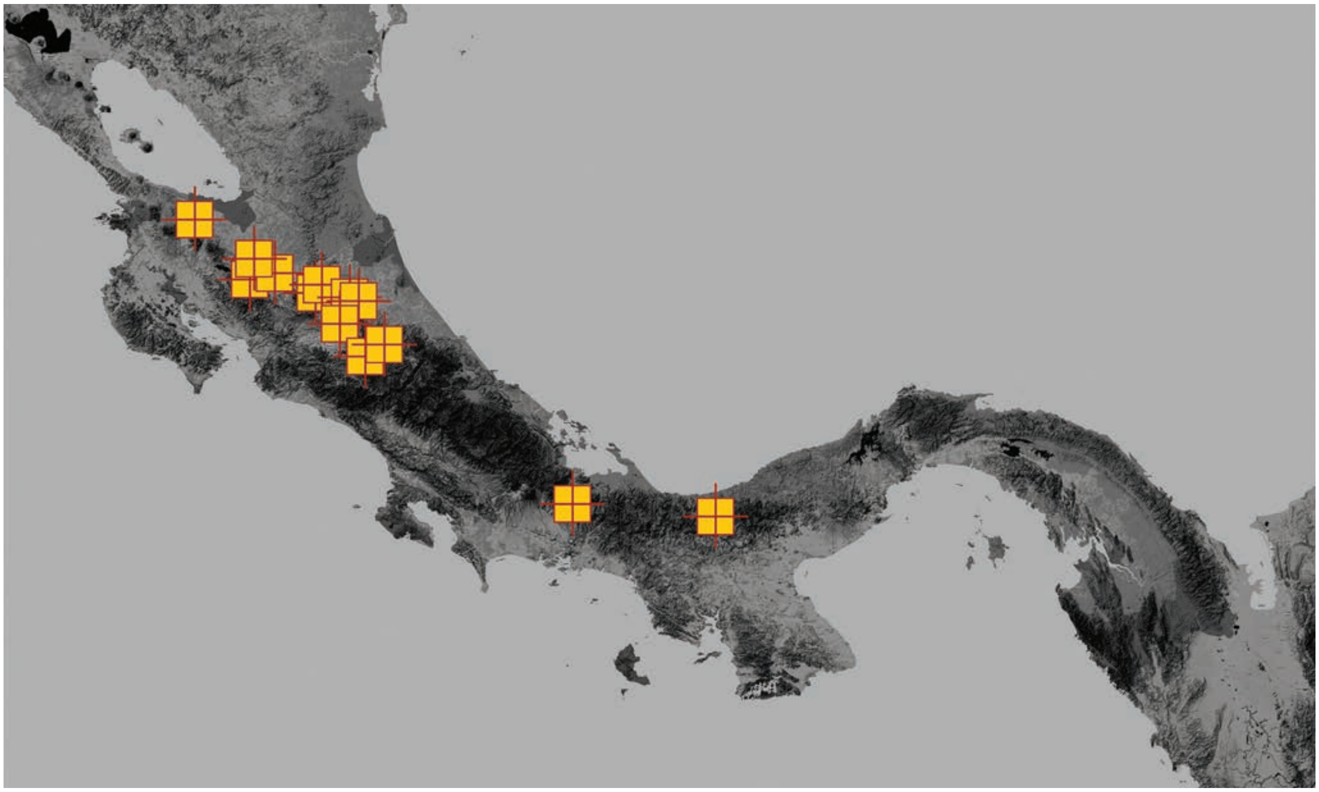


FIGURE 12. **A–D**. Species of *Dichaea* sect. *Pseudodichaea*. **A**, *Dichaea eburnea* (*Blanco 513*); **B**, *D. dressleri* (*Pupulin 8343*); **C**, *D. morrisii* (*Pupulin 6552*); **D**, *D. amazonica* (*Pupulin 6978*). Photographs by F. Pupulin.



Map 5. Distribution of *Dichaea eburnea*.

of Orchidaceae for *Flora de Nicaragua*, Hamer (2001) still records this specimen as the only voucher of this taxon collected in Nicaragua, and in the absence of any further evidence, I exclude the presence of *D. eburnea* from that country.

Distribution: Costa Rica and Panama, at elevations between 200 and 1600 m (Map 5).

I will also take the opportunity to record for the first time the presence of *Dichaea dressleri* Folsom in Costa Rica. Until now exclusively known from the provinces of Chiriquí and Veraguas in Panama, *D. dressleri* is here recorded for the flora of Costa Rica on the basis of a collection from the vicinity of Buenos Aires in the southern region of the country, along the Pacific slopes of the Talamanca mountain chain.

8. ***Dichaea dressleri*** Folsom, Novon 16: 336. 2006.
TYPE: PANAMA. Chiriquí: forest near Fortuna Lake, just beyond bridge, 1100 m, 9 Apr. 1995, J.P. *Folsom11278A* (Holotype: PMA; Isotypes: HNT, MO).

Among the species of sect. *Dichaeopsis*, characterized by the leaves articulated with the sheaths that cover the stem, *Dichaea dressleri* is most similar to *D. gracillima* C. Schweinf., known only from the type collection (Pupulin, 2007, 2010), from which it is distinguished by the shorter leaves and the larger flowers with a long-unguiculate lip and short, retrorse lateral lobes. In habit, it also resembles *D. gomez-lauritoi* Pupulin, from the Caribbean belt of the Central Cordillera in Costa Rica, but the latter species has a muricate ovary (vs. galabrous in *D. dressleri*) and much wider sepals and petals, with a length:width ratio close to 3:7 (vs. 2:8), a lip cuneate at the base (vs. distinctly humerate), and a white gymnsotemium provided with an upward, apically hirsute ligule (vs. solid purple, the glabrous ligule projecting downward).

Dichaea dressleri is illustrated here on the basis of the following material:

COSTA RICA. Puntarenas: Buenos Aires, Buenos Aires, between Santa Rosa and Convento, shores of Quebrada Santa María, confluent of Río Cañas, 9°15'3.797"N, 83°22'33.968"W, 824 m, premontane wet forest, epiphytic on trees along the creek, 20 March 2013, *F. Pupulin 8343, D. Bogarín, J. Cambronero & A.P. Karremans* (JBL) (Fig. 12B, 13, 14).

Distribution: Costa Rica and Panama, at elevations between 800 and 1200 m (Map 6).

With the additions of *Dichaea elvirae* and *D. dressleri*, as well as the recently described *D. auriculata* Pupulin & Karremans (in press) to the species recorded for the flora of Costa Rica, it could be useful including them all in a key to the species of the genus in Costa Rica:

Key to the Costa Rican Species of *Dichaea*

1a. Plants with articulate leaves, eventually deciduous; the peduncle usually straight; the hypochile of the lip glabrous 2
1b. Plants with persistent leaves, rotting in place; the peduncle usually geniculate; the hypochile of the lip frequently ciliate along the margins . . . .(sect. *Dichaea*) 15
2a. Ovary glabrous 3
2b. Ovary muricate . . . . (sect. *Pseudodichaea*) 8

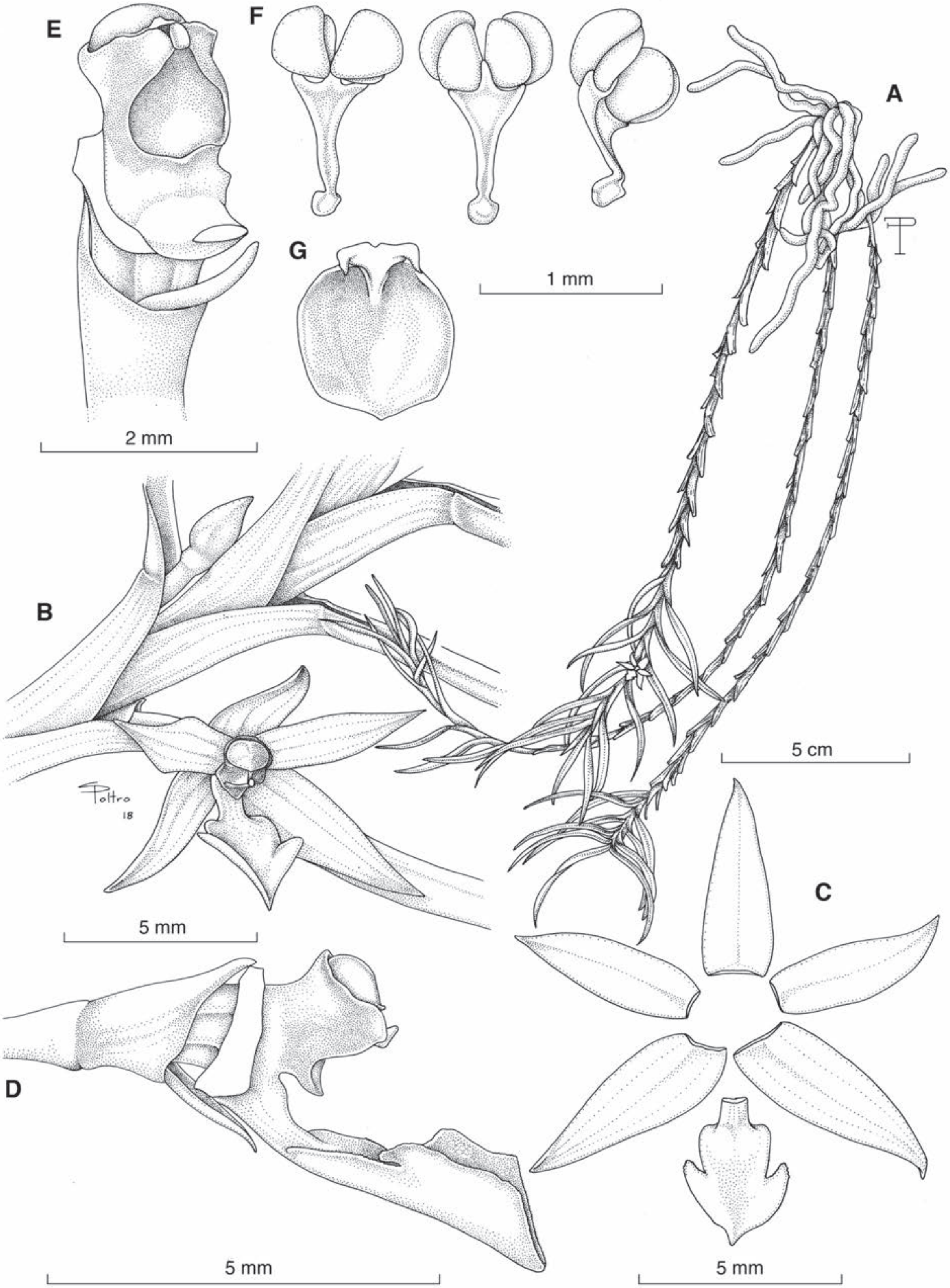


FIGURE 13. *Dichaea dressleri* Folsom. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, frontal and three-quarter views; **F**, pollinarium (three views) and anther cap. Drawn by F. Pupulin and S. Poltronieri from *Pupulin 8343* (JBL).

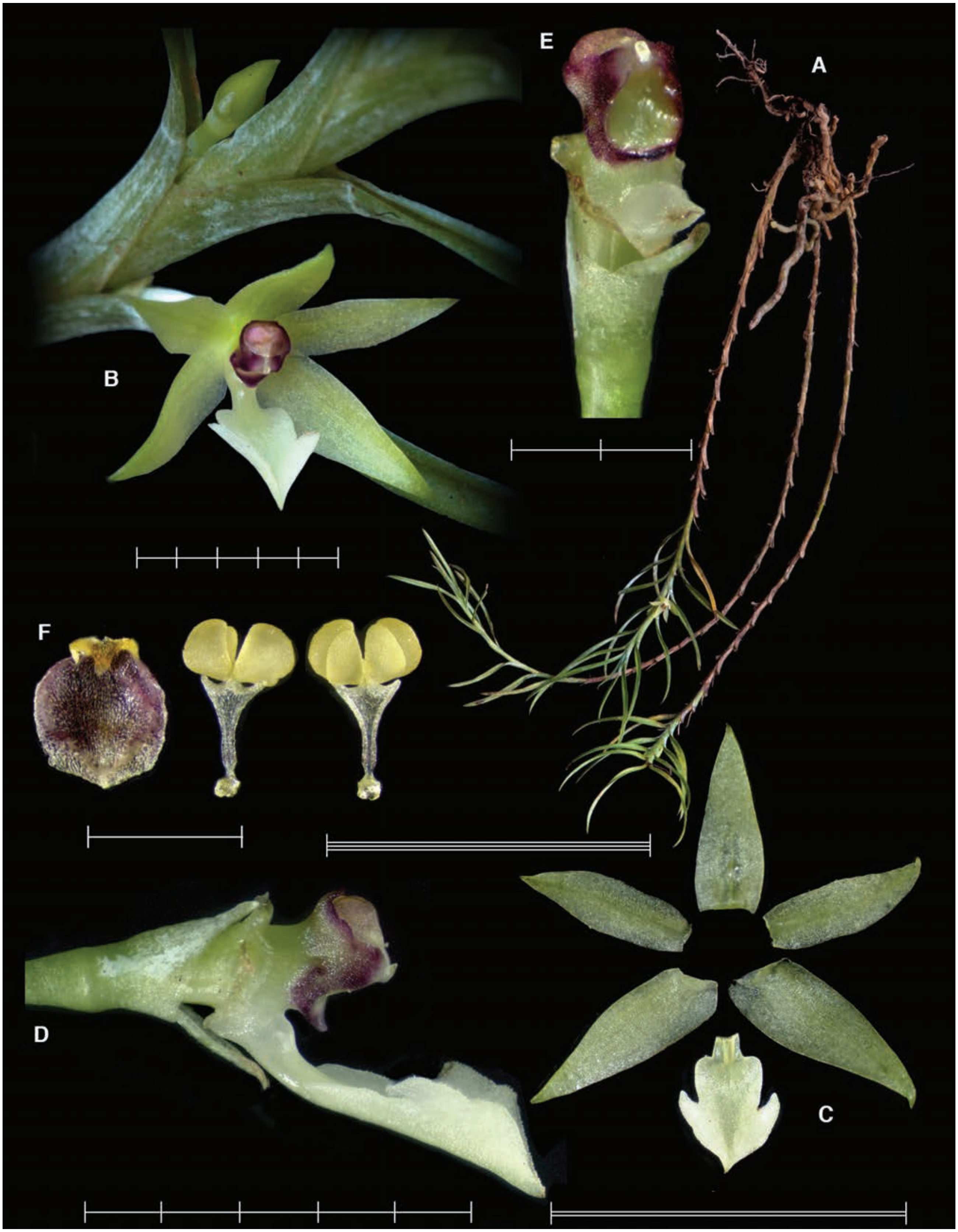


FIGURE 14. Lankester Digital Composite Plate of *Dichaea dressleri* Folsom. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, frontal and three-quarter views; **F**, pollinarium (three views) and anther cap. Single bar = 1 mm; double bar = 1 cm; triple bar = 1 dm. Prepared by F. Pupulin from *Pupulin 8343* (JBL).

Key to the Costa Rican Species of *Dichaea* cont.

3a. Stems flattened; roots thick, produced only at the base of the stem; leaves ovate-elliptic, >7 mm wide 4

3b. Stems terete; roots slender, basal and caulinar (the latter often cryptic within the leaf sheaths); leaves narrowly ligulate, <5 mm wide 5

4a. Plants spreading to pendent; mature leaves <25 mm long; inflorescences produced in succession; flowers greenish white, variously spotted/blotched with purple-red; petals much wider than sepals . . . . *D. panamensis*

4b. Plants erect; mature leaves >40 mm long; inflorescences produced simultaneously; flowers ivory white; petals smaller than sepals . . . . *D. glauca*

5a. Plant tall, the stems up to 1 m long; leaves >7 cm long . . . . *D. trulla*

5b. Plant small, the stems mostly <25 cm long; leaves <5 cm long 6

6a. Lip with distinct, rounded auricles at the base . . . . *D. auriculata*

6b. Lip sagittate, without basal auricles 7

7a. Lateral sepals asymmetrically ovate, much broader than the dorsal sepal; epichile half the length of the hypochile . . . . *D. gracillima*

7b. Lateral sepals lanceolate, subequal in width to the dorsal sepal; epichile as long as the hypochile . . . . *D. dressleri*

8a. Plants small, with leaves <40 mm long and 7 mm wide; flowers membranaceous, spreading; margins of sepals and petals glabrous 9

8b. Plants large, with leaves >50 mm long and 10 mm wide; flowers fleshy, not completely spreading; margins of sepals and petals ciliate 13

9a. Stems borne suberect to erect, becoming arcuate with age; flowers very fragrant; sepals long-acuminate; epichile as wide as long; infrastigmatic ligule glabrous 10

9b. Stems borne pendent; flowers faintly fragrant or scentless; sepals acute to shortly acuminate; epichile much wider than long; infrastigmatic ligule apically pubescent 11

10a. Flowers ivory white, the stigmatic rim pale rose; flowers boldly blotched with purple; lateral lobes of the epichile triangular . . *D. lankesteri*

10b. Flowers pale pink, spotted purple at the base of sepals and petals, the lip apically rose, the stigmatic rim purple; lateral lobes of the epichile falcate . . . . *D. amparoana*

11a. Leaves >4(to 7) mm wide; flowers sparsely and finely spotted with pink; epichile truncate, the lateral lobes to 1.5 mm long. . . . *D. elliptica*

11b. Leaves <3 mm wide; flowers concolorous white or boldly blotched with purple; the epichile obtuse to acute, the lateral lobes 2–3 mm long 12

12a. Flowers white; sepals <6 mm long; lip with a short claw, 4.5 × 6 mm when spread, the lateral lobes rounded . . . . *D. gomez-lauritoi*

12b. Sepals and petals greenish white blotched with purple, sometimes solidly purple; sepals >6.5 mm long; lip sessile, 6.5 × 7–8 mm when spread, the lateral lobes acuminate . . . . *D. acroblephara*

13a. Lateral lobes of lip <2.5 mm long, oblong from obtuse angles; ligule of column subquadrate, truncate or bifid; petals sublanceolate, narrowly acute, widest basally; flowers ivory white with greenish apices . . . . *D. eburnea*

13b. Lateral lobes of lip >2.5 (to 6.0) mm long, reflexed, acuminate; ligule of column triangular; petals ovate to obovate, widest distally; flowers green marked with red-purple 14

14a. Petals oblong-ovate, widest near middle, acute; claw of lip ligulate, 1–3 mm wide distally, with a distinct callus at base; ligule of column porrect; sepals and petals marked with lines basally. . . . . *D. morrisii*

14b. Petals distinctly obovate, widest above middle, apiculate; claw of lip broadly obovate, 6–8 mm wide distally, without basal callus; ligule of column deflexed; sepals and petals usually blotched, rarely solid green . . . . *D. globosa*

15a. Ovary glabrous 16

15b. Ovary echinate, provided with variously shaped trichomes 17

16a. Plant laxly pendent, the stems rarely branching, the leaves brownish green, undulate along the margins; flowers campanulate, pale green, unspotted; the lip anchor-shaped, with a central, low keel at the base . . . . *D. viridula*

16b. Plant creeping, the stems freely branching, the leaves medium green, with flat margins; flowers spreading, greenish white, spotted violet; the lip ovate, with two lateral, basal calli . . . . *D. tuerckheimii*

17a. Mature plants small, <20 cm long; the hypochile provided with distinct calli 18

17b. Mature plants medium to large, >20 cm long; the hypochile variously shaped, but never with basal calli 19

18a. Margins of the leaves entirely ciliate; the hypochile provided with two lateral, rounded knobs .... *D. hystricina*

18b. Margins of the leaves ciliate only toward the apex; the hypochile provided a base, cushionlike callus . . . . *D. elvirae*

19a. Stems terete, the sheaths tightly clasping 20

19b. Stems flattened, the sheaths more or less loose. 21

20a. Plants pendent, the stems pointing downward; leaves thin-textured; petals obovate . . . . *D. acostae*

20b. Plants often creeping, the stems developing in all directions along tree trunk; leaves coriaceous to succulent; petals ovate to broadly ligulate 21

21a. Roots slender, < 0.5 mm in diam.; leaves coriaceous; base of the hypochile rounded, disk-shaped . . . . *D. trichocarpa*

21b. Roots thick 1 mm in diam.; leaves succulent; base of the lip cuneate . . . . *D. squarrosa*

22a. Apex of the pendent stem upcurving; leaves very thin-textured; flowers mostly produced below foliage; peduncle straight; lip subentire . . . . *D. pendula*

22b. Apex of the pendent stem not upcurving; leaves subcoriaceous; flowers always produced above foliage; peduncle geniculate; lip with distinct lateral lobes. 23

23a. Petals obovate 24

23b. Petals ovate to lanceolate-elliptic 26

24a. Leaves >2 cm long; sepals abaxially aculeate; lip upcurved toward the column; ligule retrorse . . . . *D. dammeriana*

24b. Leaves <1 cm long; sepals abaxially glabrous; lip straight; ligule pointing forward — 25

KEY TO THE COSTA RICAN SPECIES OF *DICHAEA* CONT.

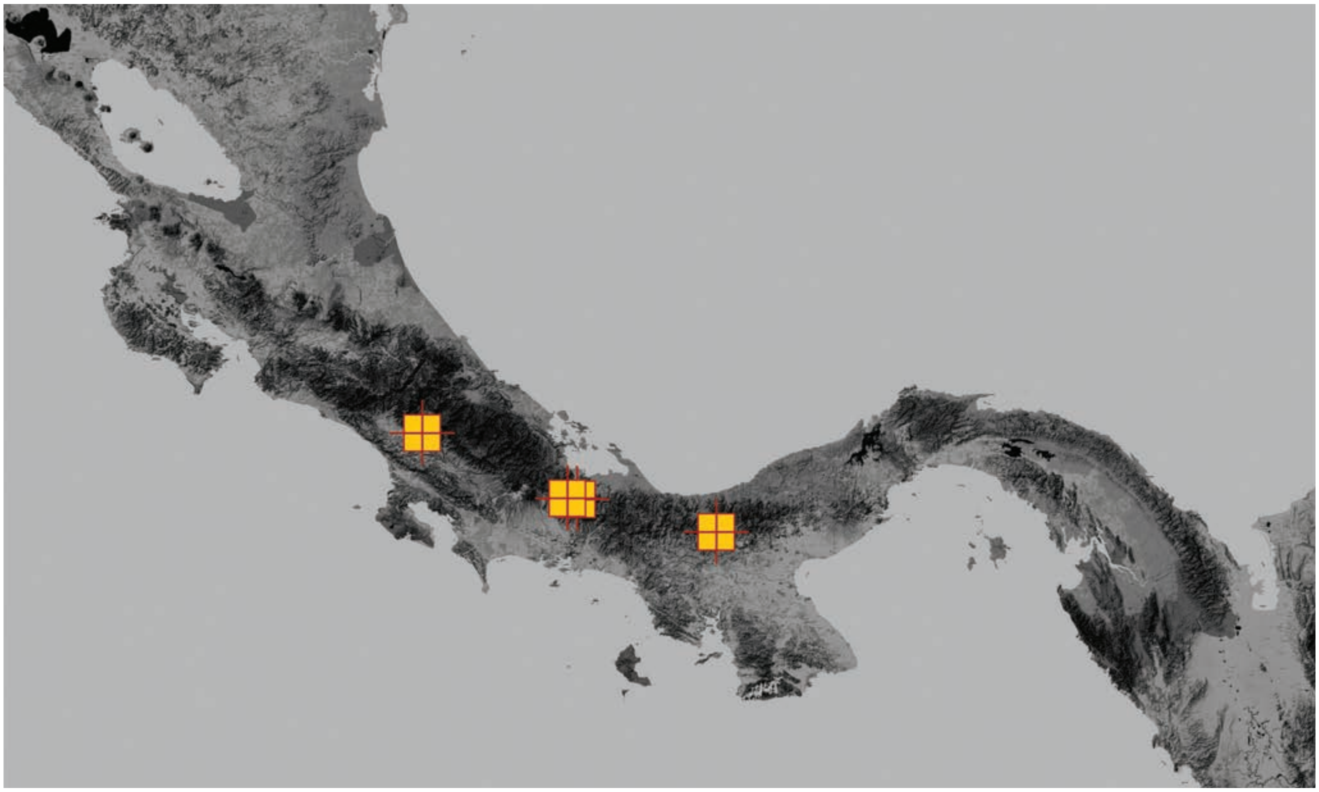
25a. Mature plants forming intricate mats, the stems highly branching; hypochile subacute, adaxially plain . . . . *D. obovatipetala*
25b. Mature plants long, pendent, the stems rarely branching; hipochile subtruncate, minutely apiculate, adaxially provided with low tubercles among the main veins toward the apex . . . . *D. sarapiquinsis*
26a. Column without infrastigmatic ligule . . . . *D. eligulata*
26b. Column with a ligule projecting from the lower lobe of the stigma 27
27a. Leaves with cross veining between main longitudinal veins 28
27b. Leaves without cross veining 29
28a. Leaves medium green with 2–3 cross veins; stems freely branching, plants forming mats; hypochile obcuneate . . . . *D. costaricensis*
28b. Leaves dark olive-brown with many cross veins; stems not branching; hypochile with distinct . . . . *D. filiarum*
29a. Leaves olive brown, mostly retrorse; pedicel to 20 mm long; ligule bifid at apex . . . . *D. oxyglossa*
29b. Leaves medium green, spreading; pedicel to 14 mm long; ligule entire, acute to truncate 30
30a. Flowers with sepals and petals gray-orange, marked purple; lateral lobes of the epichile spreading; ligule truncate . . . . *D. poicillantha*
30b. Flowers with sepals and petals greenish white, often marked violet; lateral lobes of the epichile retrorse; ligule acute 31
31a. Leaves widely elliptic, usually overlapping; sepals spotted violet; hypochile with distinct shoulders . . . . *D. cryptarrhena*
31b. Leaves lanceolate elliptic, not overlapping; sepals mostly concolorous, or with a few spots near the base; hypochile obcuneate . . . *D. similis*

Although the diversity of *Dichaea* species with tall habit belonging to sect. *Pseudodichaea* is likely well understood in the southern region of Central America, where we account for five taxa (*D. eburnea*, *D. fragrantissima*, *D. globosa*, *D. morrisii*, and *D. trulla*), the composition of the Andean contingent still requires some further clarifications. Here both the names, *D. morrisii* and *D. trulla*, have been broadly used to identify any large *Dichaea* with short, elliptic leaves, and long, narrowly ligulate leaves, respectively.

9. ***Dichaea morrisii*** Fawc. & Rendle, J. Bot. 48: 107. 1910; *emend.* in W. Fawcett & A. B. Rendle, Flora of Jamaica 1: 139, plate 30, fig. 13–16. 1910. *Epithecia morrisii* (Fawc. & Rendle) Schltr., Orchis 9. 26. 1915. *Dichaeopsis morrisii* (Fawc. & Rendle) Schltr. In Urban, Symbolae Antill. 8: 146. 1920.

SYNTYPES: JAMAICA. Mt. Moses, 3500 ft., *D. Morris s.n. (Jamaica Plants 2269),* designated by Ackerman (2014: 115) as the Lectotype (BM; Isolectotypes: NJ, K, W); JAMAICA. Hardware Gap, *G. E. Nichols s.n.* (BM; Isosyntypes: NJ, YALE).

In South America, *Dichaea morrisii* has been recorded from Venezuela (Dunsterville and Garay, 1959; Foldats, 1970), Colombia (Ortiz Valdivieso and Uribe Vélez, 2014: 334; Ortiz Valdivieso, 2016), Ecuador (Dodson and Marmol de Dodson, 1980a; Dodson and Escobar, 1993: 180), Peru



MAP 6. Distribution of *Dichaea dressleri*.

(Schweinfurth, 1961; Zelenko and Bermúdez, 2009), and Bolivia (Dodson and Vásquez, 1989; Vásquez et al., 2014). However, both Duntserville's drawings of specimens from Venezuela and the botanical plate prepared for Foldats's treatment of the Orchidaceae for *Flora de Venezuela* illustrate a completely distinct taxon, which differs from *D. morrisii* in almost every floral feature. I have not examined the specimens from Cuzco cited by Schweinfurth (1961: *Vargas 2533*, presumably at AMES), but the photograph of *D. morrisii* in Zelenko and Bermúdez (2009: 110) is misidentified and depicts a still-unnamed species, described hereafter as *D. amazonica*. Finally, the drawing published by Dodson and Vásquez (1989) to voucher *D. morrisii* in Bolivia, with its large, infundibuliform bracts of the peduncle, the short floral bract, and the very long lateral lobes of the epichile, illustrate under this name a species likely corresponding to *D. robusta* Schltr.

I may here substantiate the occurrence of the true *Dichaea morrisii* in Ecuador, on the basis of a specimen from the western slopes of the Andean chain:

ECUADOR. Azuay: road from Puerto Inca to Cuenca, between Corona de Oro and Luz Maria, 02°38'39.9"S, 79°27'00.3"W, 820 m, Pacific watershed of the Andes, litophytic in deep layer of mosses on a steep bank along the roadside, 4 May 2007, *F. Pupulin 6552 & J. Portilla* (CIOA) (Fig. 12C, 15).

Distribution: West Indies (Cuba, Dominican Republic, Haiti, Jamaica, and Tobago, according to Ackerman, 2014), Costa Rica, Panama, Colombia, Ecuador, and possibly Peru.

On the eastern side of the Andes in Ecuador, and likely in Peru, another species of sect. *Pseudodichaea* with large habit and flowers has been treated as *Dichaea morrisii* (i.e., Zelenko and Bermúdez, 2009), but it differs from the latter species in a number of significant features. I propose here to recognize it as a new species with the following name:

10. **Dichaea amazonica** Pupulin, *sp. nov.*
TYPE: ECUADOR. Morona-Santiago: Tumbes, 3°17' 59.6"S, 78°34'26.9"W, ca. 1200 m, collected by H. Medina, December 2000, grown in the collection of Ecuagenera at Gualaceo (stems striped purple), 19 December 2007, *F. Pupulin 6978* (Holotype: CIOA). Fig. 12D, 16.

Species sectionis Pseudodichaeae, Dichaea morrisii Fawc. et Rendl *affinis, caulibus suberectis, vaginis foliarum plerumque purpureo striatis, floribus claviodoribus distincte grandioribus, pallenti ochraceis, sepalis lanceolatis, lateralibus subfalcatis, hypochilo breviore multoque latiore, marginibus basalibus columnae glabris recedit*.

Epiphytic, caespitose *herb*, erect when young, becoming pendent with erect apex when old, to over 1 m long. *Roots* filiform, ca.1.0 mm in diam., exposed at the base of the stem, the caulinar roots completely hidden by the leaf sheaths. *Stems* compressed, simple, 15–110 cm long, 0.4–0.7 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, closely spaced along stem, spreading, membranaceous, narrowly elliptic, subacute to obtuse, abaxially apiculate, medium green, 3.0–5.5 × 1.0–1.5 cm; sheaths loose, strongly complanate, ancipitous, the veins neatly visible, often suffused with purple, 20–25 × 17–20 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, subpatent, 20–22 mm long, provided with a basal, cylindrical, tightly clasping bract, ca. 1 mm long. *Floral bract* double, the outer bract broadly transversely ovate, abruptly subacuminate, 9 × 14 mm, the inner bract linear-lanceolate, acuminate, 12 × 3 mm. *Pedicel* cylindric, 2 mm long. *Ovary* 2.2–2.5 mm long, densely muricate. *Flower* ringent, the sepals and petals pale yellow, shiny, striped with red along the veins in the inner half; the lip white, the hypochile blotched with pale purple, the epichile solid violet on the adaxial side, white abaxially; column yellow, flecked with red on basal wings; strongly clove-scented. *Dorsal sepa*l lanceolate, acuminate, fleshy, concave, dorsally subcarinate, the margins ciliate, 16 × 7 mm. *Lateral sepals* obliquely lanceolate-subfalcate, concave, acute, apically minutely mucronate, dorsally carinate, the margins ciliate, 18 × 1.0 mm. *Petals* lanceolate, with a distinct elliptic bulge on the basal half of the superior margin, acute to subacuminate, the margins hispid-ciliate, 13.0 × 4.5 mm. *Lip* 3-lobed, sagittate, sessile, 10 × 8 mm when spread, the hypochile linear, ca. 8 mm long, 4 mm wide, provided at the base with a central, low, short keel, flushing into the hypochile surface ca. 2 mm; the epichile triangular-sagittate, acute, 4 × 7 mm, the lateral lobes narrowly linear, acuminate, retrorse, to 2.5 × 0.4 mm. *Column* suberect, 11 mm long, with a indistinct foot; the clinandrium shallowly concave, entire; ligule broadly triangular, truncate, ciliate at apex, 1.0 × 1.4 mm. *Anther cap* transversely subrectangular, cucullate, flattened, 2-celled. *Pollinia* 4, ovate-rounded, in 2 superposed pairs of different size, on a cuneate-obflabellate, truncate stipe; viscidium hyaline, rounded, incurved. *Fruit* not seen.

Additional specimen examined: ECUADOR. Without collecting data, a plant from Ecuagenera, flowered in cultivation at Jardín Botánico Lankester, 12 January 2006, *F. Pupulin 5938* (JBL). Fig. 17A.

Etymology: named in reference to the known habit of the new species, on the eastern side of the Andean chain, known in Ecuador and Peru as the "*Amazonía*."

Distribution: currently documented only from the southern, Amazonian region of Morona-Santiago in Ecuador, where several population have been recorded. A photograph in Zelenko and Bermúdez (2009), likely belonging to the same taxon, would extend southward the range of distribution of the species to Peru (Map 7).

Habitat and ecology: an epiphyte of secondary mature and secondary young vegetation along the eastern slopes of the Ecuadoran Andes, close to the Cordillera del Condor, where it has been recorded around 1200 m elevation. The region is characterized by a warm, humid, frequently cloudy climate, which supports a tropical wet forest. The strong scent of eugenol, the major volatile constituent of clove oil, is strongly correlated with euglossine bees pollination.

11. ***Dichaea calyculata*** Poepp. & Endl., Nov. Gen. Sp. Pl. 2: 4. 1838. Fig. 17B, 18.
TYPE: PERU. Crescit cum praecedentibus [… supra arbores Peruviae Orientalis ad Pampayaco]. Floret Julio. *S. Poeppig & L. Endlicher s.n.* (Holotype: W).

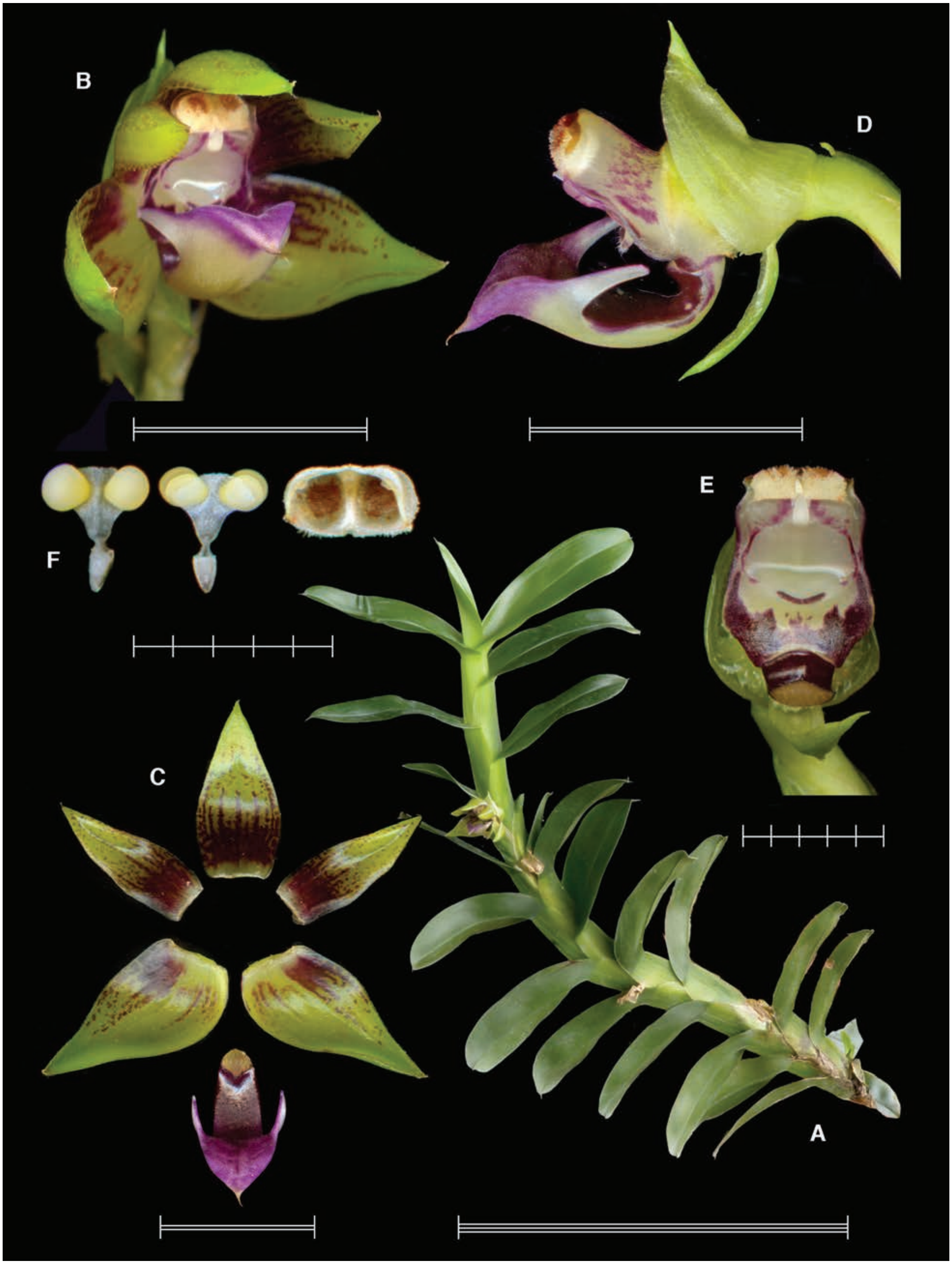


FIGURE 15. Lankester Digital Composite Plate of *Dichaea morrisii* Fawc. & Rendle. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, anther cap and pollinarium (three views). Single bar = mm; double bar = cm; triple bar = dm. Prepared by F. Pupulin from *Pupulin 6978*.

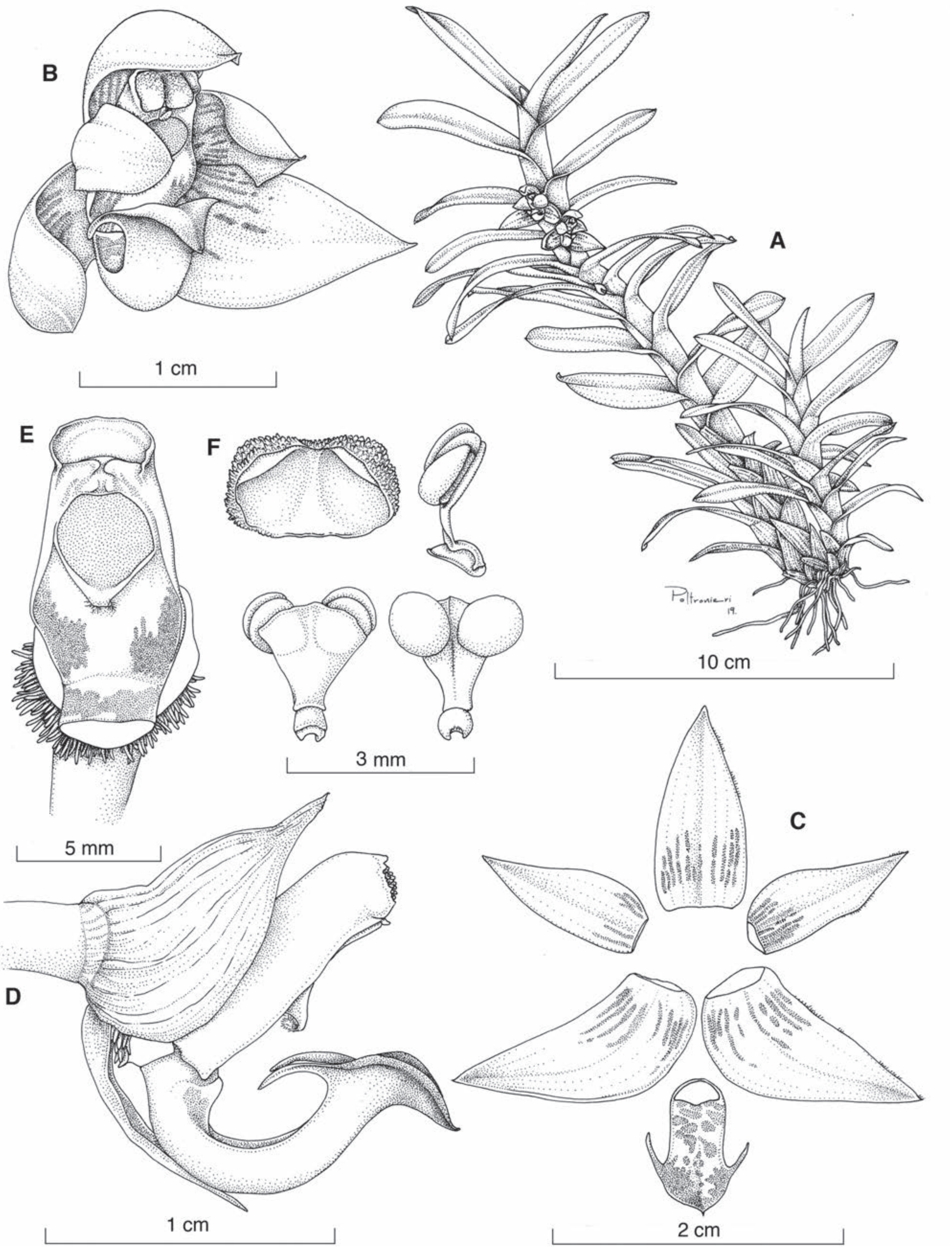


FIGURE 16. *Dichaea amazonica* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral view; **F**, anther cap and pollinarium (three views). Drawn by S. Poltronieri from *Pupulin 5938* (CIOA).

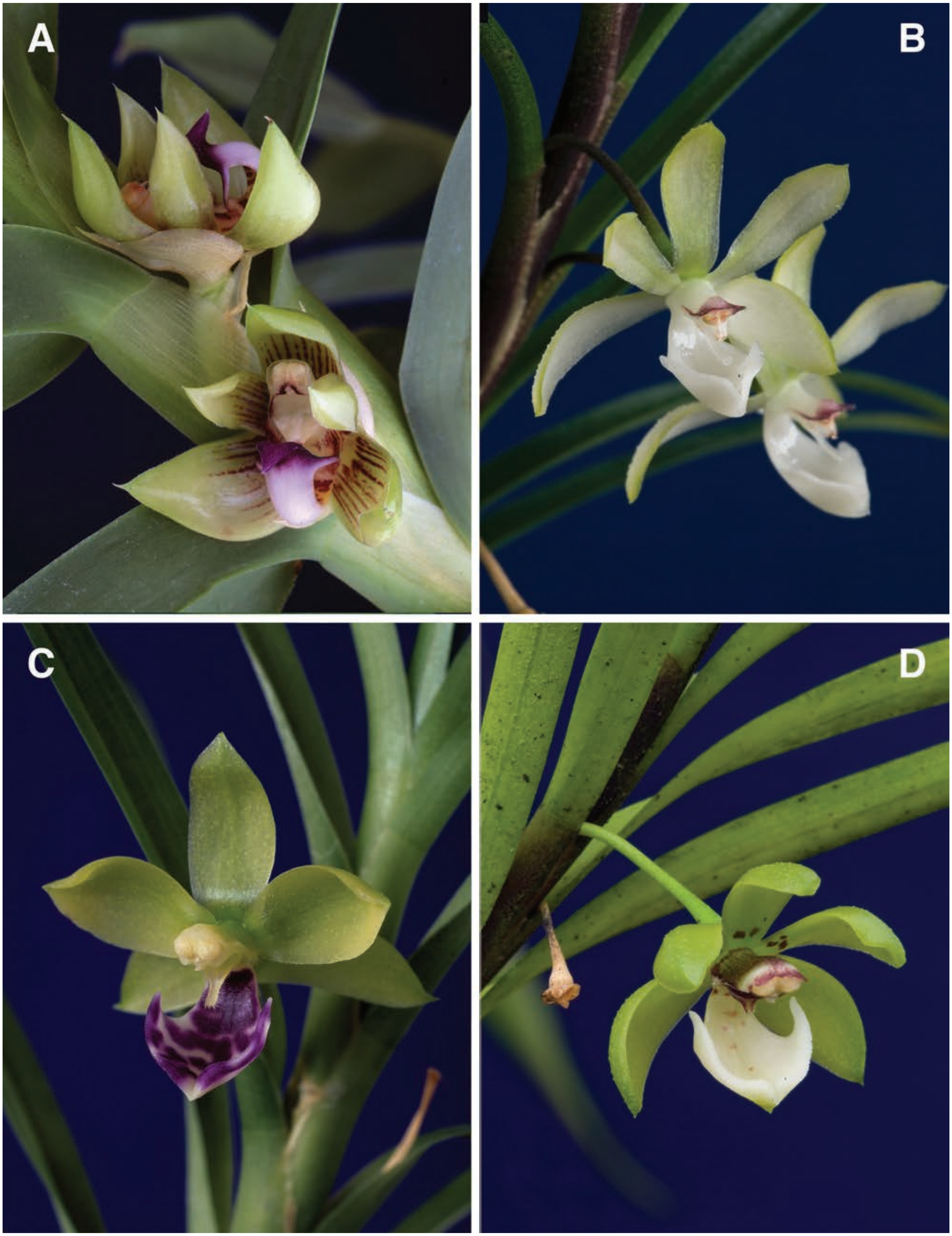
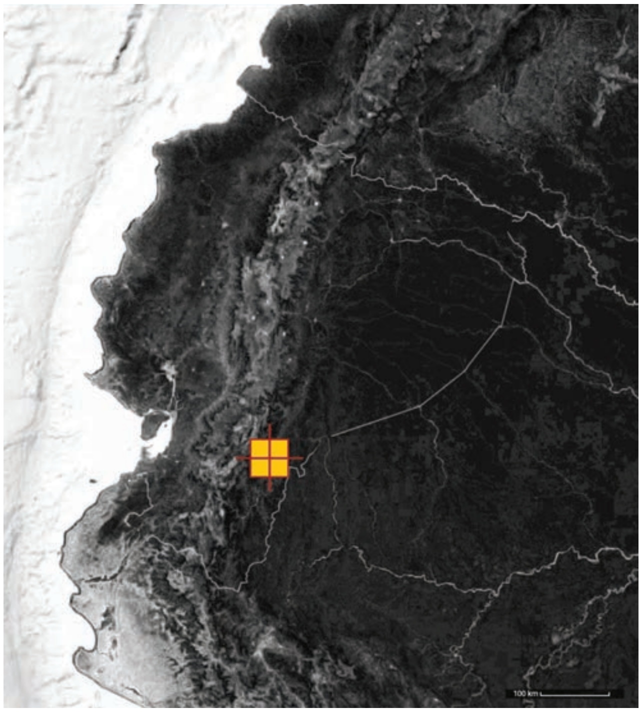


FIGURE 17. **A–D**. Species of *Dichaea* sect. *Pseudodichaea*. **A**, *Dichaea amazonica* (*Pupulin 5938*); **B**, *D. calyculata* (*Pupulin 6923*); **C**, *D. trulla* (*Pupulin 6617*); **D**, *D. superba* (*Pupulin 6901*). Photographs by F. Pupulin.



MAP 7. Distribution of *Dichaea amazonica*.

Epithecia calyculata (Poepp. & Endl.) Schltr., Orchis 9: 26. 1915.

Heterotypic synonym: *Dichaea coriacea* Barb. Rodr., Gen. Sp. Orchid. 2: 181. 1881, *syn. nov*.

SYNTYPES: BRAZIL: [Río de Janeiro]: dans les montagnes de Rodeio. Fleurit en Octobre. *J. Barbosa Rodríguez s.n.* (not found; drawing of the syntype; tracings of the drawing from the syntype); BRAZIL: Santos, Herb. Brasil. Regnellian. Museo bot. Stokcholm, *Mosén 2957* (S).

Epithecia coriacea (Barb. Rodr.) Schltr., Orchis 9: 25. 1915, *syn. nov*.

Dichaea australis Cogn., Fl. Bras. 3(6): 498. 1906, *syn. nov*. *Epithecia australis* (Cogn.) Schltr., Orchis 9: 25. 1915, *syn. nov*.

SYNTYPES: BRAZIL: S. Catharina: Blumenau, *Gull s.n.* (?); *Müller s.n.* (B, destroyed); BRAZIL. in arboribus prope S. Paulo, Comm. Geogr. e Geol. S. Paulo, *A. Cogniaux 1780* in herb. Havn. (BR?; illustration of the syntype).

Dichaea caveroi D.E.Benn. & Christenson, Icon. Orchid. Peruv. pl. 629. 2001, *syn. nov.* TYPE: PERU. Condorcanqui, from area closely surrounding the Border Guard Post 'Alfonso Ugarte' PV-3, 1300 m, *M. Cavero B. ex Bennett 6441* (Holotype: Herb. Bennettianum, according to Bennett and Christenson 2001).

The long, suberect stems with narrowly linear, acinacyform, arcuate leaves, the small flowers produced simultaneously on relatively short peduncles, and the emarginate lip of *Dichaea caveroi* are indistinguishable from the features typical of *D. calyculata*. The latter taxon is not a synonym of *Dichaea trulla* Rchb.f. as it was treated by Dodson and Marmol de Dodson (1980b), Brako and Zarucchi (1993), Stevens et al. (2001), and Zuloaga et al. (2008), as well as by eMonocot (2013) and other online taxonomic databases. *Dichaea trulla* has much larger flowers, with apple-green sepals and petals, and purple lip (Fig. 17C), which are produced singly and never simultaneously in groups.

12. **Dichaea superba** Pupulin, *sp. nov.*

TYPE: ECUADOR. Esmeraldas: San Lorenzo, Río Mataje, ca 1°12'40"N, 78°31'45"W, 300–600 m, collected by H. Medina, 2002, flowered in cultivation in the collection of Ecuagenera at El Pangui, 10 November 2007, *F. Pupulin 6901* (Holotype: CIOA). Fig. 17D, 19, 20.

Species sectionis Pseudodichaeae, habito floreque cum Dichaeam trullam Rchb.f. congruentibus, foliis distincte longioribus angustioribusque, bractea floralis ovario non excedentis, bracteola plerumque occulta intus illa externa, sepalis petalisque concavis subringentibus, labello subacuto niveo lobuli lateralibus epichili anguste ligulatis et stipite pollinarii late rhombico-obtrullato recedit.

