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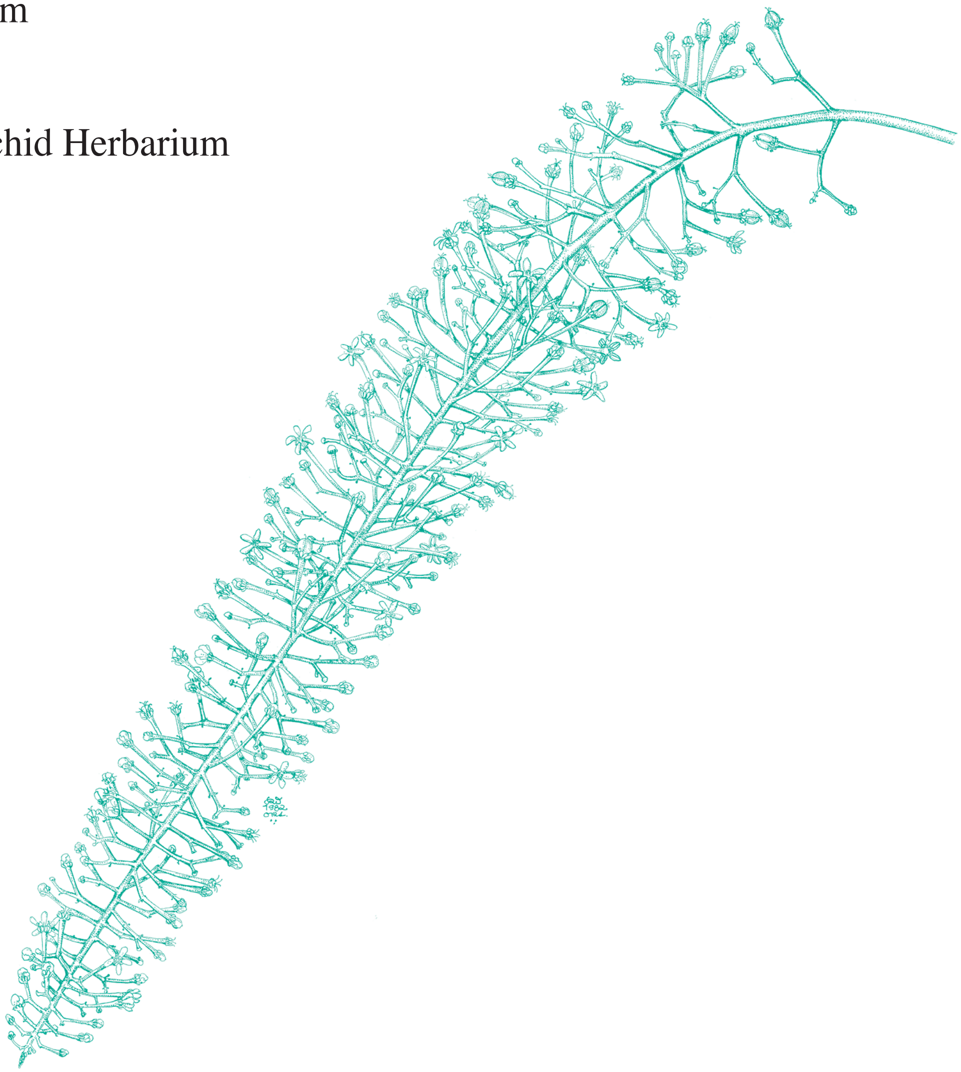

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Cover: *Andersoniella hammelii* (W.R. Anderson) C. Davis & Amorim
(See page 54, Fig. 2.) Drawing by Karin Douthit.

# Harvard Papers in Botany

Volume 25, Number 1 June 2020

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# NEW OR NOTEWORTHY TAXA IN THE SOUTH AFRICAN *HELIOPHILA* (BRASSICACEAE)

IHSAN A. AL-SHEHBAZ[1]

**Abstract.** One subspecies, *Heliophila subulata* subsp. *longipila,* is described as new. Ten new combinations (*H. agtertuinensis, H. arenaria* subsp. *acocksii*, *H. diffusa* subsp. *flacca*, *H. elata* subsp. *pillansii*, *H. glabrescens*, *H. minor*, *H. namaquana* subsp. *sarcostyla*, *H. pusilla* subsp. *macrosperma*, *H. scabrida* subsp. *salteri*, and *H. seselifolia* subsp. *nigellifolia*) are proposed. The following 35 taxa are lectotypified: *Brachycarpaea polygaloides, Carponema aggregata, H. adpressa, H. anomala, H. aspera, H. basutica, H. dolichostyla, H. dregeana* var. *induta*, *H. edentula, H. linearifolia, H. macowaniana, H. macra, H. maritima, H. maximiliani, H. natalensis, H. odontopetala, H. pearsonii, H. pearsonii* var. *prageri*, *H. pubescens, H. rivalis, H. rosea, H. rostrata, H. scandens, H. schlechteri, H. scoparia, H. stylosa, H. suavissima, H. suavissima* var. *incana*, *H. sulcata* var. *modestior*, *H. torulosa, H. trichinostyla, Leptormus caledonicus, L. tripartitus, Pachystylum glabrum,* and *Peltaria capensis*.

**Keywords:** Brassicaceae, Cruciferae, *Heliophila,* novelties, South Africa, typification

The present contribution is part of ongoing studies on the primarily South African genus *Heliophila* L. (Brassicaceae or Cruciferae) that started almost a decade and a half ago (Mummenhoff et al., 2005; Al-Shehbaz and Mummenhoff, 2005), continued recently (Al-Shehbaz, 2019, 2020a,b), and are to be concluded eventually with a comprehensive monograph that deals with the cytological, ecological, genomic, molecular phylogenetic, and detailed taxonomic accounts. The following nomenclatural adjustments are needed for the above-mentioned studies in progress. All taxa are numbered in one sequence regardless of their subheadings to facilitate easy search in the Appendix (Index to Numbered Collections) at the end of the paper.

## A NEW SUBSPECIES

*Heliophila subulata* Burch. ex DC. is one of the most variable and widespread species of the genus. The variation is continuous in almost all morphological features and does not show distinct patterns that merit formal recognition. The exception, however, is in localized populations in the Cape Province that have distinctly longer trichomes than do those elsewhere in the species range. They are formally recognized below as a distinct subspecies.

**1. Heliophila subulata** subsp. **longipila** Al-Shehbaz, *subsp. nov.* TYPE: SOUTH AFRICA. Western Cape: [Overberg District, Theewaterskloof Municipality], Swartberg, Caledon, along top of rocky ridge and on stony slopes, 30 September 1980, *E. Esterhuysen 35515* (Holotype: MO; Isotypes: BOL, M).

Plants of this subspecies are readily distinguished from those of subsp. *subulata* by having stem and leaf trichomes (0.3–)0.5–0.8(–1.0) versus 0.01–0.06(–0.08) mm long.

*Herbs,* perennial, densely hirsute to scabrous-pubescent on stems, leaves, and often pedicels. *Trichomes* (0.3–)0.5–0.8(–1.0) mm long.

**Phenology and habitat:** flowering late July into October (rarely into December). Plants restricted to rocky ridges, stony slopes, and hillsides at 300–750 m.

**Discussion:** plants of *Heliophila subulata* subsp. *longipila* are restricted to Theewaterskloof Municipality (formerly Caledon) of the Overberg District (Western Cape Province). These "Caledon"-endemics are highly restricted perennial herbs that are densely hirsute to scabrous-pubescent, especially along the stems and on leaves and pedicels, with trichomes (0.3–)0.5–0.8(–1.0) mm long. By contrast, subsp. *subulata* is widespread throughout the Western Cape (including the City of Cape Town, West Cape, Cape Winelands, Overberg, Garden Route, and Central Karoo districts), Eastern Cape, and KwaZulu-Natal provinces. They are also perennial herbs, but in some coastal populations the plants are sometimes annuals and at higher elevations they sometimes grow into subshrubs. However, throughout this subspecies range, the plants are densely to moderately puberulent with minute trichomes only 0.01–0.06(–0.08) mm long, and rarely they are subglabrous or glabrous.

Marais (1970) assigned the collections of *Heliophila subulata* to several unnamed groups, one of which included four collections from the Caledon area that have longer trichomes than the others. These collections (*Bolus 6772, Esterhuysen 18945, Schlechter 9783,* and *van Niekerk 398*) are cited below as paratypes.

**Additional specimens examined**: SOUTH AFRICA. Western Cape: Overberg, Theewaterskloof [Caledon], Swartberg, lower S slopes, *E. Esterhuysen 18945* (BOL, PRE); Houw Hoek *F. R. R. Schlechter 5578* (B, MO, Z), *G. van Niekerk 398* (BOL); Houw Hoek peak, *R. S. Adamson 4249* (BOL); Swartberg, *F. R. R. Schlechter 9783* (K, Z); foot of mountain near Caledon, *H. Bolus 6772* (BOL, PRE); Zandfontein, *E. E. Galpin 3747* (PRE).

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

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## New Combinations

The study of extensive collections of several species complexes of *Heliophila* supports raising the status of some varieties to distinct species. For others, they are either synonymized or treated as subspecies instead of varieties in order to be consistent with the concept I adopted throughout most of my career.

**2. Heliophila agtertuinensis** (O.E. Schulz) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *Heliophila maximiliani* Schltr. var. *agtertuinensis* O.E. Schulz, Bot. Arch. 31: 540. 1931. Described from: “Westregion, Agtertuin, auf Hügeln, alt. 800 ft. (R. Schlechter, It. II. 1897 n. 10858 – am 15. August blühend).” TYPE: SOUTH AFRICA. [Western Cape: West Coast, Cederberg], Clanwilliam, Agtertuin, 800 ft [ca. 244 m], 15 August 1897, *F. R. R. Schlechter 10858* (Holotype: K [000230382]; Isotypes: BM [000552478], BOL [133702, image seen], BR [0000008887214, image seen], E [00292843], G [00160955], GRA [00009890, image seen], HBG [506077, image seen], L [1827316, image seen], MO [1926510], P [00739534], PR, PRE [04064220, image seen], S [1216057], STU [image seen], W [19070005244], WAG [0000801, image seen], Z [000089792]).

This species is extremely rare and was treated by Schulz (1931) and Marais (1966, 1970) as a variety of *Heliophila maximiliani* Schltr. and *H. arenaria* Sond., respectively. *Heliophila agtertuinensis* is unique in the genus for having densely tuberculate sepals. It is further distinguished from *H. arenaria* (including *H. maximiliani*) by having nonmoniliform fruit with straight replum and smooth valves and by being glabrous throughout. By contrast, *H. arenaria* has moniliform fruit with strongly constricted replum and often callose parts of the valve facing the seeds, and it is often densely pilose especially on the sepals, though very rarely glabrescent or sparsely pilose in the young bud. Both species superficially resemble many other annual *Heliophila* for lacking the paired glands at leaf and pedicel bases and for having blue flowers, narrow fruit, one-appendaged petals and lateral stamens, and filiform to narrowly linear or trifid leaves. Therefore, their treatment as varieties of one species ignores their remarkable differences in the sepal indumentum.

Marais (1966, 1970) stated that the type of *Heliophila maximiliani* var. *agtertuinensis* is housed at B, but a search for it by some of the curatorial staff at B and I failed to locate any trace of it. It should be noted that the Brassicaceae taxa described by Schulz and deposited at B were saved during World War II. It is absolutely certain that Marais made a mistake because Schulz (1931) described this taxon and many others based on the material he studied at Kew and enumerated on pages 439–442 of that article. Therefore, *Schlechter 10858* (K), which was annotated by Schulz in 1930, is the holotype.

**3. Heliophila arenaria** subsp. **acocksii** (Marais) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *H. arenaria* var. *acocksii* Marais, Bothalia 9: 97. 1966. Described from: “Calvinia, Lokenburg, *Acocks 19750*.” TYPE: SOUTH AFRICA. [Northern Cape: Namakwa, Hantam], Calvinia, Lokenburg North, Boklandskloof, 2100 ft [640 m], 13 October 1958, *J. P. H. Acocks 19750* (Holotype: PRE [0406413-0, image seen]; Isotypes: BOL [108667, image seen], K [000230383]).

Marais (1970) used characters such as flower size, fruit indumentum, and ovule number to distinguish this subspecies (as var.) from subsp. *arenaria*. However, these characters can be quite variable in a given collection and, therefore, are unreliable for the separation of the two taxa. Instead, subsp. *acocksii* is readily separated from subsp. *arenaria* by having submoniliform or nonmoniliform (vs. strongly moniliform) fruits with straight (vs. strongly constricted) replum and cylindrical-subulate (vs. subclavate to broadly cylindrical) styles (3–)4–9 mm long (vs. 1.5–3.0[–3.5]) mm long.

**4. Heliophila diffusa** (Thunb.) DC. subsp. **flacca** (Sond.) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *H. flacca* Sond., Abh. Geb. Naturwiss. Hamb. 1: 223. 1846. Described from: “Hab. Inter frutices, (alt. II.) ad thermas prope urbem Caledon (Eckl. et Zeyh.!) Floret Augusto.” TYPE: SOUTH AFRICA. [Western Cape: Overberg, Theewaterskloof], Caledon Baths, Zwarteberg, *C. F. Ecklon & C. L. P. Zeyher s.n.* (Lectotype designated by Marais [1970: 41] as type: K [000230408]; Isolectotypes: B [100153836, 100153872], C [2 sheets], GOET [002611, image seen], M [0108061], MO [102155], P [00739579], S [G8768 and unnumbered sheet], SAM, W [0009169, 18890303879]).

Sonder (1846) provided a detailed description of the species based at least on the two duplicates at S that were not examined by Marais (1966, 1970), who indicated (pp. 98 and 41, respectively) that the lectotype (as type) is at K. However, Nordestam (1980: 257) lectotypified the name based on S (G8768), but this typification is predated by that of Marais, though this S duplicate is far more complete than that at K.

Subspecies *flacca* is distinguished from subsp. *diffusa* by having wingless or narrowly margined seeds, inflated, suborbicular-ovate to broadly elliptic silicles 2.5–3.5 × 2–3 mm, 2-ovuled ovaries, and styles 2.0–3.1 mm long. By contrast, subsp. *diffusa* has seeds winged all around, latiseptate, narrowly to broadly oblong silicles or siliques (3.5–)5.0–12(–14) × 3–4(–5) mm, (2–)4- to 8-ovuled ovaries, and styles 0.7–1.8(–2.3) mm long.

The above differences may suggest that the two taxa are sufficiently different morphologically to merit recognition at the species rank. However, their remarkable similarities in foliage, flowers, and racemes do not support that. In particular, both taxa have unappendaged stamens and petals all papillate at base, a feature extremely rare in the genus and found only in the related *H. minor* (see below).

**5. Heliophila elata** Sond. subsp. **pillansii** (Marais), Al-Shehbaz, *comb. et stat. nov.*

Basionym: *H. elata* var. *pillansii* Marais, Bothalia 9: 98. 1966. Described from: "Cape. Piketberg District, between Avontuur and Zebra Kop, Pillans 7603 (BOL, holo; GRA, K)."

TYPE: SOUTH AFRICA. [Western Cape: West Coast, Bergrivier], top of Piquetberg Range, between Avontuur and Zebra Kop, Piquetberg Div., 4000 ft (ca. 1219 m), 9 November 1934, *N. S. Pillans 7603* (Holotype: BOL [135669, image seen]; Isotypes: BOL [135668, image seen], GRA [0000996-0, image seen], K [000230364], NBG [0003141-0]).

The differences listed by Marais (1970) between vars. *elata* and *pillansii* do not hold because of the tremendous overlap, especially in characters such as the ovule number, presence versus absence of sparse trichomes on the fruiting pedicels, saccate versus nonsaccate sepals base, leaf division, and style length. Instead, subsp. *pillansii* differs by having flower-bud apices minutely puberulent (vs. glabrous), unappendaged (vs. appendaged) bases of petals and lateral stamens, and fruits 2.5–5.5 (vs. 4–8) cm long.

**6. Heliophila glabrescens** (O.E. Schulz) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *H. sabulosa* Schltr. var. *glabrescens* O.E.Schulz, Bot. Arch. 31: 541. 1931. Described from: "Piquetberg Div., Het Kmis [for Kruis], (E. L. Stephens and R. Glover in Percy Sladen Memorial Expedi. Etc. 1912 n. 8705 – am 17. Septbr. blühend und fruchtend)."

TYPE: SOUTH AFRICA. [Western Cape: West Coast, Bergrivier], Piketberg: Het Kruis, 17 September 1912, *E. L. Stephens & R. Glover 8705* (Holotype: K [000567805]).

Schulz (1931) and Marais (1966, 1970) treated *Heliophila glabrescens* as a variety of *H. sabulosa* and *H. arenaria,* respectively. From *H. arenaria* (including *H. sabulosa*), *H. glabrescens* differs substantially in being a very slender (vs. stout) plant with several decumbent and glabrous (vs. usually single, ascending, and hirsute to pilose stems), minutely puberulent (vs. pilose) sepals and pedicels with trichomes 0.01–0.03(–0.10) mm long (vs. 0.3–0.8(–1.3) mm long), puberulent (vs. hirsute to pilose) sepals the median pair of which is noncucullate (vs. cucullate), very slender (vs. stout) fruits 0.6–0.8 (vs. 1.0–1.5) mm wide and with obscure (vs. distinct) midvein, slender (vs. stout) fruiting pedicels (0.8–)1.0–2.0 cm (vs. 0.6–1.2 cm) long, and smaller seeds 0.6–0.8 × 0.5–0.6 mm (vs. 1.0–1.2 × 0.7–0.9 mm). In my opinion, these differences are substantial, and they justify the recognition of both *H. arenaria* and *H. glabrescens* as distinct species.

**7. Heliophila minor** (Marais) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *H. meyeri* Sond. var. *minor* Marais, Bothalia 9: 99. 1966.

TYPE: SOUTH AFRICA. [Western Cape: Overberg District], Swellendam Municipality, 26 September 1933, *F. M. Leighton s.n.* (Holotype: BOL [108455]).

*Heliophila minor* is a very rare species known thus far only from a handful collections made over half a century ago. It was described by Marais (1966) as a variety of *H. meyeri*, a species it resembles in the papillate bases of filaments and petals. In addition to lacking the appendaged filaments characteristic of *H. meyeri, H. minor* differs in being delicate plants 9–30 cm tall with 3- to 7-lobed basal leaves only 1–4 cm long, sepals 2.0–2.5 mm long, nonclawed petals 3–4 × 2–3 mm, filaments 1.5–1.8 mm long, ovate anthers 0.6–0.7 mm long, 8- to 14-ovuled ovaries, slightly moniliform fruits 1.0–1.7 cm × 1.2–1.7 mm, undulate replum, and suborbicular-ovate seeds 0.9–1.0 mm long. By contrast, *H. meyeri* is a more robust plant 18–50(–67) cm tall with (7–)9- to 19(–27)-lobed basal leaves 4–15(–24) cm long, sepals 3.0–4.5 mm long, short-clawed petals (5–)6–9 × 3.0–5.5 mm, filaments 2.3–4.0 mm long, oblong anthers 1.0–1.5 mm long, 12- to 18-ovuled ovaries, nonmoniliform fruit 1.5–2.5 cm × 2.5–3.0 mm, straight replum, and orbicular seeds 1.2–1.6 mm in diam.

Although both *Heliophila minor* and *H. meyeri* are restricted to the Western Cape Province, they are geographically isolated. The former occupies an easterly distribution and is confined to Langeberg and adjacent Breede Valley municipalities of the Cape Winelands District and adjacent Swellendam of the Overberg District. By contrast, *H. meyeri* occupies a further westerly range, especially in the City of Cape Town, Witzenberg, Drakenstein, Stellenbosch, and adjacent Breede Valley municipalities of the Cape Winelands District, and Theewaterskloof municipality of the Overberg District.

In conclusion, both geographical and morphological data strongly support the recognition of the above taxa as distinct species.

**8. Heliophila namaquana** Bolus subsp. **sarcostyla** (Schltr.) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *Heliophila sarcostyla* Schltr., Bot. Jahrb. Syst. 27: 138. 1899. Described from: "In regione austro-occidentali: In clivis lapidosis montis Koude-Berg, in ditione Clanwilliam, alt. c. 2600 ped., 28. Aug. 1896. – n. 8732."

TYPE: SOUTH AFRICA. [Western Cape: West Coast, Cederberg], Mt. Koudeberg, Clanwilliam, ca. 2600 ft [ca. 792 m], 28 August 1896, *F. R. R. Schlechter 8732* (Lectotype designated by and listed as type by Marais [1970: 26]: B [00154904]; Isolectotypes: BR [0000008886088, image seen], E [00193006], G [00160959], GRA [0000962-0, image seen], H [1348769, image seen], HBG [506061, image seen], K [000230437, 000230438], L [1827317, image seen], MO [1926507], P [00739692, 005445294, 05445297], PH [00014190, image seen], PR, S [1216096], SAM, US [00099879], W [18980002285], WAG [0000818, image seen], Z [000005046]).

Marais (1970) reduced *Heliophila sarcostyla* to synonymy of *H. namaquana* most likely because he examined only the isolectotype at K, which has no fruits. The study of fully mature fruits in several collections not studied by him strongly supports the recognition of the former, at least at the subspecific rank of the latter. Subspecies *sarcostyla* is distinguished from subsp. *namaquana* by having thickened, globose-to-obovoid styles to 2.5 mm wide, nonmoniliform fruits 2.0–2.2 mm wide, straight replum, subwoody valves, and seeds 2.0–2.2 × 1.2–1.5 mm. Subspecies *namaquana* differs by having cylindrical-subclavate to subclavate styles to 1 mm wide, moniliform to submoniliform fruits 1.0–1.5 mm wide, constricted to undulate replum, papery valves, and seeds 0.9–1.1(–2.2) × 0.6–0.8(–1.5) mm.

**9. Heliophila pusilla** L.f. subsp. **macrosperma** (Marais) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *Heliophila pusilla* var. *macrosperma* Marais, Bothalia 9: 100. 1966.

TYPE: SOUTH AFRICA. [Western Cape: Cape Winelands], Stellenbosch, *Prior s.n.* (Holotype: K [000230410]).

This subspecies differs from subsp. *pusilla* in having orbicular (vs. oblong) seeds 1.2–1.8 mm in diam. (vs. 0.8–1.0) mm wide, fruits (1.5–)1.7–2.3 (vs. 0.8–1.5) mm wide, orbicular (vs. elliptic) bead, as long as (vs. longer than) wide, appendaged (vs. unappendaged) and basally papillate (vs. basally glabrous) petals 4–6 × 2–3 mm (vs. 2.0–3.5 × 1.2–2.0 mm), and basally papillate (vs. glabrous) lateral filaments.

*Heliophila pusilla* subsp. *macrosperma* is almost exclusively restricted to Stellenbosch and adjacent Drakenstein municipalities of the Cape Winelands, whereas subp. *pusilla* is far more widespread in the City of Cape Town, Cape Winelands, and Overberg districts of the Western Cape Province. The two subspecies are allopatric, and I have not seen any morphologically intermediate collections to indicate possible hybridizations. Therefore, it is with some hesitation that I recognize them at the subspecific rank, and future field and experimental studies may show that they merit recognition as distinct species.

**10. Heliophila scabrida** Schltr. subsp. **salteri** (Exell) Al-Shehbaz, *comb. et stat. nov*.

Basionym: *Heliophila salteri* Exell, J. Bot. 68: 246. 1930. Described from: "*Hab.* South Africa: southern slope of the Twelve Apostles Mts., Cape Peninsula, fl. and fr. Oct.; T. M. Salter, 233/14 (type in Herb. Mus. Brit.)."

TYPE: SOUTH AFRICA. [Western Cape: City of Cape Town], south slope of 12 Apostles Mts., 16 October 1928, *T. M. Salter 233/14* (Holotype: BM [000552493]).

Marais (1970) treated both *Heliophila salteri* and *H. scabrida* as informal groups within *H. concatenata* Sond., a species he believed to be of hybrid origin between *H. meyeri* and *H. coronopifolia* L. A critical comparative study of all of the above taxa failed to support that assumption. Indeed, *H. scabrida* (together with *H. salteri*) are unrelated to the other three species above, and they are recognized as distinct taxa.

Subspecies *salteri* differs from subsp. *scabrida* by having moniliform fruits 1.0–1.5 cm × 1.5–2.0 mm, constricted to undulate at replum, cylindrical styles 1.0–1.5 mm long, and white petals 4–6 × 2–3 mm. By contrast, subsp. *scabrida* has nonmoniliform fruits (1.7–)2.0–3.6 cm × 2.5–3.2 mm, straight or rarely irregularly undulate replum, clavate to subulate or cylindrical styles 2–7 mm long, and mauve or pink petals 6–12 × 3–6 mm.

**11. Heliophila seselifolia** Burch. ex DC. subsp. **nigellifolia** (Schltr.) Al-Shehbaz, *comb. et stat. nov.*

Basionym: *Heliophila nigellifolia* Schltr., Bot. Jahrb. Syst. 49: 416. 1913. Described from: "Llein-Namaqualand: auf sandigen Hügeln bei Aus ca. 800 m ü. M. (R. Schlechter n. 11292 [for 11229]—blühend im September 1897)."

TYPE: SOUTH AFRICA. [Northern Cape: Namakwa], Namaqualand, ca. 800 m, 13 September 1897, *F. R. R. Schlechter 11229* (Lectotype designated by Marais [1970: 33] and listed as holotype: B [100153844]; Isolectotypes: BOL [135646, image seen], GRA [0000965-0, image seen], PRE [0404006-0, image seen]).

From subsp. *seselifolia*, subsp. *nigellifolia* differs by having unappendaged lateral stamens and torulose, strongly tortuose fruits that are alternately bulged above seeds on each side of fruit and strongly depressed between them on the other side. On the other hand, subsp. *seselifolia* has appendaged lateral stamens and nontorulose, nontortuose, flat fruits without any bulging above or between seeds.

## Typification

The vast majority of lectotypifications in *Heliophila* were done by Marais (1970), and his listings of the types for taxa are considered herein as lectotypifications following the excellent brief account by McNeill (2014) and the *Code* (Turland et al., 2018). The 35 cases below deal with untypified taxa or those that need a second-step lectotypification.

**12. *Brachycarpaea polygaloides*** Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 7. 1834–1835. TYPE: SOUTH AFRICA. [Western Cape: West Coast, Cederberg], Clanwilliam, [1 January 1830], *C. F. Ecklon & C. L. P. Zeyher 51* (Lectotype here designated: B [100154808]; Isolectotypes: B [100154804], C, GOET [002720, image seen], K, M [0152588], MO [1926515], P [00739470, 99739474], PRE [0409792-0, 0631917-0, images seen], SAM, W [0075577, 18890303903]).

The above name is a synonym of the widespread and highly variable *Heliophila juncea* (P. J. Bergius) Druce.

**13. *Carponema aggregata*** Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 8. 1834–1835. TYPE: SOUTH AFRICA. [Western Cape: Overberg, Theewaterskloof], Caledon, "In locis arenosis apud Vogelvalley et in Zwartland (Stellenbosch), Sep.," *C. F. Ecklon & C. L. P. Zeyher 55* (Lectotype here designated: SAM [00140640]; Isolectotypes: PRC [451623], PRE, S [1216080]).

*Carponema aggregata* is a synonym of the earlier-published *Heliophila digitata* L.f.

**14.** ***Heliophila adpressa*** O.E.Schulz, Bot. Arch. 31: 530. 1931. Described from: "*Südafrika:* Kap der Guten Hoffnung (Bergius 1815 – im September blühend, Herb. Berlin-Dahlem), an sandigen Orten des Tafelberges (Ecklon, un. it. n. 387 – im Oktober fruchtend, ad Herb. Pocker in Herb. Kew." TYPE: SOUTH AFRICA. [Western Cape]: Arenosa Mount, *C. F. Ecklon 387* (Lectotype here designated: K [000230436]; Isolectotypes: G [00161014], JE [00000396], M [0108070], PRE [0403162-0, fragments at B).

Schulz (1931) cited two syntypes (*Bergius s.n.* at B and *Ecklon 387* at K), and both were examined by Marais (1970), who did not lectypify the species. The former collection is an immature unicate, whereas the Ecklon collection has mature fruits, and the duplicate at K was annotated by Schulz in 1930 and is here designated as the lectotype.

**15.** ***Heliophila anomala*** Schltr., Bot. Jahrb. Syst. 49: 410. 1913. Described from: "Südwestliche Kap-Kolonie: auf grasigen Abhängen der Berge beim Tulbagh-Wasserfall ca. 1000 m ü. M. (R. Schlechter n. 1682 – blühend im September 1892). Auf grasigen Flächen der Berge bein Elandsfontein, im Koude Bokkeveld (Ceres-Division) ca. 1700 m ü. M. (R. Schlechter n. 10032 – blühend im Januar 1897)." TYPE: SOUTH AFRICA. [Western Cape: Cape Winelands, Witzenberg], Ceres, Koude Bokkeveld, 5500 ft [ca. 1676 m], 18 January. 1897, *F. R. R. Schlechter 10032* (Lectotype here designated: Z [000005018]; Isolectotypes: B [100153801], BM [001254227], BOL [135674, image seen], G [00160848, 00160849], GRA [0001004-0, image seen], K [000230564], PRE [0408634-0, image seen], WAG [0000825, image seen]).

*Heliophila anomala* is an illegitimate and superfluous name because one of its syntypes, *Schlechter 1682* (Z [000005049]), is the holotype of the earlier-published *H. tulbaghensis* Schinz. To my knowledge, the latter is known only from the unicate above, whereas the former has not been typified before.

**16.** ***Heliophila aspera*** Schltr., Bot. Jahrb. Syst. 49: 410. 1913. Described from: "Südwestliche Kap-Kolonie: an felsigen Stellen auf den Gydouwbergen (Ceres-Division) ca. 1800 m ü. M. (R. Schlechter n. 10050 – blühend und fruchtend im Januar 1897)." TYPE: SOUTH AFRICA. [Western Cape: Cape Winelands, Witznberg], Ceres, Koude Bokkeveld, Gydouwberg, 19 January 1897, 6000 ft [ca. 1829 m], *F. R. R. Schlechter 10050* (Lectotype here designated: B [100153804]; Isolectotypes: BM [001254229], BOL [135685, image seen], BR [0000008886170, 0000008886897, images seen], E [00193021, 00193022], G [00160853, 00160854], GRA [0001008-0, image seen], HBG [506102, 506103, images seen], K [000230558, 000230559], L [1827576, 1827577, images seen], MO [1806619, 1925722, 1925723], P [00710355, 00723708], PH [00014168, 00014169, 00014170, images seen], PR [two sheets], PRE [0408660-0, 0593974-0, 593975-0, images seen], S [1216102, 1216104], US [00099867, 00099868], W [18990003179, 18980007154], WAG [0000823, 0000824, images seen], Z [000005021, 000005022]).

Schlechter collected the type material and retained 2 of the 39 duplicates at Z. The name needed lectotypification, and because he (Schlechter, 1913) did not typify the name and, apparently later, annotated the sheet at B as "typus auct." I am designating that sheet as the lectotype.

**17.** ***Heliophila basutica*** Phillips, Ann. S. African Mus. 16: 38. 1917. Described from: "Qoqolosi Peak. January-February, flowers purple or pink. *A. Dieterlen,* 939 partly; *Philipps*, 975." TYPE: [LESOTHO] Basuntoland, Leribe, Qoqolosi Peak, January 1913, *A. Dieterlen 939* (Lectotype here designated: SAM [0006115-2]; Isolectotypes: P [00739713], SAM, US [00099870]).

Phillips (1917) cited the above two syntypes but did not designate a type for *Heliophila basutica,* though he annotated one sheet as the type, and that is taken here as the lectotype. Marais (1970) cited both *Philipps 975* and *Dieterlen 939* as syntypes, and although he annotated all sheets as *H. suavissima* Burch. ex DC., he too did not designate a lectotype.

**18.** ***Heliophila dolichostyla*** Schltr., Bot. Jahrb. Syst. 49: 414. 1913. Described from: "Kap-Kolonie: an steinigen Abhängen der Berge am Gracias-Pass (Riversdale – Division) ca. 450 m ü. M. ([*C. Leipoldt*] Herb. Bolus n. 10577 – blühend im Dezember 1904). An steinigen Stellen auf dem Montague-Pass (George-Division) ca. 300 m ü. M. (R. Schlechter n. 5787 – blühend un fruchtend im November 1894)." TYPE: SOUTH AFRICA. [Western Cape: Cape Winelands, Langeberg], Montague Pass, 1000 ft [ca. 305 m], 2 November 1894, *F. R. R. Schlechter 5787* (Lectotype here designated: B [100153878]; Isolectotypes: GRA [0001011-0, image seen], Z [00089872]).

*Heliophila dolichostyla* is a synonym of *H. elongata* (Thunb.) DC. Schlechter (1913) did not indicate which of the two syntypes cited is the type, and the more complete specimen of the two duplicates I examined is designated above as the lectotype.

**19.** ***Heliophila dregeana*** Sond. var. ***induta*** O.E. Schulz, Bot. Arch. 31: 525. 1931. Described from: "Packhuisberg, 1000 m ü. M., an felsigen Orten (R. Schlechter 1896 n. 8640, Hb. Berlin-Dahlem), Kondeberg, Cedarberge, bei Wupperthal, ca. 1000 m ü. M. (H. Bolus 1897 u. 8923, Hb. Kew), (L. Diels 1900 n. 875, Hb. Berlin-Dahlem)." TYPE: SOUTH AFRICA. [Western Cape: West Coast, Cederberg], Clanwilliam, Parkhimsberg, 3000 ft [ca. 914 m], 24 August 1896, *F. R. R. Schlechter 8640* (Lectotype here designated: K [000865600]; Isolectotypes: BOL [135677, image seen], BR [0000008886132, image seen], G [00160878, 00160879], MO [1925703], P [00739592], PR, PRE [0408643-0, 0631910-0, 0631911-0, images seen], S [1216081], W [18980002276], Z [000089729]).

Two of the three B syntypes cited by Schulz (1931) under *Heliophila dregeana* var. *induta, Schlechter 8640* and *Diels 875*, were not located, and it is likely that they were misplaced or lost during World War II. Although I have examined *Bolus 8923* (K), it is not as complete as the K duplicate of *Schlechter 8640*. Therefore, I am designating the latter as the lectotype because it is also represented by 14 duplicates that I either examined or saw images of, or both. The variety is considered a minor variant of *H. dregeana* that does not merit recognition.

**20. *Heliophila edentula*** O.E.Schulz, Bot. Arkiv 31: 527. 1931. Syn. nov. Described from: "Südafrica: Ohne genauen Standort (Drège 1838 n. 7569, Hb. Kew, Alex. Kuhn 1903), Südl. Gross-Nama-Land, Gebiet des unteren Fischflusses bei Utschoa, auf Granitupen, 700 m ü. M. (Prager 1918 n. 8), Stolzenfels-Rietfontein (J. Garf Pfeil 1890/91 n. 105), Aus, auf Hügeln, 950 m. ü. M. (R. Schlechter 1897 n. 11416), Aus, im Halbschatten niedriger Sträucher, 1400 m ü. M. (Dinter 1910 n. 1086, Blütenfarbe dunkelveilchenblau), Kuibis, Sandsteinplateau, 900 m ü. M. (Dinter 1910 n. 1240), Kubub am Felsen, 1400–1650 m ü. M. (Range 1906 n. 66, Blüten violettblau), Klein-Karas, auf Sand, 1300 m ü. M. (Schäfer 1909 n. 13, in Dinter, Kollect. n. 1292, 1300), Tafelberge bei Buntfeldschuh (Schäfer 1913 n. 508), Klinghardtgebirge, Pietab I u. II (Schäfer 1913 n. 515)." TYPE: [NAMIBIA. Karas: Lüderitz District], Klinghardtgebirge, Pietab I u. II, 14 July 1913, *Schäfer 515* (Lectotype here designated: B [100153877]).

Five of the above syntypes were not located in any of the major herbaria consulted, and the remaining four that I examined belong to three unrelated species. *Drege 7569* is *Heliophila trifurca* Burch. ex DC., *Schaefer 515* and *Garf Pfeil 105* are *H. deserticola* Schltr., and *Schlechter 11416* is *H. affinis* Sond. Schulz (1931) distinguished *H. edentula* from *H. deserticola* solely by the presence versus absence of the minute petal appendage facing the lateral stamens; a feature alone does not justify the recognition of distinct species.

**21. *Heliophila linearifolia*** Burch. ex DC., Syst. Nat. 2: 692. 1821. Described from: "H. linearifolia. *Burch! cat. geogr. pl. afr. austr. extratrop. n. 374 et 793*. Hab. ad Caput Bonae-Spei. Var. α in vicinitate Urbis Cape-Town. Var. β ad Nysna in regione Anteniqua-land (*Burchell*). *5*. (v. s. sp. in herb. Burch.)." TYPE: SOUTH AFRICA. [Western Cape: City of Cape Town], Camps Bay, *W. J. Burchell 347* (Lectotype here designated: K [000230370]; Isolectotypes: G [00207084], K [000230369], PRE).

The above syntypes cited by de Candolle (1821) are housed in Burchell's herbarium at Kew, and the name has not been typified to the present. The lectotype designated above is a plant with leaves, flowers, and young fruits, and the fragments at G-DC consist of leaves and a flower taken from the lectotype. The isolectotype at K and the syntype are mounted on the same sheet.

**22. *Heliophila macowaniana*** Schltr., Bot. Jahrb. Syst. 27: 135. 1899. Described from: "In regione austro-occidentali: In arenosis prope villam Tulbagh, alt. c. 400 ped. 13. Sept. 1896. – n. 8996." TYPE: SOUTH AFRICA. [Western Cape: Cape Winelands, Drakenstein], Tulbagh Road, 600 ft [ca. 183 m], 13 September 1896, *F. R. R. Schlechter 8996* (Lectotype here designated: Z [000005035]; Isolectotypes: BM [000593515], BOL [135655, image seen], BR [0000008886118, image seen], E [00193012], G [00160908], GRA [0000975-0, image seen], H [1348759, image seen], K [000230398], MO [1925734], NBG [0199105-0], P [05445277, 00739628], PH [00014199, image seen], PR, PRE [0407947-0, 0631908-0, 0631909-0, images seen], S [1216094], US [00099875], W [18980002279], WAG [0000815, image seen]).

*Heliophila macowaniana* needs lectotypification because Schlechter (1899) based the species description on his collection prior to distributing any duplicates, and he did not indicate where the type is housed. Marais (1970) did not lectotypify the name and listed K and PRE as the type.

**23. *Heliophila macra*** Schltr., Bot. Jahrb. Syst. 27: 136. 1899. Described from: "In regione austro-occidentali: In clivis arenosis montium pone rivulum 'Onrust-Rivier' in ditione Caledon, alt. 2000 ped., 29. Nov. 1896. – n. 9497; in arenosis montium pone rivulum 'Koude-Rivier' in ditione Bredasdrorp, alt. c. 900 ped., 4 Dec. 1896. – n. 9626." TYPE: SOUTH AFRICA. [Western Cape: Overberg, Theewaterskloof], Caledon, Onrust River Mts, 2000 ft [ca. 610 m], 29 November 1896, *F. R. R. Schlechter 9497* (Lectotype here designated: Z [000089748]; Isolectotypes: B [100153851], BM [000552489], BR [0000008886446, image seen], E [00193011], G [00160909], GRA [00001012-0, image seen: two plants on the right], HBG [506078, image seen], K [000230551], L [1827376, image seen], MO [1925732], P 00739629], PH [00014197, 00014198, images seen], PR, PRE [0409966-0, 0632500-0, 0632501-0, images seen], S [1216095], US [00099876], W [18980007155], WAG [0000816, 0000817, images seen]).

The name was not previously typified, and the collection number with more complete plants and more duplicates is taken here as the lectotype.

**24. *Heliophila maritima*** Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 11, No. 85. 1834–1835. Described from: "In collibus litoris apud 'Port Elisabeth' ad fluvium 'Zwartkopsrivier' et in 'Krakakamma' (Uitenhage), Sept. Oct." TYPE: SOUTH AFRICA. [Eastern Cape: Nelson Mandela Bay], Krakakama (Uitenhage), *C. F. Ecklon & C. L. P. Zeyher 85* (Lectotype here designated: SAM [0028110-0]; Isolectotypes: C, B [100154890], M [0152587], PRC [451625], W [0009173]).

*Heliophila maritima* is a synonym of the widespread and highly variable *H. subulata*.

**25. *Heliophila maximiliani*** Schltr., Bot. Jahrb. Syst. 27: 136. 1899. Described from: "In regione namaquensi: In sabulosis montium Karree-Bergen, alt. c. 1500 ped., 20. Jul. 1896. – n. 8229." TYPE: SOUTH AFRICA. [Western Cape: West Coast, Matzikama], Vanrhynsdorp, Karreeberg, 1500 ft [ca. 457 m], 20 July 1896, *F. R. R. Schlechter 8229* (Lectotype designated by Marais [1966: 97] as a first step, and second step here designated: B [10 0154905 (two plants on the right)]; Isolectotypes: B [10-0154907], BM [000552477, 000552478], BOL [135662, image seen], BR [0000008886880, image seen], G [00160956], GRA [00009870, image seen], HBG [506063, image seen], K [000230387], L [1827312, 1827315, images seen], MO [1926509], P [00739533], PH [00014193, image seen], PR, PRE [0406392-0, 0632490-0, images seen], S [1216055], US [552893, herb. #], W [19050000702], WAG [0000803, image seen], Z[000089791]).

Schlechter (1899) did not designate a type, and Marais (1966) indicated that the type of *Heliophila maximiliani* is at B, but he did not specify which of the two sheets was meant, though he annotated both of them on 13 March 1963 as "*Heliophila arenaria* Sond. = *H. maximiliani* Me." Of the two sheets of the type collection of *H. maximiliani* at B, the more complete is designated herein as the lectotype. The lectotype, which is represented by the two plants on the right, is a mixed collection with *H. acuminata* (Eckl. & Zeyh.) Steud.

**26.** ***Heliophila natalensis*** O.E. Schulz, Bot. Arch. 31: 534. 1931. Described from: "*Südafrika:* Natal, Winkle Spruit bei Durban, auf sandigen, spärlich begrasten Hügeln, ca. 25 m ü. M. (H. Rudatis 1911 n. 1497 – am 12. November blühend und fast fruchetend, Hb. Berlin-Dahlem), Congella, auf sandigem Boden, alt. 50 ft. (J. M. Wood 1892 n. 4676 mit *H. Woodii Conranth* – am 2. November blühend und fruchtend, Hb. Berlin-Dahlem)." TYPE: SOUTH AFRICA. [KwaZulu-Natal: e-Thekwini], Winklespruit [Winkle Spruit] (Durban City), 25 m, 12 November 1911, *H. Rudatis 1497* (Lectotype here designated: B [100153845]; Isolectotype: NBG [0218583-0]). Syntype: SOUTH AFRICA. [KwaZulu-Natal]: Congella, 2 November 1892, *J. M. Wood 4676* (B [100153846, 100154888], MO [1925737, 1925738, 1925739, 1925740], PRE [0408027-0, image seen], US).

Schulz (1931) cited and annotated two syntype collections of *Heliophila natalensis* at B. He believed that two species were represented in *Wood 4676,* and this sheet was subsequently split into two, of which one includes a larger plant annotated by Schulz as *H. natalensis* (B [100153846]), and the other is a bundle of about 14 plants believed by him to be *H. woodii* (B [100154888]). Both species names were correctly synonymized with *H. subulata* by Marias (1970).

**27.** ***Heliophila odontopetala*** Zahlbr. Ann. Nat. Hofmus. Wien, 18: 383. 1903. TYPE: SOUTH AFRICA. [Western Cape: West Coast, Cederberg], Piqueniers Mts., 22 August 1894, *A. Penther 2690* (Lectotype here designated: W [18970009359]; Isolectotypes: BM [000552492], BOL, M [0152586], W [18970006360]).

*Heliophila odontopetala* is a synonym of *H. digitata,* and its description by Zahlbruchner was based on the two duplicates at W without type designation.

**28.** ***Heliophila pearsonii*** O.E. Schulz, Bot. Arch. 31: 528. 1931. Described from: "Auf dem Hochplateau zwischen Krai Kluft und Wasserfall an einem breiten, tochenen, sandigen Wasserlauf (H. H. W. Pearson, Percy Sladen Memonrial Expedition to the Great Karasberg 1912–1913 n. 7869, Blüten seher bleich lila, Hb. Berlin-Dahlem und Kew), nördlich von Nauchas, auf granitischem Sand, Percy Sladen Mem. Exp. 1915–1916 n. 9007, Hb. Kew), Hantam-Gebirge (Meyer 1869, Hb. Berlin-Dahlem)." TYPE: [NAMIBIA. Karas]: Karasberg, between Kari Kluft and Wasserfall, 20 January 1913, *H. H. W. Pearson 7869* (Lectotype here designated: K [000230421]; Isolectotypes: B [100153841], BM [001254232], BOL [not seen]).

I have examined the same material studied by Schulz (1931), and the more complete specimen is designated as the lectotype. Both *Heliophila pearsonii* and the following var. *prageri* are synonyms of *H. minima* (Stephens) Marais.

**29.** ***Heliophila pearsonii*** var. ***prageri*** O.E. Schulz, Bot. Arch. 31: 528. 1931. Described from: "Südliches Gross-Nama-Land, Gebiet des unteren Fischflusses, Utschoa, auf sandigem Granitboden, 900 m ü. M., nichet sehr husfig (J. Prager 1918 n. 2, mit hellblauer Blüte), Garub, auf Kiesboden, ca. 900 m ü. M. (Range n. 507 in Gesellschaft von H. deserticola, mit hellblauen Blüten)." TYPE: [NAMIBIA. Karas: Lüderitz-Süd], Garub, Kiesboden, ca. 900 m, Range 507 (Lectotype here designated: B [100299423]).

The *Prager 2* syntype was not located in any of the major herbaria consulted.

**30.** ***Heliophila pubescens*** Burch. ex Sond., Abh. Ges. Naturw. Hamb. 1: 208. 1846. Described from: "Hab. Rhenosterriver d. 8. Aug. 1811 (Burchell!) in locis rupestribus ad latus meridionale montis Zuureplas, Sneeuwbergen, 4–5000'. (Drège!) Floret Augusto." TYPE: SOUTH AFRICA. [Northern Cape: Karoo Hoogland], Sutherland, between Jakhalsfontein and Kuilenberg, August 1811, *W. J. Burchell 1334* (Lectotype designated by Marais [1970: 29] as first step, and a second step is here designated: K [000230431]; Isolectotypes: K [000230433], PRE [0403177-0, image seen]).

Burchell (1822) listed his collection under *Heliophila pubescens*, but the name was a nom. nud. Sonder (1846) validated the name and cited both *Burchell 1334* and *Drège s.n.* Although Marais (1970) indicated that *Burchell 1334* (K) is the holotype, he did not specify which of the two sheets he annotated it is. Therefore, a second-step lectotypification is needed. The above-designated lectotype includes four plants, as compared with the single immature plant of K (000230433). The lectotype is a mixed collection that also includes a single plant of *Burchell 1323* (K [000230432]), but this second collection of *H. pubescens* does not concern us for the lectotypification of the name.

**31.** ***Heliophila rivalis*** Burch. ex DC., Syst. Nat. 2: 682. 1821. Described from: "H. rivalis. *Burch! cat. geogr. pl. afr. eustr. extratrop. n. 5496*. Hab. in locis humidis territorii Capitis Bonae-Spei ad Melkhout-Kraal prope Nysna (*Burch.*). φ. (v. s. sp. comm. à cl. Burchell.)." TYPE: SOUTH AFRICA. [Western Cape: Garden Route], Knysna, 29 June 1814, *W. J. Burchell 5496* (Lectotype here designated: K [000230406]; Isolectotypes: B [100153824], K [000230407], M [0108050], P [05445295, 00739689], PRE [0405043-0, image seen]).

There are two sheets of the type collection of *Heliophila rivalis* in Burchell's herbarium at K, and Marais annotated them as a synonym of *Heliophila pendula* Willd. Both sheets were anonymously annotated as type, and the one with the original handwritten description by Burchell is here designated as the lectotype.

**32.** ***Heliophila rosea*** Schltr., Bot. Jahrb. Syst. 27. 137. 1899. Described from: "In regione austro-occidentali: Juxta rivulos montium prope French-Hoek, solo arenoso, alt. c. 2500 ped., 24. Nov. 1897. – n. 9324." TYPE: SOUTH AFRICA [Western Cape: Cape Winelands, Drakenstein], French Hoek Mt., *F. R. R. Schlechter 9324* (Lectotype here designated: Z [000005042]; Isolectotypes: B [100154908], BM [000552471], BOL [135652, image seen], GRA [00009720, image seen], K [000230401], PRE [04079770, image seen]).

Taxonomic novelties described by Schlechter (1897, 1898, 1899, 1913) were based almost exclusively on his own collections. The complete set of his collections are deposited at Z, and the second set at B. In many cases, however, he annotated but did not cite the B duplicates of his novelties as types. However, in the case of *Heliophila rosea*, the B duplicate is rather fragmentary as compared with the more complete one at Z that I am designating here as the lectotype.

**33.** ***Heliophila rostrata*** C.Presl, Abh. Königl. Böhm. Ges. Wiss. ser. 5, 3: 440. 1845. Described from: "Heliophila pilosa Drege pl. Cap. exs." TYPE: SOUTH AFRICA. [Western Cape]: (as "Capland"), 1838, *J. F. Drège s.n.* (Lectotype desigated here: PRC [452647]; Isolectotypes: HBG [506065, image seen], K, P [05122862, 05445319, 00739647], PRC [452646, plant on the left]).

There are two sheets of the type collection of *Heliophila rostrata* at PRC, where Karel Presl's herbarium is housed, and the more complete one is designated above as the lectotype. The PRC isolectotype is a mixed collection of this species and *H. africana* (L.) Marais.

**34.** ***Heliophila scandens*** Harv., Thes. Cap. 2: 43. 1863. Described from: "Hab.–Back Beach, in shady places, among shrubs, D'Urban, Natal, *M. J. McKen*, Aug., 1862. Natal, *T. Cooper,* 1268. (Herb. T. C. D.)." TYPE: SOUTH AFRICA. [KwaZulu-Natal: e-Thekwini], Natal, Back Beach, near Durban, in shady places, among shrubs, August 1862, *W. T. McKen 7* (Lectotype here designated: TCD [0001710, image seen]).

Marais (1970: 66) listed both syntypes but did not lectotypify the name. Although the lectotype designated above is a unicate, it is preferred over the four-duplicate syntype *Cooper 1268* because it is more complete and carries the notes in William Harvey's handwriting. The original publication (Harvey, 1863) includes an excellent illustration (plate 166), and the species description was subsequently emended in details by Hooker (1899) and illustrated within by Matilda Smith on the basis of flowering material grown at K.

*Heliophila scandens* is unique in the genus in being a true liana that may exceed 3 m in height. It is endemic to KwaZulu-Natal and can easily be distinguished by the petiolate and undivided leaves and large elliptic to elliptic-lanceolate fruits (1.5–)2.0–3.7(–4.4) × (0.6–)0.8–1.4 cm with 1 or 2 suboricular, winged seeds.

**35.** ***Heliophila schlechteri*** Schinz, Vierteljahrsschr. Naturf. Ges. Zürich 45: 235. 1910. Described from: "Südafrika Kapkolonia George, 300 m. Schlechter 2355. bl. u. fr. 18. III. 1893." TYPE: SOUTH AFRICA. Pr. George, 300 m, 18 March 1893, *F. R. R. Schlechter 2355* (Lectotype here designated: B [100299432]; Isolectotypes: BM [001254158], G [00160962], HBG [506059, 506060, images seen], K, MO [1612411], MPU [017495, image seen], P [00739693], PRC [451628], S [1216072], W [19100007316], WU [0101784]).

As recognized by this author, the type collection of *Heliophila schlechteri* clearly falls within the limits of *H. filiformis* L.f., though the isolectotype at K is a mixture of the former with a plant of *H. tulbaghensis*, and images of the duplicates BOL (135670) and GRA (00009971 and 00009972), which carry the same collection number, clearly belong to *H. subulata*.

Marais (1970) listed *Schlechter 8550* under *Heliophila africana,* but these plants have filiform leaves and sharply reflexed immature fruits, and their overall morphology is more at home in *H. filiformis* than in *H. africana*.

**36.** ***Heliophila scoparia*** Burch. ex DC., Syst. Nat. 2: 693. 1821. Described from: "H. scoparia. *Burch! cat. geogr. pl. afr. eustr. extratrop. n.* 7887 *et* 8557. Hab. ad Cap. Bonae-Spei in vicinitat urbis Cape-Town et in montibus Baviaans-Kloof (*Burchell.*) 5. (*v. s. sp.*)." TYPE: SOUTH AFRICA. [Western Cape: Overberg, Theewaterskloof], Caledon, *W. J. Burchell 7887* (Lectotype here designated: K [000230560]; Isolectotype: G [00207081]).

The K specimen is more complete than the G duplicate, and it is not known if the latter was taken from the former.

**37.** ***Heliophila stylosa*** Burch. ex DC., Syst. Nat. 2: 692. 1821. Described from: "H. scoparia. *Burch! cat. geogr. pl. afr. eustr. extratrop. n. 3291*. Hab. ad Caput Bonae-Spei ad Komme dakka (*Burchell*). 5. (*v. s. sp.* in h. Burch.)." TYPE: SOUTH AFRICA. [Eastern Cape: Sara Baartman, Blue Crane Route], Mt. Commadagga, Somerset East, 5 July 1813, *W. J. Burchell 3291* (Lectotype here designated: K [000230553]; Isolectotypes: G [00207083], K [000230554], PRE [0410026-0, image seen]).

*Heliophila elongata, H. stylosa,* and *H. virgata* were simultaneously published by de Candolle (1821). Marais (1970) was the first to place the last two under the synonymy of the first, and therefore *H. elongata* has priority (see Article 11.5 in Turland et al., 2018).

There are two sheets of the type collection of *Heliophila stylosa* at K, and the more complete of the two (K [000230553]), which was studied by de Candolle and from which he apparently obtained fragmentary material (leaf, fruit, and flower) and deposited in his herbarium, is here designated as the lectotype. It is likely that he also examined the second sheet.

**38.** ***Heliophila suavissima*** Burch. ex DC., Syst. Nat. 2: 691. 1821. Described from: "H. suavissima. *Burch! cat. geogr. pl. afr. austr. extratrop. n.* 2742. Hab. ad Caput Bonae-Spei prope Plettenbergs-Baaken (*Burchell*). ♄. (v. s. sp. comm. À cl. Burch.)." TYPE: SOUTH AFRICA. [Western Cape: Garden Route?], Colesberg, between Rietfontein and Plettenbergs Beacon, March 1813, *W. J. Burchell 2742* (Lectotype designated by Marais (1970: 63) as a first step and second-step lectotype designation here: K [000230358]; Isolectotypes: G [00207087], GOET [002613, image seen], GRA [0001000-0, image seen]; K [000230357, two plants on the right], M [0108045], P [00739711, 05445350], PRE [0407889-0, image seen]).

There are two sheets in the folder of the type collection at K, of which the lectotype is the more complete. The second sheet is a mixture of two collections by Burchell, but only the two plants on the right are the isolectotype. Marais (1970) annotated the latter sheet but did not indicate its type status.

**39.** ***Heliophila suavissima*** Burch. var. ***incana*** Sond. in Harvey & Sond., Fl. Cap. 1: 49. 1860. Described from: "....*β*. Springbokkeel, *Zeyher*. Aug. Oct. and Feb. (Herb. Hook., Sond., T.C.D. [Trinity College in Dublin])." TYPE: SOUTH AFRICA. [Northern Cape: Namakwa, Nama Khoi], Springbokkeel, *C. L. P. Zeyher 43* (Lectotype here designated: S [1216105, plant on right]; Isolectotypes: K, SAM [0028105-0], W [18890144758]).

Sonder (1860) based this variety on Zeyher's specimens from Springbokkeel that were collected in February, August, and October and are currently deposited in K, S, and TCD. Sonder did not give any collection numbers, but the only material collected in February from Springbokkeel is *Zeyher 43*, and the S duplicate carries the species and varietal names in Sonder's handwriting. Of the three duplicates he cited, I did not have the chance to study the one at TCD.

This variety, as well as the later published and illegitimate *Heliophila suavissima* var. *velutina* O.E.Schulz, is based on the same type collection, and both are synonyms of *H. minima*.

**40.** ***Heliophila sulcata*** Conrath var. ***modestior*** O.E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 11: 228. 1931. Described from: "Südafrika: Orange Free State, Distr. Fauresmith, on Fauresmith Botanical Reserve, alt. c. 4550–4600' (blühend und mit jungen Früchten am 1. September 1925 – C. A. Smith, National Herbarium Pretoria n. 396, 400), eastern slope of hill, near top, alt. c. 4650' (fast fruchtend am 3. Mai 1927 – C. A. Smith n. 3930), hill crest near South Boundary on the Fauresmith Bot. Reserve, alt. c. 4700' (blühend und mit Fruchtresten am 24. August 1927 – C. A. Smith n. 4433), District Philippolis, Spioenkop, near crest on north slope, c. 5150' (blühend un mit jungen Früchten am 8. September 1927 – C. A. Smith n. 4466)." TYPE: SOUTH AFRICA. [Free State: Xhariep, Kopanong], Distr. Philippolis, Spioenkop, near crest on north slope, ca. 5150 ft [ca. 1570 m], 8 September 1927, *C. A. Smith 4466* (Lectotype here designated: B [10-0154889]; Isolectotype: PRE [0407936-0, image seen]).

Of the above five syntype collections of Smith, I have examined the lectotype and *Smith 396* (PRE), and both clearly belong to *Heliophila carnosa* (Thunb.) Steud.

**41.** ***Heliophila torulosa*** O.E. Schulz, Bot. Arch. 31: 537. 1931. Described from: "*Sudafrika*: Kloof village, Asbestos Mts. (W. J. Burchell 1811, Catal. geogr. pl. Afric. austr. extratrop. n. 1689 – am 25. September fruchtend, Hb. Kew), im Tale des Hex River bei Doorns, alt. ca. 1700 ft. (H. Bolus, Fl. regionis austro-occid. 1908 n. 13068 – im Januar fruchtend, Hb. Kew)." TYPE: SOUTH AFRICA. [Northern Cape: Pixley ka Seme, Siankuma], Kloof Village, Asbestos Mts, 25 September 1911, *W. J. Burchell 1689* (Lectotype, here designated: K [000230391]; Isolectotype: B [100153832]).

Marais (1970) correctly assigned Burchell and Bolus syntypes of *Heliophila torulosa* to *H. remotiflora* O.E.Schulz and *H. linoides* Schltr., respectively, but he did not lectotypify the first name. Both *H. remotiflora* and *H. torulosa* were simultaneously published by Schulz (1931), and the former will have priority by the designation of Burchell's collection as the lectotype of the latter. The B isolectotype is fragmentary material that Schulz removed from the K specimen when he annotated it in 1930.

**42.** ***Heliophila trichinostyla*** E. Phillips, Ann. S. African Mus. 9: 112. 1913. Described from: "Van Rhynsdorp Division: Giftberg Range, 1–2,000 ft., September, Phillips 7577, 7621 in *Percy sladen Memorial Expedition to the Khamieberg, Giftberg, and Oliphant's River Mountains,* 1911." TYPE: SOUTH AFRICA. [Western Cape: West Coast, Matzikama], Vanrhynsdorp, Giftberg, *E. P. Phillips 7577* (Lectotype here designated: SAM [0003244-0]).

*Heliophila trichinostyla* is one of several morphological extremes of the highly variable *H. africana,* and it is characterized by the subglobose to clavate and sparsely to densely pubescent styles. It is sporadically distributed in the Western Cape (City of Cape Town and West Coast districts) and Northern Cape (Namakawa District). *Phillips 7577*, instead of *Phillips 7621* (B [100153831], K, and SAM [0003248-0]) syntype, is designated as the lectotype because it is more complete.

**43.** ***Leptormus caledonicus*** Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 9, No. 60. 1834–1835. Described from: "As montem 'Zwarteberg' apud thermas urbis 'Caledon' altit. III. Aug." TYPE: SOUTH AFRICA. [Western Cape: Overberg, Theewaterskloof], "Mt. Zwarteberg apud thermus urbis Caledon, 3 August [no year given], *C. F. Ecklon & C. L. P. Zeyher 60*" (Lectotype here designated: SAM [00280020]; Isolectotypes: GOET [002610 [image seen], M [0108067], PR, PRC [451617], PRE, W [0009164]).

Duplicates of the type collections of South African novelties described by Ecklon and Zeyher (1834–1835) are scattered in various herbaria, and many of their taxa are yet to be lectotypified. I have examined only six duplicates and one image of the type collection of *Leptormus caledonicus,* and the above lectotype is the most complete. The name is a synonym of *H. coronopifolia* L.

**44.** ***Leptormus tripartitus*** Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 9, No. 61. 1834–1835, *non Heliophila tripartita* Thunb., Prodr. Pl. Cap. 2: 108. 1800. Described from: "In locis arenosis (alt. I) apud 'Heerelongement' (Clanwilliam), Oct." TYPE: SOUTH AFRICA. [Western Cape: West Coast, Cederberg], Clanwilliam, Heerelongement, *C. F. Ecklon & C. L. P. Zeyher 61* (Lectotype here designated: S [1216070]; Isolectotypes: PRE [04050780, image seen], S [1216071], SAM [00280040]).

Plants from Clanwilliam district described by Ecklon and Zeyher (1834–1935) as *Leptormus tripartitus* have inflated stems. Upon the transfer of the name to *Heliophila*, both Steudel (1840) and Sonder (1846) renamed the species as *H. zeyheri* and *H. fistulosa*, respectively, to avoid the creation of a later homonym of *H. tripartita* Thunb., which is a synonym of *H. carnosa*.

**45.** ***Pachystylum glabrum*** Eckl. & Zeyh., Enum. Pl. Afric. Austral. 1: 13, No. 100. 1834; *Heliophila glabra* (Eckl. & Zeyh.) Steud., Nomencl. Bot., ed. 2, 1: 742. 1840. Described from: "In montium dorsis prope 'Potberg' (Caledon). Oct." TYPE: SOUTH AFRICA. [Western Cape: Overberg, Theewaterskloof], Caledon, Oct., *C. F. Ecklon & C. L. P. Zeyher 100* (Lectotype here designated: S [1216073]; Isolectotype: PRC [451620]).

The name needs lectotypification because the authors based their description on more than one duplicate of their collections. The name is generally recognized as a synonym of *Heliophila africana*.

**46.** ***Peltaria capensis*** L.f., Suppl. 296. 1781; *Heliophila capensis* (L.f.) C.A.Sm., Bull. Misc. Inform. Kew 1931: 155. 1931, *nom illeg*., *non* Kunze, Revis. Gen. Pl. 3(3): 5. 1898. TYPE: "*Habitat* in Cap. Bonae spei." *Anonymous s.n*. (Lectotype here designated: LINN 829.3; Isolectotype: LINN 829.4; images seen).

The name is a synonym of *Heliophila diffusa* (Thunb.) DC. subsp. *diffusa,* and the more complete of the two duplicates at LINN is designated as the lectotype.

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## APPENDIX
## INDEX TO NUMBERED COLLECTIONS

*J. P. H. Acocks 19750* (**3**).

*R. S. Adamson 4249* (**1**).

*Anonymous s.n.* [no date or collection number] (**46**).

*H. Bolus 6772* (**1**).

*W. J. Burchell 347* (**21**); *1334* (**30**); *1689* (**41**); *2742* (**38**); *3291* (**37**); *5496* (**31**); *7887* (**36**).

*A. Dieterlen 939* (**17**).

*J. F. Drège s.n.* [1838] (**33**).

*C. F. Ecklon 387*(**14**).

*C. F. Ecklon & C. L. P. Zeyher 51* (**12**); *55* (**13**); *60* (**43**); *61* (**44**); *100* (**45**); *85* (**24**); *s.n.* [no date] (**4**).

*E. Esterhuysen 18945* (**1**); *35515* (**1**).

*E. E. Galpin 3747* (**1**).

*F. M. Leighton s.n.* [1933] (**7**).

*W. T. McKen 7* (**34**).

*H. H. W. Pearson 7869* (**28**).

*A. Penther 2690* (**27**).

*E. P. Phillips 7577* (**42**).

*N. S. Pillans 7603* (**5**).

*Prior s.n.* [no initials or date] (**9**).

*Range 507* [no initials] (**29**).

*H. Rudatis 1497* (**26**).

*T. M. Salter 233/14* (**10**).

*Schäfer 515* [no initials] (**20**).

*F. R. R. Schlechter 2355* (**35**); *5578* (**1**); *5787* (**18**); *8229* (**25**); *8640* (**19**); *8732* (**8**); *8996* (**22**); *9324* (**32**); *9497* (**23**); *9783* (**1**); *10032* (**15**); *10050* (**16**); *10858* (**2**); *11229* (**11**).

*C. A. Smith 4466* (**40**).

*E. L. Stephens & R. Glover 8705* (**6**).

*G. van Niekerk 398* (**1**).

*J. M. Wood 4676* (**26**).

*C. L. P. Zeyher 43* (**39**).

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# SINOPSIS DEL GÉNERO *STERCULIA* (STERCULIOIDEAE, MALVACEAE) PARA MESOAMÉRICA, Y LA VALIDACIÓN TAXONÓMICA DE TRES ESPECIES

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**Abstract.** A synopsis of *Sterculia* (Sterculioideae, Malvaceae) is presented for the Mesoamerican region, including eight native and two introduced species. The names of three species are validated (*S. allenii*, *S. petenensis*, *S. ornatisepala*) and are described in detail, illustrated, and discussed with regard to their affinities. An identification key for the species, diagnoses, phenological data, and data on uses and distribution are presented, and all examined specimens are cited.

**Resumen.** Se presenta la sinopsis del género *Sterculia* (Sterculioideae, Malvaceae) para la región mesoamericana, que incluye ocho especies nativas y dos introducidas. Se validan los nombres de tres de sus especies (*S. allenii*, *S. petenensis y S. ornatisepala*), las que se describen a detalle, se ilustran y se comentan sus afinidades. Además, se presenta una clave de identificación; diagnósticos de las especies; y datos fenológicos, de usos y de distribución; y se citan los especímenes examinados.

**Keywords:** Centro América, Mesoamerica, Malvaceae, *Sterculia*, Sterculiaceae, taxonomía

El género *Sterculia* (Malvaceae) fue válidamente publicado por Linnaeus (1753), quien registró dos especies paleotropicales: *Sterculia balanghas* L. y *Sterculia foetida* L. (Taylor, 1989; Mondragón y Castillo, 2011). Subsecuentemente *S. foetida* fue designada como la especie tipo para el género (Green, 1929, citado por Taylor, 1989).

Este es un género con distribución pantropical, constituido por árboles de dosel superior o medio, raras veces arbustos del dosel inferior. Se han estimado entre 200 (Cristóbal, 2001; Fryxell, 2004; Mondragón y Castillo, 2011) y 300 (Taylor, 1989) especies. En el Viejo Mundo crecen fundamentalmente en los trópicos y subtrópicos, mientras que en el Nuevo Mundo se restringen principalmente a la región tropical, con 44 especies (34 spp. en Ulloa Ulloa et al., 2018 onwards)—42 endémicas y 2 cultivadas (*Sterculia foetida* L. y *Sterculia lanceolata* Cav., nativas de Asia [China, Laos, Myanmar, Tailandia y Vietnam]) (Rodríguez, 2015; Taylor, 1989; Ya et al., 2007). En tanto, en la región de Mesoamérica y acorde con esta sinopsis, se reportan 8 especies nativas (5 spp. en Ulloa Ulloa et al., 2018 onwards), y se adicionan las mismas especies cultivadas.

En América el rango de distribución incluye desde el sur de México hasta Paraguay, además en las islas del Caribe. Se ha documentado que crece en bosques húmedos, muy húmedos, así como en secos, tanto en las tierras bajas como en las zonas montañosas hasta los 1600 m de elevación (Taylor, 1989; Cristóbal, 2007).

