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Volume 28, Number 1 June 2023

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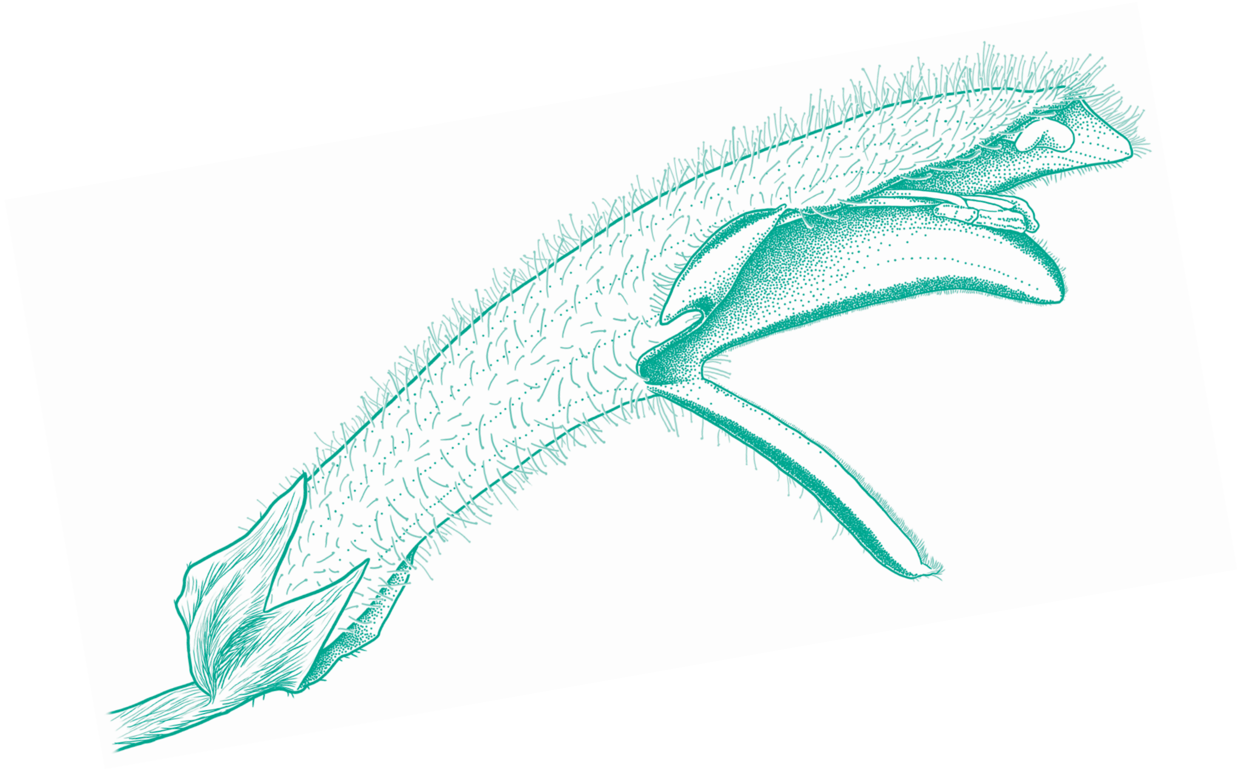

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***Harvard Papers in Botany* Volume 27, Number 2, was published online December 31, 2022.**

Columnea blancoi J.E. Jiménez, Chinchilla & Kriebel (see page 54, Fig. 2D).
Drawn by Darha Solano.

Harvard Papers in Botany

Volume 28, Number 1 June 2023

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

(Continued on page ii)

(Continued from page i)

TWO NEW SPECIES OF *NOLANA* (NOLANEAE–SOLANACEAE) FROM SOUTHERN PERU

Michael O. Dillon[1,3] and Victor Quipuscoa-Silvestre[2]

Abstract. In preparation for the publication of a monograph of *Nolana* L.f. (Nolaneae–Solanaceae), two new species*, Nolana hoxeyi* and *Nolana samaensis*, are described from the southern Peruvian Department of Tacna. These two share relationships and occur in the same geographic area, although not strictly sympatrically. Series of diagnostic morphological characteristics allow for discrimination of these two from all other species of *Nolana* with narrow leaves recorded from the Department of Tacna. Descriptions, illustrations, and a distribution map are provided for the new species. Typifications are provided for several taxa of *Nolana*.

Keywords: Solanaceae, *Nolana*, flora of Peru, coastal lomas, new species

Resumen. En preparación de la monografía de *Nolana* L.f. (Nolaneae–Solanaceae) para su publicación, se describen dos nuevas especies del departamento de Tacna en el Sur de Perú, *Nolana hoxeyi* y *Nolana samaensis*. Estas dos especies están relacionadas y se distribuyen en la misma área geográfica, aunque no son estrictamente simpátricas. Muchos caracteres morfológicos diagnósticos permiten diferenciar a estas dos, de las demás especies de *Nolana* con hojas angostas registradas en el departamento de Tacna. Se describen, ilustran y se proporciona un mapa de distribución para las dos nuevas especies. Se dan a conocer además, tipificaciones para varios taxones de *Nolana*.

Pablabras clave: Solanaceae, *Nolana*, flora del Perú, lomas costeras, nuevas especies

Nolana L.f. (Nolaneae-Solanaceae) is an easily recognized genus possessing a unique, mericarp fruit type within the family. With the addition of the two new species described here, the genus comprises 92 species confined to Peru and Chile and one endemic species in the Galapagos Islands, Ecuador (Dillon, 2005; Dillon, 2016). *Nolana* is among the five or six largest genera in the family and has its greatest species diversity in coastal southern Peru and northern Chile (Dillon, 1997; Dillon and Hoffmann, 1997). These regions are dominated by vegetation termed *lomas* formations, which exist as virtual islands of highly endemic communities all utilizing available moisture from fog (*camanchaca* or *garua*) (Rundel et al., 1991; 2007). While most species of *Nolana* have their distributions in near-shore habitats, a few occur in habitats far removed from oceanic influence at elevations over 2000 m.a.s.l., *Nolana* stands out as the most wide-ranging and conspicuous floristic element of these formations. In many modern classifications, members of *Nolana* have been recognized at familial (Nolanaceae) or subfamilial (Nolanoideae) rank due to their unusual carpel morphology, but data from molecular studies have provided unequivocal evidence that *Nolana* is nested within the Solanaceae (Dillon et al., 2007b; 2009). We have described several new species from Peru (Dillon et al., 2007a; Quipuscoa and Dillon, 2018) and the species described here do not conform to any previously encountered within *Nolana* (Dillon, 2016).

Materials and Methods

During studies of *Nolana* throughout Peru and Chile, we have encountered taxa that were obviously *Nolana* (Solanaceae) but could not be associated with any of the previously described species. The first new *Nolana* described here was represented by two herbarium sheets housed at USM, one identified as *Nolana lycioides* I. M. Johnst. (*Mueller & Chávez 3591*, USM-81298) and the other as *N. coelestis* (Lindl.) Miers ex Dunal (*Mueller et al. 12236*, USM-64133), a Chilean species quite unrelated and differing in many fundamental morphological features. The images of the herbarium specimens at USM exhibited a growth habit and inflorescence different from any species of Chilean or Peruvian *Nolana* known to us. What led to the recent discovery of this taxon were photographs by Paul Hoxey that contained geographic coordinates. In late November 2021, a field trip to the Department of Tacna was undertaken to locate and document this putative new species. Now, with ample, well-documented material available, it is possible to describe it here.

Examination of populations in the field allowed us to observe salient characteristics that are easily seen in the living state but are generally lost with drying. After studying the populations of *Nolana* and their ecological parameters, the species we describe here are based on diagnostic morphological characteristics supported by a geographic fidelity. We have also examined more than 2,600 herbarium collections and undertaken field work that has encompassed the entire geographic range of the genus. This background has given us a sound basis for describing this and the following species as new.

We thank the collection managers of F and USM for allowing us to consult their collections. We thank Maricruz Bedoya Cuno for preparing the illustrations and Margarita Esther Balvin Aguilar for preparation of the distribution map. We thank Paul Hoxey for providing photographs and geographic data of these species. We thank our field companions Cristian Tejada Pérez and Jhon Muñuico Mamani for their friendship and collaboration while collecting these new species and for making our botanical excursion a success. David Boufford is acknowledged for his useful comments in an early version of this paper.

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Table 1. Comparison of diagnostic morphological characteristics of narrow-leaved species of *Nolana* L.f. recorded from Department of Tacna, Peru.

Characters	***N. hoxeyi***	***N. samaensis***	***N. confinis***	***N. lycioides***	***N. gracillima***
Habit	shrubs	subshrubs	perennial herbs to suffrutescent	suffrutescent	herb
Inflorescence	racemose	solitary flowers	solitary flowers	solitary flowers	solitary flowers
Calyces Size	3–4.5 (–5) mm long × 2–3.5 mm at anthesis; tube 1.5–2 mm long × 2–2.5 mm diam., lobes 2.5–3 mm long × 1–1.5 mm wide	5–6.5 mm long × 4–5(–6) mm at anthesis; tube 1–1.5 mm long × 1–1.5 mm diam., lobes 4–5 mm long × 1–1.2 mm wide	3–3.5(–4) mm long × 2.5–3.5 mm at anthesis; tube 0.5–1 mm long × 1.8–2 mm diam., lobes 2.5–3 mm long × 1 mm wide	4–5.5 mm long × 3–4(–5) mm at anthesis; tube 0.5–1 mm long × 1.5–2.5 mm diam., lobes 2.5–3 mm long × 1–1.2 mm wide	5–5.5(–6) mm long × 3–4 mm at anthesis; tube 2–2.5 mm long × 1.8–2 mm diam., lobes 3–3.5 mm long × 1–1.3 mm wide
Surface	densely strigose	densely pilose	lanuginous	scabrous-glandular	glabrous to glabrescent
Corolla Size	10–13(–15) mm long × 15–20 mm at anthesis	9–11(–13) mm long × 10–15 mm at anthesis	10–13 mm long × 7–9(–10.2) mm at anthesis	13–22(–27) mm long × 11–13(–15) mm at anthesis	9–12 mm long × 7–9(–12) mm at anthesis
No. of Mericarps	7–10(–12)	6–8(or 9)	4 or 5(or 6)	5–9	4 or 5
Mericarp Size	2–2.5 mm long	1–2.5 mm long	1.5–2.5 mm long	1.6–2.5 mm long	(1–)1.5–2 mm long
Mericarp Surfaces	rugose-punctate	rugose-punctate	rugose-punctate	punctate	rugose

Taxonomy

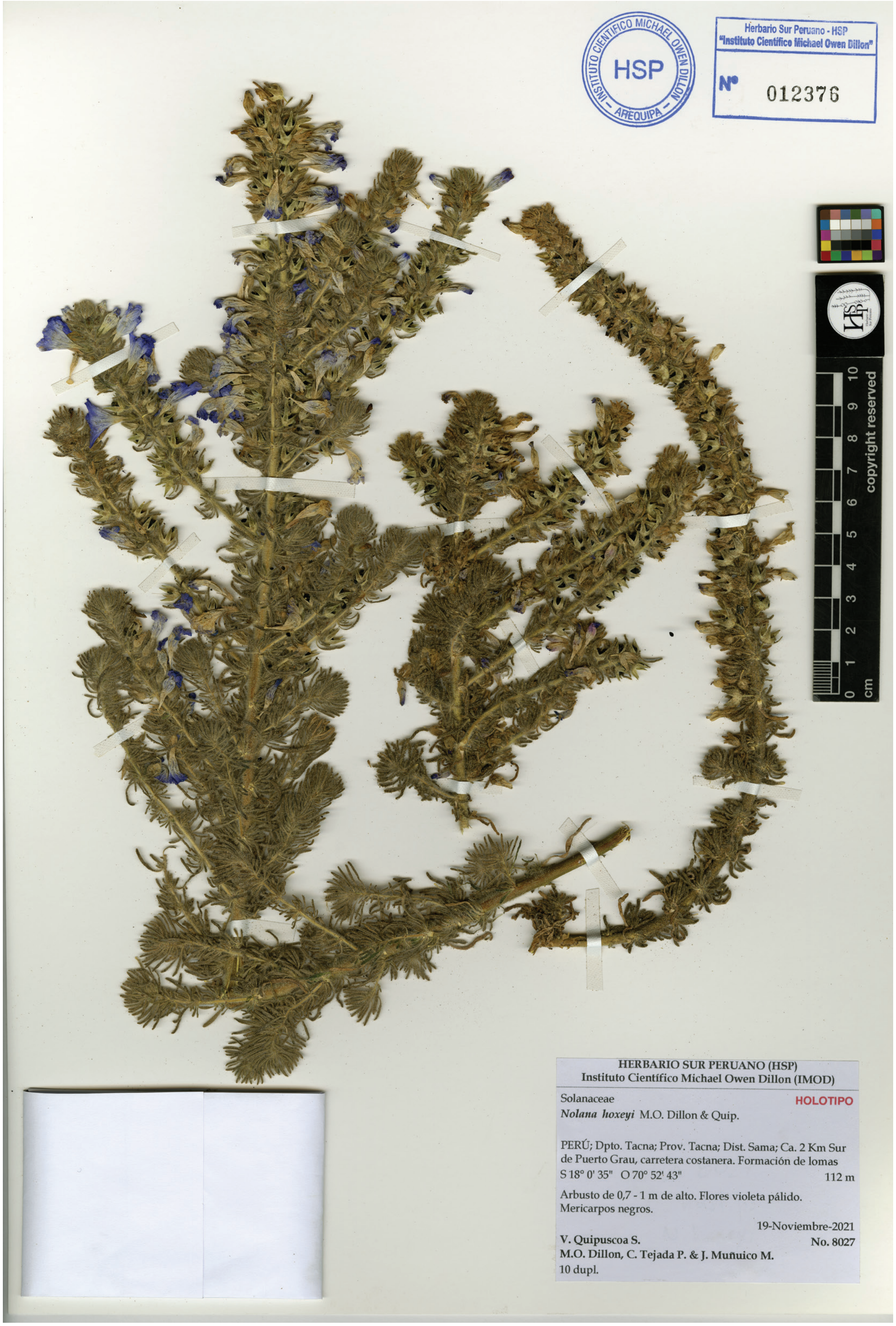
Nolana hoxeyi M. O. Dillon & Quip. *sp. nov.* TYPE. PERU. Tacna: Prov. Tacna, Dist. Sama, ca. 2 km Sur de Puerto Grau, carratera costanera, 18°00'35"S, 70°52'43"W, 112 m.a.s.l., 19 Noviembre 2021, *V. Quipuscoa S., M. O. Dillon, C. Tejada P. & J. Muñuico M. 8027* (Holotype: HSP [12376]; Isotypes: HSP [12377], F [2330851], HUT, USM). Fig. 1–6.

Nolana hoxeyi can be distinguished from all other species in the genus by the following combination of characteristics: shrubs to 1 m tall; leaves elliptic to linear-oblanceolate, strigose; inflorescences compact, densely racemose, 30–40 cm long; mericarps 7–10(–12).

Shrubs, 50–100 cm tall. *Stems* intricately branched, erect, 50 cm long, young branches densely velutinous to villous, occasionally capitate-glandular. *Leaves* alternate, fasciculate, sessile to subsessile; petiole canaliculate, blade elliptic, linear-oblanceolate, 7–11 mm long, 1–1.5(–2) mm wide, densely strigose, succulent, entire, base attenuate, apex rounded to obtuse. *Inflorescences* compact or densely racemose, 30–40 cm long; flowers subtended by leaf-like bracts, 4–5 mm long, ca. 1 mm wide, strigose; pedicels cylindrical, densely pubescent, strigose, 1–5 mm long. *Flowers* 5-merous; calyx narrowly campanulate, 2–2.5 mm wide at anthesis, densely strigose, 5-lobed, the tube 1–1.5(–2) mm long, 1–1.5 mm in diam., lobes lanceolate, unequal, 2–3 mm long, 1–1.5 mm wide, apex acute; corolla zygomorphic, infundibuliform, 15–20 mm wide at anthesis, 10–13 (–15) mm long, light lavender or lilac, throat clear, externally and internally glabrous; stamens 5, included, filaments inserted on lower third of corolla, unequal, 2 filaments 9–10 mm long, 3 filaments 6–8 mm long, glabrous; anthers dithecal, light purple, thecae ca.1 mm long, ca. 1 mm wide, glabrous; ovary glabrous, ca. 1 mm long, 0.5–1(–1.5) mm wide, nectary basal, carpels 7–9, style included, 7–9 mm long, stigma bilobed, light green, ca. 0.5 mm long. *Mericarps* 7–10(–12), 2-seriate, round, black, rugose-punctate, (1–)2–2.5 mm long, 3 or 4 large, 7 or 8 smaller, included within expanding calyx; seeds 1–5. Chromosome number: unknown.

Etymology: The epithet of *Nolana hoxeyi* commemorates Paul D. Hoxey, a prolific collector and author of publications on the Cactaceae, especially those of Central and South American genera. His photographs and documentation were critical in locating populations of this new species. He splits his residency between Cambridge, England, and Arequipa, Peru.

Distribution and Ecology: Peru, Department of Tacna; 100–600 m; restricted to sandy soils, most commonly from near-ocean localities near sea level, and to ca. 10 kms inland reaching 600 m.a.s.l.



HERBARIO SUR PERUANO (HSP)
Instituto Científico Michael Owen Dillon (IMOD)

Solanaceae HOLOTIPO
Nolana hoxeyi M.O. Dillon & Quip.

PERÚ; Dpto. Tacna; Prov. Tacna; Dist. Sama; Ca. 2 Km Sur de Puerto Grau, carretera costanera. Formación de lomas
S 18° 0' 35" O 70° 52' 43" 112 m

Arbusto de 0,7 - 1 m de alto. Flores violeta pálido. Mericarpos negros.

19-Noviembre-2021
V. Quipuscoa S. **No. 8027**
M.O. Dillon, C. Tejada P. & J. Muñuico M.
10 dupl.

FIGURE 1. Holotype of *Nolana hoxeyi* M. O. Dillon & Quip. from HSP, Arequipa, Peru [HSP-12376].

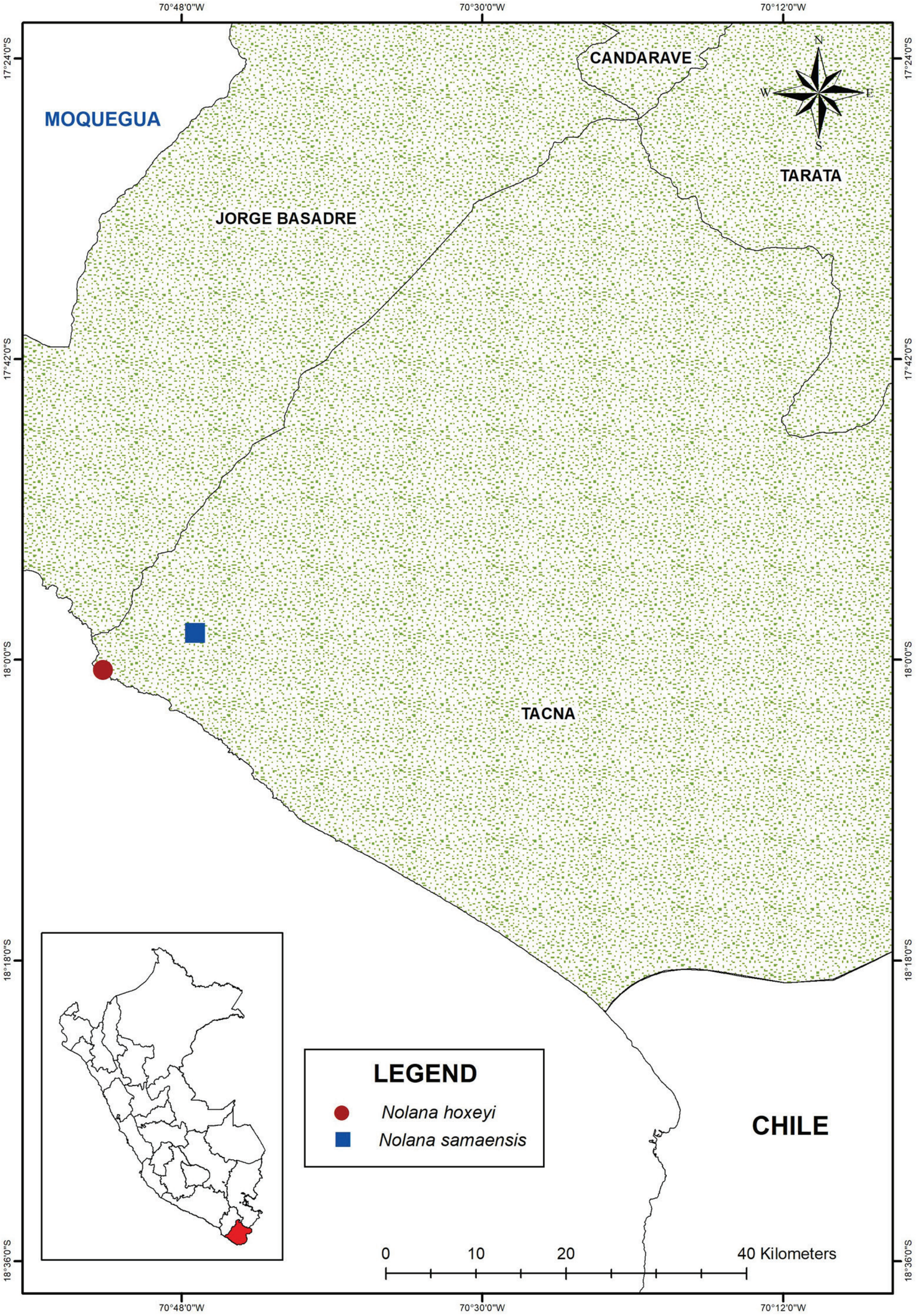


FIGURE 2. Map of known distribution of *Nolana hoxeyi* M. O. Dillon & Quip. and *N. samaensis* M. O. Dillon & Quip. in Department of Tacna, Peru. (Prepared by Margarita Balvin Aguilar).

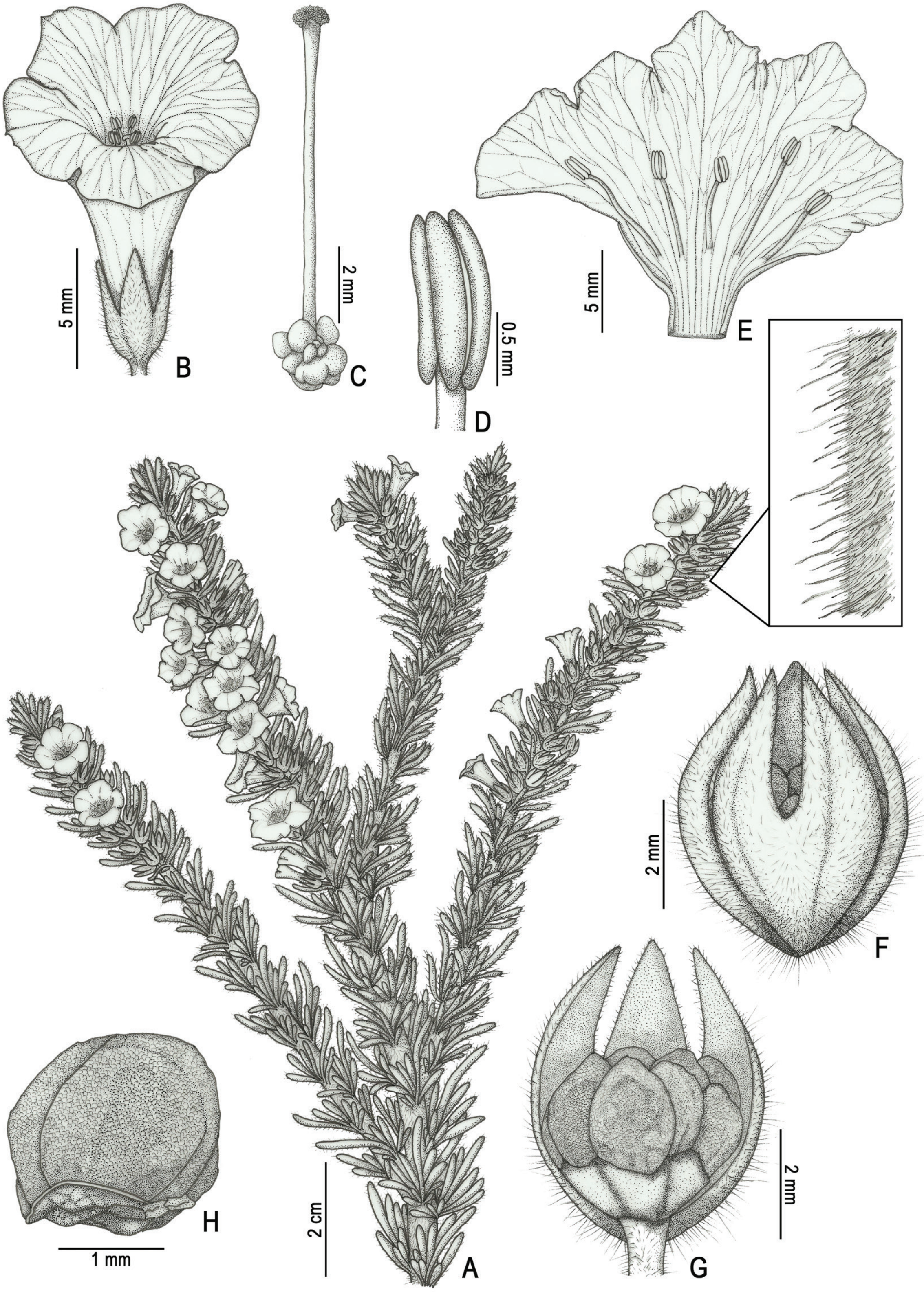


FIGURE 3. Illustration of *Nolana hoxeyi* M. O. Dillon & Quip. **A**, habit with enlargement of surface pubescence; **B**, flower; **C**, ovary and style. **D**, anther; **E**, dissected corolla; **F**, calyx; **G**, dissected calyx with mericarps; **H**, mericarp. Line drawing by Maricruz Bedoya Cuno based on the holotype.

FIGURE 4. Photograph of type locality for *Nolana hoxeyi* M. O. Dillon & Quip., ca. 2 km Sur de Puerto Grau on carratera costanera, Tacna, Peru.

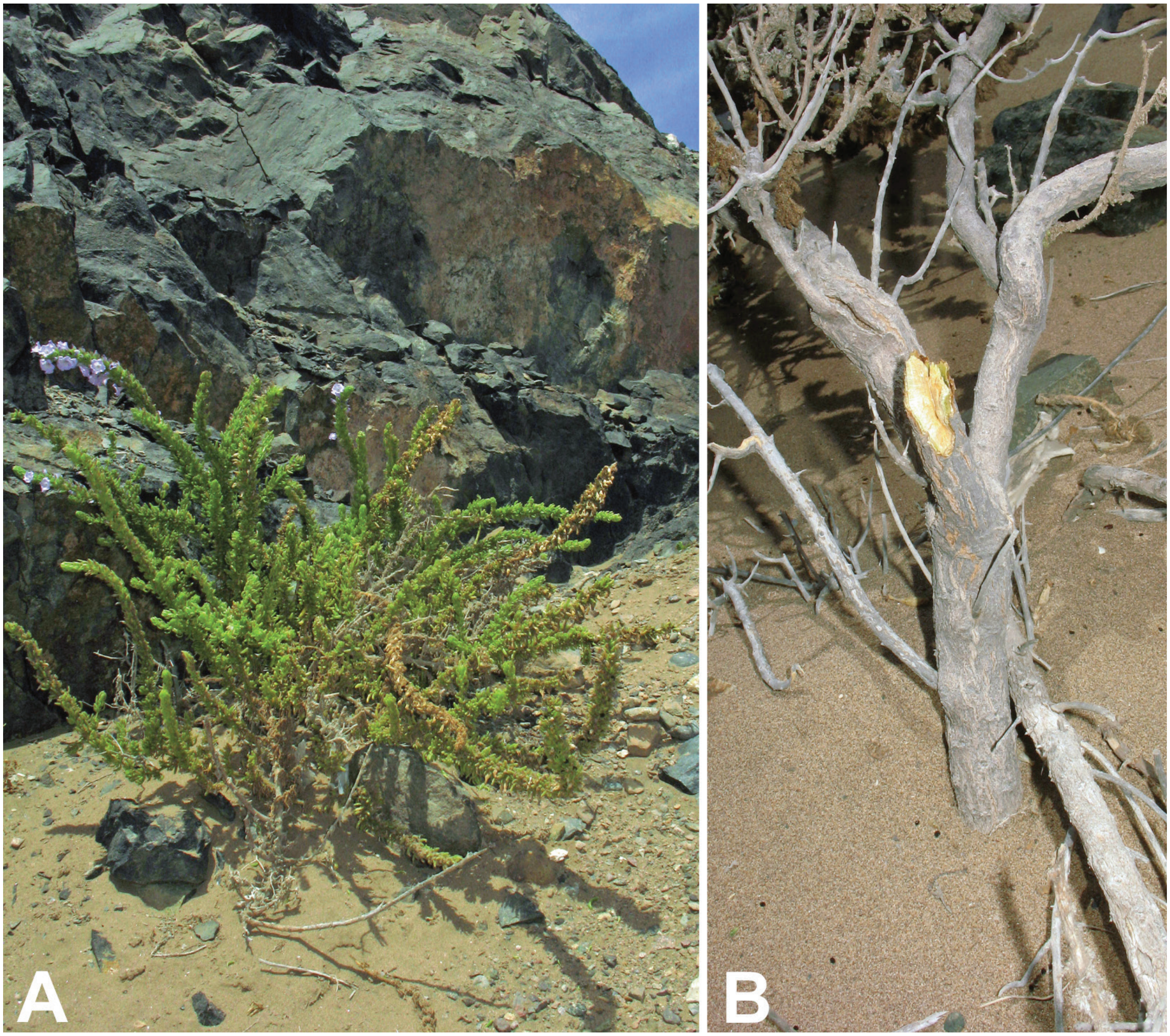


FIGURE 5. *Nolana hoxeyi* M. O. Dillon & Quip. **A**, habit; **B**, woody trunk.

Nolana hoxeyi is endemic to a small area in the Province of Sama, Department of Tacna. It is recorded from near-ocean habitats from 100 to 600 m.a.s.l. and within a few kilometers of the ocean. It is decidedly different with its non-branching, sinuate stems and densely set fasciculate leaves. There are no evident internodes; only stems covered with dense leaves on all surfaces. The apical portion of the stems are obviously racemose inflorescences that appear spicate with many flowers over the apical 20–50 cm (Fig. 6).

Nolana hoxeyi was first recognized as a potentially new species while we examined photographs of the two G. K. Muller collections identified as *Nolana lycioides* I. M. Johnst. (*Mueller & Chávez 3591*, USM-81298) and another identified as *N. coelestis* (Lindl.) Miers ex Dunal (*Mueller et al. 12236*, USM-64133), a Chilean species quite unrelated and differing in many fundamental morphological characteristics. Both sheets were collected in the Morro Sama region. MOD did not have an opportunity to examine the herbarium collections at USM, but the photographs were intriguing. When living plants were encountered on 19 November 2021 it was obvious that they represented a species new to science.

Nolana hoxeyi does not closely resemble any other species of the genus, but it does share some characteristics with the following taxon described here, *N. samaensis*. These two species share similar mericarp shape and size but differ in mericarp number. The densely leafy stems and distinct, densely racemose inflorescences are unique. The most common inflorescences in *Nolana* are solitary flowers borne in leaf axels, but sometimes, as in *N. inflata* Ruiz & Pav. and *N. weissiana* Ferreyra, they display weakly cymose inflorescences; in *N. scaposa* Ferreyra, the inflorescence is easily recognized and well-developed. The only other species of *Nolana* with such densely set leaves are *N. galapagensis*

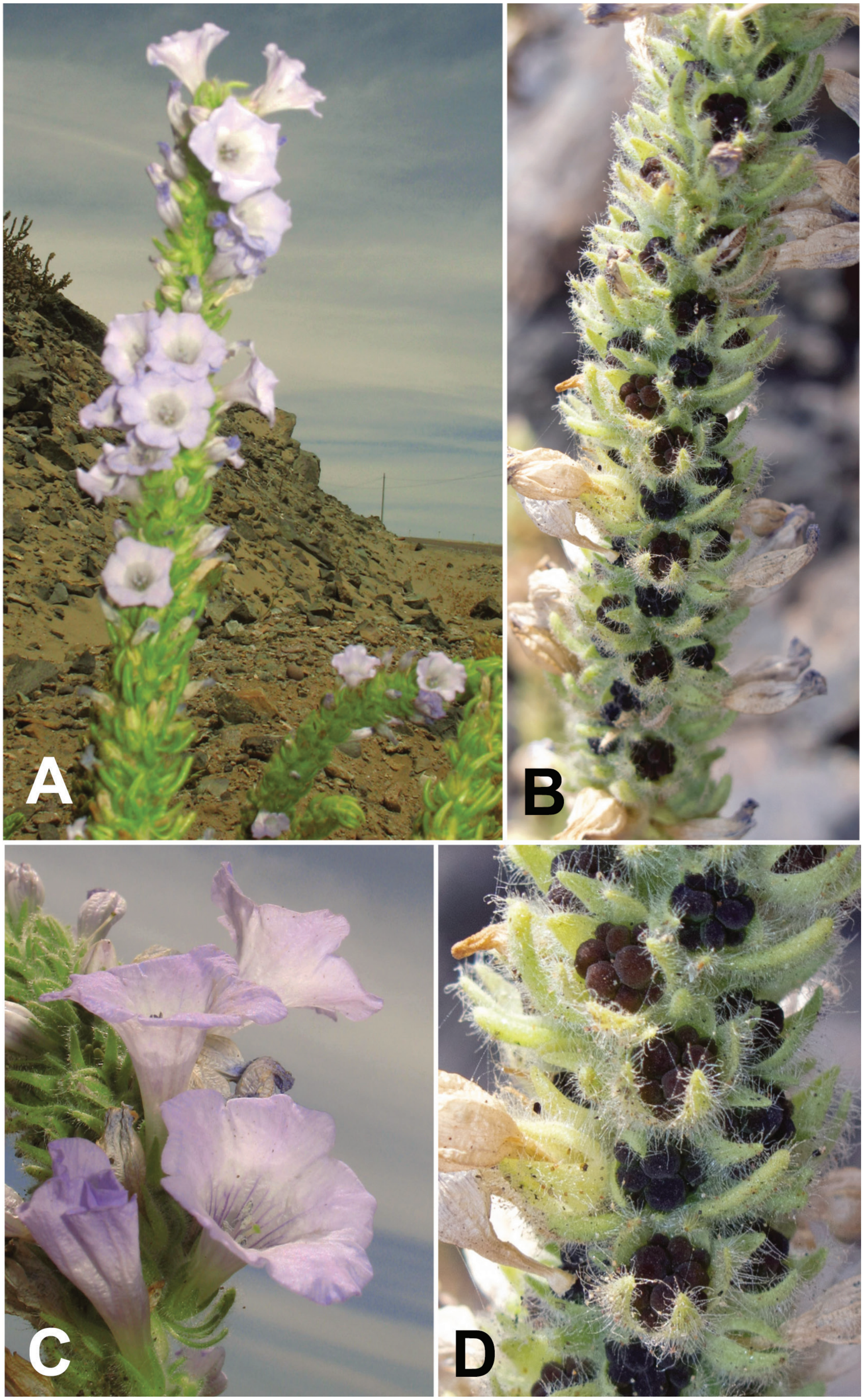


FIGURE 6. *Nolana hoxeyi* M. O. Dillon & Quip. **A**, inflorescence; **B**, closeup of fruiting inflorescence; **C**, flower; **D**, mericarps.

(Christoph.) I. M. Johnst., *N. onoana* M. O. Dillon & M. Nakaz. of northern Chile, and *N. tricotiflora* Quip. & M. O. Dillon of southern Peru. They all have very different flowers, different mericarp number and different mericarp shape.

Associated species recorded at the type locality included *Ephedra americana* Humb. & Bonpl. ex Willd. (Ephedraceae), C*ristaria multifida* (Dombey ex Cav.) Cav., *Palaua dissecta* Benth. (both Malvaceae), *Perityle emoryi* Torrey in W. H. Emory, *Trixis cacalioides* (Kunth) D. Don (both Asteraceae), *Suaeda foliosa* Moq., *Chenopodium murale* L. (both Amaranthaceae), *Spergularia collina* I. M. Johnst. (Caryophyllaceae), *Nolana adansonii* (Roem. & Schult.) I. M. Johnst., *Solanum multifidum* Lam. (both Solanaceae) and at upper reaches associated with *Neoraimondia arequipensis* (Meyen) Backeb. and other cacti.

Additional specimens examined: PERU. Tacna: Morro Sama, September 1980, 250 m.a.s.l., *G. K. Muller & R. Chávez 3591* (USM-64133); Morro de Sama, 6 August 1985, *G. K. Muller, G. Krebs & R. Chávez 12236* (USM-81298).

Nolana samaensis M. O. Dillon & Quip., *sp. nov.* TYPE. PERU. Tacna: Prov. Tacna, Dist. Sama, Lomas de Sama, 17°58'23"S, 70°46'12"W, 503 m.a.s.l., 19 Noviembre 2021, *V. Quipuscoa S., M. O. Dillon, C. Tejada P. & J. Muñuico M. 8029* (Holotype: HSP [12378]; Isotypes: HSP [12379], F [F-2330852], HUT, USM). Fig. 2, 7–9.

Nolana samaensis can be distinguished from all other species in the genus by the following combination of characteristics: subshrubs to ca. 30 cm tall; leaves linear to obovate, 4–7 mm long, densely pilose; inflorescences of solitary flowers; mericarps 6–9.

Subshrubs to ca. 30 cm tall. *Stems* intricately branched, erect to decumbent, to ca. 20 cm long, densely villous with capitate-glandular trichomes. *Leaves* alternate, fasciculate, sessile or subsessile, internodes to 1 cm long; blade linear, oblanceolate or obovate, 4–7 mm long, 1–1.5 mm wide, pilose, succulent, entire, base attenuate, margins entire, apex rounded to obtuse. *Inflorescences* of solitary flowers in leaf axils; pedicel cylindrical, densely pubescent, 1–2 mm long. *Flowers* 5-merous; calyx narrowly campanulate, 4–5(–6) mm wide at anthesis, densely pilose, 5-lobed, tube 1–1.5 mm long, 1.5–2 mm in diam., lobes oblong-lanceolate, unequal, 4–5 mm long, ca. 1.2 mm wide, apex acute; corolla zygomorphic, infundibuliform, 10–15 mm wide at anthesis, 9–11(–13) mm long, light lavender or lilac, throat with dark purple ring, externally pilose, trichomes uniseriate, internally glabrous; stamens 5, included, filaments inserted on lower third of corolla, unequal, (5–)7–8 mm long, glabrous at bases; anthers dithecal, purple, thecae ca. 0.5 mm long, ca. 0.5 mm wide, glabrous; ovary glabrous, ca. 1 mm long, 1–1.2 mm wide, basal nectary ca. 1 mm wide, carpels 5, style included, 6–7 mm long, stigma bilobate, purple, ca. 0.3 mm long. *Mericarps* 6–8(or 9), 2-seriate, polyhedrons, black, rugose-punctate, 1–2.5 mm long, 2–4 large, 4 or 5 small, included within expanding calyx; seeds 1–5. Chromosome number: unknown.

Etymology: The specific epithet is from the latinisation of the geographic locality of the type collection, Sama in Department of Tacna.

Distribution and Ecology: Peru, Department of Tacna; 100–600(–810) m.a.s.l.; restricted to sandy soils and inland localities within 10 km of the ocean.

Nolana samaensis is distinguished by a combination of characters not met in other species. It is a subshrub with small, densely pubescent leaves less than 10 mm long and 1.5 mm wide. The shape, size and pubescence of the calyx lobes in *N. samaensis* are distinctive amongst other southern Peruvian congeners. Two species recorded from Department of Tacna, *N. confinis* and *N. lycioides*, are shrubby and have similar sized leaves but very different pubescence. Their calyx lobes are longer, long-attenuate, and densely lanuginous or with short-stipitate glandular trichomes. *Nolana hoxeyi* and *N. gracillima* both have much longer leaves to 25 mm long; *N. gracillima* lacks leaf pubescence while *N. hoxeyi* leaves are densely strigose.

The flora at the type locality was depauperate, with only *Palaua dissecta* and *Nolana pallidula* I. M. Johnst. recorded.

Typifications

Nolana aenigma M. O. Dillon, S. Leiva & Quip., Arnaldoa 14: 172. 2007.

TYPE. PERU. La Libertad: Prov. Trujillo, Dist. Trujillo, Km 580, Cerro Cabezón, 10 February 1998, *S. Leiva G., M. O. Dillon, A. Sagástegui A., & V. Quipuscoa S. 2165* (Holotype: HAO, destroyed; Lectotype, designated here: HUT [031950]; Isolectotype: F [F-2329912]).

Nolana coronata Ruiz & Pav., Fl. Peruv. [Ruiz & Pavón] 2: 7, tab. 112b. 1799.

TYPE. PERU. Arequipa: Prov. Camaná, entre Pongo y Atiquipa, 30 November 1777, *J. Tafalla s.n.* [*Hb. Pavón 434*] (Lectotype, designated here: MA [815123]; Isolectotypes: B-W [03451-010], F [F-712543, F-843660, F-845176, F-845335, F-341432, F-341434, F-341435, F-341436], G [G-23240, G00383540, G00383541], HAL [HAL0115088], K [K000532272], MA [MA815121, MA815122, MA817983], MPU [MPU012108]).

Nolana crassulifolia Poepp., Not. Natur- Heilk. 23: 276. 1829.

TYPE. CHILE. Valparaíso: "in rupibus marit. ubique prope Concón," *E. F. Poeppig 67* (Lectotype, designated here, W [1889-0301807]; Isolectotypes: BM [BM000021201], HAL [HAL115090], P [P00605847], W [W0075445]).

Nolana gayana (Gaudich.) Koch, Ind. Sem. Berol. 12. 1855.

> Basionym: *Alibrexia gayana* Gaudich., Voy. Bonite, pl. 105. 1851; p. 81. 1866. **TYPE**. PERU. Lima, based upon material collected at Callao or Lurín, 11–21 July 1836, *C. Gaudichaud s.n.* [Johnston (1936) accepted the illustration as the type until the type collection could be located. Neotype, designated here: PERU, Lima, "Tablada de Lurín," *A. Mathews 837* (E00793138); Isoneotypes: BM [BM000941268], E [E00793139], K).

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Solanaceae HOLOTIPO
Nolana samaensis M.O. Dillon & Quip.

PERÚ; Dpto. Tacna; Prov. Tacna; Dist. Sama; Lomas de Sama. Formación de lomas.
S 17° 58' 23" O 70° 47' 12" 503 m

Sufrútice de 0,15 - 0,3 m de alto. Flores lavandas. Mericarpos negros.

19-Noviembre-2021
V. Quipuscoa S. **No. 8029**
M.O. Dillon, C. Tejada P. & J. Muñuico M.
7 dupl.

FIGURE 7. Holotype of *Nolana samaensis* M. O. Dillon & Quip. from HSP, Arequipa, Peru [HSP-12378].

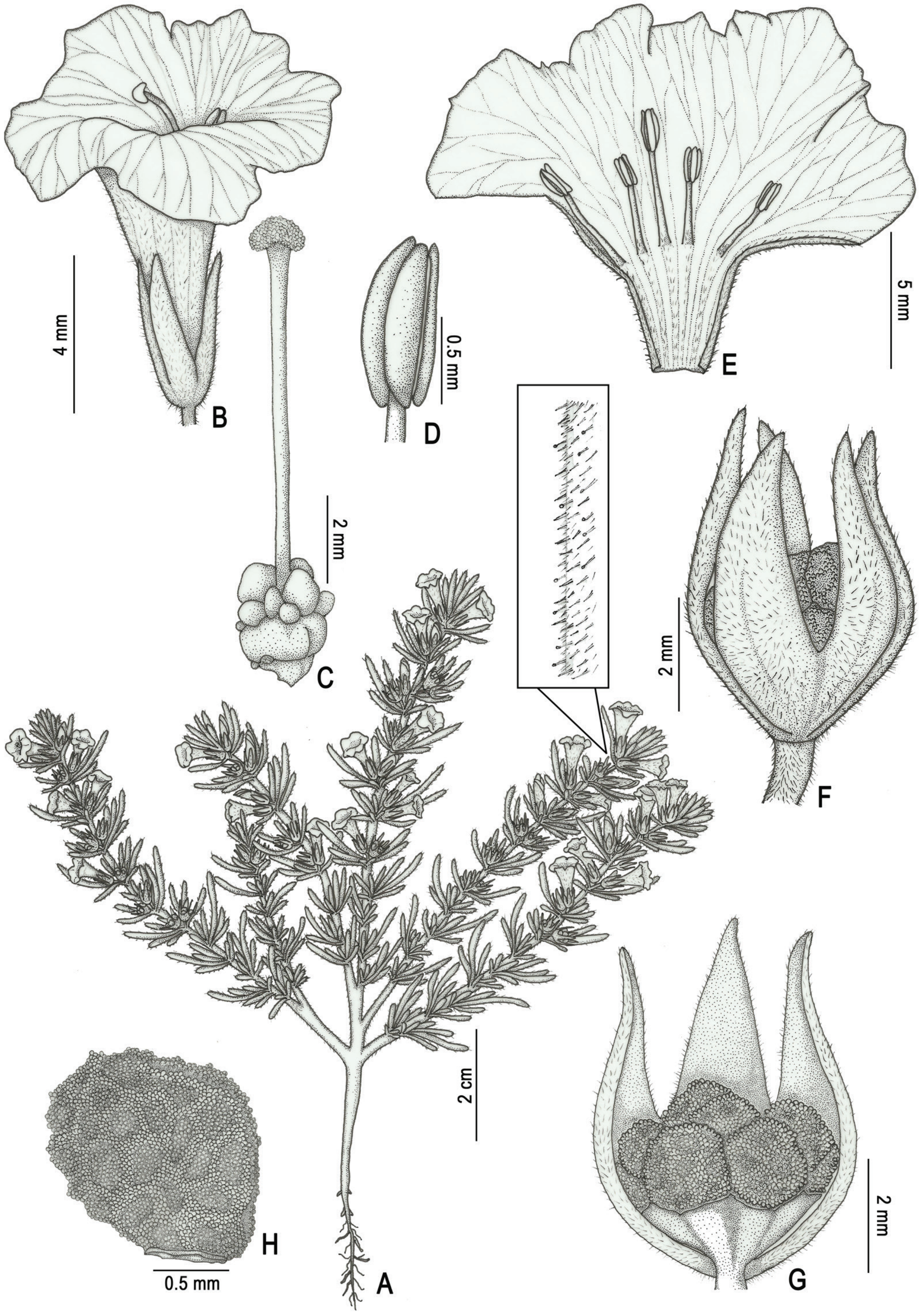

FIGURE 8. Illustration of *Nolana samaensis* M. O. Dillon & Quip. **A**, habit with enlargement of surface pubescence; **B**, flower; **C**, ovary and style; **D**, anther; **E**, dissected corolla; **F**, calyx; **G**, dissected calyx with mericarps; **H**, mericarp. Line drawing by Maricruz Bedoya Cuno based on the holotype.

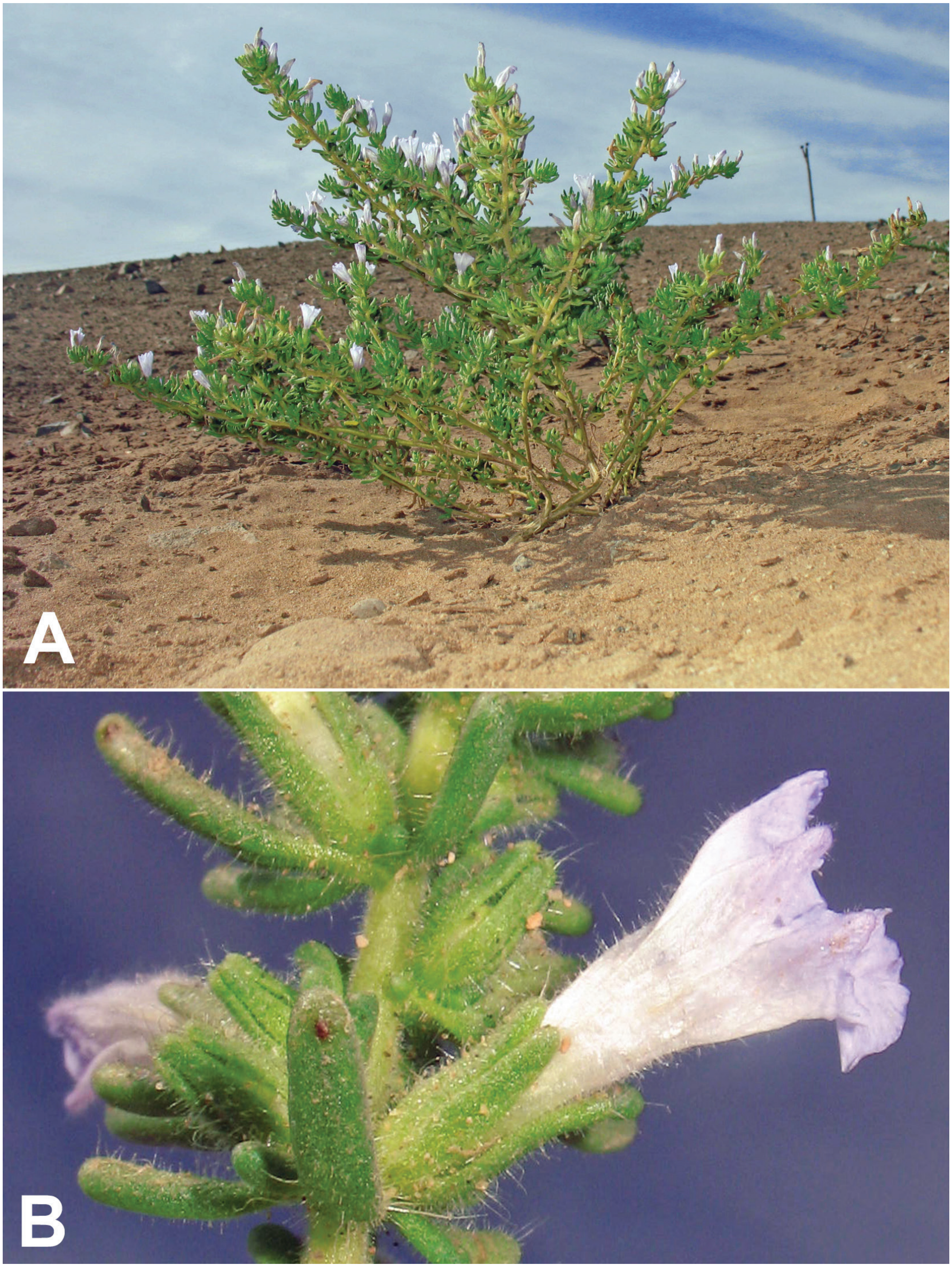

FIGURE 9. *Nolana samaensis* M. O. Dillon & Quip. **A**, habit; **B**, closeup of flowering branch.

Nolana inflata Ruiz & Pav., Fl. Peruv. [Ruiz & Pavón] 2: 7, tab. 112a. 1799.

TYPE. PERU. Arequipa: Prov. Camaná, *J. Tafalla s.n.* (Lectotype, designated here: MA [815130] ; Isolectotypes: B [B-W03450-010], F [F-712544, F-843609, F-845149], FI-Webb [FI009586], G [G00383940, G00303942, G00383943], HAL [HAL115089], K [K000532269], MA [MA815125, MA815126, MA815127, MA815129, MA815131, MA817979, MA817682, MA817683], MPU [MPU0012109], P [P00605856]).

Nolana lezamae M. O. Dillon, S. Leiva & Quip., Arnaldoa 14: 184. 2007.

TYPE. PERU. Ancash: Prov. Corongo, Dist. Corongo. Tres Cruces (entre La Pampa-Yuramarca), 8°41'S, 77°55'W, 2144 m.a.s.l., 30 June 1998, *S. Leiva G., V. Quipuscoa, P. Lezama A. & E. López 2212* (Holotype: HAO, destroyed; Lectotype, designated here: HUT [032058], Isolectotypes: E, F [F-2329913], G, GH, HSP).

Nolana sedifolia Poepp., Not. Natur- Heilk. 23: 276. 1829.

TYPE. CHILE. Valparaíso: “in rupibus maritus ubique prope Concón,” *E. F. Poeppig 68* (Lectotype, designated here: W [1889-0301807]; Isolectotypes: BM [BM000941358], F [F-870466], GH [GH00282361], HAL [HAL-115091], K [K000532209], W [W0075450].

Heterotypic synonym: *Fabiana lanuginosa* Hook. & Arn., Bot. Beechey Voy. 1: 35. 1830. **TYPE**. CHILE. Coquimbo: Coquimbo, Capt. F. W. Beechey Voyage, *A. Collie & G. T. Lay* s.n. (Lectotype, designated here: (E [00369176]).

Nolana spathulata Ruiz & Pav., Fl. Peruv. [Ruiz & Pavón] 2: 7, tab. 113a. 1799.

TYPE. PERU. Arequipa: Prov. Camaná, “Pongo et Atiquipa,” *J. Tafalla s.n.* [*435*] (Lectotype, designated here: MA [815133]; Isolectotypes: B [B-W03449], BC, F [F-843636, F-845155], FI [FI132659], G [G00383935, G00383937, FM neg 23244], MA [MA815132, MA815134, MA811535, MA817982], MPU [MPU012112]).

Discussion

Several taxa of *Nolana* require nomenclatorial changes that are best addressed here. In Mesa (1981), the last monograph for the genus, lectotype designations were provided for nearly 50 taxa. Now, for a variety of reasons, additional lectotypifications and neotypifications are required. For *Nolana aenigma* and *N. lezamae*, the holotypes were destroyed in at catastrophic fire in the Herbario Antenor Orrego (HAO) on 6 June 2010. Material deposited in Herbario Universidad de Trujillo (HUT) has been chosen as lectotypes for those two species.

In the instance of *Nolana coronata*, *N. inflata* and *N. spathulata*, Mesa (1981) designated an institution (MA) from the duplicates distributed to various herbaria, but there were several duplicates. Because no single specimen was designated as the lectotype, following the *Shenzhen Code* (Turland et al., 2018), the names are here lectotypified with one of them.

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AN UPDATED SYNOPSIS AND KEY TO THE SPECIES *MONNINA* IN THE VENEZUELAN FLORA (POLYGALACEAE, POLYGALEAE), INCLUDING TWO NEW RECORDS

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Abstract. A new checklist and key to the species of *Monnina* in the flora of Venezuela, which currently includes 16 species, are presented. *M. salicifolia* and *M. smithii*, the former previously known along the Andes from Colombia, Ecuador, Peru, and Bolivia, and the latter from Colombia, are reported here as new country records. Through the revision of the nomenclature and typification of Venezuelan *Monnina* species, six leptotypifications (*M. aestuans*, *M. cladostachya*, *M. densa*, *M. elongata*, *M. mollis* and *M. solandrifolia*) and one neotypification (*M. meridensis*) are designated. In a geographical and taxonomical context, *Monnina coriacea* is considered a synonym of *M. meridensis*, whereas *M. densa* and *M. duidae* are regarded here as distinct from *M. aestuans* and *M. cacumina*, respectively.

Keywords: Andes, Flora of Venezuela, Lectotypification, *Monnina*, Polygalaceae

Resumen. Se presenta una nueva lista y clave de las especies de *Monnina* para la Flora de Venezuela, las cuales incluyen 16 especies. Se registran para la flora de Venezuela a *M. salicifolia* y *M. smithii*, dos especies previamente conocidas de los Andes de Colombia, Ecuador, Perú y Bolivia la primera, y Colombia la segunda. A traves de la revisión de la nomenclatura de las especies venezolanas de *Monnina*, se proponen seis leptotipificaciones (*M. aestuans, M. cladostachya*, *M. densa*, *M. elongata*, *M. mollis* and *M. solandrifolia*) y una neotipificación (*M. meridensis*). En un contexto geográfico y taxonómico, *Monnina coriacea* es considerada sinonimo de *M. meridensis*, mientras que *M. densa* y *M. duidae* son consideradas diferentes de *M. aestuans* y *M. cacumina*, respectivamente.

Palabras clave: Polygalaceae, Lectotipificación, Flora de Venezuela, *Monnina*, Andes

Monnina s. l. Ruiz & Pav. is an New World genus of Polygalaceae with ca. 170 species. The genus is distributed from the southwestern United States (New Mexico; *M. wrightii* A. Gray *sensu* Blake, 1924; Eriksen, 1993a), Mexico, Central America (Taylor, 1985; Morales-Quiros, 2014), along the Andes and Coastal Cordillera (Venezuela), the Pacific coast of Ecuador and Peru to southern Paraguay, Uruguay, dry parts of southeastern Brazil Central (Marques, 1989), Chile and northeastern and central Argentina ([Río Negro; *M. dictyocarpa* Griseb] *sensu* Freire-Fierro and Pastore, 2008); it is absent in the islands of the Caribbean. The countries with the highest number of species are Peru, with 59, followed by Ecuador and Colombia with 48 and 43 species, respectively. The region with the highest number of species is the Andes of northwestern South America (Colombia, Ecuador and Peru), suggesting that this region is the center of distribution for *Monnina* (Ferreyra, 1946, 1953, 1957; Eriksen et al., 2000). Moreover, this region is the most plant species-rich of the Andean ecosystems, with 10,932 species in Colombia, 8,897 in Ecuador and 8,698 in Peru (Perez-Escobar et al., 2021).

Species of *Monnina* occur from ca. sea level (e.g., *M. denticulata* Chodat in the Pacific coastal region of Ecuador) to 4000–4500 m (e.g., *M. revoluta* (Bonpl.) Kunth in Colombia and Ecuador). However, most species are from middle to high elevations in a variety of habitats in the Andes, such as montane forests, subpáramo, páramo, roadsides, shrubby edges and *Polylepis* forests, at elevations of 1200 to 4500 m. They also occur in lowland, semiarid biomes (e.g., *M. pterocarpa* Ruiz & Pav. Ecuador, Peru and Chile), dry forests (e.g., *M. conferta* Ruiz & Pav. in Peru), over rocky slopes and Tepuis summits on the Guayana Shield (e.g., *M. cacumina* N. E. Brown), and in open savannas in Brazil (e.g., *M. stenophylla* A. St. Hil.). Some species (e.g., *M. salicifolia* Ruiz & Pav.; *M. subscandens* Triana & Planch.) are invasive and flourish in disturbed areas along the edges of roadsides, in montane forests and páramo.

The family Polygalaceae is divided at present into four tribes: *Carpolobieae* B. Eriksen, *Diclidanthereae* Reveal, *Polygaleae* Chodat and *Xanthophylleae* Chodat (Pastore et al., 2017; Mota et al., 2019). *Monnina* is included in the tribe *Polygaleae* characterized by a 3-merous, caducous corolla (rarely also with two rudimentary lateral petals), caduceus calyx, unappendaged keel, eight stamens and dehiscent fruit (Eriksen, 1993a,b,c; Eriksen and Persson, 2007).

The monophyly of *Monnina* s.l. is reflected in its subgeneric ranks (e.g., *Hebeandra* Chodat, *Monninopsis* Chodat and *Pterocarya* (DC.) Chodat) established in early classifications (Chodat, 1896a,b). However, Eriksen's morphological cladistic analysis (Eriksen, 1993a,b) showed that the genus is polyphyletic. The results of this work showed that *Monnina* subg. *Monninopsis* appeared deeply nested in *Polygaleae,* whereas *Monnina* subg. *Monnina* and *M.* subg. *Pterocarya* formed a rather basal clade.

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This result, based on fruit and seed characteristics, led Eriksen to assign generic rank to subg. *Monninopsis* and subg. *Pterocarya*, and creating the new genera *Ancylotropis* B. Eriksen and *Pteromonnina* B. Eriksen, respectively. Persson (2001) demonstrated the traditional view of a single origin of *Monnina*. He determined that *Monnina* subg. *Monninopsis* is the sister group to the strongly supported, but partly unresolved, clade of *M.* subg. *Monnina* and *M.* subg. *Pterocarya*. Otherwise, *Monnina* subg. *Pterocarya* does not possess any character that does not also occur in one of the other subgenera (Eriksen, 1993b). Since this monophyletic entity is difficult to circumscribe and distinguish morphologically from *Monnina* s.str., the genus *Pteromonnina* will most likely be put into synonomy (Eriksen and Persoon, 2007).

In addition, the genus has been treated in North American Flora (Blake, 1924), Flora of Argentina (Grondona, 1945), Flora of Peru (Ferreyra, 1946), Flora of Colombia (Ferreyra, 1953a), Flora of Ecuador (Ferreyra, 1953b; Eriksen et al., 2000), Flora of Venezuela (Ferreyra, 1957), Flora of Central America (Taylor, 1985), Flora of Brazil (Marques, 1989), Flora of the Venezuelan Guayana (Aymard et al., 2004), *Catálogo de las Plantas Vasculares del Cono Sur* (Freire-Fierro and Pastore, 2008) and *Manual de Plantas de Costa Rica* (Morales Quiros, 2014).

While conducting herbarium research for updating the checklist of Polygalaceae for the *Nuevo Catálogo de la Flora de Venezuela* (Aymard and Campbell, 2008), specimens of two species of *Monnina* were found that represent records new to the Venezuelan flora (*M. salicifolia* Ruiz & Pav. and *M. smithii* Chodat). This contribution increases to sixteen the number of *Monnina* species known from Venezuela. In addition, five lectotipifications (*M. cladostachya* Turcz.; *M. densa* Planch & Linden ex Wedd.; *M. elongata* Triana & Planch.; *M. mollis* Planch & Linden ex Wedd. and *M. solandrifolia* Triana & Planch.) and one neotypification are proposed (*M. meridensis* Planch & Linden ex Wedd.). In a geographical and taxonomical context, *M. coriacea* Chodat is considered a synonym of *M. meridensis* Planch. & Linden ex Wedd, whereas *M. densa* Planch. & Linden ex Wedd. and *M. duidae* Blake are regarded here as distinct from *M. aestuans* (L.f.) DC.and *M. cacumina* N. E. Brown, respectively.

Materials and Methods

This work is based on morphological (using a dissecting stereomicroscope) and herbarium studies in COL, GH, MER, MERF, MO, NY, PORT, US and VEN (herbarium codes after Thiers, 2019). Historical taxonomic literature on *Monnina* was examined using the Biodiversity Heritage Library (http://www.biodiversitylibrary.org), mainly Turczaninow (1854), Weddell (1857), Triana and Planchon (1862), and Chodat (1894, 1895; 1896a,b). Additional literature was reviewed: e.g., Ferreyra´s contributions (1946, 1953a,b, 1957), Flora of Brazil (Marques, 1989), Flora of Ecuador (Eriksen et al., 2000), and Flora of the Venezuelan Guayana (Aymard et al., 2004). The checklists *Nuevo Catálogo de la Flora de Venezuela* (Aymard and Campbell, 2008) and *Catálogo de plantas y Líquenes de Colombia* (Aymard and Freire-Fierro, 2016) were also reviewed.

Type specimens of *Moninna* species studied in this work were examined using online images from JSTOR Global Plants (https://plants.jstor.org/). In addition, the International Plant Names Index (https://www.ipni.org/), the online botany collections of Smithsonian Natural Museum of Natural History (https://naturalhistory.si.edu/research/botany), and Tropicos (http://legacy.tropicos.org/Home.aspx) were consulted to update the current nomenclature and geographical information.

Key to the species of *Monnina* in the flora of Venezuela

Modified from Ferreira (1957); species indicated with an asterisk (*) are endemic to Venezuela

1a. Leaves spathulate; inflorescence paniculate, the lateral branches usually divaricate . . . . *M. solandrifolia*

1b. Leaves ovate, wide-ovate, oblanceolate-elliptic, lanceolate, sometimes elliptic, lanceolate-elliptic or oblong; inflorescence racemose 2

2a. Leaves ovate, wide-ovate, oblanceolate-elliptic; lower sepals conspicuously joined, usually one-third to one-half united 3

2b. Leaves lanceolate, sometimes elliptic, lanceolate-elliptic or oblong; lower sepals free 7

3a. Apex of leaves acuminate or acute, mucronate; flower subtended by linear-lanceolate or lanceolate bracts; lower sepals half- to completely united, apex acute 4

3b. Apex of leaves obtuse, not mucronate; flower subtended by triangular bracts; lower sepals one-third to one-half united, sometimes only slightly united, obtuse, rarely acute 5

4a. Branches and branchlets lax foliose, not densely foliose, on the upper parts of its branches; leaves elliptic-lanceolate 4.8–11 × 1.5–5 cm, glabrous above, hirsute beneath, petiole 3–7 mm long; inflorescence 9–11 cm long; bract linear-lanceolate, 3–3.8 mm long, flower 5–5.5 mm long, pedicels 1.8–2.2 mm long; outer sepals triangular, slightly pubescent beneath; drupe ellipsoid, 6–7.5 mm long . . . . *M. cacumina*

4b. Branches and branchlets densely foliose on the upper parts of branches; leaves oblanceolate-elliptic, 2–5.5 × 0.5–1.2 cm, puberulent to glabrescent on both surfaces, petiole 2–3 mm long; inflorescences 2–4 cm long, bract oval-lanceolate, ca. 3 mm long; flower 3–4 mm long; pedicels 1–1.5 mm long; outer sepals ovate, glabrous beneath; drupe oblong, ca. 4 mm long . . . . *M. densa*

5a. Leaves ovate, about twice as long as wide, up to 3.5 × 1.8 cm; outer sepals acute, 1-nerved; kee1 glabrous inside . . . . *M. duidae**

5b. Leaves elliptic or lanceolate, more than 3 times as long as wide, up to 6.8 × 1.6 cm; outer sepals obtuse, 3–5-nerved; keel pubescent inside, rarely glabrescent 6

6a. Leaves elliptic, apex obtuse; flower subtended by acuminate bracts; lower sepals usually one-half united . . . . *M. aestuans*

6b. Leaves lanceolate, apex acute; flower subtended by acute bracts; lower sepals one-third united . . . . *M. meridensis**

7a. Racemes with linear-filiform or filiform bracts, apex involute 8

7b. Racemes with triangular to acute-triangular, ovate, hood-shaped or oblanceolate bracts, apex not involute 9

Key to the species of *Monnina* in the flora of Venezuela cont.

