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Cover: *Pleurothallis maduroi* Luer. (See page 236, Fig. 22).
Drawn by S. Díaz Poltronieri from *Kaes s.n.* (JBL)

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(Continued from page i)

NOMENCLATURAL ADJUSTMENTS IN *EUTREMA, CERATOCNEMUM, RHAMPHOSPERMUM, AND SINAPIS* (BRASSICACEAE, CRUCIFERAE)

IHSAN A. AL-SHEHBAZ[1]

Abstract. The following new combinations *Ceratocnemum aphanoneurum, C. ballii, Eutrema angustifolium, E. sulphureum, E. watsonii, Rhamphospermum labasii, R. nigrum,* and *R. pubescens* are proposed. As a result *Rhamphospermum* is resurrected, *Trachystoma* is reduced to synonymy of *Ceratocnemum*, and *Sinapis* becomes dispecific.

Keywords: Brassicaceae, *Ceratocnmum*, Cruciferae, *Eutrema*, *Rhamphospermum*, *Sinapis, Trachystoma*

The present study is the first in a series of forthcoming publications aimed to update the generic assignments of Brassicaceae species and infraspecific taxa to make these names available for the World Flora Online project in progress. The study is based on the critical re-examination of the boundaries of various genera in light of molecular data published so far. It deals with three species each of North African *Trachystoma* O.E. Schulz and Himalayan *Pegaeophyton* Hayek & Hand.-Mazz., and five species of Eurasian–North African *Sinapis* L.

EUTREMA–PEGAEOPHYTON

The latest revision of *Pegaeophyton* (Al-Shehbaz, 2000) recognized seven species restricted almost exclusively to the Himalayan region. Most recently, Hao et al. (2017) conducted extensive molecular phylogenetic studies on *Eutrema* R. Br., and their data strongly supported the transfer of three of them, including the generic type *P. scapiflorum* (Hook. & Thomson) C. Marq. & Airy Shaw, to *Eutrema* and a fourth species, *P. minutum* H. Hara, to *Aphragmus* Andrz. ex. DC. As currently recognized, *Eutrema* consists of 44 species centered primarily in the Himalayas and Central Asia. The diversity in plant size and fruit morphology surpasses that of any other genus in the family. For example, the fruit length can be as small as 1–2 mm (*E. nepalense* (Al-Shehbaz, Arai, & H. Ohba) Al-Shehbaz, G.Q. Hao & J. Quan Liu) to as long as 35 cm (*E. renifolium* (Boiss. & Hohen.) Al-Shehbaz, G.Q. Hao & J. Quan Liu); the fruit shape and compression can be terete, subquadrangular, latiseptate, or angustiseptate; the ovule number ranges from 2 to 96 per ovary; the seeds arrangement varies from uni- to biseriate; and the raceme ranges from fully bracteate to ebracteate.

The three remaining species of *Pegaeophyton* dealt with here were not included in any molecular studies because each is known only from the holotype sheet. However, their transfer to *Eutrema* hardly expands its generic limits, except for the development of a gamosepalous calyx in *E. watsonii*. Gamosepaly is rare in the family and has been reported in individual species of several unrelated genera that otherwise have a polysepalous calyx (Al-Shehbaz, 2001).

Eutrema angustiseptatum (Al-Shehbaz, T.Y. Cheo, L.L. Lu & G. Yang) Al-Shehbaz, *comb. nov.*
Basionym: *Pegaeophyton angustiseptatum* Al-Shehbaz, T.Y. Cheo, L.L. Lu & G. Yang in Al-Shehbaz, Edinburgh J. Bot. 57: 167. 2000.

Eutrema sulphureum (Al-Shehbaz) Al-Shehbaz, *comb. nov.*
Basionym: *Pegaeophyton sulphureum* Al-Shehbaz, Edinburgh J. Bot. 57: 169. 2000.

Eutrema watsonii (Al-Shehbaz) Al-Shehbaz, *comb. nov.*
Basionym: *Pegaeophyton watsonii* Al-Shehbaz, Edinburgh J. Bot. 57: 168. 2000.

CERATOCNEMUM–TRACHYSTOMA

The Moroccan *Ceratocnemum* Coss. & Balansa and *Trachystoma* O.E. Schulz belong to the Brassiceae, a tribe well defined morphologically by the presence of tribal-specific conduplicate cotyledons (longitudinally folded around the radicle) and/or heteroarthrocarpic (strongly segmented) fruit (Al-Shehbaz et al., 2006). However, generic delimitation in the tribe is problematic because molecular phylogenetic data (e.g., Arias and Pires, 2012, and references therein) clearly demonstrated that several genera (e.g., *Brassica* L., *Diplotaxis* DC., *Erucastrum* C. Presl, *Sinapis* L.) are polyphyletic. Genome triplication, hybridization, and reticulate evolution played a major role in the evolution and diversification of the Brassiceae (Lysak et al., 2005), and convergent evolution, even in the unique heteroarthrocarpic fruit (Hall et al., 2011), further complicates the traditional generic delimitation in the tribe. Therefore, a critical evaluation of morphology in light of molecular and genomic data would certainly lead to far more sensible taxonomy of genera than does morphology alone.

Ceratocnemum has been known for the past 177 years to be monospecific, whereas the later-published *Trachystoma* includes three species (see Al-Shehbaz, 2012). Both genera have similar leaf and flower morphology, heteroarthrocarpic fruit, and chromosome number of $2n = 16$. However, they differ in some details of fruit morphology: *Ceratocnemum*

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has oblong fruit with indehiscent, 1-seeded valvular (proximal) and distal segments, whereas *Trachystoma* has linear fruit with indehiscent or dehiscent, 1- or 3- to 15-seeded valvular segment and indehiscent 1- to 12-seeded distal segment.

Maire and Samuelsson (1939) indicated that *Ceratocnemum rapistroides* and *Trachystoma ballii* hybridize in nature, and they formally recognized their intergeneric nothogenus ×*Trachycnemum* Maire & Sam. (Type: *T.* ×*mirabile* Maire & Sam.). A detailed description of this intergeneric hybrid is given in the above publication and in Maire and Quézel (1965: 229).

Molecular phylogenetic studies (e.g., Warwick and Sauder, 2005; Warwick and Hall, 2009; Couvreur et al., 2010; Koch and Lemmel, 2019) have clearly demonstrated that *Trachystoma* is polyphyletic and that two of its species—*T. ballii* O.E. Schulz (the generic type) and *T. aphanoneurum* (Maire & Weiller) Maire & Weiller—formed with *C. rapistroides* Coss. & Balansa a strongly supported monophyletic clade. The third species, *T. labasii* Maire, was part of a clade that included *Sinapis arvensis* L. and *S. pubescens* L.

The remarkable similarities in floral, folial, and basic fruit features (e.g., heteroarthrocarpy, indehiscent segments, few- to several-seeded valvular segments), as well as chromosome number, the molecular findings above, and reported fertile hybrids, strongly support the transfer of *Trachystoma ballii* and *T. aphanoneurum* to *Ceratocnemum*. The third species, *T. labasii,* is discussed under *Sinapis*.

Ceratocnemum aphanoneurum (Maire & Weiller) Al-Shehbaz, *comb. nov.*
Basionym: *Sinapis aphanoneura* Maire & Weiller, Bull. Soc. Hist. Nat. Afrique N. 19: 32. 1928.

Ceratocnemum ballii (O.E. Schulz) Al-Shehbaz, *comb. nov.*
Basionym: *Trachystoma ballii* O.E. Schulz, Bot. Jahrb. Syst. 54(3, Beibl. 119): 52. 1916.

RHAMPHOSPERMUM–SINAPIS

In his original description of *Sinapis*, Linnaeus (1753) recognized five species, of which the first two (*S. arvensis* L. and *S. alba* L.) have been maintained in the genus to date. The third and fourth species (*S. nigra* L. and *S. juncea* L.) are currently recognized in *Brassica* L., and the fifth (*S. hispanica* L.) has been kept in *Erucaria* Gaertn. for the past 230 years. As presently delimited in BrassiBase (https://brassibase.cos.uni-heidelberg.de/), the major database of the Brassicaceae, *Sinapis* includes only four species.

All molecular phylogenetic studies of the past two decades that included a good sampling of the most common genera of the tribe Brassiceae (e.g., Warwick and Sauder, 2005; Arias and Pires, 2012; Koch and Lemmel, 2019; and references therein) placed *Sinapis alba* and *S. flexuosa* in a clade clearly unrelated to that including *S. arvensis, S. nigra* (as *Brassica nigra* [L.] W.D.J. Koch)*, S. pubescens,* and *Trachystoma labasii*. Extensive cytological data (Warwick and Al-Shehbaz, 2006; updated in BrassiBase) place the above six species in three species pairs, here designated as groups A–C. Group A (*S. alba* and *S. flexuosa*) has $2n = 24$, group B (*S. arvensis* and *S. pubescens*) has $2n = 18$, and group C (*S. nigra* and *T. labasii*) has $2n = 16$. As designated by Green (1925), *S. alba* is the generic type, and therefore *Sinapis* would include only the two species of group A. In all of the above-mentioned molecular studies, groups B and C formed one clade unrelated to that of the herein-circumscribed *Sinapis,* and they should be placed in a separate genus despite slight differences in their chromosome numbers.

The earliest validly published genus, other than *Sinapis*, that included at least one of the four species of groups B and C is *Rhamphospermum* Andrz. ex Besser (Besser, 1822: 83). Its original description listed two species: "Cal. patens, petala erecta, limbo patente. Siliqua sessilis angulata, stylo compresso-conico nervoso, basi monospermo, sponte secedente rostrata. Semina subglobosa, funiculis compressis septo adnatis adfixa uniserialia *Andrz.* Nomen a rostro s. stylo seminifero desumptum: huc. p. 28. n. 851. SINAPIS *arvensis* et 1623 *R. orientale* [=*S. orientalis* L.], quod sparsim cum priori occurrit." The mentioning of 1-seeded, conical, slightly compressed stylar segment clearly excluded *S. alba*, which has profoundly compressed, ensiform, seedless distal fruit segment. Although Schulz (1919, 1936) recognized *S. orientalis* as a variety of *S. arvensis*, subsequent students of the Brassicaceae treated it as a minor variant not worth recognition.

As delimited herein, *Rhamphospermum* consists of the four species listed above in groups B and C. *Trachystoma labasii* differs from the other three in having oblong (vs. subglobose) seeds, 1- or 2-seeded (vs. 8- to 16-seeded) valvular segment, and 9- to 11-seeded (vs. 1–4-seeded) terminal segment. However, comparable differences in fruit morphology can be found in small genera of the tribe Brassiceae such as *Ceratocnemum* (see above), *Coincya* Rouy, *Enarthrocarpus* Labill., and *Vella* L., Therefore, the above differences are considered insignificant in the generic placement of *T. labasii*.

The transfer of *Brassica nigra* to another genus would break a traditional, 188-year generic assignment, though the species remained in *Sinapis* for some 50 years following its description by Linnaeus (1753). Every Brassiceae-wide molecular phylogenetic study for the past 30+ years, starting with the pioneering, classic work of Warwick and Black (1991, 1993) and followed by others up to the present (e.g., Warwick and Sauder, 2005; Arias and Pires, 2012; Koch and Lemmel, 2019), concluded that *B. oleracea* ($2n = 18$), the generic type, and *B. nigra* are universally accepted as belonging to the two major and most speciose lineages of the tribe Brassiceae, namely the Oleracea and Nigra lineages, respectively. Together with *B. rapa* L. ($2n = 20$), the above two species formed through ancient interspecific hybridizations among them three allopolyploid species: *B. carinata* A. Braun ($2n = 34$), *B. juncea* (L.) Czern. ($2n =$

36), and *B. napus* L. (2*n* = 38). These six species have long been known as members of the U-triangle named after U (1935) who illucidated their relationships (see also Palmer et al., 1983; Xue et al., 2020).

Therefore, the placement herein of *Brassica nigra* with its three sister species of *Rhamphospermum* is long overdue. In terms of morphology, the former species differs only in having distinctly 1-veined (vs. 3-veined) fruit valves, a feature useful for its separation from the other congeners recognized here. This valve venation is basically the only difference between *Brassica* and *Sinapis*. As briefly given above, *Brassica* is quite heterogeneous in chromosome numbers, and it will have to be split into smaller but monophyletic genera. An excellent initial step, first taken by Gómez-Campo (2002) and extended by German (2015), was to recognize the genus *Guenthera* Andrz. ex Besser. What is most interesting, however, is that both Antoni L. Andrzjowski and Wilibald S. J. G. von Besser were the first to realize nearly two centuries ago that the limits of *Brassica* and *Sinapis* were so heterogeneous that they segregated *Guenthera* and *Rhamphospermum* from them, respectively.

A detailed description of *Rhamphospermum* and a key to its species is presented herein for the first time.

Rhamphospermum Andrz. ex Besser, Enum. Pl. Volhyn., ed. 2: 83. 1822.

Type: *Rhamphospermum arvensis* (L.) Andrz. ex Besser.

Homotypic synonyms: *Agrosinapis* Fourr., Ann. Soc. Linn. Lyon, ser. 2, 16: 329. 1868. TYPE: *A. arvensis* (L.) Fourr.

Sinapistrum Spach, Hist. Nat. Vég. Phan. 6: 343. 1838; non Mill., Gard. Dict. Abr., ed. 4. 1754 [Cleomaceae]; nec F.F.Cheval., Fl. Gén. Env. Paris, ed. 2, 2: 860. 1836. TYPE: *Sinapistrum arvense* (L.) Spach.

Herbs annual. *Trichomes* simple. *Multicellular glands* absent. *Stems* erect to ascending, simple or branched distally, leafy, unarmed. *Basal leaves* petiolate, rosulate or not, simple, lyrate, pinnatifid, or sinuate-dentate, with 1–5 lateral lobes on each side, sometimes undivided and dentate; cauline leaves petiolate or subsessile, cuneate, not auriculate at base, dentate. *Racemes* several to many flowered, ebracteate, corymbose, elongated considerably in fruit, secund or not; rachis straight; fruiting pedicels erect to ascending or divaricate, persistent. *Sepals* oblong to linear, free, deciduous, suberect to ascending or spreading, equal or unequal, base of lateral pair saccate or not. *Petals* bright or pale yellow, erect at base, with flaring blade, ascending, to spreading, longer than sepals; blade obovate, apex subemarginate; claw subequaling sepals, glabrous, unappendaged, entire. *Stamens* 6, exserted, suberect, tetradynamous; filaments wingless, unappendaged, glabrous, free; anthers oblong, apex obtuse. *Nectar glands* 4, distinct; median pair ovoid to oblong; lateral pair prismatic or lobed. *Ovules* 8–16(–24) per ovary; placentation parietal. *Fruit* dehiscent, capsular siliques, linear, terete, not inflated, segmented (heteroarthrocarpic); valvular segment dehiscent, well developed and 4- to 16(–24)-seeded, or highly reduced and seedless, torulose, wingless, unappendaged; valves thick papery, 3- to 5(–7)-veined, glabrous or pubescent, not keeled, wingless, unappendaged; distal segment indehiscent, longer or much shorter than valvular segment, conical to subulate or linear, terete or only slightly compressed, seedless or 1- to 12-seeded, wingless, slightly to distinctly corky, unappendaged, sometimes lomentaceous and break apart transversely into 1-seeded corky segments; gynophore absent; replum rounded, visible; septum complete and membranous, or reduced; style < 1 mm long, stout, persistent; stigma capitate, entire or slightly 2-lobed, unappendaged. *Seeds* uniseriate, wingless, globose or oblong, plump; seed coat reticulate, mucilaginous or not when wetted; cotyledons conduplicate.

Distribution: North Africa, Europe, SW and Central Asia; naturalized in Australia, North and South America, and elsewhere in Africa and Asia.

Key to the Species of *Rhamphospermum*

1a. Fruiting raceme secund; petals with dark purple to brown veins; valvular segment aborts and seedless or 1- to 3-seeded; distal segment lomentaceous, to 12-seeded, breaks apart transversely into 1-seeded segments . . . . 2. *R. labasii*

1b. Fruiting raceme not secund; petal veins yellow, same color as blade; valvular segment dehiscent, several to many seeded, not lomentaceous; distal segment 1- or 2-seeded, not lomentaceous 2

2a. Valves 1-veined; distal segment seedless . . . . 3. *R. nigrum*

2b. Valves 3- to 5(–7)-veined; distal segment 1- or 2-seeded 3

3a. Annuals; fruit (2–)2.5–4.5(–5.7) cm long, glabrous or retrorsely hairy; terminal segment straight, erect, conical to subulate, 1- or 2-seeded . . . . 1. *R. arvense*

3b. Perennials; fruit 1.5–2.5 cm long, antrorsely hairy; terminal segment strongly recurved or hooked, cylindrical, 1- to 4-seeded . . . . 4. *R. pubescens*

1. ***Rhamphospermum arvense*** (L.) Andrz. ex Besser, Enum. Pl. Volhyn., ed. 2: 83. 1822.

Basionym: *Sinapis arvensis* L., Sp. Pl. 2: 668. 1753.

Distribution: native throughout Europe except NE part, North Africa, and SE and Central Asia; naturalized in Australia, North and South America, and elsewhere in Asia and Africa.

Chromosome number: 2*n* = 18.

2. **Rhamphospermum labasii** (Maire) Al-Shehbaz, *comb. nov.*

Basionym: *Trachystoma labasii* Maire, Mém. Soc. Sci. Nat. Maroc 15: 6. 1926.

Distribution: endemic to Morocco.

Chromosome number: 2*n* = 16.

3. **Rhamphospermum nigrum** (L.) Al-Shehbaz, *comb. nov.*

Basionym: *Sinapis nigra* L., Sp. Pl. 2: 668. 1753.

Distribution: native to Austria, Belgium, England, France, Germany, Italy, Greece, the Netherlands, and NW Africa; perhaps native to some parts of Central Europe and SW Asia; naturalized in Northern Europe, Australia, North and South America, and elsewhere in Africa and Asia.

Chromosome number: $2n = 16$.

4. **Rhamphospermum pubescens** (L.) Al-Shehbaz, *comb. nov.*

Basionym: *Sinapis pubescens* L., Mantissa Pl. 95. 1767.

Distribution: Albania, Algeria, SE France, Italy.

Chromosome number: $2n = 18$.

Maire (in Maire and Quézel, 1965) divided the Algerian populations of *Rhamphospermum* (as *Sinapis*) *pubescens* into three subspecies, six varieties, and two forms. I was not able to critically evaluate these infraspecific taxa because of insufficient material, so no infraspecific taxa are recognized here. *Rhamphospermum arvense* is even more widespread and variable, and this variation necessitates critical population-based molecular and morphological studies as well before any meaningful infraspecific taxonomy is adopted.

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VALIDATION OF THE COMBINATION *MONTEVERDIA PSAMMOPHILA* (CELASTRACEAE)

LEONARDO BIRAL[1]

Abstract. *Maytenus* species bearing fruits with a coriaceous pericarp that open by two valves and having seeds that are completely covered by a white aril are currently placed in the genus *Monteverdia*. One hundred and twenty-three combinations have been proposed following these two diagnostic characters. However, according to Art. 41.5 of the *International Code of Nomenclature for algae, fungi and plants*, one of these combinations has not been validly published. The validation of the combination *Monteverdia psammophila* is provided here through the presentation of the complete citation of its basionym.

Keywords: basionym, Bahia, Code, *Maytenus*, *Monteverdia*

In a contribution to the systematics of *Maytenus* Molina (Celastraceae), Biral et al. (2017) presented a phylogenetic study based on morphological and molecular characters. Supported by molecular and morphological evidence, especially that based on fruit characters, the results obtained provided a guide to a new proposal for the delimitation of the genus. *Maytenus* had three main lineages that were then recognized as separate genera: *Maytenus*, *Tricerma* Liebm., and *Monteverdia* A. Rich. (Biral et al., 2017). One of the *Maytenus* lineages comprises the species presenting flowers with two carpels, two ovules per locule, fruits with coriaceous pericarp that open by two valves, and a white aril that completely covers the seeds. Biral et al. (2017) presented 123 new combinations transferring *Maytenus* species from this lineage to the genus *Monteverdia*.

Checking some of these combinations as part of the project Flora do Brasil, 2020 (http://floradobrasil.jbrj.gov.br), I came across one combination that according to Article 41.5 of the *International Code of Nomenclature for algae, fungi and plants* (Shenzen Code) (Turland et al., 2018) is not considered validly published. The valid combination of *Maytenus psammophila* Biral & Lombardi in *Monteverdia* is provided below.

Monteverdia psammophila (Biral & Lombardi) Biral, *comb. nov.*

Basionym: *Maytenus psammophila* Biral & Lombardi, Harvard Pap. Bot. 18(2): 129–131. 2013.

TYPE: BRAZIL. Bahia: Pilão Arcado, dunas, caatinga de areia, 10°07'11"S, 42°53'02"W, 457 m, 16 June 2007, *R. M. Santos 1357* (Holotype: HRCB [49506]; Isotype: HUEFS [122294]).

The transfer of *Maytenus psammophila* to *Monteverdia* was not validly published in Biral et al. (2017) because the text lacked the specific epithet of the basionym. According to Article 41.5. of the Shenzen Code (Turland et al., 2018) this unintentional omission, due to a typographical error, invalidated the combination.

Monteverdia psammophila is endemic to Brazil and is restricted to a few locations in northwestern Bahia, characterized by sandy soils and popularly known as "the dunes of the São Francisco river" (Biral and Lombardi, 2013).

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THE ORCHID FLORA OF BARRA HONDA NATIONAL PARK, NICOYA, GUANACASTE, COSTA RICA

Diego Bogarín[1,2,3,6] and Franco Pupulin[1,4,5]

Abstract. Barra Honda National Park (BHNP) lies in the Tempisque River Basin of the Península de Nicoya, Guanacaste, Costa Rica. The Park is well known for its limestone caverns, which date from the Upper Paleocene–Lower Eocene and are the main attraction of BHNP. The area shows a marked climatic seasonality with a predominantly semideciduous tropical dry forest. We present a floristic treatment of the orchids of BHNP based on field collections, herbarium sampling, and documentation of living specimens. We discuss the biodiversity, climate, geology, and topography of the Park and provide a novel vegetation zones map with eight floristic associations: bean plantations, disturbed secondary forest, evergreen forest, jaragua fields, mature secondary forests, pastures, rocky areas, karstic limestone pavement, and young secondary forest. For the 36 species belonging to 29 genera recorded, we provide composite line drawings and Lankester composite digital plates, descriptions, distribution, ecology, etymology, synonymy, taxonomy, photographs, and a key to the species for field identification based on morphology. Ten species of orchids (27.8%) are terrestrials and 26 are epiphytes (72.2%). The evergreen forest contains 80% of the orchid species of BHNP. We describe *Pelexia barrahondaensis* and *Sarcoglottis calcicola* as new to science, and we propose a new combination under *Specklinia* for *Pleurothallis panamensis*. Also, we record the terrestrial orchid genus *Tropidia* for the first time in Costa Rica. The present study provides new information on the Nicoya Peninsula's dry forest ecosystems for in situ conservation and research. This work can be useful for other protected areas within the same ecosystem that lack a floristic treatment of the Orchidaceae.

Keywords: Cerros de Jesús, floristics, Orchidaceae, protected areas, taxonomy, tropical dry forest

Resumen. El Parque Nacional Barra Honda (BHNP) se encuentra en la cuenca del río Tempisque de la Península de Nicoya, Guanacaste, Costa Rica. El parque es bien conocido por su sistema de cavernas de piedra caliza que datan del Paleoceno Superior–Eoceno Inferior, el principal atractivo de BHNP. El área muestra una marcada estacionalidad climática con un bosque seco tropical predominantemente semideciduo. Presentamos un tratamiento florístico de las orquídeas de BHNP basado en colecciones de campo, muestreo de herbario y documentación de especímenes vivos y discutimos la biodiversidad, el clima, la geología y la topografía del parque. Además, proporcionamos un mapa de zonas de vegetación novedoso con ocho asociaciones florísticas: plantaciones de frijol, bosque secundario perturbado, bosque siempre verde, campos de jaragua, bosques secundarios maduros, pastizales, áreas rocosas y pavimento de piedra caliza kárstica y bosque secundario joven. Proporcionamos ilustraciones y láminas compuestas digitales de Lankester, descripciones, distribución, ecología, etimología, sinonimia, taxonomía, fotografías y una clave de las especies basada en la morfología para la identificación en el campo de cada una de las 36 especies pertenecientes a 29 géneros registrados. Diez especies de orquídeas (27,8%) son terrestres y 26 son epífitas (72,2%). Aproximadamente el 80% de las especies de orquídeas de BHNP se encontraron en el bosque siempre verde. Describimos *Pelexia barrahondaensis* y *Sarcoglottis calcicola* como nuevas para la ciencia de poblaciones en BHNP y proponemos una nueva combinación bajo *Specklinia* para *Pleurothallis panamensis*. Además, registramos el género de orquídeas terrestres *Tropidia* por primera vez en Costa Rica. El presente estudio proporciona nueva información sobre los ecosistemas de bosque seco de la Península de Nicoya para la conservación in situ e investigación. Esta información se puede extrapolar a otras áreas protegidas dentro del mismo ecosistema que carecen de un tratamiento florístico de las Orchidaceae.

Palabras claves: áreas protegidas, bosque seco tropical, Cerros de Jesús, florística, Orchidaceae, taxonomía

Barra Honda National Park (BHNP) lies in the lower Tempisque River Basin of the Península de Nicoya, Guanacaste, Costa Rica (Fig. 1). The Park was established in 1974 to protect a unique system of limestone caverns present in Costa Rica that dates from the Upper Paleocene–Lower Eocene (Boza, 1986). Geologically, the Península de Nicoya is one of the most diverse and complex areas in southern Central America. Particularly, Barra Honda is a suitable place for understanding the geological evolution of the Central American Isthmus and the sedimentary regions of the Nicoya Complex (Mora, 1978; Aguilar and Denyer, 2001; Jaccard et al., 2001). The establishment of BHNP ensured the protection of water sources and the northern Pacific's dry forest ecosystems. Administratively, BHNP

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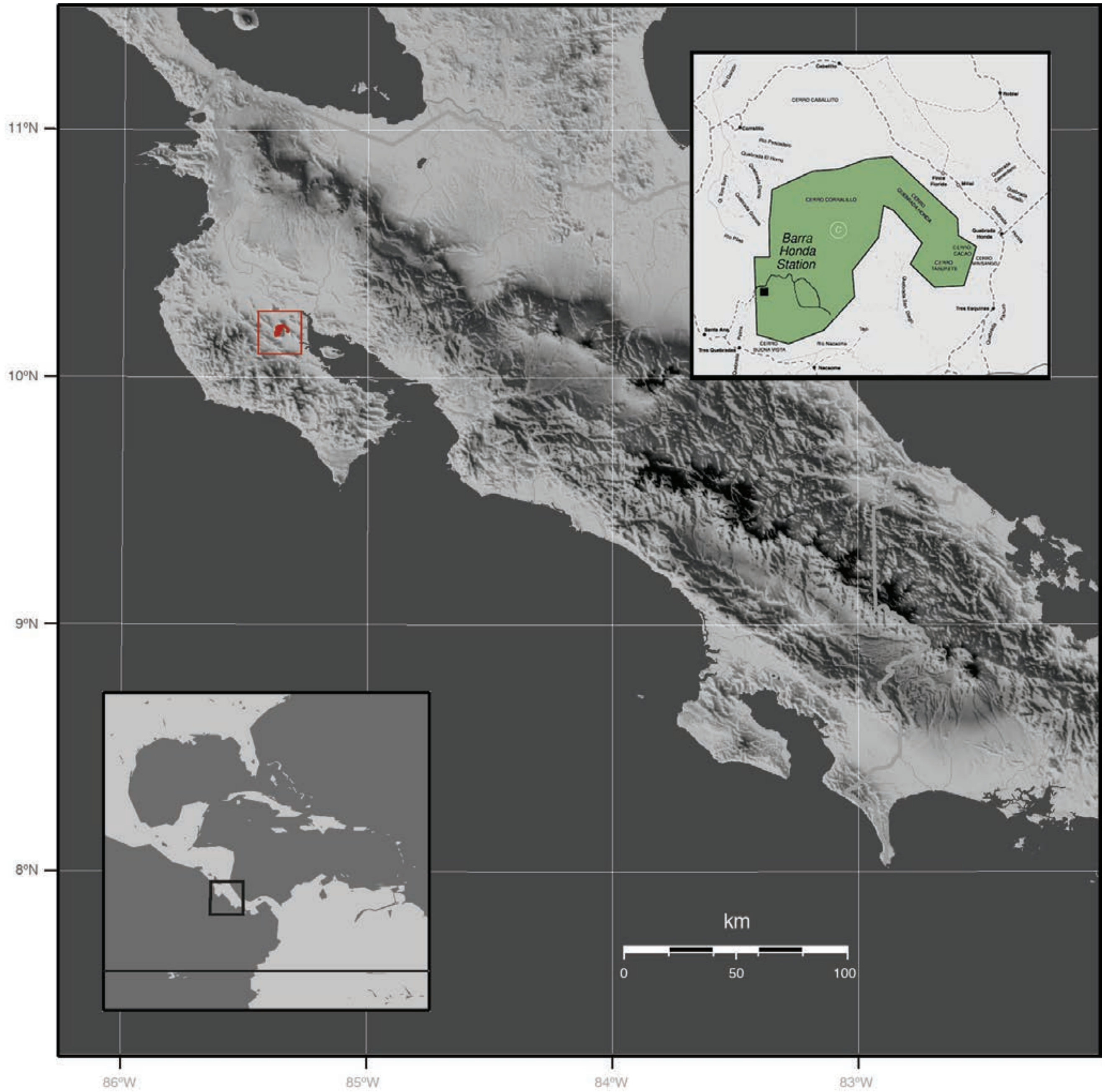

FIGURE 1. Location of BHNP in Costa Rica.

belongs to the Área de Conservación Tempisque (ACT) of the Costa Rican National System of Conservation Areas (SINAC).

The northern Pacific of Costa Rica shows a marked climatic seasonality and a predominantly semideciduous tropical dry forest. This area has suffered massive human intervention by deforestation and agricultural activities (Boza, 1986). The fragility of dry forest ecosystems such as are found in BHNP and the lack of information for understanding the natural resources protected by the SINAC make the development of floristic studies critical. Because of its geological importance, most of the research at BHNP has been published by geologists and speleologists, but little has been published to help understand its biodiversity. On the other hand, seasonally dry forests have been unattractive to orchidologists because of their low diversity as compared with the montane and premontane forests at higher elevations (Bogarín and Pupulin, 2007). Although some unpublished inventories have been undertaken, no scientific treatments on flora and fauna of BHNP are available, except for the two authors' preliminary assessment of the orchid species recorded within the Park (Bogarín and Pupulin, 2007) and a broader essay on the inventory carried out for this study (Pupulin and Bogarín, 2013).

This paper is the first botanical treatment at BHNP, aimed to clarify the Orchidaceae's diversity and provide the basis for a complete systematic revision of the flora at BHNP. This paper is part of a series of floristic studies on the orchids of protected areas in Costa Rica (Pupulin, 1998; Bogarín et al., 2011; Pupulin and Bogarín, 2013; Pupulin and Bogarín, 2018).

Description of the Study Site

BHNP lies in San Antonio, Nicoya, Guanacaste, about 12.5 km northeast of the city of Nicoya (10˚12'N, 85˚22'W, 10˚09'N, 85˚18'W) (Fig. 1–4). The Park comprises 2295 ha, with the following limits: to the north Cerro Caballito (a hill), to the south Finca San Diego (a private farm), to the west El Flor (a town), and to the east Quebrada Honda (a village). Other towns surrounding the Park are Barra Honda (Nacaome), Caballito, Corralillo, La Mansión, San Antonio, and Santa Ana. Executive Decree No. 10727-A established the boundaries of BHNP on October 5, 1979, using for reference topographic maps of the Instituto Geográfico Nacional labeled Matambú 3146-III and Talolinga 3146-IV, scale 1:50,000.

Topography

The Park comprises three main slopes: Cerro Barra Honda (423 m); the highest point, Cerro Corralillo (575 m); and Cerro Quebrada Honda (266 m) (Fig. 2), with rocky cliffs and gradients of 60–70 % observed mainly to the south of Cerro Barra Honda and Cerro Corralillo (Fig. 3). The summit of Cerro Barra Honda is a plateau of around 250 ha. The main caves, trails, and viewpoints are located here, making it the most important place for visitors. From the ranger station, a trail of about 1.7 km climbs up to the plateau's top. About 11 km of trails are available for visitors to the Park, including Quebrada Palma (at the ranger station), Ceiba, Los Laureles, Mirador Nacaome (at 423 m), Los Mesones, Bosque de Piedra on Cerro Barra Honda, and Las Cascadas at the south of Cerro Corralillo (Fig. 4). About 42 caves were documented, 19 of which have been explored. The most important are Chorotega, Los Gemelos, Nicoa, Ojoche, Ojos Verdes, Pozo Hediondo, Santa Ana (the deepest, at 180 m), La Trampa, La Cuevita, and Terciopelo (Fig. 5). The latter two are the only caves open to visitors (Barrantes et al., 1999). The slopes rise abruptly from the plains at 30–70 m on the lower Tempisque River Basin near its mouth into the Golfo de Nicoya (Fig. 6A–B).