La primera revisión taxonómica de *Sterculia* fue presentada por Schumann (1886), quien incluyó una clave para las especies, descripciones, dibujos, y sinonimia, y registró seis especies para Brasil y países vecinos. En la región mesoamericana los principales aportes al conocimiento de *Sterculia* se han presentado a través de algunas floras locales, tanto en la descripción de especies como en la contribución de nuevos especímenes, tal es el caso de la *Flora de Costa Rica* (Standley, 1937), la *Flora de Guatemala* (Standley y Steyermark, 1949), la *Flora de Panamá* (Robyns, 1960), la *Flora de Nicaragua* (Cristóbal, 2001) y el *Manual de Plantas de Costa Rica* (Rodríguez, 2015). Sin embargo, para el Neotrópico la revisión más significativa del género fue realizada por Elizabeth Louise Taylor (1989) con su tesis doctoral presentada ante la Universidad de Harvard. En esta revisión se describieron 43 especies, de las que 16 fueron propuestas como nuevas, aunque los nombres nunca fueron formalmente publicados; razón por la que luego Silva y Silva (2001) publicaron y formalizaron el nombre de una de sus especies, *Sterculia duckei* E.L. Taylor ex J.A.C. Silva & M.F. Silva. Posteriormente, Mondragón (2005, 2006) formalizó cuatro especies: *S. abbreviata* E.L. Taylor ex Mondragón, *S. amazonica* E.L. Taylor ex Mondragón, *S. steyermarkii* E.L. Taylor ex Mondragón y *S. multiovula* E.L. Taylor ex Mondragón; finalmente en la "Flora of the Venezuela Guayana" se estableció el nuevo epíteto *S. kayae* P.E. Berry, basado *S. parviflora* (Ducke) E.L. Taylor, un nombre ilegítimo (Cristóbal and Saunders, 2005).

Las angiospermas representan el primer grupo de organismos que han sido reclasificado a través de secuencias plastídicas rbcL y atpB (APG, 2016). En las actualizaciones del "Angiosperm Phylogeny Group" (http://www.mobot.org/MOBOT/Research/APweb/welcome.html) se encuentran la información acerca de los numerosos cambios a nivel de familias, subfamilias, tribus y géneros

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que se han sugeridos y realizados. La familia Sterculiaceae no ha sido exenta a estos cambios, a través de filogenias se formó el gran grupo Malvaceae, el cual es aceptado por la gran mayoría de los botánicos y agrupa a Malvaceae, Bombacaceae, Sterculiaceae y Tiliaceae (Alverson et al., 1998, 1999; Chen et al., 2016), respectivamente.

A pesar de que *Sterculia* se ha clasificado bajo la subfamilia Sterculioideae en un clado bien difereciado, tanto esta clasificación como probar la monofilia del género requieren mayor nivel de muestreo de especies, especialmente con la incorporación de taxones de la región neotropical que han sido escasamente investigados (APG, 2016; Wilkie et al., 2006. La clasificación subgenérica de *Sterculia* requiere ser ampliamente revisada (Dorr, 2004; Wilkie et al., 2006). Schumann (1895, 1905) hizo una clasificación infragenérica para *Sterculia* en la que propuso tres series con base en características de las hojas; las especies con hojas compuestas las ubicó en la serie *Digitatae* K. Schum., en tanto aquellas con hojas enteras y lobuladas las incluyó en las series *Integreae* y *Lobatae*, respectivamente; sin embargo, se ha considerado que esta es una clasificación artificial (Dorr, 2004; Wilkie et al., 2009). Luego, Chattaway (1938) separa *Sterculia* en dos grupos con base en la anatomía de la madera, pero ésto debe ser investigado con detalle (Wilkie et al., 2006).

## Tratamiento Taxónomico

Árboles hasta de 45(–50) m, o arboles pequeños a arbustos, algunas veces la base del tronco con gambas, las ramas engrosándose hacia los ápices, donde las hojas y las inflorescencias se agrupan. Funcionalmente monoicos, a veces aparentemente andromonoicos o dioicos; con ramitas terminales, hojas y estructuras reproductivas variadamente pubescentes, los tricomas simples y/o estrellados, sésiles o pediculados; con canales mucilaginosos en tallos y hojas; con estípulas laterales, aunque pronto deciduas, por lo general acompañadas por los primordios foliares. *Hojas* grandes, alternas y espiralmente arregladas, usualmente agrupadas en los extremos de las ramitas, simples, elípticas u ovadas, con frecuencia 3- a 5-lobuladas, o digitadamente compuestas, con uno o dos tamaños de tricomas estrellados por el envés; pecioladas, *pecíolos* por lo general con un pulvínulo diferenciado en la base y en el ápice, en las hojas compuestas los *peciólulos* son poco a conspicuamente diferenciados, articulados a la lámina; nervadura prominente, palmada a subpalmada (en hojas simples) o pinnada (en los folíolos de las hojas compuestas), margen generalmente entero. *Inflorescencias* ampliamente paniculadas o racemoso-paniculadas, axilares en ramitas subterminales, con frecuencias en nudos defoliados, que nacen de la ramita principal o de ramitas laterales poco desarrolladas, con numerosos tricomas glandulares rojos, gruesos en la base, multifloras, con brácteas y bractéolas tempranamente deciduas, raras veces subpersistentes. *Flores* actinomorfas, pediceladas, apétalas, unisexuales (aunque en ocasiones de apariencia bisexual) o a veces posiblemente bisexuales; perianto simple, *cáliz* sinsépalo, hasta 2 cm de largo, campanulado o urceolado, con 5 lóbulos basalmente connatos, el lado externo con tricomas estrellados y/o glandulares de diferentes tamaños, el lado interno con tricomas simples, estrellados, papilosos o vermiformes, a veces con un apéndice central. *Flores estaminadas* con un *andróforo* alargado, sigmoide o erecto, ensanchado o no en la base, filiforme distalmente, más corto que el cáliz, glabro a hirsuto, con tricomas papilosos, simples, estrellados o glandulares, con 10–15 *estambres*, sésiles o subsésiles, irregularmente agrupados en una cabezuela globosa, *anteras* subsésiles o filamentos escasamente desarrollados, bitecas, extrorsas, con dehiscencia longitudinal; con ovario rudimentario. *Flores pistiladas* (o bisexuales) con un *androginóforo* corto y curvo, generalmente erecto, ensanchado o no hacia la base, ensanchado hacia el ápice, más corto que el cáliz, glabro a hirsuto, con tricomas papilosos, simples, estrellados o glandulares; *pistilos* 5, apocárpicos, *ovario* unilocular, *lóculos* coherentes, con 2–22 óvulos por carpelo, tomentoso o piloso, estilo recurvado, tomentoso o piloso, *estigma* capitado a ligeramente 5-lobulado; estaminodios 10, 12 o 15, que rodean la base del ovario, anteras estipitadas, con el filamento claramente diferenciado, bitecas, extrorsas, con dehiscencia longitudinal. *Frutos* péndulos, compuestos de hasta 5 folículos (plurifolículos), folículos longitudinalmente obovoides, lisos, algunas veces rostrados, dehiscentes a lo largo de una sutura ventral, generalmente pardo o amarillo verdosos o rojo intensos al madurar, con pericarpio leñoso, lado externo velutino, densamente estrellado-puberulento, lado interno híspido, ferrugíneo, con tricomas rigidos, urticantes, simples o estrellados, rara vez glabro; *semillas* 1–22 por folículo, péndulas, negro azuladas, oblongo-elipsoides, no aladas, lisas, sin arilo, cotiledones carnosos, con abundante endoperma (Taylor, 1989; Cristóbal, 2001; Cristóbal and Saunders, 2005; Rodríguez, 2015).

## Clave para los Taxones de *Sterculia* en Mesoamérica

1a. Hojas digitadamente compuestas . . . . . . . . . . 2

1b. Hojas simples . . . . . . . . . . 7

2a. Flores estaminadas con el tubo del cáliz 5–6 mm de largo y 4–8(–11) mm de ancho, lóbulos 9–17 mm de largo y 3–7 mm de ancho, andróforo 10–14 mm de largo; flores pistiladas (o bisexuales) con el tubo del cáliz 6–7 mm de largo y 7–9 mm de ancho, lóbulos 10–15 mm de largo y 3–5 mm de ancho, androginóforo 9–10 mm de largo, óvulos 18–22 por carpelo; folículos glabros en el lado interno; hojas con peciólulos 0.1–0.5 mm de largo; especie cultivada . . . . . . . . . . *S. foetida*

2b. Flores estaminadas con el tubo del cáliz 1.5–5.0 mm de largo y de ancho, lóbulos 4.3–9.0(–11.0) mm de largo y 1.0–4.5 mm de ancho, andróforo 3–9 mm de largo; flores pistiladas (o bisexuales) con el tubo del cáliz 1–5 mm de largo y 1.2–4.0 mm de ancho, lóbulos 4.5–8.0 mm de largo y 1.7–4.0 mm de ancho, androginóforo 2.5–6.0 mm de largo, óvulos 6–12 por carpelo; folículos híspidos o velutinos en el lado interno (desconocidos en *S. petenensis*); hojas con peciólulos 0.2–4.3(–6) cm de largo; especies nativas . . . . . . . . . . 3

### Clave para los Taxones de *Sterculia* en Mesoamérica cont.

3a. Flores con el tubo del cáliz internamente ocluido por un anillo de tricomas densos, simples y estrellados, erectos y rígidos; inflorescencias con una yema apical persistente; peciólulos (1.4–)3.2–4.3(–6.0) cm de largo; arbustos o árboles, hasta 15(–25) m de altura . . . . . . *S. mexicana*

3b. Flores con el tubo del cáliz variadamente pubescente en el lado interno, pero nunca ocluido por un anillo de densos tricomas; inflorescencias sin una yema apical; peciólulos 0.2–3.0 cm de largo; árboles 10–45(–50) m de altura . . . . . . 4

4a. Hojas con el envés esparcida a densamente hirsuto, especialmente sobre las venas principales (notorio principalmente en hojas nuevas); foliolos terminales 12–17 cm de largo y 4–6 cm de ancho; pecíolos 7.3–22.5 cm de largo; peciólulos 0.2–1.0(–1.4) cm de largo; folículos lateralmente compresos, 2.3–3.8 cm de ancho . . . . . . *S. xolocotzii*

4a. Hojas con el envés glabro a glabrado, a veces con esparcidos e inconspicuos tricomas papilosos (aunque tempranamente deciduos y notorios sólo en hojas nuevas) o con diminutos tricomas estrellados sobre los nervios principales; folíolos terminales 5–45 cm de largo y 2.5–13.0 cm de ancho; pecíolos 3–60 cm de largo; peciólulos 0.2–3.0 cm de largo; folículos lateralmente ensanchados, 4–8 cm de ancho (desconocidos en *S. petenensis*) . . . . . . 5

5a. Lóbulos del cáliz con el lado interno apendiculado hacia la parte media, flores estaminadas con lóbulos 2–4 mm de ancho; flores pistiladas (o bisexuales) con androginóforo 5–6 mm de largo; inflorescencias (10–)25–41 cm de largo, con ejes secundarios hasta 10.5 cm de largo; hojas con 9–10 folíolos; México y Guatemala, 1000–1500 m. . . . . . . *S. ornatisepala*

5b. Lóbulos del cáliz con el lado interno sin un apéndice hacia la parte media, flores estaminadas con lóbulos 2.0–2.7 mm de ancho; flores pistiladas (o bisexuales) con androginóforo 3.0–4.3 mm de largo; inflorescencias 8–22 cm de largo, con ejes secundarios hasta 5 cm de largo; hojas con (5–)6–10 folíolos; Guatemala, Belice y Costa Rica, 0–500 m . . . . . . 6

6a. Flores pistiladas (o bisexuales) con 6–8 óvulos por carpelo; flores estaminadas con andróforo 3.0–3.5 mm de largo; botones florales con la base aguda a subtruncada; cáliz con el lado interno rosado a rojo; hojas con 7–10 folíolos, los terminales 5–45 cm de largo; pecíolos 3–60 cm de largo; árboles hasta 25(–33) m de altura; Costa Rica . . . . . . *S. allenii*

6b. Flores pistiladas (o bisexuales) con 10–11 óvulos por carpelo; flores estaminadas con andróforo 4.0–6.4 mm de largo; botones florales con la base truncada; cáliz con el lado interno verde amarillento, amarillo o crema; hojas con (5–)6–8 folíolos, los terminales 14.5–20.2 cm de largo; pecíolos 12.5–18.1 cm de largo; árboles hasta 45(–50) m de altura; Guatemala y Belice . . . . . . *S. petenensis*

7a. Flores con lóbulos del cáliz 4–6 mm de largo; folículos 5–7 cm de largo y 2.0–2.5 cm de ancho, distintivamente rojos al madurar; especie cultivada . . . . . . *S. lanceolata*

7b. Flores con lóbulos del cáliz 5–18 mm de largo; folículos 3.8–16.0 cm de largo y 2.7–13.0 cm de ancho, pardos o amarillo verdosos al madurar; especies nativas . . . . . . 8

8a. Hojas con la lámina 3- a 5-lobulada, con la base profundo-cordada (con los lóbulos basales frecuentemente traslapados), el envés, por lo general, denso-pubescente; pecíolos (5.0–)7.0–24.0(–33.5) cm de largo; cáliz con el tubo 5–18 mm de largo, lóbulos sin apéndice; estambres y estaminodios 15; árboles con gambas bien desarrolladas; bosque seco, húmedo y muy húmedo . . . . . . *S. apetala*

8b. Hojas con la lámina entera, no lobulada (excepto en las plantas juveniles de *S. recordiana*), con la base subcordada, obtusa a corto-cuneada (con los lóbulos basales nunca traslapados), el envés glabro, glabrado, glabrescente a esparcido-pubescente, con tricomas restringidos principalmente a los nervios principales; pecíolos 0.5–8.0 cm de largo (aunque hasta 18 cm de largo en plantas juveniles de *S. recordiana*, pero nótese que hojas lobuladas); cáliz con el tubo 1–4(–7) mm de largo, lóbulos con un apéndice central en el lado interno; estambres y estaminodios 8–10; árboles sin gambas o apenas diferenciadas; bosque húmedo y muy húmedo . . . . . . 9

9a. Ramitas y envés de las hojas glabras, sólo esparcido-puberulentas en estípulas relacionadas a las yemas terminales; hojas en individuos juveniles y adultos con la lámina siempre entera, el ápice sin un mucrón o, si este presente, entonces <1 mm, el haz ± plano; inflorescencias 3.1–9.0 cm de largo; cáliz con el lado interno que entremezcla tricomas estrellados y alargados, con tricomas vermiformes y cortos (<0.6 mm de largo), y tricomas papilosos . . . . . . *S. costaricana*

9b. Ramitas y envés de las hojas esparcido a densamente estrellado-pubescentes (aunque las plantas juveniles por lo general glabras o glabradas); hojas en individuos juveniles con lámina 3- a 5-lobulada, los adultos con la lámina entera, el ápice generalmente con mucrón hasta de 4 mm (aunque en ocasiones pronto-caedizo), el haz generalmente rugoso (al menos en individuos adultos); inflorescencias 2–20 cm de largo; cáliz con el lado interno que entremezcla tricomas estrellados y cortos, con tricomas vermiformes y alargados (hasta 1.2 mm de largo), y tricomas papilosos . . . . . . *S. recordiana*

**Sterculia allenii** E.L. Taylor ex Al. Rodr. & D. Santam., *sp. nov.* TIPO: COSTA RICA. Puntarenas: Osa, Sierpe, Aguabuena, Sector Oeste, Reserva Forestal Golfo Dulce, 08˚42'20"N, 83˚31'30"W, 50–150 m, 16 enero 1992 (fls), *R. Aguilar 827* (Holotipo: CR-159065; Isotipos: CR-1554878, MO). Fig. 1–2.

*Sterculia allenii* is distinguished by being a tree 15–25(–33) m tall with digitately compound leaves with leaflets 7–10, oblong-obovate, elliptical, or oblong-elliptic, glabrescent and with petiolules 0.2–3.0 cm long, petioles 3–60 cm long, calyx internally pink to red, staminate flowers with calyx lobes 5–9 mm long and 2.0–2.7 mm wide and androphore 3.0–3.5 mm long, pistillate (or bisexual) flowers with calyx lobes 4.5–7.0 mm long and 2.0–2.7 mm wide, androgynophore 3–4 mm long and carpels with 6–8 ovules, and its distribution restricted to Costa Rica.

Árbol 15–25(–33) m de altura y 25–40(–122) cm de diámetro, el tronco con gambas hasta al menos 5.5 m de altura, y algunas veces con raíces fúlcreas. *Ramitas terminales* 4–12 mm de diámetro (en ramitas foliadas), estrellado-puberulentas, tricomas pardo-ferrugíneos, en ocasiones glabrescentes. *Estípulas* 2.0–2.5 cm de largo y ca. 1.3 cm de ancho, ovadas a lanceoladas, largo-acuminadas, tempranamente deciduas (sólo presentes en las yemas terminales), el lado externo e interno con densa pubescencia estrellado-puberulenta, los tricomas pardo-ferrugíneos. *Hojas* digitadamente compuestas, rojizas cuando jóvenes (en material fresco); *pecíolos* 3–60 cm de largo, esparcidamente estrellado puberulentos a glabrescentes, con el pulvínulo basal y el apical débilmente diferenciados; *peciólulos* 0.2–3.0 cm de largo, articulados, con la base engrosada, glabrados, aunque esparcido-hirsútulos o estrellado puberulentos

Figura 1. *Sterculia allenii* E.L. Taylor ex Al. Rodr. & D. Santam. **A**, hábito; **B**, estípula; **C**, peciólulos; **D**, detalle de la ramita terminal; **E**, folículos; **F**, folículo abierto; **G**, inflorescencias; **H**, botón floral; **I**, flor pistilada (o bisexual); **J**, androginóforo; **K**, estambres de la flor pistilada (o bisexual); **L**, estigma de la flor pistilada (o bisexual); **M**, flor estaminada; **N**, andróforo; **O**, antera de la flor estaminada. A–D de *P. Riba 21* (CR); E de *N. Zamora et al. 1499* (CR); F de *L. J. Poveda et al. s.n.* (CR); G–L de *S. Lobo & A. Quesada 3234* (CR); M–O de *K. Thomsen 220* (CR).

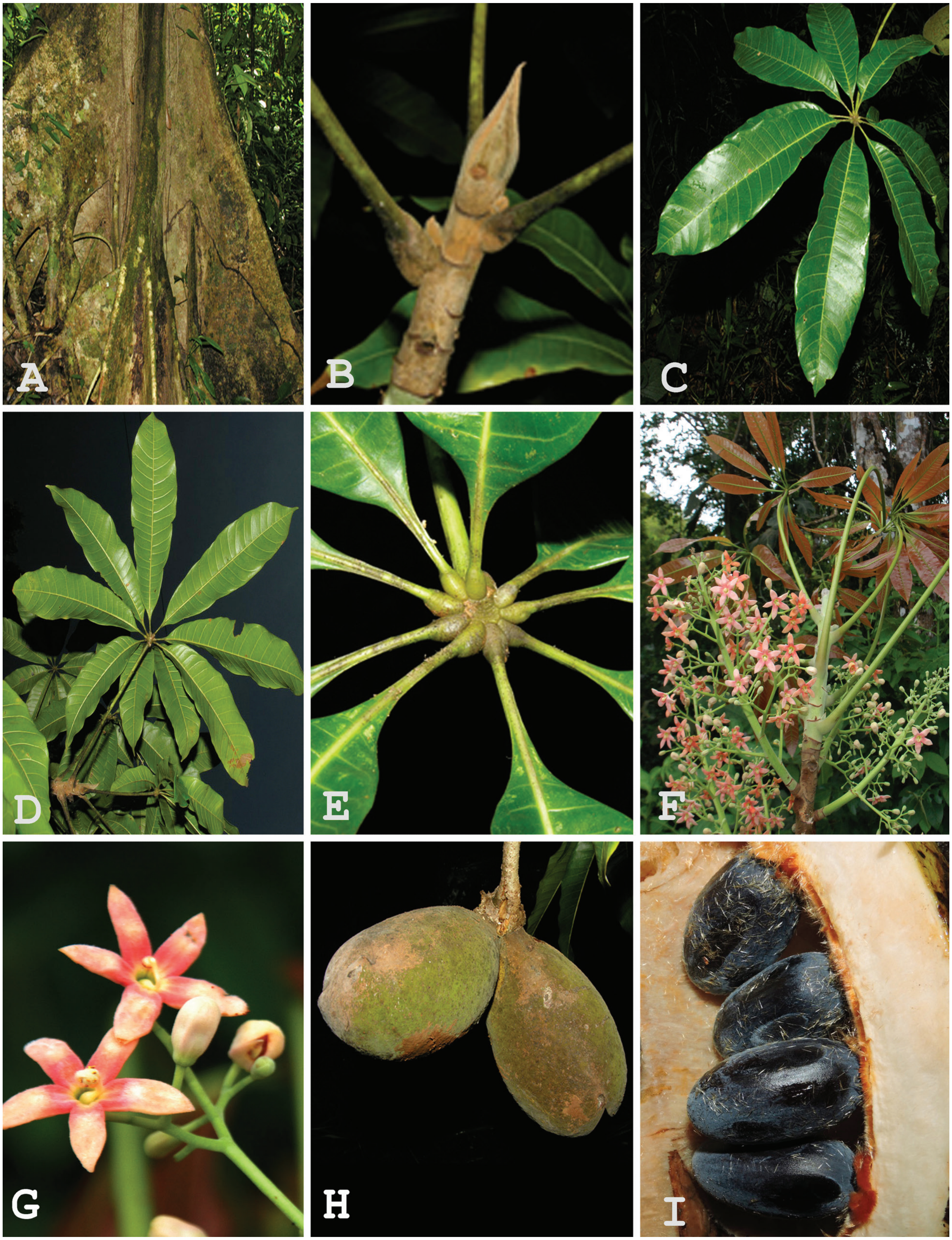


FIGURA 2. *Sterculia allenii* E.L. Taylor ex Al. Rodr. & D. Santam. **A**, base del tronco; **B**, ramita distal con yema terminal subtendida por la estípula; **C**, hoja en el lado adaxial; **D**, hoja en el lado abaxial; **E**, peciólulos; **F**, inflorescencias; **G**, flores pistiladas (o bisexuales); **H**, folículos, **I**, semillas. Fotografías A–E, H y I por R. Aguilar: A de *R. Aguilar 12149* (CR); B–E, H de *R. Aguilar 12305* (CR); I sin testigo; F y G por S. Lobo, de *S. Lobo & A. Quesada 3234* (CR).

en la base; folíolos 7–10, *lámina* oblongo-obovada, elíptica a oblongo-elíptica, los proximales 5.0–13.5 cm de largo y 1.0–4.5 cm de ancho, los terminales 5–45 cm de largo y 2.5–13.0 cm de ancho, verde-grisácea, pardo-grisácea a pardo-rojiza al secar, la base cuneada o atenuada, el ápice agudo a corto-acuminado, el margen entero y ligeramente ondulado, la nervadura pinnada, con 10–25 pares de nervios secundarios, los nervios terciarios conspicuamente reticulados, el haz y envés glabrescentes, con pardos, esparcidos e inconspicuos tricomas papilosos (notorio sólo en hojas nuevas), aunque tempranamente deciduos. *Inflorescencias* 8–22 cm de largo, en los extremos de las ramas, axilares, solitarias, generalmente en nudos defoliados, con 2–4 por ramita, en panículas erectas, sin una yema apical persistente, el *raquis* esparcidamente estrellado-puberulento, con tricomas pardo-ferrugíneos, los ejes secundarios hasta 5 cm de largo, los ejes terciarios, si presentes, hasta 3 cm de largo. Pedúnculos 1.5–4.0 cm de largo, esparcidamente estrellado-puberulentos, los tricomas pardo-ferrugíneos. *Botones florales* 2–5 mm de largo y 1.5–3.0 mm de ancho, con la base aguda a subtruncada, el ápice obtuso. Pedicelos 4–8 mm de largo, con una articulación cerca del 1/4 basal, esparcidamente estrellado-puberulentos, los tricomas pardo-ferrugíneos. *Cáliz* con 5 lóbulos erectos, oblongos a oblongo-lanceolados, el lado externo estrellado-velutino, con tricomas pardo-ferrugíneos, el lado interno rosado a rojo (en material fresco), densamente estrellado-viloso y que entremezcla papilas ferrugíneas o rojizas, sin un apéndice central, el tubo con el lado interno denso-papilado, sin tricomas, al menos en los 3/4 basales. *Flores estaminadas* con el cáliz 5–10 mm de largo, inciso por los lóbulos hasta 3/4 o más de su longitud, el tubo de 2–3 mm de largo y ancho, urceolado, los lóbulos 5–9 mm de largo y 2.0–2.7 mm de ancho; *andróforo* 3.0–3.5 mm de largo, sigmoide, con la base engrosada y densamente hirsútula, ca. de las 3/4 partes distales filiforme y esparcidamente hirsútula, que entremezcla tricomas simples y papilosos; estambres 6–15, subsésiles o con filamento hasta 0.2 mm de largo; tecas 0.25–0.50 mm de largo. Flores pistiladas (o bisexuales) con el cáliz 4–7 mm de largo, inciso por los lóbulos hasta 3/4 o más de su longitud, el tubo 1.5–2.0 mm de largo y ancho, urceolado, los lóbulos 4.5–7.0 mm de largo y 2.0–2.7 mm de ancho; androginóforo 3–4 mm de largo, por lo general curvado, con la base engrosada y denso-hirsútula, ca. 3/4 partes distales filiforme y denso-hirsútulo, que entremezcla tricomas simples y papilosos; estambres 10, filamento 0.5–1.0 mm de largo; tecas 0.20–0.35 mm de largo y 0.15–0.30 mm de ancho; ovario 1.0–1.5 mm de largo y de ancho globoso, densamente viloso; estilo 1–2 mm de largo, densamente viloso; estigma capitado, 5-lobado, rojo; óvulos 6–8 por carpelo. Folículos 6–12 cm de largo, 4–6 cm de ancho y 4–5 cm de alto (en fruto maduro aún no abierto), obovoides y lateralmente expandidos, pardos o amarillo verdosos al madurar, la base cuneada, el ápice con un rostro 5–7 mm de largo; pericarpio 5–9 mm de grosor, el lado externo velutino, densamente estrellado-puberulento, con tricomas pardo-ferrugíneos, el lado interno híspido y ferrugíneo; semillas 6–8 por folículo, ovoides, ca. 0.9 mm de largo y ca. 3 mm de diámetro (aunque aparentemente inmaduras).

**Nombres comunes:** pan de leche (Rodríguez, 2015).

**Usos:** las semillas tostadas son comestibles (León y Poveda, 2000).

**Distribución y hábitat:** endémica de Costa Rica, en la vertiente Pacífica entre Uvita y la Península de Osa, y al Norte de la Fila Costeña (Fila Retinto); 0–500 m de elevación. También ha sido observada en el Parque Nacional Carara (Jiménez Madrigal y Grayum, 2002) y en la vertiente Caribe en Baja Talamanca. Se encuentra en bosque muy húmedo, en vegetación principalmente primaria (Mapa 1).

**Fenología:** flores en enero, febrero y diciembre. Frutos en abril y setiembre.

**Etimología:** Taylor (1989) asigna el epíteto específico "allenii" en honor al botánico estadounidense Paul H. Allen (1911–1963), quien realizó importantes estudios de la flora de Costa Rica, especialmente en la región de Golfo Dulce, e incluso, es quien recolectó esta especie por primera vez en 1951.

**Especímenes adicionales examinados:** COSTA RICA. Puntarenas: Osa, Sierpe, Península de Osa, Reserva Forestal Golfo Dulce, camino a Rancho Quemado, 08˚41'00"N, 83˚32'00"W, 100 m, 20 mayo 2000 (estéril), *L. Acosta* et al. *1352* (CR); Osa, Sierpe, Aguabuena, alrededores, 08˚42'00"N, 83˚31'00"W, 50 m, 23 agosto 1992 (estéril), *R. Aguilar 1284* (CR-184826, CR-1568621, MO-2 cartulinas); Golfito, Puerto Jiménez, Agujas, Península de Osa, 08˚33'55"N, 83˚23'20"W, 1–10 m, 23 enero 1995 (fls), *R. Aguilar* et al. *3706* (CR-206434, CR-1586633); Rincón de Osa, camino a Rancho Quemado, cruce a Vaneguitas, finca de Isidro Guido, 08˚41'12"N, 83˚32'04"W, 155 m, 19 julio 2013 (estéril), *R. Aguilar* et al. *14480* (CR); forest hill above Palmar Norte, 500 m, 12 febrero 1951 (fls), *P. H. Allen 5863* (GH 2-cartulinas); Rancho Quemado, ca. 15 km Oeste de Rincón, en borde de bosque en fila antes de llegar a Rancho, 08˚42'00"N, 83˚33'00"W, 250 m, 11 enero 1993 (fls), *B. Hammel* et al. *18711* (CR, MO); Palmar, del colegio de Palmar Norte, 1.1 km al E sobre la carretera interamericana y 300 N sobre calle de lastre, sendero que cruza la quebrada Grande, 08˚58'7.7"N, 83˚26'37.3"W, 81 m, 15 diciembre 2011 (fls), *S. Lobo & A. Quesada 3234* (CR); Distrito Jiménez, Playa Llorona, 22 setiembre 1975 (frs), *L. J. Poveda* et al. *s.n.* (CR); Punta San José, Estación Biológica Marenco, 08˚41'00"N, 83˚42'00"W, 5–100 m, 20 enero 1999 (estéril), *P. Riba 21* (CR); Península de Osa, Dos Brazos de Río Tigre, trocha maderera que va al Parque Nacional Corcovado, 08˚31'55"N, 83˚24'35"W, 200–300 m, 27 abril 1999 (estéril), *A. Rodríguez* et al. *4820* (CR, MO); Agua Buena, 3.5 km W of Rincón, 08˚43'00"N, 83˚31'00"W, 300 m, 11 enero 1993 (fls), *K. Thomsen 220* (CR); Agua Buena, 3.5 km W of Rincón, 08˚43'00"N, 83˚31'00"W, 350 m, 19 noviembre 1992 (estéril), *K. Thomsen 674* (CR); Agua Buena, 3 km W of Rincón, 08˚42'00"N, 83˚30'00"W, 130 m, 19 abril 1993 (frs), *K. Thomsen 908* (CR); Distrito Bahía Ballena, Ballena, Hacienda Bahía, Uvita, 09˚09'40"N, 83˚43'30"W, 100 m, 14 abril 1988 (frs), *N. Zamora* et al. *1499* (CR-130258, CR-2930363, MO).

*Sterculia allenii* se distingue por ser un árbol 15–25(–33) m de altura, por sus hojas digitadas, con 7–10 folíolos oblongo-obovados, elípticos a oblongo-elípticos,

Mapa 1. Mapa de distribución en la región mesoamericana de *Sterculia allenii* E.L. Taylor ex Al. Rodr. & D. Santam., *sp. nov.*, *S. apetala* (Jacq.) H. Karst., *S. costaricana* Pittier, *S. foetida* L. y *S. lanceolata* Cav.

glabrescentes, y con peciólulos 0.2–3.0 cm de largo, por sus pecíolos 3–60 cm de largo, por sus flores con el cáliz rosado a rojo en el lado interno, las estaminadas con lóbulos 5–9 mm de largo y 2.0–2.7 mm de ancho y andróforo 3.0–3.5 mm de largo, las pistiladas (o bisexuales) con lóbulos 4.5–7.0 mm de largo y 2.0–2.7 mm de ancho, androginóforo 3–4 mm de largo y con 6–8 óvulos por carpelo, y por su distribución restringida a Costa Rica.

Esta entidad se podría confundir con *Sterculia mexicana*, una especie restringida al sur de México; sin embargo, esta última se diferencia debido a que sus inflorescencias tienen una yema apical persistente (vs. ausente), flores con el tubo del cáliz internamente ocluido por un anillo de densos tricomas rígidos y erectos (vs. nunca ocluidos por tricomas), por sus folículos lateralmente compresos (vs. no compresos) y por sus peciólulos comúnmente más alargados, (1.4–)3.2–4.3(–6.0) cm de largo (vs. 0.2–0.3 cm). También, se parece a *S. petenensis*, una especie endémica de la región del Petén, entre Guatemala y Belice, que se diferencia por presentar flores pistiladas (o bisexuales) con mayor número de óvulos por carpelo (10–12 vs. 6–8), las flores estaminadas con andróforo más alargado, 4.0–6.4 mm de largo (vs. 3.0–3.5 mm), el cáliz en material fresco con el lado interno verde amarillento, amarillo o crema (vs. rosado a rojo) y hojas comúnmente más pequeñas y con menor número de folíolos, ca. (5–)6–8 (vs. 7–10).

En el Neotrópico, las especies nativas de *Sterculia* con hojas digitadamente compuestas se restringen a la región mesoamericana, específicamente entre el sur de México y Costa Rica.

En el tratamiento de Sterculiaceae para el *Manual de Plantas de Costa Rica* (Rodríguez, 2015), esta entidad fue tratada como *Sterculia* sp. A.

***Sterculia apetala*** (Jacq.) H. Karst., *Fl. Columb*. 2: 35. 1862. Fig. 3.

Basionym: *Helicteres apetala* Jacq., *Enum. Syst. Pl*. 30. 1760. TIPO: COLOMBIA. Carthagenae: *N. J. Jacquin s.n*. (Holotipo: W; Isotipo: BM).

Synonyms: *Sterculia carthaginensis* Cav., Diss. 6: 353. 1788. *nom. illeg. superfl*. basado en el tipo de *Helicteres apetala* Jacq.

*Sterculia helicteres* Pers., Syn. Pl. 2: 240. 1806. *nom. illeg. superfl*. basado en el tipo de *Helicteres apetala* Jacq.

*Sterculia chicha* A. St.-Hil. ex Turpin, Dict. Sci. Nat. (ed. 2) 3: pl. 142, f. 1–2. 1817.

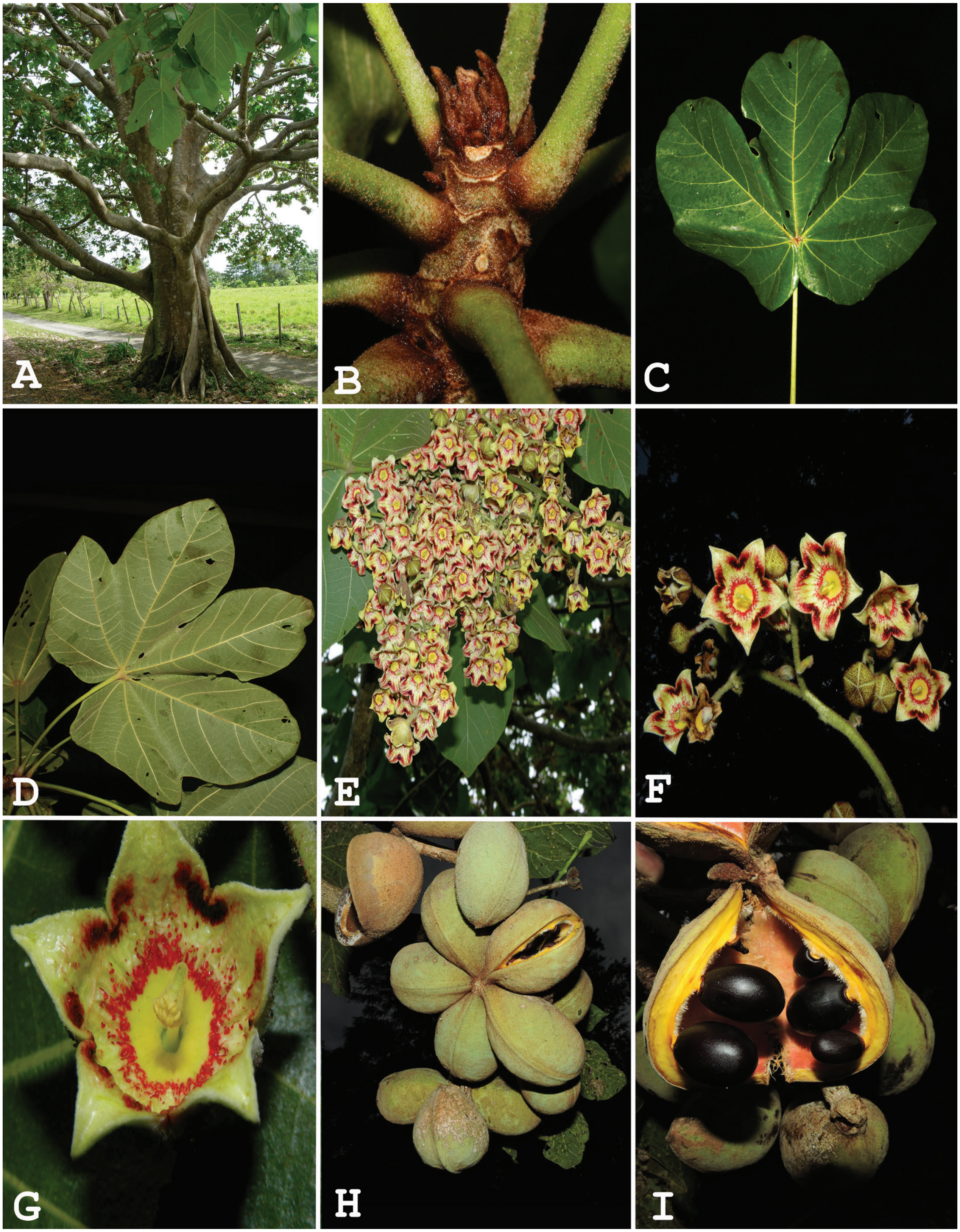


FIGURA 3. *Sterculia apetala* (Jacq.) H. Karst. **A**, tronco; **B**, ramita terminal; **C**, hoja en el lado adaxial; **D**, hoja en el lado abaxial; **E**, inflorescencias; **F**, **G**, flores estaminadas; **H**, folículos; **I**, folículo abierto con semillas expuestas. Fotografías A y E–I por R. Aguilar: A y E de *R. Aguilar 9032* (CR), F–I sin testigo; B–D por A. Rodríguez, de *A. Rodríguez 13018* (CR).

*Sterculia punctata* DC., Prodr. 1: 483. 1824.

*Chichaea acerifolia* C. Presl, Reliq. Haenk. 2(2): 141. 1835.

*Chichaea hilariana* C. Presl, Reliq. Haenk. 2: 141. 1835. *nom. illeg. superfl.* basado en el tipo de *Sterculia chicha* A. St.-Hil. ex Turpin

*Opsopea foetida* Raf., Sylva Tellur. 72. 1838. nom. illeg. superfl. basado en el tipo de *Helicteres apetala* Jacq.

*Sterculia acerifolia* (C. Presl) Hemsl., Biol. Cent.-Amer., Bot. 1(2): 126. 1879.

*Sterculia convoluta* St.-Lag., Ann. Soc. Bot. Lyon 7: 135. 1880. *nom. illeg. superfl.* basado en el tipo de *Helicteres apetala* Jacq.

*Clompanus apetalus* (Jacq.) Kuntze, Revis. Gen. Pl. 1: 78. 1891.

*Clompanus chichus* (A. St.-Hil. ex Turpin) Kuntze, Revis. Gen. Pl. 1: 78. 1891.

*Clompanus haenkeanus* Kuntze, Revis. Gen. Pl. 1: 78. 1891. *nom. illeg. superfl.* basado en el tipo de *Chichaea acerifolia* C. Presl

*Clompanus punctatus* (DC.) Kuntze, Revis. Gen. Pl. 1: 78. 1891.

*Sterculia elata* Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 211. 1922.

*Sterculia capitata* G. Karst. ex F. Seym., Phytologia Mem. 1: 195. 1980.

**Nombres comunes:** árbol del bellote (México), Bellota (México: Chiapas y Tabasco), Castaño (América Central), Guararé (Panamá), Pan de leche (Costa Rica), Panamá (Nicaragua, Costa Rica y Panamá), Petaca (México), Pepetaca (México), Temazcal (México), Tepedaca (México), Tuxtepec (México) (Taylor, 1989; Rodríguez, 2015).

**Usos:** es el árbol nacional de Panamá. La madera suave, blanca y de mediana calidad, se ha utilizado en construcciones rurales, en la elaboración de cajas, ataúdes y canoas, y como fuente de leña (Grijalva, 2006; Mondragón y Castillo, 2011; Pennington y Sarukhán, 1968; Taylor, 1989). La infusión de las hojas y de la corteza se ha empleado en el tratamiento de afecciones pulmonares y en molestias del catarro (Mondragón y Castillo, 2011); en Guatemala la corteza se ha usado contra la malaria (Standley y Steyermark, 1949; Taylor, 1989); las hojas machacadas y en cataplasma se han usado como antirreumáticas (Mondragón y Castillo, 2011), también en enfermedades inflamatorias y en dolores de cabeza (Standley, 1923; Taylor, 1989). Un jarabe obtenido a partir de las flores se ha usado como expectorante y antiasmático (Núñez, 1975); la corteza en remojo por tres días se toma para los riñones (Grijalva, 2006). Las semillas tostadas son comestibles, y molidas se han utilizado para dar sabor al chocolate o como sustituto del café. En forma de horchata se han utilizado para tratar el estreñimiento, y también como forraje para el ganado porcino (Cristóbal, 2001; González, 2002; Harmon, 2004; Grijalva, 2006; Mondragón y Castillo, 2011; Taylor, 1989). De la savia se obtiene una goma que se ha usada como sustituto de la goma de traganto, que comúnmente se ha usado como aditivo en la preparación de geles para el cabello, entre otros (Taylor, 1989).

**Distribución y hábitat:** México a Venezuela, Perú, Ecuador y Brasil, introducida y (a veces) naturalizada en Bolivia, Trinidad y Tobago, Guyana, Paraguay, Antillas y Bermudas; 0–1300(–1500) m de elevación. Se encuentra en bosque seco, húmedo y muy húmedo, en áreas perturbadas de vegetación riparia, bordes de manglares, potreros, orillas de playas y caminos (Mapa 1).

**Fenología:** flores entre enero y junio, y entre agosto y diciembre. Frutos entre enero y marzo, y entre junio y diciembre.

**Especímenes adicionales examinados:** MÉXICO. Chiapas: municipio Huixtla, a 6 km antes de Coronado, carretera de terracería El Retiro-Coronado, 600 m, 14 noviembre 1977 (frs), *J. I. Calzada* et al. *3810* (MO); 1 km al N de La Libertad, 60 m, 05 marzo 1983 (fls), *R. Fernández & Guadarrama-Zamudio 1389* (MO-2 cartulinas); municipio de Mazatlán, La Gloria, 0 m, 15 agosto 1984 (fls), *E. Ventura & E. López 188* (MO); municipio de Tapachula, Unión Miramar, 19 noviembre 1984 (fls), *E. Ventura & E. López 700* (MO); municipio Huehuetán, *E. Ventura & E. López 3367* (MO); municipio de Palenque, 50 m, 06 marzo 1983 (fls), *E. Ventura 19987* (MO); La Chacona, near Tuxtla Gutiérrez, 23 marzo 1958 (frs), *B.G. Schubert 1763* (A); Sabanilla, Finca El Carmen, 500 m, 15 julio 1983 (fls), *A. Shilom Ton 6355* (MO). Tabasco: 1 km al N de La Libertad, municipio La Libertad, 60 m, 05 marzo 1983 (fls), *R. Fernández 1389* (GH); Emiliano Zapata, 13 marzo 1968 (fls), *T. D. Pennington & J. Sarukhan 9545* (A); Heroica Cárdenas, 100 m, 04 marzo 1981 (fls), *M. Sousa* et al. *11689* (CR, MO); 1 km al NE de Libertad, municipio de Palenque, 50 m, 06 marzo 1983 (fls), *F. Ventura 19987* (GH); municipio Paraíso, 0 m, 19 julio 1983 (fls), *F. Ventura 20467* (MO). Veracruz: municipio San Andrés Tuxtla, 320 m, 21 enero 1974 (frs), *J. I. Calzada 01119* (MO); Carretera Santiago Tuxtla a Isla, ca. 8 km al SW de Santiago Tuxtla, 02 abril 1981 (fls), *D. H. Lorence 3137* (MO); vicinity Pixixiapan, 2.5 km W of Tibernal and 20 km SW of Santiago Tuxtla, 18°20'N, 95°26'W, 35 m, 05 abril 1983 (frs), *M. H. Nee & K. Taylor 26469* (MO); 1 km N of Rincon de Zapatero along Santiago Tuxtla-Isla highway, 18°23'N, 95°23'W, 100 m, 17 junio 1984 (fls), *S. L. Solheim 1603* (MO). GUATEMALA. Escuintla: Naranjo, abril 1892 (fls), *J. Donnell Smith 2545* (GH). Izabal: Antes de llegar a Brito, carretera hacia Taxisco, 300 m, 21 agosto 1993 (estéril), *J. J. Castillo & R. Luarca 1887* (GH); El Estor, El Boquerón bordering Río Sarco, about 6 km NE, 24 mayo 1975 (fls), *C. L. Lundell & E. Contreras 19351* (MO); Vicinity of Quirigua, 75–225 m, 15–31 mayo 1922 (estéril), *P. C. Standley 24542* (GH). Petén: Occupied clearing, La Libertad, 14 mayo 1933 (fls), *C. L. Lundell 3254* (A, GH); Retalhuleu. Between Retalhuleu and Nueva Linda, 120–220 m, 25 febrero 1941 (fls), *P. C. Standley 88499* (A). Sololá: San Lucas Tolimán, 11 marzo 1984 (fls), *E. Pöll 4022* (MO). EL SALVADOR. Ahuachapán: San Francisco Menéndez, El Corozo, Mariposario, zona baja “Los Sánchez,” 13°49'N, 89°59'W, 380 m, 07 febrero 2000 (fls), *J. M. Rosales 159* (MO). La Libertad: Municipio Antiguo Cuscatlan, “Laderas de La Laguna” inner slope of an ancient volcanic crater, 8 m SE de S.25, 13°40'N, 89°15'W, 830 m, 15 noviembre 1988 (fls), *R. Cruz s.n.* [Berendsohn 1211] (MO). La Unión: Laguna de Maquigüe, 60 m, 18 febrero 1922 (estéril), *P. C. Standley 20901* (GH). Isla Meanguera, sector El Peladero, 130 m, 03 diciembre 2006 (estéril), *A. Estrada* et al. *3902* (CR). San Salvador: mayo 1922 (fls), *S. Calderón 725* (GH). Santa Ana: San José Ingenio, Parque Nacional Montecristo, potrero buenavista, 14°25'N, 89°21'W, 1100 m, 05 octubre 2001 (fls), *V. M. Martínez 44* (MO). HONDURAS. Atlántida: vicinity of Tela, at sea level, 14 diciembre 1927–15 marzo 1928 (estéril), *P. C. Standley 54541* (A); Mountain Cangrejal, back of Ceiba, 06 agosto 1938 (bot fls), *T. G. Yuncker* et al. *8842* (GH, MO). Morazán: Río Guarabuquí, terrenos de los indios Xicaques de la Montaña de la Flor, 1800 m, 02 junio 1950 (estéril), *A. Molina* 3046 (GH); El Calvario, Tegucigalpa city, 04 abril 1980 (fls), *A. Molina 31806* (MO); cerca de aldea Yaguasire, 9 km S. de Tegucigalpa, 900 m, 07 febrero 1982 (estéril), *R. Perdomo 266* (MO); cercanías de la Aldea Yaguasire, 8 km S de Tegucigalpa, 900 m, 07 enero 1982 (estéril), *J. L. Segovia 190* (MO); Tegucigalpa, 936 m, 05 febrero 1945 (fls), *J. Valerio 3756* (GH, MO); San Buenaventura y Sauce, 1300 m, 16 febrero 1949 (fls), *L. O. Williams & A. Molina 15573* (GH). Lempira: Gracias, 13 mayo 1987 (fls), *S. Blackmore & M. Chorley 3916* (MO). NICARAGUA. Boaco: 1 km al W de San Lorenzo, “Río de Plato,” 12°22'N, 85°40'W, 300 m, 11 noviembre 1982 (frs inm), *P. P. Moreno 18580* (MO). Carazo: quebrada La Chota, afluente del Río Escalante, ca 7 km al NE de la estación biológica Chococenter, 11°35'05"N, 86°09'20"W, 100 m, 19 marzo 1983 (fls), *A. Grijalva 2426* (MO); Hacienda Veracruz, ca. 5 km al noroeste del Astillero, 11°33'30"N, 86°13'W, 10 m, 13 febrero 1987 (fls), *A. Grijalva 5259* (GH); Refugio de Vida Silvestre Chococente, 11°30'N, 86°07'W, 20–80 m, 14 abril 1984 (fls), *J. C. Sandino 4990* (GH, MO); km 22.5 Carretera Nueva a León, Finca La Polvosa, UCA, 12°12'N, 86°25'W, 60–80 m, 06 marzo 1982 (frs), *J. C. Sandino 2450* (MO). Chontales: 4 km NNE of highway along road to Comalapa, 12°12'26"N, 85°32'17"W, 205 m, 16 mayo 2011 (fls), *W. D. Stevens 31629* (MO); 3.5 km S of Juigalpa-La Libertad road (from 1.4 km E of Río Mayales bridge at Juigalpa) along road to Piedras Grandes #2, around vado of N-flowing stream, 12°07'09"N, 85°19'51"W, 75 m, 09 noviembre 2011 (frs), *W. D. Stevens 32383* (MO). Chinandega: Municipio de Cinco Pinos, comunidad El Jícaro, 13°11'06"N, 86°51'39"W, 250 m, 06 mayo 2004 (frs), *I. Coronado* et al. *667* (MO); municipio El Viejo, Reserva Natural Cosigüina, frente a la finca los Placeres, 13°01'N, 87°33'W, 0–600 m, 27 marzo 2001 (fls), *R. Rueda* et al. *15963* (MO). Estelí: San Diego, 3 km al NE de Condega, 13°22'N, 86°22'W, 560 m, 10 marzo 1984 (fls), *P. P. Moreno 23524* (GH, MO). Granada: Granada, 17 febrero 1903 (fls), *C. F. Baker 2441* (AMES, GH); Puerto Asese, 5 km al sureste de Granada, y Las Isletas de Granada, 40 m, 06 noviembre 1979 (frs), *A. Grijalva & M. Araquistain 712* (MO). León: San Antonio, ca. 6 km SE de Nagarote, 12°10'25"N, 86°30'40"W, 100 m, 15 noviembre 1982 (frs inm), *A. Grijalva P. & M. V. de Grijalva 1738* (MO); Reparto La Providencia, 12°26'N, 86°53'W, 01 abril 2000 (frs), *R. Rueda & D. Paguaga 13236* (MO); ca. 2.1 km NE of El Transito on road to Hwy. 12, 12°03'N, 86°41'W, 50 m, 10 diciembre 1977 (frs), *W. D. Stevens 5465* (MO). Madriz: Km 192 on Panamerican Highway, 2 km SE of entrance to Palacagüina, 13°25'08"N 86°23'59"W, 520 m, 08 enero 2009 (fls), *W. D. Stevens* et al. *27615* (MO). Managua: Along Route 10 between Managua and Masachapa, 14.8 miles south of junction with Route 12, 100 m, 18 agosto 1977 (frs), *T. Croat 43747* (CR); municipio San Rafael del Sur, reserva Natura, 11°52'N, 86°30'W, 59 m, 19 diciembre 2010 (frs), *R. Rueda* et al. *18241* (MO); municipio de Nandaime, comarca Aguas Agrias, Reserva Natural Laguna de Mecatepe y río Manares, finca Las Plazuelas, río Brujo, 11°47'N, 85°58'W, 50 m, 14 mayo 2011 (fls), *R. Rueda* et al. *18566* (MO); Esquipulas, 230 m, 15 noviembre 1976 (fls, frs), *D. Neill 1270* (MO); Between Hda. El Paraíso and old Managua-Tipitapa Hwy (Hwy 1), 12°08'30"N, 86°07'00"W, 40–45 m, 27 julio 1978 (frs. inm.), *W. D. Stevens* et al. *9512* (MO). Rivas: Puente de Ochomogo, km 80 carretera sur, sobre el camino a San Rafael, 11°39'N, 85°57'W, 50 m, 25 enero 1984 (fls), *P. P. Moreno & W. D. Stevens 22872* (GH, MO); San Jorge, adjacent *Musa* plantations and beach of Lago de Nicaragua, 11°28'N, 85°47'W, 30–50 m, 17 setiembre 1983 (frs), *M. Nee 28212* (GH, MO); Isla Ometepe, Volcán Concepción, 11°34'N, 85°38'30"W, 100–300 m, 13 febrero 1984 (frs), *W. Robleto 242* (GH, MO); along road SE from San Juan del Sur, 3–4 km NW of Río La Flor, Playa El Coco, Quebrada El Coco, and small peak S of quebrada, 11°09'N, 85°47'W, 0–95 m, 11 setiembre 1987 (frs inm), *W. D. Stevens 3722* (MO). Río San Juan: El Carmen, 2 km al N de San Miguelito, 11°25'N, 85°53'W, 35–40 m, 01 marzo 1984 (fls), *P. P. Moreno 23469* (GH, MO). Zelaya: Estación Experimental El Recreo, 12°09'N, 84°17'W, 15 m, 12 febrero 1985 (fls), *D. E. Ríos 320* (MO). COSTA RICA. Guanacaste: Parque Nacional Santa Rosa, Alrededor de la entrada a Nancite y playa Naranjo, 10°48'30"N, 85°40'55"W, 10 m, 26 abril 2000 (fls), *L. Acosta* et al. *944* (MO); Parque Nacional Santa Rosa, 12–15 km west of the Interamerican Highway, 600 ft [70 m], 27 febrero 1978 (fls), *F. Almeda & K. Nakai 3985* (MO); Comelco property near Bagaces, 17 febrero 1970 (fls), *K. S. Bawa 187* (MO); Parque Nacional Santa Rosa, 0–300 m, 7–9 mayo 1982 (fls), *K. Barringer* et al. *2858* (CR); entre Cascajal y Los Loros, 16–26 febrero 1937 (fls), *A. M. Brenes 20493* (CR); Rafael Lucas Rodríguez Reserve, Palo Verde, 10°21'N, 85°22'W, 20 m, 29–30 enero 1982 (fls, frs), *W. Burger 11356* (CR); Parque Nacional Palo Verde, sendero Guayacán, 10°21'N, 85°20'W, 10–150 m, 22 diciembre 1991 (frs), *U. Chavarría 456* (MO); Camino Hato Viejo, Parque Nacional Palo Verde, 10°23'N, 85°23'W, 10 m, 24 diciembre 1991 (fls), *U. Chavarría 458* (CR, MO); Santa Rosa National Park, 317 m, 1 marzo 1976 (estéril), *R. Chazdon 76–207* (CR); Between Murciélago and Cuajiniquil, Península de Santa Elena, 30–160 m, 26 enero 1983 (fls, fr), *G. Davidse* et al. *23263* (CR); La Cruz, Parque

Nacional Santa Rosa, Cuenca de Santa Elena, sector Junquillal, 10˚54'35"N, 85˚48'08"W, 10 m, 10 enero 1997 (fls), *R. Espinoza 1653* (CR-231540, CR-3107890); OTS research area B, Stewart property, 28 km north Cañas, 100 m, 29 setiembre 1969 (fls), *G. W. Frankie 284a* (MO); Parque Nacional Santa Rosa, Playa Naranjito, 1 m, 07 mayo 1982 (fls), *J. Gómez-Laurito 8476* (CR); Parque Nacional Santa Rosa, road to Estero Real, 0–300 m, 09 marzo 1982 (fls), *M. J. Huft* et al. *2105* (MO); Sardinal, 05 marzo 1951 (estéril), *J. León 3127* (CR); Santa Rosa National Park, beach and near it playa Naranjo, 10˚48'N, 85˚41'W, 23 junio 1977 (frs), *R. Liesner & R. Lockwood 2494* (MO); Liberia, Parque Nacional Santa Rosa, Murciélago, Cerro Murciélago, Sitio El Hachal, 10˚55'20"N, 84˚44'15"W, 150 m, 16 febrero 1994 (fls), *J. F. Morales 2379* (CR); La Cruz, Cuenca de Santa Elena, Loma Castilla, falda NE, cerca playa Cuajiniquil, 10˚56'10"N, 85˚42'33"W, 5–20 m, 03 abril 2001 (fls), *J. F. Morales 7924* (CR-244461, CR-3796699); La Cruz, Santa Elena, Península de Santa Elena, Playa Blanca, 10˚56'16"N, 85˚51'32"W, 1 m, 26 enero 2012 (estéril), *J. F. Morales 20659* (CR); Parque Nacional Santa Rosa, Naranjo, 3 m, 11 agosto 1972 (estéril), *L. J. Poveda 237* (CR); La Cruz, Parque Nacional Santa Rosa, Península de Santa Elena, Murciélago, Playa Blanca, 10˚55'20"N, 85˚44'15"W, 10 m, 15 febrero 1994 (fls, frs), *F. Quesada 90* (CR, MO); Santa Rosa National Park, 317 m, 23 febrero 1976 (estéril), *G. Scholfield 76–115* (CR); Bagaces, seasonal swamp, dry now, OTS Area A3 site Comelco, 31 marzo 1972 (fls), *D. E. Stone & P. Opler 3159* (GH, MO); La Cruz, Parque Nacional Santa Rosa, Golfo de Papagayo, Península de Santa Elena, Hacienda Santa Elena, parte baja del río Potrero Grande, 10˚50'51"N, 85˚46'40"W, 0 m, 28 enero 1998 (fls), *N. Zamora* et al. *2672* (CR-236304, CR-2825046, MO). Heredia: Sarapiquí, OET La Selva, Sendero SOC 1520 m, derecha, 17 setiembre 2009 (fls, frs), *O. Vargas* et al. *2089* (LSCR). Limón: Pocora, 100 m, 26 enero 1983 (estéril), *M. Wiemann 57* (CR). Puntarenas: Aguirre, Quepos, P. N. Manuel Antonio, de playa Manuel Antonio a Punta Catedral, orilla de playa y bosques, 09˚22'46"N, 84˚08'50"W, 0–100 m, 08 noviembre 2006 (estéril), *L. Acosta* et al. *6098* (CR); Golfito, Península de Osa, Puerto Jiménez, Playa Carbonera, 08˚24'30"N, 83˚17'00"W, 1 m, 08 enero 1994 (frs), *R. Aguilar* et al. *2995* (CR-193433, CR-1582233); Golfito, Península de Osa, Parque Nacional Corcovado, Río Claro, Estación Sirena, 08˚28'50"N, 83˚35'30"W, 10 m, 10 octubre 1994 (fls), *R. Aguilar 3606* (CR); Golfito, cuenca de Coto Colorado, río Oro, 08˚38'10"N, 83˚05'10"W, 400 m, 28 junio 1995 (fls), *R. Aguilar 4138* (CR); Osa, Palmar Norte, 30 m, 16 noviembre 1952 (fls), *P. H. Allen 6637* (GH); Puntarenas, enero 1909 (fls), *A. Biolley 17406* (GH); vicinity of Cascajal (25 km SE of Puntarenas), 30–100 m, 06 julio 1949 (frs. inm.), *R. W. Holm & H. H. Iltis 277a* (A); Reserva Biológica Carara, cerca de la carretera costanera Sur, límite Oeste, 09˚47'00"N, 84˚36'25"W, 50 m, 20 abril 1993 (fls), *Q. Jiménez* et al. *1284* (CR, MO); Garabito, cuenca del Tárcoles, camino entre Puntarenas y Jacó, 09˚49'00"N, 84˚35'55"W, 0–100 m, 31 diciembre 2002 (frs), *R. Kriebel & J. Larraguivel 2173* (CR-264355, CR-3906853); Esparza, Zona Protectora Río Tivívez, cuenca Jesús María, Finca El Silencio, 09˚53'26"N, 84˚43'10"W, 100 m, 28 noviembre 2001 (fls), *F. Murillo* et al. *185* (CR-261763, CR-3965158); Quepos, Garabito, cercanías a manglares, 09˚27'00"N, 84˚19'50"W, 0–10 m, 29 enero 1998 (frs), *O. Valverde 691* (CR); Golfito, Jiménez, Boca del río Platanares, alrededores del estero Conte, 08˚32'07"N, 83˚17'44"W, 1 m, 18 mayo 2010 (frs), *A. Rodríguez & C. Olivares 13018* (CR); Osa, Cortés, Puerto Cortés, a orilla del camino que lleva a estero Tagual, 08˚58'35"N, 83˚33'21"W, 1 m, 18 agosto 2005 (fls), *D. Santamaría & M. Moraga 2899* (CR); Puntarenas, Isla San Lucas, Playa El Coco, 09˚56'51"N, 84˚54'00"W, 1 m, 18 marzo 2005 (frs), *D. Santamaría & F. Morales 1067* (CR). PANAMÁ. Chiriquí: Vicinity of San Felix, 100 m, 29 agosto 1946 (fls), *P. H. Allen 3656* (MO). Burica Peninsula, Quebrada Manzanillo, 9 km southsouthwest of Puerto Armuelles, 03 marzo 1973 (fls), *P. Busey 732* (MO-2 cartulinas); Distrito Guanabano, Burica Peninsula, disturbed areas along Quebrada Quanabano, 0–100 m, 03 marzo 1973 (frs), *T. Croat 22527* (MO). Coclé: 1–5 mi, S Anton along old road to coast, 08 diciembre 1965 (estéril), *E. L. Tyson & K. Blum 2560* (GH, MO). Los Santos: Vicinity of Santa Ana Abajo, 5–10 m, 21 noviembre 1966 (estéril), *S. T. McDaniel 8057* (MO). Panamá: Victoria Fill, near Miraflores Locks, 06–14 marzo 1939 (fls), *P. H. Allen 1720* (MO); Barro Colorado Island, south dock, 15 setiembre 1968 (frs inm), *T. Croat 6083* (MO); Barro Colorado Island, Laboratory clearing, 21 enero 1969 (fls., frs.), *T. Croat 7402* (MO); Barro Colorado Island, North edge Slothia Isle, 11 febrero 1969 (fls), *T. Croat 7889* (MO); Barro Colorado Island, Fuertes Cove, 24 febrero 1969 (fls), *T. Croat 8141* (MO); Barro Colorado Island, North edge of Slothia Island, 06 febrero 1971 (fls), *T. Croat 13244* (MO); roadside near Panamá Viejo, 18 enero 1935 (estéril), *C. W. Dodge 17520* (MO); vicinity of El Llano, 14–19 octubre 1962 (frs inm), *J. A. Duke 5820* (MO); Parque Metropolitano, camino de La Amistad, 08˚59'43"N, 79˚32'56"W, 17 enero 2007 (fls), *C. Galdames 5722* (MO); Barro Colorado Island, sin fecha (fls), *S. Aviles 101* (MO); 8 km W from the town site of Balboa in an area called Rodman Tank Farm on the Pacific slope of Panama, 15 febrero 1978 (frs), *P. A. Garber 6* (MO); Arraijan, cerro San Silvestre, 08 junio 1971 (frs inm), *E. A. Lao 105* (MO); zona del Canal, 05 febrero 1975 (fls), *E. León 11* (MO); Madden Forest Preserve, along Las Cruces Trail and highway, 08 abril 1969 (estéril), *W. H. Lewis et al. 5362* (MO); río Pacora, ca. 15 miles west of Chepo, 28 diciembre 1969 (estéril), *S. McDaniel & E. L. Tyson 12591* (MO); pasture along old road to Bique, 5 km SW of Arraijan, 20–40 m, 31 octubre 1973 (frs), *M. Nee 7704* (GH, MO-2 cartulinas); Canal Zone, edge of secondary tropical moist forest 1.5 km W of Gamboa, near airfield, 40 m, 27 enero 1974 (fls), *M. Nee 9479* (GH, MO); Barro Colorado Island. Above E shore of Dump Cove, 03 enero 1967 (estéril), *J. R. Oppenheimer 67-1-3-1630* (MO-2 cartulinas); afueras de San Carlos, 22 noviembre 1975 (fls), *S. Pons 35* (MO); Pantera or Tigre Islands, out in Gatun Lake, 30 enero 1982 (fls), *R. J. Schmalzel 338* (MO);

Balboa, Canal Zone, noviembre 1923–enero 1924 (frs), *P. C. Standley 27160* (A, MO); Balboa, Canal Zone, noviembre 1923–enero 1924 (fls), *P. C. Standley 30856* (A); Barro Colorado Island, Donato Trail, 04 enero 1932 (estéril), *R. H. Wetmore & E. C. Abbe 114* (MO-2 cartulinas); Cocoli Island, vicinity of Miraflores Lake, 14 febrero 1940 (fls), *P. White 281* (GH, MO); Barro Colorado Island, on shore near Orchid Island, febrero-marzo 1931 (estéril), *C. L. Wilson 97* (MO); Barro Colorado Island, Canal Zone, Donato trail, 04 enero 1932 (estéril), *R. H. Woodworth & E. C. Abbe 114* (A, GH); Barro Colorado Island, Canal Zone, shore of Miller trail, 22 febrero 1932 (fls), *R. H. Woodworth & P. A. Vestal 651* (A).

*Sterculia apetala* se reconoce entre sus congéneres por sus hojas simples y por la siguiente combinación de caracteres: láminas foliares 3- a 5-lobulada (en individuos juveniles y adultos), con la base profundamente cordada (con los lóbulos basales a menudo traslapados), el envés esparcida a denso-pubescente y por sus flores conspicuamente más grandes, con el lado interno del cáliz glabro, aunque con un amplio anillo de densas papilas alrededor del andróforo y androginóforo, y con lóbulos carentes de un apéndice hacia la parte media. Además, se caracteriza por ser un árbol (3–)8–40(–50) m de altura, con gambas hasta de 1.5 m de altura, deciduo, por sus hojas con pecíolos (5.0–)7.0–24.0(–33.5) cm de largo, con la nervadura palmada, y el margen entero y leve-ondulado, por sus inflorescencias paniculadas, (4.0–)10.0–22.0(–34.5) cm de largo, por sus flores con el cáliz internamente verde-crema a verde amarillento, con manchas o puntos rojos a púrpura (en material fresco), las estaminadas con el tubo del cáliz 6–17 mm de largo y 12–21 mm de ancho, con los lóbulos 6–13 mm de largo y (3.0–)4.5–11.0 mm de ancho y con andróforo 6–14 mm de largo, las flores pistiladas (o bisexuales) con el tubo del cáliz 5–18 mm de largo y 12–25 mm de ancho, y con lóbulos 6–15 mm de largo y 4–12 mm de ancho, el androginóforo 4.5–7 mm de largo, y por sus folículos lateralmente expandidos, 3.8–16.0 cm de largo, 2.7–13.0 cm de ancho y 2.8–8.5 cm de alto (en fruto maduro aún no abierto), pardos o amarillo verdosos al madurar, internamente híspidos.

En esta especie se han reconocido dos variedades *S. apetala* var. *apetala* y *S. apetala* var. *elata* (Ducke) E.L. Taylor ex Brako & Zarucchi. El material mesoamericano pertenece a *Sterculia apetala* var. *apetala*, que ocupa todo el rango geográfico de la especie, excepto Ecuador, Perú y Brasil, mientras que *S. apetala* var. *elata* es una entidad que se restringe a la región del amazonía en Colombia, Ecuador, Perú y Brasil.

***Sterculia costaricana*** Pittier, Contr. U. S. Natl. Herb. 13: 449. 1912. TIPO: COSTA RICA. Las Delicias del Reventazon, plains of Santa Clara, ca. 40 m, September 1901 (fls), *H. Pittier 16172* (Holotipo: US-716130; Isotipo: CR, US-578036). Fig. 4.

Synonym: *Sterculia glauca* A. H. Gentry, Ann. Missouri Bot. Gard. 63(2): 370. 1976.

**Nombres comunes:** Burío, Papa, Ratón papa (Costa Rica) (Rodríguez, 2015).

**Usos:** la madera se usa en carpintería general, construcción interna, ebanistería embalaje, cajas, cajones, gabinetes, juguetes, utensilios domésticos y otros (Flores-Vindas y Obando-Vargas, 2014).

