Harvard Papers in Botany

Volume 25, Number 2 December 2020

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

Arnold Arboretum

Botanical Museum

Farlow Herbarium

Gray Herbarium

Oakes Ames Orchid Herbarium

ISSN: 1938-2944

Harvard Papers in Botany

Initiated in 1989

Harvard Papers in Botany is a refereed journal that welcomes longer monographic and floristic accounts of plants and fungi, as well as papers concerning economic botany, systematic botany, molecular phylogenetics, the history of botany, relevant and significant bibliographies, and book reviews. Harvard Papers in Botany is open to all who wish to contribute.

Instructions for Authors

http://huh.harvard.edu/pages/manuscript-preparation

Manuscript Submission

Manuscripts, including tables and figures, should be submitted via email to papers@oeb.harvard.edu. The text should be in a major word-processing program for either Microsoft Windows or the Apple macOS, or in a compatible format. Authors should include a submission checklist available at http://huh.harvard.edu/files/herbaria/files/submission-checklist.pdf

Availability of Current and Back Issues

Harvard Papers in Botany publishes two numbers per year, in June and December. The two numbers of volume 18, 2013, made up the last issue distributed in printed form. Starting with volume 19, 2014, Harvard Papers in Botany became an electronic serial. It is available by subscription from volume 10, 2005, to the present via BioOne (http://www.bioone.org/). The content of the current issue is freely available at the Harvard University Herbaria & Libraries website (http://huh.harvard.edu/pdf-downloads). The content of back issues is also available from JSTOR (http://www.jstor.org/) volume 1, 1989 through volume 12, 2007, with a five-year moving wall.

Publication Exchange Agreements

Please send inquiries to botserials@oeb.harvard.edu or to the Serials Acquisition Manager at Serials Acquisitions & Exchanges, Harvard Botany Libraries, 22 Divinity Avenue, Cambridge, MA 02138, U.S.A.

To meet our publication exchange agreements, we are currently developing a mechanism to supply an electronic copy of each issue to the institutions with which we maintain an exchange program.

For all other questions and/or to order back issues, please email papers@oeb.harvard.edu.

Cover: *Echinosepala glenioides* Pupulin
(See page 171, Fig. 9). Drawing by F. Pupulin and D. Solano Ulate.

Harvard Papers in Botany

Volume 25, Number 2 December 2020

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

(Continued on page ii)

(Continued from page i)

IDENTIFICATION OF *OUDEMANSIELLA CANARII* AND *O. CUBENSIS* (BASIDIOMYCOTA, PHYSALACRIACEAE) IN ARGENTINA USING MORPHOLOGICAL, CULTURE AND MOLECULAR ANALYSIS

Melisa Alberti,[1] Nicolas Niveiro,[2] Diego Cunha Zied,[3] and Edgardo Albertó[1,4]

Abstract. Species of *Oudemansiella* are distributed worldwide mainly in tropical to south temperate zones. Morphological identification of the species is usually complex and may even be ambiguous, especially for *O. canarii* and *O. cubensis*, since they share many similar characters. They have been considered synonyms by several authors. There are no recent descriptions or detailed illustrations of *Oudemansiella* species from Argentina, and molecular data are practically null. In this work these species were described and illustrated making use of new collections, culture data, and nrITS phylogenetic analysis. It was not possible on the basis of the results to differentiate the species macroscopically, but these were differentiated at the microscopic level, mainly by their pileipellis structure. Phylogenetic analysis from nrITS sequences enabled the molecular identification of these two species, and the cultivation of basidiomes on lignocellulosic substrate allowed us to affirm that both species have a hemiangiocarpic development.

Keywords: *Agaricales*, *Basidiomycota*, ITS, phylogeny, taxonomy

The genus *Oudemansiella* Speg. (Basidiomycota, Physalacriaceae) was proposed based on *Agaricus platensis* Speg. (Spegazzini, 1880a) and combined in *Oudemansia* Speg. (Spegazzini, 1880b). Later, it was replaced by *Oudemansiella* (Spegazzini, 1881) because *Oudemansia* already existed in Malvaceae. In the diagnosis, Spegazzini (1880b, 1881) characterized this genus as not having a manifest veil and having a central stipe, a hemispheric, fleshy, and nonliquescent pileus, and membranose lamellae, first connate, then free. The diagnostic characters presented by Spegazzini (1881) to delimit *Oudemansiella* were so broad that most agaric fungi would fit the description (Petersen and Hughes, 2010). Because of this broad description, the concept of the genus *Oudemansiella* has changed over the years. Some authors (Moser, 1955; Singer, 1962a,b, 1964; Clémençon, 1979; Pegler and Young, 1986; Singer, 1986; Yang et al., 2009) considered *Oudemansiella* a broadly circumscribed genus, which included *Xerula* Maire and *Mucidula* Pat. species. On the other hand, other authors (Dörfelt, 1979; Boekhout and Bas, 1986; Redhead et al., 1987; Petersen and Halling, 1993; Corner, 1994, 1996; Petersen and Methven, 1994; Boekhout, 1999; Halling and Mueller, 1999; Contu, 2000; Mueller et al., 2001; Horak, 2005; Petersen and Hughes, 2005; Petersen and Nagasawa, 2006; Petersen and Baroni, 2007; Petersen, 2000, 2008a,b,c) considered *Oudemansiella*, *Xerula,* and *Mucidula* as separate genera. Yang et al. (2009) and Petersen and Hughes (2010) summarized the taxonomic history of the *Oudemansiella* and *Xerula* complex.

With the advancement of molecular studies, *Oudemansiella* was placed in the *Physalacriaceae*. Petersen and Hughes (2010) completed the previous morphological and molecular studies, proposed four new genera (*Hymenopellis* R.H. Petersen, *Paraxerula* R.H. Petersen, *Pointiculomyces* R.H. Petersen, and *Protoxerula* R.H. Petersen), and redefined other previously existing genera (*Dactylosporina* (Clémençon) Dörfelt, *Mucidula*, *Oudemansiella*, and *Xerula*). In these assessments the genus *Oudemansiella* has been circumscribed to species with pileus dry to generally viscid, usually with scattered floccules; lamellae white to off-white and subdistant; and stipe central, usually without veil remnants, or with rudimentary or fugacious veil. Microscopically, basidiospores are characterized by being large, globose to subglobose, and white in prints, their pleuro- and cheilocystidia are well developed, and the pileipellis is formed of a polycystoderm or an ixotrichodermium, constructed of hyphal chains with subspherical, keg-shaped, fusiform, filamentous, or rod-shaped cells (Petersen and Hughes, 2010). The number of *Oudemansiella* species sensu stricto has been limited by these revisionary studies and 36 are recognized (Index Fungorum, 2020), with worldwide distribution, mainly in tropical to south temperate zones (Yang et al., 2009).

Morphological identification of *Oudemansiella* species is usually complex and may be ambiguous, especially for *O. canarii* (Jungh.) Höhnel. and *O. cubensis* (Berk. and M.A. Curtis) R.H. Petersen, since they share many characteristics and have been considered synonyms by several authors

---

The authors wish to thank Y. Briñoccoli for her advice on phylogenetic analysis. This research was made possible by the support of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) in Argentina (PIP 2014-0714) and by support for the International Barcode of Life (iBOL) Argentina project provided by the Consortium for the Barcode of Life (Canada).

[1] Instituto Tecnológico Chascomús INTECH (UNSAM–CONICET), Intendente Marino Km 8.2, CP 7130, Chascomús, Buenos Aires, Argentina.

[2] Instituto de Botánica del Nordeste, IBONE (UNNE–CONICET), Sargento Cabral 2131, CC 209 Corrientes Capital, CP 3400, Argentina.

[3] Facultad de Ciências Agrárias e Tecnológicas (FCAT), Universidade Estadual Paulista (UNESP), Campus de Dracena, Rod. Cmte João Ribeiro de Barros, km 651, Bairro das Antes, Dracena, SP 17900-000, Brazil.

[4] Corresponding author: ealberto@intech.gov.ar

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 131–143.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n1, Published online: 31 December 2020

(Horak, 1968; Pegler and Young, 1986; Singer, 1986; Wright and Albertó, 2002; Niveiro and Albertó, 2012). Many citations and descriptions of these two species should not be considered for identification purposes until further revisions of herbarium materials are carried out. Molecular data of *Oudemansiella* species are scarce and are often not accompanied by the corresponding morphological descriptions, which can lead to identification errors. In Argentina, *Oudemansiella* species sensu lato were cited by Spegazzini (1880b, 1881, 1899, 1926), Singer (1950), Singer and Digilio (1952), Singer (1964), Raithelhuber (1979, 1987, 1991, 1995, 2004), Wright and Albertó (2002), Wright and Wright (2005), and Wright et al. (2008), but there are no recent descriptions or detailed illustrations, and molecular data are practically null. The aim of this work is to describe and illustrate the two *Oudemansiella* species sensu stricto found in Argentina on the basis of new collections, culture data, and phylogenetic analysis formulated on molecular data.

Materials and Methods

Morphological Studies

The specimens were collected in northern and central Argentina. Strains were isolated in nature from wild specimens and conserved in glucose potato agar in the ICFC (INTECH Collection of Fungal Cultures, Laboratory of Mycology and Mushroom Cultivation, Chascomús, Argentina); reference in the WDCM database: 826. For the taxonomic identification, the specimens were analyzed macro- and microscopically following the criteria and terminology proposed by Alexopoulos and Mims (1985), Vellinga (1988), and Lodge et al. (2004). The color terminology followed Kornerup and Wanscher (1978). Microscopic observations were made from material mounted in a 5% KOH (v/w) with 1% floxin aqueous solution and Melzer's reagent to verify amyloid reaction (Wright and Albertó, 2002). The microscopic structures were measured directly through photographs taken with a Zeiss Discovery V20 SteREO camera using ZEN 2.6 (Blue Edition) software or with a BX 43 Olympus camera using Cell standard 3.0 software. For the basidiospores, "n=" indicates the number of basidiospores measured, "x=" the average value, "Q=" the Q-value (length/width), and "Qx=" the mean value of Q. The authors of scientific names agree with the *Index Fungorum* "Authors of Fungal Names" (Index Fungorum, 2020), and acronyms of herbaria follow the *Index Herbariorum* (Thiers, 2020). The collected material was dried, kept in the freezer for a week, and deposited as a reference in the CTES herbarium. One strain of each *Oudemansiella* species conserved in agar in the culture collection mentioned above was cultivated on wheat straw to obtain basidiomes in order to characterize the development. Spawn production, substrate preparation, spawning, incubation, and cultivation conditions followed the methodology proposed by Jaramillo Mejía and Albertó (2013) for cultivation of *Pleurotus ostreatus* (sterile technique), using plastic bags with substrate, and introducing the following modifications: 2-cm layer of casing soil formulated with 99% peat (Bertinat ™) and 1% $CaCO_3$ added after the incubation period. Mushrooms were grown in a room under controlled conditions with an air temperature of 24 C and relative humidity of 90%, and with periodic watering.

Molecular Genetic Analyses

Extracting DNA from basidiomes was performed in two ways: (1) by the Barcode of life Project following Ivanova and Grainger (2006) protocols, and (2) using EasyPure® Plant Genomic DNA Kit following the manufacturer's protocols. PCR amplification was performed following Ivanova et al. (2008). The nuclear ribosomal internal transcribed spacer region (ITS) was amplified using the basidiomycete-specific primer set: ITS1-F and ITS4-B (Gardes and Bruns, 1993). For samples processed through the Barcode of Life project, PCR products were sequenced in the Canadian Centre for DNA Barcoding (CCDB). For the rest of the samples, PCR products were sequenced at Macrogen, Korea.

Molecular Phylogeny

The dataset was compiled using our 15 sequences and 21 sequences selected from GenBank on the basis of BLAST results. *Hymenopellis radicata* (Relhan: Fr.) R.H. Petersen and *Xerula pudens* (Pers.) Singer were selected as outgroups (Table 1). Sequence editing and alignment were done in BioEdit (version 7.2.5). Sequences were aligned under the Clustal IW criteria. Phylogenetic reconstruction was inferred using maximum likelihood estimation (ML) and Bayesian inference (BI) separately. The best evolutionary model for ML was TrN+G; it was estimated using Bayesian information criterion (BIC) in jModelTest2 (version 1.6) (Guindon and Gascuel, 2003; Darriba et al., 2012). The evolutionary model used for BI was GTR+I+G. Maximum likelihood estimates were calculated using MEGA X (Kumar et al., 2018). The statistical support for the resulting phylogenies was assessed by bootstrapping with 1,000 replicates (Felsenstein, 1985). Bayesian inference was performed in MrBayes 3.2.7 (Ronquist et al., 2012), and it was carried out with two simultaneous runs of four Markov Monte Carlo chains. These were run for 10^6 generations, with sampling each 100 generations, and with a burnin of 1,001 generations; the final consensus was based on 17,959 trees used to estimate posterior probabilities. Only the topology of the ML tree is shown, indicating support values of Bayesian posterior probability/bootstrapping (BPP/BS) of each node. A node was considered to be strongly supported if it showed a BPP ≥ 0.95 and/or BS ≥ 90%, whereas moderate support was was indicated by a BPP ≥ 0.90 and/or BS ≥ 70%.

TABLE 1. List of sequences used in the phylogenetic analyses and their references.[1]

SPECIES	SPECIMEN VOUCHER	ORIGIN	GENBANK ACCESSION NUMBER	REFERENCE
Hymenopellis radicata	LE-BIN 1795	Russia	MK795851	Moiseenko et al. (unpubl.)
Hymenopellis radicata	TENN60080	USA	GQ913389	Petersen and Hughes (2010)
Oudemansiella australis	RV95/416	Australia	AF321473	Mueller et al. (2001)
Oudemansiella australis	RV95/297	Australia	AF321472	Mueller et al. (2001)
Oudemansiella canarii	JM98/221	China	AF321476	Mueller et al. (2001)
Oudemansiella canarii	TENN62802	USA	GQ892793	Petersen and Hughes (2010)
Oudemansiella canarii	FLAS-F-61207	USA	MH211812	Kaminsky et al. (unpubl.)
Oudemansiella canarii	**13v**	**Argentina**	**MT271880**	**This work**
Oudemansiella canarii	**14v**	**Argentina**	**MT272111**	**This work**
Oudemansiella canarii	**15v**	**Argentina**	**MT271881**	**This work**
Oudemansiella canarii	**22v**	**Argentina**	**MT271883**	**This work**
Oudemansiella canarii	**33v**	**Argentina**	**MT271882**	**This work**
Oudemansiella canarii	**36v**	**Argentina**	**MT272113**	**This work**
Oudemansiella canarii	**68v**	**Argentina**	**MT273085**	**This work**
Oudemansiella canarii	**3325**	**Argentina**	**MT272114**	**This work**
Oudemansiella canarii	**3326**	**Argentina**	**MT272115**	**This work**
Oudemansiella canarii	**3328**	**Argentina**	**MT272116**	**This work**
Oudemansiella canarii	**MA4**	**Argentina**	**MT272117**	**This work**
Oudemansiella canarii	**MA5**	**Argentina**	**MT272119**	**This work**
Oudemansiella canarii	**3060**	**Argentina**	**MT272112**	**This work**
Oudemansiella crassifolia	HKAS43500	China	AY665205	Zhang and Yang (unpubl.)
Oudemansiella crassifolia	S140148	China	MK886522	Hu et al. (unpubl.)
Oudemansiella cubensis	TENN51190	Costa Rica	GQ892794	Petersen and Hughes (2010)
Oudemansiella cubensis	TENN59771	Dominican Republic	GQ892791	Petersen and Hughes (2010)
Oudemansiella cubensis	TENN58954	Argentina	GQ892789	Petersen and Hughes (2010)

[1] Data in boldface correspond to the new sequences proposed in this work.

TABLE 1 CONT. List of sequences used in the phylogenetic analyses and their references.[1]

SPECIES	SPECIMEN VOUCHER	ORIGIN	GENBANK ACCESSION NUMBER	REFERENCE
Oudemansiella cubensis	TENN56534	Costa Rica	GQ892790	Petersen and Hughes (2010)
Oudemansiella cubensis	TENN49023	Puerto Rico	GQ892792	Petersen and Hughes (2010)
Oudemansiella cubensis	**MA2**	**Argentina**	**MT272118**	**This work**
Oudemansiella cubensis	**MA3**	**Argentina**	**MT271884**	**This work**
Oudemansiella cubensis (submitted as O. canarii)	RVPR100	Puerto Rico	AF321479	Mueller et al. (2001)
Oudemansiella cubensis (submitted as O. canarii)	RVPR33	Puerto Rico	AF321478	Mueller et al. (2001)
Oudemansiella cubensis (submitted as O. canarii)	RV96/35	Costa Rica	AF321477	Mueller et al. (2001)
Oudemansiella cubensis (submitted as O. canarii)	ECO-TA-HO 7876	Mexico	MF156259	Guillen-Navarro et al. (unpubl.)
Oudemansiella cubensis (submitted as O. canarii)	170854	Brazil	KJ620018	Vitola et al. (unpubl.)
Xerula pudens	178026	Sweden	AF321491	Mueller et al. (2001)
Xerula pudens	F. Popa1969	Germany	MF063189	Qin et al. (2018)

[1] Data in boldface correspond to the new sequences proposed in this work.

RESULTS

Taxonomy

Oudemansiella canarii (Jungh.) Höhnel, Siztgber. K. Akad. Wiss., Wien, math.- nat. Kl. 118: 276. 1909. TYPE: INDONESIA, Java. Mt. Halimun Nat. Park, loop trail from Cikiniki, ~1000 m elev., 8 Jan 1999, DE Desjadin, DED6886 (Neotype: SFSU, BO; Holotype: not present ex herb Junghuhn at L.). Fig. 1–2.

Basionym: *Agaricus canarii* Jungh. Praemissa in floram cryptogamicam Javae Insuae, Fasc. 1: 82. 1838.

Basidiomata gregarious in small cluster, xylophagous (Fig. 1A). *Pileus* up to 65 mm broad, hemispherical-convex when young, then plano-convex to plane (Fig. 1B). Surface markedly glutinous when young, embedded in translucent mucilage that disappears with maturity, hygrophanous dark brown (7F4-6) when young, clearing up when dehydrated, brownish orange (7C4-6), yellowish brown (5D-E4), finally yellow-white (4A2-3) on the disk to yellowish white (2A2) to white (2A1) at the margin at maturity. Glabrous or occasionally with scattered veil patches forming small, appressed, dark brown (7F4-6) to yellowish-brown (5D-E4) scales, in young specimens embedded in the glutinous surface. Margin smooth with tiny fragments of veil when young. *Context* thin, up to 2 mm, white (2A1) to ashen or pale (2A2, "yellowish-white"), odor farinaceus that accentuates and turns sweet when dry. *Lamellae* adnate with a decurrent tooth when young (Fig. 1C), then adnate to adnexed, ventricose to broadly ventricose, white (1A1) when young, and sometimes yellowish white (2A2) at maturity with a fimbriate margin under a lens, lamellulae of one or two orders. *Stipe* central (Fig. 1A,D), 15–80 × 4–9 mm, straight or curved, cylindrical, tapering to the apex, with a bulbose to subbulbose base, white (2A1) to pale (2A2), concolorous with the lamellae, solid, tough, fibrous, surface dry, longitudinally fibrillose, with small remnant fragments of veil toward the apex, which disappear at maturity. *Basidiome development* hemiangiocarpic (Fig. 1D). *Spore print* white (2A1) to pale (2A2) and extremely abundant (Fig. 1E). *Basidiospores* 16.79–19.96 × 17.69–21.99 μm, x = 18.11 × 19.13 μm, Qx = 1.00–1.16, Qx = 1.05, n = 25; globose to subglobose, smooth, nonamyloid, hyaline, thin walled, with multigranular contents and abundant guttules (Fig. 2A). *Basidia* 40–69 × 22–35 μm, clavate, 4-spored, hyaline, thick walled (Fig. 2B). *Pleurocystidia* 146–246 × 25.75—38.00 μm, lageniform, formed by a globose to subglobose base, and a narrower, cylindrical, long neck, thick walled at the base, thin walled toward the apex, homogeneous contents (Fig. 2C). *Cheilocystidia* 9–28 × 44–84 μm, clavate to broadly clavate, often pedicelate. *Hymenophoral trama* subregular, consisting of 4- to 35-μm-diam., thin-walled hyphae, nonamyloid. *Pileipellis* formed by two tissue types: (1) underneath, a more or less hymeniform layer, formed by spindle cells, cylindrical to

FIGURE 1. Basidiomes of *O. canarii*. **A**, general aspect; **B**, specimens obtained in culture; **C**, lamellae; **D**, partial veil; **E**, spore print. Bars = 1.3 cm (A); 2.6 cm (B); 0.15 cm (C); 0.3 cm (D); 0.92 cm (E).

thinly claviform, softly pigmented olive, 67–101 × 9.0–13.5 μm, thin walled and with homogeneous content; (2) on the surface, an ixotrichoderm formed by hyphae 4.7–6.75 μm in diam. and 90–202 μm in length, erect, occasionally branched and intermixed (Fig. 2D). Scales formed by erumpent chains cells 19.28–41.14 × 28.28–51.42 μm, broadly fusoid (basally) to subglobose or globose (apically) (Fig. 2E). *Stipitipellis* a cutis made up of smooth and parallel, 6.65- to 12.75-μm-diam. hyphae. *Caulocystidia* clavate, hyaline, thick walled (1.5 thick). *Clamp connections* present. Basidiomes obtained in culture showed a hemiangiocarpic development (Fig. 1D). Pileus 10–140 mm, convex when young and convex to plane when mature and without floccules. The other macro- and microscopic characteristics

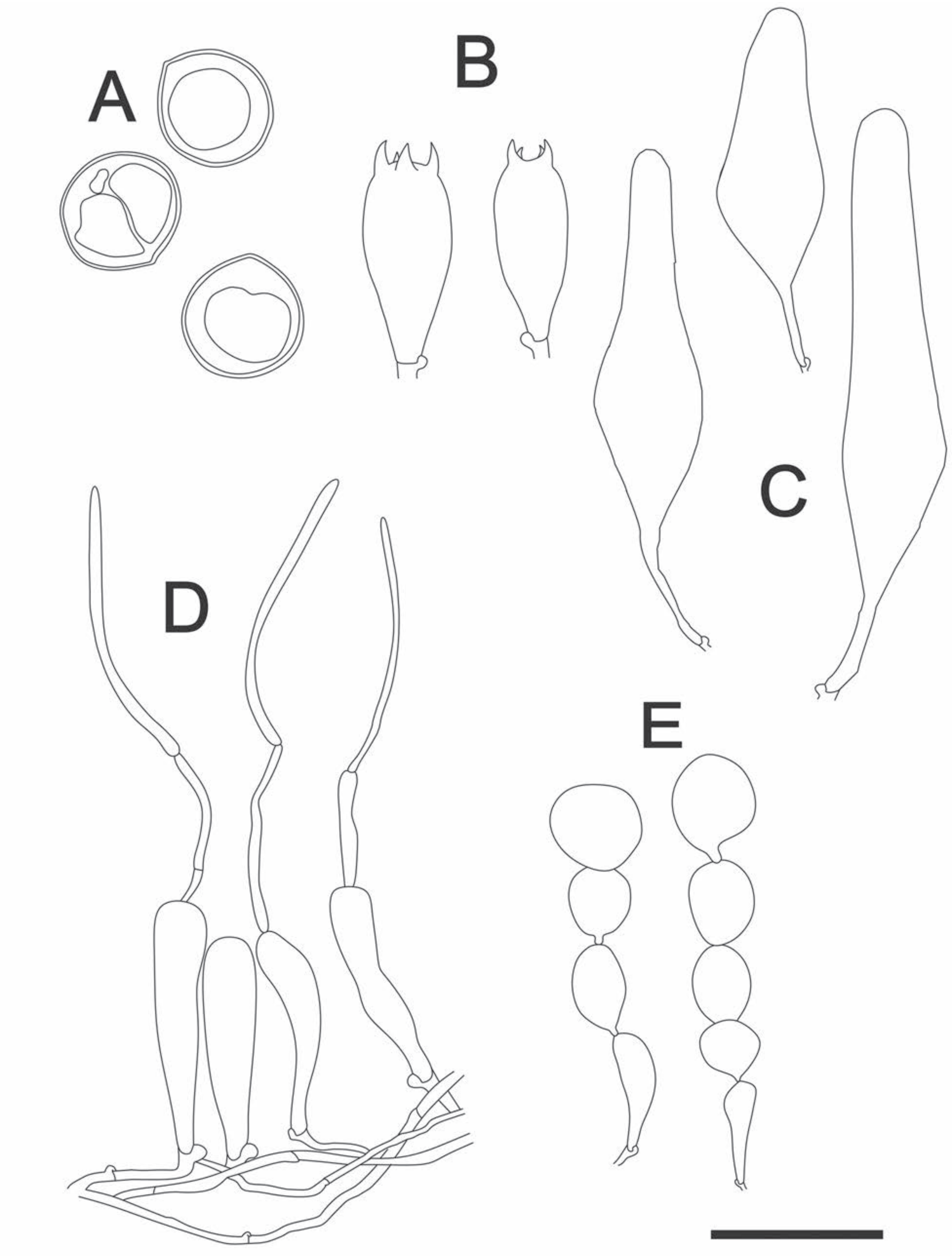


FIGURE 2. Microscopic characters of *O. canarii*. **A**, basidiospores; **B**, basidia; **C**, pleurocystidia; **D**, pileipellis elements; **E**, scale elements. Bars = 30 μm (A); 50 μm (B, E); 70μm (C, D).

agree with the descriptions of the basidiomata found in nature mentioned above.

Distribution: Southern Asia (Japan, Malaysia, Papua New Guinea, Solomon Islands) and tropical America (Argentina, Mexico, United States) (Petersen and Hughes, 2010). In Argentina, known in Buenos Aires, Corrientes, Misiones, and Tucumán Provinces.

Ecology: growing on live, decaying, or dead logs of gymnosperms and angiosperms. Solitary or forming small groups of 1–5 basidiomes.

Additional specimens examined: ARGENTINA, Buenos Aires, Reserva Ecológica Costanera Norte, 31°38'10"S, 60°40'31"W, 4/08/2016, J. Aliaga MA4 (CTES). Corrientes City, Province of Corrientes, 27°27'29"S, 58°49'17"W, 26/03/2017, N. Niveiro MA5 (CTES). Misiones, General Manuel Belgrano, Reserva Natural Estricta San Antonio, 26°03'00"S, 53°43'00"W, 23/03/2017, M. Alberti 22v, 33v, 36v (CTES). *Ib*. INTA, Campo Anexo General Manuel Belgrano, in *Araucaria angustifolia* forest, 26°38'29"S, 53°46'14"W, 23/03/2017, M. Alberti 43v (CTES). Guaraní, Reserva Privada Yasi Yateré, 27°13'26"S, 54°00'47"W, 809 m.s.n.m., 23/03/2017, M. Alberti 60v (CTES). Iguazú, Parque Nacional Iguazú, surroundings of CIES, 26°38'29"S, 53°46'14"W, 210 m.s.n.m., 22/03/2017, Ramírez 13v, 14v, 15v, 17v (CTES), *Ib*. Timbó station, N. Ramírez 16v (CTES). San Ignacio, Parque Provincial Teyú Cuaré, 27°33'43.3"S, 55°35'24.2"W, 18/10/2017, N. Niveiro MA3325, MA3326, MA3327, MA3328 (CTES). Santa Ana, Parque Provincial Cañadon de Profundidad, 27°33'23.1"S, 55°42'21.1"W, 16/10/2017, N. Niveiro MA3325 (CTES). San Pedro, Parque Provincial Moconá, Chachi trail, 27°08'35"S, 53°53'12"W, 25/03/2017, M. Alberti 68v (CTES). *Ib*. 26/03/2017, M. Alberti 93v (CTES). Reserva Privada Yagurundí, 26°41'40"S, 54°15'52"W, 23/03/2017, M. Alberti 57v (CTES).

Oudemansiella canarii is characterized by its white pileus with scattered brownish veil patches (but absent in basidiomes obtained from culture), surface markedly glutinose and darker (brownish) when young, and pileipellis formed by a superficial ixotricodermium composed by expanded cells mounted on a more or less hymeniform layer, formed by spindle cells, cylindrical to thinly claviform, olive pigmented. Pleurocystidia numerous and of large size (Petersen and Hughes, 2010). One of the most similar species that shares the pileipellis structure is *O. exannulata* (Cleland & Cheel) R.H. Petersen from eastern Australia. However, it differs from *O. canarii* by the absence of floccules in the pileus surface, and its larger pileus, up to 100 mm diam. (Petersen and Hughes, 2010). The macro- and microscopical characters of the Argentine specimens of *O. canarii* coincide with the description previously made by Corner (1994) and Petersen and Hughes (2010), although with minor differences. Petersen and Hughes (2010) describe larger basidiospores (up to 31 × 33 μm), with 1–4 sterigmated basidia and basidiomes usually with pinkish colorations. In this work, maximum measurements of basidiospores were 19.96 × 21.99 μm; the observed basidia were 4-sterigmated in all cases, and no pinkish colorations have been seen in any examined basidiomata.

Oudemansiella cubensis (Berk. & M. A. Curtis) R. H. Petersen, Nova Hedwigia, Beih. 137: 283. 2010. TYPE: CUBA. July 1857, C. Wright s.n. (FH). Fig. 3–4.

Basionym: *Agaricus (Amanita) cubensis* Berk. & M.A. Curtis. J. Linn. Soc. London 10: 282. 1869.

Synonyms: *Agaricus (Tricholoma) platensis* Speg. Anales Soc. Ci. Argent. 9(4): 161. 1880.

Oudemansia platensis (Speg.) Speg. Anales Soc. Ci. Argent. 10(6): 280. 1880. [*nom. gen. illeg*., Art. 53 ICNB].

Oudemansiella platensis (Speg.) Speg. Anales Soc. Ci. Argent. 12(1): 24. 1881.

Psalliota platensis (Speg.) Herter. Estudios Botanicos Region Uruguaya, III *Florula Uruguayensis Plantae Avasculares* (Montevideo): 43. 1933.

Basidiomata gregarious in small cluster, xylophagous (Fig. 3A). *Pileus* up to 80 mm broad, hemispherical-convex when young, then plano-convex to plane; glutinous when young, quickly turning viscid, and finally dry at maturity (in dry environmental conditions) (Fig. 3B, C); hygrophanous, brown (6E5-8) when young, becoming lighter brown when dehydrated (6D4), grayish brown (6D3), finally orange-white (6A2) in the disk to white (6A1) at the margin at maturity. Glabrous or occasionally with scattered veil patches forming appressed or recurved scales, concentrated in the center, more dispersed toward the margins, brown (7E4-6) to dark brown (7F4-6), varying considerably in size, forming from large patches (5–20 mm) to small and very abundant scales (1–3 mm) (Fig. 3D). Margin smooth with tiny fragments of veil when young. *Context* thin, up to 2 mm, white (2A1) to ashen or pale (2A2, "yellowish-white"), odor farinaceus, which accentuates and turns sweet when dry. *Lamellae* adnate when young, then adnexed, ventricose, subdistant to distant (Fig. 3E), white (1A1) when young, turning yellowish white (1A2) to pale yellow (1A3) at maturity, lamellulae of one or two orders. *Stipe* central, 17–80 × 4–8 mm, straight or curved, cylindrical, slightly tapering to the apex, with a subbulbose base, (Fig. 3A–F), white (2A1) to pale (2A2), concolorous with the lamellae, solid, tough, fibrous, surface dry, longitudinally fibrillose, with small remnant veil fragments toward the apex, which disappear at maturity. *Basidiome development* hemiangiocarpic (Fig. 3F). *Spore-print* white to pale and extremely abundant (Fig. 3G). *Basidiospores* 14.92–20.47 × 17.08–20.72 μm; x = 17.7 × 18.38 μm, Q = 1.00–1.20, Qx = 1.03, n = 25; globose to subglobose, multigranular contents and abundant guttules, nonamyloid, hyaline, smooth, thick walled (Fig. 4A). *Basidia* 45–70 × 23–36 μm, clavate, 4-spored, hyaline, thick walled (Fig. 4B). *Pleurocystidia* 140.0–190.3 × 25.38–39.24 μm, lageniform, formed by a globose to subglobose base, and a narrower, cylindrical, long neck, thick walled on the base, thin walled to the apex, homogeneous contents (Fig. 4C). *Cheilocystidia* of two types: (1) 13–28 × 39–83 μm, fusiform to broadly clavate thin walled; and (2) 12–40 × 61–150 μm, very broadly fusiform, thick walled. *Hymenophoral trama* subregular, consisting of 5- to 38-μm-diam., thin-walled hyphae, nonamyloid. *Pileipellis* formed by two tissue types: (1) underneath, a more or less hymeniform layer, formed by claviform cells,

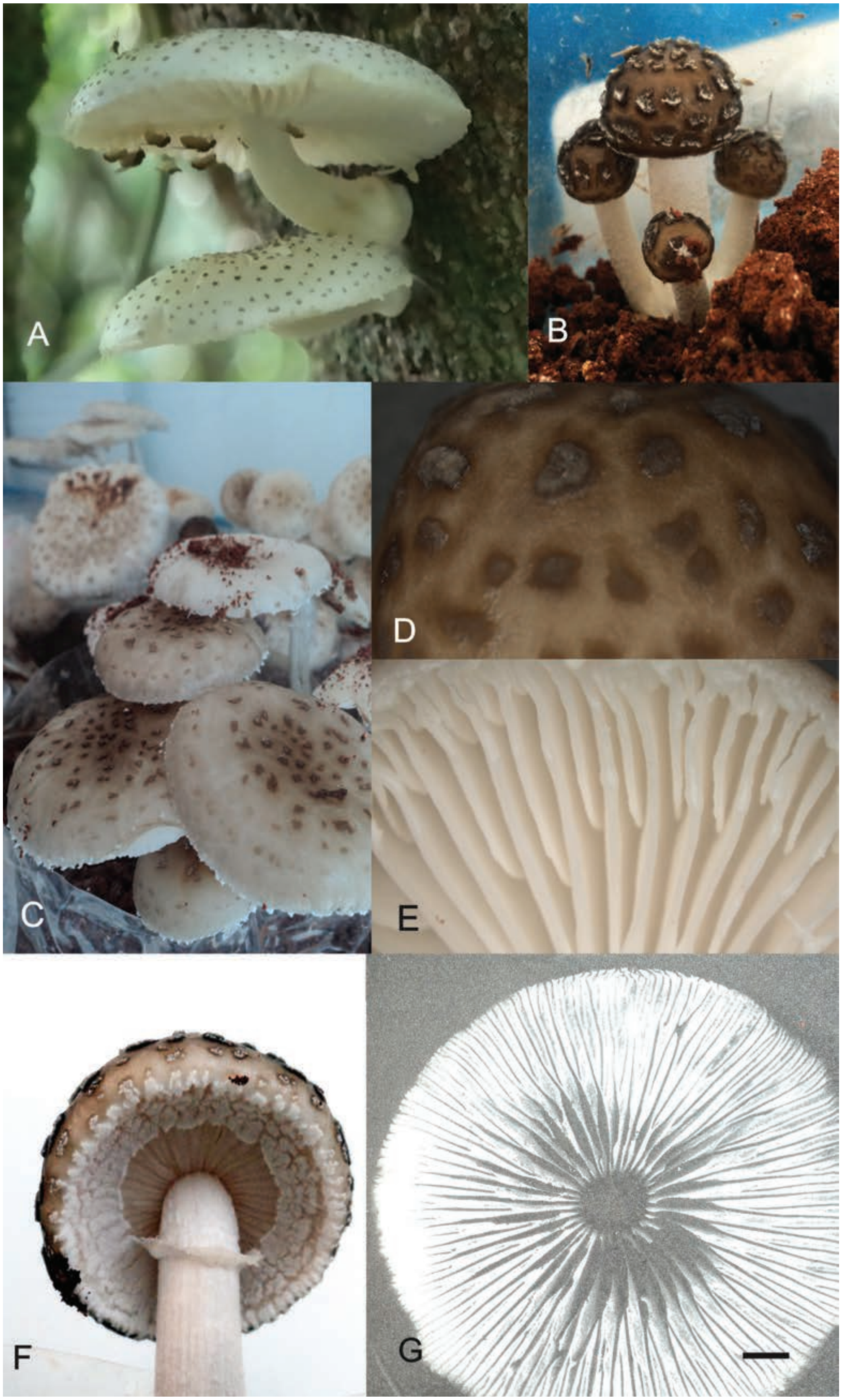


Figure 3. Basidiomes of *O. cubensis*. **A**, general aspect; **B**, primordia; **C**, specimens obtained in culture; **D**, detail of pileus scales; **E**, lamellae; **F**, partial veil; **G**, spore print. Bars = 0.75 cm (A); 1 cm (B, G); 1.75 cm (C); 0.3 cm (D, E); 0.43 cm (F).

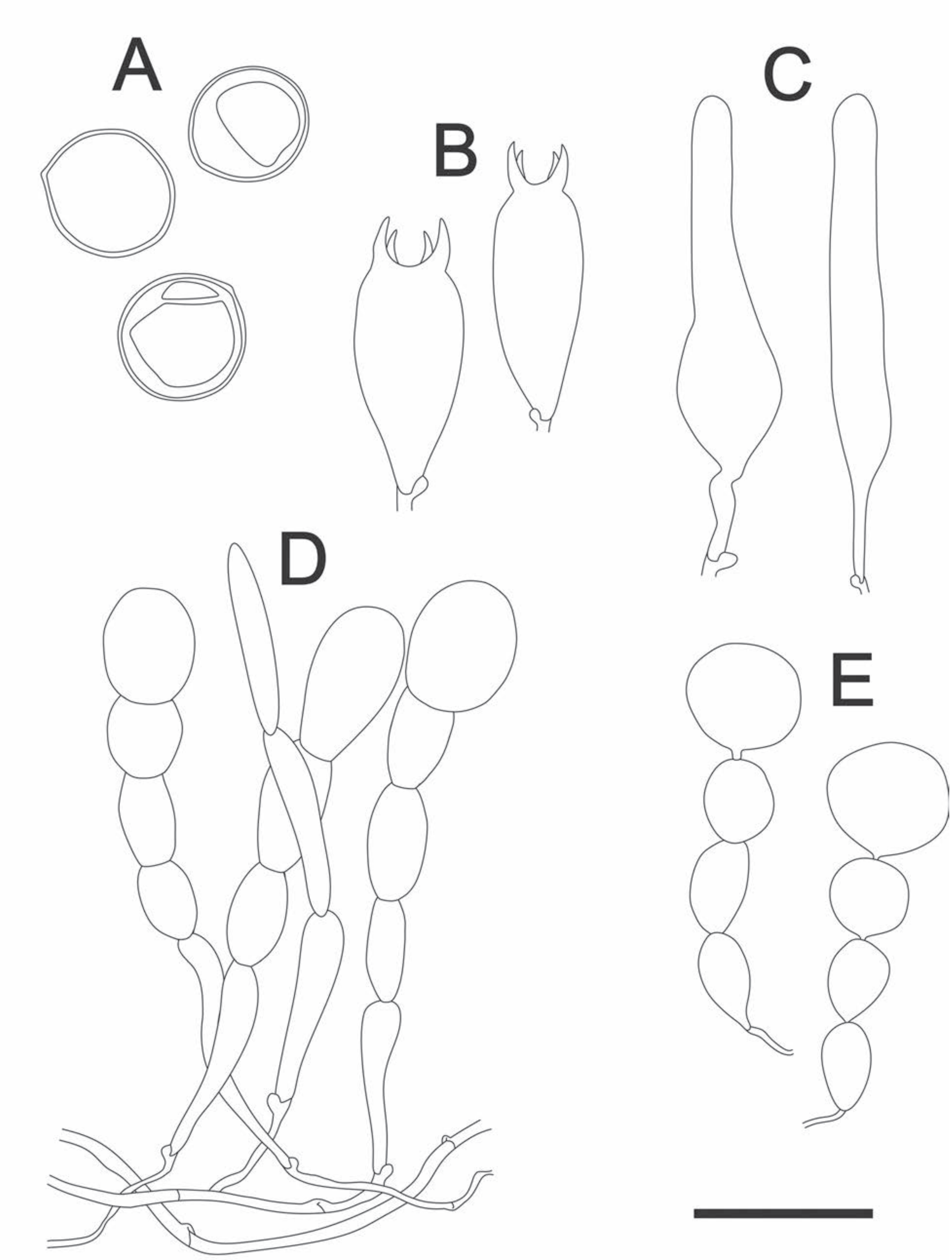


FIGURE 4. Microscopic characters of *O. cubensis*. **A**, basidiospores; **B**, basidia; **C**, pleurocystidia; **D**, pileipellis elements; **E**, scale elements. Bars = 25 μm (A, D); 50 μm (B); 70 μm (C); 80 μm (E).

20–80 × 8–10 μm, softly pigmented olive; and (2) the most superficial layer, formed by a polycystoderm, composed by chains of progressively inflated cells of 6–25 μm diam. (Fig. 4D). Scales formed by erumpent chains cells of 20–50 μm diam., broadly fusoid (basally) to subglobose or globose (apically) (Fig. 4E). *Stipitipellis* in a cutis made up of smooth and parallel, 6.68- to 14.63 μm diam. hyphae. *Caulocystidia* fusiform, hyaline, thick walled (1.4 thick). *Clamp connections* present. Basidiomes obtained by culture showed a hemiangiocarpic development (Fig. 2G). Pileus 15–99 mm diam., convex when young and convex to plane when mature with floccules present. The other macro- and microscopic characteristics coincide with the descriptions of the basidiomes found in nature mentioned above.

Distribution: Neotropical, from southern U.S.A. to northern Argentina: Argentina, Brazil, Colombia, Costa Rica, Cuba, Dominican Republic, Ecuador, United States (Petersen and Hughes, 2010). In Argentina, known to Buenos Aires, Corrientes, and Misiones Provinces.

Ecology: growing on live, decaying, or dead logs of gymnosperms and angiosperms. Solitary or forming small groups of 1–4 basidiomes.

Additional specimens examined: ARGENTINA, Buenos Aires, Reserva Natural Municipal Santa Catalina, 34°46'46"S, 58°25'36"W, 27/07/2016, S. Ponce MA3 (CTES). Corrientes, San Cosme, Paso de la Patria, Estancia Las Lagunas, 27°22'15"S, 58°32''54"W, 21/04/2016, N. Niveiro 2930/MA2 (CTES).

Petersen and Hughes (2010) define six characters that separate *O. cubensis* from similar taxa: (1) smaller spores, (2) longer and slender basidia, (3) proximal swelling of pleurocystidia less than in other species, (4) immature pileus color dark brown rather than pallid gray, pallid yellow, or pinkish, (5) conspicuous cheilocystidia, and (6) pileipellis composed of chains of cells. However, spore size, basidia, cheilocystidia, and pleurocystidia are not completely conclusive characters because of overlapping measurements in many cases. The most suitable morphological character to differentiate this species is the white to pallid-brown pileus with scattered veil patches and a pileipellis composed of a superficial polycystoderm, formed by a chain of progressively inflated cells, and underneath a more or less hymeniform layer, formed by claviform cells softly pigmented olive. *Oudemansiella apalosarca* (Berk. & Broome) Höhn. from Sri Lanka and Oceania (as *O. australis* G. Stev. & G.M. Taylor) differs from *O. cubensis* in its pileus without floccules, dry surface, and larger spores (22–25 × 20–24 μm) (Petersen and Hughes, 2010). Descriptions of Argentine specimens of *O. cubensis* are in agreement with Petersen and Hughes (2010) and with descriptions made by Corner (1994) for *O. platensis*. In this work, basidiospores with a maximum size of 20.47 × 20.72 μm are reported, which are smaller than maximum sizes described by Petersen and Hughes (2010) (22.5 × 22 μm), and by Corner (1994) (15 × 25 μm). Also, these authors reported pleurocystidia greater than 250 μm long, whereas the maximum pleurocystidia length described in this work is 190.3 μm. Concerning basidia, Petersen and Hughes (2010) reported 2- to 4-sterigmated basidia, but in this work only 4-sterigmated basidia are described.

Phylogenetic Analysis

The original dataset consisted of 36 taxa and 682 positions. The resulting tree generated in BI agreed with the ML analysis. The species studied in this work were grouped in three well-defined clades: Clade *O. canarii* (1/91); Clade *O. cubensis* (1/84); and Clade *O. apalosarca* (1/90), in which *Oudemansiella* sequences named as *O. crassifolia* and *O. australis* from the Asian continent were grouped (both synonymized with *O. apalosarca* by Petersen and Hughes, 2010) (Fig. 5).

DISCUSSION

Taking into consideration the works published by Petersen and Hughes (2010) and Niveiro and Albertó (2012), seven species of *Oudemansiella* were described for Argentina, some of which have not been revised yet. Species such as *O. aculeata* Raith. and *O. haasiana* Raith. have been poorly described and the type materials are presumably lost. After several field trips to collect mushrooms from the northern and central parts of the country, where we obtained various specimens belonging to the genus *Oudemansiella*, we found it was very difficult to determine them to specific level because of the great variation in the morphological characters that these collections presented. On the basis of morphological characters, we initially thought that the number of species present in the area was higher than we had previously assumed. Only the combined study of morphology and molecular characters allowed us to conclude that only two species were present in the area. Moreover, it was not possible to differentiate them at the macroscopic level, it being necessary to perform micromorphological studies, culture studies, and phylogenetic analyses to be able to identify them with certainty. At the microscopic level, they can be differentiated mainly by pileipellis structure, specifically its superficial layer: *O. canarii* has an ixotricodermium composed of expanded cells, whereas *O. cubensis* has a superficial polycystoderm, formed by a chain of progressively inflated cells. Some authors consider that it could be variable at different stages of development (Dörfelt, 1981; Corner, 1994; Yang et al., 2009).

Another morphological difference, noticed after repeated observations of basidiomes obtained in culture, is the consistency of the primordia, *O. canarii* primordia being more glutinous than in *O. cubensis*. However, this can vary greatly with environmental conditions, as well as the perception of the observer. In addition, when these species are cultivated under controlled conditions, they can be recognized by the presence of scales on the pileus in *O. cubensis*, which are absent in *O. canarii*. (Fig. 1C, 3C–E). Regarding basidiomes development, Corner (1994) pointed out that the development of species of the genus was gymnocarpic. The production of basidiomes in culture on substrate allowed us to observe the development of many specimens of both species. We can affirm that *O. canarii* and *O. cubensis* have a hemiangiocarpic development. According to Alexopoulos and Mims (1985), the hemiangiocarpic

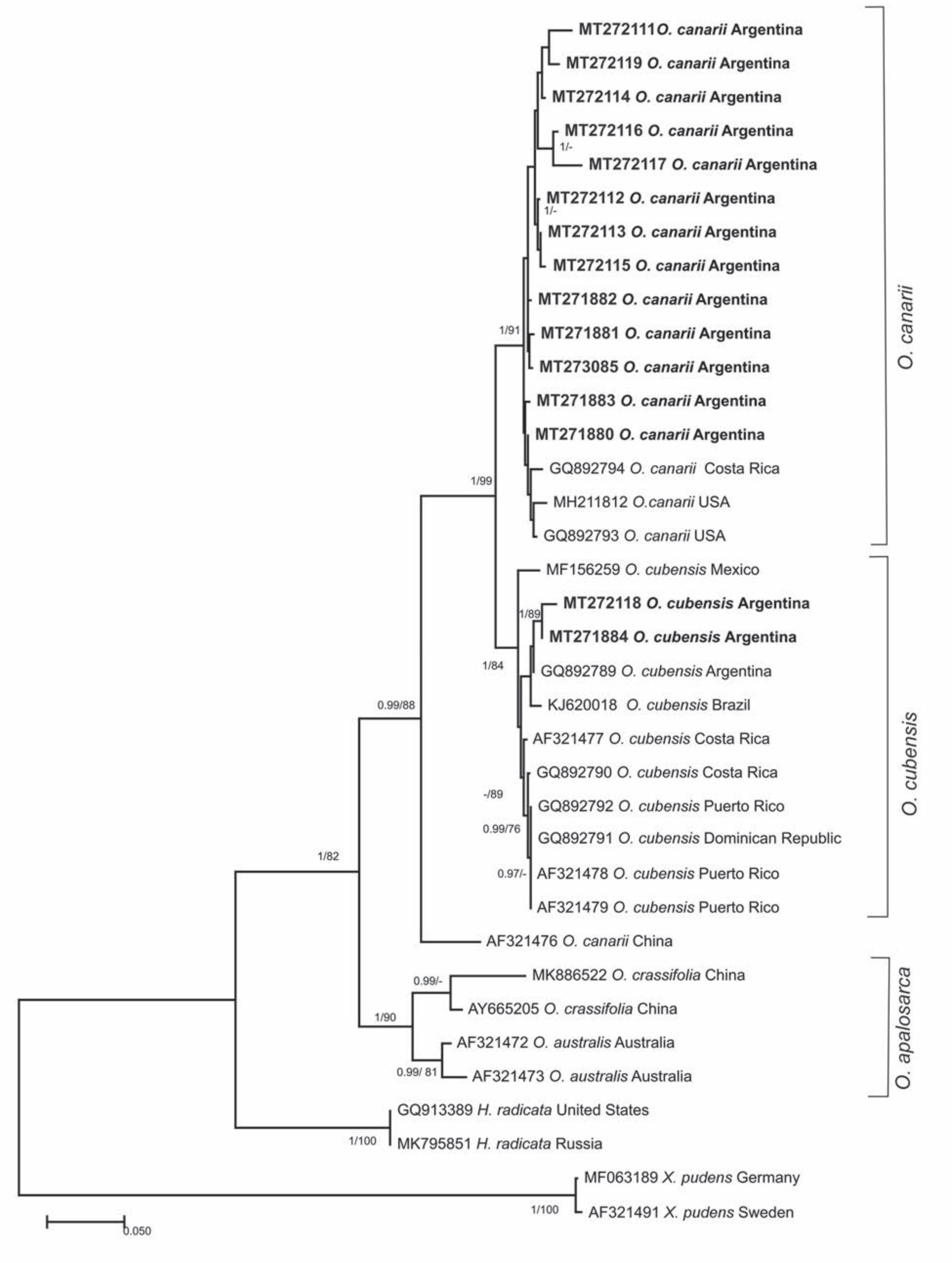


FIGURE 5. Molecular phylogeny inferred by Bayesian inference based on dataset of ITS sequences. Bayesian posterior probabilities above 0.9 (BPP ≥ 0.9) and bootstrap values above 70% (BS ≥ 70) are shown. Sequences obtained in this study are in bold.

development is characterized by the fact that during the first phases of basidiomal development, the hymenium is covered by the partial veil, which is a tissue that connects the margin of the pileus with the stipes. When the pileus expands, the partial veil tears and may or may not form a permanent ring. The phylogenetic analysis carried out from the ITS sequences allowed us to separate them into three well-supported clades (Fig. 5). Our sequences were grouped into two different clades: *O. canarii* and *O. cubensis*. These results agree with those obtained by Petersen and Hughes (2010), who also phylogenetically separated both species on the basis of ITS sequences. We assert that ITS sequences are optimal markers for phylogenetic molecular identification of these two species, which are at present the only ones found in Argentina belonging to genus *Oudemansiella* sensu stricto.

LITERATURE CITED

ALEXOPOULOS, C. J., AND C. W. MIMS. 1985. *Introducción a la micología*. 1st ed. Ediciones Omega, Barcelona.

BOEKHOUT, T. 1999. *Oudemansiella* and *Xerula*. Pages 181–184 in C. BAS, T. W. KUYPER, M. E. NOORDELOOS, AND E. C. VELLINGA, EDS., *Flora Agaricina Neerlandica 4*. A. Balkema, Brookfield.

BOEKHOUT, T., AND C. BAS. 1986. Notulae ad Floram Agaricinam Neerlandicam—XII. Some notes on the genera *Oudemansiella* and *Xerula*. Persoonia 13: 45–56.

CLÉMENÇON, H. 1979. Taxonomic structure of the genus *Oudemansiella* (*Agaricales*). Sydowia 32: 74–80.

CONTU, M. 2000. IL Genere *Xerula* (*Basidiomycotina, Agaricales*) nell'Italia Centro-Meridionale de Insulare. Micol. Veg. mediterr. 15: 18–39.

CORNER, E. J. H. 1994. *Oudemansiella*. Part 2 of *On the Agaric Genera* Hohenbuehelia *and* Oudemansiella. Speg. Gard. Bull. Singapore 46: 49–75.

———. 1996. The agaric genera *Marasmius*, *Chaetocalathus*, *Crinipellis*, *Heimiomyces*, *Resupinatus*, *Xerula* and *Xerulina* in Malesia. Nova Hedwig. Beih. 111: 1–175.

DARRIBA, D., G. L. TABOADA, R. DOALLO, AND D. POSADA. 2012. jModelTest 2: More models, new heuristics and parallel computing. Nat. Methods 9(8): 772.

DÖRFELT, H. 1979. Taxonomische Studien in der Gattung *Xerula* R. Mre. Feddes Repert. 90: 363–388.

———. 1981. Taxonomische Studien in der Gattung *Xerula* R. Mre. (V). Feddes Repert. 92: 631–674.

FELSENSTEIN, J. 1985. Phylogenies and the comparative method. Am. Nat. 125(1): 1–15.

GARDES, M., AND T. D. BRUNS. 1993. ITS primers with enhanced specificity for basidiomycetes—application to the identification of mycorrhizae and rusts. Molec. Ecol. 2: 113–118.

GUINDON, S., AND O. GASCUEL. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. Syst. Biol. 52: 696–704.

HALLING, R. E., AND G. M. MUELLER. 1999. A new species and a new record for the genus *Xerula* (*Agaricales*) from Costa Rica. Mycotaxon 71: 105–110.

HORAK, E. 1968. Synopsis Generum *Agaricalium* (Die Gattungstypen der *Agaricales*). Beit Zur Kryptogamenflora Der Schweiz. 13: 1–741.

———. 2005. *Röhrlinge und Blätterpilze in Europe*. Elsevier, Munich.

INDEX FUNGORUM. 2020. Authors of fungal names (accessed June 22, 2020). http://www.indexfungorum.org/Names/NAMES.ASP.

IVANOVA, N. V., A. J. FAZEKAS, AND P. D. N. HEBERT. 2008. Semi-automated, membrane-based protocol for DNA isolation from plants. Plant Mol. Biol. Rep. 26: 186–198.

IVANOVA, N. V., AND C. GRAINGER. 2006. CCDB protocols: Pre-made frozen PCR and sequencing plates (accessed June 22, 2020). http://ccdb.ca/site/wp-content/uploads/2016/09/CCDB_Sequencing.pdf.

JARAMILLO MEJÍA, S., AND E. ALBERTÓ. 2013. Heat treatment of wheat straw by immersion in hot water decreases mushroom yield in *Pleurotus ostreatus*. Rev. Iberoam. Micol. 30(2): 125–129.

KORNERUP, A., AND J. H. WANSCHER. 1978. *Methuen Handbook of Colour*. Eyre Methuen, London.

KUMAR, S., G. STECHER, M. LI, C. KNYAZ, AND K. TAMURA. 2018. MEGA X: Molecular evolutionary genetics analysis across computing platforms. Mol. Biol. Evol. 35: 1547–1549.

LODGE, D. J., J. F. AMMIRATI, T. E. O'DELL, G. M. MUELLER, S. M. HUHNDORF, C. J. WANG, J. N. STOKLAND, J. P. SCHMIT, L. RYVARDEN, P. R. LEACOCK, M. MATA, L. UMAÑA, Q. F. WU, AND D. CZEDERPILTZ. 2004. Terrestrial and lignicolous macrofungi. Pages 127–172 in G. M. MUELLER, G. F. BILLS, AND M. S. FOSTER, EDS., *Biodiversity of Fungi, Inventory and Monitoring Methods*. Elsevier Academic Press, Boston.

MOSER, M. M. 1955. Studien zur Gattung *Oudemansiella* Speg. Schleim–und Sammetrüblinge. Z. Mykol. 19: 4–11.

MUELLER, G. M., Q. X.WU, Y. Q. HUANG, S. Y. GUO, R. A. GOMEZ, AND R. VILGALYS. 2001. Assessing biogeographic relationships between North American and Chinese macrofungi. J. Biogeogr. 28: 271–281.

NIVEIRO, N., AND E. ALBERTÓ. 2012. Checklist of the Argentine *Agaricales* 4. *Tricholomataceae & Polyporaceae*. Mycotaxon 121: 499–500.

PEGLER, D. N., AND T. W. K. YOUNG. 1986. Classification of *Oudemansiella* (*Basidiomycota: Tricholomataceae*), with special reference to spore structure. Trans. Brit. Mycol. Soc. 87(4): 583–602.

PETERSEN, R. H. 2000. *Rhizomarasmius*, gen. nov. (Xerulaceae, Agaricales). Mycotaxon 75: 333–342.

———. 2008a. The genus *Xerula* (*Agaricale*s; Fungi) in Australia and New Zealand. Nova Hedwigia 87: 1–67.

———. 2008b. Scanning electron microscope images of basidiospores of *Xerula* (*Physalacriaceae, Agaricales*). Mycoscience 49: 19–34.

———. 2008c. Species of *Xerula* from sub-Saharan Africa. Fungal Divers. 30: 121–147.

PETERSEN, R. H., AND T. J. BARONI. 2007. *Xerula hispida* and *Xerula setulosa* (comb. nov.), two similar subtropical New World agarics. Mycotaxon 101: 113–136.

PETERSEN, R. H., AND R. E. HALLING. 1993. Mating systems in the *Xerulaceae*: *Oudemansiella*. Trans. Mycol. Soc. Japan. 34: 409–422.

PETERSEN, R. H., AND K. W. HUGHES. 2005. Une nouvelle espèce de *Xerula*: *Xerula limonispora*. Bull. Trimest. Soc. Mycol. Fr. 120: 37–49.

———. 2010. *The Xerula/Oudemansiella Complex (Agaricales)*. J. Cramer, Mörlenbach.

PETERSEN, R. H., AND A. S. METHVEN. 1994. Mating systems in the *Xerulaceae*: *Xerula*. Can. J. Bot. 72: 1151–1563.

Petersen, R. H., and E. Nagasawa. 2006. The genus *Xerula* in temperate East Asia. Rep. Tottori Mycol. Inst. 43: 1–49.

Qin, J., Horak, E., Popa, F., Rexer, K. H., Kost, G., Li, F., and Z. L. Yang. 2018. Species diversity, distribution patterns, and substrate specificity of *Strobilurus*. Mycologia. 1–21.

Raithelhuber, J. 1979. Die Gattung Oudemansiella Speg. Metrodiana 8(2–3): 40–51.

———. 1987. *Flora Mycologica Argentina. Hongos I*. Mycosur, Stuttgart.

———. 1991. *Flora Mycologica Argentina. Hongos III*. Mycosur, Stuttgart.

———. 1995. Agaric Flora of South America (10). Metrodiana 22(1): 31–38.

———. 2004. *Nueva Flora Micológica Argentina*. Mycosur, Stuttgart.

Redhead, S., J. Ginns, and R. A. Shoemaker. 1987. The *Xerula* (*Collybia, Oudemansiella*) *radicata* complex in Canada. Mycotaxon 30: 357–405.

Ronquist, F., M. Teslenko, P. van der Mark, D. L. Ayres, A. Darling, S. Höhna, B. Larget, L. Liu, M. A. Suchard, and J. P. Huelsenbeck. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61(3): 539–542.

Singer, R. 1950. Type studies in Basidiomycetes IV. Lilloa. 23: 147–246.

———. 1962a. *The Agaricales in Modern Taxonomy*. 2nd ed. J. Cramer, Weinheim.

———. 1962b. Diagnoses fungorm novorum Agaricalium II. Sydowia 15: 45–83.

———. 1964. *Oudemansiellinae*, *Macrocystidiinae*, *Pseudohiatulinae* in South America. Darwiniana 13: 146–190.

———. 1986. *The Agaricales in Modern Taxonomy*. 4th ed. Koeltz Scientific Books, Koenigstein.

Singer, R., and A. P. L. Digilio. 1952. Pródromo de la Flora Agaricina Argentina. Lilloa 25: 6–461.

Spegazzini, C. 1880a. Fungi Argentini. Pugillus 1. Anales Soc. Ci. Argent. 9(4): 158–192.

———. 1880b. Sobré la *Oudemansia platensis*. Anales Soc. Ci. Argent. 10: 279–280.

———. 1881. Fungi Argentini additis nonnullis Brasiliensibus Montevideensibusque. Pugillus quartus. Anales Soc. Ci. Argent. 12: 13–30.

———. 1899. Fungi argentini novi v. critici. Anales Mus. Nac. Buenos Aires 6: 6–365.

———. 1926. Observaciones y adiciones a la micología argentina. Bol. Acad. Nac. Cienc. 28(3–4): 267–351.

Thiers, B. 2020. *Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff*. New York Botanical Garden's Virtual Herbarium (accessed June 22, 2020). http://sweetgum.nybg.org/ih/.

Vellinga, E. C. 1988. Glossary. Pages 54–64 in C. Bas, T. W. Kuyper, M. E. Noordeloos, and E. C. Vellinga, eds., *Flora Agaricina Neerlandica*. Vol. 1. A. Balkema, Brookfield.

Wright, J. E., and E. Albertó. 2002. *Hongos con laminillas*. Vol. 1 of *Guía de hongos de la región pampeana*. Literature of Latin America, Buenos Aires.

Wright, J. E., B. E. Lechner, and O. Popoff. 2008. *Atlas pictórico de los hongos del Parque Nacional Iguazú*. Literature of Latin America, Buenos Aires.

Wright, J. E., and E. Wright. 2005. Checklist of the mycobiota of Iguazu National Park (Misiones, Argentina). Bol. Soc. Argent. Bot. 40(1–2): 23-44.

Yang, Z. L., L. F. Zhang, G. M. Mueller, G. W. Kost, and K. H. Rexer. 2009. A new systematic arrangement of the genus *Oudemansiella* s. str. (*Physalacriaceae*, *Agaricales*). Mycosystema 28(1): 1–13.

Page 144 intentionally left blank.

NEW COMBINATIONS IN *MYRIOPUS* (HELIOTROPIACEAE) FROM CENTRAL AND SOUTH AMERICA

José Iranildo Miranda de Melo[1,3] and Márcio Gleisson Medeiros Gonçalves[2]

Abstract. Five new combinations in *Myriopus* (Heliotropiaceae) are proposed in this paper: *Myriopus andrade-limae*, *M. isabellinus*, *M. mapirensis*, *M. selleanus*, and *M. subsessilis*. *Myriopus isabellinus* and *M. selleanus* are restricted to Costa Rica and Haiti, respectively, and other three species are distributed in South America; *M. andrade-limae* is endemic to Brazil.

Keywords: Boraginales, diversity, Neotropics, nomenclature

Myriopus (Heliotropiaceae; BWG, 2016) was established by Small (1933). Following Diane et al. (2003), it currently includes all the species formerly in *Tournefortia* sect. *Cyphocyema* I.M. Johnst. (Johnston, 1930). The genus is exclusively Neotropical and consists of approximately 30 species (authors' pers. obs.), with Brazil representing the principal center of taxonomic diversity (14 species) and endemism (6 species).

Species of *Myriopus*, in terms of habit, are lianas or subscandent shrubs with supporting branches; the leaves are alternate to pseudo-opposite, elliptic, and lanceolate to ovate or obovate; inflorescences are axillar or terminate, generally secundiflorous, many flowered, all them ebracteose, and fruits are fleshy 4-lobed with curved embryo (Diane et al., 2016).

According to The Plant List (2020), *Myriopus* currently encompasses only eight names at the rank of species, hardly representing the real taxonomic diversity of the genus. On the basis of Diane et al. (2003), Heliotropiaceae sensu BWG (2016), and Diane et al. (2016), five species of *Tournefortia* are here tranferred to *Myriopus*, three of them restricted to South America (*M. andrade-limae* endemic from Brazil) and the other two to Central America (one endemic to Costa Rica, and the other to Haiti).

Myriopus andrade-limae (J.I.M. Melo) J.I.M. Melo, *comb. nov.*

Basionym: *Tournefortia andrade-limae* J.I.M. Melo, Hoehnea 34(2): 156. 2007. TYPE: BRAZIL. Paraíba: São José dos Cordeiros, June 1997, *Braz s.n.* (Holotype: IPA53027).

Homotypic synonym: *Heliotropium andrade-limae* (J.I.M. Melo) Govaerts, Skvortsovia, International Journal of Salicology and Plant Biology 4(3): 91. 2018.

Distribution: Brazil.

Govaerts (2018) inadvertently combined *Tournefortia andrade-limae* under the genus *Heliotropium*. However, morphological characters of *T. andrade-limae* observed in an analysis of the type specimen and protologue indicate that this species is referable to *Myriopus*, on the basis of its narrow and involute corolla lobes and apically coherent anthers.

Myriopus isabellinus (J.S. Mill.) J.I.M. Melo, *comb. nov.*

Basionym: *Tournefortia isabellina* J.S. Mill., Novon 9(2): 232. 1999. TYPE: COSTA RICA. Puntarenas, Parque Internacional La Amistad San Vito Coto Brus. Finca Cafrosa, 4 July 1990, *R. Delgado 47* (Holotype: MO [2235010]; Isotypes: INB [0001595747], NY [01287743]).

Distribution: Costa Rica.

Myriopus mapirensis (Lingelsh.) J.I.M. Melo, *comb. nov.*

Basionym: *Tournefortia mapirensis* Lingelsh., Repert. Spec. Nov. Regni Veg. 7: 244. 1909. TYPE: BOLIVIA. La Paz, Charopampa near Mapiri, 570 m, November 1907, *O. Buchtien 1995* (Isotypes: NY [00337247]; US [00110808]).

Distribution: Bolivia and Peru.

Myriopus selleanus (Urb. & Ekman) J.I.M. Melo, *comb. nov.*

Basionym: *Tournefortia selleana* Urb. & Ekman. Ark. Bot. 20A(5): 43. 1926. TYPE: HAITI. Massif de la Selle, Montagne Noire, in low limestone forest, scandens, 1750 m, 4 September 1924, *E. L. Ekman 1770* (Holotype: S [04-2398]; Isotypes: G [00236177], GH [00096904], K [000583469], NY [00111148], US [00110824]).

Homotypic synonym: *Heliotropium selleanum* (Urb. & Ekman) Feuillet, Phytoneuron 2020-11: 3.

Distribution: Haiti.

Feuillet (2020) inadvertently combined *Tournefortia selleana* under *Heliotropium*. However, morphological characters of *T. andrade-limae* observed in an analysis

---

José I. M. Melo would like to acknowledge the National Council for Scientific and Technological Development (CNPq) for a Research Productivity Fellowship grant (#303860/2019-6 [PQ-2]). The authors thank the JSTOR Global Plants program for the information they make available.

[1] Universidade Estadual da Paraíba, Centro de Ciências Biológicas e da Saúde, Departamento de Biologia, Avenida das Baraúnas, 351, Bairro Universitário, 58429-500, Campina Grande, Paraíba, Brazil

[2] Universidade Federal de Campina Grande, Centro de Ciências e Tecnologia, Unidade Acadêmica de Engenharia de Petróleo, Rua Aprígio Veloso, 882, Bairro Universitário, 58429-900, Campina Grande, Paraíba, Brazil; marcio.gmgoncalves@yahoo.com.br

[3] Corresponding author: tournefort@gmail.com

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 145–146.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n2,

of the type specimen and protologue indicate that this species is referable to *Myriopus*, on the basis of its narrow and involute corolla lobes, apically coherent anthers, and 4-lobed fruits.

Myriopus subsessilis (Cham.) J.I.M. Melo, *comb. nov.*
Basionym: *Tournefortia subsessilis* Cham., Linnaea 8: 119. 1833. TYPE: BRASIL. s.l., s.d., *F. Sellow s.n.* (Holotype: B [destroyed], F [negative #001061, seen]).

Distribution: Brazil and Trinidad and Tobago.

The type of *Tournefortia subsessilis* was cited as "Brazil, *F. Sellow s.n.*," and it was probably housed at B, which was destroyed during World War II. Nonetheless, there is one photograph of this material at F.

Myriopus subsessilis has a disjunct geographic distribution: it is found in Brazil, where it has been recorded in three northeastern states (Pernambuco, Sergipe, and Bahia) and probably also in a southeastern state (Minas Gerais; *Flora do Brasil*, 2020), as well as in Trinidad and Tobago (according to Baksh-Comeau et al., 2016).

LITERATURE CITED

BAKSH-COMEAU, Y. S., S. S. MAHARAJ, C. D. ADAMS, S. A. HARRIS, D. L. FILLER, AND H. D. HAWTHORNE. 2016. An annotated checklist of the vascular plants of Trinidad and Tobago with analysis of vegetation types and botanical 'hotspots.' Phytotaxa 250: 1–431. http://dx.doi.org/10.11646/phytotaxa.250.1.1.

BWG (BORAGINALES WORKING GROUP). 2016. Familial classification of the Boraginales. Taxon 65: 502–522. https://doi.org/10.12705/653.5.

DIANE, N., H. FÖRTHER, AND H. H. HILGER. 2003. A systematic analysis of Heliotropiaceae (Boraginales) based on trnL and ITS1 sequence data. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 125: 19–51. http://dx.doi.org/10.1127/0006-8152/2003/0125-0019.

DIANE, N., H. H. HILGER, H. FÖRTHER, M. WEIGEND, AND F. LUEBERT. 2016. Heliotropiaceae. Pages 203–211 in J. W. KADEREIT AND V. BITTRICH, EDS., *Flowering Plants. Eudicots*. Vol. 2 of *The Families and Genera of Vascular Plants*. Springer International Publishing, Switzerland.

FEUILLET, C. 2020. Synopsis with new combinations of *Heliotropium* (Heliotropiaceae, Boraginales) for taxa from the West Indies previously in *Tournefortia*. Phytoneuron 2020(11): 1–3. http://www.phytoneuron.net/2020Phytoneuron/11PhytoN-HeliotropiumWestIndies.

FLORA DO BRASIL. 2020. Under construction. Jardim Botânico do Rio de Janeiro (accessed July 27, 2020). http://floradobrasil.jbrj.gov.br.

GOVAERTS, R. 2018. 101 Nomenclatural corrections in preparation for the Plants of the World Online (POWO). Skvortsovia 4(3): 74–99. http://skvortsovia.uran.ru/2018/4301.pdf.

JOHNSTON, I. M. 1930. Studies in Boraginaceae 8. *Cordia* and *Tournefortia* known from Brazil, Paraguay, Uruguay and Argentina. Contributions from the Gray Herbarium of Harvard University 92: 1–95.

SMALL, J. K. 1933. *Manual of the Southeastern Flora*. University of North Carolina Press, New York.

THE PLANT LIST: A WORKING LIST OF ALL PLANT SPECIES. 2020 (continuously updated). *Myriopus* in Boraginaceae (accessed July 27, 2020). http://www.theplantlist.org/tpl1.1/search?q=Myriopus.

A NEW RECORD AND SPECIES OF *DENDROBIUM* SECTION *GRASTIDIUM* (ORCHIDACEAE) FROM THE SOLOMON ISLANDS

Paul Ormerod[1]

Abstract. Two additions are proposed for the Solomon Islands orchid flora. *Dendrobium biflorum* is a new record, while *D. stella-portus* is proposed as a new species.

Keywords: *Dendrobium, Grastidium,* Solomon Islands, new record, new species

The orchid flora of the Solomon Islands and Bougainville was treated by Lewis and Cribb (1991), wherein they recorded eight native species of *Dendrobium* Swartz section *Grastidium* Blume. This section is the largest in the genus, with about 225 species, 158 of which are found in nearby New Guinea. The group is characterized by elongate, leafy stems; short, biflorous inflorescences subtended by two pairs of sheaths; and ephemeral flowers. Recent research (Ormerod, in prep.) has resulted in the discovery of two new endemic section *Grastidium* species from Bougainville, Papua New Guinea. Thus the Solomon Archipelago now has 13 species of the group, including *D. isabelense* Ormerod (Ormerod, 2010) from Santa Isabel, the new entities from Bougainville, and the two taxa dealt with here.

Dendrobium biflorum (Forst.f.) Swartz, Nova Acta Regiae Soc. Sci. Upsal. ser. 2, 6: 84. 1799.

Basionym: *Epidendrum biflorum* Forst.f., Fl. Ins. Austral. Prodr.: 60. 1786. TYPE: SOCIETY ISLANDS. Tahiti, 1774, *J. R. & G. Forster s.n.* (Lectotype [proposed by Kores, 1989: 96]: BM, not found; Isolectotypes: G [not seen]; K [, image seen]). Fig. 1.

Homotypic synonym: *Grastidium biflorum* (Forst.f.) M.A. Clem. & D.L. Jones, Lasianthera 1, 2: 64. 1997.

Distribution: Society Islands; Samoa; Fiji; Vanuatu; Solomon Islands.

Additional specimens examined: SOCIETY ISLANDS. Tahiti, 23 June 1922, *W. A. Setchell & H. E. Parks 456* (GH). NIUE. Without locality, 1775, *Capt. J. Cook s.n.* (BM, image seen). SAMOA. Tau Island, 1.6–3.2 km S of Siufuga Village, 150 m, 27 September 1939, *H. G. Yuncker 9067* (AMES). FIJI. Viti Levu, near Nandarivatu, valley of the Sigatoka River, 900 m, 17 November 1927, *J. W. Gillespie 3862* (AMES). VANUATU. Erromanga Island, near the Nouankao Camp, 150 m, 8 August 1971, *P. S. Green RSNH 1310* (A). SOLOMON ISLANDS. Vanikoro Island, Senimi, 50 m, 25 November 1928, *S. F. Kajewski 657* (AMES 38010, 37192, BRI). San Cristobal (= Makira), Star Harbour, 0 m, 18 October 1932, *L. J. Brass 3067* (AMES, BRI).

Dendrobium biflorum is a widespread and commonly collected species in the Pacific Islands. It has not been unambiguously recorded from the Solomon Islands, though Lewis and Cribb (1989) report it. They later (Lewis and Cribb, 1991) referred those reports to *D. vanikorense* Ames. Examination of material from the Santa Cruz Islands and Makira in the Solomon Islands confirms the presence of *D. biflorum* there.