Epiphytic, caespitose *herb* to 70 cm long. *Roots* filiform, ca.1.0 mm in diam., exposed at the base of the stem, the caulinar roots produced at each internode completely hidden by the leaf sheaths. *Stems* rounded, simple, suberect when young, becoming pendent with age but with the apex suberect, 20–70 cm long, 0.5–0.8 cm wide across conduplicate sheaths. *Leaves* articulate with the sheaths, closely spaced along stem, spreading, sucoriaceous, narrowly linear, acuminate, dark green, 6.0–15.0 × 0.3–0.5 cm; sheaths adpressed to the stem, slightly complanate, 20–40 × 10–16 mm. *Inflorescence* solitary, 1-flowered, emerging below foliage, subpatent, 13–17 mm long, provided with a basal, cylindrical, tightly clasping bract, ca. 1 mm long. *Floral bract* double, the outer bract tubular, obtuse, abruptly subacuminate, clasping, 2.5 × 5.0 mm when spread, the inner bractlet linear, acuminate, almost completely hidden by the outer bract, 2.5–2.8 × ca. 1 mm. *Pedicel* cylindric, ca. 1 mm long. *Ovary* 1.0–1.5 mm long, glabrous. *Flower* spreading, the sepals and petals green, blotched at the base with reddish brown, sometimes spotted with pale purple throughout; the lip white, sometimes spotted with pale red, fading ivory toward the hypochile, where it is sparsely blotched with brown; column reddish brown, fading ivory toward the apex; anther cap cream colored, suffused with red. *Dorsal sepa*l oblanceolate, acute, fleshy, concave, dorsally subcarinate, slightly bent over the column, 8 × 5 mm. *Lateral sepals* obliquely lanceolate-elliptic, concave, acute, apically minutely mucronate, dorsally subcarinate, 9 × 5 mm. *Petals* narrowly obovate, acute, concave, 8 × 5 mm. *Lip* 3-lobed, sagittate, sessile, 8 × 10 mm when spread, the hypochile obcuneate, ca. 5 mm long, 6 mm wide at apex, provided at the base with a central, low, short keel, flushing into the hypochile surface ca. 2 mm; the epichile triangular-sagittate, acute, 3.5 × 10.0 mm, the lateral lobes narrowly linear, rounded, retrorse, ca. 2 × 1 mm. *Column* suberect, hemiterete, with a indistinct foot, 7.5 mm long, 4.5 broad around the stigma; the clinandrium shallowly concave, undulate; ligule triangular-cuspidate, subacuminate, ciliate at apex, 2.5 × 1.8 mm. *Anther cap* transversely subrectangular-rheniform, cucullate, 2-celled. *Pollinia*

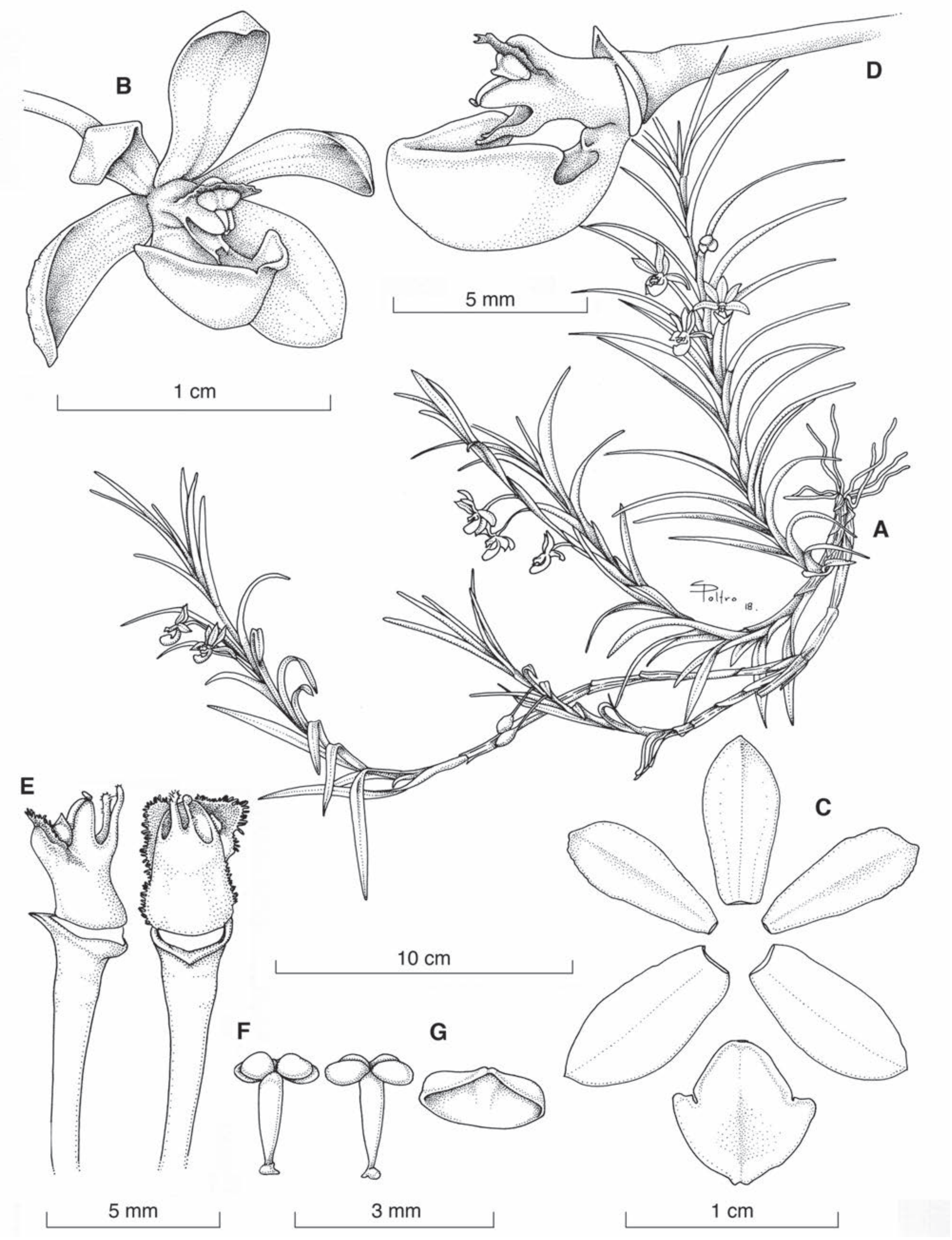


FIGURE 18. *Dichaea calyculata* Poepp. & Endl. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, lateral and ventral views; **F**, pollinarium (two views); **G**, anther cap. Drawn by S. Poltronieri from *Pupulin 6923* (CIOA).

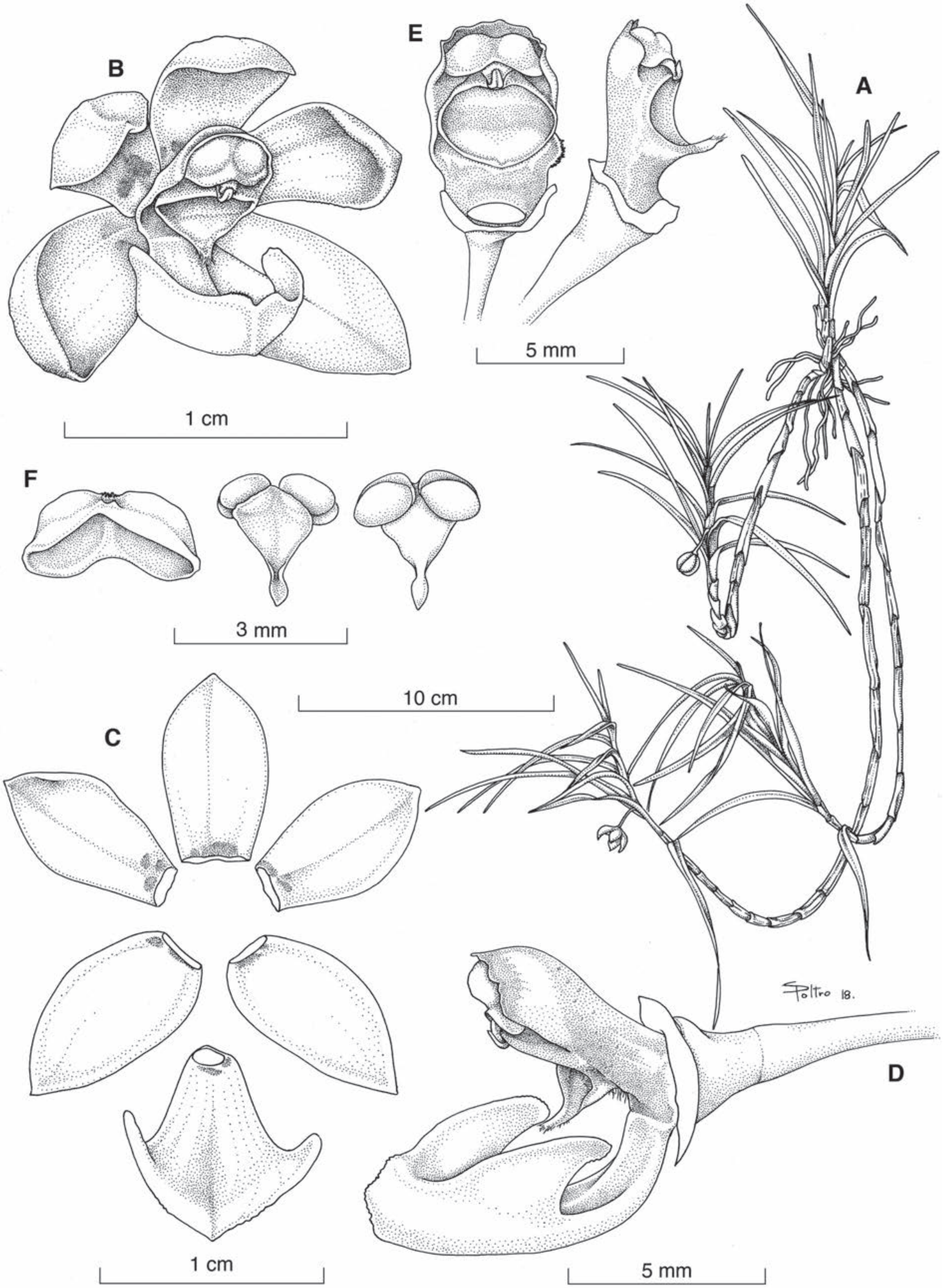


FIGURE 19. *Dichaea superba* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral and lateral views; **F**, anther cap and pollinarium (two views). Drawn by F. Pupulin and S. Poltronieri from the holotype.

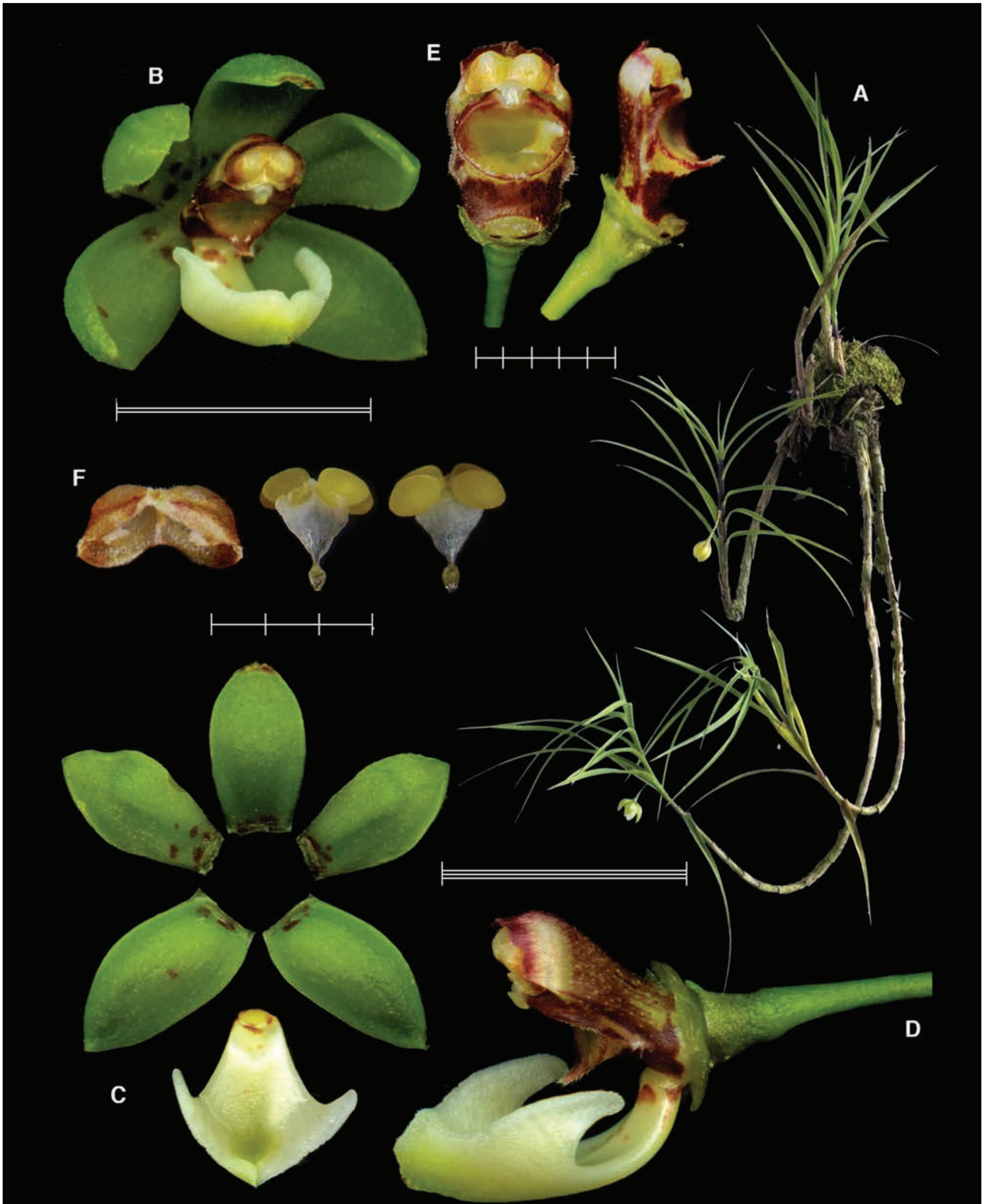


FIGURE 20. Lankester Digital Composite Plate of *Dichaea superba* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral and lateral views; **F**, anther cap and pollinarium (two views). Single bar = mm; double bar = cm; triple bar = dm. Prepared by F. Pupulin from the holotype.

4, elliptic, in 2 superposed pairs of slightly different size, on a obtrullate-rhombic, obtuse stipe; viscidium hyaline, obovate. *Fruit* not seen.

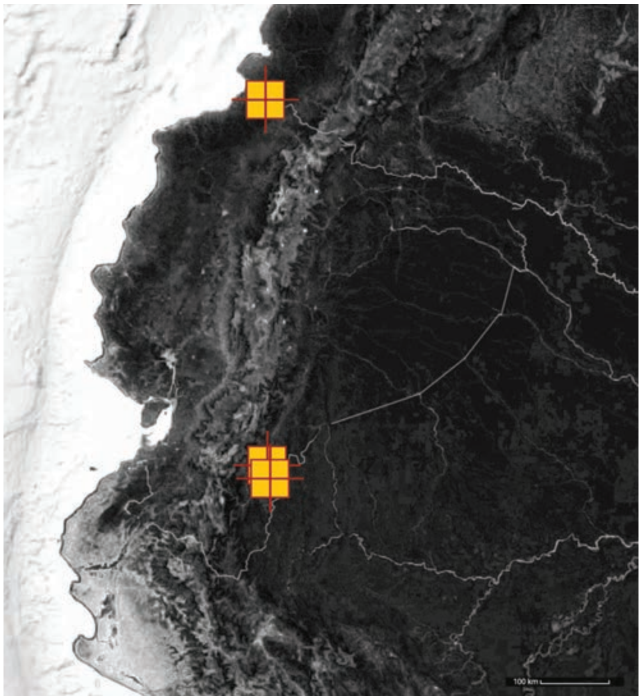
Additional specimens examined: ECUADOR. Zamora-Chinchipe: Pangui, Quebrada Pachicutza, 3˚39'50.3"S, 78˚34'09.7"W, 940 m, collected by H. Medina, December 2000, grown in the collection of Ecuagenera at Gualaceo, 18 December 2007, *F. Pupulin 6977*.

Other material studied: ECUADOR. Zamora-Chinchipe: Pangui, Río Chuchumbleza, 3˚31'51"S 78˚31'51"W, 750 m, grown in the collection of Ecuagenera at Gualaceo, 22 December 2007. Photograph (Fig. 25A), not conserved.

Etymology: from the Latin *superbus*, superb, magnificent, in allusion to the imposing habit of the tall plants and the fleshy, flower, large for the genus *Dichaea*.

Distribution: the species is known from documented collection on both watersheds of the Ecuadorean Andes, where it inhabits warm and wet regions of tropical forests at low to medium elevations (ca. 300–1000 m) (Map 8). The Río Mataje, *locus typycus* of the species, marks the border between the Ecuadorean province of Esmeraldas and Colombia, so that *Dichaea superba* must be certainly found also in the latter country. On the other side, the photograph of a Peruvian unidentified species in Zelenko and Bermúdez (2009: 110) surely represents the same species, which is probably widespread along the Andes at least from Colombia to Peru.

Dichaea superba is superficially similar to *D. trulla*, with which it shares the habit formed by very long stems that are foliaceous only toward the apex and become long and pendent with age (to 70 cm or more), the long and narrow, pointed leaves, and the comparatively large, solitary, quite fleshy, long-lasting flowers. In *D. Superba*, however, the leaves are distinctly longer and narrower (to 15.0 × 0.5 cm vs. 11.0 × 0.6 cm), the external floral bract does not exceed the length of the ovary (vs. longer) and the internal bractlet is almost completely hidden by the outer bract (vs.largely exposed), the sepals and petals remain subringent during anthesis (they become strongly reflexed at maturity in *D. trulla*), and the subacute lip is white or sparsely spotted with brownish red (vs. truncate, mostly solid violet), provided with narrowly ligulate lobes of the epichile (vs. triangular, short). Finally, the pollinaria of the two species are quite different (Fig. 21). The stipe of *D. superba* is rhombic-obtrullate, distinctly wider in the median-upper portion, where it is almost as broad as the width of two transversal pollinia, whereas in *D. trulla* the stipe is narrow and almost ligulate, apically less than half the width of that of *D. superba*; the viscidium of *D. superba* is obovate and small, vs. obpeltate and large in *D. trulla*.



MAP 8. Distribution of *Dichaea superba*.

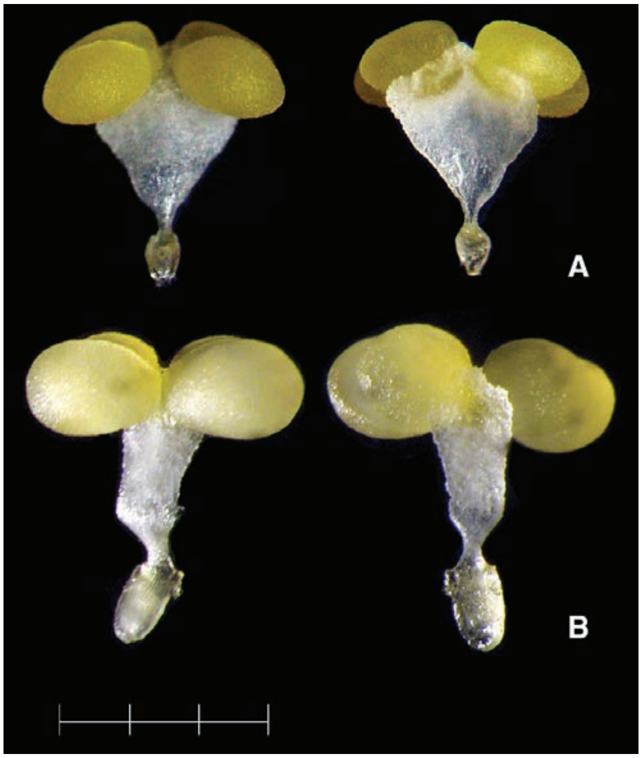


FIGURE 21. **A–B**. Comparison between the pollinaria of *Dichaea superba* and *D. trulla*. **A**, *D. superba* (*Pupulin 6901*); **B**, *D. trulla* (*Pupulin 5319*). Photographs by F. Pupulin.

At least on the Amazonian watershed of the Andes, the latter species is sometimes sympatric with *Dichaea superba*, as we documented with a collection from the Río Chuchumbleza (Zamora-Chinchipe: Pangui) (Fig. 25B).

Photographs and illustrations of *Dichaea tenuis* C.Schweinf. appearing on the Internet often mistakenly refer to *D. superba* (i.e., orchidspecies, Ecuagenera [Ecuador], and Agroriente [Peru] webages, among others). Nevertheless, *D. tenuis* is altogether a completely different species of sect. *Pseudodichaea*, with small plants less than 10 cm tall, acicular leaves ca. 10 mm long, and subglobse, small flowers with perianth parts as short as 3 mm (Schweinfurth, 1952).

Ixyophora Dressler

Robert Dressler created *Ixyophora* (in Whitten et al., 2005), typified by *I. viridisepala* (Senghas) Dressler, to accomodate a group of Andean species previously treated under a broad concept of *Chondrorhyncha*, which the molecular analyses carried out by Whitten and collaborators recovered as sister of *Aetheorhyncha* and consecutively sister to *Chaubardiella* Garay (Whitten et al., 2005). Morphologically similar to *Warszewiczella* Rchb.f. (which is nested into a sister clade), *Ixyophora* is characterized by the callus of the lip reaching the middle of the blade but scarcely separate from it, not thick and fleshy, mostly widest basally and narrow distally, not thick and fleshy, and the column flat beneath. Also the stipe of the pollinarium is quite characteristic in *Ixyophora*, being narrowed between the viscidium and the pollinia. At that time, Dressler (in Whitten et al., 2005) transferred to *Ixyophora Chondrorhyncha carinata* Ortiz, which was included in the DNA analyses together with *I. viridisepala* and *Chondrorhyncha aurantiaca*, Senghas & Gerlach, on the basis of morphological similarities. In 2008, Harding included in *Ixyophora* also *Chondrorhyncha luerorum* R. Vásquez & Dodson, which is morphologically very close to *I. aurantiaca* (Senghas & Gerlach) Dressler.

Curiously, *Chondrorhyncha velastiguii* Dodson, which is the closest species to the *typus generis* of *Ixyophora*, *I. viridisepala*, and morphologically almost indistinguishable from it (if not for the very different color) (Fig. 22, 25C, 30C), escaped the attention of systematists and remained undisturbed within *Chondrorhyncha*, contributing to the polyphily of the genus. As I already previously indicated the need for this transfer to resolve the paraphyly of *Ixyophora* (Pupulin, 2009b), here I formally propose the new combination:

13. **Ixyophora velastiguii** (Dodson) Pupulin, *comb. nov.* Fig. 23, 24, 25D, 30D.

Basionym: *Chondrorhyncha velastiguii* Dodson, Icon. Pl. Trop., ser. 2, 5: pl. 419. 1989.

TYPE: ECUADOR. Tungurahua: Río Negro, road Baños-Puyo, 1300 m, 11 Mar 1963, *Dodson & Thien 2358* (Holotype: SEL).

When Ortiz Valdivieso (2004) described *Chondrorhyncha carinata*, he made no express comparison of the new species with any other taxon of the group, basically diagnosing it for the presence of a minutely papillose keel on the underneath of the column, the 3- to 5-toothed callus, and details of the rostellum. The closest species in the *Chondrorhyncha* complex were obviously *C. viridisepala* and *C. velastiguii*, which I combined into *Ixyophora* here above. Bob Dressler (in Whitten et al. 2005) first recognized the affinities of *C. carinata* and transferred it to *Ixyophora*, which differs from other *Ixyophora* species not only for the presence of a distinct keel under the column but also for the structure of its callus. In *I. velastigui*, *I. viridisepala*, and *I. aurantiaca*, the free portion of the callus does not extend forward from the point of attachment of the callus to the lamina, forming something like a "suspended bridge" only in the frontal part. In *I. carinata*, on the contrary, the callus extends beyond the point of fusion with the blade, forming a sort of long tooth, which in turn is 2- to 3-toothed in front. Furthermore, the general outline of the lip is elliptic in *I. carinata*, whereas in the other species of *Ixyophora* it is distinctly obovate. We provide here a complete botanical illustration of *I. carinata*, from a plant grown in the rich collection of Ecuagenera in Gualaceo, to complement the quite schematic illustration originally provided by P. Ortiz Valdivieso (2004) when he described the species:

14. ***Ixyophora carinata*** (P. Ortiz) Dressler, Lankesteriana 5(2): 95. 2005.

COLOMBIA. Without further locality data, flowered in cultivation in the collection of Ecuagenera at Gualaceo, 17 Apr. 2008, *CIOA-00567* (CIOA). Fig. 26, 29A.

We also documented another Ecuadorian taxon in *Ixyophora*, whose characteristics are similar to those of *I. viridisepala* but which differs from the latter in significant details. We describe it here as a species new to science that is described next.

15. **Ixyophora imitatrix** Pupulin, *sp. nov.*

TYPE: Ecuador. Without further locality data, flowered in cultivation in the collection of Ecuagenera at Gualaceo, 5 July 2008, *CIOA-00928* (Holotype: CIOA). Fig. 27, 29B.

Species Ixyophora viridisepala (Senghas) Dressler *similis, sed habito minore foliis subsessilis, labello elliptico subtrilobo, columna alba glabra apice multo dilatata carina parva laevis munita et stipite pollinarii late rhombico-obtrullatoplerumque recedit.*

Epiphytic, caespitose, small *herbs* without pseudobulbs. *Roots* terete, thick, to 4.5 mm in diam., produced from the short rhizome. *Stem* abbreviated, enclosed by 3–5 imbricating sheaths to 2 cm long, provided with hyaline,

FIGURE 22. **A–E**. Flowers of *Ixyophora virisidisepala*. **A**, *Pupulin 5941* (JBL); **B**, *CIOA-s.n.* (not preserved); **C**, *CIOA-00492* (CIOA); **D**, *Pupulin 6554* (CIOA); **E**, *Pupulin 6979* (CIOA). Flowers not at the same scale. Photographs A, C–E, by F. Pupulin; B by G. Merino.

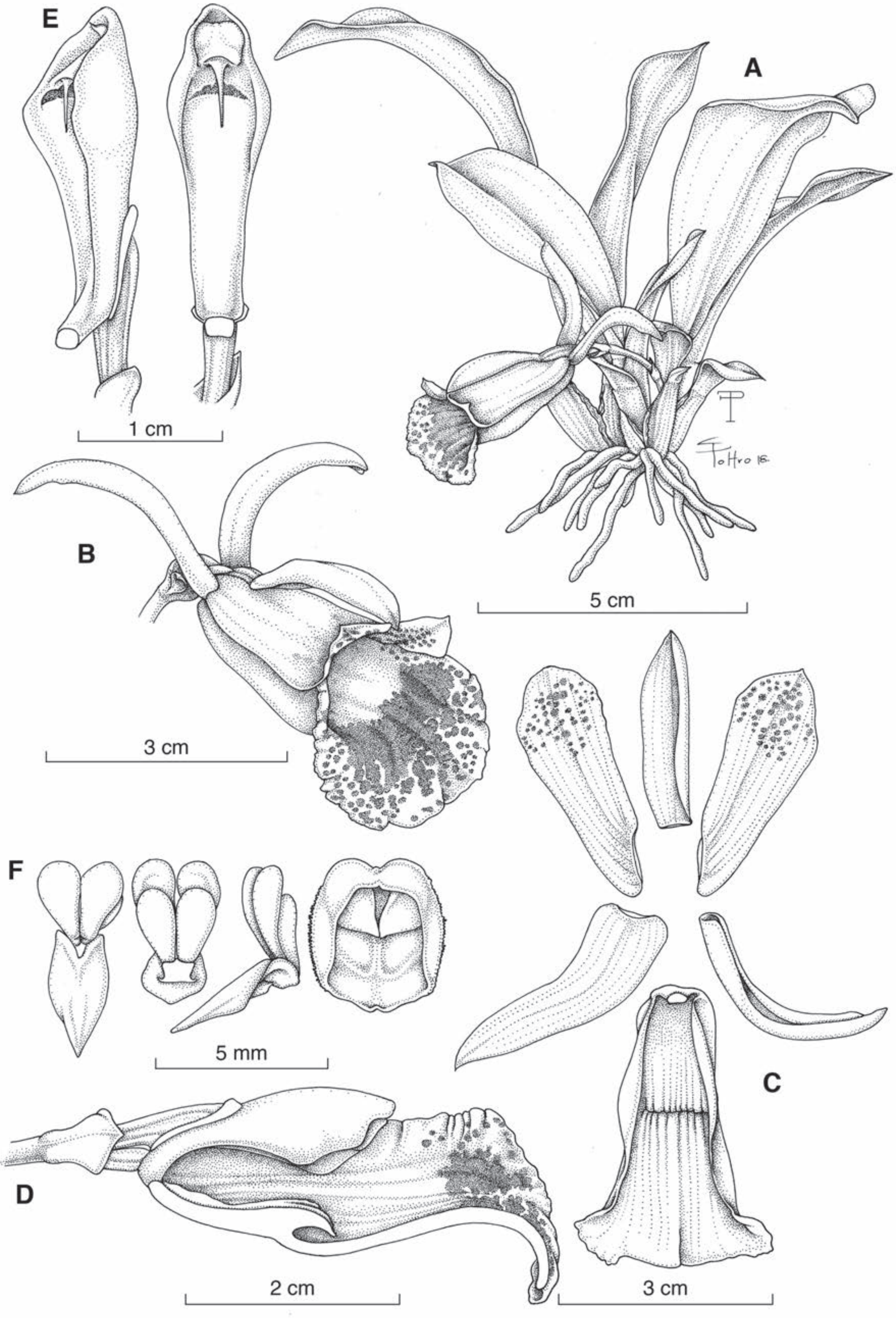


FIGURE 23. *Ixyophora velastiguii* (Dodson) Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, three-quarter and ventral views; **F**, pollinarium (three views) and anther cap. Drawn by F. Pupulin and S. Poltronieri from *Pupulin 6622* (CIOA).

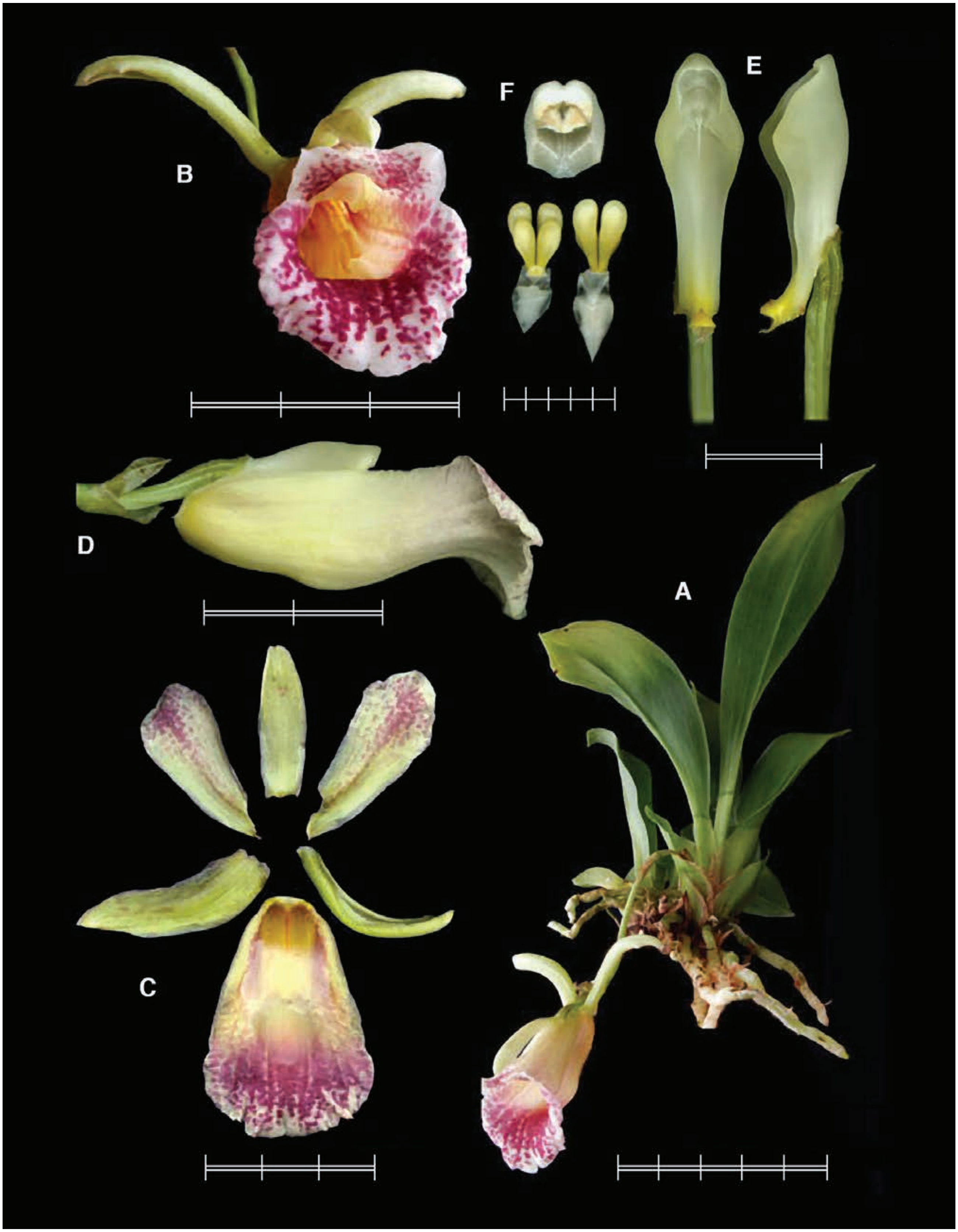


Figure 24. Lankester Digital Composite Plate of *Ixyophora velastiguii* (Dodson) Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral and lateral views; **F**, anther cap and pollinarium (two views). Single bar = mm; double bar = cm. Prepared by Hugo Medina from *Pupulin 6622* (CIOA).

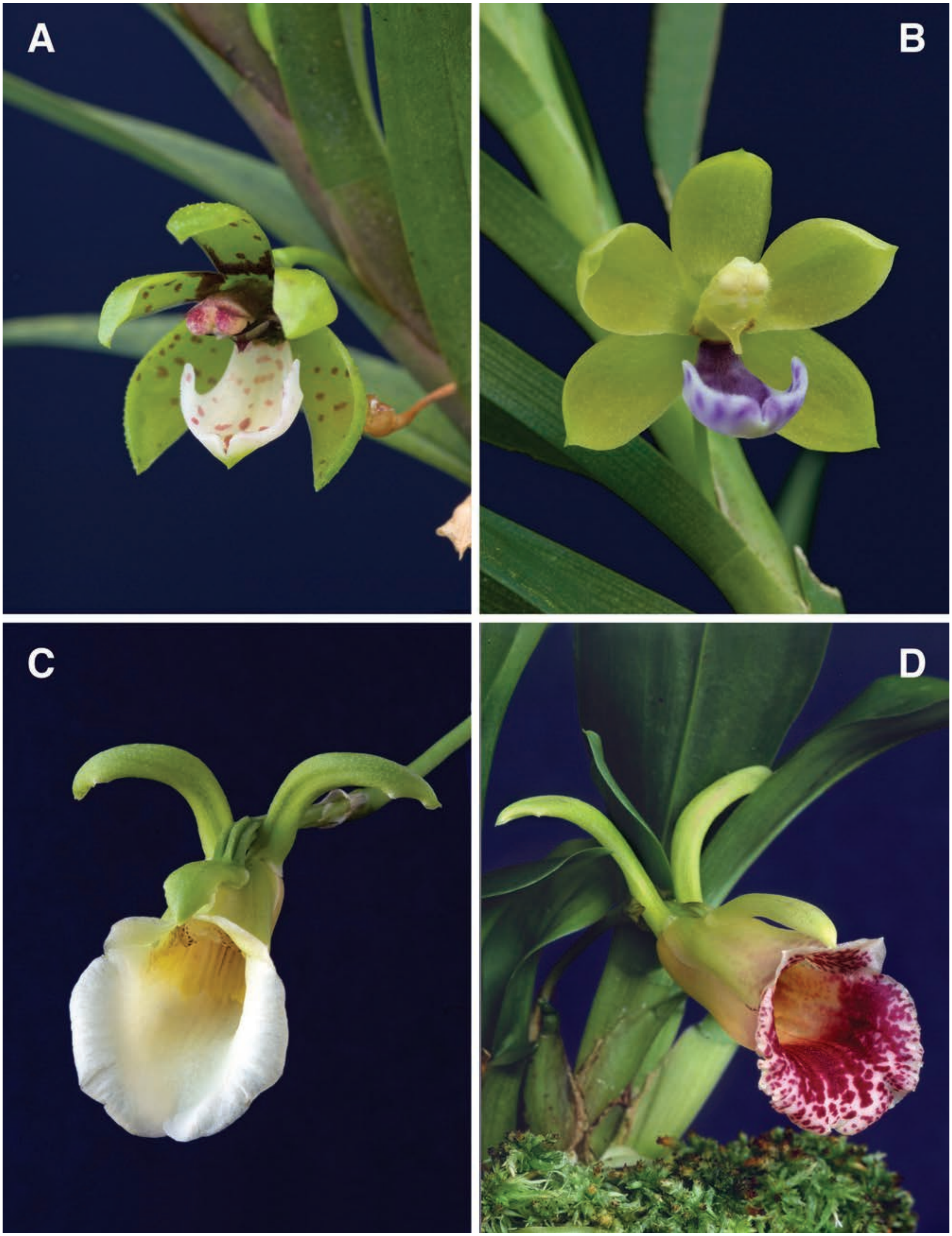


Figure 25. **A–D**. Species of Zygopetalinae. **A**, *Dichaea superba* from Pangui, Río Chuchumbleza (not conserved); **B**, *Dichaea trulla* (*Pupulin 6976*); **C**, *Ixyophora viridisepala* (*CIOA-00492*); **D**, *Ixyophora velastiguii* (*Pupulin 6622*). Photographs by F. Pupulin.

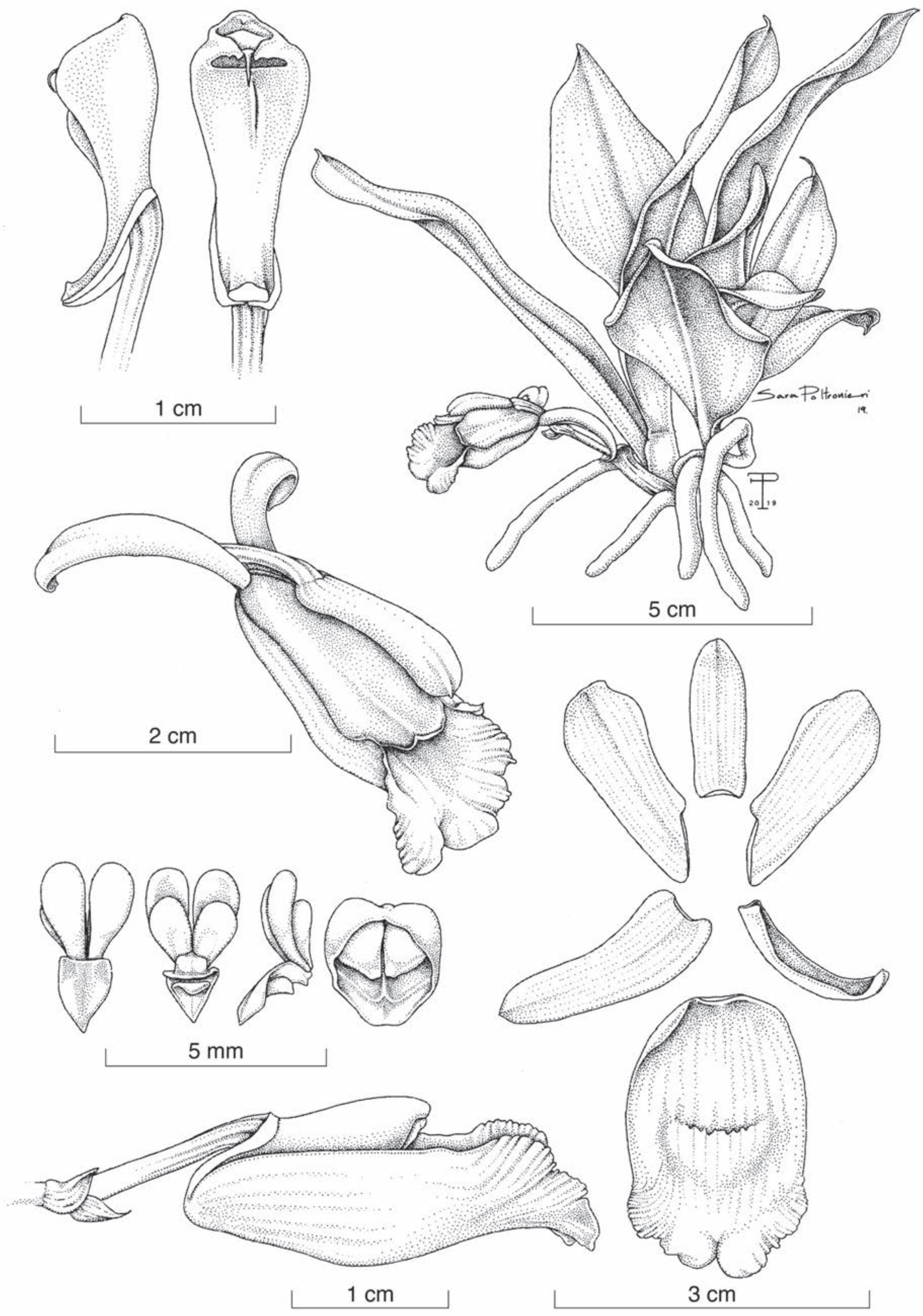


FIGURE 26. *Ixyophora carinata* (Ortiz) Dressler. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, lip, longitudinal section; **F**, column, lateral and ventral views; **G**, pollinarium (three views) and anther cap. Drawn by F. Pupulin and S. Poltronieri from *CIOA-00567* (CIOA).

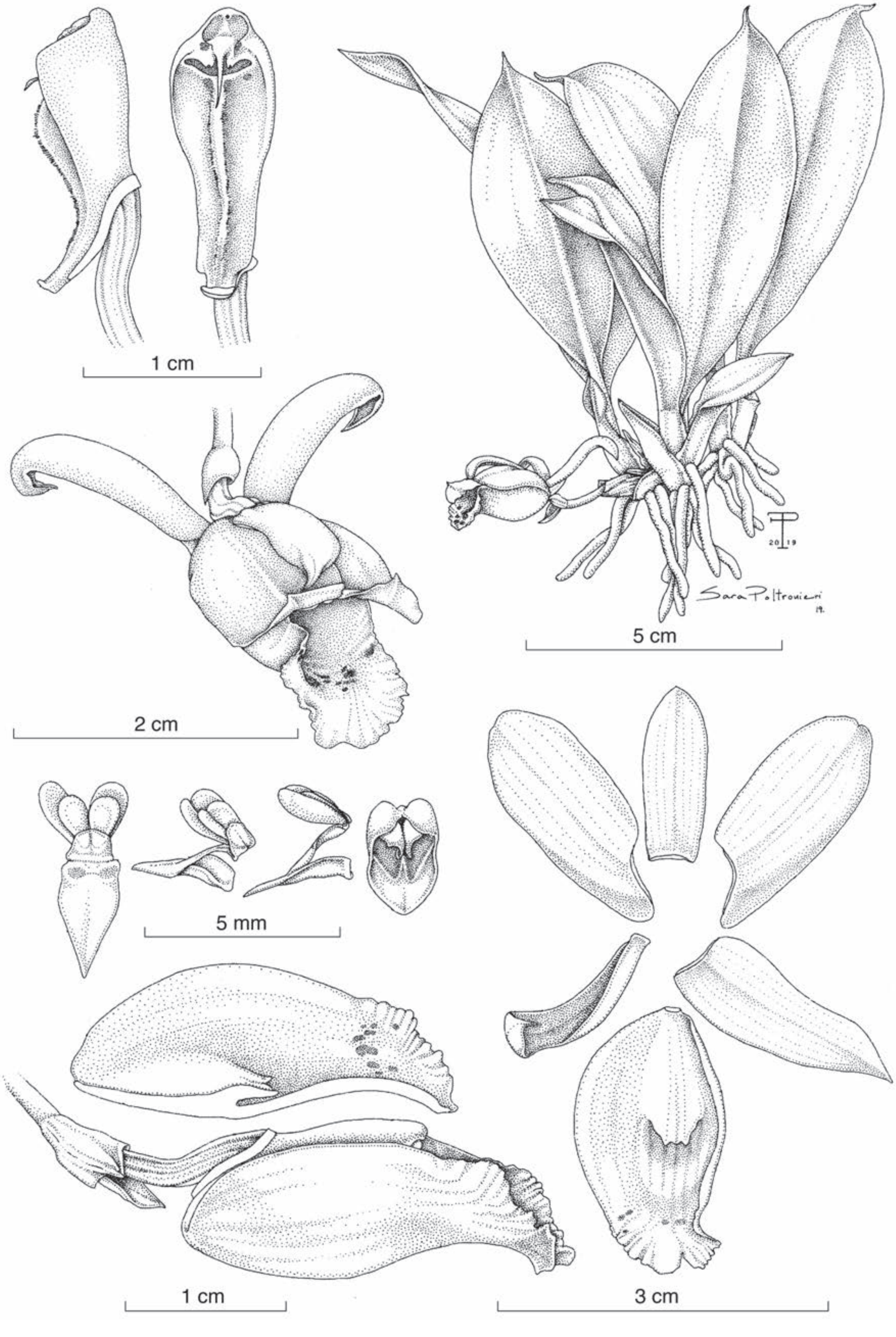


FIGURE 27. *Ixyophora imitatrix* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, lateral and ventral views; **F**, pollinarium (three views) and anther cap. Drawn by F. Pupulin and S. Poltronieri from the holotype (CIOA).

scarious margins, the upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, oblanceolate-elliptic, acute, grass green, matte, 3.7–7.5 × 2.4–3.0 cm, narrowed at the base into a indistinct, conduplicate petiole, abaxially provided with a pronounced median keel and 2–3 lateral, obscure veins on each side. *Inflorescence* lateral, slender, 1-flowered, to 3 cm long, produced from the axil of the lower sheaths; the peduncle terete, suberect, provided with a triangular, acute bract to 6 mm long; floral bract scarious, double, conduplicate, much shorter than pedicellate ovary, the external one broadly ovate, acute, ca. 3 × 3 mm, the subopposite internal bractlet lanceolate, subacuminate, 4 × 3 mm. *Flowers* resupinate, ringent, with pale yellow sepals and petals, paler toward the apex, the lip yellow at the base, white at apex, the column white, bright yellow at the base, the anther cap white. *Dorsal sepal* free, incurved, bent over the porrect petals, linear-elliptic, obtuse, shortly apiculate, concave, 15 × 6 mm. *Lateral sepals* narrowly lanceolate-subfalcate, asymmetrical, obtuse, reflexed 180 degrees, apically subuncinate, strongly inrolled-folded at the base, 22 × 7 mm. *Petals* inserted along the margins of the column foot, obliquely oblong, obtuse-rounded, porrect, apically gently revolute, 22 × 8 mm. *Lip* articulate with the column foot, elliptic, obscurely 3-lobed, 27 × 17 mm, deeply concave, forming a distinct mentum on the median portion when seen laterally, the base rounded, the apex emarginate, the proximal margins erect, flanking the column, apically bent, the distal margins undulate; disc covered from the base to the mid-lip with a laminar, flat callus, adnate to the lamina up to the lateral margins of the apex, the free apex truncate, minutely and irregularly 5-toothed, forming a narrow and shallow pocket with the base of the blade. *Column* semiterete, straight, 16 mm long, 7.5 mm broad around the stigma, with a distinct foot ca. 5 mm long, strongly dilated at apex into large, elliptic, rounded stigmatic wings, provided with a low, rounded keel running from the middle to the stigmatic opening; the stigma transverse, narrow, slit-like; the rostellum acicular, with two short, round teeth on each side. *Anther cap* incumbent, cucullate, ovate, truncate, flattened, 2-celled. *Pollinia* 4, in 2 subequal pairs, on a broad, obpeltate, incurved, apically depressed, hyaline stipe and a scarcely distinct, ventral, subrectangular, hyaline viscidium.

Etymology: from the Latin *imitatrix*, a female imitator, for the strong resemblance of the new species with *Ixyophora viridisepala*.

Distribution and ecology: the plant that served as the type was originally collected in Ecuador, but no specific locality data were recorded at the time. In cultivation, the species flowers in June-July.

Ixyophora imitatrix is at first sight almost indistinguishable from *I. viridisepala*, with which it shares the general color scheme and the subtubular flower with the lateral sepals strongly reflexed. However, whereas *I. viridisepala* has long imbricating sheaths and petiolate leaves, the foliage of the new species looks almost sessile. Furthermore, the lip of *I. imitatrix* is distinctly 3-lobed-elliptic, almost subrectangular, whereas in *I. viridisepala* it is distinctly obovate. The column of *I. imitatrix* is white (vs. feckled with purple), glabrous (vs. densely villose), strongly dilated around the stigma (vs. slightly dilated), and provided with a substigmatic low keel (vs. keel absent). Finally, the stipe of the pollinarium is broadly rhombic-obtrullate, vs. triangular in *I. viridisepala*.

KEFERSTEINIA RCHB.F.

16. ***Kefersteinia alata*** Pupulin, Harvard Pap. Bot. 8(2): 161. 2004.

TYPE: Panama. Bocas del Toro: road from David to Chiriquí Grande, around km. 74, ca. 450 m, epiphytic in premontane moist forest, 10 April 2001, flowered in cultivation at Gaia Botanical Garden, 18 August 2001, *F. Pupulin, D. Castelfranco & E. Salas 3119* (Holotype: USJ; Isotype: USJ-Spirit).

Up to now only recorded from the Caribbean watershed of the Chiriquí mountains in Panama, *Kefersteinia alata* is here documented for the first time for the flora of Costa Rica, on the basis of three collections from the lower Talamanca region, not far from the Caribbean Sea:

COSTA RICA. Limón: Amubri, Bris, 300 m West of the mouth of the Río Tskuí (a tributary of the Río Yorkín), 9°31'N, 82°52'W, collected by E. Carman, 28 July 2009, prepared from cultivation at the Lankester Botanical Garden, 30 July 2009, *F. Pupulin 7874* (JBL) (Fig. 28). Limón: Talamanca, Cahuita, ca. 1 km after the substation of ICE-Cahuita, finca of don Cipriano, shores of an affluent of orillas río Carbón toward a small waterfall, 9°43'19.87"N, 82°52'16.87"W, 107 m, tropical moist forest, 26 November 2014, flowered in cultivation at the Lankester Botanical Garden, 8 Aug. 2018, *F. Pupulin 8641 & D. Bogarín* (JBL) (Fig. 29C); same locality, epífitas on fallen branches and vines, flowered in cultivation at the Lankester Botanical Garden, 20 Aug. 2018, *D. Bogarín 11252, N. Belfort & F. Pupulin* (JBL).

Distribution and ecology: tropical rain forests and premontane wet forests along the Atlantic watershed of the Talamanca mountain chain in southern Costa Rica and Western Panama, at elevations of 100–500 m (Map 9). The species flowers in July-August.

Kefersteinia alata, exclusively recorded from the tropical rain forests at low elevations in southern Talamanca, represents the species pair of *K. orbicularis* Pupulin, which is restricted to the low-to-medium elevations on the Pacific slopes of the Talamanca chain.

PRIDGEONIA PUPULIN

17. **Pridgeonia** Pupulin, *gen. nov.*

Herbae epiphyticae, caespitosae, acaules, foliis distichis con*duplicatis inflorescentiisque lateralibus unifloris; flos insignis, tepalis labelloque manifestis, sepalis lateralibus reflexis basi profunde convolutis, petalis porrectis, labello magno trilobo, apice dilatato, expanso, geniculato, callo magno laminare humilis denticulato, in medio laminae fornito; columna hemiterete pilosa apice dilatata, stigma transversali angusto, rostello aciculare; pollinia 4 super stipitem obcuneiforme-cuspidatum viscidiumque peltatum uncinatum duobus dentibus acutis lateralis munitum.*

Type species: *Pridgeonia insignis* Pupulin.

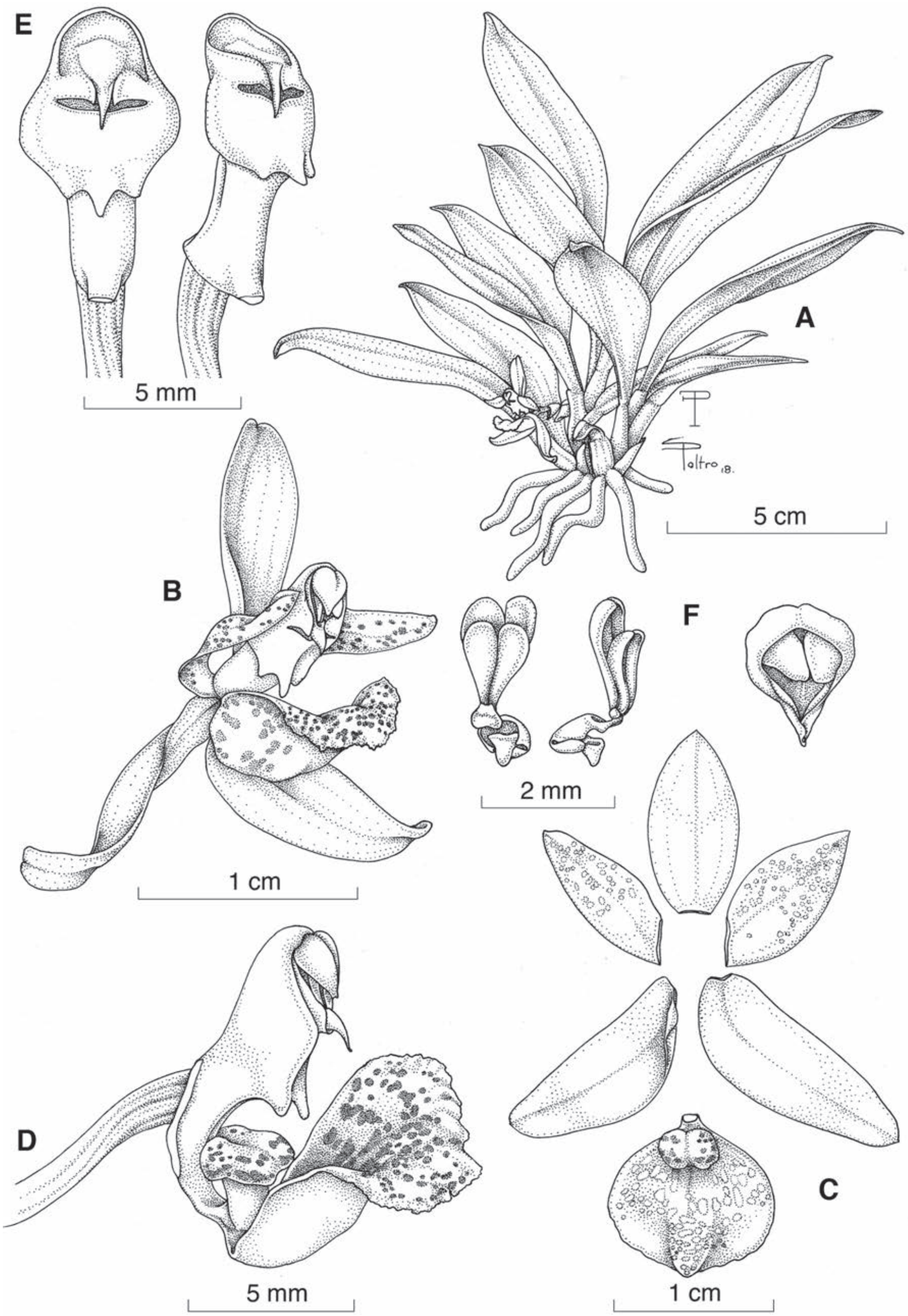


Figure 28. *Kefersteinia alata*. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, ventral and three-quarter views; **F**, pollinarium (two views) and anther cap. Drawn by F. Pupulin and S. Poltronieri from *Pupulin 8343* (JBL).