**Distribución y hábitat:** Costa Rica y Panamá; 0–450 m de elevación. Se encuentra en bosque húmedo y muy húmedo, en vegetación primaria, secundaria y bordes de bosque (Mapa 1).

**Fenología:** flores entre enero y marzo, además en setiembre y diciembre (Taylor, 1989). Frutos entre enero y marzo, además en junio y octubre.

**Especímenes adicionales examinados:** COSTA RICA. Cartago: Turrialba, Parque Nacional Barbilla, cuenca del Matina, sendero principal Río Dantas, alrededores de la Estación, 09°58'20"N, 83°27'10"W, 300–400 m, 15 febrero 2001 (frs), *E. Mora & E. Rojas 1797* (CR-230551, CR-3162108, MO). Limón: Limón, cuenca del Estrella, 09°40'30"N, 83°00'20"W, 150–200 m, 28 junio 2000 (frs), *L. Acosta* et al. *1946* (CR-252678, CR-3424319); Limón, cuenca del Estrella, Valle de las Rosas, riberas del río Cerere, 09°40'30"N, 83°00'20"W, 100–200 m, 01 febrero 2003 (fls), *J. González et al. 2850* (CR-252651, CR-3834517); Limón, cuenca del Estrella, camino de Pandora a Vesta, en los márgenes del río Suruy, 09°43'41"N, 83°02'21"W, 60 m, 18 febrero 2003 (fls), *J. González et al. 2970* (CR-259088, CR-3837724); Limón, Valle la Estrella, camino a Buena Vista, 09°47'55"N, 82°57'11"W, 325 m, 19 febrero 2003 (fls, frs), *L. González et al. 1954* (CR-252427, CR-3821087); Sixaola, Forests between headwaters of Quebrada Mata de Limón and ("Crique Azul") Quebrada Quiebra Caña, Finca Anai, 09°33'36"N, 82°39'36"W, 20–40 m, 27 enero 1987 (fls, frs), *M. H. Grayum et al. 8012* (CR-134751, CR-2913709, MO); Siquirres, río Siquirres, ca. 6 km al Suroeste de Siquirres, 10°05'20"N, 83°32'30"W, 150 m, 15 febrero 1991 (fls, frs), *B. Hammel et al. 18129* (CR, MO-2 cartulinas); cerros al sur del camino entre Puerto Viejo y Manzanillo por un camino nuevo hacia Bribri, 09°37'20"N, 82°41'20"W, 100 m, 18 enero 1992 (bot fls), *B. Hammel 18389* (MO); steep hillside along Hotel Creek, west Puerto Viejo, 150 m, 26 octubre 1976 (frs), *G. Hartshorn 1852* (CR, MO); Cordillera de Talamanca, Matina, Intersección de Río Barbilla y Quebrada Cañabral, por fila al norte, 10°01'N, 83°24'W, 100–200, 11 octubre 1988 (estéril), *G. Herrera 2164* (MO); Limón, Reserva Biológica Hitoy Cerere, Valle del río Estrella, margen izquierdo del río Hitoy, Lomas El Níspero, 09°40'10"N, 83°01'20"W, 150 m, 06 febrero 1989 (fls), *G. Herrera & A. Chacón 2348* (CR-272677, CR-1600086, MO); Limón, Talamanca, Cahuita, 3 enero 1970 (estéril), *L. R. Holdridge 5219A* (CR); Limón, cuenca del Bananito, Fila Matama, Cerro Muchilla, falda NW, río Bananito Lodge, 09°49'30"N, 83°03'50"W, 50–100 m, 24 marzo 2001 (fls), *J. F. Morales 7712* (CR-252559, CR-3520895); Limón, cuenca del Bananito, Fila Matama, Cerro Muchilla, falda NW, río Bananito Lodge, 09°49'30"N, 83°03'50"W, 50–100 m, 24 marzo 2001 (frs), *J. F. Morales 7727* (CR-252030, CR-3521102); Limón, Squirres, en las colinas montañosas, 17 setiembre 1973 (frs), *L. J. Poveda 723* (CR); Parque Nacional Tortuguero, a orillas de Caño Negro, 10°21'N, 83°24'W, 2 m, 08 febrero 1989 (fls), *R. Robles 2628* (GH);

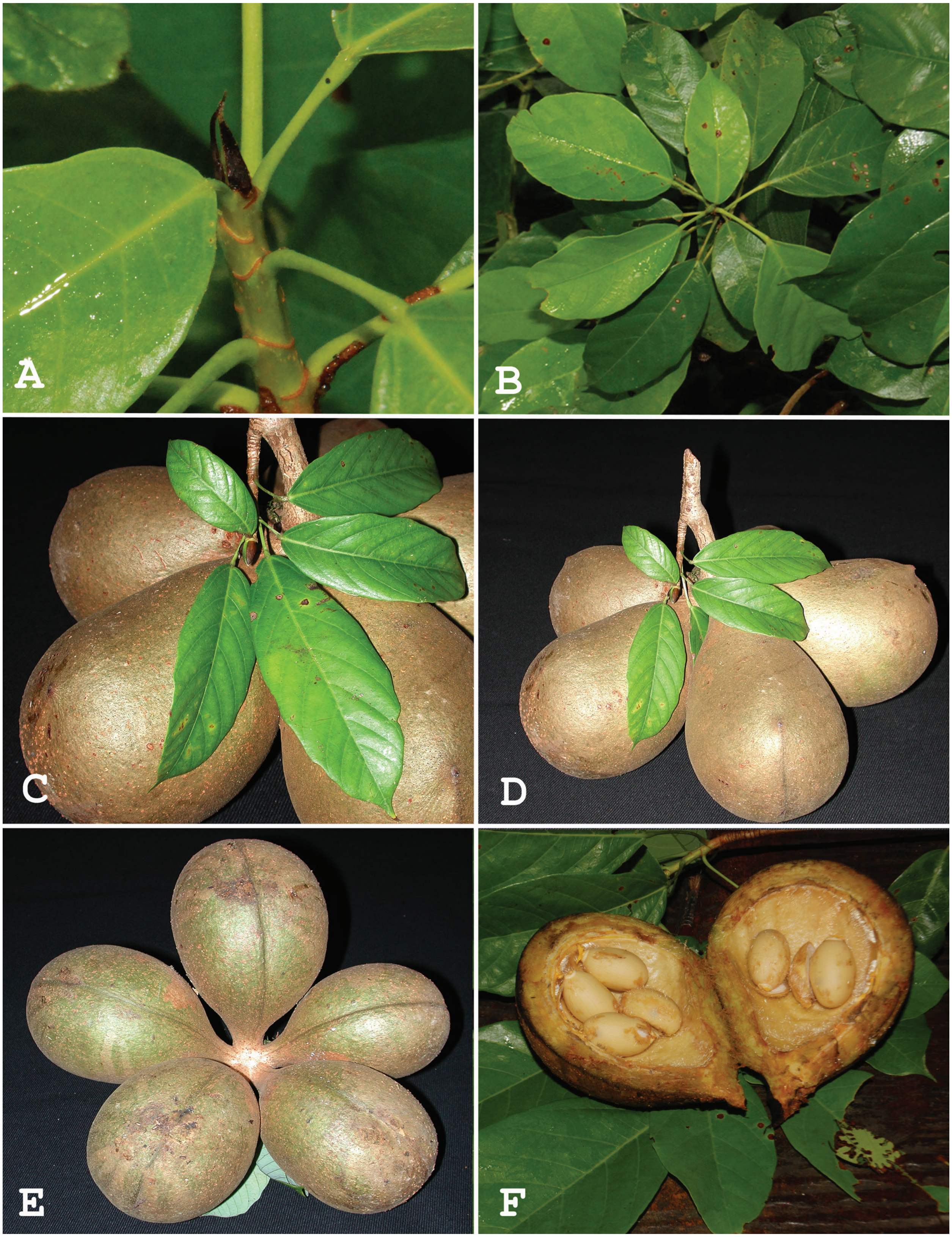


FIGURA 4. *Sterculia costaricana* Pittier. **A**, ramita terminal con estípulas; **B**, hoja en el lado adaxial; **C**, **D**, detalle de las hojas y folículos inmaduros; **E**, folículos inmaduros; **F**, folículo y semillas inmaduras. Fotografías A–B y F por J. Sánchez, de *J. Sánchez 2638* (CR); C–E por *F. Hidalgo*, de *L. González* et al. *1954* (CR).

Talamanca, Refugio Nacional de Vida Silvestre Gandoca-Manzanillo, Faja Costeña de Limón, Manzanillo, Punta Uva, 09°37'50"N, 82°41'10"W, 40 m, 24 setiembre 1995 (frs), *A. Rodríguez 730* (CR-193864, CR-1597280, MO); Limón, Reserva Biológica Hitoy Cerere, cuenca del Estrella, La Poza de las Chichis, recorrido al sendero Bobocava 2 km de la poza de las Chichis, 09°40'17"N, 83°01'42"W, 140 m, 20 enero 1999 (frs), *E. Rojas 349* (CR-234690, CR-2849807, MO); Limón, Talamanca, Sixaola, Gandoca, Trocha entre Gandoca y Manzanillo, 2 km SO, en línea recta de Gandoca, 09°35'4.7"N, 82°37'27.5"W, 20 m, 12 diciembre 2013 (frs), *J. Sánchez* et al. *2638* (CR); sendero Dema, 15 min. in motorboat W from Tortuguero Village in Parque National Tortuguero, 10°31'N, 83°30'W, 5 m, 10 febrero 1998 (fls), *K. Thomsen 1501* (CR); Limón, Valle la Estrella, point 6, forest close to edge of field adjoining Bananito Lodge, disturbed forest with many remnant trees, 09°49'02"N, 83°04'06"W, 100 m, 24 marzo 2010 (frs), *N. Zamora et al. 4867* (CR). PANAMÁ. Colón: East Santa Rita Riedge, 06 febrero 1968 (frs), *M. D. Correa & R. L. Dressler 665* (A, MO). Panamá: Chepo, carretera de Llano-Carti, km 15.5, 09°19'11"N, 78°59'34"W, 17 diciembre 2012 (frs), *J. Aranda* et al. *4369* (MO); 5–6 mi N of El Llano, near San Blas border, 395 m [1300 feet], 08 setiembre 1972 (frs), *A. H. Gentry 5822* (MO); Chepo, carretera de Llano-Carti, bosque cercano al km 8, 09°16'55"N, 78°57'59"W, 379 m, 18 diciembre 2012 (fls), *L. Martínez 1190* et al. (MO); El Llano-Cartí Road, 10–12 km from junction with Inter-American Highway, 420 m, 30 octubre 1974 (frs), *S. Mori & J. Kallunki 2884* (MO); along new El Llano-Cartí road, 8–12 km N of El Llano, 400–450 m, 12 diciembre 1973 (fls), *M. Nee et al. 8806* (MO). San Blas: Comarca de San Blas, río Cangandí, hills W of river S of confluence with Río Titamibe, 09°24'N, 79°º09'W, 50–150 m, 27 enero 1985 (fls), *G. de Nevers 4686* (GH, MO).

*Sterculia costaricana* se reconoce entre sus congéneres con hojas simples por presentar ramitas y envés de la lámina foliar glabros, sólo esparcido-puberulentas y con tricomas simples, en estípulas relacionadas a yemas terminales. Además, se caracteriza por ser un árbol (7–)10–25 m de altura, con gambas apenas diferenciadas, por su condición siempre verde, los pecíolos 1.0–7.5 cm de largo, por sus hojas con la lámina no lobulada en individuos juveniles y adultos, elíptica a oblongo-elíptica, 4.5–18.0 cm de largo y 2.0–8.5 cm de ancho, la base obtusa a corto-cuneada, con el ápice cuspidado a corto-acuminado, a veces con un mucrón <1 mm, la nervadura palmada, el margen entero y ligeramente sinuado y el envés en ocasiones levemente glauco (fresco o seco), por sus inflorescencias paniculadas, 3.1–9.0 cm de largo, por sus flores con el cáliz internamente rosado a rojo (en material fresco), esparcidamente estrellado-pubescente, que entremezcla alargados tricomas estrellados en toda la extensión de los lóbulos, pero especialmente sobre la boca del tubo del cáliz y sobre los apéndices, con tricomas vermiformes cortos y abundantes en la boca del tubo, esparcidos en los lóbulos y tricomas papilosos (esparcidos en los lóbulos y abundantes dentro del tubo) y con un apéndice central 0.5–0.8 mm de largo, aunque a veces pronto-caedizo, por sus flores estaminadas con el tubo del cáliz 1–2 mm de largo y 2–4 mm de ancho, y con lóbulos (5–)7–9 mm de largo y (1.2–)2.0–3.0 mm de ancho, con el andróforo 4–7 mm de largo, por sus flores pistiladas (o bisexuales) con el tubo del cáliz 1–2 mm de largo y 3–5 mm de ancho, con lóbulos 6–10 mm de largo y 2.0–3.3 mm ancho y con androginóforo 3–6 mm de largo, y por sus folículos lateralmente expandidos, 9–15 cm de largo, 6–12 cm de ancho y 4.5–7.0 cm de alto (en fruto maduro aún no abierto), pardos o amarillo verdosos al madurar, internamente híspidos.

Esta especie a menudo se confunde con *Sterculia recordiana*, la que se distingue por mostrar hojas con un mucrón apical hasta de 4 mm de largo, aunque a veces deciduo, el haz a menudo rugoso y el envés esparcidamente puberulento, por sus inflorescencias que llegan a ser más alargadas y por presentar lado interno del cáliz con tricomas vermiformes más alargados. Además, en *S. recordiana* las plantas juveniles muestran hojas significativamente distintas en relación con las plantas adultas; en los individuos juveniles son más grandes y 3- a 5-lobuladas, pero los individuos adultos tienen hojas más pequeñas y no lobuladas. Mientras que en *S. costaricana* las hojas de los individuos juveniles y la de adultos son siempre subiguales en tamaño y forma, siendo siempre no lobuladas. Con base en lo anterior, se determinó que un espécimen recolectado en Costa Rica, dividido en dos partes (*B. Hammel et al. 18129*; CR, MO-2 cartulinas) y aquí citado bajo esta entidad, corresponde a una mezcla de ambas especies.

Taylor (1989) dividió esta especie en dos variedades, con la var. autonímica aparentemente endémica de Costa Rica; sin embargo, nunca se hizo válido el nombre de la otra variedad panameña.

***Sterculia foetida*** L., Sp. Pl. 2: 1008. 1753. Tipo: Ceylon, ster., LINN 1143.1 [fide Tantra 1976].

Synonyms: *Clompanus molucanus* Raf., Sylva Tellur. 73. 1838.

*Sterculia mexicana* var. *guianensis* Sagot, Ann. Sci. Nat., Bot., sér. 6, 11: 153. 1881.

*Clompanus foetidus* (L.) Kuntze, Revis. Gen. Pl. 1: 77. 1891.

**Nombres comunes:** no registrados en Mesoamérica.

**Usos:** las semillas tostadas son comestibles y con sabor similar al de la castaña (*Castanea sativa* Mill., Fagaceae) y contienen un aceite que se usa con fines medicinales. La madera se emplea para hacer muebles y la corteza en la elaboración de cuerdas (Ya et al., 2007). Holdridge y Poveda (1975) mencionan que las semillas no se deben consumir crudas porque causan náuseas y vertigo.

**Distribución:** nativa de los trópicos de Asia; cultivada en el Neotrópico (Taylor, 1989), aunque poco recolectada, usualmente de individuos en jardines botánicos (Mapa 1).

**Fenología:** flores en junio. Frutos no observados.

**Especímenes adicionales examinados:** COSTA RICA. Cartago: Turrialba, CATIE, 625 m, 15 junio 1977 (fls), *L. J. Poveda & E. Camacho 1656* (CR).

*Sterculia foetida* se caracteriza por ser un árbol hasta de

20 m de altura y 30 cm de diámetro, deciduo, con estípulas densamente estrellado-vilosas en el lado externo y glabras en el interno, por sus hojas con pecíolos 9–38 cm de largo, glabros en hojas adultas, aunque en las hojas nuevas son glabrados a esparcidamente estrellado-vilosulos hacia el ápice, con pubescencia que entremezcla cortos tricomas papilosos, el pulvínulo basal es débilmente desarrollado, mientras el apical es conspicuo, por sus peciólulos obsoletos y articulados, folíolos 5–9, con la lámina elíptica a obovado-elíptica, los proximales 6–19 cm de largo y 2–5 cm de ancho, los terminales 13–26 cm de largo y 4–5 cm de ancho, por sus hojas nuevas en el haz con esparcidos tricomas estrellados que entremezclan abundantes y diminutos tricomas papilosos, aunque el punto de unión de los peciólulos y proximalmente sobre el nervio principal densamente estrellado-vilosos, el envés con esparcidos o abundantes tricomas estrellados, especialmente sobre el nervio principal, que se entremezclan con densos y diminutos tricomas papilosos, aunque pronto-glabrescente, por lo que las láminas foliares adultas, en general son glabras, por sus inflorescencias paniculadas, 9.5–32.0 cm de largo, por sus flores con olor desagradable, el cáliz rojo a púrpura externa e internamente (en material fresco), el lado externo con esparcidos tricomas estrellados, el interno denso-papilado en toda su extensión, con los lóbulos densamente estrellado-vilosos hacia el ápice, glabrados a glabros proximalmente y en el tubo del cáliz, sin un apéndice central, las flores estaminadas con el tubo del cáliz 5–6 mm de largo y 4–8(–11) mm de ancho, con los lóbulos 9–17 mm de largo y 3–7 mm de ancho y con el andróforo 10–14 mm de largo, proximalmente denso-piloso, distalmente glabrado o glabro, las flores pistiladas (o bisexuales) con el tubo del cáliz 6–7 mm de largo y 7–9 mm de ancho, con lóbulos 10–15 mm de largo y 3–5 mm de ancho y con el androginóforo 9–10 mm de largo, proximalmente denso-piloso, distalmente glabrado o glabro, y por sus folículos lateralmente expandidos, 6–8 cm de largo, 5.2–6.0 cm de ancho y 6–8 cm de alto (en fruto aun no abierto) (descripción de los folículos con base en Taylor, 1989).

Esta especie introducida en el Neotrópico se reconoce entre los congéneres nativos y con hojas digitadamente compuestas por presentar flores estaminadas y pistiladas (o bisexuales) más grandes, con el tubo del cáliz 5–7 mm de largo (vs. 1–5 mm de largo en otras especies con hojas digitadas) y los lóbulos 9–17 mm de largo y 3–7 mm de ancho (vs. 4.3–9.0 mm de largo y 1.5–4.5 mm de ancho), con mayor número de óvulos, 18–22 por carpelo (vs. [(4–]6–11[–12] por carpelo) y por sus folículos rojos al madurar (vs. pardos, amarillo verdosos a rojo anaranjados o pardo anaranjados al madurar, aunque desconocidos en *S. petenensis*) e internamente glabros (vs. híspidos o velutinos).

***Sterculia lanceolata*** Cav., Diss. 5: 287, pl. 143, f. 1. 1788.
Synonym: *Sterculia balansae* Aug. DC., Bull. Herb. Boissier Ser. II. iii. 369. 1903.

**Nombres comunes:** no registrados en Mesoamérica.

**Usos:** en los países donde ocurre de forma nativa la fibra de la corteza se ha empleado en la elaboración de bolsas y papel (Ya et al., 2007).

**Distribución:** nativa de Asia, en China, Laos, Myanmar, Tailandia y Vietnam; pocas veces cultivada en el Neotrópico (Mapa 1).

**Fenología:** flores en abril. Frutos no observados.

**Especímenes adicionales examinados:** PANAMÁ. Canal Area, 09°04'00"N, 79°39'00"W, 04 abril 1941 (fls), *P. H. Allen 534* (MO).

*Sterculia lanceolata* se reconoce entre sus congéneres por la combinación de hojas simples, las flores con lóbulos del cáliz cortos, 4–6 mm de largo, folículos pequeños, 5–7 cm de largo y 2.0–2.5 cm de ancho, y distintivamente rojos al madurar, y por ser una especie cultivada. Además, se caracteriza por ser un árbol (3–)5–10 m de altura, por sus pecíolos 1.5–5.5 cm de largo, por sus hojas con la lámina no lobulada, elíptica, ovada, lanceolada a ovado-elíptica, 9–20 cm de largo y 3.5–8.0 cm de ancho, la base obtusa a corto-cuneada, el ápice agudo o acuminado, la nervadura palmada, con 3 nervios principales que salen desde la base, el margen entero y el envés esparcido o densamente estrellado-puberulento o glabrado, por sus inflorescencias paniculadas, 4–10 cm de largo, por sus flores con el cáliz rojizo (en material fresco), esparcidamente estrellado-pubescente en el lado externo, dividido casi hasta la base, con el tubo ca. 2 mm de largo y ca. 1 mm de ancho, y los lóbulos 4–6 mm de largo y ca. 3 mm de ancho, y por sus folículos híspidos en el lado interno (descripción en parte basada en Ya et al. 2007).

Esta especie se podría confundir con individuos adultos de la nativa *Sterculia recordiana*, pero esta última se distingue por mostrar hojas con un mucrón apical hasta de 4 mm de largo (aunque a veces deciduo), el haz a menudo rugoso (vs. más o menos lisa), por sus inflorescencias que llegan a ser más alargadas y por sus flores y folículos distintivamente más grandes, con estos últimos pardo o amarillo verdosos al madurar.

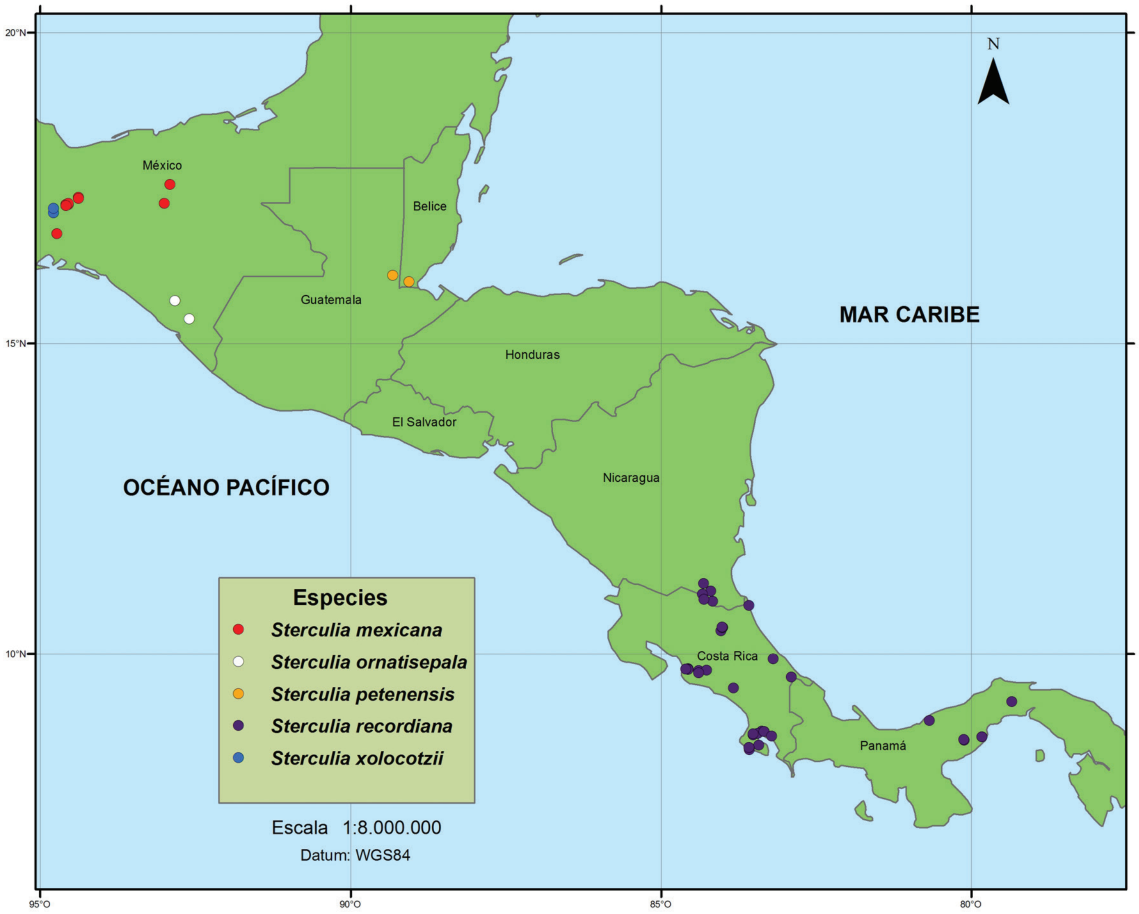
***Sterculia mexicana*** R. Br., Pl. Jav. Rar. 227. 1844. TIPO: MEXICO. Chiapas [Tabasco]: Teapa, abril 1840 (fls), *Linden s.n.* (Lectotipo: P; Isolectotipo: G).
Synonym: *Clompanus mexicanus* (R. Br.) Kuntze, Revis. Gen. Pl. 1: 77. 1891.

**Nombres comunes:** Bellota (México: en todo su rango de distribución), Pica-pica (México: Veracruz) (Taylor, 1989).

**Distribución y hábitat:** endémica de México; 100–300 m de elevación. Se encuentra en bosque tropical perennifolio, en potreros, remanentes de bosque y orillas de camino (Mapa 2).

**Fenología:** flores entre enero y abril, y entre octubre y diciembre. Frutos entre enero y agosto, además en diciembre (Taylor, 1989).

**Especímenes adicionales examinados:** MÉXICO. Chiapas: Along highway 195, 20 km S of Ixtacomitan, 17°15'N, 93°00'W, 300 m, 14 octubre 1986 (fls), *B. Hammel 15730* (GH, MO). Oaxaca: Santa María Chimalapa, Cerro 5 km al E. de Cofradia Chimalapa, 16°46'N, 94°44'W, 700 m,



Mapa 2. Mapa de distribución en la región mesoamericana de *Sterculia mexicana* R. Br., *S. ornatisepala* E.L. Taylor ex D. Santam. & Al. Rodr. *sp. nov.*, *S. petenensis* E.L. Taylor ex D. Santam. & Al. Rodr. *sp nov*, *S. recordiana* Standl. y *S. xolocotzii* T. Wendt & E.L. Taylor.

27 agosto 1986 (fls), *H. Hernández 2374* (MO). Tabasco: Cerro del Madrigal, 3 km al E de Teapa, sobre camino a Tacotalpa, 50 m, 21 febrero 1984 (fls), *R. Fernández Nava 2210* (MO). Veracruz: Municipio Hidalgotitlán, 1 km SE of San Agustín Melgar, 17˚15'N, 94˚33'W, 100 m, 02 marzo 1984 (frs), *M. Nee 29783* (GH, MO); municipio Hidalgotitlán, north side of río Solosúchil, 2–3 km, SE of Agustín Melgar, 17˚14'N, 94˚33'W, 100 m, 05 marzo 1984 (fls), *M. Nee & K. Taylor 29932* (GH); municipio Hidalgotitlán, Brecha Hnos. Cedillo-A. Melgar, 17˚13'N, 94˚35'W, 09 noviembre 1974 (fls), *B. Vázquez 1340* (MO); municipio Hidalgotitlán, río Solosuchil, más o menos 1 1/2–2 horas a pie al SE de Ejido Agustín Melgar, cerca de potrero de Ejido Pancho Villa, 17˚14'N, 94˚35'O, 150 m, 24 marzo 1982 (frs), *T. Wendt 3734* (GH); municipio Minatitlán, 13.7 km al E de la Laguna sobre terracería a Uxpanapa, luego 8 km al N sobre el camino no completo (brecha 93) a Belisario Domínguez, 17˚21'N, 94˚23'O, 130 m, 02 abril 1984 (bot fls, frs), *T. Wendt & L. Rico 4391* (GH, MO); municipio Minatitlán, 13.7 km al E de La Laguna sobre terracería a Uxpanapa, luego 6.5 km al N sobre camino nuevo no completo (brecha 93) a Belisario Domínguez, 17˚20'N, 94˚23'O, 130 m, 10 octubre 1984 (fls), *T. Wendt & S. Plettman 4474* (GH).

*Sterculia mexicana* se reconoce entre sus congéneres con hojas digitadamente compuestas por la combinación de hábito mediano a pequeño (arbusto o árbol de hasta 15 [–25] m de altura), las inflorescencias con una yema terminal persistente, el cáliz con la boca del tubo ocluido por un anillo de densos tricomas simples y estrellados, erectos y rígidos, por sus folículos lateralmente compresos y por ser una especie endémica de México. Además, esta especie se caracteriza por su condición siempreverde, estípulas densamente estrellado-velutina en ambas caras, por sus hojas con pecíolos 13.0–50.5(–60.0) cm de largo, glabros, aunque diminuto-velutino hacia el pulvínulo basal, por sus peciólulos (1.4–)3.2–4.3(–6.0) cm de largo y articulados, los folíolos 5–9, con la lámina obovada a estrechamente obovada, los proximales 10–32 cm de largo y 3–13 cm de ancho, los terminales 17.0–42.0(–50.5) cm de largo y 5–17 cm de ancho, glabros sobre ambas superficies, por sus inflorescencias paniculado-racemosas, 6.5–21.6(–31.0) cm de largo, por sus flores con el cáliz densamente estrellado-puberulento en el lado externo, el interno crema o verde-crema hacia la base y rosado-anaranjado o rosado-salmón hacia el ápice (en material fresco), con papilas ferrugíneas en toda su extensión, aunque difusas entre la pubescencia, y denso-pubescente, en especial en el ápice de los lóbulos (estrellado-vilosos), la parte distal del tubo y la base de los lóbulos, sin un apéndice central en el lado interno de los lóbulos, las flores estaminadas con el tubo del cáliz 2–3 mm de largo y 2.0–2.5 mm de ancho, con los lóbulos 4.3–6.5 mm de largo y 1.0–4.5 mm de ancho, y el andróforo ca. 4 mm de largo, proximalmente pubescente, que entremezcla tricomas hirsútulos y papilosos, y distalmente glabrado, las flores pistiladas o bisexuales, con el tubo del cáliz 2.2–5.0 mm de largo y ca. 2 mm de ancho, los lóbulos 5.0–7.5 mm de largo y 2–4 mm de ancho, y el androginóforo 3–5 mm de largo, proximalmente pubescente, que entremezcla tricomas hirsútulos y papilosos, distalmente glabrado, y por sus folículos lateralmente compresos, 5.5–10.5 cm de largo, 2.3–4.8 cm de ancho y 2.6–6.0 cm de alto (en fruto maduro aún no abierto), pardos o amarillo verdosos al madurar e internamente velutinos.

Esta especie es afín a *Sterculia xolocotzii*, con la cual fue confundida por mucho tiempo, ya que ambas comparten hojas digitadamente compuestas, el cáliz con los lóbulos sin un apéndice central en el lado interno y por los folículos lateralmente compresos; sin embargo, se distinguen ya que esta última tiene hojas y pecíolos más pequeños y denso-pubescentes, al menos en hojas nuevas, inflorescencias sin una yema terminal y el cáliz con la boca del tubo no ocluido por el indumento.

**Sterculia ornatisepala** E.L. Taylor ex D. Santam. & Al. Rodr. *sp. nov.* TIPO. MÉXICO. [Chiapas]: Mount Ovando, 1000 m, 14–18 noviembre 1939 (fls), *E. Matuda 3920* (Holotipo: A [A00057603]; Isotipos: MO, NY [imagen digital]). Fig. 5.

*Sterculia ornatisepala* is distinguished among its congeners by being the only species with digitately compound leaves with calyx lobes on the inner side that have an appendix toward the middle part. In addition, it is characterized by its leaves with 9–10 leaflets that are elliptical to narrow-elliptic, glabrate to glabrescent, and with petiolules 0.5–1.0 cm long, petioles 16.5–25.0 cm long, staminate flowers with calyx lobes 6–8(–11) mm long and 2–4 mm wide, and androphore 4–7 mm long, pistillate (or bisexual) flowers with calyx lobes 7–8 mm long and 3.0–3.8 mm wide, androgynophore 5–6 mm long and carpels with 6–8 ovules, and its distribution restricted to Mexico and Guatemala.

Árbol 10.0–30.5 m de altura y 60–100 cm de diámetro, el tronco con gambas (de tamaño desconocido). Ramitas terminales 8–12 mm de diámetro (en ramitas foliadas), estrellado-puberulentas, tricomas pardo-ferrugíneos. Estípulas ca. 1.8 cm de largo y ca. 0.9 cm de ancho, ovadas a triangulares, largo-acuminadas, tempranamente deciduas (sólo presentes en la yema terminal), el lado externo e interno con densa pubescencia estrellada, los tricomas pardo-ferrugíneos a castaño claro. Hojas digitadamente compuestas; pecíolos 16.5–25.0 cm de largo, densamente estrellado puberulentos a glabrescentes, con el pulvínulo basal y el apical débilmente diferenciados; peciólulos 0.5–1.0 cm de largo, articulados, con la base leve-engrosada, glabrados o tomentosos a estrellado puberulentos; folíolos 9–10, la lámina elíptica u angosto-elíptica, los proximales 12.4–17.5 m de largo y 4.1–6.2 cm de ancho, los terminales 17–19 cm de largo y 4.4–7.0 cm de ancho, pardo-rojiza a pardo oscuro al secar, la base cuneada o atenuada, el ápice agudo, el margen entero y ligeramente ondulado, la nervadura pinnada, con 17–27 pares de nervios secundarios, los nervios terciarios conspicuamente reticulados, el haz por lo general glabro, el envés glabrescente, sin tricomas papilosos (las hojas nuevas no vistas), algunas veces sobre ambas superficies diminutamente estrellado-tomentulosos sobre los nervios principales. Inflorescencias (10–)25–41 cm de largo, en los extremos de las ramas, axilares, solitarias, generalmente en nudos defoliados, con 2–4 por ramita, en panículas generalmente robustas, erectas, sin una yema apical persistente, el raquis tomentoso, con tricomas pardo-ferrugíneos a castaño claro, los ejes secundarios hasta 10.5 cm de largo, los ejes terciarios, si presentes, hasta 4 cm de largo. Pedúnculos 2.5–3.5 cm de largo, estrellado-tomentosos, los tricomas pardo-ferrugíneos, castaño claro o blanquecinos. Botones florales 3.5–7.0 mm de largo y 2–4 mm de ancho, con la base aguda a subtruncada, el ápice obtuso o redondeado. Pedicelos 4–8 mm de largo, con una articulación cerca del 1/4 basal o algunas veces cerca de la base, densamente estrellado-tomentosos, los tricomas pardo-ferrugíneos a castaño claro. Cáliz con los lóbulos erectos, triangulares a oblongo-lanceolados, el lado externo estrellado-velutino, con tricomas pardo-ferrugíneos, dorados o grisáceos a castaño claro, el lado interno castaño claro, pardo-ferrugíneo, dorado o negro-grisáceo (en material seco), densamente estrellado-viloso y generalmente que entremezcla papilas ferrugíneas o rojizas, con un apéndice central de 0.5–0.8 mm de largo, el tubo con el lado interno denso-papilado, sin tricomas. Flores estaminadas con el cáliz 5–13 mm de largo, inciso por los lóbulos hasta 3/4 o más de su longitud, el tubo 3–5 mm de largo y ancho, urceolado, los lóbulos 6–8(–11) mm de largo y 2–4 mm de ancho; andróforo 4–7 mm de largo, sigmoide, con la base engrosada e hirsutula, ca. 3/4 partes distales filiforme y esparcido-hirsútula, que entremezcla tricomas simples y papilosos; estambres 11–15, sésiles o con el filamento hasta 0.1 mm de largo; tecas 0.3–1 mm de largo. Flores pistiladas (o bisexuales) con el cáliz 11–12 mm de largo, inciso por los lóbulos hasta 3/4 o más de su longitud, el tubo ca. 3 mm de largo y ca. 4 mm de ancho, urceolado, los lóbulos 7–8 mm de largo y 3–3.8 mm de ancho; androginóforo 5–6 mm de largo, erecto a leve-curvado, con la base engrosada e hirsútula, que entremezcla tricomas simples y papilosos; estambres 4–14, filamento 0.2–1.0 mm de largo; tecas 0.1–0.2 mm de largo y 0.10–0.15 mm de ancho; ovario 2.0–2.1 de largo y de ancho globoso, densamente hirsuto; estilo ca. 3.1 mm de largo, densamente hirsuto; estigma capitado, 5-lobado, rojo a negruzco; óvulos 6–8 por carpelo. Folículos ca. 14 cm de largo, ca. 8 cm de ancho y ca. 7.5 cm de alto (en fruto abierto), obovoides y lateralmente expandidos, pardos o amarillo verdosos al madurar, la base cuneada, el ápice con un rostro hasta 15 mm de largo o ausente, pericarpio 4.5–5.0 mm de grosor, el lado externo velutino, densamente estrellado, con tricomas pardo-ferrugíneos a castaño claro, el lado interno híspido y ferrugíneo; semillas posiblemente 6–8 por folículo, elípticas, 25–32 mm de largo y 13–18 mm de diámetro.

**Nombre común:** Castaño (México y Guatemala) (Taylor, 1989).

**Usos:** no documentados.

FIGURA 5. *Sterculia ornatisepala* E.L. Taylor ex D. Santam. & Al. Rodr. **A**, hábito; **B**, estípula; **C**, peciólulos; **D**, folículo abierto; **E**, semilla; **F**, botón floral; **G**, flor pistilada (o bisexual); **H**, androginóforo; **I**, estambres de la flor pistilada (o bisexual); **J**, estigma de la flor pistilada (o bisexual); **K**, flor estaminada; **L**, andróforo; **M**, antera de la flor estaminada. A, C–F y K de *A. F. Skutch 1542* (A); B de *E. Matuda 3920* (MO); G–J y L–M de *C. A. Purpus 7082* (MO).

**Distribución y hábitat:** México y Guatemala; 1000–1500 m de elevación. Se encuentra en bosque tropical perennifolio (o selva alta siempre verde) (Taylor, 1989) (Mapa 2).

**Fenología:** flores en octubre (Taylor, 1989), noviembre y diciembre, ocasionalmente en febrero (Taylor, 1989). Frutos en junio y octubre (Taylor, 1989), además en agosto.

**Especímenes adicionales examinados:** MEXICO. Chiapas: municipio Angel Albino Corzo, Above Finca Cuxtepec, 1380 m, 14 diciembre 1980 (fls), *D. E. Breedlove 48644* (MO); 1913 (fls), *C. A. Purpus 7082* (GH-2 cartulinas, MO); municipio Jaltenango, Colonia Santa Rita, ca. 33 km al SO de Jaltenango en la Sierra Madre, a 3 km de Finca Prusia, filo al E de la colonia, cerca de la vereda a El Triunfo, 15°41'N, 92°50'W, 1450 m, 01 agosto 1986 (frs), *T. L. Wendt 5330* (MO-2 cartulinas). GUATEMALA. Suchitepequez: finca Mocá, 3500–5000 ft [1060–1500 m], 26 octubre 1926 (fls, frs), *A. F. Skutch 1542* (A).

*Sterculia ornatisepala* se reconoce entre sus congéneres por ser la única especie con hojas digitadamente compuestas que tiene en el lado interno de los lóbulos del cáliz un apéndice hacia la parte media. Además, se caracteriza por sus hojas con 9–10 folíolos, elípticos a estrecho-elípticos, glabrados a glabrescentes y con peciólulos 0.5–1.0 cm de largo, por sus pecíolos 16.5–25.0 cm de largo, por sus flores estaminadas con lóbulos del cáliz 6–8(–11) mm de largo y 2–4 mm de ancho y andróforo 4–7 mm de largo, las flores pistiladas (o bisexuales) tienen los lóbulos del cáliz 7–8 mm de largo y 3.0–3.8 mm de ancho, el androginóforo 5–6 mm de largo y con 6–8 óvulos por carpelo, y por su distribución restringida a México y Guatemala.

Esta entidad tiene similitud con *Sterculia allenii*, una especie endémica de Costa Rica, pero esta última se diferencia debido a que los lóbulos del cáliz en el lado interno carecen de apéndice (vs. con un ápendice), en las flores estaminadas los mismos lóbulos comúnmente son más estrechos, 2.0–2.7 mm (vs. 2–4 mm), el andróforo y el androginóforo son más cortos, 3.0–3.5 mm y 3–4 mm de largo respectivamente (vs. 4–7 mm y 5–6 mm de largo en su orden respectivo), las inflorescencias son menos robustas, 8–22 cm de largo (vs. [10–]25–41 cm), con ejes secundarios más cortos, hasta 5 cm de largo (vs. hasta 10.5 cm) y las hojas llegan a ser distintivamente más grandes.

**Etimología:** el epíteto específico "ornatisepala" fue sugerido por Taylor (1989), en alusión a los sépalos adornados o equipados de un apéndice en el lado interno y hacia la parte media.

**Sterculia petenensis** E.L. Taylor ex D. Santam. & Al. Rodr. *sp nov.* TIPO. BELICE. Toledo: Temash river, 150 ft [50 m], 18 marzo 1935 (fls), *W. A. Schipp 1321* (Holotipo: GH [GH00057605]; Isotipos: A, BM [imagen digital], MO). Fig. 6.

*Sterculia petenensis* is distinguished by being a deciduous tree 10–45(–50) m tall with digitately compound leaves, with leaflets (5–)6–8 elliptical to broad-elliptical, glabrous and with petiolules 0.6–1.5 cm long, petioles 12.5–18.1 cm long, calyx internally yellowish green, yellow, or cream, staminate flowers with calyx lobes 5–7 mm long and 1.8–2.3 mm wide and androphore 4.0–6.4 mm long, pistillate (or bisexual) flowers with calyx lobes 5–7 mm long and 1.7–2.5 mm wide, androgynophore 2.1–4.3 mm long and carpels with 10–11(–12) ovules, and its distribution restricted to the Peten region, between Guatemala and Belize.

Árbol 10–45(–50) m de altura y 150(–200) cm de diámetro, con gambas altas (de tamaño desconocido). *Ramitas terminales* 5–11 mm de diámetro (en ramitas foliadas), estrellado-velutinas, tricomas grisáceos o castaño claro. *Estípulas* 1.2–2.1 cm de largo y 2–4 cm de ancho, triangulares, largo-acuminadas, tempranamente deciduas, solo presentes en la yema terminal, lado externo con densa pubescencia estrellado-velutina, *tricomas* castaño claro, el lado interno tomentoso, con tricomas simples y estrellados, castaños claro, y que entremezcla tricomas papilosos. *Hojas* digitadamente compuestas; *pecíolos* 12.5–18.1 cm de largo, esparcida o densamente estrellado-velutino o glabrescentes, con pulvínulo basal y apical débilmente diferenciados, en ocasionalmente bien diferenciado, densamente velutino; *peciólulos* 0.6–1.5 cm de largo, articulados, con la base engrosada, glabrados o estrellado-velutino; folíolos (5–)6–8, la *lámina* elíptica a amplio-elíptica, los proximales 11.2–12.5 cm de largo y 4.2–4.9 cm de ancho, los terminales 14.5–20.2 cm de largo y 3.5–7.0 cm de ancho, café claro a oliva al secar, la base cuneada o atenuada (algunas veces con un lado oblicuo), ápice agudo o acuminado, margen entero, a veces leve-ondulado, nervadura pinnada, con 11–27 pares de nervios secundarios, nervios terciarios conspicuamente reticulados, haz y envés glabros (en hojas maduras), sin tricomas papilosos. *Inflorescencias* (7.0–)12.3–20.2 cm de largo, en los extremos de las ramas, solitarias, axilares o en nudos defoliados, 1–4 por ramita, panículas generalmente erectas, algunas veces leve-curvadas, sin una yema apical persistente, raquis estrellado-velutino, *tricomas* castaño claro, ejes secundarios hasta 2–3 cm de largo, ejes terciarios, si presentes, hasta 0.9 cm de largo. *Pedúnculos* 0.6–4.5 cm de largo, estrellado velutinos, tricomas castaño claro o grisáceos. Botones florales 2–5 mm de largo y 1.5–2.0 mm de ancho, con la base truncada o subtruncada, el ápice obtuso o redondeado. *Pedicelos* 0.8–5.0 mm de largo, con articulación cerca del 1/4 basal o menos, estrellado-velutinos, tricomas castaño claro o grisáceos. *Cáliz* con lóbulos erectos o ascendentes, oblongo-lanceolados a oblongo-obovados, el lado externo estrellado-velutino, *tricomas* pardo-amarillentos, lado interno verde amarillento, amarillo o crema (cuando fresco), densamente estrellado-velutino, sin un apéndice central, el tubo con el lado interno denso-papilado, sin tricomas. *Flores estaminadas* con el cáliz 6–8 mm de largo, inciso por los lóbulos hasta 3/4 o menos de su longitud, el tubo 1.5–3.0 mm de largo y ancho, urceolado, los lóbulos 5–7 mm de largo y 1.8–2.3 mm de ancho; *andróforo* 4.0–6.4 mm de largo, sigmoide, con la base engrosada y denso-hirsutula, ca. 3/4 partes distales más o menos filiforme y esparcido-hirsutula, que entremezcla tricomas simples y papilosos; *estambres* 12–14, subsésiles o con filamento hasta 0.3 mm de largo; tecas ca. 0.5 mm de largo. *Flores pistiladas* (o bisexuales) con el cáliz 8–9 mm de largo, inciso por los lóbulos hasta 3/4 o menos de su longitud, el tubo 1.0–1.9 mm de largo y 1.2–2.0 mm de

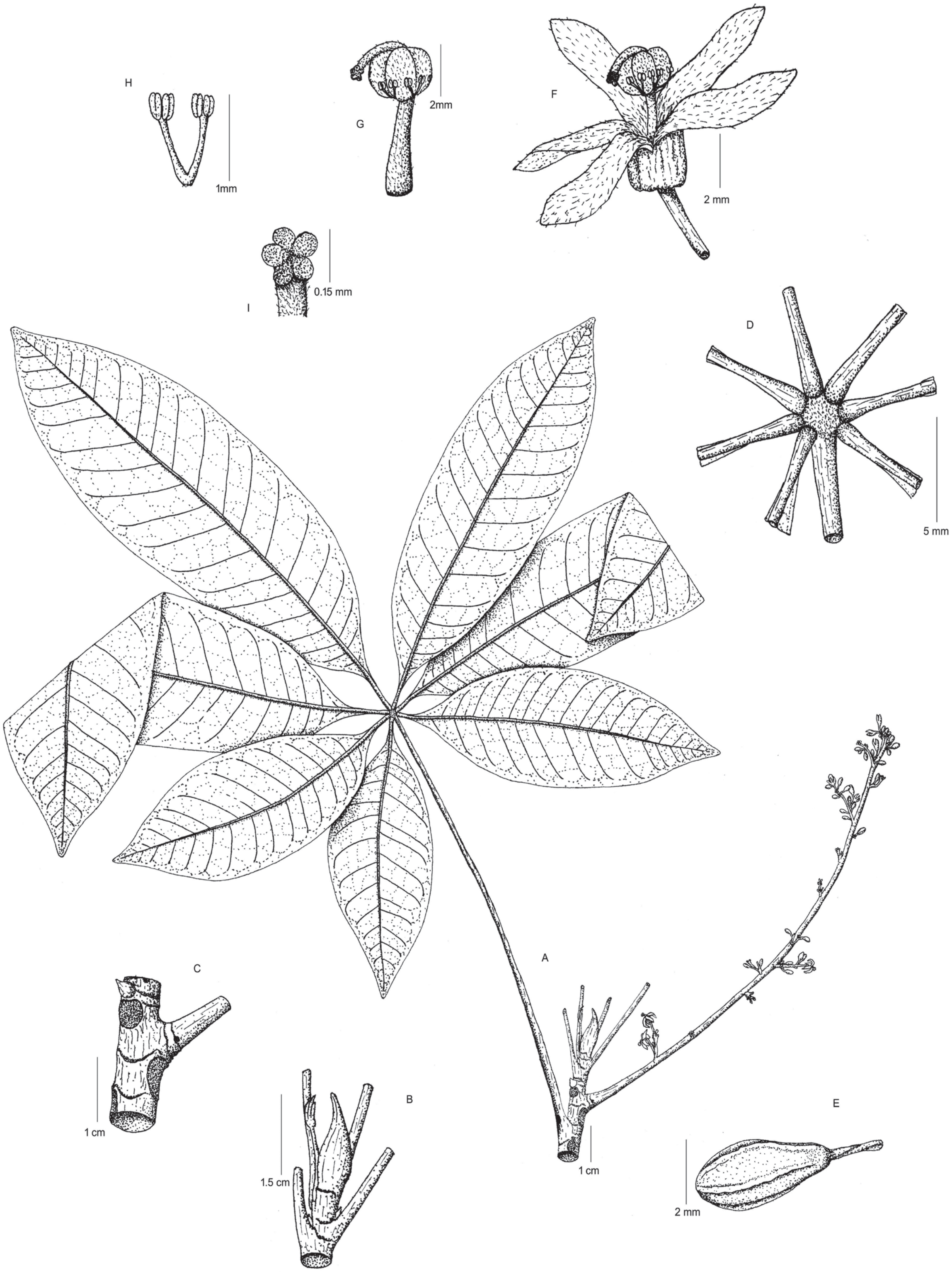


FIGURA 6. *Sterculia petenensis* E.L. Taylor ex D. Santam. & Al. Rodr. **A**, hábito; **B**, estípula; **C**, detalle de la ramita terminal; **D**, peciólulos; **E**, botón floral; **F**, flor pistilada (o bisexual); **G**, androginóforo; **H**, estambres de la flor pistilada (o bisexual); **I**, estigma. A–E de *E. Contreras 6804* (MO); F–I de *W. A. Schipp 1321* (MO).

ancho, urceolado, los lóbulos 5–7 mm de largo y 1.7–2.5 mm de ancho; *androginóforo* 2.1–4.3 mm de largo, erecto, con la base engrosada y denso-hirsútula, que entremezcla tricomas simples y papilosos; *estambres* 9–13, *filamento* 0.3–1.0 mm de largo; *tecas* 0.2–0.3 mm de largo y de ancho; ovario 1.3–2.0 mm de largo y de ancho, globoso, densamente viloso; *estilo* 0.8–1.5 mm de largo, densamente viloso; *estigma* capitado, 5-lobado, negruzco; óvulos 10–11(–12) por carpelo. *Folículos* desconocidos.

**Nombres comunes:** bola de danto (Taylor, 1989).

**Usos:** no documentados.

**Distribución y hábitat:** Guatemala y Belice; en bosque lluvioso de tierras bajas en la vertiente Caribe; 50–150 m de elevación (Mapa 2).

**Fenología:** flores en marzo.

**Etimología:** el epíteto específico "petenensis" fue sugerido por Taylor (1989), como indicativo de que la distribución conocida para la especie es la región del Petén, en Belice y Guatemala.

**Especímenes adicionales examinados:** GUATEMALA. Petén: Cadenas, 4 km bordering río Sarstun, 21 marzo 1967 (fls), *E. Contreras 6804* (GH, MO); La Cumbre, about 3 km east on Pusila Village road, 25 marzo 1977 (fls), *C. L. Lundell & E. Contreras 20673* (GH-2 cartulinas).

*Sterculia petenensis* se distingue por ser un árbol que alcanza gran tamaño, 10–45(–50) m de altura, deciduo, por sus hojas digitadamente compuestas, con (5–)6–8 folíolos elípticos a amplio-elípticos, glabros, y con peciólulos 0.6–1.5 cm de largo, por sus pecíolos 12.5–18.1 cm de largo, por sus inflorescencias poco desarrolladas, (7.0–)12.3–20.2 cm de largo, con ejes secundarios hasta 2–3 cm de largo, por sus flores con el cáliz verde amarillento, amarillo o crema en el lado interno (cuando fresco), las flores estaminadas con lóbulos del cáliz 5–7 mm de largo y 1.8–2.3 mm de ancho y el andróforo 4.0–6.4 mm de largo, las flores pistiladas (o bisexuales) con lóbulos del cáliz 5–7 mm de largo y 1.7–2.5 mm de ancho, androginóforo 2.1–4.3 mm de largo y con 10–11 óvulos (o hasta 12; Taylor, 1989) por carpelo, y por su distribución restringida a la región del Petén, entre Guatemala y Belice.

Esta entidad es similar a *Sterculia mexicana*, que también tiene hojas digidamente compuestas, pero esta última se distingue debido a que tiene inflorescencias con una yema apical persistente (vs. yema ausente), las flores con el tubo del cáliz internamente ocluido por un anillo de densos tricomas rígidos y erectos (vs. nunca ocluidos por tricomas), por sus folículos lateralmente compresos (vs. no compresos), por sus peciólulos comúnmente más alargados, (1.4–)3.2–4.3(–6.0) cm de largo (vs. 0.6–1.5 cm), y por ser una especie con porte comúnmente más pequeño, hasta 15(–25) m de altura (vs. 10–45[–50] m). También comparar con *S. allenii,* del Pacífico sur de Costa Rica, para diferencias entre estas dos especies, ver comentarios bajo esta última.

***Sterculia recordiana*** Standl., Trop. Woods 44: 25. 1935. TIPO: PANAMÁ. Changuinola Valley, mayo 1927 (fls, frs), *G. P. Cooper & G. M. Slater 104* (Holotipo: F; Isotipo: GH, US, WIS). Fig. 7.

Synonym: *Sterculia costaricana* sensu Flora of Panama, *non* Pittier.

**Nombres comunes:** Panamá, Papa, Yuco (Costa Rica) (Rodríguez, 2015).

**Usos:** en Nicaragua la madera se usa en la fabricación de casas (Salick et al., 1995).

**Distribución y hábitat:** del sureste de Nicaragua hasta el oeste de Colombia; 0–1100 m de elevación. Se encuentra en bosque húmedo y muy húmedo, en vegetación primaria, secundaria y bordes de bosque (Mapa 2).

**Fenología:** flores entre enero y abril, luego en julio y noviembre. Frutos en enero, febrero, entre mayo y julio, y entre octubre y noviembre.

**Especímenes adicionales examinados:** NICARAGUA. Río San Juan: Reserva Indio-Maíz, Municipio de el Castillo, Cerro el Diablo, 11°01'N, 84°12'W, 250 m, 07 enero 1997 (frs), *R. Rueda 5540* (MO); municipio del Castillo, Estación Biológica Bartola a 3 kilómetros de la desembocodura, 10°58'00"N, 84°19'50"W, 50–100, 26 julio 1998 (estéril), *R. Rueda 8191* (MO); municipio el Castillo, Reserva Indio-Maiz, Cerro Bolívar, 10°51'N, 84°10'W, 150–280 m, 29 noviembre 1998 (estéril), *R. Rueda 9217* (MO); Los Filos, near Loma Los Filos, Río Santa Cruz, 11°08'N, 84°19'W, 04 setiembre 1991 (estéril), *J. Salick 8045* (MO). COSTA RICA. Alajuela: Llanura de San Carlos, Proyecto Minero Placer-Dome, camino al cerro Las Crucitas, 10°52'45"N, 84°18'40"W, 100–200 m, 25 julio 1996 (frs), *J. González 1115* (MO). Heredia: Parque Nacional Braulio Carrillo, Estación El Ceibo, 10°22'29"N, 84°02'10"W, 500–600 m, 1 octubre 1989 (frs), *R. Aguilar 12* (CR, F, GH, MO-2 cartulinas); Finca La Selva, the OTS field station on the río Puerto Viejo just E of its junction with the río Sarapiquí, line 1400 between East boundary and Central Trail, 100 m, 03 abril 1980 (fls), *B. Hammel 8425* (LSCR [fotocopia DUKE]); along the road from Puerto Viejo de Sarapiquí to the río Sucio, 50 m, 1 noviembre 1974 (estéril), *G. Hartshorn 1564* (CR, MO); Puerto Viejo de Sarapiquí, 10 febrero 1957 (estéril), *B. G. Schubert & L. R. Holdridge 1357* (A); Finca La Selva, the OTS field station on the río Puerto Viejo just E of its junction with the río Sarapiquí, Sabalo-Esquina trail, on flood plain of Quebrada Sabalo, 100 m, 20 noviembre 1981 (frs), *D. Smith 578* (LSCR, [fotocopia DUKE]); Santo Domingo, Santa Rosa, INBioparque, jardines cultivados, 09°58'25"N, 84°05'36"W, 1100 m, 13 julio 2011 (fls), *D. Vargas 4621* (CR); Sarapiquí, OET, La Selva, sendero CES 150 m, 31 mayo 2001 (frs), *O. Vargas 683* (LSCR); Sarapiquí, OET, La Selva, sendero CES 150 m, 12 junio 2001 (estéril), *O. Vargas 692* (LSCR); Sarapiquí, OET, La Selva, Arboleda placa #553, 16 febrero 2006 (frs), *O. Vargas 1409* (LSCR); Sarapiquí, OET, La Selva, sendero SURA 130 m, derecha 2 m, 7 mayo 2008 (estéril), *O. Vargas 1985* (LSCR); finca La Selva, the OTS field station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, along trail through swamp on Holdridge Trail, 1800 m South, 14 julio 1982 (estéril), *B. Hammel & J. Trainer 13166* (MO); finca La Selva, Hacienda Santiago, adjacent to La Selva, 10°26'N, 84°01'W, 29 octubre 1970 (estéril), *G. S. Hartshorn 954* (MO). Limón:

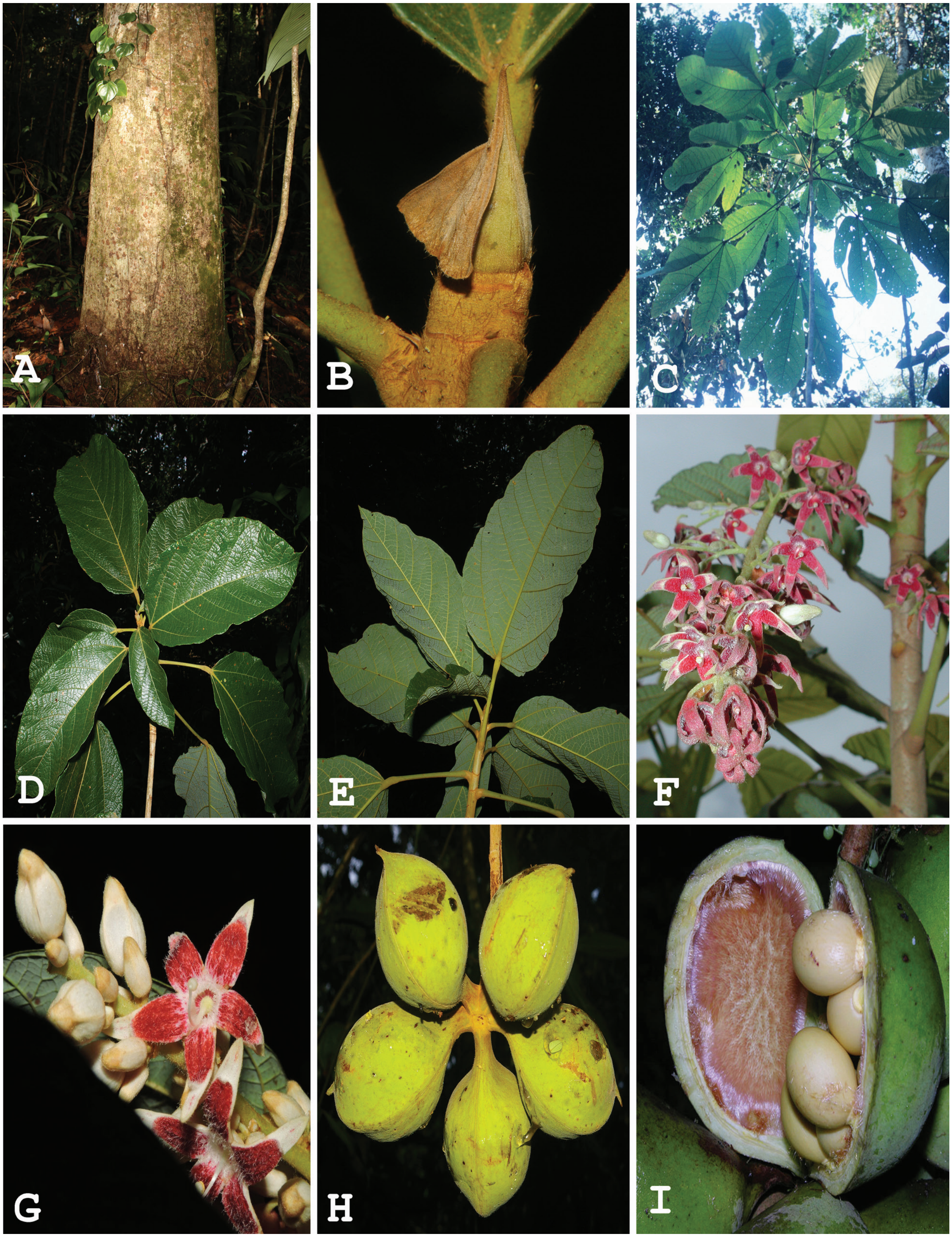


FIGURA 7. *Sterculia recordiana* Standl. **A**, base del tronco; **B**, ramita distal con yema terminal subtendida por la estípula; **C**, hojas lobuladas de un individuo juvenil; **D**, hojas en el lado adaxial; **E**, hojas en el lado abaxial; **F**, inflorescencias; **G**, flores estaminadas; **H**, folículos; **I**, folículo y semillas inmaduras. Fotografías A–B, D–E y H por A. Rodríguez, sin testigo; C por R. Aguilar, sin testigo; F por D. Solano, sin testigo; G por R. Aguilar, de *R. Aguilar 15355* (CR); I por O. Vargas, de *O. Vargas 720* (LSCR).

Limón, Pococí, Guápiles, Finca del Bosque Lluvioso, Sendero Central, 10°11'28"N, 83°51'28"W, 300–350 m, 05 setiembre 2005 (estéril), *L. Acosta 3677* (CR); Limón, Río Blanco, Las Brisas de Veragua, propiedad de Veraguas Rainforest, trayecto entre el restaurante y el serpentario, 09°55'28.7"N, 83°11'28.9"W, 387 m, 1 marzo 2011 (fls), *A. Estrada et al. 4798* (CR); Talamanca, Reserva Indígena Talamanca, cuenca del Sixaola, San Miguel Cabécar, Lomas Tsipubeta, 09°37'55"N, 82°53'55"W, 325–500 m, 18 febrero 1997 (fls), *J. González et al. 1745* (CR-221564, CR-2826980, MO); Limón, Fila Matama, Cerro Muchilla, Falda NW, Río Bananito, Selva Bananito Lodge, 09°49'30"N, 83°03'50"W, 100 m, 25 enero 2001 (frs), *J. F. Morales 7764* (CR); Limón, Barra del Colorado, N side, between town and ocean beach, 10°47'N, 83°35'W, 0–2 m, 26 enero 1986 (fls), *W. D. Stevens 24127* (CR, MO). Puntarenas: Golfito, Reserva Forestal Golfo Dulce, Península de Osa, alrededores de la Estación Agujas, 08°32'11.8"N, 83°25'31.8"W, 300 m, 22 mayo 2000 (estéril), *L. Acosta* et al. *1386* (CR-245030, CR-3387131); Golfito, Península de Osa, Reserva Forestal Golfo Dulce, Los Mogos, 08°45'30"N, 83°22'30"W, 100–200 m, 16 octubre 1991 (estéril), *R. Aguilar 542* (CR-156819, CR-2905700); Golfito, Estacion Sirena, Sendero Ollas, 08°27'36"N 83°34'48"W, 10 m, 11 febrero 1994 (fls), *R. Aguilar 3113* (MO); Rincón, Aguabuena Este, 08°42'N, 83°31'W, 50 m, 2 noviembre 1992 (fls), *R. Aguilar 1395* (CR-186924, CR-1570456, MO); Osa, Península de Osa, Reserva Forestal Golfo Dulce, Los Mogos, Bahía Chal, junto a la playa, 08°43'20"N, 83°26'30"W, 1 m, 6 enero 1994 (frs), *R. Aguilar* et al. *2973* (CR-205657, CR-1582482, MO); Osa, Península de Osa, Reserva Forestal Golfo Dulce, Bahía Chal, entrada a Chocuaco, 08°43'20"N, 83°26'40"W, 20–100 m, 18 setiembre 1995 (estéril), *R. Aguilar 4378* (CR-200629, CR-1590741); Osa, Sierpe, R. F. Golfo Dulce, Cuenca Térraba-Sierpe, Mogos, a 33 km de Chacarita, entrada San Luis cerca de la Quebrada Chal, finca de Isidro Mora, 08°44'00"N, 83°26'10"W, 100 m, 1 julio 2001 (fls), *R. Aguilar 6493* (CR-268028, CR-4151593); Osa, Península de Osa, vicinity of Sirena Field Station, Corcovado National Park, 08°30'N, 83°35'W, 0–50 m, 12 agosto 1984 (estéril), *A. Gentry 48489* (CR); Osa, Península de Osa, Reserva Forestal Golfo Dulce, Los Mogos, bosque primario en la Fila Mogos, 08°45'15"N, 83°20'32"W, 250 m, 23 octubre 1993 (frs), *J. F. Morales et al. 1938* (CR-169339, CR-1554881, MO); Puntarenas, Osa, Piedras Blancas, La Florida, Finca Bellavista, 08°47'N, 83°13'W, 300 m, 31 agosto 2011 (frs), *G. Rivera & M. Núñez 4573* (CR); Península de Osa, Alto Los Mogos, carretera a Rincón, 14 febrero 1986 (frs), *P. Sánchez 1230* (CR, F, MO); Aguabuena, 3.5 km W of Rincón, 08°43'N, 83°31'W, 350 m, 25 noviembre 1992 (estéril), *K. Thomsen* 508 (CR); Golfito, La Gamba, bosque de los Austriacos, 08°41'N, 83°13'W, 300 m, 26 mayo 1994 (estéril), *W. Huber & A. Weissenhofer 506* (CR). San José: Tarrazú, San Lorenzo, cerro Nara y alrededores, 09°29'20"N, 84°00'40"W, 800–1000 m, 26 julio 1995 (estéril), *M. M. Chavarría 912* (CR); Pérez Zeledón, Río Nuevo, Savegre Abajo, 09°27'10"N, 83°50'00"W, 600 m, 11 mayo 1999 (frs), *A. Estrada et al. 2187* (CR); Turrubares, valle del Tárcoles, Parque Nacional Carara, sector Bijagual, montaña Jamaical, 09°46'N, 84°34'W, 200 m, 27 julio 1995 (estéril), *Q. Jiménez et al. 1890* (CR-197401, CR-1578858); Puriscal, San Martín de Puriscal, Zona Protectora La Cangreja, cuenca del Río Negro, bosque primario al Este de la Fila Vara Blanca, 09°44'12"N, 84°23'28"W, 800 m, 20 noviembre 1993 (frs), *J. F. Morales 2063* (CR-173601, CR-2926319); Acosta, Sabanas, Fila Bustamante, sector Oeste, bosques residuales cerca del cruce a Teruel, 09°44'28"N, 84°16'03"W, 1000–1100 m, 25 junio 1995 (frs), *J. F. Morales 4500* (CR-197968, CR-1577281, MO); Garabito, valle del Tárcoles, Parque Nacional Carara, Estación Bijagual, 09°45'00"N, 84°33'50"W, 500 m, 23 julio 1990 (frs), *E. Rojas 116* (CR-181495, CR-1574020, MO); Reserva Biológical Carara, valle del Tárcoles, Estación Bijagual, 09°45'36"N, 84°36'00"W, 500 m, 23 julio 1990 (frs), *E. Bello 2346* (CR-201940, CR-1576078, MO); Puriscal, Cuenca del Tulín, Santa Rosa, Finca Celimo Jiménez junto al Río Negro, 09°41'50"N, 84°23'45"W, 350 m, 26 junio 1997 (estéril), *Q. Jiménez & L. Acosta 2304* (MO). PANAMÁ. Coclé: Above El Valle, short of La Mesa, 08°37'N, 80°07'W, 630 m, 23 febrero 1998 (frs), *G. McPherson 12137* (GH, MO); hills north of El Valle, 1000 m, 13 enero 1942 (frs), *P. H. Allen 2973* (MO). Colón: Site of proposed copper mine (MPSA), 08°55'43"N, 80°40'48"W, 75 m, 04 diciembre 2009 (estéril), *G. McPherson 21081* (MO). Panamá: Cerro Campana, west of Panama City, along trail to top, 08°40'N, 79°50'W, 850 m, 26 marzo 1988 (fls), *G. McPherson 12342* (GH, MO-2 cartulinas); cerro Campana, west of Panama City, along trail to top, 08°40'N, 79°50'W, 850 m, 26 marzo 1988 (fls), *G. McPherson 12354* (MO); Cerro Jefe region, 760–915 m [2500–3000 feet], 29 junio 1978 (fls), *B. Hammel 3684* (MO); along side road that turns off to west approx. 9.4 km N of Goofy Lake, 900 m, 11 marzo 1977 (estéril), *J. P. Folsom* et al. *1951* (MO).