Though Lewis and Cribb (1989) united *Dendrobium vanikorense* with *D. biflorum,* they later (Lewis and Cribb 1991) reinstated and illustrated the former. Externally the two species are quite similar, with slender stems, narrow leaves, and spidery, white flowers. However, *D. vanikorense* differs in having smaller (sepals 8–13 vs. 19–26 mm long) flowers, and an entire to weakly trilobed lip with an ovate-elliptic midlobe (vs. strongly trilobed lip, with a basally ovate, apically caudate midlobe).

Typification of *Dendrobium biflorum* is problematic because the lectotype (*J. R. & G. Forster s.n.*) chosen by Kores (1989) cannot be found in BM (Margonska and Szlachetko, 2010; N. Holstein, pers. comm.). There is one collection in BM ascribed to Captain James Cook, on whose ship the Forsters travelled during the former's second circumnavigation of the world. However, this specimen was collected on Savage Island (now Niue), and if the provenance is correct it shows that *D. biflorum* occurs on Niue alongside the recently described *D. niueense* (Ormerod, 2020).

Dendrobium stella-portus Ormerod, *sp. nov.*

TYPE: SOLOMON ISLANDS. San Cristobal (= Makira), Star Harbour, 0 m, 18 October 1932, *L. J. Brass 3066* (Holotype: AMES 50442; Isotypes: BRI, GH). Fig. 2.

Related to *D. campbellii* Cribb & B.A. Lewis but the flowers with subacute, concave (vs. obtuse, cucullate) dorsal sepal and petals, the labellum with truncate, acute-cornered (vs. obtuse) sidelobes, and shorter, acanthoid (vs. longer, hairlike) processes on the disc.

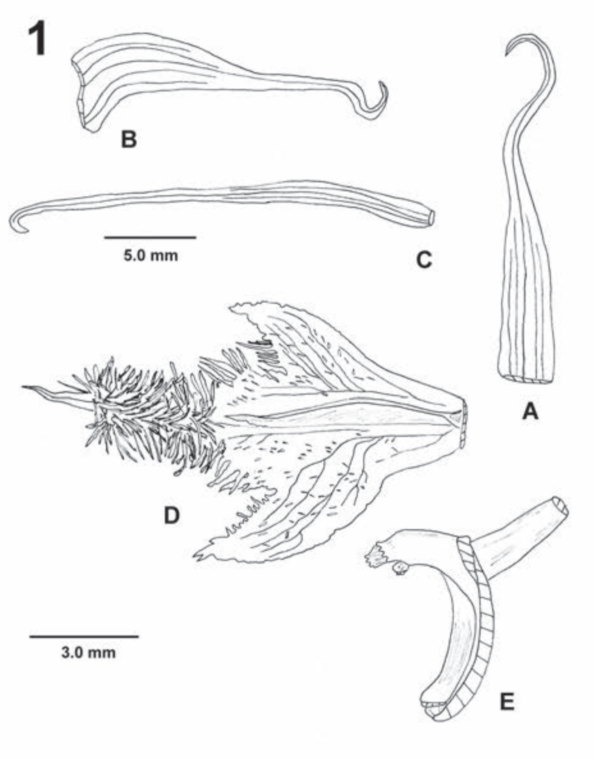
Epiphytic *herb*. *Roots* and *rhizome* not seen. *Stems* slender, elongate, subterete, laxly leafy, pendent, 100–200 cm long, 0.6 cm wide across leaf sheaths; internodes to 3.5 cm long. *Leaves* oblong-lanceolate, apex unequally obtusely bilobed, rigidly coriaceous, 11.30–12.00 × 1.90–2.65 cm; leaf sheaths tubular, striate, 1.8–2.6 cm long. *Inflorescence* biflorous, very short; inner peduncular sheaths transversely elliptic, to 5 × 6–7 mm. *Flowers* pure white. *Pedicel*

I wish to thank herbarium and library staff at BRI and the Harvard University Herbaria (A, AMES, GH) for their help and hospitality during my visits. Andrew Franks (Collections Manager, BRI) kindly imaged the BRI isotype of *Dendrobium stella-portus*. Norbert Holstein (BM) graciously searched collections at BM for the type material of *Epidendrum biflorum*.

[1] P.O. Box 8210, Cairns, Queensland 4870, Australia; wsandave1@bigpond.com

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 147–148.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n3,



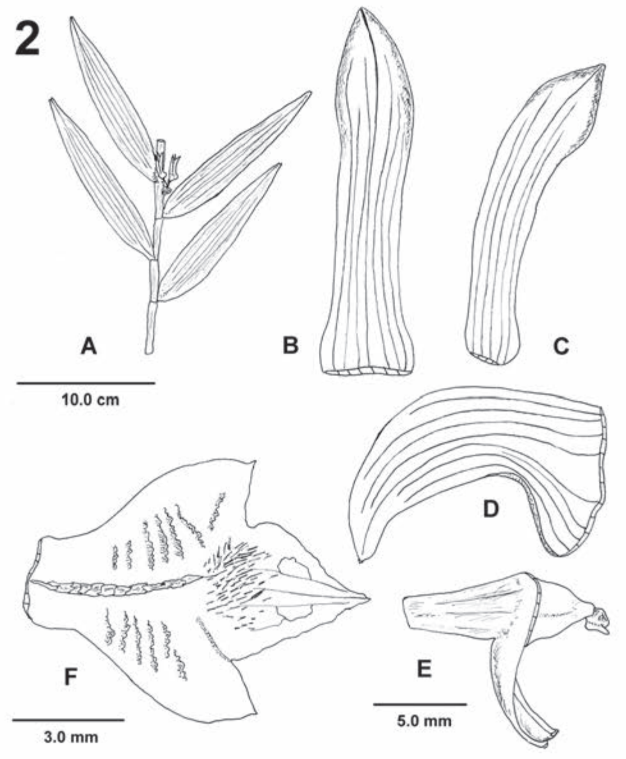


FIGURE 1. *Dendrobium biflorum* (Forst.f.) Swartz. **A,** dorsal sepal; **B,** lateral sepal; **C,** petal; **D,** labellum; **E,** column (minus anther cap). Drawn from *S. F. Kajewski 657* (AMES 38010).

FIGURE 2. *Dendrobium stella-portus* Ormerod. **A,** stem fragment; **B,** dorsal sepal; **C,** petal; **D,** lateral sepal; **E,** column; **F,** labellum. A drawn from isotype (BRI), rest from holotype.

with ovary clavate, 5.9 mm long. *Dorsal sepal* ligulate-subpandurate, subacute, apical third concave, 7-veined, 13.0 × 4.5 mm. *Lateral sepals* obliquely elliptic from a dilated base, subacute, 8-veined, 13.5–15.0 × 8.0 mm, middle 4.8 mm wide, forming with the column foot an obtuse, 6-mm-long mentum. *Petals* ligulate-oblanceolate, subacute, apical third concave, 7-veined, 16.0 × 3.8 mm. *Labellum* trilobed, 9.5 × 5.9–6.0 mm; hypochile flabellate, 6.0 × 5.9–6.0 mm, sidelobes truncate with acute corners, each side inside with transverse rows of irregular thickenings; epichile ovate-triangular, acute, 3.5 × 3.9 mm; medial keel relatively narrow, upper surface broken and jagged, apex forward pointing, triangular, acute, free, in front of which at the apex of the hypochile and base of the epichile an acanthoid patch of processes. *Column* short, stout, 3.2 mm long (minus anther cap); column foot 5.7 mm long.

Distribution: Solomon Islands (Makira).

Habitat: on trees fringing the beach, of common occurrence all along the coast.

Etymology: from the Latin *stella,* star, and *portus,* harbour, in reference to the type locality, Star Harbour.

Dendrobium stella-portus is related to *D. campbellii* Cribb & B.A. Lewis (from Rendova, Solomon Islands), sharing with it a similar external appearance, and flowers in which the lip has a narrow, broken median keel with a free apex that is terminated by a patch of subulate processes spread over the apex of the hypochile and base of the epichile. However, *D. stella-portus* differs in having subacute sepals and petals, truncate sidelobes with acute corners, and shorter prickle-like processes in front of the keel apex.

LITERATURE CITED

KORES, P. 1989. A precursory study of Fijian orchids. Allertonia 5,1: 1–222.

LEWIS, B. A., AND P. J. CRIBB. 1989. *Orchids of Vanuatu*. Royal Botanic Gardens, Kew, U. K.

———. 1991. *Orchids of the Solomon Islands and Bougainville*. Royal Botanic Gardens, Kew, U. K.

MARGONSKA, H. B., AND D. L. SZLACHETKO. 2010. *Orchidaceae of Tahiti, French Polynesia*. Gdansk University Press, Gdansk, Poland.

ORMEROD, P. 2010. Additions to the orchid flora of the Solomons. Orchadian 16,10: 465–471.

———. 2020. *Dendrobium niueense*—A new species from Niue. Orchadian 19,12: 559–561.

NOTES ON SOME MALESIAN ORCHIDACEAE II

Paul Ormerod[1,2] and Lina Juswara[3]

Abstract. Continuing studies of Malesian Orchidaceae find that it is necessary to subsume *Platystyliparis* into *Alatiliparis* requiring nine combinations, propose a small flowered but showy new *Dendrobium,* expand the circumscription of *Oberonioides,* requiring five combinations, move *Calanthe subhamata* to *Styloglossum,* and propose a new *Tropidia*.

Keywords: Malesia, new names, *Alatiliparis, Dendrobium, Oberonioides, Styloglossum, Tropidia*

This paper is a continuation of studies into Malesian Orchids (Ormerod et al. 2019; Ormerod and Juswara 2019). As noted before, the basic Malesian area extends from Malaysian peninsula to the Solomon Islands, north to the Philippines. The whole area is dominated by large tropical islands (e.g. Borneo, Sumatra, Java, New Guinea) interspersed with numerous smaller islands that are (or were) covered by various types of rainforest, though some of the Lesser Sunda Islands (e.g. Lombok through to Timor) are somewhat drier and often have Australasian elements present.

Here we mostly deal with some former members of the genus *Liparis* L.C. Rich., which in the broad sense would contain about 490-500 species. There is also a showy new *Dendrobium,* unfortunately its flowers are ephemeral. The second last plant dealt with is a natural hybrid found growing in the Bogor Botanic Gardens, possibly it arose because the parent species were planted in the same general area. The last species belongs to the rather unloved genus *Tropidia,* it is the first endemic element of that genus to be described from Sulawesi.

Alatiliparis Marg. & Szlach., Ann. Bot. Fenn. 38, 2: 78. 2001.
Type species: *Alatiliparis filicornes* Marg. & Szlach.
Heterotypic synonyms: *Malaxis* Swartz section *Platystylis* Blume, Bijdr.: 389. 1825.
Platystylis (Blume) Lindl., Gen. Sp. Orch. Pl.: 18. 1830 *nom. illeg.* (*non* Sweet 1828).
Liparis L.C. Rich. section *Platystylis* (Blume) Ridl., J. Linn. Soc., Bot. 22: 258. 1886.
Cestichis Lindl. ex Pfitz. section *Platystylis* (Blume) Pfitz., in Engl. & Prantl., Naturl. Pflanzenfam. 2, 6: 131. 1889.
Platystyliparis Marg., Richardiana 7, 1: 35. 2007.
Type species: *Malaxis decurrens* Blume
Ypsilorchis Z.J. Liu, S.C. Chen & L.J. Chen, J. Syst. Evol. 46, 4: 623. 2008.
Type species: *Liparis fissipetala* Finet

This genus of intriguing little epiphytes consists of about 20 species distributed from India and China through Malaysia and Indonesia to Timor Leste. Molecular studies by G.D. Tang et al. (2015) were the first to confirm that the group (as *Platystyliparis*) was phylogenetically distinct from *Cestichis,* and that the monospecific Chinese genus *Ypsilorchis* was nested in the former. The genus *Alatiliparis* is the oldest available name for the group and was based on two Sumatran species with slightly more complex column wings and labellum calli that do not differ in any way in habit from the plants assigned to *Platystyliparis*. They are here considered to be members of the same genus based on their aggregated morphological similarities such as small plants, 2-5 leaved pseudobulbs, tender leaves, laxly flowered, often flexuous and winged rachises, often four-winged column, and fleshy, complicated labellum callus. Nine combinations are needed for Malesian species.

Alatiliparis aptenodytes (J.J. Sm.) Ormerod & Juswara, *comb. nov.*
Basionym: *Liparis aptenodytes* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 10: 53. 1928.
TYPE: INDONESIA. Sumatra, Gunung Kerintji, 1500 m, 7 March 1920, *H.A.B. Bunnemeijer 8540* (Syntype: BO; Isosyntype: L, image seen); Gunung Kerintji, 1500 m, 7 March 1920, *H.A.B. Bunnemeijer 8535* (Syntype: BO; Isosyntype: L, image seen); Gunung Kerintji, 1600 m, 11 March 1920, *H.A.B. Bunnemeijer 8601* (Syntype: BO, not found).
Homotypic synonyms: *Platystyliparis aptenodytes* (J.J. Sm.) Marg., Richardiana 7, 1: 38. 2007.
Stichorkis aptenodytes (J.J. Sm.) Marg., Szlach. & Kulak, Acta Soc. Bot. Polon. 77, 1: 37. 2008.

Distribution: Indonesia (Sumatra).

Alatiliparis auriculifera (J.J. Sm.) Ormerod & Juswara, *comb. nov.*
Basionym: *Liparis auriculifera* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 10: 51. 1928.

The first author wishes to thank herbarium and library staff at the Harvard University Herbaria (A, AMES, GH) and Kew (K) for their help and hospitality during visits. Leiden (L) kindly loaned material for study. The second author would like to thank the head of the Research Center for Biology, the head of the Botany Division, and staff of the herbarium for technical support.

[1] P.O. Box 8210, Cairns, Queensland 4870, Australia
[2] Corrresponding author: wsandave1@bigpond.com
[3] Research Center for Biology, Botany Division, Indonesian Institute of Sciences, CSC, Jl. Raya Jakarta to Bogor KM 46, Cibinong, Bogor 16911, Java, Indonesia; lina.juswara@gmail.com

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 149–153.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n4, Published online: 31 December 2020

TYPE: INDONESIA. Sumatra, Gunung Kerintji, 1500 m, 4 March 1920, *H.A.B. Bunnemeijer 8377* (Syntype: BO; Isosyntype: L, image seen); Gunung Kerintji, 1700 m, 15 March 1920, *H.A.B. Bunnemeijer 8834* (Syntype: BO, not found); Gunung Kerintji, 1500 m, 22 March 1920, *H.A.B. Bunnemeijer 9074* (Syntype: BO).

Homotypic synonym: *Platystyliparis auriculifera* (J.J. Sm.) Marg., Richardiana 7, 1: 39. 2007.

Distribution: Indonesia (Sumatra).

Alatiliparis aurita (Ridl.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis aurita* Ridl., Natur. Wand. East. Arch.: 518. 1885.

TYPE: TIMOR LESTE. Bibicucu, 6-22 April 1883, *H.O. Forbes 3714* (Holotype: BM, image seen; Isotypes: GH; L, image seen; LISU, not seen).

Homotypic synonyms: *Leptorkis aurita* (Ridl.) Kuntze, Rev. Gen. Pl. 2: 671. 1891.

Platystyliparis aurita (Ridl.) Marg., Richardiana 7, 1: 39. 2007.

Distribution: Timor Leste; Thailand?

Alatiliparis bilobulata (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis bilobulata* J.J. Sm., Orch. Java: 279. 1905.

TYPE: INDONESIA. Java, Mt. Gede, near Tjibodas, *J.J. Smith s.n.* (Holotype: BO, not found).

Homotypic synonym: *Platystyliparis bilobulata* (J.J. Sm.) Marg., Richardiana 7, 1: 39. 2007.

Distribution: Indonesia (Java).

Alatiliparis cameronica (P.T. Ong & P. O'Byrne) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis cameronica* P.T. Ong & P. O'Byrne, Malay. Orch. Rev. 47: 72. 2013.

TYPE: MALAYSIA. Pahang, Cameron Highlands, 17 July 2012, *P.T. Ong et al. FRI 75364* (Holotype: KEP, not seen).

Distribution: Malaysia (Pahang).

Alatiliparis decurrens (Blume) Ormerod & Juswara, *comb. nov.*

Basionym: *Malaxis decurrens* Blume, Bijdr.: 390. 1825.

TYPE: INDONESIA. Java, Mt. Salak, *C.L. Blume 623* (Holotype: L, 2 sheets, images seen; Isotype: BM, not seen; P, image seen).

Homotypic synonyms: *Platystylis decurrens* (Blume) Lindl., Gen. Sp. Orch. Pl.: 18. 1830.

Liparis decurrens (Blume) Rchb.f. ex Ridl., J. Linn. Soc., Bot. 22: 291. 1886.

Cestichis decurrens (Blume) Pfitz., in Engl. & Prantl., Naturl. Pflanzenfam. 2, 6: 131. 1889.

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

Stichorkis decurrens (Blume) Pfitz., in Engl. & Prantl., Naturl. Pflanzenfam., Nachtr. 1: 103. 1897.

Platystyliparis decurrens (Blume) Marg., Richardiana 7, 1: 38. 2007.

Distribution: Indonesia (Java).

Alatiliparis hirundo (Holtt.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis hirundo* Holtt., Gard. Bull. Singap. 11: 281. 1947.

TYPE: MALAYSIA. Pahang, Cameron Highlands, November 1939 to January 1940, *A.H. Batten-Pooll s.n.* (Holotype: K).

Homotypic synonym: *Platystyliparis hirundo* (Holtt.) Marg., Richardiana 7, 1: 39. 2007.

Distribution: Malaysia (Pahang).

Alatiliparis leucophaea (Schltr.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis leucophaea* Schltr., Bot. Jahrb. Syst. 45, Beibl. 104: 15. 1911.

TYPE: INDONESIA. Sumatra, Bukit Djarat, 1300 m, 1 February 1907, *R. Schlechter 15922* (Holotype: B, destroyed; Isotypes: BO; K, P, images seen).

Homotypic synonym: *Platystyliparis leucophaea* (Schltr.) Marg., Richardiana 7, 1: 39. 2007.

Distribution: Indonesia (Sumatra).

Alatiliparis spiralipetala (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis spiralipetala* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 9: 145. 1927.

TYPE: INDONESIA. Sumatra, Palembang, Gunung Dempo, 1700 m, 17 August 1916, *E. Jacobson Exped., Ajoeb 495* (Holotype: BO).

Distribution: Indonesia (Sumatra).

Andre Schuiteman (pers. comm.) found the type species of *Alatiliparis, A. filicornes,* to be conspecific with *Liparis spiralipetala*.

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

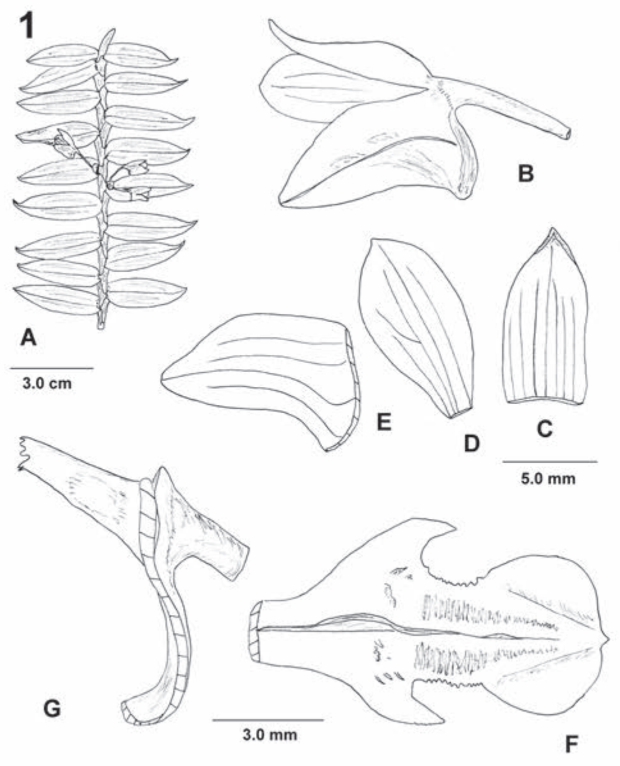
Type species: *Dendrobium moniliforme* (L.) Swartz *typ. cons.*

A genus of 1600-1800 species distributed from Sri Lanka and India to Tahiti. The species described below belongs to section *Grastidium* Blume, the largest group in the genus with about 223 species, of which 158 are now known from New Guinea. The section is characterised by its caulescent habit (plants to 3 metres long), biflorous inflorescences arising from two pairs of basal sheaths, and ephemeral flowers.

Dendrobium ornatum Ormerod & Juswara, *sp. nov.*

TYPE: PAPUA NEW GUINEA. Morobe Prov., Wantoat, 1065-1830 m, 22 February 1940, *M.S. Clemens 11167* (Holotype: AMES; Isotype: MICH, not seen). Fig. 1.

Related to *D. igneum* J.J. Sm. but the flowers with shorter pedicellate ovaries (12.0-13.0 vs. 16.3-21.0 mm), shorter sepals (8.75-8.80 vs. 13.50-17.00 mm), shorter column foot (4.0 vs. 6.6-7.0 mm), and the labellum with a broadly clawed (vs. unclawed) epichile terminated by a transversely elliptic-suborbicular (vs. epichile cuneate in overall shape) lobule.



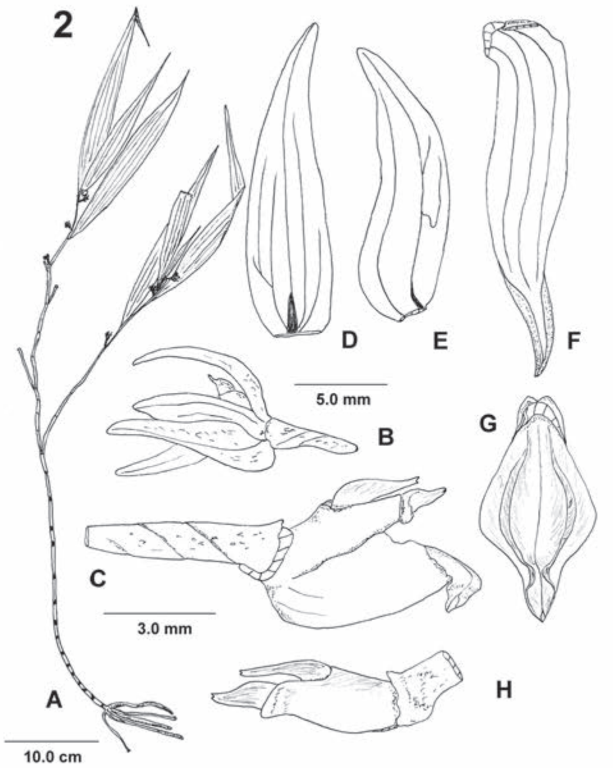


FIGURE 1. *Dendrobium ornatum* Ormerod & Juswara. **A,** stem (upper part); **B,** flower; **C,** dorsal sepal; **D,** petal; **E,** lateral sepal; **F,** labellum; **G,** column and foot. Drawn from holotype.

FIGURE 2. *Tropidia kjellbergii* Ormerod & Juswara. **A,** plant; **B,** flower; **C,** flower minus tepals; **D,** dorsal sepal; **E,** petal; **F,** lateral sepal; **G,** labellum; **H,** column. A drawn from isotype (L), rest from holotype.

Presumably epiphytic *herb*. *Roots* and *rhizome* not seen. *Stems* slender, subdensely many-leaved, compressed, preserved parts to 30 cm long, 0.4 cm wide across the leaf sheaths, 0.12 cm thick near the base. *Leaves* oblong to oblong-lanceolate, apex unequally obtusely to subacutely bilobed, 31.00-32.00 x 8.00-9.75 mm; leaf sheaths tubular-infundibuliform, compressed, apex opposite leaf lamina shallowly to deeply U-shaped, exposed part of sheaths 6-8 mm long. *Inflorescences* biflorous, almost sessile. *Flowers* sulphur to orange, a pretty soft yellow. *Pedicel with ovary* terete-subclavate, 12-13 mm long. *Dorsal sepal* ovate-elliptic, subacute, 7-veined, 8.8 x 4.0 mm. *Lateral sepals* obliquely ovate-elliptic, obtuse, 5-veined, 8.75 x 6.20 mm, forming with the column foot a 4.0-4.5 mm long obtuse mentum. *Petals* obovate-elliptic, subacute, 3-4 veined, 9.80 x 4.75 mm. *Labellum* trilobed, 8.7 x 5.0 mm; *hypochile* 4 mm long medially, 5 mm wide, lateral lobes obliquely falcate-lanceolate, acute to subacute, outer upper margin minutely denticulate, at base inside with one or two transverse lamellae and a few subulate processes, outside edge *c*. 2.5 mm long, inside edge *c*. 1.2 mm long; *epichile* in total 4.7 x 4.0 mm, claw transversely rugulose each side of central keel, margins dentate, *c*. 1.8 x 2.6 mm, terminal lobe transversely elliptic-suborbicular, obtuse, 3 x 4 mm; median keel lamellate, highest between the sidelobes but thereafter barely apparent. *Column* slightly oblique, semiterete, 3.2 mm long; *column foot* 4 mm long.

Distribution: Papua New Guinea.

Etymology: From the Latin *ornatus,* handsome, in reference to the attractive flowers.

This species is related to *D. igneum,* sharing with it compressed stems and leaf sheaths, and showy yellow flowers. *Dendrobium ornatum* differs from *D. igneum* in having smaller flowers, that have a broadly clawed lip midlobe that lacks an apical retrorse barb.

Dendrobium igneum is probably not found in general culture despite the number of cultivated plants that bear its name. Recently Thoerle et al. (2020) described *D. aurifex* Thoerle, Schuit. & Turkel from Papua New Guinea to cover some of these cultivated specimens. *Dendrobium aurifex* has some similarities with *D. ornatum* but differs in having terete stems, larger flowers (sepals 20-22 mm long), and an ovate, unclawed lip midlobe. Thoerle et al. (2020) also provided the first true photograph we have seen of *D. igneum,* showing its distinctive cuneate lip midlobe terminated by a retrorse barb.

Oberonioides Szlach., Fragm. Fl. Geobot., Suppl. 3: 134. 1995.
Type species: *Malaxis oberoniiflora* Seidenf.
Homotypic synonym: *Malaxis* Swartz section *Oberoniiflora* Seidenf., Dan. Bot. Ark. 33, 1: 43. 1978.
Type species: *Malaxis oberoniiflora* Seidenf.

This genus was originally construed to encompass two terrestrial species with small pseudobulbs that are terminated by a single cordate, conduplicate leaf, with an inflorescence bearing several tiny (sepals less than 2 mm long) flowers, the trilobed labellum with a basal linear lobule each side. Molecular analyses by G.D. Tang et al. (2015) showed that *Liparis maingayi* and *L. purpureoviridis* were sister to *Oberonioides*. Both groups (the five Malesian *"Liparis"* and the two SE Asian "type" entities) share the same habit and small flowers. However there is considerable variation in floral characters among the Malesian species, which as a whole have a longer column than the two original species. Some of the Malesian species lack a basal callus, some have an unlobed lip with fimbriate margins, others have an apically bilobed lip.

Oberonioides furcata (J.D. Hook.) Ormerod & Juswara, *comb. nov.*
Basionym: *Microstylis furcata* J.D. Hook., Icon. Plant. 19: t.1827A. 1889.
TYPE: MALAYSIA. Perak, without locality, *B. Scortechini 370* (Holotype: K, image seen; Isotype: SING, image seen).
Homotypic synonyms: *Malaxis furcata* (J.D. Hook.) Kuntze, Rev. Gen. Pl. 2: 673. 1891.
Liparis furcata (J.D. Hook.) Ridl., J. Linn. Soc., Bot. 32: 226. 1896.
Distribution: Malaysia (Peninsula).

Oberonioides maingayi (J.D. Hook.) Ormerod & Juswara, *comb. nov.*
Basionym: *Microstylis maingayi* J.D. Hook., Icon. Plant. 19: t.1826. 1889.
TYPE: MALAYSIA. Penang Island, *A.C. Maingay s.n. (= Kew Distr. 1602)* (Holotype: K, image seen).
Homotypic synonyms: *Malaxis maingayi* (J.D. Hook.) Kuntze, Rev. Gen. Pl. 2: 673. 1891.
Liparis maingayi (J.D. Hook.) Ridl., J. Linn. Soc., Bot. 32: 226. 1896.
Heterotypic synonym: *Microstylis maingayi* J.D. Hook. var. *kunstleri* J.D. Hook., Fl. Brit. Ind. 5: 689. 1890.
TYPE: MALAYSIA. Perak, Larut Hills, 1065 m, *R. King's coll. [H. Kunstler] 2427* (Holotype: K, not seen).
Distribution: Malaysia (Peninsula).

Oberonioides parvula (J.D. Hook.) Ormerod, *comb. nov.*
Basionym: *Microstylis parvula* J.D. Hook., Icon. Plant. 19: t.1827B. 1889.
TYPE: MALAYSIA. Perak, Larut, 915-1220 m, August 1884, *R. King's coll. 6457* (Holotype: K, image seen).
Homotypic synonyms: *Malaxis parvula* (J.D. Hook.) Kuntze, Rev. Gen. Pl. 2: 673. 1891.
Liparis parvula (J.D. Hook.) Ridl., J. Linn. Soc., Bot. 32: 226. 1896.
Distribution: Malaysia (Peninsula).

Oberonioides pilifera (J.J. Sm.) Ormerod & Juswara, *comb. nov.*
Basionym: *Liparis pilifera* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 12: 114. 1932.
TYPE: INDONESIA. Sumatra, Deli and Serdang, Dolok Sebajak, 1600 m, 23 January 1923, *J.A. Lorzing 8327* (Syntype: BO, not found); same area, Petani Valley, 1300 m, 27 January 1923, *J.A. Lorzing 9440* (Syntype: BO, not found; Isosyntype: L, image seen); Loeboek Sikaping, Gunung Talakmau, 2000 m, 29 May 1917, *H.A.B. Bunnemeijer 916* (Syntype: BO, not found).
Distribution: Indonesia (Sumatra).

Oberonioides purpureoviridis (Burkill ex Ridl.) Ormerod & Juswara, *comb. nov.*
Basionym: *Liparis purpureoviridis* Burkill ex Ridl., Fl. Malay Pen. 4: 21. 1924.
TYPE: MALAYSIA. Pahang, Fraser's Hill, 1220-1330 m, 16-20 September 1922, *I.H. Burkill & R.E. Holttum 8422* (Lectotype, here designated: K, image seen).
Distribution: Malaysia (Peninsula, Sarawak); Indonesia (Sumatra).

This taxon is the only *Oberonioides* species to be recorded from Borneo. It has the largest flowers in the genus (sepals 12 mm long). Wood & Cribb (1994) inadvertently designated *Burkill & Holttum 8422* in SING as lectotype of *Liparis purpureoviridis* but this collection is not found in that herbarium, so this lectotypification is not valid and is here superseded by choosing the specimen in Kew. In SING another collection (*R.E. Holttum 11345*) is listed as holotype of *Liparis purpureoviridis,* but this specimen does not have details that match those cited in the protologue by Ridley (1924), it is therefore not type material.

Styloglossum Breda, Gen. Sp. Orch. Asclep. [fasc. 2]: [t.2]. 1829.
Type species: *Styloglossum nervosum* Breda

A genus of 50 primarily terrestrial species distributed from India to Samoa. They were previously included in *Calanthe* R. Br. but may be distinguished from that genus by having glabrous flowers, and generally caducous floral bracts. One more transfer is required to the genus, this plant being a rare natural hybrid from Java.

Styloglossum subhamatum (J.J. Sm.) Ormerod & Juswara, *comb. nov.*
Basionym: *Calanthe subhamata* J.J. Sm., Bull. Jard. Bot. Buitenz. s.2, 9: 31. 1913.
TYPE: INDONESIA. Java, Buitenzorg Botanic Garden, *cult. Hort. Bogor. s.n.* (Holotype: BO, not found).
Distribution: Indonesia (Java).

This plant is a natural hybrid between *S. pulchrum* (Blume) Yukawa & Cribb and *S. speciosum* (Blume) Yukawa & Cribb. Though Smith supplied no description in the protologue, he referred to his previous description of this hybrid in 1905 in the notes for *Calanthe speciosa* (Blume) Lindl.

Tropidia Lindl., Edwards's Bot. Reg. 19: sub t.1618. 1833.
Type species: *Tropidia curculigoides* Lindl.

This is a genus of about 30 species distributed from Sri Lanka and India to Samoa, with one or two taxa in the New

World (Ormerod 2018). The plants often resemble small palm seedlings, and have dull white to greenish flowers, often beset with a scurfy pubescence.

Tropidia kjellbergii Ormerod & Juswara, *sp. nov.*
TYPE: INDONESIA. Sulawesi, Todjamboe, 700 m, 15 December 1929, *G. Kjellberg 2933* (Holotype: AMES; Isotypes: BO, L; S, not seen). Fig. 2.

Related to *T. squamata* Blume but the labellum inside with strongly lamellate (vs. low ridges) keels which meet on the epichile and diverge again (vs. keels or low ridges parallel on the epichile).

Terrestrial *herb*. *Roots* thickly wiry, rigid, terete, to 4 mm thick. *Stems* erect, caespitose, laxly few branched, each branch apically 3-4 leaved, to 60 cm tall, 0.4 cm thick, branches to 25 cm long. *Leaves* ligulate-lanceolate to lanceolate, apex subcaudate-subacuminate, gramineous, 3-5 veined, 17.5-24.0 x 2.0-2.6 cm. *Inflorescences* axillary, 16-21 mm long; peduncle covered by two 5-6 mm long sheaths, 8 mm long; rachis sequentially 6 or more flowered, to 13 mm long; floral bracts lanceolate, acute, 5-6 mm long. *Flower* color not known, outside laxly furfuraceous. *Pedicel with ovary* clavate, furfuraceous, 4 mm long. *Dorsal sepal* oblong-lanceolate, subacute, 4-5 veined, 7.5 x 2.3 mm. *Lateral sepals* asymmetric, obliquely oblong-lanceolate, subacute, 3-4 veined, basally joined for 1.2 mm, 8.9-9.0 x 2.0-2.5 mm. *Petals* obliquely oblong-lanceolate, subacute, 2 veined, 6.9 x 2.0 mm. *Labellum* cymbiform-rhombic, subacute, 6 x 4 mm; hypochile cymbiform-rhombic, inside each side with a lamellate keel, these meet and diverge on the epichile, 5.8 x 4.0 mm; epichile ovate, subacute, recurved, 1.2 x 1.2 mm. *Column* stout, twisted, 4.1 mm long.

Distribution: Indonesia (Sulawesi).

Etymology: Named after Swedish botanist G.K. Kjellberg (1885-1943), collector of the type.

Tropidia kjellbergii is most similar to *T. squamata* Blume in habit (laxly 2-3 branched stems, each branch with a few leaves in the upper half), but the former differs in having lamellate (vs. low ridges, or very low lamellae) in the labellum hypochile that converge on the base of the epichile and then diverge (vs. parallel ridges on the epichile). *Tropidia curculigoides* Lindl. has 8-11 leaved stems, but the labellum is subpandurate with lamellate keels that are parallel on the epichile (vs. rhombic with diverging keels).

Tropidia mindorensis Ames has 13-14 leaved stems, and the labellum has lamellate keels that meet and diverge on the epichile. However the labellum hypochile is subpandurate (vs. rhombic), and the epichile is elliptic and concave (vs. ovate, subacute).

Literature Cited

Ormerod, P. 2018. Notes on Asiatic *Tropidia* (Orchidaceae: Tropidieae). *Harvard Pap. Bot.* 23, 1: 77–83.

Ormerod, P. and L. Juswara. 2019. New Names in Indonesian Orchids. *Harvard Pap. Bot.* 24, 2: 27–30.

Ormerod, P., M. A. Naive, and J. Cootes. 2019. Notes on Some Malesian Orchidaceae. *Harvard Pap. Bot.* 24, 2: 281–290.

Ridley, H. N. 1924. The Flora of the Malay Peninsula IV–Monocotyledones. L. Reeve & Co., London.

Smith, J. J. 1905. *Die Orchideen von Java*. E.J. Brill, Leiden.

Tang, G. D., G. Q. Zhang, W. J. Hong, Z. J. Liu, and X. Y. Zhuang. 2015. Phylogenetic analysis of Malaxideae (Orchidaceae: Epidendroideae): two new species based on the combined *nr*DNA ITS and chloroplast *mat*K sequences. *Guihaia* 35, 4: 447–463.

Thoerle, L., A. Schuiteman, and M. Turkel. 2020. *Dendrobium aurifex* (Orchidaceae). *Orchideen J.* 27, 1: 42–47.

Wood, J. J. and P. J. Cribb. 1994. A Checklist of the Orchids of Borneo. Royal Botanic Gardens, Kew, U.K.

Page 154 intentionally left blank.

FLORAE COSTARICENSIS SUBTRIBUI PLEUROTHALLIDINIS PRODROMUS—SYSTEMATICS OF *ECHINOSEPALA* (ORCHIDACEAE)

Franco Pupulin,[1–4] Noelia Belfort-Oconitrillo,[1,5] Adam P. Karremans,[1,6] and Diego Bogarín[1,7]

Abstract. We provide a general introduction to the *prodromi* to *Flora Costaricensis*, and an introduction to the precursors of subtribe Pleurothallidinae. We present a systematic revision of the genus *Echinosepala* for the flora of Costa Rica and a detailed discussion of molecular evidence with regard to most Costa Rican taxa, aimed at phylogenetically framing *Echinosepala* within the subtribe Pleurothallidinae, recognizing internal relationships among the species in the genus, and proposing evolutionary hypotheses. We recognize 10 species of *Echinosepala* in Costa Rica. Each species is described and illustrated with one or more botanical drawings and photographs, all based on Costa Rican material. Etymology, distribution, ecology, distinguishing features, and affinities with other taxa in the genus are discussed, taxonomic notes are provided, and a list of selected material examined for this study is included for each taxon. Two new species of *Echinosepala*, *E. glenioides* and *E. isthmica*, are described and illustrated, and their relationships are discussed. New combinations are proposed in *Echinosepala* for *Pleurothallis alexandrae* and *P. pastacensis*, and the former species is neotypified.

Keywords: flora of Costa Rica, new species, new combination, *Pleurothallis alexandrae*, *Pleurothallis pastacensis*, Pleurothallidinae

With this work, a first *prodromus* (Latin for "precursor") to *Flora Costaricensis*, we are starting a series of papers that aim to present partial but coherent results obtained by our group of researchers in the study and critical appreciation of the orchid flora of Costa Rica. These *prodromi* will discuss the systematics of selected genera or phylogenetically related groups of species in larger genera, which will be included in forthcoming volumes of *Flora Costaricensis*. This *magnus opus* devoted to the rich flora of Costa Rica started in 1965 with the visionary effort of William Burger and has since been led by the Field Museum of Natural History in Chicago. Thirteen volumes of *Flora Costaricensis* have been published to date over a period of almost 40 years, covering entire plant families or parts thereof (Burger, 1971; Burger et al., 1977, 1983, 1991, 2000; Pohl, 1980; Durkee and Burger, 1986; Burger and van der Werff, 1990; Burger and Taylor, 1993; Burger and Huft, 1995; Atwood and Mora de Retana, 1999; Luteyn and Wilbur, 2005; Pupulin, 2010).

As the general structure of *Flora Costaricensis* was conceived as individual volumes embracing complete families or at least vast taxonomic groups (to the ranks of subfamilies, tribes, and subtribes), the completion of Orchidaceae, with its high internal diversity and the rarity of certain taxa, proves to be an overwhelming challenge. A more convenient approach is the publication of individual papers dealing with the systematics of genera and/or groups already understood at the specific and intraspecific level, in anticipation of the final, comprehensive treatment (see, e.g., Pupulin and Bogarín, 2010, 2014b; Pupulin et al., 2010a; Bogarín, Serracín, and Samudio, 2014; Karremans et al., 2020). The present *prodromus* offers the first systematic insight into a complete group of Pleurothallidinae orchids for *Flora Costaricensis*.

Flora Costaricensis: Pleurothallidinae

When, in 2009, we inscribed a project devoted to the systematic treatment of the subtribe Pleurothallidinae Lindl. ex G. Don (Orchidaceae: Epidendreae) for *Flora Costaricensis* at the University of Costa Rica (UCR), we knew that a work of such magnitude had never been attempted before in a country as highly biodiverse as Costa Rica. Modern orchid treatments intended for *Flora Costaricensis* (see Atwood and Mora de Retana, 1999; Pupulin, 2010) are aimed at critically discussing the typification and identity of each taxon to the specific rank, including subspecific taxa and morphs when required, and to illustrate from living material all the taxa of a given group. Subtribe Pleurothallidinae encompasses in Costa Rica one-third of the total number of orchid species (Pupulin et al., 2019), making this vast assemblage of taxa one of the taxonomically more challenging in the country's flora.

We would like to thank the staff and curators at AMES, CR, JBL, K, SEL, USJ, and W for their help in retrieving the *Echinosepala* specimens kept there and their supportive cooperation. We acknowledge our colleagues at the research department of Lankester Botanical Garden for the unselfish support they gave throughout the stages of the present work, sharing with us most of the fieldwork and providing stimulating ideas, discussion, and materials. Darha Solano Ulate splendidly rendered most of the illustrations for this paper, proving to be one of the most gifted botanical illustrators active today. The horticulture staff at Lankester Botanical Garden is thanked for their help in cultivating the living plants documented here. Acknowledgments are extended to the Costa Rican Ministry of Environment and Energy (MINAE) and its National System of Conservation Areas (SINAC) for issuing the scientific collection permits under which all the wild specimens for this study were collected. The present paper is part of Project 814-B0-052, "Flora Costaricensis: taxonomía y filogenia de la subtribu Pleurothallidinae, Orchidaceae," supported by the Vice-Presidency of Research, University of Costa Rica.

[1] Lankester Botanical Garden, University of Costa Rica, P.O. Box 302-7050 Cartago, Costa Rica
[2] Harvard University Herbaria, Cambridge, Massachusetts, U.S.A.
[3] The Marie Selby Botanical Gardens, Sarasota, Florida, U.S.A.
[4] Corresponding author: franco.pupulin@ucr.ac.cr
[5] Orchid Conservation Project, Bosque de Paz Biological Reserve, Bajos del Toro, Costa Rica
[6] Naturalis Biodiversity Center, Endless Forms group, Leiden, The Netherlands
[7] Herbario UCH, Universidad Autónoma de Chiriquí, David, Panamá

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 155–190.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n5, Published online: 31 December 2020

In the 15 years elapsed since the publication of the senior author's checklist of Costa Rican Orchidaceae (Pupulin, 2002), which recorded 427 species of Pleurothallidinae, and up to the last catalog of pleurothallid orchids given by Pupulin and coworkers (2019), 134 new species and new records for the flora of Costa Rica have been added by our group (Pupulin and Bogarín, 2004, 2007, 2010, 2011a,b, 2012, 2014a,b; Pupulin et al., 2007, 2009, 2010a,b, 2011, 2012; Bogarín et al., 2008, 2013, 2015; Bogarín and Fernández, 2010; Bogarín and Karremans, 2010, 2016; Pupulin, Bogarín, and Smith, 2010; Pupulin, Medina, et al., 2010; Bogarín and Pupulin, 2011; Fernández, 2011; Fernández and Bogarín, 2011, 2013; Karremans and Bogarín, 2011, 2013; Karremans and Muñoz García, 2011; Bogarín, Karremans, et al., 2012; Bogarín, Smith, et al., 2012; Karremans, 2012, 2014; Karremans and Smith, 2012; Karremans et al., 2012; Smith and Pupulin, 2012; Fernández, 2013; Smith et al., 2013, 2015; Bogarín and Kisel, 2014; Bogarín, Serracín, and Samudio, 2014; Fernández et al., 2014; Bogarín and Jiménez, 2015; Karremans, Bogarín, et al., 2015; Karremans, Pupulin, et al., 2015; Oses Salas and Karremans, 2016; Karremans and Díaz-Morales, 2017; Pupulin, Díaz-Morales, Aguilar, et al., 2017; Pupulin, Díaz-Morales, Fernández, et al., 2017; Pupulin, Karremans, et al., 2017). The last available enumeration of Pleurothallidinae in Costa Rica (Pupulin et al., 2019), which includes data published until 2017, accounts for 561 species in 30 genera. After that list, another 20 species were published as new for science or new records for the flora of the country (Bogarín et al., 2017, 2020; Karremans and Bogarín, 2017; Rojas-Alvarado and Karremans, 2017; Bogarín, Fernández, et al., 2018; Bogarín, Karremans, et al., 2018; Bogarín, Pérez-Escobar, et al., 2018; Karremans and Jiménez, 2018; Karremans, 2019; Karremans et al., 2019; Pridgeon, 2020; Pupulin, 2020; Pupulin and Bogarín, 2020; Pupulin and Oses, 2020). Several additional species, patiently awaiting their turn within the drawers of the research department at Lankester Botanical Garden, shall be published in the coming years.

Species richness is not evenly distributed among Costa Rican Pleurothallids. Traditionally smaller genera (but please remember that generic definitions and circumscriptions in the subtribe are still problematic, and that alternative systems of classification have been proposed and are sometimes in parallel use) have shown reduced growth in terms of diversity and number of species, with increments in overall diversity probably proportional to the total number of taxa for each genus in the concerned region. Nonetheless, it is noteworthy that also in most of the groups that are not centered in Mesoamerica in terms of species diversity, like *Acianthera* Scheidw., *Anathallis* Barb. Rodr., *Dracula* Luer, *Dresslerella* Luer, *Myoxanthus* Poepp. & Endl., *Octomeria* R. Br., *Pabstiella* Brieger & Senghas, *Restrepiella* Garay & Dunst., and *Trichosalpinx* Luer, new taxa and new records are continually added to the checklist of the country's Pleurothallidinae. The case is different for the more specious genera like *Lepanthes* Sw., *Pleurothallis* R. Br., and *Stelis* Sw., each of which already accounts for around 100–150 species in Costa Rica, and which together represent more that half of the known species of Pleurothallidinae in the country. Each of these genera will include, once their monographic treatments have been concluded, no less than 150 species.

With the advent of new techniques for the analysis of molecular data, the supraspecific systematics of the Pleurothallidinae have been discussed extensively (see, at least, Pridgeon et al., 2001; Luer, 2002; Karremans, 2016). However, less emphasis has been put into the effort of clarifying the internal relationships within the major groups, which would have greatly contributed to a better understanding not only of the phytogeographic and phylogenetic patterns of dispersion and speciation of the largest genera in the different regions of the American tropics, but also of their true diversity. For almost two centuries, pleurothallid orchids have been mainly described within the limits of a strictly floristic approach, with little or no consideration of either the relationships between species within any given genus or the delineation of groups of close relative taxa that could reflect the natural history of the largest genera. Molecular taxonomy mainly focuses on distinguishing and circumscribing monophyletic genera, rejecting artificial or erroneous systematic frameworks, but the difficulty of obtaining enough samples and molecular markers for analyses (Bogarín, Pérez-Escobar, et al., 2018) has in part obscured the true relationships among the species of the concerned groups. As a result, those genera whose monophyly received strongest molecular support were poorly investigated as to their internal relationships, irrespective of their size.

The five-year term sponsored by the University of Costa Rica for our study of the Subtribe Pleurothallidinae (the maximum period of funding for research projects by UCR) was highly productive, but it is obvious that the effort made by the team of Lankester Botanical Garden botanists to complete the chapter on Pleurothallidinae for *Flora Costaricensis* still has to offer novel results. To organize and present these results, we split Pleurothallidinae into blocks of genera, and the largest genera into smaller complexes of related species. Here we introduce the results of our systematic studies on *Echinosepala*.

Materials and Methods

The general methods adopted for this study follow that presented in Pupulin, Karremans, et al. (2017). Plants of *Echinosepala* were collected around the country, from type localities and other critical areas, and brought to Lankester Botanical Garden (LBG) for cultivation and subsequent documentation. At least five specimens per morphospecies were collected at any given locality whenever possible. Field notes were taken during fieldwork, including GPS and political data, elevation, ecological zones, and main types of vegetation. Plants were cultivated at JBL, and phenological data recorded.

Morphological Analysis

Over 180 individuals of *Echinosepala*, belonging to most of the morphospecies known for the country, were studied and documented. High-resolution macro- and microphotographs were taken according to the methods and with the camera and microscopic equipments detailed in Pupulin, Karremans, et al. (2017). Drawings of flowers and floral dissection were prepared according to the methods described therein. Vouchers were conserved in the liquid collection of JBL and/or in the herbaria of the National Museum of Costa Rica (CR) and the University of Costa Rica (USJ). Measurements were mostly taken under a dissecting stereoscope, or with the aid of the electronic scale bars inserted in the high-definition images of the floral details. Collections of the country, as well as relevant herbaria that allow digital access to their collections, were revised to study specimens of the taxa in this study, and specimens annotated when required.

Floral Ecology

Notes on floral ecology were taken from direct observation of the plants under the semiartificial conditions of the LBG open greenhouses. Photographs were taken of individual flowers over a lapse of two to three days to document temporal activity of the perianth.

DNA Extraction and Sequencing

The selection of the material was based on availability and interspecific variability. Vouchers of the specimens are kept in the liquid collections at JBL or L, unless specified otherwise. The list of the vouchers used in the phylogenetic analyses and their NCBI GenBank accession numbers are provided in Pupulin, Karremans, et al. (2017: Tab. 1). Methodology for DNA extraction, amplification, and sequencing of the material followed the steps given therein under the same heading.

Building the Data Sets

The STADEN (Staden et al., 2003) package was used for editing the sequences, and the Unicode nomenclature (IUPAC) was adopted where more than one base pair was equally probable. In the few cases when Pregap was unable to build a contig, sequences were merged by filling in missing positions with N's. Sequences were aligned manually in Mesquite v2.72 (Maddison and Maddison, 2007). After the alignments had been edited, additional sequences were obtained from GenBank, the latter using nBLAST. *Arpophyllum giganteum* AF266742 (ITS) was used as outgroup in all cases, as it is suggested to be the furthest related of all included species (Pridgeon et al., 2001; Pupulin, Karremans, et al., 2017).

Phylogenetic Analysis

The Bayesian Evolutionary Analysis Sampling Trees (BEAST; Drummond and Rambaut, 2007) was used to analyze the ITS matrix. Substitution and clock models were unlinked. GTR + Γ model, estimated frequencies, and eight categories were used. The Lognormal relaxed clock model was used. The tree prior was speciation-yule birth, and the number of generations was set to 30,000,000. The first 20% of the resulting trees were used as burin. Trees were visualized in FigTree v.1.3.1 (Rambaut, 2009). Posterior probability (PP) values were added to the branches of the trees using the labeling option, and branches were reordered for better visualization as discussed in Pupulin, Karremans, et al. (2017).

SYSTEMATICS OF *ECHINOSEPALA*

Echinosepala Pridgeon & M.W. Chase, Lindleyana 17(2): 100–101. 2002.

Synonyms: *Echinella* Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg. homonym*, *non* Ach. (1810, Closteriaceae). Type species: *Pleurothallis aspasicensis* Rchb.f. ≡ *Echinosepala aspasicensis* (Rchb. f.) Pridgeon & M.W. Chase.

Myoxanthus subgen. *Satyria* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 44: 5. 1992. *Pleurothallis* subgen. *Acianthera* sect. *Satyria* (Luer) Luer, Lindleyana 11: 118. 1996. Type species: *Pleurothallis pan* Luer ≡ *Echinosepala pan* (Luer) Pridgeon & M.W. Chase.

Myoxanthus subgen. *Silenia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 44: 6. 1992. *Pleurothallis* subgen. *Acianthera* sect. *Silenia* (Luer) Luer, Lindleyana 11: 118. 1996. Type species: *Pleurothallis aspasicensis* Rchb. f. ≡ *Echinosepala aspasicensis* (Rchb. f.) Pridgeon & M.W. Chase.

Epiphytic, lithophytic or terrestrial, caespitose to repent, small to large *herbs*. *Stems* erect to curved, terete to slightly complanate, homoblastic, composed of 2 or more nodes, enclosed by ancipitous, loose, rarely pubescent sheaths, commonly disintegrating with age. *Leaf* coriaceous, narrowly ovate to linear-elliptic, subacute to acuminate, cuneate below into a conduplicate, sessile base, with the veins typically very apparent. *Inflorescence* a fascicle of single, successive flowers from the base or the apex of the stem, or both; the peduncle terete. *Floral bract* loose, usually pubescent. *Ovary* minutely scaberulous to tomentose or long-haired. *Flowers* bilabiate, fleshy, with temporal activity, usually with putrid, reddish-purple colors, with sepals externally glabrous, scabrous or pubescent. *Dorsal sepal* free, subtriangular to lanceolate-elliptic to oblanceolate, obtuse to acuminate, abaxially glabrous to verrucose. *Lateral sepals* connate into an elliptic to obovate synsepal, subacute-rounded to broadly obtuse, the apices sometimes free, glabrous to verruculose within. *Petals* fleshy, lanceolate to obovate, asymmetric, rounded to acute or truncate. *Lip* 3-lobed, elliptic from a small claw, the apical lobe rounded to subtruncate, thickened at apex into a cushion-like pad, with a pair of intramarginal thin keels, lateral lobes erect, uncinate; the disc with an erect callus arising above the base, the lip sometimes with a horseshoe-shaped pseudoglenion. *Column* semiterete, footed, with narrow wings above the middle. *Anther cap* globose, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, on a short, bilobed caudicle.

Before molecular systematics, *Echinosepala* species had been difficult to adequately place into a phylogenetic context, and only in the present century has its position in the groups of basal Pleurothallidinae (sensu Karremans, 2016) been fully understood. Of the 14 species currently recognized as belonging to the genus (Epidendra, 2019; IPNI, 2020), only 2 were originally described under the name *Echinosepala* (Pupulin, Karremans, et al., 2017); all others have been classified as species of *Acianthera*, *Myoxanthus*, and *Pleurothallis*.

Carlyle Luer (1992) first recognized that most species of the group were closely related and gathered them into *Myoxanthus* subgen. *Silenia* Luer and *Satyria* Luer. The two subgenera were mainly distinguished from other groups of *Myoxanthus* by the non-scurfy sheaths (except *Myoxanthus pan* [Luer] Luer ≡ *Echinosepala pan* [Luer] Pridgeon & M.W. Chase) and the flowers produced from low on the ramicaul or terminally at the base of the leaf (instead of from near the apex of the stem). The long verrucose-ciliate upper margin of the anther cap is a common synapomorphy of the two subgenera.

Because of the strong morphological affinities of *Myoxanthus* subgen. *Satyria* and *Silenia* with *Pleurothallis* subgen. *Acianthera* (Scheidw.) Luer—a relationship also recovered by molecular analyses (see particularly Karremans et al., 2016)—Luer moved most species to *Pleurothallis* subgen. *Acianthera*, creating two new sections (Luer, 1995; validated in Luer, 1996).

The analyses of DNA data (Pridgeon and Chase, 2001; Pridgeon et al., 2001) confirmed that the species of *Myoxanthus* subgen. *Silenia* and subgen. *Satyria* formed a monophyletic group deserving generic recognition, and Pridgeon and Chase (2001) gave it formal status by creating *Echinella* Pridgeon & M.W. Chase (later corrected to *Echinosepala* Pridgeon & M.W. Chase [Pridgeon and Chase, 2002]). The phylogenetic analyses also confirmed a close relationship between *Echinosepala* and *Myoxanthus*, as noted by Luer. Together with *Barbosella* Schltr., *Dresslerella* Luer, *Pleurothallopsis* Porto & Brade, *Restrepia* Kunth, and *Restrepiella* Garay & Dunst., *Echinosepala* forms one of the nine major clades within the Pleurothallidinae, sister to the basal clade of *Octomeria*, and consecutively sister to the *Acianthera* clade (Karremans, 2016).

Morphologically, species of *Echinosepala* are characterized by caespitose to repent plants with monophyllous stems covered by tubular-ancipitous, minutely warty to (rarely) pubescent sheaths; the leaf coriaceous; the inflorescence solitary-flowered, produced from the apical or lower nodes of the stem; the flower fleshy, with the sepals frequently hirsute abaxially and variously verrucose adaxially, the lateral sepals connate into a concave to cymbiform synsepal; the lip 3-lobed, with the erect lateral lobes oblong to uncinate, provided with a tall basal callus; the anther apical incumbent, the anther cap papillose to ciliate at apex; the 2 pollinia provided with whale-tail-shaped caudiculae (Luer, 1992; Pridgeon, 2005a).

The point of insertion of the inflorescence along the stem has been used as the main character to distinguish the two assemblages of species within the group. Luer (1992) created *Myoxanthus* subgen. *Silenia* to separate those species with a basal inflorescence (erroneously reported to be produced from the rhizome; e.g., Luer, 1992, 2003; Dressler, 1993; Pridgeon, 2005a) from the rest of the group, which supposedly have a terminal inflorescence. Pupulin, Karremans, et al. (2017) showed that the inflorescences of *Echinosepala* species are never rhizomic but are rather produced along the stem, where it is exerted from the apex of the second to third internode (see fig. 1 in Pupulin, Karremans, et al., 2017), and they expressed doubts that flowering from the nodes of the rhizome occurs at all in the Pleurothallidinae. Producing inflorescences from the lower nodes of the secondary stem is apparently an obligate feature in *E. lappiformis* (A.H. Heller & L.O. Williams) Pridgeon & M.W. Chase, *E. pan*, and *E. stonei* (Luer) Pridgeon & M.W. Chase, but it is facultative in *E. expolita* Pupulin & Belfort, where both apical and basal inflorescences are sometimes produced simultaneously. This condition has evolved in other groups of Pleurothallids, especially in *Acianthera*, and according to our molecular analyses even in *Echinosepala* it could have arisen independently in two different groups of species.

The "basal" position of the inflorescence in species of *Echinosepala* convinced Luer (2004) to revive the genus *Brenesia* Schltr. (1923), created to accommodate the anomalous *Brenesia costaricensis* Schltr., a species with pendent inflorescences produced from the lower nodes of the stem and hirsute flowers. He transferred eight species previously treated under *Echinosepala* (Luer, 2004) to *Brenesia*, under the belief that they were related to each other. However, the relationship between species of *Brenesia sensu stricto* (i.e., *B. costaricensis*, *B. herrerae* [Luer] Luer, and *B. johnsonii* [Ames] Luer, plus *Acianthera sotoana* Solano) and species of *Echinosepala* is not supported by DNA studies. The broad phylogenetic analysis of *Acianthera* carried out by Karremans et al. (2016) retrieved that the clade including the type species of *Brenesia* is sister to a clade that includes *Antilla* and *Kraenzlinella*, which all together are highly supported as sisters to the rest of *Acianthera*.

Florally, species of *Echinosepala* are mostly characterized by the putrid, reddish-purple color of the bilabiate perianth, often spreading only partially, and the complicate abaxial indumentum of the sepals, which vary from almost glabrous (*E. isthmica*, described below), to sparsely warty-verruculose (*E. alexandrae* [Schltr.] Pupulin & Bogarín, *E. aspasicensis*, *E. glenioides* [hereafter], *E. uncinata* [Fawc.] Pridgeon & M.W. Chase), the warts sometimes grouped into small tufts (*E. longipedunculata* Pupulin & Karremans and *E. vittata* [Pupulin & M.A. Blanco] C.O. Morales & N. Villalobos), to sparsely spiny (*E. expolita* Pupulin & Belfort), densely tomentose (*E. tomentosa* [Luer] Pridgeon & M.W. Chase), hirsute with soft trichomes (*E. lappiformis* [A.H. Heller & L.O. Williams] Pridgeon & M.W. Chase, *E. stonei* [Luer] Pridgeon & M.W. Chase), or echinate with stiff hairs (*E. pan*). Adaxially, the sepals are almost glabrous (*E. alexandrae, E. aspasicensis, E. uncinata, E. vittata*), sparsely warty (*E. tomentosa*), to covered with irregular, low (*E. lappiformis*) or tall (*E. stonei*) warts, or stiff, short, rounded (*E. longipedunculata*) or pointed (*E. expolita*, *E. pan*) warts. In some species, the base of the dorsal sepal is semitransparent (e.g. *E. aspasicensis, E. expolita, E. glenioides*), forming a window under the dark purple blotches (Pupulin, Karremans, et al., 2017: fig. 3). The petals are mostly glabrous to sparsely verruculose, but they may be distinctly warty toward the apex (*E. expolita*, *E. lappiformis, E. pan, E. stonei*). The lip is glabrous in most species, but it is warty at apex in *E. alexandrae* and *E. shuarii* (Luer) Luer (= *Pupulinia shuarii* [Luer] Karremans & Bogarín). It always presents a tall callus at the base, which can be rounded and broad, massive, slightly concave, smooth or transversely rugose, occupying all the lip base (*E. alexandrae, E. isthmica, E. lappiformis*, *E. stonei, E. uncinata*), or provided with a horseshoe-shaped, concave pseudoglenion (*E. aspasicensis, E. expolita, E. glenioides, E. longipedunculata, E. pan, E. tomentosa, E. vittata*). This produces a gelatinous, non-viscous, shiny exudate, which is spread through a longitudinal groove to the apex of the lip, where it apparently dries, becoming matte in two to three days. In most species, the midline of the lip presents a pair of intramarginal low lamellae, typically undulate on the upper margin.

According to our analyses, species of *Echinosepala* form a highly supported clade, consecutively sister to *Myoxanthus*, *Dresslerella*, and a clade grouping species of *Pleurothallopsis* and *Restrepia*, and species of *Restrepiella* and *Barbosella*, on two branches (Fig. 1). Within *Echinosepala*, *E. glenioides* (as *E. aspasicensis*) and *E. longipedunculata* are highly supported as sister species, and in turn they are well supported as sister of *E. pan* and *E. expolita,* which cannot be differentiated by their ITS sequences. *Echinosepala alexandrae* (as *E. sempergemmata*) and *E. isthmica* (as *E. uncinata*) form a well-supported group, which in turn is sister (with low support) to *E. stonei*. In our analysis, the phylogenetic position of *E. stonei* is not resolved, but the species is surely not closely related to the group of *E. expolita*/*E.pan*. *Echinosepala tomentosa* and *E. vittata*, both characterized by miniature plant habits and flowers, are sister to all the other species in a highly supported group.

The actual diversity of this group has still to be fully understood. Pridgeon (2005a) reported only 8 species for the genus, but we have recorded 10 species in Costa Rica alone (Pupulin, Karremans, et al., 2017; herein) (Fig. 2–3). Including the new taxa described and resurrected in the present paper, at least 17 species are recognized today in the genus, distributed from Belize to the West Indies (Jamaica), to the Guyanas and Brazil, and down to Bolivia, including Peru (Zelenko and Bermudez, 2009), along the Andes, but the diversity of *Echinosepala* is likely much higher.

References: Pridgeon et al. (2001, 2005a,b), Karremans (2016), Pupulin, Karremans, et al. (2017).

GENUS DISCUSSION FOR *FLORA COSTARICENSIS*

Echinosepala is a genus of 17 or more species, distributed from Belize to the West Indies (Jamaica), the Guyanas and Brazil, and down to Bolivia along the Andes. According to the number of species recorded in Costa Rica alone, the diversity of *Echinosepala* is likely higher. Species of *Echinosepala* occur mostly epiphytically (rarely as lithophytic or terrestrial herbs) in warm tropical, premontane or cloud, evergreen, wet forests at elevations of 300–2000 m. Flowering has been mostly recorded from June to December. Morphologically, species of *Echinosepala* are characterized by caespitose to repent plants with monophyllous stems covered by tubular-ancipitous, minutely warty to (rarely) pubescent sheaths and coriaceous leaves; the inflorescence solitary-flowered, produced from the apical or lower nodes of the stem; the bilabiate flower fleshy, with putrid colors and complicate indumenta of the sepals, frequently hirsute abaxially and variously warty adaxially, the lateral sepals connate into a synsepal; the lip 3-lobed, with the erect lateral lobes oblong to uncinate, provided with a tall basal callus occupying all the disc, which can be rounded and broad, massive, smooth, or provided with a horseshoe-shaped, concave pseudoglenion, producing a shiny, gelatinous exudate, and a pair of intramarginal, low keels; the apical anther incumbent, papillose to ciliate at apex; the 2 pollinia provided with whale-tail-shaped caudiculae. *Echinosepala* is likely to be pollinated by flies that hook the pollinarium to the rear portion of the scutellum. No pollination studies have been published to date, but flies of the Drosophilidae family were recorded visiting the flowers. Molecular analyses carried out by Pridgeon and collaborators (2001) and by our group (Pupulin, Karremans, et al., 2017) support the monophyly of *Echinosepala*, whose species form a highly supported clade, sister to *Myoxanthus*, *Dresslerella*, and a clade grouping species of *Pleurothallopsis* and *Restrepia*, and species of *Restrepiella* and *Barbosella*, on two branches. Within *Echinosepala*, the species with a pseudoglenion are highly supported as sister species, whereas those with a plate-like, bare callus form another well-supported group, which in turn is sister to *E. stonei* (Fig. 4). The species with miniature plant habits and flowers are sister to all the other species in a highly supported group.

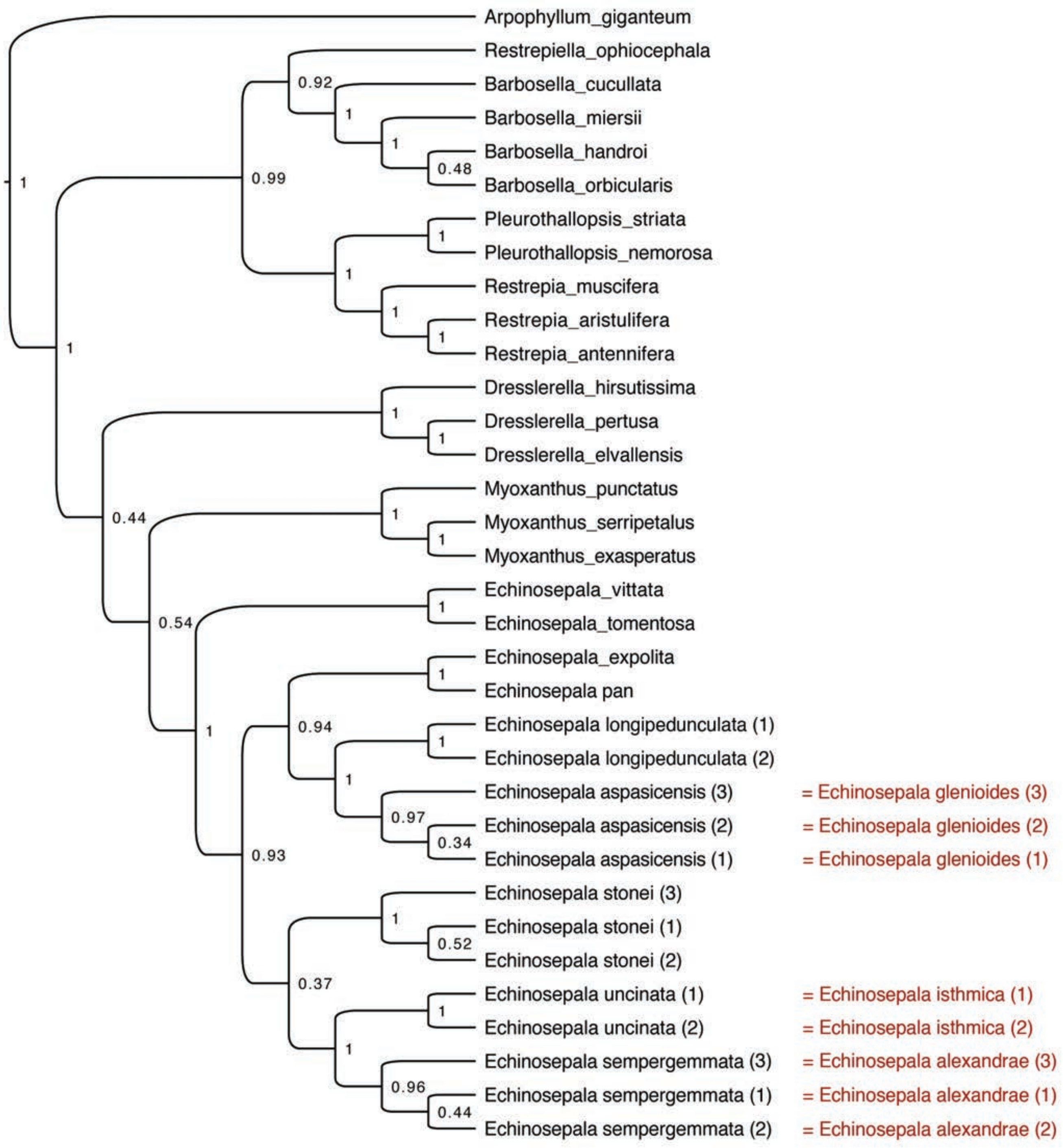


FIGURE 1. Phylogenetic relationship among the species of *Echinosepala* (modified from Pupulin, Karremans, et al., 2017). Species names in red are updated to the nomenclature proposed in the present paper.

FIGURE 2. Flowers of *Echinosepala* species from Costa Rica. **A–B**, *E. alexandrae* (*Bogarín 7137*); **C–D**, *E. expolita* (*Bogarín 1871*; *Pupulin 7030*); **E–F**, *E. glenioides* (*Bogarín 3063*; *Bogarín 8211*); **G–H**, *E. isthmica* (*Bogarín 5855*; *Bogarín 5871*); **I**, *E. lappiformis* (*Bogarín 9554*). All the vouchers at JBL. Photographs by F. Pupulin.

FIGURE 3. Flowers of *Echinosepala* species from Costa Rica. **A–B**, *E. longipedunculata* (*Bogarín 5449*; *Karremans 4994*); **C**, *E. pan* (*Bogarín 10270*); **D**, *E. stonei* (*Bogarín 5713*); **E**, *E. tomentosa* (*Bogarín 5622*); **F**, *E. vittata* (*Blanco 1324*). All the vouchers at JBL. Photographs by F. Pupulin.

KEY TO THE SPECIES OF *ECHINOSEPALA* IN COSTA RICA

1a. Callus of the lip with an inverted U-shaped callus (pseudoglenion) at the base 2
1b. Callus of the lip with the basal callus smooth to rugulose 8
2a. Inflorescences produced from the lower nodes of the stem 3
2b. Inflorescences produced from the apex of the stem 4
3a. Sheaths of the ramicauls hirsute; leaves narrowly linear-anceolate, >2.5 cm wide: sepals long-echinate abaxially . . . . *E. pan*
3b. Sheaths of the radical glabrous; leaves ligulate, <3 cm wide; sepals shortly tomentose abaxially . . . . *E. expolita*
4a. Mature plants <20 cm tall; flowers small, synsepal >1 mm long, lip >4 mm long 5
4b. Mature plants >30 cm tall; flowers large, synsepal < 15 mm long, lip <7 mm long 6
5a. The dorsal sepal yellow, the synsepal deep purple, adaxially densely tomentose . . . . *E. tomentosa*
5b. Sepals whitish, striped with red, abaxially with stiff hairs along the veins . . . . *E. vittata*
6a. Ovary and abaxial surface of the sepals tomentose; adaxial surface spiny . . . . *E. expolita*
6b. Ovary and abaxial surface of the flowers warty; adaxial surface verruculose 7
7a. Pedicel <3 cm long; flowers purple-maroon; lip elliptic, acute, purple-red . . . . *E. glenioides*
7b. Pedicel >6 cm long; flowers yellow-orange; lip sub rectangular, truncate, yellow . . . . *E. longipedunculata*
8a. Inflorescences produced from the lower nodes of the stem 9
8b. Inflorescences produced from the apex of the stem 10
9a. Dorsal sepal narrowly triangular-lanceolate . . . . *E. lappiformis*
9b. Dorsal sepal broadly oblong . . . . *E. stonei*
10a. Leaves ligulate; flowers autogamous, mostly cleistogamous, adaxially warty, midlobe of lip ovate, narrower than the lip base . . . . *E. alexandrae*
10b. Leaves lanceolate; flowers not autogamous, adaxially subglabrous, midlobe of lip transversely rectangular, as wide as the lip base . . . . *E. isthmica*

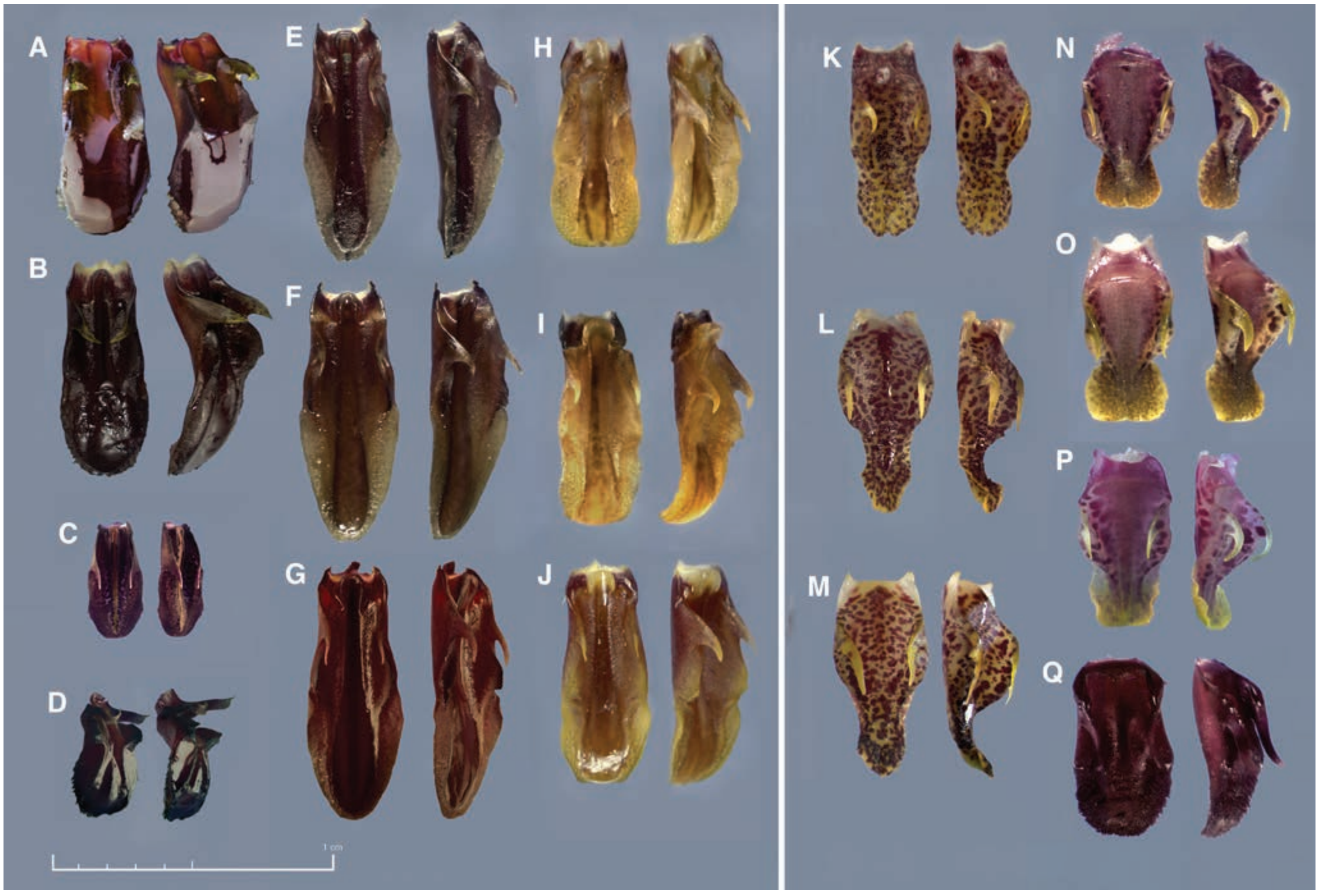


Figure 4. Labella of *Echinosepala* species. **A–J** (left of the bar), species provided with a pseudoglenion; **K–Q** (right of the bar), species without pseudoglenion. **A–B**, *Echinosepala expolita*; **C**, *E. tomentosa*; **D**, *E. pan*; **E–G**, *E. glenioides*; **H–J**, *E. longipedunculata*; **K–M**, *E. alexandrae*; **N–P**, *E. isthmica*; **Q**, *E. stonei*. Vouchers (all at JBL): *Pupulin 7030* (A); *Bogarín 1871* (B); *Bogarín 5822* (C); *Bogarín 10274* (D); *Bogarín 1945* (E); *JBL-20660* (F); *JBL-27660* (G); *Bogarín 3863* (H); *Bogarín 5449* (I); *Karremans 4994* (J); *Bogarín 4601* (K); *Bogarín 4678* (L–M); *Bogarín 5855* (N); *Bogarín 5871* (O); *Bogarín 5855* (P); *Bogarín 7190* (Q). Photographs by F. Pupulin.