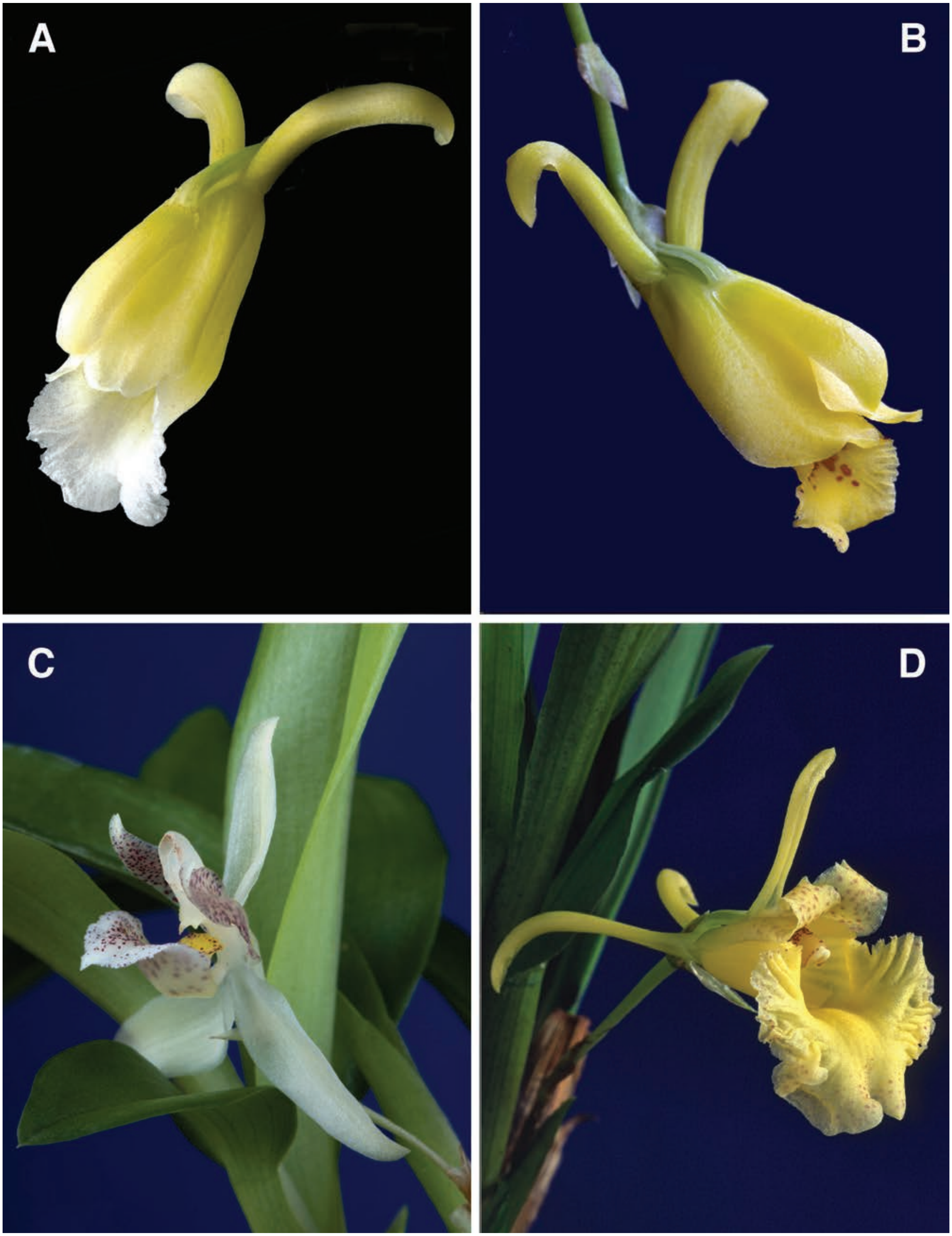


FIGURE 29. **A–D**. Species of Zygopetalinae. **A**, *Ixyophora carinata* (*CIOA-00567*); **B**, *Ixyophora imitatrix* (CIOA-*00928*); **C**, *Kefersteinia alata* (*Pupulin 8641*); **D**, *Pridgeonia insignis* (*Pupulin 6605*). Photographs by F. Pupulin.

Map 9. Distribution of *Kefersteinia alata*.

Eponymy: the genus honors Alec M. Pridgeon, Ph.D., former Sainsbury Orchid Fellow at Jodrell Laboratory, Royal Botanic Gardens, Kew, in recognition of his outstanding career in scientific orchidology.

The flowers of *Pridgeonia* immediately call attention for their size and color, which make them some of the most striking flowers of the whole *Chondrorhyncha* group of the Zygopetalinae (Fig. 30). They are comparable in size to those of *Chondroscaphe* (Dressler) Senghas & G. Gerlach, *Cochleanthes* Raf., and *Euryblema* Dressler, and particularly bring to mind the latter for the shape of the flower and the beautiful foliage. They are born on short, patent to patent, single-flowered inflorescences, from rather stout, erect plants provided with long, oblong, dark green leaves, which are matte on both surfaces. Besides their larger sizes, the shape, color, and texture of the leaves (with the vein not protruding but clearly visible on both the abaxial and adaxial surfaces) are reminiscent of those of *Chaubardiella* Garay, *Aetheorhyncha*, and *Ixyophora*. Florally, *Pridgeonia* is very similar to *Ixyophora*, with the porrect petals forming quite a narrow tube with the lip, whose lateral lobes are erect and flank the column, whereas the apex is spread-geniculate. Along with *Aetheorhyncha* and *Ixyophora*, the new genus presents a low, laminar callus in the center of the disc, the free part of which only occupies the central part of the lip, but the callus is much broader than that of *Aetheorhyncha* and it is not multiseriate as its lobes are erect and flank the column, although the apex is spread-geniculate as those of *Aetheorhyncha* and *Ixyophora*. The flowers are distinctly larger than those of any other species in *Aetheorhyncha* and *Ixyophora* and of a bright yellow color, with the petals sometimes spotted with pale brown, a combination not found in any other species of the supposedly closest relatives. The column of *Pridgeonia* is unique for its ventral surface covered with a densely and finely pilose indumentum, more prominent at the base and more sparse toward the apex. The pollinarium has four large pollinia in two pairs of different sizes, mounted on a reddish brown, transversely rectangular stipe and a peltate viscidium provided with lateral, narrow, acicular extensions in the middle, which are unique among the genera of the *Chondrorhyncha* clade.

18. **Pridgeonia insignis** Pupulin, *sp. nov.*
TYPE: ECUADOR. Zamora-Chinchipe: Zumbi, 3°53'29"S, 78°46'43"W, ca. 1100 m, collected by G. Merino and H. Medina, 2003, flowered in cultivation in the collection of Ecuagenera at Gualaceo, 15 May 2007, *F. Pupulin 6605* (Holotype: CIOA). Fig. 29D, 30A, 31.

Herba epiphytica, caespitosa, acaulis, foliis oblanceolatis acuminatis indistincte petiolatis, inflorescentiae una vel duabus uniflorae; flos insignis, luteo, petalis labelloque rubro pallente notatis; sepalis marginibus involutis, postico erecto subuncinato, lateralibus reflexis; petalis oblongo-ellipticis obtusis porrectis; labello magno trilobo, ellittico-obovato, profunde emarginato, marginibus proximalibus erectis, apicaliter geniculato, callo magno laminare humilis denticulato in medio laminae fornito; columna hemiterete pilosa apice dilatata, stigma transversali angusto, rostello aciculare; pollinia 4, stipite obcuneiforme-cuspidato, viscidio peltato uncinato duobus dentibus acutis lateralis fornito.

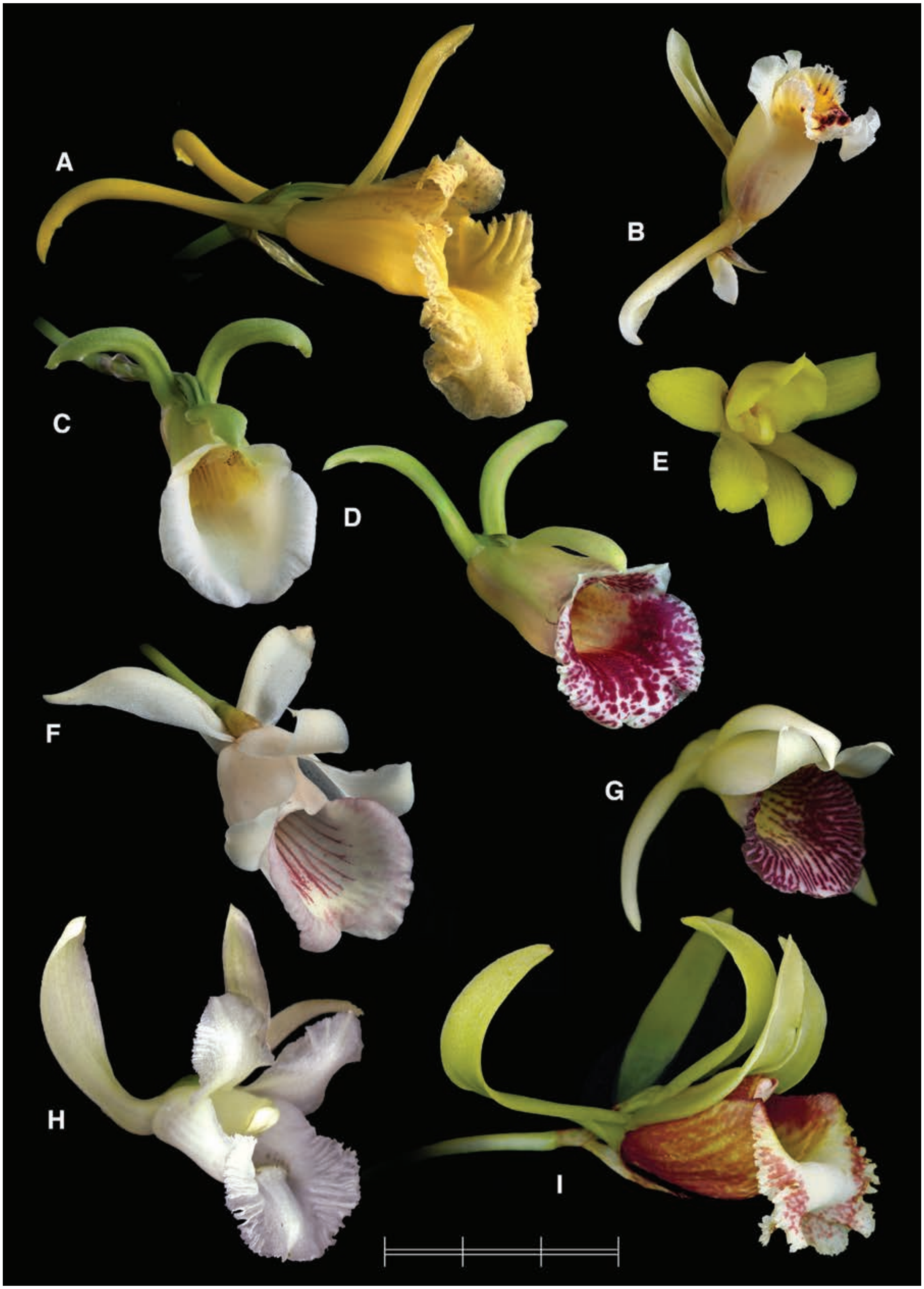


FIGURE 30. **A–I**. Comparison between the flower of *Pridgeonia* (A), those of other closely allied genera (B–G), and other large-flowered genera of the *Chondrorhyncha* complex (H–I). **A**, *Pridgeonia insignis* (*Pupulin 6605*); **B**, *Aetheorhyncha andreettae* (*Pupulin 6560*); **C**, *Ixyophora viridisepala* (*CIOA-00492*); **D**, *Ixyophora velastiguii* (*Pupulin 6622*); **E**, *Chaubardiella subquadrata* (*Pupulin 6614*); **F**, *Warszewiczella lipscombiae* (*Pupulin 8032*); **G**, *Stenotyla picta* (*Pupulin 4702*); **H**, *Chondroscaphe yamilethae* (*Pupulin 4637*); **I**, *Euryblema anatonum* (*Pupulin 5726*). All the flowers at the same scale. Scale bar = 3 cm. Photographs by F. Pupulin.

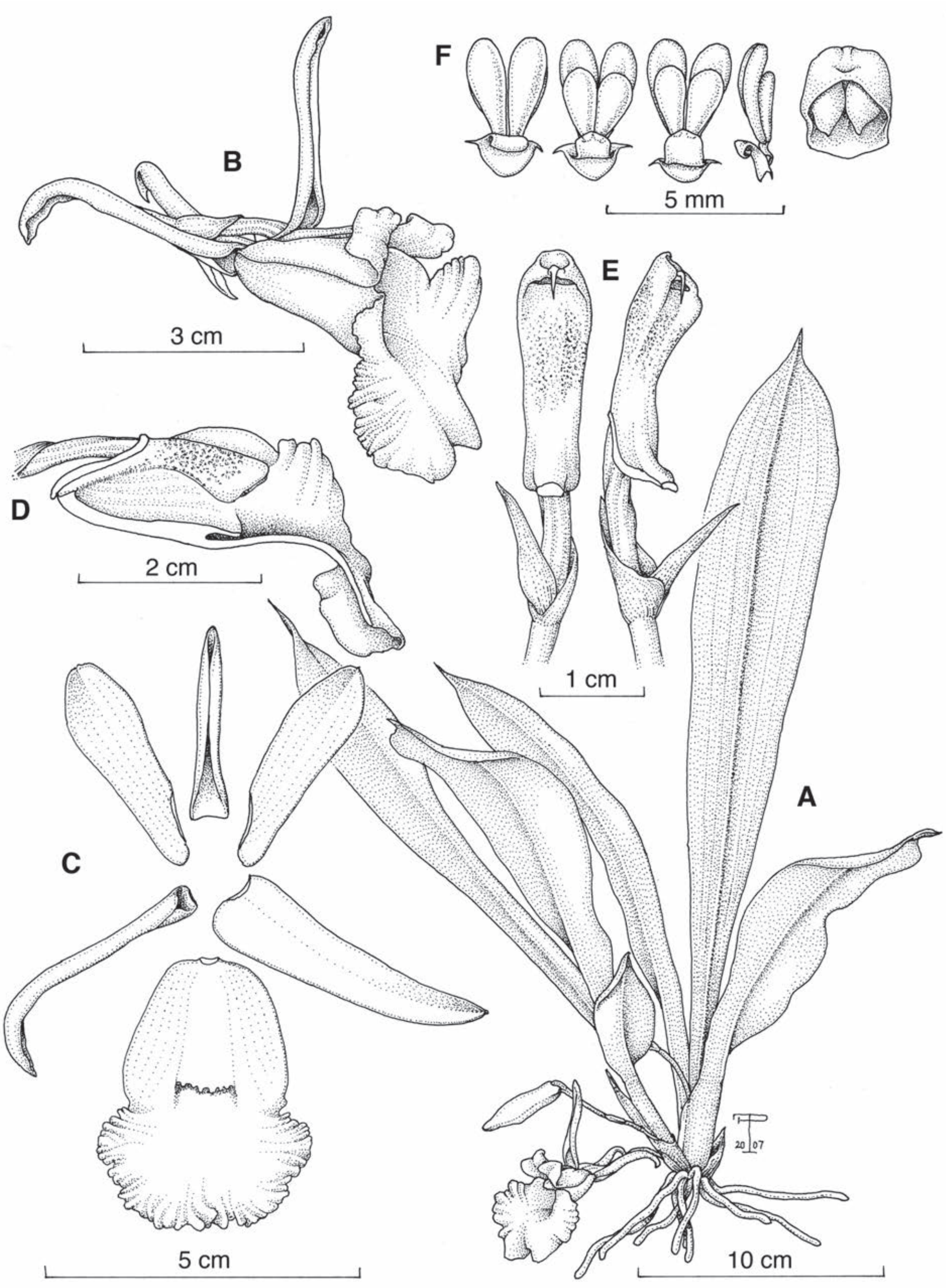
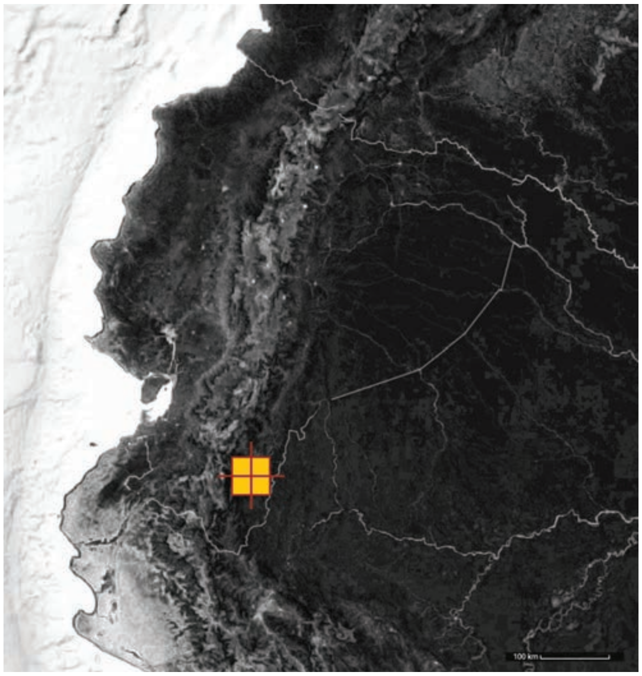


FIGURE 31. *Pridgeonia insignis* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view (the lip longitudinally dissected); **E**, column, ventral and three-quarter views; **F**, pollinarium (four views) and anther cap. Drawn by F. Pupulin from the holotype.

Epiphytic, caespitose *herbs* without pseudobulbs. *Roots* terete, thick, 2.5–3.0 mm in diam., produced from the short rhizome. *Stem* abbreviated, enclosed by 4–7 imbricating sheaths to 6.5 cm long, provided with hyaline, scarious margins, the upper ones foliaceous. *Leaves* conduplicate, articulate, membranaceous, oblanceolate to narrowly obovate, acuminate, grass green, 13–34 × 3.2–5.3 cm, narrowed at the base into a indistinct, conduplicate petiole, abaxially provided with a pronounced median keel and 2–3 lateral, obscure veins. *Inflorescence* lateral, slender, 1–2 per shoot, 1-flowered, to 8 cm long, produced from the axil of the lower sheaths; the peduncle terete, suberect to patent, provided with 2–3 narrow, conduplicate-tubuliform, acute bracts to 15 mm long; floral bract double, conduplicate, shorter than pedicellate ovary, the external one broadly ovate-suborbicular, shortly acuminate, 13 × 11 mm, the subopposite internal bractlet narrowly lanceolate, 11 × 3 mm. *Flowers* resupinate, large, no perfume detected, yellow, the petals sparsely spotted with pale brown, the column spotted and striped with reddish brown, the callus yellow. *Dorsal sepal* free, erect, narrowly lanceolate, acute to shortly acuminate, apically subuncinate, the lateral margins strongly inrolled-folded, 3.2 × 0.6–0.7 cm. *Lateral sepals* narrowly lanceolate, slightly subfalcate, asymmetrical, acute, reflexed 180 degrees, apically falcate-uncinate, strongly inrolled-folded, 4.0 × 1.2 cm. *Petals* inserted along the margins of the column foot, obliquely oblong-elliptic, obtuse, minutely apiculate, porrect, apically gently arcuate-revolute, 3.5 × 1.3 cm. *Lip* articulate with the column foot, elliptic-obovate, obscurely 3-lobed, 4.3 × 3.0 cm, the base rounded, the apex deeply emarginate, the proximal margins erect, flanking the column, apically deflexed, the distal margins crisped; disc with a low, flat, laminar callus, borne at the middle of the lip, apically provided with 2 acute teeth, and 2 lateral, shorter, rounded teeth on each side. *Column* semiterete, gently curved, 1.5 cm long, with a distinct foot ca. 8 mm long, slightly dilated at apex into inconspicuous stigmatic wings, pale yellow, fading bright yellow toward the base, irregularly spotted with purple, more densely toward the apex, adaxially densely pilose-hirsute toward the base; the stigma transverse, narrow, slit-like; the rostellum acicular. *Anther cap* incumbent, cucullate, subrectangular, flattened, 2-celled. *Pollinia* 4, in 2 subequal pairs, on a broad, obcuneiform-cuspidate, sigmoid, brown stipe and a shield-shaped, basally uncinate, hyaline, brown viscidium provided with 2 lateral, narrow, acute teeth at its widest point.



Map 10. Distribution of *Pridgeonia insignis*.

Etymology: from the Latin *insigne-insignis*, remarkable, distinguished, in reference to the remarkable flower, one of the largest flowers in the whole complex of Zygopetalinae genera and species allied to *Chondrorhyncha*.

Distribution and ecology: *Pridgeonia insignis* is known only from the wet region of Zumbi along the Amazonian watershed of the Andes in southern Ecuador, where it has been found in a tropical rainforests patch (Map 10). The species flowers in cultivation in May-June.

The first, unfortunate attempt at describing *Pridgeonia insignis* was done by Harding (2008), who in her proposal of *Chondrorhyncha panguensis*, and in the absence of any fresh material at hand for study, ended up mixing several collections and creating a chimaera. Fortunately, the type of *C. panguensis* selected by the author is a specimen of *Aetheorhyncha andreettae*, so that Harding's name has no nomenclatural effects on *Pridgeonia* (see discussion here above, under *Aetherorynhca andreettae*).

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A NEW SPECIES OF *EPERUA* (LEGUMINOSAE, DETARIOIDEAE) FROM AMAZONAS STATE, VENEZUELA

Gustavo A. Romero-González[1,2] and Gerardo A. Aymard C.[3]

Abstract. A new species of *Eperua* from the upper basin of the San Miguel River, Amazonas state, Venezuela, is described and illustrated. Its affinities within the genus are discussed and an updated key to identify the 20 currently recognized taxa is provided.

Keywords: Amazonas state, banas, Detarioideae *Eperua*, Fabaceae, San Miguel River, Venezuela

Resumen. Se describe y se ilustra una nueva especie de *Eperua* de la cuenca alta del Río San Miguel, en el estado Amazonas de Venezuela. Se discuten sus afinidades dentro del género y se incluye una clave actualizada para identificar los 20 taxones que hasta el momento se reconocen, los que incluyen cuatro subespecies y cuatro variedades.

Palabras claves: banas, Detarioideae, *Eperua*, estado Amazonas, Fabaceae, Río San Miguel, Venezuela

Eperua Aubl. (Leguminosae, Detarioideae) is a Neotropical genus that currently includes 19 taxa (including four varieties and four subspecies) of small to large trees. It is found in Brazil, Colombia, Venezuela, and the Guianas (Guyana, Surinam, and French Guiana). Species occur in humid forest formations on sandy and clay soils (lowland, montane slopes, gallery and flooded forests, and Amazonian caatinga), and on the edge of shrubby savannas from sea level to 1200 m of elevation. *Eperua* is characterized by a combination of characters, including leaves always evenly pinnate, epunctate leaflets in 2–6 pairs, flowers with 1 petal and 4 scale-like petaloida, (5–)10 fertile stamens, anthers dehiscing by longitudinal slits, and non-arillate seeds (Cowan, 1975; Cowan and Berry, 1998).

Until recently, *Eperua* was treated as a natural group in subfamily Caesalpinioideae, subtribe Detarieae (Cowan and Polhill, 1981; Mackinder, 2005). However, a new classification of Fabaceae, based on a comprehensive phylogenetic analysis of the family, placed *Eperua* in subfamily Detarioideae (LPWG, 2017). A revision of the genus was published by Cowan (1975), who documented 14 species, including four varieties and four subspecies; since then, only a single new species, *E. praesagata* R.S. Cowan, has been described (Cowan, 1985). In addition, a treatment of the genus for the Venezuelan Guayana was published by Cowan and Berry (1998), and more recently, Reis (2014) revised the genus for his Master's thesis.

The woods of several species of *Eperua* are of economic importance. *Eperua falcata* Aubl. is a valuable timber tree: its wood, "Wallaba," is used for telephone poles, fence posts, house frames, fuel, and charcoal, and especially for heavy construction and, more recently, for roof shingles, which by far outperform cedar shingles (the latter manufactured from the wood of *Thuja plicata* Donn ex D. Don, Cupressaceae; see a comparison at https://www.turadashingles.com/wallaba-vs-cedar-shingles/). The wood of *E. purpurea* Bentham, a species found in the Río Negro basin in Brazil, Colombia, and Venezuela (see common names in Cowan and Berry, 1998), is locally used for bridges and general construction, but like the wood of *E. falcata*, it exudes resin after it is cut and cannot be used for fine cabinetry work. *Eperua falcata* is planted in Cameroon, Trinidad, and West Java, and *E. jenmanii* Oliv. in Cameroon, Jamaica, Mexico, Singapore, and Trinidad (Cowan, 1975).

Here we describe and illustrate a new species of *Eperua* from a "bana" (see discussion under Etymology below) in the basin of the San Miguel River, Amazonas state, Venezuela (see Romero-González et al., 2019, for a description of this basin).

Eperua banaensis G.A. Romero & Aymard, *sp. nov.* TYPE: VENEZUELA. Amazonas: Municipio Autónomo Maroa, cuenca del río San Miguel, alto caño Mee, bana sobre arena blanca al sur de la serranía de Cariche, 2°44'14"N 66°20'7"W, 106 m, 18 septiembre 2011, *G. A. Romero, C. Gómez y J. Fernández 4079* (Holotype: VEN; Isotypes: GH, TFAV). Fig. 1–3.

Eperua banaensis is vegetatively similar to *E. obtusata* R.S. Cowan, from which it differs by having 2 adaxial, lanose structures near the margins of the petal (vs. absent), 10 fertile stamens (vs. 7), and the ovary longer than the gynophore (vs. shorter).

Glabrous *treelet* 3–5 m tall; *stipules* intrapetiolar, minute, caducous; *petiole* terete, 2–4 cm long, the *rachis* slender, terete, 2.5–4.5 cm long; *leaflets* 2-jugate, the *petiolules* 7–9 mm long, the *blades* flat, glabrous, slightly oblique, obovate, ovate to narrowly elliptic, 9–14 cm long, 3.7–6.5 cm wide,

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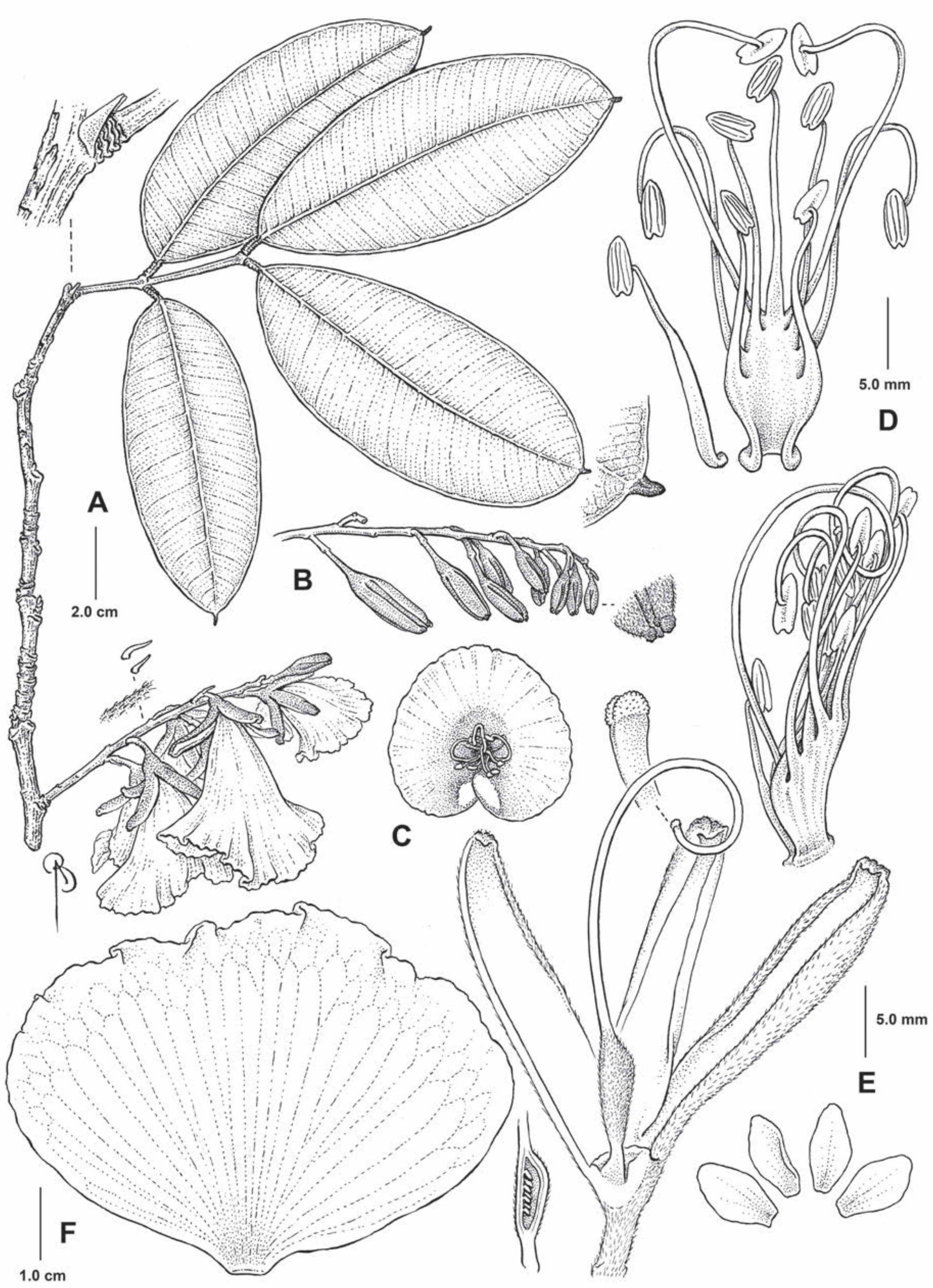

FIGURE 1. *Eperua banaensis* G.A. Romero & Aymard. **A**, a fertile branch; **B**, the inflorescence bearing flower buds, showing the single large, raised nectar gland near the apex of the outer sepals; **C**, view of the flower, showing the two lanose structures along the margins of the petal; **D**, two views of the androecium, showing the 10 fertile stamens, including the free, dorsal one; **E**, partial cutout view of the hypanthium, three sepals, and the gynoecium, showing a sagittal section of the ovary and the bilobed stigma; **F**, abaxial view of the petal, expanded. Drawing by Bobbi Angell based on the type collection.

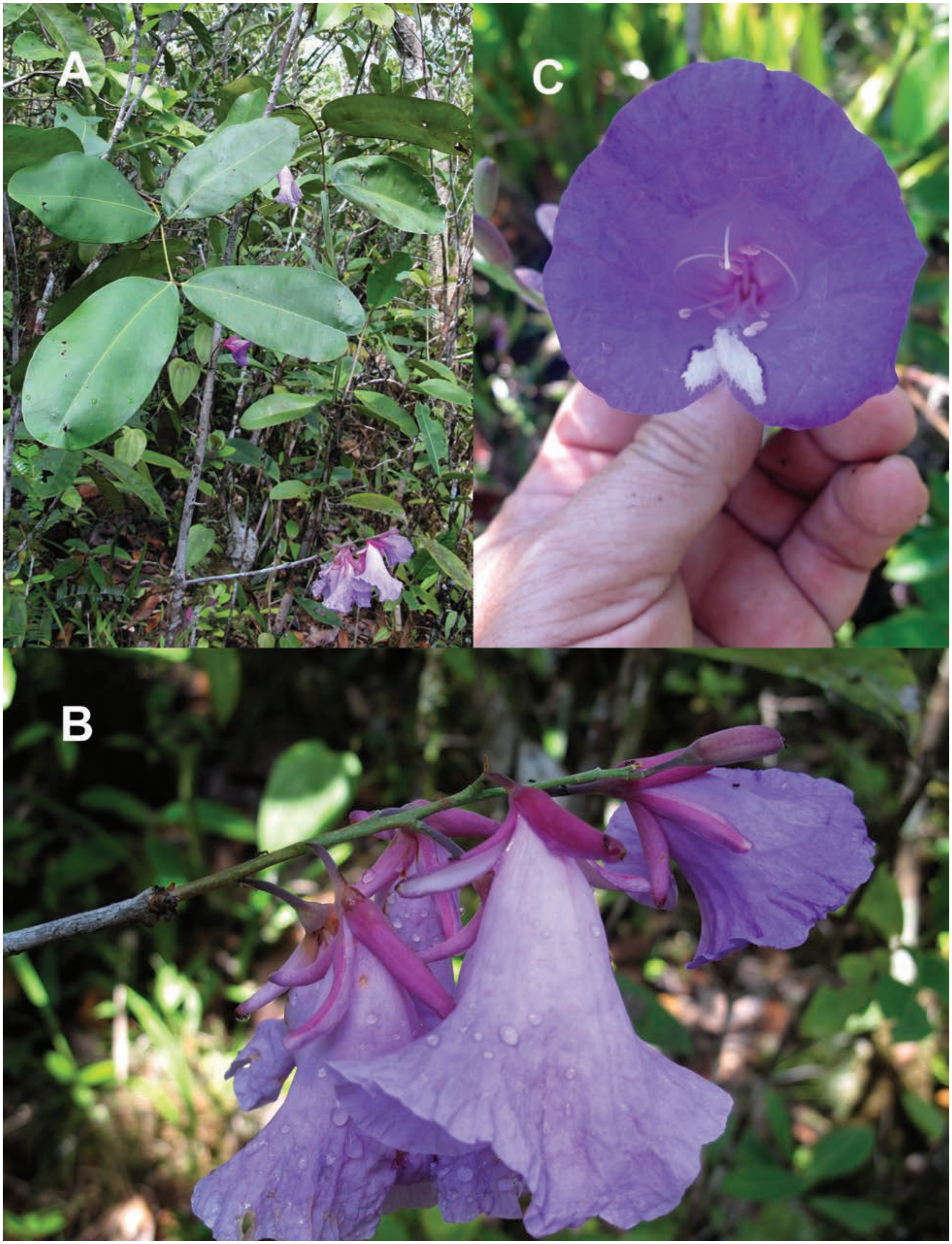

FIGURE 2. *Eperua banaensis* G.A. Romero & Aymard. **A**, habit (notice the emarginate leaflet); **B**, close-up of the raceme (notice the ants on the inflorescence axis and particularly on the tip of the terminal flower bud); **C**, view of the flower, showing in particular the petal with the two lanose structures along the margins. Photographs by G. A. Romero-González based on the type collection.

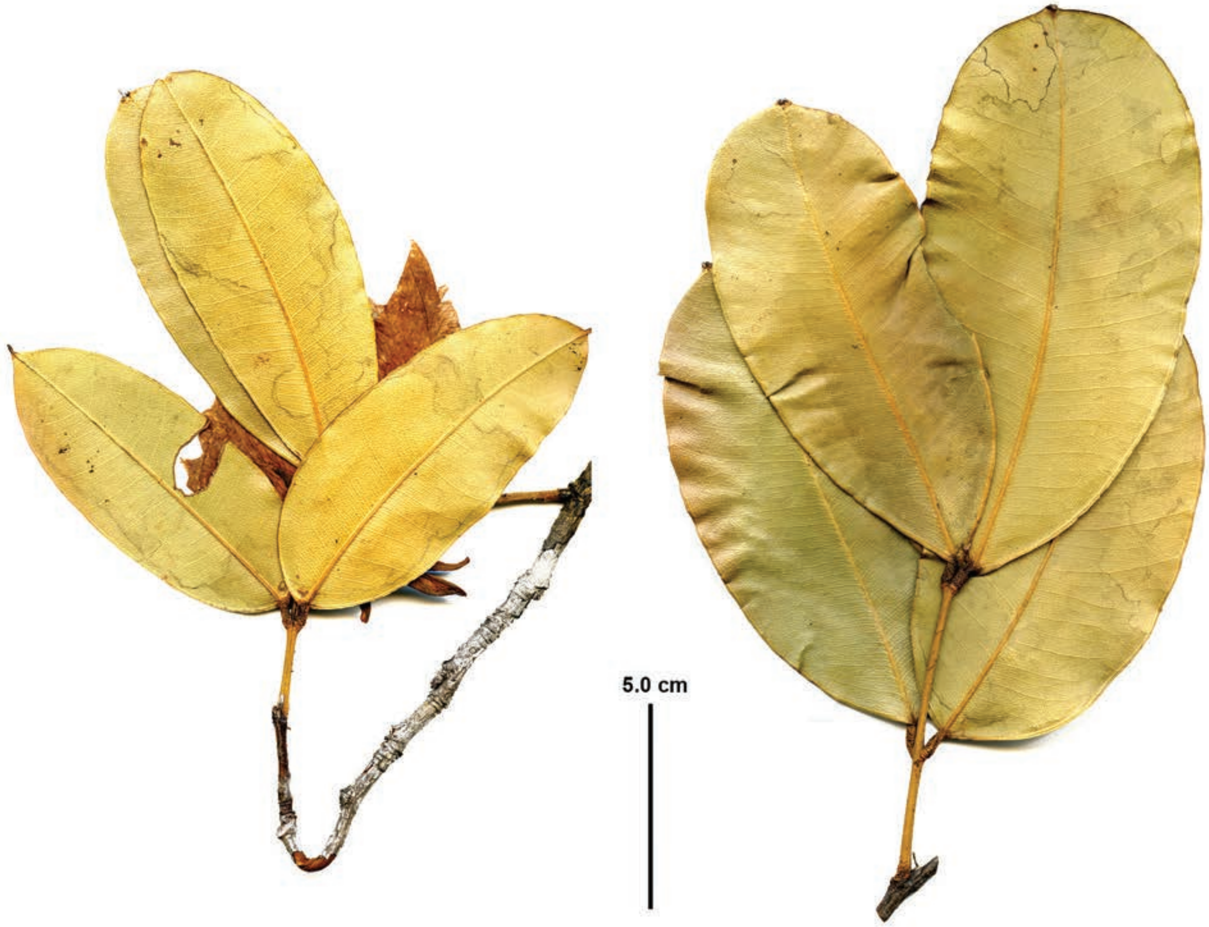

FIGURE 3. *Eperua banaensis* G.A. Romero & Aymard. **A–B**, leaf size and shape variation in type collection. Photographs by G. A. Romero-González.

rigidly coriaceous, nitid, slightly discolorous, the upper surface darker, the base usually cuneate, the apex apiculate (the apiculum brittle, most often deciduous), acute, obtuse, rounded to emarginate; *inflorescences* either individual, cauliflorous flowers or erect short racemes 1.5–11.0 cm long; the *axis* minutely strigulose, the *bracts* cupulate, the bracteoles caducous, broadly triangular, 7–8 mm long and wide, arising near the base of the pedicels; flowers generally pendent, the *pedicels* ca. 10 mm long, compressed below the bracteoles but cylindric above; *hypanthium* cylindric or cupulate, ca. 5 mm long and wide; *sepals* 4, abaxially pink, adaxially light purple, pubescent, unequal in size and shape, oval or oblong, obtuse, the 2 outer ones 25–27 mm long, 8–9 mm wide, with a single large, raised nectar gland near the apex on the outer surface, the inner ones ca. 23 mm long, marginally scarious; petal 1 (*petalodia* 4), purple, flabelliform, sessile, ca. 50 mm long and 70 mm wide, abaxially glabrous, adaxially with 2 white, lanose structures near the margins, the *petalodia* oval or elliptic-oblong, 6–7 mm long, 2.6–3.5 mm wide; *stamens* 10, glabrous, connate basally 9–10 mm, strongly inequilateral, the *filaments* light lilac, the free portion 13–30 mm long, the dorsal one 16 mm long, the anthers adaxially pink, abaxially white, narrowly oblong, 6.5–7.5 mm long, 2–3 mm wide; the *stigma* bilobate, papillate, the style ca. 36 mm long, slender, the *ovary* sericeous, oblong-obovate, 7–8 mm long and 2.5 mm wide, the *gynophore* glabrous, 2–3 mm long; *fruits* not seen (description of the flower based on samples preserved in 50% ethanol).

Etymology: from "bana," or "low Amazon caatinga… an evergreen sclerophyllous woodland …[that] occupies relatively small 'islands' amidst tall Amazon caatinga" (Bongers et al., 1985; see also Huber and Riina, 1997: 36). This type of vegetation occurs mainly in the drainage of black-water tributaries of the Río Negro in Brazil (Amazonas, Pará, and Roraima states), Colombia (Amazonas, Guainía, Vaupés, and Vichada departments), and Venezuela (Amazonas state; Aymard et al., 2014).

Ecology: no pollinator activity was observed during the collecting period, but many ants were observed on the inflorescences and flowers (especially on the tip of flower buds; Fig. 2B).

Distribution: known only from a small population at the type locality, in the sources of the San Miguel River (the upper basin of this river locally known as the Mee or Mé River), a tributary of the Guainía River, in the basin of the Rio Negro, one of the largest tributaries of the Amazon.

Eperua banaensis is apparently related to *E. obtusata* (Fig. 4), with which it shares vegetative characters. Although

FIGURE 4. Holotype of *Eperua obtusata* R.S. Cowan. Image courtesy of the Smithsonian Institution.

the protologue of the latter describes a tall tree (*Arbor alta*; Cowan, 1975: 33), an additional collection from the vicinity of the type locality, *M. Colella et al. 1864* (VEN 328381), referred here to *E. obtusata*, is described as a small tree of 2–3 m ("Arbolito de 2–3 m"), and habit alone is insufficient to separate these two species. Nonetheless, they can be distinguished easily using the floral characters presented in the diagnosis given above. We call particular attention to the two lanose structures in the margins of the petal (Fig. 1C, Fig. 2C), first reported in the genus herein, which either are found only in *E. banaensis* or have not been detected yet in live or herbarium material of other taxa.

The remote type locality of *Eperua banaensis* also yielded a new, diminutive species of *Cleistes* Rich. ex Lindl. (Orchidaceae), which remains undescribed, and *Gleasonia uaupensis* Ducke (Rubiaceae), a new report for the flora of Venezuela.

In the following key (modified from Cowan, 1975) we found it most convenient to initially separate two group of species on the basis of number of leaflet pairs (always 2 vs. 3–6). Trees of *Eperua purpurea*, however, can often bear 2-jugate leaves, but this species is distinguished easily from others bearing 2-jugate leaves by the leaflets, the surfaces of which are strongly discolorous and have "the undersurface…obscured by a microscopic layer of tangled wax filaments" (Cowan, 1975).

Key to the Taxa of *Eperua*

1a. Leaflets always 2-jugate 2

1b. Leaflets mostly 3- to 6-jugate (sometimes 2-jugate in *E. purpurea*). 6

2a. Inflorescences pendent, terminal racemes of racemes (85–)145–188 cm long; petal 2.5–3.4 cm long, abaxially sericeous at the base . . . . *E. venosa* (Guiana Shield, Bolívar state, Venezuela, endemic)

2b. Inflorescences individual cauliflorous flowers or erect short racemes 1.5–11.0 cm long; petal 4–8 cm long, abaxially glabrous to strigulose at the base 3

3a. Rachis 2.5–5.5 cm; petioles 2.0–4.5 cm long; ovary sericeous 4

3b. Rachis 7–85 cm long; petioles 8–30 cm long; ovary glabrous 5

4a. Inflorescences axillary racemes, 7.0–9.5 cm long; petal adaxially without 2 basal lanose structures near the margins; stamens fertile 7; ovary ca. as long as gynophore (5 vs. 4 mm), stigma obtuse to capitate . . . . *E. obtusata* (macrothermic forest, basin of Casiquiare canal, Amazonas state, Venezuela, endemic)

4b. Inflorescences cauliflorous flowers or axillary racemes 1.5–11.0 cm long; petal adaxially with 2 basal lanose structures near the margin; fertile stamens 10; ovary longer than the gynophore (7–8 vs. 2–3 mm), stigma bilobed . . . . *E. banaensis* (macrothermic shrubby white sand vegetation, Amazonas state, Venezuela, endemic)

5a. Leaflets narrowly revolute marginally; inflorescence axes glabrous; bracteoles 9–10 mm long, oval-ovate; pedicels and sepals glabrous, unequal in size and form; "terra firme" forest . . . . *E. glabriflora* (macrothermic forests, Amazonas and Pará states, Brazil, endemic)

5b. Leaflets flat; inflorescence axes puberulous; bracteoles ca. 5 mm long, oblate; pedicels and sepals puberulous, equal in size and form; flooded forest. . . . . *E. bijuga* (macrothermic forest, Amapá, Amazonas and Pará states, Brazil; French Guiana)

6a. Inflorescence long-pendent, 48–300 cm long 7

6b. Inflorescences erect or at least not pendent, only a few cm long 13

7a. The base of the leaflets cuneate; inflorescence not longer than 50 cm; ovary shorter than gynophore . . . . *E. praesagata* (macrothermic forest, Pará state, Brazil, endemic)

7b. The base of the leaflets rounded-obtuse, obtuse, or cordulate; inflorescence 60–300 cm long; ovary longer than the gynophore 8

8a. Leaflets falcate; stipules intrapetiolar or rarely more-or-less fused into one intrapetiolar body. 9

8b. Leaflets not falcate (elliptic, obovate, oval, ovate, lanceolate, or combinations of them); stipules free from each other, lateral at the base of the petiole 11

9a. Leaflet surfaces strongly discolorous, densely papillate-ceriferous on the undersurfaces (at least x 30), the "wax bodies" contiguous, obscuring epidermis; bracteoles scarious marginally, triangular-ovate . . . . *E. purpurea* (Río Negro and upper Orinoco basins forest, Brazil, Colombia, and Venezuela)

9b. Leaflet surfaces not discolorous, never ceriferous; bracteoles membranaceous marginally, broadly ovate or oval. 10

10a. Petal white, 2.5–3.0 × 4–5 cm; buds with a gray bloom (minutely puberulous); inflorescences 60–90 cm long, the axis of the lateral branches mostly 10–15 mm long at anthesis; staminal tube strigose-sericeous; fruits minutely strigulose . . . . *E. leucantha* (Amazon caatinga forest, sometimes near edges of shrubby savannas, Amazonas state, Brazil; Guianía and Vaupés departments, Colombia; Amazonas state, Venezuela)

10b. Petal pink to scarlet, 1.3–1.8 cm × 1.9–2.5 cm; buds brownish-strigulose; inflorescences 10–14 cm long, the axis of the lateral branches about 30–50 mm long or even longer at anthesis; staminal tube villose; fruits more or less minutely puberulous . . . . *E. falcata* (macrothermic forest, Amapá state, Brazil; Vaupés department, Colombia; Guianas; Amazonas and Bolivar states, Venezuela)

11a. Plant glabrous in all its parts; base of the leaflets cordulate; petal cream-colored, 2.8–3.0 × 3.5–5.0 cm; filaments ca 7.8 cm long, the anthers ca. 9 mm long . . . . *E. glabra* (macrothermic forest, Guyana, endemic)

11b. Plant with many parts minutely tomentulose, the hairs multicellular, irregularly branching, rusty-colored (at least x 60); base of the leaflets rounded-obtuse; petal dark pink to red or purple-red, 1.3–2.0 × 2.2–3.5 cm; filaments 3.5–5.5 cm long, anthers 5.5–7.0 mm long 12

Key to the Taxa of *Eperua* cont.

12a. Leaf rachis usually 12.5 cm long or shorter, the leaflets 3-jugate; sepals 13–20 × 4–9 mm. . . . . *E. rubiginosa* var. *rubiginosa* (macrothermic forests, Amapá, and Pará states, Brazil; Guianas)

12b. Leaf rachis usually more than 15 cm long, the leaflets 4- or 5-jugate; sepals 21–35 × 7–15 mm. . . . . *E. rubiginosa* var. *grandiflora* (macrothermic forests, Suriname, endemic)

13a. Petal white; bracteoles caducous; fruits more or less oblong, more than twice as long as wide 14

13b. Petal pink, lilac, rose-purple, or purple; bracteoles persistent; fruits more or less quadrate, less than twice as long as wide 15

14a. Leaflets mostly 5- or 6-jugate; sepals 2.2–3.0 cm long; petal 2.5–3.5 × 3.5–6.0 cm; ovary rarely with a few hairlets on the dorsal margin near the base, gynophore glabrous; staminal tube equilateral, 1.0–1.5 cm long . . . . *E. schomburgkiana* (macrothermic forests, Amazonas and Pará states, Brazil; Guianas)

14b. Leaflets mostly 4-jugate; sepals 1.2–1.8 cm long; petal 1.4–2.5 × 2.2–3.5 cm; ovary and gynophore densely tomentulose; staminal tube somewhat zygomorphic, 3.5–9.0 mm long . . . . *E. duckeana* (macrothermic forests, Amazonas and Pará states, Brazil, endemic)

15a. Petal dark lavender to purple with darker purple and white markings, mottled, basally white, 5–10 × 4.0–8.5 cm 16

15b. Petal pink to purple, 2.5–4.0 × 2.5–5.0 cm 17

16a. Bracts, bracteoles, inflorescence axes, pedicels, and hypanthium minutely puberulous; bracts 4–5 mm long . . . . *E. jenmanii* ssp. *jenmanii* (macrothermic to mesothermic forests, Roraima state, Brazil; Guianas; Bolívar state, Venezuela)

16b. Bracts and bracteoles glabrous except somewhat ciliolate; inflorescence axes, pedicels, and hypanthium glabrous; bracts 2–3 mm long . . . . *E. jenmanii* ssp. *sandwithii* (macrothermic to mesothermic forests, Roraima state, Brazil; Guianas; Bolívar state, Venezuela)

17a. Petal lilac to purple; branchlets, petioles and rachis pubescent sparingly; hypanthium equilateral; staminal tube villose 18

17b. Petal pink; branchlets, petioles, and rachis glabrous; hypanthium inequilateral; staminal tube puberulous to glabrescent. 19

18a. Large trees; leaflets oval to elliptic, the base rounded-obtuse; petal pale lilac . . . .*E. oleifera* var. *oleifera* (macrothermic forests, Amazonas state, Brazil, endemic)

18b. Treelets to small tree ca. 8 m; leaflets ovate, base cordate, petal rose-purple or purple. . . . . *E. oleifera* var. *campestris* (white sand Campina, Amazonas state, Brazil, endemic)

19a. Leaflets margins revolute, minutely venulose; anthers minutely puberulous; ovary and gynophore densely pilosulose. . . . .*E. grandiflora* ssp. *guyanensis* (macrothermic to mesothermic forests, Guyana; Bolívar state, Venezuela)

19b. Leaflets flat, the venation subobscure; anthers and gynoecium glabrous . . . . *E. grandiflora* ssp. *grandiflora* (macrothermic forests, Amazonas and Amapá states, Brazil; Guianas; Bolívar state, Venezuela)

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NOMENCLATURAL NOTES ON *CYPERUS ODORATUS* AND RELATED SPECIES (CYPERACEAE)

Gordon C. Tucker[1, 2] and Kanchi N. Gandhi[3]

Abstract. We discuss nomenclatural and taxonomic matters pertaining to three species of *Cyperus* subg. *Diclidium* (Schrad. ex Nees) C. B. Clarke, viz., *C. acicularis* (Schrad. ex Nees) Steud., *C. flexuosus* Vahl, and *C. macrocephalus* Liebm. We examined the relevant available type materials of the three species and their associated synonyms. Our study shows that based on priority, the names *C. ferax* Rich. and *C. conglobatus* Link replace *C. flexuosus* and *C. macrocephalus*, respectively. For *C. acicularis*, a later homonym (non (L.) With.), *C. strongii* G.C. Tucker & Gandhi is proposed as the replacement name. A key is provided for identification of all the *Cyperus* subg. *Diclidium* species occurring in the New World.

Keywords: Neotropical, *Cyperus*, Sedge, nomenclature

The genus *Cyperus* L. includes about 900 species, occurring worldwide in warm temperate and tropical regions (Larridon et al., 2011a, 2011b). The distribution of the individual species ranges from nearly cosmopolitan, e.g., *C. squarrosus* L. and *C. flavescens* L., to regional and narrow endemics found in most tropical and temperate regions (Alves et al., 2007; Kükenthal, 1935–1936; Tucker, 1994, 2013; Tucker et al., 2002). In the New World, areas of high diversity and endemism include the southeastern United States, Mexico, the Greater Antilles, the Guiana Shield, and eastern Brazil (Ribeiro et al., 2015; Tucker, 2007, 2013). Recent molecular studies (Larridon et al., 2011a; 2011b; 2013) demonstrated that the "Cyperus Clade" comprises 13 or more genera traditionally segregated from *Cyperus* (e.g., *Kyllinga* Rottb., *Lipocarpha* R. Br., *inter alia*), as well as confirming the majority of subgenera and sections proposed by Kükenthal (1935–1936).