*Sterculia recordiana* se reconoce entre sus congéneres con hojas simples por presentar hojas con el ápice cuspidado a obtuso, por lo general, con un mucrón apical alargado de hasta 4 mm de largo, aunque en ocasiones tempranamente caedizo, y la superficie a menudo rugosas en plantas adultas. Además, se caracteriza por ser un árbol 7–35 m de altura, con gambas apenas diferenciadas, por su condición siempre verde, por sus pecíolos 0.5–8.0 cm de largo, aunque hasta cerca de 18 cm en plantas juveniles, por sus hojas, en individuos adultos, con la lámina entera en contorno, oblonga, oblongo-elíptica a obovada, 4.5–18.0 cm de largo y 2–8 cm de ancho, mientras en los individuos juveniles la lámina es de 3- a 5-lobulada, hasta 50 cm de largo y 30 cm de ancho; la base obtusa a subcordada, la nervadura palmada, el margen entero y leve-sinuado, el envés esparcido a denso-puberulento, especialmente sobre los nervios principales, con tricomas estrellados y corto-estipitados, aunque en individuos juveniles, por lo general, glabrado o glabrescente y leve-glauco (fresco o seco), ramitas esparcida a densamente estrellado-pubescentes, aunque pronto-glabrescentes, por sus inflorescencias paniculadas, 2–20 cm de largo, por sus flores con el cáliz internamente rosado, rojo o rojo-castaño (en material fresco), pubescente, que entremezcla tricomas corto-estrellados (en la parte distal de los lóbulos, a partir del punto de inserción del apéndice), tricomas vermiformes alargados (esparcidos sobre los lóbulos debajo del punto de inserción de los apéndices, pero formando un anillo denso en la boca del tubo del cáliz) y tricomas papilosos (principalmente en el tubo del cáliz, debajo del anillo de tricomas vermiformes, esparcidos en los lóbulos), con un apéndice central 0.30–0.75(–1.20) mm de largo, aunque a menudo pronto-caedizo, por sus flores estaminadas con el tubo del cáliz 1–4(–7) mm de largo y 3.5–8.0 mm de ancho, y con lóbulos 6–15 mm de largo y 2–6 mm de ancho, con andróforo 4–10 mm de largo, por sus flores pistiladas o bisexuales, con el tubo del cáliz 2–4 mm de largo y 3–8 mm de ancho, y con lóbulos 9–16 mm de largo y 2.5–4.0 mm ancho, con androginóforo 4–7 mm de largo, y por sus folículos lateralmente expandidos, 6–10 cm de largo, 4–6 cm de ancho y 3.8–6.5 cm de alto (en frutos maduros aún no abierto), pardos o amarillo verdosos al madurar e internamente híspidos.

Taylor (1989) dividió esta especie en dos variedades, ambas registradas en la región mesoamericana; no obstante, nunca se hizo válida la nomenclatura.

***Sterculia xolocotzii*** T. Wendt & E.L. Taylor. Lundellia 2: 128. 1999. TIPO: MÉXICO. Veracruz: Municipio Minatitlán, 13.7 km al E de La Laguna sobre terracería a Uxpanapa, luego 3.8 km al N sobre camino nuevo (no completo) a Belisario Domínguez, afloramientos cársticos selva pertubada, rodeada por acahual, 17°18'30"N, 94°23'W, 130 m, 7 abril 1981 (fls y frs*), T. Wendt, A. Villalobos & I. Navarete* 3149 (Holotipo: MEXU; Isotipos: CHAPA, ENCB, F, GH, TEX).

**Nombres comunes:** Apompo, Apompillo (Wendt y Taylor, 1999), Majahua y Pepetaca (*T. Wendt 4241*).

**Distribución y hábitat:** endémica de México; 140–150 m de elevación. Se encuentra en las tierras bajas de los bosques lluviosos de la Región de Uxpanapa, en el límite de los estados de Veracruz, Oaxaca, Chiapas y Tabasco y a lo largo de la costa del Golfo de Veracruz (Taylor, 1989) (Mapa 2).

**Fenología:** flores en abril y mayo (Taylor, 1989). Frutos en abril (inmaduros) (Taylor, 1989) y octubre.

**Especímenes adicionales examinados:** MÉXICO. Oaxaca: Municipio Matías Romero, 8.3 km al S de Esmeralda, sobre camino al río Verde, luego 0.3 km al E sobre el camino al río Escondido, 17°06'N, 94°47'O, 140 m, 2 abril 1982 (fls), *T. Wendt 3819* (GH-2 cartulinas); Municipio Chimalapa, arroyo Choncolín, población de Nicolás Bravo, cerca rancho de Agustín Montero, más 3–4 km al S de la población de río Alegre, 17°10'30"N, 94°47"O, 150 m, 21 octubre 1983 (frs), *T. Wendt et al. 4241* (GH, LSU).

*Sterculia xolocotzii* se reconoce entre sus congéneres con hojas digitadamente compuestas por sus folíolos con el envés denso-hirsuto sobre las venas principales, aunque el resto de la lámina esparcido-hirsuto (notorio principalmente en hojas nuevas). Además, se caracteriza por ser un árbol de mediano porte, hasta 22 m de altura y 80 cm de diámetro, deciduo, con estípulas densamente estrellado-velutinas en el lado externo e interno, por sus hojas con pecíolos 7.3–22.5 cm de largo, denso-velutinos, pulvínulo basal débilmente desarrollada, apical conspicuo, por sus peciólulos 0.2–1.0(–1.4) cm de largo y articulados, folíolos 6–8, con lámina elíptica a estrecho-elíptica, proximales 7–12 cm de largo y 2–4 cm de ancho, terminales 12–17 cm de largo y 4–6 cm de ancho, glabras adaxialmente, por sus inflorescencias paniculadas, 11.0–25.5 cm de largo, por sus flores con el cáliz internamente rojo (en material fresco), el lado externo densamente estrellado-puberulento, el interno con papilas ferrugíneas en toda su extensión (aunque difusas entre la pubescencia) y densamente estrellado-viloso en los lóbulos y en la parte distal del tubo, tricomas ausente en la base del tubo, sin un apéndice central en el lado interno de los lóbulos, las estaminadas con el tubo del cáliz 2–4 mm de largo y 2.0–2.5 mm de ancho, los lóbulos 6.0–7.5 mm de largo y 1.8–3.0 mm de ancho y el andróforo ca. 5 mm de largo, proximal y distalmente esparcido-pubescente, que entremezcla tricomas hirsútulos y papilosos, las pistiladas (o bisexuales) con el tubo del cáliz 2.5–3.0 mm de largo y 2–3 mm de ancho, los lóbulos 5.2–8.0 mm de largo y 1.8–3.7 mm de ancho, y el androginóforo 4–5 mm de largo, proximal y distalmente esparcido-pubescente, que entremezcla tricomas hirsútulos y papilosos, y por sus folículos lateralmente compresos, 6.5–8.0 cm de largo, 2.3–3.8 cm de ancho y 3.5–5.5 cm de alto (en frutos maduros aún no abiertos), pardos o amarillo verdosos al madurar e internamente híspidos.

Esta especie es afín a *Sterculia mexicana,* de la que se distingue por las características presentadas en la clave y bajo los comentarios de la primera.

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# *CAPPARIDASTRUM ALBOANNULATUM*: A NEW SPECIES AND NEW RECORDS OF CAPPARACEAE FROM COLOMBIA

Xavier Cornejo[1,2] and William Vargas[3]

**Abstract.** *Capparidastrum alboannulatum*, a new species of tree of the Capparaceae, endemic to western Colombia, is described and illustrated. Its conservation status is here assessed as endangered. In addition, *Capparidastrum discolor*, *C. mollicellum*, and *Quadrella isthmensis* subsp. *isthmensis*, all species of Capparaceae previously known only from Mexico and Mesoamerica, are reported as new records for the flora of Colombia and South America.

**Keywords:** Capparaceae, Colombia, *Capparidastrum alboannulatum*, endemic

**Resumen.** Se describe e ilustra *Capparidastrum alboannulatum*, una nueva especie de árbol de Capparaceae, endémica del occidente de Colombia. El estado de conservación de *Capparidastrum alboannulatum* aquí asignado es en peligro. Además, *Capparidastrum discolor*, *C. mollicellum* y *Quadrella isthmensis* subsp. *isthmensis*, todas estas especies de Capparaceae previamente conocidas como restringidas a México y Mesoamérica, se reportan por primera vez para la flora de Colombia y América del Sur.

**Palabras claves:** Capparaceae, Colombia, *Capparidastrum alboannulatum*, endémica

*Capparidastrum* (DC.) Hutch. (Capparaceae) is a Neotropical genus of shrubs and trees, comprising two subgenera (*Capparidastrum* subgen. *Capparidastrum* and *C*. subgen. *Pulviniglans*) and 24 species, ranging from western Mexico to Bolivia in dry, moist, and wet forests, from sea level to 1600 m (Cornejo and Iltis, 2008; Cornejo and Iltis, 2016; Mercado et al., 2020; Cornejo, in prep.).

The following new species and three new records of Capparaceae, all from Colombia, were found after the publication of Capparaceae for the *Catalogue of the Plants and Lichens of Colombia* (Cornejo and Iltis, 2016), and the synopsis of Capparaceae for the flora of Colombia (Mercado-Gómez et al., 2019).

## TAXONOMY

**1. Capparidastrum alboannulatum** Cornejo & W. Vargas, *sp. nov.* TYPE**:** COLOMBIA. Valle del Cauca: Mun. Palmira, vereda El Tenjo, margen del río Nima, en la cordillera Central, en transición entre piedemonte seco y bosque húmedo subandino, 3°31'4.62"N, 76˚10'06.55"W, 1570 m, 20 April 2018 (fl, fr), *William Vargas 18923* (Holotype: ICESI; Isotype: COL). Fig. 1.

*Capparidastrum alboannulatum* is a new species from western Colombia that resembles *C. cuatrecasasianum* (Dugand) Cornejo & Iltis from Cundinamarca and Santander departments, but differs from the latter by the leaf blades glabrous (vs. densely pilose at least on veins beneath), the presence of a lower number of lateral veins, 7–9 (vs. 10–14), the flowers with an infracalycine white ring (vs. infracalycine white ring absent), larger floral nectaries, 6–7 mm wide (vs. 4–5 cm wide), and purplish-green ovary (vs. deep-purple ovary) at anthesis. It is also similar to *C. dugandii* Mercado-Gómez J. and M. E. Morales (2020) from Antioquia and Valle del Cauca in Colombia, but differs from the latter by the distinctively narrower leaf blades, 3–7 cm wide (vs. leaf blades 7.4–14.0 cm wide), flowers with an infracalycine white ring (vs. infracalycine white ring absent), purplish-green ovary (vs. yellowish-green to yellow ovary) at anthesis, seeds with a white embryo (vs. seeds with a light-yellow embryo), and a higher altitudinal pattern, at 1570 m (vs. 200 to 1200 m).

*Tree* to 5 m tall and 20 cm dbh; glabrous. Stipules not seen. *Leaf blades* chartaceous, elliptic to elliptic-obovate, 6–16 × 3–7 cm, cuneate to obtuse at base, acute and minutely apiculate at apex to barely obtuse, dark green and glabrous above, paler green and glabrous beneath; lateral veins 7– 9 on each side of the midrib; petioles 0.5–6.0 × 0.1–0.2 cm, glabrous, the pulvinus 2–7 mm, dark brown (dried). *Inflorescences* terminal, erect racemes, 6–15 cm, glabrous; central floral bract linear-lanceolate or narrowly oblong, ca. 3 mm, deciduous, the pair of lateral bracts narrowly triangular, ca. 1 mm, ± persistent; pedicels 2.0–2.5 cm, glabrous. Sepals deltoid, 4–5 × 7–8 mm, broadly divergent, yellowish-cream without, light green within, shallowly erose at margins. Floral nectaries conspicuous, ca. 2–3 × 6–7 mm, pink (fresh), black (dried). *Corolla* buds just preceding anthesis subglobose. Petals ovate-elliptic to elliptic, 16–20 × ca. 7–8 mm, divergent, more-or-less entire to erose at margins, green and glabrous without. Stamens ca. 27–40; filaments 5–7 cm; anthers ca. 3.0–3.5 mm, dorsifixed in basal third, white. Gynophore 6–7 cm, purplish at distal half, pink at base (fresh), glabrous. Ovary sublanceolate, 6–7 × 2 mm, inconspicuously ribbed, purplish green (fresh), glabrous; stigma truncate (fresh). Infructescences with gynophores 6–9 cm × ca. 3 mm, green (fresh). *Fruits* ovoid to irregularly obovoid, 3.5–8.0 × 3–7 cm, at maturity yellow, glabrous; fruit wall 4–8 mm thick,

Jorge Mercado, Rodrigo Botina, and Jorge Vélez-Puerta shared with the senior author their field images of *Capparidastrum dugandii*.

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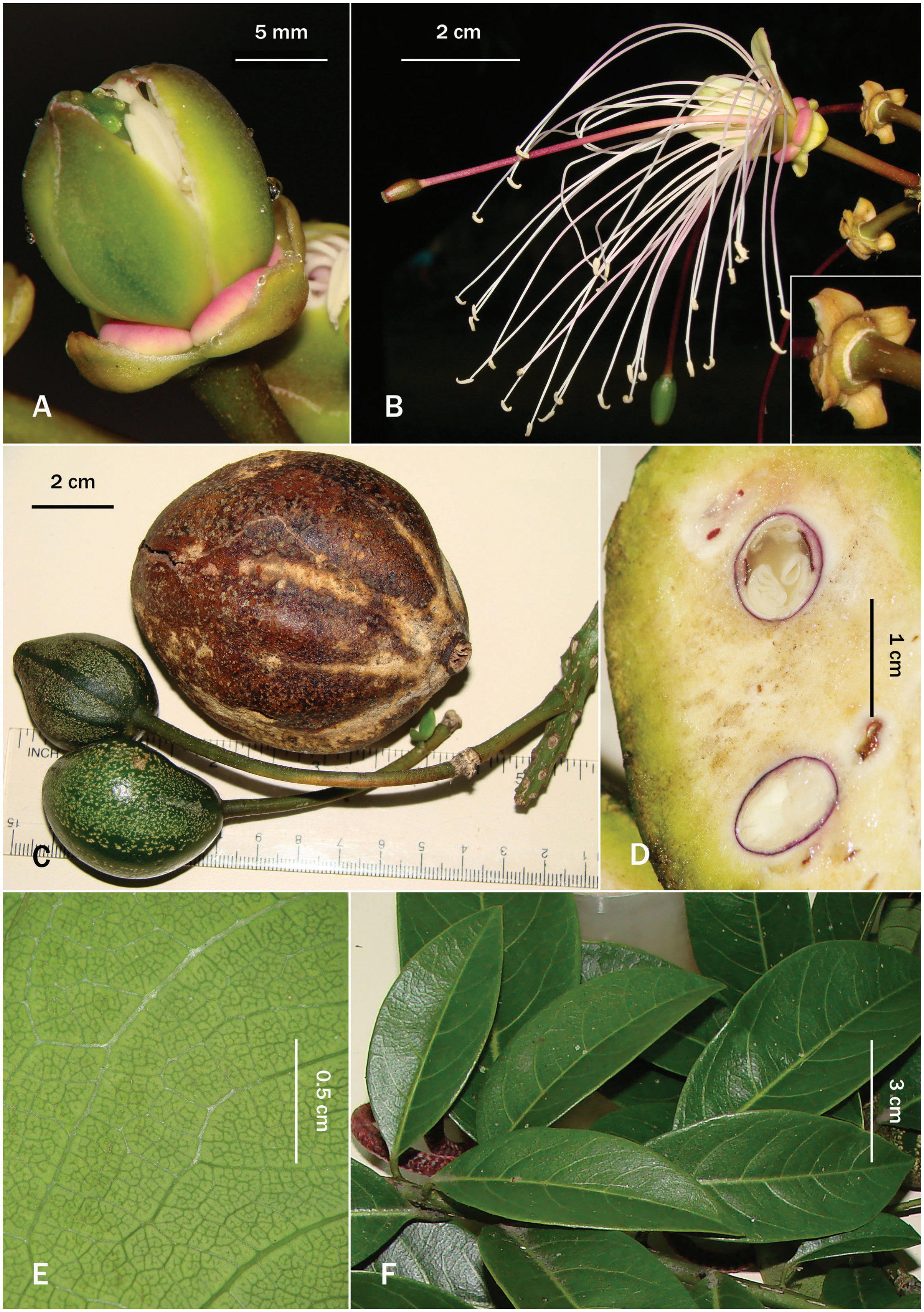

FIGURE 1. *Capparidastrum alboannulatum* Cornejo & W. Vargas. **A**, flower bud, lateral view; **B**, flower at anthesis, lateral view, and abaxial view of calyx at lower right square, note the white ring at the infracalycine zone; **C**, fruits; **D**, close up of a sectioned fruit, note the cut-open seeds with white embryos and convolute cotyledons; **E**, close up of reticulate tertiary veins, abaxial view; **F**, mature leaves, adaxial view. Photographs based on the holotype, *W. Vargas 18923* (ICESI). Photos by William Vargas.

coriaceous, flexible; pulp creamish white. Seeds 7–20, ca. 0.8 × 0.7 cm. Embryo white, convolute.

The placement of this new taxon in *Capparidastrum* subgen. *Pulviniglans* is supported by morphological evidence as the presence of glabrous leaves, 4 cushion-shaped rounded floral nectaries and pepo fruits. *Capparidastrum alboannulatum* may resemble two other species from Colombia, *C. cuatrecasasianum* and *C. dugandii*, but differs from both by the characters described in the diagnosis. This novelty is the only species in *Capparidastrum* and among all Neotropical Capparaceae that has flowers with a distinctive infracalycine white ring.

**Etymology:** the epithet *alboannulatum* of this taxonomic novelty refers to the white ring present at the base of calyx.

**Habitat and distribution:** known only from the type. *Capparidastrum alboannulatum* occurs in the Río Nima dry Andean foothills in Valle del Cauca, western Colombia. The type locality is characterized by steep slopes, with small alluvial valleys and hills dominated by secondary vegetation and pastures. It is found associated with species of the genera *Miconia* Ruiz & Pav., *Croton* L., *Casearia* Jacq., *Nectandra* Rol. ex Rottb., *Cinnamomum* Schaeff., *Ocotea* Aubl., *Ficus* L., and *Piper* L., among others. The fruits are consumed by rodents, but when they fall to the ground, they are also eaten by livestock, making their regeneration more difficult. It is a little known species without current uses. The populations are reduced to a few individuals, most of them seedlings and juveniles.

**Conservation status:** at present, the native vegetation of the area where *Capparidastrum alboannulatum* occurs is disturbed by selective timber cutting, deforestation, and forest fragmentation due to the advancement of the agricultural frontier and cattle farming. Therefore, the preliminary status of Endangered (EN B1ab[iii]) (IUCN, 2012) is assigned to this species.

In addition, three new records for the flora of Colombia and South America were found while studying the collections of Capparaceae in COL herbarium. Those are reported here for first time.

**2. *Capparidastrum discolor*** (Donn. Sm.) Cornejo & Iltis, Harvard Pap. Bot. 13(2): 233. 2008.

Basionym: *Capparis discolor* Donn. Sm., Bot. Gazette 24: 389. 1897. TYPE. COSTA RICA. Bois du Rodeo de Pacaca, 1100 m, January 1891, *H. Pittier 3537* (Holotype: CR [not seen]; Isotypes: BR [2, fragm. and photo at WIS], US [1392173]).

Synonym: *Morisonia discolor* (Donn. Sm.) Christenh. & Bing, The Global Flora 4: 139. 2018.

COLOMBIA. Antioquia. Mun. Amalfi, vereda Peldar, mina La Viborita, 6°55'N, 75°04'W, 1490–1600 m, 3 Oct 1992, *R. Fonnegra and Curso Palinología SEM 4537* (COL).

**Distribution:** the cited collection represents the southernmost record of this species, extending the geographical range from Mexico to Colombia.

**3. *Capparidastrum mollicellum*** (Standl.) Cornejo & Iltis, Harvard Pap. Bot. 13(2): 234. 2008.

Basionym: *Capparis mollicella* Standl., Proc. Biol. Soc. Wash. 37: 44. 1924. TYPE. MEXICO. Nayarit: La Bajada, 80 m, 1923, *J. G. Ortega 103* (Holotype: US [1111324]; Isotype: K [000220516]).

Synonym: *Morisonia mollicella* (Standl.) Christenh. & Bing, The Global Flora 4: 141. 2018.

COLOMBIA. Antioquia. Mun. Mutatá, Hoya del Río León o Bacubá, villa Arteaga, Las Caucheras, on a Hill nearby, rainforest, 140 m, 3 Oct 1961, *J. Cuatrecasas and L. Willard 26202* (COL).

**Distribution:** the cited collection represents the southernmost record of this species, extending the geographical range from Mexico to Colombia.

**4. *Quadrella isthmensis*** (Eichler) Hutch. subsp. ***isthmensis***, Gen. Fl. Pl. 2: 308. 1967.

Basionym: *Capparis isthmensis* Eichler in Martius, Fl. Bras. 13: 269. 1865. TYPE. COSTA RICA. "Habitat ad Costa Rica et Veraguas Americae Centralis," without date, *C. Hoffmann and J. Warszewicz 217* (Lectotype: B, B fragm. at M, WIS, designated by Iltis and Cornejo, 2010).

Synonym: *Morisonia isthmensis* (Eichler) Christenh. & Bing, The Global Flora 4: 141. 2018.

COLOMBIA. Chocó. Mun. Acandí, camino Sapzuro-la Maloka, rainforest, 25 Jul 2005, *S. E. Hoyos-Gómez, A. Upegui, E. Norena and I. Loaiza 362* (COL).

**Distribution:** the cited collection represents the southernmost record of this species, extending the geographical range from Mexico to Colombia.

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# *ACANTHOCAPPARIS* (CAPPARACEAE): A NEW GENUS FROM MESOAMERICA

Xavier Cornejo[1]

**Abstract.** On the basis of defined morphological characters, *Acanthocapparis*, a new monospecific genus of Capparaceae from Mesoamerica and a segregate of *Capparicordis*, is formally proposed. The new combination *Acanthocapparis yunckeri* is also provided. The genus occurs from northern Honduras to Campeche, in the Yucatan Peninsula of Mexico.

**Keywords:** *Acanthocapparis,* Capparaceae, Mesoamerica, new genus

**Resumen.** Con base en caracteres morfológicos definidos se propone formalmente un nuevo género monoespecífico de Capparaceae de Mesoamérica, *Acanthocapparis,* un segregado de *Capparicordis*. También se provee la nueva combinación *Acanthocapparis yunckeri*. Este nuevo género se distribuye desde el norte de Honduras hasta Campeche, en la Península de Yucatán, México.

**Palabras claves:** *Acanthocapparis,* Capparaceae, género nuevo, Mesoamérica

*Capparis yunckeri* Standl. was originally described as an outstanding taxon of Neotropical Cappar-aceae with "no species to which it is at all similar" and recognized by the "scandent habit and for the small, broad, copiously stellate-tomentose leaves" (Standley in Yuncker, 1940), a unique combination of traits among Mesoamerican Capparaceae (Cornejo and Iltis, 2015). The species was initially known only from the type collection, which consists of a branch with leaves and one (F) or two fruits (NY) gathered by T. G. Yuncker from a thicket in woodland, in the semiarid region near Coyoles, Department of Yoro, northern Honduras (Standley in Yuncker, 1940). After the original publication, the flowers of *C. yunckeri* remained unknown to the scientific community for almost 80 years.

Despite the different habit, the distinct leaf shape with prominent venation and dense stellate pubescence, and the pepo fruits that the type exhibits, *Capparis yunckeri* was provisionally placed in *Capparicordis* Iltis & Cornejo, a South American genus, pending availability of flowering specimens (Iltis and Cornejo, 2007). Since the establishment of *Capparicordis* in 2007, *C. yunckeri* remained a taxonomic puzzle until field images sent to the author by Paul House† from the Department of Yoro, northern Honduras, exhibited for first time the distinctive floral features of this species that do not fit those of *Capparicordis*. Furthermore, the presence of brachyblasts and/or thorn derived brachyblasts, a unique character among Neotropical Capparaceae, makes clear at first glance that *C. yunckeri* cannot be placed in *Capparicordis* nor in any other known genus, deserving to be recognized in its own. In addition, a collection with fruits held in MEXU from southeastern Campeche, which has remained without identification since 1996, turned out to be a new record of distribution for this taxon from the Yucatan Peninsula in southeastern Mexico. Therefore, a new genus, the respective new combination, and a full description for the species are formally presented here.

## Taxonomy

**Acanthocapparis** Cornejo, *gen. nov*.

TYPE**:** *Capparis yunckeri* Standl., Field Mus. Nat. Hist., Bot. Ser.9(4): 291–292. 1940.

*Acanthocapparis* has leaf blades densely stellate, similar in shape to those of *Capparicordis* Iltis & Cornejo but differing from the latter by the climbing (vs. shrubby) habit; presence (vs. absence) of brachyblasts and/or thorns; calyx with open (vs. closed) aestivation from early bud; petals oblong-obovate, white to creamish (vs. narrowly elliptic, yellow to orange), the nerves strongly ascendant and longitudinal toward apex (vs. pinnatinerved along petal blade); stamens in a higher number, ca. 20–25 (vs. 4–8); nectary dish bearing 4 nectary glands, each one attached on basal half of sepals (vs. nectary cup with 4 erect minute appendages inserted at the inner edge of calyx cup and apart from sepals); and pepo (vs. capsular) fruits.

*Woody liana*. *Brachyblasts* supraxillary, those often turning to thorns, densely ferrugineous stellate-tomentose, glabrescent. Stipules apparently absent. *Blades* subcordate to ovate or lanceolate. *Flowers* arranged at distal third of brachyblasts. *Floral buds* oblongoid. *Calyx* 1-seriate, valvate, sepals 4, equal, exhibiting the corolla from early bud. *Nectary dish* present, bearing 4 episepal green glands, the glands attached on basal half of sepals. *Petals* 4, oblong-obovate, white to cream, pinnatinerved from lower third, the nerves strongly ascendant and longitudinal toward apex. *Fruit* pepo; *seeds* cochleate-reniform, with a hair-infiltrated sarcotesta.

**Etymology:** *Acanthocapparis* is composed of the Greek prefix *Acantho*, which means spiny or thorny, and the genus *Capparis*, a name coined by Theophrastus (4th century BC; Inocencio et al., 2006), which became the mother genus that once comprised a significant part of the whole New World Capparaceae diversity and refers to the spiny New World *Capparis* L.

Thanks are due to Lilian Ferrufino, Paul House† (both TEFH), and Emily Lott (MEXU) for sharing images of *Acanthocapparis yunckeri* from their respective countries.

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**Distribution:** a monotypic genus ranging in the lowlands from northern Honduras to the Yucatan Peninsula of southeastern Mexico.

The generic name highlights the presence of spines, which is a rarity considering that none of the remaining genera of Capparaceae native to America is armed. Thorns that are present in most Old World *Capparis* s.str. (e.g., *C. spinosa* L., the type, and closely related species) are short, paired, stipular, clawlike, mostly retrorse or antrorse, and not solitary, supraxillary, ± straight, elongate, and derived from a brachyblast as in *Acanthocapparis*, the latter suggesting a different evolutionary origin.

The cordate-to-ovate leaves and densely stellate pubescence that *Acanthocapparis* presents resemble those of the South American genera *Capparicordis* (western Ecuador to southern Brazil and northern Argentina; Iltis and Cornejo, 2007) and *Mesocapparis* from Brazil (Cornejo et al., 2015). However, the liana habit, presence of supraxillary flowering brachyblasts and/or thorn-derived brachyblasts, and the respective floral differences as nectary structure and pattern of veins of petals are strong morphological support for not allowing the placement of *C. yunckeri* in any of those genera. The vegetative similarity among *Acanthocapparis*, *Capparicordis*, and *Mesocapparis* could be regarded as a case of convergent evolution (for differences see Table 1).

**Acanthocapparis yunckeri** (Standl.) Cornejo, *comb. nov.* (Fig. 1).

Basionym: *Capparis yunckeri* Standl., Field. Mus. Nat. Hist., Bot. Ser. 9 (4): 291. 1940. TYPE**:** HONDURAS. Dept. Yoro, Aguan River Valley, climbing in a thicket in woodland, semi-arid region near Coyoles, ca. 15°28'N 86°43'W, ca. 240 m, 25 July 1938 (fr), *T. Yuncker, J. Koepper & K. Wagner 8615* (Holotype: F; Isotype: NY; photo: WIS [F-neg.51614]).

Synonym: *Capparidastrum yunckeri* (Standl.) Iltis & Cornejo, Brittonia, 59(3): 251–254, f. 4A–I. 2007, *syn. nov.*

*Woody liana*. *Brachyblasts* supraxillary, (sub)patent to somewhat retrorse, 0.5–7.0(–10.0) cm, densely ferrugineous stellate-tomentose, glabrescent; after flowering, the brachyblasts often turning deciduous at terminal third and

Table 1. Comparison of *Acanthocapparis* and related Neotropical genera with cordate-to-ovate leaves and densely stellate pubescence.

| Feature | *Acanthocapparis* | *Capparicordis* | *Mesocapparis* |
|---|---|---|---|
| Habit | Liana | Shrub, occasionally with shortly scandent branches | Liana or scandent shrub |
| Supraxillary brachyblasts turning to thorns with age | Present | Absent | Absent |
| Flowering | Nocturnal | Diurnal | Diurnal |
| Floral bracts | Unknown | Shortly linear, deciduous from very early buds | Absent |
| Calyx aestivation | Open | Closed until near anthesis | Closed until near anthesis |
| Calyx | 1-seriate, valvate | 1-seriate, reduplicate-valvate | 2-seriate, decussate |
| Shape and color of petals | Oblong-obovate, white to cream | Narrowly elliptic, lemon-yellow to orange | Broadly obovate, white to cream or yellow |
| Petal nerves | Longitudinal, pinnatinerved from lower third | Pinnatinerved along midvein | Longitudinal-palmate |
| Number of stamens | Ca. 20–25 | 4–8 | Ca. 20–30 |
| Inflorescence | 1–3 flowers, on distal part of brachyblasts | Corymbose or racemose, subterminal and opposite to distal leaves | Solitary flower, axillary |
| Calyx nectary glands | 4 nectary glands adnate to sepals | 4 erect nectary appendages, linear to linear-triangular | 4 suberect nectary scales |
| Fruit type | Pepo | Capsular, opening along sutures at maturity, the soft and very flexible fruit wall splitting and falling apart in 2–4 segments at maturity | Pepo |

FIGURE 1. *Acanthocapparis yunckeri* (Standl.) Cornejo. **A**, flower at postanthesis; **B**, habit: thorns indicated by arrows; **C**, leafy branch bearing brachyblasts (*House et al*. *5427*, TEFH); **D**, thorny liana bearing a fruit (*Alvarez 6077*, MEXU); **E**, thorn and leaf base, detail. A–B, courtesy of Paul House, from Department of Yoro, northern Honduras.

remaining as thorns. *Stems and leaves* densely stellate-tomentose throughout, at least when young, the *blades* subcordate to ovate or lanceolate, 2.5–5.0(–7.0) × 2–4 cm, subcordate to broadly obtuse at base, entire and often rolled inward at margins, broadly obtuse to acute and mucronate at apex, coriaceous and evergreen, soon glabrescent, dark green above, matte beneath (fresh), on drying, often becoming brittle and sharply rolled inward in herbarium material. *Petioles* 3–8 mm, ferrugineous stellate-tomentose, glabrescent. *Flowers* 1–3, but only 1 developed and open at time, the 2 remaining as very young buds otherwise abortive, all arranged at distal third of brachyblasts. *Pedicels* 5–8 mm, stellate-tomentose. *Calyx* 1-seriate, valvate, sepals 4, equal, shortly lanceolate, 2–3 × 1–2 mm, patent at anthesis, exhibiting the corolla from early bud, stellate-tomentose. *Nectary dish* present, bearing 4 episepal green glands, the glands attached on basal half of sepals. *Petals* 4, oblong-obovate, ca. 1.2 × 0.7 cm, white to cream, pinnatinerved from lower third, the nerves strongly ascendant and longitudinal toward apex. *Stamens* ca. 20–25, exserted; filaments ca. 0.8 cm length, white, glabrous; anthers cream. *Gynophore* 2–4 mm, densely stellate-tomentose; *ovary* oblong-elliptic, ca. 5 mm, longitudinally sulcate, greenish-white, densely stellate-tomentose; stigma capitate, sessile, green. *Fruit* pepo, narrowly obovoid to oblong, 4.5–6.0 × 1.3–2.5 cm, densely stellate, glabrescent; *seeds* ca. 20–25, cochleate-reniform, with a hair-infiltrated sarcotesta.

**Habitat and distribution:** from northern Honduras to southeastern Campeche in the center of the Yucatan Peninsula of southeastern Mexico, 150–240 m, in thicket in woodland, in semiarid regions to evergreen tropical forest (“selva baja perennifolia”).

**Additional specimens examined:** HONDURAS. Atlántida: (based mostly on R.A. Howard’s [Arnold Arboretum] letter to Iltis of November 1965) Los Dragos pine lands at a place called Jutiapa 15°47'N, 86°35'W, and ca. 1 km from, and the first village due south of, the coastal town of Nuevo Armenia, 3 Aug 1951 (fr), *R. Howard, W. Briggs, P. Kamb, I. Lane & R. Ritland 540* (A, photocopy WIS). **Yoro:** Municipio Arenal, 15°22'50"N 86°61'31"W, 260 m, 8 Apr 2011 (fl), *P. House, H. Vera, I. Rivera 5427* (TEFH, 2 sheets). MEXICO. Campeche: Mun. Champotón, a 120 km SO de Xpujil, alrededores de la zona arqueológica de Calakmul, 18°06'N, 89°50'W, 150 m, 7 Jul 1996 (fr), *Pascual Alvaro 340* (MEXU, 2 sheets).

Among Neotropical Capparaceae, *Acanthocapparis yunckeri* is the only liana that produces flowering brachyblasts and/or brachyblast-derived thorns. The highly reduced to essentially absent gynophores in flowers or fruits is an unusual characteristic shared with few other genera of New World Capparoids that also occur in xerophytic lowland areas, like *Quadrella quintanarooensis* Iltis & Cornejo, endemic to the state of Quintana Roo, Mexico (Yucatan Peninsula), and *Cynophalla heterophylla* (Ruiz & Pav. ex DC.) Iltis & Cornejo in coastal Ecuador and northwestern Peru.

## Key to the Neotropical Genera of Capparaceae with Cordate to Ovate Leaves and Densely Stellate Pubescence

1a. Shrubs; inflorescence racemose or corymbose, subterminal and opposite to distal leaves; petals narrowly elliptic, pinnatinerved, the secondary nerves inserted along midvein; stamens 4–8; fruit capsular, dehiscent with a thin, soft, and very flexible fruit wall . . . . . . . . . . *Cappariicordis*

1b. Lianas; flowers solitary, axillary, or on brachyblasts; petals broadly obovate or shortly oblong, with longitudinal nerves, the secondary nerves inserted at basal third of midvein; stamens 20–30; fruit pepo . . . . . . . . . . 2

2a. Flowering brachyblasts and/or thorns absent, the flowers solitary, axillary; calyx 2-seriate, decussate, with closed aestivation until near anthesis, petals broadly obovate, the nerves longitudinal-palmate; nectary scales suberect; Brazil. . . . . . . . . . . *Mesocapparis*

2b. Flowering brachyblasts and/or thorns present; calyx 1-seriate, valvate, with open aestivation from very young buds, petals shortly oblong, the nerves pinnate and strongly ascending at lower third of blade, longitudinal at distal two thirds; nectary glands adnate to sepals on adaxial side; northern Honduras to southeastern Mexico . . . . . . . . . . .*Acanthocapparis*

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# *PELLICIERA BENTHAMII* (TETRAMERISTACEAE): A NEW STATUS AND LECTOTYPIFICATION OF AN OVERLOOKED NEOTROPICAL MANGROVE

XAVIER CORNEJO[1,2] AND CARMEN BONIFAZ[1]

**Abstract.** On the basis of previously documented genetic, morphological, and ecological evidence, a new status at specific rank and the respective lectotypification are formally presented for *Pelliciera rhizophorae* var. *benthamii* (Tetrameristaceae). A key to identify the species is provided.

**Keywords:** Mesoamerica, *Pelliciera,* Tetrameristaceae

**Resumen.** Con base en evidencia genética, morfológica y ecológica previamente presentada se establece formalmente un nuevo estatus a nivel de especie y se lectotipifica a *Pelliciera rhizophorae* var. *benthamii* (Tetrameristaceae). Se presenta una clave para la identificación de las especies de *Pelliciera*.

**Palabras claves**: Mesoamérica, *Pelliciera,* Tetrameristaceae

*Pelliciera* Planch. & Triana (Tetrameristaceae) is a Neotropical genus of mangrove that inhabits the Pacific coast from the Nicoya Gulf in the province of Puntarenas, western Costa Rica, to the Muisne estuary in the province of Esmeraldas, northwestern Ecuador; and on the Caribbean side, from the Gracias a Dios department in eastern Honduras, to the Bolivar department, northern Colombia (Kobuski, 1951; Jiménez, 1984; Cornejo, 2014). The genus is represented solely by *Pelliciera rhizophorae* Planch. & Triana, a species of mangrove with conspicuous flowers visited by hummingbirds and pollinated by bats and regarded as the oldest living mangrove, fossil records of which date back to the Eocene (Wijmistra, 1968). *P. rhizophorae* comprises two varieties, both formally presented at the same time in the original publication of the genus and species (Triana and Planchon, 1862). The typical variety is characterized by flowers with greenish floral bracts; the second variety, *P. rhizophorae* var. *benthamii* Triana & Planch., can be recognized at first glance in the field or fresh material by the pink to crimson-red floral bracts. Unfortunately, the original color of the floral bracts, which is regarded as among the main distinguishing morphological characters, and the color of the flower, which turns dark brown during the herborization process, cannot be observed in herbarium material (obs. pers.). Subsequently, *P. rhizophorae* var. *benthamii* has been reduced to synonymy with the typical species, even in regions where the former variety does not occur, such as in coastal Ecuador (Kobuski, 1951; Jørgensen and León-Yánez, 1999).

In recent years, on the basis of molecular and morphological traits, as well as on geographical and climatic distribution, two well-defined groups, named variants or morphotypes, have been found in populations of *Pelliciera rhizophorae* that occur on both coasts of America (Castillo-Cárdenas et al., 2014, 2015; Garzón-Bautista et al., 2018). "Variant A," a group that comprises individuals with greenish, white-to-cream floral bracts that correspond to clade A (sensu Castillo-Cárdenas et al., 2014, 2015), is consistent with the typical variety; "variant B," represented by individuals with pink-to-red floral bracts that correspond to clade B (sensu Castillo-Cárdenas et al., 2014, 2015), is consistent with *P. rhizophorae* var. *benthamii*. Both groups have been interpreted as "geographically isolated genetic variants" and "intraspecific lineages that inhabit different climatic niches" (Castillo-Cárdenas et al., 2014, 2015; Garzón-Bautista et al., 2018). However, differences in molecular and morphological traits among both highly differentiated groups and in their geographical and climatic distributions, the fact that neither intermixed populations nor hybrids between these two "variants" have been found in the field, and the lack of shared haplotypes in each group are here regarded as strong support for the recognition of *P. rhizophorae* var. *benthamii* at the rank of species and not merely as a second intraspecific lineage under *P. rhizophorae*, as had been previously suggested (Castillo-Cárdenas et al., 2014, 2015). Therefore, a new status is formally proposed for a second species of tea mangrove in the Neotropics. As no holotype was designated in the original publication of *P. rhizophorae* var. *benthamii*, just a reference of Bentham's communication that was collected on the western coast of Central America by Sutton Hayes (Triana and Planchon, 1862), a lectotypification is also proposed following Arts. 7.11, 9.3, and 9.17 of the ICBN *Shenzhen Code* (Turland et al., 2018).

## TAXONOMY

**Pelliciera benthamii** (Triana & Planch.) Cornejo, *stat. nov.* Fig. 1.

Basionym: *Pelliciera rhizophorae* var. *benthamii* Triana & Planch., Ann. Sci. Nat., Bot. sér. 4, 17: 381. 1862. TYPE: PANAMA. Rio Grande swamp with mangroves, June 1861 (fl, fr), *S. Hayes 76* (Lectotype: K-000630592 designated here; Isotype: K-000648531).

Synonym: *Pelliciera rhizophorae* var. *rhizophorae non auct*.

**Local name:** mangle piñuelo (Calderón-Sáenz, 1982).

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Thanks are due to K herbarium for permission to reproduce the image of *Pelliciera rhizophorae* var. *benthamii*.

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FIGURE 1. *Pelliciera benthamii* (Triana & Planch.) Cornejo. Photograph of the lectotype proposed herein, *S. Hayes 76* (K-000630592) © The Board of Trustees of the Royal Botanic Gardens, Kew. Reproduced with the consent of the Royal Botanic Gardens, Kew.

**Habitat and distribution:** Pacific coast of Panama and Caribbean basin, in river mouth at mangroves located in zones under 1850 mm of annual average precipitation (as variant B in Castillo-Cárdenas et al., 2014, 2015). Different from other mangroves in the Neotropics, the small trees of *Pelliciera benthamii* often look like a dwarf version of *P. rhizophorae* (Calderón-Sáenz, 1982). Taking into account that *P. rhizophorae* is pollinated by bats, particularly the leaf-nosed bat (*Glossophaga soricina* Pallas, Phyllostomidae), as first hypothesized by Cornejo (2014) and more recently confirmed in a photograph by Chein Lee at Utría National Park, Department of Choco, Colombia (photograph available at https://www.flickr.com/photos/25872797@N02/42642738092), the notorious differences in floral sizes and colors of bracts among *P. rhizophorae* and *P. benthamii* may suggest different pollinators. Additional field studies are suggested for this interesting mangrove species.

## KEY TO THE SPECIES OF *PELLICIERA*

1a. Trees to 30 m tall; floral bracts light green, white, or cream, often 8.8–10.2 cm long × 4.0–4.7 cm wide; sepals 1.5–2.5 cm long, pure white; petals pure white; pistil 5.8–7.2 cm long; in mangroves located in areas with over 1900 mm of annual average precipitation. . . . . . . . . . . . . . . . *Pelliciera rhizophorae*

1b. Trees to 10 m tall; floral bracts pink to red, often 4.5–6.3 cm long × 1.4–1.8 cm wide; sepals 1.0–1.7 cm long, white to pink or reddish; petals often pink, few times white; pistil 3.2–5.0 cm long; in mangroves located in areas with less than 1850 mm of annual average precipitation. . . . . . . . . . . . . . . . *Pelliciera benthamii*

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# *ANDERSONIELLA*: A NEW GENUS OF NEOTROPICAL MALPIGHIACEAE

Charles C. Davis,[1,2] Lucas C. Marinho,[1,3] and André M. Amorim[4]

**Abstract.** Morphological and molecular investigations of the galphimioid clade in the angiosperm family Malpighiaceae revealed that three species previously assigned to *Lophanthera* are more closely allied with *Spachea*. These species are transferred to the newly described genus *Andersoniella* and include *A. hammelii*, *A. marcelae*, and *A. spruceana*, the type species of the genus.

**Keywords:** galphimioid clade, *Lophanthera*, Malpighiales, *Spachea*, taxonomy

**Resumo.** Investigações moleculares e morfológicas no clado galphimioide da família Malpighiaceae revelaram que três espécies previamente associadas ao gênero *Lophanthera* são mais intimamente relacionadas ao gênero *Spachea*. Essas espécies são transferidas para o novo gênero *Andersoniella* e incluem *A. hammelii*, *A. marcelae*, and *A. spruceana*, esta última, a espécie tipo do gênero.

Malpighiaceae are an angiosperm family of trees, shrubs, and vines in tropical and subtropical forests and savannas (Anderson, 2004). They comprise approximately 1,300 species in 77 genera. The majority of their genera and species are found in the New World and typically possess unicellular, two-branched hairs, simple opposite leaves, bilaterally symmetrical flowers with two large oil glands on the abaxial surface of four or all five sepals, five clawed petals, 10 stamens, and a tricarpellate gynoecium with one ovule per locule (Anderson, 2004). The relative floral uniformity in the group (Anderson, 1979; Davis et al., 2014) led earlier researchers to define genera and tribes principally on the basis of fruit morphology (e.g., Niedenzu, 1928; Davis et al., 2001). Numerous phylogenetic investigations over the past two decades, however, have highlighted the problematic nature of this single-character taxonomy (Cameron et al., 2001; Davis et al., 2001, 2004; Davis, 2002; Davis and Anderson, 2010).

These phylogenetic investigations have largely supported, and inspired, extensive taxonomic revisions in the family, especially the recircumscription and description of several genera (Anderson and Davis, 2005a,b, 2006, 2007, 2012, 2013; Anderson, 2011). They also revealed uncertainties about the status of other genera that merit further attention. These uncertainties relate to generic circumscription on morphological grounds, combined with a lack of phylogenetic support, insufficient taxon sampling, or both. In particular, previous efforts revealed the non-monophyly of several genera that still lack proper or more comprehensive taxonomic treatment, including *Janusia* A. Juss. (and close relatives *Aspicarpa* Rich. and *Gaudichaudia* Kunth), *Lophanthera* A. Juss., *Mascagnia* (Bertero ex DC.) Colla, *Sphedamnocarpus* Planch. ex Benth & Hook. f., and *Tetrapterys* Cav. (Davis and Anderson, 2010). A major goal of our efforts for nearly two decades has been to improve the resolution of the Malpighiaceae phylogeny by comprehensively sequencing representatives of all genera plus a much broader species sampling of the larger and more problematic genera (Davis et al., 2001; Davis and Anderson, 2010). Resolving these uncertainties and evaluating these inferred phylogenies in light of morphology continue to be a major focus of our research and the basis for this taxonomic update.

Here, we focus our efforts on taxonomic delimitation within the galphimioid clade sensu Davis et al. (2001) which comprises four genera whose species are widely distributed across the neotropics: *Galphimia* Cav., *Lophanthera*, *Spachea* A. Juss., and *Verrucularia* A. Juss. In particular, Davis and Anderson (2010) previously identified the genus *Lophanthera* as non-monophyletic using a combination of plastid, nuclear, and morphological data, but opted not to make any formal taxonomic or nomenclatural changes at that time. Ongoing efforts to apply plastid genome data to these questions have reinforced published findings that *Lophanthera* should be recircumscribed. Along these lines, preliminary results combining plastid *mat*K, *ndh*F, and *rbc*L data with nuclear ribosomal ITS data (Fig. 1; C. Davis et al., unpubl.) identify a well-supported core *Lophanthera* clade

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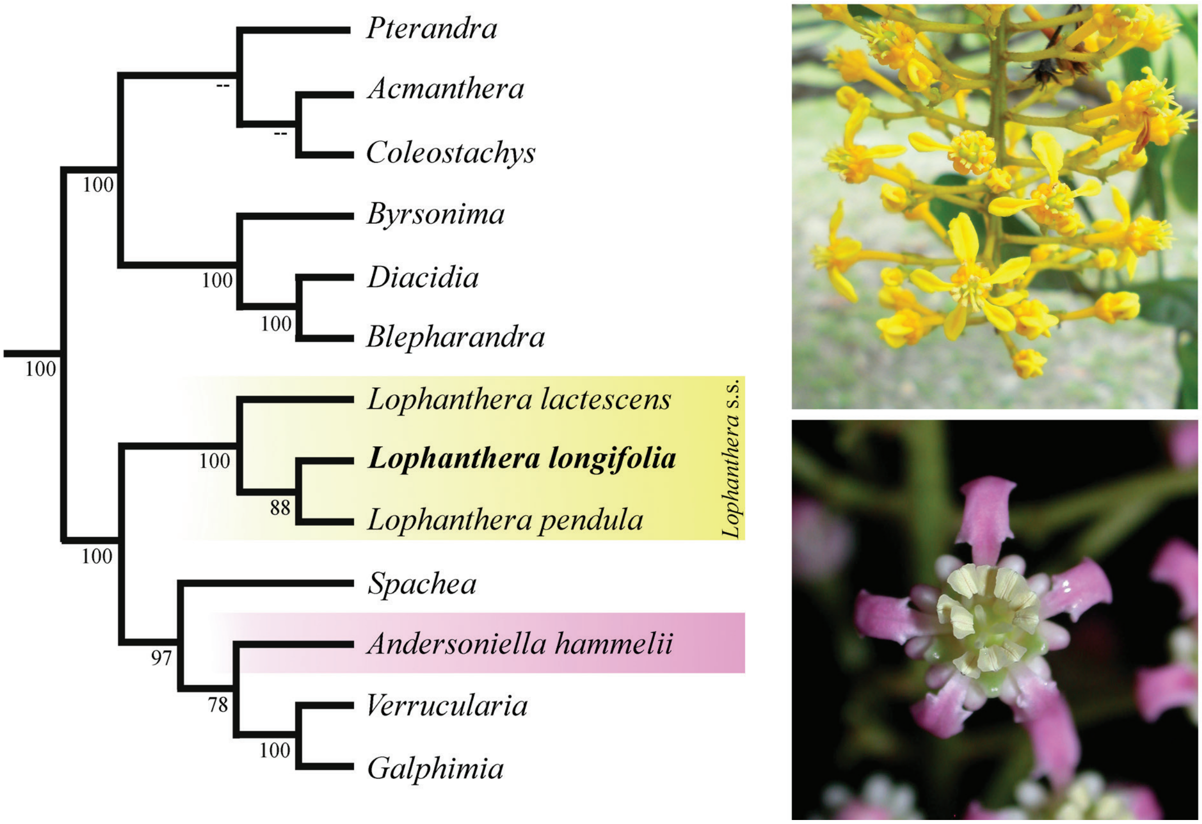

FIGURE 1. Phylogenetic tree showing the placement of *Andersoniella* and *Lophanthera* s. str. in the galphimioid clade of Malpighiaceae. Name in boldface indicates the type species of the genus *Lophanthera*. Bootstrap values are given above branches. The majority rule consensus tree shown here is summarized from a larger phylogenetic analysis of Malpighiaceae using combined plastid *mat*K, *ndh*F, and *rbc*L, and nuclear ITS; all genes were sequenced for all taxa (C. Davis et al., unpubl.). Voucher for *Andersoniella hammelii* sequenced: *Schatz 1034*, MICH.

(100% BP; hereafter *Lophanthera* sensu stricto [s. str.]), which includes the type species of the genus [*L. longifolia* (Kunth) Griseb.]. In contrast, the Mesoamerican species *Lophanthera hammelii* W. R. Anderson is more closely related to the genera *Galphimia*, *Verrucularia*, and *Spachea*. In light of these investigations, combined with new insights into the morphology of these groups, we newly describe this *Lophanthera* segregate as the genus *Andersoniella*.

**Andersoniella** C. Davis & Amorim, *gen. nov.* TYPE: *Andersoniella spruceana* (Nied.) C. Davis & Amorim (≡*Lophanthera spruceana* Nied.).

Species of *Andersoniella* differ from species of *Lophanthera* s. str. by their petal color (pink or white to pink vs. vivid yellow), dorsal surface of petal (rounded, smooth, or if carinate only slightly in the claw vs. keeled or carinate), cocci dorsum (smoothly rounded vs. keeled), and ventral areole of cocci (broad and flat vs. very narrow); and from species of *Spachea* in their leaves with persistent glands found only on the abaxial surface (vs. glands on both surfaces), bisexual flowers (vs. functionally unisexual flowers), anthers winged (vs. unwinged), and stigma minute and apical (vs. stigma large and reniform or bilobed).

Small- to medium-sized shrubs or trees, stems densely or loosely sericeous to glabrate, hairs copper-colored to reddish when present, lenticels present or not. Lamina abaxially ± persistently sericeous with hairs initially dense on midrib, bearing 2–3(–5) impressed glands restricted to abaxial surface, glands borne singly along midrib, or in pairs on opposite side of midrib, rarely several small glands borne in a row along each side, lamina adaxially glabrate or sparsely sericeous on midrib; petiole densely and ± persistently sericeous to glabrate, eglandular (but sometimes glands on decurrent base of lamina seeming to be on apex of petiole); stipules intrapetiolar, narrowly or distinctly triangular, abaxially sericeous, adaxially sericeous proximally to glabrescent, completely connate or free at apex. Inflorescence terminal, rarely axillary, pendent, rarely erect, with a pair of sterile and much-reduced leaves at base or not, thyrse composed of cincinni of 1–3(–4–5) bisexual flowers, axis loosely to densely sericeous like stems; bracts triangular, abaxially sericeous, eglandular; primary and secondary peduncles loosely sericeous, smaller or bigger than pedicels, bearing 2 bracteoles borne slightly below its apex; bracteoles like bract but smaller, eglandular or bearing 1(–2) gland(s), gland sessile or bearing a spatulate apical (peltate?) extension terminating in a discoid gland.

Pedicel loosely sericeous. Sepals bearing glands or not, slightly revolute in anthesis, rarely sericeous or glabrescent on both sides but occasionally bearing a few hairs along margin, lateral sepal eglandular, biglandular or 2 adjacent sepals bearing a single gland each, glands white, ellipsoidal, anterior sepal eglandular or biglandular; glands distally free from sepals and slightly reflexed. Petals generally pink (white to pink in *A. spruceana*), glabrous, dorsally rounded, smooth or slightly carinate on claw, nearly entire or minutely denticulate; posterior petal (the "flag") different from lateral 4 petals, more erect and with a slightly longer and thicker claw. Stamens 10, all fertile, filaments straight, free or slightly connate only at very base, glabrous; anthers ± alike, with membranous wings, connective widest at base on apex. Gynoecium glabrous or densely sericeous, bi- or tricarpellate; ovary glabrous to densely sericeous, all locules fertile; styles 2–3, subulate, long, slightly incurved at apex; stigma minute and apical. Fruit schizocarpic, breaking apart into 2 or 3 dry, 1-seeded cocci, cocci separating from a pyramidal base, glabrous to thinly sericeous, narrowly or irregularly ovoid, dorsally smoothly rounded, not or only obscurely carinate at apex; ventral areole broad and flat.

**Eponymy:** this genus honors William R. Anderson (1942–2013), friend and life-long student of Malpighiaceae. For nearly 25 years, Bill served as our closest mentor, guiding us in the beauty and intellectual pursuits of this fascinating plant family. For those who knew him, he set a high bar and shared his time and comments generously and often candidly. He has been an inspiration to us and is deeply missed.

**Distribution:** *Andersoniella* occurs in Central America (Nicaragua and Costa Rica) and southward to northwest South America in the Amazon region (Colombia and the Brazilian state of Amazonas).

Species of *Andersoniella* can be recognized by the presence of 2–3(–5) impressed glands on each side of the midrib or in pairs on the abaxial surface of the lamina (Fig. 2A), thyrsoid inflorescences composed of 1–3(–4–5) flowered cincinni, flowers bisexual (Fig. 2E), sepals distally free from the petals and slightly reflexed (Fig. 3C), pink or white to pink petals, dorsally rounded, smooth or slightly carinate on the claw, posterior petal differentiated from the 4 lateral petals, more erect and with a slightly longer and thicker claw, gynoecium bi- or tricarpellate; coccus dorsally smoothly rounded (Fig. 3D), ventral areole broad and flat.

*Andersoniella* is closely related to *Spachea*, *Galphimia*, and *Verrucularia*. Despite its closer relationships to *Galphimia* and *Verrucularia*, *Andersoniella* shows a greater morphological affinity with *Spachea*. Shared features of members of *Andersoniella* and *Spachea* include glands on the lamina, 1(–2) bracteole(s) bearing a discoid gland, petals white to pink, and a bi- to tricarpellate gynoecium. Species of *Andersoniella* are clearly distinguished from members of *Spachea* in their laminas with glands present only on the abaxial surface (vs. glands on both sides of lamina), bisexual (vs. unisexual) flowers, anthers with wings (vs. anthers unwinged), and stigma minute and apical (vs. stigma large and reniform or bilobed).

*Andersoniella* differs from *Galphimia* and *Verrucularia* in the presence of glands on the abaxial lamina surface, borne singly along midrib, or in pairs on opposite side of the midrib (vs. glands absent in *Verrucularia* or borne on the margin near or at the base, or on the petiole as in *Galphimia*), sepals generally with oil glands (vs. sepals without oil glands in *Galphimia*), petals pink or white to pink (vs. petals yellow to reddish in *Galphimia* and yellow in *Verrucularia*), the posterior petal unequal (vs. the posterior petal hardly differentiated from the lateral 4 petals in *Galphimia* and *Verrucularia*), anthers ± alike, with membranous wings (vs. anthers subequal, unwinged in *Galphimia* and alike, or with vesicular outgrowths in *Verrucularia*).

In addition to the characters outlined in our diagnosis, we can include geographical distribution to distinguish species of *Andersoniella* from species of *Lophanthera* s. str. Species of *Lophanthera* s. str. are distributed in South America, east of the Andes, while *Andersoniella* occurs in Central America southward to northwestern South America in the Amazon region (*A. spruceana*). Geographical distribution and habitat are also useful in distinguishing species of *Andersoniella* from species of *Galphimia* and *Verrucularia*. Among species in the galphimioid clade genera, *Galphimia* species are the most widely distributed and most strongly associated with dry habitats. The majority of *Galphimia* species are found in dry forests of Mexico extending south to Central America, with a few species reaching the Amazon basin, Bolivia, and southern/eastern Brazil to northern Argentina (Anderson, 2007). The distribution of *Verrucularia* species is restricted by soil and altitude. *Verrucularia* has only two species disjunctly distributed between the *Chapada Diamantina*, in the Brazilian state of Bahia, and *Serra do Aracá*, in the Brazilian state of Amazonas. Species in this genus inhabit waterways in high rocky outcrops.

**Andersoniella hammelii** (W.R. Anderson) C. Davis & Amorim, *comb. nov.*

Basionym: *Lophanthera hammelii* W.R. Anderson, Brittonia 35(1): 37, f. 1–2. 1983. TYPE: COSTA RICA. Província de Heredia: Finca La Selva, OTS Field Station on Río Puerto Viejo just E of its junction with Río Sarapiquí, elev. about 100 m, Rafael's point on the river, about 300 S × 1300 E m grid, 1 August 1980 (fl. and fr.), *B. Hammel 9397* (Holotype: MICH; Isotypes: DUKE, F).

**Distribution:** *Andersoniella hammelii* occurs from Nicaragua south to Costa Rica (Anderson, 1983).

**Andersoniella marcelae** (W.R. Anderson) C. Davis & Amorim, *comb. nov.*

Basionym: *Lophanthera marcelae* W.R. Anderson, Acta Bot. Mex. 109: 37. 2014. TYPE: COLOMBIA. Chocó: Región del (Bajo) Río Baudó, 6 February 1967 (im. fl.), *H. P. Fuchs, L. Zanella & J. H. Torres R. 21771* (Holotype: COL).

**Distribution:** *Andersoniella marcelae* occurs in the Chocó region of Colombia, on the western side of the Andes (Anderson, 2014).

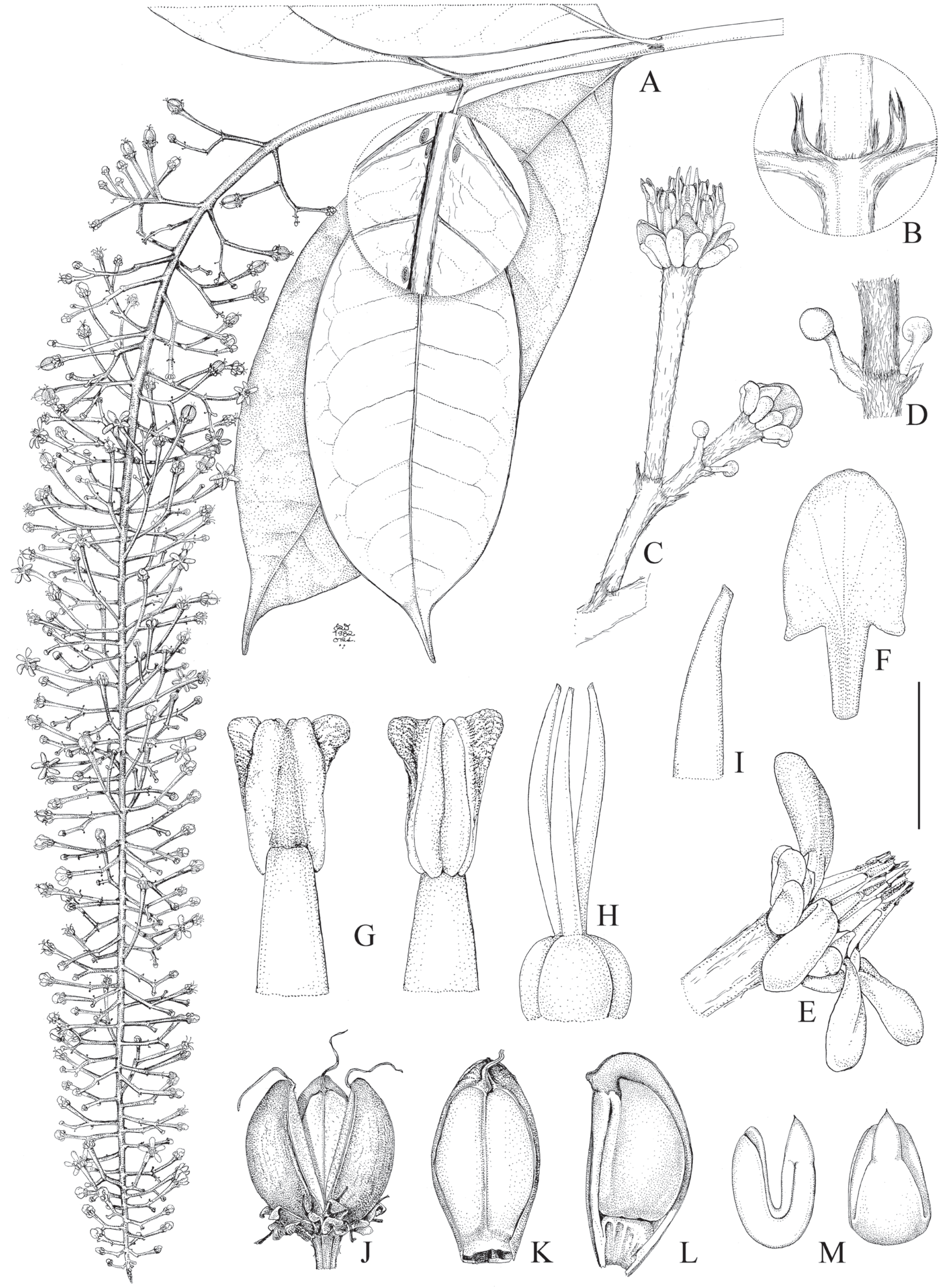

FIGURE 2. Morphology of *Andersoniella hammelii* (W.R. Anderson) C. Davis & Amorim. **A**, flowering branch; **B**, stem node magnification to show stipules; **C**, 2-flowered cincinnus; **D**, bracteole glands; **E**, flower, side view, posterior banner petal upright; **F**, banner petal, adaxial view; **G**, anthers, abaxial view (left) and adaxial view (right); **H**, gynoecium; **I**, distal portion of style; **J**, fruit; **K**, single mericarp, adaxial view; **L**, mericarp in longitudinal section, with seed; **M**, embryos, side view (left) and abaxial view (right). Scale-bar equivalents: A, 3 cm (6 mm); B–C, 6 mm; D, 3 mm; E, 4 mm; F, 3 mm; G, 1 mm; H, 1.4 mm; I, 0.7 mm; J, 5 mm; K–M, 3.3 mm. A–B based on *Grayum 2231A*, DUKE; C–M based on *Hammel 9397*, MICH. Drawn by Karin Douthit.

FIGURE 3. *Andersoniella hammelii* (W.R. Anderson) C. Davis & Amorim. **A**, flowering branch, detail showing the distal part of the inflorescence; **B**, floral buds; **C**, flower, front view, posterior petal upright; **D**, immature fruits. Photos by O. Vargas, from the *Florula Digital de La Selva*.

**Andersoniella spruceana** (Nied.) C. Davis & Amorim, *comb. nov.*

Basionym: *Lophanthera spruceana* Nied., Arbeiten Bot. Inst. Königl. Lyceums Hosianum Braunsberg 5: 30. 1914. TYPE: BRAZIL. Amazonas: prope Panuré ad Rio Uaupés, October 1852–January 1853 (fl.), *R. Spruce 2518/2632* (Holotype: B†; Lectotype, here designated: BR; Isolectotypes: BM, C, E, G [2 sheets, K [2 sheets], NY, P [2 sheets]).

**Distribution:** *Andersoniella spruceana* occurs in the eastern Andes from Colombia eastward to the Brazilian Amazon (Anderson, 1983). It is the only species of the genus *Andersoniella* that occurs in sympatry with *Lophanthera* s. str.

Because the holotype at B was destroyed during World War II, we designate the duplicate at BR, annotated by Niedenzu, as the lectotype. This specimen was annotated by Bruce MacBryde as “lectotype” in 1970; however, MacBryde never published his choice.

## Taxonomic Key for the Species of *Andersoniella* (first provided as *Lophanthera* by Anderson [2014])

1a. Gynoecium densely sericeous; bracteole gland, when present, sessile and covering much of the abaxial surface of the bracteole; stipules 1.5–3.0 mm long, connate their whole length; northwestern Amazonia (Brazil and Colombia) . . . . . . . . . . . . . . . . . . . . . . . . . . *A. spruceana*

1b. Gynoecium glabrous; bracteole gland, when present, terminal and peltate; stipules 3–6 mm long, at least partially connate but often distally distinct . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2a. Gynoecium tricarpellate; calyx bearing 10 abaxial glands; anther wings 0.2–0.4 mm wide, widest distally; Costa Rica and Nicaragua . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. hammelii*

2b. Gynoecium bicarpellate; calyx bearing 0–2 abaxial glands; anther wings 0.10–0.15 mm wide and of uniform width; Colombia (Chocó) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *A. marcelae*

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# VALIDATION OF "*VIBURNUM* × *CARLCEPHALUM*" (VIBURNACEAE)

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**Abstract.** The name "*Viburnum* × *carlcephalum*" has hitherto not been validly published. It is validated here by the provision of a description in English and holotype citation.

**Keywords:** Burkwood, Pike, *Viburnum*, "*Viburnum* × *carlcephalum*"

"*Viburnum* × *carlcephalum*" (Viburnaceae), commonly known as fragrant viburnum, fragrant snowball, or *Carlcephalum viburnum*, has been widely cultivated. This hybrid shrub, created around 1932 by Albert Burkwood in England, was raised from a cross between *V. carlesii* Hemsl. and *V. macrocephalum* Fortune and received an "Award of Merit" in 1946 in a floral exhibition (Pike, 1946).