A depression separates Cerro Barra Honda and Cerro Corralillo, which continues to the south bordering Finca San Diego. This depression is covered by evergreen forest locally known as Las Cascadas (47 ha). To the southeast of Cerro Barra Honda, there is a patch of evergreen forest named Los Mesones (27 ha). The depression between Cerro Barra Honda and Cerro Corralillo and the top of Cerro Corralillo have been disturbed by the action of fire and human activities. This area of about 210 ha comprises grassy lands and bean plantations. A narrow depression separates Cerro Corralillo from Cerros Quebrada Honda, a less explored region without trails for visitors and scientists. Other smaller slopes are Cerro Taburete, Cerro Cacao, and Cerro Misingo, located toward the southeast boundary. Other geologically related slopes in the neighborhood of BHNP are, to the north, Cerro Caballito (448 m) and Cerros del Rosario; to the northeast, Cerros Corral de Piedra and Sonzapote; to the east, Cerros Copal; and to the south, Cerros de Jesús.

Hydrology

The few rivers in BHNP flow mainly between Cerro Corralillo and Cerro Barra Honda in Las Cascadas and Los Mesones, the most humid area of the Park, with gallery forests that run along their edges. The most important rivers and streams are Quebrada San Diego, a system of small creeks from Las Cascadas and Los Mesones that flows into Río Nacaome to the south; Quebrada Horno, Grande, and Río Pescadero to the north of Cerro Corralillo; Quebrada Palma at the main station of the BHNP east of Cerro Barra Honda; and Quebrada Gradas on the slopes of Cerro Taburete, Cacao, and Misingo. Most of the rivers and creeks are intermittent and dry up during the dry season.

Geology

Barra Honda is part of the Barra Honda Limestone Platform of Upper Paleocene–Lower Eocene age (58 to 49 million years ago). Jaccard et al. (2001) studied the age of the structural setting of platform limestones of the Río Tempisque area, recognizing two distinct carbonate platform systems: the El Viejo Platform, represented by Cerros Ballena and Cebollín (Filadelfia, Guanacaste), and the Barra Honda Platform, from the classical outcrops at Cerro Barra Honda in the south to Palo Verde in the north. In the Barra Honda Platform, most facies contain larger benthic and planktonic porcelaneous foraminifera, specially *Morozovella velascoensis* Cushman, rotaliids, crinoids, and abundant red algae such as the Squamariacean *Ethelia alba* (Pfender) Johnson, characteristic of the Paleocene–Eocene (Aguilar and Denyer, 2001; Jaccard et al., 2001). The action of these organisms and the resulting calcium carbonate deposition led to the formation of limestone. According to Jaccard et al. (2001), the docking of the Nicoya Terrane during the Late Paleocene could have caused the uplift initiating the deposition of the Barra Honda Platform. The slopes at BHNP are surrounded by sedimentary plains made up of Cretaceous-Paleogene deep-water sediments and Quaternary alluvial, colluvial sediments (Denyer and Alvarado, 2007).

The water at BHNP contains high calcium carbonate levels, dissolved by rainwater and deposited by rivers and streams on the ground and rocks as travertine. The rivers show carbonate-staggered terraces and travertine columns, produced through slow precipitation and deposition of calcium carbonate. This phenomenon is evident in Las Cascadas, where several streams flow from Cerro Corralillo to Quebrada San Diego (Fig. 7A–B).

Barra Honda is considered a karst characterized by its limestone plateau and underground caverns. The action of

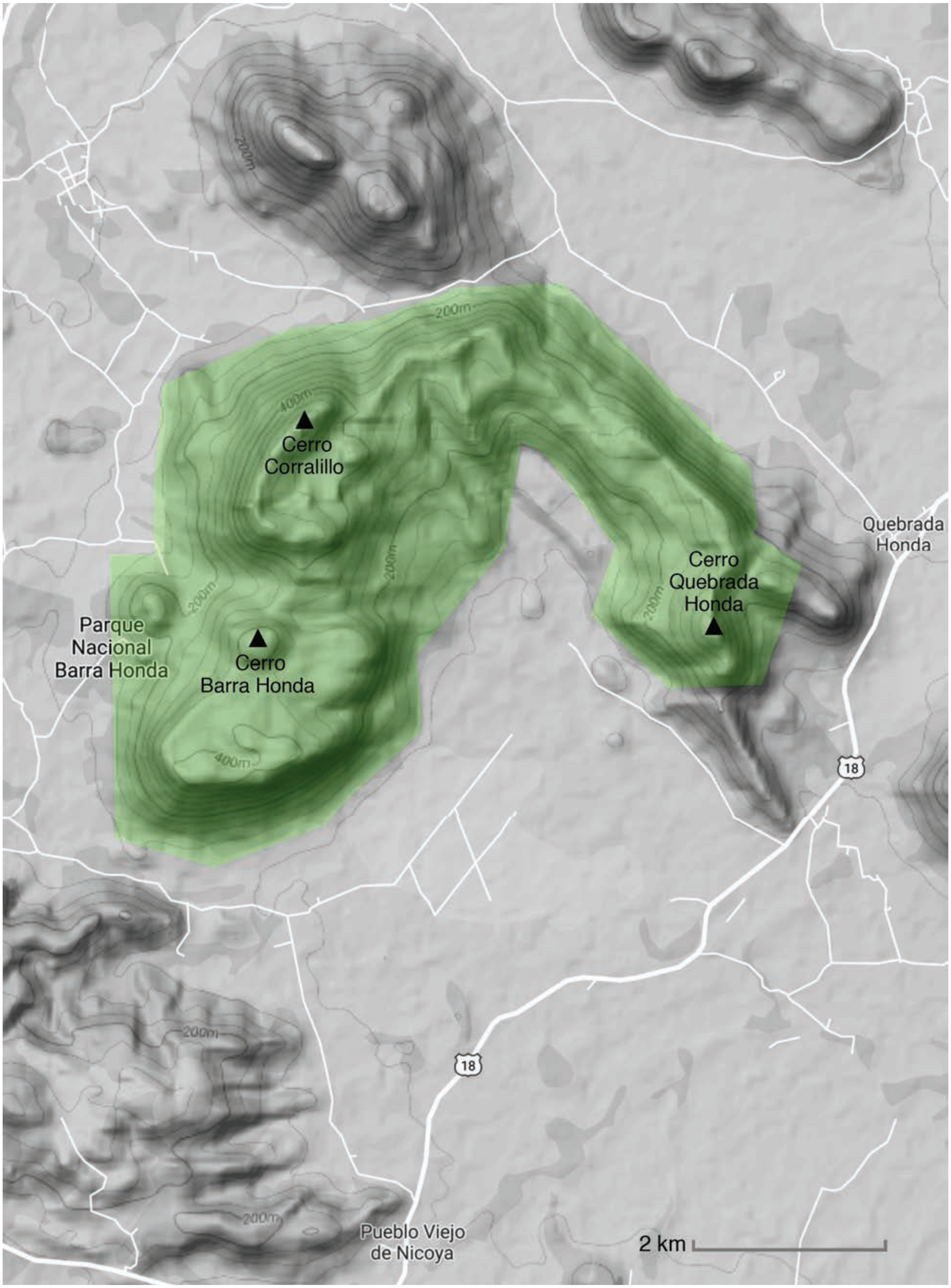

FIGURE 2. The topography of BHNP, showing the position of the highest peaks. Level curves every 20 m.

FIGURE 3. View of the limestone hills of BHNP. Photograph by F. Pupulin.

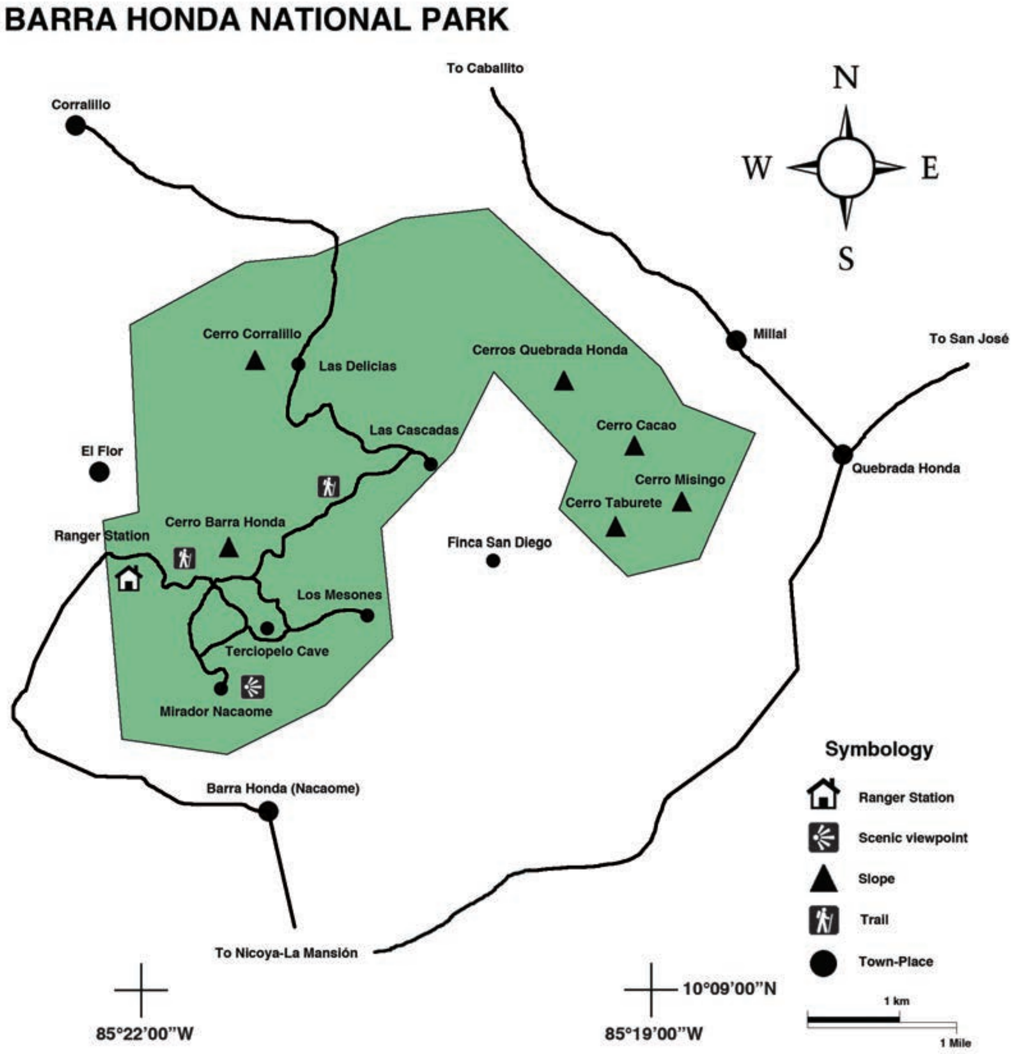

FIGURE 4. Map of Barra Honda National Park showing the main trails and places sampled. Map by D. Bogarín.

FIGURE 5. Calcium stalactites in the Terciopelo cave at BHNP. Photographs by D. Bogarín.

rainwater on soluble limestone also produced the erosion and deposition of calcium carbonate, resulting in the formation of vertical caverns adorned by stalactites and stalagmites, dolines, and sinkholes. Cerro Barra Honda has a stratification of limestone 300 m thick. It is not considered a young karst because of the deep vertical caves such as Santa Ana and La Trampa (170 m deep). However, it lacks the horizontal caverns characteristic of a mature karst (Mora, 1978). Other slopes with similar karstic features are Cerro Corralillo, Quebrada Honda, Corral de Piedra, and El Rosario, all surrounding BHNP.

Climate

The climate has two marked seasons: a dry season from late November to late April and a wet season from May to November (Fig. 6A–B, 7A–B). Precipitation can reach 1500–2000 mm/year, with less than 100 rainy days per year. During the rainy season, the total rainfall is 1800 mm, contrasting with 55 mm during the driest period. Rainfall increases in May (243 mm), slightly diminishes in July–August (191 mm), but later reaches a peak in September–October (up to 372 mm). From November to December, it decreases significantly (11 mm) until March (< 7 mm). The driest month is January, with less than 1 mm of rainfall. The average temperature is > 28 C, with minimum and maximum averages of 23.3 and 33.5 C. The warmest period is from February to April, with an average of 35.8 C.

Trade winds from the north influence the rainfall patterns at BHNP. These winds flow from the Caribbean to the Pacific watershed, but after passing the Cordillera de Guanacaste, they lose moisture and produce the typically dry conditions of the Península de Nicoya. The southwest trade winds and sea breezes from the Golfo de Nicoya interact with the northern trade winds, producing storms and rains from May to November. The intensification of the trade winds from the north during July–August causes a slight decrease in rainfall called *veranillo de San Juan* or *canícula* ("short St. John's summer"). Later in September–October, a stronger influence of southern trade winds increases rainfall levels that diminish in December when the northern trade winds blow again (Kohlmann et al., 2002). According to Bolaños et al. (2005), the life zone is the tropical dry forest, moist province transition with tropical dry forest and premontane moist forest, basal belt transition in the nearby areas.

Biodiversity

The Park lacks a floristic treatment and map of the vegetation types. Plant information is dispersed in unpublished checklists and databases in herbaria. About 200 plant species have been documented, most of them typical of Guanacaste and Puntarenas's seasonally dry forests. Most of the Park comprises secondary forest, and almost 80% of the species are deciduous during the dry season (Barrantes et al., 1999). The fauna includes 18 species of amphibians, 35 species of reptiles, 140 species of birds, and 66 species of mammals, of which about 50% are bats.

Here we propose the subdivision of the vegetation into eight types: pastures, rocky areas and karstic limestone pavement, jaragua fields, bean plantations, and disturbed, young, mature, and evergreen secondary forest (Fig. 8, 9A–H). We established these vegetation types on the basis of field observations and analysis from satellite imagery and aerial photography from 2010 to 2020 provided by Google Earth Pro 7.3.3.©

Vegetation

Evergreen forest (238 ha). Scattered patches of gallery forest cover the edges of rivers and streams, where humidity is constant throughout the year (Fig. 9H). The major areas are located at Las Cascadas and Los Mesones, where several streams flow into Quebrada San Diego. Other sites are located along the base of the western side

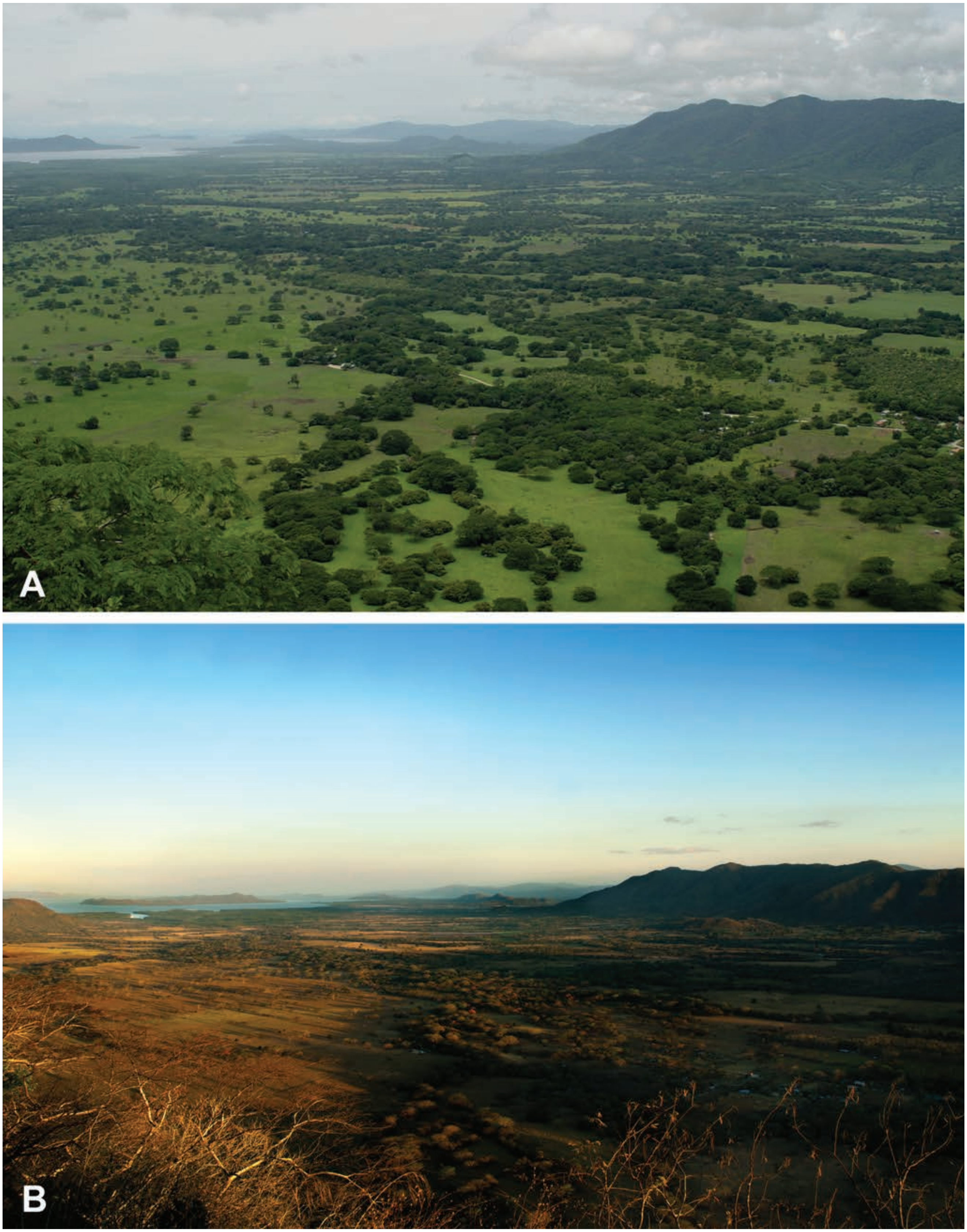

FIGURE 6. The plains of the lower Tempisque River from the top of Cerro Barra Honda, with the Cerros de Jesús on the right and the Nicoya Gulf on the background. **A,** Photo taken during the rainy season by D. Bogarín. **B,** Photo taken during the dry season by F. Pupulin.

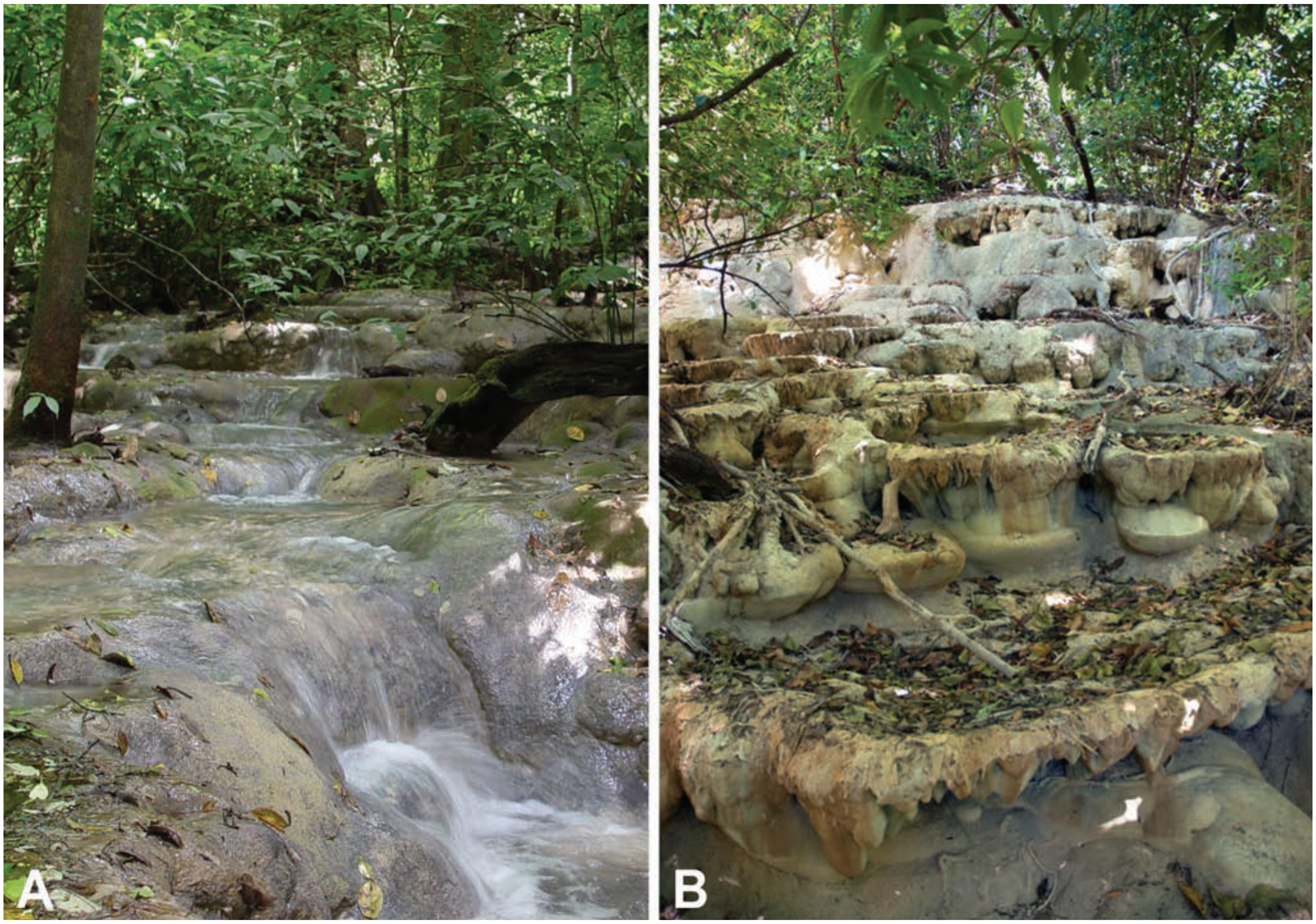

FIGURE 7. Rivulet with carbonate-staggered terraces at Las Cascadas, BHNP. **A,** Photo taken during the rainy season by D. Bogarín. **B,** Photo taken during the dry season by F. Pupulin.

of Cerro Barra Honda and Corralillo. The tallest trees of BHNP (ca. 15–30 m) are mainly found in the evergreen forest: *Anacardium excelsum* (Bertero & Balb. ex Kunth) Skeels, *Aspidosperma megalocarpon* Müll. Arg., *Astronium graveolens* Jacq., *Brosimum alicastrum* L., *Cedrela odorata* L., *Ceiba pentandra* (L.) Gaertn., *Dalbergia retusa* Hemsl., *Enterolobium cyclocarpum* (Jacq.) Griseb., *Ficus goldmanii* Standl., *Genipa americana* L., *Lonchocarpus phaseolifolius* Benth., *Luehea candida* (DC.) Mart., *Luehea semannii* Triana & Planch, *Pachira fendleri* Seem., *Samanea saman* (Jacq.) Merr., *Syderoxilum capiri* (A.DC.) Pittier, and *Tabernaemontana donnell-smithii* Rose. Some of the common shrubs are *Annona reticulata* L., *Ardisia revolute* Kunth, *Cordia* spp., *Garcia nutans* Vahl, *Inga* spp., *Jacquinia nervosa* C. Presl, *Lysiloma divaricatum* Hook. & Jackson, *Pouzolzia guatemalana* (Blume) Wedd., and *Psidium guineense* Sw. Common herbs present are *Dichorisandra hexandra* (Aubl.) Standl., *Dorstenia contrajerva* L., *Olyra latifolia* L., *Psychotria carthagenensis* Jacq., *Rhynchospora nervosa* (Vahl) Boeckeler, and *Selaginella sertata* Spring. Among the species of vines and lianas are *Dalbergia glabra* (Mill.) Standl., *Desmodium infractum* DC., *Heteropterys laurifolia* (L.) A. Juss., *Luffa aegyptiaca* L., *Monstera adansonii* Schott, *Petrea volubilis* L., *Smilax spinosa* Mill., and *Xylophragma seemannianum* (Kuntze) Sandwith.

Mature secondary forests (672 ha). Areas of mature secondary forest are located surrounding evergreen forest and steep areas of BHNP, mostly to the north of Cerro Barra Honda and Cerro Corralillo, and along the depression between Las Delicias and Las Cascadas. The forest is dense and semideciduous (Fig. 9G), with the following representative tree species: *Alvaradoa amorphoides* Liebm., *Annona reticulata, Brosimum aliscastrum, Bursera simaruba* (L.) Sarg., *Casearia corymbosa* Kunth, *Celtis trinervia* Lam., *Coccoloba caracasana* Meisn., *Dalbergia retusa, Ficus* L. spp., *Genipa americana, Hymenaea courbaril* L., *Inga vera* Kunth, *Nectandra martinicensis* Mez, *Phyllanthus acuminatus* Vahl, *Pisonia aculeata* L., *Plumeria rubra* L., *Sapranthus palanga* R.E. Fr., *Semialarium mexicanum* (Miers) Mennega, *Shizolobium parahyba* (Vell.) S.F. Blake, *Sideroxylon capiri,* and *Tamarindus indica* L. Common shrubs are *Aegiphila panamensis* Moldenke, *Allophylus racemosus* Sw., *Bourreria quirosii* Standl., *Bunchosia polystachia* (Andrews) DC., *Calliandra coriacea* (Humb. & Bonpl. ex Willd.) Benth., *Chomelia spinosa* Jacq., *Croton niveus* Jacq., *Erythroxylum havanense* Jacq., *Exostema caribaeum* (Jacq.) Schult., *Jacquinia nervosa*, *Lippia cardiostegia* Benth., *Margaritaria nobilis* L.f., *Vachellia collinsii* (Saff.) Seigler & Ebinger, and *Zanthoxylum setulosum* P. Wilson. Other common plants include the ferns

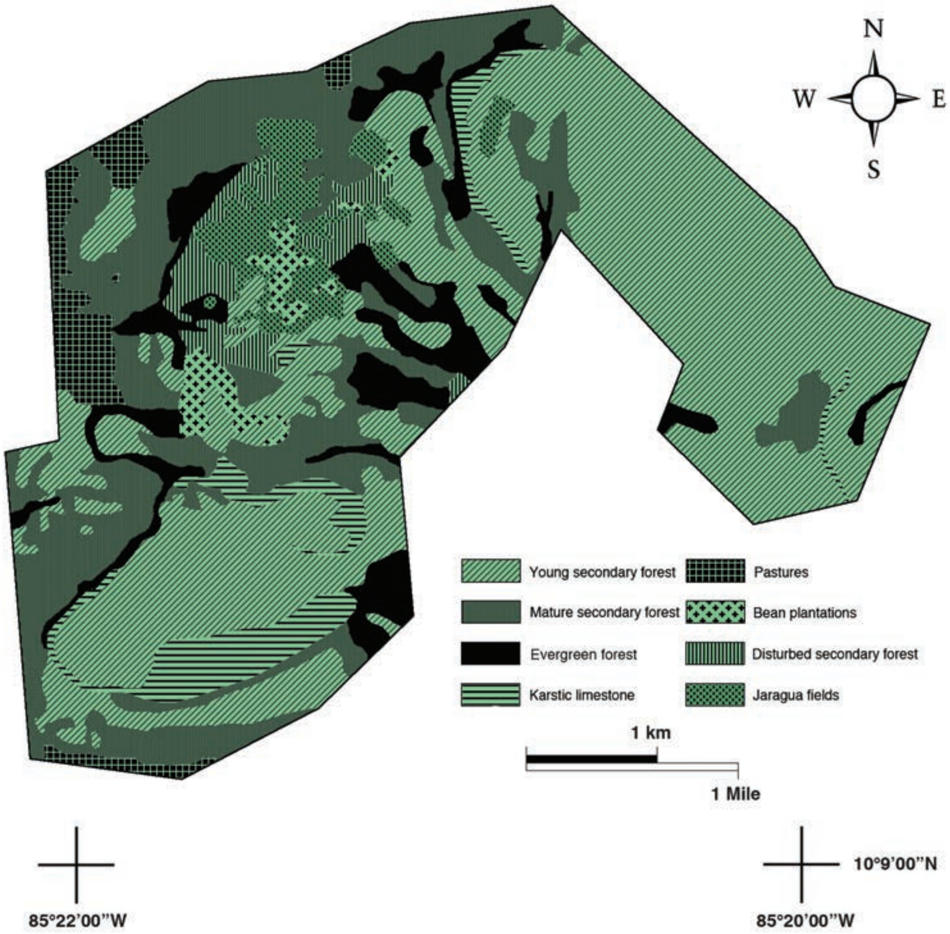

FIGURE 8. Map of vegetation types at Barra Honda National Park, by D. Bogarín.

and herbs *Adianthum* Manetti spp., *Ageratum conyzoides* L., *Coursetia caribea* (Jacq.) Lavin, *Eugenia hiraeifolia* Standl., *Euphorbia* L. spp., *Lasiacis divaricata* (L.) Hitchc., and *Mitreola petiolata* (Walter ex J.F. Gmel.) Torr. & A. Gray; and the vines *Centrosema sagittatum* (Humb. & Bonpl. ex Willd.) Brandegee, *Cydista diversifolia* (Kunth) Miers, *Desmodium infractum* DC., *Mandevilla subsagittata* (Ruiz & Pav.) Woodson, *Melothria trilobata* Cogn., *Passiflora platyloba* Killip, *Pleonotoma variabilis* (Jacq.) Miers, and *Trigonia rugosa* Benth.

Young secondary forest (1017 ha). Extensive secondary deciduous forest areas with scattered trees are located at Cerro Barra Honda, Cerros Quebrada Honda, Taburete, and Misingo (Fig. 9F). Some fine timber trees have been selectively logged in the past, while other areas have suffered the effects of fire, thus changing the areas' floristic composition. The vegetation comprises a mixture of shrubs and trees: *Albizia adinocephala* (Donn.Sm.) Britton & Rose ex Record, *Astronium graveolens, Bursera simarouba*, *Byrsonima crassifolia* (L.) Kunth, *Cedrela* L. spp., *Cecropia peltata* L., *Enterolobium cyclocarpum*, *Guazuma ulmifolia* Lam., *Handroanthus* Mattos spp., *Lonchocarpus phaseolifolius, Luehea seemannii*, *Muntingia clabura* L., *Pisonia aculeata, Plumeria rubra, Sideroxylon capiri*, *Spondias mombin* L., *Tabebuia* Gomes ex DC. *spp*., *Trichilia* P. Browne *spp*., *Sapranthus palanga,* and *Schizolobium parahyba*. On the slopes of Taburete, Cacao, and Misingo, tree species *Cochlospermum vitifolium* (Willd.) Spreng., *Handroanthus chrysanthus* (Jacq.) S.O. Grose, and *Schyzolobium parahyba* produce a conspicuous yellow bloom during the dry season. Understory vegetation comprises mainly *Acacia* Mill. spp., *Aegiphila panamensis, Jacquinia nervosa,* and various *Piper* L. spp.

Bean plantations (42 ha). Occupied lands inside the boundaries of BHNP owned by local farmers have been traditionally used to cultivate beans (*Phaseolus vulgaris* L.) until the present (Fig. 9D). The area is called Las Delicias, and it is located between Cerro Corralillo and Cerro Barra Honda. The land is surrounded by steep slopes of grassy lands and disturbed secondary forest. Scattered palm trees of *Acrocomia aculeata* (Jacq.) Lodd. ex Mart. (Coyol) are observed around the bean plantations and jaragua fields. Local farmers often burn this area before they begin sowing beans.

Jaragua fields (104 ha). Disturbed areas mostly covered by exotic jaragua grass, *Hyparrhenia rufa* (Nees) Stapf, are located on the summit of Cerro Corralillo at Las Delicias (Fig. 9C). The area has suffered severe deforestation, the original vegetation having been destroyed by fire. It is surrounded by bean plantations, which are burned by farmers every year during the dry season.

FIGURE 9. **A–H.** Vegetation types at Barra Honda National Park. **A,** Pastures with scattered trees. **B,** Rocky areas and karstic limestone pavement. **C,** Jaragua fields. **D,** Bean plantations. **E,** Disturbed secondary forest. **F,** Young secondary forest. **G,** Mature secondary forest. **H,** Evergreen secondary forest. Photographs by D. Bogarín (B, E–H) and F. Pupulin (A, C–D).

Disturbed secondary forest (68 ha). Areas surrounding jaragua fields and bean plantations have been severely disturbed by fire and human activities. This vegetation type is located mostly on Cerro Corralillo. The vegetation comprises scattered bushes mixed with grasses on rocky soils (Fig. 9E). Among the species observed are *Acrocomia aculeata, Bursera simarouba, Cecropia peltata, Ceiba pentandra, Chomelia spinosa, Cordia* L. spp., *Crescentia cujete* L., *Tabebuia* spp., *Enterolobium cyclocarpum*, *Ficus* spp., *Gliricidia sepium* (Jacq.) Kunth ex Walp., *Guazuma ulmifolia, Hymenaea courbaril, Luehea* Willd. spp., *Mutingia calabura, Pachira fendleri* Seem., and *Sideroxylum capiri*, among others.

Pastures (56 ha). Disturbed areas and fields, remnants of farms in the Park, are located mainly on the northwest boundary above El Flor (Fig. 9A). The area comprises grassy lands and scattered trees of *Crescentia cujete, Enterolobium cyclocarpum*, *Guazuma ulmifolia, Mutingia calabura*, *Samanea saman*, *Tabebuia rosea*, *Tamarindus indica,* and *Tectona grandis* L.f., among others.