Modified from Ferreira (1957); species indicated with an asterisk (*) are endemic to Venezuela

8a. Branches and branchlets hirsute, glabrescent when mature; petioles unwinged; racemes 8–10 cm long: bracts linear-filiform; outer sepals larger than the wings and keel, 5–6 mm long, lanceolate, apex acute; keel slightly pubescent inside . . . . *M. bracteata*

8b. Branches and branchlets finely pubescent; petioles slightly winged; racemes 14–23 cm long: bracts filiform; outer sepals smaller than wings and keel, 1.4–4 mm long, triangular, apex obtuse; keel glabrous inside . . . . *M. smithii*

9a. Ovary pubescent, sometimes slightly pubescent 10

9b. Ovary glabrous 12

10a. Leaves acute; flower subtended by bracts 1.8–2.2 mm long, acute-triangular, glabrescent to slighty pubescent on the lower surface; lower sepals triangular, 3-nerved, glabrescent beneath . . . . *M. cladostachya**

10b. Leaves acuminate to long-acuminate; flower subtended by bracts 6–7 mm long, triangular or oblanceolate, densely pubescent on the lower surface; lower sepals spathulate or ovate-triangular, 1-, rarely 2- or 5-nerved, glabrous or densely pubescent beneath, apex obtuse; keel pubescent beneath 11

11a. Leaves long-acuminate; bracts triangular, densely pubescent on the lower surface; lower sepals spathulate, 5-nerved, densely pubescent beneath, apex obtuse; keel pubescent beneath . . . . *M. tatei**

11b. Leaves acuminate; bracts oblanceolate, slightly pubescent on the lower surface; lower sepals ovate-triangular, 1-, rarely 2,-nerved, glabrous beneath, apex acute; keel glabrous beneath . . . . *M. elongata*

12a. Flowers subtended by ovate or hood-shaped bracts 13

12b. Flowers subtended by triangular to acute-triangular bracts 14

13a. Flowers subtended by ovate bracts, apex obtuse; lower sepals spathulate, densely pubescent beneath; wings pubescent beneath . . . . *M. venezuelensis**

13b. Flowers subtended by hood-shaped bracts, apex acute, lower sepals ovate-triangu lar; wings glabrous beneath . . . . *M. mollis*

14a. Leaves elliptic, canescent pubescent on both sides, 5–6 pairs of lateral veins, apex obtuse; bracts finely pubescent beneath; upper petals slightly pubescent to glabrous . . . . *M. salicifolia*

14b. Leaves lanceolate or elliptic-lanceolate, glabrescent above, sparsely hirsute beneath; 6–10 pairs of lateral veins, apex acute or acuminate; bracts hirsute or glabrescent beneath; upper petals dense pubescent 15

15a. Branches and branchlets hirsute; leaves 4–21 × 1.4–8 cm, hirsute beneath, apex acuminate; flowers subtended by bracts 3–5 mm long, 3-nerved, glabrescent beneath; outer sepals obtuse . . . . *M. pubescens**

15b. Branches and branchlets glabrescent; leaves 4–8.8 × 1–2.3cm, glabrescent beneath; apex acute; flowers subtended by bracts 1.5–2.2 mm long, l-nerved, hirsute beneath; outer sepals acute . . . . *M. steyermarkii**

Synopsis of the species of *Monnina* in the Flora of Venezuela

Monnina aestuans (L.f.) DC. Prodr.1: 338. 1824.

Basionym: *Polygala aestuans* L. f., Supplementum Plantarum 315. 1781[1782]. TYPE: COLOMBIA [Nouvelle-Grenade]. *J. J. Mutis 59* (Lectotype, designated here: LINN [882.23], image seen; Isotype: LINN [882.24], image seen).

Habitat and ecology: Shrub 1–1.5 m tall; montane forests and páramo. At elevations of 1800–4000 m.

Distribution: Along the Andes in Colombia (Antioquia, Bolívar, Boyacá, Cauca, Cesar, Cundinamarca, Huila, Magdalena, Norte de Santander, and Santander), Venezuela (Táchira and Trujillo), and Ecuador.

Linnaeus f. cited in the protologue "*Habitat* in Nova Granada. *Mutis*." There are three specimens identified as *Polygala aestuans* in LINN (one of *Mutis 79* [882.22] and two of *Mutis 59* [882.23 and 882.24]). Ferreyra (1953, 1957) suggested that the type specimen probably was collected by J. C. Mutis in Cundinamarca, Colombia, but he did not propose a lectotype.

Monnina bracteata Chodat, Bulletin de l'Herbier Boissier 3: l33. 1895. TYPE: VENEZUELA. Prope Truxillo et Mérida, 4000–4500 pieds., 1842, *J. J. Linden 339* (Holotype: G [image seen]; Isotypes: GENT [image seen], K [image seen]).

Habitat and ecology: Shrub or slender tree to 3 m tall, branched; montane forests, subpáramo shrubby edges and páramo. At elevations of 1300–3000 m.

Distribution: Andes of Colombia (Boyacá, Quindío, Norte de Santander, and Santander) and Venezuela (Barinas, Lara, Mérida, Táchira, and Trujillo).

The author cited in the protologue "*Prope Truxillo et Mérida*, *J. J. Linden 339* (hr. Delessert)." The only specimen at G, where the Delessert Herbarium is housed, annotated by Chodat, is without any ambiguity the holotype.

Monnina cacumina N. E. Brown, Trans. Linn. Soc. Bot. 6: 10, 11: 1910. TYPE: GUYANA [British Guiana], Summit Roraima, 5600 ft. alt., 1898, *R. V. McConnell & J. J. Quelch 645* (Holotype: K).

Heterotypic Synonym: *Monnina uaipanensis* Wurdack, Mem. New York Bot. Gard. 9: 479. 1957. TYPE: VENEZUELA, Bolivar state, cumbre Uaipán Tepui, 1900 m, 1–15 February 1948, *K. D. Phelps; C. B. Hitchcock 368* (Holotype: NY).

Habitat and ecology: Erect or scandent shrub 1–6 m tall; montane forests, on rocky slopes and tepui summits. At elevations of 1300–2800 m.

Distribution: Endemic to the Guayana Shield in Brazil (Amazonas and Roraima), Guyana, and Venezuela (Amazonas and Bolívar).

Monnina cladostachya Turcz., Bull. Soc. Nat. Mosc. 27(2): 357. 1854. TYPE: VENEZUELA: Prope Porto Cabello [Carabobo state, Puerto Cabello], 01 September 1843, *N. Funck 758* (Lectotype, designated here: KW, image seen).

Residual syntypes: VENEZUELA: Provincia Caracas–ana, prope la Guayra [La Guaira, La Guaira state], 1842, *N. Funck 374* (KW, image seen); *H. G. Galeotti 469* (KW, image seen).

Habitat and ecology: Shrub 1 to 4 m tall, branched; montane forests to subpáramo shrubby edges. At elevations of 1200–2800 m.

Distribution: Endemic to the Andes and Northern Venezuela (Coastal Cordillera); Anzoátegui, Aragua, Distrito Capital, Lara, Mérida, Miranda, and Táchira states. Probably in Boyacá, Cesar, Norte de Santander, and Santander departments, Colombia.

The author of this species cited three specimens in the protologue from the Coastal Cordillera in Venezuela: **"…** provincia Caracasana, prope la Guayra. *Funck 374*, *Galeotti 469,* and *Funck 758*, prope Porto Cabello." Ferreyra (1957), in his revision of the Venezuelan species of *Monnina*, did not propose a lectotype.

Monnina densa Planch. & Linden ex Wedd., Chloris Andina 2: 268. 1857. TYPE: [Nouvelle-Grenade] COLOMBIA. Cordillères de la province d'Ocaña [Norte de Santander Department]: 2600–3250 m, 1846–1852, *L. J. Schlim 345* (Lectotype, designated here: BR; Isolectotypes: K [image seen], MPU [image seen]).

Protologue specimen citations: Nouvelle-Grenade: Sierra Nevada de Santa Marta!, h. 3575–3900 m (*L. J. Schlim*, n. 820); environs de Pamplona (*J. J. Linden 734*); Cordilléres de la province d´Ocaña, 2600–3250 m (*L. J. Schlim 345*).

Residual syntypes: COLOMBIA [Nouvelle-Grenade]. prov. de Rio Hacha [Magdalena Department), Sierra Nevada de Santa Marta, 3575–3900 m, March, 1852, *L. J. Schlim 820* (BR, G, MPU, P [images seen]). Environs de Pamplona [Norte de Santander Department], November, 1849, *J. J. Linden 734* (BR, G, K, MPU [images seen]).

Habitat and ecology: Shrub to 2 m tall; montane forests and páramo. At elevations of 2800–3800 m.

Distribution: Along the Andes in Colombia (Boyacá, Cundinamarca, Magdalena, and Norte de Santander) and Venezuela (Mérida and Táchira).

In the protologue, H. A. Weddell cited three specimens from the Western Cordillera and Sierra de Santa Marta, Colombia, but he did not designate a type collection. In his revisions of the Colombian and Venezuelan species of *Monnina*, Ferreyra (1953, 1957, respectively) treated *M. densa* as a synonym of *M. aestuans* (L.f.) DC. These two taxa are small-leaved shrubs bearing single stems with a much branched crown. There are several species (i.e., *M. loxensis* Benth. and *M. pycnophylla* B. Eriksen) of *Monnina* growing in the Paramo ecosystem that are sympatric and bear the same morphological features. *Monnina aestuans* is sympatric with *M. densa* but differs in the characters cited in the key to species above.

Monnina duidae Blake, Bull. Torrey Club 58: 381. 1931. TYPE: VENEZUELA. Amazonas: Mount Duida, summit of the peak, No. 7., 7100 ft, October 1928, *G. H. G. Tate 604* (Lectotype, effectively designated by Ferreira (1957): NY; Isosyntype: US).

Habitat and ecology: Frutescent 0.6 m tall; tepui summits. At elevations of 2200 m.

Distribution: Endemic to the Guayana Shield of Venezuela (Amazonas).

Eriksen (in Aymard et al., 2004) treated *M. duidae* as a synomym of *M. cacumina*. Here, I follow the morphological concepts proposed by Ferreyra (1957), who recognized both taxa. The main characters to separate both species are in the key to the species above.

Monnina elongata Planch. & Linden ex Triana & Planch., Annales des Sciences Naturelles; Botanique, série 4, 17: 137. 1862. TYPE: COLOMBIA [Nouvelle-Grenade]. La Enllanada, province d'Ocaña [Norte de Santander Department], 1500 m; 1846; *L. J. Schlim 1137* (Lectotype, designated here: BM [image seen]; Isolectotypes: G [image seen], GH [image seen], K [image seen], P [image seen], US [image seen]).

Protologue specimen citations: Nouvelle-Grenade: La Enllanada, prov. d'Ocaña, alt. 1500 metres (*J. J. Triana s.n.*); ibid. (*L. J. Schlim 1137*); prov. de Pamplona, alt. 2600 metres et Ocaña (*L. J. Schlim 87, 674, 679*).

Residual syntypes: COLOMBIA [Nouvelle-Grenade]. prov. de Pamplona, Ocaña, 2600 m. *L. J. Schlim* 87 (G, MPU, P [images seen]), *Schlim 674* (BM [image seen], BR [image seen], GH [image seen], K [image seen], MPU [image seen], P [image seen], US [image seen]), *Schlim 679* (P, image seen).

Habitat and ecology: Subfrutescent to 2 m tall; montane forests and páramo. At elevations of 1500–3500 m.

Distribution: Along the Andes in Colombia (Cundinamarca, Norte de Santander, and Santander) and Venezuela (Mérida, Táchira, Trujillo, and Zulia).

In the protologue, J. J. Triana and J. E. Planchon cited four specimens from the Western Cordillera in Colombia, but they did not designate a type collection. In his revision of Colombian species of *Monnina*, Ferreyra (1953) did not make any reference to the specimens cited by Triana and Planchon. Sprague (1926), in Linden and Planchon's *Plantae Columbianae*, suggested that *J. J. Linden 339* from Venezuela, Trujillo state, San Urbino, may be regarded as the type specimen. However, the Venezuelan specimen is not available and, moreover, only the Colombian localities were cited by J. J. Triana and J. E. Planchon.

Monnina meridensis Planch. & Lind. ex Wedd. Chlor. And. 2: 268. 1857. Neotype [designated here]: VENEZUELA. Mérida. Sierra Nevada de Mérida, Río Nuestra Señora, 3100 m., 16 Junio 1911. *A. Jahn 81* (US [images seen]).

Habitat and ecology: Frutescent, or slender tree to 6 m. tall; montane forests, subparamo and páramo. At elevations of 2000–3500 m.

Distribution: Along the Andes in Venezuela (Lara, Mérida, Táchira, and Trujillo); a single collection from Colombia (La Guajira; *H. Cuadros 2247*, MO).

In the protologue, Weddell cited a single specimen (*J. J. Linden 586*) from the Sierra Nevada de Mérida, 2870–3250 m. A search for type material of *M. meridensis* was unsuccessful, including herbaria likely to hold type material of plants described by Weddell. Currently, the interpretation of this species is based solely on Weddell's protologue and Ferreyra´s description (Ferreyra, 1957). Therefore a neotype is designated here for *M. meridensis*, a species first described from Venezuela.

Monnina mollis Planch. & Linden ex Wedd. Chloris Andina 2: 268. 1857. TYPE: COLOMBIA [Nouvelle-Grenade]. Sierra Nevada de Santa Marta, h. 3250 m, 1852; *L. J. Schlim 119* (Lectotype, designated here: BM [image seen]; Isolectotypes: G [image seen], GH [image seen], K [image seen], US [image seen]).

Habitat and ecology: Frutescent, or slender tree to 6 m. tall, branched; montane forests and páramo. At elevations of 1500–3500 m.

Distribution: Along the Andes in Colombia (Antioquia, Caldas, Cundinamarca, Magdalena, Norte de Santander, Putumayo, and Santander); in Venezuela in the Andes (Mérida) and Coastal Cordillera (Aragua, Distrito Capital, and Miranda).

In the protologue, Weddell cited a single specimen from the Sierra de Santa Marta in Colombia, but he did not assign a type. In his revisions of the Colombian species of *Monnina*, R. Ferreyra (1953) made no reference to the protologue or to the specimen cited by H. A. Weddell.

Monnina pubescens (Bonpl.) H.B.K. Nov. Gen. Sp. (quarto ed.) 5: 418, t. 505. 1821 [1823]).

Basionym: *Hebeandra pubescens* Bonpl. 2: 43. 1808. TYPE: VENEZUELA. Prope Caracas, Cerro Avila, *H. von Humboldt & A. Bonpland s.n.* (Lectotype, designated by Eriksen (1996): P [00677994], image seen; Isolectotype: B-W [13049-010] [image seen]; F [photograph ex B-W], US [photograph ex B-W]).

Habitat and ecology: Shrub or slender tree to 5 m. tall; montane forests, disturbed subpáramo and páramo slopes. At elevations of 1500–2900 m.

Distribution: Endemic to the Andes and Northern (Coastal Cordillera) Venezuela (Aragua, Distrito Capital, Miranda, Táchira). Probably in Boyacá, Cesar, Norte de Santander and Santander departments of Colombia.

Monnina salicifolia Ruiz & Pav., Systema Vegetabilium Florae Peruvianae et Chilensis 172. 1798. TYPE: PERU. Huarocherí, Tarmae et Panatahuarum Provincias, 1778–1788, *H. Ruiz & J. A. Pavon s.n.* (Lectotype, designated by Ferreyra (1946): US, image seen).

Habitat and ecology: Shrub 0.5 to 3 m tall; montane forests, páramo, roadsides, shrubby edges and *Polylepis* forests. At elevations of 1200–3800 m.

Distribution: Along the Andes in Venezuela (Mérida), widespread in Colombia to Ecuador, Peru, and Bolivia. The specimens *H. van der Werff 7669* (MO, US, VEN) and *J. J. Wurdack, M. L. Wurdack & H. Rodriguez 2754* (US), identified by *J. J. Wurdack* (US), represent the first records for the flora of Venezuela.

Monnina smithii Chodat, Bulletin de la Société Botanique de Genève 25: 216. 1934. TYPE: COLOMBIA. Santander. Between Piedecuesta and Las Vegas, 2000–2500 m, 19–24 December 1926, *E. Killip & A. C. Smith 15568* (Lectotype, designated by Ferreyra (1953): US, image seen; Isolectotypes: A [image seen], G [image seen], NY [image seen]).

Habitat and ecology: Frutescent 1 to 2 m tall; montane forests, subparamo and páramo. At elevations of 2000–3700 m.

Distribution: Along the Andes of northern Colombia (Cesar, Norte de Santander, Santander) and Venezuela (Táchira, Trujillo). The specimens *G. Aymard 4390* (PORT, US), *A. Licata 282* (PORT, US), *R. E. Ruiz-Terán 8139* (MERF, US), *B. Stergios 2548, 17575, 18969, 19119* (PORT, US), *J. A. Steyermark 118374* (US, VEN), identified by *J. J. Wurdack* (US), represent the first records for the flora of Venezuela.

Monnina solandrifolia Triana & Planch., Annales des Sciences Naturelles; Botanique, série 4, 17: 138–139. 1862. TYPE: COLOMBIA [Nouvelle-Grenade]. porv. d'Antioquia, Montagnes d'Herveo, versant occidental, 2900 m, 1851, *J. J. Triana s.n.* (Lectotype: BM, designated here [image seen]; Isolectotype: K [images seen].

Protologue specimen citations: Nouvelle-Grenade: Montagnes d'Herveo, versant occidental, prés du Paramo, porv. d'Antioquia, *J. J. Triana s.n.*; prov. de Velez, entre Chiquinquirá et el Puente nacional, alt. 2270 metres, *J. J. Linden s.n.*

Residual syntypes: COLOMBIA [Nouvelle-Grenade]. prov. de Velez (Santander department), entre Chiquinquirá et el Puente nacional, alt. 2270 metres, 1842 *J. J. Linden 742* (BM [image seen], K [image seen], G [image seen], NY [image seen]).

Habitat and ecology: Shrub 1–3 m tall; montane forests to shrubby páramo edges. At elevations of 1500–3000 m.

Distribution: Along the Andes in Colombia (Antioquia, Boyacá, Caquetá, Chocó, Cauca, Cundinamarca, and Norte de Santander) and Venezuela (Táchira).

In the protologue, J. J. Triana and J. E. Planchon cited two collections from the Central and Western Cordilleras of Colombia, but they did not designate a type. In his revision of the Colombian species of *Monnina*, Ferreyra (1953) cited *J. J. Triana* and *J. J. Linden* specimens incorrectly. Chodat (1894) later based his *Monnina platyphylla* on *Linden 742*, which is currently treated as a synonym of *M. solandrifolia* (Ferreyra, 1953).

Monnina steyermarkii Ferreyra, Brittonia 9: 17. 1957. TYPE: Venezuela. Anzoátegui, Cerro Peonia above Santa Cruz, headwaters of Río Manantiales, 1800–2000 m, 20 March 1945, *J. A. Steyermark 61611* (Holotype: F, Isotypes: NY, VEN).

Habitat and ecology: Shrub 1 to 2 m tall; montane forests. At elevations of 1500–2500 m.

Distribution: Endemic to northern Venezuela (Coastal Cordillera) in Anzoátegui and Sucre states. Probably in the Andes of Venezuela.

Monnina tatei Ferreyra, Brittonia 9: 14–15. 1957. TYPE: VENEZUELA. Anzoátegui. Carapas, 1680 m, 1925, *G. H. H. Tate 74* (Holotype: US).

Habitat and ecology: Shrub 1 to 2 m tall; montane forests at an elevation of 1680 m.

Distribution: Endemic to Northern Venezuela (Coastal Cordillera) in Anzoátegui state.

Monnina venezuelensis Ferreyra, Brittonia 9: 16. 1957. TYPE: VENEZUELA. Monagas, Valley of Caripe, summit of Cerro de la Cueva de Doña Anita, 1300 m, 07 April 1954, *J. A. Steyermark 61926* (Holotype: F, Isotypes: NY, US, VEN).

Habitat and ecology: Shrub to 3 m tall; montane forests, over limestone outcrops at an elevation of 1380 m.

Distribution: Endemic to Northern Venezuela (Coastal Cordillera) in Monagas state.

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FLORISTIC INVENTORY OF AN ESTUARINE AREA IN NORTHEASTERN BRAZIL (PONTA DO TUBARÃO SUSTAINABLE DEVELOPMENT RESERVE)

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Abstract. We examined the floristic composition and similarity of the Ponta do Tubarão Reserve of Sustainable Development, Diogo Lopes District, Macau, Rio Grande do Norte State, Brazil. During the Field Course of Ecology I and II of the Postgraduate Program in Ecology and Conservation of the State University of Paraíba (PPGEC-UEPB), herbarium collections of fertile specimens were made in the four recognized phytophysiognomies of the area; Caatinga, Dunes, Islands, and Mangrove. Our results were complemented by data from the speciesLink network. A total of 140 species, belonging to 102 genera and 47 families, were collected and identified. Four of the species are new records for the state of Rio Grande do Norte: *Calliandra depauperata* Benth., *Calliandra spinosa* Ducke and *Bauhinia dubia* G. Don (Fabaceae), which is also a new record for the Caatinga vegetation area, and *Schultesia doniana* Progel (Gentianaceae). Fabaceae was the most represented family with 23 species. Similarity analyses indicated three distinct vegetation groups, composed of the combined Dunes and Mangrove areas, the Island area, and the Caatinga area.

Keywords: Semiarid flora; Northeastern Brazil; Conservation Units.

Vegetation represents one of the world's most important natural resources, providing food and shelter for humans and other organisms and preventing soil erosion, among other things. Studies that can aid in its management and preservation are critical, including descriptions of vegetation types and analyses of local floristic compositions (Pescott and Stewart, 2014).

The Caatinga ecoregion of Brazil is the largest nucleus of seasonally dry tropical forests and woodlands biome (SDTFW, *sensu* Queiroz et al., 2017). It predominates in all northeastern states, including portions of Minas Gerais. This ecoregion is home to a heterogeneous variety of vegetation types, but frequently has low rainfall rates and extended dry periods, resulting in leafless vegetation cover for much of the year (e.g., Moro et al., 2014, 2015; Queiroz et al., 2017; Fernandes et al., 2020).

The entire area occupied by Caatinga vegetation has experienced some degree of anthropogenic modification due to agricultural and pastoral uses, and 30–50% of the biome is considered to have been extremely impacted (Castelletti, 2003). The anthropogenic alterations of the Caatinga region are mainly related to the substitution of native species with cultivated crops and non-native grasses, deforestation, burning for agro-pastoral uses, and the direct use and consumption of native plant resources (MMA, 2002). However, recent studies reveal an extraordinary richness, with 3,347 recorded species, of which 526 are endemic (Fernandes et al., 2020).

The Caatinga is currently the most threatened Brazilian biome, with only 1.3% of its total area under some form of legal protection, including 16 federal and seven state-level conservation areas (Silva et al., 2004; Leal et al., 2005a, b; Teixeira et al., 2021). These conservation areas are typically fairly old, and their administration is often driven by economic aspects distinct to each locality, with larger considerations of environmental protection often ignored. Nonetheless, these areas are extremely important, not only for the preservation of the biological heritage of the nation, but also for scientific research (e.g., Camphora and May, 2006).

The Ponta do Tubarão Sustainable Development Reserve (PTSDR) is located between the municipalities of Macau and Guamaré on the northern coast of Rio Grande do Norte State, Northeast Brazil. Artisanal fishing provides the economic basis of the region. PTSDR covers an area of more than 12,000 ha, and includes Caatinga vegetation, mangrove swamps, sand dunes, restinga (sandy coastal

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vegetation), oceanfront cliffs, and beaches. The reserve was created in 2003 and was the first Sustainable Development Reserve in Rio Grande do Norte State (Cunha, 2006). Despite its phytophysiognomic richness, the knowledge of the species that comprise the different vegetation formations is still limited.

We performed a floristic survey of the plant formations of the Reserve, that we found to harbor almost 100 species of flowering plants. Additionally, we assessed the composition of plant formations with a similarity analysis. These surveys are especially relevant in Sustainable Development Reserves, and, in parallel with species compilations, they can support policies for the sustainable use and management of local flora (e.g., Mattos et al., 2011).

MATERIALS AND METHODS

Study area

Ponta do Tubarão Sustainable Development Reserve (5˚05'37"S, 36˚32'21"W), is located in Diogo Lopes district, Macau municipality, northern coast of Rio Grande do Norte State, Brazil (Fig. 1). The regional rainy season lasts 3 to 4 months, usually occurring from February to May, with the greatest rainfall rates between March and May. The dry period generally extends for 8 to 9 months, from June to January (INMET, 2012–2013). These factors characterize a semiarid climate with evapotranspiration rates greater than the annual precipitation (IDEMA, 2004). The reserve is located at the estuary of the Tubarão River, which is bordered by mangrove vegetation, and includes Caatinga, restinga, moving and fixed dune fields, and ocean-front cliffs (Dias, 2006), characterizing different phytophysiognomies (Fig. 2).

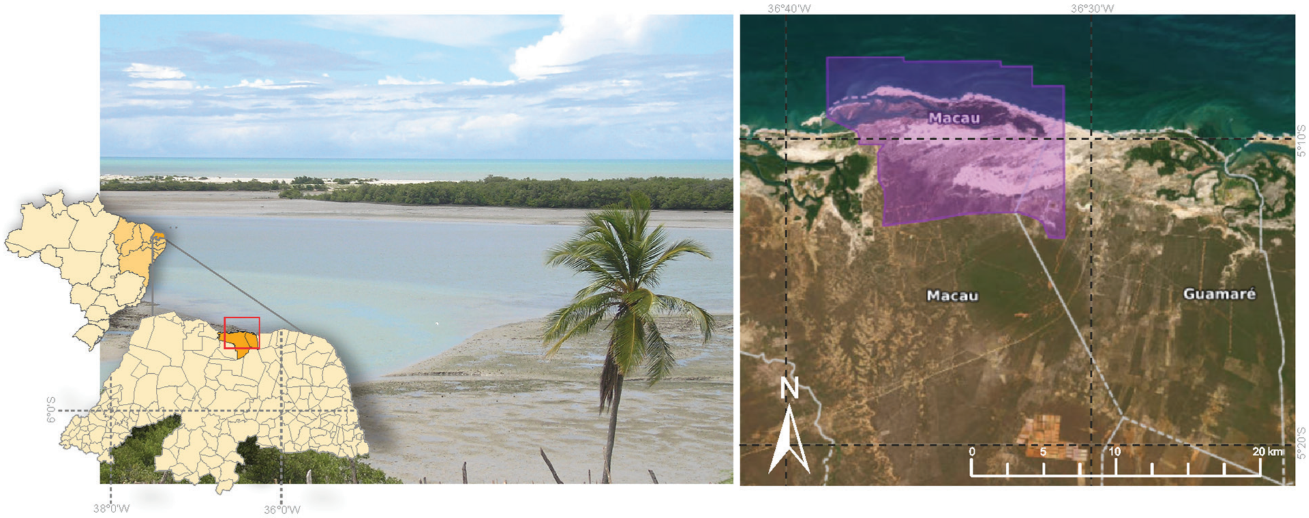

FIGURE 1. Map indicating the location of the Ponta do Tubarão Sustainable Development Reserve (PTSDR) study area, in the district of Diogo Lopes, municipality of Macau, Rio Grande do Norte State, Brazil. Photographs by R.G.V. Camacho.

FIGURE 2. The phytophysiognomies of the study areas. **A**, Caatinga; **B**, Dunes; **C**, Mangrove. Photographs: J. M. Oliveira and T. L. P. Dias.

Sampling techniques and floristic composition

The characterization of the floristic composition of the PTSDR was undertaken mostly during the Field Course of Ecology I and II of the Postgraduate Program in Ecology and Conservation at the State University of Paraíba (PPGEC-UEPB) in May 2015 through botanical collections in four formations within the reserve: Caatinga, island, mangrove, and dune vegetation. Random but massive collections were performed in each environment, where we collected at least five specimens of each fertile species found (with flowers and/or fruits). Our results were complemented by data from the speciesLink network. Taxonomic identifications were based on specialized literature, comparisons with online herbaria collections (e.g., Flora e Funga do Brasil, 2022) and by specialists in each taxonomic group. The checklist was based on classifications from the Angiosperm Phylogeny Group (APG) IV (2016).

Similarity analyses

To evaluate the similarities of the floristic compositions of the different phytophysiognomies, a presence/absence binary matrix based exclusively on the species encountered in the study area was prepared using Microsoft's EXCEL software. Clustering was determined based on the Jaccard similarity index using PRIMER 6 (Clarke and Gorley, 2006) and PERMANOVA (McArdle and Anderson, 2001) software.

Results and Discussion

Characterization of the vegetation

The predominant vegetation type in the PTSDR was hyperxerophilic Caatinga, composed of low to medium sized plants. Halophyte vegetation is found in lowland areas bordering watercourses where salt water penetrates during high tides. Restinga vegetation develops on near-shore sand dunes and sandy plains (and is protected by Federal legislation identifying those areas as permanent preservation sites). Coastal mangrove vegetation is dominated by plant species adapted to soils that are flooded by salt water during high tides, with large internal variations in salinity. In general, the PTSDR comprises lowland and periodically flooded tidal plains, and dune, mangrove, and Caatinga vegetation (the latter being found inland). Fixed and mobile sand dunes surround the entire central-southern area of the reserve.

Floristic richness

A total of 140 species belonging to 102 genera and 47 families of Angiosperms (APG IV) were recorded during the survey (Table 1; Fig. 3). Of this total, 86% of the species (120) were identified to the species level. Of the 16% (22 species) not identified to the species level, 14% (20) were identified to the genus level, while 1.4% (2) remain unidentified. The families Fabaceae (23 spp.), Euphorbiaceae (13 spp.), Malvaceae (10 spp.), Convolvulaceae (9 spp.), Poaceae (7 spp.), Rubiaceae (6 spp.), and Amaranthaceae (5 spp.) comprised 52% of all the species encountered in the study area. In the other families, four were represented by three species each, six contained two species each, and 26 families were represented by only a single species; 118 genera were represented by a single species. Four species are new records for the state of Rio Grande do Norte: *Calliandra depauperata* Benth., *Calliandra spinosa* Ducke and *Bauhinia dubia* G. Don (Fabaceae), and *Schultesia doniana* Progel (Gentianaceae). *B. dubia* G. Don is also a new record for the Caatinga vegetation area.

Caatinga vegetation contains the greatest species richness (66%), with 93 species, while island formations comprise 23% of the total number of species (33), dune areas comprise 24 species (19%), and mangrove areas contain 4 species (3%). Dune and Caatinga vegetations have seven species in common (5%); the islands and Caatinga vegetations also share seven species (5%). Considering only the Caatinga areas sampled in the present study, the numbers of families encountered there (47) was greater than those encountered in other Caatinga vegetation areas (e.g., Andrade et al., 2005; Cabral et al., 2013; Lucena et al., 2015). The predominance of species of Fabaceae is consistent with the results of other floristic surveys undertaken in other semiarid areas in Brazil, where the family typically has the highest number of species, including many woody representatives (e.g., Andrade et al., 2005; Oliveira et al., 2009; Cabral et al., 2013; Oliveira et al., 2013; Calixto-Júnior and Drumond, 2014; Apagaua et al., 2014).

Mangrove species collected along the margins of the islands (*Avicennia schaueriana* Stapf & Leechm. ex Moldenke, *Conocarpus erectus* L., *Laguncularia racemosa* (L.) C.F. Gaertn., and *Rhizophora mangle* L.) were also reported by Costa et al. (2014) in the estuary of the Apodi-Mossoró River in Rio Grande do Norte State.

In dune vegetation, the best-represented families were Convolvulaceae, Rubiaceae, and Euphorbiaceae. Of these three families, only Euphorbiaceae is represented in floristic surveys undertaken in other areas of dune vegetation in the state of Rio Grande do Norte (Freire 1990), in addition to species of Poaceae, Myrtaceae, and Asteraceae.

Floristic similarity

Similarity analyses (Fig. 4) indicated the formation of three distinct groups: (1) dune and mangrove vegetation, with 83% similarity; (2) the islands, with 60% similarity; and (3) Caatinga, with 20% similarity. The quantitative floristic similarity analyses of the sampled areas pointed to clear differences between the four phytophysiognomies in the study area. The dune and mangrove combined group may be related to a sampling bias, since the fewest numbers of species were collected in these areas. Environmental pressures specific to the dune and mangrove areas may prevent the establishment of larger numbers of successful species compared to the other two phytophysiognomies that were sampled (e.g., Costa, 2001).

Table 1. Floristic list of the study area in the Ponta do Tubarão Sustainable Development Reserve (PTSDR), in the district of Diogo Lopes, municipality of Macau, Rio Grande do Norte State, Brazil.

Family	Species	Vegetation Formation
1-Acanthaceae	*Avicennia schaueriana* Stapf & Leechm. ex Moldenke	Mangrove
2-Aizoaceae	*Sesuvium portulacastrum* (L.) L.	Island
3-Amaranthaceae	*Alternanthera brasiliana* (L.) Kuntze	Dunes
	Blutaparon portulacoides (A. St.-Hil.) Mears	Island
	Froelichia humboldtiana Seubert	Caatinga
	Pfaffia gnaphalioides (L.) Mart.	Island
	Pfaffia sp.	Island, Caatinga
4-Anacardiaceae	*Spondias lutea* L.	Island
5-Apocynaceae	*Allamanda blanchetii* A.DC.	Caatinga
	Aspidosperma pyrifolium Mart.	Caatinga
	Calotropis procera (Aiton) W.T. Aiton	Dunes
	Ibatia cf. ganglinosa (Vell.) Morillo	Island
6-Arecaceae	*Copernicia prunifera* (Mill.) H.E.Moore	Dunes
7-Asteraceae	*Blainvillea acmella* (L.) Philipson	Caatinga
	Delilia biflora Kuntze	Caatinga
	Emilia sonchifolia (L.) DC.	Caatinga
	Pectis linifolia L.	Island, Caatinga
8-Bataceae	*Batis maritima* L.	Dunes, Island
9-Boraginaceae	*Euploca polyphylla* (Lehm.) J.I.M. Melo & Semir	Dunes, Caatinga
	Myriopus salzmannii (DC.) Diane & Hilger	Caatinga
10-Bromeliaceae	Indet.	Caatinga
11-Burseraceae	*Commiphora leptophloeos* (Mart.) J.B. Gillet	Caatinga
12-Cactaceae	*Cereus jamacaru* DC.	Island, Caatinga
	Melocactus sp.	Caatinga
	Tacinga inamoena Taylor	Caatinga
	Xiquexique gounellei (F.A.C. Weber ex K. Schum.) Lavor & Calvente	Caatinga
13-Capparaceae	*Cynophalla flexuosa* J. Presl	Island
14-Celastraceae	*Monteverdia rigida* (Mart.) Biral	Island
15-Cleomaceae	*Tarenaya longicarpa* Soares-Neto & Roalson	Caatinga
16-Combretaceae	*Combretum lanceolatum* Pohl ex Eickl.	Caatinga
	Combretum leprosum Mart.	Caatinga
	Conocarpus erectus L.	Mangrove
	Laguncularia racemosa C. F. Gaertn.	Mangrove
17-Commelinaceae	*Commelina erecta* L.	Island
	Commelina obliqua Vahl	Island
	Commelina sp.	Island
18-Convolvulaceae	*Distimake aegyptius* (L.) A.R. Simões & Staples	Caatinga
	Evolvulus sericeus Sw.	Caatinga
	Ipomoea asarifolia Roem. & Schult.	Dunes
	Ipomoea incarnata Choisy	Caatinga
	Ipomoea longiracemosa Choisy	Caatinga
	Ipomoea sp.	Dunes
	Jacquemontia confusa Meisn,	Dunes
	Jacquemontia evolvuloides Meisn.	Caatinga
	Jacquemontia glaucescens Choisy	Caatinga

TABLE 1 CONT. Floristic list of the study area in the Ponta do Tubarão Sustainable Development Reserve (PTSDR), in the district of Diogo Lopes, municipality of Macau, Rio Grande do Norte State, Brazil.

FAMILY	SPECIES	VEGETATION FORMATION
19-Cyperaceae	*Bulbostylis* sp.	Dunes
	Cyperus crassipes Vahl	Island
	Cyperus ligularis L.	Caatinga
	Eleocharis filiculmis Kunth	Dunes
20-Erythroxylaceae	*Erythroxylum pyan* Costa-Lima	Caatinga
21-Euphorbiaceae	*Bernardia sidoides* (Klotzsch) Müll. Arg.	
	Chamaesyce sp.	Dunes, Caatinga
	Cnidoscolus urens (L.) Arthur	Caatinga
	Cnidoscolus quercifolius Pohl ex Baill.	Caatinga
	Croton blanchetianus Baill.	Caatinga
	Croton heliotropiifolius Kunth	Caatinga
	Croton pedicellatus Kunth	Caatinga
	Jatropha curcas L.	Caatinga
	Jatropha gossypifolia L.	Caatinga
	Jatropha mollissima (Pohl) Baill.	Caatinga
	Jatropha mutabilis Baill.	Dunes, Caatinga
	Jatropha ribifolia (Pohl) Baill.	Caatinga
	Manihot pseudoglaziovii Pax & K. Hoffm.	Caatinga
22-Fabaceae	*Bauhinia dubia* G. Don	Caatinga (New record for RN and Caatinga vegetation)
	Calliandra depauperata Benth.	Caatinga (New record)
	Calliandra spinosa Ducke	Caatinga (New record)
	Calopogonium caeruleum (Benth.) C. Wright	Caatinga
	Cenostigma bracteosum (Tul.) Gagnon & G.P. Lewis	Caatinga
	Centrosema sagittatum Humb. & Bonpl. ex Willd. Brandegee	Caatinga
	Centrosema sp.	Caatinga
	Chamaecrista hispidula (Vahl) H.S. Irwin & Barneby	Island
	Chamaecrista rotundifolia (Pers.) Greene	Caatinga
	Chamaecrista sp.	Caatinga
	Chloroleucon foliolosum (Benth.) G.P. Lewis	Caatinga
	Indigofera microcarpa Desv.	Dunes, Caatinga
	Libidibia ferrea (Mart. ex Tul.) L.P. Queiroz	Caatinga
	Mimosa acutistipula Benth.	Caatinga
	Mimosa sensitiva L.	Caatinga
	Piptadenia moniliformis Benth.	Caatinga
	Pithecellobium diversifolium Benth.	Caatinga
	Pityrocarpa moniliformis (Benth.) Luckow & R.W. Jobson	Caatinga
	Senna occidentalis (L.) Link	Island
	Tephrosia egregia Sandwith	Island
	Tephrosia purpurea (L.) Pers.	Island
	Zornia sp. 1	Caatinga
	Zornia sp. 2	Caatinga
23-Gentianaceae	*Schultesia doniana* Progel	Caatinga (New record)
24-Krameriaceae	*Krameria grandiflora* A. St.-Hil.	Caatinga
25-Lamiaceae	*Mesosphaerum suaveolens* (L.) Kuntze	Caatinga
26-Malvaceae	*Herissantia crispa* (L.) Brizicky	Island, Caatinga
	Herissantia tiubae (K. Schum.) Brizicky	Dunes, Caatinga
	Hibiscus sp.	Island
	Sida brittonii León	Caatinga
	Sida galheirensis Ulbr.	Caatinga
	Waltheria brachypetala Turcz.	Caatinga
	Waltheria sp. 1	Caatinga
	Waltheria sp. 2	Caatinga
	Wissadula sp.	Dunes
	Indet.	Dunes

TABLE 1 CONT. Floristic list of the study area in the Ponta do Tubarão Sustainable Development Reserve (PTSDR), in the district of Diogo Lopes, municipality of Macau, Rio Grande do Norte State, Brazil.

FAMILY	SPECIES	VEGETATION FORMATION
27-Molluginaceae	*Mollugo verticillata* L.	Caatinga
28-Nyctaginaceae	*Boerhavia coccinea* Mill.	Dunes
29-Oxalidaceae	*Oxalis debilis* Kunth	Caatinga
30-Passifloraceae	*Passiflora cincinnata* Mast.	Island, Caatinga
	Passiflora subrotunda Mast.	Island
31-Plantaginaceae	*Bacopa monnieri* (L.) Wettst.	Dunes
	Stemodia maritima L.	Dunes
32-Plumbaginaceae	*Plumbago scandens* L.	Caatinga
33-Poaceae	*Anthephora hermaphrodita* Kuntze	Caatinga
	Digitaria ciliaris (Retz.) Koeler	Island
	Eleusine indica (L.) Gaertn.	Caatinga
	Eragrostis amabilis (L.) Wight & Arn.	Caatinga
	Hymenachne amplexicaulis (Rudge) Nees	Island
	Melinis minutiflora P. Beauv.	Island
	Sporobolus indicus (L.) R. Br.	Island
34-Polygalaceae	*Polygala* sp.	Caatinga
35-Portulacaceae	*Portulaca hirsutissima* Cambess.	Caatinga
	Portulaca oleracea L.	Island
	Portulaca umbraticola Kunth	Dunes, Caatinga
	Portulaca sp.	Island, Caatinga
36-Primulaceae	*Jacquinia armillaris* Jacq.	Restinga
37-Rhamnaceae	*Sarcomphalus joazeiro* (Mart.) Hauenschild.	Caatinga
38-Rhizophoraceae	*Rhizophora mangle* L.	Mangrove
39-Rubiaceae	*Borreria multiflora* (DC.) Bacigalupo & E.L. Cabral	Dunes
	Coutarea sp.	Island
	Hexasepalum apiculatum (Willd. ex Roem. & Schult.) Delprete & J.H. Kirkbr.	Caatinga Dunes
	Mitracarpus sp.	
	Richardia brasiliensis Gomez	Caatinga
	Richardia grandiflora (Cham. & Schltdl.) Steud.	Dunes
40-Santalaceae	*Phoradendron* sp. 1	Caatinga
	Phoradendron sp. 2	Caatinga
41-Sapindaceae	*Cardiospermum corindum* L.	Island
42-Sapotaceae	*Bumelia sartorum* Mart.	Caatinga
	Sideroxylon obtusifolium (Roem. & Schult.) T.D. Penn.	Caatinga
43-Solanaceae	*Nicotiana glauca* Graham	Dunes, Caatinga
44-Talinaceae	*Talinum fruticosum* (L.) Juss.	Caatinga, Island
45-Turneraceae	*Piriqueta viscosa* Griseb.	Caatinga
	Turnera subulata Sm.	Island
46-Verbenaceae	*Stachytarpheta coccinea* Schauer	Caatinga
	Stachytarpheta microphylla Walp.	Caatinga
47-Ximeniaceae	*Ximenia americana* L.	Caatinga

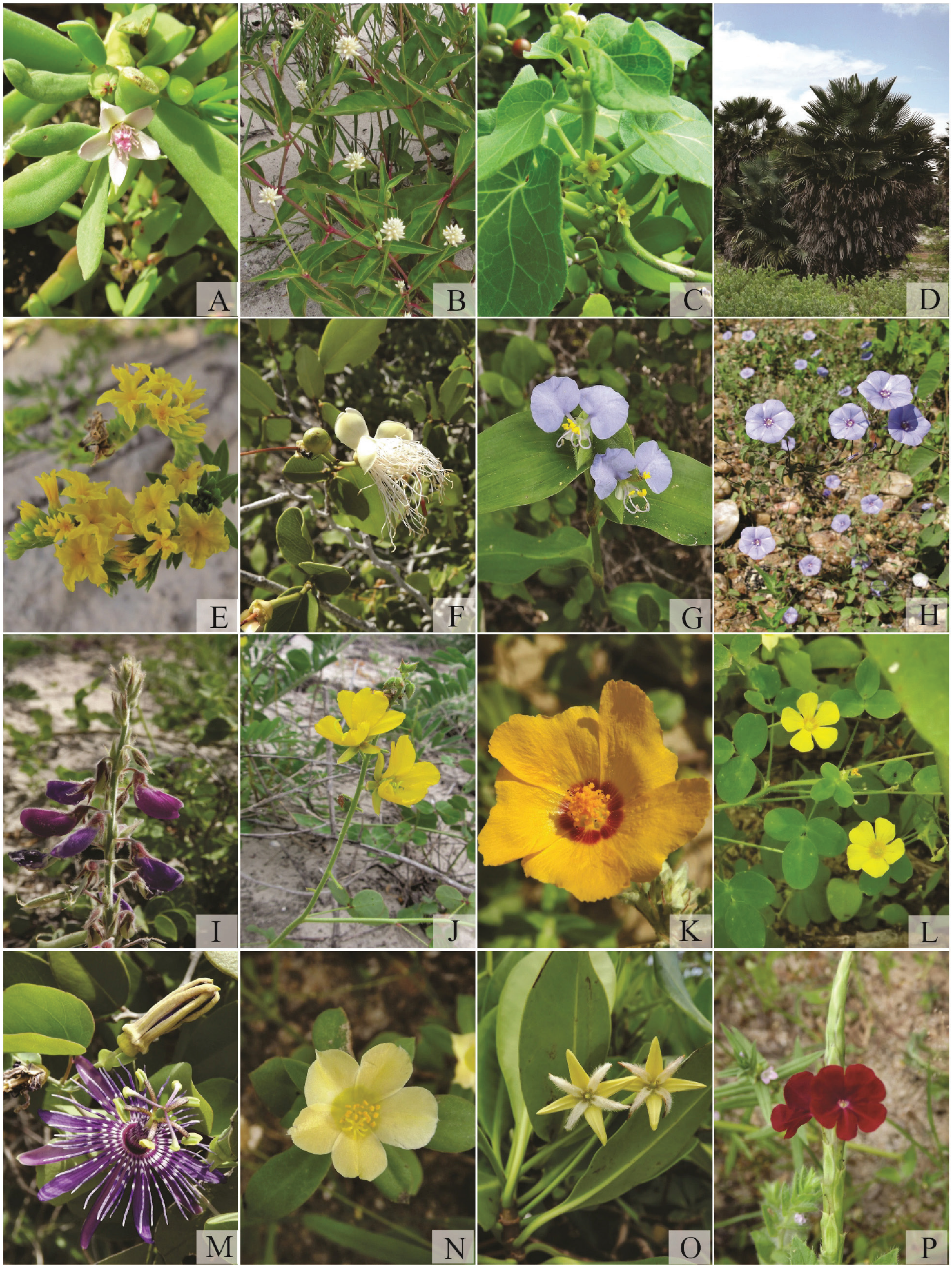

FIGURE 3. Plant species in the Ponta do Tubarão Sustainable Development Reserve (PTSDR) study area, in the district of Diogo Lopes, Macau, Rio Grande do Norte State, Brazil. **A**, *Sesuvium portulacastrum* (L.) L.; **B**, *Pfaffia glomerata* (Spreng.) Pedersen; **C**, *Ibatia ganglinosa* (Vell.) Morillo; **D**, *Copernicia prunifera* (Mill.) H.E. Moore; **E**, *Euploca polyphylla* (Lehm.) J.I.M. Melo & Semir; **F**, *Cynophalla flexuosa* J. Presl; **G**, *Commelina erecta* L.; **H**, *Jacquemontia evolvuloides* Meisn.; **I**, *Tephrosia egregia* Sandwith; **J**, *Chamaecrista hispidula* (Vahl) H.S. Irwin & Barneby; **K**, *Sida galheirensis* Ulbr.; **L**, *Oxalis debilis* Kunth; **M**, *Passiflora cincinnata* Mast.; **N**, *Portulaca hirsutissima* Cambess.; **O**, *Rhizophora mangle* L.; **P**, *Stachytarpheta microphylla* Walp. Photographs: J. M. Oliveira.

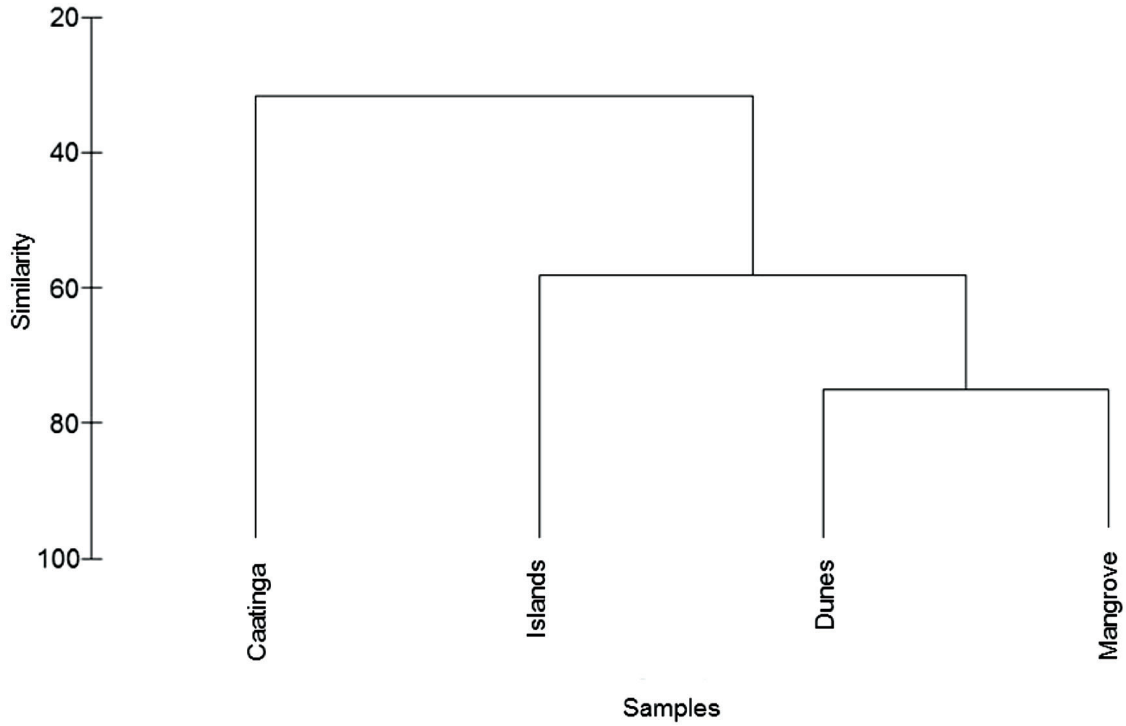

FIGURE 4. Floristic similarity dendrogram obtained from the grouping analyses of the four phytophysiognomies identified in the study area (Caatinga, Dune, Islands, and Mangrove) at the Ponta do Tubarão Sustainable Development Reserve (PTSDR) study area, in the district of Diogo Lopes, Macau, Rio Grande do Norte State, Brazil.

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THE REINSTATEMENT OF *APHANANDRIUM* (ACANTHACEAE), A NEW SPECIES FROM ECUADOR AND FOUR NEW COMBINATIONS

XAVIER CORNEJO,[1,2] DIETER WASSHAUSEN,[3] NOLAN EXE,[4] AND MIA JOHNSON [5]

Abstract. *Aphanandrium*, a genus of herbs and shrubs in the Acanthaceae from the Neotropics, is reinstated based on a previous phylogenetic study, and the following new combinations are herein presented: *Aphanandrium grandifolius*, *A. harlingii* var. *harlingii*, *A. harlingii* var. *longifolius*, and *A. nitidus*. Also, *Aphanandrium narupayacuensis*, a distinctive new species from the lowlands of northeastern Ecuador, is formally described and illustrated, and its relationship to morphologically closely related species is discussed.

Keywords: Ecuador, Narupayacu, *Neriacanthus*, Neotropics

Resumen. *Aphanandrium* Lindau, un género de pequeños arbustos of Acanthaceae del Neotrópico es validado con base en un estudio filogenético previo y se presentan las siguientes nuevas combinaciones: *Aphanandrium grandifolius*, *A. harlingii* var. *harlingii*, *A. harlingii* var. *longifolius*, y *A. nitidus*. Además, se presenta formalmente a *Aphanandrium narupayacuensis*, una distintiva nueva especie de las tierras bajas del noreste de Ecuador, se discute sus relaciones con las especies morfológicamente cercanas.

Palabras claves: Ecuador, Narupayacu, *Neriacanthus*, neotrópicos

Aphanandrium Lindau (Lindau, 1895), is a small Neotropical genus in the Acanthaceae that was originally based on *A. lehmannianum* Lindau (Lindau, 1895), a species from western Colombia (Leonard, 1958). Previously, *A. lehmannianum* was transferred to *Neriacanthus* Benth. (Bentham and Hooker, 1876), a genus proposed to accommodate *N. purdieanus* Benth. (Bentham and Hooker, 1876), a species endemic to Jamaica. The latter species has been placed in synonymy with *Salpixantha* (1845), the older generic name, that comprises two species endemic to Jamaica (Franck and Daniel, 2015).

In the treatment of the Acanthaceae of Colombia (Leonard, 1958) and Ecuador (Wasshausen, 2013), the mainland species of *Aphanandrium* were treated as *Neriacanthus* s.l. However, a molecular analysis reveals that the mainland species of *Neriacanthus* s.l. are a monophyletic lineage, sister to the clade that contains *Salpixantha* (Manzitto-Tripp et al., 2022); therefore, the Central and South American species of *Neriacanthus* should be assigned to another genus (Franck and Daniel, 2015). Morphologically, *Neriacanthus* s.s. can be recognized by tricolpate pollen grains with each colpus flanked by a pair of pseudocolpi. ¨Pseudocolpi are not otherwise known in Acantheae and thus appear to be a synapomorphy for mainland *Neriacanthus*¨ (McDade et al., 2005).

In this paper, *Aphanandrium* is reinstated based on previous molecular work (McDade et al., 2005), and four new combinations from *Neriacanthus* s.l. to *Aphanandrium* are presented to accommodate the mainland members of this genus. Furthermore, a highly distinctive new species of *Aphanandrium* has been discovered from field work in northeastern Ecuador and is formally presented here.

TAXONOMY

Aphanandrium Lindau, Nat. Pflanzenfam. 4 (3b): 323. 1895.

TYPE: *Aphanandrium lehmannianum* Lindau, Nat. Pflanzenfam. 4 (3b): 323. 1895.

Homotypic synonym: *Neriacanthus lehmannianus* (Lindau) Lindau, Symb. Antill. 2: 209. 1900. TYPE: COLOMBIA. Valle del Cauca: Cali, 2000–2200 m, June–July (without year, fl), *F. C. Lehmann 7852* (Neotype: [designated here] K [000534388]; Isoneotype: K [000534387]).

A Neotropical genus that comprises five species of herbs and subshrubs, ranging from Panama to Venezuela and Peru. In the original publication (Lindau, 1895: 323), the genus *Aphanandrium* was proposed based on *Aphanandrium lehmannianum* from Colombia, but without reference to a type or herbarium collection. Later, *Lehmann 7852*, referred to as gathered in Ecuador, is cited as the type collection of *A. lehmannianum* which was transferred to *Neriacanthus* (Lindau, 1900: 209, Leonard, 1958: 123). However, since the specimen originally at B has not been found, it is most likely that it was destroyed during the allied bombing of Berlin in World War II. Two duplicates of *Lehmann 7852* from Cali, Colombia, both studied by Leonard and handwritten as ¨type¨, were found at K. Since these were not

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included in the protologue in the original publication, they cannot be designated as lectotypes. Therefore, one of those (K [000534388]) is selected here as the neotype, following Arts. 7.9, 9.8, 8.13, 9.19c of ICBN (2022).

The following new combinations transferred from *Neriacanthus* to *Aphanandrium* are formally presented here.

1. Aphanandrium grandiflorum (Leonard) Wassh., *comb. nov.*

Basionym: *Neriacanthus grandiflorus* Leonard, Contr. US. Natl. Herb. 31(2): 121, f. 41. 1953. TYPE: COLOMBIA. El Valle: cordillera occidental, vertiente occidental, Hoya del río Sanguininí, lado izquierdo, La Laguna, bosques, 1250–1400, 10–20 December 1943 (fl), *J. Cuatrecasas 15625* (Holotype: US [1852711]; Isotype: F [1335149]).

Additional specimens examined: PANAMA. Veraguas: Cerro Tute, western slopes, 1100 m, 23 October 1980 (fl), *P. J. M. Maas & R. L. Dressler 5042* (US); ridge east of cerro Tute, NW of Santa Fe, 08°29'15"N, 081°07'30"W, 900–1250 m, 25 October 1975 (fl), *R. L. Dressler 5202* (US).

Habitat: From premontane to montane rain forests.

2. Aphanandrium harlingii var. **harlingii** (Wassh.) Wassh., *comb. nov.*

Basionym: *Neriacanthus harlingii* var. *harlingii* Wassh., Opera Bot. 92: 271. 1987. TYPE: ECUADOR. Morona-Santiago: Road Limón (General Plaza)-Gualaceo, km 20–30 from Limón, 2000–2300 m, 25 March 1974 (fl), *G. Harling & L. Andersson 12830* (Holotype: US [2791223]; Isotype: GB).

Additional specimens examined: ECUADOR. Morona Santiago: Between Campanas and Arenillas, along Río Tintas SE of El Pan, 2195 m, 13 July 1943 (fl), *J. A. Steyermark 53640* (F, US); road Cuenca-General Plaza (Limón), km 45, c. 2000 m, without date, *B. Sparre 18706* (S). Gualaceo-Limón road, 27.4 km SE and below highest pass, 2310 m, 15 June 1989 (fl), *L. J. Dorr & I. Valdespino 6296* (US); eastern slopes of the cordillera, valley of the Río Negro, down to the Río Pailas (on the trail to Mendez), 1800–2200 m, 20–24 August 1945 (fl), *W. H. Camp E-4923* (US).

Habitat: In montane wet forest.

3. Aphanandrium harlingii var. **longifolium** (Wassh.) Wassh., *comb. nov.*

Basionym: *Neriacanthus harlingii* var. *longifolius* Wassh., Opera Bot. 92: 271. 1987. TYPE: ECUADOR. Napo: Cerro Huacamayos, on road Baeza-Tena, ca. 34 km from Baeza, ca. 0°41'S, 77°50'W, ca. 2000 m, 9–10 August 1980 (fl), *B. Ollgaard, S. Roth & C. Sperling 35851* (Holotype: US [2993116]; Isotypes: AAU [×2], US [3280014]).

Additional specimens examined: ECUADOR. Napo: Km 33 Baeza-Tena road, cordillera de Huacamayos, 0°39'S, 77°51'W, 2000 m, 4 May 1986 (fl), *P. M. Jørgensen et al. 61274* (AAU); El Chaco, sitio Tres Cruces, hda. El Mirador, 0°11' S, 77°42'W, 2000 m, 23 January 1991 (fl), *W. Palacios 6895* (MO, QCNE, US); S slope, cordillera de Guacamayos, c. 5 km below pass, 0°40'S, 77°55'W, 1950 m, 27 April 1985 (fl), *B. A. Stein 2645* (MO, US).

Habitat: Occasional on steep slopes, ridges, ravines and road banks in montane rain forests, at elevations between 2000 and 3000 m (Wasshausen, 2013).

4. Aphanandrium nitidum (Leonard) Wassh., *comb. nov.*

Basionym: *Neriacanthus nitidus* Leonard, Fieldiana, Bot. 28:563. 1953. TYPE: VENEZUELA. Mérida: quebrada de Los Salchichales, tributary of Río Canaguá, 1950–2135 m, 9 May 1944 (fr), *J. A. Steyermark 56424* (Holotype: F [1205072]; Isotype: US [1997546]).

Habitat: In ravines, montane moist forests.

A distinctive new species of *Aphanandrium* has recently been found in northeastern Ecuador and is formally described here.

5. Aphanandrium narupayacuensis Cornejo, Wassh. & Exe, *sp. nov.*

TYPE: ECUADOR. Napo: Narupayacu Reserve, c. 21 km NE from Archidona, 0°43'S, 77°46'W, ca. 1170 m, 5 November 2022 (fl, fr), *N. Exe 001* (Holotype: GUAY; Isotype: QCA). Fig. 1.

The new species of *Aphanandrium* is similar to *A. harlingii (Wassh.) Wassh.,* but differs by having lorate leaves and narrower floral bracts.

Herbs to 60 cm tall; stems red on top, simple or few-branched, the branches loose, spreading to subtract, subquadrangular at apex, glabrous throughout. *Leaf blades* lorate, distally straight to laterally curved upward, thinly chartaceous, 5–12 × 0.25–0.4 cm, cuneate at base, entire to somewhat sinuate revolute (dry) at margin, acute to caudate at apex, mid vein prominent, the blades olive-green and nitid (living) adaxially, mid vein prominent to impressed, blade light green (living), glandular dark brown-punctate (dry) abaxially, secondary veins inconspicuous on both sides, glabrous; petioles 1–2 mm, glabrous. *Inflorescence* spicate, terminal 6–21 × 1.0–1.5 cm, the peduncles 2.5–6 cm, the rachis subquadangular, glabrous; *floral bracts* lanceolate 3–7 × 1.0–1.5 mm obtuse at base minutely obscurely dentate to sinuate at margins, acute to acuminate at apex, green, glabrous; *bractlets* narrowly lanceolate or linear lanceolate, 2–3 × 0.3–0.5 mm, gradually narrowed to the tip, maroon to dark purple; *calyx* 4–5 mm long, lobes linear-lanceolate, gradually narrowed to a subulate tip, the posterior lobe 1 mm wide, the lateral ones 0.5 mm wide, the anterior ones 0.75 mm wide, all inconspicuously striate, red, glabrous; *corolla* white, ca. 15–16 mm long, glabrous, the tube cylindric, straight or curved ca. 15 × 1.2 mm, swollen, ca. 2 mm wide at base and ca. 2.5 mm at apex, the swollen apex with short trichomes within, abaxially yellow, the limb ca. 8–9 mm wide, the lobes ovate to oblong, obtuse to notched, the posterior lobe 3 × 2.5 mm, the lateral lobes ca. 5 × 2.5 mm, the anterior lobe transversely reniform, 5–6 × 8–9 mm, inconspicuously bilobed, the terminal somewhat vestigial, otherwise without lobes; *stamens* inserted at base of swollen upper third of corolla tube, filaments 1.5–2.5 mm, glabrous, the anthers oblong, 1.5–2 mm, 1-thecous, dorsifixed midway

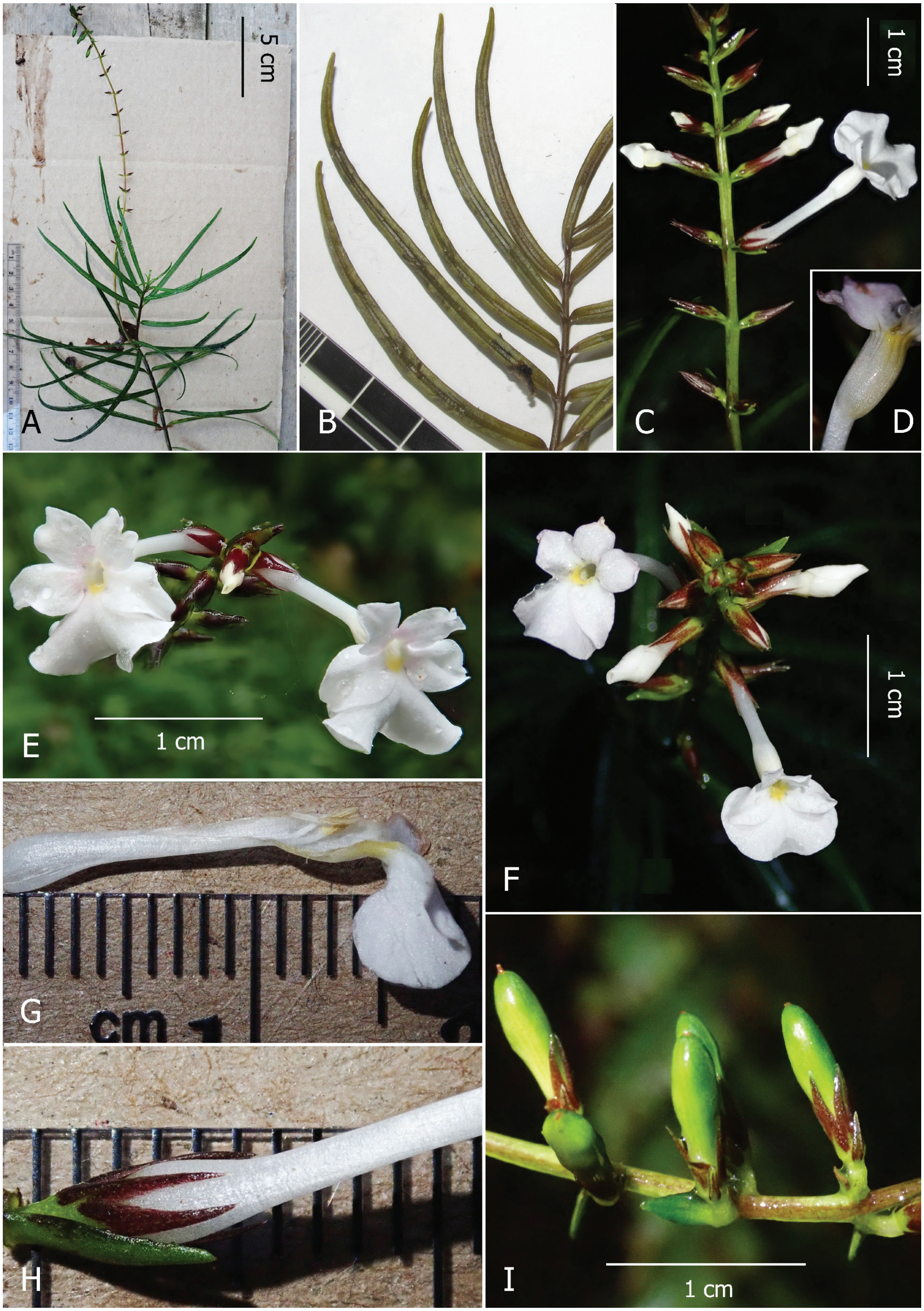

FIGURE 1. *Aphanandrium narupayacuensis* Cornejo, Wassh. & Exe. **A**, habit; **B**, terminal leafy branch, abaxial view; **C**, inflorescence; **D**, close-up of swollen distal part of corolla tube; **E**, **F**, flowers at anthesis; **G**, longitudinal section of corolla, lateral view; **H**, floral bract, calyx, and base of corolla tube; **I**, fruits nearly to maturity attached to the rachis of infructescence, lateral view. A–I are based on the type. Photographs A, B, G, and H by X. Cornejo; C, D, E, F, and I, by N. Exe.

TABLE 1. Morphological comparison of species of *Aphanandrium*.