Although the name "*Viburnum* × *carlcephalum*" has been in existence since 1946 (Pike, 1946; Burkwood, 1947; USDA-GRIN, 2020), the hybrid name has not been validly published. Neither Pike (1946) nor Burkwood (1947) provided a description or diagnosis in Latin, a requirement for valid publication of hybrid species and infraspecies names published during 1935–2011 (vide Shenzhen Code Art. 39.1, H.10.1; Turland et al., 2018). Both Pike and Burkwood provided descriptions in English. We note that citation of a type was not mandatory for validation of names published before 1958 (Art. 40).

We herewith validate "*Viburnum* × *carlcephalum*" by provision of a short description in English and citation of the holotype housed at A (see Arts. 39.2, 40.1, 40.2, 40.6, 40.7).

**Viburnum** × **carlcephalum** Burkwood *ex* Rullo, Brach & Gandhi, *nothosp. nov.*

TYPE: U.S.A. Maryland: Montgomery County, Silver Spring, in a small triangle and the Metro Station near Colesville Road, 28 April 1986, *F. G. Meyer 21250* (Holotype: A). Fig. 1.

Synonyms: "*Viburnum* × *carlcephalum*" Burkwood ex A.V. Pike Gard. Chron. ser. 3, 119: 217, t. 96. 1946, not valid (*sine* Latin).

"*Viburnum* × *carlcephalum*" Burkwood, J. Hort. Soc. London 72: 361, t. 132. 1947, not valid (*sine* Latin).

Deciduous multistemmed *shrub*, attaining a round form reaching 1.8–3.0 m high and 1.8–2.4 m in diam. *Leaves* opposite, *petiole* 0.6–1.5 cm long; *lamina* elliptic-ovate, 5–10 cm long, 3.0–4.5 cm wide, grayish-green (turning reddish-maroon in fall), serrulate-serrate or shallowly toothed along the margin, the apex subacute to acute, sometimes abruptly so, the base truncate to subcordate, or acute, sometimes oblique. *Inflorescence* cymose, composed of 7- to 13-cm-wide, snowball-like clustered cymes. *Flowers* 20–100+ per cyme, fragrant; *corolla* sympetalous, ca. 1.7 cm across apically, 0.9–1.1 cm long, white, often pink in bud. *Fruits* red berrylike drupes turning black at maturity.

**Hybrid parents:** *Viburnum carlesii* and *V. macrocephalum*.

**Phenology:** April to early May.

**Distribution:** widely cultivated.

**Etymology:** the epithet *carlcephalum* was derived from the parent specific epithets, combining the first part of *carlesii* and the second part of *macrocephalum*. Since neither epithet is unaltered, *carlcephalum* is a true epithet (see Shenzhen Code Rec. H.10.2 Ex. 5)

**Additional specimen examined:** U.S.A. Maryland: Anne Arundel County, Edgewater, woodland, London Town Publik House Garden, 839 Londontown Road, 1 May 1986, *F. G. Meyer & P. M. Mazzeo 21281* (A).

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**CULTIVATED PLANTS**

MARYLAND

<u>Viburnum</u> x <u>carlcephalum</u> Burkw. Cv. ?
(<u>V</u>. <u>carlesii</u> x <u>macrocephalum</u>) det. T.R. Dudley

Deciduous shrub, much branched, multistemmed from base, spreading habit; ca. 4-5 ft.tall; lvs. gray-green; fls. white, very fragrant.

In a small triangle and the Metro Station near Colesville Rd., Silver Spring, Montgomery Co.

F. G. Meyer 21250 28 April 1986

coll.

HERBARIUM, U.S. NATIONAL ARBORETUM, WASHINGTON, D.C.

FIGURE 1. *Viburnum* × *carlcephalum* Burkwood ex Rullo, Brach & Gandhi. Holotype. Image courtesy of the Arnold Arboretum Herbarium (A). See original at https://kiki.huh.harvard.edu/databases/specimen_search.php?mode=details&id=1366322

# PLANTS NAMED “LOTUS” IN ANTIQUITY: HISTORIOGRAPHY, BIOGEOGRAPHY, AND ETHNOBOTANY

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**Abstract.** In ancient times, several plants were named “lotus.” They assumed very important roles in the religions and art of many cultures, but historiography and descriptions of the various plants called “lotus” have always been poor. The aim of this work is to define what plant species correspond to the ancient name “lotus.” Through analysis of classical texts and other historiographical sources, three types of “lotus” have been identified: “arboreal lotus,” “herbaceous lotus,” and “aquatic lotus.” From the sources examined, several botanical species have been identified for each “lotus” category. In the “arboreal lotus” category there are two species of *Ziziphus*: *Z. lotus* and *Z. spina-christi*. The “herbaceous lotus” include several species in Fabaceae that have been called “lotus,” more specifically in the genera *Melilotus*, *Lotus*, *Trifolium*, and *Trigonella*. In the last category, “aquatic lotus,” are two species of *Nymphaea* L. (*N. lotus* and *N. nouchali* var. *caerulea*) and the sacred Indian lotus (*Nelumbo nucifera*). The attributions of these species have been validated by research on their biogeography and ethnobotanical uses.

**Keywords:** Lotus, ethnobotany, historiography, *Ziziphus*, *Nymphaea*

In ancient times, the name “lotus” was applied to several plants, and each had a relevant economic importance: some produced wood and bark, and others produced beautiful flowers, fodder, fruits, seeds, or rhizomes. Very often people attributed a mystical-religious symbolic meaning to these plants, or used them as design elements in their legends and traditions. Historiography about plants with the name “lotus” has always been poor, and there have been many different interpretations of the original lotus plant. In the early Greek and Latin literature, the name “lotus” did not refer to one plant but to a whole group of plants, which differed in their uses, locations, and local customs. In all literatures, from Arabic to Christian and Hindu, there occur different plant species called “lotus” that assume very important roles in religion and art; emblematic cases are the Egyptian water lilies and *Ziziphus spina-cristi* (L.) Desf., exploited for ethnobotanical uses. Of great historical and botanical importance is the famous legend of the “lotus of the Lotophages,” a plant mentioned in Homeric literature, in Theophrastus, and in works of subsequent authors. This plant was a food source and provided many products to the populations living on Gerba Island (modern-day Djerba) and on the nearby coasts. The plant has often been indicated as belonging to the genus *Ziziphus* but has also been referred to *Paliurus* Mill. These attributions, sometimes generic or incorrect, were influenced by rough descriptions and questionable morpho-anatomical and bio-geographical references. There is an interesting discussion of the presence of an “Italian arboreal lotus” and a “fodder lotus” in the Latin literature. There are also references to the Oriental Lotus (species of *Nelumbo* Adans., Nelumbonaceae), but these are provided with only fragmentary and sparse descriptive sources. The aim of this study is to clarify attributions made in historical descriptions and biogeographical references to reliable botanical species. Several descriptive sources will be used, and the ethnobotanical uses will be analyzed together with any cultural symbolism.

## Materials and Methods

Many historiographical sources have been consulted for descriptions of plants given the name “lotus,” especially the ones that, in different ways, gave clear vision of the diversity among the botanical species to which plants with this common name have been ascribed (Supplementary Table 1; Supplementary Material). Homer (Ciani, 2001: 86–169), in *The Odyssey*, distinguishes a “lotus of the Lotophages” (described as a tree), a “herbaceous lotus,” and a “floral lotus.” Moreover, since the time of Herodotus (fifth century BC), there was a plant known in Greece by the name “Egyptian aquatic lotus.” In Theophrastus (Theophrastus, 1644: 59–116) (fourth to third century BC), both the “herbaceous lotus” and the floral one constitute two different groups of plants, each of which comprise several botanical species. Virgil (Virgilio, 1965: 71) declares clearly that many species of “arboreal lotus” were known. Pliny (Plinio, 1985, Book XIII: 17) insists on the explicit division of “lotus” plants into many varieties: arboreal, herbaceous, and aquatic; this division is implicitly accepted by Dioscorides (Mattioli, 1583: 16–594), who spends a lot of time on the “herbaceous lotus” description and less on the arboreal one. In addition to the sources deriving from Egyptological studies about *Nymphaea* spp. (the famous “Egyptian lotus”) and to those from Indian culture describing the “oriental lotus” (*Nelumbo nucifera* Gaert.), special attention has been paid to those sources preceding the ninth century BC. In these sources, the great herbalists and botanical humanists of the sixteenth and seventeenth centuries who comment on the works of Theophrastus, Dioscorides, and Pliny, help clarify the ancient “lotus” terminology and propose

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the first schemes of identification. In this context, the work of Bodaeus is fundamental (1644: 323). Also considered were several authors of the nineteenth and twentieth centuries who cite historical texts from Herodotus, Strabo, Pomponius Mela, and Athenaeus, among others. In their texts, "lotus" is mentioned with varying levels of detail. Among the treatises on ethno-anthropology, Thomas Shaw's text (1738: 225–570) was analyzed, which already frames the "lotus" plant in a geographic and phenotypic context. Among the botanical treatises, Louiche Desfontaines's text (1789: 433) was fundamental. Another work consulted was the commentary on the Flore de Virgile by Fèe (1822: 81), who focuses on all antique "lotuses" benefiting from the Napoleonic expedition in Egypt. For the geobotany, texts of Pampanini (1914a: 203–248,b: 5, 1917, 1926), with descriptions of North African vegetation, and those of Bonacelli (1929), with interpretations of sources relating to plants that in antiquity were under the name "lotus," were used for reference. Essentially, all the major and most reliable texts related to the topic of this research from antiquity up to the beginning of the twentieth century have been examined. Therefore, this study's sources encompass botany, ethno-pharmacology, economic history, geography, art history, religion, and other ethno-botanical uses.

## Results and Discussion

### *The Legend of the "Lotus of the Lotophages"*

The first reference to a "Lotus of the Lotophages" appears in Homer's *Odyssey* (Ciani, 2001: 86–169). Ulysses tells Alcinoo how, during his journey back to Ithaca, adverse north winds drove him and his men off Cape Malea and made them land in an unknown place. Ulysses sent ambassadors to explore the place where the storm had driven them and discover the manners of the people living on the island. This place was inhabited by Lotophages, people who nourished themselves with "lotus," a mysterious plant that was offered to Ulysses' ambassadors. Those who accepted and ate the strange plant, sweet as honey, did not want to come back to Ulysses. So he forced them back to the ships, made them fast under the benches, and sailed quickly, freeing the crew from the "temptation of the lotus." This famous legend, also referred to in another passage of the *Odyssey* (canto XXIII, verse 311), is later mentioned in Euripides' *Troads* (Susanetti, 2014: 36), where the prophetic Cassandra announces the tribulations of Ulysses, quoting also the "temptations of the lotus." This effect of the fruit is very often evoked in ancient sources. Xenophon (Baccarini, 1991, book III: 2) tells his soldiers not to forget the way back to their houses, like the "lotus eaters" did. In sources written in Latin, the expressions which reevoked the legend come along with truly passionate and aesthetic delicacy. Propertius (Canali, 1987: book III: canto II) says that the "lotus" and the "bewitching herbs" (lotosque, herbaeque tenaces) were tribulations for Ulysses, and Ovid (Bovincini, 2005, book IV: canto I) says the same. In writers of the first century of the Roman Empire, we commonly find the epithet "too hospitable," referring to the fruit and the earth that produces it. In Virgil's *Culex* (Barelli, 2000: 71), in Silio Italico (Vinchesi, 2001, Book III, 311), as well as in Pliny (Plinio, 1985: Book XIII: 17), this "lotus" is regarded as a sweet berry ("Et dulci pasci lotos nimis hospita bacca").

Identification and Geographical Distribution of "Lotus of the Lotophages." Among the oldest historical references to the region inhabited by the Lotophages we found is by Herodotus (Sgroj, 1968: 175–183). Herodotus is sure that the coast of the ancient Tripolitania was inhabited to the east by the Maci and more to the west by the Gindans, while the coast of the area running toward the current Tripoli was occupied by the Lotophages. He adds that the shortest route to the Garamantes, a tribe inhabiting the Fezzan, started from the village of the Lotophages. Scylax (Perretti, 1979: 108), a geographer from Asia Minor who lived in the sixth and fifth centuries BC (the same period in which Herodotus wrote), confirms in the *Periplo* this distribution of these peoples. According Scylax, the Maci, a Syrtic tribe of shepherds, reached the country of Cinipide and Neapoli (and the city of Leptis Magna); he places the Lotophages to the west, up to the Lesser Syrtis (or Gulf of Gabès). Moreover, Scylax mentions Brachion Island (also known by the historical name Gerba), said to be the island of the Lotophages, where "lotus" grew spontaneously and was eaten by the people living there. Theophrastus (Theophrastus, 1644: 59–116) adds that numerous "lotus trees" were on the island of Gerba, which he called "Faride" and home of the Lotophages, who lived also on the coast across the island. Later geographical accounts agree on the location of the Lotophages on the island of Gerba, in antiquity also called "Meninge" and, by Polybius (Cardona, 1968, 1: 39), "of Lotophages." Pliny (Plinio, 1985, Book XIII: 17), in his *Naturalis Historia*, following Eratosthenes, calls the island of Gerba by the name "Lotofagitida." Strabo (Biffi, 1999; Trotta, 1996: 305) resumes the ancient concept of "lotus" in saying that the Lesser Syrtis is called "Sirte Lotofagitide."

There is no lack of quite controversial interpretations that confuse the location of those people, called Lotophages in northern Libya. One of these is Pomponius Mela (Muratori, 1855, I: 7), who locates them on the beaches of Cyrenaica, from Cape Borion (now Ras Tejonas to SW of Benghazi) to Cape Ficunte (now Ras Sem to NW of Cyrene). Moreover, Scylax (Perretti, 1979: 108) mentions the presence of the "lotus" in Cyrenaica by counting it among the plants of the famous and legendary Garden of the Hesperides. These ancient geographical designations are preserved by Ptolemy (Ruscelli and Malombra, 1574: 190), who mentions the people of the Lotophages along the River Cinipe and nicknames Meninge (Djerba) as "Lotofagitide." Meninge is the island about which, in more modern times, Torquato Tasso (Savini, 2015, XV: 18) is quoted as saying, "*Alzerbe, già dè Lotofagi albergo*." (Alzerbe, which was the home of the Lotophages). Summarizing, the most ancient data agree in indicating the position of the Lotophages on the island of Gerba and its adjacent coasts, although some sources extend the "lotus eaters" to the whole of Cyrenaica.

Descriptive Sources of the Plant. Homer, in the *Odyssey*, did not describe the “lotus” plant or its fruit. According to Herodotus (Sgroj, 1968: 175–183), the fruit was as large as a fruit of the lentisk tree (*Pistacia lentiscus* L., Anacardiaceae) and as sweet as a date (*Phoenix dactilifera* L., Arecaceae), and was also used to prepare wine. Scylax (Perretti, 1979: 108) claims that the fruit was as large as a strawberry (*Fragaria x ananassa* Duchesne, Rosaceae) and that wine was made from some species of it. Theophrastus (Theophrastus, 1644: 59–116), reporting observations of his own and other authors, claims that the plant was fruticose and dense with branches, and had a large stem. The fruits were opposite and arranged in a dense manner as in myrtle (*Myrtus communis* L., Myrtaceae). They turned color during maturation and were as big as a broad bean, sweet, pleasant, and harmless–even useful–for the womb. He reports that there was a variety that had a fruit without a kernel, which was tastier and used to make wine. But he also reports that, according other observers, the fruit was always provided with a large kernel, had little pulp, was covered by a rather rigid membrane, and was more pleasant than sweet. The wine it produced did not last more than two or three days. In any case, it was the preferred fruit of the Lotophages. The plants were numerous and produced a great quantity of fruits. A testimony of its great value comes from the “Stories” from Polybius (Cardona, 1968). In fact, he claims that “the lotus plant is not large, but rough and thorny, has green leaves, like the buckthorn, but a little darker and wider.” Continuing, he claims that “the whole fruit crushed when ripe, is stored in the pots and is used to feed the servants, while, deprived of the kernel and preserved in the same way, it is food for the free people. Macerated in water and minced, it is used to make a wine-like drink.” Pliny (Plinio, 1985, Book XIII: 17) reports the opinion of Cornelio Nepote, according to whom “the plant was small”; he also claims that “the fruit was abundant and dense as in myrtle; it was as big as a saffron-colored bean, changing color as it matured. Very sweet food in Africa, preserved from stomach ache.” “From it we obtained a drink like wine with honey,” which, Nepote states, “was not kept more than ten days.” The crushed fruits were kept in large vessels for food. According to numerous authors (e.g., Bauhin, 1671: 328–447), the ancient edible lotus fruits were like jujubes. All these descriptions seem to strengthen the identification of the “lotus of the Lotophages” as *Ziziphus lotus* (L) Lam. (Rhamnaceae). It is widespread, growing wild, in arid regions of North Africa, from Egypt to Morocco: in Tripolitania, the classic Lotophages’ country, it was extensively studied from the botanical point of view at the beginning of the twentieth century. In Tripolitania, as in Cyrenaica, it has mostly a bushy aspect, which evolves to a small tree in some particular soil conditions. Pampanini (1914a,b) describes it with these words: “Although we meet it in the low scrub here and there, in the garrigue, and sometimes even in the rock sites, the *Z. lotus*, also called *sedr*, never assumes great importance for its frequency, nor for its size. Instead it constitutes a particular type of vegetation. They are wide and thick bushes, sometimes very frequent, especially on loose and flat soils where the action of the wind is freer. They cover small mounds, produced from the sand carried by the wind and stopped by the intricate bushes. When conditions are favorable, and perhaps when the man intervenes by thinning the bush, the shrub becomes a sapling or a tree. However, the fruit is not very juicy, much smaller than a common jujube. On the other hand, in some of the places that were once inhabited by the Lotophages, there are no other spontaneous species that bear fruit outside the *sedretum*. Today has a greater intensity of development, and according to the same words of Theophrastus, the -*lotus of the Lotophages* was a fruit all skin and bones, tastier than sweet.-”. All these descriptions tend increasingly to reinforce the belief that the “lotus of the Lotophages” is identifiable with *Z. lotus*, a shrub with gray, supple, glabrous branches when young; alternate leaves, oblong, obtuse, glandular-crenate, with short petiole; and few flowers, gathered in small axillary peaks shorter than the peduncle. Drupe 1.0–1.5 cm long, subglobose, dark yellow (Tutin et al., 2010) (Fig. 1).

FIGURE 1. “Ziziphus lotus” postal stamp, representing *Z. lotus* (L.) Lam. branches, leaves, and fruits. Printed in Mauritania.

### *The Lotus of Cyrenaica*

Theophrastus (Theophrastus, 1644: 59–116) claims that in Cyrenaica there was another plant used for the fruits called *paliuro*, whose name recurred in ancient place names; in fact, Paliuro was a locality outside the Gulf of Bomba, in view of the island of Platea, east of Cyrene. More important in this regard is a passage from Athenaeus (Dalechamp, 1612), where he speaks of plants called *connari* and *paliuri*, near Alexandria in Egypt. Agatocle from Cizico (Montanari, 1988: 26–31) describes this plant as a small tree, big like an elm (*Ulmus* spp. L., Ulmaceae) or a poplar (*Populus* spp. L., Salicaceae), with long, thorny branches and green, ovate leaves. It bore fruit twice a year, in spring and autumn, and fruits were sweet, as big as olives, also similar to olives in the pulp and kernel, and of delicate sweetness. The fruit was eaten fresh, but also slightly dried. It was ground into flour, which was kneaded with the feet and used to make coarse flat breads. Athenaeus (Jacob, 2001: 1686–1751) adds that those fruits were used on the tables of Alexandria in Egypt. The *paliurus* is known to have been present in the regions on either side of the Red Sea. Agatarchide (Burstein, 1989:

152), also cited by Photius (Bianchi and Schiano, 2016: 27–38) and Diodorus Siculus (Baldelli, 1575, XX: 6–7), claims that the Ittiofagi, people living along the African coasts of the Red Sea, had the habit of preparing a paste with fermented fish meat, in which they mixed *paliurus* seeds, to improve the texture and as a condiment. Of the Troglitidi, shepherds who inhabited the region east of the Nile near the Red Sea, Agatarchide says that the most miserable drank the juice of *paliurus* plants, and with the young branches they made bindings to tie corpses in a certain way (Bonacelli, 1929). Diodorus Siculus (Baldelli, 1575, XX: 6–7) reports that the Panchei, inhabitants of oceanic islands in front of "Arabia Felix" [now Yemen], collected the fruit of the *paliurus*, using it for food and drink, and as a remedy for stomach ailments. The descriptions herein reported all lead back to the same plant, *Ziziphus spina-christi* (L.) Desf. (Rhamnaceae). Widespread and widely cultivated, it is a plant typical of arid climates. It is mentioned in the Qur'an (Mandel, 2016) with the name *sedr*. The specific epithet *spina-christi*, assigned first by Linnaeus, derives from a Christian legend according to which its thorns formed the crown of Christ (Fig. 2). The tree, and parts of it, seems to have been used in Egyptian carpentry, diet, and medicine. Theophrastus (Theophrastus, 1644: 59–16) writes, "The (Egyptian) Spine of Christ is thicker than the lotus [presumably *Z. lotus*]," also describing the fruit. Pliny (Plinio, 1985: Book XIII: 17) mentions the plant in comparison with related species: "The region of Cyrenaica classifies the 'lotus' under the epithet Spina-christi." Pliny also states that Egyptians eat the kernels of the plant (Manniche, 1989: 157). Athenaeus (Jacob, 2001: 1686–1751) talks about it in the *Deipnosophistes*, describing the plant. This species is frequently mentioned in the Christian, Jewish, and Muslim traditions. In Hebrew, the plant is called *sheisaf*, and many Bible commentators identify it with *atad* (Scarpa, 2003; Job 40:21–22), *n'atsuts*, and *tse'elym*. In rabbinic literature, the plant is called *rimin* (Sefaria, 2019), and in the Talmud, it is called *kanari* (Jewish Virtual Library, 2019). Botanical scholars of the Bible (Scarpa, 2003) and the Gospels (Conferenza Episcopale Italiana, 2014) have long debated what constitutes the "bramble" or "thorns" (Scarpa, 2003; Judges 9:14–15; Conferenza Episcopale Italiana, 2014; Matthew 27:27–29) and the "crown of thorns" (Conferenza Episcopale Italiana, 2014, John 19:5). Today these quotations refer to *Z. spina-christi*, indicating the shrub with which Jesus was crowned before his crucifixion (Conferenza Episcopale Italiana, 2014; Matthew 27:27–29; John 19:5; Mark 15:17).

The Qur'an (Mandel, 2016) mentions the tree twice (53:13–18; 56:28–32). The "arboreal lotus" is commonly associated with *Z. spina-christi* and is consequently respected by the Muslims of the Middle East. The plant has been widely used as a source of fruit and a medicinal plant both in the past and in recent times. Many common Arabic names are still in use today: for example, *nabq*, *dum*, *sidr*, *tsal*, and *sadr*. According to various authors, the Libyan name of the plant, *sedr*, and that of its fruit, *nabeq*, are the interchangeable, and are generalized everywhere in Arabic usage; however, in modern Tunisia and Libya the word *sedr* also indicates *Z. lotus* (Dafni et al., 2005). Muslim and Christian pilgrims and other travelers describe *Z. spina-christi* as a great tree that grows in Israel. Estori ha-Parhi (1897 cited in Dafni et al., 2005), during the Mammelucchi period (thirteenth to sixteenth centuries) in Israel, writes that the *rimin* is the *nabaq* in Egyptian, and the *dum* in the land of Canaan, and it coincides with the tree called *sidar* in Israel(Dafni et al., 2005). It is reported by Pampanini in Cyrenaica in Egypt, where it was known as *paliuro* (1917, 1926). In Tripolitania, the plant is reported by Durand and Barratte (1910: 220) and again by Pampanini (1914a,b). The Arabs used *Z. spina-christi* as a hedge to keep goats and cattle out of cultivated land; when it grew in the wild, the cattle were grazed on it (Dafni et al., 2005). The fruits, which have the flavor of dried apples, were eaten by Arabs and made a good liqueur (Dafni et al., 2005). The bark was used as a source of tannins. Its hard, heavy, and termite-resistant wood was used in African carpentry (Dafni et al., 2005). Various parts of the plant were used in Ancient Egypt, and are still used in traditional Middle Eastern medicine by various cultures that make up the ethnic mosaic of the area: Arabs, Bedouins, Bedouins particularly from Sinai and Negev, Yemenite Jews, Iraqi Jews, and Israelites (Dafni et al., 2005). The plant has been used to treat tumors; its antitumor activity has been attributed to the presence of β-sitosterol, a proven tumor inhibitor (Dukes, 1985: 717). For Muslims, the tree must be respected, as an ancient legend holds that *Z. spina-christi* has as many leaves as there are people of humanity. According to the legend, on the central day of Ramadan the leaves that fall from the shaking of the tree represent the people who will go to their death during the year. In the Hebrew tradition, the plant was associated with the saints (Dafni et al., 2005). There are also many proverbs in the various cultures investigated that mention the tree, and many traditions that are linked to not destroying, or at least to respecting, these plants because the red sap produced by the species is associated with human blood (Dafni et al., 2005).

FIGURE 2. Reproduction of the Crown of Thorns made with branches of *Ziziphus spina-christi* (L.) Desf.

*Herbaceous and Fodder Lotus*

As mentioned above, in antiquity three types of “lotus” were mentioned: an “arboreal lotus,” which we have already discussed, a “herbaceous lotus,” and a “floral lotus.” Homer, in the *Iliad* and the *Odyssey* (Ciani 2001, 2016: 75–155), cites a “fodder lotus,” a delicious fodder for horses, which was associated with plants that grow in humid meadows or on river margins. The Homeric hymn to Mercury (Zanetto, 1996: 135) quotes this “fodder lotus” as useful to cattle. Athenaeus (Jacob, 2001: 1686–1751) gives us the color of the herbaceous lotus flower, stating that “the flower of the *helichrysum* was like the lotus, but the latter was a more intense yellow.” Euripides (Medda, 2006: 287) speaks more generally about “fruitful lotus lawns.” In the *Iliad*, again, we read that from the land to the summit of Mount Ida (Crete), during the embrace of Zeus and Hera, the “dewy lotus” germinated. These plants had showy flowers and, the poems from Homer suggest that they were of different species (Ciani, 2016: 75–155), when he speaks about a “floral lotus” very different from that designated for fodder. The Greeks made crowns by intertwining the showy flowers, as cited by Athenaeus (Jacob, 2001: 1686–1751), who specifically speaks of “lotine and melilotine crowns”; he also recalls, quoting Anacreonte, the “lotus crowns” composed by the Athenians. Cratino also mentions the “coronary lotus,” or “melilotus,” in the Effeminati (Bonacelli, 1929). The same Athenaeus speaks of the color of the flowers (Jacob, 2001: 1686–1751) and states that the flower of helichrysus is like the “lotus.” With slight variations in the transcriptions, the “herbaceous lotus” of Theophrastus (Theophrastus, 1644: 59–116), of Dioscorides (Mattioli, 1583: 16–594) and of Pliny (Plinio, 1985, Book XIII: 17) is described as a sylvan flower suitable for making crowns, and many times it is said that the “lotus” plants are also odorous. Theophrastus (1644: 59–116) and Pliny (Plinio, 1985, Book XIII: 17), describing the ointments used by the Frankish King of the Parts, listed among the aromas the “herbaceous lotus.” Of the “melilotus,” Pliny (Plinio, 1985, Book XIII: 17) specifically states that it was odorous and used to make ointments and a fragrant oil. Dioscorides (Mattioli, 1583: 16–594) confirms its use as an ingredient for ointments, which he referred to as *telino*. Pliny (Plinio, 1985, Book XIII: 17) includes “melilotus” among the aromatic herbs and fragrant flowers to be planted as bees’ flowers; furthermore, etymologically, its root (meli-) probably derives from the Latin *mellitus* or *melinus* (Greek *melinos*), pertaining to honey. Statement of Dioscorides was also present in Aristotle (Aristotele, 2018), who stated that, at the time, the bees feeded on plants that then flourish, including the “melilotus.” Ovid reports the appearance of flowers (Canali, 1998: 96–97), saying that “the young companions of Proserpina picked up the melilotus with other flowers.” The Greek habit of braiding crowns also occurred in Italy, especially in the Hellenic colonies of Campania. The fame of the local variety of the plant used for this purpose there soon reached Rome and is remembered by Cato (Canali and Lelli, 2000: 85), who called it *serta campanica*. This name is connected with the name “melilotus” in explicit declarations dating back to the first century of the Empire. For example, Scribonius Largo (Mantovanelli, 2012: 101–126) states that “the melilotus is what we say *sertula Campana*,” and Pliny (Plinio, 1985: Book XIII: 17) says that “*Sertula Campana* is called melilotus, because in ancient times was used for crowns.” In Italy, the ecotype found in Campania was very famous, while in Greece the ecotypes on the promontory south of Attica, Chalkidiki, and Crete were well known. Dioscorides (Mattioli, 1583) says that “the melilotus is celebrated in Attica, in Cizico and in Calcedone, had color close to the saffron and with a good smell,” adding that “it is also born in Campania near Nola reddish and slightly odorous.” For this plant, we can even make a fairly accurate hypothesis attributing it to *Melilotus neapolitanus* Ten. (Fabaceae), since the morphological descriptions and the uses found in the ancient citations correspond sufficiently to this entity. The species appears through reports to match the Steno-Mediterranean corotype (Pignatti, 2017); this fact lends evidence to the possibility that the species described by historical sources is *M. neapolitanus*.

Despite some ancient partial confusion between “herbaceous lotus” and “melilotus,” the two entities were different. Nevertheless, neither the “herbaceous lotus” nor the “melilotus” was a single species; rather they constituted two groups, each of which included botanically related plants of different species. So, the “lotuses” included herbaceous forage species common in the natural pastures of central Mediterranean countries, with leaves present along the stem, generally yellow and fragrant. The “melilotus” had the yellowish flower tending to red, although sometimes the color was lighter, as in Campania, and even white; the flower was fragrant and the aroma recalled saffron (Bonacelli, 1929). In conclusion, it is essential to know what Dioscorides (Mattioli, 1583) writes about “herbaceous lotuses.” The “lotus clover of the meadows” described by Dioscorides, which Pliny (Plinio, 1985: Book XIII: 17) claimed to be the best among all grasses of the meadows, is presumably referable to *Trifolium boissieri* Guss. (Fabaceae). The hypothesis that the “lotus clover of the meadows” corresponds to the previously mentioned species (i.e., *Trifolium boissieri*) is corroborated by analysis of the area of origin and distribution of the species (Euro+Med, 2006). The most typical of autochthonous plants used for fodder is *Lotus corniculatus* L. (Fabaceae), which has yellow flowers and rich nectar sought by bees. Therefore, the reference to the genus *Lotus* for herbaceous and foraging lotuses is well justified. There are also references to the use of this plant in traditional medicine; for example, the plant was used as an astringent and to treat wounds (Gras et al., 2017). Among mentions of fodder in classical literature one often sees “fenugreek,” which, although not specifically referred to as “lotus,” is among the edible species present in pastures and known in antiquity. “Fenugreek” is probably referable to *Trigonella foenum-graecum* L. (Fabaceae). This species is noted in texts and articles on ethnobotany for its uses in traditional medicine in the Mediterranean area: as an emollient, antalgic, and antacid, and for improving sight (Gras et al., 2017). It was also used to treat diabetes

(Asadi-Samani et al., 2017). For both *Lotus corniculatus* and *Trigonella foenum-graecum*, was made the analysis of the origin and geographical distribution (Euro+Med, 2016) to avoid errors in the attribution hypotheses. Ultimately, because of the very general descriptions of classical authors, it seems rather imprudent to attribute the presumed "herbaceous lotus" to a precise botanical species. It is likely that several species belonging to Fabaceae have been assigned the common names "herbaceous and fodder lotus" and "melilotus," more specifically species belonging to *Melilotus*, *Lotus*, *Trifolium*, and *Trigonella*.

### *Aquatic Lotus*

Since the first dynasties in ancient Egypt, some Nymphaeaceae were considered sacred so they acquired symbolic meaning, and their forms were reproduced as stylistic motifs in architecture and in the art of the Empire. Studies of the flowers' stylization, reproduced on capitals of columns, on sculptures, and on paintings, always lead back to *Nymphaea* L. Depictions of leaves, which have the insertion of the petiole in the cordiform inlet, support the referral to this genus. Kandeler and Wolfram (2009) report iconographic sources, related to hieroglyphic culture, representing flowers related to the *Nymphaea* that highlight the morphological, descriptive, and biogeographic similarities. More precisely, these depictions represent *Nymphaea nouchali* var. *coerulea* (Savigny) B. Verdcourt and *Nymphaea lotus* L., both present in Egypt and reported (Muschler, 1912: 1294) for the Delta, Fayun, and other neighboring areas. Recent sources (Euro+Med, 2006) confirm the area of origin of *N. nouchali* var. *coerulea* and *N. lotus*, species hypothesized as corresponding to the "Egyptian aquatic lotus." Hieroglyphic documents include references to the aforementioned Nymphaeaceae. The hieroglyphic personification of the god Nefrtem (called ZŠŌŠĔN), corresponding with the desired transformation of dead's soul, has been identified with *N. nouchali* var. *coerulea*; the depiction of the leaf (called ḪA') with the typical cordiform insertion, is undoubted testimony of the genus, and the species can be identified in the schematic figure of the flower with long, acute petals in the oldest texts (Bonacelli, 1929). The historical sources, generic and descriptive, of "Egyptian lotus" are Herodotus (Sgroj, 1968: 175–183), Theophrastus (Theophrastus, 1644: 59–117), Diodorus Siculus (Baldelli, 1575, XX: 6–7), Pliny (Plinio, 1985, Book XIII: 17), Dioscorides (Mattioli, 1583), and Galenum (Gaudano, 1543: 20–322). The Greeks first used the name "lotus" to refer to a white-colored water lily (*N. lotus*), and later Athenaeus (Jacob, 2001: 1686–1751) designated with the same name the blue water lily (*N. nouchali* var. *coerulea*) and some ecotypes with reddish flowers (presumably local variations derived from variations in soil and climate). The relation between Hellenic references to "lotus" and the sacred Egyptian plants is strengthened by the sun myth of the god Horo, born on the water lily flower: "the flower rose from the primordial waters of Nù on the day of creation." In artistic depictions, the flower seems to be *N. lotus* as often as *N. nouchali* var. *coerulea* (Spanton, 1917: 1–20). This "Egyptian lotus" lived on the flooded lands of the Nile and the Euphrates. Descriptions (Baldelli, 1575, XX: 6–7; Mattioli, 1583; Plinio, 1985: Book XIII: 17; Sgroj, 1968: 175–183; Theophrastus, 1644: 59–116) indicate that the "lotus" flower was white; the fruit was like a large poppy capsule, equally divided into lodges, but with more-dense seeds like millet, which, extracted by maceration of the shell, served to make bread. Indeed, Diodorus Siculus (Baldelli, 1575, XX: 6–7) says that in Egypt bread was made from the seeds of lotus plants. Pliny (Plinio, 1985, Book XIII: 17) specifies that the "*lotometra* was produced from the lotus"; and that "from the seed like the millet, macerated in water or milk, the Egyptian shepherds made excellent breads to be cooked, but when cooled they became indigestible." *Nymphaea* spp. are still found in Egypt, offering, at least until the beginning of our century, seeds and edible roots to the peoples of the upper Nile. From there to Senegal, the genus *Nymphaea* is distributed widely during marsh floods and has spread south throughout all of tropical Africa, often offering a substantial contribution of seeds and tubers to the diets of native peoples. Today the blue water lily has almost disappeared from the Nile, but during the dynastic periods it was found from the Delta to the Nubia (Koemoth, 1997). The range of meanings and symbols, linked to the sacred and ritual sphere, that were attributed to these plants over the centuries was of great importance. The blue water lily, which emerges from the water during the day and plunges into it at sunset, has become the symbol of the rising sun and eternal life (Kandeler and Wolfram, 2009). The Egyptian *ankh*, symbol of eternal life, a mystic knot in ancient depictions (Lurker, 1987, cited in Kandeler and Wolfram, 2009), was composed of three stamens or petioles bound together, most likely coming from the water lily. The water lilies were used in funerary rites, as evidenced by limestone reliefs (Kandeler and Wolfram, 2009). Wreaths of dried flowers, including the blue water lily, were found in the tomb of Tut-ankh-Amun (Newberry, 1973, cited in Kandeler and Wolfram, 2009). The sacredness of water lilies in Pharaonic Egypt was also linked to their use by priests and druids as a drug for trances and to connect with the other world (Kandeler and Wolfram, 2009). The hypothesis that the Egyptian blue water lily has narcotic properties is found in the decorative motifs of Egyptian funerary art. Often, in the depictions, it is united with the narcotic fruit of the mandrake (*Mandragora officinarum* L., Solanaceae); the rhizome of the *Nymphaea* is never represented, always and only the flower, often with one or more fruits of *M. officinarum* in the center. Further evidence in ancient iconography of the psychoactive properties of *N. nouchali* var. *caerulea* can be found in the combination of blue water lilies and opium poppies, as shown in the gold sanctuary of Tut-ankh-amun (Emboden, 1978). Goris and Crete (1910, cited in Emboden, 1978) isolated an alkaloid, which they called nupharina, from the species *Nymphaea lutea* L. In 1941 some explorers indicated water lilies as substitutes for opium, and in the same year, Delphaunt and Balansard (1941, cited in Emboden, 1978) described their experiments using *Nymphaea alba* L. rhizomes on some animals and verified their soporific effects after initial spasms. Raymond-Hamet (1941, cited in Emboden, 1978) reports that the water lily flowers are narcotic and lead to a hypnotic state if swallowed. It can be assumed that the other species of *Nymphaea* (*lotus* and *nouchali* var. *caerulea*) can have similar effects and for that reason have been used in shamanic rites in Egypt. A relevant clue to these shamanic practices involving *N. nouchali* var *caerulea* is seen in representations of ritual vessels used in the rites. The vessels were made of calcite and shaped like water lily flowers, often inlaid with blue pigments and lapis lazuli (Fig. 3).

In the tomb of Tut-ankh-amun, a specimen of a white flower-shaped chalice was found. The Egyptologist I. E. S. Edwards, observing the differences between the chalices, asserted that the white chalices (*Nymphaea lotus*) were vessels for drinking and the blue chalices (*N. nouchali* var. *caerulea*) were for rituals (Emboden, 1978). *Nymphaea nouchali* var. *caerulea* could also have been used for medical purposes in ancient Egypt. A proof of this can be seen in some hieroglyphics concerning Tut-ankh-amun. The sovereign, of notoriously delicate health, is often portrayed with his queen offering him fruits of mandrake and blue water lily buds and blue water lily shaped chalices containing liquid. These findings suggest a use of the flower in ritual healing practices (Emboden, 1978). Dioscorides associates the "Egyptian lotus" with *Nelumbo nucifera* Gaertn. (Bonacelli, 1929), a species referred to Nelumbonaceae, but this attribution is doubtful. Already in 1834, Cattaneo tried to reorganize historical sources to address the confusion created between *N. nucifera* and Egyptian water lilies (Cattaneo, 1834). Analysis of the biogeography of the species shows that it is not native to Egypt (Euro+Med, 2006). Testimonies from Herodotus (Sgroj, 1968: 175–183) to Strabo (Jones, 1924, VIII: 383) document that in antiquity a plant of the genus *Nelumbo* Adans., almost certainly the same *N. nucifera*, also lived in Egypt, but it is a species introduced for ornamental purposes during Persian hegemony and cultivated in Egypt for a definite period. In the mosaic of the House of the Faun, the aquatic species in the Nilotic scene (Fig. 4) was analyzed.

Leaving aside any anatomical differences, presumably due to stylistic issues, the presence of capsules of *N. nucifera* is clear. There are also flowers, in blossom and not, and leaves that could be attributable to *Nelumbo*. Given the similarities of this genus with water lilies, the importation of *Nelumbo* in Egypt has generated over time a terminological confusion that can now be cleared up. On the basis of this analysis, and considering the historical and biogeographical data mentioned above, it can be said that the various species generically called "Egyptian lotus" collectively in ancient times are very distinct and actually represent *Nymphaea lotus* (white water lily), *Nymphaea nouchali* var. *caerulea* (blue water lily), and *Nelumbo nucifera* (Indian lotus).

FIGURE 3. Blue lily (*Nimphaea nouchali* Burm. var. *caerulea* (Sav.) Verdc.) shaped chalice used in Egyptian rites.

The Oriental Sacred Lotus or Indian Lotus. *Nelumbo nucifera* has a wide range of common names (e.g., Indian lotus, Indian bean, Chinese water lily, and sacred lotus). Historically, three countries have venerated this plant: India, China, and Egypt. Illustrations depicting this species are present in all the cultures of these countries, being a symbol of perfection, purity, and beauty. On the aspect of diet, different parts of the plant were used to prepare various

FIGURE 4. The Nilotic scene depicted in the mosaic of the House of the Faun. Museo Archeologico Nazionale di Napoli.

dishes in the respective cultures (Paudel and Panth, 2015: 1–33). The white or pink flower of *N. nucifera* emerges from the water together with the peltate leaves. The flower axis has the shape of an inverted cone, on whose flat upper part the carpels are reduced to holes during the maturation process (Kandeler and Wolfram, 2009). The "Indian lotus" is widespread in the stagnant waters of the Indian subcontinent and in Southeast Asia. It was introduced into Egypt during the period of Persian hegemony (Germer, 1985, cited in Kandeler and Wolfram, 2009), although today it no longer grows there. Some scholars have mistakenly called it "Egyptian lotus;" however, no evidence was found before 700 BC, when the Assyrians imported it. Moreover, at the beginning of 1900 it was no longer found in Egypt (Emboden, 1978). An important source of disambiguation is represented by the Ani Papyrus, also known as the Book of the Dead, dated between 1500 and 1350 BC; in this text, there is a chapter entitled "Transformation in a water lily." Some translators have linked the term "water lily" to the term "lotus," creating confusion between the genus *Nymphaea* and the genus *Nelumbo*. Given the gap between the historical period of the reference text and the period of importation of the *N. nucifera* species in Egypt, it is impossible for the "sacred Egyptian lotus" to be attributable to it (Emboden, 1978). However, when it was introduced into Egypt, it supplanted the native water lilies species (*Nymphaea* spp.) in the Isis cult. Isis became the goddess of fertility and the queen of the kingdom of the dead (Helck, 1979, cited in Kandeler and Wolfram, 2009). In Buddhism, the plant is a central symbol because it is said that Buddha, at birth, took seven steps and lotus flowers sprang up in his footsteps; moreover, the holy figures of Buddhism are often represented sitting on lotus flowers or on the flat part of the flower gynoecium (Majupuria and Joshi, 1988, cited in Kandeler and Wolfram, 2009). Sacred for Hindus since ancient times, it represents the firstborn of creation and the magic womb from which the gods and the world were born (Kandeler and Wolfram, 2009). It is a symbol, in India, of fertility, long life, health, and knowledge. In the early stages of Christianity, in the Council of Ephesus, the name "Theotokos" (God-bringer) was attributed to St. Mary, and the figure of the lotus is associated with her (Kandeler and Wolfram, 2009). In traditional medicine, the whole plant, the rhizomes, the stems, the leaves, the flowers, and the seeds have been used as the main components of recipes to cure several diseases (Paudel and Panth, 2015: 1–33).

When we consider descriptions found in the ancient literature, it is difficult to make correct and precise botanical attributions of plants referred to as "lotus." Many ancient descriptions appear to have little botanical reliability and are often the result of imagination. We present here only verifiable data from a large number of carefully examined sources, eliminating descriptions of questionable logic and reporting and interpreting only those that show a certain reliability. In this context, the name "lotus" is not attributable to a single plant but to a group of plants of different habitus and biogeography. The distinction between the "lotus of the Lotophages" (*Z. lotus*) and the "lotus of Cyrenaica" (*Z. spina-christi*) appears to be definite and reliable. In historical sources, there is a slight overlap of distribution areas of the two species, specifically in North Africa; this overlap, although there is a risk of interpretative confusion in the analysis of texts, can be accepted, as validated by the literature (Tutin et al., 2010). Different results have been obtained for the "herbaceous lotuses," since the sources in our possession make possible a precise reconstruction of the entities identified with this name. In the cases of *M. neapolitanus*, *T. foenum-graecum*, and *L. corniculatus*, the specific attribution is clear and certain. In *Trifolium*, we have indicated *T. boissieri*, but a wider range of species of this genus among the "lotuses" cannot be excluded. It is no wonder that various species of fodder were attributed to the epithet "lotus": it is typical of classical literature to refer to an entity by what it most "resembles," on the basis of impressions of the author and ancient vernacular names from the most disparate ethnobotanical uses. From this tendency of classical authors, confusion arises in relation to the "aquatic lotuses." This name has been given to plants similar to each other in shape, habit, and habitat. Historical events, over the centuries, have led to a temporary overlap of the habitats of these species in Egypt, confusing reports related to them. The native water lilies of Egypt, used for widely varying purposes since pre-dynastic periods, are the species *N. lotus* (white water lily) and *N. nouchali* var. *caerulea* (blue water lily). Joining them in the iconography from the time of Persian domination in Egypt (sixth to fifth centuries BC) is *N. nucifera* (Indian lotus). Similar to the indigenous water lilies, it supplanted or at least appeared side by side with these in uses and descriptions. The confusion generated in the past is clarified by a careful analysis of the sources and areas of origin and distribution of the species. This is confirmed by the fact that *N. nucifera* has disappeared from Egypt, regressing in that environment to which it was not fully adapted, while the native water lilies are still present, even if less widespread than in the past.

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Supplementary Table 1. Sources for "*lotus*." Analyzed sources, with authors, dates, titles, and citations. Sorted by date.

| Author | Date | Title | Investigated terms and interpretations |
|---|---|---|---|
| Egyptian traditions | IV millennium BC –Ptolemaic period (III century BC) | Myth of the birth of the god Horo | "the flower rose from the primordial waters of Nù in the day of creation" (*Nymphaea lotus* L.; *Nymphaea nouchali* var. *coerulea* (Savigny) B. Verdcourt) |
| Islamic and Hebrew culture | | Common names | "nabq," "dum," "sidr," "tsal," "sadr" (*Ziziphus spina-christi* Mill.) |
| Various authors | | | "fenugreek" (*Trigonella foenum-graecum* L.) |
| Homer | IX–VIII century BC | Odissey; Iliad | "lotus of the Lotophages" (*Ziziphus lotus* L.); "fodder lotus," "dewy lotus" (*Trifolium boissieri* Guss.; *Trifolium* spp.); "floral lotus" (*Melilotus neapolitanus* Ten.; *Trigonella foenum-graecum* L.) |
| Bible | VI century BC | Judges 9:14-15; Jobs 40:21-22 | "bramble," "thorns," "sheisaf," "atad," "n'atsuts," "tse'elym" (*Ziziphus spina-christi* Mill.) |
| Scylax | VI–V century BC | The *Periplo* | "lotus of the Lotophages," "Brachion, Lotophages's island," "Lotus of the Hesperides," "the fruit was as large as a strawberry tree fruit and from a species was made wine" (*Ziziphus lotus* L.) |
| Cratino | 520–423 BC | The *Effemminati* | "coronary lotus or melilotus" (*Melilotus neapolitanus* Ten.) |
| Euripides | 485–407 BC | The *Troadi*; The *Fenicie* | "lotus of the Lotophages" (*Ziziphus lotus* L.); "fruitful lotus lawns" (*Trifolium boissieri* Guss.; *Trifolium* spp.) |
| Herodotus | 484–430 BC | The *Histories* | "lotus of the Lotophages," "the fruit was as large as a lentisk, it was as sweet as the date, from it was also made of wine" (*Ziziphus lotus* L.); "Egyptian white-colored water lily," "the flower was white; the fruit like a large poppy capsule, equally divided into lodges, but with more dense seeds like millet, which, extracted by maceration of the shell, served to make bread" (*Nymphaea lotus* L.); "Egyptian blue water lily" (*Nymphaea nouchali* var. *coerulea* (Savigny) B.Verdcourt) |
| Xenophon | 430–355 BC | *Anabasi* | "Lotus eaters" (*Ziziphus lotus* L.) |
| Aristotle | 384–322 BC | *Historia animalium* | "at the time the bees wax, they feed on plants that then flourish, including the melilotus" (*Melilotus neapolitanus* Ten.) |
| Theophrastus | 371–287 BC | *De Historia Plantarum* | "*Faride*, home of the Lotophages," "the plant was fruticose, dense with branches and had a large stem. The fruits were arranged in opposite and dense manner as in myrtle; they turned color during maturation, were as big as a broad bean, sweet and pleasant, were harmless, even useful for the womb," "there was a variety that had the fruit without kernel, which was tastier and needed to make wine," "the fruit was always provided with a large kernel, had little pulp, covered by a rather rigid membrane, more pleasant than sweet, and the wine it produced did not last more than two or three days" (*Ziziphus lotus* L.); "paliurus" "The (Egyptian) Spine of Christ is thicker than the lotos" (*Ziziphus spina-christi* Mill.); "sylvan flower suitable for making crowns" (*Melilotus nepolitanus* Ten.); "Egyptian white-colored water lily," "the flower was white; the fruit like a large poppy capsule, equally divided into lodges, but with more dense seeds like millet, which, extracted by maceration of the shell, served to make bread" (*Nymphaea lotus* L.); "Egyptian blue water lily" (*Nymphaea nouchali* var. *coerulea* (Savigny) B. Verdcourt) |

Supplementary Table 1 cont. Sources for “*lotus*.” Analyzed sources, with authors, dates, titles, and citations. Sorted by date.

| Author | Date | Title | Investigated terms and interpretations |
|---|---|---|---|
| Agatocle from Cizico | III century BC | *History of Cizico* | “a small tree, big like an elm or a poplar, with long and thorny branches, green and ovate foliage. It bears fruit twice a year: in spring and autumn, fruits were sweet, as big as an olive, similar to this in the pulp and kernel and of delicate sweetness; the fruit was eaten fresh, but also a little dried, it was ground to obtain a flour, which was kneaded with the feet, to prepare coarse flat breads” (*Ziziphus spina-christi* Mill.) |
| Cato | 234-149 BC | *De Re Rustica* | “*serta campanica*” (*Melilotus neapolitanus* Ten.) |
| Agatarchide | 220-145 BC | *About the Red Sea* | “the Ittiofagi, people living along the African coasts of the Red Sea, had the habit of preparing a paste with fermented fish meat, to which they mixed paliurus seeds, to make it more consistent, and as a condiment,” “the most miserable drank the juice of the paliurus plants, and with the young branches they made bindings to tie the corpses in a certain way” (*Ziziphus spina-christi* Mill.) |
| Polybius | 206-124 BC | *Histories* | “Meninge, Lotophages’ island,” “the lotus plant is not large, but rough and thorny, has green leaves, like the buckthorn, but a little darker and wider, the whole fruit crushed when ripe, is stored in the pots and is used to feed the servants, while, deprived of the kernel and preserved in the same way, it is food for the free people. Macerated in water and minced, it is used to make a wine-like drink” (*Ziziphus lotus* L.) |
| Diodorus Siculus | 90-27 BC | *Bibliotheca Historia* | “Agatocle cit.,” “Panchei, that those peoples collected the fruit of the paliurus, using it for food and drink, obtaining benefit against the flow of the stomach” (*Ziziphus spina-christi* Mill.); “Egyptian white-colored water lily,” “the flower was white; the fruit like a large poppy capsule, equally divided into lodges, but with more dense seeds like millet, which, extracted by maceration of the shell, served to make bread,” “in Egypt bread was made” (*Nymphaea lotus* L.); “Egyptian blu water lily” (*Nymphaea nouchali* var. *coerulea* (Savigny) B. Verdcourt) |
| Virgil | 70-19 BC | *Culex*;<br>The *Georgiche* | “lotus too hospitable” (*Ziziphus lotus* L.); |
| Strabo | 60 BC-24 | *Geography* | “Sirte Lotofagide” (*Ziziphus lotus* L.) |
| Propertius | 47-15 BC | The *Elegie* | “lotosque, herbaeque tenaces” (*Ziziphus lotus* L.) |
| Ovid | 43 BC-17 | The *Tristia*;<br>The *Fasti* | “lotosque, herbaeque tenaces” (*Ziziphus lotus* L.); “the young companions of Proserpina picked up the melilotus with other flowers” (*Melilotus neapoletanus* Ten.) |
| Pomponius Mela | I century-43 | *De Chorografia* | “Lotophages in Cyrenaic” (*Ziziphus lotus* L.) |
| Bible, Gospels | I century | Mattew 27:27-29;<br>Jon 19:5 | “bramble,” “thorns,” “crown of thorns” (*Ziziphus spina-christi* Mill.) |
| Scribonius Largo | I century | The *Compositiones* | “the melilotus is what we say sertula Campana” (*Melilotus neapolitanus* Ten.) |

*continued*

SUPPLEMENTARY TABLE 1 CONT. Sources for "*lotus*." Analyzed sources, with authors, dates, titles, and citations. Sorted by date.

| **AUTHOR** | **DATE** | **TITLE** | **INVESTIGATED TERMS AND INTERPRETATIONS** |
|---|---|---|---|
| Pliny | 23-79 | *Naturalis Historia* | "Lotus too hospitable," "Gerba Lotofagida," "the plant was small; the fruit was abundant and dense as in myrtle; it was as big as a saffron-colored bean, changing color as it matured. Very sweet food in Africa, preserved from stomach ache. From it we obtained a drink like wine with honey which was not kept more than ten days. The crushed fruits were kept in large vessels for food" (*Ziziphus lotus* L.); "Spina-christi" (*Ziziphus spina-christi* Mill.); "a sylvan flower suitable for making crowns," "it was odorous and was used to make ointments and with it was prepared a fragrant oil," "the ointments used by the King of the Parts," "*Sertula Campana* is called melilotus, because in ancient times was used for crowns," "aromatic herbs and the fragrant flowers to be planted as bees' pasturage" (*Melilotus neapolitanus* Ten.); "be the best among all the grasses of the meadows" (*Trifolium boissieri Guss*.; *Trifolium* spp.); "*lotometra* was produced from the lotus," "Egyptian white-colored water lily," "the flower was white; the fruit like a large poppy capsule, equally divided into lodges, but with more dense seeds like millet, which, extracted by maceration of the shell, served to make bread," "from the seed like the millet, macerated in water or milk, the Egyptian shepherds made excellent breads to be cooked, but when cooled they became indigestible" (*Nymphaea lotus* L.); "Egyptian blue water lily" (*Nymphaea nouchali* var. *coerulea* (Savigny) B. Verdcourt) |
| Silio Italico | 25-101 | *Punica* | "Lotus too hospitable" (*Ziziphus lotus* L.) |
| Dioscorides | 40-90 | *De Materia Medica* | "a sylvan flower suitable for making crowns," "ingredient for ointments, which he defined as *telino*," "the melilotus is celebrated in Attica, in Cizico and in Calcedone, had color close to the saffron and with a good smell," "it is also born in Campania near Nola reddish and slightly odorous" (*Melilotus neapolitanus* Ten.); "lotus clover of the meadows" (*Trifolium boissieri* Guss.; *Trifolium* spp.); "Egyptian white-colored water lily" (*Nymphaea lotus* L.); "Egyptian blue water lily" (*Nymphaea nouchali* var. *coerulea* (Savigny) B. Verdcourt) |
| Ptolemy | 100-175 | *Geography* | "*Gerba Lotofagida*," "*Meninge Lotofagida*" (*Ziziphus lotus* L.) |
| Galeno | 129-201 | *De simplicium medicamentorum facultatibus* | "Egyptian white-colored water lily" (*Nymphaea lotus* L.); "Egyptian blue water lily" (*Nymphaea nouchali* var. *coerulea* (Savigny) B. Verdcourt) |
| Talmud | II-III century | Bava Bathra, 48b | "*kanari*" (*Ziziphus spina-christi* Mill.) |
| Mishnah | 217 | Demai, 1:1; Kil'ayim, 1:4 | "*rimin*" (*Ziziphus spina-christi* Mill.) |
| Ateneo | II sec. | The *Deipnosofisti, Propontis* | "*connari* and *paliuri*," "those fruits were used on the tables of Alexandria in Egypt," "*spina-christi* (description)" (*Ziziphus spina-christi* Mill.); "the flower of the *helichrysum* was like the lotus, but the latter was a more intense yellow" (*Trifolium boissieri* Guss.; *Trifolium* spp.); "*lotine* and *melilotine* crowns" (*Melilotus neapolitanus* Ten.) |
| Qur'an | 650 | LIII: 13-18;<br>LVI: 28-32 | "*sedr*" (*Ziziphus spina-christi* Mill.) |
| Photius | 820-893 | Biblioteca | "Agatocle cit." (*Ziziphus spina-christi* Mill.) |
| Estori ha-Parhi | 1280-1355 | Sepher Kaftor va-Ferah | "*rimin*," "*nabaq*," "*dum*," "*sidar*" (*Ziziphus spina-christi* Mill.) |
| Mattioli P. A. | 1501-1577 | Commentarii | "the flower was white; the fruit like a large poppy capsule, equally divided into lodges, but with more dense seeds like millet, which extracted by maceration of the shell, served to make bread" (*Nymphaea lotus* L.) |
| Torquato Tasso | 1544-1595 | Gerusalemme Liberata | "Alzerbe, già dè lotofagi albergo" (*Ziziphus lotus* L.) |
| Pampanini Renato | 1875-1949 | Various | "*Sedr*" (*Ziziphus lotus* L.) |

SUPPLEMENTARY MATERIAL. Summary of “lotus” ancient names and definitions related to hypothesized species.

I. Arboreal lotus
**_Ziziphus lotus_ Lam.**
1) Lotus of the Lotophages (Homer, Herodotus, Theophrastus, Scylax, Polybius, Pomponius Mela, Pliny, Strabo, Ptolemy, Torquato Tasso).
Tempting lotus (Euripides).
Lotus too hospitable (Virgil, Silio Italico, Pliny).
Lotus and bewitching herbs (Propertius).
Lotus makes forget the way home (Xenophon, Ovid).
Lotus of the Hesperides (Scylax).

**_Ziziphus spina-Christi_ Willd.**
2) Paliurus of Cyrenaic (Theophrastus, Agatocle from Cizico).
Paliurus and connaro (Athenaeus).
Paliurus of the African coasts (Agatarchide cited by Photius and Diodorus Siculus).
Paliurus of the *Arabia felix* (Diodorus Siculus).
*Sedr* (Qur’an).
Tree of *nabeq* fruit (Qur’an, Estori ha-Parhi).
The Egyptian Spine of Christ (Theophrastus).
Spina Christi Lotus (Pliny).
*Atad* (Bible).
*N’atsuts* (Bible).
*Tse’elym* (Bible).
*Rimin* (Talmud, Estori ha-Parhi).
*Kanari* (Talmud).
Bramble and thorns (Bible, Gospels).
*Sidar* (Estori ha-Parhi).
*Dum* (Estori ha-Parhi).

II. Herbaceous and fodder lotus
**_Lotus, Melilotus, Trigonella and Trifolium_ spp.**
1) Fodder lotus (Homer).
Herbaceous lotus (Athenaeus, Theophrastus, Pliny, Dioscorides).
Floral lotus (Homer)
Lotus flower like helichrysus (Athenaeus)
Coronary lotus or melilotus (Athenaeus, Anacreonte, Cratino).
Lotus as ingredient for ointments (Theophrastus, Pliny).
Odorous melilotus, ingredient for ointments (Pliny, Dioscorides).
Melilotus as bees’ pasturage (Pliny, Aristotle).
Floral melilotus (Ovid).
Melilotus called *serta campanica* (Cato).
Melilotus called *sertula campana* (Pliny, Scribonius Largo)
Lotus clover of meadows (Dioscorides, Pliny).
Dewy lotus from mount Ida (Homer).
Lotus in fruitful lawns (Euripides).
Clover lotus (Dioscoride, Galeno).

III. Aquatic lotus
**_Nymphaea lotus_ L.**
1) Egyptian lotus (Herodotus, Theophrastus, Diodorus Siculus, Pliny, Dioscorides, Galenum).
Lotus from which bread is made (Diodorus Siculus, Pliny)
Lotus from which the *lotometra* is obtained (Pliny)

**_Nymphaea nouchali_ var. _coerulea_ (Savigny) B. Verdecourt**
*2) ZŠŌŠĔN* (Hieroglyphic documents).
3) Egyptian lotus (Athenaeus).

**_Nelumbo nucifera_ Willd.**
4) Egyptian lotus (Dioscorides).

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# *EUPHORBIA SHEHBAZIANA* (EUPHORBIACEAE), A NEW SPECIES FROM KURDISTAN IRAQ

Sakar Y. Hama[1] and Saman A. Ahmad[1,2,3]

**Abstract.** *Euphorbia shehbaziana* is described and illustrated as a new species from Kurdistan Iraq, and its distinguishing characters from its nearest relatives, *E. denticulata* and *E. craspedia*, are discussed.

**Keywords:** *Euphorbia*, Iraq, Gmo Mt., Kurdistan

One of us (SYH) has been involved in the past two years in intensive floristic studies of Gmo Mountain in partial fulfillment of the requirements for an M.S. degree in botany. This mountain, which is only about 6 km from the Iran-Iraq border, is part of the extensive Zagros Range that extends from eastern Turkey into SW Iran. Gmo was previously inaccessible to botanical fieldwork because of its strategic border location. We collected plants from several populations of a *Euphorbia* species that proved to represent an undescribed species, after checking floristic accounts from Iraq (Radcliffe-Smith, 1980), Iran (Rechinger and Schiman-Czeika, 1964), and Turkey (Radcliffe-Smith, 1982). It is described and illustrated below, and its relationships to nearest relatives are discussed.

**Euphorbia shehbaziana** S.Y. Hama and S.A. Ahmad, *sp. nov*.

TYPE: IRAQ. Kurdistan region, Sulaimani Province: Gmo Mountain, Rashakani village, mountainside, eroded place, sandy and rocky soil, 1803 m, 35°53'91"N, 45°33'26"E, 17 June 2019, *S. A. Hama, S. A. Ahmad, and A. Hama 2019-1581* (Holotype: KBFH; Isotypes: SUFAH). Fig. 1.

*Euphorbia shehbaziana* is readily distinguished from its nearest woody relatives by having entire leaves, 3- to 5-rayed umbels, denticulate glands, bracteate male flowers, and rugose seeds.

*Subshrubs* or perennial herbs, glabrous throughout. *Stems* 15–50 cm tall, erect, woody except herbaceous current-year growth, 3–10 mm wide at base, many branched below, simple to the base of inflorescence; sterile shoots with dense imbricate, narrowly oblanceolate to linear-oblanceolate leaves 1.0–2.5 cm × 1–5 mm. *Cauline leaves*, glabrous, not glaucus, oblanceolate to oblong-obovate, 0.9–3.2 cm × 4–12 mm, margin entire, apex mucronate. *Inflorescence* 3- to 5-rayed umbel; involucral bracts 3–5, obovate to broadly so, 1.3–2.0 × 0.7–0.6 cm, apex mucronate, margin entire; rays ending with 3-flowered dichasial cymes subtended by minutely petioled pair of reniform bracts 0.7–1.0 × 1.2–1.6 cm; central *cyathium* sessile, two lateral cyathia on short stalks each subtended by 2 bracts similar to those at base of the dichasium but smaller; cyathium cup-shaped, 2.0–3.5 mm long, glabrous; teeth acute ca. 0.5 mm long; glands short stalked to subsessile (2–)3- to 5-toothed, teeth simple or minutely divided into 2 or 3 teeth. *Male flowers* on pedicels 0.9–2.0 mm long, surrounded by linear distally ciliate bracts 1.5–2.0 mm long; filament 0.5–0.8 mm long; anthers 0.5–0.7 mm long. *Fruit* glabrous, ovoid, (3.5–)4.5–6.0 × 2.5–4.0 mm, slightly lobed. *Seeds* gray, including caruncle 3–4 × 1.5–2.0 mm, surface rugose; caruncle 0.5–0.7 mm long, cordate, 1/6–1/8 the length of seed.

**Etymology:** *Euphorbia shehbaziana* is named in honor of our mentor and friend Dr. Ihsan A. Al-Shehbaz (MO) in recognition of his devotion to promoting botany in Kurdistan Iraq.

**Additional specimens examined:** IRAQ. Kurdistan region, Sulaimani Province, Gmo Mountain: Rashakani village, near stream, sandy and rocky soil, 1779 m, 35°53'96"N, 45°33'06"E, 17 June 2019, *S. A. Hama, S. A. Ahmad, and A. Hama 2019-1592* (KBFH, SUFAH); Shaxa spi area, mountainside, timberline, wetlands, sandy soil, 1800 m, 35°53'52"N, 45°34'05"E, 20 May 2019, *S. A. Hama, S. A. Ahmad, and M. Abdulla 2019-1024* (KBFH, HKS); Basne, Darui Zuberan, mountainside, near orchard, sandy and rocky soil, 1815 m, 35°89'81"N, 45°56'75"E, 25 Jun 2019, *S. A. Hama, S. A. Ahmad, and M. Abdulla 2019-1654* (KBFH); Rashakani village, mountainside, near orchards, sandy and rocky soil, 1767 m, 35°53'79"N, 45°33'58"E, 17 June 2019, *S. A. Hama, S. A. Ahmad, and A. Hama 2019-1467* (KBFH); Rashakani village, mountainside, eroded place, sandy and rocky soil, 1803 m, 35°53'91"N, 45°33'26"E, 17 June 2019, *S. A. Hama, S. A. Ahmad, and A. Hama 2019-1564* (KBFH); Basne, Darui Zuberan, mountainside, near orchard, sandy and rocky soil, 1815 m, 35°89'81"N, 45°56'75"E, 25 June 2019, *S. A. Hama, S. A. Ahmad, and M. Abdulla 2019-1658* (KBFH); Rashakani village/ Kani chankan, mountainside, eroded place, sandy and rocky soil, 1726 m, 35°53'10"N, 45°33'70"E, 12 June 2019, *S. A. Hama, S. A. Ahmad, and A. Hama 2019-1422* (KBFH); Shaxa swr, mountainside, eroded place, roadside, sandy and rocky soil, 1602 m, 35°55'11"N, 45°34'36"E, 29 May 2019, *S. A. Hama, S. A. Ahmad, and Z. S. Mustafa 2019-1216* (KBFH).

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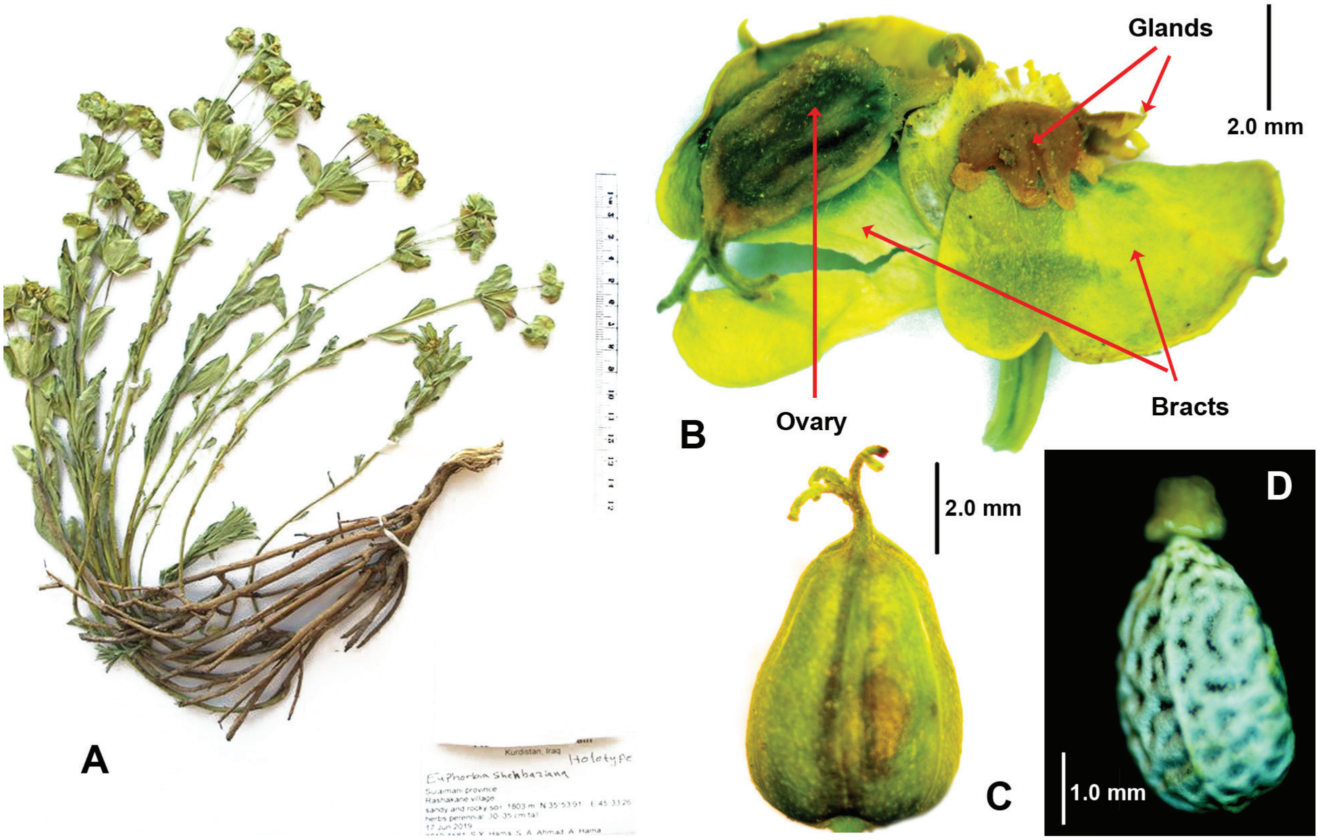

FIGURE 1. *Euphorbia shehbaziana* S.A. Hama & S.A. Ahmad. **A**, plant; **B**, cyathium; **C**, fruit; **D**, seed with caruncle. Photographs by Saman A. Ahmad based on the holotype.