Rocky areas and karstic limestone pavement (98 ha). The area is represented by small trees and bushes interspersed with limestone pavement in exposed sunny conditions (Fig. 9B). They are evident on top of Cerro Barra Honda near Mirador Nacaome. Vegetation includes *Albizia adinocephala, Andira inermis* (Sw.) Kunth, *Ayenia micrantha* Standl., *Bursera simaruba, Casearia corymbosa, Cordia inermis* (Mill.) I.M. Johnst., *Eugenia hiraeifolia* Standl., *Hymenaea courbaril, Lippia cardiostegia, Maclura tinctorial* (L.) D. Don ex Steud., *Mariosousa centralis* (Britton & Rose) Seigler & Ebinger, *Pitcairnia calcicola* J.R. Grant & J.F. Morales, *Plumeria rubra, Senna skinneri* (Benth.) H.S. Irwin & Barneby, *Simarouba glauca* DC., and *Trophis racemosa* (L.) Urb. The cactus *Stenocereus aragonii* (F.A.C. Weber) Buxb. is a common plant observed growing among calcareous rocks. Plants form large populations, mostly in the open, exposed sunny areas on the top of the main slopes of BHNP.

Materials and Methods

We conducted this study at the Barra Honda National Park, Guanacaste (Fig.1–4), Costa Rica, and the Lankester Botanical Garden (JBL, the acronym from its name in Spanish), University of Costa Rica. Living specimens were collected, cultivated, and documented at JBL between 2005 and 2019. We collected along the main trails of BHNP, along the Park boundaries, and in other places not accessible to visitors. Vegetation maps and georeferences were obtained using a Garmin GPSMAP® 64s, Google Earth Pro 7.3.3,© and field observations. Ecological zones were estimated using the Holdridge Life Zone System (Holdridge, 1967) and the ecological map of Costa Rica (Bolaños et al., 2005). Climatic data were taken from the Atlas Climatológico de Costa Rica (2019) and La Ceiba Station N.157 at Nicoya (10˚06'N, 85˚19'W; 20 m) of the Instituto Meteorológico Nacional de Costa Rica. Phenology data were recorded both in the field and in cultivated specimens, or from herbarium labels. Individual plants were photographed, illustrated, and preserved as herbarium specimens or spirit specimens in FAA (5% formaldehyde:5% glycerol:53% ethanol + 37% water) (including flowers, portions of the stems, or entire plants) for future reference. Herbarium and spirit vouchers may consist of wild-collected specimens or material collected entirely from cultivated plants, and they were deposited at CR, JBL, and USJ. Vouchers were complemented with sketches, photographs, and FAA material deposited at JBL. Drawings and images were prepared with Leica® MZ7.5 and MZ9.5 stereomicroscopes fitted with drawing tubes, Nikon® D5100 and D750 digital cameras with an AF-S VR Micro-NIKKOR 105mm f/2.8G IF-ED lens, and an Epson Perfection Photo Scanner V600. Composite plates were diagramed in Adobe Photoshop.® Ink drawings were prepared on smooth Fabriano® paper of 240 g/m^2 with a Rotring® Rapidograph 0.1 mm using black capillary cartridges and traced on an Artograph LightPad® A920. All taxa were illustrated with composite line drawings from living specimens. Illustrations include a typical plant habit, inflorescences or part of the inflorescences, the flower, and a dissection of the perianth. Descriptions were prepared from living specimens and herbarium material. Materials from AMES, CR, INB, JBL, K, and USJ were studied. Taxonomy of the genera that were recently subject to taxonomic changes, such as *Laelia* Lindl., *Specklinia* Lindl., and *Stelis* Sw., follow Pridgeon et al. (2005).

Results

We documented 36 orchid species at Barra Honda National Park, belonging to 29 genera (Fig. 10–14). Nine species (27.8%) were terrestrials, whereas 26 were epiphytes (72.2%) (Table 1). The most diverse genera were *Epidendrum* L., with 4 species, *Sarcoglottis* C. Presl with 3 species, and *Scaphyglottis* Poepp. & Endl. and *Specklinia*, each with 2 species recorded in the study area. While several elements are typical of the orchid flora of the dry region in northern Pacific Costa Rica or, more generally, of the Pacific lowlands, a surprise was the finding at BHNP of *Malaxis aurea* Ames, whose type is from the basal belt of the Talamanca mountain chain at over 1000 m of elevation. Even though its presence was expected in Costa Rica, the genus *Tropidia* Lindl., with *T. polystachya* (Sw.) Ames, is recorded from the BHNP for the first time for the flora of Costa Rica. *Pelexia barrahondaensis* Bogarín & Pupulin and *Sarcoglottis calcicola* Bogarín & Pupulin are described as new to science on the basis of populations found within BHNP. *Pleurothallis panamensis* Schltr. is recognized as a species distinct from *Specklinia microphylla* (A. Rich. & Galeotti) Pridgeon & M.W. Chase, transferred to the latter genus, and recorded for the first time for the Costa Rican flora from BHNP. With *Trichosalpinx reflexa* Mel. Fernández & Bogarín also described from BHNP (Fernández & Bogarín, 2011), the study of the orchid flora of the Park revealed three new species of Orchidaceae and resulted in the record of a new genus for the flora of Costa Rica.

Orchid Distribution within BHNP

Orchids at BHNP are distributed within the following vegetation types:

Table 1. Orchid species recorded at Barra Honda National Park.

Species	Epiphyte	Terrestrial	Deciduous	Evergreen
1. *Barkeria obovata* (C.Presl) Christenson	x		x	
2. *Beloglottis costaricensis* (Rchb.f.) Schltr.		x	x	
3. *Brassavola nodosa* (L.) Lindl.	x			x
4. *Catasetum maculatum* Kunth	x		x	
5. *Cohniella brachyphylla* (Lindl.) Cetzal-Ix & Carnevali	x			x
6. *Cycnoches warszewiczii* Rchb.f.	x		x	
7. *Cyrtopodium macrobulbon* (La Llave & Lex.) G.A.Romero-Gonzalez & Carnevali		x	x	
8. *Dichaea panamensis* Lindl.	x			x
9. *Dimerandra emarginata* (G.Mey.) Hoehne	x			x
10. *Encyclia macrochila* (Hook.) Neumann	x			x
11. *Epidendrum congestoides* Ames & C.Schweinf.	x			x
12. *Epidendrum coronatum* Ruiz & Pav.	x			x
13. *Epidendrum stamfordianum* Bateman	x			x
14. *Epidendrum vulgoamparoanum* Hágsater & L.Sánchez S.	x			x
15. *Guarianthe skinneri* (Bateman) Dressler & W.E.Higgins	x			x
16. *Habenaria macroceratitis* Willd.		x	x	
17. *Heterotaxis sessilis* (Sw.) F.Barros	x			x
18. *Laelia rubescens* Lindl.	x			x
19. *Lalexia quadrifida* (La Llave & Lex.) Luer	x			x
20. *Leochilus scriptus* (Scheidw.) Rchb.f.	x			x
21. *Lophiaris oerstedii* (Rchb. f.) R.Jiménez, Carnevali & Dressler	x			x
22. *Malaxis aurea* Ames		x	x	
23. *Maxillariella acervata* (Rchb.f.) M.A.Blanco & Carnevali	x			x
24. *Oeceoclades maculata* (Lindl.) Lindl.		x		x
25. *Pelexia barrahondaensis* Bogarín & Pupulin		x	x	
26. *Sarcoglottis acaulis* (Sm.) Schltr.		x	x	
27. *Sarcoglottis calcicola* Bogarín & Pupulin		x	x	
28. *Sarcoglottis sceptrodes* (Rchb.f.) Schltr.		x	x	
29. *Scaphyglottis micrantha* (Lindl.) Ames & Correll	x			x
30. *Scaphyglottis stellata* Lodd. ex Lindl.	x			x
31. *Sobralia fenzliana* Rchb.f.	x			x
32. *Specklinia grobyi* (Bateman ex Lindl.) F.Barros	x			x
33. *Specklinia panamensis* (Schltr.) Bogarín & Pupulin	x			x
34. *Trichosalpinx reflexa* Mel.Fernández & Bogarín	x			x
35. *Trigonidium egertonianum* Bateman ex Lindl.	x			x
36. *Tropidia polystachya* (Sw.) Ames		x		x

Evergreen forest. This vegetation type, located mainly at Las Cascadas, Quebrada San Diego, and Los Mesones, is the most diverse area in terms of orchid species at BHNP (Fig. 9H). We recorded 27 of the 36 (75%) species of orchids of BHNP in the evergreen forest. The only population of *Lophiaris oerstedii* (Rchb.f.) R. Jiménez, Carnevali & Dressler is found at Las Cascadas. Because of their high orchid diversity, these areas are a priority in terms of orchid conservation.

Mature secondary forests. This vegetation zone (Fig. 9G) contains many species of orchids typical of the northern Pacific dry forest ecosystems of Península de Nicoya, such as *Barkeria obovata* (C. Presl) Christenson*, Brassavola nodosa* (L.) Lindl.*, Catasetum maculatum* Kunth*, Cohniella brachyphylla* (Lindl.) Cetzal & Carnevali*, Dimerandra emarginata* (G. Mey.) Hoehne*, Epidendrum stamfordianum* Bateman*, Encyclia macrochila* (Hook.) Neumann*, Laelia rubescens* Lindl.*, Scaphyglottis micrantha* (Lindl.) Ames & Correll, and *S. stellata* Lodd. ex Lindl. Also, a population of the national flower of Costa Rica, *Guarianthe skinneri* (Bateman) Dressler & W.E. Higgins, was found. Other similar areas are located at Cerro Corralillo, Taburete, and Misingo. A section of mature secondary forest located around Cerro Barra Honda has the only population of fewer than 10 individuals of *Tropidia polystachya*. This species had not been previously recorded in Costa Rica. Together with the cactus forest and rocky areas with scattered trees of Cerro Barra Honda, this area has abundant populations of orchids that are rare or absent in other regions of BHNP, such as *Beloglottis costaricensis* (Rchb.f.) Schltr., *Habenaria macroceratitis* Willd.*, Malaxis aurea*, and *Sarcoglottis* spp. The exotic *Oeceoclades maculata* (Lindl.) Lindl. is common in the understory vegetation and even among rocks mixed with *Beloglottis costaricensis* and *Sarcoglottis calcicola*. We recorded 26 of the 36 (66.6%) species of orchids of BHNP in the mature secondary forest.

Young secondary forest. In this vegetation type (Fig. 9F), we observed *Barkeria obovata, Brassavola nodosa, Catasetum maculatum, Cohniella brachyphylla, Dimerandra emarginata, Epidendrum stamfordianum, Encyclia macrochila, Laelia rubescens, Scaphyglottis micrantha,* and *S. stellata*. However, orchids are not common, and they are mostly found on scattered old trees. Common terrestrial orchids are *Beloglottis costaricensis*, *Oeceoclades maculata,* and *Sarcoglottis* spp. We recorded 13 of the 36 (36.1%) species of orchids of BHNP in the young secondary forest.

Disturbed secondary forest, bean plantations, and jaragua fields. These areas (Fig. 9C–E) have very few orchid species because of the massive human intervention. The only orchids observed are growing on scattered trees surrounding the bean plantations and jaragua fields. The trees host mainly *Brassavola nodosa, Catasetum maculatum, Cohniella brachyphylla, Encyclia macrochila, Epidendrum stamfordianum,* and *Laelia rubescens*. Two rare terrestrial orchids were found in a secondary patch neighboring the jaragua fields: *Malaxis aurea* and *Pelexia barrahondaensis*. We recorded 8 of the 36 (22.2%) species of orchids of BHNP in these vegetation types.

Pastures. The scattered trees in pastures, such as large old specimens (Fig. 9A) of *Samanea saman* and *Tabebuia rosea* (Bertol.) DC., host mainly *Brassavola nodosa, Catasetum maculatum, Cohniella brachyphylla, Encyclia macrochila, Epidendrum stamfordianum, E. vulgoamparoanum* Hágsater & L. Sánchez, and *Laelia rubescens*. Isolated trees of *Crescentia cujete* are common in pastures and host *Leochilus scriptus* (Scheidw.) Rchb.f. on twigs. We did not find terrestrial orchids in pastures. We recorded 8 of the 36 (22.2%) species of orchids of BHNP in this vegetation type.

Rocky areas and karstic limestone pavement. Trees of *Cedrela odorata, Plumeria rubra,* and *Tabebuia rosea* are suitable phorophytes for *Barkeria obovata, Brassavola nodosa, Catasetum maculatum, Cohniella brachyphylla, Encyclia macrochila, Epidendrum stamfordianum, Laelia rubescens, Lalexia quadrifida* (La Llave & Lex.) Luer, *Specklinia grobyi* (Bateman ex Lindl.) F. Barros, and *S. panamensis* (Schltr.) Bogarín & Pupulin. Among rocks, we observed *Beloglottis costaricensis*, *Cyrtopodium macrobulbon* (Lex.) G.A. Romero & Carnevali, and *Sarcoglottis calcicola*. We recorded 13 of the 36 (36.1%) species of orchids of BHNP in this vegetation type.

Biogeography and Orchid Floristic Composition at BHNP

The seasonal dry forests of Central America, extending along the Pacific coast from Mexico to northern Costa Rica and then from eastern Panama to the Caribbean coast of Colombia and Venezuela, have the lowest diversity in terms of orchid species among Mesoamerican life zones (Pupulin and Bogarín, 2013). Some species at BHNP have wide distribution ranges and inhabit the entire Pacific coast of Costa Rica to Nicaragua, the humid areas of the central and southern Pacific to Panama, and the seasonal areas of Valle Central. These species are *Epidendrum coronatum*, *E. stamfordianum*, *E. vulgoamparoanum*, *Specklinia panamensis,* and *Scaphyglottis stellata*. Three species, *Lalexia quadrifida*, *Scaphyglottis micrantha,* and *Sobralia decora*, have the same distribution, but they can also be found in the humid areas of the northern Caribbean. Furthermore, *Brassavola nodosa*, *Catasetum maculatum*, *Dimerandra emarginata, Specklinia grobyi,* and *Trigonidium egertonianum* are distributed along the Pacific and the Caribbean slopes.

Within the biogeographic region of the northern Pacific, another group of species is found in the seasonally dry areas of the Northern Río Grande de Tárcoles Basin, reaching the seasonal areas of western Valle Central. Those species have their southern distribution limit in the surrounding regions of Cerro Turrubares and the Tárcoles and Candelaria rivers. Their habitat corresponds to the northern dry seasonal forests (Jiménez and Grayum, 2002). Within this group, we found *Barkeria obovata*, *Cohniella brachyphylla*, *Cyrtopodium macrobulbon*, *Encyclia macrochila*, *Guarianthe skinneri* (now extremely rare in the wild because of overcollection), *Laelia rubescens,* and *Trichosalpinx reflexa*. These observations are supported by floristic studies on the central and southern Pacific coast (Jiménez and Grayum, 2002; Pupulin, 1998; Pupulin and Rakosy, 2013; Weber et al., 2001). The Río Grande de Tárcoles Basin area is also the biogeographical limit for some species that range from the central and southern Pacific coast to Panama. They are mostly found in humid areas of the southern Pacific to the northern Península de Nicoya but without reaching the seasonal drier regions of the North Pacific. This pattern is observed in the orchid flora of BHNP, where we did not record *Aspasia epidendroides* Lindl., *Ionopsis satyrioides* (Sw.) Rchb.f., *Specklinia corniculata* (Sw.) Steud., *Trizeuxis falcata* Lindl., *Prosthechea abbreviata* (Schltr.) W.E. Higgins, *Campylocentrum multiflorum* Schltr., or *C. micranthum* (Lindl.) Maury, among others (Pupulin, 1998; Jiménez and Grayum, 2002). Other species not recorded in BHNP but commonly found in humid areas of Península de Nicoya are also found in the wet forest of the central and southern Pacific, such as *Anathallis lewisiae* (Ames) R. Solano & Soto Arenas, *Coryanthes kaiseriana* G. Gerlach, *Epidendrum anceps* Jacq., *Prosthechea chacaoensis* (Rchb.f.) W.E. Higgins, and *Stanhopea cirrhata* Lindl., among others. Méndez and Obregón (2019) compiled most of the orchids of the Península de Nicoya. Some of these orchid species might appear at BHNP in the future.

Plants of *Beloglottis* and *Sarcoglottis* are deciduous during the dry season when they bloom. Their habitat is similar to the species found in the dry areas of Mexico toward Nicaragua. They grow mostly among rocks and organic litter. The widespread *Tropidia polystachya* and the exotic *Oeceoclades maculata* retain their leaves throughout the year. *Oeceoclades maculata* is common in some regions of BHNP and form large groups of individuals, mainly in the secondary forest. Its presence is reported for dry areas of the Park Nacional Santa Rosa and has been collected in the central and southern Pacific and the Caribbean lowlands (Dressler, 2003). Plants of *Cyrtopodium macrobulbon* grow in rocky areas with organic matter in secondary forests. The only species of the genus in Costa Rica, it is also found in the seasonal areas of the Candelaria River Basin. Another curious finding is *Malaxis aurea*, a terrestrial species only recorded from the montane rainforest of eastern Cartago.

Among the most apparent elements of the seasonally dry forest ecosystems of the northern Pacific of Costa Rica are *Barkeria obovata, Brassavola nodosa, Catasetum maculatum, Cohniella brachyphylla, Dimerandra emarginata, Epidendrum stamfordianum, Encyclia macrochila, Laelia rubescens,* and *Scaphyglottis micrantha*. In addition to those well-known species, the present study provides new information on the dry forest ecosystems of Península de Nicoya. It attempts to explain the orchid flora of BHNP on the basis of the general distribution of species. This treatment can be useful for other protected areas within the same ecosystem that share several orchid species.

Key to the Orchids of Barra Honda National Park, Costa Rica

1a. Plant terrestrial 2
1b. Plant epiphytic 11
2a. Plant with pseudobulbs 3
2b. Plants without pseudobulbs 5
3a. Plants with several plicate leaves along the pseudobulb . . . . . . *Cyrtopodium macrobulbon*
3b. Plants with one conduplicate leaf at the apex of the pseudobulb 4
4a. Leaf cordate, concolorous green, inflorescence apical . . . . . . *Malaxis aurea*
4b. Leaf oblong-elliptic, maculate, inflorescence lateral . . . . . . *Oeceoclades maculata*
5a. Stems elongated > 3.5 cm long, leaves arranged along the stem, persistent when in flower, roots < 2.5 mm 6
5b. Stems abbreviated < 2 cm, leaves rosulate, deciduous when in flower, roots > 4 mm 7
6a. Plants without tubers, leaves plicate, lip without spur . . . . . . *Tropidia polystachya*
6b. Plants with tubers, leaves conduplicate, lip with a conspicuous spur . . . . . . *Habenaria macroceratitis*
7a. Leaves sessile or subsessile 8
7b. Leaves petiolate 9
8a. Inflorescence congested, floral bracts shorter than the ovary . . . . . . *Sarcoglottis calcicola*
8b. Inflorescence lax, floral bracts longer or as long as the ovary . . . . . . *Sarcoglottis acaulis*
9a. Petiole reddish-pinkish at the base, 13–23 cm long, stem monophyllous, inflorescence up to 8 flowers, brownish-green with white with the mesochile yellow . . . . . . *Pelexia barrahondaensis*
9b. Petiole white-green at base 10
10a. Inflorescence with 5–11 flowers, green or brownish green . . . . . . *Sarcoglottis sceptrodes*
10b. Inflorescence with 15–70 flowers, white with a central green stripe in the perianth parts . . . . . . *Beloglottis costaricensis*
11a. Plants with pseudobulbs 12
11b. Plants without pseudobulbs 27
12a. Leaves terete or semiterete 13
12b. Leaves flattened, plicate or conduplicate, not terete 14
13a. Leaves semiterete, flowers white . . . . . . *Brassavola nodosa*
13b. Leaves terete, flowers yellow . . . . . . *Cohniella brachyphylla*

Key to the Orchids of Barra Honda National Park, Costa Rica cont.

14a. Stems prolific, with pseudobulbs arising from the top of old pseudobulbs, forming chains . . . . *Scaphyglottis stellata*

14b. Stems not prolific, with pseudobulbs arising from the side of old pseudobulbs, not forming chains 15

15a. Leaves plicate 16

15b. Leaves conduplicate 17

16a. Plants without a mass of secondary roots, inflorescence lateral from near the apex of the pseudobulb, staminate flowers with ovate lip, the column thin, elongated, arcuate without setae . . . . *Cycnoches warszewiczii*

16b. Plants with a mass of secondary roots, inflorescence lateral from the base of the pseudobulb, staminate flowers with saccate lip, the column thick, short, erect with two setae . . . . *Catasetum maculatum*

17a. Inflorescence apical 18

17b. Inflorescence lateral 22

18a. Leaves (several) arranged along the stem, deciduous . . . . *Barkeria obovata*

18b. Leaves (1 or 2) arranged at the apex of the stem, evergreen 19

19a. Leaves < 8 mm wide, flowers < 5 mm in diam. . . . . *Scaphyglottis micrantha*

19b. Leaves > 1.5 cm wide, flowers > 2 cm in diam. 20

20a. Pseudobulbs clavate, the inflorescence shortly pedunculate and developed from a conspicuous papyraceous spathe . . . *Guarianthe skinneri*

20b. Pseudobulbs not clavate, the inflorescence pedunculate and not developed from a conspicuous papyraceous spathe 21

21a. Pseudobulbs 1-leaved, laterally flattened, ancipitous, flowers with the lip purple-lavender with the center dark purple . . . . *Laelia rubescens*

21b. Pseudobulbs 2-leaved, not laterally flattened, conic-ovoid, flowers with the lip white . . . . *Encyclia macrochila*

22a. Inflorescence many-flowered 23

22b. Inflorescence 1-flowered 25

23a. Pseudobulbs > 15 cm long, apically 2-leaved . . . . *Epidendrum stamfordianum*

23b. Pseudobulbs < 3 cm long, apically 1-leaved 24

24a. Leaves fleshy-coriaceous, > 30 cm long, > 7 cm wide; flowers white with purple-brown blotches, lip pandurate . . . . *Lophiaris oerstedii*

24b. Leaves coriaceous, < 10 long, < 2 cm wide; flowers greenish-yellow, lip obovate . . . . *Leochilus scriptus*

25a. Rhizome long, pseudobulbs distant from one another (plant repent) . . . . *Maxillariella acervata*

25b. Rhizome short, pseudobulbs close each other (plant caespitose) 26

26a. Pseudobulbs conspicuous, not hidden by the sheaths, bifoliate; leaves subcoriaceous, inflorescence to 20 cm long . . . . *Trigonidium egertonianum*

26b. Pseudobulbs inconspicuous, hidden by the foliaceous sheaths, monophyllus; leaves fleshy-coriaceous; inflorescence to 3.5 cm long . . . . *Heterotaxis sessilis*

27a. Leaves plicate . . . . *Sobralia fenzliana*

27b. Leaves conduplicate, lenticular or cylindrical 28

28a. Plants creeping, leaves granulose-verrucose, superposed . . . . *Specklinia panamensis*

28b. Plants erect or subpendent, leaves smooth, not superposed 29

29a. Leaves cylindrical or semiterete 30

29b. Leaves flattened 31

30a. Leaves semiterete, flowers white . . . . *Brassavola nodosa*

30b. Leaves terete, flowers yellow . . . . *Cohniella brachyphylla*

31a. Plants with one leaf at the apex of the stem 32

31b. Plants with more than one leaf distributed along the stem 34

32a. Stems covered by lepanthiform bracts . . . . *Trichosalpinx reflexa*

32b. Stems without lepanthiform bracts 33

33a. Mature plants < 4 cm tall . . . . *Specklinia grobyi*

33b. Mature plants > 5 cm tall . . . . *Lalexia quadrifida*

34a. Leaves < 1 cm wide 35

34b. Leaves > 1.5 cm wide 37

35a. Inflorescence lateral; leaves subcoriaceous, glaucous on the upper surface . . . . *Dichaea panamensis*

35b. Inflorescence apical; leaves coriaceous, not glaucous 36

36a. Stems short, < 6 cm tall; flowers green, suffused brown . . . . *Epidendrum congestoides*

36b. Stem long, > 20 cm tall; flowers pink-purple . . . . *Dimerandra emarginata*

37a. Inflorescence subumbellate, subsessile, with 3–5 green flowers . . . . *Epidendrum vulgoamparoanum*

37b. Inflorescence racemose, pedunculate, with > 6 cream flowers . . . . *Epidendrum coronatum*

Taxonomic Treatment

1. ***Barkeria*** Knowles & Westc., Floral Cabinet 2: 7–8. 1838. TYPE: *Barkeria elegans* Knowles & Westc.

Plants epiphytic or lithophytic, caespitose, often growing on twigs but not considered obligate twig epiphytes. *Stems* forming slender, ellipsoid, stipitate pseudobulbs bearing tight leaf sheaths. *Leaves* distichous, linear-lanceolate to broadly ovate, conduplicate, arranged along the stem, clustered toward the apex, deciduous during the dry season. *Inflorescence* a terminal raceme, sometimes branched or paniculate. *Flowers* often showy, 1–6 cm in diam., perianth parts reflexed or projected forward, resupinate. *Sepals* and *petals* subequal, or the petals wider than the sepals. *Lip* simple, conspicuous, basally adnate to the column, callus absent or consisting of verrucose keels extending beyond the apex of the column. *Column* appressed against the lip or divergent, often winged. *Anther* terminal. *Pollinia* 4, waxy, sometimes united in loose pairs by the caudicles.

A Neotropical genus of about 17 species ranging in the Pacific of Mesoamerica from Mexico (with 15 species) to Western Panama. Two species occur in Costa Rica, with a single species in BHNP.

Barkeria obovata (C. Presl) Christenson, Lindleyana 3(4): 221. 1988 [1989]. Fig. 10A, 15.

Basionym: *Oncidium obovatum* C. Presl., Reliquiae Haenkeanae 99. 1827. TYPE: MEXICO. *Thaddeus Haenke s.n.* (Holotype: PR).

Heterotypic synonyms: *Broughtonia chinensis* Lindl., London J. Bot. 1: 492. 1842. TYPE: Central America. *Richard B. Hinds s.n.* (Holotype: K).

Laeliopsis chinensis (Lindl.) Lindl., Paxton's Fl. Gard. 3: 156. 1853.

Epidendrum nonchinense Rchb.f. in W.G. Walpers, Ann. Bot. Syst. 6: 324. 1862.

Barkeria nonchinensis (Rchb.f.) Schltr., Orchideen: 206. 1915.

Epidendrum chinense (Lindl.) Ames, Schedul. Orchid. 7: 4. 1924.

Barkeria chinensis (Lindl.) Thien ex Dressler, Taxon 15: 241. 1966.

Plants epiphytic, caespitose, up to 25 cm high. *Roots* thick, coarse, up to 3 mm in diam., white with green tips. *Pseudobulbs* ellipsoid to fusiform, leafy, to 2.5–20 × 0.5–2.3 cm, concealed by green leaf sheaths, scarious when deciduous. *Leaves* 7–8, arranged along the stem, distichous, linear-lanceolate to elliptic-lanceolate, acute, conduplicate, subcoriaceous, articulate, deciduous before flowering and during the dry season, 5–14 × 0.7–1.6 cm. *Inflorescence* terminal, racemose simple or paniculate, 2–14 flowers, peduncle 5–35 cm long, elongated, slender, covered by tubular scarious sheaths, raceme 5–12 cm long, with 1–2 branches in large plants. *Floral bracts* subtending the floral branches, triangular, scarious, up to 10 mm long. *Ovary* pedicellate, cylindrical, up to 23 mm long. *Flowers* rather small and showy, spread, often cleistogamous, up to 1.7 cm long, white to yellowish or cream, the lip yellow, white or pink, often with reddish spots. *Dorsal sepal* lanceolate, acute, 9.5–10.0 × 1.5–2.0 mm. *Lateral sepals* ovate to lanceolate, acute, slightly thickened at apex, 9.5–10.0 × 1.5–2.0 mm. *Petals* lanceolate to elliptic, acute, 9–11 × 1.5–2.0 cm. *Lip* rhombic-ovate or elliptic-obovate, shortly acute, the margins involute around the column, disc sulcate, with 3 longitudinal keels, laterally branched, veins warty, verruculose, 9–11 × 6–7 mm. *Column* short, crenate at the apex, 3.0–3.5 mm. *Pollinia* 4, obovate. *Anther cap* cucullate. *Capsule* ellipsoid, about 2 cm long.

Distribution: from southern Mexico to western Panama.

Distribution in the Park: widespread in the Park. Populations were found near the cactus forest, along Ceiba and Mirador trails, and Cerro Corralillo around Las Delicias.

Etymology: from the Latin *obovatus*, "obovate," in allusion to the lip shape.

Habitat and ecology: plants grow on twigs of *Alophyllus* L. sp. (Sapindaceae), *Bursera* Jacq. ex L. spp. (Burseraceae), *Cedrela* L. spp. (Meliaceae), and *Erythroxylum havanense* (Erythroxylaceae) in rocky areas, rarely growing on thick branches or tree trunks.

Phenology: flowering occurs from December to April.

Discussion: it is distinguished by the fusiform pseudobulbs, with elliptic-lanceolate, subcoriaceous, conduplicate leaves arranged along the stem. The leaves are deciduous during the dry season and just before flowering. The terminal inflorescence is racemose or paniculate, bearing whitish-yellowish flowers. The lip is yellow, immaculate, or often with small red spots with a callus formed by several verrucose veins. The flowers are not as showy as other species of *Barkeria*, and they are often cleistogamous.

Additional specimens examined: BHNP, Bosque de Cactus, 10°10'32.1"N, 85°21'13.3"W, 639 m, bosque húmedo premontano transición a basal, epífitas en lomas rocosas, 28 enero 2009, *D. Bogarín 6149 y F. Pupulin* (JBL, CR). BHNP, San Antonio, Parque Nacional Barra Honda, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, epífitas en bosque secundario, 26 julio 2005, *D. Bogarín 1756 y F. Paniagua* (CR). Guanacaste: Nicoya, San Antonio, Parque Nacional Barra Honda, Cerro Corralillo, Sector Las Delicias, en bosque al final de las plantaciones de frijol, 10°11'11.82"N, 85°21'09.28"W, 481 m, epífitas en bosque húmedo premontano transición a basal, 5 noviembre 2011, *D. Bogarín 9387 & E. Artavia* (JBL).

2. ***Beloglottis*** Schltr., Beih. Bot. Centralbl., Abt. 2 37(2, Heft 3): 364–365. 1920.
TYPE: *Beloglottis costaricensis* (Rchb.f.) Schltr.

Plants terrestrial, sometimes epiphytic. *Roots* fasciculate, fleshy, puberulent. *Leaves* arranged in a basal rosette, strongly petiolate, lanceolate or elliptic-lanceolate, acute, deciduous in the seasonally dry forest before flowering. *Inflorescence* slender, erect, exceeding the leaves, covered by several tight sheaths, the rachis with loosely or densely, secund or subsecund flowers. *Flowers* inconspicuous, tubular, usually greenish or white. *Sepals* subsimilar, sometimes glandular outside, free or connate. *Petals* linear to linear-spathulate,

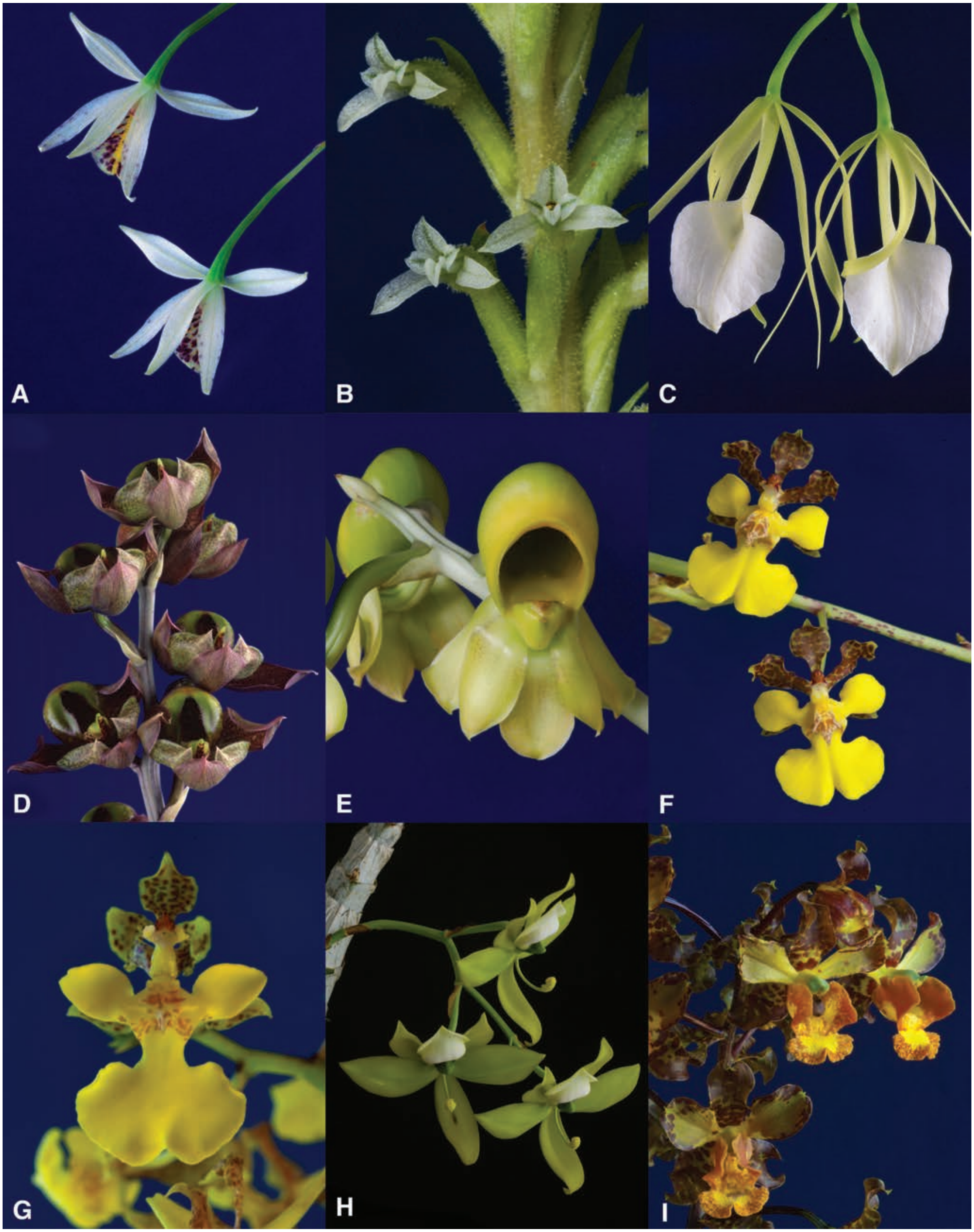

FIGURE 10. **A–I.** Orchid species found at Barra Honda National Park. **A,** *Barkeria obovata* (*Bogarín 6149*, JBL). **B,** *Beloglottis costaricensis* (*Bogarín 9415*, USJ). **C,** *Brassavola nodosa* (*Bogarín 1763*, JBL). **D,** *Catasetum maculatum*, male flowers (*Bogarín 2609*, JBL). **E,** *C. maculatum*, female flowers (*Pupulin 8331*, JBL). **F,** *Cohniella brachyphylla* (*Bogarín 2610*, JBL). **G,** *C. brachyphylla* (*Pupulin 8184*, JBL). **H,** *Cycnoches warszewiczii* (*Pupulin 8895*). **I,** *Cyrtopodium macrobulbon* (*Bogarín 2596*, JBL). Photographs by the authors.