	A. LEHMANNIANUM	*A. GRANDIFLORUM*	*A. HARLINGII VAR. HARLINGII*	*A. HARLINGII VAR. LONGIFOLIUM*	*A. NITIDUM*	*A. NARUPAYACUENSIS*
Habit	herb	suffrutescent herb	suffrutescent herb	shrub or subshrub	woody vining epiphyte	herb
Color of corolla	white or yellow proximally	Lilac	white	white	unknown	white
Length of corolla	2 cm	4 cm	1.7 cm	2.5 cm	unknown	1.5–1.6 cm
Length and width of floral bracts	8–15 × 3–7 mm	23 × 9 mm	ca. 8.5 × 3–9 mm	ca. 10.5 × 2 mm	ca. 15 × 8 mm	3–7 × 1–1.5 mm
Shape of leaves	oblong elliptic to oblanceolate	oblong elliptic	elliptic	elliptic to obovate	elliptic	lorate
Length and width of leaves	8–13 × 2–4 cm	3–10 × 1.5–4.5 cm	3–6 × 0.6–2.0 cm	9–13.5 × 3.3–4.0 cm	6–8 × 1.8–3.0 cm	5–12 × 0.25–0.4 cm
Secondary veins	8–12 pairs	8–9 pairs	5–10 pairs	9–14 pairs	5–7 pairs	inconspicuous
Length of petioles	10–15 mm	10–15 mm	4–13 mm	8–10 mm	3–7 mm	1–2 mm
Size of capsules	ca. 12 × 4 mm	ca. 15 × 5 mm	ca. 10 mm	ca. 14 mm	ca. 18 × 5 mm	7–8 × 1.5–2.0 mm
Distribution	Colombia, Western cordillera	Panama and Colombia, Western cordillera	SE Ecuador, eastern Andean slopes	NE Ecuador, eastern Andean slopes	Venezuela, Eastern Andean cordillera	NE Ecuador, eastern Andean slopes
Altitudinal range	1700–2900 m	900–1400 m	1800–2300 m	2000–2300 m	1950–2150 m	ca. 1170 m

between middle and base, dorsally pilose, the trichomes pluricellular, univariate, hyaline; *ovary* oblong, 1.5 × 1 mm long; *style* ca. 8 mm, glabrous; *stigma* papillose, flattened. *Capsule* oblong-clavate to clavate 7–8 × 1.5–2 mm, obtuse and apiculate at apex, green (living), brown and glossy (dry), short-glandular-depressed, 4-seeded; *seeds* broadly ovate to suborbicular, brown, ca. 1.5 × 1.5 mm, glabrous, retinacula ca. 1.5 mm.

Aphanandrium narupayacuensis is easy to recognize by the elongate narrowly-oblong to lorate leaves with very short petioles, 1–2 mm long, and inconspicuous secondary veins, which is a unique feature among species in this genus. Further distinguishing characteristics in *A. narupayacuensis* are: longer spikes, 6–21 cm; the peduncles and spike axis are not purplish; the bracts are lanceolate, 3–7 × 1.0–1.5 mm; the bractlets are narrowly lanceolate to linear lanceolate, 2–3 × 0.3–0.5 mm, maroon to dark purple; the calyx is red, and the corolla is 15–16 mm long. In contrast, in *A. harlingii* the spikes are 1.7–7 cm long, the peduncles and spike axis are dark purplish, the bracts subulate, 8.5–10.5 × 2–3 mm, the bractlets are lanceolate-subulate, 4 × 0.75–0.85 mm, mucronulate and glabrous, the calyx is purplish and the corolla is 17–25 mm long.

Etymology: The epithet refers to the Narupayacu river, for which the Narupayacu Reserve, the type locality, is named. Narupayacu is a Quichua word that is composed of *Narupa*, meaning palm, and *yacu*, meaning river (José A. Simbaña, pers. comm.).

Common names: Unknown.

Habitat and distribution: Known only from the type locality.

Aphanandrium narupayacuensis is restricted to vertical cliff bands located to the south of the Narupayacu waterfall (left side when viewing the waterfall from below), at the Narupayacu Hummingbird Gardens. The exposed cliff outcrops range from a few meters to approximately 15 meters high. The cliff substrate consists of various sedimentary rock types, crumbling in layers and allowing water from the river to seep through the cliffs. The rocks of the cliffs naturally exude bitumen, and the oily black substance oozes from the cliffs on a hot day. A distinctive lithophytic plant community is found in areas with wet seeps, including *A. narupayacuensis* as a dominant species. *A. narupayacuensis* plants are multi-stemmed with long rhizomes, running beneath a thick layer of bryophytes, anchored directly to rock. The plant community in wet areas of the cliff includes bryophytes, vascular epiphytes such as ferns, *Selaginella*, and multiple species of Gesneriaceae. The surrounding area is a patchwork of primary- and secondary- growth forest with a rich shrub layer. The plant community on sections of the cliff lacking wet seeps is notably different from the wet areas, indicating that the steady, year-round moisture provided by the seeps is an important factor in the growth of *A. narupayacuensis*.

Phenology: Flowers have been observed from October to February, and fruits from November to March.

Conservation status: At least 100 individuals estimated (Nolan Exe obs. pers. in the field). At present, due to the scarce information, the new species is designated as DD (data deficient; IUCN 2022).

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REVISION OF *CALYCACANTHUS* (ACANTHACEAE: JUSTICIEAE: MONOTHECIINAE) WITH A NEW SPECIES FROM PAPUA NEW GUINEA

THOMAS F. DANIEL[1]

Abstract. *Calycacanthus* is treated as comprising two species, *C. magusianus* and a newly described species, *C. insularis*. The genus is endemic to New Guinea and several adjacent islands. *Calycacanthus magnusianus* is widespread in Papua New Guinea, whereas *C. insularis* is only known from several islands of that country in the southern Solomon Sea. The two species are similar in corolla size, shape, and coloration, but differ in calyx coloration, anther size, and pollen morphology. Both species are described (macromorphology and pollen), their distributions are mapped, habitats and phenological data are summarized, and preliminary conservation assessments are discussed.

Keywords: *Calycacanthus*, Acanthaceae, New Guinea, pollen, lectotypification

The region from India through Indo-China and Malesia is a major center of diversity for the large, and mostly tropical family, Acanthaceae (Lawrence, 1951; Daniel, 1993). Islands comprising Papuasia, which lie at the southeastern extent of the Malesian Region, harbor a relatively rich assemblage of acanthaceous taxa, including endemic genera and species. There is no comprehensive taxonomic account of Acanthaceae for New Guinea, nor one for either of the political entities that comprise that island and the surrounding smaller islands; i.e., the Indonesian provinces of western New Guinea (formerly known as Irian Jaya) and the nation of Papua New Guinea on the eastern side of the island. The indigenous Acanthaceae of New Guinea, including surrounding islands of Indonesia (e.g., Aru Islands) and Papua New Guinea (e.g., Louisiade Archipelago), consist of 24 genera and 95 species (Cámara-Leret et al., 2020, with updates herein). Three currently recognized genera (*Calycacanthus* K. Schum., *Jadunia* Lindau, *Hulemacanthus* S. Moore; the unispecific genus *Gymnophragma* Lindau, described from Papua New Guinea, was excluded by Manzitto-Tripp et al., 2021) and 47 species of the family are endemic to the region. Another genus, *Leptosiphonium* F. Muell., is nearly endemic to the region, but also occurs in the nearby Solomon Islands. Recent studies involving these genera include: chromosome numbers (Daniel, 2000), molecular phylogenetics (Tripp et al., 2013; McDade et al., 2008, 2020), classification and identification keys (Manzitto-Tripp et al., 2021), and taxonomy (Wearn and Darbyshire, 2013).

Calycacanthus was described as a unispecific genus from Papua New Guinea by K. Schumann in an account of the flora of Kaiser Wilhelms Land (Schumann and Hollrung, 1889). *Calycacanthus magnusianus* K. Schum. has since been found to be widespread in that nation, both on the mainland and on several surrounding islands. That species has been noted among Acanthaceae for its cauliflory (Manzitto-Tripp et al., 2021), which is rare in the family. In the most recent classification of Acanthaceae (Manzitto-Tripp et al., 2021), the genus was included in tribe Justicieae, subtribe Monotheciinae, with seven other Paleotropical genera. Based on sampling to date, the closest relatives of *Calycacanthus* are certain species of *Jadunia* and *Ptyssiglottis* T.Anderson, both of which are endemic to New Guinea (McDade et al., 2020).

Studies of *C. magnusianus* in Papua New Guinea and in several herbaria have revealed the existence of a second species of the genus that is restricted to islands of that country in the southern Solomon Sea. Herewith, a monographic revision of *Calycacanthus* is provided to document the macromorphology and known ecological parameters (e.g., distribution, habitats, flowering/fruiting phenology) of both species. Because of their systematic importance among Acanthaceae, descriptions and/or discussions of pollen morphology and chromosome numbers are included. Preliminary conservation assessments based on IUCN (2022) criteria are discussed for both species.

MATERIALS AND METHODS

From 9 July to 6 August in 1992, I collected Acanthaceae in Madang and Morobe provinces of Papua New Guinea, and studied a portion of the Acanthaceae collection at the herbarium (LAE) of that country's Forest Research Institute. In addition to my collections and selected materials at LAE, specimens of *Calycacanthus* were studied at BM, K, L, MO, RSA, and UC. Information from images of specimens at P and US (and some additional specimens at L) was also utilized; in specimen citations these are noted as "-image." For pollen studies, individual grains were removed from

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exposed anthers of herbarium specimens with an insect pin, mounted (untreated) onto scanning electron microscope (SEM) stubs coated with double-stick tape, sputter coated with gold/palladium for 50 seconds, and examined under 15KV on a Hitachi SU3500 SEM at CAS. Pollen measurements reported here are from specimens of *C. insularis* (*Brass 27599* at L, *28507* at L, *28517* at L) and *C. magnusianus* (*Daniel & Jebb 6518* at CAS, *Hoogland 5178* at LAE, *Reeve 1628* at K, *Sohmer & Katik 75123* at K). Measurements consist of the polar diameter (P) and the equatorial diameter (E). Palynological terminology generally follows that proposed by Walker and Doyle (1975), supplemented by Hesse et al. (2009). Preliminary conservation assessments are based on IUCN (2022) criteria for geographic range and GeoCat (2022) for calculations of extent of occurrence (EOO) and area of occupancy (AOO; based on IUCN default cell width of 2 km). Collections lacking latitude and longitude on labels were georeferenced (where possible) based on the locality data provided. In such cases, the coordinates are enclosed with brackets in the specimen citations.

Taxonomy

Calycacanthus K. Schum. in K. M. Schumann & M. U. Hollrung, Fl. Kais. Wilh. Land, 126. 1889. TYPE: *Calycacanthus magnusianus* K. Schum.

Shrubs to small trees, older stems lenticellate. *Leaves* opposite, subsessile to petiolate, blades ± membranaceous to subcoriaceous. *Inflorescences* of sessile to pedunculate dichasia or thyrses (bearing pedunculate dichasia) from axils of young leaves or from woody branches or trunks on older growth (i.e., cauliflorous, at least in *C. magnusianus*); dichasia up to 10 (or more)-flowered, sometimes modified and appearing ± linear. *Bracts* (when present) and bracteoles small, triangular to subulate. *Flowers* pedicellate, nototribic. *Calyces* dark red to pink or green, 5-lobed, lobes similar. *Corollas* pinkish to salmon colored or bright red, 38–50 mm long, externally pubescent with some or all trichomes glandular, tube funnelform, tube length:corolla length = 0.21–0.40 (–0.58), narrow proximal portion of tube ± abruptly expanded distally into throat, upper lip ± hoodlike, lacking a rugula, 2-lobed, lower lip often reflexed, 3-lobed. *Stamens* 2, inserted in tube at or near junction of narrow proximal portion and throat, sometimes exserted beyond upper lip of corolla, filaments glabrous, anthers 2-thecous, thecae equally to subequally inserted, parallel, equal to subequal in size, staminodes absent. *Pollen* 2- or 3-aperturate, exine reticulate. *Capsules* clavate, 15–34 mm long, with a sterile basal stipe and an ellipsoid fertile head having a slight medial constriction. *Seeds* up to 4 per capsule, ± discoid, rugose or tuberculate-ridged, lacking trichomes.

Calycacanthus consists of two species endemic to Papuasia. *Calycacanthus insularis* is restricted to the islands of southeastern Papua New Guinea in the Solomon Sea, and *C. magnusianus* occurs throughout much of Papua New Guinea and is also known from the northeastern portion of the Indonesian province of Papua on the Island of New Guinea (Fig. 1). Based on molecular phylogenetic data (McDade et al., 2020; Manzitto-Tripp et al., 2021), the genus pertains to subtribe Monotheciinae of the tribe Justicieae.

Floral Morphology

Flowers of the two species differ in calyx color, anther length, and pollen morphology. However, corollas of both species are very similar in size, morphology, and (to a lesser extent) in coloration, all features that likely reflect adaptation to similar avian pollinators. A collection of *C. insularis* (*Frodin 2177*) from Rossel Island notes that flowers were visited by a nectar-sucking "hummingbird-like bird." Given the location of this species, this possibly refers to either the honeyeater White-chinned Myzomela (*Myzomela albigula albigula* E. Hartert, Meliphagidae) or the Louisiade Flowerpecker (*Dicaeum nitidum rosseli* Rothschild & Hartert, Nectariniidae), both of which taxa are endemic to islands in southeastern Papua New Guinea, including Rossel Island (Pratt and Beehler, 2015; Tarburton, 2020).

Chromosome Numbers

Subtribe Monotheciinae consists of eight Paleotropical genera that occur in Africa/Madagascar (*Ambongia* Benoist, *Champluviera* I. Darbysh., T.F. Daniel & Kiel, and *Monothecium* Hochst.) and primarily Asia/Malesia (*Calycacanthus, Cyclacanthus* S. Moore, *Jadunia*, *Marcania* J.B. Imlay, *Monothecium*, and *Ptyssiglottis*). Daniel (2000) reported a chromosome number of *n* = 16 for *Calycacanthus magnusianus* and an approximate count of *n* = ca. 16 for *Jadunia biroi* (Lindau & K. Schum.) Lindau, one of its closest relatives (McDade et al., 2020). These appear to be the only known chromosome counts for taxa in the subtribe. Although the data are insufficient to be conclusive, *n* = 16 might be a common number elsewhere in the subtribe, at least among Papuasian taxa.

Palynology

The two species of *Calycacanthus* have pollen of similar size and exine sculpturing. However, they differ in shape and in the number and types of apertures. Pollen of *C. magnusianus* (Fig. 2G–L) is prolate spheroidal to euprolate (likely varying in shape due to harmomegathic responses), 3-colporate, and 6-pseudocolpate. Pollen of this species resembling that studied here has been previously documented from other collections: drawing on *Clemens 970* at L, *Hoogland 4864* at BM (Scotland, 1990), and *Schodde 2396* (APSA, 2007). Similar 3-colporate, 6-pseudocolpate pollen occurs elsewhere among most genera of Monotheciinae, including in *Ambongia* (Muller et al., 1989), *Champluviera* (Darbyshire et al., 2019), *Monothecium* (e.g., Raj, 1961), and *Ptyssiglottis* (Hansen, 1992). Pollen of *C. insularis* (Fig. 2A–F) is globose-elliptic, 2-pororate, and lacking in pseudoapertures. It is perhaps noteworthy that pollen among species currently treated in *Ptyssiglottis* include grains with various numbers and types of apertures, including colpori, pseudocolpi, and pores (Hansen, 1992). Two-pororate pollen is known elsewhere among the acanthaceous tribes

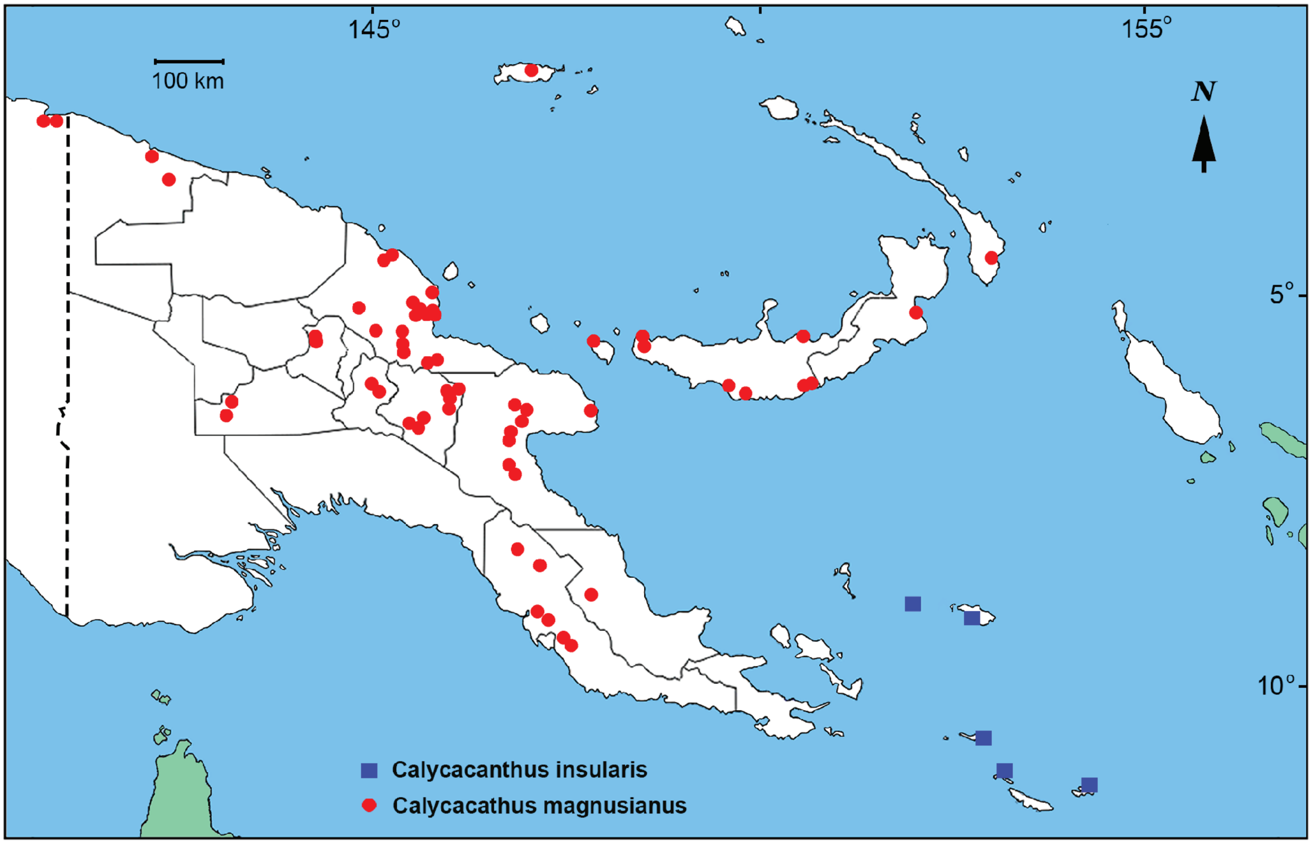

FIGURE 1. Map of eastern portion of the island of New Guinea showing part of the province of Papua in Indonesia (left of dotted line) and Papua New Guinea (showing all provinces) with distributions of *Calycacanthus insularis* and *C. magnusianus*. Portions of Australia (south of Papua New Guinea) and the Solomon Islands (east of Papua New Guinea) are highlighted in green.

Whitfieldieae (e.g., *Whitfieldia* Hook.; Manktelow et al., 2001) and Isoglossinae (e.g., *Stenostephanus* Nees; Daniel, 1998). However, 2-pororate pollen in *Whitfieldia* and *Stenostephanus* differs from that of *C. insularis* by having very large and round ectoapertures. In addition, pollen of *C. insularis* has the appearance of being 2-brevicolporate because of the tapering of the ectoapertures at two opposite ends (i.e., diamond-shaped). However, the length:width ratio of the ectoapertures (1.4–1.7) places them well within the limits of pores rather than colpi (length:width > 2; e.g., Raj, 1961; Hesse et al., 2009). Given their shape, they are likely derived from shortened colpi. Other Acanthaceae that show markedly different apertural types in a monophyletic clade include *Ruellia* L. (colporate and porate, Tripp et al., 2009). Given the importance of pollen morphology in the classification of many taxa of Acanthaceae (Lindau, 1895; Scotland and Vollesen, 2000; Manzitto-Tripp et al., 2021), it is possible that the two species of *Calycacanthus*, which appear to be related to one another based on macromorphological characters, might pertain to different genera. Molecular phylogenetic studies should help to clarify their relationship to one another.

KEY TO THE SPECIES OF *CALYCACANTHUS*

1a. Leaves subcoriaceous; inflorescence of thyrses of dichasia in axils of leaves on new growth or in axils of leaf scars on woody branches or trunks (i.e., cauliflorous); calyx usually dark red during anthesis (rarely pink but usually fading to pink following anthesis); corolla pinkish to salmon colored; anther thecae 2.9–3.8 (–4.4) mm long; pollen 3-colporate, 6-pseudocolpate; capsule (18–) 20–33 mm long . . . . *C. magnusianus*

1b. Leaves ± membranaceous; inflorescence of dichasia in axils of leaves; calyx green; corolla bright red; anther thecae 2.5–3.0 mm long; pollen 2-pororate; capsule 15–19 mm long . . . . *C. insularis*

1. *Calycacanthus insularis* T.F. Daniel, *sp. nov*. TYPE: PAPUA NEW GUINEA. Milne Bay: Misima Island, Narian [ca. 10˚41'21.63"S, 152˚49'25.76"E], 20 m, frequent in shrubberies on coral limestone, 4 August 1956 (fl, fr), *L. Brass 27599* (Holotype: L [Herb. Lugd. Bat. 958.003 106]; Isotype: US-image). Fig. 3–4.

Shrubs to 3 m tall, bark dark greenish brown, ± smooth, older stems sparsely pubescent to glabrate, younger stems quadrate-sulcate, at first ± evenly and sparsely pubescent with antrorse to antrorsely appressed eglandular trichomes 0.1–0.2 mm long and sometimes also puberulent with erect subglandular trichomes to 0.05 mm long (subglandular

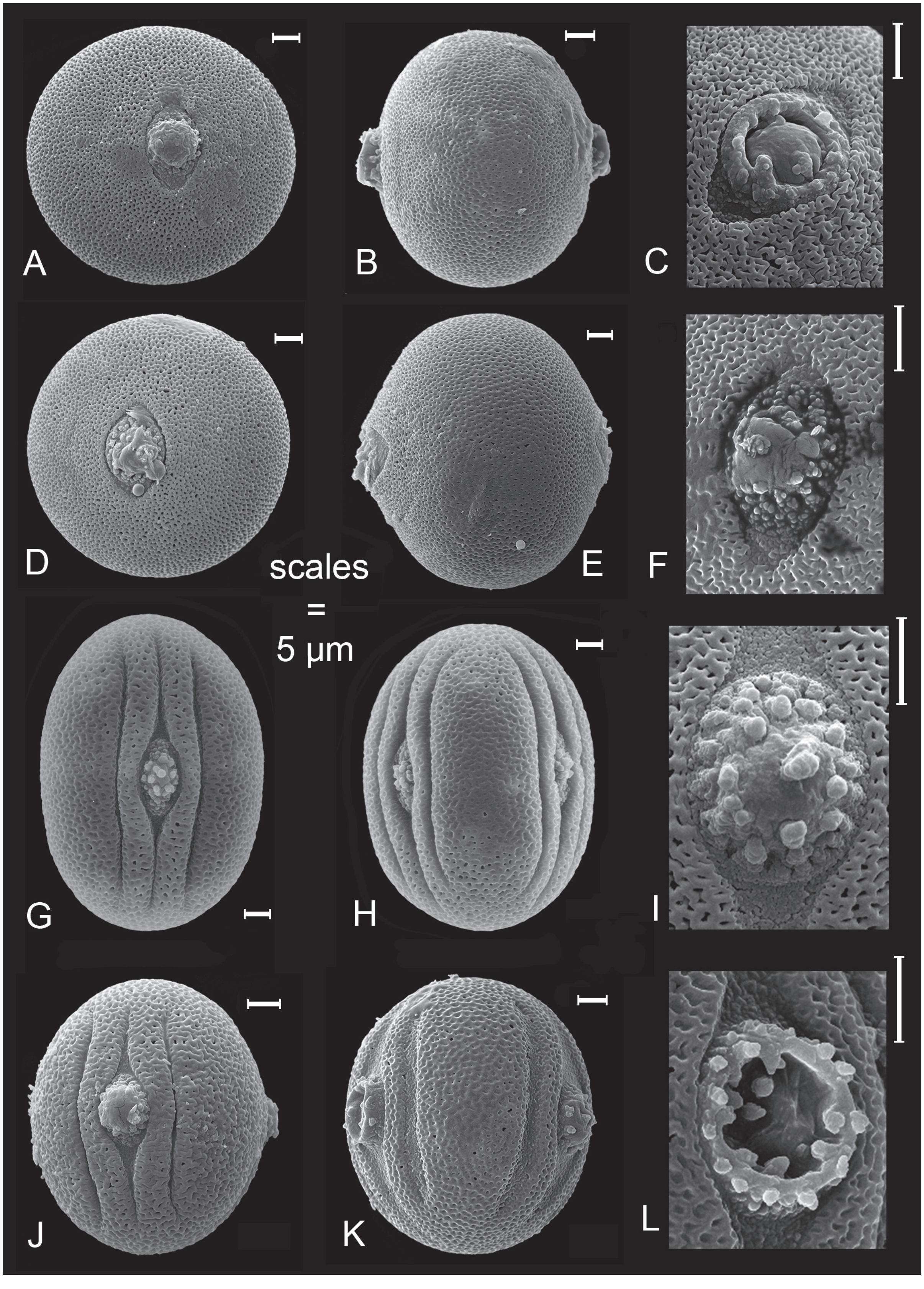

FIGURE 2. Pollen of *Calycacanthus*. **A**–**F**. C. *insularis*. **A**, equatorial/apertural view; **B**, polar or interapertural view; **C**, aperture (pororus); **D**, equatorial/apertural view; **E,** polar or interapertural view; **F,** aperture (pororus). **G**–**L**. *C. magnusianus*. **G,** equatorial/apertural view; **H,** equatorial/interapertural view; **I,** endoaperture (os); **J,** equatorial/apertural view; **K,** equatorial/interapertural view; **L,** endoaperture (os). A from *Brass 28517*; B, D, and F from *Brass 27599*; C and E from *Brass 28507*; G–H from *Daniel & Jebb 6518*; I from *Hartley 13163*; J from *Reeve 1628*; K–L from *Hoogland 5178*.

FIGURE 3.Holotype of *Calycacanthus insularis* (*Brass 27599* at L).

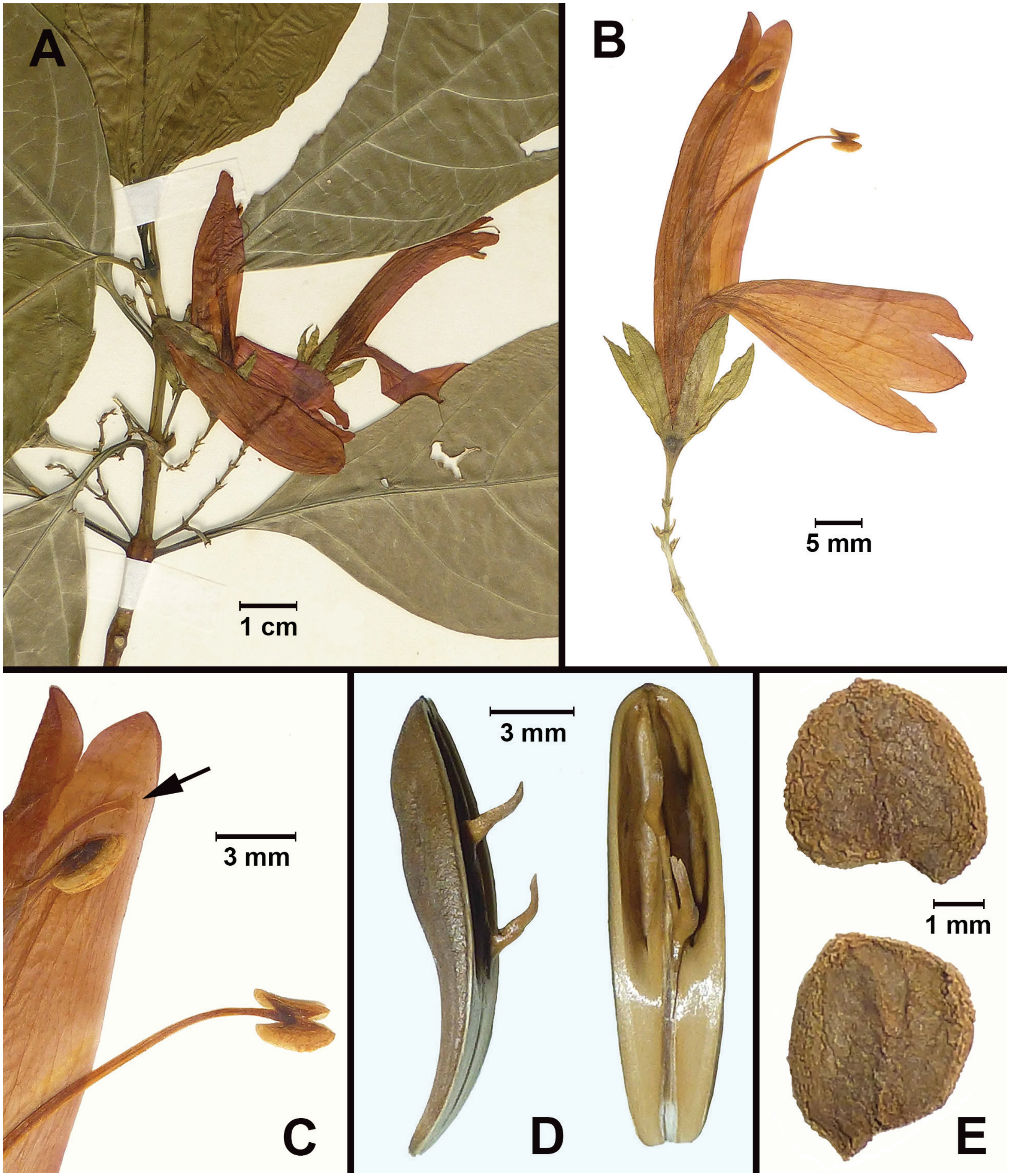

FIGURE 4. *Calycacanthus insularis*. **A**, nodes with inflorescences; **B**, dichasial branch with bracteoles and flower; **C**, distal portion of upper lip of corolla with stamens, style, and stigma (arrow); **D**, capsule valves, lateral view (left) and internal view (right); **E**, seeds. A from *Brass 28517* (L); B–C from *Brass 28507* (L); D–E from *Gillison NSG 25326* (L).

puberulent), trichomes soon ± concentrated in 2 or 4 lines on younger stems or becoming sparse to absent as stems age. *Leaves* petiolate, petioles to 28 mm long, blades dark green and ± shiny above, yellow-green below, ± membranaceous, (ovate-elliptic to) elliptic, 55–182 mm long, 17–67 mm wide, (1.8–) 2.2–3.4 times longer than wide, cuneate to subattenuate at base, acuminate at apex, both surfaces glabrous. *Inflorescences* of pedunculate dichasia from axils of leaves (i.e., with leaves present), dichasia opposite at nodes, 1 (–2) per axil, (1–) 3–10 (or more)-flowered, dichotomous or sometimes modified such that development occurs in only one axil per node of bracteoles for multiple nodes resulting in a ± linear appearance to dichasium, peduncles 4–14 mm long, secondary peduncles often shorter, both peduncles and secondary peduncles nearly glabrous to pubescent with antrorse to antrorsely appressed eglandular trichomes 0.05–0.10 mm long, sometimes also subglandular puberulent. *Bracteoles* and secondary bracteoles triangular to subulate, 1–2 mm long, 0.5–0.9 mm wide, abaxially pubescent with cauline type trichomes. *Flowers* with pedicels 6–15 mm long, pedicels pubescent like peduncles (or with subglandular trichomes absent when present on peduncles). *Calyces* green, 9.5–16.0 (–18.0 in fruit) mm long, lobes (lance-linear to) linear to oblong to elliptic to oblanceolate, 7–15 (–17) mm long, 1.3–4.5 mm wide, generally widest above base, subequal in size (variation mostly in width rather than length), abaxially glabrous or nearly so (sometimes with a few antrorse eglandular trichomes present, especially along midvein), margin ciliolate with trichomes like those of peduncles (or with the eglandular trichomes to 0.2 mm long). *Corollas* bright red, 39–46 mm long, externally pubescent with erect to flexuose glandular and eglandular trichomes 0.05–0.20 mm long, tube 8–18 mm long, 3.5–4.0 mm in diameter near midpoint, tube length:corolla length = 0.2–0.4, narrow proximal portion of tube (3.5–) 6.0–12.0 mm long, throat 4–7 mm long, 7–9 mm in diameter (measured flat) at mouth, throat length:narrow proximal portion of tube length = 0.3–0.9 (–1.3), upper lip 26–36 mm long, lobes 2.5–8.0 mm long, lower lip 23–33 mm long, lobes 4–9 mm long. *Stamens* 30–35 mm long, not exserted beyond upper lip of corolla, anther thecae white, equally to subequally inserted, 2.5–3.0 mm long, lacking basal appendages. *Pollen* globose-elliptic, 2-pororate, P (and apertural E) = 43–51 μm diam., interapertural E = 36–40 μm wide, apertural E: interapertural E = 1.1–1.2, ectoaperture tapered on 2 opposite sides (diamond-shaped), 16.0–16.5 × 10.2–11.7 μm, L:W = 1.4–1.7. *Styles* 37–45 mm long, distally glabrous, proximally sparsely pubescent with eglandular trichomes or nearly glabrous, stigma subcapitate (lobes inconspicuous or not evident), 0.2–0.4 mm long. *Capsules* 15–19 mm long, glandular puberulent with trichomes to 0.05 mm long, stipe 5–6 mm long, head 10–11 mm long. *Seeds* discoid, 3.5–3.7 × 2.8–3.8 mm, surfaces rugose-reticulate.

Phenology: flowering: April, August–October; fruiting: October.

Distribution and habitat: southeastern Papua New Guinea among the islands of Milne Bay Province in the southern half of the Solomon Sea (Fig. 1). Plants occur frequently to commonly at edges of clearings in rain forest, in secondary forest, and among shrubs on coral limestone at elevations from 10–25 m.

Local name: “kakuleia” (*Gillison NGF 25326*).

Conservation: Based its calculated EOO of 21,046 km^2 (mostly open ocean) and the AOO of 20 km^2, the species could be assessed as Endangered (EN) if sufficient information on fragmentation of the population and potential threats was known. Because its occurrences are restricted to small and relatively small islands, the distribution of *C. insularis* might be severely fragmented. However, dispersal distances remain unknown for its propagules. Little is known about potential threats on some of the islands on which the species occurs (e.g., Gawa and Nasai), but others are heavily populated (e.g., Misima and Sabari; Anonymous, 2021, 2022). Misima Island has a long history of mining activities (Anonymous, 2022), and known threats on Rossel Island include local timber harvests and shifting agricultural practices (Lamei, 2021). Although *C. insularis* is not specifically known to be impacted by these threats, and has been noted by collectors to be locally frequent to common, given the few known collections of the species, the possible severe fragmentation of its population, and the threats noted above on the islands, it could potentially be assessed as Endangered as B2(a)(b) with an inferred or projected decline in either habitat or the number of locations or subpopulations.

Because the dichasia are borne in the axils of leaves, only bracteoles are present in the inflorescences (Fig. 4A). The dichasia are sometimes expanded and elongate with branches bearing up to eight flower-bearing nodes. Dichasia are often asymmetric with one dichasial branch expanded to many more orders than other branches, and beyond the initial central (terminal) flower, they often bear only a single flower at each node of the paired bracteoles. On herbarium specimens the color of corollas is variously described as red, bright red, and deep red-pink.

Additional specimens examined: PAPUA NEW GUINEA. Milne Bay: Rossel Island, Jinjo (as “Jinju”) [ca. 11°19'10.70"S, 154°14'29.02"E], *L. Brass 28507* (K, L); Rossel Island, Jinjo (as “Jinju”), *L. Brass 28517* (K, L); without specific locality, *D. Frodin 2177* (K, L); Nasai (as “Nassai”) Island [09°10'20.32"S, 152°39'18.97"E], *H. Gay 984* (K); Gawa Island [ca. 08°57'22.62"S, 151°59'12.37"E], *A. Gillison NGF 25326* (K, L); Sabari (as “Sabara”) Island, 11°05'S, 153°05'E, *E. Mann NGF 43370* (L-image only).

2. *Calycacanthus magnusianus* K. Schum. in K. M. Schumann & U. M. Hollrung, Fl. Kais. Wilh. Land, 126. 1889. TYPE: PAPUA NEW GUINEA. Madang (“Kaiser Wilhelmsland”): Wald bei Hatzfeldthafen [Hatzfeldhavn, ca. 04°24'’13.86"S, 145°11'47.27"E], October 1886 (fl), *M. Hollrung 365* (Lectotype: [designated here]: K: [000884408]). Fig. 5.

Shrubs or small to medium-sized trees to 10 (–15) m tall, branches sometimes ± clambering, older stems glabrous or glabrate, younger stems subterete to subquadrate, glabrous or

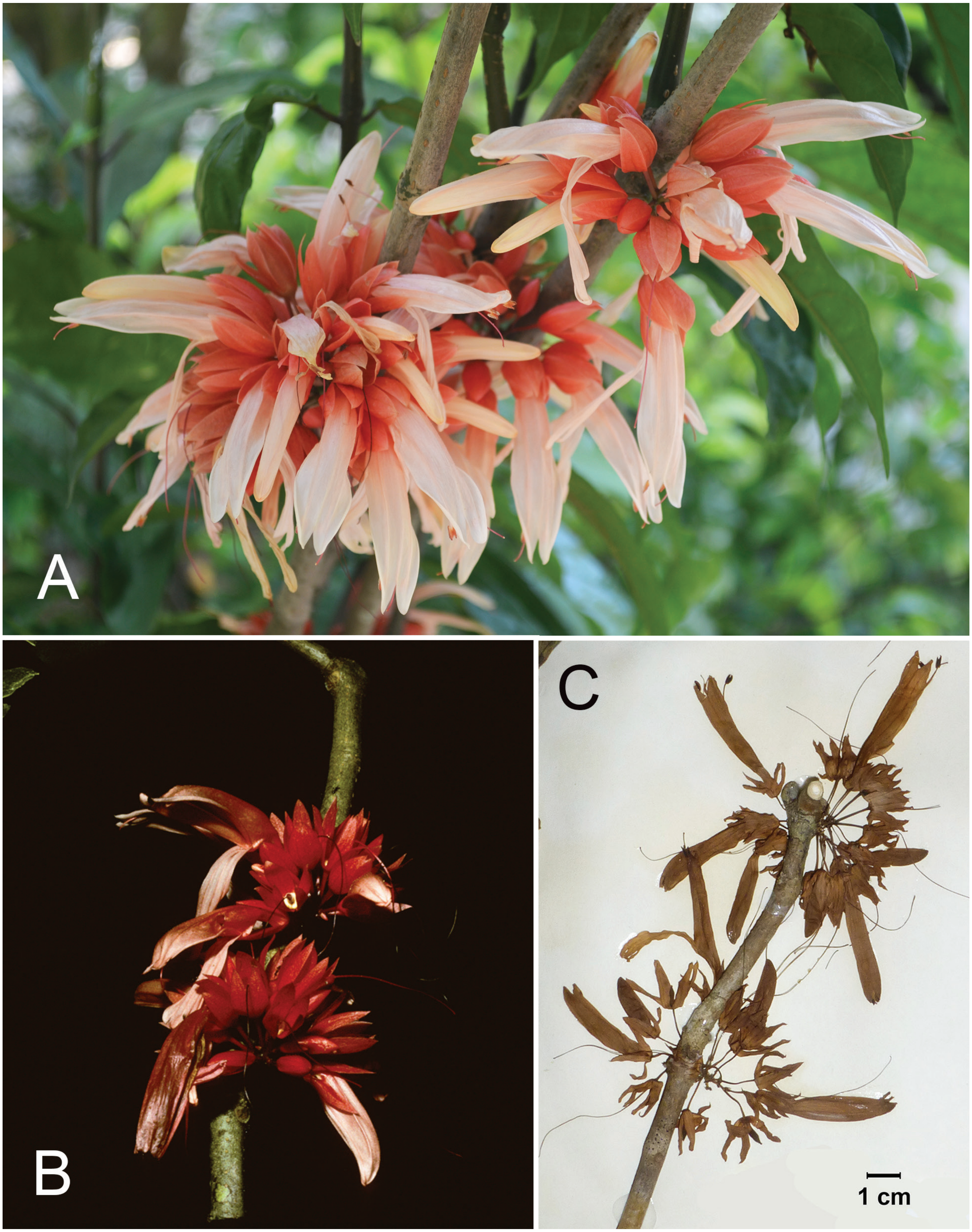

FIGURE 5. *Calycacanthus magnusianus*, inflorescences with flowers on woody stems. **A**, live plant cultivated in Singapore; **B**, plant in native habitat in Papua New Guinea; **C**, portion of herbarium specimen. A photo by K. H. Ooi, used with permission; B from *Daniel & Jebb 6518*, photo by T. Daniel; C from *Hoogland 4864* (K).

± evenly pubescent (sometimes sparsely so) with antrorsely appressed to antrorse to erect eglandular trichomes to 0.3 mm long. *Leaves* subsessile to petiolate, petioles to 17 mm long, sometimes reddish tinged, blades subcoriaceous, dull dark green above, paler green below, elliptic to obovate-elliptic, 77–290 mm long, 25–145 mm wide, 2.2–4.6 times longer than wide, acute at base, acuminate to caudate at apex, abaxial surface glabrous (or pubescent with eglandular trichomes to 0.6 mm long), adaxial surface glabrous (or sparsely pubescent along midvein with eglandular trichomes to 0.6 mm long). *Inflorescences* of sessile to short pedunculate thyrses (bearing pedunculate dichasia) in axils of leaves of younger growth or in axils of leaf scars on older (woody and leafless) branches and trunks (i.e., plants at least partially cauliflorous), peduncles (if present) to 7 mm long, thyrses 1 (–2) per axil or leaf scar, up to 13-flowered, ± compact (i.e., rachis usually less than 2 cm long) or with well-developed lateral dichasia (i.e., much branched), opposite or alternate at nodes, dichasia dichotomous or sometimes modified such that development occurs in only one axil per node of bracteoles for multiple nodes resulting in a ± linear appearance to dichasium, rachis pubescent (sometimes sparsely so) with erect to antrorse (to antrorsely appressed) eglandular trichomes to 0.1 (–0.2) mm long and sometimes also with evenly disposed erect glandular trichomes to 0.1 mm long (i.e., glandular puberulent), secondary peduncles (i.e., those subtending dichasia) pubescent like rachis (and usually glandular puberulent even if rachis is not). *Bracts* and bracteoles triangular to subulate, 1–3 mm long, 0.3–1.1 mm wide, abaxially pubescent like rachis. *Flowers* with pedicels 2–13 (–16 in fruit) mm long, pedicels pink, pubescent like rachis and usually also glandular puberulent (especially distally) and sometimes also with erect to flexuose eglandular trichomes to 0.5 mm long (rarely nearly glabrous). *Calyces* usually dark red (rarely pink but usually fading to pink with age), 9–19 mm long, persistent and ± accrescent in fruit, lobes sometimes incompletely or irregularly separating from one another, usually spreading with age, lance-linear to linear to linear-elliptic, (5–) 9–17 mm long, (1.5–) 2.0–6.0 mm wide, widest at base or near midpoint, subequal in size, abaxially and marginally glabrous or pubescent like rachis. *Corollas* pinkish to salmon colored, 38–50 mm long, externally glandular puberulent (and sometimes also with a few eglandular trichomes to 0.1 mm long as well), tube 10–19 mm long, 2.5–3.7 mm in diameter near midpoint, tube length:corolla length = 0.3–0.4 (–0.6), narrow proximal portion of tube 4–12 mm long, throat 4–8 (–10) mm long, 6.5–8.0 mm diam. (measured flat) at mouth, throat length:narrow proximal portion of tube length = 0.3–1.5 (–2.0), upper lip 23–40 mm long, lobes to 4.5 mm long, lower lip 25–33 mm long, lobes to 5 mm long. *Stamens* 26–40 mm long, not exserted or exserted up to 5 mm beyond upper lip of corolla, anther thecae cream to yellowish to pinkish or reddish, equally inserted, 2.9–3.8 (–4.4) mm long, lacking a basal appendage or with a minute and inconspicuous appendage-like swelling or extension (0.1–0.2 mm long) at base. *Pollen* prolate spheroidal to euprolate, 3-colporate, 6-pseudocolpate, P = 43–56 μm, E = 36–44 μm (P:E = 1.1–1.4). *Styles* pinkish, 37–52 mm long, proximally glandular puberulent, distally glabrous, stigma appearing subcapitate or distinctly and subequally 2-lobed, 0.2–0.4 mm long. *Capsules* (18–) 20–34 mm long, glabrous or glandular puberulent with trichomes to 0.1 mm long, stipe (6–) 9–17 mm long, head 11.0–18.5 mm long. *Seeds* 3–4 × ca. 2.5–3.9 mm, surfaces coarsely rugose or tuberculate-ridged. (n = 16; Daniel, 2000).

Phenology: flowering: throughout the year; fruiting: January–June, September–October. Collections with fruits are rare, but span much the same period as flowering; thus, fruiting likely also occurs throughout the year.

Distribution and habitat: island of New Guinea—Papua New Guinea (the mainland and several islands of the Bismarck Archipelago to the east) and in the northeasternmost portion of the province of Papua, Indonesia (Fig. 1). In addition to the collections noted below, Lindau (1894) cited a collection of "Turner" that he treated as *C. magnusianus* from Duke of York Island (East New Britain Province, between New Britain and New Ireland islands). Specimens identified as or attributed to *Calycacanthus* from the Solomon Islands at L (e.g., *Womersley & Whitmore BSIP1141*, *Lipaqeto BSIP3505*, *Gafui et al. BSIP9173*) do not appear to conform to *C. magnusianus* based on images of them. Plants occur infrequently to commonly, especially along streams, in primary and secondary lowland to montane rain forests, *Lithocarpus* (and *Lithocarpus-Castanopsis*) forests, and *Araucaria* forests at elevations from 25–2060 m. The species attains its highest elevation in the Eastern Highlands Province of Papua New Guinea near Okapa (*White NGF 9571*).

Local names: "fivis" (Bembi), "pidom bidom" (Rawa), "pissa'o" (Jal)—all from *Hoogland 4864*; "pisau" (*Pullen 1144 at LAE*); "qwasasang" (*Katik NGF 46741*); "tumeda" (Kutubu language; *Schodde 2396*); "marip" (Sambui Village; *van Royen 16092*); "navilovilo" (*Frodin NGF 26270*); "Ikowote" (Ipma-Baruya language, Wauko Village) and "Wusale" (Ipma-Baruya language, Ande Village)—both from Jorim et al. (2012).

Uses: Fresh, macerated leaves are used to treat all types of external sores in the Eastern Highlands Province of Papua New Guinea (Jorim et al., 2012). The species is sometimes cultivated for ornamental use in botanical gardens of southeastern Asia (e.g., China and Singapore) and Australia.

Conservation: The EOO was calculated as 617,941 km^2 (half or more consisting of open ocean), and the AOO as 300 km^2. Based on the AOO, the species could be assessed as Endangered (EN), if information on threats was known. Without such information, this relatively widespread and sometimes locally common species is best treated as Data Deficient (DD) at the present time.

A holotype was not designated in the protologue. Specimens of Hollrung's collection were distributed from B, where a specimen was undoubtedly retained, but which is no longer extant there. A duplicate specimen at K (ex B) with information corresponding to the protologue is herewith designated as the lectotype.

Although mostly erect shrubs or trees, collections of *C. magnusianus* have rarely noted "scrambling branches" (e.g., *Verdcourt & Galore 5130*) and indicated (possibly erroneously) a climbing habit (e.g., *Paijmans 1419*). No evidence of an adaptation for climbing (e.g., twining, adventitious roots, tendrils, etc.) was observed on any of the specimens studied. The thyrses possess at least two nodes that bear dichasia with up to four or more orders of development, and they sometimes appear to terminate in a dichasium. The density of glandular puberulence on parts of the inflorescence (except the corolla, ovary, and capsule) varies from absent (e.g., *Brass 5191* at UC) to sparse to dense; corollas, ovaries, and capsules are always externally glandular puberulent. Flowers are borne from ca. one meter above ground to near the shoot apex along the trunks of shrubs or trees, or "cauliflorous from youngest branchlets down to base of the plant" (*van Royen NGF 16254*). Cauliflory appears to be rare among Acanthaceae. In addition to its common occurrence in *C. magnusianus*, a similar occurrence (with inflorescences from leaf axils of young growth and from older woody stems) is reported for Neotropical *Justicia cauliflora* Durkee, which occurs in wet forests of Panama (Durkee, 1999). Colors of the "flower" provided on herbarium specimens are variously listed as red, light red, salmon-red, reddish orange, pink-red, bright pink, rose, rose-pink, pink, and white with pink patches. Based on most herbarium specimens that distinguish corolla from calyx colors, images, and personal observations of living plants, the calyx is red and the corolla is pinkish or salmon colored during anthesis (Fig. 5). Whatever descriptive terms are used for colors, the calyx is both colored (other than green) and darker in color than the corolla when both are present in the flower. However, the calyx fades to pink or nearly white after the corolla dehisces. *Hartley 13163* appears to differ from other collections by having anthers 4 to 4.4 mm long (vs. 2.9 to 3.8 mm long) and dark pink calyces and corollas simultaeously. In most other respects, including pollen, this collection generally conforms well to others of the species.

Additional specimens examined: INDONESIA. Papua: Hollandia Stad, small wooded hill near post office, *H. McKee 1829* (K, L-image, LAE); Dessa Staat Hollandia, Kpg. Nemo, Eiland NNG bij de Tami River, [ca. 02°40'33.78"S, 140°54'0.31"E], *F. Rappard 875* (K, L, LAE); Onderafd. Hollandia, Nafri (Jautefah-baai), [02°40'25.08"S, 140°42'39.08"E], *F. Schram 2875* (L, LAE). PAPUA NEW GUINEA. Central: Mafulu [ca. 08°31'0"S, 147°01'00"E], *L. Brass 5191* (K, UC, US-image); Koitaki [ca. 09°24'49.11"S, 147°26'57.46"E], *C. Carr 12287* (BM, K, L); Sogeri Region, 09°28'S, 147°31'E, *H. Forbes 887* (BM); Tapini Subdistrict, Tapini area, 08°18'S, 146°48'E, *Y. Lelean NGF 46388* (K, L, US-image); Rubulogo Creek, ca. 18 mi N of Port Moresby [ca. 09°11'42.99"S, 147°13'30.13"E], *R. Pullen 6654* (K, L); Pt. Moresby Subdistrict, Kuriva Forestry Area, near Veimauri Rv., 09°05'S, 147°05'E, *H. Streimann & A. Kairo LAE 51530* (K, L, US-image); between S coast and Owen Stanley Range, Comm. M. Veitch 1897, *Burke s.n.* (K); Bisiatabu (near Rouna Falls), [ca. 09°25'26.20"S, 147°23'09.54"E], *C. White 360* (BM). Chimbu**:** Gumine Subdistrict, 25 km NE of Karimui [ca. 06°12'04.17"S, 144°58'22.86"E], *K. Paijmans 1419* (L); Chuave Distsrict, Kenangi, near Mai River [06°17'33.90"S, 145°05'14.15"E], *T. Reeve 1628* (K). Eastern Highlands: Purosa [ca. 06°39'57.46"S, 145°33'52.90"E], Okapa area, *L. Brass 31763* (K, L, US-image); Arau [ca. 06°20'49.68"S, 145°54'52.72"E], *L. Brass 32067* (K, L, US-image); Kassam, [ca. 06°13'58.05"S, 146°00'01.28"E], *L. Brass 32425* (L, US-image); Kainantu Subdistrict, Kassam, 06°15'S, 145°55'E, *R. Donunaba NGF 49116* (L); near Wanatabi, ca. 15 mi SW of Okapa [ca. 06°39'55.05"S, 145°26'12.45"E], *T. Hartley 13163* (K, L, RSA, US-image); Okapa Patrol Post, 06°35'S, 145°40'E, *E. Henty NGF 10612* (K, L); Kainantu Subdistrict, Kassam Pass, 06°12'S, 146°02'E, *E. Henty & M. Coode NGF 29185* (L); Kainantu Subdistrict, Kassam Pass, 06°15'S, 146°03'E, *A. Kairo & H. Streimann NGF 35717* (K, L, US-image); Kainantu Subdistrict, Aiyura–Lae Road, 3 miles from Station [ca. 06°20'51.08"S, 145°55'46.63"E], *A. Millar NGF 22719* (L); Kainantu Subdistrict, Kassam Pass, *A. Millar NGF 22734* (L); Akinantu Sub-district, Kainatu–Ramu Divide, *R. Robbins 984* (L); Kainantu Subdistrict, top of Kassam Pass, 06°13'S, 146°04'E, *H. Streimann NGF 47901* (L); Kainantu Subdistrict, above Aiyura and Noreikora valleys, "06°30'S, 145°75'E" [ca. 06°30'S, 145°55'E], *J. Wheeler ANU 5924* (K, L); Okapa Patrol Post, 06°35'S, 145°40'E, *K. White NGF 9571* (K, L); Okapa Subdistrict, vicinity Wonatabe, 15 mi S from Okapa, 06°35'S, 145°40'E, *J. Womersley NGF 17631* (K); Kainantu Subdistrict, Andandara, 06°30'S, 145°55'E, *J. Womersley NGF 24713* (L); Awande near Okapa, 06°35'S, 145°40'E, *J. Womersley NGF 24935* (K, L). East New Britain: Malpas, near Milim Wide Bay, 05°13'S, 152°02'E, *G. Weiblen 512* (L-image). Madang: Josephstaal District, 04°30'S, 145°02'E, *Ama & Takeuchi s.n.* (L-image); ca. 8 km WNW of Christensen Research Institute, ca. 2 km W of Baitabag Mission just W of Amron village, 05°08'S, 145°45'E, *T. Daniel & M. Jebb 6518* (CAS, K, LAE, MO); ca. 8 km W of Bagildik on Madang–Bogia Hwy., 04°55'S, 145°43'E, *T. Daniel & P. Forster 6575* (CAS); Ramu Valley, 68 km SW of Gum River, S of Madang toward Lae, 05°34'S, 145°25'E, *T. Daniel et al. 6529* (CAS); vic. of headwaters of Gogol River, ca. 20 km NW of Utu Mission, ca. 45 km (air) WNW of Madang, 05°05'S, 145°22'E, *T. Daniel et al. 6606* (CAS, LAE); Usino Subdistrict, Amiaba River, 05°25'S, 145°25'E, *D. Foreman et al. NGF 45850* (L, LAE), *NGF 45903* (L, LAE), *NGF 45989* (L, LAE); Bundi Subdistrict, Brahman, 05°44'S, 145°25'E, *E. Henty 49268* (L, LAE); Dumpu Subdistrict, Boringe, [05°50'S, 145°50'E], *E. Henty & Sayers NGF 20576* (K, L, LAE, US-image); near Amele village in hills behind Madang, [ca. 05°15'54.52"S, 145°38'36.97"E], *R. Hoogland 4864* (BM, K, L, LAE, US-image); along Puria River, foot (NE) of Mt. Hellwig, [ca. 05°52'11.87"S, 145°40'52.84"E], *R. Hoogland 5178* (BM, K, L, LAE, US-image); Madang Subdistrict, Gogol River, 05°10'S, 145°25'E, *P. Katik NGF 46504* (K, L, LAE); Urikina (Usino), 05°35'S, 145°25'E, *K. Kerenga & Y. Lelean LAE 73890* (LAE); hills of upper Ramu, *Lane-Pooke 637* (K); Constantinhafen [ca. 05°30'33.58"S, 145°01'28.69"E], *Lauterbach CAG 12* (L); Gogol TRP, 05°15'S, 145°45'E, *W. Moi 146* (LAE); Gogol Sapi-Catchment, 05°15'S, 145°35'E, *K. Rau 179* (LAE); Madang District, hill above Gum River near Ohu Village, 05°15'S, 145°41'E, *Regalado & Katik 1111* (F, K); Madang Subdistrict, Ramu Valley, ca. 5 mi SE

Faita airstrip, [ca. 05˚40'05.20"S, 145˚20'02.53"E], *J. Saunders 197* (BM, K, L, LAE, US-image); Ramu Subdistrict, N of Walium Patrol Post, 05˚30'S, 145˚24'E, *S. Sohmer & P. Katik LAE 75123* (BM, K, L, LAE); near Gogol River, Nara logging area block 8, *Verdcourt & Galore 5130* (K, L); 4 km N of Baisarik village, road to Taipensarik village, 05˚13'S, 145˚30'E, *J. Waikabu LAE 70351* (LAE); Constantinhafen, *O. Warburg 21212* (BM); Gogol Valley, 05˚10'S, 145˚25'E, *J. Womersley NGF 13470* (K, L, LAE); Tiganuntz River, near Aiome, tributary of main stream, [ca. 05˚08'22.72"S, 144˚43'46.08"E], *J. Womersley NGF 24762* (LAE). Manus: Manus Island, 02˚02'S, 147˚01'E, *M. Sands 2679* (K). Morobe: Oomsis,[ca. 06˚41'00.83"S, 146˚48'03.27"E], *L. Brass 29177* (K, US-image), *29278* (K, L, US-image); Sattelberg, [ca. 06˚29'04.09"S, 147˚45'59.92"E], *Clemens 970* (L); Boana, [ca. 06˚25'46.39"S, 146˚49'32.02"E], *M. Clemens 41657* (L, RSA, UC, US-image); Finschhafen-Umboi Is. Subdistrict, Sisilla River area, 05˚29'S, 147˚47'E, *B. Conn & P. Katik LAE 66043* (L); near Garagos Creek, on Bulolo Rd., *A. Floyd 7240* (L); ca. 2.5 miles N of Gurukor, 06˚50'S, 146˚38'E, *T. Hartley 9906* (L); Oomsis Creek, ca. 18 miles W of Lae, 06˚43'S, 146˚47'E, *T. Hartley 10441* (L, P-image); Kuali Creek, ca. 5 miles S of Wau, [ca. 07˚22'22.85"S, 146˚46'17.86"E], *T. Hartley 11471* (L); Wau Subdistrict, head of Sandy Creek, 07˚20'S, 146˚45'E, *A. Kairo & H. Streimann NGF 30936* (K, L); Wau Subdistrict, Upper Watut Valley, 07˚11'S, 146˚35'E, *A. Kairo & H. Streimann NGF 45238* (K, L); Lae Subdistrict, 3 mi from Suinim Village near Busu River, 06˚35'S, 146˚55'E, *P. Katik NGF 46741* (K, L); Lae Subdistrict, Gurako log. rd. 1 mile from Gabansis, [ca. 06˚43'44.65"S, 146˚46'22.07"E], *P. Katik & G. Larivita 38090* (L); Bulolo Subdistrict, Bulolo Forestry Plantation Road 6, 07˚15'S, 146˚40'E, *P. Katik & G. Larivita LAE 62039* (K, L, MO, US-image); Lae Subdistrict, Bupu Village, 06˚20'S, 146˚45'E, *A. Millar NGF 40979* (K, L); Lae Subdistrict, Garagos, 27 miles from Lae on Wau Road, [ca. 06˚43'35.39"S, 146˚42'33.27"E], *H. Streimann LAE 51927* (L); Bumsi River, tributary of Busu River, 06˚27'S, 147˚00'E, *P. van Royen NGF 16074* (K, L); Sambui-Gawan, Mon Hill, Rawlinson Range, 06˚26'S, 147˚00'E, *P. van Royen 16092* (K); Kauli Creek above Wau, 07˚20'S, 146˚45'E, *P. van Royen NGF 16254* (K, L, US-image); Lae Subdistrict, Oomsis Forestry Station, 06˚43'S, 146˚47'E, *J. Wiakabu & K. Kerenga LAE 73357* (K, L); Oomsis logging area, 20 mi from Lae, 06˚40'S, 146˚45'E, *J. Womersley NGF 17620* (K, L). New Ireland**:** Namatanai Subprovince, Hans Meyer Range, E of Mandih Lake, ca. 6 km WNW of Taron on east coast, 04˚26'S, 152˚59'E, *M. Sands et al. 2162* (K). Northern (Oro): Kokoda trail, 08˚50'S, 147˚45'E, *A. Millar NGF 23587* (K). Southern Highlands: near Waro airstrip, 20 km SSW of Kutubu, 06˚31'S, 143˚10'E, ca. 10 km farther E, *M. Jacobs 9135* (L); near Moro, Lake Kutubu [ca. 06˚21'12.20"S, 143˚15'43.39"E], *R. Schodde 2396* (K, L, US-image). Western Highlands**:** Hagen Subdistrict, Hallstrom Flora and Fauna Sanctuary, 05˚35'S, 144˚10'E, *A. Millar NGF 37701* (K, L); Jimmi Valley, Tagan River Valley, 05˚30'S, 144˚10'E, *J. Womersley & A. Millar NGF 8513* (K, L). West New Britain: 9 mi N of Kandrian, "16˚15'S, 149˚35'E" [06˚07'50.59"S, 149˚31'14.87"E], *J. Buderus NGF 23918* (K, L, US-image); District E. New Britain, Subdistrict Pomio, road W of Fulleborne Harbour, ca. 1 mi, "06˚10'S, 150˚40'E" [ca. 06˚07'23.80"S, 150˚35'47.91"E], *J. Croft et al. NGF 12999* (K, L); West Nakanai, Galilo Village, near Cape Hoskins, [05˚28'30.49"S, 150˚32'55.97"E], *A. Floyd 3548* (L); E of Airagilpua, Talasea, *D. Frodin NGF 26270* (K, L); Talasea, near Cape Gloucester Patrol Post, "05˚27'S, 148˚30'E," [05˚26'50.04"S, 148˚25'8.84"E], *D. Frodin NGF 26614* (K, L); Kandrian Sub-district, Dandeng Village, 06˚15'S, 149˚45'E, *A. Gillison NGF 22453* (L); ridge above Kilenge, "05˚25'S, 148˚25'E" [ca. 05˚28'40.61"S, 148˚22'3.36"E], *C. Ridsdale NGF 30416* (L); Kandrian Subdistrict, 06˚06'S, 150˚40'E, *D. Sayers NGF 21904* (L). West Sepik: 22 km E of Lumi, 03˚29'S, 142˚14'E, *P. Heyligers 1642* (LAE, CANB-image); 26 km W of Aitape, 03˚08'S, 142˚06'E, *P. Heyligers 1697* (LAE, CANB-image). Province not determined: Kaiser-Wilhelmsland, Rl. Baum in den Wäldesu des Rani Geb. [Kani Mt, Range?], *R. Schlechter 17498* (UC).

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COLUMNEA BLANCOI (GESNERIACEAE), A NEW SPECIES FROM THE CENTRAL PACIFIC REGION OF COSTA RICA

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Abstract. We describe and illustrate a new species of *Columnea* from the Central Pacific region of Costa Rica. *Columnea blancoi sp. nov.* is morphologically similar to *Columnea canarina*, from Panama which it can be distinguished by having stems that are flaky and sericeous distally, ovate bracts, entire, green and shorter calyx lobes, yellow corolla that is glandular-pilose externally, with a marginal purple-red line 1–2 mm wide on all lobes internal and externally, and a shorter ventral corolla lobe and style. A taxonomic description, illustrations, a distribution map, conservation status, and comments on how *C. blancoi* differs from other morphologically related species are provided.

Keywords: *Columnea canarina, Columnea lariensis*, Endemism, Premontane Forest, Fila Costeña, Zona de Los Santos

Resumen. Describimos e ilustramos una nueva especie de *Columnea* de la región del Pacífico Central de Costa Rica. *Columnea blancoi sp. nov.* es morfológicamente similar a *Columnea canarina*, de Panamá la que se distingue por tener tallos escamosos y seríceos distalmente, brácteas ovadas, los lóbulos del cáliz enteros, verdes y más cortos, la corola amarilla, glandular-pilosa externamente y con una línea rojo-púrpura marginal de 1–2 mm de ancho en todos los lóbulos interna y externamente, y el lóbulo ventral de la corola y el estilo más cortos. Ade**má**s, se proporciona su descripción taxonómica, ilustración, mapa de distribución, estado de conservación y comentarios de c**ó**mo difiere *C. blancoi* de especies morfológicamente relacionadas.

Palabras claves: *Columnea canarina, Columnea lariensis*, Endemism, Premontane Forest, Fila Costeña, Zona de Los Santos

Gesneriaceae is the third largest family in the order Lamiales with around 3400 species (Stevens, 2001; Weber et al., 2013). It is divided into subfamilies Coronantheroideae, Cyrtandroideae, and Gesnerioideae, the latter of which encompasses most of the New World species (Weber et al., 2013). Gesnerioideae is itself subdivided into five tribes, of which Beslerieae and Gesnerieae account for most of the species. Gesnerieae includes the species rich genus *Columnea* L., in which new species continue being described, particularly from Colombia and Ecuador (Amaya-Márquez et al., 2015; Clark et al., 2021; Smith et al., 2013b; Tobar et al., 2022).

Columnea comprises more than 200 species ranging from Mexico through Central and South America, and the Antilles (Clark et al., 2020). Species in the genus have mostly red or yellow flowers that are pollinated exclusively by hummingbirds (Serrano-Serrano et al., 2017). In addition, *Columnea* can be distinguished by its epiphytic habit and berry fruits and is very diverse in morphology, with variation in whether plants are erect or pendant, bear isophyllous or anisophyllous leaves with or lacking markings, as well as variation in corolla shape and color. Morphological and molecular phylogenetic studies have started to elucidate the relationships within the genus testing previous sectional classifications (Smith, 1994; Smith and Sytsma, 1994a; 199b; 1994c; Smith et al., 2013b).

In this study, we propose a new species of *Columnea* from Costa Rica, another rich country for this genus. The new taxon is known from the Central Pacific slope, in the Zona de Los Santos region (Cordillera de Talamanca), which has high endemicity, and in the north of the Fila Costeña. Unfortunately, the Zona de Los Santos has been slowly deforested to cultivate coffee plantations in the last decades (Fig. 1). Despite this, new endemic plant species have recently been found and described in this region, which is now threatened by the expansion of coffee plantations (Estrada and Santamaría, 2010; Jiménez et al., 2016; Morales, 2018a; 2018b; Cedeño et al., 2020; Jiménez and Hidalgo-Mora, 2021; Juárez and Morales, 2021).

Materials and Methods

This study was based on fieldwork performed in 2022, and all specimens prepared were deposited at CR and USJ. Measurements were taken from fresh material and one previously collected herbarium specimen. The illustrations were digitized and diagrammed in a composite plate using Adobe Photoshop CS6,® and the drawing was digitally delineated and shaded with an Apple Pencil® in Procreate application for iPad Pro® tablet (Apple Inc.). *Columnea* specimens of CAS, CR, MO, PMA, and USJ herbaria were examined physically. The type material of the species

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FIGURE 1. Habitat at the type locality of *Columnea blancoi* J.E. Jiménez, Chinchilla & Kriebel in Zona de Los Santos region, showing the alteration of the natural habitat as a result of the human settlements and the expansion of coffee plantations.

of *Columnea* most morphologically similar to the new taxon were studied through digital images available in the JSTOR repository (https://www.jstor.org). Herbarium acronyms follow Thiers (2022). Terminology for vegetative and reproductive structures follows Kriebel (2010) and Tovar et al. (2002). Morphological characters used in Table 1 were extracted from Kriebel (2010).