Within *Cyperus (sensu stricto)*, a small but well-marked group of species is characterized by the disarticulation of the rachilla of mature spikelets into one-seeded segments. This group has been treated as either *C.* subg. *Diclidium* (Schrad. ex Nees) C. B. Clarke (Kükenthal, 1936) or given generic status as *Torulinium* Desv. ex Ham. or *Diclidium* Schrad. ex Nees (Koyama, 1978). In a DNA-based phylogeny of the genus, Reid et al. (2017) included three species of subgenus *Diclidium*: *C. odoratus* L., *C. macrocephalus* Liebm., and *C. filiformis* Sw. We have examined images of their vouchers and agree with the identifications. In the phylogeny, however, *C. odoratus* and *C. macrocephalus* were sister species, whereas *C. filiformis* was placed in sect. *Laxiglumi* (C.B. Clarke) Kük. It is emphasized here that the three species have never been the focus of a taxonomic revision, although several nomenclatural changes were made by Jones et al. (1996). In this paper, we discuss issues pertaining to the application of three species of *Cyperus* subg. *Diclidium*. We also provide a key to all species of the subgenus.

An Earlier Name for *Cyperus flexuosus*

Cyperus flexuosus has been considered to be a regional endemic species of the West Indies and northern South America (Kükenthal, 1935–1936; McLaughlin, 1944; Acevedo and Strong, 2005). This species can readily be distinguished from C. *odoratus* by the outline of its spikes, broadly ovoid or egg-shaped, with the lower spikelets reflexed (*C. odoratus* has broadly cylindric spikes with all the spikelets spreading). *Cyperus ferax* was generally included in the synonymy of *C. odoratus*. However, examination of the type of *C. ferax* (Fig. 1) shows that it is indistinguishable from the type of *C. flexuosus* (Fig. 2) Therefore, *C. flexuosus* should be removed from the synonymy of *C. odoratus*, and instead be treated as a taxonomic synonym of *C. ferax*, the oldest name for this species, as given below.

Cyperus ferax Rich., Act. Soc. Hist. Nat. Paris 1: 106. 1792. TYPE: "Cayenna Missarum A Domino Le Blond." French Guiana: Cayenne, 1792, *J. B. Le Blond s.n.* (Lectotype, here designated: P; Isolectotypes: G, P).

Homotypic synonyms: *Diclidium ferax* (Rich.) Schrad. ex Nees in C.F.P. Martius, Fl. Bras. 2(1): 54. 1842 (as *ferox*).

Mariscus ferax (Rich.) C.B. Clarke in J.D. Hooker, Fl. Brit. India 6: 624. 1894. *Torulinium ferax* (Rich.) Ham., Prodr. Pl. Ind. Occid. 15. 1825 (as *Feroci*); Urb., Symb. Antill. 2: 165. 1900 (isonym).

Except for mentioning the locality (as Cayenne) and the collector's name (as Le Blond), Richard did not cite or indicate the holotype, and the name *Cyperus ferax* needs

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FIGURE 1. *Cyperus ferax* Rich. Type specimen, conserved at the Museum Nationale d'Histoire Naturelle, Paris.

FIGURE 2. *Cyperus flexuosus* Vahl. Type, conserved at Copenhagen Herbarium. Image courtesy Field Museum of Natural History.

to be typified. Acevedo-Rodríguez and Strong (Contr. U.S. Natl. Herb. 52: 280. 2005) cited: "Type: French Guiana; Cayenne. *Leblond s.n.* (Holotype: P; Isotypes: G, P)" (sic). Since they did not use the phrase "designated here" or an equivalent, their usage of the type term "holotype" cannot be corrected to lectotype (ICN Arts. 7.10, 9.9).

Heterotypic synonyms: *Cyperus flexuosus* Vahl, Enum. Pl. 2: 359. 1805. TYPE: "Habitat in America meridionali v. Rohr [*s.n.*, *s.d.*]" Virgin Islands, [*J.P.B. Rohr 173* (Lectotype: C; photograph: F# 22395)

Diclidium vahlii Schrad. ex Nees in C.F.P. Martius, Fl. Brasil. 2(1): 53. 1842. *Cyperus vahlii* (Schrad. ex Nees) Steud., Syn. Pl. Glumac. 2(7): 48. 1854. *Torulinium vahlii* (Schrader ex Nees) C.B. Clarke in Urban, Symb. Antill. 2(1): 56. 1900. TYPE: "Habitat in America meridionali: *J. P. B. Rohr s.n.*, *s.d.* An quoque in Brasilia?" (sic; not located).

Cyperus ehrenbergii Kunth, Enum. Pl. 2: 89. 1837. TYPE: "C. strigosus (sensu) Schlechtend. in Ehrenb. herb. Ins. St. Thomae. (nec Linn.) - Insulae St. Thomae (*Ehrenb.*) et Cubae (*Poeppig*)." Virgin Islands. St. Thomas, [*C.A. Ehrenberg 77* (Lectotype (vide P. Acevedo-Rodríguez and M.T. Strong, Contr. U.S. Natl. Herb. 52: 269. 2005): HAL; isolectotype: B!).

Cyperus insignis Kunth, Enum. pl. 2: 92. 1837; *C. flexuosus* f. *insignis* (Kunth) Kuk., Pflanzenreich IV. 20 (Heft 101, 4): 622. 1936. TYPE: Trinidad: *F. W. Sieber 7* (not located).

Diclidium fuscatum Schrad. ex Nees in C.F. P. Martius, Fl. Brasil. 2(1): 52. 1842. TYPE: Brazil: Minas Gerais, Serro Frio, *C.F.P. Martius s.n.*, *s.d.* (Lectotype: M; photo F # 18870).

Herbs, perennial, cespitose, 20–40 cm tall. Rhizome 0.5–2.0 cm long, 0.5–1.5 cm in diameter, indurate, horizontal to slightly oblique. Culms 2–3 mm in diameter, trigonous, smooth (base tuberous-thickened). Leaves 2–5, 10–50 cm long, 5–10 mm wide, flanged v–shaped or inversely w–shaped, the margins scabrellate especially distally; sheaths stramineous to light brown. *Inflorescence bracts* (4–) 6 or 7, (3–) 10–28 cm long, 3–9 mm wide, the margins and keel scabrellate, horizontal to ascendant at 30–60°. Rays 8–10, 1–6 cm long; prophyll 5–10 mm long, with two apical teeth up to 3 mm long; secondary rays up to 1 cm long. *Spikes* 1–3, 10–20 (–40) mm long, (8–) 10–30 (–35) mm wide, loosely spherical (spikelets radiate, the lower reflexed); bractlets 1–2 cm long, 0.5–1.5 mm wide; prophyll 3–4 mm long, tubular, sheathing. *Spikelets* 20–40, 5–8 mm long, 0.8–1.1 mm wide, linear, subulate; rachilla articulate at the bases of the scales at maturity, ca. 0.5 mm wide, 0.1–0.4 mm thick, straight to slightly flexuous, becoming corky or spongy thickened with achene maturation, stramineous, wings 0.2–0.5 mm wide, membranous to corky, yellow to brown (clasping the mature achene), successive scales 1–1.5 mm apart. *Scales* persistent, appressed to slightly spreading, partly covering the next scale above, 6–12, 2–2.5 mm long, 2 mm wide, obovate, obtuse, slightly mucronulate (semicircular in cross-section), laterally faintly 1 (–3) nerved, reddish to stramineous to shiny brown or beige, medially 3–5 nerved, green. *Stamens* 3; filaments ca. 2 mm long; anthers ca. 0.5 mm long, ellipsoid, the connective apex minute, less than 0.1 mm long, reddish. Styles 0.5–1.2 mm long; stigmas 3, ca. 1 mm long. *Achenes* 1–1.5 mm long, ca. 0.5 mm wide, trigonous (dorsiventrally flattened or equilateral in cross-section), oblong-obovoid, slightly falcate, acute to barely obtuse, apiculate, the stipitate base 0.1–0.2 mm long, the faces flat to convex, the surface finely papillose, light brown to grayish brown.

Additional Specimens Examined: CUBA: Matanzas: near Guamá, *W.W. Thomas et al. 14767* (NY). Oriente: Sierra Maestra, Bayamo, Mina Christina, *H. Lippold 16039* (JE). DOMINICAN REPUBLIC. *L. Ekman 14454* (NY, US). HAITI. *L. Ekman 8279* (US), *Leonard & Leonard 15716* (NY, US). JAMAICA. Kingston, *Fuller 144* (ILL). MARTINIQUE. *Duss 709, 765* (NY). VIRGIN ISLANDS. St. John: Lamosure, *N.L. Britton & Shafer* 623 (MO, NY, US); St. Thomas: *N.L. Britton & Marble 1224* (NY, US). TRINIDAD. *Broadway 4312* (US). MEXICO. Quintana Roo: sur de Cozumel, rumbo al Cedral, *J.J. Ortiz 937* (MO). GUYANA. Mazaruni Station, *Forestry Dept. M394* (U). SURINAME. Toekoemoetoe-Kreek, fluv. Saramacca sup. bank 1 km S of Base Camp, *A.G.H. Daniels & F.P. Jonker 1307* (U).

An Earlier Name for *Cyperus macrocephalus*

Cyperus macrocephalus is a regional endemic species of the Caribbean and northern South America (Kükenthal 1935–1936; O'Neill, 1940; Benedict Ayers, 1946). This species can be distinguished readily from C. *odoratus* (and the other members of the subgenus) by the outline of its inflorescence, lacking rays, and having the spikelets congested into a dense mass. *Cyperus oxycarioides* has sometimes been treated as a synonym of *C. eggersii* Boeck. However, the type of *C. oxycarioides* has dense inflorescences, not the pyramidal spikes composed of ascending appressed spikelets, characteristic of *C. eggersii*. *Cyperus macrocephalus* was sometimes included in the synonymy of *C. odoratus* (Tucker, 1994; Tucker et al., 2002). Examination of the type of *C. conglobatus* (Fig. 3), however, shows that its taxonomy is the same as that of *C. macrocephalus*. Thus, the oldest name for this species is *C. conglobatus*, as shown below.

Cyperus conglobatus Humb. ex Link, Jahrb. Gewächsk. 1(3): 87. 1820.

TYPE: VENEZUELA. [Bolívar]: "[Venezuela] von Humboldt am Orinoko," in arenosis Carichane, *F.N.H.A. Humboldt 845* (Lectotype, here designated: B) [Kükenthal gives A.J.A. Bonpland as collector].

Homotypic synonyms: *Cyperus ferax* var. *conglobatus* (Humb. ex Link) Kük., Pflanzenreich IV. 20 (Heft 101, 4): 617. 1936.

C. cephalophorus J. Presl & C. Presl, Reliq. Haenk. 1(3): 170. 1828, *nom. superfl. & illegit.* [the protologue includes *C. conglobatus* Willd. Herb. in synonymy].

Diclidium conglobatum Nees in C.F.P. Martius, Fl. Bras. 2(1): 51. 1842, *nom. invalid* [Nees assigned *C. conglobatus* to *Diclidium*, but did not make the new combination].

FIGURE 3. *Cyperus conglobatus* Humb. *ex* Link. Type specimen from Berlin Herbarium.

Heterotypic synonyms: *Cyperus ignoratus* Boeck., Linnaea 36: 395. 1870. TYPE: not located ["(Ex herb. F. Ottonis) Patria?" (sic)]. Application of name follows Kükenthal (1935–1936).

Cyperus macrocephalus Liebm., Mexic. halvgr. 33. 1850. TYPE: Mexico. Veracruz, Denne udmærkede Art voxer i den oestlige Kystregion paa Bredderne af Río Nautla ved Pital (faa Mil fra dens Udloeb i mex. Bugt), og blomstrer i April og Mai." Lectotype (here designated): *F.M. Liebmann 14367* (C; Isolectotypes: GH, HAL, K, LL, MICH; photograph: F).

Torulinium macrocephalum (Liebm.) Koyama, Phytologia 29: 74. 1974.

Cyperus oxycarioides Britton, Bull. Torrey Bot. Club 11: 86. 1884.—TYPE: U.S.A. Texas, valley of the lower Rio Grande, 1878–83, *S. B. Buckley s.n.* (Holotype: NY).

Herbs, perennial, cespitose, 15–65 cm tall. Rhizome 0.5–2.0 cm long, 0.5–1.5 cm in diameter, indurate, horizontal to slightly oblique. Culms 12 mm in diameter, trigonous, smooth. Leaves 2 or 3, 15–40 cm long, 2–7 mm wide, sub-coriaceous, flat, revolute, the margins and keel scabrellate and upper surface distally; sheaths reddish brown. *Inflorescence bracts* 4–7, 4–10 (–15+) cm long, 1–8 mm wide, the margins and keel scabrellate, spreading to reflexed. Rays absent. *Spikes* aggregated into a globose head. *Spikelets* 50–100+, 5–12(–15) mm long, 0.9–1.1 mm wide, oblong to linear-lanceolate, subcylindrical; rachilla 0.3–0.4 mm wide, 0.1–0.4 mm thick, straight to slightly flexuous, becoming corky or spongy thickened with achene maturation, stramineous, wings 0.2–0.5 mm wide, membranous to corky, stramineous to bronze or carmine, rhomboidal (clasping the lower half of the mature achene), rachilla articulate at the bases of the scales at maturity. *Scales* persistent, 5–12, ca. 2 mm long, 1.5 mm wide, ovate, obtuse, sometimes mucronulate (semicircular in cross-section), laterally faintly 1 (-3) nerved, light brown or beige, medially faintly to rather conspicuously 5-nerved, green. *Stamens* 3; filaments 2–3 mm long; anthers ca. 0.5 mm long, ellipsoid, the connective apex minute, less than 0.1 mm long, reddish. Styles 0.6 mm long; stigmas 3, 1.0-1.3 mm long. *Achenes* ca. 1.2 mm long, ca. 0.5 mm wide, compressed trigonous (dorsiventrally flattened in cross-section), ellipsoid, obtuse, the stipitate base ca. 0.1 mm long, the faces flat to convex, the surface finely papillose, dull brown.

Additional Specimens Examined: CUBA. Matanzas: Mun. Ciénaga de Zapata: near Guamá, *Thomas et al. 14767* (NY). MEXICO. Campeche: Tuxpena, *C. Lundell 1042* (GH, LCA, MO, US). Quintana Roo, sur de Cozumel, 29 Aug 1985, *Ortiz 937* (MO). Sinaloa: Meseta de Cacaxtla, *Ruiz G. et al. 2006-151* (ARIZ, EIU). Veracruz: Antigua, *Purpus 6252* (GH, MO, NY); 89 km ESE of Ébano on hwy. 70, *M. Nee & Hansen 18343* (AAU). Yucatán: Uxmal, *J. Swallen 2587* (US). BELIZE. Corozal Dis., Corozal-Consejo road, *Lundell 4974* (LL). Cayo Dis., Grano de Oro, *T. Croat 23370* (AAU, MO). GUATEMALA. Petén: Uaxactun, *H. Bartlett 12769*; Remate, *C. Lundell 2091*.

A New Name for *Cyperus acicularis*

The name *C. acicularis* (Nees) Steud.(based on *Diclidium aciculare* Schrad. ex Nees), used in some floras (e.g. O'Neill, 1940), is illegitimate because of the existence of the earlier homonym *C. acicularis* (L.) With., dated 1796. Therefore, we provide a new name for this species. As in the case of *C. macrocephalus*, *C. acicularis* (Nees) Steud. and its relative *C. engelmannii* Steud. together have sometimes been treated as either varieties or synonyms of *C. odoratus*. The lapse may be explained by the fact that earlier treatments (e.g., Tucker, 1994) relied heavily on the work of Benedict Ayers (1946) who noted the difficulty in distinguishing *C. engelmannii* from *C. odoratus*, especially in South America. However, in contrast, in the earlier work by his doctoral supervisor, O'Neill (1940) provided a somewhat better account of *C. engelmannii* and *C. acicularis*. The two species can be distinguished from *C. odoratus*, provided mature spikelets are compared. Both *C. engelmannii* and *C. acicularis* can be distinguished from other species of the *C. odoratus* group by the internode of the spikelet rachilla being always longer than the corresponding floral scale. [In contrast, younger spikelets can have more closely spaced, even slightly overlapping scales (cf. Mears, 1995)] Worldwide, very few species of *Cyperus* have spikelets with such widely spaced scales. These differences are summarized in the key below.

Cyperus strongii G.C. Tucker & Gandhi, *nom. nov.*

Replaced synonym: *Diclidium aciculare* Schrad. *ex* Nees in C.F.P. Martius, Fl. Bras. 2(1): 55. 1842. TYPE: Brazil. "Habitat in ad Engenho da *Ponta Praedium et Caxoeira oppidum prov. Bahiensis*, *C.F.P. Martius* [*s.n. s.d.*]*;* "Cyperus variabilis Herb. Lindl."; "Cyperus lomentaceus Nees … quoad locum natalem Bahiam et syn. Lindl., excl. syn. Cyp. ferocis Link" (Lectotype here designated: M-0243949). Fig. 4.

C. acicularis (Schrad. ex Nees) Steud., Syn. Glum. 2(7): 45. 1854, not *Cyperus acicularis* (L.) With. (1796; based on *Scirpus acicularis* L.); *C. ferax* var. *acicularis* (Schrad. ex Nees) Kük. in A. Engler, Pflanzenreich IV. 20 (Heft 101, 4): 619. 1936.

Herb, perennial, cespitose, 30–90 cm tall. Rhizome 0.5–1.0 cm long, 1–2 cm in diameter, indurate, slightly oblique. Culms 2–5 mm in diameter, trigonous, smooth. Leaves 3–5, 15–80 cm long, 5–20 mm wide, flanged v-shaped, coriaceous, the margins and keel scabrellate; sheaths stramineous to reddish-brown. *Inflorescence bracts* 6–8, 10–60 cm long, 5–20 mm wide, the margins and keel spinulose-scabrellate, ascendant at 30–60°. Rays 4–12, 2–30 cm long; secondary rays 1–9 cm long. *Spikes* 1–5, 20–50 mm long, 20–35 mm wide, loosely ovoid. *Spikelets* (10–) 20–30, 5–25 mm long, 0.55–0.8 mm wide, linear, cylindrical; rachilla articulate at the bases of the scales at maturity, 0.3-0.4 mm wide, 0.1–0.4 mm thick, straight to slightly flexuous, becoming corky or spongy thickened with achene maturation, stramineous, wings 0.2–0.5 mm wide, membranous to corky, stramineous to bronze or carmine (clasping the mature achene and barely reaching its apex), successive scales 2.7–2.8 mm apart. *Scales* persistent, appressed, not reaching the next scale

FIGURE 4. *Diclidium aciculare* Schrad. *ex* Nees. Lectotype at Munich Herbarium. Photo from negative courtesy Field Museum of Natural History.

above, (4–) 8–12, 2.0–2.3 mm long, ca. 1.6 mm wide, ovate, obtuse, sometimes slightly mucronulate (semicircular to C-shaped in cross-section), chartaceous, laterally faintly to conspicuously 1 (–3) nerved, reddish to stramineous to shiny brown or beige, medially 2–5 nerved, green to brownish. *Stamens* 3; filaments 2.0–2.5 mm long; anthers 0.3–0.35 mm long, linear, the connective apex minute, less than 0.1 mm long, reddish. Styles 0.7–1 mm long; stigmas 3, 0.7-1.0 mm long. *Achenes* 1.6–1.7 mm long, 0.3–0.45 mm wide, trigonous (dorsiventrally flattened or equilateral in cross-section), linear to linear-oblong, slightly falcate, acute to barely obtuse, scarcely apiculate, the stipitate base 0.1(–0.2) mm long, the faces flat to convex, the surface finely papillose, dull brown.

Additional Specimens Examined: CUBA. *N.L. Britton et al. 525* (NY); *H.S. Wright 704* (US). HAITI. *Nash 330* (NY). PUERTO RICO. Mpio. Yauco, Cordillera Central, 1.6–2 km S of hwy 365 along hwy 3365, *R.D. Worthington 37549* (ILLS, UTEP). TRINIDAD AND TOBAGO. Trinidad, *N.L. Britton et al. 1142* (GH). BELIZE. El Cayo Dis., *H. Bartlett 12047*, *12872* (MICH). GUATEMALA. Izabal: Lago Izabal, El Estor, *Morales & Pérez 2978* (MO). COSTA RICA. Puntarenas: Isla del Coco, *J.L. Trusty & Kesler 468* (FTG). ARGENTINA. Jujuy: Dep. Santa Bárbara: entre El Palmar y Laguna de la Brea, *A. Cabrera et al. 29831* (AAU, SI). BOLIVIA. Chuquisaca: Hernando Siles: Sauces: Azero Norte, *Peñarenda et al. 1311* (MO). BRAZIL. Mato Grosso, Corumbá, *Silva 44* (ILL, SP). Paraiba: São Joko do Cariri, *J. Mattos 9378* (SP). Paraná: between Urai and Cornélio Procópio, *T. Koyama et al. 13738* (NY, SP). Rio Grande do Sul: Porto Alegre, *W.D. Clayton 4453* (K, SP). São Paulo: São Bernardo do Campo, *J. Mattos 15428* (SP). COLOMBIA. Antioquía: alrededores del río Ampurrumiado, *Gutiérrez & Barkley17C188* (COLO, CORD). ECUADOR. Guayas: km 5.5 Balao–Naranjal, *Laegaard 70431* (AAU). Sucumbios: Reserva Faunistica de Cuyabeno, *H. Balslev et al. 84896* (AAU). PERU. Loreto: Lower Uyucali River, 3 km W of Jenaro Herrera, *Kvist 1244* (AAU).

Eponymy: The new name honors Mark T. Strong (b. 1954), botanist at the U.S. National Herbarium, for his contributions to the botany of the Caribbean and northern South America, especially his publications on Cyperaceae.

Key to Species of *Cyperus* subg. *Diclidium*

1a. Spikelets few, ± erect or spreading; inflorescence unbranched; longest inflorescence bract erect 2

1b. Spikelets numerous; inflorescence branched (if unbranched, spikelets numerous and congested in head); inflorescence bract not erect. 3

2a. Culms single or clustered; creeping rhizome absent; Caribbean, Florida, N. South America . . . . *Cyperus filiformis* (*C. floridanus*)

2b. Culms borne singly, 2- 5 mm apart, from creeping rhizome; Jamaica endemic . . . . *Cyperus harrisii*

3a Achene linear to linear-oblong; scales not overlapping on the same side of the rachilla (separated by 0.3–0.8 mm); wings of rachilla about 0.2 mm wide, usually reaching the apex of the achene 4

3b. Achene oblong to obovoid; scales overlapping on the same side of the rachilla (by 0.4–0.9 mm); wings of rachilla 0.4–0.5 mm wide, not usually extending beyond the middle of the achene. 5

4a. Leaves and bracts membranous, 1–4(–6) mm wide; culms 1–2 mm wide below bracts; anthers ca. 0.4 mm long; secondary rays absent; plants annual, rhizome absent; primarily in eastern and central United States . . . . *C. engelmannii*

4b. Leaves and bracts coriaceous, 8–16 mm wide; culms 3–5 mm wide below bracts; anthers 1.5–1.8 mm long; secondary rays usually present, up to 15 cm long; plants perennial (sometimes flowering the first year), rhizome present; primarily in tropical America (Cuba to southern Mexico, southern to northern Argentina) . . . . *C. strongii* (*C. acicularis*)

5a. Inflorescence congested into a single ± globose, compact head, 2–3 cm in diameter; bracts reflexed; achene ellipsoid; culms sharply trigonous; leaves 4–6 mm wide . . . . *C. conglobatus* (*C. macrocephalus*)

5b. Inflorescence with some rays; bracts spreading or ascendant; achenes obovoidoblong to linearoblong 6

6a. Spikelets suberect, penicillate, very densely fascicled at the ends of the rays, into head-like or pyramidal clusters . . . . *C. eggersii*

6b. Spikelets divaricate, subdense, scattered along the rachis 7

7a. Achenes with transverse notch on the abaxial surface; Pacific coast of Central America (also Venezuela). . . . . *C. hayesii*

7b. Achenes without notch 8

8a. Plants diminutive, 2–6 cm tall, culms spreading to prostrate; endemic to Chile . . . . *C. poeppigii*

8b. Plants taller, stems erect; widespread (but not occurring in Chile).

9a. Scales orbiculate, conduplicate; Bahamas endemic . . . . *C. correllii*

9b. Scales elliptic, involute in cross-section (especially at or before anthesis); widespread species 10

10a. Spikes elliptic to egg-shaped in outline; lower spikelets reflexed, the medial spreading, the upper ascending . . . . *C. ferax* (*C. flexuosus*)

10b. Spikes broadly ovoid to shortly cylindric in outline; spikelets all spreading.

11a. Scales 1.8–2.6 mm long, laterally reddish to reddish-brown; achenes 0.8–1.1 mm long, (0.3–) 0.4–0.5 mm wide; each ray bearing 1(–3) spikes, secondary bracts usually absent or minute . . . . *C. odoratus* var. *squarrosus* (*C. ferruginescens*)

11b. Scales 1.8-3.0 mm long, laterally light to medium brownish; achenes (1.2–)1.3–1.5 mm long, (0.5–) 0.6–0.7 mm wide; rays each bearing 3–4 spikes, subtended by secondary bracts up to 6 cm long . . . . *C. odoratus* var. *odoratus*

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REVISION OF *MECONOPSIS CASTANEA* (PAPAVERACEAE) AND ITS ALLIES[1]

Toshio Yoshida[2, 3] and Hang Sun[4]

Abstract. *Meconopsis castanea* and the related *M. georgei* and *M. bijiangensis* are revised, and a related new species, *M. atrovinosa*, is described and illustrated. A distribution map of the treated species is provided.

Keywords: *Meconopsis atrovinosa, Meconopsis bijiangensis, Meconopsis castanea, Meconopsis georgei,* section *Racemosae,* series *Racemosae*

The identification of *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun (Papaveraceae) has been confused by various botanists. Taylor (1934) treated *M. castanea* in a broad sense (including its hybrids) as *M. lancifolia* (Franch.) Franch. ex Prain var. *solitariifolia* Fedde, which belongs in section *Forrestianae* C.Y. Wu & H. Chuang. However, *M. lancifolia* differs from *M. castanea* of section *Racemosae* C.Y. Wu & H. Chuang in many features. C. Grey-Wilson (2014) treated *M. castanea* as a form of *M. georgei* G. Taylor. *M. castanea,* however, differs from *M. georgei* not only in flower color but in the inflorescence and other features mentioned below, making it reasonable and proper to treat it as distinct from the latter.

The confusion of *Meconopsis castanea* with *M. lancifolia* and *M. georgei,* and occasionally with Myanmar plants of *M. bijiangensis* H. Ohba, T. Yoshida & H. Sun, is partly due to ambiguity of the localities of specimens collected from 1921 to 1932, especially those of G. Forrest.

On specimens of *Meconopsis castanea sensu lato* collected by G. Forrest, the localities were written as Mekong [Lancang Jiang, 澜沧江]-Salwin [Nu Jiang, 怒江] divide, or Fuchuan Shan [富川山]; on specimens collected by J. F. Rock, who followed G. Forrest's routes, the localities were written as Mount Fu-Chuan, west of the Mekong-Salwin divide and west of Wei-hsi [Weixi, 维西], or Fuchuan range, Mekong-Salwin divide and west of Wei-hsi. The specimen of *G. Forrest 30101* wrongly records the locality as Fuchuan Shan, Mekong-Yangtse [Jinsha Jiang, 金沙江] divide. In fact, Fuchuan Shan is not part of the Mekong-Yangtse divide, but in the Mekong-Salwin divide. On these specimens, the flower color was given as pale to dark purplish rose and blue or deep purple crimson by G. Forrest and pale blue, bluish purple, and red or dark purple by J. F. Rock.

Although the name Fuchuan (富川) is not shown on maps published in China, it is shown on sheet 2 of the maps accompanying Rock (1947) to be a large village located around 26°55'57"N, 99°08'32"E, on the eastern foot of Biluo Xueshan (碧罗雪山), or the southern part of Nu Shan (怒山), or in the Mekong-Salwin divide.

Fuchuan had been a prosperous village at the junction of trade routes supplied with many forest products such as timber, walnuts, medicinal plants, and lacquerware in the days when Forrest and Rock visited and before the modern motor road was constructed along the bottom of the Lancang Jiang valley. From Fuchuan to the west, a well-trodden path connects to Lumadeng (鹿马登), which is located near the bottom of Nu Jiang valley via Xinhua (新化) village and the pass on the main ridge of Biluo Xueshan. No other path, except for narrow, tricky footpaths, crossed the main ridge of Biluo Xueshan in the region west of Weixi. "Fuchuan Shan" on Forrest's specimens is considered to refer to the mountainous area around the pass (Fig. 1, 2).

Meconopsis georgei G. Taylor was also collected by Forrest and Rock in a region similar to where *M. castanea sensu lato* was collected. The localities given for *M. georgei* by Forrest were written on the specimen as Fuchuan Shan, Mekong-Yangtze [mistaken for Salwin] divide, or simply as Wei-hsi area; those collected by Rock were written as Fuchuan range, west of the Mekong-Salwin divide and west of Wei-hsi. The flower color was given as clear primrose-yellow on *Forrest 30100*, and yellow on *Rock 22696*. Taylor (1934) recognized these specimens as being a distinct species, *M. georgei* G. Taylor, and different from *M. castanea sensu lato*, which he treated as *M. lancifolia* (Franch.) Franch. ex Prain var. *solitariifolia* Fedde. He (Taylor, 1934) wrote in a note under *M. georgei*, "The specific epithet commemorates George Forrest, who discovered the species in the Fu-chuan mountains in 1931 during his last expedition. It was collected the following year by Rock in the same mountains, and specimens have also been sent to this country by Forrest's native collectors. As seed accompanied these collections it may be hoped that the species, which in nature grows on scree, will become established in gardens. It is quite unlike the other yellow-

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[1] Comments in the text placed in between square brackets are by the authors.

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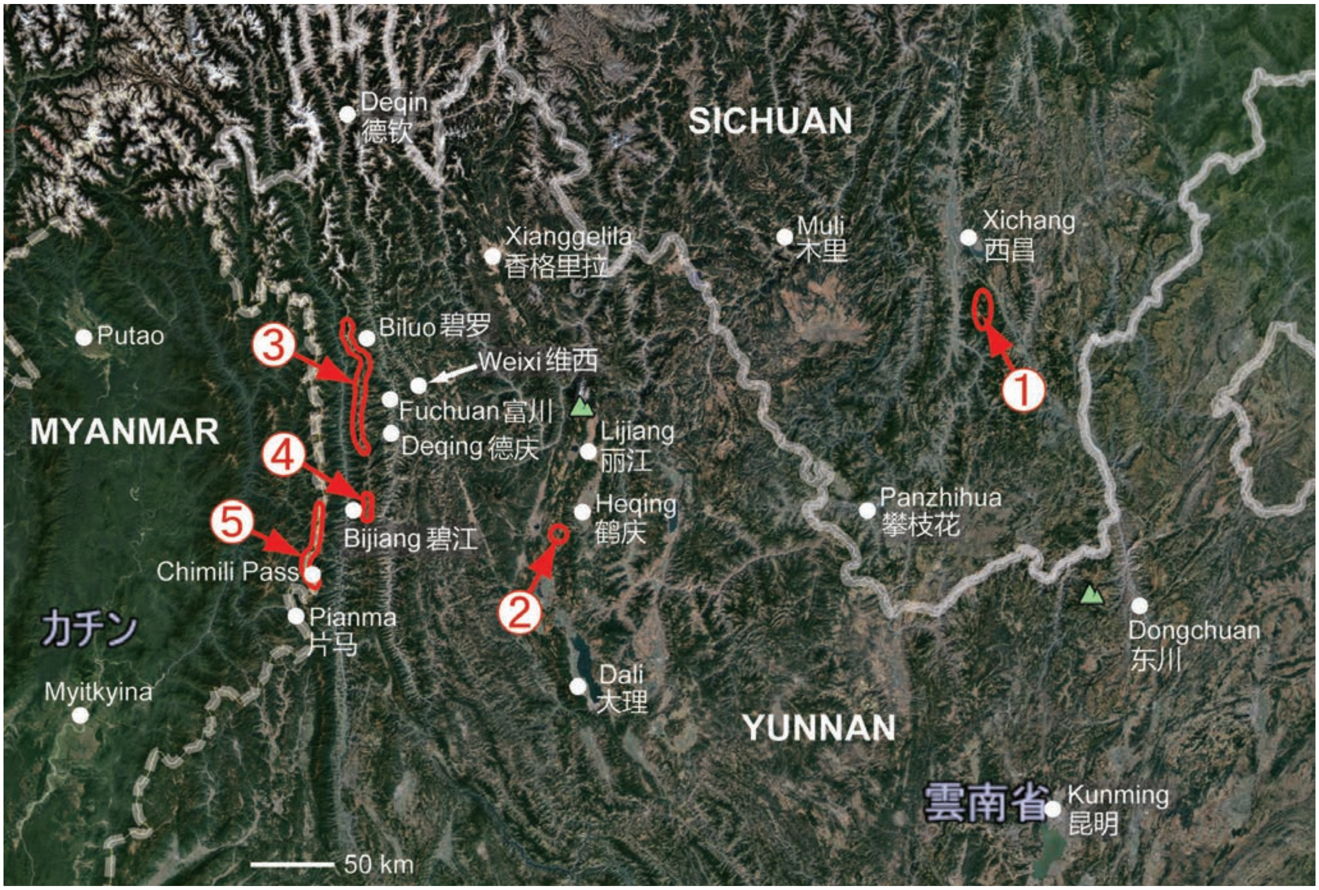


FIGURE 1. Distribution map of *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun and allies based on Google Earth with supposed delineations of five regions that each include the locality of at least one specimen of the species. Region 1: SW Sichuan, Luoji Shan; Region 2: NW Yunnan, Heqing Xian; Region 3: NW Yunnan, Fugong Xian and Weixi Xian, Biluo Xueshan (southern part of Nu Shan); Region 4: NW Yunnan, Bijiang region, Biluo Xueshan (southernmost part of Nu Shan); Region 5: NE Myanmar, Kachin State, western slopes of Gaoligong Shan around Chimili Valley, and NW Yunnan, Bijiang region, Gaoligong Shan. Treated species with their distribution regions: *M. atrovinosa* T. Yoshida & H. Sun (Regions 1, 2); *M. bijiangensis* H. Ohba, T. Yoshida & H. Sun (Regions 4, 5); *M. castanea* H. Ohba, T. Yoshida & H. Sun (Region 3); *M. georgei* G. Taylor (Region 3).

flowered members of the genus in having harsh prickles, while the flowers are borne on comparatively long pedicels arising near the base of the stem.

In the summer of 2008, one of us (Yoshida) crossed Biluo Xueshan by following narrow footpaths between Laowo (老窝), west of Deqing (德庆) on the eastern flank of Biluo Xueshan, and Fugong (福贡), located near the bottom of the Nu Jiang gorge, and collected the type specimens of *Meconopsis castanea, T. Yoshida K3*, on the western side of the main ridge. The flowers of these plants were dark red.

In the following summer of 2009, Yoshida visited the pass on the route between Xinhua (新化), located west of Fuchuan village, and Luomadeng, located on the eastern bank of the Nu Jiang, and collected specimens (*T. Yoshida K20*) of *Meconopsis* aff. *castanea*. Most plants in the population around the pass were on the eastern side of the pass, but some plants were also close to the pass on the western side. The flowers of this population were pale purplish blue, pale pink or whitish, occasionally deep red, with populations of plants with different flower colors growing together. No plants of *M. georgei* with yellow flowers were found around the pass.

In 2011, Yoshida visited Biluo Xueshan by following narrow footpaths from Tuobaluo (托八洛), west of Biluo Cun (碧罗村), and collected specimens (*T. Yoshida K68*) of *Meconopsis castanea* on west- or south-facing gentle slopes on the main ridge of Biluo Xueshan. The flowers of those plants were dark red.

On the basis of our collaborative studies of the specimens, photographs, literature, and geography of *Meconopsis castanea* sensu lato, we have determined that *T. Yoshida K20* is a hybrid between *M. castanea* and *M. georgei* and that many of the specimens collected by Forrest and Rock on Fuchuan Shan and on Biluo Xueshan west of Weixi are also hybrids between the two species, although it is difficult to distinguish hybrids from *M. castanea* in old specimens.

The specimens of the taxa treated below were assigned to regions to generate the distribution map (Fig. 1).

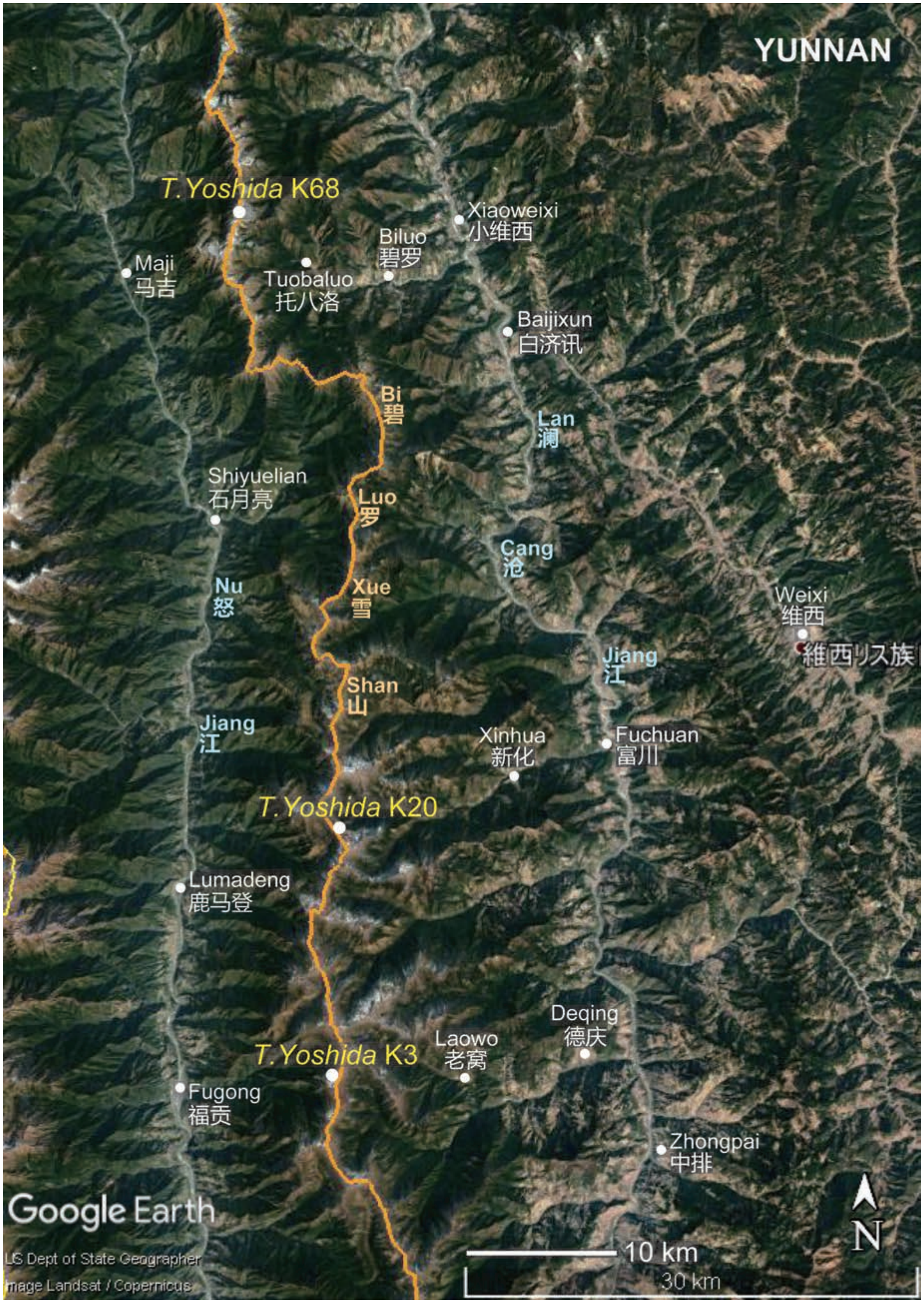


FIGURE 2. Enlarged map of Region 3 based on Google Earth with specimen localities of *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun, *T. Yoshida K3* and *K68*, and its hybrid with *M. georgei* G. Taylor, *T. Yoshida K20*.

TAXONOMY

Meconopsis* section *Racemosae C.Y. Wu & H. Chuang series ***Racemosae*** C.Y. Wu & H. Chuang, *Acta Bot. Yunnan.* 2 (4): 374 (1980), emend. excl. series *Grandes*.

The section *Racemosae* and the series *Racemosae* were revised by C. Grey-Wilson in *The Genus Meconopsis—Blue Poppies and Their Relatives* (2014: 45).

Herbs, monocarpic, most parts prickly with spine-like hairs. Inflorescence a raceme, usually simple, or occasionally scapose (*M. horridula*) or subscapose (*M. georgei* and *M. horridula*), ebracteate except lowermost flowers. Petals 4–9, blue, mauve, purple, pink, or occasionally dark purple, dark red, yellow, or white. Filaments filiform or thickly filiform, similar to or darker than petals in color, occasionally with whitish vascular bundles protruding from apex (*M. elongata* and *M. atrovinosa*).

Thirteen species are included in series *Racemosae*: *M. atrovinosa* T. Yoshida & H. Sun, *sp. nov.*; *M. bijiangensis* H. Ohba, T. Yoshida & H. Sun; *M. castanea* H. Ohba, T. Yoshida & H. Sun; *M. elongata* T. Yoshida, R. Yangzom & D.G. Long; *M. georgei* G. Taylor; *M. horridula* Hook. f. & Thomson; *M. lhasaensis* Grey-Wilson; *M. merakensis* T. Yoshida, R. Yangzom & D.G. Long; *M. prainiana* Kingdon-Ward; *M. prattii* Prain; *M. racemosa* Maxim.; *M. rudis* (Prain) Prain; and *M. zhondianensis* Grey-Wilson.

KEY TO *MECONOPSIS CASTANEA* AND RELATED SPECIES

1a. Inflorescence subscapose, with short rachis and long ascending pedicels; petals yellow, apex triangular, acute or acuminate. . . . . .*M. georgei*

1b. Inflorescence racemose; petals blue, mauve, purple, pink, or occasionally dark purple, dark red, or white, apex rounded or obtuse. 2

2a. Flowers deeply cup-shaped; petals 4, rarely 5 or 6, mauve or pale purple; capsules 2.0–4.7 cm long . . . . *M. bijiangensis*

2b. Flowers dish-, bowl-, or cup-shaped; petals (4–)5–9, maroon, dark red, dark wine-colored, or dark purple; capsules 1.5–3.0 cm long 3

3a. Prickles pale brown or reddish-brown, not tinged dark purple at base; margin of lamina coarsely and irregularly crenate, toothed or lobed; petals 4 or more; anthers orange; capsules 2–3 cm long. . . . .*M. castanea*

3b. Prickles pale yellowish green, tinged dark purple at base; margin of lamina usually entire; petals 5 or more; anthers dull yellow tinged dark purple; capsules 1.5–2.0 cm long . . . . *M. atrovinosa*

Meconopsis georgei G. Taylor, *The Genus Meconopsis* 86. 1934. TYPE: CHINA. NW Yunnan, Fugong Xian (福贡县): Fuchuan Shan [富川山], Mekong-Yangtze [mistake for Salwin] divide, 12,000–13,000 ft, July–August, 1931, *G. Forrest 30100* (Holotype: E; Isotype: BM). Fig. 1–5.

Herbs, monocarpic, 15–32 cm tall. *Taproot* elongate, to 10 cm long or more, 5–10 mm across, contracted at junction with stem. Most parts of plant prickly; *prickles* to 5 (–7) mm long. *Stem* (below lowermost flower) simple, 1.5–6.0 cm long, mostly underground. *Leaves* alternate on short stem, petiolate; *petiole* membranous, linear or broadly linear, 3–7 cm long, 1–4 mm wide; *lamina* oblanceolate, lanceolate, or oblong, occasionally linear-oblong, or elliptic or ovate on lowest leaves, 1.5–11.0 cm long, 0.5–2.0 cm wide, base attenuate or occasionally cuneate, margin entire or occasionally coarsely crenate or toothed, apex acute, acuminate or occasionally obtuse. *Inflorescence* subscapose with short rachis and long ascending pedicels, ebracteate except for a few flowers near base of inflorescence; *rachis* 2–5 mm across near base in dried specimens; *bracts* similar to leaves but with shorter petiole; *pedicels* 5–15 cm long. *Flowers* 5–9, 3-dimensional shape unknown. *Calyx* 0.8–1.5 cm long. *Petals* (4 or)5–8, yellow, rhombic-elliptic or obovate, 2.5–3.3 cm long, 0.8–1.7 cm wide, base cuneate, margin irregularly denticulate near apex, apex triangular, acute or acuminate. *Stamens* numerous; *filaments* filiform, 7–12 mm long; *anthers* oblong, 0.8–2.0 mm long, color unknown. *Ovary* ovoid, 7–12 mm long, with dense ascending prickles; *style* 2–6 mm long in flower; *stigma* capitate, 1.0-1.8 mm across. *Capsules* ellipsoid, 1.7–2.4 cm long, 6–15 mm across, with dense prickles; carpels 3–5, often 4, dehiscent in upper 1/5–1/4.

Distribution: CHINA. NW Yunnan: Fugong Xian (福贡县), Fuchuan Shan [富川山], or Biluo Xueshan (碧罗雪山), 3600–4350 m.

Habitat: open stony alpine meadows (according to Forrest); in scree (according to Rock).

Specimens examined: CHINA. NW Yunnan, Fugong Xian, Biluo Xueshan, **Region 3:** Fuchuan Shan, Mekong-Yangtze divide, lat. 27˚N, long. 99˚30'E. [Fuchuan Shan is not on the Mekong-Yangtse divide, but on the Mekong-Salwin divide as indicated on Rock's specimens, *J. F. Rock 22696*, *23287*], July–August 1931, *G. Forrest 30100* (BM, E); Wei-hsi area, 1931, *G. Forrest 30595* (BM, E); Fuchuan range, west of the Mekong-Salwin divide and west of Wei-hsi, alt. 13,500–14,500 ft, May–June, 1932, *J. F. Rock 22696* (BM, K); same locality, August–September 1932, *J. F. Rock 23287* (K).

Meconopsis bijiangensis H. Ohba, T. Yoshida & H. Sun, *J. Jap. Bot.* 84 (5): 294. 2009. TYPE: CHINA. NW Yunnan, Fugong Xian (福贡县): Bijiang (碧江) region, Biluo Xueshan (碧罗雪山), around the head of Pi-he (匹河) valley, 3700–4000 m, 8 July 2008, *T. Yoshida K1* (Holotype: KUN; Isotypes: KUN, TI). Fig. 1, 6–10.

Homotypic Synonym: *M. bijiangensis* H. Ohba, T. Yoshida & H. Sun subsp. *chimiliensis* Grey-Wilson, *The Genus Meconopsis—Blue Poppies and Their Relatives* (2014: 271).

Herbs, monocarpic, 15–40 cm tall in flower. *Taproot* elongate, to 15 cm long or more, 5–13 mm across. Most parts of plant prickly; *prickles* pale brown or amber, to 4 mm long, moderately stiff, borne on raised, rounded, or elliptic pustules tinged dark purple. *Stem* (below lowermost flower) simple, 3–10 cm long, 5–12 mm across. *Basal leaves* petiolate; *petiole* membranous, broadly linear, 3–10 cm long, 2–4 mm wide; *lamina* ovate or lanceolate, 2.5–10.0 cm long, margin coarsely crenulate or subentire. *Stem leaves and bracts* short petiolate or sessile; *lamina* linear-oblong with parallel sides, 5–15 cm long, 7–17 mm wide, base attenuate,

FIGURE 3. Holotype of *Meconopsis georgei* G. Taylor, *G. Forrest 30100* (E) from "Fu-chuan Shan," with note "Flowers clear primrose-yellow."

FIGURE 4. Isotype of *Meconopsis georgei* G. Taylor, *G. Forrest 30100* (BM), with apex of petal magnified.

PLANTAE ROCKIANAE
Expedition of the University of California Botanical Garden to Southwestern China.
Plants of Yunnan

Meconopsis Georgei G. Tayl.

In scree.
Altitude 13,500-14,500 feet.

Fuchuan range, west of the Mekong-Salwin divide and west of Wei-hsi.
Joseph F. Rock, No. 23287 August–September 1932

FIGURE 5. Fruiting specimen of *Meconopsis georgei* G. Taylor, *J. F. Rock 23287* (K), collected on “Fuchuan range, west of the Mekong-Salwin divide and west of Wei-hsi.”

Figures 6–9. **6**. *Meconopsis bijiangensis* H. Ohba, T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 8, 2008. **7**. *Meconopsis bijiangensis* H. Ohba, T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 8, 2008. **8**. Habitat of *Meconopsis bijiangensis* H. Ohba, T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 8, 2008. **9**. Dead plant of *Meconopsis bijiangensis* H. Ohba, T. Yoshida & H. Sun with previous year's capsules at the type locality. Photograph by T. Yoshida, July 8, 2008.

FIGURE 10. Type specimen of *Meconopsis bijiangensis* H. Ohba, T. Yoshida & H. Sun subsp. *chimiliensis* Grey-Wilson, *R. J. Farrer 1159* (E), collected in NE Myanmar, Chimili Valley, Hpawshi Bum, with provisional name *M. "cyanochlora"* by the collector.

margin coarsely crenate or toothed, sometimes undulate, occasionally subentire, apex obtuse to acute, upper surface dark green, somewhat shiny, sometimes tinged dark purple along margin, lower surface somewhat paler, both surfaces with dense patent prickles. *Inflorescence* a simple raceme occupying most of plant above ground, ebracteate except on lowermost third to fifth; *pedicels* 2–12 cm long in flower, to 15 cm long in fruit, densely prickly. *Flowers* 7–12, often 10, deeply cup-shaped, usually nodding. *Calyx* 1.2–1.7 cm long, with dense spreading prickles. *Petals* 4, rarely 5 or 6, pale mauve or pale purple, rounded, broadly ovate or elliptic, 2.0–3.5 cm long, 1.7–3.5 cm wide, margin entire, sometimes denticulate and minutely undulate near apex, apex rounded or obtuse. *Stamens* numerous; *filaments* somewhat darker than petals, filiform, 7–10 mm long; *anthers* orange, ellipsoid or oblong, 1.5–2.0 mm long. *Ovary* ellipsoid, 5–10 mm long, with dense ascending prickles. *Style* 2.5–5.0 mm long, to 7 mm long in fruit. *Stigma* capitate, 1.0–1.5 mm across. *Capsules* cylindrical-ellipsoid, narrowly ellipsoid or narrowly obovoid, 2.0–4.7 cm long, 6–13 mm across, 3- to 4-grooved, with dense spreading prickles shorter than those on stem. *Seeds* black, reniform, 2.0–2.3 mm long, longitudinally wrinkled or obscurely pitted.

Distribution: CHINA. NW Yunnan: Bijiang (碧江) region, Biluo Xueshan (between 26°37'24"N, 99°00'48"E and 26°31'10"N, 99°00'35"E) and Gaoligong Shan (高黎贡山). MYANMAR. Kachin State: western slopes of Gaoligong Shan around Chimili valley. 3500–4000 m.

Habitat and ecology: on Biluo Xueshan, *Meconopsis bijiangensis* is often gregarious on west-facing (Nu Jiang side), gentle, stony alpine slopes near the main ridge, sometimes among dwarf shrubs of *Rhododendron*, just above the steep head of valleys where ascending foggy winds from the southwest summer monsoon gather and swiftly flow over the slopes and bring moisture to the plants growing there; rooting in thick, dry, peaty soils derived from half-decomposed mosses and other plants. Alpine meadows, moors, or rarely rocky places, according to the specimen, *R. J. Farrer 1159*, collected in Chimili, NE Myanmar.

