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A Publication of the Harvard University Herbaria Including
The Journal of the Arnold Arboretum

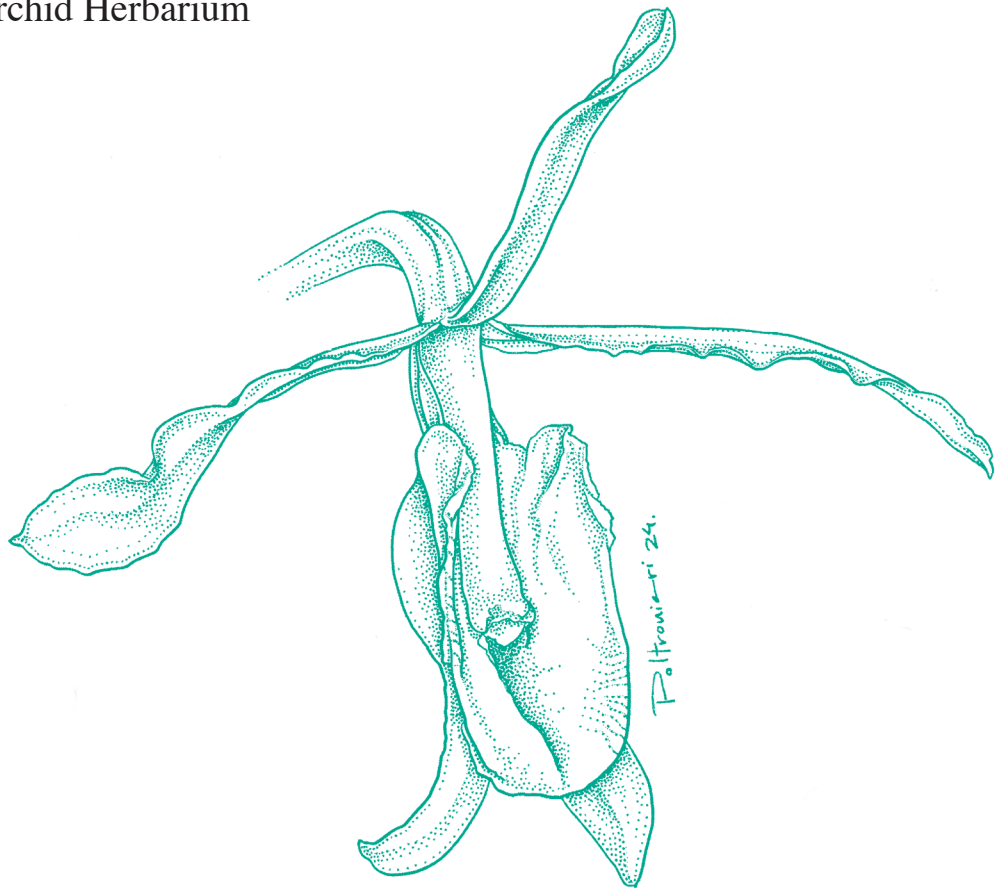
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EDITORIAL ANNOUNCEMENT

My tenure as editor of *Harvard Papers in Botany* ends with this issue (volume 29, number 2).

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Gustavo A. Romero

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NOTES ON THE CARIBBEAN, MEXICAN, AND CENTRAL AND SOUTH AMERICAN *CARDAMINE* (CARDAMINEAE, BRASSICACEAE)

IHSAN A. AL-SHEHBAZ^{1,4} AND KAROL MARHOLD^{2,3}

Abstract. The present study deals with the native *Cardamine* species of the New World south of the United States, because previous studies failed to clarify their distribution, delimitation, and endemism. The status of 12 species (*C. carrii*, *C. cebollana*, *C. chilensis*, *C. hispidula*, *C. killipii*, *C. marginata*, *C. nana*, *C. obliqua*, *C. pacensis*, *C. pygmaea*, *C. speciosa*, and *C. subterranea*) is discussed. The new name *C. hintonii* and the new combination *Rorippa pygmaea* are proposed. Three species (*C. aschersoniana*, *C. nana*, and *C. obliqua*) are lectotypified, and *C. carrii*, *C. cebollana*, *C. chilensis*, and *Rorippa austroamericana* are reduced to synonymy of *C. macrocarpa*, *C. longipedicellata*, *C. africana*, and *R. pygmaea*, respectively. Mexico has eleven native species (three endemic), Central America has eight (three endemic), and the Caribbean Islands have three (two endemic). A key to the South American species and another to the Mexican, Central American, and Caribbean species are presented.

Keywords: Brassicaceae, *Cardamine*, Caribbean Islands, Central America, Cruciferae, Mexico, South America.

Cardamine L., the second largest genus in the Brassicaceae (Cruciferae) with about 280 species (Šlenker et al., 2021; Marhold et al., 2022) and updated here to 284, is represented by native species on all continents except mainland Antarctica. It includes a number of weedy species, including *C. africana* L., *C. flexuosa* With., *C. hirsuta* L., *C. impatiens* L., *C. occulta* Hornem., and *C. parviflora* L.

In order to determine the number of native species per continent or region, we checked all *Cardamine* names, regardless of their rank, in worldwide databases, including CardaBase (<https://cardamine.sav.sk>), BrassiBase (<https://brassibase.cos.uni-heidelberg.de>), and IPNI (International Plant Name Index: <https://ipni.org>). Our compilation indicates that Africa has the fewest native species (six, or perhaps seven), of which four are endemic, whereas Australia has 13 native species (11 endemic), and New

Zealand has 42 spp., all of which, except a pair that also grows in Australia, are endemic (Heenan, 2017; Heenan and de Lange, 2018). The majority of species, herein compiled, are Eurasian (153), of which 61 (39.8%) are native to Europe and 54 (ca. 28.3%) to China (32 endemic). North America north of Mexico has 37 native species, all of which grow in the United States (14 endemic), Canada (20), and three in Greenland (Al-Shehbaz et al., 2010).

The present study deals with the New World *Cardamine* species from the US-Mexico border southward through the southernmost tip of Patagonia in South America, an area covering a distance of over 9200 air miles (ca. 14,806 km). It aims to resolve the status of several controversial binomials that have been either recognized as distinct species or overlooked in some or all the databases listed above.

SOUTH AMERICAN SPECIES

The native South American species of *Cardamine*, estimated by Al-Shehbaz & Marhold (2023) to be 23 species, are updated to 24 by the recognition of Venezuelan *C. aschersoniana* O.E. Schulz. *Cardamine albertii* O.E. Schulz is not recognized here and has been treated by Al-Shehbaz (2024) as only a trivial variant of the widespread *C. ovata* Benth. The country distribution of all species is presented in Table 1. Chile has 15 species, of which five are endemic, and *C. bonariensis* Pers. is the only species that grows in all countries excluding French Guyana, Guyana, and Suriname that have no native species. This species is by far the most variable in the New World, especially in habit, leaf morphology, and the bracteate part of the raceme.

Although the following species names are based on South American plants, they were recognized, synonymized, overlooked, or remained in obscurity for more than a century (see the three databases above).

1. *Cardamine aschersoniana* O.E. Schulz, Bot. Jahrb. Syst. 32 : 410. 1903. TYPE: VENEZUELA. Tovar, May 1836, J. W. K. Moritz 369 (Lectotype, here designated; B [0-0386988]).

Schulz (1903) cited four syntypes under *Cardamine aschersoniana*. Fendler 23 β (GH) was cited under this species, whereas Fendler 23 was cited as the single type collection of *C. fulcrata* var. *scabra* O.E. Schulz. However, plants of both collections are indistinguishable, and they

We are grateful to curators of the herbaria cited. We thank Gustavo Romero and anonymous reviewers for their comments on the manuscript. This work was partially funded by the Slovak Research and Development Agency (APVV; Grant No. APVV-21-0044). We are grateful to Anthony R. Brach (GH), Carol Kelloff (US), Emily Sessa and Amy Weiss (NY), and Weston Testo (VT) for information about any duplicates of the collection Pringle 5327 in the databases and holdings in their herbaria. We are equally grateful to Barbara Hellenthal (NDG) for sending the image of the holotype of *Cardamine fulcrata*, as well as to Nicholas Fumeaux (G) for locating the Caribbean specimens of *Cardamine*. We also thank Carla Maldonado (LPB) and Mats Wedin (S) for their opinion on the type material of *C. pacensis* and *C. pygmaea*, respectively. We are much indebted to Diego L. Salariato (SI) and Mary Stiffler (MO) for providing literature.

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TABLE 1. Country distribution of the native South American species of *Cardamine*. An asterisk (*) indicates presence, and E means endemic to that country. Country abbreviations are: ARG: Argentina; BOL: Bolivia; BRA: Brazil; CHL: Chile; COL: Colombia; ECU: Ecuador; PRY: Paraguay; PER: Peru; URY: Uruguay; and VEN: Venezuela.

SPECIES	ARG	BOL	BRA	CHL	COL	ECU	PRY	PER	URY	VEN
<i>C. armoracioides</i> Turcz.					*					*
<i>C. aschersoniana</i> O.E.Schulz										E
<i>C. bonariensis</i> Pers.	*	*	*	*	*	*	*	*	*	*
<i>C. chenopodiifolia</i> Pers.	*	*	*	*			*		*	
<i>C. cordata</i> Barnéoud	*			*						
<i>C. fulcrata</i> Greene					*					*
<i>C. geraniifolia</i> (Poir.) DC.	*			*						
<i>C. glacialis</i> (G.Forst.) DC.	*			*						
<i>C. hispidula</i> Phil.				E						
<i>C. jamesonii</i> Hook.					*	*				*
<i>C. kruesselii</i> Johow				E						
<i>C. lojanensis</i> Al-Shehbaz						E				
<i>C. marginata</i> Phil.				E						
<i>C. nana</i> Barnéoud	*			*						
<i>C. ovata</i> Benth.		*			*	*		*		*
<i>C. peruviana</i> Al-Shehbaz & Marhold								E		
<i>C. picta</i> Hook.					*	*				
<i>C. rostrata</i> Griseb.				E						
<i>C. speciosa</i> Britton		E								
<i>C. tenuirostris</i> Hook. & Arn.	*			*						
<i>C. tuberosa</i> DC.				E						
<i>C. variabilis</i> Phil.	*			*						
<i>C. volkmannii</i> Phil.	*			*						
<i>C. vulgaris</i> Phil.	*			*						

are clearly synonyms of *C. fulcrata* Greene. *Cardamine aschersoniana* is easily distinguished from the latter by having long-acuminate (vs. acute) leaflets.

2. *Cardamine chilensis* DC., Syst. Nat. 2: 254. 1821. TYPE: CHILE. "Dubia tetradyname siliquosa. Ruiz et Pavón! in Lamb." (Holotype: BM [000583653]).

The examination of the holotype of *Cardamine chilensis* was quite a surprise because it is indistinguishable from, and herein synonymized with, the earlier-published *C. africana*. Unless the type locality of the former was from a different country, Candolle (1821) is the only record to date of *C.*

africana from Chile. We have examined collections of the latter from Argentina, Bolivia, Brazil, Colombia, Ecuador, Peru, and Venezuela, but none from Chile. Therefore, all other reports of *C. chilensis* from Argentina and Chile in the past two centuries represent a different species recognized below as *C. nana*.

3. *Cardamine hispidula* Phil., Anales Univ. Chile 81: 79. 1892; *Cardamine alsophila* var. *hispidula* (Phil.) Reiche, Anales Univ. Chile 90: 99. 1895. TYPE: CHILE. [Region XVI] Andes of Prov. Ñuble, October 1878, *F. Puga s.n.* (Holotype, not seen).

Schulz (1903) justifiably recognized *Cardamine hispidula* (pp. 452, 453) and examined and indicated that its type is housed at the Museo Nacional in Santiago Chile (cited as H.Ch., presently SGO). However, a search for its type by one of us (IAS) and the curatorial staff of SGO, where the herbarium of Rodolfo Amando Philippi (1804–1904) is housed, did not yield any results (see Al-Shehbaz et al., 2011), and we assume that it is lost.

Except for the following description, hardly anything else is known about *Cardamine hispidula*, a well-defined species easily distinguished from the other South American species by the key below.

Herbs, perennial. *Rhizomes* globose-tuberous, stolon filiform, tuberous at apex. *Stems* 2–15 cm tall, erect, simple or branched at base, flexuous, slender, subangular, sparsely hirsute to glabrescent. *Rhizomal leaves* rosulate, 1.2–3.0 cm long, petiolate, 3-foliolate; terminal leaflet orbicular, base subcordate, obscurely crenate or 6-angled, long petiolulate, 3.5–8.0 × 2.5–8.0 mm; lateral leaflets ovate, entire, short petiolulate; cauline leaves 0.8–2.5 cm long, lower ones 3–5-foliolate; terminal leaflet ovate, strongly 1- or 2-crenate, short petiolulate, 2.5–8.0 × 1.5–6.0 mm; lateral leaflets similar but sessile; upper leaves short petiolate, 3-foliolate, leaflets 1-toothed; uppermost leaves subsessile, simple, lanceolate, entire or 1-toothed; hirsute to long ciliate. *Racemes* ebracteate, ca. 10-flowered, flowers small, ca. 3 mm long. Ovary 20–28 ovuled. Fruit ca. 1.8 cm × 0.7 mm.

4. *Cardamine killipii* O.E. Schulz, Notizbl. Bot. Gart. Berlin-Dahlem 10: 341. 1928. TYPE: COLOMBIA. Santander, eastern Cordillera, edge of Páramo de las Vegas, 3300–3700 m, 20–21 December 1926, *E. P. Killip & A. C. Smith 15596* (Holotype: B [10-0386986]; Isotypes: F [009295F], GH[00312548], K [000485032], NY [00172742], PH [00000959], S-R [7296], US [00100037]).

With its simple, suborbicular to broadly ovate to subreniform, and entire cauline leaves, the casual observer would believe that *Cardamine killipii* is quite distinct from *C. bonariensis*, the type of which and most of its populations have pinnately compound cauline leaves. However, the latter is extremely variable in leaf morphology, number of lateral leaflets, bracteate portion of the raceme, and habit. The species is adapted to wet habitats (ponds, streams, seepage areas, bogs, moist slopes, wet bluffs, muddy banks, wet paramo, moist turf, gravel, wet grass fields, swales, marshes) and grows at elevations from sea level to 4500 m. Its distribution ranges from Patagonian Argentina and Chile into Central America and Mexico, and as many as 26 species and varieties were described from its entire range. The examination of hundreds of collections from all of the major herbaria of the world clearly demonstrates that all features appearing to be sufficiently distinct are in fact continuous, and it is not possible to maintain any of the variants. A comprehensive molecular phylogenetic study of this complex covering its entire range is much needed and, without that, it is advisable to recognize a single polymorphic species.

5. *Cardamine marginata* Phil., Anales Univ. Chile 27(2): 324. 1865; *C. vulgaris* var. *marginata* (Phil.) O.E. Schulz, Bot. Jahrb. Syst. 32: 545. 1903. TYPE: CHILE. Región VIII, near Chillán, *Manuel Antonio de Solis Obando s.n.* (Lectotype, designated by Al-Shehbaz et al. (2011: 281); SGO [63903]; Isolectotype: SGO [49376]).

Schulz (1903) reduced *Cardamine marginata* to a variety of *C. vulgaris* and examined a single specimen, *Delfin s.n.* (SGO), but this collection definitely belongs to the latter species. *Cardamine marginata* resembles the small-sized forms of *C. vulgaris* by having a tuberous stem base, attenuate styles, and fruit forming a distinct angle with the fruiting pedicels. However, the two species are quite different in flower, infructescence, fruit, and seed morphology. *Cardamine marginata* has smaller flowers (sepals 1.0–1.5 × 0.5–0.7 mm; petals 2.5–3.2 × 0.7–1.0 mm), a flexuous rachis of fruiting racemes, smaller and wider, linear-lanceolate fruit 1.0–1.5(–1.7) cm × 1.8–2.5 mm, fewer ovules (6–10) per ovary, and orbicular to broadly ovate seeds 2.0–2.5 × 1.2–1.5 mm that are winged all around. By contrast, *C. vulgaris* has larger flowers (sepals 2.5–3.5 × 1.0–1.5 mm; petals (5–)6–9 × 2.0–3.5 mm), a straight rachis of fruiting racemes, larger and narrower linear fruits 2.0–3.5(–4.0) cm × 1.0–1.5 mm, more ovules (20–34) per ovary, and ovate, wingless seeds 1.2–1.6 × 0.8–1.2 mm. Unfortunately, *C. marginata* is known thus far only from the type collection and those cited below.

Additional specimens examined: CHILE. Región VII. Ñuble, 2 km E of Chillán on road to El Carmen, 36°37'S, 72°5'W, *Bliss 512* (CONC), *Keeley et al. 25824* (CONC). Región VIII. BíoBío, Antuco, *Barros 2790* (SI). Región IX. Araucanía, Malleco, Mininco, [37°47'S, 72°28'W], *Montero 5254* (CONC, SI), *Montero 9416* (CONC).

6. *Cardamine nana* Barnéoud in Gay, Fl. Chil. 1: 108. 1846; *C. chilensis* var. *nana* (Barnéoud) O.E. Schulz, Bot. Jahrb. Syst. 32: 445. 1903. TYPE: CHILE. [Región XIV. Los Ríos] Valdivia, 1839, *C. Gay s.n.* (Lectotype, here designated; P [00747619]; Isolectotype: P [00747620]).

Schulz (1903), who reduced the species to a variety of *Cardamine chilensis*, was followed by subsequent authors (e.g., Boelcke & Romanczuk, 1984; Al-Shehbaz & Salariato, 2012), but none examined the types of both species. That confusion persisted to the present, and our examination of both types reveals that the type of *C. chilensis* is indistinguishable from plants of *C. africana* (see above). *Cardamine nana* differs substantially from *C. africana* (including *C. chilensis*) by having simple (vs. trifoliolate) cauline leaves, bracteate (vs. ebracteate) racemes with a flexuous (vs. straight) rachis, and a tuberous (vs. non-tuberous) stem base.

A full description of *Cardamine nana* and citation of Chilean plants are provided herein, but for a complete synonymy and cited Argentinean specimens, the reader should consult Al-Shehbaz & Salariato (2012).

Labels of the type collection of *Cardamine nana* were annotated by Barnéoud, and that of the designated lectotype has Valdivia, the type locality cited in the original publication.

Herbs, perennial, often with a thickened, tuber-like stem base, sometimes rooting from the lower nodes, glabrous or with trichomes 0.1–0.2 mm long. Stems (2–)4–30 cm tall, erect, simple or several from the base, simple or branched above, glabrous or pubescent near the base. *Basal leaves* not rosulate, simple or rarely with 1 or 2 lateral leaflets; *cauline leaves* (0.8–)1.4–4.0(–5.5) cm long, petiolate, not auriculate; petiole (0.4–)0.8–3.0(–3.5) cm long; blade (2–)7–15(–25) × (1–)3–8(–12) mm, oblanceolate to spatulate or obovate to ovate, glabrous or sparsely pubescent, usually minutely ciliate, cuneate to attenuate at the base, entire or repand, rounded to obtuse at the apex. *Racemes* several flowered, bracteate throughout or at least along the proximal half; rachis slightly to strongly flexuous, glabrous; fruiting pedicels (2–)4–10(–17) mm long, ascending, slender, straight. *Sepals* oblong, 1.2–1.5(–2.0) mm long, glabrous, caducous; *petals* white, oblanceolate, 2.5–3.5(–4.0) × 0.7–1.0(–1.5) mm, apex obtuse; filaments 1–2 mm long; anthers ovate, 0.1–0.2 mm long; ovules (16–)20–30 per ovary. *Fruit* 0.7–1.5(–2.0) cm × 0.7–0.8(–1.0) mm; style 0.1–0.5(–1.0) mm long. *Seeds* light brown, oblong to ovate, 0.7–0.9 × 0.5–0.6 mm, usually with a distal wing ca. 0.1 mm wide.

The species grows in seepy sites, streamsides, pond margins, sloughs in dry sandy matorral at sea level to 1000 m. It is distributed in Argentina (Chubut, Nuequén, Río Negro, Salta) and Chile (Región V, Santiago, VI, VII, VIII, IX, X).

Additional specimens examined: CHILE. Región V (Valparaíso): Catapilco, *Philippi* 67 (SGO); Las Láunas, *Jaffuel* 3005 (CONC, GH), *Jaffuel* 3114 (CONC, GH); Olmué, *Garaventa* 2024 (CONC, SI); Cerro de La Campana, 27 Sep. 1962, *Weisser* s.n. (CONC); Quilpué, *Zöllner* 4601 (BACP, SI); Marga, *Zöllner* 7103 (CONC, NA), *Jaffuel & Pirion* 3056 (GH); Limache, *Garaventa* 2230 (BACP, CONC, SI); Viña del Mar, 30 August 1932, *Behn* s.n. (CONC); Concón, *Pöppig* 171 (W); El Pangal, *Garaventa* 4090 (BAA, BACP, SI). Región VI (Santiago): Santiago: Batuco, *Garaventa* 2206 (BAA, CONC, SI); Caro, 0.6 km W of RR crossing in Alcones on road to Pichilemu, *Bliss* 547 (CONC); Mine La Leona, Oct. 1935, *Grandjot* s.n. (MO); Lolol, *Barros* 2797 (CONC, SI); Colchagua, Lolol, *Bliss* 754 (CONC); Rancagua, *Bertero* 145 (GH, P); Leona, *Bertero* 146 (G, MO, NY, P, W). Región VII (Maule): Talca, *Claude-Joseph* 4321 (US); SE Linares along Río Ancoa, along road to Melado and Medina, 38.2 km upstream to Peñasco, *Taylor & Gereau* 10997 (CONC, MO); Itahue, Fdo. “El Colorado,” *Garaventa* 4539 (BACP, CONC, SI); N Colbun, *Bliss* 670 (CONC); 10 km E Cauquenes on road to Parral, *Bliss* 538 (CONC). Región VIII (Bíobío): Ñuble, 5 km W San Nicholas, *Bliss* 850 (CONC); La Posada, *Barros* 2804 (CONC, SI); 2 km S Escuadrón on hwy 160, *Lammers, Baeza, & Peñailillo* 7490 (CONC, MO); Vegas de San Vicente, *Junge* 992 (CONC, SI). Región IX (Araucanía): Biobio, Cabrero, 5–8 km N Salto El Laja, *Bliss et al.* 2005 (CONC); Antuco, *Barros* 2803 (SI); Malleco, Mininco, *Montero* 5253 (CONC, SI); 5–6 km SE Minico

on road to Collipulli, *Bliss* 864 (CONC); Araucanía, Nov. 1887, *Philippi* s.n. (SGO); E Pucón, from the Río Turbio along road to Termas de Huife, *Taylor & Taylor* 10870 (MO). Región X (Los Lagos): Valdivia, *Hohenacker* 275 (G, P), *Buchtein* s.n. (US); Talcahuano, *Pöppig* 168 (P, W); Quinchilca, *Hollermayer* 870 (CONC, SI); Llanquihue, Peulla, *Pennell* 12669 (GH); San Miguel, *Barros* 798 (BACP).

7. *Cardamine pacensis* Díaz Rom., Bol. Direcc. Nac. Estad. Estud. Geogr., La Paz, Segunda Epoca iii. Nos. 25–27: 64. 1920. [as *C. pacense*]. TYPE: BOLIVIA. No collection data were given.

A search for any authentic material of this species did not yield anything, and according to the director of LPB, where such material is most likely to be found, there is no such material, and if it exists, it is either misfiled or lost. Although the species was compared to watercress, *Nasturtium officinale* W.T. Aiton, it was said to resemble *Cardamine andicola* Phil. However, Díaz Romero (1920) provided a detailed species description, all indications of which clearly indicate that the species belongs to a family quite unrelated to the Brassicaceae. Translation of the description from Spanish indicates that: the plants are aquatic with opposite submerged and emergent leaves, axillary aerial inflorescences, a bell-shaped and five-toothed (as quinquedentate), 5-angled calyx, 1–2 cm long intensely yellow flowers with 2 parallel series of small red spots in the throat, and with ovoid, bifurcate silicles. No Brassicaceae species has any of these features and, therefore, it is excluded here from the family. However, we are not in a position to suggest a family to which this species belongs.

8. *Cardamine pygmaea* Dusén

According to Stafleu & Cowan (1976: 712), Dusén’s herbarium is housed at S, and a search for it during an earlier visit by one of us (IAS), as well as a communication with the current director of botany, Mats Wedin, did not yield anything, and it may be misplaced or lost. The original publication included the illustration of two plants but without additional details of the other parts. However, the description and illustration of the fruit clearly exclude the species from *Cardamine*. Schulz (1903) did not examine any material of it, but he suspected (p. 595) that it belongs to *Nasturtium*, a genus he broadly circumscribed to include *Rorippa* Scop. The only diminutive Patagonian species of *Rorippa* that perfectly matches *C. pygmaea* is *R. austroamericana* (see below). Plants of this species can be as minute as 1.5 cm long, with pinnatisect basal and cauline leaves as short as 1.5 cm and with as few as three lateral lobes. These features, as well as the white flowers and oblong fruits, confirm the generic and species assignments. It is the southernmost Patagonian *Rorippa* that also grows elsewhere in Argentina, Chile, and Peru along irrigation canals and edges of ponds at elevations of 2000–4270 m (Al-Shehbaz & Salariato, 2012). Therefore, the following new combination is needed.

Rorippa pygmaea (Dusén) Al-Shehbaz & Marhold, *comb. nov.*

Basionym: *Cardamine pygmaea* Dusén, *Wiss. Ergebn. Schwed. Exped. Magellansl. 1895–1897*, 3(5): 175, pl. 8. 1900.

TYPE: CHILE. [Región de Magallanes y de la Antártica Chilena], Rfo San Martín, *Dusén s.n.* (S, not located).

Rorippa austroamericana Mart.-Laborde, *Parodiana* 2: 73. 1983, *syn. nov.* TYPE: CHILE. [Región V: Vaparaíso.] Los Andes, Potrero Escondido, ca. 3500 m, 22 February 1947, *O. Boelcke 2444* (Holotype: BAA).

9. *Cardamine speciosa* Britton, *Bull. Torrey Bot. Club* 16: 16. 1889; *C. jamesonii* var. *speciosa* (Britton) O.E. Schulz, *Bot. Jahrb. Syst.* 32: 422. 1903. TYPE: BOLIVIA. La Paz, Undavi, 1885, 10,000 ft [3048 m], *H. H. Rusby 1199* (Holotype: NY [00172744]; Isotypes: NY [00172745], US [09919955]).

Schulz (1903) reduced *Cardamine speciosa* to a variety of *C. jamesonii*, but the two are quite distinct morphologically. They are also disjunct by some 1840 air km from the range of the former in Undavi (Bolivia) to that of the latter in the southernmost part of Loja Province (Ecuador). *Cardamine speciosa* can easily be separated from *C. jamesonii* by having ebracteate (vs. bracteate) racemes, entire or repand (vs. crenate, incised-crenate, or serrate leaflets), petiolulate (vs. sessile) lateral leaflets, and leaflets of cauline leaves drastically narrower and smaller (vs. about the same shape and size) as the lowermost leaves.

Cardamine speciosa is very rare, under collected, and known thus far only from the type gathering and the following two collections.

Additional specimens examined: BOLIVIA. La Paz: Undavi, North Yungas, 3300 m, November 1910, *Buchtien 126* (E, F, G, GH, NY), *Buchtien 585* (NY).

10. *Cardamine subterranea* Larrañaga, *Escritos Damaso Antonio Larranaga* 2: 205. 1923. Type indication and diagnosis: “floribus hermaphroditis, terminalibus siliquosis, foemineis siliculosis, subterraneis. Folia simplicibus. Julio 5 de 1809.” TYPE: Not located.

The above brief diagnosis is everything known to date about the species. It is absolutely clear that the above name is a synonym of *Cardamine chenopodiifolia* Pers., a species distributed in Argentina, Bolivia, Brazil, Chile, Paraguay, and Uruguay. It is most unique in the entire Brassicaceae for having two fruit types: aerial, dehiscent, 12–20-seeded, linear siliques 1.7–4.0 cm long and with seeds 1.8–2.3 mm long, as well as hypogeal (geocarpic), indehiscent, 1–4-seeded, obovoid to fusiform silicles 0.5–1.0 cm long and with seeds 2.5–3.5 mm long (Al-Shehbaz & Salariato, 2012).

In addition to *Cardamine chenopodiifolia*, geocarpic fruits evolved independently in five other tribes of the Brassicaceae. These include the Aphragmeae in one of 13 species of *Aphragmus* Andr. ex DC., Euclidieae in the Himalayan monospecific *Pyconoplinthopsis* Jafri, Eutremeae in two of 44 species of *Eutrema* R. Br., Microlepidieae in monospecific Australian *Geococcus* J. Drumm. ex Harv, and Brassiceae in monospecific *Morisia* J. Gay (Corsica, Sardinia), and both species of Algerian-Moroccan *Raffenaldia* Godr. Unlike *C. chenopodiifolia*, geocarpic plants in these five tribes do not produce fruits on aerial racemes.

KEY TO THE NATIVE SOUTH AMERICAN SPECIES

The Argentinean species of *Cardamine* can be identified in Al-Shehbaz & Salariato (2012), but no updated key is available for the native species of the entire continent. Three naturalized species (*C. africana*, *C. hirsuta*, *C. flexuosa*) are not as widespread in South America as they are in the Caribbean islands, Central America, and Mexico. They are included in the species key of these three areas, but not in the following.

- 1a. Plants annual; fruits heteromorphic, linear siliques on aerial racemes and ovate to oblong silicles on subterranean solitary pedicels *C. chenopodiifolia*
- 1b. Plants perennial; fruit only on aerial stems 2
- 2a. Racemes bracteate at least proximally 3
- 2b. Racemes ebracteate, rarely a basal flower bracteate 13
- 3a. Cauline leaves almost always simple, rarely lowermost minutely trifoliolate 4
- 3b. Cauline leaves compound 6
- 4a. Fruit 3.0–5.5 cm long; leaves lanceolate to ovate, serrate, long acuminate; Colombia, Venezuela *C. armoracioides*
- 4b. Fruit (0.7–)1.5–2.2(–2.8) cm long; leaves entire or repand 5
- 5a. Stem base not tuberous; fruit 1.0–1.5 mm wide; cauline leaves orbicular, broadly cordate to reniform, lowermost with a pair of small leaflets; petiole 1.5–2.5 cm long; Colombia, Ecuador *C. bonariensis*
- 5b. Stem base tuberous especially in older plants; fruit 0.7–0.8 mm wide; cauline leaves simple, oblanceolate; petiole <1 cm long; Argentina, Chile *C. nana*
- 6a. Cauline leaves trifoliolate 7
- 6b. Cauline leaves pinnately compound 8
- 7a. Leaflets long-acuminate to subcaudate *C. aschersoniana*
- 7b. Leaflets acute *C. fulcrata*
- 8a. Rhizomes fleshy, thickened, usually tuberous, scaly; basal and lowermost cauline leaves 13–23-foliolate *C. lojanensis*
- 8b. Rhizomes not fleshy, slender, not scaly; basal and lowermost cauline leaves (3–)5–11(–13)-foliolate, very rarely simple 9

KEY TO THE NATIVE SOUTH AMERICAN SPECIES CONT.

- 9a. Petals 2–4 mm long; fruit (0.7–)1.5–2.2(–2.8) cm long 10
 9b. Petals (5–)6–22 mm long; fruit (2.5–)3.5–5.5(–7.0) cm long 11
 10a. Replum glabrous; ovules 20–40 per ovary; rachis straight *C. bonariensis*
 10b. Replum pilose; ovules 18–22 per ovary; rachis flexuous *C. kruessellii*
 11a. Lower and middle cauline leaves (3–)5(–7)-foliolate; petals white or rarely pale lavender, 5–7 mm long *C. ovata*
 11b. Lower and middle cauline leaves 7–11(–13)-foliolate; petals dark purple, violet or rarely pale lavender, (8–)10–22 mm long 12
 12a. Lowermost fruiting pedicels 1–2(–3) cm long; style 3–8(–10) mm long; racemes bracteate only basally; petals (8–)10–14 mm long
 *C. jamesonii*
 12b. Lowermost fruiting pedicels (2.0–)2.5–4.2(–5.0) cm long; style (6–)8–16(–20) mm long; racemes bracteate throughout; petals 1.5–2.0 cm long
 *C. picta*
 13a. Cauline leaves simple, rarely lowermost with 1 or 2 minute lateral leaflets 14
 13b. Cauline leaves compound, 3-, 5- or 7-foliolate 17
 14a. Plants with numerous tubers *C. tuberosa*
 14b. Plants not tuberous 15
 15a. Cauline leaves lanceolate to ovate *C. variabilis*
 15b. Cauline leaves cordate or flabellate 16
 16a. Stems 6–25 cm tall; leaves 3–5-toothed; sepals 3.5–4.0(–4.5) mm long *C. cordata*
 16b. Stems 20–60 cm tall; leaves undulate-crenate; sepals 1–2 mm long *C. rostrata*
 17a. Plants tuberous 18
 17b. Plants not tuberous 21
 18a. Rhizomal and lowermost cauline leaves 3-foliolate; rhizomes and stolons tuberous at apex; stem and rachis angular-flexuous *C. hispidula*
 18b. All leaves 5- or 7-foliolate; only stem base tuberous; stem and rachis straight or (in *C. marginata*) flexuous but not angular 19
 19a. Style stout, almost as wide as fruit apex *C. glacialis*
 19b. Style slender, distinctly narrower than fruit apex 20
 20a. Petals 2.5–3.2 × 0.7–1.0 mm; rachis of raceme flexuous; ovules 6–10 per ovary; fruit 1.0–1.7 cm × 1.8–2.5 mm *C. marginata*
 20b. Petals (5–)6–9 × 2.0–3.5 mm; rachis of raceme straight; ovules 20–34 per ovary; fruit 2–4 cm × 1.0–1.5 mm *C. vulgaris*
 21a. Leaflets strongly lobed or compound 22
 21b. Leaflets entire, dentate, crenate, or serrate 23
 22a. Lateral leaflets with sessile lobes; petals broadly obovate, (0.8–)10.0–15.0 × 4–8 mm; Patagonian Argentina and Chile *C. geraniifolia*
 22b. Lateral leaflets 3-foliolate; petals oblong-oblongate, 8–12 × 3–4 mm; Peru *C. peruviana*
 23a. Petals purple, 4.0–6.5 mm wide; Bolivia *C. speciosa*
 23b. Petals white, 1.5–4.0(–6.0) mm wide, central Chile and Patagonian Chile and Argentina 24
 24a. Leaflets of basal and lower cauline leaves orbicular to reniform or broadly ovate, those of upper leaves filiform, linear, or narrowly oblong
 25
 24b. Leaflets of basal leaves similar morphologically to cauline but larger 26
 25a. Rhizomes slender; sepals (3.2–)3.5–4.5 mm long; petals (6–)7–12 mm long; terminal lobe of lower cauline leaves broadly ovate, 3-toothed
 *C. tenuirostris*
 25b. Rhizomes robust; sepals 2.2–3.0 mm long; petals 5.0–6.5 mm long; terminal lobe of lower cauline leaves orbicular to reniform, crenate to
 subentire *C. vulgaris*
 26a. Terminal leaflet distinctly longer than lateral ones 27
 26a. Terminal leaflet about as long as lateral ones 28
 27a. At least some leaves simple; leaflets obovate to flabellate *C. cordata*
 27b. All leaves pinnately compound; leaflets ovate to oblong *C. variabilis*
 28a. Rhizomes thickened apically; petals 1.5–3.0 mm wide; style stout, almost as thick as fruit apex *C. glacialis*
 28b. Rhizomes slender apically; petals 2.5–4.0(–5.0) mm wide; style slender, distinctly narrower than fruit apex *C. volckmannii*

MEXICAN AND CENTRAL AMERICAN CARDAMINE

Rollins (1993) recognized 15 native species of *Cardamine* in Mexico and Central America excluding the Caribbean Islands. Of those, *C. ramosa* Rollins, *C. flaccida* Cham. & Schltdl., and *C. innovans* O.E. Schulz are minor variants of *C. longipedicellata* Rollins, *C. bonariensis*, and *C. africana*, respectively. By contrast, a recent floristic account of Central America and southern Mexico (Al-Shehbaz & Fuentes Soriano, 2015) recognized only eight species. Finally, Sjöstedt (1975) recognized only five species in all of Central and South America and drastically reduced the vast

majority of 97 names to their synonymy. Such a very broad species concept was not followed by subsequent workers.

With the addition of *Cardamine guatemalensis* Al-Shehbaz and *C. karol-marholdii* Al-Shehbaz, which are endemic to Guatemala and Mexico, respectively, Central America and Mexico combined have 15 native species, of which Mexico has 11 (three endemic) and Guatemala has eight (three endemic) (Table 2). Belize, El Salvador, and Nicaragua are the only countries in the region without native species. The following species require some notes.

TABLE 2. Country distribution of the native Caribbean, Central American, and Mexican species of *Cardamine*. An asterisk (*) indicates presence, and E means endemic to that country. Country abbreviations are: CRI: Costa Rica; CUB: Cuba; DOM: Dominican Republic; GTM: Guatemala; HND: Honduras; HTI: Haiti; MEX: Mexico; and PAN: Panama.

SPECIES	CRI	CUB	DOM	GTM	HND	HTI	MEX	PAN
<i>Cardamine auriculata</i> S.Watson							E	
<i>Cardamine balnearia</i> Standl. & Steyerl.				E				
<i>Cardamine bonariensis</i> Pers.	*			*			*	
<i>Cardamine californica</i> (Nutt.) Greene							*	
<i>Cardamine eremita</i> Standl. & Steyerl.				E				
<i>Cardamine fulcrata</i> Greene	*			*	*		*	*
<i>Cardamine guatemalensis</i> Al-Shehbaz				E				
<i>Cardamine hintonii</i> Marhod & Al-Shehbaz			*			*	*	
<i>Cardamine jejuna</i> Standl. & Steyerl.	*			*			*	
<i>Cardamine karol-marholdii</i> Al-Shehbaz							E	
<i>Cardamine longipedicellata</i> Rollins				*			*	
<i>Cardamine macrocarpa</i> Brandegees							*	
<i>Cardamine mexicana</i> O.E.Schulz							E	
<i>Cardamine ocoana</i> O.E.Schulz			E					
<i>Cardamine oligosperma</i> Nutt.							*	
<i>Cardamine ovata</i> Benth.	*			*				*
<i>Cardamine porphyrophylla</i> Ekman ex Urb.		E						

1. *Cardamine carrii* B.L. Turner

Turner (2012) described this species from South-Central Texas, and he closely compared it with, and annotated it in 1997 as, *Cardamine macrocarpa*, a species distributed in Texas (Brewster, Kinney, Jeff Davis, and Uvalde counties) and Mexico (Chihuahua and Nuevo Leon). Since then, we have studied several additional collections, and it is evident that *C. carrii* is indistinguishable from the former. The holotype has aborted flowers with smaller petals than those of typical *C. macrocarpa*, and the other alleged differences between them in fruit width and pedicel length show continuous variation and are unreliable. In every other aspect, plants of the two are indistinguishable. Therefore, a single species is involved, and its synonyms are listed below.

Cardamine macrocarpa Brandegees, Zoe 5: 233. 1906. TYPE: MEXICO. Coahuila, Sierra de Parras, March 1905, *C. A. Purpus 1029* (Holotype: UC [136075]; Isotypes: GH [00018932], NY [00172736]).

Cardamine macrocarpa var. *texana* Rollins, J. Arnold Arbor. 21: 394. 1940. TYPE: UNITED STATES. Brewster Co., Camp Mountain, Chisos Mountains, September 1933, *V. L. Cory 7141* (Holotype: GH [00018914]).

Cardamine carrii B.L. Turner, Phytoneuron 49: 1. 2012, syn. nov. TYPE: UNITED STATES. Texas, Kinney Co.: Kickapoo Cavern State Park, ca. 400 ft NW of BM 1822, ca. 1700 ft SE of windmill at BM 1717, SW ¼ of park, 29°35'48"N, 100°27'25"W, clay loam and duff over rock rubble on slope at shaded base of NW-facing limestone bluff, 1700–1720 ft, 20 April 1990, *W. R. Carr 10,458* (Holotype: TEX [00208722]; Isotype: TEX [00028533]).

2. *Cardamine cebollana* B.L. Turner

This Mexican species was based on a single diffuse plant that was most likely grazed at the tips, became multibranching at the base, and appeared as if it is perennial. It resembles diffuse plants of *Cardamine longipedicellata*, especially in leaf morphology, flower size, second racemes, fruiting pedicels, fruits, and seeds. The examination of many collections of this species from Mexico and Guatemala leaves no doubt that *C. cebollana* is conspecific with *C. longipedicellata*, as indicated below.

Cardamine longipedicellata Rollins, J. Arnold Arbor. 21: 395. 1940: 395. TYPE: MEXICO. [Nuevo León]:

Sierra Madre Oriental, San Francisco Canyon, about 15 miles southwest of Pueblo Galeana, 11 May 1934, 7500–8500 ft [2286–2591 m], *C. H. Mueller & M. T. Mueller 298* (Holotype: GH [00018931]).

Cardamine cebollana B.L. Turner, *Phytologia* 94: 384. 2012, syn. nov. TYPE: MEXICO. Nuevo León: Mpio. Montemorelos, 6 km SE of La Trinidad, in La Sierra Cebolla, just below the summit, 2900 m, 25°11'N, 100°07'W, 5 August 1988, *T. F. Patterson 6150* (Holotype: TEX [00147820]).

3. *Cardamine obliqua* Hochs. ex A. Rich.

Schulz (1903) confused the limits of the African *Cardamine obliqua* Hochs. ex A. Rich., and cited (p. 518) two collections from Africa and a third from Mexico. Rollins (1940, 1993) followed Schulz and recognized that Mexican collection and another as a distinct variety of this species.

The typification of *Cardamine obliqua* is incomplete, and Jonsell (1982) listed the holotype at P but did not annotate any of the duplicates cited below. However, P has three sheets, of which two, as well as duplicates in other herbaria, have printed labels, whereas the one designated below as the lectotype has a handwritten label most likely by Achille Richard. It is unknown if Richard examined the two duplicates at P and both sheets at TUB, where Hochstetter's types are housed (see Stafleu & Cowan, 1979). Furthermore, Jonsell indicated that the type locality is Begemdir [sic], but this name is not listed on any sheet of the type collection or in Richard (1847), who gave the locality Boauhit in (Prov. Semien), a name listed as Bachit on all labels of the type collection. Gillett (1972) indicated that Bachit, or Bauhit, is located at 13°15'N, 38°15'E of Province Semien, which is north of Prov. Begemder.

Cardamine obliqua Hochs. ex A. Rich., *Tent. Fl. Abyss.* 1: 19. 1847. TYPE: AETHIOPIA. "In regione superioris montis Bachit ad rivulos," 24 June 1838, [W. G.] *Schimper 989* (Lectotype, here designated; P [00364836]; Isolectotypes: B [10-0386989], BR [0000008248770], BR [0000008886973], HAL [0081734], K [000230709], K [000230711], KW [001000745], M [0108035], P [00364834], P [00364835], S-G-[8719], STU [000327], TUB [000540], TUB [00541]).

Cardamine obliqua grows in the alpine belt, on lake and stream shores, and in moist mountain forests at 2000–4900 m in its native range in Ethiopia, Kenya, Rwanda, Tanzania, Uganda, and Zaire (Jonsell, 1982). It is not known from any other African country. Its disjunct distribution (as var. *stylosa*) in Mexico is highly dubious, and there is no other Brassicaceae that has such an allegedly disjunct African-American native distribution. A closer examination of numerous collections (including types) from Africa and fewer from Mexico show that there are some settled differences between the two, though there is also a great deal of overlap in morphology, especially in leaf characters.

Unfortunately, there is no molecular phylogenetic study that dealt with samples from both continents, and such study should reveal whether or not those bicontinental populations are somewhat related or not. Moreover, according to the data by Jonsell (1976) from East Africa, this species represents a polyploid complex, comprising hypertetraploids ($2n = 36$), heptaploids ($2n = 56$), (hypo)octoploids ($2n = 62$, c.64) and nonaploids ($2n = 72$). For now, however, the Mexican populations are treated as the following distinct species, and a complete description is given.

Cardamine hintonii Marhold & Al-Shehbaz, nom. nov.

Basionym: *Cardamine obliqua* var. *stylosa* Rollins, *J. Arnold Arbor.* 21: 392. 1940; non *C. stylosa* D.C., *Syst. Veg.* 2: 248. 1821. TYPE: MEXICO. [State of Mexico] Las Cruces, Tamascaltepe, 3350 m, 13 June 1934, *G. B. Hinton 6080* (Holotype: GH [0001834]; Isotypes: K [000485041], MICH [1115033], NY [00172737]; US [00100046]).

Perennial herbs; rhizomes non-fleshy, not scaly. *Stems* 30–60 cm tall, erect to ascending, simple or few-branched above, glabrous to occasionally pubescent. Basal and lowermost cauline *leaves* pinnately compound, 5–7-foliolate; *leaflets* subsessile to short petiolulate, ovate to suborbicular, entire or somewhat dentate, glabrous, sparsely ciliate along the margin; terminal leaflets slightly larger than to subequaling laterals; middle and upper leaves similar to basal, not auriculate. *Raceme* several flowered, ebracteate, glabrous, elongated in fruit; fruiting pedicels ascending, straight, lowermost 1.0–2.3 cm long. *Sepals* erect, 2–3 mm long, ovate, green, glabrous; *petals* white, obovate, 4.5–7.0(–8.0) mm long, cuneate to claw-like base; *stamens* white, slender; *anthers* 1.0–1.5 mm long. *Fruit* linear, 2.3–4.0 cm × 1.0–1.8 mm, glabrous; *style* slender, (2–)3–5 mm long.

The species grows in wet areas in mountains, steep gullies, winding gorges, and along creek and stream margins. It is distributed in Hispaniola (see below) and México (Ciudad de México, Durango, Estad. México, Morelos).

Cardamine hintonii generally resembles *C. obliqua* in habit, foliage, and ebracteate racemes that are elongated in fruit. However, the basal and lowermost leaves in *C. hintonii* are 5–7-foliolate (vs. (7–)9–11-foliolate), the petals are always white (vs. violet, pink, or white), the styles are slender (vs. stout), and the fruit is usually subappressed (vs. divaricate). Ranges of the two species are separated by a distance of some 12,000–15,000 air km.

Schulz (1903) cited *Pringle 5327* (GH, as H.C.) as a representative of *Cardamine obliqua* from the New World, and Rollins (1940) cited that collection as a paratype of his Mexican *C. obliqua* var. *stylosa*. A recent search for that specimen in the Harvard University Herbaria failed to locate it despite the fact that one of us (IAS) examined it several years ago, and it is likely misplaced. There are no duplicates of this collection in Pringle's Herbarium (VT) or herbaria in Europe and the United States (e.g., CAS, NY, UC, US).

CARIBBEAN SPECIES

The vast majority of Caribbean Islands have one or more naturalized weedy species of *Cardamine*, including *C. africana*, *C. flexuosa*, *C. hirsuta*, and *C. impatiens* (see Adams, 1972; Al-Shehbaz, 1988; Fournet, 2002; Liogier &

Martorell, 2000; Liogier, 1983). The last author reported *C. pensylvanica* Muhl. ex Willd. from Haiti based on a collection (Sto. Dominigo, *Ventenant s.n.* (G)) that was annotated by Schulz on 26 March 1902 and cited by him

(Schulz, 1903: 521) as *C. flexuosa* subsp. *pensylvanica* (Muhl.) O.E. Schulz. One of us (IAS) examined the specimen in May 2024, and it definitely belongs to *C. hirsuta*. *Cardamine pensylvanica* is restricted to southern Canada and the United States (see Al-Shehbaz et al., 2010). Furthermore, Liogier who reported *C. debilis* Don from the Dominican Republic based on *Turchheim 2949* (G), and based on its examination, it is definitely *C. occulta*, a species shown by Marhold et al. (2016) to be widely naturalized worldwide and often misidentified as *C. flexuosa*.

Schulz (1903) broadly delimited *Cardamine jamesonii* Hook. (Colombia, Ecuador, Venezuela) to include at least three species, and Liogier (1983) listed its occurrence in Hispaniola (Haiti and the Dominican Republic). An examination of several of Ekman's collections from Haiti, all annotated by Schulz as *C. jamesonii*, revealed that these collections clearly do not belong to this species. Instead, they belong to *C. hintonii*, which differs from the latter by having 5–7-foliolate (vs. 7–11(–13)-foliolate) leaves, basally ebracteate (vs. bracteate) racemes, green (vs. dark purple)

sepals, white (vs. purple, violet, or red but rarely lavender) petals 4.5–7.0(–8.0) (vs. (8–)10–14) mm long, fruit 2.3–4.0 (vs. 3–7) cm long, and (2–)3–5) (vs. (3–)5–8(–10) mm long. It is not known if these disjunct Hispaniola populations of *C. hintonii* are remnants of a wider distribution that included Mexico, or were introduced around the turn of the 20th century.

The Caribbean Islands have two native *Cardamine* species, of which *C. porphyrophylla* Ekman ex Urb. is endemic to Cuba and currently known from a number of localities (Rodríguez & Greuter, 2009). The other, *C. ocoana* O.E. Schulz, is known previously only from the type collection in the Dominican Republic, *Ekman 11702* (Holotype: S-R [7298]; Isotype: B [10-0243591]). A second collection that perhaps belongs here is *Hill 23933* (MO [4320943]) from Dominica, a small island of the Lesser Antilles disjunct from the above type locality by some 1000 km, and it is likely a recent introduction. Plants of both collections have procumbent stems that produce several well-spaced rosettes with 5–7-foliolate leaves and terminate in ebracteate racemes.

KEY TO THE CARIBBEAN, CENTRAL AMERICAN, AND MEXICAN *CARDAMINE* SPECIES

In addition to the 17 native species present in the countries and areas above, the key also includes the five weedy species *Cardamine africana*, *C. flexuosa*, *C. hirsuta*, *C. impatiens*, and *C. occulta*. This should help in their separation from each other and the native species. Šlenker et al. (2018) is followed in separating *C. flexuosa* from *C. occulta*.

- 1a. Plants annual 2
- 1b. Plants perennial 11
- 2a. Petiole base of cauline leaves auriculate *C. impatiens*
- 2b. Petiole base of cauline leaves not auriculate 3
- 3a. Bases of at least some leaflet petiolules with stalked or sessile auricles *C. auriculata*
- 3b. Bases of leaflet petiolules without auricles 4
- 4a. Stems and petioles usually densely hirsute with long trichomes; terminal leaflets crenate, suborbicular, usually cordate or oblique at the base *C. mexicana*
- 4b. Stems and petioles glabrous to sparsely pubescent; terminal leaflets entire or dentate, variously shaped but rarely cordate 5
- 5a. Basal leaves forming well-developed rosettes with ciliate petioles 6
- 5b. Basal leaves not rosulate, or forming loose rosettes usually with glabrous petioles 8
- 6a. Racemes 3–5-flowered; cauline leaves few, reduced, or absent; alpine endemic of Guatemala *C. jejuna*
- 6b. Racemes many flowered; cauline leaves several, well developed 7
- 7a. Stamens 4, rarely 5 or 6; seeds narrowly margined; fruit usually appressed to rachis; valves glabrous; widespread weed. *C. hirsuta*
- 7b. Stamens 6; seeds not margined; fruit not appressed to rachis; valves glabrous or pubescent; native to Baja California. *C. oligosperma*
- 8a. Racemes secund; lowermost fruiting pedicels (0.8–)1.0–2.5 cm long *C. longipedicellata*
- 8b. Racemes not secund; lowermost fruiting pedicels rarely to 1 cm long 9
- 9a. Racemes strongly flexuous at geniculate; fruit (2.5–)3.0–4.6 cm × 1.7–2.0 mm; petals 6–8 mm long *C. macrocarpa*
- 9b. Racemes not or hardly flexuous at base; fruit 1.0–2.5(–3.2) cm × 1.0–1.5 mm; petals 2–4(–5) mm long 10
- 10a. Basal rosette absent; upper surfaces of middle cauline leaves and upper stems usually glabrous; petals more than two times wider than sepals; terminal leaflet of middle cauline leaves with (1–)3–5(–7) sinuses *C. occulta*
- 10b. Basal rosette present; upper surfaces of middle cauline leaves and upper stems usually pubescent; petals less than two times wider than sepals; terminal leaflet of middle cauline leaves with 1–7(–9) sinuses. *C. flexuosa*
- 11a. Plants woody at base; stem and raceme rachis strongly flexuous, geniculate; leaves pinnatisect *C. karol-marholdii*
- 11b. Plants herbaceous throughout; stem and raceme rachis straight, not geniculate; leaves pinnately compound or trifoliolate, rarely simple . 12
- 12a. Basal leaves simple, reniform to orbicular, palmately veined, rarely with minute 1 or 2 lateral lobes; cauline leaves absent or 1 *C. guatemalensis*
- 12b. Basal leaves compound, trifoliolate or pinnate; cauline leaves usually several 13
- 13a. Rhizomes bulbous; plants of Baja California *C. californica*
- 13b. Rhizomes not bulbous; plants from elsewhere 14
- 14a. Rhizomes thickened, simple; leaves 9–13-foliolate *C. balnearia*
- 14b. Rhizomes slender, often branched; leaves 3–7(–9)-foliolate 15
- 15a. Racemes bracteate at least basally 16
- 15b. Racemes ebracteate 19
- 16a. Fruit (0.7–)1.5–2.2(–3.0) cm long; petals to 5 mm long; terminal leaflet 0.3–2.5 cm long 17
- 16b. Fruit (2.8–)3.5–5.5(–6.5) cm long; petals 4.5–9.0 mm long; terminal leaflet (2–)3–9 cm long 18

KEY TO THE CARIBBEAN, CENTRAL AMERICAN, AND MEXICAN *CARDAMINE* SPECIES CONT.

- 17a. Terminal leaflet orbicular, reniform, or rarely ovate; raceme not secund in fruit *C. bonariensis*
 17b. Terminal leaflet linear-oblongate to oblongate; raceme secund in fruit *C. eremita*
 18a. Middle cauline leaves trifoliolate *C. fulcrata*
 18b. Middle cauline leaves 5–9-foliolate *C. ovata*
 19a. Leaves trifoliolate throughout 20
 19b. Leaves pinnate, 5–7-foliolate 21
 20a. Terminal leaflet lanceolate to ovate, acute at apex, on petiolule 2–5 cm long; fruit (2.5–)3.5–5.0(–6.0) cm long; sepals 1.5–4.0 mm long; petals 3.5–9.0 mm long; widespread naturalized weed *C. africana*
 20b. Terminal leaflet suborbicular, rounded at apex, on petiolule 1.0–1.5 cm long; fruit 2.5–3.0 cm long; sepals to 2 mm long; petals to 5 mm long; endemic to Cuba *C. porphyrophylla*
 21a. Plants erect to ascending; fruit 2.3–4.0 cm long; petals 4.5–7.0(–8.0) mm long; style (2–)3–5 mm long *C. hintonii*
 21b. Plants prostrate or procumbent; fruit 1.5–2.5 cm long; petals 3–4 mm long; style 0.5–1.0(–1.5) mm long *C. ocoana*

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PHYTOSOCIOLOGICAL CLASSIFICATION OF FOREST VEGETATION IN VENEZUELAN LLANOS

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Abstract. The forest vegetation of Venezuelan Llanos (Anzoátegui, Barinas, Guárico, Monagas, Portuguesa, and Táchira states) was characterized using 68 units (plots) between 500 m² and 1000 m². All individuals with a diameter at breast height (DBH) \geq 10 cm were measured, and the basal area (m²), relative abundance (%), relative dominance (%), and a reduced importance value index (IVI) were calculated. The Sigmatis school guidelines were used to classify the forests, using the floristic composition data. The forests were grouped in the *Guazuma ulmifoliae-Spondiadetea mombinis* class (65,000 m², 630 species, and a richness index of 0.97×10^{-2} sp/m²). This class has two orders: the *Cupanio americanae-Protietalia heptaphylli* order (38,000 m², 510 species, and a richness index of 1.3×10^{-2} sp/m²), which is mixed with palm communities (*Protio heptaphylli-Attaleion* alliance) and the forests of the alliance *Xylopia aromatica-Protium heptaphylli*, has three associations; and the *Cupanio americanae-Tabebuialia roseae* order, which harbors the *Ceibo pentandrae-Trichilion martianae* alliance with three associations. In the latter order, a total of 9554 individuals were counted (average 245) with a density index of 25.1×10^{-2} individuals per square meter. The vegetation of both the Venezuelan Llanos and the Colombian Llanos contain *Attalea butyracea* palm communities. Another interesting affinity is found with the Colombian Caribbean vegetation: both regions share the *Spondias mombin* and *Attalea butyracea* community at the class level, and *Protium heptaphyllum*, *Anacardium excelsum*, and *Pterocarpus acapulcensis* at the alliance level. The dominance shown by *Guazuma ulmifolia* and *Cupania americana* in the vegetation units in the Venezuelan Llanos is a very important floristic characteristic observed between the two Llanos regions of Colombia and Venezuela. This floristic-ecological convergence between the two regions may be related to the lower levels of precipitation in many places in the Venezuelan Llanos. This phytosociological study allowed for the characterization of one class, two orders, three alliances, and ten associations. These results highlight the importance of this methodology to define and classify the vegetation of northeastern South America.

Keywords: Tropical forests, phytosociology, floristic composition, structural aspects, Llanos, Venezuela

Resumen. La vegetación boscosa de los Llanos de Venezuela (estados Anzoátegui, Barinas, Guárico, Monagas, Portuguesa y Táchira) es caracterizada utilizando la información de 68 levantamientos (parcelas) entre 500 m² y 1000 m². Se midieron todos los individuos con un diámetro a la altura del pecho (DAP) \geq 10 cm, y se calculó el área basal (m²), abundancia relativa (%), dominancia relativa (%). Con estos valores se estimó el índice de valor de importancia “reducido” (IVI). Para la clasificación de la vegetación, se siguieron los lineamientos de la escuela sigmatista. De acuerdo con la composición florística, los bosques se agruparon en la clase *Guazuma ulmifoliae-Spondiadetea mombinis* (65,000 m², con 630 especies y un índice de riqueza de 0.97×10^{-2} sp./m²). Esta clase posee dos órdenes: *Cupanio americanae-Protietalia heptaphylli* (38,000 m², 510 especies un índice de riqueza de 1.3×10^{-2} sp./m²), el cual incluye las comunidades mixtas de palmas (*Protio heptaphylli-Attaleion* alliance) y los bosques de la alianza *Xylopia aromatica-Protium heptaphylli*, la cual posee tres asociaciones. El otro orden: *Cupanio americanae-Tabebuialia roseae* incluye la alianza *Ceibo pentandrae-Trichilion martianae*, la cual posee tres asociaciones. En este orden, 9554 individuos fueron censados (una media de 245) con un índice de densidad de 25.1×10^{-2} de individuos por m². La vegetación boscosa de los Llanos de Venezuela comparte con los Llanos de Colombia las comunidades de la palma *Attalea butyracea*. Se encontraron dos interesantes afinidades con la región del Caribe colombiano, a nivel de clase con las comunidades de *Spondias mombin* y *Attalea butyracea*, y a nivel de alianza, las comunidades de *Protium heptaphyllum*, *Anacardium excelsum* y *Pterocarpus acapulcensis*. Los valores de dominancia de *Guazuma ulmifolia* y *Cupania americana* esrepresentan importantes rasgos florísticos observados en los Llanos de Colombia y Venezuela. Esta convergencia ecológica/florística entre ambas regiones quizás está relacionada a los bajos valores de precipitación de varios sectores de los Llanos venezolanos. El presente estudio fitosociológico permitió caracterizar una clase, dos órdenes, tres alianzas, y diez asociaciones. Estos resultados demuestran la importancia de esta metodología para clasificar la vegetación del noreste de Sudamérica.

Palabras clave: Bosques tropicales, fitosociología, composición florística, estructura, Llanos, Venezuela.

The Orinoco plains or “Llanos del Orinoco” have an area of ca. 532,000 km² (Fig. 1), of which 254,000 km² correspond to Colombia and 278,000 km² to Venezuela (Aymard, 2017). Due to its species richness and numerous types of vegetation, this region is considered one of the most diverse biogeographic areas in the Neotropics (Huber et al., 2006; Duno de Stefano et al., 2007; Rangel-Ch. and Minorta-C., 2014; Rangel-Ch., 2015; Rangel-Ch. et al., 2022). This large sector comprises an almost uninterrupted region

of plains that gradually descends from the base of the Andes (250–500 m) in a west-east direction, ending on the left bank and in the deltaic plain of the Orinoco River (Schargel, 2007).

Previous studies of the flora and vegetation of Llanos in Venezuela were by P. Loeffling (1754–1756), A. von Humboldt and A. Bonpland (1800), A. Codazzi (1840), and K. Karsten between 1846–1847 (Aymard and González, 2014). At the beginning of the 19th century, A. von Humboldt and A. Bonpland (Humboldt, 1818–1819) traveled through

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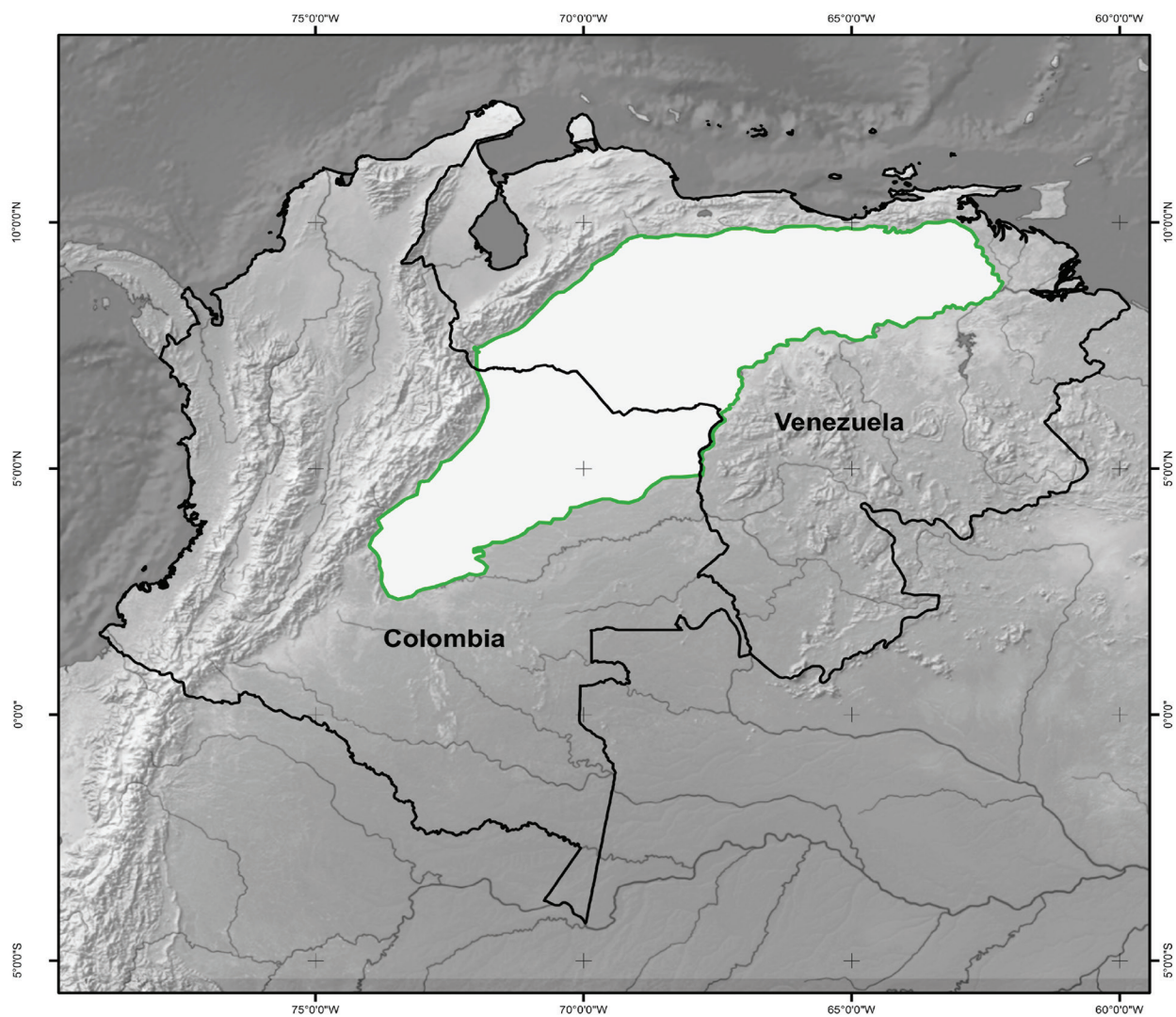


FIGURE 1. Geographic area (within green lines) of Colombian and Venezuelan Llanos (from Aymard, 2017).

the central Llanos of Venezuela and continued up the Orinoco river, making numerous botanical collections in the mouths of the rivers Apure, Arauca, and Meta, and in the Atures (today in Venezuela) and Maypures (today in Colombia) regions (Sandwith, 1925). These naturalists made the first geographical and botanical descriptions of the wide interior savannas and forests of Venezuela, called “Llanos” (Humboldt, 1818–1819). Based on geological processes that differentiated soils and vegetation, A. Jahn applied the terms “Llanos Occidentales” and “Llanos Orientales” to separate these two regions (Jahn, 1921). H. Pittier developed the first map of the vegetation of Venezuela (Pittier 1920, 1937) based on structural characteristics and floristic composition. Other early studies in this region were made by Veillon et al. (1949), Beard (1955), Tamayo (1958, 1972a, b), Hueck (1960), Aristeguieta (1968), Finol (1976), and Veillon (1976). More recently, the Llanos vegetation has been studied by González (1985, 1987), Montes et al.

(1987, 2013), Cuello et al. (1989), Arends et al. (1993), Vareschi (1992), and Hernández and Guevara (1994). For a detailed historical review see Aymard and González (2007) and Aymard (2017). In their vegetation map of Venezuela, Huber and Alarcón (1988) mentioned gallery forests, palm communities, deciduous, semi-deciduous, and evergreen forests in this bioregion. Additional contributions documenting the vegetation types of the Llanos of Colombia and Venezuela can be found in Galán de Mera et al. (2006), Fernández (2007), Rojas and Aymard (2010), Aymard (2011, 2015), Rangel-Ch. and Minorta-C. (2014), Cárdenas-L. et al. (2016), Madriñan et al. (2017), and Rangel-Ch. (2024). This last set of contributions represent the current state of knowledge of the floras and types of vegetation of the Colombian and Venezuelan Llanos, and the ecological importance of the Orinoquía bioregion through its floristic richness and the descriptions of its numerous plant communities.

The Venezuelan Llanos are limited to the north by the Coastal Cordillera mountain system (of Upper Tertiary origin), to the south-southwest by the ancient (Precambrian) and massive mountain system of the Guayana Shield and the Colombian Llanos, to the west by the Andean Cordillera of mid-Tertiary age, and to the east by the alluvial Quaternary deposits located in the muddy plains of the Guarapiche and San Juan rivers and the Orinoco river delta (Schargel, 2007, 2015). The southwestern limit of the Venezuelan Llanos extends from the Arauca and Meta rivers toward the Vichada and Guaviare river basins, a region known as the Colombian Eastern Plains (Blydenstein, 1967) or the Colombian Orinoquia (van der Hammen and Rangel, 1997). The Llanos extend along a larger, southwest-northeast-oriented geosyncline occurring between the base of the Guayana Shield and the Coastal Cordillera (Schargel, 2007). As a result of the orogenic processes caused by the Andean uplift, an enormous depression was formed and originally flooded by marine waters. This depression has filled up since the Upper Tertiary and during the Quaternary with sediments that currently dominate the superficial geology of the region (Huber et al. 2006; Zinck, 2015). Moreover, during the mid- and late-Tertiary periods, the Llanos depression was subject to differential tectonic processes (Huber et al., 2006). Its central and eastern sectors have suffered from a moderate uplift causing subsequent pronounced erosion in the area, whereas in the western sector, subsidence prevailed, which was then followed by intense sediment accumulation (Schargel, 2007, 2015; Zinck, 2015). According to Schargel (2007, 2015), the core Venezuela Llanos region includes four principal geomorphological landscapes. The alluvial plains (“planicies aluviales”), which are plains with low

slopes (usually < 1%) produced mainly by overflow of the rivers with consequent periodic accumulation of sediment. They are most evident in the west and the extreme northeast Llanos. The aeolian plains (“planicies eólicas”) are plains covered by sand and silt, which were deposited by wind during the Pleistocene. In the Llanos, aeolian plains with stabilized Pleistocenic dunes more than 10 m high are distinguished from completely flat aeolian plains covered by silt strata. These plains extend principally from the south-central Llanos to the lower Arauca-Cinaruco basins in the western Llanos. The high plains or plateaus (“altiplanicies”) are plains formed by flat or slightly undulated extensions where the rivers are flowing in valleys or fluvial incisions more than 10 m deep (in some cases >150 m deep). They consist of flat mesas elevated by tectonic movements and are most frequent and visible in the eastern Llanos. The hills and denuded surfaces (“colinas y superficies de denudación”), where erosion has dismantled a high plain, hills less than 300 m high remain, including low “Mesa” remnants and colluvial glacia. This landscape can be seen mainly in the central Llanos.

In this study, new data from the Venezuelan Llanos are presented to establish the structural and compositional characteristics of these forests. We established 68 forest plots distributed across the Venezuelan Llanos region and studied local tree abundance, dominance, and frequency to perform a hierarchical forest classification. This forest vegetation characterization follows the combined approaches of the European Sigmatis School (Braun-Blanquet, 1979) and the Anglo-Saxon forest schools method based on structural parameters (Curtis and McIntosh, 1950; Curtis and Cottam, 1962).

STUDY AREA

The Venezuelan Llanos, a well-defined bioregion in northern South America, occupy an area of approximately 278,000 km² lying between 7° and 10° N (Huber et al. 2006; Aymard, 2017). These wide lowland plains consist mainly of Quaternary alluvial sediments covered by a mosaic of savannas, gallery forests, and dry to semideciduous forests. The climate is markedly macrothermic (>24 C) and tropophilous, with a strong alternation between one rainy and one dry season, and with an average rainfall between 800 and 2200 mm/year, and average annual temperatures between 25 and 35 C (Huber et al. 2006). Therefore, the core Llanos region of Venezuela and adjacent Colombia is subject to a strongly seasonal climate, with a single dry season extending between November and April–May and a single rainy season between April–May and October (Huber et al., 2006). The rainless period of the year is locally called “verano” (summer). During

April and May, the sky becomes cloudy due to the activation of the intertropical convergence zone (ITCZ), which annually operates north and south of the equator zone (Richards et al., 2015). This climatic phenomenon loads humidity and generates large local precipitation until August and September (Andressen, 2003). ITS is generated by the trade winds, which circulate freely through the Caribbean Sea and enter the Llanos bioregion. The trade winds also increase their drying power due to the low pressures that originate in the Llanos (Andressen, 2003; Ranseyer and Miller, 2021). Torrential rains begin in April (more than 80% of the annual rainfall falls during the 5–6 months of the rainy season), and extensive flooding occurs in the lower-lying parts of the Llanos, such as Apure and southern Guárico states (Huber et al., 2006). The altitude ranges between 0 to 450 m in the Andean foothills (Schargel, 2007).

MATERIALS AND METHODS

The localities that were visited are found in the forest vegetation of the Venezuelan Llanos, mainly in gallery forests, palm communities, and deciduous, semi-deciduous, and evergreen forests. The study area is represented by 68 plots that were established in Anzoátegui, Barinas, Guárico, Monagas, Portuguesa, and Táchira states (Table 1). In these

localities, the forest vegetation was characterized using sample plots with areas between 500 m² and 1000 m². The ecological parameters that were estimated in the field were height (m), number of individuals, and diameter at breast height (DBH) ≥ 10 cm. With these measurements, basal area, relative density, and importance value index

(IVI) were calculated (Curtis and McIntosh, 1950; Curtis and Cottam, 1962). The botanical samples were processed and determined in the Herbario Universitario (PORT) at UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Portuguesa state, Venezuela. The species names and nomenclatural validity were revised and updated by consulting Tropicos (<http://legacy.tropicos.org/Home.aspx>) and the International Plant Names Index (<https://www.ipni.org/>). The syntaxonomy names follow the International Code of Phytosociological Nomenclature rules (Izco and del Arco, 2003; Theurillat et al., 2021). The vegetation characterization follows the combined approaches of the European Sigmata School (Braun-Blanquet, 1979) and the Anglo-Saxon forest schools method based on dominance and other structural parameters (Curtis and McIntosh, 1950; Curtis and Cottam, 1962). Based on

floristic composition information, vegetation hierarchical classification was carried out by using the TWINSpan algorithm (a two-way divisive technique: plots, species with indicator species) with the PC-ORD version 6 program (McCune and Mefford, 2011). This classification was used to prepare floristic composition tables, that were used to assemble the vegetation into classes, orders, alliances, and associations. Each unit was described according to its floristic composition, focusing on species with the highest values in cover, and structural variables such as frequency, basal area, and the number of individuals (Avella and Rangel-Ch., 2012). These tables were processed to obtain a classification of communities or associations defined in their floristic composition and contrasted with field observations. The fidelity score was estimated according to the Szafer and Pawlowski scale (1934; in Braun-Blanquet, 1979).

RESULTS

The Syntaxonomical units

The present phytosociological study assembles vegetation into one class, two orders, three alliances, ten associations, and two well-defined forests. The syntaxonomic units are described below. These results represent an innovative proposal to classify the Venezuelan Llanos forest vegetation.

Class *Guazuma ulmifoliae-Spondiadetia mombinis* class nov., in this contribution. (Tables 2, 3).

Typus: *Cupania americanae-Protietalia heptaphylli*

Physiognomy-floristic composition: This new class grouped the “guadales” (vegetation dominated by *Guadua* spp., Poaceae) mixed with palm communities and forests.

The characteristic-dominant species (40) include *Spondias mombin*, *Guazuma ulmifolia*, *Cecropia peltata*, *Leptobalanus apetalus*, *Sapium glandulosum*, *Cochlospermum vitifolium*, *Tapirira guianensis*, *Astronium graveolens*, *Zanthoxylum caribaeum*, *Apeiba tiburoubo*, *Sorocea sprucei*, *Schnella (Bauhinia) guianensis*, *Platymiscium pinnatum*, and *Annona purpurea*. There are 26 other species in this class. The species with the highest value in the importance value index (IVI) are *Luehea candida*, *Guettarda divaricata*, *Bactris major*, *Inga ingoides*, *Inga interrupta*, *Annona jahnii*, *Guarea guidonia*, *Machaerium robinifolium*, *Enterolobium cyclocarpum*, *Vismia cayenensis*, *Casearia silvestris*, *Ceiba pentandra*, *Cordia toqueve*, and *Tabebuia rosea*.

Distribution: This forest vegetation is established in Barinas, Portuguesa, Táchira, Anzoátegui y Monagas states, at altitudes of 20–322 m.

There are three surveys that present very high values in species, individual number, and basal area, which showed different trends compared with the remaining surveys. These surveys are: plot-52, Barinas state, Pedro Morales (130 species, 986 individuals and 16.8 m² of basal area); plot-32, Barinas state, Las Colinas (105 species, 697 individuals and 17.71 m² of basal area); and plot-14, Barinas state, El Trueno, with 82 species, 932 individuals and 21.75 m² of basal area. All three of these survey areas are humid forests located on the Andean foothills (Rojas and Aymard, 2010).

In 66 surveys, the total number of species was 630, average 30 and variation per survey between 12 and 75 and the total number of individuals was 13,469. For the remaining 63 surveys, the number of individuals fluctuates between 35 and 614 with an average of 172 individuals. The species with the highest number of individuals are *Guazuma ulmifolia*, *Cecropia peltata*, *Spondias mombin*, *Leptobalanus (Licania) apetalus*, and *Sapium glandulosum*. Total basal area is 323.6 m² in 66 surveys. For the remaining 63 surveys, the basal area was 267.37 m² with variation between 0.79 and 16.99 m² and average of 4.24 m². The species with the largest basal area are *Spondias mombin*, *Guazuma ulmifolia*, *Cecropia peltata*, and *Leptobalanus apetalus*. The species with the highest IVI values are *Spondias mombin*, *Guazuma ulmifolia*, *Cecropia peltata*, *Leptobalanus apetalus*, and *Sapium glandulosum*.

Order *Cupania americanae-Protietalia heptaphylli* ord. nov., in this contribution. (Table 2).

Typus: *Xylopio aromatae-Protion heptaphylli*

Physiognomy-floristic composition: palm communities, mixed palm, guadales, and forests

The characteristic-dominant species in this order are *Protium heptaphyllum*, *P. tenuifolium*, *P. stevensonii*, *Ceiba pentandra*, *Guarea guidonia*, *Cupania americana*, *Ardisia foetida*, *Didymopanax morototoni*, *Clitoria dendrina*, *Allophyllus racemosus*, *Cordia alliodora*, *Vitex compressa*, *Ocotea puberula*, and *Casearia silvestris*.

The diagnostic species (order differentials) are *Annona montana*, *Aspidosperma cuspa*, *Bauhinia pauletia*, *Bertiera guianensis*, *Casearia aculeata*, *Cecropia peltata*, *Coccoloba caracasana*, *Cordia sericicalyx*, *Couroupita guianensis*, *Euterpe precatória*, and nine other species (see Table 2).

Information on floristic composition and structure of the *Cupania americanae-Protietalia heptaphylli* order, such as species, number of individuals, basal area, and IVI values, is found in Table 3.

Alliance *Protio heptaphylli-Attaleion butyraceae* all. nov., in this contribution. Table 2.

Typus: *Attaleo butyraceae-Rudgetum crassilobae*

Floristic composition: Among the characteristic-dominant species (23) are *Attalea butyracea*, *Guatteria pilosula*, *Protium heptaphyllum*, *Pradosia caracasana*, *Hirtella triandra*, *Citharexylum venezuelense*, *Anacardium excelsum*, *Vitex orinocensis*, *Guadua angustifolia*, *Rudgea crassiloba*, *Guarea guidonia*, *Spondias mombin*, *Xylopia aromatica*, *Platypodium elegans*, *Pochota fendleri*, *Ocotea bofo*, *Zanthoxylum rhoifolium*, and *Tanaecium tetragonolobum*. Other dominant species included in this alliance are *Ficus insipida*, *Rudgea crassiloba*, *Xylopia aromatica*, *Astronium graveolens*, *Cecropia peltata*, and *Erythrina fusca*.

Physiognomy: The alliance is dominated by palm communities and mixed forests. It is very rare to find an upper tree stratum; only *Hirtella triandra* was measured with individuals 30 m high. In the lower tree layer, *Guarea guidonia*, *Guatteria pilosula*, *Tapirira guianensis*, and *Zanthoxylum caribaeum* are very common, and in the sub-arboreal layer *Attalea butyracea*, *Citharexylum venezuelense*, *Guarea guidonia*, *Protium heptaphyllum*, and *Protium tenuifolium* are very common. In the shrub layer, the dominant species are *Miconia magdalenae*, *Calathea lutea*, and young individuals of *Protium heptaphyllum*, *Brosimum alicastum*, *Notopleura macrophylla*, and *Spondias mombin*.

Distribution: This alliance is found in Barinas, Portuguesa, Táchira, Anzóategui, and Monagas states between 20–322 m (Table 1).

Information on floristic composition and structure of this alliance, such as species, number of individuals, basal area, and IVI values, is found in Table 4.

Association Attaleo butyraceae-Guaduetum angustifoliae ass. nov., in this contribution. (Table 2).

Typus: Aymard 52-2012

Floristic composition: Among the characteristic-dominant species (32) are *Cecropia peltata*, *Guadua angustifolia*, *Spondias mombin*, *Brosimum alicastrum*, *Aiphanes horrida*, *Astronium graveolens*, *Cupania americana*, *Protium heptaphyllum*, *P. crenatum*, *P. tenuifolium*, *Guarea guidonia*, *Attalea butyracea*, *Ficus insipida*, *Guatteria pilosula*, *Terminalia amazonia*, *Bixa urucurana*, *Notopleura macrophylla*, *Anacardium excelsum*, *Acalypha diversifolia*, and *Pleurothyrium trianae*.

The differential diagnostic species are *Machaerium humboldtianum*, *Stylogyne micrantha*, *Triplaris americana*, and *Parinari pachyphylla*.

Physiognomy: The vegetation in this association is compound by mixed palm and bambu communities (“guadual-palmar”); *Hirtella triandra* (30 m high) and *Notopleura macrophylla* were found in the upper tree layer. The lower tree stratum is dominated by *Guadua angustifolia* accompanied by *Luehea seemanii*, *Cochlospermum vitifolium*, *Ficus insipida*, *Terminalia amazonia*, *Cecropia peltata*, *Protium tenuifolium*, *Anacardium excelsum*, *Chrysophyllum argenteum*, *Zanthoxylum caribaeum*, and *Guarea guidonia*. The sub-arboreal stratum is dominated by *Guadua angustifolia*, *Attalea butyracea*, *Cupania americana*, *Acalypha diversifolia*, *Aiphanes horrida*, *Erythrina fusca*, *Guarea guidonia*, *Inga edulis*, *Vitex orinocensis*, and 15 other species distributed in the

three surveys (Plots 14, 52 and 32). In the shrub layer, there are shoots of *Brosimum alicastum*, *Hura crepitans*, *Dendropanax arboreus*, *Spondias mombin*, *Notopleura macrophylla*, *Pleurothyrium trianae*, *Ardisia foetida*, and *Guadua angustifolia*.

The climbing (vines, lianas) taxa that reach the upper strata of the forest are represented by several species of *Fridericia*.

Distribution: Localities are in El Trueno, Pedro Morales, and Las Colinas, Barinas state (Rojas and Aymard, 2010).

Information on floristic composition and structure of this association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Association Attaleo butyraceae-Rudgeetum crassilobae ass. nov., in this contribution. Table 2.

Typus: Aymard 60-2012

Floristic composition: Among the characteristic-dominant species (26) are *Protium heptaphyllum*, *P. tenuifolium*, *Attalea butyracea*, *Rudgea crassiloba*, *Guarea guidonia*, *Xylopia aromatica*, *Myrcia splendens*, *Deguelia (Lonchocarpus) picta*, *Guatteria pilosula*, *Didymopanax morototoni*, *Oenocarpus mapora*, *Pochota fendleri*, *Astronium graveolens*, *Hymenaea courbaril*, *Spondias mombin*, and *Pradosia caracasana*. The diagnostic species in this association are *Warszewiczia coccinea*, *Inga sapindoides*, and *Bunchosia argentea*.

Physiognomy: The vegetation of this association is composed of mixed palm communities and forest, where the upper tree stratum is not differentiated. *Hymenaea courbaril* (25 m high) is the tallest species in this layer. In the sub-arboreal layer, the dominant species are *Rudgea crassiloba*, *Triplaris caracasana*, *Myrcia splendens*, *Protium heptaphyllum*, *P. stevensonii*, *Ocotea puberula*, *Miconia magdalenae*, and *Swartzia pittieri*. The lower stratum is dominated by *Miconia magdalenae*, *Rudgea crassiloba*, *Triplaris caracasana*, *Protium heptaphyllum*, *Myrcia splendens*, and *Genipa americana*. In some surveys (i.e., plot-60), a marked dominance of *Calathea lutea* and *Bactris major* was observed. In survey plot-40, the understory is dominated by juvenile individuals of *Oenocarpus mapora*. The climbing species (vines, lianas) that reach the upper strata of the forest are *Davilla nitida*, *Fridericia platyphylla*, and *Xylophragma seemannianum*.