The locations of the specimens examined were classified according to the Holdridge life zone system (Holdridge, 1967). The phenology was determined from the examination of herbarium specimens and their labels. A map was prepared using the QGIS 3.8 Zanzibar program (QGIS Development Team, 2019), based on a satellite image of the year 2000 from NASA's Jet Propulsion Laboratory, National Imagery and Mapping Agency of the U.S. The conservation status of each species was assessed according to the methodology of the International Union for Conservation of Nature (IUCN, 2019). The Extent of Occurrence (EOO) and Area of Occupancy (AOO) were estimated based on the studied specimens using geographical data with the Geospatial Conservation Assessment Tool (GeoCAT, Royal Botanic Gardens, Kew: http://geocat.kew.org).

TAXONOMY

Columnea blancoi J.E. Jiménez, Chinchilla and Kriebel, *sp. nov.*

TYPE: COSTA RICA. San José, Tarrazú, San Lorenzo, San Joaquín, bosque secundario, 1250 m, 9°35'28.41"N, 83°59'40.20"W, 22 September 2022 (fl), *J. E. Jiménez 6500* (Holotype: USJ, isotype: CR). Fig. 2–3.

Similar to *Columnea canarina* Wiehler because of its anisophyllous leaves, larger leaf blade with a red to deep purple red or fuchsia red spot abaxially, and pubescent yellow corolla, but differs in having flaky stems, sericeous distally (vs. not flaky, completely sericeous), ovate floral bracts (vs. lanceolate), entire and green calyx lobes, 1.1–2.3 cm long (vs. serrate, yellow, 2.5–3.6 cm long), with a marginal purple-red line of 1–2 mm wide on all corolla lobes, glandular-pilose externally (vs. without marginal purple-red line, eglandular-pilose), shorter ventral lobe (1.0–1.3 cm vs. 1.9 cm), and shorter style (3.4–5.3 cm vs. 6.2 cm).

Epiphytic *herb* up to 2.0 m tall. *Stems* terete, branched with shoots to 1.5–1.9 m long, 0.7–1.6 cm in diameter, flaky, sericeous distally to glabrescent with age; internodes 1.5–

Table 1. Morphological differences between *Columnea blancoi* and *C. canarina*, and the four most similar species present in Costa Rica.

Character	*C. blancoi*	*C. canarina*	*C. lariensis*	*C. maculata*	*C. verecunda*
Stem	Flaky, sericeous distally	Smooth, sericeous	Not flaky, villous	Flaky, pilose	Flaky, sericeous distally
Large leaf blade shape dimensions (cm)	6.4–16.5 × 1.9–5.0	12–20 × 4.0–5.5	8.5–15 × 1.6–3.0	17–26 × 6.0–9.5	6.0–12.5 × 1.4–3.0
Abaxial surface of the larger leaf blade	Irregular red to deep purple-red or fuchsia red spot covers the apex or up to the apical third	Light green with dark red tips and sometimes additional red spotting below	Irregular red spot in the apex or up to half of the blade	Irregular red spot in the apex or up to the apical third	Irregular red to fuchsia red spot covers the apex, or light purple to green purplish in all its extension
Number of flowers per inflorescence	1–4	1–4	1–3	1–3	1–5
Calyx lobe shape	Ovate to ovate-lanceolate	Lanceolate-elliptic	Oblong to obovate	Lanceolate	Lanceolate to linear-lanceolate
Calyx lobe margin	Entire	Serrate	Denticulate to lobulate	Fimbriate	Entire
Calyx color	Green	Yellow	Unknown	Green to purple greenish	Green with the purple apex to purple
Corolla indument	Glandular-pilose	Eglandular-pilose	Villose	Sericeous	Sericeous
Corolla color	Yellow with a marginal purple-red line of 1–2 mm wide on all lobes	Yellow	Yellow	Yellow with longitudinal purple lines and irregular spots	Usually yellow to red or pinkish
Distribution	720–1500 m, Central Pacific of Cordillera de Talamanca (Zona de Los Santos) and north of Fila Costeña, Costa Rica	1000–1400 m, Caribbean Watershed of Cordillera de Talamanca (Fortuna Dam site, Chiriquí, Panama)	1300–1500 m, Caribbean Slope, Cordillera de Talamanca (cuenca Río Lari), Costa Rica	100–900 m, Caribbean Slope, Cordillera Volcánica Central and Cordillerade de Talamanca, Costa Rica, and Panama	550–1650 m, Caribbean and Slope of Cordilleras Guanacaste, Tilarán, Central and E Talamanca, Costa Rica

3.5 cm long near the base, then 0.5–1.3 cm long clustered at branch apex. *Leaves* opposite, strongly anisophyllous with age, isophyllous when seedling and young; petioles terete, 0.2–0.9 mm long, sericeous; larger blade oblong to oblanceolate, 6.4–16.5 × 1.9–5.0 cm, basally obliquely rounded, apically acute to acuminate, coriaceous, adaxially green, slightly sericeous to glabrescent, abaxially light green or whitish green to light purple red with irregular red to deep purple red or fuchsia red spot, that covers the apex or up to the apical third, sericeous; margin entire shallowly and remotely crenate, ciliate; veins adaxially impressed, glabrescent, abaxially raised, sericeous, light-green to pinkish or light purple red, lateral veins 5–7; smaller blade linear, sessile, 0.4–2.7 × 0.2–1.1 cm, sericeous, adpressed to the stem and sometimes deciduous. *Inflorescences* axillary, reduce cyme of 1–4 flowers; bracts ovate, acuminate, 0.2–1.1 cm, long sericeous, deciduous; pedicels terete, 0.4–1.7 cm long, sericeous. *Calyx* clasping, 5-lobed, erect, green, white-sericeous, with abaxially raised main vein; lobes ovate to lanceolate, obtuse to acuminate, 1.1–2.3 cm long, entire. *Corolla* funnel-shaped, 5.2–6.7 cm long, erect, zygomorphic, gibbous at the base, yellow with a marginal purple-red line of 1–2 mm wide on all lobes, sparsely glandular-pilose internally, densely glandular-pilose externally; tube 2.9 a 4.1 cm long, 0.35–0.60 cm wide proximally, 0.5–0.7 cm wide distally, the mouth of the tube ca. 0.5–0.8 cm in diameter; limb bilabiate, upper limb with two fused dorsal lobes and two lateral lobes, lower limb with an extended ventral lip; dorsal lobes connate, concave, subquadrate with a small rounded apiculum at the

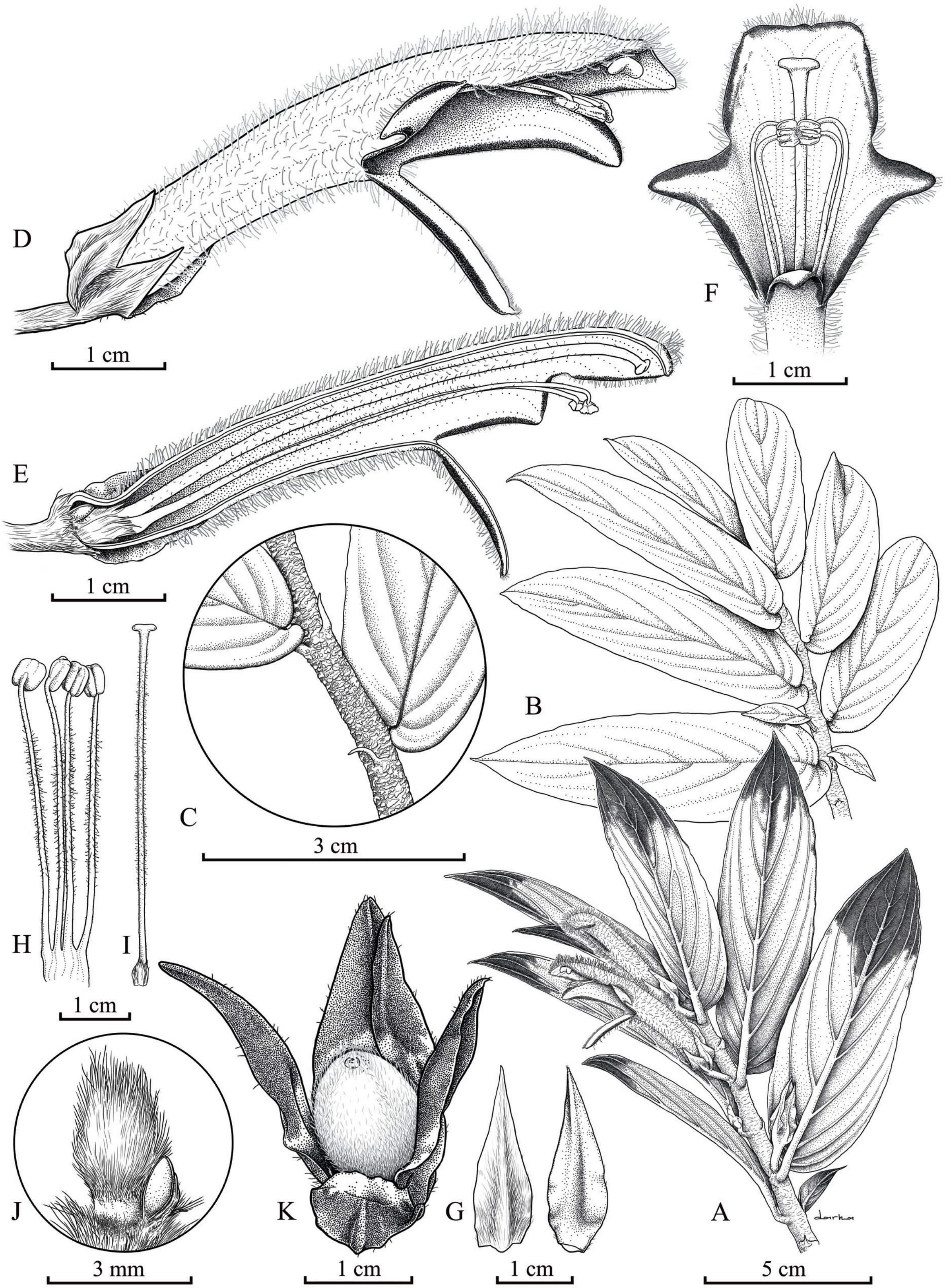

FIGURE 2. *Columnea blancoi* J.E. Jiménez, Chinchilla & Kriebel. **A–B**, Leaves and flowers in their natural position in abaxial (A) and adaxial (B) surfaces. Note the irregular red to fuchsia red spot on the abaxial surface; **C**, Close-up of the flaky stems and the linear smaller blade shape; **D**, Close-up of the flower. Note the glandular-pilose indument externally, and the marginal purple line in all corolla lobes; **E**, Lateral dissected view of the corolla; **F**, Ventral view of the flower distally; **G**, Abaxial (right) and adaxial (left) view of the sepals; **H**, Stamens; **I**, Pistil; **J**, Ovary (left) and nectary gland (right); **K**, Fruit with the marcescent calyx. Drawing based on live specimens of *J. E. Jiménez 6500* and *J. E. Jiménez et al. 6576* (USJ).

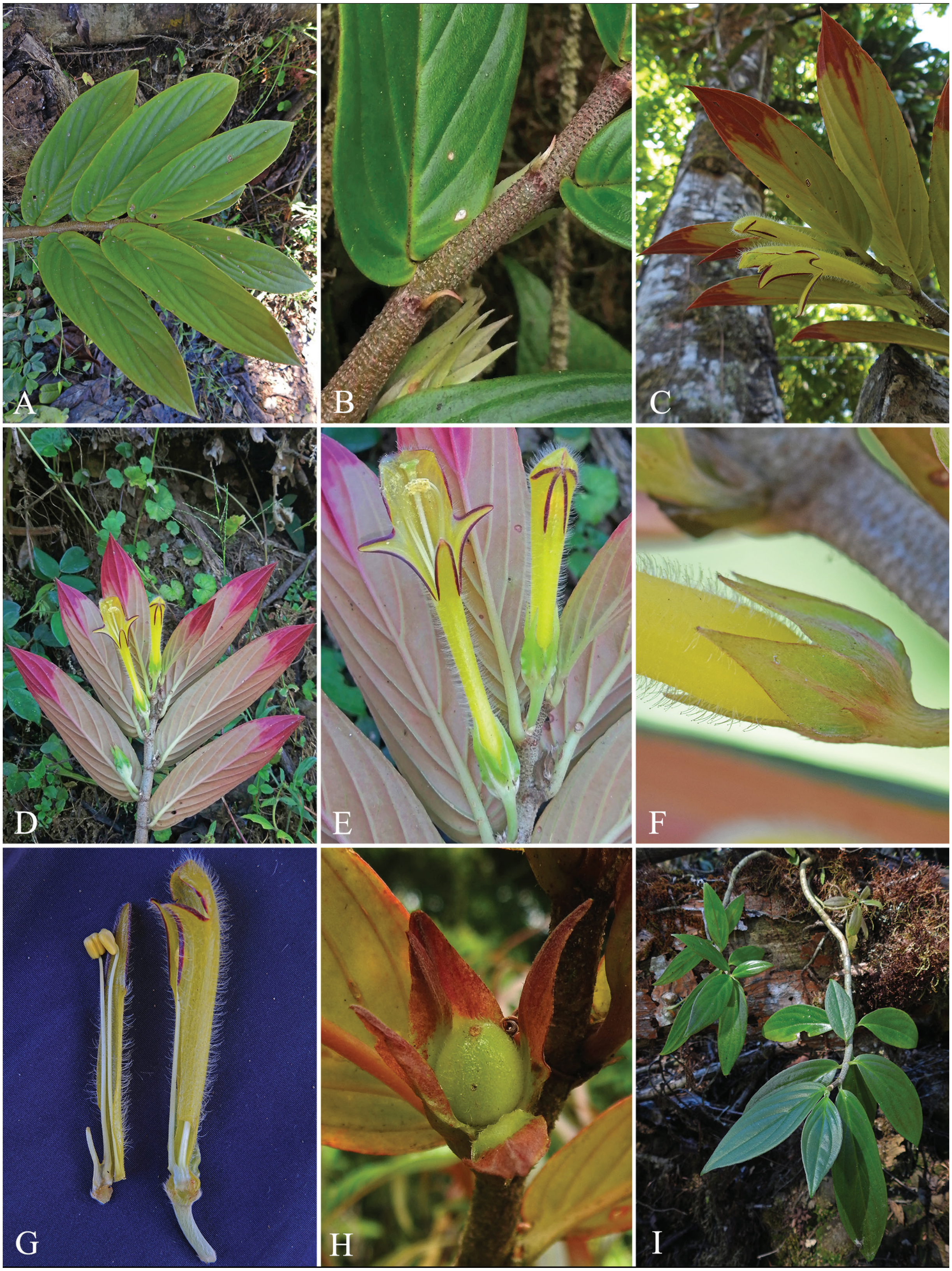

FIGURE 3. *Columnea blancoi* J.E. Jiménez, Chinchilla & Kriebel. **A**, Anisophyllous leaves; **B**, Close-up of the flaky stems and the linear smaller blade shape; **C**, Leaves and flowers in their natural position; **D**, Abaxial surface of the larger leaf blade with the irregular red to fuchsia red spot; **E**, Ventral view of the flower. Note the indument and the marginal purple line in all corolla lobes; **F**, Calyx and the close-up of the glandular-pilose indument on the corolla; **G**, Laterally dissected flower; **H**, Fruit and the marcescent calyx; **I**, A juvenile individual with isophyllous leaves. Photos based on live specimens of *J. E. Jiménez 6500* and *J. E. Jiménez et al. 6576* (USJ).

apex, 1.2–1.5 × 1.0–1.4 cm; lateral lobes triangular, 0.3–0.9 × 0.2–0.7 cm, incurved; ventral lobe narrowly oblong, ca. 1.0–1.3 × 0.2–0.7 cm, recurved. *Stamens* 4; filaments connate at the base, 0.2–0.6 cm long, free ca. 3.8–4.7 cm long, white, pilose-glandular anthers ca. 0.3 × 0.2 cm, not included in the corolla throat, dehiscing by longitudinal slits, fused. *Pistil* 1; ovary ca. 0.3 mm long, conical, densely sericeous; style 3.4–5.3 cm long, white, pilose-glandular stigma bilobed, papillate, green, included in the corolla tube; nectary a bilobed dorsal gland, light green. *Fruits* a berry, subglobose to ovate, 0.9–1.2 cm in diameter, green when immature, pilose to sericeous, with marcescent red calyx. Mature fruit and seeds unknown.

Distribution and habitat: Currently known only from the Central Pacific slope of Costa Rica where it grows at 720–1500 m of elevation. It has been collected in the Zona de Los Santos region (Cordillera de Talamanca), specifically San Lorenzo de Tarrazú, and Sukia de Dota, and north of the Fila Costeña, in Dos Bocas de Quepos, near the border of the provinces of Puntarenas and San José (Fig. 4). It inhabits the primary and secondary forest in the premontane pluvial forest.

Phenology: Plants have been collected flowering in March, April, October to December, and bearing fruits in May.

Eponymy: The specific epithet honors the Costa Rican botanist and professor Mario Alberto Blanco Coto, who is a professor at the University of Costa Rica (UCR). Professor Blanco has contributed to the study of neotropical flora, has taught botany courses at the UCR and the Organization for

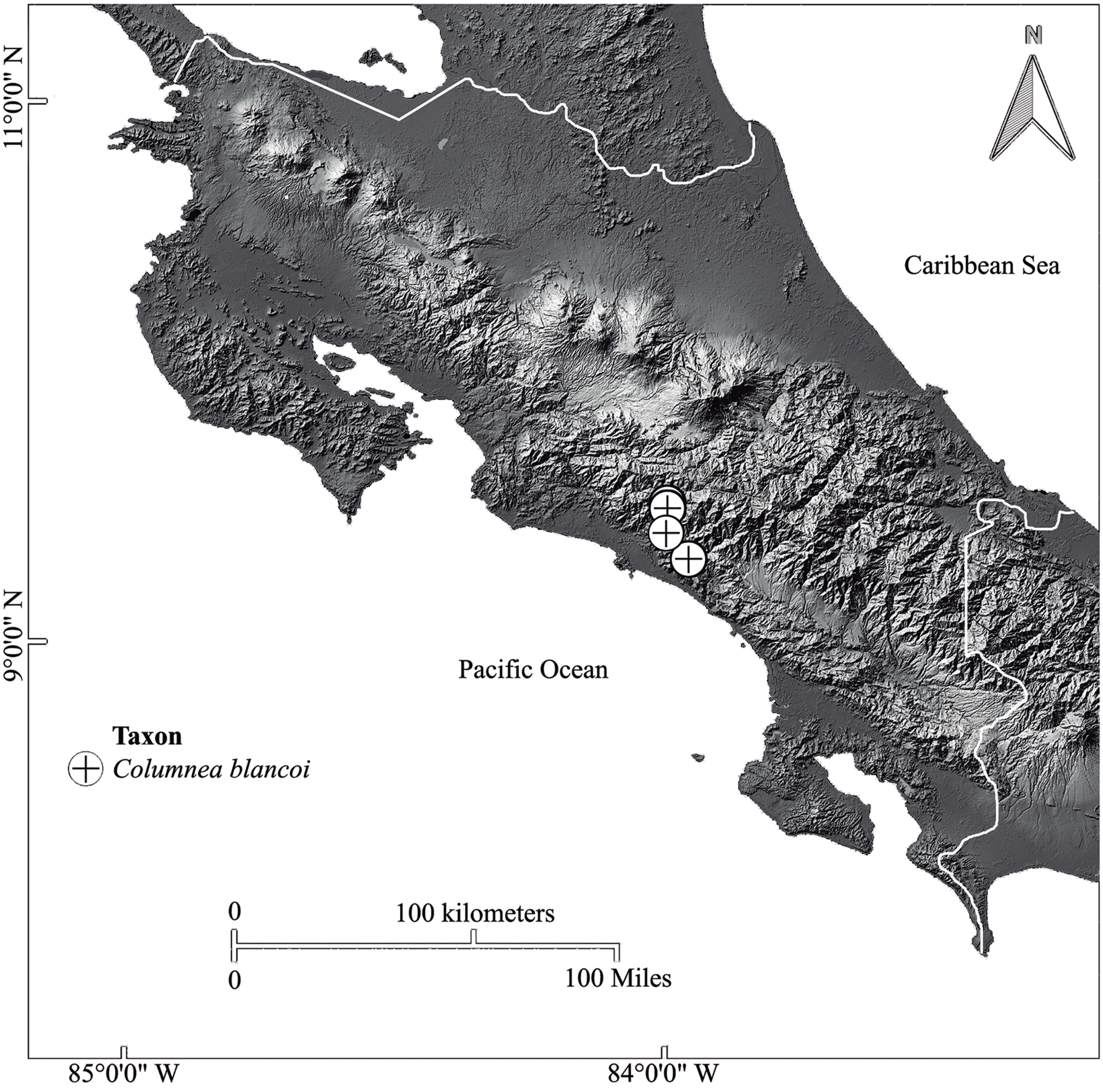

FIGURE 4. Distribution of *Columnea blancoi* J.E. Jiménez, Chinchilla & Kriebel based on herbarium specimens.

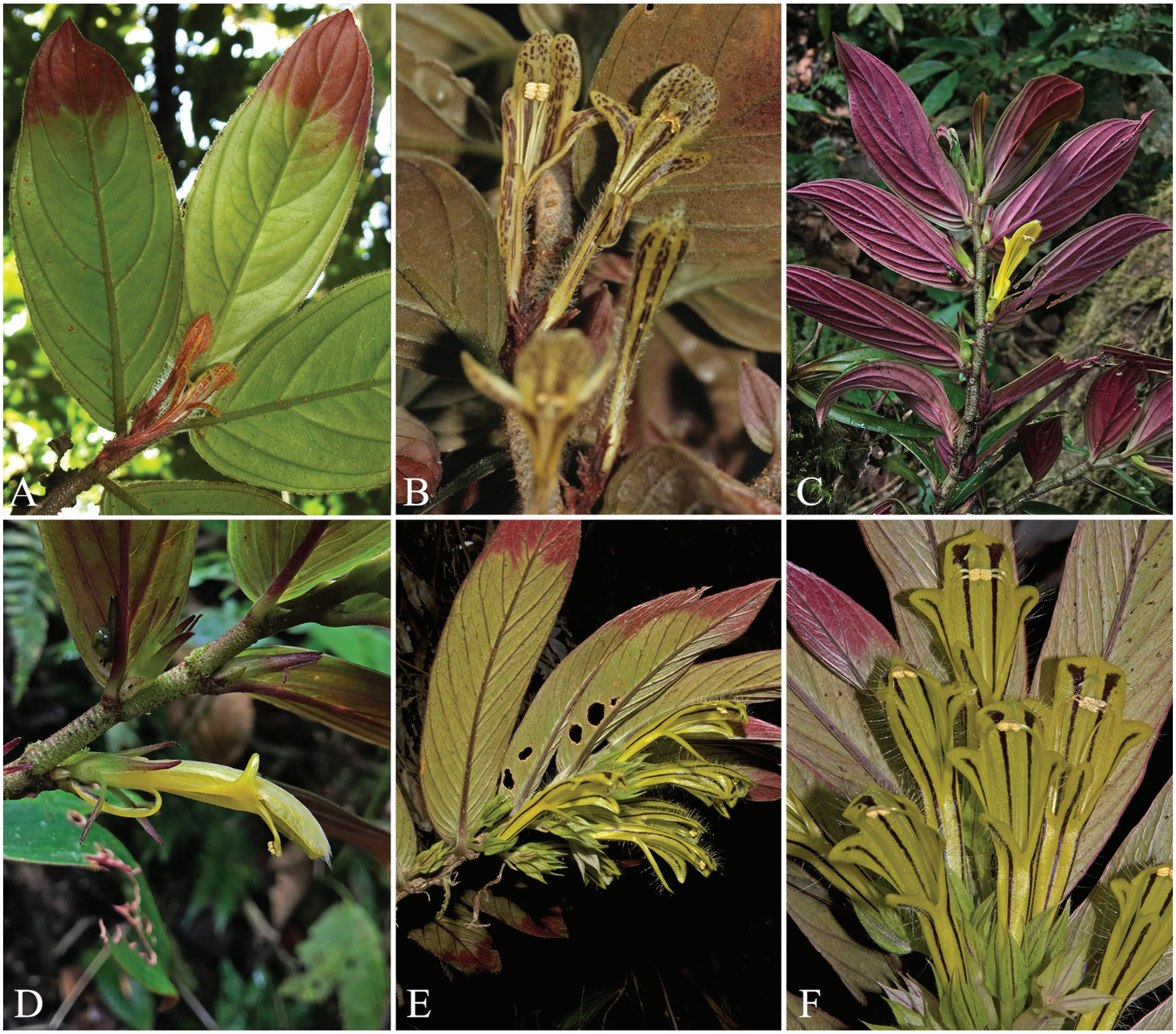

FIGURE 5. Three morphologically similar species of *Columnea blancoi* J.E. Jiménez, Chinchilla & Kriebel in Central America; **A–B**, *Columnea maculata* C.V. Morton: A, from Costa Rica (*J. E. Jiménez 6692*, USJ), and B, from Panamanian Caribbean (*L. E. Skog and S. S. Hodapp 5438*, US); **C–D**, *Columnea verecunda* C.V. Morton (*J. E. Jiménez et al. 4357*, USJ); **E–F**, *Columnea zebrina* Raymond (*J. L. Clark 12601*, US).

Tropical Studies (OTS), and is one of the most influential mentors of the new generations of botany students in the country.

Vernacular name: Known as "*panza de mono*," monkey belly.

Conservation status: *Columnea blancoi* is endemic to Costa Rica, known from three locations in the Central Pacific. Its extent of occurrence (EOO) was estimated at 23.372 km^2 with an area of occupancy (AOO) of 16 km^2. The species is known from two disturbed localities by deforestation in the Los Santos Forest Reserve, and the third location at the forest edge in the Fila Costeña outside protected wilderness areas. Currently, its populations are threatened by fragmentation and habitat loss caused by deforestation, and the expansion of human settlements, livestock, and coffee plantations. Further studies on the ecology and population size of this species are required to promote its long-term conservation. Therefore, the species is listed as Endangered (EN) under criteria B1ab(i, ii)+2ab (i, ii).

Additional Specimens Examined: COSTA RICA. San José: Dota, Santa María, Reserva Forestal Los Santos, Sukia, a la orilla de la calle frente a la Escuela de Sukia, 9°29'37.34"N, 83°58'30.58"W, 720 m, 2 November 2022 (fl), *I. Chinchilla 4776* (CR, USJ); Tarrazú, San Lorenzo, 1 km antes de llegar al puente sobre el río Naranjillo, viniendo desde Santa Marta, 9°35'28.36"N, 83°59'40.24"W, 1250 m, 3 April 2022 (fl), *J. E. Jiménez and J. Flores 6415* (USJ); Tarrazú, San Lorenzo, San Joaquín, 9°34'45.35"N, 83°59'34.11"W, 1417 m, 22 April 2022 (fl), *J. E. Jiménez 6490* (USJ); Tarrazú, San Lorenzo, San Joaquín, 9°35'28.41"N, 83°59'40.20"W, 1250 m, 21 May 2022 (fr), *J. E. Jiménez et al. 6576* (USJ); Tarrazú, San Lorenzo, Cerro El Milagro, entrando por San Joaquín de Tarrazú, sobre carretera a mano izquierda antes de llegar a la escuela, 9°34'45.35"N, 83°59'34.11"W, 1417 m, 26 December 2022 (fl), *J. E. Jiménez and M. F. Cordero 6766* (USJ). Puntarenas: Aguirre [Quepos], Savegre, Dos Bocas, Finca Las Filipinas, propiedad de Adolfo Chinchilla, 9°24'13.54"N, 83°55'7.72"W, 935 m, 18 April 2013 (fl), *I. Chinchilla 283* (CR).

Columnea blancoi is recognized by its flaky stems that are sericeous distally, anisophyllous leaves, the larger leaf blade with a red to deep purple-red or fuchsia red spot distally abaxially, the calyx lobes ovate, green, and entire, and the corolla yellow with a marginal purple-red line of 1–2 mm wide on all lobes with glandular-pilose indument externally. This new species is similar to *C. canarina*, and apart from the morphological characteristics mentioned in the diagnosis, there is marked allopatry between the two species. *Columnea blancoi* grows in the Central Pacific slope of Costa Rica in the Cordillera de Talamanca and the north of the Fila Costeña, whereas *C. canarina* is found in the Caribbean Slope of Panama in the Cordillera de Talamanca, specifically in Fortuna Dam site (Table 1).

Columnea blancoi is also similar to *Columnea lariensis* Kriebel, but differs from the latter in having flaky stems and sericeous distally (vs. not flaky, villous), the calyx lobes ovate and entire (vs. oblong to obovate and denticulate to lobulate), and the corolla yellow with a marginal purple-red line of 1–2 mm wide in all lobes (vs. yellow without purple-red line), and glandular-pilose externally (vs. glabrous to villose). In addition, the larger leaf blade of *Columnea blancoi* is oblong to oblanceolate with an irregular red to deep purple-red or fuchsia red spot covers the apex or up to the apical third, while those in *C. lariensis* have elliptic to oblong or oblanceolate with an irregular red spot in the apex or up to half of the blade. There is marked allopatry between the two species. *Columnea blancoi* grows in the Pacific slope of the Cordillera de Talamanca, whereas *C. lariensis* inhabits in the Caribbean slope of the same range.

Due to the irregular red to deep purple red or fuchsia red spot covering the apex of the abaxial surface of the larger blade and the yellow corolla, *Columnea blancoi* may also be confused with *Columnea maculata* C. V. Morton and *C. zebrina* Raymond. It differs from *C. maculata* by having a smaller leaf blade of 6.4–16.5 × 1.9–5.0 cm (vs. 17–26 × 6–9.5), calyx lobes ovate to ovate-lanceolate with an entire margin and green (vs. lanceolate, fimbriate, and green to purple greenish), corolla glandular-pilose with a marginal purple line of 1–2 mm wide in all lobes (vs. sericeous with longitudinal purple lines and irregular spots), and distributed in the Central Pacific of Cordillera de Talamanca (Zona de Los Santos) and north of Fila Costeña between 720–1500 m (vs. Caribbean Slope of Cordillera Volcánica Central and Cordillera de Talamanca between 100–900 m) (Table 1). From the allopatric Panamanian species *C. zebrina* differs notably by having the purple line of the corolla restricted to the margin, whereas *C. zebrina* has four purple lines running longitudinally within the surface and never on the margins (Fig. 5).

Lastly, *Columnea blancoi* also resembles *C. verecunda* C. V. Morton due to its similar leaf size and number of lateral veins, entire calyx lobes, and the usually yellow corolla (Fig. 5). However, *C. blancoi* differs because of its inflorescence with a solitary flower (vs. 1–5), the ovate to ovate-lanceolate, green calyx lobes (vs. lanceolate to linear-lanceolate, green with the purple apex to purple), the yellow corolla with pilose-glandular trichomes (vs. yellow, red or pinkish and sericeous), the corolla lobes with a marginal purple-red line of 1–2 mm wide in all lobes (vs. without any marginal purple-red line), and being distributed in Central Pacific of Cordillera de Talamanca (Zona de Los Santos) and north of Fila Costeña between 720–1500 m (vs. Caribbean Slope of Cordilleras de Guanacaste, Tilarán, Central and E Talamanca between 550–1650 m) (Table 1).

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KARMA, A NEW GENUS IN THE PLEUROTHALLIDINAE (ORCHIDACEAE)

Adam P. Karremans[1,2]

Abstract. The new generic name *Karma* (Orchidaceae: Pleurothallidinae) is proposed to substitute the concept of *Tubella* (Luer) Archila [2009], which is illegitimate on account of the prior homonym *Tubella* Archila [2006], a genus in the Gentianaceae. The latter was proposed together with the illegitimate genus *Xenia* Archila in the Asclepiadaceae, and the invalid *Pseudolepanthes* Archila in the Orchidaceae. All three names were "hidden" at the end of an unrelated paper in *Revista Guatemalensis* volume 2 number 2 and had been forgotten or ignored until now. Taxonomic proposals published in this inconsistent, self-published, cryptic journal are good candidates for suppression, especially given the existence of alternative contents and pre-dated covers, among other issues.

Keywords: *Karma*, new genus, priority, Revista Guatemalensis, *Trichosalpinx*, *Tubella*

Phylogenetic studies in the *Lepanthes* affinity (sensu Karremans, 2016) evidenced that *Trichosalpinx*, as defined by Luer (1997) and Pridgeon (2005), is polyphyletic (Bogarín et al., 2019). Several groups of taxa were shown to represent isolated lineages, prompting the recognition of several new generic concepts required to adequately explain the phylogenetic relationships in this group (Bogarín et al., 2018). *Trichosalpinx* subgen. *Tubella* Luer was found to be composed of unrelated taxa, neither of which belong to *Trichosalpinx* in the strict sense (Bogarín et al., 2019). The type species, *Trichosalpinx acremona* (Luer) Luer as well as most other members of the genus were shown to form a clade more closely related to *Anathallis* Barb. Rodr. (Karremans, 2014; Pérez-Escobar et al., 2017; Bogarín et al., 2019), from which they are easily distinguished morphologically (Fernández, 2013, 2016; Bogarín et al., 2018). *Tubella* (Luer) Archila, which had been previously elevated to generic rank, therefore became the accepted name for this group of species.

The taxonomic history of *Tubella* (Orchidaceae), as of many other taxa published in *Revista Guatemalensis*, has been rather unfortunate (Govaerts et al., 2022). The name was originally published as *Tubella* Archila (2000 [2009]: 46). However, *Trichosalpinx* subgen. *Tubella* Luer was explicitly stated as the basionym, and therefore the correct authority for the generic name is *Tubella* (Luer) Archila. The genus was published once again in Archila (2014 [2015]: 47), this time without citing a basionym. The reasoning for the second, superfluous, proposal was allegedly to avoid "misinterpretations in prior publications," presumably to secure having complied with all the necessary requirements for effective and valid publication. The former *Revista Guatemalensis* volume 3, number 1, like many early issues of this journal, was later shown to bear a pre-dated cover (Govaerts et al., 2022). Rather than being printed and distributed in June of the year 2000, as the cover suggests, it was effectively published in February 2009 when first received physically at a botanical institution. *Revista Guatemalensis* volume 17, number 1, on the other hand was effectively published in 2015. Bearing the corrected publication dates, the first generic name applicable to this group of species is *Tubella* (Luer) Archila [2009], while *Tubella* Archila [2015] is an illegitimate posterior homonym.

Among the many questionable practices surrounding the publication of this obscure journal, producing volumes with conflicting publication dates, alternative covers and alternative contents is also commonplace (Govaerts et al., 2022). One such case occurs with the different issues of volume 2, allegedly published in the year 1999. The most common, physically available version of volume 2 includes both issues 1 and 2 (Fig. 1A). Nevertheless, there is also a much rarer version of volume 2 that includes only the second issue (i.e., number 2; Fig. 1B–C). Volume 2, numbers 1–2 has a cover date July 1999, while the second version, volume 2, number 2, has a cover date November 1999. The latter, of which we have received copies from the Gray Herbarium at the Harvard University Botany Libraries and from a private collection in Guatemala, is key to the taxonomic issue discussed here. One would expect the contents of *Revista Guatemalensis* 2(1–2) to be the sum of contents of volume 2 number 1 plus those of number 2, and, on the surface, this would appear to be true. Volume 2 number 1 has yet to surface, but the five articles contained in volume 2 number 2 are also contained in the combined volume 2 numbers 1–2. Unfortunately, the contents of those two issues of the journal are not exactly the same.

A single article in volume 2 deals with taxonomy. In volume 2 number 2 it appeared as "Monografía del género Brassia en Guatemala" on page 28, and in volume 2 numbers 1–2, as "Monografía del género Brassia/Orchidaceae en Guatemala" on page 49. Besides a slight difference in the title, page numbers and publication date, there is also an important modification in the contents. Hidden at the very end of the *Brassia* paper in volume issue 2 number 2 is a brief proposal of three new genera (Fig. 2) which does not appear in volume 2 numbers 1–2. Proposed therein are the names *Xenia* Archila (Asclepiadaceae), *Tubella* Archila (Gentianaceae) and *Pseudolepanthes* Archila (Orchidaceae).

I am very grateful to the staff at the Harvard University Botany Libraries, Missouri Botanical Garden, Royal Botanic Gardens Kew, Lankester Botanical Garden, and numerous private persons. The Vice Presidency of Research of the University of Costa Rica financed this study through research project 814-C3-021 – Flora costaricensis: sistemática molecular y taxonomía del clado *Trichosalpinx* (Orchidaceae: Pleurothallidinae) de Costa Rica.

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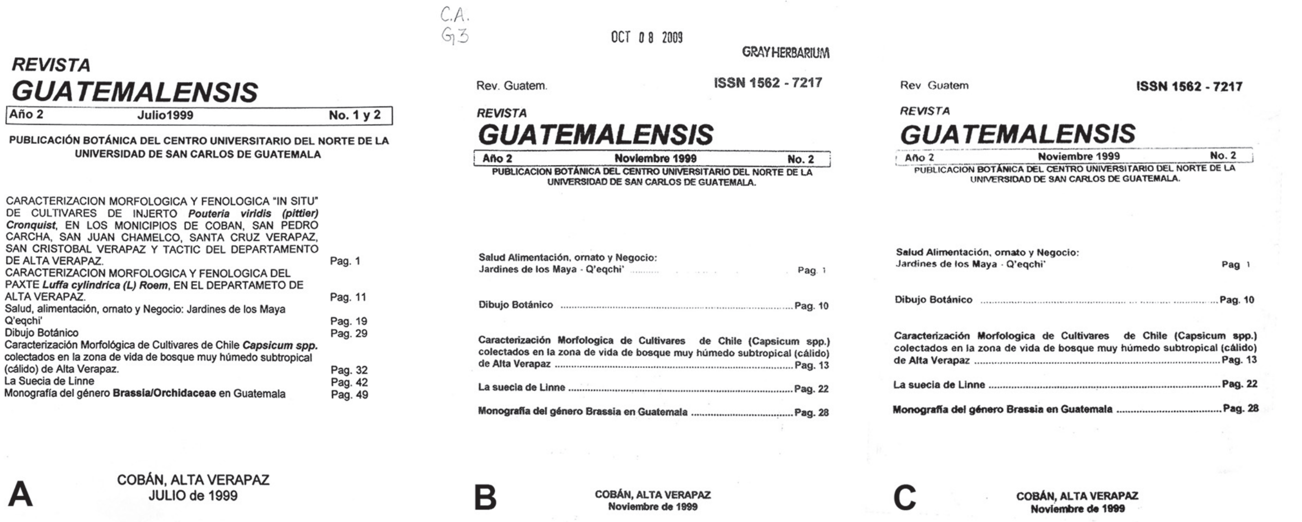


REVISTA
GUATEMALENSIS
Año 2 Julio1999 No. 1 y 2
PUBLICACIÓN BOTÁNICA DEL CENTRO UNIVERSITARIO DEL NORTE DE LA UNIVERSIDAD DE SAN CARLOS DE GUATEMALA

CARACTERIZACION MORFOLOGICA Y FENOLOGICA "IN SITU" DE CULTIVARES DE INJERTO ***Pouteria viridis* (pittier) *Cronquist***, EN LOS MONICIPIOS DE COBAN, SAN PEDRO CARCHA, SAN JUAN CHAMELCO, SANTA CRUZ VERAPAZ, SAN CRISTOBAL VERAPAZ Y TACTIC DEL DEPARTAMENTO DE ALTA VERAPAZ. Pag. 1
CARACTERIZACION MORFOLOGICA Y FENOLOGICA DEL PAXTE ***Luffa cylindrica* (L) Roem**, EN EL DEPARTAMETO DE ALTA VERAPAZ. Pag. 11
Salud, alimentación, ornato y Negocio: Jardines de los Maya Q'eqchi' Pag. 19
Dibujo Botánico Pag. 29
Caracterización Morfológica de Cultivares de Chile ***Capsicum* spp.** colectados en la zona de vida de bosque muy húmedo subtropical (cálido) de Alta Verapaz. Pag. 32
La Suecia de Linne Pag. 42
Monografía del género **Brassia/Orchidaceae** en Guatemala Pag. 49

A

COBÁN, ALTA VERAPAZ
JULIO de 1999

C.A.
G73

OCT 08 2009
GRAY HERBARIUM

Rev. Guatem. ISSN 1562 - 7217
REVISTA
GUATEMALENSIS
Año 2 Noviembre 1999 No. 2
PUBLICACION BOTÁNICA DEL CENTRO UNIVERSITARIO DEL NORTE DE LA UNIVERSIDAD DE SAN CARLOS DE GUATEMALA.

Salud Alimentación, ornato y Negocio: Jardines de los Maya - Q'eqchi' .... Pag. 1
Dibujo Botánico .... Pag. 10
Caracterización Morfologica de Cultivares de Chile (Capsicum spp.) colectados en la zona de vida de bosque muy húmedo subtropical (cálido) de Alta Verapaz .... Pag. 13
La suecia de Linne .... Pag. 22
Monografía del género Brassia en Guatemala .... Pag. 28

B

COBÁN, ALTA VERAPAZ
Noviembre de 1999

Rev Guatem ISSN 1562 - 7217
REVISTA
GUATEMALENSIS
Año 2 Noviembre 1999 No. 2
PUBLICACION BOTÁNICA DEL CENTRO UNIVERSITARIO DEL NORTE DE LA UNIVERSIDAD DE SAN CARLOS DE GUATEMALA.

Salud Alimentación, ornato y Negocio: Jardines de los Maya - Q'eqchi' Pag 1
Dibujo Botánico .... Pag. 10
Caracterización Morfologica de Cultivares de Chile (Capsicum spp.) colectados en la zona de vida de bosque muy húmedo subtropical (cálido) de Alta Verapaz .... Pag. 13
La suecia de Linne .... Pag. 22
Monografía del género Brassia en Guatemala .... Pag. 28

C

COBÁN, ALTA VERAPAZ
Noviembre de 1999

FIGURE 1. Alternative covers of *Revista Guatemalensis* volume 2. **A**, The common version, volume 2, No. 1–2, held at Lankester Botanical Garden; **B**, The rarer version, volume 2, No. 2, kept at the Gray Herbarium, Harvard University Library, physically received on the 8th of October 2009; **C**, Another cover of the rarer version, volume 2, number 2, kept in a private collection in Guatemala, physically received in 2006.

These names cannot be considered preliminary because the author clearly states that the requirements for valid publication are met. These three generic names have passed completely unnoticed, probably on account of the odd placement, in addition to the rarity of the issue volume 2 number 2, and the fact that Archila himself had forgotten or ignored them, speculatively for good reasons. *Xenia* Archila [2006] is illegitimate because it is a posterior homonym of *Xenia* Gerbaulet (Anacampserotaceae) [1992]. *Pseudolepanthes* Archila [2006] is invalid because no type species is explicitly designated, but *Tubella* Archila [2006] complies with all the requirements for valid publication in accordance with ICN Articles 38.5 and 40.6.

Regardless of the alternative covers and predated publication, the generic name *Tubella* is occupied since its publication in volume 2 number 2 of *Revista Guatemalensis* (effectively published in 2006) for a genus in the Gentianaceae and cannot be used in Orchidaceae at the same rank as proposed in volume 3, number 1 (effectively published in 2009) and volume 17, number 1 (effectively published in 2015). A new name is proposed here to substitute the illegitimate *Tubella* (Luer) Archila [2009]. However, the lack of peer-review and faithful editorial process, the inconsistency, paucity and unavailability of the publication, existence of alternative contents and pre-dated covers, republication of taxa, often using different types, and a multitude of other ethical and technical violations make taxonomic proposals published in *Revista Guatemalensis* good candidates for overall suppression.

Karma Karremans, *gen. nov.*
Type species: *Pleurothallis arbuscula* Lindl., Edwards's Bot. Reg. 28: Misc. 72–73. 1842.

Habit slender, often with proliferating ramicauls, covered by lepanthiform sheaths, the inflorescence longer than the leaf, the ovary glabrous, the sepals membranaceous, glabrous, acuminate, concave, the petals much shorter, entire, elliptic, the lip simple, often three-lobed, the base unguiculate, lacking lobules, column elongate, apically winged, with a prominent column foot.

Synonyms: *Tubella* (Luer) Archila, Revista Guatemal. 3(1): 46. 2000 [2009], *nom. illeg. Pro parte*. Basionym: *Trichosalpinx* subgen. *Tubella* Luer, Monogr. Syst. Bot. 15:66. 1986. TYPE: *Pleurothallis acremona* Luer, Selbyana 5(2): 157. 1979.

Tubella Archila, Revista Guatemal. 17(1): 47. 2014 [2015], *nom. illeg. Pro parte*. TYPE: *Pleurothallis acremona* Luer, Selbyana 5(2): 157. 1979.

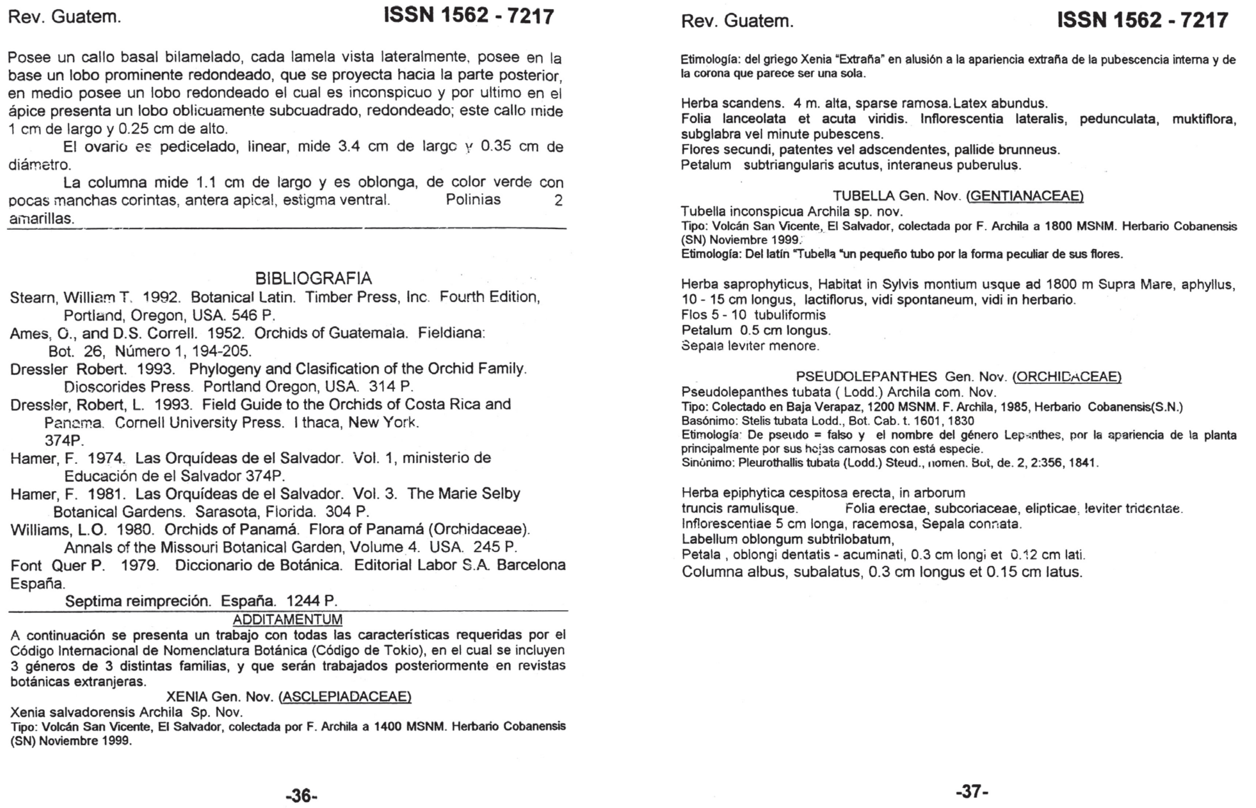
Non Tubella Archila, Revista Guatemal. 2(2): 37. 1999 [2006]. TYPE: *Tubella incospicua* Archila, Revista Guatemal. 2(2): 37. 2000 [2006].

NEW COMBINATIONS

Karma adnata (I. Jiménez) Karremans, *comb. nov.*
Basionym: *Trichosalpinx adnata* I. Jiménez Lankesteriana 15(3): 194. 2015.
Homotypic synonym: *Tubella adnata* (I. Jiménez) Mel. Fernández & Bogarín, Phytotaxa 340(2): 133. 2018.

Karma alabastra (Luer & R. Escobar) Karremans, *comb. nov.*
Basionym: *Pleurothallis alabastra* Luer & R. Escobar, Orquideología 16: 17. 1983.
Homotypic synonyms: *Trichosalpinx alabastra* (Luer & R. Escobar) Luer, Phytologia 54(5): 394. 1983. *Tubella alabastra* (Luer & R. Escobar) Archila, Revista Guatemal. 3(1): 49. 2000 [2009]. *Tubella alabastra* (Luer & R. Escobar) Archila, Revista Guatemal. 17(1): 48. 2014 [2015].

Karma amygdalodora (Kraenzl.) Karremans, *comb. nov.*
Basionym: *Pleurothallis amygdalodora* Kraenzl., Bot. Jahrb. Syst. 37: 521. 1906.



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Posee un callo basal bilamelado, cada lamela vista lateralmente, posee en la base un lobo prominente redondeado, que se proyecta hacia la parte posterior, en medio posee un lobo redondeado el cual es inconspicuo y por ultimo en el ápice presenta un lobo oblicuamente subcuadrado, redondeado; este callo mide 1 cm de largo y 0.25 cm de alto.

El ovario es pedicelado, linear, mide 3.4 cm de largo y 0.35 cm de diámetro.

La columna mide 1.1 cm de largo y es oblonga, de color verde con pocas manchas corintas, antera apical, estigma ventral. Polinias 2 amarillas.

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ADDITAMENTUM

A continuación se presenta un trabajo con todas las características requeridas por el Código Internacional de Nomenclatura Botánica (Código de Tokio), en el cual se incluyen 3 géneros de 3 distintas familias, y que serán trabajados posteriormente en revistas botánicas extranjeras.

XENIA Gen. Nov. (ASCLEPIADACEAE)

Xenia salvadorensis Archila Sp. Nov.
Tipo: Volcán San Vicente, El Salvador, colectada por F. Archila a 1400 MSNM. Herbario Cobanensis (SN) Noviembre 1999.

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Etimología: del griego Xenia "Extraña" en alusión a la apariencia extraña de la pubescencia interna y de la corona que parece ser una sola.

Herba scandens. 4 m. alta, sparse ramosa. Latex abundus.
Folia lanceolata et acuta viridis. Inflorescentia lateralis, pedunculata, muktiflora, subglabra vel minute pubescens.
Flores secundi, patentes vel adscendentes, pallide brunneus.
Petalum subtriangularis acutus, interaneus puberulus.

TUBELLA Gen. Nov. (GENTIANACEAE)

Tubella inconspicua Archila sp. nov.
Tipo: Volcán San Vicente, El Salvador, colectada por F. Archila a 1800 MSNM. Herbario Cobanensis (SN) Noviembre 1999.
Etimología: Del latín "Tubella "un pequeño tubo por la forma peculiar de sus flores.

Herba saprophyticus, Habitat in Sylvis montium usque ad 1800 m Supra Mare, aphyllus, 10 - 15 cm longus, lactiflorus, vidi spontaneum, vidi in herbario.
Flos 5 - 10 tubuliformis
Petalum 0.5 cm longus.
Sepala leviter menore.

PSEUDOLEPANTHES Gen. Nov. (ORCHIDACEAE)

Pseudolepanthes tubata (Lodd.) Archila com. Nov.
Tipo: Colectado en Baja Verapaz, 1200 MSNM. F. Archila, 1985, Herbario Cobanensis(S.N.)
Basónimo: Stelis tubata Lodd., Bot. Cab. t. 1601, 1830
Etimología: De pseudo = falso y el nombre del género Lepanthes, por la apariencia de la planta principalmente por sus hojas carnosas con está especie.
Sinónimo: Pleurothallis tubata (Lodd.) Steud., nomen. Bot, de. 2, 2:356, 1841.

Herba epiphytica cespitosa erecta, in arborum
truncis ramulisque. Folia erectae, subcoriaceae, elipticae, leviter tridentae.
Inflorescentiae 5 cm longa, racemosa, Sepala connata.
Labellum oblongum subtrilobatum,
Petala , oblongi dentatis - acuminati, 0.3 cm longi et 0.12 cm lati.
Columna albus, subalatus, 0.3 cm longus et 0.15 cm latus.

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FIGURE 2. Pages 36 and 37 of Revista Guatemalensis 2, number 2 showing the proposal of three generic names under the title "*Additamentum*" at the end of the article "Monografía del género Brassia en Guatemala". Reproduced with the kind permission of the Gray Herbarium, Harvard University Library.

Homotypic synonyms: *Trichosalpinx amygdalodora* (Kraenzl.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 43. 1997. *Tubella amygdalora* (Kraenzl.) Archila, Revista Guatemal. 3(1): 49. 2000 [2009]. *Tubella amygdalora* (Kraenzl.) Archila, Revista Guatemal. 17(1): 48. 2014 [2015].

Karma arbuscula (Lindl.) Karremans, *comb. nov.*
Basionym: *Pleurothallis arbuscula* Lindl., Edwards's Bot. Reg. 28: Misc. 72. 1842.
Homotypic synonyms: *Humboldtia arbuscula* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 667. 1891. *Trichosalpinx arbuscula* (Lindl.) Luer, Phytologia 54(5): 394. 1983. *Tubella arbuscula* (Lindl.) Archila, Revista Guatemal. 3(1): 49. 2000 [2009]. *Tubella arbuscula* (Lindl.) Archila, Revista Guatemal. 17(1): 49. 2014 [2015].

Karma atropurpurea (Luer & Hirtz) Karremans, *comb. nov.*
Basionym: *Trichosalpinx atropurpurea* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 46. 1997.
Homotypic synonyms: *Tubella atropurpurea* (Luer & Hirtz) Archila, Revista Guatemal. 3(1): 50. 2000 [2009]. *Tubella atropurpurea* (Luer & Hirtz) Archila, Revista Guatemal. 17(1): 49. 2014 [2015].

Karma ballatrix (Luer & R. Escobar) Karremans, *comb. nov.*
Basionym: *Trichosalpinx ballatrix* Luer & R. Escobar, Orquideología 16(2): 178. 1984.
Homotypic synonyms: *Tubella ballatrix* (Luer & R. Escobar) Archila, Revista Guatemal. 17(1): 49. 2014 [2015]. *Tubella ballatrix* (Luer & R. Escobar) Archila, Revista Guatemal. 3(1): 50. 2000 [2009].

Karma barbelifera (Luer & R. Vásquez) Karremans, *comb. nov.*
Basionym: *Trichosalpinx barbelifera* Luer & R. Vásquez, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 46. 1997.
Homotypic synonyms: *Tubella barbelifera* (Luer & R. Vásquez) Archila, Revista Guatemal. 3(1): 51. 2000 [2009]. *Tubella barbelifera* (Luer & R. Vásquez) Archila, Revista Guatemal. 17(1): 49. 2014 [2015].

Karma carinilabia (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis carinilabia* Luer, Selbyana 3(3–4): 256. 1977.
Homotypic synonyms: *Pleurothallis broadwayi* var. *tricarinata* C. Schweinf., Bot. Mus. Leafl. 8(2): 42–43. 1940. *Trichosalpinx carinilabia* (Luer) Luer, Phytologia 54(5): 394. 1983. *Tubella carinilabia* (Luer) Archila, Revista Guatemal. 3(1): 51. 2000 [2009]. *Tubella carinilabia* (Luer) Archila, Revista Guatemal. 17(1): 50. 2014 [2015].

Karma carmeniae (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx carmeniae* Luer, Harvard Pap. Bot. 17(2): 366. 2012.
Homotypic synonym: *Tubella carmeniae* (Luer) Mel. Fernández & Bogarín, Phytotaxa 340(2): 133. 2018.

Karma carvii (Archila) Karremans, *comb. nov.*
Basionym: *Tubella carvii* Archila, Revista Guatemal. 3(1): 71. 2000 [2009].
Homotypic synonyms: *Trichosalpinx carvii* (Archila) J.M.H. Shaw, Orchid Rev. 122(1305): 18. 2014 [2015]. *Tubella tactiquensis* Archila, Revista Guatemal. 17(1): 62. 2014, *nom. illeg*. Definitively includes the type of *T. carvii* (see Karremans et al. 2021).

Karma cedralensis (Ames) Karremans, *comb. nov.*
Basionym: *Pleurothallis cedralensis* Ames, Sched. Orch. 4: 18. 1923.
Homotypic synonyms: *Trichosalpinx cedralensis* (Ames) Luer, Phytologia 54(5): 394. 1983. *Tubella cedralensis* (Ames) Archila, Revista Guatemal. 3(1): 52. 2000 [2009]. *Tubella cedralensis* (Ames) Archila, Revista Guatemal. 17(1): 50. 2014 [2015].

Karma chaetoglossa (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis chaetoglossa* Luer, Selbyana 3: 262. 1977.
Homotypic synonyms: *Trichosalpinx chaetoglossa* (Luer) Luer, Phytologia 54(5): 394. 1983. *Tubella chaetoglossa* (Luer) Archila, Revista Guatemal. 3(1): 52. 2000 [2009]. *Tubella chaetoglossa* (Luer) Archila, Revista Guatemal. 17(1): 50. 2014 [2015].

Karma costata (Luer & R. Vásquez) Karremans, *comb. nov.*
Basionym: *Pleurothallis costata* Luer & R. Vásquez, Phytologia 46(6): 364. 1980.
Homotypic synonyms: *Trichosalpinx costata* (Luer & R. Vásquez) Luer, Phytologia 54(5): 395. 1983. *Tubella costata* (Luer & R. Vásquez) Archila, Revista Guatemal. 3(1): 53. 2000 [2009]. *Tubella costata* (Luer & R. Vásquez) Archila, Revista Guatemal. 17(1): 50. 2014 [2015].

Karma crucilabia (Ames & Correll) Karremans, *comb. nov.*
Basionym: *Pleurothallis crucilabia* Ames & Correll, Bot. Mus. Leafl. 10(4): 76. 1942.
Homotypic synonyms: *Trichosalpinx crucilabia* (Ames & Correll) Luer, Phytologia 54(5): 395. 1983. *Tubella crucilabia* (Ames & Correll) Archila, Revista Guatemal. 3(1): 53. 2000 [2009]. *Tubella crucilabia* (Ames & Correll) Archila, Revista Guatemal. 17(1): 50. 2014 [2015].

Karma cunorensis (Archila) Karremans, *comb. nov.*
Basionym: *Tubella cunorensis* Archila, Revista Guatemal. 3(1): 68. 2000 [2009].
Homotypic synonyms: *Trichosalpinx cunorensis* (Archila) J.M.H. Shaw, Orchid Rev. 122(1305): 18. 2014 [2015]. *Tubella cobanensis* Archila, Revista Guatemal. 17(1): 60. 2014, *nom. illeg*. Definitively includes the type of *T. cunorensis* (see Karremans et al. 2021).

Karma dalstroemii (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx dalstroemii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 52–53. 1997.
Homotypic synonyms: *Tubella dalstroemii* (Luer) Archila, Revista Guatemal. 3(1): 53. 2000 [2009]. *Tubella dalstroemii* (Luer) Archila, Revista Guatemal. 17(1): 51. 2014 [2015].

Karma dirhamphis (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis dirhamphis* Luer, Selbyana 3(3,4): 292. 1977.
Homotypic synonyms: *Trichosalpinx dirhamphis* (Luer) Luer, Phytologia 54(5): 395. 1983. *Tubella dirhamphis* (Luer) Archila, Revista Guatemal. 3(1): 53. 2000 [2009]. *Tubella dirhamphis* (Luer) Archila, Revista Guatemal. 17(1): 51. 2014 [2015].

Karma dressleri (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx dressleri* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 54. 1997.
Homotypic synonyms: *Tubella dressleri* (Luer) Archila, Revista Guatemal. 3(1): 54. 2000 [2009]. *Tubella dressleri* (Luer) Archila, Revista Guatemal. 17(1): 51. 2014 [2015].

Karma drosoides (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx drosoides* Carnevali & I. Ramírez, Ernstia 42: 1. 1987.
Homotypic synonyms: *Tubella drosoides* (Carnevali & I. Ramírez) Archila, Revista Guatemal. 3(1): 54. 2000 [2009]. *Tubella drosoides* (Carnevali & I. Ramírez) Archila, Revista Guatemal. 17(1): 51. 2014 [2015].

Karma dunstervillei (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx dunstervillei* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 55–56. 1997.
Homotypic synonyms: *Tubella dunstervillei* (Luer) Archila, Revista Guatemal. 3(1): 54. 2000 [2009]. *Tubella dunstervillei* (Luer) Archila, Revista Guatemal. 17(1): 51. 2014 [2015].

Karma dura (Lindl.) Karremans, *comb. nov.*
Basionym: *Pleurothallis dura* Lindl., Fol. Orchid. 9(Pleurothallis): 32. 1859.
Homotypic synonyms: *Humboldtia dura* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 667. 1891. *Trichosalpinx dura* (Lindl.) Luer, Phytologia 54(5): 395. 1983. *Tubella dura* (Lindl.) Archila, Revista Guatemal. 3(1): 54. 2000 [2009]. *Tubella dura* (Lindl.) Archila, Revista Guatemal. 17(1): 51. 2014 [2015].

Karma escobarii (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx escobarii* Luer, Orquideología 18(2): 168–170. 1991.
Homotypic synonyms: *Trichosalpinx escobarii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 114–115. 1997, *nom. superfl. Tubella escobarii* (Luer) Archila, Revista Guatemal. 3(1): 55. 2000 [2009]. *Tubella escobarii* (Luer) Archila, Revista Guatemal. 17(1): 52. 2014 [2015].

Karma fasciculata (Luer & Hirtz) Karremans, *comb. nov.*
Basionym: *Trichosalpinx fasciculata* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 58–59. 1997.
Homotypic synonyms: *Tubella fasciculata* (Luer & Hirtz) Archila, Revista Guatemal. 3(1): 55. 2000 [2009]. *Tubella fasciculata* (Luer & Hirtz) Archila, Revista Guatemal. 17(1): 52. 2014 [2015].

Karma fissa (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx fissa* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 59. 1997.
Homotypic synonyms: *Tubella fissa* (Luer) Archila, Revista Guatemal. 3(1): 56. 2000 [2009]. *Tubella fissa* (Luer) Archila, Revista Guatemal. 17(1): 52. 2014 [2015].

Karma fruticosa (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx fruticosa* Luer, Lindleyana 11(2): 105. 1996.
Homotypic synonyms: *Trichosalpinx fruticosa* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 59–60. 1997, *nom. superfl. Tubella fruticosa* (Luer) Archila, Revista Guatemal. 3(1): 56. 2000 [2009]. *Tubella fruticosa* (Luer) Archila, Revista Guatemal. 17(1): 52. 2014 [2015].

Karma gabi-villegasiae (I. Jiménez) Karremans, *comb. nov.*
Basionym: *Trichosalpinx gabi-villegasiae* I. Jiménez, Lankesteriana 15(3): 196. 2015.
Homotypic synonym: *Tubella gabi-villegasiae* (I. Jiménez) Mel. Fernández & Bogarín, Phytotaxa 340(2): 133. 2018.

Karma gentryi (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx gentryi* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 60. 1997.
Homotypic synonyms: *Tubella gentryi* (Luer) Archila, Revista Guatemal. 3(1): 56. 2000 [2009]. *Tubella gentryi* (Luer) Archila, Revista Guatemal. 17(1): 52. 2014 [2015].

Karma giovi-mendietae (I. Jiménez) Karremans, *comb. nov.*
Basionym: *Trichosalpinx giovi-mendietae* I. Jiménez, Lankesteriana 15(3): 199. 2015.
Homotypic synonym: *Tubella giovi-mendietae* (I. Jiménez) Mel. Fernández & Bogarín, Phytotaxa 340(2): 133. 2018.

Karma hamiltonii (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx hamiltonii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 61. 1997.
Homotypic synonyms: *Stelis hamiltonii* (Luer) Pridgeon & M.W. Chase, Lindleyana 16(4): 263. 2001. *Specklinia hamiltonii* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 261. 2004. *Tubella hamiltonii* (Luer) Archila, Revista Guatemal. 3(1): 56. 2000 [2009]. *Tubella hamiltonii* (Luer) Archila, Revista Guatemal. 17(1): 52. 2014 [2015].

Karma hirtzii (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx hirtzii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 61. 1997.
Homotypic synonyms: *Tubella hirtzii* (Luer) Archila, Revista Guatemal. 3(1): 57. 2000 [2009]. *Tubella hirtzii* (Luer) Archila, Revista Guatemal. 17(1): 52. 2014 [2015].

Karma hypocrita (Garay & Dunst.) Karremans, *comb. nov.*
Basionym: *Pleurothallis hypocrita* Garay & Dunst., Venez. Orchid. Ill. 6: 344. 1976.
Homotypic synonyms: *Trichosalpinx hypocrita* (Garay & Dunst.) Luer, Phytologia 54(5): 395. 1983. *Tubella hypocrita* (Garay & Dunst.) Archila, Revista Guatemal. 3(1): 57. 2000 [2009]. *Tubella hypocrita* (Garay & Dunst.) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma inaequisepala (C. Schweinf.) Karremans, *comb. nov.*
Basionym: *Pleurothallis inaequisepala* C. Schweinf., Bot. Mus. Leafl. 10: 180. 1942.
Homotypic synonyms: *Trichosalpinx inaequisepala* (C. Schweinf.) Luer, Phytologia 54(5): 394. 1983. *Tubella inaequisepala* (C. Schweinf.) Archila, Revista Guatemal. 3(1): 57. 2000 [2009]. *Tubella inaequisepala* (C. Schweinf.) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma intricata (Lindl.) Karremans, *comb. nov.*
Basionym: *Pleurothallis intricata* Lindl., Orchid. Linden. 1. 1846.
Homotypic synonyms: *Humboldtia intricata* (Lindl.) Kuntze, Revis. Gen. Pl. 2: 667. 1891. *Trichosalpinx intricata* (Lindl.) Luer, Phytologia 54(5): 396. 1983. *Tubella intricata* (Luer) Archila, Revista Guatemal. 3(1): 57. 2000 [2009]. *Tubella intricata* (Luer) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma jimburae (Luer & Hirtz) Karremans, *comb. nov.*
Basionym: *Trichosalpinx jimburae* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 64. 1997.
Homotypic synonyms: *Tubella jimburae* (Luer & Hirtz) Archila, Revista Guatemal. 3(1): 58. 2000 [2009]. *Tubella jimburae* (Luer & Hirtz) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma jostii (Luer & Hirtz) Karremans, *comb. nov.*
Basionym: *Trichosalpinx jostii* Luer & Dalström, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 255. 2006.
Homotypic synonym: *Tubella jostii* (Luer & Dalström) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma lamellata (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx lamellata* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 64. 1997.
Homotypic synonyms: *Tubella lamellata* (Luer) Archila, Revista Guatemal. 3(1): 58. 2000 [2009]. *Tubella lamellata* (Luer) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma lenticularis (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis lenticularis* Luer, Selbyana 3(1/2): 132. 1976.
Homotypic synonyms: *Trichosalpinx lenticularis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 65. 1997. *Tubella lenticularis* (Luer) Archila, Revista Guatemal. 3(1): 58. 2000 [2009]. *Tubella lenticularis* (Luer) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma ligulata (Luer & Hirtz) Karremans, *comb. nov.*
Basionym: *Trichosalpinx ligulata* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 65. 1997.
Homotypic synonyms: *Tubella ligulata* (Luer & Hirtz) Archila, Revista Guatemal. 3(1): 58. 2000 [2009]. *Tubella ligulata* (Luer & Hirtz) Archila, Revista Guatemal. 17(1): 53. 2014 [2015].