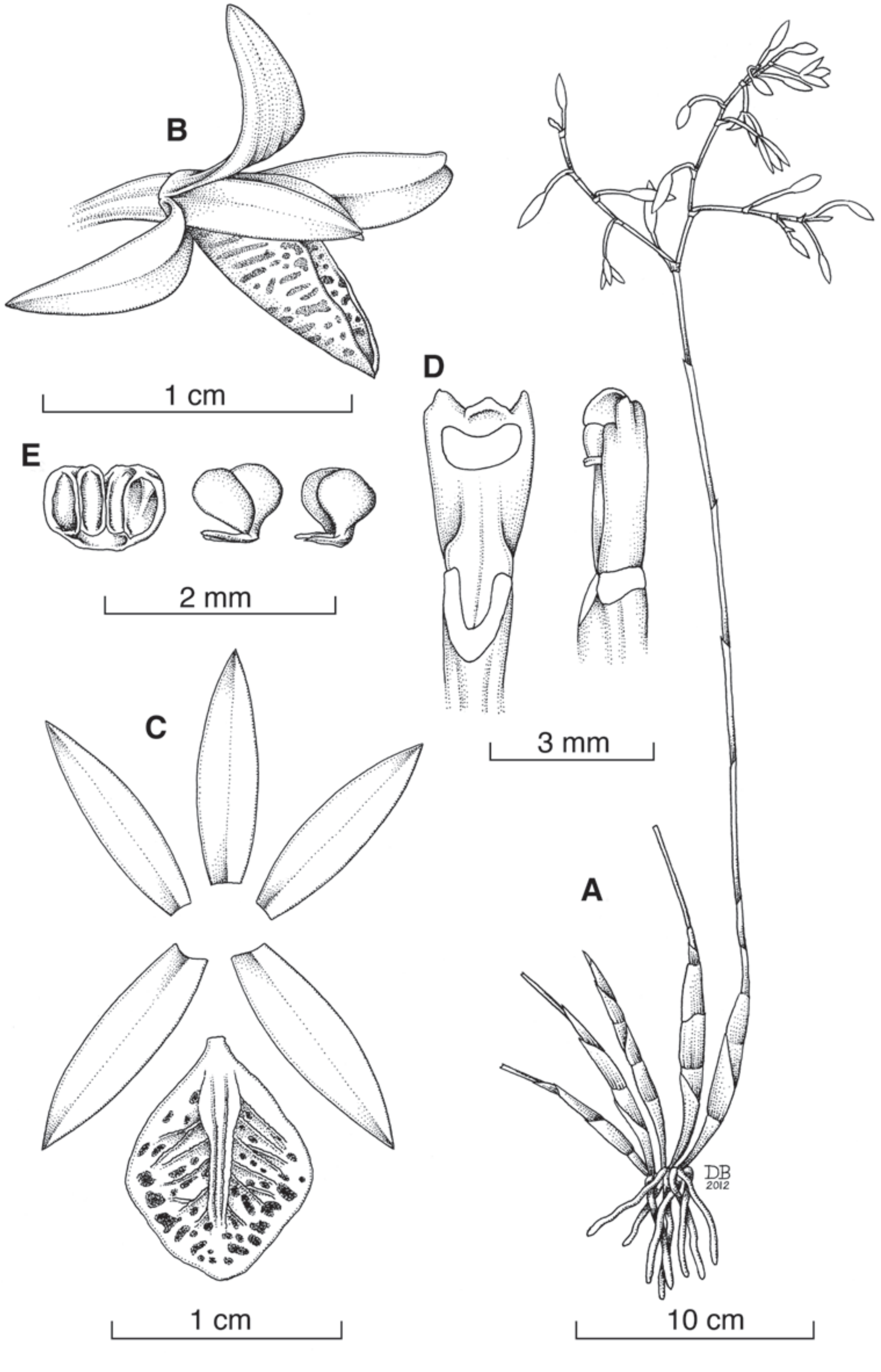

FIGURE 15. *Barkeria obovata* (C.Presl.) Christenson. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column. **E,** Pollinarium and anther cap. Drawn by D. Bogarín from *Bogarín 4041* (JBL).

acute to obtuse. *Lip* clawed, the claw basally connate with the lateral sepals, the lamina constricted near the apex, with basal auricles, the lateral margins agglutinate with the clinandrium. *Column* short, dilated below the stigma and forming a chin structure, footed. *Anther* erect, ovate to oblong-cordate. *Pollinia* 2–4, oblong-ovoid, powdery.

A Neotropical genus of about 10 species ranging from Mexico to Argentina. Four species occur in Costa Rica, with a single species in BHNP.

Beloglottis costaricensis (Rchb.f.) Schltr., Beih. Bot. Centralbl., Abt. 2 37(2, Heft 3): 365. 1920. Fig. 10B, 16, 17.

Basionym: *Spiranthes costaricensis* Rchb.f., Bonplandia 3:214. 1855. TYPE: [COSTA RICA. Alajuela:] Naranjo in Costarica, *A. S. Oersted s.n.* (Holotype: W, Mus. Hafn.).

Homotypic synonyms: *Gyrostachys costaricensis* (Rchb.f.) Kuntze, Rev. Gen. 2:664. 1981.

Plants terrestrial or lithophytic up to 45 cm tall, deciduous when in flower. *Roots* thick, fusiform, puberulent, fasciculate, 5.0–11.3 cm long, 7 mm in diam. *Leaves* 3–6, arranged in a basal rosette, petiolate, 9.5–22.2 × 3.8–6.7, ovate-elliptic to elliptic-lanceolate, acute, petiolate, petiole 2.5–9.0 cm long, the margin wavy. *Inflorescence* terminal, erect, pubescent, 38.5–43.0 cm long, peduncle 20–28 cm long with 6–10 appressed, tubular, ovate, acute bracts 2.8 × 0.6 cm, rachis 13–21 cm, with about 70 helical flowers opening in succession. *Floral bracts*, ovate, acute to acuminate, up to 12 × 3 mm. *Ovary* cylindrical, glandular-pubescent, to 4.3 mm long. *Flowers* inconspicuous, tubular, up to 5 mm long, perianth white with a green stripe in the middle, resupinate. Sepals connate at base, glandular-pubescent adaxially up to the middle, slightly reflexed toward the apex. *Dorsal sepal* oblong, conduplicate, acute, 5.0–6.1 × 1.0–1.6 mm. *Lateral sepals* oblong, conduplicate, acute, 5.8–7.5 × 1.2–1.6 mm. *Petals* narrowly linear-oblong to narrowly spathulate, acute, slightly falcate, 4.5–5.0 × 0.8–1.1 mm. *Lip* clawed, sagittate, with 2 basal filiform, falcate auricles up to 1.2 mm long, the blade oblong, wider near the middle and narrowing toward the acute apex, conduplicate and folded downward apically, glandular-pubescent, 4.6 × 3.5 cm. *Column* oblong, cylindrical, bidentate, rostrate, pubescent abaxially, 2-chambered, 2.0 × 1.1 cm. Anther erect, dorsal. *Anther cap* cucullate, rostrate, with 2 cells. *Pollinia* 2, obovate to elliptic, puberulent.

Distribution: Mexico to Peru and the West Indies.

Distribution in the Park: widespread around Cerro Barra Honda, Cerro Corralillo, Las Cascadas, and Los Mesones.

Etymology: named after Costa Rica, where the type specimen was collected.

Habitat and ecology: plants grow on rocky areas of secondary mature forest and cactus areas. They grow in medium-shaded conditions, terrestrially or in the humus and litter between fissures of rocks. During the dry season, the plants start to bloom while the leaves fall. They grow sympatrically with *Sarcoglottis acaulis* and *S. sceptrodes*.

Phenology: flowering occurs during the dry season from December to March.

Discussion: plants are terrestrial without pseudobulbs, with thickened roots and petiolate leaves with somewhat undulate margins. They are deciduous during the dry season when the plants bloom, developing an elongated scape of several inconspicuous, tubular white flowers. The perianth parts are glandular-pubescent, white with a green stripe along the middle. Within the Park, it can be confused with the other rosulate terrestrial species of the genus *Sarcoglottis*. During the wet season, they bear several leaves arranged in a basal rosette growing in the same habitat (in humus and litter among calcareous or limestone rocks). However, *Beloglottis costaricensis* shows green, petiolate leaves against those of *S. acaulis* and *S. sceptrodes*, which are white spotted. When in bloom, they are easily distinguished, mainly by the shape, size, and color of the flowers (see discussion and description of *Sarcoglottis* spp.).

Additional specimens examined: BHNP, Bosque de Cactus hacia una loma rocosa, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, terrestres en sitio rocoso con hojarasca, 21 febrero 2006, *D. Bogarín 2591* (JBL-spirit). Same locality, *D. Bogarín 2590* (CR). BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, al lado derecho, en dirección a La Mantequilla, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, 22 febrero 2006, *D. Bogarín 2611* (JBL-spirit). Same locality, *D. Bogarín 2612* (CR). BHNP, camino principal de la estación al Sendero Ceiba, parte alta antes de llegar al parqueo, 10°10'21.53"N, 85°21'42.50"W, 342 m, bosque húmedo premontano transición a basal, terrestre a orillas del camino, bosque secundario, 7 noviembre 2011, *D. Bogarín 9414 and 9415* (USJ). BHNP, rocky hill in Cactus forest toward La Mantequilla, 10°10'34.48"N, 85°21'19.08"W, 368 m, epiphytic in premontane moist, transition to tropical moist forest, 21 February 2012, *F. Pupulin 8185 & D. Bogarín* (JBL-spirit).

3. *Brassavola* R. Br., Hort. Kew. (ed. 2) 5: 216. 1813.
TYPE: *Brassavola cucullata* (L.) R. Br.

Plants epiphytic or lithophytic, caespitose or shortly creeping, erect or pendent. *Pseudobulbs* short, terete, monophyllous, cylindrical in cross section, covered by tightly fitting, papery sheaths. *Leaves* fleshy, subcylindric or terete, rarely flattened, articulate, conduplicate, channeled on the upper side, erect, stiff, rarely pendent. *Inflorescence* a terminal or lateral 1- to many-flowered raceme shorter than the leaves. *Flowers* generally large and showy, on an elongated peduncle, white, resupinate or pendent, scented during the night. *Sepals* and *petals* subequal, free, narrowly linear or linear-lanceolate, acute. *Lip* unguiculate, trumpet-like, conspicuous, with a tubular claw enfolding the column and a broad acute lamina. Column very short, usually shorter than the claw, footless, winged, straight or recurved, toothed at apex. *Anther* operculate, incumbent. *Pollinia* 8, 4 in each cell of the anther, laterally compressed, hard, waxy.

A Neotropical genus of about 17 species ranging from Mexico to Brazil, northern Argentina, and the West Indies. Two species are found in Costa Rica, 1 species in BHNP.

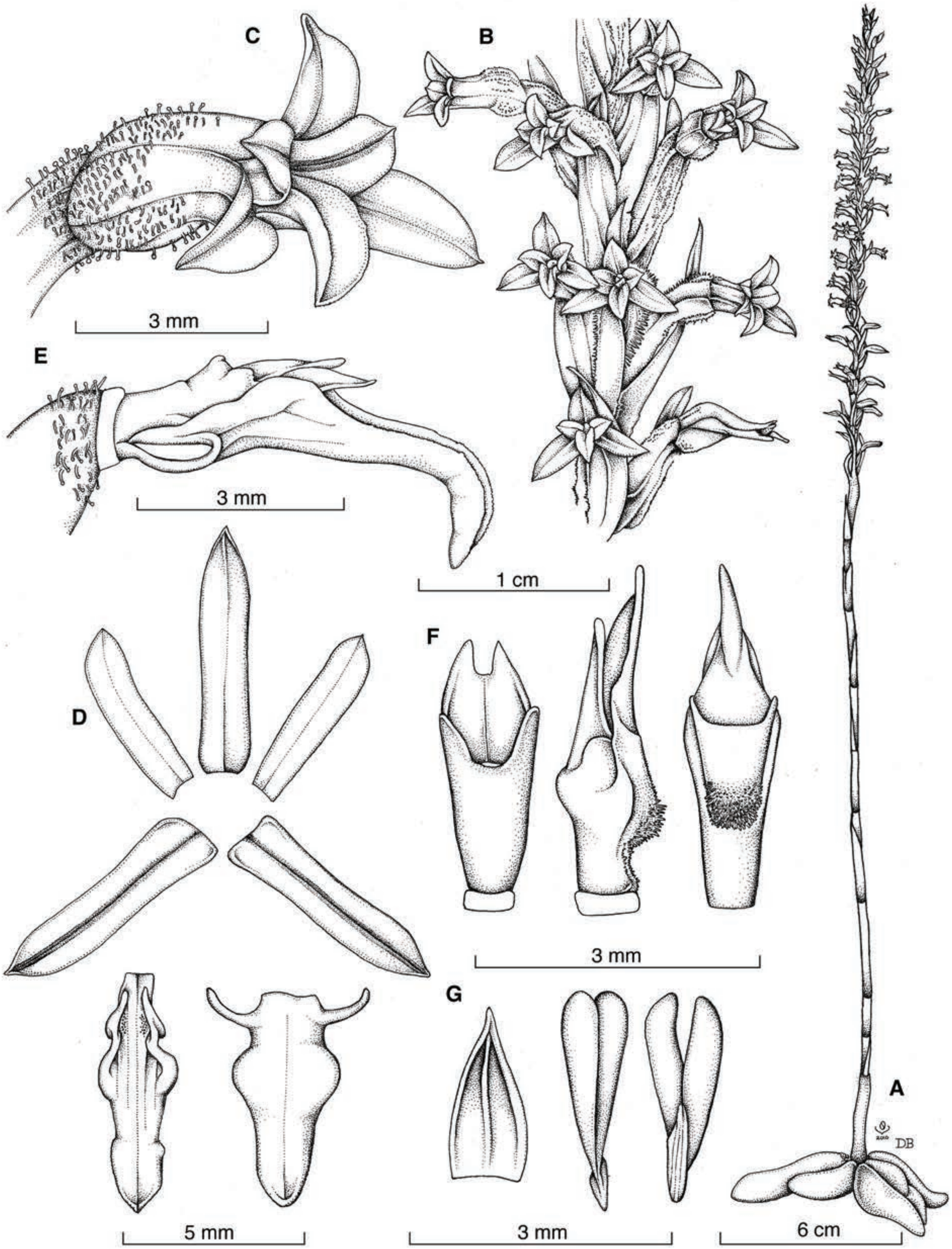

FIGURE 16. *Beloglottis costaricensis* (Rchb.f.) Schltr. **A,** Habit. **B,** Portion of the inflorescence. **C,** Flower. **D,** Perianth flattened. **E,** Column and lip, side view. **F,** Column, dorsal, lateral, and ventral view. **G,** Pollinarium and anther cap. Drawn by D. Bogarín & L. Oses from *Bogarín 9415* (JBL).

FIGURE 17. *Beloglottis costaricensis* flowering in situ among arborescent cacti at BHNP. Photograph by F. Pupulin.

Brassavola nodosa (L.) Lindl., Gen. Sp. Orchid. Pl. 114. 1831. Fig. 10C, 18–19.

Basionym: *Epidendrum nodosum* L., Species Plantarum 2: 953. 1753. TYPE: Habitat in America meridionali (Holotype: S).

Homotypic synonyms: *Cymbidium nodosum* (L.) Sw., Nova Acta Regiae Soc. Sci. Upsal. 6: 73. 1799.

Bletia nodosa (L.) Rchb.f. in W.G. Walpers, Ann. Bot. Syst. 6: 437. 1862.

Plants epiphytic or lithophytic, medium sized, up to 50 cm tall, with short, terete rhizome. *Roots* fleshy, with green to brownish vegetative apex, up to 4 mm in diam. *Pseudobulbs* terete to clavate, slender, 2.5–8.5 × 0.4–0.6 cm, covered by 2–3 scarious, tubular sheaths, monophyllous. Leaf linear to linear-elliptic, conduplicate, very fleshy-coriaceous, subcylindrical, rarely flattened, acuminate to slightly mucronate, erect, sulcate on the upper surface, 5–20 × 0.9–1.5 cm. *Inflorescence* terminal, slender, elongated, usually shorter than the leaves, to 15 cm long, 1- to many-flowered (mostly 2- to 3-flowered); peduncle terete; bracts triangular-lanceolate, acute, scarious, 7–10 mm long. *Ovary* pedicellate, slender, smooth, to 4–5 cm long. *Flowers* large and showy, with pale green sepals and petals, and white lip spotted by pale purple on the interior of the tubular claw. Sepals subequal, linear-lanceolate, acute, to 5–9 × 0.3–0.6 cm. *Petals* linear, attenuate above, somewhat falcate, 5.0–8.5 × 0.2–0.5 cm. *Lip* with a tubular-cymbiform claw enfolding the column, abruptly expanding into an ovate-cordate lamina, venose, abruptly apiculate-acuminate at apex and often recurved backward, to 7.8–8.0 × 4.0–4.5 cm at midpoint of the lamina; claw about 3 cm long, 1.2 cm wide, with erose-dentate margins. *Column* short, with a pair of triangular-subfalcate, acute wings, 3-lobed at apex, to 8 mm long. *Pollinia* 8, in 2 subequal groups of 4, on 2 powdery, bilobed caudicles. *Anther cap* hemiglobose, 8-celled. *Capsule* ellipsoidal, conspicuously ridged, up to 5 cm long.

Distribution: from Mexico to Venezuela, Brazil, and the Antilles.

Distribution in the Park: common along the main trails of BHNP, Cerro Barra Honda, Cerro Corralillo, Las Delicias, and the boundaries of the Park with private farms.

Etymology: from the Latin *nodosus*, “knotted” or “knobby.”

Habitat and ecology: plants are usually found in exposed to medium-shaded conditions, often forming large specimens on the host tree (Fig. 19). They are found growing on several trees, such as *Lonchocarpus* Kunth sp. (Fabaceae-Papilionaceae), *Pachira fendleri* (Bombacaceae), *Plumeria rubra* (Apocynaceae), and *Tabebuia* spp. (Bignoniaceae). Pollination may be carried out by sphingid moths (Pupulin, 1998).

Phenology: flowering occurs from January to October, but mainly from June to August.

Discussion: it is distinguished by the cylindrical short pseudobulbs bearing 1 semiterete leaf. The terminal inflorescences have 2–3 white, showy flowers that are fragrant in the evenings. The sepals and petals are subequal, linear, and pale green. Variation in the floral fragrances among populations suggests that there could be more than one species under a broad concept of *Brassavola nodosa* (Williams, 1981). However, no morphological differences have been found to allow a proper distinction among the names proposed, such as *B. grandiflora* Lindl. Within the park, *B. nodosa* is vegetatively similar to *Cohniella brachyphylla* because of the terete leaves; however, *C. brachyphylla* has thin roots (< 3 mm in diam.), subglobose pseudobulbs, and a panicle of smaller yellow flowers with brown spots.

Additional specimens examined: BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, epífitas en bosque secundario, 26 julio 2005, *D. Bogarín 1763 y F. Paniagua* (JBL-spirit). Same locality, *D. Bogarín 1762 and F. Paniagua* (JBL-spirit).

4. *Catasetum* Rich. Ex Kunth, Syn. Pl. 1: 330–331. 1822. TYPE: *Catasetum macrocarpum* Rich. Ex Kunth.

Plants epiphytic (often on rotten trunks), rarely terrestrial or lithophytic. *Pseudobulbs* slender-ovoid or fusiform with several leaves arranged along the stem, deciduous during the dry season, leaving spines at the apex of the imbricating sheaths when the leaves are dropped. *Leaves* distichous, usually large and plicate, thin, elliptic-lanceolate. *Inflorescence* lateral, arising from the base of the pseudobulb, erect or pendent, few- to many-flowered raceme. *Flowers* usually large and conspicuous, unisexual, dimorphic, nonresupinate. *Sepals* and *petals* subequal, free, fleshy, or membranaceous. *Lip* deeply saccate or rigid to almost flat, sessile, lateral compressed, with entire, dentate, or deeply fimbriate margins. *Column* erect, footless, thickened, elongated with or without a pair of reflexed antennae or tendrils surrounding the stigma and developed at the base in male flowers; shorter and thicker, without antennae in female flowers. *Anther* terminal, operculate, incumbent. *Pollinia* 4, or 2.

A genus of about 130 species extending from Mexico through Central America to Brazil and Argentina. One species in Costa Rica and BHNP.

Catasetum maculatum Kunth, Syn. Pl. 1: 331. 1822. Fig. 10D–E, 20.

TYPE: *Crescit in Regno Novo-Granatensi, prope Turbaco, alt. 180 hex. Floret Majo, A. de Humboldt & A. Bonpland s.n.* (Lectotype designated by Romero and Jenny, 1993).

Heterotypic synonyms: *Catasetum oerstedii* Rchb.f., Bonplandia (Hannover) 3: 218. 1855. TYPE: NICARAGUA. Herr Dr. Oersted sammelte die Art in Nicaragua, *A. Oersted s.n.* (Holotype: W).

Catasetum brenesii Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 136, 225 (1923). TYPE: COSTA RICA. Clairiéres des bois aux plaines du Pacifique, pres Guacimal, alt. 100–150 m, *A. M. Brenes no. 294*, VIII. 1922. Fleurs tachetées et lavées de rouge-brun au fond vert (Holotype: B, destroyed; Lectotype designated by Barringer, 1986: NY).

Plants epiphytic, ascending, stout *herb*s with abbreviated rhizome, to 70 cm tall. *Roots* fleshy, glabrous, with many

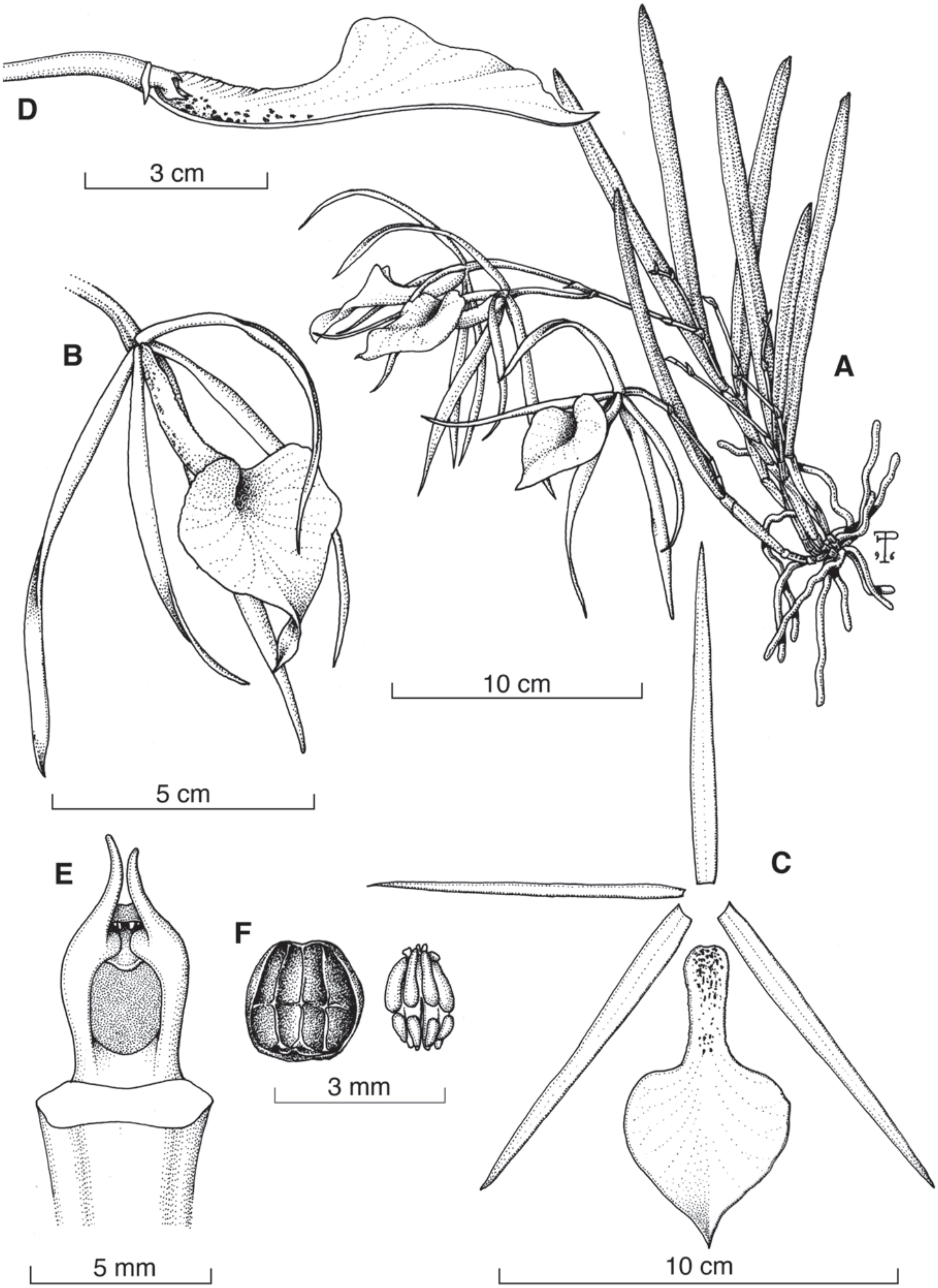

FIGURE 18. *Brassavola nodosa* (L.) Lindl. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 331* (USJ).

FIGURE 19. *Brassavola nodosa* flowering in situ on the trunk of a *Ceiba* sp. at BHNP. Photograph by F. Pupulin.

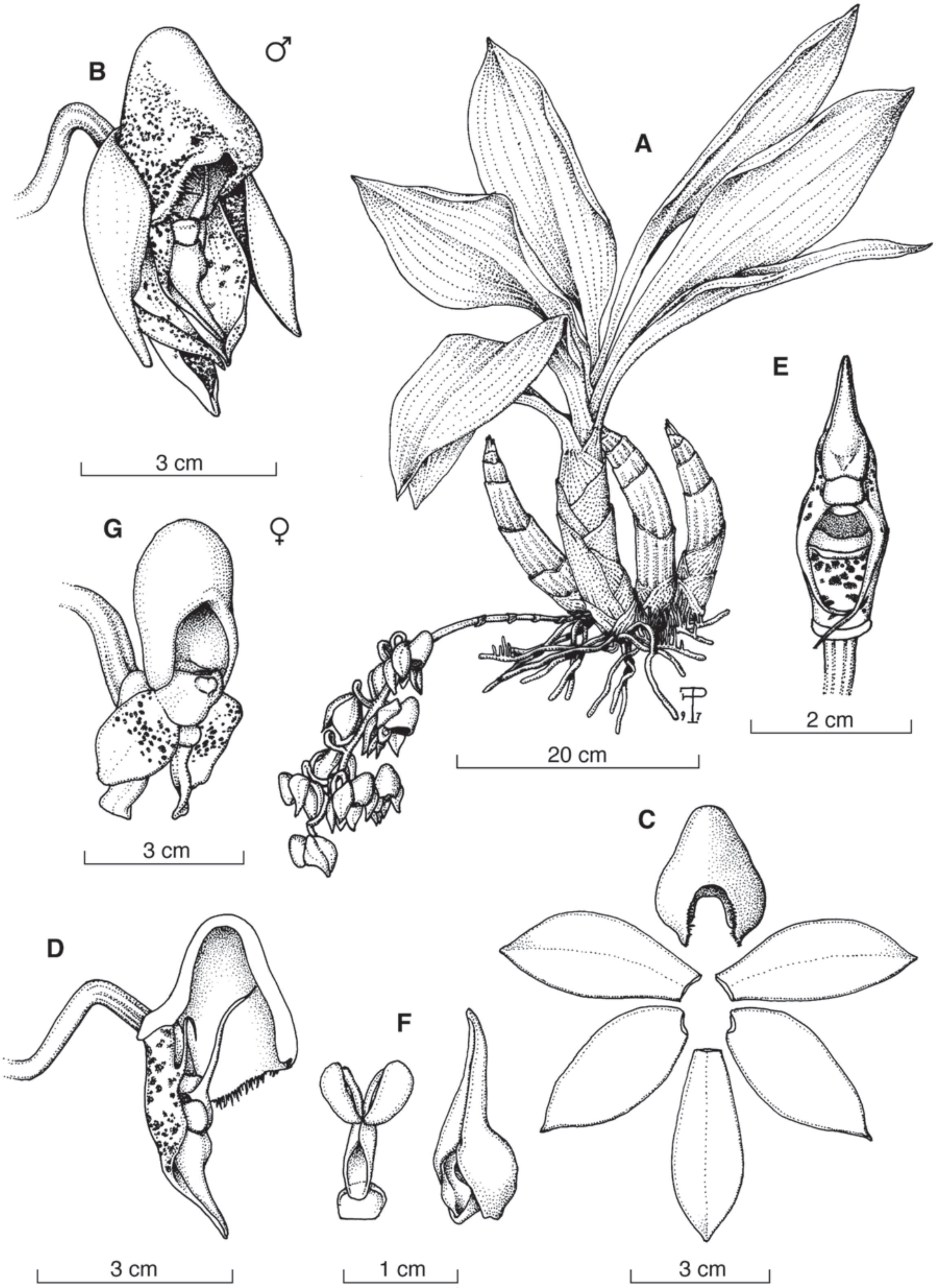

FIGURE 20. *Catasetum maculatum* Kunth. **A,** Habit. **B,** Male flower. **C,** Male column and lip, lateral view (the lip longitudinally sectioned). **D,** Dissected male flower. **E,** Male column, ventral view. **F,** Pollinarium and anther cap. **G,** Female flower. Drawn by F. Pupulin from *Pupulin 323* and *327* (USJ).

slender, erect, secondary rootlets, forming dense mats around the plant base. *Pseudobulbs* subfusiform-conical, to 30 × 5–8 cm, covered by 5–6 scarious, imbricating leaf-sheaths. *Leaves* 6 to 8, distichous, elliptic-lanceolate to oblong-elliptic, acute to acuminate, plicate, strongly nerved, up to 45 × 8–12 cm, the blades deciduous during the dry season, the persistent bracts enveloping the pseudobulbs armed at the apex with sharp spines. *Inflorescence* lateral, basal, erect to arching, racemose, 3- to 14-flowered, up to 40 cm long. Ovaries pedicellate, stout, arcuate, to 3 cm long. *Flowers* relatively large, nonresupinate, unisexual, dimorphic; staminate, and pistillate flowers produced on separate inflorescences. Staminate *flowers* (male), yellowish-green, suffused, and spotted by purple. *Dorsal sepal* membranaceous, oblong-elliptic to lanceolate, acuminate, concave, to 4.2 × 1.6 cm. *Lateral sepals* membranaceous, obliquely lanceolate, acuminate, to 4.4 × 1.9 cm. *Petals* membranaceous, elliptic-lanceolate, acuminate, mucronate at apex, 4.0 × 1.8 cm. *Lip* fleshy, rigid, saccate, obconic, 3.0 × 2.5 cm, margins of the basal portion of the orifice ciliate, the apex of the orifice slightly emarginate. *Column* stout, rostrate, concave, 3.2 × 1.2 cm, with 2 slender, elongate antennae projecting downward, one unciform, the other undulate, extending into the calceolate lip. *Pollinia* 2, obovate, sulcate, on an obtriangular deflexed stipe; viscidium peltate. *Anther cap* cucullate-rostrate, 2-celled. Pistillate *flowers* (female) yellowish-green, spotted by purple at the base of petals. *Sepals* and *petals* reflexed, fleshy. *Sepals* subequal, broadly ligulate, apiculate at apex, to 2.8 × 2.0 cm. *Petals* elliptic-lanceolate, acute, to 2.5 × 1.9 cm. *Lip* fleshy, rigid, saccate, 3.1 cm long, about 2 cm wide, margins of the orifice smooth. *Column* fleshy, very stout, to 1.4 × 1.2 cm, with a short apicule on upper apex.