Taxonomic Treatment

1. **Echinosepala alexandrae** (Schltr.) Pupulin & Bogarín, *comb. nov*.

Basionym: *Pleurothallis alexandrae* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 103. 1923. TYPE: COSTA RICA. [San José: Cerro el] Tablazo, 1900 m, blühend im Juli 1909, *A. Brade & C. Brade 1159* (Holotype: B, destroyed; Neotype: designated here, tracings of Schlechter's drawings of the habit and floral analysis, mounted on the same sheet, AMES 00074034, Fig. 5A–B). Fig. 6–7 (Vouchers: *Bogarín 5755*, JBL, and *Bogarín 4678*, JBL).

Heterotypic synonyms: *Pleurothallis sempergemmata* Luer, Selbyana 3(3–4): 386. 1977. TYPE: PANAMA. Chiriquí: epiphytic in forested valley above Guadalupe, alt. 2200 m, 17 Dec 1976, *C. Luer 1360, A. Luer, R. Dressler, N. Williams & F. L. Stevenson* (Holotype: SEL).

Myoxanthus sempergemmatus (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 38. 1986.

Echinella sempergemmata (Luer) Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg*.

Echinosepala sempergemmata (Luer) Pridgeon & M.W. Chase, Lindleyana 17(2): 101. 2002.

Brenesia sempergemmata (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Epiphytic, caespitose, erect *herb* up to 30 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, thicker in the distal portion, 5–13 cm long, homoblastic, composed by 5–8 internodes different in length, completely enclosed by 6–8 papyraceous, tubular, ancipitous, apically loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the apex, 1.8–5.2 × 0.8–1.5 cm, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, narrowly elliptic to lanceolate-elliptic, subacute to acute, minutely emarginate at apex, 12–20 × 2.6–5.0 cm, the midvein distinctly protruding abaxially. *Inflorescence* a fascicle of single, successive (or few simultaneous) flowers produced from a quickly degrading spathe at the apex of the ramicaul; the peduncle terete, suberect to prostrate, glabrous to minutely puberulous, 2.0–3.2 mm long. *Floral bract* papyraceous, inflated, lanceolate, acute, ca. 1.0–1.8 cm long.

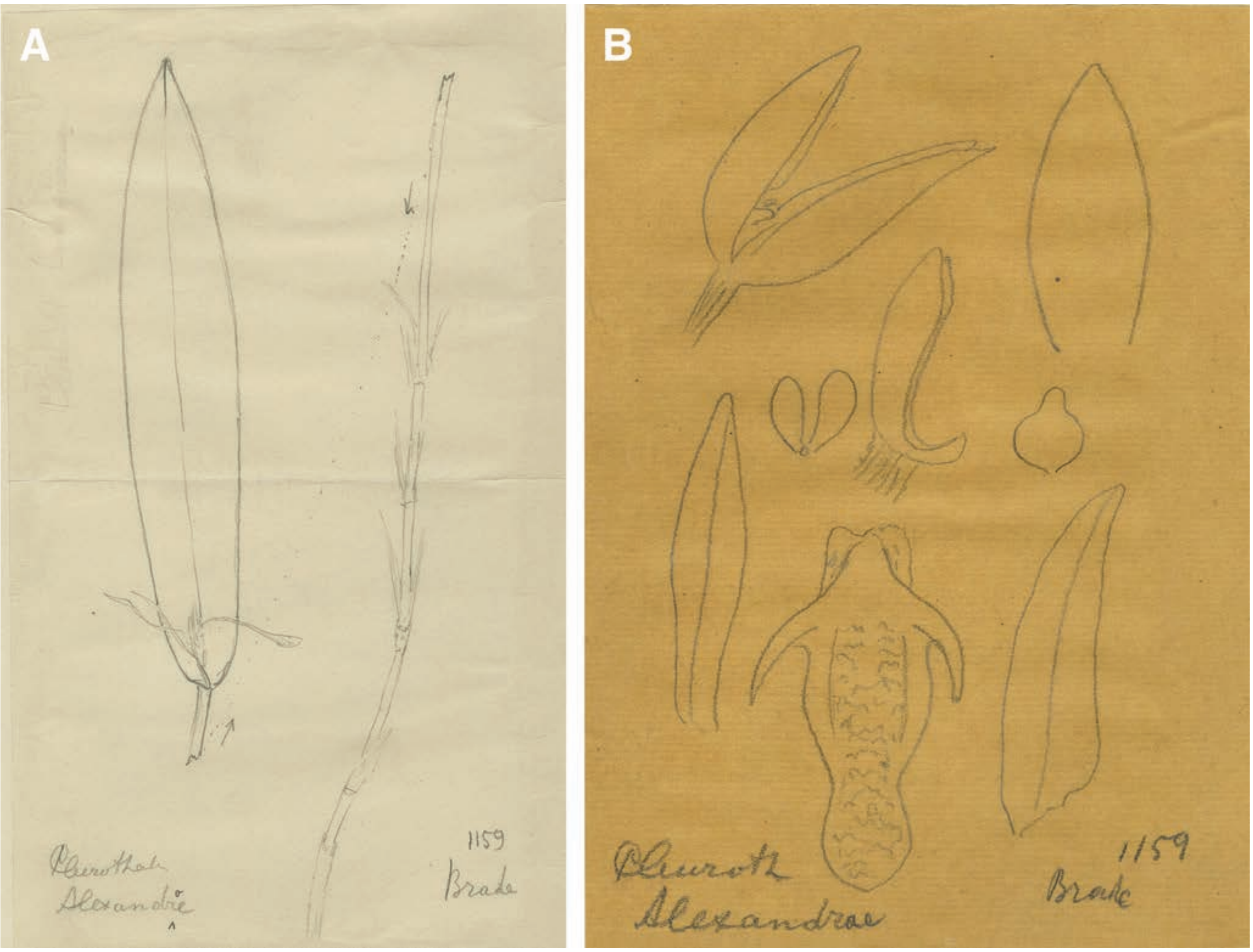


FIGURE 5. Neotype of *Pleurothallis alexandrae*. **A**, habit; **B**, flower analysis. Tracings of Schlechter's original illustrations based on the original collection *A. Brade & C. Brade 1159* (AMES 00074034). Reproduced with the kind permission of the Curator, Oakes Ames Orchid Herbarium, Harvard University Herbaria.

Pedicel terete, 0.8–1.0 cm long; *ovary* linear-subclavate, to 7 mm long, papillous-puberolous, the short warts apically provided with a tuft of stiff, somewhat stellate bristles. *Flowers* bilabiate, autogamous, mostly cleistogamous and quickly developing into a fruit before reaching anthesis; when opening, the flowers self-pollinating during the first or second day of anthesis, if flowering more than one day, without temporal activity of the perianth; the sepals light to dull green, the adaxial basal half blotched and spotted purple-brown, abaxially striped with pale purple; the petals yellow, blotched with purple-red, sparsely verrucose; the lip purple-red. *Sepals* fleshy, densely and shortly stellate-puberolous on the abaxial side; *dorsal sepal* lanceolate-oblong, concave, narrowly obtuse, 14–18 × 6–8 mm, 5-veined, the inner surface glabrous, abaxially densely warty-pubescent, the warts apically provided with a stellate tuft of short hairs; *lateral sepals* connate into an ovate, obtuse to shortly bifid, abaxially warty-pubescent synsepal, the warts terminating with a stellate tuft of short hairs, 15–19 × 10–12 mm, each half 3-veined, the apices sometimes free to about 1 mm. *Petals* fleshy, elliptic-lanceolate to oblong-lanceolate, obliquely asymmetric, narrowly obtuse to acute, 7–10 × 2.5–3.0 mm, 3-veined. *Lip* 3-lobed, ovate-elliptic, pandurate, from a small, thin, rectangular, white-hyaline claw, 7.2–8.0 × 2.8–3.1 mm (5.5 mm across the lateral lobes), the base subtruncate; the apical lobe elliptic to ovate-elliptic, obtuse, the margins more or less incurved, provided at the base with a pair of intramarginal, thin, crenulate keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly triangular-uncinate, antrorse; the disc with an erect, tall, broad, glabrous laminar callus. *Column* subarcuate, semiterete, ca. 8 mm long, provided with thickened, small, elliptic wings above the middle, the foot ca. 1 mm long. *Anther cap* ovate, cucullate, with long, stiff apical hairs, 2-celled. *Pollinia* 2, ovoid, flattened, on a short bifid caudicle. Fig. 2A–B.

Eponymy: named in honor of Rudolf Schlechter's wife, Alexandra, née Sobenikoff.

Distribution: Costa Rica to central Panama (Cerro Campana).

Ecology: in Costa Rica, *Echinosepala alexandrae* is an uncommon epiphyte, seemingly restricted to the Caribbean,

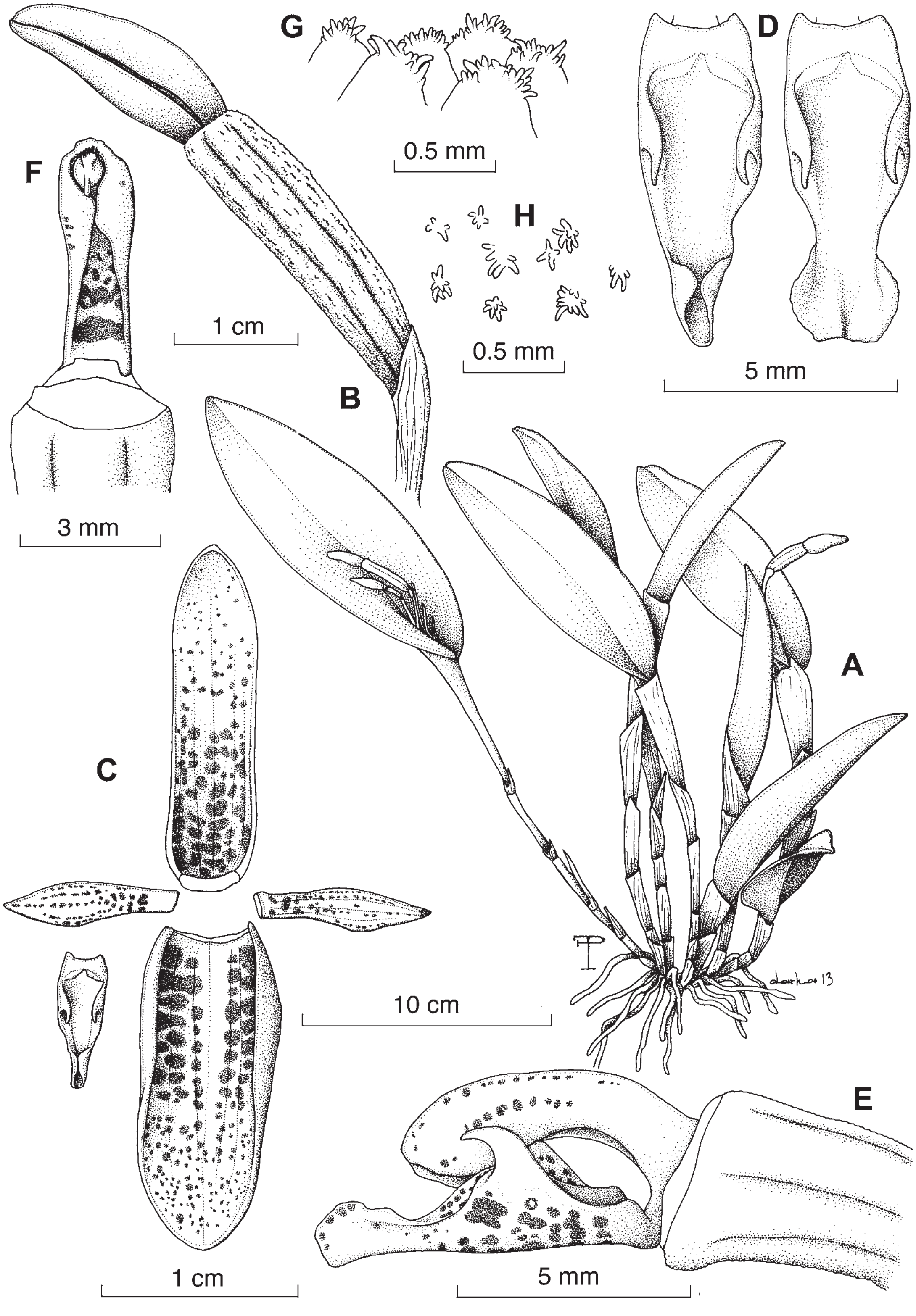


FIGURE 6. *Echinosepala alexandrae* (Schltr.) Pupulin & Bogarín. **A**, habit; **B**, developing ovary and flower remnants; **C**, dissected perianth; **D**, lip, ventral view (the apical lobe in natural position and spread); **E**, column and lip, lateral view; **F**, column of self-pollinated flower, ventral view; **G–H**, details of the ovary indumentum. Drawn from *Bogarin 5775* by F. Pupulin and D. Solano Ulate.

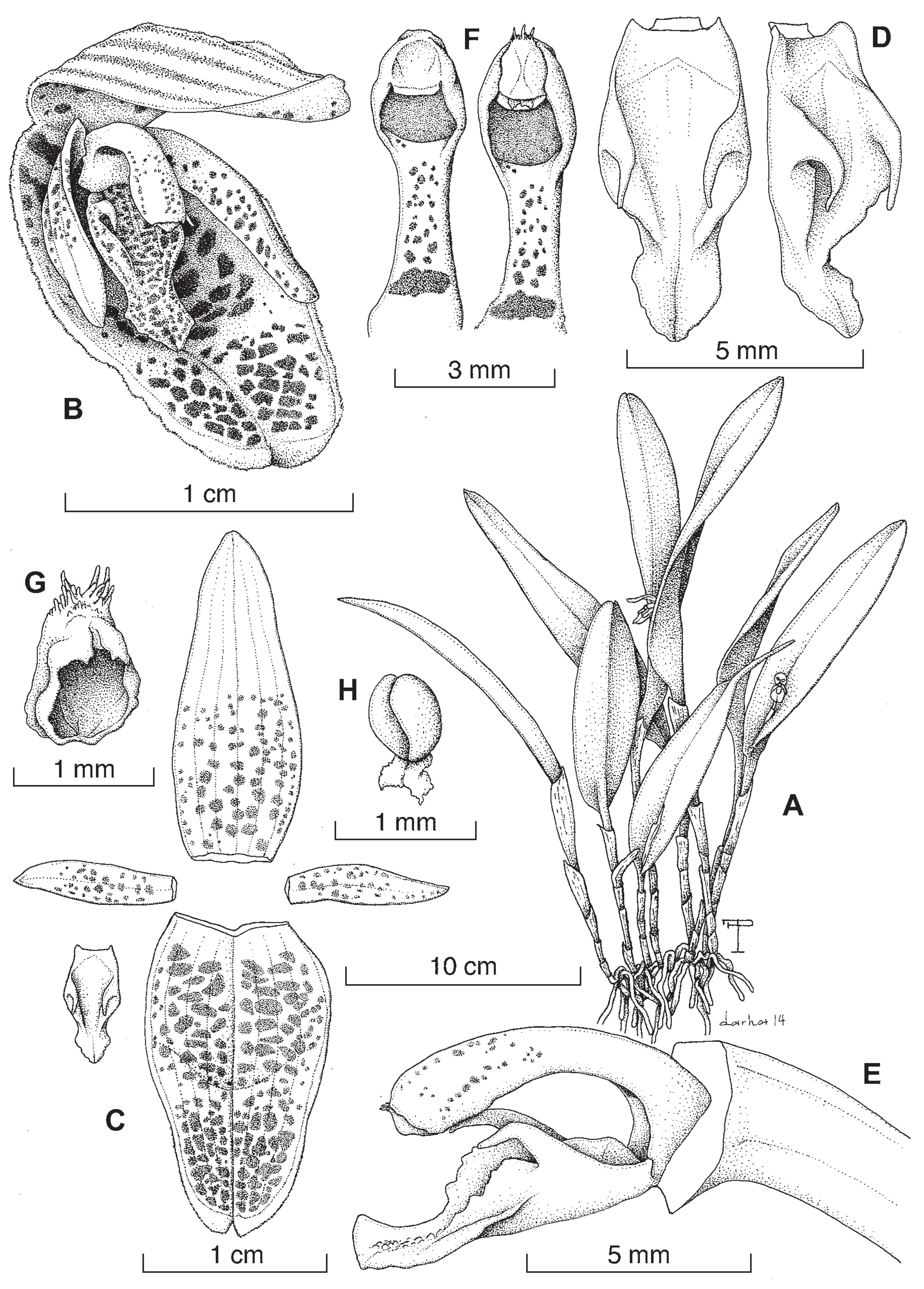


FIGURE 7. *Echinosepala alexandrae* (Schltr.) Pupulin & Bogarín. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip in ventral and three-quarters views; **E**, column and lip, lateral view; **F**, column in ventral view (emasculate on the left); **G**, anther cap; **H**, pollinarium. Drawn from *Bogarin 4678* by F. Pupulin and D. Solano Ulate.

submontane wet forests of the Tilarán, Central Volcanic, and Talamanca mountain ranges, at elevations between 1400 and 2600 m. The species mostly flower during the months of July–August, but sporadic flowering has been recorded from November to February.

Distinguishing features: the large plants with large, coriaceous leaves, the flowers buds quickly developing into fruits before or immediately after anthesis, the stellate appearance of the bristles covering the ovary and the abaxial surface of the sepals, and the elliptic-pandurate lip with the apical lobe narrow and with incurved margins distinguish this species.

The specific epithet *alexandrae*, created by Schlechter to honor his wife and conferred to a species of "*Pleurothallis*" collected in Costa Rica by the Brade brothers, is the first available name for the species that Carl Luer described in 1977 as *Pleurothallis sempergemmata* on the basis of a collection from Chiriquí, Panama (Luer, 1977). The type of *P. alexandrae* was lost during the bombing of the Berlin Herbarium in 1943, but fortunately Oakes Ames at Harvard University had Schlechter's drawings traced for his own files before they were destroyed. The two sketches that Luer (1995) selected as the species lectotype show the large habit typical of the species, and the pandurate lip with a tall basal callus—with no pseudoglenion—and a small apical lobe, which are characteristic of *Echinosepala alexandrae* and its synonym *P. sempergemmata*. Even though Luer (1992) thought that *P. alexandrae* was a name for one of Endrés's detailed illustrations of *Echinosepala* (W0021295) on the basis of material collected in Costa Rica (*Endrés s.n*, *Restrepia* 156, W0021295, W18890142222), which he treated as *Myoxanthus aspasicensis*, the two species are only superficially similar. Endrés's illustration in Vienna (reproduced in Ossenbach et al., 2013: 173, fig. 171) depicts a species hereafter treated as *E. glenioides*, which has a horseshoe-shaped structure on the top of the basal callus (pseudoglenion), whereas *E. alexandrae* has a massive, tall plate-like callus without a pseudoglenion, similar to that of *E. isthmica*, to which it is phylogenetically related.

In his treatment of the Orchidaceae for the *Flora of Panama*, Williams (1946) dubitatively included *Pleurothallis alexandrae* in synonymy with *P. uncinata*, and this induced Dressler (1981) to retain this name, based on Costa Rican populations, for a Panamanian species distinct from *P. uncinata*. However, what Williams considers as possibly different from *Echinosepala uncinata* sensu lato—a collection by Cope from el Valle de Antón (Coclé)—cannot be *E. alexandrae*, because Williams describes the callus of this specimen as "prominent retrorse […] and membranaceous at the base of the side lobes" (Williams, 1946), that is, provided with a pseudoglenion, a feature that is lacking in the true *E. alexandrae*. Bogarín, Serracín, Samudio, Rincón, et al. (2014) correctly recognize the affinity of this species, treating it as *E. aspasicensis* (or *E. glenioides*, according to the present treatment). Also, Luer (1976) interpreted as *P. alexandrae* a species locally common in Panama, ranging south to Venezuela and possibly Colombia. He correctly stated that *P. alexandrae* is closely allied to *P. uncinata*, but the specimen he illustrated (Luer, 1976: fig. 125, likely from Veraguas), does not match Schlechter's concept however, as it clearly presents a lip with a basal pseudoglenion, and we interpret it as the species described hereafter as *E. glenioides*. Luer (1976) also compared the supposed *P. alexandrae* with his *P. pastacensis*, described from an Ecuadorean collection (Luer, 1976: 156, fig. 181), which in fact also belongs to the group of species provided with a pseudoglenion and has been treated as conspecific with *E. aspasicensis* (e.g., Luer, 1986; Renner et al., 1990; Vásquez and Ibisch, 2000; Luer, 1992, 1995; Jørgensen and León-Yánez, 1999; Pupulin, 2002; Bogarín, Serracín, Samudio, Rincón, et al., 2014; Jørgensen et al., 2014; Kolanowska, 2014). Even though it has been treated under several names, for example, *P. pastacensis* (Luer 1976) and *Myoxanthus pastacensis* (Luer) Luer (Luer, 1986), and as a synonym of *Brenesia aspasicensis* (Jørgensen et al., 2014), *Echinella aspasicensis* (Pupulin, 2002), *Echinosepala aspasicensis* (Bogarín, Serracín, Samudio, Rincón, et al., 2014), *M. aspasicensis* (Luer, 1992; Renner et al., 1990), and *P. aspasicensis* (Luer, 1995; Jørgensen et al., 1999; Vásquez and Ibisch, 2000), we consider it a distinct and good species. As it lacks specific recognition as a member of *Echinosepala*, we propose it here:

Echinosepala pastacensis (Luer) Pupulin, *comb. nov.*

Basionym: *Pleurothallis pastacensis* Luer, Selbyana 3(1/2): 156. 1976. TYPE: ECUADOR. Pastaza: epiphytic in felled tree 20 km east of Puyo, 1000 m, 19 Mar 1976, *C. Luer 949, J. Luer & P. Taylor* (Holotype: SEL).

To prevent possible claims of confusion between *Pleurothallis alexandrae* Schltr. (1923) and *P. alexandri* Schltr. (1922), we would like to emphasize that the names are different, were created to honor different people, and refer to different species. Both are therefore legitimate as they are not likely to be confused under Article 53 of the International Code of Nomenclature (Turland et al., 2018).

Costa Rican material examined: Cartago: Alvarado, Cervantes, Parque Nacional Tapantí-Macizo Cerro de la Muerte, Sendero Arboles Caidos, 9.9016667, -83.7908333, 20 Aug 1992, *J. F. Morales 415, V. Nilsson & R. Chacón Coto* (CR). Macizo de la Muerte, southern Panamerican Highway, km 47, Palo Verde, epiphytic on large trees, remnants of primary and secondary vegetation, lower montane wet forest, 2000 m, Nov 2011, *F. Pupulin 4284, E. Salas, H. Léon-Páez & A. C. Rodríguez* (JBL). El Guarco, San Isidro, Casa Mata, Carretera Panamericana Sur, km 47, Palo Verde, 2000 m, 16 Nov 2002, *F. Pupulin 4284, E. Salas, H. Montealegre & E. Salas* (JBL). El Guarco, San Isidro, Casa Mata, Carretera Interamericana, km 40, desvío a San Cristóbal Norte, epífitas en árboles a orillas de la calle, bosque muy húmedo montano bajo, 9˚46'32.21"N 83˚56'34.40"W, 1869 m, 24 Apr 2008, *D. Bogarín 4601, A. Karremans, Y. Kisel & R. Phillips* (JBL). El Guarco, San Isidro, Madreselva, Tres de Junio, Carretera Interamericana Sur, km 66, entrada a la finca El Jaular, 9˚40'11.7"N 83˚51'55.9"W, 2609 m, bosque pluvial montano, en bosque secundario a la entrada de la finca, 24 Apr 2008, *D. Bogarín*

4678, A. Karremans, Y. Kisel & R. Phillips (JBL). El Guarco, El Empalme, Carretera Interamericana, Cartago to Cerro de La Muerte, km 66, epiphytic in roadside trees, 9˚42'N 83˚56'W, 2545 m, 23 Jul 2003, *M. Whitten 2153, M.A. Blanco & D. Bogarín* (JBL). Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, bosque pluvial montano bajo, epífitas en árboles en potreros y borde de bosque, 9˚48'36.7"N 83˚45'16.2"W, 1396 m, 24 Nov 2008, *D. Bogarín 5775, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Turrialba, Santa Cruz–Santa Teresita, Guayabo Arriba, Torito, 50 m después del Caño Seco, en árboles solitarios del potrero de los Mesén, 10˚00'06.23"N 83˚41'47.85"W, 1470 m, 18 Dec. 2010, *A. P. Karremans 3499 & M. Contreras Fernandez* (JBL). **Guanacaste**: Monteverde Reserve, 1500 m, 13 Jul 1992, *S. Ingram 1515, K. Ferrell & N. Edmondson* (SEL). **Heredia**: Cerro Chompipe, 2300 m, 27 Aug 1997, *R. L. Dressler s.n. & D. E. Mora* (JBL). San Rafael, Reserva Biológica "El Chompipe," 2000–2050 m, 9 Aug 1991, *S. Ingram 843 & K. Ferrell* (SEL). **San José**: Cerro El Tablazo, 1900 m, fl. Jul 1909, *A. Brade & C. Brade 1159* (drawings, AMES).

2. ***Echinosepala expolita*** Pupulin & Belfort, Lankesteriana 17(2): 294. 2017. TYPE: Costa Rica. Alajuela: San Ramón, Piedades, Piedades Norte, road to Bajo La Paz, ca. km 3, along the Río San Pedro, 10˚08'58.7"N 84˚34'03.3"W, 1300 m, premontane wet forest, secondary and remnants of primary vegetation, 19 February 2008 *F. Pupulin 7030, R. L. Dressler & A. P. Karremans* (Holotype: JBL; Isotype: JBL). Fig. 8 (Voucher: *Pupulin 7030*, JBL).

Epiphytic, caespitose, erect *herb* up to 35 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, thicker in the distal portion, 6.0–12.5 cm long, homoblastic, composed of 5 internodes different in length, completely enclosed by 3–5 papyraceous, tubular, ancipitous, apically loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the upper one, 1.4–7.7 × 0.20–0.85 cm, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaf* erect, coriaceous, linear-elliptic, subacute, minutely emarginate at apex, 16.2–27.0 × 1.8–2.4 cm, with the midvein strongly protruding abaxially. *Inflorescence* a fascicle of single, successive flowers produced facultatively at the apex and the base of the ramicaul at once; the peduncle terete-subclavate, erect, glabrous, 1.8–2.5 cm long. *Floral bract* papyraceous, loose, obliquely truncate-subobtuse, 1.8–2.4 cm long. *Pedicel* terete-subclavate, 1.8–2.5 mm long; *ovary* lanate-hirsute, completely covered by the bract, linear-subclavate, 3 mm long. *Flowers* bilabiate, with temporal activity, fully opening during the morning and closing in late afternoon; the sepals light greenish-yellow, with the adaxial basal half mottled purple-red and the distal half with pointed warts becoming denser toward the apex, abaxially flushed purple and densely warty-pubescent; the petals yellow, blotched with purple-red, sparsely verrucose; the lip dark purple, apically covered with a translucent wax in fresh flowers. *Dorsal sepal* elliptic-oblong, 0.4–0.9 × 1.9–2.0 cm, 7- to 9-veined, showing a semitransparent base, forming a window under the dark purple-red blotches, tomentose abaxially, adaxially provided with spiny warts in the apical half. *Lateral sepals* connate into an elliptic, abaxially tomentose synsepal, 0.6–1.7 × 0.4–1.0 cm, each half 5-veined, the apices free about 6 mm, subacute-rounded, with pointed-spiny warts in the distal half. *Petals* fleshy, rhombic, obliquely asymmetric, acute, 6–7 × 1–3 mm, 3-veined, apically provided with spiny warts. *Lip* 3-lobed, narrowly elliptic from a small, rounded, thin, dark purple claw, 7.5 × 2.2 mm (5.0 mm across the lateral lobes), the base subtruncate; the apical lobe rounded-truncate, thickened at apex into a cushion-like, elliptic, low pad, provided with a pair of intramarginal, thin keels running inside the lateral lobes toward the disc, more prominent to the base of the disk; lateral lobes erect, narrowly lanceolate, antrorse; the disc with an erect, narrow callus arising above the base the lip, covered on top by a horseshoe-shaped, channeled pseudoglenion extending in front into a low keel flushing into the apical pad. *Column* straight to subarcuate, semiterete, 4.4–5.5 mm long, provided with narrow, uncinate wings above the middle, the foot ca. 2.3 mm long. *Anther cap* globose, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, obovoid, flattened, on a short bifid caudicle. Fig. 2C–D.

Etymology: from the Latin *expolitus*, shining, glossy, in allusion to the the glossy apex of the lip in the fresh flowers.

Distribution: known only from the Caribbean watershed of the Cordillera de Tilarán in central Costa Rica.

Ecology: epiphytic in tropical, transition to premontane, and premontane wet forests along the Caribbean watershed of the Cordillera de Tilarán, at 800–1300 m elevation. Flowering has been recorded at least from March to June, and in November, but probably plants may flower at any time of the year. Flowers show temporal activity, fully opening during the morning and closing in late afternoon; usually they are almost to completely closed in the evening. During anthesis they emit a subtle but pungent smell, reminiscent of urea. The breakdown of urea to ammonia and carbon dioxide is known to lure insects, particularly certain flies.

Distinguishing features: the species may be distinguished by the large plants with narrowly lanceolate leaves longer than the subtending ramicauls, the inflorescences produced both at the apex and from one of the lower nodes of the stem, the lanate-hirsute ovary, and the large flower with the abaxial side of the sepals tomentose.

Florally, *Echinosepala expolita* is similar to *E. pan*, to which it appears related in the phylogenetic reconstruction, and from which it can be distinguished by the glabrous, inflated sheaths that cover the stem (vs. hirsute, tight), the distinctly broader ligulate-lanceolate leaves (vs. narrowly lanceolate), the lanate-hirsute ovary (vs. echinate), the much larger flower (sepals >15 mm vs. <10 mm long), and the tomentose abaxial indumentum of the sepals (vs. hirsute-echinate). At anthesis and in fresh flowers, the adaxial surface of the lip is covered with a translucent wax exudate, apparently produced within the basal pseudoglenion, which becomes progressively matte until the lip appears dry during the last days of anthesis.

The plant architecture of *Echinosepala expolita* is similar to *E. aspasicensis*, but the basal inflorescences distinguish the two species, also in sterile material. The inflorescences

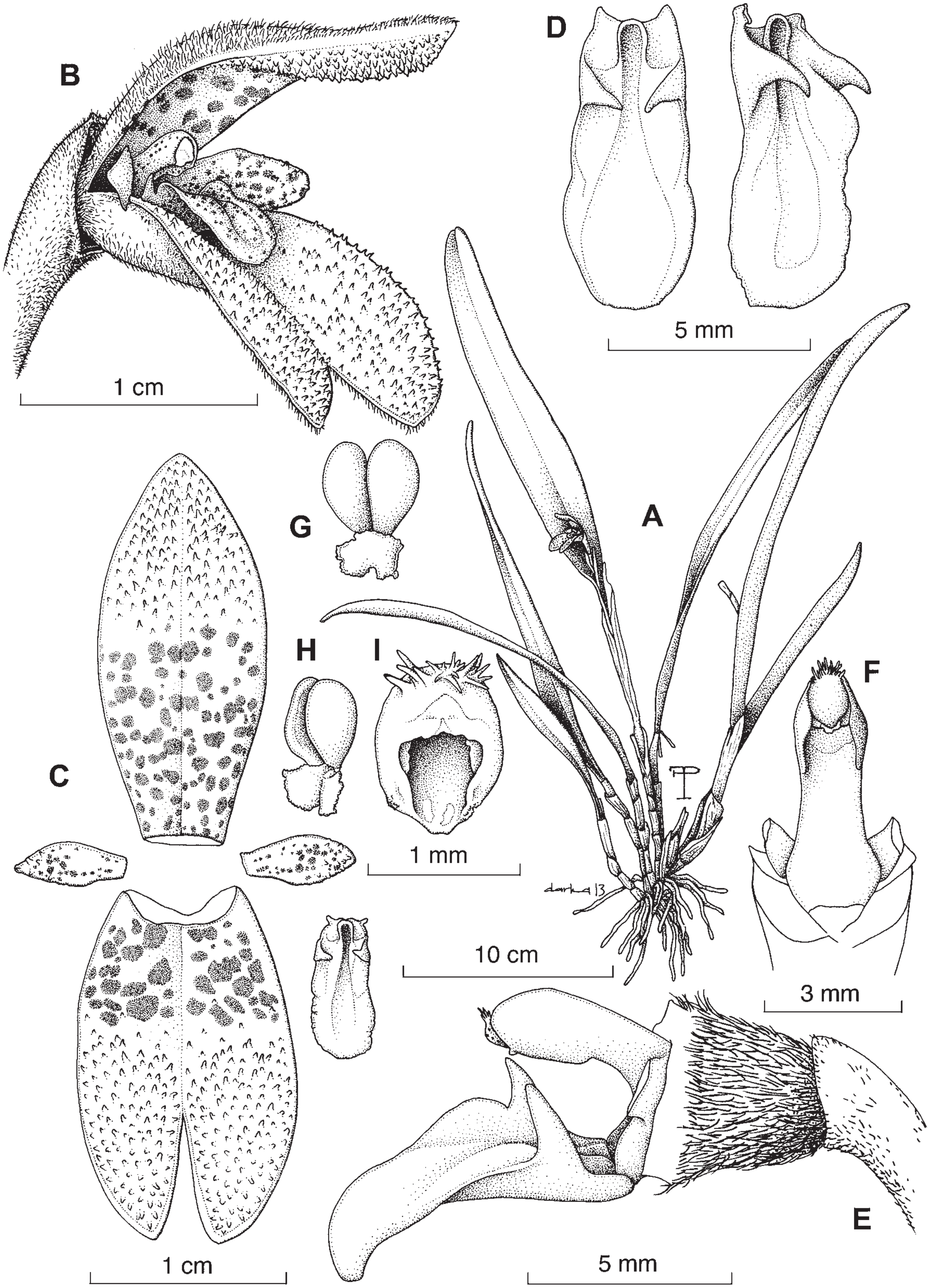


FIGURE 8. *Echinosepala expolita* Pupulin & Belfort. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip in ventral and three-quarters views; **E**, column and lip, lateral view; **F**, column in ventral view; **G–H**, pollinarium (two views); **I**, anther cap. Drawn from *Pupulin 7030* by F. Pupulin and D. Solano Ulate.

produced from a lower node of the stem may have originated twice independently (in the *E. expolita* + *E. pan* clade and the clade of *E. stonei*). Alternatively, it may have evolved only once, with one or two reversals to the ancestral state (apical inflorescence). Either scenario indicates that species with basal inflorescence do not form a monophyletic group in *Echinosepala*.

Costa Rican material examined: Alajuela: San Ramón, Piedades, Piedades Norte, road to Bajo La Paz, ca. km 3, along the Río San Pedro, 10°08'58.7"N 84°34'03.3"W, 1300 m, premontane wet forest, secondary and remnants of primary vegetation, 19 February 2008 *F. Pupulin 7030, R. L. Dressler & A. P. Karremans* (JBL). San Ramón, Ángeles, Reserva Biológica Alberto M. Brenes, 10°13'06"N 84°36'11"W, 850 m, bosque muy húmedo tropical transición a premontano, sobre el Sendero La Catarata, epífitas en borde de bosque secundario a orillas del Río San Lorencito, 24 setiembre 2005, *D. Bogarín 1871* (JBL). San Ramón, Piedades S[ur] de San Ramón, Cerros de Laguna, 1190 m, 7 Nov 1922, *A. M. Brenes 26219* (*425 Herb. Brenes*) (CR). San Ramón, Cordillera de Tilarán, cerca a Balsa, ca. 12 km NE de San Ramón, 10°10'30"N 80°30'30"W, 1100 m, 18 June 1995. Epífita a 2 m. Flores grises con manchas moradas y rayos blanco-hueso, suculentas, *B. Hammel 19870* (CR).

3. **Echinosepala glenioides** Pupulin, *sp. nov.*
TYPE: Costa Rica. Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, camino entre el portón del Mirador hacia el Río Humo, Proyecto Hidroeléctrico Tapantí, 9°41'32.9"N 83°47'03.2"W, 1650 m, bosque pluvial premontano "*supra arbores et ad truncos prostratos vetustos ad sylvarum versuras ad viam flumen Humo in Tapantí*," 18 Nov 2010, *D. Bogarín 8211, R. Gómez, A. Karremans, B. Klein, G. Meza & F. Pupulin* (Holotype: JBL). Fig. 9 (Voucher: *Bogarín 8211*, JBL).

Species Echinosepala aspasicensis (Rchb. *f.*) Pridgeon & M.W. Chase *similis sed ovario glabro versus pubescentem, sepalo postico anguste obovato versus oblongo-lanceum, petalis obtrullatis versus falcata, labello obtrullato rotundato versus ligulatum attenuatum retusum, columna dimidio longa quam labello versus aequilongam recedit.*

Epiphytic, caespitose, erect *herb* up to 50 cm tall. *Roots* coarse, flexuous, 1.3–2.0 mm in diam. *Ramicauls* stout, erect, rarely subpendent, terete, thicker in the distal portion, 10.0–22.5 cm long, homoblastic, composed of 4–6 internodes different in length, completely enclosed by 4–6 papyraceous, tubular, ancipitous, loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the upper one, 1.5–9.0 × 0.3–1.0 cm, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, ligulate to oblong-elliptic, subacute, minutely emarginate at apex, 16–29 × 1.9–3.3 cm, with the midvein strongly protruding abaxially and the lateral veins also faintly visible on both sides. *Inflorescence* a fascicle of single, successive flowers produced at the apex of the ramicaul; the peduncle terete-subclavate, erect, microscopically pubescent, 1.0–2.2 mm long. *Floral bract* papyraceous, loose, obliquely obtuse, longer than the pedicel, 2.2–3.2 cm long. *Pedicel* terete-subclavate, ca. 5 mm long; *ovary* terete, linear-subclavate, glabrous, ca. 5 mm long. *Flowers* bilabiate, mostly ringent, with temporal activity, fully opening during the morning and closing in late afternoon; the sepals light greenish-yellow, the dorsal semitransparent-fenestrate at the base, mottled purple-maroon particularly on the basal half, the dots and blotches more or less aligned with the veins, abaxially flushed purple and densely warty-pubescent; the petals dull yellow, heavily blotched or boldly striped with purple-maroon; the lip purple-red, apically covered with a translucent wax in fresh flowers; the column yellow, flecked with purple. *Dorsal sepal* oblanceolate to narrowly obovate, subobtuse, reclinate, rarely erect, 2.1–2.6 × 0.7–0.9 cm, 5-veined, with a semitransparent base, forming a window under the dark purple-red blotches, shortly and sparsely pubescent abaxially, adaxially provided with low warts in the apical half. *Lateral sepals* connate into an elliptic, obtuse, shortly bifid, abaxially shortly and sparsely pubescent synsepal, 1.80–2.20 × 0.9–1.1 cm, each half 4-veined, the apices free about 1 mm, with low rounded warts in the distal half. *Petals* fleshy, obtrullate, acute, 6–7 × 1.6–2.0 mm, 3-veined. *Lip* 3-lobed, elliptic-subrhombic from a small, rectangular, thin, hyaline claw, 7.0–8.0 × 2.3–2.6 mm (ca. 5 mm across the lateral lobes), the base truncate with two short, digitate-conical, retrorse auricles; the apical lobe ovate, acute, minutely rounded, the apex with sparse warts, provided with a pair of intramarginal, thin, rounded keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly uncinate-acuminate, antrorse; the disc with an erect, narrow callus arising above the base the lip, covered on the top by a horseshoe-shaped pseudoglenion, channeled in front up to the apical lobe. *Column* subarcuate, terete, 5 mm long, provided with narrow, elliptic, stigmatic wings above the middle, the foot ca. 1 mm long. *Anther cap* globose, subspherical, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, pyriform, on a broad, obreniform, bifid caudicle. Fig. 2E–F.

Etymology: from the words *glene*, the Greek for "socket or eyeball," and the suffix *-oides*, from the Greek εἶδος (*eîdos*, "likeness"), to suggest the imperfect resemblance of the ornamentation at the base of the callus with the glenion of other groups of Pleurothallidinae. The pseudoglenion is apparently an ancestral character in *Echinosepala*, as it has been recorded in both the basal *E. vittata* + *E. tomentosa* clade and in the clade including *E. glenioides* + *E. longipedunculata* and *E. expolita* + *E. pan*, whereas it is absent in the derived clades of *E. lappiformis* + *E. stonei* and *E. alexandrae* + *E. uncinata*.

Distribution: known at least from central Costa Rica to the Chiriquí province in western Panama, perhaps ranging to central Panama.

Ecology: an epiphyte of the large branches and trunks of trees in pristine and mature vegetation, *Echinosepala glenioides* is apparently restricted to the premontane and lower montane wet forests along the Caribbean watershed of the Costa Rican cordilleras, ranging from the Tilarán mountain chain southward to the cordillera of Talamanca, at elevations between 850 and 2000 m. Flowering mostly occurs from July to September, but sporadic flowering has been recorded as early as May.

Distinguishing features: the large plant (the largest of the genus in Costa Rica), with almost linear-ligulate leaves,

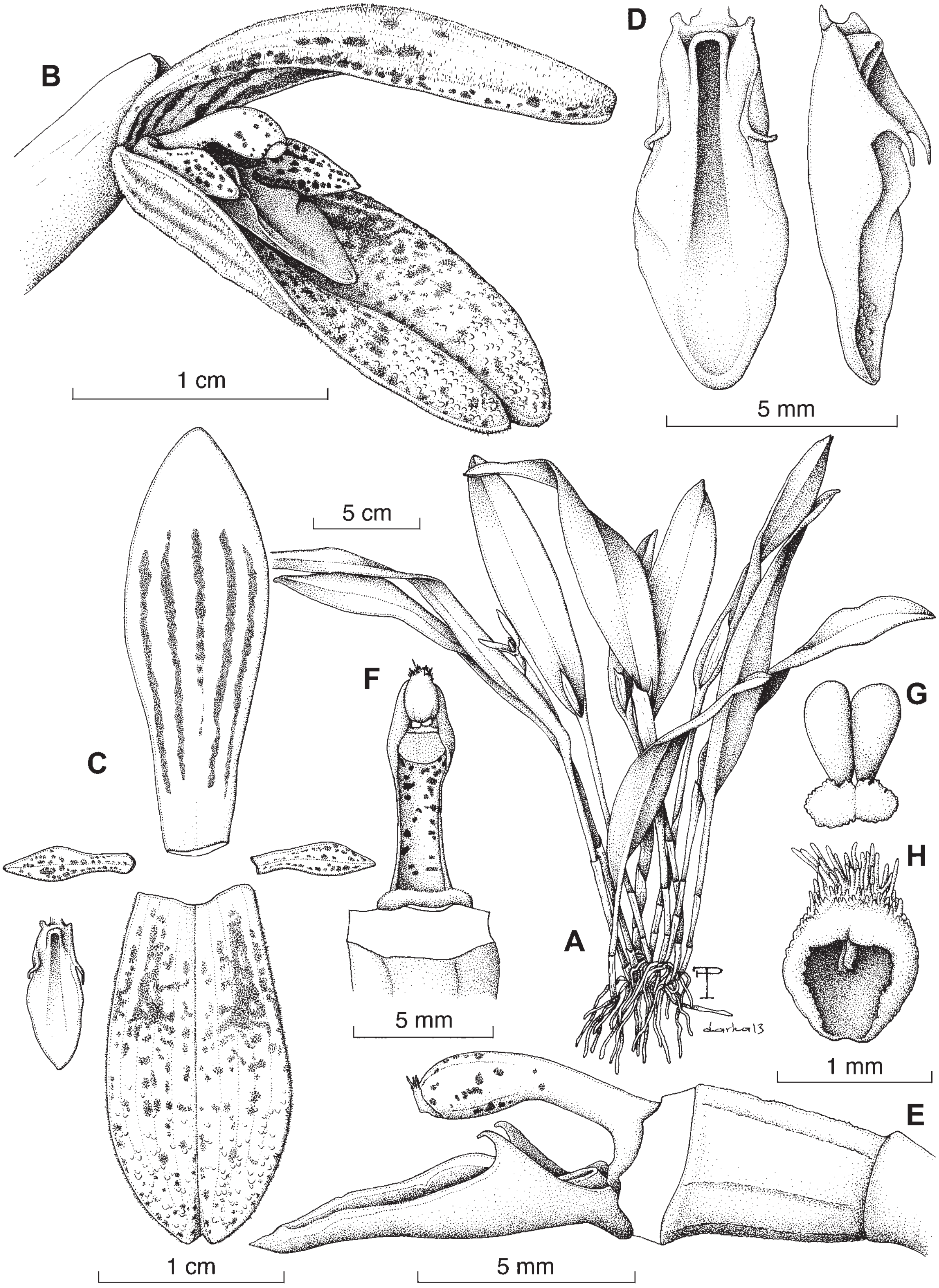


FIGURE 9. *Echinosepala glenioides* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip in ventral and three-quarters views; **E**, column and lip, lateral view; **F**, column in ventral view; **G**, pollinarium; **H**, anther cap. Drawn from *Bogarin 8211* by F. Pupulin and D. Solano Ulate.

the glabrous ovary, the large flowers (with sepals over 2.5 cm long) mostly ringent, the dorsal sepal fenestrate at the base, the long, elliptic-subrhombic lip provided with narrow uncinate lateral lobes, and a basal pseudoglenion distinguish this species among other relatives in Costa Rica.

Populations of *Echinosepala glenioides* have been traditionally treated as the northernmost records of *E. aspasicensis*, originally described from the Colombian Andes (Dressler, 1981, 1993; Luer, 1992, 1995, 2003; Hamer, 2001; Pupulin, 2002; Ossenbach et al., 2010; Bogarín, Serracín, Samudio, Rincón, et al., 2014; Pupulin et al., 2019), a poorly known species allegedly distributed from Costa Rica to Guyana, Brazil, and down to Bolivia along the Andean chain (Luer, 1992). The plant material on which the description of *Pleurothallis aspasicensis* was based had been sent to Reichenbach by Hermann Wagener from Caracas, where he was collecting orchids for the firm of Jean Linden (Reichenbach, 1855). The holotype specimen, supposedly among Reichenbach's materials in Vienna, has not been located. Nevertheless, during one of his visits to Lindley, Reichenbach gave him a piece of the original collection, today housed at Kew, which Luer (1992) selected as lectotype. No vegetative parts are included, and the crushed flower lacks the lip, so our understanding of Reichenbach's concept of *P. aspasicensis* is largely based on the original protologue. Several of the features described by Reichenbach prevent the application of this name to Costa Rica populations here described as *E. glenioides*. The leaves were described as lanceolate, versus oblong-ligulate in Costa Rican material; the sepals as "oblongo-lanceis," versus the dorsal sepal distinctly oblanceolate to obovate; the lip apically attenuate and retuse, versus acute in *E. glenioides*; and the column as long as the lip ("gynostemio labello aequilongo"), versus barely half the length of the lip in Costa Rican material.

Florally, *Echinosepala glenioides* is also similar to *Pleurothallis pastacensis* Luer (which has been generally treated as a synonym of *E. aspasicensis*), but it differs from the Ecuadorean taxon by the caespitose habit with narrow leaves (vs. distinctly repent with wider leaves), the 1-flowered inflorescence (vs. simultaneously many-flowered), the distinctly larger flowers, the sparse hairs of the sepals' indumentum (vs. arranged in tufts), and the glaborus midlobe of the lip (vs. verucose).

Broadly distributed in Costa Rica, *Echinosepala glenioides* is florally variable among populations (Fig. 2E–F). One of the vouchers used for the molecular analyses does not group with the other two accessions of *E. glenioides* (Fig. 1), leaving an open question about the existence in Costa Rica on another, cryptic taxon closely related to *E. glenioides*. We were unable, however, to characterize this genetically distinct individual on the basis of distinguishing morphological features, so given the present status of our knowledge we favored including it within the variation of *E. glenioides*.

Costa Rican material examined: Alajuela: San Carlos, Fortuna, volcán Chato, sobre el sendero a la laguna de la cima de volcán, en bosque primario, muy húmedo premontano, 10.4427778 -84.6808333, 27 Jul 2011, *A. P. Karremans 4407* (CR, JBL). San Ramón, Candelaria, March–June 1867, *A. Endrés s.n.* [Restrepia 156] (W). San Ramón, Candelaria, 1867, *A. Endrés s.n.* [Restrepia 156] (W). San Ramón, Piedades, Potrerillos, road to Socorro de Piedades Sur, slopes of Cerro La Palma, premontane wet forest, 10°08'09.9"N 84°34'47.5"W, 1300–1450 m, 12 Apr 2006, *F. Pupulin 6045, R. L. Dressler & A. Carbajal* (JBL). San Ramón, Ángeles, Reserva Biológica Alberto Brenes, ascenso por el sendero Saíno, bosque muy húmedo tropical transición a premontano, epífita en bosque secundario, 10°13'08"N 84°35'48"W, 900–1000 m, 25 Sept 2005, *D. Bogarín 1945* (JBL). San Ramón, Ángeles, Reserva Biológica Alberto Brenes, sobre el sendero Pájaro Sombrilla, 10°13'N 84°37'W, 850 m, 3 Oct 2003, *D. Bogarín 436* (JBL). San Ramón, Ángeles, Reserva Río San Lorenzo de UCR, headwaters of the Río San Lorenzo below Fila Volcán Muerte. 10- 23 N. 14 Jul 1983, *K. A. Barringer 3783 & B. Pérez* (CR). San Ramón, Ángeles, Balsa, road between San Ramón and La Fortuna de San Carlos, epiphytic on trees in pastures close to Río Balsa, premontane rain forest, 10°10'03.6"N 84°29'35.7"W, 1150 m, 29 may 2013, *F. Pupulin 1150, D. Bogarín, M. Díaz, & M. Fernández* (JBL). San Ramón, Ángeles, Ángeles Sur, road 141 to La Fortuna, deviation point on the left to Ángeles Sur, premontane rain forest, epiphytic on scattered trees in pastures along the border of a secondary, mature forest, 10°08'32.78"N 84°29'28.30"W, 1140 m, 22 Apr 2011, *F. Pupulin 8033 & M. Pupulin* (JBL). San Ramón, Santiago, finca of Jesús Salas Jiménez, mountains toward the towers of Berlín, lower montane rain forest, epiphytic in old trees along coffee plantations, 10°02'21"N 84°12'02"W, 1300 m, 30 May 2013, *F. Pupulin 8497, D. Bogarín, M. Díaz, & M. Fernández* (JBL). **Cartago**: Orosi, Purisil, Parque Purisil, 1400–1500 m, 15 Feb 2005, *H. León-Páez 92* (JBL). **Heredia**: Heredia–San Rafael, Vara Blanca, 2 km noreste de Alto del Roble, faldas al norte del Cerro Chompipe, Refugio de Vida Silvestre Cerro Dantas, márgenes de la Quebrada Grande, epífitas en bosque secundario, bosque pluvial premontano, 10°05'30,5"N 84°03'51,4"W, 1981 m, 14 Apr. 2005, *D. Bogarín 1521, M. G. Gei & A. Vaughan* (JBL). **Limón**: Matina, Batán, Parque Nacional Braulio Carrillo, Carrillo Station, along trail SE of Station, W of Quebrada González, 10.1625 -83.25, 19 Sept 1990, *S. Ingram 530 & K. Ferrell* (CR). **San José**: Vásquez de Coronado, Jesús, Bajo La Hondura, Parque Nacional Braulio Carrillo, camino de la ermita hacia Río Blanco, bosque pluvial premontano, epífitas en árboles a orillas del camino, 10°03'03"N 83°59'14"W, 900–1100 m, 21 Jan 2007, *D. Bogarín 3063, R. L. Dressler, F. Pupulin & W. Rossi* (JBL).

4. **Echinosepala isthmica** Pupulin, *sp. nov.*

TYPE: COSTA RICA. Limón: Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, bosque pluvial premontano, epífitas en árbol caído a orillas del camino, 10°1'1.5"N 83°28'29.3"W, 627 m, 3 Dec 2008, flowered in cultivation at Lankester Botanical Garden, 29 Sept. 2102, *D. Bogarín 8571, R. L. Dressler, R. Gómez & R. Trejos* (Holotype: JBL). Fig. 10 (Voucher: *Bogarín 8571*, JBL).

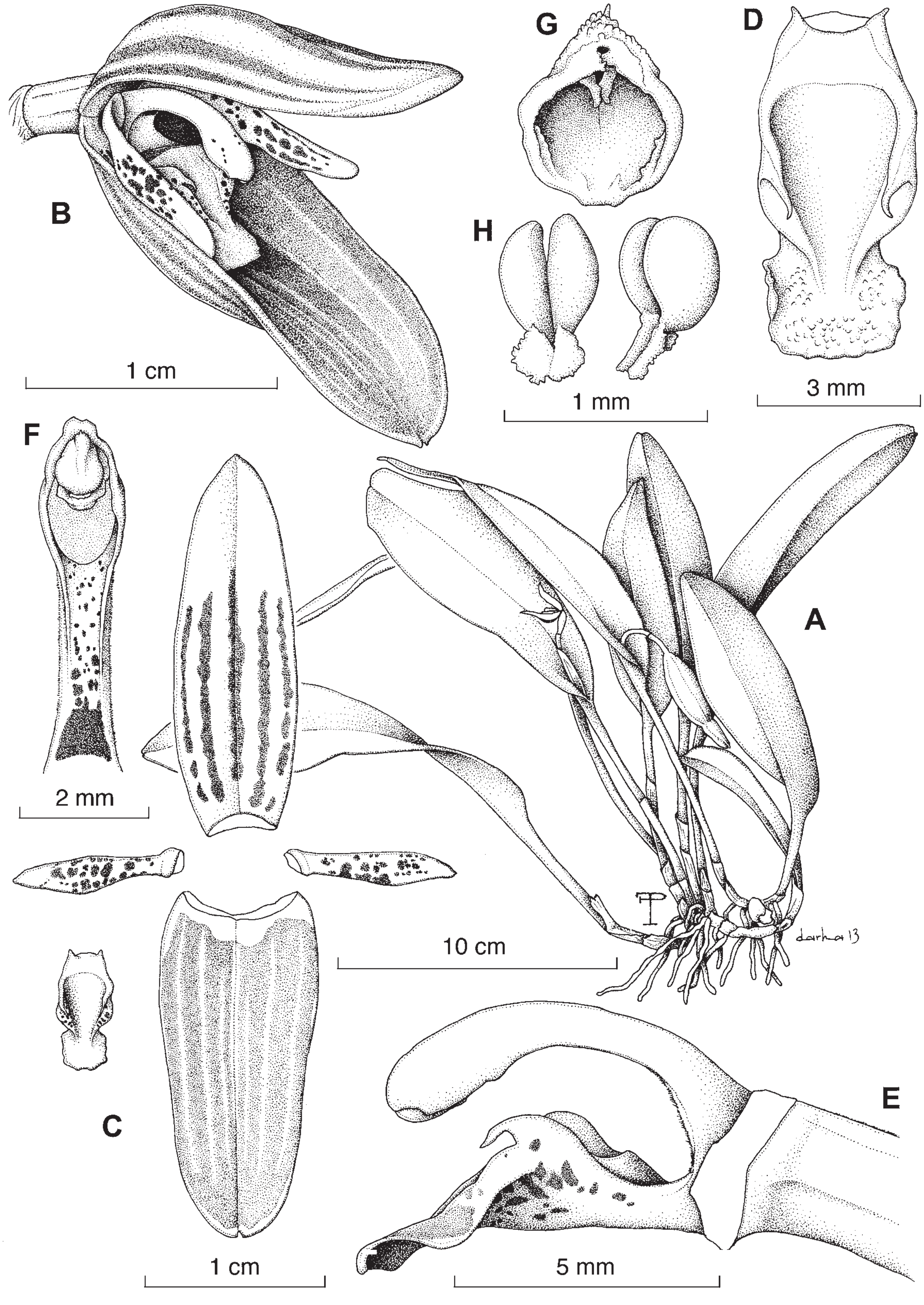


FIGURE 10. *Echinosepala isthmica* Pupulin. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, ventral view; **E**, column and lip, lateral view; **F**, column in ventral view; **G**, anther cap; **I**, pollinarium, two views. Drawn from *Bogarin 8571* by F. Pupulin and D. Solano Ulate.

A Echinosepala uncinata (Fawc.) Pridgeon *et* M.W. Chase *similis, sed caulibus dimidio brevioribus et foliis parvioribus, labello multo breviore et latiore, lobo apicali rectangulari vel late obovato integro vs. subrotundatum minute denticulatum, callo basali insignis massivo altoque vs. sublaevem, columna longiore distincte curvata plerumque recedit.*

Epiphytic, caespitose to shortly repent, erect *herb* up to 25 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, 6.0–13.5 cm long, homoblastic, composed of 5–7 internodes different in length, rarely producing secondary shoots from the apex, completely enclosed by 5–8 papyraceous, tubular, ancipitous, apically loose, obliquely truncate, whitish, glabrous, inflated sheaths, increasing in size toward the upper one, 1.5–4.6 × 0.3–0.9 cm, eventually disintegrating with age. *Leaf* erect, coriaceous, narrowly ovate to lanceolate-elliptic, acute, minutely emarginate at apex, 13.2–16.0 × 2.2–4.2 cm, the midvein distinctly protruding abaxially. *Inflorescence* a fascicle of single, successive flowers produced at the apex of the ramicaul from a narrowly rectangular, papery, loose, obliquely truncate spathe to about 1.5 cm long; the peduncle terete, prostrate, furfuraceous to minutely and sparsely pubescent, 1.8–2.5 cm long. *Floral bract* papyraceous, loose, triangular, subacute, 1 cm long. *Pedicel* terete-subclavate, 1.8–2.3 mm long; *ovary* sparsely pubescent, completely covered by the bract, linear-subclavate, ca. 5 mm long. *Flowers* bilabiate, not completely spreading, remaining fully opening after anthesis with no temporal activity observed; the sepals greenish-cream, striped to almost solidly mottled purple, subglabrous to sparsely pubescent abaxially; the petals yellow, blotched with purple-red; the lip yellow, densely spotted brown apically, rose-purple, blotched purple at the base, the lateral lobes yellow; the column white, sparsely dotted purple at the apex, flushed yellow basally. *Dorsal sepal* elliptic-lanceolate, acute, 1.3–1.9 × 0.6–0.9 cm, 5-veined, translucent. *Lateral sepals* connate into a narrowly ovate, obtuse to subrounded, minutely excised synsepal, 0.4–1.7 × 1.6–1.7 cm, each half 3-veined, glabrous within. *Petals* fleshy, oblanceolate, obliquely asymmetric, acute, 7–12 × 2–3 mm, 3-veined. *Lip* 3-lobed, subrectagular-pandurate from a small, transversely rectangular, thin, hyaline claw, 6.2–7.3 × 2.5–3.0 mm (5.0 mm across the lateral lobes), the base subtruncate, provide with 2 small, acicular, retrose, pointed auricles; the apical lobe transversely rectangular to broadly obovate, truncate, the margins sometimes subundulate, provided with a pair of intramarginal, thick keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly uncinate, antrorse; the disc with an erect, broad, massive plate-like callus arising above the base the lip, flushing in front to the base of the midlobe. *Column* arcuate, semiterete, 6.3–7.0 mm long, provided with inconspicuous, elliptic wings above the middle, the foot ca. 1.5 mm long. *Anther cap* globose, cucullate, with short, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, ovoid, laterally flattened, on a short bifid caudicle. Fig. 2G–H.

Etymology: named in reference to the Central American isthmus, where the species ranges at least from Nicaragua southward to Panama.

Distribution: Nicaragua, Costa Rica, Panama, and Colombia.

Ecology: in Costa Rica, *Echinosepala isthmica* has the widest ecologic tolerance, spanning from the tropical forests close to sea level (50 m) to the premontane wet forest at about 1500 m of elevation. The species has been recorded from both the Caribbean watersheds of the continental divide. It mostly flowers from July to September, with sporadic, early flowerings recorded in June.

Distinguishing features: the distinctly lanceolate leaves on a medium-sized plant, the comparatively large, subglabrous to minutely and sparsely tomentose flowers, with the purple blotches of the dorsal sepal arranged in stripes and the synsepal almost solidly purple-maroon, and the rectangular-pandurate lip with the apical lobe broader than long and a massive callus but no pseudoglenion distinguish this species.

Echinosepala isthmica has been treated as conspecific with *E. uncinata* (Williams, 1946; Dressler, 1981, 1993; Luer, 1992, 1995, 2003; Hamer, 1984, 2001; Pupulin, 2002; Ossenbach et al., 2010; Bogarín, Serracín, Samudio, Rincón, et al., 2014), originally described from Jamaica by William Fawcett (1895). Plants of *E. uncinata* are however much larger, approaching in size and appearance those of *E. alexandrae*, with ramicauls reaching almost 25 cm in length (vs. up to 13.5 cm in *E. isthmica*). The flowers are also different. The lip of *E. uncinata* is comparatively longer, with minute denticulations on the margin (vs. rectangular to broadly obovate, entire, in *E. isthmica*), the basal callus is low and narrow (vs. massive, as wide as the hypochile and high), and the column is stout, straight (vs. slender, distinctly curved), more similar to that of *E. alexandrae*. The illustration of *Pleurothallis uncinata* in *Flora of Jamaica* (Fawcett and Rendle, 1910: pl. 10) shows a large plant with several fruits and, if not for the midlobe of the lip as wide as the hypochile, we would have been tempted to consider the native species of Jamaica as the first available name for the Costa Rican and Panamanian populations described later as *P. alexandrae* and *P. sempergemmata*.

Echinosepala isthmica may occasionally produce new vegetative shoots, made up of stem and leaf, and ultimately roots, at the apex of the pseudobulb (e.g., *Bogarín 5855*; Fig. 11). These adventitious plantlets could eventually detach from the main stem and, on finding the appropriate conditions, form new individuals independent of the mother plant. This form of vegetative reproduction is rare in *Echinosepala*, and up to now it has been observed only in *E. isthmica*, but it is not uncommon in other groups of Pleurothallidinae.

We are not including Belize at this time in the distribution of *E. isthmica*, as the species recorded there by McLeish and colleagues (1995) could well be conspecific with the true *E. uncinata* from the Antilles. Florally, the collection by Adams (no. *253*, K) from the Mountain Pine Ridge in Cayo District, Belize, is very close to *E. isthmica*, but the plant is much larger, with ligulate-oblong leaves, quite distinct from populations from Nicaragua southward. The close relationships of the coastal flora of Belize with that of the West Indies are well known, even in the subtribe

FIGURE 11. Adventitious plantlets on the apex of the stem in *Echinosepala isthmica* (*Bogarín 5855*). Scale bar = 5 cm. Photograph by F. Pupulin.

Pleurothallidinae, and the species has not been recorded so far south of Belize. Populations of *E. uncinata* previously recorded from Nicaragua (Hamer, 1984, 2001; van den Berghe and van den Berghe, 2008) and Caribbean Costa Rica (Atwood, 1987) surely belongs to *E. isthmica*.

Costa Rican material examined: Alajuela: San Ramón: Camino a San Carlos, between Potrero Volio and Legua, July, *A. Endrés s.n.* [*Restrepia 262*] (W). Upala, Bijagua. Parque Nacional Volcán Tenorio, sobre los senderos principales del parque, bosque primario y secundario, 10˚42'58.3"N 84˚59'33.1"W, 1121 m, 28 Jul 2011, *A. P. Karremans 4446* (JBL). Upala, Bijagua. Parque Nacional Volcán Tenorio, sobre los senderos principales del parque. Epífitas en bosque primario, bosque húmedo premontano, 10˚42'54"N 84˚59'14"W, 686 m, 19 May 2016, *A. P. Karremans 7112, N. Davin & J. E. Jiménez* (JBL). **Cartago**: Jiménez, Pejibaye, entre Taus y Tausito, Selva, orillas del Río Taus y Quebrada Selva, bosque pluvial premontano, epífitas en bosque secundario a orillas del camino, 9˚47'10.3"N 83˚45'37.5"W, 1095 m, 24 Nov 2008, *D. Bogarín 5853, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Paraíso, Orosi, Tapantí, sobre el camino a Tausito, unos 1.5 km del cruce al Parque Nacional Tapantí, epífitas y semi-terrestres sobre el acantilado al lado de la calle, bosque pluvial premontano, 9˚46'18.48"N 83˚47'34.36"W, 1412 m, *A. P. Karremans 6678 & I. Chinchilla* (JBL). Turrialba Santa Cruz–Santa Teresita, Guayabo Arriba, Torito, 50 m después del Caño Seco, en árboles solitarios del potrero de los Mesén, 10˚00'06.23"N 83˚41'47.85"W, 1470 m, 18 Dec 2010, *A. P. Karremans 3199 & M. Contreras Fernandez* (JBL). **Heredia**: Sarapiquí, Puerto Viejo, Estación Biológica La Selva, epífitas en ramas caídas, 50 m, 3 Nov 2006, *G. Rojas 144* (JBL). **Limón**: Pococí, Guápiles, Hacienda La Cuenca, bosque pluvial premontano, falda norte del Volcán Turrialba, 10˚8'7.81"N 83˚46'46.2"W, 611 m, 1 Jan 2005, *M. A. Blanco 2762, A.Cháves, L. duToit & C. Ugalde* (JBL). Pococí, Guápiles, Guápiles, Pocora, La Argentina Sur, márgenes del río Dos Novillos, sendero Las Cataratas, bosque premontano muy húmedo, vegetación primaria madura, 500–700 m, 12 Sept 2004, *R. Valverde 1303* (JBL). Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, bosque pluvial premontano, epífitas en árbol caído a orillas del camino, 10˚01'1.5"N 83˚28'29.3"W, 627 m, 3 Dec 2008, *D. Bogarín 5853, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Same collecting data, *D. Bogarín 5871, R. L. Dressler, R. Gómez & R. Trejos* (JBL). **Puntarenas**: Buenos Aires, Olán, ascenso por la falda sur del Cerro Tinuk, bosque pluvial premontano, epífita en bosque secundario y primario, 9˚17'23.5"N 83˚10'33.5"W, 2164 m, 5 Jul 2012, *D. Bogarín 9716, E. Herrera, D. Jiménez, A. P. Karremans & V. H. Zúñiga* (JBL). **San José**: Pérez Zeledón, Montecarlo, without collector, 20 Sept 1991, *JBL-02659* (JBL).

5. ***Echinosepala lappiformis*** (A. Heller & L.O. Williams) Pridgeon & M.W. Chase, Lindleyana 17(2): 101. 2002.

Basionym: *Pleurothallis lappiformis* A. Heller & L.O. Williams, Fieldiana, Botany 31(2): 42, f. 8. 1964. TYPE: NICARAGUA. Chontales: epiphytic at Pistacho Peak near Babilonia Mine, alt. 650 m, Jul 1962, *A. Heller 6620* (Holotype: F). Fig. 12 (Voucher, *Bogarín 9554*, JBL).

Homotypic synonyms: *Myoxanthus lappiformis* (A. Heller & L.O. Williams) Luer, Monogr. Syst. Bot. Missouri Bot. Gard.15: 38. 1986.

Echinella lappiformis (A. Heller & L.O. Williams) Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg.*

Brenesia lappiformis (A. Heller & L.O. Williams) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Epiphytic, shortly repent, erect to subprostrate *herb* up to 25 cm tall. *Roots* coarse, flexuous, ca. 2.0 mm in diam. *Ramicauls* stout, terete, 15–50 mm long, homoblastic, composed of 2–3 nodes, the lower one much shorter, completely enclosed by 3 papyraceous, fibrous, tubular, obtuse, whitish sheaths, increasing in size toward the upper one, to 3 cm long, fragmented with age. *Leaf* thickly coriaceous, elliptic, acute, minutely emarginate, 6–12 × 2–3 cm, cuneate below into a conduplicate, sessile base, the midvein strongly protruding abaxially. *Inflorescence* a single flower emerging from the lower nodes of ramicauls; the peduncle terete, suberect to erect, minutely pubescent, 3–4 mm long, subtended by a fibrous, brown, acute bract ca. 3 mm long. *Floral bract* fibrous-papyraceous, brownish, inflated, obliquely truncate, 7–8 mm long. *Pedicel* obconical, pubescent, 2–3 mm long; *ovary* clavate, purple, 3 mm long, densely long-pubescent to echinate. *Flowers* bilabiate, the dorsal sepals apically connate to the tip of the synsepal, fleshy, nonresupinate, held almost vertically, neither temporal activity of the perianth nor scent detected, bright red-purple, the petals basally white, densely long pubescent-echinate externally, rugose-verrucose within. *Dorsal sepal* narrowly triangular, acute, 17–20 × 4–5 mm, 3-veined. *Lateral sepals* connate to the apex into an obovate, obtuse, concave synsepal, the margins erect, adaxially transversely verruculose, 20–22 × 14–16 mm. *Petals* fleshy, linear-oblong, acute, fleshy, adaxially verrucose in the distal half, 11–12 × 3 mm, 3-veined. *Lip* 3-lobed, elliptic from a thin, rectangular, rose-hyaline claw, 7–8 × 3–4 mm (6 mm across the lateral lobes), the base truncate; the apical lobe ovate, minutely truncate, denticulate, verrucose, provided with a pair of intramarginal, thick, apically verrucolose keels running inside the lateral lobes toward the disc; lateral lobes erect, elliptic-subuncinate, antrorse; the disc transversely rugose-sulcate. *Column* straight, semiterete, 6–7 mm long, provided with narrow, rectangular wings above the middle ending at apex into pointed teeth, the foot ca. 1 mm long. *Anther cap* globose, cucullate, with stiff hairs on the upper margin, 2-celled. *Pollinia* 2, ovoid, laterally compressed, on a short bilobed caudicle. Fig. 2I.

Etymology: from the Latin *lappa*, "bur," for the similarity of the flower to a spiny fruit.

Distribution: originally described from Nicaragua (Williams, 1964), the species is reported to range southward to northern South America, where it was recorded from Colombia (Misas Urreta, 2005), Ecuador, and Venezuela (Luer, 1992). We have examined specimens from Nicaragua,

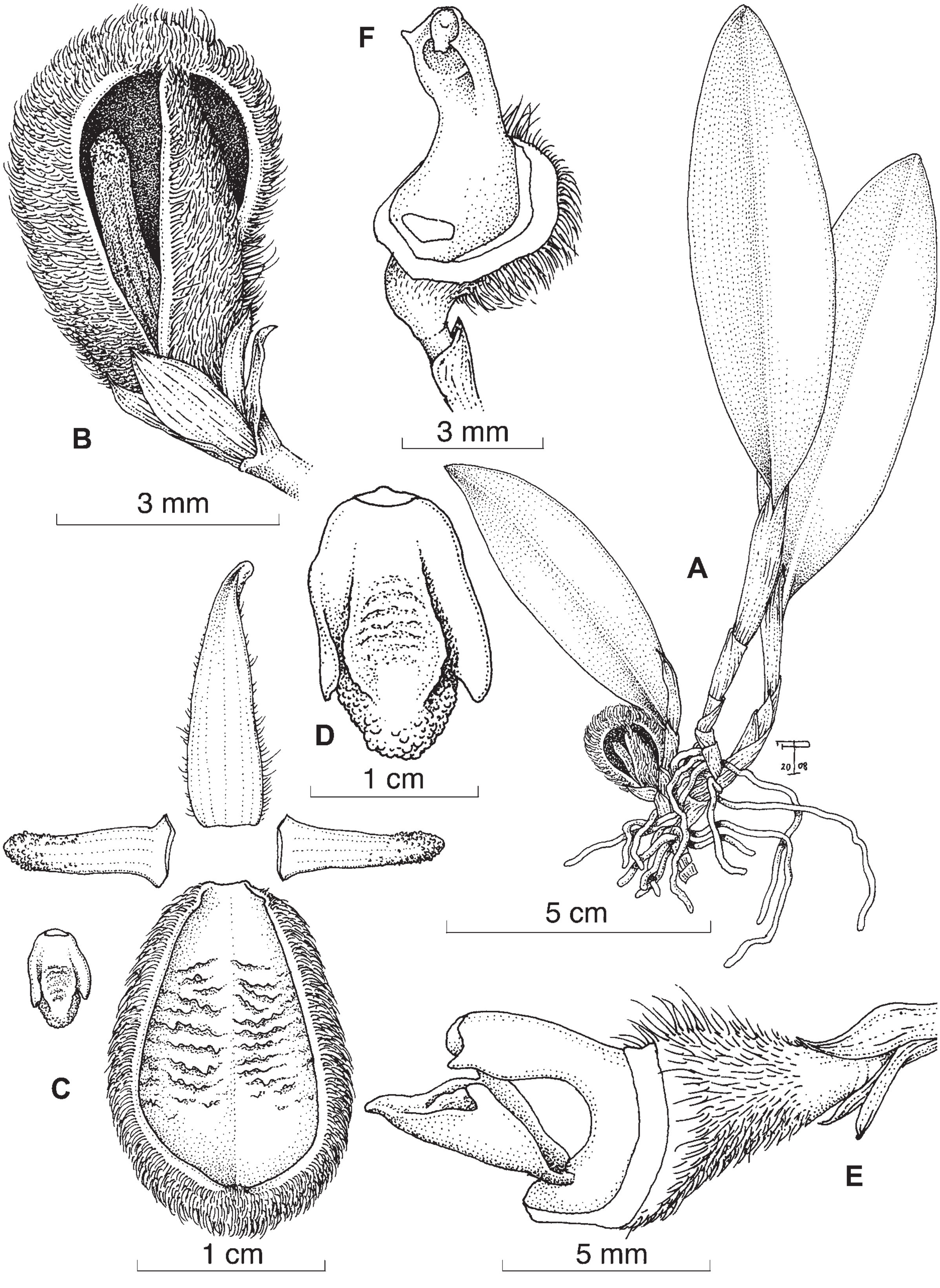


FIGURE 12. *Echinosepala lappiformis* (A. Heller & L.O. Williams) Pridgeon & M.W. Chase. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, ventral view; **E**, column and lip, lateral view; **F**, column, three-quarters view. Drawn from *Bogarín 95541* by F. Pupulin.