Karma lilliputalis (Luer & Hirtz) Karremans, *comb. nov.*
Basionym: *Lepanthopsis lilliputalis* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 118. 1994.
Homotypic synonyms: *Trichosalpinx lilliputalis* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 115. 1997. *Tubella lilliputalis* (Luer & Hirtz) Archila, Revista Guatemal. 3(1): 58. 2000 [2009]. *Tubella lilliputalis* (Luer & Hirtz) Archila, Revista Guatemal. 17(1): 54. 2014 [2015].

Karma macphersonii (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx macphersonii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 66. 1997.
Homotypic synonyms: *Tubella macphersonii* (Luer) Archila, Revista Guatemal. 3(1): 59. 2000 [2009]. *Tubella macphersonii* (Luer) Archila, Revista Guatemal. 17(1): 54. 2014 [2015].

Karma membraniflora (C. Schweinf.) Karremans, *comb. nov.*
Basionym: *Pleurothallis membraniflora* C. Schweinf., Bot. Mus. Leafl. 5(6): 91–92. 1938.
Homotypic synonyms: *Trichosalpinx membraniflora* (C. Schweinf.) Luer, Phytologia 54(5): 396. 1983. *Tubella membraniflora* (C. Schweinf.) Archila, Revista Guatemal. 3(1): 59. 2000 [2009]. *Tubella membraniflora* (C. Schweinf.) Archila, Revista Guatemal. 17(1): 54. 2014 [2015].

Karma metamorpha (Luer & Hirtz) Karremans, *comb. nov.*
Basionym: *Trichosalpinx metamorpha* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 67. 1997.
Homotypic synonyms: *Tubella metamorpha* (Luer & Hirtz) Archila, Revista Guatemal. 3(1): 59. 2000 [2009]. *Tubella metamorpha* (Luer & Hirtz) Archila, Revista Guatemal. 17(1): 54. 2014 [2015].

Karma montana (Barb. Rodr.) Karremans, *comb. nov.*
Basionym: *Lepanthes montana* Barb. Rodr., Gen. Sp. Orchid. 1: 22. 1877.
Homotypic synonyms: *Trichosalpinx montana* (Barb. Rodr.) Luer, Phytologia 54(5): 396. 1983. *Tubella montana* (Barb. Rodr.) Archila, Revista Guatemal. 3(1): 59. 2000 [2009]. *Tubella montana* (Barb. Rodr.) Archila, Revista Guatemal. 17(1): 54. 2014 [2015].

Karma multicuspidata (Rchb. f.) Karremans, *comb. nov.*
Basionym: *Pleurothallis multicuspidata* Rchb. f., Linnaea 41: 117. 1877.
Homotypic synonyms: *Trichosalpinx multicuspidata* (Rchb. f.) Luer, Phytologia 54(5): 396. 1983. *Tubella multicuspidata* (Rchb. f.) Archila, Revista Guatemal. 3(1): 60. 2000 [2009]. *Tubella multicuspidata* (Rchb. f.) Archila, Revista Guatemal. 17(1): 54. 2014 [2015].

Karma nana (Ames & C. Schweinf.) Karremans, *comb. nov.*
Basionym: *Pleurothallis nana* Ames & C. Schweinf., Sched. Orch. 8: 29–30. 1925.
Homotypic synonyms: *Trichosalpinx nana* (Ames & C. Schweinf.) Luer, Phytologia 54(5): 396. 1983. *Tubella nana* (Ames & C. Schweinf.) Archila, Revista Guatemal. 3(1): 60. 2000 [2009]. *Tubella nana* (Ames & C. Schweinf.) Archila, Revista Guatemal. 17(1): 55. 2014 [2015].

Karma notosibirica (T. Hashim.) Karremans, *comb. nov.*
Basionym: *Pleurothallis notosibirica* T. Hashim., Bull. Natl. Sci. Mus., Tokyo, B 4: 11. 1978.
Homotypic synonyms: *Trichosalpinx notosibirica* (T. Hashim.) Luer, Phytologia 54: 396. 1983. *Tubella notosibirica* (Hashim.) Archila, Revista Guatemal. 3(1): 61. 2000 [2009]. *Tubella notosibirica* (Hashim.) Archila, Revista Guatemal. 17(1): 55. 2014 [2015].

Karma nymphalis (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis nymphalis* Luer, Phytologia 49: 212–213. 1982.
Homotypic synonyms: *Trichosalpinx nymphalis* (Luer) Luer, Phytologia 54(5): 396. 1983. *Tubella nymphalis* (Luer) Archila, Revista Guatemal. 3(1): 61. 2000 [2009]. *Tubella nymphalis* (Luer) Archila, Revista Guatemal. 17(1): 55. 2014 [2015].

Karma otarion (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis otarion* Luer, Selbyana 7: 120–121. 1982.

Homotypic synonyms: *Trichosalpinx otarion* (Luer) Luer, Phytologia 54(5): 396. 1983. *Tubella otarion* (Luer) Archila, Revista Guatemal. 3(1): 61. 2000 [2009]. *Tubella otarion* (Luer) Archila, Revista Guatemal. 17(1): 55. 2014 [2015].

Karma parsonsii (Luer & Dod) Karremans, *comb. nov.*
Basionym: *Trichosalpinx parsonsii* Luer & Dod, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 72. 1997.
Homotypic synonyms: *Tubella parsonsii* (Luer & Dod) Archila, Revista Guatemal. 3(1): 62. 2000 [2009]. *Tubella parsonsii* (Luer & Dod) Archila, Revista Guatemal. 17(1): 55. 2014 [2015].

Karma pumila (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis pumila* Luer, Selbyana 1(3): 268. 1975.
Homotypic synonyms: *Trichosalpinx pumila* (Luer) Luer, Phytologia 54(5): 397. 1983. *Tubella pumila* (Ames) Archila, Revista Guatemal. 3(1): 62. 2000 [2009]. *Tubella pumila* (Ames) Archila, Revista Guatemal. 17(1): 55. 2014 [2015].

Karma pusilla (Kunth) Karremans, *comb. nov.*
Basionym: *Dendrobium pusillum* Kunth, Nov. Gen. Sp. 1: 357. 1816.
Homotypic synonyms: *Humboldtia pusilla* (Kunth) Kuntze, Revis. Gen. Pl. 2: 668. 1891. *Pleurothallis pusilla* (Kunth) Lindl., Edwards's Bot. Reg. 28: Misc. 82–83. 1842. *Specklinia pusilla* (Kunth) Lindl., Edwards's Bot. Reg. 21: sub. t. 1797. 1835. *Trichosalpinx pusilla* (Kunth) Luer, Phytologia 54(5): 397. 1983. *Tubella pusilla* (Kunth) Archila, Revista Guatemal. 3(1): 62. 2000 [2009]. *Tubella pusilla* (Kunth) Archila, Revista Guatemal. 17(1): 56. 2014 [2015].

Karma quitensis (Rchb. f.) Karremans, *comb. nov.*
Basionym: *Pleurothallis quitensis* Rchb. f., Bonplandia (Hannover) 3: 240. 1855.
Homotypic synonyms: *Humboldtia quitensis* (Rchb. f.) Kuntze, Revis. Gen. Pl. 2: 668. 1891. *Trichosalpinx quitensis* (Rchb. f.) Luer, Phytologia 54(5): 397. 1983. *Tubella quitensis* (Rchb. f.) Archila, Revista Guatemal. 3(1): 63. 2000 [2009]. *Tubella quitensis* (Rchb. f.) Archila, Revista Guatemal. 17(1): 56. 2014 [2015].

Karma reticulata (Thoerle & C. Soto) Karremans, *comb. nov.*
Basionym: *Trichosalpinx reticulata* Thoerle & C. Soto, Lankesteriana 15(1): 95. 2015.
Homotypic synonym: *Tubella reticulata* (Thoerle & C. Soto) Mel. Fernández & Bogarín, Phytotaxa 340(2): 133. 2018.

Karma robledorum (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis robledorum* Luer, Orquideología 14: 170. 1981.
Homotypic synonyms: *Trichosalpinx robledorum* (Luer) Luer, Phytologia 54(5): 397. 1983. *Tubella robledorum* (Luer) Archila, Revista Guatemal. 3(1): 63. 2000 [2009]. *Tubella robledorum* (Luer) Archila, Revista Guatemal. 17(1): 56. 2014 [2015].

Karma scabridula (Rolfe) Karremans, *comb. nov.*
Basionym: *Pleurothallis scabridula* Rolfe, Mem. Torrey Bot. Club 4: 260. 1895.
Homotypic synonyms: *Trichosalpinx scabridula* (Rolfe) Luer, Phytologia 54(5): 397. 1983. *Tubella scabridula* (Rolfe) Archila, Revista Guatemal. 3(1): 64. 2000 [2009]. *Tubella scabridula* (Rolfe) Archila, Revista Guatemal. 17(1): 56. 2014 [2015].

Karma sipapoensis (G.A. Romero & Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx sipapoensis* G.A. Romero & Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 111–112. 2007.
Homotypic synonym: *Tubella sipapoensis* (G.A. Romero & Luer) Archila, Revista Guatemal. 17(1): 56. 2014 [2015].

Karma solomonii (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx solomonii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 79. 1997.
Homotypic synonyms: *Tubella solomonii* (Luer) Archila, Revista Guatemal. 3(1): 64. 2000 [2009]. *Tubella solomonii* (Luer) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma steyermarkii (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx steyermarkii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 79–80. 1997.
Homotypic synonyms: *Tubella steyermarkii* (Luer) Archila, Revista Guatemal. 3(1): 64. 2000 [2009]. *Tubella steyermarkii* (Luer) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma strumifera (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx strumifera* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 80. 1997.
Homotypic synonyms: *Tubella struminifera* (Luer) Archila, Revista Guatemal. 3(1): 65. 2000 [2009]. *Tubella struminifera* (Luer) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma systremmata (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis systremmata* Luer, Phytologia 49(3): 219. 1981.
Homotypic synonyms: *Trichosalpinx systremmata* (Luer) Luer, Phytologia 54(5): 397. 1983. *Tubella systremmata* (Luer) Archila, Revista Guatemal. 3(1): 65. 2000 [2009]. *Tubella systremmata* (Luer) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma tantilla (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis tantilla* Luer, Selbyana 5(2): 183–184. 1979.

Homotypic synonyms: *Trichosalpinx tantilla* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 81. 1997. *Tubella tantilla* (Luer) Archila, Revista Guatemal. 3(1): 65. 2000 [2009]. *Tubella tantilla* (Luer) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma teaguei (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx teaguei* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 82. 1997.
Homotypic synonyms: *Tubella teaguei* (Luer) Archila, Revista Guatemal. 3(1): 65. 2000 [2009]. *Tubella teaguei* (Luer) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma tenuiflora (Schltr.) Karremans, *comb. nov.*
Basionym: *Pleurothallis tenuiflora* Schltr., Repert. Spec. Nov. Regni Veg. 12: 488. 1913.
Homotypic synonyms: *Trichosalpinx tenuiflora* (Schltr.) Luer, Phytologia 54(5): 397. 1983. *Tubella tenuiflora* (Schltr.) Archila, Revista Guatemal. 3(1): 65. 2000 [2009]. *Tubella tenuiflora* (Schltr.) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma tenuis (C. Schweinf.) Karremans, *comb. nov.*
Basionym: *Pleurothallis tenuis* C. Schweinf., Bot. Mus. Leafl. 10: 190–192. 1942.
Homotypic synonyms: *Trichosalpinx tenuis* (C. Schweinf.) Luer, Phytologia 54(5): 397. 1983. *Tubella tenuis* (C. Schweinf.) Archila, Revista Guatemal. 3(1): 66. 2000 [2009]. *Tubella tenuis* (C. Schweinf.) Archila, Revista Guatemal. 17(1): 57. 2014 [2015].

Karma teres (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx teres* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 64: 83. 1997.
Homotypic synonyms: *Tubella teres* (Luer) Archila, Revista Guatemal. 17(1): 58. 2014 [2015]. *Tubella teres* (Luer) Archila, Revista Guatemal. 3(1): 66. 2000 [2009].

Karma todziae (Luer) Karremans, *comb. nov.*
Basionym: *Trichosalpinx todziae* Luer, Lindleyana 11(2): 111. 1996.
Homotypic synonyms: *Tubella todziae* (Luer) Archila, Revista Guatemal. 3(1): 66. 2000 [2009]. *Tubella todziae* (Luer) Archila, Revista Guatemal. 17(1): 58. 2014 [2015].

Karma trilobata (Fawc. & Rendle) Karremans, *comb. nov.*
Basionym: *Pleurothallis trilobata* Fawc. & Rendle, J. Bot. 47: 4. 1909.
Homotypic synonyms: *Trichosalpinx trilobata* (Fawc. & Rendle) Luer, Phytologia 54(5): 398. 1983. *Tubella trilobata* (Fawc. & Rendle) Archila, Revista Guatemal. 3(1): 66. 2000 [2009]. *Tubella trilobata* (Fawc. & Rendle) Archila, Revista Guatemal. 17(1): 58. 2014 [2015].

Karma tropida (Luer) Karremans, *comb. nov.*
Basionym: *Pleurothallis tropida* Luer, Phytologia 49(3): 219–220. 1981.
Homotypic synonyms: *Trichosalpinx tropida* (Luer) Luer, Phytologia 54(5): 398. 1983. *Tubella tropida* (Luer) Archila, Revista Guatemal. 3(1): 67. 2000 [2009]. *Tubella tropida* (Luer) Archila, Revista Guatemal. 17(1): 58. 2014 [2015].

Karma vagans (Garay & Dunst.) Karremans, *comb. nov.*
Basionym: *Pleurothallis vagans* Garay & Dunst., Venez. Orchid. Ill. 6: 372. 1976.
Homotypic synonyms: *Trichosalpinx vagans* (Garay & Dunst.) Luer, Phytologia 54(5): 398. 1983. *Tubella vagans* (Garay & Dunsterville) Archila, Revista Guatemal. 3(1): 67. 2000 [2009]. *Tubella vagans* (Garay & Dunsterville) Archila, Revista Guatemal. 17(1): 58. 2014 [2015].

Karma webbiae (Luer & R. Escobar) Karremans, *comb. nov.*
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A REPORT ON THE NOMENCLATURAL SECTION OF THE SECOND INTERNATIONAL SYMPOSIUM ORGANIZED BY THE BOTANICAL SURVEY OF INDIA AT KOLKATA, INDIA

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Gopal Krishna,[1] and Kanchi N. Gandhi[2,3]

The Botanical Survey of India (BSI) organized the second International Symposium on February 13–14, 2023, at the National Library, Kolkata. Ashiho Asosii Mao, Director, BSI, was the patron of the symposium; Sudhansu Sekhar Dash and C. Murugan, both Scientists-E, BSI, served as the organizing secretary and a joint organizing secretary, respectively; and Gopal Krishna, Scientist-C, BSI, was an organizing committee member. The dates of the first symposium held in 2020 in Kolkata, and of the second symposium, coincided with the 131st and 134th foundation days of the BSI, respectively. The objective of both symposia was to provide a platform for botanical researchers to address the current issues in Plant Taxonomy, Ethnobotany, and Botanic Gardens. At the second symposium, besides the 400 delegates (including 22 international delegates), Shri Bhupender Yadav, Honorable Union Minister of Ministry of Labour and Employment, and of Ministry of Environment, Forest, and Climate Change, and Ms. Nameeta Prasad, Joint Secretary, Ministry of Environment, Forest & Climate Change, participated. The Minister spoke on current efforts and initiatives of the Government of India to promote conservation, biodiversity, and a seed bank for species pertaining to agriculture and horticulture and an intended seed bank for native plant species. The delegates spoke on their ongoing research. In this regard, the section on nomenclature, addressed by Kanchi N. Gandhi, is highlighted here. Furthermore, as a recognition of Gandhi's efforts in promoting botanical nomenclature knowledge across India, Prasad, Mao, and Dash honored Gandhi with a *Lifetime Achievement Award*.

Nomenclature and Etymologies

As per the Shenzhen Code Art. 20.1 (Turland & al., 2018), a genus name "may be taken from any source whatever and may even be composed in an absolutely arbitrary manner." In other words, it is not essential for each and every generic name to have an acceptable etymology. In this regard, a few examples are addressed here.

According to Linnaeus (1751: 174–175), etymologies of some currently/then used generic names that are of Greek and Latin origin are obscure. Under the headings "LATINA obscura, quorum fontes ignoramus, vel quæ origine dubia evadunt, assumenda sunt, sed non imitanda: e. gr." and "GRÆCA obscura, quamplurima eruuntur difficillime, et eruta dubia tamen persistunt," he listed several generic names, e.g., Latin: *Acer, Berberis*, *Ficus*, *Ilex*, *Lilium*, *Malva*, *Pinus*, *Rosa, Solanum*, *Tilia*, *Verbena*, *Viola*, *Vitex,* etc.; Greek: *Aloe, Cactus, Citrus*, *Cycas*, *Exacum*, *Fucus*, *Gossipium*, *Hibiscus*, *Lemna*, *Morus*, *Myrtus*, *Nerium*, *Oryza*, *Piper*, *Rhamnus*, *Saccharum*, *Thalictrum*, *Xyris, Zea*, etc. From the preceding list, it is evident that Linnaeus was unaware of the derivations of some generic names from Indian languages, e.g., *Oryza* (from *Arici*, rice) and *Saccharum* (from *Sacchar*, sugar).

Andira Lam. (Fabaceae)

Lamarck mentioned that the genus name *Andira* was derived from the common name *Angelyn*. Although the term angel may be traced to Greek, Lamarck mentioned *Angelyn* as a Brazilian Portuguese term. The initial speculation on the etymology of the name Angelyn was that it probably alludes to a tree's form and height. However, Michael J. Hopkins (INPA, pers. comm. to KNG) asserted that *Angelyn* was derived from Malayalam/Tamil/Sanskrit.

Sanskrit/Tamil/Malayalam: Offering to divinity with two hands joined creating a basin/bowl (or cavity) simulating the shape of a boat. In Kerala, the common name *Anjali* or *Anjili* refers to *Artocarpus hirsutus* Lam. (Moraceae). The wood of *Andira hirsutus* has been extensively used in making boats. Portuguese, who were in Kerala, assigned the same common name to *Andira* in Brazil.

Ephedra L. (Ephedraceae).

The species occur in deserts and arid regions and are occasionally found in wet areas. The plant's unique characters include small, decussate or whorled, ephemeral leaves on photosynthetic stems and branches, vessels for water and mineral transport (an anatomical character of most Angiosperms), and the presence of ephedrine and other alkaloids. *Casuarina* L. (Angiosperm), *Ephedra* (Gymnosperm), *Equisetum* L. (Pteridophyte), and *Polygonum* L. (Angiosperm) have, in common, jointed branches and/or stems.

Perhaps, for the above reason, for what is currently

We thank Carl Lenhart (Retired, Latin and Greek Teacher, Boston) for providing the translated text from Giovanni Battista Ferrari's work, Robert Rice for his analysis and critical remarks on the etymology of *Anthriscus*, Anthony R. Brach (A, GH) for helpful suggestions on the text, and Avishek Bhattacharjee (CAL) and Sanjay Kumar (CAL) for providing the photographs used in this report.

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known as *Ephedra*, Bauhin (1623: 15) used the name *Polygonum* (as *Polygonum bacciferum maritimum minus*), whereas Woods (1944: 95, 96, 118) assigned the common name "horse tail" to *Ephedra*, *Equisetum* and *Hippuris* L. In Greek, the common name for *Ephedra* is "horse tail." The green shoots of *Hippuris* look similar to those of *Ephedra*. An analysis on the etymology of *Ephedra* is given below.

One of the literal meanings of *Ephedra* is "sitting upon;" *epi,* upon, and *hedros*, seat (c.f., Sanskrit *Api*, also, besides; and *sad*, sit; *sidati*, sits; and *niddah*, resting place, nest) [see Online Etymology Dictionary]. It is a puzzle about the plant "sitting/resting on something". In ancient times, the name *Ephedra* seems to have been applied to an unknown epiphyte or parasite; if so, the literal meaning is justified (Smith in Rees, 1809: 290).

Linnaeus (1751: 185), however, gave the etymology as: *Ephedra Aqua* ύδωϱ, and *prasu* επi. This can be slightly elaborated as follows: *Aqua* = ύδωϱ = hydor: water; *prasu* επi": *epi*- = upon; *prasu* = leek green, tender grass, shoot, mare, etc.

Ephedra is a desert plant, whereas Linnaeus mentioned *aqua* for habitat! This was a puzzle. Linnaeus also mentioned "*prasu* επi," and this is another puzzle about linking "green shoot" with the word 'upon.' Linnaeus treated two species, and neither were in a wet place (one is marine & the other is in Siberia). It is likely that Linnaeus mistook the aquatic habitat of similar looking *Equisetum* and/or *Hippuris* and misapplied the same habitat to *Ephedra*. Peter Raven (MBG, pers. comm.) agreed about the error of Linnaeus, and asserted that Linnaeus most likely did not see *Ephedra* in its habitat and misapplied the habitat of similar looking *Equisetum* to *Ephedra*.

The acceptable etymology is: Greek *epi*, upon, and *hydor*, water, probably alluding to habitat of similar looking green shoots of *Equisetum* and/or *Hippuris*, misapplied to *Ephedra*.

Citrus L. (Rutaceae)

About 600 years ago, "oranges" were commonly known as "Chinese apples" (cf. the phrase "comparing oranges and apples"!). As mentioned before, Linnaeus (1751: 174) listed *Citrus* as of obscure Greek origin. Scora (1975: 369-375), however, provided detailed information on the history and origin of *Citrus*, and a portion of his text is quoted below in three paragraphs.

"The oldest known reference to *Citrus* appears in the Sanskrit literature. In the Vajasaneyi Samhita, a collection of devotional texts dated prior to 800 B.C., and which is part of the Brahmin sacred book called the White Yahir-veda, the name applied to *citron* and lemon is *Jambhila*."

"The *citron* (*Citrus medica* L.) was sanctified in India, and consecrated to…Ganesh, God of knowledge and wisdom. The Buddhist art of Java features the treasure god Kuvera (aka Kubera) holding a *citron* in his hands."

"Once this fruit was dispersed over the hellenistic Near East, it became an important part of the Jewish feast of Tabernacles, which was originally based upon Canaanite manhood rites. Through the Jewish communities, the fruit was traded over the entire Mediterranean region. Its sanctity, pleasant odor, good appearance, and relative imperishability suited for prolonged travel made the citron the forerunner of all Citrus to reach the West and the first citrus fruit to come to the attention of Europeans. From the records of Alexander's scientific staff accompanying his Macedonian army into Persia, Theophrastus, in about 310 B.C., described the citron as the apple from the lands of the Medes. The fruit was also described in Latin by Virgil, Dioscorides and Plinius."

Linnaeus (1751: 189) referred *Citrus* to *Kitros* Dioscorides. Therefore, the derivation of the name is evident, but the allusion is uncertain. Linnaeus (1754: 341) attributed "Citreum" to Tournefort (1700: 620). Tournefort, in turn, attributed "Citreum" to the work *Hesperides*, authored by Giovanni Battista Ferrari (1646: 41–2). A translation of the relevant portions of the text from pages 41–42, kindly provided by Carl Lenhart, is quoted below in five paragraphs.

> "Lusitania (Portugal) echoes Greece, which proclaims in a common vocabulary trees and fruit-trees having thorns. But the Athenians (as their ancestor is Horus) from a place, which they do not name, think the name refers to a fruit-tree. I am of the opinion that this is a city, which was called *Kixus* or *Citrus*, a secondary city, by the formerly well-celebrated Thessalonican Episcopate. And perhaps as the town Cerasus got its name from *ceracis* (cherry trees), so the land of *Citrus* got its name from *malis citreis, the citrus-apple* trees. In other respects, *Isidorus* affirms that the tree itself, the *kedromelon (= kitrion,* the *citron-tree)* is called the *citriam (citron-tree* or *citrus-tree)* by the Latins: because the *cedrum* (cedar tree) imitates it with its fragrance."
>
> "If you follow Jannis Goropius Becanus, that man will steer you first to the Arabs and Africans, and to the other *cedrum* (cedar tree), as celebrated for its resin as well as its wood, either people more accurately calling the cedar resin itself in their own local languages as *chitran* or (as he says similarly) *chatra*n: from which he affirms that the fruit-bearing *citrum* has been designated with a similar appellation."
>
> "Then he will lead you to his own people, the Cimbri, among whom he ingeniously devised falsely the Aboriginal gushing/babbling of all their tongues. He would announce that the ancestor of our universal mortality, the very head of the human family, Adam, was not said to be a Hebrew name, but a Cimbri name; and clearly, he would place the land of the Cimbri in Mesopotamia. Therefore, he thinks *citrum* is called that because it will defraud with distinguished honor large drinking vessels. While with one's thirst quenched by his own very cold juice/liquor, he does not finish the same among those who are parched or given to drink, if mortals should be lacking the citrus-apple tree (*malo citreo*)" (Ferrari, 1646: 41).

FIGURE 1. **A**, Kanchi N. Gandhi interacting with Shri Bhupender Yadav (on the podium, not shown in the photograph) and Sadhana Babbar, S. B. Babbar, G. K. Dhingra, R. K. Gupta, S. S. Hameed, P. J. Matthews, C. A. Pendry, B. Prasad, P. K. Pusalkar, V. Ranjan, D. K. Singh, Harish Singh, Paramjith Singh, V. Sampath Kumar, M. Sanjappa, M. F. Watson, J. Yesilyurt, et al. seen in the back rows; **B**, Gandhi honored (L–R): S. S. Dash, A. A. Mao, Gandhi, and Nameeta Prasad.

> “For in Cimbrian speech *Chit* signifies a large drinking vessel or jug. The form *eer* is trustworthy, but the form *hoon* sounds like a deception. So that, from these three members of this word, the name *Chiteerhoon* is connected together. And with the benefit of syncope (omission of letters) *citron* or *citrum* (is created), by means of his own position (office, authority) without a doubt deceiving with the term “large drinking vessel.” But (and I shall speak rather more equally than that of the man praising his country during a time of peace) the suggestion of the force and strength of the name *citreus*, (praelo = spoken before?) as coming from a Cimbrian etymology, flows much too awkwardly and too forcefully.”
>
> “For who does not know, from even that the coldness of citrus trees is total (?), that the ardor of the intoxicated drinker is imperishable, who with drinking vessels as large as you can imagine does not cheat or defraud, his honor (office, position, authority) drying up in the process? Why do we not rejoice over the felicitous interpretation of this same name found among our several regions, an interpretation not long searched for but obvious? Let us deduce *citrum* from *citra,* an adverb of place: and let us proclaim that its own name comes from *citro* precisely because Palladij (Palladio?) caused this tree, (its origin) for a long time across the sea, to be brought here to us, having been tried to do so rather often, by the intense efforts of earlier people. And (the tree) accepted hospitably into a very skillful culture, widely propagated in a woodland setting throughout the orchards of Italy. Palladij (Palladio?) brought this tree to us.” (Ferrari, 1646: 42)

For the etymology, from the above text, “... the *kedromelon* (= *kitrion,* the citron-tree) is called the *citriam (citron-tree or citrus-tree)* by the Latins: because the cedrum (cedar tree) imitates it with its fragrance*”* may be acceptable.

Greek *kitros* is an ancient name possibly alluding to fragrance, as in *cedrum*.

Anthriscus Pers. (Apiaceae)

Persoon (1805: 320) derived *Anthriscus* from the species name *Scandix anthriscus* L. (Linnaeus 1753: 257), the type species of the genus name, but he did not provide an etymology. For his *S.* “*Anthriscus,*” Linnaeus indicated that the epithet is a noun but did not provide a reference for the epithet.

Pliny ([ca. AD 77] 1856: 349, 423) seems to be the only classical Latin source. He mentioned *anthriscum* twice (book 21, chapter 52, and book 22, chapter 38) as shown below in quoted translated text.

> “The other plants that are commonly eaten in Egypt are the *chondrylla* … the *anthriscum* …” (book 21, chapter 52, p. 349); and “The *anthriscum* would be exactly the same plant as the *scandix*, if its leaves were somewhat thinner and more odoriferous. Its principal virtue is that it reinvigorates the body when exhausted by sexual excesses, and acts as a stimulant upon the enfeebled powers of old age. It arrests leucorrhœa in females” (book 22, chapter 38, p. 423)

For *Scandix australis* L, the southern chervil, Lewis and Short (1879) mentioned “*anthriscus*, i, f., or -*um*, i, n., = *ἄνθρισκον*.” However, Robert Rice (pers. comm. to KNG), Vice-President of the Passiflora Society International, disagreed with Lewis and Short and remarked that, “There certainly does not seem to be a Greek form *ἄνθρισκον*.” According to Rice, Pliny did not mention *anthriscum*, and whatever he wrote was unfamiliar to the later scribes, so *anthriscum* was likely a mistake of the scribes. Rice added that “although the reading *enthryscum* (as given in the Oxford Latin Dictionary) is now generally accepted, we have variant readings such as *Enthyriscum, Inthyriscum, Entriscum* and *Anthriscum*; in addition, as its appearance in the accusative opens up to an uninformed reader the possibility that the nominative may be *Anthriscus* or the like.” Rice provided the following additional remarks:

> “1. *Enthryscum* (Pliny) (N) = *Scandix australis*, chervil, following Theophrastus ἐνθρύσκον, spelt by other classical authors (Sappho and Cratinus the comic playwright) ἀνθρύσκον; in Pherecrates, another playwright, it is ambiguous due to crasis with a preceding καὶ, giving κᾀνθρύσκον, which could conceal either a leading ἀ or an ἐ. But in all cases, it is spelt with an ύ and not an ί, except in the late secondary sources Hesychius the lexicographer (C5AD), who instances ἀνθρίσκιον, and the grammarian Pollux (C2AD), ἀνθρίσκος. Only in the last case is it masculine, elsewhere always neuter. Not found in Dioscorides.”
>
> “2. ἀνθέρικος (Theophrastus) (M) = *Anthriscum* (Pliny) = the epigeal part of an asphodel; i.e., its flowering stem or scape (as opposed to ἀσφόδελος = the hypogeal portion, also used for the entire plant). Pliny gave the name in Greek correctly, but Bauhin (1651: 70, 83) gave its Latin name as *Antriscus* or *Anthriscus*, whereas Linnaeus (1753: 240, 257) used *Anthriscus* as an epithet (i.e., *Scandix* “*Anthriscus*” and *Tordylium* “*Anthriscus*”), which has not been found anywhere in classical Latin.”
>
> “As before, this could derive from a failure to understand that both contexts in Pliny required it to be in the accusative, viz. *anthricum*. In this case Lewis and Short correctly give it as *Anthericus*.”
>
> “3. ἀνθέριξ gen. -ικος (Homer, Hesiod etc.) (M) = awn/barb/beard of an ear of corn; the ear itself; also = ἀνθέρικος.”

"4. ἀθήϱ, -έϱος (Hesiod onwards) (M) = awn, barb, spike."

"So, what can we say about etymology? It looks as if there are 2 strands, which are hard to disentangle, and in any case may themselves be related:

a) ἀθήϱ with the core concept of spike
b) ἄνθος = flower"

"What we do *not* have is the idea of a bare stalk, still less a hollow one. The stem of most asphodels is terete, not hollow.

The "hollow stem" or at least "stem" theory can be traced in the first instance back to Klaas Dijkstra's website:

https://wilde-planten.nl/fluitenkruid.htm

Google Translation: "Fluitenkruid [Dutch for Cow parsley] owes its name to the fact that whistles can be made from the stem. To make a flute, a hollow cow parsley pipe with a closed knot at the bottom must be cut lengthwise about halfway. *Anthriscus* comes from Greek. In ancient Greek, *Anthriskon* was the name for an umbrella flower unknown to us. The name has been passed on to this genus and is said to be related to *antherix* (culm). *Sylvestris* means growing in the forest."

Rice remarked that that the first two sentences in the above translation are explaining the etymology of the Dutch common name, not the botanical name. It is emphasized here that, in summary, we do not know the allusion of the genus name. In this regard, Rice's remark is quoted below.

> "One may find this [unknown allusion] disappointing, but at a certain point, one has to stop etymologizing: one cannot always chop words into pieces and say one piece means x and another y, hence the combined meaning; all one can say is that there is such-and-such a Greek or Latin word, which appears to have a Greek, Latin, Indo-European, etc., root meaning Z, cf., e.g., Sanskrit."

Finally, an acceptable etymology is given below as:

> Greek *Anthriskon*, and Latin *Anthriscum or Anthriscus,* ancient names for southern chervil, *A. cerefolium*.

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A NEW SPECIES OF *VOCHYSIA* (VOCHYSIACEAE, SECTION *CILIANTHA*, SUBSECTION *FERRUGINEA*) FROM THE COLOMBIAN AMAZON FOREST

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Abstract. A new species of *Vochysia*, *V. wilsonii* (section *Ciliantha*, subsection *Ferruginea*), is described, and its morphological relationships with other similar *Vochysia* species are discussed. *Vochysia wilsonii* is found in wet forests over sandstone tabletop outcrops ("Mesetas") and white sand soils in the Araracuara ("medio río Caquetá") and Chiribiquete areas, a megadiverse region in the Colombian Guayana Shield, Caquetá department. This new species is a tree up to 25 m tall, and shares features with four species (*Vochysia biloba*, *V. casiquiarensis, V. sabatieri*, and *V. vismiifolia*). However, it differs in the size and shape of the leaves, stipules, inflorescence, cincinni, spur, spurred sepal, flower, central petal and stamen, as well as in its pubescence size and shape. An updated key of 45 Colombian species of *Vochysia* is provided.

Keywords: Wet forest, Sandstone outcrops, Araracuara, Medio Río Caquetá, *Vochysia,* Vochysiaceae

Resumen. Una nueva especie de *Vochysia*, *V. wilsonii* (section *Ciliantha*, subsection *Ferruginea*) es descrita y sus relaciones morfológicas con sus especies afines son discutidas. *Vochysia wilsonii* se encuentra en los bosques sobre mesetas en los afloramientos de arenisca y en suelos de arenas blancas de Araracuara (medio río Caquetá) y Chiribiquete, una región megadiversa del escudo guayanés colombiano, en el departamento del Caquetá. Esta nueva especie es un arbol de hasta 25 m de altura, que presenta similitudes morfológicas con cuatro especies (*Vochysia biloba, V. casiquiarensis, V. sabatieri* and *V. vismiifolia*). Sin embargo, esta difiere en la pubescencia, tamaño y forma de sus hojas, estípulas, inflorescencias, cincinos, espolón, cáliz espolonado, flores, el pétalo central y el estambre. Se incluye una clave actualizada de las 45 especies de *Vochysia* presentes en Colombia.

Palabras clave: Bosques húmedos, afloramientos de arenisca, Araracuara, Medio Rìo Caquetá, *Vochysia,* Vochysiaceae

Vochysia Aublet (Vochysiaceae) is a Neotropical genus found in southern Mexico (Chiapas, Oaxaca, Tabasco and Veracruz states) through Central America, Colombia, Venezuela, The Guianas, Ecuador, Perú, Brazil, Bolivia, and Paraguay (Marcano-Berti, 1998, 2005; Marcano-Berti and Aymard, 2021). The genus encompasses 146 species, including the new species described herein, and is the most diverse and most representative genus in *Vochysiaceae*, a pantropical family of eight genera and ca. 238 species (Kawasaki, 2007). *Vochysia* has its highest diversity in the Amazon and Orinoco river basins and the Guayana Shield region (ca. 86 species; Marcano-Berti, 2005, 2014). The genus is characterized by its opposite or verticillate leaves in whorls of 3, 4 or 5; stipules present, often deciduous; inflorescences thyrses or racemes, usually terminal; spurred calyx-lobe, persistent; petals usually 3, yellow, sometimes 1–2 or absent; stamen in the plane of symmetry; stigma terminal or lateral; ovules 2 per locule; and seeds, 3, unilaterally winged (Stafleu, 1948; Marcano-Berti, 1998, 2005; Kawasaki, 2007).

Stafleu (1948) did a worldwide monograph of *Vochysia* and divided the genus into three sections (*Ciliantha* Stafleu, *Pachyantha* Stafleu and *Vochysiella* Stafleu) and 8 subsections, recognizing 97 species, and describing 14. Later, based on vegetative and flower features, Marcano-Berti (2014) established the section *Apopetala*, to which he also transferred nine species of section *Ciliantha* Stafleu.

The present contribution increases to 45 the number of *Vochysia* species known from Colombia. This new species was identified during research on Vochysiaceae conducted by the senior author in the herbarium COAH of Instituto Amazónico de Investigaciones Científicas (SINCHI) in Bogotá, Colombia.

Materials and Methods

This work is based on morphological (using a dissecting stereomicroscope) and herbarium studies at COAH and COL (herbarium codes after Thiers, 2019). Additionally, all type specimens, as well as general collections, hosted by virtual herbaria, were consulted, including those maintained by the Field Museum (F; http://emuweb.fieldmuseum.org/botany/taxonomic.php), Instituto Nacional de Pesquisas da Amazônia (INPA; http://inst.florabrasil.net/en/), JSTOR Global Plants (http://plants.jstor.org), Museum of Natural History, Paris (P; http://www.mnhn.fr), Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/), speciesLink (https://specieslink.net/), the Smithsonian

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Institution (US; https://collections.si.edu/search/), and the National Herbarium of The Netherlands (U; https://www.nationaalherbarium.nl/). A historical and current taxonomic literature review on *Vochysia* was done, mainly using Stafleu's *Vochysia* monograph (1948), the treatments of Vochysiaceae in *Flora of Guianas* (Marcano-Berti, 1998), *Flora of the Venezuelan Guayana* (Marcano-Berti, 2005), the updated key of the Colombian *Vochysia* species (Marcano-Berti and Aymard, 2021), "*Catálogo preliminar comentado de la flora del medio Caquetá – Amazonia colombiana*" (Sánchez, 1997), "*Catálogo de plantas y líquenes de Colombia"* (Marcano-Berti, 2016), and *"Catálogo de las plantas con flores de la Amazonia colombiana*" (Infante-Betancour and Rangel-Ch., 2018a). Type specimens of *Vochysia* species involved in this study were examined using online images from JSTOR Global Plants (https://plants.jstor.org/). The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), Marcano-Berti (2005) and Harris and Harris (2006). To determine the conservation status (IUCN, 2022), the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the supporting Red List threat assessments with GeoCAT (Geospatial Conservation Assessment Tool; Bachman et al., 2011), which is continually updated (https://geocat.kew.org/.). The GeoCAT is an open source, browser-based tool that performs rapid geospatial analysis for Red List assessment. The EOO is defined by the IUCN (2022) as the minimum convex polygon encompassing all known occurrences of a species. In addition, AOO is the area within the EOO, which is comprised of 2 × 2 km grid cells containing known occurrences records.

TAXONOMY

Vochysia wilsonii Marc.-Berti, J.M. Vélez. & Aymard, *sp. nov.* TYPE: COLOMBIA. Caquetá: Araracuara, sobre la mesa de arenisca cerca de la pista aérea, 0°37'S, 72°24'W. 200–300 m, 09 November 1991 (fl). *Joost Duivenvoorden, Noé Matapí & Diego Restrepo 2723* (Holotype: COAH [4950]; Isotypes: COAH [4945]; COAH [4946]; COAH [75473]). Fig. 1.

Vochysia wilsonii resembles *V. biloba, V. casiquiarensis, V. sabatieri* and *V. vismiifolia*, but can be differentiated from these species by having leaves obovate to obovate-elliptic, 7.0–14.2 × 4.2–6.0 cm, apex emarginated, truncate to truncate-emarginate, short mucronate, base obtuse, lateral veins 24–29, at a 50°–60° angle with the midrib, stipules triangular, inflorescences 16–19 cm long, cincinni 3-flowered, rarely 2- or 4-flowered, spurred sepal 1.3–1.4 cm long, spur 6.5–7 mm long, subsigmoidal, and stamen glabrous dorsally, laxly pubescent on internal surface.

Trees up to 25 m tall and 60 cm DBH. Young and adult *branchlets* tetragonal, sulcate to flat, bark persistent, dark brown, densely ferruginous adpressed pubescent. *Leaves* opposite, obovate to obovate-elliptic, 7.0–14.2 × 4.2–6.0 cm, shiny, glabrous above, except the midrib, which is densely pubescent, covered with white and ferruginous trichomes; *trichomes* 2-branched (t-shaped), sessile, densely ferruginous below, with the same type of pubescence above, base obtuse, apex emarginate, truncate to truncate-emarginate, short mucronate 1–5 mm long; midrib impressed above, prominent below; *main lateral veins* 24–29 on each side, plain above, prominent below, not decurrent over the midrib, forming with an angle of 45°–55° (at least the veins located in the middle); *minor lateral veins* inconspicuous; *veinlets* inconspicous, scaleriform, submarginal vein ca 0.05 mm from margin; *stipules* triangular, persistent, 1.0–1.5 mm long, 2.5–3.0 mm at the base, densely adpressed ferruginous; petiole 1.0–1.8 × 0.20–0.25 cm, adaxially depressed, slighty striate abaxially, pubescence like the branchlets. *Inflorescence* paniculate, terminal, sometimes axillary, 16–19 cm long, axis tetragonal, slightly sulcate, ferruginous adpressed pubescent; cincinni 3-flowered, rarely 2- or 4-flowered, 1.5–2.7 cm long, peduncle of cincinni 4–6 mm long, pubescent; *pedicel* in mature flower 0.3–0.6 mm long; bracts and bracteoles early deciduous, lanceolate, ca. 1.5 × ca. 1.0 mm, densely golden-ferruginous adpressed pubescent. *Flower bud* near anthesis, arcuate, ca. 2 mm wide near apical third, subrounded at apex; Spur sepal 1.3–1.4 cm long at anthesis, sparsely ferruginous pubescent; *spur* subsigmoidal, 6.5–7 mm long, 1.5–1.8 mm wide at the base, ca. 1 mm wide at the apex, at an angle of 10°–15° with the pedicel, smaller sepals 0.25–0.4 mm long, subequal; *petals* 3, central petal about 1/3 shorter than stamen, apex acute, densely adpressed pubescent dorsally; lateral petal about 1/3 shorter than central petal, pubescent near the base and at the margin of the apex; *stamen* subobtuse at the apex, glabrous dorsally, laxly pubescent adaxially, glabrous abaxially, tecae glabrous; *anther* ca. 10 times longer than the filament; *staminodes* pilose at the margin, trichomes larger than staminode; *ovary* glabrous; *stigma* terminal, punctiform. *Fruit* 2.5–2.8 × 1.0–1.2 cm, oblong to oblong-obovate, densely verruculose, brown; *seed* winged, wing ca. 1.8 × ca. 0.5 cm, glabrous, light brown.

Phenology: This new species was collected with flowers in November and with fruit in February.

Etymology: *Vochysia wilsonii* is named after Wilson Rodríguez, a most enthusiast Colombian botanist, with an extraordinary knowledge of the floras of the Amazon and Orinoco river basins, of neotropical ferns, and, more recently, of Vochysiaceae.

Common names: The name "Peraikz" (Uitoto) was recorded on the specimen *Sastre & Raichel-Dolmatoff 4956*.

Distribution and ecology: The new species is known to occur in the Araracuara and Chiribiquete regions, in wet forests on dissected and tabletop terrain over sandstone outcrops, in spodozols and quartzizaments soils, between 200–300 m elevation. The former is a region located in the middle Caquetá river, in the department of Caquetá. The first botanical samples for the Colombian Amazon were collected in Araracuara by Karl Friedrich Philipp von Martius in 1820 (Martius and Zucarini, 1824; Dugand, 1942). The most prolific Amazonian plant collector, W. A. Ducke, collected in the Caquetá river (Cerro de Cupati = Cerro de La Pedrera) in 1912 (Dugand, 1948); the relevant collections made by R. E. Schultes and H. García-Barriga also should be mentioned.

FIGURE 1. Holotype of *Vochysia wilsonii* Marc.-Berti, J.M. Vélez & Aymard (*Duivenvoorden, Matapí & Restrepo 2723*, COAH [4950]).

Sastre-Blanco and Reichel-Dolmatoff (1978) published the pioneer contribution to the flora of the Araracuara. The vegetation, soils, geology, and geomorphology of this area have also been studied (especially the sector from Araracuara to the mouth of the Cahuinari river) through the establishment of the Amazon herbarium in Araracuara in 1982 and the various research projects of the Tropenbos-Colombia Foundation, the Colombian Corporation for the Amazon "Araracuara" and "Universidad Nacional de Colombia" (Infante-Betancour and Rangel-Ch., 2018b). The Corporation subsequently formed the "Instituto Amazónico de Investigaciones Científicas" –SINCHI (Sánchez, 1997). Among the detailed studies in Araracuara and adjacent areas are those by Duivenvoorden et al. (1988), Urrego (1991, 1992), Álvarez (1993), Duivenvoorden (1994), Duivenvoorden and Cleef (1994), Duivenvoorden and Lips (1995), Londoño-V. et al. (1995), Sánchez (1997), Arbeláez and Callejas (1999), Duque et al. (2001), and Londoño-V. (2011). Based on floristic compostion, these authors recognized 22 communities, of which 14 are forest. The area where *Vochysia wilsonii* is found is composed of sandstone outcrops of the Guayana shield, located on isolated hills and on the "mesetas" on spodozols soils. This habitat has plant formations with several types of low forests with a high density of individuals (Sánchez, 1997; Arbeláez and Callejas, 1999), and it harbors the endemic genus *Araracuara* Fern. Alonso (Rhamnaceae; Fernández-Alonso and Arbeláez, 2008). Additionally, these forests are intermixed with shrubby communities and savannas over white sand soils. They harbor several species (e.g., *Brocchinia hechtioides* Mez, *B. paniculata* Schult.f. [Bromeliaceae], *Ocotea neblinae* C.K. Allen [Lauraceae], and *Xyris esmeraldae* Steyerm. [Xyridaceae]) that share affinities with the vegetation of Amazonian savannas and tepuis areas located in the Guayana shield in The Guianas, Brazil and Venezuela (Duivenvoorden and Cleef, 1994; Arbeláez and Callejas, 1999). Duivenvoorden and Cleef (1994) differentiated seven types of vegetation (one community and six associations) for the Araracuara region; the shrubby and savannas communities over white sand soils dominated by endemic species such as *Steyerbromelia garcia-barrigae* (L. B. Sm.) Aguirre-Santoro, Betancur & B. Holst. (Bromeliaceae), and *Schoenocephalium martianum* Seub. (Rapataceae) are especially remarkable.

TABLE 1. Comparison of diagnostic morphological characters of *Vochysia wilsonii* and closely related species.

CHARACTER	*V. BILOBA*	*V. CASIQUIARENSIS*	*V. SABATIERI*	*V. VISMIIFOLIA*	*V. WILSONII*
Leaves	obovate or cuneate, 11–17 × 5–9 cm, apex deeply truncate-emarginate to bilobulate forming a two-lobed obcordate shape, base rounded, obtuse or cuneate	elliptic, 12–18 × 5.0–7.5 cm, apex obtuse to obtuse-retuse, base obtuse	elliptic to sub-elliptic, 17–21 × 5–6 cm; apex acuminate, acumen ca. 10 mm long, base obtuse	elliptic; 8–12 × 3–4 cm; apex acute, obtuse or short acuminate, base acute	obovate to obovate-elliptic, 7.0–14.2 × 4.2–6.0 cm, apex truncate to truncate-emarginate, short mucronate, base obtuse
Lateral nerves	16–19, 45°–60° angle to the midrib, strongly impressed above, sharply elevated below	16–20, 60°–70° angle to the midrib, inconspicous above, slightly prominent below	30–35, ca. 50° angle to the midrib, inconspicous above, slightly prominent below	15–18, 50°–60° angle to the midrib, inconspicous above, slightly prominent below	24–29, 45°–55° angle to the midrib, inconspicous above, slightly prominent below
Stipules	deltoid	triangular	triangular	deltoid	triangular
Inflorescence and cincinni	20–25 cm long; cincinni 3-to 5-flowered	ca. 15 cm long; cincinni 2 to 3-flowered	ca. 20 cm long; cincinni 2 to 3-flowered	9.0–11.5 cm long; cincinni 1 to 3-flowered	16–19 cm long; cincinni 3-flowered, rarely 2- or 4-flowered
Spur and spurred sepal (including the hypanthium or calyx tube) at anthesis	spurred sepal 12–15 mm long; spur 6–8 mm long, straight, at an angle of 0°–30° to the spurred sepal at anthesis	spurred sepal 6.5–7.5 mm long; spur 5.3–6.2 mm long, slightly incurved, at an angle of 60°–90° to the spurred sepal at anthesis	spurred sepal ca. 16 mm long; spur ca. 9 mm long, slightly curved, at an angle of ca. 120° to the spurred sepal at anthesis	spurred sepal 8–10 mm long; spur 5–7 mm long, incurved, at angle of 60°–90° to the spurred sepal at anthesis	spurred sepal 1.3–1.4 cm long; spur 6.5–7 mm long, subsigmoidal, at an angle of 70°–90° to the spurred sepal at anthesis
Anther	pubescent on both sides	glabrous abaxially, pubescent elsewhere	pubescent on both sides	glabrous abaxially, pubescent elsewhere	laxly pubescent adaxially, glabrous abaxially

Additional specimens examined: COLOMBIA. Amazonas, río Caquetá, Araracuara, aereopuerto, aprox. 0°36'03.70"S, 72°23'45.45"W. 22 December 1977(fl), *Claude H. L. Sastre & Gerardo Raichel-Dolmatoff 4956* (COL [249769], F [2310416], P [04776105]). Caquetá: Araracuara, sobre la mesa de arenisca cerca de la pista aérea, 0°25'S, 72°30'W, 250 m, 02 November 1991 (fl) *D. Restrepo & A. Matapí 423* (COAH [18063]). Solano. Araracuara, sector Chiribiquete, bosque medio en la base del tepui, 0°17'56"S, 72°22'54"W. 165 m, 15 November 2010 (fl), *F. Castro 10756* (COAH [79383]). Solano, Araracuara, ruta Araracuara-Pista-Cueva de Guácharos, bosque húmedo, 0°35'S, 74°24'W, 165 m, 14 November 1993 (fl), *D. Cárdenas-López, G. Gangi & G. Silvano 4019* (COAH [020990]). Solano, Araracuara-Río Yarí, bosque de sabanas, 0°13'51.7"S, 72°25'45"W, 236 m, 17 February 2011 (fr), *D. Caicedo 2843* (COAH [79728]).

Conservation status: Currently, *Vochysia wilsonii* is known from six collections; three from the type locality, one near the type locality (see the additional specimens), and the other two from the SE portion of "Parque Nacional Natural Serranía de Chiribiquete." Under IUCN (2022) guidelines, there are not sufficient data (DD) to accurately determine its conservation status. However, it should be regarded as Endangered (EN) according to our calculations that estimate its Area of Occupancy (AOO) to be 16,000 km^2 and its Extent of Occurrence (EOO) to be 1,223,552 km^2 (following guidelines in IUCN, 2022). These guidelines estimate the EOO as the minimum convex polygon that includes all known occurrences of any taxon, and the AOO as the region inside the EOO that is occupied by the species (using a grid of 2 × 2 km). For threatened species, the AOO value recommended by IUCN is above 10,000 km^2 (IUCN, 2022). Although conservation status assessments can be made for species with such small numbers of collections (Rivers et al. 2011), it may be difficult to determine whether the appearance of rarity in a species is due to the lack of, or outdated, data, collection artifact, or to its actual rarity (Verspagen and Erkens, 2022).

Because of its opposite leaves, pubescent petals on the abaxial side, pubescent stamens, ciliate staminodes, and glabrous ovary, *Vochysia wilsonii* belongs in section *Ciliantha* Stafleu, and from the latter features, and the leaves below being densely ferruginous pubescent, this new species belongs to subsection *Ferruginea* Warm. (Stafleu, 1948).

This new species is morphologically related to four others taxa in section *Ciliantha*: *V. biloba* Ducke, *V. casiquiarensis* Stafleu, *V. sabatieri* Marc.-Berti, and *V. vismiifolia* Spruce ex Warm.

Nonetheless, *Vochysia wilsonii* differs from these four species in the characters discussed in the diagnosis, Table 1, and in the following key.

Key to the Colombian species of *Vochysia*

Based on Marcano-Berti and Aymard (2021)

1a. Ovary pubescent 2

1b. Ovary glabrous 9

2a. Corolla present 3

2b. Corolla absent 7

3a. Cincinni 1-flowered, petals ciliate at the apex 4

3b. Cincinni (1)2- to 4-flowered; petals not ciliate at the apex 5

4a. Stigma terminal . . . . *V. expansa*

4b. Stigma lateral. . . . . *V. diversa*

5a. Plants dried black in herbarium specimens; spurred sepal (including the hypanthium or calyx tube) 1.0–1.1 cm long at anthesis; inflorescence1.6–1.8 cm long, cincinni 1- to 2-flowered; style glabrous; stigma (lateral part) 0.3 × 0.4–0.5 mm . . . . *V. obscura*

5b. Plants dried brown or green in herbarium specimens; spurred sepal (including the hypanthium or calyx tube) 1.2–1.6 cm long at anthesis; inflorescence 2.5–3.5 cm long, cincinni 2- to 4-flowered; style sparsely pubescent in the lower 1/3; stigma (lateral part) 1.0–1.2 × 0.8–1.0 mm 6

6a. Cincinni 2- to 3-flowered; spurred sepal (including the hypanthium or calyx tube) 1.2–1.3 cm long at anthesis; central petal slightly shorter than the stamen . . . . *V. lehmannii*

6b. Cincinni 3- to 4-flowered; spurred sepal (including the hypanthium or calyx tube) 1.4–1.6 cm long at anthesis; central petal one-half shorter to slightly shorter than the stamen . . . . *V. venezuelana*

7a. Lower surface of leaf blade densely appressed pubescent, with sessile or subsessile malpighiaceous trichomes . . . . *V. pinkusii*

7b. Lower surface of leaf blade pubescent on the veins with 2-branched trichomes, one branch, erect or suberect, larger than the other 8

8a. Leaves opposite, 7–12 × 3–6 cm; spurred sepal (including the hypanthium or calyx tube) ca. 1.8 cm long at anthesis . . . . . *V. steyermarkiana*

8b. Leaves 3- to 4-verticillate, 23–27 × 11–13 cm; spurred sepal (including the hypanthium or calyx tube) 3.0–3.2 cm long at anthesis . . . . *V. pachyantha*

9a. Corolla absent 10

9b. Corolla present (1 or 3 petals) 11

10a. Leaf blades 14–18 cm long; glabrous on both sides, submarginal vein lacking and the lateral veins irregularly joined near margin forming a submarginal pseudovein . . . . *V. megalophylla*

10b. Leaf blades 6–12 cm long, sparsely to adpressed pubescent on the lower surface, trichomes 2-branched, sessile or subsessile; submarginal vein present . . . . *V. punctata*

11a. Petals 1 12

11b. Petals 3 16

12a. Lower surface of leaf blade densely ferruginous tomentose, mostly along the midrib and secondary veins, trichomes ca. 2 mm; spurred sepal (including the hypanthium or calyx tube) no longer than 12 mm at anthesis; petal 1/3 shorter than stamen . . . . *V. moskovitsiana*

12b. Lower surface of leaf blade glabrous, sparsely pilose to pilose, greyish-brownish, trichomes 0.5–1.0 mm long; spurred sepal (including the hypanthium or calyx tube) 15–24 mm long at anthesis; petal 2/3–4/5 shorter than stamen. 13

Key to the Colombian species of *Vochysia* cont.

Based on Marcano-Berti and Aymard (2021)

13a. Petiole 2–3 mm long; petal 4/5 shorter than stamen . . . *V. pacifica*

13b. Petiole 12–27 mm long; petal 2/3–3/4 shorter than stamen . . . 14

14a. Apex of the leaf blade subrounded-retuse; inflorescence ca. 4 cm long; spurred sepal (including the hypanthium or calyx tube) ca. 16 mm long at anthesis . . . *V. jefensis*

14b. Apex of leaf blade acuminate or cuspidate. Inflorescence 9–30 cm long . . . 15

15a. Petiole 1.3–1.5 cm long; leaf blade 9.8–12.0 × 4.7–5.9 cm, apex acuminate, glabrous on the lower surface; inflorescence 9–13 cm long; staminal filament ca. 7 times shorter than anther; staminodes ciliate . . . *V. gentryi*

15b. Petiole 1.7–2.7 cm long; leaf blade 16.0–19.5 × 7.0–9.5 cm, elliptic oblong, apex cuspidate; sparsely adpressed pubescent on the entire lower surface; inflorescence 17–30 cm long, staminal filament ca. 5 times shorter than the anther; staminodes glabrous . . . *V. antioquiae*

16a. Stamen glabrous . . . 17

16b. Stamen ciliate or pubescent on one or both sides . . . 21

17a. Leaves opposite, lower surface of leaf blade densely adpressed pubescent . . . *V. calophylla*

17b. Leaves 3- to 5-verticillate; lower surface of leaf blade glabrous, glabrescent on the midvein or sparsely patent pilose . . . 18

18a. Stigma lateral, 2-branched . . . *V. grandis var. uaupensis*

18b. Stigma terminal, not 2-branched . . . 19

19a. Apex of the leaf rounded to rounded-emarginate . . . *V. catingae*

19b. Apex of the leaf acute to acuminate . . . 20

20a. Leaf margin plain; no marginal vein present; spurred sepal at anthesis ca. 17 mm long . . . *V. guatemalensis*

20b. Leaf margin strongly revolute; marginal vein present; spurred sepal at anthesis ca. 7 mm long . . . *V. parviflora*

21a. Leaves opposite . . . 22

21b. Leaves 3- to 5-verticillate . . . 38

22a. Spurred sepal (including the hypanthium or calyx tube) 0.6–1.4 cm long at anthesis . . . 23

22b. Spurred sepal (including the hypanthium or calyx tube) 1.4–2.6 cm long at anthesis . . . 33

23a. Spur incurved-uncinate; leaf on the lower surface densely pubescent, mainly on the venation, with 2-branched trichomes, each with an erect or suberect end much longer than the other, nearly obsolete end; main lateral veins ca. 12 . . . *V. ferruginea*

23b. Spur straight or slightly curved; leaf on the lower surface glabrous or densely ferruginous adpressed pubescent, with 2-branched sessile to subsessile trichomes; main lateral veins 15–29 . . . 24

24a. Leaf on the lower surface densely pubescent, with ferruginous trichomes . . . 25

24b. Leaf on the lower surface densely pubescent, with grey to pale golden trichomes . . . 30

25a. Apex of the leaf deeply truncate-emarginate to bilobulate forming a two-lobed obcordate shape . . . *V. biloba*

25b. Apex of the leaf short acuminate, obtuse to obtuse-retuse; emarginate, slightly truncate to truncate-emarginate, short mucronate . . . 26

26a. Petals glabrous; leaf blade with 2 submarginal veins . . . *V. elegans*

26b. Petals pubescent dorsally (at least the central one), leaf blade with one submarginal vein . . . 27

27a. Inflorescence 30–43 cm long; central petal cucullate, larger than the stamen and covering the apex of it . . . *V. splendens*

27b. Inflorescence 9–19 cm long; central petal one-quarter to one-half shorter than the stamen . . . 28

28a. Leaf blade obovate to obovate-elliptic, apex truncate to truncate-emarginate, short mucronate, lateral veins 24–29; inflorescences 16–19 cm long; spurred sepal 1.3–1.4 cm long; spur incurved; flowers 12–13 cm long . . . *V. wilsonii*

28b. Leaf blade elliptic, apex obtuse to obtuse-retuse, acute or short acuminate, lateral veins 8–20; inflorescences 5–15 cm long; spurred sepal 5–7.5 cm long; spur, slightly curved or recurved; flowers 7–9 cm . . . 29

29a. Leaf blade 8–12 cm long, apex acute, obtuse or shortly acuminate, lateral nerves 8–15, base acute; stipules deltoid; inflorescence 5–10 cm long *V. vismiifolia*

29b. Leaf blade 12–18 × 5.0–7.5 cm, apex obtuse to obtuseretuse, lateral nerves 16–29, base obtuse; stipules triangular; inflorescence ca. 15 cm long *V. casiquiarensis*

30a. Central petal 2/3 shorter than the stamen; lateral petals pubescent dorsally . . . *V. carol-scottii*

30b. Central petal as long as or 1/3 shorter than the stamen; lateral petals glabrous dorsally, sometimes ciliate at the margin . . . 31

31a. Apex of the leaf blade obtuse-retuse to rounded-retuse . . . *V. angustifolia*

31b. Apex of the leaf blade acute to acuminate . . . 32

32a. Apex of the leaf blade acute; central petal as long as the stamen, sparsely pubescent dorsally . . . *V. artantha*

32b. Apex of the leaf blade acuminate; central petal covers ca. 2/3 of the stamen, with a narrow strip of adpressed trichomes at the central portion dorsally, glabrous at the borders . . . *V. calamana*

33a. Leaf blade glabrous on both surfaces; main lateral veins 24–26 . . . 34

33b. Leaf blade pubescent on lower surface; main lateral veins 13–18 . . . 35

34a. Spurred sepal 2.4–2.6 cm long; central petal 4.7–5.8 mm long; staminodes ciliate at the base . . . *V. garcia-barrigae*

34b. Spurred sepal ca. 1.8 cm long; central petal ca. 3 mm long; staminodes glabrous . . . *V. complicata*

35a. Spur inflated, almost as long as wide . . . *V. densiflora*

35b. Spur not inflated, 4–7 times longer than wide . . . 36

36a. Leaf blade 14–21 × 4.5–9.0 cm; inflorescence 30–60 cm long . . . *V. saccata*

36b. Leaf blade 6.5–13 × 2.5–4.0 cm; inflorescence no longer than 26 cm . . . 37

Key to the Colombian species of *Vochysia* cont.
Based on Marcano-Berti and Aymard (2021)

37a. Main lateral veins 10–15 . . . . *V. calamana*
37b. Main lateral veins 20–25 . . . . *V. allenii*
38a. Leaves 3-verticillate 39
38b. Leaves 4- to 5-verticillate 42
39a. Central petal glabrous, glabrous or ciliate dorsally, ciliate at the margin 40
39b. Central petal pubescent dorsally 41
40a. Leaf blade densely adpressed ferruginous pubescent on the entire lower surface . . . . *V. elegans*
40b. Leaf blade sparsely gray pilose along the midrib on the lower surface . . . . *V. macrophylla*
41a. Leaf blade 1–2 times longer than wide; central petal ca. 2/3 as long as the stamen . . . . *V. braceliniae*
41b. Leaf blade 3–4 times longer than wide; central petal ca. 3/4 as long as the stamen . . . . *V. magna*
42a. Staminodes ciliate 43
42b. Staminodes glabrous 46
43a. Spur strongly incurved . . . . *V. spathiphylla*
43b. Spur straight to slightly recurved 44
44a. Leaf blade 1–2 times longer than wide; central petal ca. 2/3 as long as the stamen . . . . *V. braceliniae*
44b. Leaf blade ca. 4 times longer than wide; central petal as long as the stamen 45
45a. Main lateral veins 20–25 . . . . *V. lomatophylla*
45b. Main lateral veins not more than 16 . . . . *V. laxiflora*
46a. Cincini 1- to 2-flowered; central petal cucullate . . . . *V. aurantiaca*
46b. Cincini 1-flowered; central petal not cucullate 47
47a. Young branchlets, stipules and leaves on both surfaces glabrous . . . . *V. meridensis*
47b. Young branchlets and stipules pilose; leaves sparsely pilose on the lower surface, mainly on the venation . . . . *V. duquei*

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NEW RECORDS FOR NORTHEASTERN BRAZIL AND LECTOTYPIFICATIONS IN *DYSCHORISTE* (ACANTHACEAE)

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Abstract. This work presents two new records of *Dyschoriste* (Acanthaceae) for northeastern Brazil, *D. erythrorhiza* and *D. maranhonis*. Both species are endemic to Brazil. Additionally, lectotypes are proposed for *D. maranhonis* and *D. pulegium*. Geographic distribution and flowering and fruiting data are also presented.

Keywords: Brazil, Lamiales, lectotype, Ruellieae

Dyschoriste Nees (Acanthaceae) is placed in the tribe Ruellieae of subfamily Acanthoideae (Mabberley, 2008) and comprises approximately 60–80 species distributed in tropical and subtropical areas of America, Africa, and Asia (Ezcurra, 2014; Chumchim et al., 2015). Southern South America (southern Brazil, Paraguay, Bolivia and northern Argentina) is one of the main centers of diversity of this genus (Kobuski, 1928; Daniel, 1995; Wasshausen and Wood, 2003). According to Monteiro (2020), thirteen species of *Dyschoriste* are recognized in Brazil, associated with dry and humid habitats in Caatingas in the Northeast, Midwest, South and Southeast regions.

Dyschoriste species are characterized by the lobes of the calyx fused by translucent parts, generally small flowers, anthers mostly appended at the base, triaperturate pollen with sexine lips and 0–48 pseudocolpi, and capsules with 2–4 seeds covered with hygroscopic hairs (Furness, 1995; Daniel, 1995, 2004; Tripp et al., 2013).