Additional specimens examined: MYANMAR. Kachin State, western slopes of Gaoligong Shan around Chimili valley, **Region 5:** Hpawshi Bum, 11,000–12,500 ft, 1 August 1919, *R. J. Farrer 1159* (E) [The plant was referred as "a new Poppy" in E. H. M. Cox's *Farrer's Last Journey* (1926: 131)]; western flank of Chimi-li, N'Maikha-Salwin divide, 26°23'N, 98°48'E, 11,000–12,000 ft, June 1924, *G. Forrest 24655* (E); same locality, August 1924, *G. Forrest 24886* (E, K); western flank of N'Maikha-Salwin divide, N of the Chimi-li, 26°35'N, 98°48'E, 12,000–13,000 ft, June 1925, *G. Forrest 26831* (BM, E, K); western flank of N'Maikha-Salwin divide, 26°24'N, 98°48'E, 12,000 ft, June 1925, *G. Forrest 26902* (BM, E, K); same locality, October 1925, *G. Forrest 27277* (E, K); western flank of the N'Maikha-Salwin divide, N of the Chimili, 26°35'N, 98°48'E, 12,000–13,000 ft, at the same location as *G. Forrest 26831*, October 1925, *G. Forrest* 27284 (E, K); Chimili, 1931, *G. Forrest* 29934 (BM, E). CHINA. NW Yunnan, Bijiang region, Gaoligong Shan, **Region 5:** Bijiang Gaoligong Shan (碧江高黎贡山), on the main ridge of the range running along the boundary between China and Myanmar (中缅国界境山背上), 14 July 1978, *Bijiang Research Team* (碧江考查队) *1135* (KUN). NW Yunnan, Bijiang region, Biluo Xueshan, **Region 4:** Bijiang Biluo Xueshan (碧江碧罗雪山), near Jiumingfang (救命房附近), 4250 m, 12 September 1964, *Sugong Wu* (武素功) *8832* (KUN) [The roots are used for an indigenous drug with a name of Paoshen, 泡参, according to the note]; Bijiang Xian (碧江县), Biluo Xueshan Longtan (碧罗雪山龙潭), 3900–4000 m, 16 June 1978, *Nujiang Research Team* (怒江考查队) *0848* (KUN); around the head of Pi-he (匹河) valley, 3700–4000 m, 8 July 2008, *T. Yoshida K1* (KUN, TI).

Bijiang region refers to the former Bijiang Xian (碧江县). In 1986 the northern part of Bijiang Xian was incorporated in Fugong Xian and the southern part was incorporated in Lushui Xian.

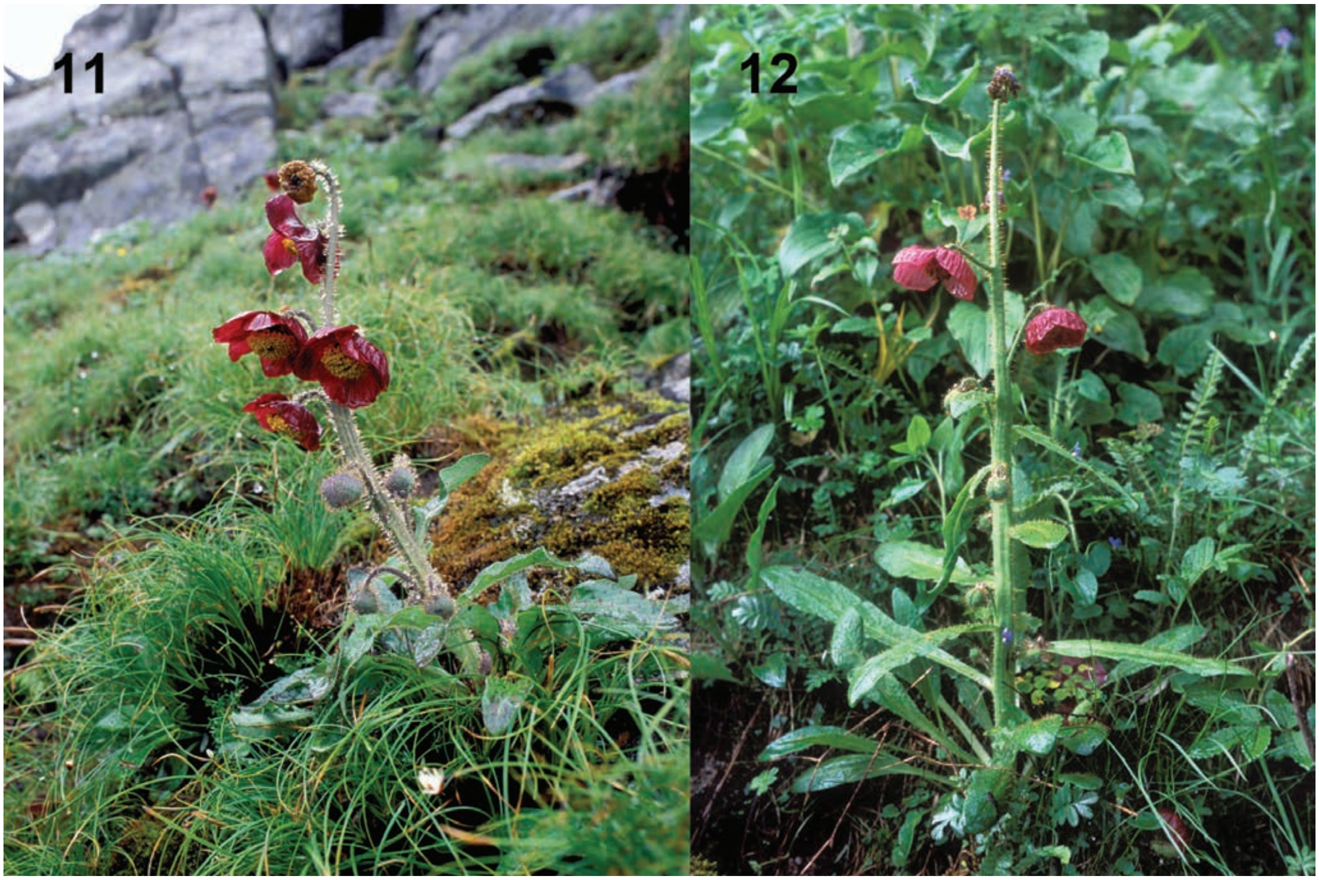
Gaoligong Shan runs along the boundary between Kachin State, Myanmar, and Fugong Xian (福贡县) and Lushui Xian (泸水县) in Yunnan, China. The location of Chimili, on specimens collected by G. Forrest and R. J. Farrer, appears on the map on the front page of F. Kingdon-Ward's (1949) *Burma's Icy Mountains* as "Chimeli" Pass, which is located on the boundary between Myanmar (Burma) and China, as indicated here in Fig. 1.

Grey-Wilson (2014) described *Meconopsis bijiangensis* subsp. *chimiliensis* Grey-Wilson in his monograph of *Meconopsis* for the population of *M. bijiangensis* in Myanmar on the basis of differences in diagnostic characters from the typical plant that include greater height, larger leaves with longer petioles, and relatively narrower fruit capsules. However, plants within a population can vary continuously and are not distinguishable from typical plants as different taxa. Grey-Wilson, in his monograph of *Meconopsis* (2014: 276), wrongly indicated the distribution of *M. bijiangensis* subsp. *chimiliensis* to be west of N'Maikha, a tributary of the Irrawaddy (Ayeyarwady), far from the boundary between Myanmar and China. There are no mountains taller than 3000 m elevation where *M. bijiangensis* can grow in the region marked by him.

Meconopsis castanea H. Ohba, T. Yoshida & H. Sun, *J. Jap. Bot.* 84 (5): 300. 2009. TYPE: CHINA. NW Yunnan, Fugong Xian (福贡县): S of Laowo Shan (老窝山) on Biluo Xueshan (碧罗雪山), between 26°55'35"N, 98°57'56"E and 26°56'11"N, 98°58'58"E, 3650–4000 m, 17 July 2008, *T. Yoshida K3* (Holotype: KUN; Isotypes: KUN, TI). Fig. 1–2, 11–16.

Homotypic synonym: *M. Georgei* G. Taylor forma *castanea* Grey-Wilson, *The Genus Meconopsis—Blue Poppies and Their Relatives* 274. 2014.

Herbs, monocarpic, 20–40 cm tall in flower, to 50 cm or more in fruit. *Taproot* elongate, 10–25 cm long, 5–10 mm across. Most parts of plant moderately or densely prickly; *prickles* pale brown or reddish-brown, to 4(–5) mm long, moderately stiff, without blackish spots at base. *Stem* (below lowermost flower) simple, 2.5–10.0 cm long, 4–7 mm across. *Basal leaves* petiolate; *petiole* membranous, broadly linear, 3–7 cm long, 2.5–4.0 mm wide; *lamina* ovate, elliptic or lanceolate, 3–5 cm long, margin coarsely



FIGURES 11–12. **11**. *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun at the type locality, 4000 m elevation. Photograph by T. Yoshida, July 17, 2008. **12**. *Meconopsis castanea* at the type locality, 3650 m elevation. Photograph by T. Yoshida, July 16, 2008.

crenulate, or subentire in smaller leaves. *Stem leaves and bracts* short petiolate or sessile; *lamina* ovate, lanceolate, oblanceolate, oblong, or more often linear-oblong, 5–12 cm long, 5–20 mm wide, base attenuate, margin coarsely and irregularly crenate, toothed or lobed, apex obtuse or acute, upper surface green, lower surface somewhat paler, whitish in dried specimens, both surfaces with spreading prickles, somewhat densely so on upper surface. *Inflorescence* a simple raceme occupying most of plant above ground, ebracteate except in lower half; *rachis* 4–7 mm across near base in dried flowering specimens; *pedicels* 2.5–7.0 cm long in flower, to 15 cm long in fruit. *Flowers* 6–10, often 8, dish- or cup-shaped, usually half nodding. *Calyx* 10–14 mm long, with dense spreading prickles. *Petals* 5–9, occasionally 4, maroon, dark red or dark reddish-purple, obovate, rounded, ovate, elliptic, 2.5–3.5 cm long, 1.3–2.5 cm wide, margin entire, sometimes denticulate near apex, apex rounded or obtuse. *Stamens* numerous; *filaments* darker than petals, filiform, 7–10 mm long; *anthers* orange, oblong, 1.7–2.0 mm long. *Ovary* ellipsoid, 5–8 mm long, with dense ascending prickles; *style* 2–5 mm long in flower, to 7 mm long in fruit; *stigma* capitate, 1.5–2.5 mm across. *Capsules* obovoid, ellipsoid or cylindrical-ellipsoid, 2–3 cm long, 6–10 mm across, with dense spreading prickles.

Distribution: CHINA. NW Yunnan: Fugong Xian (福贡县) and Weixi Xian (维西县), Biluo Xueshan (碧罗雪山), or the southern Nu Shan (怒山), 3650–4150 m elevation.

Habitat and ecology: on steep boulder slopes partly covered with mosses or stony alpine slopes thinly covered with lichens, mosses, and other dwarf plants exposed to wet summer monsoon; rooting deeply into blackish muddy soil among stones.

Additional specimens examined: CHINA. NW Yunnan, Biluo Xueshan, Fugong Xian and Weixi Xian, **Region 3:** Mekong-Salwin divide, 27°30'N, 98°56'E, 13,000 ft, July 1921, *G. Forrest 19490* (BM); same locality, July 1921, *G. Forrest 19790* (BM, E); west of Tuobaluo (托八洛) and Biluo Cun (碧罗村), on the boundary between Fugong Xian and Weixi Xian, 27°25'31"N, 98°54'55"E, 3850–3950 m, 22 July 2011, *T. Yoshida K68* (KUN).

Forrest 19490 and *19790* were collected in the same locality. If the coordinates recorded on the specimens are accurate, the location is on the northern periphery of the distribution of *Meconopsis castanea*, indicated as Region 3 in Fig. 1.

Forrest 19790 (E) is unusually branched at the base with 5 flowering branches (Fig. 16). As already suggested by C. Grey-Wilson (2014: 274) in his monograph of the genus, the branching may be due to damage of the young shoot. However, such branching sometimes occurs in *Meconopsis elongata* T. Yoshida, R. Yangzom & D.G. Long of series *Racemosae*, which is somewhat related to *M. castanea*.

FIGURE 13. *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun (*T. Yoshida K68*) on Biluo Xueshan, west of Tuobaluo and west of Biluo Cun, 3800 m elevation. Photograph by T. Yoshida, July 22, 2011.

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FIGURES 14–15. **14**. Habitat of *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun at the type locality, 3750 m elevation. Photograph by T. Yoshida, July 17, 2008. **15**. Habitat of *Meconopsis castanea* (*T. Yoshida K68*), on west-facing slope of Biluo Xueshan, west of Tuobaluo and west of Biluo Cun, 3900 m elevation. Photograph by T. Yoshida, July 22, 2011.

FIGURE 16. Specimen of *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun, *G. Forrest 19790* (E), an odd plant unusually branched from base of stem, collected on "Mekong-Salwin divide, 27°30'N, 98°56'E."

These species have a tendency for unusual branching.

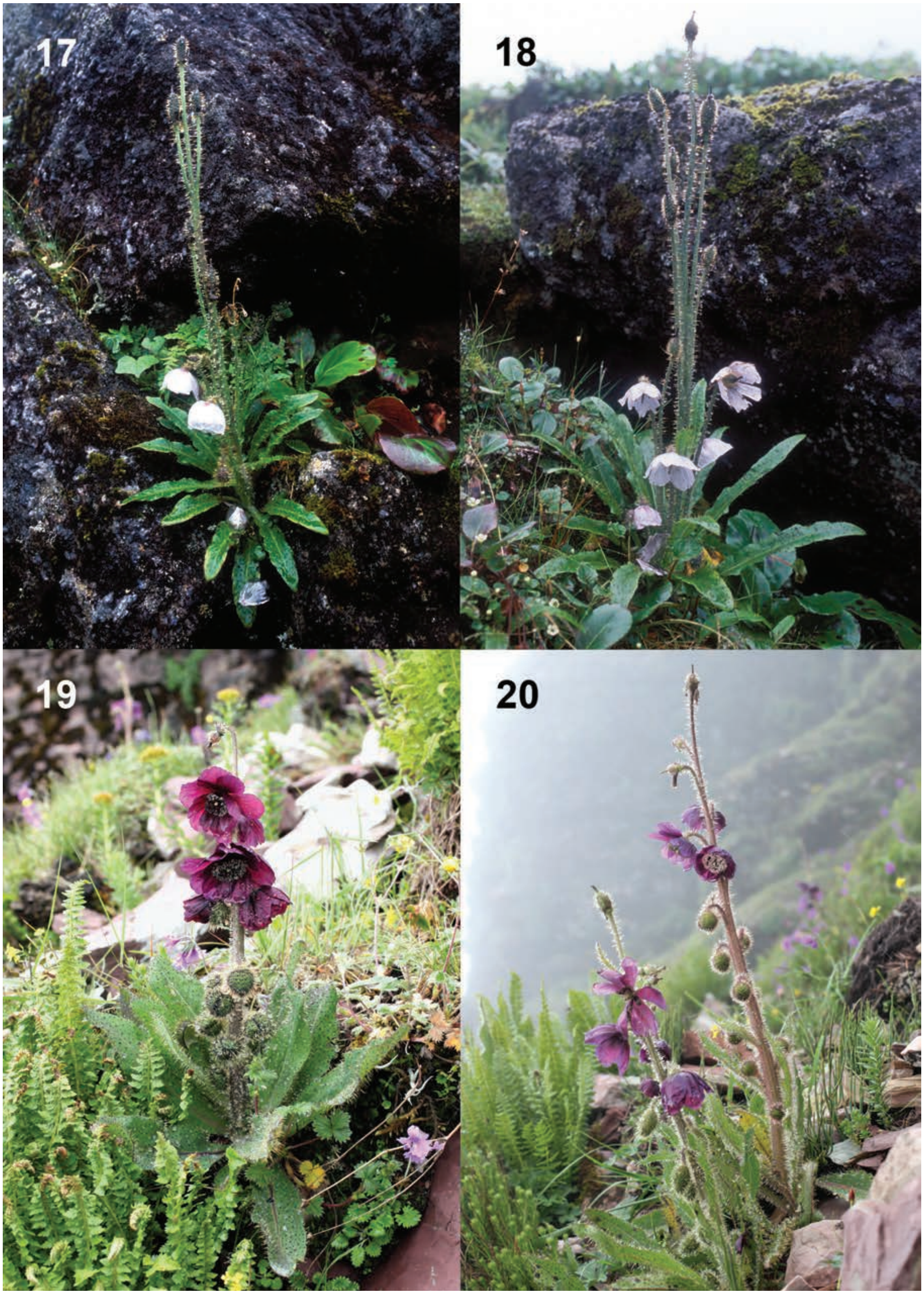
C. Grey-Wilson (2014) treated *Meconopsis castanea* as a form of *M. georgei* G. Taylor. However, *M. castanea* is a distinct species, different from the related *M. georgei* in being larger, to 40 cm tall in flower (to 32 cm tall in flower in the latter), having the margin of the lamina coarsely and irregularly crenate, toothed, or lobed or occasionally subentire (usually entire in the latter), in the racemose inflorescence with elongate thicker rachis to 7 mm across in flower and shorter pedicels to 7 cm long in flower (subscapose with a short, narrower rachis to 5 mm across in flower and long ascending pedicels, to 15 cm long in flower, in the latter), dark red petals (yellow in the latter) with margin usually entire (irregularly denticulate near the apex in the latter) and apex rounded or obtuse (triangular-acute or acuminate in the latter) and the capsules larger, to 3.0 cm long (to 2.4 cm long in the latter).

Additional specimens examined of *Meconopsis castanea sensu lato* (including hybrids with *M. georgei*): CHINA. NW Yunnan, Biluo Xueshan, Fugong Xian or Weixi Xian, **Region 3:** Fuchuan Shan (富川山), 1931, *G. Forrest 30099* (BM, E) [Petals blue according to note]; Fuchuan Shan, Mekong-Yangtse [mistake for Salwin] divide, 27˚N, 99˚30'E, 13,000 ft, July–August. 1931, *G. Forrest 30101* (BM, E) [petals deep purple crimson according to note]; Ma-k'a-ho, Wei-hsi [Weixi, 维西], July 1932, *McLaren "D" Collection 134* (E); Mount Fu-Chuan [富川], southwest of Wei-Hsi [维西, Weixi], Mekong-Salwin divide, 4450 m, May–June 1928, *J. F. Rock 17029* (E) [Flower color is pale blue according to the note]; Fuchuan range, west of the Mekong-Salwin divide and west of Wei-hsi, 13,500–14,500 ft, May–June 1932, *J. F. Rock 22697* (E) [Flower color bluish purple and red according to note]; same locality and date, *J. F. Rock 22699* (BM, E, K) [Flower color is dark purple according to the note]; same locality, August–September 1932, *J. F. Rock 23253* (BM, E); same locality and date, *J. F. Rock 23286* (E); mountain of Weixi region (维西后山), Fuchuan Shan (富川山), without collection number and date, *KUN No. 0201676* (KUN) [Flower color deep red according to note]; mountain of Weixi region (维西后山), without collection number and date, *KUN No. 0201677* (KUN); same locality, *KUN No. 0201689* (KUN); mountain of Weixi region (维西后山), Fuchuan Shan (富川山), without collection number and date, *KUN No. 0201693* (KUN) [Flower color deep red according to note]; around pass on main ridge of Biluo Xueshan, west of Xinhua (新化) and west of Fuchuan (富川), 27˚04'14"N, 98˚58'36"E, 3650–3850 m, 23 July 2009, *T. Yoshida K20* (KUN) [Flower color pale purplish blue, pale pink, or whitish, occasionally deep red]. Fig. 2, 17, 18.

Meconopsis atrovinosa T. Yoshida & H. Sun, *sp. nov.* TYPE: CHINA. SW Sichuan: Luoji Shan (螺髻山), near boundary of Xichang Shi (西昌市), Puge Xian (普格县) and Dechang Xian (德昌县), 27˚36'02"N, 102˚20'45"E, 4000 m, 1 July 2013, *T. Yoshida K90* (Holotype: KUN; Isotypes: E, TI); same locality, 2 September 2012, T. Yoshida K80 (Paratypes: E, KUN, TI). Fig. 1, 19–23.

Meconopsis atrovinosa resembles *M. castanea* H. Ohba, T. Yoshida & H. Sun, but differs from the latter in having prickles tinged dark purple at the base (usually not tinged at the base in the latter), the lamina elliptic, oblong, or oblanceolate, margin usually entire (often linear-oblong, margin coarsely and irregularly crenate, toothed or lobed in the latter), the flowers 7–25 (6–10 in the latter), the petals 5 or more (4 or more in the latter), the anthers dull yellow tinged dark purple (orange in the latter), the capsules to 2 cm long (to 3 cm long in the latter). *Meconopsis atrovinosa* resembles *M. racemosa* Maxim. and *M. prattii* Prain, but differs from these species in the prickles tinged dark purple at the base (usually not tinged at the base in these species), the petals dark wine colored or dark purple (bluish purple in these species), the filaments similar to or darker than the petals, thickly filiform, occasionally with whitish vascular bundles protruding from the apex (similar to petals in color, filiform, without whitish vascular bundles protruding from the apex in these species), the anthers dull yellow tinged dark purple (yellow or orange in these species), the capsules larger, to 2.0 cm long (to 1.7 cm long in *M. racemosa,* to 1.5 cm long in *M. prattii*). *Meconopsis atrovinosa* resembles *M. elongata* T. Yoshida and R. Yangzom & D.G. Long (Yoshida et. al., 2016) especially in the thick, darker filaments with the whitish vascular bundle protruding from the apex, but differs from the latter in petal color (pale blue or pink in the latter), the whitish vascular bundle of filaments inconspicuously protruding to 0.8 mm from the apex (conspicuously protruding to 2 mm from the apex in the latter), the anthers tinged dark purple (not tinged in the latter), and shorter capsules to 2.0 cm long (to 3.5 cm long in the latter).

Herbs, monocarpic, 25–47 cm tall in flower, to 60 cm tall in fruit. *Taproot* elongate, to 30 cm long or more, 7–11 mm across. Most parts of plant densely prickly; *prickles* pale yellowish green, uneven in length, to 4(–5) mm long, rather thin but hard, base broadened and unequally tinged dark purple. *Stem* (below lowermost flower) simple, 2.3–5.0(–8.0) cm long, 7–9 mm across. *Leaves* crowded near base of stem, petiolate; *petiole* broadly linear, 3–6 cm long, 2–4 mm wide; *lamina* elliptic, oblong, or oblanceolate, 5–13 cm long, 1.5–3.0 cm wide, base cuneate or attenuate, margin usually entire, sometimes coarsely toothed or sinuate, apex obtuse, acute or acuminate, both surfaces with patent prickles. *Upper leaves (bracts)* shortly petiolate or sessile; *lamina* oblong or oblanceolate, 2–5 cm long, 7–12 mm wide. *Inflorescence* a simple raceme occupying most of plant above ground, upper half to two-thirds of flowers ebracteate; *pedicels* 1.5–5.0 cm long in flower, to 18 cm long in fruit; rachis and pedicels densely hairy with patent prickles. *Flowers* 7–25, nodding or half nodding, dish- or bowl-shaped, occasionally cup-shaped, 2.5–3.5 cm across. Calyx 10–15 mm long; petals 5–7(–9), dark wine colored or dark purple, occasionally chocolate colored, or rarely red (*R. C. Ching 23487* from Heqing), obovate or broadly obovate, 1.7–3.0 cm long, 1–2 cm wide, margin subentire, sometimes irregularly crenulate, apex obtuse or rounded; *stamens* numerous; *filaments* similar to or darker than petals in color, thickly filiform, 7–11 mm long, occasionally with whitish vascular bundles protruding to 0.8 mm beyond apex; *anthers* dull yellow tinged dark purple to various degrees or often entirely dark purple, 1.0–1.5 mm



FIGURES 17–20. **17**. *Meconopsis castanea* H. Ohba, T. Yoshida & H. Sun × *georgei* G. Taylor (*T. Yoshida K20*) with whitish flowers; east side of Biluo Xueshan, west of Xinhua and west of Fuchuan, 3800 m elevation. Photograph by T. Yoshida, July 23, 2009. **18**. *Meconopsis castanea* × *georgei* (*T. Yoshida K20*) with palest purple flowers, on east side of Biluo Xueshan, west of Xinhua and west of Fuchuan, 3800 m elevation. Photograph by T. Yoshida, July 23, 2009. **19**. *Meconopsis atrovinosa* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 30, 2013. **20**. *Meconopsis atrovinosa* at the type locality. Photograph by T. Yoshida, June 30, 2013.

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FIGURES 21–22. **21**. Habitat of *Meconopsis atrovinosa* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 1, 2013. **22**. Habitat of *Meconopsis atrovinosa* T. Yoshida & H. Sun on northern ridge of Luoji Shan, 3750 m elevation. Photograph by T. Yoshida, July 2, 2013.

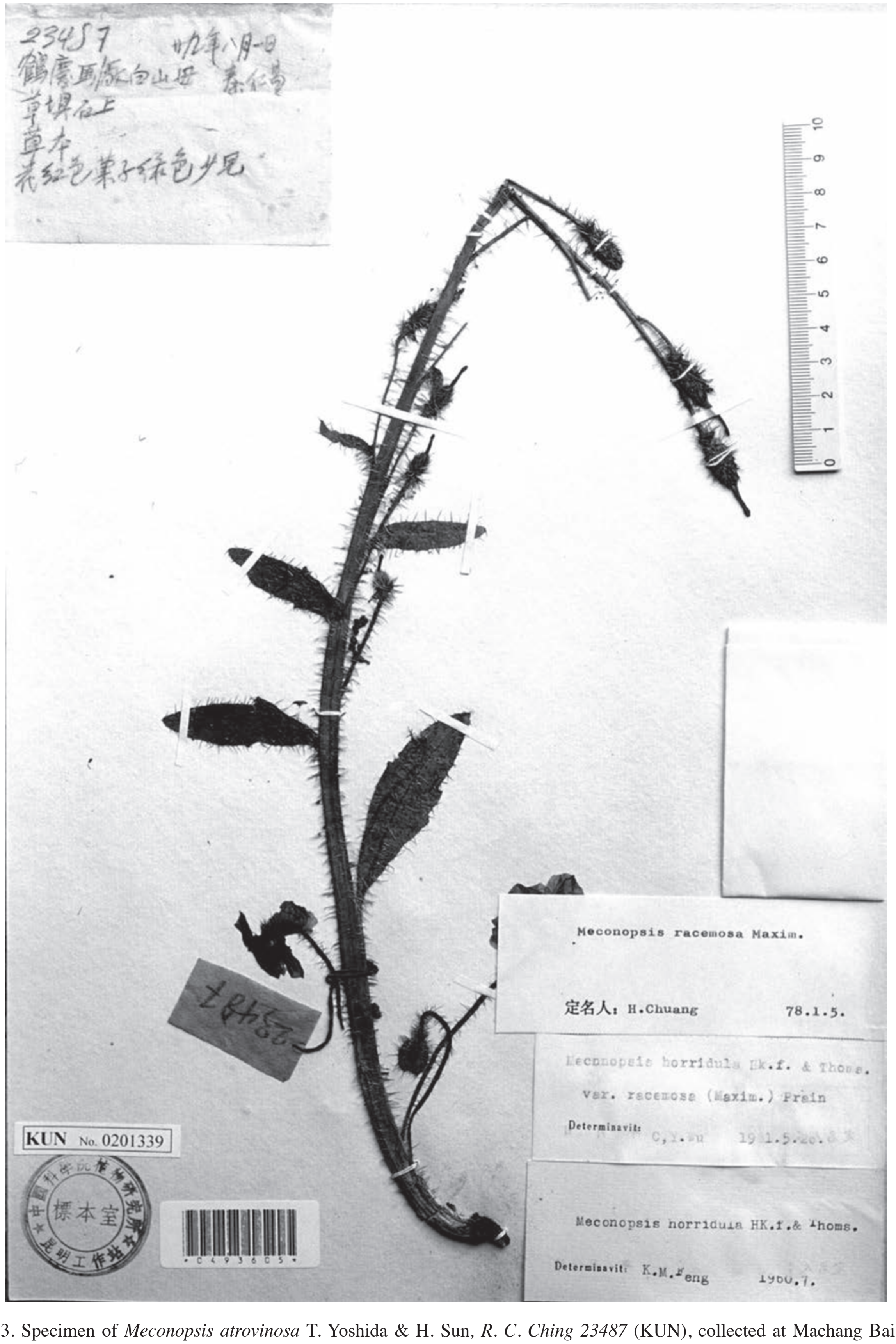

FIGURE 23. Specimen of *Meconopsis atrovinosa* T. Yoshida & H. Sun, *R. C. Ching 23487* (KUN), collected at Machang Baishanmu, Heqing Xian, northwest Yunnan; with red flowers and green fruit according to note on label.

FIGURES 24–27. **24**. *Meconopsis atrovinosa* T. Yoshida & H. Sun (*T. Yoshida K80a*) at the type locality. Taproots of twin plants are partly fused. Photograph by T. Yoshida, September 2, 2012. **25**. Specimen of twin plants of *Meconopsis atrovinosa* T. Yoshida & H. Sun (*T. Yoshida K80a*) with partly fused taproots. **26**. Branched plant of *Meconopsis elongata* T. Yoshida, R. Yangzom & D.G. Long at the type locality, west of Tsabjo La, Haa district, western Bhutan, 4100 m elevation. Photograph by T. Yoshida, July 8, 2015. **27**. Branched plant of *Meconopsis elongata* on the eastern side of Yaktu La, Haa district, western Bhutan, 4250 m elevation. The plant has two branches from base of stem; flowering branch on left is again two-branched in inflorescence. Photograph by T. Yoshida, July 11, 2015.

long; *ovary* ovoid, 4–7 mm long, with dense ascending prickles; *style* 2–3 mm long in flower, to 7 mm long in fruit, 4- to 6-ridged; *stigma* capitate, 0.7–1.5 mm across, lobes (rays) 4–6, 0.5–2.0 mm long. *Capsule*s elliptic-ovoid or ellipsoid, 1.5–2.0 cm long, 6–10 mm across, 4- to 6-ridged, with dense patent prickles; prickles on capsules rather short, with enlarged dark purple base before maturity.

Distribution: CHINA. SW Sichuan: Xichang Shi, Puge Xian and Dechang Xian, Luoji Shan. NW Yunnan: Heqing Xian (鹤庆县), around Machang (马厂). 3700–4100 m elevation.

Habitat and ecology: with grasses, herbs, and mosses on west-facing, rarely east-facing, alpine slopes on calcareous mountains; rooting deeply in blackish loam among iron-rich, reddish mudstone and limestone.

Etymology: specific epithet "atrovinosa" derives from the dark-wine-colored petals.

Additional specimens examined: CHINA. SW Sichuan, Luoji Shan, **Region 1:** 27°36'02"N, 102°20'45"E, 4000 m, 2 September 2012, *T. Yoshida K80* (E, KUN, TI); same locality, 1 July 2013, *T. Yoshida K90* (E, KUN, TI). NW Yunnan, Heqing Xian, **Region 2:** Heqing Machang Baishanmu (鹤庆马厂白山母), 1 August 1940, *R. C. Ching* (秦仁昌) *23487* (KUN) [Flowers red (花红色) according to note] (Fig. 23).

Meconopsis atrovinosa was collected only once in Region 2 by R. C. Ching in 1940. The locality "Machang (马厂)," where *R. C. Ching 23487* was collected, is a flat pastureland for horses surrounded by mountains less than 3800 m elevation located around 26°28'38"N, 100°03'14"E in the northwestern part of Heqing Xian. One of us (Yoshida) explored the region in the summer of 2018 for *Meconopsis atrovinosa,* and *M. lancifolia* Franch. subsp. *lancifolia*. Yoshida rediscovered *M. lancifolia* subsp. *lancifolia* at the type locality, Yen-tze-hay, or Ma-er Shan (马耳山), some 20 km south of Machang earlier in 2108. It was the first collection in some 130 years after Delavay's collections. *Meconopsis betonicifolia* was first collected by Delavay near Machang, but Yoshida was unable to find it.

Meconopsis atrovinosa is rarely branched at the base. One example has the taproots of two plants in fruit partly fused, as shown in Fig. 24 and 25. Such plants branched at the base have also been observed in *M. castanea* (Fig. 16) and *M. elongata* (Fig. 26–27). Further studies are needed to clarify the phenomenon and to compare them with other characteristics. As mentioned in the diagnosis, *M. atrovinosa* resembles *M. elongata* from western Bhutan, some 2,000 km west of *M. elongata*. Related taxa, as well as *M. castanea,* may occur between the two distribution areas.

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REVISION OF *MECONOPSIS* SECTION *FORRESTIANAE* (PAPAVERACEAE)[1]

Toshio Yoshida[2, 3] and Hang Sun[4]

Abstract. *Meconopsis* section *Forrestianae* is revised. Three new species, *M. aprica, M. purpurea,* and *M. wengdaensis*; two new subspecies of *M. lancifolia*, subsp. *daliensis* and subsp. *shikaensis*; and a new variety of *M. yaoshanensis,* var. *luojiensis*, are described and illustrated. A new combination is proposed, *Meconopsis lancifolia* subsp. *xiangchengensis*. Distribution maps of the taxa treated are provided.

Keywords: *Meconopsis,* section *Forrestianae,* revision, new species, series *Barbisetae,* series *Forrestianae,* series *Henricnae*

Meconopsis lancifolia (Franch.) Franch. ex Prain of section *Forrestianae* C. Y. Wu & H. Chuang (Papaveraceae) was first collected on 7 June 1886 by Jean Marie Delavay, French missionary and botanist, on calcareous rocky hills around the depression of Yen-tze-hay, Lan-kong, at 3200 m in elevation according to the type specimen, *J. M. Delavay 2080* (P). On another sheet of *J. M. Delavay 2080* (P), which was not annotated as one of the type specimens, it is written on the label: "on a calcareous rocky hill above the pass of Konalapo (Ho-kin), 3500 m in elevation on 13 July 1886." Ho-kin, or Heqing (鹤庆) in modern Chinese, is the main region where Delavay was engaged as a missionary and where he conducted many of his botanical activities. The exact location of the type locality of *M. lancifolia,* Yen-tze-hay, was unknown until one of us (Yoshida) discovered it in July 2018 through information provided by Siyuang Wang (王思源), committee secretary of Xiyi Village (西邑村), located at the eastern foot of Ma-er Shan (马耳山). According to Mr. Wang, Yen-tze-hay, or Yen-tzu-ai in more precise pronunciation, is a place name in the language of the local people, the Bai-zu (白族), referring to a depression with two lakes on Ma-er Shan. On the basis of the information from Mr. Wang, Yoshida successfully reached Yen-tze-hay with a key local person as a guide, and there on the slopes near Yen-tze-hay was a blue poppy resembling the plant in the photograph of *Meconopsis lancifolia* taken by him on Shika Xueshan. It was the first collection of *M. lancifolia* at the type locality in some 130 years since Delavay made his collections. New collections of *M. lancifolia* and field observation enabled us to compare the features to related taxa.

Plants resembling typical *Meconopsis lancifolia* have been collected in many places in northwest Yunnan, northeast Myanmar, southeast Xizang (Tibet), western Sichuan, and southern Gansu by others since Delavay's time. Some were described as new species, such as *M. eximia* Prain and *M. lepida* Prain, or included in *M. lancifolia*.

Taylor (1934) included *Meconopsis eximia* and *M. lepida* within *M. lancifolia* var. *solitariiflora* Fedde in his monograph of the genus. He treated *M. concinna* Prain as *M. lancifolia* var. *concinna* (Prain) G. Taylor in the monograph, but *M. concinna* is quite different from *M. lancifolia*, especially in often having pinnately or bi-pinnately lobed leaves. Grey-Wilson (2014) treated *M. eximia* as *M. lancifolia* subsp. *eximia* (Prain) Grey-Wilson, and *M. lepida* as *M. lancifolia* subsp. *lepida* (Prain) Grey-Wilson in his monograph of the genus. *Meconopsis lepida* in southern Gansu is, however, distinct from *M. lancifolia* in the elliptic or rounded anthers with incurved thecae (short oblong or ellipsoid anthers with straight thecae in the latter) and in the inflorescence with 1–4, most often 2, flowers, and without flowers at the base (3–7 flowers, often with basal flowers in the latter), as mentioned by Yoshida and Sun (2017).

On the basis of our studies of *Meconopsis lancifolia* and related plants using herbarium specimens, newly collected materials, and field observations, we present a revision of section *Forrestianae* in which we recognize three series; *Forrestianae* C.Y. Wu & H. Chuang, *Henricanae* C.Y. Wu & H. Chuang, and *Barbisetae* T. Yoshida & H. Sun, provided with descriptions of the included species, except those recently revised or described by T. Yoshida and H. Sun (2017, 2018).

In this paper, "scapose plant" refers to plants with the stem, peduncle, and rachis all contracted and not exposed above ground and with flowers borne on long erect or ascending pedicles; subscapose refers to plants with a short inflorescence rachis partly or entirely exposed above ground and with long ascending pedicels.

The taxa treated below are mapped to show their distributions (Fig. 1).

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[1] Corrections and comments by the authors are in square brackets. Figures 85–100 (S.E.M. images) are cited out of sequence throughout the text.

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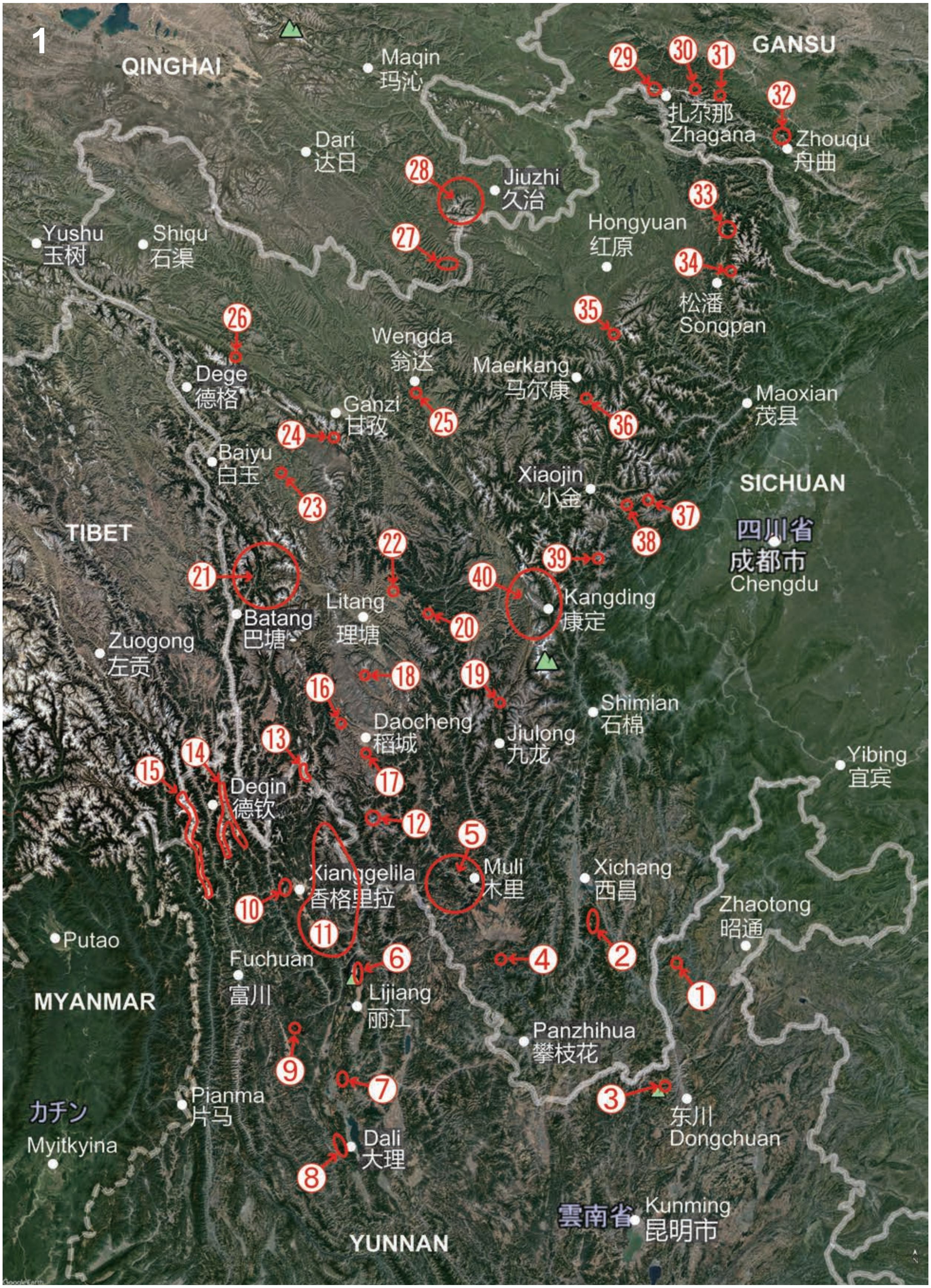
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昆明市
YUNNAN

FIGURE 1. Distribution of taxa of *Meconopsis* Vig. section *Forrestianae* based on Google Earth with proposed delineation of 39 regions that include the locality of at least one specimen of the taxa of concern. **Region 1**: NE Yunnan, Qiaojia Xian, Yao Shan; **Region 2**: SW Sichuan, Luoji Shan; **Region 3**: NE Yunnan, Dongchuan Qu; **Region 4:** SW Sichuan, Yan-yuang Xian; **Region 5**: SW Sichuan, Muli Xian; **Region 6**: NW Yunnan, Lijiang Shi; **Region 7**: NW Yunnan, Heqing Xian; **Region 8**: NW Yunnan, Yangbi Xian and Dali Shi, Cang Shan; **Region 9**: NW Yunnan, Jianchuan Xian; **Region 10**: NW Yunnan, Xianggelila Shi, around Shika Xueshan; **Region 11**: NW Yunnan, Xianggelila Shi; **Region 12**: SW Sichuan, Daocheng Xian, Daocheng Gongga Shan; **Region 13**: NW Yunnan, Xianggelila Shi, and SW Sichuan, Xiangcheng Xian, Da Xueshan; **Region 14**: NW Yunnan, Deqin Xian, Yunling including Baima Xueshan; **Region 15**: NW Yunnan, Deqin Xian and Gongshan Xian, and SE Xizang, Chayu Xian, northern part of Nu Shan including Meili Xueshan; **Region 16**: SW Sichuan, Daocheng Xian and Xiangcheng Xian, Wuming Shan; **Region 17**: SW Sichuan, Daocheng Xian, Bowa Shan; **Region 18**: SW Sichuan, Litang Xian, Haizi Shan; **Region 19**: SW Sichuan, Jiulong Xian, Jichou Shan; **Region 20**: SW Sichuan, Yajiang Xian, west of Yajiang; **Region 21**: SW Sichuan, Batang Xian; **Region 22**: W Sichuan: Yajiang Xian, Kazi La Shan; **Region 23**: W Sichuan, Baiyu Xian, Ganbailu Yakou; **Region 24**: NW Sichuan, Ganzi Xian, around Zhuoda La; **Region 25**: NW Sichuan, Wengda Xian, Laozhe Shan; **Region 26**: NW Sichuan, Dege Xian, Dege Haizi Shan; **Region 27**: SE Qinghai, Banma Xian, Makehe; **Region 28**: SE Qinghai, jiuzhi Xian, around Nianbaoyuze Shan; **Region 29**: S Gansu, Diebu Xian, W of Zhagana; **Region 30**: S Gansu, Diebu Xian, Gansu Min Shan; **Region 31**: S Gansu, Zhuoni Xian, Gansu Min Shan; **Region 32**: S Gansu, Zhouqu Xian and Dangchang Xian, Leigu Shan; **Region 33**: N Sichuan, Songpan Xian, Gonggaling; **Region 34**: N Sichuan, Songpan Xian, around Xueshanliang; **Region 35**: N Sichuan, Heishui Xian and Hong-yuan Xian, Yanggong Shan; **Region 36**: NW Sichuan, Xiaojin Xian, Mengbi Shan; **Region 37**: W Sichuan, Xiaojin Xian, Balang Shan; **Region 38**: W Sichuan, Xiaojin Xian, Jiajin Shan; **Region 39**: W Sichuan, Kangding Shi, Baoding Shan; **Region 40**: W Sichuan, Kangding Shi. Taxa treated and their region(s) of distribution: *M. aprica* T. Yoshida & H. Sun: Region 24; *M. barbiseta* C.Y. Wu & H. Chuang ex L.H. Zhou: Region 27, 28; *M. forrestii* Prain: Region 5, 6, 8, 11; *M. henrici* Bureau & Franch.: Region 5, 40; *M. hispida* T. Yoshida & H. Sun: Region 35; *M. huanglongensis* T. Yoshida & H. Sun: Region 34; *M. inaperta* T. Yoshida & H. Sun: Region 22, 23; *M. lancifolia* (Franch.) Franch. ex Prain subsp. *daliensis* T. Yoshida & H. Sun: Region 3, 8; *M. lancifolia* subsp. *eximia* (Prain) Grey-Wilson: Region 11, 12, 13, 14, 15; *M. lancifolia* subsp. *lancifolia*: Region 7, 9; *M. lancifolia* subsp. *shikaensis* T. Yoshida & H. Sun: Region 10; *M. lancifolia* subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun: Region 4, 5, 16, 17, 18, 19, 20, 21; *M. lepida* Prain: Region 32; *M. pleurogyna* W.T. Wang: Region 28, 35, 36; *M. psilonomma* Farrer var. *calcicola* T. Yoshida & H. Sun: Region 29; *M. psilonomma* var. *psilonomma*: Region 30, 31; *M. psilonomma* var. *sinomaculata* (Grey-Wilson) H. Ohba: Region 33; *M. psilonomma* var. *zhaganaensis* T. Yoshida & H. Sun: Region 29; *M. purpurea* T. Yoshida & H. Sun: Region 37, 38, 39; *M. trichogyna* T. Yoshida & H. Sun: Region 26; *M. wengdaensis* T. Yoshida & H. Sun: Region 25; *M. yaoshanensis* T. Yoshida, H. Sun & Boufford var. *luojiensis* T. Yoshida & H. Sun: Region 2; *M. yaoshanensis* var. *yaoshanensis*: Region 1.

TAXONOMY

Meconopsis section Forrestianae C. Y. Wu & H. Chuang, *nomen emend*.

Synonyms: *Meconopsis* section *Forrestii* C.Y. Wu & H. Chuang, *Acta Bot. Yunnan*. 2 (4): 375. 1980; *M.* section *Simplicifoiae* series *Henricanae* C.Y. Wu & H. Chuang, *Acta Bot. Yunnan*. 2 (4): 376. 1980, *pro parte, quoad M. henrici* Bureau & Franch. et *M. barbiseta* C.Y. Wu & H. Chuang ex L.H. Zhou; *M.* section *Forrestianae* sensu Grey-Wilson, *The Genus Meconopsis—Blue Poppies and Their Relatives*: 46. 2014.

Herbs, monocarpic, bristly; bristles hard but thin and brittle, composed of agglutinated long, thin cells, less than 6 mm long, simple except on ovary in series *Barbisetae,* which are branched near the base. Leaves all basal; lamina entire. Inflorescence racemose, subscapose or scapose. Flowers 1–16, ebracteate except those near base of plant; petals 4–10, blue, violet, mauve, purple, or magenta-purple.

Three series are included: series *Forrestianae* C.Y. Wu & H. Chuang, series *Henricanae* C.Y. Wu & H. Chuang, and series *Barbisetae* T. Yoshida & H. Sun.

Type species: *M. forrestii* Prain.

KEY TO SERIES OF SECTION *FORRESTIANAE*

1a. Hairs on ovary simple 2
1b. Hairs on ovary branched near base . . . . . series *Barbisetae*
2a. Filaments filiform throughout . . . . . series *Forrestianae*
2b. Filaments, at least innermost ones, dilated toward base . . . . . series *Henricanae*

Series Forrestianae C.Y. Wu & H. Chuang, *nomen emend.*

Synonym: *Meconopsis* section *Forrestii* series *Forrestii* C.Y. Wu & H. Chuang, *Acta Bot. Yunnan*. 2 (4): 375. 1980.

Filaments filiform throughout. Hairs on ovary simple. Nine species are included: *Meconopsis aprica* T. Yoshida & H. Sun, *sp. nov., M. forrestii* Prain, *M. inaperta* T. Yoshida & H. Sun, *M. lancifolia* (Franch.) Franch. ex Prain, *M. lepida* Prain, *M. pleurogyna* W.T. Wang, *M. purpurea* T. Yoshida & H. Sun, *sp. nov., M. wengdaensis* T. Yoshida & H. Sun, *sp. nov.,* and *M. yaoshanensis* T. Yoshida, H. Sun & Boufford.

KEY TO SPECIES OF SERIES *FORRESTIANAE*

1a. Inflorescence racemose, lowermost 2 or 3 flowers bracteate . . . . . *M. yaoshanensis*
1b. Inflorescence racemose, subscapose or scapose; flowers of raceme, except basal ones, ebracteate 2
2a. Style indistinct, less than 1 mm long; capsules to 6 cm long; inflorescence without basal flowers . . . . . *M. forrestii*
2b. Style distinct, more than 1 mm long; capsules less than 4.5 cm long; inflorescence with or without basal flowers 3
3a. Flowers cup-shaped, often half-closed at mouth . . . . . *M. inaperta*
3b. Flowers widely open 4

Key to Species of Series *Forrestianae* cont.

4a. Inflorescence racemose, occasionally subscapose with short rachis and long ascending pedicels 5
4b. Inflorescence scapose 8
5a. Anthers short oblong or ellipsoid, thecae straight 6
5b. Anthers ellipsoid or rounded, thecae incurved 7
6a. Taproot dauciform or elongate, inflorescence with or without basal flowers, ovary uniformly colored . . . . *M. lancifolia*
6b. Taproot napiform, inflorescence without basal flowers, ovary with dark purple streaks . . . . *M. wengdaensis*
7a. Taproot napiform, inflorescence without basal flowers, anthers uniformly colored . . . . *M. lepida*
7b. Taproot elongate; inflorescence with basal flowers; anthers bicolored, with dark purple central part and pale yellow periphery . . . . *M. purpurea*
8a. Leaves dimorphic, lamina to 19 mm wide, petals to 3.1 cm long, filaments to 8 mm long, ovary densely to sparsely bristly or occasionally glabrous . . . . *M. pleurogyna*
8b. Leaves uniform, lamina to 9 mm wide, petals to 4.2 cm long, filaments to 12 mm long, ovary densely covered with bristles in close contact with each other . . . . *M. aprica*

Meconopsis yaoshanensis T. Yoshida, H. Sun & Boufford, *Plant Diversity and Resources* 34 (2): 145–149. 2012. TYPE: CHINA. NE Yunnan, Qiaojia Xian (巧家县): Yao Shan (药山), 27°12'40"N, 103°04'31"E, 3750 m, 7 July 2011, *T. Yoshida K55* (Holotype: KUN; Isotype: KUN).

Herbs, monocarpic, 15–50 cm tall in flower, to 60 cm tall or more in fruit. *Taproot* elongate, 7–20 cm long, 5–13 mm across, sometimes few branched near head. Most part of plant bristly; *bristles* golden brown or reddish brown, to 4(–6) mm long, stiff but not spine-like. *Stem* (below uppermost leaf) simple, 1–8 cm long, 5–10 mm across. *Leaves* crowded on short stem; *petiole* broadly linear, 1.5–8 cm long, 1.5–5 mm wide; *lamina* oblong, oblanceolate, elliptic or ovate, 2–18 cm long, 0.7–3 cm wide, base cuneate or attenuate, margin entire, sometimes coarsely crenate or toothed, sometimes undulate, apex obtuse or acute, rarely acuminate, lower surface somewhat canescent, both surfaces covered with bristles. *Inflorescence* racemose, composing most of plant above ground, ebracteate except for few lowest flowers; *pedicels* erect along rachis, 1–7 cm long in flower, to 12 cm long or more in fruit, recurving distally, abruptly swollen at base of calyx. *Flowers* 5–16 per individual, half nodding, cup- or bowl-shaped, 2.0–3.5 cm across. *Calyx* 1.0–1.5 cm long. *Petals* 4–7, pale blue or violet, elliptic, obovate, broadly ovate or broadly obovate, 1.5–2.4 cm long, 0.7–1.7 cm wide, margin often coarsely and irregularly dentate near apex, apex triangularly obtuse, acute, or rounded. *Stamens* numerous; *filaments* filiform, 7–11 mm long, similar to or paler than petals; *anthers* dark purple, orange, yellow, pale brown, or white, ellipsoid, 0.8–1.5 mm long. *Ovary* ellipsoid, 5–9 mm long, densely hairy with ascending or patent bristles; *style* 1.0–2.5 mm long, to 7.0 mm long in fruit; *stigma* capitate, lobes 3–5, 0.5–1.5 mm long. *Capsules* ellipsoid, narrowly obovoid, or cylindrical-oblong, 1.5–5.2 cm long, 5–10 mm across, densely covered with patent or retrorse bristles; carpels 4–5.

Distribution: CHINA. NE Yunnan, Qiaojia Xian, Yao Shan. SW Sichuan: Xichang Shi, Puge Xian and Dechang Xian, Luoji Shan. 3650–3900 m elevation.

Habitat: stony or grassy slopes at edge of thickets.

Meconopsis yaoshanensis T. Yoshida, H. Sun & Boufford var. ***yaoshanensis*.** Fig. 1–4.