Distribution: from Mexico to Colombia, Ecuador, and Venezuela.

Distribution in the Park: widespread in open areas and along Sendero Ceiba and Mirador. Large populations were observed at Las Delicias in exposed dead rotten trunks.

Etymology: from the Latin *maculatus*, "spotted" or "speckled," referring to the red-brown spots on the flower.

Habitat and ecology: common in humid coastal lowlands often below 500 m in both Caribbean and Pacific lowlands. They grow mostly on rotten branches or main trunks of *Guazuma ulmifolia* (Sterculiaceae), *Spondias mombin*, *Tabebuia* sp. (Bignoniaceae), and, most frequently, on *Acrocomia aculeata* (Arecaeae), "palma coyol," in disturbed areas fully exposed to sunlight. Flowers are pollinated by the bee *Eulaema cingulata* (Allen, 1952).

Phenology: flowering mainly occurs from July to September. *Catasetum maculatum* shows unisexual flowers and environmental sex determination, in which plants can produce staminate or pistillate flowers under specific ecological conditions (Pérez-Escobar et al., 2016). We observed staminate flowers more often than pistillate flowers.

Discussion: *Catasetum maculatum* is distinguished by the epiphytic plants, with elongated pseudobulbs with distichously arranged plicate leaves. The leaves are deciduous, leaving spiny sheaths during the dry season. The flowers are produced from a basal racemose inflorescence of few unisexual flowers, with a saccate lip. The staminate flowers are greenish with red spots, and the column has 2 antennas projected into the lip. The pistillate flowers are yellow with red dots. Large specimens show dense mats of rootlets around the plant base. In the BHNP, it is vegetatively similar to *Cyrtopodium macrobulbon* because both species have long plicate leaves grouped along the pseudobulbs, becoming spiny when they fall. However, *C. macrobulbon* is mostly terrestrial or lithophytic, with a paniculate inflorescence bearing prominent bracts and several hermaphrodite yellow-brown spotted flowers, without a saccate lip.

Additional specimens examined: BHNP, camino del Sendero Ceiba hacia la Caverna Terciopelo, 10°10'N, 85°21'W, 420 m, epífita en Jobo, *Spondias mombin,* bosque húmedo premontano transición a basal, 21 febrero 2006, *D. Bogarín 2609* (JBL-spirit).

5. *Cohniella* Pfitzer, Nat. Pflanzenfam 2(6): 194. 1889.
TYPE: *Cohniella quekettioides* (Rchb. f.) Pfitzer

Plants epiphytic or lithophytic caespitose herbs. *Pseudobulbs* short, subglobose, 1-leaved. *Leaf* terete, fleshy, sulcate, often spotted with red or purple, erect or pendent. *Inflorescences* lateral from the base of the pseudobulbs, paniculate or racemose. *Flowers* showy, resupinate, spreading, yellow with red or maroon spots or blotches. *Sepals* and *petals* subsimilar, clawed, often spotted with red-brown. *Lip* conspicuously 3-lobed, yellow, rarely white, the midlobe larger than the laterals with the callus made up of small teeth and spotted with red or maroon. *Column* short, cylindrical, the stigmatic surface suborbicular, usually with small horns or wings on each side and a tabula infrastigmatica. *Anther* terminal, operculate. *Pollinarium* 2, yellow, obpyriform, with stipe and viscidium.

A Neotropical genus of about 30 species distributed from northern Mexico to Brazil and northern Argentina. Two species in Costa Rica and one in BHNP.

Cohniella brachyphylla (Lindl.) Cetzal-Ix & Carnevali, Brittonia 62(2): 163. 2010. Fig. 10F–G, 21.

Basionym: *Oncidium brachyphyllum* Lindl., Edwards's Bot. Reg. 28: sub t. 4. 1842. TYPE: This is a Mexican species, with very short stiff leaves, and smaller panicles, not above 18 inches high (Holotype: K).

Plants epiphytic, cespitose, erect, rarely pendent *herb*s up to 50 cm long, with short rhizome. *Roots* up to 1.5 mm in diam., white with reddish tips. *Pseudobulbs* oblate to globose to broadly ovoid, short, 0.7–2.0 × 0.7–1.1 cm, unifoliate, enclosed by imbricate sheaths 3.2–10.0 × 1.0–2.1 cm. *Leaves* terete, subcylindrical, fleshy-coriaceous, 5–50 × 0.5–2.0 cm, dark green, purple-spotted, sulcate dorsally, gradually attenuated apically. *Inflorescence* basal, lateral, racemose or paniculate, green and purple spotted, up to 40 cm long with 1–8 branches, the branches 3- to 7-flowered, erect to arched, peduncle bracts 10–20 × 4–10 mm, oblanceolate, acuminate, tubular; bracts subtending the lateral branches 4–12 × 1.5–3.5 mm, elliptic, acuminate; floral bracts 1.5–7.0 × 1.0–1.5 mm, narrowly elliptic,

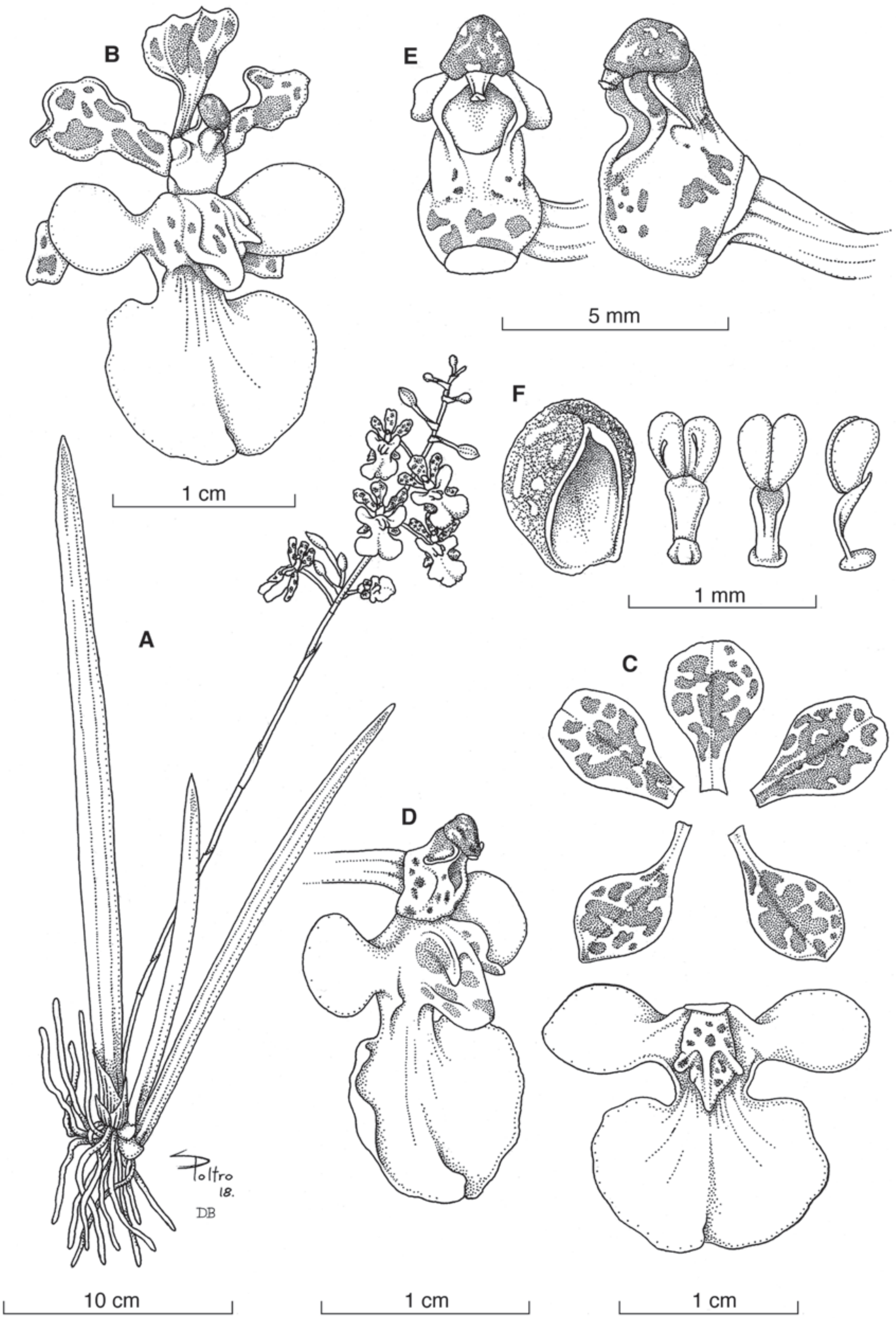

FIGURE 21. *Cohniella brachyphylla* (Lindl.) Cetzal & Carnevali. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, side and ventral view. **F,** Pollinarium and anther cap. Drawn by D. Bogarín and S. Poltronieri from *Bogarín 2610* (JBL).

acuminate. *Ovary* pedicellate, cylindric, 2 mm long. *Flowers* showy, resupinate, medium-sized for the genus, spread, the lip yellow, the callus white stained with reddish-brown, sepals and petals greenish-yellow with brown spots. *Dorsal sepal* unguiculate, spathulate, suborbicular to ovate, obtuse, shortly apiculate, apically concave, 8–9 × 5.5–6.0 mm. *Lateral sepals* subsimilar to the dorsal sepal, unguiculate, subfalcate, ovate, acute, apically concave, 9.5–10.0 × 4.5–5.0 mm. *Petals* slightly unguiculate, oblong to oblanceolate, subtruncate, sometimes reflexed, with undulate margins, 8–9 × 4.5–5.0 mm. *Lip* deeply 3-lobed, 1.5 cm long from the base to the apex, 1.9 cm wide across the lateral lobes, the lateral lobes perpendicular to the disc, slightly unguiculate, suborbicular, ovate or obovate, obtuse, the midlobe transversely oblong to reniform, retuse or deeply emarginate, appearing bilobate, slightly undulate, 0.9–1.0 × 1.3–1.6 cm, the isthmus 2.0–3.0 × 4.5–5.0 mm, the disc 4.5–5.0 × 4–5 mm with a callus formed by a central rounded keel and 2 smaller divergent lateral teeth. *Column* short, up to 5.5 mm long, basally thick, with 2 short stigmatic wings, the tabula infrastigmatica sulcate. Pollinarium with 2 obpyriform, cleft pollinia in a narrow spathulate stipe with viscidium. *Anther cap* cucullate, operculate, papillose, ellipsoid, spotted with purple.

Distribution: it ranges from Mexico to Costa Rica.

Distribution in the Park: this species was observed growing on several phorophytes but mainly on *Plumeria rubra* and *Tabebuia rosea* in the forest mixed with cacti at Cerros Barra Honda and on insolated trees in disturbed areas surrounding the park.

Etymology: from the Greek *brachys*, "short," and *phyllo*, "leaf," referring to the very short, stiff leaves and smaller panicles, not above 18 inches high.

Habitat and ecology: plants are found in the lowland tropical dry forest of Península de Nicoya and the drier areas of the Valle Central up to 900 m of elevation. It is the species of *Cohniella* from the driest environments, often found growing under fully exposed conditions (Carnevali et al., 2010).

Phenology: plants were recorded in flower from November to May.

Discussion: it is characterized by the subglobose pseudobulbs bearing one fleshy, succulent, dorsally grooved, cylindrical leaf. The inflorescence is lateral, paniculate with several yellow flowers spotted with brown. *Cohniella ascendens* is similar but differs in the inflorescences usually shorter than the subtending leaves and the erect lateral lobes of the lip that are partially enfolding the column (Carnevali et al., 2010). Within BHNP, it is similar in habit to *Brassavola nodosa*, though the latter has terminal inflorescences, elongated, cylindrical pseudobulbs, and night-scented white flowers. The species is found mostly in tropical rain forest, in warm, humid areas, whereas *C. brachyphylla* is found in the seasonal dry forest. Nevertheless, the variation in flower morphology, both among and within populations of *Cohniella* at BHNP (Fig. 7F–G), is so pronounced as to challenge any attempt at a firm application of the names previously proposed for this group of plants. Here, we tentatively accept *C. brachyphylla* (Carnevali et al., 2010) for the specimens previously treated as *C. cebolleta* (Dressler, 2003).

Additional specimens examined: BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, al lado derecho, en dirección a La Mantequilla, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, epífitas en *Plumeria rubra* (Apocynaceae), 22 febrero 2006, *D. Bogarín 2618* (JBL-spirit). Same locality, *D. Bogarín 2610* (JBL-spirit).

6. *Cycnoches* Lindl., Gen. Sp. Orchid. Pl. 154. 1832.
TYPE: *Cycnoches loddigesii* Lindl.

Plants epiphytic (often on rotten trunks). *Pseudobulbs* slender-ovoid or fusiform with several leaves arranged along the stem, deciduous during the dry season. *Leaves* distichous, usually large and plicate, thin, elliptic-lanceolate. *Inflorescence* lateral, arising above the middle or from near the apex of the pseudobulb, pendent, few- to many-flowered raceme. *Flowers* usually large and conspicuous, unisexual, rarely bisexual, dimorphic, nonresupinate. *Sepals* and *petals* subequal, free, fleshy, or membranaceous. *Lip* convex to almost flat, entire with a prominent callus at the base. *Column* deeply arcuate, footless, thin, elongated. *Anther* terminal, operculate, incumbent. *Pollinia* 2 with stipe and viscidium.

A genus of about 30 species extending from Mexico through Central America to Brazil. Two or three species in Costa Rica and one found in BHNP.

Cycnoches warszewiczii Rchb.f., Bot. Zeit. (Berlin) 10: 734. 1882. Fig. 10H, 22–23.

Basionym: *Cycnoches ventricosum* var. *warszewiczii* (Rchb.f.) P.H.Allen, Orchid J. 1: 401. 1952. TYPE: [PANAMA]: Chiriqui, *J. Warszewicz s.n.* (Holotype: W).

Heterotypic synonym: *Cycnoches tonduzii* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 298. 1923. TYPE: COSTA RICA: San Ramon, im Mai 1913, *A. Tonduz s.n.* (Holotype: B, destroyed; Neotype, selected by Pupulin et al., 2016, copy of the original drawing of the type made in 1934 by Mansfeld: AMES).

Plants epiphytic, cespitose, tall *herb*s up to 70 cm tall. *Rhizome* stout, with very short internodes. *Roots* thick, numerous, flexuous, to about 3 mm in diam. *Pseudobulbs* homoblastic, cylindrical, tapering at apex, made up of 7–19 internodes, 15–45 cm long, 2.5–5.0 cm wide, leafy at maturity, then deciduous, covered by distichous, thin, tightly adpressed, persistent, papery, fibrous, broadly triangular leaf sheaths, becoming dry, papyraceous, white with age, the apex of the sheaths unarmed. *Leaves* distichous, plicate, lanceolate-elliptic, acute to subacuminate, narrowed at the base into a short, conduplicate petiole, 15–50 × 3–10 cm, ultimately deciduous. *Inflorescence* lateral, produced from the middle to upper portion of the pseudobulb (after the leaves have fallen at BHNP), a stout, arching-pendent raceme, few-flowered (2–4 flowers) raceme to about 20 cm long; the peduncle terete, to 10 cm long, with 3–5 adpressed, triangular-lanceolate, acute, papyraceous, adpressed brown bracts to 15 mm long. *Floral bracts* narrowly triangular-

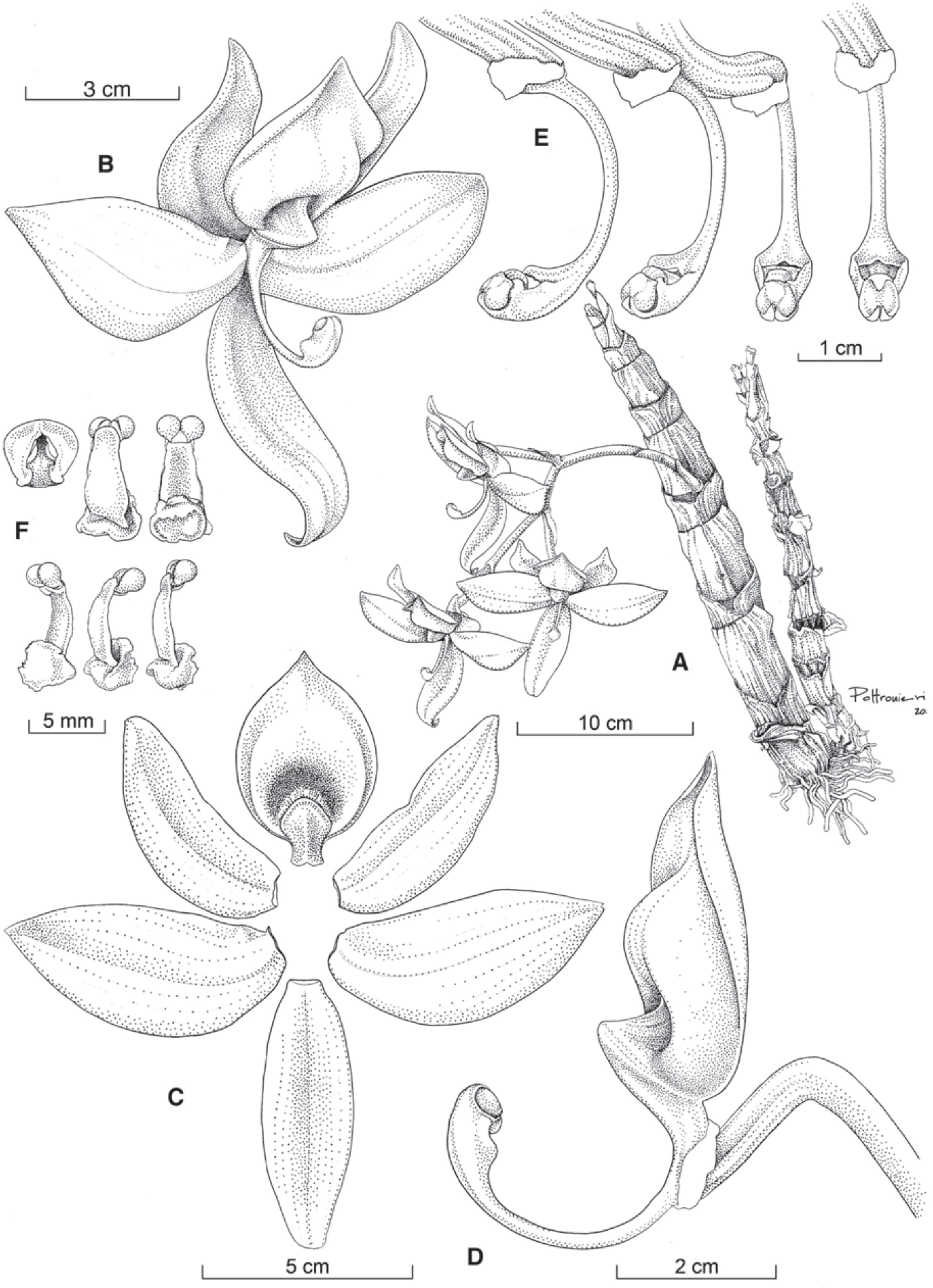

FIGURE 22. *Cycnoches warszewiczii* Rchb.f. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, lateral, three-quarter, and ventral views. **F,** Anther cap and pollinarium, several views. Drawn by S. Poltronieri from *Pupulin 8895* (JBL).

FIGURE 23. *Cycnoches warszewiczii* flowering in situ at BHNP. Photograph by O. Cubero.

lanceolate, acute, scarious, brown, to 25 × 8 mm. Pedicellate *ovary* cylindric, round in section, to 6 cm long including the pedicel. *Flowers* quite variable in size, but usually large, nonresupinate, fleshy, unisexual, staminate and pistillate flowers produced on separate inflorescences, the male and female flowers similar except for the column (see below), the sepals and petals spreading, yellowish-green, the lip white with an emerald green callus, the column pale green, flushing yellow at apex. Dorsal sepal erect, lanceolate to elliptic-lanceolate, acute, concave, the apex gently recurved, 4–7 × 1–2 cm. *Lateral sepals* lanceolate, subfalcate, acute, recurved at apex, 4–6 × 1.3–2.5 cm. *Petals* elliptic-lanceolate, asymmetric-subfalcate, acute, 4.5–7.0 × 1.9–3.7 cm. *Lip* shortly clawed, ovate-elliptic, very fleshy, obtuse, abruptly acute, strongly convex-ventricose, the margins and the apex gently reflexed, 3.5–4.0 × 2.5–3.5 cm; basal callus triangular, acute, fleshy, elevated, projecting, surrounded by a semicircular, lunate, dark depression. *Column* of *staminate flowers* very slender, arcuate, 2.5–3.5 cm long, abruptly dilated at the apex into a subtrigonous, shortly winged, thick clinandrium; in *pistillate flowers*, the column terete, stout, arcuate, 2.0–2.5 cm long, ca. 5 mm thick, provided with auricular, fleshy wings around the stigmatic cavity. *Anther cap* deeply cucullate, flattened, obovate, rounded, 2-celled. *Pollinia* 2, waxy, pyriform, on a ligulate, thick, apically bilobed, green stipe and a massive, transversely elliptic to transversely ovate, brown viscidium.

Distribution: along the Pacific coast from northern Costa Rica to western Panama.

Distribution in the Park: rare, seen only along the calcareous rocky areas mixed with cacti and other scattered trees in Cerro Barra Honda.

Eponymy: named after Józef Warszewicz Ritter von Rawicz, a Polish botanist who collected the type specimen.

Habitat and ecology: rather common in humid coastal lowlands often below 1000 m along the Pacific coast. It grows mostly in exposed full sunlight, usually on dead, rotten branches or main trunks.

Phenology: flowering occurs from January to July.

Discussion: the long, almost cylindrical pseudobulbs with distichous, plicate leaves easily distinguish this species; during the dry season and at flowering, the leaves are deciduous, but the remaining sheaths are unarmed. The inflorescences produced from a node on the central or the upper parts of the pseudobulb are also unmistakable in BHNP. Staminate (more common) and pistillate flowers are similar but essentially distinguished by the morphology of the column, which is longer and filiform in male flowers, and shorter and thicker in female flowers. The other species with similar (but larger) pseudobulbs at BHNP with which *C. warszewiczii* could be confused when not in flower is *Cyrtopodium macrobulbon*, but the latter is a mostly terrestrial or lithophytic plant, and its pseudobulbs are distinctly spiny after shredding the leaves.

Additional specimen examined: BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, terrestres en sitio rocoso con hojarasca, 3 enero 2016, *O. Cubero s.n.* (digital voucher, JBL).

7. *Cyrtopodium* R.Br., Hort. Kew. (ed. 2) 5: 216. 1813.
TYPE: *Cyrtopodium andersonii* (Lamb. ex Andrews) R. Br.

Plants large, terrestrial or lithophytic, rarely epiphytic, caespitose. *Stems* ovoid, fusiform, or ellipsoid pseudobulbs bearing several leaves. *Leaves* distichous, linear-lanceolate or elliptic-linear, plicate, arranged along the stem, deciduous during the dry season leaving spines at the apex of the imbricating sheaths when the leaves are dropped. *Inflorescence* a large spreading panicle of numerous flowers and bracts developed at the base of the pseudobulb. *Flowers* medium-sized, often showy, with free, spreading parts. *Sepals* and *petals* subequal, the lateral ones slightly oblique and adnate to the column foot, the petals shorter and wider than the sepals, with the margins undulate. *Lip* attached to the column foot, 3-lobed, the lateral lobes incurved over the column, with verrucose margins, the callus warty or tuberculate toward the middle or near the margin. *Column* stout, elongate, semiterete, footed. *Anther* terminal, operculate, incumbent. *Pollinia* 2 or 4, waxy.

A Neotropical genus of about 44 species ranging from Florida (USA), Mexico, and Central America through northern Argentina and the Antilles. One species in Costa Rica and BHNP.

Cyrtopodium macrobulbon (La Llave & Lex.) G.A. Romero-González & Carnevali, Harvard Pap. Bot. 4(1): 331, f. 2–4. 1999. Fig. 10I, 24.

Basionym: *Epidendrum macrobulbon* La Llave & Lex., Nov. Veg. Descr. Orchid. Opusc.: 42. 1825. TYPE: MEXICO. *Habitat supra arbores, prope Turicato in regione calida provinciae Michuacanensis*, *J. J. M. de Lexarza s.n.* (Holotype: not located, presumably lost; Neotype designated by Romero-González and Carnevali Fernández-Concha, 1999: Mexico. Michoacán: Coalcomán, Aguililla, 800 m, *G. B. Hinton 15928*, AMES).

Plants terrestrial or lithophytic, robust, caespitose, up to 1.2 m tall. *Roots* thick, 4–5 mm in diam., white with yellowish-green tips. *Pseudobulbs* fusiform, elongated, rostrate, bearing several leaves during wet season, the old pseudobulbs wrinkled, enclosed by the spiniferous leaf sheaths or naked, 13–55 × 2.2–5.5 cm. *Leaf sheaths* distichously imbricated, papyraceous with age, tightly adpressed to the pseudobulbs, spiniferous, grayish-white when the leaves fall, spines stout, sharp to 3 cm long. *Leaves* several (up to 25), distichously arranged along the pseudobulbs, plicate, with 3 main veins, narrowly elliptic-lanceolate to linear-lanceolate, recurved, acute to acuminate, thin, chartaceous, the blades articulated with the leaf sheaths and deciduous during the dry season and when in bloom, 37–64 × 3.9–8.2 cm. *Inflorescence* lateral, stout, a panicule of several flowers developed from the base of the pseudobulbs, to 90 cm tall; peduncle to 50 cm long erect, basally fusiform, bearing foliaceous, green, ovate-oblong bracts, 4.5 × 4.2 cm; the bracts subtending the branches and flowers ovate-oblong or oblong-lanceolate, undulate, purple-spotted, resembling the sepals in coloration and markings, 5.4–2.1 × 1.3–4.0 cm. *Ovary* pedicellate, arcuate, to 2.3 cm long, including the pedicel. *Flowers* resupinate, showy, yellow, irregularly stained with red-brown, the lip bright yellow with orange margins and spots at the center, the column basally yellow, apically green. *Dorsal sepal* ovate to elliptic, obtuse, truncate, slightly undulate, convex, 1.7 × 1.1 cm. *Lateral sepals* subsimilar to the dorsal sepal, ovate to elliptic, obtuse, slightly reflexed, 1.5 × 1.1 cm. *Petals* obovate to spathulate, obtuse, 1.5 × 1.0 cm. *Lip* basally adnate to the column, deeply 3-lobed, the lateral lobes wider than the midlobe, rounded, reniform, folded, erect and flanking the column in natural position, 0.9 × 2.4 across the lateral lobes, 1.2 from the base to the apex, the midlobe reniform, 0.5 × 1.2 cm, basally verrucose, the margin erose tuberculate, crispate, the disc with a median fleshy oblong, tuberculate callus, running up to the base of the midlobe. *Column* clavellate, arcuate, footed, apically subauriculate, the anther apical, the stigma ventral, 1.2 × 0.4 cm. *Pollinarium* with 2 pollinia, obovate, slightly sulcate, in a triangular stipe. *Anther cap* cucullate, 2-celled.

Distribution: from Mexico (Sinaloa to Yucatán) to Panama and possibly Venezuela.

Distribution in the Park: it is commonly observed in calcareous rocky areas mixed with cacti and other scattered trees in Cerro Barra Honda, Los Mesones, Bosque de Piedra, and Las Delicias.

Etymology: from the Greek *makros,* "long," and *bulbos*, "bulb or fleshy tuber," in reference to the long pseudobulbs.

Habitat and ecology: terrestrial or lithophytic in rocky or sandy soils in tropical dry to seasonal forest up to 800 m. Plants are deciduous and spiniferous when in bloom and during the dry season. They are pollinated by *Centris* bees (Romero-González and Carnevali Fernández-Concha, 1999).

Phenology: plants become deciduous and develop inflorescences in late November and flower from March to May.

Discussion: it is easily recognized by the terrestrial or lithophytic stout plants, the long pseudobulbs with several plicate leaves arranged along the stem and deciduous during the dry season. The inflorescences are basal, paniculate, several to many yellow-brown spotted, hermaphrodite flowers. In habit, they could be confused with *Cyrtopodium maculatum* because of the fusiform pseudobulbs bearing several plicate leaves; however, the latter is mostly epiphytic and somewhat smaller, having racemose inflorescences of few unisexual flowers with saccate lip. Romero-González and Carnevali Fernández-Concha (1999) treated *C. macrobulbon* as a distinct entity ranging from Mexico to Panama, stating that *C. paniculatum* (Ruiz & Pav.) Garay

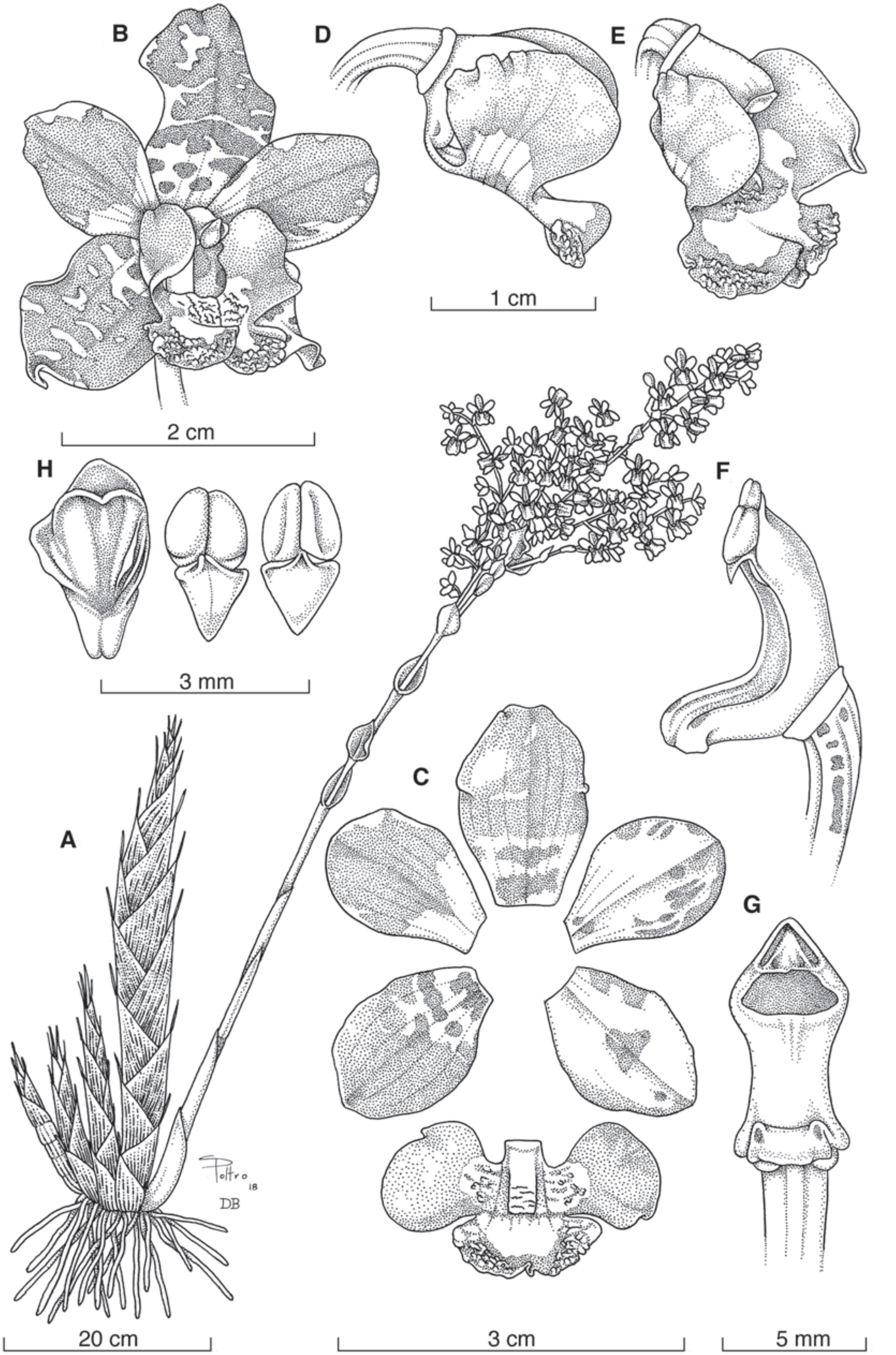

FIGURE 24. *Cyrtopodium macrobulbon* (La Llave & Lex.) G.A. Romero-González & Carnevali. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column and lip, three-quarter view. **F,** Column, lateral view. **G,** Column, ventral view. **H,** Anther cap and pollinarium, two views. Drawn by D. Bogarín from *Bogarín 2596* (JBL).

from Venezuela to Peru, and *C. punctatum* (L.) Lindl. from Florida, the Antilles, and the northwestern Caribbean coast of South America, do not occur in Costa Rica.