According to Scotland and Vollesen (2000), the genus is placed in tribe Ruellieae, subtribe Ruellineae. More recently, Tripp et al. (2013) published a phylogeny of Ruellieae based on molecular data that places *Dyschoriste* in subtribe Petalidiineae. Species of this genus have features that help characterize this subtribe, such as four or fewer ovules per ovary, seeds with hygroscopic trichomes that cover their entire surface (in all species), and the presence of anthers with basal appendages.

Dyschoriste is one of the most difficult genera to place within Acanthaceae, because the species have few distinguishing characters (Ezcurra, 2013; Chunchim et al., 2015), often have restricted distribution, are poorly collected, and are morphologically variable and difficult to differentiate from related species (Ezcurra, 2014). Furthermore, taxonomic treatments of this genus are scarce: there is only one monograph of American *Dyschoriste* (Kobuski, 1928), although most of its species have been included in floristic and taxonomic surveys, mainly in Brazil.

We propose herein lectotypes for *Dyschoriste maranhonis* (Nees) Kuntze and *D. pulegium* (Nees) Kuntze, and present two new records for *Dyschoriste* for northeastern Brazil. Geographic distribution and notes on flowering and fruiting habits of these species are also provided.

Materials and Methods

Type analyses were based on high-resolution photographs from BR, GZU, LE, M, and W (acronyms according to Thiers, 2022, continuously updated), from the JSTOR Global Plants website, or from herbaria websites. Specimens from Brazil were examined at BHCB, CEPEC, HST, HUEFS, IPA, MBM, PEUFR, RB, and UB. Protologues were consulted for all names.

SpeciesLink, Reflora Virtual Herbarium, and Plants of the World Online (POWO, 2022) were consulted for geographic distributions. Typification follows the International Code of Nomenclature for algae, fungi and plants (ICN) (Turland et al., 2018).

Results and Discussion

Lectotypes for *Dyschoriste maranhonis* (Nees) Kuntze and *D. pulegium* (Nees) Kuntze are proposed herein (see rationale for each proposal below). In addition, the species *Dyschoriste erythrorhiza* (Nees) Lindau and *D. maranhonis* (Nees) Kuntze are newly reported for the northeastern region of Brazil.

Dyschoriste erythrorhiza (Nees) Lindau, Nat. Pflanzenfam. [Engler & Prantl] 4, Abt. 3b: 302. 1895. *Homotropium erythrorhizum* Nees, Fl. Bras. (Martius) 9: 47, t. 48. 1847. TYPE: BRAZIL. In sylvis Catingas ad Formigas, prov. Minarum, Augusto, et in deserto Bahiensi, *C. F. P. Martius s.n.* (Lectotype, proposed by Monteiro et al. 2020, M [0186270]).

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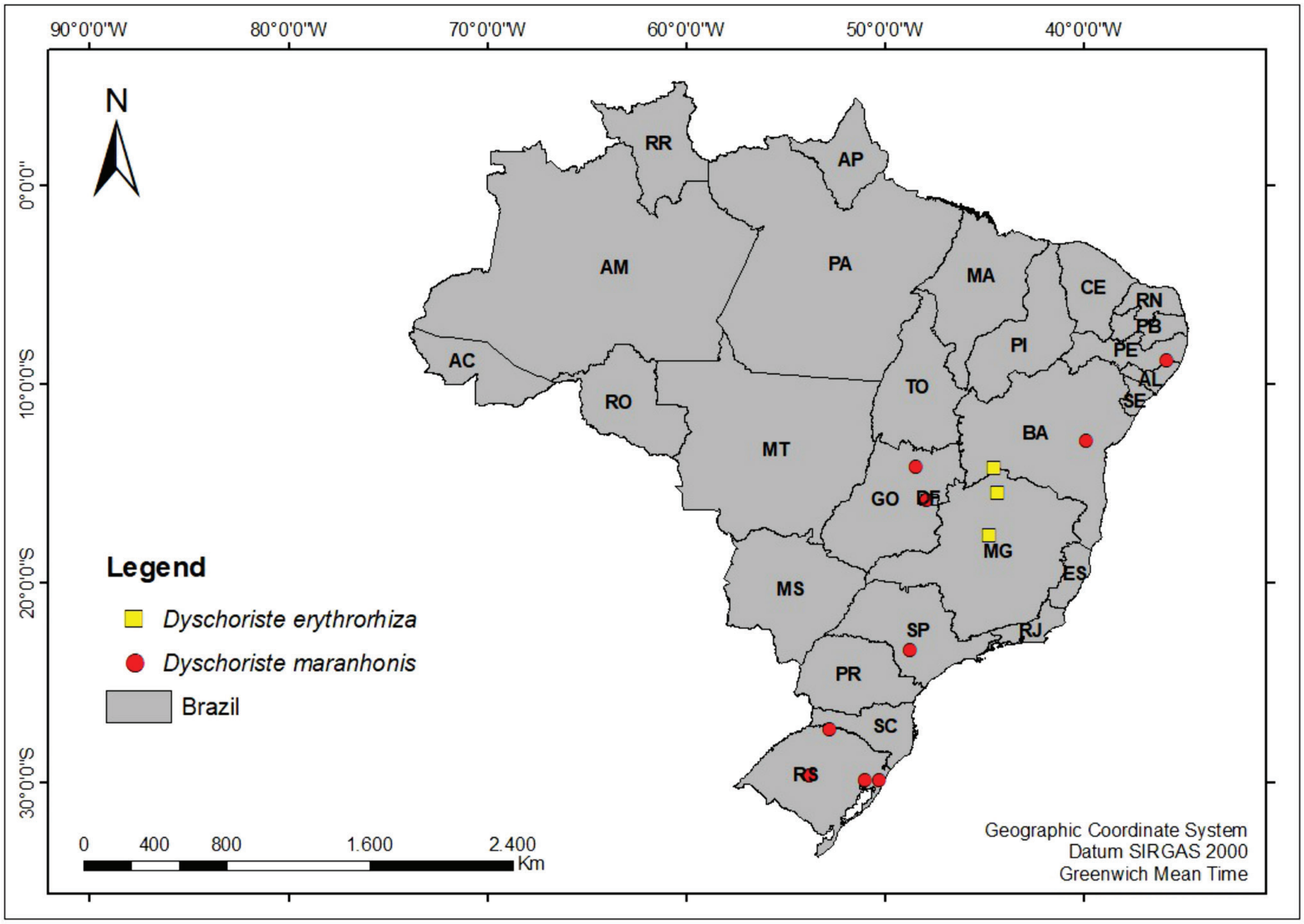

FIGURE 1. Distribution map of *Dyschoriste erythrorhyza* (Nees) Kuntze and *D. maranhonis* (Nees) Kuntze.

Heterotypic synonym: *Homotropium erythrorhizum* var. *latifolium* Nees. Fl. Bras. (Martius) 9: 48. 1847. TYPE: BRAZIL. *J. B. E. Pohl s.n.* (Lectotype, proposed by Monteiro et al. (2020), W [0056792]; Isolectotypes: M [0186271], W [0056791], W [0056793].

This species is endemic to Brazil, occurring only in the Cerrado phytogeographic domain from Minas Gerais state (Monteiro, 2020). In this work, *Dyschoriste erythrorhiza* is being reported as a new record for northeastern Brazil in Bahia state (Fig. 1). It was found with flowers from March to July and with fruits in April and July. *Dyschoriste erythrorhiza* can be distinguished by its red corollas, a rare feature in this genus.

Additional material examined: BRAZIL. Bahia: Cocos, Espigão Mestre, ca. 13 km Sul de Cocos e 3 km Sul do Rio Itaguarí, 15 March 1972 (fl.), 560 m, *W. Anderson, M. Stieber & J. H. Kirkbride-Junior 36976* (NY, US); Minas Gerais: Januária, Distrito de Fabião, 23 May 1997 (fl.), *J. A. Lombardi & A. Salino 1719* (BHCB, US); Vale do rio Peruaçu, Cerrado do Judas, 21 September 1997 (fl., fr.), *A. Salino & J. R. Stehmann 3302* (US); Montalvânia, 18 March 1972 (fl.), 550 m, *W. R. Anderson, M. Sieber & J. H. Kirkbride-Junior 37157* (UB); Várzea da Palma, Fazenda Mãe d'Água, 26 April 1963 (fl., fr.), *A. P. Duarte 7713* (NY, US).

Dyschoriste maranhonis (Nees) Kuntze, Revis. Gen. Pl. 2: 486. 1891.

Basionym: *Calophanes maranhonis* Nees, Fl. Bras. (Martius) 9: 25. 1847. TYPE: BRAZIL. Ad Maranhão flumen, *J. B. E. Pohl 1765* (Lectotype, designated here, W [0049974], image seen; Isolectotype: GZU [000249902], image seen).

In the protologue of *Calophanes maranhonis*, Nees (1847a) noted an unpublished name ("*Ruellia viscosa Pavon in Herb. Moricand.*"), *"Ruellia quitensis (?) Schlechtendal in Linn. V. 1. p. 96. n. 122.?*" (referring to a name published by Kunth from Ecuador and a synonym of *D. quitensis* (Kunth) O. Kuntze), and an unpublished illustration ("*Zahlbrucknera maranhonis* Pohl ic."). He also cited collections from Brazil and Peru ("*ad Maranhâo flumen: Pohl; ad praedium S. Ignacio in prov. Rio Grande do Sul: Sellow; in Peruvia: Pavon*!"). In a subsequent account of the species (Nees, 1847b), he noted these same collections and indicated the herbaria in which he saw them. Thus, *Pohl 1765* from the Rio Maranhão in Brazil (W [0049974] [image seen]); *Sellow 59* and *185* collected at San Ignacio, Brazil (B [destroyed]); and Pavon's collection labeled as "*Ruellia viscosa* Pavon" from Peru in herbarium Moricand are syntypes. Kobuski (1928) indicated that the type was Sellow's collection from "St. Ignacio" housed at B (destroyed, as indicated above).

A duplicate of *Pohl 1765* at GZU was chosen as an isolectotype, in order to stabilize the name associated to the species. In addition, the selected material has well-preserved vegetative and reproductive structures and can be compared with the original description of the species.

Dyschoriste maranhonis is endemic to Brazil and grows in the phytogeographic domains of the Atlantic Forest and Pampa from Distrito Federal, São Paulo and Rio Grande do Sul states (Monteiro et al., 2020). It is being reported for the first time from Pernambuco and Bahia states (Fig. 1), with flowers in November, January, and March. *D. maranhonis* can be characterized by its purple, tetragonal, and highly branch stems.

Additional material examined: BRAZIL. Bahia: Milagres, 22 February 1993 (fl., fr.), 350 m, *G. Hatschbach 42454* (CEPEC, HUEFS, MBM, US); Rod. BA-046, 22 February 1993 (fl., fr.), *G. Hatschbach 45130* (CEPEC, MBM); Pernambuco: Maraial, Engenho Curtume, 22 September 2006 (fl.), 248 m, *M. S. Leite 196* (HST, IPA); Rio Grande do Sul: Gravataí, Cachoeirinha, 7 January 1949 (fl.), *B. Rambo s.n.* (PACA-AGP 39625); Nonoai, March 1945 (fl.), *B. Rambo s.n.* (PACA-AGP 28115); Osório, Fazenda do Arroio, 23 January 1958 (fl.), *B. Rambom s.n.* (PACA-AGP 63522); Santa Maria, 1943 (fl.), *A. Heidler s.n.* (PACA-AGP 11367); São Paulo: Paranapanema, Campo Capivary, 26 November 1899 (fl.), *A. C. G. G. Loefgren 4494* (SP).

Dyschoriste pulegium (Nees) Kuntze, Revis. Gen. Pl. 2: 486. 1891.

Basionym: *Calophanes pulegium* Nees, Fl. Bras. (Martius) 9: 25 (1847). TYPE: BRAZIL. In prov. S. Pauli, *L. Riedel 70* (Lectotype: designated here: LE [00007839], image seen).

Nees (1847a), in the protologue of *C. pulegium*, cited two collections for this species *in prov. S. Pauli: Sellow, Riedel,* which are currently treated as syntypes. Kobuski (1928) in his monograph of American *Dyschoriste* mentioned only a photograph of a Sellow's collection, deposited in the Berlin herbarium (possibly destroyed), but he did not mention the existence of Riedel's collection. Kobuski also ignored "*Sellow 173* (FMNH-B-Types 5900)" as a possible lectotype of *D. pulegium*. After analyzing these collections, we propose *Riedel 70* (LE 00007839) as a lectotype of *D. pulegium* in order to bring nomenclatural stability to this species. The proposed lectotype has reproductive structures and conforms to the original description.

Additional material examined: BRAZIL. Paraná: Lapa, Engenho Bley, 26 September 1948 (fl.), *G. Hatschbach 1014* (PACA-AGP). São Paulo: without additional locality data (fl., fr.), without additional locality data (fl.), *F. Sellow* (B 173, GZU H-72).

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LEPANTHES CARRIZOSANA, A NEW SPECIES OF *LEPANTHES* (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM THE SOUTHWESTERN ANDES IN COLOMBIA

Juan Sebastián Moreno,[1,2,3,5] Robinson Galindo-tarazona,[1] and Alejandro Zuluaga Tróchez[2,4]

Abstract. A new species of *Lepanthes* from the southwestern Andes of Colombia is described, illustrated and compared with morphologically similar species. The new species was found in two localities in the municipality of San José del Salado, in the department of Valle del Cauca, where several new species have been found and described in the past several years.

Keywords: Colombia, Dagua, *Lepanthes*, Orchidaceae, San José del Salado, Sistemática, Valle del Cauca

Resumen. Se describe, ilustra y compara una nueva especie de *Lepanthes* del suroeste de los Andes occidentales de Colombia con especies morfológicamente similares. La especie nueva fue encontrada en el municipio de San José del Salado en el departamento del Valle del Cauca donde se han encontrado y descrito varias especies nuevas en los últimos años.

Palabras claves: Colombia, Dagua, *Lepanthes*, Orchidaceae, San José del Salado, Sistemática, Valle del Cauca

Lepanthes Sw. is one of the most diverse genera in the Orchidaceae, with more than 1158 species described (Karremans and Vieira, 2020), of which 376 are reported from Colombia (Farfán et al., 2003; Luer and Thoerle, 2012; Betancur et al., 2015; Bernal et al. 2016). The Western Cordillera of the Andes is the most diverse region, with Valle del Cauca Department second in diversity after Antioquia. Seven new species of *Lepanthes* have been described from San José del Salado, a region within the Cauca department (Luer, 2009; Moreno et al., 2017, 2021, 2021, 2022). In 2022, we carried out new expeditions to the mountains of San José del Salado and discovered a new species of *Lepanthes*. Here we describe and illustrate it, provide information about its distribution, and compare it with the most similar species, adding the 377th species of *Lepanthes* to the flora of Colombia.

Materials and Methods

The description and drawings were prepared from living specimens and flowers preserved in 70% alcohol. Flowers were dissected, measured, and photographed using Celestron Handheld Digital Microscope Pro. Vegetative structures were measured from dried material and reproductive structures from spirit material. Digital images were taken with a Nikon D610 and a Nikon 105mm f/2.8 macro lens. Sketches from living and preserved specimens were digitized, and the images were used for diagramming a draft composite template in Adobe Photoshop® CS6. A digital composite line drawing was then made (lines and stippling) in Procreate illustration application for iPad 6th generation tablet computer (Bogarín et al., 2019). The new species was described following the botanical terminology by Beentje (2012) and Stearn (1992). All original descriptions of related species were consulted for detailed comparisons (Luer 1996; Luer and Thoerle 2012). Specimens from the following herbaria, AMES, COL, CUVC, HUA, JAUM, JBB, VALLE, CAUP and MO (online), were consulted, and no additional material of the new species was found.

Taxonomic Treatment

Lepanthes carrizosana Gal.-Tar., Zuluaga & J.S.Moreno, *sp. nov.*
TYPE: COLOMBIA, Valle del Cauca, municipality of Dagua, corregimiento de San José del Salado, predio El Almorzadero, 1730 m, 28 August 2022, *R. Galindo-Tarazona & D. L. Mora 1586* (Holotype: CUVC). Fig. 1–2.

Lepanthes carrizosana is most similar to *Lepanthes darioi* Luer & R.Escobar. It can be distinguished by having a pubescent, obovate, bilaminate lip with cuneate connectives (vs. narrowly ovate lip and oblong connectives), and a small appendix with a pair of minute apical lobes that come from a slightly short pubescent, concave base (vs. broadly triangular appendix held directly below the stigma).

Plant 4.5–6.8 cm tall, epiphytic, weak, caespitose. *Roots* slender, flexuous 0.7 mm in diameter. *Ramicauls* slender, 2.7–4.0 cm long, suberect, enclosed by 15 lepanthiform sheaths, reducing in size towards the base, furrowed, with a dilated and ciliated ostia, long-acuminate. *Leaves* pendent, 2.5–2.8 × 0.6–0.8 cm, thinly coriaceous, ovate, long-acuminate, the apex emarginate with an abaxial central apiculum, 1.5 mm long, the base cuneate contracted into a petiole 0.5–1 mm long. *Inflorescence* a congested, successively flowered raceme, up to 0.8–1.0 cm long, including the peduncle, borne on top of the leaf by a filiform

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We are very grateful to Danny Leandro Mora for his support during the field trips to the areas of San José del Salado where the new and several other species were found. Finally, to Luisa Calderón who helped us dissect and measure the flowers of the new species.

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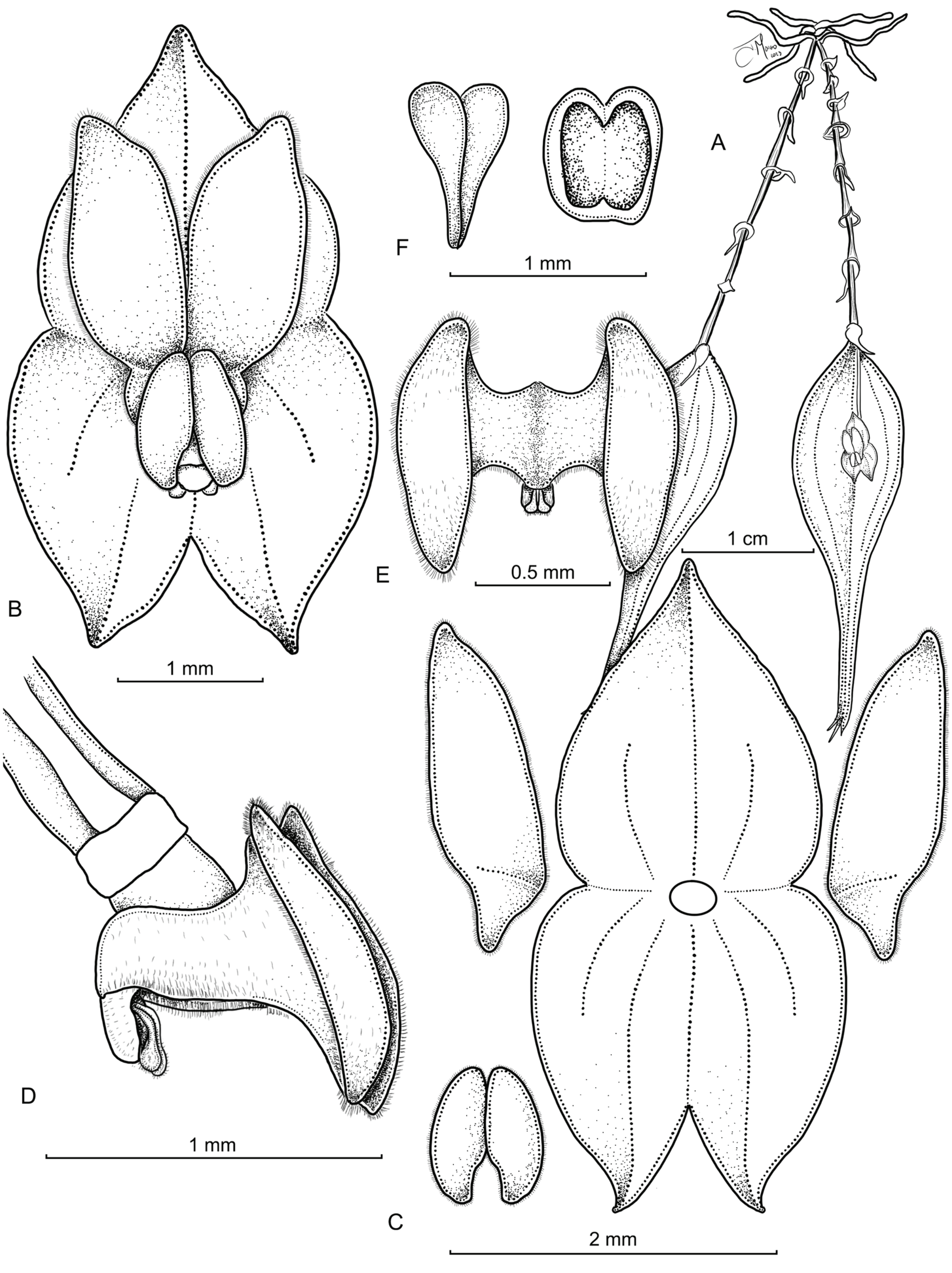

FIGURE 1. *Lepanthes carrizosana* Gal.-Tar., Zuluaga & J.S. Moreno. **A**, Habit and plant; **B**, Flower; **C**, Dissected perianth; **D**, Lip, column and ovary; **E**, Lip expanded; **F**, Pollinia and anther cap. Drawing by J. S. Moreno based on the holotype.

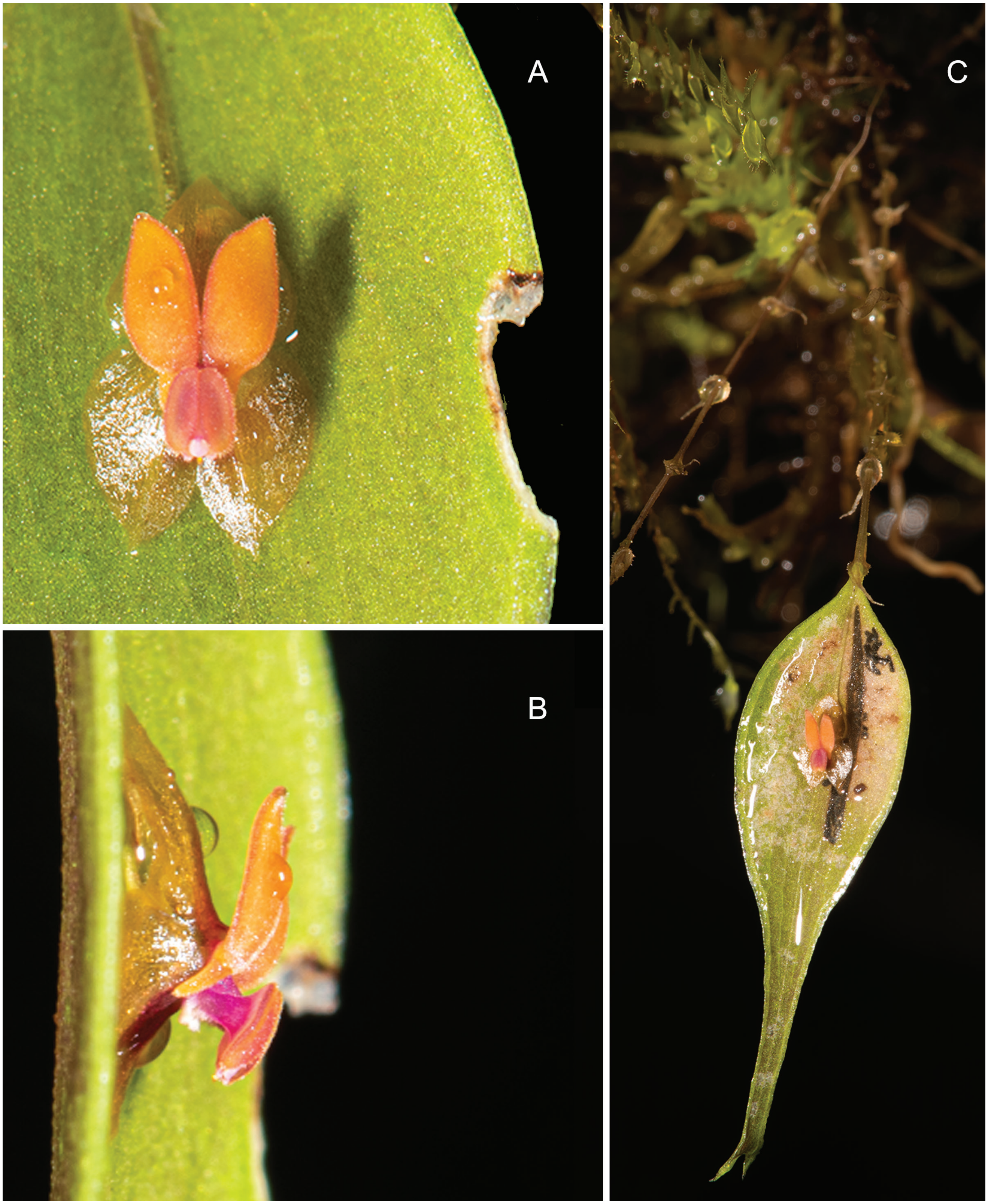

FIGURE 2. In-situ photographs of *Lepanthes carrizosana* Gal.-Tar., Zuluaga & J.S. Moreno. **A**, Flower; **B**, Flower from the side; **C**, Habit and plant. In-situ photographs by R. Galindo-Tarazona.

peduncle,7.0 mm long; *floral bract*, acuminate, 0.7–0.9 mm long; *pedicel* 1.2–1.5 mm long, terete, persistent, longer than floral bract. *Flower* 7–7.5 mm long, 4–4.2 mm wide. *Ovary* costate, up to 1 mm long. *Sepals* convex, glabrous, similar in size. *Dorsal sepal* ovate-acute, 1.8–2 mm long, 1.3–1.4 mm wide, 3–veined, connate to the lateral sepals for 1.4 mm. *Lateral sepals* ovate, oblique, acute, 1.5–1.7 × 0.9–1.1 mm, 2-veined, connate for 0.7 mm. *Petals* transversely bilobed, 0.4–0.5 × 1.6–1.8 mm, the upper lobe much longer than the lower lobe, oblong-ovate, pubescent; the lower lobe short, triangular, acute. *Lip* pubescent, bilaminate, the blades obovate, with rounded ends, the apex of each lobe short pubescent towards the base, 0.7–0.8 × 0.4–0.5 mm, the connectives short, cuneate, the body thick, rounded, pubescent, connate to the base of the column, the sinus obtuse, the appendix small with a pair of minute apical lobes that are borne from a slightly concave base, short pubescent. *Column* terete, slender, 0.9–1 mm long, the anther dorsal and stigma ventral. *Anther cap* pink, cordate, cucullate, 0.5 mm wide. *Pollinia* two, yellow, pyriform, 0.4 mm long.

Eponymy: The name of the new species honors Julio Carrizosa Umaña, a scientist, environmentalist and thinker with a great vision of the connection between environmental institutionalism and strategies aimed at sustainable development in Colombia. He was the Director of the Institute of Environmental Studies of the National University of Colombia from 1993 to 1998. He currently coordinates the Natural Parks Committee of the Colombian Academy of Exact, Physical, and Natural Sciences. He has been designated a full member of the Colombian Society of Engineers, a full member of the Geographical Society of Colombia, vice president of the Colombian Society of Ecology in 1978, an honorary member of the Cartographic Society of Colombia and the Association of Fisheries Researchers, president of the Environment Committee of the Pan-American Institute of Geography and History between 1973 and 1976, and corresponding member of the Ecuadorian Institute of Natural Resources.

Conservation status: *Lepanthes carrizosana* is known only from its type locality. Therefore, the species is classified within the IUCN categories as data deficient (DD), because we lack adequate distribution and population information to make an assessment (IUCN Standards and Petitions Subcommittee 2017; IUCN 2023).

Lepanthes carrizosana is a medium size species with small flowers that are borne in a congested raceme above the leave. The leaves are thin coriaceous, ovate, long-acuminate, the apex emarginate with an abaxial apiculum in the middle. Its petals, which are its most striking feature, have an oblong-ovate upper lobe, much longer than the small triangular lower lobe. It is most easily distinguished by its pubescent, bilaminate lip, with obovate blades and a small, short pubescent appendix with a pair of minute apical lobes that comes from a slightly concave base. The most similar species is *Lepanthes darioi* from the Western Andes of the Department of Antioquia, but its flowers are borne in a congested raceme below the leaves (*vs*. above the leaves). Also, the leaves are elliptical and obtuse (*vs*. ovate and long-acuminate) and the lip has narrowly ovate blades at the anterior margins of erect, oblong connectives, with a broad triangular appendix held directly below the *stigma* (*vs*. small appendix with a pair of minute apical lobes that comes from a slightly concave base, short pubescent).

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NOTES ON SOME MALESIAN ORCHIDACEAE V

PAUL ORMEROD[1,2] AND LINA JUSWARA[3]

Abstract. Continuing herbarium and literature research on the Malesian orchid flora reveals the need to propose 12 new synonyms in the genera *Calanthe, Coelogyne, Dendrobium, Didymoplexis,* and *Pinalia*. Two new combinations are also proposed, *Crepidium auriculatum,* and *Pinalia puberula*.

Keywords. Malesia, orchids, *Calanthe, Crepidium, Dendrobium, Pinalia*

This paper is a continuation of our studies (e.g., Ormerod and Juswara, 2022) that are intended as an effort to update knowledge of Malesian orchids. Most of the taxa dealt with here occur in Indonesia.

Calanthe R. Br., Bot. Reg. 7: sub t.573. 1821 *nom. cons.*
Type species: *Limodorum veratrifolium* Willd. *nom. illeg.* [= *Orchis triplicata* Willemet].

A genus of about 150 species of mostly terrestrial herbs that favour forested environments. They bear upright racemes of white, yellow, or purple flowers. Many are quite attractive plants in full flower. The flowers are small to medium sized, usually with spreading sepals and petals, a simple to four lobed lip that is united to the lower margins of the column and spurred at the back.

Calanthe triplicata (Willemet) Ames, Philipp. J. Sci., Bot. 2: 326. 1907.
Basionym: *Orchis triplicata* Willemet, Ann. Bot. (Usteri) 18: 52. 1796.
LECTOTYPE (Designated by Clements 1989: 32) Tab. 52, fig. 2 of *Flos triplicatis* Rumph, Herb. Amboin. 6: 115. 1750.
Heterotypic synonym: *Calanthe sumatrana* Blume ex Boerl., Bijdr. Fl. Midden-Sumatra 4, 2: 33. 1884 *syn. nov.* TYPE: INDONESIA. Sumatra, Korintji Peak, 13 December 1877, *A.L. van Hasselt s.n.* (Lectotype, here designated: L [1493711], image seen); Mt. Singgalang, *P.W. Korthals s.n.* (Syntype: L [1493713], image seen).

Distribution: Sri Lanka; India; Bhutan; China; Myanmar; Laos; Cambodia; Vietnam; Thailand; Taiwan; Japan; Philippines; Malaysia; Singapore; Indonesia; Timor Leste; Papua New Guinea; Australia; Solomon Islands; Vanuatu; New Caledonia; Fiji; Samoa; Tahiti.

Calanthe sumatrana has long been considered a synonym (e.g. Smith, 1933) of *C. ceciliae* Rchb.f. due to the misleading description and figure in the protologue of the former. Rediscovery of its type material shows that it is properly considered a synonym of *C. triplicata*. We choose the collection of A. L. van Hasselt as lectotype since this is the basis of the figure in the protologue. Both lectotype and syntype have been correctly identified by J.J. Smith as *C. veratrifolia* (Willd.) Ker Gawl., an illegitimate synonym of *C. triplicata*.

Calanthe triplicata has a vast synonymy already (Clayton and Cribb, 2013) partly due to its variation and broad distribution.

Coelogyne Lindl., Coll. Bot. (Lindley): sub t. 33. 1821.
Type species: *Coelogyne cristata* Lindl.

A genus of about 270 species (excluding *Dendrochilum* Blume) distributed from India and Sri Lanka to Samoa. Most species are epiphytic herbs, and quite a number have showy medium to large flowers. The flowers occur in shades of white, yellow, green, brown, or more rarely red. The taxon discussed here belongs to section *Speciosae* Pfitz. & Kraenzl., a group of fifteen species that was revised by Barbara Gravendeel and Ed de Vogel in 1999.

Coelogyne caloglossa Schltr., Repert. Sp. Nov. Regni Veg. 10: 16. 1911. TYPE: INDONESIA. Sulawesi, Minahassa Peninsula, Mt. Klabat, 1000 m, December 1909, *R. Schlechter 20571* (Holotype: B, destroyed). Lectotype, here designated: Fig. 91, Taf. 23 in Repert. Sp. Nov. Regni Veg., Beih. 74. 1933.
Heterotypic synonyms: *Coelogyne celebensis* J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 2, 25: 3. 1917 *syn. nov.*
TYPE: INDONESIA. Sulawesi, *leg. J. Elbert, cult. Hort. Bogor. s.n.* (Lectotype [designated by Gravendeel and de Vogel, 1999: 268]: L [0267278] image seen; L [0267279], image seen); Kolaka, 1909, *leg. J. Elbert, cult. Hort. Bogor. 4* (Syntype: BO, lost); Kampung Tapalang, near Makassar, L. van Vuuren Exped., *leg. Noerkas, cult. Hort. Bogor. 388* (Syntype: BO, lost); Gunung Paka-Paka, 1913 L. van Vuuren

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Exped., September 1913, *Rachmat 678* (Syntype: BO, lost); Bili-Bili, 1913 L. van Vuuren Exped., *leg. Rachmat, cult. Hort. Bogor. 29* (Syntype: BO, lost).

Coelogyne platyphylla Schltr., Repert. Sp. Nov. Regni Veg. 21: 129. 1925. TYPE: INDONESIA. Sulawesi, Donggala (?), *leg. native collector, cult. Becker s.n.* (Holotype: B, destroyed).

Distribution: Indonesia (Sulawesi).

We have been unable to find any differences between *C. caloglossa* and the later *C. celebensis*. Therefore the two entities are treated as conspecific. Gravendeel and de Vogel (1999) overlooked *C. caloglossa* in their monograph of section *Speciosae*.

Crepidium Blume, Bijdr. Fl. Ned. Ind.: 387. 1825.

Type species: *Crepidium flavescens* Blume

A genus of Malaxidiinae with about 270 species distributed from Sri Lanka and India to Tahiti. In Indonesia there are about 133 species with approximately 87 of them endemic. Most of the plants are forest floor terrestrials, sometimes growing in colonies. They have soft, pleated leaves and terminal racemes of small flowers, often in shades of yellow or purple.

Crepidium auriculatum (P. O'Byrne & J.J. Verm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Malaxis auriculata* P. O'Byrne & J.J. Verm., Malay. Orch. Rev. 40: 101. 2006.

TYPE: INDONESIA. Sulawesi, Luwu Prov., 8 July 2006, *P. O'Byrne SBGO 5376* (Holotype: SING [0282245, spirit], not seen).

Distribution: Indonesia (Sulawesi).

This species is a member of section *Hololobos* (Schltr.) Marg., of which there are 74 species, 37 of which are found in Indonesia.

Dendrobium Swartz, Nova Acta Regiae Soc. Sci. Upsal. ser. 2, 6: 82. 1799 *nom. cons.*

Type species: *Dendrobium moniliforme* (L.) Swartz *typ. cons.*

This is a genus of about 1520–1530 species distributed from India and Sri Lanka to Tahiti. Most taxa are epiphytic herbs though several are known to grow on rocks and terrestrially. It is a popular genus in horticulture, with many species and artificial hybrids being grown. The species discussed here belong to sections *Grastidium* Blume (*D. heteroglossum* Schltr.), *Pedilonum* Blume (*D. cymbiforme* Rolfe), *Spatulata* Lindl. (*D. jennyanum* Kraenzl., *D. enigmaticum* Ormerod), and nothosection *Spatulanthe* Ormerod (*D. leeanum* O'Brien).

Dendrobium cymbiforme Rolfe, Bull. Misc. Inf. Kew: 192. 1898. TYPE: INDONESIA. Sumatra, without locality, cultivated in Horgen, near Zurich, April 1896, *L. Kienast s.n.* (Holotype: K [001085028], image seen).

Homotypic synonym: *Eurycaulis cymbiformis* (Rolfe) M.A. Clem., Telopea 10, 1: 286. 2003.

Heterotypic synonyms: *Dendrobium ventrilabium* J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 3, 5: 84. 1922 *syn. nov.* TYPE: INDONESIA. Sumatra, Padang Highlands, Agam, Bukit Batoe Banting, *cult. W. Groeneveldt 1740* (Holotype: BO, spirit, not found).

Eurycaulis ventrilabius (J.J. Sm.) M.A. Clem., Telopea 10, 1: 288. 2003.

Distribution: Indonesia (Sumatra).

This species is easily recognised by its deeply concave, broadly flabellate labellum. Comber (2001) distinguished *D. cymbiforme* from *D. ventrilabium* by the former having a much shorter (8 vs. 15.3 mm) labellum claw. This error arose from the protologue of *D. cymbiforme* due to the labellum claw being broken off halfway when the flower was dissected for study. We find *D. cymbiforme* and *D. ventrilabium* are identical in all features, thus requiring the latter to be reduced to synonymy.

Dendrobium enigmaticum Ormerod, Oasis 4, 1: 3. 2009.

TYPE: WITHOUT ORIGIN. Flowering October 1907, *cult. H. Low & Co. s.n.* (Holotype: K).

Heterotypic synonyms: *Dendrobium taurinum* Lindl. var. *moluccense* Hort., Orchidee (Bandoeng) 4, 5: 122. 1935 *nom. inval.* [no Latin]; Anschutz, Orchidee (Bandoeng) 7, 1: 355 (25), ph. 1938 *nom. inval.* [no Latin] *syn. nov.*

Basis for name: INDONESIA. Papua or Maluku, cultivated, *sine coll. s.n.* (lost).

Dendrobium stockelbuschii Schettler, Orchideen J. 23, 2: 84. 2016 [Orchideen J. 22, 4: 173. 2015 *nom. inval.* (no Latin or English)] *syn. nov.*

TYPE: INDONESIA. Java, Bandung, in cultivation, *A. Stockelbusch s.n.* (Holotype: BO, not found).

Distribution: Indonesia [Maluku Prov. (Tanimbar Islands)].

Additional specimens examined: WITHOUT ORIGIN. *Ex Herbarium Sander s.n.* (AMES [6202]). "GERMAN NEW GUINEA": 1898, *leg. W. Micholitz, ex Herbarium Sander s.n.* (AMES [5781]).

The true origin of this species has long been a mystery but clearly it was a place where horticultural collectors often travelled to. Recently we have been able to ascertain through one of the collectors who found the material that served the basis for *D. stockelbuschii* that the plants came from one of the Tanimbar Islands (sometimes called Timor Laut). These islands were indeed visited by horticultural collectors and proved to be of great value because the attractive *D. bigibbum* Lindl. var. *schroederianum* (Rchb.f ex W. Watson) Peter B. Adams was sourced from here for the European market in the late 19th and early 20th century.

Dendrobium enigmaticum resembles both *D. nindii* W. Hill and *D. taurinum* Lindl. but its flowers are colored in shades of yellow and brown (vs. white to pale green with purple), also the labellum has three apically elevated keels (vs. midkeel elevated in *D. taurinum,* and all three keels apically decurrent in *D. nindii*). The first author also examined fresh material named *D. stockelbuschii* through the courtesy of Mr. Ross McLaren. This matched the protologue of *D. stockelbuschii* and showed it to have all the critical characters of *D. enigmaticum,* thus requiring the reduction to synonymy of the former.

Dendrobium heteroglossum Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 593. 1912.

TYPE: PAPUA NEW GUINEA [as Kaiser Wilhelm's Land]: Waria District, Maboro Range, 1200 m, June 1909, *R. Schlechter 19866* (Holotype: B, destroyed). Fig. 1.

Homotypic synonym: *Grastidium heteroglossum* (Schltr.) Rauschert, Repert. Sp. Nov. Regni Veg. 94: 449. 1983.

Heterotypic synonyms: *Dendrobium coloratum* J.J. Sm., Repert. Sp. Nov. Regni Veg. 12: 113. 1913 *syn. nov.*

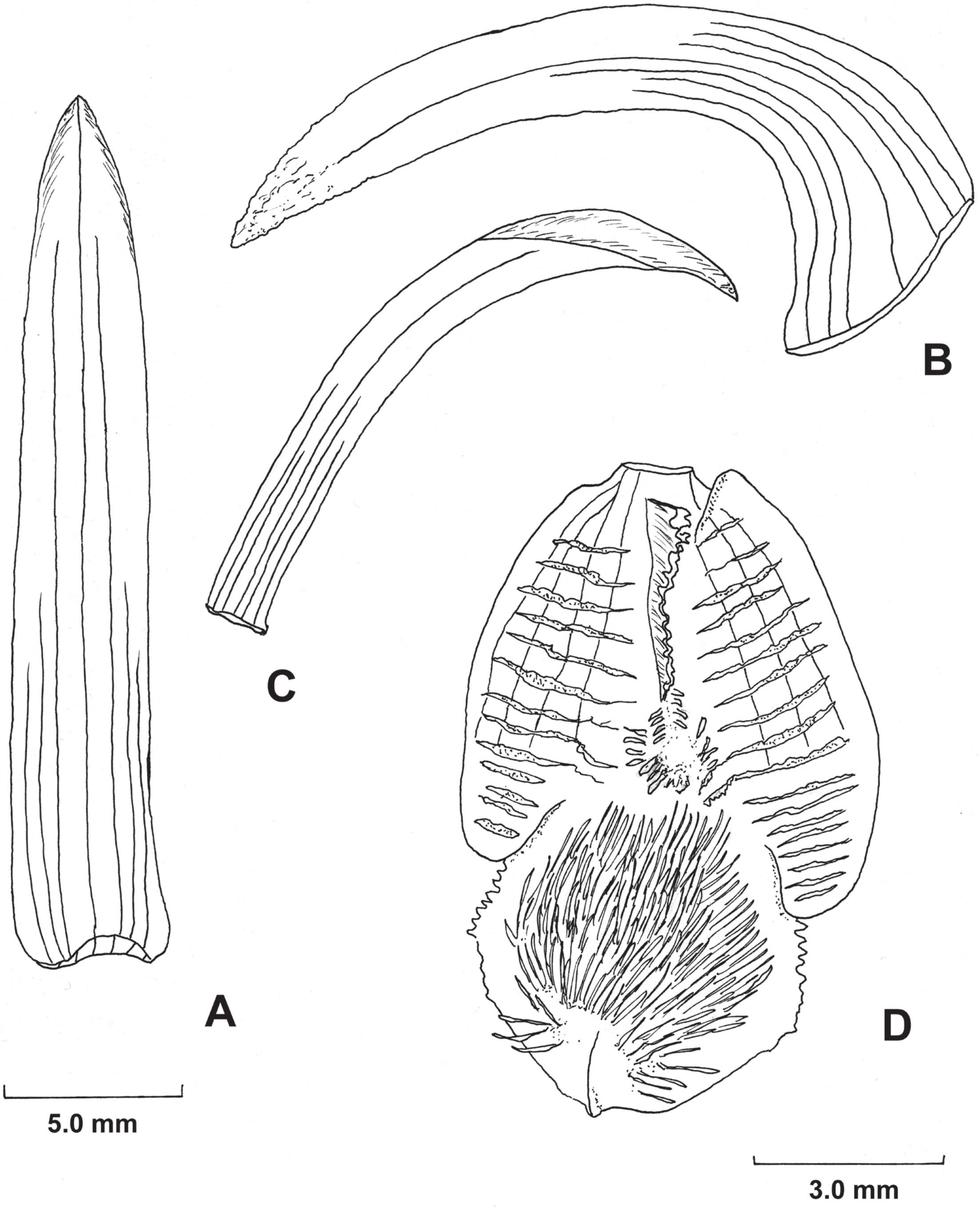

FIGURE 1. *Dendrobium heteroglossum* Schltr. **A,** dorsal sepal; **B,** lateral sepal; **C,** petal; **D,** labellum. Drawn from *A.N. Millar NGF 13816* (A).

TYPE: INDONESIA. Papua Prov., Mt. Goliath, 150 m, April 1911, *A.C. de Kock 183* (Holotype: BO, spirit, not found).

Grastidium coloratum (J.J. Sm.) Rauschert, Rep. Sp. Nov. Regni Veg. 94: 448. 1983.

Dendrobium donacoides Ridl., Trans. Linn. Soc. ser. 2, Bot. 9: 166. 1916. TYPE: INDONESIA. Papua Prov., Utakwa River, Camp 1, 215 m, November to December 1912, *C.B. Kloss s.n.* (Holotype: BM [000038246]; Isotype: AMES [00090027]).

Distribution: Indonesia (Papua); Papua New Guinea.

Additional Specimens Examined: PAPUA NEW GUINEA. Morobe Prov., Oomsis Ridge, 485 m, 12 April 1961, *A.N. Millar NGF 12290* (A); Oomsis Ridge, cult. Lae Botanic Garden, 60 m, August 1961, *A.N. Millar NGF 13816* (A).

Despite its ephemeral flowers this species is a rather attractive member of section *Grastidium* Blume. The first author was sent images by William Cavestro of this species from Papua Province in Indonesia with the suggestion these represented *D. coloratum*. Further studies convince us that *D. coloratum* is not different from *D. heteroglossum,* both taxa agreeing in habit, flower color (dark purple to carmine red sepals and petals), sepals and petal shape, and in details of the labellum (such as the relatively large epichile covered in setose appendages, obtuse sidelobes, and the inside of the sidelobes covered in transverse lamellae). The slightly smaller flowers described and depicted by Smith (1916) are in our opinion due to their immature nature.

Dendrobium jennyanum Kraenzl., Gard. Chron. ser. 3, 20: 329. 1896.

TYPE: ORIGIN UNKNOWN ["Eastern"]. Flowering in Zurich, August 1896, *cult. E. Zollinger-Jenny s.n.* (Lectotype [here designated]: HBG [501541] [image and drawing seen]).

Homotypic synonym: *Durabaculum jennyanum* (Kraenzl.) M.A. Clem. & D.L. Jones, Orchadian 13, 11: 488. 2002.

Heterotypic synonym: *Dendrobium aries* J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 2, 13: 64. 1914 *syn. nov.*

TYPE: INDONESIA [as New Guinea]. Papua Prov., *cult. Odenthal s.n.* (Holotype: BO [not found]; probable Isotype: L [0059354] [image seen]).

Distribution: Indonesia (Papua); Papua New Guinea (?).

Additional specimen examined: INDONESIA. Papua Prov., Pionier Bivak, 10 m, 20 July 1920, *H.J. Lam 452* (L [1497306] [image seen]).

In the protologue of *D. jennyanum* Kraenzlin described the flowers as being yellowish on the outside, brown on the inside and varnished all over, the lip being paler, especially in the basal part, adorned with chocolate brown veins, and with whitish calli that are pale violet basally. He noted that the pedicel with ovary was 35 mm long, the sepals 30 mm long, petals 40 x 5 mm, lip 30 x 18 mm, and the epichile 6 mm long and 12 mm wide. In HBG there is a sheet with three flowers that has been identified as type material by Kraenzlin. Dr. Szlachetko was kind enough to study a flower for the first author and found the pedicel with ovary was 40 mm long, the sepals 28 to 36 mm long, petals 30 x 9 mm, the lip 34 x 20 mm with the epichile 11 mm long and 13 mm wide.

The flower color given by Kraenzlin for *D. jennyanum* and the specimen treated by him as type in HBG accord very well with the expanded description and figure given by Smith (1916) for *D. aries*. The only minor difference is that *D. aries* has a more circular labellum epichile (10 x 10 mm). However the specimen cited above (*H.J. Lam 452*) that was identified by Smith as *D. aries* has the more transversely elliptic epichile of *D. jennyanum*. We assume that the epichile shape in *D. jennyanum* is a little variable and that *D. aries* is therefore a synonym.

The statements by Kraenzlin in the protologue of *D. jennyanum* regarding petal width and epichile dimensions have no doubt clouded the identity of this taxon.

Dendrobium leeanum O'Brien, Gard. Chron. ser. 3, 10: 640. 1891.

TYPE: WITHOUT ORIGIN. Imported with *Dendrobium phalaenopsis* Fitzg. var. *schroederianum* Rchb.f. ex W. Watson [i.e. from the Tanimbar Islands, Indonesia], *cult. Messrs. F. Sander & Co. s.n.* (Holotype: K [001085362] [image seen]).

Homotypic synonym: *Vappodes leeana* (O'Brien) M.A. Clem. & D.L. Jones, Orchadian 13, 11: 492. 2002.

Heterotypic synonyms: *Dendrobium leeanum* O'Brien var. *atropurpureum* H.J. Veitch, Gard. Chron. ser. 3, 11: 664. 1892.

TYPE: WITHOUT ORIGIN. Exhibited RHS 17 May 1892 (sent to K, 30 May 1892), *cult. W.H. Young for F. Wigan s.n.* (Holotype: K [001085365] [image seen]).

Dendrobium enfieldense H.J. Veitch, Gard. Chron. ser. 3, 20: 535. 1896 *syn. nov.*

TYPE: WITHOUT ORIGIN. Exhibited RHS 27 October 1896, *cult. Messrs. H. Low & Co. s.n.* (Holotype: [lost]).

Dendrobium leeanum O'Brien var. *enfieldense* (H.J. Veitch) H.J. Veitch, Gard. Chron. ser. 3, 26: 156. 19 Aug. 1899 as *enfieldiense*; Hort., Garden (London, 1871-1927) 56: 149. 19 Aug. 1899.

Dendrobium fleischeri J.J. Sm., Repert. Sp. Nov. Regni Veg. 12: 111. 1913 *syn. nov.*

TYPE: WITHOUT ORIGIN. Cultivated in Java, *M. Fleischer s.n.* (Holotype: BO; possible Isotype: L [0059599] [image seen]).

Vappodes fleischeri (J.J. Sm.) M.A. Clem. & D.L. Jones, Orchadian 13, 11: 492. 2002.

Distribution: Indonesia [Maluku Prov. (Tanimbar Islands)].

This taxon appears to be a natural hybrid between *D. bigibbum* Lindl. var. *schroederianum* (Rchb.f. ex W. Watson) Peter B. Adams (section *Phalaenanthe* Schltr.) and *D. antennatum* Lindl. (section *Spatulata* Lindl.). The type form of *D. leeanum* has a rather shorter labellum epichile and relatively broader hypochile. This could be expected from backcrosses onto the *D. bigibbum* var. *schroederianum* parent. The later synonyms are closer to the primary hybrid between the two supposed parent taxa.

Didymoplexis Griff., Calcutta J. Nat. Hist. 4: 383. 1844.
Type species: *Didymoplexis pallens* Griff.

A genus of about 21 species of holomycoheterotrophic terrestrial herbs distributed from Africa and Madagascar to Samoa. The delicate flowers are often produced sequentially and are mostly white in color except for some yellow on the labellum.

Didymoplexis torricellensis Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 44. 1911.
TYPE: PAPUA NEW GUINEA [as Kaiser Wilhelm's Land]. Torricelli Range, 800 m, September 1909, *R. Schlechter 20309* (Holotype: B, destroyed).
Heterotypic synonym: *Didymoplexis cornuta* J.J. Sm. var. *betungkerihunensis* Tsukaya & H. Okada, Acta Phytotax. Geobot. 62, 2-3: 92. 2012 *syn. nov.*
TYPE: INDONESIA. Kalimantan, Betung Kerihun National Park, along Sungei Tobang Kopang, 203 m, 27 December 2010, *H. Okada, H. Nagamasu & H. Tsukaya HT1011A* (Holotype: BO [not found]).

Distribution: Indonesia (Kalimantan); Papua New Guinea.

This species is related to *D. cornuta* J.J. Sm. but differs from that taxon in the shorter, more rounded mentum, labellum lacking an erect basal appendage, and more distinctly lamellate keels on the labellum. We find that *D. cornuta* var. *betungkerihunensis* has the same features as *D. torricellensis* and therefore we treat these two taxa as synonyms.

Pinalia Buch.-Ham. ex Lindl.
Type species: *Pinalia alba* Lindl.

A genus of Eriinae with about 185 species distributed from Sri Lanka and India to Tahiti. About 73 species can be found in Indonesia, which is the center of speciation. The plants have rather soft stems (thus, herbarium specimens look rather shrunken) usually bearing two or more leaves. Flowers are usually rather smallish (sepals 5-12 mm long), often in shades of white, yellow, and pink.

Pinalia fitzalanii (F. Muell.) Kuntze, Rev. Gen. Pl. 2: 679. 1891.
TYPE: AUSTRALIA. Queensland, Mulgrave River, *E. Fitzalan s.n.* (Holotype: lost). Neotype [designated by Clements 1989: 76]: Australia, Queensland, McIlwraith Range, Massey Creek, 60 m, 4 September 1979, *J.R. Clarkson 2604* (Holoneotype: BRI [AQ 0381865] [image seen]; Isoneotype: K [000482434] [not seen]).
Basionym: *Eria fitzalanii* F. Muell., South. Sci. Rec. 2: 252. 1882.
Homotypic synonym: *Hymeneria fitzalanii* (F. Muell.) M.A. Clem. & D.L. Jones, Orchadian 13, 11: 501. 2002.
Heterotypic synonyms: *Eria solomonensis* Rolfe, Bull. Misc. Inf. Kew: 63. 1909. TYPE: SOLOMON ISLANDS. Tulagi, *cult. C.M. Woodford 11* (Holotype: K [000827422] [image seen]).

Eria hollandiae J.J. Sm., Bull. Dep. Agr. Ind. Neerl. 45: 7. 1911. TYPE: INDONESIA. Papua Prov., Hollandia Bivouac, 50 m, 8 August 1910, *K. Gjellerup 302* (Lectotype [here designated]: BO [0066317]; Isolectotypes: BO [0066601], BO, spirit [19.13], K [000827428]; L [0059879] [image seen]).

Eria indivisa Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 662. 1912. TYPE: PAPUA NEW GUINEA [as Kaiser Wilhelm's Land]. Djamu Gorge, 400 m, October 1907, *R. Schlechter 16686* (Syntype: B, destroyed; Isosyntypes: G [00165701], L [0059873] [images seen]); Kani Range, 600 m, August 1908, *R. Schlechter 18086* (Syntype: B, destroyed).

Bryobium indivisum (Schltr.) J.J. Wood, Orch. Review 113, 1261: 41. 2005.

Eria ledermannii Schltr., Bot. Jahrb. Syst. 58: 125, 127. 1923 *syn. nov.*

TYPE: PAPUA NEW GUINEA [as Nordostl. Neu-Guinea]. Sepik District, April River, Strand Camp, 100 m, September 1912, *C. Ledermann 8616* (Holotype: B, destroyed).

Pinalia ledermannii (Schltr.) Schuit., Y.P. Ng & H.A. Pedersen, Bot. J. Linn. Soc. 186, 2: 197. 2018.

Bryobium rendovaense J.J. Wood, Orch. Review 113, 1261: 41. 2005 *syn. nov.*

TYPE: SOLOMON ISLANDS. Rendova, track from Ughele Village to Rendova Peak, 450 m, 10 September 1991, *B.A. Lewis 6* (Holotype: K [000827418], image seen).

Distribution: Indonesia (Papua); Papua New Guinea; Australia (NE Queensland); Solomon Islands.

Additional Specimens examined: PAPUA NEW GUINEA. Western Prov., Lake Daviumbu, Middle Fly River, April 1936, *L. J. Brass 7780* (AMES); same data, *L. J. Brass 7871* (AMES, BRI).

Habitat: Epiphytic on lakeside tree (*L.J. Brass 7780*); in *Melaleuca* swamp forest *(L.J. Brass 7871*).

This species is a widespread taxon, most commonly found in tropical lowland forests. The flowers are smallish (sepals 6-8 mm long), and usually a pale yellow (but can be white with yellow on the lip). The lip is somewhat oblong-rectangular, entire to weakly trilobed, the apex more or less truncate-emarginate. The keels on the lip appear as two broadened inflexed lamellae on the lower half, these continue as three low ridges on the upper half.

Eria ledermannii possibly has had its identity obscured due to a typesetting error that occurred in the protologue whereby the text for *Eria molliflora* Schltr. (= *Trichotosia* Blume) was mismatched with that of the former. For this reason the wrong type data appeared in the first author's treatment of it (Ormerod 2017). It also seems Schlechter omitted to describe the three low upper keels on the labellum. Otherwise all details in the protologue of *Eria ledermannii* match those of *Pinalia fitzalanii* and therefore we treat them as conspecific.

Bryobium rendovaense was described from unopened flowers (hence the slightly lesser floral lengths) and is not distinguishable from *Pinalia fitzalanii* in any feature. Thus, it too is added to the synonymy.

Pinalia puberula (Ridl.) Ormerod & Juswara, *comb. nov.*

Basionym: *Eria puberula* Ridl., J. Bot. (Lond.) 24: 326. 1886. TYPE: PAPUA NEW GUINEA. South Cape, *H.O. Forbes s.n.* (Holotype: BM [000506690]).

Heterotypic synonyms: *Eria oligotricha* Schltr., in Schum. & Laut., Fl. Deutsch. Schutzgeb. Sudsee, Nachtr. 2: 181. 1905 *syn. nov.* TYPE: PAPUA NEW GUINEA [as Kaiser Wilhelm's Land]: Torricelli Range, 1000 m, April 1902, *R. Schlechter 14353* (Holotype: B [destroyed]; Isotype: K [00827430]).

Pinalia oligotricha (Schltr.) T.C. Hsu, Taiwania 61, 1: 25. 2016.

Eria papuana J.J. Sm., Bull. Dep. Agr. Ind. Neerl. 19: 23. 1908. TYPE: INDONESIA. Papua Prov., Noord River, at confluence with Reiger River, June 1907, *G.M. Versteeg 1208* (Syntype: BO; Isosyntype: L [0063893] [image seen]); near Geluks Hill, August 1907, *G.M. Versteeg 1556 [*as *1555]* (Syntypes: L [1510657], P [00360346] [images seen]).

Eria oligotricha Schltr. var. *acutiloba* Schltr., Repert. Sp. Nov. Regni Veg., Beih. 1: 666. 1912.

TYPE: PAPUA NEW GUINEA [as Kaiser Wilhelm's Land]: Ibo Range, 1000 m, December 1908, *R. Schlechter 19031* (Holotype: B [destroyed]).

Distribution: Indonesia (Sulawesi, N Maluku, Maluku, Papua); Papua New Guinea; Solomon Islands.

Additional specimens examined: INDONESIA. Papua Prov., 4 km SW of Bernhard Camp, Idenburg River, 850 m, March 1939, *L.J. Brass 13281* (AMES); same data, *L.J. Brass 13348* (AMES); Mt. Carstensz Expedition, Camp 3, *C.B. Kloss s.n.* (BM); Camp 6a, January 1913, *C.B. Kloss s.n.* (AMES, BM); Camp 6b, *C.B. Kloss s.n.* (BM); Camp 6c, Pundok Padang, 17 February 1913, *C.B. Kloss s.n.* (AMES, BM); Camps 6-7, *C.B. Kloss s.n.* (BM). Salawati Island, Kaloal, 0 m, 28 October 1956, *C. Versteegh BW 4663* (A). PAPUA NEW GUINEA. Madang Prov., Finisterre Range, 1100 m, 20 January 1909, *R. Schlechter 19158* (GH); Simbu Prov., 10 km E of Haia, Crater Mountain Biological Research Station, 850-1350 m, 18 May 1991, *A. Mack 458* (A). Enga Prov., Porgera District, Paiela Census Division, Taronga to Komanga, 1500-1800 m, 15 October 1979, *T.M. Reeve 1640* (AMES). Western Highlands Prov., Lake Kopiago Subdistrict, 17.6 km from Kopiago, top of Paga Hill, 1555 m, 1 November 1968, *J. Vandenberg, J.S. Womersley & M. Galore NGF 39965* (A); Eastern Highlands Prov., Kainantu Subdistrict, Arona side of Kassam Pass, 1300 m, 23 August 1973, *J.S. Womersley NGF 46424* (A). Western Prov., Palmer River, 3.2 km below junction with Black River, 100 m, July 1936, *L. J. Brass 7230* (AMES); same data, *L. J. Brass 7236* (AMES).

Habitat: Epiphytic in floodplain rainforest (*L. J. Brass 13281, 13348*); riverine forest (*L. J. Brass 7230*) primary forest along seashore (*C. Versteegh BW 4663*); ridge forest (*L. J. Brass 7236*); roadside regrowth (*NGF 39965*).

This species has long been known as *Eria oligotricha;* it is a commonly collected plant in New Guinea. It was however first described by Ridley based on one of Henry Forbes' collections from South Cape in Papua New Guinea. The plant Forbes found was the rare form with ligulate sidelobes on the lip (see however orchids of New Guinea website https://www.orchidsnewguinea.com for images of this form such as *Leiden cult 32054* from Southern Highlands Prov., Papua New Guinea, and J. J. Smith's drawing of *L.S.A.M. von Roemer 888* from Papua Prov., Indonesia). More commonly the sidelobes of the lip are shortly elliptic, subquadrate or triangular.

A very similar plant was described from Sulawesi in 1911 as *Eria oreogena* by Schlechter. Further material is needed from Sulawesi to assess this name since the holotype was destroyed in the second World War.

The protologue of *Eria papuana* J.J. Sm. cites *G.M. Versteeg 1208* and *1555* as syntypes. We believe the second collection should be *Versteeg 1556* since the specimen *Versteeg 1555* is the type collection of the fern species *Polypodium versteegii* Christ.

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BIOGEOGRAPHICAL HISTORY OF THE YUCATAN PENINSULA ENDEMIC FLORA (SPERMATOPHYTA) FROM A PHYLOGENETIC PERSPECTIVE[1]

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Abstract. The increased availability of phylogenetic, morphological, and geographic information from different biological groups has allowed for the testing of several scenarios on the origin and assembly of the biota around the world. The biogeographical approaches used to understand the origin of the Yucatan Peninsula Biotic Province (YPBP) flora were previously based on floristic comparisons and do not consider the phylogenetic relationships among taxa, complicating the understanding of their biogeographical history. In order to improve the understanding of biogeographical and evolutionary processes implied in the occurrence of the endemic flora of the YPBP, we constructed a geobiotic scenario, which integrates lineage divergence events obtained from previous phylogenetic and biogeographical studies, along with geological/tectonic and climatic events occurring in the area. To strengthen the biogeographical hypotheses, we constructed a phylogenetic tree as a framework for an approximation of the periods of history with the greatest influence on the evolution of the flora. Additionally, we searched for morphological traits of relevance for dispersal, establishment, and adaptation to the current environmental conditions of the YPBP. The evidence gathered in the present work strongly suggests that the origin of the endemic flora of the YPBP has been driven by various factors and processes that occurred at different times in the history of the Earth (mainly in the Pliocene and early Pleistocene). These include hybridization, isolation after long-distance dispersal from the Antilles, as well as the influence of environmental changes during the Pleistocene. Those climatic fluctuations reduced the geographic range of some ancestral lineages, leading to geographic isolation of populations in the northern part of the YPBP, where the climate has been more stable over time.

Keywords: Dispersal syndromes, divergence times, extinction, geographic isolation, Pleistocene, phylogenetic relationships, speciation

Endemic species are species distributed exclusively in a natural, predefined area and are considered unique results of evolution (Hobohm, 2014), highlighting the importance of "endemism" for biogeography. Specific locations across the Earth with high levels of endemism are often associated with climatic stability, serving as refugia for paleoendemic lineages that had broader distributions in the past (Anderson, 1994). Additionally, endemism is associated with sites of rugged relief, high levels of environmental heterogeneity (Noroozi et al., 2018), and geographical isolation, such as on oceanic islands or mountain peaks, which promote genetic differentiation and subsequent allopatric differentiation (Kier et al., 2009; Losos and Ricklefs, 2009). In contrast, sites with a history of high climatic instability tend to host fewer endemic species, often of recent local divergences known as neoendemic lineages (Merckx et al., 2015; Noguera-Urbano, 2016). Endemic species are useful for establishing the boundaries of biogeographical areas (Crother and Murray, 2011; Morrone, 2014) and are essential criteria for the conservation of biological diversity at local, regional, and global scales (Fattorini, 2017).

Phylogenetic hypotheses provide direction for the reconstruction of geographic distributions and for the elucidation of the processes of diversification, dispersal, extinction, and vicariance (Santiago-Valentín and Olmstead, 2004; Kadereit, 2017; Morrone, 2022). The study of the geographic distribution of phylogenetically related endemic species can improve the understanding of the biogeographical processes which shaped the biota of a given area. For example, areas with geographically restricted sister species suggest in situ diversification processes, where the time elapsed has been insufficient for the expansion of their distribution range (Kadereit, 2017), and/or where there are geographic or ecological barriers preventing the sister species from achieving more extensive distributions (Merckx et al., 2015). Moreover, allopatric speciation resulting from vicariant divergence can be inferred from geographically isolated sister species (Morrone, 2004; Luebert and Weigend, 2014; Chiapella and Demaio, 2015; Kadereit, 2017). The increased availability of phylogenetic, morphological, and geographic information from different biological groups has allowed for the testing of several scenarios on the origin and assembly of the biota around the world (e.g., Chiapella and Demaio, 2015; Kadereit, 2017; Zizka, 2019). Additionally, knowledge of the divergence times of closely related species, evaluated in the context of tectonic or paleoclimatic events, helps to elucidate speciation events by isolation after long-distance dispersal (Grandcolas et al., 2008; Andrus et al., 2009; Luebert and Weigend, 2014). Furthermore, the analysis of functional traits of relevance for their distribution and establishment, such as growth form and dispersal syndrome, may strengthen the biogeographical hypotheses of interest (Wen et al., 2014).

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The Yucatan Peninsula Biotic Province (YPBP) is considered a biogeographical unit based on its biotic, physiographic, morphotectonic, and environmental attributes (Barrera, 1962; Morrone, 2019). It is located in the Neotropics (Fig. 1) on the karst platform impacted by the meteorite that triggered the fifth mass extinction on Earth, approximately 65 Mya (Renne et al., 2013). The southern YPBP re-emerged from the seabed during the Oligocene (~32 Mya) and continued to be exposed in staggered episodes up to the Holocene (<0.01 Mya) on the northern coast (Bryant et al., 1991; Lugo-Hubp et al., 1992). This geological phenomenon suggests a recent establishment and evolution of the flora in this region, particularly in coastal zones (Miranda, 1958). Today, this area (ca. 300, 000 km^2) harbors a floristic diversity of ca. 2, 860 taxa of vascular plants (modified from Carnevali et al., 2010b), of which around 6% are endemic (180 spp.) and quasi-endemic species (8 spp.) (Carnevali et al., 2021b). Quasi-endemics are limited to the area of endemism but also reach the border or transition zones with adjacent biogeographical provinces or are represented by a few isolated populations beyond the boundaries and into neighboring provinces. This percentage is relevant considering the relatively short time that has elapsed since the re-emergence of the YPBP, its low relief complexity, and its relatively close connection with the rest of Mexico and Central America (Ramos, 1975; Lugo-Hupb et al., 1992; Morrone, 2019).