Herbs, monocarpic, 20–50 cm tall in flower, to 60 cm tall or more in fruit. *Taproot* elongate, 8–20 cm long, 6–13 mm across, sometimes few branched near head. Most parts of plant bristly; *bristles* golden brown or reddish brown, to 5(–6) mm long, stiff but not spine-like, patent except those on fruit. *Stem* (below uppermost leaf) simple, 2–8 cm long, 5–10 mm across. *Leaves* 12–25 per individual, on short stem; *petiole* broadly linear, 2–8 cm long, 2–3 mm wide; *lamina* oblong or oblanceolate, rarely elliptic, 4–17 cm long, 1–3 cm wide, base cuneate or attenuate, margin entire, sometimes coarsely crenate and undulate, apex obtuse or acute, rarely acuminate, both surfaces somewhat yellowish green, covered with patent bristles, less densely so on lower surface; lower surface canescent in dried specimens. *Upper leaves* (bracts) short petiolate or sessile; *lamina* similar to basal leaves but gradually smaller. *Inflorescence* racemose, composing most of plant above ground, ebracteate except for few lowest flowers; *rachis* thick and hollow in lower part; *pedicels* erect, 2–7 cm long in flower, to 12 cm long or more in fruit, often winding around rachis in fruit, recurving distally, abruptly swollen at base of calyx; base of pedicel decurrent as rounded ridges on rachis. *Flowers* 8–16 per individual, half nodding, cup- or bowl-shaped in fine weather, 2.0–3.5 cm across. *Calyx* 1.0–1.5 cm long. *Petals* 4 or 5, rarely 6, pale blue or violet, elliptic, broadly ovate or obovate, 1.5–2.4 cm long, 0.7–1.7 cm wide, margin often coarsely and irregularly dentate near apex, apex triangularly obtuse, acute or rounded. *Stamens* numerous; *filaments* filiform, 7–11 mm long, similar to petals; *anthers* dark purple, yellow, or orange, ellipsoid, 1.0–1.5 mm long, often curved. *Ovary* ellipsoid, 5–7 mm long, with dense ascending hairs; *style* 1–2 mm long, to 7 mm long in fruit; *stigma* capitate, 1.0–1.5 mm long. *Capsules* cylindrical-oblong, 3.5–5.2 cm long, 6–10 mm across, narrowed at both ends, with 3–5 ridges, densely covered with retrorse bristles; mature fruits often spirally arranged around rachis, pedicel twisted, elongate. *Seeds* blackish, 2.3–2.9 mm long.

Distribution: CHINA. NE Yunnan: Qiaojia Xian, Yao Shan, only in the vicinity of the type locality, 3650–3800 m elevation.

Habitat and ecology: South-, southeast-, and east-facing steep slopes covered with basaltic debris and scattered grasses and herbs among the stones, subject to wet monsoon in summer.

Additional specimens examined: CHINA. NE Yunnan, Qiaojia Xian (巧家县), **Region 1:** Yao Shan (药山), 27°12'40"N, 103°04'31"E, 3750 m, 2 August 2010, *T. Yoshida K46* (KUN); same locality, 7 July 2011, *T. Yoshida K55* (KUN).

FIGURES 2–5. **2**. *Meconopsis yaoshanensis* T. Yoshida, H. Sun & Boufford var. *yaoshanensis* at the type locality. Photograph by T. Yoshida, July 6, 2011. **3**. *Meconopsis yaoshanensis* T. Yoshida, H. Sun & Boufford var. *yaoshanensis* at the type locality. Photograph by T. Yoshida, August 2, 2010. **4**. *Meconopsis yaoshanensis* T. Yoshida, H. Sun & Boufford var. *yaoshanensis* at the type locality. Photograph by T. Yoshida, August 2, 2010. **5**. *Meconopsis yaoshanensis* T. Yoshida, H. Sun & Boufford var. *luojiensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 1, 2013.

Meconopsis yaoshanensis var. luojiensis T. Yoshida & H. Sun, *var. nov.* TYPE: CHINA. SW Sichuan: Luoji Shan (螺髻山), near boundary of Xichang Shi (西昌市), Puge Xian (普格县), and Dechang Xian (德昌县), 27°36'57"N, 102°20'37"E, 3900 m, 1 July 2013, *T. Yoshida K91* (Holotype: KUN; Isotype: TI). Fig. 1, 5–7.

Var. *luojiensis* differs from var. *yaoshanensis* in the ellipsoid or narrowly obovoid capsules to 2.5 cm long (cylindrical-oblong, to 5.2 cm long in the latter), the lamina to 2.2 cm wide (to 3 cm wide in the latter), and petals (4 or)5–8 (4 or 5, rarely 6, in the latter).

Herbs, monocarpic, 15–40 cm tall. *Taproot* elongate, to 18 cm long or more, 5–12 mm across. Most parts of plant with patent or retrorse bristles; *bristles* pale reddish brown except pale apex and pale green base, to 4(–5) mm long, dense on rachis, pedicels, calices and ovaries, less dense on leaves. *Stem* (below uppermost leaf) simple, usually less than 1.5 cm long, rarely to 6 cm long in plants growing among shrubs. *Leaves* crowded near base of stem; *petiole* broadly linear, 1.5–6.0 cm long, 1.5–5.0 mm wide; *lamina* oblong, oblanceolate, elliptic or ovate, 2–18 cm long, 0.7–2.2 cm wide, base cuneate or attenuate, margin entire, sometimes undulate and coarsely wavy or toothed, apex acute or obtuse, upper surface green, lower surface somewhat canescent, both surfaces with bristles. *Inflorescence* racemose, composing most of plant above ground, ebracteate except lowest 1 or 2 flower(s); *pedicels* mostly erect, curving downward near apex, 1–5 cm long in flower, to 9 cm long in fruit, abruptly swollen at base of calyx. *Flowers* (4 or)5–7 per individual, half nodding, cup-shaped, 2–3 cm across. *Calyx* 1.2–1.5 cm long. *Petals* (4 or)5–8, violet, obovate, broadly obovate or elliptic, 1.5–2.4 cm long, 0.7–1.7 cm wide, apex usually triangular, obtuse or rarely rounded. *Stamens* numerous; *filaments* filiform, 8–11 mm long, similar to or paler than petals; *anthers* white or pale brown, ellipsoid, 0.8–1.2 mm long. *Ovary* ellipsoid, 5–9 mm long, densely hairy with ascending or patent whitish bristles; *style* 2.0–2.5 mm long in flower, to 4 mm long in fruit; *stigma* capitate, 1.0–1.5 mm across; lobes 4–5, 0.5–1.0 mm long. *Capsules* ellipsoid or narrowly obovoid, 1.5–2.5 cm long, 5–8 mm across, with dense patent or retrorse bristles; carpels 4 or 5. *Seeds* unknown.

Distribution: CHINA. SW Sichuan: Xichang Shi, Puge Xian and Dechang Xian, Luoji Shan, only in the vicinity of the type locality, ca. 3900 m elevation.

Habitat and ecology: with other herbs at edge of thickets of *Berberis* L., *Spiraea* L., and *Rhododendron* L., on a gentle west-facing slope in calcareous soil.

Meconopsis forrestii Prain, *Bull. Misc. Inform., Kew, 1907*: 316. 1907. TYPE: CHINA. NW Yunnan, Lijiang Shi (丽江市): eastern flank of Lichiang Range [Yulong Xueshan, 玉龙雪山], 10,000–11,000 ft, June 1906, *G. Forrest 2314* (Lectotype: E, designated here; Isolectotypes: BM, E, K, P). Fig. 1, 8–10, 85–86.

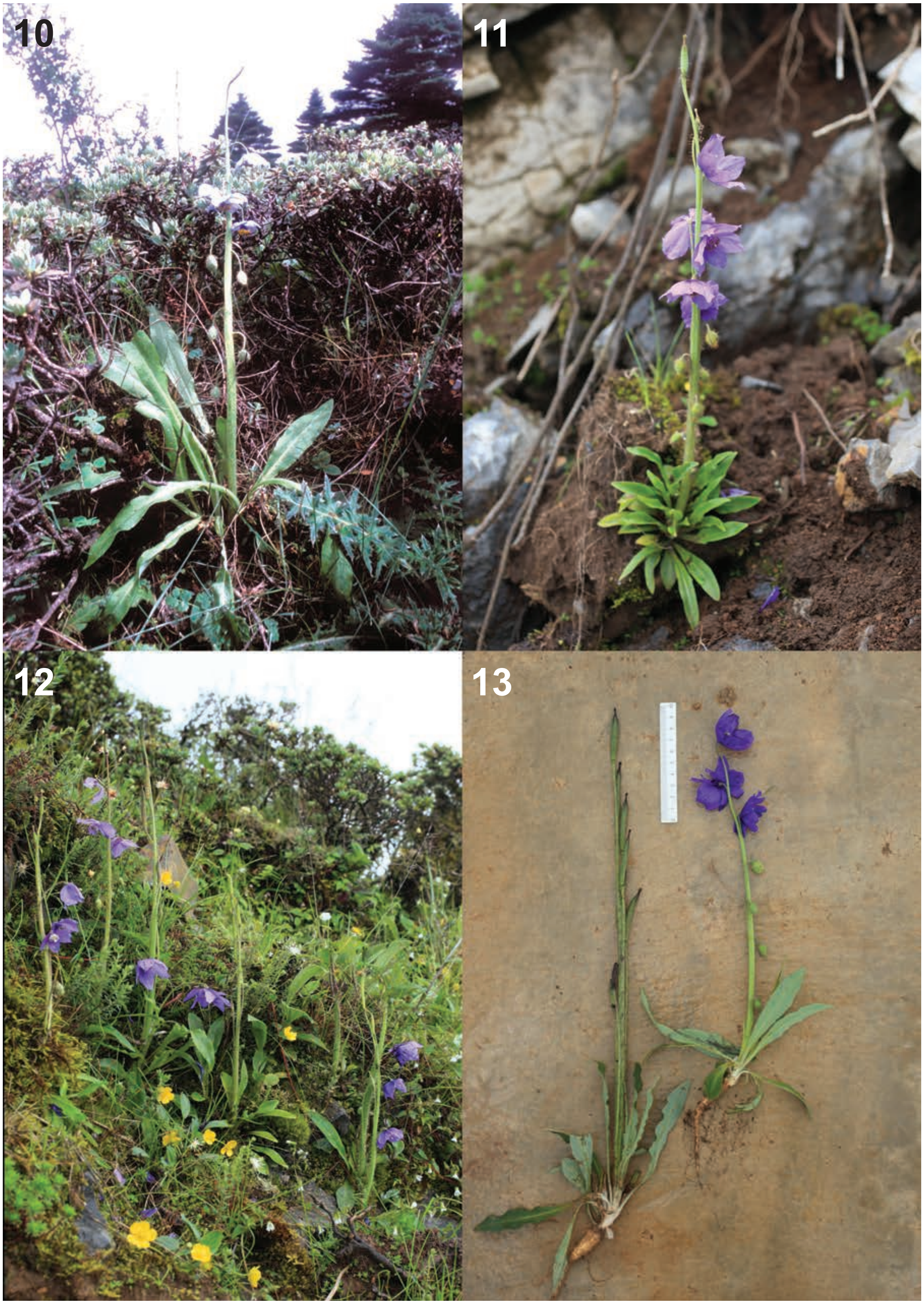
Herbs, monocarpic, 15–42 cm tall in flower, to 47 cm tall in fruit. *Taproot* dauciform, napiform or slightly elongate, 2–7 cm long, 6–13 mm across, often fusiform with contracted head, distally gradually narrowed and with a slender extension. Most parts of plant bristly; *bristles* to 2.5(–3.5) mm long, sometimes tinged reddish brown except at base. *Stem* (below uppermost leaf) simple, 0.3–5.5 cm long. *Leaves* crowded near base of stem, petiolate; *petiole* linear or broadly linear, 1.5–7.0 cm long, 1.5–3.0 mm wide; *lamina* oblong, linear-oblong, narrowly oblanceolate or lanceolate, elliptic or ovate in small leaves, 1.5–14.0 cm long, 0.5–3.0 cm wide, base attenuate, occasionally cuneate in small leaves, margin entire, apex acute or obtuse, upper surface green, lower surface somewhat paler, both surfaces moderately or sparsely bristly. *Inflorescence* racemose, without basal flowers, ebracteate; *peduncle* 1–6 mm across in dried specimens; *pedicels* 1–7 cm long in flower, to 12 cm long in fruit, those of racemose flowers shorter; peduncle, rachis, and pedicels sparsely or moderately hairy with retrorse bristles, bristles denser on peduncle. *Flowers* (2 or)3–7(–10), usually on upper half of plant, nodding, half nodding, or facing laterally, opening flat or dish-shaped, 2.5–3.8 cm across. *Calyx* 0.8–1.2 cm long, densely or moderately bristly. *Petals* 4, rarely 5, pale blue, occasionally tinged purple, ovate, broadly ovate or rhombic, 1.2–2.2 cm long, 1.0–1.8 cm wide, base rounded or cuneate, margin entire, occasionally crenulate near apex, apex triangular-acute or obtuse, rarely rounded. *Stamens* numerous; *filaments* darker than petals, paler near base, filiform, 4–7 mm long; *anthers* orange, ellipsoid, 0.7–1.1 mm long, thecae straight. *Ovary* narrowly ovoid or narrowly ellipsoid, 4–10 mm long, sparsely or moderately hairy with ascending bristles, occasionally glabrous; *style* less than 1 mm long, often negligible even in fruit; *stigma* capitate, 0.7–1.0 mm across; lobes 2–4, 0.8–1.5 mm long, erect in fruit. *Capsules* cylindrical-oblong, 3–6 cm long, 3.5–5.5 mm across, sparsely bristly or glabrous; carpels 2–4, upper 1/7–1/6 dehiscent. *Seeds* unknown.

Distribution: CHINA. NW Yunnan: Lijiang Shi, Xianggelila Shi (香格里拉市, or Shangri-La County in English), Yangbi Xian (漾濞县). SW Sichuan: Muli Xian (木里县). 3300–3800 m elevation.

Habitat and ecology: humid grassy slopes with scattered dwarf shrubs, with or without moss; rooting in blackish, stony soil or sometimes growing close to or within dwarf shrubs with rachis protruding through canopy.

Additional specimens examined: CHINA. SW Sichuan, Muli Xian, **Region 5**: Muli, 28°12'N, 12,000 ft, June 1918, *G. Forrest 16309* (K); Muli, 18°12'N, 11–12,000 ft, August 1918, *G. Forrest 16799* (E); east of Yunging [Yongning, 永宁], 27°48'N, 101°E, 13,000 ft, June 1922, *G. Forrest 21251* (K); Szechuan aust. [probably in Muli Xian], 3200–3500 m, June 1913, *Schneider 1514* (A, K). NW Yunnan, Lijiang Shi, **Region 6:** NE of Yangtze bend, 27°45'N, 11,000–12,000 ft, August 1913, *G. Forrest 10799* (E); eastern slopes of Likiang Snow Range, Yangtze watershed, 11,500 ft, June 1923, *J. F. Rock 8681* (K); Lichung [Lijiang], July 1933, *McLaren collection 53* (K); Nguluko, Lichiang (丽江雪松村), 3400 m, 7 June 1937, *T. T. Yü* (俞德俊) *15136* (KUN); Sandaowan, Yulong Shan, Lijiang, 3500 m, 7 June 1985, *Chamberlain et al. 625* (E); Yulong Xueshan, 27°11'04"N, 100°13'18"E, 3700 m, 24 June 2010, *T. Yoshida K29* (KUN, TI). NW Yunnan, Yangbi Xian, **Region 8:** above Malutang [马鹿塘], W side of Diancang Shan [点苍山], Yangbi Xian, 54°46'N, 100°01'E, 3450 m, 26 June 1984, *Bartholomew et*

FIGURES 6–9. **6**. *Meconopsis yaoshanensis* T. Yoshida, H. Sun & Boufford var. *luojiensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 30, 2013. **7**. *Meconopsis yaoshanensis* T. Yoshida, H. Sun & Boufford var. *luojiensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 30, 2013. **8**. *Meconopsis forresttii* Prain, near Maoniuping (牦牛坪), eastern side of Yulong Xueshan, 3550 m. Photograph by T. Yoshida, June 16, 2015. **9**. *Meconopsis forresttii* Prain, near Maoniuping, eastern side of Yulong Xueshan, 3700 m. Photograph by T. Yoshida, June 24, 2010.



FIGURES 10–13. **10**. *Meconopsis forresttii* Prain, near Maoniuping, eastern side of Yulong Xueshan, 3700 m. Photograph by T. Yoshida, June 24, 2010. **11**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *lancifolia*, near the type locality on Ma-er Shan, 3500 m. Photograph by T. Yoshida, July 21, 2018. **12**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *lancifolia*, near the type locality on Ma-er Shan, 3500 m. Photograph by T. Yoshida, July 21, 2018. **13**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *lancifolia*, near the type locality on Ma-er Shan, 3500 m. Photograph by T. Yoshida, July 21, 2018.

al. 559 (KUN). NW Yunnan, Xianggelila Shi, **Region 11:** Chungtien [Zhongdian,中甸] Plateau, 27˚30'N, 12,000–13,000 ft, June 1914, *G. Forrest 12507* (E); Chungtien Plateau, 27˚30'N, 12,000 ft, July 1914, *G. Forrest 12672* (E, K); Chungtien, 3200 m, 2 June 1937, *T. T. Yü 11601* (KUN); NW flank of Haba Snow Range (哈巴雪山), 22 June 1939, *K. M. Feng* (冯国楣) *1360* (KUN); Haba Shan, July 1943, *J. F. Rock 9635* (E); Tianbao Shan (天宝山), 27˚37'55"N, 99˚55'18"E, 3800 m, 8 July 2010, *T. Yoshida 4384* (TI); same locality, 24 June 2011, *T. Yoshida 4397* (TI).

The typification of *Meconopsis forrestii* has been ambiguous. To resolve this issue, lectotype and isolectotypes are designated here. Prain (1907) first described *M. forrestii* on the basis of a Forrest specimen but did not cite a collection number or the herbarium where it was deposited. When he redescribed it in 1915, he cited *G. Forrest 2314*, collected in 1906, *G. Forrest 10799*, collected in 1913, and *G. Forrest 12507* and *12672*, both collected in 1914, but again did not indicate the herbarium where the specimens were deposited. The collections from 1913 and 1914 were obviously not available in 1907 when the name *M. forrestii* was first proposed, leaving *Forrest 2314* as the only original material at the time of the original description. From the five sheets of *Forrest 2314* we have chosen the specimen at E, which was available to Prain and matches the original description well.

Meconopsis lancifolia (Franch.) Franch. ex Prain, *J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist.* 64 (2): 311. 1896.

Basionym: *Cathcartia lancifolia* Franch., *Bull. Soc. Bot. Fr.* 33: 391. 1886. TYPE: CHINA. NW Yunnan, Heqing Xian (鹤庆县): Yen-tze-hay, Lankong, 3200 m, 7 June 1886, *J. M. Delavay 2080* (Holotype: P; Isotypes: E, K, P).

Herbs, monocarpic, 8–35 cm tall in flower. *Taproot* dauciform or elongate, 1.5–12.0 cm long, 4–15 mm across, distally gradually narrowed and with a slender extension. Most parts of plant bristly; *bristles* to 2.5–4.0(–5.0) mm long. *Stem* (below uppermost leaf) simple, 0.3–7.0 cm long. *Leaves* crowded near base of stem, petiolate; *petiole* linear or broadly linear, 0.5–7.0 cm long, 1–5 mm wide; *lamina* oblong, linear-oblong, strap-shaped or oblanceolate, 2–13 cm long, 0.3–2.5 cm wide, smaller leaves elliptic or ovate, base attenuate, margin entire, occasionally undulate, apex acute, obtuse or rounded. *Inflorescence* racemose or subscapose, with or without basal flowers, ebracteate except lowermost flowers, occasionally with lowest flower bud(s) borne on diminutive pedicel and much smaller and abortive; *rachis* 2–9 mm across in dried specimens; *pedicels* (except those of abortive flower buds) 1–12 cm long in flower, to 15 cm long in fruit. *Flowers* 4–13, half nodding, occasionally nodding, or facing laterally, bowl- or dish-shaped, 2.3–7.0 cm across. *Calyx* 0.7–1.5 cm long. *Petals* 4–9, violet, purple, magenta-purple, deep purplish blue, pale purplish blue, obovate, broadly obovate, rhombic, elliptic or ovate, 1.5–4.0 cm long, 0.6–3.0 cm wide, base cuneate or rounded, margin entire, sometimes irregularly crenulate near apex, occasionally cleft in various degree, apex obtuse, rounded or triangular-acute. *Stamens* numerous; *filaments* filiform, 5–12 mm long; *anthers* pale yellow, yellow or orange, ellipsoid or oblong, 0.8–2.0 mm long, thecae straight. *Ovary* ovoid, ellipsoid or narrowly ellipsoid, 4–8 mm long; *style* 1–4 mm long in flower; *stigma* capitate or ovoid, ca. 1 mm across; lobes 3–5, ovate, 0.8–3.5 mm long in flower, erect, occasionally ascending, in fruit. *Capsules* cylindrical-oblong, oblong, narrowly ellipsoid, ellipsoid, broadly ellipsoid, ovoid, obovoid or narrowly obovoid, 1.0–4.5 cm long, 3–12 mm across; carpels 3–5, upper 1/7–2/3 dehiscent.

Distribution: CHINA. NW Yunnan: Heqing Xian (鹤庆县), Jianchuan Xian (剑川县), Dali Shi (大理市), Yangbi Xian (漾濞县), Xianggelila Shi (香格里拉市), Deqin Xian (德钦县), Gongshan Xian (贡山县). SE Xizang: Chayu Xian (察隅县), or Zayu County. SW Sichuan: Xiangcheng Xian (乡城县), Daocheng Xian (稻城县), Jiulong Xian (九龙县), Litang Xian (理塘县), Yan-yuang Xian (盐源县), and Muli Xian (木里县). 3200–4700 m.

We were unable to find a specimen to support Grey-Wilson's (2014) claim of *Meconopsis lancifolia* on Yulong Xueshan, or even from Lijiang Shi (丽江市), which includes Yulong Xueshan.

KEY TO SUBSPECIES OF *MECONOPSIS LANCIFOLIA*

1a. Petals 4 or more; inflorescence with or without basal flowers 2
1b. Petals 5 or more; inflorescence always with basal flowers 3
2a. Taproot dauciform; lamina to 1.2 cm wide; inflorescence racemose, usually without basal flowers; petals to 2.2 cm long; capsules cylindrical-oblong, to 4.5 cm long, 5.5 mm across . . . . subsp. *lancifolia*
2b. Taproot elongate; lamina to 2.5 cm wide; inflorescence short racemose, sometimes appearing subscapose with short rachis and long ascending pedicels, with or without basal flowers; petals to 3.4 cm long; capsules ellipsoid, obovoid or narrowly obovoid, to 2.5 cm long, 7.5 mm across . . . . subsp. *daliensis*
3a. Rachis 4–9 mm across in dried flowering specimens; petals to 4 cm long; capsules ellipsoid or broadly ellipsoid . . . . subsp. *eximia*
3b. Rachis 2–4 mm across in dried flowering specimens; petals to 2.5 cm long; capsules narrowly ellipsoid or narrowly obovoid 4
4a. Petals 5–7; anthers dull yellow; style 2–4 mm long in flower; capsules narrowly obovoid, to 3 cm long . . . . subsp. *shikaensis*
4b. Petals 6–9; anthers yellow, pale orange, or orange; style 1.0–1.8 mm long in flower; capsules narrowly ellipsoid, to 1.8 cm long . . . . subsp. *xiangchengensis*

Meconopsis lancifolia (Franch.) Franch. ex Prain subsp. ***lancifolia*.** Fig. 1, 11–13, 87.

Herbs, monocarpic, 15–35 cm tall in flower, to 42 cm tall in fruit. *Taproot* dauciform, 1.5–4 cm long, 5–12 mm across, distally gradually narrowed and with a slender extension. Most parts of plant bristly; *bristles* to 2.5(–3.0) mm long, rather weak, sometimes on short purplish streaks on surface of rachis and pedicels. *Stem* (below uppermost leaf) simple, 0.8–7.0 cm long. *Leaves* crowded near base of stem, petiolate; *petiole* membranous, linear or broadly linear, 1.5–5.0 cm long, 1–5 mm wide; *lamina* oblong or narrowly oblanceolate, or elliptic in small leaves, 2–8 cm long, 4–13 mm wide, base attenuate, margin entire, often undulate, apex acute or obtuse, upper surface green or yellowish green, lower surface somewhat canescent, both surfaces sparsely or moderately bristly, occasionally glabrous. *Inflorescence* racemose, usually without basal flowers, ebracteate, lowest flower occasionally in axil of uppermost leaf (bract), occasionally with lowest flower bud borne on diminutive pedicel much smaller and abortive; *rachis* 2.8–5.5 mm across in dried specimens; *pedicels* 1–10 cm long in flower, to 13 cm long in fruit; rachis and pedicels densely hairy with patent or retrorse bristles. *Flowers* 5–12, half nodding, bowl- or dish-shaped, 2.3–3.8 cm across. *Calyx* 7–9 mm long, densely bristly. *Petals* 4–7, often 5 or 6, violet or purple, obovate, elliptic or ovate, 1.5–2.2 cm long, 0.6–1.5 cm wide, base cuneate or rounded, margin entire, sometimes irregularly crenulate near apex, occasionally cleft to various degrees, apex triangular-acute, obtuse or rounded. *Stamens* numerous; *filaments* similar to or paler than petals, filiform, 5–8 mm long; *anthers* pale yellow, ellipsoid, 0.8–1.3 mm long, thecae straight. *Ovary* ellipsoid, 4–5 mm long, sparsely or moderately hairy with ascending bristles, occasionally glabrous; *style* 1–2 mm long in flower, to 5 mm long in fruit; *stigma* capitate, ca. 1 mm across; lobes 3 or 4, ovate, 1.0–1.5 mm long, erect in fruit. *Capsules* cylindrical-oblong, 2.0–4.5 cm long, 3.0–5.5 mm across, sparsely or moderately hairy with patent or retrorse bristles, occasionally glabrous; carpels 3 or 4, upper 1/6–1/5 dehiscent. *Seeds* blackish, 1–1.3 mm long.

Distribution: CHINA. NW Yunnan: Heqing Xian (鹤庆县), Jianchuan Xian (剑川县), 3200–3900 m elevation.

Habitat and ecology: west-facing humid, steep, rocky slopes covered with mosses, often below lower margin of dwarf thickets; rooting in humus-rich soil among rocks.

Specimens examined: CHINA. NW Yunnan, Heqing Xian, **Region 7:** Yen-tze-hay, Lankong, 3200 m, 7 June 1886, *J. M. Delavay 2080* (E, K, P); same locality, 8 July 1886, *J. M. Delavay s.n.* (P); same locality, 9 May 1887, *J. M. Delavay s.n.* (E); same locality, 3300 m, 6 June 1888, *J. M. Delavay s.n.* (P); same locality, 3500 m, 6 June 1888, *J. M. Delavay s.n.* (P); same locality, 3200 m, 7 August 1888, *J. M. Delavay s.n.* (P); same locality, 3500 m, 7 August 1888, *J. M. Delavay s.n.* (P); Lao-long-tong, Yen-tze-hay [without elevation], 18 July 1889, *J. M. Delavay s.n.* (P); Yen-tze-hay, 3500 m [without collection date], *J. M. Delavay s.n.* (K); Kona-lo-po, Ho-kin, 3500 m, 13 July 1886, *J. M. Delavay 2080* [duplicated number assigned to a different collection] (P); Fang-yang-tchang, Mo-so-yn, 3200 m, 17 June 1887, *J. M. Delavay s.n.* (P); Maeulchan [probably Machang, 马厂], Gnou-kay, 9 July 1889, *J. M. Delavay s.n.* (P); Sung-kwe pass between Likiang and Ho-king, south of Likiang, 13,500 ft, July–August 1932, *J. F. Rock 25192* (KUN) [there are no mountains higher than 13,000 ft between Likiang (Lijiang) and Ho-king (Heqing). The locality, Sung-kwe pass, could be in the vicinity southwest of Songgui (松桂), south of Heqing.]; Ma-er Shan (马耳山), 26°16'32"N, 100°06'05"E, 3500 m, 21 July 2018, *T. Yoshida K127* (KUN, TI). NW Yunnan, Jianchuan Xian (剑川县), **Region 9:** Chienchuan [Jianchuan, 剑川]– Mekong divide, 26°45'N, 99°40'E, 13,000 ft, *G. Forrest 21576* (E) [the locality seems to be on the northwestern spur of Laojun Shan (老君山), NW of Jianchuan (Chienchuan), according to the locality records].

Meconopsis lancifolia (Franch.) Franch. ex Prain **subsp. daliensis** T. Yoshida & H. Sun, *subsp. nov.* TYPE: CHINA. NW Yunnan, Yangbi Xian (漾濞县): western flank of Tali Range, 12,000 ft, July 1917, *G. Forrest 15502* (Holotype: K; Isotypes, BM, E). Fig. 1, 14–15.

Subsp. *daliensis* differs from subsp. *lancifolia* in the elongate taproot (dauciform in the latter), ellipsoid, obovoid or narrowly obovoid capsules (cylindrical-oblong in the latter), differs from subsp. *shikaensis*, subsp. *xiangchengensis*, and subsp. *eximia* in the petals 4 or more (5 or more in the latter three subspecies) and the lamina to 2.5 cm wide (less than 1.3 cm wide in the latter three subspecies).

Herbs, monocarpic, 13–25 cm tall in flower, to 35 cm tall in fruit, *Taproot* elongate, to 12 cm long or more, 5–12 mm across, distally gradually narrowed and with slender extensions. Most parts of plant bristly; *bristles* rather hard, to 4(–5) mm long. *Stem* (below uppermost leaf) simple, 1–5 cm long. *Leaves* crowded on short stem, distinctly petiolate; *petiole* membranous, linear or broadly linear, 1–5 cm long, 1–3 mm wide; *lamina* oblong, elliptic or narrowly oblanceolate, rarely ovate in small leaves, 2.5–13.0 cm long, 1.0–2.5 cm wide, base attenuate, rarely cuneate, margin entire, occasionally undulate, apex obtuse or acute, both surfaces sparsely or moderately bristly, occasionally glabrescent. *Inflorescence* short racemose, sometimes subscapose with short rachis and long ascending rachis, with or without basal flowers, ebracteate except basal flowers; *rachis* 4–8 mm across in dried flowering specimens; *pedicels* (scapes) 1.5–12.0 cm long in flower, to 15 cm long in fruit; rachis and pedicels moderately, densely, or sparsely hairy with patent bristles. *Flowers* 4–11, three-dimensional shape unknown. *Calyx* 0.9–1.5 cm long, densely, moderately, or sparsely bristly. *Petals* 4, 5 or occasionally 6, deep satiny purple, deep purple, deep purplish blue, or pale purplish blue (according on *G. Forrest* 1950, 1999, 2950, 13517, 13714, 15502), obovate or broadly obovate, 2.2–3.4 cm long, 1.5–2.7 cm wide, base cuneate, margin entire, occasionally irregularly crenate near apex, apex rounded or occasionally obtuse. *Stamens* numerous; *filaments* filiform, 6–12 mm long; *anthers* ellipsoid or oblong, 1.0–1.7 mm long; thecae straight. *Ovary* ellipsoid, 4–8 mm long, densely hairy with ascending bristles; *style* 1.0–2.5 mm long in flower, to 5 mm long in fruit; *stigma* ovoid, c. 1 mm across; lobes 3 or 4, 1–2 mm long, erect in fruit. *Capsules* ellipsoid, obovoid or narrowly obovoid, 1.8–2.5 cm long, 5.0–7.5 mm across, moderately, densely, or sparsely hairy with patent stiff bristles; carpels 3 or 4, dehiscent in upper 1/4–1/3. *Seeds* unknown.

Distribution: CHINA. NW Yunnan: Dali Shi (大理市) and Yangbi Xian (漾濞县), Cang Shan (苍山). NE Yunnan: Kunming Shi (昆明市), Donchuan Qu (东川区). 3500–4100 m elevation.

Habitat and ecology: among shifting stones, among stones near ridge and on granite rocks near ridge, according to label data on specimens, *J. M. Delavay s.n.* 19 August 1887 (P) and *J. M. Delavay s.n.* 29 August 1889 (P).

Specimens examined: CHINA. NW Yunnan, Yangbi Xian and Dali Shi, **Region 8:** western flank of Tali Range [Cang Shan, 苍山], 12,000 ft, July 1917, *G. Forrest 15502*

FIGURES 14–17. **14**. Holotype of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *daliensis* T. Yoshida & H. Sun, *G. Forrest 15502* (K). **15**. Paratype of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *daliensis* T. Yoshida & H. Sun, *G. Forrest 13517* (K). **16**. Holotype of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *shikaensis* T. Yoshida & H. Sun, *T. T. Yü 12093* (KUN). **17**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *shikaensis* T. Yoshida & H. Sun on Shika Xueshan, 4400 m. Photograph by T. Yoshida, July 27, 2005.

(BM, E, K); same locality, 25°40'N, 12,000 ft, August 1914, *G. Forrest 13517* (E, K); same locality, 25°25'N, 12,000 ft, May 1917, *G. Forrest* 13714 (E); parmi les pierres mouvants sur le Tsang-chan [Cang Shan, 苍山] au dessus de Ta-li [Dali, 大理], 4000 m, 19 August 1887, *J. M. Delavay s.n.* (P); parmi les pierres, sur le Tsang-chan, tout près de l'arête, 4000 m, 19 August 1887, *J. M. Delavay s.n.* (P); des rochers granitiques tout près de l'arête sur le Tsang chan, 4000 m, 29 August 1889, *J. M. Delavay s.n.* (P); eastern flank of the Tali range, 25°40'N, 11,000 ft, June 1906, *G. Forrest 1950* (BM, E); eastern flank of the Tali range, 25°40'N, 12–13,000 ft, July–August 1906, *G. Forrest 1999* (BM); Tali range, August 1929, *G. Forrest 28224* (BM, E); Tali range, 1931, *G. Forrest 30946* (BM); Tsangshan [Cang Shan, 苍山] range, west of Talifu [Dali-fu, 大理府], August 1922, *J. F. Rock 6324* (E); Dali, Top of Yingle Feng (应乐峰山顶), 1941, *Hanchen Wang* (王汉臣) 974 (KUN). NE Yunnan, Kunming Shi, Donchuan Qu (东川区), **Region 3:** Shekuai Xiang, Huoshi-liangzi, Baishi-ya, Jinfengkou, (舍块乡火石梁子白石崖紧风口), 26°09'21.5"N, 102°55'40.2"E, 4100 m, 18 July 2009, *Liu Ende & Fang Wei 2100* (KUN).

As far as known, there is no recent record of collection or photography of the subspecies from Cang Shan since the collection by *Hanchen Wang* in 1941.

The specimen collected from Dongchuan Qu, *Liu Ende & Fang Wei 2100* (KUN), is in fruit and with a note "Flower: blue." Identification of the specimen needs further studies, especially the inflorescence and the number and size of the petals.

Meconopsis lancifolia (Franch.) Franch. ex Prain **subsp. shikaensis** T. Yoshida & H. Sun**,** *subsp. nov.* TYPE: CHINA. NW Yunnan: Sianrentung (仙人洞雪山) [Shika Xueshan, 石卡雪山], Chungtien (Zhongdian, 中甸) [Xianggelila, 香格里拉], 3500–3550 m, 12 July 1937, *T. T. Yü* (俞德俊) 12093 (Holotype: KUN). Fig. 1, 16–20, 88.

Subsp. *shikaensis* differs from the related subsp. *lancifolia* in the taproot usually elongate, occasionally dauciform (dauciform in the latter), and the petals 5 or more (4 or more in the latter), the inflorescence always with basal flowers (usually without basal flowers in the latter). It differs from the related subsp. *xiangchengensis* in the petals 5–7 (6–9 in the latter), the style 2–4 mm long (1–1.8 mm long in the latter), and the capsules narrowly obovoid, to 3 cm long (narrowly ellipsoid, to 1.8 cm long in the latter).

Herbs, monocarpic, 12–28 cm tall in flower, to 34 cm tall in fruit. *Taproot* usually elongate, occasionally dauciform, to 8 cm long or more, 4–10 mm across, sometimes with a smaller branch, distally gradually narrowed and with slender extensions. Most parts of plant usually bristly; *bristles* to 2.5 mm long, occasionally to 3 or 4 mm long. *Stem* (below uppermost leaf) simple, 0.4–2.0 cm long. *Leaves* crowded on short stem, petiolate; *petiole* membranous, linear, 0.5–2.0 cm long, 1–2 mm wide; *lamina* linear-oblong or oblong, 2–7 cm long, 4–9 mm wide, base attenuate, margin entire, sometimes coarsely undulate, apex obtuse, rounded or acute, upper surface green, moderately bristly, lower surface somewhat canescent, sparsely or moderately bristly. *Inflorescence* racemose, with basal flowers, occasionally subscapose with short rachis and long ascending pedicels in windy habitats, sometimes with a few lowest flower buds borne on diminutive pedicels much smaller and abortive, ebracteate except basal flowers; *rachis* 2–4 mm across in dried flowering specimens; *pedicels* (except those of abortive flower buds) 2–8 cm long in flower, to 15 cm long in fruit; rachis and pedicels moderately or sparsely hairy with retrorse or patent bristles, or rarely glabrous. *Flowers* 4–13 except abortive ones, half nodding or nodding, dish- or bowl-shaped in fine weather, 2.5–3.8 cm across. *Calyx* 8–10 mm long, moderately bristly. *Petals* 5–7, violet or purple, occasionally magenta-purple, obovate or broadly obovate, 1.8–2.3 cm long, 0.7–1.7 cm wide, base cuneate, margin entire, sometimes irregularly crenulate near apex, occasionally cleft in various degree, apex obtuse or rounded. *Stamens* numerous; *filaments* similar to or darker than petals, filiform, 7–9 mm long; *anthers* dull yellow, narrowly ellipsoid, 1.0–1.2 mm long; thecae straight. *Ovary* narrowly ellipsoid, 4–7 mm long, densely or moderately hairy with ascending bristles; *style* 2–4 mm long in flower, to 5 mm long in fruit; *stigma* capitate, ca. 1 mm across, lobes 3–4, ovate, 0.8–1.5 mm long, erect in fruit. *Capsules* narrowly obovoid, 1.5–3.0 cm long, 4–6 mm across, moderately or densely hairy with patent bristles, rarely glabrous; carpels 3 or 4, upper 1/6–1/7 dehiscent. *Seeds* brownish, 1.3–1.8 mm long.

Distribution: CHINA. NW Yunnan: Xianggelila Shi (香格里拉市), around Shika Xueshan (石卡雪山), 3400–4350 m elevation.

Habitat and ecology: on southwest- or south-facing stony slopes covered with thin layer of soil composed of old plants, partly covered with mosses; occasionally growing among dwarf shrubs.

Additional specimens examined: CHINA. NW Yunnan, Xianggelila Shi, around Shika Xueshan, **Region 10:** Sianrentung (仙人洞雪山) [Shika Xueshan], Chungtien (Zhongdian, 中甸), 3500–3550 m, 12 July 1937, *T. T. Yü* (俞德俊) *12093* (KUN); same locality, 3400 m, 12 July 1937, *T. T. Yü 12117* (KUN); same locality, 3400m, 12 July 1937, *T. T. Yü 12127* (KUN); Juatze, Chungtien, 3700 m, 20 July 1937, *T. T. Yü 12305* (KUN); Zhongdian Shigao Xueshan (中甸石膏雪山) [Shika Xueshan], Dege Niuchang Houshan (德哥牛场後山), 6 July 1939, *K. M. Feng* (冯国楣) *1519* (KUN); Zhongdian Chengjiao (中甸城郊), Buluzhai (布吕寨), near Songlu (松如), 4200 m, 20 July 1963, *Zhongdian Team* (中甸队) *3626* (KUN); Zhongdian Xian Shika Xueshan (中甸县石卡雪山), 4200 m, 21 June 1981, *Qinghai-Xizang Team* (青藏队) *1295* (KUN); Shika Xueshan, 27°47'41"N, 99°35'06"E, 4350 m, 24 July 2018, *T. Yoshida K128* (KUN); same locality, 27°48'10"N, 99°34'30"E, 4250 m, 24 July 2018, *T. Yoshida K129* (KUN, TI).

The plants in the photographs appearing in Grey-Wilson (2014: 322, middle right and below left; 323, above right), with captions of *Meconopsis lancifolia* subsp. *eximia,* are *M. lancifolia* subsp. *shikaensis* in this paper.

FIGURE 18. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *shikaensis* T. Yoshida & H. Sun on Shika Xueshan, 4400 m. Photograph by T. Yoshida, July 27, 2005.

FIGURES 19–20. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *shikaensis* T. Yoshida & H. Sun. **19**. On Shika Xueshan, 4350 m. Photograph by T. Yoshida, July 24, 2018. **20**. Capsules and seeds, from *T. Yoshida K129*.

Meconopsis lancifolia (Franch.) Franch. ex Prain subsp. ***eximia*** (Prain) Grey-Wilson, *The Genus Meconopsis—Blue Poppies and Their Relatives*: 324. 2014. TYPE: CHINA. NW Yunnan, Deqin Xian (德钦县): Kari Pass, Mekong-Yangtzi divide, 27˚40'N, alt. 12,000 ft, August 1914, *G. Forrest 13020* (Lectotype: E, designated by Grey-Wilson, 2014; Isolectotype: K). Fig. 1, 21–27, 89.

Basionym: *Meconopsis eximia* Prain, *Bull. Misc. Inform., Kew, 1915*: 159 (1915). TYPE: CHINA. NW Yunnan, Xiangelila Shi (香格里拉市): Chungtien [Zhongdian, 中甸] Plateau, 27˚30'N, 12,000 ft, July 1914, *G. Forrest 12691* (Syntypes: E, K); same locality, September 1914, *G. Forrest 13352* (Syntype: K). NW Yunnan, Deqin Xian (德钦县): Kari Pass, Mekong-Yangtzi divide, 27˚40'N, alt. 12,000 ft, August 1914, *G. Forrest 13020* (Syntypes: E, K); Mekong-Salwin divide, 28˚10'N, 14,000 ft, August 1914, *G. Forrest 13238* (Syntypes: E, K).

Herbs, monocarpic, 15–35 cm tall in flower, to 40 cm tall in fruit, occasionally to 58 cm tall on lower edge of shrubberries (around Hong Shan) in fruit. *Taproot* hard and woody, elongate, to 10 cm long or more, 7–12 mm across, often fusiform, distally gradually narrowed and with slender extensions. Most parts of plant bristly; *bristles* to 3.5 mm long, occasionally to 4 or 5 mm long. *Stem* (below uppermost leaf) simple, 3–12 mm long. *Leaves* all basal, petiolate; *petiole* not membranous, linear or broadly linear, 0.5–3.5 cm long, 1.5–3.0 mm wide; *lamina* rather thick, strap-shaped, oblong or oblanceolate, 2.5–6.0 cm long, 5–10 mm wide, base attenuate, margin entire, often undulate, apex obtuse or acute, upper surface green or dark green, densely or moderately bristly, lower surface pale green, moderately or sparsely bristly. *Inflorescence* racemose, with basal flowers, occasionally subscapose with short rachis and long ascending pedicels in windy habitats, ebracteate except basal flowers; *rachis* 4–9 mm across in dried flowering specimens; *pedicels* (scapes) 2–11 cm long in flower, to 13 cm long in fruit; rachis and pedicels densely or moderately hairy with retrorse or patent bristles. *Flowers* 6–11, half nodding or occasionally facing laterally, bowl-shaped or occasionally dish-shaped in fine weather, 3.5–7.0 cm across. *Calyx* 1.0–1.5 cm long, densely bristly. *Petals* 5–9, purple or magenta-purple, obovate or broadly obovate, 1.8–4.0 cm long, 0.8–3.0 cm wide, base cuneate, margin entire, occasionally crenulate near apex, sometimes cleft in various degree, apex rounded or obtuse. *Stamens* numerous; *filaments* darker than petals, filiform, rather thick, 7–12 mm long; *anthers* yellow, pale yellow or dull orange, oblong, 1.3–2.0 mm long; thecae straight. *Ovary* ovoid or ellipsoid, 4–8 mm long, densely hairy with ascending bristles; *style* 1–2 mm long in flower, to 3 mm long in fruit; *stigma* ovoid, 1–2 mm across; lobes 4–5, 2.0–3.5 mm long, erect or

FIGURES 21–24. **21**. Syntype of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *eximia* (Prain) Grey-Wilson, *G. Forrest 12691* (E), collected on "Chungtien Plateau" [Zhongdian Plateau]. **22**. Specimen of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *eximia* (Prain) Grey-Wilson, *G. Forrest 14087* (K), collected on "Mekong-Salween divide." **23**. Syntype of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *eximia* (Prain) Grey-Wilson, *G. Forrest 13238* (K), collected on "Mekong-Salwin divide." **24**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *eximia* (Prain) Grey-Wilson on Da Xueshan, 4300 m. Photograph by T. Yoshida, June 15, 1999.

FIGURES 25–26. **25**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *eximia* (Prain) Grey-Wilson on Baima Xueshan, 4650 m. Photograph by T. Yoshida, July 26, 2018. **26**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *eximia* (Prain) Grey-Wilson on Baima Xueshan, 4650 m. Photograph by T. Yoshida, July 25, 2018.

FIGURE 27. Habitat of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *eximia* (Prain) Grey-Wilson on Baima Xueshan, 4650 m. Photograph by T. Yoshida, July 25, 2018.

ascending in fruit. *Capsules* ellipsoid or broadly ellipsoid, 1.2–2.2 cm long, 8–12 mm across, densely bristly; carpels 4–5, upper 1/3–2/3 dehiscent. *Seeds* unknown.

Distribution: CHINA. NW Yunnan: Xiangelila Shi (香格里拉市), Deqin Xian (德钦县), Gongshan Xian (贡山县). SE Xizang: Chayu Xian (察隅县). SW Sichuan: Xiangcheng Xian (乡城县), Daocheng Xian (稻城县). 3500–4700 m elevation.

Habitat and ecology: on southwest-, west-, or south-facing stony slopes or stable scree slopes covered with thin soil composed of old plants; occasionally growing among dwarf shrubs.

Additional specimens examined: CHINA. NW Yunnan, Xiangelila Shi, **Region 11:** mountains of Chungtien Plateau, 27˚30'N, 12,000 ft, July 1914, *G. Forrest 12691* (E, K); same locality, September 1914, *G. Forrest 13352* (K); Geza (格咱) – Langdou (浪都), 4400 m, 25 June 1988, *Z. D. Fang & X. H. Li 753* (KUN); Shangri-La County, Geza Township, 28˚08'23.7"N, 99˚54'28.8"E, 4385m, 16 July 2007, *R. Li & Z. Dao 009C* (MO); Hon Shan (红山), 28˚06'35"N, 99˚53'59"E, 4200 m, 27 July 2018, *T. Yoshida K133* (KUN, TI). NW Yunnan, Xianggelila Shi, Da Xueshan (大雪山), **Region 13:** Da Xueshan Yakou (大雪山丫口), 4300 m, 5 June 1999, *T. Yoshida 2840* (TI); same locality, 4350 m, 22 June 1999, *T. Yoshida 2890* (TI). NW Yunnan, Deqin Xian, Yunling (云岭) including Baima Xueshan (白马雪山), **Region 14:** Kari Pass, Mekong-Yangtzi divide, 27˚40'N, alt. 12,000 ft, August 1914, *G. Forrest 13020* (E, K); Beima Shan, 28˚12'N, 11,000 ft, August 1917, *G. Forrest 14625* (BM, E, K); Mekong-Yangtzi divide, 27˚36'N, 99˚10'E, 14,000 ft, July 1921, *G. Forrest 19683* (BM, E); Beima Shan, 28˚18'N, 99˚10'E, 13,000 ft, September 1921, *G. Forrest 20406* (E); mountains east of Atuntzi, 28˚36'N, 99˚E, 14,000 ft, *G. Forrest 22642* (E); mountains of Moting [Maoding, 茂顶], NE of the Yangtze-Mekong watershed, June 1923, *J. F. Rock 10339* (E); Moting Shan, northeast of Atuntze, eastern slopes of Yangtze-Mekong divide, 15,000 ft, June 1932, *J. F. Rock 22768* (E); Deqen, Beima Shan, north side of road, 28˚22'N, 99˚02'E, 4322 m, 28 June 1994, *ACE 744* (E); Baima Xueshan, 28˚28'57"N, 99˚00'29"E, 4650 m, 26 July 2018, *T. Yoshida K132* (KUN, TI). NW Yunnan, Deqin Xian and Gongshan Xian, northern part of Nu Shan (怒山) including Meili Xueshan (梅里雪山), **Region 15:** Mekong-Salwin divide, 28˚10'N, 14,000 ft, August 1914, *G. Forrest 13238* (E, K); Mekong-Salween divide, 28˚20'N, 14,000 ft, July 1917, *G. Forrest 14087* (E, K); Londre pass [Kongque Shan Yakou, 孔雀山丫口], Mekong-Salwin divide, 28˚14'N, 98˚40'E, 14,000 ft, July 1921, *G. Forrest 19694* (BM, E); Mekong-Salwin divide, 27˚30'N, 98˚56'E, 14,000 ft, August 1921, *G. Forrest 20032* (E). SE Xizang, Chayu Xian, **Region 15:** Sarong [Chawalong, 察瓦龙, or Tsarong], Ka-gwr-pu [Meili Xueshan], Mekong-Salwin divide, 28˚25'N, 14,000 ft, July 1917, *G. Forrest 14473* (BM, E, K). SW Sichuan, Daocheng Xian, **Region 12:** Daocheng Gongga Shan (稻城贡嘎山), Jiamairong Feng (贾迈荣峰), 4600 m, 29 Aug. 1981, *Qinghai-Xizang Team* (青藏队) *5544* (KUN). SW Sichuan, Xiangcheng Xian, **Region 13:** Rewu Gongshe (热乌公社) [located on the northern side of Da Xueshan], Balang (巴朗), 4700 m, 6 August 1981, *Qinghai-Xizang Team* (青藏综合科学考察队) *3901* (KUN).

Kari Pass, where *G. Forrest 13020*, the lectotype of *Meconopsis lancifolia* subsp. *eximia* (Prain) Grey-Wilson, was collected, is an old pass located at 28˚08'27"N, 99˚13'34"E southeast of Baima Xueshan. "Kari" is written in Chinese as 更里 in Rock (1947, volume I: 349).

The mountain range written as Mekong-Salwin divide on the specimen labels of G. Forrest or other collectors appears in modern Chinese maps as Nu Shan (怒山). The northern part of Nu Shan is called Meili Xueshan, whereas the southern part of Nu Shan is often called Biluo Xueshan (碧罗雪山).

According to determination labels on specimens, Taylor (1934) included specimens collected in the southern part of Nu Shan, such as *G. Forrest 19490* (BM), *19790* (E) and *J. F. Rock 23253* (E), and those collected around Chimili valley on the western (Myanmar) side of Gaoligong Shan (高黎贡山), such as *R. Farrer 1159* (E), *G. Forrest 24886* (E) and *G. Forrest 27284* (K), in *Meconopsis lancifolia* var. *solitariifolia* Fedde. However, those specimens are not *M. lancifolia*. The specimens from the southern Nu Shan are *M. castanea* H. Ohba, T. Yoshida & H. Sun; those collected around Chimili valley are *M. bijiangensis* H. Ohba, T. Yoshida & H. Sun. Both Taylor (1934) and Grey-Wilson (2014) included northern Myanmar (Burma) in the distribution of *M. lancifolia,* but we have not found any specimens of *M. lancifolia* collected in Myanmar.

The photographs in Grey-Wilson (2014: 322, above right and below left; 323, above right), taken on Shika Shan, are not *Meconopsis lancifolia* subsp. *eximia* as indicated in the captions, but *M. lancifolia* subsp. *shikaensis* described above; the photographs in Grey-Wilson (2014: 323, above left, below middle, and below right), taken on Balang Shan, are not *M. lancifolia* subsp. *eximia* as indicated in the captions, but *M. purpurea* described below.

As far we know, there have been no collection or photograph of subsp. *eximia* on Nu Shan (Region 14) since the collection by G. Forrest in August 1921.

Meconopsis lancifolia (Franch.) Franch. ex Prain **subsp. xiangchengensis** (R. Li & Z.L. Dao) T. Yoshida & H. Sun, *stat. nov.* Fig. 1, 28–34, 90.

Basionym: *M. xiangchengensis* R. Li & Z.L. Dao, *Novon* 22 (2):180. 2012. TYPE: CHINA. SW Sichuan: Xiangcheng Xian (乡城县), Shagong (沙贡) township, Wuming Snow Mountains Pass [Wuming Shan, 无名山], 29˚08'15.5"N, 100˚02'38.6"E, 4684 m, 19 July 2007, *R. Li & Z. Dao 036* (Holotype: KUN).

Subsp. *xiangchengensis* differs from the related subsp. *shikaensis* T. Yoshida & H. Sun in the petals 6–9 (5–7 in the latter), the style 1.0–1.8 mm long (2–4 mm long in the latter), and the capsules narrowly ellipsoid, to 1.8 cm long (narrowly obovoid, to 3 cm long, in the latter). It differs from the related subsp. *eximia* (Prain) Grey-Wilson in the petals to 2.5 cm long (to 4.0 cm long in the latter) and the capsules narrowly ellipsoid (ellipsoid or broadly ellipsoid in the latter).