Panama, and Colombia, which surely correspond to this taxon, but we have not had access to materials from Ecuador and Venezuela to confirm their identities.

Ecology: epiphytic in partial to deep shade on large branches of trees, in primary and mature secondary vegetation, *Echinosepala lappiformis* has been recorded in Costa Rica exclusively from the warm, wet tropical forests of the Caribbean plains at elevations between 50 and 650 m. Flowering has been recorded in cultivation from March to June.

Distinguishing features: *Echinosepala lappiformis* is easily recognized by the red-purple, long pubescent-echinate flowers borne at the base of the stems, with the narrowly triangular dorsal sepal apically connate to the apex of the synsepal. *Echinosepala stonei*, superficially similar, has the dorsal sepal obtuse, free. The Panamanian *E. balaeniceps*, not recorded from Costa Rica, has a much larger flower with a tall, longitudinal callus on the disc.

Costa Rican material examined: Heredia: Sarapiquí, Horquetas, ca. 80 m, Feb 2005, *C. Ossenbach s.n.* (JBL). **Limón**. Siquirres, Pacuarito, 5 km después de la Estación del Parque Nacional Barbilla, bosque pluvial premontano, epífitas en árbol caído a orillas del camino, 10˚1'1.5"N 83˚28'29.3"W, 627 m, 3 Dec 2008, *D. Bogarín 5876, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Pococí, Guápiles, Parque Nacional Braulio Carrillo, Sector Quebrada González, Sendero Las Palmas, detrás de las instalaciones, 10°9'9.3"N 83°56'43.5"W, 467 m, bosque muy húmedo tropical transición a premontano, epífitas en bosque secundario alrededor del sendero, 22 Mar 2012, *D. Bogarín 9554, M. Fernández, A. P. Karremans & C. Smith* (JBL). Pococí, Guápiles, 5 km al sur de la carretera, fin del camino paralelo con el Río Blanco, cerca de la Finca Tintoreras, bosque muy húmedo tropical, 10˚2'16.2"N 83˚53'2.1"W, 350–400 m, 15 Jun 2006, *R. L. Dressler 6768, D. Bogarín, J. Gómez-Laurito & F. Pupulin* (JBL). Guápiles, carretera Braulio Carrillo, ca. 2 km hacia abajo de la entrada del Teleférico del Bosque Lluvioso, en lomas a orilla de la carretera, bosque muy húmedo tropical transición a premontano, epífitas en árboles caídos en bosque secundario, 10˚11'32"N 84˚54'27"W, 520 m, 9 Jul 2004, *D. Bogarín 890 & F. Pupulin* (JBL).

6. ***Echinosepala longipedunculata*** Pupulin & Karremans, Lankesteriana 17(2): 299. 2017. TYPE: COSTA RICA. Cartago: La Unión, San Rafael, Cerros de La Carpintera, Campamento Escuela Iztarú, 9˚53'08.2"N 83˚58'15.6"W, 1778 m, bosque húmedo premontano, epífitas en potreros arbolados, 30 octubre 2008, floreció en cultivo en el Jardín Botánico Lankester, 19 de junio 2012, *D. Bogarín 5449, R. L. Dressler, R. Gómez, F. Pupulin, & R. Trejos* (Holotype, JBL). Fig. 13 (Voucher: *Bogarín 5449*, JBL).

Epiphytic, caespitose, erect *herb* up to 30 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, terete, slightly complanate, thicker in the distal portion, 5.5–10.0 cm long, homoblastic, composed of 2 nodes different in length, the lower one much shorter (to 1.5–2.2 cm long), completely enclosed by 3 papyraceous, tubular, ancipitous, apically loose, obliquely truncate, whitish sheaths, increasing in size toward the upper one, 2.0–6.5 × 1.3–2.0 cm, the oldest ones breaking longitudinally into long fibers and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, linear-elliptic, subacute, minutely emarginate at apex, 14–18 × 2.3–3.0 cm, cuneate below into a conduplicate, sessile base, with the midvein strongly protruding abaxially and several lateral veins faintly visible on the adaxial blade. *Inflorescence* a fascicle of single, successive flowers at the apex of ramicaul; the peduncle terete, suberect to gently arching, sparsely and minutely pubescent, 3–8 cm long, subtended by a papyraceous, whitish, ancipitous, obliquely truncate spathe 2.7–4.2 cm long. *Floral bract* papyraceous, loose, obliquely truncate-subobtuse, 7–10 mm long. *Pedicel* terete-subclavate, 4–5 mm long; *ovary* completely covered by the bract, linear-subclavate, 5 mm long, minutely scaberulous. *Flowers* bilabiate, with temporal activity, opening early in the morning and closing in the afternoon during three or four days; the sepals yellow, mottled dark purple in the inner side, flushed purple and densely scabrous to shortly pubescent externally, abaxially verrucose, the warts scattered at the base and becoming denser toward the apex, the petals yellow, heavily blotched with purple-red, the lip orange yellow. *Dorsal sepal* oblanceolate, obtuse, 19–21 × 6–7 mm, 7- to 9-veined. *Lateral sepals* connate into an elliptic synsepal, verruculose in the distal half, 17–19 × 9–10 mm, each sepal 5-veined, the free apices subacute-rounded. *Petals* fleshy, narrowly lanceolate, obliquely asymmetric, acute, 6–7 × 1.5–1.8 mm, 3-veined, the central vein raised into a rounded keel. *Lip* 3-lobed, narrowly elliptic from a small, rectangular, thin, hyaline claw, 7 × 2 mm (4.5 mm across the lateral lobes), the base subtruncate; the apical lobe rounded to subtruncate, thickened at apex into a cushion-like, elliptic, low pad, provided with a pair of intramarginal, thin keels running inside the lateral lobes toward the disc; lateral lobes erect, narrowly uncinate, antrorse; the disc with an erect, narrow callus arising at the base of the lip, the highest part covered by a horseshoe-shaped, channeled pseudoglenion extending in front into a low keel flushing into the apical pad. *Column* straight to subarcuate, semiterete, 5.0–5.5 mm long, provided with narrow, elliptic wings above the middle, the foot ca. 1.5 mm long. *Anther cap* globose, cucullate, with long, stiff hairs on the upper margin, 2-celled. *Pollinia* 2, obovoid, flattened, on a short bilobed caudicle. Fig. 3A–B.

Etymology: from the Latin *longipedunculatus*, “with a long peduncle,” in reference to the unusually elongate peduncle of the flower, which can reach 8 cm in length.

Distribution: known only from Costa Rica, where it has been recorded from the Caribbean watershed of the Talamanca, Central Volcanic, and Guanacaste mountain chains.

Ecology: epiphytic in partial shade on large branches and trunks of trees, in primary and mature secondary vegetation, recorded in lower montane wet, premontane rain, and premontane wet forests at elevations of about 1300–1800 m. Flowering has been recorded under cultivation from March to June, September, and November.

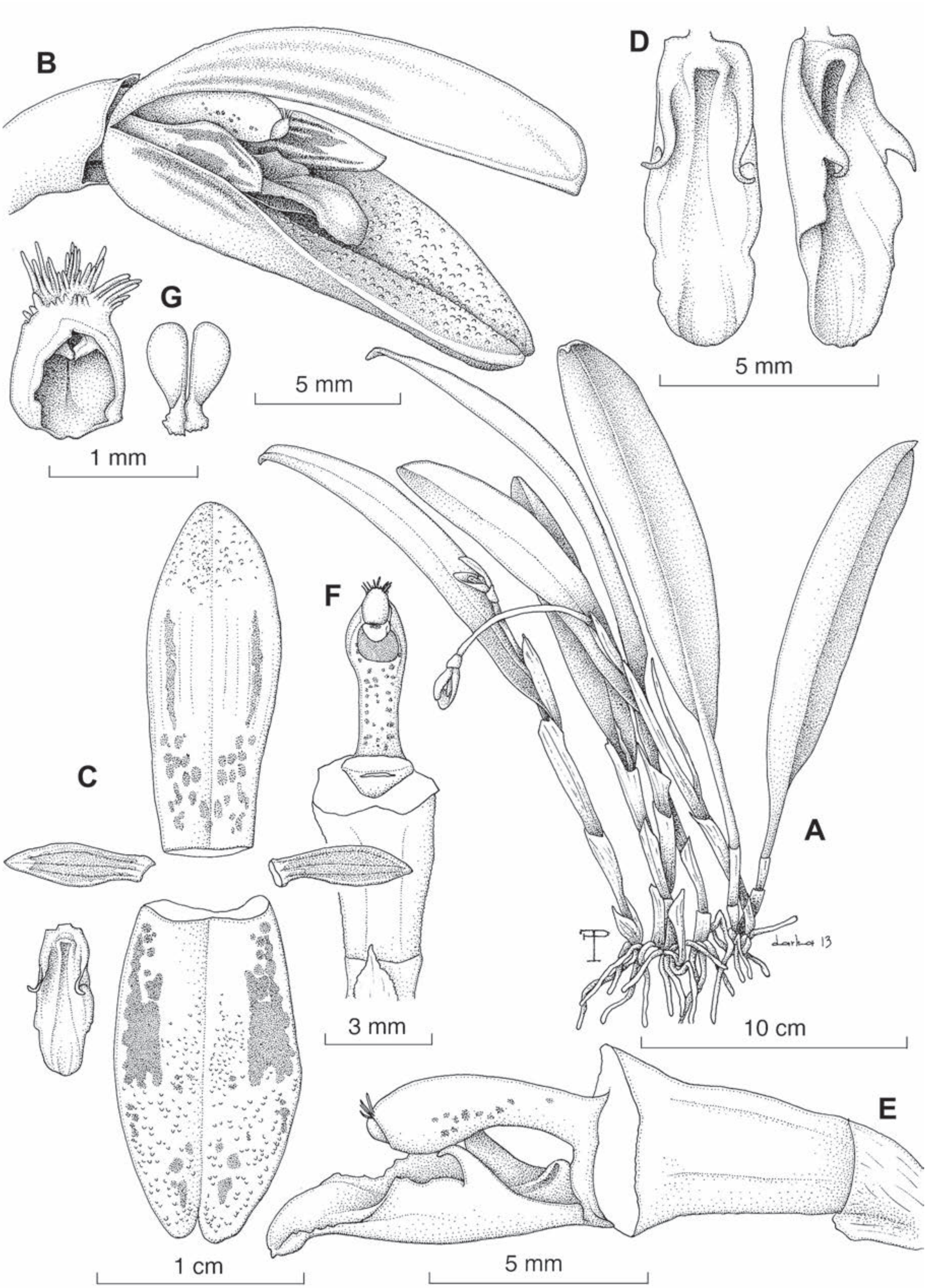


FIGURE 13. *Echinosepala longipedunculata* Pupulin & Karremans. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, ventral view; **E**, column and lip, lateral view; **F**, column, ventral view; **G**, anther cap and pollinarium. Drawn from *Bogarin 5449* by F. Pupulin and D. Solano Ulate.

Distinguishing features: *Echinosepala longipedunculata* is most similar to *E. aspasicensis*, with which it shares the large habit of the plant and the general morphology of the flower. Nevertheless, *E. longipedunculata* can be recognized by the unusually long floral pedicel, which can reach 8 cm in length (vs. 2.0–3.5 cm in *E. aspasicensis*), the greenish-yellow flowers (vs. purple-brown), the verrucose-tuberculate adaxial surface of the sepals (vs. glabrous), and the shorter, truncate, orange lip (vs. 1.5 × longer, obtuse to acute, purple).

Costa Rican material examined: Cartago: Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'50.3"N 83°54'21.1"W, 1430–1620 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 23 mayo 2007, floreció en cultivo en el Jardín Botánico Lankester, 30 marzo 2013, *D. Bogarín 3863, M. Bonilla, R. Gómez, R. Trejos & J. D. Zúñiga* (JBL). Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, unos 9 km después de la entrada principal del parque, 500 m después del puente superior sobre el río Grande de Orosi sobre la calle que va a la represa, 9°41'56.24"N 83°46'53.12"W, 1570 m, epífitas en árboles al lado de la calle principal, bosque pluvial premontano, 10 de febrero 2012, floreció en cultivo en el Jardín Botánico Lankester, 9 marzo 2013, *A. P. Karremans 4994* (JBL). **Guanacaste**: Liberia, Liberia. Parque Nacional Rincón de la Vieja, sendero que recorre el sector Volcán Santa María, 10°47'26.00"N, 85°19'16.00"O, 1304 m, bosque húmedo montano bajo, epífita, 24 Jan. 2015, flowered in cultivation at Lankester Botanical Garden, 29 nov 2016, *I. Chinchilla 2216, R. Espinoza, C. Moraga, A. Guadamuz & A. Rojas-Alvarado* (JBL).

7. ***Echinosepala pan*** (Luer) Pridgeon & M.W. Chase, Lindleyana 17(2): 101. 2002.

Basionym: *Pleurothallis pan* Luer, Selbyana 3(3–4): 360–362, f. 280. 1977. TYPE: PANAMA. Veraguas: epiphytic in cloud forest northwest of Santa Fé, alt. *ca.* 750 m, *R. L. Dressler s.n.* (Holotype: SEL). Fig. 14 (Voucher: *Bogarín 10274*, JBL).

Homotypic synonyms: *Myoxanthus pan* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 38. 1986.

Echinella pan (Luer) Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg*.

Brenesia pan (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Epiphytic, caespitose to shortly repent *herb*, up to 25 cm tall. *Roots* coarse, flexuous, 1.5–2.0 mm in diam. *Ramicauls* stout, erect, 4.5–5.7 cm long, homoblastic, composed of 2–3 nodes different in length (increasing from the basal to the apical internode), each completely enclosed by equally long, tubular, ancipitous, papyraceous, obliquely truncate, hirsute, tight, apically loose sheaths, the oldest ones breaking longitudinally and eventually disintegrating with age. *Leaves* erect, coriaceous, narrowly linear-lanceolate, acute, 1.4–1.8 × 10–22 cm, the base sessile. *Inflorescence* a fascicle of flowers produced singly from the lower nodes of the ramicauls; the peduncle terete-subclavate, short, 6–10 mm long, pubescent. *Floral bract* papyraceous, loose, obliquely truncate-subobtuse, 5–8 mm long, densely pubescent. *Pedicel* 2 mm long, pubescent; *ovary* obconical, 2 mm long, densely long-echinate. *Flowers* bilabiate, fleshy, short pedunculate, no temporal activity detected, emitting an urine-like odor, the sepals dull greenish-yellow, spotted and blotched with dark purple, the petals yellow, dotted with purple, the lip dark purple-red, the column white to rose-purple, spotted dark purple. *Dorsal sepal* elliptical-obovate, obtuse, fleshy, concave, reclined over the column, 11–15 × 6–9 mm (ca. 4 mm wide at the base), 5-veined, adaxially provided with spiny warts becoming denser toward the apical portion, abaxially long-echinate. *Lateral sepals* connate into a broadly elliptic-obovate elliptic-ovate, apically excised for about half their length, 8.3–12.0 × 7.5–9.3 mm, each half 3-veined, adaxially provided with spiny warts from the distal half and becoming denser to the apical portion, abaxially long-echinate. *Petals* rhombic, fleshy, obliquely asymmetric, subacute, subacutely angled on both margins, 4.3–5.0 × 2.9–3.8 mm, 3-veined, adaxially verrucose in the thickened apical portion. *Lip* 3-lobed, narrowly elliptic-oblong from a small, truncate, dark purple claw, 5.3–6.0 × 2.1–3.6 mm (6.8 mm wide across the expanded lateral lobes), the base truncate, with two small, conical, retrorse auricles; the lateral lobes erect, narrowly uncinate; the apical lobe elliptic to broadly elliptic, rounded-truncate, thickened at apex into a cushion-like, low pad, covered with a translucent wax in fresh flowers and provided with a pair of intramarginal, thin keels running inside the lateral lobes toward the disc; the disc with an erect, narrow callus arising above the base of the lip, covered on the top by an inverted U-shaped (horseshoe-shaped), channeled pseudoglenion flushing into the apical pad. *Column* stout, straight, semiterete, to 3.2 mm long, 1.5 mm wide, provided with narrow stigmatic wings, the foot ca. 2.5 mm long. *Anther cap* globose, cucullate, 2-celled, with long stiff hairs in the upper margin, red-colored abaxially. *Pollinia* 2, ovoid, laterally flattened, on a short bilobed caudicle. Fig. 3C.

Etymology: named after the Greek god of the forest and leader of the Satyrs, Pan, whose hair was short-horned and bristly, resembling the abaxial indumentum of the sepals.

Distribution: known exclusively from Costa Rica and Panama, ranging from the Tilarán mountain chain in northern Costa Rica, to the regions of El Valle de Antón and Santa Fé in central Panama.

Ecology: *Echinosepala pan* is apparently a rare species, growing epiphytically in primary and secondary forests, usually along streams. In Costa Rica it has been recorded in the premontane wet forests along the Caribbean watershead of the Cordillera de Tilarán, Cordillera Volcánica Central, and Cordillera de Talamanca, at elevations ranging between 550 and 1150 m. Flowering has been recorded from June to September.

Distinguishing features: *Echinosepala pan* is close to *E. expolita*, with which it shares the dark flowers and the lip provided with a narrow, horseshoe-shaped callus. It can be distinguished from the latter by the narrowly linear-lanceolate leaves (vs. broader ligulate-lanceolate), the smaller flowers (sepals <10 mm vs. >15 mm long), the hirsute and tight sheaths clasping the ramicauls (vs. glabrous and inflated), and the abaxial long-echinate indumentum of the sepals (vs. shortly tomentose).

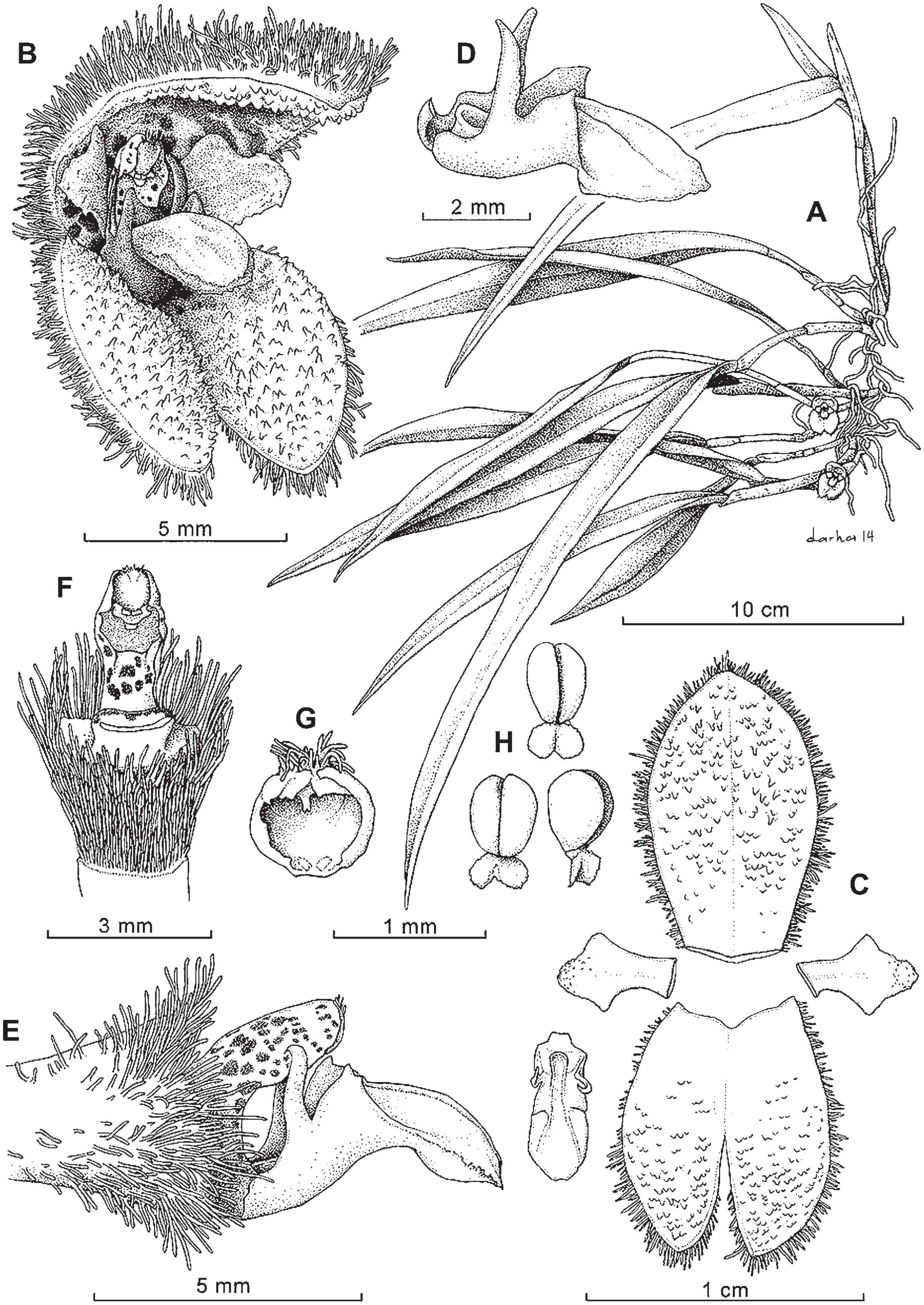


FIGURE 14. *Echinosepala pan* (Luer) Pridgeon & M.W. Chase. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, three-quarters view; **E**, column and lip, lateral view; **F**, column, ventral view; **G**, anther cap; **H**, pollinarium, three views. Drawn from *Bogarin 10274* by D. Solano Ulate.

Costa Rican material examined: Alajuela: San Ramón, 1867, *A. Endrés s.n.* [*Pleurothallis No. 315*] (W). San Ramón, Ángeles, Reserva Biológica A.M. Brenes, 30 Dec. 1990, *M. Freiberg s.n.* (JBL). Same collecting data, flowered in cultivation at Lankester Botanical Garden, Sept 2066, *M. Freiberg s.n.* (JBL). San Ramón, Ángeles, Reserva Forestal de San Ramón, 850–1000 m, Aug. 1991, *M. Germani 115* (JBL). San Ramón, Los Ángeles, deviation point to Villa Blanca, km 1.5, epiphytic in windward premontane forest, secondary vegetation, 10°19'11"N 84°28'28"W, 1120 m, 27 Feb 2003, *F. Pupulin 4327, D. Bogarín, H. Montealegre & A. C. Rodríguez* (JBL). **Limón**: Pococí, Guápiles, Bellavista 600 m oeste de la Escuela La Guaria de Bellavista, 10°8'35.111"N 83°48'43.052"W, 569 m, bosque muy húmedo tropical, epífitas en bosque secundario a orillas de una quebrada, 7 jun 2013, *D. Bogarín 10270* (JBL).

8. ***Echinosepala stonei*** (Luer) Pridgeon & M.W. Chase, Lindleyana 17(2): 101. 2002.

Basionym: *Pleurothallis stonei* Luer, Phytologia 44(3): 171. 1979. TYPE: COSTA RICA. San José: epiphytic in cloud forest southeast of San José, cultivated in California, flowered in cult. 3 Mar 1978, submitted to the OIC, no. 2022, *C. Luer 2781* (Holotype, SEL). Fig. 15 (Voucher, *Bogarín 5777*, JBL).

Homotypic synonyms: *Myoxanthus stonei* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard.15: 38. 1986.

Echinella stonei (Luer) Pridgeon & M.W. Chase, Lindleyana 16(4): 253. 2001, *nom. illeg.*

Brenesia stonei (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Epiphytic, shortly repent, erect *herb* up to 25 cm tall. *Roots* stout, flexuous, coarse, 1–2 mm in diam. *Ramicauls* erect, stout, terete, 6–8 cm long, homoblastic, composed of 2–4 internodes different in length (increasing from the basal to the apical internode), each completely enclosed by equally long, tubular, papyraceous, loose, obliquely truncate-subobtuse, glabrous sheath, the oldest breaking longitudinally and eventually disintegrating with age. *Leaves* sessile, erect, coriaceous, broadly elliptic, 9–13 × 2–4 cm, conduplicate, with a prominent midvein, the apex asymmetrically retuse, the base cuneate. *Inflorescence* a fascicle of flowers produced singly from the lower nodes of the ramicauls; the peduncle terete-subclavate, short, glabrous, ca. 1 cm long. *Floral bract* papyraceous, inflated, loose, obliquely truncate, acuminate, glabrous, 5–7 mm long. *Pedicel* terete, arcuate, glabrous, 5 mm long; *ovary* obconical, densely pubescent, not covered by the bract, ca. 4 mm long. *Flowers* held vertically, nonresupinate, deeply concave-cucullate, fleshy, short pedunculate, with a faint urine-like scent, the apex of the dorsal sepal not connate to the synsepal but accommodated inside forming two lateral entrances; the sepals dark red-purple colored with whitish hairs abaxially, petals and lip dark red-purple, column dark red. *Dorsal sepal* broadly elliptic-oblong, acute, fleshy, 14 × 7 mm, 5-veined, the free apex accommodated inside the synsepal, adaxially covered with irregular, tall warts; abaxial indumentum hirsute with soft trichomes. *Lateral sepals* connate into a broadly oblong, concave, apiculate synsepal, fleshy, to 17 × 13 mm, each half 3-veined, adaxially covered with irregular, tall warts, abaxially hirsute with soft trichomes. *Petals* clavate, fleshy, narrowly rounded, obtuse, transversely rugose, 3 × 8 mm, warty from the middle portion toward the apex. *Lip* 3-lobed, fleshy, elliptic-ovate from a small, thin, rectangular, white-hyaline claw, 4 × 8 mm (ca. 6 mm across the lateral lobes), the base truncate; the apical lobe elliptic-ovate, obtuse, smooth becoming densely rugose in the distal portion; the lateral lobes suberect, narrowly uncinate, antrorse, acuminate; the disc provided with a massive, tall, rounded and broad, slightly concave callus, occupying all the lip base and extending to the disc; pseudoglenion absent. *Column* stout, straight, semiterete, 5–6 mm long, 1–2 mm wide, provided with narrow, uncinate wings above the middle, the foot ca. 3 mm long. *Anther cap* globose, 2-celled, cucullate, with stiff hairs in the upper margin. *Pollinia* 2, ovoid, on a granulose, short, bifid caudicule. Fig. 2I.

Eponymy: named for Richard L. Stone of Los Altos Hills, California, who discovered the species and flowered it in the United States.

Distribution: known only from Costa Rica.

Ecology: a rare epiphyte on trees, paddocks, and secondary forest edges. *Echinosepala stonei* is apparently restricted to the lower montane and premontane rain forests along the Caribbean watershed of the Talamanca mountain chain (and perhaps the Central Volcanic Cordillera), where it has been recorded from 800 to 1900 m in elevation. Flowering has been recorded from January to March.

Distinguishing features: the purple-red, hirsute flowers borne at the base of the ramicaul, with the dorsal sepal broad, elliptic, obtuse, apically free, and the clavate petals with tall warts distinguish *Echinosepala stonei* from the closely related *E. lappiformis*, which has a narrowly triangular, acute dorsal sepal apically connate to the apex of the synsepal, and narrowly lanceolate, low-tuberculate petals.

Echinosepala stonei is apparently a very rare species, for a long time exclusively known from the type collection, flowered in cultivation in California, and allegedly collected "southeast of San José" (Luer, 1979), an imprecise locality. Here we can substantiate the presence of *E. stonei* in Costa Rica, on the basis of three collections from the Caribbean slopes of Cerro Duán, in the northern region of the Talamanca cordillera.

Costa Rican material examined: Cartago: Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, 9°48'36.7"N 83°45'16.2"W, 1396 m, bosque pluvial montano bajo, epífitas en árboles en potreros y borde de bosque, 24 Nov 2008, *D. Bogarín 5714, R. L. Dressler, R. Gómez & R. Trejos* (CR). Jiménez, Pejibaye, Tucurrique, Bajos del Humo, entre ríos Humo y Vueltas, ladera este de Cerros Duán, bosque pluvial montano bajo, epífitas en árboles en potreros y borde de bosque. 9°48'36.7"N 83°45'16.2"W, 1396 m, 24 Sept 2008, *D. Bogarín 5740, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Same locality data, *D. Bogarín 5777, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Paraíso,

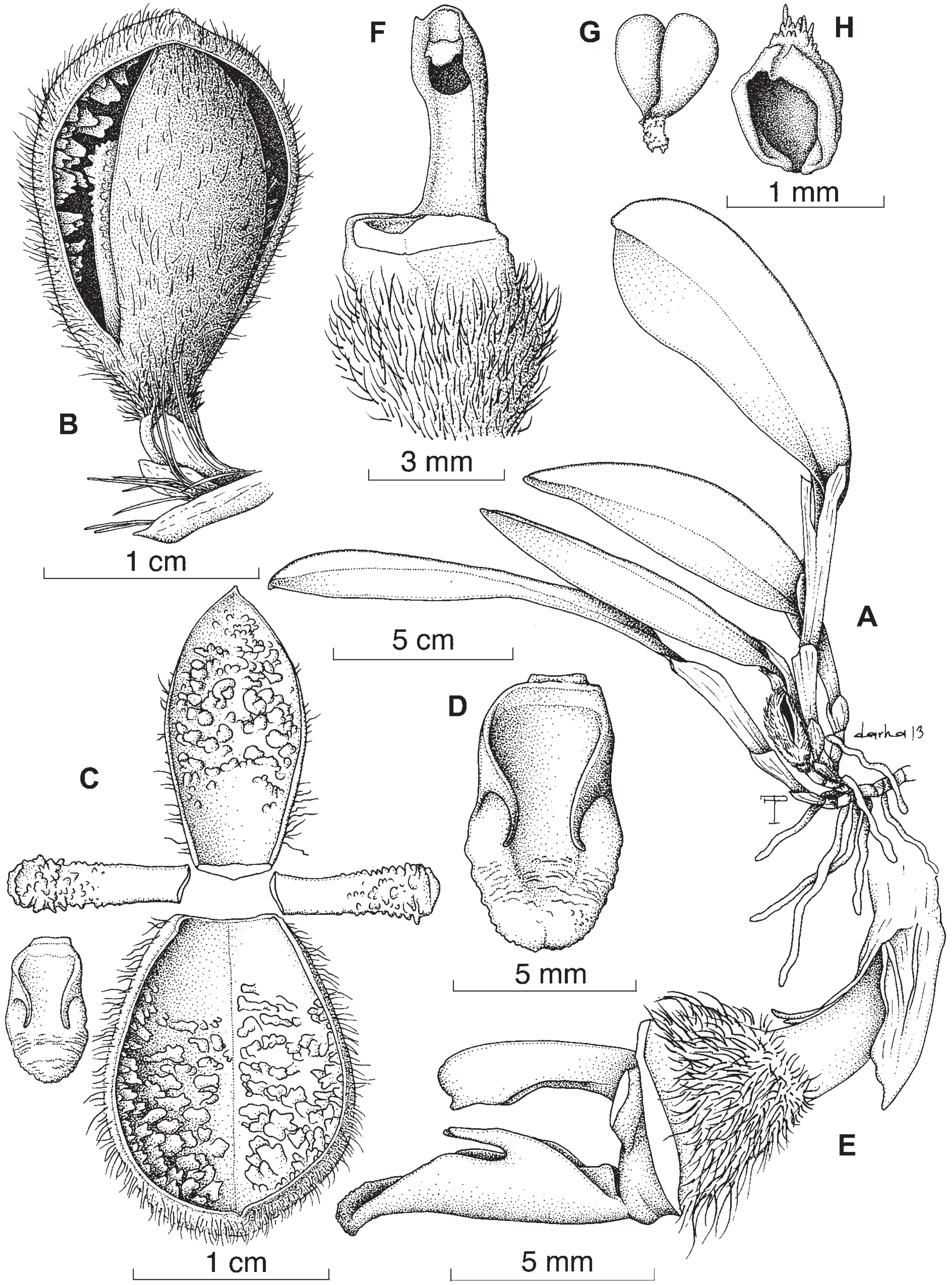


FIGURE 15. *Echinosepala stonei* (Luer) Pridgeon & M.W. Chase. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, ventral view; **E**, column and lip, lateral view; **F**, column, ventral view; **G**, anther cap; **H**, pollinarium. Drawn from *Bogarin 5777* by D. Solano Ulate.

Cachí, Peñas Blancas, entre Cerros Duán y Alto Velo de Novia, 9°48'43.76"N 83°46'36.61"W, 1829 m, bosque muy húmedo premontano, epífitas en árboles en potreros y borde de bosque, 11 Mayo 2009, *D. Bogarín 7190, R. Gómez, Y. Kisel, P. Renshaw & R. Trejos* (JBL).

9. ***Echinosepala tomentosa*** (Luer) Pridgeon & M.W. Chase, Lindleyana 17: 101. 2002.

Basionym: *Pleurothallis tomentosa* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 76: 177. 1999. TYPE: COSTA RICA. Without locality, [San José: Candelaria] ca. 1867, *A. R. Endres 630* (Holotype: W). Fig. 16 (Voucher: *Bogarín 5622*, JBL).

Homotypic synonyms: *Pleurothallis tomentosa* Luer, Orquideología 21: 337. 2000, *nom. illeg*.

Echinella tomentosa (Luer) Pridgeon & M.W. Chase, Lindleyana 16: 253. 2001.

Myoxanthus tomentosus (Luer) Pupulin & M.A. Blanco, Lankesteriana 2: 18. 2001.

Brenesia tomentosa (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 255. 2004.

Epiphytic, caespitose, erect *herb* up to 2 cm tall. *Roots* coarse, flexuous, 1 mm in diam. *Ramicauls* stout, erect, terete, slightly complanate, thicker in the distal portion, 2.5–12.5 long, homoblastic, composed of 2 internodes different in length, the lower one much shorter (to 1.0–1.5 cm long), completely enclosed by four papyraceous, tubular, ancipitous, apically loose, obliquely truncate, greenish sheaths, increasing in size toward the upper one, 1.5–5.0 × 0.5 cm, the youngest with purple spots, the oldest ones breaking longitudinally into long fibers and eventually disintegrating with age. *Leaf* erect, thickly coriaceous, narrowly elliptic, subacute, minutely emarginate at apex, 8.2–11.2 × 1.5–2.4 cm, cuneate below into a conduplicate, sessile base, with the midvein strongly protruding abaxially and several lateral veins faintly visible on the adaxial blade. *Inflorescence* a fascicle of single, successive flowers at the apex of ramicaul; the peduncle terete, suberect, sparsely and minutely pubescent, 3 mm long, subtended by a papyraceous, whitish, ancipitous, obliquely truncate spathe 7 mm long. *Floral bract* papyraceous, loose, obliquely truncate-subobtuse, 7 mm long. *Pedicel* terete-subclavate, 4 mm long, pubescent; *ovary* completely covered by the bract, linear-subclavate, 1.5 mm long, pubescent. *Flowers* bilabiate, no temporal activity of the perianth observed; the dorsal sepal yellow, blotched with dark purple in the inner side along the veins, the synsepal deep purple, adaxially densely tomentose, the lip dark purple, column yellow with purple blotches. *Dorsal sepal* linear-elliptic, obtuse, 11.5–13.0 × 3.3–4.0 mm, 5-veined, adaxially tomentose. *Lateral sepals* connate into an elliptic, synsepal, verruculose in the distal half, 11–13 × 5–6 mm, each half 8-veined, the free apices subacute-rounded, adaxially tomentose. *Petals* fleshy, narrowly lanceolate, obliquely asymmetric, acute, 4.5–5.0 × 1.3–2.0 mm, 3-veined, the central vein raised into a rounded keel. *Lip* 3-lobed, ovate to oblong from a small, rectangular, thin, hyaline claw, 6 × 2 mm (3.2 mm across the lateral lobes), the base subtruncate; the apical lobe obtuse, narrowly uncinate, antrorse; with a pair of intramarginal, thin keels running toward the apex and canaliculate along the middle; lateral lobes suberect, with a horseshoe-shaped, channeled pseudoglenion at the base. *Column* straight to subarcuate, semiterete, clavate, 4.3 × 1.2 mm long, the foot ca. 1.3 mm long. *Anther cap* globose, cucullate, with a fimbriate crest, 2-celled. *Pollinia* 2, obovoid, flattened, on a short bilobed caudicle. Fig. 3E.

Etymology: from the Latin *tomentosus*, "covered by short, rigid hairs," in reference to the adaxial surface of sepals.

Distribution: endemic to the central Pacific watershed of the Cordillera de Talamanca, Costa Rica.

Ecology: epiphytic in partial shade on large branches and trunks of trees, in primary and mature secondary vegetation, in premontane rain, and premontane wet forests at elevations of about 1200–1400 m. Flowering has been recorded in cultivation in April and March.

Distinguishing features: *Echinosepala tomentosa* is distinguished by the inflorescences developed at the apex of the stem, the leaves of fertile stems less than 12 cm long and the adaxially densely tomentose sepals, the yellow dorsal sepal and the purple synsepal. It is similar to *E. vittata*, but that species has sepals abaxially with stiff hairs along the veins and they are whitish, striped with red.

Luer (1999) described *Pleurothallis tomentosa* based on a collection by A. R. Endrés in 1867, apparently without locality data. However, the description made by A. R. Endrés (*Restrepia* 630, W0020266) states "Candelaria, March," a place comprising the drainage basins of the Tarrazú, Alumbre, and Santa Elena rivers flowing into the Pacific watershed of Cordillera de Talamanca (Ossenbach et al., 2010). Luer suspected the species to be extinct, as no collections after 1867 were known. However, we found populations of this species in the Central Pacific region (Tarrazú) of Costa Rica, where the species is locally relatively frequent.

Additional Costa Rican material examined: Puntarenas: Parrita, Parrita, 9 km suroeste de San Carlos de Tarrazú, La Virgen, potreros hacia la cumbre de Fila Chonta, 9°34'33.92"N 84°9'24.49"W, 1240.2 m, bosque pluvial montano bajo, epífitas en bosque secundario remanente y potreros, 25 Febrero 2020, *D. Bogarín 12945, S. Abarca, I. Chinchilla, G. Parra & R. Parra* (JBL). **San José**: Tarrazú, San Lorenzo, ca. 4 km al sureste de Santa Marta, camino a Bajo Reyes, 9°36'38.2"N 84°00'52.1"W, 1475 m, bosque muy húmedo premontano, en parche de bosque secundario maduro, 20 Noviembre 2008, *D. Bogarín 5622, R. L. Dressler, M. Fernández, R. Gómez & R. Trejos* (JBL).

10. ***Echinosepala vittata*** (Pupulin & M.A. Blanco) C.O. Morales & N. Villalobos, Lankesteriana 4(3): 203. 2004.

Basionym: *Myoxanthus vittatus* Pupulin & M.A. Blanco, Lankesteriana 2: 16. 2001. TYPE: COSTA RICA. San José: Pérez Zeledón, El Brujo, near Río División, 450 m, 30 Jan. 2000, flowered in cultivation at Jardín Botánico Lankester, 3 June 2001, *M. A. Blanco 1324* (Holotype: USJ, Isotype: JBL). Fig. 17 (Voucher: *Blanco 1324*, USJ).

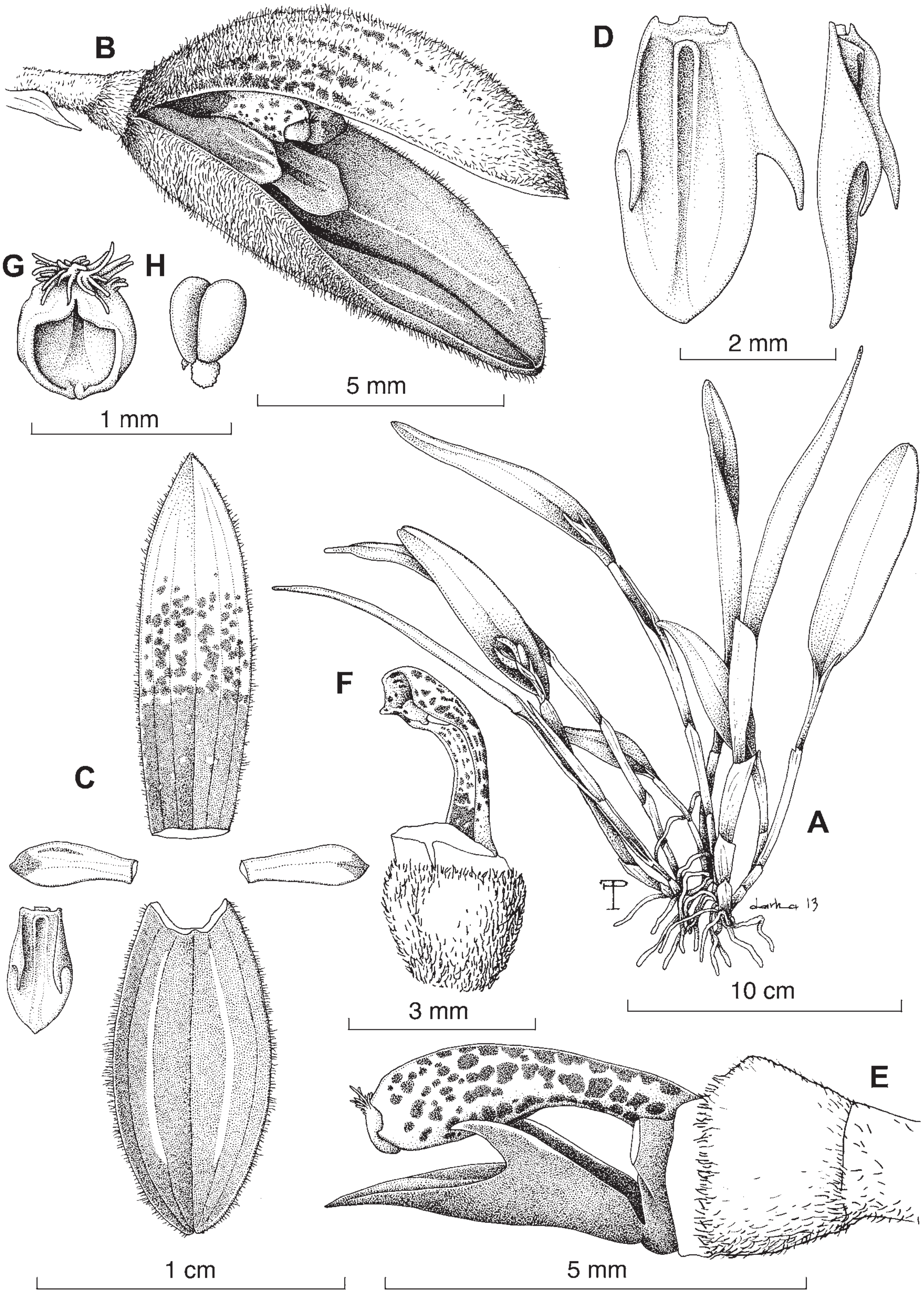


FIGURE 16. *Echinosepala tomentosa* (Luer) Pridgeon & M.W. Chase. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, ventral and three-quarters views; **E**, column and lip, lateral view; **F**, column, three-quarters view; **G**, anther cap; **H**, pollinarium. Drawn from *Pupulin 5622* by F. Pupulin and D. Solano Ulate.

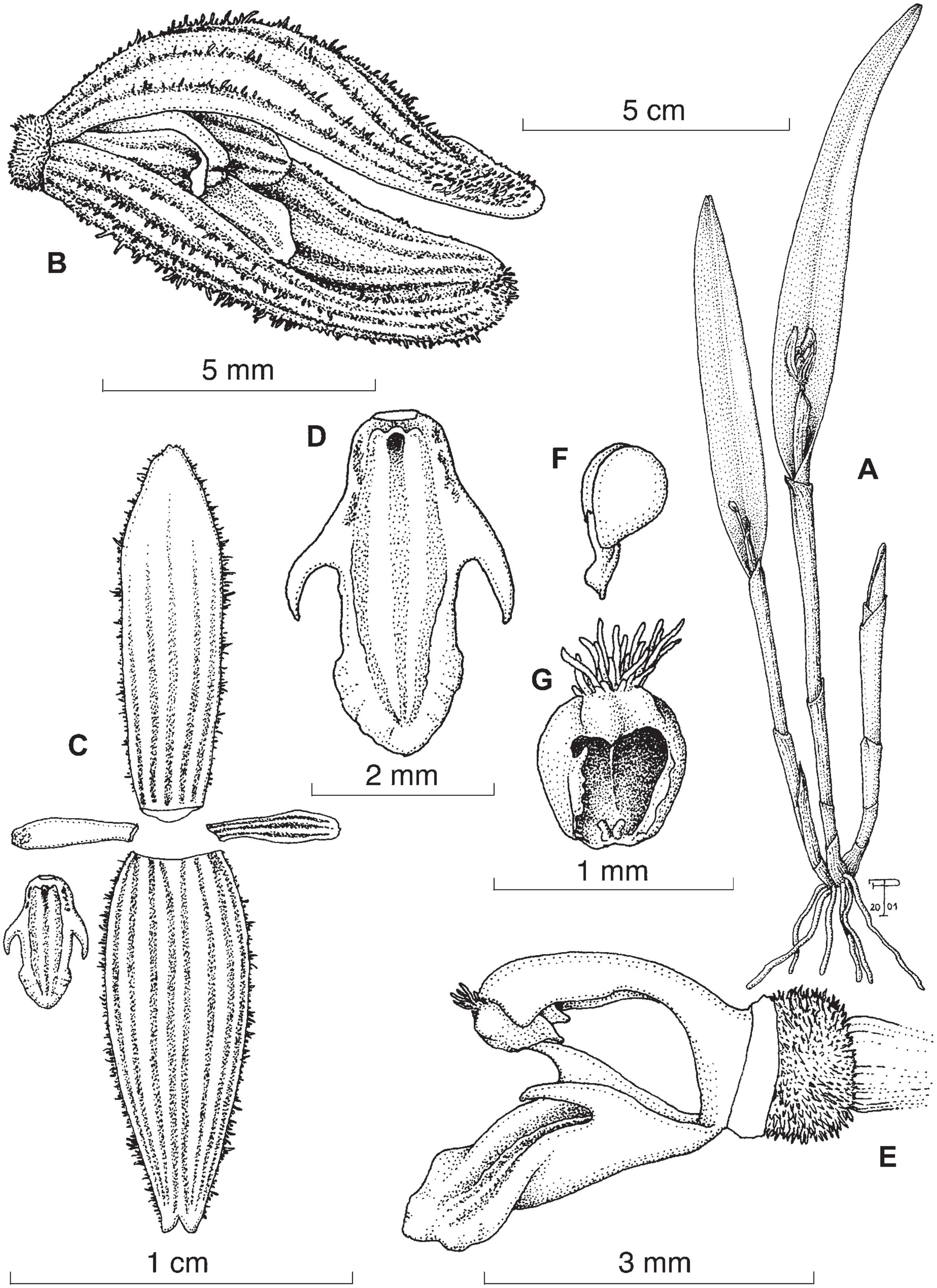


FIGURE 17. *Echinosepala vittata* (Pupulin & M.A. Blanco) C.O. Morales & N. Villalobos. **A**, habit; **B**, flower; **C**, dissected perianth; **D**, lip, ventral view; **E**, column and lip, lateral view; **F**, pollinarium; **G**, anther cap. Drawn from *Blanco 1324* by F. Pupulin.

Homotypic synoyms: *Echinella vittata* (Pupulin & M.A. Blanco) Pupulin, Lankesteriana 4: 17. 2002, *nom. illeg*.

Pleurothallis grammata Dressler, Lankesteriana 3: 28. 2002, *nom. subst*.

Echinosepala vittata (Pupulin & M.A. Blanco) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 112: 119. 2007, *nom. illeg., nom. superfl*.

Epiphytic, caespitose *herb* up to 17 cm tall. *Roots* coarse, ca. 2 mm in diam. *Ramicauls* stout, erect, 4–7 cm long, enclosed by 3–4 loose, tubular sheaths, fragmented with age. *Leaf* erect, thickly coriaceous, narrowly lanceolate-elliptic, minutely emarginate, 7–10 × 1.3–1.5 cm, cuneate below into a conduplicate, sessile base. *Inflorescence* a fascicle of single, successive flowers, produced at the apex of ramicaul, the peduncle terete, sparsely pubescent, 0.8–1.3 cm long, subtended by a papyraceous, ancipitous spathe 1.4–1.6 cm long. *Pedicel* terete-subclavate, 2–3 mm long; *ovary* less than 1 mm long, densely pubescent. *Flowers* small, fleshy, whitish, longitudinally striped with purple, densely short-pubescent externally, glabrous within. *Dorsal sepal* linear-oblanceolate, obtuse, 1.0–1.2 × 0.3 cm, 5-veined. *Lateral sepals* connate into a lanceolate, shortly emarginate, concave synsepal, 1.0–1.3 × 0.4–0.5 mm, each half 4-veined. *Petals* fleshy, linear-oblong, obtuse, minutely apiculate, adaxially provided with a tuft of short papillae near the apex, 4 × 1 mm, 3-veined. *Lip* 3-lobed, ligulate, subacute, 4 mm long, 2.5 mm wide between lateral lobes; the apical lobe smooth, slightly undulate along the margins; the lateral lobes erect, narrowly uncinate, antrorse; the disc with an erect, narrow, low, horseshoe-shaped, channeled callus above the base, extending in front into a low keel just to near the lip apex, laterally provided with a pair of low lamellae extending to the apex, hinged on the end. *Column* arcuate, semiterete, 1.6 mm long, provided with narrow wings above the middle, the foot less than 1 mm long. *Anther cap* globose, cucullate, with long hairs on the upper margin, 2-celled. *Pollinia* 2, obovoid, flattened, on a short, bifid caudicle. Fig. 3F.

Etymology: from the Latin *vittatus*, "longitudinally striped," in reference to the stripes on sepals and petals.

Distribution: known only from northern and central Costa Rica, where it has been recorded on both watersheds of the continental divide.

Ecology: epiphytic in tropical wet forest, premontane belt transition, at 450–750 m in elevation. Flowering has been recorded from November to June.

Distinguishing features: *Echinosepala vittata* is closely related to *E. glenioides*, *E. longipedunculata*, and particularly to *E. tomentosa*, all provided with a pseudoglenion at the base of the lip, but it is distinguished by the small size, the densely pubescent ovary, the whitish flower striped with purple, the sepals adaxially smooth, and the ligulate, obtuse lip. *Echinosepala tomentosa* may be distinguished from *E. vittata* by the purple-black flowers with an oblong lip, rounded at apex.

Together with *Echinosepala tomentosa*, the other species with a short vegetative habit and small flower, *E. vittata* groups into the basal-most clade of *Echinosepala*, sister to all the other species in the genus.

Additional Costa Rican material examined: Alajuela: Upala, Bijagua. En la calle nueva desde el Celeste Moutain Lodge al parque Volcán Tenorio, orillas del bosque y potrero al lado del camino, 10°43'8.46"N 85°0'2.07"W, 729 m, 14 Dec 2016, *A. P. Karremans 7524, M. Cedeño, I. Chinchilla, M. Díaz y G. Rojas-Alvarado* (JBL). **San José**: León Cortés, San Pablo, R.F. Los Santos, El Abejonal, 7 Jan 1935, *E. Azofiefa 286* (CR). Pérez Zeledón, El Brujo, near Río División, 450 m, 30 Jan. 2000, flowered in cultivation at Jardín Botánico Lankester, 3 June 2001, *M. A. Blanco 1324* (JBL). Pérez Zeledón, Viento Fresco de El Brujo, 9°25'13"N 83°56'27"W, 450 m, 21 Jan 2001, *F. Pupulin 2878, D. Castelfranco & E. Elizondo* (JBL).

LITERATURE CITED

Atwood, J. T. 1987. The vascular flora of la Selva Biological Station, Costa Rica. Orchidaceae. Selbyana 10(1): 76–145.

Atwood, J. T., and D. E. Mora de Retana. 1999. Family #39, Orchidaceae: Tribe Maxillarieae: Subtribes Maxillariinae and Oncidiinae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 40.

Bogarín, D., I. F. Chinchilla and M. Cedeño Fonseca. 2020. Two new species of *Lepanthes* (Orchidaceae: Pleurothalldinae) from Costa Rica and their phylogenetic affinity. Plant Systematics and Evolution 306(2): 20.

Bogarín, D., and M. Fernández. 2010. *Lepanthes arenasiana* (Pleurothallidinae: Orchidaceae), a new species from Costa Rica. Lankesteriana 9(3): 487–489.

Bogarín, D., M. Fernández, and Z. Serracín. 2018. *Lepanthes aures-ursinae* and *L. vertebrata spp. nov.* (Orchidaceae: Pleurothallidinae) from Panama. Nordic J. Bot., 36(1–2), njb-01292.

Bogarín, D., and D. Jiménez. 2015. *Lepanthes novae Durikaensis*. Lindleyena [in Orchids (Bull. Amer. Orchd. Soc.)] 84: 430–440.

Bogarín, D., and A. P. Karremans. 2010. A new *Platystele* (Orchidaceae: Pleutothallidinae) from central Costa Rica. Orquideología 27: 208–220.

———. 2016. A New *Brachionidium* (Orchidaceae: Pleurothallidinae) from the First Botanical Expedition to the Volcán Cacho Negro, Costa Rica. Syst Bot. 41(4): 919–923(5).

Bogarín, D., A. P. Karremans, and M. Fernández. 2018. Genus-level taxonomical changes in the *Lepanthes* affinity (Orchidaceae, Pleurothallidinae). Phytotaxa 340(2): 128–136.

Bogarín, D., A. P. Karremans, and M. Muñoz García. 2015. *Brachionidium kirbyi*, eine neue Art zu Ehren des Gründers des Orchideenprojektes "Bosque de Paz" in Costa Rica. Die Orchidee 66: 404–409.

Bogarín, D., A. P. Karremans, and F. Pupulin. 2008. New species and records of Orchidaceae from Costa Rica. Lankesteriana 8(2): 53–74.

Bogarín, D., A. P. Karremans, R. Rincón, and B. Gravendeel. 2013. A new *Specklinia* (Orchidaceae: Pleurothallidinae) from Costa Rica and Panama. Phytotaxa 115(2): 31–41.

Bogarín, D., and Y. Kisel. 2014. A new *Lepanthes* from Costa Rica. Orchid Rev. 122(1305): 28–31.

Bogarín, D., L. Oses, and C. M. Smith. 2017. *Masdevallia luerorum* (Orchidaceae: Pleurothallidinae), a new species from Costa Rica. Lankesteriana 17(2): 235–244.

Bogarín, D., O. A. Pérez-Escobar, D. Groenenberg, S. D. Holland, A. P. Karremans, E. M. Lemmon, A. R. Lemmon, F. Pupulin, E. Smets, and B. Gravendeel. 2018. Anchored hybrid enrichment generated nuclear, plastid and mitochondrial T markers resolve the *Lepanthes horrida* (Orchidaceae: Pleurothallidinae) species complex. Molec. Phylogen. Evol. 129(2018): 27–47.

Bogarín, D., and F. Pupulin. 2011. *Lepanthes daniel-jimenezii* Bogarín & Pupulin, *spec. nov*. (Pleurothallidinae: Orchidaceae), a new species from Costa Rica close to *Lepanthes guardiana*. Die Orchidee 62(2): 111–115.

———. 2012. Three new *Lepanthes* (Orchidaceae: Pleurothallidinae) from South-East Costa Rica. Lankesteriana 12(2): 107–114.

Bogarín, D., Z. Serracín, and Z. Samudio. 2014. Illustrations and studies in Neotropical Orchidaceae, The *Speccklinia condylata* group (Pleurothallidinae) in Costa Rica and Panama. Lankesteriana 13(3): 185–206.

Bogarín, D., Z. Serracín, Z. Samudio, R. Rincón, and F. Pupulin. 2014. An updated checklist of the Orchidaceae of Panama. Lankesteriana 14(3): 135–364.

Bogarín, D., C. M. Smith, and D. Jiménez. 2012. The *Lepanthes ovalis* group (Pleurothallidinae) with three new species from Costa Rica. J. Bot. Res. Inst. Texas 6(2): 361–373.

Burger, W. C. 1971. Family #40, Casuarinaceae. Family #41, Piperaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. 35.

Burger, W. C., K. Barringer, A. Gentry, and L. D. Gómez. 2000. Family #193, Scrophulariaceae; Family #193a, Schlegeliaceae; Family #194, Bignoniaceae; Family #195, Pedaliaceae; Family #196, Martyniaceae; Family #197, Orobanchaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 41.

Burger, W. C., J. G. Furlow, L. D. Gómez P., and D. E. Stone. 1977. Family #42, Chlorantaceae; Family #43, Lacistemaceae; Family #44, Salicaceae; Family #45, Garryaceae; Family #46, Myricaceae; Family #47, Juglandaceae; Family #48, Bataceae; Family #49, Betulaceae; Family #50, Fagaceae; Family #51, Ulmaceae; Family #52, Moraceae; Family #52a, Cannabaceae; Family#53, Urticaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. 40.

Burger, W. C., and M. Huft. 1995. Family #113, Euphorbiaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 36.

Burger, W. C., J. Kuijt, K. Barringer, L. D. Gómez, and R. Baker. 1983. Family #54, Podostemaceae; Family #55, Proteaceae; Family #56, Olacaeae; Family #57, Opiliaceae; Family #58, Loranthaceae; Family #59, Aristolochiaceae; Family #60a, Hydnoraceae; Family #60b, Rafflesiaceae; Family #61, Balanophoraceae; Family #62, Polygonaceae; Family #63, Chenopodiaceae; Family #64, Amaranthaceae; Family #65, Nyctaginaceae; Family #66, Phytolaccaceae; Family #67, Aizoaceae; Family #68, Portulacaceae; Family #69, Basellaceae; Family #70, Caryophyllaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 13.

Burger, W. C., T. Plowman, B. B. Simpson, and N. Zamora. 1991. Family #97, Krameriaceae; Family #98, Oxalidaceae; Family #99, Geraniaceae; Family #100, Tropaeolaceae; Family #101, Linaceae; Family #101a, Humiriaceae; Family #102, Erythroxylaceae; Family #103, Zygophyllaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 28.

Burger, W. C., and C. M. Taylor. 1993. Family #202, Rubiaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 33.

Burger, W. C., and H. van der Werff. 1990. Family #80, Lauraceae; Family #81, Hernandiaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 23.

Dressler, R. L. 1981. *The Orchids: Natural History and Classification*. Harvard University Press, Cambridge, Massachusetts, U.S.A.

Pleurothallidinae1993. *Phylogeny and Classification of the Orchid Family*. Cambridge University Press, Cambridge.

Drummond, A. J., and A. Rambaut. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7: 214.

Durkee, L. H., and W. Burger. 1986. Family #200, Acanthaceae; Family #201, Plantaginaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 18.

Epidendra. 2019. The Global Orchid Taxonomic Network. Jardín Botánico Lankester, Universidad de Costa Rica (accessed June 2019). Available from: http://epidendra.org/taxones/index.html

Fawcett, W. 1895. Two new orchids from Jamaica. J. Bot. 33(385): 12.

Fawcett, W., and A. B. Rendle. 1910. *Flora of Jamaica: Orchidaceae*. British Museum, London.

Fernández, M. 2011. A reconsideration of *Trichosalpinx minutipetala* (Ames & C.Schweinf.) Luer (Orchidaceae: Pleurothallidinae). Orquideología 28(2): 119–134.

———. 2013. *Tubella*—those other *Trichosalpinx*. Die Orchidee 64(4): 310–317.

Fernández, M., and D. Bogarín. 2011. A new *Trichosalpinx* (Orchidaceae: Pleurothallidinae) from the northern Pacific lowlands of Costa Rica. Phytotaxa 38: 41–48.

———. 2013. A new species of *Trichosalpinx* (Orchidaceae: Pleurothallidinae) from Costa Rica. Brittonia 65(1): 96–101.

Fernández, M., D. Bogarín, A. P. Karremans, and D. Jiménez. 2014. New species and records of Orchidaceae from Costa Rica. III. Lankesteriana 13(3): 259–282.

Hamer, F. 1984. Orchids of Nicaragua, Part 5. *Icones Plantarum Tropicarum* 12: pl. 1101–1200.

———. 2001. Orchidaceae. Pages 1612–1853 in W. D. Stevens, C. Ulloa Ulloa, A. Pool, and O. M. Montiel, eds., *Flora de Nicaragua*. Monogr. Syst. Bot. Missouri Bot. Gard. 85(2).

IPNI. 2020. International Plant Names Index (accessed May 2020. http://www.ipni.org/

Jørgensen, P. M. and S. León-Yánez, eds. 1999. Catalogue of the vascular plants of Ecuador. Monographs in Systematic Botany from the Missouri Botanical Garden 75: 1-1181.

Jørgensen, P. M., M. H. Nee and S. G. Beck, eds. 2014. Catálogo de las plantas vasculares de Bolivia. Monographs in Systematic Botany from the Missouri Botanical Garden 127(1-2): 1-1744.

Karremans, A. P. 2012. Illustrations and studies on Neotropical Orchidaceae. 3. On the identity of *Dracontia pachyglossa* and *D. ramonensis*; with a new species, *D. lueriana* (Pleurothallidinae). Ann. Naturhist. Mus. Wien, B. 113: 119–132.

———. 2014. *Lankesteriana*, a new genus in the Pleurothallidinae (Orchidaceae). Lankesteriana 13(3): 319–332.

———. 2016. *Genera Pleurothallidinarum*: An updated phylogenetic overview of Pleurothallidinae. Lankesteriana 16(2): 219–241.

———. 2019. To be or not to be a *Stelis*. Lankesteriana 19(3): 281–343.

Karremans, A. P., D. Aguilar Sandí, M. Artavia-Solís, M. Cedeño-Fonseca, I. F. Chinchilla, K. Gil, G. Rojas-Alvarado, N. Solano-Guindon, and J. Villegas-Murillo. 2019. Nomenclatural notes in the Pleurothallidinae (Orchidaceae): Miscellaneous. Phytotaxa 406(5): 259–270.

Karremans, A. P., and D. Bogarín. 2011. *Pleurothallis adventurae* (Orchidaceae: Pleurothallidinae), eine neue Art aus einer unerforschten Region in Costa Rica/*Pleurothallis adventurae* (Orchidaceae: Pleurothallidinae), una nueva especie de una región inexplorada en Costa Rica. Orchideen Journal 18(3): 111–114.

———. 2013. Three new species of *Dracontia* (Pleurothallidinae, Orchidaceae) from Costa Rica. Syst. Bot. 38(2): 307–315.

———. 2017. Two novelties in *Platystele* (Ochidaceae: Pleurothallidinae) from Costa Rica. Lankesteriana 17(2): 215–221.

Karremans, A. P., D. Bogarín, M. Díaz-Morales, M. Fernández, L. Oses, and F. Pupulin. 2016. Phylogenetic reassessment of *Acianthera* (Pleurothallidinae: Orchidaceae). Harvard Pap. Bot. 21(2): 171–187.

Karremans, A. P., D. Bogarín, M. Fernández, C. M. Smith, and M. A. Blanco. 2012. New species and records of Orchidaceae from Costa Rica. II. Lankesteriana 12(1): 19–51.

Karremans, A. P., D. Bogarín, and B. Gravendeel. 2015. *Specklinia lugduno-batavae* (Pleurothallidinae: Orchidaceae), a new species in the *S. digitalis* group. Blumea 59(3): 180–184(5).

Karremans, A. P., and M. Díaz-Morales. 2017. Novelties in Costa Rican *Stelis* (Orchidaceae: Pleurothallidinae): Two new species and a new record in the "Dracontia Group." Lankesteriana 17(2): 193–202.

Karremans, A. P., and J. E. Jiménez. 2018. *Pleurothallis hawkingii* and *Pleurothallis vide-vallis* (Orchidaceae; Epidendroideae), two new species from Cordillera de Guanacaste in Costa Rica. Phytotaxa 349(2): 185–191.

Karremans, A. P., and M. Muñoz García. 2011. *Pleurothallis silvae-pacis*, a new species. Orchid Rev. 119(1295): 155–159.

Karremans, A. P., F. Pupulin, and B. Gravendeel. 2015. *Specklinia dunstervillei*, a new species long confused with *Specklinia endotrachys* (Orchidaceae: Pleurothallidinae). PLoS One 10(7): e0131971.

Karremans, A. P., G. Salguero, D. Bogarín, L. Oses, and M. Cedeño-Fonseca. 2020. Illustrations and studies in Neotropical Orchidaceae: The *Specklinia brighamii* group (Pleurothallidinae) in Costa Rica. Phytotaxa 447(1): 16–30.

Karremans, A. P., and C. M. Smith. 2012. A note on genus *Dracontia* (Orchidaceae: Pleurothallidinae), with a new species. Harvard Pap. Bot. 17(1): 13–17.

Kolanowka, M. 2014. *Orchids of the Darien gap*. Koeltz Scientific Books, Koenigstein, Germany.

Luer, C. A. 1976. *Icones Pleurothallidinarum*. Miscellaneous species of *Pleurothallis*. Selbyana 3: 38–201.

———. 1977. *Icones Pleurothallidinarum* (Orchidaceae). Miscellaneous species in the Pleurothallidinae. Selbyana 3(3–4): 386–387, f. 293.

———. 1979. Miscellaneous new species in the Pleurothallidinae. Phytologia 44: 164.

———. 1986. *Icones Pleurothallidinarum*. 1. Systematics of *Pleurothallidinae*. Monogr. Syst. Bot. Missouri Bot. Gard. 15: 65–69.

———. 1992. *Icones Pleurothallidinarum*. 9. Systematics of *Myoxanthus*. Addenda to *Platystele, Pleurothallis* subgenus *Scopula,* and *Scaphosepalum* (Orchidaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 44: 1–128.

———. 1995. A reevaluation of the Pleurothallid subgenera *Satyria* and *Silenia* (Orchidaceae). Page 146 in *Icones Pleurothallidinarum*. 12. Systematics of *Brachionidium*. Addenda to *Dresslerella, Platystele* and *Porroglossum*. Monogr. Syst. Bot. Missouri Bot. Gard. 57.

———. 1996. Validation of taxa in the Pleurothallidinae. Lindleyana 1(2): 118.

———. 1999. *Icones Pleurothallidinarum*. 18. Systematics of *Pleurothallis* subgen. *Pleurothallis* sect. *Pleurothallis* subsect. *Antenniferae,* subsect. *Longiracemosae,* subsect. *Macrophyllae-Racemosae,* subsect. *Perplexae,* subgen. *Pseudostelis,* subgen. *Acuminatia*. Monogr. Syst. Bot. Missouri Bot. Gard. 76: 177, f. 33a.

———. 2000. Miscellaneous new species in the Pleurothallidinae. Orquideologia 21(3): 318–340.

———. 2002. A systematic method of classification of the Pleurothallidinae versus a strictly phylogenetic method. Selbyana 23(1): 57–110.

———. 2003. *Pleurothallis*. Pages 386–452 in B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora, eds., *Monocotiledóneas (Orchidaceae–Zingiberaceae)*. Vol. 3 in *Manual de Plantas de Costa Rica*. Monogr. Syst. Bot. Missouri Bot. Gard. 93.

———. 2004. *Icones Pleurothallidinarum*. 26. New genera and combinations in the Pleurothallidinae. Monogr. Syst. Bot. Missouri Bot. Gard. 95: 253–265.

———. 2007. *Icones Pleurothallidinarum*. 29. A third century of *Stelis* of Ecuador. Systematics of *Apoda–Prorepentia*. Systematics of miscellaneous small genera. Addenda: New genera, species, and combinations (Orchidaceae). Monogr. Syst. Bot. Missouri Bot. Gard. 112: 119.

Luteyn J. L., and R. L. Wilbur. 2005. Family #172, Ericaceae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 45.

Maddison, W. P., and D. R. Maddison. 2007. Mesquite: A modular system for evolutionary analysis. Mesquite v. 2.72. Available at http://mesquiteproject.org

McLeish, I., N. R. Pearce, B. R. Adams, and J. S. Briggs. 1995. *Native Orchids of Belize*. A. A. Balkema, Rotterdam, The Netherlands.

Misas Urreta, G. 2005. Orquídeas de la Serranía del Baudó, Chocó, Colombia. Corporacion Capitalina de Orquideología, Bogotá, Colombia.

Oses Salas, L., and A. P. Karremans. 2016. A note on *Masdevallia zahlbruckneri* and *M. utriculata* (Orchidaceae). Harvard Pap. Bot. 21(2): 325–336.

Ossenbach, C., F. Pupulin, and R. Jenny. 2010. Orchid itineraries of Augustus R. Endrés in Central America: A biographic and geographic sketch. Lankesteriana 10(1): 19–47.

———. 2013. *The Illustrations and the Catalogue*. Vol. 2 of *Orchids in the Life and Work of Auguste R. Endrés*. Verlag des Naturhistorischen Museums, Vienna.

Pohl, R. W. 1980. Family #15, Gramineae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 4.

Pridgeon, A. M. 2005a. *Echinosepala*. Pages 356–358 in A. M. Pridgeon, P. J. Cribb, M. W. Chase, and F. N. Rasmussen, eds., *Epidendroideae*. Part 1.Vol. 4 of *Genera Orchidacearum*. Oxford University Press, Oxford.

———. 2005b. *Echinosepala*. Pages 246–249 in F. Pupulin, ed., *Acianthera—Kegeleilla*. Vol. 1 of *Vanishing Beauty. Native Costa Rican Orchids*. Editorial de la Universidad de Costa Rica, San José.

———. 2020. *Pleurothallis*. Pages 850–909 in F. Pupulin, ed., *Lacaena—Pteroglossa*. Vol. 2 of *Vanishing Beauty. Native Costa Rican Orchids*. Koeltz Botanical Books, Oberreifenberg, Germany.

Pridgeon, A. M., and M. W. Chase. 2001. A phylogenetic reclassification of Pleurothallidinae (Orchidaceae). Lindleyena 16(4): 235–271.

———. 2002. Nomenclatural notes on Pleurothallidinae (Orchidaceae). Lindleyana 17(2): 98–101.

Pridgeon, A. M., R. Solano, and M. W. Chase. 2001. Phylogenetic relationships in Pleurothallidinae (Orchidaceae): Combined evidence from nuclear and plastid DNA sequences. Amer. J. Bot. 88(12): 2286–2308.

Pupulin, F. 2002. Catálogo revisado y anotado de las Orchidaceae de Costa Rica. Lankesteriana 4: 1–88.

———. 2010. Family #39, Orchidaceae: Tribe Cymbidieae: Subtribe Zygopetalinae. In W. Burger, ed., *Flora Costaricensis*. Fieldiana, Bot. n.s. 49.

———. 2020. *Pabstiella*. Pages 809–811 in F. Pupulin, ed., *Lacaena–Pteroglossa*. Vol. 2 of *Vanishing Beauty. Native Costa Rican Orchids*. Koeltz Botanical Books, Oberreifenberg, Germany.

Pupulin, F., and D. Bogarín. 2004. Two new species of *Lepanthes* (Orchidaceae: Pleurothallidinae) from Costa Rica. Kew Bull. 59: 559–563.

———. 2007. A second species of *Restrepiella* (Orchidaceae: Pleurothallidinae). Willdenowia 37(1): 323–329.

———.2010. Illustrations and studies in Neotropical Orchidaceae—The *Lepanthes jimenezii* group (Pleurothallidinae). Harvard Pap. Bot. 15(1): 111–121.

———. 2011a. Two *Lepanthes* (Orchidaceae: Pleurothallidinae) with strongly reduced corolla. OrchidsJournal 1(1): 31–35.

———. 2011b. Two New *Lepanthes* from Costa Rica. Lindleyana [in Orchids (Bull. Amer. Orch. Soc.)] 80(3): 178–181.

———. 2012. *Lepanthes novae Tapantienses*. Orch. Digest 76(1): 20–29.

———. 2014a. *Aliae Lepanthes Machogaffenses* (Orchidaceae: Pleurothallidinae). Harvard Pap. Bot. 19(2): 193–200.

———.2014b. Illustrations and studies in Neotropical Orchidaceae. 6. The "*Lepanthes guatemalensis*" group (Pleurothallidinae) in Costa Rica. An. Jard. Bot. Madrid 71(1): 1–17.

———.2020. *Lepanthes.* Pages 444–511 in F. Pupulin, ed., *Lacaena–Pteroglossa*. Vol. 2 of *Vanishing Beauty. Native Costa Rican Orchids*. Koeltz Botanical Books, Oberreifenberg, Germany.

Pupulin, F., D. Bogarín, and M. Fernández. 2010a. Illustrations and studies in Neotropical Orchidaceae. 2. A note on *Pleurothallis luctuosa* (Orchidaceae: Pleurothallidinae), with a new species. Ann. Naturhist. Mus. Wien. B.112: 239–252.