It has been hypothesized that the origin of endemism in the northern YPBP was strongly influenced by Pleistocene climatic fluctuations that resulted in the fragmentation of tropical dry forests (TDF), leading to the isolation and differentiation of many plant groups (Carnevali et al., 2003; Espadas-Manrique et al., 2003; Espadas-Manrique, 2004). Miranda (1958) suggested that the origin of these endemic species may be explained by edaphic conditions in the area and the establishment of lineages from southern Mexico and northern Central America in these new environmental conditions. However, the biogeographical approaches used to understand the origin of the YPBP flora have been based on floristic comparisons (Estrada-Loera, 1991; Ibarra-Manríquez et al., 2002; Espadas-Manrique et al., 2003; Ramírez-Barahona et al., 2009) and do not consider phylogenetic relationships. Studying the phylogenetic relationships of the endemic flora of the YPBP is necessary for understanding past scenarios of the origin of the biota (Morrone, 2022) and a first step to estimating possible responses to anthropogenic disturbances and future environmental changes (e.g., Edwards and Still, 2008).

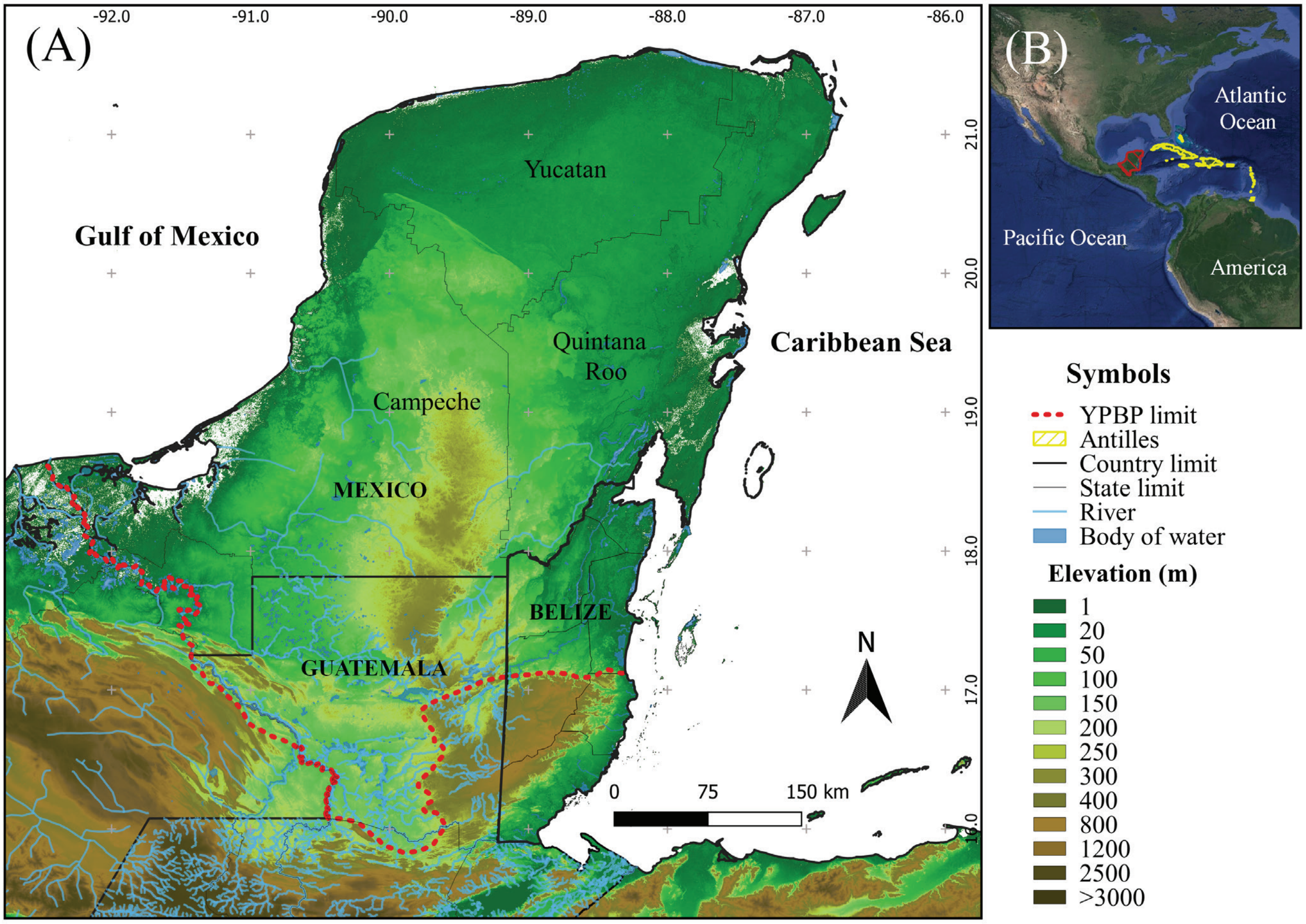

FIGURE 1. Study area. **A**, Elevations of the YPBP karst platform and the occurrence of surface rivers, concentrated mainly in the south; **B**, Geographic location of the Yucatan Peninsula Biotic Province (YPBP) in the Neotropics, note the proximity to the Antilles (highlighted in yellow).

Here, we review the documentation of geological/tectonic and climatic events that have occurred in the area, as well as lineage divergence events obtained from previous phylogenetic and biogeographical studies, in order to improve the understanding of the biogeographical and evolutionary processes implied in the occurrence of the endemic flora of YPBP. We constructed a phylogenetic tree as a framework for an approximation of the periods of history with the greatest influence on the evolution of the flora. To strengthen the biogeographical hypotheses, we searched for morphological traits of relevance for dispersal, establishment, and adaptation to the current environmental conditions of the YPBP.

We hypothesized that the origin of the endemic flora was mostly influenced by climatic changes that occurred during the Pleistocene, reflected in the current geographical distribution of allopatric sister species with high niche conservatism in seasonally dry habitats and in recent divergence times. This geographic isolation should be independent of the ability of the lineages to disperse long distances. However, the environmental characteristics of the YPBP, insularity (at least of the northern dry ecosystems), and climatic gradient, could have promoted another evolutionary process that contributed to the diversity of the endemic flora, such as isolation after a long-dispersal event (either from the West Indies and from other parts of America) or ecological divergence (with respect to adjacent areas or inside the environmental gradient).

Methods

For the compilation of phylogenetic and biogeographical hypotheses, we performed a metasearch of evolutionary and biogeographical scientific publications based on molecular phylogenetic and/or morphological evidence of endemic and quasi-endemic taxa of the YPBP. First, we used the Datataxa script (Ruiz-Sánchez et al., 2019) to extract meta-information on articles from the Genbank database (Benson et al., 2018). The search categories were Phylogenetic studies (including the terms phylogen*, monop*, systemat*, sistemat*, relationsh*, relacio*), Phylogeographic studies (phylogeog*, filogeog*), Phylogenomic analysis (phylogenom*, genome-scale, "plastid genome"), Diversity studies (diver*, geneti*, pop*, pobl*) and Biogeography (biogeog*). The endemic species list of Carnevali et al. (2021b) was updated with the addition of taxa recently recognized as endemic (e.g., *Echites yucatanensis* Millsp. ex Standl.; Carnevali et al., 2021a) and recently described species (e.g., *Matelea falcata* Juárez-Jaimes, G.M. Hernández-Barón & W.D. Stevens; *Gonolobus caamali* Carnevali & R. Duno) (Apocynaceae). Additionally, other taxa were included that were not considered endemic by those authors (e.g., *Harpalyce torresii São-Mateus & M. Sousa*, *H. yucatanense* Miranda ex São-Mateus & M. Sousa, *Gouinia latifolia* var. *guatemalensis* (Hack.) J.J. Ortiz), sometimes because they were found at the southernmost boundary of the YPBP (e.g., *Miconia hondurensis* Donn. Sm., (Melastomataceae), *Rhynchospora pusilla* Chapm. ex M.A. Curtis (Cyperaceae)).

Second, a search for biogeographical and systematic studies based on morphological data was conducted for each taxon endemic to the YPBP from the academic search engine Google Scholar (https://scholar.google.com/), with the name of the taxon in question as a keyword (e.g., *Justicia_dendropila*).

The nomenclature used follows the Angiosperm Phylogenetic Group IV classification system (APG, 2016). Information on phylogenetic relationships and divergence dates was extracted based on bootstrap, Neighbor-joining (NJ), Maximum Parsimony (MP) or Maximum Likelihood (MV) methods. Only those phylogenetic relationships whose statistical support was above 60% and whose analyses included a sampling of more than 50% of the species of the genus present in the study area were considered. Where possible, divergence dates were extracted both for cladogenetic events at the species level and for the most recent clade in which the endemic species was included, if the phylogenetic resolution did not reach the specific level.

In order to have an approximation of the age of origin of the endemic taxa, two data sources were used. In one approach, divergence dates, and their confidence intervals, were extracted from previously published chronograms (e.g., Cuenca et al., 2007; Cuevas-Chapa, 2016; Lavor et al., 2018). This information was contextualized within the framework of paleoclimatic and geological events that have occurred since the exposure of the YPBP seafloor 32 Mya (Szabo et al., 1978; Lugo-Hubp et al., 1992; Aragón-Moreno et al., 2012). Additionally, a phylogenetic reconstruction was performed with V.Phylomaker (Jin and Qian, 2019), a package implemented in the open source software R (Core Team, 2021. This software generates dated phylogenies (timelines) from a list of species and compared them with a mega phylogenetic tree of vascular plants (GBOTB.extended.tre) that includes 74, 533 species and all 479 families known to date. For this purpose, a list of vascular plant species obtained from the YPBP Digital Flora (Duno et al., 2019) and updated with the aforementioned endemic species list was used. Because V.Phylomaker uses the list of species accepted by The Plant List (TPL; http://www.theplantlist.org/) as a reference, in order for the program to identify the correct branch insertion position, new names were updated using the r.bind function. Since the phylogeny obtained is not resolved at the species level, the values for divergence times are probably overestimated for some plant lineages, especially those with few representatives in the YPBP. FIGTREE package (Rambaut, 2009) was used for phylogeny visualization.

To document the general distribution patterns of the endemic flora, as well as its related taxa, a search of herbarium records in national (CICY, MEXU) and foreign (MO, SELBY) institutions was performed, and records with supporting collections were obtained from the GBIF online database (www.gbif.org). This information was compared and supplemented with information obtained from other online databases (e.g., SEINet, Jstor, Tropicos), protologues, and regional floras, such as Flora of Guatemala (Gentry and Standley, 1974), Flora Mesoamericana (e.g., Davidse et al., 1994), Digital Flora of the Yucatan Peninsula (Duno et al., 2019), Flora of the Valley of Mexico (Rzedowski & Rzedowski, 2001), and Flora Novogaliciana (McVaugh, 1987; 1995). A database containing information on habit, habitat, phenology, pollination and dispersal syndromes, reproductive aspects of the species, as well as morphological characters of possible adaptive relevance, was compiled from the review of these data sources. Biogeographical provinces follow Morrone (2019), except in the case of the southern limits of the YPBP, which follow Lundell (1934) and Carnevali et al. (2010b). Those authors have a broader geographic delimitation of the area based on topography and hydrology, characteristics which could help explain the role of the southern transitional zone.

RESULTS

Phylogenetic hypothesis

A total of 184 endemic and quasi-endemic species were included in the search. According to Datataxa, only 63 YPBP endemic taxa have been included in studies with genetic data recorded in GenBank, either phylogenetic (49), biogeographical (9), phylogeographic (2) or population genetic diversity (1) (some of these studies include more than one taxon, i.e., González Martínez, 2019 and Majure et al., 2012). However, phylogenetic hypotheses based on molecular information with high support and resolution were only found for 34 endemic species, representing 18 vascular plant families, and 18.4% of the endemic flora diversity (Appendix 1). Most of the hypothetical relationships were found at the species level, with five species belonging to unsolved clades consisting of two or three taxa.

Divergence times

We found 12 divergence times based on dated phylogenies, eight of them (66%) corresponding to the Pleistocene (Appendix 1; Fig. 2A). Regarding the phylogenetic tree constructed with V.Phylomaker (Fig. 2B), the greatest peak of evolutionary divergence (32 divergence nodes; 17% of endemic species) occurred 4–2 Mya, corresponding to the late Pliocene and early Pleistocene.

Distribution patterns

Most of the hypothesized sister species of the endemic taxa compiled in this work have an allopatric distribution and are absent in the YPBP (17 spp.). Of these, three are in the Antilles region, 11 taxa have their distribution limits in adjacent biogeographical provinces to the YPBP, and three are in provinces farther away from continental America, mainly in the Chiapas Highlands, the Mexican Plateau, and Pacific Lowlands provinces. Three pairs of taxa are allopatric within the limits of the YPBP, and are distributed along the north-south humidity and temperature gradients of the YPBP. Sympatric distributions were found in eight pairs of phylogenetical related taxa, which have the following distribution: three of them are fully restricted to the YPBP, four have a broader distribution along YPBP and the neotropics, and two are widely distributed in Central America but are limited to the southern part of the YPBP (Appendix 2).

Morphological characteristics

There is a great diversity of growth forms in the YPBP endemic taxa, including parasitic herbs, climbing shrubs, and epiphytes, but the most common are trees (47), shrubs (38), and terrestrial herbs (29). Most of the endemic species have dispersal mechanisms that can reach long distances, such as animal-dispersed berries (84) and those with adaptations for wind (67) or water dispersal (12). Another less diverse group of species have mechanisms for medium- to short-distance dispersal, such as explosive (36) or gravity dispersal (4).

DISCUSSION

Influence of the Pleistocene on the origin of the YPBP endemic flora

During the Miocene (23–5.3 Mya), xeric, savannah, and tropical dry forest (TDF) communities dominated the YPBP and many other Neotropical areas (Becerra, 2005; De-Nova et al., 2011; Leyden, 1984; Pennington et al. 2000, 2009, 2018; Islebe and Leyden, 2006). The climatic instability that characterized the Pleistocene (2.6–0.01 Mya) led to local and mass extinctions that affected lineages in different areas of the YPBP. On one hand, the biotic dispersal of plant communities of boreal affinity led to the replacement of whole biomes in the Neotropics, particularly in the southern part of the YPBP (Gutiérrez-Ayala et al., 2012; Islebe and Leyden, 2006). Expansions and contractions of the distribution ranges of these plant communities resulted in the fragmentation of the TDF and increased its isolation by restricting it to the northern part of the YPBP. This could have promoted allopatric speciation processes in lineages with high niche conservatism, as has occurred in many Neotropical lineages (Becerra, 2005; De-Nova et al., 2011; Montaño-Arias et al., 2018; Pennington et al., 2000, 2009; Rivera-Martínez et al., 2022). Therefore, the origin and current distribution of these species are the result of contraction in the geographic range of the ancestral species, which inherently led to local extinction processes (Habel et al., 2010).

The northern part of the YPBP has experienced greater climatic stability over time, with generally warm and dry environments (Torrescano-Valle and Islebe, 2015), so it likely functioned as a refuge for lineages adapted to these environments, such as some groups of plants and reptiles (Rzedowski, 1991; Espadas-Manrique et al., 2003; Lee, 2010). This area coincides with the tropical deciduous forest with columnar cacti (TDFCC), a variant of the TDF endemic to parts of Yucatan associated with limestone outcrops and consistent flooding during the rainy season (Perry et al., 1989; Beach, 1998; Espadas-Manrique et al., 2003; Batllori-Sanpedro et al., 2006). It is also home to a great diversity of endemic plant species (91 spp.), which represent about 54% of the total endemic spermatophyta flora, mainly in the Apocynaceae, Cactaceae, and Euphorbiaceae families (Carnevali et al., 2021). Although

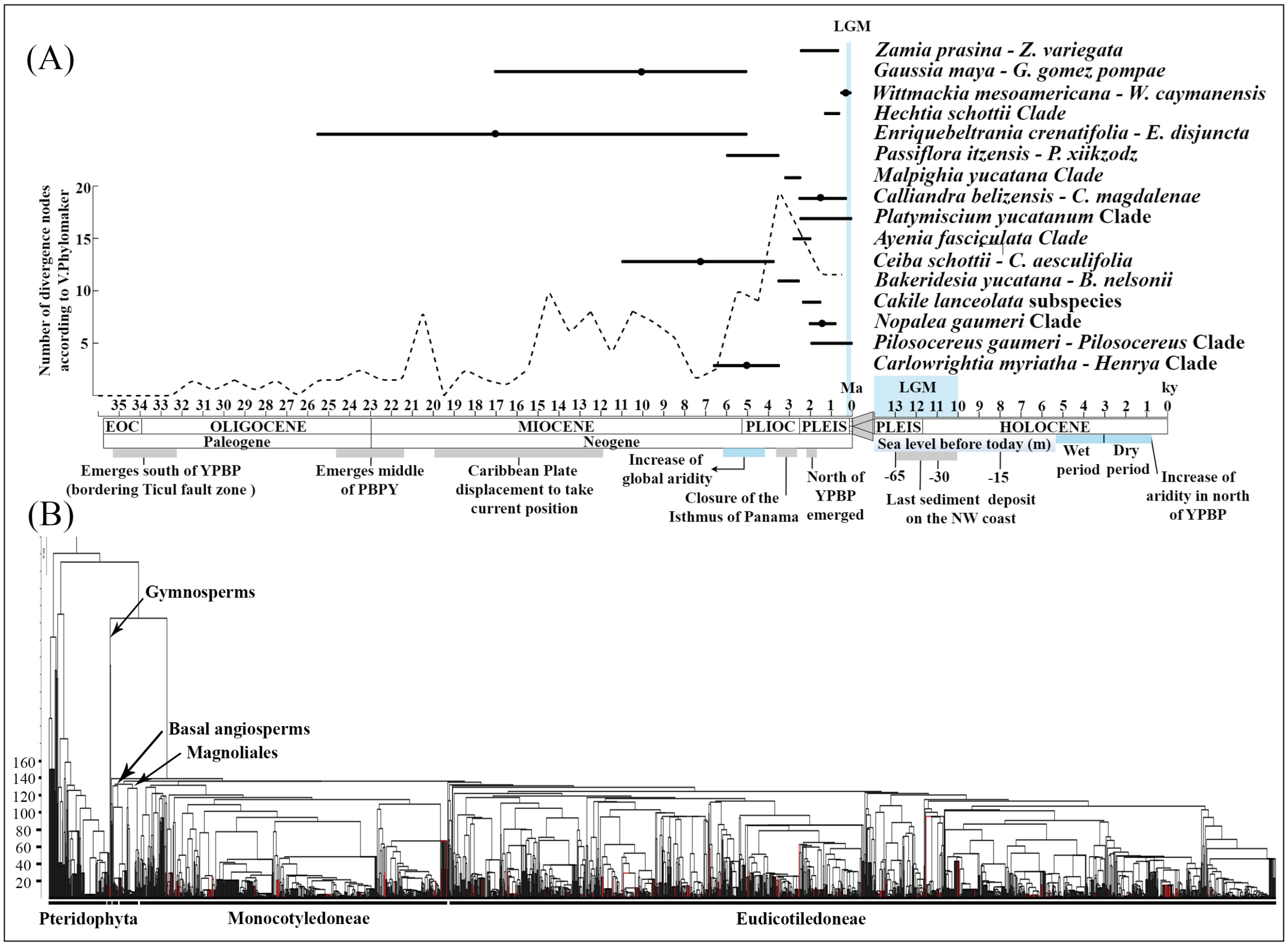

FIGURE 2 (above). Geobiotic scenario of the Yucatan Peninsula Biotic Province (YPBP). Constructed from divergence dates of endemic vascular plants of the YPBP published in previous works (black circles), and their confidence intervals (black lines), and complemented with the number of cladogenetic events (dashed line) according to a phylogenetic tree (below) generated from V.Phylomaker (2, 824 native taxa = black branches; 184 endemic taxa = red branches) in relation to the geological and climatic events that have occurred since their resurgence from the seafloor. Geological data based on Ramos (1975) and climatic data taken from Orellana et al. (1999).

many of these species inhabit diverse environments in the northern part of the YPBP (Carnevali et al., 2021), others are restricted to a single vegetation association, such as *Zephyranthes orellanae* Carnevali, Duno & J.L. Tapia in the TDFCC, or to a few localities, such as *Ruehssia calichicola* (Carnevali & Juárez-Jaimes) L.O. Alvarado (Carnevali et al. 2010a, 2016). These restrictions could be related to the micro-scale environmental heterogeneity of the area (see *In situ speciation* section).

It is well known that climate variations in the Pleistocene (2.6–0.01 Mya) played a central role in the recent biogeographical distribution of many vascular plant species (Gentry, 1982; Ramírez-Barahona and Eguiarte, 2013; Tribsch and Schönswetter, 2003). The influence of the Pleistocene on the YPBP biota has been reported for various biological groups, including endemic plants and several vertebrate groups (Lee, 2010; Espadas-Manrique, 2004; Stinnesbeck et al., 2021). Geographic isolation between species endemic to the YPBP and their phylogenetically related congeneric species, especially those restricted to TDF habitats and that diverged after the late Pliocene (<3.5 Mya), supports this hypothesis (Fig. 2; Appendix 1).

We found evidence of vicariance processes in the continental Neotropics such as in geographically isolated TDF sister species. For example, *Myrmecophila christinae* Carnevali & Gómez-Juárez (Orchidaceae) is geographically separated by the Isthmus of Tehuantepec from *M. grandiflora* (Lindl.) Carnevali, Tapia-Muñoz & I. Ramírez, which is distributed on the Mexican portion of the Pacific Lowlands and Veracruz provinces (Carnevali et al., 2003) (Fig. 3A). The vicariant distribution patterns observed for several groups of *Myrmecophila* Rolfe sister species, all native to the TDF, suggest that this genus previously had a much wider distribution (Carnevali et al., 2003). Also, *Bakeridesia yucatana* (Standl.) D.M. Bates (Malvaceae), currently restricted to the eastern part of the YPBP, diverged from *B. nelsonii* (Rose) D.M. Bates during the last quarter of the Pleistocene (Donnell, 2012; Hoorn et al., 2019). The latter species thrives in dry forests from southeastern Mexico to northern Nicaragua. *Platymiscium yucatanum* Standl.

(Fabaceae) diverged during the Quaternary period and has a wide distribution in the YPBP, but it is geographically isolated from all of its congeners (Saslis-Lagoudakis et al., 2008). We found 18 similar evolutionary hypotheses proposed in taxonomic studies based on morphological similarity and species sharing the same distribution pattern (Appendix 1).

Other studies on lineages distributed in the YPBP which did not include endemic species have also demonstrated the influence of the Pleistocene on the current flora. For instance, the genus *Neomillspaughia* S.F. Blake (Polygonaceae) is composed of three species restricted to fragments of TDF in Central America (Ortiz-Díaz et al., 2013). However, only *N. emarginata* (H. Gross) S.F. Blake is found in the YPBP, while the other two species grow within a minimum distance of 300 km between southern Guatemala and northern Nicaragua (Ortiz-Díaz et al., 2013). Also, the phylogenetic and geographic structure among some Capparaceae groups reflects the isolation of ancestral populations that were previously connected (Mercado and Escalante, 2019). The evolution of many lineages within families such as Malpighiaceae and Fabaceae is closely linked to the history of the TDF (da Silva et al., 2012; Willis et al., 2014a). Given the geographic distance between the remaining TDF fragments, and the role of humid tropical forests of the mountains of southern Mexico and Guatemala as environmental barriers for TDF communities, vicariance is the likely factor which restricted these taxa to the YPBP.

The multiple evolutionary divergence events of endemic species between the late Pliocene (<5.3 Mya) and the early Pleistocene (Fig. 2) support the notion that climatic changes during this period influenced the divergence of species. However, it is important to consider that the lack of phylogenetic resolution of the outermost nodes (species level) may lead to overestimating the age of the divergence of some groups, such as several groups with few representatives in the YPBP [e.g., *Loeselia campechiana* C. Gut. Báez & Duno] or others with unresolved relationships (e.g., *Justicia* L.). Therefore, it is estimated that a larger number of more recent divergence events may have occurred. Despite this, the calibrated phylogenetic framework (e.g., V.Phylomaker trees) has contributed to several biogeographical and ecological studies (Capichoni and Gerdhold, 2020), and they provide approximations of the time of divergence at the level of genera or clades within genera.

Although most cases correspond to lineages restricted to TDF habitats, the Pleistocene also influenced the evolution of lineages typical of colder and humid environments. The southern portion of the YPBP was arid during glacial peaks alternating with humid interglacial periods (Leyden, 1984; Islebe and Leyden, 2006; Metcalfe et al., 2009; Gutiérrez-Ayala et al., 2012). This climatic change possibly caused the extinction of entire communities of boreal species, leaving only a few relict communities of endemic species or 'paleoendemic' species, respectively. A phylogeographic study of *Zamia prasina* W. Bull (Zamiaceae) shows that its populations remained restricted to the southeastern YPBP during the Last Glacial Maximum (Pleistocene-Holocene) (Montalvo-Fernández et al., 2019). Paleoclimatic reconstruction models employed in that work indicate very few or no environments available for successful establishment of populations in the YPBP at that time, which suggests scenarios of local extinction followed by the re-expansion of the distribution range throughout the warmer Mid-Holocene periods. This pattern is consistent with the glacial refuge hypothesis (Ramírez-Barahona and Eguiarte, 2013). Additionally, the genetic structure of *Pinus caribaea* var. *hondurensis* (Sénécl.) W.H. Barret & Golfari (Pinaceae) indicates a demographic history associated with expansion and contraction events (Rebolledo et al., 2018). Populations of this species in northern Belize are more closely related to populations in Honduras than to populations closer to southern Belize.

Enriquebeltrania Rzed. (Euphorbiaceae) is a genus endemic to Mexico with just two known species: *E. crenatifolia* (Miranda) Rzed., and *E. disjuncta* De-Nova & Sosa. Separated by more than 2,000 km and by the Mexican Highlands, both taxa grow in similar coastal environments (De-Nova et al., 2006) (Fig. 3B). It has been hypothesized that this geographic separation occurred as a result of the displacement of the Chortis Block in a west-to-east direction along the Mexican Pacific coast approximately 45–38 Mya (Cuevas-Chapa, 2016). However, there is still uncertainty about the validity of this displacement model due to the complex tectonic history of the Caribbean (Moreno and Manea, 2021). An alternative hypothesis, proposed here, is that during the Oligocene-Miocene, this group was more diverse and widespread along coastal areas, but the marine fluctuations during the Pleistocene and Holocene led to extinctions that resulted in the geographic separation of these species. No fossils belonging to this genus have been found; therefore, we can only speculate that both species come from a common ancestral species whose intermediate populations went extinct in other coastal regions due to changes in sea level or climatic shifts. The surviving populations had to be highly resilient and moved to the newly emerged coastal environments. Moreover, the myrmechocorous dispersal syndrome of the genus may have contributed to its geographic restriction.

While geographic isolation may shed light on the processes involved in the generation of endemism, dispersal may obscure interpretations. We found ten cases where the most likely phylogenetically related species to an endemic taxon is present in the YPBP but has a broad distribution in Mexico, Central America, and the Antilles (Appendix 1). Some of these species pairs are sympatric in the YPBP, such as *Bonellia flammea* (Millsp. ex Mez) B. Ståhl & Källersjö and *B. macrocarpa* (Cav.) B. Ståhl & Källersjö (Primulaceae); *Ceiba schottii* Britten & Baker f. and *C. aesculifolia* (Kunth) Britten & Baker f. (Malvaceae); *Coccoloba spicata* Lundell and *C. diversifolia* Jacq. (Polygonaceae); *Gliricidia maculata* (Kunth) Kunth ex Walp. and *G. sepium* (Jacq.) Kunth ex Walp. (Fabaceae); *Metastelma yucatanense* W.D. Stevens and *M. schlechtendalii* Decne. (Apocynaceae); *Tillandsia dasyliriifolia* Baker and *T. limbata* Schltdl. (Bromeliaceae). Distinguishing between different allopatric

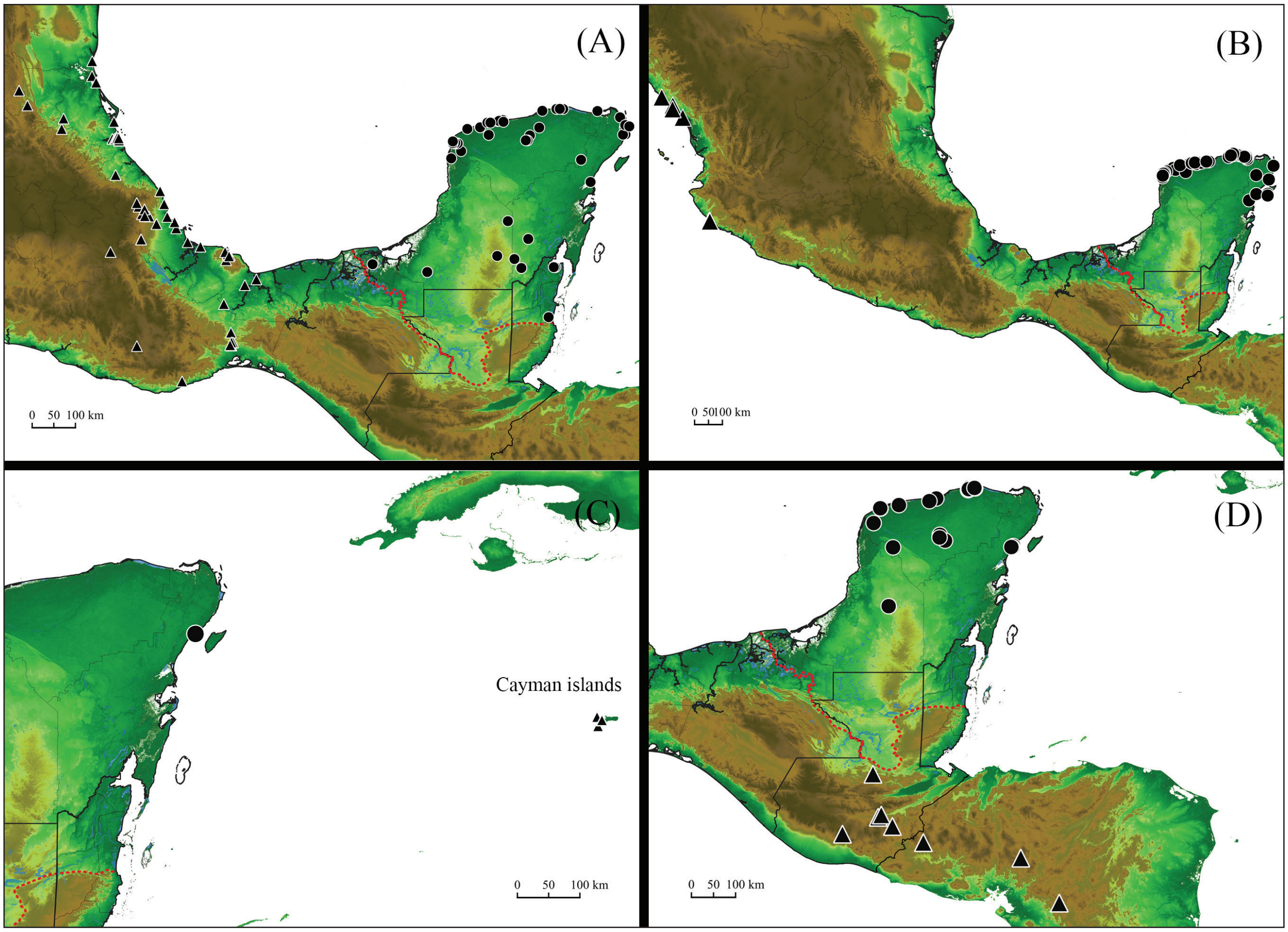

FIGURE 3. Geographic distribution of endemic taxa and their phylogenetically most closely related relatives, representing some of the potential biogeographical settings that gave rise to the endemic flora of the YPBP. **A**, *Myrmecophila christinae* (●) and *M. grandiflora* (▲); **B**, *Enriquebeltrania crenatifolia* (●) and *E. disjuncta* (▲); **C**, *Wittmackia mesoamericana* (●) and *W. caymanesis* (▲); **D**, *Beaucarnea pliabilis* (●) and *B. guatemalensis* (▲).

mechanisms (vicariance or establishment after dispersal) is one of the main challenges in biogeography (Runemark et al., 2012). However, these patterns may suggest dispersal processes that took place after divergence by isolation of these species in the past. This scenario is supported by the relative accessibility to the YPBP territory for several groups of plants.

Other endemic TDF species may have experienced incipient divergence processes given the geographical separation of their populations during the Pleistocene. Today, isolated populations in the Central Depression of Chiapas (Mexico) and Central America of near endemic species of the YPBP, such as *Bakeridesia gaumeri* (Standl.) D.M. Bates (Malvaceae), *Chiococca motleyana* Borhidi (Rubiaceae), *Mammillaria columbiana* subsp. *yucatanensis* (Britton & Rose) D.R. Hunt (Cactaceae), and *Stenocereus laevigatus* (Salm-Dyck) Buxb. (Cactaceae), might well be in the process of genetic and morphologic differentiation. These taxa have not been recognized as separate species, likely due to the lack of thorough systematic studies.

Long-Distance Dispersal Followed by Geographic Isolation

Floristic affinities of the YPBP and the Antilles have been reported for some groups within Apocynaceae, Arecaceae, Icacinaceae, Orchidaceae, Rubiaceae and Salicaceae, among others (Miranda, 1958; Rzedowski, 1978; Estrada-Loera, 1991; Chiappy-Jhones et al., 2001; Trejo-Torres and Ackerman, 2001; Ibarra-Manríquez et al., 2002). However, the main affinity between these two regions is for widely distributed taxa, especially those from coastal environments, suggesting recent dispersal and establishment (Espejel, 1987; Estrada-Loera, 1991).

The endemic flora of the YPBP originating from the Caribbean may have arisen as a result of long-distance dispersal followed by geographic isolation, along with the processes of gene drift and adaptation to new local conditions (Lomolino, 2016). Long-distance dispersal is a relatively rare phenomenon in nature, where migrating populations would have to circumvent the effects of bottleneck phenomena, such as inbreeding depression (Levin et al., 2003). This could explain why there are only three cases of endemic taxa with sister species from the Caribbean. Additionally, the geographic proximity between the YPBP and the Antilles has probably allowed continued gene flow between populations of species with long-distance dispersal capabilities (anemochory, hydrochory, or zoochory). For example, a great diversity of birds, such as *Vireo olivaceus* L. (Vireonidae), disperse the fruits of species such as *Erythroxylum havanense* Jacq. (Erythroxylaceae) (Islam, 2011). A high dispersal capacity of fruits and seeds limits speciation as it increases gene flow, while limited dispersal promotes rapid genetic differentiation and speciation (Givnish, 2010; Levin et al., 2003).

The best documented case of this speciation mechanism is that of *Wittmackia mesoamericana* (I. Ramírez, Carnevali & Cetzal) Aguirre-Santoro (Bromeliaceae), the only member of the genus in continental Central America. The other species of the genus are concentrated in the Antilles (Aguirre-Santoro, 2018) (Fig. 3C). This species diverged from *W. caymanensis* (Britton ex L.B. Sm.) Aguirre-Santoro about 0.1 Mya (Aguirre-Santoro et al., 2015; Aguirre-Santoro et al., 2016), and its fleshy berries are likely dispersed by birds. The fruits of most members of the subfamily Bromelioideae (Smith and Downs, 1979) have similar dispersal scenarios. However, only a single wild population of this species is known to exist on the east coast of the YPBP (Quintana Roo, Mexico). This is most likely due to the low success of the expansion of its range, coupled with local extinction events that are associated with land use changes in that area of the YPBP (Ellis et al., 2017). Two similar cases occur within the Eudicotyledoneae, although these endemic species have a wider geographical distribution in the YPBP, suggesting an older origin and a better adaptation to the local conditions: e.g., *Thouinia paucidentata* Radlk. (Sapindaceae), whose sister species, *T. portoricensis* Radlk., is endemic to Puerto Rico (Acevedo-Rodríguez et al., 2017). Members of this genus that display anemochory are distributed in the Caribbean, and they diversified mainly in limestone soils (González-Gutiérrez et al., 2016). Finally, *Randia truncata* Greenm. & C.H. Thomps. (Rubiaceae), restricted to the northern YPBP, appears to be closely related to *R. ciliolata* C. Wright (Appendix 1), a species restricted to Jamaica and western Cuba (Gustafsson and Persson, 2002).

The biotic exchange between these land masses has occurred in both directions and has had different implications for the evolution of the flora. In the west-to-east direction, the YPBP has served as a bridge for the dispersal of the biota from Mexico and Central America to the Antilles, where some groups of plants have experienced adaptive radiation by occupying the multiple available niches in these islands. For example, in *Encyclia* Hook. (Orchidaceae), at least three lineages have dispersed to the Antilles, and one of them subsequently, and rapidly, diversified there (Carnevali et al., 2022). In the east-to-west direction, there are diverse Antillean lineages with few representatives in the YPBP, such as *Casearia yucatanensis* (Standl.) T. Samar. & M.H. Alford (Salicaceae) and *Coccothrinax readii* H.J. Quero (Arecaceae) (Jestrow et al., 2017). This distribution pattern suggests sporadic dispersal events with little or no subsequent diversification.

Although the YPBP has not been an area of great plant diversification, the conditions there have facilitated the passage of lineages from the Antilles and northern South America to other parts of Mexico, where groups such as *Diospyros* L. (Ebenaceae) and *Pilosocereus* Byles & G.D. Rowley (Cactaceae) have diversified (García-Díaz et al., 2015; Lavor et al., 2018, 2020). Additional geographic disjunctions with the Caribbean have been reported for genera of Arecaceae, such as *Sabal* Adans. (Zona, 1990; Heyduk et al., 2016) and *Pseudophoenix* H. Wendl. ex Sarg. (Zona, 2002); however, neither phylogenetic nor biogeographical studies have addressed this.

In situ speciation

The present review found phylogenetic evidence of four clades completely restricted to the YPBP in the genera *Dictyanthus* Decne. (Fig. 4A), *Matelea* Aubl. (Apocynaceae), *Nopalea* Salm-Dyck (Cactaceae, often included in *Opuntia* Mill.) (Fig. 4B), and *Passiflora* L. (Passifloraceae), each including two species. The low species diversity found in these clades may indicate two important aspects of the history of the region. First, this pattern may suggest that cladogenetic events occurred very recently: i.e., these are neoendemic lineages that have been unable to expand their distribution range or diversify further (Bruchmann and Hobohm, 2014). The times of divergence between *Nopalea inaperta* Schott ex Griffiths and *N. gaumeri* Britton & Rose (~2 Mya) (Majure et al., 2012) support this hypothesis (Fig. 2). Also, *Passiflora itzensis* (J.M. MacDougal) Port.-Utl. and *P. xiikzodz* J.M. MacDougal diverged 6–4 Mya but have not spread to other areas of the Neotropics (Porter-Utley, 2014). Second, the relative orographic and environmental homogeneity in the YPBP does not provide a broad variety of niches where lineages can undergo adaptive radiation, as has occurred on many islands worldwide (Kier et al., 2009; Givnish et al., 2014). Nonetheless, the YPBP has an environmental gradient and a microenvironmental heterogeneity that have favored in situ evolutionary divergence processes at different geographic scales, as detailed below.

On a microenvironmental scale, selective local adaptation processes also seem to have led to the divergence of some lineages in the YPBP. For example, morphological differences in androgynophore length and the position of floral nectaries between the sister species *Passiflora itzensis* and *P. xiikzodz* (Porter-Utley, 2014) may have led to selective pressures and, ultimately, sympatric speciation among them. The biogeographical evidence indicates that this genus underwent rapid diversification spreading to Central America from North America (Muschner et al., 2012) involving large floral variation among its species (Acha et al., 2021). In the Apocynaceae, *Dictyanthus aeneus* Woodson and *D. yucatanensis* Standl. are sister species (González-Martínez, 2019) that coexist in TDFs in the northern part of the YPBP, although in different microenvironments (Fig. 4A). *Dictyanthus aeneus* grows in the shady understory, while *D. yucatanensis* thrives in open environments, such as forest margins and along road edges (Carnevali, 2021b). However, the infrequent occurrence of natural hybrids between the two species (Carnevali, 2011) suggests that barriers to gene flow between them are still not well-established.

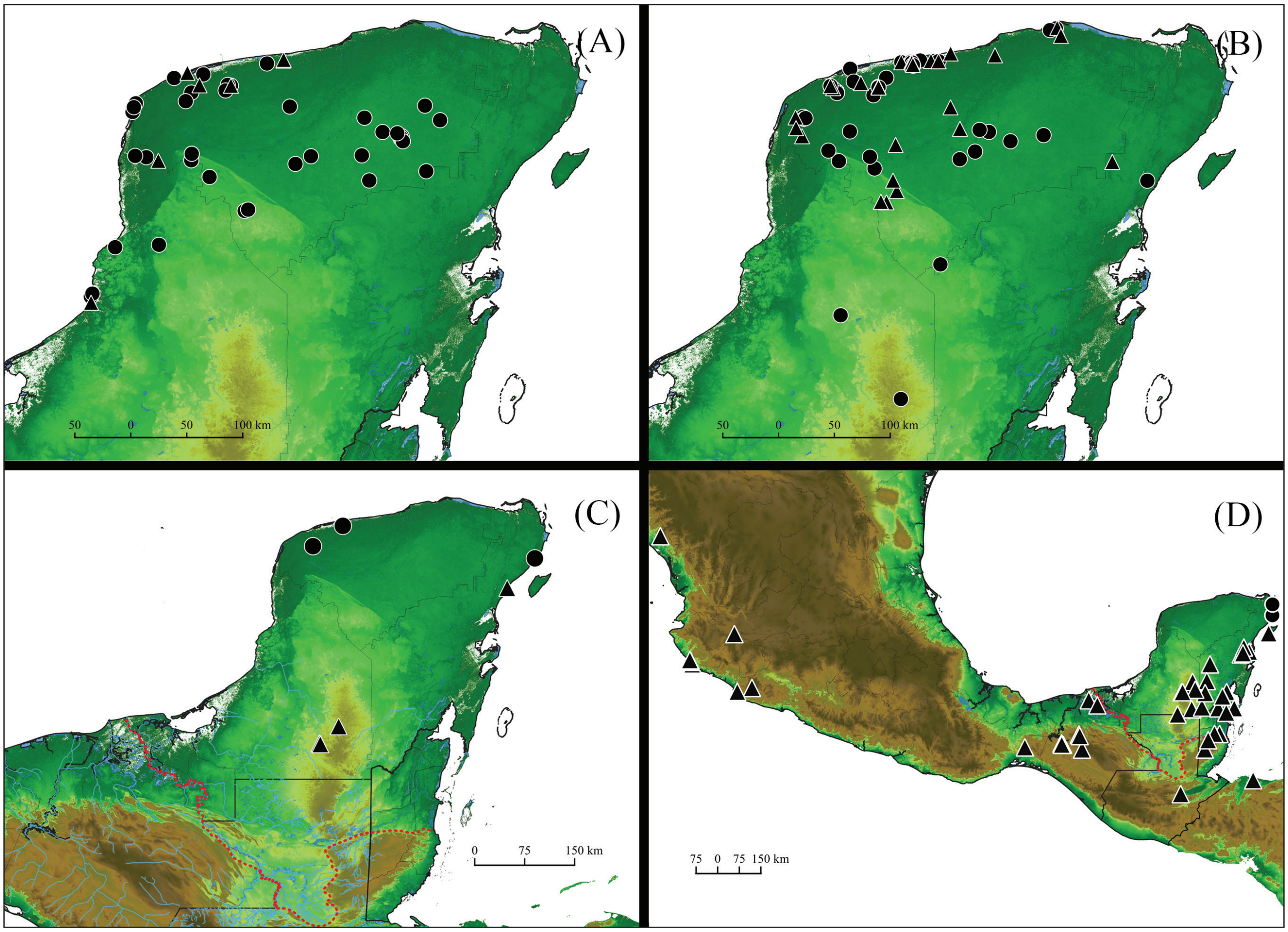

FIGURE 4. Geographic distribution of endemic taxa and their phylogenetically most closely related relatives, representing some of the potential biogeographical scenarios that gave rise to the endemic flora of the YPBP. **A**, *Dictyanthus aeneus* (▲) and *D. yucatanensis* (●); **B**, *Nopalea gaumeri* (●) and *N. inaperta* (▲); **C**, *Wimmeria lundelliana* (▲) and *W. obtusifolia* (●); **D**, *Citharexylum calvum* (●) and *C. hirtellum* (▲).

The relatively more complex orographic conditions in the southern portion of the YPBP (Duch, 1991), combined with higher moisture and nutrient levels in the soil (Bautista et al., 2011; 2015), led to a greater number of available niches than in the northern part of the YPBP. These conditions possibly favored sympatric diversification processes in these rainforests, which gave rise to neoendemic species; however, these divergences are likely very recent due to the climatic instability during the Pleistocene. The availability of humid niches in the southern YPBP may be a plausible explanation for the endemism of *Syngonanthus* Ruhland (Eriocaulaceae) (3 endemic spp.) rather than a limitation in their dispersal capacity (anemochory or hydrochory), as observed in the large number of microendemics within the genus (Echternacht, 2012). Also, although the phylogenetic relationships of many *Justicia* species inhabiting the YPBP are unknown, at least five are microendemic taxa, restricted to humid sites in the central and southern areas of the YPBP.

On a regional scale, climatic and edaphic gradients in the YPBP may have favored adaptive processes, resulting in differentiated populations over time. According to some studies on the biogeography of the flora of the YPBP (Espadas-Manrique et al., 2003; Ibarra-Manríquez et al., 2002), there is a marked separation in the biotic components between the north and south of the YPBP, where the climatic conditions are markedly different (Orellana et al., 1999). This environmental divergence seems to have shaped the speciation between sister species that inhabit different geographic areas within it, such as *Harpalyce torresii* São-Mateus & M. Sousa and *H. yucatanense* São-Mateus & M. Sousa (Fabaceae) (São-Mateus, 2018), and, based on morphological similarity, between *Wimmeria lundelliana* Carnevali, R. Duno, J.L. Tapia & I. Ramírez and *W. obtusifolia* Standl. (Celastraceae) (Carnevali et al., 2009) (Fig. 4C). Also, *Citharexylum calvum* Moldenke (Verbenaceae) has a few populations inhabiting the driest tropical forests of the northeast YPBP, and its most likely related species, *C. hirtellum* Standl., has a wider distribution in the wetter forests in the southern YPBP, Mexico, and Central America (Frost et al., 2017; 2020) (Fig. 4D). This genus originated in the mesic environments of central-northern Mexico, with at least three transitions to arid environments (Frost et al., 2017). Additionally, the pattern of geographic divergence between the legumes *Mariosousa dolichostachya* (S.F. Blake) Seigler & Ebinger, endemic to the central and northern areas of the YPBP, and *M. usumacintensis* (Lundell) Seigler & Ebinger, distributed in Mexico, Central America, and the south of the YPBP, coincides with the environmental gradient of this province (Miller et al., 2017).

In the YPBP, many endemic species are not restricted to a single vegetation type but are widely distributed throughout the territory (Carnevali et al., 2021b). This suggests that environmental barriers have not been strong enough to promote diversification processes within the YPBP. The lack of important geographic barriers, coupled with dispersal capabilities observed in many endemic species, probably favored broad distribution within the YPBP. Nonetheless, some cases suggesting divergence processes at the subspecies level within the YPBP have been documented from phylogeographic and population structure studies. *Cakile lanceolata* subsp. *alacranensis* (Millsp.) Rodman (Brassicaceae) is a taxon restricted to the driest areas of the coastal dune vegetation in the Alacrán reef, an ecologically restrictive area in terms of humidity and temperature. In fact, the subspecific taxa of *C. lanceolata* (Millsp.) O.E. Schulz diverged less than 2 Mya (Willis et al., 2014b). A study on *Metastelma schlechtendalii* Decne. (Apocynaceae) also reported genetic differentiation between populations in the southern and northern areas of the YPBP (Liede-Schumman et al., 2014).

Evolutionary Divergence in Areas Adjacent to the YPBP from Adaptation to Local Conditions

Some authors have highlighted the strong floristic affinity of the YPBP with Central America and Mexico (Miranda, 1958; Estrada-Loera, 1991; Ibarra-Manríquez et al., 2002; Duno de Stefano et al., 2012). However, this region has significantly different environmental restrictions compared to contiguous geographic areas, including complex microtopology and northwest-to-southeast edaphic and climate gradients (Vargas et al., 2014). The combination of the climatic, orographic, and edaphic characteristics of the YPBP has likely acted as an ecological filter for several plant lineages. Despite the lack of obvious geographic barriers, some families which are widely distributed in the Neotropics, such as Crassulaceae and Ericaceae, are completely absent in this area. Other families, such as Marcgraviaceae, Melastomataceae, Polemoniaceae, and Pinaceae, barely reach the southern, more humid, limits of this province. This pattern is interesting because the absence of orographic barriers that could prevent the arrival of lineages from the southern part of the YPBP indicates the likelihood that ecological factors restrict the establishment of many biological groups in this area.

The environmental conditions of the YPBP possibly promoted evolutionary divergence between populations in this area and neighboring areas of southern Mexico and Central America. This phenomenon has already been evidenced in biogeographical works indicating a marked pattern of biotic separation between these areas (e.g., Poaceae, Dávila-Aranda et al., 2004; amphibians and reptiles, Barrera, 1962). This same pattern of geographic divergence was found in 13 taxa endemic to the YPBP; the phylogenetically closest relatives of these taxa have a relatively broad distribution and long-distance dispersal characteristics, but do not penetrate the YPBP territory (Appendix 2). Taxonomic studies of selected groups based on morphological similarity indicate that at least 18 other pairs of hypothetically related species show the same distribution pattern. Since most of these species have long-distance dispersal mechanisms, this low diversity cannot be attributed to a limited dispersal capability. Also, it is important to note that quasi-endemic species, such as *Acalypha gentlei* Atha (Euphorbiaceae), *Eugenia winzerlingii* Standl. (Myrtaceae) or *Haematoxylum campechianum* L. (Fabaceae), which also appear in the Gulf of Mexico province, could reflect the transitional zone characteristic of the southern portion of the YPBP, and explain the historical challenge of its southern delimitation (Morrone, 2019). These species grow in the more atypical humid conditions of the YPBP, which is mainly dry.

Some taxa endemic to the YPBP have morphological characteristics that are particularly distinctive from the rest of the species in the same genus. These adaptive morphological characters may be of evolutionary importance for the taxa. For example, *Beaucarnea pliabilis* (Baker) Rose (Nolinaceae) has a larger number of foliar papillae that protect stomata in contrast to its sister species *B. guatemalensis* Rose, which grows in humid tropical forests from central Guatemala to northern Nicaragua (Rojas-Piña et al., 2014) (Fig. 3D). As observed in other species of Asparagaceae (Solano et al., 2017), these differential adaptations between lineages suggest that their evolutionary divergence may be associated with the colonization of drier environments and provide indications of the selective pressures that shaped their diversification. *Pilostyles maya* P. Ortega, Gonz.-Martínez & S. Vázquez is the only species in the genus that has hermaphroditic flowers, a condition considered ancestral and rare in Apodanthaceae, where most species are dioecious or monoecious (Azevedo, 2010; Schaefer and Renner, 2011). Additionally, *P. maya* presents cleistogamous flowers, an autapomorphic character in the genus (Ortega-González et al., 2020). Both characters require low energy expenditure and are deemed reproductive strategies that increase the likelihood of self-pollination (Bawa and Beach, 1981; Cardoso et al., 2018). This may be advantageous in the absence of pollinators or in the variable seasonal conditions of the YPBP.

In some cases, the occurrence of species with highly atypical morphological traits within their group has caused them to be considered separate, monotypic genera. This may be evidence of the ecological divergence mentioned above. For example, *Plagiolophus* Greenm. (Asteraceae) is the only member of the tribe *Ecliptinae* that has a projection on the apex of the cypsela (or apical rostrum) (Azevedo-Bringel, 2014). This structure facilitates its attachment to mammalian hair or to the feathers of birds, thus promoting long-distance dispersal (Sorensen, 1986). However, this genus is restricted to the Yucatan peninsula and is phylogenetically related to the genus *Jefea* Strother, which is absent from the YPBP. *Attilaea abalak* E. Martínez & Ramos (Anacardiaceae) has characteristics similar to species of *Spondias* L., but it is distinguished by having a climbing (vs. arborescent) habit, and a bicarpellary (vs. unicarpellary) gynoecium (Martínez and Ramos, 2007; Mitchell and Daly, 2015). Both characters can be ecologically favorable for faster establishment when invading new areas and for increasing the possibility of seed dispersal relative to members of *Spondias* (Howe and Smallwood, 1982).

Finally, the only two species of *Manfreda* Salibs. (Asparagaceae) present in the YPBP, *M. paniculata* L. Hern., R.A. Orellana & Carnevali and *M. petskinil* R.A. Orellana, L. Hern. & Carnevali, have different characteristics than the rest of the genus: perennial (vs. deciduous) leaves, paniculate (vs. racemose) inflorescences, and flowers subtended by a single bracteole (vs. two bracteoles) (Hernández-Sandoval et al., 2008). These authors suggest that geographic isolation may have promoted its evolutionary and morphological divergence. However, an intergeneric hybrid origin between *Manfreda* and *Agave* L. has also been proposed for *M. paniculata* L. Hern., R.A. Orellana & Carnevali (Carnevali, 2013). The uniqueness or peculiarity of the morphological characters in these species may be the result of the extinction of morphologically similar lineages or ancestral lineages, or of morphological divergences arising from selective pressures related to the YPBP environment.

Hybridization

In vascular plants, hybridization is a process that regulates and catalyzes biological diversity, being more common in some groups than in others (Rieseberg et al., 2007; Schley et al., 2022). Natural hybrids have been documented within families, such as Orchidaceae [*Maxillariella* × *yucatanensis* (Carnevali & R. Jiménez) M.A. Blanco & Carnevali, and *Myrmecophila* × *laguna-guerrerae* Carnevali, Ibarra-González & J.L. Tapia] and Fabaceae [*Vachellia* × *cedilloi* (L. Rico) Seigler & Ebinger]. Also, in *Tillandsia* L. (Bromeliaceae), *T. maya* I. Ramírez & Carnevali has intermediate morphology between *T. brachycaulos* Schltdl. and *T. balbisiana* Schult. f., suggesting a hybrid origin (Ramírez et al., 2000). However, we only found phylogenetic evidence for the hybrid origin of *Stylosanthes quintanarooensis* Gama & Dávila (Fabaceae), a tetraploid species which likely arose from a single clone locally adapted to humid conditions in southeastern YPBP (Stappen et al., 2002).

Another work suggests hybrid origin in Anthericaceae. The genus *Echeandia* Ortega has a large variation in the number of chromosomes between species, suggesting that hybridization has been a key driver of diversification (Cruden, 1999; Rodríguez and Castro-Castro, 2005). In fact, *E. luteola* Cruden, endemic to the YPBP, is pentaploid (n = 40), which supports the hypothesis of a hybrid origin (Cruden, 1994). The populations mentioned above thrive mainly in flooded plant communities, particularly in the southern YPBP, where communities of seasonal and perennial environments converge. These hybrid zones are usually common in overlapping areas of different environments, also known as ecotones (Schley et al., 2022). However, only a few isolated individuals (in some cases, only a single individual) have been found in these areas. Thus, whether hybridization processes lead to successful hybrid speciation events is still an unanswered question (Mallet, 2007).

It is worth noting that the study of natural populations in the YPBP is biased by the lack of specialists for multiple taxonomic groups in the region; therefore, hybrid speciation events are probably more common than reported, since that adaptive introgression is especially common in novel or disturbed environments (Rieseberg et al., 2007).

Anthropogenic influence

Anthropogenic activities have impacted the flora of the YPBP since the establishment of the Mayan civilization about 10, 000 years ago (Binford, 1983; Rico-Gray and García-Franco, 1991). The plant communities inhabiting the YPBP have been modified throughout its long anthropogenic history (Rico-Gray and García-Franco, 1991; Chiappy et al., 2000; Fedick and Morrison, 2004; Dupuy et al., 2015). At the peak of the Mayan civilization, some 3,000–4,000 years ago, the high population density caused a profound impact on the vegetation, climate, and soil in the region (Binford, 1983; Islebe et al., 1996). However, the forests are highly resilient and have recovered, even after the sisal industry significantly impacted the landscape (Ceccon et al., 2002; González-Iturbe et al., 2002). These forests currently account for the second largest patch of continuous vegetation in America, but the region has the highest deforestation rates in the Neotropics (Ellis et al., 2017).

The flora of the YPBP currently faces serious anthropogenic threats from changes in land use due to urban and agricultural expansion, as well as from energy and tourism projects (Sánchez-Sánchez et al., 2015; Reyes-García et al., 2019). Approximately 51% of the endemic taxa are listed in a risk category, of which some 44% are listed as threatened or critically threatened (Carnevali et al., 2021b).

Conclusions

The evidence gathered in the present review strongly suggests that the origin of the endemic vascular flora of the YPBP has been driven by various factors and processes that occurred at different times in the history of the Earth. However, the biogeographical and phylogenetic patterns of most of the species studied show the influence of Pleistocene climatic fluctuations on the processes of speciation. Such environmental changes may have had different consequences for the flora and resulted in different distribution patterns, depending on the dispersal and adaptive capabilities of the lineages. Additionally, although less frequently, other processes such as hybridization, local adaptation, and geographic isolation after long-distance dispersal, must also have contributed to the creation and diversification of the endemic flora of this region.

Greater climatic stability in the northern region of the YPBP allowed for the isolation of lineages associated with drier and more seasonal environments compared to the southern region. The environmental conditions of the YPBP promoted ecological divergence within this area, while the regional environmental conditions led to processes of large-scale divergence. However, the probability of dispersal between the YPBP and the Antilles, given their geographic proximity and the various dispersal capabilities of species, has prevented differentiation by isolation in the lineages that have arrived in the YPBP.

Added at proof stage

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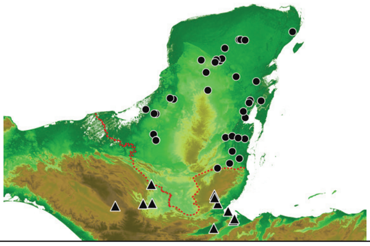
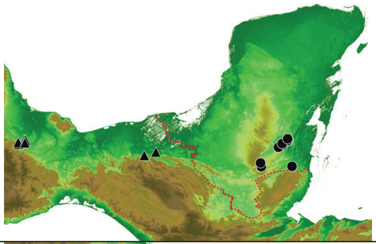
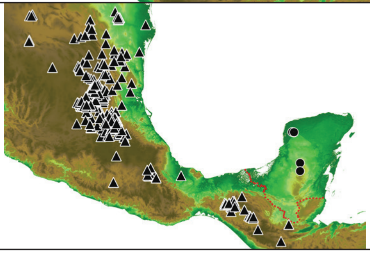
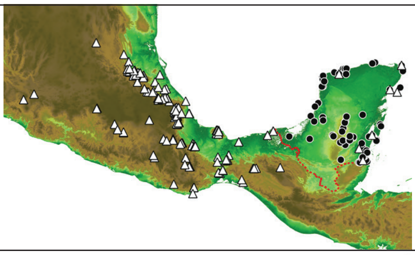
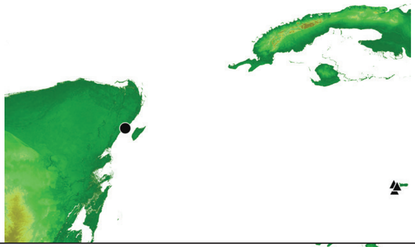
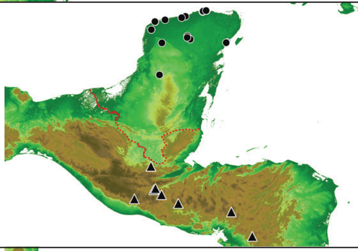
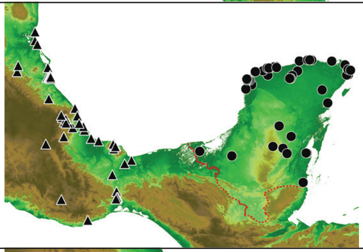
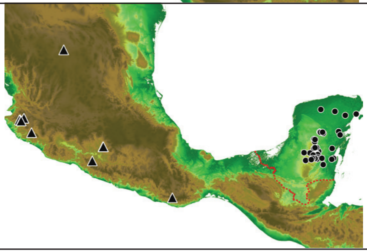
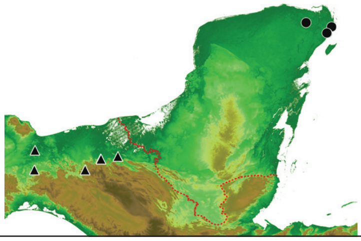
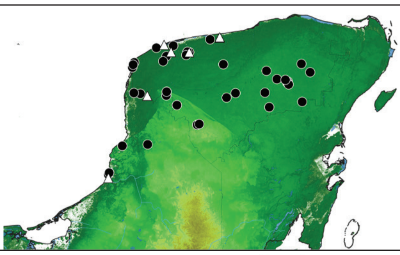
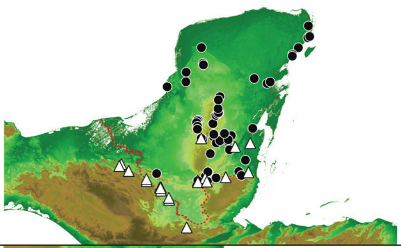
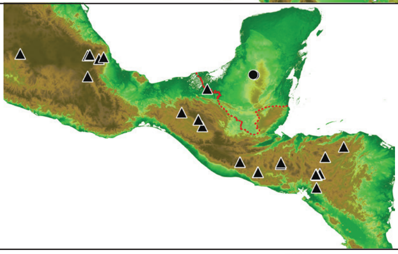
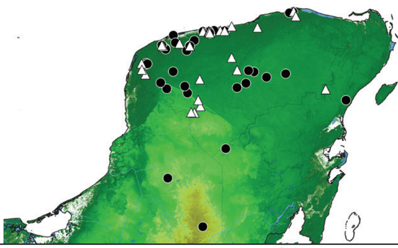
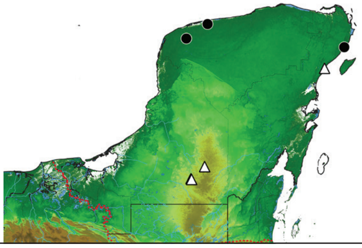
APPENDIX 1

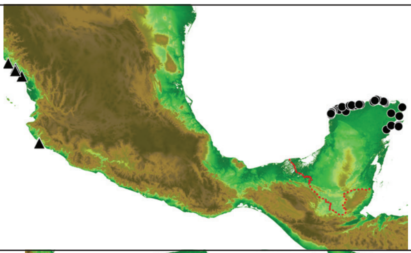
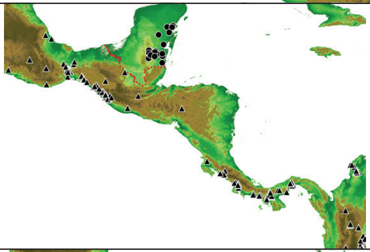
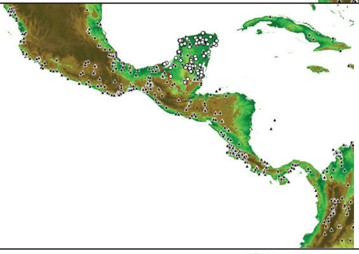
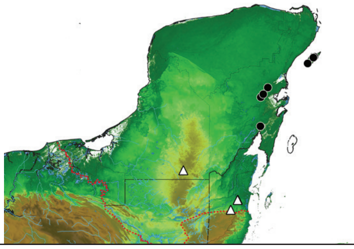
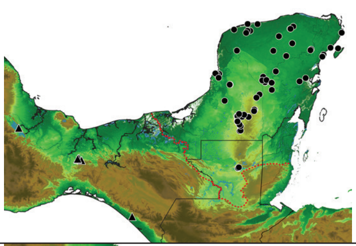
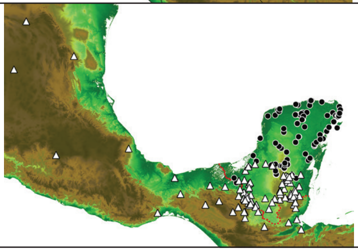
Possible biogeographic hypothesis about origin of YPBP endemic species, according to their phylogenetic relationships and estimated divergences times taken from previous work (values in parenthesis), and according to a phylogenetic reconstruction with the V.Phylomaker package [values in brackets], as well as biological attributes of biogeographical relevance. YPBP endemic or quasiendemic taxa (●) and their sister taxon or taxa (▲), unless otherwise noted when both of them are endemic.

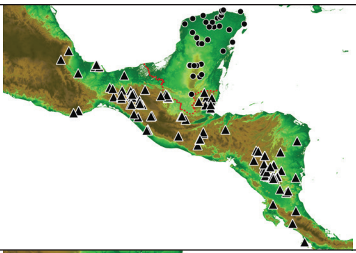
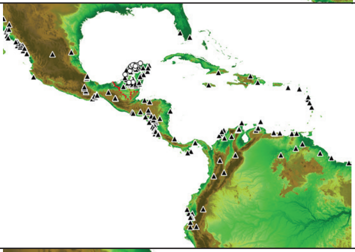
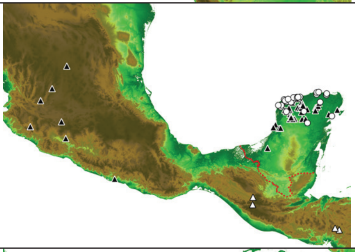
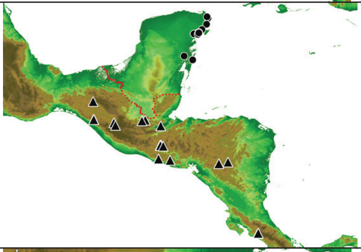
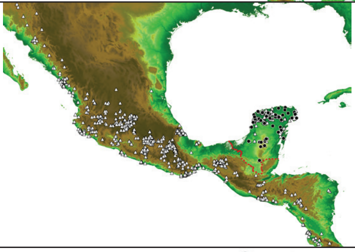
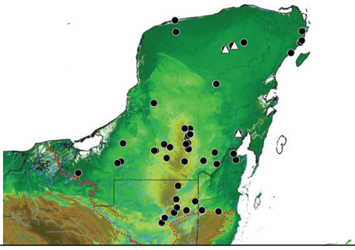
Abbreviations. **Growth forms, (Categories)** ARB = Arborescent, EPI = Epiphyte, HER = Herbaceous, LIA = Liane, SHR = Shrubby, SUC = Succulent; (Subcategories) Cli = Climbing, Palm = Palm, Par = Parasitic, Ros = Rosseted, Shr = Shrubb, Shr-l = Shrubb-like, Suf = Suffrutex, Tree = Tree, Tree-l = Tree-like. **Dispersal syndromes**, ANE = Anemochory, BAL = Balochory, BAR = Barochory, HYD = Hydrochory, ZOO = Zoochory; (Subcategories) Chi = Chiropterophily, Epi = Epizoochory, Mast = Mastocory, My = Myrmecochory, Orn = Ornithophily. **Phylogenetic evidence**, N= Nuclear, C= Chloroplast, BS = Bootstrap, CF= Concordance factors, ML = Maximum Likelihood, MP =Maximum Parsimony, JN = Jacknife, PP = Posterior Probability.