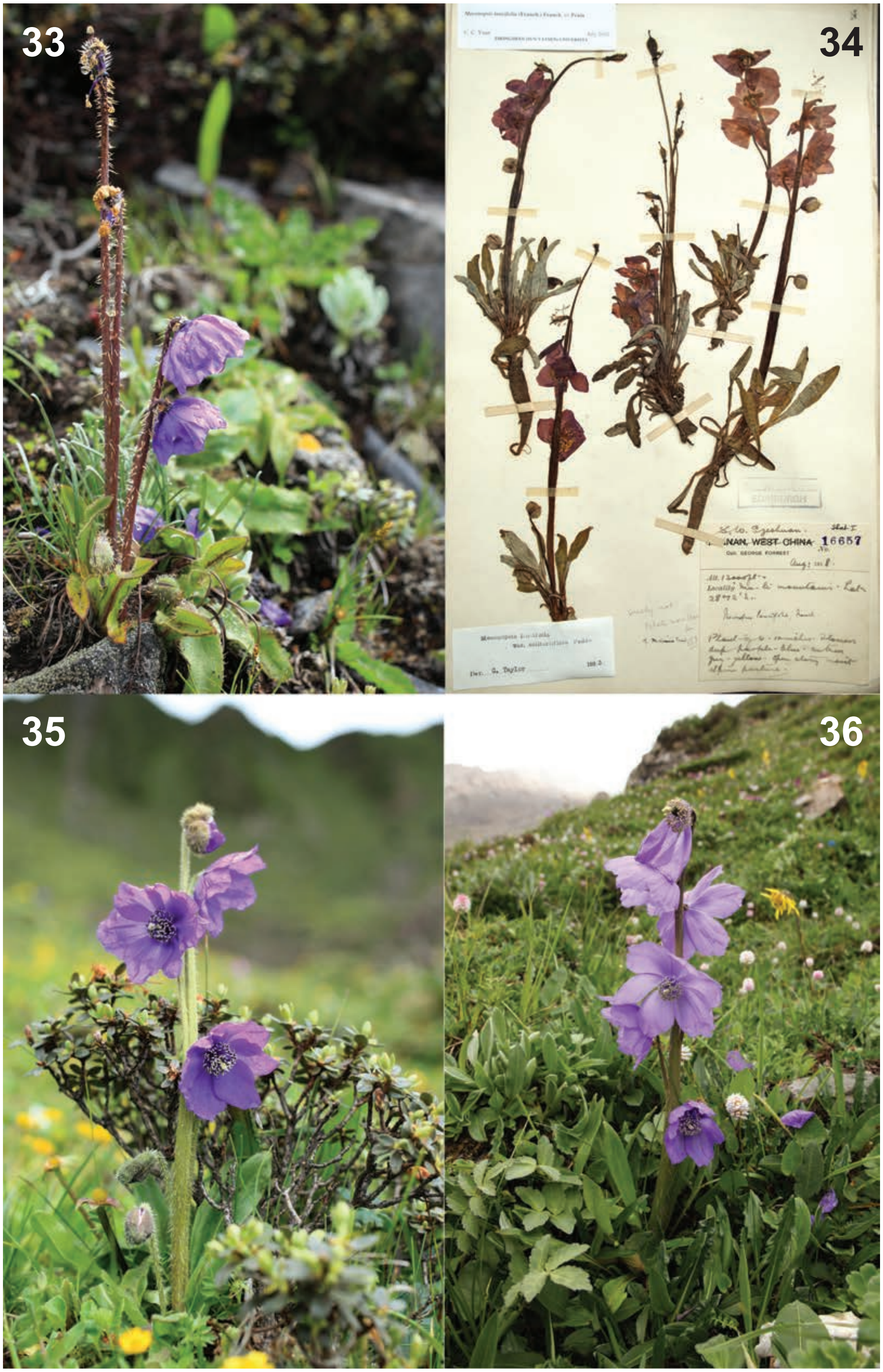
Flora of China

Collection number: 036
Collectors: Li Rong and Dao Zhiling
Collection date: 19 July, 2007
Family number: 32 Family name: Papaveraceae
Field name: Meconopsis
Description: Perennial herb ca. 10 cm tall. Flowers blue, root fleshy, inflorescence glabrous, leaves with hair.
Habitat: Alpine meadow.
Where growing: On the slope.
Locality: Sichuan Province, Ganzi Tibet people zizhi Prefecture, Xiangcheng Xian, Shagong Xiang, Wuming snow Mountains pass, along the road from Xiangcheng to Daocheng.
Latitude and Longitude: N 29⁰ 08' 15.5", E 100⁰ 02' 38.6" Elevation: 4684 m

HOLOTYPE!
Coll.No.: **R. Li *et al.* 036, Papaveraceae**
香城绿绒蒿
***Meconopsis xiangchengensis* R. Li & Z. L. Dao, sp. nov.**
鉴定人（Det.）: R. Li & Z. L. Dao 2012.11.30

FIGURE 28. Holotype of *Meconopsis xiangchengensis* R. Li & Z.L. Dao, *R. Li & Z. L. Dao 036* (KUN).

FIGURES 29–32. **29**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun on Wuming Shan, 4500 m. Photograph by T. Yoshida, June 21, 2017. **30**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun on Wuming Shan, 4500 m. Photograph by T. Yoshida, June 21, 2017. **31**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun on Jichou Shan, 4400 m. Photograph by T. Yoshida, June 30, 2018. **32**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun on Jichou Shan, 4350 m. Photograph by T. Yoshida, June 30, 2018.



FIGURES 33–36. **33**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun on Jichou Shan, 4400 m. Photograph by T. Yoshida, June 30, 2018. **34**. Specimen of *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun, *G. Forrest 16657* (E), collected on "Mu-li mountains." **35**. *Meconopsis purpurea* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 28, 2018. **36**. *Meconopsis purpurea* T. Yoshida & H. Sun on the western side of Balang Shan, 4250 m. Photograph by T. Yoshida, July 14, 2013.

Herbs, monocarpic, 8–27 cm tall in flower, to 30 cm tall in fruit. *Taproot* often elongate, occasionally dauciform in milder habitats, to 10 cm long or more, 7–15 mm across, distally gradually narrowed and with slender extensions. Most parts of plant bristly; *bristles* to 3.5 mm long, occasionally to 4 or 5 mm long. *Stem* (below uppermost leaf) simple, 0.5–2.2 cm long. *Leaves* all basal, petiolate; *petiole* membranous, linear, 1–7 cm long, 1–2 mm wide; *lamina* linear-oblong or oblanceolate, 2–8 cm long, 3–11 mm wide, base attenuate, margin entire, usually coarsely undulate, apex obtuse, occasionally acute, upper surface green or yellowish green, lower surface somewhat paler, both surfaces densely, moderately, or occasionally sparsely bristly. *Inflorescence* racemose often with basal flowers or occasionally without basal flowers in milder habitats, occasionally subscapose with short rachis and long ascending pedicels in windy habitats especially when uppermost flower buds are damaged or removed, ebracteate except in basal flowers; *rachis* 2.0–3.5 mm across in flower, to 4.5 mm across in fruit; *pedicels* (scapes) 1–10 cm long in flower, to 13 cm long in fruit; rachis and pedicels densely, moderately or occasionally sparsely hairy with retrorse or patent bristles. *Flowers* 6–11, rarely 4 or 5, half nodding or facing laterally, dish- or occasionally bowl-shaped, 2.8–4.5 cm across. *Calyx* 8–12 mm long, densely bristly. *Petals* 6–9, often 6 or 7, violet or purple, occasionally magenta purple, obovate, rhombic, broadly obovate or elliptic, 1.7–2.5 cm long, 0.7–2.2 cm wide, base cuneate, margin entire, apex triangular-obtuse or rounded, occasionally irregularly crenulate, scarcely cleft. *Stamens* numerous; *filaments* similar to or darker than petals, filiform, 7–11 mm long; *anthers* yellow, pale orange, or orange, ellipsoid or oblong, 0.8–1.5 mm long. *Ovary* ellipsoid, 5–7 mm long, densely hairy with ascending bristles; *style* 1.0–1.8 mm long in flower; *stigma* capitate, ca. 1 mm across; lobes 3–4, rarely 5, to 2.5 mm long in fruit, erect in fruit. *Capsules* narrowly ellipsoid, 1.0–1.8 cm long, 3–6 mm across, moderately or densely hairy with patent or ascending bristles; carpels 3 or 4, rarely 5. *Seeds* unknown.

Distribution: CHINA. SW Sichuan: Daocheng Xian (稻城县), Xiangcheng Xian (乡城县), Jiulong Xian (九龙县), Yajiang Xian (雅江县), Litang Xian (理塘县), Batang Xian (巴塘县), Yan-yuang Xian (盐源县), Muli Xian (木里县), 3500–4650 m elevation.

Habitat and ecology: on rocky slopes covered with humid blackish soil composed of old plants and partly covered with moss; with other herbs and grasses, often among dwarf shrubs of *Rhododendron* or *Potentilla* L. (*Dasiphora* Raf.).

Additional specimens examined: CHINA. SW Sichuan, Yan-yuang Xian, **Region 4:** at foot of Huolu Shan (火炉山脚), Yan-yuan Yuanbao Qu (盐源元宝区) [Yuanbao is located at 27°16'15"N, 101°26'15"E, southwest of town of Yan-yuan], 3600 m, 21 July 1983, *Qinghai-Xizang Team* (青藏队) *12816* (KUN). SW Sichuan, Muli Xian, **Region 5:** Muli mountains, 28°12'N, 13,000 ft, August 1918, *G. Forrest 16657* (BM, E, K); mountains around Muli, 28°12'N, 100°E, 14,000 ft, July 1930, *G. Forrest 28388* (E); Yenching Shan, N. 6 days from Muli, 1931, *G. Forrest 30086* (BM); Litang River divide, just below the pass south of Muli, 12,000 ft, 6 June 1921, *F. Kingdon-Ward 4008* (E); Muli Kingdom, 10,000–14,000 ft, June 1922, *J. F. Rock 5501* (E, K); same locality and date, *J. F. Rock* 5557 (E); Muti Konka, snow range east of the Yalung, Mutirong, territory of Muli, 14,000–15,000 ft, May–June 1932, *J. F. Rock 23711* (BM, E, K); mountains of Kulu, Muli territory, 13,000 ft, June 1932, *J. F. Rock 23946* (BM, E); Muli, 21 June 1937, *T. T. Yü* (俞德俊) *6524* (KUN). SW Sichuan, Daocheng Xian and Xiangcheng Xian, **Region 16:** Xiangcheng Xian, Shagong (沙贡) township, Wuming Snow Mountains Pass [无名山], 29°08'15.5"N, 100°02'38.6"E, 4684 m, 19 July 2007, *R. Li & Z. Dao 039* (KUN); Daocheng Xian, Wuming Shan (无名山), 29°08'42"N, 100°04'15"E, 4550 m, 21 June 2017, *T. Yoshida K114* (KUN, TI); same locality, 29°08'02"N, 100°02'33"E, 4600–4700 m, 2 July 1998, *D. E. Boufford et al. 28160* (A, KUN). SW Sichuan, Daocheng Xian, **Region 17:** near pass of Daocheng Bowa Shan (稻城波瓦山丫口附近), 4600 m, 29 June 1973, *Sichuan Team* (四川省植被调查队) *1934* (KUN). SW Sichuan, Litang Xian, **Region 18:** Haizi Shan (海子山), 29°31'00"N, 100°16'22"E, 4550 m, 20 June 2017, *T. Yoshida K133* (KUN). SW Sichuan, Jiulong Xian, **Region 19:** Jichou Shan [鸡丑山], 29°20'03"N, 101°29'58"E, 4365–4620 m, 21 July 2005, *Boufford et al. 33308* (A); Jichou Shan, 29°20'00"N, 101°30'11"E, 4400 m, 30 June 2018, *T. Yoshida K126* (KUN, TI). SW Sichuan, Yajiang Xian, **Region 20:** Yajiang County, Jian Zikou pass west of Yajiang [雅江], 30°00'15"N, 100°51'40"E, 4380 m, 2 September 2010, *Kunming & Edinburgh Expedition to Sichuan 126* (E). SW Sichuan, Batang Xian, **Region 21:** Thibet oriental, province de Batang [巴塘], Yar-gong, 1903, *J. A. Soulié 3919* (P).

On Wuming Shan, which is located along the boundary between Xiangcheng Xian and Daocheng Xian, SW Sichuan, subsp. *xiangchengensis* grows around the pass on the main ridge of the mountain and adjacent eastern (Daocheng-side) slopes from 4400 m to 4650 m in elevation. The inflorescence in this population is racemose with basal flowers, or occasionally subscapose with a short rachis and long ascending pedicels in windy habitats especially when the uppermost flower buds are damaged or removed.

The holotype of *Meconopsis xiangchengensis* was collected near the pass on Wuming Shan. According to the description, the plant has a scapose inflorescences with solitary flowers borne on slender pedicels arising from the basal rosette. In the type specimens of *M. xiangchengensis*, *R. Li & Z. Dao 036* (Holotype: KUN) and *R. Li & Z. Dao 039* (Paratype: KUN), however, it is discernible that a few central pedicels were removed above the base. In the photograph of the fresh plants before pressing in Grey-Wilson (2014: 289), they appear to have been damaged by animal grazing. The thicker pedicels in the damaged center of each plant could possibly be peduncles with a few flowers.

Meconopsis purpurea T. Yoshida & H. Sun, *sp. nov.* TYPE: CHINA. W Sichuan, Xiaojin Xian (小金县): northern side of Jiajin Shan Yakou (夹金山丫口), 30°52'16"N, 102°41'02"E, 3950 m, 28 June 2018, *T. Yoshida K124* (Holotype: KUN; Isotypes: KUN, TI). Fig. 1, 35–39, 91.

FIGURES 37–40. **37**. *Meconopsis purpurea* T. Yoshida & H. Sun at the type locality; scapose plant with 4-petaled flower. Photograph by T. Yoshida, June 28, 2018. **38**. Flower of *Meconopsis purpurea* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 28, 2018. **39**. *Meconopsis purpurea* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, August 26, 2011. **40**. *Meconopsis lepida* Prain on northern side of Leigu Shan, 3500 m. Photograph by T. Yoshida, July 16, 2016.

Meconopsis purpurea differs from the related *M. lancifolia* in having both surfaces of the lamina covered with bristles shorter and thinner than those on other parts of the plant (with similar bristles on all parts of the plant in the latter); anthers bicolored with a dark purple central part and pale yellow periphery (unicolor in the latter), ellipsoid or rounded (ellipsoid or short oblong in the latter); and thecae incurved (straight in the latter).

Herbs, monocarpic, 12–30 cm tall in flower, to 38 cm tall in fruit. *Taproot* elongate, to 20 cm long or more, 4–10 mm across, distally gradually narrowed and with a slender extension. Most parts of plant bristly; *bristles* to 3(–4) mm long, often tinged reddish brown. *Stem* (below uppermost leaf) simple, 0.3–2.0 cm long. *Leaves* all basal, petiolate; *petiole* linear or broadly linear, 1.5–4.0 cm long, 1.0–3.5 mm wide; *lamina* oblong, narrowly lanceolate, narrowly elliptic, elliptic, or small leaves occasionally ovate, 1.5–7.0 cm long, 0.5–1.5 cm wide, base cuneate or attenuate, margin entire, sometimes undulate, occasionally coarsely toothed, apex obtuse, triangular or subacute, both surfaces moderately or sparsely covered with shorter and thinner bristles (as seen in Fig. 91). *Inflorescence* racemose with basal flower(s) or entirely scapose, ebracteate except in basal flowers, occasionally with lowest flower bud borne on diminutive pedicel and much smaller and abortive; *rachis* 2–4 mm across in dried flowering specimens; *pedicels* (scapes) 1.5–13.0 cm long in flower, to 20 cm long in fruit; rachis and pedicels moderately, densely, or sparsely hairy with retrorse or patent bristles. *Flowers* including abortive ones (3 or)4–9, facing laterally or half nodding, dish- or bowl-shaped in fine weather, 3–5 cm across. *Calyx* 10–13 mm long, densely or moderately bristly. *Petals* 4–10, purple or occasionally magenta-purple, obovate, broadly obovate or elliptic, 2.0–3.3 cm long, 0.9–2.2 cm wide, base cuneate, margin entire, occasionally irregularly crenulate near apex, apex rounded or occasionally triangular. *Stamens* numerous; *filaments* similar to petals, filiform, 6–12 mm long; *anthers* bicolored with dark purple central part and pale yellow periphery, ellipsoid or globose, 0.7–1.0 mm long, thecae incurved. *Ovary* pale green, often with 3–5 dark purple streaks, occasionally entirely tinged dark purple, ellipsoid or obovoid, 6–9 mm long, densely, moderately or occasionally sparsely bristly, rarely glabrous; *style* pale green, sometimes tinged dark purple, 1.5–3.0 mm long in flower, to 4 mm long in fruit; *stigma* capitate, ca. 1 mm across; lobes 3–5, 0.8–1.5 mm long, to 2.2 mm long in fruit. *Capsules* obovoid or narrowly obovoid, 1.2–2.2 cm long, 3.5–10.0 mm across, densely, moderately, or sparsely hairy with retrorse or patent bristles, rarely glabrous; carpels 3–5, dehiscent in upper 1/4–1/3. *Seeds* blackish, 1.3–2.0 mm long.

Distribution: CHINA. W Sichuan: Xiaojin Xian (小金县), Wenchuan Xian (汶川县), Baoxing Xian (宝兴县), Kangding Shi (康定市), 3900–4500 m elevation.

Habitat and ecology: southwest-, south-, and southeast-facing rocky slopes in blackish soil of old plants; growing together with other herbs, occasionally close to cushion plants of *Arenaria,* dwarf shrubs of *Rhododendron* or *Potentilla* (*Dasiphora*), or prostrate shrubs of *Salix*; rooting deeply in thin soil among rocks.

Additional specimens examined: CHINA. W Sichuan, Xiaojin Xian, **Region 37:** western side of Balang Shan Yakou (巴朗山丫口), 30°54'49"N, 102°53'21"E, 4300 m, 19 July 2010, *T. Yoshida K40* (KUN, TI); same locality, 17 July 2013, *T. Yoshida K93* (KUN, TI). W Sichuan, Xiaojin Xian, **Region 38:** northern side of Jiajin Shan Yakou (夹金山丫口), 30°52'16"N, 102°41'02"E, 3950 m, 20 July 2010, *T. Yoshida K42* (KUN, TI); same locality, 26 August 2011, *T. Yoshida K78* (KUN, TI); same locality, 18 July 2013, *T. Yoshida K94* (KUN, TI); same locality, 28 June 2018, *T.Yoshida K124* (KUN, TI). W Sichuan, Kangding Shi, **Region 39:** Baoding Shan (宝顶山), southern part of Jiajin Shan range, east of Pengta (捧塔), 30°26'23"N, 102°24'40"E, 4200 m, 24 July 2010, *T. Yoshida K44a* (KUN).

The plants in the photographs in Grey-Wilson (2014: 323, above left, below center, and below right), cited as *Meconopsis lancifolia* subsp. *eximia,* are *M. purpurea*; the upper plant on the same publication, on page 296, cited as *M. pulchella* and on page 297, cited as *M.* aff. *pulchella,* are not *M. pulchella*, but *M. purpurea*.

Meconopsis lepida Prain, *Bull. Misc. Inform. Kew, 1915,* No. 4: 158. 1915. TYPE: CHINA. S Gansu: Mountains of Thundercrown (Lei-go-shan) [Leigu Shan, 雷古山], Siku Alps, 12,000–13,000 ft, June 1914, *R. Farrer 123* (Holotype: E; Isotypes, BM, K). Fig. 1, 40, 41.

Synonyms: *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *lepida* (Prain) Grey-Wilson, *The Genus Meconopsis—Blue Poppies and Their Relatives*: 324. 2014.

See revision of *Meconopsis lepida* Prain by Yoshida and Sun (2017).

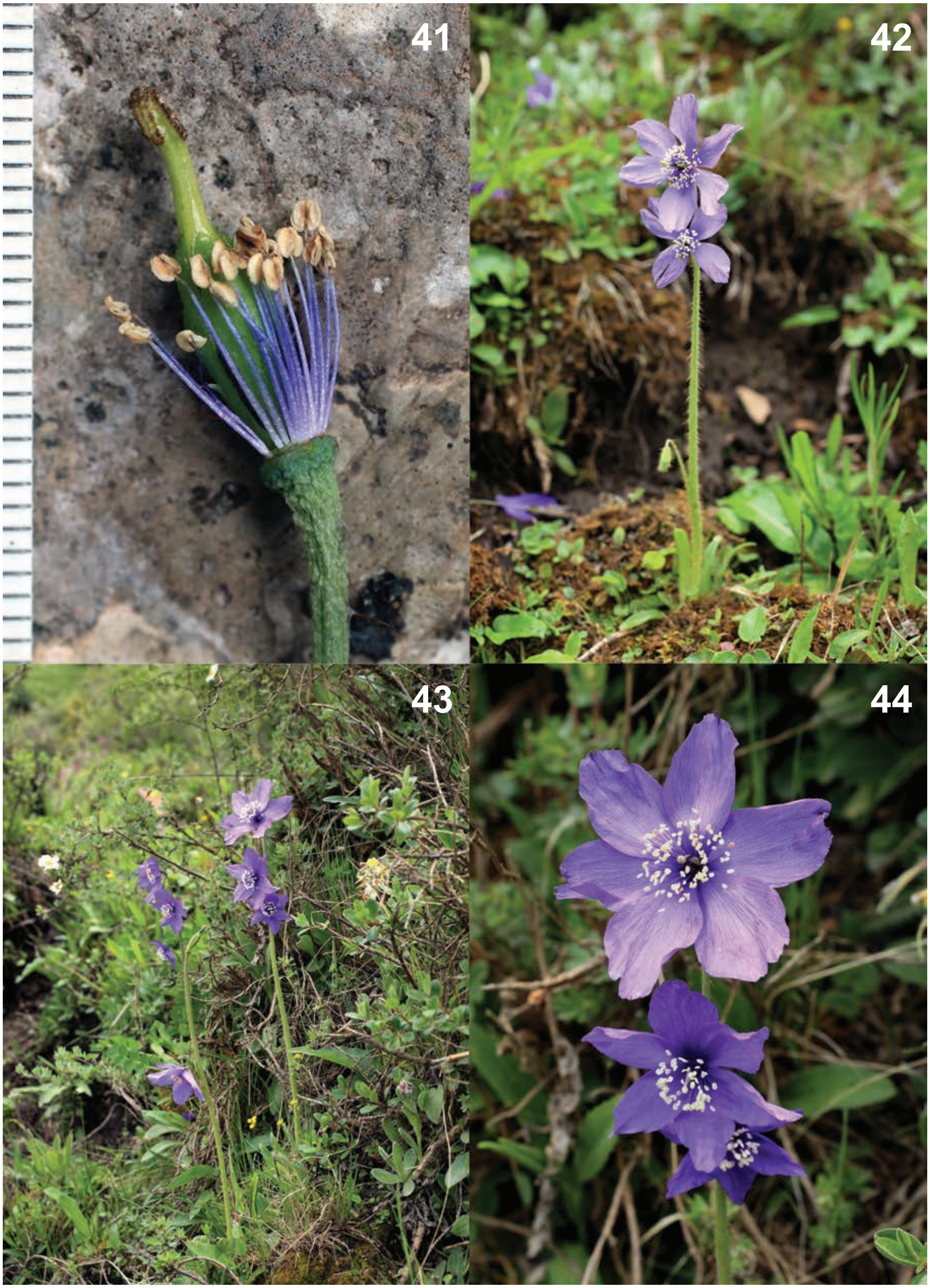
Distribution: CHINA. S Gansu: Zhouqu Xian (舟曲县) and Dangchang Xian (宕昌县), around Leigu Shan (雷古山), 3450–3900 m elevation.

Additional specimens examined: CHINA. S Gansu, Zhouqu Xian and Dangchang Xian, around Leigu Shan, **Region 32:** mountains of Thundercrown (Lei-gu-shan), Siku Alps, 12,000–13,000 ft, June 1914, *R. Farrer 123* (BM, E, K); Danchang Xian, northern side of Leigu Shan [Thundercrown in Farrer], 33°53'36"N, 104°19'01"E, 3500 m, 16 July 2016, *T .Yoshida K108* (KUN, TI).

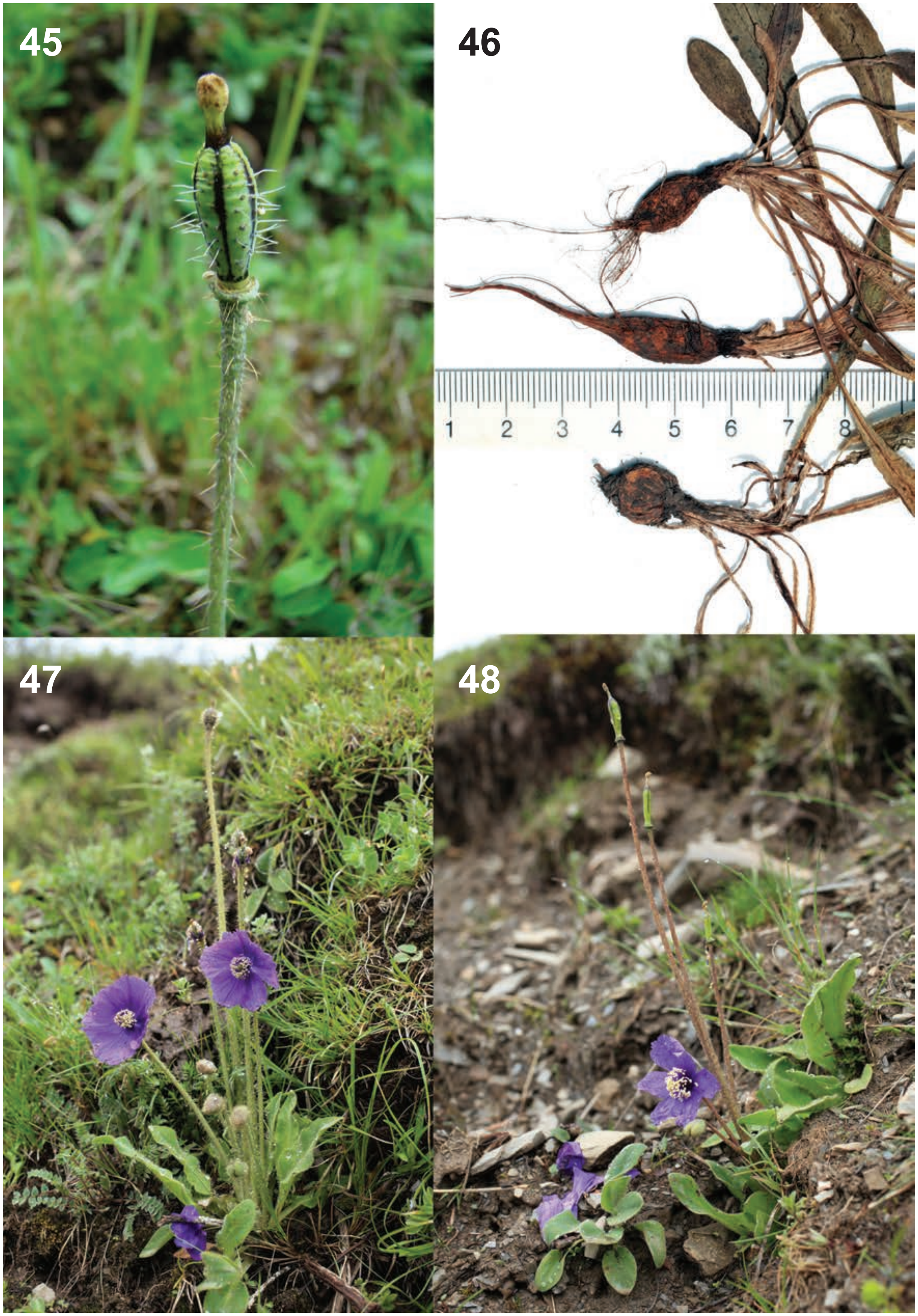
Meconopsis wengdaensis T. Yoshida & H. Sun, *sp. nov.* TYPE: CHINA. NW Sichuan, Wengda Xian (翁达县): northern side of laozhe Shan (老折山), 31°46'15"N, 100°45'19"E, 3950 m, 27 June 2016, *T. Yoshida K104* (Holotype: KUN; Isotypes: KUN, TI). Fig. 1, 42–46, 92.

Meconopsis wengdaensis differs from the related *M. lepida* in its larger size, to 40 cm tall (to 33 cm tall in the latter), rachis to 4.5 mm across (to 3.0 mm across in the latter), longer bristles to 4.0(–5.0) mm long (to 2.5 mm long in the latter), pedicels scarcely warty distally (prominently warty distally in the latter), petals 4–8 (6–9 in the latter), to 3.2 cm long (to 2.5 cm long in the latter), straight thecae (incurved thecae in the latter), and ovary streaked with dark purple (scarcely streaked with dark purple in the latter).

Herbs, monocarpic, 17–40 cm tall in flower, to 45 cm tall in fruit. *Taproot* napiform, 1.0–2.5 cm long, 7–10



FIGURES 41–44. **41**. Flower of *Meconopsis lepida* Prain with petals removed; on northern side of Leigu Shan, 3500 m. Photograph by T. Yoshida, July 16, 2016. **42**. *Meconopsis wengdaensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 27, 2016. **43**. *Meconopsis wengdaensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 29, 2016. **44**. *Meconopsis wengdaensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 29, 2016.



FIGURES 45–48. **45**. Young fruit of *Meconopsis wengdaensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Kobayashi, June 27, 2016. **46**. Napiform taproots of *Meconopsis wengdaensis* T. Yoshida & H. Sun, from *T. Yoshida K104*. **47**. *Meconopsis pleurogyna* W.T. Wang on eastern side of Yanggong Shan, 3900 m. Photograph by T. Yoshida, June 26, 2018. **48**. *Meconopsis pleurogyna* W.T. Wang on eastern side of Yanggong Shan, 3900 m. Rosette leaves of young plant with ovate lamina are on the left. Photograph by T. Yoshida, June 26, 2018.

mm across, distally abruptly narrowed and with a slender extension. Most parts of plant bristly; *bristles* to 4(–5) mm long, often tinged purple except near base. *Stem* (below uppermost leaf) simple, 0.8–2.0 cm long. *Leaves* all basal, petiolate; *petiole* membranous, linear or broadly linear, 2.0–4.5 cm long, 1–3 mm wide; *lamina* narrowly oblanceolate, oblong or narrowly elliptic, or small leaves elliptic, 1.5–6.0 cm long, 5–13 mm wide, base attenuate or cuneate, margin entire, apex obtuse or acute, upper surface green, lower surface somewhat paler or canescent, both surfaces moderately, densely, or sparsely bristly. *Inflorescence* short racemose, without basal flowers, ebracteate; *rachis* 2.0–4.5 mm across in dried specimens; *pedicels* 0.8–3.0 cm long in lateral flowers, to 6 cm long in terminal flowers, to 10 cm long in terminal flowers in fruit, scarcely warty toward apex; rachis and pedicels densely or moderately hairy with retrorse or patent bristles. *Flowers* 2–5, usually on upper half of plant, facing laterally or half nodding, opening flat or dish-shaped in fine weather, 3.0–5.5 cm across. *Calyx* 9–11 mm long, densely or moderately bristly. *Petals* 4–8, violet or purple, sometimes more deeply colored near base, obovate, elliptic or broadly obovate, 1.8–3.2 cm long, 0.7–2.0 cm wide, base cuneate or rounded, margin entire, sometimes irregularly crenulate near apex, occasionally cleft in various degree, apex rounded or obtuse. *Stamens* numerous; *filaments* similar to or more deeper colored than petals, filiform, 6–10 mm long; *anthers* pale yellow or dull orange, ellipsoid, 0.8–1.2 mm long; thecae straight. *Ovary* pale green with (3 or)4 or 5 dark purple streaks, ovoid or ellipsoid, 4–6 mm long, moderately or sparsely hairy with ascending bristles, occasionally glabrous; *style* pale green sometimes tinged dark purple near base, 1.0–2.5 mm long in flower, to 4 mm long in fruit; *stigma* capitate, ca. 1 mm across; lobes (3 or)4 or 5, 1–2 mm long, to 3 mm long in fruit, erect in fruit. *Capsules* narrowly ellipsoid or narrowly obovoid, 1.5–2.0 cm long, sparsely to moderately bristly, occasionally glabrous; carpels (3 or)4 or 5. *Seeds* unknown.

Distribution: CHINA. NW Sichuan: Wengda Xian (翁达县), known only from the vicinity of the type locality, 3950 m elevation.

Habitat and ecology: among shrubs such as *Salix* and *Potentilla* (*Dasiphora*) on southwest-facing, moist, moss-clad slopes; with other herbs and grasses; rooting in humus-rich soil.

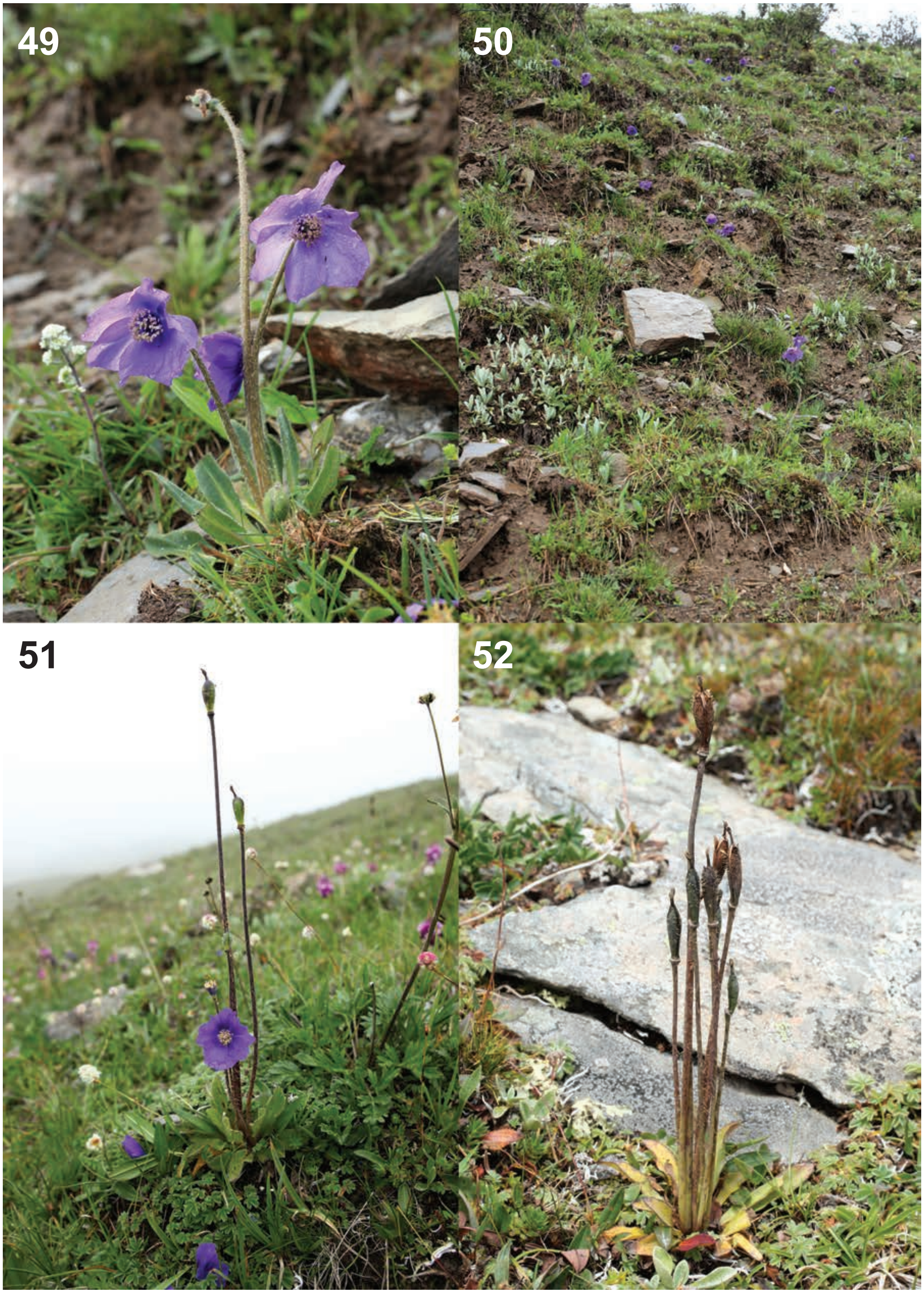
Meconopsis pleurogyna W.T. Wang, *Guihaia* 30 (1): 2. 2019. TYPE: CHINA, N Sichuan: Maerkang Xian (马尔康县), Mengbi Shan (梦笔山), 4150 m, 29 June 1983, *Z. X. Tang* (汤宗孝) *1201* (Holotype: PE; Isotype: PE). Fig. 1, 47–56, 93–96.

Herbs, monocarpic, 7–25 cm tall in flower, to 35 cm tall in fruit. *Taproot* hard and woody, elongate, to 12 cm long or more, 8–13 mm across, sometimes fusiform, distally gradually narrowed and with slender extension. Most parts of plant bristly; *bristles* to 3 mm long. *Stem* (below uppermost leaf) simple, 0.4–4.0 cm long. *Leaves* all basal, dimorphic (as shown in Fig. 48); rosette leaves on vegetative shoots with distinct long petioles and ovate or elliptic lamina, central leaves of flowering plants with indistinct short petiole and oblong, oblanceolate or narrowly elliptic lamina. *Petiole* pale green, linear or broadly linear, 1.5–4.5 cm long, 1.5–4.0 mm wide; *lamina* oblong, oblanceolate, elliptic or ovate, 1.5–6.0 cm long, 7–18 mm wide, base attenuate or cuneate, occasionally rounded in ovate lamina, margin entire, sometimes coarsely undulate, apex obtuse or acute, upper surface green or yellowish green with canescent sheen, lower surface somewhat paler, both surfaces densely hairy with shorter and narrower bristles, entirely covered with raised and thickened reticulation formed by adjacent epidermal cell walls (Fig. 94–95) resulting in canescent appearance of leaves. *Inflorescence* scapose, occasionally with central scapes connate to various degree in less windy habitats, few lowest (outermost) flower buds occasionally borne on diminutive scapes and much smaller and abortive; *scapes* 4–18 cm long in flower, to 28 cm long in fruit, densely or moderately hairy with retrorse, patent or occasionally ascending bristles. *Flowers* (4 or)5–13, facing laterally or half nodding, dish- or bowl-shaped in fine weather, 2.8–4.5 cm across. *Calyx* 1.0–1.6 cm long, usually densely bristly. *Petals* 5 or 6, occasionally 4 or 7, purple or violet, obovate, broadly to narrowly obovate, 1.8–3.1 cm long, 0.8–2.7 cm wide, base cuneate, margin entire, sometimes irregularly crenate near apex, apex rounded, obtuse or triangular. *Stamens* numerous; *filaments* similar to petals, filiform, 4–8 mm long; *anthers* pale yellow or dull orange, ellipsoid, 0.8–1.0 mm long; thecae straight or slightly incurved. *Ovary* ellipsoid, 4–7 mm long, densely, moderately or sparsely hairy with ascending bristles, occasionally glabrous, often with 3 or 4(or 5) dark purple streaks; *style* 1–2 mm long in flower, to 4 mm long in fruit; *stigma* capitate, ca. 1 mm across; lobes 3 or 4, rarely 5, 1.0–2.5 mm long in flower, to 4 mm long in fruit, erect in fruit. *Capsules* obovoid or narrowly obovoid, 0.9–2.3 cm long, 3.5–11.0 mm across, densely, moderately, or sparsely hairy with retrorse, patent, or ascending bristles, occasionally glabrous; carpels 3 or 4, rarely 5, dehiscent in upper 1/3–1/4. *Seeds* dark brown, 1.3–2.0 mm long.

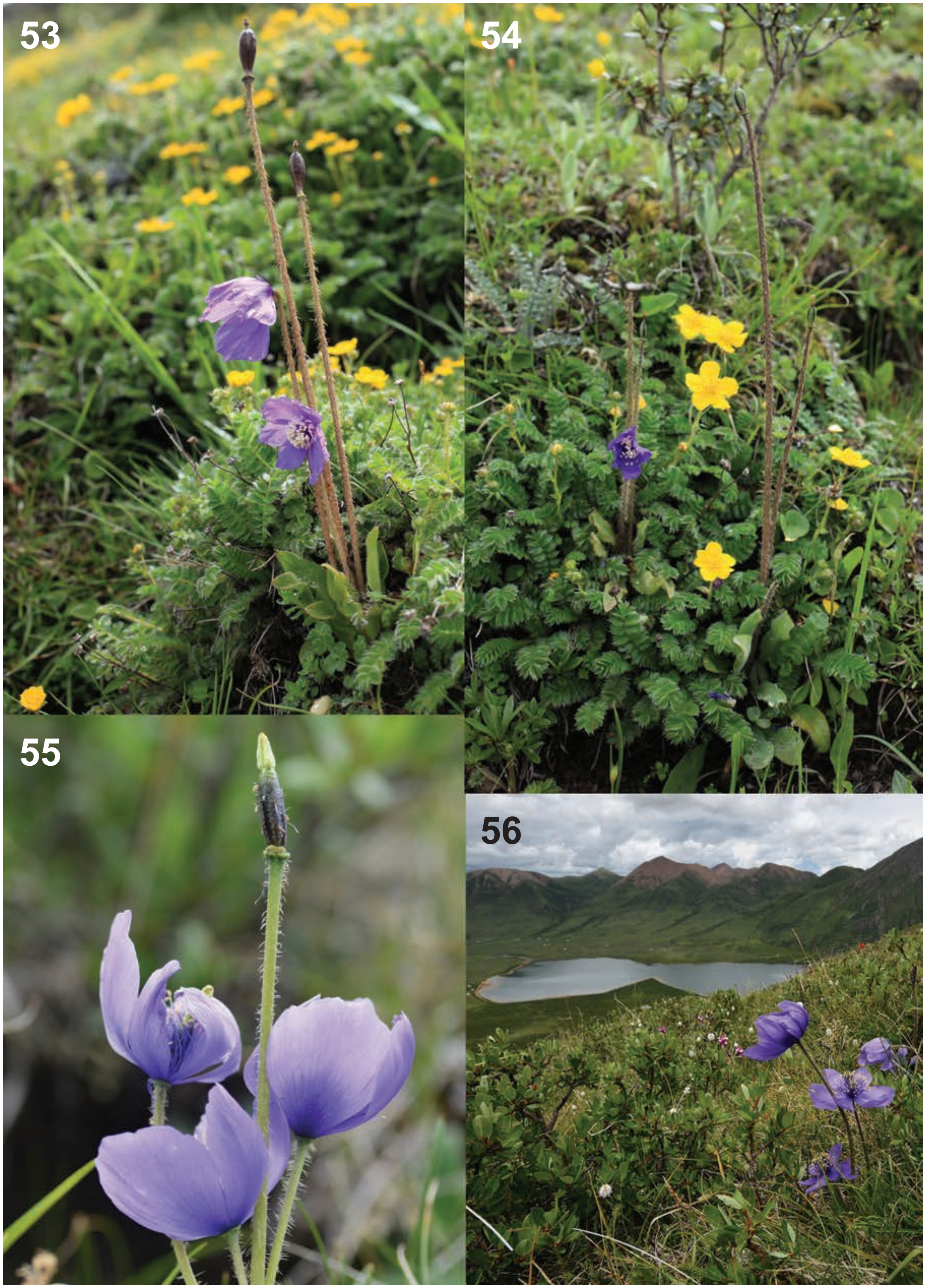
Distribution: CHINA. N Sichuan: Heishui Xian (黑水县), Hong-yuan Xian (红原县), Xiaojin Xian (小金县), Mian-yang Shi (绵阳市). SE Qinghai: Jiuzhi Xian (久治县). 3900–4400 m elevation.

Habitat and ecology: southwest-, south-, and southeast-facing windy alpine slopes**;** usually with other herbs and grasses, occasionally among dwarf shrubs such as *Salix* or *Potentilla* (*Dasiphora*); rooting in blackish soil composed of old plants mixed with stones.

Additional specimens examined: CHINA. SE Qinghai, Jiuzhi Xian (久治县), **Region 28:** Nianbaoyuze Shan (年保玉则山), above Emu Cuo (鄂木措), 4400 m, 3 July 2013, *Y. Niu* (牛洋) *QH2013048* (KUN). N Sichuan, Heishui Xian (黑水县) and Hong-yuan Xian (红原县), **Region 35:** Hong-yuan Xian, near the top of Yanggong Shan (羊拱山) pass, 32°14'01"N, 102°35'56"E, 4200 m, 24 August 2011, *T. Yoshida K76* (KUN, TI); same locality, 16 July 2013, *T. Yoshida K92* (KUN, TI); Heishui Xian, eastern side of Yanggong Shan, 32°13'13"N, 102°36'18"E, 3900 m, 26 June 2018, *T. Yoshida K122* (KUN, TI). NW Sichuan, Maerkang Xian (马尔康县) and Xiaojin Xian (小金县), **Region**



FIGURES 49–52. **49**. *Meconopsis pleurogyna* W.T. Wang with connate central scapes; on eastern side of Yanggong Shan, 3900 m. Photograph by T. Yoshida, June 26, 2018. **50**. Habitat of *Meconopsis pleurogyna* W.T. Wang on eastern side of Yanggong Shan, 3900 m. Photograph by T. Yoshida, June 26, 2018. **51**. *Meconopsis pleurogyna* W.T. Wang on Yanggong Shan, 4200 m. Photograph by T. Yoshida, July 16, 2013. **52**. *Meconopsis pleurogyna* W.T. Wang on Yanggong Shan, 4200 m. Photograph by T. Yoshida, August 24, 2011.



FIGURES 53–56. **53**. *Meconopsis pleurogyna* W.T. Wang on Mengbi Shan, 4000 m. Photograph by T. Yoshida, June 27, 2018. **54**. *Meconopsis pleurogyna* W.T. Wang on Mengbi Shan, 4000 m. Plant on right has connate central scapes. Photograph by T. Yoshida, June 27, 2018. **55**. *Meconopsis pleurogyna* W.T. Wang above Emu Cuo, Nianbaoyuze Shan, 4400 m. Photograph by Y. Niu (牛洋), July 3, 2013. **56**. Habitat of *Meconopsis pleurogyna* W.T. Wang above Emu Cuo, Nianbaoyuze Shan, 4400 m. Photograph by Y. Niu, July 3, 2013.

36: Maerkang Xian, Mengbi Shan (梦笔山), 4150 m, 29 June 1983, *Z. X. Tang* (汤宗孝) *1201* (PE); Xiaojin Xian, southwestern side of Mengbi Shan (梦笔山), 31°42'28"N, 102°18'55"E, 4150 m, 25 August 2011, *T. Yoshida K77* (KUN, TI); same locality, 27 June 2018, *T. Yoshida K123* (KUN, TI).

According to Wang (2019), *Meconopsis pleurogyna* is related to *M. lhasaensis* Grey-Wilson in subgenus *Cunmminsia* (Prain) Grey-Wilson section *Racemosae* C.Y. Wu & H. Chuang, but the relationship of *M. pleurogyna* to *M. lhasaensis* is rather obscure. *Meconopsis lhasaensis* has thicker and harder bristles (spine-like hairs), a racemose inflorescence (never scapose), lowermost flowers bracteate, and capsules more or less ellipsoid; *M. pleurogyna* has thin, brittle bristles, scapose inflorescence with occasional central scapes connate to various degrees, flowers on connate scapes ebracteate, and capsules obovoid or narrowly obovoid. We consider *Meconopsis pleurogyna* to be related to *M. lancifolia* (Franch.) Franch. ex Prain in section *Forrestianae* C.Y. Wu & H. Chuang series *Forrestianae* C.Y. Wu & H. Chuang, as treated here. *Meconopsis pleurogyna* differs from the related *M. lancifolia* in the dimorphic leaves (all alike in the latter) and scapose inflorescence (usually racemose in the latter). Wang (2019) used the longitudinally ribbed ovary as a key character and for the specific epithet, *pleurogyna*. However, ribbed (streaked) ovaries are common in some species such as *M. purpurea*, *M. wengdaensis*, and *M. lepida* in series *Forrestianae* and is not useful as a key character to separate species.

Meconopsis aprica T. Yoshida & H. Sun, *sp. nov.* TYPE: CHINA. NW Sichuan, Ganzi Xian (甘孜县): Zhuoda La (卓达拉), 31°24'14"N, 99°57'58"E, 4650 m, 28 June 2016, *T. Yoshida K106* (Holotype: KUN; Isotypes: KUN, TI). Fig. 1, 57–61, 97–100.

Meconopsis aprica differs from the related *M. pleurogyna* W.T. Wang in the uniform leaves (dimorphic in the latter), lamina less than 9 mm wide (to 19 mm wide in the latter), surfaces of the lamina without prominently raised and thickened reticulation formed by epidermal cell walls (prominently raised and thickened reticulation formed by epidermal cell walls in the latter), flowers fewer than 6 (to 12 in the latter), petals larger, to 4.2 cm long, 3.7 cm wide (less than 3.1 cm long, 2.7 cm wide in the latter) and usually prominently concave (only slightly concave in the latter), filaments to 12 mm long (less than 8 mm long in the latter), ovary densely bristly with bristles in close contact with each other (densely, moderately, or sparsely bristly, or occasionally glabrous, in the latter) and capsules narrowly ellipsoid (obovoid or narrowly obovoid in the latter).

Herbs, monocarpic, 12–25 cm tall in flower. *Taproot* hard and woody, elongate, to 6 cm long or more, 6–10 mm across, sometimes fusiform, distally gradually narrowed and with slender extension. Most parts of plant bristly; *bristles* to 3 mm long. *Stem* (below uppermost leaf) diminished, 3–5 mm long. *Leaves* all basal, petiolate; *petiole* pale green, linear or broadly linear, 1.5–4.0 cm long, 1.0–3.5 mm wide; *lamina* rather thick, linear-oblong, strap-shaped, narrowly oblanceolate, 1.5–6.0 cm long, 3–9 mm wide, base attenuate, margin entire, sometimes coarsely undulate, apex obtuse or acute, upper surface green or dark green, lower surface somewhat paler, both surfaces moderately, densely, or sparsely bristly. *Inflorescence* scapose, occasionally lowest (outermost) flower bud borne on diminutive much smaller and abortive scape; *scapes* 8–19 cm long in flower, densely, moderately, or sparsely hairy with retrorse (occasionally patent) bristles. *Flowers* 4–6, ascending, facing upward or laterally, parabola-shaped, bowl-shaped, or dish-shaped in fine weather, 4.0–7.5 cm across. *Calyx* pale green, occasionally tinged dark purple, 1.3–1.6 cm long, densely or moderately bristly; bristles sometimes with thick, blackish base. *Petals* 5–7, purple, occasionally tinged dark red near base, broadly obovate, rounded or obovate, usually prominently concave, 2.5–4.5 cm long, 1.1–3.8 cm wide, base cuneate, margin entire, occasionally crenate and undulate near apex, apex usually rounded, occasionally obtuse. *Stamens* numerous; *filaments* more deeply colored or similar to petals, sometimes bluish distally, filiform, 7–12 mm long; *anthers* pale yellow or whitish, ellipsoid or oblong, 1.0–1.5 mm long; thecae straight. *Ovary* pale green, often with 3–5 dark purple stripes, occasionally partly tinged dark purple, ellipsoid or ovoid, 4–7 mm long, densely hairy with whitish ascending bristles in close contact with each other; *style* 0.5–1.5 mm long in flower, often tinged dark purple near base; *stigma* narrowly ovoid, 1.5–2.0 mm across; lobes 3–5, often 4, 2–3 mm long in flower, to 5 mm long in fruit, erect in fruit. *Capsules* narrowly ellipsoid, 1–2 cm long, 3–5 mm across, densely or moderately bristly. *Seeds* unknown.

Distribution: CHINA. NW Sichuan: Ganzi Xian (甘孜县), known only from the vicinity of the type locality, 4150–4900 m elevation.