Distribution: The vegetation of this association is found in Morador 1, Morador 4, Tucupido, and Morador 2 surveys located in Portuguesa state, and Navay and Culebra 1 surveys in Táchira state (Table 1).

Information on richness and structure of this association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Undefined alliance

Association Protio heptaphylli-Euterpetum precatioriae ass. nov., in this contribution. Appendix II.

Typus: Aymard 33-2012

Floristic composition: Among the characteristic-dominant species (18) are *Cupania americana*, *Spondias mombin*, *Euterpe precatioria*, *Tapirira guianensis*, *Sapium glandulosum*, *Inga ingoides*, *Jacaranda obtusifolia*, and

Protium heptaphyllum. Other species in this association are *Attalea maripa*, *Macrobium acaciifolium*, *Alchornea glandulosa*, *Maquira coriacea*, *Abarema jupumba*, and *Guarea guidonia*. The diagnostic species of the association are *Conceveibum cordatum* and *Tanaecium tetragonolobum*.

Physiognomy: The vegetation is composed of mixed palm communities. The dominant species of the lower arboreal and small tree strata are *Maquira coriacea*, *Euterpe precatória*, *Inga ingoides*, *Protium heptaphyllum*, *Macrobium acaciifolium*, *Abarema jupumba*, *Jacaranda obtusifolia*, *Lonchocarpus hedyosmus*, *Leptobalanus apetalus*, *Cordia collococca*, and *Attalea maripa*. The understory layer is dominated by *Virola elongata*, *Calathea lutea*, and *Ischnosiphon arouma*.

Distribution: This association is found in Río Guanipa, Los Pozos de Guanipa, Oeste de La Hormiga, and Las Coloradas, Monagas state, and Navay and Urimán 2, Táchira state (Table 1).

Data on richness and structure of this association, such as species, number of individuals, basal area, and IVI values, are found in Appendix I.

Alliance *Xylopio aromatica*-*Protium heptaphyllum* all. nov., in this contribution. Table 5.

Typus: *Vochysia lehmannii*-*Protium heptaphyllum*

Floristic composition: Among the characteristic-dominant species (23) are *Cecropia peltata*, *Xylopio aromatica*, *Spondias mombin*, *Astronium graveolens*, *Cupania americana*, *Protium heptaphyllum*, *P. stevensonii*, *Croton fragrans*, *Annona purpurea*, and *Cassia moschata*. Other dominant species are *Anacardium excelsum*, *Leptobalanus apetalus*, *Vochysia lehmannii*, *Virola elongata*, *Hura crepitans*, *Allophyllum racemosus*, and *Uniosium velutinifolium*. The diagnostic-differential species are *Inga vera*, *Genipa americana*, *Petrea pubescens*, *Swartzia pittieri*, and *Chrysophyllum argenteum*.

Physiognomy: The vegetation of this alliance includes forests, which in some cases have a discontinuous upper tree layer represented by *Anacardium excelsum*, *Cassia grandis*, *Petrea pubescens*, *Astronium graveolens*, *Xylopio aromatica*, *Protium heptaphyllum*, and *Hura crepitans*. *Guazuma ulmifolia*, *Mauritia flexuosa*, and *Pradosia caracasana* are found in the lower tree layer. The shrub layer is dominated by *Ardisia foetida*, *Croton fragrans*, *Guarea guidonia*, *Leptobalanus apetalus*, and *Protium heptaphyllum*. Other species with local importance are *Calathea lutea*, *Montrichardia arborescens*, *Piper tuberculatum*, and *Stylogyne micrantha*.

Distribution: The vegetation of this alliance was found in La Productora, Bumbi Pastoreña 1, 2, 3; Smurfit, Ospino, La Cabaña 1 and 3; Los Alacranes 1, 2, 3, Saltanejas 1, 2, 3, El Tesoro 1, Tacamajaca 1, 2, and 3, Portuguesa state. Other localities are Cerro Negro, Boca del Cogollal, El Rincón, Río Yabo, Paso Marcano, Río Orocuál, and Puente Amarillo, Monagas state (Table 1).

Information on richness and structure of this alliance, such as species, number of individuals, basal area, and IVI values, is found in Table 4.

Association *Ingo verae*-*Anacardietum excelsi* ass. nov., in this contribution. Table 5.

Typus: Aymard 9-2012

Floristic composition: Among the characteristic-dominant species (28) are *Cecropia peltata*, *Inga vera*, *Leptobalanus apetalus*, *Anacardium excelsum*, *Guazuma ulmifolia*, *Cupania americana*, *Ardisia foetida*, *Neea ovalifolia*, *Ormosia macrocalyx*, *Acalypha diversifolia*, *Pradosia caracasana*, *Guarea guidonia*, *Protium tenuifolium*, *Melicoccus bijugatus*, and *Parinari campestris*. The differential species are *Rudgea trujilloi*, *Coursetia ferruginea*, and *Apuleia leiocarpa*.

Physiognomy: The upper tree layer in plot-26 is dominated by emergent individuals of *Anacardium excelsum* (40 m), *Ormosia macrocalyx* (35 m), and *Cassia grandis* (30 m). Usually, *A. excelsum* has a higher basal area and IVI values, because it is one of the largest trees in the Venezuelan Llanos (Aymard et al., 2011; Lugo et al., 2020). In general, the lower tree layer is dominated by *A. excelsum*, *Melicoccus bijugatus*, *Hirtella triandra*, *Aspidosperma cuspa*, *Vitex compressa*, *Protium heptaphyllum*, and *Zanthoxylum caribaeum*. The sub-arboreal stratum is composed of *Protium heptaphyllum*, *Hirtella triandra*, *Inga vera*, *Vitex compressa*, *Pseudalbizzia niopoides*, *Pouteria glomerata*, *Cupania americana*, *Guapira ferruginea*, and 19 other species measured in the nine surveys that are included in this association. The lower layer is composed of *Melicoccus bijugatus*, *Calathea lutea*, *Ardisia foetida*, *Piper tuberculatum*, *Guapira ferruginea*, *Stylogyne micrantha*, *Leptobalanus apetalus*, *Ormosia macrocalyx*, and 15 other species.

The climbing species (vines, lianas) that reach the upper strata of the forest are *Mascagnia ovatifolia*, *Friedericia florida*, *Friedericia dichotoma*, *Davilla nitida*, *Xylophragma seemannianum*, and *Carolus sinemariensis*.

Distribution: The *Ingo verae*-*Anacardietum excelsi* association is found in La Productora, Bumbi, Pastoreña 1 and 2, Smurfit, Ospino, La Cabaña 1 and 3, and Los Alacranes 3 localities, Portuguesa state.

Information on richness and structure of the *Ingo verae*-*Anacardietum excelsi* association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Association *Vochysia lehmannii*-*Protium heptaphyllum* ass. nov., in this contribution. Table 5.

Typus: Aymard 54-2012

Floristic composition: Among the characteristic-dominant species (30) are *Cecropia peltata*, *Spondias mombin*, *Vochysia lehmannii*, *Astronium graveolens*, *Cupania americana*, *Mabea occidentalis*, *Protium heptaphyllum*, *Ardisia foetida*, *Protium tenuifolium*, *Protium stevensonii*, *Cassia moschata*, *Uniosium velutinifolium*, and *Genipa americana*. The differential species are *Zanthoxylum rhoifolium*, *Miconia prasina*, *Amaioua glomerulata*, *Nectandra bartlettiana*, *Roupala montana*, *Myrciaria floribunda*, and *Pterocarpus acapulcensis*.

Physiognomy: This association has forest with an upper tree layer composed of *Astronium graveolens*, *Xylopia aromatica*, and *Protium heptaphyllum*. The lower arboreal layer is dominated by *Ocotea puberula*, *Cecropia peltata*, *Cordia sericicalyx*, *Protium heptaphyllum*, *Petrea pubescens*, *Cordia bicolor*, and *Vochysia lehmannii*. Common in the lower stratum are *Croton fragrans*, *Protium tenuifolium*, *Cupania americana*, *Nectandra bartlettiana*, *Allophylus racemosus*, *Ocotea puberula*, *Xylopia aromatica*, *Zanthoxylum rhoifolium*, *Vochysia lehmannii*, *Guarea guidonia*, *Inga vera*, *Mabea occidentalis*, and 26 other species. The climbing species (vines, lianas) that reach the upper strata are *Fridericia mollissima*, *Fridericia oxycarpa*, *Davilla nitida*, *Fridericia florida*, *Xylophragma seemannianum*, and *Davilla kunthii*.

Distribution: The *Vochysia lehmannii*-*Protium heptaphyllum* association is found in Los Alacranes 1 and 2, Bumbi, Pastoreña 3, La Productora, Saltanejas 1, 2, and 3; Smurfit, Ospino, El Tesoro 1 and Tacamajaca 1, 2, and 3 localities, Portuguesa state.

Information on richness and structure of the *Vochysia lehmannii*-*Protium heptaphyllum* association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Association *Eschweilero subglandulosae-Protium heptaphyllum* ass. nov., in this contribution, Table 5.

Typus: Aymard 51-2012

Floristic composition: Among the characteristic-dominant species (30) of this association are *Cecropia peltata*, *Tapirira guianensis*, *Eschweilera subglandulosa*, *Vismia cayennensis*, *Protium heptaphyllum*, *Guarea guidonia*, *Virola elongata*, *Mauritia flexuosa*, *Symphonia globulifera*, *Calophyllum brasiliense*, *Tabebuia insignis*, *Ceiba pentandra*, *Hura crepitans*, *Chrysobalanus icaco*, and *Xylopia aromatica*. The differentiating species include *Coccoloba latifolia* and *Maprounea guianensis*.

Physiognomy: In plot-20, *Hura crepitans* is an important species in the upper tree layer. In the lower tree layer, the dominant species are *Protium heptaphyllum*, *Tapirira guianensis*, *Mauritia flexuosa*, *Symphonia globulifera*, *Didymopanax morototoni*, *Virola elongata*, *Trichilia pallida*, *Zanthoxylum caribaeum*, *Eschweilera pedicellata*, and *E. subglandulosa*. The lower stratum is dominated by *Calophyllum brasiliense*, *Chrysobalanus icaco*, *Eschweilera subglandulosa*, *Protium heptaphyllum*, *Swartzia polyphylla*, *Monteverdia guyanensis*, *Virola elongata*, and 18 species placed in the four surveys present in this association.

Distribution: The *Eschweilera subglandulosae-Protium heptaphyllum* association is found in Cerro Negro, Boca del Cogollal, El Rincón, Río Yabo, Paso Marcano, Río Orocuál, and sector Puente Amarillo, Anzoátegui state.

Information on richness and structure of the *Eschweilera subglandulosae-Protium heptaphyllum* association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Cassia moschata and Chomelia spinosa forest, Appendix II.

Physiognomy: The *Cassia moschata* and *Chomelia spinosa* forest has a tree layer composed of *Spondias mombin*, *Cochlospermum vitifolium*, *Handroanthus chrysanthus*, *Cassia moschata*, and *Xylopia aromatica*. The lower stratum is dominated by *Cupania americana*, *Annona jahonii*, *Luehea candida*, *Chomelia spinosa*, and *Copaifera officinalis*. Also, armed (thorny) elements, such as *Leuenergeria (Pereskia) guamacho*, *Randia aculeata*, and *Xylosma benthamii*, are common in this community.

The climbing species (vines, lianas) that reach the upper strata of this forest are *Fridericia mollissima*, *F. oxycarpa*, and *Xylophragma seemannianum*.

Floristic composition: The characteristic-dominant species are *Chomelia spinosa*, *Genipa americana*, *Cupania americana*, *Guettarda divaricata*, *Luehea candida*, and *Lonchocarpus macrocarpus*.

Distribution: The community is based on Gentry's survey (1980) in Guárico state, Calabozo, Llanos Biological Station, 110 m (Phillips and Miller, 2002).

Information on richness, floristic composition, and structure of the *Cassia moschata* and *Chomelia spinosa* forest, such as species, number of individuals, basal area, and IVI values, is found in Appendix II.

Order Cupanio americanae-Tabebuialia roseae ord. nov., in this contribution, Table 6.

Typus: *Ceiba pentandrae-Trichilion martianae*

Physiognomy: The vegetation of the *Cupanio Americanae-Tabebuialia roseae* order includes "guadales" and forest communities.

Floristic composition: Among the characteristic-dominant species (25) are *Tabebuia rosea*, *Genipa americana*, *Cupania americana*, *Deguelia picta*, *Bursera simaruba*, *Coursetia ferruginea*, *Hymenaea courbaril*, *Guettarda divaricata*, *Luehea candida*, *Annona jahonii*, *Doliocarpus dentatus*, *Cordia toqueve*, *Agonandra brasiliensis*, and *Margaritaria nobilis*.

The diagnostic species (differential) are *Aralia excelsa*, *Clitoria arborecensens*, *Enterolobium cyclocarpum*, *Machaerium biovolatum*, *Ormosia macrocalyx*, *Stylogyne micrantha*, and *Triplaris caracasana*.

Information on richness, floristic composition, and structure of the *Cupanio Americanae-Tabebuialia roseae* order, such as species, number of individuals, basal area, and IVI values, is found in Table 3.

Alliance Ceiba pentandrae-Trichilion martianae all. nov., in this contribution, Table 6.

Typus: *Ingo interruptae-Pterocarpum acapulcensis*

Floristic composition: Among the characteristic-dominant species (22) are *Ceiba pentandra*, *Trichilia martiana*, *Sterculia apetala*, *Guazuma ulmifolia*, *Spondias mombin*, *Deguelia picta*, *Casearia guianensis*, *Erythrina fusca*, *Sapium glandulosum*, *Tabebuia rosea*, *Hura crepitans*, *Coccoloba latifolia*, *Pterocarpus acapulcensis*, *Pithecellobium lanceolatum*, *Cochlospermum vitifolium*, *Allophylus racemosus*, and *Guadua angustifolia*.

Physiognomy: The vegetation of this alliance includes "guadales" and forest communities. The vegetation

has a well-defined upper tree layer, where *Erythrina fusca*, *Anacardium excelsum*, *Pterocarpus acapulcensis*, *Doliocarpus dentatus*, and *Pachira aquatica* are dominant. The lower arboreal stratum is dominated by *Erythrina fusca*, *Tabebuia rosea*, *Guazuma ulmifolia*, *Spondias mombin*, *Inga ingoides*, *Sterculia apetala*, and *Euterpe oleracea*. *Seguiera macrophylla*, *Guadua angustifolia*, *Casearia guianensis*, and *Trichilia martiana* are present in the lower stratum.

The woody climbers (vines) that reach the upper strata are *Fridericia mollissima*, *F. platyphylla*, and *F. pubescens*.

Distribution: The vegetation of the *Ceibo pentandrae-Trichilion martiana* alliance is found in Río Amana (sector Caño Amarillo), NE of Sta. Bárbara de Maturín, Río Guarapiche, Los bajos del Furrial and Carmen del Guarapiche, Los Colorados, San José de Buja, El Rabanal, localities, Monagas state, as well as in Montelar, La Productora, Papelón 1, Portuguesa state, Chaparito 2, Los Cocos, Chaparrito 1, and Caño San Rafael, Barinas state.

Information on richness, floristic composition, and structure of the *Ceibo pentandrae-Trichilion martiana* alliance, such as species, number of individuals, basal area, and IVI values, is found in Table 4.

Association *Huro crepitantis-Guaduetum angustifoliae* ass. nov., in this contribution. Table 6.

Typus: Aymard 38-2012

Floristic composition: Among the characteristic-dominant species (24) are *Ceiba pentandra*, *Trichilia martiana*, *Guadua angustifolia*, *Sterculia apetala*, *Tanaecium tetragonolobum*, *Tabebuia rosea*, *Guazuma ulmifolia*, *Pterocarpus acapulcensis*, *Casearia guianensis*, *Samanea saman*, *Spondias mombin*, *Coccoloba latifolia*, *Cecropia peltata*, *Sapium glandulosum*, and *Hura crepitans*. The diagnostic species are *Roystonea oleracea*, *Desmoncus orthacanthos*, *Faramaea occidentalis*, *Strychnos mattogrossensis*, and *S. panamensis*.

Physiognomy: The vegetation of this association is composed of guadales, with forests that harbor an upper tree layer (>25 m) with *Erythrina fusca*, *Anacardium excelsum*, and *Pterocarpus acapulcensis*. In the lower tree layer, the dominant species are *Erythrina fusca*, *Tabebuia rosea*, *Guazuma ulmifolia*, *Mauritia flexuosa*, *Spondias mombin*, *Inga ingoides*, *Hura crepitans*, *Sterculia apetala*, and *Ruprechtia cruegeri*. *Coccoloba latifolia*, *Seguiera macrophylla*, *Guadua angustifolia*, *Casearia guianensis*, and *Tanaecium tetragonolobum* are dominant in the sub-arboreal stratum.

The climbing species (vines, lianas) that reach the upper strata are *Fridericia pubescens*, *Fridericia platyphylla*, and *Davilla kunthii*.

Distribution: The vegetation of this association is found in Río Amana, NE of Sta. Bárbara de Maturín, Río Guarapiche, and bajos del Furrial, Monagas state, as well as in Montelar and La Productora localities, Portuguesa state.

Information on richness, floristic composition, and structure of the *Huro crepitantis-Guaduetum angustifoliae* association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Association *Ingo interruptae-Pterocarpetum acapulcensis* ass. nov., in this contribution. Table 6.

Typus: Aymard 28-2012

Floristic composition: Among the characteristic-dominant species (25) are *Guazuma ulmifolia*, *Cochlospermum vitifolium*, *Inga interrupta*, *Spondias mombin*, *Pterocarpus acapulcensis*, *Coccoloba caracasana*, *Ruprechtia ramiflora*, *Pithecellobium lanceolatum*, *Sapium glandulosum*, *Bravaisia integerrima*, *Ceiba pentandra*, and *Deguelia picta*.

The diagnostic species are *Pseudalbizia niopoides*, *Cordia tetrandra*, *Samanea saman*, *Tetracera volubilis*, *Casearia completa*, *Pisonia aculeata*, and *Libidibia punctata*.

Physiognomy: This forest has a well-defined upper tree layer (> 25 m) with *Hymenaea courbaril*, *Pterocarpus acapulcensis*, and *Spondias mombin* as dominant species. In the lower tree layer, *Ceiba pentandra*, *Cecropia peltata*, *Bravaisia integerrima*, *Cochlospermum vitifolium*, *Guazuma ulmifolia*, *Pithecellobium lanceolatum*, and *Astronium graveolens* were observed. In the lower stratum, *Pterocarpus acapulcensis*, *Clitoria dendrina*, *Lonchocarpus velutinus*, *Sapium glandulosum*, and *Machaerium robinifolium* were dominant species.

The climbing species (vines, lianas) that reach the upper strata of the forest are *Fridericia dichotoma*, *F. mollissima*, *F. platyphylla*, and *F. pubescens*.

Distribution: The vegetation of the *Ingo interruptae-Pterocarpetum acapulcensis* association is found in La Productora and Papelón 1–2, Portuguesa state, as well as in the Chaparito 1–2, Los Cocos, and Caño San Rafael localities, Barinas state, and in Carmen del Guarapiche, Monagas state.

Information on richness, floristic composition, and structure of the *Ingo interruptae-Pterocarpetum acapulcensis* association, such as species, number of individuals, basal area, and IVI values, is found in I.

Association *Spondiado mombinis-Trichilietum pallidae* ass. nov., in this contribution. Table 6.

Typus: Aymard 22-2012

Floristic composition: Among the characteristic-dominant species (20) are *Guazuma ulmifolia*, *Spondias mombin*, *Sapium glandulosum*, *Cupania americana*, *Genipa americana*, *Hymenaea courbaril*, *Trichilia martiana*, *Trichilia pallida*, *Neea spruceana*, *Attalea maripa*, *Coccoloba latifolia*, *Vismia cayennensis*, *Couropita guianensis*, and *Cordia collococca*.

The diagnostic species are *Pachira aquatica*, *Eugenia cribrata*, *Casearia sylvestris* var. *sylyvestris*, and *Protium laxiflorum*.

Physiognomy: This forest has an open upper tree layer (>25 m) with *Pachira aquatica* (Plot 8). The lower tree layer is dominated by *Tapirira guianensis*, *Cochlospermum orinocense*, *Attalea maripa*, *Euterpe oleracea*, *Cupania americana*, *Spondias mombin*, and *Jacaranda obtusifolia*. The lower stratum is composed of *Tapirira guianensis*, *Attalea maripa*, *Brownea coccinea*, *Cupania americana*, *Coccoloba latifolia*, *Trichilia pallida*, and *Casearia aculeata*.

The most common climbing species (vines, lianas) that reaches the upper strata of the forest is *Davilla kunthii*.

Distribution: The vegetation of this association is found in Los Colorados, río Amana, San José de Buja and Rabanal, Monagas state.

Information on richness, floristic composition, and structure of the *Spondiado mombinis-Trichilietum pallidae* association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Undefined alliance

Anacardium excelsum and Guazuma ulmifolia forest community. Table 7.

Floristic composition and physiognomy: This forest has an upper stratum dominated by *Guazuma ulmifolia*, *Cecropia peltata*, *Coccoloba caracasana*, *Anacardium excelsum*, *Inga vera*, *Bactris major*, *Guadua* sp., and *Annona purpurea*. The lower tree layer is dominated by *Guadua* sp., *Guazuma ulmifolia*, *Anacardium excelsum*, and *Annona purpurea*.

The most common climbing species (vines, lianas) that reaches the upper strata of the forest is *Xylophragma seemannianum*.

Distribution: The vegetation of this forest community is found in Smurfit, Ospino, and La Cabaña 2 localities, Portuguesa state.

Information on richness, floristic composition, and structure of the *Anacardium excelsum* and *Guazuma ulmifolia* forest community, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Connarus araucanus and Eugenia punicifolia forest Table 7.

Floristic composition: Among the dominant species (20) are *Deguelia picta*, *Coursetia ferruginea*, *Hymenaea courbaril*, *Guettarda divaricata*, *Cordia alliodora*, *Connarus araucanus*, *Eugenia punicifolia*, *Lonchocarpus violaceus*, *Senegalia polyphylla*, *Casearia ulmifolia*, *Machaerium myrianthum*, *Cupania latifolia*, *Strychnos fendleri*, and *Unioostium velutinifolium*.

This phytosociological arrangement grouped vegetation into one class, two orders, five alliances, 10 associations, and two forest communities. This classification allowed the definition of the *Guazumo ulmifoliae-Spondiadetea mombinis* class with two orders: the *Cupanio americanae-Protietalia heptaphylli* order, in which the mixed palm groves dominated by *Attalea butyracea* and the forests dominated by *Protium heptaphyllum* meet; and the *Cupanio americanae-Tabebuietalia roseae* order, that harbors the forests dominated by *Trichillia* spp., *Pterocarpus acalpuensis*, *Connarus araucanus*, and *Guarea guidonia*, among other species. The syntaxonomic units described here represent the first modern proposal to classify the forest vegetation in the Venezuelan Llanos. The analysis technique used showed the floristic differences between the groups. In general, these forests have between three and four well-defined strata, with an average canopy height of 25 m, with emergent individuals to 40 m.

The species and individuals (by species) values of each

Physiognomy: This forest has a lower tree layer dominated by *Cordia alliodora*, *Lonchocarpus violaceus*, *Senegalia polyphylla*, and *Unioostium velutinifolium*. The lower stratum is dominated by *Eugenia punicifolia*, *Connarus araucanus*, *Guettarda divaricata*, *Eugenia cribata*, and *Unioostium velutinifolium*.

The most common climbing species (vines, lianas) that reach the upper strata of the forest are *Fridericia mollissima* and *Strychnos fendleri*.

Distribution: The vegetation of this forest is found in río Amana locality, Monagas state, and Cerro Negro, Anzoátegui state.

Information on richness, floristic composition, and structure of the *Connarus araucanus* and *Eugenia punicifolia* forest, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

Association Homalolepidis cedrontis-Guareetum guidoniae ass. nov., in this contribution. Table 7.

Typus: Aymard 48-2012

Floristic composition: Among the characteristic-dominant species (15) are *Sapium glandulosum*, *Tabebuia rosea*, *Homalolepis (Simaba) cedron*, *Guarea guidonia*, *Ficus máxima*, *Protium heptaphyllum*, *Didymopanax morototoni*, *Vismia guianensis*, *Zygia latifolia*, *Tapirira guianensis*, *Spondias mombin*, and *Ocotea leptobotra*.

Physiognomy: This forest has a lower tree layer dominated by *Tapirira guianensis*, *Zygia latifolia*, *Guarea guidonia*, *Protium heptaphyllum*, *Xylopi aromaticum*, *Ocotea aurantiodora*, *Homalolepis cedron*, *Croton megalodendron*, *Annona fendleri*, and *Duguetia lucida*.

Distribution: The vegetation of this association is found in Navay, Urimán 1, Culebra 2, Los Monos 1 and El Tesoro 2, Táchira state.

Information on richness, floristic composition, and structure of the *Homalolepidis cedrontis-Guareetum guidoniae* association, such as species, number of individuals, basal area, and IVI values, is found in Appendix I.

DISCUSSION

syntaxonomic unit are shown in Table 8.

In the *Guazumo ulmifoliae-Spondiadetea mombinis*, 630 species were found in 65,000 m² (6.5 ha), with an average of 30 species/plot in the 66 surveys carried out. The richness index (species per square meter) is 0.97 x 10⁻². In total, 13,469 individuals were found (average 188) and the density index was 20.7 x 10⁻² individuals per m². In the order *Cupanio americanae-Protietalia heptaphylli* in 38,000 m² (3.8 ha), 510 species were found with an average of 38 species/plot. The richness index is 1.3 x 10⁻² species per m². In total 9554 individuals were found (average 245) and density index 25.1 x 10⁻² individuals per m².

At the alliance level, the highest values were found in the *Protio heptaphylli-Attaleion butyraceae*, with 295 species, a richness index of 4 x 10⁻² and 3470 individuals with a density index of 43 x 10⁻² in eight surveys covering 8000 m².

In the other order *Cupanio americanae-Tabebuietalia roseae* in 27000 m² (2.7 ha) 278 species were found with an average of 22 species/survey and density index

14.5×10^{-2} individuals per m^2 . In the *Ceibo pentandrae-Trichilion martianae* alliance 236 species were found and a richness index of 1×10^{-2} . In total, 3078 individuals (average 154) were measured, with a density index 16×10^{-2} individuals per m^2 /survey.

At the association level, the highest number of species (215) was found in *Attaleo butyraceae-Guaduetum angustifoliae* in an area of 3,000 m^2 , the richness index ($sp./m^2$) is 7×10^{-2} . The lowest values in number of species were found in the communities of *Anacardium excelsum*, *Guazuma ulmifoliae* (26), *Connarus araucanus*, and *Eugenia puniceifolia* (47). Regarding the number of individuals, the highest value (3045) was found in the association *Vochysia lehmanni-Protietum heptaphylli* and the lowest (212) in *Homalolepidis cedrontis-Guareetum guidoniae*.

The lowest values of species number were found in the *Anacardium excelsum* and *Guazuma ulmifolia* (26) and the *Connarus araucanus* and *Eugenia puniceifolia* (47) forest communities. The highest individual value (3045) was found in the *Vochysia lehmanni-Protietum heptaphylli* association, and the lowest (212) in the *Homalolepidis cedrontis-Guareetum guidoniae* association.

The information from A. Gentry's field plots using 0.10 ha (1000 m^2 ; each consisting of ten 2 m \times 50 m subplots/subtransects) is based on the worldwide woody plant abundance records in 197 localities (Gentry, 1995; Phillips and Miller, 2002). In dry forests, Gentry found between 50 and 70 species (60 average, I.R. = 6×10^{-2} species per square meter). He pointed out that the richest dry forests in Latin America are located in Los Colorados, Colombia (121 species), Coloso, Colombia (113 species), and in Chamela, Mexico (103). The highest richness value in this work was 106 species (0.1 ha) in the "palm-guadual" community in the *Attaleo butyraceae-Guaduetum angustifoliae* association. Gentry's forest transect data have been frequently used to assess global patterns of plant diversity and plant species compositional changes along environmental and geographical gradients. However, Gentry's data were collected along narrow transects, and, therefore, the dependence among sampled individuals due to spatial aggregation is generally weak (Chao et al., 2023). The same authors also pointed out that coverage-based standardization analysis reveals latitudinal beta diversity patterns/trends not

only for richness-based, but also for abundance-sensitive beta diversity. Additionally, Fajardo et al. (2005) mentioned between 110–170 species for Venezuelan dry forests in an area of 10 hectares.

This syntaxonomic scheme of the Venezuelan Llanos is compared with other regions, such as the Caribbean and the Colombian Llanos, resulting in interesting floristic convergence between these regions. A notable feature is the dominance of *Cupania americana* in the Venezuelan Llanos. In the Orinoquia of Colombia, the latter species is a companion taxon in the *Protio tenuifoli-Himatanthion articulati* alliance and of the *Jacarando copaiaie-Luehetea seemani* class (Rangel-Ch. et al., 2022). In the Venezuelan Llanos, *Guazuma ulmifolia* is a very important taxon at a higher level (class), a condition that does not occur in the vegetation of the eastern "Llanos" of Colombia. The Llanos of Colombia and Venezuela share vegetation associations, such as the palm communities with *Attalea butyracea*, the forests with *Spondias mombin* and *Protium heptaphyllum*, and the forests of *Connarus araucanus* and *Guadua angustifolia*.

Like many biomes in Latin America, the Orinoco Llanos have been subjected (especially since the last century) to excessive exploitation of their natural resources based on the expansion of the agricultural frontier, logging, and the extraction of hydrocarbons (Pacheco-Angulo et al., 2011, 2017). The anthropogenic transformations have been manifested in changes in the species composition and structure of the forests. The changes may translate into a response of the vegetation that is associated with a higher level of dominance of a few widely distributed species. This floristic composition is associated with pioneer species in the processes of plant succession. The final objective is the restoration of the original conditions in the pattern of plant richness to continue offering the varied environmental services that vegetation provides. The conservation efforts carried out by governmental and non-governmental organizations can be improved with original scientific information such as that offered here. It is essential to implement management plans based on knowledge of the natural environment in such a way as to ensure the persistence of the biodiversity of the very important natural region.

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TABLE 1. Location of sampling sites (States and localities).

PLOT AYMARD 2012	LOCALITIES	ALT. (M)	PLOT AYMARD 2012	LOCALITIES	ALT. (M)
State Anzoátegui, Cerro Negro			State Portuguesa		
6	Boca del Cogollal	80	10	Bumbi Pastoreña 3	200
7	Boca del Cogollal	80	24	La Cabaña 1	176
13	El Rincón, Río Yabo	80	25	La Cabaña 2	184
51	Paso Marcano, Río Yabo	80	26	La Cabaña 3	176
Estado Barinas			34	Los Alacranes 1	220
14	El Trueno	300	35	Los Alacranes 2	254
32	Las Colinas	300	36	Los Alacranes 3	228
37	Los Cocos, ca. 30 S de Guanare	300	49	Papelón 1, ca. 25 SE de Guanare	180
52	Pedro Morales	300	50	Papelón- 2, ca. 25 SE de Guanare	180
12	Chaparito 2	87	53	Saltanejas 1	180
11	Chaparrito 1, Caño San Rafael	123	54	Saltanejas 2	180
State Monagas			55	Saltanejas 3	180
15	Bajo del Carmen del Guarapiche, SO de Jusepín	230	61	Smurfit, Ospino	176
19	Caserío La Laguna, 15 km al Norte de Jusepín	230-241	62	Smurfit, Ospino	176
4	Lower Río Amana	50	63	Smurfit, Ospino	200
33	Oeste de la Hormiga, sector Las Coloradas	20	64	Smurfit, Ospino	200
2	Río Amana (sector Caño Amarillo)	125	65	Smurfit, Ospino	200
18	Río Amana, NE Sta. Bárbara de Maturín	90	67	Smurfit, Ospino	200
1	Río Amana, 2 km S de Musipán	122	57	Tacamajaca 1	260
3	Río Amana, 5 km N de Morón	125	58	Tacamajaca 2	256
5	Río Amana, NE de Sta. Barbará de Maturín	150	59	Tacamajaca 3	260
17	Río Amana, sector Amana abajo	48	9	Bumbi Pastoreña 2	200
16	Río Guarapiche, sector bajos del Furrial, Norte del Furrial	110	27	Finca La Productora, 20 km NE de Guanare	180
56	San José de Buja, sector el Rabanal	20	28	Finca La Productora, 20 km NE de Guanare	180
23	Río Guanipa, sector Los Pozos de Guanipa	110	29	Finca La Productora, 20 km NE de Guanare	180
20	Río Orocuai, sector Puente Amarillo, 15 km Norte de La Toscana	105-112	30	Finca La Productora, 20 km NE de Guanare	180
21	San José de Buja, sector El Rabanal	12	31	Finca La Productora, 20 km NE de Guanare	180
22	Sector Los Colorados, Oeste del Caserío La Hormiga	10-14	38	Finca Montelar, 50 km NE de Guanare	181
State Táchira, Navay			39	Morador 1	300
46	Culebra 1	188	40	Morador 2	316
47	Culebra 2	188	41	Morador 4	322
42	El Tesoro 1	188	60	Tucupido dam	250
43	El Tesoro 2	188	8	Bumbi Pastoreña 1	200
48	Los Monos 1	188	Estado Guárico, Calabozo		
44	Urimán 1	188	Gentry, 1980	Llanos Biological station	110
45	Urimán 2	188			

TABLE 2. Floristic composition of *Guazuma ulmifoliae-Spondiadetea mombinis* class and *Cupanio americanae-Protietalia heptaphylli* order.

PLOT AYMARD 2012	14	52	32	39	41	46	60	40
SURFACE PLOT. (M²):	1000							
ALTITUDE (M):	300	300	300	300	322	188	250	316
	Relative Density (%)							
Class <i>Guazuma ulmifoliae-Spondiadetea mombinis</i>								
<i>Cecropia peltata</i>	1,2	1,0	0,7			2,0	1,4	0,6
<i>Spondias mombin</i>	1,0	0,5	0,6			6,0	0,9	
<i>Astronium graveolens</i>		0,4	2,6	0,4			0,9	3,0
<i>Fissicalyx fendleri</i>	0,2	0,2	0,3				0,5	
<i>Cochlospermum vitifolium</i>	0,2		0,1		0,5			
<i>Guazuma ulmifolia</i>	0,1	0,2	0,7					
<i>Sorocea sprucei</i>		1,6	0,7				0,9	
<i>Apeiba tibourbou</i>	0,1		0,1					0,6
<i>Tapirira guianensis</i>		0,5	0,1				2,3	
<i>Sapium glandulosum</i>	0,3	0,1						0,6
<i>Jacaranda obtusifolia</i>	0,1	0,1	1,6					
<i>Inga ingoides</i>	0,9	0,1					0,9	
<i>Annona montana</i>	0,4	0,2	0,9					
<i>Schnella guianensis</i>		0,1	0,9					
<i>Zanthoxylum caribaeum</i>			1,4				2,8	
<i>Platymiscium pinnatum</i>			0,1					0,6
<i>Leptobalanus apetalus</i>	0,2		0,1					
<i>Inga interrupta</i>		0,1					1,4	
<i>Hymenaea courbaril</i>				1,3	0,5			
<i>Luehea candida</i>		0,3						1,2
<i>Phyllanthus acuminatus</i>	0,2							
<i>Clitoria arborescens</i>							0,5	
<i>Cordia toqueve</i>		0,1						
Order <i>Cupanio americanae-Protietalia heptaphylli</i>								
<i>Didymopanax morototoni</i>	0,2	0,6	1,1	3,0	1,5	12		0,6
<i>Cupania americana</i>	0,2	0,5	2,0	0,4	0,5	4		
<i>Guarea guidonia</i>	2,8	1,5	1,4		1,5	30	0,5	
<i>Protium heptaphyllum</i>				7,0	9,7	4	2,3	4,2
<i>Protium tenuifolium</i>		2,8	0,3		1,5		0,5	9,1
<i>Ardisia foetida</i>			4,3		1,0		0,9	0,6
<i>Casearia sylvestris</i>	0,5		0,1				0,5	
<i>Allophylus racemosus</i>				3,0			0,5	
<i>Ocotea puberula</i>				4,8	4,6			
<i>Vitex compressa</i>		0,2					1,9	
<i>Protium stevensonii</i>				2,2			0,5	
<i>Agonandra brasiliensis</i>					1,0		0,5	
<i>Neea amplifolia</i>			0,3					0,6
<i>Oenocarpus mapora</i>				0,4				22,4

TABLE 2 CONT. Floristic composition of *Guazuma ulmifoliae*-*Spondiadetea mombinis* class and *Cupanio americanae*-*Protietalia heptaphylli* order.

PLOT AYMARD 2012	14	52	32	39	41	46	60	40
<i>Cordia alliodora</i>				3,9				
<i>Ceiba pentandra</i>		0,2						
<i>Amphilophium paniculatum</i>		0,5						
<i>Cestrum latifolium</i>		0,4						
<i>Casearia aculeata</i>		0,2						
<i>Euterpe precatoria</i>	0,9							
<i>Ouratea castaneifolia</i>							0,5	
<i>Ouratea guildingii</i>		0,1						
<i>Piper arboreum</i>								1,2
<i>Piper marginatum</i>	0,3							
<i>Psychotria carthagenensis</i>	0,1							
<i>Sloanea</i> sp.				1,3				
<i>Miconia minutiflora</i>					0,5			
<i>Protio heptaphylli</i>-<i>Attaleion butyraceae</i>								
<i>Attalea butyracea</i>	2,7	3,8	5,9	0,9	2,6	2	3,3	4,8
<i>Guatteria pilosula</i>	0,3	0,8	0,9	3,0	2		0,5	
<i>Miconia magdalenae</i>	0,4	0,1	0,4	4,3				7,9
<i>Pradosia caracasana</i>	0,1	0,1	0,3				2,8	
<i>Hirtella triandra</i>	0,7	0,1	0,4				2,3	
<i>Clavija ornata</i>	0,1	0,1	1,1				0,5	
<i>Citharexylum venezuelense</i>		0,3	0,7				1,9	0,6
<i>Anacardium excelsum</i>	0,1		0,9				0,9	
<i>Bixa urucurana</i>	1,5	5,7					0,9	
<i>Vitex orinocensis</i>		0,1	0,3		0,5			
<i>Cyathea microdonta</i>			0,1					3,6
<i>Nectandra hihua</i>		0,4						2,4
<i>Platypodium elegans</i>			0,3				0,5	
<i>Serjania atrolineata</i>		0,3					0,5	
<i>Pochota fendleri</i>			0,6				1,4	
<i>Stylogyne longifolia</i>		0,2					0,5	
<i>Pombalia prunifolia</i>		0,2					0,5	
<i>Ficus maxima</i>		0,1				2,0		
<i>Myrtaceae</i>		0,2					0,5	
<i>Ocotea bofo</i>			0,9				1,4	
<i>Croton gossypifolius</i>	0,1						1,9	
<i>Zanthoxylum rhoifolium</i>		0,3			2,6			
<i>Tanaecium tetragonolobum</i>		0,2					0,9	
<i>Attaleo butyraceae</i>-<i>Guaduetum angustifoliae</i>								
<i>Guadua angustifolia</i>	52,7	41,1	9,3					
<i>Brosimum alicastrum</i>	2,4	0,3	1					
<i>Paullinia cururu</i>	1,3	1,1	0,1					
<i>Fridericia</i> sp.	0,7	1,1	2,2					

TABLE 2 CONT. Floristic composition of *Guazuma ulmifoliae*-*Spondiadetea mombinis* class and *Cupanio americanae*-*Protietalia heptaphylli* order.

PLOT AYMARD 2012	14	52	32	39	41	46	60	40
<i>Machaerium humboldtianum</i>	0,5	0,2					0,9	
<i>Stylogyne micrantha</i>	0,9	0,2	1,4					
<i>Aiphanes horrida</i>	0,6	0,7	2,7					
<i>Dendropanax arboreus</i>	0,2	0,6	2,6					
<i>Ficus insipida</i>	0,2	0,4	0,7					
<i>Protium crenatum</i>	0,3	0,3	5,9					
<i>Smilax purhampuy</i>	0,2	1,1	0,6					
<i>Triplaris americana</i>	0,2	0,1	0,4					
<i>Inga</i> sp2	0,1	0,4	0,3					
<i>Ocotea</i> sp2	0,2	0,1						
<i>Ocotea</i> sp3	0,1	0,1						
<i>Costus guanaiensis</i>	0,1	0,7						
<i>Parinari pachyphylla</i>		2,9	0,1					
<i>Herrania albiflora</i>	1,9		1,7					
<i>Myrcia</i> sp.		0,3	6,2					
<i>Inga</i> sp.	1,2	1,2						
<i>Mabea macrocalyx</i>		1,5	1,0					
<i>Adenocalymma</i> sp.	0,3		0,1					
<i>Myrcia splendens</i>		0,5	0,9					
<i>Myrcia</i> sp2	0,3		0,1					
<i>Nectandra</i> sp.	0,5	0,3						
<i>Notopleura macrophylla</i>	2,8		2,7					
<i>Erythrina fusca</i>	1,0	0,5						
<i>Gouania polygama</i>	0,1		0,4					
<i>Protium opacum</i> subsp. <i>exaggeratum</i>		0,4	0,6					
<i>Tabernaemontana grandiflora</i>		0,3	0,7					
<i>Luehea seemanii</i>	0,2		1,4				2,3	
<i>Siparuna guianensis</i>	0,1		1					
<i>Pleurothyrium trianae</i>	2,6	1,5						1,2
<i>Rudgea hostmanniana</i>		0,1	1,7					
<i>Cordia</i> sp.		0,2	0,3					
<i>Paullinia leiocarpa</i>	0,3		0,3					
<i>Talisia</i> sp.		0,3	0,3					
<i>Urera caracasana</i>	1,0	0,4						
<i>Roystonea oleracea</i>		1	1,7					
<i>Annona glabra</i>	0,2	1						
<i>Himatanthus articulatus</i>		0,2	0,7					
<i>Acalypha diversifolia</i>	4,0	2,5	0,6					
<i>Pouteria baehniana</i>	0,1	0,1						
<i>Attaleo butyraceae</i>-<i>Rudgeetum crassilobae</i>								
<i>Rudgea crassiloba</i>			2,3	16,5	48,5		0,5	1,2
<i>Xylopia aromatica</i>		0,2		5,2	8,7			0,6

TABLE 2 CONT. Floristic composition of *Guazumo ulmifoliae-Spondiadetea mombinis* class and *Cupanio americanae-Protietalia heptaphylli* order.

PLOT AYMARD 2012	14	52	32	39	41	46	60	40
<i>Serjania adusta</i>				2,2	4,1			2,4
<i>Warszewiczia coccinea</i>			0,4			2	1,9	
<i>Inga sapindoides</i>		0,1				2	0,5	
<i>Myrcia splendens</i>				9,1	2,6			
<i>Bunchosia argentea</i>					1		0,5	
<i>Deguelia picta</i>				0,9			2,8	
<i>Petrea pubescens</i>				0,4			0,5	
<i>Rudgea trujilloi</i>					0,5		0,5	
<i>Triplaris caracasana</i>				10,4			0,5	
<i>Bactris major</i>							4,2	5,5
<i>Miconia prasina</i>							0,5	3,6
<i>Miconia serrulata</i>			1,9		0,5			1,2
<i>Cassia moschata</i>				0,4				0,6
<i>Genipa americana</i>		0,2			0,5			11
Species number	82	130	105	36	26	21	75	31

Other species present:

Strychnos panamensis (14/0,11), (32/0,14), *Terminalia oblonga* (14/0,11), *Aegiphila elata* var. *macrophylla* (14/0,11), *Aristolochia odoratissima* (14/0,11), *Stigmaphyllon sinuatum* (14/0,11), *Celtis iguanaea* (14/0,21), *Dioscorea polygonoides* (14/0,21), Indeterminado (14/0,21), *Mucuna urens* (14/0,21), *Ocotea* sp5 (14/0,21), *Acalypha macrostachya* (14/0,32), *Ocotea* sp4 (14/0,32), *Matelea* sp. (14/0,43), *Salacia elliptica* (14/0,43), *Hura crepitans* (14/0,53), *Piper tenue* (14/0,53), *Inga subnuda* (14/0,64), *Ocotea* sp1 (14/1,39), *Ocotea* sp. 1 (52/0,1), (32/0,86), *Aralia excelsa* (52/0,1), *Jupunba trapezifolia* (52/0,1), *Ocotea leptobotra* (52/0,1), *Maclura tinctoria* (52/0,1), *Libidibia punctata* (52/0,1), *Conarus araucanus* (52/0,1), *Fridericia* sp.2 (52/0,1), Bignoniaceae sp.1 (52/0,1), Bignoniaceae sp.4 (52/0,1), *Dilodendron bipinnatum* (52/0,1), *Hieronyma alchorneoides* (52/0,1), *Monteverdia macrocarpa* (52/0,1), *Miconia ibaguensis* (52/0,1), *Ochroma pyramidale* (52/0,1), *Passiflora foetida* (52/0,1), *Paullinia pinnata* (52/0,1), *Senna macrophylla* (52/0,1), *Trigonia bracteata* (52/0,1), *Verbesina caracasana* (52/0,1), *Zanthoxylum setulosum* (52/0,1), *Chrysophyllum argenteum* (52/0,2), (32/0,43), *Amphilophium paniculatum* (52/0,2), *Carludovica palmata* (52/0,2), *Cestrum alternifolium* (52/0,2), *Machaerium kegelii* (52/0,2), *Matayba guianensis* (52/0,2), *Piper demeraranum* (52/0,2), *Terminalia amazonia* (52/0,3), *Annona exsucca* (52/0,3), *Mangifera indica* (52/0,3), *Protium mucronatum* (52/0,3), *Trichilia maynasiana* (52/0,41), *Inga punctata* (52/0,51), *Piper hispidum* (52/0,61), *Pterocarpus* sp. (32/0,14), (46/2), *Combretum fruticosum* (32/0,14), *Heisteria acuminata* (32/0,14), *Amaioua glomerulata* (32/0,14), *Lonchocarpus hedyosmus* (32/0,14), *Syagrus sancona* (32/0,14), *Aphelandra scabra* (32/0,14), *Guettarda tobagensis* (32/0,14), Indeterminado (32/0,14), *Machaerium arboreum* (32/0,14), *Phyllanthus* sp. (32/0,14), *Posoqueria latifolia* (32/0,14), *Piper tuberculatum* (32/0,29), *Rinorea pubiflora* (32/0,29), *Randia venezuelensis* (32/0,43), *Zanthoxylum syncarpum* (32/0,43), *Adelia ricinella* (32/1), *Casearia mollis* (32/1), *Lonchocarpus* sp. (32/1,15), *Annona mucosa* (39/0,43), *Albizia* aff. *barinensis* (39/0,43), *Macropsychnanthus malacocarpus* (39/0,43), *Eugenia pseudopsidium* (39/0,43), *Vitex capitata* (39/0,87), *Jacaranda caucana* (39/0,87), *Acaciella angustissima* (39/0,87), *Fridericia platyphylla* (39/0,87), *Casearia arborea* (39/1,3), *Swartzia pittieri* (39/2,61), *Xylophragma seemannianum* (39/3,91), *Machaerium biovulatum* (41/0,51), *Davilla nitida* (41/1,02), *Machaerium inundatum* (41/1,53), *Homalolepis cedron* (46/2), *Tabebuia rosea* (46/2), *Trigynaea duckei* (46/2), *Socratea exorrhiza* (46/4), *Vismia guianensis* (46/4), *Cochlospermum orinocense* (46/6), *Handroanthus serratifolius* (46/6), *Pseudoalbizia niopoides* (60/0,47), *Pseudo-samanea guachapele* (60/0,47), *Cratava tapia* (60/0,47), *Bromelia chrysantha* (60/0,47), *Centrolobium paraense* (60/0,47), *Coccoloba padiformis* (60/0,47), *Guadua latifolia* (60/0,47), *Ocotea leptobotra* (60/0,47), *Rinorea lindeniana* (60/0,47), *Simira lezamae* (60/0,47), *Solanum bicolor* (60/0,47), *Zanthoxylum culantrillo* (60/0,47), *Inga vera* (60/0,93), *Ormosia macrocalyx* (60/0,93), *Bursera simaruba* (60/0,93), *Trichanthera gigantea* (60/0,93), *Coccoloba ovata* (60/0,93), *Costus comosus* (60/0,93), *Strychnos schultesiana* (60/0,93), *Mouriri pseudogeminata* (60/1,4), *Pseudobombax septenatum* (60/1,87), *Croton fragrans* (60/1,87), *Euphorbia cotinifolia* (60/2,34), *Fareamea occidentalis* (60/5,61), *Calathea lutea* (60/16,82), *Vochysia lehmannii* (40/0,61), *Lacistema aggregatum* (40/2,42), *Inga capitata* (40/1,21), *Erythroxylum macrophyllum* (52/0,1), (32/1), (39/3,91), *Myrcia* sp. (32/0,29), *Neea* sp. (32/0,29), *Acalypha villosa* (14/0,11), *Licania* sp. (14/0,11), *Miconia* sp1 (14/0,11), *Myrcia* sp1 (14/0,11), Fabaceae (52/0,1), *Inga nobilis* (52/0,1), *Maripa* sp. (52/0,1), *Ocotea* sp6 (52/0,1), *Turpinia* sp. (52/0,1), *Fridericia* sp.1 (52/0,2), *Piper aequale* (52/0,2), *Guatteria* sp. (52/0,3), *Inga edulis* (52/0,41), *Piper amalago* (52/0,41), *Herrania* sp (52/0,91), *Miconia trinervia* (32/0,14), *Andira inermis* (32/0,14), *Hippocratea* sp. (32/0,14), *Dioclea* sp. (32/0,14), *Inga* sp. 1 (32/0,14), *Myrcia* sp. (32/0,29), *Neea* sp. (32/0,29), *Ouratea* sp. (32/0,43), *Ocotea* sp. 2 (32/0,57), *Simira* sp. (32/0,72), *Piper* sp. (40/3,64), Lauraceae 1 (46/2), Lauraceae 2 (46/2), *Bactris* sp. (46/2), *Psidium* sp. (39/1,3), *Machaerium* sp. (32/0,14), Fabaceae 1 (39/0,43), *Pouteria* sp. 5 (52/0,1), *Pouteria* sp.1 (52/0,1), *Theobroma* sp. (52/0,1), *Pouteria* sp. (52/0,1), *Protium* sp4 (32/0,14), *Guapira* sp. (60/0,47).

TABLE 3. Importance Value Index (IVI) to *Guazuma ulmifoliae*-*Spondiadetea mombinis* class and *Cupanio americanae*-*Protietalia heptaphylli* and *Cupanio americanae*-*Tabebuietalia roseae* orders.

SPECIES	IND.	IND. %	FREC. ABS.	FREC. %	A.B.(CM ²) ABS.	A.B. %	IVI ABS.	IVI %
Class <i>Guazuma ulmifoliae</i>-<i>Spondiadetea mombinis</i>								
<i>Spondias mombin</i>	157	9,14	31	9,31	158819,32	27,72	46,17	15,39
<i>Guazuma ulmifolia</i>	294	17,11	32	9,61	72392,17	12,63	39,36	13,12
<i>Cecropia peltata</i>	242	14,09	34	10,21	45477,89	7,94	32,23	10,74
<i>Leptobalanus apetalus</i>	126	7,33	8	2,4	57358,48	10,01	19,75	6,58
<i>Sapium glandulosum</i>	92	5,36	20	6,01	35959,78	6,28	17,64	5,88
<i>Cochlospermum vitifolium</i>	90	5,24	20	6,01	24455,12	4,27	15,51	5,17
<i>Tapirira guianensis</i>	89	5,18	15	4,5	26518,06	4,63	14,31	4,77
<i>Astronium graveolens</i>	57	3,32	17	5,11	26805,25	4,68	13,1	4,37
<i>Zanthoxylum caribaeum</i>	45	2,62	15	4,5	21786,9	3,8	10,93	3,64
<i>Apeiba tibourbou</i>	58	3,38	12	3,6	12870,84	2,25	9,23	3,08
<i>Sorocea sprucei</i>	57	3,32	13	3,9	6235,23	1,09	8,31	2,77
<i>Schnella guianensis</i>	51	2,97	15	4,5	4067,51	0,71	8,18	2,73
<i>Platymiscium pinnatum</i>	31	1,8	15	4,5	7442,99	1,3	7,61	2,54
<i>Annona purpurea</i>	51	2,97	7	2,1	12905,13	2,25	7,32	2,44
Subtotal	1440	83,83	254	76,26	513094,67	89,56	249,65	83,22
Other taxa: 26 species	278	16,18	79	23,72	59873,51	10,45	50,36	16,79
Subtotal: 40 species	1718	100	333	100	572968,18	100	300	100
Remaining taxa: 590 species	11751				2663336,09			
Total 630 species	13469	NA	NA	NA	3236304,27	NA	NA	NA
Order <i>Cupanio americanae</i>-<i>Protietalia heptaphylli</i>								
<i>Protium heptaphyllum</i>	624	24,55	23	8,42	55078,36	13,53	46,5	15,5
<i>Ceiba pentandra</i>	7	0,28	6	2,2	126418,33	31,05	33,52	11,17
<i>Protium tenuifolium</i>	375	14,75	15	5,49	29333,98	7,2	27,45	9,15
<i>Protium stevensonii</i>	368	14,48	9	3,3	30143,85	7,4	25,18	8,39
<i>Guarea guidonia</i>	177	6,96	19	6,96	36940,62	9,07	23	7,67
<i>Cupania americana</i>	139	5,47	26	9,52	15186,52	3,73	18,72	6,24
<i>Ardisia foetida</i>	185	7,28	20	7,33	9033,88	2,22	16,82	5,61
<i>Didymopanax morototoni</i>	60	2,36	19	6,96	25901,29	6,36	15,68	5,23
<i>Clitoria dendrina</i>	87	3,42	13	4,76	8245,81	2,03	10,21	3,4
<i>Allophylus racemosus</i>	109	4,29	13	4,76	3602	0,88	9,93	3,31
<i>Vitex compressa</i>	28	1,1	10	3,66	10381,77	2,55	7,31	2,44
<i>Cordia alliodora</i>	33	1,3	7	2,56	13456,09	3,3	7,17	2,39
<i>Ocotea puberula</i>	55	2,16	8	2,93	4479,64	1,1	6,19	2,06
<i>Casearia sylvestris</i>	21	0,83	9	3,3	1866,38	0,46	4,58	1,53
Subtotal	2268	89,23	197	72,15	370068,52	90,88	252,26	84,09
Other taxa: 35 species	274	10,78	76	27,86	37087,46	9,11	47,73	15,91
Subtotal: 49 species	2542	100	273	100	407155,96	100	300	100
Remaining taxa: 461 species	7012				1637052,91			
Total: 510 species	9554	NA	NA	NA	2044208,87	NA	NA	NA
Order <i>Cupanio americanae</i>-<i>Tabebuietalia roseae</i>								
<i>Tabebuia rosea</i>	35	11,15	15	16,85	40757,78	46,88	74,88	24,96
<i>Genipa americana</i>	44	14,01	12	13,48	6417,91	7,38	34,88	11,63
<i>Hymenaea courbaril</i>	20	6,37	6	6,74	16403,52	18,87	31,98	10,66
<i>Cupania americana</i>	30	9,55	9	10,11	2212,01	2,54	22,21	7,4
<i>Deguelia picta</i>	38	12,1	2	2,25	2297,92	2,64	16,99	5,66
<i>Bursera simaruba</i>	23	7,32	2	2,25	4612,6	5,31	14,88	4,96
<i>Coursetia ferruginea</i>	24	7,64	2	2,25	568,32	0,65	10,54	3,51
<i>Guettarda divaricata</i>	10	3,18	5	5,62	327,99	0,38	9,18	3,06
<i>Annona jahnii</i>	15	4,78	3	3,37	644,32	0,74	8,89	2,96
<i>Luehea candida</i>	8	2,55	4	4,49	1263,68	1,45	8,5	2,83
<i>Doliocarpus dentatus</i>	4	1,27	2	2,25	2617,53	3,01	6,53	2,18
<i>Cordia toqueve</i>	8	2,55	2	2,25	1280,25	1,47	6,27	2,09
<i>Agonandra brasiliensis</i>	7	2,23	2	2,25	1353,09	1,56	6,03	2,01
<i>Margaritaria nobilis</i>	8	2,55	2	2,25	716,45	0,82	5,62	1,87
Subtotal	274	87,25	68	76,41	81473,37	93,7	257,38	85,78
Other taxa: 11 species	40	12,74	21	23,6	5459,19	6,27	42,61	14,19
Subtotal: 25 species	314	100	89	100	86932,59	100	300	100
Remaining taxa: 253 species	3601				1105162,81			
Total: 278 species	3915	NA	NA	NA	1192095,4	NA	NA	NA

TABLE 4. Importance Value Index (IVI) to *Protio heptaphylli-Attaleion butyraceae*, *Xylopio aromatica-Protion heptaphylli* and *Ceibo pentandrae-Trichilion martianae* alliances.

SPECIES	IND.	IND. %	FREC. ABS.	FREC. %	A.B.(CM ²) ABS.	A.B. %	IVI ABS.	IVI %
alianza <i>Protio heptaphylli-Attaleion butyraceae</i>								
<i>Guadua angustifolia</i>	963	27,75	3	0,59	88788,92	11,18	39,53	13,18
<i>Attalea butyracea</i>	126	3,63	8	1,57	112866,53	14,22	19,42	6,47
<i>Ficus insipida</i>	11	0,32	3	0,59	74184,19	9,34	10,25	3,42
<i>Rudgea crassiloba</i>	152	4,38	5	0,98	13587,59	1,71	7,08	2,36
<i>Guarea guidonia</i>	70	2,02	6	1,18	21633,38	2,72	5,92	1,97
<i>Spondias mombin</i>	23	0,66	5	0,98	29509,59	3,72	5,36	1,79
<i>Guatteria pillosula</i>	29	0,84	6	1,18	19700,66	2,48	4,5	1,5
<i>Didymopanax morototoni</i>	33	0,95	7	1,38	15458,95	1,95	4,28	1,43
<i>Xylopio aromatica</i>	32	0,92	4	0,79	16636,81	2,1	3,81	1,27
<i>Anacardium excelsum</i>	9	0,26	3	0,59	21636,62	2,73	3,58	1,19
<i>Bixa urucurana</i>	72	2,07	3	0,59	6799,16	0,86	3,52	1,17
<i>Astronium graveolens</i>	30	0,86	5	0,98	12453,8	1,57	3,42	1,14
<i>Terminalia amazonia</i>	3	0,09	1	0,2	23170,03	2,92	3,2	1,07
<i>Cecropia peltata</i>	31	0,89	6	1,18	8020,7	1,01	3,08	1,03
<i>Erythrina fusca</i>	14	0,4	2	0,39	17931,57	2,26	3,06	1,02
<i>Protium heptaphyllum</i>	49	1,41	5	0,98	5191,16	0,65	3,05	1,02
Subtotal	1647	47,45	72	14,15	487569,66	61,42	123,06	41,03
Other taxa: 278 species	1823	52,54	436	85,82	306394,33	38,58	176,95	58,99
Total	3470	100	508	100	793963,99	100	300	100
alianza <i>Xylopio aromatica-Protion heptaphylli</i>								
<i>Protium heptaphyllum</i>	575	9,86	18	2,02	49887,2	4,45	16,33	5,44
<i>Anacardium excelsum</i>	37	0,63	9	1,01	138447,51	12,35	13,99	4,66
<i>Ceiba pentandra</i>	4	0,07	4	0,45	121417,05	10,83	11,34	3,78
<i>Protium stevensonii</i>	362	6,21	7	0,78	29945,48	2,67	9,66	3,22
<i>Protium tenuifolium</i>	326	5,59	10	1,12	26064,13	2,32	9,04	3,01
<i>Leptobalanus apetalus</i>	123	2,11	6	0,67	56723,3	5,06	7,84	2,61
<i>Cecropia peltata</i>	156	2,67	17	1,91	21558,18	1,92	6,5	2,17
<i>Vochysia lehmannii</i>	129	2,21	9	1,01	33077,35	2,95	6,17	2,06
<i>Virola elongata</i>	138	2,37	3	0,34	33015,81	2,94	5,65	1,88
<i>Cupania americana</i>	111	1,9	19	2,13	10458,02	0,93	4,97	1,66
<i>Annona purpurea</i>	64	1,1	9	1,01	31442,39	2,8	4,91	1,64
<i>Cassia moschata</i>	26	0,45	11	1,23	35189,6	3,14	4,82	1,61
<i>Ardisia foetida</i>	150	2,57	16	1,79	4991,75	0,45	4,81	1,6
<i>Xylopio aromatica</i>	75	1,29	13	1,46	22207,72	1,98	4,72	1,57
<i>Croton fragrans</i>	217	3,72	5	0,56	3941,25	0,35	4,63	1,54
<i>Guarea guidonia</i>	98	1,68	12	1,35	11897,26	1,06	4,09	1,36
<i>Clitoria dendrina</i>	87	1,49	13	1,46	8245,81	0,74	3,68	1,23
<i>Uniosium velutinifolium</i>	25	0,43	8	0,9	23945,81	2,14	3,46	1,15
<i>Hura crepitans</i>	5	0,09	2	0,22	33788,72	3,01	3,32	1,11
<i>Allophylus racemosus</i>	101	1,73	11	1,23	3386,52	0,3	3,27	1,09
Subtotal	2809	48,17	202	22,65	699630,84	62,39	133,2	44,4
Other taxa: 305 species	3023	51,83	690	77,35	421796,57	37,61	166,8	55,6
Total	5832	100	892	100	1121427,41	100	300	100
alianza <i>Ceibo pentandrae-Trichilion martianae</i>								
<i>Spondias mombin</i>	114	3,7	17	2,67	114749,3	11,52	17,9	5,97
<i>Guazuma ulmifolia</i>	220	7,15	19	2,99	54475,5	5,47	15,61	5,2
<i>Hura crepitans</i>	31	1,01	7	1,1	81297,36	8,16	10,27	3,42
<i>Coccoloba latifolia</i>	169	5,49	9	1,42	16962,85	1,7	8,61	2,87
<i>Pterocarpus acapulcensis</i>	80	2,6	7	1,1	46889,83	4,71	8,41	2,8
<i>Erythrina fusca</i>	23	0,75	7	1,1	52095,98	5,23	7,08	2,36
<i>Pithecellobium lanceolatum</i>	83	2,7	5	0,79	33560,02	3,37	6,85	2,28
<i>Sapium glandulosum</i>	74	2,4	9	1,42	27311,19	2,74	6,56	2,19
<i>Casearia guianensis</i>	119	3,87	7	1,1	11951,01	1,2	6,17	2,06
<i>Ruprechtia cruegeri</i>	20	0,65	1	0,16	53211,23	5,34	6,15	2,05
<i>Tabebuia rosea</i>	29	0,94	10	1,57	35231,57	3,54	6,05	2,02
<i>Ceiba pentandra</i>	20	0,65	14	2,2	27344,69	2,75	5,6	1,87
<i>Cochlospermum vitifolium</i>	60	1,95	9	1,42	11722,17	1,18	4,54	1,51
<i>Allophylus racemosus</i>	102	3,31	4	0,63	3436,45	0,35	4,29	1,43
<i>Guadua angustifolia</i>	78	2,53	6	0,94	7842,49	0,79	4,27	1,42
<i>Cecropia peltata</i>	46	1,49	7	1,1	14559,53	1,46	4,06	1,35
Subtotal	1268	41,2	138	21,7	592641,15	59,52	122,41	40,8
Other taxa: 219 species	1810	58,8	498	78,3	403130,98	40,48	177,59	59,2
Total	3078	100	636	100	995772,13	100	300	100

TABLE 5 CONT. Floristic composition of alliance *Xylopia aromatica*-*Proton heptaphylli*.

PLOT NUMBER-AYMARD 2012	31	9	64	26	8	36	67	24	30	34	35	10	29	53	65	54	42	57	63	58	59	55	62	7	13	20	51		
<i>Cordia sericealax</i>										1,4				0,9															
<i>Dolichandra unguis-cati</i>				0,5	0,4																								
<i>Miconia minutiflora</i>								0,8				0,8																	
<i>Coccoloba caracasana</i>				2				0,8															5,2						
<i>Samanea saman</i>				1,5																									
<i>Couroupita guianensis</i>				0,5					0,6																				
<i>Sapindus saponaria</i>	0,4			0,5																									
Alliance <i>Xylopia aromatica</i>-<i>Proton heptaphylli</i>																													
<i>Inga vera</i>	3	2,2	4,5	0,5	1,2	2,9	3,2	0,8	0,6	1,4	1,5	1,5		0,9															
<i>Xylopia aromatica</i>	0,6				10					4,4	2,3	1,1				1,6		1,2	2,3	1,5	5,7	1,7		0,3	0,6			1,3	
<i>Genipa americana</i>			0,1	1,5	2,4	0,4			4,6	0,7	0,5	6				0,8			0,6	0,5			0,6					0,3	
<i>Cassia moschata</i>	0,4				0,6			0,4	0,6			1,1	1,4	0,5		4				1	0,9	0,7							
<i>Petrea pubescens</i>	0,9	1,1			0,6	1,8	0,5	2,9				1,1	0,9		0,6	5,6													
<i>Davilla nitida</i>	1,1				2,4	0,7	0,5					7,7						3,5	2,3	1	2,8	0,7							
<i>Annona purpurea</i>	2,2			5,4	1,5	2,1	3,4	1,4					3,9	3,7		4,8													
<i>Uniositium velutinifolium</i>	0,9					0,5	0,4	0,6				0,8	3	0,9								1							
<i>Swartzia pittieri</i>					0,6	3,6				1,4		1,5			0,6			0,8											
<i>Xylophragma seemannianum</i>					0,6			0,4		2,8			6,5		9,6							16							
<i>Chrysophyllum argenteum</i>	1,7	1,1			18									1,8				0,6				0,3							
<i>Croton fragrans</i>						28		3,8	0,6	46	31																		
<i>Bactris major</i>				6,3	0,4			17		2,1		2,7																	
<i>Parinari campestris</i>	2,8			3,4	0,6																0,6							3	
<i>Pradosia caracasana</i>	1,7								4,0				0,7													3,3			
<i>Vitex capitata</i>																0,8													
<i>Bursera simaruba</i>	1,7								0,6																		1,1		
<i>Terminalia oblonga</i>									1,2																				
<i>Deguelia picta</i>	0,6								0,6				2,3									0,3						2,9	
<i>Fridericia florida</i>							10								2,9				6,3										
<i>Myrcia splendens</i>									0,6						0,6				6,9		6,6								
<i>Machaerium biovulatum</i>	1,3								1,7				0,2																
<i>Cochlospermum orinocense</i>																6,8												0,3	
Association <i>Ingo verae</i>-<i>Anacardietum excelsti</i>																													

TABLE 5 CONT. Floristic composition of alliance *Xylopia aromatica*-*Protium heptaphyllum*.

PLOT NUMBER-AYMARD 2012	31	9	64	26	8	36	31	31	69	27	25	38	55	37	15	63	58	59	55	62	7	13	20	51
<i>Euterpe oleracea</i>																					1	0,6		
<i>Swartzia polyphylla</i>																					2,4	0,9		
<i>Andira surinamensis</i>																					0,9			0,3
<i>Dolichopus brevipedicellatus</i>																				0,7			1,3	
<i>Guapira cuspidata</i>																					0,3	0,3		
<i>Guatteria inundata</i>																					1	1,3		
<i>Hirtella racemosa</i>																					1,3			2,3
<i>Ilex jennamii</i>																					1,7	5,4		
<i>Inga heterophylla</i>																					0,7			1
<i>Macrobium acaciifolium</i>																								0,3
<i>Maquira coriacea</i>																							0,6	
<i>Montichardia arborescens</i>																							9,7	1,3
<i>Trichilia pallida</i>																								11
<i>Desmoncus orthacanthos</i>																								0,3
<i>Himatanthus articulatus</i>																								1,1 1,3
Species number	58	38	21	36	36	38	31	31	69	27	25	38	55	37	15	63	58	59	55	62	39	29	26	43

Other species present:

Myrcia sp. (31/2,55), *Siparuna guianensis* (31/0,43), *Heliconia bihai* (31/1,28), *Banara guianensis* (31/0,43), *Fridericia dichotoma* (31/0,43), *Curatella americana* (31/0,43), *Aralia excelsa* (31/0,43), *Aristolochia maxima* (31/0,85), *Hirtella triandra* (31/2,98), *Smilax oblongata* (31/0,85), *Hura crepitans* (31/1,28), (20/2,22), *Annona mucosa* (9/0,55), (55/0,34), *Leptobalanus octandrus* (63/5,75), *Conceveiba guianensis* (7/0,35), *Heisteria acuminata* (51/0,33), *Protium paniculatum* (51/0,33), *Rinorea melanodonita* (31/0,85), *Strychnos panamensis* (31/0,43), *Homalolepis cedron* (42/1,35), *Vismia macrophylla* (42/4,05), *Carolus sinemariensis* (26/1,95), *Croton gossypifolius* (8/0,61), *Morrisonia frondosa* (64/0,02), *Ruprechtia ramiflora* (64/0,05), *Eugenia galatensis* (64/0,07), *Stylogyne micrantha* (64/0,38), *Alchornea glandulosa* (42/9,46), *Socratea exorrhiza* (42/20,27), *Jupunba trapezifolia* (42/4,05), *Casearia arborea* (42/4,05), *Monteverdia guyanensis* (7/2,42), *Gmelina arborea* (34/2,76), *Clusia* sp. (7/0,35), *Guarea* sp. (7/0,35), *Coccoloba* sp. (64/0,02), *Paulinia cururu* (26/7,32), *Bignoniaceae* (29/0,23), *Claviia ornata* (8/0,61), *Senna vicifolia* (8/1,83), *Vigna luteola* (8/4,27), *Fabaceae* 2 (53/0,46), *Ficus citrifolia* (67/0,53), *Ocotea bofo* (67/0,53), *Indeterminado* (9/1,66), *Acacia* sp. (51/0,33), *Mabea trianae* (63/1,15), *Eugenia puniceifolia* (55/0,34), *Guatteria inundata* (7/0,35), *Casearia corymbosa* (59/1,27), (62/1,73), *Brownea coccinea* (20/24,44), *Banisteriopsis muricata* (36/0,36), *Guatteria pilosula* (31/0,43), (10/0,38), *Tabebuia ochracea* (36/0,36), (62/2,31), *Zanthoxylum jagara* (67/1,06), (62/0,58), *Tetracera costata* subsp. *costata* (51/1,64), *Strychnos mattogrossensis* (63/0,57), *Rudgea crassiloba* (30/1,73), (29/0,23), *Macluerium humboldtianum* (30/1,73), *Senegalia polyphylla* (34/0,69), (54/0,8), *Bigonia aequinoctialis* (24/1,26), (62/0,58), *Rosenbergiodendron formosum* (36/1,09), *Dolichopus dentatus* (13/0,32), *Henriettea multiflora* (13/0,32), *Handroanthus ochraceus* (54/0,8), *Trichanthera gigantea* (67/1,06), *Lonchocarpus punctatus* (62/3,47), *Casearia completa* (62/0,58), *Machaerium myrianthum* (62/1,16), *Tanaecium pyramidalatum* (30/0,58), *Erythrina poeppigiana* (30/0,58), *Acalypha macrostachya* (30/0,58), *Chomelia venezuelensis* (29/0,46), *Tournefortia bicolor* (67/1,06), *Tabernaemontana cymosa* (67/1,06), *Citharexylum venezuelense* (67/1,59), *Casearia mariquitensis* (67/1,59), *Deguelia utilis* (29/1,15), *Anacardium occidentale* (7/0,35), *Rudgea hostmanniana* (20/2,22), *Conmarus lambertii* (51/0,98), *Lycoseris triplinervia* (24/0,84), *Casearia guianensis* (36/2,91), *Ipomoea corymbosa* (26/0,49), *Trichilia maritima* (30/0,58), *Guadua paniculata* (30/0,58), *Guapira pubescens* (26/1,46), *Clitoria glabrata* (30/0,58), *Dianthera secunda* (30/0,58), *Platypodium elegans* (30/1,16), *Zanthoxylum schreberi* (29/8,49), *Heliconia marginata* (30/1,73), *Senna robinifolia* (30/1,73), *Fridericia dichotoma* (30/2,31), *Cordia collococca* (62/2,31), *Eugenia cribrata* (62/3,47), *Copaifera officinalis* (51/0,66), *Eugenia coffeifolia* (35/0,38), *Vismia baecifera* (35/0,38), *Casearia hirsuta* (29/0,23), *Miconia sericea* (30/0,58), *Piptocoma acuminata* (29/0,46), *Guadua angustifolia* (29/0,69), *Tetracera volubilis* (29/0,69), *Mansoa verrucifera* (24/0,42), *Davilla kunthii* (29/1,15), *Cordia tetrandra* (29/1,61), *Bauhinia aculeata* (30/1,16), *Muellera fendleri* (62/0,58), *Eumachia microdon* (62/0,58), *Pachira quinata* (62/1,16), *Alibertia edulis* (51/3,28), *Cupania latifolia* (51/0,98), *Coutarea hexandra* (53/0,46), *Serjania atrolineata* (53/0,93), *Tetrapterys crispa* (53/0,93), *Prionostemma aspera* (53/1,85), *Bonania trichantha* (53/3,7), *Annona mucosa* (53/4,63), *Pinzona corticea* (65/0,59), *Pouteria stipitata* (54/0,8), *Eugenia monticola* (54/0,8), *Homalium racemosum* (54/0,8), *Terminalia amazonia* (42/1,35), *Balizia pedicellaris* (51/0,66), *Eschweilera pedicellata* (51/2,3), *Ilex guianensis* (51/0,33), *Ormosia coccinea* (51/7,87), *Parinari excelsa* (51/2,3), *Cissus alata* (57/0,39), *Duguetia* sp. (7/0,35), *Duroia eriopila* (7/0,35), *Pera glabrata* (51/2,3), *Licania hypoleuca* (20/1,11), *Delonix regia* (64/0,38), *Bixa urucurana* (26/0,49), *Ficus maxima* (42/1,35), *Pseudobalizia niopoides* (31/1,7), *Calathea lutea* (31/2,13), *Tovomita* sp. (7/0,69), *Hiraea reclinata* (20/2,22), *Swartzia pinnata* (20/5,56), *Guadua* sp. (62/28,9), *Myrtaceae* (7/0,35), *Annona glabra* (35/1,15).

TABLE 6 CONT. Floristic composition of *Gtiazumo ulmifoliae-Spondiadea mombinis* class and *Cupanio americanae-Tabebititalia roseae* order.

PLOTS AYMARD 2012	2	5	18	16	38	27	1	4	28	12	15	37	11	49	50	22	17	56	19	21	
	<i>Warszewiczia coccinea</i>						0,3			0,3											
<i>Fridericia mollissima</i>									1												
<i>Clitoria arborescens</i>					0,4			4,3						1,9							
<i>Cordia toqueve</i>																	4,3				
<i>Enterolobium cyclocarpum</i>					0,4	0,3			0,2	0,4											
<i>Machaerium biovulatum</i>					0,4								0,4								
<i>Stylogyne micrantha</i>					0,4																
<i>Bursera simaruba</i>					0,4				3,6												5,7
<i>Coursetia ferruginea</i>																					
<i>Paullinia cururu</i>						1,7				1,2											
<i>Triplaris caracasana</i>						1,7				0,8											
<i>Ormosia macrocalyx</i>					0,4																
<i>Aralia excelsa</i>									0,2												1
Alliance Ceibo pentandrae-Trichilion martianae																					
<i>Ceiba pentandra</i>	2	1,6	1,7	3,7	0,4	0,3	2,9	1,1	0,8	0,4	0,5		0,4		1,8		1,1				
<i>Trichilia martiana</i>	2	3,3	3,4	2,6	0,4	0,3	4,3	0,2	0,5	0,4	0,5		0,4		2,2		2,4	1	2,6		
<i>Sterculia apetala</i>		1,6	1,7	0,4	0,4	0,3	1,1	0,3	0,4								1,1				
<i>Tanaecium tetragonolobum</i>	4	3,3	3,4	3,4	0,9	2,1	2,1		0,8	0,4	3,1			3,8		1,1	2,1	2,4	1	1,8	
<i>Deguelia picta</i>					0,9	2,1							10	3,8	1,8						
<i>Casearia guianensis</i>	8	8,1	7,6	0,4	0,4		6,4			2,4			3,5				6,4	38		34	
<i>Erythrina fusca</i>		0,8	0,8				2,9											0,8			
<i>Coccoloba caracasana</i>	4	17,1	18	2,4	0,9	1,7	11	31	0,2	0,4	19	3,4	9,3		5,5		31	10		11	
<i>Coccoloba latifolia</i>	2				1,3		5,3		0,4	0,4	14	3,4					6,4				
<i>Cordia collococa</i>				0,2	0,9						0,5	3,4	0,8								1
<i>Machaerium humboldtianum</i>		0,8	0,8				8,5									1,1	8,5				
<i>Bixa urucurana</i>	2		0,8				2,9		3,2	1			0,4								
<i>Fridericia</i> sp.		0,8				1		3,2	4,2												1,6
<i>Genipa americana</i>	2						5,7	4,3									5,3	3,2	3,8	3,5	
<i>Casearia aculeata</i>					3,4				2,4					1,9			7,4	0,8		0,9	
<i>Lonchocarpus hedyosmus</i>					0,9	1,4			0,7	12											29
<i>Deguelia utilis</i>																					
<i>Ruprechtia ramiflora</i>		0,8	0,8						1,2				8,1	3,8	3,6						

TABLE 6 CONT. Floristic composition of *Guazuma ulmifoliae-Spondiadea mombinis* class and *Cupania americanae-Tabebuia roseae* order.

PLOTS AYMARD 2012	2	5	18	16	38	27	1	4	28	12	15	37	11	49	50	22	17	56	19	21	
<i>Leptobalanus apetalus</i>		0,8	0,8																		
<i>Annona montana</i>		0,8	0,8				2,9														
<i>Fridericia platyphylla</i>					0,9	0,7			2,9												
<i>Allophylus racemosus</i>				0,2	4,7	4,2			13												
<i>Margaritaria nobilis</i>				0,4		0,3															
<i>Ingo interruptae-Pterocarpum acapulcensis</i>																					
<i>Inga interrupta</i>						4,2			0,7												
<i>Pterocarpus acapulcensis</i>					1,3	5,2															
<i>Pseudoalbizia niopoides</i>					2,2																
<i>Pithecellobium lanceolatum</i>				12																	
<i>Cordia tetrandra</i>						0,7															
<i>Crateva tapia</i>																					
<i>Samanea saman</i>					0,4	1															
<i>Tetracera volubilis</i>		0,8	0,8																		
<i>Casearia completa</i>																					
<i>Pisonia aculeata</i>					0,4	1,4															
<i>Libidibia punctata</i>																					
<i>Bravaisia integerrima</i>										16	13										
<i>Copernicia tectorum</i>													3,1	1,9							
<i>Malvaviscus arboreus</i>												3,4		1,9							
<i>Trichilia trifolia</i>										1,2			2,7								
<i>Sarcophthalmus saeri</i>													2,3	1,9							
<i>Fissicalyx fendleri</i>										0,4	0,5										
<i>Machaerium robinifolium</i>				0,4						4,6	0,4										
<i>Acrocomia aculeata</i>										0,4											
<i>Neea amplifolia</i>										0,3			1,7								
<i>Myrcia</i> sp.										0,2			1,6								
<i>Spondiadea mombinis-Trichilitetum pallidae</i>																					
<i>Trichilia pallida</i>																1,1	4,3	0,8	1,9	0,9	

TABLE 6 CONT. Floristic composition of *Guazuma ulmifoliae-Spondiadea mombinis* class and *Cupanio americanae-Tabebuitalia roseae* order.

PLOTS AYMAR 2012	2	5	18	16	38	27	1	4	28	12	15	37	11	49	50	22	17	56	19	21
<i>Pachira aquatica</i>																1,1		2,4		2,6
<i>Neea spruceana</i>								3,2			0,5						3,2	1,6	1	1,8
<i>Eugenia cribrata</i>																		4		4,4
<i>Davilla kunthii</i>					1													0,8		0,9
<i>Casearia sylvestris</i>																			2,9	0,9
<i>Cordia panamensis</i>																		0,8		0,9
<i>Virola surinamensis</i>						2,9										2,2				
<i>Zanthoxylum fagara</i>																				1
<i>Swartzia pinnata</i>																		0,8		0,9
<i>Protium laxiflorum</i>																		1,6		1,8
<i>Psidium acutangulum</i>																		3,2		1,8
<i>Phyllanthus acuminatus</i>																		0,8		0,9
<i>Vismia cayennensis</i>																		7,1		7,9
<i>Didymopanax morototoni</i>																		0,8		0,9
Species number	22	27	28	22	61	46	16	25	54	58	21	21	46	24	12	31	24	30	36	30

Other species present:

Seguiera macrophylla (2/4), *Mauritia flexuosa* (2/6), *Hamelia patens* (27/0,35), *Adelia ricinella* (27/2,08), *Maclura* sp. (5/0,7), *Ruprechtia cruegeri* (5/50,99), *Heliconia bihai* (4/3,19), *Randia armata* (38/0,43), *Paulinia leiocarpa* (38/0,43), *Fabaceae* (38/0,43), *Hippocratea* sp. (38/0,43), *Indeterminado* (38/0,43), *Rubiaceae* (38/0,43), *Trichilia* sp. (38/0,43), *Clerodendrum* sp. (38/3,88), *Prionostemma aspera* (12/1,2), *Casearia ulmifolia* (27/4,84), *Leptobalanus apetalus* (1/5,71), *Trema micrantha* (28/0,16), *Cedrela odorata* (28/0,33), *Cassia moschata* (28/0,49), *Platypodium elegans* (28/0,49), *Anacardium excelsum* (38/1,72), *Melicoccus bijugatus* (38/2,16), *Pradosia caracasana* (28/0,98), *Cornutia pyramidata* (28/1,14), *Lecythis minor* (38/2,16), *Handroanthus billbergii* (19/1,9), *Acacia* sp. (11/0,39), *Lonchocarpus velutinus* (28/4,72), *Clitoria dendrina* (28/6,19), *Ficus maxima* (12/0,4), *Cassia grandis* (12/0,4), *Syagrus sancona* (12/0,4), *Rudgea* sp. (11/0,39), *Cissus erosa* (12/0,4), *Cupania scrobiculata* (12/0,4), *Funarium clausum* (12/0,4), *Lecythis ollaria* (12/0,4), *Ruprechtia apurensis* (12/0,4), *Piper tuberculatum* (12/0,8), *Lonchocarpus (Derris)* sp. (11/0,39), *Strychnos fendleri* (19/4,76), *Ayenia catalpifolia* (15/0,52), *Coccoloba ovata* (37/1,72), *Terminalia guyanensis* (37/1,72), *Senegalia polyphylla* (11/0,39), *Attalea maripa* (22/34,41), *Machaerium* sp. (11/0,39), *Securidaca divaricata* (11/0,39), *Aspidosperma cuspa* (11/0,78), *Muelleria fendleri* (11/1,16), *Phyllanthus elisia* (11/2,71), *Fridericia dichotoma* (11/3,1), *Trichilia trifolia* (49/1,92), *Morisonia odoratissima* (49/3,85), *Conceveitium cordatum* (22/1,08), *Conarus lamBERTII* (19/0,95), *Baulinia aculeata* (27/3,46), (28/0,33), *Zanthoxylum schreberi* (28/1,95), *Uniosium velutinifolium* (28/2,61), *Erythroxylum orinocense* (28/0,49), *Brosimum alicastrum* (5/0,06), (12/0,4), *Vitex orinocensis* var. *multiflora* (27/1,04), *Pseudosamanea guachapele* (11/0,78), *Cochlospermum orinocense* (22/6,45), *Pseudosamanea guachapele* (12/1,2), *Coccoloba portuquesana* (12/2,39), *Maprounea guianensis* (15/0,52), *Tanacetium tetragonolobum* (5/0,11), *Agonandra brasiliensis* (38/0,43), *Handroanthus chrysanthus* (28/2,77), *Aibertia edulis* (15/0,52), *Machaerium inundatum* (22/1,08), *Astrocarium aculeatum* (22/1,08), *Manilkara bidentata* (22/1,08), *Chrysophyllum* (22/1,08), *Protium* (22/1,08), *Ischnosiphon arouma* (22/2,15), *Pouteria* sp. (22/3,23), *Calathea lutea* (22/4,3), *Cordia* sp. (22/4,3), *Euterpe oleracea* (22/4,3), *Heliconia caribaea* (17/2,13), *Bromelia pinguin* (56/0,79), *Trichilia pallida* (56/0,79), *Parinari campestris* (22/1,08), *Mabea occidentalis* (19/0,95), *Guapira pubescens* (19/0,95), *Dalbergia frutescens* (19/0,95), *Erythroxylum gracilipes* (19/0,95), *Melicoccus oliviformis* (19/0,95), *Randia* sp. (19/0,95), *Alseis labatiooides* (19/1,9), *Copaifera officinalis* (19/2,86), *Myrtaceae* (19/2,86), *Bromelia* sp. (21/0,88), *Erythrina fusca* (21/0,88).