*Euphorbia shehbaziana* is most closely related to *E. denticulata* Lam. and *E. craspedia* Boiss., which it resembles in having glabrous leaves, woody lower stems, and denticulate nectar glands. However, it differs from both of them in having ciliate bracts (vs. no bracts) between male flowers, entire (vs. denticulate) cauline leaves, 3- to 5-rayed (vs. 5- to 17-rayed) pseudoumbels, and denticulate versus pectinate glands. It also differs from *E. denticulata* by having umbels 3- to 5-rayed (vs. 5- to 7[–9]-rayed), smaller fruits 3.5–6.0 mm (vs. ca. 8 mm), and ovoid rugose (vs. quadrangular-ovoid and tuberculed-regulose) seeds. From *E. craspedia,* the novelty differs by having 3- to 5-rayed (vs. 8- to 17-rayed) umbels and smaller seeds 3–4 (vs. ca. 5) mm long that are rugose (vs. tuberculate).

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# A REPORT ON THE FOURTH BOTANICAL NOMENCLATURE COURSE ORGANIZED BY THE BOTANICAL SURVEY OF INDIA AT SHILLONG

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The Botanical Survey of India (BSI) held its fourth Botanical Nomenclature Course on January 27–31, 2020 at BSI-Eastern Regional Centre (BSI-ERC), Shillong. The course drew 66 participants from across the country, including 45 from outside BSI (Fig. 1). Ashiho A. Mao, director of BSI, was the convener of the course; P. Lakshminarasimhan, ex-joint director of BSI, and Nripemo Odyuo, head, BSI-ERC, served as the coordinator and facilitator, respectively. Kanchi N. Gandhi served as the course director. Participants were provided with the latest International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code; Turland et al., 2018) and a user's guide to the International Code of Nomenclature (Turland, 2019).

Chaya Deori (BSI-ERC) anchored the inaugural activities. Odyuo gave a welcome speech, followed by remarks from Lakshminarasimhan, Gandhi, and chief guest Mao. Rajalakshmi Prasad and Anupama Jayasimha (former students of Gandhi's at National College, Bengaluru) were the guests of honor. Uma Shankar (North-Eastern Hill University, Shillong) also attended the inaugural function.

Gandhi began the course with a historical review of botanical nomenclature. He provided a detailed review of

FIGURE 1. Fourth Botanical Nomenclature Course organized by the Botanical Survey of India at Shillong. Delegates of the course.

We thank A. R. Brach (A, GH) for helpful suggestions on the text, C. M. Gallagher, and D. Medhanie (A, GH).

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FIGURE 2. Fourth Botanical Nomenclature Course organized by the Botanical Survey of India at Shillong. Discussion session.

the Shenzhen Code and discussed the Code Articles, with special emphasis on correct names and solving nomenclatural problems of the participants. Gandhi covered the following topics at the various sessions: an overview of nomenclature from pre-Linnaeus to the Shenzhen Code; review of the physical structure of the Code: preamble, ranks, and names of taxa (appropriate Articles 1–5 and 16–28); status, typification, starting points, conservation, and sanctioning (Articles 6–15); effective publication; validity of names (Articles 29–45); authorship citation (Articles 46–50); rejection of names-I (Articles 51–59); and orthography (Articles 60–62). In addition, he discussed hybrid names and fungal code. Each day ended with an interactive discussion with the participants (Fig. 2).

## SOME DISCUSSED TOPICS

### *Tomato and Circumscription:*

*Solanum lycopersicum* L. (1753); *Lycopersicon esculentum* Mill. (1768), *nom. cons*.; *Lycopersicon lycopersicum* (L.) H. Karst. 1882 ("*Lycopersicum lycopersicum*")

For tomato, Gandhi mentioned that for those who use *Solanum s.l.* (including *Lycopersicon*), the correct name is *S. lycopersicum*, and for those who recognize *Lycopersicon* as a distinct genus, the correct name is *L. esculentum*.

### *Berlin Code (1988):*

*Pongamia* Vent., Jard. Malm. T. 28. 1803. (nom.cons.); *Typus*: *P. glabra* Vent., nom. illegit. (*P. pinnata* (L.) Pierre, *Cytisus pinnatus* L.)

*Pongam* Adans., Fam. Pl. 2: 322, 593. 1763; *Typus*: *Dalbergia arborea* Willd.

*Derris* Lour., Fl. Cochinch.: 423, 432. 1790, *nom. cons*.; *Typus*: *D. trifoliata* Lour. (*typ. cons*.)

### *Tokyo Code (1994):*

*Pongamia* Adans., Fam. Pl. 2: 322, 593. 1763 ("*Pongam*."), (*nom.* & *orth. cons*.); *Typus*: *P. pinnata* (L.) Pierre (*Cytisus pinnatus* L.) (*typ. cons*.); *nom. rej*. vs. *Millettia* Wight & Arn. 1834 (*nom. cons*.)

*Derris* Lour., Fl. Cochinch.: 423, 432. Sep 1790, *nom. cons*.; *Typus*: *D. trifoliata* Lour. (*typ. cons*.)

Gandhi explained that occasionally the Code concepts may change and remarked that, as per the Berlin Code, *Pongam* Adans. and *Pongamia* Vent. were heterotypic and that *Derris* had priority over *Pongamia* Vent., and that in contrast, as per the Tokyo Code, *Pongam* Adans. was correctable to *Pongamia* Adans., typified with *P. pinnata*, and has priority over *Derris*.

### *English Grammar and Validity:*

Gandhi's discussion included two examples showing how English grammar could affect validity of a plant name. For example, Haworth (1821: 81-82) validly published the name *Mesembryanthemum* section *Minima* Haw. and remarked that "if this section proves to be a genus, the name of *Conophyton* would be apt." The designation "*Conophyton*," suggested by Haworth (1821), was not a validly published generic name because Haworth did not adopt or accept the genus (see Art. 36.1 Ex. 4). In contrast to the preceding situation, Gandhi provided a different example, viz., *Crepis sancta* (L.) Bornm. (1913). On his new combination, Bornmüller remarked that "if one unites the genus *Lagoseris* with *Crepis*, as Muschler has done recently, the plant has to be named *Crepis sancta*." Gandhi mentioned that he and John Wiersema (the chief editor of Code Appendices II–VIII) discussed the validity of the name *C. sancta* and asserted that it is a validly published species name. Gandhi elaborated by stating that in the first example (*Conophyton*), the verb in the second part of the sentence ("would be apt") is the simple future resulting in a conditional sentence and thus causing invalidity, whereas in the second example the verbs ("unites" and "has to be") are in the simple present, resulting in a zero-conditional sentence in which one can replace "if" with "when," because both express general truths. The meaning will be unchanged as shown here: "When (= "If") one unites the genus *Lagoseris* with *Crepis*, as Muschler has done recently, the plant has to be named *Crepis sancta*."

## VALEDICTORY FUNCTION

A valedictory function was held on January 31, 2020, anchored by Debonina Dutta (BSI-ERC). Odyuo and Lakshminarasimhan gave short talks. Gandhi was presented with a memento of appreciation by Odyuo (Fig. 3), a painting of an orchid (*Paphiopedilum venustum* (Wall. ex Sims) Pfitzer) by L. Ibemhal Chanu, a botanist at BSI-ERC (Fig. 4), as were Rajalakshmi Prasad and Anupama Jayasimha. Gandhi acknowledged several people, especially Gopal Krishna (BSI-Central National Herbarium) and Chanu, for helping to make the course a success. Feedback on the course was given by four participants: Suman Datta (Serampore College, Hooghly), Kh. Sangeeta Devi (BSI-ERC), Rajeev Kumar Yadav (Bareilly College, Bareilly), and B.R. Kailash (ATREE, Bengaluru). Certificates were then distributed to all the participants).

FIGURE 3. Fourth Botanical Nomenclature Course organized by the Botanical Survey of India at Shillong. Presentation of a memento to K. N. Gandhi by N. Odyuo.

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FIGURE 4. Artwork presented to K. N. Gandhi (*Paphiopedilum venustum* (Wall. ex Sims) Pfitzer, Orchidaceae). Painting by L. Ibemhal Chanu.

# AN ILLUSTRATED DIAGNOSTIC KEY TO SPECIES IN THE VENEZUELAN CLADE OF *ESPELETIA* (ASTERACEAE)

Jesús Mavárez[1,2]

**Abstract.** An illustrated key is presented to species in the Venezuelan clade of *Espeletia* (Asteraceae), based on herbarium specimens, virtual herbaria, and fresh samples from field collections. The 54 *Espeletia* species in this clade are documented: (i) 48 entirely endemic to the Venezuelan Andes, (ii) 2 found as well in the Venezuelan Cordillera de la Costa, the eastern section of the Colombian Cordillera Oriental, and the Sierra Nevada de Santa Marta, and (iii) 4 endemic to the northern section of Colombian Cordillera Oriental and Sierra de Perijá. Schematic representations of leaves of all species are provided, including important diagnostic characters such as length-to-width ratios, and the shape, density, or angles of secondary nerves. Additional diagnostic characters are also described or illustrated for some species, such as the type of indumentum on leaves, the structure of the inflorescence, the size of the capitulum, and the color of ray ligules. The key has been shown to allow identification of species using both herbarium samples and fresh material, and given the predominant use of vegetative characters it is also useful on some monocarpic rosette species that are frequently found in the vegetative stage.

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

The plants in the genus *Espeletia* Mutis ex Bonpl. (Asteraceae; Humboldt and Bonpland, 1809) represent the best example of taxonomic, morphological, and ecological diversification in the tropical high-elevation grassland ecosystem of the Northern Andes known as páramo (Diazgranados, 2012; Cuatrecasas, 2013; Diazgranados and Barber, 2017; Pouchon et al., 2018; Mavárez, 2019). The genus evolved from a single ancestor quite recently, about 2.5 MYA (Pouchon et al., 2018), after the final uplift of the Northern Andes that facilitated environmental conditions for the páramo habitat (Hooghiemstra et al., 2006; Torres et al., 2013). The approximately 140 *Espeletia* species are distributed phylogenetically in two major groups (Diazgranados and Barber, 2017; Pouchon et al., 2018; Mavárez, 2019): (i) a northeastern clade of 54 species, known as the "Venezuelan," almost entirely restricted to the Venezuelan Cordillera de Mérida, with some species found in the Venezuelan Cordillera de la Costa, the northern section of the Colombian Cordillera Oriental, the Sierra de Perijá, and the Sierra Nevada de Santa Marta, and (ii) a southwestern clade of about 80 species, known as the "Colombian," distributed across the Colombian Andes, the Sierra de Perijá, and northern Ecuador. The Venezuelan clade is morphologically more diverse, since it includes shrubs and unbranched, dichotomous, or profusely branched trees, and also monocarpic and polycarpic rosettes that can be sessile, short-branched, or unbranched. The Colombian clade is composed exclusively of polycarpic rosettes, almost all of them unbranched, with the exception of one species that always is profusely branched (Mavárez and Becerra, 2019) and two that can occasionally be sparsely branched (Cuatrecasas, 1996).

The identification of *Espeletia* species can sometimes be a real challenge, most particularly when attempted directly in the field. An important number of taxa are indeed very similar morphologically, differing mainly on quantitative traits associated with the shape and size of leaves, inflorescences, and capitula. On the other hand, sympatry is also particularly common among members of this genus, and it is not unusual to find several species living near each other in some locations, as for instance in Sierra de la Culata, Venezuela, where up to 11 rosette species can be found in close sympatry (Mavárez, pers. obs.). Furthermore, interspecific hybridization can be relatively frequent between certain species pairs, contributing thereby to the morphological variation observed within some taxa (Berry et al., 1988; Pouchon et al., 2018; Mavárez, 2019). Researchers studying *Espeletia* are therefore often confronted with situations in which groups of morphologically similar and closely related species in this genus coexist in sympatry and, in some cases, hybridize. This identification challenge can be especially difficult in Venezuela, where about half of the rosette species are monocarpic, spending many years in a vegetative state before flowering for a few days or weeks, after which they die. The identification of these taxa must often rely on vegetative traits of the rosettes, yet available identification keys for these plants usually depend strongly on reproductive traits (Cuatrecasas, 1996, 2013).

In this work I present an illustrated diagnostic key for the 54 species in the Venezuelan clade of *Espeletia* (Mavárez, 2019), leaving the analysis of the species in the Colombian clade for another work to be presented in the near future. The key is mainly aimed at the identification of live plants directly in the field, but several of the diagnostic traits used can also be retrieved from dry samples, so that the key may be used to identify herbarium specimens as well.

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## MATERIALS AND METHODS

### *Samples*

The key is based on the analysis of 2,264 samples reliably identified to the species level: 1,450 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 (Thiers, continuously updated), and 814 plants identified during fieldwork by the author and some colleagues (250 of which are now deposited at herbarium IVIC). These samples include all 54 species currently known to belong to the Venezuelan clade of *Espeletia* and 13 interspecific hybrid taxa that have received binomials in the past (Mavárez, 2019). However, hybrid taxa will not be treated in this key.

### *Morphological Characters*

The key uses interspecific variation observed in several diagnostic macroscopic morphological attributes of the plants' stems, leaves, inflorescences, and capitula, all of which can be easily measured on both living plants and herbarium samples without need for complex equipment:

Growth form. Habitus (tree or rosette), type of stem branching (branched or unbranched, monopodial or sympodial), stem size and aspect (naked or covered by marcescent leaves).

Leaf. Sheath type (open or closed) and shape, pubescence on sheaths (present or absent). Lamina type (sessile or pseudopetiolate), shape (linear, lanceolate, oblong, etc.), length, width, length-to-width ratio, type of adaxial pubescence (absent, sericeous, lanuginous, etc.). Pseudopetiole length. Angle and density of secondary nerves.

Inflorescence. Position (lateral or terminal), structure (simple or compound), organization of main branches (monochasial or dichasial), axis length, number and distribution of bracts in the vegetative section.

Capitulum. Diameters of capitulum, ligular circle, and disc, number or proportion of ray and disc flowers, length and color of ray corollas, shape and texture of sterile phyllaries.

### *Key Testing*

The key was tested blindly, that is, without the user's knowing the identity of the individual beforehand, on living plants of the *Espeletia* species shown in Fig. 1. Whenever possible, the key was tested on adult individuals that were in reproduction at the moment of the test or that held remnants of past reproduction events (dry inflorescences with attached capitula). However, tests of key performance were also tried in juvenile/sterile individuals when fertile ones were exceedingly rare in the population assayed.

The key was also tested on herbarium samples of the following species: *Espeletia albarregensis* (Cuatrec.) Mavárez, *E. angustifolia* Cuatrec., *E. arborea* Aristeg., *E. aristeguietana* Cuatrec., *E. atropurpurea* A.C. Sm., *E. badilloi* Cuatrec., *E. banksiifolia* Sch. Bip. & Ettingsh. ex Wedd., *E. batata* Cuatrec., *E. bracteosa* Standl., *E. bromelioides* Cuatrec., *E. chardonii* A.C. Sm., *E. cuatrecasasii* Ruiz-Terán & López-Fig., *E. elongata* A.C. Sm., *E. figueirasii* Cuatrec., *E. floccosa* Standl., *E. griffinii* Ruiz-Terán & López-Fig., *E. grisea* Standl., *E. hanburyana* Cuatrec., *E. jabonensis* Cuatrec., *E. jahnii* Standl., *E. leucactina* Cuatrec., *E. lindenii* Sch. Bip. ex Wedd., *E. liscanoana* Cuatrec., *E. lopezpalacii* Ruiz-Terán & López-Fig., *E. lucida* Aristeg., *E. marcescens* S.F. Blake, *E. margarita* Cuatrec., *E. marthae* Cuatrec., *E. moritziana* Sch. Bip. ex Wedd., *E. nana* Cuatrec., *E. neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd., *E. occulta* S.F. Blake, *E. paltonioides* Standl., *E. palustris* (Diazgr. & Morillo) Mavárez, *E. pannosa* Standl., *E. parvula* (Cuatrec.) Mavárez, *E. ruizii* Cuatrec., *E. schultzii* Wedd., *E. semiglobulata* Cuatrec., *E. spectabilis* Cuatrec., *E. spicata* Sch. Bip. ex Wedd., *E. tamana* Cuatrec., *E. tenorae* Aristeg., *E. thyrsiformis* A.C. Sm., *E. timotensis* Cuatrec., *E. trujillensis* Cuatrec., *E. ulotricha* Cuatrec., *E. vergarae* (Cuatrec. & López-Fig.) Mavárez, *E. viridis* Aristeg., and *E. weddellii* Sch. Bip. ex Wedd. Specimens of these species were collected by the author and colleagues and are now deposited at IVIC, where the identification tests were performed blindly by a group of staff members.

## RESULTS

Almost all living plants were correctly identified with this key. The few failures corresponded to some juvenile or sterile individuals with no remnants of past reproduction events, which did not allow the determination of diagnostic traits such as the position and structure of the inflorescence or the size of the capitula. This occasional difficulty did not prevent the correct identification of any species, since in all populations evaluated there were always individuals with inflorescences and capitula from on-going or past reproduction events. However, fertile individuals can be relatively rare in certain monocarpic species, for example, fewer than 1% in *Espeletia jabonensis* or *E. paltonioides* (Mavárez, pers. obs), probably as a consequence of a high degree of reproductive synchronization. The identification of individuals in this type of species was attempted using vegetative traits alone, with complete success.

The rate of correct identification for herbarium samples was also relatively high, about 90%. The failures occurred in some herbarium sheets in which diagnostic information, such as the description of the pubescence of sheaths, the position of the inflorescence, or the length and color of ray corollas, could not be retrieved from the specimens or their labels.

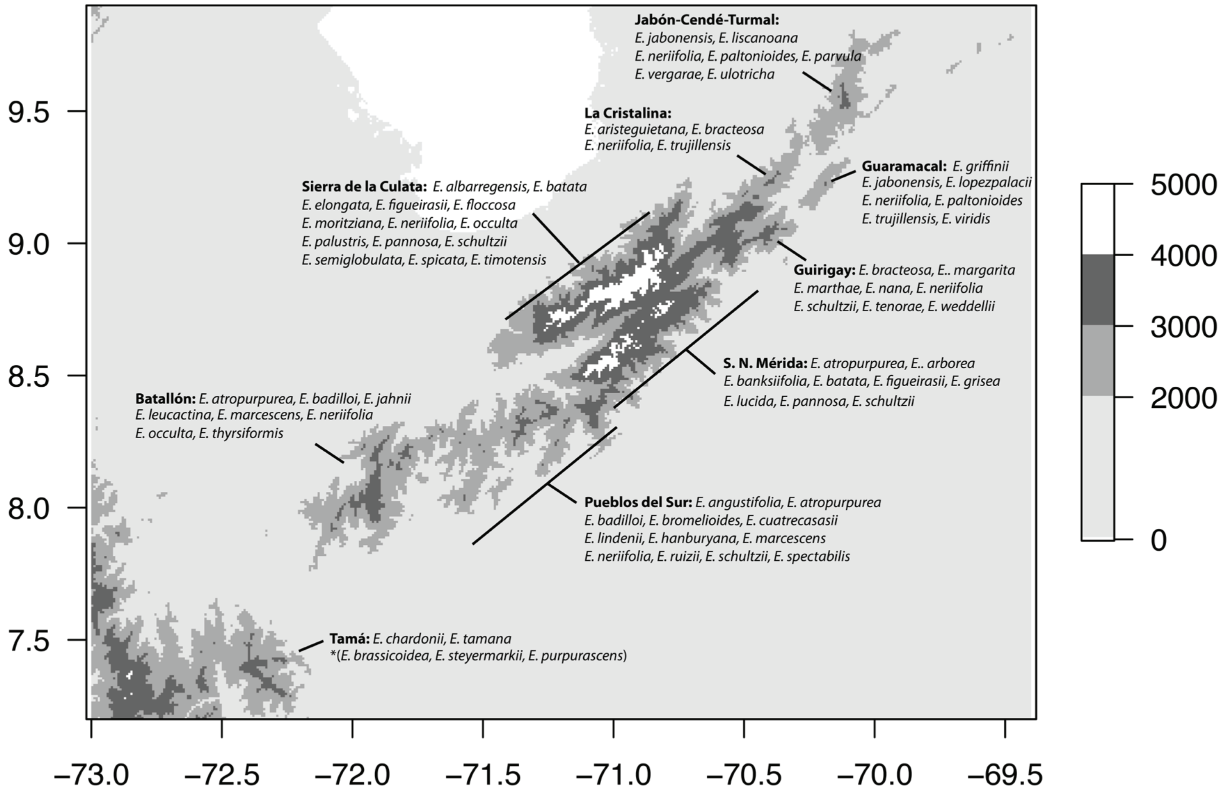

FIGURE 1. *Espeletia* species used for tests of key performance in living plants and their geographic locations (páramo names given in boldface). The three *Espeletia* species marked with (∗) are found in Páramo de Tamá but do not belong to the Venezuelan *Espeletia* clade.

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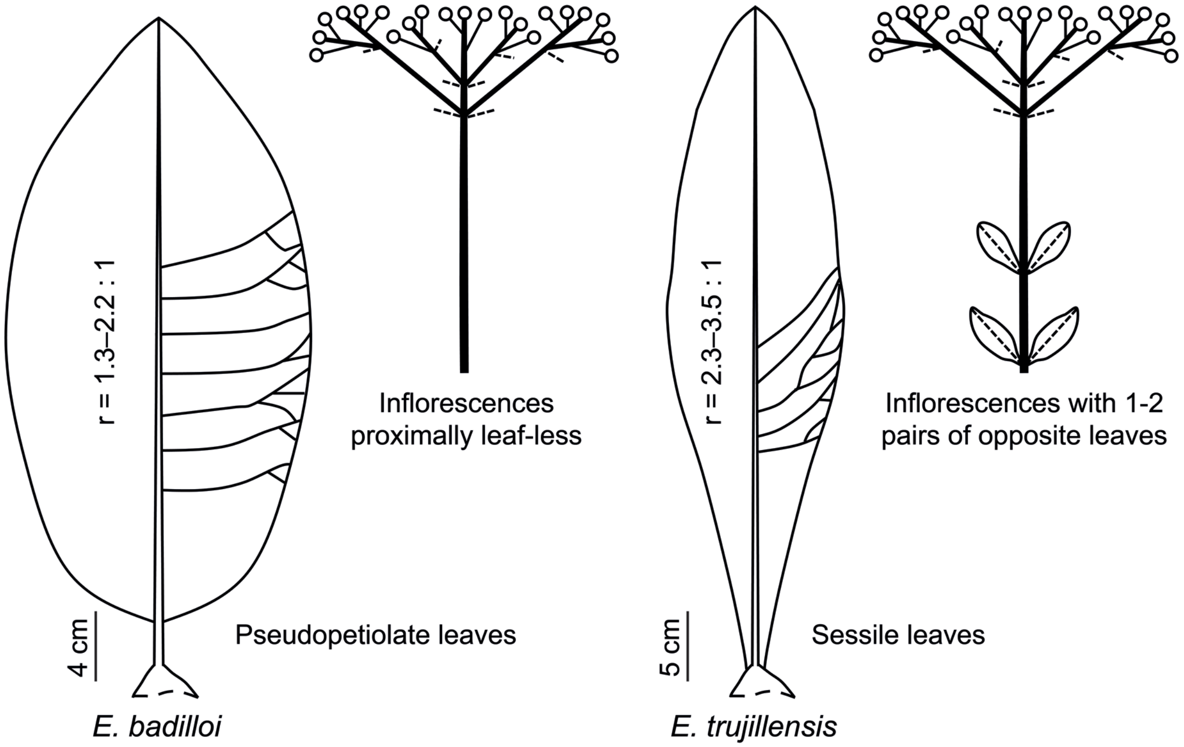
## An Illustrated Diagnostic Key to Species in the Venezuelan Clade of *Espeletia* (Asteraceae)

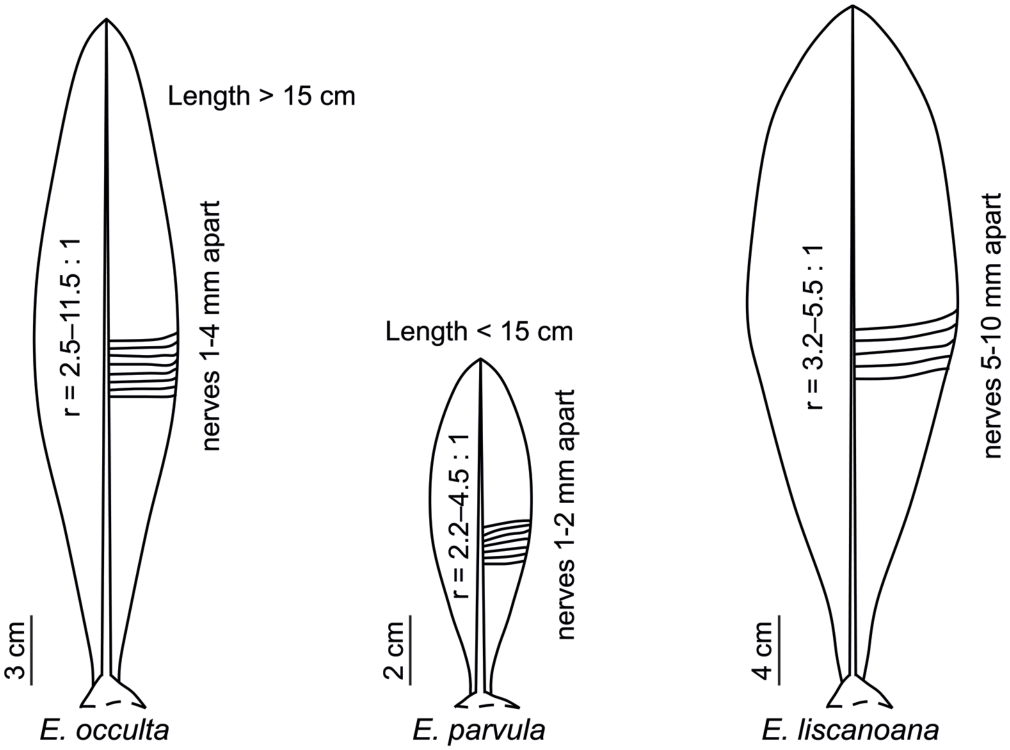
Plates 1–7. Schematic representations of leaf outlines, inflorescences, and phyllaries of species in the Venezuelan *Espeletia* clade. Leaf sheaths not shown unless otherwise stated. Abbreviations: **r**, leaf length-to-width ratio; **Ø**, capitulum diameter; **LC**, ligular circle diameter; **disc**, disc diameter; **%RF**, proportion of ray flowers. All leaf and inflorescence drawings by J. Mavárez (LECA). Plant drawings of *E. atropurpurea* A.C. Sm., *E. chardonii* A.C. Sm., and *E. jahnii* Standl. by C. Perrier (SAJF).

1a. Trees . . . . . . . . . . 2
1b. Rosettes . . . . . . . . . . 14
2a. Inflorescence structure primarily dichasial and in lateral position with regard to branch axis . . . . . . . . . . 3 (plate 1A)
2b. Inflorescence structure primarily monochasial and in terminal position with regard to branch axis . . . . . . . . . . 4
3a. Leaves pseudo-petiolate. Vegetative part of the inflorescence ebracteate . . . . . . . . . . *E. badilloi*
3b. Leaves sessile. Vegetative part of the inflorescence with 1–2 pairs of opposite bracts . . . . . . . . . . *E. trujillensis*
4a. Leaves sessile . . . . . . . . . . 5 (plate 1B)
4b. Leaves pseudopetiolate . . . . . . . . . . 7 (plate 2)
5a. Secondary nerves > 4 mm apart . . . . . . . . . . *E. liscanoana*
5b. Secondary nerves < 4 mm apart . . . . . . . . . . 6
6a. Leaf length > 15 cm . . . . . . . . . . *E. occulta*
6b. Leaf length < 15 cm . . . . . . . . . . *E. parvula*
7a. Stems sparsely branched, sympodial (pseudodichotomous). Sheaths open, semiamplectant. Ray corollas bright yellow . . . . . . . *E. chardonii*
7b. Stems profusely branched, monopodial. Sheaths either closed or open but entirely amplectant. Ray corollas eligulate or white, cream, pale-yellow . . . . . . . . . . 8
8a. Secondary nerves > 4 mm apart . . . . . . . . . . *E. neriifolia*
8b. Secondary nerves < 4 mm apart . . . . . . . . . . 9
9a. Ray corollas eligulate . . . . . . . . . . *E. lucida*
9b. Ray corollas ligulate . . . . . . . . . . 10
10a. Small shrubs and trees, usually < 4 m high. Leaf length < 15 cm . . . . . . . . . . *E. griffinii*
10b. Large trees, usually > 4 m high. Leaf length > 15 cm . . . . . . . . . . 11
11a. Sheaths adaxially barbate . . . . . . . . . . 12
11b. Sheaths adaxially glabrous . . . . . . . . . . 13
12a. Leaves with oblong outline (ratio 2–5:1) and dentate margins . . . . . . . . . . *E. banksiifolia*
12b. Leaves with lanceolate outline (ratio 6–9:1) and entire margins . . . . . . . . . . *E. tamana*
13a. Capitulum diam. > 12 mm . . . . . . . . . . *E. arborea*
13b. Capitulum diam. < 12 mm . . . . . . . . . . *E. divisoriensis*
14a. Terminal inflorescences (monocarpic rosettes) . . . . . . . . . . 15
14b. Lateral inflorescences (polycarpic rosettes) . . . . . . . . . . 38
15a. Leaves adaxially glabrous . . . . . . . . . . 16
15b. Leaves adaxially pubescent . . . . . . . . . . 28
16a. Sessile rosettes or with short-branched stems . . . . . . . . . . 17 (plate 3A)
16b. Caulescent rosettes with unbranched stems . . . . . . . . . . 22 (plate 3B)
17a. Leaves with oblong outline, pseudopetiolate or strongly attenuated near the base . . . . . . . . . . 18
17b. Leaves with linear or cuneiform outline . . . . . . . . . . 20
18a. Leaves strongly attenuated toward the base but not distinctly pseudopetiolate. Ray corollas white . . . . . . . . . . *E. usubillagae*
18b. Leaves distinctly pseudopetiolate. Ray corollas eligulate or yellow . . . . . . . . . . 19
19a. Rosettes occasionally branched with monopodial architecture. Ray corollas eligulate . . . . . . . . . . *E. atropurpurea*
19b. Rosettes occasionally branched with sympodial architecture (usually < 4 rosettes per individual). Ray corollas yellow . . . . . . . *E. bracteosa*
20a. Rosettes almost invariably branched with sympodial architecture, usually profusely so (up to 10 rosettes per individual). Leaves with strictly linear outline (ratio > 50:1) and strongly revolute margins. Secondary nerves obsolete. Ray flowers eligulate . . . . . . . . . . . *E. jahnii*
20b. Rosettes occasionally branched. Leaves with linear-lanceolate or cuneiform outline (ratio < 50:1) and flat margins . . . . . . . . . . 21

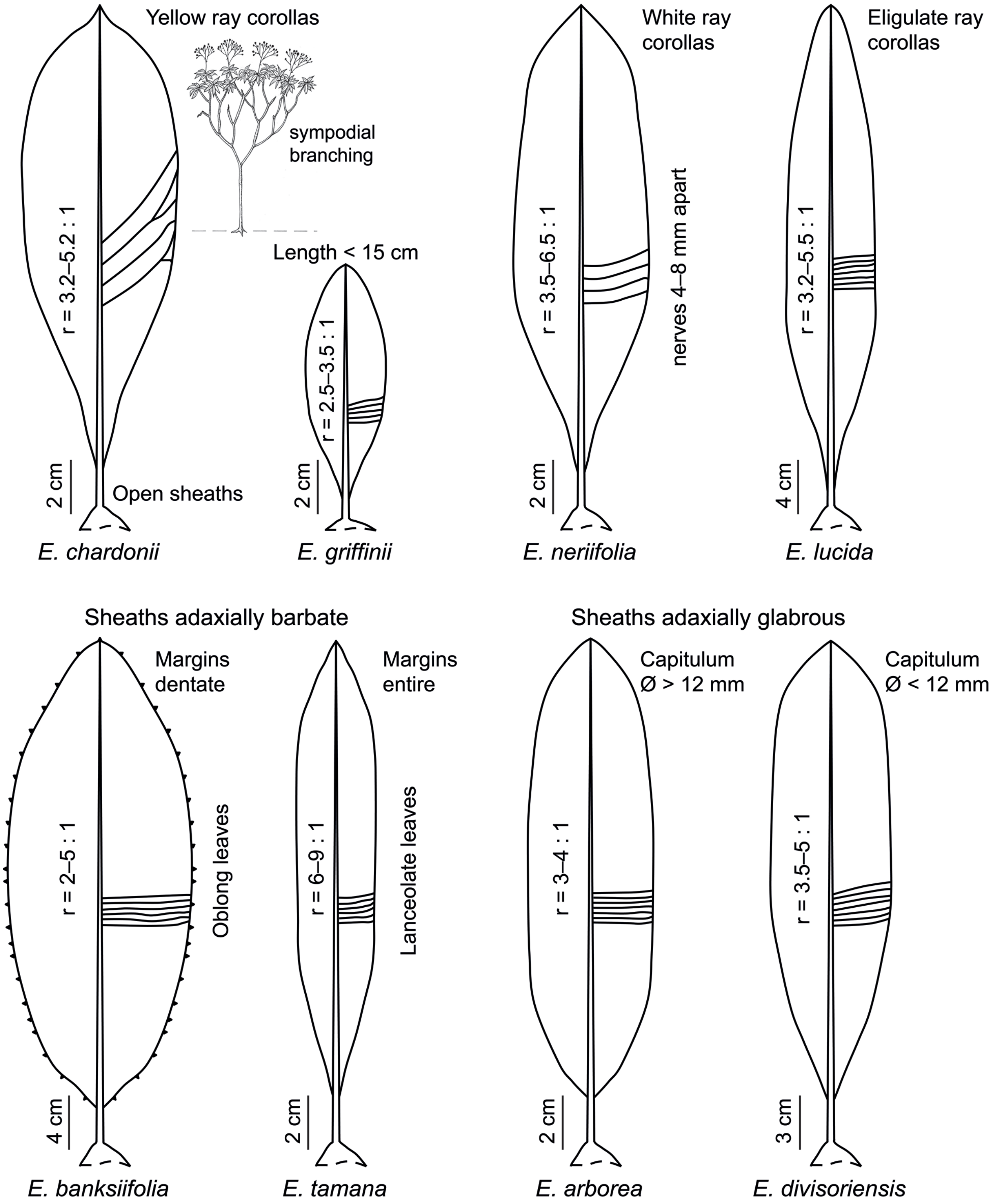
## 1A. Trees with dichasial inflorescences



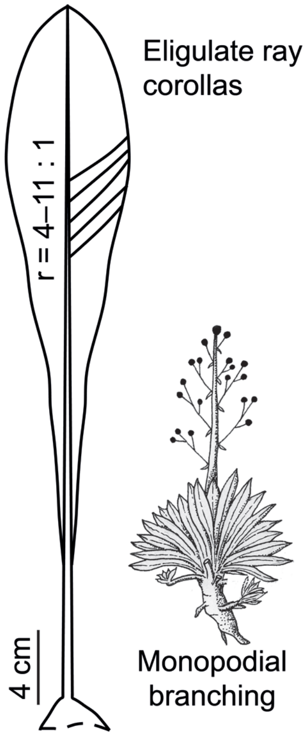
## 1B. Trees with monochasial inflorescences, sessile leaves



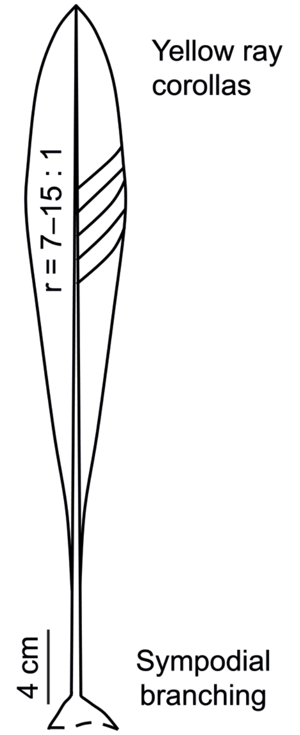
**2. Trees with monochasial inflorescences, pseudopetiolate leaves**



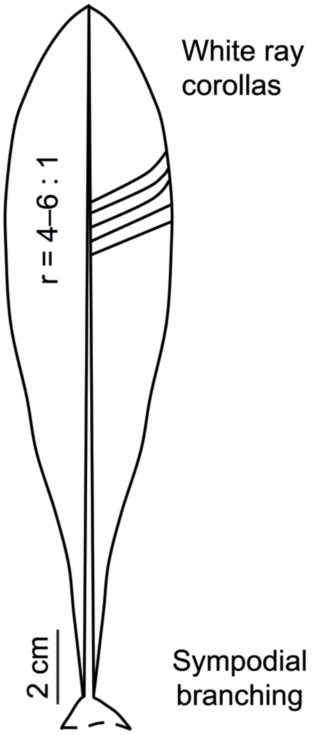
## 3A. Monocarpic rosettes, sessile or short-branched, adaxially glabous leaves



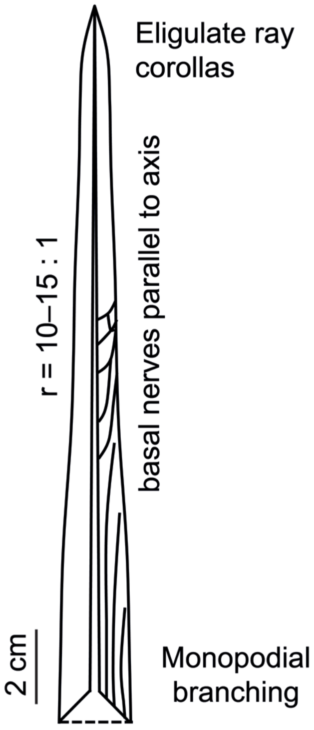
*E. atropurpurea*



*E. bracteosa*

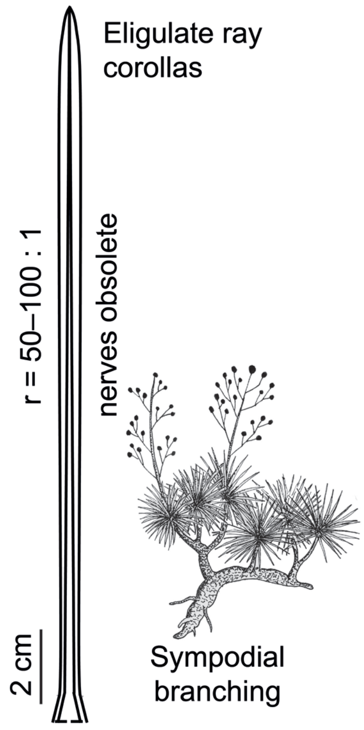


*E. usubillagae*



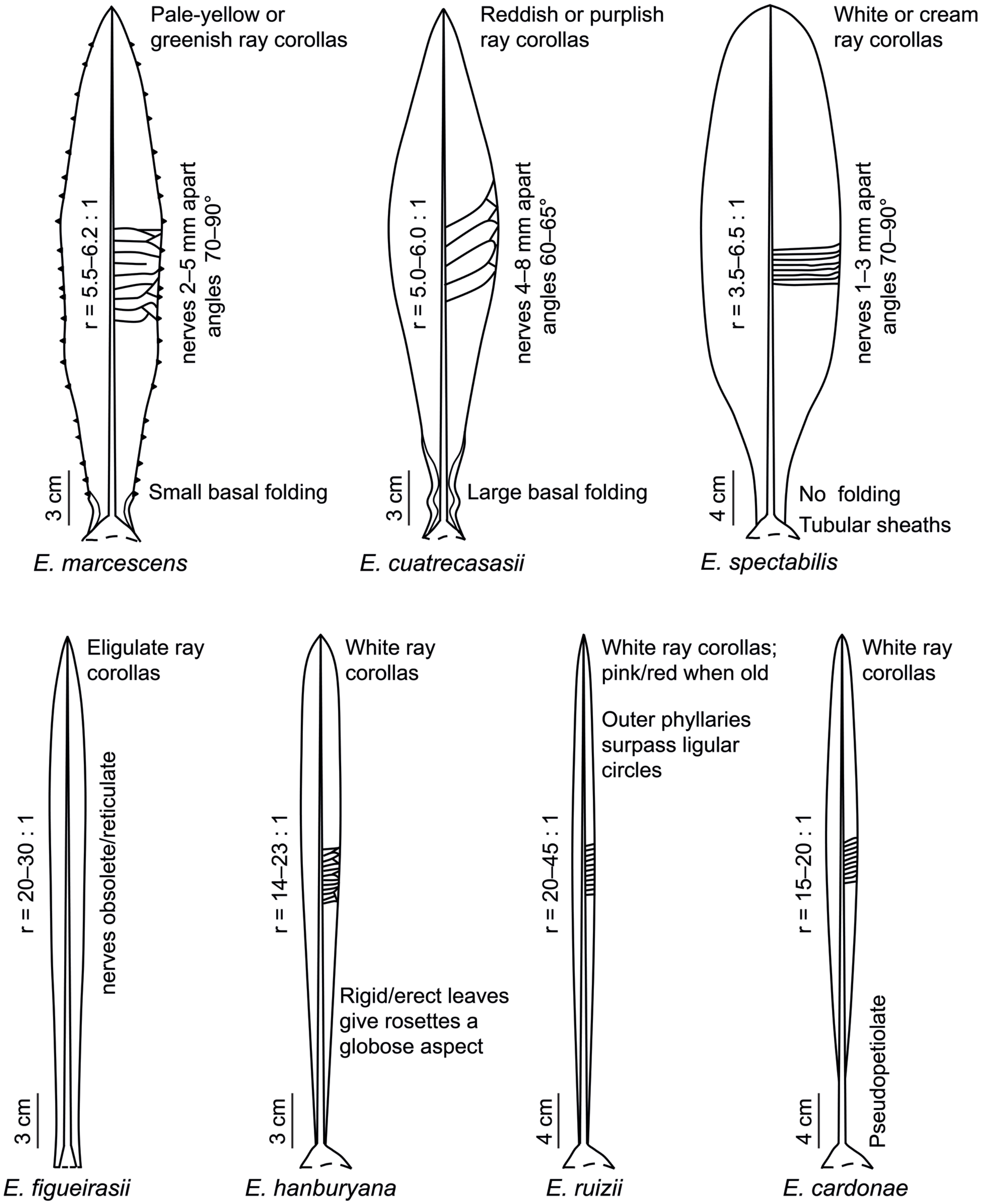
*E. bromelioides*

*E. viridis*



*E. jahnii*

**3B. Monocarpic unbranched caulescent rosettes, adaxially glabrous leaves**



21a. Rosettes occasionally branched with sympodial architecture (usually < 3 rosettes per individual). Leaves with linear-lanceolate outline (ratio 15–50:1). Nerves reticulate or obsolete. Ray corollas yellow . . . . . . . . *E. viridis*

21b. Rosettes occasionally branched with monopodial architecture. Leaves with cuneiform outline (ratio < 10–15:1). Basal nerves parallel to axis. Ray corollas eligulate . . . . . . . . *E. bromelioides*

22a. Leaves with broadly oblong outline (ratio < 6.5:1) . . . . . . . . 23

22b. Leaves with linear or linear-lanceolate outline (ratio > 14:1) . . . . . . . . 25

23a. Tubular sheaths. Leaves with unfolded margins and obtuse apex, secondary nerves 1–3 mm apart, deviation angles 70–90° . . . *E. spectabilis*

23b. Open sheaths. Leaves with folded margins near the base and acute apex . . . . . . . . 24

24a. Leaves usually with small margin folding near the base, secondary nerves 2–5 mm apart, deviation angles 70–90°, capitulum diam. > 20 mm. Ray ligules pale-yellow or greenish . . . . . . . . *E. marcescens*

24b. Leaves usually with large margin folding near the base, secondary nerves 4–8 mm apart, deviation angles 60–65°, capitulum diam. < 18 mm. Ray corollas pinkish-reddish. . . . . . . . . *E. cuatrecasasii*

25a. Leaves rather flexible. Secondary nerves very thin, reticulate or obsolete. Ray corollas eligulate . . . . . . . . *E. figueirasii*

25b. Leaves rather rigid. Secondary nerves visible. Ray corollas ligulate, white or pinkish . . . . . . . . 26

26a. Leaves pseudopetiolate. Ray corollas white . . . . . . . . *E. cardonae*

26b. Leaves sessile . . . . . . . . 27

27a. Leaves with linear outline (ratio 20–45:1). Ray corollas white when young, turning pink-reddish when old. Tips of external phyllaries surpass the ligular circle . . . . . . . . *E. ruizii*

27b. Leaves with linear-lanceolate outline (ratio 14–23:1). Ray corollas white. Tips of external phyllaries do not surpass the ligular circle. . . . . . . . . *E. hanburyana*

28a. Sessile rosettes or with short stems . . . . . . . . 29 (plate 4A)

28b. Caulescent rosettes with unbranched stems . . . . . . . . 34 (plate 4B)

29a. Ray corollas white, cream, or pale-yellow . . . . . . . . 30

29b. Ray corollas yellow . . . . . . . . 32

30a. Leaves with oblong-oblanceolate outline (ratio 7–9:1). Outer phyllaries broad, green, foliaceous, and reticulate . . . . . . . . *E. lindenii*

30b. Leaves with linear-lanceolate outline (ratio > 15:1). Outer phyllaries linear-triangular, pubescent. Ray corollas white . . . . . . . . 31

31a. Leaves with linear outline (ratio 20–40:1), secondary nerves obsolete or scarce, deviation angles 20–30°. Length of ray corollas > 13 mm. . . . . . . . . *E. margarita*

31b. Leaves with linear-lanceolate outline (ratio 15–30:1), secondary nerves 1–3 mm apart, deviation angles 60–80°. Length of ray corollas < 10 mm. . . . . . . . . *E. leucactina*

32a. Sheaths rectangular and slightly broader than lamina. Leaves with linear outline (ratio 30–40:1), secondary nerves obsolete, silvery-sericeous indumentum. . . . . . . . . *E. jabonensis*

32b. Sheaths oblong and clearly broader than lamina. Leaves with linear-lanceolate outline (ratio < 20:1) . . . . . . . . 33

33a. Leaves with silvery-sericeous indumentum, secondary nerves obsolete or thin, 2–4 mm apart, deviation angles 25–50°. Ligular circles > 40 mm. . . . . . . . . *E. floccosa*

33b. Leaves with appressed-sericeous indumentum, secondary nerves 10–15 mm apart, deviation angles 15–30°. Ligular circles < 35 mm. . . . . . . . . *E. vergarae*

34a. Length of ray corollas > 8 mm . . . . . . . . 35

34b. Length of ray corollas < 8 mm . . . . . . . . 36

35a. Leaves pseudopetiolate, secondary nerves 5–8 mm apart, deviation angles 45–75°. Ray corollas yellow . . . . . . . . *E. emmanuelis*

35b. Leaves sessile, secondary nerves 2–4 mm apart, deviation angles 70–85°. Ray corollas white or pale-yellow, outer phyllaries broad, green, foliaceous, and reticulate . . . . . . . . *E. lindenii*

36a. Secondary nerves 1–3 mm apart, deviation angles 50–70°. Capitulum diam. > 12 mm, ligular circle > 15 mm . . . . . . . . *E. grisea*

36b. Secondary nerves > 4 mm apart, deviation angles < 40°. Capitulum diam. < 12 mm, ligular circle < 15 mm . . . . . . . . 37

37a. Stems covered with old leaves/sheaths, up to 1 m high. Capitulum radiate, ray corollas 4.5–6.5 mm long, ligules white . . . . *E. lopezpalacii*

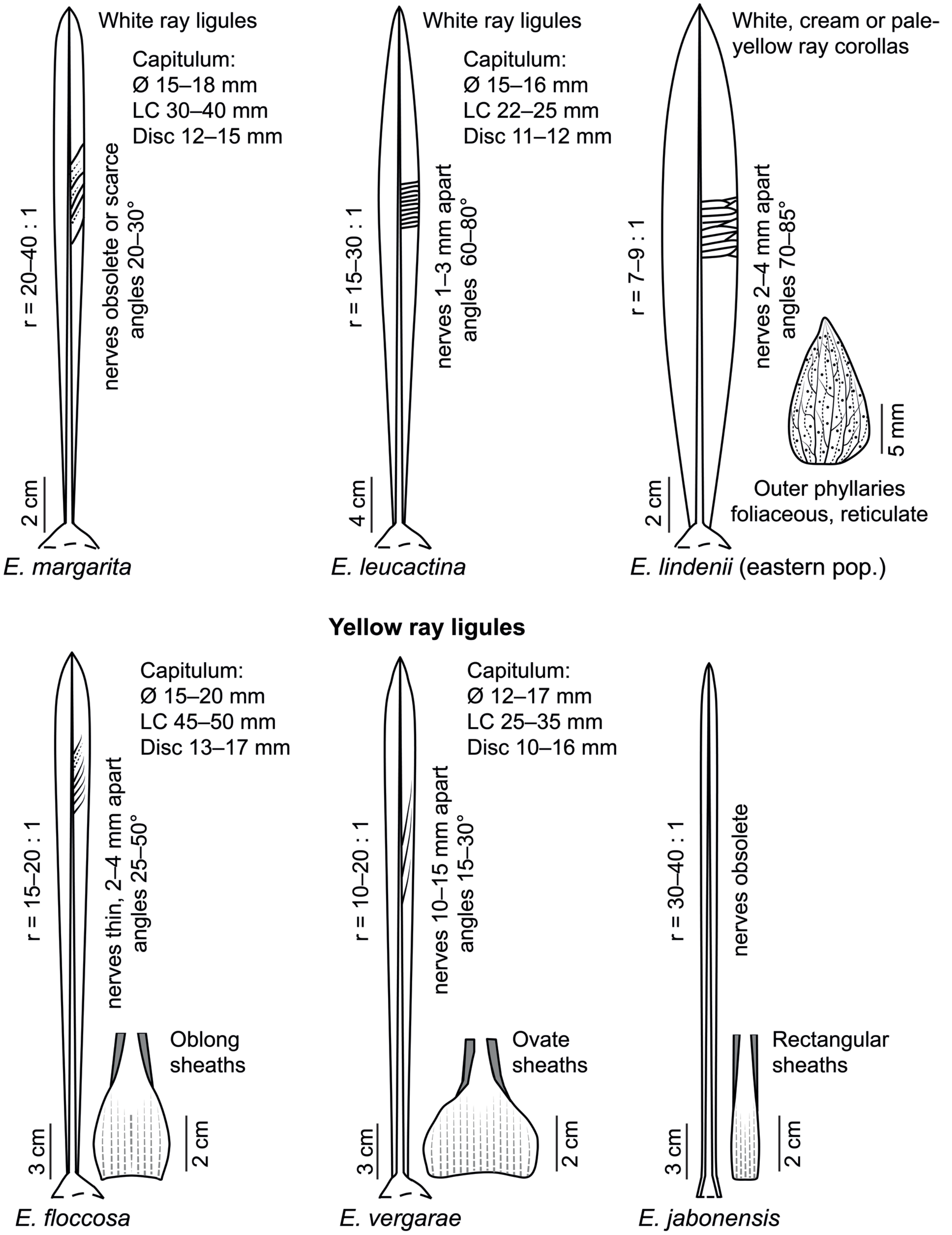
37b. Stems mostly leafless, up to 10 m high. Capitulum short-radiate, ray corollas 2.0–3.5 mm long, ligules pale yellow . . . . . . . *E. paltonioides*

38a. Inflorescences mono- or oligocephalous (< 5 capitula). . . . . . . . . 39 (plate 5)

38b. Inflorescences polycephalous (> 5 capitula) . . . . . . . . 46

39a. Large rosettes (leaf length > 25 cm) . . . . . . . . 40

39b. Small rosettes (leaf length < 15[–25] cm) . . . . . . . . 41



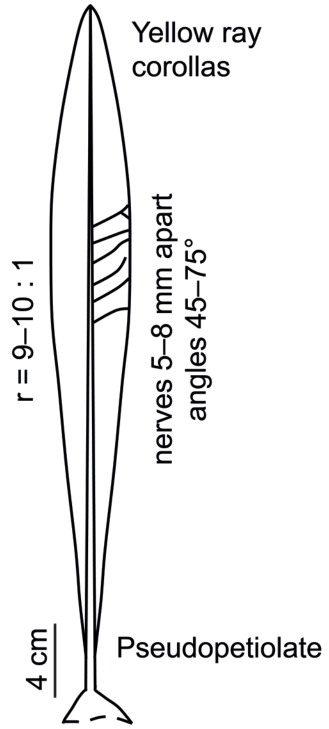
**4A. Monocarpic rosettes, sessile or short-branched, adaxially pubescent leaves**

**White, cream or pale-yellow ray ligules**

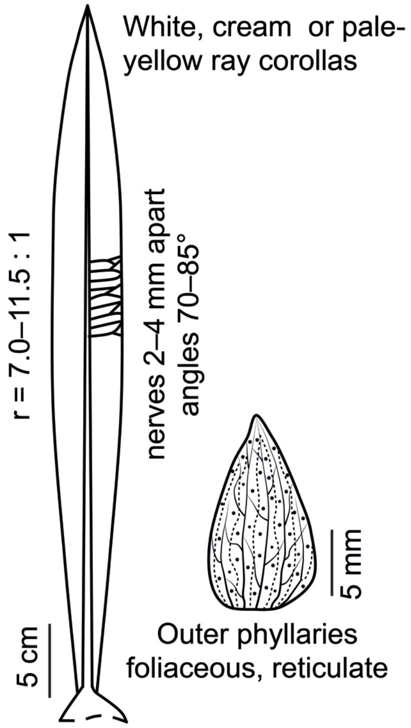
**Yellow ray ligules**

## 4B. Monocarpic unbranched caulescent rosettes, adaxially pubescent leaves

### Ray corollas > 8 mm

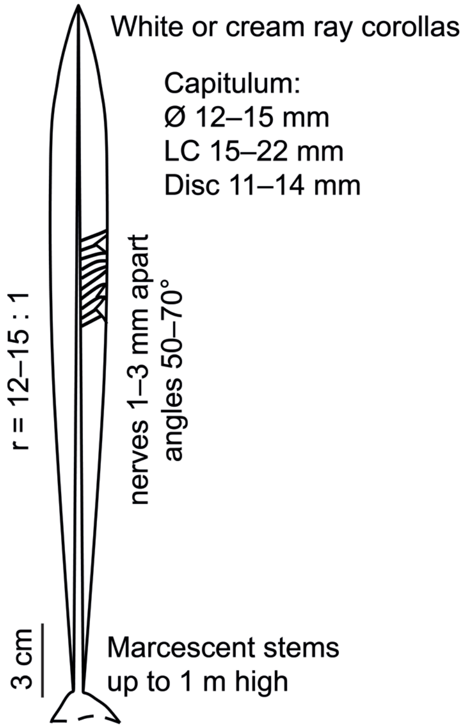


*E. emmanuelis*

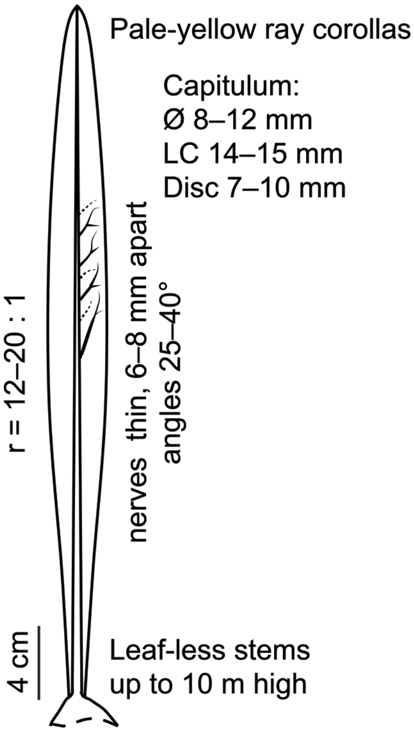


*E. lindenii* (western pop.)

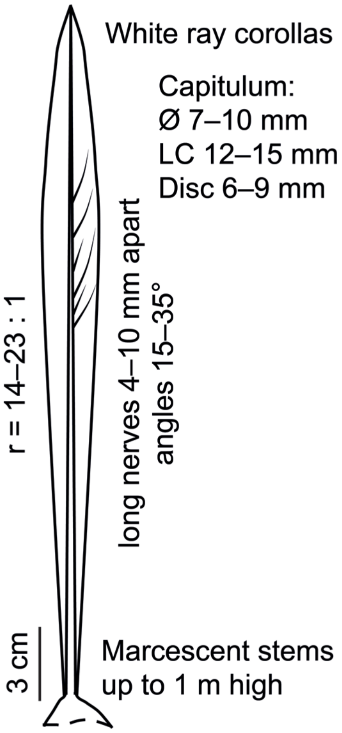
### Ray corollas < 7 mm



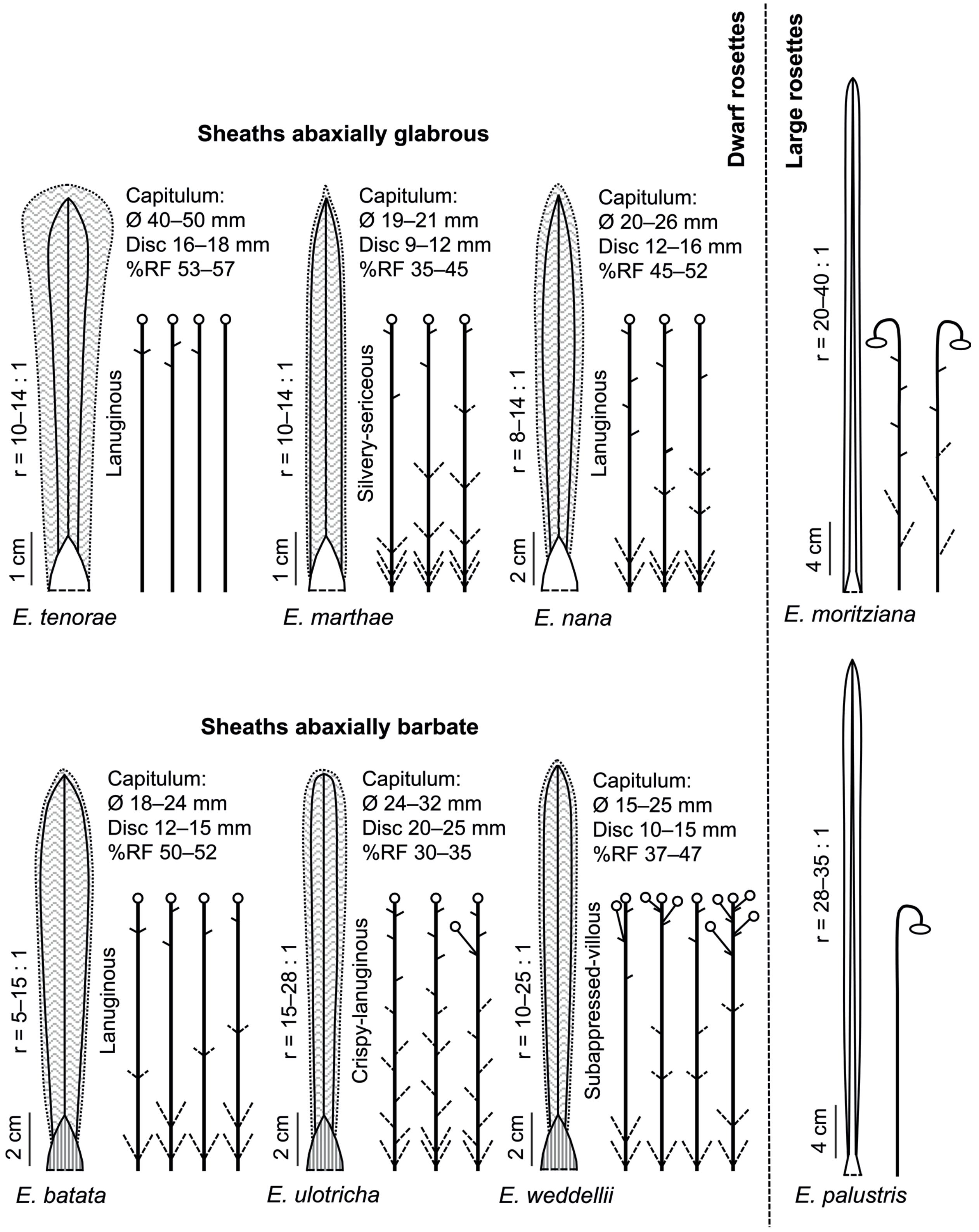
*E. grisea*



*E. paltonioides*



*E. lopezpalacii*



**5. Polycarpic rosettes, mono- or oligocephalous inflorescences**

40a. Sheath length 5.0–7.0 cm, sheath width 0.9–2.2 cm. Leaves with yellowish–greenish indumentum. Inflorescences bracteate. Capitulum with 600–860 disc flowers and 400–740 ray flowers . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. moritziana*

40b. Sheath length 7.0–10.0 cm, sheath width 2.2–2.5 cm. Leaves with white indumentum. Inflorescences aphyllous. Capitulum with 215–280 disc flowers and 95–200 ray flowers . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. palustris*

41a. Sheaths abaxially glabrous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 42

41b. Sheaths abaxially barbate... 44

42a. Leaves usually with cub-shaped outline and with lanuginous indumentum. Inflorescences frequently aphyllous, sometimes with 1–2 alternate or opposite bracts in the upper half. Capitulum densely pubescent, diam. 40–50 mm, ligular circle smaller than the involucre (diam. 20–30 mm), disc diam. 16–18 mm. Capitulum with 53–57% ray flowers . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. tenorae*

42b. Leaves with lanceolate or oblong-lanceolate outline and with silvery-sericeous or lanuginous indumentum. Inflorescences with 2 or more pairs of opposite bracts. Capitulum diam. < 30 mm, ligular circle larger than the involucre and with < 53% ray flowers . . . . . . . . . . . . . . 43

43a. Leaves with lanceolate outline and with silvery-sericeous indumentum. Inflorescences with 3–5 pairs of opposite bracts. Capitulum diam. 19–21 mm, ligular circle diam. 30–35 mm, disc diam. 16–18 mm. Capitulum with 35–45% ray flowers . . . . . . . . . . . . . . *E. marthae*

43b. Leaves with oblong-lanceolate outline and with lanuginous indumentum. Inflorescences with 2 pairs of opposite bracts. Capitulum diam. 20–26 mm, ligular circle diam. 24–35 mm, disc diam. 12–16 mm. Capitulum with 45–52% ray flowers . . . . . . . . . . . . . . . . . *E. nana*

44a. Leaves with revolute margins, cylindrical outline, and crispy-lanuginous indumentum. Inflorescences frequently monocephalous, rarely with 2–3 capitula, also with 1–2 pairs of opposite bracts. Capitulum diam. 24–32 mm, ligular circle diam. 40–45 mm, disc diam. 20–25 mm. Capitulum with 30–35% ray flowers . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. ulotricha*

44b. Leaves with lanceolate or oblong-lanceolate outline and with lanuginous or villous indumentum. Capitulum diam. < 25 mm, ligular circle diam. < 40 mm, disc diam. < 15 mm. Capitulum with > 35% ray flowers . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 45

45a. Leaves with oblong-lanceolate outline and with lanuginous indumentum. Inflorescences with 2–3 pairs of opposite bracts. Capitulum diam. 18–24 mm, ligular circle diam. 30–40 mm, disc diam. 12–15 mm. Capitulum with 50–52% ray flowers . . . . . . . . . . . . . . . . . . . . . *E. batata*

45b. Leaves with lanceolate outline and with subappressed villous indumentum. Inflorescences frequently with 2–5 capitula, rarely 1, also with 2 pairs of opposite bracts (rarely 1 or 3). Capitulum diam. 15–25 mm, ligular circle diam. 20–30 mm, disc diam. 10–15 mm. Capitulum with 37–47% ray flowers . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. weddellii*

46a. Capitula erect, ligular circles much larger than the involucres . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 47 (plate 6)

46b. Capitula dropping or nodding. Ligular circles usually smaller than the involucres, occasionally equal or slightly larger . . . . . . . 50 (plate 7)

47a. Inflorescences monochasial, corymboid-paniculate. Ray corollas white . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 48

47b. Inflorescences dichasial, thyrsoid. Ray corollas yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 49

48a. Leaves with linear outline (ratio 30–40:1) and silvery-sericeous indumentum . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. pannosa*

48b. Leaves with linear-lanceolate outline (ratio 20–25:1) and lanuginous indumentum . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. angustifolia*

49a. Leaves with oblong outline (ratio 4.0–5.7:1) and green tomentose-velvety indumentum. Capitulum diam. 10–14 mm, ligular circle diam. 24–28 mm, disc diam. 10–11 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. aristeguietana*

49b. Leaves with oblong outline (ratio 4.7–12.0:1) and whitish-grayish lanuginose indumentum. Capitulum diam. 20–30 mm, ligular circle diam. 30–50 mm, disc diam. 12–18 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. schultzii*

50a. Inflorescences simple, monochasial (strict botryoid) . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 51

50b. Inflorescences compound (at least basal peduncles polycephalous), monochasial or dichasial . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 53

51a. Leaves with linear-lanceolate outline (ratio 20–35:1). Inflorescences with 14–38 monocephalous peduncles. Capitulum diam. 15–25 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. spicata*

51b. Leaves with lanceolate outline (ratio < 20:1). Inflorescences with < 15 monocephalous peduncles. Capitulum diam. > 25 . . . . . . . . . . . . 52

52a. Leaves with lanceolate outline (ratio 10–18:1). Inflorescences with 8–15 monocephalous peduncles. Capitulum diam. 35–55 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. timotensis*

52b. Leaves with lanceolate outline (ratio 9–10:1). Inflorescences with 9–11 monocephalous peduncles. Capitulum diam. 35–55 mm . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. albarregensis*

53a. Leaves with oblong outline (ratio 4–10:1), sessile, with secondary nerves 5–10 mm apart. Inflorescences monochasial, with 17–35 peduncles, basal ones usually polycephalous (rarely monocephalous). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. thyrsiformis*