Additional specimens examined: BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, terrestres en sitio rocoso con hojarasca, 21 febrero 2006, *D. Bogarín 2596* (JBL-spirit).

8. ***Dichaea*** Lindl., Gen. Sp. Orchid. Pl. 208. 1833.
TYPE: *Dichaea echinocarpa* (Sw.) Lindl., *nom. illeg.* = *Dichaea pendula* (Aubl.) Cogn.

Plants epiphytic monopodial caespitose, or scandent, pendent or rarely erect, with foliaceous stem, lacking pseudobulbs. *Roots* terete, filiform to fleshy. *Stems* 1 to several, elongate, erect to arching or laxly pendent, terete or dorsiventrally flattened, often freely branching, entirely enclosed by persistent imbricating leaf sheaths. *Leaves* conduplicate, articulate or not, membranaceous or coriaceous. *Inflorescence* lateral from the axils of the leaves, 1-flowered on a short peduncle. *Flowers* small or medium-sized, resupinate, ringent to spreading, the sepals and petals ivory-white to greenish white or orange-grey, the sepals mostly flecked with purple-violet toward the base. *Sepals* and *petals* subequal, free or the laterals sepals slightly connate, spreading; lip clawed, 3-lobed or rarely entire. *Column* short, erect, with a short foot, provided with an infrastigmatic ligule. *Pollinia* 4, in 2 subequal pairs, on a laminar, apically expanding stipe, continuous with the elliptic, sulcate, hyaline viscidium.

A Neotropical genus of about 60 species ranging from Mexico to Brazil and the Antilles. About 30 species in Costa Rica and 1 at BHNP.

Dichaea panamensis **Lindl.**, Gen. Sp. Orchid. Pl. 209. 1833.
TYPE: Hab. in Panama, et Columbia occidentali, [Taboga Island], 1831, *H. Cuming 1292* (Holotype: K). Fig. 11A, 25.
Homotypic synonyms: *Dichaeopsis panamensis* (Lindl.) Schltr., Beih. Bot. Centralbl., Abt. 2 36(2): 519. 1918.
Epithecia panamensis (Lindl.) Schltr., Orchis 9: 25. 1915.
Heterotypic synonyms: *Dichaea brachypoda* Rchb. f., Beitr. Orch. Centr.-Amer. 78: 1866. TYPE: COSTA RICA. San Miguel in Costa Rica, 14 May 1857, *H. A. Wendland s.n.* (Holotype: W).
Dichaeopsis brachypoda (Rchb. f.) Schltr., Beih. Bot. Centralbl. 36(2): 519. 1918.
Epithecia brachypoda (Rchb. f.) Schltr., Orchis 9: 25. 1915.

Plants epiphytic, caespitose, to 20 cm long. *Roots* basal, glabrous, flexuous, very thick, wider than the stem, about 2 mm in diam. *Stems* flattened, suberect to spreading or pendent, simple, rarely producing new plantlets with roots at the nodes, 6–21 cm long, 0.15 cm wide across conduplicate sheaths. *Leaves* widely spaced along stem, oblique to spreading, medium to dark green, frequently glaucous on one or both surfaces, subcoriaceous, narrowly linear-elliptic to lanceolate, acute, apiculate, 12–20 × 3–4 mm, usually varying in length along the stem, the blade articulated to the sheath encircling the stem and ultimately deciduous; sheaths tightly clasping, to 4 × 3 mm. *Inflorescence* solitary, 1-flowered, emerging below the foliage, the peduncle straight, to 15 mm long, provided at the base with 2 tubular, acute bracts, about 1.5 mm long. *Floral bract* double, the outer bract suborbicular-funnelform, obtuse, shorter than pedicel, 2 × 2 mm, the inner bract narrowly lanceolate, 2.5 mm long. *Ovary* pedicellate cylindric-subclavate, glabrous, ca. 2.5 mm long, including the pedicel. *Flower* ringent, rarely subspreading, the sepals and petals greenish cream spotted and blotched with purple, sometimes almost solidly purple, the lip cream white, sparsely spotted with purple, mostly toward the apex, rarely solid purple, the column greenish white, flecked violet along the margins of the stigma, anther cap purple-red; no fragrance detected. *Dorsal sepal* elliptic-lanceolate, acute, dorsally carinate, 6–9 × 2.5–3.2 mm. *Lateral sepals* lanceolate-elliptic, asymmetrical, slightly falcate, acute, apiculate, usually upcurved in natural position, 7.5–12.0 × 3.0–4.1 mm. *Petals* obliquely ovate, shortly acute, much wider than sepals, 6.0–8.5 × 4–5 mm. *Lip* 3-lobed, from a fleshy claw, 7–10 × 6–9 mm when spread, the hypochile obcuneate, sometimes provided at the base with a thickened area, 4–5 mm wide apically, the epichile broadly triangular-sagittate, obtuse to subrounded, minutely apiculate, adaxially carinate toward the apex, the lateral lobes narrowly triangular, acute, spreading-retrorse, decurring in the lamina, 1.5 × 1.0 mm. *Column* erect, 5–6 mm long, with a distinct foot about 2 mm long, the reclined clinandrium shallow; ligule small, widely triangular, projecting downward, subacute, glabrous, 0.6 × 1.5 mm. *Anther cap* transversely elliptic-suborbicular, flattened, 2-celled. *Pollinia* 4 in 2 superposed pairs of slightly different size, on a narrowly obtriangular-ligulate, subtruncate stipe with inrolled margins; viscidium elliptic. *Fruit* an elliptic, glabrous capsule.

Distribution: Mexico to Venezuela, Ecuador, and Brazil.

Distribution in the Park: it was observed at Cerros de Jesús. Likely found in the humid evergreen forest of Los Mesones and Las Cascadas at BHNP.

Habitat and ecology: from warm tropical to premontane wet forests on both drainages, at 50–1350 m elevation, but most commonly found between 400 and 900 m. It is a shade-loving epiphyte, occupying many different niches, with a preference for old, moist branches and trunks of the understory vegetation.

Etymology: named after Panama, where the type specimen was found initially.

Phenology: flowering occurs year-round, with a peak between April and June, corresponding to the beginning of the rainy season.

Discussion: *Dichaea panamensis* is vegetatively and florally unmistakable. The plants, rooting only at the base of the stems, have very thick roots wider than the stems. The leaves are distichous, articulate, narrowly linear-elliptic to lanceolate, usually glaucous beneath. The flowers are ringent and vary in color from pale greenish white to almost solid purple, with any combination of purple spotting, blotching, and flushing.

Figure 11. **A–I.** Orchid species found at Barra Honda National Park. **A,** *Dichaea panamensis* (*Bogarín s.n.*). **B,** *Dimerandra emarginata* (*Bogarín 9500*, JBL). **C,** *Encyclia macrochila* (*Bogarín 6148*, JBL). **D,** *Epidendrum congestoides* (*Bogarín s.n.*). **E,** *E. coronatum* (*Pupulin 1835*, JBL). **F,** *E. stamfordianum* (*Bogarín 1665*, JBL). **G,** *E. vulgoamparoanum* (*Bogarín 1686*, JBL). **H,** *Guarianthe skinneri* (*Bogarín 2607*, JBL). **I,** *Habenaria macroceratitis* (*Bogarín 1724*, JBL). Photographs by the authors.

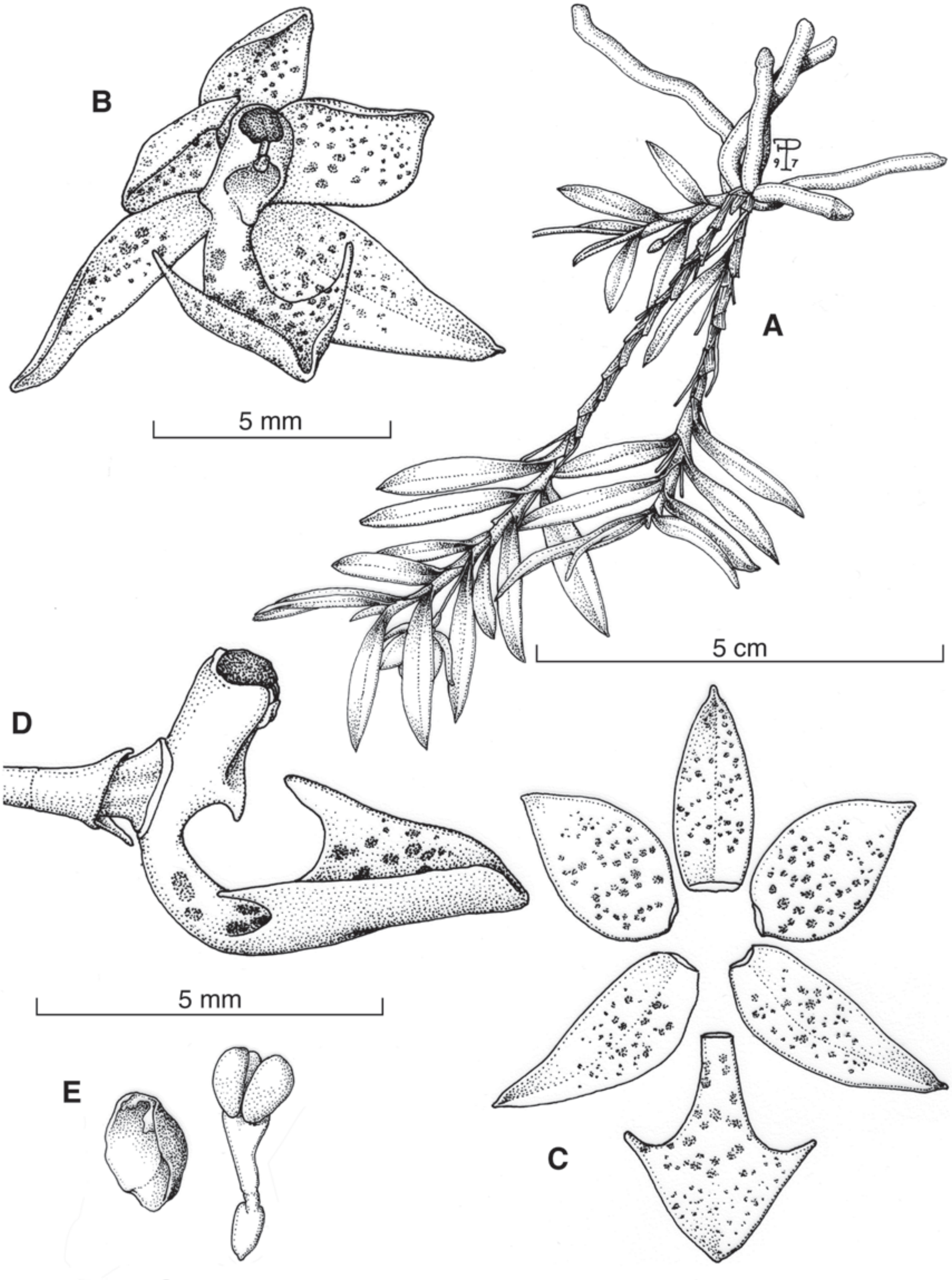

FIGURE 25. *Dichaea panamensis* Lindl. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 304* (JBL).

Additional specimens examined: Guanacaste: Nicoya, Mansión, Zona Protectora Cerros de Jesús, 10°05'41.7"N, 85°18'59.58"W, 370 m, premontane moist, transition to tropical moist forest, epiphytic in secondary mature vegetation along a seasonal stream with high trees, en bosque secundario maduro sobre una quebrada estacional con árboles altos, 23 February 2012, *F. Pupulin 8192 & D. Bogarín* (unvouchered).

9. ***Dimerandra*** Schltr., Repert. Spec. Nov. Regni Veg. Beih., 17: 43–44. 1922.
TYPE: *Dimerandra rimbachii* (Schltr.) Schltr.

Plants epiphytic, caespitose herbs. *Stems* thickened, narrowly fusiform, foliaceous, covered with thin, imbricating sheaths articulated with the leaves, erect or pendent, the old stems striate and often without leaves. *Leaves* conduplicate, distichous, linear to narrowly elliptic, subcoriaceous, often scattered along the upper part of the stems. *Inflorescence* terminal, a very short, successively and few-flowered raceme. *Flowers* of medium size, showy, resupinated, rose-purple with a white center. *Sepals* linear-lanceolate, acute, spreading. *Petals* wider than sepals, rhombic or elliptic. *Lip* simple with a short claw, obovate or rhombic-obovate, the disc under the column provided with a callus formed by several obscure carinae or imbricating lamellae in rows. *Column* short, apically with 2 prominent rows of the clinandrium. *Anther* small, incumbent. Pollinia 4, waxy, laterally flattened, with caudicles.

A genus probably monotypic, ranging from Mexico to Brazil and Trinidad. One species in Costa Rica and BHNP.

Dimerandra emarginata (G. Mey.) Hoehne, Bol. Agric. (Sao Paulo). 34: 618. 1934. Fig. 11B, 26.

Basionym: *Oncidium emarginatum* G. Mey., Prim. Fl. Esseq. 259. 1818. TYPE: [GUYANA]. In arboribus plantationis Hof. van Holland, floret Sept, *H. van Holland s.n.* (Holotype: GOET).

Plants epiphytic, caespitose, with fleshy, foliaceous stem, up to about 60 cm tall. *Roots* fleshy, glabrous. *Pseudobulbs* cylindrical to fusiform from a narrow stalk, slightly fractiflex, of several nodes, bearing leaves in the upper portion, sometimes purplish and wrinkled. *Leaves* arranged distichously on the stems, narrowly linear-elliptic, subcoriaceous, unequally bilobed at apex, 4.0–9.0 × 0.7–1.0 cm, produced at the nodes of the pseudobulb, articulate with the leaf sheaths. *Inflorescence*s terminal, a short raceme bearing 1 to few flowers produced successively, about 1 cm long. *Ovary* pedicellate, cylindrical, up to 4 cm long. *Flowers* very flat, with spreading parts, often self-pollinating, rose-purple with a white blotch at the base of the lip. *Dorsal sepal* lanceolate to elliptic-lanceolate, acute, conduplicate, 15 × 5 mm. *Lateral sepals* subsimilar, elliptic-lanceolate, acute to acuminate, conduplicate, somewhat oblique, 15 × 5 mm. *Petals* broad-obovate to subrhombic, acute, 17 × 10 mm. *Lip* flabellate, with a fleshy claw partially adnate to the column, the lamina broadly obovate to suborbicular, truncate, slightly apiculate, the disc with a callus made up by obscure lines or rows of imbricating lamellae, the entire lip 16 × 15 mm. *Column* short, slightly arcuate, without a foot, provided at the apex with 2 large, subquadrate, deflexed wings, about 5 mm long. *Pollinia* 4, laterally compressed, in 2 pairs on short, bilobed caudicles. *Anther cap* hemiglobose, 4-celled.

Distribution: from Mexico to South America and the West Indies.

Distribution in the Park: it was observed at Cerro Barra Honda near Sendero Ceiba and around Terciopelo cave.

Habitat and ecology: commonly found in tropical moist lowland forest of both the Caribbean and Pacific at elevations below 1000 m in disturbed forest or open areas. The plants often form big clumps of many stems, usually pendent in mature specimens. Sometimes the flowers are self-pollinating soon after anthesis, and the plants bear several capsules.

Etymology: from the Latin *emarginatus*, "emarginate," in allusion to the emarginate apex of the lip.

Phenology: flowering occurs from September through April.

Discussion: it is easily distinguished by the narrowly fusiform, many-leaved pseudobulbs, the linear-elliptic leaves, and the small, successively pink-purple flowers produced at the apex. The sepals and petals are subsimilar, and the lip is broadly obovate to suborbicular with the column basally adnate.

Additional specimens examined: Guanacaste: Nicoya, San Antonio, Parque Nacional Barra Honda, Cerros Barra Honda, bosque cercano al parqueo en el inicio del sendero Ceiba, 10°10'23.24"N, 85°21'38.22"W, 367 m, epífita en bosque húmedo premontano transición a basal, 21 febrero 2012, *D. Bogarín 9500 y F. Pupulin* (unvouchered).

10. ***Encyclia*** Hook., Bot. Mag. 55: pl. 2831. 1828.
TYPE: *Encyclia viridiflora* Hook.

Plants epiphytic or lithophytic, rarely terrestrial, caespitose. *Pseudobulbs* spherical, subovoid, ovoid, conic-ovoid, fusiform, pyriform or subpyiriform, heteroblastic, subtended by scarious bracts. *Leaves* 2–3, on short tubular petioles at the apex of pseudobulbs, ligulate, oblong, linear or elliptic, acute or subacute, conduplicate. *Inflorescence* apical, erect or arching, racemose or paniculate. *Flowers* showy, spread, sometimes scented. *Sepals* and *petals* elliptic, ovate, obovate or spathulate, simple, free, membranaceous to fleshy. *Lip* 3-lobed, narrowing to the middle conforming an isthmus, free or basally adnate to the column, the lateral lobes arching and clasping the column, midlobe sessile, or separated by a clear isthmus, with a central keeled callous. *Column* straight, semiterete, truncate, lateral wings or teeth present or absent. *Anther* incumbent anther, the stigma dorsal. *Pollinia* 4, of equal size, ovate or obovate, with caudicles. *Anther cap* cucullate, 4-celled. *Capsule* pyriform to fusiform, smooth or warty.

A Neotropical genus of about 120 species ranging from Mexico (Sonora) and Florida (USA) through Central America and the West Indies to Peru, Argentina, and Brazil (Rio Grande do Sul). Nine species are reported from Costa Rica. A single species occurs in BHNP.

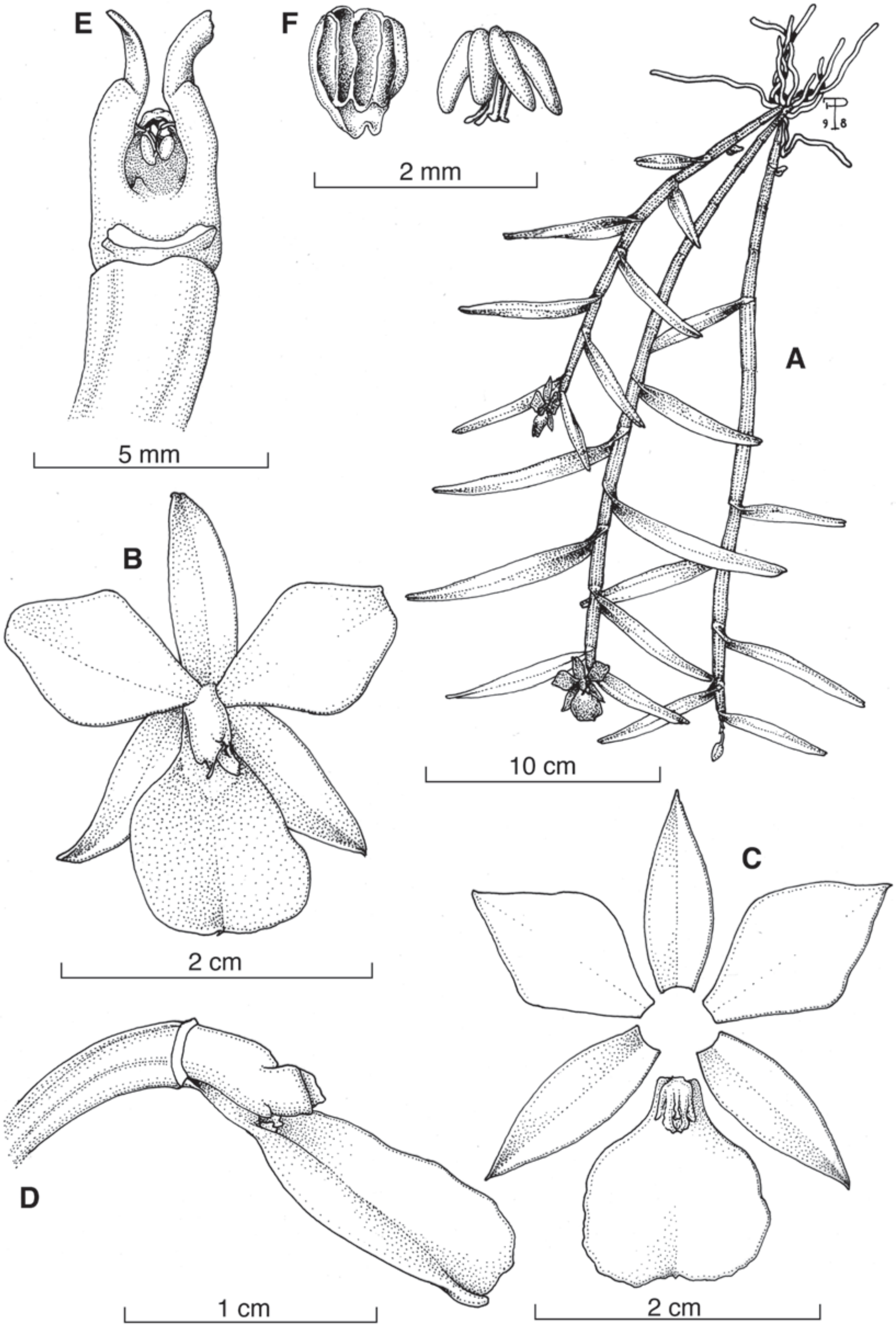

Figure 26. *Dimerandra emarginata* (G. Mey.) Hoehne. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 325* (JBL).

Encyclia macrochila (Hook.) Neumann, Rev. Hort., II, 4: 137. 1846. Fig. 11C, 27.

Basionym: *Epidendrum macrochilum* Hook., Bot. Mag. 63: t. 3534 (1836). TYPE: [MEXICO.] "A charming epiphyte, introduced from Mexico, by Charles Horsfall, Esq., in whose fine collection at Everton it flowered in June, 1836, when a drawing and specimen of the handsome flowers were kindly communicated by Mrs. Mrs. Horsfall," *C. Horsfall s.n.* (Holotype: K).

Heterotypic synonyms: *Cymbidium cordigerum* and homotypic synonyms from the authors, *non Cymbidium cordigerum* Kunth in F.W.H.A. von Humboldt, A.J.A. Bonpland & C.S. Kunth, Nov. Gen. Sp. 1: 341 1816.

Epidendrum atropurpureum and homotypic synonyms from the autors, *non Epidendrum atropurpureum* Willd., Sp. Pl. 4: 115. 1806. *Epidendrum macrochilum* var. *albopurpurea* C. Morren, Ann. Soc. Roy. Agric. Gand 2: 365, t. 86. 1846. TYPE*:* not designated.

Encyclia atropurpurea var. *leucantha* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 45. 1922. *Encyclia cordigera* f. *leucantha* (Schltr.) Withner, Cattleyas & Relatives 5: 104. 1998. TYPE: PANAMA (Lectotype: designated by Christenson, 1991: PANAMA. Sehr selten auf Hügeln bei Panama City, *C. W. Powell 149*: AMES; Isolectotype: MO).

Plants epiphytic, caespitose, to 80 cm tall. *Roots* produced from the base of the pseudobulb and the rhizome, flexuous, 2–3 mm in diam., whitish with green tips. *Pseudobulbs* ovoid to pyriform, 8–11× 3–6 cm, subtended by ovate, acute papery sheaths, shredded with age, 2(rarely 3)-foliate at the apex. *Leaves* on short tubular petioles at the apex of pseudobulbs, oblong or elliptic-oblong, ensate, coriaceous, conduplicate, dorsally keeled, acute to subacute, the apex irregularly bilobed, curving with age, 10–50 × 2–4 cm. *Inflorescence* apical, racemose, distichous, peduncle 13–35 cm, bracts 6–8 mm, acute, adpressed, infundibuliform, raceme 6–25 cm, rarely with 1 basal branch. *Floral bracts* triangular, acute, adpressed, scarious, 1–3 × 3–4 mm. *Ovary* and pedicel 2.5–3.3 cm, smooth, with minute lenticels. *Flowers* showy, resupinate, scented, the sepals and petals greenish to brownish, lip white, striped with magenta at base of lateral lobes and along the callus, strongly suffused with pink or magenta at the middle toward the apex (rarely pure white). *Dorsal sepal* spathulate, elliptic-oblanceolate, acute to subacute, dorsally carinate, apically curved, 2.6–3.6 × 0.5–1.1 cm. *Lateral sepals* spathulate, cuneate-oblanceolate, acute, slightly apiculate, strongly curved toward the apex, dorsally carinate, 2.4–3.5 × 0.8–1.2 cm. *Petals* unguiculate, spathulate-ovate or cuneate-ovate, acute or apiculate, dorsally carinate, 2.3–3.5 × 1.0–1.8 cm. *Lip* basally adnate to the column for 3 mm, deeply 3-lobed, shortly unguiculate, 2.9–3.1 × 2.8–3.1 cm across lateral lobes, lateral lobes oblong-lanceolate, falcate, obtuse, suberect and flanking the column in natural position, slightly stripped with magenta, 0.7–1.5 × 0.5–0.8 cm, isthmus about 1 mm long, subquadrate; midlobe 2.0–3.6 × 1.3–3.0 cm, suborbicular, obovate or oblong, retuse or obtuse, callus with 2 longitudinal fleshy keels, which made up a fovea on the isthmus, 0.8–1.1 × 0.3–0.6 cm, sulcate, with a second callous with 3 magenta veins running and reducing slightly toward the apex. *Column* subterete, truncate, cuneate-obovate, subpandurate, basally sulcate, 1.0–1.8 cm, midtooth triangular, subequal to lateral teeth, without wings; anther apical; stigma dorsal. *Anther cap* 4-celled, cucullate, ovate to orbicular. *Pollinia* 4, in 2 pairs with caudicles, without viscidium. *Capsule* 4 × 2.3 cm, fusiform to obovoid-ellipsoid.

Distribution: from Mexico to Colombia and Venezuela.

Distribution in the Park: fairly common around the main trails at Cerro Barra Honda and Las Delicias.

Etymology: from the Greek *macro,* "big," *and cheilon*, "lip," in reference to the large size of the labellum.

Habitat and ecology: epiphytic in tropical moist forest, premontane moist forest, basal belt transition and tropical dry forest, moist province transition. Plants are restricted to the northern and central Pacific lowlands of Puntarenas, Guanacaste, and San José (Puriscal and Turrubares) from 0 to 700 m of elevation. They are common in sunny areas and disturbed lands such as pastures, river edges, tree fences, and primary and secondary forest. At BHNP, it is observed growing on several hosts such as *Bursera simarouba* (Burseraceae), *Cedrela* spp. (Meliaceae), and *Plumeria rubra* (Apocynaceae), both in secondary forest and disturbed areas around the Park boundaries.

Encyclia macrochila is reported to be pollinated by medium-sized, black female carpenter bees (*Xylocopa* sp., Hymenoptera: Anthophoridae) (Janzen et al., 1980), and another species of *Xylocopa*; these authors suggested that the shape and color of the flower of *E. macrochila* are similar to the common legume tree, *Gliricidia sepium* (Fabaceae), which is frequently visited by the same bees in search of nectar.

Phenology: plants flower from November to April.

Discussion: it is easily distinguished by the racemose inflorescences (never branched) with showy, scented, large flowers. The pseudobulbs are ovoid to pyriform, and very conspicuous in healthy and well-developed specimens. The brown spathulate sepals are strongly curved at the apex, the suborbicular, obovate, or oblong midlobe of the lip is white with three magenta stripes at the base. The lip is larger (2.4–3.5 × 0.8–1.2 cm) than those of other species of the genus and is the most conspicuous structure of the flower. The column is not winged or toothed apically, with an evident yellow anther cap.

Additional specimens examined: BHNP, Bosque de Cactus, 10°10'32.1"N, 85°21'13.3"W, 639 m, bosque húmedo premontano transición a basal, epífitas en lomas rocosas, 28 enero 2009, *D. Bogarín 6148 y F. Pupulin* (JBL-Spirit).

11. ***Epidendrum*** L., Sp. Pl. ed. 2: 1347. 1763., *nom. cons.* TYPE: *Epidendrum nocturnum* Jacq. *type. cons.*

Plants epiphytic or rarely terrestrial herbs to subshrubs, small to large, variable in size and habit, caespitose, creeping, erect to pendent, occasionally with pseudobulbs. *Leaves* distichously arranged along the stem, occasionally 1 apical leaf or several apical leaves distributed throughout the stem or aggregate at the apex of the stem or pseudobulb, flattened, conduplicate or terete, subcoriaceous to fleshy, not

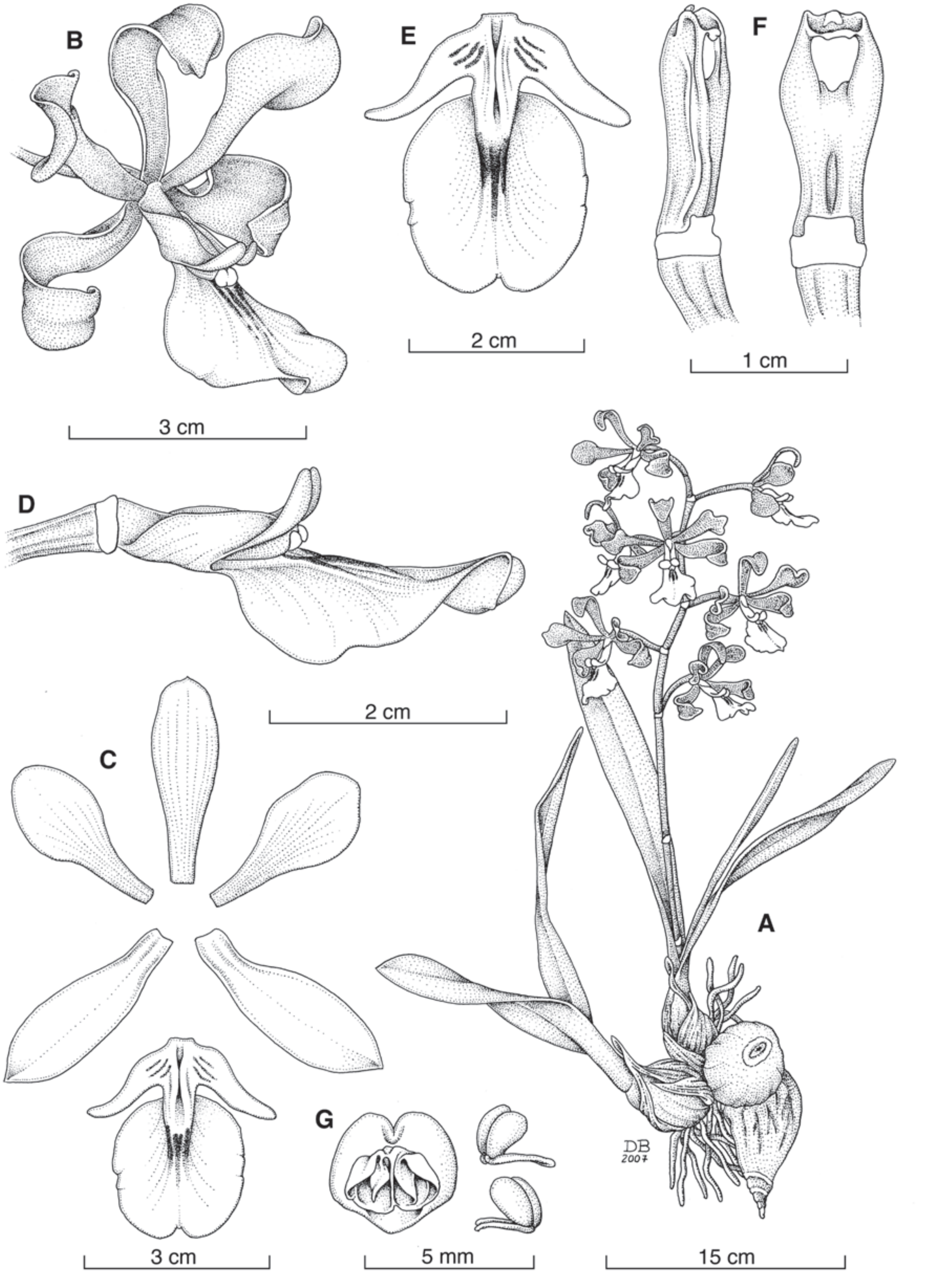

FIGURE 27. *Encyclia macrochila* (Hook.) Neumann. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Lip, flattened. **E,** Column and lip, side view. **F,** Column, side and ventral view. **G,** Pollinarium and anther cap. Drawn by D. Bogarín from *Bogarín 13* (JBL).

petiolate. *Inflorescence* apical, rarely lateral, a 1- to many-flowered raceme, spike, panicle, umbel or subumbellate. *Flowers* resupinate or not, small to large and showy. *Sepals* and *petals* subsimilar, free, usually spreading. *Lip* simple or lobed, mostly united to the ventral portion of the column, usually with fleshy calli at the base, simple or 3-lobed, callose. *Column* mostly fused with the lip, but sometimes totally free or half fused with the lip just to the apex, often provided with a hooded clinandrium. Anther cap cucullate. *Pollinia* 2, 4, or rarely 8, waxy.

Epidendrum is one of the largest genera of Neotropical orchids with more than 1500 species. The genus is widely distributed throughout the Neotropics, from North Carolina to northern Argentina, including the Antilles. About 200 species are reported from Costa Rica. Four species occur in BHNP.