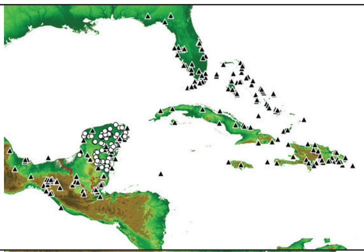
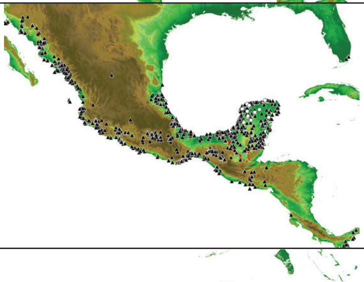
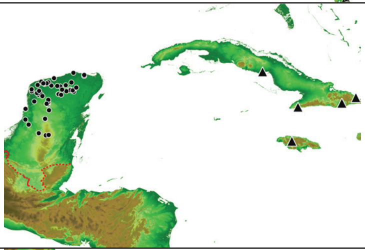
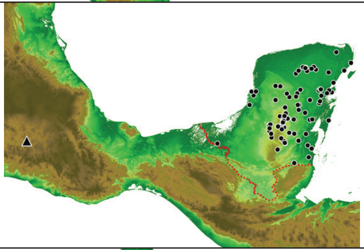
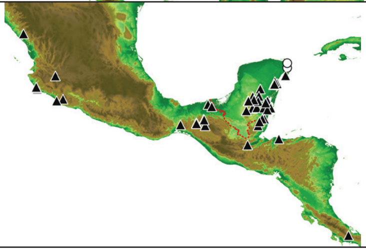
LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Zamiaceae *Zamia* ~60 (2/2)	*Zamia prasina* / *Z. variegata* **1.7** (0.74–2.28) **[12.9]**		**SHR** **Shr-l**	**ZOO** **Mast**	Molecular (N+C) Montalvo-Fernández et al., 2019
Arecaceae *Gaussia* 5 (1/1)	*Gaussia maya* / *G. gomez-pompae* **10** (5–17) **[12.97]**		**ARB** **Palm**	**ZOO** **Orn, Chi**	Molecular (N+C) 100 BS / 0.95 PP Cuenca et al., 2007; Cuenca and Asmussen-Lange, 2007
Bromeliaceae *Hechtia* > 90 (1/1)	*Hechtia schottii* / Clade (*H. lepidophylla*, *H. glomerata*, *H. ghiesbreghtii*) ~1 **[24.2]**		**SUC** **Ros**	**BAR**	Molecular (N+C) & Morphology 0.56 PP Ramírez-Morillo et al., 2018; Rivera-Martínez et al., 2022

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Bromeliaceae *Tillandsia* > 650 (21/6)	*Tillandsia dasyliriifolia* / *T. limbata* **[0.02]**		**EPI**	**ANE**	Molecular (N+C) & Morphology >0.85 PP Pinzón et al., 2016; Granados et al., 2017
Bromeliaceae *Wittmackia* 44 (1/1)	*Wittmackia mesoamericana* / *W. caymanensis* **(<0.3)** **[8.26]**		**EPI (Facul)**	**ZOO (Orn)**	Molecular (N+C) & Morphology 43 ML / 0.49 CF Aguirre-Santoro, 2015; Aguirre-Santoro et al., 2016
Nolinaceae *Beaucarnea* ~12 (1/1)	*Beaucarnea pliabilis* / *B. guatemalensis* **[25.7]**		**ARB** **Tree-l**	**ANE**	Molecular © 99 BS / 0.99 PP + (N) 88 BS /1.0 PP Rojas-Piña et al., 2014
Orchidaceae *Myrmecophila* 8 (4/1)	*Myrmecophila christinae* / *M. grandiflora* **[0.91]**		**EPI**	**ANE**	Molecular & Morphology (N) 79 MP Carnevali et al., 2003
Acanthaceae *Carlowrightia* 28 (2/2)	1. *Carlowrightia myriantha* / *Chalarothyrsus amplexicaulis* 2. *Henrya* Clade **5** (3.5–6.8) **[2.54]**		**SHR** **Suf**	**BAL**	1. Molecular 0.95 PP / 89 ML McDade et al., 2018 2. Molecular 100 BS / 89 MP Daniel et al., 2008
Acanthaceae *Justicia* > 700 (22/7)	*Justicia dendropila* / *J. valvata* **[14.3]**		**SHR** **Shr**	**BAL**	Molecular (N+C) (0.98 PP / 51 BS) Kiel et al., 2018

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Apocynaceae *Dictyanthus* 17 (4/2)	*Dictyanthus aeneus* (▲) / *D. yucatanensis* (●) **[15.4]**		**HER** **Cli**	**ANE**	Molecular (N+C) + Morphology 0.99 PP González-Martínez, 2019
Apocynaceae *Matelea* ~100–200 (8/4)	*Matelea gentlei* / *M. micrantha* **[3.32]**		**HER** **Cli**	**ANE**	Molecular (C) 98 ML McDonnell et al., 2018
Apocynaceae *Metastelma* > 70 (4/1)	*Metastelma yucatanense* / *M. schlechtendalii* **[0.19]**		**HER** **Cli**	**ANE**	Molecular (C) Ev_supp Liede-Schumann et al. 2014
Apodanthaceae *Pilostyles* 11 (1/1)	*Pilostyles maya* / *P. mexicana* **[15.08]**		**HER** **Par**	**ND**	Molecular (C) 0.67 PP / 61 BS Ortega-González et al., 2020
Cactaceae *Nopalea* 10 (2/2)	*Nopalea inaperta* (▲) / *N. gaumeri* (●) **1.5** (1–2) **[2.56]**		**SUC** **Shr**	**ZOO**	Molecular (C+N) 0.55 PP / 60 BS Majure et al., 2012; Hernández-Hernández et al., 2014
Celastraceae *Wimmeria* ~15 (4/2)	*Wimmeria lundelliana* (▲) / *W. obtusifolia* (●) **[5.49]**		**ARB** **Tree**	**ANE**	Morphological similarity Carnevali et al., 2009

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Euphorbiaceae *Enriquebeltrania* 2 (1/1)	*Enriquebeltrania crenatifolia* / *E. disjuncta* **17.6** (6.21–32.2) **[22.03]**		**SRH** **Shr**	**ZOO (Myr)**	Molecular (C+N) (100 BS / >0.98 PP) De Nova et al., 2006; Cuevas-Chapa, 2016
Fabaceae *Calliandra* ~135 (6/2)	*Calliandra belizensis* / *C. magdalenae* <2.6 **[20.8]**		**SHR** **Shr**	**BAL**	Molecular (N+C) (0.98 PP / 0.94 BS) Souza et al., 2013
Fabaceae *Gliricidia* 3 (2/1)	*Gliricidia maculata* / *G. sepium* **[0.85]**		**ARB** **Tree**	**BAR**	Molecular (N+C) (99 BS) Lavin et al., 2001, 2003
Fabaceae *Harpalyce* 34 (4/2)	*Harpalyce torresii* (▲) / *H. yucatanense* (●) **[9.78]**		**ARB** **Tree**	**BAL**	Molecular (N) 99 BS / 100 ML São Mateus, 2018
Fabaceae *Lonchocarpus* ~180 (12/3)	*Lonchocarpus yucatanensis* / *L. wendtii* **[6.6]**		**ARB** **Tree**	**ANE**	Molecular (N) (100 PP) Sousa et al., 2014
Fabaceae *Mariosousa* 13 (1/1)	*Mariosousa dolichostachya* / *M. usumacintensis* **[25.1]**		**ARB** **Tree**	**BAR**	Molecular (N+C) (100 BS / 1 PP) Seigler et al., 2006; Miller et al., 2017

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Fabaceae *Platymiscium* ~20 (1/1)	*Platymiscium yucatanum* / *P. dimorphandrum* + *P. jejunum* **<2.5** **[62.36]**		**TREE** **Tree**	**ANE**	Molecular (N+C) + Morphology 96 BS / 1 PP Saslis-Lagoudakis et al., 2008
Malpighiaceae *Malpighia* >50 (8/2)	*Malpighia souzae* / *M. emarginata* + *M. stevensii* **[2.14]**		**SHR** **Shr**	**ZOO**	Molecular (N+C) + Morphology (54 BS) Davis and Anderson, 2010
Malvaceae *Ayenia* ~70 (3/1)	*Ayenia fasciculata* / *A. simulatrix* + *A. abutilifolia* **~2.6** **[9.8]**		**SHR** **Shr**	**BAL / ZOO (EPI)**	Molecular (C) 59 BS Sharber, 2018
Malvaceae *Bakeridesia* ~30 (4/1)	*Bakeridesia yucatana* / *B. nelsonii* **~3** **[6.63]**		**SHR** **Shr**	**ZOO (Epi)**	Molecular (N+C) Donnell et al., 2012; Donnell, 2012; Hoorn et al., 2019
Malvaceae *Ceiba* 18 (2/1)	*Ceiba schottii* / *C. aesculifolia* + one accession of *C. samauma* **7.3** (3.7–11) [3.05]		**TREE** **Tree**	**ANE**	Molecular (N+C) Pezzini et al., 2021
Passifloraceae *Passiflora* ~500 (21/6)	*Passiflora itzensis* (▲) / *P. xiikzodz* (●) **[13.7–6.2*]**		**HER** **Cli**	**ZOO**	Molecular (N) & Morphology Porter-Utley, 2014

LINEAGE **Family** *Genus* # spp. (# spp. in YPBP / # endemic species)	**Endemix taxa / Related taxa & Stimated time divergence in My (Literature) [V.Phylomaker]**	**Geographic distribution**	**Growth form**	**Dispersal syndrome**	**Phylogenetic evidence (References)**
Polygonaceae *Coccoloba* ~150 (14/5)	*Coccoloba spicata* / *C. diversifolia* **[4.5]**		**TREE** **Tree**	**ZOO**	Molecular (N+C) 26 MP / 70 ML Burke et al., 2010
Primulaceae *Bonellia* ~22 (5/3)	*Bonellia flammea* / *B. macrocarpa* **[5.7]**		**SHR** **Shr**	**ZOO**	Molecular (C) & Morphology 91 JN Källersjö and Stahl, 2003
Rubiaceae *Randia* >110 (5/3)	*Randia truncata* / *R. ciliolata* [+ *R. mitis* in Borges et al., 2021] **[1.6]**		**TREE** **Tree**	**ZOO**	Molecular (N+C) 0.99 PP / 98 BS Gustafsson and Persson, 2002; Borges et al., 2021
Sapindaceae *Serjania* ~230 (14/2)	*Serjania yucatanensis* / *Balsas guerrirensis* **[4.3]**		**LIA**	**ANE**	Molecular (N+C) 0.93 PP / 81 BS Acevedo-Rodríguez et al., 2017
Sapindaceae *Thouinia* ~30 (3/1)	*Thouinia paucidentata* / *T. portoricensis* **[12.5]**		**LIA**	**ANE**	Molecular (N+C) 82 BS Acevedo-Rodríguez et al., 2017
Verbenaceae *Citharexylum* ~130 (7/1)	*Citharexylum calvum* / *C. hirtellum* **[2]**		**SHR** **Shr**	**ZOO**	Molecular (N+C) 60 ML / 100 PP Frost et al., 2017; 2020

NOTES ON SEVERAL ARGENTINEAN AND CHILEAN SPECIES OF *LEPIDIUM* (BRASSICACEAE)

Darío J. Schiavinato,[1] Adriana Bartoli,[1] and Ihsan A. Al-Shehbaz[2,3]

Abstract. *Lepidium graminifolium* is reported for the first time for South America. New first records are given for *L. argentinum, L. brevicaule,* and *L. santacruzense* from the Argentinean provinces San Juan, Mendoza, and Chubut, respectively. *Coronopus leptocarpus* is lectotypified and the status of the types of *C. leptocarpus* var. *microcarpus, L. abrotanifolium* var. *steinmannii, L. boelckeanum*, and *L. inclusum* are briefly discussed.

Keywords: Argentina, Brassicaceae, Chile, Cruciferae, *Lepidium*

Lepidium L. (ca. 270 spp.), the fourth largest genus in the Brassicaceae (Cruciferae), is represented by native species on all continents except Antarctica. Its limits were expanded in the past two decades to include the genera *Cardaria* Desv., *Coronopus* Zinn, *Cyphocardamum* Hedge, *Lithodraba* Boelcke, *Stroganowia* Kar. & Kir., *Stubendorffia* Schrenk, and *Winklera* Regel (Al-Shehbaz et al., 2002; Al-Shehbaz & Mummenhoff, 2011; Al-Shehbaz, 2021). Except for the monospecific *Cyphocardamum* and *Lithodraba*, molecular phylogenetic studies (e.g., Mummenhoff et al., 2001, 2009, and references therein) have shown that the other five genera are polyphyletic and nested within *Lepidium*. The features on which all seven genera were recognized as distinct from *Lepidium* are artificial and independently evolved within *Lepidium*. Therefore, a more-inclusive *Lepidium* is far more acceptable and practical than recognizing ill-defined, much smaller genera.

The South American species of *Lepidium* have been subjected to several recent studies (e.g., Al-Shehbaz 2010, 2012, 2017), and the continent includes 12 naturalized and 55 native species, including 32 narrowly endemic: Argentina (10), Chile (7), Bolivia (6), Ecuador (4), Peru (4), and Brazil (1).

The present paper is based primarily on an undergraduate degree thesis by the first author (Schiavinato, 2015) and a world monograph of *Lepidium* (in progress) by the last author.

New Records

1. ***Lepidium graminifolium*** L. This species is native to southern Europe, northwestern Africa, the Caucasus, and southwestern Asia (Syria, and Turkey). It is naturalized elsewhere in Europe and western Asia. It was recorded for North America as a ballast plant, but, despite being a short- to long-lived perennial, the species never became established on the continent (Al-Shehbaz and Gaskin, 2010). The following first record for South America may also represent an early introduction that has not become naturalized in Argentina, which has nine of the 12 alien species on the continent.

Lepidium graminifolium is a perennial easily distinguished by a combination of linear, entire cauline leaves not auriculate at the base, 6 stamens, and elliptic to ovate-elliptic fruits, (1.8–)2–3 × (1.4–)1.8–2 mm, that have an obsolete apical notch and exserted style. The new record is based on: Argentina. Buenos Aires, La Plata Partido, La Plata, 15 October 1932, *A. L. Cabrera s.n.* (BAA [00008189], BAB [66708]).

2. ***Lepidium argentinum*** Thell. The following collection represents the first record of the species from San Juan Province.

Argentina. San Juan, Iglesia Department, Quebrada de Agua Negra, 7 November 1980, *R. Kiesling 2987* (BAA [00008191], NY, SI).

3. ***Lepidium brevicaule*** Barnéoud. Al-Shehbaz (2012) treated this name as a synonym of *L. reichei* Phil. ex Reiche because it was considered to be a later homonym of *L. brevicaule* Hoppe ex W.D.J. Koch. However, further study of the literature clearly showed that the last name was a *nomen nudum*. Therefore, Barnéoud's name should be recognized instead of *L. reichei* Phil. ex Reiche. *Lepidium brevicaule* is reported here for the first time from Mendoza Province.

Argentina. Mendoza, Tunuyán Department, Valle del Arroyo Grande, between Puesto de Gendarmería "Alférez Portinari" and the bridge over Arroyo Arenal, 21 January 1963, *O. Boelcke 10163* (BAA-00008192).

4. ***Lepidium santacruzense*** Al-Shehbaz. This species was previously known only from the type collection (Al-Shehbaz, 2010) that was made from Santa Cruz Province in 1963. The following collection is the second for the species and the first record for Chubut Province.

Argentina. Chubut, Florentino Ameghino Department, Punta Tombo, 19 September 1970, *J. Daciuk XIII-11* (BAA [00008190]).

We are grateful to the directors and curators of the herbaria cited.

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TYPIFICATIONS

1. *Coronopus leptocarpus* Boelcke. This taxon was described by Boelcke (1975) from his Chilean collection, *Boelcke 7309,* and he indicated that its holotype and isotype are deposited at SI and BAA, respectively. The holotype was not found by two of the authors (DJS and IAS) or by the curatorial staff of SI, so we conclude that it has been lost. However, there are two isotypes at BAA (BAA [00007661] and BAA [00007662]), and, as per Article 9.3 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018), we designate the former BAA isotype as the lectotype. It is the most complete specimen of the two and has a handwritten annotation by Boelcke.

Coronopus leptocarpus Boelcke. Type: Chile, Biobío, Arauco Province, Playa Laraquete, 11 November 1955, *O. Boelcke 7309* (Lectotype: [designated here]: BAA [00007661]; Isolectotype: BAA [00007662]).

2. *Coronopus leptocarpus* var. ***microcarpus*** Boelcke. Boelcke (1975) described this variety from a unicate, *Barros 2722,* and the holotype is SI [094831].

The following specimen is an isotype that was not previously recorded.

Chile, Maule, Curicó Province, Vichuquén, Llico, 20 October 1938, *E. Barros 2722* (BAA [00007665]).

3. *Lepidium abrotanifolium* Turcz. var. ***steinmannii*** Thell. This taxon was lectotypifid by Al-Shehbaz (2010) from a unicate. The following specimen is an isosyntype that was not previously recorded.

Bolivia. Tarija, Cercado Province, Tarija, *K. Fiebrig 2772* (BAA [00004778]).

4. *Lepidium boelckeanum* Prina. This species was described by Prina (1993) from the collection *Troiani & Prina 8193,* and he indicated that its holotype and isotype are deposited at SRFA and BACP, respectively. The BACP collections were dismantled in 2004, and almost all of the Brassicaceae holdings were moved to BA and BAA (see Thiers, continuously updated). A recent search by the first author resulted in locating the isotype at BA, so the following adjustments should be made.

Lepidium boelckeanum Prina. Type: Argentina. La Pampa, Chapaleufú Department, between Bernardo Larroudé and Río Quinto, *H. O. Troiani & A. Prina 8193* (Holotype: SRFA; Isotype: BA [93599]).

5. *Lepidium inclusum* O.E. Schulz. This is a synonym of the earlier published *L. pseudodidymum* Thell. The former name was previously known only from the holotype. Below is the first report of isotypes.

Argentina. Tierra del Fuego, Río Grande Department, Río Grande, *A. Castellanos s.n.* (Isotypes: BA [7757], BAA [00001162], BAA [00004228]).

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REPORT ON THE BOTANICAL NOMENCLATURE COURSE ORGANIZED BY ST. XAVIER'S COLLEGE AT MUMBAI, INDIA

Rajendra D. Shinde,[1] Alok Gude,[1] and Kanchi N. Gandhi[2,3]

The St. Xavier College (SXC), Mumbai, held its Botanical Nomenclature Course in February 2023. The course drew about 50 participants from across the State of Maharashtra. Rajendra Shinde, Principal (also known as administrative head) of the college and Director, Blatter Herbarium (BLAT), was the Convener; and Alok Gude, Associate Professor and Head of the Department of Botany, served as the Coordinator and Facilitator. Participants were provided in advance with information on the latest International Code of Nomenclature for algae, fungi, and plants ("the Shenzhen Code") (Turland et al., 2018). Gandhi served as the instructor. He reviewed the physical structure of the Code: ranks, and names of taxa (Articles 1–5 and 16–28 of the Shenzhen Code); 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 (Articles 51–59); and orthography (Articles 60–62).

COMMON NAMES VS. BOTANICAL NAMES

Gandhi began the course with his remark that, although the saying "a rose by any other name would smell as sweet," from William Shakespeare's play, *Romeo and Juliet*, is well known, such an expression might not be universally applicable to all biological names. In this regard, Gandhi observed that in ancient and medieval Greek and Latin, fleshy edible fruits of different taxa imported from other countries had "apple" (pome) or "melon" (derived from *Malos* (Greek) or *Malus* (Latin) as part of their names; e.g., Chinese apple (*Citrus ×aurantium* L. var. *sinensis* L.), custard apple (*Annona squamosa* L.), Indian apple (*Ziziphus jujuba* Mill.), Persian apple (peach, *Prunus persica* (L.) Batsch), pineapple (*Ananas comosus* (L.) Merr.), poisonous apple (tomato, *Solanum lycopersicum* L., also known as, *Lycopersicon esculentum* Mill.), rage or raging apple (mad apple or eggplant, "*Solanum* ***pomi****ferum fructu oblongo*" (Bauhin 1623: 167); *Solanum* "***Melon****gena*" L.; cf., genus name "***Melon****gena* Tourn." (Tournefort 1700: 151), seedy apple (pomegranate, *Punica granatum* L.), thornapple (*Datura Stramonium* L.), and watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai).

COMPOUND NAME FORMATION

Gandhi instructed the participants on how to make compound words or names and how to derive family names from relevant generic names. The first thing to do is find the genitive form of the first term from which its stem can be deduced and used in name formation. If the second term starts with a consonant, a connecting vowel ("o" for Greek words and "i" for Latin words) is needed between the stem of the first word and the whole of the second word. The plural adjectival suffixes, *-aceae*, *-eae*, and *-inaei,* are added to stems of generic names to make family, tribe, and subtribe names, respectively; e.g., *Anacardium* (nominative), *Anacardii* (genitive), *Anacardi* (stem) + *aceae* = Anacardiaceae; *Myrtus* (nominative), *Myrti* (genitive), *Myrt-* (stem) + *aceae* = Myrtaceae; *Rosa* (nominative), *Rosae* (genitive), *Ros-* (stem) + *aceae* = Rosaceae.

For generic names with an "*-is*" ending, the genitive suffix may be *-is* itself; e.g., *Batis* (nominative and genitive) with *Bat-* as the stem, and *Vitis* (nominative and genitive) with *Vit-* as the stem, resulting in the family names Bataceae and Vitaceae, respectively. In contrast, the *-idis*/*itis* genitive suffix applies to some "*-is*" ending names; e.g., *Amaryllis* (*Amaryllidis*, *Amaryllid-* (stem), Amaryllidaceae), *Orchis* (*Orchidis*, *Orchid-* (stem), Orchidaceae), *Oxalis* (*Oxalidis*, *Oxalid-* (stem), Oxalidaceae), *Pteris* (*Pteridis*, *Pterid-* (stem), Pteridaceae, Pteridophyta), *Xyris* (*Xyridis*, *Xyrid-*, Xyridaceae); *Hydrocharis* (*Hydrocharitis*, *Hydrocharit-* (stem), Hydrocharitaceae). For those with an "*-o*" ending, the genitive suffix may be "*-inis*"; e.g., *Borago* (*Boraginis*, *Boragin–* (stem), Boraginaceae), *Plumbago* (*Plumbaginis*, *Plumbagin–* (stem), Plumbaginaceae).

Generic names of Greek origin with endings "*-as*" and "*-ma*" were also mentioned; e.g., *Asclepias* (*Asclepiadis* (genitive), *Asclepiad-* (stem), Asclepiadaceae; and *Cycas* (*Cycadis* (genitive), *Cycad-* (stem), Cycadaceae). The ending, "*-ma*," may denote either feminine or neuter gender; e.g., *Alisma* (neuter; *Alismatis* (genitive), *Alismat-* (stem), Alismataceae), *Sperma* (neuter; *Spermatis* (genitive), *Spermat-* (stem), Spermatophyta); *Hedeoma* (feminine; *Hedeomae* (genitive), *Hedeom-* (stem), Hedeominae (name of subtribe).

We thank Anthony R. Brach (A, GH) for helpful suggestions on the text. We also thank Vijaya Lobo (BLAT), Rajdeo Singh (BLAT), and Praveen Kale (BLAT) for their assistance in organizing the course. Gandhi thanks Suchandra Dutta (RDNCP) and Manek K. Mistry (Retired; BLAT) for their gracious hospitality given to him during the course.

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Gandhi added that whether the origin is Greek or Latin, and despite several scholarly publications, determining the genitive form of some generic names ending with *-is* continues to be a daunting task for many botanists, since the genitive form ending may be *-is* itself (i.e., the nominative and genitive forms look alike) or *-idis* or *-inis*. He illustrated this problem with a few examples provided below.

Cannabis L.

In the past, the family name of *Cannabis* was variously spelled Cannabaceae, Cannabiaceae, Cannabidaceae, Cannabinaceae, and Cannabisaceae. Accordingly, the genitive form of the genus name varied. 1) Cannabaceae (widely used): *Cannabis* (genitive), *Cannab-* (stem); 2) Cannabiaceae (Punja et al., 2023): *Cannabii* (genitive), *Cannabi-* (stem)), but this usage is not justifiable; 3) Cannabidaceae (Zabinkova (1968: 26): *Cannabidis* (genitive), *Cannabid-* (stem); 4) Cannabinaceae (Lindley 1846: 265; Lawrence 1951: 463): *Cannabinis* (genitive), *Cannabin-* (stem); and 5) Cannabisaceae (De Candolle (1869: 28 (in synonymy)): *Cannabis* as indeclinable, but no evidence exists for such a concept.

Bullock's proposal (1958: 160) to conserve the family name "Cannabiaceae Endl." was accepted, but what was conserved was Cannabaceae (vide Montreal Code; Lanjouw & al., 1961: 189).

Capparis L.

In the past, the genitive form of *Capparis* was in dispute; i.e., whether it is *Capparidis* with *Capparid-* as stem, or *Capparis* with *Cappar-* as stem. Several authors chose to accept *Capparidis* and spelled the family name as "Capparidaceae"; e.g., Orr (1921: 259), Pax and Hoffmann (1936: 146), Raghavan (1937: 43), Stoudt (1941: 664), and Lawrence (1951: 518). Lanjouw and Sprague (1935: 81) proposed to conserve the family name *Capparidaceae*, and their proposal was listed in Appendix V of the Stockholm Code (Lanjouw et al., 1952: 66). The name was subsequently conserved as *Capparaceae* (vide Montreal Code; Lanjouw & al., 1961: 190). Crosswhite and Iltis's (1966: 205-211) proposal to "correct" *Capparaceae* to *Capparidaceae* was not accepted (Stafleu & al. 1972: 225).

Genders of Generic Names and Intraspecific Names in Flora of British India

In the Flora of British India, genders of generic names and intraspecific names are not consistent with present day standards. For example, Clarke (in Hooker, 1884: 429–477) treated the genus *Strobilanthes* and included 154 species. In this treatment, almost all species names have the masculine ending, -us, as in *S. acuminatus*, *S. heyneanus*, *S. rhamnifolius*, *S. viscosus*, etc. However, as per the Shenzhen Code Art. 62.4, all *-anthes* ending names are feminine.

Clarke (in Hooker, 1884: 345–355) also treated *Didymocarpus* and included 40 species, almost all with the feminine ending, -a, as in *D. aromatica*, *D. oblonga*, *D. pedicellata*, *D. villosa*, etc. As per Art. 62.2, all generic names ending in *-carpus*/*carpos* are masculine.

Hooker, in publications from 1874 to 1885, also "erred" in assigning feminine gender to his adjectival infraspecific names in neuter or masculine gendered genus names; e.g., *Biophytum sensitivum* var. *nervifolia* (Hooker, 1874: 437), *Hieracium umbellatum* var. *lanceolata* (Hooker, 1881: 400), *Ocimum sanctum* var. *hirsuta* (Hooker, 1885a: 609), *Polygonum lapathifolium* var. *laxa* (Hooker, 1885b: 35), and *Rubus niveus* var. *microcarpa* (Hooker, 1876: 335). In his treatment of *Exacum*, Clarke (in Hooker, 1883: 95–99), published *E. axillare* var. *pentamera*, *E. courtallense* var. *travancorica*, *E. tetragonum* var. *stylosa*, and *E. zeylanicum* var. *macrantha*.

Peter Raven (MO, pers. comm. to KNG) remarked that in the past, regardless of the gender of a genus name, it was a convention practiced by some botanists to assign feminine gender to infraspecific names with adjectival epithets.

Nomenclature Stability and Revision of Conserved Names

Gandhi noted that as per the Code, Art. 14.12, "The lists of conserved names will remain permanently open for additions and changes …". He gave one example pertaining to a conserved genus name listed in two botanical codes.
Berlin Code (Greuter et al., 1988: 214, 217).

Pongamia Ventenat, Jard. Malm. t. 28. 1803 (*nom. cons.*).
Typus: *P. glabra* Vent., nom. illegit. (*P. pinnata* (L.) Pierre, *Cytisus pinnatus* L.)
[conserved over *Pongam* Adanson, Fam. Pl. 2: 322, 593. 1763, *nom. rej.*; Typus: *Dalbergia arborea* Willdenow].

Millettia Wight et Arnott, Prodr. 263. 1834 (*nom. cons.*).
Typus: *M. Rubiginosa* Wight et Arnott
[conserved over *Pongam* Adanson (1763) and *Pongamia* Ventenat (1803)]

Gandhi noted that, unless specifically conserved, a conserved name does not have priority over an earlier legitimate name, and that, regardless of priority, a conserved name may be conserved over another conserved name. For example, the conserved genus name *Millettia* (1834) was conserved over the conserved genus name *Pongamia* (1803). Gandhi added that, in the past, some works treated the conserved genus name *Pongamia* (1803) as a heterotypic synonym of *Derris* Loureiro (1790), nom. cons. However, in the next Code (i.e., Tokyo Code), what was previously listed as "*Pongam* Adans." (type: *D. arborea*)" was revised to "*Pongamia* Adans., nom. cons." (type: *Cytisus pinnatus*). Although it was a conserved name, *Pongamia* remained a rejected name vs. *Millettia* Wight & Arn. 1834 (*nom. cons.*), as shown below.

Tokyo Code (Greuter & al. 1994: 244, 246).

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

Millettia Wight & Arn., Prodr. Fl. Ind. Orient: 263. 14 Aug 1834, *nom. cons*. Typus: *M. rubiginosa* Wight & Arnott [conserved over *Pongamia* Adans. (1763)]

Gandhi explained that prior to the Tokyo Code, one could have treated the conserved genus name, "*Pongamia* Vent. (1803)," as a heterotypic synonym of the conserved genus name *Derris* Loureiro (dated 1790), but from the Tokyo Code, *Pongamia* (dated 1763) has priority over *Derris*. In the event of their merging, *Derris* would become a heterotypic synonym, because it is not specifically conserved over *Pongamia*.

TYPE CITATION

As per Art. 8.1 (Turland et al., 2018), the type "(holotype, lectotype, or neotype) of a name of a species or infraspecific taxon is either a single specimen conserved in one herbarium or other collection or institution …". The type specimen "… may be mounted as more than one preparation ..." (vide Art. 8.3). For the validity of post-1957 names of species and infraspecies, the type of the name must be indicated by reference to an entire gathering, or a part thereof (vide Arts. 40.1, 40.2), and from 1990, the indication of the type must include one of the words "typus" or "holotypus," or its abbreviation, or its equivalent in a modern language. Also, the single herbarium, collection, or institution in which the type is conserved must be specified (vide Arts. 40.6, 40.7).

With regard to the above, Gandhi told participants that in a few cases, the protologues may seemingly satisfy the above requirements for valid publications, but the relevant herbaria might not have a single specimen as the holotype, as given in the Code Example shown below.

> "Art. 40 Ex. 3. Radcliffe-Smith (in Gen. Croton. Madag. Comoro: 169. 2016) indicated the type of *Croton nitidulus* var. *acuminatus* Radcl.-Sm. as "Cours 4871 (holotypus P)". In the herbarium P, there are four duplicates of Cours 4871. The name is validly published because a single gathering in a single herbarium was indicated as type. These specimens are syntypes, and one of them was subsequently designated as the lectotype by Berry & al. (in Phytokeys 90: 69. 2017)."

Gandhi remarked that the above protologue did not meet the requirements of Arts. 8.1, 40.6 and 40.7, and that the situation might be addressed in the next Congress. For type citation, listing a single gathering and/or name of a single herbarium is not necessarily an indication of the citation of a holotype. Concrete wording is needed within the protologue, and, in this regard, he provided one example from Art. 9.

> "Ex. 1. When Tuckerman established *Opegrapha oulocheila* Tuck. (Lich. Calif.: 32. 1866) he referred to 'the single specimen, from Schweinitz's herbarium (Herb. Acad. Sci. Philad.) before me'. Even though the term "type" or its equivalent was not used in the protologue, that specimen (in PH) was clearly the one specimen used by the author and is therefore the holotype."

AUTHORSHIP CITATION

For a new taxon, whoever provides the name and description/diagnosis, and accepts the proposed name, is the author of the taxon's name. It was mandatory that the relevant description/diagnosis was in Latin for the validity of names proposed between 1935 and 2011. For a post-1957 name, besides the provision of description/diagnosis, type citation from a single gathering is mandatory for validation of the proposed name. In this regard, for the validity of a name and its authorship citation, the importance of the description over the type citation is explained from Art. 46.

> "*Ex. 23. 'Pancheria humboldtiana'* was published by Guillaumin (in Mém. Mus. Natl. Hist. Nat., Ser. B, Bot. 15: 47. 1964), but not validly so because no type was indicated. Valid publication was effected by Hopkins & Bradford (in Adansonia 31: 119. 2009), who designated "*Baumann-Bodenheim 15515* (P! P00143076)" as the holotype, ascribed the name to Guillaumin, and by citing "*Pancheria humboldtiana* Guillaumin, *Mémoires du Muséum national d'Histoire naturelle,* sér. B, botanique 15: 47 (1964), nom. inval.," provided a full and direct reference to a validating description that is unequivocally associated with Guillaumin. Art. 46.10 notwithstanding, the name is therefore attributed to Guillaumin, not 'Guillaumin ex H. C. Hopkins & J. Bradford' as given by Hopkins & Bradford."

Gandhi emphasized that, although both description and type citation are required for the validity of a post-1957 name, the provision of a description is primary, and, for this reason, Guillaumin is the author of the name validly published in 2009.

FIGURE 1. **A**, Class group picture; **B**, Kanchi N. Gandhi and Rajendra D. Shinde interacting with the course participants during a question and answer session.

HOMONYMY

Homonyms, regardless of their priority, are valid names, have types, and may be legitimate or illegitimate. Later homonyms are illegitimate, when published, and can become legitimate by conservation. Gandhi added that homonyms of equal priority are legitimate and illustrated the concept with the following example.

> "Art. 53.5. When two or more legitimate homonyms have equal priority (see Note 1), the first of them that is adopted in an effectively published text (Art. 29–31) by an author who simultaneously rejects the other(s) is treated as having priority. Likewise, if an author in an effectively published text replaces with other names all but one of these homonyms, the homonym for the taxon that is not renamed is treated as having priority (see also Rec. F.5A.2).
>
> *Ex. 19*. Linnaeus simultaneously published "10." *Mimosa cinerea* (Sp. Pl.: 517. 1753) and "25." *M. cinerea* (Sp. Pl.: 520. 1753). In 1759 (Syst. Nat., ed. 10: 1311), he renamed species 10 as *M. cineraria* L. and retained the name *M. cinerea* for species 25, so that the latter is treated as having priority over its homonym."

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A NEW SPECIES OF *BULBOPHYLLUM* (ORCHIDACEAE) FROM THE ANDEAN REGION OF COLOMBIA

Mario Alexei Sierra-Ariza,[1,4] Jose Armando Alvarez diaz,[2] and Juan Sebastián Moreno[1,3]

Abstract. A new species of *Bulbophyllum*, section *Xiphyzusa*, found in the Andean region of Colombia, in the department of Huila, is described and illustrated. The species is discussed in relation to its morphologically similar and closest relatives. Information on its distribution, ecology, and habitat is provided.

Keywords: Huila, section Xiphyzusa, systematics, taxonomy

Resumen. Se describe e ilustran una nueva especie para el género *Bulbophyllum* sección *Xiphyzusa* encontrada en la región andina de Colombia, en el departamento del Huila. La especie se discute con las especies morfológicamente más cercanas y se proporciona información sobre su distribución, ecología y hábitat.

Palabras claves: Huila, sección *Xiphyzusa*, sistematica, taxonomía

Bulbophyllum Thouars (Orchidaceae) is one of the largest genera of angiosperms comprising more than 2200 species of epiphytic, lithophytic, and occasionally terrestrial orchids. These plants are characterized by their unique floral structures, which include a prominent lip and a column that is generally adorned with intricate appendages (Vermeulen et al., 2015). In terms of distribution, *Bulbophyllum* species are found mainly in tropical regions around the world, with the majority located in Southeast Asia, Africa, and South America, with some species present in Australia and the Pacific Islands (Gravendel, 2014, Chase et al., 2015, Naive and Cootes, 2022).

In the Neotropical region, there are around 70 species of *Bulbophyllum*, primarily found in the Andes, the Amazon basin, and the Brazilian Atlantic Forest. Brazil has the highest representation of *Bulbophyllum* with 60 species, most of which are endemic (Smidt et al., 2007, Mancinelli and Smidt, 2012, Santos et al., 2020). In Colombia, only seven species have been reported to date (Ministerio de Ambiente y Desarrollo Sostenible y Universidad Nacional de Colombia, 2015).

The Neotropical section *Xiphizusa* Rchb. f. of *Bulbophyllum* comprises approximately 25 species. Morphologically, it is characterized by having discoid, compressed, aggregated, and small monofoliate pseudobulbs; long inflorescences with a thin rachis and flowers arranged distichously; the lateral sepals fused to form a synsepal in most species; ciliated margins on the petals; a trilobed labellum with erect and occasionally ciliated lateral lobes; a smooth or longitudinally crested disk, which can be thin, slightly thick, or fleshy, sometimes sessile or more commonly constricted in some species; the lamina can be flat or concave, and usually smooth or rarely ciliated on the margin and surface (Borba and Smidt, 2004; Smidt and Borba, 2007)

Here, we describe and illustrate a new species of *Bulbophyllum* in the subsection *Xiphizusa*, found in the department of Huila, Colombia.

Materials and Methods

Field trips were conducted to forest fragments located in the municipality of Tello-Huila between the months of November and December 2022. At the location, a single population of this species was found in its natural habitat. The individuals under study were photographed in detail in order to record each of their morphological characteristics, using a Nikon D5300 camera, accompanied by a NIKKOR AF 105 mm f/2.8 D Macro lens. Additionally, ecological and geographical data of the species were recorded.

The type specimens were prepared by storing vegetative structures on newspaper soaked in 75% ethanol. The floral structures were preserved in a plastic container with glycerol in a concentration of equal parts of glycerin and alcohol. Subsequently, the collected material was dried in an electric oven at 75°C for 14 hours and entered into the collection of the TOLI Herbarium, Dendrology section of the University of Tolima. The floral structures in glycerol were examined under a Motic Series SMZ 168 Led stereoscope and were deposited and entered into the collection. Finally, to confirm the identity of the new species, online revisions of international herbaria, such as AMES (www.huh.harvard.edu) and KEW (apps.kew.org/herbcat/gotoHomePage.do), and national herbaria, such as TOLI, HPUJ, JBB and COL, were carried out (www.biovirtual.unal.edu.co/es/colecciones/search/plants/colecciones/search/plants/).

We thank Biota Consultancy and Environment, especially its directors and professionals in the Flora component, who participated and accompanied field trips during the project when this species was first collected. We also thank the company Atención Social Integral (ASI) for their participation in the process of finding the species. We thank the Research Seedbed in Ethnobiology for their support and motivation to carry out these studies. Finally, we thank the TOLI Herbarium, directed by Professor Hilda Rocío Mosquera Mosquera, who facilitated access to the collection.

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To illustrate the new species, sketches from living and preserved specimens were digitized, and the images were used for diagramming a draft composite template in Adobe Photoshop® CS6. A digital composite line drawing was then made (lines and stippling) in Procreate illustration application for iPad 6th generation tablet computer (Bogarín et al., 2019), and a composite dissection plate Lankester (LCDP) was created using Adobe Photoshop® CS6.

Taxonomic Treatment

Bulbophyllum parex J.Alvarez-Diaz & J.S.Moreno *sp. nov*.
TYPE: COLOMBIA. Huila, municipality of Tello, road to Sierra la cañada, 1070 m, Dec 10 2022. *J. Alvarez-Diaz & B. Tovar 01* (Holotype: TOLI). Fig. 1–2.

Bulbophyllum parex is morphologically closest to *Bulbophyllum bidentatum* (Barb.Rodr.) Cogn., from which it differs in having lanceolate petals with a ciliate margin (*vs*. ovate-lanceolate petals with a lacerate-ciliate margin), the labellum with slightly ciliate lateral lobes (*vs*. to entire

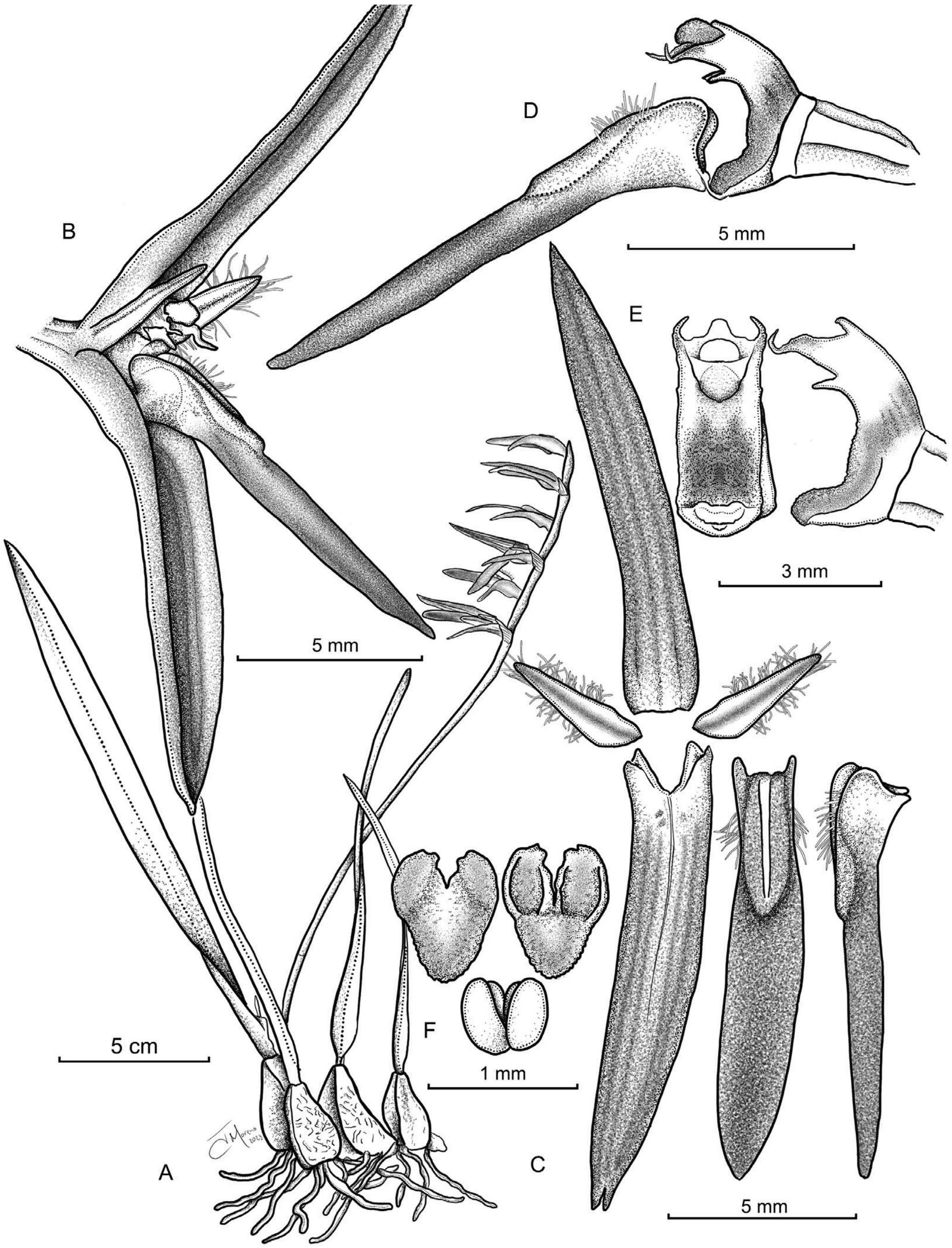

Figure 1. *Bulbophyllum parex* J. Alvarez-Diaz & J.S. Moreno. **A**, Habit; **B**, Flower; **C**, Dissected perianth; **D**, Lip and column lateral view; **E**, Column; **F**, Anther and Pollinia. Illustration by A. J. S. Moreno based on the plant that served as the holotype.

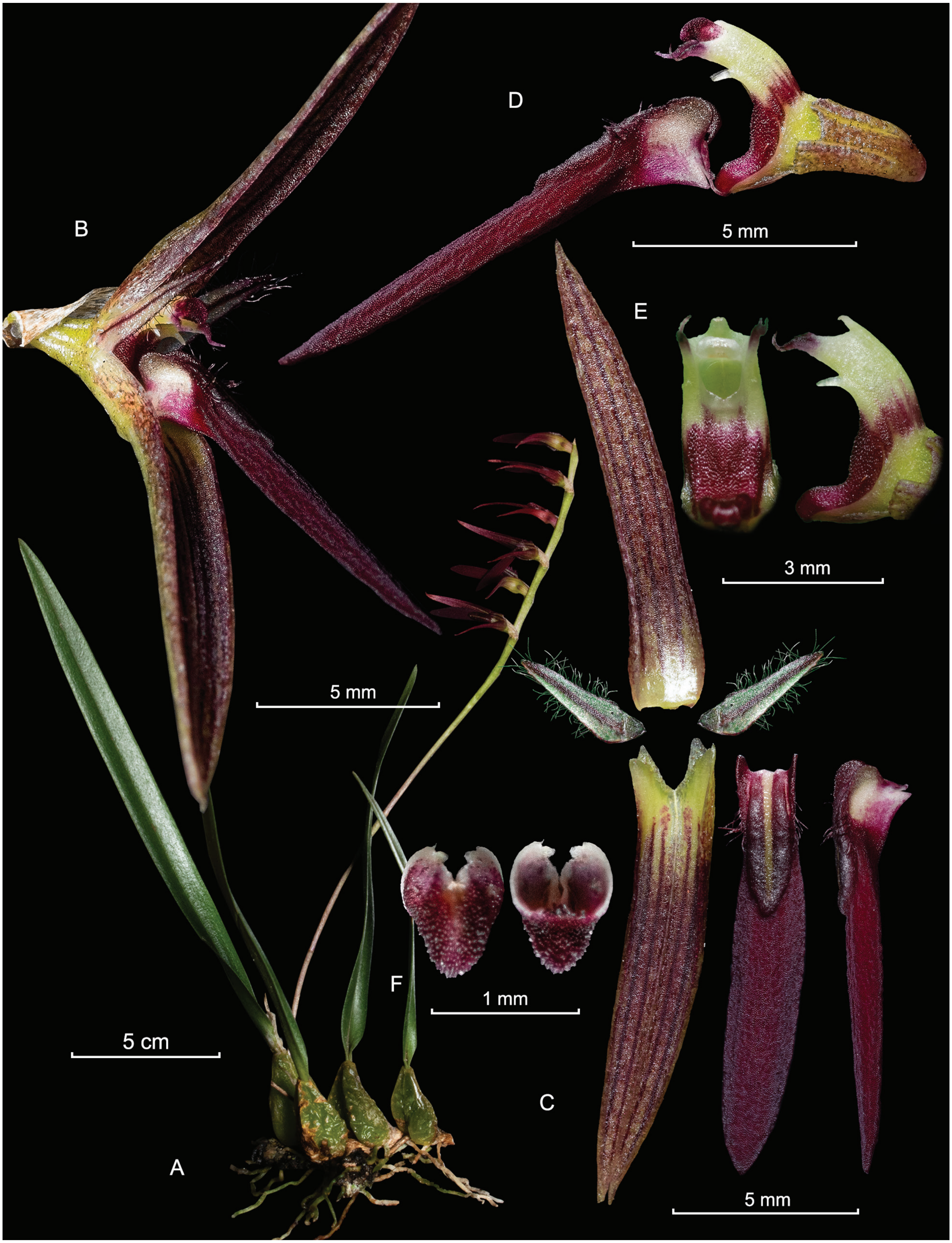

FIGURE 2. *Bulbophyllum parex* J. Alvarez-Diaz & J.S. Moreno. **A**, Habit; **B**, Flower; **C**, Dissected perianth; **D**, Lip and column lateral view; **E**, Column; **F**, Anther. LCDP by M. A. Sierra-Ariza, based on the holotype.

lateral lobes), and the middle lobe oblong-elliptic (vs. linear-ligulate).

Plant epiphytic. *Heteroblastic pseudobulbs* grouped, ovate, rigid, rough, covered by narrow, papery, whitish sheaths, which are lost when the stem matures, unifoliate, 11–16 × 10–12 mm (dry, 10–14 × 8–11 mm). *Leaf* linear-oblong, coriaceous, keeled, with the base conduplicate, acute apex, 5–10.5 × 0.5–0.8 cm. *Inflorescence* a spike, erect to slightly inclined, 12–16 cm long, the rachis not thickened; floral bracts ovate, papery, acute up to 3 mm long. *Flowers* arranged in two columns, intercalated between resupinate and non-resupinate. *Sepals* purple with darker veins, yellowish towards the base, membranous, papillose. *Dorsal sepal* oblong-lanceolate, 3-veined, slightly concave, acute, 14–16 × 2.5–3.0 mm. *Lateral sepals* connate into an oblong-lanceolate synsepal, 7-veined, concave, sagittate at the base, bifid at the apex, 14–16 × 3–4 mm. *Petals* white with purple edges and veins, lanceolate, membranous, ciliate margin, acute, 5–4 × 1.5–2.0 mm. *Lip* dark purple with a white line in the callus, papillose, striated, 10–12 × 2–3 mm, trilobed, small, basal, rounded, oblique side lobes, with slightly ciliate margins, 2–3 mm long, prominent, fleshy, oblong-elliptic mid-lobe, acute, 9–10 mm long; basal callus prominent, fleshy, flat, oblong when viewed from above, 4 × 1.5 mm, sulcate with a central division that extends from the base to near the apex. *Column* white with purple base and apex, slightly curved, semi-terete, flat in the lower part, 4 mm long, with 4 teeth, 2 lateral teeth towards the center, acute, oblique, 2 long apical teeth. Apical stigma, noticeable, rounded. *Anther* purple with white edges, papillose, thickened, ovate, cordate, 1.3 × 1.0 mm. *Pollinia* 2, light yellow, round.

Etymology: The specific epithet, *parex*, is given in gratitude to Parex Resources company, for their financial and logistic support in the process of studying and publishing the new species.

Distribution and ecology: The species was only recorded in a fragment of low secondary vegetation, in a transition from tropical forest to premontane forest, located in the municipality of Tello-Huila, at elevations between 950 and 1150 meters, growing as an epiphyte and lithophyte. As an epiphyte, it was observed inhabiting trees of the genus *Roupala* (Proteaceae) and *Myrsine* (Primulaceae). As a lithophyte, it was growing on large rocks with a high presence of organic matter and lichens (Parmeliaceae) associated with the plant roots (Fig. 3–4).

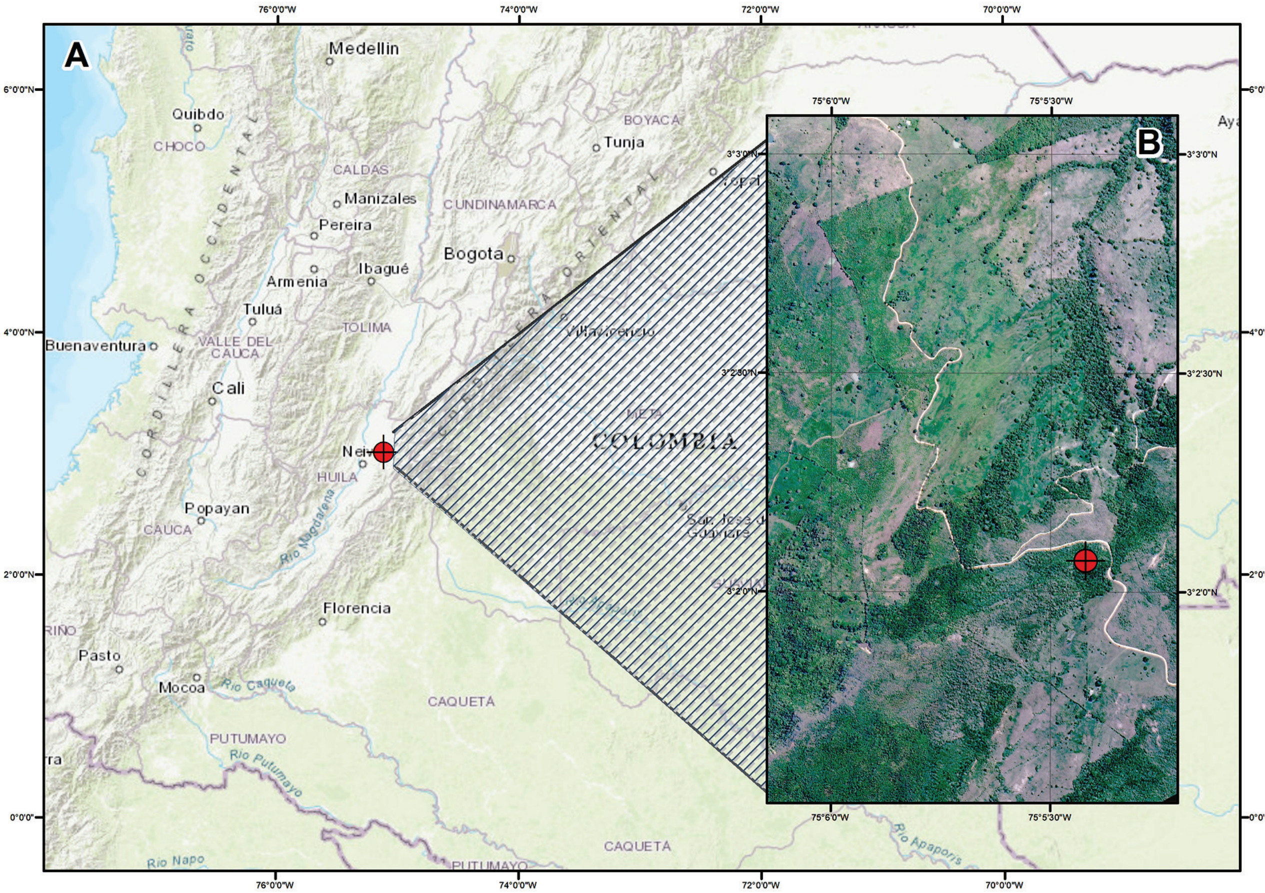

FIGURE 3. Distribution map of *Bulbophyllum parex* J. Alvarez-Diaz & J.S. Moreno. Prepared by J. A. Alvarez-Diaz.

FIGURE 4. In-situ pictures of *Bulbophyllum parex* J. Alvarez-Diaz & J.S. Moreno. **A**, Growing on a rock as a lithophyte; **B**, Growing on a stem as an epiphyte. Prepared by J. A. Alvarez-Diaz.

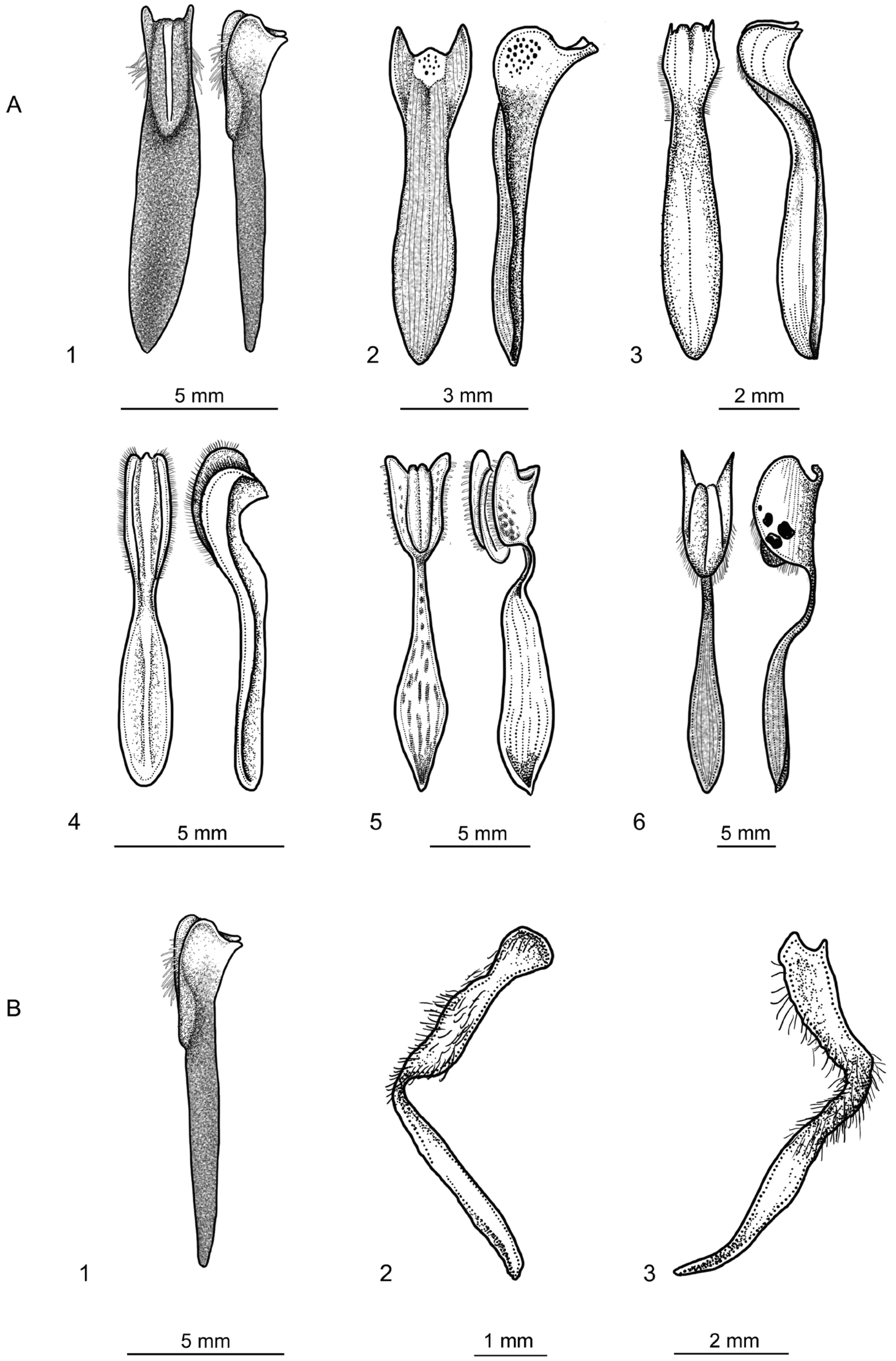

Figure 5. **A**, Adaxial and lateral view of the labellum of species of *Bulbophyllum* from South America. **A1**, *Bulbophyllum parex* J. Alvarez-Diaz & J.S. Moreno; **A2**, *B. bidentatum* (Barb.Rodr.) Cogn.; **A3**, *B. gehrtii* E.C. Smidt & Borba; **A4**, *B. filifolium* Borba & E.C. Smidt.; **A5**, *B. weberbauerianum* Kraenzl.; **A6**, *B. plumosum* (Barb.Rodr.) Cogn. **B**. Lateral view of the labellum of species of *Bulbopyllum* from Colombia. **B1**, *B. parex*; **B2**, *B. antioquiense* Kraenzl.; **B3**, *B. lehmannianum* Kraenzl. Redrawn by A. J. S. Moreno: A1 and B1 based on the Holotype (TOLI); A2 on Cogniaux (1902, t. 1188-II); A3–4 on Borba and Smidt (2004) and Smidt and Borba (2009), respectively; A5 on a drawing by F. Hammer (see Holotype: Ames [00106060]); A6 on Cogniaux (1902: t. 118-I); and B2–3 on drawings by F. Hammer (See Isotype: Ames [00000508] and *Lehmann 7274*, AMES [00000390], respectively).

Conservation status: Data Deficient (DD). *Bulbophyllum parex* is currently only known from the locality where the type specimen was found, where few individuals are observed. Therefore, further field efforts are necessary to assess its current conservation status.

The species morphologically most similar to *Bulbophyllum parex* are *Bulbophyllum bidentatum* (Barb. Rodr.) Cogn., *Bulbophyllum filifolium* Borba & E.C. Smidt, *Bulbophyllum gehrtii* E.C.Smidt & Borba, and *Bulbophyllum plumosum* (Barb.Rodr.) Cogn, which are endemic to Brazil. However, it differs from them by having a lip with slightly ciliated lateral lobes and a fleshy, oblong-elliptic, acute mid-lobe. *Bulbophyllum bidentatum* is distinguished by having a lip with entire lateral lobes, a slightly fleshy mid-lobe, and a linear-ligulate, obtuse apex. *Bulbophyllum filifolium* is characterized by having mid-lobes with the margin densely covered with short cilia, a fleshy, linear-elliptic mid-lobe with an adaxial longitudinal crest, and a rounded apex. *Bulbophyllum gehrtii* has a lip with pubescent lateral lobes in the distal half, a concave, lanceolate central lobe with a constricted base, and an acute apex. *Bulbophyllum plumosum* is characterized by having a lip with glabrous lateral lobes, a slightly fleshy, linear-ligulate mid-lobe with a slightly constricted base and obtuse apex. In Colombia, this new species could be similar to *Bulbophyllum antioquiense* Kraenzl. and *Bulbophyllum lehmannianum* Kraenzl. *B. antioquiense* is distinguished by having a lip with long cilia on the lateral lobes and a linear mid-lobe with cilia at the base. *B. lehmannianum* is distinguished by having a lip with separated cilia on the lateral lobes and a linear-lanceolate median lobe with a pilose base and an acute apex. The new species also resembles *Bulbophyllum weberbauerianum* Kraenzl., but this species only inhabits Bolivia and Peru, and is characterized by having a lip with fimbriated lateral lobes and a median lobe tapered at the base and lanceolate towards the apex (Fig. 5).

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THE REINSTATEMENT OF *PETROGENIA* (CONVOLVULACEAE)

George Staples[1]

Abstract. The reinstatement of the generic name *Petrogenia* is proposed, from synonymy under *Bonamia,* as an accepted genus of Convolvulaceae.

Keywords: Dichondreae, systematics, taxonomy

Austin and Staples (1985) reduced *Petrogenia repens* I.M. Johnst. (Convolvulaceae) to the synonymy of *Bonamia* Thouars, and proposed a new combination for the species, *Bonamia repens* (I.M.Johnst.) Austin & Staples. The morphological and palynological evidence at the time seemed clear and compelling. Subsequently, however, molecular evidence contradicted this placement (Stefanović et al., 2002) and showed that *Petrogenia repens* is part of a clade that was later recognized as tribe Dichondreae (Stefanović et al., 2003).

More intensive molecular sampling across the /Dicranostyloideae clade since that time (Delgado pers. comm.; Moreira, pers. comm.) has corroborated that *Petrogenia* is a distinct, monospecific genus that is the sister group to *Dichondra* J.R.Forst. & G.Forst. plus *Falkia* L.f.

I take this opportunity, then, to formally reinstate the genus *Petrogenia*, restoring the original binomial, *Petrogenia repens*.

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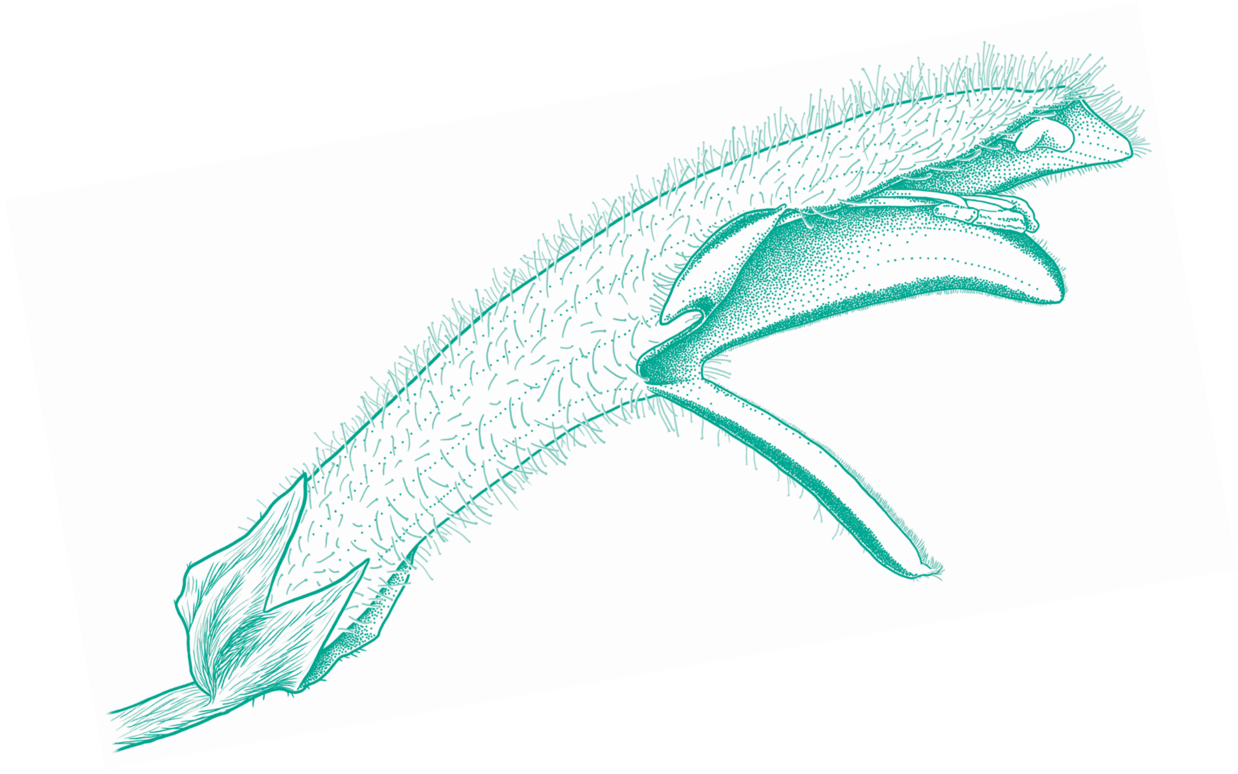

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