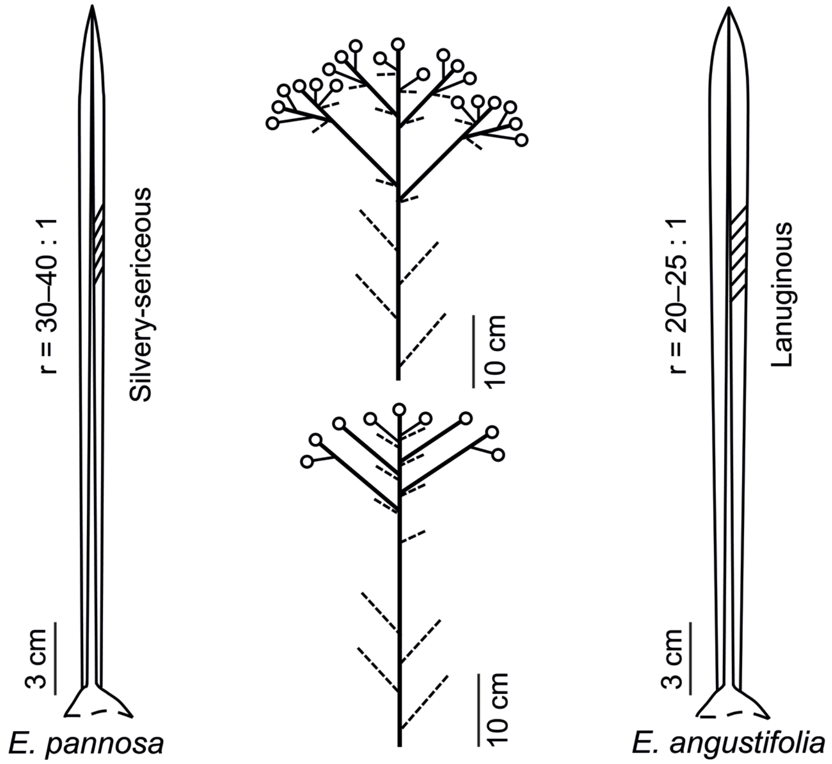
53b. Leaves with lanceolate outline (ratio 9–20:1), distinctly pseudopetiolate . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 54

54a. Secondary nerves 5–7 mm apart. Inflorescences monochasial, with 30–60 peduncles, basal one polycephalous . . . . . . . . . . . . . . *E. elongata*

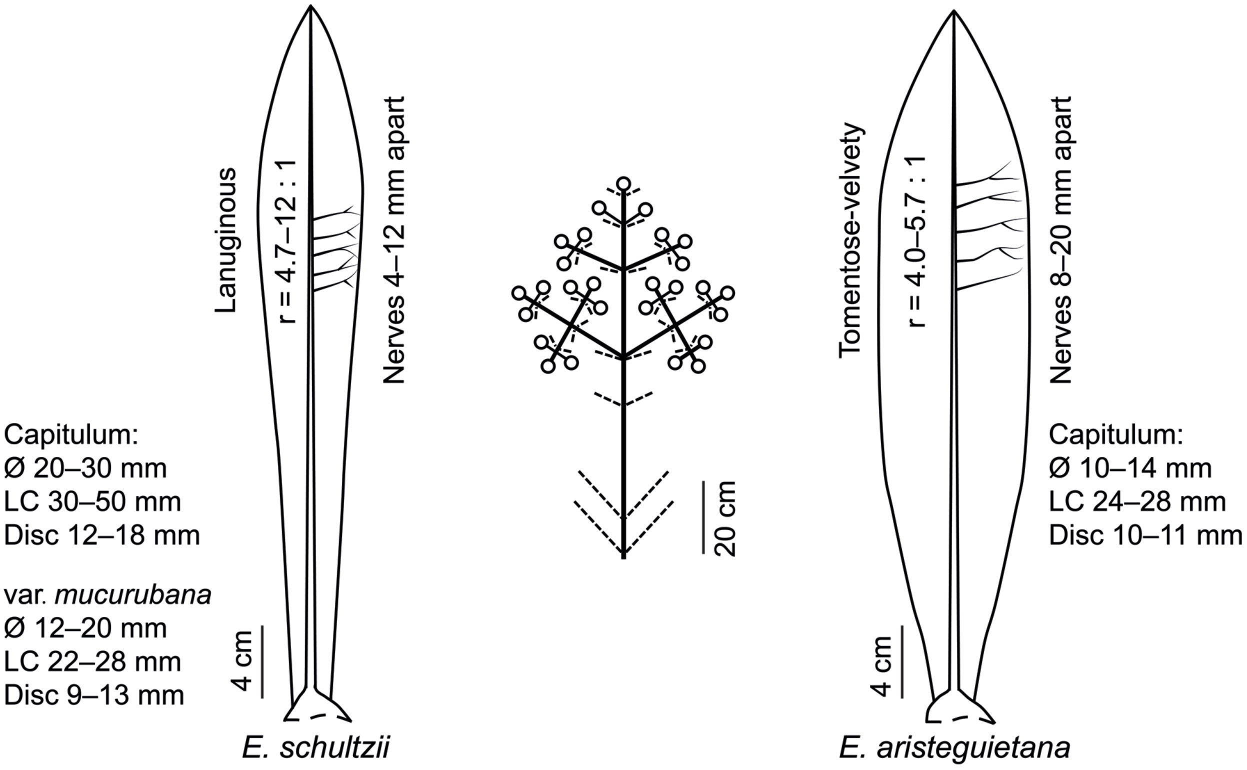
54b. Secondary nerves 2–4 mm apart. Inflorescences dichasial, thyrsoid . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *E. semiglobulata*

## 6. Polycarpic rosettes, polycephalous, ligular circles larger than involucres

### Monochasial inflorescences, white ray corollas

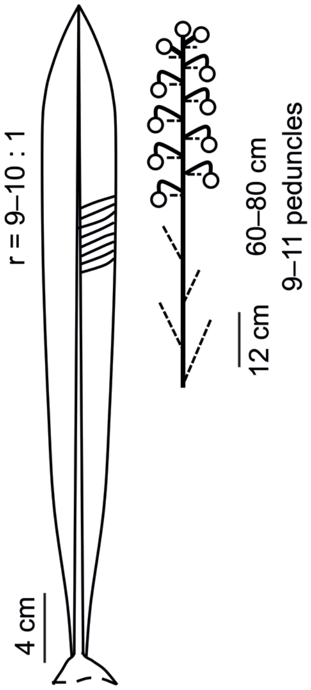


### Dichasial inflorescences, yellow ray corollas

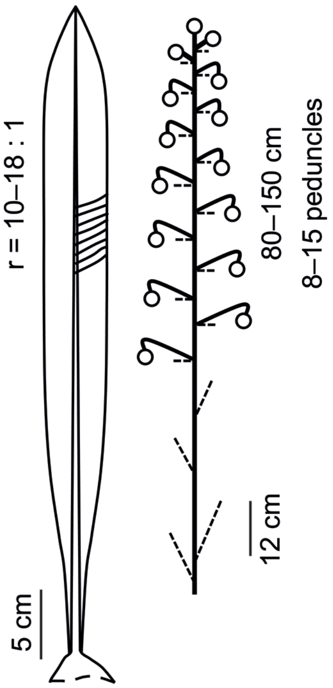


## 7. Polycarpic rosettes, polycephalous, ligular circles smaller than involucres

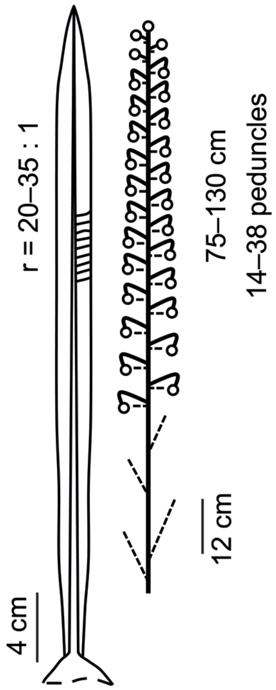
### Simple inflorescences (strict botryoid)



*E. albarregensis*

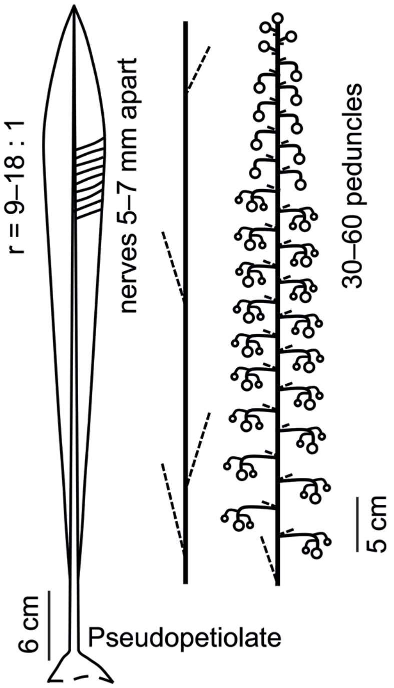


*E. timotensis*

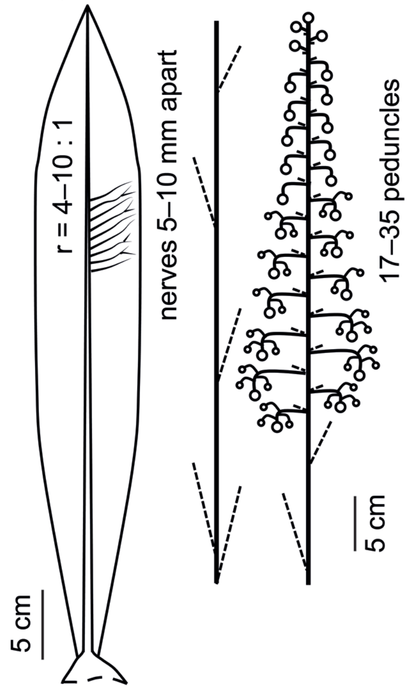


*E. spicata*

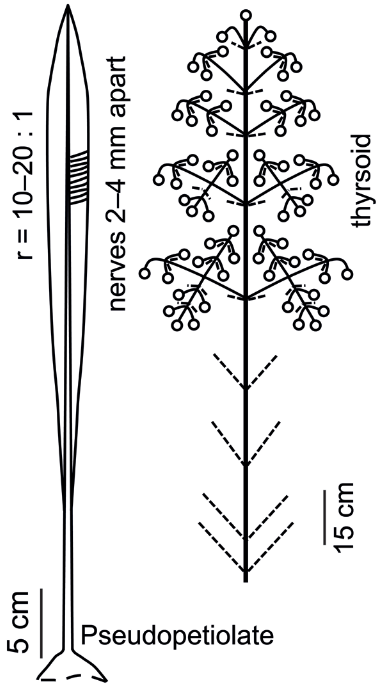
### Compound inflorescences



*E. elongata*



*E. thyrsiformis*



*E. semiglobulata*

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# NEW RECORDS OF RAUVOLFIOIDEAE (APOCYNACEAE, GENTIANALES) FOR PARAÍBA STATE, BRAZIL

Mickaelly De Lucena Mamede,[1] Luan Pedro-Silva,[2] And José Iranildo Miranda De Melo[2,3]

**Abstract.** This paper presents five new records of Rauvolfioideae for Paraíba state, northeastern Brazil: *Aspidosperma discolor*, *A. melanocalyx*, *Macoubea guianensis*, *Tabernaemontana catharinensis*, and *T. flavican*s, with the genus *Macoubea* being recorded for the first time in Paraíba state. Notes on distinghishing morphological features as well as data on geographical distribution and reproductive phenology of the species are provided.

**Keywords:** Caatinga, diversity, flora, Brazil

Apocynaceae encompass 5,000 species belonging to 375 genera (Rapini, 2012), distributed in pantropical regions with a few species in temperate regions (Endress, 2004; Sennblad and Bremer, 2002). This family is subdivided into five subfamilies: Rauvolfioideae, Apocynoideae, Asclepiadoideae, Secamonoideae, and Periplocoideae.

Rauvolfioideae comprise 11 tribes and 79 genera (Endress et al., 2014), which are commonly recognized by small flowers; hypocrateriform corolla; anthers free of the gynoecium; fruit a berry, capsule, drupe, or follicle; and seeds naked, winged, or arillate.

To address the scarcity of floristic and taxonomic studies focused on this taxonomic group in some regions of Brazil, particularly in the region located north of the São Francisco River basin, a taxonomic survey for Apocynaceae subfamily Rauvolfioideae was carried out in Paraíba state, in northeastern Brazil. Here we report five new records, including one genus (*Macoubea*). In addition, data on distribution and reproductive phenology are provided for each species.

## Material and Methods

Our study was based on field collections housed in the main herbaria of Paraíba State (Fig. 1) (EAN, Jayme Côelho de Moraes; JPB, Lauro Pires Xavier; and HACAM, Manuel de Arruda Câmara) and Bahia state (HUEFS, Herbarium of State University of Feira de Santana) (acronyms follow Thiers, continuously updated) and websites (*Flora do Brasil*, 2020, in progress; Tropicos, 2020). The website JSTOR Global Plants (2019) was used to consult type specimens, mainly from P, S, MO, L, and B. Geographic distribution and phytogeographic domains were consulted in *Flora do Brasil* (2020, in progress) and Tropicos (2020). Data on reproductive phenology were obtained from the labels of the exsiccatae consulted.

Five new records of species of Rauvolfioideae (Apocynaceae), including the first record of *Macoubea* Aubl., were detected for Paraíba state and are reported for the first time herein.

1. ***Aspidosperma discolor*** A. DC., Prodr. 8:398.1844.
TYPE: BRAZIL. Bahia, *J. S. Blanchet 3388* (Holotype: P [P00645118], photograph seen).

**Distribution and habitat:** this species is found exclusively in South America: Brazil, Suriname, and Venezuela (Tropicos, 2020). In Brazil, it is distributed in northeastern region (Alagoas, Bahia, Pernambuco, and Sergipe), and associated with the Caatinga and Atlantic forest domains (Flora do Brasil, 2020, in progress).

**Phenology:** flowering in November and fruiting in March.

**Additional specimens examined:** BRAZIL. Paraíba: Espírito Santo, 25 November 1968, fl., *D. Andrade-Lima 68-5.471* (IPA); João Pessoa, 10 March 1995, fr., *M. R. Barbosa et al. 1456* (JPB); Rio Tinto, 21 November 1991, fl., *L. P. Félix et al. 4554* (EAN).

This species can be recognized by its sulcate stalks, alternate leaves, discolored with base revolute, brochidodromous venation, and muricate follicle, inconspicuous lenticels, and rounded apex.

2. ***Aspidosperma melanocalyx*** Müll. Arg., Fl. Bras. (Martius) 6(1): 52.1860.
TYPE: BRAZIL. Minas Gerais, *A.-St. Hilaire s.n.* (Holotype: P [P0038777], photograph seen).

**Distribution and habitat:** this species is endemic to Brazil and found in northeastern (Alagoas, Bahia, Pernambuco, and Sergipe), central-western (Distrito Federal, Goiás, and Mato Grosso), and southeastern (Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo) regions, and associated with the Atlantic Forest and Cerrado domains (Flora do Brasil 2020, in progress; Tropicos, 2019).

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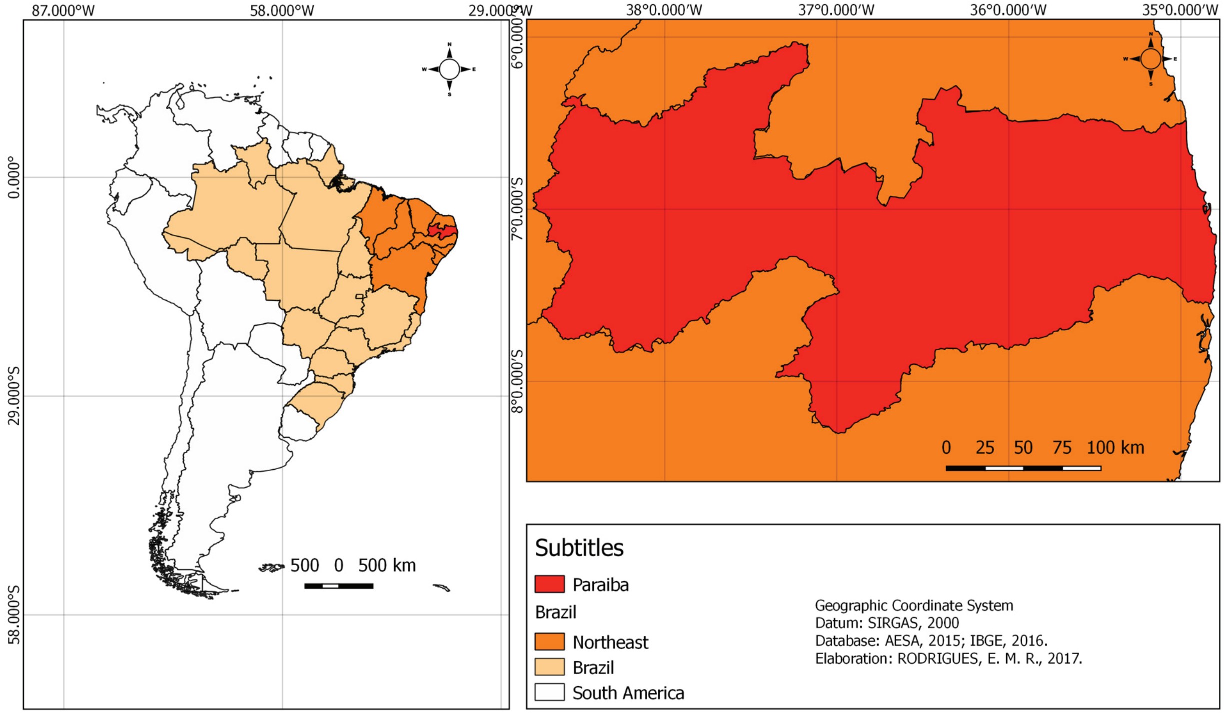

FIGURE 1. Map of the location of Paraíba state, Brazil.

**Phenology**: flowering in February and October and fruiting in March.

**Additional specimens examined:** BRAZIL. Paraíba: João Pessoa, 09 March 1995, fr., *M. R. Barbosa et al. 1446* (JPB); João Pessoa, 08 October 1988, fl., *C. A. B. Miranda 7767* (JPB); João Pessoa, 24 February 1984, fl., *C. Alonso 56697* (JPB).

It is characterized by its red latex, smooth stalk, alternate leaves, leaf blade with craspedodromous venation, and fruits dark green, densely tomentose, and sulcate.

3. ***Macoubea guianensis*** Aubl., Hist. Pl. Guiane 2 (Suppl.): 18, t. 378. 1775.

TYPE: FRENCH GUIANA. *J. B. C. F. Aublet s.n.* (Holotype: BM [000952638], photograph seen).

**Distribution and habitat:** this species is found in Brazil, Bolivia, French Guiana, Guiana, Peru, Suriname, and Venezuela (Tropicos, 2020). In Brazil it is distributed in northern (Acre, Amazonas, Pará, and Rondônia), northeastern (Bahia, Maranhão, and Pernambuco), central-western (Mato Grosso), and southeastern (Espírito Santo) regions associated with the Amazon and Atlantic Forest domains (Flora do Brasil, 2020, in progress).

**Phenology:** flowering in May and fruiting in February.

**Additional specimens examined:** BRAZIL. Paraíba: João Pessoa, 03 May 2016, fl., *P. C. Gadelha-Neto 4034* (JPB); Mamanguape, 10 February 2012, fr., *W. W. Thomas et al. 15653* (JPB).

This species can be recognized by its arboreal habit as well as by the smooth stalks, white latex, opposite leaves, leaf blade presenting craspedodromous venation, fruit (berry) with dry pericarp, and seeds oblong and viscous.

4. ***Tabernaemontana catharinensis*** A. DC., Prodr. 8: 365. 1844.

TYPE: BRAZIL. Ile de Ste Catherine, *C. Gaudichaud 186* (Isotype: P [P00646818]; Lectotype: G-DC; Isolectotypes: F, FI-W, G, P [photograph seen]).

**Distribution and habitat:** this species is found only in South America: Brazil, Argentina, Bolivia, Paraguay, and Uruguay (Tropicos, 2020). In Brazil it can be found in northeastern (Bahia, Ceará, Maranhão, Pernambuco, and Sergipe), central-western (Mato Grosso do Sul), southeastern (Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo), and southern (Paraná, Rio Grande do Sul, and Santa Catarina) regions, associated with the Atlantic Forest and Cerrado domains (Flora do Brasil 2020, in progress).

**Phenology:** flowering and fruiting in March.

**Additional specimens examined:** BRAZIL. Paraíba: Alagoa Nova, 05 March 2012, fl., *E. Melo et al. 10910* (HUEFS); Alagoa Nova, 08 March 2012, fl., fr., *E. Melo et al. 11052* (HUEFS); Alagoa Nova, 08 March 2012, fl., fr., *E. Melo et al. 11064* (HUEFS).

This species can be recognized by its membranaceous leaf blades, unequal on the same node, presenting eucamptodromous venation, calyx with lobes triangulate and revolute, white corolla presenting yellow mouth, and muricate follicle, convex-concave.

5. ***Tabernaemontana flavicans*** Willd. ex Roem. & Schult., Syst. Veg. ed. 15 bis. 4: 797. 1819.

TYPE: BRAZIL. Brasilia, *J. C. Hoffmannsegg s.n.* (Holotype: B [B-W05195-020], photograph seen).

**Distribution and habitat:** this species is found only in South America: Bolivia, Brazil, Colombia, Peru, and Venezuela (Tropicos, 2020). In Brazil it can be found in northern (Amazonas, Pará, and Rondônia), northeastern (Alagoas, Bahia, Maranhão, and Pernambuco), central-western (Mato Grosso), and southeastern (Espírito Santo, Minas Gerais, and Rio de Janeiro) regions associated with the Atlantic Forest, Cerrado, and Amazon domains (Flora do Brasil 2020, in progress).

**Phenology:** flowering in August, September, and October and fruiting in January and September.

**Additional specimens examined:** BRAZIL. Paraíba: Baía da Traição, 11 October 2004, fl., *P. C. Gadelha-Neto et al. 1264* (JPB); João Pessoa, 06 September 2005, fr., *N. T. Amazonas et al. 44* (JPB); João Pessoa, 20 January 2012, fr., *P. C. Gadelha-Neto 3147* (JPB); João Pessoa, 12 August 2002, fl., *P. C. Gadelha-Neto et al. 727* (JPB); João Pessoa, 12 September 2011, fl., *P. C. Gadelha-Neto 3053* (JPB); Mamanguape, 04 September 2004, fl., *M. R. Barbosa et al. 3045* (JPB).

This species can be recognized by its chartaceous leaves, unequal on the same node, brochidodromous venation, white corolla presenting yellow mouth, and smooth follicle, ellipsoid with acute apex.

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# TWO NEW SPECIES OF *LEPANTHES* (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM THE ANCHICAYÁ RIVER VALLEY IN COLOMBIA

Juan Sebastián Moreno,[1,2,3] Luis E. Baquero R.,[4] and Sebastián Vieira-Uribe[1,5,6]

**Abstract.** Two new species of *Lepanthes* from the Anchicayá River Valley in the department of Valle del Cauca in Colombia, in the Pacific lowlands of the Chocó biogeographic region, are described and illustrated. Both species are discussed and compared with their closest relatives, and information about their distribution, conservation, habitat, and ecological characteristics is provided.

**Keywords:** conservation, Chocó biogeographic region, distribution, taxonomy

**Resumen.** Se ilustran y se describen dos nuevas especies de *Lepanthes* del Valle del Rio Anchicayá en el departamento del Valle del Cauca en Colombia, en las tierras bajas del Pácifico del Chocó biogeográfico. Ambas especies son discutidas y comparadas con sus parientes más cercanos y se provee información acerca de su distribución, conservación, habitát y caracteristicas ecológicas.

**Palabras claves:** conservación, región biogegráfica del Chocó, distribución, taxonomía

*Lepanthes* Sw. (Orchidaceae) is a relatively recent group of species that diverged ca. 5–10 MYA with the highest net diversification rate among genera in subtribe Pleurothallidinae (Pérez-Escobar et al., 2017; Bogarín et al., 2018), possibly correlated with pollination by pseudocopulation. Flowers are pollinated by male fungus gnats of the family Sciaridae, probably attracted by a pheromone-mimicking strategy. *Lepanthes*, with morphological features such as a bilaminate lip with a central and very small appendix of different shapes, exhibits a highly specialized pollination system involving sexual deception (Blanco and Barboza, 2005; Luer and Thoerle, 2012; Bogarín et al., 2019).

*Lepanthes* in Colombia has been studied extensively thanks to the collaboration of Carlyle A. Luer (1922–2019) and Rodrigo Escobar (1935–2009), who described 208 species between 1980 and 2011. A year later, Luer and Thoerle (2012) provided a comprehensive review of the genus. Despite this revision, *Lepanthes* is a taxonomic group that continues to be challenging to study, primarily because of the generally minute size of its flowers and the complexity of its floral structures (a lip composed of two blades and a central appendix). Typically, press-and-dry practices used to prepare herbarium specimens make the study of these structures difficult, and the careful examination of living plants and the preservation of material in alcohol are essential to identify most species.

Little work has been done on Colombian *Lepanthes* since Luer and Thoerle (2012) published their monograph. From 2014 to 2019, nine new species were described (Vieira-Uribe and Larsen, 2014a,b; Moreno et al., 2017, 2018; Vieira-Uribe and Moreno, 2018, 2019); two species described by Pérez-Escobar et al. (2013a,b) and one by Szlachetko et al. (2019) are excluded because they are most likely synonyms of already known taxa.

As a result of several field trips conducted two years ago to document flora and fauna of the Anchicayá River Valley in the Cauca Valley, carried out by the members of the Schultes Investigation Group of the Ecotonos Foundation, two new species of *Lepanthes* were detected and are described and illustrated here, with information about their ecology and comparisons with similar species.

## Materials and Methods

### *Descriptions and Drawings*

The descriptions were prepared from living specimens. Specimens were preserved in alcohol and dissected under a stereo microscope (AmScope SM-1TNZ-144A-3M). Digital images were taken with a Nikon D750 with a Nikkor 105 mm f/1.8 macro lens. Sketches from living and preserved specimens were digitized, and the images were used for diagramming draft composite templates in Adobe Photoshop® CS6. Digital drawings were prepared (using lines and stippling) in Procreate illustration for Apple iPad 6th generation tablet computer (Bogarín et al., 2019).

The first author thanks CELSIA and the Corporación Paisajes Rurales for their financial support, which made possible the description of the two new species in this investigation. Also, JSM would like to thank the Harvard University Herbaria for a travel grant used to review all the specimens and literature related to the genus *Lepanthes*, especially to Gustavo A. Romero and Irina Ferreras for their kind help during the stay at AMES. We are grateful to Robinson Galindo Tarazona, director of the regional Los Farallones National Natural Park (Parque Nacional Natural; PNN), who let us collect the species within the PNN and the central hydroelectric complex of Empresa Energía del Pacífico S. A. (EPSA); to Gilberto Collazos Bolaños, Camilo E. Sánchez, and Alejandra Herrera, who kindly invited the first author to participate in the Global Big Day (the day the two new species were found). Luis Baquero thanks Universidad de Las Américas (UDLA) for funding research on orchids in Ecuador. Two anonymous reviewers and the editor improved this manuscript greatly and their help is appreciated. Finally, we thank the Missouri Botanical Gardens Press for letting us use drawings by C. A. Luer in figure 5.

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### *Plant Material*

*Lepanthes* specimens at AMES, CAUP, ICESI, JAUM, HPUJ, HUA, FMB, VALLE, JBB, CUVC, SEL, MO (online), TOLI, and COL (online) were consulted, although no additional material was found in these collections to include in the description of the new species.

### *Study Area*

The Anchicayá River Valley (Fig. 1) in the department of Valle del Cauca, located in the Pacific slope of the Western Cordillera, receives constant rainfall (up to 183 mm in 24 hr, in higher proportion at night), has a mean temperature of 26 C, and a relative humidity of 86% (Tovar, 2004). This valley is located close to the Pacific Ocean in the Chocó biogeographic region, the world's ninth most biodiverse hotspot and perhaps one of the least understood in terms of species diversity (Pérez-Escobar et al., 2019). The area hosts nearly 3% (~11,000) of all plant species, of which ~2,750 are endemic (Gentry, 1982; Myers et al., 2000; Pérez-Escobar et al., 2019).

FIGURE 1. Landscape view of the Anchicayá River Valley in the department of Valle del Cauca in Colombia. Photograph by J. S. Moreno.

## TAXONOMY

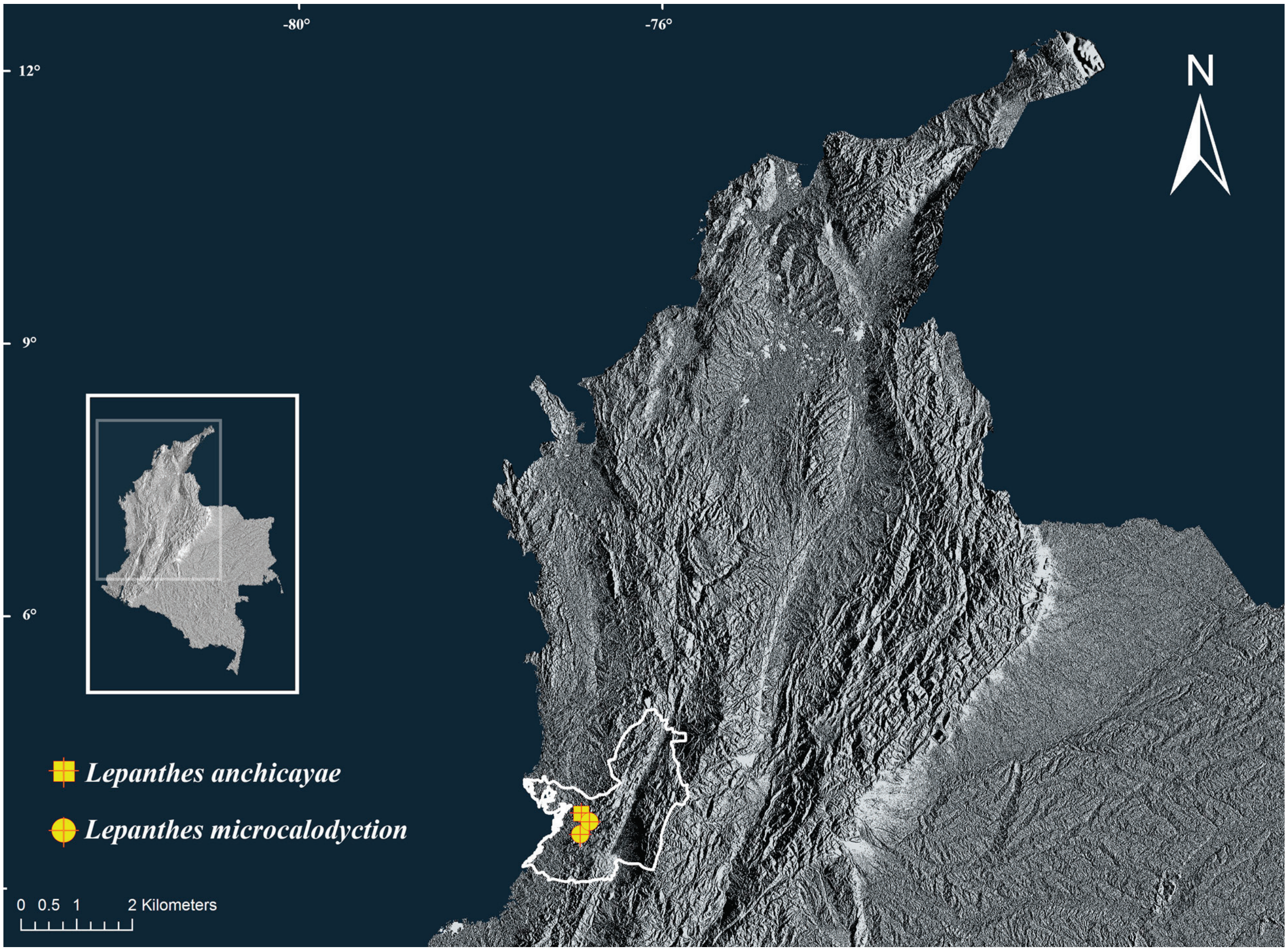
**Lepanthes anchicayae** J.S. Moreno & S. Vieira-Uribe, *sp. nov*. TYPE: COLOMBIA. Valle del Cauca: Buenaventura, Cañón del Rio Anchicayá, La Cascada, 3°37'33.5"N, 76°56'34.7"W, 300 m, 4 May 2018, *Juan Sebastián Moreno and Astrid Erazo* 429 (Holotype: CAUP) (Fig. 2, 3, 4A, 5A).

*Lepanthes anchicayae is similar to Lepanthes pleurorachis Luer but can be distinguished by its wider petals, the lip transversely bilobed with cuneate lobes (vs. transversely bilobed-cordate with rounded lobes) with margins not ciliate (vs. ciliate,) and the stigma ventral and widely dilated (vs. stigma apical).*

*Plant* small, epiphytic, caespitose; *roots* slender, terete. *Ramicauls* slender, erect, 2.25–3.00 cm long, enclosed by 5–6 microscopically ciliate-scabrous lepanthiform sheaths. *Leaves* suffused with purple on the abaxial side, erect, coriaceous, narrowly ovate, acute, 2.25–2.50 × 0.5–0.6 cm, the base cuneate into a petiole 1–2 mm long. *Inflorescence* a congested, distichous, successively several-flowered raceme, up to 7.5–12.0 mm long, borne underneath the leaf by a slender peduncle 4–7 mm long; *floral bracts* muricate, acute, 1 mm long; pedicels 1.5 mm long. *Ovary* costate, 1.5 mm long. *Sepals* translucent yellow, suffused with burgundy at the base, glabrous, carinate, reflexed. *Dorsal sepal* ovate to elliptical, acute, 3-veined, 2 × 1.2–1.3 mm, connate to the lateral sepals for 0.5 mm. *Lateral sepals* ovate, oblique, apiculate, 2 × 1.5–1.7 mm, connate at the base for 0.8 mm, 2-veined. *Petals* orange strongly suffused with burgundy at the base, microscopically pubescent, 0.75–0.80 × 3.3–3.5 mm, transversely bilobed, the upper lobe ovate, oblique, acute, with a second point midway on the inner margin, the lower lobe triangular, oblique, shorter than the upper, with the apex attenuate, incurved. *Lip* burgundy, microscopically pubescent, 2-veined, transversely bilobed, the lobes cuneate, 0.5 × 1 mm embracing the column, the apex retuse with a wide sinus, connate close to the base of the column. *Column* magenta, terete, 0.5 mm long, the anther apical, stigma ventral and widely dilated.

**Etymology:** the specific epithet refers to the region of the Anchicayá River Valley in the department of Valle del Cauca, Colombia, the type locality where the species was found.

**Habitat and ecology:** an epiphyte of secondary vegetation along the western slope of the Western Cordillera, where it has been recorded at 300 m of elevation (Map 1). The species was found growing on small branches close to a very wet clump of *Sphagnum* moss located on the rocks under a waterfall. *Lepanthes anchicayae* is probably distributed all along the road to Agua Clara, Buenaventura, and may be very well protected within the area occupied by the hydroelectric power station of the Bajo Anchicayá, located within the perimeter of Los Farallones National Natural Park, where access for the general public is highly restricted.



MAP 1. Distribution of *Lepanthes anchicayae* J.S. Moreno & S.Vieira-Uribe and *Lepanthes microcalodyction* J.S. Moreno & L. Baquero in the Anichayá River Valley, Valle del Cauca, Colombia.

*Lepanthes anchicayae* belongs to a group of species with very congested, distichous racemes, reflexed sepals, transversely bilobed petals with the lobes somewhat triangular and a lip without appendix, transversely bilobed-cordate to subcordate and reniform, which embraces the column. Among this informal group, three species share some similar traits with the new species: *Lepanthes petalopteryx* Luer & R. Escobar (Fig. 4B), *Lepanthes pleurorachis* Luer (Fig. 4C), and *Lepanthes viahoënsis* Luer & R. Escobar (Fig. 4D) (Luer and Thoerle, 2012). *Lepanthes petalopteryx*, from the Western Cordillera in the department of Antioquia, has sepals minutely denticulate along the margins (vs. smooth margins), transversely bilobed petals with the lobes truncate (vs. transversely bilobed with the upper lobe ovate, and the lower triangular, attenuate), and a reniform transversely bilobed lip (vs. transversely bilobed with lobes cuneate; Fig. 5B). It is most similar to *Lepanthes pleurorachis*, but it can be easily distinguished from the latter by its wider petals, the lip transversely bilobed with the lobes cuneate and the microscopically pubescent (vs. transversely bilobed with the lobes cordate and the margins ciliate; Fig. 5C). The only other species to which it can be compared, *Lepanthes viahöensis*, is characterized mainly by its 3-veined lateral sepals (vs. 2-veined in *L. anchicayae*), petals transversely bilobed, with the upper lobe erect, obliquely triangular, the lower lobe oblong, shorter, oblique at the apex (vs. transversely bilobed), with the upper lobe ovate, oblique, triangular, the lower lobe triangular, oblique, shorter than the upper, lip microscopically ciliate (vs. microscopically pubescent), and subcordate lobes (vs. transversely bilobed, cuneate lobes; Fig. 5D). The new species is also recognized by its widely dilated ventral stigma.

**Lepanthes microcalodyction** J.S. Moreno & L. Baquero, *sp. nov*. TYPE: COLOMBIA. Valle del Cauca: Buenaventura, Cañón del Rio Anchicayá, PNN Farallones, Campamento Yatacué, EPSA, 3˚34'32.6"N 76˚52'46.4"W, 640 m, 11 September 2016, *Juan Sebastián Moreno and Astrid Erazo 432* (Holotype: CAUP) (Fig. 6, 7, 8B, 9B).

*Lepanthes microcalodyction is similar to Lepanthes calodyction Hook., but it can be distinguished by its unique very small, diminutive flowers and plants; petals with the margin velvety (vs. ciliate) acaudate (vs. long caudate), and the lip transversely reniform (vs. transversely oblong-reniform).*

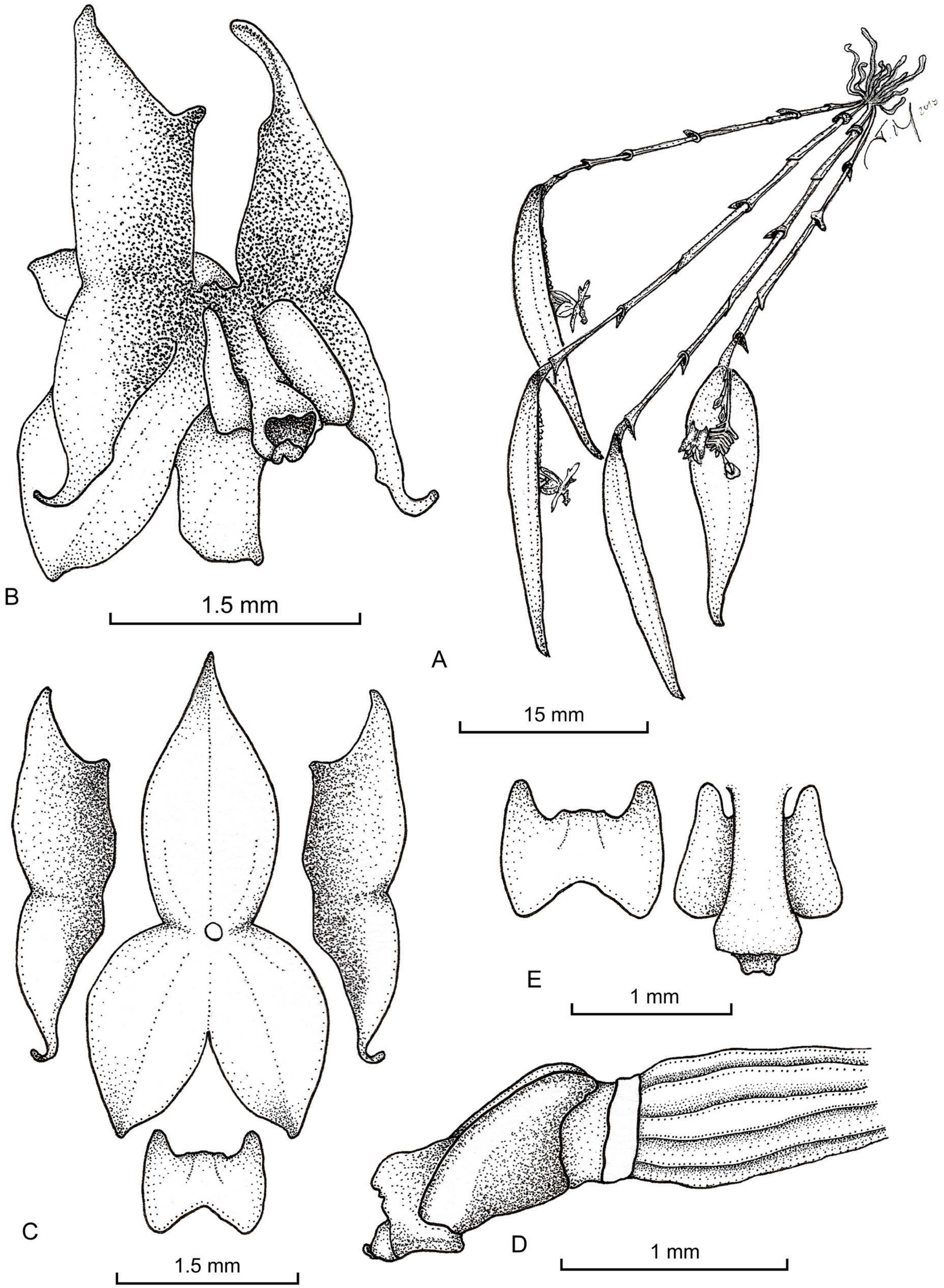


FIGURE 2. Illustration of *Lepanthes anchicayae* J.S. Moreno & S.Vieira-Uribe. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column, lip, and ovary lateral view (pollinia and anther cap absent); **E**, lip. Drawn by J. S. Moreno based on *J. S. Moreno & A. L. Erazo 429* (CAUP).

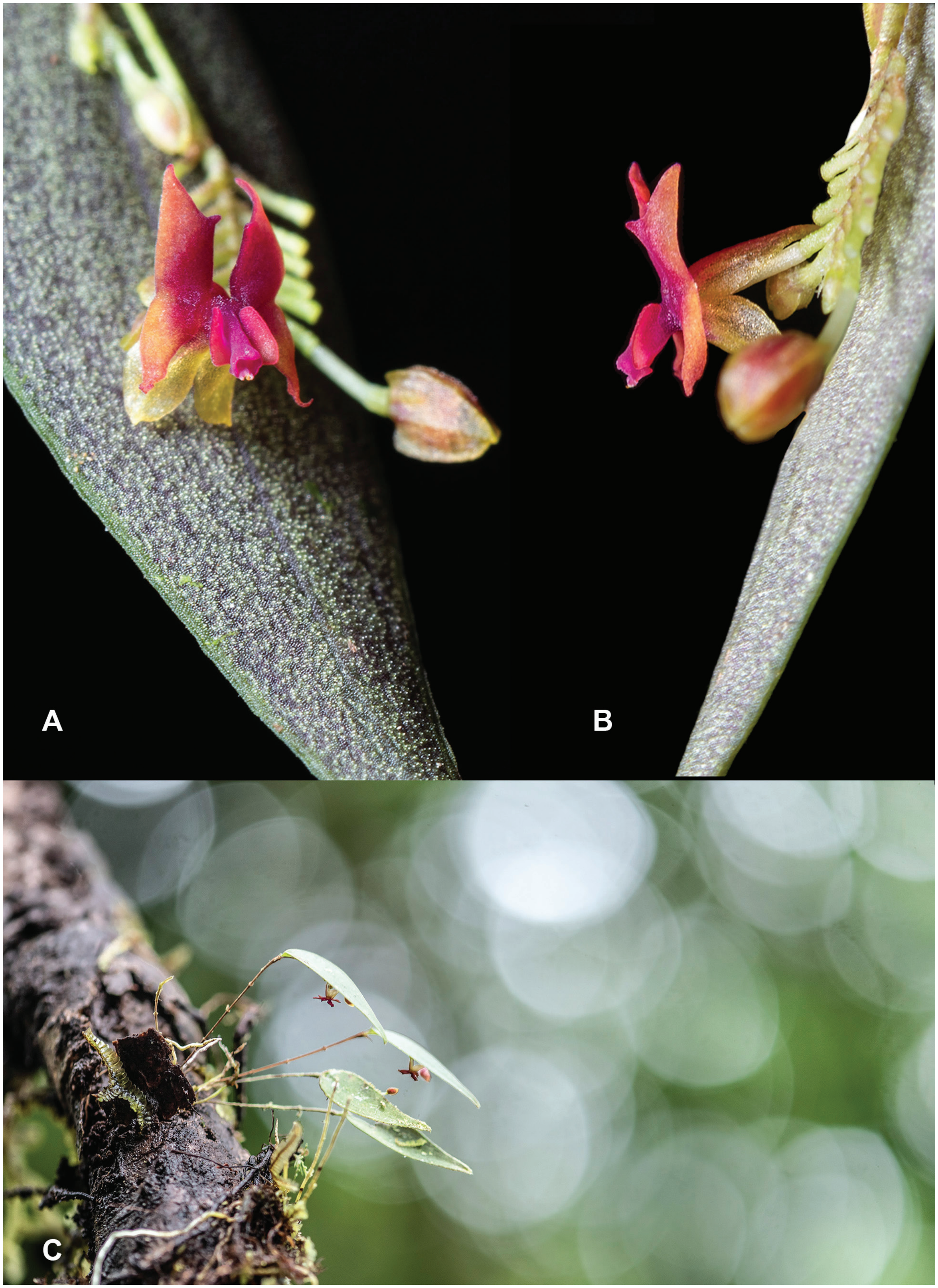


FIGURE 3. *Lepanthes anchicayae* J.S. Moreno & S.Vieira-Uribe. **A**, frontal view; **B**, lateral view; **C**, plant and habit, in situ. Photographs by J. S. Moreno.

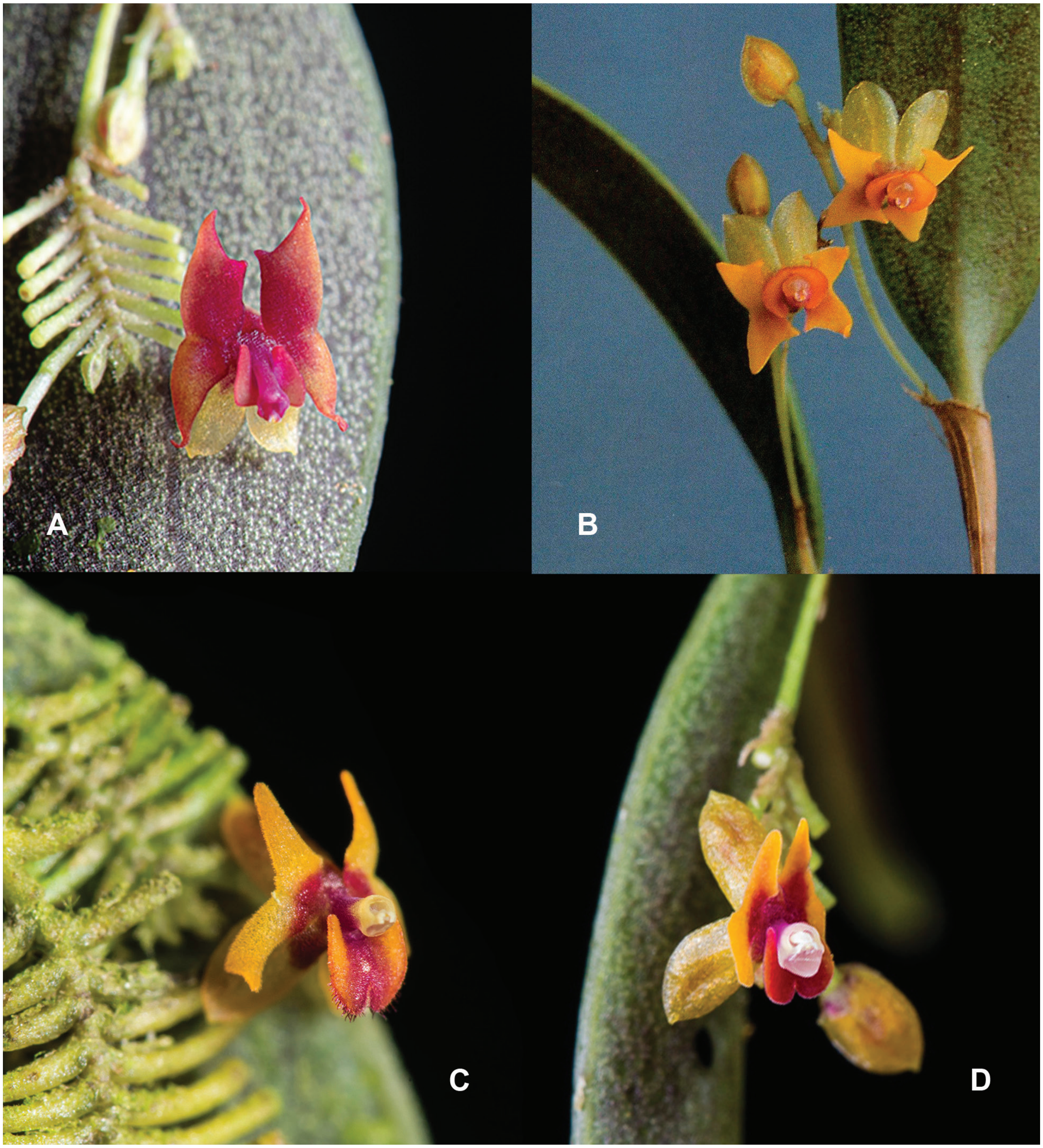


FIGURE 4. Comparison of the most similar species to *Lepanthes anchicayae* J.S. Moreno & S. Vieira-Uribe. **A**, *Lepanthes anchicayae*; **B**, *L. petalopteryx* Luer & R. Escobar; **C**, *L. pleurorachis* Luer; **D**, *L viahöensis* Luer & R. Escobar. Photographs by J. S. Moreno (A, C), Sebastián Vieira-Uribe (D), and Rodrigo Escobar (B), courtesy of the Sociedad Colombiana de Orquideología.

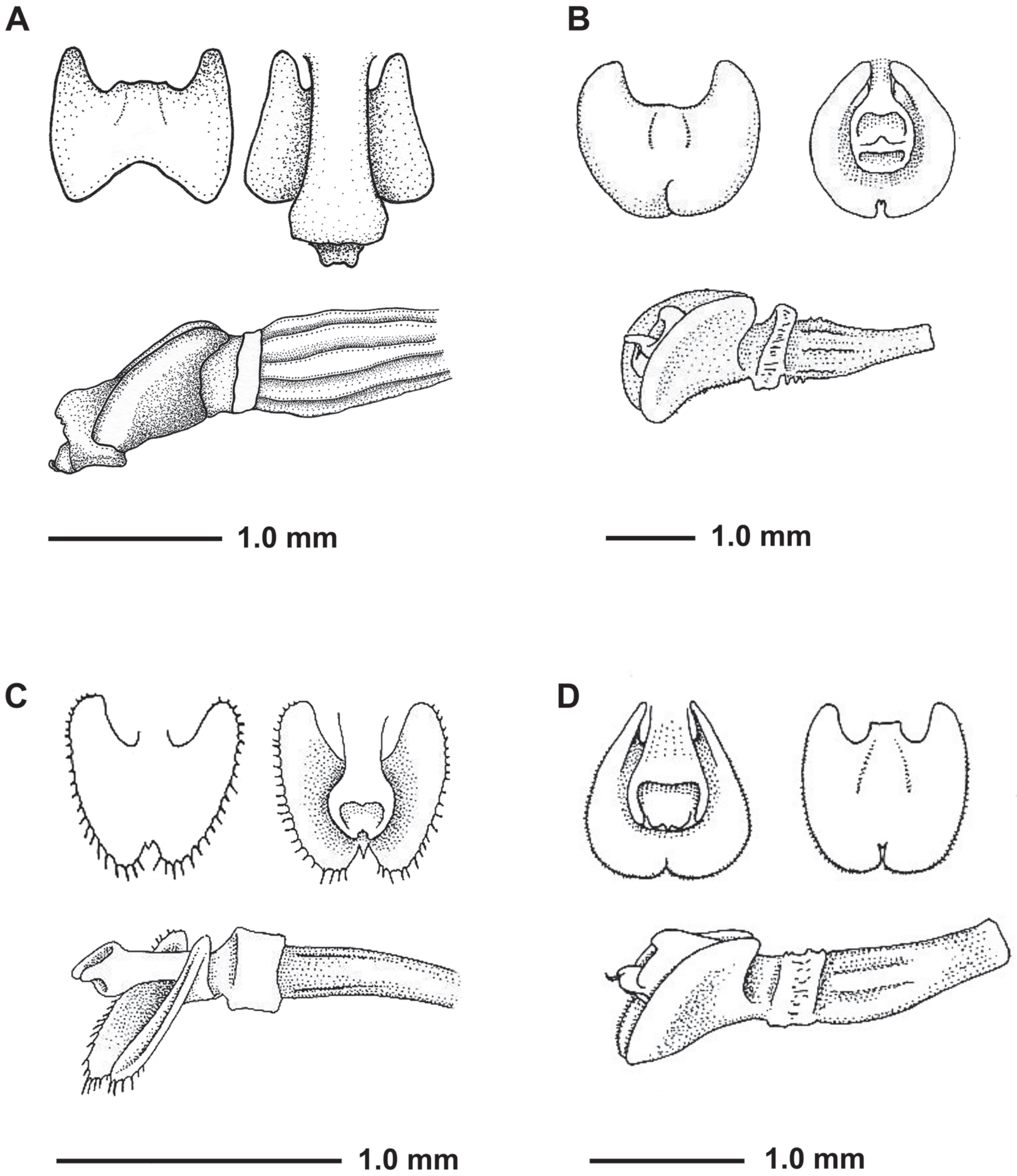


FIGURE 5. Illustration and comparisons of the lip and columns of the species most similar to *Lepanthes anchicayae* J.S. Moreno & S. Vieira-Uribe. **A**, *L. anchicayae*; **B**, *L. petalopteryx* Luer & R. Escobar; **C**, *L. pleurorachis* Luer; **D**, *L. viahöensis* Luer & R. Escobar. Original drawings by J. S. Moreno (A) and Carlyle Luer (B–D), courtesy of the Missouri Botanic Gardens Press.

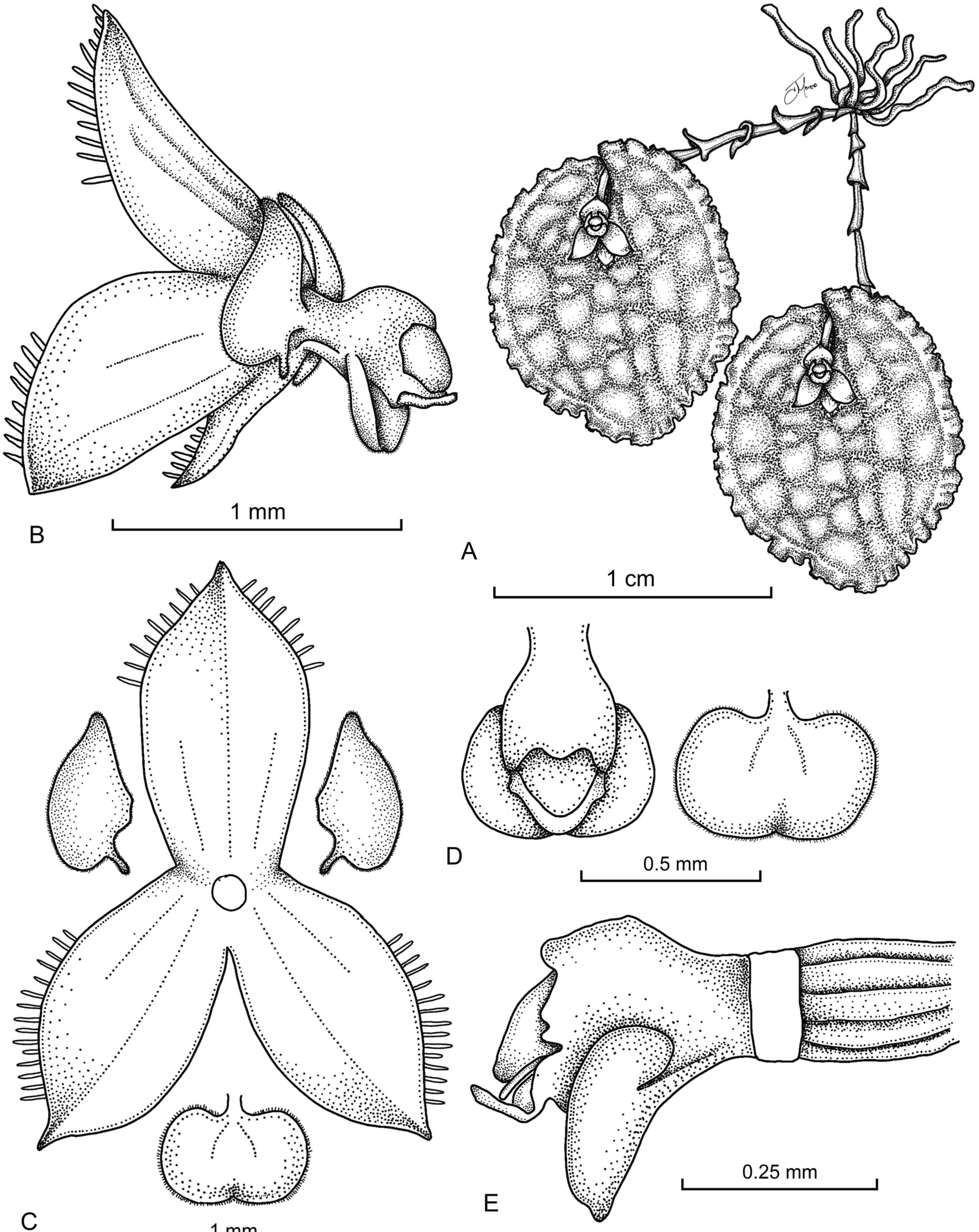


FIGURE 6. Illustration of *Lepanthes microcalodyction* J.S. Moreno & L. Baquero. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip; **E**, column, lip, and ovary lateral view (pollinia and anther cap absent). Drawn by J. S. Moreno based on *J. S Moreno & A. L. Erazo 432* (CAUP).

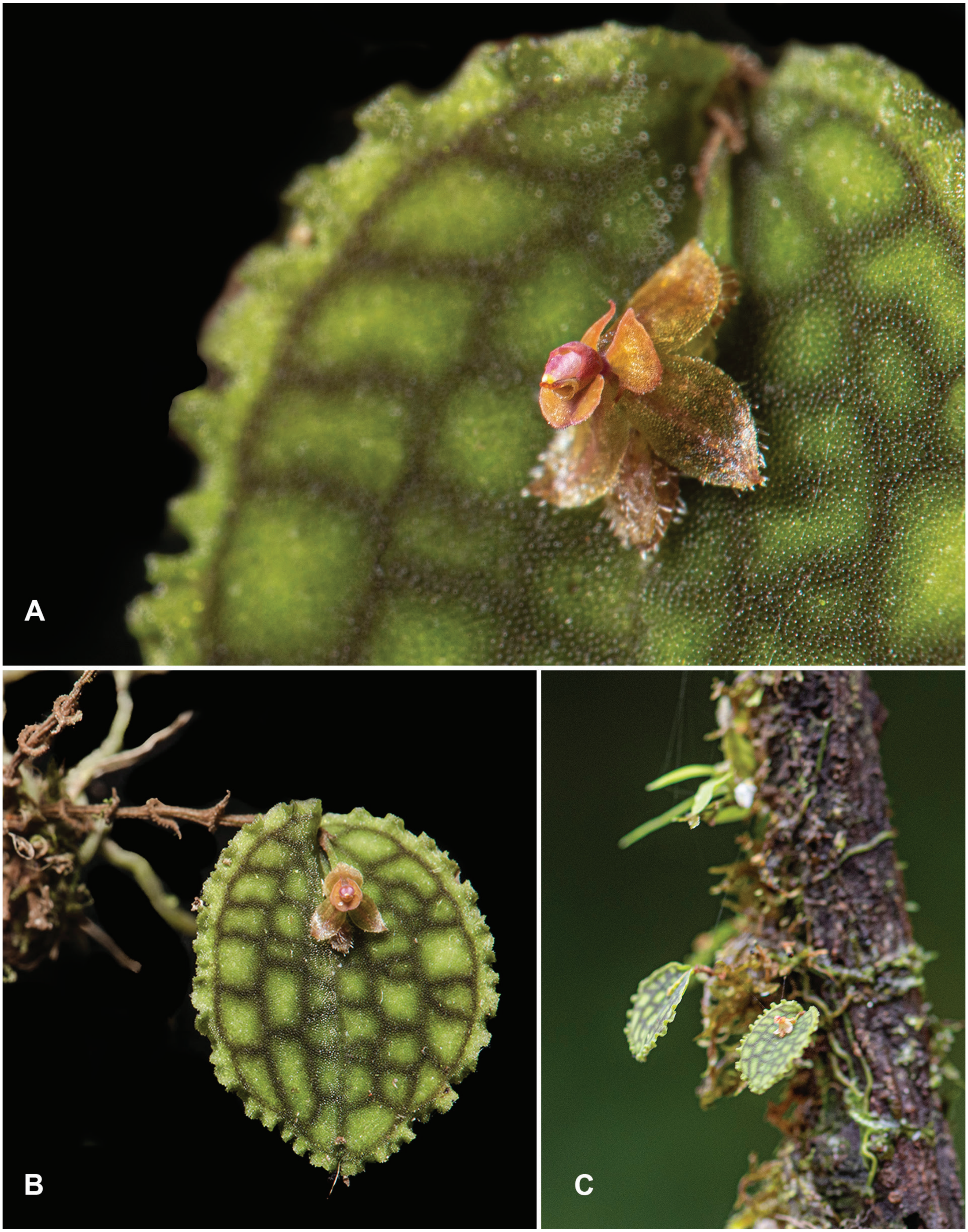


FIGURE 7. *Lepanthes microcalodyction* J.S. Moreno & L. Baquero. **A**, 3/4 frontal view; **B**, plant; **C**, habit and plant, in situ. Photographs by J. S. Moreno.

FIGURE 8. Comparison of the most similar species to *Lepanthes microcalodyction* J.S. Moreno & L. Baquero. **A**, *L. calodyction* Hook.; **B**, *L. microcalodyction*. Both photographs represent the real scale of the two species. Photographs by J. S. Moreno.

*Plant* very small, up to 2 cm tall, epiphytic, caespitose; *roots* slender. *Ramicauls* erect, slender, 6.0–6.5 cm long, enclosed by 5–6 microscopically ciliate-scabrous lepanthiform sheaths. *Leaves* thinly coriaceous, light green, heavily reticulated with purple, subcircular to broadly ovate, broadly obtuse, 1.0 × 0.8 cm, a marginal vein, margins undulate, the base cordate, abruptly contracted into a petiole ca. 0.5 mm long. *Inflorescence* a congested, distichous, successively several-flowered raceme up to 3–4 mm long, borne on top of the leaf including the 2-mm-long, slender peduncle; *floral bracts*, echinate 0.5 mm long; pedicels 1 mm long. *Ovary* costate, 0.3–0.4 mm long. *Sepals* tawny translucent, glabrous, reflexed, carinate at the abaxial side with long spiculate margins toward the apex. *Dorsal sepal* obovate, acute, 3-veined, 1.0 × 0.5 mm, connate to the lateral sepals for 0.1 mm. *Lateral sepals* obovate, acute, 2-veined, 1.0 × 0.5 mm, connate for 0.1 mm. *Petals* coppery, velvety, transversely bilobed, 0.25 × 1 mm, the upper lobe ovate, oblique, with the apex obtuse, the lower lobe ovate, oblique, the base rounded and abruptly contracted into a short, filiform structure. *Lip* coppery, minutely pubescent, transversely reniform, bent upward at each side of the column, 0.3 × 0.6–0.7 mm, connate to the column close to the base. *Column* scarlet, clavate, papillose, terete, 0.25 mm long; the anther apical; stigma with the tip of the rostellum acute and facing upward.

**Additional specimen examined:** COLOMBIA. Valle del Cauca: Buenaventura, Cañón del Rio Anchicayá, La Cascada, 3°37'33.5"N, 076°56'34.7"W, 300 m, 4 May 2018, *J. S. Moreno and A, Erazo 433*: CAUP).

**Etymology:** the specific epithet "microcalodyction" refers to the diminutive flower with a strong resemblance to *Lepanthes calodyction*.

**Habitat and ecology:** *Lepanthes microcalodyction* was found in two different locations within the Anchicayá River Valley, the first one characterized by having a fairly pristine wet forest located inside Los Farallones National Natural Park and one of the oldest hydroelectrical dams built by CELSIA known as Alto Anchicayá (Map 1). Thanks to the creation of the National Natural Park and the construction of the dam, the forests are well preserved because, as mentioned above, access to the general public is carefully supervised by the company and park authorities. It was also collected in the type locality of *Lepanthes anchicayae* where both species were found growing together in small, continuous tree branches close to the bajo Anchicayá. As a result, anthropic pressure on *Lepanthes microcalodyction* will be minimal and its conservation status will be of least concern in the future.

*Lepanthes microcalodyction* belongs to an informal group of species from the lowlands of the Pacific Ocean in South America and Panamá, characterized mainly by having heavily reticulate leaves (except for the Panamanian species *Lepanthes pantomima* Luer & Dressler and *Lepanthes arachnion* Luer & Dressler; Baquero, 2018) with margins undulate, small flowers with caudate petals, lip transversely reniform, oblong, cordate, and without an appendix, connectives and body. Several species, such as *Lepanthes pretiosa* Luer & Hirtz, *L. volador* Luer & Hirtz, *L. barbelifera* Luer & Hirtz, *L. tentaculata* Luer & Hirtz, *L. tortuosa* Luer & Hirtz, *L. bibarbullata* Luer, *L. saltatrix* Luer & Hirtz (Luer and Thoerle, 2011), and the recently described species *L. kayii* L. Baquero (Baquero, 2018), share very similar flowers and plants with the new species. The most similar species is *Lepanthes calodyction* (Fig. 8–9), characterized mainly by larger, transversely bilobed petals, 0.5–1.0 × 1.25–2.00 with ciliate margins and the upper and lower lobe long, caudate (vs. petals transversely bilobed, 0.25 × 1 mm, with margins smooth, acaudate, with the base of the lower lobe rounded and abruptly contracted into a short, filiform structure), and a larger lip of 0.66–1.00 × 1.25–2.00 mm, (vs. smaller lip 0.3 × 0.6–0.7 mm).