TABLE 7. Floristic composition of *Anacardium excelsum* and *Guazuma ulmifoliae*, *Connarus araucanus* and *Eugenia puniceifolia* forests and the *Homalolepidis cedrontis*-*Guareetum guidoniae* association.

PLOT AYMARD 2012	61	25	3	6	44	47	48	43
SURFACE PLOT. (M²):	1000		500	1000				
ALTITUDE (M):	176	184	125		188	188	188	188
Relative Density (%)								
Class <i>Guazuma ulmifoliae</i>-<i>Spondiadetea mombinis</i>								
<i>Guazuma ulmifolia</i>	11	23			2,1			
<i>Spondias mombin</i>								3,6
<i>Sapium glandulosum</i>		1,9					1,8	5,4
<i>Cochlospermum vitifolium</i>			1,5					
<i>Cecropia peltata</i>	1	3,8				7,7		
<i>Annona purpurea</i>		25						
<i>Platymiscium pinnatum</i>		1,9						
<i>Tapirira guianensis</i>					38			
<i>Astronium graveolens</i>	0,5							
<i>Bactris major</i>		13						
<i>Cordia alliodora</i>			4,4					
<i>Casearia sylvestris</i>			2,9					
<i>Schnella guianensis</i>		1,9					1,8	
<i>Apeiba tibourbou</i>		3,8						
<i>Zanthoxylum caribaeum</i>			1,5					
Order <i>Cupanio americanae</i>-<i>Tabebuietum roseae</i>								
<i>Cupania americana</i>			1,5					
<i>Tabebuia rosea</i>			2,9		2,1	1,9	1,8	1,8
<i>Guettarda divaricata</i>			5,9					
<i>Hymenaea courbaril</i>				3,5				
<i>Luehea candida</i>		3,8						3,6
<i>Warszewiczia coccinea</i>								1,8
<i>Fridericia mollissima</i>				0,6				
<i>Coursetia ferruginea</i>				5,8				
<i>Deguelia picta</i>	5,7			8,7				
<i>Agonandra brasiliensis</i>		1,9		1,9				
<i>Margaritaria nobilis</i>				1,9				3,6
Undifines alliance								
<i>Anacardium excelsum</i> and <i>Guazuma ulmifolia</i> forest								
<i>Coccoloba caracasana</i>	2,1	3,8						
<i>Anacardium excelsum</i>		7,5						
<i>Inga vera</i>		1,9						
<i>Neea ovalifolia</i>		1,9						

TABLE 7 CONT. Floristic composition of *Anacardium excelsum* and *Guazuma ulmifoliae*, *Connarus araucanus* and *Eugenia puniceifolia* forests and the *Homalolepidis cedrontis*-*Guareetum guidoniae* association.

Plot AYMARD 2012	61	25	3	6	44	47	48	43
<i>Connarus araucanus</i> and <i>Eugenia puniceifolia</i> forest								
<i>Connarus araucanus</i>			8,8	3,5				
<i>Eugenia puniceifolia</i>			21	0,6				
<i>Tabernaemontana cymosa</i>			5,9					
<i>Homalolepidis cedrontis</i>-<i>Guareetum guidoniae</i>								
<i>Homalolepis cedron</i>					6,4	5,8	3,5	3,6
<i>Guarea guidonia</i>						48	25	18
<i>Ficus maxima</i>					2,1	1,9		1,8
<i>Protium heptaphyllum</i>					2,1	3,8	3,5	
<i>Casearia arborea</i>					4,3		3,5	
<i>Didymopanax morototoni</i>						1,9	3,5	3,6
<i>Vismia guianensis</i>					2,1			1,8
<i>Zygia latifolia</i>					11			11
Lauraceae						3,8		1,8
Species number	13	16	19	30	14	13	17	23

Other species present:

Pterocarpus acapulcensis (61/0,52), *Genipa americana* (61/0,52), *Senegalia polyphylla* (61/0,52), *Combretum fruticosum* (61/0,52), *Pseudosamanea guachapele* (61/1,03), *Coccoloba* sp. (61/1,03), *Xylophragma seemannianum* (61/9,28), *Guadua* sp. (61/66,49), *Acalypha diversifolia* (25/1,89), *Sterculia apetala* (25/3,77), *Casearia guianensis* (3/1,47), *Cassia moschata* (3/1,47), *Gouania polygama* (3/1,47), *Guapira* sp. (3/1,47), *Mabea piriri* (3/2,94), *Deguelia utilis* (3/4,41), *Machaerium myrianthum* (3/4,41), *Tanaecium tetragonolobum* (3/7,35), *Lonchocarpus violaceus* (3/19,12), *Randia armata* (6/0,32), *Erythroxylum gracilipes* (6/0,32), *Hirtella paniculata* (6/0,32), *Myrcia* sp. (6/0,32), *Copaifera officinalis* (6/0,65), *Cordia bicolor* (6/0,65), *Handroanthus ochraceus* (6/0,65), *Bredemeyera floribunda* (6/0,65), *Bourreria exsucca* (6/0,97), *Ouratea grosourdyi* (6/0,97), *Bunchosia mollis* (6/1,29), *Zanthoxylum martinicense* (6/1,29), *Casearia sylvestris* (6/1,61), *Pouteria stipitata* (6/1,61), *Connarus lambertii* (6/1,94), *Vitex capitata* (6/2,26), (48/1,75), *Uniosium velutinifolium* (6/3,55), *Senegalia polyphylla* (6/4,84), *Casearia ulmifolia* (6/4,84), *Cupania latifolia* (6/8,39), *Eugenia cribrata* (6/9,35), *Strychnos fendleri* (6/26,45), *Rudgea crassiloba* (44/2,13), Lauraceae 1 (44/4,26), Lauraceae 2 (44/4,26), *Himatanthus articulatus* (44/8,51), *Ocotea glomerata* (44/10,64), *Vismia macrophylla* (47/1,92), *Trigynaea duckei* (47/1,92), *Alchornea discolor* (47/1,92), *Pterocarpus* sp. (47/7,69), *Croton megalodendron* (47/11,54), *Zanthoxylum rhoifolium* (48/1,75), *Albizia* sp. (48/1,75), *Talisia macrophylla* (48/1,75), *Ocotea leptobotra* (48/3,51), *Duguetia lucida* (48/7,02), *Ocotea aurantiadora* (48/8,77), *Annona fendleri* (48/12,28), *Xylopia aromatica* (48/17,54), *Parinari pachyphylla* (43/1,79), *Pouteria caimito* (43/1,79), *Gustavia macarenensis* (43/1,79), *Euterpe precatoria* (43/1,79), *Conceveibum cordatum* (43/3,57), *Socratea exorrhiza* (43/3,57), *Lonchocarpus* sp. (43/3,57), *Miconia prasina* (43/7,14), *Dichapetalum* sp. (43/7,14), *Virola sebifera* (43/7,14).

TABLE 8. Pattern of richness and density of Venezuelan Llanos vegetation units described.

UNITS	SPECIES						INDIVIDUALS			
	NUMBER. PLOT.	SURFACE (M ²)	AVERAGE SP.	VARIATION NO. SPP.	TOTAL SPP.	I. RICH. X10 ⁻² (SPPXM ²)	AVERAGE. IND.	VARIATION NO. IND.	NUMBER IND.	I. DEN. X10 ⁻² (INDXM ²)
<i>Attalea butyraceae</i> - <i>Guaduetum angustifoliae</i>	3	3000	106	82-131	215	7	872	697-986	2615	87
<i>Attalea butyraceae</i> - <i>Rudgeetum crassilobae</i>	5	5000	38	21-75	135	3	171	50-230	855	17
All. Protio heptaphylli - Attaleion butyraceae	8	8000	63	21-131	295	4	434	50-986	3470	43
<i>Ingo verae</i> - <i>Anacardietum exce/lsi</i>	9	9000	37	22-58	176	2	199	128-275	1787	20
<i>Vochysia lehmanni</i> - <i>Protietum heptaphylli</i>	14	14000	28	15-55	176	1	218	74-436	3045	22
<i>Eschweilero subglandulosae</i> - <i>Protietm heptaphylli</i>	4	4000	34	26-43	88	2	250	90-316	1000	25
All. Xylopio aromatica - Protion heptaphylli	27	27000	33	15-69	322	1	216	74-436	5832	22
<i>Protio heptaphylli</i> - <i>Euterpetum preceptoriae</i>	3	3000	21	14-30	57	1,9	84	69-95	252	8,4
Order Cupanio americanae - Protietalia heptaphylli	38	38000	38	14-131	510	1,3	245	50-986	9554	25,1
<i>Huro crepitantis</i> - <i>Guaduetum angustifoliae</i>	8	7500	31	16-61	108	1	133	35-289	1066	14
<i>Ingo interruptae</i> - <i>Pterocarpetum acapulcensis</i>	7	7000	34	12-59	129	2	211	52-614	1480	21
<i>Spondiaco mombinis</i> - <i>Trichilitetum pallidae</i>	5	5000	30	24-36	93	2	106	93-126	532	11
All. Ceibo pentandrae - Trichilion martianae	20	19500	32	12-61	236	1	154	35-614	3078	16
<i>Com. de Anacardium excelsum and Guazuma ulmifoliae</i>	2	2000	14	13 y 16	26	1,3	123	53 y 194	247	12,4
<i>Com. de Conarus araucanus and Eugenia punicifolia</i>	2	1500	24	19 y 30	47	3,1	189	68 y 310	378	25,2
<i>Homalolepidis cedronis</i> - <i>Guareetum guidoniae</i>	4	4000	17	13 y 23	48	1,2	53	47 y 57	212	5,3
Order Cupanio americanae - Tabebuitalia roseae	28	27000	22	12-61	278	1,03	130	35-614	3915	14,5
Class. Guazumo ulmifoliae - Spondiadea mombinis	66	65000	30	12-131	630	0,97	188	35-986	13469	20,7

APPENDIX I

Importance Value Index (IVI) by species.

SPECIES	IND.	IND. %	FREC. ABS.	FREC. %	A.B.(CM ²) ABS.	A.B. %	IVI ABS.	IVI %
Association Attaleo butyraceae-Guaduetum angustifoliae								
<i>Guadua angustifolia</i>	963	36,83	3	0,94	88788,92	15,78	53,55	17,85
<i>Attalea butyracea</i>	103	3,94	3	0,94	88991,84	15,82	20,7	6,9
<i>Ficus insipida</i>	11	0,42	3	0,94	74184,19	13,19	14,55	4,85
<i>Spondias mombin</i>	18	0,69	3	0,94	21431,44	3,81	5,44	1,81
<i>Guatteria hirsuta</i>	17	0,65	3	0,94	19051,87	3,39	4,98	1,66
<i>Guarea guidonia</i>	51	1,95	3	0,94	10061,97	1,79	4,68	1,56
<i>Terminalia amazonia</i>	3	0,11	1	0,31	23170,03	4,12	4,55	1,52
<i>Bixa urucurana</i>	70	2,68	2	0,63	6769,36	1,2	4,51	1,5
<i>Erythrina fusca</i>	14	0,54	2	0,63	17931,57	3,19	4,35	1,45
<i>Notopleura macrophylla</i>	45	1,72	2	0,63	9599,22	1,71	4,05	1,35
<i>Protium crenatum</i>	47	1,8	3	0,94	6007,08	1,07	3,81	1,27
<i>Anacardium excelsum</i>	7	0,27	2	0,63	16373,19	2,91	3,81	1,27
<i>Acalypha diversifolia</i>	66	2,52	3	0,94	1122,66	0,2	3,66	1,22
<i>Pleurothyrium trianae</i>	39	1,49	2	0,63	8451,11	1,5	3,62	1,21
<i>Brosimum alicastrum</i>	32	1,22	3	0,94	7723,1	1,37	3,54	1,18
<i>Cecropia peltata</i>	26	0,99	3	0,94	7398,88	1,32	3,25	1,08
<i>Aiphanes horrida</i>	32	1,22	3	0,94	5961,2	1,06	3,22	1,07
Subtotal	1544	59,04	44	13,79	413017,65	73,41	146,25	48,75
Other taxa: 197 especies	1071	40,96	275	86,21	149563,16	26,59	153,75	51,25
Total	2615	100	319	100	562580,81	100	300	100
Association Attaleo butyraceae-Rudgeetum crassilobae								
<i>Rudgea crassiloba</i>	136	15,91	4	2,12	12972,17	5,61	23,63	7,88
<i>Attalea butyracea</i>	23	2,69	5	2,65	23874,69	10,32	15,65	5,22
<i>Xylopia aromatica</i>	30	3,51	3	1,59	16604,61	7,18	12,27	4,09
<i>Protium heptaphyllum</i>	49	5,73	5	2,65	5191,16	2,24	10,62	3,54
<i>Deguelia picta</i>	8	0,94	2	1,06	18493,92	7,99	9,99	3,33
<i>Guarea guidonia</i>	19	2,22	3	1,59	11571,41	5	8,81	2,94
<i>Didymopanax morototoni</i>	17	1,99	4	2,12	9376,7	4,05	8,16	2,72
<i>Oenocarpus mapora</i>	38	4,44	2	1,06	2112,33	0,91	6,42	2,14
<i>Pochota fendleri</i>	3	0,35	1	0,53	11949,62	5,16	6,04	2,01
<i>Astronium graveolens</i>	8	0,94	3	1,59	7953,15	3,44	5,96	1,99
<i>Hymenaea courbaril</i>	4	0,47	2	1,06	8714,63	3,77	5,29	1,76
<i>Spondias mombin</i>	5	0,58	2	1,06	8078,15	3,49	5,13	1,71
<i>Pradosia caracasana</i>	6	0,7	1	0,53	8611,84	3,72	4,95	1,65
<i>Zanthoxylum caribaeum</i>	6	0,7	1	0,53	7834,51	3,39	4,62	1,54
<i>Myrcia splendens</i>	26	3,04	2	1,06	770,09	0,33	4,43	1,48
<i>Protium tenuifolium</i>	19	2,22	3	1,59	1062,44	0,46	4,27	1,42
Subtotal	397	46,43	43	22,79	155171,42	67,06	136,24	45,42
Other taxa: 118 especies	458	53,57	146	77,21	76211,76	32,94	163,76	54,58
Total	855	100	189	100	231383,18	100	300	100
Association Protio heptaphylli-Euterpetum precatoriae								
<i>Attalea maripa</i>	24	9,52	1	1,56	17208,13	13,36	24,44	8,15
<i>Macrolobium acaciifolium</i>	11	4,37	1	1,56	21127,75	16,4	22,33	7,44
<i>Alchornea glandulosa</i>	10	3,97	1	1,56	14728,06	11,43	16,96	5,65
<i>Maquira coriacea</i>	27	10,71	1	1,56	5534,89	4,3	16,57	5,52
<i>Abarema jupumba</i>	14	5,56	1	1,56	11528,72	8,95	16,07	5,36
<i>Leptobalanus apetalus</i>	7	2,78	1	1,56	8668,86	6,73	11,07	3,69
<i>Jacaranda obtusifolia</i>	12	4,76	2	3,13	2311,24	1,79	9,68	3,23
<i>Inga ingoides</i>	12	4,76	2	3,13	2300,19	1,79	9,67	3,22
<i>Guarea guidonia</i>	9	3,57	1	1,56	3409,98	2,65	7,78	2,59
<i>Euterpe precatoria</i>	8	3,17	2	3,13	1809,72	1,4	7,7	2,57
<i>Vismia macrophylla</i>	6	2,38	1	1,56	2970,95	2,31	6,25	2,08
<i>Protium heptaphyllum</i>	3	1,19	3	4,69	207,24	0,16	6,04	2,01
<i>Ceiba pentandra</i>	1	0,4	1	1,56	4899,19	3,8	5,76	1,92
<i>Lonchocarpus hedyosmus</i>	8	3,17	1	1,56	1206,81	0,94	5,67	1,89
<i>Sapium glandulosum</i>	3	1,19	1	1,56	3723,6	2,89	5,64	1,88
Subtotal	155	61,5	20	31,24	101635,33	78,9	171,63	57,2
Other taxa: 42 especies	97	38,48	44	68,75	27182,14	21,1	128,35	42,78
Total	252	100	64	100	128817,47	100	300	100

APPENDIX I CONT.

Importance Value Index (IVI) by species.

SPECIES	IND.	IND. %	FREC. ABS.	FREC. %	A.B.(CM ²) ABS.	A.B. %	IVI ABS.	IVI %
Association Ingo verae-Anacardietum excelsi								
<i>Anacardium excelsum</i>	37	2,07	9	2,49	138447,51	32,55	37,11	12,37
<i>Leptobalanus apetalus</i>	117	6,55	4	1,1	56562,93	13,3	20,95	6,98
<i>Ardisia foetida</i>	116	6,49	9	2,49	4379,1	1,03	10,01	3,34
<i>Annona purpurea</i>	31	1,73	5	1,38	24509,07	5,76	8,88	2,96
<i>Cecropia peltata</i>	54	3,02	7	1,93	6579,98	1,55	6,5	2,17
<i>Croton fragrans</i>	88	4,92	3	0,83	1306,74	0,31	6,06	2,02
<i>Acalypha diversifolia</i>	84	4,7	4	1,1	1044,8	0,25	6,05	2,02
<i>Ormosia macrocalyx</i>	21	1,18	4	1,1	15883,73	3,73	6,01	2
<i>Inga vera</i>	37	2,07	9	2,49	4242,98	1	5,55	1,85
<i>Neea ovalifolia</i>	29	1,62	6	1,66	8083,11	1,9	5,18	1,73
<i>Allophylus racemosus</i>	51	2,85	6	1,66	1331,63	0,31	4,82	1,61
<i>Cupania americana</i>	27	1,51	8	2,21	4055,1	0,95	4,67	1,56
<i>Melicococcus bijugatus</i>	44	2,46	3	0,83	4396,55	1,03	4,32	1,44
<i>Combretum fruticosum</i>	57	3,19	3	0,83	870,77	0,2	4,22	1,41
<i>Pradosia caracasana</i>	11	0,62	2	0,55	12316,61	2,9	4,06	1,35
<i>Bactris major</i>	54	3,02	3	0,83	795,32	0,19	4,04	1,35
<i>Vitex compressa</i>	16	0,9	5	1,38	7373,2	1,73	4,01	1,34
Subtotal	874	48,91	90	24,86	292179,16	68,69	142,46	47,49
Other taxa: 159 especies	913	51,09	272	75,14	133167,09	31,31	157,54	52,51
Total	1787	100	362	100	425346,25	100	300	100
Association Vochysio lehmanni-Protietum heptaphylli								
<i>Protium stevensonii</i>	355	11,66	4	1,02	29517,22	7,55	20,22	6,74
<i>Protium heptaphyllum</i>	348	11,43	10	2,54	21107,42	5,4	19,37	6,46
<i>Protium tenuifolium</i>	297	9,75	6	1,53	22277,02	5,7	16,98	5,66
<i>Vochysia lehmannii</i>	126	4,14	8	2,04	31464,88	8,05	14,22	4,74
<i>Cassia moschata</i>	22	0,72	7	1,78	31189,01	7,98	10,48	3,49
<i>Xylopia aromatica</i>	50	1,64	8	2,04	16852,45	4,31	7,99	2,66
<i>Cecropia peltata</i>	69	2,27	7	1,78	13580,15	3,47	7,52	2,51
<i>Cupania americana</i>	83	2,73	10	2,54	6383,29	1,63	6,9	2,3
<i>Uniosium velutinifolium</i>	20	0,66	4	1,02	19880,44	5,08	6,76	2,25
<i>Guarea guidonia</i>	52	1,71	5	1,27	10445,61	2,67	5,65	1,88
<i>Mabea occidentalis</i>	62	2,04	5	1,27	8350,69	2,14	5,44	1,81
<i>Croton fragrans</i>	129	4,24	2	0,51	2634,52	0,67	5,42	1,81
<i>Clitoria dendrina</i>	56	1,84	8	2,04	4496,55	1,15	5,02	1,67
<i>Didymopanax morototoni</i>	11	0,36	8	2,04	7716,85	1,97	4,37	1,46
<i>Genipa americana</i>	32	1,05	7	1,78	5527,2	1,41	4,25	1,42
Subtotal	1712	56,22	99	25,19	231423,3	59,18	140,6	46,87
Other taxa: 160 especies	1333	43,78	294	74,81	159609,12	40,82	159,4	53,13
Total	3045	100	393	100	391032,43	100	300	100
Association Eschweilero subglandulosae-Protietum heptaphylli								
<i>Ceiba pentandra</i>	1	0,1	1	0,73	119398,5	39,14	39,97	13,32
<i>Protium heptaphyllum</i>	200	20	4	2,92	25890,96	8,49	31,41	10,47
<i>Viola elongata</i>	138	13,8	3	2,19	33015,81	10,82	26,81	8,94
<i>Tabebuia insignis</i>	69	6,9	3	2,19	7666,34	2,51	11,6	3,87
<i>Tapirira guianensis</i>	46	4,6	3	2,19	7578,78	2,48	9,27	3,09
<i>Hura crepitans</i>	2	0,2	1	0,73	24570,5	8,05	8,98	2,99
<i>Mauritia flexuosa</i>	12	1,2	3	2,19	10283,19	3,37	6,76	2,25
<i>Symphonia globulifera</i>	33	3,3	3	2,19	2685,34	0,88	6,37	2,12
<i>Eschweilera subglandulosa</i>	18	1,8	4	2,92	4663,21	1,53	6,25	2,08
<i>Cecropia peltata</i>	33	3,3	3	2,19	1398,05	0,46	5,95	1,98
<i>Calophyllum brasiliense</i>	19	1,9	3	2,19	5509,45	1,81	5,9	1,97
<i>Chrysobalanus icaco</i>	29	2,9	3	2,19	1814,01	0,59	5,68	1,89
<i>Brownea coccinea</i>	22	2,2	1	0,73	6865,51	2,25	5,18	1,73
<i>Montrichardia arborescens</i>	32	3,2	2	1,46	494,19	0,16	4,82	1,61
<i>Ormosia coccinea</i>	24	2,4	1	0,73	2959,62	0,97	4,1	1,37
Subtotal	678	67,8	38	27,74	254793,47	83,53	179,06	59,69
Other taxa: 73 especies	322	32,2	99	72,26	50255,26	16,47	120,94	40,31
Total	1000	100	137	100	305048,73	100	300	100

APPENDIX I CONT.

Importance Value Index (IVI) by species.

SPECIES	IND.	IND. %	FREC. ABS.	FREC. %	A.B.(CM ²) ABS.	A.B. %	IVI ABS.	IVI %
Association <i>Huro crepitantis-Guaduetum angustifoliae</i>								
<i>Hura crepitans</i>	30	2,81	6	2,43	80151,27	14,54	19,79	6,6
<i>Spondias mombin</i>	44	4,13	7	2,83	63132,1	11,46	18,42	6,14
<i>Guazuma ulmifolia</i>	89	8,35	8	3,24	26504,92	4,81	16,4	5,47
<i>Ruprechtia cruegeri</i>	20	1,88	1	0,4	53211,23	9,66	11,94	3,98
<i>Coccoloba latifolia</i>	78	7,32	5	2,02	11092,33	2,01	11,35	3,78
<i>Guadua angustifolia</i>	78	7,32	6	2,43	7842,49	1,42	11,17	3,72
<i>Tabebuia rosea</i>	18	1,69	6	2,43	29731,71	5,39	9,51	3,17
<i>Erythrina fusca</i>	7	0,66	4	1,62	31539,52	5,72	8	2,67
<i>Ceiba pentandra</i>	10	0,94	8	3,24	19357,44	3,51	7,69	2,56
<i>Pterocarpus acapulcensis</i>	18	1,69	2	0,81	20696,91	3,76	6,25	2,08
<i>Casearia guianensis</i>	26	2,44	4	1,62	6588,34	1,2	5,25	1,75
<i>Samanea saman</i>	4	0,38	2	0,81	22050,04	4	5,19	1,73
<i>Cecropia peltata</i>	26	2,44	2	0,81	8356,69	1,52	4,77	1,59
<i>Inga ingoides</i>	17	1,59	4	1,62	8471,81	1,54	4,75	1,58
<i>Pithecellobium lanceolatum</i>	20	1,88	1	0,4	12647,52	2,29	4,58	1,53
<i>Trichilia martiana</i>	19	1,78	5	2,02	3098,47	0,56	4,37	1,46
Subtotal	504	47,3	71	28,73	404472,79	73,39	149,43	49,81
Other taxa: 109 especies	562	52,72	176	71,24	146633,3	26,6	150,58	50,19
Total	1066	100	247	100	551106,105	100	300	100
Association <i>Ingo interruptae-Pterocarpetum acapulcensis</i>								
<i>Guazuma ulmifolia</i>	119	8,04	7	2,94	25065,48	7,68	18,67	6,22
<i>Spondias mombin</i>	63	4,26	5	2,1	37907,84	11,62	17,98	5,99
<i>Pterocarpus acapulcensis</i>	62	4,19	5	2,1	26192,92	8,03	14,32	4,77
<i>Pithecellobium lanceolatum</i>	63	4,26	4	1,68	20912,5	6,41	12,35	4,12
<i>Sapium glandulosum</i>	52	3,51	5	2,1	15032,42	4,61	10,22	3,41
<i>Cochlospermum vitifolium</i>	52	3,51	6	2,52	9645,66	2,96	8,99	3
<i>Bravaisia integerrima</i>	64	4,32	2	0,84	11531,32	3,53	8,7	2,9
<i>Erythrina fusca</i>	15	1,01	2	0,84	19984,18	6,13	7,98	2,66
<i>Ruprechtia ramiflora</i>	28	1,89	4	1,68	11738,9	3,6	7,17	2,39
<i>Allophylus racemosus</i>	78	5,27	1	0,42	2255,87	0,69	6,38	2,13
<i>Inga interrupta</i>	24	1,62	5	2,1	6028,39	1,85	5,57	1,86
<i>Deguelia picta</i>	35	2,36	5	2,1	2805,26	0,86	5,33	1,78
<i>Ceiba pentandra</i>	9	0,61	5	2,1	7414,69	2,27	4,98	1,66
<i>Coccoloba caracasana</i>	31	2,09	5	2,1	2010,96	0,62	4,81	1,6
<i>Uniosium velutinifolium</i>	16	1,08	1	0,42	9502,86	2,91	4,41	1,47
<i>Machaerium robiinifolium</i>	38	2,57	3	1,26	1851,73	0,57	4,4	1,47
Subtotal	749	50,59	65	27,3	209880,98	64,34	142,26	47,43
Other taxa: 115 especies	731	49,39	173	72,69	116346,88	35,67	157,74	52,57
Total	1480	100	238	100	326227,84	100	300	100
Association <i>Spondiado mombinis-Trichilietum pallidae</i>								
<i>Attalea maripa</i>	32	6,02	1	0,66	21809,69	18,41	25,09	8,36
<i>Casearia guianensis</i>	93	17,48	3	1,99	5362,67	4,53	24	8
<i>Spondias mombin</i>	7	1,32	5	3,31	13709,37	11,58	16,2	5,4
<i>Coccoloba latifolia</i>	55	10,34	3	1,99	4461,86	3,77	16,09	5,36
<i>Deguelia utilis</i>	30	5,64	1	0,66	3633,84	3,07	9,37	3,12
<i>Guazuma ulmifolia</i>	12	2,26	4	2,65	2905,11	2,45	7,36	2,45
<i>Neea spruceana</i>	8	1,5	4	2,65	3259,99	2,75	6,91	2,3
<i>Vismia cayennensis</i>	18	3,38	2	1,32	2461,4	2,08	6,79	2,26
<i>Casearia aculeata</i>	17	3,2	4	2,65	875,34	0,74	6,58	2,19
<i>Cupania americana</i>	16	3,01	4	2,65	1037,93	0,88	6,53	2,18
<i>Tanaecium tetragonolobum</i>	9	1,69	5	3,31	1624,77	1,37	6,37	2,12
<i>Hymenaea courbaril</i>	5	0,94	3	1,99	3370,63	2,85	5,77	1,92
<i>Trichilia pallida</i>	9	1,69	5	3,31	620,76	0,52	5,53	1,84
<i>Lonchocarpus hedyosmus</i>	9	1,69	3	1,99	2072,19	1,75	5,43	1,81
<i>Copaifera officinalis</i>	3	0,56	1	0,66	4718,14	3,98	5,21	1,74
<i>Couropita guianensis</i>	1	0,19	1	0,66	4417,86	3,73	4,58	1,53
<i>Trichilia martiana</i>	9	1,69	4	2,65	234,09	0,2	4,54	1,51
<i>Genipa americana</i>	6	1,13	4	2,65	790,01	0,67	4,44	1,48
<i>Cordia collococca</i>	6	1,13	1	0,66	3078,28	2,6	4,39	1,46
Subtotal	345	64,85	58	38,41	80443,93	67,92	171,18	57,06
Other taxa: 73 especies	187	35,15	93	61,59	37994,26	32,08	128,82	42,94
Total	532	100	151	100	118438,19	100	300	100

APPENDIX I CONT.

Importance Value Index (IVI) by species.

SPECIES	IND.	IND. %	FREC. ABS.	FREC. %	A.B.(CM ²) ABS.	A.B. %	IVI ABS.	IVI %
Anacardium excelsum and Guazuma ulmifolia forest community								
<i>Guadua</i> sp.	129	52,23	1	3,45	3098,4	6,03	61,7	20,57
<i>Anacardium excelsum</i>	4	1,62	1	3,45	28138,33	54,73	59,8	19,93
<i>Guazuma ulmifolia</i>	33	13,36	2	6,9	7700,12	14,98	35,23	11,74
<i>Annona purpurea</i>	13	5,26	1	3,45	5137,49	9,99	18,7	6,23
<i>Astronium graveolens</i>	1	0,4	1	3,45	3245,57	6,31	10,17	3,39
<i>Coccoloba caracasana</i>	6	2,43	2	6,9	244,72	0,48	9,8	3,27
<i>Cecropia peltata</i>	4	1,62	2	6,9	406,15	0,79	9,31	3,1
<i>Deguelia picta</i>	11	4,45	1	3,45	403,69	0,79	8,69	2,9
<i>Bactris major</i>	7	2,83	1	3,45	87,31	0,17	6,45	2,15
Subtotal	208	84,2	12	41,4	48461,78	94,27	219,85	73,28
Other taxa: 16 especies	39	15,8	17	58,6	2953,43	5,73	80,15	26,72
Total	247	100	29	100	51415,21	100	300	100
Conarus araucanus and Eugenia punicifolia forest community								
<i>Strychnos fendleri</i>	82	21,69	1	2,04	2614,27	6,18	29,92	9,97
<i>Hymenaea courbaril</i>	11	2,91	1	2,04	5888,36	13,93	18,88	6,29
<i>Senegalia polyphylla</i>	15	3,97	1	2,04	4071,4	9,63	15,64	5,21
<i>Copaifera officinalis</i>	2	0,53	1	2,04	5080,43	12,02	14,59	4,86
<i>Deguelia picta</i>	27	7,14	1	2,04	1894,24	4,48	13,66	4,55
<i>Uniosium velutinifolium</i>	11	2,91	1	2,04	3138,92	7,42	12,38	4,13
<i>Cupania latifolia</i>	26	6,88	1	2,04	967,39	2,29	11,21	3,74
<i>Vitex capitata</i>	7	1,85	1	2,04	2980,44	7,05	10,94	3,65
<i>Eugenia cribata</i>	29	7,67	1	2,04	431,15	1,02	10,73	3,58
<i>Eugenia punicifolia</i>	16	4,23	2	4,08	726,91	1,72	10,03	3,34
<i>Conarus araucanus</i>	17	4,5	2	4,08	582,03	1,38	9,96	3,32
<i>Lonchocarpus violaceus</i>	13	3,44	1	2,04	1545,67	3,66	9,14	3,05
<i>Coursetia ferruginea</i>	18	4,76	1	2,04	442,14	1,05	7,85	2,62
<i>Casearia ulmifolia</i>	15	3,97	1	2,04	681,69	1,61	7,62	2,54
<i>Tabebuia rosea</i>	2	0,53	1	2,04	1986,21	4,7	7,27	2,42
Subtotal	291	76,98	17	34,68	33031,25	78,14	189,82	63,27
Other taxa: 32 especies	87	23,01	32	65,3	9248,7	21,88	110,19	36,74
Total	378	100	49	100	42279,97	100	300	100
Association Homalolepidis cedrontis-Guareetum guidoniae								
<i>Guarea guidonia</i>	49	23,11	3	4,48	20531,64	20,01	47,6	15,87
<i>Tapirira guianensis</i>	18	8,49	1	1,49	7916,52	7,71	17,7	5,9
<i>Homalolepis cedron</i>	10	4,72	4	5,97	4754,6	4,63	15,32	5,11
<i>Ficus maxima</i>	3	1,42	3	4,48	8504,76	8,29	14,18	4,73
<i>Zygia latifolia</i>	11	5,19	2	2,99	3338,16	3,25	11,43	3,81
<i>Tabebuia rosea</i>	4	1,89	4	5,97	3539,99	3,45	11,31	3,77
<i>Xylopia aromatica</i>	10	4,72	1	1,49	3895,46	3,8	10,01	3,34
<i>Virola sebifera</i>	4	1,89	1	1,49	6315,72	6,15	9,53	3,18
<i>Didymopanax morototoni</i>	5	2,36	3	4,48	1986,14	1,94	8,77	2,92
<i>Spondias mombin</i>	2	0,94	1	1,49	5863,04	5,71	8,15	2,72
<i>Protium heptaphyllum</i>	5	2,36	3	4,48	1296,62	1,26	8,1	2,7
<i>Sapium glandulosum</i>	4	1,89	2	2,99	1892,15	1,84	6,72	2,24
<i>Annona fendleri</i>	7	3,3	1	1,49	1284,39	1,25	6,05	2,02
<i>Pterocarpus acapulcensis</i>	4	1,89	1	1,49	2661,06	2,59	5,97	1,99
<i>Ocotea aurantiodora</i>	5	2,36	1	1,49	1905,48	1,86	5,71	1,9
Subtotal	141	66,53	31	46,27	75685,73	73,74	186,55	62,2
Other taxa: 32 especies	71	33,47	36	53,73	26942,36	26,26	113,45	37,8
Total	212	100	67	100	102628,09	100	300	100

APPENDIX II

Floristic composition of *Protio heptaphylli-Euterpetum precatoriae* association (A)
and *Cassia moschata* and *Chomelia spinosa* forest (B)

A. *Protio heptaphylli-Euterpetum precatoriae* association

PLOT AYMARD 2012	23	33	45
SURFACE PLOT (M²):	1000	1000	1000
ALTITUDE (M):	110	20	188
	Relative density (%)		
Class <i>Guazuma ulmifoliae-Spondiadetea mombinis</i> and Order <i>Cupanio americanae -Protietalia heptaphylli</i>			
<i>Cupania americana</i>		3,4	
<i>Guarea guidonia</i>			13
<i>Spondias mombin</i>		3,4	
<i>Tapirira guianensis</i>		4,5	
<i>Sapium glandulosum</i>			4,3
<i>Tabebuia rosea</i>		1,1	
<i>Annona montana</i>	1,1		
<i>Ceiba pentandra</i>	1,1		
<i>Guazuma ulmifolia</i>		1,1	
<i>Cecropia peltata</i>		1,1	
<i>Didymopanax morototoni</i>			1,4
<i>Cordia alliodora</i>			1,4
Alliance undefined			
<i>Protio heptaphylli-Euterpetum precatoriae</i>			
<i>Protium heptaphyllum</i>	1,1	1,1	1,4
<i>Euterpe precatoria</i>		4,5	5,8
<i>Conceveibum cordatum</i>		1,1	1,4
<i>Inga ingoides</i>	11,6	1,1	
<i>Jacaranda obtusifolia</i>	9,5	3,4	
<i>Tanaecium tetragonolobum</i>	2,1	3,4	
Species number	20	30	14

Other species present:

Maquira coriacea (23/28,42), *Maclobium acaciifolium* (23/11,58), *Lonchocarpus hedyosmus* (23/8,42), *Leptobalanus apetalus* (23/7,37), *Cordia collococca* (23/3,16), *Ormosia paraensis* (23/2,11), *Stryphnodendron guianense* (23/2,11), *Stylogyne micrantha* (23/1,05), *Coccoloba latifolia* (23/1,05), *Desmoncus orthacanthos* (23/1,05), *Sequiera macrophylla* (23/1,05), *Dalbergia monetaria* (23/1,05), *Cochlospermum orinocense* (33/6,82), *Cordia panamensis* (33/4,55), *Astrocaryum aculeatum* (33/3,41), *Brownea coccinea* (33/3,41), *Virola surinamensis* (33/2,27), *Ischnosiphon arouma* (33/2,27), *Trichilia martiana* (33/1,14), *Parinari campestris* (33/1,14), *Machaerium inundatum* (33/1,14), *Manilkara bidentata* (33/1,14), *Jupunba trapezifolia* (45/20,29), *Alchornea glandulosa* (45/14,49), *Oenocarpus bataua* (45/11,59), *Vismia macrophylla* (45/8,7), *Miconia trinervia* (45/7,25), *Hernandia guianensis* (45/4,35), *Fridericia* sp. (23/1,05), *Pouteria* sp. (33/3,41), *Ficus maxima* (45/4,35), *Chrysophyllum* (33/1,14), *Bixa urucurana* (33/2,27), *Virola elongata* (23/4,21), *Attalea maripa* (33/27,27), *Trichilia pallida* (33/2,27), *Calathea lutea* (33/4,55), *Xylopia discreta* (33/1,14), *Pachira aquatica* (33/1,14).

APPENDIX II CONT.

B. *Cassia moschata* and *Chomelia spinosa* forest

PLOT	Gentry, 1980
SURFACE OF PLOT. (M ²):	1000
ALTITUDE (M).	110
	Relative density (%)
Class <i>Guazuma ulmifoliae</i>-<i>Spondiadetea mombinis</i>	
<i>Spondias mombin</i>	2,7
<i>Cochlospermum vitifolium</i>	5,3
<i>Guazuma ulmifolia</i>	1,3
<i>Guettarda divaricata</i>	6,7
<i>Jacaranda obtusifolia</i>	1,3
<i>Luehea candida</i>	4,0
<i>Annona jahnii</i>	6,7
<i>Fridericia mollissima</i>	2,7
Order <i>Cupanio americanae</i>-<i>Protietalia heptaphylli</i>	
<i>Cupania americana</i>	1,3
<i>Allophylus racemosus</i>	5,3
<i>Casearia sylvestris</i>	2,7
<i>Handroanthus chrysanthus</i>	1,3
<i>Ouratea guildingii</i>	1,3
<i>Fridericia oxycarpa</i>	4,0
Alliance <i>Xylopio aromatica</i>-<i>Protion heptaphylli</i>	
<i>Xylopio aromatica</i>	1,3
<i>Genipa americana</i>	1,3
<i>Cassia moschata</i>	6,7
<i>Xylophragma seemannianum</i>	1,3
<i>Cassia moschata</i> -<i>Chomelia spinosa</i> forest	
<i>Chomelia spinosa</i>	6,7
<i>Lonchocarpus macrocarpus</i>	4
<i>Pleonotoma clematis</i>	4
<i>Byrsonima crassifolia</i>	2,7
<i>Copaifera officinalis</i>	2,7
<i>Eugenia biflora</i>	2,7
<i>Erythroxylum orinocense</i>	2,7
<i>Bowdichia virgilioides</i>	1,3
<i>Casearia decandra</i>	1,3
<i>Connarus araucanus</i>	1,3
<i>Godmania aesculifolia</i>	1,3
<i>Guapira pacurero</i>	1,3
<i>Leuengeria (Pereskia) guamacho</i>	1,3
<i>Passiflora serrulata</i>	1,3
<i>Pterocarpus rohrii</i>	1,3
<i>Randia aculeata</i>	1,3
<i>Securidaca diversifolia</i>	1,3
<i>Senegalia polyphylla</i>	1,3
<i>Vochysia venezuelana</i>	1,3
<i>Xylosma benthamii</i>	1,3
Species number	38

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SCOTTMORIA TENUICAULE (LECYTHIDACEAE) A NEW SPECIES WITH A NEW ARIL VARIATION FOR THE GENUS, FROM THE TROPICAL RAINFOREST OF THE CARIBBEAN SLOPE OF PANAMA

JUVENAL ENRIQUE BATISTA GUERRA¹

Abstract. *Scottmoria tenuicaule*, a new tree species from this recently described genus in Lecythidaceae and native to the tropical forests of the Caribbean slope of central and western Panama, is described and illustrated, and taxonomic affinities inferred for this species are offered. In addition to the description of this species is a new detail in aril shape. It has the same “half I-beam” shaped aril previously reported for *Scottmoria*; however, the detail is that the seed aril of this new species is laterally more developed, “L-shaped,” with a 3-lobed end. This trait has not been previously reported or known for other species in the genus. Information on its distribution, habitat, ecology, phenology, and conservation status according to the IUCN for this new taxon is also provided.

Keywords: Bocas del Toro mountains, Central America, Donoso mountains, endemic, L-shaped aril

Resumen. *Scottmoria tenuicaule*, una nueva especie de árbol del género *Scottmoria*, Lecythidaceae, género descrito recientemente, es nativa de los bosques tropicales del centro y oeste de la vertiente caribeña de Panamá; también se ilustra y se ofrecen afinidades taxonómicas inferidas para esta especie, junto con la descripción de un nuevo detalle en la forma del arilo. Tiene el mismo arilo en forma de “I” reportado previamente para *Scottmoria*, sin embargo, el detalle es que el arilo de la semilla de esta nueva especie está más desarrollado lateralmente, en forma de “L,” con un extremo trilobulado, ese rasgo no había sido reportado previamente ni conocido para las especies del género. También se proporciona aquí información sobre su distribución, hábitat, ecología, fenología y estado de conservación según la IUCN para este nuevo taxón.

Palabras claves: Arilo en forma de L, América Central, endémico, montañas de Bocas del Toro, montañas de Donoso

The Neotropical Lecythidaceae are represented by trees and shrubs with zygomorphic flowers of the subfamily Lecythidoideae (Prance and Mori, 1979; Mori and Prance, 1990; Mori et al., 2017; Vargas et al., 2024). These trees are diverse in the Amazon basin and the Guiana Shield (Vargas and Dick, 2020). Currently, the most diverse and complex genera are *Eschweilera* Mart. ex DC. s. str. and *Scottmoria* Cornejo, the latter recently described in honor of the American botanist Scott Allan Mori (Vargas et al., 2024). These genera have notable differences in their androecial hoods of the flowers and the arils of their mature seeds. *Eschweilera* s. str. has flowers with an androecial hood with two inner coils, seeds with a lateral, thick, white, rubbery aril with ends that do not overlap (Vargas et al., 2024), sometimes splitting at the chalazal end into 2–3 branches (Batista and Mori, 2017a, b), and the sarcotesta or rubbery coat is absent. *Scottmoria* has flowers with an androecial hood with three to four inner coils and seed coverings of two types: (1) a soft, thin, white sarcotesta that is infiltrated with testa, arranged over the entire

or most of the mature seed or at least present in young seeds and mostly dissolving at maturity, and with a thick, yellow to white, lateral aril, often half I-beam shaped with a rubber-like texture and overlapping ends on the seed; or (2) seeds surrounded by a mostly free, white, rubbery coat (Vargas et al., 2024), also called a spreading aril. In Mesoamerica, species of understory trees with slender trunks are few, among the best known of which are *Scottmoria calyculata* (Pittier) Cornejo and *Scottmoria jacquelyniae* (S.A. Mori) Cornejo (Mori et al., 2010). *Scottmoria tenuicaule* J.E. Bat., a species described in this manuscript, is characterized by having a very slender trunk and low height, as well as having a type of aril different from those described in *Scottmoria* in the latest reclassification of the Bertholletia Clade, according to Vargas et al. (2024). The new type of aril will be called “L-shaped.” In this contribution the new species is illustrated, and information on distribution, habitat, ecology, phenology, and conservation status according to the IUCN, and a key to the Central American species are presented.

MATERIALS AND METHODS

For the description of this new species, fresh branches with flowers and fruit were collected at different times, and the most important characteristics were documented with photographs. The transverse section of the androecial hood was very important to seeing the internal chambers of the androecial hood, and the fruit section to seeing the arils of the seeds (protocol used followed Mori et al., 2011). Specimens from the herbaria PMA, MO, NY, and SCZ of the species

related to this one were reviewed and their differences compared (herbarium acronyms follow Thiers, 2022), as well as the Lecythidaceae page of the New York Botanical Garden (Mori et al., 2010). The species distribution map was made using ArcGIS (ESRI, 2017), and the conservation status treatments were made following the IUCN (2022) Red List of Threatened Species criteria and the GeoCAT geospatial conservation assessment tool (Bachman et al., 2011).

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TAXONOMY

Scottmorria tenuicaule J.E. Bat., *sp. nov.* TYPE: PANAMÁ. Colón, Distrito de Donoso, Chicheme, Costal Road, Pipeline, km 19, a un costado de la parcela de restauración, camino hacia Punta Rincón. Bosque secundario intervenido, concesión de una Mina de cobre a cielo abierto, 8°53'25.9"N, 80°38'42.3"W, 115 m, 28 noviembre 2015, *J. Batista, L. Rojas, I. Vergara, & E. González 1478* (Holotype: PMA [accession number, 130895; barcode, 129681]; Isotypes: MO [accession number 6972135; barcode, 3207508], NY [barcode 02840635]). Fig. 1–5.

Scottmorria tenuicaule has a pedicel/hypanthium 10–15 mm long, smooth lenticels, calyx lobes that are imbricate at the base, and an androecial hood with a triple inner coil; the fruit is conical-depressed, without prominent woody knobs at the calycine ring. The smooth testa of the seed is covered with a thin, white sarcotesta that features multiple faintly marked veins and is covered with a white, lateral, L-shaped aril with a rubber-like texture, and splitting at the chalazal end into three branches.

Understory trees, 2.5–8.0 m tall × 3–8 cm DBH and the trunk cylindrical to the base, bark deep brown, thin, smooth and a few brown lenticels, inner bark cream. Leaves, petiole 8–14 × 2.5–4.0 mm, terete, black when dry; blade 17.0–32.4 × 5.7–10.5 cm, lanceolate to ovate-elliptic, reddish punctations associated with veins abaxially (seen only with magnification), chartaceous, base acute to rounded, margin entire; secondary veins in 14–16 pairs, plain adaxially, raised abaxially. Inflorescences from branches below leaves (ramiflorous), axillary, or terminal (suprafoliar), unbranched, rachis, 2.2–7.8 cm long, cylindrical, puberulous; pedicel/hypanthium 10–15 mm long, puberulous (seen only under magnification). Flowers 6–8 cm in diam.; hypanthium puberulous, cylindrical; calyx with 6–7 (–8) lobes, ovate, 6–9 × 3–8 mm, green-yellowish, horizontally oriented at anthesis, imbricate at the base; 6 petals, pale yellow, 19–35 × 10–16 mm; androecial hood with a triple inner coil, intense yellow, ligule 27–35 × 10–18 mm, ovary with two locules and 3–4 ovules per locule. Fruit conical-depressed, brown, 3 (including operculum) × 3.0–3.5 cm in diam.; calycine ring visible, remnants of calyx-lobes usually visible, persistent; supracalycine zone erect, infracalycine zone conical, lenticellate, operculum convex. Seeds globose, 2.0–2.5 × 2.5–3.0 cm, 1–3 per fruit, the smooth testa of the seed is covered with a thin, white sarcotesta that features multiple, faintly marked veins and is topped with a white lateral L-shaped aril with a rubber-like texture, splitting at the chalazal end into three branches, that sometimes may resemble the footprint of a Central American Tapir or *Tapirus bairdii* Gill.

At first glance, *Scottmorria tenuicaule* resembles the lowland rainforest species, *Scottmorria hondurensis* Standl., *Eschweilera pittieri* R. Knuth, and *Eschweilera biflora* S.A. Mori, because it is a small tree, has yellow flowers and turbinate to depressed fruits. However, *S. hondurensis* is an understory to canopy tree 7–25 m tall (vs. understory tree 2.5–8 m), with flowers 3–5 cm in diam. (vs. flowers 6–8 cm in diam.) and the smooth testa of the seed has a white, lateral aril that is often half I-beam shaped with a rubber-like texture not splitting at the chalazal end into three

branches (vs. the smooth testa of the seed covered with a thin white sarcotesta that features multiple faintly marked veins and is topped with a white, lateral L-shaped aril, with a rubber-like texture, splitting at the chalazal end into three branches; Fig. 5). *E. pittieri* differs from *S. tenuicaule* by having an androecial hood with a double inner coil (vs. three to four inner coils), a lateral aril (vs. L-shaped aril), and fruit with the calycine ring with calyx-lobes persisting as prominent woody knobs (vs. the calycine ring with calyx-lobes persisting without prominent woody knobs). *E. biflora* differs from *S. tenuicaule*, by having an androecial hood with a double coil (vs. three to four inner coils), deep brown seeds (vs. cream-colored seeds) and a lateral aril (vs. L-shaped aril).

Scottmorria species in Mesoamerica generally have fuchsia, magenta, or pink flowers. However, in 2017 several species with yellow flowers were described, such as *Scottmorria rotundicarpa* (J.E. Bat. & S.A. Mori) Cornejo, *Scottmorria jefensis* (J.E. Bat. & S.A. Mori) Cornejo, and *Scottmorria roseocalyx* (J.E. Bat., S.A. Mori, & J.S. Harrison) Cornejo, all endemic to Panama (Batista and Mori, 2017a, c; Vargas et al., 2024). *Scottmorria tenuicaule* can be a shrub from 2–5 m to a low tree of 6–8 (–10) m in height. It has a thin trunk and cream-colored inner bark, while other *Scottmorria* species are generally trees ranging from 10–35 m. This species has leaves with lanceolate to ovate-elliptic blades in the Donoso region, and one collection in Bocas del Toro has ovate-elliptic blades.

Etymology: The specific epithet refers to the tree's slender trunk, 3–8 cm DBH, and thin bark.

Common names: Known as “Ollito” in the Donoso communities.

Habitat and Distribution: Understory trees of lowland, non-flooded, primary rainforest at 40–113 m elevation, near the Quebrada Jujuca and Río Del Medio River, in the Donoso mountains. This species is associated at both sites with these species: *Scottmorria calyculata* (Pittier) Cornejo, *Taralea oppositifolia* Aubl., and *Pausandra trianae* (Müll. Arg.) Baill. The species is also known from Isla Bastimento Marine National Park, Bocas del Toro (Fig. 4).

Phenology: Flowering collections were made in February. (*I. Vergara et al. 1070*), March (*Batista et al. 1557, 1558*), July (*L. Martínez et al. 884*), September (*De Sedas et al. 420*), October (*A. Espinosa & B. Fuentes 5764*), November (*Batista et al. 1478*), and December (*Zapata et al. 2616*). Fruiting specimens were collected in September (*De Sedas et al. 420*), February (*I. Vergara et al. 1070*), March (*Batista et al. 1557*), and December (*Zapata et al. 2616*).

Conservation status: *Scottmorria tenuicaule* is known from seven collections which were found in two occurrences. A single collection was registered on Isla Bastimentos (Bocas del Toro), which is included in a protected area (Isla Bastimentos National Park). The other collections were made within a working mining concession area located in the Donoso district (Colón). This species has an EOO of 817.2 km² and an AOO 25 km². Considering the imminent peril of mining activities on the suitable habitats, this species must be considered as endangered [EN B1ab(ii,iii,iv,v) + B2ab(ii,iii,iv,v)].

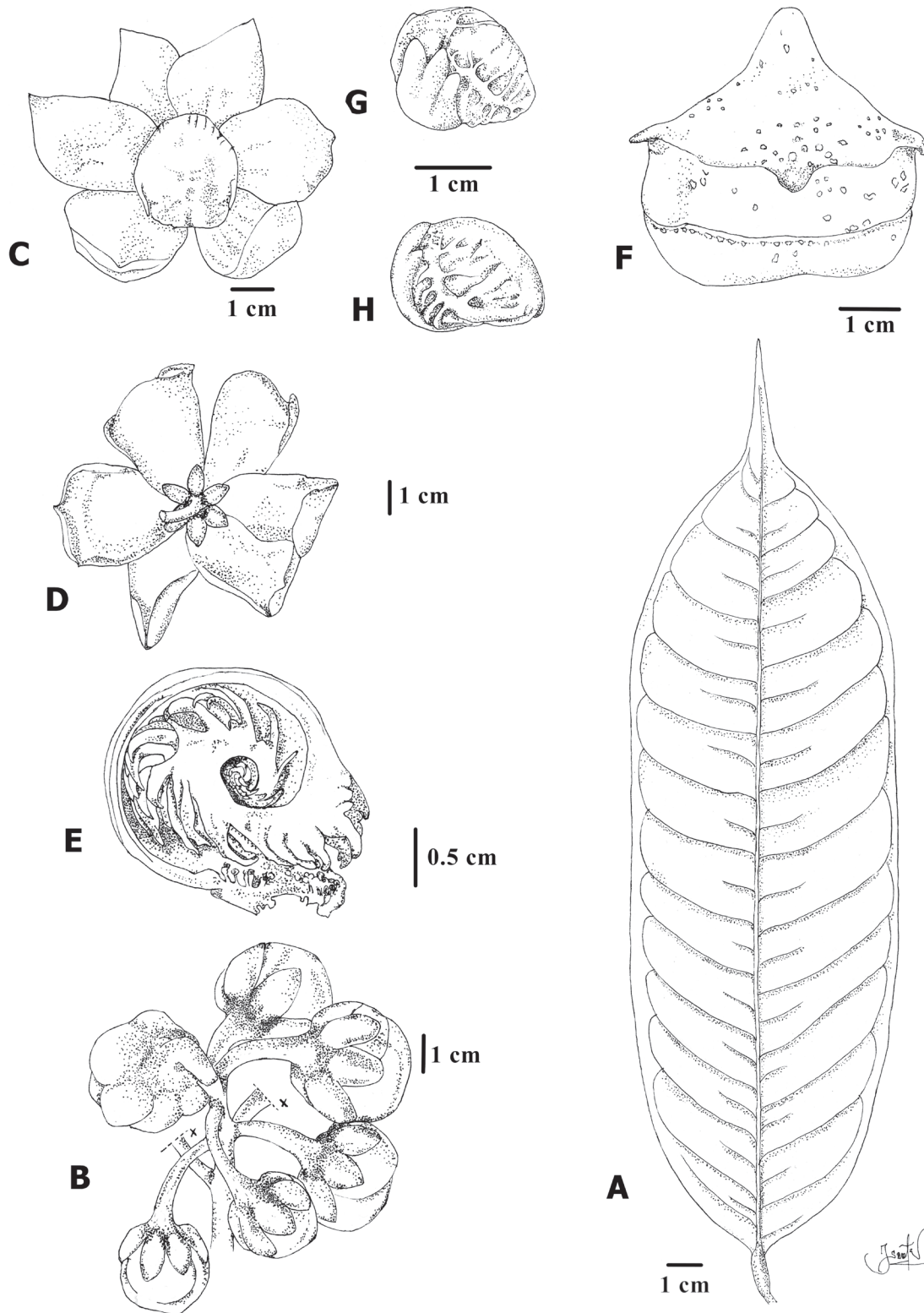


FIGURE 1. Drawing of *Scottmoria tenuicaule* J.E. Bat. **A**, adaxial view of leaf blade showing venation; **B**, magnified view of buds in the inflorescence; **C**, apical view of flower; **D**, basal view of flower showing the calyx; **E**, cross section of the hood showing the coils; **F**, side view of a closed fruit; **G**, apical view of seed showing sarcotesta branching of veins and L-shaped aril with branches; **H**, lateral view of seed showing sarcotesta branching of veins and L-shaped aril. A–E, are based on the holotype; F–H, are based on the paratype *J. Batista* et al. 1557. Drawn by Jeraldin Vergara.



FIGURE 2. *Scottmorium tenuicaule* J.E. Bat. **A**, slender cylindrical trunk, thin, dark-brown bark, cream inner bark; **B**, leaf blade showing abaxial surface; **C**, leaf blade showing adaxial surface. A–C are based on the paratype *J. Batista et al. 1557*; B is based on the holotype.

Additional specimens examined: PANAMA. Colon: Distrito de Donoso, Coclé del Norte, Helipat C11, 79 m, 8°57'34.21"N 80°37'01.17"W, 18 Octubre 2010 (fl), *A. Espinosa & B. Fuentes 5764* (PMA); Coclé del Norte, Donoso, área del Helipat PR09, 99 m, 9°00'28"N, 80°41'35"W, 10 Diciembre 2010 (fl, fr), *A. Zapata, D. Santana, & R. López 2616* (PMA); Coclé del Norte, Donoso, Helipat T02A, tomando la ruta Sur, a orilla de trocha, 109 m, 8°53'28"N, 80°40'42"W, 18 Julio 2012 (fl), *L. Martínez, A. Espinosa, A. Morris, & E. Sánchez 884* (PMA); Omar Torrijos H., Área de construcción de helipuerto, Petaquilla, ± 15 km del campamento Colina (Parcela 2), área de bosque maduro bien conservado, 100–200 m, 8°52'32"N, 80°39'27"W, 13 Septiembre 2007 (fl), *A. De Sedas 420*

(PMA); Camino Costero, Pipeline, KM 19+700, a 50 metros del camino, 130 m, 8°53'25"N, 80°38'43"W, 23 Febrero 2016 (fl, fr), *I. Vergara, L. Rojas, & M. Madrid 1069* (NY, MO, PMA, SCZ, UCH); Presa Norte, Coffor Dam, bosque maduro intervenido, 80 m, 8°53'25.8"N, 80°40'32.3"W, 21 Marzo 2016 (fl, fr), *J. Batista, I. Vergara, E. González, & L. Rojas 1557* (NY, MO, PMA); Chicheme, Costal road, Pipeline, km 19, bosque maduro intervenido, 113 m, 8°53'24"N, 80°38'43"W, 21 Marzo 2016 (fr), *J. Batista, I. Vergara, E. González, & L. Rojas 1558* (NY, PMA). Bocas Del Toro: Parque Nacional Marino Isla Bastimento. Área de Bahía Honda, 42 m, 9°17'42"N, 82°09'07"W, 4 Octubre 2013 (fl), *J. Aranda & L. Martínez 4480* (PMA).

KEY TO *SCOTTMORIAM* SPECIES OF CENTRAL AMERICA

- 1a. Flowers with petals and androecial hood magenta, fuchsia or rose, occasionally androecial hood yellow 2
- 1b. Flowers with petals and androecial hood pale yellow, deep yellow or white 8
- 2a. Inflorescence cauline, sometimes ramiflorous; fruit turbinate or weakly globose 3
- 2b. Inflorescence axillary, terminal or ramiflorous; fruit depressed-globose 4
- 3a. Blade elliptic to narrowly elliptic; flowers 5–7 cm diam.; seeds with yellow lateral aril, often half I-beam shaped with rubber-like texture and overlapping ends on seed *Scottmorium caudiculata*
- 3b. Blade oblong; flowers 4–5 cm diam.; seeds with yellow to white sarcotesta that is infiltrated with testa in most of the mature seed *Scottmorium jacquelyniae*
- 4a. Blades coriaceous to chartaceous; inflorescence unbranched; flower fuchsia to pink 5
- 4b. Blades coriaceous; inflorescence once-branched, paniculate arrangement of racemes; petals pink or fuchsia and androecial hood yellow 7

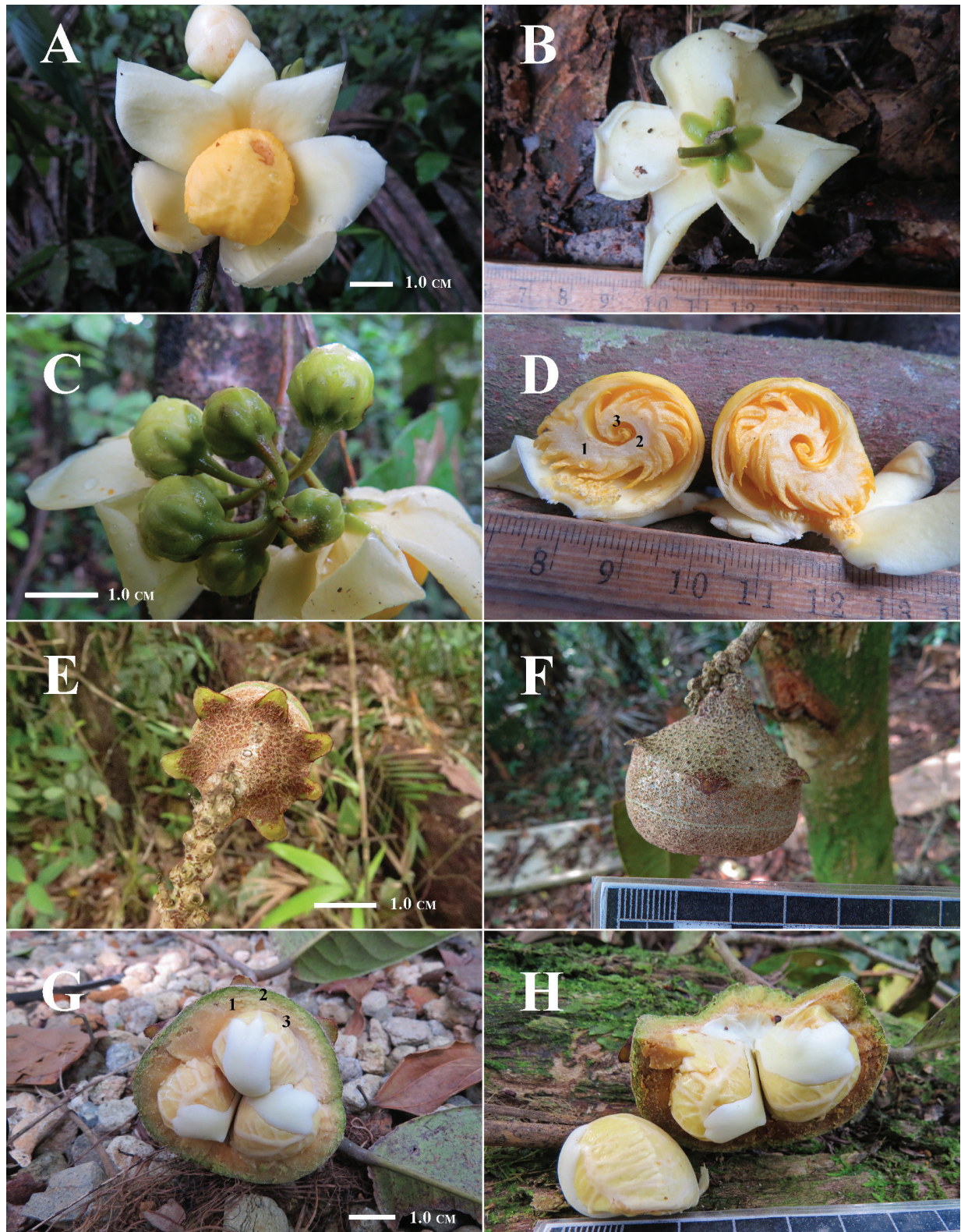


FIGURE 3. *Scottmoria tenuicaule* J.E. Bat. **A**, apical view of flower; **B**, basal view of flower showing the imbricate calyx lobes at the base; **C**, unbranched inflorescence in bud, showing pedicel/hypanthium and calyx lobes; **D**, medial longitudinal section of androecial hood showing the first, second, and third coils; **E**, basal view of an immature fruit showing the persistent, woody calyx lobes; **F**, lateral view of a nearly mature fruit; **G**, artificially opened fruit, lateral view, showing a smooth testa, topped with a thin white sarcotesta that features multiple, faintly marked veins and a lateral L-shaped aril; **H**, apical view of the seeds showing a smooth testa, topped with a thin, white sarcotesta that features multiple, faintly marked veins and a white, lateral L-shaped aril. A–D are based on the holotype. E–H are based on *J. Batista et al. 1557*.

KEY TO *SCOTTMORIA* SPECIES OF CENTRAL AMERICA CONT.

- 5a. Blade base clasping the petiole apex and the lower midrib; inflorescence terminal (suprafoliar), rachis 1–3 cm long, pedicel/hypanthium zone ca. 4 mm long; flower ca. 2.0–3.5 cm in diam., calyx lobe widely ovate, 3.0–5.5 × 2.5–4.0 mm; fruit 5–7 × 6.0–9.5 cm, widely depressed globose, infracalycine and supracalycine zone with small brown lenticels; species endemic to the Caribbean coast of Panama *Scottmoria amplexifolia*
- 5b. Blade base not clasping the petiole apex and the lower midrib; inflorescence usually from branches (ramiflorous) or axillary, rachis 1–15 cm long, pedicel/hypanthium zone 1–3 mm long; flower ca. 3–5 cm diam., calyx lobe ovate, 2–10 × 1.5–10.0 mm; fruit 5–7 × 4–7 cm, depressed globose, infracalycine and supracalycine zone with large brown lenticels; species from Central to Eastern Panama 6
- 6a. Rachis 1.0–4.5 cm long., pedicel/hypanthium zone narrowly short. Calyx lobe narrowly ovate, 2.5–3.0 × 1.5–4.0 mm., abaxial side narrowly carinate, bases not imbricate, sometimes scarcely imbricate in the base. Fruit 4–5 cm diam., calycine ring narrowly conspicuous forming a knob with the calyx lobe woody to inconspicuous, operculum umbonate to narrowly umbonate; species from Darien, Panama to Ecuador *Scottmoria integrifolia*
- 6b. Rachis 3–15 cm long, pedicel/hypanthium zone widely short; calyx lobe widely ovate to rounded, 8–10 × 8–10 mm, abaxial side not carinate, base imbricate for much of length; fruit 7–6 cm in diam., calycine ring with calyx lobes acrescent and persisting but not woody, operculum umbonate; morphotype species endemic from Central Panama *Scottmoria calyculata*
- 7a. Blades with 10–35 (50) × 4–12 cm, adaxial side with reddish punctation; inflorescence once-branched in racemes; flowers ca. 3.5–5.0 cm diam.; fruit with infracalycine and supracalycine zone with few brownish lenticels *Scottmoria antioquiensis*
- 7b. Blades with 3.2–14.5 × 1.5–7.5 cm, adaxial side with dark punctation; inflorescence once-branched, paniculate arrangement of racemes, often scarcely branched or infrequently unbranched; flower ca. 2.5–4.0 cm diam.; fruit with infracalycine and supracalycine zone with large whitish lenticels *Scottmoria jefensis*
- 8a. Canopy tree, laminate or scalloped bark, peeling in irregularly-shaped, thick plates; fruit depressed globose to globose; seeds with spreading aril or sarcotesta 9
- 8b. Understory tree, smooth bark, sometimes peeling in irregularly-shaped, thin plates; fruit cup-shaped to conical-depressed; seeds with lateral aril, half I-beam shaped or L-shaped with rubber-like texture 14
- 9a. Inflorescence unbranched or weakly branched 10
- 9b. Inflorescence once-branched 11

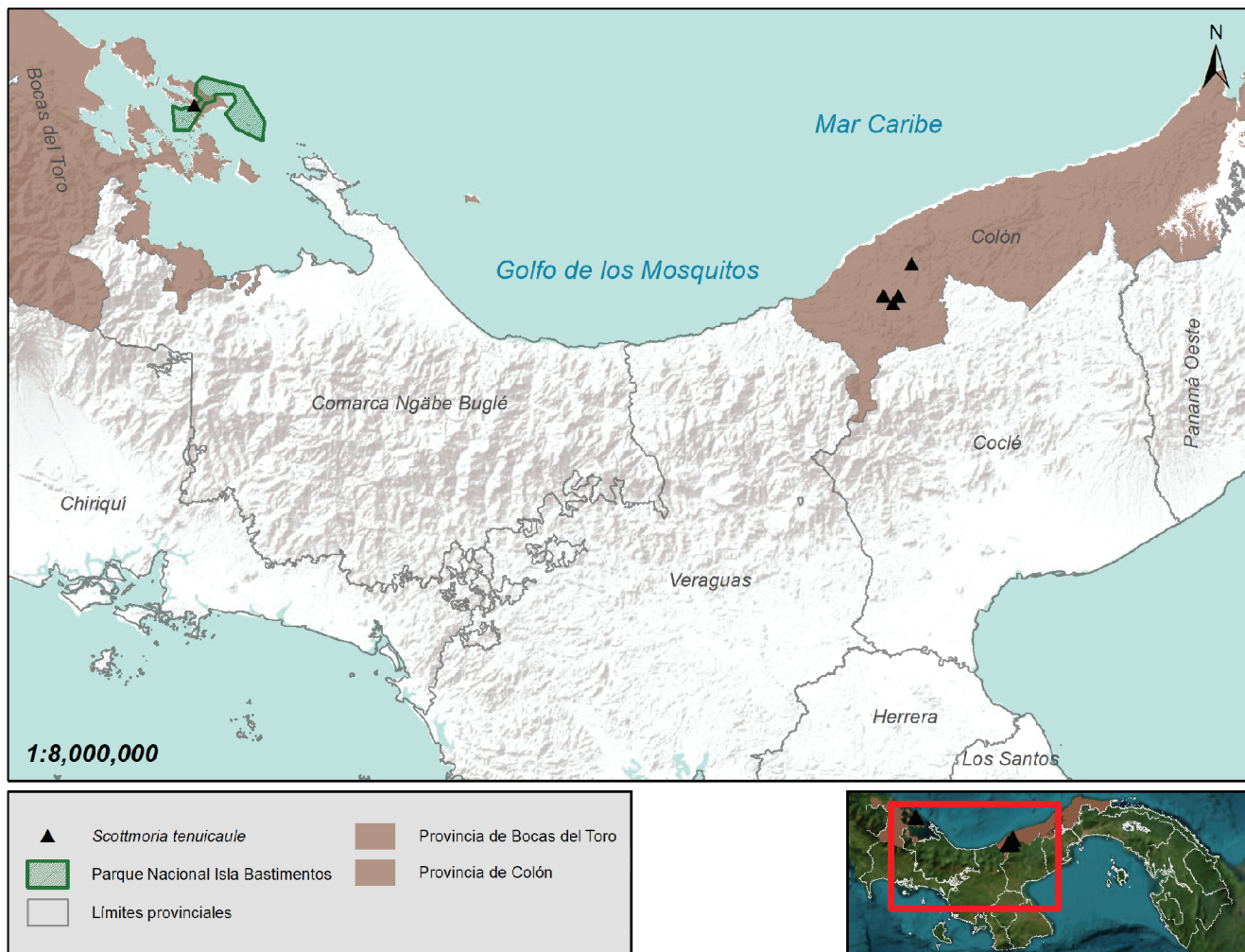


FIGURE 4. *Scottmoria tenuicaule* J.E. Bat. Distribution map. Prepared by Vayron De Gracia.

KEY TO *SCOTTMORIA* SPECIES OF CENTRAL AMERICA CONT.

- 10a. Blade 10–15 × 3–5 cm, elliptic to narrowly elliptic, blackish punctations; flower 2.0–2.5 cm diam., pedicel/hypanthium zone 5–9 mm long, calyx lobe weakly ovate, 1.5–2.0 × 1.5–2.5 mm, base not imbricate; fruit weakly depressed globose to nearly globose; species endemic to Peninsula Osa, Costa Rica *Scottmoria aguilarii*
- 10b. Blade 10–35 × 4–12 cm, oblong to narrowly elliptic, reddish punctations; flower 3.5–4.0 cm diam., pedicel/hypanthium zone 3 mm long, calyx lobe widely ovate, 7–8 mm × 7.0–8.5 mm, base imbricate much of its length; fruit widely depressed globose; morphotype species from Costa Rica to Western Panama *Scottmoria calyculata*
- 11a. Secondary veins not impressed adaxially; principal rachis of inflorescence 5.0–7.5 cm long; fruit with conspicuous calycine ring with individual sepal lobes expanded; trees from lowland rainforest from Osa Peninsula, Costa Rica to Caribbean slope Panama *Scottmoria panamensis*
- 11b. Secondary veins impressed adaxially; principal rachis of inflorescence 4–35 cm long; fruit with the calycine ring inconspicuous, sometimes conspicuous forming a continuous ring; trees from mid-altitude rainforests to cloud rainforest 12
- 12a. Blade elliptic, 3.1–11.0 × 1.2–6.7 cm long; principal rachis of inflorescence 4–7 cm long, pedicel/hypanthium zone 4–5 mm long, yellow; flower 2–3 cm. diam.; fruit globose to weakly depressed globose. *Scottmoria rotundicarpa*
- 12b. Blade widely elliptic to oblong, 15–39 × 5.5–15.5 cm long, principal rachis of inflorescence 4–35 cm long, pedicel/hypanthium zone 5–10 mm long, pink to yellow greenish; flower 3–5 cm. diam.; fruit depressed globose, conical or conical-depressed 13
- 13a. Bark brown, slightly fissured; principal rachis of inflorescence 9–35 cm long, secondary rachises well-developed, to 40 cm long, pedicel/hypanthium zone yellow to yellow greenish; fruit 6–9 cm diam., depressed globose, calycine ring conspicuous, forming a continuous ring; seeds to 10 per fruit, surrounded by a mostly free, white, rubbery coat, thin *Scottmoria collinsii*
- 13b. Bark scalloped, grayish brown, peeling in longitudinal plates; principal rachis of inflorescence 4–8 cm long, secondary rachises developed, to 6 cm long, pedicel/hypanthium zone pink to pale yellow pinkish; fruit 5–6 cm diam., turbinate to conical, calycine ring weakly conspicuous, not forming a continuous ring; seeds 3 per fruit, surrounded by a mostly free, white, rubbery coat, thick, especially along major veins *Scottmoria roseocalyx*
- 14a. Tree 10–30 m tall; flower 3–5 cm diam.; fruit cup-shaped; seeds with lateral aril, often half I-beam shaped, with a rubber-like texture, without branches; species from Honduras, Nicaragua, Costa Rica, and west to Pacific coast of Central Panama. *Scottmoria hondurensis*
- 14b. Tree 2.5–8.0 m tall; flower 6–8 cm diam.; fruit conical-depressed; seeds with lateral L-shaped aril with a rubber-like texture, with three branches; endemic species from Caribbean coast of Central Panamá *Scottmoria tenuicaule*

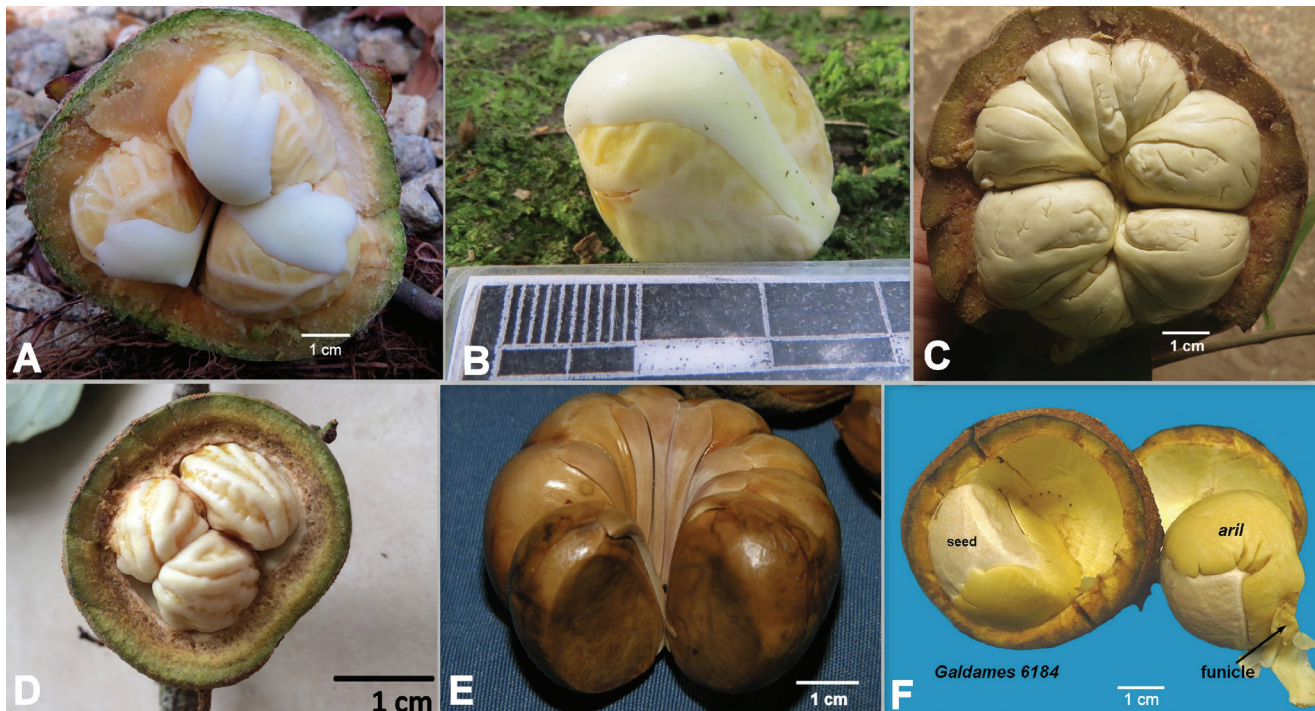


FIGURE 5. Aril types of *Scottmoria* s. str. **A**, open fruit of *Scottmoria tenuicaule*, showing three seeds with a thin white sarcotesta that features multiple, faintly marked veins and a fleshy, white, lateral L-shaped aril, splitting at the chalazal end into three branches; **B**, lateral view of seed of *S. tenuicaule* showing thin white sarcotesta that features multiple, faintly marked veins and fleshy white lateral L-shaped aril; **C**, open fruit of *Scottmoria integrifolia* showing seven seeds fully surrounded by a fleshy, thin, white sarcotesta, which in turn is surrounded by a white spreading aril, with a rubber-like texture; **D**, open fruit of *Scottmoria roseocalyx*, showing apical view of three seeds with spreading aril, growing on a thin, white sarcotesta; **E**, open fruit of *Scottmoria hondurensis* showing the seeds with lateral aril, often half I-beam shaped, with a rubber-like texture; **F**, open fruit of *Scottmoria jacquelyniae* showing two seeds with testa covered by a thin, white layer of sarcotesta and a yellow aril with a rubber-like texture that is infiltrated with testa and sarcotesta, arranged over most of the mature seed. A–B are based on the paratype *J. Batista et al.* 1557; C is based on *J. Batista et al.* 1659 (NY, PMA); D is based on *J. Batista et al.* 1682 (NY, PMA, SCZ, UCH); E is based on *R. Aguilar 11748* (NY), photo by R. Aguilar; F is based on *C. Galdames 6142* (NY, PMA, SCZ), photo by C. Galdames.

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APPENDIX

Since the key on pages 248–251 could not be presented as a continuous text, readers can obtain it on a single page [here](#).

ANDINOCLEOME COMPLANATICARPA (CLEOMACEAE): A NEW SPECIES FROM SOUTHWESTERN ECUADOR

XAVIER CORNEJO¹

Abstract. *Andinocleome complanaticarpa*, a new species from southwestern Ecuador characterized by the strongly complanate ovaries and fruit, is formally described and illustrated, and its relationship to morphologically closely related species is discussed.

Keywords: Ecuador, endemics, Cleomaceae, Neotropics

Resumen. *Andinocleome complanaticarpa*, una nueva especie del suroeste de Ecuador caracterizada por los ovarios y frutos fuertemente aplanados es descrita e ilustrada, se discute sus relaciones con las especies morfológicamente cercanas.

Palabras claves: Ecuador, endémicas, Cleomaceae, neotrópicos

Andinocleome (Iltis and Cochrane, 2014; *sensu* Cornejo, 2024) is a small Neotropical genus in Cleomaceae centered in the northern and north-central Andes of South America, except for one isolated species, *A. magnifica*, which occurs in southern Mexico and Guatemala (Cornejo and Cochrane, submitted). The genus was originally defined in a broad sense, including the *lechleri* and *chilensis* clades (McGinty and Roalson, 2020). Subsequent examination of morphology in fresh material related to the geographic pattern of distribution, and, based on previous phylogenetic studies, led the author to the recognition of *Andinocleome* in a strict sense as a monophyletic genus only based on the *lechleri* clade. In the *chilensis* clade, a closely related sister genus, *Incacleome*, is recognized and is restricted to the Andes and coastal deserts of Peru and Chile (Cornejo, 2024). *Andinocleome* is the only genus of subwoody shrubs to woody treelets in the Cleomaceae, reaching from 0.8 m up to 4 m high, the tallest in this family in the Neotropics. Currently, *Andinocleome* comprises seven species, including the new species presented here. These species can

be recognized by: the palmately compound leaves, folioles with brochodromous venation and tertiary veins that are sulcate above and conspicuously prominent beneath, the highly distinctive and unique floral nectaries that are thick, bowl-shaped, subhexagonal, 5–10 mm wide, with six shallow infrastaminal depressions often separated by six radial interstaminal fleshy elevations or crests, margins that are wavy or dentate, petals that are light green to yellowish or purple, fruit valves that are thick, coriaceous to subwoody, usually crowned by a short and thick style, otherwise the style is absent (Cornejo, 2024). Similar to the case of *Capparidastrum* in the closely related Capparaceae family (Cornejo and Iltis, 2005; Cornejo et al., 2021), during the revision of Cleomaceae for the Flora of Ecuador project, it was observed that in *Andinocleome*, the shape and size of the ovaries in fresh material can provide useful characters for separating and recognizing species. Based on these characters in some specimens from southwestern Ecuador with strongly flattened ovaries and fruit, a new species is formally described here.

TAXONOMY

1. *Andinocleome complanaticarpa* Cornejo, *sp. nov.*

TYPE: ECUADOR. El Oro: Cerro de Chilla, 3°43'S, 79°38', 3595 m, 3 May 1997 (fl), *H. Vargas & C. Canaday 1389* (Holotype: MO [5339848]; Isotypes: MO [5185823], QCNE, US [3396031], US [3396031]). Fig. 1.