KEY TO SPECIES OF *EPIDENDRUM*

1a. Plants with pseudobulbs . . . . *E. stamfordianum*
1b. Plants without pseudobulbs 2
2a. Plants with abbreviated stems < 5 cm long . . . . *E. congestioides*
2b. Plants with elongated stems >10 cm long 3
3a. Inflorescence subumbellate, subsessile, 3–5 green flowers . . . . *E. vulgoamparoanum*
3b. Inflorescence racemose, pedunculate, > 6 white flowers . . . . *E. coronatum*

11a. ***Epidendrum congestoides*** Ames & C.Schweinf., Schedul. Orch. 10: 61–63. 1930. Fig. 11D, 28.
TYPE: COSTA RICA. Guanacaste: vicinity of Tilarán, 10–31 Jan 1926, alt. 500–650 m, *P. C. Standley & J. Valerio 44933* (Holotype: AMES).
Homotypic synonyms: *Nanodes congestioides* (Ames & C. Schweinf.) Brieger, Orchideen 8(29–32): 512. 1976.

Plants epiphytic, cespitose, without pseudobulbs, with abbreviated, foliaceous stems, up to 5 cm tall. *Roots* filiform, flexuous, glabrous. *Stems* flattened, to 5 cm long, 0.8 cm in diam., entirely concealed by closely appressed leaf sheaths, 5- to 11-leaved. *Leaves* distichous, elliptic-ovate, imbricate basally, fleshy, conduplicate, retuse, carinate, dorsally apiculate, 1.0–2.3 × 0.6–0.9 cm, glaucous-green or suffused with purple when exposed to sunlight, not articulated with the sheaths, the margins somewhat revolute, dentate-fimbriate or erose. *Inflorescence* terminal from the upper leaf, sessile, 1- to 2-flowered, flowering only once. *Floral bracts* shorter than the ovary, obovate, rounded, imbricating, denticulate, unequal. *Flowers* small, fleshy, pale green with purplish suffusion, the lip emerald green. *Ovary* triquetrous, keeled. *Dorsal sepal* ovate-lanceolate, acuminate, dorsally carinate near the apex, 10 × 4 mm. *Lateral sepals* subsimilar, elliptic-lanceolate, acute, the margins somewhat denticulate, dorsally carinate, the lateral sepals falcate, concave, with a serrulate keel, 10–12 × 4 mm. *Petals* oblique, narrowly lanceolate, acute or subacute, the apical margins denticulate, nearly as long as the sepals, 9 × 2.8 mm. *Lip* with a ligulate claw adnate to the column, partially enfolding the column in natural position, the lamina ovate, somewhat cordate at the base, acute, mucronate, 9 × 5.5 mm. *Column* short, stout, up to 6.6 mm. *Clinandrium-hood* 3-toothed, the margins erose or fimbriate-dentate, 1 mm long. *Pollinia* 4, ovoid, laterally compressed, on a short caudicle. *Anther cap* hemiglobose, 4-celled.

Distribution: Guatemala to Costa Rica.

Distribution in the Park: only one population was located at Las Cascadas.

Etymology: from the Latin *congestum*, "congested," in allusion to the crowded leaves and flowers, and the Greek *oides*, "resembling," in allusion to the similar *Epidendrum congestum* Rolfe.

Habitat and ecology: it is found on tropical wet and moist lowland forest to up to 1000 m of elevation in both the Caribbean and Pacific. Plants were observed growing on tall trees of *Brosimum alicastrum* (Moraceae) in the humid areas of the gallery forest at BHNP. It is usually found in well-lit spots, and when exposed to full sunlight the plants can present a strong purple pigmentation on the leaves and flowers instead of glaucous-green leaves.

Phenology: from December to June.

Discussion: plants are characterized by the small, compact, cespitose, creeping habit with fleshy distichous leaves arranged along the stems. Mature specimens can form a mass of stems closely appressed to the phorophyte, and juveniles may grow loosely hanging from branches or main tree trunks. The inconspicuous green flowers suffused with purple are produced in pairs on a short inflorescence closely appressed to the leaves. From other species of *Epidendrum* of BHNP it is distinguished by the lack of pseudobulbs, abbreviated stems less than 5 cm long, and the 2-flowered inflorescences (vs. many-flowered, usually more than 3 flowers in *E. coronatum*, *E. satmfordianum*, and *E. vulgoamparoanum*).

Additional specimens examined: BHNP, Las Cascadas (the waterfalls), entering from Finca San Diego (Finca Los Trejos), 10°10'59.86"N, 85°20'17.4"W, 86 m, premontane moist, transition to tropical moist forest, epiphytic in gallery forest on *Brosimum alicastrum* "Ojoche" (Moraceae) close to a stream, 22 February 2012, *D. Bogarín s.n.* (unvouchered).

11b. ***Epidendrum coronatum*** Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 242. 1798. Fig. 11E, 29.
TYPE: PERU. Habitat in Pozuzo supra arbores et saxa. Floret Septembri et Octobri, *H. Ruiz & J. A Pavón s.n.* (Holotype: MA).
Heterotypic synonyms: *Epidendrum sulphuroleucum* Barb. Rodr., Gen. Spec. Orchid. 1: 56. 1877. TYPE: BRAZIL. Dans la serra da fazenda de Santa Rosa, au Carmo do Rio Claro, province de Minas Geraes. Fleurit en Septembre, *J. Barbosa Rodrígues s.n.* (Holotype: at Herb. Barb. Rodr., destroyed; Lectotype: designated by Jiménez and Hágsater, Icon. Orchid. (Mexico) 11: text with t. 1113, 2008a: AMES, copy, K).

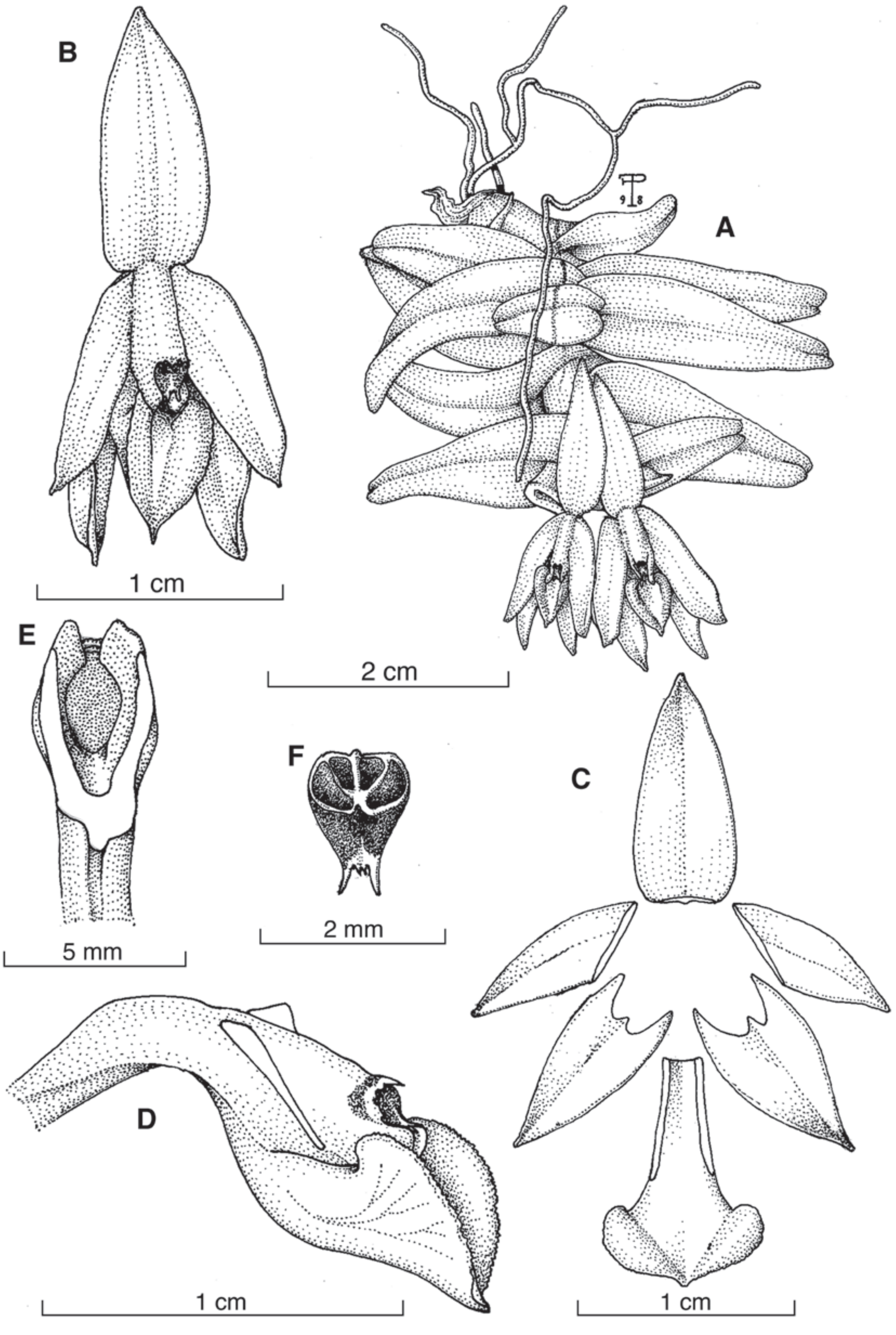

FIGURE 28. *Epidendrum congestoides* Ames & C.Schweinf. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 296* (JBL).

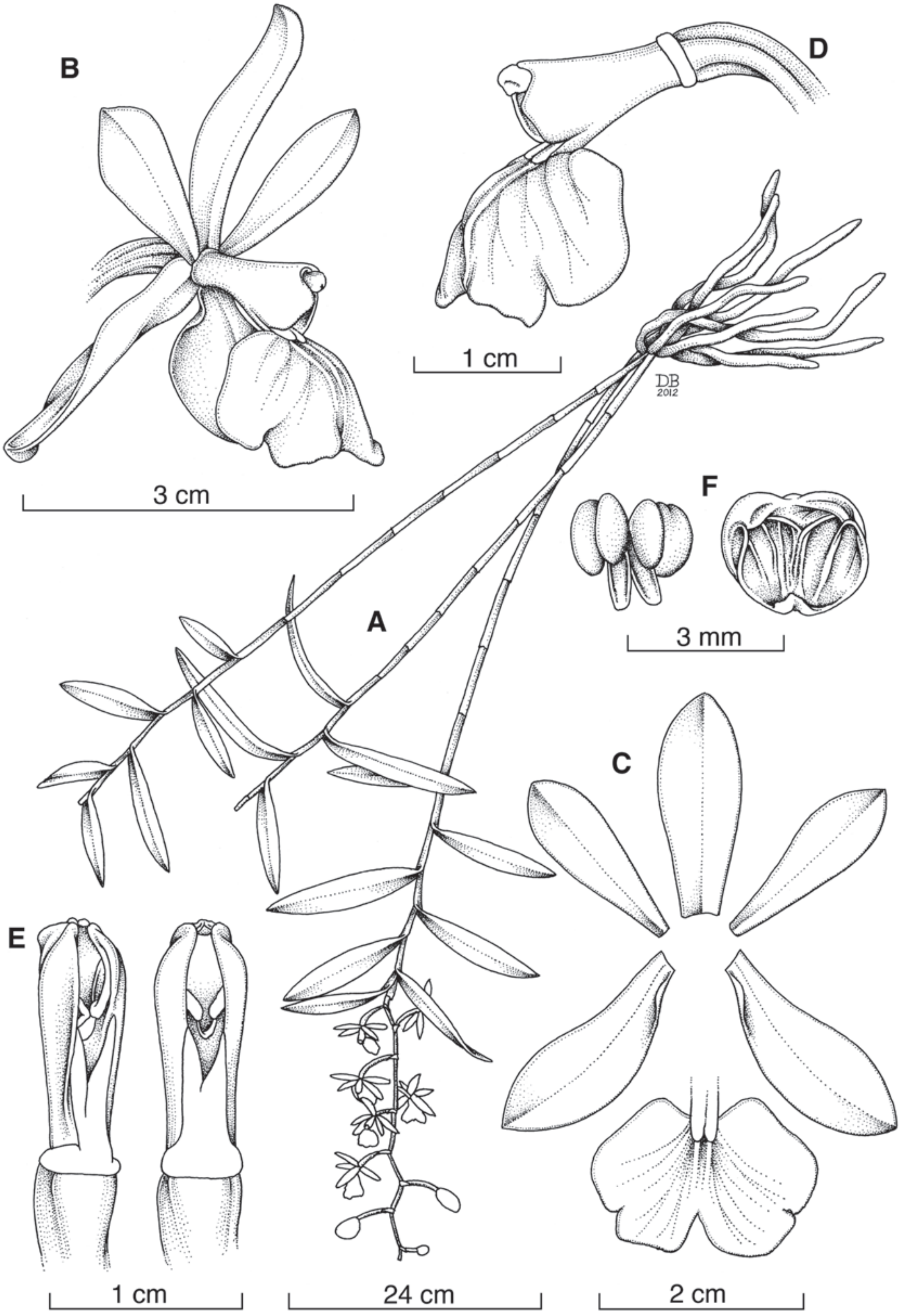

FIGURE 29. *Epidendrum coronatum* Ruiz & Pav. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, side and ventral view. **F,** Pollinarium and anther cap. Drawn by D. Bogarín from *Bogarín 1699* (JBL).

Epidendrum moyobambae Kraenzl., Repert. Spec. Nov. Regni Veg. 1: 185. 1905. TYPE: PERU. Dep. Loreto, bei Moyobamba. Wald (ziemlich trocken, Sträucher spärlich) in 800–900 m, *A. Weberbauer 4563* (Holotype: B, destroyed, photo: AMES, F, MO, NY, SEL).

Epidendrum subpatens Schltr., Repert. Spec. Nov. Regni Veg. Beih. 17: 40. 1922. TYPE: PANAMA. Im Gebiete des Gatun-Sees und auch in Veraguas bei Santiago, *C. W. Powell 86* (Holotype: B, destroyed; Lectotype designated by Christenson, 1991: AMES-23943; Isolectotypes: K, photo: AMES, MO-955940).

Epidendrum benignum Ames, Schedul. Orchid. 2: 26. 1923. TYPE: COSTA RICA. Forêts de Nicoya, May 1900, *A. Tonduz 13928* (Holotype: US).

Epidendrum amazonicum Schltr., Beih. Bot. Centralbl. 42(2): 78. 1925. TYPE: BRAZIL. Amazonas: Baixo, Rio Branco, 1913, *G. Kuhlmann 780* (Holotype: B).

Plants epiphytic, pendent to suberect, stout, caespitose, without pseudobulbs, with short rhizome and foliaceous stems up to 70 cm tall. *Roots* fleshy, flexuous, glabrous, to 5 mm in diam. *Stems* elongate, cane-like, straight to flexuous, ridged, cylindrical, to 9 mm in diam., to 62.5 cm long, entirely enfolded by the tubular, leaf-bearing sheaths, purple-spotted, which are 1–5 cm long, 5- to 16-leaved. *Leaves* oblong-elliptic to elliptic-lanceolate, acute or subacute, conduplicate, distichous, distributed toward the apical half of the stem, coriaceous or subcoriaceous, dark green glossy or light green, sometimes suffused with purple, retuse, 7.0–18.2 × 1.8–4.4 cm. *Inflorescence* apical, racemose, distichous, slightly fractiflex, hanging or arching-nutant, elongate, lax, peduncle short with 3 oblong-triangular, acute bracts, with up to 25 flowers, to 40 cm long, basally with several appressed sheaths. *Floral bracts* scale-like, subacute, concave, to 2 mm long. *Ovary* pedicellate, smooth, grooved, arcuate, 2.0–2.5 cm long, including the pedicel. *Flowers* medium-sized, spread, ivory-white or white-cream, column greenish, the sepals and petals greenish white, resupinate. *Dorsal sepal* elliptic-spathulate to obovate, cuneate, slightly revolute basally, acute 2.0–2.2 × 0.7–0.8 cm. *Lateral sepals* subsimilar, subfalcate and slightly revolute basally, obovate to elliptic or spathulate, acute, fleshy, 2.0–2.3 × 0.9–1.0 cm. *Petals* narrowly obovate to spathulate or oblanceolate, fleshy acute, 1.9–2.0 × 0.6–0.7 mm. *Lip* adnate to the column, clawed, entire, arcuate, convex, the lamina 3-lobed, the lateral lobes deflexed suborbicular, trapezoid to dolabriform, the midlobe retuse or with the apex deeply slit appearing bilobulate, 2.1–2.7 × 1.7 cm; the disc laminar, shortly bicarinate in front of the column, with several low keels radiating toward the sides of the lamina and 1 prominent keel running toward the apex of the midlobe. *Column* straight, wider at the apex, wholly adnate to the lip, 1.4 × 0.5 cm. *Clinandrium hood* abbreviated, entire, 1.2 cm long. *Pollinia* 4, laterally compressed, ovoid, subequal, with granulose caudicles and viscidium. *Rostellum* apical, slit. *Anther cap* hemiglobose, 4-celled with lamellae.

Distribution: from Mexico to Brazil and Peru.

Distribution in the Park: found at Las Cascadas on a main tree trunk along a creek. It probably also occurs at Los Mesones. Another plant was found growing at La Jaralosa in Zona Protectora Cerros de Jesús, 6 km from BHNP in humid evergreen forest.

Etymology: from the Latin *coronatum*, "crowned," probably referring to the inflorescence that crowns the stem.

Habitat and ecology: it is found in tropical wet forest from the central to northern Pacific and the dry western areas of Valle Central from 0 to 700 m of elevation. It was observed growing on *Spondias mombin* and *Guazuma ulmifolia* (Sterculiaceae).

Phenology: from April to August, but flowers mainly from May to June.

Discussion: it is distinguished by the relatively large pendant or suberect plants, with elongate, cylindrical stems covered by several dark-green, glossy, coriaceous, distichous leaves articulated with the leaf sheaths. The inflorescences are apical, racemose, hanging, with several ivory-white flowers with a prominent 3-lobed lip. From other species of *Epidendrum* in BHNP it is easily distinguished by the lack of pseudobulbs and the elongate, racemose inflorescences bearing 6–25 white-ivory flowers.

Additional specimens examined: Guanacaste: Nicoya, Mansión, Zona Protectora Cerros de Jesús, ascenso por el sector de La Jaralosa, 10°05'58.1"N, 85°19'11.7"W, 436 m, bosque húmedo premontano transición a basal, epífitas en bosque secundario sobre un yurro con árboles altos, 14 julio 2005, *D. Bogarín 1699, F. Villalobos, C. Aguilar, O. Durán, F. Paniagua* (JBL). BHNP, Las Cascadas (the waterfalls), entering from Finca San Diego (Finca Los Trejos), 10°10'59.86"N, 85°20'17.41"W, 86 m, premontane moist, transition to tropical moist forest, epiphytic in gallery forest on *Brosimum alicastrum* "Ojoche" (Moraceae) close to a stream, 22 February 2012, *F. Pupulin 8190 & D. Bogarín* (JBL-spirit).

11c. ***Epidendrum stamfordianum*** Bateman, Orchid. Mexico & Guatemala, t. 11. 1838. Fig. 11F, 30.

TYPE: GUATEMALA. Isabal, 1837, *G. U. Skinner s.n.* (Holotype: K).

Homotypic synonyms: *Auliza stamfordianum* (Batem.) Brieg., Die Orchideen 3. Aufl. 1 (9): 548. 1977.

Heterotypic synonyms: see Jiménez and Hágsater, 2008b.

Plants epiphytic, cespitose, erect, to about 50 cm tall. *Roots* fleshy, flexuous, glabrous, to 2.5 mm in diam. Pseudobulbs stalked, fusiform, enfolded by many large bracts becoming papyraceous with age, 8–28 cm long, 1.5–2.2 cm in diam., 2- to 4-leaved near the apex. *Leaves* rather variable, oblong-elliptic to ligulate or oblanceolate, conduplicate, obtuse, slightly retuse, coriaceous, 10–22 × 2.5–6.5 cm. *Inflorescence* appearing basal, apical from a short abortive shoot along the rhizome, erect to slightly arcuate, racemose or paniculate, usually many-flowered raceme to 50 cm long, peduncle 4–8 cm long, enfolded by 2–3 triangular bracts. *Ovary* terete, smooth, up to 3.5 cm long. *Flowers* medium-sized, 8–30 flowers, showy, sepals

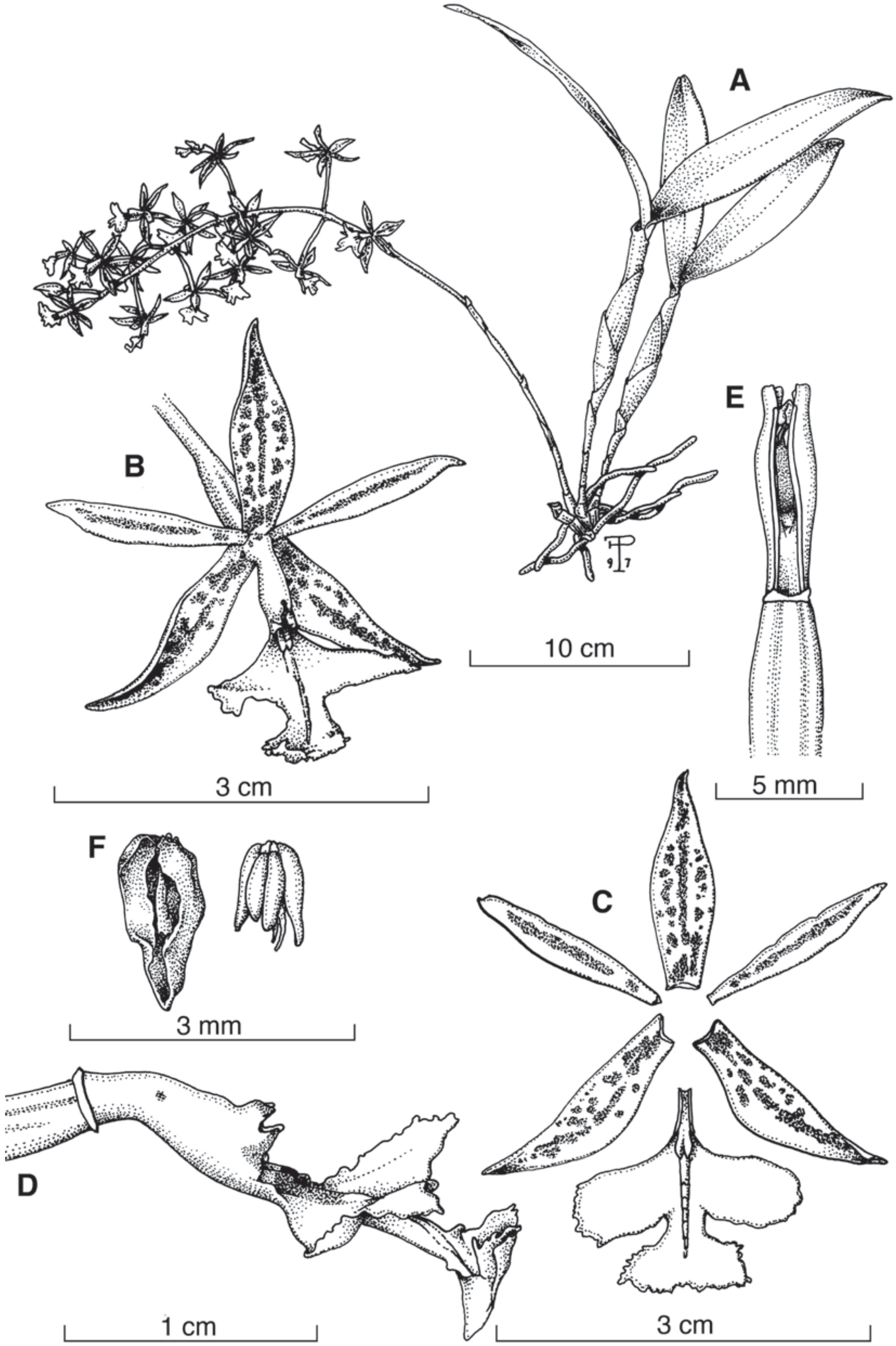

FIGURE 30. *Epidendrum stamfordianum* Bateman. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 370* (USJ).

and petals greenish yellow marked with dark purple, the lip with the lateral lobes white and the midlobe yellow, variously spotted or suffused with lilac to purple. *Dorsal sepal* elliptic-lanceolate, acute, concave and submucronate near the apex, 11.8–2.0 × 0.3–0.5 cm. *Lateral sepals* spreading, free, entire, subequal, elliptic-oblanceolate, acute, falcate, concave and submucronate near the apex, 1.8–2.0 × 0.3–0.5 cm. *Petals* oblique, linear-elliptic or linear-oblong, acute to acuminate, entire, slightly crenulate at the apex, 1.2–1.8 × 0.3–0.6 cm. *Lip* unguiculate, the claw adnate to the column, the lamina prominently 3-lobed, the midlobe transversely oblong, with a short claw at the base, crenulate to serrulate; the lateral lobes broad, subquadrate-elliptic to reniform, rounded, crenulate; disc provided with a short bilobed callus at the base and a median, low keel running to the middle of the midlobe; the entire lip 1.7 × 2.0 cm between the lateral lobes. *Column* clavate, stalked, arcuate basally, adnate to the lip just to the apex. *Clinandrium hood* cucullate, funnel-shaped, 3-toothed, 9 mm long. *Pollinia* 4, laterally compressed, semiovoid, ancipitose, in 2 pairs of different size, on a short caudicle. *Rostellum* apical, slit. *Anther cap* cucullate, lanceolate, 4-celled.

Distribution: Mexico to Colombia and Venezuela.

Distribution in the Park: widespread in BHNP. It is commonly observed in the evergreen forest of Las Cascadas, along the Ceiba trail at Cerros Barra Honda and Las Delicias.

Eponymy: in honor of the Earl of Stamford and Warrington, who put together an extensive collection of tropical orchids in Enville Hall, England, in the middle of the 19th century.

Habitat and ecology: plants can be found in seasonal tropical wet or moist forest in the Pacific lowlands of Península de Nicoya, central Pacific, and the dry areas of western Valle Central from 0 to 700 m. It was observed in disturbed areas or in secondary forest mostly on *Brosimum aliscastrum* (Moraceae), *Cedrela odorata* (Meliaceae), *Samanea saman* (Fabaceae), *Sideroxylum capiri*, and *Spondias mombin*.

Phenology: plants flower from November to May.

Discussion: plants are distinguished by the fusiform pseudobulbs having 2–4 coriaceous leaves, the inflorescence racemose or paniculate, arching, developed from a short abortive shoot along the rhizome appearing basal and the flowers with yellow sepals and petals spotted with magenta and the white lip with the midlobe yellow. At BHNP, it is the only species of *Epidendrum* having pseudobulbs. Because of the vegetative resemblance, it could be confused with *Guarianthe skinneri*. However, *E. stamfordianum* has 2–4 leaves in each pseudobulb (vs. 2 in *G. skinneri*), the inflorescence is developed from a short abortive shoot at the base (vs. apical from a fully developed pseudobulb), the flowers are white-yellow with magenta spots (vs. rose-purple), and the pseudobulb lacks a green spathe that becomes papery before flowering, as happens in *G. skinneri*.

Additional specimens examined: BHNP, Sendero Ceiba, desviación hacia Las Cascadas, La Mantequilla, 10°10'37.0"N, 85°21'09.6"W, 415 m, bosque húmedo premontano transición a basal, epífitas sobre Myrtaceae, en bosque secundario, 11 julio 2005, *D. Bogarín 1665 y F. Paniagua* (JBL-spirit).

11d. ***Epidendrum vulgoamparoanum*** Hágsater & L. Sánchez S., Icon. Orchid. (Mexico) 8: t. 898. 2006. Fig. 11G, 31.

TYPE: COSTA RICA: Alajuela: entre Río Grande de Atenas y Balsa, 400–485 m, colectada por Clarence Kl. Horich 20 Dec. 1982, prensado de material cultivado 13 oct. 1983, *E. Hágsater 6963* (Holotype: INB; Isotype: AMO).

Plants epiphytic, cespitose, erect or subpendent, without pseudobulbs, with short rhizome and foliaceous stems up to 35 cm tall. *Roots* fleshy, flexuous, glabrous, to 1.5 mm in diam. *Stems* elongate, flattened or laterally compressed, 35 cm long, to 1.4 cm in diam., completely enfolded by the tubular, leaf-bearing sheaths, 5- to 9-leaved. *Leaves* distichously arranged, elliptic-oblong to ovate, coriaceous, retuse, conduplicate, entire, persistent, 3.5–8.0 × 1.0–3.0 cm. *Inflorescence* apical, a short subumbellate, subsessile raceme bearing 3–5 flowers, produced from the axil of the upper leaf, flowering only once. *Floral bracts* smaller than the ovary, triangular, acute. *Ovary* smooth, terete, wider apically, to 2.5 cm long. *Flowers* medium-sized, green, resupinate, producing a plastic-like smell. *Dorsal sepal* elliptic, acute, entire, revolute basally, 3.0 × 0.9 cm. *Lateral sepals* subsimilar, lanceolate-elliptic to obliquely-elliptic, acute, somewhat falcate, revolute basally, 3.2 × 1.0 cm. *Petals* linear-elliptic to elliptic-oblanceolate, acute, spreading, entire, 2.8 × 0.5 cm. *Lip* adnate to the column, clawed, the lamina 3-lobed, concave, arching toward the apex, widely reniform or obovate, deeply cordate at the base, somewhat 3-lobed at apex, apiculate, 2.8 × 3.5 cm; the disc with 2 thickened, subglobose, slightly diverging calli. *Column* straight, clavate, with a terminal tooth and a nectary. *Clinandrium hood* prominent, entire, erose-fimbriate, 1.2 cm long. *Pollinia* 4, laterally compressed, subequal, with caudicles and viscidium. *Rostellum* subapical, slit. *Anther cap* hemiglobose, 4-celled.

Distribution: from the Pacific lowlands of Costa Rica and Panama (probably also in Rivas, Nicaragua).

Distribution in the Park: widespread in disturbed areas close to the boundaries of BHNP on insolated *Tamarindus indica* (Fabaceae-Mimosaceae) or *Tabebuia* spp. and along the main trails of the Park at Cerro Barra Honda, Las Delicias, and Las Cascadas.

Etymology: from the Latin *vulgo*, "commonly, generally," and *amparoanum*, in reference to the fact that this species has been wrongly identified as *Epidendrum amparoanum* Schltr.

Habitat and ecology: a widespread epiphyte of the tropical wet or tropical moist forest of the Pacific lowlands and the dry areas of western Valle Central, from sea level to 800 m of elevation. The flowers emit a plastic-like smell that is stronger in the last hours of the day.

Phenology: from December to July.

Discussion: it is characterized by a lack of pseudobulbs and having elongate, flattened, or laterally compressed

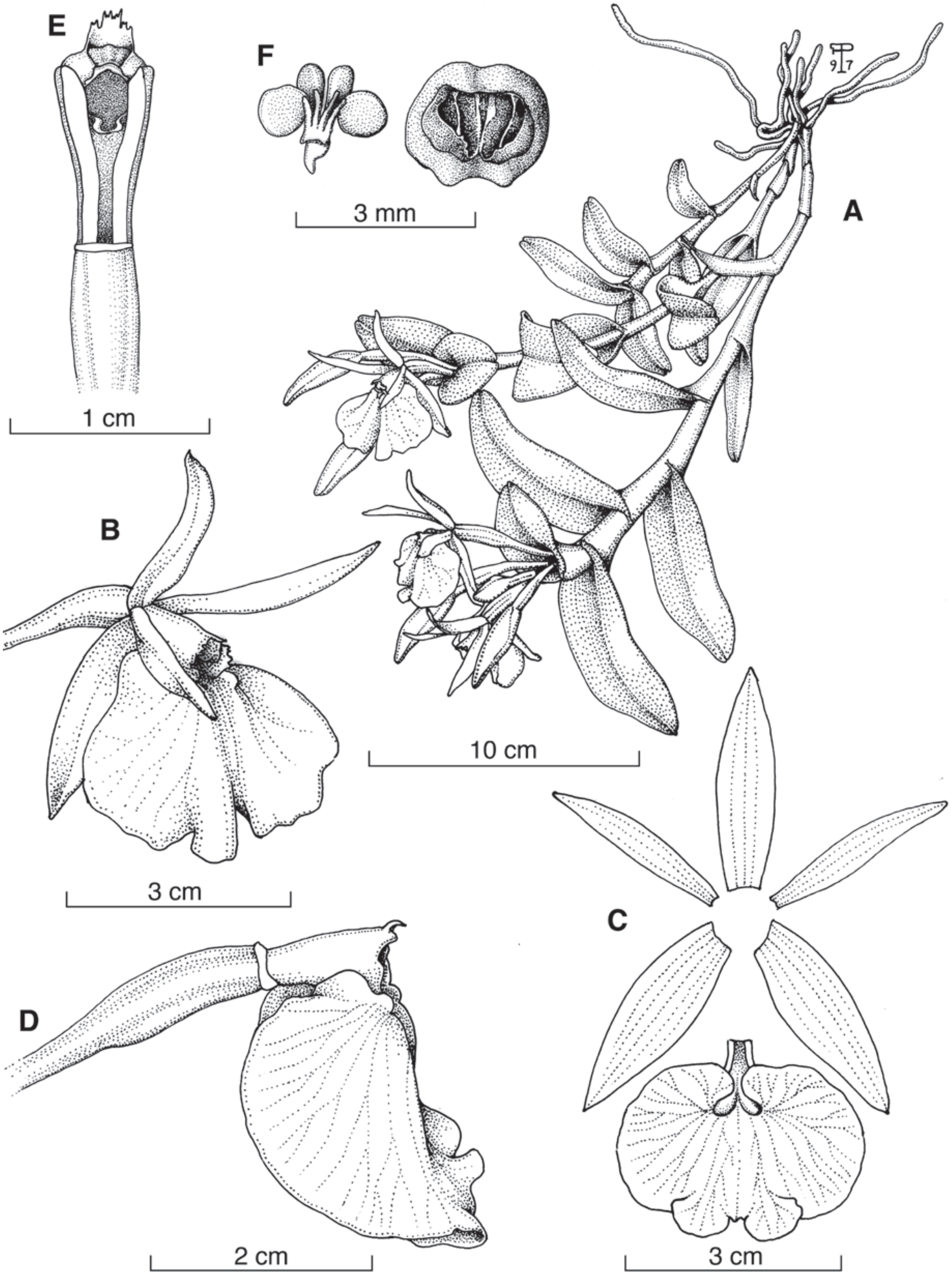

FIGURE 31. *Epidendrum vulgoamparoanum* Hágsater & L.Sánchez. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 328* (JBL).

foliaceous stems with subumbellate, subsessile, apical racemes bearing 3–5 simultaneous green fragrant flowers. The name *E. amparoanum* (=*Epidendrum barbeyanum* Kraenzl.) was applied to this species (Pupulin 1998; Dressler, 2003; Hágsater and Sánchez, 2006).