———. 2010b. On the identity of *Myoxanthus scandens* (Orchidaceae: Pleurothallidinae), with a new species. Lankesteriana 9(3): 467–473.

Pupulin, F., D. Bogarín, and D. Jiménez. 2009. New species and records in Mesoamerican *Lepanthes*. Orchid Digest 73: 136–145.

Pupulin, F., D. Bogarín, and A. P. Karremans. 2019. How many species of Pleurothallidinae are there? Pages 301–362 in A. Pridgeon, ed., *Proceedings of the Sixth Scientific Conference on Andean Orchids, 2017*. Guayaquil, Ecuador.

Pupulin, F., D. Bogarín, and C. M. Smith. 2010. Two new species of *Lepanthes* from Costa Rica close to *L. schizocardia* (Orchidaceae: Pleurothallidinae). Lankesteriana 9(3): 423–430.

Pupulin, F., M. Díaz-Morales, J. Aguilar, and M. Fernández. 2017. Two new species of *Pleurothallis* (Orchidaceae: Pleurothallidinae) allied to *P. cardiothallis*, with a note on flower activity. Lankesteriana 17(2): 329–356.

Pupulin, F., M. Díaz-Morales, M. Fernández, and J. Aguilar. 2017. Two new species of *Pleurothallis* (Orchidaceae: Pleurothallidinae) from Costa Rica in the *P. phyllocardia* group. Lankesteriana 17(2): 153–164.

Pupulin, F., A. P. Karremans, and N. Belfort Oconitrillo. 2017. Two new species of *Echinosepala*. Lankesteriana 17(2): 285–304.

Pupulin, F., A. P. Karremans, and B. Gravendeel. 2012. A reconsideration of the empusellous species of *Specklinia* (Orchidaceae: Pleurothallidinae) in Costa Rica. Phytotaxa 63: 1–20.

Pupulin, F., H. Medina, and D. Bogarín. 2010. Two *Lepanthes* (Orchidaceae: Pleurothallidinae) with a reduced corolla. Orchideen J. 17(3): 117–121.

Pupulin, F., and L. Oses. 2020. *Masdevallia*. Pages 572–609 in F. Pupulin, ed., *Lacaena–Pteroglossa*. Vol. 2 in *Vanishing Beauty. Native Costa Rican Orchids*. Koeltz Botanical Books, Oberreifenberg, Germany.

Pupulin, F., C. Ossenbach, R. Jenny, and E. Vitek. 2011. Typi Orchidacearum ab Augusto R. Endresio in Costa Rica lecti. Annalen Naturhistorisches Museums Wien, Ser. B, Botanik. Zoologie. 112: 265–313.

Pupulin, F., G. Rojas, and J. D. Zúñiga. 2007. Three new species of *Acianthera* (Orchidaceae: Pleurothallidinae) from Costa Rica. Harvard Pap. Bot. 12(1): 163–170.

Rambaut, A. 2009. FigTree v1.3.1. Available at http://tree.bio.ed.ac.uk/ software/

Reichenbach, H. G. 1855. Wagener's Orchideen aus Ocaña. Bonplandia 3(5): 65–73.

Renner. S. S., H. Balslev and L. B. Jolm-Nielsen. 1990. Flowering plants of Amazonian Ecuador–A checklist. AAU Reports 24: 1–241.

Rojas-Alvarado, G., and A. P. Karremans. 2017. Additions to the Costa Rican *Myoxanthus* (Orchidaceae: Pleurothallidinae). Lankesteriana 17(2): 203–214.

Schlechter, R. 1923. Beiträge zur Orchideenkunde von Zentralamerika. II. Additamenta ad Orchideologiam Costaricensem. Repert. Spec. Nov. Regni Veg. Beih. 19: 200.

Smith, C. M., D. Bogarín, and F. Pupulin. 2015. A new *Reichantha* (Orchidaceae: Pleurothallidinae) from Nicaragua and Costa Rica. Syst. Bot. 40(1): 83–87.

Smith, C. M., D. Jiménez, and F. Pupulin. 2013. *Lepanthes variabilis* (Orchidaceae: Pleurothallidinae), a new endemic species from Costa Rica. Brittonia 65: 469–476.

Smith, C. M., and F. Pupulin. 2012. Contributions to a taxonomic revision of *Masdevallia* (Orchidaceae: Pleurothallidinae) in Costa Rica. A note on *Masdevallia attenuata*. Harvard Pap. Bot. 17(1): 25–38.

Staden, R., D. P. Judge, and J. K. Bonfield. 2003. Analyzing sequences using the Staden Package and EMBOSS. In S. A. Krawetz and D. D. Womble, eds., *Introduction to Bioinformatics. A Theoretical and Practical Approach*. Humana Press, Totawa, New Jersey.

Turland, N. J., J. H. Wiersema, F. R. Barrie, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, W.-H. Kusber, D.-Z. Li, K. Marhold, T. W. May, J. McNeill, A. M. Monro, J. Prado, M. J. Price, and G. F. Smith, eds. 2018. *International Code of Nomenclature for Algae,Fungi, and Plants (Shenzhen Code) Adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017*. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten.

van den Berghe, E. P., and I. G. van den Berghe. 2008. Las orquídeas de Nicaragua, una guía de campo (accessed July 17, 2019). http:// www.caftadr-environment.org/spanish/outreach/publications/37_cafta_Orquideas_final.pdf.

Vásquez, R. and P. L. Ibisch. 2000. *Orchids of Bolivia, diversity and conservation status, Subtribu Pleurothallidinae*. Editorial F.A.N., Santa Cruz de la Sierra, Bolivia.

Williams, L. O. 1946. Orchidaceae. Pages 107–246 in W. G. D'Arcy, ed., *Flora of Panama*. Part 3. Fascicle 2. Ann. Missouri Bot. Gard. 33: 1–140.

———.1964. Tropical American plants. 6. Orchidaceae. Fieldiana, Bot. 31(2): 17–44.

Zelenko, H., and P. Bermúdez. 2009. *Orchids. Species of Peru*. ZAI Publications, Quito, Ecuador.

FIRST RECORD OF *CALLIANDRA SUBSPICATA* (FABACEAE) IN PARAÍBA STATE, BRAZIL

Aureliana Santos Gomes,[1] Erimágna de Morais Rodrigues,[2,5] Rubens Teixeira de Queiroz,[3]
Débora Coelho Moura,[1] and José Iranildo Miranda de Melo[4,5]

Abstract. *Calliandra subspicata* (Fabaceae) hitherto had been reported from Pernambuco and Bahia, states of the Northeast Region of Brazil. Here we report this species from Paraíba state, the third state of this region. It was observed and collected at the Pico do Jabre State Park, a conservation unit situated at the residual massif of the Depression Sertaneja on the Borborema Plateau, which reaches an altitude of 1197 m. The identification was made on the basis of current literature. A morphological description, images, information about the area where the taxon was collected, and a key for identification of the species of *Calliandra* recorded in Paraíba state are provided.

Keywords: northeastern Brazil, diversity, Fabaceae

Fabaceae, in the order Fabales (APG IV, 2016), is the third largest family of angiosperms in the world. It is currently divided into six subfamilies: Caesalpinioideae, Cercidoideae, Detarioideae, Dialioideae, Duparquetioideae, and Papilionoideae (LPWG, 2017). This family has a cosmopolitan distribution and is found in a variety of habitats: from coastal plains and mountains to tropical forests and deserts, in equatorial regions and close to the poles (Queiroz, 2009; Hartmann et al., 2019). This family comprises approximately 20,000 species distributed in 727 genera (LPWG, 2017). In Brazil, Fabaceae includes the largest number of species of all flowering plants in Brazil, namely, 2854 species in 222 genera, and is associated with a variety of phytogeographic domains and environments (*Flora do Brasil*, 2020).

Calliandra is an important genus included in tribe Ingae and belonging to the Mimosoideae clade, subfamily Caesalpinioideae. *Calliandra* has a Neotropical distribution, and species are found in areas with strong climatic seasonality, such as seasonally dry tropical forests, savannas, and seasonal deciduous and semi-deciduous forests (*Flora do Brasil*, 2020). It encompasses ca. 132 species (Barneby, 1998; Souza, 2001; Renvoize, 1981).

Morphologically, species of *Calliandra* are shrubs or subshrubs, and rarely trees. The genus is recognized mainly by the shape of the inflorescences, glomeruli, or terminal pseudo-racemes, as well as by the androecium with monadelphous stamens, bipinnate leaves devoid of extra floral nectaries, and fruits of the typical legume type with thick margins and elastic dehiscence from the apex toward the base (Souza, 2007; *Flora do Brasil*, 2020).

Calliandra is commonly found throughout Brazil and is represented by 74 species, 46 of which are recorded from Chapada Diamantina, Bahia state (Northeast Region), the area with the highest diversity of this genus in the country (Souza et al., 2013; *Flora do Brasil*, 2020). A recent study revealed several Fabaceae in the Cariri region of Paraíba state (Rodrigues et al., 2020). However, no record of this genus was reported. Here we report the first record of *Calliandra subpiscata* Benth. for Paraíba in a locality at relatively high altitude.

The species was found at the Pico do Jabre State Park (-7°15'11"S, -37°23'04"W), in a conservation unit located in the municipalities of Maturéia and Mãe d'Água (Fig. 1), metropolitan region of the municipality of Patos, Paraíba state, in northeastern Brazil (IBGE, 2017). Pico do Jabre State Park is part of the Borborema Plateau in the geotectonic zone of Teixeira, covering 500 ha and reaching a maximum elevation of 1197 m, the highest point in Paraíba state (Carvalho, 1982). The climate of this region is characterized as hot and dry, of the Bsh (hot, semi-arid) type, according to the Köppen classification (Francisco et al., 2015). However, because of the altitude and orography, Pico do Jabre has a wetter microclimate and mild temperatures, with rainfall records that vary from 800 to 1000 mm annually. This conservation unit is a high-altitude swamp with a remarkable mosaic of vegetation: it is possible to find the typical caatinga vegetation of northeastern Brazil (as opposed to Amazonian caatinga forest, an entirely different ecosystem), seasonal forest, and rupestrian vegetation in its various altitudinal levels, an exceptional area within the surrounding caatinga (Cunha and Silva-Júnior, 2018; Araújo et al., 2019).

The authors would like to thank the administration of the Pico do Jabre State Park for their permission to carry out botanical collections. José I. M. Melo would like to acknowledge the National Council for Scientific and Technological Development (CNPq) for a Research Productivity Fellowship grant (#303860/2019-6 [PQ-2]).

[1] Centro de Humanidades, Unidade Acadêmica de Geografia, Universidade Federal de Campina Grande, R. Aprígio Veloso, 882, Universitário, CEP: 58428-830, Campina Grande, Paraíba, Brazil

[2] Instituto de Biologia, CCS Jardim Didático, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, Cidade Universitária, Ilha do Fundão, CEP: 21941-971, Rio de Janeiro, Rio de Janeiro, Brazil

[3] Departamento de Botânica, *Campus* I, Jardim Cidade Universitária, CEP: 58051-090, João Pessoa, Paraíba, Brazil

[4] Departamento de Biologia, Centro de Ciências Biológicas e da Saúde, Universidade Estadual da Paraíba, Rua Baraúnas 351, Bairro Universitário, CEP 58429-500, Campina Grande, Paraíba, Brazil

[5] Corresponding author: tournefort@gmail.com

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 191–194.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n6,

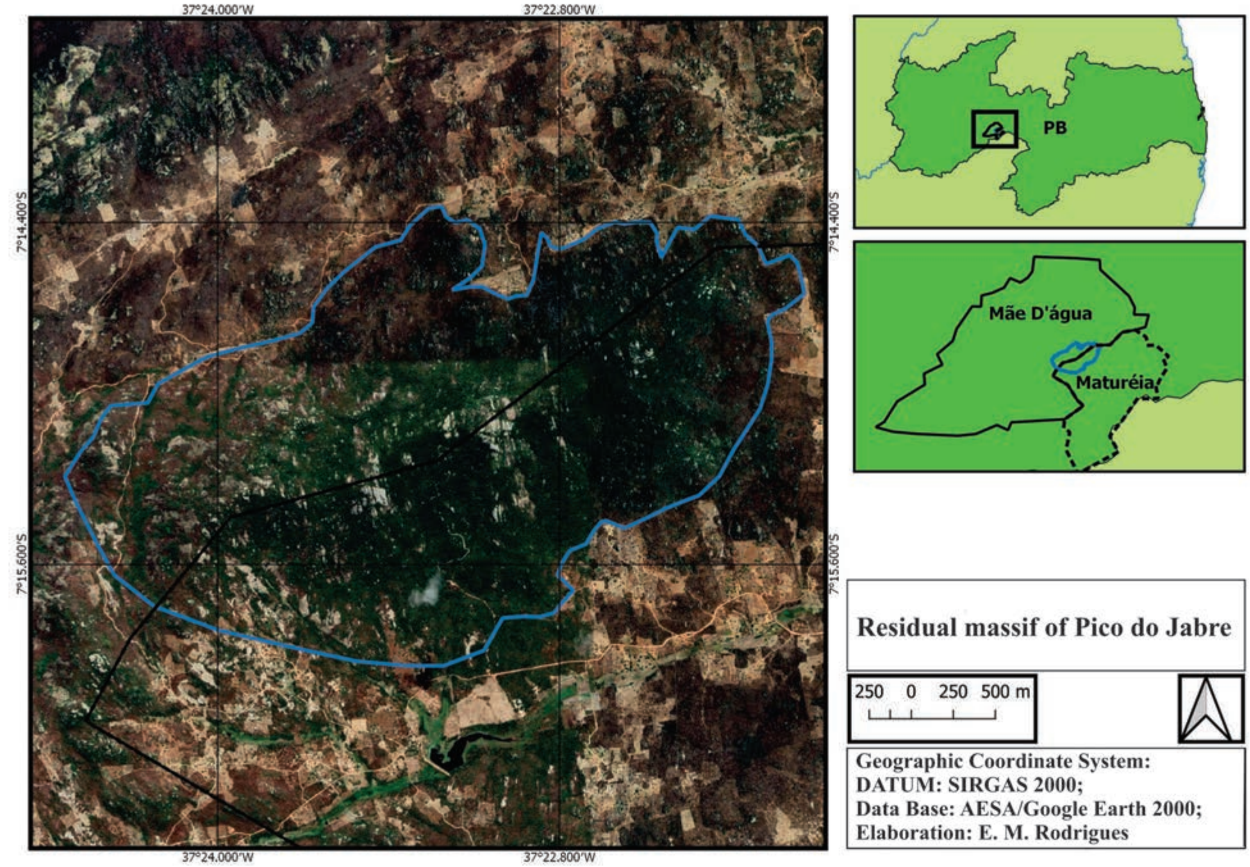


FIGURE 1. Location of the Pico do Jabre State Park (between the municipalities of Maturéia and Mãe d'Água), Paraíba state, northeastern Brazil.

Data Collection and Taxonomic Treatment

Specimens of *Calliandra subspicata* were collected during monthly excursions from December 2018 to February 2020 while exploring the windward part of the massif. During field trips, fertile branches (with flowers) were obtained and the samples herborized according to the techniques used in taxonomic studies described by Peixoto and Maia (2013), using an air circulation oven at 50 C for a period of 24 to 48 hours. Herborization was carried out at the Botany Laboratory, Department of Biology, State University of Paraíba (UEPB), *Campus* I. The samples were incorporated into the collections of the Herbaria Manuel de Arruda Câmara (HACAM) and Lauro Pires-Xavier (JPB), in the State and Federal Universities of Paraíba (UEPB and UFPB), respectively.

We followed the Leguminosae Phylogeny Working Group (LPWG, 2017) in classifying the subfamilies, and Queiroz (2009) and Souza et al. (2013) for genera and species classifications. Type of habit was defined on the basis of field observations. The morphological characterization of the species was based on the material obtained in the study area, consulting exsiccates incorporated into the Virtual Herbarium of the Flora and Fungi (Reflora). Acronyms follow Thiers (2020). The spelling of authors' names was based on Brummitt and Powell (1988). The descriptive terminologies of plant and reproductive structures were based on Hickey (1973), Radford et al. (1974), Rizzini (1977), Payne (1978), and Harris and Harris (2001). The type of inflorescence was based on Weberling (1992). The names were verified in Tropicos (2020). The species of *Calliandra* found in Paraíba state can be identified using the following key.

Key to *Calliandra* Species

1a. Leaves 2-foliolate; flowers sessile . . . . *Calliandra brevipes*
1b. Leaves 4- to 8-foliolate; flowers pedicellate 2
2a. Leaves 4- to 6-foliolate; inflorescence a raceme . . . . *C. subspicata*
2b. Leaves 7- to 8-foliolate; inflorescence an umbel . . . . *C. pedicellata*

Calliandra subspicata Benth., Trans. Linn. Soc. London 30(3): 556. 1875. TYPE: BRAZIL, *M. Wied s.n.* (Holotype: BR [BR0000005194421, photograph seen]). Fig. 2.

Distribution and habitat: the species is endemic to Brazil and is distributed in the Northeast Region (Bahia and Pernambuco); it is associated with the morphoclimatic domains of the Caatinga and Atlantic Forest (Tropicos, 2020), here representing a new record for Paraíba state. In the study area (Pico do Jabre State Park), it was found at an altitude of 1197 m (Fig. 1) on the Borborema Plateau of the massif, close to boulders in a stretch of Litolic Neosoils.

Phenology: found flowering in December 2018 and August 2019.

Additional specimens examined: BRAZIL. Bahia, Camacã, Rodovia Camacã, 09 May 2003, fl., fr., *E. Souza 109585* (CEPEC); Ilhéus, Cachoeira river bank, 08 July 1965, fr., *R. P. Belém et al. 1325* (CEPEC).

Shrub, erect, ca. 2 m high, cylindrical branches, striate, pubescent, unarmed. *Stipules* narrow-triangular to triangular, 1–12 × 2–4 mm. *Leaves* bipinnate, 4- to 6-bifoliolate, alternate, petiole 0.9–3.0 cm long, apex rounded-acute, margin entire, base truncate; chartaceous, adaxial surface glabrous, abaxial surface puberulent. *Inflorescence* axillary, raceme, 7.2 × 2.2 cm. *Pedicellate* flowers, pentamerous, actinomorphic, monoclines, hypogynous, polistemonous; pedicel ca. 0.1 long; campanulate calyx 5 × 3 mm, lobes 5, ca. 1 mm long; tubular corolla, white, 6.5 × 7.0 mm, lobes 5.4 × 35.0 mm; stamens 30–35, isodynamous, monadelphous; fillaments white with pinkish apex, 5–6 cm long; superior ovary, unicarpelar, unilocular, marginal placentation, pluriovulate. *Legume* 0.5–0.6 × 6.0–7.3 cm, linear, flat, seeds not seen.

Two other species of *Calliandra* (*C. brevipes* Benth. and *C. parvifolia* [Hook. & Arn.] Speg.) can be found in Paraíba state. These species are distinguished from *C. subspicata* mainly by the number of leaflets, the presence of pedicels, and the color of the filaments: *C. brevipes* has two pairs of leaflets, glomerulus-type inflorescence, and sessile flowers, versus leaves with 4–8 pairs of leaflets and flowers pedicellate in *C. parvifolia* and *C. subspicata*. The latter two species can be differentiated by the number of leaflets and the shape of the inflorescence: the former has leaves with 7–8 pairs of leaflets and umbellate inflorescences, whereas the latter has leaves with 4–6 pairs of leaflets and racemose inflorescences (see key above).

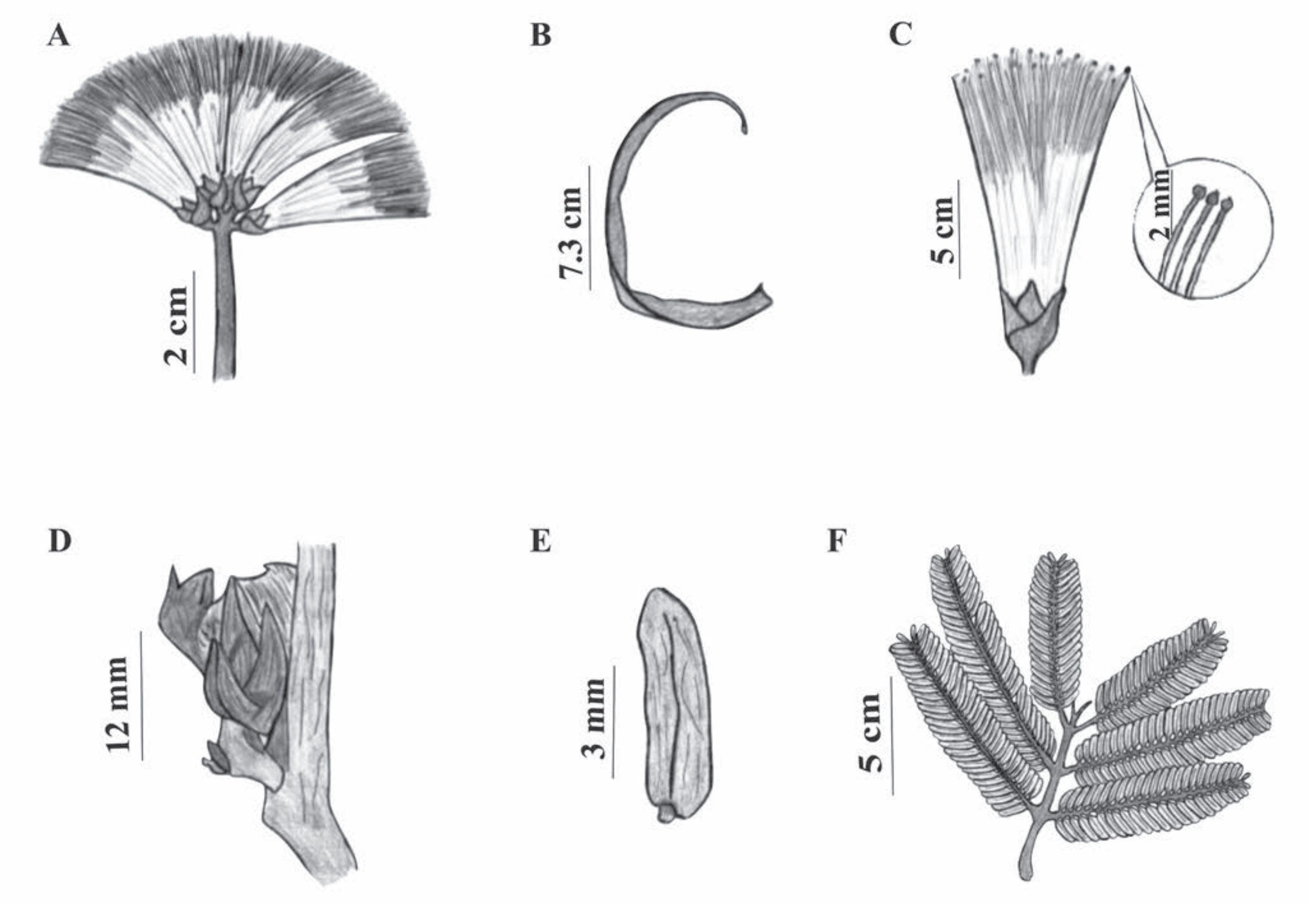


FIGURE 2. *Calliandra subspicata* Benth. **A,** inflorescence; **B,** fruit; **C,** flower; **D,** stipule; **E,** leaflet; **F,** leaf.

Literature Cited

APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. Botanical Journal of the Linnean Society 181(2): 1–20.

Araújo, E. D. S., C. C. C. Machado, and J. O. P. Souza. 2019. Considerações sobre as paisagens semiáridas e os enclaves subúmidos do Nordeste seco—uma abordagem sistêmica. Revista de Geografia Física 36(3): 128–146.

Barneby, R. C. 1998. *Calliandra*. Part 3 of *Tree, Guanacaste, Monkey's Earring: A Generic System for the Synandrous Mimosaceae of the Americas*. Memoirs of the New York Botanical Garden 74(3): 1–223.

Brummitt, R. K., and C. E. Powell. 1988. *Authors of Plant Names*. Royal Botanic Gardens, Kew, U. K.

Carvalho, M. G. R. F. 1982. Estado da Paraíba: classificação geomorfológica. João Pessoa, Editora Universitária UFPB, Castelo Branco, João Pessoa, Paraíba, Brazil.

Cunha, M. C. L., and M. C. Silva-**Júnior**. 2018.Comunidades de Árvores Na Floresta Estacional Semidecidual Montana do Pico do Jabre, Paraíba. Ciência Florestal, Santa Maria 28(4): 1365–1380.

Flora do Brasil. 2020 (under construction). *Fabaceae*. Jardim Botânico do Rio de Janeiro (accessed April 29, 2020). http://reflora.jbrj.gov.br/reflora/floradobrasil/FB115.

Francisco, P. R. M., R. M. Medeiros, D. Santos, and R. M. Matos. 2015. Classificação climática de Köppen e Thornthwaite para o Estado da Paraíba. Revista Brasileira de Geografia Física 8(4): 1006–1016.

Harris, J. G., and M. W. Harris. 2001. *Plant Identification Terminology: An Illustrated Glossary*. 2nd ed. Spring Lake Publishing, Spring Lake, Utah.

Hartmann, L. S., R. S. Rodrigues, and A. S. Flores. 2019. O gênero *Aeschynomene* (Leguminosae: Papilionoideae) no Estado de Roraima, Brasil. Rodriguésia 70(40): 2–14.

Hickey, L. J. 1973. Classification of the architecture of dicotyledonous leaves. American Journal of Botany 60(1): 17–33.

IBGE (Instituto Brasileiro de Geografia e Estatística). 2017. Divisões regionais do Brasil: Regiões geográficas da Paraíba (accessed April 29, 2020). ftp://geoftp.ibge.gov.br/organizacao_do_territorio/divisao_regional/divisao_regional_do_brasil/divisao_regional_ do_brasil_em_regioes_geograficas_2017/.

LPWG (The Legume Phylogeny Working Group). 2017. A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny. Taxon 66: 44–77.

Payne, W. W. 1978. A glossary of plant hair terminology. Brittonia 30: 239–255.

Peixoto, A. L., and L. C. Maia. 2013. *Manual de Procedimentos para Herbários*. INCT Herbário Virtual para a Flora e os Fungos. Editora Universitária UFPE, Recife.

Queiroz, L. P. 2009. Leguminosas da Caatinga. Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil.

Radford, A. E., W. C. Dickison, J. R. Massey, and C. R. Bell. 1974. *Vascular Plant Systematics*. Harper & Row, New York.

Renvoize, S. A. 1981. The genus *Calliandra* (Leguminosae) in Bahia, Brazil. Kew Bulletin 36(1): 63–83.

Rizzini, C. T. 1977. Sistematização terminológica da folha. Rodriguésia 42(1): 103–210.

Rodrigues, E. M., R. T. Queiroz, L. P. Silva, F. K. S. Monteiro, and J. I. M. Melo. 2020. Fabaceae em um afloramento rochoso no semiárido brasileiro. Rodriguésia 71(22): 1–25.

Souza, E. R. 2001. Aspectos taxonômicos e biogeográficos do gênero *Calliandra* Benth. (Leguminosae–Mimosoideae) na Chapada Diamantina, Bahia, Brasil. Dissertação (Mestrado em Botânica), Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil.

———. 2007. Estudos filogenéticos na tribo *Ingeae* (Leguminosae: Mimosoideae) com ênfase em *Calliandra* Benth. e gêneros afins. Tese (Doutorado em Botânica), Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil.

Souza, E. R., G. P. Lewis, F. Forest, A. S. Schnadelbach, C. V. D. Berg, and L. P. Queiroz. 2013. Phylogeny of *Calliandra* (Leguminosae: Mimosoideae) based on nuclear and plastid molecular markers. Taxon 62(6): 1201–1220.

Thiers, B. 2020 (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium (accessed April 29, 2020). http://sweetgum.nybg. org/science/ih/.

Tropicos. 2020 Continuously updated. Missouri Botanical Garden, 2019 (accessed April 29, 2020). http://www.tropicos.org.

Weberling, F. 1992. *Morphology of Flowers and Inflorescences*. Cambridge University Press, Cambridge.

NOTES ON THE GENUS *BACOPA* (PLANTAGINACEAE, GRATIOLEAE) IN THE ORINOQUIA REGION OF COLOMBIA AND VENEZUELA

Gerardo A. Aymard C.,[1,2,3] J. Orlando Rangel-Ch.,[3]
Vladimir Minorta-Cely,[4] and Francisco Castro-Lima[5]

Abstract. *Bacopa llanorum*, a new species from the seasonally flooded savannas of the "Llanos" region of Colombia (Arauca department) is described and illustrated, and its morphological relationships are discussed. On the basis of its dimorphic leaves (the innermost blade filiform, uppermost lanceolate-ovate), the new species does not appear to be allied to any other *Bacopa* species. However, it shares several other features with *B. reptans*. A new combination, *Bacopa debilis*, is proposed to replace *Caconapea debilis*. In addition, ecological information of the genus in "Los Llanos" of Colombia and Venezuela, and ecological and floristic notes about the eolic-limose plains, are included. A key for identifying species of *Bacopa* in this region is also provided. *Bacopa llanorum* is remarkable for its foliar dimorphism, in an otherwise predominantly homomorphic-leaved genus, and it increases to 20 the number of species of the genus in the "Llanos del Orinoco" bioregion.

Keywords: *Bacopa*, Plantaginaceae, "Llanos del Orinoco," foliar dimorphism, wetlands, eolic-limose plains

Resumen. *Bacopa llanorum* de las sabanas estacionalmente inundables de "los Llanos" de Colombia (departamento de Arauca) es descrita, ilustrada, y sus relaciones morfológicas son discutidas. Por su dimorfismo foliar (láminas basales filiformes y lanceolado-ovadas las superiores), *B. llanorum* no se relaciona con ninguna de las otras especies de *Bacopa*. Sin embargo, comparte algunos caracteres morfológicos con *B. reptans*. Se propone la nueva combinación *Bacopa debilis* para subtituir *Caconapea debilis*. Adicionalmente, se presenta información acerca de la ecología del género en los Llanos, notas ecológicas y florísticas acerca de la planicie eólica-limosa, y una clave de las especies registradas en la Orinoquia de Colombia y Venezuela. *Bacopa llanorum* es notable por su dimorfismo foliar, en un género donde predominan las hojas homomorfas. Este nuevo hallazgo eleva a 20 el número de especies del género para la bioregión de los Llanos del Orinoco.

Palabras claves: *Bacopa*, Plantaginaceae, "Llanos del Orinoco," dimorfismo foliar, humedales, planicies eólicas-limosas

Bacopa Aubl. (Aublet, 1795: 128–130), encompassing ca. 60 species, is the largest genus in tribe *Gratioleae* (Fischer, 2004). It is a mostly Pantropical group (Ahedor and Elisens, 2015), with few taxa in temperate areas (Pennell, 1919, 1935; Spencer et al., 1978) and with its highest diversity in the Neotropics (46 species; *fide* Ulloa Ulloa et al., 2018 Onward). The life forms of the genus are variable, including mostly annual prostrate, diffuse, or erect succulent and flaccid stems, aquatic or swamp-inhabiting rhizomatous to completely submerged herbs (Holmgren and Vincent, 2005; Souza, 2012; Sosa et al., 2018). A few taxa are perennial, terrestrial, erect suffrutexes (e.g., *B. angulata* (Benth.) Loefgr. & Edwall; *B. lisowskiana* R. Mielcarek).

The genus has been treated as a member of the tribe *Gratioleae* (Bentham, 1835) of Scrophulariaceae. Molecular-phylogenetic studies have greatly altered concepts of families of the traditional Scrophulariaceae (e.g., Olmstead et al., 2001; Oxelman et al., 2005; Tank et al., 2006; Barker et al., 2012; APG, 2016), placing several genera (e.g., *Bacopa, Mecardonia* Ruiz & Pav., and *Scoparia* L.) within Plantaginaceae.

Bacopa is characterized by leaves all opposite or verticillate, pedicels (2.0–)4.5–10.0 mm long, bractlets present at the summit of the pedicel (often appearing to be part of the calyx), rarely absent, calyx segments divided to or nearly to the base, distinctly dissimilar, 3 broad segments (1 posterior and 2 anteriolateral) and 2 narrower, posteriolateral ones, corolla throat open, fertile stamens four (rarely 5) or two stamens plus two staminodes, anthers with both thecae fertile and capsules 1–4 mm long (Holmgren and Vincent, 2005; Souza, 2012; Barringer, 2015).

Species of *Bacopa* (mainly *B. monnieri* [L.] Wettst.) are herbs and important sources of various biochemical compounds, such as alkaloids, bacosides, flavonoids, glycosides, triterpenoids, and saponins (Reddy, 2019). Clinical studies show it to have anxiolytic, antidepressant, cognitive-enhancing, antioxidant, cholinergic, and adaptogenic actions (Abascal and Yarnell, 2011). These properties make it a highly useful herb in helping patients cope with physical and emotional stress and with the cognitive impairment that usually accompanies aging, such as from dementia, Parkinson's disease, and epilepsy (Aguiar and Borowski,

---

The authors are grateful to Parques Nacionales Naturales de Colombia (PNN) for sponsoring the fieldwork in Arauca Department, and to Gustavo A. Romero-G. (AMES) for his comments on an earlier version of the text and his help locating historical literature. We also thank Liseth Paola Piñeros U. (COL) for preparing the illustration and for providing herbarium and morphological notes, Larry Niño for his help with the Orinoquia map, and the staff of Herbario Nacional de Colombia (COL) and the Gray Herbarium (GH) for making their facilities available for our research. This work could not have been completed without the invaluable JSTOR Global Plants database (https://plants.jstor.org/).

[1] UNELLEZ-Guanare, Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), Mesa de Cavacas, estado Portuguesa 3350, Venezuela; Compensation International Progress S.A. Ciprogress–Greenlife, Bogotá, D.C., Colombia

[2] Corresponding author; cuyuni24@hotmail.com

[3] Grupo de Investigación en Biodiversidad y Conservación, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, P.O. Box 7495, Bogotá, D.C., Colombia

[4] Departamento de Ciencias Naturales, Universidad Central de Colombia, Grupo de Investigación en Biodiversidad y Conservación, Instituto de Ciencias Naturales, Universidad Nacional de Colombia

[5] Investigador Independiente, Mz A. Casa 2. Vereda Vanguardia, Villavicencio, Meta, Colombia

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 195–203.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n7, Published online: 31 December 2020

2013; Sukumaran et al., 2019).

No worldwide monograph of *Bacopa* has been completed; however, several attempts have been made to organize the genus after G. Bentham's treatment of Scrophulariaceae (Bentham, 1846). For instance, von Wettstein (1891) divided the genus into six sections, described two species, and made seven combinations. Edwall (1897) transferred *Herpestis* C.F. Gaertn. to *Bacopa*, and with J. A. C. Loefgren described seven species and made 14 combinations. Pennell (1935) initially placed the species in five genera but later merged them in *Bacopa*, recognizing six sections and six subsections (Pennell, 1946); these form the basis for the most recent taxonomic treatments (Ahedor and Elisens, 2015; Sosa et al., 2018). Since then, 12 new species have been described from the Neotropics (Williams, 1950, 1952; Pennell, 1953; Descole and Borsini, 1954; Alain, 1968; Ichaso and Barroso, 1974; Borhidi and Muñiz, 1975a,b; Rossow, 1986; Souza, 2001).

The genus has been treated for the Flora of Colombia (Pennell, 1920), *Flora of the Venezuelan Guayana* (Holmgren and Vincent, 2005), *Flora Mesoamericana* (Christenhusz, 2014), and *Manual de Plantas de Costa Rica* (Barringer, 2015). In addition, a revision of the genus in Argentina was published by Sosa et al. (2018).

Currently, a third of *Bacopa* species are found in the Orinoco "Llanos" region of Colombia and Venezuela (Fig. 1), also known as "Orinoquia" in Colombia (Minorta-Cely and Rangel-Ch., 2014). These taxa occur in wetlands (e.g., estuaries, edges of abandoned meanders ["madreviejas"], lagoons, and swamps). In these habitats they constitute ecologically interesting communities of dense aquatic or swamp-inhabiting rhizomatous plants. Their roots are able to penetrate the substrate, and remain submerged or re-emerge, as is the case in swamps. The permanence throughout the year of populations of *Bacopa* spp. and other aquatic plants is highly affected by the marked seasonality in the Orinoquia region, primarily by loss of the water column (Vera-Ospina et al., 2020). These communities are common in the seasonally flooded savannas over the vast eolic-limose plains, which extend from northeastern Colombia through western-central Venezuela (Schargel and Aymard, 1992; Rangel-Ch. et al., 2020). Several taxa of *Bacopa* also occur from Mesoamerica, Amazonia, the Andes, the Guianas, and southeastern and central Brazil to the Southern Cone (Holmgren and Vincent, 2005; Christenhusz, 2014; Barringer, 2015; Sosa et al., 2018).

This contribution increases to 20 the number of *Bacopa* species known from the Orinoco "Llanos" (Table 1). This new species was detected during herbarium research for aquatic vegetation and other physical and biotic studies conducted in seasonally flooded savannas over the eolic-limose plains, Arauca department, Colombia (Rangel-Ch. et al. 2020).

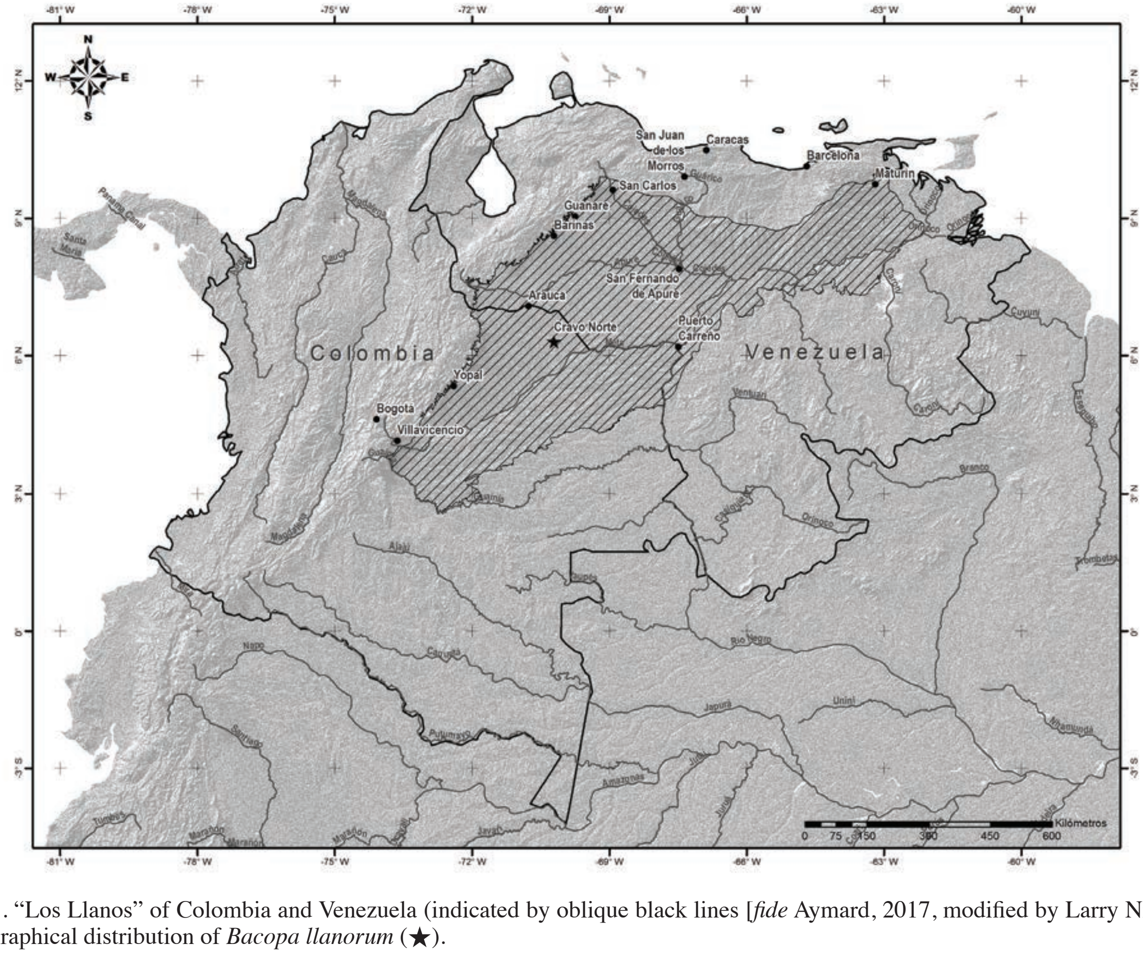


FIGURE 1. "Los Llanos" of Colombia and Venezuela (indicated by oblique black lines [*fide* Aymard, 2017, modified by Larry Niño]) and the geographical distribution of *Bacopa llanorum* (★).

TABLE 1. Comparative checklists of *Bacopa* in the Orinoquia region of Colombia and Venezuela.

TAXA OF *BACOPA*	MINORTA AND RANGEL (2014); COLOMBIA, 7 TAXA	CÁRDENAS-L. ET AL. (2016); COLOMBIA, 7 TAXA	AYMARD (2017); VENEZUELA, 16 TAXA	BERNAL (2020); COLOMBIA, 7 TAXA	TAXA ACCEPTED IN THIS STUDY: 20 TAXA COLOMBIA (10 SSP.) AND VENEZUELA (18 SSP.)
B. albida (Pennell) Standl.				X	X (COL)
B. aquatica Aubl.			X		X (VEN)
B. axillaris (Benth.) Standl.			X	X	X (COL, VEN)
B. bacopoides (Benth.) Pulle			X		X (VEN)
B. callitrichoides (Kunth) Pennell		X	X		X (COL, VEN)
B. gratioloides (Cham.) Chodat & Hassl.			X		X (VEN)
B. innominata (M. Gómez) Alain					X (VEN)
B. llanorum Aymard & Rangel-Ch.					X (COL)
B. laxiflora (Benth.) Wettst. ex Edwall	X	X	X	X	X (COL, VEN)
B. monnieri (L.) Wettst.			X		X (VEN)
B. monnierioides (Cham.) B.L. Rob.	X	X	X	X	X (COL, VEN)
B. myriophylloides (Benth.) Wettst.	X	X	X	X	X (COL, VEN)
B. reflexa (Benth.) Edwall	X	X	X		X (COL, VEN)
B. repens (Sw.) Wettst.			X		X (VEN)
B. reptans (Benth.) Wettst. ex Edwall	X	X	X	X	X (VEN)
B. salzmannii (Benth.) Wettst. ex Edwall	X	X	X		X (COL, VEN)
B. serpyllifolia (Benth.) Pennell					X (VEN)
B. sessiliflora (Benth.) Edwall	X		X	X	X (COL, VEN)
B. valerii Standl. & L.O. Williams			X		X (VEN)
B. verticillata (Pennell & Gleason) Pennell			X		X (VEN)

MATERIALS AND METHODS

This work is based on a morphological study of specimens in COL, GH, and NY (herbarium codes after Thiers, 2019), and the examination of historical and current taxonomic literature on *Bacopa*. Type specimens of *Bacopa* species were studied through the use of on-line images from the JSTOR Global Plants database (https://plants.jstor.org/). The specific terminology for vegetative characters, vestiture descriptions, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), Harris and Harris (2001), and Endress (2010).

TAXONOMIC TREATMENT

Bacopa llanorum Aymard & Rangel-Ch. *sp. nov*. TYPE: COLOMBIA. Arauca: Cravo Norte, Vereda Campo Abierto, Finca de los hermanos Mojica, estero en la base de médanos, 06°23'49.55"N; 70°25'13.17"W, 105 m. 29 August 2016 (fl and fr), *Vladimir Minorta-Cely, Francisco Castro-Lima, Luis F. Gopar, Andrés Vera-Ospina & Diego Yasnó 2749* (Holotype: COL; Isotype: HORA). Fig. 2.

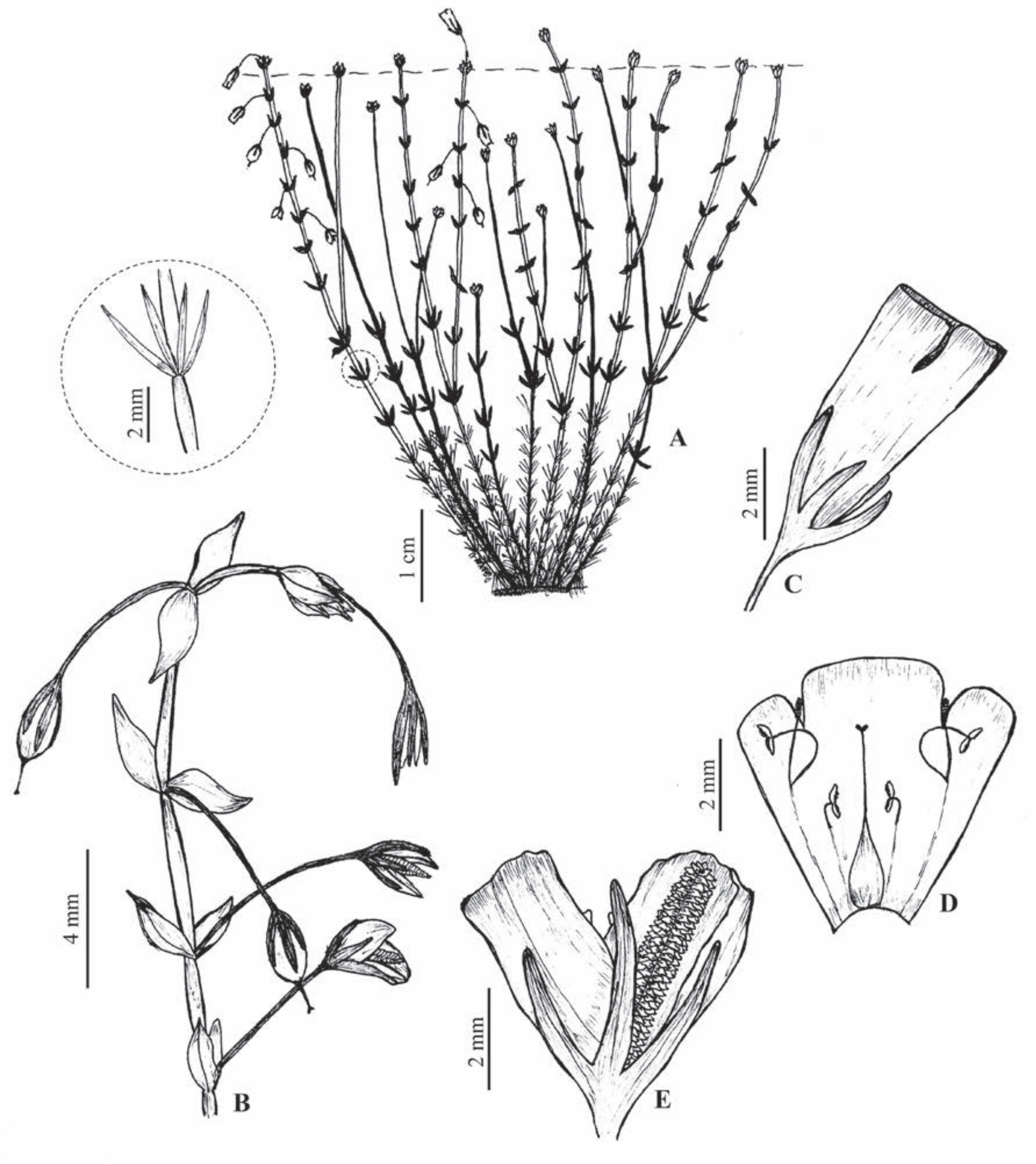


FIGURE 2. *Bacopa llanorum* Aymard & Rangel-Ch. **A**, habit showing the filiform innermost blade; **B**, top of the main stem with capsules showing lanceolate-ovate uppermost blade; **C**, corolla; **D**, inside of corolla showing the stamens and ovary; **E**, mature capsules showing the placenta and seeds.

Bacopa llanorum is morphologically similar to *B. reptans* (Benth.) Wettst. ex Edwall but differs in its habit (stout herbs, 20–40 cm tall), having dimorphic leaves, the innermost blade filiform, the uppermost lanceolate-ovate 3.5–4.6 × ca. 1.9 mm, opposite or 4–6 verticillate, margins entire, apex acute, flowers axillary or terminal, calyx lobes 2.0–2.2 mm long, lanceolate, entire at the margin and the apex acute.

Herbs 20–40 cm, stout, mat-forming, aquatic. *Stems* ascending, becoming erect, branched at the base, quadrangular, glabrate, succulent, creeping and rooting at nodes. *Leaves* dimorphic, opposite or 4- to 6-verticillate, sessile, glabrous and minute punctate on both sides, margin entire, midvein impressed on the upper surface, elevated on the lower surface; the innermost blade filiform, ca. 3.2 × ca. 0.8 mm, base attenuate, apex acute, the uppermost blade lanceolate-ovate, 3.5–4.6 × ca. 1.9 mm, base cuneate, apex acute. *Flowers* solitary, axillary or terminal, pedicel 7.0–7.8 mm long, glabrous, ebracteate; *calyx* 5-lobed, lanceolate, glabrous, apex acute, margins entire, the external dorsal lobe ca 2.2 mm, the 2 lateral and the 2 internal ca. 2 mm long; *corolla* pale lilac, 3-lobed, tube 5–6 mm long, lobes ca. 2 mm, glabrous; *stamens* 4, didynamous; *ovary* ca. 4 mm long, glabrous, style ca. 2.3 mm long, stigmatic apex bifid. *Capsule* ovoid, apex obtuse, ca. 5 × ca. 2 mm. *Seed* ellipsoid, flattened, ca. 0.5 mm.

Phenology: collected with flowers and fruits in August.

Distribution and habitat: the species is known from seasonally flooded savannas over oligotrophic soils, in the eolic-limose plains that extend from northeastern Colombia through western Venezuela, between 100 and 300 m. A recent phytosociological study showed that *Bacopa llanorum* is associated with the *Leersia hexandra* Sw. (Poaceae) and *Pontederia subovata* (Seub.) Lowden (Pontederiaceae) community of the Arauca River floodplains (Vera-Ospina et al., 2020). In estuaries located in Cravo Norte and Puerto Rondón (Arauca department, Colombia), this species forms colonies with high cover values (64%). It is found with other submerged aquatic species, such as *Cabomba furcata* Schult. & Schult. f. (Cabombaceae) and *Eriocaulon setaceum* L. (Eriocaulaceae), and emergent rooted herbs, such as *Sagittaria platyphylla* (Engelm.) J.G. Sm. (Alismataceae) (Vera-Ospina et al., 2020). In other cases, this new species was observed in communities of *Cabomba furcata* Schult. & Schult. f. and *Ludwigia sedioides* (Bonpl.) H. Hara (Onagraceae) as an emergent herb with relatively low cover values, between 8 and 50% (Vera-Ospina et al., 2020).

Conservation status: according to IUCN criteria ((IUCN, 2017), this species would be ranked as DD (data deficient). This indicates that, while the species has been overlooked until recently, future research may show that a threatened classification is appropriate. Currently, *Bacopa llanorum* is known only from the type collection; however, we expect this new species to have a wider distribution across seasonally flooded savannas that extend from northeastern Colombia through western Venezuela. Notwithstanding, "Los Llanos" have experienced intense human activity in the last six decades, which has led to changes in the species composition and structural complexity of its vegetation (Aymard, 2017). However, the region remains in a good state of conservation, the main threats being the transformation of savannas into pastures and selective logging. Currently, these activities are relatively local and with low impact, but transformation into pastures is the greatest pressure because of the removal of biomass and soils.

Given its dimorphic leaves (the innermost blade filiform, uppermost lanceolate-ovate), in a predominantly homomorphic-leaved genus, *Bacopa llanorum* is not evidently allied to any other *Bacopa* species. This new species does share several features with *B. reptans* (Benth.) Wettst. ex Edwall from Honduras, Colombia, Venezuela, Guyana, and Bolivia (Santa Cruz) south to Brazil (Minas Gerais): both species have succulent stems, leaf blade minute punctate on both sides, inflorescences of solitary flowers, pedicels ebracteate, and capsules ovoid. Nevertheless, this new species differs from *B. reptans* in the vegetative and reproductive characters discussed in the diagnosis, in Table 2, and in the Key to the Species presented here.

Dimorphism or phenotypic plasticity in leaf form is a remarkable feature among aquatic plants (Deschamp and Cooke, 1983). How aquatic plants form such different leaves has been largely investigated among Eudicots

TABLE 2. Comparison of diagnostic morphological characters of *Bacopa llanorum* Aymard & Rangel-Ch. and *B. reptans* (Benth.) Wettst. ex Edwall.

CHARACTER	*BACOPA LLANORUM*	*BACOPA REPTANS*
Habit	Herbs 20–40 cm tall, stout	6–20 cm, slender
Leaves	Dimorphic (the innermost blade filiform, uppermost lanceolate-ovate), opposite or 4–6 verticillate, margins entire	Homomorphic (all linear-lanceolate), opposite or 4-verticillate, margins dentate
Uppermost leaves	Lanceolate-ovate, 3.5–4.6 × ca. 1.9 mm, apex acute	Linear-lanceolate, 6–9 × 3–4 mm, apex obtuse
Inflorescence	Flowers axillary or terminal	Always axillary
Calyx lobes	2–2.2 mm long, external and internal lanceolate, margin entire, apex acute	Ca. 6 mm long, external oblong-lanceolate, internal linear, margin ciliate, apex obtuse

(e.g., Lamiales and Ranunculales), monocots (e.g., Alismatales and Poales), and basal angiosperms such as Nymphaeales (for a review see Koga et al., 2020). This feature is common in several genera, such as *Callitriche* L. (Plantaginaceae), *Elatine* L. (Elatinaceae), *Hydrophila* R. Br. (Acanthaceae), *Potamogeton* L. (Potamogetonaceae), and *Ranunculus* L. (Ranunculaceae). However, dimorphism in *Bacopa* is an uncommon morphological attribute; of the ca. 60 known species, dimorphic leaves has been reported only in *B. verticillata* (Pennell & Gleason) Pennell (Gleason, 1929; Sosa et al., 2018) and in *B. llanorum* herein (see couplets 2a and 2b in the key that follows for differences between these two species).

Caconapea Cham. is one of the genera that Pennell (1946) placed in the synonymy of *Bacopa*. The genus was described by L. K. A. von Chamisso (1833) on the basis of a single species, *C. gratioloides* Cham. Over the years, species of *Caconapea* were transferred to *Bacopa*, except for *C. debilis* Pennell, a species originally collected by F. W. Pennell (1886–1952) in the Colombia Llanos, which is formally combined here:

Bacopa debilis (Pennell) Aymard & Rangel-Ch., *comb. nov.* Basionym: *Caconapea debilis* Pennell, Proc. Acad. Nat. Sci. Philadelphia 75:151. 1920. TYPE: COLOMBIA. Intendencia del Meta: Villavicencio, shallow pools, 450 m, 1–2 September 1917, *Francis W. Pennell 1623* (Holotype: NY; Isotypes: GB, K, PH).

Current taxonomic status: *Caconapea debilis* is currently treated as a synonym of *Bacopa reptans* (Pennell, 1946; Holmgren and Vincent, 2005).

KEY TO *BACOPA* SPECIES OF THE ORINOQUIA REGION

Based on Holmgren and Vincent (2005); distribution outside Orinoquia not included.

1a. Leaves dimorphic along the stems 2
1b. All leaves homomorphic along the stems 3
2a. Leaves filiform only at the base and lanceolate-ovate at the top of the stem, blade punctate, the base attenuate or cuneate; flowers with pedicels 7–7.8 mm long, ebracteate . . . . . ***B. llanorum*** (Colombia: Arauca)
2b. Leaves pinnatisect or pinnatifid at the base and pinnatifid to entire at the top of the stem, the base amplexicaul or auriculate, epunctate; flowers sessile or with brief pedicels ca. 5 mm long, bracteate . . . . . ***B. verticillata*** (Venezuela: Guárico)
3a. Leaves deeply pinnately dissected into filiform divisions 4
3b. Leaves linear, oblong-lanceolate, narrowly lanceolate, lanceolate or broader 5
4a. Leaves 10–14 leaves per node, 0.9–1.5 × ca. 3 mm, with 5–7 segments on each side; pedicels 2–3 cm, with 2 bracteoles; calyx unequal, the external lobes ovate-lanceolate, the internal linear, disc 4- to 8-dentate . . . . . ***B. myriophylloides*** (Colombia: Arauca, Meta, Vichada; Venezuela: Apure)
4b. Leaves 6–8 leaves per node, 0.2–3.5 × 0.1–1.4 cm, with 5–20 segments on each side; pedicels 0.05–1.80 cm, ebracteate; calyx equal, disk 5- to 10-dentate . . . . . ***B. reflexa*** (Colombia: Casanare, Meta; Venezuela: Cojedes, Guárico, Portuguesa)
5a. Leaves linear, relatively thick and conduplicate-folded; calyx segments barely differentiated; pedicels 1.0–2.5(–3.5) mm long; flowers often in pairs in each axis, sometimes only 1; bractlets present. . . . . ***B. gratioloides*** (Venezuela: Guárico, Portuguesa)
5b. Leaves oblong-oblanceolate, obovate, lanceolate or broader, if narrower neither thick nor conduplicate-folded; calyx segments distinctly differentiated except in *B. callitrichoides* and some *B. repens* and *B. reptans*, flowers in fascicles of 4–8 or solitary; bractlets present or absent 6
6a. Pedicels < 1.5 mm long or absent 7
6b. Pedicels > 1.5 mm long. 11
7a. Inflorescences of 1 or 2 axillary flowers; calyx 3.5–7.0 mm long; corolla 3–5 mm long; stems glabrous. 8
7b. Inflorescences in fascicles of 1–8 flowers in leaf axils; calyx 1.5–3.0 mm long, corolla 1.5–3.0 mm long; stems hispid with conspicuous spreading trichomes. 9
8a. Leaves linear to narrowly oblanceolate, the margins entire or shallowly dentate, pedicels 0.2–1.5 mm . . . . . ***B. sessiliflora*** (Colombia: Meta; Venezuela: Apure, Guárico, Monagas)
8b. Leaves ovate to lanceolate, obovate-spathulate, the margins serrulate in the upper part; pedicels 5–15 mm 10
9a. Leaves 1–5 mm wide, narrowly oblong, margins entire or minutely denticulate; the outer lobes of the calyx ovate, punctate with sessile glands, the inner minutely ciliate; stigma convolute, crestlike . . . . . ***B. monnierioides*** (Colombia: Meta; Venezuela: Apure, Cojedes, Guárico, Portuguesa)
9b. Leaves 6–12 mm wide, narrowly lanceolate, margins obtusely serrate in the distal part, entire at the basal half; the outer lobes of the calyx broadly ovate, sometimes ciliate, glandular-punctate, the inner densely glandular-punctate; stigmas flattened . . . . . ***B. axillaris*** (Colombia: Meta; Venezuela: Guárico, Portuguesa)
10a. Plants dried brown in herbarium specimens; leaves ovate to lanceolate, apex acuminate, the midvein with 2 veins on each side; pedicels with bracteoles 2 . . . . . ***B. bacopoides*** (Guárico, Portuguesa)
10b. Plants dried black in herbarium specimens; leaves obovate-spathulate, apex obtuse, the midvein without 2 veins on each side; pedicels ebracteolate . . . . . ***B. valerii*** (Venezuela: Portuguesa)
11a. Bractlets present at the summit of the pedicel or attached to the base of the calyx 12
11b. Bractlets absent (or rudimentary in some *B. salzmannii* and *B. serpyllifolia*) 15
12a. Stems prostrate to decumbent or trailing. 13
12b. Stems erect or ascending. 14
13a. Leaves, lanceolate to oblong-lanceolate; 3–9 × 1–2 cm, margins obtusely serrate in the distal part, entire at the basal half; pedicels 1.8–3.6 cm long; calyx 8.5–13.5 mm long; stamens 5 . . . . . ***B. aquatica*** (Venezuela: Anzoátegui, Apure, Cojedes, Guárico)
13b. Leaves obovate, 0.5–2.0 × 0.1–0.8 cm, margins entire or minutely denticulate; pedicels 0.5–1.0(–3.5) cm long; calyx 4–7 mm long; stamens 4 . . . . . ***B. monnieri*** (Venezuela: Portuguesa)

Key to *Bacopa* Species of the Orinoquia Region cont.

Based on Holmgren and Vincent (2005); distribution outside Orinoquia not included.

14a. Stems 20–45 cm long, with a few short gland-tipped hairs near the apex; posterior calyx segment ovate, scrabrous at the margen; leaves opposite . . . . **B. laxiflora** (Colombia: Casanare, Meta; Venezuela: Apure, Guárico, Portuguesa)

14b. Stems 3–15 cm long, glabrous; posterior calyx segment (the largest one) lanceolate to broadly lanceolate; glabrous at the margen, leaves opposite to 4-whorled . . . . **B. reptans** (Colombia: Meta; Venezuela: northwestern Amazonas, Anzoátegui, Cojedes, Guárico, Portuguesa)

15a. Calyx 3.5–7.5 mm long, the posterior segment truncate-rounded to cordate at the base, becoming reticulate-venose; capsule firm-walled 16

15b. Calyx 1.2–4.2 mm long, the posterior segment broadly cuneate at the base, not strongly reticulate; capsule membranous-walled 19

16a. Stems appressed to ascending-pubescent or glabrous; outer calyx segments glabrous; pedicels 1.5–14.0 mm long. 17

16b. Stems spreading-pubescent; outer calyx segments pubescent; pedicels (4.5–)8.0–22.0 mm long 18

17a. Stems appressed to ascending-pubescent; pedicels 1.5–6.5 mm long; stamens 2(–4) . . . . **B. innominata** (Venezuela: Portuguesa)

17b. Stems glabrous; pedicels 7–14 mm; stamens 4; capsule elliptic-oblong . . . . **B. albida** (Colombia: Meta)

18a. Pubescence of the stems, pedicels, and calyx-segment margins of fine, yellowish hairs; corolla 3–6(–7) mm long, mostly concealed by the calyx; stems 5–20 cm long . . . . **B. salzmannii** (Colombia: Casanare, Meta; Venezuela: Apure, Cojedes, Guárico, Monagas, Portuguesa)

18b. Pubescence of the stems, pedicels, and calyx-segment margins of coarse, whitish, multicellular hairs; corolla 6–7 mm long, the limb exserted from the calyx; stems usually shorter, 3–6 cm long . . . . **B. serpyllifolia** (Venezuela: northwestern Amazonas)

19a. Leaves > 12 × 7 mm; calyx 2.7–4.2 mm long, usually consisting of 5 segments, 3 broad ones and 2 narrow ones, sometimes reduced to 4 with 1 slightly broader than the others; capsule 2.5–3.5 mm long . . . . **B. repens** (Venezuela: Barinas, Guárico, Portuguesa)

19b. Leaves < 7 × 5.5 mm; calyx 1.2–2.3 mm long, reduced to 4 segments, 1 slightly broader than the others; capsule 1.2–1.8 mm long. **B. callitrichoides** (Colombia: Vichada; Venezuela: Apure, Barinas, Guárico, Portuguesa)

Notes about the Orinoco "Llanos" Region and Its Eolic-Limose Plains

The broad lowland region that extends from northeastern Colombia to eastern Venezuela, occupying an area of ca. 532,000 km^2 (ca. 240,000 in Colombia and ca. 292,000 in Venezuela; Fig. 1), is known as "Los Llanos del Orinoco," or as "Orinoquia," particularly in Colombia (Minorta-Cely and Rangel-Ch., 2014); elsewhere, Orinoquia refers to the entire Orinoco River basin. The "Llanos" are regarded as the largest savanna area in northwestern South America, with rich sedimentary deposits of Quaternary origin (Huber et al., 2006; Schargel, 2015), and they are considered one of the most biodiverse regions in the Neotropics (Rangel-Ch., 2014, 2015; Aymard, 2015). This large region is a flat, almost uninterrupted expanse that gradually descends from the base of the Andes (250–500 m) in a west–east direction, ending on the left bank and the deltaic plain of the Orinoco River. The southwestern boundary of the Venezuelan llanos extends from the Arauca and Meta rivers in the direction of the Vichada and Guaviare basins, a region known as "Llanos Orientales Colombianos" (Cortés-Lombana, 1981). Nonetheless, recent evidence indicates that the Vichada and Guaviare watersheds contain a large belt of Amazonian vegetation rather than "Llanos" vegetation itself (Minorta-Cely et al., 2020).

Currently, the vegetation of "Los Llanos" is composed of a mosaic of savannas mixed with pastures, shrubby vegetation, gallery forests, an array of thorn dry forest communities, and a transition of dry semideciduous to evergreen forests highly transformed by human activity.

The eolic-limose plains located in Colombia and Venezuela Llanos are notable for their physical and biological characteristics and their ancestral inhabitants, and lately there has been particular interest in conserving their ecosystems (Rangel-Ch. et al., 2020). Moreover, these plains are recognized as having a fluvial network composed of several rivers (e.g., the Capanaparo, the Cinaruco, and the Cravo Norte) that are part of the Orinoco River basin. This large sector is characterized by numerous gallery forests and by its large and continuous area of dunes and savannas over oligotrophic soils (Schargel, 2007). Perhaps one the most peculiar features of these extensive plains is the presence of large, dense tree communities of *Caraipa llanorum* Cuatr., *C. savannarum* Kub. (Calophyllaceae, "Saladillo"), and *Leptolobium nitens* Vogel (Fabaceae, "Congrio"), the former called "Saladillales" and the latter "Congriales" (Aymard and Campbell, 2008; Montes et al., 2013). This region is important biologically because of its endemics elements, such as *Cuphea apurensis* Lourteig (Lythraceae) and *Xyris apureana* Kral & L.B. Sm. (Xyridaceae), and because it is the northwestern limit of distribution of many Amazonian taxa, such as *Leptobalanus wurdackii* (Prance) Sothers & Prance (Chrysobalanaceae), *Spathanthus unilateralis* (Rudge) Desv. (Rapateaceae), and *Salacia negrensis* Lombardi (Celastraceae) (Aymard, 2015, 2017).

Literature Cited

Abascal, K., and E. Yarnell. 2011. *Bacopa* for the brain (a smart addition to Western medicine). Alternative and Complementary Therapies 17(1): 21–25.

Aguiar, S., and T. Borowski. 2013. Neuropharmacological review of the nootropic herb *Bacopa monnieri*. Rejuvenation Research 16(4): 313–326.

Ahedor, A. R., and W. Elisens. 2015. Seed morphology and its taxonomic significance in the subtribe *Gratiolinae* (Plantaginaceae). Systematic Botany 40(3): 845–852.

Alain, H. L. 1968. Novitates Antillanae. III. Brittonia 20: 148–161.

Angiosperm Phylogeny Group (APG). 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1–20.

Aublet, J. B. C. F. 1775. *Bacopa*. Pages 128–130 in *Histoire des Plantes de la Guiana Françoise*. Vol. 1. Pierre François Didot Jeune, London and Paris.

Aymard, G. 2015. Bosques de los Llanos de Venezuela: Estructura, composición florística, diversidad y estado actual de conservación. Pages 241–268 in R. López-Falcón, J. M. Hétier,

D. López-H., R. Schargel, and A. Zinck, eds., *Tierras llaneras de Venezuela*. 2nd ed. IRD-CIDIAT, Mérida, Venezuela.

———. 2017. Adiciones a la flora vascular de los Llanos de Venezuela: Nuevos registros y estados taxonómicos. Biollania (Edic. Esp.) 15: 1–296.

Aymard, G., and L. Campbell. 2008. A new species of *Caraipa* Aublet (Clusiaceae) from the Venezuelan Andes and its biogeographical implications. Rodriguesia 59(2): 1–6.

Barker, W. R., G. L. Nesom, P. M. Beardsley, and N. S. Fraga. 2012. A taxonomic conspectus of Phrymaceae: A narrowed circumscription for *Mimulus*, new and resurrected genera, and new names and species. Phytoneuron (2012)39: 1–60.

Barringer, K. 2015. Scrophulariaceae. In B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora, eds. *Manual de Plantas de Costa Rica*. Vol. 8. Monographs in Systematic Botany from the Missouri Botanical Garden 131: 149–192.

Bentham, G. 1835. *Scrophularineae indicae*. J. Ridgeways and Sons, London.

———.1846. Scrophulariaceae. Pages 186–586 in A. P. Candolle, ed., *Prodromus systematis naturalis regni vegetabilis* 10. Victor Masson, Paris.

Bernal, R. 2020. *Bacopa*. In R. Bernal, S. R. Gradstein, and M. Celis, eds. *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (accessed May 31, 2020). http://catalogoplantasdecolombia.unal.edu.co

Borhidi, A., and O. Muñiz. 1975a. Combinationes novae florae Cubanae II. Botanikae Közlemények 62: 25–27.

———. 1975b [1976]. New plants in Cuba. IV. Acta Botanica Academiae Scientiarum Hungaricae 21: 221–230.

Cárdenas-López, D., H. Mendoza, M. F. González, and S. Sua. 2016. Flora de la cuenca del río Orinoco en Colombia: Grado de conocimiento, uso y conservación. Revista Colombia Amazónica 9: 93–146.

Chamisso, L. K. A., von. 1833. Scrofularineae. Linnaea 8: 17–30.

Christenhusz, M. J. M. 2014. Plantaginaceae. Pages 1–73 in G. Davidse, M. Sousa Sánchez, S. Knapp, and F. Chiang Cabrera, eds. *Flora Mesoamericana*. Vol. 5. Missouri Botanical Garden Press, St. Louis.

Cortés-Lombana, A. 1981. Capacidad de uso actual y futuro de las tierras de la Orinoquía Colombiana. Un enfoque ecológico. Boletín Sociedad Venezolana de Ciencias Naturales 139: 427–448.

Deschamp, P. A., and T. J. Cooke. 1983. Leaf dimorphism in aquatic angiosperms: Significance of turgor pressure and cell expansion. Science 219: 505–507.

Descole, H. R., and O. H. Borsini. 1954. Scrophulariaceae. In H. R. Descole, ed., *Genera et Species Plantarum Argentinarum* 5: 1–167.

Edwall, G. 1897. Flora Paulista II. Familias Solanaceae e Scrophulariaceae. Commissao Geographica e Geologica de Sao Paulo: Boletim 13: 149–210.

Endress, P. K. 2010. Disentangling confusions in inflorescence morphology: Patterns and diversity of reproductive shoot ramification in angiosperms. Journal of Systematics and Evolution 48: 225–239.

Fischer, E. 2004. Scrophulariaceae. Pages 333–388 in J. W. Kadereit, ed., *The Families and Genera of Vascular Plants*. Vol. 7. Springer-Verlag, New York.

Font-Quer, P. 2001. *Diccionario de Botánica*. Ediciones Península, Barcelona.

Gleason, H. A. 1929. The Tate collection from Mount Roraima and vicinity. Vol. 13 of *Studies on the Flora of Northern South America*. Bulletin of the Torrey Botanical Club 56(8): 391–408.

Harris, J. G., and M. W. Harris. 2001. *Plant Identification Terminology: An Illustrated Glossary*. 2nd ed. Spring Lake Publishing, Spring Lake, Utah.

Holmgren, N. H., and K. A. Vincent. 2005. Scrophulariaceae. Pages 144–167 in P. E. Berry, K. Yatskievych, and B. K. Holst, eds., *Rutaceae—Zygophyllaceae*. Vol. IX of *Flora of the Venezuelan Guayana*. Missouri Botanical Garden Press, St. Louis.

Huber, O., R. Duno de Stefano, G. Aymard, and R. Riina. 2006. Flora and vegetation of the Venezuelan Llanos: A review. Pages 95–120 in T. R. Pennington, G.P. Lewis, and J. A. Ratter, eds., *Neotropical Savannas and Seasonal Dry Forests: Plant Diversity, Biogeography, and Conservation*. Taylor & Francis, Boca Raton, Fla.

Ichaso, C. L. F., and G. M. Barroso. 1974. Uma nova Scrophulariaceae do Estado do Pará. Rodriguesia 27: 95.

IUCN. 2017. Guidelines for using the IUCN Red List Categories and Criteria. Version 12. Prepared by the Standards and Petitions Subcommittee (accessed May 2020). http://www.iucnredlist.org/documents/ RedList Guidelines.pdf

Koga H., Y. Doll, K. Hashimoto, K. Toyooka, and H. Tsukay. 2020. Dimorphic leaf development of the aquatic plant *Callitriche palustris* L. through differential cell division and expansion. Frontiers in Plant Science 11: 269. doi: 10.3389/fpls.2020.00269

Minorta-Cely, V., and J. O. Rangel-Ch. 2014. La riqueza y la diversidad de las plantas con flores de la Orinoquia colombiana. Pages 237–418 in J. O. Rangel-Ch., ed., *La región de la Orinoquia de Colombia*. Vol. 14 of *Colombia Diversidad Biótica*. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.

Minorta-Cely, V., J. O. Rangel-Ch., G. Aymard, and F. Castro-L. 2020. La vegetación en el territorio de las selvas transicionales de Cumaribo, Vichada (Colombia): Composición florística y principales aspectos estructurales. Pages 165–222 in J. O. Rangel-Ch., G. Andrade, C. Jarro, and G. Santos, eds., *Selvas transicionales de Cumaribo (Vichada—Colombia)*. Vol. 19 of *Colombia Diversidad Biótica*. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.

Montes, R., J. San José, and G. Aymard. 2013. Disposición espacial de las comunidades vegetales de la altiplanicie de mesa y planicie de explayamiento en el sistema hidrológico Aguaro-Guariquito, estado Guárico, Venezuela. Caldasia 35: 1–22.

Olmstead, R. G., C. W. Depamphilis, A. D. Wolfe, N. D. Young, W. J. Elisons, and P. A. Reeves. 2001. Disintegration of the Scrophulariaceae. American Journal of Botany 88: 348–361.

Oxelman, B., P. Kornhall, R. G. Olmstead, and B. Bremer. 2005. Further disintegration of Scrophulariaceae. Taxon 54(2): 411–425.

Pennell, F. W. 1919. Scrophulariaceae of the southeastern United States. Proceedings of the Academy of Natural Sciences of Philadelphia 71: 224–291.

———.1920. Scrophulariaceae of Colombia: I. Proceedings of the Academy of Natural Sciences of Philadelphia 72: 136–188.

———. 1935. The Scrophulariaceae of eastern temperate North America. Academy of Natural Sciences of Philadelphia Monographs 1: 1–650.