Andinocleome complanaticarpa is similar to *A. longifolia* (C. Presl) Iltis ex E.M. McGinty & Roalson, but differs by the narrowly elliptic or elliptic-oblong, strongly complanate ovaries, 3–4 mm wide (vs. ovaries linear-cylindric, 1–2 mm wide), and complanate fruit (vs. cylindric fruit).

Shrubs, ca 1.3 m tall, generally short-pilose to glabrous, hairs simple. *Leaves* 5(–9?)-foliolate; petioles 2–10 cm long; leaflets sessile or with petiolule up to 5 mm long; blades narrowly elliptic, central leaflet ca 10–12 × 1.5–2.0 cm, narrowly cuneate or attenuate at base, entire or finely serrulate-ciliate at the margin, acute to shortly caudate at the apex, lateral veins ca 14–20 on each side, short pilose

abaxially. *Racemes* terminal and lateral, to 0.8 m long, flowers few at any one time, very dense [bracts and buds numerous on older racemes]; bracts lanceolate, 2.0–3.5 × 0.7–1.5 cm. *Pedicels* 2.5–3.0 cm long, (sub)glabrous; *sepals* fused at the base, lanceolate, ca 5–6 × 2–3 mm, glabrous; *petals* oblong, spatulate, 20–27 × 5–9 mm, gradually to abruptly attenuate at base, entire to irregularly denticulate at the margins, rounded and often cucullate at the apex, yellow to purplish-yellow, glabrous; filaments 6–9 cm long; *anthers* 8–11 mm long, purple; *gynophore* 5–9 cm long; *ovary* narrowly elliptic or elliptic-oblong, 1.2–1.7 × 0.3–0.4 cm, strongly complanate and irregularly torulose (fresh), glabrous; style gradually narrowed from ovary apex, nearly absent or oblong; stigma undeveloped, narrower than or equaling style in diameter. *Capsules* subpendulous to pendulous, narrowly elliptic, 5–7 × 0.5–0.6 cm, strongly complanate, undulate along both sutures and irregularly

Thanks to the MO herbarium for the reproduction of the isotype image of *Andinocleome complanaticarpa*.

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MISSOURI
BOTANICAL GARDEN
HERBARIUM
Nº 5339848



147

ECUADOR

DAPPARACEAE
Cleome longifolia C. Presl ?

det. S.F. Smith (US), August 2000
El Oro: Chilla

Cerro de Chilla. Vegetación de páramo, arbustiva y herbácea.
03°30'S 079°38'W 3595 m

Arbusto de 1.30 m. Flor terminal amarilla con varios filamentos que salen del interior de la flor.

3 Mayo 1997

Homero Vargas & C. Canaday 1389
HERBARIO NACIONAL DEL ECUADOR (QCNE)
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

FIGURE 1. *Andinocleome complanaticarpa* Cornejo, Vargas & Canaday 1389, the holotype.

torulose, smooth, glabrous; style 1–3 mm long; carpophore 5–9 cm long; pedicel ca 3 cm long; *seeds* not seen.

Andinocleome complanaticarpa vegetatively resembles *A. longifolia*, but the new species is differentiated from the latter and from all other species in the genus by the compressed ovary and fruit as described in the diagnosis.

Etymology: The epithet *complanaticarpa* is composed from the Latin words *complanatus*, meaning flattened, and *carpus*, meaning fruit, and refers to the laterally compressed fruit, a conspicuous character of this taxonomic novelty.

Habitat and distribution: Known only from the type locality, in cerro de Chilla, where it was collected and later photographed in the disturbed upper montane Andes in the province of El Oro, southwestern Ecuador. An image

of *Andinocleome complanaticarpa* with fruit from the type locality is posted on iNaturalist (<https://ecuador.inaturalist.org/observations/109709231>).

Phenology: Flowering and fruiting specimens have been collected and observed in March and May.

Conservation status: *Andinocleome complanaticarpa* is known only from the type locality. As the area of occupancy of the species is less than 100 km², and due to the steady deforestation and fragmentation in the region, with small patches of native vegetation remaining, all surrounded by extensive grass areas for cattle (pers. obs.), it is suggested that this new species should be assigned as Critically Endangered (CR) following the IUCN criterion B1 ab(iii) (IUCN, 2022).

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A TAXONOMIC SURVEY OF THE RAUVOLFOID GRADE (APOCYNACEAE) IN PARAÍBA STATE, BRAZIL

MICKAELLY DE LUCENA MAMEDE,¹ INGRID KOCH,² AND JOSÉ IRANILDO MIRANDA DE MELO^{3,4}

Abstract: This study presents a taxonomic treatment of the Rauvolfioideae grade (Apocynaceae) in Paraíba state, Brazil. Morphologically, Rauvolfioideae are distinguished from the other groups in the family by including representatives with white flowers, stamens free from the style head and fully fertile anthers, and sinistrorse corolla lobes. We carried out field trips to municipalities in Paraíba state between September 2018 and August 2019, visited the herbaria of Paraíba, Pernambuco, and Bahia states, and consulted records of Apocynaceae available at: Virtual Herbarium of Flora and Fungi (Reflora) and SpeciesLink. We found seven genera and 16 species: *Allamanda* (three spp.), *Aspidosperma* (six spp.), *Hancornia* (one sp.), *Himatanthus* (one sp.), *Macoubea* (one sp.), *Rauvolfia* (one sp.), and *Tabernaemontana* (three spp.). *Aspidosperma confertiflorum* A.C.D. Castello and *A. discolor* A.D.C. are recorded for Paraíba state for the first time in this study. The treatment presents a key, taxonomic descriptions, comments on the morphological characters for species recognition, data on flowering and fruiting, distribution and preferential environments, images of the main characters for species identification, and distribution maps.

Keywords: Conservation, diversity, flora, Gentianales, taxonomy

Resumo: Este estudo apresenta um levantamento taxonômico do grau Rauvolfioideae (Apocynaceae) no Estado da Paraíba, Brasil. Morfologicamente, o grau Rauvolfioideae se diferencia dos demais grupos da família por incluir representantes com flores brancas, estames livres da cabeça do estilete e anteras totalmente férteis, e geralmente apresentam os lobos da corola sinistrorsos. Foram realizadas expedições para coletas em municípios da Paraíba entre setembro/2018 e agosto/2019, analisados os materiais incorporados aos herbários da Paraíba, Pernambuco e Bahia, além de consultados os registros de Apocynaceae disponíveis para a área de estudo nas plataformas: Herbário Virtual da Flora e Fungos (Reflora) e SpeciesLink. Foram encontrados sete gêneros e 16 espécies: *Allamanda* (três spp.), *Aspidosperma* (seis spp.), *Hancornia* (uma sp.), *Himatanthus* (uma sp.), *Macoubea* (uma sp.), *Rauvolfia* (uma sp.), e *Tabernaemontana* (três spp.). *Aspidosperma confertiflorum* A.C.D. Castello e *A. discolor* A.D.C. estão sendo registradas pela primeira vez para a Paraíba nesse estudo. O tratamento taxonômico apresenta chave de identificação, descrições taxonômicas e comentários sobre os caracteres morfológicos para o reconhecimento das espécies, dados de floração e frutificação, distribuição, ambientes preferenciais, imagens dos principais caracteres para a identificação das espécies e mapas de distribuição.

Palavras-chave: Conservação, diversidade, flora, Gentianales, taxonomia

According to Endress et al. (2014), Rauvolfioideae are an Apocynaceae subfamily comprising 11 tribes and 79 genera with a pantropical distribution. However, Fishbein et al. (2018) recognizes the Rauvolfioideae grade, a group comprising 12 tribes. In Brazil, Rauvolfioideae comprises 206 species in 24 genera, with 74 species in 18 genera in the Northeast region, and, in the state of Paraíba, nine species and six genera were initially recorded (Flora e Funga do Brasil, 2024).

The species in this grade have latex, flowers with gamopetalous corollas, epipetalous stamens, and usually a superior ovary (semi-inferior in *Himatanthus*), formed by two carpels united to different degrees, with a style and a style head with compartmentalized functions. However, members of the Rauvolfioideae grade can be recognized by typically having white flowers, usually with sinistrorse corollas, stamens free of the style head, and fully fertile anthers. Within Apocynaceae, Rauvolfioideae has great

morphological variation, with its representatives exhibiting all types of habits and phyllotaxis, and an impressive diversity of fruits.

Some representatives of the subfamily have edible fruits, such as ‘mangaba’ (*Hancornia speciosa* Gomes), which has a sweet flavor and is highly appreciated in northeastern Brazil, has high nutritional value and protein content compared to other fruit species (Vieira-Neto, 1994). The latex of the Amazon ‘sorva’ (*Couma utilis* (Mart.) Müll. Arg.) is edible and employed on a large scale in the industrial production of chewing gum. It also provides varnishes and rubber (Falcão and Lleras, 1981). Some species of *Aspidosperma* are appreciated for their wood (Carvalho 2003, 2010), and *Allamanda* and *Thevetia* are cultivated as ornamental species (Sakane and Shepherd, 1986; Lorenzi et al., 2003).

Several species of Rauvolfioideae have pharmacological and toxic properties. Species of *Himatanthus* Willd. Ex Schult. have been tested for their effectiveness for the treatment of

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external wounds, worm infections, and arthritis (Endo et al., 1994; Villegas et al., 1997; Miranda et al., 2000; Camaioni-Neto et al., 2002; Rodrigues et al., 2010), and species of *Aspidosperma* have anti-inflammatory, antineoplastic properties, and are used for treating malaria and fevers (Oliveira et al., 2009; Trindade et al., 2016). Lactonic iridoids (plumericin, alamandin, and isoplumericin) were observed on the bark of *Himatanthus*; plumericin and isoplumericin are toxic to fungi (Silva et al., 1998). Confluence acid, a mono-amino oxidase B inhibitor, has also been isolated from *Himatanthus* spp. and used in studies to treat Parkinson's disease (Endo et al., 1994). Indole alkaloids are recorded for several species of *Aspidosperma*, and these substances are known to act on the central nervous system (Oliveira et al., 2009). The genus *Rauvolfia* L. has species with antimicrobial

actions in addition to toxic potential (Agra et al., 2007; Agra et al., 2008). Indole alkaloids, such as reserpine, with hypotensive and sedative properties, have been widely used in the pharmaceutical industry (Koch, 2002) and isolated from several species of *Rauvolfia*, especially *R. serpentina* (L.) Benth. ex Kurz (Monachino, 1954).

Considering the attributes of this taxonomic group and the importance of expanding studies on the diversity of Apocynaceae in the flora of northeastern Brazil, we present the taxonomic treatment of the Rauvolfioideae grade (Apocynaceae) for Paraíba state, Brazil. We include an identification key, descriptions, examined material, and comments on the diagnostic morphological characters for each species, as well as data on reproductive phenology, preferential environments, and geographical distribution maps.

MATERIALS AND METHODS

Study area

Paraíba state (Fig. 1) has an area of 56,467.239 km² (IBGE, 2018) and comprises predominantly Caatinga vegetation, which occupies approximately 90% of its territory. The other vegetation types include semideciduous seasonal forest, open ombrophilous forest, wooded savanna, forested savanna, mangrove, palm trees, 'tabuleiros' [a Brazilian type of coastal natural formation like cliffs], and the pioneer vegetation of beaches, 'restingas,' and open areas (IBGE, 2004; SERVIÇO FLORESTAL BRASILEIRO, 2019).

According to Francisco et al. (2015), the Paraiban Forest is characterized by a hot and humid tropical climate. In the Borborema region, in central Paraíba, the climate is hot semi-arid with summer rains and between February and May, the greatest amounts of rain occur in the Cariri/Curimataú and Sertão regions and in the west of the state, the climate is tropical hot semi-humid, also with summer rains (BSHw). The rainy season in the Midwest sector is the most intense during the months from February to May, while in the East sector, it takes place from April to July

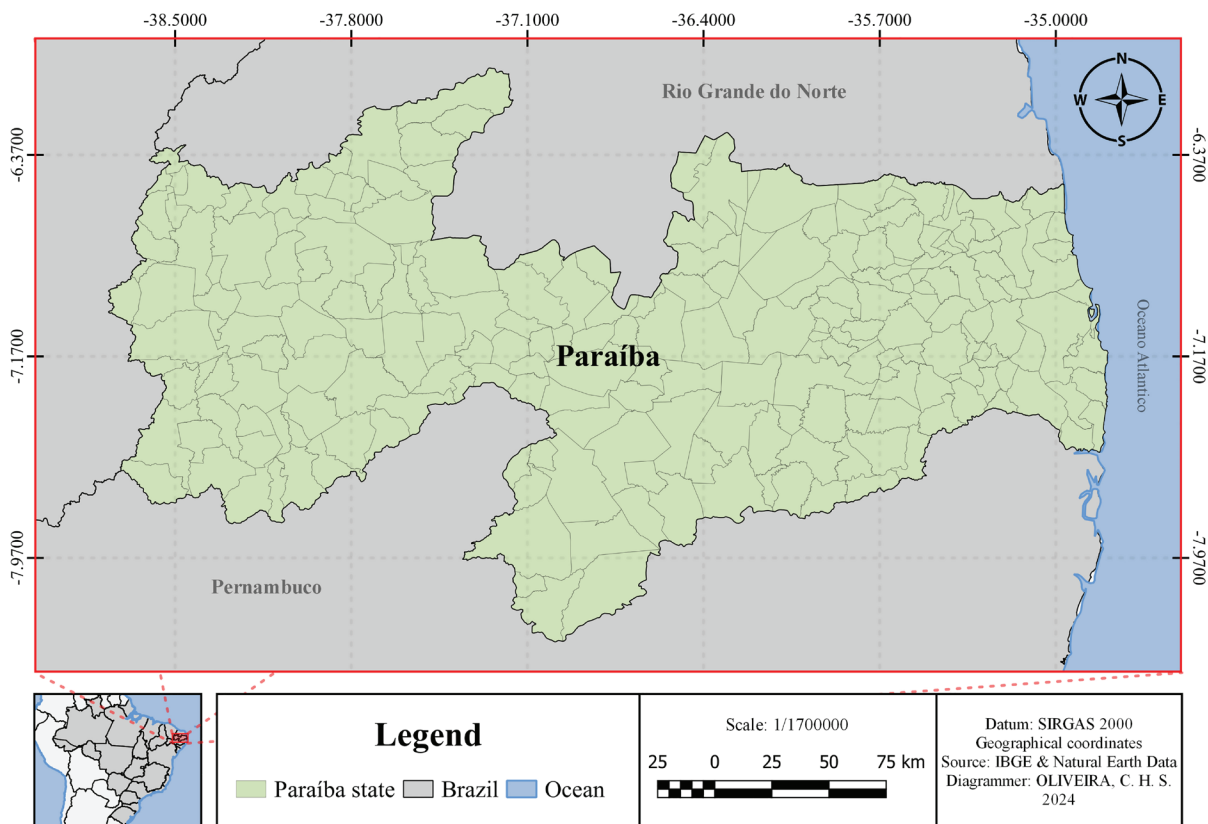


FIGURE 1. Location of the study area, Paraíba state, Brazil.

(AES, 2006) with the annual rainfall ranges from 300 to 1900 mm, with the lowest precipitation occurring in the West and central regions with greater rainfall averages on the Paraíba coast. (Francisco et al., 2015).

Taxonomic treatment

We conducted field expeditions from September 2018 to August 2019, covering the Paraíba state, including dry and rainy seasons, and all intermediate regions. Specimens were collected and processed according to the methods outlined in Judd et al. (2009). We incorporated the specimens into the João Vasconcelos-Sobrinho Herbarium (PEUFR) at the Rural Federal University of Pernambuco (UFRPE) and sent duplicates to the Manuel de Arruda Câmara Herbarium (HACAM) at the State University of Paraíba, *Campus I*. We visited the herbaria of Paraíba state (CSTR, EAN, HACAM, and JPB) as well as the herbaria of Pernambuco state (HST, IPA, and PEUFR) and Bahia state (ALCB and HUEFS). The herbaria acronyms are in accordance with Thiers (continuously updated). We also consulted the platforms of the INCT: Virtual Herbarium of the Flora and Fungi (2024) and SpeciesLink (2024). We checked the correct spelling of taxon names in the database 'Flora and Fungi

of Brazil' (Koch et al., continuously updated) and Tropicos (continuously updated). We also used these databases to obtain data on the Brazilian and general distribution of each species.

We used specialized literature for the identification of genera and species (Sakane and Shepherd, 1986; Leeuwenberg, 1994; Koch and Kinoshita, 1999; Koch, 2002; Simões and Kinoshita, 2002; Matozinhos and Konno, 2008, 2011; Morokawa et al., 2013; Pereira et al., 2016; Castelo et al., 2018; Fernandes et al., 2018), and consulted protologues and nomenclatural types. We used the terminologies of Harris and Harris (2000) and Gonçalves and Lorenzi (2011), in addition to those of the classic studies for Apocynaceae for taxonomic descriptions. We based species morphological and flowering and fruiting data on field observations and information on the labels of the analyzed exsiccatae; when pertinent, we complemented this with literature data. We used our observations and exsiccatae labels to obtain geographical distribution data and preferential environments of the species in Paraíba state. We used the studies of Cabrera (1973), Morrone (2014, 2015), and Boechat and Longhi-Wagner (2000) to determine the distribution patterns of the species.

RESULTS AND DISCUSSION

We identified 16 species in seven genera: *Allamanda blanchetii* A.DC., *Allamanda cathartica* L., *Allamanda doniana* Müll. Arg., *Aspidosperma confertiflorum* A.C.D. Castello, *Aspidosperma cuspa* (Kunth) S.F. Blake ex Pittier, *Aspidosperma discolor* A.DC., *Aspidosperma melanocalyx* Müll. Arg., *Aspidosperma nigricans* Handro, *Aspidosperma pyriforme* Mart. & Zucc., *Hancornia speciosa* Gomes, *Himatanthus bracteatus* (A.DC.) Woodson, *Macoubea guianensis* Aubl., *Rauvolfia ligustrina* Willd., *Tabernaemontana catharinensis* A.DC., *Tabernaemontana flavicans* Willd. ex Roem. & Schult., and *Tabernaemontana laeta* Mart. *Aspidosperma confertiflorum*, *A. discolor*, *A. melanocalyx*, *Macoubea guianensis*, *Tabernaemontana catharinensis*, *T. flavicans*, *T. laeta*, and the genus *Macoubea* were first recorded in Paraíba state by Mamede et al. (2020). Furthermore, three species are restricted to the Northeast region: *Aspidosperma confertiflorum*, *A. nigricans*, and *A. discolor*. *Aspidosperma pyriforme* and *Allamanda blanchetii* are the most widely distributed species in the state.

We found Rauvolfioid species in upland forests ('Brejos de altitude'), dry forests (*Aspidosperma confertiflorum*, *Tabernaemontana laeta*), Caatinga (*Aspidosperma pyriforme*), and coastal Atlantic vegetation, including 'restingas' and 'tabuleiros' (*Hancornia speciosa* and *Himatanthus bracteatus*). We also observed species of Rauvolfioid in forest edges, roadsides, and disturbed areas. *Allamanda cathartica* and *A. doniana* had few collection records, many of which were in areas disturbed by humans. However, because these species are widely used in gardening projects, we are unsure of their native distribution.

We found several species in the Atlantic Forest and the Caatinga protected areas, including the upland forests. In the municipality of Mamanguape, there are records for

Hancornia speciosa, *Himatanthus bracteatus*, and *Macoubea guianensis* at the 'Reserva Biológica de Guaribas,' and for *Tabernaemontana flavicans*, *Aspidosperma discolor*, and *H. bracteatus* at the 'Estação Ecológica do Pau-Brasil.' Some species have been recorded at the 'Jardim Botânico Benjamin Maranhão,' known as 'Mata do Buraquinho,' municipality of João Pessoa, such as *Aspidosperma melanocalyx*, *Hancornia speciosa*, *H. bracteatus*, *M. guianensis*, and *T. flavicans*. *Allamanda blanchetii*, *Aspidosperma nigricans*, and *A. pyriforme* were recorded at the 'Parque Estadual do Pico do Jabre,' in the municipality of Maturéia. The species *H. bracteatus* and *Rauvolfia ligustrina* were recorded at the 'Parque Estadual Mata do Pau-Ferro,' municipality of Areia. At the 'Parque Estadual da Pedra da Boca,' located between the municipalities of Araruna and Tacima, we found *Allamanda blanchetii*, *Himatanthus bracteatus*, and *Rauvolfia ligustrina*. At the Monumento Natural (MONA) do Vale dos Dinossauros, municipality of Sousa, we recorded *Aspidosperma pyriforme*, *Himatanthus bracteatus*, and *Rauvolfia ligustrina*.

Aspidosperma pyriforme and *Allamanda blanchetii* were recorded at the 'Área de Proteção Ambiental (APA) de Onças,' municipality of São João do Tigre; *Himatanthus bracteatus* and *Hancornia speciosa* were found at the Tambaba APA, municipality of Conde; *Rauvolfia ligustrina* and *Tabernaemontana laeta* were obtained at the Roncador APA, municipality of Bananeiras.

Regarding Private Natural Heritage Reserves (RPPN), *Allamanda blanchetii* and *Aspidosperma pyriforme* were recorded at the Fazenda Almas RPPN, municipality of São José dos Cordeiros; *A. pyriforme* at the Fazenda Tamanduá RPPN, municipality of Santa Terezinha; and *Hancornia speciosa*, *Himatanthus bracteatus*, and *Tabernaemontana laeta* at the Fazenda Pacatuba RPPN, municipality of Sapé.

Aspidosperma discolor and *A. melanocalyx* have a few records of occurrence in these conservation units. Still, these records are quite old, dated from 1995, and new searches for the species are necessary to assess their current occurrence in Paraíba state.

We used the following characters to identify the

Rauvolfioid grade species in the study area: stem surface, latex coloration, foliar phyllotaxy, leaf size, texture, shape, base and apex of the leaf blade, venation type, bract shape, calyx lacinia, length relationship between tube and lobes, corolla shape and color, nectariferous disc shape, characters related to the ovary, fruit type, fruit surface, and fruit shape.

TAXONOMIC TREATMENT

Rauvolfioideae Kostel

Shrubs, with climbing *branches* or not, and *trees*, with woody, subwoody, flat, or grooved *stems*, usually white or reddish *latex*; *branches* lenticellate or non-lenticellate, glabrous or pilose. *Leaves* petiolate or sessile, simple, alternate, opposite, or verticillate, lax or congested at the apex of the branches; blade oblanceolate, elliptical, lanceolate, obovate, with margin flat, slightly undulate, or revolute, chartaceous, or membranaceous, concolorous or discolorous; brochidodromous, craspedodromous, camp-todromous, or reticulodromous venation. *Inflorescence* terminal or axillary; bracts linear, oval, or navicular. *Flowers* pink, white, cream, dark red, or yellow; calyx usually with 5 sepals, with subequal lacinia or unequal to

each other; hypocrateriform or infundibuliform corolla; stamens longitudinal, anthers free from the head of the style, triangular, lanceolate, or oval; ovary bicarpellar, hemisyncarpic (rarely syncarpous: *Allamanda* spp.; *Rauvolfia ligustrina*), usually superior, rarely semi-inferior (*Himatanthus*), glabrous or tomentose; style head fusiform or spool-shaped, with two apical appendages and trichomes forming small crowns at the apex and/or base. Nectariferous disc present or absent, lobed, or entire. *Fruit* a follicle, berry, capsule, or drupe with a smooth, costate, verrucose, or spinescent surface; sessile or stipitate, lenticels conspicuous or inconspicuous; seeds smooth or rough, orbicular, rounded, elliptical, ovate, or oblong, naked, with aril, or winged.

KEY TO SPECIES OF RAUVOLFOID GRADE (APOCYNACEAE) IN PARAÍBA STATE, BRAZIL

- 1a. Leaves opposite 2
 1b. Leaves whorled or alternate 6
 2a. Tree ca. 20 m tall; leaves 8.2–16.0 × 5.4–10.0 cm, blade obovate, base rounded to obtuse, apex rounded; calyx lacinia oval; fruit a berry, with a dried pericarp *Macoubea guianensis*
 2b. Tree 2–8 m tall; leaves 2.5–10.8 × 0.8–4.0 cm, blade oblong or elliptical, base obtuse or cuneate, apex cuneate, acuminate or acute; calyx lacinia deltoid, oval, or triangular; fruit a follicle or a berry, when a berry, with a fleshy pericarp 3
 3a. Leaves 2.5–5.2 × 0.8–2.6 cm, blade oblong to elliptical, apex acuminate; flowers pubescent, calyx lacinia deltoid; corolla with tube 29–31 × 2–3 mm, lobes 5–9 × 1–2 mm, fruit a berry *Hancornia speciosa*
 3b. Leaves 5.3–10.8 × 2.3–4.0 cm, blade elliptical, apex cuneate, acute, or acuminate; flowers glabrous, calyx lacinia triangular or oval; corolla tube 5–27 × 1–2 mm, lobes 4–21 × 4–8 mm, fruit a follicle 4
 4a. Venation brochidodromous; follicle smooth, ellipsoid *Tabernaemontana flavicans*
 4b. Venation campitodromous venation; follicle muricate, ellipsoid, or convex concave 5
 5a. Leaf apex cuneate to acuminate, chartaceous; bracts 1.5 × 1.0 mm, oval; calyx 3 × 2 mm, lacinia oval; floral tube shorter than lobes; follicle ellipsoid *Tabernaemontana laeta*
 5b. Leaf apex acute, membranaceous, bracts ca. 2 × 2 mm, lanceolate; calyx ca. 4 × 3 mm, lacinia triangular; floral tube longer than lobes; follicle convex-concave *Tabernaemontana catharinensis*
 6a. Leaves whorled; fruit a capsule or drupe 7
 6b. Leaves alternate; fruit a follicle 10
 7a. Leaves 2.4–3.7 × 1.0–1.5 cm; blade elliptical to oval; corolla hypocrateriform; fruit a drupe *Rauvolfia ligustrina*
 7b. Leaves 3.5–8.0 × 2.0–3.3 cm; blade lanceolate to elliptical; corolla infundibuliform; fruit a capsule 8
 8a. Branches and leaves hispid; leaves sessile, 3 per node, flowers dark red or pinkish *Allamanda blanchetii*
 8b. Branches glabrous or pubescent; leaves petiolate, 4 per node; flowers yellow 9
 9a. Blade lanceolate, margin flat; lower corolla tube longer than the upper corolla tube and lobes; corolla lobes orbicular; nectariferous, disc slightly 5-lobed *Allamanda cathartica*
 9b. Blade oblanceolate to oval, margin slightly bullate; lower corolla tube shorter than the upper corolla tube and the lobes; corolla lobes obovate; nectariferous disc entire *Allamanda doniana*
 10a. Inflorescence bracts navicular (3.8 × 2.2 cm); ovary semi-inferous; follicle oblong *Himatanthus bracteatus*
 10b. Inflorescence bracts non-navicular (ca. 1 mm long) or absent; ovary superior; follicle falcate, dolabriform, or pyriform 11
 11a. Cataphylls protecting the gems; leaves congested at the apex of branches 12
 11b. Cataphylls absent, leaves lax at the apex of branches 14
 12a. Leaf blade concolorous, glabrous adaxially and strigose abaxially; venation brochidodromous; flowers white; corolla tube shorter than the lobes; follicle pyriform *Aspidosperma pyrifolium*
 12b. Leaf blade discolorous, adaxially pubescent to glabrous, abaxially pubescent, tomentose or glabrous; venation craspedodromous or eucampitodromous; flowers cream or yellowish green; corolla tube equal to or longer than the lobes; follicle dolabriform 13

KEY TO SPECIES OF RAUVOLFOID GRADE (APOCYNACEAE) IN PARAÍBA STATE, BRAZIL CONT.

- 13a. Leaf blade with margin slightly undulated, base acute and strongly revolute, adaxial surface pubescent to glabrous, abaxial surface tomentose to glabrous; venation craspedodromous; flowers cream; corolla with tube equal to or longer than the lobes; ovary tomentose; follicle yellow brown, densely tomentose. *Aspidosperma nigricans*
- 13b. Leaf blade with margin flat, base cuneate, adaxial and abaxial surfaces pubescent; venation eucamptodromous; flowers yellowish to green; corolla tube longer than the lobes; ovary glabrous; follicle brown, glabrous. *Aspidosperma confertiflorum*
- 14a. Venation reticulodromous; follicle falcate, smooth surface *Aspidosperma cuspa*
- 14b. Venation brochidodromous or craspedodromous; follicle dolabriform or pyriform, grooved or muricate. 15
- 15a. Stem grooved, latex white; blade elliptical; flowers white; follicle dolabriform, muricate, glabrous, midrib inconspicuous *Aspidosperma discolor*
- 15b. Stem cylindrical, latex red; blade oblong; flowers yellow; follicle pyriform, grooved, tomentose, midrib conspicuous *Aspidosperma melanocalyx*

Allamanda L., Mant. Pl. 2:146, 214–215. 1771.

Type: *A. cathartica* L., Mant. Pl. 2:214–215. 1771.

Shrubs or subshrubs, herbaceous or subwoody stem, white latex; branches non-lenticellate. Leaves petiolate or sessile, whorled, 3–4 per node, lax; blade lanceolate to elliptical, with flat margin, chartaceous, discolorous; brochidodromous; colleters axillary or absent. Inflorescences terminal, cymose; bracts linear. Flowers pink, dark red, or yellow; calyx with 5 sepals, equal in length or unequal to each other; corolla infundibuliform. Stamens with trichomes at the base. Ovary globose, superior; nectariferous disc present. Fruit capsular, circular-compressed, or elliptical, thorny. Seeds winged, orbicular.

Allamanda blanchetii has a wide distribution in the remaining areas of Caatinga and upland forests. This species is the only one in the genus to have flowers with dark red or pink coloration, which facilitates its identification. The other species have yellow flowers and similar characteristics. The two species with yellow flowers recorded in this study, *A. cathartica* and *A. doniana*, have few collection records from the state of Paraíba. As they are widely used in gardening projects, their native distribution is not well known.

Allamanda blanchetii A.DC., Prodr. 8:319. 1844. (Fig. 2; Fig. 3A–D; Fig. 10A).

Shrubs, 1.5–4.0 m tall, stem subwoody; branches hispid. Leaves sessile, 3 per node; blade 3.5–8.0 × 2.0–3.3 cm, lanceolate to elliptical, margin flat, base cuneate, apex cuspidate to acuminate, discolorous, hispid on both surfaces, prominent midrib; brochidodromous; axillary colleters. Inflorescence 6–10 cm long; peduncle ca. 4 mm long, hispid; bracts 1.5 × 1.0 mm, linear, pubescent. Flowers dark red or pink; calyx 2.8 × 0.7 cm, lacinia lanceolate to ovate, subequal, hispid to glabrescent on the outer surface, hispid on the inner surface; corolla infundibuliform, 2.3 × 0.4 cm lower tube, 2.8 × 1.4 cm upper tube, 2.0 × 2.7 cm lobes, orbicular with slightly undulating margin. Anthers ca. 3 mm long. Ovary 2–3 mm long, globose, glabrous; nectariferous disc ca. 0.5 mm long, 5-lobed. Capsule 4.3 × 3.7 cm, elliptic to obovate-compressed, thorny, glabrous. Seeds 2.1 × 1.7 mm, orbicular, winged.

Specimens examined: BRAZIL. Paraíba: Alagoa Grande, 28 January 2010, fl., *Félix 16011* (EAN); Alcantil, 21 December 2007, fl., *Félix 12059* (EAN); Araruna, 14 April 2002, fl., *Barbosa 2412* (JPB); Areia, 26 May 2001,

fl., *Félix 7104* (HST); Cuité, 11 March 2008, fl., *Félix 12135* (EAN); Cuitégi, Sítio Palmeira, 22 April 2009, fl., *Gadelha-Neto 2575* (JPB); Coremas, 7 February 2015, fl., *Whelley s/n* (HCSTR); Esperança, 17 June 2003, fl., *Pitrez 273* (EAN); Guarabira, Serra da Jurema, 03 April 2015, fl., *Gadelha-Neto 3930* (JPB); Itaporanga, 7 February 2015, fl., fr., *Souza 81* (CSTR); Itapororoca, 17 November 2008, fr., *Félix 12633* (EAN); Juazeirinho, 3 March 1993, fl., *Agra et al. 1593* (IPA); Mamanguape, ReBio Guaribas, 26 November 2002, fl., *Sevilha 2564* (CEN); Maturéia, 8 April 1999, fl., *Agra 5443* (JPB); Monte Horebe, 15 March 2000, fl., *Barbosa 2054* (JPB); Monteiro, 9 July 2009, fl., fr., *Siqueira-Filho 2176*; Ibidem, 13 May 2009, fr., *Carvalho-Sobrinho 2189* (HVASF); Patos, 24 April 2015, fl., *Mamede 04* (CSTR); Ibidem, Inselberg Espinho Branco, 26 April 2012, fl., *Angelis 201* (HCSTR); Picuí, 29 January 1998, fl., *Rocha 256* (IPA); Pilões, Serra do Espinho, 7 March 2012, fl., *Guedes 19665* (HUEFS); Queimadas, 27 May 2014, fl., *Oliveira 5802* (IPA); Ibidem, 29 January 2006, fl., *Dantas 748* (HACAM); Remígio, 30 April 2019, fl., *Mamede 30* (PEUFR); São Bentinho, 28 May 2015, fr., *Silva 5942* (CSTR); São João do Tigre, 13 March 2010, fl., fr., *Pessoa 566* (JPB); São José de Piranhas, 03 April 2018, fl., *Mamede16* (PEUFR); Ibidem, 17 July 2008, fl., *Andrade 61* (PEUFR); São José dos Cordeiros, 20 May 2017, fl., *Figueira 621* (JPB); Serraria, 26 January 2007, fl., *Félix 12385* (EAN); Serra Branca, 26 April 2006, fl., fr., *Gadelha-Neto 1510* (JPB); Sobrado, 28 January 2010, fl., *Félix 16010* (EAN); Solânea, 30 August 2001, fl., fr., *Grisi-Veloso 287* (JPB); Tenório, 7 February 2006, fl., *Aurino 08* (JPB).

Distribution and habitat: *Allamanda blanchetii* is endemic to Brazil, with a disjunct geographical distribution and a Caatinga-Cerrado pattern (Flora e Funga do Brasil, 2024). The species can be found throughout the Northeast (Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, and Sergipe) and in the states of Goiás and Minas Gerais (Flora e Funga do Brasil, 2024). In Paraíba, it is frequently observed in the Caatinga and upland forests on sandy, stony soils. It has been found on roadsides, at forest edges, on slabs, inselbergs, and mountains and can be found in high altitudes and cattle pastures. The species is found in protected areas, such as Parque Estadual da Pedra da Boca, municipalities of Araruna and Tacima; Parque Estadual do Pico do Jabre, Maturéia; Fazenda Almas RPPN, São José dos Cordeiros; and Onças APA, São João do Tigre.

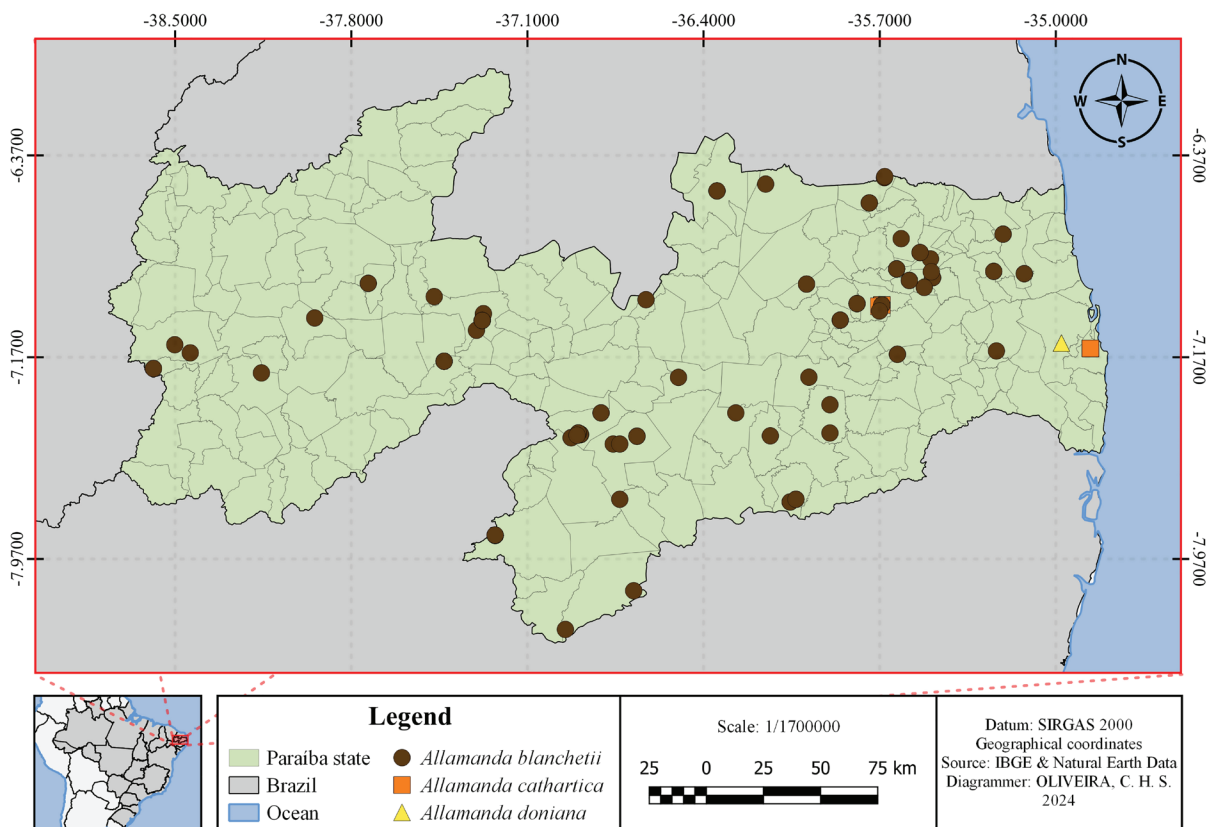


FIGURE 2. Distribution of the *Allamanda* species in Paraíba state, Brazil.

Phenology: It blooms from December to August and bears fruit from February to November.

It is a shrub covered with a hispid indumentum, has a pink to dark red corolla that stands out in the landscape, and it has a 5-lobed nectariferous disc.

Allamanda cathartica L., Mant. Pl. 2:214. 1771. (Fig. 2; Fig. 3E–G; Fig. 10B–C).

Climbing *shrubs* or *subshrubs*, ca. 0.5 m high, *stem* herbaceous or subwoody; *branches* glabrous. *Leaves* petiolate, 4 per node; blade 6.5–10.2 × 2.9–4.1 cm, lanceolate, margin flat, base cuneate, apex acuminate, discolorous, glabrous, glossy dark green adaxially, glabrous light green abaxially, with a prominent midrib; brochidromous. *Petiole* 0.3–0.5 cm long, glabrous. *Inflorescence* 8–9 cm long; peduncle 2–6 cm long, glabrous; bracts 1–4 mm long, linear, glabrous. *Flowers* yellow, pedicel 0.5–1.0 cm long, glabrous; calyx 1.2–1.5 × 0.4–0.6 cm, lacinia lanceolate, unequal to each other, glabrous to pilose only on the abaxial surface; corolla infundibuliform, 3.0–3.8 × 0.3 cm lower tube, 2.8–3.0 × 1.9–2.8 cm upper tube, lobes 2.2–3.5 × 2.2–3.4 cm, apex rounded, glabrous. *Anthers* ca. 6 × 2 cm, oblong. *Ovary* ca. 2 × 2 mm, globose, glabrous; nectariferous disc ca. 1 × 3 mm, slightly 5-lobed. *Capsule* ca. 3.2 × 3.0 cm, circular-compressed, thorny, glabrous. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Areia, 13 August 2013, fl., *Félix 14295* (EAN); João Pessoa, 29 August 1982, fl., *Montenegro 21* (JPB).

Additional specimen examined (outside Paraíba): BRAZIL. Bahia: Mucuri, 23 September 2018, fr., *Martinelli et al. 20598* (RB).

Distribution and habitat: This species occurs from Central America to Brazil and Bolivia and was introduced in Mexico, South Asia, and Southeast Africa (POWO, 2024). In Brazil, it occurs throughout the territory, mainly in coastal regions (Sakane and Shepherd, 1986; Simões and Kinoshita, 2005; Flora e Funga do Brasil, 2024) at forest edges. It has a continuous distribution and an Amazonian-Cerrado-Atlantic pattern. It is found in capoeira, high and humid places, and urbanized areas, often in gardens. The records found do not clarify whether the species occurs in native areas.

Phenology: Recorded with flowers in August.

Allamanda cathartica can be climbing or a subshrub that is glabrous, and can be recognized mainly by its yellow, showy flowers, with unequal calyx lacinia and a slightly 5-lobed nectariferous disc.

Allamanda doniana Müll. Arg., Fl. Bras. 6(1):11. 1860. (Fig. 2; Fig. 3H–K; Fig. 10D).

Shrubs, ca. 1.5 m high, stem subwoody; *branches*

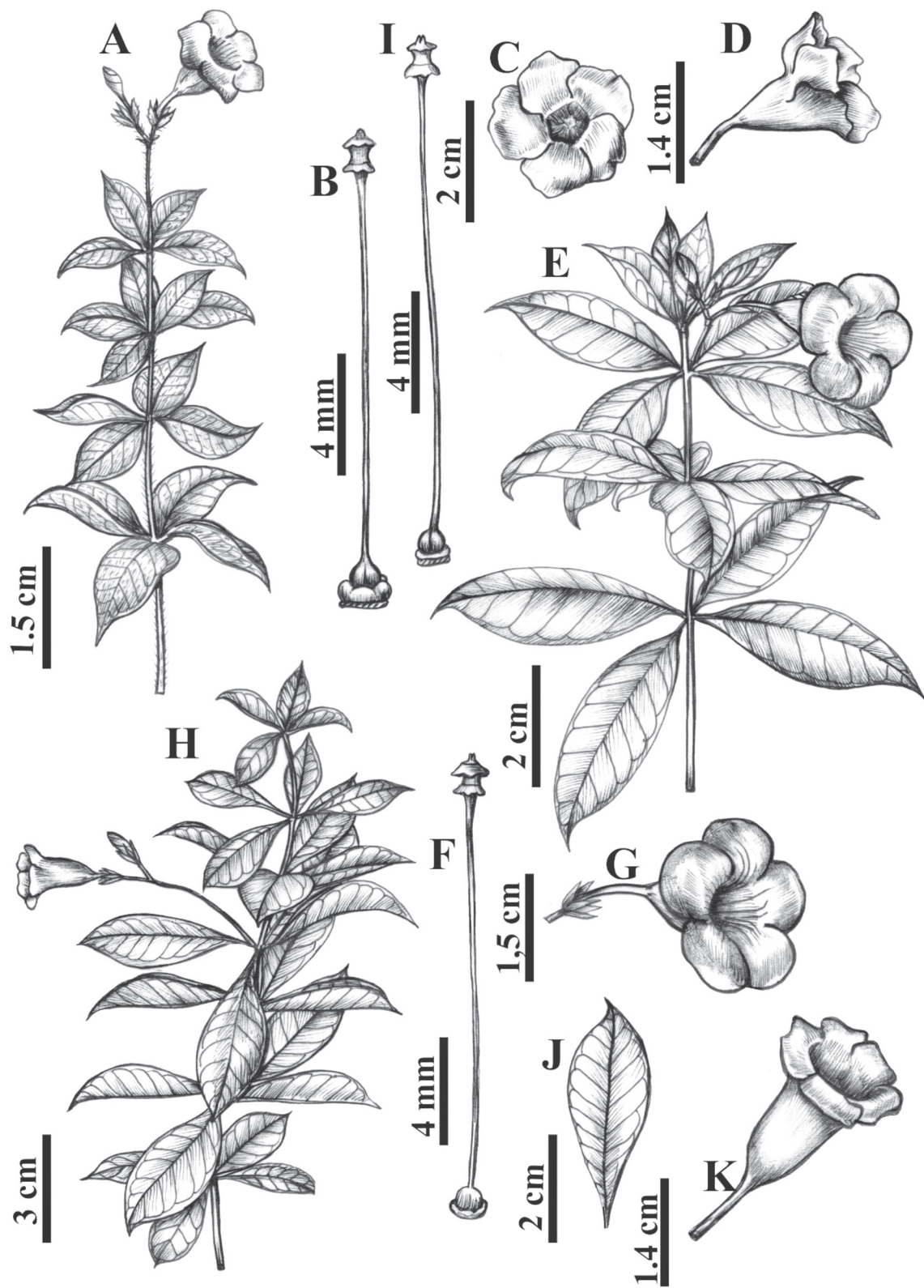


FIGURE 3. A–D, *Allamanda blanchetii*: A, flowering branch; B, gynoecium; C, flower (front view); D, flower (lateral view); E–G, *Allamanda cathartica*: E, flowering branch; F, gynoecium; G, flower (lateral view); H–K, *Allamanda doniana*: H, flowering branch; I, gynoecium; J, leaf; K, flower (lateral view). Photos: M. L. Mamede.

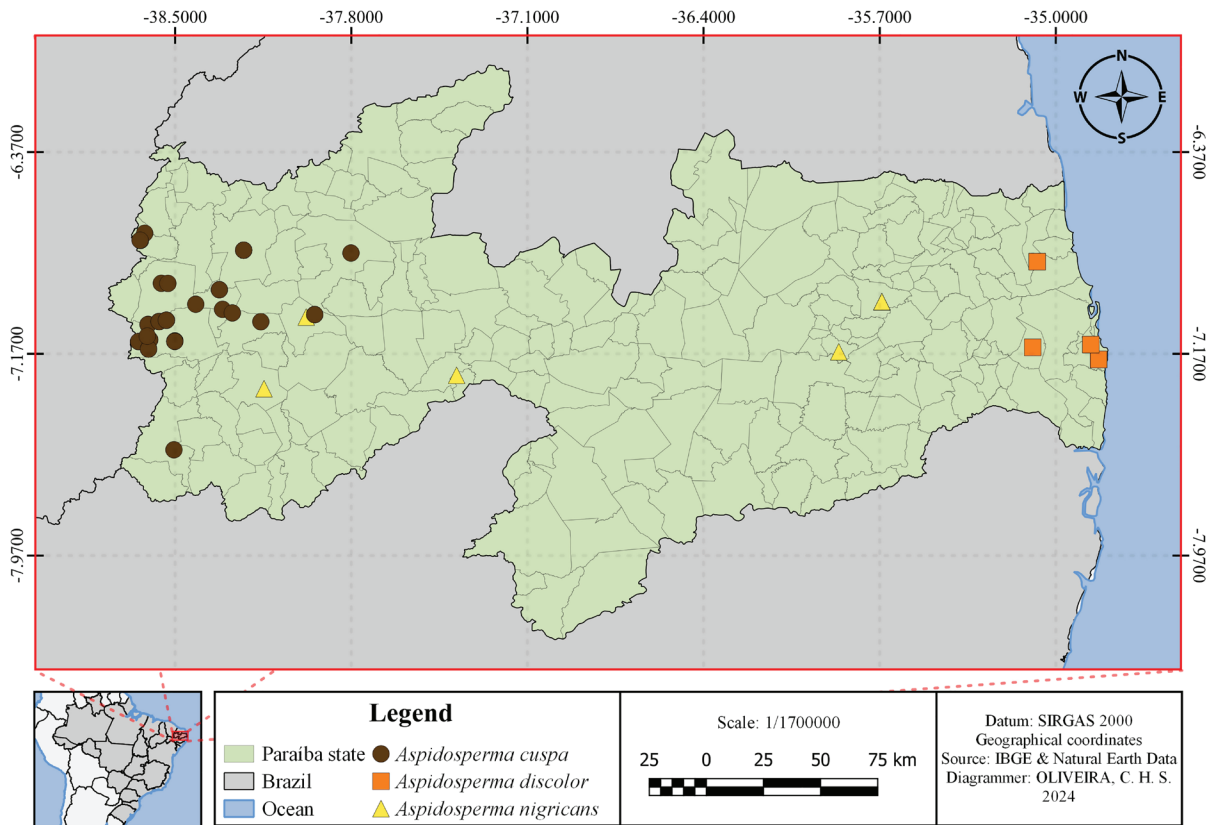


FIGURE 4. Distribution of the *Aspidosperma* species in Paraíba state, Brazil: *A. cuspa*, *A. discolor*, and *A. nigricans*.

pubescent. *Leaves* petiolate, 4 per node; blade 7.0–10.7 × 2.5–3.8 cm, oblanceolate to obovate, margin slightly undulate, base attenuate, apex acuminate, concolorous, sparsely pubescent adaxially, pubescent abaxially with hispid midrib and secondary veins; brochidodromous. *Petiole* 0.5–1.0 cm long, hispid. *Inflorescence* ca. 12 cm long; peduncle ca. 3 cm long, hispid; bracts 3 × 1 mm, linear, glabrous. *Flowers* yellow, pedicel 0.3–0.7 cm long, hispid; calyx 1.5–2.0 × 0.4 cm, lacinia lanceolate to oval, pubescent; *corolla* infundibuliform, lower tube 2.8 × 0.2–0.3 cm, upper tube 3–4 × 1.6–2.6 cm, lobes 2 × 2.0–2.4 cm, obovate, glabrous. *Anthers* ca. 5 × 2 mm, oblong. *Ovary* ca. 2 × 2 mm, globose, glabrous; nectariferous disc ca. 1 × 3 mm, slightly undulated. *Capsule* 2.7 × 2.3 cm, circular-compressed, thorny, glabrous. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Areia, 10 March 1997, fl., fr., *Félix et al.* 7094 (HST); Santa Rita, 15 October 2018, fl., *Mamede* 22 (PEUFR); Ibidem, 7 April 2008, fl., *Félix et al.* 12262 (EAN).

Distribution and habitat: This species is endemic to Brazil, occurring in the North (Amazonas, Amapá, and Pará) and Northeast (Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, and Sergipe) regions (Flora e Funga do Brasil, 2024). It has a restricted, continuous distribution and an Amazonian-Caatinga-Cerrado distribution pattern. In Paraíba, it is found only in the municipalities of Areia and Santa Rita, on

roadsides, sandy soils, and ‘capoeira’ in urbanized places. Few collections were obtained in the natural environment, which leaves doubt about its current native distribution.

Phenology: It blooms in March and April and bears fruit in March.

Allamanda doniana morphologically resembles *A. cathartica*, differing by the ratio between the length of the lower and upper corolla tube (the lower tube is smaller than the upper tube and lobes in *A. doniana*, while in *A. cathartica* the lower tube is larger than the upper tube and lobes) and because it presents an entire nectariferous disc, while in *A. cathartica*, the nectariferous disc is 5-lobed.

Aspidosperma Mart. & Zucc. in *Flora* 7(1, Beil. 4): 135. 1824.

Type: *A. tomentosum* Mart., *Flora* 7(1):135. 1824.

Trees or *shrubs*, stem cylindrical or grooved, white or red latex; *branches* densely or sparsely lenticellate. *Leaves* with flattened *petioles*, canaliculate, cylindrical, pilose or glabrous, alternate, congested at the apex or lax; elliptical, oblanceolate, oblong, or obovate blade, margin flat or revolute, chartaceous, concolorous, or discolorous; craspedodromous, eucamptodromous, brochidodromous, or reticulodromous. *Inflorescence* terminal or axillary, corymbiform, paniculate, or multiflora; bracts absent. *Flowers* yellow, white, or cream; calyx lanceolate, filiform, or oval, with lacinia equal or unequal to each other; corolla

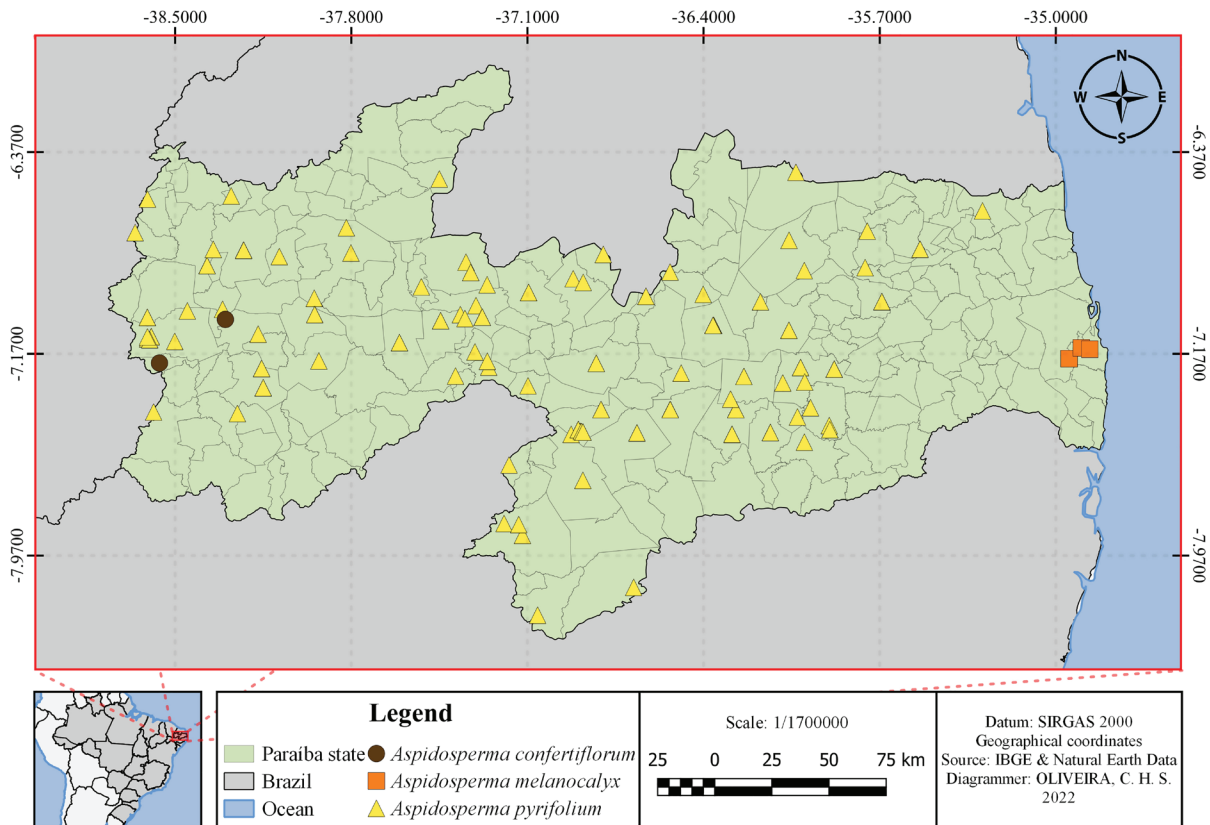


FIGURE 5. Distribution of the *Aspidosperma* species in Paraíba state, Brazil: *A. confertiflorum*, *A. melanocalyx*, and *A. pyriformum*.

hypocrateriform. Stamens with free, triangular, lanceolate, or oval anthers. *Ovary* globose, superior, tomentose, or glabrous. Nectariferous disc absent. *Follicle* falcate, dolabriform, or piriform, smooth, muricate, or grooved; lenticels conspicuous or inconspicuous, midrib evident or absent; stipe present or absent; apex mucronate or rounded, pilose or glabrous. *Seeds* oblong, rounded, ovate, or elliptical, winged.

Aspidosperma had the highest number of species (six) among the Rauvolfioid grade for Paraíba state. The record of *Aspidosperma confertiflorum* is the first for the state. The most widely recorded species were *A. pyriformum* and *A. cuspa*, respectively, in Caatinga. *Aspidosperma* can be found mainly in drier areas, predominating in Caatinga vegetation, associated with stony soils, inselbergs, the interior and at the edge of semideciduous forests. However, it is also possible to observe species of this genus, such as *A. discolor* and *A. melanocalyx*, in humid forests along the Atlantic Forest, including in swampy areas near the coast.

Aspidosperma confertiflorum A.C.D. Castello, Syst. Bot. 43(4):1040. 2018. (Fig. 5).

Trees, ca. 5 m high, *stem* cylindrical, white *latex*; *branches* glabrous. *Leaves* petiolate, congested at apex; *blade* 4.0 × 1.3 cm, elliptical to oblanceolate, margin flat, base cuneate, apex acuminate, discolorous, pubescent adaxially and abaxially; eucamptodromous. *Petiole* 0.5–

0.7 cm long, cylindrical, tomentose. *Inflorescence* ca. 1.5 cm long, terminal, corymbiform; *peduncle* ca. 2 mm long, pubescent. *Flowers* yellow-green, *pedicel* ca. 1 mm long; ca. 3 × 1 mm, *lacinia* ovate to triangular, apex unequally acute, externally pubescent, internally glabrous; *corolla* hypocrateriform, tube ca. 3 mm long, pubescent outer and inner surfaces, *lobes* ca. 2.5 × 0.6 mm, oblong, pubescent. *Anthers* ca. 2 mm long. *Ovary* ca. 1 mm long, globose, glabrous. *Follicle* ca. 2.5 × 1.5 cm, dolabriform, brown, smooth, lenticels conspicuous, midrib evident, with stipe, mucronate apex, glabrous. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Carrapateira, Guaribas, 27 November 2014, fl., *Fontana 8886* (HUEFS); Monte Horebe, 31 May 2012, fr., *Silva 1981* (HVASF).

Distribution and habitat: This species is endemic to the Northeast region, presenting a Caatinga pattern and a very restricted geographical distribution. *Aspidosperma confertiflorum* has been recorded in the state of Ceará, mainly in high-altitude areas and in dry forests (Castello et al., 2024), but it is recorded for the first time in Paraíba state in this study.

Phenology: It was recorded with flowers in November and with fruit in May.

Aspidosperma confertiflorum can be recognized mainly by having eucamptodromous venation, a corolla with a tube larger than the lobes, a glabrous ovary, and a dolabriform, glabrous follicle.

Aspidosperma cuspa (Kunth) S.F. Blake, Manual de las plantas usuales de Venezuela 110. 1926. (Fig. 4; Fig. 6A–C).

Trees, ca. 4 m high, *stem* cylindrical, white latex; *branches* glabrous. *Leaves* petiolate, lax; *blade* 2.1–4.0 × 0.9–1.3 cm, elliptic to obovate, margin revolute, base cuneate to obtuse, apex cuneate to rounded, chartaceous, discolorous, sparsely pubescent on both surfaces; reticulodromous. *Petiole* 0.7–0.9 cm long, canaliculate, pubescent. *Inflorescence* ca. 4.5 cm long, axillary, paniculate; *peduncle* ca. 2 mm long, tomentose. *Flowers* yellow, *pedicel* ca. 1 mm long, glabrous; *calyx* 1.5–1.9 × 1.0 mm, lacinia ovate, equal, apex acute, externally tomentose, internally glabrous; *corolla* hypocrateriform, tube ca. 3 mm long, cylindrical, slightly inflated at the corolla apex, externally glabrous, internally pubescent to glabrescent, *lobes* ca. 1.0 × 0.5 mm, oblong, glabrous on both surfaces, tomentose at the insertion of the stamens. *Anthers* ca. 1 mm long, lanceolate, glabrous. *Ovary* ca. 1 mm long, globose, glabrous. *Follicle* 1.6–3.7 × 0.7–2.0 cm, falcate, brown, smooth, lenticels conspicuous, midrib evident, with stipe, apex mucronate, pubescent. *Seeds* ca. 1.2 × 0.7 cm, oblong, apical wing 1.3 × 0.9 cm.

Specimens examined: BRAZIL. Paraíba: Aguiar, Serra de Santa Catarina, Sítio Mata Fresca, 29 May 2014, fl., Fontana 8082 (HUEFS); Cajazeiras, Sítio Campos de Fora, 27 May 2014, fr., Fontana et al. 8076 (HUEFS); Ibidem, Serra do Vital, 25 February 2010, fl., Fontana 6522 (HVASF); Coremas, 17 July 2009, fr., Andrade 27 (PEUFR); Lagoa, 31 July 2011, fr., Laboratório de Etnoecologia s/n (EAN - 17.564); Nazarezinho, 8 September 2002, fl., Gadelha-Neto 755 (JPB); Santa Helena, 21 May 2014, fr., Costa-Lima et al. 1272 (HUEFS); São José de Piranhas, 8 June 2010, fr., Oliveira 4946 (IPA); Ibidem, 25 February 2010, fl., Fontana et al. 6522 (IPA); Ibidem, Povoado de Boa Vista, 18 September 2009, fr., Carvalho-Sobrinho 2378 (HUEFS); Ibidem, 17 July 2008, fr., Andrade 62 (PEUFR); Ibidem, 8 June 2010, fr., Oliveira 4946 (HVASF); Ibidem, Reservatório Cuncas, 21 February 2013, fr., Silva 684 (HVASF); Sousa, 07 February 1998, fl., Gadelha-Neto 403 (JPB).

Distribution and habitat: This species is distributed from the Caribbean and Panama to South America (POWO, 2024). In Brazil, it is found in the Northeast (Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, and Rio Grande do Norte), North (Pará and Tocantins), Midwest (Goiás, Mato Grosso do Sul, and Mato Grosso), and Southeast (Minas Gerais, Rio de Janeiro, and São Paulo) (Castello et al., 2024). It has a wide, continuous geographical distribution and an Amazonian-Caatinga-Cerrado-Atlantic pattern. In Paraíba, *A. cuspa* was found in the arboreal, shrubby Caatinga, in stony and sandy soils, and near the mountains.

Phenology: It blooms in February, May, and September and bears fruit in May, June, July, and September.

Aspidosperma cuspa differs from the other congener species recorded by its discolorous leaves, with reticulodromous venation (*vs.* brochidodromous in *A. discolor* and *A. pyrifolium*; craspedodromous in *A. melanocalyx* and *A. nigricans*), falcate follicles (piriform in *A. pyrifolium* and *A. melanocalyx*, dolabriform in the other species), and by the apical wings of the seeds (central in the seeds of the other analyzed species).

Aspidosperma discolor A.DC., Prodr. 8:398. 1844. (Fig. 4; Fig. 6D–F).

Trees, ca. 20 m high, *stem* grooved, white latex; *branches* glabrous. *Leaves* petiolate, lax; *blade* ca. 9 × 3 cm, elliptic, margin flat, base cuneate and strongly revolute, apex obtuse to cuneate, chartaceous, discolorous, pubescent in both surfaces; brochidodromous. *Petiole* ca. 0.6 cm long, flattened, canaliculate, pubescent. *Inflorescence* ca. 4 cm long, terminal, corymbiform; *peduncle* 1–3 mm long, pubescent. *Flowers* white, *pedicel* ca. 1 mm long, pubescent; *calyx* 1–2 × 1 mm, lacinia lanceolate, unequal, apex acute, externally pubescent and internally glabrous; *corolla* hypocrateriform, tube ca. 4 × 1 mm, slightly inflated at the apex, pubescent internally and externally; *lobes* ca. 2 × 1 mm, oval, internally glabrous and externally pubescent. *Anthers* ca. 1 mm long, lanceolate, glabrous. *Ovary* 1.2–1.3 mm long, globose, tomentose. *Follicle* ca. 4.5 × 3.0 cm, dolabriform, brown, muricate, lenticels inconspicuous, midrib inconspicuous to absent, with stipe, round apex and glabrous. *Seeds* ca. 2.0 × 1.6 cm, oval, membranous eccentric wings.

Specimens examined: BRAZIL. Paraíba: Cruz de Espírito Santo, 25 November 1968, fl., Andrade-Lima 68–5471 (IPA); João Pessoa, 10 March 1995, fr., Barbosa et al. 1456 (JPB); Rio Tinto, 21 November 1991, fl., Félix et al. 4554 (EAN).

Distribution and habitat: *Aspidosperma discolor* is an endemic species of the Brazilian Northeast, found in the states of Alagoas, Bahia, Pernambuco, and Sergipe (Castello et al., 2024), and is recorded in Paraíba state for the first time in this study. It has a Caatinga-Atlantic pattern and a disjunct distribution. In Paraíba, it can be found in the Atlantic Forest, in forest remnants, and in a protected area, the Estação Ecológica do Pau-Brasil.

Phenology: It blooms in November and bears fruit in March.

This species can be characterized by its grooved stem, lax leaves, discolorous leaf blades, and strongly revolute base and by its muricate, glabrous fruit.

Aspidosperma melanocalyx Mull. Arg., in Mart. Fl. Bras. 6(1):52. 1860. (Fig. 5; Fig. 6M).

Trees, ca. 20 m high, *stem* cylindrical, red latex; *branches* glabrous. *Leaves* petiolate, lax; *blade* 6.2–10.4 × 2.9–4.5 cm, oblong, margin flat, base cuneate, apex cuneate, chartaceous, discolorous, glabrous on both surfaces; craspedodromous. *Petiole* ca. 0.6 cm long, flattened, glabrous. *Inflorescence* ca. 6.5 cm long, axillary, multiflora; *peduncle* 5–8 mm long, tomentose. *Flowers* yellow, *pedicel* 1–3 mm long, tomentose; *calyx* 2.0–2.5 × 1.5 mm, oval, lacinia equal, tomentose, apex acute, glabrous; *corolla* hypocrateriform, tube ca. 3 × 1 mm, slightly inflated at the base, externally glabrous, internally tomentose, *lobes* ca. 2 × 1 mm, linear, glabrous. *Anthers* ca. 4 mm long, oval, glabrous. *Ovary* ca. 1 mm long, flattened, globose, glabrous. *Follicle* ca. 10.0 × 5.2 cm, piriform, dark green, surface sulcate, lenticels inconspicuous, midrib evident, with stipe, round apex, densely tomentose. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: João Pessoa, 9 March 1995, fr., Barbosa et al. 1446 (JPB); Ibidem, 8

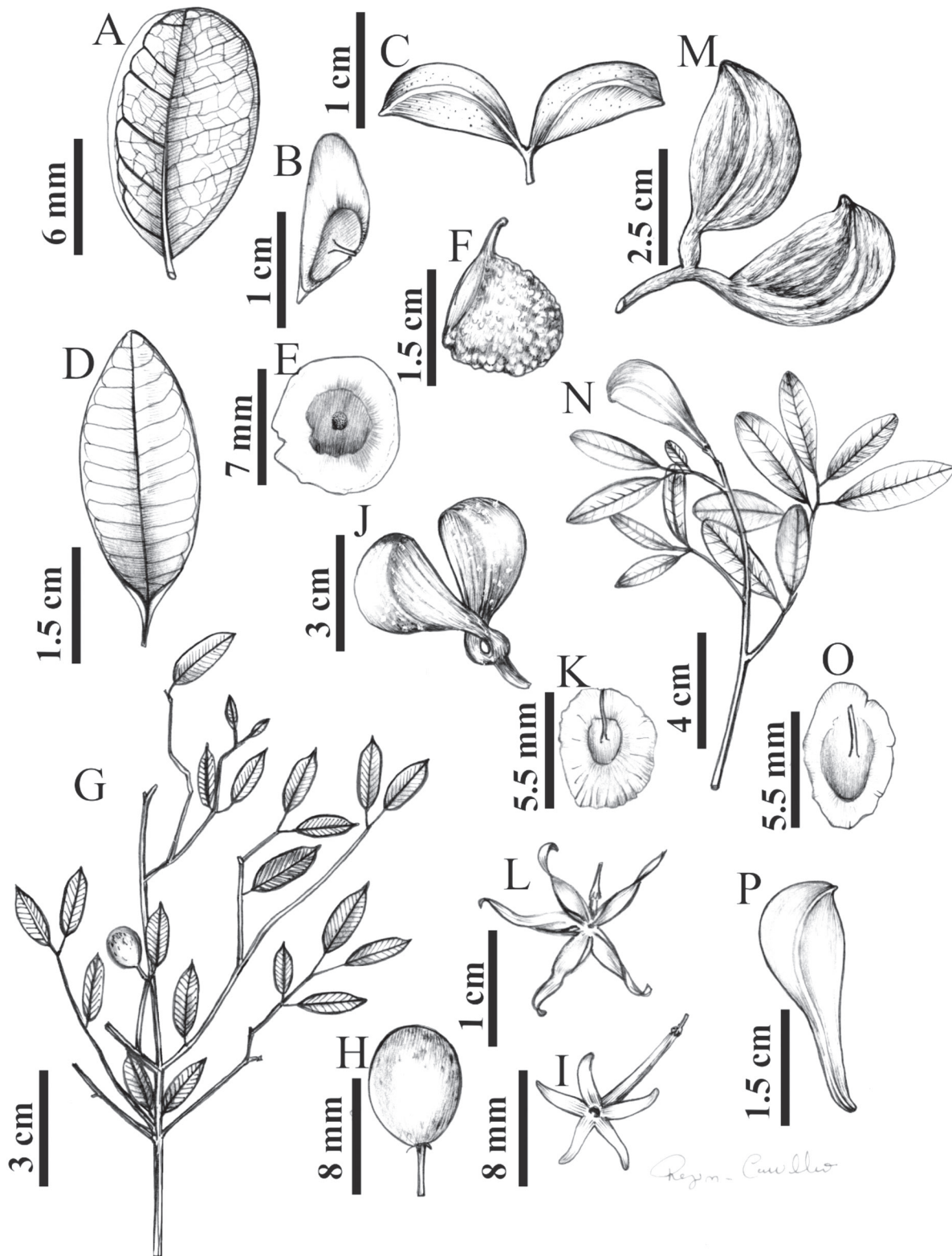


FIGURE 6. A–C, *Aspidosperma cuspa*: A, leaf; B, seed; C, fruit; D–F, *Aspidosperma discolor*: D, leaf; E, seed; F, fruit; G–L, *Hancornia speciosa*: G, fructified branch; H, fruit; I, flower; J–L, *Aspidosperma pyriformium*: J, fruit; K, seed; L, flower. M, *Aspidosperma melanocalyx* fruit; N–P, *Aspidosperma nigricans*: N, fructified branch; O, seed; P, fruit.

October 1988, fl., *Miranda 7767* (JPB); *Ibidem*, 24 February 1984, fl., *Alonso 56697* (JPB).

Distribution and habitat: This species is restricted to the Brazilian territory, being found in the Northeast (Alagoas, Bahia, Pernambuco, and Sergipe), Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo), and Midwest (Federal District, Goiás, and Mato Grosso) (Castello et al., 2024). It has a Cerrado-Atlantic pattern and a disjunct distribution. *Aspidosperma melanocalyx* was recorded in the Atlantic Forest of Paraíba, in a permanent preservation area at Jardim Botânico Benjamin Maranhão, known as 'Mata do Buraquinho,' in the municipality of João Pessoa.

Phenology: *Aspidosperma melanocalyx* blooms from October to February and bears fruit in March.

This species can be recognized by its red latex, oblong, glabrous leaves, yellow flowers, and piriform follicles, that are densely tomentose, sulcate, and dark green. It is often confused in herbarium collections with *A. spruceanum* Benth. ex Müll. Arg.; in Brazil, the latter is restricted to the state of Amazonas (Castello et al., 2024). *Aspidosperma melanocalyx* can be recognized by its leaves with oblong blades and a cuneate apex, a glabrous abaxial surface, and a piriform follicle, while *A. spruceanum* has leaves with an obovate blade with a rounded apex, a whitish abaxial surface, and dolabriform follicles (Castello et al., 2024).

Aspidosperma nigricans Handro, Arq. Bot. Estado São Paulo 3:282, t. 69. 1962. (Fig. 4; Fig. 6N–P).

Trees, ca. 4–8 m high, *stem* cylindrical, white *latex*; *branches* glabrous. *Leaves* petiolate, congested at the apex of the branches; *blade* 6.0–7.4 × 1.2–2.0 cm, oblanceolate to oblong, margin slightly undulated, base acute, strongly revolute; apex acute to cuneate, chartaceous, discolorous, pubescent to glabrescent adaxially, tomentose to glabrous abaxially; craspedodromous. *Petiole* ca. 3 mm long, flattened, pubescent to glabrous. *Inflorescence* ca. 3 cm long, terminal, corymbiform; *peduncle* ca. 1.5 mm long, pubescent. *Flowers* cream, *pedicel* ca. 2 mm long, pubescent; *calyx* 1.5–2.0 × 0.7–1.0 mm, oval, *lacina* subequal to each other with acute apex, pubescent outer surface, glabrous inner surface; *corolla* hypocrateriform, tube 2–4 × 1 mm, cylindrical, slightly inflated in the upper portion, pubescent; *lobes* ca. 2 × 1 mm, oval, pubescent. *Anthers* ca. 1 mm long, oval. *Ovary* ca. 1 mm long, globose, tomentose. *Follicle* 3.7–6.5 × 1.5–3.0 cm, dolabriform, yellow-brown, smooth, lentils conspicuous, midrib prominent, stipe elongated, apex mucronate, densely tomentose. *Seeds* ca. 14 × 7 mm, caramel-colored, elliptical to ovate, membranous surrounding wing, 12 × 5 mm.

Specimens examined: BRAZIL. Paraíba: Areia, May 1944, fl., *Moraes 243* (EAN); *Ibidem*, Mata da Escola de Agronomia, 15 May 1944, fl., *Vasconcelos 243* (USP); Areia–Cuité ou Campina Grande, 25 May 1978, fr., *Andrade-Lima 78-8.412* (IPA); Coremas, 16 July 2008, fr., *Andrade et al. 07* (PEUFR); Itaporanga, 1 March 2015, fr., *Souza 72* (CSTR); Lagoa Seca, 29 July 2001, fr., *Lourenço et al. 241* (JPB); *Ibidem*, 10 December 2000, fr., *Carneiro et al. 56* (JPB); Maturéia, 29 July 2014, fr., *Cordeiro et al. 330* (EAN); *Ibidem*, 10 May 1998, fr., *Agra et al. 5153* (JPB); *Ibidem*, 17 November 1997, fr., *Agra et al. 4396* (JPB).

Distribution and habitat: This species is endemic to the Northeast region of Brazil, in the states of Paraíba, Pernambuco, and Alagoas (Castello et al., 2024). It has a Caatinga pattern and a very restricted geographical distribution. In Paraíba, it was found in Caatinga, generally associated with the shrub-tree stratum, forest edges, near the mountain area, at high altitudes. *A. nigricans* was recorded in a Conservation Unit, the Parque Estadual do Pico do Jabre, municipality of Maturéia.

Phenology: It blooms in May and bears fruit from November to July.

Aspidosperma nigricans can be recognized by its congested leaves at the apex of the branches, cream-colored flowers, and yellow-brown fruit, densely tomentose, with an elongated stipe.

Aspidosperma pyrifolium Mart. & Zucc., Flora 7(1, Beil.):136. 1824. (Fig. 5; Fig. 6J–L; Fig. 10E–G).

Trees, ca. 5 m high, *stem* cylindrical, white *latex*; *branches* densely lenticellate, glabrous. *Leaves* petiolate, congested at the apex of the branches; blade 3.9–5.0 × 4.0 cm, elliptical, margin flat, base acute, apex acute to acuminate, chartaceous, concolorous, glabrous adaxially, strigose abaxially; brochidodromous. *Petiole* 1.1–1.5 cm long, cylindrical, glabrous. *Inflorescence* ca. 4 cm long, terminal, corymbiform; *peduncle* 5–8 mm long, pubescent. *Flowers* white, *pedicel* ca. 3 mm long, pubescent; *calyx* 1.0–2.9 × 0.5 mm, filiform, *lacina* equal or unequal to each other, *corolla* glabrous, hypocrateriform, tube ca. 4 × 1 mm, cylindrical slightly inflated at the apex, tomentose in the median portion and the throat, lobes ca. 12 × 2 mm, linear, flat margin, glabrous. *Anthers* ca. 1 mm long, triangular. *Ovary* ca. 2.2 mm long, globose, glabrous. *Follicle* 4.0–6.5 × 2.5–4.0 cm, piriform, brown, smooth, densely lenticellate, lenticels conspicuous, midrib inconspicuous to absent, round apex, glabrous. *Seeds* ca. 2 cm long, rounded, with concentric wings.

Specimens examined: BRAZIL. Paraíba: Aparecida, 18 May 2019, fr., *Mamede 31* (PEUFR); Areia, 14 November 2016, fr., *Félix 16118* (EAN); Boa Vista, 15 April 2010, fl., *Machado-Filho 140* (HACAM); Cabaceiras, 21 November 2007, fr., *Pessoa 204* (JPB); Campina Grande, 20 November 2006, fl., *Félix 11314* (EAN); Carrapateira, Guaribas, 27 November 2014, fr., *Fontana et al. 8883* (RB); Catingueira, 17 March 2010, fl., *Santos 01* (CSTR); Coremas, 16 February 2019, fr., *Mamede 27* (PEUFR); Diamante, 2 May 2011, fr., *Diniz 2082* (CSTR); Itaporanga, 12 October 2011, fr., *Félix 17261* (EAN); Malta, 12 February 2013, fr., *Ferreira 3910* (CSTR); Maturéia, Pico do Jabre, 29 July 2014, fr., *Cordeiro et al. 330* (HUEFS); Monteiro, Serra do Morcego, 6 June 2010, fr., *Araújo 1649* (HVASF); Natuba, 26 September 1971, fl., *Andrade-Lima 1038* (IPA); Patos, 5 October 2018, fr., *Mamede 21* (PEUFR); *Ibidem*, 22 September 2018, fr., *Mamede 19* (PEUFR); *Ibidem*, 28 May 2015, fr., *Mamede 11* (CSTR); *Ibidem*, 25 June 2006, fr., *Nóbrega 70203* (IPA); *Ibidem*, 29 November 2000, fr., *Silva 411* (JPB); Pocinhos, 21 June 2011, fr., *Nóbrega 247* (CSTR); *Ibidem*, Parque das Pedras, 19 November 2001, fl., *Heringer et al. 2357* (EAC); Pombal, 28 October 2011, fl., *Queiroga 151* (CSTR); Queimadas, 18 December 2013, fr., *Félix 14629* (EAN);

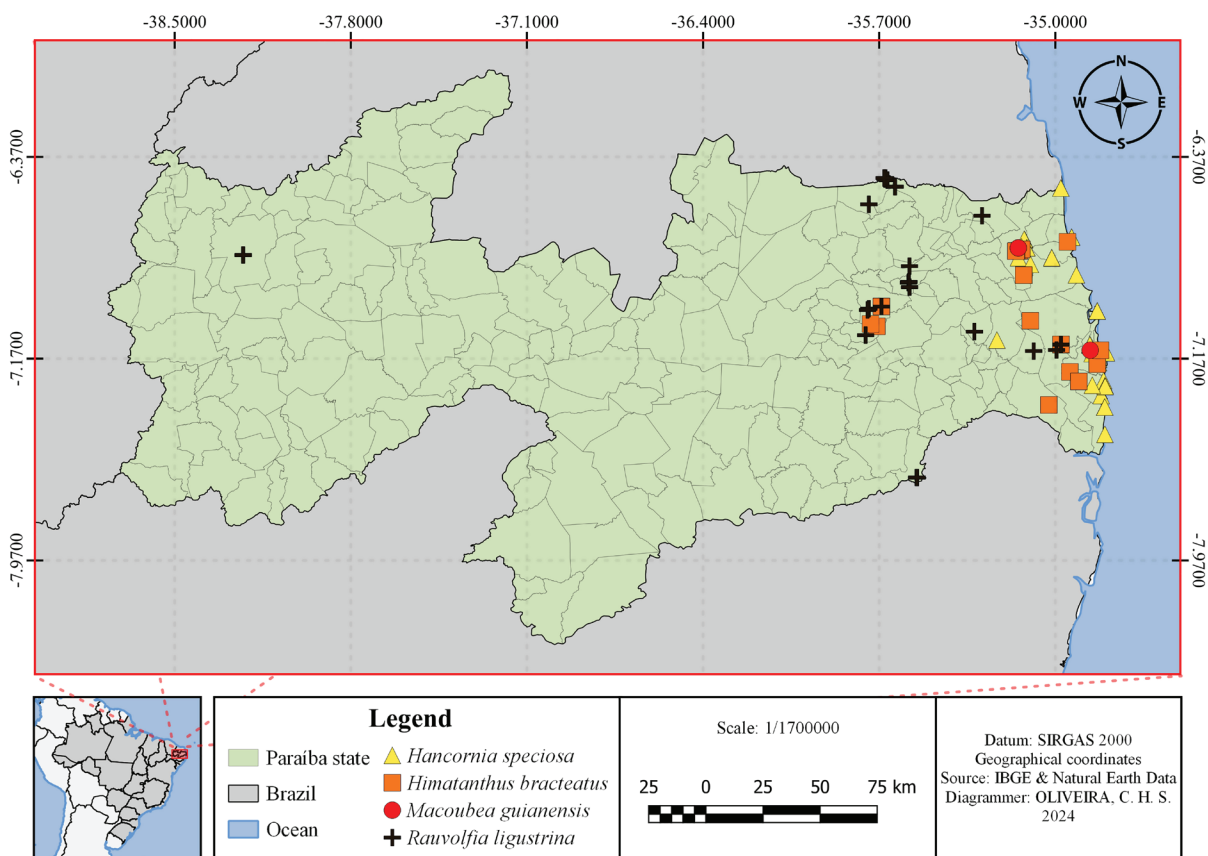


FIGURE 7. Distribution of the species: *Hancornia speciosa*, *Himatanthus bracteatus*, *Macoubea guianensis*, and *Rauvolfia ligustrina* in Paraíba state, Brazil.

Santa Helena, Sítio Retiro, 6 June 2013, fr., *Oliveira et al.* 2570 (HVASF); Santa Terezinha, 18 April 2006, fr., *Pegado* 24 (EAN); São Bento, 12 April 2015, fr., *Silva* 5928 (CSTR); São João do Cariri, 13 March 2003, fr., *Lacerda* 51 (JPB); São João do Tigre, 13 March 2010, fr., *Pessoa* 567 (JPB); São João do Rio do Peixe, Sítio Pititinga, 29 August 2012, fr., *Oliveira et al.* 1529 (HVASF); São José de Piranhas, 14 January 2009, fr., *Andrade* 63 (PEUFR); Ibidem, Riacho da Boa Vista, 18 May 2011, fr., *Silva* 423 (HVASF); São José do Bonfim, 23 April 2010, fr., *Duarte* 22 (CSTR); São José dos Cordeiros, RPPN Fazenda Almas: Lajedo Aveloz, 25 October 2009, fr., *Costa* 43 (HUEFS); São José do Sabugi, 3 October 2018, fr., *Mamede* 20 (PEUFR); São Sebastião do Umbuzeiro, Povoado Capitão Mor., 29 November 2012, fl., *Oliveira et al.* 2035 (HVASF); Serra Branca, 11 March 2002, fr., *Baracho* 5696 (JPB); Solânea, 21 January 2000, fl., fr., *Grisi* 84 (JPB); Soledade, 30 March 2006, fr., *Lucena* 216 (PEUFR); Ibidem, 22 February 2006, fr., *Sá* 342 (HST); Sousa, 3 October 2000, fl., *Gadelha-Neto* 602 (JPB); Ibidem, Riacho João Gonçalves, Sítio Pedregulho, 23 January 2013, fl., fr., *Silva* 705 (HVASF); Ibidem, Vale dos Dinossauros, 9 August 2003, fl., *Gadelha-Neto* 927 (JPB); Taperoá, 20 July 1986, fr., *Agra* 525 (JPB); Ibidem, 1 July 1986, fr., *Agra et al.* 48681 (IPA); Triunfo, Sítio Gamela, 29 August 2012, fr., *Oliveira et al.* 1540 (HVASF).