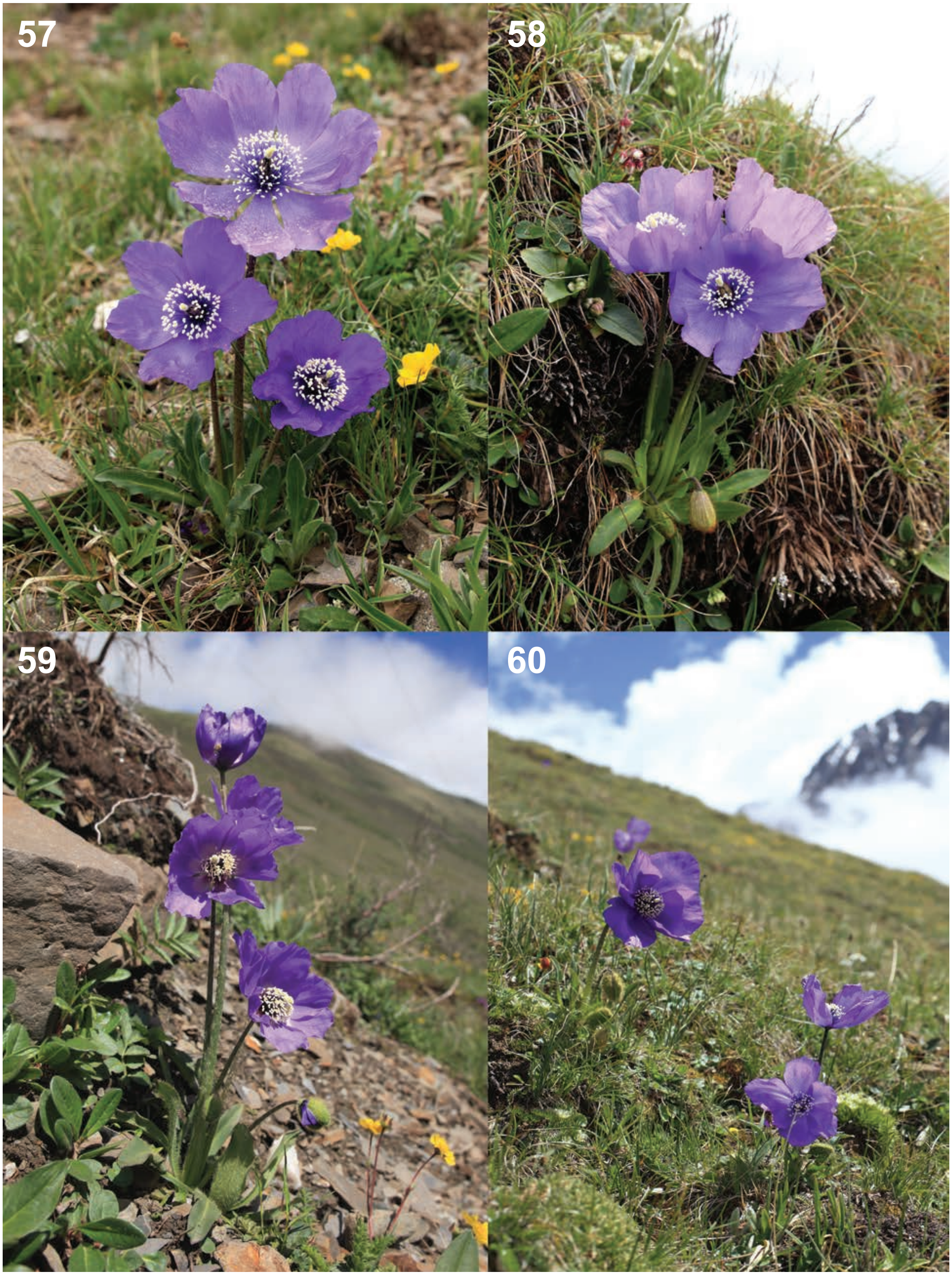
Habitat and ecology: south-, southwest-, and southeast-facing, windy and relatively dry, stony slopes thinly covered with herbs and grasses; rooting in sandy soil among stones. Flies frequent the flowers in fine weather.

Additional specimens examined: CHINA. NW Sichuan, Ganzi Xian, around Zhuoda La, **Region 24:** S of Ganzi on road (Gan-Bai Lu) to Baiyu, first pass after Ganzi, 31°24'14"N, 99°57'58"E, 4785–4900 m, 3 August 2015, *Boufford et al*. 34065 (A); Zhuoda La, 31°24'14"N, 99°57'58"E, 4650 m, 28 June 2016, *T. Yoshida K106* (KUN, TI).

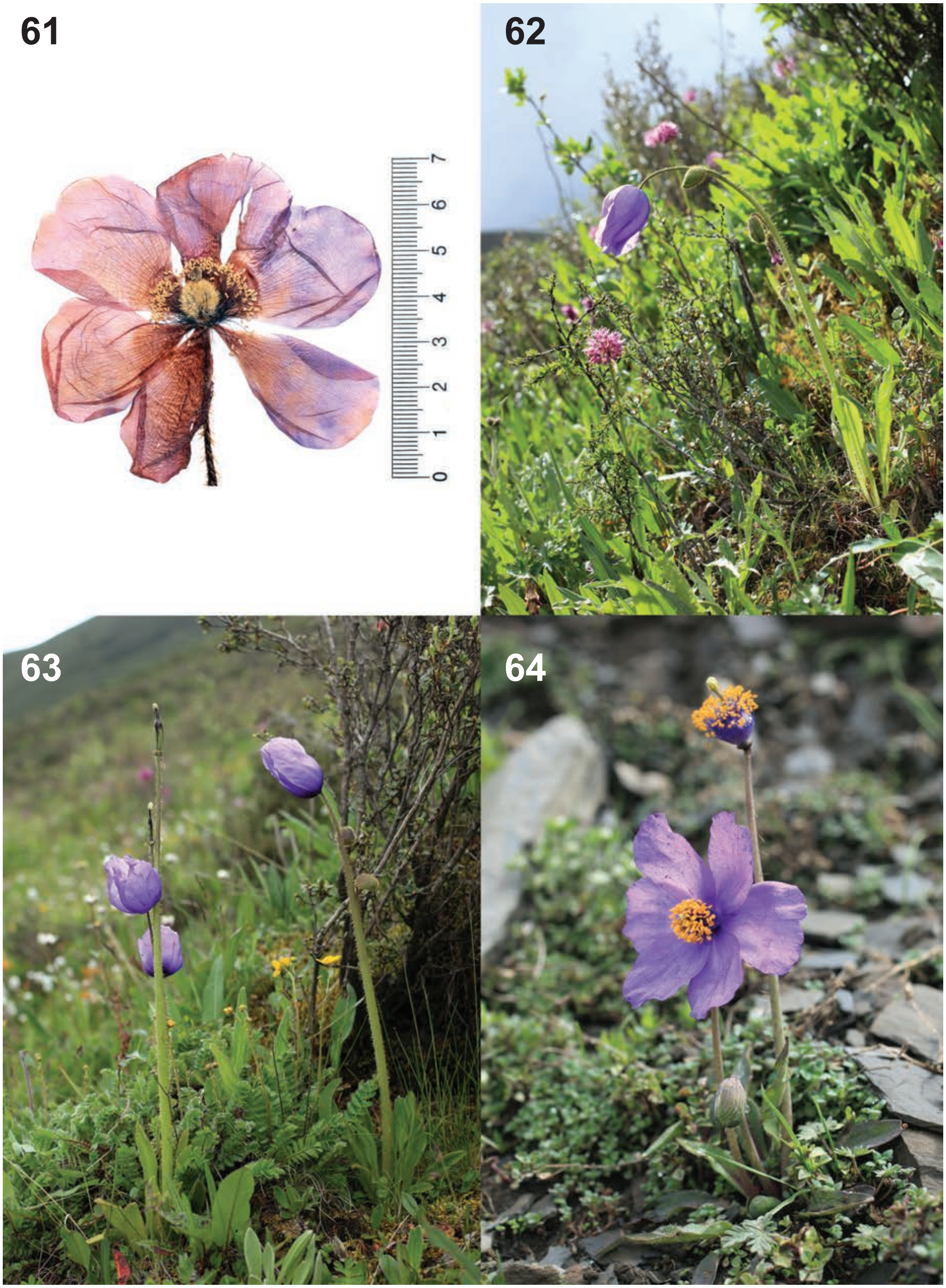
Various forms of a hybrid between *Meconopsis aprica* and *M. wengdaensis* grow intermixed on a roadside flat densely covered with dwarf herbs and grasses and scattered dwarf shrubs on the northern flank of Zhuoda La, 31°25'28"N, 99°57'50"E, at 4150 m elevation.

Meconopsis inaperta T. Yoshida & H. Sun, *Harvard Papers in Botany* 23 (2): 317. 2018. Type: CHINA. NW Sichuan, Baiyu Xian (白玉县): western side of Ganbailu Yakou (甘白路丫口) near Acha (阿察), 31°06'25"N, 99°26'17"E, 4000 m, 16 July 2017, *T. Yoshida K120* (Holotype: KUN; Isotype: TI). Fig. 1, 62–63.

Distribution: CHINA. W Sichuan: Baiyu Xian (白玉县), Litang Xian (理塘县), Yajiang Xian (雅江县), 3950–4200 m elevation.



FIGURES 57–60. *Meconopsis aprica* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 28, 2016.



FIGURES 61–64. **61**. Flower of type specimen of *Meconopsis aprica* T. Yoshida & H. Sun, *T. Yoshida K106*. **62**. *Meconopsis inaperta* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 16, 2017. **63**. *Meconopsis inaperta* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 16, 2017. **64**. *Meconopsis henrici* Bureau & Franch. on Zheduo Shan, 4200 m. Photograph by T. Yoshida, July 1, 2018.

Additional specimens examined: CHINA. W Sichuan, Yajiang Xian, **Region 22:** Kazi La Shan (卡子拉山), 30°01'05"N, 100°48'42"E, 4150 m, 19 June 2017, *T. Yoshida K112* (KUN). W Sichuan, Baiyu Xian, **Region 23:** western side of Ganbailu Yakou near Acha, 31°06'25"N, 99°26'17"E, 4000 m, 16 July 2017, *T. Yoshida K120* (KUN, TI).

Series Henricanae C.Y. Wu & H. Chuang, Acta Bot. Yunnan. 2 (4): 376. 1980, emended to exclude *M. barbiseta, M. concinna, M. neglecta*, and *M. wumungensis*.

Inflorescence scapose. Filaments, at least innermost ones, dilated toward the base. Hairs on ovary simple. Three species are included: *Meconopsis henrici* Bureau & Franch., *M. huanglongensis* T. Yoshida & H. Sun, and *M. psilonomma* Farrer.

C. Grey-Wilson (2014, p. 306) wrote, "In both *M. henrici* and *M. sinomaculata* [*M. psilonomma* var. *sinomaculata* in this paper] and to some extent *M. psilonomma* also, the most prominently dilated filaments are those of the outer stamens and they are not so obviously air-filled but simply expanded in the lower half, and neither do the stamens form a protective jacket around the ovary." However, the outermost filaments of *M. psilonomma* Farrer, including *M. psilonomma* var. *sinomaculata* (Grey-Wilson) H. Ohba, are sometimes scarcely dilated, whereas the innermost filaments are usually dilated toward the base. The dilated parts of the filaments are considered to provide a protective jacket for the ovary, even if they are not air-filled.

Key to Species of Series Henricanae

1a. Flowers cup-shaped even in fine weather . . . . *M. psilonomma*

1b. Flowers opening flat or dish-shaped in fine weather 2

2a. Flowers 2–12; all filaments similarly dilated in lower half . . . . *M. henrici*

2b. Flower 1; inner filaments dilated toward base, outermost filaments often scarcely dilated . . . . *M. huanglongensis*

Meconopsis henrici Bureau & Franch., *J. Bot. (Morot)* 5:19. 1891. TYPE: CHINA. W Sichuan: Tatsienlu [Kangding, 康定], *P.G.E. Bonvalot & Henri d'Orleans s.n.* (Holotype: P). Fig. 1, 64–67.

Synonym: *M. principis* Bulley, *Fl. & Silva* 3:84 (1905); *M. wardii* Kingdon-Ward, *Gard. Chron*. Ser. 3, 72: 268. 1922. *nomen nudum*.

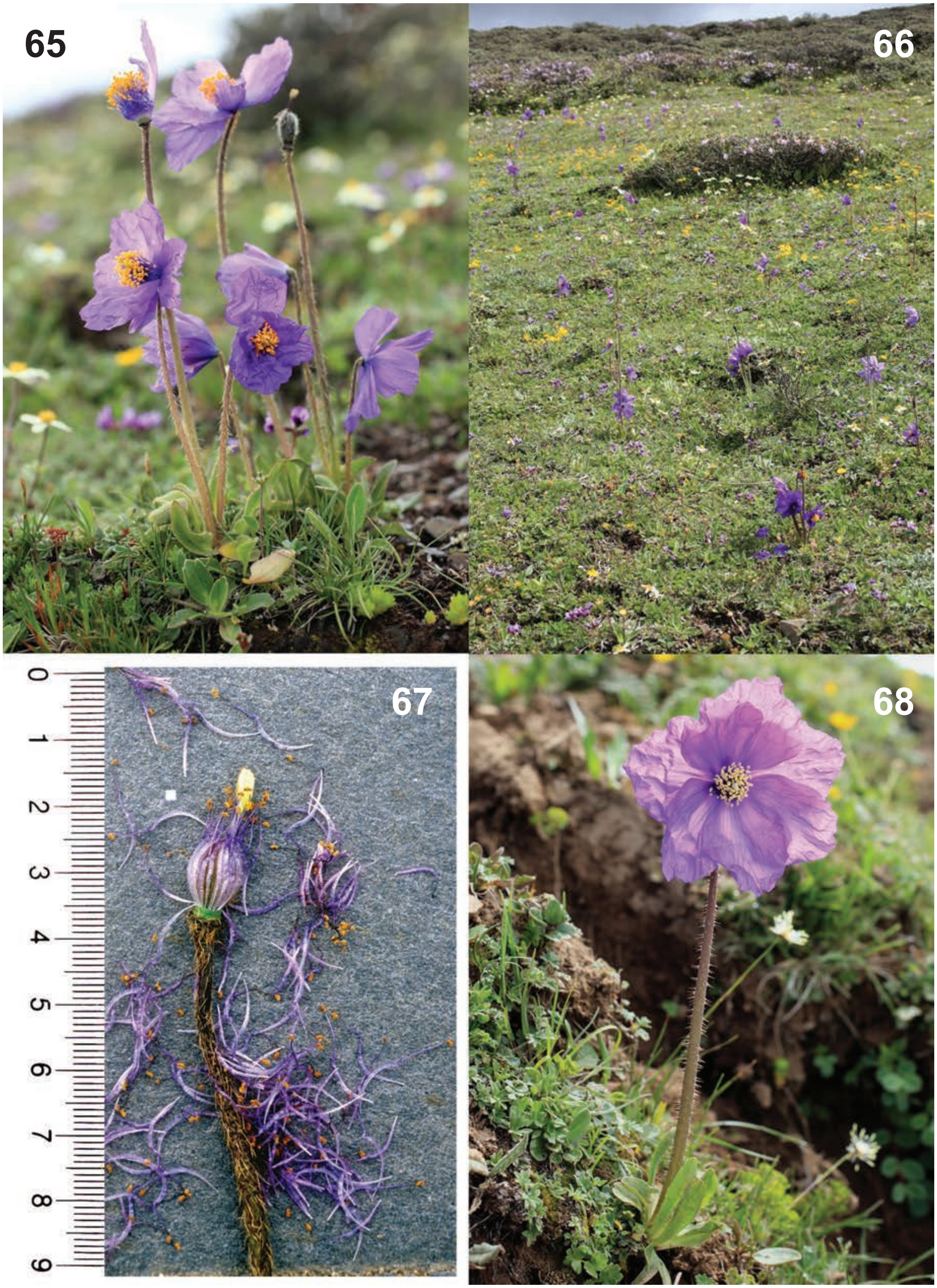
M. henrici var. *genuina* G. Taylor, *The Genus Meconopsis*: 80. 1934.

Herbs, monocarpic, 8–25 cm tall in flower, to 30 cm tall in fruit. *Taproot* napiform or dauciform, occasionally shortly elongate, 1.5–7.0 cm long, 4–12 mm across, contracted at junction with stem, distally with slender roots. Most parts of plant bristly; *bristles* usually pale colored, occasionally straw-colored, rather weak, to 4 mm long. *Stem* (below uppermost leaf) simple, 0.3–2.5 cm long. *Leaves* crowded near base of stem, petiolate; *petiole* membranous, linear or broadly linear, 0.4–4.5 cm long, 1.0–2.3 mm wide; *lamina* rather thick, lanceolate, oblong or elliptic, or lowest small leaves ovate, 1.5–10.0 cm long, 0.4–1.5 cm wide, base attenuate, margin usually entire, sometimes coarsely wavy, rarely coarsely toothed, apex acute or obtuse, both surfaces densely hairy with weaker and shorter bristles. *Inflorescence* scapose, central scapes rarely connate in various degree; *scapes* 1–3 mm across when dried, with dense retrorse bristles. *Flowers* 1 per scape, 2–12, often 3–6, rarely solitary per individual, laterally facing, dish-shaped in fine weather, 3.0–5.5 cm across. *Calyx* 1.0–1.5 cm long, densely hairy. *Petals* 4–8, often 6, mauve or purple, obovate, broadly obovate or elliptic, 1.8–3.6 cm long, 0.8–2.7 cm wide, base cuneate, margin entire or sometimes undulate and denticulate near apex, apex rounded or occasionally obtuse. *Stamens* numerous; *filaments* 0.7–1.7 cm long, lower half usually pale, dilated to 0.8 mm wide, somewhat boat-shaped, overlapping and surrounding ovary, upper half purple, filiform, usually erect along style; *anthers* orange, ellipsoid or globose, 0.7–1.0 mm long. *Ovary* ellipsoid, 4–7 mm long, densely hairy with ascending whitish bristles; *style* 1–3 mm long in flower, to 7 mm long in fruit; *stigma* capitate, ca. 1 mm across; lobes 3–5, to 3 mm long in fruit. *Capsules* obovoid, 1.0–2.3 cm long, 4–7 mm across, densely bristly. *Seeds* unknown.

Distribution: CHINA. W Sichuan: Kangding Shi (康定市) and Muli Xian (木里县), 3800–4500 m elevation.

Habitat and ecology: alpine slopes of various aspects; with herbs, grasses, mosses, and scattered dwarf shrubs such as *Rododendron nivale* Hook. f. subsp. *boreale* M.N. Philipson & Philipson, rarely on bare slopes; sometimes with dwarf shrubs; rooting in humid blackish, stony soil. Flies frequent the flowers in fine weather.

Additional specimens examined: CHINA. SW Sichuan, Muli Xian, **Region 5:** Litang [理塘]- Yalung [Yalong, 雅砻] divide, 28°20'N, 101°05'E, 8 July 1921, *F. Kingdon-Ward 4421* (E); southwestern Szechwan [Sichuan], Muli Kingdom, between Baurong and Kulu, west of the Yalung River [Yalong Jiang, 雅砻江], 4660 m, July 1929, *J. F. Rock 17829* (E, P); S Muli, Wa-chin, Wulinsi (屋林司), 4100 m, 20 June 1937, *T. T. Yü* (俞德俊) *6484* (KUN). W Sichuan, Kangding Shi, **Region 40:** Se-Tchuen [Sichuan], avant Ta Tsien Lou [Kangding], *P. G. E. Bonvalot & Henri d'Orléans s.n.* (P); Ta p'as chang, NE of Tachienlu [Kangding], 12,000–15,000 ft, 7 July 1908, *E. H. Wilson 3028* (E, K); Sikang [Xikang, 西康], Kangting (Tachienlu) distr., Yülingkong [Yulin Gou, 榆林沟], in montibus Yachiagan [Yajiageng, 雅加梗, located on the northern ridge of Gongga Shan, 贡嘎山], ca. 4000 m, 24 July 1934, *Harry Smith 10676* (BM); same locality, *Harry Smith* 10688 (BM); Sikang, Kangting (Tachienlu) distr., Tapaoshan, ca. 4500 m, 22 August 1934, *Harry Smith 11509* (BM); Szechuan [Sichuan], Tatsienlu [Kangding], summit of mountain, June 1938, *McLaren's Collectors AC6* (E, P); west Szechuen and Tibetan Frontier, chiefly near Tachienlu, 9,000–13,500 ft, before 1890, *A. E. Pratt 600* (BM, K); Bois à Tongolo [Dong-e-luo, 东俄洛; the region around Xindouqiao, 新都桥], June–July 1891, *J. A. Soulié 25* (P); Principauté de Kiala [Jiarong, 嘉絨], Thibet oriental, 1891, *J. A. Soulié 29* (P); Thibet Oriental,



FIGURES 65–68. **65**. *Meconopsis henrici* Bureau & Franch. on Zheduo Shan, 4200 m. Photograph by T. Yoshida, July 1, 2018. **66**. Habitat of *Meconopsis henrici* Bureau & Franch. on Zheduo Shan, 4200 m. Photograph by T. Yoshida, July 1, 2018. **67**. Flower of *Meconopsis henrici* Bureau & Franch. dissected to show dilated stamens, on Zheduo Shan, 3950 m. Photograph by T. Yoshida, July 21, 2010. **68**. *Meconopsis huanglongensis* T. Yoshida & H. Sun during fine weather at type locality. Photograph by T. Yoshida, July 11, 2016.

Ta-tsien-lou [Kangding], Principauté de Kiala, 1893, *J. A. Soulié 523* (P), Tatsienlou, Thibet oriental, June–July 1894, *J. A. Soulié 2090* (P); Thibet Oriental, Tongolo environs Bois, June 1894, *J. A. Soulié 2434* (P); Thibet Oriental, Tongolo, 1893, *J. A. Soulié s.n.* (P); plantes du Setchuen [Sichuan] oriental, [without collection date], *J. A. Soulié s.n.* (P); Xikang (西康), Kangding (康定), 13 July 1930, *G. Huang* (黄给平) *et al. 1393* (KUN); Sichuan Zheduo Shan Yakou (四川折多山丫口), 4150 m, 20 July 1959, *Nanshui Beidiao Team* (南水北调队) *2084* (KUN); Sichuan, Kangding Shi (康定市), Zheduo Shan (折多山), 4200 m, 9 August 1976, *Yunnan Botanical Institution* (云南省植物研究所) *805* (KUN); Zheduo Shan, 30°04'27"N, 101°48'15"E, 4250 m, 21 July 2010, *T. Yoshida K43* (KUN); same locality, 13 July 2013, *T. Yoshida K95* (KUN); upside of Kangding Airport, 30°09'43"N, 101°43'58"E, 4200 m, 29 June 2018, *T. Yoshida K125* (KUN).

Meconopsis angustipetala was described as a new species related to *M. henrici* on the basis of a specimen without collector, *PE 1306833* (PE), collected on 31 July 1982 on the mountain behind Gongga Temple, Shade Xiang, Kangding Xian (康定县沙德乡贡嘎寺后山), 4700 m. According to Wang, *M. angustipetala* differs from *M. henrici* in the glabrous leaves with narrow blade to 7 mm wide and the narrow petals to 8 mm wide. Although we have not examined the specimen, we consider it to be a form of *M. henrici*. If confirmed, the range of Region 40 in Fig. 1 should be extended somewhat toward the south.

Meconopsis huanglongensis T. Yoshida & H. Sun, *Harvard Papers in Botany* 23 (2): 313. 2018. TYPE: CHINA. N Sichuan, Songpan Xian (松潘县): Xueshanliang (雪山梁), near Huanglong (黄龙), 32°44'23"N, 103°44'02"E, 4000 m, 11 July 2016, *T. Yoshida K107* (Holotype: KUN; Isotype: TI). Fig. 1, 68–70.

Distribution: CHINA. N Sichuan: Songpan Xian, around Xueshanliang near Huanglong, 3900–4100 m elevation.

Additional specimens examined: CHINA. N Sichuan, Songpan Xian (松潘县), **Region 34:** Top of Pass "Deng Zhanzwa" toward Huanglong Si [黄龙寺], 32°45'08"N, 103°44'46"E, 2 July 2000, *SBQE* (Sino-British Qinghai Alpine Garden Society Expedition) *594* (E); Xueshanliang, near Huanglong, 32°44'23"N, 103°44'02"E, 4000 m, 28 July 2014, *T. Yoshida K98* (KUN, TI); same locality, 11 July 2016, *T. Yoshida K107* (KUN, TI).

Meconopsis psilonomma Farrer, *Gard. Chron.* 3 (57): 110. 1915. TYPE: CHINA. S Gansu: Min Shan [岷山], above Ardjeri [Ajiao, 阿角], 30 July 1914, *R. Farrer 255* (Holotype: K [lost]; Isotype: E); S Gansu, Mt. Lissedzadza, 12,500 ft, 7 July 1925, *J. F. Rock 12613* (Epitype, designated by Yoshida and Sun (2017); Isoepitypes: BM, E, K).

Meconopsis psilonomma Farrer was revised by Yoshida and Sun (2017).

Distribution: CHINA. S Gansu and N Sichuan, 3400–4150 m elevation.

KEY TO VARIETIES OF *MECONOPSIS PSILONOMMA*

1a. Petals pale purple or lavender purple, without prominent blotch at base; thecae dull orange .... var. *psilonomma*

1b. Petals purple or deep purple, with prominent dark purple blotch at base; thecae blackish purple, dull orange, or dull yellow.......... 2

2a. Thecae and style blackish purple .... var. *sinomaculata*

2b. Thecae dull orange or dull yellow; style pale green, sometimes tinged purple 3

3a. Plants 30–55 cm tall in flower; flowers cup-shaped; filaments slightly dilated toward base and tightly or loosely surrounding ovary .... var. *zhaganaensis*

3b. Plants 15–30 cm tall in flower; flowers bowl-shaped; filaments scarcely dilated or slightly dilated toward base, radiating or loosely surrounding ovary ....var. *calcicola*

Meconopsis psilonomma var. ***psilonomma***. Fig. 1, 71–72.

Synonym: *Meconopsis henrici* Bur. & Franch. var. *psilonomma* (Farrer) Taylor, *The Genus Meconopsis* 81 (1934).

Distribution: CHINA. S Gansu: Zhuoni Xian (卓尼县) and Diebu Xian (迭部县), eastern Die Shan (迭山), head of Dayugou (大峪沟) valley, 3500–3800 m elevation.

Additional specimens examined: CHINA. S Gansu, Diebu Xian, **Region 30:** Gansu Min Shan, Donsari Khikha at the head of Dayugou (大峪沟), 34°18'12"N, 103°26'21"E, 3750 m, 24 July 2016, *T. Yoshida K109* (KUN, TI). S Gansu, Zhuoni Xian, **Region 31:** Min Shan, above Ardjeri, 30 July 1914, *R. Farrer 255* (E, K); Mt. Lissedzadza, 12,500 ft, 7 July 1925, *J. F. Rock 12613* (A, BM, E, K).

Meconopsis psilonomma var. ***sinomaculata*** (Grey-Wilson) H. Ohba, *J. Jap. Bot.* 81(5): 296. 2006. Fig. 1, 73–74.

Basionym: *M. sinomaculata* Grey-Wilson, *Plantsman,* n. s., 1 (4): 221. 2002. TYPE: CHINA. N Sichuan, Songpan Xian (松潘县): top of Gonggan Len [Gonggaling, 贡嘎岭], 33°00'46"N, 103°42'53"E, 3400–3600 m, 29 June 2000, *SBQE* (Sino-British Qinghai Alpine Garden Society expedition) *500* (Holotype: E; Isotypes: E, GB, HNWP, WSY).

Distribution: CHINA. N Sichuan: Songpan Xian (松潘县) and Jiuzhaigou Xian (九寨沟县), around Gonggaling (贡嘎岭), 3400–3750 m elevation.

Additional specimens examined: CHINA. N Sichuan, Songpan Xian, **Region 33:** top of Gonggan Len [Gonggaling], from Jiuzhaitou to Songpan, west-side, 33°00'46"N, 103°42'53"E, 3,400–3600 m, 29 June 2000, *SBQE 500* (E, GB, HNWP, WSY); same locality, 30 June 2000, *SBQE 511* (E); same locality, *SBQE 513* (E); top of Huangshen Guan, 45 km east [mistaken for west according to the coordinates] from Chuanzhusi [川主寺], 32°57'41"N, 103°20'52"E, 1 July 2000, *SBQE 569* (E); on western side of Gonggaling pass, 33°02'58"N, 103°41'42"E, 3700 m, 9 July 2017, *T. Yoshida K116* (KUN, TI).

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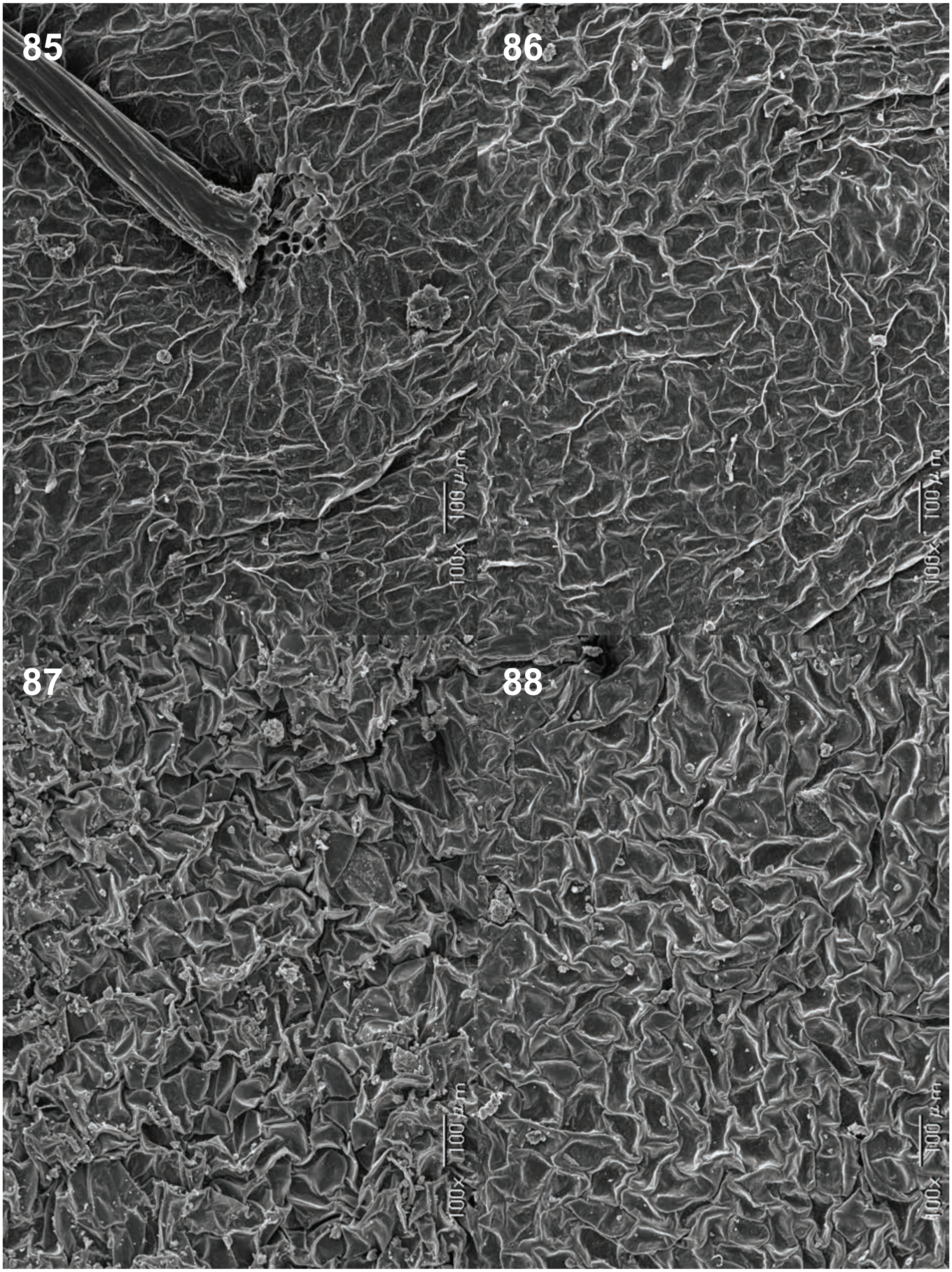
FIGURES 69–72. **69**. Habitat of *Meconopsis huanglongensis* T. Yoshida & H. Sun during foggy weather at type locality. Photograph by T. Yoshida, July 8, 2017. **70**. Dissected flowers of *Meconopsis huanglongensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 11, 2016. **71**. *Meconopsis psilonomma* Farrer var. *psilonomma* at Donsari Khikha, Gansu Min Shan, 3750 m. Photograph by T. Yoshida, July 24, 2016. **72**. *Meconopsis psilonomma* Farrer var. *psilonomma* at Donsari Khikha, Gansu Min Shan, 3750 m. Photograph by T. Yoshida, July 24, 2016.

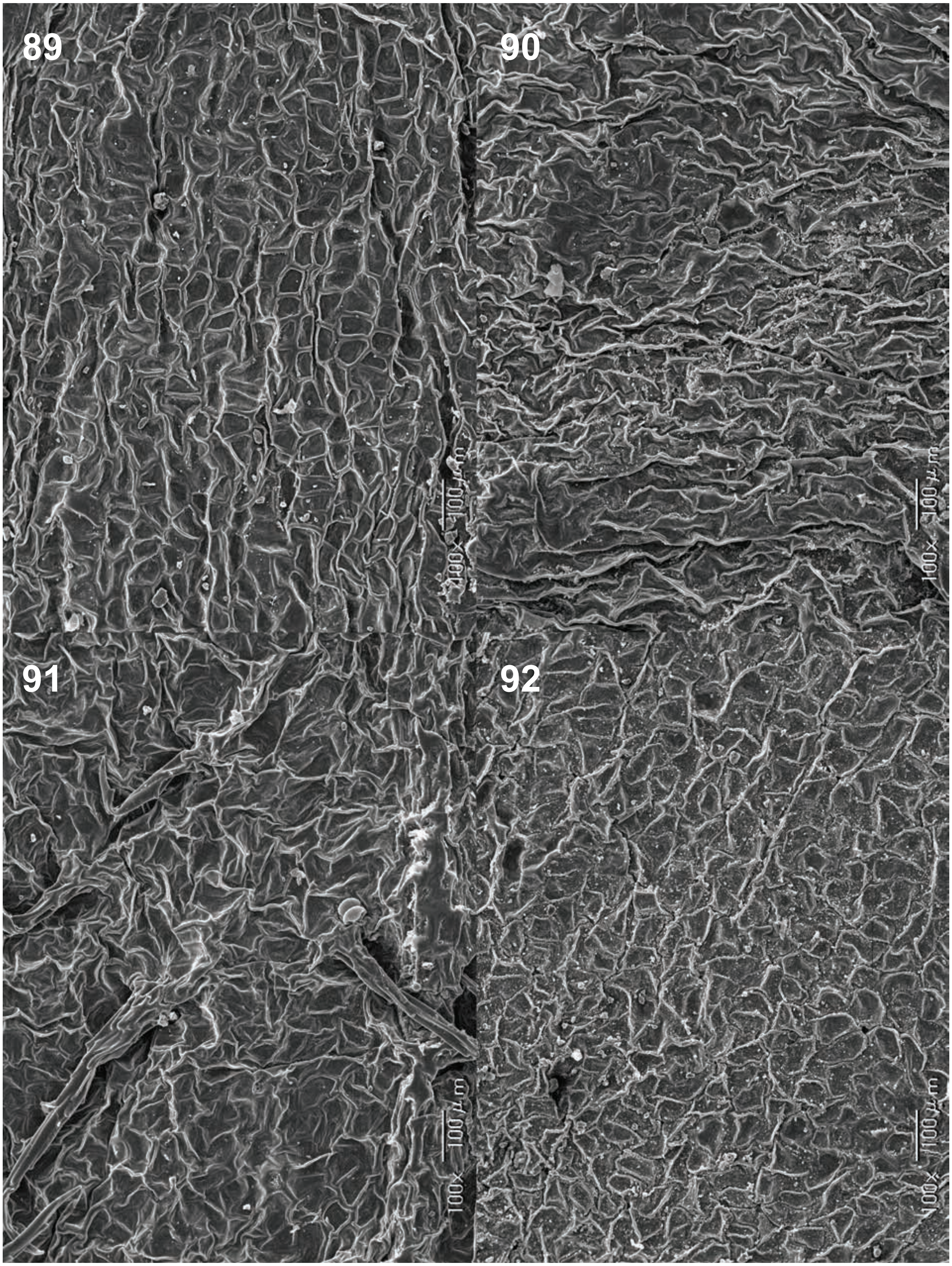
FIGURES 73–76. **73**. *Meconopsis psilonomma* Farrer var. *sinomaculata* (Grey-Wilson) H. Ohba on Gonggaling, 3700 m. Photograph by T. Yoshida, July 9, 2017. **74**. *Meconopsis psilonomma* Farrer var. *sinomaculata* (Grey-Wilson) H. Ohba on Gonggaling, 3700 m. Foreground petals were removed to show the stamens. Photograph by T. Yoshida, July 9, 2017. **75**. *Meconopsis psilonomma* Farrer var. *zhaganaensis* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 24, 2014. **76**. *Meconopsis psilonomma* Farrer var. *zhaganaensis* T. Yoshida & H. Sun at the type locality. Plants with young fruits. Photograph by T. Yoshida, July 23, 2014.

FIGURES 77–80. **77**. *Meconopsis psilonomma* Farrer var. *calcicola* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 24, 2014. **78**. *Meconopsis psilonomma* Farrer var. *calcicola* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 24, 2014. **79**. *Meconopsis barbiseta* C.Y. Wu & H. Chuang ex L.H. Zhou at Luanshitou Yakou, 4000 m. Photograph by T. Yoshida, June 23, 2016. **80**. Mature ovary of *Meconopsis barbiseta* C.Y. Wu & H. Chuang ex L.H. Zhou with dense, minute, dark purple branched hairs, at Luanshitou Yakou, 4000 m. Photograph by T. Yoshida, July 11, 2017.

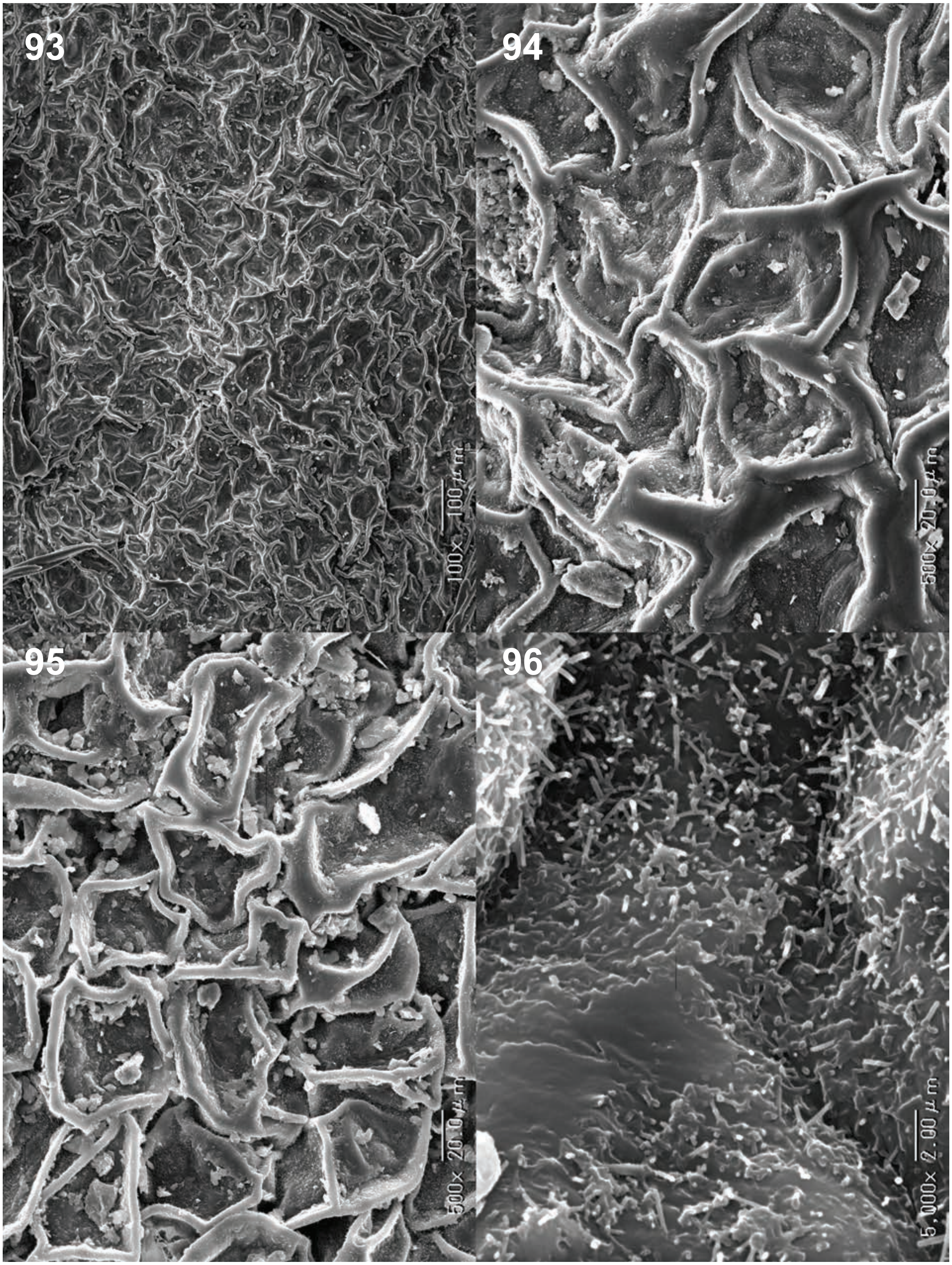
Figures 81–84. **81**. *Meconopsis hispida* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, June 20, 2016. **82**. *Meconopsis hispida* T. Yoshida & H. Sun on the western side of Yanggong Shan, 3900 m. A flower opened to show the ovary on the right and a young fruit on the left. Photograph by T. Yoshida, July 18, 2017. **83**. *Meconopsis trichogyna* T. Yoshida & H. Sun at the type locality. Photograph by T. Yoshida, July 14, 2017. **84**. Open flower of *Meconopsis trichogyna* T. Yoshida & H. Sun at the type locality with petals and stamens removed to show hairiness of ovary. Photograph by T. Yoshida, July 14, 2017.



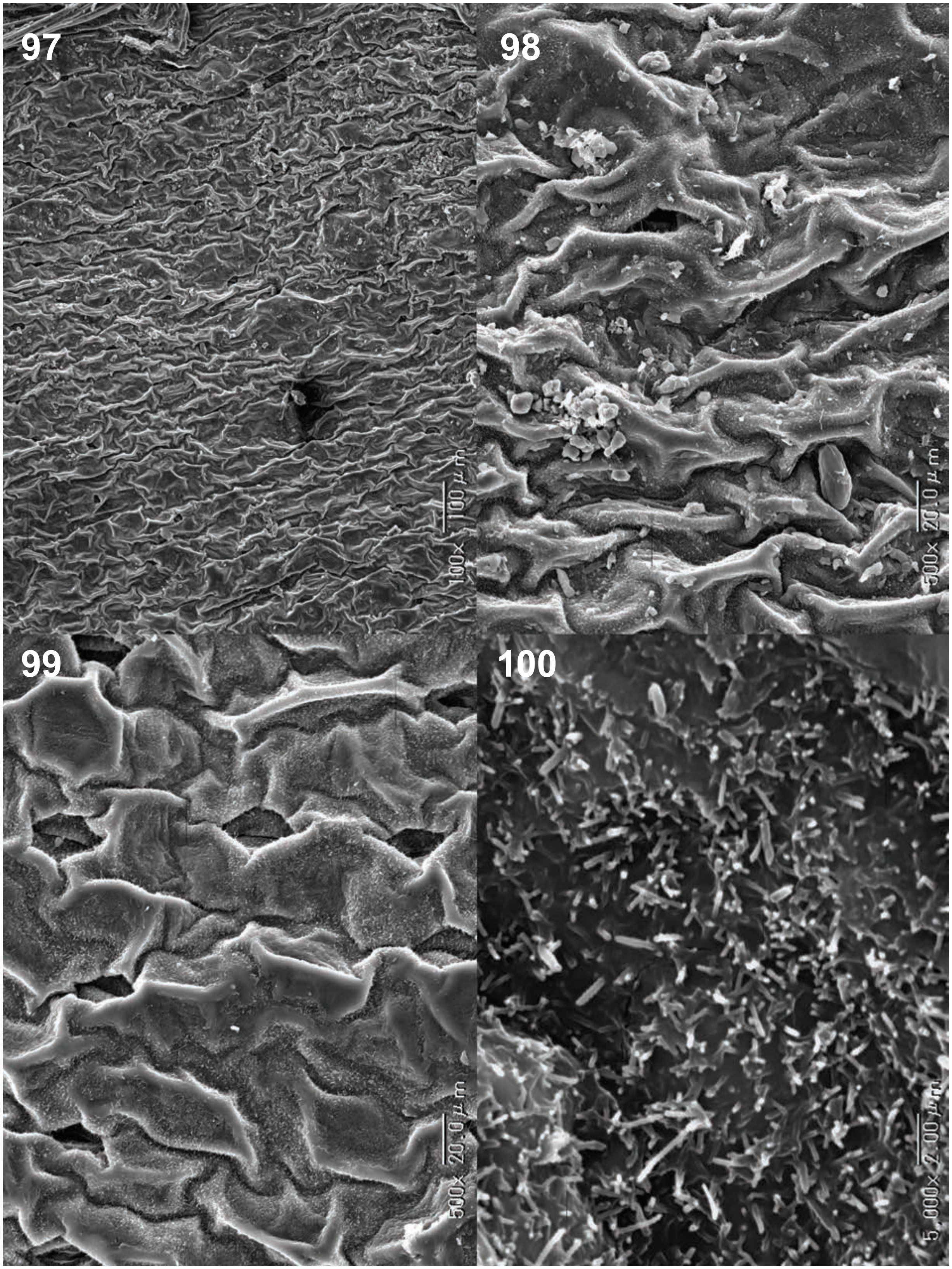
FIGURES 85–88. Scanning electron microscope images of upper surface of dried leaves at 100x magnification. **85**. *Meconopsis forrestii* Prain (*T. Yoshida K29*). Cross section at base of a bristle composed of agglutinated long and thin cells is visible. **86**. *Meconopsis forrestii* Prain (*T. Yoshida K29*). Reticulation formed by cell walls of epidermis is indistinct. **87**. *Meconopsis lancifolia* (Franch.) Franch. ex Prain subsp. *lancifolia* (*T. Yoshida K127*). Epidermis finely cracked by desiccation. **88**. *Meconopsis lancifolia* subsp. *shikaensis* T. Yoshida & H. Sun (*T. Yoshida K129*).



FIGURES 89–92. Scanning electron microscope images of upper surface of dried leaves at 100x magnification. **89**. *Meconopsis lancifolia* subsp. *eximia* (*T. Yoshida K132*). Reticulation formed by cell walls of epidermis is somewhat distinct. **90**. *Meconopsis lancifolia* subsp. *xiangchengensis* (R. Li & Z.L. Dao) T. Yoshida & H. Sun (*T. Yoshida K114*). **91**. *Meconopsis purpurea* T. Yoshida & H. Sun (*T. Yoshida K124*). Surface covered by many smaller bristles. **92**. *Meconopsis wengdaensis* T. Yoshida & H. Sun (*T. Yoshida K104*).



FIGURES 93–96. Scanning electron microscope images of surface of a dried leaf from a specimen of *Meconopsis pleurogyna* W.T. Wang, *T. Yoshida K122*. Reticulation formed by cell walls of epidermis is prominent. **93**. Upper surface of leaf at 100x magnification. **94**. Upper surface of leaf at 500x magnification. Reticulation raised and thickened. **95**. Lower surface of the leaf at 500x magnification. Reticulation raised and thickened and more prominent than on upper surface. **96**. Lower surface of the leaf at 5000x magnification. More studies are needed to clarify structures of epidermis visible in the image.



FIGURES 97–100. Scanning electron microscope images of the surface of a dried leaf from the type specimen of *Meconopsis aprica* T. Yoshida & H. Sun, *T. Yoshida K106*. Reticulation formed by cell walls of epidermis is indistinct. **97**. Upper surface of leaf at 100x magnification. **98**. Upper surface of the leaf at 500x magnification. **99**. Lower surface of leaf at 500x magnification. **100**. Lower surface of the leaf at 5000x magnification. Surface appears be densely covered with minute fibrous emergences to 5 µm long. More studies are needed to clarify epidermal structures visible in image.

Meconopsis psilonomma var. ***zhaganaensis*** T. Yoshida & H. Sun, *Harvard Papers in Botany* 22 (2): 183. 2017. TYPE: CHINA. S Gansu, Diebu Xian (迭部县): W of Zhagana (扎尕那), 34°15'27"N, 103°06'10"E, 3700 m, 23 July 2014, *T. Yoshida K96* (Holotype: KUN; Isotype: TI). Fig. 1, 75–76.

Distribution: CHINA. S Gansu: Diebu Xian, western Die Shan (迭山), 3500–3800 m elevation.

Additional specimen examined: CHINA. S Gansu, Diebu Xian, **Region 29:** W of Zhagana, 34°15'27"N, 103°06'10"E, 3700 m, 23 July 2014, *T. Yoshida K96* (KUN, TI).

Meconopsis psilonomma var. **calcicola** T. Yoshida & H. Sun, *Harvard Papers in Botany* 22 (2): 183. 2017. TYPE: CHINA. S Gansu, Diebu Xian (迭部县): W of Zhagana (扎尕那), 34°16'14"N, 103°03'57"E, 4050 m, 24 July 2014, *T. Yoshida K97* (Holotype: KUN; Isotype: TI). Fig. 1, 77–78.

Distribution: CHINA. S Gansu: Diebu Xian, western Die Shan (迭山), 4000–4150 m elevation.

Series ***Barbisetae*** T. Yoshida & H. Sun, *Harvard Papers in Botany* 23 (2): 325. 2018.

Hairs on ovary branched near base. Three species are included: *Meconopsis barbiseta* C.Y. Wu & H. Chuang ex L.H. Zhou, *M. hispida* T. Yoshida & H. Sun, *M. trichogyna* T. Yoshida & H. Sun.

Key to Species of Series *Barbisetae*

1a. Inflorescence short racemose, with basal flowers; flowers opening widely; hairs on ovary with root-like branches at base and several rounded ridges on surface . . . . *M. trichogyna*
1b. Inflorescence a solitary scape and solitary flower; flower cup-shaped 2
2a. Hairs on ovary straight, ascending, with branches at base and with many longitudinal ridges on surface, apex sharply pointed; branches of hairs often gradually upturned. . . . . *M. hispida*
2b. Hairs on ovary usually incurved, with branches in lower half and with several rounded longitudinal ridges on surface, apex rather obtuse; branches of hairs retrorse, imbricate, not upturned . . . . *M. barbiseta*

Meconopsis barbiseta C.Y. Wu & H. Chuang ex L.H. Zhou, *Acta Phytotax. Sin.* 17 (4): 113–114. 1979. TYPE: CHINA. SE Qinghai, Jiuzhi Xian (久治县): eastern bank of Xiemu Cuo (斜木措), north side of Nianbao Shan (年保山), 4400 m, 1971, *Guoluo Team* (果洛队) *438* (Holotype: HNWP). Fig. 1, 79–80.

Meconopsis barbiseta C.Y. Wu & H. Chuang ex L.H. Zhou was revised by Yoshida and Sun (2018).

Distribution: CHINA. SE Qinghai: Jiuzhi Xian (久治县) and Banma Xian (班玛县), 3650–4100 m elevation.

Additional specimens examined: CHINA. SE Qinghai, Banma Xian, **Region 27:** Makehe (玛可河) Forest Reserve, southern side of Nianbao Yuze (年保玉则), 32°47'53"N, 101°04'42"E, 3650 m, 25 June 2016, *T. Yoshida K103* (KUN, TI). SE Qinghai, Jiuzhi Xian, **Region 28:** eastern bank of Xiemu Cuo, north side of Nianbao Shan, 4400 m, 1971, *Guoluo Team* (果洛队) *438* (HNWP); Jiuzhi (久治), July 1974, *Guoluo Grassland Station* (果洛草原站) *289* (HNWP); Sangchi Shan (桑赤山), 33°22'03"N, 101°19'18"E, 3950 m, 21 June 2016, *T. Yoshida K100* (KUN, TI); Luanshitou Yakou (乱石头丫口), 33°25'23"N, 101°13'30"E, 4000 m, 23 June 2016, *T. Yoshida K101* (KUN, TI).

Meconopsis hispida T. Yoshida & H. Sun, *Harvard Papers in Botany* 23 (2): 323. 2018. TYPE: CHINA. N Sichuan, Hongyuan Xian (红原县): western side of Yanggong Shan (羊拱山), 32°13'22"N, 102°35'04"E, 3850 m, 20 June 2016, *T. Yoshida K99* (Holotype: KUN; Isotype: TI). Fig. 1, 81–82.

Distribution: CHINA. N Sichuan: Hongyuan Xian and Heishui Xian (黑水县), Yanggong Shan, 3750–4000 m elevation.

Additional specimen examined: CHINA. N Sichuan, Hongyuan Xian, **Region 35:** western side of Yanggong Shan, 32°13'22"N, 102°35'04"E, 3850 m, 20 June 2016, *T. Yoshida K99* (KUN, TI).

Meconopsis trichogyna T. Yoshida & H. Sun, *Harvard Papers in Botany* 23 (2): 325. 2018. TYPE: CHINA. NW Sichuan, Dege Xian (德格县): Dege Haizi Shan (德格海子山), 32°03'13"N, 99°00'43"E, 4450 m, 14 July 2017, *T. Yoshida K119* (Holotype: KUN; Isotype: TI). Fig. 1, 83–84.

Distribution: CHINA. NW Sichuan: Dege Xian (德格县), 4400–4550 m elevation.

Additional specimen examined: CHINA. NW Sichuan, Dege Xian, **Region 26:** Dege Haizi Shan, 32°03'13"N, 99°00'43"E, 4450 m, 14 July 2017, *T. Yoshida K119* (KUN, TI).

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