———. 1946. Reconsideration of the *Bacopa–Herpestis* problem of the Scrophulariaceae. Proceedings of the Academy of Natural Sciences of Philadelphia 98: 83–98.

———. 1953. Scrophulariaceae. In J. A. Steyermark, ed., *Botanical Exploration in Venezuela*. Vol. 3. Fieldiana (Botany) 28: 516–520.

Rangel-Ch., J. O. 2014. Ecosistemas de la Orinoquia Colombiana. Pages 807–847 in J. O. Rangel-Ch., ed., *La región de la Orinoquia de Colombia*.Vol. 14 of *Colombia Diversidad Biótica*. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.

———. 2015. La biodiversidad de Colombia: Significado y distribución regional. Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales 39(151): 176–200.

Rangel-Ch., J. O., G. Andrade, C. Jarro, and G. Santos, eds. 2020. *Territorio sabanas y humedales de Arauca, Colombia*. Vol. 20 of *Colombia Diversidad Biótica*. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.

Reddy E., S. R. 2019. *Bacopa monnieri*—A review. International Journal of Trends in Scientific Research and Development 3(2): 503–507.

Rossow, R. A. 1986. Notas sobre Scrophulariaceae II. Parodiana 4: 163–181.

Schargel, R. 2007. Geomorfología y suelos. Pages 15–31 in R. Duno de Stefano, G. Aymard, and O. Huber, eds., *Catálogo Anotado e Ilustrado de la Flora Vascular de los Llanos de Venezuela*. FUDENA–Fundación Polar–FIBV, Caracas.

———. 2015. Suelos llaneros: Geomorfología, distribución geográfica y caracterización. Pages 63–153 in R. López-F., J. M. Hétier, H. D. López., R. Schargel, and A. Zinck, eds., *Tierras llaneras de Venezuela*. IRD–CIDIAT, Mérida, Venezuela.

Schargel, R., and G. Aymard. 1992. Observaciones en suelos y vegetación en la planicie eólica-limosa del alto río Cinaruco. Distrito Muñoz, Estado Apure, Venezuela. Biollania 9: 119–147.

Sosa, M. M., P. Moroni, and N. O´Leary. 2018. A taxonomic revision of the genus *Bacopa* (*Gratioleae*, Plantaginaceae) in Argentina. Phytotaxa 336(1): 001–027.

Souza, V. C. 2001. Uma nova espécie de *Bacopa* Aubl. (Scrophulariaceae) da América do Sul. Acta Botânica Brasilica 15: 57–61.

———. 2012. Neotropical Plantaginaceae. In W. Milliken, B. Klitgäard, and A. Baracat, eds. (2009 onwards), Neotropikey—Interactive key and information resources for flowering plants of the Neotropics (accessed October 15, 2020). https://www.kew.org/science/tropamerica/neotropikey/families/Plantaginaceae.htm

Spencer C., H. Barrett, and John L. Strother. 1978. Taxonomy and natural history of *Bacopa* (Scrophulariaceae) in California. Systematic Botany 3(4): 408–419.

Sukumaran, N. P., A. Amalraj, and S. Gopi. 2019. Neuropharmacological and cognitive effects of *Bacopa monnieri* (L.) Wettst—A review on its mechanistic aspects. Complementary Therapies in Medicine 44: 68–82.

Tank, D. C., P. M. Beardsley, S. A. Kelchner, and R. S. Olmstead. 2006. Review of the systematics of Scrophulariaceae s.l. and their current disposition. L.A.S. Johnson Review No. 7. Australian Systematic Botany 19: 289–307.

Thiers, B. 2019 (continuously updated). Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium (accessed July 15, 2020). Available from: http://sweetgum.nybg.org/ih/

Ulloa Ulloa, C., P. Acevedo-Rodríguez, S. G. Beck, M. J. Belgrano, R. Bernal, P. E. Berry, L. Brako, M. Celis, G. Davidse, S. R. Gradstein, O. Hokche, B. León, S. León-Yánez, R. E. Magill, D. A. Neill, M. H. Nee, P. H. Raven, H. Stimmel, M. T. Strong, J. L. Villaseñor Ríos, J. L. Zarucchi, F. O. Zuloaga, and P. M. Jørgensen. 2018 (continuously updated). An integrated assessment of vascular plants species of the Americas (accessed May 10, 2020). http://legacy.tropicos.org/Project/VPA

Vera-Ospina, A., J. O. Rangel-Ch., y G. Aymard. 2020. Vegetación acuática del territorio sabanas y humedales de Arauca. Pages 359–385 in J. O. Rangel-Ch., G. Andrade, C. Jarro, and G. Santos, eds., *Territorio sabanas y humedales de Arauca, Colombia*. Vol. 20 of *Colombia Diversidad Biótica*. Universidad Nacional de Colombia, Instituto de Ciencias Naturales, Bogotá, Colombia.

von Wettstein, R. 1891. Scrophulariaceae. Pages 39–107 in A. Engler and K. Prantl, eds., *Die Natürlichen Pflanzenfamilien* IV, 3b. Wilhelm Engelmann, Leipzig.

Williams, L. O. 1950. New plants from Honduras. Ceiba 1(3): 163–164.

———. 1952. Plantae Centrali-Americanae, IV. Ceiba 3(2): 101–131.

Page 204 intentionally left blank.

BESLERIA NAQUENENSIS (BESLERIEAE, BESLERIACEAE), A NEW SPECIES FROM SERRANÍA DE NAQUÉN, GUIANÍA RIVER BASIN (COLOMBIA)

Gerardo A. Aymard C.,[1,2] Henry Arellano-P.,[1,3] Adela Lozano,[1] María C. Montilla,[1]
Albeiro Calero-Cayopare,[1] and Reinaldo A. Gómez-Yuvabe[4]

Abstract. *Besleria naquenensis* is described and illustrated on the basis of a collection from the understory of seasonally flooded forests drained by black waters located in the lower “Río (Caño) Naquén,” northwestern base of “Serranía de Naquén,” upper Guainía River basin, Guainía Department, Colombia, and its relationships with related species are discussed. This new species shares features with three species (*B. gibbosa*, *B. neblinae*, and *B. yatuana*) of section *Neobesleria* subsection *Axillares*. Morphologically, it is closest to *B. yatuana*, but it differs in its leaves, inflorescences, calyx, and corolla. In addition, habitat information, a distribution map, and data of its conservation status are included. An identification key of 27 species of *Besleria* found in the Rio Negro basin (Brazil, Colombia, and Venezuela) and adjacent regions is also provided. This new species elevates to 66 the number of *Besleria* taxa for the flora of Colombia, the country with the highest diversity of the genus.

Keywords: Guianía River basin, “Serranía de Naquén,” black water, seasonally flooded forests, *Besleria*, Gesneriaceae

Resumen. *Besleria naquenensis* se describe e ilustra a través de una colección en bosques estacionalmente inundables sobre aguas negras, situados en el río (caño) Naquén, noroeste de la base de la Serranía de Naquén, alto río Guianía, Departamento del Guianía, Colombia, y sus relaciones con las especies afines son discutidas. La nueva especie presenta similitudes morfológicas con tres especies (*B.* gibbosa, *B. neblinae y B. yatuana*) de la sección *Neobesleria* subsección *Axillares*. Sin embargo, está más relacionada con *B. yatuana*, de la cual difiere en sus hojas, inflorescencias, cáliz y corola. Se incluye información acerca de su hábitat, un mapa de distribución, datos del status de conservación, y una clave para la identificación de las 27 especies de *Besleria* presentes en la cuenca del río Negro (Brasil, Colombia y Venezuela) y regiones adyacentes. Esta nueva especie eleva actualmente en 66 el número de especies de *Besleria* para la flora de Colombia, el país con la mayor diversidad del género.

Palabras clave: Cuenca del río Guianía, Serranía de Naquén, aguas negras, bosques periódicamente inundables, *Besleria*, Gesneriaceae

Yaakuti iipenaa (Abstract in Kuripako). *Besleria naquenensis,* padana jnete pakajñeta linapjian nerikuda jnaja paniwampe jaikulima alape likuperi uni itajnai liko, aperi Naquén liko, noroeste de la base de la Serranía de Naquén, alto río Guianía, Departamento del Guianía, Colombia. Pakajñeta padeniri linakuapana jlieje *B. naquenensis* jnete kuameka napidzawaka jnaja likaishuperi. Jlieje waline jaiko wadepe pakuaka likapakana naine jnaja madalina jaiko (*B. gibbosa*, *B. neblinae y B. yatuana*) de la subsect. *Axillares*. Metsa, kadzu likapakana *B. yatuana* kametsa puadzalika jnaja lipje, liwi, jnete liwi idakipeda. Wakaite kuamekawaka litawiñawa, kuamekawaka jipai lipedzu litawiñakawa, jlinapjian, jnete papera inipu pajneshopa jnakani jnaja 27 nadzawaka *Besleria* aperi itawiña waja rio negro liko (Brasil, Colombia y Venezuela). Jlieje waline waaketaka jaiko 66 shupa namanupeka jnaja *Besleria* Colombia isruwa, katsa jipai isrukada pja manupena.

The genus *Besleria* Plumier *ex* Linnaeus (Gesneriaceae) currently includes 167 species (Ulloa Ulloa et al., 2018; Clark et al., 2020) of terrestrial, perennial herbs, suffrutexes, or shrubs with fibrous roots, growing in the understory of rainforests (Feuillet and Steyermark, 1999; Skog and Feuillet, 2008). It is rarely epiphytic (e.g., *B. macropoda* Donn Sm.) or small trees not taller than 7 m (e.g., *B. arborescens* C.V. Morton, *B. decipiens* C.V. Morton). The genus has a Neotropical distribution and ranges from southern Mexico (Chiapas, Oaxaca, Puebla, Tabasco, and Veracruz States) through Central America, the Caribbean, Colombia, Venezuela, Guianas, Ecuador, Peru, Brazil, and Bolivia (Morton, 1939; Ferreira et al., 2016; Ferreira, 2019).

Besleria is most diverse throughout the foothills to the high mountains of the Andes (Wiehler, 1975) and the Coastal Cordillera in Venezuela, where 57% (95) of the species are found growing in nutrient-rich soils. The remaining species appear to require more specific habitats, as is the case with the Amazon/Guayana lineage (e.g., *B. neblinae* Feuillet, *B. saxicola* C.V. Morton, *B. yatuana* Feuillet), which occurs in vegetation that grows on rocky slopes and oligotrophic soils derived from the Precambrian crystalline basement of the Guayana Shield and drained by black waters. Some taxa are found along the Pacific Coast of Colombia and Ecuador. Several species have wide geographic distributions (e.g., *B. aggregata* [Mart.] Hanst., *B. pauciflora* Benth., *B. solanoides* Kunth), whereas others are endemic to particular geographical areas, such as some species found only in Caribbean islands, or in Southeast Brazil (Ferreira et al., 2016).

We gratefully acknowledge the support provided by Compensation International Progress S.A.–Greenlife (Ciprogress–Greenlife) and the Kuripako indigenous alliance for our botanical expedition to the Cui(y)arí, Isana, and Naquén Rivers. The trip was sponsored by the Flor de Inírida REDD+ Project of the Guayana–Amazonian Transition Region, which made this undertaking possible. We also thank Germán Bernal Gutíérrez, Daniel S. Bernal Linares, Juan S. Bernal García, Martha Rivera, and Claudia Restrepo for logistic support, and Alírio Yavinape, Roberto Garrido, and Jahir Bedoya for their field assistance. We are indebted to the Kuripako people of the communities of Berrocal, San José del Guianía, and Manacal (Guianía River) for their help during different stages of the expedition. Finally, we thank Sylvia Mota de Oliveira (L) for her help finding literature, and Gustavo A. Romero-G. (AMES) for his help finding literature and his comments on early versions of this text. This work would not be possible without JSTOR Global Plants (https://plants.jstor.org/).

[1] Compensation International Progress S.A. Ciprogress–Greenlife, Bogotá, D.C., Colombia
[2] Corresponding author: gaymard@ciprogress.com
[3] Nuevo Estándar Biotropical NEBIOT SAS, Bogotá, D.C., Colombia
[4] Comunidad Kuripako Manacal, Río Guianía, Corregimiento departamental Puerto Colombia, departamento del Guianía, Colombia

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 205–214.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n8, Published online: 31 December 2020

Ethnobotanical information about *Besleria* in the lowlands is scarce. However, Lizot (1978) reported that in the Upper Orinoco River (Venezuela), the leaves of *B. laxiflora* Benth. are used by children and teenagers of the Yanomani nation as a tobacco substitute. This species is known in their language as "Tescho kënahekí" (hummingbird's tobacco).

Recent phylogenetic studies indicate that the genus is monophyletic and belongs in the also-monophyletic tribe *Beslerieae* Bartl. within subfamily Gesnerioideae Link (Perret et al., 2013; Weber et al., 2013). According to these authors, *Beslerieae* diverged about 30 million years ago within the Gesnerioideae. Moreover, diversification rates of Gesneriaceae have increased through time since the Early Miocene (25 Ma), a time frame coinciding with the evolution of hummingbird-adapted flowers and their arrival in South America (Serrano-Serrano et al., 2017).

Besleria is characterized by its mostly terrestrial habit, opposite leaves, stomata of the abaxial leaf surface well-spaced**,** axillary, pedunculate, or sessile inflorescences, bractless, campanulate or urceolate calyx, conspicuous, ventricose or subcampanulate succulent corollas, nectary in the majority of species evenly ring-shaped, superior ovary, and fleshy berries (Morton, 1939; Wiehler, 1975; Skog, 1978a).

Besleria was monographed worldwide by Morton (1939), who divided the genus into four sections (*Eubesleria* [Hanst.] Benth. & Hook., *Gasteranthus* [Benth.] Benth. & Hook. f., *Neobesleria* Morton, and *Rhynchobesleria* [Hanst.] Benth. & Hook.) and 18 subsections, recognizing 141 species and describing 43. Later, on the basis of vegetative and fruit features, Wiehler (1975) recognized *Gasteranthus* Benth., to which he also transferred five subsections of section *Neobesleria* (Skog and Kvist, 2000).

Molecular phylogenetic studies in *Besleria* have demonstrated that the four sections proposed by Morton (1939) were not monophyletic (Roalson and Clark, 2005; Clark et al., 2010). Therefore, the circumscription of many species of *Besleria* is still unclear, and the genus needs a detailed revision (Ferreira et al., 2016). Since C. V. Morton's contributions (Morton, 1939, 1944, 1968), 22 new species have been described (Steyermark, 1970; Skog, 1974, 1978a,b, 1982, 1987; Nowicke, 1974; Skog and Steyermark, 1991; González et al., 2001; Feuillet, 2008; Salinas, 2008; Ferreira, 2017, 2019; Ferreira et al., 2016; Cortés-C. et al., 2017; Sánchez-Taborda et al., 2020). The genus has been treated for Peru (Morton, 1968), *Flora of Panama* (Skog, 1978a), *Flora of the Venezuelan Guayana* (Feuillet and Steyermark, 1999), *Flora of the Guianas* (Skog and Feuillet, 2008), and *Manual de Plantas de Costa Rica* (Kribel, 2010). The present contribution increases to 66 the number of *Besleria* species known from Colombia, the country with the highest diversity of the genus. This new species was detected during fieldwork for forest studies being conducted in the upper Guianía River, Guianía Department, Colombia.

Materials and Methods

This work is based on morphological (using a dissecting stereomicroscope) and herbarium studies in COAH, COL, GH, NY, and PORT (herbarium codes after Thiers, 2019) of a specimen collected on a botanical expedition to the Río (Caño) Naquén in 2019, Guainía Department, Colombia. In addition, historical and current taxonomic literature on *Besleria* were examined, mainly the treatment of Gesneriaceae in *Flora of Venezuelan Guayana* (Feuillet and Steyermark, 1999), the original descriptions of *B. neblinae* Feuillet and *B. yatuana* Feuillet (Feuillet, 2008), and the checklists *Catálogo de plantas y líquenes de Colombia* (Clavijo et al., 2016) and *Catálogo de las plantas con flores de la Amazonia colombiana* (Infante-Betancour and Rangel-Ch., 2018). Type specimens of *Besleria* species involved in this study were examined using on-line images from JSTOR Global Plants (https://plants.jstor.org/). The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), Harris and Harris (2006), and Endress (2010).

Taxonomy

Besleria naquenensis Arellano-P. & Aymard. *sp. nov.* TYPE: COLOMBIA. Guainía: Corregimiento departamental Puerto Colombia. Sector noroeste de la base de la Serranía de Naquén, río (Caño) Naquén, bosques estacionalmente inundables sobre aguas negras, 2°42'04.5"N; 68°16'41.2"W, 100 m. 15 March 2019 (fl and fr), *Gerardo Aymard, Adela Lozano, María C. Montilla, Albeiro Calero Cayopare & Reinaldo A. Gómez Yuvabe 15087* (Holotype: COL; Isotypes: COAH, FMB). Fig. 1–2.

Besleria naquenensis is morphologically similar to *B. yatuana* Feuillet but differs in its larger ovate or elliptic to lanceolate-elliptic leaves, sparsely appressed-pubescent on both sides (denser in midrib abaxially), subtended by petioles 2.8–7.5 cm long, its 5–10-flowered inflorescence, 8- to 10-mm long pedicels, 3– 3.5 mm long calyx lobes, broadly lanceolate, appressed-pubescent outside, glabrous inside, and its 3.5- to 3.8-cm long corolla, glabrous outside.

Suffrutescent *herb*, 1.0–1.5 m tall, spreading branches. *Stem* terete, somewhat succulent, ca. 0.5 cm diam., appressed-pubescent, trichomes 5–10 mm long. *Leaves* dimorphic, opposite, membranaceous, appressed-pubescent on both sides, denser in midrib abaxially, trichomes ca. 1 mm long, margin serrulate; the uppermost pair equal, ovate, 10–12 × 4.0–5.5 mm, base slighty asymmetric, rounded, apex long acuminate, acumen ca. 15 mm long, 8–9 secondary veins on each side, petiole 8–10 mm long, appressed-pubescent. The innermost pairs mostly unequal; smaller leaves lanceolate-elliptic, ca. 17.8 × ca. 5.4 cm, base asymmetric, attenuate, apex long acuminate, acumen ca. 15 mm long, 11–12 secondary veins on each side, petiole 1.2–2.3 cm long, appressed-pubescent; larger leaves elliptic to lanceolate-elliptic, ca. 24.7 × ca. 7.8 cm, base asymmetric, attenuate, apex long acuminate, acumen ca. 15 mm long, 12–15 secondary veins on each side, petiole 2.8–7.5 cm long, appressed-pubescent. *Inflorescences* sessile or with short peduncle up to 2 mm long, appressed-pubescent, 5- to 10-flowered; pedicels 0.8–10.0 mm long, sparsely appressed-pubescent. *Flowers* with calyx sparsely appressed-pubescent, lobes free to base, broadly lanceolate, 3.0–3.5 × ca. 2.5 mm, attenuate at apex; *corolla* horizontal

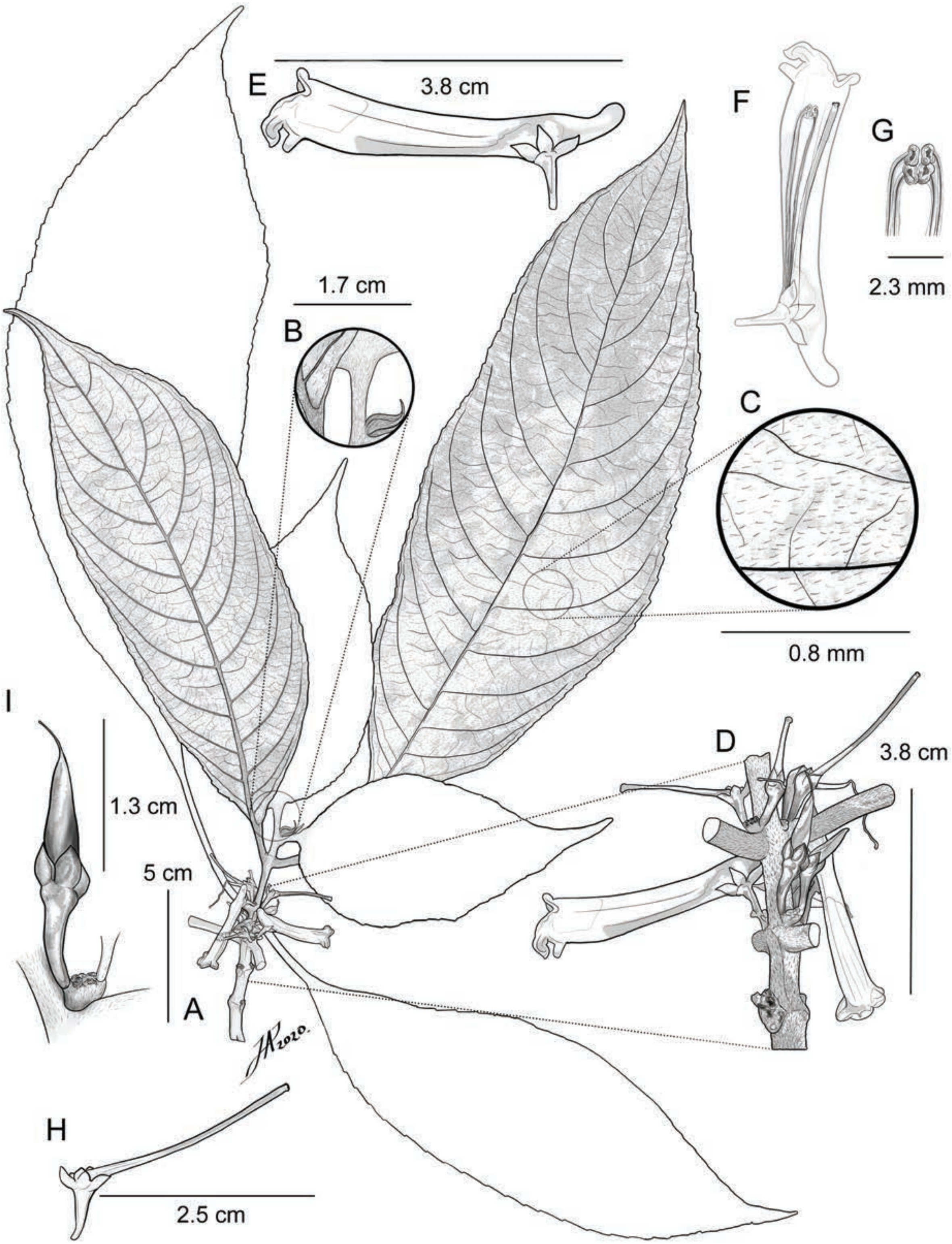


FIGURE 1. *Besleria naquenensis* Arellano-P. & Aymard. **A**, habit showing the unequal leaves and inflorescence; **B**, base of petiole and axillar bud; **C**, adaxial leaf surface showing the sparsely appressed pubescence; **D**, view of the inflorescence; **E**, calyx and corolla in lateral view; **F**, calyx and corolla showing the four stamens and the style and stigma; **G**, anthers view; **H**, calyx and style in lateral view; **I**, immature fruit.

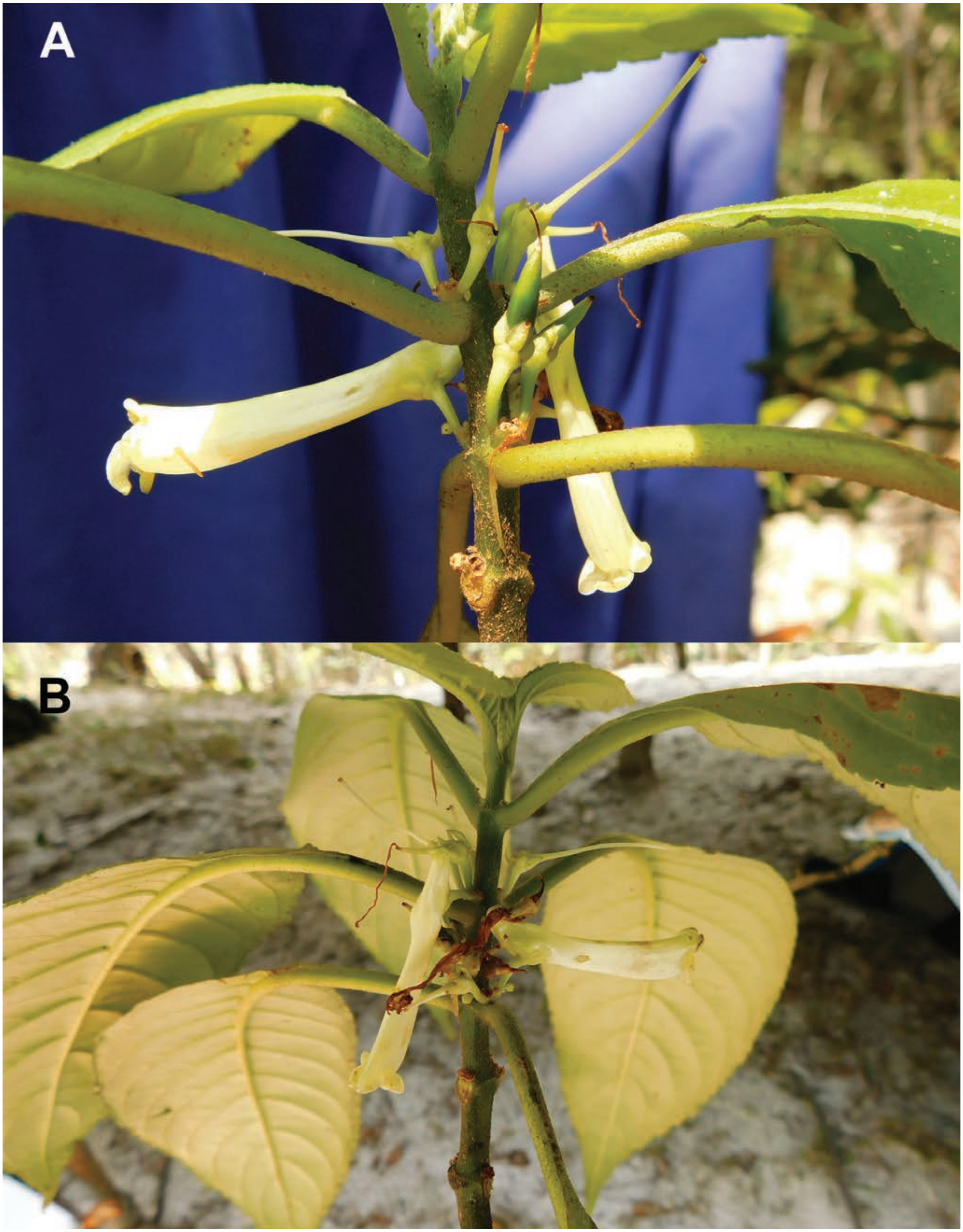


FIGURE 2. *Besleria naquenensis* Arellano-P. & Aymard. **A**, lateral views of the calyx and corolla and young fruits; **B**, flowering branch showing the glaucous leaves on the lower surface and lateral views of calyx and corolla. Based on *Aymard et al. 15087*. Photographs by María C. Montilla. ©Ciprogress Greenlife.

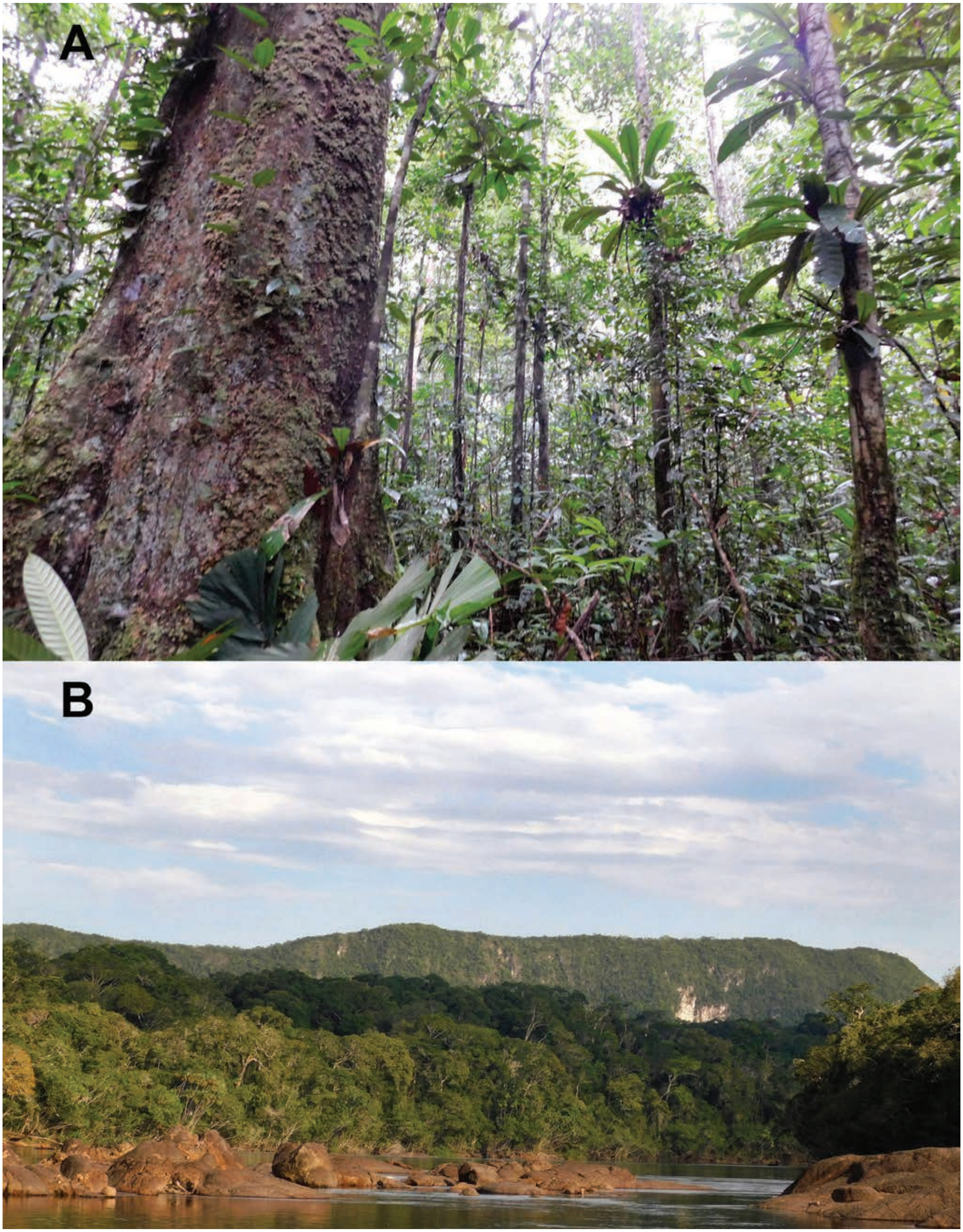


FIGURE 3. **A**, habitat of *Besleria naquenensis*—seasonally flooded forests on alluvial plains drained by black waters of the lower Río ("Caño") Naquén. Photograph by Adela Lozano. ©Ciprogress Greenlife; **B**, Río ("Caño") Naquén and a view of the "Serranía de Naquén." Photograph by María C. Montilla. ©Ciprogress Greenlife.

in the calyx, white, glabrous outside, prominently spurred, spur 5–6 × 4–5 mm, ovoid-oblong, rounded, protruding upward at an angle of ca. 25°; tube 3.5–3.8 × ca. 4 mm at the base and up to 1 cm at the mouth, lobes suborbicular, ca. 5 × ca. 2 mm; 4 stamens, ca. 2.3 cm long, anthers orbicular-reniform, dorsal glands fused into one, staminode not seen; *ovary* superior, ovoid, glabrous, ca. 2 mm long, style ca. 2.5 cm, glabrous. *Immature fruits* 1.0–1.3 cm, conical, glabrous.

Phenology: the type specimen with flowers and young fruits was collected in March (Fig. 2).

Etymology: *Besleria naquenensis* is named after "Serranía de Naquén," the type locality. The "Serranía de Naquén" or "Caparro" (also known as Naquén Mountains) is located in the southeastern portion of Guianía Department

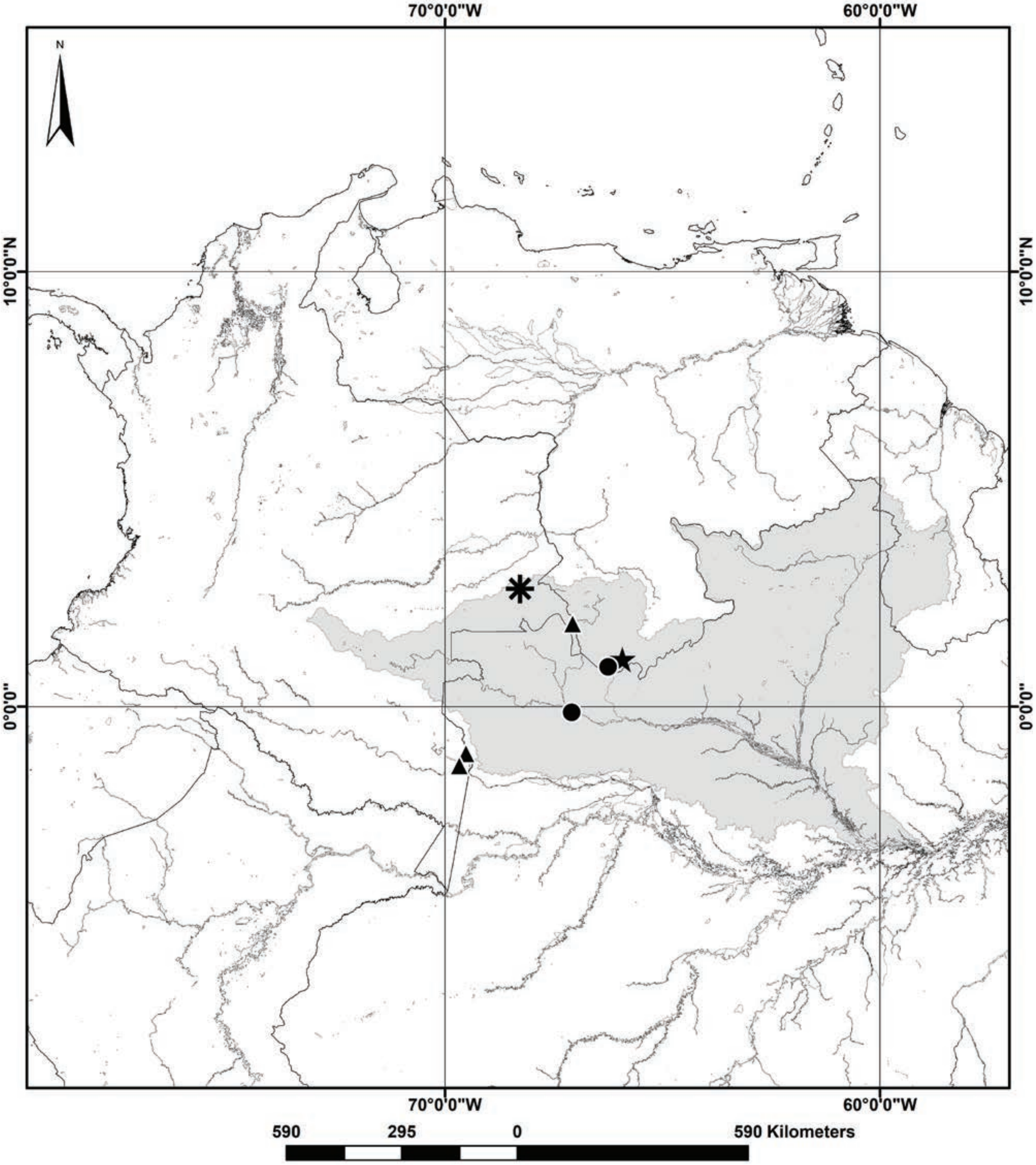


FIGURE 4. The Río Negro basin region of Brazil, Colombia, and Venezuela is outlined by gray shadow; symbols show geographical distribution of *Besleria* species belonging to subsection *Axillares* present in Rio Negro basin: *B. gibbosa* (Poepp.) Hanst. (▲), *B. naquenensis* Arellano-P. & Aymard (✱), *B. neblinae* Feuillet (●), and *B. yatuana* Feuillet (★).

along the border of northwestern Brazil and southern Colombia. It is ca. 70 km long (ca. 40 km in Colombia, the remaining portion in Brazil), 1–2 km wide. This Precambrian geological formation belongs to the Statherian basement that conforms the Mitú Complex (Bonilla et al., 2020). This metasedimentary sequence is associated with the Tunui Group in Brazil that was deposited around 1720–1600 Ma and extended north into the Naquén and Caranacoa Mountains (for a review see Bonilla et al., 2019, 2020). The Naquén area harbors several endemic species (e.g., *Steyerbromelia naquenensis* Betancur & Aguirre-Santoro, Bromeliaceae), and it forms part of the system of highlands of the Guayana Shield known as "tepuis." The tepuis are areas rich in numerous endemic species and unique habitats (Maguire, 1970; Riina et al., 2019).

Distribution and habitat: the species is known to occur only along small channels in the understory of seasonally flooded forests growing on oligotrophic and acid soils drained by black waters (Fig. 3A) in the type locality (Fig. 3B, 4). These plant communities are common in alluvial plains of the upper Rio Negro basin in Brazil, Colombia, and Venezuela. A recent phytosociological study (Arellano-Peña et al., in press) showed that *Besleria naquenensis* grows in forest associations that exhibit medium tree statures and densities, composed of trees with an average DBH greater than 10 cm. The species of these forests that presented a high physiognomic expression are: *Micrandra sprucei* (Müll. Arg.) R.E. Schult. (Euphorbiaceae), *Aspidosperma verruculosum* Müll. Arg. (Apocynaceae), *Henriquezia nitida* Spruce ex Benth. (Rubiaceae), *Caraipa longipedicellata* Steyerm. (Calophyllaceae), *Moronobea riparia* Planch. & Triana (Clusiaceae), *Parahancornia surrogata* Zarucchi (Apocynaceae), and *Pradosia schomburgkiana* (A. DC.) Cronquist (Sapotaceae).

Conservation status: according to IUCN criteria (IUCN, 2017), this species would be ranked as DD (data deficient), suggesting that future research may show that a threatened classification is appropriate. Currently, *Besleria naquenensis* is known only from the type collection, but we expect this species to have a wider distribution along seasonally flooded forests drained by black waters in the upper Rio Negro basin. This region copes with legal and illegal exploitation of minerals (mainly surface gold mining), as well as other economic activities that threaten the territorial rights of indigenous people and promote soil and habitat degradation and toxic contamination by heavy metals (e.g., mercury).

On the basis of its corolla with a spur at the base protruding from the tube at an angle of ca. 25° (Fig. 1) and its thickened, glabrous disk, *Besleria naquenensis* belongs in section *Neobesleria* C. V. Morton. Its sessile inflorescence, axillary pedicels, the corolla horizontal in the calyx, limb regular, not over 10 mm wide, and glabrous ovary place it in subsection *Axillares* C. V. Morton (Morton, 1939). This new species is morphologically similar to three others in subsection *Axillares* (Feuillet, 2008), that is, *B. gibbosa* (Poepp.) Hanst.,

TABLE 1. Comparison of diagnostic morphological characters of *Besleria* species in subsection *Axillares* present in the basin of the Rio Negro.

CHARACTER	*BESLERIA GIBBOSA*	*BESLERIA NAQUENENSIS*	*BESLERIA NEBLINAE*	*BESLERIA YATUANA*
Stems, petioles, and pedicels	Strigose	Appressed-pubescent	Densely villous with lax spreading trichomes	Appressed-pubescent
Leaves	Blade equal or subequal, broadly elliptic, 8–12 cm wide, sparsely strigose adaxially, the midrib and main veins abaxially densely strigose with patent white trichomes, apex acute to acuminate	Blade strongly unequal, ovate or elliptic to lanceolate-elliptic, 4.0–7.8 cm wide, sparsely appressed-pubescent on both sides (denser in midrib abaxially), apex long acuminate	Blade strongly unequal, lanceolate to elliptic, 3.0–5.5 cm wide, appressed-pubescent on both sides (denser and spreading on midrib and main veins on both sides), apex acute to acuminate	Blade strongly unequal, lanceolate to elliptic, 4–6 cm wide, glabrous on both sides, the midrib and main veins abaxially sparsely appressed–short pilose, apex long acuminate
Petioles on larger leaves	1.5–5.0 cm long	2.8–7.5 cm long	1.5–4.5 cm long	3–5 cm long
Inflorescence	3- to 6-flowered, pedicels 6–8 mm long, strigose	5- to 10-flowered, pedicels 8–10 mm long, appressed-pubescent	2-flowered, pedicels 3–5 mm long, densely villous	1- to 2-flowered; pedicels 3–6 mm long, appressed- pubescent
Calyx lobes	Free to base, ca. 4.5 mm long, ovate or ovate-lanceolate, glabrous or with few long trichomes outside, glabrous inside	Free to base, 3.0–3.5 mm long, broadly lanceolate, minutely appressed-pubescent outside glabrous inside	Connate, 5–6 mm long, lanceolate, hirsute on both sides	Free to base, 6–10 mm long, narrowly lanceolate, minutely appressed-pubescent on both sides
Corolla	2.4–3.0 cm long, pilosulous outside, spur acute at the apex	3.5–3.8 cm long, glabrous outside, spur rounded at the apex	2.5–3.5 cm long, puberulent outside, spur rounded at the apex	Ca. 2.5 cm long, sparsely to moderately pilose outside, spur rounded at the apex

B. neblinae, and *B. yatuana*, but it is most closely related to *B. yatuana* from the upper Rio Negro basin of Venezuela. Both species have stems, petioles, and pedicels appressed-pubescent; leaf blades strongly unequal, apex long acuminate and calyx lobes free to base. However, *B. naquenensis* differs from *B. yatuana* in the characters discussed in Table 1 and the key to the species represented here.

This new species for the flora of Colombia in an unexplored portion of the upper Guainía River is an incentive to continue vegetation studies in the region, an area unique in the Amazonian basin that deserves more research and conservation efforts.

Key to the Species of *Besleria* to Rio Negro Basin and Adjacent Regions into the Amazon Basin

(Modified from Feuillet and Steyermark, 1999; distribution outside Amazon basin and the Guianas not included)

1a. Inflorescence with a peduncle 0.5–7.0 cm long 2
1b. Inflorescence without a peduncle, or with short peduncle not longer than 3 mm 13
2a. Leaf blade with 16–18 primary veins; pendunce 3-branched at apex, pedicels borne throughout the length of the branches .... *B. minutiflora* (Brazil, Colombia, Peru)
2b. Leaf blade with 5–14 primary veins; penducle 1-branched at apex, pedicels being crowded near the apex 3
3a. Pedicels 4–6 mm long; calyx 2–3 mm long, the lobes suborbicular or oval; corolla white, 3–8 mm long .... *B. flavovirens* (Brazil, Colombia, Venezuela)
3b. Pedicels 6–35 mm long; calyx 3–15 mm long, the lobes linear-lanceolate, lanceolate, lanceolate-ovate, oblong, oblong-lanceolate, ovate, ovate-oblong or suborbicular (in *B. mucronata*); corolla yellow, orange, or red, 13–40 mm long 4
4a. Calyx lobes connate near base or in the middle of the tube, rarely free 5
4b. Calyx lobes always free, or nearly so 7
5a. Calyx lobes connate to middle of the tube, without a conspicuous mucro in the apex .... *B. patrisii* (Guianas)
5b. Calyx lobes connate near base of the tube, rarely free, with a conspicuous mucro in the apex 6
6a. Leaf blades lanceolate-elliptic, 11–13 × 4–5 cm, the midrib and lateral veins in the lower surface finely strigillose; the calyx lobes ca. 4 mm long, suborbicular, mucro arising below the apex; corolla 13–14 mm long .... *B. mucronata* (Brazil, Venezuela)
6b. Leaf blades elliptic or narrowly oblong, 15–21 × ca. 8.5 cm, the midrib and lateral veins in the lower surface slightly pubescent; calyx lobes 7–15 mm long, oblong-lanceolate, attenuate into a mucro, corolla 17–22 mm long .... *B. laxiflora* (Brazil, Colombia, Venezuela)
7a. Leaf blades subentire, inconspicuously shallowly serrulate or crenate at the margin; corolla yellow 8
7b. Leaf blades serrulate, serrate, minutely denticulate or sharply denticulate at the margin; corolla red or orange 9
8a. Stems, lower surface of the leaf blade, and petioles densely sericeous; calyx lobes unequal; corolla 35–40 mm long, spurred at base; ovary finely pilose .... *B. penduliflora* (Brazil?, Venezuela)
8b. Stems, lower surface of the leaf blade, and petioles densely hirsute, hirsute tomentose; calyx lobes equal; corolla 14–16 mm long, not spurred at base; ovary glabrous .... *B. trichiata* (Brazil, Peru)
9a. Leaf blade broadly elliptic; calyx lobes ovate or oblong 10
9b. Leaf blade elliptic or oblanceolate; calyx lobes linear, linear-lanceolate to subulate-attenuate 11
10a. Stem stout, hirsute; petioles 2–4 cm long; pedicels ca. 1 cm long; calyx lobes oblong, long white ciliate .... *B. barbata* (Colombia)
10b. Stem slender, glabrous; petioles 4–11 cm long; pedicels 2.0–3.5 cm long; calyx ovate, short brown ciliate .... *B. variabilis* (Colombia)
11a. Primary veins of the leaf blades 13–14, lobes of the calyx glabrous inside; corolla 12–15 mm long, glabrous outside; ovary glabrous .... *B. concinna* (Brazil, Venezuela)
11b. Primary veins of the leaf blades 8–11, lobes of the calyx hirsute inside; corolla 14–22 mm long, pilose outside; ovary pilose 12
12a. Leaf blades obliquely elliptic; calyx lobes hirsute inside; corolla equal size throughout the length .... *B. pauciflora* (Colombia, Peru)
12b. Leaf blades elliptic or oblanceolate; calyx lobes glabrous inside; corolla ventricose upwardly .... *B. sprucei* (Brazil, Colombia)
13a. Leaves of a pair equal to subequal, stem internodes straight 14
13b. Leaves of a pair unequal (at least the petiole), stem internodes at an angle to each other 27
14a. Stem and petioles densely hirsute or densely long villose 15
14b. Stem and petioles glabrescent, strigose, sericeous, hirsute, or with short pubescence 21
15a. Leaf blades elliptic or elliptic-oblong; lobes connate about 2/3 their length .... *B. insolita* (Brazil, French Guiana, Guyana)
15b. Leaf blades oblanceolate, elliptic-oblanceolate, oblong, lanceolate, elliptic-lanceolate to elliptic or narrowly elliptic; lobes free, nearly so or connate 1/3 their length (*B. iara*) 16
16a. Petioles 4–8 mm long; calyx lobes narrow-lanceolate, ovate lanceolate, lanceolate, or linear 17
16b. Petioles 10–45 mm; calyx lobes rounded, ovate, or linear-lanceolate 19
17a. Stem and petiole strigose; leaf blade ca. 10 × ca. 3.5 cm, margin entire; pedicels stout; lobes of calyx unequal, narrow-lanceolate or ovate lanceolate, densely pilose externally .... *B. inaequalis* (Colombia)
17b. Stem and petiole densely hirsute; leaf blade 12–19 × 4–7 cm, margin crenulate or lightly serrate, pedicels slender; lobes of calyx equal, lanceolate or linear hirsute, externally 18
18a. Margins of the leaves lightly serrate; calyx lobes 10–11 mm long, corolla ca. 13 mm long, slightly ventricose .... *B. immitis* (Colombia, Ecuador, Peru)
18b. Margins of the leaves minutely crenulate; calyx lobes ca. 4.5 mm long, lanceolate, corolla ca. 17 mm long, ventricose upwardly .... *B. leucostoma* (Colombia)
19a. Stems very densely long-villous; leaf blade elliptic-oblanceolate, petioles 5–15 mm long; calix ca. 4 mm long, the lobes rounded; corolla equal size throughout its length .... *B. villosa* (Colombia)
19b. Stems densely hirsute, with short hairs, leaf blade oblanceolate or oblong; petioles 1–4 cm long; calyx 10–14 mm long; lobes linear-lanceolate or ovate; corolla slightly ventricose 20

Key to the Species of *Besleria* to Rio Negro Basin and Adjacent Regions into the Amazon Basin cont.

(Modified from Feuillet and Steyermark, 1999; distribution outside Amazon basin and the Guianas not included)

20a. Leaf oblong, 15–19 × 5.5–6.4 cm, cuneate at the base, margins entire; calyx lobes linear-lanceolate; corolla orange to scarlet . . . . *B. aggregata* s. l. (Brazil, Colombia, Peru)

20b. Leaf oblanceolate, 18–30 × 7.3–11.4 cm, long-attenuate at the base, margins serrate; lobes of the calyx ovate; corolla yellow . . . . *B. iara* (Brazil, Peru)

21a. Leaf blade elliptic, broadly elliptic, elliptic-lanceolate, elliptic to oblanceolate or obovate, lateral veins of the leaf blade 5–9 on each side of the midrib, margin entire, minutely denticulate toward apex 22

21b. Leaf blade narrowly oblong or obliquely elliptic, lateral veins of the blade leaf 10–15 on each side of the midrib, margin serrate toward apex 26

22a. Leaf blade broadly elliptic or elliptic to lanceolate; pedicels 2–10 mm long 23

22b. Leaf blades narrow elliptic or elliptic to oblanceolate; pedicels 12–25 mm long. 25

23a. Stem hirsute throughout the length; lobes of the calyx oblong, long white ciliate; corolla orange or red . . . . *B. barbata* (Colombia)

23b. Stem strigose or pubescent near apex; lobes of the calyx lanceolate to ovate or ovate-oblong, short brown ciliate; corolla white, greenish white to yellow 24

24a. Leaf blades broadly elliptic, thin membranous calyx lobes free, ovate-oblong; corolla white. . . . . . *B. gibbosa* (Brazil, Colombia, Venezuela)

24b. Leaf blades elliptic to lanceolate, subcoriaceous to papyraceous when dry; calyx lobes connate 1/4 to 1/3 their length, lanceolate to ovate; corolla greenish white to yellow . . . . *B. parviflora* (Brazil, Venezuela)

25a. Leaf blades narrow elliptic; inflorescence fasciculate; calyx lobes green, oblong; corolla 13–15 mm long . . . .*B. solanoides* (Colombia)

25b. Leaf blades elliptic to oblanceolate, sometimes falcate; inflorescence in congested cymes; calyx lobes white or bluish, rounded; corolla 5–7 mm long . . . . *B. stricta* (Colombia)

26a. Leaf blade narrowly oblong, 12–22 × 5–7 cm; lobes of the calyx connate in the middle; corolla 3–6 mm long . . . .*B. flavovirens* (Brazil, Colombia, Venezuela)

26b. Leaf blade obliquely elliptic, 20–30 × 7–13 cm; lobes of the calyx free; corolla 12–20 mm long . . . . *B. saxicola* (Guyana)

27a. Calyx, pedicels, petioles, and stems either sparsely strigose or appressed-pubescent 28

27b. Calyx, pedicels, petioles, and stems densely villous with lax spreading hairs 30

28a. Stems, petioles, and pedicels sparsely strigose; leaf blades with apex acute to acuminate; calyx lobes ovate or ovate-lanceolate . . . . *B. gibbosa* (Brazil, Colombia, Venezuela)

28b. Stems, petioles, and pedicels appressed-pubescent; leaf blades with apex long acuminate; calyx lobes narrowly lanceolate or broadly lanceolate 29

29a. Leaves lanceolate to elliptic, glabrous on both sides, the midrib . . . . .abaxially with sparse, appressed, short hairs, petioles on larger leaves 3–5 cm long; inflorescence 1- to 2-flowered; pedicels 3–6 mm long; calyx lobes 6-10 mm long, narrowly lanceolate, minutely appressed-pubescent in both sides; corolla ca. 2.5 cm long, sparsely to moderately pilose outside . . . .*B. yatuana* (Colombia, Venezuela)

29b. Leaves ovate or elliptic to lanceolate-elliptic, with sparse, appressed hairs on both sides (denser in midrib abaxially), petioles on larger leaves 2.8–7.5 cm long; inflorescence 5- to 10-flowered, pedicels 8–10 mm long; calyx lobes 3.0–3.5 long, broadly lanceolate, with appressed pubescence outside, glabrous inside, corolla 3.5–3.8 cm long, glabrous outside . . . . *B. naquenensis* (Colombia)

30a. Large leaf blade 3.0–5.5 cm wide, lanceolate to elliptic, base acute to obtuse, occasionally nearly rounded, apex acute to acuminate, margins ciliate, with lax spreading hairs; calyx tube 1.5 mm long; corolla white, spurred, ovary glabrous . . . . *B. neblinae* (Brazil, Venezuela)

30b. Large leaf blade 3.0–5.5 cm wide, 6–7 cm wide, base narrowly cuneate, apex attenuate, margin not ciliate; calyx lobes free to base; corolla red, not spurred, ovary pilose . . . . *B. immitis* (Colombia, Ecuador, Peru)

Literature Cited

Arellano-Peña H., D. Cárdenas-López, J. Stropp, N. Castaño, G. Romero-González, F. Castro-Lima, A. Lozano, M. C. Montilla, H. ter Steege, and G. A. Aymard Corredor. (In press). The forests of the Rio Negro basin in the north-western Amazon: A phytosociological classification. In O. Huber and A. Zinck, eds. *Psammic Peinobiomes of the Upper Orinoco and Rio Negro Basins in Southern Venezuela*. Springer-Verlag, Berlin, Germany.

Bonilla, A., T. Cramer, M. Poujol, H. Cano, J. F. Franco, and Z. Amaya. 2019. Petrografía, geoquímica y geocronología U/Pb en circones de rocas ígneas y metamórficas a lo largo del Río Cuiarí en el sur del Departamento de Guainía, Colombia. Boletín de Geología 41(1): 55–84.

Bonilla, A., J. A. Franco, T. Cramera, M. Poujol, N. Cogné, S. Nachtergaele, and J. De Grave. 2020. Apatite LA-ICP-MS U–Pb and fission-track geochronology of the Caño Viejita gabbro in E-Colombia: Evidence for Grenvillian intraplate rifting and Jurassic exhumation in the NW Amazonian Craton. Journal of South American Earth Sciences 98. https://doi.org/10.1016/j.jsames.2019.102438.

Clark, J. L., D. A. Neill, A. Weber, J. A. Gruhn, and T. Katan. 2010. *Shuaria* (Gesneriaceae), an arborescent new genus from the Cordillera del Cóndor and Amazonian Ecuador. Systematic Botany 35: 662–674.

Clark, J. L., L. E. Skog, J. K. Boggan, and S. Ginzbarg. 2020. Index to names of New World members of the Gesneriaceae (Subfamilies Sanangoideae and Gesnerioideae). Rheedea 30: 190–256. https://doi.org/10.22244/rheedea.2020.30.01.14.

Clavijo, L., L. E. Skog, and J. L. Clark. 2016 (continuously updated). Gesneriaceae. Pages 1356–1387 in R. Bernal, S. R. Gradstein, and M. Celis, eds., *Catálogo de plantas y líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (accessed October 7, 2020). Available at www.catalogoplantasdecolombia.unal.edu.co.

Cortés-C., O. L., A. Giraldo-R., and A. M. Torres-G. 2017. Two new species of *Besleria* (Gesneriaceae) from the department of Valle del Cauca, Colombia. Phytotaxa 332(2): 181–188.

Endress, P. K. 2010. Disentangling confusions in inflorescence morphology: Patterns and diversity of reproductive shoot ramification in angiosperms. Journal of Systematics and Evolution 48: 225–239.

Ferreira, G. E. 2017. A new species of *Besleria* (Gesneriaceae) from the western Amazon rainforest. Brittonia 69(2): 241–245.

———. 2019. A new species and two new records of *Besleria* (Gesneriaceae) from Brazil. Systematic Botany 44(4): 887–892.

Ferreira, G. E., I. G. Costa, A. O. de Araújo, M. G. Hopkins, and A. Chautems. 2016. Three new species of *Besleria* (Gesneriaceae) from southeastern Brazilian Atlantic rainforest. Phytotaxa 263(3): 270–278.

Feuillet, C. 2008. Folia Taxonomica 6. Two new species of *Besleria* (Gesneriaceae) from the Venezuelan Guayana. Journal of the Botanical Research Institute of Texas 2(1): 269–273.

Feuillet, C., and J. A. Steyermark. 1999. Gesneriaceae. Pages 542–573 in J. A. Steyermark, P. E. Berry, and K. Yatskievych, eds., *Flora of the Venezuelan Guayana*. Vol. 5. Missouri Botanical Garden Press, St. Louis.

Font-Quer, P. 2001. *Diccionario de Botánica*. Ediciones Península, Barcelona.

González, C. E., L. E. Skog, and M. Amaya-Márquez. 2001. Una nueva especie de *Besleria* (Gesneriaceae) para Colombia. Caldasia 23(2): 401–404.

Harris, J. G., and M. W. Harris. 2006. *Plant Identification Terminology: An Illustrated Glossary*. Spring Lake Publishing, Spring Lake, Utah.

Infante-Betancour, J., and J. O. Rangel-Ch. 2018. Catálogo de las plantas con flores de la Amazonía colombiana. Pages 171–1008 in O. J. Rangel-Ch., ed., *La Riqueza Vegetal de la Amazonía de Colombia*. Fundación Natura, Bogotá, Colombia.

IUCN. 2017. Guidelines for using the IUCN Red List Categories and Criteria. Version 12. Prepared by the Standards and Petitions Subcommittee (accessed August 25, 2020). Available at http://www.iucnredlist.org/documents/ RedList Guidelines.pdf.

Kriebel-H., R. 2010. Gesneriaceae. In B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora, eds., *Manual de Plantas de Costa Rica*. Vol. 5. Monographs in Systematic Botany from the Missouri Botanical Garden 119: 844–939.

Lizot, J. 1978. Connaissance et usages del plantes sauvages chez les Yanomami. Pages 129–171 in E. Wagner and A. Zucchi, eds., *Unidad y Variedad (Ensayos Antropológicos en Homenaje J. M. Cruxent)*. Departamento de Antropología, Instituto Venezolano de Investigaciones Científicas (IVIC), Caracas, Venezuela.

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

Morton, C. V. 1939. A revision of *Besleria*. Contributions from the United States National Herbarium 26(9): 395–474.

———. 1944. New species of *Besleria* (Gesneriaceae). Contributions from the United States National Herbarium 29(1): 19–31.

———. 1968. The Peruvian species of *Besleria* (Gesneriaceae). Contributions from the United States National Herbarium 38(4): 125–151.

Nowicke, J. W. 1974. Two new species of *Besleria* (Gesneriaceae) from Panama. Brittonia 26(1): 37–41.

Perret, M., A. Chautems, A. O. Araujo, and N. Salamin. 2013. Temporal and spatial origin of Gesneriaceae in the New World inferred from plastid DNA sequences. Botanical Journal of the Linnean Society 171: 61–79.

Riina, R, P. E. Berry, O. Huber, and F. A. Michelangeli. 2019. Pantepui plant diversity and biogeography. Pages 121–147 in V. Rull, T. Vegas-Vilarrúbia T., O. Huber, and J. Señaris, eds., *Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands*. Academic Press, Cambridge.

Roalson, E. H., and J. L. Clark. 2005. Phylogenetic patterns of diversification in the *Beslerieae* (Gesneriaceae). Pages 251–268 in A. K. Sharma and A. Sharma, eds., *Phanerogams*. Vol. 2, Part C of *Plant Genome: Biodiversity and Evolution*. Science Publishers, Enfield, N.H.

Salinas, I. 2008. *Besleria beltranii* (Gesneriaceae), a new species from Peru. Novon 18(2): 244–246.

Sánchez-Taborda, J. A., A. Zuluaga, and L. Clavijo. 2020. A new species of *Besleria* (Gesneriaceae) from the Serranía El Pinche (Cauca), southwestern Colombia. PhytoKeys 162: 71–80.

Serrano-Serrano, M. L., J. Rolland, J. L. Clark, N. Salamin, and M. Perret. 2017. Hummingbird pollination and the diversification of angiosperms: An old and successful association in Gesneriaceae. Proceedings of the Royal Society B: Biological Sciences 284(1852): 20162816. http://dx.doi.org/10.1098/rspb.2016.2816.

Skog, L. E. 1974. A new Colombian species of *Besleria* (Gesneriaceae). Phytologia 27(6): 502–503.

———. 1978a. *Besleria* (Gesneriaceae). In *Flora of Panama*. Annals of the Missouri Botanical Garden 65(3): 802–821.

———. 1978b. New Panamanian species of Gesneriaceae. Brittonia 30(3): 319–326.

———. 1982. New Gesneriaceae from Peru and Ecuador. Selbyana 7(1): 94–99.

———. 1987. New species of Gesneriaceae from tropical America. Opera Botanica 92: 231–233.

Skog, L. E., and C. Feuillet. 2008. Gesneriaceae (Fascicle 26). Pages 1–126 in M. Jansen-Jacobs, ed., *Phanerogams*. Series A of *Flora of the Guianas*. Royal Botanic Gardens, Kew, U.K.

Skog, L. E., and L. P. Kvist. 2000. Revision of *Gasteranthus* (Gesneriaceae). Systematic Botany Monographs 59: 1–118.

Skog, L. E., and J. A. Steyermark. 1991. Novae Gesneriaceae Neotropicarum III. Additional new species from Venezuela. Novon 1(4): 211–222.

Steyermark, J. A. 1970. A new species of *Besleria* (Gesneriaceae) from Venezuela. Brittonia 22(4): 303–304.

Thiers, B. 2019 (continuously updated). *Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium* (accessed August 15, 2020). Available from: http://sweetgum.nybg.org/ih/.

Ulloa Ulloa, C., P. Acevedo-Rodríguez, S. G. Beck, M. J. Belgrano, R. Bernal, P. E. Berry, L. Brako, M. Celis, G. Davidse, S. R. Gradstein, O. Hokche, B. León, S. León-Yánez, R. E. Magill, D. A. Neill, M. H. Nee, P. H. Raven, H. Stimmel, M. T. Strong, J. L. Villaseñor **Ríos, J. L.** Zarucchi, F. O. Zuloaga, and P. M. Jørgensen. 2018 (continuously updated). An integrated assessment of vascular plants species of the Americas (accessed October 10, 2020). http://legacy.tropicos.org/Project/VPA.

Weber, A., J. Clark. and M. Möller. 2013. A new formal classification of Gesneriaceae. Selbyana 31: 68–94.

Wiehler, H. 1975. *Besleria* L. and the re-establisnment of *Gasteranthus* Benth. (Gesneriaceae). Selbyana 1: 150–156.

A NEW *LEPANTHES* (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM PENÍNSULA DE OSA, PUNTARENAS, COSTA RICA

Isler F. Chinchilla,[1–3] Reinaldo Aguilar,[4] and Diego Bogarín[1,5,6]

Abstract. *Lepanthes* is one of the most species-rich genera of orchids in the Neotropics, with most of the species found in medium to high elevation forests and few species in lowlands. We describe and illustrate *Lepanthes osaensis*, a new species from the very wet lowland forest of Península de Osa, Costa Rica. It is similar to *Lepanthes cuspidata* but differs mostly in the vinous leaves; smaller sepals; the narrower, bilobed petals; and the smaller lip with triangular blades. Notes on its distribution, habitat, flowering, and conservation status, as well as discussion of a taxon with similar morphology, are provided.

Keywords: *Lepanthes cuspidata*, orchid endemism, Pleurothallidinae taxonomy, twig epiphytes, very wet lowland forest

Lepanthes Sw. is one of the most species-rich genera of Pleurothallidinae (Orchidaceae), with over 1200 species from southern Mexico and the Antilles to Bolivia and northern Brazil (Pridgeon, 2005; Luer and Thoerle, 2012; Vieira-Uribe and Moreno, 2019; Bogarín et al., 2020). *Lepanthes* comprises plants with ramicauls enclosed by several infundibular sheaths, named "lepanthiform sheaths," racemose inflorescences of successive flowers, subsimilar, glabrous sepals, petals wider than long, frequently bilobed with divergent lobes, the lip usually trilobed with the lateral lobes surrounding the column, and the midlobe minute, modified as an appendix, connate at the base of the column (Luer, 2003; Pridgeon, 2005). In Central America, Costa Rica harbors the highest species diversity of *Lepanthes* with 153 spp., followed by Panama with 61 spp. (Luer, 2003; Bogarín et al., 2020). In Costa Rica, about 77% of the species inhabit cloud, premontane, and montane forests between 1000 and 2500 m, whereas only 23% of *Lepanthes* species inhabit forests lower than 1000 m (Luer, 2003; Bogarín and Kisel, 2014; Bogarín et al., 2020). In addition, only four species have been found at lower than 100 m elevation: *Lepanthes confusa* Ames & C. Schweinf., *L. crucitasensis* Chinchilla, M. Cedeño & Bogarín, and *L. truncata* Luer & Dressler, from the Caribbean plains; and only one species from the southern Pacific lowlands, *L. glicensteinii* Luer, from Refugio Nacional de Vida Silvestre Golfito (Luer, 2003; Bogarín et al., 2020).

Recently, two new species of *Lepanthes* were described from the Caribbean of Costa Rica, one occurring in the lowlands (Bogarín et al., 2020). The extremely low diversity of *Lepanthes* (and members of the Pleurothallidinae) in the Pacific lowlands of Costa Rica is not an artifact of undercollecting, as demonstrated by comprehensive orchid inventories in the region (Pupulin, 1998; Weber et al., 2001; Jiménez and Grayum, 2002; Bogarín and Pupulin, 2007; Rakosy et al., 2013) and the continued long-term fieldwork by the second author (RA). A possible explanation is the marked seasonality between dry and wet seasons from the north toward the central Pacific, contrasting with the prevailing wet conditions in the Caribbean throughout the year (Kohlmann et al., 2002). The most suitable areas for lowland *Lepanthes* in the Pacific are the tropical wet forests from Carara in the central Pacific to Península de Osa and Burica. However, curiously, in very wet lowland forests at the Península de Osa (a region adjacent to Golfito), no *Lepanthes* species has previously been recorded. Nonetheless, this region potentially habored *Lepanthes* species because of its very humid forests (Luer, 2003).

The Costa Rican lowland humid forests of the southern Pacific continuously reveal new plant species. Most of these new species have been described from Península de Osa: *Chrysophyllum moralesianum* Aguilar, D. Santam. & J.M. Chaves, *Chrysophyllum sierpense* Aguilar, D. Santam. & J.M. Chaves (Sapotaceae), *Epidendrum zunigae* Hágsater, Karremans & Bogarín (Orchidaceae), *Hirtella crusa* Aguilar & D. Santam. (Chrysobalanaceae), *Pentagonia osapinnata* Aguilar, N. Zamora & Hammel (Rubiaceae; it is the first species reported from this family that has opposite, pinnately compound leaves), *Peperomia sierpeana* Callejas (Piperaceae), *Protium aguilarii* D. Santam. (Burseraceae), *Sterculia allenii* E.L. Taylor ex Al. Rodr. & D. Santam. (Malvaceae), *Virola chrysocarpa* D. Santam. & Aguilar (Myristicaceae), among others, demonstrating the need for floristic studies in the region (Bogarín et al., 2008; Hammel, 2015; Santamaría-Aguilar et al., 2016, 2019; Santamaría-Aguilar and Lagomarsino, 2017; Santamaría-Aguilar and Aguilar Fernández, 2017; Callejas Posada, 2020; Rodríguez

---

We thank the Vice-Rectory for Research of the University of Costa Rica for support through research project 814-B6-140. Also, we thank the Ministerio de Ambiente y Energía (MINAE) and Sistema Nacional de Áreas de Conservación (SINAC) of Costa Rica for issuing the scientific permit, SINAC-SE-GASP-PI- R-019-2015. Thanks to D. Santamaría for his support in the field.

[1] Jardín Botánico Lankester, Universidad de Costa Rica, P.O. Box 302-7050, Cartago, Costa Rica
[2] Herbario Luis Fournier Origgi, Universidad de Costa Rica, Apdo. 11501-2060, San José, Costa Rica
[3] Corresponding author: isler.chinchilla@ucr.ac.cr
[4] Los Charcos de Osa, Centro de Diversidad de Plantas Regionales, Osa, Puntarenas, Costa Rica
[5] Herbario UCH, Universidad Autónoma de Chiriquí, David, Panama
[6] Naturalis Biodiversity Center, Endless Forms group, P.O. Box 9517, 2300 RA Leiden, The Netherlands

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 215–219.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n9, Published online: 31 December 2020

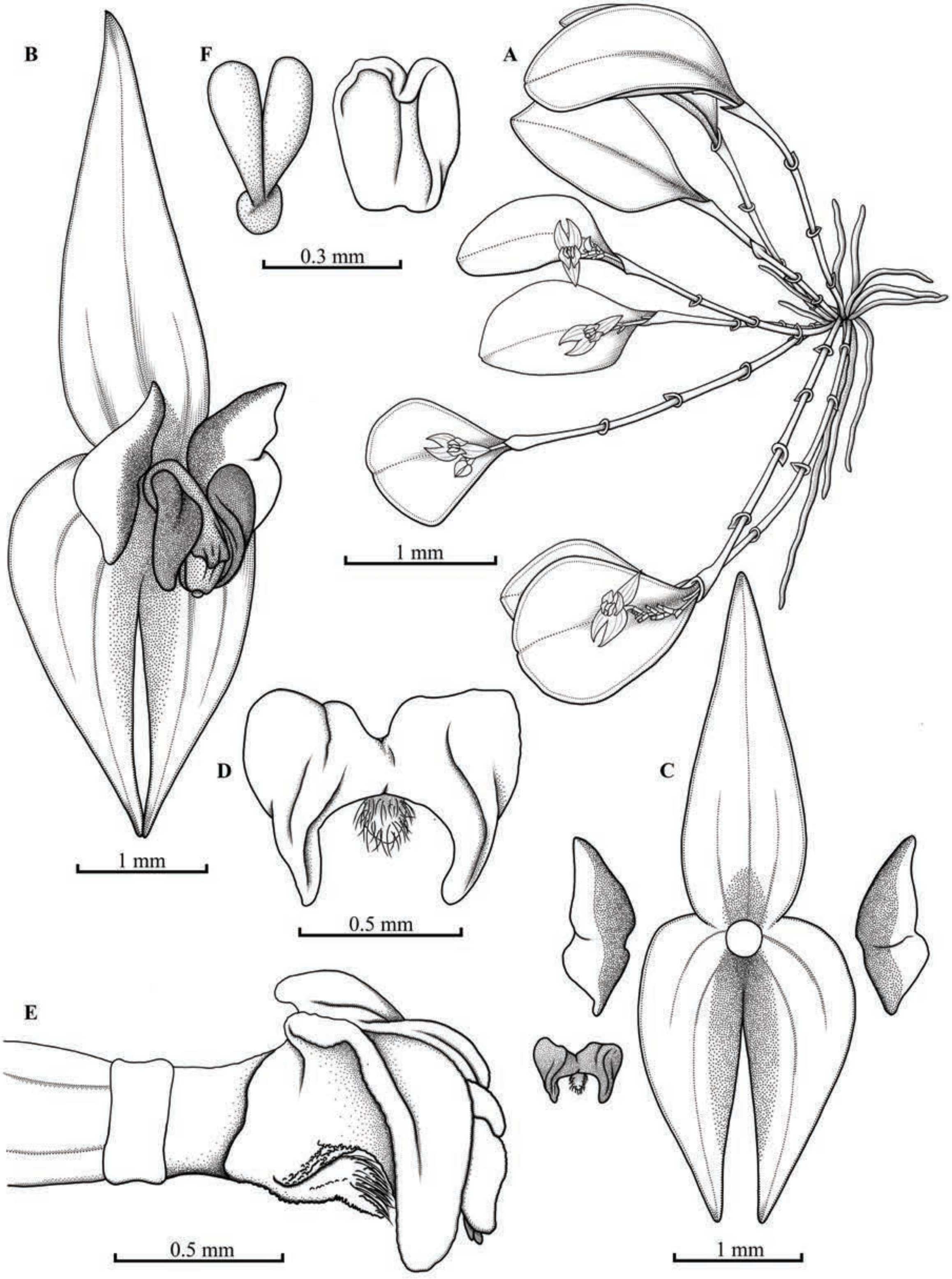


FIGURE 1. **A–F**. *Lepanthes osaensis* Chinchilla, Aguilar and Bogarín. **A**, habit; **B**, flower in natural position; **C**, dissected perianth, flattened; **D**, lip spread, adaxial view; **E**, lip, ovary, and column, lateral view; **F**, pollinarium (left) and anther cap (right). Prepared by I. F. Chinchilla and D. Bogarín from the holotype.

and Santamaría-Aguilar, 2020). In addition, some of these plant species could inhabit areas highly vulnerable to habitat fragmentation and loss (Karremans and Lehmann, 2018; Bogarín, et al., 2020). To update the inventory of the lowland orchid species of Costa Rica, we propose a new species of *Lepanthes* as a result of the extensive fieldwork in the area. This species is the first record of the genus in Península de Osa.

Materials and Methods

This study was based on field collections in Península de Osa in southern Costa Rica. Living plants were documented with photographs and sketches using a Nikon® D7100, and a Leica® MZ 9.5 stereomicroscope with a drawing tube at Jardín Botánico Lankester, Universidad de Costa Rica. The sketches were digitalized and diagrammed in a composite plate using Adobe Photoshop CS6® and digitally inked with the aid of an Apple Pencil® in Procreate application for iPad Pro® tablet (Apple Inc.). Phenological data were recorded in the field and in cultivation. Georeferences were obtained using a Garmin eTrex Vista GPS. We prepared a map based on a satellite image of the year 2000 from NASA's Jet Propulsion Laboratory, National Imagery and Mapping Agency of the United States. We examined specimens and types at the following herbaria: CR, JBL, K, MO, SEL, US, USJ, and W.

Taxonomic Treatment

Lepanthes osaensis Chinchilla, Aguilar and Bogarín, *sp. nov.* TYPE: COSTA RICA. Puntarenas: cantón Osa, distrito Sierpe, no estación no sendero a Mogos, a 33 km de Chacarita, entrada de San Luis, fin del camino, antes de llegar a la finca de Luis Mejía, 08˚45'00"N, 083˚26'05"O, 179 m, 24 abril 2017, *R. Aguilar 16206* (Holotype: JBL [J0571]). Fig. 1, 2B, and 3.