Distribution and habitat: This species occurs in Paraguay, Brazil, and Bolivia (POWO, 2024). In Brazil,

it can be found in the Northeast (Alagoas, Bahia, Ceará, Maranhão, Paraíba, Pernambuco, Piauí, Rio Grande do Norte, and Sergipe), North (Tocantins), Midwest (Federal District, Goiás, Mato Grosso do Sul, and Mato Grosso), and Southeast (Minas Gerais) (Castello et al., 2024). It has a Caatinga-Cerrado pattern and a disjunct distribution. In Paraíba, it is distributed in the Caatinga, mainly in the interior of the state, and it is associated with sandy, stony soils and dry forests. It was found in the interior and at the edge of woods, roadsides, inselbergs, and surrounding granitic rock outcrops. It has been recorded in protected áreas, such as Fazenda Almas RPPN, in São José dos Cordeiros; Parque Estadual Vale dos Dinossauros, in Sousa; Fazenda Tamanduá RPPN, in Santa Terezinha; Onças APA, in São João do Tigre; and Pico do Jabre, in Maturéia.

Phenology: It blooms in October, November, April, May, and August and bears fruit in January.

Aspidosperma pyriforme can be especially recognized by its white flowers, with lobes ca. 12 mm long being larger than the tube, which is ca. 4 mm long, and by its piriform, densely lenticellate follicles.

Hancornia speciosa Gomes, Mem. Math. Phis. Acad. Real Sci. Lisboa 2:1, pl. 1. 1803. (Fig. 6G–I; Fig. 7; Fig. 11A).

Trees, 2–5 m high, stem straight, white latex; branches lenticellate, glabrous. *Leaves* petiolate, opposite, lax; *blade* 2.5–5.2 × 0.8–2.6 cm, oblong to elliptical, margin flat,

base cuneate, apex acuminate, chartaceous, concolorous, glabrous on both surfaces, profuse secondary veins parallel and close together; craspedodromous. *Petiole* 0.6–1.0 cm long, glabrous. *Inflorescence* ca. 6 cm long, terminal, sessile; bracts absent. *Flowers* white, pedicel 0.8–0.9 cm long, pubescent; *calyx* 1.8–2.0 × 1.0 mm, deltoid, glabrous on inner surface and pubescent on outer surface; *corolla* hypocrateriform, tube 2.9–3.1 × 2–3 mm, externally glabrous, internally hirsute, lobes 5–9 × 1–2 mm, deltoid, glabrous. *Anthers* ca. 2.3 mm long, triangular, glabrous. *Ovary* 1–2 × 1 mm, ovoid, superior, glabrous. *Nectariferous disc* absent. *Drupe* 1.9–2.6 × 1.3–2.3 cm, globose, yellow, smooth, lenticels absent, midrib absent, fleshy pericarp, glabrous. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Baía da Traição, Aldeia São Miguel, 26 April 2008, fl., *Lima et al.* 2265 (JPB); Cabedelo, 19 November 1999, fl., *Pontes* 292 (JPB); Conde, 6 October 2012, fl., *Lima* 23 (EAN); Ibidem, Assentamento Tambaba, 10 July 2012, fr., *Brito* 250 (JPB); Ibidem, Área de Preservação Permanente de Tambaba, 11 August 2008, fr., *Gadelha-Neto et al.* 2404 (JPB); Ibidem, Área de Preservação Permanente de Tambaba, 20 November 2009, fr., *Araújo* 209 (RB); João Pessoa, Mangabeira, 25 March 2019, fr., *Mamede* 28 (PEUFR); Ibidem, Mangabeira, Mata Ciliar do Rio Cabelo, 22 February 2011, fr., *Pereira* 158 (JPB); Ibidem, Cabo Branco, Falésia do Cabo Branco, 28 March 2008, fr., *Araújo* 125 (JPB); Ibidem, 7 August 1993, fl., fr., *Moura* 1036 (JPB); Mamanguape, 27 October 2013, fr., *Félix* 14519 (EAN); Ibidem, Reserva Biológica Guaribas, 25 November 2002, fl., *Sevilha et al.* 2511 (CEN); Ibidem, Reserva Biológica Guaribas, 19 August 2002, fr., *Sevilha et al.* 2258 (CEN); Marcação, Aldeia Tramataia, 26 September 2006, fl., fr., *Freitas et al.* 166 (JPB); Mataraca, 4 October 2007, fl., fr., *Gadelha-Neto* 1859 (JPB); Rio Tinto, Tabuleiro do Miriri, falésia costeira, 3 March 2003, fr., *Barbosa et al.* 2753 (JPB); Ibidem, without dated, fr., *Gadelha-Neto* 3266 (W); Santa Rita, 5 February 1992, fr., *Agra* 1365 (JPB); Ibidem, Mata de Jacuípe, Tabuleiro Cova do Caboclo, 27 March 2013, fr., *Pontes* 861 (NY); Ibidem, 29 March 2012, fr., *Gadelha-Neto* 3266 (NY); Sapé, 9 March 2001, fr., *Dionísio* 100 (JPB).

Distribution and habitat: This species is distributed from the Brazilian North to Paraná (Flora e Funga do Brasil, 2024), as well as in Peru, Bolivia, and Paraguay (POWO, 2024). It has an Amazonian-Caatinga-Cerrado-Atlantic pattern and a wide, continuous geographic distribution. In Paraíba, it was recorded in the Atlantic Forest on sandy soil. It can be found in the interior of ‘tabuleiros’ forests, roadsides, and cliffs. *Hancornia speciosa* was registered in environmental preservation areas, such as Reserva Biológica (ReBio) Guaribas, in the municipalities of Mamanguape and Rio Tinto; Fazenda Pacatuba RPPN, in Sapé; Tambaba APA, in Conde; and Jardim Botânico Benjamin Maranhão, in the municipality of João Pessoa.

Phenology: Flowering and fruiting between August and March.

Hancornia speciosa is characterized by opposite leaves with profuse secondary veins parallel to each other and

globular berries. This species is known as ‘mangaba,’ an edible fruit with a pleasant aroma (Kinoshita, 2005). According to Flora and Funga of Brasil (2024), as well as the treatment on cultivated Brazilian and exotic fruits (Lorenzi et al., 2003), the individuals of the region belong to the typical variety, called ‘mangaba-da-restinga,’ being recognized for having leaves with a distinct, reddish petiole, and glabrous blades.

Himatanthus bracteatus (A. DC.) Woodson, Ann. Missouri Bot. Gard. 25(1):200. 1938[1937]. (Fig. 7; Fig. 9A–C; Fig. 11B–C).

Trees, 2–6 m high, *stem* straight, white latex; *branches* woody, glabrous. *Leaves* petiolate, alternate, congested at the apex of the branches; blade 12.7–21.5 × 4–7 cm, oblanceolate, flat margin, base attenuated, apex cuspidate to rounded, chartaceous, concolorous, glabrous on both surfaces; brochidodromous. *Petiole* 1–4 cm long, hispid. *Inflorescence* ca. 10 cm long, terminal, thyrsoid; *peduncle* 0.8–0.9 cm long, glabrous; *bracts* 3.8 × 2.2 cm, petaloid, navicular, glabrous. *Flowers* white with yellow throat, pedicel 3–9 mm long; calyx with 1 conspicuous lacinia and the others reduced, glabrous; *corolla* hypocrateriform, tube 20–25 × 3 mm, glabrous externally and pilose on the inside, lobes 36–48 × 9 mm, oblanceolate to obovate, glabrous. *Anthers* 2.5–3.0 mm long, triangular, glabrous. *Ovary* 2.0–2.5 × 2 mm, ovoid, hypanthium, glabrous. *Nectariferous disc* absent. *Follicle* 16–18 × 3.9–4.0 cm, oblong, brown, smooth, glabrous, lenticels and midrib absent. *Seeds* 2.0–2.3 cm long, elliptic, elliptical wings.

Specimens examined: BRAZIL. Paraíba: Alagoa Nova, 8 March 2012, fl., *Guedes* 19715 (HUEFS); Ibidem, Mata do Urucu, 12 December 2011, fl., *Melo* 10867 (HUEFS); Areia, 28 February 2001, fl., *Nascimento* 26565 (JPB); Ibidem, Chão do Jardim, 13 March 1975, fl., *Perazzo Barbosa* 130 (RB); Ibidem, Próximo a Mata Pau Ferro, 23 November 1980, fl., *Fevereiro et al.* 104 (K); Baía da Traição, 24 January 2007, fl., *Lima* 2168 (JPB); Conde, 15 October 2018, fl., fr., *Mamede* 23 (PEUFR); Ibidem, 22 August 2008, fr., *Gadelha-Neto* 2411 (JPB); João Pessoa, Mangabeira, 25 March 2019, fl., *Mamede* 29 (PEUFR); Ibidem, 28 March 2008, fl., *Araújo* 128 (JPB); Ibidem, 23 November 2002, fr., *Gadelha-Neto* 849 (JPB); Ibidem, Cabo Branco, 25 February 2005, fl., *Carauta* 962 (RB); Mamanguape, 6 January 2008, fl., *Satyro* 08 (JPB); Ibidem, 22 May 1994, fl., *Rodrigues* 89 (HST); Ibidem, 1 February 1989, fl., *Félix* 6336 (EAN); Ibidem, Reserva de Guaribas, 21 October 2012, fr., *Silva* 198 (HUEFS); Ibidem, Reserva Biológicas Guaribas, 30 November 2002, fl., *Sevilha* 2600 (EMBRAPA); Ibidem, Reserva Biológicas Guaribas, 20 August 2002, fr., *Sevilha et al.* 2298 (UEC); Pedra de Fogo, 28 February 1998, fl., *Lucena* 403 (PEUFR); Santa Rita, 7 February 1986, fl., *Plumel* 6528 (JPB); Sapé, 27 October 2000, fl., *Dionísio* 58 (JPB).

Distribution and habitat: This species is endemic to Brazil, occurring in the coastal regions of the Northeast (Alagoas, Bahia, Paraíba, Pernambuco, Rio Grande do Norte, and Sergipe) and Southeast (Espírito Santo, Minas

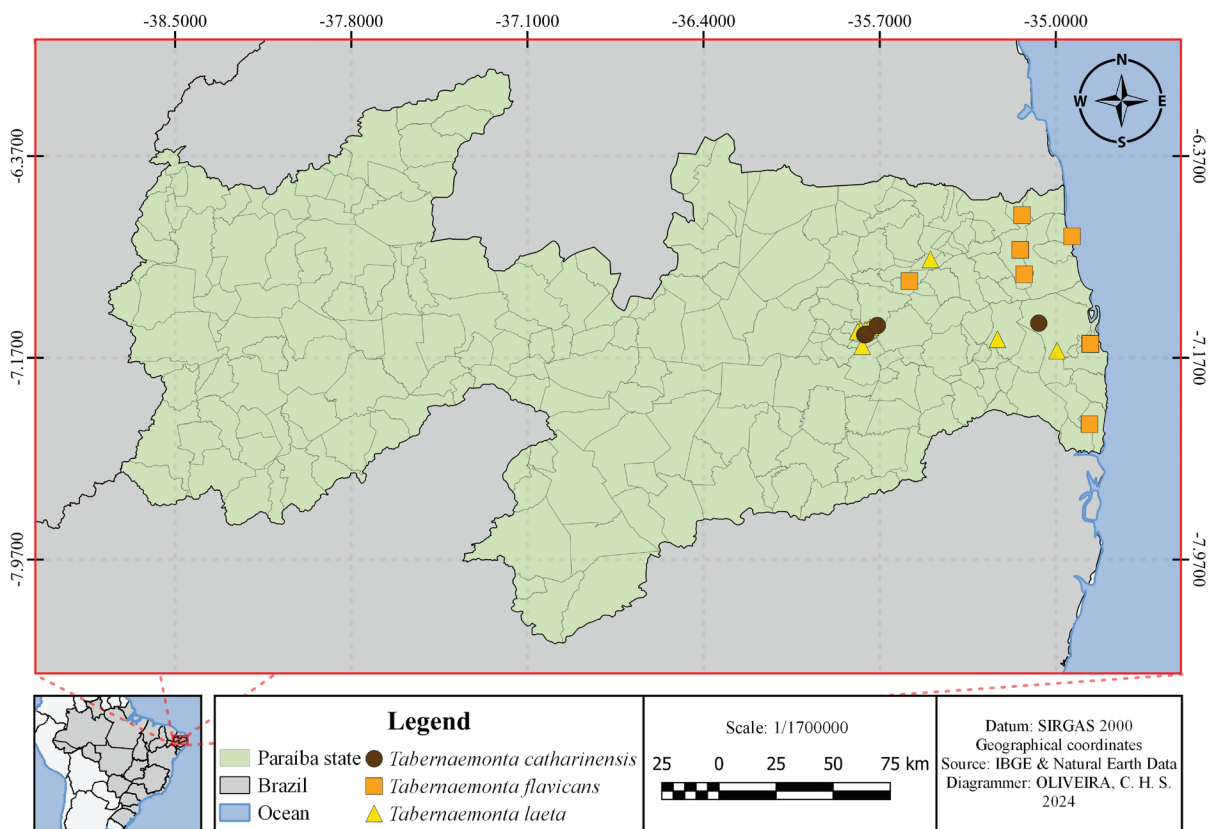


FIGURE 8. Distribution of the *Tabernaemontana* species in Paraíba state, Brazil.

Gerais, and Rio de Janeiro) (Flora e Funga do Brasil, 2024; Spina, 2004). It has an Atlantic pattern and a very restricted geographical distribution. In Paraíba, this species is mainly associated with the Atlantic Forest vegetation, including upland forests, in ‘restinga,’ ‘tabuleiro,’ and riparian forests. Its individuals have been sighted on the edges and interior of forests, cliffs, capoeiras, and roadsides. It has been recorded in the APA of Parque Estadual da Pedra da Boca, in the municipalities of Araruna and Tacima; Parque Estadual Mata do Pau Ferro, in Areia; Parque Estadual Vale dos Dinossauros, in Sousa; Reserva Biológica de Guaribas, in Mamanguape and Rio Tinto; Tambaba APA, in Conde; Estação Ecológica do Pau-Brasil, in Mamanguape; Fazenda Pacatuba RPPN, in Sapé; and Jardim Botânico Benjamin Maranhão, in João Pessoa.

Phenology: Flowering from January to October and fruiting from August to November.

It is characterized by having congested leaves at the apex of the branches, oblanceolate leaf blades, and large white flowers with lobes longer than the corolla tube. The buds are protected by petaloid bracts, navicular, and elongated oblong follicle-like (2) fruit.

Macoubea guianensis Aubl., Hist. Pl. Guiane 2(Suppl.):18, t. 378. 1775. (Fig. 7; Fig. 9D–F; Fig. 11D–E).

Trees, ca. 20 m high, *stem* straight, white *latex*; *branches*

lenticellate, glabrous. *Leaves* petiolate, opposite, lax; blade 8.2–16.0 × 5.4–10.0 cm, obovate, margin flat, base rounded to obtuse, apex rounded; chartaceous, concolorous, glabrous on both surfaces; craspedodromous. *Petiole* 1.5–2.0 cm long, glabrous. Inflorescence ca. 3 cm long, terminal, corymbiform; *peduncle* ca. 1.5 cm long, glabrous; *bracts* ca. 2 mm long, navicular, glabrous. Flowers white; *pedicel* ca. 0.6 mm long, glabrous; *calyx* ca. 2.5 mm long, oval, *lacinia* subequal to each other, glabrous; corolla hypocrateriform, lower tube ca. 2 mm long, cylindrical, upper tube ca. 4 mm long, cylindrical; lobes ca. 1.6 × 1 mm, linear, glabrous. *Anthers* 4–5 mm long, glabrous; ovary 2.0–2.3 mm long, pubescent. *Drupe* 5.8 × 5.5 cm, subglobose, smooth, dry pericarp, glabrous. *Seeds* 1.7 × 0.6 cm, rough, oblong, not winged, *arils* viscous.

Specimens examined: BRAZIL. Paraíba: João Pessoa, Jardim Botânico, 3 May 2016, fl., *Gadelha-Neto* 4034 (JPB); Mamanguape, Reserva Biológica Guaribas: Área de cabeça do boi – Sema II, 10 February 2012, fr., *Thomas et al.* 15653 (JPB).

Distribution and habitat: This species occurs in Panama and South America (Suriname, Venezuela, Guyana, French Guiana, Bolivia, Brazil, and Peru) (POWO, 2024). In Brazil, it has a disjunct geographical distribution from the North (Acre, Amazonas, Pará, and Rondônia), Northeast (Bahia, Maranhão, and Pernambuco), Midwest (Mato

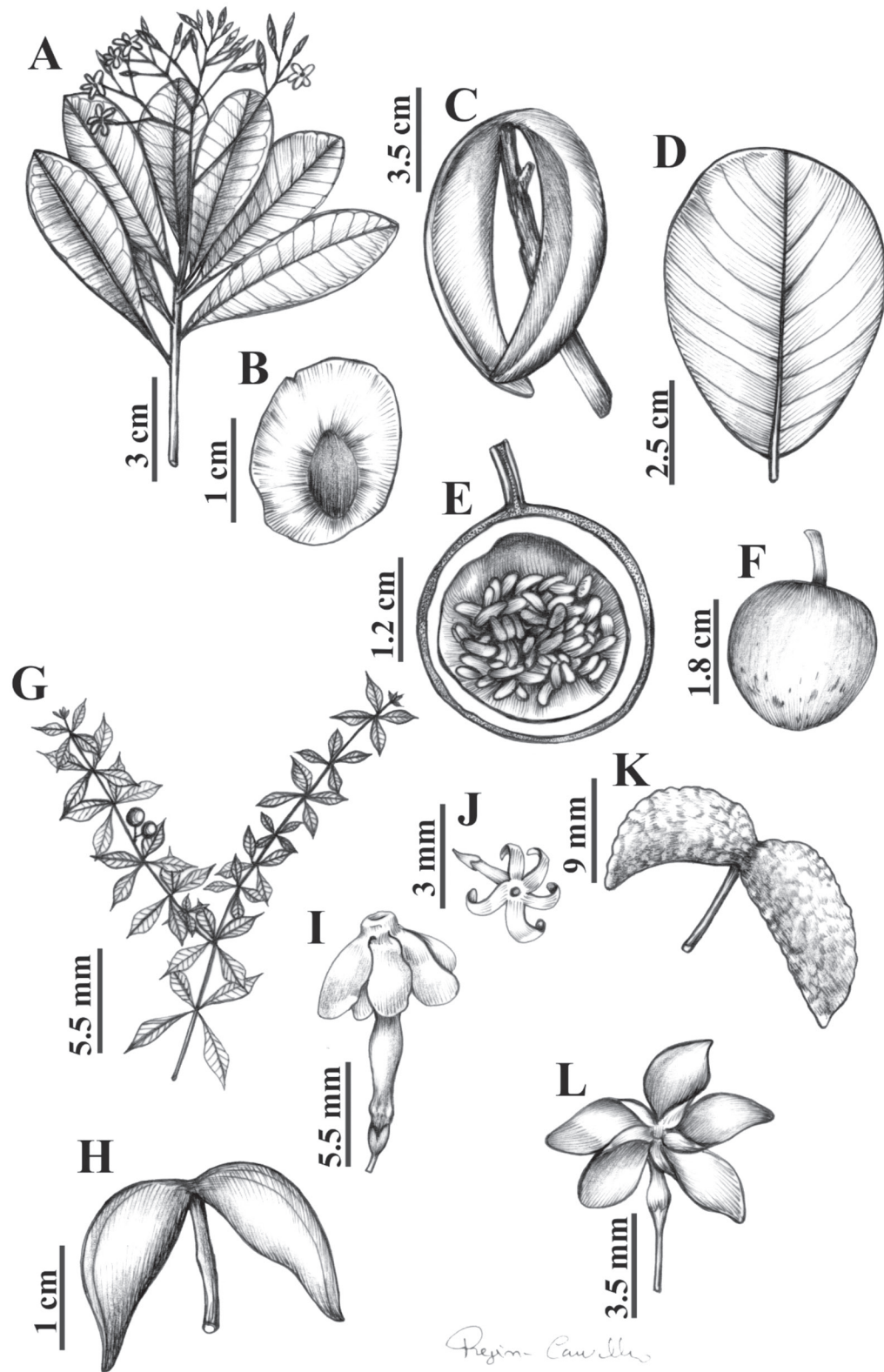


FIGURE 9. A–C, *Himatanthus bracteatus*: A, flowering branch; B, seed; C, fruit; D–F, *Macoubea guianensis*: D, leaf; E, fruit and seeds; F, fruit; G, *Rauvolfia ligustrina* fructified branch; H–I, *Tabernaemontana flavicans*: H, fruit; I, flower; J–K, *Tabernaemontana catharinensis*: J, flower; K, fruit; L, *Tabernaemontana laeta* flower.

Grosso) to the Southeast (Espírito Santo) (Flora e Funga do Brasil, 2024), presenting an Amazonian-Atlantic pattern. In Paraíba, the species can be found in the Atlantic Forest, in the APA of Jardim Botânico Benjamin Maranhão, in João Pessoa, on sandy, clay substrate soils, and in the Reserva Biológica Guaribas: Área de Cabeça do Boi, municipality of Mamanguape.

Phenology: Flowers and fruit were recorded in May and February, respectively.

Macoubea guianensis can be recognized by its opposite leaves, obovate leaf blade, and subglobose drupe, with a dry pericarp, oblong seeds, and viscous arils.

Rauvolfia ligustrina Willd., Syst. Veg. 4:805. 1819. (Fig. 7; Fig. 9G).

Trees, ca. 0.5–1.0 m high, *stem* cylindrical, white latex; *branches* lenticellate, pubescent. *Leaves* petiolate, whorled, 3 per node, lax; blade 2.4–3.7 × 1.0–1.5 cm, elliptical to oval, margin flat to slightly undulating, base obtuse, apex cuspidate; membranaceous, discolorous, glabrous surfaces with trichomes on the main vein; brochidodromous. *Petiole* ca. 1 mm long, pubescent. *Inflorescence* ca. 3 cm long, terminal, cymose, pleiochasium; peduncle 8–5 mm long, pubescent; bracts ca. 1 mm long, linear, glabrous. *Flowers* white, *pedicel* ca. 2 mm long, glabrous; calyx 2 × 1 mm; *lacinia* triangular, equal, green, apex acute, margin ciliate; *corolla* hypocrateriform, tube ca. 2 × 1 mm constricted in the throat, *lobes* ca. 1 mm long, oval, apex rounded, glabrous. *Anthers* ca. 0.6 mm long, triangular, glabrous. *Ovary* ca. 1.5 mm long, superior, glabrous. *Nectariferous disc* ca. 0.5 mm long. *Drupe* 5–7 × 6 mm, syncarpous, globose, red to black, smooth, lenticels and midrib absent. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Alagoa Nova, Sítio do Preguiçoso, May 2012, fl., fr., *Guedes et al. 19451*(UFPB); Araruna, Parque Estadual da Pedra da Boca, 17 March 2003, fl., *Lima 1755* (JPB); Ibidem, Parque Estadual da Pedra da Boca, 14 April 2002, fr., *Barbosa et al. 2419* (JPB); Ibidem, 18 October 2003, fl., fr., *Pessoa et al. 7* (JPB); Areia, Mata do Pau-Ferro, 16 February 2000, fr., *Barbosa et al. 1957* (JPB); Ibidem, 17 March 1992, fr., *Félix 4733* (HST); Ibidem, Engenho Cepilho, 16 March 1975, fl., *Perazzo Barbosa 175* (RB); Borborema, 16 January 1998, fl., *Schindwein 869* (JPB); Cruz de Espírito Santo, 29 January 1991, fr., *Moura 525* (JPB); Dona Inês, 10 April 1971, fr., *Carvalho 3495* (JPB); Mari, 25 April 2017, fr., *Figueira et al. 579* (IPA); Natuba, 13 August 1952, fr., *Xavier 1623* (JPB); Ibidem, 26 November 1971, fl., *Andrade-Lima et al. 1038* (PEUFR); Pilões, Cruzeiro do Espinho, 7 III 2012, fr., *Melo 10993* (HUEFS); Ibidem, Serra do Espinho, 6 III 2012, fl., *Melo 10960* (HUEFS); Ibidem, Serra do Espinho, 7 III 2012, fl., *Guedes 19651* (HUEFS); Santa Rita, Lagoa do Paturi, 16 VI 2001, fl., fr., *Agra 5594* (JPB); Ibidem, 12 December 1992, fr., *Agra et al. 1509* (JPB); Ibidem, Usina São João, Tibirizinho, 12 July 1990, fl., fr., *Agra 1185* (K); Sousa, Vale dos Dinossauros, 6 September 2002, fl., *Gadelha-Neto 751* (JPB); Ibidem, 1 January 1992, fr., *Gadelha-Neto 399* (JPB); Tacima, 11 March 2002, fl., fr., *Agra 5627* (JPB); Ibidem, 8 March 2002, fl., fr., *Agra 5637* (JPB).

Distribution and habitat: This species is recorded from Mexico to South America and the Caribbean (Argentina, Belize, Bolivia, Brazil, Colombia, Costa Rica, Cuba, El Salvador, Guatemala, Guyana, Mexico, Nicaragua, Paraguay, Suriname, Trinidad and Tobago, and Venezuela) (POWO, 2024). In Brazil, it has a wide distribution, with an Amazonian-Caatinga-Cerrado-Atlantic pattern and disjunct populations, being found in the North (Amazonas and Pará), throughout the Northeast and Midwest, and in the Southeast (Rio de Janeiro) (Koch et al., 2007; Flora e Funga do Brasil, 2024), and is associated with the interior of forests. In Paraíba, it was recorded in the Atlantic Forest, including upland forest. It can be found in the interior of forests, capoeira, rocky outcrop surroundings, near streams, slabs, and roadsides. It has been recorded in the APA of Parque Estadual da Pedra da Boca, municipalities of Araruna and Tacima; Parque Estadual Mata do Pau-Ferro, in Areia; Parque Estadual Vale dos Dinossauros, in Sousa; and Roncador APA, in Bananeiras.

Phenology: It can be found with flowers and fruit from March to September.

Rauvolfia ligustrina is characterized by having whorled leaves, 3 per node, an elliptical to oval blade, and small, white flowers, with a tube ca. 2 mm long, and syncarpous drupes. In some regions, it is called ‘arrebenta-boi’ (ox-buster) for its toxic properties.

Tabernaemontana L., Sp. Pl. 1:210. 1753.

Type: *T. citrifolia* L., Sp. Pl. 1:210. 1753.

Trees or shrubs, *stem* cylindrical, white latex, *branches* non-lenticellate, glabrous. *Leaves* opposite, lax, unequal at the same node; *petiole* cylindrical, glabrous; blade elliptic, margin flat or slightly undulate, membranous or chartaceous, concolorous; brochidodromous or camptodromous. *Inflorescences* axillary or terminal, cymose; bracts oval. *Flowers* white, yellow throat; *calyx* with subequal or unequal *lacinia*, with or without collectors on the inside of the sepals; *corolla* hypocrateriform. *Stamens* with free *anthers*, triangular. *Ovary* globose, superior, glabrous. *Nectariferous disc* absent. *Follicles* convex-concave or ellipsoid, smooth or muricate, lenticels and midrib absent, round, or acute apex, glabrous.

Tabernaemontana catharinensis A.DC., Prodr.8:365. 1844. (Fig. 8; Fig. 9J–K).

Trees, ca. 8 m high. *Leaf* blade 5.3–10.8 × 2.3–3.6 cm, elliptical, margin flat, base cuneate, apex acute, membranous, glabrous in both surfaces; camptodromous. *Petiole* 0.5–0.7 cm long. *Inflorescence* ca. 5 cm long, axillary; peduncle 0.4–0.6 cm long, glabrous; bracts ca. 2 × 2 mm, lanceolate. *Flower* pedicel ca. 7 mm long, glabrous; *calyx* ca. 4 × 3 mm, with triangular, revolute, glabrous *lacinia*, collectors arranged on the inner surface of the sepal; *corolla* hypocrateriform, yellow-green, spiral, glabrous, tube 5 × 2 mm, cylindrical inflated at the base, lobes 4 × 4 mm, dolabriform. *Anthers* ca. 4 × 1 mm, glabrous. *Ovary* ca. 2 × 2 mm. *Follicle* 2.4–3.0 × 1.3–1.4 cm, convex-concave, brown, muricate. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Alagoa Nova, 8 March 2012, fl., fr., *Melo et al. 11052* (HUEFS); Ibidem,

Fazenda Sr. José Roberto, 8 March 2012, fl., fr., *Melo et al. 11064* (HUEFS); Ibidem, 5 March 2012, fl., *Melo et al. 10910* (HUEFS); Ibidem, Brejo Paraibano, 5 March 2012, fl., *Melo 10910* (HUEFS).

Distribution and habitat: *Tabernaemontana catharinensis* is native to South America and occurs in Argentina, Bolivia, Paraguay, Uruguay, and Brazil; however, it is also cultivated in the United States of America and Italy (POWO, 2024). In Brazil, it has a disjunct distribution and a Cerrado-Atlantic pattern. It can be found in the Northeast (Bahia, Ceará, Maranhão, Pernambuco, and Sergipe), Midwest (Mato Grosso do Sul), and in all states of the Southeast and South (Flora e Funga do Brasil, 2024). Mamede et al. (2020) recorded *T. catharinensis* for the first time in Paraíba state. In Paraíba it occurs in upland forests, on roadsides, in the forest's interior, capoeira, pasture areas, and riparian forests.

Phenology: It was found with flowers and fruit in March.

This species can be recognized by its membranous leaf blades with camptodromous venation; its flowers with triangular and revolute calyx lacinia; its corolla tube that is inflated at the base, yellow inside, white outside; its spiral corolla lobes that are yellow-green and smaller than the tube; and its muricate, convex-concave follicle.

Tabernaemontana flavicans Willd. ex Roem. & Schult., Syst. Veg., ed. 15 bis. 4:797. 1819. (Fig. 8; Fig. 9H–I; Fig. 11F).

Shrubs, ca. 2 m high. *Leaf* blades 8.5–10.8 × 3.4–3.9 cm, elliptical, margin flat, base cuneate, apex acuminate, chartaceous, glabrous on both surfaces; brochidodromous. *Petiole* 0.7–1.0 cm long. *Inflorescence* ca. 6 cm long, axillary; peduncle 0.6–0.4 cm long, glabrous; bracts ca. 1 mm long, oval. *Flowers* white with yellow throat extending to the beginning of the lobes, *pedicel* 1.4–2.0 cm long, glabrous; calyx 2–3 mm long, oval, *lacinia* unequal to each other, glabrous; corolla hypocrateriform, *tube* ca. 27 mm long, cylindrical, white, slightly inflated at the beginning of the tube, *lobes* ca. 21 × 8 mm, dolabriform, glabrous. *Anthers* 2.5 × 1.0 mm, glabrous. *Ovary* ca. 1 × 1 mm. *Follicle* 3.7 × 1.0 cm, ellipsoid, brown, apex acute, smooth. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Baía da Traição, 11 October 2004, fl., *Gadelha-Neto et al. 1264* (JPB); João Pessoa, Jardim Botânico, 20 January 2012, fr., *Gadelha-Neto 3147* (JPB); Ibidem, Jardim Botânico, 12 September 2011, fl., *Gadelha-Neto 3053* (JPB); Ibidem, 6 September 2005, fr., *Amazonas et al. 44* (JPB); Ibidem, 12 August 2002, fl., *Gadelha-Neto et al. 727* (JPB); Mamanguape, 4 September 2004, fl., *Barbosa et al. 3045* (JPB); Pilões, Cruzeiro do Espinho, 7 March 2012, fl., *Melo 10985* (HUEFS).

Distribution and habitat: This species occurs from Venezuela, Colombia, Peru, Bolivia, to Brazil (POWO, 2024). In Brazil, it has a continuous, restricted distribution and an Amazonian-Cerrado-Atlantic pattern, being found in the North (Amazonas, Rondônia, and Pará), Northeast (Pernambuco, Maranhão, Alagoas, and Bahia), Midwest (Mato Grosso), and Southeast (Espírito Santo, Minas Gerais, and Rio de Janeiro) (Flora e Funga do Brasil, 2024).

Mamede et al. (2020) verified *T. flavicans* as a new record in Paraíba state. It occurs in the Atlantic Forest, inside the forest between trails in sandy, clay soils, and was recorded at the Pau-Brasil Ecological Station-Mamanguape and at the Benjamin Maranhão Botanical Garden, municipality of João Pessoa.

Phenology: It was found with flowers between August and October and with fruit between September and January.

This species is characterized by its chartaceous leaf blades, with brochidodromous venation, a white corolla with a yellow throat extending to the beginning of the lobes, a tube that is longer than the lobes and slightly inflated, and the smooth, ellipsoid follicle with an acute apex.

Tabernaemontana laeta Mart., Flora 20(2): Beibl. 98. 1837. (Fig. 8; Fig. 9L).

Trees, ca. 6 m high; *branches* striated. *Leaf* blade 8.4–10.5 × 3–4 cm, elliptical, margin slightly undulated, base obtuse to cuneate, apex cuneate to acuminate, chartaceous, glabrous on both surfaces; camptodromous; colleters in the nodal region. *Petiole* 1.0–1.4 cm long. *Inflorescences* ca. 7 cm long, terminal; peduncle ca. 8 mm long, glabrous; *bracts* 1.5 × 1.0 mm, oval. *Flowers* white with yellow throat, *pedicel* ca. 7 mm long, glabrous; *calyx* 3 × 2 mm, lacinate, oval, glabrous, colleters on the inner surface of the sepal; *corolla* hypocrateriform, *tube* 10–12 × 2 mm, cylindrical, inflated at the base, greenish-yellow, *lobes* 13–16 × 7 mm, dolabriform, outer basal portion yellowish, glabrous. *Anthers* 5 × 1 mm, glabrous. *Ovary* 2 × 1 mm. *Follicle* 3.3 × 2.1 cm, ellipsoid, brown, apex round, muricate. *Seeds* not seen.

Specimens examined: BRAZIL. Paraíba: Alagoa Nova, 19 November 2016, fl., *Bordon and Chaves 6* (UEC); Ibidem, 19 November 2016, fl., *Bordon and Chaves 8* (UEC); Ibidem, 19 November 2016, fl., *N.G. Bordon and C. L. Chaves 4* (UEC); Matinhas, 6 December 2000, fl., *Barbosa et al. 2091* (JPB); Pirpirituba, 2 April 2008, fl., *Gadelha-Neto et al. 2152* (JPB); Santa Rita, 8 November 1995, fr., *Agra et al. 3681* (JPB); Sapé, 25 November 2000, fl., *Dionísio 74* (JPB); Ibidem, 10 November 2000, fl., *Dionísio 69* (JPB).

Distribution and habitat: This species constitutes a new record for Paraíba state. *Tabernaemontana laeta* is endemic to Brazil, where it has a disjunct geographical distribution, occurring in the Northeast (Pernambuco, Alagoas, Bahia, and Sergipe), Midwest (Federal District), and Southeast (Espírito Santo, Minas Gerais, Rio de Janeiro, and São Paulo) regions (Flora e Funga do Brasil, 2024), presenting a Cerrado-Atlantic distribution pattern. It can be found in Paraíba forest uplands, in sandy, clay soils. It was recorded in the protected areas of the RPPN - Fazenda Pacatuba, municipality of Sapé, and APA do Roncador, municipality of Bananeiras.

Phenology: Flowering in April, November, and December and fruiting in November.

It is distinguished from other congeneric species recorded in the study area by the corolla with lobes longer than the tube and by the ellipsoid, muricate follicle.

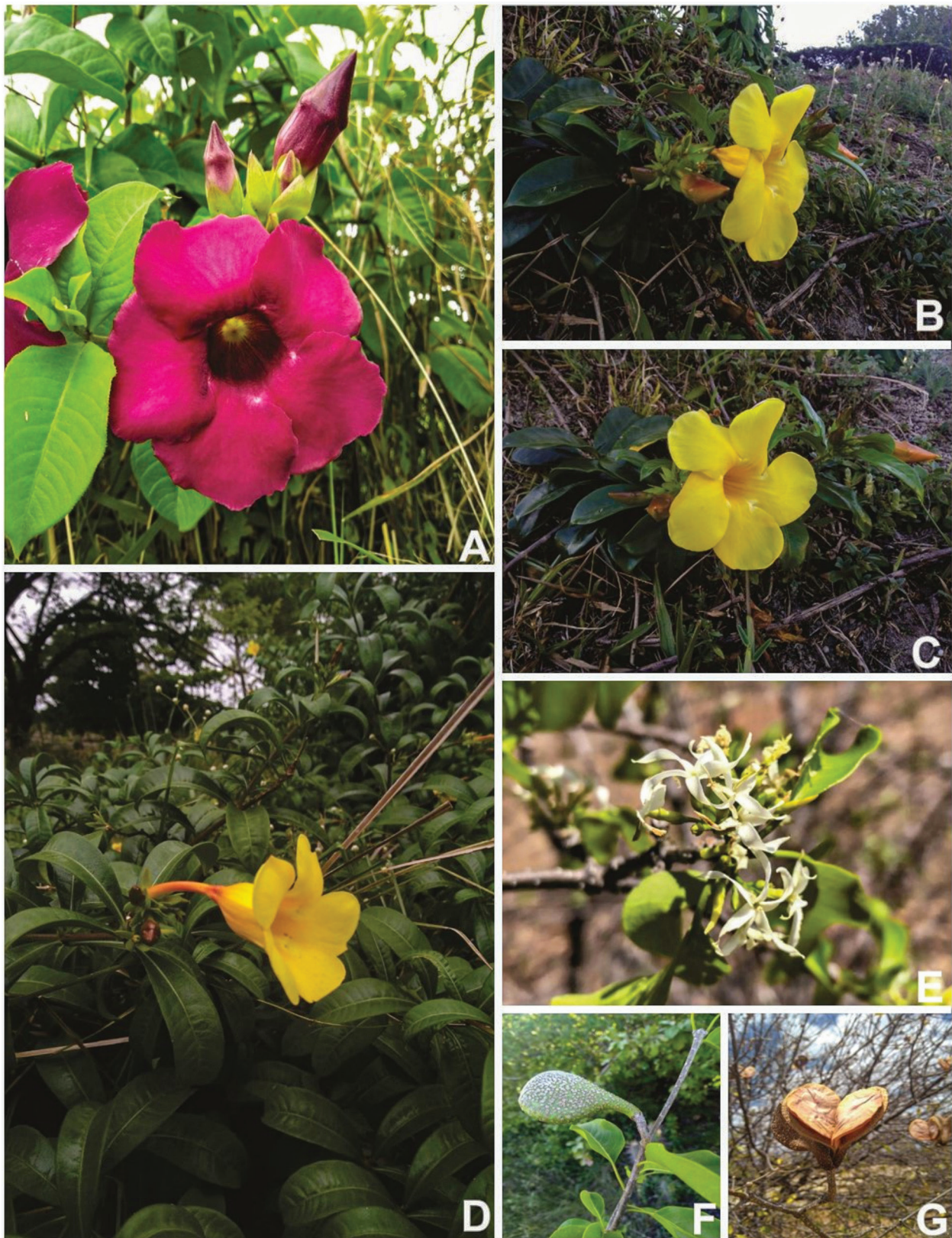


FIGURE 10. Species of Rauvolfioid grade in Paraíba state, Brazil. A, *Allamanda blanchetii*; B–C, *Allamanda cathartica*; D, *Allamanda doniana*; E–G, *Aspidosperma pyriformium*. Photographs by M. L. Mamede (A–D, F–G) and E. M. P. Fernando (E).

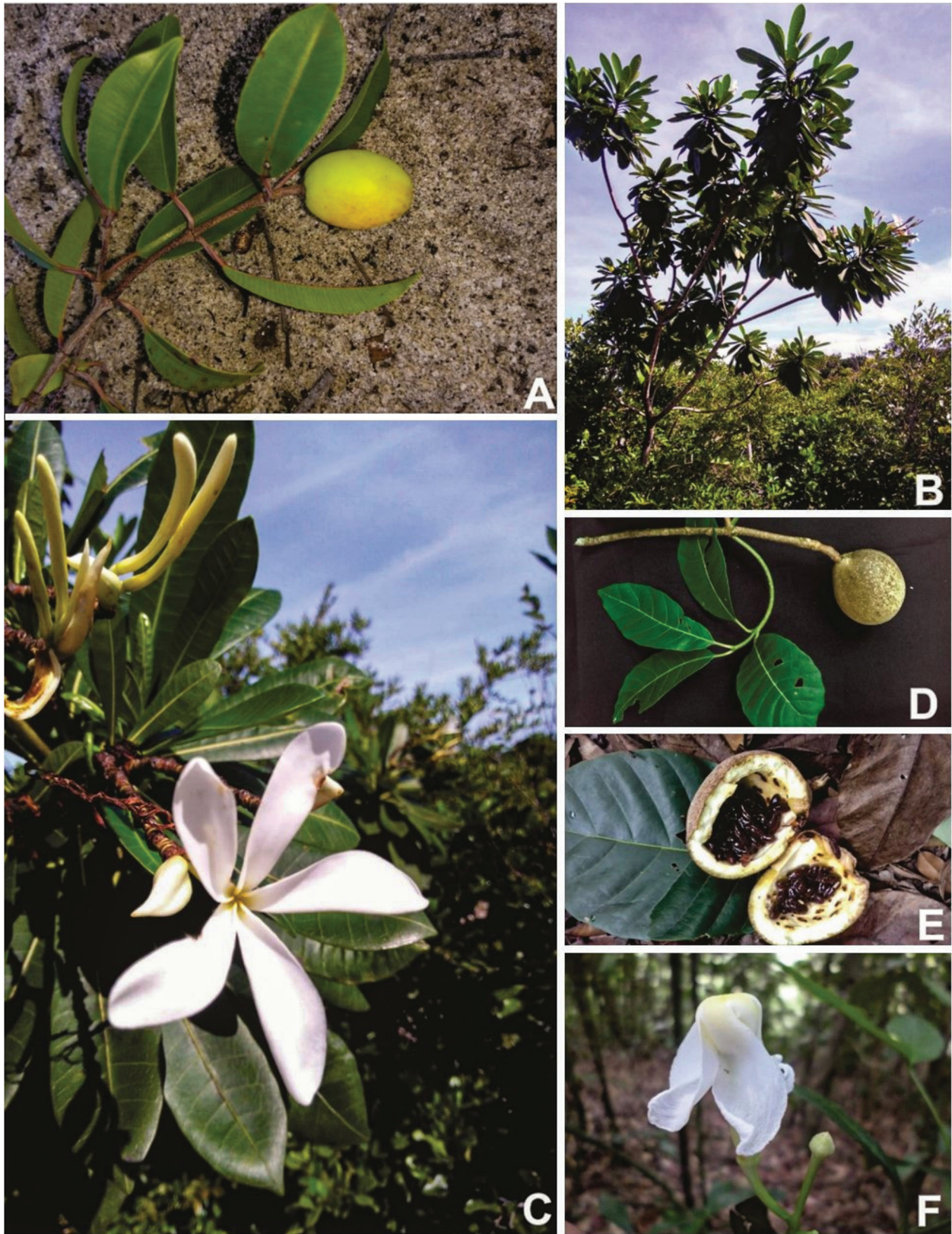


FIGURE 11. Species of Rauvolfioideae in Paraíba state, Brazil. **A**, *Hancornia speciosa*; **B–C**, *Himatanthus bracteatus*; **D–E**, *Macoubea guianensis*; **F**, *Tabernaemontana flavicans*. Photographs by M. L. Mamede (A–C), Lucas Monteiro (D–E), and Thales Coutinho (F).

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ENCYCLIA TULUAENSIS (ORCHIDACEAE: LAELIINAE),
A NEW SPECIES FROM A TROPICAL DRY FOREST IN
THE DEPARTMENT OF VALLE DEL CAUCA, COLOMBIA

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Abstract. *Encyclia tuluaensis* is a newly discovered orchid species, endemic to the tropical dry forests of Valle del Cauca, Colombia, a region characterized by high biodiversity and significant conservation relevance, primarily due to extensive habitat loss. This species was identified through comprehensive morphological analysis of cultivated specimens at the Juan María Céspedes Botanical Garden, in the municipality of Tuluá, Valle del Cauca. Initially, the species, which we hypothesize belongs to the Andean clade, was misidentified as *Encyclia betancourtiana* during the first collection due to its superficial similarity. However, detailed morphological analysis ultimately revealed significant differences, leading to its recognition as a new species. The species exhibits a range of distinctive floral and vegetative features, including three apical leaves, a pronounced fold in the central lobe of the lip, and marked color changes from anthesis to senescence. This discovery underscores the taxonomic complexity and biodiversity within the genus *Encyclia*, emphasizing the need for continued taxonomic and ecological research. *Encyclia tuluaensis* is part of the Andean species complex and is currently only known from its type locality. It requires particular conservation efforts due to its restricted distribution and the vulnerability of its habitat, which is threatened by deforestation, agricultural expansion, and urban development.

Keywords: systematics, taxonomy, tropical dry forest, Andean clade

Resumen. *Encyclia tuluaensis* es una especie de orquídea recientemente descubierta, endémica de los bosques secos tropicales del Valle del Cauca, Colombia, una región caracterizada por su alta biodiversidad y un significativo valor de conservación, principalmente debido a la extensa pérdida de hábitat. Esta especie fue identificada mediante un análisis morfológico exhaustivo de especímenes cultivados en el Jardín Botánico Juan María Céspedes, en el municipio de Tuluá, Valle del Cauca. Inicialmente, la especie, que pertenece al clado andino, fue identificada erróneamente como *Encyclia betancourtiana* durante la primera colecta debido a sus características similares. Sin embargo, un análisis morfológico detallado reveló finalmente diferencias significativas, lo que llevó a su reconocimiento como una nueva especie. La especie exhibe una serie de características florales y vegetativas distintivas, que incluyen tres hojas apicales, un pliegue pronunciado en el lóbulo central del labelo y cambios de color marcados desde la antesis hasta la senescencia. Este descubrimiento subraya la complejidad taxonómica y la biodiversidad dentro del género *Encyclia*, enfatizando la necesidad de continuar con la investigación taxonómica y ecológica. *E. tuluaensis* forma parte del complejo de especies andinas y actualmente está confinada a su localidad tipo, lo que requiere esfuerzos de conservación enfocados debido a su distribución restringida y la vulnerabilidad de su hábitat, el cual está amenazado por la deforestación, la expansión agrícola y el desarrollo urbano.

Palabras claves: sistemática, taxonomía, bosque seco tropical, clado Andino

Encyclia Hook. (Orchidaceae) is the second most diverse genus within the Neotropical subtribe Laeliinae. Species of *Encyclia* range from southern Florida in the United States, through the Antilles, Mexico, Central America, northern South America (primarily the Andes, mostly below 1500 meters, with a secondary center of diversity in the combined Guianas/Amazon area), southeastern Brazil, and northern Argentina (Dressler and Pollard, 1974; van den Berg and Carnevali, 2005; Leopardi-Verde et al., 2016; Carnevali et al., 2022). Currently, the genus comprises approximately 213 taxa and nothotaxa, of which 180 have been formally described (Carnevali et al., 2022; Ocupa-Horna et al., 2024).

Systematic studies of *Encyclia* have revealed a complex phylogenetic structure, comprising several well-defined internal clades. These clades exhibit distinct geographic affinities, which may or may not correspond with marked morphological and ecological similarities. For instance, certain *Encyclia* species complexes are morphologically diagnosable as monophyletic groups; however, resolving internal relationships within these groups remains challenging (Leopardi-Verde et al., 2016; Bastos et al., 2018; Carnevali et al., 2018a, b; Tamayo-Cen et al., 2020; Carnevali et al., 2022, see differing perspectives in Lipińska et al., 2023). In contrast, some phylogenetic patterns in the

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recovered clades exhibit robust geographic structuring, with less pronounced morphological similarities that include hyperdivergent floral elements, particularly in the labellum (Leopardi-Verde et al., 2016). Additionally, these clades may include elements that demonstrate ecological divergence, such as altitudinal preferences. For example, some topologies suggest cladogenesis events associated with shifts in altitudinal preferences, as seen in the *Encyclia mooreana* complex (Tamayo-Cen, 2022).

The remarkable diversity within *Encyclia*, along with the continuous discovery of new species, underscores the necessity of ongoing exploration and taxonomic refinement. Future efforts could benefit from the use of advanced molecular techniques, such as next-generation sequencing and integrative taxonomy approaches that combine genetic, morphological, and ecological data to refine species boundaries and enhance our understanding of evolutionary relationships. Many regions with suitable habitats remain botanically unexplored or only partially studied, particularly the tropical dry forests of Colombia and the Andean

foothills in northern South America (Leopardi-Verde et al., 2014). Consequently, the taxonomic status of several populations requires further evaluation, highlighting the complexity of the genus and the potential for additional discoveries.

During an extensive review of orchids from the tropical dry forests of Valle del Cauca, two specimens deposited in the herbarium of the Juan María Céspedes Botanical Garden (TULV) were initially identified as *Encyclia betancourtiana* Carnevali & I. Ramírez. However, these specimens exhibited morphological characteristics inconsistent with the known description of that species. Consequently, a field investigation was conducted at the botanical garden to examine a cultivated plant in bloom, originating from the same population as the herbarium specimens. Detailed morphological analysis confirmed that the plant represents a new entity, differing from *E. betancourtiana* and other species within the same group. Based on these collections and comparisons with previous specimens from the same region, this species is formally recognized as new to science.

MATERIALS AND METHODS

The description and illustrations were prepared from the living type specimens cultivated at the Botanical Garden of Juan María Céspedes, deposited in the herbarium of TULV with the accession number 17657 (Fig. 1). Digital images were taken with a Nikon D750 and a Nikkor 105mm f/2.8 macro lens. Sketches from living and preserved specimens were digitized, and the images were used for

diagramming a Lankester Composite Digital Plate (LCDP) in Adobe Photoshop® CS6. The new species was described following the botanical terminology by Beentje (2012) and Stearn (1992). Specimens from the herbaria AMES, CICY, CUVC, TULV, and VALLE were consulted, and no further herbarium material referable to this taxon was found.

TAXONOMIC TREATMENT

Encyclia tuluensis J.S. Moreno, Tamayo-Cen, & Carnevali *sp. nov.*

TYPE: COLOMBIA. Valle del Cauca: Municipio de Tuluá, corregimiento de Mateguadua, *ex Hort.* Jardín Botánico Juan María Céspedes, 1085 m, 14 August 2012, A. Castaño 49 (Holotype: TULV [17657]; Isotype: TULV 17656) Fig. 2–3.

Encyclia tuluensis is most similar to *E. betancourtiana*, distinguished by its lip with lateral lobes that are oblong-elliptic (vs. oblong and rounded), and a mid-lobe that is transversely subquadrate-rhomboid (vs. obovate in the new species).

Epiphytic *plant*, up to 80 cm tall including the inflorescence. *Pseudobulbs* heteroblastic, with two distinct internodes, which are located between three prominent nodes in the apical portion, ovoid-cylindrical, apically 2–3 foliate, 5.96–7.54 × 2.7–3.2 cm, smooth when recently developed, rough with time or dehydration, subtended by 1 or 2 white papyraceous, non-persistent sheaths, shredding with age. *Leaves* erect when recently developed; when mature, the leaves bend due to their larger and longer size, causing the plant to arch, 14.32–48.10 × 1.43–3.17 cm, conduplicate, coriaceous, oblong-linear, obtuse. *Inflorescence* apical, borne from the mature pseudobulb, erect to suberect, paniculate, up to 70 cm long, with ca. 60 flowers; peduncle, rachis, and pedicels dark-brown tinged, coarsely verruculose, cylindrical; *peduncle* up to 30 cm long, with 4 internodes; *rachis* up to 50 cm long; floral bract triangular, acute, 2.2–2.5 × 4.2–4.4 mm; *pedicel* up

to 2.5 cm. *Ovary* dark-brown at the base, greenish toward the pedicel, costate, straight to sigmoid, terete, distally dilated, verruculose at the base, with the verrucosity diminishing progressively toward the pedicel, 6.2–6.5 mm long. Flowers change color during the period from anthesis to senescence, with greenish-brown sepals and petals when freshly opened, turning red as they age, sepals with yellow margins toward the apex, petals with the base, apex, and margins yellow; mid-lobe of the lip white with the callus white with purple nerves at the base, which turn yellow as they age, lateral lobes yellow with white toward the apex, tinged with red, column yellow, tinged with red dorsally, ventrally, and laterally, anther pale yellow to white, capsule dark-brown. *Sepals* slightly verruculose, oblong-elliptic, slightly concave at the apex, acute, 1.07–1.13 × 0.40–0.43 cm, 7-veined. *Petals* projected forward, slightly concave toward the apex, oblanceolate, subacute, 1.07–1.08 × 0.30–0.33 cm, 6-veined. *Lip* trilobed, 0.97–1.30 × 1.2–1.5 cm expanded; *lateral lobes* with 3–4 dark-red nerves, embracing the column, apex of the lobes curves outward, oblong, inclined at an angle of approximately 30° from the vertical axis of the base, rounded, 0.60–0.67 × 0.22–0.24 cm; *mid-lobe* obovate, emarginate, verruculose, undulate margins and a prominently textured surface characterized by parallel ridges and grooves, 0.45–0.58 × 0.58–0.62 cm; callus oblong-elliptic, sulcate, elevated, formed by 4 longitudinal keels that do not reach the apical end of the callus, with a prominent central sulcus, a deep, longitudinal groove running from the base to the trifid apex ending in



FIGURE 1. Holotype of *Encyclia tuluaensis* J.S. Moreno, Tamayo-Cen, & Carnevali, identified initially as *Encyclia betancourtiana* Carnevali & I. Ramírez. Based on A. Castaño 49 (TULV [17657]).

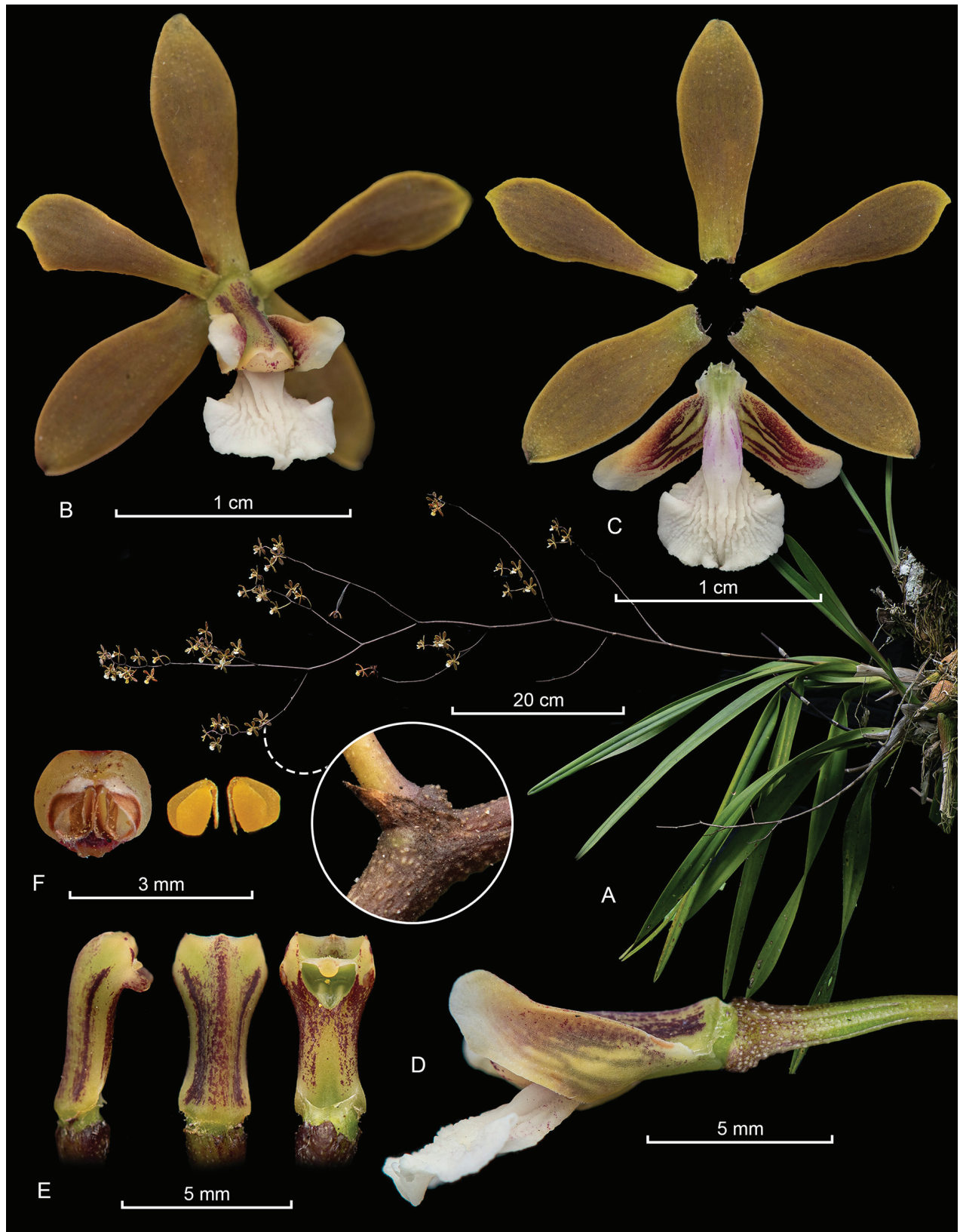


FIGURE 2. LDCP of *Encyclia tuluaensis* J.S. Moreno, Tamayo-Cen, & Carnevali. A, habit and growth; B, flower C, dissected perianth; D, lip, column, and ovary; E, column, lateral, dorsal, and ventral view; F, anther cap and pollinia. LDCP by J. S. Moreno, based on the holotype.

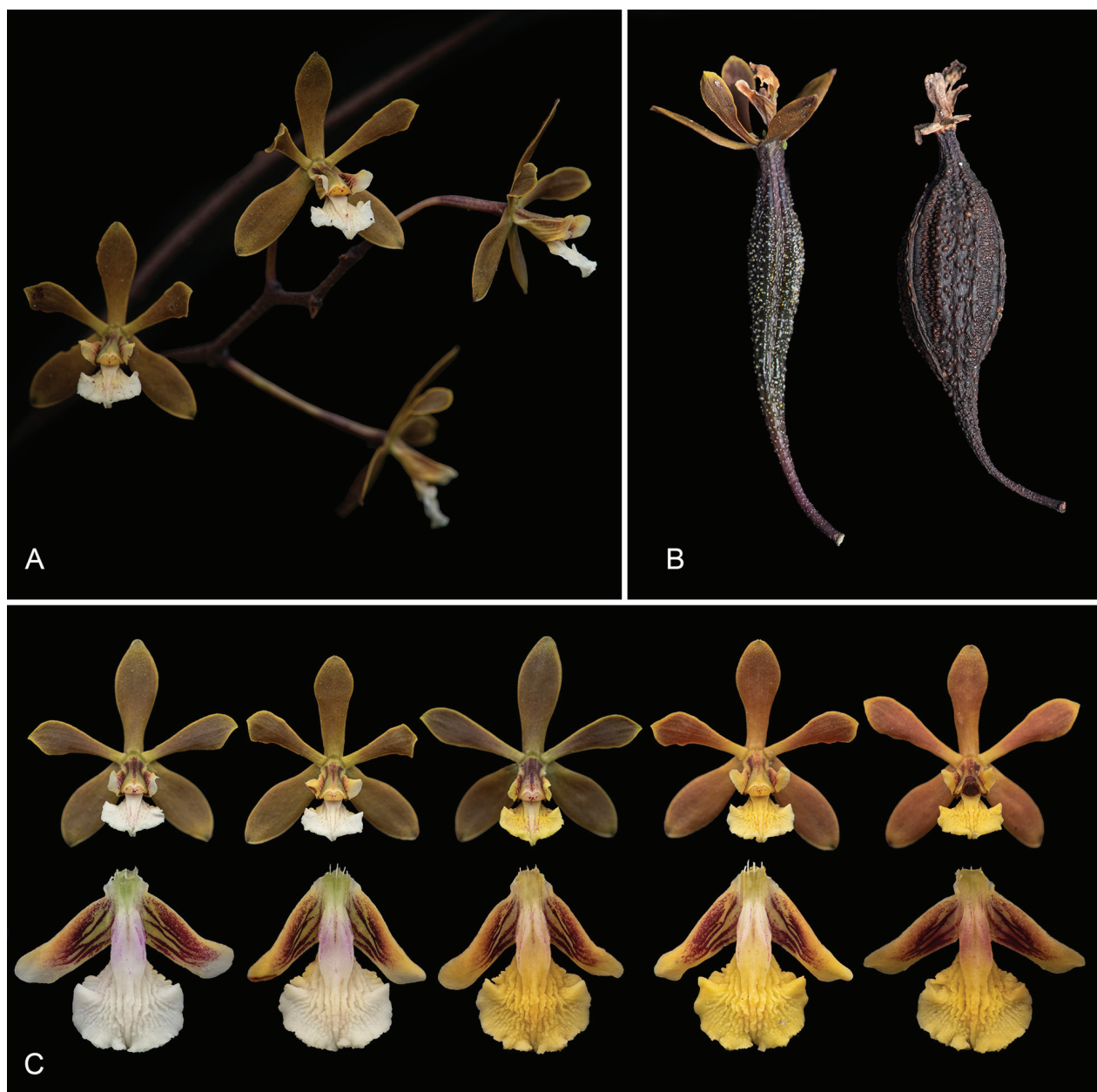


FIGURE 3. *Encyclia tuluensis* J.S. Moreno, Tamayo-Cen, & Carnevali. **A**, inflorescence; **B**, capsules in two stages of maturation. On the left, the immature ovary with dark brown color, and on the right, the mature ovary with black-purple color. Both show a verruculose (warty) surface; **C**, front view of the flower from anthesis to senescence, showing the progression from initial colors to aged appearance and a detailed view of the lip showing the color transition from initial vivid hues to the final coloration as the flower ages. Photographs by J. S. Moreno.

three central longitudinal keels extending toward the mid-lobe, $0.45\text{--}0.46 \times 0.19\text{--}0.20$ cm long. *Column* claviform, in lateral view somewhat curved toward the apex, $5.44\text{--}5.79 \times 1.67\text{--}2.81$ mm long, ventral view canaliculated at the base, where the cuniculus is formed, clinandrium superficially tridentate, with a pair of rounded stelidia. *Anther cap* yellow with small, irregularly scattered wine-red spots, lacking a discernible pattern, sub-cordate, 1.74×1.89 mm. *Pollinia* 4, in two pairs, 0.94×0.53 mm, obovoid, bright yellow, with granular caudicles. *Capsule* verruculose up to 3 cm long.

Additional specimens examined: COLOMBIA. Valle

del Cauca: Municipio de Tuluá, corregimiento de Mateguadua, quebrada Valenzuela, 1117 m, 23 June 2010, *G. Reina-Rodríguez* & *N. H. Ospina-Calderón* 1217 (CUVC).

Toponymy: The name honors the municipality of Tuluá, where the new species was found.

Although we have no molecular evidence for *Encyclia tuluensis*, the geography and overall morphology suggest that it probably belongs in the Andean Clade. The species in this clade have a lip with a conspicuously raised, sinuous callus that extends toward the central lobe; the nerves may or may not converge with the edge of the margin and end



FIGURE 4. Type specimen photograph of *Encyclia betancourtiana* Carnevali & I. Ramírez. **A**, flower; **B**, plant. Photographs by A. Betancourt.

trifid. They are also markedly verruculose on the pedicel and ovary, as well as on the rachis of the inflorescence, which is coppery brown. This species group of *Encyclia* exhibits thick, elevated, and relatively flat calli with a less pronounced central depression compared to other groups in the genus. Additionally, the keel or nerves originating from the callus and extending into the mid-lobe of the labellum are thick and coarsely verrucose. The column's auricles or wings are small, rounded, and acute, and the capsules are verruculose to warty (Carnevali and Ramirez, 2004). This Andean complex includes such taxa as *E. angustiloba* Schlechter, *E. aspera* (Lindl.) Schltr., *E. asperirhachis* Garay, and *E. microtos* (Reichenbach f.) Hoehne. Other species that could be considered relatively similar, and are found outside the Andean clade, include *E. betancourtiana* and *E. parkeri* Reina-Rodr. & Leopardi (Tamayo-Cen, 2022).

The most similar species is *E. betancourtiana* (Carnevali and Ramirez, 2004) (Fig. 4) from western Venezuela, which can be recognized by its lip with lateral lobes that are oblong-elliptic, with an obliquely obtuse to rounded apex, $0.90\text{--}0.95 \times 0.35$ cm, spreading forming an angle of less than 45° in relation to the main *labelar axis* (vs. oblong, rounded, $0.6\text{--}0.67 \times 0.22\text{--}0.24$ cm spreading with an angle of approximately 30°) and the mid-lobe is transversally subquadrate-rhomboid, $0.6\text{--}0.7 \times 0.95$ cm (vs. obovate, $0.45\text{--}0.58 \times 0.58\text{--}0.62$ cm).

Encyclia aspera (Fig. 5) is distinguished by the short, broad, and rounded lateral lobes of the lip (vs. longer and narrower lateral lobes) and a median lobe with a slightly pronounced wavy margin (vs. a median lobe with markedly defined undulations), which is orbicular to orbicular-elliptic

(vs. obovate). Additionally, the labellum of *E. tuluensis*, when viewed from the front, has an anchor-like shape due to a slight fold in the proximal portion that retracts the labellum slightly, a feature absent in *E. aspera*. This distinct folding pattern gives *E. tuluensis* a characteristic form not present in *E. aspera*.

Encyclia microtos (Fig. 6), with a restricted distribution in Ecuador and Peru, is also similar to *E. tuluensis* but differs mainly by its narrower leaves, its oblong-cuneate, acute sepals, about 1.5 cm long (vs. oblong-elliptic, slightly concave at the apex, acute, $1.07\text{--}1.13$ cm long), with oblong-spatulate, obtuse petals (vs. oblanceolate, subacute), a three lobed lip with the lateral lobes obliquely triangular-oblong, slightly retrorse, and sub-obtuse (vs. oblong and rounded), and a mid-lobe suborbicular from a cuneate base mid-lobe (vs. obovate).

Additionally, described from Colombia and also growing in a tropical dry forest, and probably distributed to Peru, *Encyclia parkeri* (Fig. 7) is also similar to the new species, but it can be recognized by its three-lobed lip with an orbicular to suborbicular mid-lobe, rounded at the apex, $0.70\text{--}0.75 \times 0.80\text{--}0.85$ cm (vs. with an obovate, emarginate mid-lobe, $0.45\text{--}0.58 \times 0.58\text{--}0.62$ cm). *Encyclia parkeri* also has larger lateral lobes, $0.90\text{--}0.95 \times 0.30\text{--}0.40$ cm (vs. shorter $0.60\text{--}0.67 \times 0.22\text{--}0.24$ cm). Finally, the callus in *E. parkeri* is sub-rhombic to quadrangular, composed of two broad, high keels running from just above the base of the lip, $0.58\text{--}0.65 \times 0.24\text{--}0.30$ cm (vs. oblong-elliptic, sulcate, composed of four longitudinal keels that do not reach the apical end of the callus, $0.45\text{--}0.46 \times 0.19\text{--}0.20$ cm wide).

Habitat and ecology: The new species was found growing epiphytically in a tree of *Erythroxylum* sp. in the



FIGURE 5. Type specimens of *Epidendrum asperum* Lindl. **A**, specimen at AMES (barcode 00070082) with a photograph of the holotype in the Lindley Herbarium (K); **B**, close up of the labellum shown in A, drawn by J. Lindley; **C**, detail of the inflorescence, showing the dried flowers from an isotype at E (barcode 00373980).

Botanical Garden Juan María Céspedes, which is located in the district of Mateguadua, 7 km from the municipality of Tuluá. The botanical garden covers an area of 154 hectares of undulating terrain, with elevations ranging between 1050 and 1300 meters above sea level. The average temperature is the same as that of the central plain of the Valle del Cauca department, ca. 25 C, and the annual rainfall averages ca. 1000 mm, with two quarterly rainy periods alternating with two dry periods. It is situated within the life zone known as Tropical Dry Forest.

Conservation status: *Encyclia tuluaensis* is known only from its type locality in the Juan María Céspedes

Botanical Garden, located within the Natural Regional Park Mateguadua in Tuluá. Despite being found in the most threatened ecosystem in Colombia, the Tropical Dry Forest, its position within the protected park ensures its protection, at least for the type population. Assuming continued protection, the species could be categorized under the criteria of the IUCN as Least Concern (LC). However, because we lack adequate distribution and population information to make a proper assessment and the necessary data to apply the IUCN categorization protocols, we propose categorizing the new species as Data Deficient (DD) (IUCN Standards and Petitions Subcommittee, 2017; IUCN, 2024).

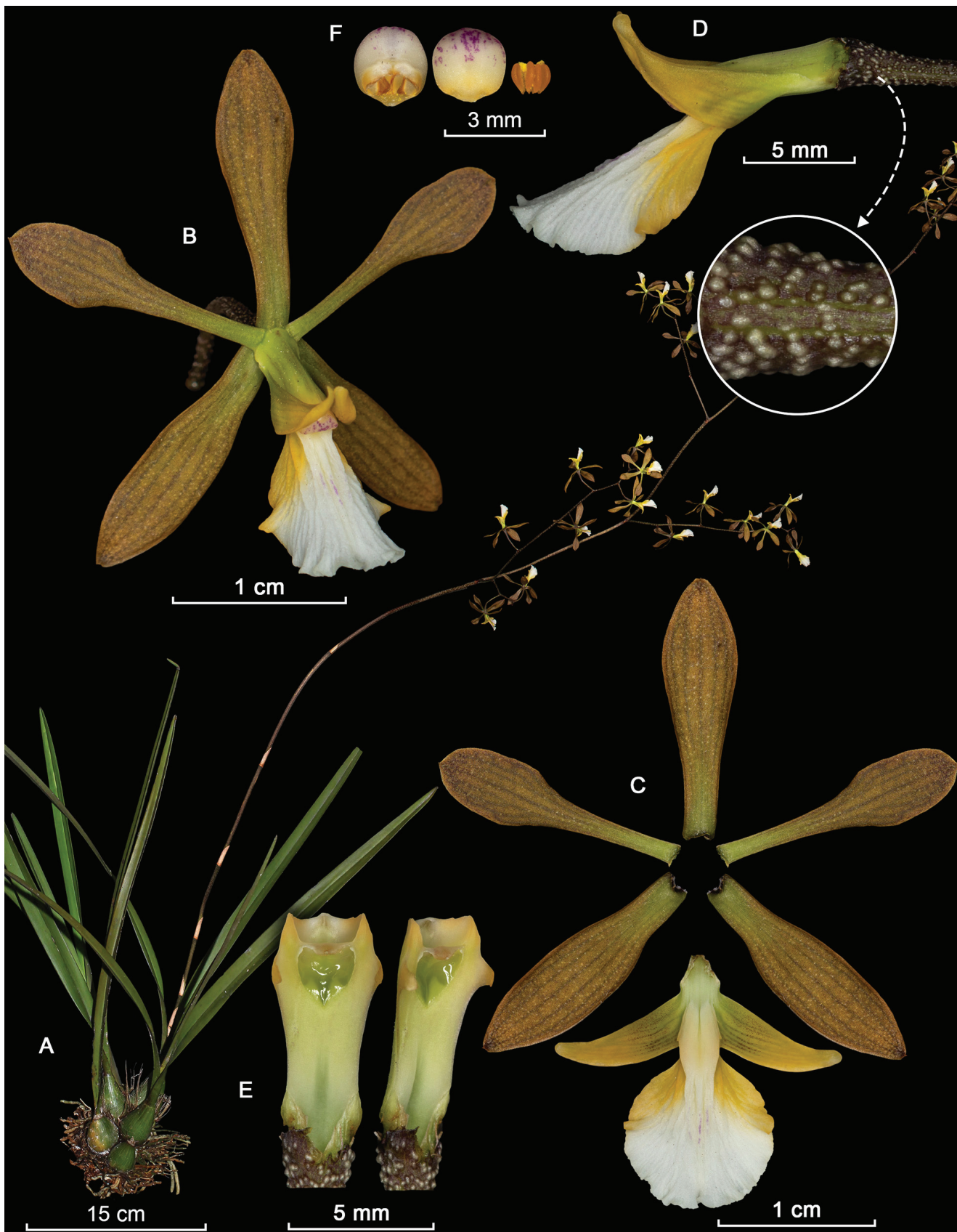


FIGURE 6. LDCP of *Encyclia microtos* (Reichenbach f.) Hoehne. A, habit and growth; B, flower; C, dissected perianth; D, lip, column, and ovary; E, column, ventral views; F, anther cap and pollinia. LDCP by L. Ocupa-Horna based on a plant from Tumbes department, northern Perú.

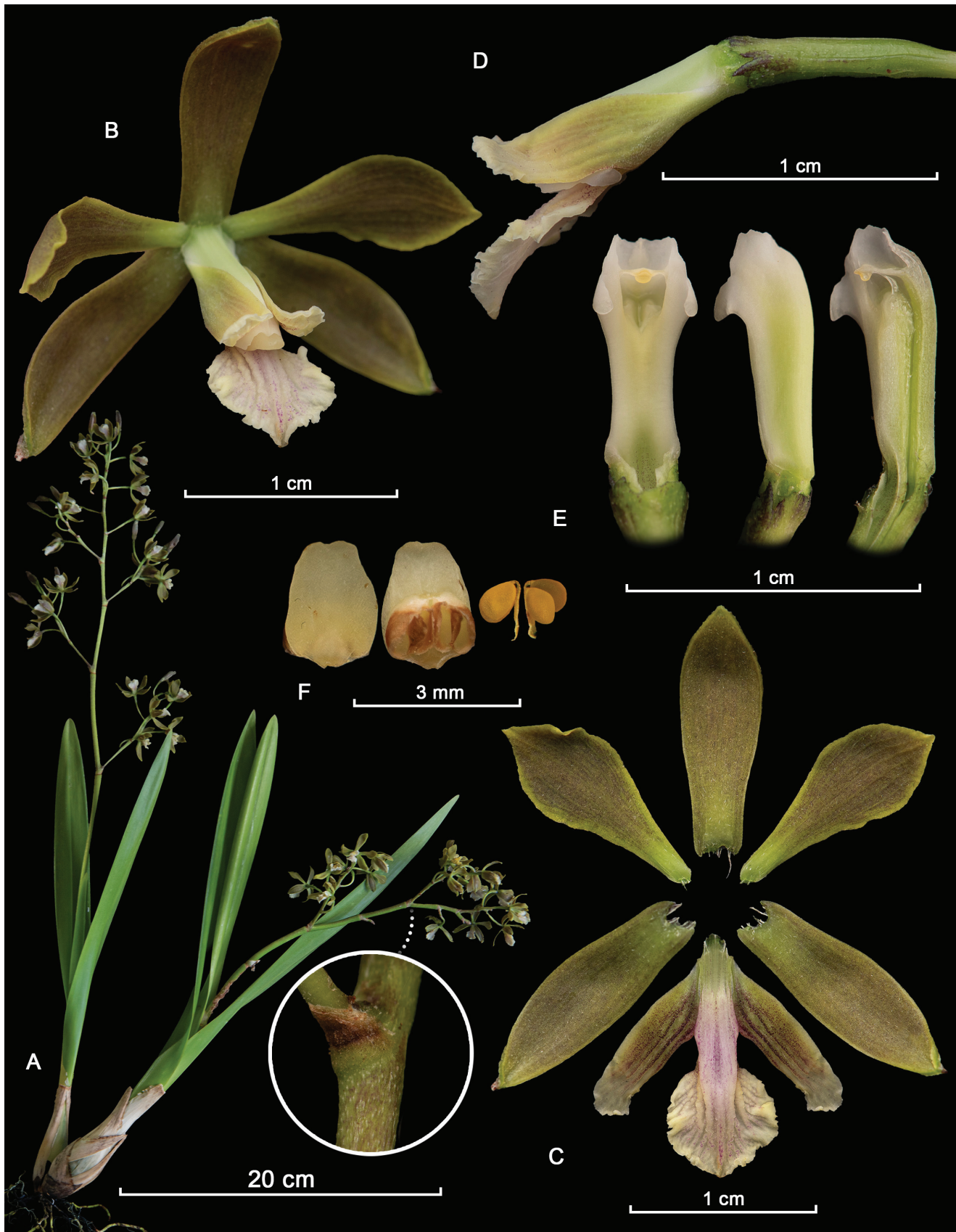


FIGURE 7. LDCP of *Encyclia parkeri* Reina-Rodr. & Leopardi. **A**, habit and growth; **B**, flower; **C**, dissected perianth; **D**, lip, column, and ovary; **E**, column, lateral, dorsal, and ventral view; **F**, anther cap and pollinia. LDCP by J. S. Moreno based on a plant from Colombia.

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REINSTATEMENT OF *LITSEA DISCOLOR* OVER *L. TIMORIANA* (LAURACEAE)

PAUL ORMEROD¹

Abstract. *Litsea discolor* (based on *Tetranthera discolor*) is found to be the first validly published name for the widespread Malesian species currently known under the invalid name *L. timoriana*. Typification where required is proposed for the various taxa discussed.

Keywords: Lauraceae, Malesia, *Litsea discolor*, synonymy, reinstatement

This paper deals with a nomenclatural issue detected while preparing a checklist of Papuasian Lauraceae. The opportunity to deal with the broader synonymy of *Litsea discolor* is taken here, rather than in a narrowly defined regional checklist.

Litsea discolor (Blume) Boerl., Handl. Fl. Ned. Ind. (Boerlage) 3(1): 144. 1900.

Basionym: *Tetranthera discolor* Blume, Mus. Bot. Lugd. Bat. 1(24): 382. 1851. TYPE: INDONESIA. Timor, A. Zippel 53 (Lectotype, 1st step, Kostermans 1969: 508 as Typus; 2nd step lectotype, here designated; L [1806261], image seen; Isolectotypes: L [1806251]; L [1806252]; L [1806253]; L [1806254], images seen); Timor, J. B. Spanoghe 73 (Syntype: L [1806249], image seen); specimen annotated “*Tetranthera apetala*” ex Herb. Mus. Paris (Syntype: not found).

Homotypic synonyms: *Cylicodaphne discolor* (Blume) Meissn., Prodr. (A.P. de Candolle) 51(1): 204. 1864.

Litsea timoriana Span. ex Fawc., Naturalist’s Wanderings E. Archipel. (H. O. Forbes): 516. 1885 *nom. illeg.*

Malapoenna discolor (Blume) O. Kuntze, Rev. Gen. Pl. 2: 572. 1891.

Heterotypic synonyms: *Tetranthera forstenii* Blume, Mus. Bot. Lugd. Bat. 1(24): 383. 1851. TYPE: INDONESIA. Sulawesi, near Tondano, July 1840, E. A. Forsten *s.n.* (Lectotype, here designated; L [1806294], image seen); Isolectotypes: K [00081522]; L [1806288]; L [1806289], images seen).

Malapoenna forstenii (Blume) O. Kuntze, Rev. Gen. Pl. 2: 572. 1891.

Litsea forstenii (Blume) Boerl., Handl. Fl. Ned. Ind. (Boerlage) 3(1): 142. 1900.

Tetranthera riparia Blume, Mus. Bot. Lugd. Bat. 1(24): 383. 1851. TYPE: INDONESIA. Maluku Prov., Banda Islands, A. Zippel 77 (Lectotype, Kostermans 1969: 508 as Typus: L [1806225], image seen).

Malapoenna riparia (Blume) O. Kuntze, Rev. Gen. Pl. 2: 573. 1891.

Litsea riparia (Blume) Boerl., Handl. Fl. Ned. Ind. (Boerlage) 3(1): 143. 1900.

Cylicodaphne pallida Blume, Mus. Bot. Lugd. Bat. 2(1–8): 11. 1856. TYPE: INDONESIA. Maluku

Prov., Banda Islands, *sine coll. s.n.* (Lectotype, here designated; L [0819867], image seen).

Malapoenna cylicodaphne O. Kuntze, Rev. Gen. Pl. 2: 572. 1891.

Litsea pallida (Blume) Boerl., Handl. Fl. Ned. Ind. (Boerlage) 3(1): 145. 1900 *nom. illeg.* [non (Blume) Boerl. 1900: 143].

Litsea stickmanii Merrill, Interpr. Herb. Amb.: 235. 1917. TYPE: INDONESIA. Maluku Prov., Ambon, Hitoe Messen and Paso, 3–200 m, 1 and 25 November 1913, C. B. Robinson 471 (Lectotype, 1st step, Merrill 1917: 235; 2nd step lectotype, here designated; US [00099375], image seen; Isolectotypes: A [00041801]; BO [1246541]; CAL [0000021804]; F [0061433F]; L [1806229]; MO [247336], images seen).

Actinodaphne novoguineensis Teschn., Bot. Jahrb. Syst. 58(4): 388. 1923. TYPE: PAPUA NEW GUINEA. Sepik [as Kaiserin Augusta] River, Camp 18, 200–400 m, 22 November 1912, C. Ledermann 9816 (Lectotype, here designated; B [10-0241826], image seen; Isolectotypes: B [10-0241827]; L [0036818], images seen).

Litsea kauloensis Teschn., Bot. Jahrb. Syst. 58(4): 396. 1923. TYPE: PAPUA NEW GUINEA. Kaulo [River], 400 m, 23 November 1907, R. Schlechter 16877 (Holotype: B, destroyed; Isotypes: P [00745270]; P [00745271]; P [00745272]; P [00745273]; SING [0069611]; UC [226449], images seen).

Tetradenia longifolia Teschn., Bot. Jahrb. Syst. 58(4): 389. 1923. TYPE: PAPUA NEW GUINEA. Sepik [as Kaiserin Augusta] River, Camp 18, 200–400 m, 19 November 1912, C. Ledermann 9759 (Lectotype, here designated; B [10-0277524], image seen; Isolectotypes: B [10-0277525]; B [10-0277526]; B [10-0277527]; L [0036819], image seen).

Neolitsea longifolia (Teschn.) Kamik., Trans. Nat. Hist. Soc. Kagoshima Imp. Coll. Agric. 3(15): 130. 1935.

Litsea solomonensis C.K. Allen, J. Arnold Arbor. 23: 127. 1942. TYPE: SOLOMON ISLANDS. Santa Isabel [as Ysabel], Maringe, 150 m, 23 November 1932, L. J. Brass 3183 (Holotype: A [00041818], image seen; Isotypes: BISH [1005941]; BRI [AQ0340635]; L [0036832], images seen).

I wish to thank Lina Juswara (BO) for kindly looking for requested materials, and Kanchi Gandhi (HUH) for nomenclatural research and advice, and for sourcing literature.

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Usage Synonyms: *Lignum leve latifolium* Rumph., Herb. Amboin. 3: 71, t.43. 1743.

Tetranthera roxburghii auct. non Nees, Decaisne, Nouv. Ann. Mus. Hist. Nat. 3: 369. 1834.

Litsea timoriana Span., Comp. Bot. Mag. 1: 350. 1836 nom. nud.

Tetranthera timoriana Span., Linnaea 15(4): 346. 1841 nom. nud.

Cryptocarya discolor Zipp. ex Span., Linnaea 15(4): 346. 1841 pro syn.

Litsea discolor Zipp. ex Blume, Mus. Bot. Lugd. Bat. 1(24): 382. 1851 pro syn.

Litsea papuana auct. non K. Schum., S. Moore, J. Bot. (London) 61, (Suppl.): 43. 1923.