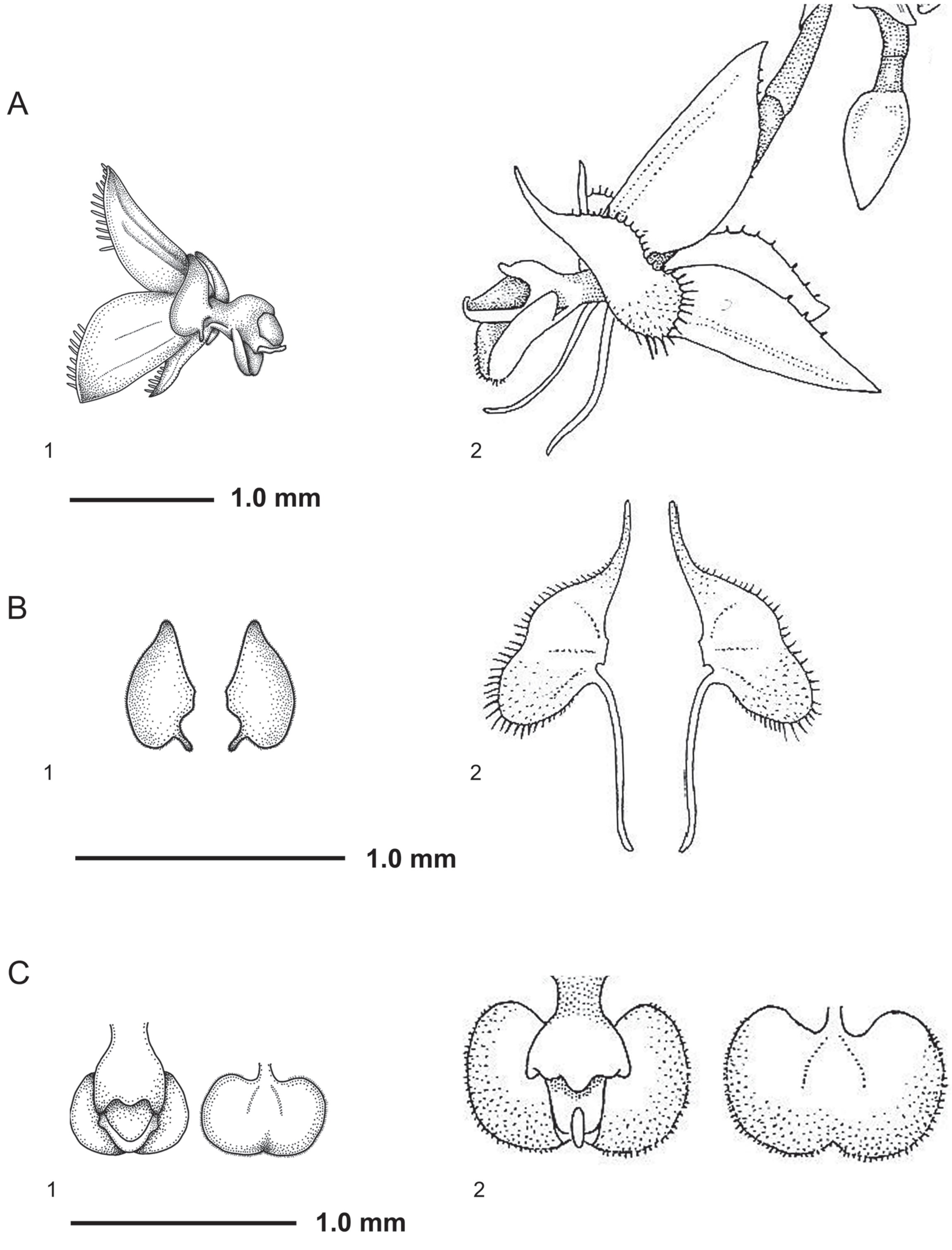


FIGURE 9. Floral illustration and comparisons of *Lepanthes microcalodyction* J.S. Moreno & L. Baquero (1) and *L. calodyction* Hook. (2). **A**, flower; **B**, petals; **C**, lip. Original drawings by J. S. Moreno (1) and Carlyle Luer (2), courtesy of the Missouri Botanic Gardens Press.

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# DISTRIBUTION MODELS AND SPATIAL ANALYSES PROVIDE ROBUST ASSESSMENTS OF CONSERVATION STATUS OF ORCHID SPECIES IN COLOMBIA: THE CASE OF *LEPHANTES MUCRONATA*

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**Abstract.** Orchidaceae is one of the most threatened families of vascular plants in the world, and in recent years, species distribution models (SDM) have been used as a tool to inform the conservation status of several species. However, the usefulness of SDM depends on appropriate knowledge of the use and limitations of these tools, otherwise there is a risk of getting erroneous models leading to wrong decisions in conservation plannning. We present the distribution model of *Lepanthes mucronata* in South America based on current and accepted knowledge in this discipline. The representativeness of protected areas for Colombia is evaluated, as well as ecosystems where it is present and its risk of extinction based on criteria of the IUCN. After reviewing these parameters, we found that *Lepanthes mucronata* meets the criteria for Least Concern (LC) IUCN status. We expect this investigation to serve as an appropriate example of this type of analysis and as a reference for future work in the conservation of this plant family.

**Keywords:** biogeography, conservation, MaxEnt, Orchidaceae

**Resumen.** Orchidaceae es una de las familias de plantas vasculares más amenazadas, y en años recientes se han utilizado modelos de distribución (MDS) como una herramienta para informar el estado de conservación de varias especies. No obstante, la utilidad de los MDS depende de un conocimiento apropiado sobre el uso y limitaciones de estas herramientas, de lo contrario existe el riesgo de obtener modelos erróneos que pueden llevar a malas decisiones en el establecimiento de planes de conservación. Presentamos la modelación de la distribución de *Lepanthes mucronata* en Suramérica con base en el conocimiento actual y aceptado en esta disciplina, donde se evalúa para la especie la representatividad de las áreas protegidas en Colombia, los ecosistemas donde está presente y su riesgo de extinción bajo los criterios de la IUCN, como un ejemplo más adecuado para realizar este tipo de análisis y un aporte que sirva de referencia para futuros trabajos en la conservación de las orquídeas.

**Palabras claves:** biogeografía, conservación, MaxEnt, Orchidaceae

Species distribution models (SDMs) predict the distribution of a species linking the occurrence records with environmental variables (Peterson and Soberón, 2012). They have been used widely to understand how biotic and abiotic factors limit distributions of species (Graham et al., 2010). In conservation studies, SDM have been used to identify the representativeness of species distributions in currently protected areas (Ortega-Andrade et al., 2015) and suggest new priority areas for conservation (Yan et al., 2018). Furthermore, SDMs have been used to predict biological invasions (Parsa et al., 2015) and to assess the exposure and sensitivity of a species distribution area to climate change (del Rosario and Hernández, 2015). Thus, SDMs are currently one of the primary tools for assessing the spatial conservation of biodiversity (Richardson and Whittaker, 2010; Ladle and Whittaker, 2011; Cox et al., 2016). However, many taxonomic groups still do not have proper distribution assessments in a context that allows the design of suitable conservation plans, and the inclusion or suggestion of potential geographic areas needed for the survival of certain species are going unnoticed. Such is the case of the Orchidaceae family, one of the largest families within vascular plants, with about 880 genera and over 28,000 species, and representing approximately 8% of all vascular flora in the world (Christenhusz and Bying, 2016; Givnish et al., 2016).

Colombia currently has 185 species of orchids in one of the threatened categories, constituting 10% of the Colombian orchid flora (Betancur et al., 2015). In these threatened categories, cultivated genera, such as *Masdevallia* Ruiz & Pav., *Dracula* Luer, and *Anguloa* Ruiz & Pav., are some of the main threatened groups because of

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their well-known distribution, being easily recognized, and importance as horticultural plants (Calderón-Sáenz, 2007). These threatened species lists leave out genera with higher numbers of species, such as the genus *Lepanthes* Sw. with more than 300 species (Bernal et al., 2019), which have minimal collection pressures from commercial growers and hobbyists because of their small flowers and overall size. However, *Lepanthes*'s distribution ranges are restricted to well-preserved forests meeting specific biological requirements, such as high humidity and particular symbiotic relationships (Crain, 2012). Therefore, estimating accurate distribution models is needed to determine or assess new threat categories.

One of the best examples of how SDMs have been used to evaluate the conservation status of species in Colombia is the *Red Book of Birds of Colombia* (Renjifo et al., 2014). This can be considered the first work that evaluated the conservation status of a large number of species using SDMs and IUCN criteria in this country. We believe that it should be a precedent for work done on orchid species, including *Lepanthes* species. Currently, *L. mucronata* Lindl is an endemic and common orchid species of the tropical Andes Hotspot region. This species has a conservation status of Least Concern (LC) according to the IUCN, indicating that the species is quite common in its distribution and has no direct threats at present. However, there are no specific data on populations of *L. mucronata*, its commercial use, or, especially, impacts and threats of habitat loss to their populations. Therefore, in this study we assess the conservation status of *L. mucronata* using SDMs as a backbone for conducting posterior spatial conservation analysis, following the methods used in the *Red Book of Birds of Colombia*. We had four major objectives: (1) estimate *L. mucronata* distribution using multiple model algorithms, (2) provide an assessment of how well this distribution is represented in protected areas in Colombia, (3) record the ecosystems where it occurs and the amount of habitat lost; and (4) assess the risk of extinction of *L. mucronata* following IUCN criteria. With this study of *L. mucronata*, we expect to provide a baseline for future orchid conservation studies of species with similarly limited information using distribution models and posterior spatial analyses.

## Materials and Methods

*Case Study: Lepanthes mucronata* Lindl. (Fig. 1)

*Lepanthes mucronata* is one of the most common species within the genus distributed in South America. This species has wide floral and vegetative variation; from small to large plants, leaves varying from ovate to acuminate or even linear, flowers 4–6 mm in length, varying in shape of the margins of upper lobe of the petals, from truncated to erose. The species has a very consistent and distinctive lip, with a pair of thin, fragile blades overlying a proportionally large, scaphoid appendix (Luer and Thoerle, 2012). It can grow as an epiphyte or lithophyte in humid, high Andean forests and páramos. In Colombia, it is found in 13 departments (from Santander to Putumayo).

Figure 1. *Lepanthes mucronata*. **A**, habit; **B**, flower. Photographs by J. S. Moreno.

### *Occurrence Data*

A total of 159 occurrence records were obtained from herbaria AMES, CAUP, COL, CUVC, FMB, JAUM, and TOLI; along with the W3 TROPICOS database (Missouri Botanical Garden, www.tropicos.org); GBIF (Global Biodiversity Information Facility, www.gbif.org), and KEW (Royal Botanical Gardens, Kew, www.kew.org), and a review of literature (Luer, 1996; Farfán et al., 2003; Viveros and Higgins, 2007; Idárraga-Piedrahita et al., 2011; Luer, 2010; Luer and Thoerle, 2011, 2012; Bernal et al., 2019).

In order to reduce the sampling bias, which can negatively affect the distribution models (Reddy and Davalos, 2003; Peterson et al., 2014; Radosavljevic and Anderson, 2014), spatial filters were applied and 93 records were obtained. The 66 records that were deleted were all within the same 10-km radius. One point was also discarded in Cochabamba, Bolivia, because it did not have exact geographic coordinates and was the only collection record in this area, making its determination questionable.

### *Environmental Data*

Environmental information was obtained from the Worldclim database (www.worldclim.org, Hijmans et al., 2005), which presents 19 bioclimatic variables that summarize annual trends, seasonality, and extreme values of temperature and precipitation. In addition, evapotranspiration and aridity variables obtained from the CGIAR-CSI (Consortium for Spatial Information, http://www.cgiar-csi.org) were used. To avoid overfitting of the model due to co-linearity of climatic variables, six variables were selected that were not strongly correlated (Pearson <0.8) to an approximate resolution of 1 km$^2$: annual mean temperature (Bio1), mean diurnal range (Bio2), temperature seasonality (Bio4), annual precipitation (Bio12), precipitation seasonality (Bio15), and precipitation of warmest quarter (Bio18).

The modeling area was selected considering the accessible area of species M (diagram by BAM; Barve et al., 2011) over relevant periods of time, in order to include historical aspects related to the distribution of the species, which does not consider species distribution models (SDM). On the basis of records obtained from terrestrial ecoregions of the World Wide Fund for Nature (WWF) and biogeographic regions of endemism (Morrone, 2014; Hazzi et al., 2018), it was hypothesized that the accessible area of *Lepanthes mucronata* is the northern Andes of South America (> 900 m of elevation), between latitude 9˚27'N and 13˚74'S, and between longitude 80˚41'W and 69˚26'W. The selection of this area is consistent with the fact that this species is endemic to the Andes and that its elevation range is 900–3800 m.

### *Distribution Modeling*

To make SDM models, the maximum entropy algorithm was used (MaxEnt program version 3.3.3K) (Phillips et al., 2006; Elith et al., 2011), which is considered to be among the best methods when using only occurrence data (Elith et al., 2006). In addition, models were made exploring other algorithms, because implementation of a single algorithm can lead to suboptimal models (Qiao et al., 2015). The following algorithms were used in Openmodeller program version 1.3 (Muñoz et al., 2011): Support Vector Machine (SVM), Euclidean Distance (MinDist), and GARP with the correction of “Best Subsets.” All models were made with default settings presented by each algorithm.

The models obtained with the various algorithms were evaluated by the partial ROC (Receiver Operating Characteristic Curve), which estimates the area under the curve (AUC) only in the sectors of the ROC where error of omission is minimal (Peterson et al., 2008). This methodology is a correction of the traditional ROC and allows a more accurate comparison of the performance of different algorithms. For example, MaxEnt tends to have high AUCs in regions of the curve that are not important for the evaluation of the model and therefore can erroneously indicate how much greater one model’s performance is than another. The partial ROC was carried out in the “Tool for Partial-ROC” program (Barve, 2008), taking two subsets of data, 70% of presence records to calibrate the models and 30% to validate them. We performed 100 pseudo-replicates with bootstrap and an $E = 10\%$ omission error allowed. To compare the performances of these models, the normality of the data was evaluated with the Shapiro-Wilks test. Because the data did not present a normal distribution ($p<0.05$), a nonparametric Kruskal-Wallis test was performed; these analyses were carried out using Past 3.14 software (Hammer et al., 2001). Finally, the continuous models with highest partial AUC values were assembled into a consensus map, averaging the continuous values of suitability.

Habitat suitability values obtained in the distribution consensus model were converted into binary values of presence and absence (or adequate and not adequate), using the 5th percentile as the threshold value. Basically, the distribution area obtained with this value covers 95% of the presence records of the species, excluding 5% of the records ($E = 5\%$; Peterson et al., 2011), which we assumed are in atypical areas or those of low habitat suitability for the species. The maps were edited in ArcMaP version 10.3 (ESRI, 2015).

### *Representativeness of the National System of Protected Areas and Ecosystems*

After obtaining the final model of the distribution of *Lepanthes mucronata*, the representativeness of the species in the National System of Protected Areas of Colombia (SINAP, 2014; http://sinap.parquesnacionales.gov.co) and the percentage of the species’ distribution represented was evaluated in each of the following categories: National Natural Parks, National Protective Forest Reserves, Regional Integrated Management Districts, Regional Natural Parks, Regional Protective Forest Reserves, Natural Reserves of Civil Society, Soil Conservation Districts, and Recreation Areas. This calculation was made with a resolution of 0.0083 degrees, which is equivalent to ~ 1 km$^2$. To evaluate the availability of ecosystems, the methodology of Ortega-Andrade et al. (2015) was applied.

The areas of the ecosystems within the distribution model were calculated and organized in descending order by their size, and then the Importance Factor was calculated (FI = [area of the ecosystem predicted by the model × 100] / total area of the suitability model).

To evaluate habitat loss of the species, we used the methodology proposed by Ortega-Andrade et al. (2015) and Figueroa et al. (2016). A map with anthropic coverage from 2012 obtained from SIAC (www.siac.gov.co), with a resolution of 30 m, was superimposed on the distribution model of *Lepanthes mucronata*. Subsequently, the types of coverage suitable for the presence of viable populations of the species that were found in the distribution model were selected. The coverage types "forest" and "forest and semi-natural areas" (the latter category being conserved areas that have had some degree of disturbance) were chosen as suitable habitats and the other types of coverage were excluded, such as human settlements, urban centers, livestock, and agricultural areas. Finally, the modeling map of *Lepanthes mucronata* without anthropic influence was labeled "historical distribution," and the map with anthropic influence was labeled "current distribution or "remnant habitat of the species." These analyses were done with software ArcGIS version 10.3.

### *Risk of Extinction*

To evaluate the extinction risk for *Lepanthes mucronata*, the categories and criteria of the IUCN red lists (2016) were used, which are based on population sizes, geographical distribution, and reduction of one or both variables. The IUCN system allows the uncertainty associated with these measurements to be considered, while providing an objective method of categorizing risk of extinction of even diverse biological groups (Collen et al., 2016). Here we present a description of criteria A and B, since they usually generate confusion in their correct application. We suggest the revision of the *Red Book of Birds of Colombia* (Renjifo et al., 2014) as an example of how to use these criteria correctly.

**Criterion A: Reduction in population size.** As population information is scarce for most species, the loss of vegetative cover in a given period can be used to obtain estimates of population reduction rates in the same period (Buchanan et al., 2008; Tracewski et al., 2016). For example, a 20% coverage loss rate can be interpreted as a 20% reduction in populations. Better estimates can be obtained if more associated information is known. The minimum threshold for a species to qualify as threatened is a reduction in population size of 30%.

**Criterion B: Geographic distribution.** Two measurements of geographic distribution are used within this criterion: the extension of presence (EOO, B1) and the occupation area (AOO, B2). EOO is the area contained in the shortest imaginary limits drawn to cover all the sites where a species is found; this area is calculated using a minimum convex polygon using its known, inferred, or projected distribution (IUCN, 2016). Note that the EOO is not the range of the potential species or habitat obtained through an SDM; it is a measure of spatial correlation, based on the observation that zones in proximity are more likely to be exposed to the same risk factors, which can disperse throughout the species' distribution and increase its risk of extinction. The minimum threshold EOO for a species to qualify as threatened is < 20,000 km$^2$.

In addition to exceeding the thresholds for criteria A or B, at least two of three subcriteria must be met:

(1) Severe fragmentation or threshold of localities of the species.

(2) Continuous decrease observed, estimated, inferred, or projected.

(3) Extreme fluctuations in populations, mature individuals, EOO, or AOO.

## RESULTS

### *Distribution Models of* Lepanthes mucronata

The models developed with the four algorithms (MaxEnt, Garp, MinDist, and SVM) indicate that the areas suitable for *Lepanthes mucronata* are Andean and high Andean ecosystems, altitude being primarily the main factor (approximately 1700–4000 m of elevation) (Fig. 2). A reduction in suitable environments for the species toward the southern end of its distribution is indicated, with few adequate areas in northern Peru and no areas further south (however, as mentioned above the species is recorded in Bolivia). On the other hand, the models indicate that part of the Venezuelan Andes is also a suitable environment for this species, although it has not been reported there. The algorithms with the highest AUC radius values were MaxEnt and SVM, with no significant difference between them ($p < 0.05$), but they were significantly different from other algorithms (Fig. 3). Therefore, these two models were chosen to generate the consensus map of the distribution of *Lepanthes mucronata* (Fig. 4).

### *Representativeness of the System of Protected Areas and Ecosystems*

In Colombia, 10.14% of the distribution of *Lepanthes mucronata*, which covers approximately 198,282 km$^2$, is within various categories of the protected area system (PAS). As expected, the National Natural Parks (Table 1; Fig. 5A) is the category that most represents the distribution of this species, covering 24,820 km$^2$ (6.33%) of its distribution and 62.40% within all PAS. Other important categories are the Integrated Management Districts and the National Protective Forest Reserves, which together cover 2.40% (9441 km$^2$) and 23.74% of the PAS. The largest ecosystems in the area (Table 2) were the montane forests of the Magdalena Valley (79,494 km$^2$, FI = 40.09), the montane forests of the Eastern Cordillera (34,459 km$^2$, FI = 17.40), the montane forests of the Northwest (28,793 km$^2$, FI = 14.54), and the montane forests of Valle del Cauca (28,182 km$^2$, FI = 14.23).

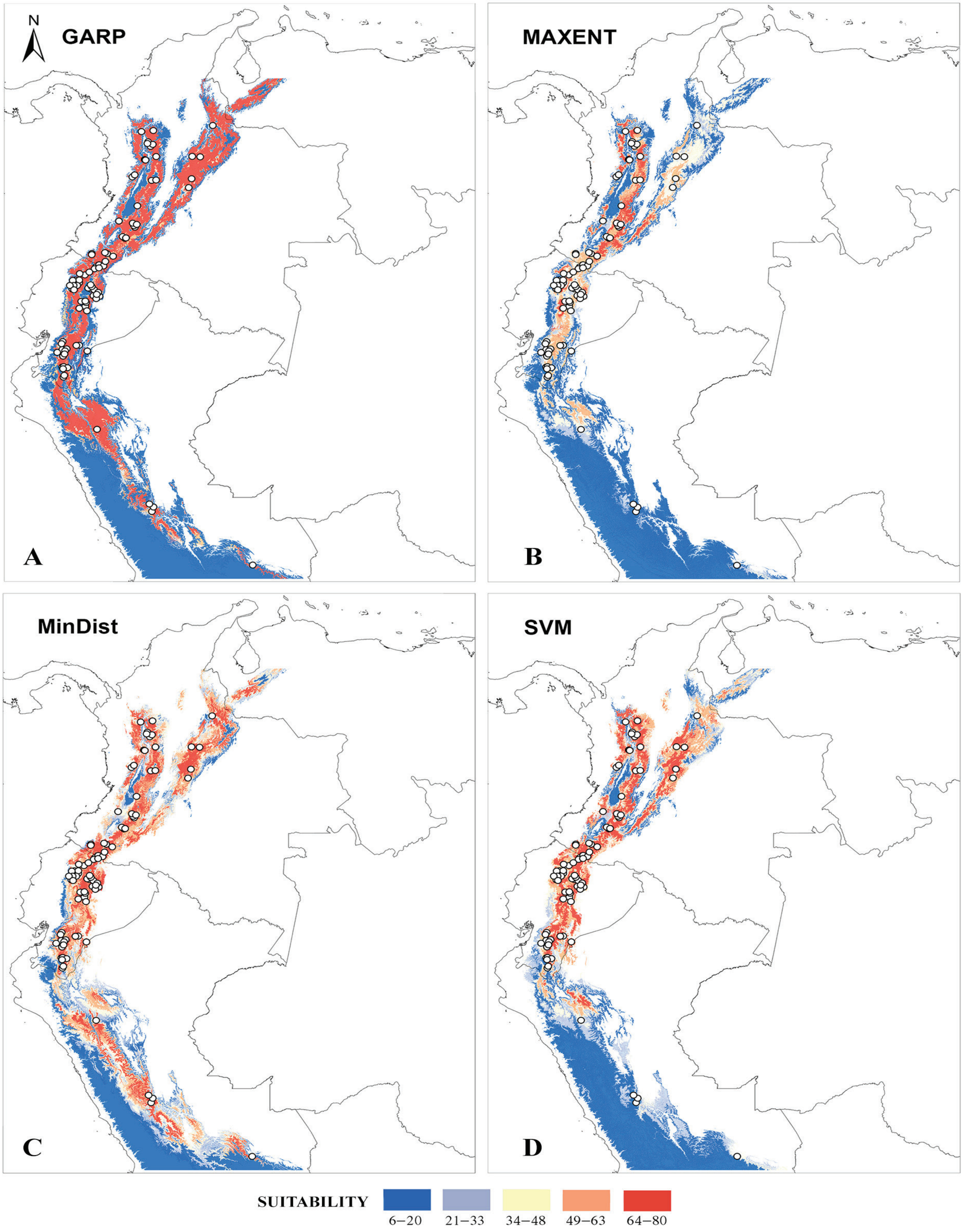

FIGURE 2. Distribution models of *Lepanthes mucronata* obtained with four algorithms in the northern Andes.

Table 1. Representativeness of the National System of Protected Areas of Colombia (SINAP) in the distribution of *Lepanthes mucronata*.

| Category | Model area (km2) | Percentage within SINAP (%) | Percentage within distribution (%) |
|---|---|---|---|
| National natural parks | 24,820 | 62.40 | 6.327 |
| Regional integrated management districts | 4826 | 12.13 | 1.230 |
| National protective forest reserves | 4615 | 11.60 | 1.176 |
| Regional natural parks | 3846 | 9.67 | 0.980 |
| Regional protective forest reserves | 1142 | 2.87 | 0.291 |
| Soil conservation districts | 429 | 1.08 | 0.109 |
| Natural Reserves of Civil Society | 91 | 0.23 | 0.023 |
| Recreation areas | 5 | 0.01 | 0.001 |
| TOTAL | 39,774 | 100.000 | 10.139 |

Table 2. Ecosystem availability (km$^2$) according to the distribution model (km$^2$) of *Lepanthes mucronata* in Colombia.

| Ecosystem | Available area in Colombia (km2) | Area in the model (km2) | Importance factor (FI%) | Cumulative importance (%) |
|---|---|---|---|---|
| Montane forests of the Magdalena Valley | 90,277.000 | 79,404.000 | 40.095 | 40.095 |
| Montane forests of the Cordillera Oriental | 45,312.000 | 34,459.000 | 17.400 | 57.496 |
| Montane forests of the northwestern Andes | 36,363.000 | 28,793.000 | 14.539 | 72.034 |
| Montane forests of Valle del Cauca | 35,720.000 | 28,182.000 | 14.231 | 86.265 |
| Northern páramo of the Andes | 16,615.000 | 16,077.000 | 8.118 | 94.383 |
| Andean montane forests of the Eastern Cordillera | 9751.000 | 9733.000 | 4.915 | 99.298 |
| Wet forests of Chocó-Darién | 542.000 | 381.000 | 0.192 | 99.49 |
| Dry forests of Valle del Cauca | 5098.000 | 341.000 | 0.172 | 99.662 |
| Dry forests of the Magdalena Valley | 3298.000 | 335.000 | 0.169 | 99.831 |
| Wet forests of Napo | 528.000 | 208.000 | 0.105 | 99.936 |
| Dry forests of Apure and Villavicencio | 100.000 | 100.000 | 0.050 | 99.986 |
| Dry forests of the Patía Valley | 698.000 | 22.000 | 0.011 | 99.997 |
| Montane forests of the Venezuelan Andes | 8.000 | 2.000 | 0.001 | 99.998 |
| Wet forests of Magdalena-Urabá | 8.000 | 1.000 | 0.001 | 99.999 |
| TOTAL | 24,4318.000 | 19,8038.000 | 100.000 | 100.000 |

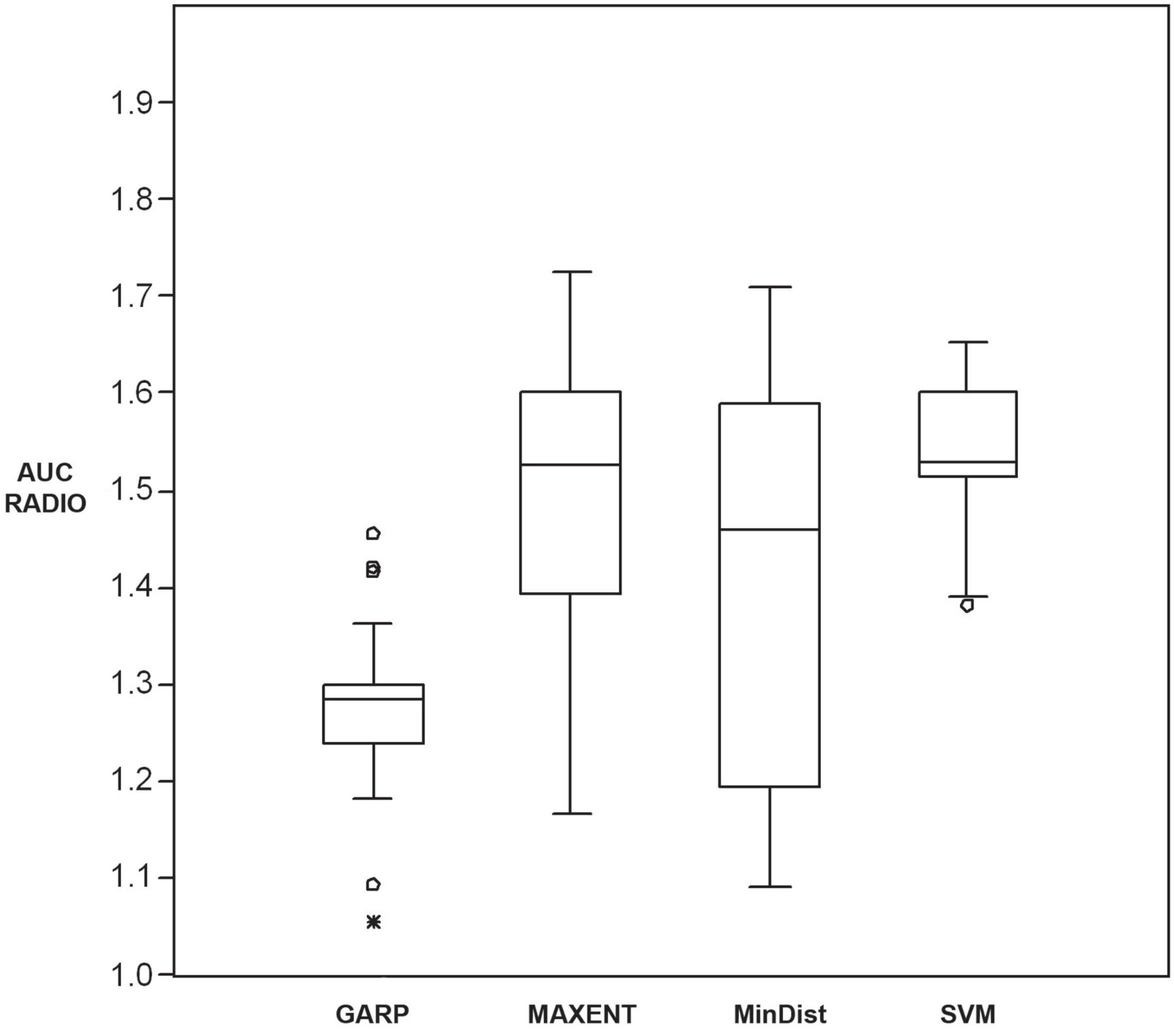

FIGURE 3. Performance of each of the models obtained using four algorithms, through partial ROC.

*Risk of Extinction*

**Criterion A.** Anthropic influence analyses (Fig. 5B) indicate that *Lepanthes mucronata* has lost 47% (93,961km$^2$) of its historical habitat, caused mainly by deforestation and the loss of vegetation cover. This is the result of the high anthropic impacts in the Colombian Andes, where the country's largest population resides (Etter and van Wyngaarden, 2000). However, in recent years there has been a recovery of plant cover in the Andes and a decrease in deforestation rates (Sánchez-Cuervo et al., 2012; IDEAM, 2016). Because of this decrease, and because the species has not had a population decline of more than 30% in the past 10 years or three generations, *Lepanthes mucronata* does not qualify as threatened under Criterion A.

**Criterion B.** B1. EOO >> 20,000 km$^2$ for *Lepanthes mucronata*. The geographic area of *L. mucronata* in Colombia far exceeds the threshold for Criteria B1, so the species does not qualify as threatened under this criterion. B2. Estimated area of occupancy = 104,321 km$^2$> 2000 km$^2$. Although the AOO must be smaller, it would be well above the threshold; thus the species does not qualify as threatened under Criterion B2.

Subcriterion 1. There is no estimated size of the population, but it is an abundant species with a large remaining habitat area, so the species does not qualify as threatened under Subcriterion 1.

Subcriterion 2. The species does not qualify as threatened under Subcriterion 2, since it does not have a very small or restricted population.

Subcriterion 3. There are not enough data to evaluate the species under this criterion of quantitative analysis.

*Conclusion*

*Lepanthes mucronata* does not meet any of the criteria of the categories In Danger, In Critical Danger, Vulnerable, or Near Threatened of the Red List prepared by the IUCN organization (2016). It therefore meets the criteria for a status of Least Concern (LC).

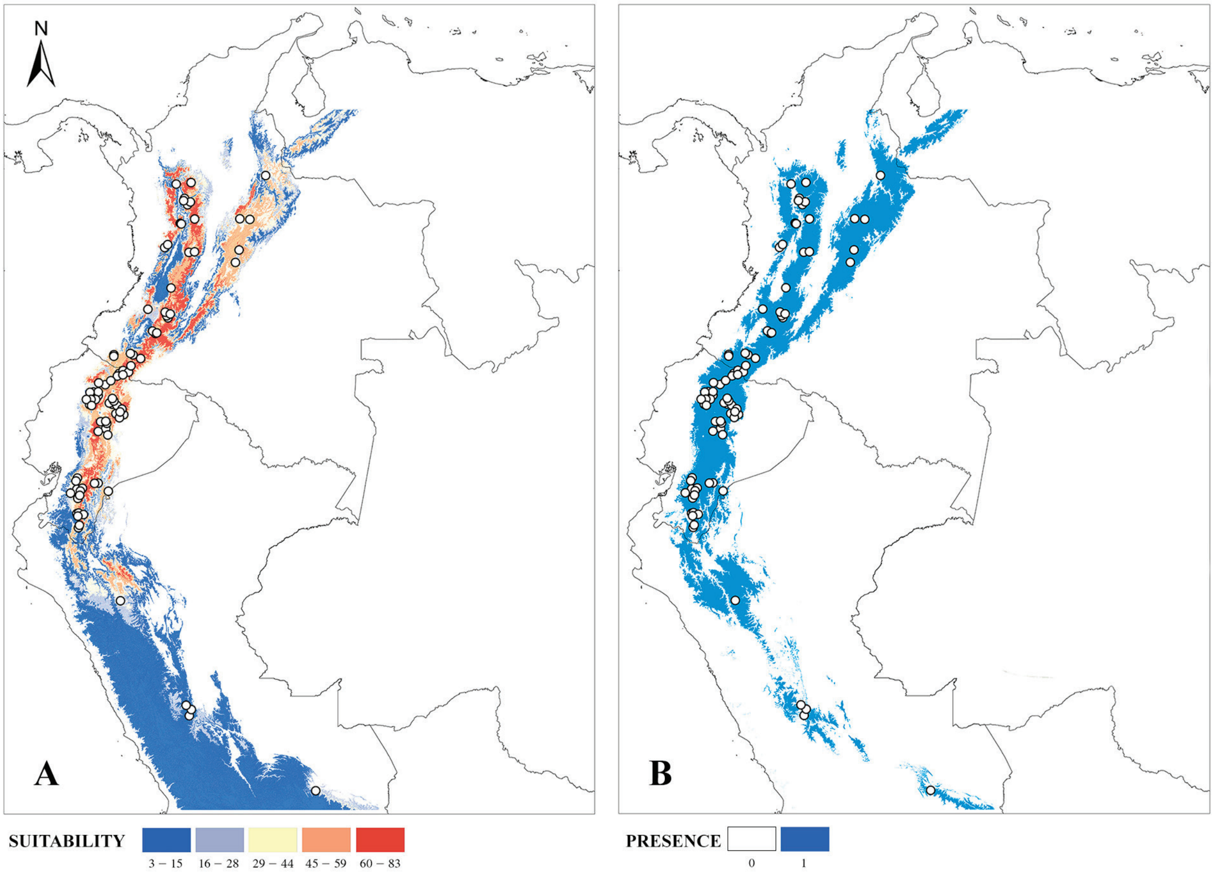

FIGURE 4. Consensus model of the distribution of *Lepanthes mucronata* obtained combining models generated by MaxEnt and SVM. **A**, continuous model; **B**, binary model.

## DISCUSSION

The present study integrated SDMs, geographic information systems (GIS), and biogeographic concepts (Richardson and Whittaker, 2010) to estimate the distribution and assess the conservation status of *Lepanthes mucronata*. In our model, we found that the species is present mainly in the Andean and high Andean cloud forests of Colombia and Ecuador. It has a low climatic suitability in Peru, and its distribution area decreases toward the south of Peru. These results are consistent with studies that show that the diversity of *Lepanthes* is much lower in Peru and in the southern Andes (Luer and Thorle, 2012; Crain and Tremblay, 2014). The genus *Lepanthes* is little known in Peru and Bolivia and has been in taxonomic oblivion for decades (Luer, 2010; Damian and Larsen, 2017). At the present time, Peru and Bolivia have 55–63 and 67 known species of *Lepanthes*, respectively, of which the majority are endemic (Luer, 2010; Damian and Larsen, 2017). In these countries the species are distributed mainly in the narrow strip of humid forest that stretches from Peru to central Bolivia, along the eastern edge of the Andes between the páramo and the warm lowlands (Luer, 2010). As extensive exploration studies continue, and with more sampling data, the prediction of the suitability in these countries may become higher, but *Lepanthes mucronata* would continue to be limited to the montane and humid ecosystems. This pattern of habitat suitability decreases toward the south and can be explained by precipitation regimes in the Andes, where there is a gradual decrease of precipitation from north to south, transitioning to large areas of dry montane ecosystems (Cheng et al., 2013). These dry areas are not suitable for most *Lephantes* species. However, as mentioned above, there are a few records from Bolivia that were not included in the model because we could not confirm their identification and exact location.

The distribution area with the largest representation of *Lepanthes mucronata* was located in montane forests of Andean and high Andean ecosystems (Table 1). These high-elevation habitats (1800–4200 m) present humid, low-temperature conditions that allow populations of *Lepanthes mucronata* and other species of this genus to be found easily here (Luer and Thoerle, 2011). The humidity of most Andean tropical ecosystems, caused by the almost permanent fog, results in high coverage of moss and other bryophytes that apparently form commensal relationships with this genus (Crain, 2012). This hypothesis is supported by the positive correlation between *Lephantes* richness and area cover of bryophytes (Crain, 2012).

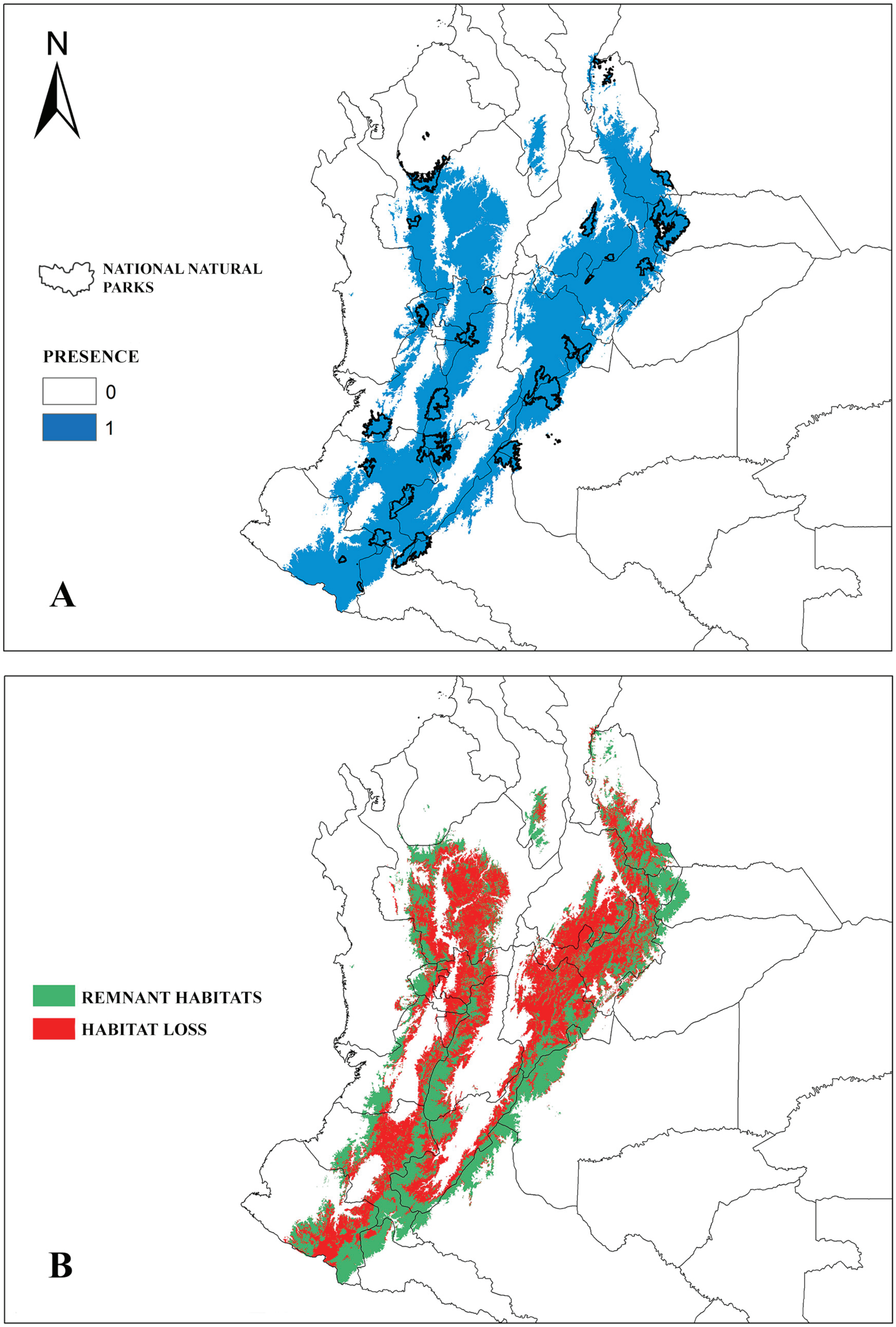

FIGURE 5. Consensus model of the distribution of *Lepanthes mucronata* in Colombia. **A**, representativeness of Natural National Parks (PNN); **B**, lost and remaining habitat.

The spatial analyses allowed us to determine that 10% of the distribution of *Lepanthes mucronata* is represented in some category of protected areas and that it has lost 47% of its habitat in Colombia. However, this species is not yet under any category of threat according to the criteria of the IUCN (2016) because of its extensive remaining range. In Colombia there are three main factors that may be affecting populations of orchids: excessive collection for ornamental purposes of species with showy and/or large flowers (Calderón-Sáenz, 2007); fragmentation and loss of habitat due to excessive deforestation and indiscriminate use of the soil (Orejuela, 2012); and finally, climate change, which can have a strong impact on species restricted to high altitudes, such as *Lepanthes mucronata* (Thuiller, 2007). *Lepanthes* is a genus of very small orchids in floral and vegetable size, and they go almost unnoticed by commercial growers, so the pressure by collection is minimal and its risk of extinction is reduced as compared with other orchid genera. Therefore, it may be safe from the anthropic intervention with the greatest impact locally and globally.

Thus, our study found that the main threat for *Lepanthes mucronata* is loss of habitat, of which 47% has disappeared, indicating that the greatest pressure exerted on this species is not overcollecting but the loss of forest cover in the three mountain ranges of Colombia. In addition, habitat loss could be one of the main threats of extinction for most of Andean *Lephanthes* species, because this genus is one of the most diverse genera in Orchidaceae, presenting high levels of endemism and association with well-conserved habitats in Colombia. Other species of this genus with more restricted ranges in the Andes could be in danger, and conservation assessments should be carryed out using methodologies of the type proposed in this study. Therefore, we expect that this work will be used as a guideline for future conservation assessments of other species of orchids.

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# *PINALIA TAUNGGYIENSIS* (ORCHIDACEAE), A NEW SPECIES FROM MYANMAR

PAUL ORMEROD[1,2] AND HUBERT KURZWEIL[3]

**Abstract.** A new species of *Pinalia, P. taunggyiensis,* is described and illustrated based on a single collection from Myanmar.

**Keywords:** *Eria*, *Pinalia*, Orchidaceae, Myanmar, Thailand

The genus *Pinalia* Lindl. (Orchidaceae) contains about 210 species (Ng et al., 2018), distributed from Sri Lanka and India to Tahiti. Many of its species were formerly placed in a broadly construed *Eria* Lindl. For the most part its species are epiphytic herbs with ovoid to slender pseudobulbs that generally bear two to six leaves near the apex, inflorescences usually emerge from nodes in the upper half of the pseudobulbs and are quite often pubescent, floral bracts may be small to relatively large and showy, the flowers are glabrous to pubescent, varying from small to modest (sepals 1.5-12.0 mm long) in size, the lateral sepals form a mentum with the column foot, the labellum is usually variously ornamented with keels and/or calli, and the column bears eight pollinia.

During our studies on the orchid flora of Myanmar, we were unable to identify a species of *Pinalia* despite comparison with taxa from nearby Southeast Asian nations. It is here described as a new species.

**Pinalia taunggyiensis** Ormerod & Kurzweil, *sp. nov.* Fig. 1. TYPE: MYANMAR. Shan State, Taunggyi, 1370 m, 26 April 1939, *F. G. Dickason 8282* (Holotype: AMES).

Similar to *Pinalia lineoligera* (Rchb.f.) Ormerod in habit, but the inflorescence with ovate-elliptic (vs. ligulate-lanceolate) floral bracts, and the labellum epichile with radiating, irregular low and partly verrucose lamellae (vs. glabrous with a low medial keel).

Lithophytic *herb*. *Rhizome* very short, creeping. *Roots* slender. *Pseudobulbs* subcylindric, erect, uninodal, probably 2- to 3-leaved apically, 15–45 mm long, 6–8 mm thick. *Leaves* not developed at time of collection. *Inflorescence* emerging with the developing pseudobulb and leaves (synanthous), erect, 55–60 mm long; peduncle 40–50 mm long; rachis 3-flowered, 10–15 mm long; floral bracts ovate-elliptic, subacuminate, lemon colored, 5- to 7-veined, to 12 mm long, 5 mm wide. *Flowers* creamy white, the labellum lemon-tipped. *Pedicel with ovary* narrowly clavate, laxly pubescent, 9–10 mm long. *Dorsal sepal* oblong-lanceolate, obtuse, 5-veined, 9.8–9.9 mm long, 2.8 mm wide. *Lateral sepals* oblong-lanceolate, acute, 7-veined, 8 mm long, 5.5 mm wide, forming with the column foot an obtuse, 3-mm-long mentum. *Petals* oblong-lanceolate, acute, 5-veined, 9 mm long, 2.85 mm wide. *Labellum* trilobed, 7 mm long, 4.2 mm wide; hypochile broadly obtriangular, 4 mm long, 4.2 mm wide, lateral lobes obliquely oblong-elliptic, obtuse, ca. 2.5 × 1.5 mm; epichile ovate-suborbicular, subacute, 3 × 3 mm; 3 keels on the hypochile, lamellate, the 2 lateral ones highest, obliquely truncate, lamellae on the epichile 3–4, parallel, low, thin, irregularly dentate, with radiating, sparsely verrucose veins. *Column* semiterete, ca. 2.9 mm long; column foot ca. 3 mm long.

**Distribution:** Myanmar.

**Habitat:** unknown, found on rocks, 1370 m.

**Etymology:** named after Taunggyi, the type locality.

This species is most similar to *Pinalia lineoligera* (Rchb.f.) Ormerod from Myanmar and Thailand, but it differs in having much broader (not narrow) floral bracts and in flowers having a labellum epichile with low, radiating, irregular, partly verrucose lamellae (vs. being glabrous with a low central keel).

Two other species with a similar aspect to *Pinalia taunggyiensis* are *P. annapurnensis* (L.R. Shakya & M.R. Shreshta) Schuiteman et al. from Nepal, and *P. leucantha* Kuntze (*Eria alba* Lindl.) from India, Nepal, and Bhutan. However, both these taxa have smaller (less than 5 mm long) floral bracts, and neither has the radiating irregular lamellae on the labellum epichile.

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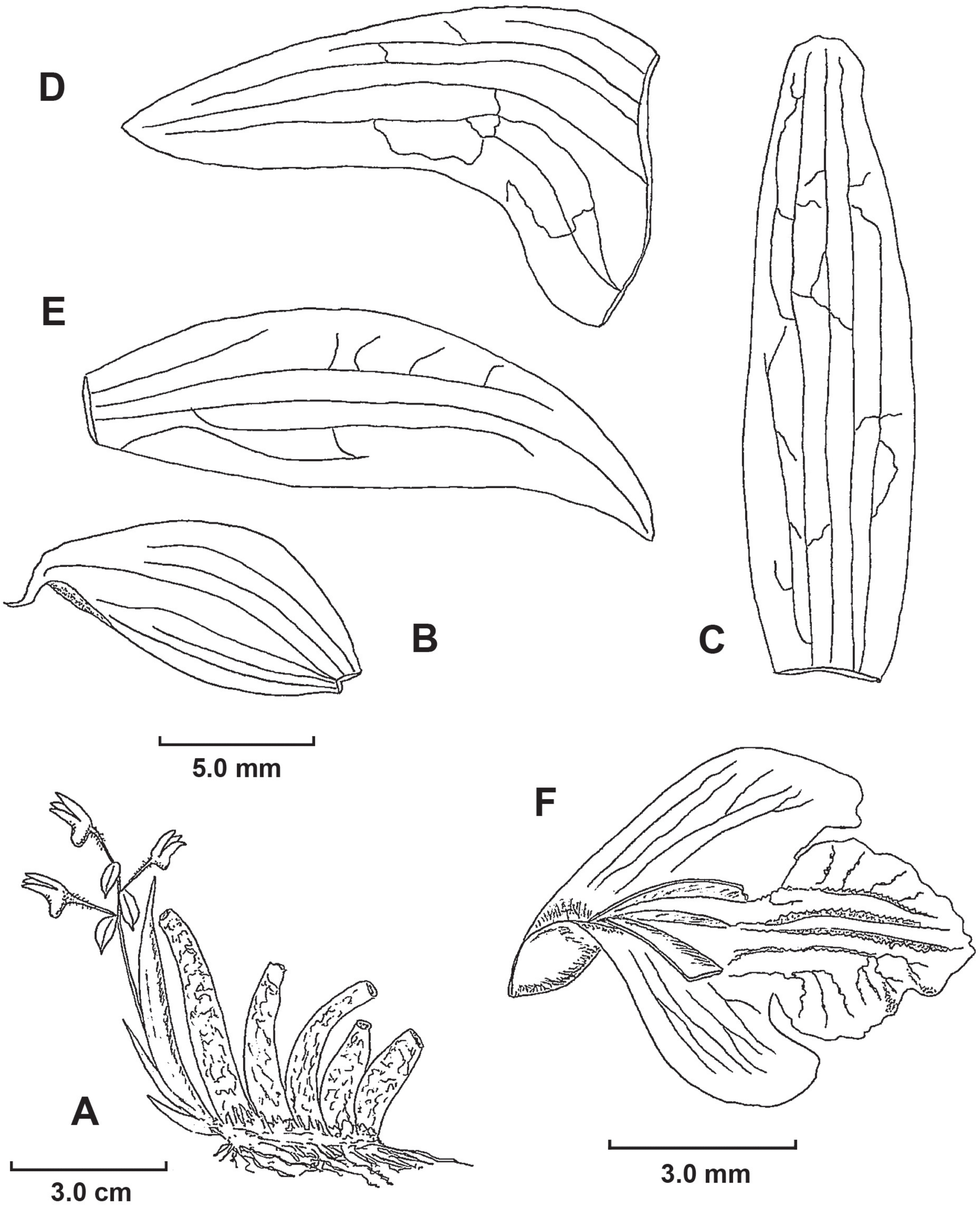

FIGURE 1. *Pinalia taunggyiensis* Ormerod & Kurzweil. **A**, plant; **B**, floral bract; **C**, dorsal sepal; **D**, lateral sepal; **E**, petal; **F**, labellum. Drawn by P. Ormerod from holotype.

# A NEW BHUTANESE *GASTROCHILUS* (ORCHIDACEAE), AND ANOTHER TRANSFER IN INDIAN *CYLINDROLOBUS*

Paul Ormerod[1,2] and C. Sathish Kumar[3]

**Abstract.** *Gastrochilus pearcei* is described as new from Bhutan, and *Eria khasiana* is transferred to *Cylindrolobus*.

**Keywords:** India, Bhutan, *Cylindrolobus, Gastrochilus,* new species, generic transfer

Ongoing literature and herbarium studies of various orchids found in Bhutan and India have revealed a new *Gastrochilus* species and the need to transfer *Eria khasiana* to *Cylindrolobus*, as part of continuing studies of the latter genus begun by the first author in 2014.

***Cylindrolobus*** Blume, Fl. Javae Praef.: 6. 1828.
Type species: *Ceratium compressum* Blume.

This genus of tribe Podochileae, subtribe Eriinae, has about 80 species distributed from Sri Lanka and India, through Malesia to Papua New Guinea. They are caulescent plants with stems up to 3 m long, but generally shorter, the flowers are borne in short axillary racemes, usually with prominent and showy peduncular bracts. The relatively attractive flowers are often in shades of white, yellow, or pink, sometimes with spotting. Key identification characters lie in the labellum, which may be ornamented with various keels, the latter often pubescent. Taxonomy of the group is hampered by the tenderness of the flowers, the parts of which when pressed can adhere to each other, rendering it difficult to separate them without causing damage.

Previously, Ormerod and Kumar (2018) transferred *Eria lindleyi* Thwaites to *Cylindrolobus* for nomenclatural reasons, since the name *C. bicolor* (Lindl.) Rauschert had been wrongly used for that species. The combination below is made for taxonomic reasons, since it seems obvious to us that *Eria khasiana* is a distinct species, worthy once more of recognition.

**Cylindrolobus khasianus** (Lindl.) Ormerod & C.S. Kumar, *comb. nov.*
Basionym: *Eria khasiana* Lindl., J. Proc. Linn. Soc., Bot. 3: 59. 1858.
TYPE: INDIA. Khasia, *W. Griffith s.n.* (Holotype: K-L, not seen).

**Distribution:** India.

Hooker (1890) united *Eria khasiana* with *E. clavicaulis* Wall. ex Lindl., and this reduction has been accepted ever since. In view of our studies of the genus *Cylindrolobus*, it seems that two outwardly similar taxa have been confounded and that Lindley's original position is correct. Hooker (1895) depicted flowers from the type of *E. khasiana* showing it to have a labellum with two lamellate keels near the apex of the hypochile, between which is a short, obovate, medially sulcate callus. The aforementioned figure also depicts a plant and a flower of the true *E. clavicaulis,* showing its distinctive pink-margined labellum sidelobes and lanceolate medial keel on the epichile. Seidenfaden (1982) published a more-detailed sketch of the flowers, which shows the thick medial keel on the hypochile terminated by two tubercles, and then continuing onto the epichile as a lanceolate keel. This is in agreement with Lindley's description in the protologue of *E. clavicaulis*.

There are also further important differences in the shape of the lip that distinguish the two. *Cylindrolobus clavicaulis* (Lindl.) Rauschert has almost truncate lateral lobes that spread at right angles, and therefore the epichile is unflanked by them when the lip is flattened. In *C. khasianus* the sidelobes are more rounded, and when the lip is flattened the sidelobes are subequal with the apex of the epichile.

***Gastrochilus*** D. Don, Prodr. Fl. Nepal.: 32. 1825.
Type species: *Aerides calceolaris* Buch.-Ham. ex J.E. Sm.

This is a genus of Aeridinae with about 63 species and one natural hybrid distributed from Sri Lanka and India to Indonesia and the Philippines. The center of diversity is China, where about 40 species have been found, about half of which are endemic. The plants are epiphytic herbs with short to elongate stems, with axillary inflorescences of one to several flowers, the flowers are variously colored, often in shades of yellow to green, usually variously spotted with brown or red, the lip usually has a large bowl-shaped to conical hypochile, and at its front is a variously shaped and adorned epichile, the column is short and broad.

Tsi (1996) published a preliminary revision of *Gastrochilus,* dividing it into three sections, section *Gastrochilus,* section *Caespitosi* Tsi, and section *Microphyllae* (Benth. & J.D. Hook.) "Seidenf." Subsequent molecular studies (Liu et al., 2019) show that there may be at least five sections, two of which appear to be undescribed.

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The same study also indicated that section *Microphyllae* needed recircumscribing and that taxa with a pubescent (vs. glabrous) labellum epichile were better placed in section *Caespitosi*.

***Gastrochilus*** D. Don section ***Microphyllae*** (Benth. & J.D. Hook.) Tsi, Guihaia 16, 2: 143. 1996.

Basionym: *Saccolabium* Blume series *Microphyllae* Benth. & J.D. Hook., Gen. Pl. 3: 579. 1883.

Type species: *Saccolabium distichum* Lindl.

Homotypic synonyms: *Saccolabium* Blume section *Microphyllae* (Benth. & J.D. Hook.) Pfitz., in Engler & Prantl, Nat. Pflanzenfam. 2, 6: 213. 1889.

*Saccolabium* Blume section *Distichophyllae* J.D. Hook., Fl. Brit. Ind. 6: 55. 1890 *nom. illeg.*

Type species: *Saccolabium distichum* Lindl.

*Saccolabium* Blume section *Disticha* J.D. Hook., Fl. Brit. Ind. 6: 64. 1890 *nom. illeg.*

Type species: *Saccolabium distichum* Lindl.

Tsi (1996) credited the transfer of section *Microphyllae* to *Gastrochilus* to Seidenfaden (1988), but no such transfer was made in that publication. The combination should be attributed to Tsi (1996), since he fully cites the basionym with a minor error in rank (section instead of series). According to Lui et al. (2019), section *Microphyllae* is defined by its pendent habit, leaves less than 5 cm long, flowers mostly with sepals about 5 mm long or less, and the lip with a glabrous epichile. The new species belongs to section *Microphyllae,* which in its revised circumscription contains about 14 species, namely, *G. affinus* (King & Pantl.) Schltr., *G. alatus* X.H. Jin & S.C. Chen, *G. corymbosus* A.P. Das & Chand, *G. distichus* (Lindl.) Kuntze, *G. dulongjiangensis* Q. Liu & J.Y. Gao, *G. fargesii* (Kraenzl.) Schltr., *G. fuscopunctatus* (Hayata) Hayata, *G. kadooriei* P. Kumar et al., *G. matsuran* (Makino) Schltr., *G. nepalensis* Raskoti, *G. pearcei* Ormerod & C.S. Kumar, *G. prionophyllus* H. Jiang, D.P. Ye & Q. Liu, *G. pseudodistichus* (King & Pantl.) Schltr., and *G. sonamii* Lucksom.

***Gastrochilus pearcei*** Ormerod & C.S. Kumar, *sp. nov.* TYPE: BHUTAN. Eastern part, Dongala, west side, 2590 m, 23 April 1949, *F. Ludlow, G. Sherriff & J. H. Hicks 20512* (Holotype: A; Isotypes: BM, E, images seen). Fig. 1.

Related to *Gastrochilus distichus* (Lindl.) Kuntze but the flowers differ in having a labellum with broadly rounded (vs. truncate), raised hypochile sidelobes, and a bilobed (vs. entire) epichile.

Epiphytic *herb*. *Roots* emerging from base of stem, semi-applanate, white, glabrous, 0.5–1.7 mm wide. *Stem* terete, simple to occasionally branching, subdensely leafy, 145–163 mm long, 0.8–1.5 mm thick; internodes 4 mm long. *Leaves* obliquely lanceolate, apex variably tridentate, tips acute to obtuse, thinly fleshy, 13–20 × 3–5 mm; leaf sheaths tubular-infundibuliform, truncate. *Inflorescence* axillary, 11–25 mm long; peduncle 8–21 mm long, 0.5 mm thick, widening to 1.2 mm wide below rachis; peduncular bract one, about midway on peduncle, short, ca. 1.8 mm long; rachis 2- to 3-flowered, 3–4 mm long; *floral bracts* ovate to ovate-lanceolate, acute to subacute, 1.2–2.8 × 1.5–1.8 mm. *Flowers* "green, lip white, spotted purple." *Pedicel with ovary* clavate, 3.2 mm long. *Dorsal sepal* ovate-elliptic, obtuse-subacute, concave, 5 veined, 4.75 × 3.00 mm. *Lateral sepals* obliquely ovate-elliptic, subacute, saccate at base, midvein with a lamellate keel that becomes thicker toward the apex, 5 veined, 5.75 × 3.00–3.10 mm. *Petals* obliquely oblong-oblanceolate, subacute, 3 veined, 4.5 × 1.5 mm. *Labellum* 5 veined, trilobed, joined to column for ca. 2 mm, ca. 7.5 × 7.2 mm spread; hypochile broadly and relatively shallowly subglobose, each side with an erect, shortly and broadly elliptic, broadly rounded sidelobe (sides asymmetric, one 3 × 2 mm wide, the other 4.2 × 2.5 mm wide); epichile transversely elliptic, deeply obtusely bilobed, medially with a triangular, obtuse, bipartite callus that arises from the apex of the hypochile margins, 2.5–2.7 × 4.5–4.7 mm, lobules to 2.7 × 2.5 mm. *Column* stout, 3.3 mm long, 1.9 mm wide laterally; anther cap with a minutely serrate front edge.

**Distribution:** Bhutan.

**Habitat:** dense rainforest, 2590 m.

**Etymology:** named after Dr. Nicholas R. Pearce, for his contributions to Bhutanese orchidology as co-author of the *Orchids of Bhutan*.

This species is seemingly indistinguishable vegetatively from *Gastrochilus distichus*, and indeed the type number was listed as that taxon in the *Orchids of Bhutan* (Pearce and Cribb, 2002). However, *G. pearcei* can be distinguished from *G. distichus* and most other taxa in section *Microphyllae* by its labellum having raised sidelobes on the hypochile (vs. truncate hypochile sides without lobes). *Gastrochilus nepalensis* also has raised sidelobes but these are subquadrate and the hypochile is conical (not subglobose). *Gastrochilus pearcei* further differs from *G. distichus* in having the labellum hypochile relatively longer than wide (excluding lobes), whereas in *G. distichus* it is the opposite, the hypochile being shorter than wide. There are also other differences in epichile shape and ornamentation: that of *G. pearcei* is bilobed with two thick medial protrusions arising from the hypochile margins and forming a triangular extension, whereas *G. distichus* has an entire epichile with two well-separated conical calli.

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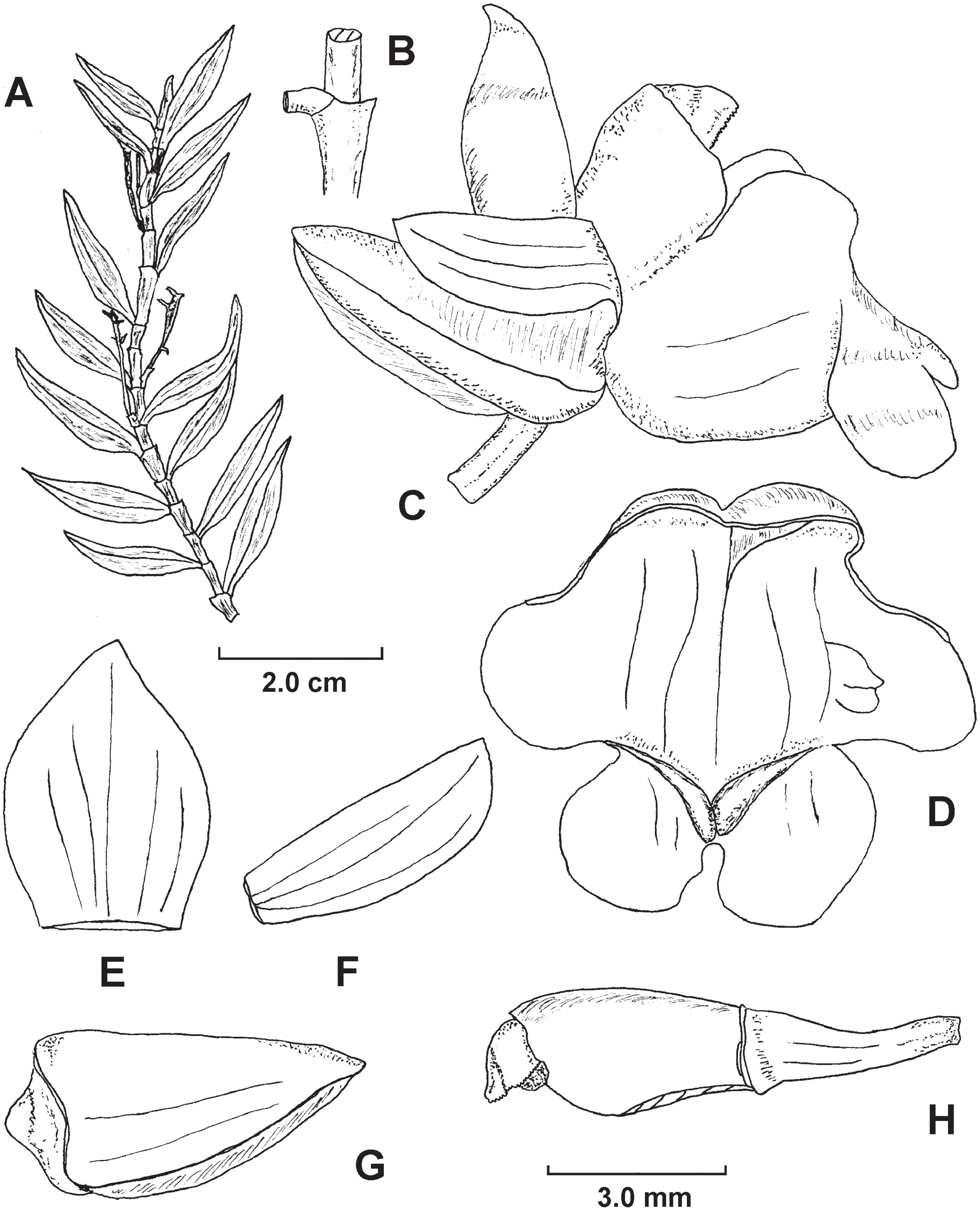

FIGURE 1. *Gastrochilus pearcei* Ormerod & C.S. Kumar. **A**, stem, upper part; **B**, stem section; **C**, flower; **D**, labellum; **E**, dorsal sepal; **F**, petal; **G**, lateral sepal; **H**, column. Drawn by P. Ormerod from the holotype.

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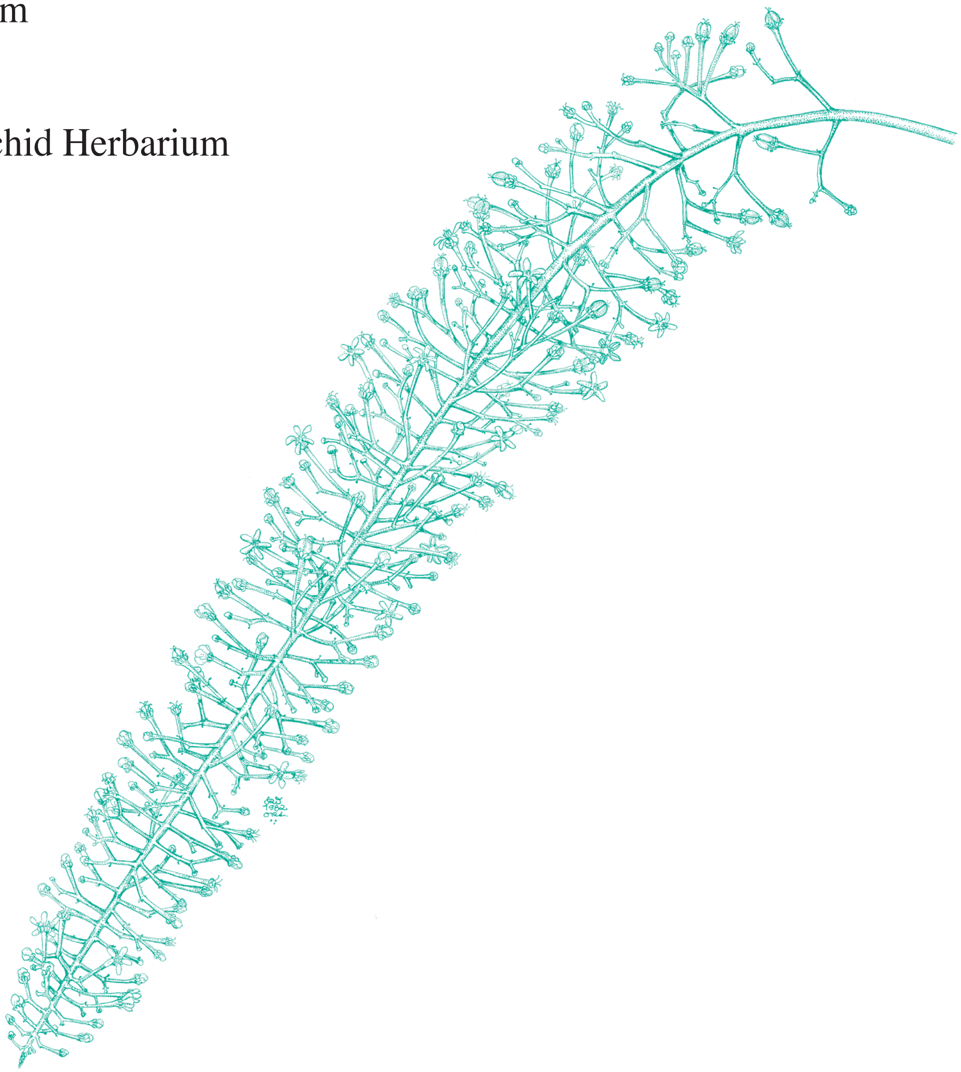

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