Lepanthes osaensis is distinguished from *L. cuspidata* Luer by the abaxially vinous leaves with the adaxial margin vinous, greenish yellow, the smaller sepals, the narrower, bilobed petals, vinous up to the midbase and apically yellow, and the smaller lip with triangular blades.

Plant epiphytic, caespitose, erect, up to 3.5 cm tall. *Roots* slender, flexuous, up to 3.4 cm long, 0.6 mm in diam.

Figure 2. Comparison of flowers in *Lepanthes cuspidata* Luer and *L. osaensis* Chinchilla, Aguilar and Bogarín. **A**, *Lepanthes cuspidata*, oblique view; **B**, *L. osaensis*, oblique and frontal view, and lateral view with the dorsal sepal removed. Photographs: A, by D. Bogarín from *Bogarín 7237* (JBLspirit); B, by I. F. Chinchilla from the holotype, *Aguilar* 16206 (JBLspirit).

Ramicauls slender, suberect or erect, 1.0–2.1 cm long, enclosed by 4–5 beige, ciliate, adpressed lepanthiform sheaths, the ostia ciliate, ovate, acuminate. *Leaves* elliptical, coriaceous, papillose, with the adaxial margin vinous, abaxially vinous, stained greenish yellow; obtuse, emarginate, apiculate, 1.0–1.5 × 0.7–1.0 cm, the obtuse base narrowing into a petiole ca. 1.3 mm long. *Inflorescence* racemose, distichous, papillose, successively flowered, extending on abaxial or adaxial surface of the leaf, shorter than the leaves, up to 6.7 mm long, peduncle up to 3.7 mm long, rachis up to 3.5 mm long. *Floral bracts* yellowish green, ovate, acuminate, muricate, 0.6–1.0 mm long. *Pedicels* 0.8–1.4 mm long, persistent. *Ovary* microscopically papillose, 0.70–0.75 mm long. *Flowers* with greenish-yellow, translucent sepals, the petals vinous up to close to midbasal and apically yellow, the lip light fuchsia, the column light fuchsia, abaxially whitish. *Dorsal sepal* lanceolate, acute, abaxially 1-carinate, entire, connate to the lateral sepals for about 0.3 mm, 2.6 × 0.96 mm, 3-nerved. *Lateral sepals* obliquely lanceolate, acute, apically convergent, abaxially 1-carinate, connate for 0.83 mm, 2.2 × 0.85 mm, 2-nerved. *Petals* transversely bilobed, microscopically papillose, 0.5 × 1.4 mm, the upper lobe obliquely deltate, acute, diverging, 0.85 mm long, the lower lobe, obliquely ovate, acute, diverging, 0.55 mm long. *Lip* bilaminate, adnate to the column base, 0.70 × 0.75 mm, not exceeding the column length, the blades triangular, obtuse to rounded, slightly convergent toward the apex; the connective cuneate, 0.4 × 0.1 mm; the body narrowly oblong, thick, adnate to the column base, 0.16 × 0.10 mm; appendix cylindric, obtuse, pubescent, 0.1 mm long. *Column* cylindric, 1.1 mm long; anther apical; stigma ventral. *Pollinia* 2, claviform, 0.32 × 0.10 mm, joined at the base by a rounded viscidium. *Anther cap*, obovate, abaxially concave, 0.34 × 0.30 mm. *Fruit* not seen.

Etymology: the specific epithet refers to the type locality of Osa, and the homonymous Península de Osa, one of the most plant-species-rich regions in the Neotropics. Osa derives from the Cacique Osa, an indigenous Boruca ruler who reigned in most of the territory that comprises the canton of Osa at the time of the Spanish colonization.

Distribution: only known from the type locality in Costa Rica (Fig. 3).

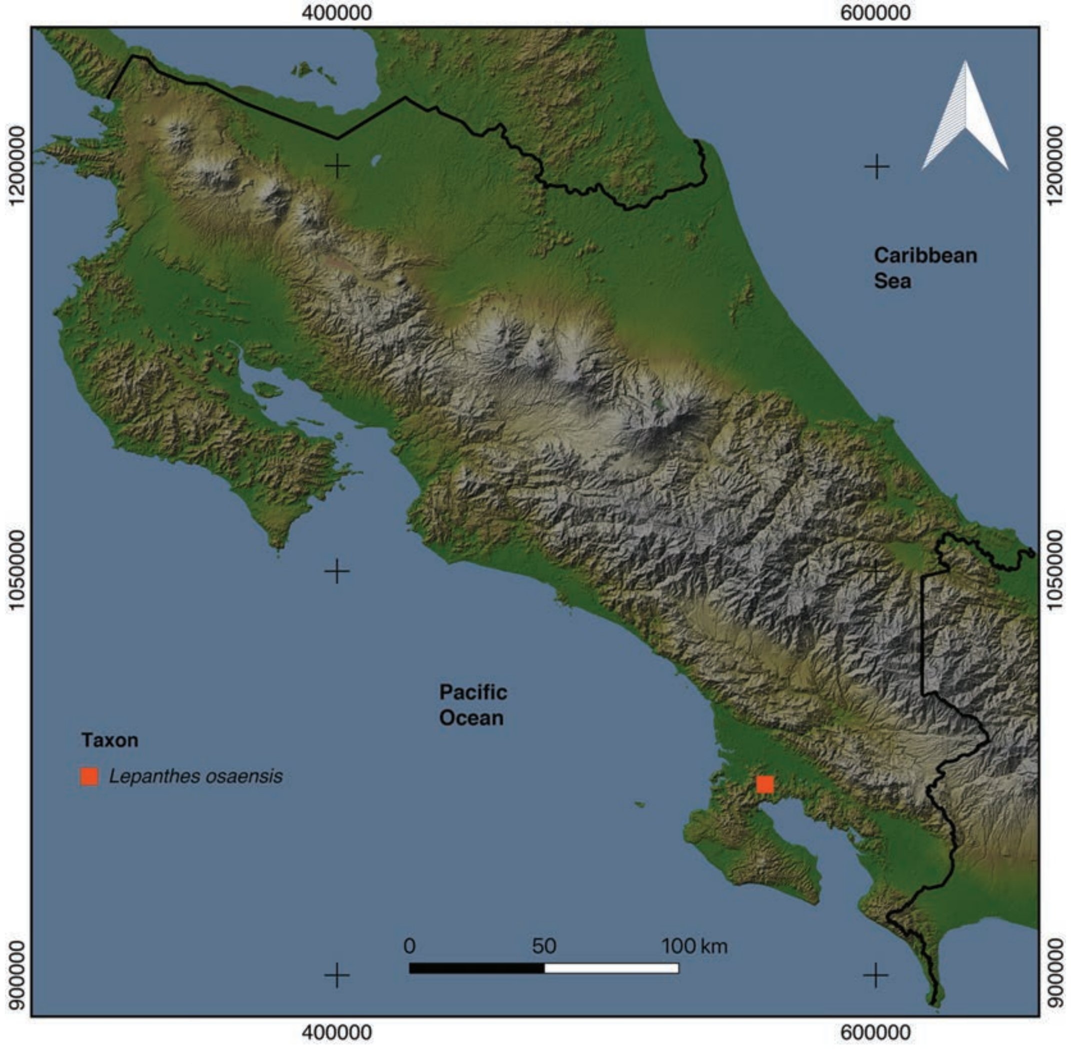


FIGURE 3. Distribution of *Lepanthes osaensis* Chinchilla, Aguilar and Bogarín. Satellite image source: NASA/JPL/NIMA (2000). Prepared by I. F. Chinchilla.

Habitat: plants were found growing as epiphytes on twigs of *Hirtella* L. sp. (Chrysobalanaceae) at around 15–20 m above the ground, in very wet forest on the Reserva Forestal Golfo Dulce, at 129 m elevation. Other common plants in the area are *Copaifera camibar* Poveda, N. Zamora & P.E. Sánchez, *Dialium guianense* (Aubl.) Sandwith, *Peltogyne purpurea* Pittier (Fabaceae), and *Pouteria laevigata* (Mart.) Radlk. (Sapotaceae). Also present are less common species such as *Parkia pendula* (Willd.) Benth. ex Walp. (Fabaceae), *Oenocarpus mapora* H. Karst. (Arecaeae), and *Ruptiliocarpon caracolito* Hammel & N. Zamora (Lepidobotryaceae), as well as epiphytic bromeliads such as *Araeococcus pectinatus* L.B. Sm., *Guzmania lingulata* (L.) Mez, *Tillandsia anceps* G. Lodd., and *Tillandsia monadelpha* (E. Morren) Baker (Bromeliaceae).

Phenology: plants flower in April and May in the field and in cultivation.

Conservation status: data deficient; only a few plants are known from the type locality. It is most probably found in the Parque Nacional Corcovado.

Lepanthes osaensis is morphologically similar to several Central America species characterized by the small habit (<5 cm tall), elliptical to broadly elliptical leaves, flowers with narrowly ovate-elliptical sepals, transversely bilobed, flabelliform-bilobed petals (often with an apiculus in the sinus), oblong and the bilobed lip with falcate lobes embracing the column and a pyramidal, pubescent appendix. Some of the species sharing these characters are *Lepanthes cuspidata*, *L. excedens* Ames & Correll, *L. empis* Luer, *L. mariposa* Luer, *L. pygmaea* Luer, and *L. volsella* Luer & R. Escobar.

Among them, *Lepanthes osaensis* resembles *L. cuspidata*; however, it differs in the leaves with the adaxial vinous margin, abaxially vinous, stained greenish yellow (vs. green on both surfaces), smaller sepals (2.2–2.6 × 0.85–0.96 mm vs. 3.50–4.85 × 1.25–1.70 mm), the petals vinous up to close to midbase and apically yellow (vs. the upper lobe red, the midlobule and the lower lobe yellow), narrower (1.4 mm vs. 2.0–3.0 mm), bilobed (vs. trilobed, with an obtuse lobule between the lobes), and smaller lip (0.70 × 0.75 mm vs. 0.9–1.0 × 0.90–1.35 mm), with triangular blades (vs. oblong blades) (Fig. 1 and 2).

LITERATURE CITED

Bogarín, D., I. F. Chinchilla, and M. Cedeño-Fonseca. 2020. Two new species of *Lepanthes* (Orchidaceae: Pleurothallidinae) from Costa Rica and their phylogenetic affinity. Plant Syst. Evol. 306(2): 1–13.

Bogarín, D., A. Karremans, and F. Pupulin. 2008. New species and records of Orchidaceae from Costa Rica. Lankesteriana 8(2): 53–74.

Bogarín, D., and Y. Kisel. 2014. A new *Lepanthes* from Costa Rica. Orchid Rev. 122: 28–31.

Bogarín, D., and F. Pupulin. 2007. Las orquídeas del Parque Nacional Barra Honda, Guanacaste, Costa Rica. Lankesteriana 7(1–2): 446–449.

Callejas Posada, R. 2020. Piperaceae. Pages 1–590 in G. Davidse, C. Ulloa Ulloa, H. M. Hernández Macías, and S. Knapp, eds., *Fl. Mesoamer.* 2(2): i–xix. Missouri Botanical Garden, Saint Louis.

Hammel, B. E. 2015. Three new species of *Pentagonia* (Rubiaceae) from southern Central America, one foreseen, two surprising. Phytoneuron 46: 1–13.

Jiménez, Q., and M. H. Grayum. 2002. Vegetación del Parque Nacional Carara, Costa Rica. Brenesia 57–58: 25–66.

Karremans, A. P., and P. C. Lehmann. 2018. A highly threatened new species of *Vanilla* from Costa Rica. Orchids 87: 304–307.

Kohlmann, B., J. Wilkinson, O. García Valverde, and K. Lulla. 2002. *Costa Rica desde el espacio*. *Costa Rica from Space*. Editorial Heliconia, Fundacion Neotropica, San José, Costa Rica.

Luer, C. 2003. *Lepanthes*. Pages 216–255 in B. E. Hammel, M. H. Grayum, C. Herrera, and N. Zamora, eds., *Orchidaceae-Zingiberaceae*. Vol. 3 of *Manual de Plantas de Costa Rica*. Monogr. Syst. Bot. Missouri Bot. Gard. 93.

Luer, C., and L. Thoerle. 2012. Lepanthes *of Colombia (Orchidaceae)*. Vol. 32 of *Icones Pleurothallidinarum*. Monogr. Syst. Bot. Missouri Bot. Gard. 123: 1–300.

Pridgeon, A. M. 2005. *Lepanthes*. Pages 362–365 in A. M. Pridgeon, P. J. Cribb, M. W. Chase and F. N. Rasmussen, eds., *Epidendroideae (Part 1)*.Vol. 4 of *Genera Orchidacearum*. Oxford University Press, New York.

Pupulin, F. 1998. Orchid florula of Parque Nacional Manuel Antonio, Quepos, Costa Rica. Rev. Biol. Trop. 46(4): 961–1031.

Rakosy, D., M. Speckmaier, A. Weber, W. Huber, and A. Weissenhofer. 2013. *Orchids: Botanical Jewels of the Golfo Dulce Region, Costa Rica*. Verein zur Förderung der Tropenstation La Gamba, University of Vienna.

Rodríguez. A., and D. Santamaría-Aguilar. 2020. Sinopsis del género *Sterculia* (Sterculioideae, Malvaceae) para Mesoamérica, y la validación taxonómica de tres especies. Harvard Pap. Bot. 25(1): 13–37.

Santamaría-Aguilar, D., and R. Aguilar fernández. 2017. *Hirtella crusa* (Chrysobalanaceae), una especie nueva de la Península de Osa, Costa Rica. Phytoneuron 74: 1–9.

Santamaría-Aguilar, D., R. Aguilar, and L. P. Lagomarsino. 2019. A taxonomic synopsis of *Virola* (Myristicaceae) in Mesoamerica, including six new species. PhytoKeys 134: 1–82.

Santamaría-Aguilar, D., J. M. Chaves-Fallas, and R. Aguilar. 2016. Two new species of *Chrysophyllum* (Sapotaceae) endemic to Costa Rica. Brittonia 69(2): 222–230.

Santamaría-Aguilar, D., and L. P. Lagomarsino. 2017. Two new species and a new combination in *Protium* (Burseraceae) from Costa Rica. PhytoKeys 76: 89–113.

Vieira-Uribe, S., and J. S. Moreno. 2019. Three new *Lepanthes* (Orchidaceae: Pleurothallidinae) from the Alto de Ventanas Ecoregion in Antioquia, Colombia. Lankesteriana 19(2): 63–75.

Weber A., W. Huber, A. Weissenhofer, N. Zamora, and G. Zimmermann. 2001. *An Introductory Field Guide to the Flowering Plants of the Golfo Dulce Rain Forests, Costa Rica—Corcovado National Park and Piedras Blancas National Park ("Regenwald der Österreicher")*. Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria.

Page 220 intentionally left blank.

NEW SPECIES OF *PODANDROGYNE* (CLEOMACEAE) IV. TWO SPECIES FROM WESTERN ECUADOR AND WESTERN COLOMBIA

Theodore S. Cochrane[1,2] and Xavier Cornejo[3]

Abstract. Two new species of *Podandrogyne*, *P. flammea*, endemic to Pacific coastal and western Andean Ecuador and Colombia, and *P. websteri*, restricted to four northern provinces of Ecuador but found mostly in Pichincha, are described and illustrated. These taxa are generally distinguished by flower and fruit size and leaf blade number and texture. A general likeness suggests affinity to the species cluster represented by *P. glabra*.

Keywords: Cleomaceae, Colombia, Ecuador, new species, *Podandrogyne*

The only comprehensive account of *Podandrogyne* Ducke (Cleomaceae) is the outdated provisional synopsis by Woodson (1948), and regional lists remain incomplete for countries like Colombia and Ecuador, well-known centers of astounding biodiversity and endemism (Groombridge, 1992; Davis et al., 1997; Jørgensen and León-Yánez, 1999; Bernal et al., 2015), where the highest concentrations of *Podandrogyne* taxa occur. In Colombia there are at least 21 species and in Ecuador as many as 14 species, the majority of which grow in primary or secondary, tropical to subtropical rainforests on the slopes of the Andes except for three species: *P. glabra* Ducke in lowland Amazonia, *P. trichopus* (Benth.) Iltis & Cochrane in the Pacific coastal lowlands, and *P. brevipedunculata* Cochrane on the lower western Andean slopes and adjoining lowlands.

Since 1979, as part of a taxonomic revision of *Podandrogyne*, the first author has been distinguishing *P. flammea* from *P. glabra* and two unpublished, seemingly distinct, close allies from Colombia. However, he found the former species disquietingly difficult to characterize, owing not only to the amount of variability accommodated by included material but also to an unresolved situation involving additional, ambiguous collections resulting from ongoing collecting in northern Ecuador. Eventually, having seen several populations of *P. flammea* in the field and having studied pertinent specimens in GUAY, co-author Cornejo realized that still another, quite similar but subtly distinct population, described below as *P. websteri*, was involved. In the spring of 2002, he sent the first author a short description based on two collections of the latter entity, bringing together the most important traits allowing its description and helping solve the existing taxonomic problems.

Podandrogyne flammea Cochrane, *sp. nov.* TYPE: ECUADOR. Guayas: Cordillera Chongón-Colonche, Bosque Protector Loma Alta, bosque de garúa muy húmedo premontano estación seca, secundario, 600 m, 22 December 1996 (fl, y fr, fr), *X. Cornejo & C. Bonifaz 5488* (Holotype: WIS [barcode v0402832WIS]; Isotypes: AAU [2], COL, GUAY, K, MO [2], QCNE [2], US, WIS [2]). Fig. 1, 2, 5.

Herba robusta, frutex vel arbor parva. Folia 1–5-foliolata, foliolis formis et amplitudinibus variantibus, glaberrima vel subtus basi et ad nervos sparsim vel manifeste pilosula. Flores flammei, in racemum subelongatum densum multiflorum dispositi; pedicelli gracillimi (9–)14–28(–32) mm. Sepala 2–6 mm. Petala 7–12 mm. Flores pistillatos: ovarium anguste oblongum, 6–8 mm vel anguste ovoideo-oblongum, 4–5 mm, gynophoro dimidio breviore quam androgynophoro. Flores staminatos: filamenta 5–17 mm, androgynophoris (12–)15–25(–32) mm. Capsulae oblongae ad anguste oblongae, raro subcylindraceae, 2–8 cm, rostro brevi ad manifesto ca. 2–8 mm. Semina reniformo-obovoidea, 3–4 × 2.3–3.2 mm.

Erect or rarely scandent, unbranched or few-branched *herbs*, *shrubs*, or *treelets* 1–4 m tall, glabrous or less often youngest shoots, lower leaf surfaces, and, more permanently, petioles, petiolules, and veins beneath irregularly scurfy-pilosulous or even shaggy-pilose; hairs (if present) bent, twisted, or rarely matted, mostly 0.3–0.9 mm but sometimes as short as 0.1–0.2 or as long as 0.6–1.9 mm. *Leaves* 1–5 (mostly 3)-foliolate, at least some on typical plants generally compound; petioles 1–28 cm; blades elliptic to narrowly elliptic, the larger 7–30 × 2–13 cm, obtuse to cuneate at base, acuminate to caudate, if 1-foliolate shaped as above or very rarely ovate-elliptic or ovate with rounded to subcordate bases, if compound on a short to long petiolule (central one 2–13, rarely up to 21 mm), commonly glabrous on both sides or lower surface scaberulous or thinly (blades) to moderately (veins) pilose, with 11–19(8–17 in Prov. Carchi) main lateral veins on each side. *Racemes* mostly erect, 7–29 cm (rarely to 63 cm in Carchi), 6–12 cm thick (seldom secund, then 4–8 cm), conspicuously many flowered and usually dense, ebracteate altogether or lowest 1 or 2 pedicels (6–8 pedicels in one collection) subtended by a large (9–15 × 2–4 cm) to small (1–8 × 0.5–4.0 cm),

---

We thank the curators and staffs of the herbaria cited for loaning specimens and Kandis Elliot, Senior Artist Emerita, of the Department of Botany, University of Wisconsin–Madison, for preparing all the figures with her usual proficiency.

[1] Department of Botany, University of Wisconsin, 430 Lincoln Drive, Madison, Wisconsin 53706, U.S.A.

[2] Corresponding author: tscochra@wisc.edu

[3] Herbario GUAY, Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Av. Raúl Gómez Lince s.n. y Av. Juan Tanca Marengo, P.O. Box 09–01–10634, Guayaquil, Ecuador, xcornejoguay@gmail.com

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 221–230.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n10,

1-foliolate leaf (bract) and upper pedicels by a short, stiff, gland-tipped hair or row of such hairs 0.05–0.50 mm, in pubescent collections these accompanied by minute curly hairs; peduncle 1–7 cm, rachis often brownish maroon or dark purple, up to 25 cm (rarely to 40 cm or more in Carchi), bearing at any one time 0–20 open flowers and ca. 55–310 buds (0–25 buds in fruit or when very old or up to only 113 buds in Carchi), usually not greatly elongating but producing a total of 110–390(–465) flowers (including pedicel scars). *Flowers* monosymmetric, with deep red to bright scarlet or orange pedicels and sepals and paler gynophore-androgynophore axes; pedicels horizontally divergent to slightly declined, 15–28(–33) mm or seldom 9–14 mm. *Sepals* ovate-oblong or ovate-triangular, (2–)3–6 × 1–2 mm, basally connate for 0.7–2.0 mm (ca. 20–50[–60]% of their length), narrowly acute, apiculate. *Petals* bright red to orange, seldom orangish yellow to yellow, commonly yellowish orange at base grading to red-orange toward apex, drying pinkish red or more often pale yellow suffused with a pinkish hue, upper pair narrowly oblong, ca. 0.5–2.0 mm shorter than the obliquely and narrowly oblong-elliptic lower pair, 7–12 × 2–3(–4) mm, exceeding the sepals by 5–9 mm, sessile, obtuse at apex. *Disk* a ± fleshy gland, light yellow, broadly depressed-obovoid in face view (*fide* fluid-preserved flower), almost disk-like but expanded adaxially, grooved on top opposite the petals, concave on the side facing the androgynophore, abaxially reduced to a filmlike band of tissue sometimes contracted into a minute lobe when dried, summit on upper side forming an undulate rim or in dried material shrinking into 3 alternipetalous lobes or ridges, 1.0–2.7 (high) × 1.1–3.3 mm (across), 0.7–2.1 mm thick (side view), not particularly conspicuous in fruit. *Pistillate flowers*: ovary either narrowly oblong to oblong-lanceoloid (and terete?), 6–8 mm, 2 mm thick, or oblong to narrowly oblong-ovoid and compressed, 4–5(–6) × 1–2 mm, glabrous or sometimes minutely papillose to scabridulous-puberulent; stigma 0.5–0.9 mm diam. (1.3 mm in a fluid-preserved flower), essentially sessile (style ≤ 1 mm); gynophore 5–10 mm, glabrous; androgynophore 15–19 mm. *Staminate flowers*: stamens inserted high up on a prominent androgynophore (12–)15–25(–32) mm; filaments red to pink, distally yellow, subequal, (5–)7–17 mm, upper and median pairs subverticillate, arising 0.6–3.7 mm above the insertion of lowest pair; anthers gray and (on side away from line of dehiscence) green, (1.8–)2.2–3.6 mm, pollen yellow. *Capsules* 0–17, light green to yellow, narrowly oblong to subcylindric, 2–7(–8) cm, 4–10 mm thick (in one fluid-preserved collection ± laterally compressed, 11–13 mm wide and 8–9 mm thick), often cuneate at base and acute to almost or quite rounded at apex; style (0–3 mm) and stigma (0.5–1.7 mm diam.) forming merely a depressed cap < 1 mm or more often with the short, tapered apices of the valves an apiculus or beak 2–7(–8) mm; gynophore (5–)8–17 mm; androgynophore 12–24 mm; pedicel declined or deflexed, 9–21(–28) mm, androgynophore-gynophore axis and silique pendant from it. *Seeds* presumably black (dark brown when dried), 11–(ca.)107 per capsule, obovoid- to suborbicular-reniform, a little irregular due to close packing, 3–4 × 2.2–3.2 mm, 1.8–2.3 mm thick, slightly compressed but hardly beveled, essentially smooth (sometimes very faintly and uniformly rugulose).

Distribution, ecology, and phenology: known primarily from Ecuador from the province of Loja (reaching its southern limit at 04°05'S) to the province of Carchi, reappearing at an apparently disjunct station on the border between the departments of El Valle and Chocó, Colombia (*Dugand & Jaramillo 3023*), in mature lowland tropical and subtropical forests (including premontane, lower montane, and "cloud" forests) along the western slopes of the Andes at elevations of 430–1760(–2200) m, and on the isolated hills of the coastal ranges at elevations of 280–600 m. More fieldwork in poorly collected forests of Colombia presumably will result in the discovery of additional populations. Flowering and probably also fruiting throughout the year.

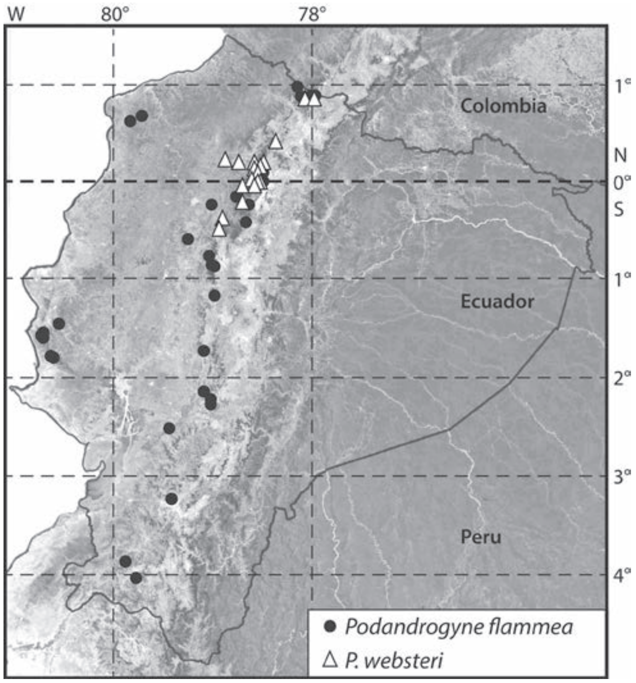


FIGURE 1. The distributions of *Podandrogyne flammea* and *P. websteri*. A single Colombian station is not shown (see text).

Additional specimens examined: COLOMBIA. Department uncertain [probably Valle del Cauca]: Cordillera Occidental, western slope near the dividing line between Valle and Chocó, north of Albán, 17 August 1941, *A. Dugand & R. Jaramillo 3023* (COL). ECUADOR. Province uncertain [Cotopaxi?]: "prp. Pangoa, R. Riofrio [sic, for Pangua?]," August 1891 [?, as ".891."], *A. Sodiro 67* (B [photos GH, US, WIS]). Azuay: road from Jesús María to Molleturo, near Azuay-Guayas border, 16 July 1977, *J. D. Boeke & H. Loyola 2168* (WIS [2]); Bosque Protector Molleturo Mullopungo, along main road near the village, ca. 2 km east, 12 April 1996, *J. L. Clark et al. 2470* (MO, QCNE); SE and E side of Río Norcay across from Molleturo, 6 June 1943, *J. A. Steyermark 52853* (F). Bolívar:

Sta. Rosa de Agua Clara, 12 January 1996, *X. Cornejo & C. Bonifaz 4709* (GUAY, WIS); [E of] Balsapampa [also spelled Balzapamba], 19 May 1968, *G. Harling et al. 9661* (GB, WIS). Cañar: km 110 from Durán, 15 January 1962, *C. H. Dodson & L. B. Thien 2093* (SEL, WIS); between Quillallpa and Kirpud, 25 October 1952, *F. Fagerlind & G. Wibom 717* (S). Carchi: km 20, Maldonado-Tulcán [road], 25 November 1985, *L. Besse et al. 2278* (WIS), *2283* (WIS); S side of upper Río Blanco, Cerro Golondrinas, 6 February 1993, *B. Boyle & A. Boyle 1486* (WIS); trail from Rafael Quindís mountain finca above Río Verde, 27 November 1987, *W. S. Hoover & S. Wormley 1764* (MO); approaching headwaters of Río Verde at base of Cerro Golondrinas, 30 November 1987, *W. S. Hoover 2096* (MO), *2108* (MO); Río Verde "...beyond principal drainage stream of large Cerro Golondrinas into drainage streams of medium Golondrinas mountains," 1 December 1987, *W. S. Hoover 2152* (MO), *2174* (MO); N bank of Quebrada Mongon, 19 January 1988, *W. S. Hoover et al. 2951* (MO); trail NW of Awá encampment to Rodrigues Finca, Gualpi-Chico area, 21 January 1988, *W. S. Hoover et al. 3486* (MO); north of Carmen, road to Chical, 10 February 1992, *W. Palacios et al. 9806* (QCNE, WIS). Cotopaxi: km 52–53 between Quevedo and Latacunga at Tenefuerste, Río Pilaló, 29 October 1981, *C. H. Dodson & P. M. Dodson 11998* (MO, SEL, WIS); *idem*, 12 June 1983, *C. H. Dodson et al. 13920* (MO, SEL); *idem*, 9 April 1984, *C. Dodson et al. 14206* (MO); Cantón La Maná, Reserva Ecológica Los Ilinizas, Cord. Tilinche, Cerro Tilipulo, 24 July 2003, *P. Silverstone-Sopkin et al. 9418* (MO, WIS); *idem*, 25 July 2003, *P. Silverstone-Sopkin et al. 9490* (MO, WIS). Esmeraldas: Reserva Mache-Chindul, Cuchilla de Bunca, 28 April 2003, *X. Cornejo & C. Bonifaz 7739* (AAU, GUAY, MO, QCA, QCNE [2], US [2], WIS [4]); Fila de Bilsa, 7 km E of San José de Bilsa, ca. 80 km due SW of Esmeraldas, 29 January 1991, *A. Gentry et al. 72873* (MO). Guayas: Cordillera Chongón-Colonche, Bosque Protector Loma Alta, 1 July 1996, *C. Bonifaz et al. 3433* (GUAY [topotype], WIS [topotype]); Guayaquil water-supply intake near Bucay, 28 September 1939, *O. Haught 2884* (BKL [photos GB, S, WIS, UC], F, US). Loja: Cantón Catacocha, Hda. "La Hamaca," El Almendral, 16 April 1944, *M. Acosta Solís 7889* (F); [Cordillera de] Chinchanza, June 1882, *E. André 477* (K). Los Ríos: La Corina, 20 km E of Patricia Pilar, 6 km E of La Centinela, 29 September 1979, *A. Gentry & G. Schupp 26668* (MO, SEL). Manabí: [Cordillera de Chongón,] San Sebastián-La Mocora, Parque Nacional Machalilla, 9 January 1994, *X. Cornejo & C. Bonifaz 1298* (GUAY); *idem*, 21 January 1991, *A. Gentry et al. 72505* (MO); *idem*, 24 March 1993, *B. Øllgaard et al. 100786* (AAU); San Sebastián, vic. Agua Blanca, ca. 15 km [sic] from Puerto López, 20–22 November 1987, *F. Hekker & W. H. A. Hekking 10251* (AAU [2]). Pichincha: Canchacoto [Canzacoto], 21 June 1876, *E. André 3774* (K); Chiriboga, 19 August 1955, *E. Asplund 17402* (S); SW of Chiriboga, km 82–84 from Quito on old road to Santo Domingo, 8 July 1979, *B. Løjtnant & U. Molau 15666* (AAU); Guanacilla, September 1883 [as "9.83"], *P. L. Sodiro 68* (B [photos GH, NY, US, WIS]).

The leaves of *Podandrogyne flammea* are variable as to leaflet number, shape, and pubescence. Although multifoliolate on most specimens, they are primarily 1-foliolate on those from the province of Carchi. There is no obvious correlation between the presence or amount of pubescence and altitudinal or geographical distribution. The blades are typically elliptic or narrowly elliptic and up to 11 cm wide, but a few individual blades on certain specimens are wider. *Sodiro 67* has large and perhaps atypical 1-foliolate leaves that are ovate to ovate-elliptic and up to 13 cm wide with obtuse to subcordate bases. Its solitary, separately mounted fruit, missing the pedicel and distal end, is cylindrical, more than 6 cm long and only 4 mm thick, and thus also atypical. However, the inflorescence has the correct shape, dimensions, and floral density for *P. flammea*.

When well developed, the showy inflorescences are usually up to about 30 cm and eventually produce close to 400 or more flowers. Except in *Acosta Solís 7889* and *Fagerlind & Wibom 717* (in which they are as short as in *Podandrogyne glabra*), the pedicels are long, so that buds, even young ones toward the apex, stand well out from the rachis, conferring a dome shape to the summit of the inflorescence (Fig. 2B). The same is true for *P. websteri* (Fig. 3A–D) and *P. pubescens* Aspl., but in *P. glabra* and other unpublished Colombian allies the pedicels are short; their inflorescences narrow toward the tip, retaining a more conical shape. Material from the province of Manabí differs in having slightly smaller flowers (sepals 2–3 mm, petals 6–8 mm) and fruits that are uniform in diameter and rounded at both ends rather than being somewhat narrowed toward each end. One specimen, *Silverstone-Sopkin 9490* (WIS), exhibits alternating zones of functionally pistillate and functionally staminate flowers, an exceedingly rare condition in the normally androgynous *Podandrogyne*, which must be analogous to the cyclical sterility frequently observed in *Tarenaya hassleriana* (Chodat) Iltis.

Local populations from the province of Carchi deserve further discussion (see also under *Podandrogyne websteri*, below). The leaves are mostly 1-foliolate, yet their blades, like the inflorescences, most often resemble those of *P. flammea* but sometimes resemble *P. websteri*. The flowers and especially the fruits of the Carchi plants match well those of *P. flammea* except that the perianths (like those from Manabí) average just slightly smaller (petals 7–10 mm vs. 8–12 mm in all other collections) and the stamens a little shorter (proximal and median filaments 5–14 mm vs. 9–17 mm). However, inflorescences and fruits (when available) are almost always too robust for *P. websteri*. Inflorescence axes are variable in angle of divergence, length, and diameter, often diverging from the bulk of the material representing *P. flammea*, and they are less densely flowered. They sometimes have relatively long rachises that may be slender and curved or sinuous instead of strong and straight, and at least occasionally they even dangle instead of being erect. However, these peculiarities are neither expressed in all specimens nor always evident in herbarium material. The only plants described in field notes as being scandent (*sub Boyle & Boyle 1486*) were found along the upper Río Blanco, Cerro Golondrinas.

In summary, the inclusion of collections from Carchi has expanded the definition of *Podandrogyne flammea*. To also embrace such specimens as *Hoover 2096* and *Hoover et al. 2951*, which have particularly elongate, slender rachises reaching 41 and 60 cm (the latter flexuous and sharply bent at the tip) and producing a total of 415 and 465 small flowers, respectively, would be more problematic were it not for the fact that other collections from along the same stretch of the Río Verde and the nearby Quebrada Mongon, both at the base of Cerro Golondrinas, have rachises that possess acceptable architecture and dimensions for *P. flammea*. In their inflorescences and relatively small and narrow leaves these two collections exhibit morphological similarity to the recently described, poorly known *P. nutibarana* Cochrane (Cochrane, 2016) from the department of Antioquia, Colombia. Inflorescences of the latter species are generally longer and less densely flowered; the petals average larger (8–14 vs. 6–11 mm); and the fruits are wider, scarcely or barely beaked, and, so far as known, borne on pedicels and androgynophores that are longer than any on specimens of *P. flammea* from Carchi. Even though most collections lack fruits and fruiting collections often lack open flowers, there is scarcely sufficient evidence at this time to justify giving taxonomic recognition to the indistinct, albeit geographically marginal, Carchi population.

Podandrogyne websteri Cochrane & Cornejo, *sp. nov.* TYPE: ECUADOR. Pichincha: Quito-Tandayapa road, 1838 m, shrub to 2 m, flower bright orange, anthers green, fruit yellow-green, seeds black-purple, 14 May 1989 (fl, fr), *J. Smith 1926* (Holotype: WIS [barcode v0402835WIS]; Isotypes: AAU, MO, QCA, QCNE [not seen]). Fig. 1, 3–5.

Herba, frutex vel arbor parva usque ad 4 m, admodum omnino glaber (petiolis et surculis juvenissimus villosulis excepto). Folia 1-foliolata vel aliquando 3-foliolata, foliolis plerumque parvis crassiusculis. Flores aurantiaci ad rubro-aurantiaci vel lutei, in racemum corymbosum densum multiflorum dispositi, pedunculo brevi et rhachi non elongato; pedicelli (9–)12–20 mm. Florae parvae, sepala 2–4 mm et petala 5–7 (flores pistillatos) vel 7–10 (staminatos) mm. Flores pistillatos: ovarium anguste ovoideum vel anguste ovoideo-oblongum, 2–3 mm, breviter glanduloso-puberulum, gynophoro dimidio longiore quam androgynophoro. Flores staminatos: filamenta 5–14 mm, androgynophoris 12–19 mm. Capsulae ovoideae, ellipsoideae, vel anguste oblongae, 0.5–3.0 cm, in rostra brevia (ca. 1–5 mm) contractae. Semina reniformo-obovoideae, 3.2–4.4 × 2.7–3.4 mm, laevia.

Erect, unbranched or sparsely branched *herbs* to *shrubs* 0.5–3.0 or *treelets* 4 m tall, glabrous except for youngest shoots, petioles, and midveins beneath, hairs (if present) 0.1–0.6 mm, rather stiff, incurved or crinkled and glandular; stems apparently woody at least at base but all collected material herbaceous, a little hairy at the very beginning but soon glabrous. *Leaves* 1-foliolate or infrequently some lower or occasionally higher on the plant 3-foliolate; petioles 1–16 cm, pilosulous, hairs incurved-curly and glandular, glabrate; blades elliptic to narrowly elliptic, (1–)5–25(–30) × 1.5–11.0(–13.0) cm, obtuse to broadly cuneate at base, attenuate to caudate, if 3-foliolate, of similar shape and size but relatively large, on petiolules 8 or 2–3 mm (central or lateral blades, respectively), firmly membranous to generally chartaceous, essentially glabrous on both sides to sparsely pilosulous beneath chiefly along the veins, with 9–14 main lateral veins either side of the midrib. *Racemes* erect, corymbiform and ± short, 3–8(–9) cm, 5–8 cm thick, densely many-flowered; lowest 1 or 2 (rarely 3) flowers usually subtended by a 1-foliolate, leaflike bract, blade elliptic or narrowly elliptic to narrowly oblong-elliptic or the smallest lanceolate to subulate, 1–12 × ca. 0.5–3.0 cm, petiole to 8(–11) mm, remaining flowers appearing ebracteate but each pedicel subtended by a dense cluster (lower flowers on selected specimens) to sparse row of 1–9, buff-colored to yellow-brown, tiny, mostly curly or bent hairs, central 1–3 of these (especially in pistillate flowers) longer (0.4–1.9 mm), straighter, and stiffer than the others; peduncle only (0.5–)1.0–2.5(–3.5) cm, rachis dark purple, (1.5–)2.5–9.5 cm, with 0–(ca.)24 (or more?) open flowers or 0–13(–20) fruits and 0–145 buds present at any one time (depending on age of the inflorescence), hardly elongated but eventually producing a total of up to ca. 273(–340) flowers (including pedicel-scars). *Flowers* monosymmetric, with orange to greenish-yellow pedicels and sepals and similarly colored but paler androgynophores and filaments; pedicels horizontally divergent to slightly declined, 8–16 (pistillate flowers) or 12–20(–23) (staminate) mm, minutely granulose-papillate. *Sepals* orange, ovate-oblong or ovate-triangular, 2–4 × 1–2 mm, basally connate for 0.4–1.4 mm (ca. 10–40% of their length), narrowly acute, often minutely apiculate. *Petals* vivid orange to red-orange, yellow-orange, or yellow, drying pinkish red or more often pale yellow with suffusion of pink, upper pair narrowly oblong, ca. 0.5–1.5 mm shorter than the obliquely and narrowly oblong-elliptic lower pair, 5–7 (pistillate flowers) or 5–10 (staminate) × 2–4 mm, exceeding the sepals by 2–5(–6) mm, essentially sessile (short, cuneate base ca. 0.5 or 1 mm in upper and lower petals, respectively), obtuse at apex. *Disk* ± fleshy, adaxially expanded into 3 alternipetalous, pointed lobes (these forming a barely undulate rim in dried material), sunken across the top when dried, concave on the side facing the androgynophore, abaxially nearly obsolete, consisting of a filmlike band of tissue (sometimes contracted into a minute lobe when dried), 1.0–2.1 × 1.5–2.3 mm, 0.7–1.4 mm thick (side view), not particularly conspicuous when dried. *Pistillate flowers*: ovary narrowly ovoid to narrowly ovoid-oblong, somewhat compressed, 2–3(–4) × 1 mm, puberulent; style 0.5–1.1 mm; stigma 0.5–0.9 mm diam.; apiculus (style + stigma) 1–2 mm; gynophore green, 4–6 mm (very rarely 9 mm), virtually glabrous (sparsely and very minutely scabridulous-puberulent); androgynophore pinkish red, 8–12 mm. *Staminate flowers*: stamens well-exserted, filaments red or orange, subequal, 5–14 mm, the 2 upper pairs subverticillate, inserted 1.3–2.7 mm beyond the lowest 2 stamens, one or both members of the distal pair sometimes notably reduced, then only 1–5 mm; anthers gray and (on side away from line of dehiscence) green, 2.2–2.8(–3.1) mm, pollen violet; androgynophore 12–20 mm. *Capsules* 0–20, yellow to greenish yellow or

FIGURE 2. *Podandrogyne flammea*. **A**, habit; **B**, inflorescence; **C**, flowers, pistillate below, staminate above (lowest one in each case from fluid-preserved material); **D**, close-up of rachis, showing bases of pedicels and subtending bracteal hairs; **E–G**, representative infructescences, E showing dehisced fruits with curled repla. A from *Cornejo & Bonifaz 5488* (holotype, WIS); B photograph taken on Centinela Ridge, Los Ríos, by A. H. Gentry; C pistillate from *Silverstone-Sopkin et al. 9490* (WIS), staminate from *Cornejo & Bonifaz 5488* (holotype, WIS); D from *Løjtnant & Molau 15666* (AAU); E from *Cornejo & Bonifaz 5488* (isotype, WIS); F from *Dodson et al. 13920* (MO); G from *Palacios et al. 9806* (QCNE).

light green, variable in shape and size, ovoid (obliquely ovoid if very small), ellipsoid, oblong, or narrowly oblong, the bodies 0.5–4.0 cm, 2–10(–12) mm thick, base obtuse to rounded, acuminate into a beak 2–6 mm; style (beyond apices of tapered valves) 1–3 mm; stigma subcapitate, 0.5–1.1 mm diam.; gynophore 8–16 mm; androgynophore 9–13 mm (very rarely to 16 mm); pedicel 8–18 mm, deflexed, the gynophore and frequently silicle-like capsule pendant from it. *Seeds* 1–48 per capsule, purple-black (brown when dried), obovoid-reniform, a little irregular due to close packing in the capsule, 3.2–4.7 × 2.7–3.4 mm, 1.6–2.5 mm thick, slightly compressed but not beveled, smooth.

Distribution, ecology, and phenology: restricted to western Andean slopes from the central portion of the province of Pichincha north to very near the international border with Colombia, in secondary to primary, premontane, lower montane, and montane rainforests, often on slopes or banks along rivers, at elevations of (600–)1600–2200 m; apparently not weedy. Cited as a "dominant or abundant plant" in montane cloud forests of the Maquipucuna area (Webster and Rhode, 2001). Flowering throughout the year; fruiting March to October (probably throughout the year).

Eponymy: named in honor of Grady L. Webster, distinguished plant systematist and lecturer and important plant collector in various areas of the world, especially Ecuador, who made more than half of the collections that led us to distinguish this new species.

Additional specimens examined.—LOCATION UNKNOWN [presumably Ecuador]: "Temperate forests of the Andes," s.d. [ca. 1820–1860], *W. Jameson s.n.* (E [photo WIS]). ECUADOR. Carchi: Cantón Mira, Cerro Golondrinas, El Carmen, 18–25 August 1994, *M. Tirado et al. 1174* (MO, WIS); Reserva Golondrinas, El Corazón, path to La Cortadera and El Mirador, 23 January 2004, *H. Vargas et al. 4310* (MO, QCNE). Cotopaxi: Parr. San Francisco de Las Pampas, Reserva La Otonga, 9 September 1992, *P. Delprete et al. 6220* (NY); Cantón Sigchos, Reserva Ecológica Los Ilinizas, ca. 4 km before Saguambi, via Triunfo Grande-Las Pampas, 13 August 2003, *J. E. Ramos et al. 7337* (MO, WIS). Imbabura: Cantón Cotacachi, Hda. La Florida, 28 August 1992, *A. Álvarez & R. Castro 636* (MO, QCNE). Pichincha: 10 km from Pachijal, NE of El Paraíso, banks of Río Pachijal, 15 June 1997, *F. D. Brown 048* (QCA); Reserva Orquideológica Pahuma, 25 August 2007, *C. E. Cerón & C. I. Reyes 60601* (MO [photo WIS]); along road and trail from Maquipucuna Lodge to Ecolodge Santa Lucia, 2 km N of Maquipucuna entrance, 15 March 2006, *T. B. Croat et al. 95953* (MO); Bellavista Cloud Forest, along road from Tandayapa to Mindo, 7.2 "m" [sic] S of Tandayapa, 27 March 2006, *T. B. Croat et al. 97413* (MO); Calacalí-Los Bancos road, km 22, Reserva Orquideológica El Pahuma, 19 October 1999, *T. Delgado y Grupo Post-grado MO-QCNE 15* (MO, WIS); *idem*, *F. Nicolalde y Grupo Post-grado MO-QCNE 333* (MO, QCNE), *350* (MO); between Nono and Tandayapa, Quito-Nono-Pacto road, 24 March 1979, *L. Holm-Nielsen 16150* (AAU); Nono-Pacto-Río Yacuambi road, 5–10 km above Nanegalito, 21 July 1980, *L. Holm-Neilsen et al. 24444* (AAU); km 59 of the old Quito-Santo Domingo de Los Colorados road, Estación Cientifica Río Guajalito, 23 June 1985, *J. Jaramillo & V. Zak 7827* (MO, WIS); *idem*, 5 March 1987, *V. Zak 1794* (MO, WIS); 16.5 km W of Calacalí along new road to Nanegalito, Río Pachán valley, 15 February 1988, *U. Molau & B. Eriksen 3050* (AAU, GB, QCA); 16 km from Calacalí on road to Nanegalito, 26 April 1995, *B. Ståhl 1348* (QCA); along Río Alambre, Hda. Guarumus, 10 km NW of Nono, 9 May 1943, *J. A. Steyermark 52654* (F); Parcela Permanente, Reserva Biológica Maquipucuna, 10 km N of Nanegalito, 17 May 1991, *G. Tipaz 140* (MO, QCNE); Cerro de Sosa, Reserva Biológica Maquipucuna, 6 km airline distance SE of Nanegal, 17 September 1989, *G. L. Webster & G. Goodstein 27676* (DAV); *idem*, 3 July 1991, *G. L. Webster et al. 28691* (DAV, QCNE, WIS); *idem*, 3 July 1991, *G. L. Webster et al. 28707* (AAU [2], DAV [2], QCNE); *idem*, 20 November 1998, *G. L. Webster et al. 32958* (DAV); Cerro Sta. Lucia (Cerro Campana), Maquipucuna area, 6 km airline distance E of Nanegal, 20 July 1990, *G. L. Webster & B. Bonning 28330* (DAV, QCNE, WIS); *idem*, 7 January 1995, *G. L. Webster et al. 31078* (DAV); slopes above Río Pichán, Bosque Protector Maquipucuna, 7.5 km airline distance SE of Nanegalito, 1 September 1993, *G. L. Webster et al. 30118* (DAV); *idem*, 1 September 1993, *G. L. Webster et al. 30217* (DAV, QCNE); Quebrada Santa Rosa, steep slopes SW of Río Pichán, 10 km airline distance WSW of Calacalí, 12 January 1995, *G. L. Webster & J. Cooper 31184* (DAV); *idem*, 24 June 1996, *Webster et al. 31829* (DAV, QCNE); along Río Umachaca, river trail, Bosque Protector Maquipucuna, 17 June 1996, *G. L. Webster et al. 31559* (DAV, QCNE); Reserva El Pahuma, trail to waterfall, 18 June 1996, *G. L. Webster & A. del Hierro 31570* (DAV, QCNE); 11 km by road W of Pacto, 17 November 1998, *G. L. Webster et al. 32872* (DAV); La Vuelta Brava zone, Nanegalito-Armenia-Loma de San José road, 9 December 1987, *V. Zak & J. Jaramillo 3237* (WIS).

Podandrogyne websteri grows on the same western slopes in the same kind of forests as *P. flammea*, and the two species closely approach or overlap one another morphologically and geographically. The differences separating them are both qualitative and quantitative and, although not great, are usually correlated. Their geographic ranges approach one another really closely only in the Los Ilinizas and Cerro Golondrinas reserves. Morphological differentiation in combination with local distribution, embedded as it is within the collective range, supports the description of *P. websteri* as a new species.

The earliest specimen seen, collected by Jameson in the 1800s, lacks data; subsequent collections were not made until 1943, then 1979. Nearly all of the collections were made during the 1980s, by various collectors representing Scandinavian herbaria, and the 1990s, mostly by G. L. Webster and his students of the University of California–Davis; both groups have contributed significantly to our knowledge of the rainforests of this part of Ecuador.

The leaves of *Podandrogyne websteri* are all or mostly 1-foliolate, seldom in part 3-foliolate, and have shorter petioles and generally decidedly smaller, thicker-textured blades with more prominent secondary veins than those of *P. flammea*, in which the leaves are generally 3-foliolate,

FIGURE 3. *Podandrogyne websteri*. **A–B**, habits with inflorescences in pistillate phase (A missing distal end of rachis); **C–D**, habits with inflorescences in late (C) and early (D) staminate phase; **E**, flowers, pistillate below, staminate above; **F**, close-up of rachis, showing pedicellar scars and patchy distribution of hairs. A from *Webster et al. 31829* (QCNE); B from *Webster et al. 30217* (DAV); C from *Nicolalde & Grupo de Post-Grado 350* (MO); D from *Webster et al. 31559* (QCNE); E pistillate from *Webster et al. 30217* (DAV), staminate from *Smith 1926* (holotype, WIS); F from *Delgado y Grupo Post-grado MO-QCNE 15* (WIS).

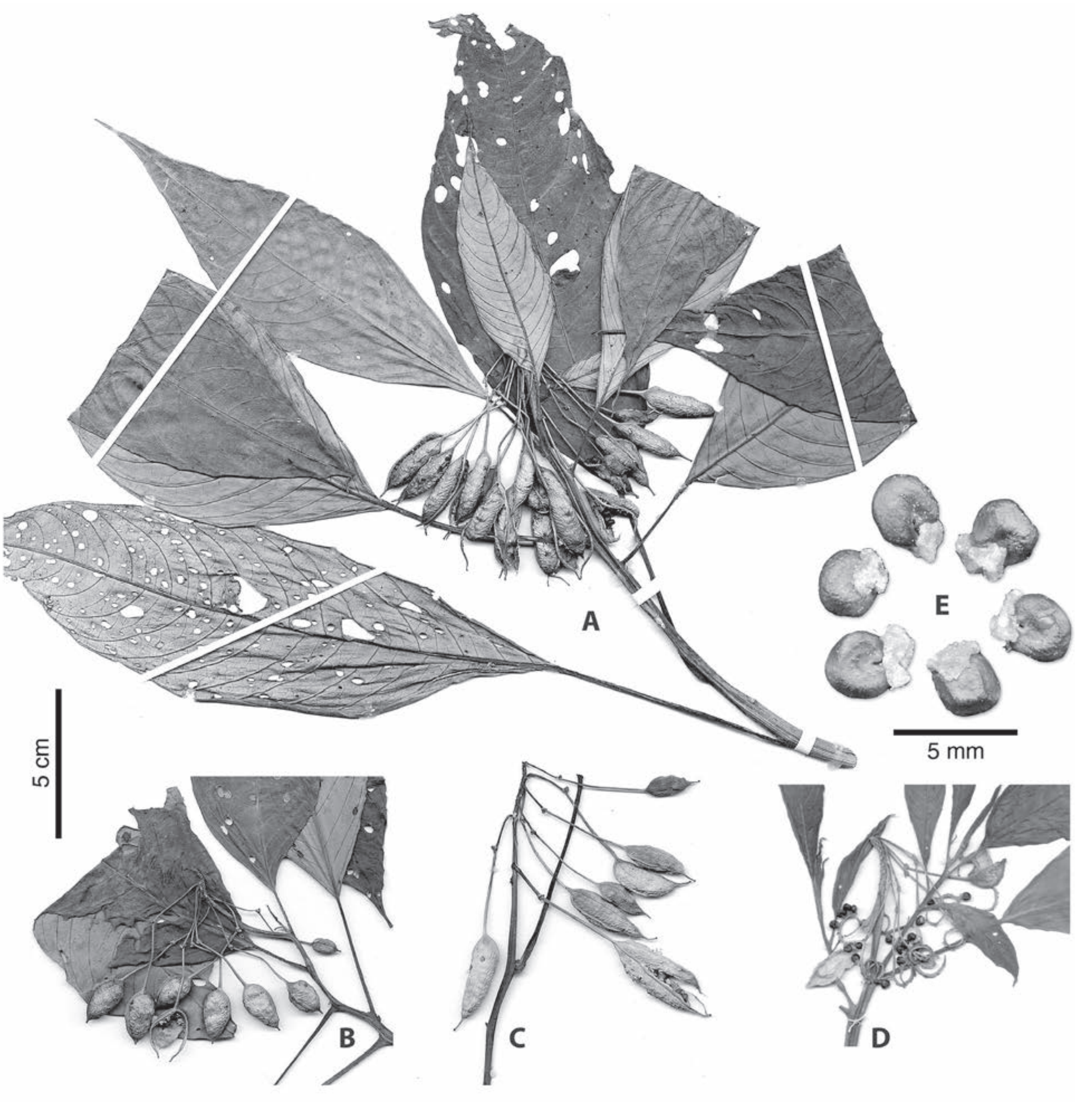


FIGURE 4. *Podandrogyne websteri*. **A–D**, representative infructescences, D with dehisced fruits; **E**, seeds. A from *Webster & del Hierro 31570* (DAV); B from *Webster et al. 28691* (DAV); C from *Zak 1794* (WIS); D from *Nicolalde & Grupo de Post-Grado 333* (QCNE); E from *Nicolalde & Grupo de Post-Grado 333* (MO).

sometimes partly 1- or 5-foliolate, and membranous. The inflorescences in *P. websteri* tend to be more strongly corymbiform from the outset, and they are smaller and less showy, as are the flowers themselves. The staminate flowers in the two species are quite similar, overlapping as they do in androgynophore, filament, and anther lengths, but the pistillate flowers differ, those of *P. websteri* having smaller ovaries (2.0–3.5 mm instead of 3.5–8.0 mm) and shorter gynophores (4–6 vs. 6–10 mm) and androgynophores (8–12 vs. 15–18 mm). The same trends are evident in the fruits, which in *P. websteri* can be similar in shape but on average are smaller and invariably stylose-beaked (Fig. 4A–C, 5), whereas in *P. flammea* they vary from lacking even a nubbin to being apiculate or shortly beaked (Fig. 2F–G, 5). The scatter diagram (Fig. 5) shows that there is a strong association between fruit shape and androgynophore length. A complete sample of each of the two species grouped them into distinct clusters and emphasized that, apart from shape, *P. websteri* does not show much variation with respect to fruit characters.

The close morphological similarity between *Podandrogyne websteri* and *P. flammea* means that occasional collections, especially if lacking pistillate flowers or fruits, can be difficult to identify. For example, both sheets of *Molau*

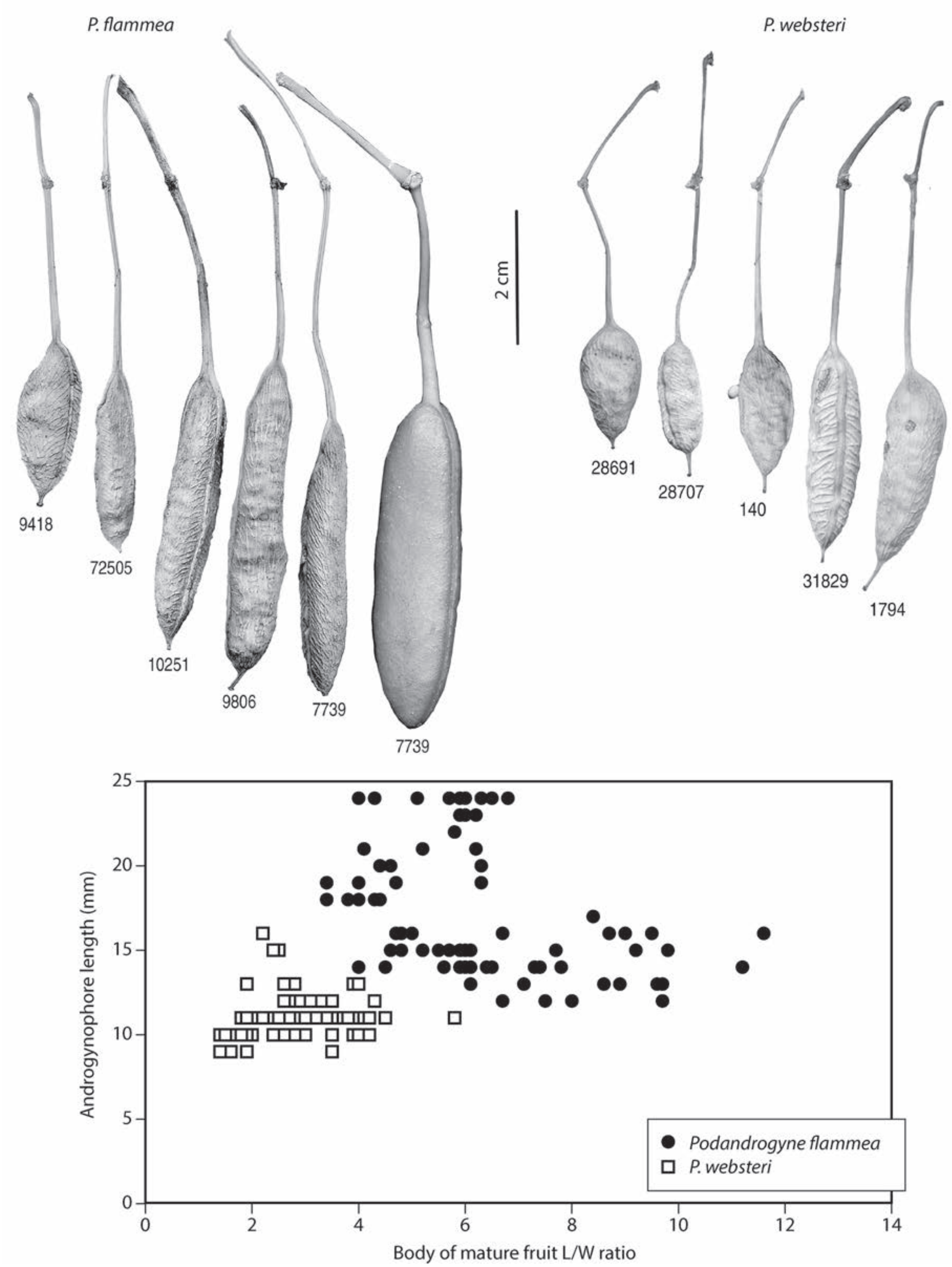


FIGURE 5. Morphological variation in fruits of *Podandrogyne flammea* (upper left) and *P. websteri* (upper right). Each fruit obtained from a different dried herbarium collection (number cited) except the largest one of *P. flammea*, which came from fluid-preserved material and was one of the largest fruits in the population. The scatter diagram illustrates the correlation of fruit length/width (if ± compressed) or length/thickness (if terete) and androgynophore length in the two species. Total morphological variation shown: *P. flammea*: 82 fruits/12 collections; *P. websteri*: 89 fruits/12 collections. (Due to overlapping values, only 128 data points appear in the diagram.)

and Eriksen 3050 have fairly robust inflorescences, large leaf blades that are closer to membranous than coriaceous, and large staminate flowers; overall, they have the gestalt of *Podandrogyne flammea*. All dimensions, however, overlap the largest extremes of *P. websteri*, and *3050*, which is also a good match for *Webster et al. 32872*, now succeeds the latter collection as the most robust representative of *P. websteri*. Furthermore, several other collections taken from the same short stretch of highway as *3050* have all been identified as the latter species. Judging by leaf characters and rachis length, the sheet of *Jaramillo & Zak 7827* at WIS and the right-hand stem on the sheet of *Delgado and Grupo Post-Grado 15* at MO seem closest to *P. flammea*, but the axillary shoot on the otherwise old, leafless, left-hand branch on the Delgado specimen has narrower, thicker leaves and a modest inflorescence, thus not only resembling *P. websteri* but also suggesting that what material is chosen for collection can confound specimen identification. Be that as it may, duplicate specimens of these two collections (*7827* and *15*) and others from the same reserves are clearly *P. websteri*. Leaves on the WIS specimen of *Tirado et al. 1174* have blades that are large, thin-textured, and pubescent, matching in size and indumentum those of *Harling et al. 9661* and *Palacios 9806* better than those typical of *P. websteri*. However, the leaves on the MO sheet numbered *1174* are typical of *P. websteri* in every way, as are the fruits on both the MO and WIS sheets. From a vegetative standpoint, the WIS sheets of *1174* and *9806* could easily be duplicates of one another, but the fruits on all sheets of *9806*, like *1174* also taken from the vicinity of El Carmen, province of Carchi, are indisputably those of *P. flammea*. Annotation decisions in these cases mean not only that leaves on specimens from Carchi are extremely variable but also that both species occur in the protected Cerro Golondrinas forest. Moreover, they raise the question of whether plants from Carchi represent a recently speciated, unstable complex of plants in which the geographical structuring of morphological variation in the *P. flammea–P. websteri* species pair is somewhat blurred.

Literature Cited

Bernal, R., S. R. Gradstein, and M. Celis, eds. 2015. *Catálogo de Plantas y Líquenes de Colombia*. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá. http://catalogoplantasdecolombia.unal.edu.co/es/ (consulted July 31, 2020).

Cochrane, T. S. 2016. New species of *Podandrogyne* (Cleomaceae) II. Two species endemic to the southwestern and northern Colombian Andes. Harvard Pap. Bot. 21: 125–130. DOI: 10.3100/hpib.v21iss1.2016.n10

Davis, S. D., V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos, and A. C. Hamilton, eds. 1997. *The Americas*. Vol. 3 of *Centres of Plant Diversity. A Guide and Strategy for Their Conservation*. World Wide Fund for Nature (WWF) and World Conservation Union (IUCN) Publications Unit, Cambridge, U.K.

Groombridge, B., ed. 1992. *Global Biodiversity. Status of the Earth's Living Resources*. A report compiled by the World Conservation Monitoring Center. Chapman & Hall, London, Glasgow, New York, Tokyo, Melbourne, and Madras.

Jørgensen, P. M., and S. León-Yánez, eds. 1999. *Catalogue of the Vascular Plants of Ecuador*. Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 75. Botanical Garden Press, St. Louis.

Webster, G. L., and R. M. Rhode. 2001. *Plant Diversity of an Andean Cloud Forest. Checklist of the Vascular Flora of Maquipucuna, Ecuador*. Appendix B. Univ. California Publ. Bot. 82. University of California Press, Berkeley.

Woodson, R. E., Jr. 1948. *Gynandropsis, Cleome*, and *Podandrogyne*. Ann. Missouri Bot. Gard. 35: 139–146. DOI: 10.2307/2394390.

THE REINSTATEMENT OF *HILAIRANTHUS* (ACANTHACEAE): A GENUS FROM NEOTROPICAL AND WESTERN-PALEOTROPICAL MANGROVES

Xavier Cornejo[1]

Abstract. On the basis of previously documented genetic evidence, which correlates with morphological traits and a well-defined biogeographic pattern of distribution, *Hilairanthus* Tiegh. is recognized and reinstated as a genus of mangrove segregated from *Avicennia* (Acanthaceae). The genus is lectotypified, and the following combinations are formally proposed for *Hilairanthus germinans*, *H. bicolor*, and *H. schaueriana*.

Keywords: *Avicennia*, Acanthaceae, mangroves, Neotropics, Paleotropics

Resumen. Con base en evidencia genética, correlacionada con caracteres morfológicos y un definido patrón de distribución biogeográfica, se reconoce y restaura *Hilairanthus* Tiegh., un género de mangle segregado de *Avicennia* (Acanthaceae). Se lectotipifica a *Hilairanthus* y además se proponen formalmente las siguientes combinaciones: *Hilairanthus germinans*, *H. bicolor* y *H. schaueriana*.

Palabras claves: *Avicennia*, Acanthaceae, manglares, Neotrópico, Paleotrópico

Avicennia L. (1753) is a well-known and widely distributed woody genus of Acanthaceae, found in mangroves, beaches, and salt marshes along tropical coastlines around the world (Bakhuizen, 1921; Moldenke, 1960; Duke, 1991; Daniel, 2016). The species of this genus, regarded as true mangroves, are characterized by the presence of subsuperficial cable roots bearing pencil-thick erect pneumatophores, decussate evergreen leaves, and water-dispersed fruits, adapted to settling in periodically inundated habitats with high levels of salinity (Tomlinson, 1986; Cornejo, 2014). On the basis of fossil records and molecular analysis, the calibrated basal position of *Avicennia* dates back 100 MYA; the genus began to diversify during the Eocene, 55 to 35 MYA; and the assumed range of divergence time of the main lineages has been estimated to be from 10 to 50 MYA (Tripp and McDade, 2014). Molecular phylogenetic studies based on chloroplast and nuclear sequences have revealed the presence of two monophyletic clades within the genus (Li et al., 2016): the Indo–Western Pacific (IWP) lineage and the Atlantic–Eastern Pacific (AEP) lineage. The IWP lineage comprises five species and three varieties grouped into three subclades: (1) *A. officinalis* L. and *A. integra* N.C. Duke; (2) *A. marina* var. *marina* (Forssk.) Vierh., *A. marina* var. *eucalyptifolia* (Zipp. ex Moldenke) N.C. Duke, and *A. marina* var. *australasica* (Walp.) Moldenke; and (3) *A. alba* Blume and *A. rumphiana* Hallier f. The AEP lineage is represented by the transoceanic *A. germinans* (L.) L., the Mesoamerican–Eastern Pacific *A. bicolor* Standl., and the western Atlantic and South American *A. schaueriana* Stapf & Leechm. ex Moldenke. These two clades, currently gathered under the same generic name, have well-defined and disjunct biogeographical patterns of distribution and are correlated with morphologically different floral structures (Table 1). Therefore, the diphyletic *Avicennia* s. l. nomenclature does not reflect natural taxonomic units. As the South Asian *A. officinalis* is the nomenclatural type of the genus (Linnaeus, 1753; Moldenke, 1960), the molecular results suggest that the name *Avicennia* must be kept for the IWP clade. Consequently, a proper generic name must be found for the remaining species included in the sister AEP clade, which do not fit biogeographically or morphologically the IWP clade of *Avicennia* s. str. The aim of this article is to provide an accurate generic name that is useful taxonomically and for conservation and management of AEP black mangroves, which are currently threatened by turistic and aquacultural development throughout its geographical range. The choice to recognize the AEP *Avicennia* s. l. as a distinct taxon at generic rank is based not only on biogeographical disjunction correlated to morphological differences but on the fact that the AEP clade is the outer group of *Avicennia* s. str. (Li et al., 2016), and that each of the three IWP subclades is characterized by distinctive morphological floral characters. These characters include corolla aestivation, stigma position in relation to the anthers, length of style, and insertion of filaments (Tomlinson, 1986; Li et al., 2016), suggesting that further studies are needed for the IWP subclades and that those taxa may deserve subgeneric recognition. Moreover, the species of the IWP and AEP clades are geographically isolated, so given the great distances that separate them, at least at present, the possibility of exchanging genetic material by natural means does not exist.

A review of the literature throughout the complex nomenclatural history shows that *Hilairanthus* Tiegh. (1898) is the only genus proposed as a segregate from *Avicennia* for the American and West African species. Morphological features, pattern of geographical distribution, and citation of species names assigned to the then-new genus perfectly match the AEP clade. In the original publication, *Hilairanthus* was described in French and without Latin; however, the genus fulfills the requirements

Thanks are due to Sajid Sheikh from the Department of Botany, Shivaji University, Kolhapur, India, and to Mandar Datar from Agharkar Research Institute, Pune, India, for the permission to use his images of *Avicennia officinalis* L. and *A. marina* (Forssk.) Vierh. in Fig. 1C; and to the Biodiversity Heritage Library (BHL) for the availability of digital versions of valuable old publications. Astrid Freire made field observations on the floral morphology of *Hilairanthus germinans* in the Galapagos Islands.

[1] Herbario GUAY, Departamento de Botánica, Facultad de Ciencias Naturales, Universidad de Guayaquil, Av. Raúl Gómez Lince s.n. y Av. Juan Tanca Marengo (campus Mapasingue), P.O. Box 09-01-10634, Guayaquil, Ecuador; xcornejoguay@gmail.com

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 231–235.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n11, Published online: 31 December 2020

Table 1. Morphological comparison of *Hilairanthus* Tiegh. and *Avicennia* L.

	Hilairanthus	*Avicennia*
Flower buds	Often asymmetric, ± curved upward, especially young ones	All symmetric and straight
Color of corollas	White or creamish white, yellow at inner throat	Full yellow to golden yellow or orange
Symmetry of corollas	Distinctly zygomorphic	Somewhat zygomorphic (in *A. officinalis*) and strictly actinomorphic
Corolla aestivation	Imbricate	Barely imbricate (in *A. officinalis*) to mostly valvate
Length of stamen filament	Didynamous, lower-inserted outer pair ± longer than upper-inserted inner pair	± equal length
Insertion of stamen filament	Adnate only at inner base and mostly free from corolla tube	Inserted at mouth of corolla tube, connate, or adnate along full length of inner corolla tube (in *A. officinalis*)
Arrangement of stamen filament	Upper-inserted inner pair closer to central pistil, lower-inserted outer pair at maturity turning divergent from pistil	All equidistant or nearly so from all points of a square or pentagon and ± equally placed around corolla tube mouth
Arrangement of anthers	Two on each side of pistil, all in a row or arc at upper half of corolla, ± horizontal under upper corolla lobe	All equidistant or nearly so from all points of a square or pentagon and ± equally placed on or over corolla tube mouth and around pistil
Distribution	Atlantic–East Pacific	Indo–West Pacific

of Art. 11, 38, and 39 of the ICN (Turland et al., 2018) and therefore, supported by the molecular, biogeographical, and morphological evidence, deserves to be recognized as valid. The genus was represented by *H. tomentosus* (Jacq.) Tiegh. and *H. nitidus* (Jacq.) Tiegh., without designation of a nomenclatural type. Both names previously published together by Jacquin (1760) under *Avicennia* were later regarded as synonyms of the well-known and widespread black mangrove *A. germinans* (1764), which at that time was placed and remained in *Bontia* L. (since 1759). In this work, *Hilairanthus* is reinstated, a nomenclatural type is designated, and the corresponding new combinations in *Hilairanthus* are presented for the three species of the AEP clade.

TAXONOMY

Hilairanthus Tiegh., J. Bot. (Morot.) 12: 358. 1898. Fig. 1A–B.

Lectotype: *Hilairanthus nitidus* (Jacq.) Tiegh., J. Bot. (Morot.) 12: 358. 1898, designated here. = *Hilairanthus germinans* (L.) Cornejo, *comb. nov.*

Hilairanthus can be recognized by its zygomorphic white or creamish-white corollas, stamens didynamous, filament adnate at inner base of corolla tube, upper-inserted inner pair somewhat shorter and upright, close to central pistil, lower-inserted outer pair at maturity turning divergent from pistil, ± longer than the inner pair, four anthers arranged into a row or arc at upper half of corolla under dorsal lobe and ± horizontal to spike (vs. corollas yellow or golden-yellow to orange, filament of stamens of ± equal length, all inserted or apparently inserted under the sinus between lobes and equally placed at the mouth of corolla tube, and anthers equidistant or nearly so from all points of a square or pentagon but never forming a row or arc). The white color of corollas as a distinct character has been noted by van Tieghem (1898) and Moldenke (1960: part 3). The distinctive zygomorphic corollas and arrangement of the stamens of *Hilairanthus*, most likely a result of coevolution, allow the more ample access at the lower part of corolla mouth that is preferred by entomophilous visitors and pollinators (Tomlinson, 1986; Cornejo, 2014).

Trees or shrubs. *Secondary subsuperficial cable roots* with many pneumatophores, those narrow, pencil-thick, erect to 50 cm high, lenticellate. *Leaves* decussate; blade simple, entire, petiolate. *Stipules* absent. *Inflorescences* terminal and axillary, in dense panicles or spikes. *Flowers* sessile. *Calyx* dialisepalous, sepals 5, persistent in fruit. *Corolla* white to creamish-white, zygomorphic, gamopetalous, forming a tube at basal third to half, the lobes 4(–5), free (2 fused at dorsal lobe). *Stamens* 4, didynamous, the filaments alternipetalous at base, mostly free, adnate at inner base of corolla tube, the upper-inserted inner pair upright closer to central pistil and somewhat shorter, the lower-inserted outer pair farther from pistil and at maturity turning divergent, the 4 anthers arranged into a row or arc at upper half of corolla under dorsal lobe and ± horizontal to spike, longitudinally dehiscent, initially white, turning black at maturity. *Ovary* 1, superior; style 1, white; stigma bifid, the lobes shortly linear. *Fruit* asymmetric, laterally compressed, dehiscent in 2 valves after falling in water, the epicarp nearly smooth to usually rugose; *seed* 1, without testa, cotyledons 2, thick, folded, the outer cotyledon enclosing the inner, the radicle white, densely pilose.

Distribution: a genus found along both coasts of the American continent—on the eastern Pacific coast from western Mexico to northwestern Peru (Piura) and the Galapagos Islands, and on the Atlantic coast from southern North America (southeastern United States and Mexico), Bermuda, West Indies, and Central America to South America (to southern Brazil and Uruguay)—and in tropical Western Africa (van Tieghem, 1898; Moldenke, 1960).