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

Select specimens examined: INDONESIA. Maluku Prov., Halmahera, Gunung Sahu, near Susupu, 500 m, 6 October 1974, *E. F. de Vogel* 3278 (BO [1247913], image seen); Gunung Sahu, near Susupu, 8 October 1974, *E. F. de Vogel* 3338 (BO [1247915], image seen); Bacan, Gunung Sibela, near Waiaua, 250 m, 27 October 1974, *E. F. de Vogel* 3697 (BO [1247923], image seen); Gunung Sibela, near Waiaua, 250 m, 28 October 1974, *E. F. de Vogel* 3714 (BO [1247927], image seen); Gunung Sibela, near Waiaua, 250 m, 31 October 1974, *E. F. de Vogel* 3785 (BO [1247926], image seen); Ambon, Hitoe Messen and Paso, 3–200 m, 1 and 25 November 1913, *C. B. Robinson Pl. Rumph. Amb.* 470 (BM [000799051]; BO [1246540]; GH [02499406]; K [000815268]; L [1806228]; NY [4748344], images seen). PAPUA NEW GUINEA. Mt. Korkoro, 855 m, 27 January 1886, *H. O. Forbes* 624 (P [02010724], image seen); lower Fly River, E bank opposite Sturt Island, October 1936, *L. J. Brass* 8106 (A [02499763]; BO [1248481], images seen). New Ireland, Feni Island Group, Ambitle Island, Nanum Caldera, 60 m, 16 November 2003, *W. Takeuchi* 16794 (A [02499753], image seen). Bougainville, Marmaromino, 50 m, 29 September 1930, *S. F. Kajewski* 2200 (A [02499757], image seen).

Kostermans (1969) used the name *Litsea timoriana* Span. for this taxon, but it is a *nomen nudum* and thus not available for consideration. It was eventually superfluously validated as a name by Fawcett in 1885 (see above). There are three competing east Malesian names for this taxon, namely *Tetranthera discolor*, *T. forstenii*, and *T. riparia*. Since the name *Tetranthera discolor* has material of Spanoghe's *Litsea timoriana* among its syntypes, I have chosen that binomial over the others. *Tetranthera forstenii* has not been formally reduced to *Litsea discolor*, but Kostermans has combined the material at Leiden under *L. timoriana*, a position I agree with. *Tetranthera riparia* is based on rather incomplete or young flowering material from the Banda Islands. It has rather shorter leaves than most of the material seen. Kostermans sunk it under *L. timoriana* in 1969.

Kostermans (1988) reduced *Cylicodaphne pallida* from the Banda Islands to *Litsea timoriana* (= *L. discolor*). A position here agreed with. Unfortunately, on POWO this has been confused with *Litsea pallida* (Blume) Boerl. (Basionym: *Tetranthera pallida* Blume), a species from Sulawesi. Part of the synonymy cited belongs to the taxon from Banda.

I also concur with Kostermans (unpublished) that *Actinodaphne novoguineensis*, *Litsea kauoensis*, and *Tetradenia longifolia* are all synonyms of *Litsea discolor*. Original material survives in Berlin of *Actinodaphne novoguineensis* and *Tetradenia longifolia*. For those two taxa I have chosen the sheets that bear Teschner's original sketches as lectotypes.

Litsea tuberculata (Blume) Boerl., Handl. Fl. Ned. Ind. (Boerlage) 3(1): 144. 1900.

Basionym: *Cylicodaphne tuberculata* Blume, Mus. Bot. Lugd. Bat. 2(1–8): 12. 1856. TYPE: INDONESIA. Sumatra, *Herbarium F.A.C. Waitz s.n.* (Lectotype, here designated; L [1789788], image seen; Isolectotypes: L [1789784]; L [1789785]; L [1789787]; L [1789789], images seen); Sumatra, *P. W. Korthals s.n.* (Syntypes: L [0036836]; L [1789841], images seen); Sumatra, *P. W. Korthals* 967 (Syntypes: L [1789790]; L [1789791], images seen); Sumatra, *C. F. E. Praetorius s.n.* (Syntype: L [1789786], image seen); Sumatra, *sine coll. s.n.* (Syntype: K [000815264], image seen). Homotypic synonyms: *Lepidadenia tuberculata* (Blume) Miq., Fl. Ned. Ind. 1(1): 937. 1858.

Malapoenna tuberculata (Blume) O. Kuntze, Rev. Gen. Pl. 2: 573. 1891.

Distribution: Indonesia (Sumatra).

Kostermans (1969, sub *L. timoriana*) listed a collection “*sine coll.* (L)” as the type of *Litsea tuberculata*, but all the possible syntypes found in Leiden can be assigned to a collector. Possibly he meant a sterile Korthals collection in Leiden (L [0036836]), because that is the only one that bears a type label. Since “*sine coll.* (L)” cannot be found, I have chosen as lectotype a specimen annotated by Blume from Herbarium Waitz that bears the distinctive tubercular fruit cups that gave the species its name. Waitz did not collect in Sumatra, but it is probable that the specimens of *L. tuberculata* in his possession were actually gathered by Christiaan Praetorius.

The status of *L. tuberculata* is unclear to me. Though Kostermans (1969) reduced it to synonymy with *L. timoriana*, he seems to have had second thoughts about this by keeping the material separate at Leiden (rather than combining it with *L. timoriana*).

In the material aggregated at Leiden there are some specimens in WAG from Papua Prov., Indonesia. In my opinion these are better referred to *L. discolor*.

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NOTES ON SOME MALESIAN ORCHIDACEAE VIII

PAUL ORMEROD^{1,2} AND LINA JUSWARA³

Abstract. Continuing herbarium and literature studies reveal the need for further transfers in three genera and the need to raise one taxon from subspecific status to species level. *Liparis brachystele* is found to be a synonym of *Cestichis pullei*. The new names are *Appendicula thymifolia*, *Cestichis affinis*, *C. carinatifolia*, *C. glaucescens*, *C. misoolensis*, *C. tunensis*, *Crepidium ventilabrum*, and *Dendrobium yudistirae*.

Keywords: *Appendicula*, *Cestichis*, *Crepidium*, *Dendrobium*, transfers, synonymy

This paper is a continuation of our research (e.g., Ormerod and Juswara, 2024) on Malesian orchids. Here we deal with four genera, making transfers in three, and raising one taxon to species status in another.

Appendicula Blume, Bijdr. Fl. Ned. Ind. 7: 297. 1825.

Type species: *Appendicula alba* Blume.

A genus of about 160 species distributed from India, through Malesia to Samoa. About 82 species may be found in Indonesia. The plants are epiphytic herbs, with slender, leafy stems, bearing axillary to terminal inflorescences of small whitish to greenish flowers.

Appendicula thymifolia (Ridl.) Ormerod & Juswara, *comb. nov.*

Basionym: *Podochilus thymifolius* Ridl., J. Fed. Mal. St. Mus. 8(4): 112. 1917.

TYPE: INDONESIA. Sumatra, Barong Bharu, Tapan, 1220 m, 5 June 1914, *leg. N. S. Jaggat, H. C. Robinson & C. B. Kloss* 72 (Syntype: BM [000509269], image seen); Barong Bharu, Tapan, 1220 m, 6 June 1914, *leg. N. S. Jaggat, H. C. Robinson & C. B. Kloss* 88 (Syntype: BM [001234408], image seen).

Distribution: Indonesia (Sumatra).

In the protologue, Ridley clearly mentioned this taxon had six pollinia, a feature of the genus *Appendicula*. *Podochilus* Blume has four pollinia. We believe that *Appendicula thymifolia* is closely related to *A. rubens* (Schltr.) Schltr. but differs in having much longer (3–4 times longer than vs. as long as) leaves, and mostly terminal (vs. mostly axillary, rarely terminal) inflorescences.

Cestichis Thouars ex Pfitz., Entwurf Anordn. Orch.: 56. 1887.

Type species: *Malaxis cespitosa* (Lam.) Thouars.

A genus of about 100 species distributed from Africa, Madagascar to Sri Lanka and India, throughout southeast Asia and Malesia to Tahiti. The plants are mostly epiphytes

in warm to mildly temperate forests. The pseudobulbs may bear one to three leaves, inflorescences are terminal and usually have numerous small, often greenish flowers. The labellum is usually simple with one or two basal calli. We transfer here another five species to the genus while placing one from New Guinea into synonymy.

Cestichis affinis (Blume) Ormerod & Juswara, *comb. nov.*

Basionym: *Malaxis affinis* Blume & Hasselt, Bijdr. Fl. Ned. Ind. 8: 392. 1825; Tabellen: fig. 54C. 1825.

TYPE: INDONESIA. Java, Bantam Prov., near Lebak, August [June in protologue], *J. C. van Hasselt s.n.* (Lectotype, here designated; L [0061482], image seen; Isolectotype: L [0061483], image seen).

Homotypic synonyms: *Liparis affinis* (Blume) Lindl., Gen. Sp. Orch. Pl.: 31. 1830.

Leptorkis affinis (Blume) O. Kuntze, Rev. Gen. Pl. 2: 671. 1891.

Distribution: Indonesia (Java).

Later collections of this species have not been made; it is known only from the type.

Cestichis carinatisejala (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis carinatisejala* J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 3(9): 456. 1928.

TYPE: INDONESIA. Maluku Prov., Buru, Wakollo, 700 m, 25 June 1921, *leg. Saprin, L. J. Toxopeus* 241 (Lectotype, here designated; L [0061446], image seen; Isolectotype: BO [1303031]); Buru, between Leksoela and Fakal, 1100 m, 27 August 1921, *leg. Saprin, L. J. Toxopeus* 415 (Syntype: L [0061447], image seen).

Distribution: Indonesia (Maluku).

We have chosen *Toxopeus* 241 (L) as lectotype because it bears good flowers; the other syntype (*Toxopeus* 415) bears developing capsules.

Cestichis glaucescens (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

The first author would like to thank herbarium and library staff at A, AMES, and GH for facilitating his research. Leiden (L) kindly loaned material for study. The second author would like to thank colleagues at the Directorate of Scientific Collection Management, National Research and Innovation Agency, BO, for their ongoing help and advice.

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Basionym: *Liparis glaucescens* J.J. Sm., Icon. Bogor. 2: 47. 1903.

TYPE: INDONESIA. Kalimantan, [treated with soda sublimate 20 May 1901], leg. J. G. Hallier, cult. Hort. Bogor. s.n. (Lectotype, here designated; L [0061554], image seen); Kalimantan, [treated with soda sublimate 19 November 1901], leg. J. G. Hallier, cult. Hort. Bogor. s.n. (Syntype: L [0061556], image seen); Kalimantan, [treated with soda sublimate 28 April 1902], leg. J. G. Hallier, cult. Hort. Bogor. s.n. (Syntype: L [0061555], image seen).

Distribution: Indonesia (Kalimantan).

No type material could be located in the spirit or dried collections at Bogor, so we have designated the sheet with the best flowering material in Leiden as lectotype. Vegetative parts of this species were not preserved, only inflorescences.

Cestichis misoolensis (Ormerod) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis misoolensis* Ormerod, Orchadian 16(11): 520. 2011.

TYPE: INDONESIA. Papua Prov., Misool Island, along road to Tip, 80 m, 23 September 1948, D. R. Pleyte 994 (Holotype: L [0630118]).

Distribution: Indonesia (Papua).

Cestichis pullei (J.J. Sm.) M.A. Clem. & D.L. Jones, Orchadian 15(1): 39. 2005.

Basionym: *Liparis pullei* J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 2(13): 56. 1914.

TYPE: INDONESIA. Papua Prov., Idenburg River, 400 m, 1 September 1914, W. K. H. Feuilletau de Bruyn 80 (Neotype, designated by Margonska, 2017: 146; BO, not found). Beaufort River, 100 m, November 1912, A. A. Pulle 272 (Lectotype [Lewis and Cribb, 1989: 66 as holotype]: BO, lost); Hellwig Range, December 1909, L. S. A. M. von Roemer 1335 (Syntype: BO, lost).

Homotypic synonym: *Stichorkis pullei* (J.J. Sm.) Marg., Szlach., & Kulak, Acta Soc. Bot. Polon. 77(1): 39. 2008.

Heterotypic synonyms: *Liparis brachystele* Ridl., Trans. Linn. Soc. London ser. 2, Bot. 9: 162. 1916 *syn. nov.*

TYPE: INDONESIA. Papua Prov., Camp 3, 760 m, January 1913, C. B. Kloss s.n. (Holotype: BM [000088805]).

Cestichis brachystele (Ridl.) M.A. Clem. & D.L. Jones, Orchadian 15(1): 38. 2005.

Stichorkis brachystele (Ridl.) Marg., Szlach., & Kulak, Acta Soc. Bot. Polon. 77(1): 37. 2008.

Distribution: Indonesia (Papua).

Margonska (2017) neotypified this species because the original syntypes appear to be lost. We find *Liparis brachystele* to be a synonym of this species since it shares all critical characters such as elongate, unifoliate pseudobulbs, large (sepals ca. 14 mm long) brownish flowers, a transversely elliptic labellum, and a short, stout column with additional lateral wings.

Cestichis tunensis (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis tunensis* J.J. Sm., Icon. Bogor. 2: 44. 1903.

TYPE: INDONESIA. Maluku Prov., Ambon, Tuna, leg. J. J. Smith, cult. Hort. Bogor. s.n. (Holotype: BO, not found).

Distribution: Indonesia (Maluku).

Crepidium Blume, Bijdr. Fl. Ned. Ind. 8: 387. 1825.

Type species: *Crepidium flavescens* Blume.

This genus of Malaxidinae contains about 270 species distributed from the Seychelles, Sri Lanka and India to Tahiti. The center of speciation is Indonesia, where 134 (87 endemic) species are found. The plants are primarily tender, terrestrial herbs bearing soft, pleated leaves, and with terminal racemes of small, often non-resupinate, greenish to purple flowers.

Crepidium ventilabrum (Rchb.f.) Ormerod & Juswara, *comb. nov.*

Basionym: *Microstylis ventilabrum* Rchb.f., Gard. Chron. n.s. 16: 717. 1881.

TYPE: SUNDA ISLANDS. *Cult. Messrs. H. Low s.n.* (Syntype: W-R [41020], not seen); *cult. H. Messrs. Low, icon F. C. Lehmann s.n.* (Syntype: W-R, not seen).

Homotypic synonym: *Malaxis ventilabrum* (Rchb.f.) O. Kuntze, Rev. Gen. Pl. 2: 673. 1891.

Distribution: "Sunda Islands" [Borneo?].

The origin of this species is unclear, but it may have originated from Borneo, a place where Low sourced a number of horticulturally attractive orchids (e.g., *Dendrobium lowii* Lindl.).

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

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

About 1530 species of this genus are distributed from Sri Lanka and India to Tahiti. The taxon treated below is a member of section *Pedilonum* Blume

Dendrobium yudistirae Ormerod & Juswara, *nom. et stat. nov.*

Basionym: *Dendrobium kruiense* J.J. Sm. subsp. *alboflavum* Yudistira, Romiyadi, & Cootes, Orchidee, Taxon. Mitt. 6(12): 96. 2020.

TYPE: INDONESIA. Sumatra, Aceh, Kute Panang Tropical Forest Range, 1400–2000 m, *cult. Y. R. Yudistira s.n.* (Holotype: BO, not found).

Distribution: Indonesia (Sumatra).

Etymology: Named after Yuda Rehata Yudistira, who cultivated and co-authored this taxon.

We believe this taxon should be treated as a species distinct from *D. kruiense* J.J. Sm. It differs from *D. kruiense* in its pure white sepals and petals, white lip with a strong

medial yellow patch, abbreviated retrorse basal spine of the lip, the main medial callus only shallowly sulcate on the lower half of the disc (but convex in its upper part), and the elliptic stigmatic cavity. In *D. kruiense* the sepals and petals are white with a pink blush (this sometimes restricted to the basal parts), the lip is white, sometimes with pink markings

near the apex or on the lower part of the medial callus (but never with a strong yellow patch), the basal retrorse spine of the lip is prominent and thorn-like, the main medial callus is strongly sulcate throughout its length, and the stigmatic cavity is subquadrate.

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TWO NEW SPECIES OF MYRTACEAE FROM THE SÁPARA TERRITORY IN THE ECUADORIAN AMAZON

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ROY H. J. ERKENS,^{6,7} AND THOMAS L. P. COUVREUR⁸

Abstract. Two new species of Myrtaceae, *Eugenia saparensis* and *Plinia oblongifolia*, from the remote Sápara territory in the Amazonian province of Pastaza in Ecuador are described and illustrated. A distribution map is provided, their morphological relationships to the putative closest species in these genera are discussed and a preliminary conservation status of Data Deficient (DD) is assigned for each species.

Keywords: Amazonia, Conservation, Ecuador, *Eugenia*, *Plinia*, Pastaza, Sápara, Taxonomy

Resumen. Dos nuevas especies de Myrtaceae, *Eugenia saparensis* y *Plinia oblongifolia*, del remoto territorio Sápara en la provincia amazónica de Pastaza en Ecuador son descritas e ilustradas. Se presenta un mapa de distribución, se discuten sus relaciones morfológicas con las especies más cercanas en cada género y el estado de conservación de Datos Insuficientes (DD) es asignado para cada especie.

Palabras claves: Amazonia, Conservación, Ecuador, *Eugenia*, *Plinia*, Pastaza, Sápara, Taxonomía

Myrtaceae (Myrtales) are a diverse tropical and subtropical family with numerous economically and ecologically important species. In Ecuador, it is represented by 15 genera and more than 130 species (Kawasaki et al. 2019); *Eugenia* is the largest genus in the country, with ca. 50 species and *Plinia* is represented by at least five species. Within the study of the Myrtaceae for the Flora of Ecuador, several new species of both genera were described (Kawasaki et al. 2019; Kawasaki and Pérez, 2012, 2016; Kawasaki and Holst, 2009a, 2009b; Holst and Kawasaki, 2006).

Two additional new species of *Eugenia* and *Plinia* are here described and illustrated; they were collected during a botanical expedition to the Sápara Nation in the Pastaza province, more specifically the Balsaura community, along the Pintuyacu river. These new species honor the Sápara nationality, which is under threat by the loss of their language and traditions. Indeed, this nationality used to have a much larger distribution across the Ecuadorian Amazon into neighboring Peru, covering 380000 ha, but has severely declined in population since the seventeenth century (Bilhaut, 2011). In recognition of the Sápara oral

and cultural traditions, the United Nations Educational, Scientific, and Cultural Organization (UNESCO) declared in 2001 for them to be an “Intangible Cultural Heritage of Humanity” (Bilhaut, 2011). The Nacionalidad Sápara del Ecuador (NASE) recently published their “Model of Territorial Management and Governance” called “Rapaka Nakujinia” or “Forest for Living Well” (Nacionalidad Sápara del Ecuador [NASE], 2024), where they call for increased collaboration with universities and research organizations to conduct studies on the biodiversity (flora and fauna) of the Sápara territory. With the discovery of these two new species of Myrtaceae we encourage more conservation research and biodiversity related co-exploration of this fascinating territory and culture.

Eugenia saparensis Á.J. Pérez, M.L. Kawas. & B. Holst, *sp. nov.* TYPE: ECUADOR. Pastaza: Cantón Pastaza, Parroquia Río Tigre, Comunidad Sápara de Balsaura, Río Pintuyacu, sendero Uksha Ñambi, 01°56'44"S, 76°18'25"W, 180–220 m, 22 September 2022 (fl), Á.J. Pérez, J.N. Zapata, R.H.J. Erkens & T.L.P. Couvreur 11882 (Holotype: QCA-251802; Isotypes: F, LOJA, QCNE). Fig. 1.

We thank the curators and staff of F, QCA, SEL, and VT for their support with this study and Weston Testo for help with the manuscript. We thank the Nacionalidad Sápara del Ecuador (NASE) for granting us permission to work in their territory, and Cesario Santi for his help organizing the field expedition. We are also grateful to the people from the Balsaura Community, in Pastaza Province, for their hospitality and friendship. Results presented here were funded by the European Research Council (ERC) under the European Union’s Horizon 2020 research and innovation program (grant agreement no. 865787). Ministerio del Ambiente, Agua y Transición Ecológica del Ecuador issued a permit under number MAE-ARSFC-2022-2237 and MAATE-ARSFC-2024-0434.

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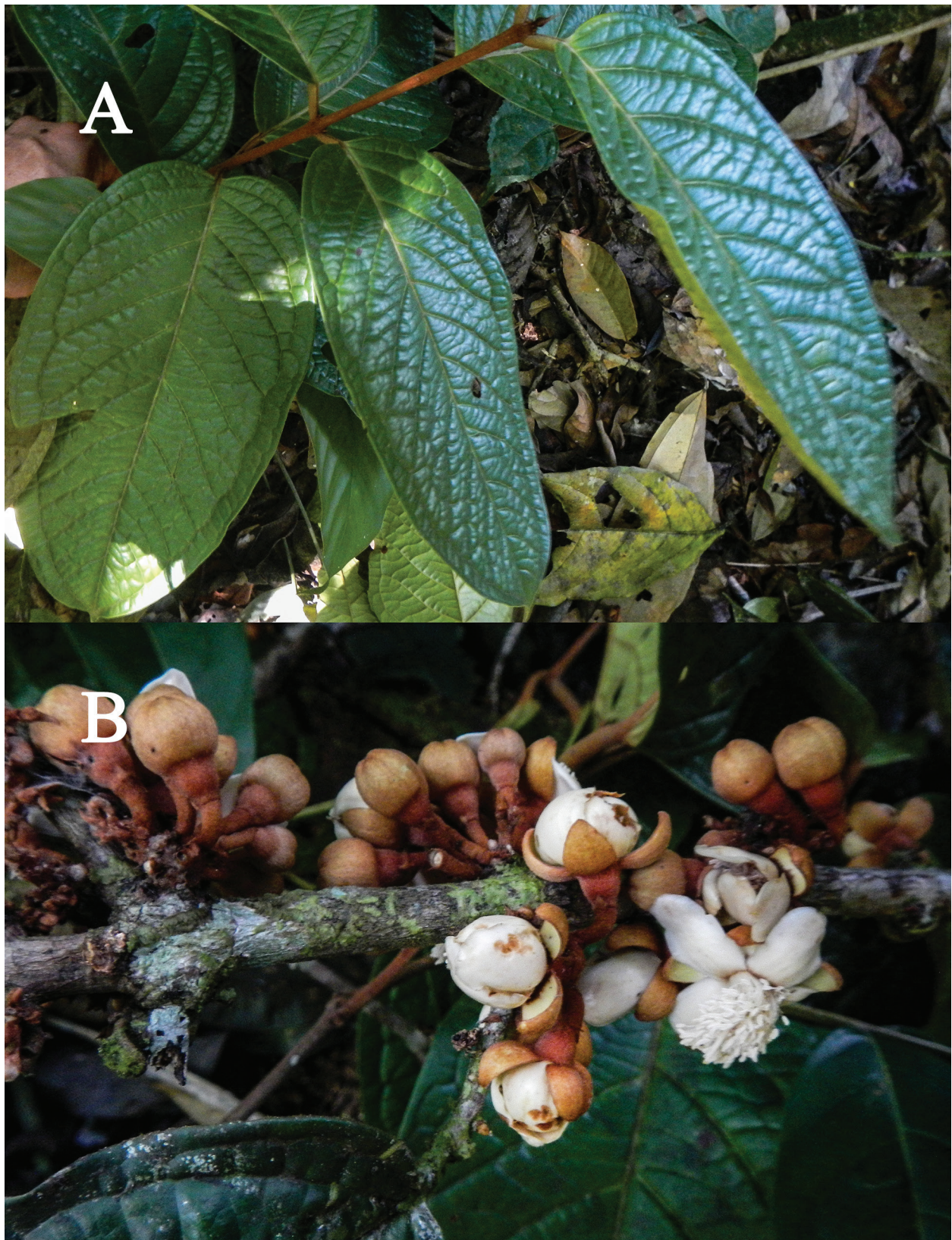


FIGURE 1. *Eugenia saparensis* Á.J. Pérez, M.L. Kavas. & B. Holst. **A**, Branchlet with leaves; **B**, Inflorescences. A, B from Pérez *et al.* 11882 (QCA). For measurements see description. Photographs by Á. J. Pérez.

This new species is similar to *Eugenia feijoi* O. Berg and *E. schunkei* McVaugh in the morphology of the inflorescences and flowers, but it is distinguished by the bullate leaves.

Trees ca. 25 m high, 25–40 cm dbh; trichomes reddish to yellowish-brown on branchlets, leaves and inflorescences. *Leaves* opposite; petioles 1–1.5 cm long, pubescent; leaf blades broadly elliptic to elliptic or ovate, 14–18 × 7–9.5 cm, coriaceous and bullate, drying greenish-brown to dark-brown on the upper surface, paler on the lower surface, puberulous to glabrous above, sparsely appressed-pubescent below, the trichomes especially evident near the veins; glands punctiform, indistinct above, dark and salient below; midvein narrowly convex above, convex below; lateral veins 8–12 pairs, strongly impressed above, convex below; marginal veins 2, the innermost 5–8 mm from margin; apex abruptly acuminate, the acumen 1–1.5 cm long; base obtuse. *Inflorescences* on leafless branchlets, of abbreviated racemes, the flowers appearing fasciculate, densely pubescent, the pedicels 5–10 mm long; bracteoles borne at the base of the ovary, ovate, 1–2 mm long. *Flowers* 4-merous; buds pyriform or obovoid, ca. 1 cm long; calyx lobes oblong to lanceolate, ca. 6–9 × 3–5 mm, obtuse, the margins connate for most of their length, cucullate at anthesis; petals white, ca. 1 cm long, obtuse, ciliate; disk ca. 4 mm diam, densely pubescent; stamens numerous, white, the filaments to 1 cm long, the anthers linear, grayish when dry, ca. 2 mm long; style ca. 1 cm long, the stigma punctiform; ovary 2-locular, with several ovules per locule. *Fruits* not known.

The new species *Eugenia saparensis*, *E. feijoi* O. Berg (a species from Colombia, Venezuela, French Guiana, Amazonian Brazil, Peru, Bolivia, and Ecuador), and *E. schunkei* McVaugh (known from Peru and Ecuador) share the following characteristics: the racemes are abbreviated, appearing fasciculate, with reddish to yellowish brown trichomes; the flowers have lanceolate or oblong, cucullate calyx lobes that are partially to nearly completely connate in bud, with grayish when dry, linear anthers; the midvein of leaves are narrowly convex on the upper surface. *Eugenia saparensis*, however, is distinguished by the elliptic leaves that are conspicuously bullate in the field, the secondary leaf venation appearing strongly sulcate on the upper surface in dried material (vs. lateral leaf venation plane to salient, leaves most narrowly elliptic or oblong-lanceolate in *E. feijoi* and *E. schunkei*).

Among the species of *Eugenia* in Ecuador, *Eugenia bullatifolia* M.L. Kawas. & Á.J. Pérez (known only from Orellana Province) also has bullate leaves, but the flowers are in irregular racemes, with yellowish white trichomes.

Etymology: The specific epithet honors the Sápara nationality that inhabits the Ecuadorian and Peruvian Amazon. In 2001, the Sápara's oral and cultural traditions were declared an "Intangible Cultural Heritage of Humanity" by the United Nations Educational, Scientific, and Cultural Organization (UNESCO) (Bilhaut, 2011).

Distribution and habitat: The species is known thus far only from the type locality, a hilly terra firme forest around the Balsaura community, to the right side downstream the

Pintuyacu river, in the Pastaza Province (Fig. 2). According to the Ministerio del Ambiente del Ecuador (2013), this area lies in the Tigre-Pastaza lowland evergreen forest (BsTa03). Field observations indicate that *Eugenia saparensis* co-occurs with the following tree species: *Guatteria ucayalina* Huber (Annonaceae), *Iriartea deltoidea* Ruiz & Pav. and *Wettinia maynensis* Spruce (Arecaceae), *Magnolia equatorialis* A. Vázquez (Magnoliaceae), and *Roucheria* sp. (Linaceae). This locality is ca. 15 km from the Peruvian border, and the forest cover is continuous; for that reason, *E. saparensis* could be present in Peru.

Phenology: Collected with flowers in September and possibly fruiting in January.

Preliminary IUCN conservation status: This species is only known from the type locality and a single individual. The forest cover is well preserved and extends from the Corrientes and Pintuyacu river into Peru (Fig. 2). There is no evidence of any threats. Since there is a lack of data and its population size is unknown, we suggest that this species be assessed as Data Deficient (DD).

Plinia oblongifolia Á.J. Pérez, M.L. Kawas. & B. Holst, *sp. nov.* TYPE: ECUADOR. Pastaza: Cantón Pastaza, Parroquia Río Tigre, Comunidad Sápara de Balsaura, Río Pintuyacu, 10 min aguas abajo, sendero en tierra firme, lado izquierdo del río, 01°57'08"S, 76°16'28"W, 180–220 m, 24 September 2022 (fr), Á.J. Pérez, J.N. Zapata, R.H.J. Erkens & T.L.P. Couvreur 11888 (Holotype: QCA-251803; Isotypes: F, QCNE, VT). Fig. 3.

Plinia oblongifolia differs from *P. yasuniana* M.L. Kawas. & Á.J. Pérez in the habit (trees ca. 22 m high vs. shrubs 1–3 m high), in the narrow leaves, ca. 6–8 times longer than wide (vs. ca. 3.5–5 times longer than wide) and in the glabrescent (vs. puberulous) fruits.

Trees ca. 22 m high, 20–30 cm dbh, puberulous, the trichomes yellowish white, mostly on young branches. *Bark* grayish, smooth, peeling in plates of different sizes. *Leaves* opposite or verticillate; petioles to 7 mm long, terete, puberulous; leaf blades narrowly oblong or narrowly oblanceolate, coriaceous, 25–38 × 3–6 cm, the upper surface mostly glabrous except for a few trichomes especially on the veins, drying olive-green to greenish brown, the lower surface paler, pubescent, the trichomes densely on the veins; glands numerous, punctiform, indistinct above, salient below; midvein sulcate on upper surface, salient on lower surfaces; lateral veins 16–25 pairs, sulcate above, salient below; marginal vein 1, almost parallel to the margin, ca. 4 mm from it, similar to the lateral veins in prominence; apex abruptly acuminate; base subcordate to truncate. *Inflorescences* ramiflorous, of glomerules; bracts and bracteoles in several pairs, lanceolate, 3–7 mm long, puberulous. *Flower buds* not seen; calyx lobes irregularly shaped, with conspicuous glands, puberulous without, glabrous within; petals, stamens, and style not seen. *Fruits* immature, globose, 1.7–5 cm diam, green when immature, glabrescent, crowned by remnants of the calyx lobes; seed 1, the seed coat membranous; embryo eugenoid, the cotyledons fleshy, connate, the radicle indistinct.

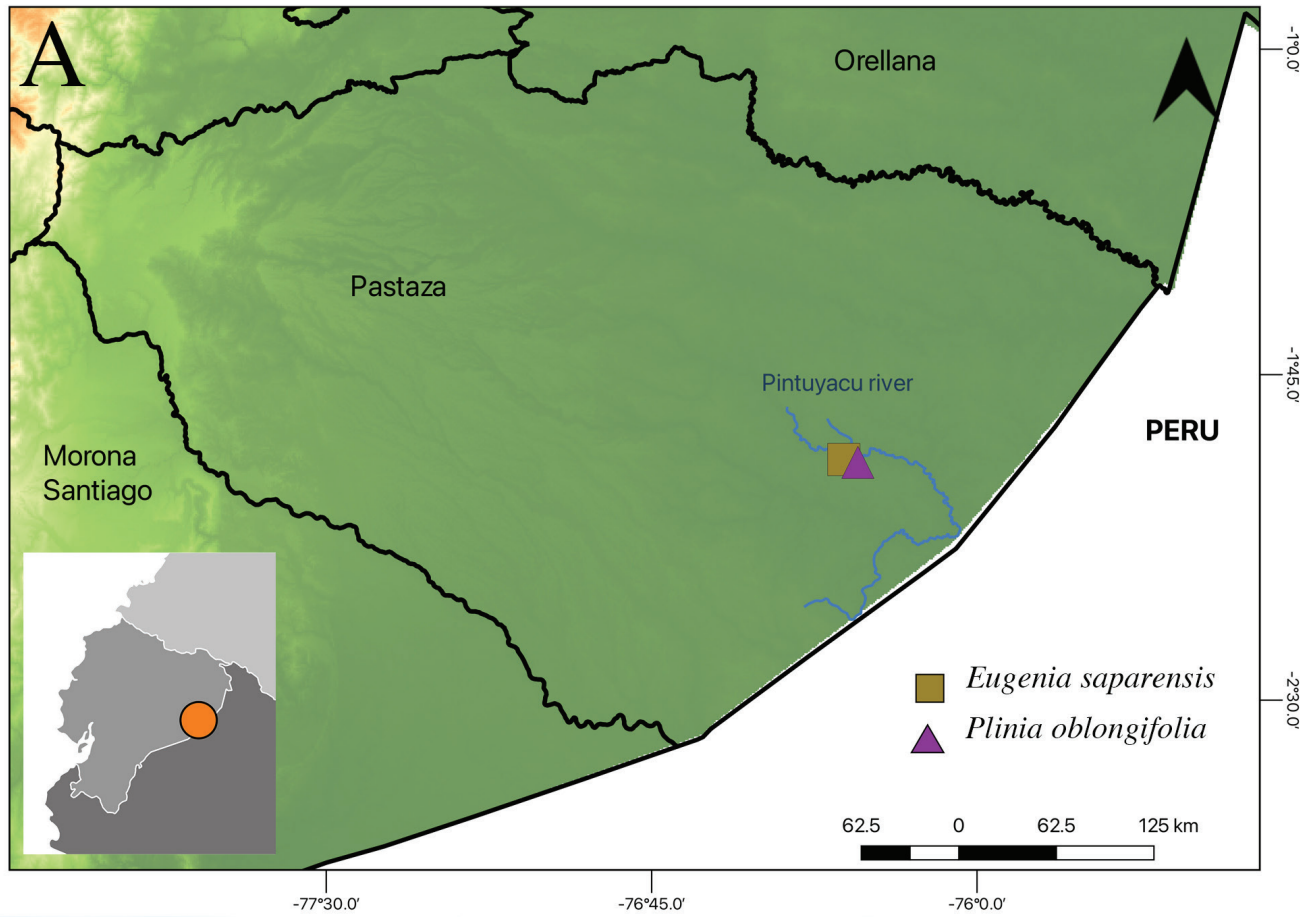


FIGURE 2. **A**, Location of *Eugenia saparensis* and *Plinia oblongifolia* in Pastaza province; **B**, Aerial view of the forest cover around the Balsaura Community. Photograph by T. L. P. Couvreur.

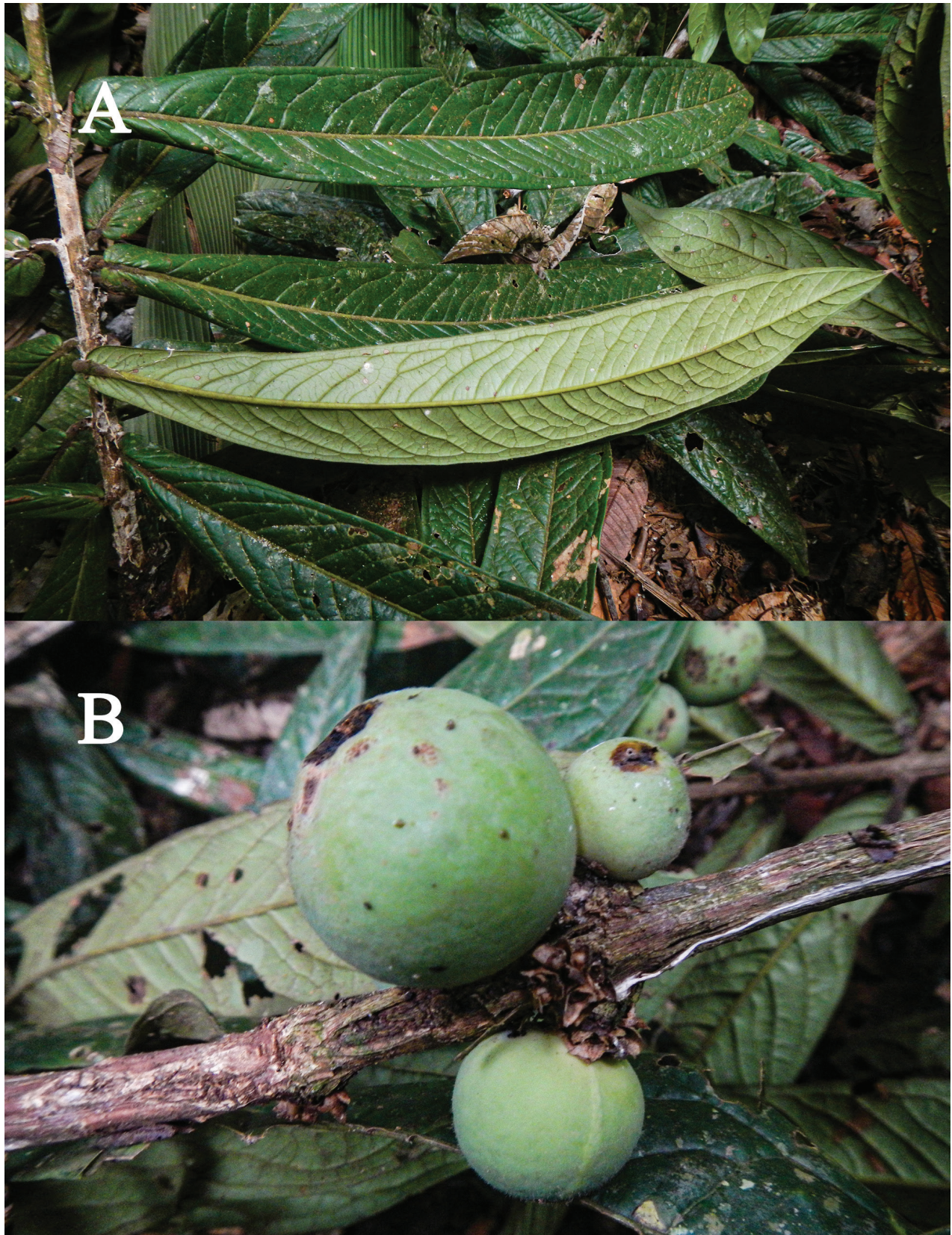


FIGURE 3. *Plinia oblongifolia* Á.J. Pérez, M.L. Kawas. & B. Holst. A, Leaves; B, Fruits. A, B from Pérez *et al.* 11888 (QCA). For measurements see description. Photographs by Á. J. Pérez.

Plinia oblongifolia is characterized by the combination of these features: trees with large, narrowly oblong or narrowly oblanceolate leaves, opposite or verticillate, 25–38 × 3–6 cm, ca. 6–8 times longer than wide, and glabrescent fruits. In leaf morphology, it resembles *Plinia yasuniana* M.L. Kawas. & Á.J. Pérez, a species known from Sucumbíos and Orellana Provinces in Ecuador, possibly also occurring in Peru; this species, however, is a shrub 1–3 m high (versus ca. 22 m), the leaves are narrowly elliptic or oblanceolate, 28–32 × 5.5–8.5 cm, ca. 3.5–5 times longer than wide, and the fruits are puberulous.

Etymology: The specific epithet denotes the commonly oblong leaf blades.

Distribution and habitat: The species is known thus far only from the type locality, a hilly terra firme forest around the Balsaura community, to the left side downstream the Pintuyacu river, in the Pastaza Province (Fig. 2). According to the Ministerio del Ambiente del Ecuador (2013), this area lies in the Tigre-Pastaza lowland evergreen forest

(BsTa03). Field observations indicate that *P. oblongifolia* co-occurs with the following tree species: *Iriartea deltoidea* Ruiz & Pav. and *Wettinia maynensis* Spruce (Arecaceae), *Magnolia equatorialis* A.Vázquez (Magnoliaceae), *Roucheria* sp. (Linaceae), and *Virola elongata* (Benth.) Warb. (Myristicaceae). This locality is ca. 15 km from the Peruvian border and the forest cover is continuous so *P. oblongifolia* might also occur in Peru.

Phenology: Collected with fruits in September and probably flowering during June to August.

Preliminary IUCN conservation status: As with *Eugenia saparensis*, this new species is only known from the type locality and a single individual. Its population size is unknown. There is no evidence of any threat, with a forest cover well preserved and expanding from the Corrientes and Pintuyacu river to Peru (Fig. 2); for these reasons, we suggest assigning it a preliminary conservation status of Data Deficient (DD).

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A RARE AND EXTRAORDINARY NEW SPECIES OF *TRICHOPILIA* FROM COSTA RICA

FRANCO PUPULIN^{1,2,3,4} AND ADAM P. KARREMANS¹

Abstract. A new species belonging to the popular orchid genus *Trichopilia* is described from southern Costa Rica. *Trichopilia gustavoi* appears to be rare, and is known only from the type locality, a pristine forest in Finca Las Alturas de Cotón on the outskirts of La Amistad National Park, close to the border between Costa Rica and Panama. The new species is vegetatively similar to *T. marginata*, but is unusual in the petals that are falcate, a lip that is boat-shaped, with a tuft of scattered, low verrucae in the center of the disc, and a column that is distinctly sigmoid. The extraordinary *T. gustavoi* honors the rector of the University of Costa Rica, Gustavo Gutiérrez Espeleta, for his support of biological research and conservation of Costa Rican biodiversity.

Keywords: flora of Costa Rica, new species, Orchidaceae, *Trichopilia*

Flowers of *Trichopilia* Lindl. are among the more showy orchids in Costa Rica. Their large colorful flowers are very appealing, and they have important cultural significance. Species belonging to the genus are highly valued by Costa Ricans, who refer to them as “tricopilia.” These orchids are often found cultivated in gardens and depicted in paintings and on stamps. Their beauty and exotic fragrance is spoken of in popular books, and they are even alluded to in the names of typical local sweets.

The genus currently includes about 30 epiphytic species occurring from Mexico to Brazil, with one species found in the Antilles. They can be found growing in pristine, mature forests on the trunks and large branches of trees. Species of *Trichopilia* are distinguished by their compact, caespitose habit with notoriously narrow, flattened pseudobulbs bearing a single apical leaf. The inflorescence is borne at the base, and may bear a single large flower or a few simultaneous, large flowers, that are sometimes fragrant. The column is elongate, often fused partially to the lip, and bears a lacerate clinandrium (Pupulin, 2022).

Costa Rica is one of the major centers of diversity for *Trichopilia* (Pupulin, 2022). The catalogue of Costa Rican orchids (Pupulin, 2002) accounted for six species and one natural hybrid, while Pupulin et al. (2023) recorded 12 species and one natural hybrid. In just two decades the number of recognized species in the genus has doubled in the

country, and this certainly speaks to the challenge of correctly determining herbarium specimens due to poorly preserved flowers (Dressler and Pupulin, 2005) and the amount of cryptic diversity that requires careful study in our region (Dressler and Pupulin, 2006; Dressler and Bogarín, 2009). It also speaks to the natural rarity of certain taxa, resulting in novelties even in large-flowered, botanically well-sampled, previously monographed genera (Bogarín, 2011).

Cryptic diversity can greatly impact studies on speciation, diversification processes, ecosystem development, and conservation priorities, and, as such, the underestimation of neotropical orchid diversity is a concern (Karremans, 2021). Just recently, Pupulin et al. (2023) predicted that, despite centuries of botanical collection and inventorying, novelties in the orchid flora of Costa Rica are likely to be found in the near future. Indeed, this has been the case, and several new orchid species have already been published since, but who would have suspected one of those novelties would be in the charismatic genus *Trichopilia*? Although unexpected, Pupulin and Karremans (2017) point out that the Costa Rican orchid flora still reveals striking novelties because of the natural rarity and restricted distribution of certain plants. Undetermined *Trichopilia* specimens recently discovered in a pristine privately conserved forest in Finca Las Alturas de Cotón on the Costa Rica-Panama border represent a most extraordinary example.

TAXONOMY

Trichopilia gustavoi Pupulin & Karremans, *sp. nov.* Fig. 1–3.

TYPE: COSTA RICA. Puntarenas: Coto Brus, Pittier, Cedro Norte, entrada noroeste de Finca Las Alturas, 9°00'00.50"N, 82°54'11.30"W, 1715 m, Zona Protectora Las Tablas, Finca Las Alturas, sector Cedro Norte, a la orilla del sendero, bosque muy húmedo montano bajo, epífita, 20 noviembre 2023, preparado 2 agosto 2024, I. F. Chinchilla, A. P. Karremans, & G. Rojas-Alvarado 5711 (Holotype: JBL, spirit).

Species Trichopilia marginata Henfr. *affinis*, *petalis falcatis vel subsigmoideis*, *labello naviculare subrectangularis vel anguste ovato*, *auriculis retrorsis ellipticis parvis in base munito*, *verrucis diminutis in disco ornato*, *columna sigmoidea plerumque recedit*.

An epiphytic, caespitose, erect *herb* to 35 cm tall. *Roots* slender, flexuous, branching, to 2.5 mm in diameter. *Pseudobulbs* linear, laterally flattened, subancipitous, 8.0–11.0 × 0.8–1.4 cm, base covered by 3–4 triangular,

We are extremely grateful to Lourdes Martínez Estévez and Fernando Castañeda from Finca Las Alturas de Cotón for allowing us to conduct research at the private reserve. We thank the vice presidency of research of the University of Costa Rica for funding our study. Permits were issued by the Costa Rican Ministry of Environment and Energy (MINAE) and its National System of Conservation Areas (SINAC).

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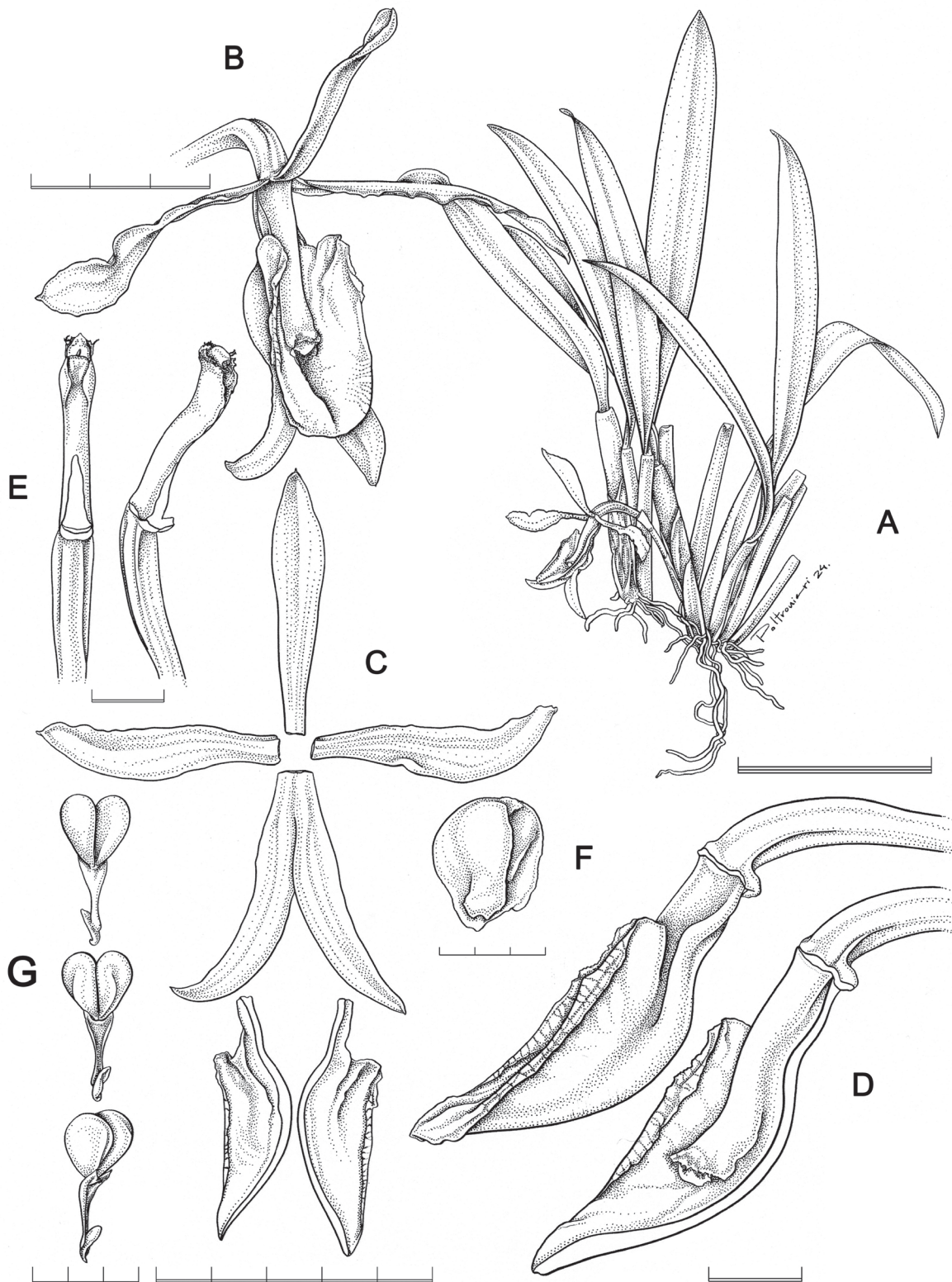


FIGURE 1. *Trichopilia gustavoi* Pupulin & Karremans. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, ovary, column and lip, side view and longitudinal section; **E**, column, side and ventral views; **F**, anther cap side view; **G**, pollinarium dorsal, side and ventral views. Scale bars: simple bar = mm; double bar = cm; triple bar = dm. Drawn by Sara Poltronieri from the holotype.

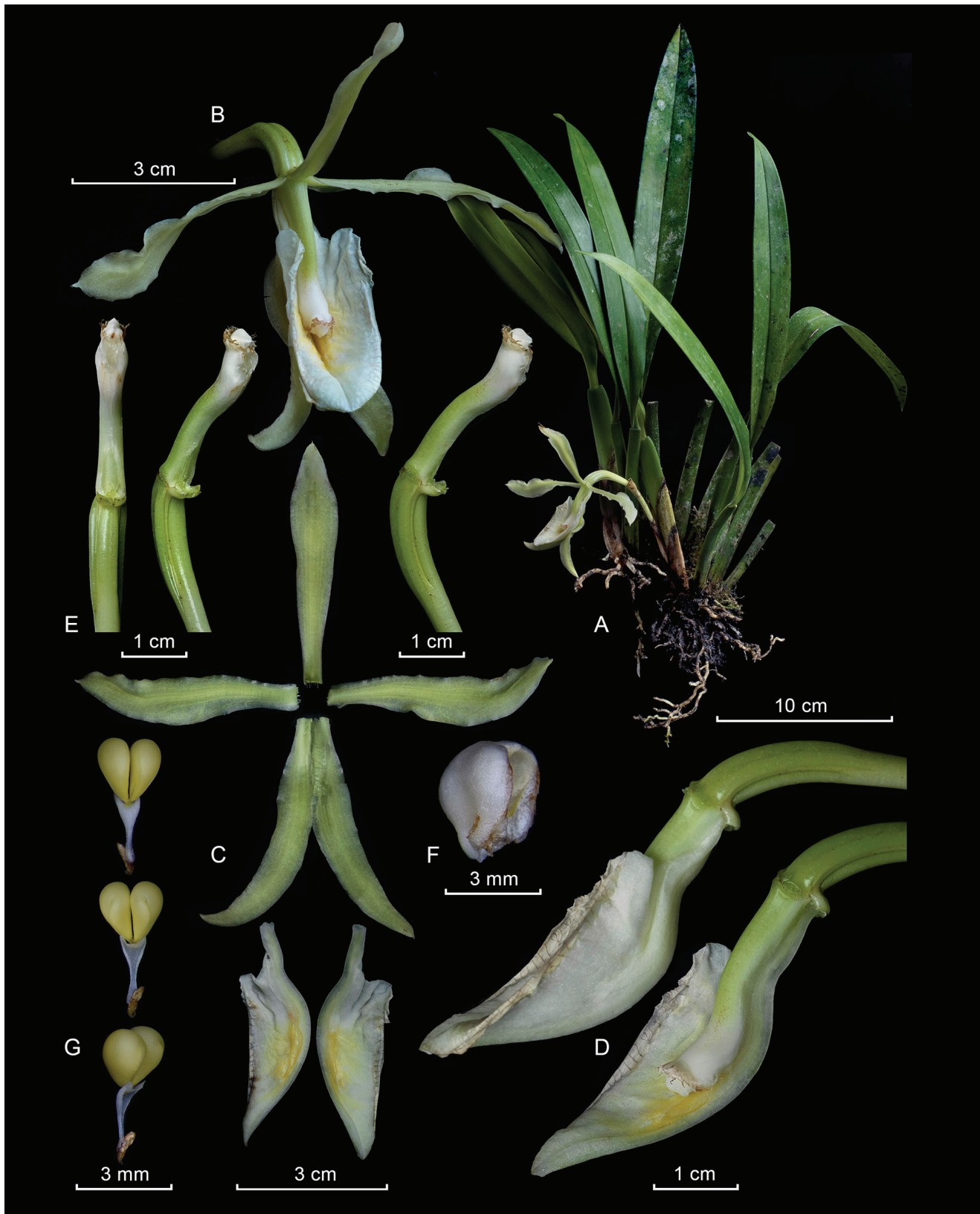


FIGURE 2. Lankester Composite Digital Plate of *Trichopilia gustavoi* Pupulin & Karremans. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, ovary, column and lip, side view and longitudinal section; **E**, column, ventral and lateral views; **F**, anther cap side view; **G**, pollinarium dorsal, ventral and side views. Photographs by FP based on *Chinchilla et al. 5711*.

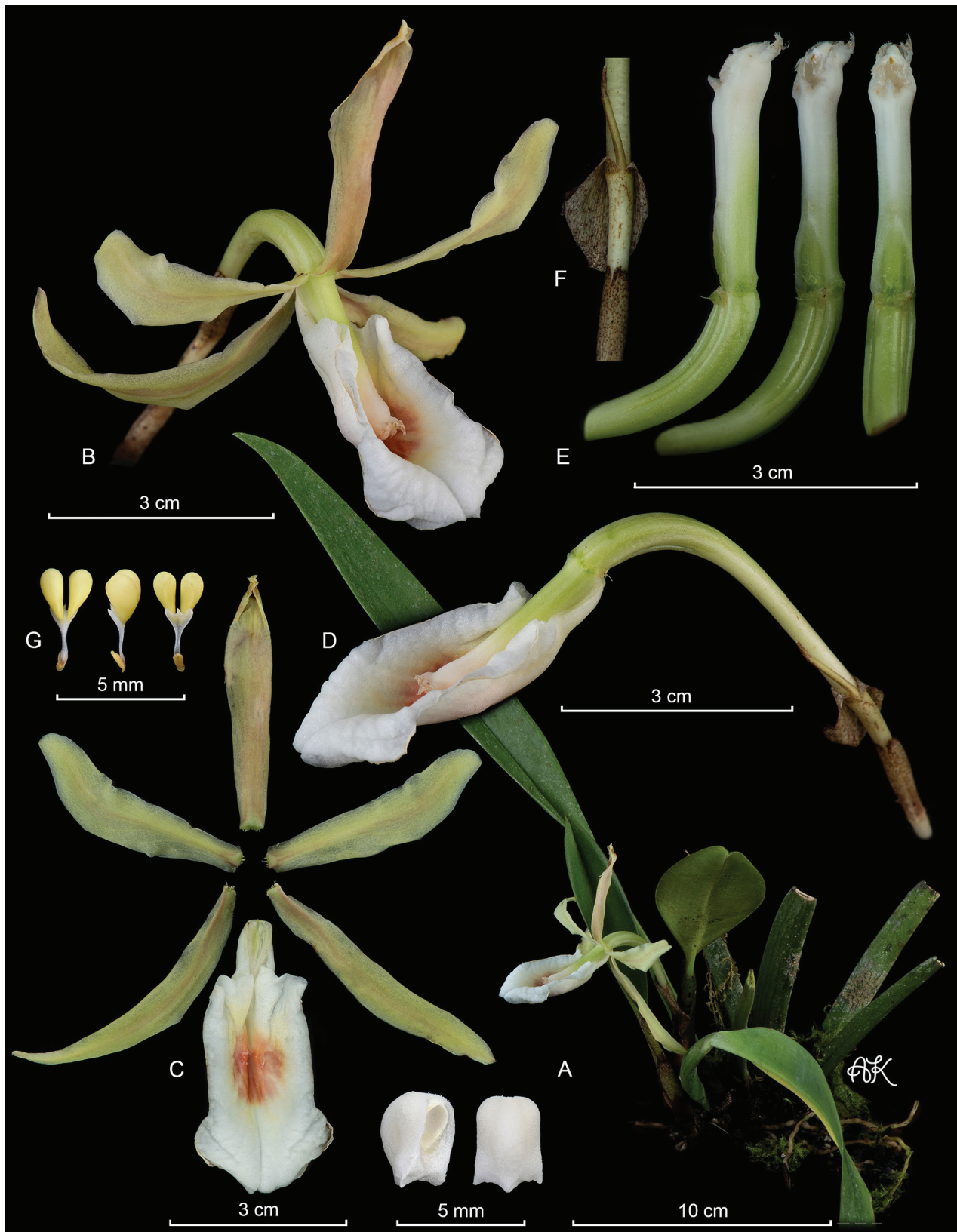


FIGURE 3. Lankester Composite Digital Plate of *Trichopilia gustavoi* Pupulin & Karremans. A, habit; B, flower; C, dissected perianth; D, ovary, column and lip, lateral view; E, column, lateral and ventral views; F, vestige of the racemose inflorescence; G, anther cap side and dorsal views; H, pollinarium dorsal, side and ventral views. Photographs by AK based on Karremans *et al.* 9598.

acute, tightly clasping, ancipitous, thinly fibrous, brown-papyraceous sheaths $2.3\text{--}6.0 \times 1.8\text{--}3.0$ cm, eventually disintegrating with age, monophyllous. *Leaf* erect, elliptic to narrowly elliptic, acute, provided with a minuscule abaxial apicule, $12.5\text{--}24.0 \times 2.2\text{--}4.0$ cm, gradually narrowed at the base into a conduplicate petiole ca. 1 cm long. *Inflorescence* a single-flowered, suberect raceme, 10–12 cm long, borne from the previous mature growth; peduncle terete, ca. 5 cm long, covered near the base by 2 amplectent, triangular, acuminate, apically diverging, fibrous bracts, 3.0×0.6 cm. *Floral bract* glumaceous, becoming thin-papyraceous with

age, oblong, acute to minutely acuminate, loose, 2.0×0.5 cm. *Pedicellate ovary* terete-clavate, curved towards the tip, 5 cm long, ovary strongly ribbed. *Flower* spreading, sepals and petals with undulate margins, greenish white, sometimes suffused with pale pink, lip white with a tuft of low papillae on the yellow or pink disk; column white from a greenish base, anther white. *Dorsal sepal* oblong, acute, conduplicate, slightly concave at the base, $4.2\text{--}4.5 \times 0.8\text{--}1.0$ cm. *Lateral sepals* ligular-falcate, acute, $4.8\text{--}5.5 \times 0.7$ cm, free or connate at the base for ca. 1.6 cm, apexes diverging. *Petals* oblong-falcate to subsigmoid, obtuse, minutely apiculate,

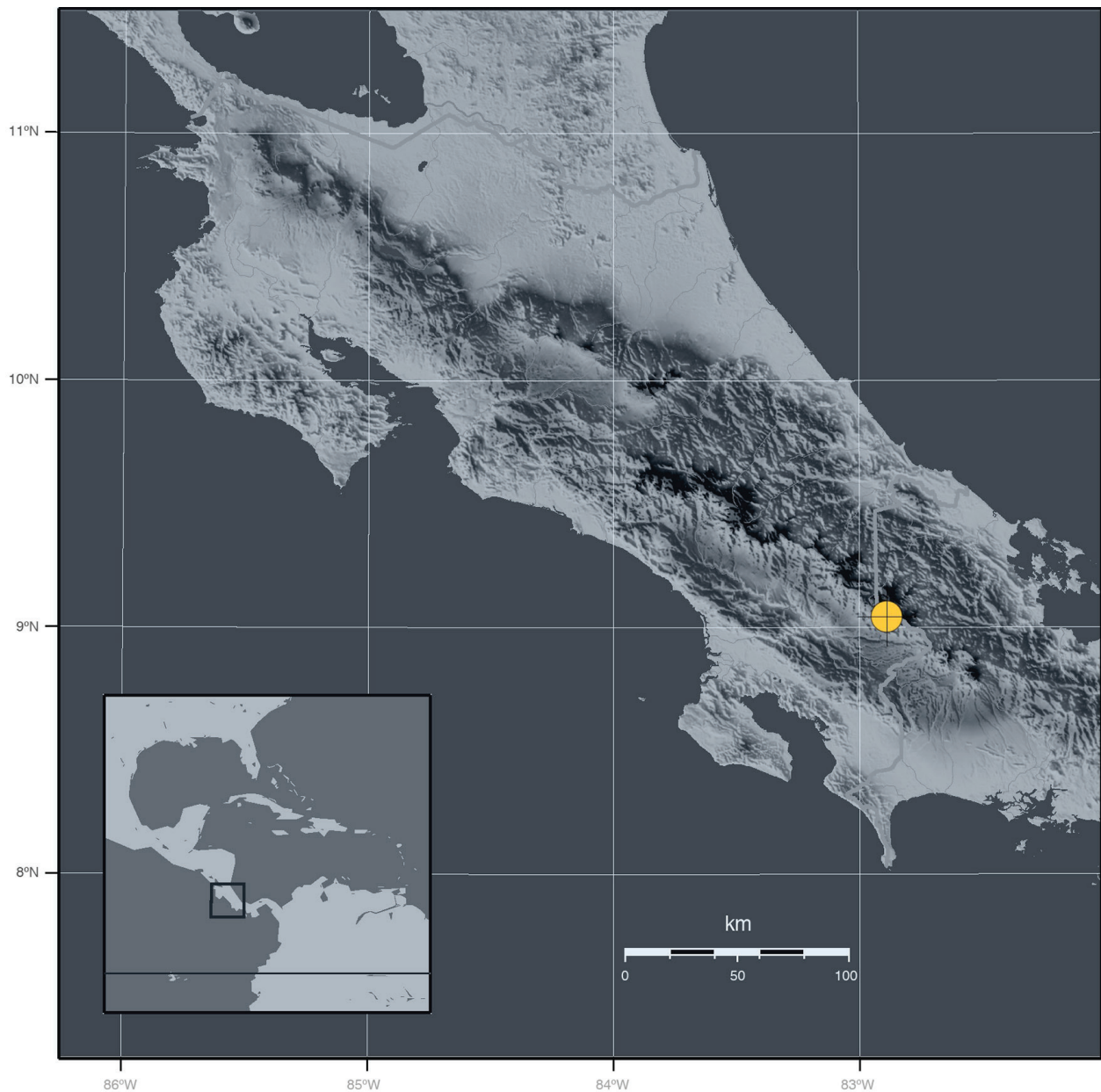


FIGURE 4. Distribution map of *Trichopilia gustavoi* Pupulin & Karremans.

4.0–4.6 × 0.9–1.0 cm, margins slightly wavy, particularly so the upper one and the base on the labellar margin. *Lip* deeply navicular, subrectangular to narrowly ovate in adaxial view, 4.4–4.6 × 1.9–2.3 cm when spread, blade provided with two small retrorse, narrowly elliptic auricles, ca. 3 × 5 mm, margins slightly undulate-reflexed, abruptly expanding from an obcuneate, narrow base 10 × 4 mm, the central portion of the disk with a few, small, low, rounded papillae. *Column* terete, distinctly sigmoid, slightly swollen at apex, 28 × 5 mm, basally fused with the lip for ca. 8 mm, provided with small, elliptic, irregularly dentate-lacerate, incurved stigmatic wings, clinandrium deeply concave, margins lacerate; anther incumbent, stigma recessed, obovate. *Anther cap* ovate-subrectangular, truncate, 2-celled. *Pollinia* 2, cleft, ovoid-pyriform, on a triangular, basally subcordate, apically rounded, hyaline stipe, affixed to a narrowly elliptic, brown viscidium. (Description based on the holotype and the specimen cited below as an additional specimen examined.)

Additional specimen examined: COSTA RICA. Puntarenas: Coto Brus, Pittier, Cedro Norte, entrada noroeste de Finca Las Alturas, 8°58'45"N, 82°54'30"W, 1350 m, epifitas al orillas de la trocha, bosque pluvial montano bajo-muy húmedo montano bajo, 20 noviembre 2023, preparado 2 agosto 2024, A. P. Karremans, I. F. Chinchilla, & G. Rojas-Alvarado 9598 (JBL, spirit). Fig. 3.

Eponymy: The name honors biologist and geneticist Gustavo Gutiérrez Espeleta, current Rector of the University of Costa Rica, for his painstaking support of biological research and conservation of Costa Rican biodiversity.

Distribution and habitat: The new species is currently known only from the type locality, a pristine forest in Finca Las Alturas de Cotón, a privately founded, protected area established for conservation purposes on the outskirts of La Amistad National Park, on the border between Costa Rica and Panama (Fig. 4).

As understood today, *Trichopilia* is a monophyletic group, which includes *Leucohyale* Klotzsch, *Helcia* Lindl.,

and *Pilumna* Lindl. Due to the lack of support for infra-generic relationship patterns in early molecular studies (Williams et al., 2001), Dressler and Klíkunas (2006) proposed a classification system using mainly characters of the pseudobulbs, leaves, and inflorescence. Section *Trichopilia*, typified by *T. tortillis* Lindl., is by far the most diverse group in the genus, with over 20 species and one nothospecies. Dressler and Klíkunas (2006) recognized two main alliances within this section: the *T. tortillis* alliance, characterized by a one-flowered inflorescence and a median groove on the lip; and the *T. suavis* alliance, with two to several flowers on each inflorescence and one to three keels running longitudinally on the lip blade. All of the species and nothospecies included in the former alliance—which is restricted in distribution to Mexico and Central America—have been recorded in Costa Rica, which is probably the main diversification center for the group. Species of the *T. tortillis* alliance typically have narrow and compressed pseudobulbs and a campanulate lip that from a narrow base forms a chamber around the apex of column.

Trichopilia gustavoi is most similar to *T. marginata* Henfr., and, vegetatively, is practically indistinguishable from the latter if not for the smaller size. The flower, however, is quite different and can be only approximately assigned to the *T. tortillis* alliance. In *T. gustavoi*, the petals are falcate and almost sigmoid (vs. straight) and the lip is boat-shaped (instead of infundibular). When spread, the lip of *T. gustavoi* is narrowly ovate to subrectangular, with two basal, retrorse auricles, while in *T. marginata* it is broadly obovate from a cuneate base, assuming a trumpet-shape in natural position. Furthermore, the groove on the midline of the lip is barely visible in *T. gustavoi*, and the basal osmophores are substituted by a tuft of scattered, low verrucae in the center of the disc. Finally, the column of *T. gustavoi* is distinctly sigmoid in lateral view (vs. straight), a feature that, together with the unusual indumentum of the lip, seems to suggest a different pollination syndrome.

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KEFERSTEINIA NOVA ISTHMII AMERICANI AUSTRALIS CUM GENERIS SYNOPSIS

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Abstract. A new species of *Kefersteinia* (Orchidaceae) from the southern region of the Central American isthmus is described and illustrated, and its affinities with *K. elegans* are discussed. In Panama, *Kefersteinia luteola* was previously misidentified as the Colombian *K. elegans*, but the new species appears to be restricted to the Cordillera de Guanacaste and Talamanca in Costa Rica and Panama. Among *Kefersteinia* species, *K. luteola* is distinguished by its small yellowish flowers, broadly extensively excised lip with a depressed laminate, trullate callus, and a column recognized by large, triangular, rounded wings with subciliate margins. The most similar species is *Kefersteinia elegans*, from which it differs in plant and flower size, with subringent sepals and petals, a sessile entire lip, and minutely glandular-ciliate wings of the column. A synopsis of the genus *Kefersteinia* is presented, and the species grouped according to their overall similarity.

Keywords: floristics, *Huntleya* clade, New Species, taxonomy, Zygopetalinae

Among the genera of Zygopetalinae (Orchidaceae) within the *Huntleya* clade (sensu Whitten et al., 2005), characterized by sympodial plants with shortened stems and leaves arranged fan-like, without pseudobulbs (or, in rare cases, rudimentary and concealed within basal leaf sheaths), *Kefersteinia* Rchb.f. stands out as the most diverse. With over 80 published names, likely corresponding to slightly more than 50 species, *Kefersteinia* generally comprises small epiphytic plants. These feature dark green, subcoriaceous-flexuous leaves, often with a prominent central vein on the abaxial side, and basal inflorescences that frequently produce numerous flowers opening simultaneously.

The inflorescence peduncle is typically slender, arching under the weight of the flower until the inflorescence becomes pendulous. Flowers are usually resupinate, except for *K. carolorum* Carnevali & Cetzal and *K. universitatis-tolimae* Sierra-Ariza. Given the very thin nature of the peduncle in species of *Kefersteinia*, which is always arched-pendent or completely pendent in natural conditions, it is possible that variations in the position of the flower may depend on the growing conditions of the studied specimens. *Kefersteinia carolorum* was described from a plant cultivated in pot (Carnevali et al., 2015), and the illustrations of *K. universitatis-tolimae* show a plant growing almost horizontally (Sierra-Ariza and Harding, 2023), a feature rarely seen in wild specimens of the genus. The non-resupinate condition of *Kefersteinia* flowers could perhaps be tested through controlled cultivation experiments to better evaluate the hypothesis that this feature is naturally inherent in these two aberrant species and to gain insight into a possible distinct pollination system in the genus.

Species of *Kefersteinia* range from southern Mexico to Bolivia (Pupulin, 2009), with notable presence in the Andes of Ecuador and Peru (over 30 recorded species) and the humid forests along the mountain chains of Costa Rica and Panama (twelve known species; Pupulin and Merino, 2008).

In the type species of the genus, *Kefersteinia graminea* Lindley, the lip lamina is broadly rounded, with a low-laminar callus typically restricted to the proximal third of the blade. About half of *Kefersteinia* species share this lip morphology, while others exhibit distinctly stalked or highly anomalous calli. However, the genus includes over 40 names that often refer to poorly characterized taxa, making identification challenging. Molecular evidence from Whitten et al. (2005) indicates that informal species groups based on callus structure are not monophyletic and lack formal taxonomic recognition.

Costa Rica hosts 12 *Kefersteinia* species, half described within the last 30 years, and two-thirds endemic to the country (Pupulin, 2001, 2010). Many species feature a prominent, fungus-like callus that forces visiting bees to twist their bodies while collecting floral fragrances, ensuring pollinaria attachment to the basal segment of an antenna (Pupulin, 2009). The function of the callus in species with low, laminar ornaments is less clear, though in some taxa, upturned basal callus margins are evident. It is possible that these species rely on a combination of the callus maintaining a longitudinal position and the column's prominent central keel, pressing against the scutellum, to direct the bee's movement and prevent lateral escape (see also discussion on putative pollination mechanisms in *Kefersteinia* by Carnevali et al. 2015).

We are grateful to the Costa Rican Ministry of Environment and Energy (MINAEC) and the National System of Conservation Areas (SINAC) for issuing the scientific permit "R-SINAC-SE-DT-PI-006-2023," which allowed us to collect the wild species studied. We also thank the Vice-Presidency of Research at the University of Costa Rica for providing support under the project "Inventario y taxonomía de la flora epífita de la región Mesoamericana" (814-A7-015). Additionally, we thank Karol Sandi for inking the illustration of the new species.

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Kefersteinia alba Schltr., *K. lactea* (Rchb.f.) Schltr., and *K. microcharis* Schltr. are among the Costa Rican species in this latter group. They are characterized by predominantly white flowers, occasionally with scattered magenta spots on the labellum's apical region, which abruptly folds downward in the middle, exposing the callus's apical and lower surfaces from the front (Pupulin, 2010). *Kefersteinia lactea* appears to exhibit two distinct vegetative forms: one with larger plants and obovate leaves, the other with smaller plants, narrow ligulate leaves, and typically smaller flowers. However, specific floral characteristics distinguishing these forms have not been definitively identified, warranting their treatment as variable (Pupulin, 2001, 2010).

TAXONOMIC TREATMENT

Kefersteinia luteola Pupulin, E. Salas, & Bogarín, *sp. nov.* TYPE: COSTA RICA. Guanacaste: Abangares, Sierra, Santa Elena Cloud Forest Reserve, close to Treetopia Park, 10°20'36"N, 84°47'40"W, 1710 m, premontane rain forest, epiphytic in mature forest, 1 May 2023, flowered in cultivation and prepared 16 Aug. 2023, A. P. Karremans 9383 & T. Vieira (holotype, JBL). Fig. 1–2.

Inter species generis Kefersteiniae callo laminato depresso in labello munitis floribus parvis luteolis callo late trullato exciso, columna alis magnis triangulis rotundatis marginibus subciliatis dignoscenda; a Kefersteinia eleganti Garay plus minusve similis, sed planta foribusque distincte minoribus, sepalis petalisque subbringentibus, labello sessile integro, alis columnae minute glandulari-ciliatis recedit.

A small, caespitose, epiphytic herb without pseudobulbs, to about 15 cm tall. Roots thick, flexuous, white with green apex, up to 2 mm in diameter. Stem abbreviated, completely enclosed by the fibrous, conduplicate leaf-sheaths up to 2.5 cm long, the lower ones triangular, glumaceous, becoming dry-papyraceous with age, the upper ones articulated with the foliaceous blades. Leaves 3–5, arranged like a fan, narrowly elliptic-oblong, acute to abruptly subacuminate, 5.5–14.0 × 1.3–1.7 cm, grass green, cuneate at the base into a short conduplicate petiole to 1 cm long, the midvein distinctly protruding abaxially. Inflorescence a single-flowered raceme, slender, born erect and becoming patent to pendent, ca. 3 cm long; peduncle terete, slender, provided in the middle with a short, triangular, glumaceous bract ca. 4 mm long. Floral bract glumaceous, double, outer bract transversely broadly ovate, obtuse, amplexant, loose, 5 × 2 mm; inner bractlet narrowly lanceolate-ligulate, acute, 7.5 × 1.5 mm. Pedicellate ovary terete subclavate, subsigmoid, green, 12 mm long including the pedicel. Flowers relatively small, subbringent, suberect to slightly pendulous, sepals and petals pale yellow, lip of the same color with a central band darker yellow, column yellowish cream, anther cap white. Dorsal sepal lanceolate, acute, 5-veined, reclinate over the column in natural position, 16 × 6 mm. Lateral sepals obliquely lanceolate-subfalcate, longitudinally asymmetrical, obtuse, minutely apiculate, 7-veined, 18 × 5 mm. Petals adnate to the side of the column, asymmetrically lanceolate, subfalcate toward the apex, acute to subacuminate, 5-veined, 17 × 7 mm. Lip sessile, broadly ovate, 18 × 18 mm, 11–13-veined, basal margins erect, then abruptly folded down to orientate the distal portion of the lamina vertically and leaving a

semicircular opening toward the column, apex of the blade excise, slightly reflexed, with crenulate to subundulate margins; callus laminar, low, thick, broadly trullate, excise-emarginate, from the base to about 2/5 of the lamina, 4 × 4 mm. Column semiterete, subrectangular, 10 mm long, 7.5 mm wide across the wings, with a short foot less than 2 mm long, provided at the middle with substigmatic, triangular, rounded wings with glandular-ciliate margins and a thin, short, high, rectangular-subrhombic keel just below the slit-like, transversal stigma; androclinium transversely elliptic, low; rostellum triangular, truncate. Anther cap cucullate, obovate pandurate, apically truncate, 2-celled. Pollinia 4, narrowly oblong, strongly dorsiventrally compressed-lenticular, in two superposed pairs of different size, on a large, hyaline, lanceolate-trullate stipe that strongly curls after removal; viscidium hyaline, transversely rectangular, ventral to the stipe and scarcely distinct from it.

During recent fieldwork in northern Costa Rica, along the Northern slopes of Cordillera de Tilarán, a *Kefersteinia* specimen was collected and subsequently cultivated in Lankester Botanical Garden's greenhouses until it flowered. Given that its floral characteristics do not align with any known *Kefersteinia* species, we hereby describe it as a new species to science.

semicircular opening toward the column, apex of the blade excise, slightly reflexed, with crenulate to subundulate margins; callus laminar, low, thick, broadly trullate, excise-emarginate, from the base to about 2/5 of the lamina, 4 × 4 mm. Column semiterete, subrectangular, 10 mm long, 7.5 mm wide across the wings, with a short foot less than 2 mm long, provided at the middle with substigmatic, triangular, rounded wings with glandular-ciliate margins and a thin, short, high, rectangular-subrhombic keel just below the slit-like, transversal stigma; androclinium transversely elliptic, low; rostellum triangular, truncate. Anther cap cucullate, obovate pandurate, apically truncate, 2-celled. Pollinia 4, narrowly oblong, strongly dorsiventrally compressed-lenticular, in two superposed pairs of different size, on a large, hyaline, lanceolate-trullate stipe that strongly curls after removal; viscidium hyaline, transversely rectangular, ventral to the stipe and scarcely distinct from it.

Etymology: From the Latin *luteus*, yellow, *luteolus*, yellowish, in reference to the color of the flowers.

Distribution: Known from Costa Rica and Panama (Fig. 3).

Habitat and ecology: Epiphytic in premontane rain forests, at 1700–1800 meters elevation. Flowered in cultivation in August.

Additional specimen examined: PANAMA. Bocas del Toro, without more specific locality, A. Olmos III, flowered at Finca Dracula and documented on 11 July 2001 (JBL, illustration: Gabinete de Diseños y Estampas FP3:1–2, 7–8).

Kefersteinia luteola is the depauperate counterpart of the Colombian *K. elegans* Garay, to which it bears a superficial resemblance. *Kefersteinia elegans* features larger, spreading flowers nearly 5 cm across its petals (Garay, 1969), reminiscent of the equally large *K. taurina* Rchb.f., one of the genus's largest-flowered species. Despite their similar flower size, these species are distantly related. In *Kefersteinia taurina*, the callus is stipitate, and the column is apterous and basally gibbous, whereas *K. elegans* features a laminar callus and a column distally adorned with prominent wings and a high, rectangular keel. In contrast, flowers of *K. luteola* are under 3 cm in diameter, with subbringent tepals. The lip is sessile, lacking the distinct, long, cuneate claw characteristic of *K. elegans*. The wings of the column in *K. luteola*, while prominent like those of *K. elegans*, are comparatively smaller, broadly triangular, and ciliate to minutely tuberculate along the margins.

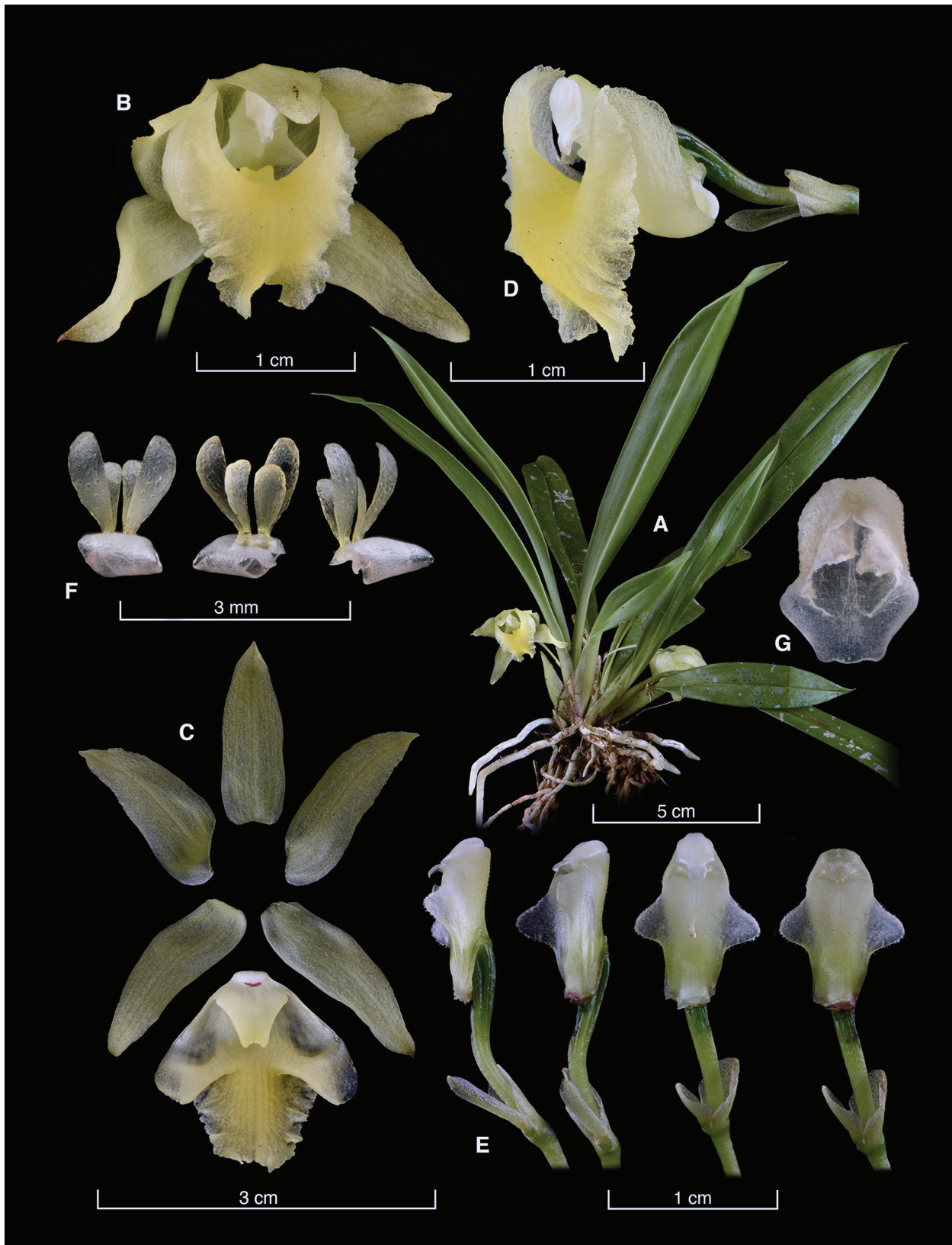


FIGURE 1. Lankester Composite Digital Plate of *Kefersteinia luteola* Pupulin, E. Salas, & Bogarín. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, several views; on the right, emasculate; **F**, pollinarium, dorsal, ventral, and three quarters views; **G**, anther cap. Photos and composition by F. Pupulin & D. Bogarín from *Karremans 9383*.

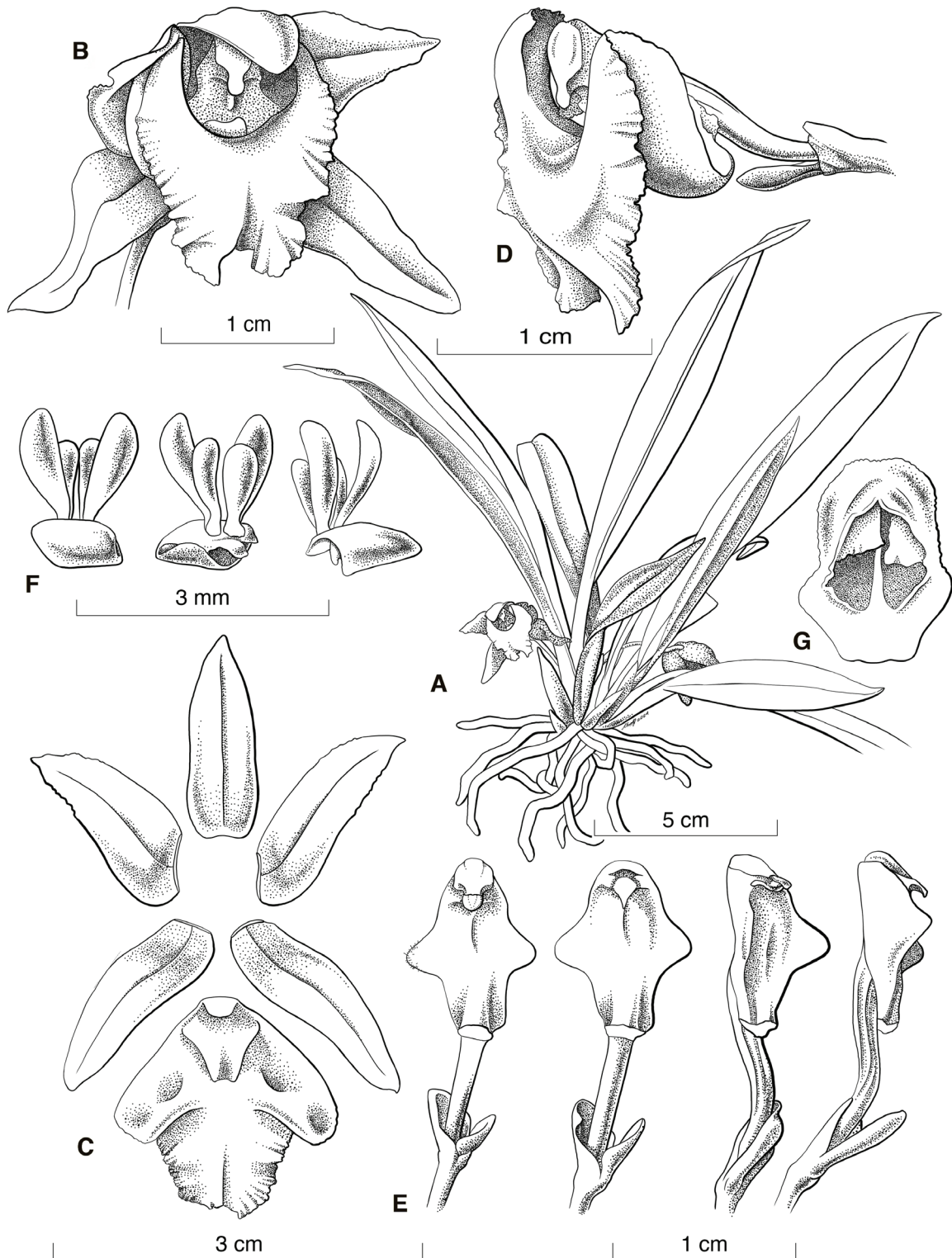


FIGURE 2. *Kefersteinia luteola* Pupulin, E. Salas, & Bogarín. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, lateral view; **E**, column, several views; on the right, emasculate; **F**, pollinarium, dorsal, ventral, and three quarters views; **G**, anther cap. Drawing by Karol Sandi, based on *Karremans* 9383.

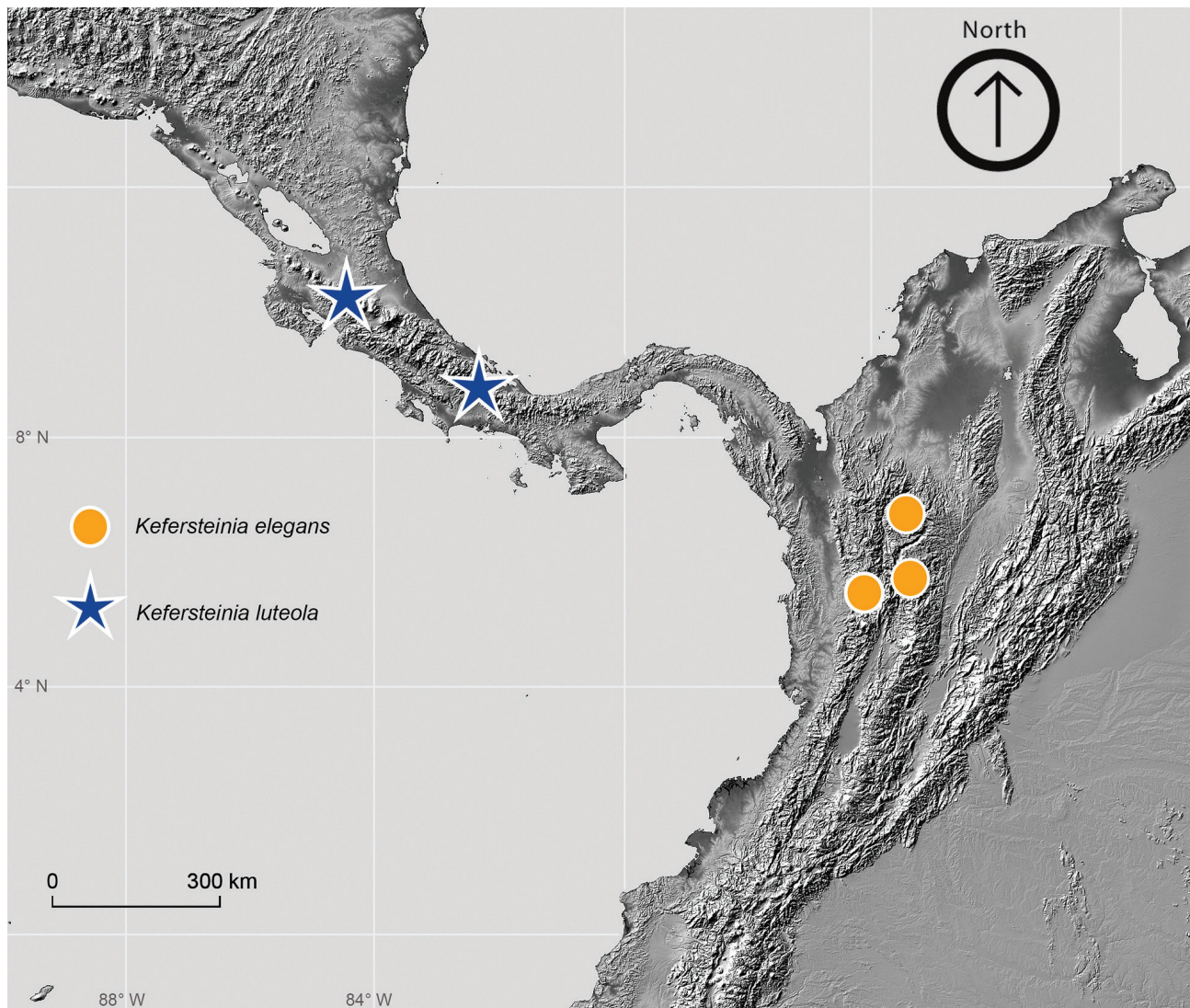


FIGURE 3. The known localities of *Kefersteinia luteola* (blue star) and *K. elegans* (yellow circle).

Kefersteinia elegans was described from a specimen collected by Gilberto Escobar in the Colombian Department of Antioquia, though the type (*G. Escobar 507*, AMES) lacks precise locality. The Missouri Botanical Garden database specifies its origin as the old colonial settlement of Abejorral (Tropicos, 2023), situated approximately 2200 m above sea level in the Central Cordillera, about 50 km south of Medellín. The few documented collections of *K. elegans* are restricted to Colombia (Fig. 3). Among Andean *Kefersteinia* species, *K. elegans* is distinguished by its large, yellowish flowers and distinct ligulate-elliptic wings of the column. Initially, only a photograph of the flower from the type was used for illustration, but a sketch by Leslie Garay attached to the holotype sheet at AMES (accession 090588, barcode 00100388) well illustrates the long, cuneate claw of the lip, with a sublobate blade at the middle, and the ligulate wings of the column.

Originally thought to be endemic to the Colombian Andes, *K. elegans* was later allegedly recorded and illustrated from Panama by Pupulin (2004), based on collections from Bocas del Toro by J. Núñez and E. Olmos,

cultivated at Finca Dracula in Cerro Punta, Panama (also cited by Dressler, 2023). Another herbarium collection at the Missouri Botanical Garden, likely from the same locality (*A. Maduro & E. Olmos 156*, not seen), is mentioned by Bogarín et al. (2014) in their updated checklist of Panamanian Orchidaceae, and by Dressler (2023) in his treatment of *Kefersteinia* for *Flora Mesoamericana*. Although Harding (2008) mentioned the presence of *K. elegans* in Panama, no herbarium voucher supports her claim.

Recent findings confirm that collections from Bocas del Toro, Panama, previously attributed to *K. elegans*, actually represent *K. luteola* (Fig. 4), expanding its known range to the southern Cordillera de Talamanca in Panama. *Kefersteinia luteola* exhibits smaller plants (up to 15 vs. 20 cm), leaves (up to 14.0×1.7 vs. 20×3 cm), inflorescences (3 vs. 5 cm), and flowers. The sepals measure 15–18 mm in *K. luteola* vs. 20–28 mm in *K. elegans*; petals are 17 vs. 23 mm long. The lip of *K. luteola* is sessile (vs. clawed), entire (vs. sublobed), measuring 18×18 mm (vs. 23×20 mm in *K. elegans*), and the column's wings are broadly triangular (vs. ligulate-elliptic) and glandular-ciliate (vs. entire).

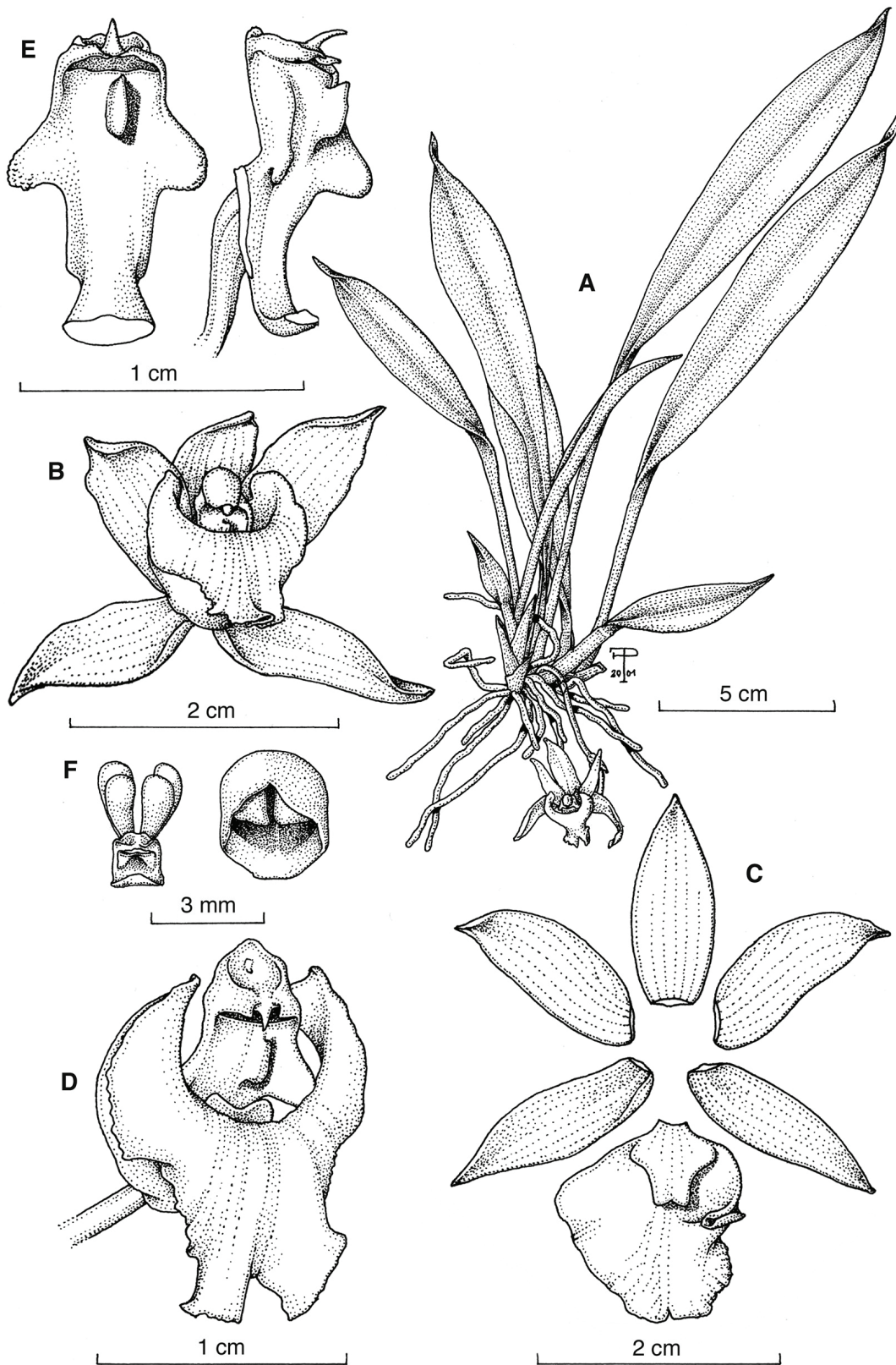


FIGURE 4. *Kefersteinia luteola* Pupulin, E. Salas, & Bogarín. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, column and lip, three quarters view; **E**, column, ventral, and three-quarters view; **F**, pollinarium and anther cap. Drawn by F. Pupulin from Nuñez & Olmos III.

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A SYNOPSIS OF *KEFERSTEINIA***Species with laminar callus**

1. *Kefersteinia alba* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 19: 228. 1923. TYPE: Costa Rica.
2. *Kefersteinia andreettae* G. Gerlach, Neudecker, & Seeger, *Orchidee (Hamburg)* 40(4): 133. 1989. TYPE: Ecuador.
= *Kefersteinia salustiana* D.E. Benn. & Christenson, *Brittonia* 46(1): 37. 1994. TYPE: Peru.
3. *Kefersteinia bismarckii* Dodson & D.E. Benn., *Icon. Pl. Trop.*, ser. 2. 1: t. 83. 1989. TYPE: Peru.
4. *Kefersteinia candida* D.E. Benn. & Christenson, *Brittonia* 46(3): 238. 1994. TYPE: Peru.
5. *Kefersteinia carolorum* Carnevali & Cetzal, *Phytotaxa* 239(2): 166. 2015. TYPE: Venezuela.
6. *Kefersteinia delcastilloi* D.E. Benn. & Christenson, *Brittonia* 46(1): 32. 1994. TYPE: Peru.
7. *Kefersteinia elegans* Garay, *Orquideología* 4(2): 80. 1969. TYPE: Colombia.
8. *Kefersteinia escobariana* G. Gerlach & Neudecker, *Orquideología* 19(3): 46. 1996. TYPE: Ecuador.
9. *Kefersteinia forcipata* (hort. ex Rchb.f.) P.A. Harding, *Huntleyas* 165. 2008. TYPE: Unknown.
= *Kefersteinia laminata* (Rchb.f.) Schltr., *Gard. Chron.* 2: 70. 1885. TYPE: Ecuador.
10. *Kefersteinia gemma* Schltr., *Gard. Chron.* 1: 406. 1874. TYPE: Ecuador.
= *Kefersteinia oscarii* P. Ortiz, *Orquideología* 20(2): 240. 1996. TYPE: Colombia.
11. *Kefersteinia graminea* (Lindl.) Rchb f., *Bot. Zeitung (Berlin)* 10: 634. 1852. TYPE: Venezuela.
12. *Kefersteinia heideri* Neudecker, *Orquideología* 19(3): 97. 1994. TYPE: Bolivia.
13. *Kefersteinia klabochii* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 7: 267. 1920. TYPE: Colombia.
14. *Kefersteinia lactea* (Rchb.f.) Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 19: 228. 1923. TYPE: Costa Rica.
15. *Kefersteinia lojiae* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 8: 93. 1921. TYPE: Ecuador.
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= *Kefersteinia lindneri* Dodson, *Icon. Pl. Trop.* 5: t. 439. 1982. TYPE: Ecuador.
= *Kefersteinia vollesii* Jenny, *Orchideen* 36(5): 185. 1985. TYPE: Colombia.
= *Kefersteinia lafontainei* Senghas & G. Gerlach, *Orchideen* 41: 47. 1990. TYPE: ??.
= *Kefersteinia benvenathar* D.E. Benn. & Christenson, *Brittonia* 46(3): 235. 1994. TYPE: Peru.
= *Kefersteinia bengasahra* D.E. Benn. & Christenson, *Brittonia* 46(3): 235. 1994. TYPE: Peru.
= *Kefersteinia jarae* D.E. Benn. & Christenson, *Brittonia* 46(1): 34. 1994. TYPE: Peru.

A SYNOPSIS OF *KEFERSTEINIA* CONT.**Species with laminar callus cont.**

- = *Kefersteinia licethyae* D.E. Benn. & Christenson, *Brittonia* 46(1): 34. 1994. TYPE: Peru.
 = *Kefersteinia richardhegerlii* R. Vásquez & Dodson, *Revista Soc. Boliv. Bot.* 3(1–2): 12. 2001. TYPE: Bolivia.
 16. *Kefersteinia luteola* Pupulin, E. Salas, & Bogarín, *Harvard Papers in Botany* 29(2): 308. TYPE: Costa Rica.
 17. *Kefersteinia microcharis* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 19: 300. 1923. TYPE: Costa Rica.
 18. *Kefersteinia minutiflora* Dodson, *Icon. Pl. Trop.* 5: t. 440. 1982. TYPE: Ecuador.
 19. *Kefersteinia niesseniae* P. Ortiz, *Orquideología* 20: 239. 1996. TYPE: Colombia.
 20. *Kefersteinia pulchella* Schltr., *Repert. Spec. Nov. Regni Veg.* 27: 68. 1929. TYPE: Bolivia.
 = *Kefersteinia vasquezii* Dodson, *Icon. Pl. Trop.*, ser. 2. 4: pl. 345. 1989. TYPE: Bolivia.
 21. *Kefersteinia ricii* R. Vásquez & Dodson, *Revista Soc. Boliv. Bot.* 2(1): 4. 1998. TYPE: Bolivia.
 22. *Kefersteinia stapelioides* Rchb.f., *Bot. Zeitung (Berlin)* 10: 634, 1852. TYPE: [Mittelamerika].
 23. *Kefersteinia tinschertiana* Pupulin, *Harvard Pap. Bot.* 8(2): 166. 2004. TYPE: Guatemala.
 24. *Kefersteinia tolimensis* Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 7: 161. 1920. TYPE: Colombia.
 25. *Kefersteinia universitatis-tolimae* Sierra-Ariza, *Harvard Pap. Bot.* 28(2): 728. 2023. TYPE: Colombia.
 26. *Kefersteinia villenae* D.E. Benn. & Christenson, *Brittonia* 46(3): 241. 1994. TYPE: Peru.
 27. *Kefersteinia villosa* D.E. Benn. & Christenson, *Lindleyana* 13(1): 51. 1998. TYPE: Peru.
 = *Kefersteinia pellita* Rchb.f. ex Dodson & D.E. Benn., *Icon. Pl. Trop.*, ser. 2. 1. 1989. TYPE: Ecuador.
 = *Kefersteinia pastorellii* Dodson & D.E. Benn., *Icon. Pl. Trop.*, ser. 2. 1. 1989. TYPE: Peru.
 = *Kefersteinia aurorae* D.E. Benn. & Christenson, *Brittonia* 46(3): 233. 1994. TYPE: Peru.
 = *Kefersteinia koechlinorum* Christenson, *Orchid Digest* 64: 139. 2000. TYPE: Peru.
 = *Kefersteinia pseudopellita* P.A. Harding, *Orquideología* 25(2): 160. 2008. TYPE: Ecuador.

Species with stalked callus

28. *Kefersteinia alata* Pupulin, *Harvard Pap. Bot.* 8(2): 161. 2004. TYPE: Panama.
 29. *Kefersteinia angustifolia* Pupulin & Dressler, *Harvard Pap. Bot.* 8(2): 164. 2004. TYPE: Costa Rica.
 30. *Kefersteinia auriculata* Dressler, *Orquideología* 16(1): 49. 1983. TYPE: Panama.
 31. *Kefersteinia chocoensis* G. Gerlach & Senghas, *Orchideen* 41: 45. 1990. TYPE: Colombia.
 32. *Kefersteinia costaricensis* Schltr., *Beih. Bot. Centralbl.*, Abt. 2 36(3): 413. 1918. TYPE: Costa Rica.
 33. *Kefersteinia escalerensis* D.E. Benn. & Christenson, *Brittonia* 46(3): 238. 1994. TYPE: Peru.
 34. *Kefersteinia excentrica* Dressler & Mora-Ret., *Orquídea (Mexico City)*, n.s. 13(1–2): 261. 1993. TYPE: Costa Rica.
 35. *Kefersteinia guacamayoana* Dodson & Hirtz, *Icon. Pl. Trop.*, ser. 2. 6: pl. 505. 1989. TYPE: Ecuador.
 36. *Kefersteinia maculosa* Dressler, *Orquideología* 16(1): 52. 1983. TYPE: Panama.
 37. *Kefersteinia medinae* Pupulin & G. Merino, *Willdenowia* 38: 190. 2008. TYPE: Ecuador.
 38. *Kefersteinia ocellata* Garay, *Orquideología* 4(2): 83. 1969. TYPE: Colombia.
 39. *Kefersteinia orbicularis* Pupulin, *Lindleyana* 15(1): 25. 2000. TYPE: Costa Rica.
 40. *Kefersteinia perlonga* Dressler, *Native Colomb. Orchids* 2: 224. 1991. TYPE: Colombia.
 41. *Kefersteinia retanae* G. Gerlach, *Brenesia* 52: 75. 1999 [2000]. TYPE: Costa Rica.
 42. *Kefersteinia saccata* Pupulin, *Willdenowia* 38: 188. 2008. TYPE: Costa Rica.
 43. *Kefersteinia sanguinolenta* Rchb.f., *Bot. Zeitung (Berlin)* 10: 635. 1852. TYPE: Venezuela.
 44. *Kefersteinia stevensonii* Dressler, *Orquideología* 7(3): 135. 1972. TYPE: Ecuador.
 45. *Kefersteinia taggesellii* Neudecker, *Orquideología* 19(3): 98. 1994. TYPE: Colombia.

A SYNOPSIS OF *KEFERSTEINIA* CONT.**Species with stalked callus cont.**

46. *Kefersteinia taurina* Rchb.f., Linnaea 41: 5. 1877 [1876]. TYPE: Colombia?
 = *Kefersteinia lehmannii* P. Ortiz, Orquideología 20: 234. 1996. TYPE: Colombia.
47. *Kefersteinia trullata* Dressler, Native Colomb. Orchids 2: 225. 1991. TYPE: Colombia.
48. *Kefersteinia wercklei* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 531. 923. TYPE: Costa Rica.

Species with anomalous callus

49. *Kefersteinia endresii* Pupulin, Ann. Naturhist. Mus. Wien, B 103B: 543. 2001. TYPE: Costa Rica.
50. *Kefersteinia expansa* Rchb.f., Otia Bot. Hamburg. 9. 1872. TYPE: Ecuador.
51. *Kefersteinia hirtzii* Dodson, Icon. Pl. Trop., ser. 2. 6: pl. 506. 1989. TYPE: Ecuador.
52. *Kefersteinia mystacina* Rchb.f., Gard. Chron., n.s. 15(382): 530. 1881. TYPE: Colombia.
 = *Kefersteinia lacerata* Fowlie, Orchid Digest 32: 145. 1968. TYPE: Colombia.
53. *Kefersteinia parvilabris* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 52. 1923. TYPE: Costa Rica.
 = *Kefersteinia deflexipetala* Fowlie, Orchid Digest 30(4): 117. 1966. TYPE: Costa Rica.

Excluded species

- Kefersteinia bicallosa* (Rchb.f.) Rchb.f., Otia Bot. Hamburg. 1: 31. 1878 = *Inti bicallosa* (Rchb.f.) M.A. Blanco
- Kefersteinia flaveola* (Linden & Rchb.f. ex Rchb.f.) Schltr., Repert. Spec. Nov. Regni Veg. Beih. 7: 266. 1920
 = *Chondroscaphe flaveola* (Linden & Rchb.f. ex Rchb.f.) Senghas & G. Gerlach
- Kefersteinia leucantha* Rchb.f. ex L. Linden, Ill. Hort. 29: 52. 1882, *nomen nudum*.
- Kefersteinia sanguinea* Pritz., Icon. Bot. Index 2: 161 Orchidaceae, *sphalm*.
- Kefersteinia subquadrata* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 300. 1923
 = *Chaubardiella subquadrata* (Schltr.) Garay

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CARPOTROCHE PAUSANDRIFOLIA (ACHARIACEAE), UNA NUEVA ESPECIE DE COSTA RICA

DANIEL SANTAMARÍA-AGUILAR,^{1,2} REINALDO AGUILAR FERNÁNDEZ³ Y ALEXANDRE K. MONRO⁴

Resumen. Se describe e ilustra una nueva especie de *Carpotroche*, de la vertiente Pacífica de Costa Rica, el cual es nombrado *C. pausandrifolia*, debido a su similitud morfológica con *Pausandra* (Euphorbiaceae). Hasta el momento es la única especie en Costa Rica, que se encuentra sobre esta vertiente, y que además tiene frutos blanco-verdosos. Históricamente fue confundido con *C. platyptera*, una especie de la vertiente Caribe, con frutos rojos. Evaluamos el estado de conservación de *Carpotroche pausandrifolia* como Casi Amenazada (NT) y se proporciona información sobre su distribución, hábitat, fenología y observaciones taxonómicas. También comparamos a *C. pausandrifolia* con aquellas especies morfológicamente afines.

Abstract. We describe and illustrate *Carpotroche pausandrifolia*, a new species from the Pacific drainage of Costa Rica. The species epithet refers to the morphological similarity of *C. pausandrifolia*'s leaves to species of *Pausandra* (Euphorbiaceae). *Carpotroche pausandrifolia* is the only species in Costa Rica distributed on the Pacific slope and is unique because of its fruits that are pale green at maturity. Historically *C. pausandrifolia* has been confused with *C. platyptera*, a species from Costa Rica's Caribbean drainage that has red fruits. We assess the conservation status of *C. pausandrifolia*'s risk of extinction as Near Threatened (NT) and provide information on the distribution, habitat, phenology and taxonomy of *C. pausandrifolia*. We also provide the means to distinguish *C. pausandrifolia* from morphologically similar species in the genus.

Palabras clave: Flora de Costa Rica, Malpighiales, Osa, Osa Peninsula

Achariaceae (Malpighiales) cuentan con 31 géneros y un estimado de 133 especies (Stevens, 2001). En Costa Rica, esta familia es representada por los géneros *Chiangiodendron* T. Wendt, *Lindackeria* C. Presl, y *Mayna* Aubl., (Fig. 1) cada uno con una especie en la zona (González, 2010), mientras *Carpotroche* Endl. es representado por cuatro especies: *C. crassiramea* Pittier, *C. glaucescens* Pittier, *C. platyptera* Pittier, y la especie propuesta en esta contribución (Santamaría-Aguilar et al., 2021).

Carpotroche está restringido al Neotrópico, y cuenta con alrededor de 15 especies, seis de ellas en América Central y 11 en América del Sur (Sleumer, 1980; Santamaría-Aguilar et al., 2021). El género es llamativo por los frutos capsulares, los cuales por lo general son alados y generalmente cauli-

floros. Otras características que presenta este género, son las láminas foliares agrupados hacia la parte distal de las ramas, y que carecen de puntos o líneas translúcidas, tricomas simples, presencia de estípulas, pecíolo pulvinado en ambos extremos (aunque es más frecuente el distal); flores unisexuales, poligamomonoicas o dioicas, con más pétalos que sépalos; estambres numerosos con los filamentos pubescentes y más cortos que las anteras; un pistilo con 4–8 (–10) estilodios capitados o lacerados (Sleumer, 1980; Alford, 2003; Fiaschi y Groppo, 2008; Groppo et al., 2013).

La presente contribución, ilustra y describe un nuevo *Carpotroche* de la vertiente Pacífica de Costa Rica, el cual fue confundido con *C. platyptera*, de la vertiente Caribe de Nicaragua y Costa Rica.

MATERIALES Y MÉTODOS

Se revisaron físicamente los especímenes de *Carpotroche* de Centro y Sur América de los herbarios BM, COAH, COL, CR (incluido ex INB), GH, K, HOXA, LSCR, LSU, MO, NO y NY. Así como las imágenes digitales de los especímenes tipos y de las colecciones generales de los herbarios, instituciones o plataformas digitales de: EAP, F (<https://collections-botany.fieldmuseum.org/>), HUH (https://kiki.huh.harvard.edu/databases/specimen_index.html),

JSTOR Global Plants (<http://plants.jstor.org>), L (<https://www.naturalis.nl/en/collections-of-naturalis>), MEXU (<https://dato.sabiertos.unam.mx/biodiversidad/>), P (<http://www.mnhn.fr>), US (<https://collections.si.edu/search/results.htm?q=&view=grid>) y USJ.

La descripción morfológica y dimensiones de las estructuras vegetativas y reproductivas se tomaron de especímenes de herbario y se complementaron con observaciones de campo.

Agradecemos a los siguientes herbarios e instituciones: BM, COAH, COL, CR, EAP, F, GH, HUH, K, HOXA, L, LSCR, LSU, MEXU, MO, NO, NY, P, US y USJ, por permitir el acceso y uso de sus colecciones, ya sea forma física o por medio de imágenes digitales, así como también a su personal por las facilidades brindadas. Ronald Zuñiga y Paul E. Hanson muy amablemente colaboraron en la identificación de las abejas (Fig. 1A, 3B). De la misma manera, la Dr. Eugenia Flores-Vindas por los comentarios y observaciones relacionados con los frutos y semillas, el Dr. Kanchi N. Gandhi por revisar la escritura del epíteto específico y al Dr. Ricardo Kriebel Haehner por sus valiosos comentarios y observaciones a este documento. A Isler Fabián Chinchilla Alvarado por la elaboración de las ilustraciones (Fig. 7). A David E. Granados facilitó imágenes de los frutos de *C. pacifica* (Fig. 6), mientras Isidro Chacón, Barry E. Hammel, Robbin C. Moran, los frutos de la Fig. 5; J. Esteban Jiménez de los ejemplares depositados en USJ. Daniel Santamaría-Aguilar expresa su sincero agradecimiento al Biological Sciences y al Shirley C. Tucker Herbarium of Louisiana State University; así como al Bentham-Moxon Trust (K) y al Instituto Amazónico de Investigaciones Científicas SINCHI (COAH) que permitió la visita a los herbarios de sus respectivas instituciones. A Jennifer Kluse, Laura P. Lagomarsino y Julio C. Betancur, por su apoyo en diferentes aspectos.

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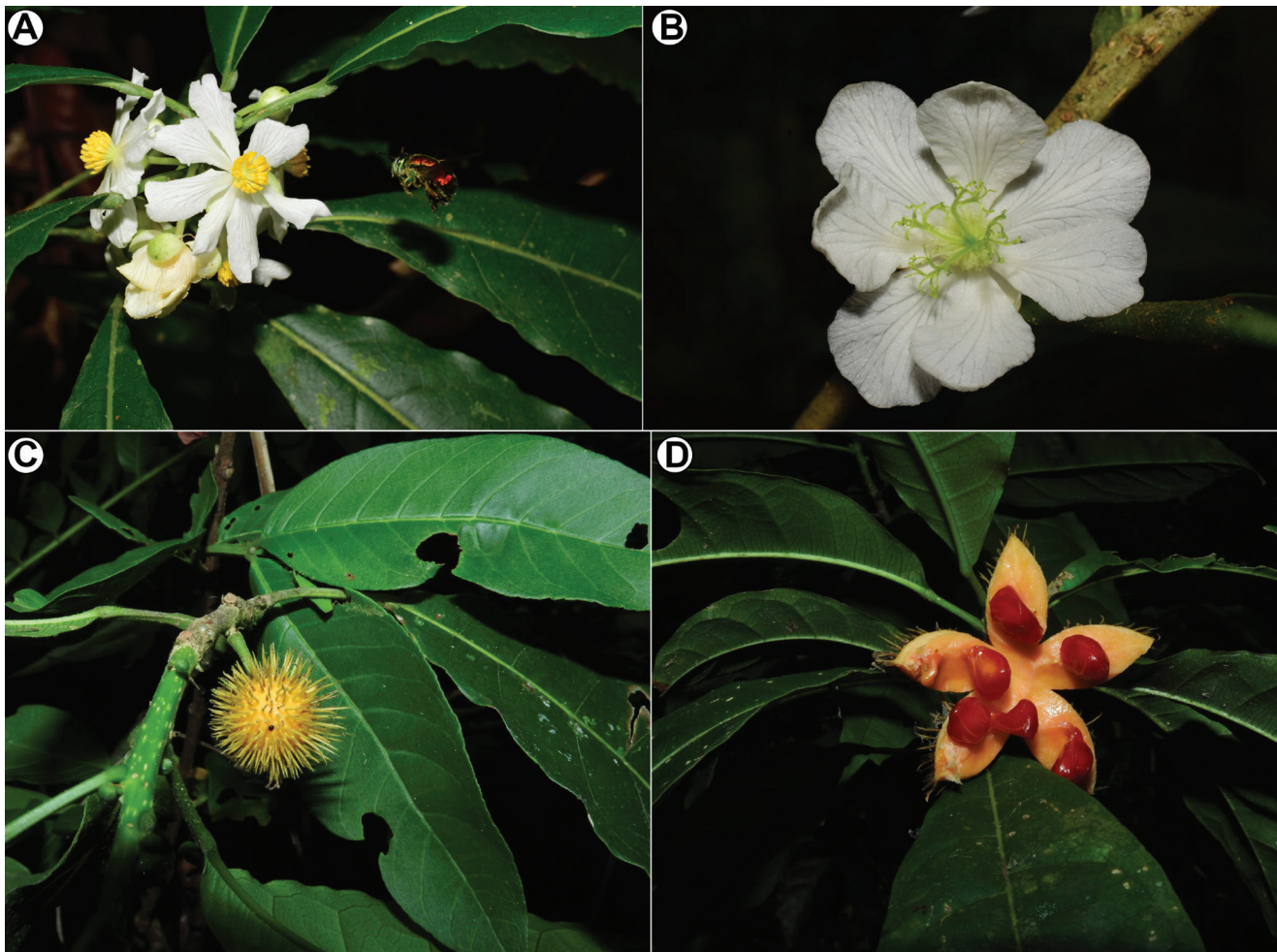


FIGURA 1. *Mayna odorata* el otro miembro de Achariaceae en la Península de Osa. **A**, flores estaminadas, visitadas por *Euglossa* sp. (*Euglossini*); **B**, flor pistilada; **C**, fruto; **D**, fruto mostrando la parte interna y las semillas. Fotografías por Reinaldo Aguilar.

El mapa fue elaborado con el programa SimpleMapp (Shorthouse, 2010), con las coordenadas geográficas proporcionadas en las etiquetas y editado en Adobe Photoshop.

Los datos fenológicos fueron tomados de los ejemplares de herbario estudiados. En la lista de ejemplares examinados,

donde se denota un asterisco (*) al lado del acrónimo de herbario (p. ej. USJ*), corresponden a imágenes digitales observadas.

Imágenes adicionales de esta nueva especie se encuentran disponibles en el siguiente enlace: <https://www.flickr.com/photos/plantaspeninsulaosa/>

TAXONOMÍA

Carpotroche pausandrifolia D. Santam. & Aguilar, *sp. nov.* TIPO: COSTA RICA. Puntarenas: Parque Nacional Corcovado, Sirena, Los Patos, Mirador Trail, 08°28'N, 083°35'W, 200–300 m, 26 Octubre 1999 (bot. fls. y fr.), *C. Kernan 1313* (Holotipo: MO [3872092, código de barras 917183]; Isotipo: CR [15420]). Fig. 2–8.

Most similar to *C. platyptera*, from which it may be distinguished based on the densely pubescent lamina on lower surface (vs. usually puberulous, rarely tomentose to tomentulose), the markedly dentate lamina margin (vs. subentire, rarely crenate to serrulate, especially towards the apex), and red fruits (vs. fruit yellowish, white, cream or lemon-green). It is distinguished from the other species by the depth of the wings on the fruit (*C. amazonica* [almost no wings], *C. integrifolia* [ca 0.3 cm deep], *C. surinamensis*

[0.4–0.8 cm high] vs. 1–1.7 cm high in *C. pausandrifolia*), the wings are lacerated and/or dentate and tubercled between them (*C. brasiliensis*, *C. caceresiae*, *C. crispidentata*, *C. longifolia*, *C. pacifica*), and wings papery and overlapping (*C. froesiana*, *C. grandiflora*).

Arbusto o árbol pequeño, 1.5–7 m de altura × 3–9 cm de diámetro (o hasta 20 cm; *C. Morales* y *A. Chacón 74*, MO), posiblemente las plantas andromonoicas; tronco recto, corteza externa pardo claro, con pequeñas lenticelas, la corteza interna rojiza, sin olor. Tricomas usualmente blanquecinos, amarillentos a pardo claro sobre las ramitas, lámina foliar, pétalos, estambres, arilo y testa de la semilla. Ramitas que llevan hojas 0.2–0.8 cm de grueso, teretes, densamente pubescentes hacia la parte distal, con tricomas simples de 0.2–0.3 (–0.5) mm y con una capa basal esparcida

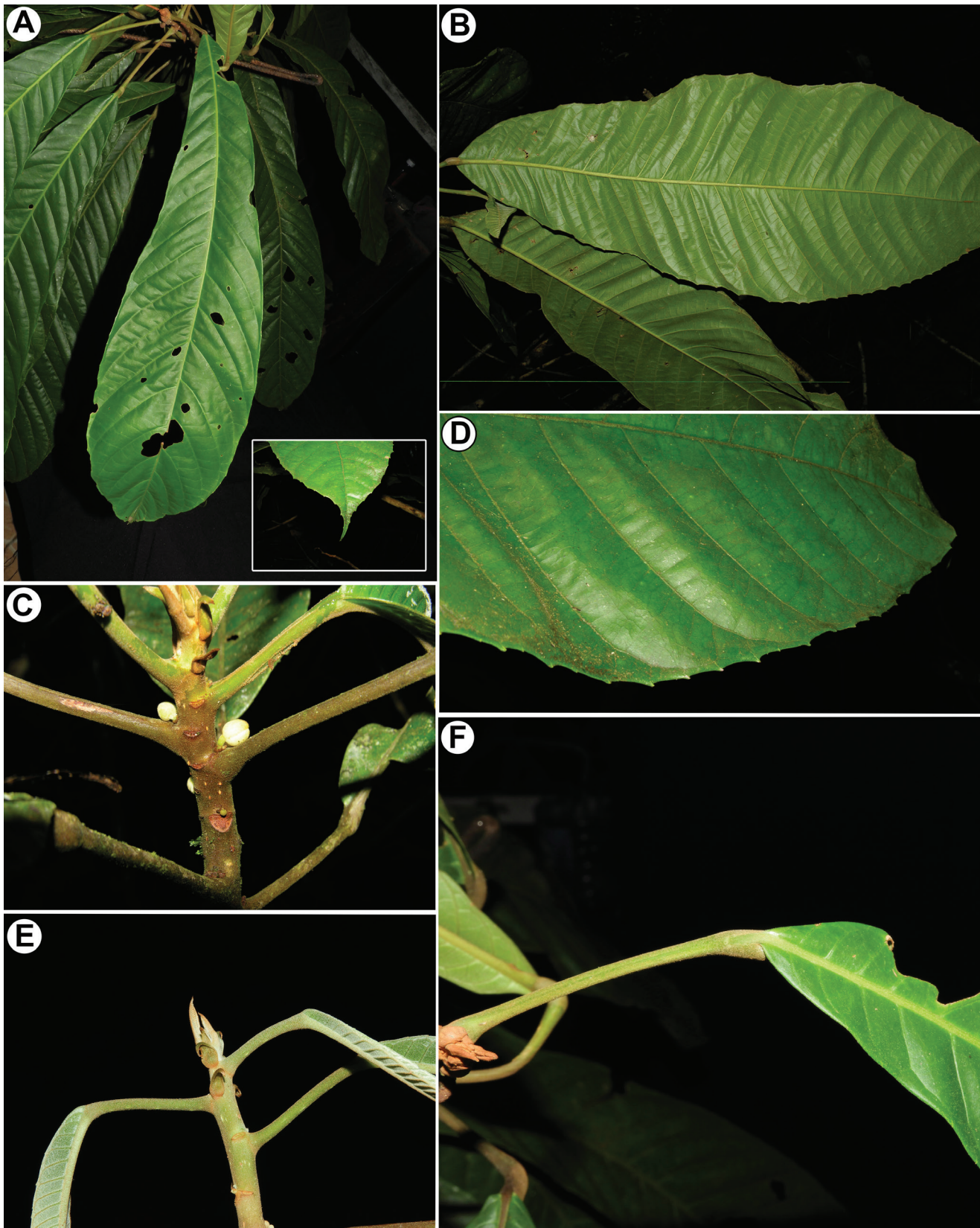


FIGURA 2. *Carpotroche pausandrifolia*. **A**, Haz de la lámina foliar y el ápice en recuadro; **B**, envés de la lámina foliar; **C**, parte apical de la ramita; **D**, margen de la lámina foliar; **E**, estípulas; **F**, pecíolo mostrando el pulvino apical. Fotografías por Reinaldo Aguilar.

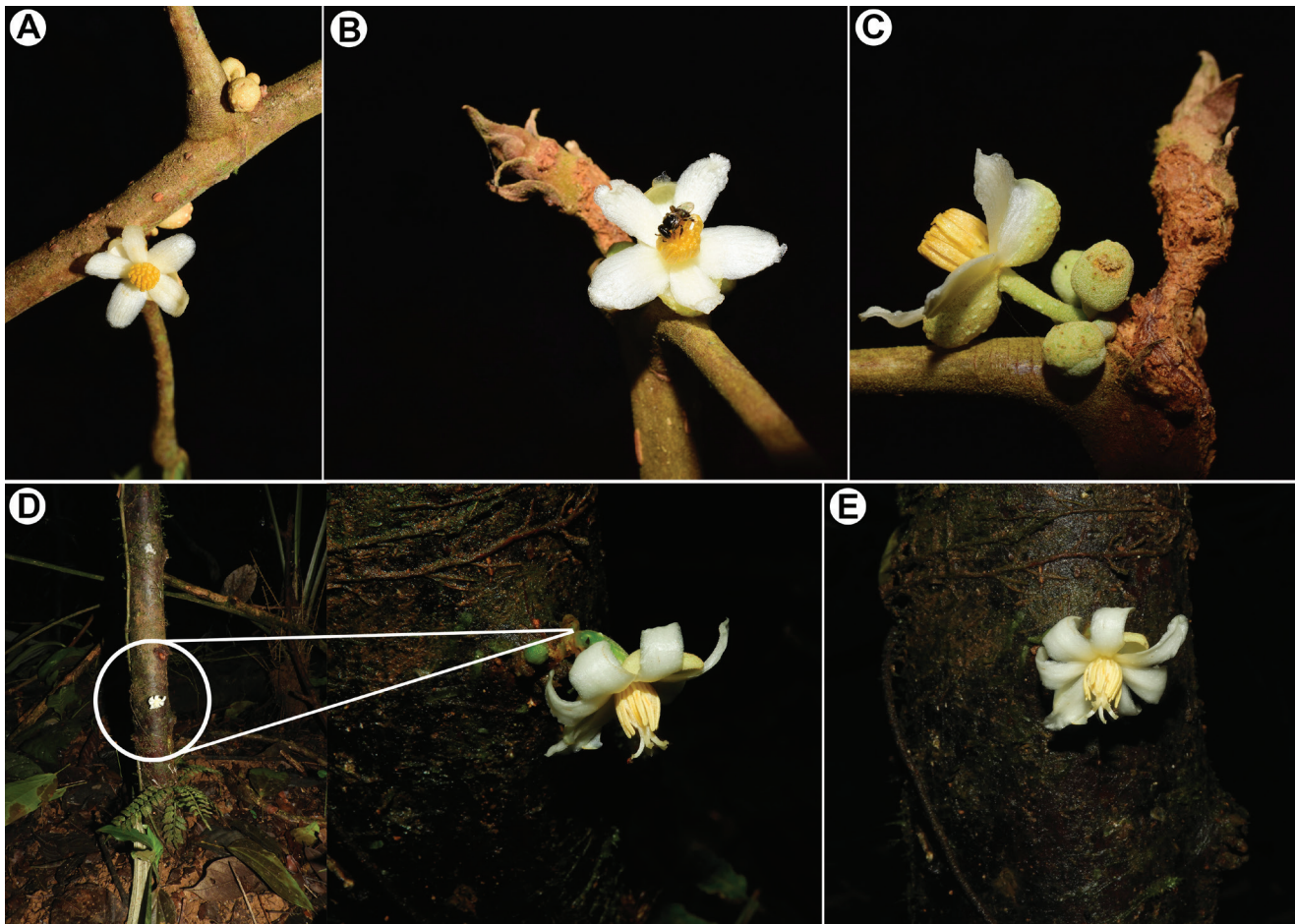


FIGURA 3. *Carpotroche pausandrifolia*. A–C, flores estaminadas y visita de *Plebeia* sp., (Meliponini); D–E, flores hermafroditas saliendo del tronco. Fotografías por Reinaldo Aguilar.

a densa de tricomas diminutos pardo oscuro; lenticelas ausentes o cuando presentes muy esparcidas, 1–1.5 × 0.7–1 mm, elípticas o redondeadas; *estípulas* 0.5–1 × 0.2–0.4 cm, caedizas y dejando una cicatriz, deltoides a angostamente deltoides, densamente pubescentes en ambas caras, la cara externa tiene una capa basal esparcida a densa de tricomas diminutos pardo oscura y otra de tricomas más claro y largos (ca. 0.2–0.5 mm longitud), la cara interna con un solo tipo y los tricomas son más claros, alguna veces nervadas, los márgenes enteros. *Hojas* alternas, espiraladas; *pecíolos* 2.5–8 cm de largo × 0.2–0.4 cm de ancho, desiguales en longitud, con pubescencia similar a la de las ramitas, plano o levemente canaliculado adaxialmente, redondeada abaxialmente, algunas veces fistulosos, pulvinado en ambos extremos, aunque más frecuente el del ápice; lámina 33.5–50 (–60) × 5.3–11.5 (–19) cm, oblanceolada a oblongo-elíptica; haz en la madurez usualmente glabro (densamente pubescente en láminas foliares jóvenes); envés usualmente pubérulo, pocas veces tomentosas a tomentulosas (p. ej. *M. Grayum* 10666, MO; *J. F. Morales* 276, MO), los tricomas blanquecinos o amarillentos; nervio central plano o ligeramente elevado en el haz, marcadamente elevado en el envés (1.3–4 mm de ancho), pubescente; venas secundarias semicraspedódromas, con 18–36 venas por lado, planas en

el haz, elevadas en el envés, algunas veces con 1–2 venas intersecundarias; venas terciarias que cruzan entre las venas secundarias adyacentes, rectas o sinuadas, sobresalientes sobre ambas caras, pero siendo más destacados por el envés; nervios cuaternarios reticulados; base angostamente cuneada a atenuada; ápice acuminado a largo acuminado; margen con 22–56 dientes, subentero, frecuentemente los dientes muy inconspicuos (ca. 0.2–0.5 mm de altura), pocas veces crenado a serrulado (especialmente hacia el ápice, ca. 0.9–1.5 mm de altura), o la combinación de los dos anteriores (i.e. *T. B. Croat* y *D. Hannon* 79273, MO), cada diente llevando una pequeña glándula, la glándula glabra o pubescente, prontamente caduca. *Inflorescencias* estaminadas en la axila de las hojas, con 1–5 flores fasciculadas en botón floral. *Flores estaminadas* con el pedicelo 1.5–5.5 mm de largo en botón floral, pubescente; sépalos 2, 3.7–5 × 2.6–3 (–4.7) mm, usualmente el externo ligeramente más grande que el interno, amarillentos a crema (cuando frescos), algunas veces la superficie levemente verrucosa, elípticos a ovados, densamente pubescentes en la cara externa, excepto glabro hacia los márgenes del sépalo interno, los tricomas pardo claro a castaños, o algunas veces similares a los de las ramitas, glabros en la cara interna; pétalos 5–7, 2.8–5.5 mm de largo, blancos o

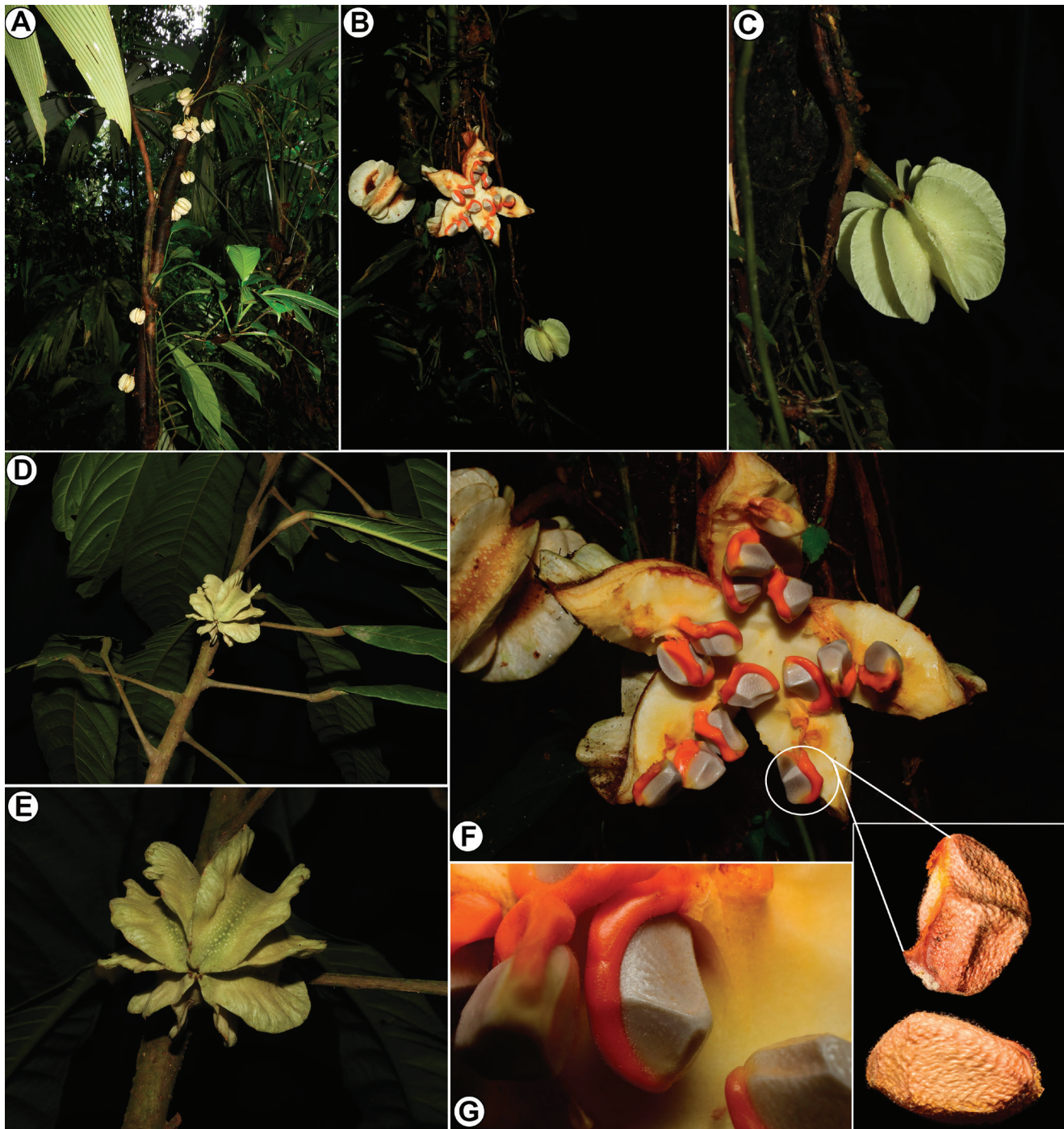


FIGURA 4. *Carpotroche pausandrifolia*. A, hábito y frutos en el tronco; B, frutos; C, frutos mostrando las alas; D–E, frutos en la axila de las hojas; F–G, fruto abierto mostrando las semillas, ariloide y detalle de la semilla (derecha en recuadro). Fotografías por Reinaldo Aguilar.

crema, oblongo-elípticos, esparcidamente pubescentes en la cara externa, el indumento especialmente en la parte central en casi todo su longitud, glabro hacia los márgenes, glabros o esparcidamente pubescente en la cara interna; estambres 25–33 (–57); filamento 0.2–0.4 mm de largo, pubescente; anteras 1.9–2.5 mm de largo, ca. 0.7 mm de ancho y ca. 0.5 mm de grueso, dehiscentes por 2-poros, loceladas, pubescentes; ovario ausente. *Inflorescencias* y *flores*

hermafroditas no vistas en especímenes de herbario. *Frutos* caulifloros o en la axila de las hojas, longitudinalmente alados, amarillentos, blancos, crema o verde-limón externa e internamente en material fresco, tardíamente dehiscente por (3–) 5 valvas; pedicelo 0.8–1.7 cm; el cuerpo 2.4–3.5 × 1.2–2.6 cm, elíptico, cubierto por una capa de tricomas cortos y otra capa de pocos tricomas rectos o uncinados, o con un solo tipo de los anteriores, sin crestas entre las alas

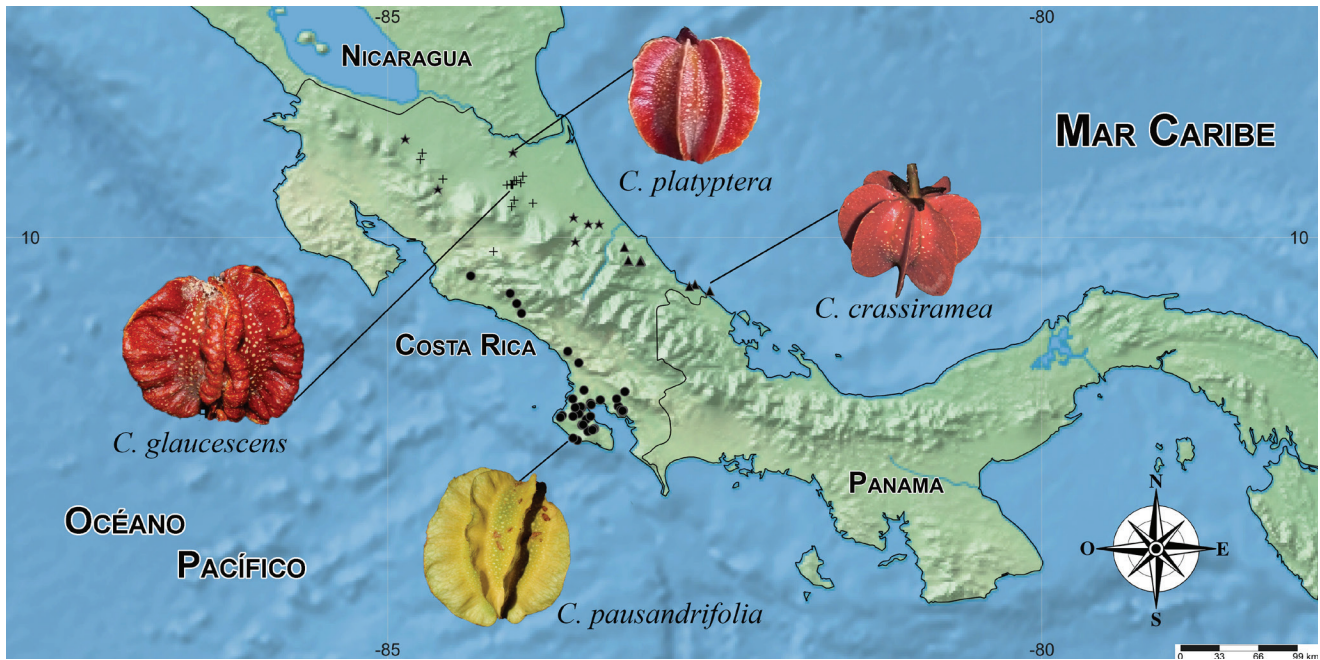


FIGURA 5. Mapa de distribución y comparación de los frutos de las especies de *Carpotroche* en Costa Rica. *Carpotroche crassiramea* (▲), *C. glaucescens* (+), *C. pausandrifolia* (●) y *C. platyptera* (★). Fotografías por Reinaldo Aguilar (*C. pausandrifolia*), Isidro Chacón (*C. platyptera*), Barry E. Hammel (*C. crassiramea*), Robbin C. Moran (*C. glaucescens*).

(i.e. liso), algunas veces cuando frescos con puntuaciones blanquecinas o anaranjadas; estilos persistentes, ca. 4 mm de largo, pubescentes en la mitad proximal, los tricomas blanquecinos a castaño; alas 8–10 (12), usualmente dos por cada valva, 1–1.7 cm de alto, erectas y cartáceas, el margen entero o levemente ondulado, 3–4.2 cm de longitud, con tricomas como los del cuerpo; pericarpo 2 mm de grueso; semillas 13–23 por fruto, 0.9–1 cm de altura, 0.4–0.6 cm de largo, 0.44–0.6 cm de ancho, con 3–5 lados, uno de los márgenes cubierto parcialmente por un ariloide anaranjado, amarillento o raramente blanco (*T. B. Croat* y *D. Hannon* 79273, MO), aceitoso, pubescente; testa ca. 0.2–0.3 de gruesa, pardo rojiza a blanquecina cuando seca (blanca a grisáceo cuando fresca), ligeramente rugosa, esparcidamente pubescente; endospermo blanco, aceitoso.

Hábitat, distribución y ecología: *Carpotroche pausandrifolia* es una especie endémica de Costa Rica. Especímenes en colecciones indican que dicha especie ha sido recolectado en el Pacífico Central y Sur (Fig. 5), en las provincias de Puntarenas y San José, entre los 0–1400 metros de elevación. En la región de Golfito, Golfo Dulce y el Parque Nacional Corcovado, por lo general se le encuentra creciendo entre los 0–400 (–600) m de elevación; mientras que las estribaciones de Tarrazú y la Fila Costeña se le

encuentra a mayor elevación (900–1400 m). Allen (1956) menciona que esta especie es frecuente en las montañas de Palmar Norte. En la Península de Osa, esta especie solo ha sido observada creciendo en áreas no perturbadas y sobre terrenos planos.

Hasta el momento, *Carpotroche pausandrifolia*, es la única especie conocida de la vertiente del Pacífico de Costa Rica, y que además, tiene frutos amarillentos, blancos, crema o verde-limón. Las otras tres especies en el país (*C. crassiramea*, *C. glaucescens* y *C. platyptera*; Fig. 7) se encuentran en la vertiente Caribe y tienen frutos rojos (Fig. 5).

Fenología: Según la información que brindan los ejemplares estudiados de *Carpotroche pausandrifolia*, las flores y frutos en diferentes estados de maduración han sido recolectado en casi todos los meses, ver Tabla 1.

Nombre común: Cacao de montaña, Caraña (*S. Salas* S-607, USJ).

Etimología: El epíteto específico, *pausandrifolia* hace alusión a la similitud morfológica del hábito y las hojas con *Pausandra* Radlk. (Euphorbiaceae), específicamente con *P. trianae* (Müll. Arg.) Baill., que se puede encontrar en los mismos bosques donde habita *C. pausandrifolia*. Sin embargo, *Pausandra* presenta savia, que por lo general es rojiza, y un par de glándulas en el ápice del pecíolo.

TABLA 1. Fenología de *Carpotroche pausandrifolia* D. Santam. & Aguilar.^a

	ENE	FEB	MAR	ABR	MAY	JUN	JUL	AGO	SET	OCT	NOV	DIC
Flores	7	2							4	1	1	
Frutos	4	3		1	3	2	4	7	2	4	1	1

^a Números corresponden a la cantidad de ejemplares colectados durante ese mes.

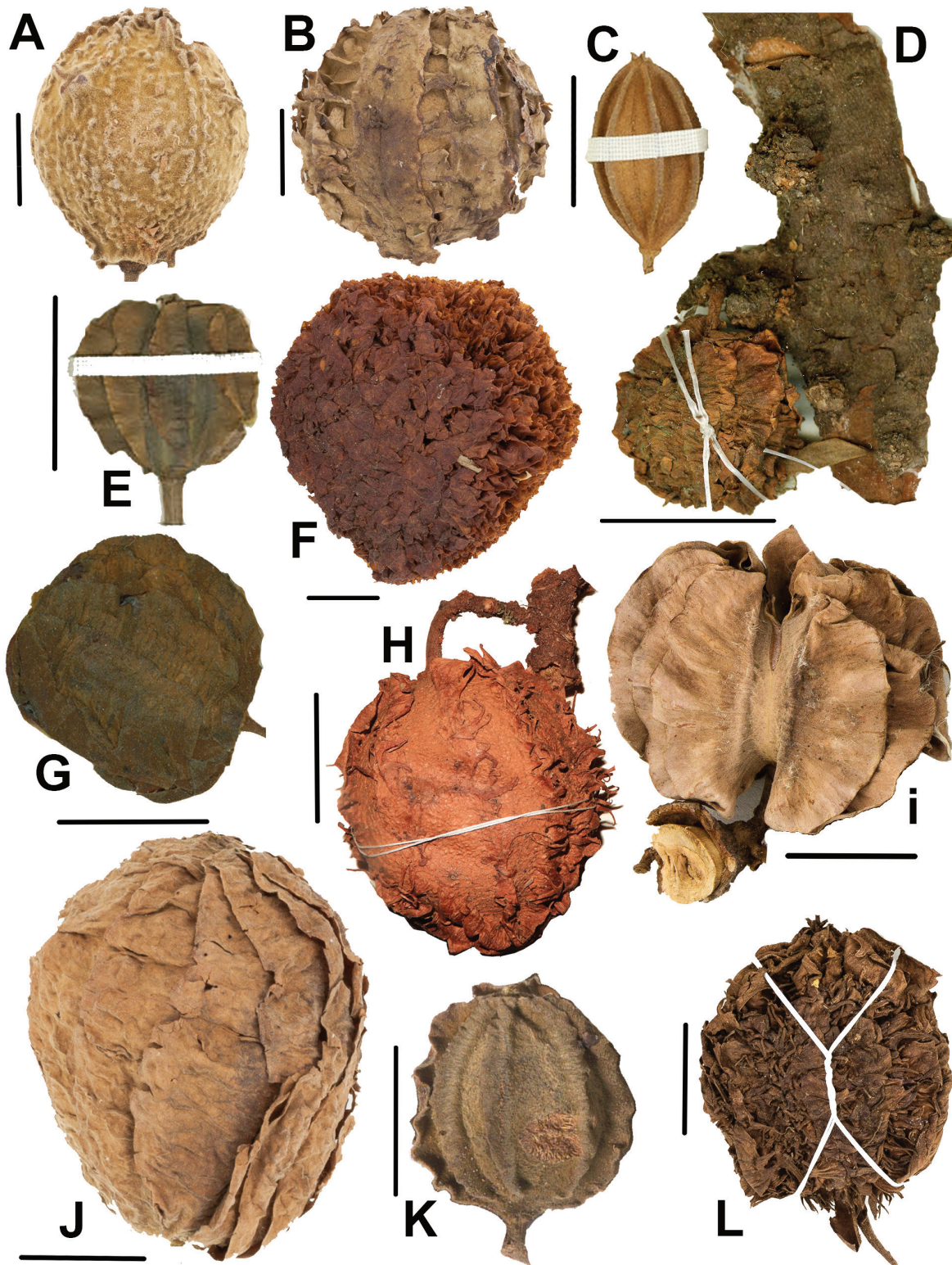


FIGURA 6. Comparación de los frutos de las especies de *Carpotroche* que son descritos con frutos blancos y/o verdes. **A**, *C. amazonica* (R. de Lemos Fróes 20762); **B**, *C. brasiliensis* (R. M. Deda et al. 96); **C**, *C. integrifolia* ([A.] Ducke 405); **D**, *C. caceresiae* (I. Coronado et al. 1953); **E**, *C. ramosii* (J. Cuatrecasas 14206); **F**, *C. crispidentata* (C. A. Cid [Ferreira] 3901); **G**, *C. froesiana* (R. de Lemos Fróes 21324); **H**, *C. pacifica* (J. M. Idrobo 1887); **I**, *C. pausandrifolia* (R. Liesner 3095); **J**, *C. grandiflora* (B. A. Krukoff 9001); **K**, *C. surinamensis* (A. Gröger et al. 1354); **L**, *C. longifolia* (D. Cárdenas et al. 23552). Fotos por New York Botanical Garden (A, B, D, F, G, L), Missouri Botanical Garden (C), Field Museum (E, H), Universidad Nacional de Colombia (J), y Naturalis Biodiversity Center (K).

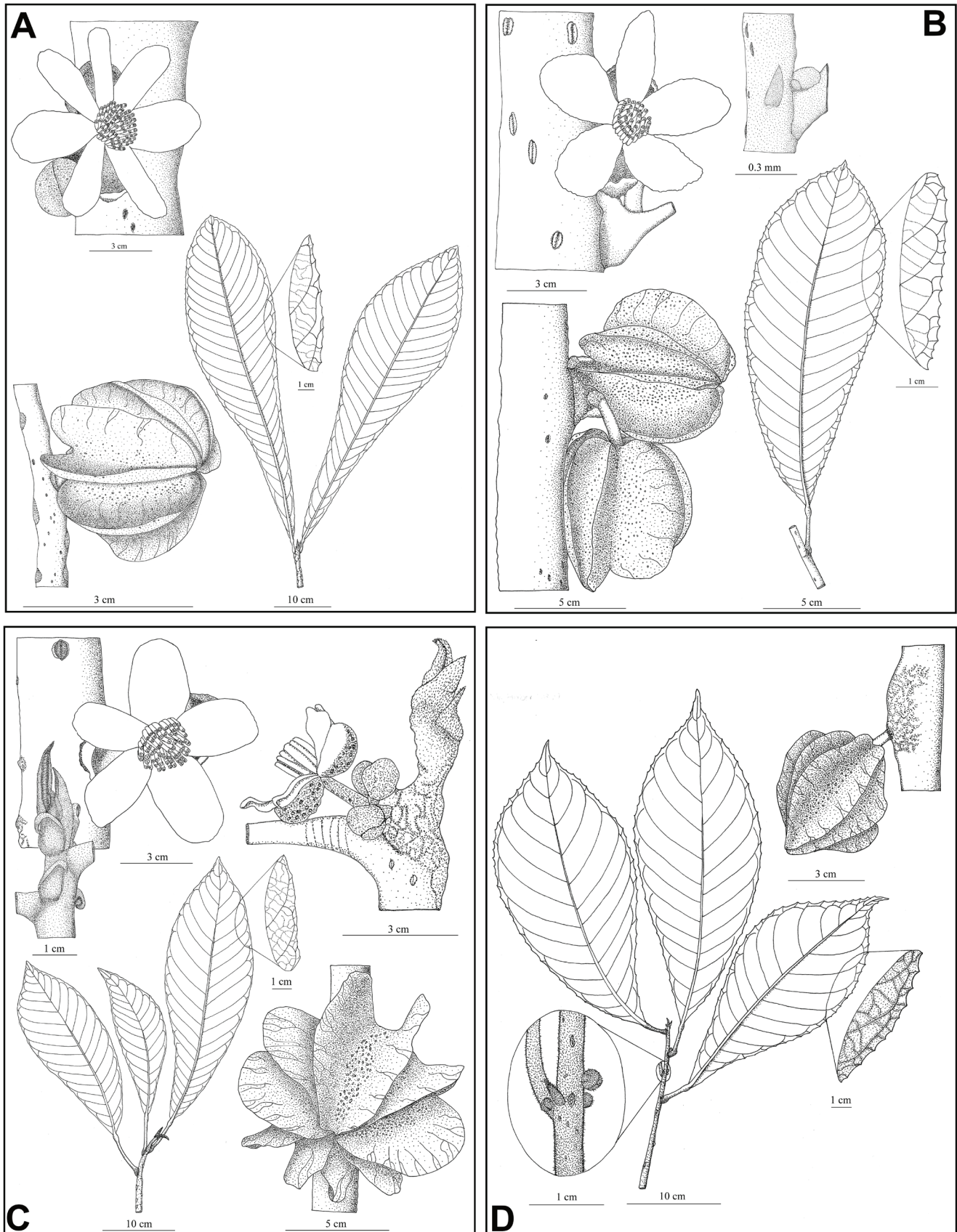


FIGURA 7. Especies de *Carpotroche* presentes en Costa Rica. A, *C. crassiramea*; B, *C. glaucescens*; C, *C. pausandrifolia*; D, *C. platyptera*. Ilustraciones por Isler Fabián Chinchilla Alvarado.



FIGURA 8. Comparación de los ejemplares de herbario de *Carpotroche crassiramea* (A; O. F. Cook y C. B. Doyle 424, US), *C. glaucescens* (B; H. Pittier s.n., US-1383131), *C. pausandrifolia* (C; C. Kernan 1313), y *C. platyptera* (D; H. Pittier 16634). Imágenes por: The Smithsonian Institution (A, B), Missouri Botanical Garden (C), y Royal Botanic Gardens, Kew (D).

Estado de conservación: *Carpotroche pausandrifolia* se conoce a partir de 34 recolecciones realizadas en 26 localidades, entre 1955 y 2009. Utilizando la herramienta Geocat Redlisting (Bachman et al. 2011), calculamos la extensión de ocurrencia (EOO) en 6272 km² y el área de ocurrencia en 108 km², que según el criterio B del protocolo de la Lista Roja de la UICN (UICN 2016) calificaría como Vulnerable (VU) o En Peligro (E). Casi el 75% de la EOO se encuentra dentro de áreas protegidas (capa Geocat Protected Planet). Utilizando la capa de la vegetación en Geocat (VCI, un servidor de la condición de humedad, NOAA STAR Central for Satellite Applications and Research 2023), aproximadamente el 60% de las localidades de las recolecciones conocidas se clasifican como buenas. En cambio, el 85% del EOO se clasifica como bueno. Una revisión visual de las localidades de recolección en Google Earth (2023) indica que cuatro (aproximadamente 3/4) de las localidades de recolección están adyacentes a tierras agrícolas donde el bosque ha sido talado y el riesgo de deforestación futura probablemente sea alto. Las amenazas activas incluyen la deforestación asociada con la agricultura y el cambio climático. Dado que aproximadamente el 75% del EOO está protegido y que el 85% de la vegetación está clasificada como buena y se han identificado amenazas en curso, evaluamos a *Carpotroche pausandrifolia* como Casi Amenazada (NT).

Observaciones taxonómicas: *Carpotroche pausandrifolia* históricamente ha sido confundido con *C. platyptera*. De acuerdo con el concepto morfológico aquí adoptado, *C. platyptera* es una especie de la vertiente Caribe de Nicaragua y Costa Rica, que tiene láminas foliares densas y suavemente pubescentes en el envés y los frutos rojos (Fig. 5). Mientras que *Carpotroche pausandrifolia* tiene láminas foliares por el envés usualmente pubérrulas, o pocas veces tomentosas a tomentulosas y los frutos siempre son amarillentos, blancos, crema o verde-limón (Fig. 4). Otras características que pueden ayudar a distinguir estas dos especies, son los márgenes de las láminas foliares, en *C. platyptera* son por lo general marcadamente dentados (vs. subentero o pocas veces crenado a serrulado en *C. pausandrifolia*).

Carpotroche caceresiae D. Santam. y *C. longifolia* (Poepp.) Benth. son otras especies en América Central, que tienen una coloración similar en los frutos con esta nueva especie. La primera tiene un ámbito de distribución en la vertiente Caribe de Honduras (departamentos de Atlántida, Gracias a Dios, y Yoro), y Nicaragua (departamentos de Atlántico Norte y Jinotega); mientras la segunda en Panamá (provincia de Panamá) y que ha sido ampliamente recolectada en América Sur. Sin embargo, *C. caceresiae* tiene numerosas protuberancias entre las alas (vs. sin protuberancias entre las alas). Por otro lado, *Carpotroche longifolia* tiene los márgenes de alas profundamente laceradas (vs. enteras) y con protuberancias entre las alas (vs. sin protuberancias entre las alas en *C. pausandrifolia*).

Los frutos inmaduros de *Carpotroche ramosii* (Cuatrec.) Cuatrec. de la vertiente del Pacífico de Colombia y Ecuador, también tiene una coloración similar con *C. pausandrifolia* (ver Santamaría-Aguilar et al., 2021: Fig. 1). Sin embargo, en la madurez los frutos de la primera especie se tornan anaranjados externa e internamente (vs. siempre amarillentos, blancos, crema o verde-limón) y las semillas son completamente cubiertas por un arilo rojo (vs. ariloide en un solo lado y anaranjado, amarillento o raramente blanco).

Aparte de las especies anteriormente discutidas, en América del Sur se encuentran las siguientes especies de *Carpotroche*: *C. amazonica* Mart. ex Eichler, *C. brasiliensis* (Raddi) A. Gray., *C. crispidentata* Ducke, *C. grandiflora* Spruce ex Eichler, *C. froesiana* Sleumer, *C. integrifolia* Kuhl., *C. longifolia*, *C. pacifica*, y *C. surinamensis* Uittien, que tiene una coloración similar en los frutos con *C. pausandrifolia*. Sin embargo, se distinguen debido a que algunos de ellas casi no tienen alas (*C. amazonica*), o son muy cortas (*C. integrifolia* [ca. 0.3 cm de altura], *C. surinamensis* [0.4–0.8 cm altura]), las alas son laceradas y/o dentadas y con protuberancias entre ellas (*C. brasiliensis*, *C. crispidentata*, *C. longifolia*, *C. pacifica*), y las alas papiráceas y que se traslapan (*C. brasiliensis*, *C. froesiana*, *C. grandiflora*). Comparar estos atributos en la Fig. 6.

En el área donde se distribuye esta nueva especie, la

literatura menciona que los frutos son rojizos o morados (p. ej. Quesada Quesada et al., 1997; Zimmermann y Zamora, 2001). Sin embargo, este color nunca ha sido observado y tampoco descrito en ninguna etiqueta de algún ejemplar de herbario del Pacífico de Costa Rica.

En la Península de Osa, en un invernadero, las semillas duran hasta un año para germinar (R. Aguilar, observación personal).

El nombre *Carpotroche platyptera* en el sentido estricto del tipo y del material citado en el Apéndice I, se aplica con confianza a los ejemplares provenientes de Nicaragua y Costa Rica. Estudios adicionales, son necesarios para esclarecer la identidad de los ejemplares provenientes de Panamá, que posiblemente abarca dos identidades.

Como se puede notar, la taxonomía aquí propuesta es basado principalmente en la morfología de los frutos, ya que son los mejor representados y preservados en colecciones. Como se mencione en una contribución previa (Santamaría-Aguilar et al. 2021), flores en líquido y fotografías, sin duda pueden aportar mucha más información.

Especímenes adicionales examinados: COSTA RICA. Puntarenas: Aguirre. Quepos, San Cristóbal, camino hacia EL Brujo, 09°25'12"N, 083°58'39"W, 522 m, 7 Diciembre 2000 (fr.), *A. Estrada et al. 2609* (CR). Golfito. R. F. [Reserva Forestal] Golfo Dulce, alrededor de la Estación Agujas, 08°32'22"N, 083°25'07"W, 300 m, 23 Mayo 2000 (fr. inm.), *L. Acosta et al. 1433* (CR-2 cartulinas); P. N. [Parque Nacional] Corcovado, estación Los Patos, 900 m por el sendero que va a Sirena, 08°34'00"N, 083°31'00"W, 200 m, 15 Enero 1993 (bot. fl.), *R. Aguilar 1584* (CR-2 cartulinas, MO); Jiménez, Reserva Forestal Golfo Dulce, La Palma, Guadalupe, 08°36'39"N, 083°28'55"W, 123 m, 31 Agosto 2009 (fr.), *R. Aguilar 12263* (USJ*); Sendero Los Patos, Río Cedral, 08°34'00"N, 083°31'00"W, 200 m, 26 Mayo 1955 [1995] (fr. inm.), *L. Angulo 312* (CR-2 cartulinas, MO); Parque Nacional Corcovado, Cerro Brujo, 08°38'N, 083°35'W, 600 m, 23 Enero 1991 (bot. fl.), *E. Castro 248* (MO, USJ*); Parque Nacional Corcovado, Jiménez, Dos Brazos de río Tigre, cerro Rincón, 08°31'30"N, 083°28'00"W, 744 m, 3 Agosto 1990 (fr.), *A. Chacón 955* (CR, MO); along road between Chacarita and Rincón de Osa, ca. 6 km W of Interamerican Highway at Chacarita, 08°45'N, 083°18'W, 160 m, 2 Marzo 1985 (fr. inm.), *T. B. Croat y M. H. Grayum 59708* (MO); Parque Nacional, Sector Esquinas, vicinity of Fila Gamba hills behind Esquinas Rain Forest Lodge, along Quebrada Negra, at end of side road off of Villa Bricena [Briceño] Golfito Road, 08°42'00"N, 083°12'30"W, 200–300 m, 12 Setiembre 1996 (fr.), *T. B. Croat y D. Hannon 79273* (MO); Refugio de Vida Silvestre Golfito, La Gamba, parcela UCR a orilla de Quebrada La Gamba, 08°40'00"N, 083°12'30"W, 150 m, 10 Agosto 2007 (fr.), *M. Fernández et al. 82* (USJ*); Estación Río Bonito, sendero Fila Río Bonito, 08°42'35"N, 083°14'15"W, 420 m, 22 Mayo 1996 (fr. inm.), *E. Fletes y S. González 311* (CR); P. N. [Parque Nacional] Corcovado, Sendero entrada Los Patos, 08°34'00"N, 083°31'00"W, 200 m, 15 Marzo 1995 (est., fr. inm.), *B. Gamboa 86* (CR-2 cartulinas); Estación Agujas, Sendero Zamia, 08°32'11"N, 083°25'31"W, 300 m,

20 Junio 1997 (fr.), *B. Gamboa 1516* (CR); P. N. [Parque Nacional] Corcovado, 08°31'05"N, 083°28'10"W, 700 m, 28 Enero 1998 (bot. fls.), *B. Gamboa et al. 2098* (CR, MO); Fila before Rancho Quemado, near Rincón, 08°42'N, 083°33'W, 300 m, 12 Enero 1993 (est.), *A. Gentry et al. 78744* (CR, MO); R. N. V. S. [Refugio Nacional de Vida Silvestre] Golfito, Valle del Coto Colorado, fila Gamba, camino entre Golfito y La Gamba, 08°40'40"N, 083°11'55"W, 250–300 m, 11 Enero 1997 (bot. fl.), *J. Gómez-Laurito y V. Mora 12914* (USJ*); ridge between Quebrada Aguabuena and Quebrada Banegas, ca. 5 km W of Rincón de Osa, [08°42'00"N, 083°33'00"W], 300–400 m, 8 Octubre 1984 (fr.), *M. Grayum et al. 4054* (MO); La Gamba, bosque de los Austriacos, 08°41'N, 083°13'W, 300 m, 15 Diciembre 1993 (est.), *W. Huber y A. Weissenhofer 53* (CR); Parque Nacional Corcovado, Sirena, Pavo trail, 08°27'N, 083°33'W, 0–150 m, 17 Febrero 1988 (fr.), *C. Kernan 171* (CR, MO); 30 SE Palmar Sur, on Panamerican highway, 100 m, 6 Agosto 1964 (fr.), *R. W. Lent L-168* (o 2579) (USJ*); Rincon de Osa, slopes adjacent to airport, [08°42'N, 083°31'W], 20–300 m, 08 Enero 1974 (bot. fl.), *R. Liesner 1856* (L*, MO); Osa Peninsula, Corcovado National Park, trail from base of hills to Los Chiles, 08°31'N, 083°31'W, 20–400 m, 9 Julio 1977 (fr.), *R. Liesner 3095* (MO); P. N. [Parque Nacional] Corcovado, Estación Agujas, Sendero La Bonanza, 08°31'47"N, 083°26'06"W, 400 m, 5 Noviembre 1999 (fr.), *E. Mora et al. 620* (CR, MO); Estación Los Patos, cerca de la Estación, 08°34'09"N, 083°30'23"W, 250 m, 27 Mayo 1995 (fr. inm.), *M. Moraga 236* (CR, MO); Bahía de Chal, ca. 5 Km al N de Rincón, 08°44'N, 083°27'W, 50–150 m, 20 Agosto 1990 (fr. inm.), *C. Morales y A. Chacón 74* (CR, MO); R. N. V. S. [Refugio Nacional de Vida Silvestre] Golfito, quebrada Rancho, 08°40'20"N, 083°12'10"W, 250 m, 28 Enero 1992 (bot. fls., fr. inm.), *A. Moreno et al. 120* (CR); Aguabuena, Rincón, 08°42'20"N, 083°31'30"W, 60–70 m, 21 Enero 1991 (fr. inm.), *V. Nielsen 63* (CR-2 cartulinas); Golfito, 100 m, 06 Agosto 1966 (fr.), *S. Salas S-171* (o 1485) (USJ*); Rincón de Osa, cerros alrededor de Osa, 07 Agosto 1967 (bot. fl.), *S. Salas S-607* (o 2018) (USJ*); Estación Esquinas, sendero a la Calathea, 08°46'00"N, 083°15'00"W, 100 m, 27 Junio 1993 (fr. inm.), *M. Segura y F. Quesada 89* (CR); Guad[a] elu pe, 3 km S of La Palma, 08°38'N, 083°27'W, 4 Mayo 1993 (fr.), *K. Thomsen 365* (CR). Osa. Forested hills above Palmar Norte, trail to Buenos Aires, 830 m, 17 Febrero 1951 (fr.), *P. H. Allen 5895* (EAP*, US*); R. F. [Reserva Forestal] Golfo Dulce, Los Mogos, 08°45'30"N, 083°22'30"W, 100–200 m, 5 Septiembre 1991 (bot. fls.), *R. Aguilar 355* (CR-2 cartulinas, MO); Los Mogos, 08°45'30"N, 083°22'30"W, 100–200 m, 16 Octubre 1991 (bot. fl. y fr.), *R. Aguilar 541* (CR, MO); Bahía Chal, entrada Chocuaco, 08°43'20"N, 083°26'40"W, 20–100 m, 13 Septiembre 1995 (bot. fls.), *R. Aguilar et al. 4366* (CR-2 cartulinas); Balsar, San Rafael de Bella Vista, 09°02'30"N, 083°32'22"W, 400 m, 9 Enero 2000 (fr. inm.), *M. Blanco et al. 1113* (CR, K); Corcovado National Park, Los Planes, 08°38'39.8"N, 083°40'0.8"W, [sin elev.], 14 Abril 2008 (fr.), *X. Cornejo y R. Aguilar 8040* (USJ*); Parque Nacional Corcovado Los Planes (La Gloria), [08°37'12"N, 083°40'48"W], 100 m, 15 Febrero

1991 (bot. fl. ♂), *R. González 24* (K, MO); along new road from Piedras Blancas to Rincón de Osa, 08°45'N, 083°21'W, 200 m, 2 Julio 1984 (fr.), *M. H. Grayum et al. 3410* (MO); Fila Costeña, Fila Cruces, cabeceras del río Piedras Blancas, Cerro Anguciana, 08°49'18"N, 083°11'15"W, 950–1150 m, 10 Diciembre 1993 (bot. fls.), *M. Grayum 10666* (CR, MO); Los Planes, Bosque comunal, La Gloria, 08°37'30"N, 083°40'50"W, 170 m, 15 Febrero 1991 (bot. fls., fr. inm.), *G. Induni 242* (CR-2 cartulinas, MEXU*, MO); ríos Piedras Blancas y Esquinas, 75 m, 06 Agosto 1965 (est.), *A. Jiménez 2247* (CR); Rancho Quemado, Fila División, entre Banegas y Rancho Quemado, [08°40'48"N, 083°32'24"W], 300 m, 16 Julio 1991 (fr.), *J. Marín 17* (MO); Rancho Quemado, sector sureste, Sierpe, 08°39'10"N, 083°32'20"W, 400 m, 4 Noviembre 1991 (bot. fls.), *J. Marín 248* (CR-2 cartulinas, MO); Rancho Quemado, Finca de Delfín, Rincón, 08°42'N, 083°34'W, 200 m, 24 Enero 1991 (fr. inm.), *F. Quesada y M. M. Chavarría 407* (CR); camino de Altura, 2 to 5 miles west of Rincón de Osa, 400–1000 ft [120–305 m], 02 Agosto 1967 (fr.), *P. H. Raven 21487* (CR); Estero Guerra

de Sierpe, 08°46'00"N, 083°35'10"W, 200 m, 5 Junio 1995 (est.), *A. Rodríguez 780* (CR); Puerto Cortés, Fila Cuesta del Burro, 09°41'25"N, 083°30'31"W [Coordenada equivocada. Coordenada aproximada: 08°50'N, 083°30'W], 500–600 m, 17 Agosto 2005 (bot. fls.), *D. Santamaría y M. Moraga 2842* (CR). San José: *Pérez Zeledón, Sierra de Pejibaye*, 09°07'45"N, 083°37'25"W, 1140 m, 24 Enero 2000 (bot. fls.), *E. Alfaro et al. 2767* (CR-2 cartulinas); Puriscal, Z. P. [Zona Protectora] La Cangreja, Santa Rosa de Puriscal, bosque primario y secundario en las márgenes del río Negro, 09°42'06"N, 083°23'35"W, 350 m, 29 Julio 1992 (fr.), *J. F. Morales 276* (MO); P. N. [Parque Nacional] La Cangreja, Alto Concepción, Quebrada Grande, Sendero a Río Negro, 09°42'20"N, 084°21'55"W, 500–600 m, 14 Setiembre 2003 (bot. fls., fr.), *J. F. Morales y J. González 9843* (CR-2 cartulinas); Tarrazú, Zona Protectora Cerro Nara, 09°29'40"N, 084°00'50"W, 900 m, 22 Octubre 1998 (fr.), *A. Estrada y J. Solano 1836* (CR, MEXU*); San Lorenzo, 09°34'20"N, 084°03'52"W, 1400 m, 9 Julio 1997 (fr.), *L. Gutiérrez 66* (CR, K).