1. Hilairanthus germinans (L.) Cornejo, *comb. nov.* Fig. 1A–B.

Basionym: *Bontia germinans* L., Syst. Nat. ed. 10 (2): 1122. 1759. TYPE: JAMAICA. *P. Browne s.n.* (Lectotype, designated by Stearn, 1958: LINN-813.2).

Homotypic synonym: *Avicennia germinans* (L.) L., Sp. Pl. ed. 3 (2): 891. 1764, *syn. nov.*

Heterotypic synonyms: *Avicennia nitida* Jacq., Enum. Syst. Pl. 25. 1760. TYPE: WEST INDIES. Without date, *N. Jacquin s.n.* (Lectotype, designated by Moldenke, 1960: BM-992851).

Avicennia officinalis var. *nitida* (Jacq.) Kuntze, Revis. Gen. Pl. 2: 502. 1891.

Hilairanthus nitidus (Jacq.) Tiegh., J. Bot. (Morot) 12: 358. 1898.

Avicennia tomentosa Jacq., Enum. Syst. Pl. 25. 1760. TYPE: WEST INDIES. Without date, *N. Jacquin s.n.* (Lectotype, designated by Moldenke, 1960: BM-992852).

Hilairanthus tomentosus (Jacq.) Tiegh., J. Bot. (Morot) 12: 358. 1898.

Avicennia tomentosa Jacq. var. *cumanensis* Kunth, Nov. Gen. Sp. 2: 229 (ed. folio); 284 (ed. quarto). 1818 (“1817”). TYPE: VENEZUELA. Cumana: “Crescit ad litora maris Cumanensis,” *A. Bonpland 68* (Lectotype: B, not found).

Avicennia tomentosa Jacq. var. *campechensis* Kunth, Nov. Gen. Sp. 2: 229 (ed. folio); 284 (ed. quarto). 1818 (“1817”). TYPE: MEXICO. Campeche: “Crescit prope Campeche Mexicanorum,” *A. Bonpland s.n.* (Lectotype, designated here: P-00670135; Isolectotype: P-00689943).

Avicennia tomentosa Jacq. var. *guayaquilensis* Kunth, Nov. Gen. Sp. 2: 230 (ed. folio); 284 (ed. quarto). 1818 (“1817”). TYPE: ECUADOR. Guayas: Guayaquil, “Crescit prope Guayaquil Quitensium,” *A. Bonpland s.n.* (Lectotype, designated here: P-00670136; Isolectotypes: P-00689945, P-00689946, P-00689947).

Avicennia africana P. Beauv., Fl. Oware 1: 80. 1806. TYPE: Oware et Benin, *A.M.F. Palisot de Beauvois s.n.* (Lectotype, designated here: G-00023640; Isolectotype: G-00023641).

Avicennia floridana Raf., Atlantic J. 1:148. 1832. TYPE: Not designated (no specimens cited).

Avicennia oblongifolia Chapm., Fl. South. U.S. 310. 1860. TYPE: U.S.A. Florida: Monroe County, Oct, Key West (fide protologue); specimens would be in the Chapman herbarium at NY, but not found (Daniel, 2016).

Avicennia floridana Gand., Bull. Soc. Bot. France 65: 64. 1918, *homon. illegit*. TYPE: U.S.A. Florida: Lee County, Fort Meyers, *A. Hitchcock 270* (see discussion in Daniel, 2016).

Avicennia tonduzii Moldenke, Phytologia 1: 273. 1938. TYPE: COSTA RICA. Puntarenas: Punta Mala [ca. 09°03'54.48"N, 083°39'04.84"W], zone littorale du Pacifique, Mar 1892, *A. Tonduz 6776* (Holotype: BR, fragment of holotype at NY; Isotypes: BM, M, MICH, US).

Habitat and distribution: southern North America (southeastern USA and Mexico), West Indies, Central America, and South America (Colombia, Ecuador [including the Galapagos islands]), and Peru on the Pacific coast; Venezuela, French Guiana, Guyana, Suriname, and Brazil on the Atlantic coast. Habitats include beaches, mangrove swamps, and salt marshes, at elevations at or near sea level (Moldenke, 1960; Cornejo, 2014; Daniel, 2016).

2. Hilairanthus bicolor (Standl.) Cornejo, *comb. nov.*

Basionym: *Avicennia bicolor* Standl., J. Wash. Acad. Sci. 13(15): 354. 1923. TYPE: PANAMA. Coclé. Aguadulce, along the outskirts of the tidal belt, 08°14'30"N 080°32'30"W, 5 Dec 2011 (fl), *H. Pittier 4968* (Holotype: US-715142; Isotypes: BM-992849, F-636788, K-573632, NY-337274, P, US-715141).

Habitat and distribution: Pacific coast of southern Mexico (Chiapas) to southern Panama; in beaches, mangrove swamps, and salt marshes, at elevations at or near sea level (Moldenke, 1960; Cornejo, 2014; Daniel, 2016).

3. Hilairanthus schaueriana (Stapf & Leechm. ex Moldenke) Cornejo, *comb. nov.*

Basionym: *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, Lilloa 4: 336. 1939.

Heterotypic synonyms: *Avicennia nitida* var. *trinitensis* Moldenke, Phytologia 1: 96. 1934. TYPE: TRINIDAD AND TOBAGO. Caroni swamp, 29 May 1932 (fl), *R. L. Brooks 12656* (Holotype: NY-337279), *syn. nov.*

Avicennia schaueriana f. *glabrescens* Moldenke, Phytologia 34: 485. 1976. TYPE: TRINIDAD AND TOBAGO. Caroni swamp, 9 May 1932 (fl), *R. C. Marshall 12651* (Holotype: NY-337281), *syn. nov.*

Avicennia schaueriana f. *candicans* Moldenke, Phytologia 35: 13. 1976. TYPE: BRAZIL. Rio de Janeiro, Manguinhos, 16 Sep 1948 (fl), *A. L. Moldenke & H. L. Moldenke 19606* (Holotype: NY-337280), *syn. nov.*

Habitat and distribution: Atlantic coast of Brazil to Uruguay, in mangrove swamps, at elevations at or near sea level (Moldenke, 1960; Tomlinson, 1986).

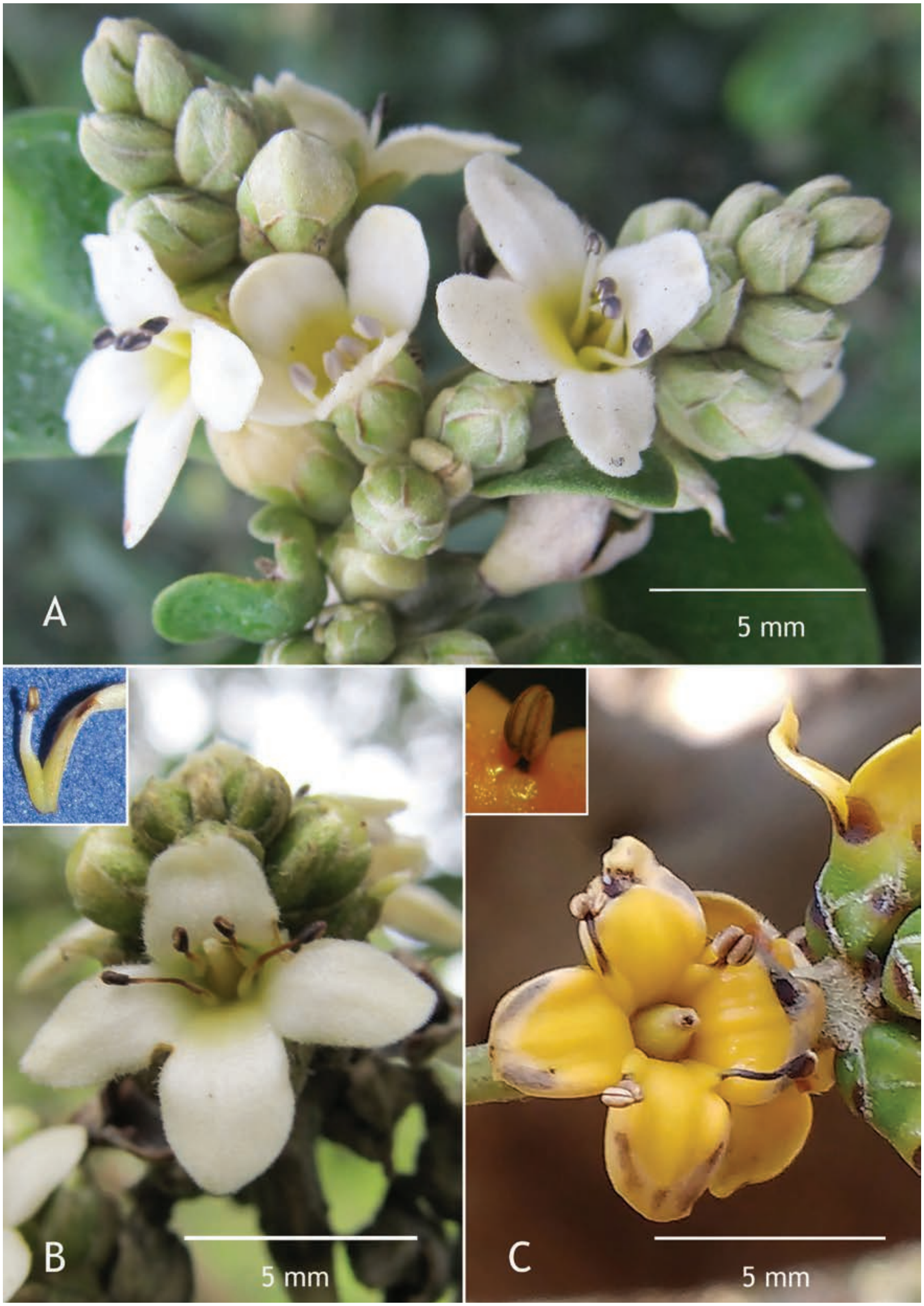


FIGURE 1. **A**–**B.** *Hilairanthus germinans* (L.) Cornejo. **A,** three dense spikes bearing open flowers, note the ± horizontal one-row arrangement of anthers; **B,** flower, adaxial view, note the zygomorfic white corolla, stamens mostly free from corolla tube, and the filament adnate at inner base of corolla tube (upper left square). **C.** *Avicennia officinalis* L. and *A. marina* (Forssk.) Vierh. **C,** flower, adaxial view, note the mostly actinomorphic pale orange corollas, stamens arranged from all points of a square and ± equally placed around corolla tube mouth, the filaments adnate along full length of inner corolla tube and apparently inserted under sinus at the mouth of corolla (*A. officinalis*) or the filament inserted at the mouth of corolla tube (*A. marina*, upper left square). C, *A. officinalis* courtesy of Mandar Datar and *A. marina* courtesy of Sajid Sheikh, both from Maharashtra, India.

LITERATURE CITED

BAKHUIZEN VAN DEN BRINCK, R. C. 1921. *Revisio generis Avicenniae*. Bull. Jard. Bot. Buitenz. 3: 199–226.

CORNEJO, X., ED. 2014. *Plants of the South American Pacific Mangrove Swamps (Colombia, Ecuador, Peru)*. Universidad de Guayaquil, Ecuador.

DANIEL, T. 2016. *Avicennia* (Acanthaceae: Avicennioideae) in North America and Mesoamerica. Proceedings of the California Academy of Sciences 63(5): 163–189.

DUKE, N. C. 1991. A systematic revision of the mangrove genus *Avicennia* (Avicenniaceae) in Australasia. Australian Systematic Botany 4: 299–324.

JACQUIN, N. 1760. *Enumeratio Systematica Plantarum, quas in insulis Caribaeis vicinaque Americes continente detexit novas, aut jam cognitas emendavit*. Lugduni Batavorum, Leiden.

LI, X., N. C. DUKE, Y. YANG, L. HUANG, Y. ZHU, Z. ZHANG, R. ZHOU, C. ZHONG, Y. HUANG, AND S. SHI. 2016. Re-evaluation of phylogenetic relationships among species of the mangrove genus *Avicennia* from Indo-West Pacific based on multilocus analyses. PloS One 11(10): e0164453.

LINNAEUS, C. 1753. *Species Plantarum*. Impensis Laurenti Salvii, Stockholm.

MOLDENKE, H. N. 1960. Materials toward a monograph of the genus *Avicennia*. I–III. Phytologia 7: 123–168, 179–232, 259–293.

STEARN, W. T. 1958. A key to West Indian Mangroves. Kew Bulletin 13: 33–37.

TOMLINSON, P. B. 1986. *The Botany of Mangroves*. Cambridge University Press, Cambridge, England.

TRIPP, E. A., AND L. A. MCDADE. 2014. A rich fossil record yields calibrated phylogeny for Acanthaceae (Lamiales) and evidence for marked biases in timing and directionality of intercontinental disjunctions. Systematic Biology 63(5): 660–684.

TURLAND, N. J., J. H. WIERSEMA, F. R. BARRIE, W. GREUTER, D. L. HAKSWORTH, P. S. HERENDEEN, S. KNAPP, W. H. KUSBER, D. Z. LI, K. MARHOLD, AND T. W. MAY. 2018. *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)*. Adopted by the 19th International Botanical Congress, Shenzhen, China, July 2017. Koeltz Botanical Books, Königstein.

VAN TIEGHEM, P. E. L. 1898. Avicenniacées et Symphorémacées place de ces deux nouvelles familles dans la classification. Journal de Botanique (Morot) 12: 353–364.

Page 236 intentionally left blank.

A NEW LARGE-LEAVED SPECIES OF *CALYPTRANTHES* (MYRTACEAE) FROM ECUADOR

Maria Lucia Kawasaki,[1,2] Bruce K. Holst,[3] and Alvaro J. Perez[4]

Abstract. *Calyptranthes magna*, a new species of Myrtaceae from Yasuní National Park (Orellana, Ecuador), is described and illustrated.

Resumen. Se describe *Calyptranthes magna*, una especie nueva de Myrtaceae del Parque Nacional Yasuní (Orellana, Ecuador).

Keywords: *Calyptranthes*, Myrtaceae, Ecuador, Yasuní

In a recent treatment of Myrtaceae from Ecuador (Kawasaki et al., 2019), we reported 131 species, including 28 species of *Calyptranthes* Sw.; it was mentioned, however, that there were many more undescribed taxa in the country. In this paper, an additional new species is described and illustrated.

Calyptranthes magna B. Holst, M.L. Kawas. & Á.J. Pérez, *sp. nov*.
TYPE: ECUADOR. Orellana: Yasuní National Park, Yasuní Scientific Station, 50-ha plot, 00˚38'S, 76˚30'W, 200–300 m, 15 Feb 2009 (fl), Á. J. Pérez & P. *Alvia 4087* (Holotype: QCA). Fig. 1–2.

Tree; trichomes yellowish brown; leaves obovate, subcordate, truncate at base; inflorescences to 8 cm long, multiflorous; flower buds obovoid, 7–9 mm long, furfuraceous.

It is distinguished from *Calyptranthes nervata* M.L. Kawas. & B. Holst by the obovate leaves with biconvex midvein and shorter inflorescences with larger flower buds.

Trees 5–10 m high, the branchlets terete; trichomes bifurcate, yellowish brown. *Leaf blades* obovate, coriaceous, 25–42 × 15–24 cm, drying olive-green above, yellowish-green below, puberulous to glabrous on both surfaces; glands indistinct above, punctiform and salient below; midvein biconvex on the upper surface, convex below, with glands throughout its length on both surfaces; lateral veins 25–30 pairs, salient above, plane below; marginal vein 1, almost parallel to the margin, ca. 2–5 mm from it; apex abruptly acuminate; base subcordate, truncate; petioles 6–8 mm long, terete, glabrous, drying reddish brown. *Inflorescences* paired panicles, subterminal, multiflorous, to 8 cm long, the axes puberulous; bracts lanceolate, ca. 1.5 cm long, hirsutulous; bracteoles not seen, early deciduous; flower buds obovoid, 7–9 mm long, sessile, furfuraceous, the calyx closed; petals not seen; disk ca. 4 mm diam., glabrous; stamens ca. 6 mm long; style 6–7 mm long; ovary 2-locular, with 2 ovules per locule. *Fruits* not seen.

Phenology: collected with flowers in February.

Distribution, habitat, and ecology: *Calyptranthes magna* is endemic to Yasuní National Park in the Orellana province, growing at 200–300 m elevation. According to the Ministerio del Ambiente del Ecuador (2013), the area is dominated by "bosque siempre verde de tierras bajas del Napo-Curaray (BsTa02)"; to date it is only recorded from the 50-ha plot and the forests surrounding the Yasuní Scientific Station (Valencia et al., 2004, 2009). Population dynamics data for this species come from a 25-ha area, where 11 individuals with dbh ≥ 1 cm were recorded; between 1995 and 2007, the annual mortality rate was 4.11%, recruitment rate was 2.15 individuals per year, average growth rate was 0.55 mm per year, and above-ground biomass was 0.13 ton.

Etymology: the specific epithet refers to the large leaves and flowers.

Conservation status: following IUCN (2017) criteria, its status would be Data Deficient (DD). However, its population should be protected within the Yasuní National Park.

Among the species of *Calyptranthes* from Ecuador, *C. magna* is similar to *C. nervata* M.L. Kawas. & B. Holst in the large leaves with many pairs of lateral veins and in the subterminal, multiflorous inflorescences; it is distinguished by the obovate (vs. narrowly elliptic to elliptic, oblong, or oblanceolate) leaves with biconvex (vs. impressed) midvein, plane (vs. salient) lateral veins on the lower surface, and shorter inflorescences (to 8 cm long vs. 12–31 cm long) with larger flower buds (7–9 mm long vs. 5–6 mm long).

This new species could also be confused with *Calyptranthes maxima* McVaugh, a species from Colombia and Peru. These two species have large flower buds in short panicles and large leaves with biconvex midvein on the upper surface; however, in *C. magna*, the leaves are obovate (vs. narrowly elliptic in *C. maxima*).

Literature Cited

IUCN. 2017. Guidelines for using the IUCN red list categories and criteria, version 13. Prepared by the Standards and Petitions Subcommittee. Available from: http://www.iucnredlist.org/documents/redlistGuidelines.pdf (accessed April 1, 2020).

Kawasaki, M. L., B. K. Holst and A. J. Perez. 2019. Myrtaceae. Fl. Ecuador 95: 1–186.

Ministerio de Ambiente del Ecuador. Sistema de clasificación de los ecosistemas del Ecuador continental. 2013. Subsecretaría de Patrimonio Natural, Quito.

Valencia, R., R. Condit, H. C. Muller-Landau, C. Hernandez, and H. Navarrete. 2009. Dissecting biomass dynamics in a large Amazonian forest plot. J. Trop. Ecol. 25: 473– 482.

Valencia, R., R. Foster, G. Villa, R. Condit, J.-C. Svenning, C. Hernández, K. Romoleroux, E. Losos, E. Margård, and H. Balslev. 2004. Tree species distribution and local habitat variation in the Amazon: Large forest plot in eastern Ecuador. J. Ecol. 92: 214–229.

We thank Renato Valencia and Consuelo Hernández for providing data on this species from the 50-ha plot in Yasuni.

[1] Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605-2496, U.S.A.
[2] Corresponding author: lkawasaki@fieldmuseum.org
[3] Marie Selby Botanical Gardens, 811 South Palm Avenue, Sarasota, Florida 34236-7726, U.S.A.; bholst@selby.org
[4] Herbario QCA, Pontificia Universidad Católica del Ecuador, Apartado 17-01-2184, Quito, Ecuador; ajperzc@puce.edu.ec

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 237–239.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n12,

FIGURE 1. *Calyptranthes magna* B. Holst, M.L. Kawas. & Á.J. Pérez. **A**, leaves, inflorescences, and detail of flower bud. From *Pérez & Alvia 4087* (Holotype: QCA).

FIGURE 2. *Calyptranthes magna* B. Holst, M.L. Kawas. & Á.J. Pérez. From *Pérez & Alvia 4087* (Holotype: QCA).

Page 240 intentionally left blank.

TWO NEW SYNONYMS IN *OXOSSIA* (TURNERACEAE, PASSIFLORACEAE S. L.)

LAMARCK ROCHA[1]

Abstract. The transfer of *Turnera acangatinga* and *T. ibateguara* to the genus *Oxossia*, as synonyms of the names *O. annularis* and *O. pernambucensis* (Turneraceae, Passifloraceae s. l.), respectively, is proposed herein.

Resumo. Propõe-se a transferência de *Turnera acangatinga* e *Turnera ibateguara* para o gênero *Oxossia*, como sinônimos para os nomes *Oxossia annularis* e *Oxossia pernambucensis* (Turneraceae, Passifloraceae s. l.), respectivamente.

Keywords: Genus *Turnera*, Malpighiales, nomenclature, Brazilian rainforests

Phylogenetic relationships within Turneraceae have been increasingly elucidated through analyses involving large datasets based on morphology and DNA (Truyens et al., 2005; Thulin et al., 2012; Tokuoka, 2012; Rocha et al., 2019). Currently, the family is considered monophyletic (Thulin et al., 2012) but remains included in the broad circumscription of Passifloraceae (sensu APG IV, 2016). Turneraceae covers 14 genera (sensu Rocha et al., 2019) with predominantly Neotropical distribution, occurring in a variety of environments, but most species are found in areas of savanna vegetation (Cerrado domain) or dry forest (Caatinga domain) (Arbo and Mazza, 2011). Recently, 15 species of the genus *Turnera* L. were circumscribed in a new genus *Oxossia* L. Rocha. The genus includes all species previously included in *Turnera* ser. *Capitatae* Urb. (11 spp.), *T.* ser. *Conciliatae* Arbo (1 sp.), part of *T.* ser. *Annulares* Urb. (1 sp.), and *T.* ser. *Microphyllae* Urb. (2 spp.) (Rocha et al., 2019).

Oxossia is endemic to Brazil, occurring mainly in the rainforests and sandbanks (restingas) of the Atlantic Forest and the Amazon. This genus can be easily recognized by the combination of conspicuous stipules and bracts, inflorescences in elongated to abbreviated racemes, head-like, spike-like, terminal or lateral flowers with white corolla and sometimes yellow base, stamens pilose, adnate only at the base to the floral tube, styles pilose, sometimes geniculate, and seeds with prominent chalaza and concave surface (Rocha et al., 2019).

Species in Turneraceae frequently exhibit wide morphological variation. This variation can be evident in the height and density of the branches, e.g., *Oxossia calyptrocarpa* (Urb.) L. Rocha and *O. maracasana* (Arbo) L. Rocha, ranging from 0.2 to 2.5 m tall depending on the environment; (sub)glabrous to tomentose indumentum, e.g., *O. calyptrocarpa* and *Turnera melochioides* Cambess.; leaf shape, e.g., *T. subulata* Sm., *T. ulmifolia* L., and so many others from *T.* ser. *Turnera*; even the color of the petals, e.g., *T. incana* Cambess., which presents white to lilac petals (Arbo, 2000, 2005, 2008; Rocha and Rapini, 2015). Morphological variation within the same species in *Oxossia* may also be pronounced, especially among widely distributed populations. *Oxossia calyptrocarpa*, for example, has high plasticity in leaf morphology, regarding the blade size (4–33 × 2–18 mm) and phyllotaxis (congested in terminal brachyblasts or with long internodes), in addition to the inflorescence arrangement pattern (solitary or congested at the apex of brachyblasts) (e.g., Arbo, 2000; Rocha and Rapini, 2015).

Some species of *Oxossia* were known to have few representative specimens or were known only from the type, for example, *O. hatschbachii* var. *miniata* (Arbo) L. Rocha, *O. princeps* (Arbo) L. Rocha, and *O. pernambucensis* (Urb.) L. Rocha. Recently, Zelenski et al. (2016) rediscovered *O. pernambucensis* in the state of Pernambuco and provided a detailed discussion of the species' morphological limits. On the basis of specimens analyzed by Zelenski et al. (2016) and some additional collections from the Atlantic Forest of northeastern Brazil, Costa-Lima and Chagas (2019) proposed a new species but incorrectly included it in the genus *Turnera*: *T. ibateguara* Costa-Lima & E.C.O. Chagas. In the same study, the authors proposed another new species with specimens corresponding to *T. annularis* var. *conglomerata* Urb., which was called *T. acangatinga* Costa-Lima & E.C.O. Chagas.

The species proposed by Costa-Lima and Chagas (2019) belong to the genus *Oxossia* because of the presence of generally developed stipules, (0.5–)1.5–3.0 mm long, conspicuous bracts (3–14 mm long), flowers with white corolla, stamens and styles pilose, the latter geniculate, and seeds with prominent chalaza, in addition to occurring predominantly in the Atlantic Forest. However, this generic adscription had been already elucidated in previous studies based on part of the specimens cited by the authors. Specimens of *Turnera ibateguara* have been studied by Zelenski et al. (2016) and referred to *T. pernambucensis*, a name recently combined in *Oxossia* (i.e., *O. pernambucensis*) by Rocha et al. (2019), on the basis of extensive morphological and DNA data. Costa-Lima and Chagas (2019) showed the equivalence

---

The author would like to thank all cited herbaria for access to specimens, and Darlan Amancio de Macêdo Filho for proofreading the English version.

[1] Universidade Federal do Rio Grande do Norte, Centro de Biociências, Departamento de Botânica e Zoologia, Natal, Rio Grande do Norte, Brazil; lamarck.rocha@gmail.com

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 241–243.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n13, Published online: 31 December 2020

between specimens of *T. acangatinga* and *T. annularis* var. *conglomerata*, but this variety is already a synonym of *O. annularis* (Urb.) L. Rocha (Rocha et al., 2019).

Turnera acangatinga has notable overlaps with *Oxossia annularis*, and characters indicated as diagnostic of *T. ibateguara* overlap with *O. pernambucensis*. Publishing new names associated with species that have extensive overlap with others, without previous population-genetics work assessing the limits between the species, may result in the unnecessary publication of new species (e.g., Jalal et al., 2014; Moonlight and Jara-Muñoz, 2017; Sotuyo et al., 2017; Tucker and Gandhi, 2019; Tebbitt et al., 2020). Following this argument, *T. acangatinga* and *T. ibateguara* may also be the result of this variation and should be considered synonyms for *O. annularis* and *O. pernambucensis*, respectively.

Turnera acangatinga: A New Synonym For *Oxossia annularis*

Oxossia annularis has petioles ranging from 2 to 10 mm long, overlapping the measurement of those of *T. acangatinga*, 3–8 mm long; the indumentum in the former may be hirsute or pilose in the adult branches, and the leaves may be rigid (dry or fresh) (see Rocha and Rapini, 2015), similar to *T. acangatinga*. Like *T. acangatinga*, the leaf blade of *O. annularis* can be elliptical, ovate, or obovate, and have serrate-crenate margins and wide teeth (Arbo, 2000, fig. 1C; Rocha and Rapini, 2015). *Turnera acangatina* also overlaps with *O. annularis* in several structural shapes and dimensions (see Rocha and Rapini, 2015), casting doubt on its new species status. Referring to the two varieties of *O. annularis* (written as *T. annularis*), Costa-Lima and Chagas (2019: 840) mention, "However, in some cases we find overlapping characters in the specimens listed by Urban (1883) of both varieties." Nevertheless, just below that statement they indicate, "It is likely that *T. annularis* var. *conglomerata* corresponds to the same species that we are describing here," that is, *T. acangatinga*. These comments show once again that the uncertainty of this new name was already known to the authors. Therefore, the characters adopted by the authors can certainly be considered variations within the same species, *O. annularis*.

Oxossia annularis (Urb.) L. Rocha, Molec. Phylogen. Evol. 137: 59. 2019.

Basionym: *Turnera annularis* Urb. var. α, Jahrb. Königl. Bot. Gart. Berlin 2: 124. 1883. TYPE: BRAZIL. Rio de Janeiro, Jurujuba, près de la mer, fl jaunes, 19 Oct.1873, *A. Glaziou 6812* (Lectotype, designated by Arbo, 2000: P [P00715474]; Isolectotypes: C, K [K000373173], K [K000373172], P [P00715475], P [P00715476], B [destroyed], F [F0BN013565]).

Heterotypic synonym: *Turnera acangatinga* Costa-Lima & E.C.O. Chagas, Syst. Bot. 44(4): 838. 2019. *syn. nov*. TYPE: BRAZIL. Alagoas, Mun. Boca da Mata, Fazenda Daniel, 28 Mar. 2009, *Chagas-Mota, E. Gonçalves & N. Ramos 2454* (Holotype: MAC [MAC0037739]).

Turnera ibateguara: A New Synonym For *Oxossia pernambucensis*

Contrary to what was pointed out by Costa-Lima and Chagas (2019), in *Oxossia pernambucensis* (as *Turnera pernambucensis*) the leaves are not always concentrated at the apex of the branches, and neither do plants of *T. ibateguara*. In both species, the branches and leaves may have an indumentum ranging from strigose to sparse-strigose to glabrescent (Arbo, 2000; Zelenski et al., 2016). Species of the genus *Oxossia* can also vary widely in the arrangement of the branches; this is evident in *O. maracasana* and *O. calyptrocarpa*, which can be very branched shrubs or not. Leaf blade shape also does not seem to be a useful differentiating character, because *T. ibateguara* may have lanceolate leaves with short petioles (ca. 1 mm long) (Zelenski et al., 2016, fig. 1A), as described in *O. pernambucensis* (Arbo 2000). Unlike what was mentioned in Costa-Lima and Chagas (2019), *T. ibateguara* has terminal or axillary inflorescences and fruits without appendages, two features common in *O. pernambucensis*. Consequently, *T. ibateguara* should be also synonymized under *O. pernambucensis*.

Oxossia pernambucensis (Urb.) L.Rocha, Molec. Phylogen. Evol. 137: 59. 2019.

Basionym: *Turnera pernambucensis* Urb., Jahrb. Königl. Bot. Gart. Berlin 2: 133. 1883. TYPE: BRAZIL. Pernambuco: Catucá (aprox. 48 km a W de Recife), shady woods, Nov. 1837, *G. Gardner 1154* (Lectotype, designated by Arbo, 2000): K [K000373158]; Isolectotypes: K [K000373157], B [destroyed], F [F0BN013596]).

Heterotypic synonym: *Turnera ibateguara* Costa-Lima & E.C.O. Chagas, Syst. Bot. 44(4): 840. 2019. *syn. nov.* TYPE: BRAZIL. Alagoas: Mun. Ibateguara, Coimbra, Grota da Burra, 29 Mar. 2011, *Chagas-Mota 10666* (Holotype: MAC [MAC0052576]; Isotypes: CTES not located, HUEFS not located, IPA not located, UFRN not located, W not located).

LITERATURE CITED

APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181(1): 1–20.

ARBO, M. M. 2000. Estudios sistemáticos en *Turnera* (Turneraceae) II. Series *Annulares*, *Capitatae*, *Microphyleae* y *Papilliferae*. Bonplandia 10(1–4): 1–82.

———. 2005. Estudios sistemáticos en *Turnera* (Turneraceae) III. Series *Anomalae* y *Turnera*. Bonplandia 14: 115–318.

———. 2008. Estudios sistematicos en *Turnera* (Turneraceae). IV. Series *Leiocarpae*, *Sessilifoliae* y *Conciliatae*. Bonplandia 17: 107–334.

ARBO, M. M., AND S. M. MAZZA. 2011. The major diversity centre for neotropical Turneraceae. Syst. Biodivers. 9: 203–210.

COSTA-LIMA, J. L., AND E. C. O. CHAGAS. (2019) Two new species of *Turnera* (Passifloraceae s.l., Turneroideae) from northeastern Brazil and considerations on the identity of *T. pernambucensis*. Syst. Bot. 44(4): 838–843.

JALAL, J. S., J. JAYANTHI, AND A. SCHUITEMAN. 2014. *Xenikophyton* Garay (Orchidaceae—Aeridinae), a new synonym of *Schoenorchis* Reinw. ex Blume. Kew Bull. 69: 9508.

MOONLIGHT, P. W., AND A. JARA-MUÑOZ. 2017. A revision and recircumscription of *Begonia* Section *Pilderia* including one new species. Phytotaxa 307: 1–22.

ROCHA, L., AND A. RAPINI. 2015. Flora da Bahia: Turneraceae. Sitientibus, Sér. Ciênc. Biol. 15: 1–72.

ROCHA, L., P. L. RIBEIRO, P. K. ENDRESS, AND A. RAPINI. 2019. A brainstorm on the systematics of *Turnera* (Turneraceae, Malpighiales) caused by insights from molecular phylogenetics and morphological evolution. Mol. Phylogenet. Evol. 137: 44–63.

SOTUYO, S., J. L. CONTRERAS, E. GAGNON, AND G. P. LEWIS. 2017. A synopsis of *Coulteria* (Leguminosae), including new names and synonyms. Phytotaxa 291(1): 33–42.

TEBBITT, M., C. REYNEL, L. LIMACHI, AND C. MARTÍN. 2020. A taxonomic revision of *Begonia veitchii* (Begoniaceae). Edinb. J. Bot. 77(1): 127–144.

THULIN, M., S. G. RAZAFIMANDIMBISON, P. CHAFE, N. HEIDARI, A. KOOL, AND J. S. SHORE. 2012. Phylogeny of the Turneraceae clade (Passifloraceae s.l.): Trans-Atlantic disjunctions and two new genera in Africa. Taxon 61(2): 308–323.

TOKUOKA, T. 2012. Molecular phylogenetic analysis of Passifloraceae sensu lato (Malpighiales) based on plastid and nuclear DNA sequences. J. Plant. Res. 125(4): 489–497.

TRUYENS, S., M. M. ARBO, AND J. S. SHORE. 2005. Phylogenetic relationships, chromosome and breeding system evolution in *Turnera* (Turneraceae): Inferences from its sequence data. Am. J. Bot. 92(10): 1749–1758.

TUCKER, G. C., AND K. N. GANDHI. 2019. Nomenclatural notes on *Cyperus odoratus* and related species (Cyperaceae). Harvard Pap. Bot. 24(2): 349–357.

URBAN, I. 1883. Monographie der familie der Turneraceen. Jahrb. Königl. Bot. Gart. Berlin 2: 1–152.

ZELENSKI, A., L. ROCHA, AND R. B. LOUZADA. 2016. Rediscovery of *Turnera pernambucensis* (Passifloraceae *s.l.*) in the northern Atlantic Forest and an update for its description. Phytotaxa 286: 177–185.

Page 244 intentionally left blank.

IN MEMORY OF PROFESSOR YAN-CHENG TANG—A BRIEF BIOGRAPHY AND ACADEMIC CONTRIBUTIONS

Jin-Xiu Wang,[1,2,3] Qiu-Yun (Jenny) Xiang,[4] Zhi-Duan Chen,[1] Hai-Ning Qin,[1] and An-Min Lu[1]

Abstract. Professor Yan-Cheng Tang, also known as Yen-Cheng Tang, (汤彦承, given name Yan-Cheng, surname Tang; abbreviated Y. C. Tang), passed away on August 6, 2016, in Beijing at the age of 90. He was a highly respected plant taxonomist for his massive contributions to plant taxonomy in China and for the number of botanists he influenced. A brief biography and a summary of his importance in the development of plant taxonomy in China during the latter half of the 20th century is presented.

摘要. 中国科学院植物研究所汤彦承教授 (简称Y.C.Tang) 于2016年8月6日在北京去世，享年90岁。他是一位倍受尊敬的植物分类学家，为中国植物分类学做出了重要贡献，影响深远。 本文简要记述了汤先生的学术生平及他对20世纪下半叶中国植物分类学发展的贡献。

Keywords: Yan-Cheng Tang, plant taxonomy, Institute of Botany, Chinese Academy of Sciences, Beijing

Professor Yan-Cheng Tang (汤彦承; surname Tang, given names Yan-Cheng or Yen-Cheng, abbreviated Y. C. Tang) (Fig. 1), was born in Xiaoshan, Zhejiang Province, China, on 7 July 1926; he passed away on 6 August 2016 in Beijing at the age of 90. From 1942 to 1945 he attended the private Suzhou Taowu Middle School in Shanghai. He was influenced by one of his Chinese teachers, Bin-Liu Wang, who advocated the ideals of the "Seven Wise Men in the Bamboo Forest," a group of Chinese scholars, writers, and artisans of the third century CE who followed Daoism, which essentially promoted living in harmony with nature. In 1945, he entered the College of Agriculture at St. John's University in Shanghai, a private university for undergraduate study, but transferred to the Advanced Class at Shanghai Temporary University in October 1946. From there, he was recommended and admitted to Tsinghua University in Beijing. During his time at Tsinghua University (Fig. 2), as the only student majoring in botany in the Department of Biology, he studied plant taxonomy under the supervision of Zheng-Yi Wu (吴征镒; Cheng-Yih Wu [C. Y. Wu]) (1916–2014) and also benefited greatly from the rigorous teaching of plant morphology and systematics by Professor Jing-Yue Zhang (张景钺; Chin-Yueh Chang [C. Y. Chang]) (1895–1975), a student of the American botanist Professor Charles J. Chamberlain (1863–1943).

In August 1950, Tang was hired by the Institute of Plant Taxonomy (now the Institute of Botany), Academia Sinica (whose name was changed to Chinese Academy of Sciences [CAS] later), where he remained for the rest of his life. From October 1958 to October 1960, Tang was a visiting scholar at the Komarov Botanical Institute (Fig. 3) in Saint Petersburg (at that time, Leningrad), in the former Soviet Union. From 1972 to 1981, he was director of the Department of Plant Taxonomy and Phytogeography at the Institute of Botany, CAS. Although he officially retired in 1987, he continued to work actively throughout his life.

His initial taxonomic interests were in Poaceae. In 1954, Tang was selected to lead a group of young researchers to the East China Workstation of the Institute of Botany (now the Jiangsu Institute of Botany) for training by Prof. Yi-Li Keng (Y. L. Keng; 1897–1975), an expert on Poaceae, and to organize and direct the research and writing of the *Flora Illustralis Plantarum Primarum Sinicarum—Gramineae*. After about two and a half years of work, the team accomplished their objective in August 1956 and the book was published in April 1959 (Keng, 1959). The book, a landmark for research on the Poaceae of China, was welcomed by plant taxonomists; it was reprinted in 1965. During this project, Tang trained a team of Chinese taxonomists in agrostology and also gained experience and expertise for the subsequent compilation and editing of the series *Iconographia Cormophytorum Sinicorum* (ICS; Institute of Botany, Chinese Academy of Sciences, 1972–1976). As one of the key organizers of the national projects ICS, 中国植物志 (*Flora Reipublicae Popularis Sinicae* [FRPS]; Editorial Committee, 1959–2004), and *Flora Xizangica* (Comprehensive Expedition to Qinghai-Tibet Plateau, Chinese Academy of Sciences; Wu, 1983–1987), he not only contributed to and edited several volumes in these three important projects but also devoted much of his time to leading and coordinating them.

During the 1970s, Tang actively organized a team of taxonomists and plant illustrators in his department and at other institutions throughout China to promote the compilation of ICS, which aimed to serve as a reference for the identification of common Chinese plants. Tang assigned plant groups to the authors and oversaw the progress on each group. He, along with Wen-Tsai Wang (王文采; W. T. Wang; b. 1926) and others, reviewed and revised the manuscripts. In addition to his management duties, he also undertook the task of compiling the treatments of Araceae, Caprifoliaceae (s. l.), Acanthaceae, Nyctaginaceae, and Polygalaceae

---

We thank David E. Boufford and Yan Tang for providing photos as well as for contributing information about Professor Tang via their personal experiences and Jin-Shuang Ma, Jun Wen, Qin-Er Yang and Tian-Gang Gao for their suggestions.

[1] State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Beijing 100093, China.

[2] CAS Center for Excellence in Tibetan Plateau Earth Sciences, Chinese Academy of Sciences, Beijing 100101, China

[3] Corresponding author: heather@ibcas.ac.cn; telephone +86-10-62836582; fax: +86-10-62836095.

[4] Department of Plant Biology, North Carolina State University, Raleigh, North Carolina 27607, U.S.A.

Harvard Papers in Botany, Vol. 25, No. 2, 2020, pp. 245–251.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n14, Published online: 31 December 2020

FIGURES 1–3. **1**, Yan-Cheng Tang in the Shennongjia Forest District, Hubei Province, China, 1980. Photograph courtesy of David E. Boufford; **2**, Yan-Cheng Tang as a student at Tsinghua University, 1948. Photograph courtesy of Yan Tang; **3**, Yan-Cheng Tang at the Komarov Botanical Institute in the former Soviet Union, 1958–1960. Photograph courtesy of Yan Tang.

for ICS. The resulting five volumes were successful in providing an important tool for identifying Chinese plants; it has been reprinted seven times by Science Press. The ICS series and the companion volume,中国高等植物科属检索表 (*Claves Familiarum Generumque Cormophytorum Sinicorum* [*Keys to Families and Genera of Higher Plants of China*]; Institute of Botany, Chinese Academy of Sciences, 1979), received China's National Natural Science First Prize Award in 1987. Although Professor Tang and others were intimately involved in these publications, their names do not appear on the title page, nor elsewhere in the books, which was customary during the years of the Great Proletarian Cultural Revolution in China (1966–1976) and in the years immediately following. At the time, it was the workers' group that was credited, not the individual(s) who carried out the work.

During the 1970s and 1980s, Tang was involved in the compilation of the *Flora Reipublicae Popularis Sinicae* (FRPS). In 1973, he served as a member of the Editorial Committee and made great efforts to speed up progress on the project. As the director of the Department of Plant Taxonomy and Phytogeography at the Institute of Botany, where the Office of the Editorial Committee was located, Tang allowed taxonomists to work on plant families that he knew well, while he himself selected families that he had not previously studied. He shared his academic notes and accumulated manuscripts without reservation with colleagues who were interested in groups that had been the focus of his research. This material included important data collected during his visit to the Soviet Union, information compiled on type specimens, and drafts of his taxonomic treatments. In collaboration with his colleagues, he published treatments of Ulmaceae, Liliaceae, and Cyperaceae (*Carex*) in three volumes of FRPS (Tang, 1978, 1998, 2000a). His treatment of *Polygonatum* in FRPS received high praise from Charles Jeffrey, a well-known taxonomist from the Royal Botanic Gardens, Kew, UK (Jeffrey, 1980), who also had an interest in the genus. To improve the quality of FRPS, Tang encouraged his colleagues to study and translate articles representing the latest progress in taxonomy. He took the lead in those efforts, resulting in the compilation and publication of the Translated Series on Plant Taxonomy in Chinese (published internally). In the early 1980s, Tang organized a series of lectures on the principles of plant taxonomy, which were later published by the Chinese Botanical Society in mimeographed form. He contributed a booklet entitled "Introduction to the Two Schools in Taxonomy—Cladistics and Evolutionary Systematics" (Tang, 1984a). Around 1990, he was invited to serve as an advisor to the Editorial Committee of FRPS to answer questions posed by authors on the treatments of various plant families.

The compilation of *Flora Xizangica* (vols. 1–5) in the 1970s was an important achievement based on the first Qinghai-Tibet scientific expedition sponsored by the CAS. Compilation of the five volumes began in late 1976. The Institute of Botany was the leading institution and Tang was one of the key organizers. Tang assisted Professor Zheng-Yi Wu, the editor-in-chief, in organizing two review meetings and contributed the treatments of Oxalidaceae, Tropaeolaceae, Linaceae, Zygophyllaceae, Tamaricaceae, Flacourtiaceae, Lythraceae, Punicaceae, Droseraceae, and part of the Asteraceae (Tang, 1985b, c, d; 1986).

During the 1970s and 1980s, Tang expanded the traditional approach of using only morphology (Fu et al., 1979; Tang and Liang, 1984; Tang and Xiang, 1989b) to incorporate experimental data from karyotype analyses (Tang et al., 1984; Tang and Xiang, 1987) and palynology (Tang et al., 1983; Tang and Zhang, 1985). In the early 1970s, Tang introduced the concepts and methods of biosystematics and cladistics to taxonomists in China. He kept abreast of new developments in taxonomy and systematics and advocated for obtaining as much taxonomic evidence as possible through experimental approaches of morphology, anatomy, embryology, palynology, and cell biology. He was the first to introduce the principles and methods of Hennig's cladistical approach to Chinese plant taxonomists (Tang, 1984a). He emphasized dividing taxonomic characters into plesiomorphies, autapomorphies, and synapomorphies and carefully analyzing all characters to infer phylogenetic relationships. In the 1970s, when the compilation of treatments for FRPS was nearing completion, he worked with colleagues to establish laboratories for gathering data from morphology, cytology, anatomy, and palynology using experimental techniques. He employed experimental approaches in his own collaborative research with colleagues and students on Stachyuraceae (Tang et al., 1983; Zhu et al., 2006), Triplostegiaceae of Dipsacales (Zhang et al., 2001, 2003), Lardizabalaceae and Convallarieae (Liliaceae) (Tang and Zhang, 1985), and *Carex* (Tang and Xiang, 1989a; Li and Tang, 1990). In 1984, he supervised graduate student Haining Qin on a systematics study of the Lardizabalaceae. Through analyses of the micromorphology of carpels, ovules, fruits, seeds, pollen, and karyology, they inferred the evolutionary relationships within the family and assessed the phylogenetic position of the family within a larger framework (Qin, 1987). Those studies were regarded as leading research in China at that time. In 1985, when Tang was nearly 60 years old, he attended courses in molecular biology at Peking University so that he could gain an understanding of molecular systematics. In the 1990s, nucleotide sequences of the plastid *rbc*L gene and ribosomal DNA ITS regions were already widely used in plant systematics, but in China molecular systematics was still in its infancy. There were debates on the value of molecular data to solve systematic problems due to fear of losing ground in traditional taxonomy and to a lack of understanding of the principles of molecular systematics. Tang firmly supported molecular systematics. He not only encouraged the young scholars and graduate students at the Institute to read the literature and use molecular methods in their research, but he also set an example by gathering with them to study the most recent literature (Xiang et al., 1998). Through those efforts, he nurtured a fertile academic environment that led to the rapid and prosperous development of molecular systematics in China under the leadership of Prof. De-Yuan Hong and Prof. An-Min Lu from Institute of Botany, Chinese Academy of Sciences.

The species concept is the key to research in taxonomic biology. Two main groups are frequently referred to in practice, namely the "splitters" and the "lumpers." As the director of the Department of Taxonomy and Phytogeography, he advocated for a national discussion on the species concept among the taxonomists of China (Tang, 1982) and encouraged young taxonomists to study the monographs prepared by world-renowned botanists, such as G. Ledyard Stebbins. He also advocated applying a population-based species concept in taxonomic practice. He had a preference for the methods employed by such taxonomists as Vernon H. Heywood in the treatment of species. In his work, he was especially concerned about morphological patterns of variation and was not constrained by characters previously employed by others. When a sufficient number of specimens were available, he proposed using a statistical approach to analyze character variation and synthesize morphological and geographic evidence in taxonomic revisions. His revisions of *Tofieldia* (Tang, 1975) and *Clematoclethra* with Qiu-Yun Xiang (Tang and Xiang, 1989b) represented new advances in plant taxonomy in China at that time.

Prof. Tang retired in 1987 but continued to work at the frontiers of plant systematics and biogeography (Fig. 4). He participated in the National Natural Science Foundation's major project, "Studies on the Seed Plant Flora of China," under the auspices of academician Zheng-Yi Wu and published important research papers on the historical elements and the Tertiary origins of the East Asian angiosperm flora based on his studies of Staphyleaceae, Morinaceae, and Caprifoliaceae sensu lato. He proposed that the eastern Asian flora had a Tertiary origin and that the Miocene could be considered to be the boundary between paleo- and neo-endemic genera in China (Tang and Li, 1994, 1996). This hypothesis was supported by several recent studies (e.g., Chen et al., 2018; Lu et al., 2018). After 20 years, they are still important historical references for understanding and studying the flora of eastern Asia. In 2000, he published *The Floristic Relationship of the Chinese Flora with Other Regional Floras and the Status and Role of the Chinese Flora in Flora of the World* (Tang, 2000b). Tang and his colleagues proposed that there were 60 "primitive" angiosperm families (Tang et al., 2002). By comparing them with the 32 basal families defined by molecular-systematic methods, they concluded that the eastern Asian flora was unique. It had a close relationship with the eastern and western North American floras but was much closer to the flora of Indochina. They considered that the four circum-Pacific districts (eastern Asia; eastern and western North America; part of tropical Asia, eastern Australia, and the southwestern Pacific islands; and tropical South America) are the areas of greatest concentration of primitive angiosperm families. This distribution pattern obviously relates to the birthplace and dispersal routes of angiosperms and the history of the Pacific Ocean. In his later years, Tang made further attempts to study the floristic range and division of the Tangut endemic flora using historical evidence (Tang and Wang, 2015).

From 1995 to 2005, Prof. Tang participated in the National Natural Science Foundation's key project, "The Structure, Differentiation, and Systematic Relationships of Primitive Angiosperms," organized by Professor An-Min Lu., Prof. Tang and his colleagues proposed a new classification for angiosperms, called the "*Eight-Class System*"

FIGURES 4–9. **4**, Yan-Cheng Tang at the Kunming Botanical Garden, Chinese Academy of Sciences, Kunming, Yunnan, China, 2007. Photograph courtesy of Jin-Xiu Wang; **5**, Left to right: Yan-Cheng Tang, Prof. An-Min Lu, and Prof. Zheng-Yi Wu at the Beijing Friendship Hotel when Wu won the National Preeminent Science and Technology Award, January 2008. Photograph courtesy of Jin-Xiu Wang; **6**, Left to right: Yan-Cheng Tang, Bruce Bartholomew, and Zong-Zhi Ran during the joint Sino-American Botanical Expedition to the Shennongjia Forest District, Hubei Province, China, 1980. Photograph courtesy of Yan Tang; **7**, American members of the joint Sino-American Botanical Expedition at the Institute of Botany, Beijing, prior to departure for fieldwork in western Hubei Province, China, August 1980. Left to right: David Boufford, Stephen Spongberg, Theodore Dudley, Bruce Bartholomew, James Luteyn, and Yan-Cheng Tang. Photograph courtesy of D. E. Boufford; **8**, Yan-Cheng Tang celebrating his 80th birthday with his students, Beijing, 2006. Left to right: Yu-Ping Zhu, Hai-Ning Qin, Yan-Cheng Tang, and Jin-Xiu Wang. Photograph courtesy of Jin-Xiu Wang; **9**, Qiu-Yun (Jenny) Xiang visiting Yan-Cheng Tang, Beijing, 2013. Left to right: Qiu-Yun (Jenny) Xiang, Prof. Pei-Yu Yu (wife of Prof. Tang and a famous entomologist), Yan-Cheng Tang, and Yan Tang (their daughter). Photograph courtesy of Qiu-Yun (Jenny) Xiang.

(Wu et al., 1998, 2002) (Fig. 5). This was the first system of classification for angiosperms proposed by Chinese botanists since the system proposed by Hu Hsen-Hsu (1950). Two important books later published were *The Families and Genera of Angiosperms in China: A Comprehensive Analysis* (Wu et al., 2003) and *The Origin and Evolution of Primitive Angiosperms* (Lu and Tang, 2020).

Prof. Tang actively promoted the advancement and prominence of plant taxonomy, plant systematics, and phytogeography in China. He was a versatile and knowledgeable scholar and an excellent mentor and friend in the Chinese plant taxonomy community. He excelled in his knowledge of classic literature, botanical nomenclature, and botanical Latin. Those endeavors had a significant impact on the development of modern plant taxonomy/systematics in China. To ensure the highest quality of the treatments in FRPS, Prof. Tang emphasized adherence to the International Code of Botanical Nomenclature (ICBN). He translated the ICBN (Montreal edition) published in 1959 into Chinese in the early 1960s, although his name does not appear in the translated version. In 1982, he taught the ICBN to young taxonomists at the Northwestern Institute of Botany (Shaanxi Province). Prof. Tang's lecture notes were mimeographed and distributed to the authors and editors of FRPS to be used as an important reference. On the basis of the lecture notes, Prof. Tang subsequently published a series of papers on nomenclature (1983a, b; 1984b–f; 1985a; Tang and Zheng, 1985). They became important references for Chinese plant taxonomists in the 1980s and 1990s. In addition to his publications on the ICBN, he also proposed a reasonable nomenclature for Chinese plant names (Wang and Tang, 2005, 2007). In addition to English, Prof. Tang also knew Latin, German, French, and Russian, which allowed him to make full use of the diverse botanical literature. He compiled an extensive index-card file on botanical literature, which resulted in the booklet "A Brief Introduction to One Hundred Kinds of Plant Taxonomy Literature" in mimeograph in 1986 to use in the training of young taxonomists. Inspired by *A Bibliography of Eastern Asiatic Botany* by E. D. Merrill and E. H. Walker (1938), he proposed a similar compilation of Chinese systematic botanical literature to the Chinese Botanical Society and generously donated his index-card file toward its production. His advocacy resulted in the publication of the *Bibliography of Chinese Botany* (vols. 1–4) (Chinese Botanical Society, 1983–1995).

Prof. Tang undertook management of many scientific research programs, especially during his 10-year tenure as director of the Department of Plant Taxonomy and Phytogeography of the Institute of Botany, CAS. Chief among them was organizing and promoting the completion of FRPS and ICS. Following his leadership, the department developed four major areas of research: phylogeny, experimental taxonomy (biosystematics), floristics and phytogeography, and monographic revisions. In the area of phylogenetics, he emphasized research at three levels, global phylogeny, class/order phylogeny, and family/genus phylogeny, referred to in China as "big system—medium system—small system." He selected young leaders for the research teams, entrusted them with important tasks, and sent them to study abroad. He proposed hiring Ke-Xue Xu, a mathematician, in the early 1980s to undertake research on numerical taxonomy and to create a database of images of Chinese plants. At the end of the 1970s, he led the committee to design the present herbarium building of the Institute of Botany (herbarium acronym PE). The design included space for laboratories of anatomy, cytology, palynology, and chemistry and extra space for future expansion of the herbarium and additional laboratories.

Prof. Tang was particularly concerned with the long interruption in academic exchanges with foreign colleagues during the tumultuous years of the 1960s. To remedy the situation, he met with Dr. Shiu-Ying Hu, a botanist from Harvard University who was visiting China at the Beijing Hotel in August of 1975. He arranged for Dr. Hu to visit the Institute of Botany, CAS. His efforts led to the reestablishment of Sino-U.S. botanical exchanges after the end of the Cultural Revolution. In 1980, from August 15 to October 15, he led a joint Sino-American botanical expedition to the Shennongjia Forest District and to Lichuan Xian (the type locality of *Metasequoia glyptostroboides* Hu and W. C. Cheng) in western Hubei (Bartholomew et al., 1983; Fig. 6–7). He also made arrangements and acted as guide for the American members of the team on visits to the leading botanical institutions in China, where they met with potential collaborators. Reciprocating the visit of the five American botanists to China, five Chinese botanists spent a year at botanical institutions in the United States. It was most unfortunate that Prof. Tang's poor health at the time prevented him from participating. He arranged for other researchers in his department to study in the United States, carried out cooperative research, and opened the way for Chinese plant taxonomists to study abroad. His vision for the future and scientific planning for the department laid a solid foundation for subsequent interdisciplinary development that led to the transformation of the department into the Laboratory of Systematic and Evolutionary Botany, CAS (now the State Key Laboratory of Systematic and Evolutionary Botany, CAS), in 1987.

Prof. Tang served as a member of the editorial committee and standing member of the editorial boards, deputy editor, and editor-in-chief of *Acta Phytotaxonomica Sinica* (now *Journal of Systematics and Evolution*) for more than 30 years, from the 1970s until 2014. He reviewed and revised many manuscripts. He was also a permanent member of the Chinese Botanical Society and the director of the Plant Taxonomy Professional Committee, where he put forward important suggestions for the development of Chinese botany.

Although Prof. Tang trained few Ph.D. students (Fig. 8), he mentored many young scientists in the department going back to the 1950s. In the 1980s he mentored Qiu-Yun Xiang (Jenny Xiang) in cytotaxonomic and quantitative taxonomic research, using a population-based species concept. His guidance provided the impetus for Xiang, now a professor at North Carolina State University, to choose a career in plant systematics. She obtained further training

FIGURE 10. Yan-Cheng Tang with his colleagues and students, Beijing, 2010. Left to right: Song Ge, De-Zhu Li, Hong Wang, De-Yuan Hong, Xiao-Guo Xiang, Zhi-Duan Chen, Yan-Cheng Tang, Jun-Sheng Ying, and An-Min Lu. Photograph courtesy of Xiao-Guo Xiang.

under Douglas E. and Pamela S. Soltis for her Ph.D. degree (Fig. 9). Numerous young scholars, especially graduate students in the CAS systematics and evolutionary laboratory, were influenced by Tang's thinking and benefited from his advice (Fig. 10).

Tang admired Wen-Lan Fan's (1891–1969) work ethic: I rather be totally ignored than pen a single meaningless word for attention (板凳要坐十年冷，文章不写半句空). Although he did not publish as many papers as his peers, most of his work was carefully thought through and was novel and pioneering in China. In his later years, he continued his research, working until the last moments of his life. Prof. Tang was knowledgeable, modest, and tolerant. He was selfless and dedicated to plant taxonomy. He was a humble person who worked tirelessly and quietly to enhance the development of plant taxonomy in China. He never sought honors or attention for himself but instead always tried to help and promote others. His outstanding attitude and contributions to plant taxonomy and scientific research, and his moral character, will continue to inspire not only those of us who were privileged to have known him but future generations in China as well.

LITERATURE CITED

BARTHOLOMEW, B., D. E. BOUFFORD, A. L. CHANG, Z. CHENG, T. R. DUDLEY, S. A. HE, Y. X. JIN, Q. Y. LI, J. L. LUTEYN, S. A. SPONGBERG, S. C. SUN, Y. C. TANG, J. X. WAN, AND T. S. YING. 1983. The 1980 Sino-American botanical expedition to western Hubei Province, People's Republic of China. J. Arnold Arbor. 64(1): 1–103.

CHEN, Y. S., T. DENG, Z. ZHOU, AND H. SUN. 2018. Is the East Asian flora ancient or not? National Science Review, 5(6): 920-932.

INSTITUTE OF BOTANY, CHINESE ACADEMY OF SCIENCES, ED. 1979. 中国高等植物科属检索表; *Claves Familiarum Generumque Cormophytorum Sinicorum* (*Keys to Families and Genera of Higher Plants of China*). Science Press, Beijing.

CHINESE ACADEMY OF SCIENCES, ED. 1983–1987. *Flora Xizangica*. Vols. 1–5. Report of the Comprehensive Expedition to Qinghai-Tibet Plateau. Science Press, Beijing.

CHINESE BOTANICAL SOCIETY. 1983–1995. *Bibliography of Chinese Botany*. Science Press, Beijing.

EDITORIAL COMMITTEE, EDS. 1959–2004. 中国植物志; *Flora Reipublicae Popularis Sinicae*. Vols. 1–80. Science Press, Beijing.

FU, L. G., J. R. CHEN, AND Y. C. TANG. 1979. Materiae ad Floram Ulmacearum Sinensium. Acta Phytotax. Sin. 17(1): 45–51.

HU, H. H. 1950. A polyphyletic system of classification of angiosperms. Sci. Record 3(2–4): 221–230.

INSTITUTE OF BOTANY, CHINESE ACADEMY OF SCIENCES, ED. 1972–1976. 中国高等植物图鉴; *Iconographia Cormophytorum Sinicorum*. Vols. 1–5. Science Press, Beijing.

JEFFREY, C. 1980. The genus *Polygonatum* (Liliaceae) in Eastern Asia. Kew Bull. 34: 435–471.

KENG, Y. L., ED. 1959. *Flora Illustralis Plantarum Primarum Sinicarum—Gramineae*. Science Press, Beijing.

LI, L. Q., AND Y. C. TANG. 1990. A conspectus and phytogeography of the genus *Carex* subgen. *Vignea* (P. Beauv.) Kirsch. in China. Acta Phytotax. Sin. 28(3): 237–260.

LU, A. M., AND Y. C. TANG. 2020. *The Origin and Evolution of Primitive Angiosperms*. Science Press, Beijing.

LU, L. M., L. F. MAO, T. YANG, J. F. YE, B. LIU, H. L. LI, M. SUN, J. T. MILLER, S. MATHEWS, H. H. HU, Y. T. NIU, D. X. PENG, Y. H. CHEN, S. A. SMITH, M. CHEN, K. L. XIANG, C. T. LE, V. C. DANG, A. M. LU, P. S. SOLTIS, D. E. SOLTIS, J. H. LI, AND Z. D. CHEN. 2018. Evolutionary history of the angiosperm flora of China. Nature 554: 234–238.

Merrill, E. D., and E. H. Walker. 1938. *A Bibliography of Eastern Asiatic Botany*. Sponsored by the Smithsonian Institution, Arnold Arboretum of Harvard University, New York Botanical Garden, and the Harvard-Yenching Institute.

Qin, H. N. 1987. A systematics study of the family Lardizabalaceae. Master's thesis, Institute of Botany, Chinese Academy of Sciences.

Tang, Y. C. 1975. Note on the methodology of plant taxonomy. Acta Phytotax. Sin. 13(1): 137–139.

———. 1978. *Polygonatum*. Pages 52–80 in Editorial Committee, ed., *Flora Reipublicae Popularis Sinicae*. Vol. 15. Science Press, Beijing.

———. 1982. A discussion on the species concept in the angiosperms. (mimeograph, published internally)

———. 1983a. Brief introduction to the International Code of Botanical Nomenclature (I). Chin. Bull. Bot. 1(1): 55–58.

———. 1983b. Brief introduction to the International Code of Botanical Nomenclature (II). Chin. Bull. Bot. 1(2): 57–59.

———. 1984a. Introduction to the two schools in taxonomy—cladistics and evolutionary systematics. (mimeograph, published internally)

———. 1984b. Brief introduction to the International Code of Botanical Nomenclature (III). Chin. Bull. Bot. 2(1): 59–61.

———. 1984c. Brief introduction to the International Code of Botanical Nomenclature (IV). Chin. Bull. Bot. 2(2–3): 87–92.

———. 1984d. Brief introduction to the International Code of Botanical Nomenclature (V). Chin. Bull. Bot. 2(4): 51–57.

———. 1984e. Brief introduction to the International Code of Botanical Nomenclature (VI). Chin. Bull. Bot. 2(5): 58–61.

———. 1984f. Brief introduction to the International Code of Botanical Nomenclature (VII). Chin. Bull. Bot. 2(6): 49–54.

———. 1985a. Brief introduction to the International Code of Botanical Nomenclature (VIII). Chin. Bull. Bot. 3(1): 59–62.

———. 1985b. Dipsacaceae. Pages 518–530 in Chinese Academy of Sciences, ed., *Flora Xizangica*. Vol. 4. Science Press, Beijing.

———. 1985c. Droseraceae. Pages 411–412 in Chinese Academy of Sciences ed., *Flora Xizangica*. Vol. 2. Science Press, Beijing.

———. 1985d. Mutisieae and Lactuceae. Pages 919–970 in Chinese Academy of Sciences, ed., *Flora Xizangica*. Vol. 4. Science Press, Beijing.

———. 1986.Various family treatments. In Chinese Academy of Sciences, ed., *Flora Xizangica*. Vol. 3. Science Press, Beijing.

———. 1998. Ulmaceae. Pages 334–431 in Editorial Committee, eds., *Flora Reipublicae Popularis Sinicae*. Vol. 22. Science Press, Beijing.

———. 2000a. *Carex*. Pages 56–519 in Editorial Committee, eds., *Flora Reipublicae Popularis Sinicae*. Vol. 12. Science Press, Beijing.

———. 2000b. On the affinities and the role of the Chinese flora. Acta Bot. Yunnanica 22(1): 1–26.

Tang, Y. C., Y. L. Cao, Y. Z. Xi, and J. He. 1983. Systematic studies on Chinese Stachyuraceae (I)—Phytogeographical, cytological, palynological. Acta Phytotax. Sin. 21(3): 236–253.

Tang, Y. C., and L. Q. Li. 1994. The phytogeography of Caprifoliaceae. s. str. with its implications for understanding eastern Asiatic flora. Acta Phytotax. Sin. 32(3):197-218.

Tang, Y. C., and L. Q. Li. 1996. On historical elements and tertiary precursors of eastern Asiatic angiospermous flora—Based on phytogeography of Staphyleaceae, Morinaceae and Caprifoliaceae. Acta Phytotax. Sin. 34(5): 453–478.

Tang, Y. C., and S. J. Liang. 1984. On convergent characters in Chinese Liliaceae (s.l.)—Berry vs. capsule. Bull. Bot. Res. 4(2): 35–58.

Tang, Y. C., A. M. Lu, Z. D. Chen, Y. Zhang, and F. M. Zhang. 2002. On extant primitive angiosperms and their phytogeography. Acta Phytotax. Sin. 40(3): 242–259.

Tang, Y. C., and J. X. Wang. 2015. Notes on the term "Tangut" in botanical names. Plant Diver. and Res. 37 (3): 253–266.

Tang, Y. C., and Q. Y. Xiang. 1987. Cytological studies on some plants of East China (I). Acta Phytotax. Sin. 25: 1–8.

———. 1989a. Cytological studies of *Carex siderosticta* Hance (Cyperaceae) and its importance in phytogeography. Cathaya 1: 49–60.

———. 1989b. A reclassification of the genus *Clematoclethra* (Actinidiaceae) and further note on the methodology of plant taxonomy. Acta Phytotax. Sin. 27: 81–95.

Tang, Y. C., Q. Y. Xiang, and Y. L. Cao. 1984. Cytological studies on some plants of Sichuan and its neighboring regions (I). Acta Phytotax. Sin. 22: 343–350.

Tang, Y. C., and W. X. Zhang. 1985. Pollen morphology of Convallarieae (Liliaceae) and systematic position of *Theropogon* Maxim. Acta Phytotax. Sin. 23(2): 91–96.

Tang, Y. C., and R. Y. Zheng. 1985. Brief introduction to the International Code of Botanical Nomenclature (IX). Chin. Bull. Bot. 3(02): 53–56.

Wang, J. X., and Y. C. Tang. 2005. Discussion on the nomenclature of Chinese names of seed plants. China Terminology 7(3): 61–63.

———. 2007. Brief discussion on the unity of Chinese names for plants. Pages 135–143 in Ma Ke-Ping, ed., *Advances in Biodiversity Conservation and Research in China* (VII). Proceedings of the Seventh National Symposium on the Conservation and Sustainable Use of Biodiversity of China. China Meteorological Press, Beijing.

Wu, Z. Y., ed. 1983–1987. 西藏植物志; *Flora Xizangica*. Vols. 1–4. Science Press, Beijing.

Wu, Z. Y., A. M. Lu, Y. C. Tang, Z. D. Chen, and D. Z. Li. 2002. Synopsis of a new "polyphyletic-polychronic-polytopic" system of the angiosperms. Acta Phytotax. Sin. 40(4): 289–322.

———. 2003. *The Families and Genera of Angiosperms in China: A Comprehensive Analysis*. Science Press, Beijing.

Wu, Z. Y., Y. C. Tang, A. M. Lu, and Z. D. Chen. 1998. On primary subdivisions of the Magnoliophyta—Towards a new scheme for an eight-class system of classification of the angiosperms. Acta Phytotax. Sin. 36(5): 385–402.

Xiang, Q. Y., D. J. Crawford, A. D. Wolfe, Y. C. Tang, and C. W. DePamphilis. 1998. Origin and biogeography of *Aesculus* L. (Hippocastanaceae): A molecular phylogenetic perspective. Evolution 52: 988–997.

Zhang W. H., Z. D. Chen, H. B. Chen, Y. C. Tang. 2001. Phylogenetic relationships of the disputed genus *Triplostegia* based on *trn*L-F sequences. Acta Phytotax. Sin. 39(4): 337-344.

Zhang W. H., Z. D. Chen, J. H. Li, H. B. Chen, and Y. C. Tang. 2003. Phylogeny of the Dipsacales s.l. based on chloroplast *trn*L-F and *ndh*F sequences. Molecular Phylogenetics and Evolution 26:176-189.

Zhu Y. P., J. Wen, Z. Y. Zhang, and Z. D. Chen. 2006. Evolutionary relationships and diversification of Stachyuraceae based on sequences of four chloroplast markers and the nuclear ribosomal ITS region. Taxon 55: 931-940.

Page 252 intentionally left blank.

ON *ENCYCLIA RHIZOMATOSA* (LAELIINAE: ORCHIDACEAE)

Iván Tamayo-Cen,[1] German Carnevali,[1,2] and Gustavo A. Romero [1,2,3]

In a recent publication (Tamayo-Cen et al., 2020), we proposed the new name *Encyclia rhizomatosa* Tamayo-Cen, Carnevali & G.A. Romero, to replace *Encyclia sclerocladia* Hoehne, itself based on an illegitimate later homonym, *Epidendrum sclerocladium* Lindl. ex Rchb.f. The protologue of the new name is indicated below.

Encyclia rhizomatosa Tamayo-Cen, Carnevali & G.A. Romero, *nom. nov*.

Basionym: *Epidendrum sclerocladium* Lindl., Catalogue. 1853 [162/21]. *Epidendrum sclerocladium* Lindl. *ex* Rchb.f., Bonplandia 4: 326. 1856, *nom. illeg., nom. superfl*. Blocking name: *Encyclia sclerocladia* (Lindl. ex Rchb.f.) Hoehne, Arq. Bot. Estado Sao Paulo 2: 155. 1952, *nom. illeg., nom. superfl.*, where "[162/21]" is the image of the holotype in the microfiche of the Lindley Herbarium, which includes the entry in the "Catalogue" that describes the basionym (IDC Publishers, 1987).

However, it has been brought to our attention (K. Gandhi, pers. comm. to the authors) that, in the protologue of the new name, the remark on the blocking name *Epidendrum sclerocladium* Lindl. *ex* Rchb.f. and the parenthetical authorship citation for *Encyclia sclerocladia* were not appropriate. In other words, the usage of "*nom. illeg., nom. superfl*." and the parenthetical authorship citation ["(Lindl. *ex* Rchb.f.)"] are found to be unwarranted, because "*Epidendrum sclerocladium* Lindl." (1853) and "*Epidendrum sclerocladium* Lindl. *ex* Rchb.f." (1856) are heterotypic, and the 1856 name is illegitimate; consequently, *Encyclia sclerocladia* is a new name for the 1856 name and does not have parenthetical authorship.

We herewith make a revision and present the information on the new name, as follows:

Encyclia rhizomatosa Tamayo-Cen, Carnevali & G.A. Romero

Replaced synonym: *Epidendrum sclerocladium* Lindl., Catalogue. 1853.

Blocking name: *Encyclia sclerocladia* Hoehne, Arq. Bot. Estado Sao Paulo 2: 155. 1952 (based on *Epidendrum sclerocladium* Lindl. ex Rchb.f., Bonplandia 4: 326. 1856, *nom. illeg*.; later homonym, non *Epidendrum sclerocladium* Lindl., 1853).

TYPE: PERU. Sources of the Marañon, *J. R. Warszewicz 30* (Holotype: K-Lindl.; Epitype (selected by Tamayo-Cen et al., 2020): PERU: Amazonas: Distrito de Cumba, 0.3 km al W de la reserva de Las Tinajas, carretera Corral Quemado-Cumba-Utcubamba, 492 m, 5°55029.22"S, 78°39035.180"W, 25 noviembre 2018, *L. Ocupa Horna* 264 (HUT).

Literature Cited

IDC [Inter Documentation Company] Publishers. 1987. Lindley Herbarium [Royal Botanic Gardens, Kew]. Leiden, the Netherlands.

Tamayo-Cen, I., G. Carnevali, L. Ocupa Horna, J. L. Tapia, and G. A. Romero-González. 2020. *Encyclia sclerocladia* (Orchidaceae: Laeliinae) revisited: A new name, its phylogenetic position, and an annotated checklist of Peruvian *Encyclia*. Systematic Botany 45(1): 11–25.

We are grateful to Kanchi Gandhi (GH) for pointing out inconsistencies in the protologue of *Encyclia rhizomatosa* and for help with nomenclatural matters.

[1] Herbarium CICY, Centro de Investigación Científica de Yucatán, A. C., Calle 43 #130 x 32 y 34, Colonia Chuburná de Hidalgo, 97205, Mérida, Yucatán, México

[2] Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138, U.S.A.

[3] Corresponding author: romero@oeb.harvard.edu

Harvard Papers in Botany, Vol. 25, No. 2, 2020, p. 253.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n15, Published online: 31 December 2020

Page 254 intentionally left blank.

INDEX TO NEW NAMES AND COMBINATIONS

Harvard Papers in Botany, Vol. 25, No. 2, 2020, p. 255.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.n16, Published online: 31 December 2020

Page 256 intentionally left blank.

(Continued from the back cover)

Harvard Papers in Botany was initiated in 1989 to consolidate the following journals published by the Harvard University Herbaria: *Botanical Museum Leaflets—Harvard University* (vols. 1–30, 1932–1986), *Contributions from the Gray Herbarium of Harvard University* N.S. (nos. 1–214, 1891–1984), and *Occasional Papers of the Farlow Herbarium of Cryptogamic Botany* (nos. 1–19, 1969–1987). Starting with no. 8, it incorporates the *Journal of the Arnold Arboretum* (vols. 1–71, 1920–1990) and the *Journal of the Arnold Arboretum Supplementary Series* (1, 1991).

Harvard Papers in Botany was published as individually paginated issues up to number 10 (April 1997). Starting with the next issue, it has been published in volumes, each volume consisting of two numbers with continuous pagination. Number 1–10, published between May 1989 and April 1997, constitute Volume 1. Volume 1, number 10, includes a cumulative, comprehensive index for the first volume. Print Copies for most volumes 1 through 18 are available. Please contact papers@oeb.harvard.edu for more information.

This issue of *Harvard Papers in Botany* was composed by Barbara Kroner Morra, using Adobe InDesign CS6 for the Macintosh. The body of the text is set in 10-point Times Roman on 11 points of leading.

Harvard Papers in Botany

Volume 25, Number 2 December 2020

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

(Continued on the inside back cover)

Harvard Papers in Botany

Volume 25, Number 2 December 2020

A Publication of the Harvard University Herbaria Including

The Journal of the Arnold Arboretum

Arnold Arboretum

Botanical Museum

Farlow Herbarium

Gray Herbarium

Oakes Ames Orchid Herbarium

Harvard Papers in Botany, Vol. 25, No. 2, 2020, Front matter, Table of Contents, End matter.

ISSN: 1938-2944, DOI: 10.3100/hpib.v25iss2.2020.fmem, Published online: 31 December 2020