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APÉNDICE I

Ejemplares examinados de *Carpotroche platyptera* Pittier.

NICARAGUA. Río San Juan: Municipio El Castillo, Comunidad Boca de Escalera, 5 km al sur de la Comunidad Las Maravillas, 11°03'59"N, 084°20'56"W, 12 Abril 2005 (fr.), *W. Garrido 3905* (MO); Municipio El Castillo, La Bijagua, 3 km al N, 11°02'28"N, 084°18'52"W, 101 m, 20 Abril 2005 (bot. fls.), *R. Guzmán 4685* (MO); Municipio El Castillo, Comunidad Las Maravillas, Escaleritas al Este de la comunidad, 11°07'15"N, 084°21'04"W, 100 m, 19 Julio 2005 (fr.), *J. Luna 4278* (MO); Municipio El

Castillo, Comunidad Samaria, a 2 km del puesto sobre el carril norte, 11°06'03"N, 084°16'49"W, 400 m, 26 Mayo 2005 (bot. fls. y fr.), *J. Manzanares 3591* (MO); 1 km al E de Río Sábalo, 11°02'N, 084°27'W, 100 m, 21 Febrero 1984 (fr.), *P. P. Moreno 23188* (MO); Santa Crucita de la Gloria, 5 km al NE de Sábalo, 11°03'N 084°25'W, 70 m, 26 Febrero 1984 (fr.), *P. P. Moreno 23374* (MO, P-2 pliegos*); La Gloria, 3.5 km al NE del poblado de Boca de Sábalo, 11°03'N 084°26'W, 70 m, 20 Marzo 1985 (fr.), *P. P. Moreno 25455* (MO, P*); Boca de Sábalo, camino a Buenavista, [11°02'30"N 084°28'00"W], 70 m, 24 Marzo 1995 (fr.), *P.*

- P. Moreno 25641* (MO); Río San Juan, sobre el Río Sábalo, 11°03'N, 084°28'W, 40 m, 7–8 Julio 1984 (bot. fls.), *P. P. Moreno 26006* (MO); near Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed), [11°08'N, 084°12'W], 200 m, 7–9 Marzo 1978 (fr.), *D. Neill 3366* (MO); Municipio El Castillo, Boca de Sábalo, Estación de Investigación en Bosque Húmedo Tropical La Lupe, 11°08'N, 084°38'W, [40–50 m], 18 Enero 1995 (bot. fls.), *R. Rueda et al. 2910* (MO); Reserva Indio-Maíz, Municipio de El Castillo, a lo largo del caño el Pavon, a 3 km de su desembocadura en el Río Bartola, 11°01'N, 084°16'W, [150–200 m], 31 Diciembre 1996 (fr.), *R. Rueda et al. 5162* (MO); Reserva Indio-Maíz, Municipio de El Castillo, 3 km al norte de la desembocadura del Caño Chontaleño, 11°05'N, 084°15'W, [150–200 m], 13 Febrero 1997 (fr.), *R. Rueda et al. 5708*; Municipio el Castillo, Reserva Indio-Maíz, Cerro el Diablo, 11°01'N, 084°13'W, 100–200 m, 7 Diciembre 1998 (fr.), *R. Rueda et al. 9496* (MO); Municipio de El Castillo, Refugio Bartola, 10°58'N 084°20'W, 70 m, 15–22 Febrero 2005 (bot. fl.), *R. Rueda et al. 17887* (MO); Municipio El Castillo, Comunidad Nueva Samaria, a los alrededores del Río Romerón, sur del puesto, 11°06'03"N, 084°16'49"W, 400 m, 11 Enero 2005 (bot. fls.), *N. Toval y F. Guido 91* (MO); Municipio El Castillo, Comunidad Las Maravillas, 4 km al este, Finca La Estrella, 11°07'15"N, 084°21'04"W, 100 m, 8 Noviembre 2004 (bot. fls.), *D. Urbina 122* (MO). COSTA RICA. Alajuela: Río Peñas Blancas canyon, Nene Castro farm, 4 km NW of La Tigra, 10°22'00"N, 084°37'00"W, 200 m, 8 Setiembre 1994 (bot. fls.), *W. Haber 11860* (CR, MO); Guatuso, asentamiento campesino La Garroba, 10°45'N, 084°52'W, 80–100 m, 9 Noviembre 1987 (fr.), *G. Herrera 1179* (CR, MO); Boca Tapada, finca Daniel Murillo, parcela #9, 10°42'02"N, 084°13'08"W, 200–300 m, 6 Julio 2005 (est.), *D. Santamaría et al. 2305* (CR); San Carlos, Boca Tapada, Laguna de Lagarto lodge, 10°38'47"N, 084°02'33"W, 50 m, 5 Diciembre 2004 (fr.), *D. Solano 1503* (CR). Cartago: 24 km NE of Turrialba on hwy to Limón, then E at Tres Equis on jeep road 1.5 km, 09°58'N, 083°34'W, 450–525 m, 10 Mayo 1983 (fr.), *R. Liesner et al. 15350* (CR, MBM*, MO). Limón: [Bonilla], La Colombiana Farm of the United Fruit Co, [10°09'00"N, 083°34'48"W], 70 m, 6–7 Marzo 1924 (fr.), *P. C. Standley 36751* (US*); *ibid.*, 06–7 Marzo 1924 (bot. fls.), *P. C. Standley 36851* (US*); *ibid.*, 6–7 Marzo 1924 (fr. probablemente en el sobre), *P. C. Standley 36860* (US*); *ibid.*, 6–7 Marzo 1924 (bot. fls.), *P. C. Standley 36953* (US*); finca Montecristo, on the Río Reventazón below Cairo, [10°07'N, 83°32'W], 25 m, 18–19 Febrero 1926 (bot. fls.), *P. C. Standley y J. Valerio 48471* (US*); *ibid.*, 18–19 Febrero 1926 (bot. fls.), *P. C. Standley y J. Valerio 48547* (US*); *ibid.*, 18–19 Febrero 1926 (bot. fls.), *P. C. Standley y J. Valerio 48558* (US*); *ibid.*, 18–19 Febrero 1926 (bot. fls.), *P. C. Standley y J. Valerio 48585* (US*); *ibid.*, 18–19 Febrero 1926 (bot. fls. y fr.), *P. C. Standley y J. Valerio 48588* (US*); *ibid.*, 19 Febrero 1926 (bot. fls.), *P. C. Standley y J. Valerio 48788* (US*); [Matina], Finca La Lola, Madre de Dios, [10°06'N, 83°23'W], 50–75 m, 25 Marzo 1949 (fr.), *L. Holdridge 2526* (CR, MO); P. N. [Parque Nacional] Barbilla, sendero Topoyiyo, 10°59'25"N, 083°26'30"W, 300 m, 5 Mayo 1999 (fr.), *E. Mora 320* (CR, MO); Siquirres, cerca de la quebrada el Diablo, Altos de Pacuarito, [10°06'N, 083°28'W], 100 m, 24 Octubre 1986 (fr.), *Q. Jiménez 434* (CR, F*); La Alegría, Alto la Botella, 800–1000 m, 11 Agosto 2006 (bot. fls., y fr. inm.), *J. González et al. 8074* (LSCR); Siquirres, en las colinas montañosas, 17 Octubre 1973 (fr.; fr. no visto en MO), *L. J. Poveda 725* (CR, MO); Finca de don J. Berrocal, 60–70 m, 4 Octubre 1986 (fr.), *N. Zamora et al. 1305* (CR-2 pliegos, MO).

DOS NUEVAS ESPECIES DE *OTOBA* (MYRISTICACEAE) PARA ECUADOR Y UN NUEVO REGISTRO PARA COLOMBIA

DANIEL SANTAMARÍA-AGUILAR¹ Y ÁLVARO J. PÉREZ²

Resumen. Dos nuevas especies de *Otoba* del Ecuador, son descritas, ilustradas y comparadas con sus especies morfológicamente similares. *Otoba awaensis* se encuentra en los bosques húmedos de la Reserva Étnica Awá, Carchi; se reconoce por las marcas de vernación en el envés de la lámina y las venas laterales broquidódromas, con la vena intramarginal prominente, las flores estaminadas con la columna de los filamentos cilíndrica con anteras oblongas y los frutos glabros, con el pericarpo grueso en la madurez. *Otoba llanganatensis*, hasta el momento se conoce de una colección realizada en los bosques nubosos del Corredor Ecológico Llanganates-Sangay, Tungurahua; es un árbol de hasta 40 m de altura, con láminas foliares pequeñas, la base revoluta, las flores pistiladas con el gineceo glabro, y los frutos con el pericarpo grueso. Se registra por primera vez a *O. cyclobasis* en el departamento del Cauca, Colombia, esta especie se consideraba restringida a la costa Pacífica de Esmeraldas, Ecuador.

Palabras claves: Bosque nublado, Cauca, Distribución, Endemismo, Llanganates-Sangay, Magnoliales, Reserva Étnica Awá, Taxonomía

Otoba (A. DC.) H. Karst (Myristicaceae) es uno de los seis géneros Neotropicales de Myristicaceae que conforman la tribu *Viroleae* (Helmstetter et al., 2024). El género es monofilético y está representado por 14 especies incluidas las dos especies aquí propuestas (Jaramillo-Vivanco y Balslev, 2020; Frost et al. 2022; Santamaría-Aguilar y Lagomarsino (2022; Fig. 1). Cuatro de ellas se encuentran entre Nicaragua y Panamá, mientras 10 especies entre Colombia, Ecuador, Perú, Bolivia, Brasil y Venezuela (Santamaría-Aguilar et al., 2019; Jaramillo-Vivanco y Balslev, 2020; Santamaría-Aguilar y Lagomarsino, 2022). Al presente, este género no ha sido documentado en Guyana, Guyana Francesa y Surinam. Los países que tienen el mayor número de especies son Colombia (10 especies) y Ecuador (8 especies), las cuales habitan principalmente en las faldas y bosques montanos de los Andes y en el Chocó biogeográfico (Fig. 2).

En Ecuador la mayor diversidad regional en número de especies (5 especies) se encuentra entre la vertiente occidental de los Andes y la región biogeográfica del Chocó, desde el nivel del mar hasta los 2200 m de elevación. *Otoba glycyarpa* (Ducke) W. A. Rodrigues & T. S. Jaram. y *O. parvifolia* (Markgr.) A. H. Gentry se distribuyen ampliamente en los bosques tropicales amazónicos, y *Otoba llanganatensis* es el primer registro para los bosques nublados de la vertiente oriental de los Andes. En Ecuador, se las conoce comúnmente con el nombre de coco, cuángare

o sangre de gallina, son un componente estructural importante de los bosques debido a sus valores de abundancia (Pérez et al., 2013; Pinto et al., 2018). Todas las especies de *Otoba* son aprovechadas por su madera de mediana calidad en la construcción de viviendas y fabricación de aglomerados (de la Torre et al., 2008; Jaramillo-Vivanco y Balslev, 2020).

Morfológicamente el género se puede reconocer por los tricomas malpigiáceos, usualmente sésiles o algunas veces corto pediculados, mezclados con otros que son como escamas y usualmente cristales hialinos, nunca dendríticos o estrellados (Aymard et al., 2021). La vernación es conduplicada, que por lo general puede dejar marcas en el envés de la lámina a través de 2 a 4 pseudovenas o líneas paralelas en el nervio medio (Fig. 3) (Aymard et al. 2021). Las inflorescencias son pareadas en la axila de las hojas (Fig. 4), sin bractéolas (aunque pueden estar presentes en algunas flores pistiladas). Las flores estaminadas con los filamentos fusionados en una columna (excepto *O. novogranatensis* Moldenke en América del Sur), con las anteras fusionadas o libres; los frutos verdes a marrones, globosos a elipsoides (Fig. 5). Las semillas generalmente se encuentran cubiertas por un arilo laciniado blanco y dulce, usualmente con la presencia de una giba lateral o apical (de Wilde, 1991; Kühn y Kubitzki, 1993; van Roosmalen et al., 1996; Jaramillo-Vivanco y Balslev, 2020).

Los autores agradecen a las instituciones (B, COAH, COL, CR (incluido INB), F, HOXA, INPA, K, LSCR, LSU, MEXU, MO, NO, NY, P, QCA, QCNE y USJ) y su personal que mantienen y protegen las colecciones citadas en este texto, así como permitir el acceso, uso y préstamo de las mismas y poner a disposición numerosas imágenes digitales. Agradecemos a John L. Clark, Robin Foster, Rudy Gelis, Field Museum, The Smithsonian Institution, Missouri Botanical Garden, C. V. Starr Virtual Herbarium del New York Botanical Garden, por las imágenes que ilustran esta contribución. A Efraín Freire (QCNE) por su apoyo incondicional para la revisión de los especímenes depositados en su institución. Gerardo Aymard-Corredor muy amablemente realizó valiosos comentarios a esta contribución. Daniel A. Santamaría A. agradece profundamente al Department of Biological Sciences y al Shirley C. Tucker Herbarium, Louisiana State University por el apoyo brindado, así como a Laura P. Lagomarsino y Jennie Kluse, al Bentham-Moxon Trust (K) y el Instituto Amazónico de Investigaciones Científicas SINCHI (COAH), que permitió una visita para estudiar las colecciones de sus herbarios. Finalmente, a Julián Aguirre-Santoro, Julio C. Betancur, Nicolás Castaño, Cristian Castro, Laura Clavijo, David Granados, Alex K. Monro, Wilson Prada, Wilson Rodríguez, Rocío Rojas, Rodolfo Vásquez y Jorge M. Vélez por el apoyo brindado y hacer muy amena la visita a sus instituciones.

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FIGURA 1. Algunas de las especies de *Otoba* que se encuentran en el Ecuador. *Otoba glycyarpa* (A–C). A, envés de la lámina foliar; B, pecíolo y yema foliar; C, frutos. *Otoba gordoniiifolia* (D–F). D, haz de la lámina foliar; E, inflorescencia estaminada; F, flor estaminada. *Otoba parvifolia* (G–H). G, haz de la lámina foliar; H, frutos. *Otoba cyclobasis* (I). I, envés de la lámina foliar. Fotos por Álvaro J. Pérez.

MATERIALES Y MÉTODOS

La presente contribución se basa en el estudio de las colecciones depositadas en los siguientes herbarios: B, COAH, COL, CR (incluido INB), HOXA, K, LSCR, LSU, MO, NO, NY, QCA, QCNE y USJ; así como material en préstamo de F, GH, NY, y US (los acrónimos siguen Thiers [continuamente actualizado]). También se consultaron los especímenes depositados en los herbarios virtuales de: Field Museum (F; <http://emuweb.fieldmuseum.org/botany/taxonomic.php>), speciesLink (<https://specieslink.net/>), JSTOR Global Plants (<http://plants.jstor.org>), Muséum National d'Histoire Naturelle, París (P; <http://www.mnhn.fr>), Naturalis Biodiversity Center (<https://biportal.naturalis.nl/>), y Universidad Nacional Autónoma de México (MEXU; <https://datosabiertos.unam.mx/biodiversidad/>).

Las flores de los especímenes se rehidrataron (cuando el material lo permitió) antes de la medición. Se utilizó una regla para medir las hojas y las inflorescencias; un calibrador digital Neiko para medir frutos, semillas y el grosor de las ramitas, pecíolos y pedúnculos; y, finalmente, las flores, los tricomas y el grosor del pericarpo se midieron con una herramienta de calibración micrométrica (1div = 1 mm) bajo un estereoscopio de disección (Nikon SMZ800). Las medidas que exponen una sola dimensión indican la longitud de una estructura.

Los mapas fueron elaborados con SimpleMappr (Shorthouse, 2010). El mapa (Fig. 2) fue elaborado con 194 colecciones fértiles, siguiendo las coordenadas dadas por la base de datos Tropicos (<https://www.tropicos.org>).

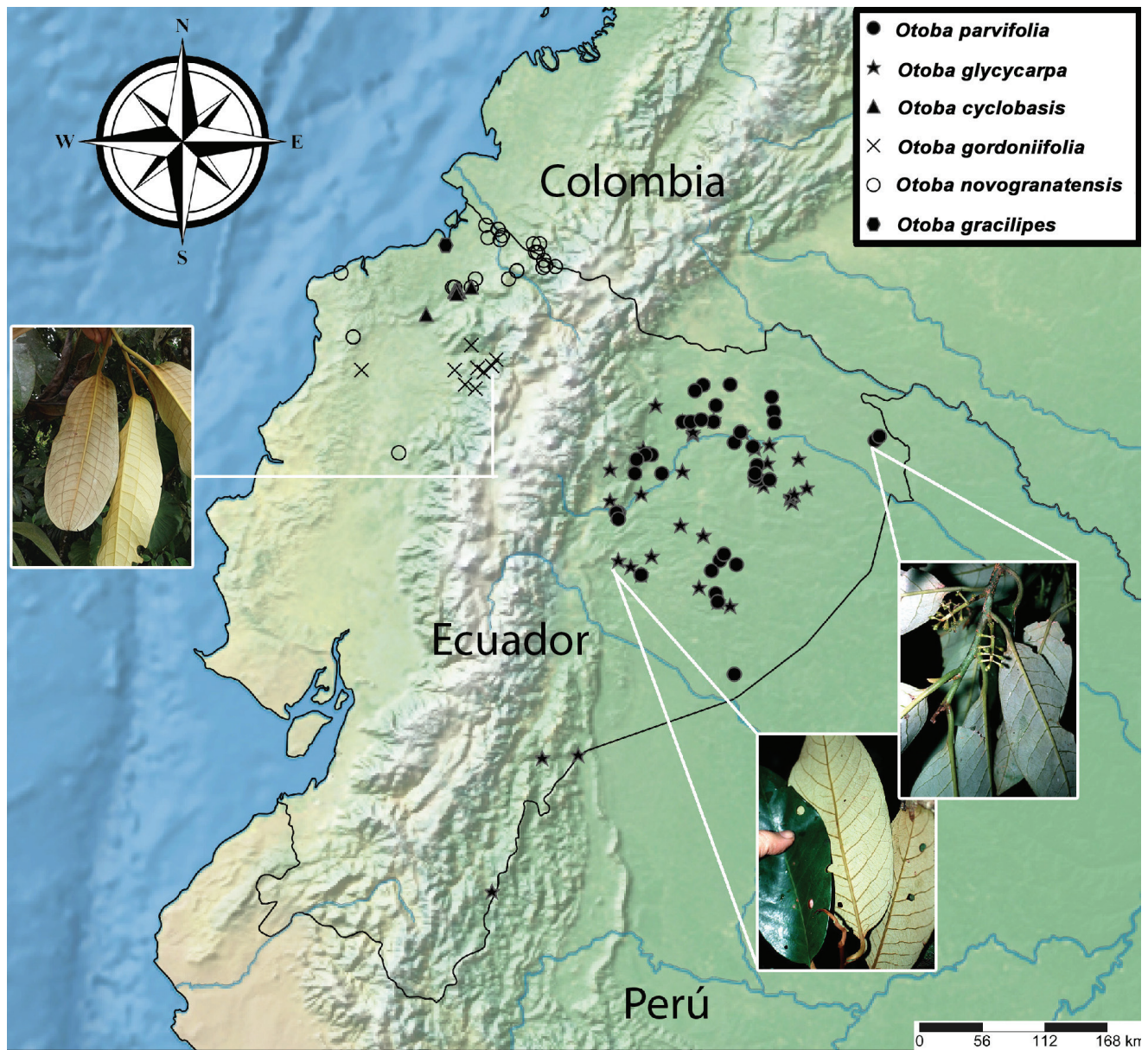


FIGURA 2. Distribución de seis especies de *Otoba* en Ecuador. Fotos por Rudy Gelis (*O. gordoniiifolia*), Robin Foster y Field Museum (*O. glycyarpa* y *O. parvifolia*).

TAXONOMÍA

Otoba awaensis D. Santam. & Á. J. Pérez, *sp. nov.* TIPO: ECUADOR. Reserva Étnica Awá, Parroquia El Chical, Centro San Marcos, 01°06'N, 078°14'W, 750 m, 20–30 abril 1993 (fr. inm.), P. Méndez, M. Aulestia y J. Pai 173 (Holotipo: MO [5028795, código de barras 1599889]); Isotipo: QCNE [74154]). Fig. 6.

Otoba awaensis is morphologically similar to *O. squamosa* D. Santam., from Colombia (1330–1450 m elevation), by the leaf blades with marks of vernation lines on abaxial side, short-winged petiole, and staminate flowers with lanceolate to oblong anthers. *Otoba awaensis* differs from *O. squamosa* by the staminate inflorescence with 7–14 (vs. 2–5) fascicles of flowers, short perianth (2.5–3 vs. 3.5–4.7 mm long), and fruits with thick pericarp (ca. 5 mm vs. 2.6–3 mm thick).

Árbol de 10–20 de altura y 16–35 cm DAP, la corteza externa e interna no descrita. Exudado rojizo, sin especificar en cual parte de la planta. Ramitas 1.1–1.8 (–2.4) mm diámetro, teretes a ligeramente angulada, la corteza pardoclaro a negruzca, proximal y distalmente glabrescentes a glabras, lenticeladas (proximalmente), lenticelas 1.5–2 mm, elípticas, blanquecinas a grisáceas. Yema foliar ca. 1.1 cm, densamente pubescente, los tricomas cobrizos. Hojas: pecíolo 1.3–2 (–2.5) cm longitud × 1.2–1.7 (–2) mm grueso, acanalado, glabrescente, angostamente alado, el ala ca. 0.5–0.7 mm de altura; lámina (8.6–) 10.2–15.7 × 4.4–6.3 (–6.8) cm, ovada a elíptica; el haz glabro, cuando seco negruzco a pardo claro a pardo oscuro, la superficie verrucosa (algunas veces áspera, i.e., en D. Rubio *et al.* 1057, MO, QCNE); el envés blanquecino o pardusco en material fresco, pardo

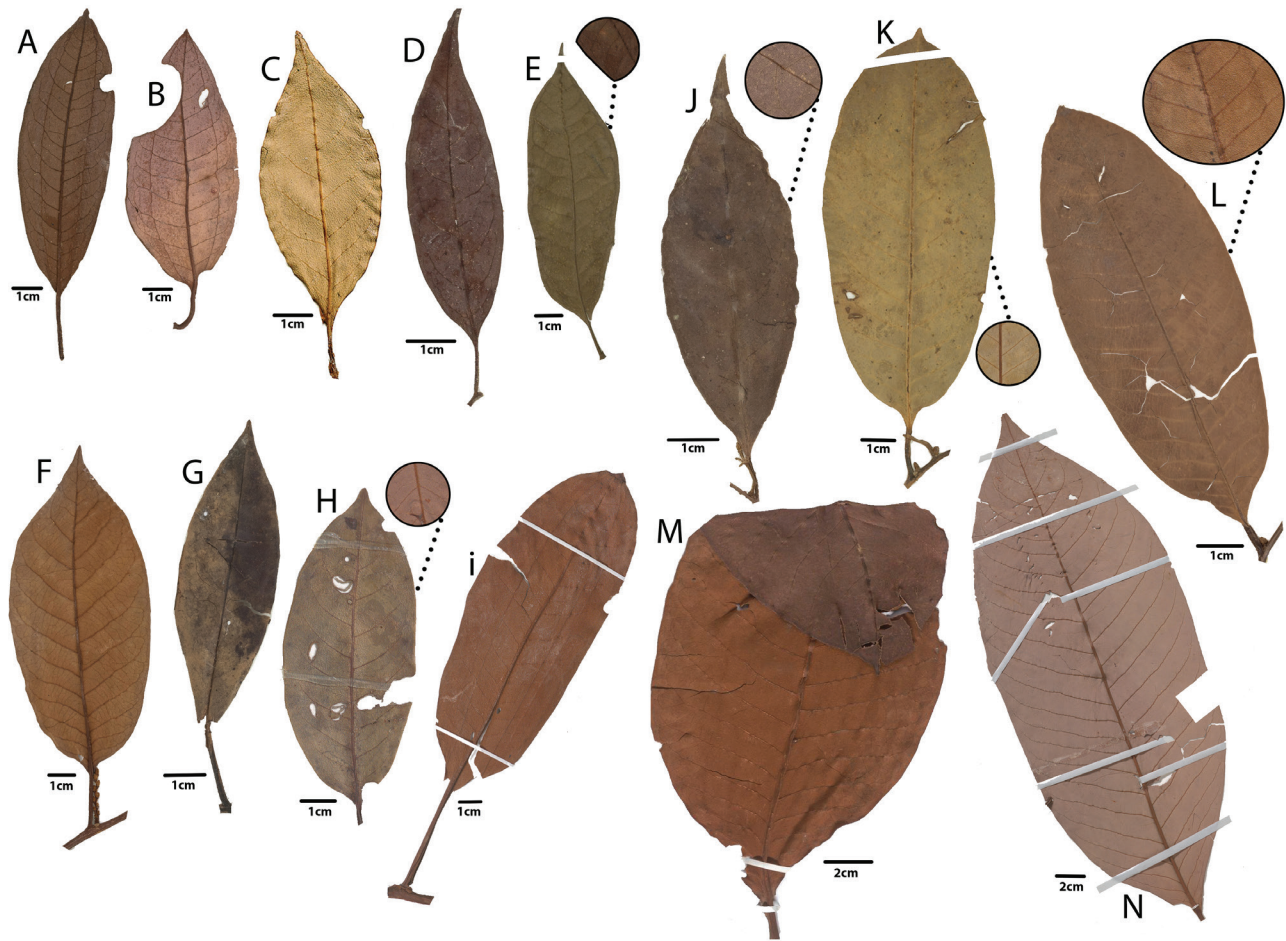


FIGURA 3. Láminas foliares de *Otoba*. **A**, *Otoba squamosa* (Á. Cogollo et al. 6279, NY); **B**, *Otoba awaensis* (B. Øllgaard et al. 57592, NY); **C**, *Otoba acuminata* (S. Aguilar et al. 993, F); **D**, *Otoba scottmorii* (R. Callejas et al. 5509, NY); **E**, *Otoba cyclobasis* (P. Méndez et al. 156, F; recuadro MO); **F**, *Otoba glycyarpa* (SEF No. 8772, NY); **G**, *Otoba llanganatensis* (J. L. Clark et al. 13971, NY); **H**, *Otoba gracilipes* (J. Cuatrecasas 14252, US); **I**, *Otoba gordoniiifolia* (J. Betancur et al. 2589, US); **J**, *Otoba vespertilio* (R. Aguilar et al. 5024, NY); **K**, *Otoba parvifolia* (D. Neill et al. 6231, F); **L**, *Otoba novogranatensis* (C. Játiya y C. C. Epling 2035, NY); **M**, *Otoba lehmannii* (A. Gentry et al. 68565, U); **N**, *Otoba latialata* (J. A. Steyermark y P. H. Allen 17227, US). Fotografías del Field Museum (C, E, K), Naturalis Biodiversity Center (M), New York Botanical Garden (A, B, D, F, G, J, L), y The Smithsonian Institution (H, I, N).

oscuro a pardo claro cuando seco, la superficie rugosa, algo ásperas, pubescente, que mezcla escasos tricomas malpigiáceos hasta 0.6 mm, sésiles a subsésiles, cobrizos, con la parte central más oscura, y abundantes tricomas escamosos de <0.1 mm, uniformes en color o con la parte central oscura y contrasta con los márgenes que son más claros; líneas de vernación presentes, de 2.6–3.9 cm de ancho (en la parte central de la lámina), a 0.7–1.3 cm de distancia del margen, del mismo color que la superficie; vena media por el haz plana a levemente elevada (especialmente en la sección distal), glabra, por el envés elevada, 1–1.2 mm de gruesa, glabrescente; venas laterales 12–14 por lado, 3–4 venas por 3 cm, broquidódromas, planas a ligeramente acanaladas en haz, planas a levemente elevadas en el envés, vena marginal indistinta por el haz, distintiva por el envés, venas terciarias indistintas en ambas caras; base atenuada a cuneada, plana; ápice acuminado a agudo, ca. 0.2 cm. *Inflorescencia estaminada* axilar, con 2 ejes principales, espiciformis, los ejes (3.8–) 5.2–7 cm, pubescentes, los tricomas cobrizos,

cada eje con 7–14 fascículos de flores, cada fascículo con 3–9 flores; bráctea 2–2.5 × 1.5–1.6 (–) mm (B. Øllgaard et al. 57592, MO), pubescente en la cara externa, los tricomas cobrizos, ciliadas; pedicelo (2–) 2.5–3.2 mm, pubescente. *Flores estaminadas* (A. Barfod 41438, MO): perianto 2.5–3 mm, amarillo (en material fresco), subcarnoso, connato 1–1.3 mm, la cara externa pubescente, la cara interna glabra; lóbulos 3, ca. 2 × 1.5 mm, sin puntos o líneas; columna de filamentos 1.2–1.6 mm, distalmente separada por 0.4 mm, usualmente cilíndrica, ligeramente más angosta distalmente, carnosa, glabra; anteras 3, 0.6–0.7 mm, libres, oblongas, el ápice levemente incurvado. *Inflorescencias y flores* pistiladas no vistas. Infrutescencia (con frutos inmaduros) ca. 5.5 cm, con 1 o 3 frutos, pedicelo ca. 1 cm. *Frutos* ca. 4.1 × 2.7 cm (en B. Øllgaard et al. 57426, QCA), verdes, globosos, la superficie glabra, sin lenticelas, lisos sobre la sutura de la dehiscencia, la base obtusa, el ápice acuminado, el acumen ca. 4 mm; pericarpo ca. 5 mm de grueso; semilla ca. 2 × 1.8 cm, similar en forma al fruto, pardo oscura cuando seca,



FIGURA 4. Inflorescencias parciales de *Otoba*. **A**, *Otoba scottmorii* (W. W. Thomas y C. J. Castaño 5501, NY); **B**, *Otoba latialata* (T. M. Antonio 1343, MO); **C**, *Otoba acuminata* (L. D. Vargas 3362, MO); **D**, *Otoba lehmannii* (M. Monsalve 3104, MO); **E**, *Otoba novogranatensis* (G. Tipaz 2699, MO); **F**, *Otoba vespertilio* (G. McPherson 11114, MO); **G**, *Otoba squamosa* (J. Pipoly et al. 16902, MO); **H**, *Otoba glycyarpa* (W. Palacios 1694, MO); **I**, *Otoba parvifolia* (W. Palacios 12837, MO); **J**, *Otoba gordoniiifolia* (L. B. Holm-Nielsen et al. 24457, MO); **K**, *Otoba cyclobasis* (E. Narváez et al. 1072, MO); **L**, *Otoba awaensis* (B. Øllgaard et al. 57592, MO). Todas las inflorescencias son con flores estaminadas.

gibosa, la giba lateral a un lado del ápice, ca. 4 mm, grosor de la testa no medido; arilo cuando fresco amarillo, cuando seco pardo oscuro, de textura membranácea, laciniado casi hasta la base; endospermo no visto.

Distribución: Endémica de Ecuador, hasta el momento solo ha sido recolectada en la provincia de Carchi (Fig. 7), cerca de la frontera con Colombia, en bosques planos inundables o de tierra firme, entre los 750–1500 m. El hábitat de esta especie se circunscribe en la región biogeográfica del Chocó-Darién definido por Morrone (2014), y con la provincia biogeográfica del Chocó Ecuatorial descrito por

el Ministerio del Ambiente del Ecuador (2013), un *hotspot* de biodiversidad y numerosos endemismos (Mittermeier et al., 2011).

Fenología: Especímenes con flores estaminadas fueron recolectados en enero y febrero; flores pistiladas no vistas. Frutos maduros en abril e inmaduros en noviembre.

Usos y nombres comunes: Cuángare (*P. Méndez et al. 173*), cuanyore (*D. Rubio et al. 1000*). Usos no mencionados entre los ejemplares estudiados, pero tradicionalmente su madera es utilizada para la construcción de viviendas como tablas de encofrado.

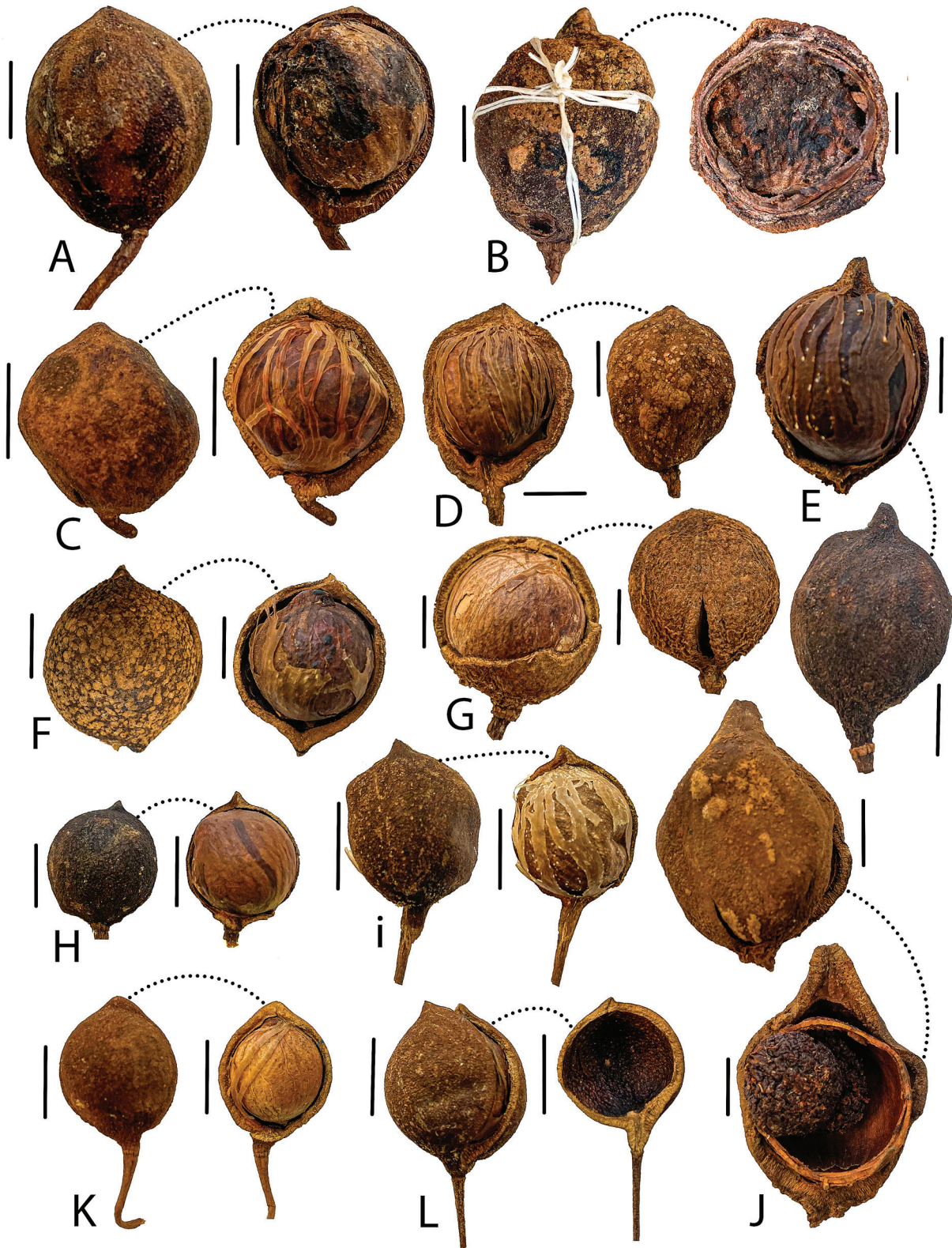
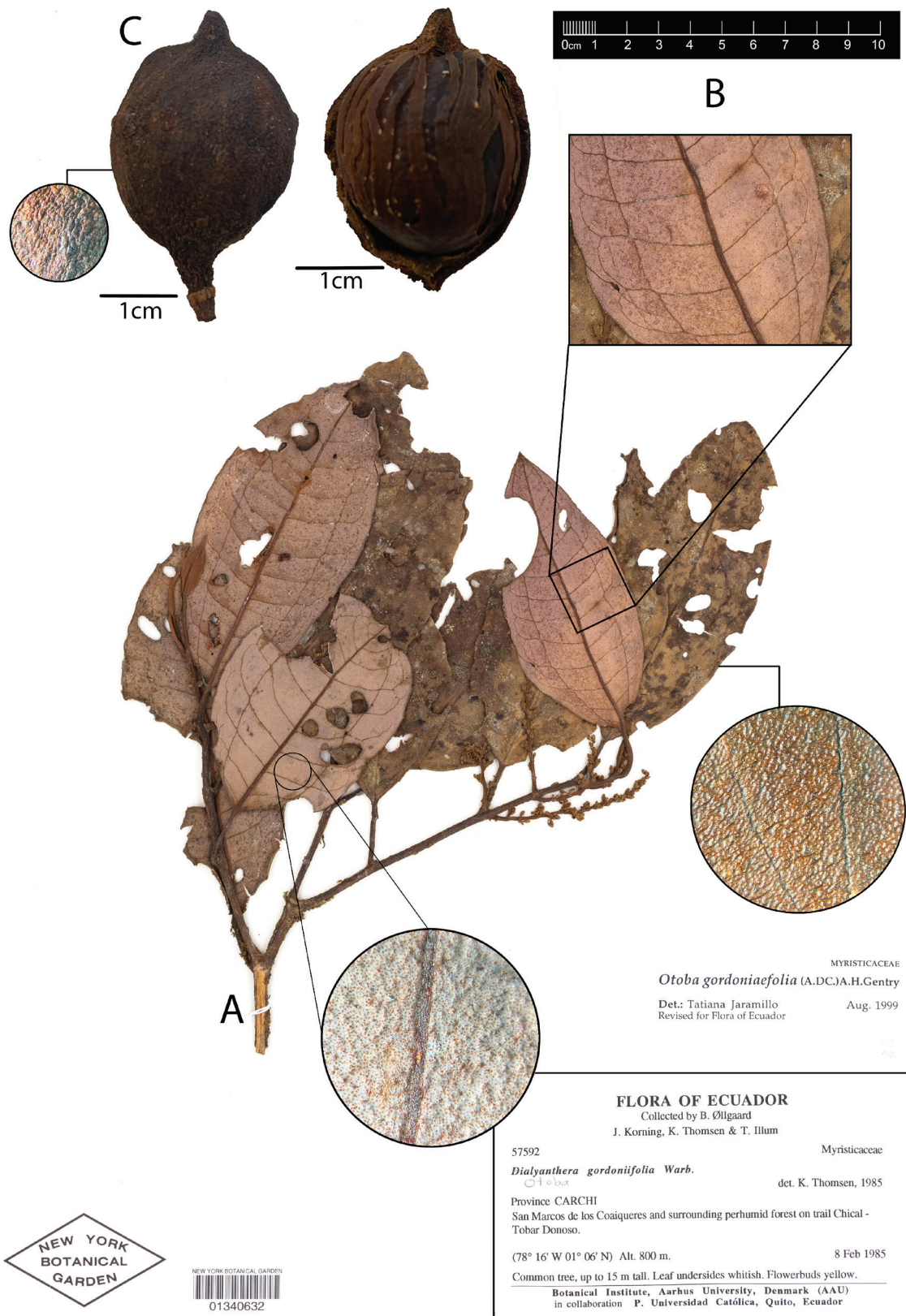


FIGURA 5. Frutos de *Otoba*. **A**, *Otoba llanganatensis* (J. L. Clark et al. 13971, MO); **B**, *Otoba novogranatensis* (C. Aulestia y A. Grijalva 1188, MO [izqda.], A. Grijalva et al. 476, MO [dcha.]); **C**, *Otoba gracilipes* (C. Játiva y C. C. Epling 775, NY); **D**, *Otoba. glycyarpa* (V. Zak 4087, MO); **E**, *Otoba awaensis* (P. Méndez et al. 173, MO, fr. inm.); **F**, *Otoba acuminata* (T. B. Croat 25225, MO); **G**, *Otoba gordoniiifolia* (J. Betancur et al. 2589, NY; fr. inm.); **H**, *Otoba parvifolia* (N. Revelo 52, MO); **I**, *Otoba cyclobasis* (W. A. Palacios y M. Tirado 11318, MO); **J**, *Otoba squamosa* (J. J. Pipoly 16745, MO); **K**, *Otoba latialata* (A. Juncosa 1254, MO; fr. inm.); **L**, *Otoba scottmorii* (R. Callejas et al. 5789, MO). Escalas: 1 cm.



MYRISTICACEAE
Otoa gordoniaefolia (A.DC.)A.H.Gentry
 Det.: Tatiana Jaramillo Aug. 1999
 Revised for Flora of Ecuador

FLORA OF ECUADOR

Collected by B. Øllgaard
 J. Korning, K. Thomsen & T. Illum

57592 Myristicaceae
Dialyanthera gordonifolia Warb. det. K. Thomsen, 1985

Province CARCHI
 San Marcos de los Coaiqueros and surrounding perhumid forest on trail Chical -
 Tobar Donoso.

(78° 16' W 01° 06' N) Alt. 800 m. 8 Feb 1985

Common tree, up to 15 m tall. Leaf undersides whitish. Flowerbuds yellow.

Botanical Institute, Aarhus University, Denmark (AAU)
 in collaboration P. Universidad Católica, Quito, Ecuador

FIGURA 6. *Otoa awaensis*. A, rama mostrando el haz y envés de las láminas foliares e inflorescencias estaminadas, en círculos un acercamiento de la superficie por el haz (dcha.) y el envés (izqda.); B, detalle de la vena marginal y las marcas por la vernación; C, frutos inmaduros, con un acercamiento de la superficie del fruto (izqda.) Basado en B. Øllgaard et al. 57592 (A, B; NY), D. Rubio et al. 1000 (A en círculos; MO), P. Méndez et al. 173 (C; NY). Fotografía del C. V. Starr Virtual Herbarium, New York Botanical Garden (A).



FIGURA 7. Distribución de *Otoba llanganatensis* (▲), *O. awaensis* (★), y *O. cyclobasis* (●) en Colombia y Ecuador. Fotografías de John L. Clark (▲), y Álvaro J. Pérez (●).

Otoba awaensis se puede reconocer por sus láminas foliares por las marcas que deja la vernación y las venas laterales broquidódromas en el envés, con la vena intramarginal prominente, y los escasos tricomas malpigiáceos y abundantes tricomas escamosos. Las flores estaminadas con la columna de los filamentos cilíndrica con anteras oblongas; y los frutos glabros. Algunas veces el haz y el envés cuando secos pueden ser algo ásperos.

Además de *Otoba squamosa* (discutida en la diagnosis), *O. gordoniiifolia* (A. DC.) A. H. Gentry, de Colombia y Ecuador, y (algunas veces) *O. lehmannii* (A. C. Sm.) A. H. Gentry, de Colombia, son otras especies que potencialmente

se podrían confundir con la nueva especie, esto debido a las marcas de la vernación en el envés de la lámina. Sin embargo, estas dos especies tienen láminas foliares más grandes ([13–] 24–43 cm vs. 4.4–6.3 [–6.8] cm), pecíolos más largos (3.2–7 cm vs. 1.3–2 [–2.5] cm) (Fig. 3I, M) y son prominentemente alados (vs. angostamente alados), el envés densamente pubescente, las flores estaminadas con el perianto más grandes (4–6 mm vs. 2.5–3 mm) (Fig. 4I, J).

En Ecuador, otra especie que puede presentar marcas por la vernación en el envés de la lámina es *O. novogranatensis* Moldenke (i.e. A. Grijalva et al. 484, MO; G. Tipaz 2699, MO). Sin embargo, la columna de filamentos es separada

por la mitad de su longitud o hasta la base (ver Jaramillo-Vivanco y Balslev, 2020: Fig. 1E), con anteras y frutos más grandes.

Notas: La mayor parte de las colecciones aquí referidas a *Otoba awaensis* fueron distribuidas como *O. gordonifolia*, *O. gracilipes* o *O. parvifolia*. El ejemplar *B. Øllgaard et al.* 57592 (MO), lleva dos ramas con flores estaminadas y un fruto separado de las ramas que podría corresponder con *B. Øllgaard et al.* 57426 (MO).

Especímenes adicionales examinados: ECUADOR. Carchi: N of San Marcos, along small streams and trails in primary rain forest on terra firme, 01°07'N, 078°20'W, 660 m, 17 enero 1983 (fl. ♂), *A. Barfod* 41438 (AAU [imagen digital], MO, NY, QCA); Perhumid forest on wet plateau above San Marcos de los Coaiqueres, on trail towards Gualpí bajo, 01°06'N, 078°17'W, 1000 m, 7 febrero 1985 (fr.), *B. Øllgaard et al.* 57426 (AAU [imagen digital], QCA); San Marcos de los Coaiqueres and surrounding perhumid forest on trail Chical-Tobar Donoso, 01°06'N, 078°16'W, 800 m, 8 febrero 1985 (fl. ♂), *B. Øllgaard et al.* 57592 (AAU [imagen digital], MO, NY, QCA); Reserva Etnica Awá, comunidad San Marcos, 25 km al NW de El Chical, parroquia Maldonado, 01°06'N, 078°17'W, 1500 m, 16–30 noviembre 1990 (fr. inm.), *D. Rubio et al.* 975 (INPA [imagen digital], MO, QCNE); ibid., 16–30 noviembre 1990 (fr. inm.), *D. Rubio et al.* 1000 (INPA [imagen digital], MO, QCNE); ibid., 16–30 noviembre 1990 (fr. inm.), *D. Rubio et al.* 1057 (INPA [imagen digital], MO, QCNE).

Otoba llanganatensis D. Santam. & Á. J. Pérez, *sp. nov.* TIPO: ECUADOR. Tungurahua: Cantón Baños, parroquia Río Negra[ro], Río Zuñac Reserve (EcoMinga Foundation), Llanganates-Sangay Ecological Corridor, 01°22'09"S, 078°09'07"W, 1855 m, 12 Mayo 2014 (fl. ♀, fr.), *J. L. Clark, D. [A.] Neill & L. Clavijo* 13971 (Holotipo: NY [código de barras 03108282]; Isotipos: ECUAMZ, not seen, US [3693655, código de barras: 03802336]). Fig. 8.

Species morphologically resembling *Otoba cyclobasis* T. S. Jaram. & Balslev from Ecuador and Colombia, and *O. vesperilio* D. Santam. & J. E. Jiménez from Costa Rica and Panama, by the small leaf blades, with the abaxial side without vernations marks, thin petioles, pistillate flowers with a glabrous gynoeceum; but differing by its leaf blades with revolute base (vs. plane), and fruits with tick pericarp (ca. 2.5 mm vs. 1–1.8 mm tick), also *O. llanganatensis* grows at high elevations (1855 m vs. 0–800 m elevations) in cloud forest (vs. humid forest).

Árbol de 40 m de altura y 40 cm DAP, la corteza externa e interna no descrita. **Exudado** no descrito. **Ramitas** 1.4–2 mm diámetro, teretes a ligeramente angulada, la corteza pardo-oscuro a negruzca, pubescentes distalmente, los tricomas ca. 0.3 mm, malpigiáceos, cobrizos, proximalmente glabras, lenticeladas, las lenticelas 0.7–1.5 mm, elípticas, blanquecinas a grisáceas. **Yema foliar** hasta 4 cm, densamente pubescente, los tricomas cobrizos. **Hojas:** pecíolo (1.1–) 1.5–1.8 cm longitud × 1.1–1.4 mm grueso, acanalado, glabrescentes o pubescentes en hojas jóvenes, angostamente alado, el ala ca. 0.5–0.8 mm de altura; lámina 7.7–10.2 × 2.5–3.5 cm, elíptica; el haz glabro, cuando seco negruzco a pardo, la superficie ligeramente verrucosa;

el envés blanquecino en material vivo, pardo cuando seco, rugosa, no áspera, pubescente, que mezcla tricomas malpigiáceos hasta 0.5 mm, sésiles, cobrizos o pocas veces algunos blanquecinos, con la parte central más oscura, y escamas de <0.1 mm, con la parte central oscura y contrasta con los márgenes que son más claros; líneas de vernación ausentes; vena media por el haz acanalada, glabra, por el envés elevada, ca. 0.1 mm de gruesa, glabrescente, el indumento más prominente en láminas jóvenes; venas laterales ca. 8 por lado, 3 venas por 3 cm, planas en el haz, levemente elevadas en el envés, vena marginal y venas terciarias casi indistintas en ambas caras; base atenuada, revoluta por ca. 2.5 cm; margen entero, plano; ápice acuminado, ca. 0.5 cm. **Inflorescencias y flores** estaminadas desconocidas. **Inflorescencia pistilada** ca. 1.1 cm, los ejes esparcidamente pubescentes, los tricomas cobrizos, el eje con 3 flores, solitarias; brácteas no vistas; pedicelo ca. 3–4 mm, pubescente; bractéola ca. 1 × 1.2 mm, en forma de “D,” diminutamente pubescente. **Flores pistiladas:** perianto (en botón floral) ca. 3 mm, carnoso, la cara externa pubescente, los tricomas cobrizos, la cara interna glabra, connato por ca. 1.2 mm; lóbulos 3, ca. 1.6 × 1.6 mm, ca. 0.3 mm de grueso, sin puntos o líneas traslúcidas; disco ausente; gineceo ca. 1.5 × 1 mm, glabro, sésil, estigma 2-labiado, ca. 0.5 mm de longitud. **Infrutescencia** posiblemente de un fruto solitario; pedicelo ca. 1.5 cm, glabro. **Frutos** 2.8–3.2 × 2.1–2.2 cm, verdes, globosos, la superficie glabra, sin lenticelas, lisos sobre la sutura de la dehiscencia, la base obtusa, el ápice obtuso a acuminado, el acumen 0–3 mm; pericarpo ca. 2.5 mm de grueso; semilla ca. 2.1 × 1.9 cm, similar en forma al fruto, pardo oscuro cuando seca, gibosa en el ápice, la giba ca. 6–7 mm, grosor de la testa no medido; arilo cuando fresco no descrito, cuando seco pardo a oliváceo, de textura membranácea, laciniado casi hasta la base; endospermo no visto.

Distribución: Endémica de Ecuador, hasta el momento se conoce sólo de la localidad tipo, en un bosque nublado de la Cordillera Oriental de los Andes Ecuatorianos, específicamente en el Corredor Ecológico Llanganates-Sangay, en la provincia de Tungurahua, a 1855 m de elevación (Fig. 7). Crece junto a *Magnolia llanganatensis* A. Vázquez & D. A. Neill (Magnoliaceae), descrita y endémica de esta localidad (Vázquez-García et al., 2016).

Fenología: Hasta el momento solo es conocida de flores pistiladas y frutos, que fueron recolectados en Mayo.

Usos y nombres comunes: Desconocidos.

Otoba llanganatensis se puede reconocer por sus láminas foliares pequeñas, con los pecíolos relativamente largos y delgados, el envés sin marcas de la vernación, y la base revoluta; flores pistiladas con el gineceo glabro; y frutos relativamente grandes (2.8–3.2 × 2.1–2.2 cm), con el pericarpo grueso (ca. 2.5 mm). Además, es un árbol de gran tamaño que crece en bosques montanos.

Además de las especies mencionadas en la diagnosis y los caracteres morfológicos (i.e. láminas foliares pequeñas, pecíolos delgados, hábitat), la nueva especie es morfológicamente similar a *O. scottmorii* D. Santam. de Colombia. Aunque el gineceo es desconocido en esta última, se presume que es glabro, ya que los frutos no tienen rastros de tricomas. Estas especies se pueden distinguir por las características enumeradas en la Tabla 1.

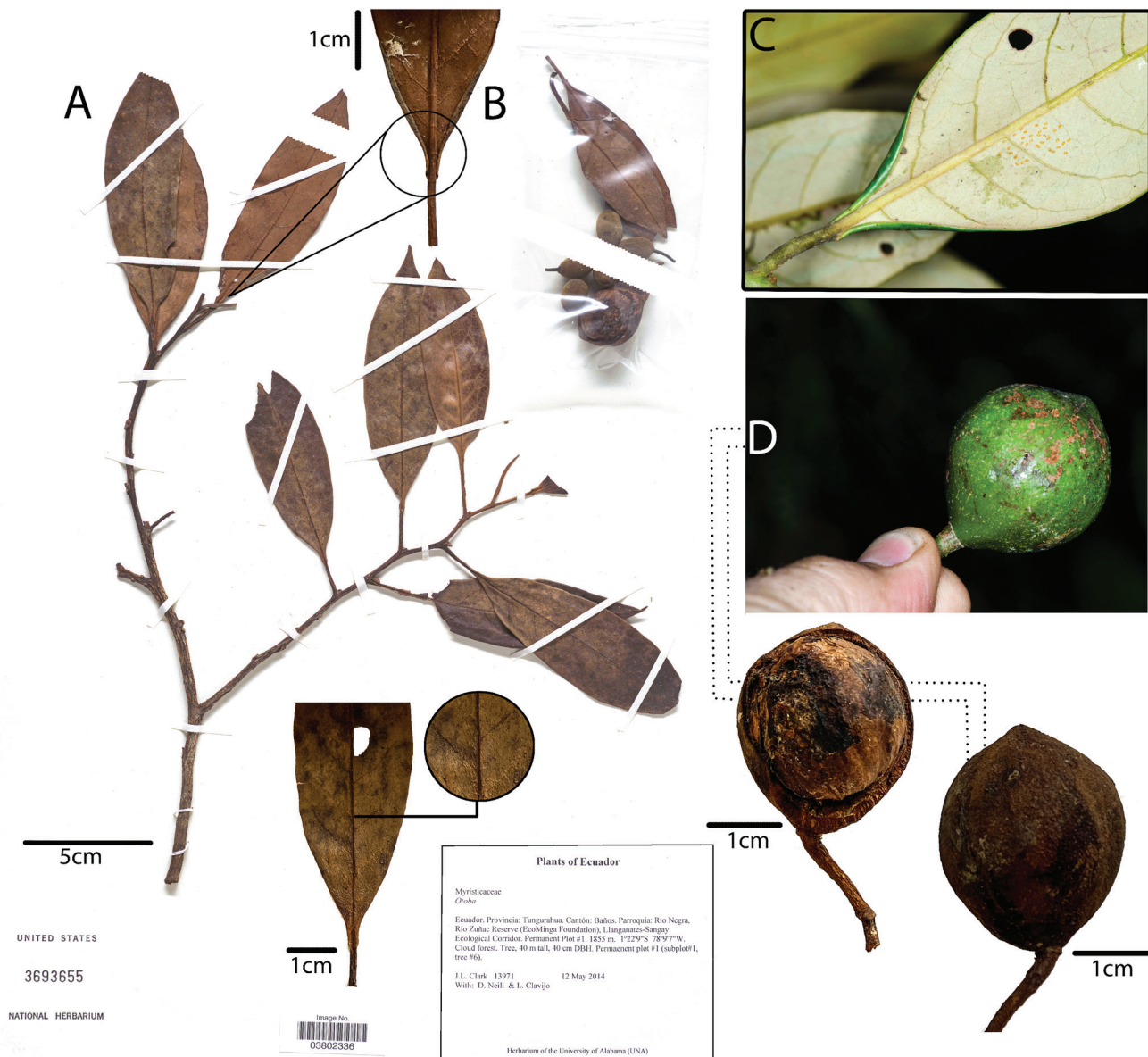


FIGURA 8. *Otoba llanganatensis*. **A**, rama mostrando el haz y envés de las láminas foliares y base de la lámina con un detalle en círculo mostrando la vena central y la superficie; **B–C**, base revoluta de lámina foliar; **D**, frutos frescos y en herbario. Basado en *J. L. Clark et al. 13971* (US). Foto por The Smithsonian Institution (A) y John L. Clark (C y D).

Otoba acuminata (Standl.) A. H. Gentry, de Costa Rica y Panamá (100–900 m y 500–1000 m de elevación, respectivamente), y *O. squamosa* D. Santam. de Colombia (1330–1450 m de elevación), son otras especies que también tiene láminas foliares similares en tamaño con *O. llanganatensis* (Fig. 3A, C), con *O. squamosa* además comparte el gineceo glabro. Sin embargo, la primera especie tiene el gineceo pubescente (vs. glabro) y los frutos con la superficie rugoso-granulosos, esparcidamente pubescentes a glabrescentes (vs. lisos y glabros), y el pericarpio más delgado (1–2.1 mm vs. ca. 2.5 mm de grueso). Mientras que *O. squamosa* tiene láminas foliares con el envés con marcas de vernación (vs. sin marcas; Fig. 3A, C), y frutos más anchos ([1.9–] 2.8–3 cm vs. 2.1–2.2 cm) (Fig. 5A, J).

Además de la nueva especie aquí propuesta, al este de los

Andes en Ecuador, se encuentran también *O. glycyarpa* y *O. parvifolia*, las cuales también se distribuyen principalmente en las tierras bajas de Colombia, Perú, Bolivia, y Brasil. *Otoba glycyarpa* tiene gineceo pubescente y frutos con pericarpio más grueso (Fig. 5D). Mientras que *Otoba parvifolia*, que tiene el gineceo glabro (característica que comparte en la nueva especie), se distinguen porque en general las láminas foliares son más grandes (Fig. 3K), con venas laterales más prominentes y mayor cantidad, con la base plana, el eje principal de la inflorescencia pistilada más largo, frutos con el ápice mucronado, y el pericarpio más delgado (Fig. 5H).

Nota: El ejemplar depositado en US (Fig. 8), lleva un paquete que tiene un fruto de esta nueva especie, y otros más pequeños que posiblemente corresponden con un *Drypetes* Vahl (Putranjivaceae).

Tabla 1. Comparación de *Otoba llanganatensis* con aquellas morfológicamente similares.

	<i>O. LLANGANATENSIS</i>	<i>O. CYCLOBASIS</i>	<i>O. SCOTTMORII</i>	<i>O. VESPERTILIO</i>
Longitud del pecíolo (cm)	(1.1–) 1.5–1.8	1–1.5*	0.5–1.1	0.8–2
Tamaño de la lámina foliar (cm)	7.7–10.2 × 2.5–3.5	9–14 (–18) × 3–5 ^a	5.5–8.5 (–11.2) × 1.7–2.5 (–3.7)	5.3–12.5 × 2–3.5 (–4.8)
# de venas laterales	ca. 8	14–17 ^a	4–7	6–8
Base de la lámina	revoluta	plana	plana	plana
Tamaño del fruto (cm)	2.8–3.2 × 2.1–2.2	1.5–2.5 × 1.5–2 ^a	1.8–2.1 × 1.5–1.7	2.2–2.7 × 1.6–1.7
Grosor del pericarpo (mm)	ca. 2.5	1–2 ^a	0.68–0.89	1.3–1.8
Tamaño de la semilla (cm)	ca. 2.1 × 1.9 cm	1–2 × 1–1.5 ^a	1.6 × 1.5	1.8–1.9 × ca. 1.7

^a Información tomada de Jaramillo-Vivanco y Balslev, 2020.

ADICIÓN A LA FLORA DE COLOMBIA

Otoba cyclobasis T.S. Jaram. & Balslev, se consideraba restringida a los bosques húmedos de la costa Pacífica en Esmeraldas, Ecuador (Fig. 7). Los autores de esta especie mencionaron que podría ser encontrada en Colombia (Jaramillo y Balslev, 2001; Jaramillo-Vivanco y Balslev, 2020). Este registro corológico es debido a la región biogeográfica de donde provienen las colecciones de esta especie. Aquí se confirma y se extiende el ámbito de distribución de esta especie para este país, basado en un ejemplar con flores recolectado en el Departamento del Cauca.

Otoba cyclobasis T.S. Jaram. & Balslev, *Nordic J. Bot.* 21(6): 563 (–566; fig. 2) (2001). TIPO: ECUADOR. Esmeraldas: Eloy Alfaro, Reserva Ecológica Cotacachi-Cayapas, Charco Vicente, río San Miguel de Cayapas, 00°43'N, 78°55'W, 150 m, [20–27] Mar. 1993 (fl. ♂), [P.] Méndez et al. [G. Tipaz, A. García] 156 (Holotipo: MO [5028796, código de barras:

288193]; Isotipos: F [imagen digital; 2162651, código de barras: F0064668F], QCNE, UPCB [imagen digital, 28933, código de barras: 0002308]).

Fenología: En Colombia el único ejemplar estudiado tiene flores estaminadas, y fue recolectado en abril; mientras en Ecuador entre febrero y abril. Colecciones con frutos en Ecuador fueron realizadas en febrero, marzo, septiembre, y noviembre.

Nombre vernáculo y usos: Hasta el momento para Colombia esta información es desconocida. Mientras en Ecuador se le llama: cuángare de monte, piimujchi (Chapalaachi) (A. P. Yáñez et al. 1514). La madera se utiliza para fabricar casas y canoas (A. P. Yáñez et al. 1514).

Especimen examinado: COLOMBIA. Cauca: López, Micay, río Naya, margen izquierda, ca. 1 km arriba de la vereda El Carmen, ca. 1 km de la orilla del río, 50–150 m, 2 abril 1992 (fl. ♂), A. Cogollo et al. 5162 (MO).

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ZYGIA NATALIAGOMEZAE (FABACEAE: LEGUMINOSAE-MIMOSOIDAE),
A NEW SPECIES FROM THE TRANSITIONAL DRY FOREST IN THE
CENTRAL ANDES IN THE DEPARTMENT OF VALLE DEL CAUCA, COLOMBIA

WILLIAM G. VARGAS¹ AND JUAN SEBASTIÁN MORENO^{2,3,4}

Abstract. *Zygia nataliagomezae*, a new species of Fabaceae from Colombia, is described and illustrated. The new species was found in a transitional foothill between a tropical dry forest and a sub-Andean Forest in the Central Andes in the Department of Valle del Cauca, Colombia. It can be recognized by its habit, a small tree of thin stems with little branching, and by its red inflorescence, which is borne on the defoliated branches rather than on the stem, as in many other species within the genus.

Keywords: Systematics, taxonomy, tropical dry forest

Resumen. Se describe e ilustra *Zygia nataliagomezae*, una nueva especie de Fabaceae de Colombia. La nueva especie se encontró en un piedemonte transicional entre un bosque seco tropical y un bosque subandino en los Andes Centrales, en el Departamento del Valle del Cauca, Colombia. Se puede reconocer por su hábito, un pequeño árbol de tallos delgados, poco ramificado y por su inflorescencia roja que se encuentra en las ramas desfoliadas y no en el tallo como en muchas otras especies del género.

Palabras claves: Sistemática, taxonomía, bosque seco tropical.

Zygia P. Browne (Fabaceae, Mimosoideae) is a neotropical genus distributed from Central America to South America (Rico-Arce, 1991; Barneby and Grimes, 1997). The genus comprises ca. 60 species of small to medium-sized, thornless trees with pinnate leaves and petiolar nectaries. The inflorescences are cauliflorous or ramiflorous, appearing in spikes or pseudoracemes, and the flowers are homomorphic, with some exceptions featuring an interstaminal disc that covers the base of the ovary. The seeds lack an aril and have a thin seed coat without a pleurogram. Species within the genus are ecologically associated with humid lowlands and

riparian forests, although most species are found in lowland areas, with a few exceptions occurring above 2000 meters in elevation (Britton and Rose, 1928; Barneby and Grimes, 1997; López-Contreras et al., 2015; Ferm et al., 2019).

In Colombia, *Zygia* is represented by 21 species, eight of which are endemic. These species are distributed from sea level to high Andean forests at nearly 2800 meters in elevation, with the Andes and the Amazon being the regions where the greatest number of species are found (Romero-Hernández, 2017). Here, we describe and illustrate a new species of *Zygia* from the Central Andes of Colombia.

MATERIALS AND METHODS

The description and illustrations were prepared from living specimens and flowers. Flowers and plants were dissected and measured, and digital images of those parts were taken with a Canon EOS 50D camera equipped with a macro lens. The description and photographic plate were based on specimens collected. The photographic compositions, including plant habit, leaves, views of the flower, inflorescence, and the dissected flower, were

digitally retouched in Adobe Photoshop CS6 and exported as JPEG files. 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 (Romero-Hernández, 2017). Specimens from the following herbaria, COL, CUVC, JBB, VALLE, CAUP, and MO (online), were consulted, and no additional material of the new species was found.

TAXONOMIC TREATMENT

Zygia nataliagomezae Vargas & J.S.Moreno, *sp. nov.*

TYPE: COLOMBIA. Valle del Cauca: Municipio de Palmira, vereda La Quisquina, en las márgenes de la quebrada Los Negros, 3°34'45"N 76°10'59"O, 1540 m, 27 March 2008, W. Vargas 18858 (Holotype: COL) Fig. 1–2.

Zygia nataliagomezae can be recognized by its growth habit: a small tree with thin branches and little branching,

leaves with 2–4 pairs of pinnae with numerous papyraceous folioles, inflorescences that are borne in the last defoliated branches and not on the stem, as in other species within the genus. The most similar species is *Zygia dinizii*, which has inflorescences in short and grouped spikes.

Tree, up to 4–5 m tall, stem 3–10 cm in diameter. *Apical buds* purple to light brown; *branches* reddish, terete,

We would like to thank the Corporación Autónoma Regional del Valle del Cauca - CVC for their support in the research of the first author in 2000 when this species was found. We also thank the Corporación Paisajes Rurales and Restaurar for their support during the investigation, and Maricel Arenas and Luis Ander Ruiz for their assistance in the search for specimens in the field, as well as in the collection of fruit and nursery propagation. Finally, we are grateful to Robert Anderson from the Canadian Museum of Nature and Jennifer Giron Duque from the Museum of Texas Tech University, who identified the weevil found in the new species.

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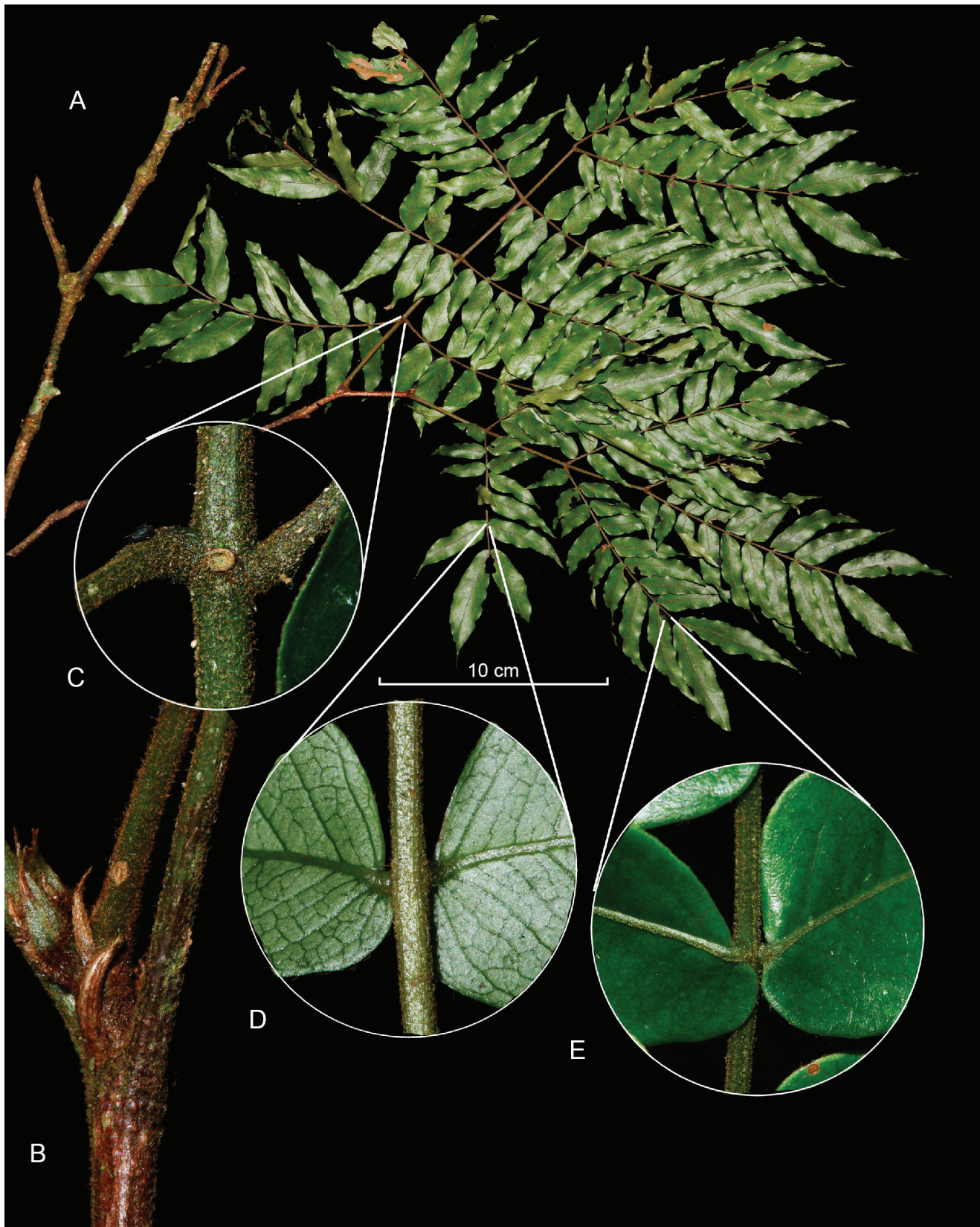


FIGURE 1. *Zygia nataliagomezae* Vargas & J.S. Moreno. **A**, habit; **B**, branch and apical bud; **C**, nectary; **D**, abaxial view of leaflet base and petiolule; **E**, adaxial view of leaflet base and petiolule. Composite digital plate by J. S. Moreno based on the holotype and photographs by W. Vargas.



FIGURE 2. *Zygia nataliagomezae* Vargas & J.S. Moreno. **F**, immature inflorescence and peduncle; **G**, mature inflorescence; **H**, dissected flower showing from right to left up to the stamen; **I**, close-up of the calyx; **J**, legume, and seeds. Composite digital plate by J. S. Moreno based on the holotype and photographs by W. Vargas.

tomentulose to glabrous, lenticellate. *Leaves* bipinnate, with tomentose axes, *stipules* linear, 3–4 × 1 mm, free, slightly falcate, tomentose ferruginous; *pulvinus* 2–4 mm long, tomentose, obscure; *petiole* 4.5–8.5 cm long, lenticellate, tomentose, with ferruginous brown hairs toward the base and the pinna insertion, striated; *rachis of the leaves* 8.5–12.0 cm long, tomentose, with a cupular gland, 0.8–1.0 mm wide between every pair of pinna, frequently absent or reduced in the apical pinna, the basal always present; *pinna* 3 pairs, eventually 2 or 4 pairs, the inferior pair shorter, *rachis* (interpetiolar segment) 5.5–11.0 cm long, 6–9 pairs of folioles, *petiolule* 0.3–0.7 cm long, the middle pair with a *petiolule* 0.3–0.5 cm long, *rachis* 12.0–13.5 cm, 10–11 pairs of folioles, the apical pair with a *petiolule* 0.3–0.7 cm long and 10–12 pairs of folioles; *folioles* unequal, elliptic-lanceolate, membranaceous, glabrous, rounded base, notoriously unequal, acute, margins undulate, central and laterals veins prominent, tertiary veins reticulate, basal 1.5–3.5 × 0.9–1.2 cm, middle 3.5–6.5 × 1.2–1.5 cm, apical 5.4–9.5 × 1.5–2.1 cm. *Inflorescence* a pendulous, solitary raceme that is borne over the defoliate apical branches, sometimes in the apex of foliate branches or very sporadically on the trunk; *peduncle* 0.8–1.2 cm long, purple; *rachis* 3.5–4.5 cm long, reddish to green purple; *bracts* reddish, linear, 0.8–1.5 mm long, less than 1 mm wide, persistent and subtending each flower. *Flowers* 120–140 per inflorescence, 40–45 open at once; *pedicel* red, 0.5–0.8 cm long; *calyx* tube red to yellowish, 3–5 mm long, apex and lobes green-yellow, glabrous, margins softly toothed to smooth, lobes 5, triangular, 0.5–1.0 mm long; *corolla* red, glabrous, tube 1.5–1.7 mm long, 2.0–2.5 mm wide at the base, 6.0–6.5 mm in diameter at the apex, lobes 5, triangular, 3 × 3.5–5.0 mm, margins sometimes green; *stamens* red, 55–75, basal half light-pink, 4.0–4.7 mm long, exceeding the corolla by 2.5–3.0 mm. *Ovary* 2–3 mm long, glabrous, white; *style* white-yellow, 4.8–5.5 cm long, longer than the stamens. *Legume* brown, tomentose, erect when immature; at maturity the apex is curved toward the ventral face or erect when short, 18–37 × 2.5–3.2 cm, laterally compressed, dorsal suture thick and prominent, dehiscent by ventral suture, valves ligneous, thick, alveolate-reticulate, acute. *Seeds* 11–18 per legume, oblong-applanate, compressed in the ends, 17–21 × 12–17 mm, 7–11 mm thick; testa brown-red, glabrous, papyraceous, smooth.

Additional specimens examined: COLOMBIA. Valle del Cauca: Florida, vereda La Diana, 1595m, 3°19'32.78"/76°10'13.01", WV37335 (CUVC), W. Vargas, M. Arenas, y L. Ander Ruiz, enero 23 de 2023. Pradera, vereda Canadá, 1638m, 3°23'21.94"/76°11'07.44", WV37338 (CUVC), W. Vargas, M. Arenas, y L. Ander Ruiz, enero 23 de 2023.

Eponymy: In honor of Natalia Gómez, wife of the first author, who in the year 2000 promoted the exploration of the area where the new species was discovered. She, from the Corporación Autónoma Regional del Valle del Cauca (CVC), has led the effort to establish nearly 300,000 hectares of protected areas in the department of Valle del Cauca.

Habitat and ecology: *Zygia nataliagomezae* is a species restricted to the Central Andes in the department of Valle

del Cauca, Colombia, with a range of distribution from 1200 to 1800 m in elevation. It is a small tree up to 2–5 m, and 4–10 cm in diameter and grows near water sources on rocky soils in the transition between tropical dry forest and montane humid forest. It is associated with trees such as *Aiouea montana* (Sw.) R. Rohde, *Nectandra turbacensis* (Kunth) Nees (Lauraceae), *Toxicodendron striatum* (Ruiz & Pav.) Kuntze (Anacardiaceae), *Cupania americana* L. (Sapindaceae), *Croton gossypifolius* Vahl (Euphorbiaceae), *Ficus* spp. (Moraceae), *Inga* spp. (Fabaceae), and *Chamaedorea pinnatifrons* (Jacq.) Oerst (Arecaceae), and shrubs and herbs such as *Picramnia* sp., *Heliconia griggsiana* L.B. Sm. (Heliconiaceae), *Aphelandra* sp. (Acanthaceae), *Renalmia aromatica* (Aubl.) Griseb. (Zingiberaceae), and *Anthurium buganum* Engl. (Araceae). It has been recorded flowering in January, May, and June and fruiting in January, September, and October.

In addition to deforestation, high seed predation increases the risk of extinction for *Zygia nataliagomezae*, which partially explains the absence of seedlings and young trees. In the two known isolated trees, predation affects 100% of the fruit and up to 80% of the seeds while they are still maturing. In some cases, seeds contained up to three larvae, resulting in 100% predation (Fig. 3). Ten larvae were raised to the adult stage and identified as belonging to the genus *Conotrachelus* Dejean (Coleoptera: Curculionidae) (Fig. 4), a genus with over 1200 species, many of which are pests in economically important crops such as avocado and apple (Mancera et al., 2018).

Predation before fruit dehiscence causes the loss of all or almost all seeds, even before maturity. Within the forest, predation is less pronounced, but fruit production is very low; during 22 years of observation, only three fruits were collected in a state of maturity and seeds free of damage. In January of 2023, we collected 42 fruits from two isolated trees, which contained 597 seeds, of which 87% presented some level of predation. The partially damaged seeds were immersed in a solution of insecticides and fungicides (Sulfoxaflor, Carboxin + Captan) for 12 hours, and we discarded 50% of the seeds due to high levels of damage. A final germination rate of 78.6% was obtained, these being the only plants obtained so far and they are being used in ecological restoration processes and conservation of this threatened species (Fig. 5).

Conservation status: *Zygia nataliagomezae* is known only from eight adult individuals and two juveniles in the type locality. This population is strongly threatened by deforestation, and little regeneration has been observed within the forest. Fewer individuals remain because of logging, as has been observed in at least fifteen visits to the site over the last twenty years, when more than twenty adult individuals were originally observed in the area. The species is not known to be cultivated despite the beauty of its inflorescences and the great potential it has as an ornamental plant. Unfortunately, it is a very slow growing species and only grows in the understory. The new species is classified as Data Deficient (DD) because we do not have the distribution and population information necessary to apply the IUCN categorization protocols. (IUCN Standards and Petitions Subcommittee, 2017; IUCN, 2024).



FIGURE 3. Seed predation in *Zygia nataliagomezae* Vargas & J.S. Moreno. **A**, seed predation within the legume showing damaged seeds; **B**, close-up sequence showing larva infestation and emergence from the seed.

Zygia nataliagomezae is recognized by its growth habit. It is a small tree with thin stems and sparse branching; leaves with 2–4 pairs of pinnae with numerous narrow, papery leaflets and compact; red, pendulous, and highly conspicuous inflorescences on the most recently defoliated branches or the subterminal portion of the branches, rather than on the main stem or the base of the branches as in most species of the genus. Among the six species of *Zygia* present in the region (Romero-Hernández, 2017), *Zygia nataliagomezae* is the only species found in the transitional zone between dry forest and sub-Andean Forest in the Cordillera Central. Together with *Zygia longifolia* (Humb. & Bonpl. ex Willd.) Britton & Rose, it is found at the lowest elevations in this part of the Cauca River basin. However, *Zygia longifolia* differs greatly in tree architecture, being tall with leaves having a single pair of pinnae and spike-like inflorescences clustered on the branches. In this sector of the Central Cordillera, *Zygia*

latifolia var. *communis* Barneby & J.W. Grimes might also be found. It differs from *Zygia nataliagomezae* by having much broader leaflets over 10 cm in length, and short, dense spike inflorescences on the stem and main branches. The greatest foliar similarity is with *Zygia dinizii* (Ducke) D.A. Neill, G.P. Lewis, & Klitg., but this species is found in lowland areas of the Amazon, Pacific, and Caribbean regions (Romero-Hernández, 2017), and it also has short, clustered spike inflorescences (Romero-Hernández, 2017). Regarding the type of large, showy, compact, and red inflorescences, the only species in the region is *Zygia lehmannii* (Harms) Britton & Rose ex Britton & Killip, which is found in the Amazonian foothills and the western slope of the Western Cordillera up to Valle del Cauca. It differs from *Zygia nataliagomezae* by having leaves with a single pair of pinnae, large broad leaflets sometimes over 15 cm in length, and inflorescences on the stems and main branches.



FIGURE 4. *Conotrachelus* sp. (Coleoptera: Curculionidae). **A**, adult *Conotrachelus* sp. on a branch of *Zygia nataliagomezae* Vargas & J.S. Moreno; **B**, various developmental stages of *Conotrachelus* sp, showing different phases of its lifecycle, including larvae and adult. The scale bar represents 5 mm. Photographs by W. Vargas.



FIGURE 5. Germination and early growth stages of *Zygia nataliagomezae* Vargas & J.S. Moreno seedlings. A, initial germination stage; B, early seedling development; C, intermediate growth stage; D, advanced seedling stage with developing leaves. Photographs by W. Vargas.

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VALIDATION AND CORRECTION OF *LEPANTHES* NAMES (ORCHIDACEAE: PLEUROTHALLIDINAE)

JUAN SEBASTIÁN MORENO,^{1,2,4,5} ROBINSON GALINDO-TARAZONA,¹
ALEJANDRO ZULUAGA,^{2,5} AND MARIO ALEXEI SIERRA-ARIZA³

When describing *Lepanthes nidiagongorana* Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza (Moreno et al., 2023: 682), the authors inadvertently failed to list the herbarium where the holotype was deposited, thus rendering the name invalid according to Art. 40.7 of the current International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018).

The name is hereby validated:

Lepanthes nidiagongorana Gal.-Tar., J.S. Moreno, Zuluaga, & Sierra-Ariza, *sp. nov.* TYPE: COLOMBIA, Valle del Cauca, municipality of Dagua, corregimiento del Queremal,

Cerro Tokio, predio sr. Álvaro, Parque Nacional Natural Farallones, 1852 m, 17 August 2020, *R. Galindo-Tarazona, L. Mamian & V. Varón & D. L. Mora 1497* (Holotype: CUVC).

Furthermore, the specific epithet in *Lepanthes nubiamuñozana* J. S. Moreno, Gal.-Tar. & Zuluaga (Moreno et al., 2023: 686) does not conform with articles 60.7 and 60.8 (d) of the code (turland et al., 2018), although it is still a valid name. Here we propose an orthographically correct epithet:

Lepanthes nubiomunoziana J. S. Moreno, Gal.-Tar. & Zulu.

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