Additional specimens examined: BHNP, Sendero Ceiba y Mirador, 10°10'06.1"N, 85°21'47.4"W, 430 m, bosque húmedo premontano transición a basal, epífitas sobre *Spondias mombin*, en bosque secundario, 12 julio 2005, *D. Bogarín 1686 y F. Paniagua* (JBL-spirit).

12. ***Guarianthe*** Dressler & W.E. Higgins, Lankesteriana. 7: 37. 2003.

TYPE: *Guarianthe skinneri* (Bateman) Dressler & W.E. Higgins

Plants epiphytic, caespitose, erect, often in large, dense clumps. *Pseudobulbs* clavate, fleshy, apically bifoliate, concealed by long tubular scarious sheaths, the oldest pseudobulbs striated and without leaves. *Leaves* subopposite, conduplicate, elliptic to oblong-lanceolate, coriaceous, thick. *Inflorescence* terminal, racemose, from a prominent papyraceous spathe with 4–12 flowers clustered together. *Flowers* showy, spread, resupinated, purple-rose, or orange. *Sepals* subsimilar, elliptic, free, spreading, or connivent. *Petals* broader than the sepals, widely elliptic to rhombic-ovate, free, sometimes waved along the margins. *Lip* infundibuliform, funnel-shaped, folded closely over the column, and spreading apically in natural position. *Column* clavate, wingless, more or less arcuate. *Anther* incumbent, terminal, operculate. *Pollinia* 4, ceraceous, with caudicles. *Capsule* ellipsoid, prominently ribbed.

A genus of four species ranging from Mexico through Central America and northern South America. Three species in Costa Rica and one in BHNP.

Guarianthe skinneri (Bateman) Dressler & W.E. Higgins, Lankesteriana. 7: 37. 2003. Fig. 11H, 32.

Basionym: *Cattleya skinneri* Bateman, Orchid. Mexico & Guatemala, t. 13. 1839. TYPE: GUATEMALA. *G. U. Skinner s.n.* (Holotype: K).

Plant epiphytic, caespitose, erect, stout, to about 50 cm tall. *Rhizome* cylindric, repent, covered by tightly appressed scarious, imbricate bracts, to 5 cm long. *Roots* fleshy, flexuous, glabrous to 2–3 mm in diam., whitish, the tips green. Pseudobulbs stalked, fusiform or clavate, attenuated into a terete jointed stalk, laterally compressed, wrinkled and furrowed with age, enfolded by many tightly appressed bracts becoming papyraceous, 8–40 cm long, 1.5–3.5 cm in diam., 2 leaved apically. *Leaves* oblong-elliptic, conduplicate, fleshy-coriaceous, acute to obtuse, slightly retuse, arching, 9.0–22.0 × 2.5–6.5 cm. *Inflorescence* apical, racemose, erect, usually with 4–15 flowers, to 15 cm long, peduncle to 10 cm long, developed from a prominent papyraceous spathe to 6–12 cm long. *Ovary* terete, slender, smooth, pedicellate, up to 6.5 cm long. *Flowers* medium-sized, showy, rose-purple, rarely white, the lip with the center white, rarely yellow or purple. *Dorsal sepal* linear-lanceolate to elliptic-lanceolate, acute, erect, entire, somewhat reflexed, 3.5–6.5 × 0.8–1.8 cm. *Lateral sepals* spreading, free, entire, subequal, elliptic-lanceolate, acute, somewhat oblique, 4.0–6.5 × 1.0–1.8 cm. *Petals* broadly ovate or elliptic to lanceolate, acute or obtuse, entire, somewhat undulate, wider than sepals, 3.5–6.7 × 1.6–6.5 cm. *Lip* infundibuliform in the lower half, funnel-shaped or folded closely over the column, apically expanded and somewhat undulate, the lamina oblong-elliptic, obovate, somewhat pandurate or obscurely 3-lobed when spread out, truncate, emarginate or obtuse, with a prominent keel along the middle, 3.5–8.0 × 2.0–4.5 cm. *Column* semiterete, clavate, straight, 3-toothed at the apex, to 1.7 cm long. *Pollinia* 4, laterally compressed, ovoid, with granulose caudicles. *Anther cap* cucullate, 4-celled.

Distribution: from southern Mexico to Costa Rica.

Distribution in the Park: one population was found at Cerro Barra Honda near the cactus forest, in a rocky area of scattered trees of *Bursera simarouba*, *Plumeria rubra*, and *Cedrela odorata*. A flower was collected on the ground at Cerros de Jesús, probably below where the plant was located high in the canopy.

Eponymy: dedicated to the Briton George Ure Skinner (1804–1867), businessman, diplomat, amateur botanist, and the most crucial figure in the history of orchids in Central America during the first half of the 19th century.

Habitat and ecology: epiphytic or lithophytic in premontane wet and premontane moist forest, tropical dry forest and moist province transition, in the seasonal warm, humid areas of the Cordillera de Guanacaste, Tilarán, and Central, around Valle Central toward Península de Nicoya and the seasonal areas of Valle del Térraba from 200 to 1400 m of elevation.

Phenology: from January to April, rarely in December and May.

Discussion: it is distinguished by the fusiform, bifoliate pseudobulbs, the apical racemose inflorescence developed from a prominent papyraceous spathe, and the rose-purple flowers with a trumpet-like lip, folded around the column in the lower half and spreading apically. It is the national flower of Costa Rica. Populations are reduced in the wild because of overcollection and the destruction of the habitat. At BHNP, it could be confused with *Epidendrum stamfordianum*, but plants have 2-leaved pseudobulbs with shorter, apical, racemose inflorescences and bigger, rose-purple flowers.

Additional specimens examined: BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, al lado derecho, en dirección a La Mantequilla, 421 m, bosque húmedo premontano transición a basal, epífita en *Plumeria rubra* (Apocynaceae), 21 febrero 2006, *D. Bogarín 2607* (JBL-spirit). Guanacaste: Nicoya, Mansión, Zona Protectora Cerros de Jesús, 370 m, bosque húmedo premontano transición a basal, epífitas en bosque secundario maduro sobre una quebrada estacional con árboles altos, 23 febrero 2012, *D. Bogarín 9515 y F. Pupulin* (JBL-spirit).

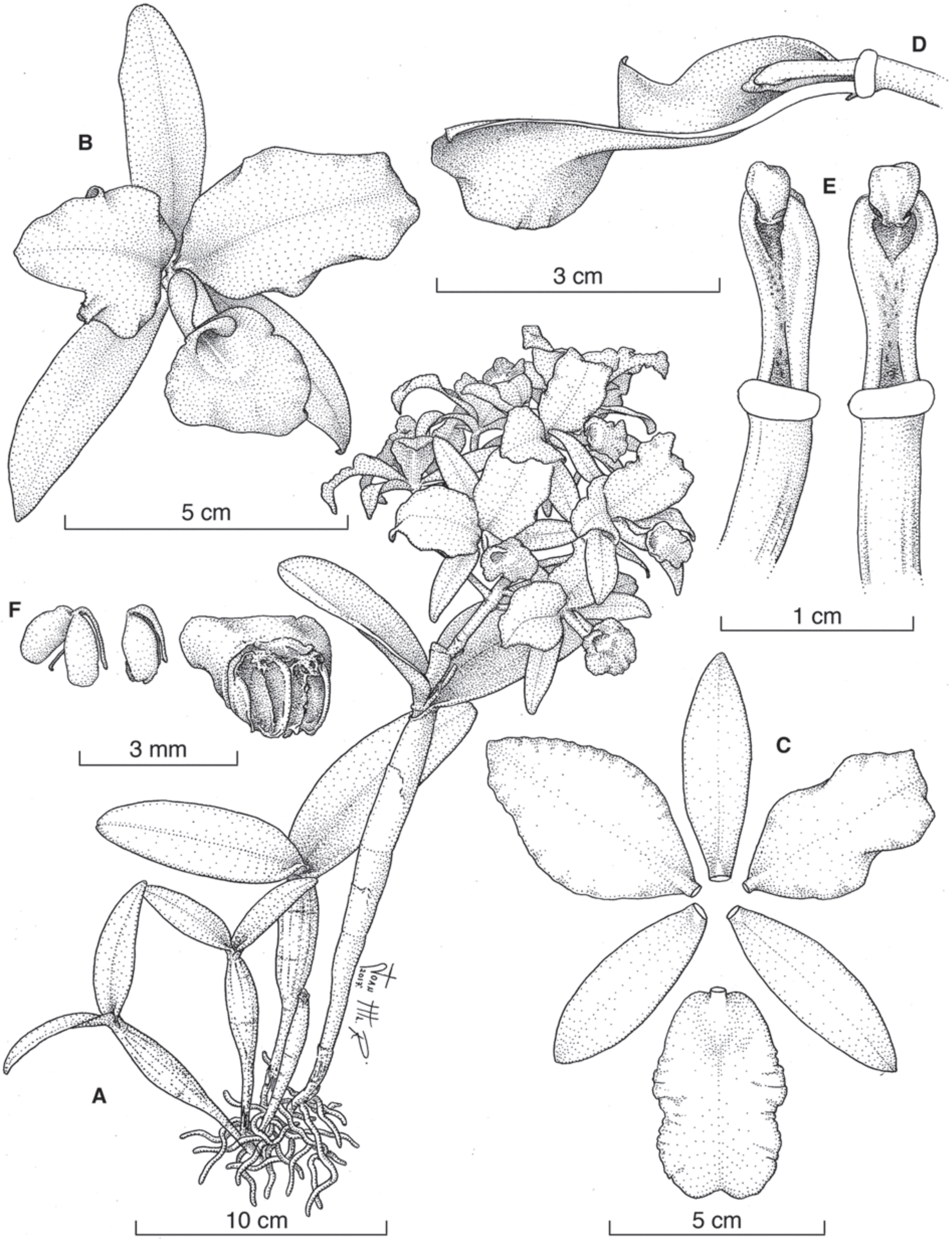

FIGURE 32. *Guarianthe skinneri* (Bateman) Dressler & W.E. Higgins. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip (longitudinal section), side view. **E,** Column, side and ventral view. **F,** Pollinarium and anther cap. Drawn by Joan M. Ramírez from *Bogarín 2607* (JBL).

13. *Habenaria* Willd., Sp. Pl. 4(1): 5, 44. 1805.
TYPE: *Habenaria macroceratitis* Willd.

Plants terrestrial or palustrine, erect herbs. *Roots* fleshy or tuberous. *Tubers* ovoid, fusiform, or subglobose. *Stem* erect, with cauline or basal leaves, the leaves rarely reduced to bracts. *Leaves* thin to fleshy, rosulate, or spiralate, usually prominent, deciduous during the dry season. *Inflorescence* terminal, erect, few- to many-flowered, spicate or racemose. *Flowers* spurred, spread, often showy, in racemes, rarely solitary. *Floral bracts* often large and conspicuous. *Sepals* subequal, free or connate at the base, the dorsal erect, usually concave, forming a hood over the column, the laterals spreading or deflexed. *Petals* similar to the sepals but usually smaller, or more or less deeply bifid (rarely trifid or polyfid), usually connivent with the dorsal sepal. *Lip* simple or 3-lobed, often adnate to the column, spreading or pendulous, at the base producing a spur. *Column* short, footless. *Stigmas* often 2-lobed and elongated into short or comparatively long processes. *Anther* erect, more or less resupinate, persistent. *Pollinia* granular, sectile, with short or sometimes long separated caudicles from the base.

A Pantropical genus of about 600 species found mainly in grasslands, woodlands, savannas, meadows, or swamps. About 20 species in Costa Rica. A single species in BHNP.

Habenaria macroceratitis Willd., Sp. Pl. 4(1): 44. 1805. Fig. 11I, 33.
TYPE: Jamaica. *Habitat in graminosis depressis subalpinis Jamaicae* (Lectotype designated by Cafferty and Jarvis, 1999: LINN-1054.14).

Plants terrestrial, with a single slender, foliaceous stem, without pseudobulbs, up to 1.2 m tall, stem, and leaves deciduous during the dry season. *Tuber* ovoid, subglobose, up to 4 cm in diam. *Roots* fibrous, numerous, up to 4 mm in diam. *Leaves* obovate or oblong-elliptic, acute or obstuse, caulinar, subcoriaceous, keeled, somewhat plicate, helical, 10–17 leaves, the lower leaves smaller than the apical, articulate with the leaf sheaths, 6–24 × 2–7 cm. *Leaf sheaths* tubular, appressed to the stem, 3.5–4.0 cm long. *Inflorescence* apical, racemose, lax, with several helical flowers, 15–25 cm long, covered by prominent leafy bracts to 4 cm long. *Floral bracts* prominent ovate, acute, up to 8 cm. *Ovary* pedicellate, up to 3.5 cm long. *Flowers* showy, resupinate, the lateral sepals and the spur green, the petals and the dorsal sepal white with the apex cream, the anther yellowish, provided with long, filiform spurs. *Dorsal sepal* ovate to orbicular, deeply concave, slightly emarginate, obtuse, margins recurved, 1.0 × 1.2 mm. *Lateral sepals* ovate to elliptic, subfalcate, free, spread, conduplicate, somewhat concave, with revolute margins, reflexed apically, 4.5 × 2.0 cm. *Petals* bifid, the upper lobe 1.2 × 3.5 mm, oblong, subfalcate, erect, connivent with the dorsal sepal forming a hood over the column, the lower lobe linear-filiform, attenuate, expanded, falcate apically, up to 5.0 × 0.1 cm. *Lip* strongly trilobed, the midlobe oblong, 2.0 × 0.3 cm, the lateral lobes longer than the middle, linear, deflexed, attenuate, 4.0 × 0.1 mm, the spur prominent, linear, widened apically, laterally flattened, hanging, 8.2–10.0 cm long. *Column* with 2 falcate arms, papillose at the base, the anther with 2 chambers in which the 2 hemipollinaria are inserted, surrounded by membranous sacciform tissue with a longitudinal opening, stigma 2-lobed, the lobes falcate, connivent, leaving a rounded spur entrance, 3.5 × 1.2 cm. *Pollinarium* 2, obovate, granular, and sectile, with a filiform stipe, viscidium peltate. *Anther cap* membranaceous.

Distribution: from Florida (USA) and Mexico to Guyana, Trinidad, and the Antilles.

Distribution in the Park: common at the beginning of Ceiba and Mirador trails and around the parking area at Cerro Barra Honda.

Etymology: from the Greek *macro*, "large," *keras*, "horn," and *itis*, "swollen," probably in allusion to the large swollen spur of the lip.

Habitat and ecology: terrestrial in seasonal tropical premontane wet and premontane moist forest from 0 to 250 m of elevation. Plants grow vegetatively during the wet season starting in May and develop inflorescences after June. During the dry season the leaves fall, and the tuber remains alive underground. Plants may be pollinated by nocturnal moths, as the white flowers with long spurs suggest.

Phenology: from August to October.

Discussion: it is easily characterized by the terrestrial plants with a subglobose tuber and a single elongate, slender, foliaceous stem with helical caulinar leaves, which are deciduous during the dry season. The flowers are showy, white with green sepals. The lip is deeply 3-lobed with a long filiform spur.

Additional specimens examined: BHNP, bifurcación del camino en Sendero Ceiba y Mirador, 10°10'25.4"N, 85°21'40.1"W, 410 m, bosque húmedo premontano transición a basal, terrestres a orillas del camino, bosque secundario, 23 julio 2005, *D. Bogarín 1726 y F. Paniagua* (JBL-spirit). Same locality, *D. Bogarín 1724 y F. Paniagua* (JBL-spirit). BHNP, camino principal de la estación al Sendero Ceiba, parte alta antes de llegar al parqueo, 10°10'21.53"N, 85°21'42.50"W, 342 m, bosque húmedo premontano transición a basal, terrestres orillas del camino, bosque secundario, 7 noviembre 2011, *D. Bogarín 9413* (CR).

14. *Heterotaxis* Lindl., Bot. Reg. 12: t. 1028. 1826.
TYPE: *Heterotaxis crassifolia* Lindl.

Plants epiphytic, pendent, with sympodial growth and laterally compressed, oblong, unifoliate, aggregate pseudobulbs subtended by several foliaceous sheaths (rarely without pseudobulbs). *Leaves* coriaceous, linear to linear-oblong or ensiform, obtuse to acute. *Inflorescence* produced from the axil of the leaves, 1-flowered. *Flowers* fleshy, yellowish, campanulate with perianth fibers. *Sepals* oblong, fleshy, acute. *Petals* linear-oblanceolate, acute. *Lip* simple, obscurely 3-lobed, elliptic, articulate with the column foot with a thickened, often farinose callus. *Column* elongate, arcuate, semiterete, produced at the base into a short foot. Pollinia 4, in 2 different sized pairs, on a short, rounded, basally dilated stipe. *Anther cap* cucullate, glabrous, 1-celled. *Capsules* ellipsoid, with lateral dehiscence.

A Neotropical genus of about 13 species ranging from northern Mexico to Brazil, Bolivia, and the Caribbean. Three species in Costa Rica, one in BHNP.

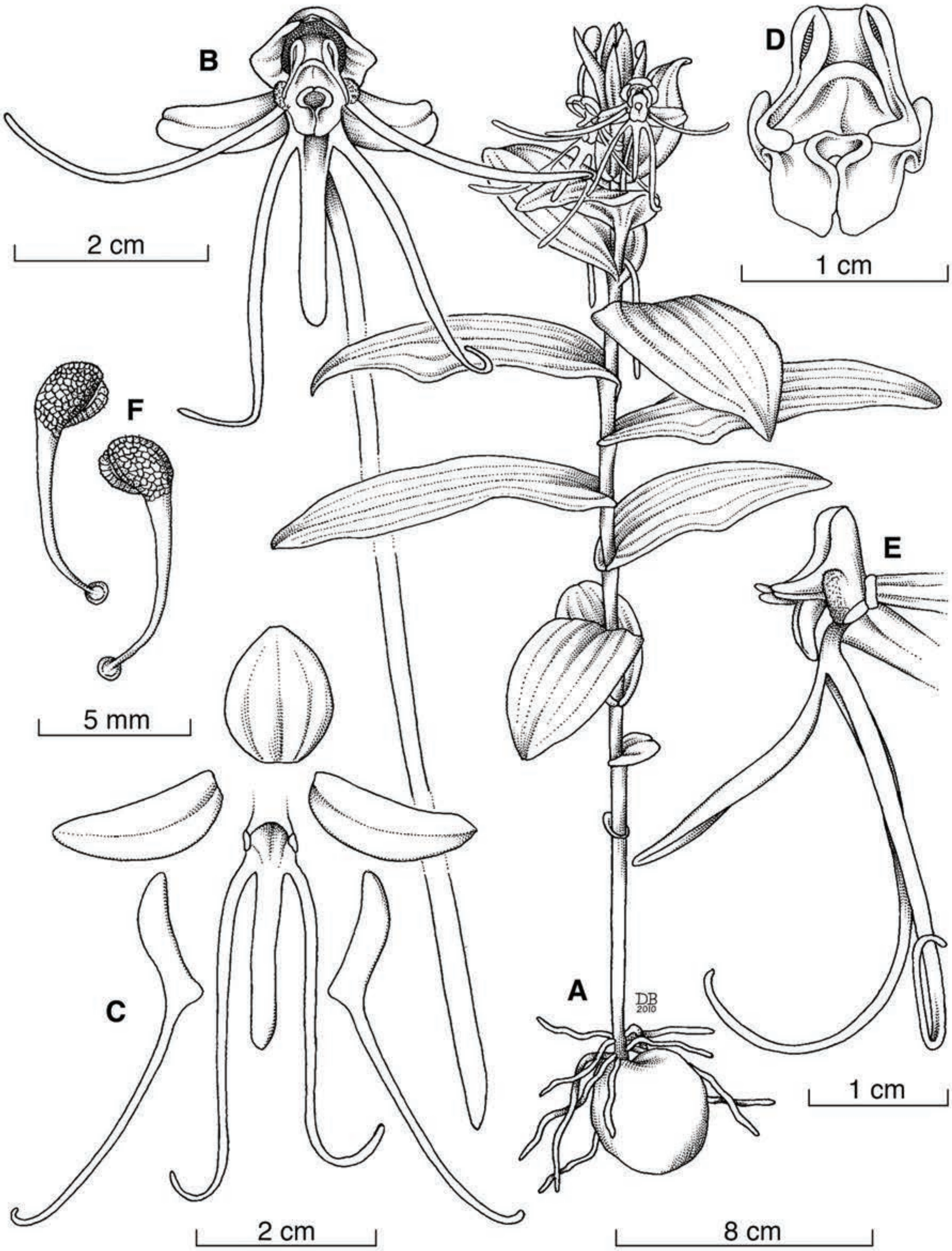

FIGURE 33. *Habenaria macroceratitis* Willd., **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium. Drawn by D. Bogarín from *Bogarín 1726* (JBL).

Heterotaxis sessilis (Sw.) F. Barros, Hoehnea 29(2): 11. 2002. Fig. 12A, 34.

Basionym: *Epidendrum sessile* Sw., Prodr. 122. 1788. TYPE: JAMAICA. *O. Swartz s.n.* (Holotype: BM).

Homotypic synonyms: *Maxillaria sessilis* (Sw.) Fawc. & Rendle, Fl. Jamaica 1: 120–121. 1910, *nom. illeg.*

Plants epiphytic, cespitose, pendent, with a short rhizome, to about 50 cm tall. *Roots* filiform, glabrous, to 2 mm in diam. *Pseudobulbs* oblong, inconspicuous, monophyllous, subtended by 2–3 distichously imbricating, fleshy, foliaceous sheaths, to 3.0 × 1.5 cm. *Leaves* coriaceous, linear to linear-oblong, obtuse to subacute, forming at the base a more or less complanate petiole, 7.0–47.0 × 1.4–2.8 cm. *Inflorescence* produced from the axils of the upper leaves, generally 1-flowered, with a short peduncle 1 to 3.5 cm long, provided by a scarious bract. *Ovary* pedicellate, subclavate, about 1 cm long. *Flowers* of moderate size, pale yellow, the lip marked with purple. *Dorsal sepal* oblong-elliptic to lanceolate, subacute, conspicuously concave, fleshy, 17.0 × 6.5–7.0 mm. *Lateral sepals* obliquely ovate-oblong, subacute, dorsally carinate, 16 × 6 mm, adnate to the column, forming an inconspicuous, rounded mentum. *Petals* linear-oblanceolate, acute, curved, 13 × 4 mm. *Lip* obscurely 3-lobed, elliptic-lanceolate, contracted at the base and articulate with the column foot, to 16 × 9 mm when spread out; lateral lobes rounded, erect; midlobe subobtuse, thickened and farinose to minutely papillose; disc with a ligulate, fleshy, thickened, farinose callus. *Column* elongate, arcuate, semiterete, to 12 mm long, produced at the base into a short foot. *Pollinia* 4, in two different sized pairs, on a short, rounded, basally dilated stipe. *Anther cap* cucullate, glabrous, 1-celled. *Capsule* ellipsoid, 6-ridged, to 3 cm long.

Distribution: widespread from southern Mexico and Florida (USA) to Brazil and the Antilles.

Distribution in the Park: it is found at Las Cascadas and Los Mesones in the humid evergreen forest. The specimen studied was collected at Cerros de Jesús.

Etymology: from the Latin *sessilis*, "sessile, stalkless," in allusion to the compressed leaf base.

Habitat and ecology: plants are common in tropical seasonal or deciduous dry forest and humid tropical moist forest along the Caribbean and Pacific lowlands at elevations below 800 m. Plants are generally found on large trunks in medium-shaded conditions, often forming large clumps on the host tree. Mostly found on *Anacardium excelsum*, *Brosimum aliscastrum*, and *Sideroxylum capiri*.

Phenology: flowering season occurs from February to May, but may extend to October.

Discussion: it is characterized by the pendent, fan-shaped plants with fleshy, conspicuously veined leaves; the pseudobulbs are obsolete, 1-leaved, subtended by several foliaceous sheaths. The flowers are inconspicuous, campanulate, yellow with the lip purple-spotted, and produced at the base of the pseudobulbs.

Additional specimens examined: BHNP, Las Cascadas (the waterfalls), entering from Finca San Diego (Finca Los Trejos), 10°10'59.86"N, 85°20'17.41"W, 86 m, premontane moist, transition to tropical moist forest, epiphytic in gallery forest on *Brosimum alicastrum* "Ojoche" (Moraceae) close to a stream, 22 February 2012, *D. Bogarín s.n.* (unvouchered).

15. *Laelia* Lindl., Gen. Sp. Orchid. Pl. 96, 115. 1831. *nom. cons.*

TYPE: *Laelia grandiflora* (La Llave & Lex.) Lindl.

Plants epiphytic or rupicolous, caespitose. *Pseudobulbs* aggregate, compressed or terete, thickened, discoid, clavate, orbicular, laterally compressed, rugulose to sulcate. *Leaves* 1–3 at the pseudobulb apex, elliptic to linear, coriaceous, subsessile. *Inflorescence* apical, a simple or compound raceme developed on an elongated scape with flowers arranged in a helical, subdistichous or distichous pattern. *Flowers* large and showy, clustered at the apex of the inflorescence, resupinate. *Sepals* subequal to the petals, often narrower, free, spreading, flat or undulate. *Petals* subequal or broader than the sepals, spreading, often undulate-crispate. *Lip* free or slightly adnate to the column, more or less 3-lobed, the lateral lobes usually convolute enfolding the column, flat to crispate, with a callus of several keels or lamellae running toward the apex. *Column* winged or wingless, often toothed at the apex. *Anther* operculate, incumbent. *Pollinia* 8, unequal, waxy, ovoid, laterally compressed. *Capsule* ellipsoid.

A Neotropical genus of about 25 species ranging from northern Mexico to Brazil, Bolivia, and the Caribbean. Two species in Costa Rica, one in BHNP.

Laelia rubescens Lindl., Edwards's Bot. Reg. 26: t. 41, also misc. 20. 1840. Fig. 12B, 35–36.

TYPE: "For this specimen I am indebted to Mr. Barker, who purchased it some time ago from Mr. Joseph Knight, Nurseryman, in the King's Road. Its native country is unknown, but is probably Mexico," *J. Knight s.n.* (Holotype: K).

Homotypic synonyms: *Amalia rubescens* (Lindl.) Heynh., Alph. Aufz. Gew. 2: 29. 1846.

Cattleya rubescens (Lindl.) Beer, Prakt. Stud. Orchid.: 214. 1854.

Bletia rubescens (Lindl.) Rchb.f. in W.G.Walpers, Ann. Bot. Syst. 6: 425. 1862.

Encabarcenia rubescens (Lindl.) Archila & Szlach., Revista Guatemalensis 17: 26. 2014.

Schomburgkia rubescens (Lindl.) Peraza & Carnevali, Taxon 65: 1259. 2016.

Plants epiphytic, rarely rupicolous, slightly repent, caespitose up to 75 cm tall. *Roots* filiform, flexuous, to 2 mm in diam., with green or reddish tips. *Rhizome* short, covered by papyraceous bracts. *Pseudobulbs* aggregate, sessile, elliptic to orbicular, subglobose, laterally flattened, subprostrate, rugulose, or somewhat wrinkled appearance, especially in the old pseudobulbs, 3.0–8.2 × 2.5–6.2 cm, subtended by clasping ovate, membranaceous, conduplicate sheaths up to 6.5 cm long. *Leaves* 1 (rarely 2), at the apex of the pseudobulb, oblong-elliptic, obtuse to obliquely retuse at the apex, fleshy-coriaceous, glossy, conduplicate, somewhat cuneate abaxially, 3.5–20.0 × 3.1–5.5 cm. *Inflorescence*

FIGURE 12. **A–I.** Orchid species found at Barra Honda National Park. **A,** *Heterotaxis sessilis* (*Pupulin 8201*, JBL). **B,** *Laelia rubescens* (*Bogarín 1666*, JBL). **C,** *Lalexia quadrifida* (*Bogarín 1676*, JBL). **D,** *Leochilus scriptus* (*Bogarín 9385*, JBL). **E,** *Lophiaris oerstedii* (*Pupulin 8189*, JBL). **F,** *Malaxis aurea* (*Bogarín 1755*, JBL). **G,** *Maxillariella acervata* (*Pupulin 4053*, JBL). **H,** *Oeceoclades maculata* (*Bogarín 4061*, JBL). **I,** *Pelexia barrahondaensis* (*Pupulin 8168*, JBL). Photographs by the authors.

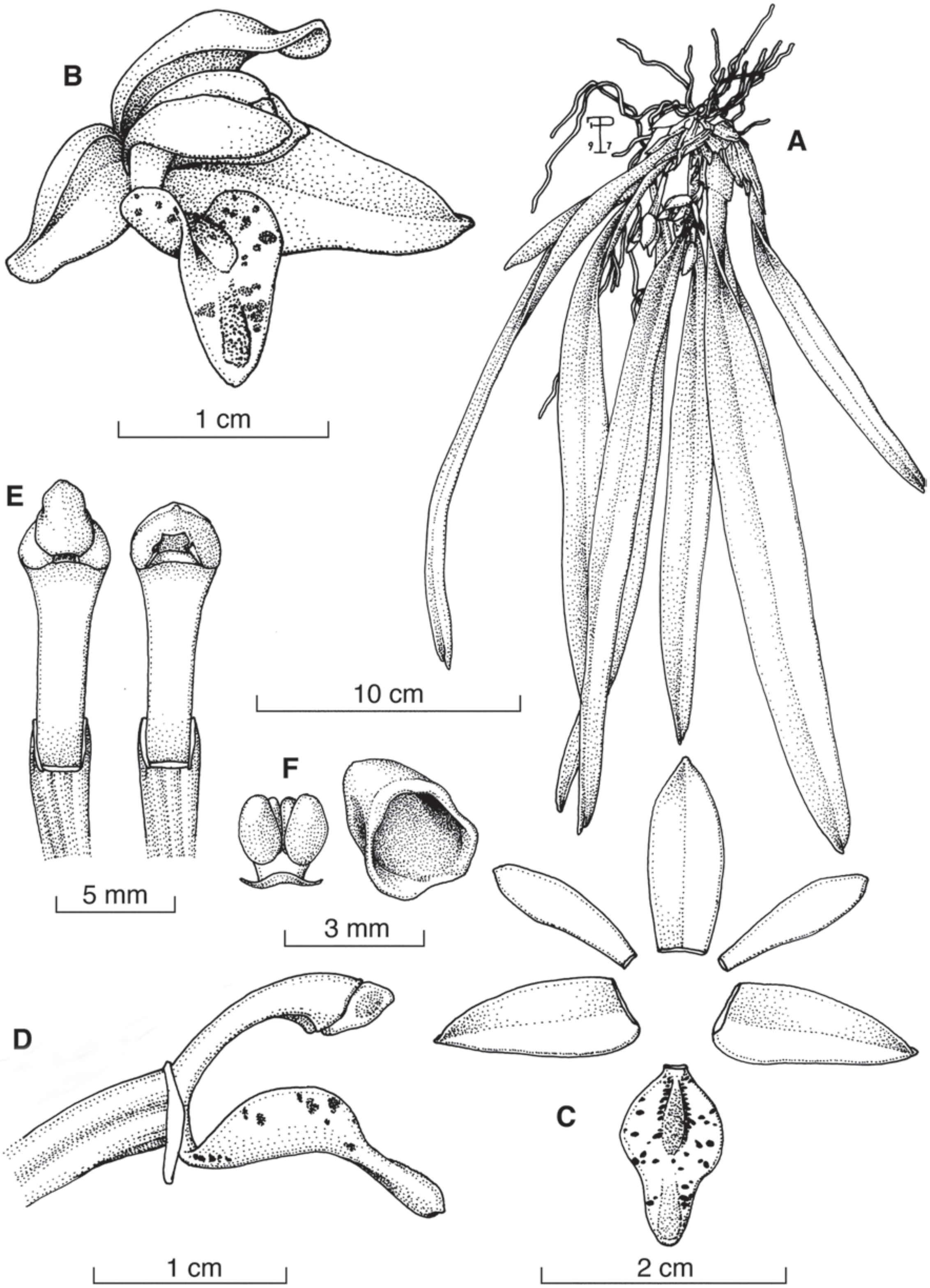

FIGURE 34. *Heterotaxis sessilis* (Sw.) F. Barros. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, side and ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 312* (JBL).

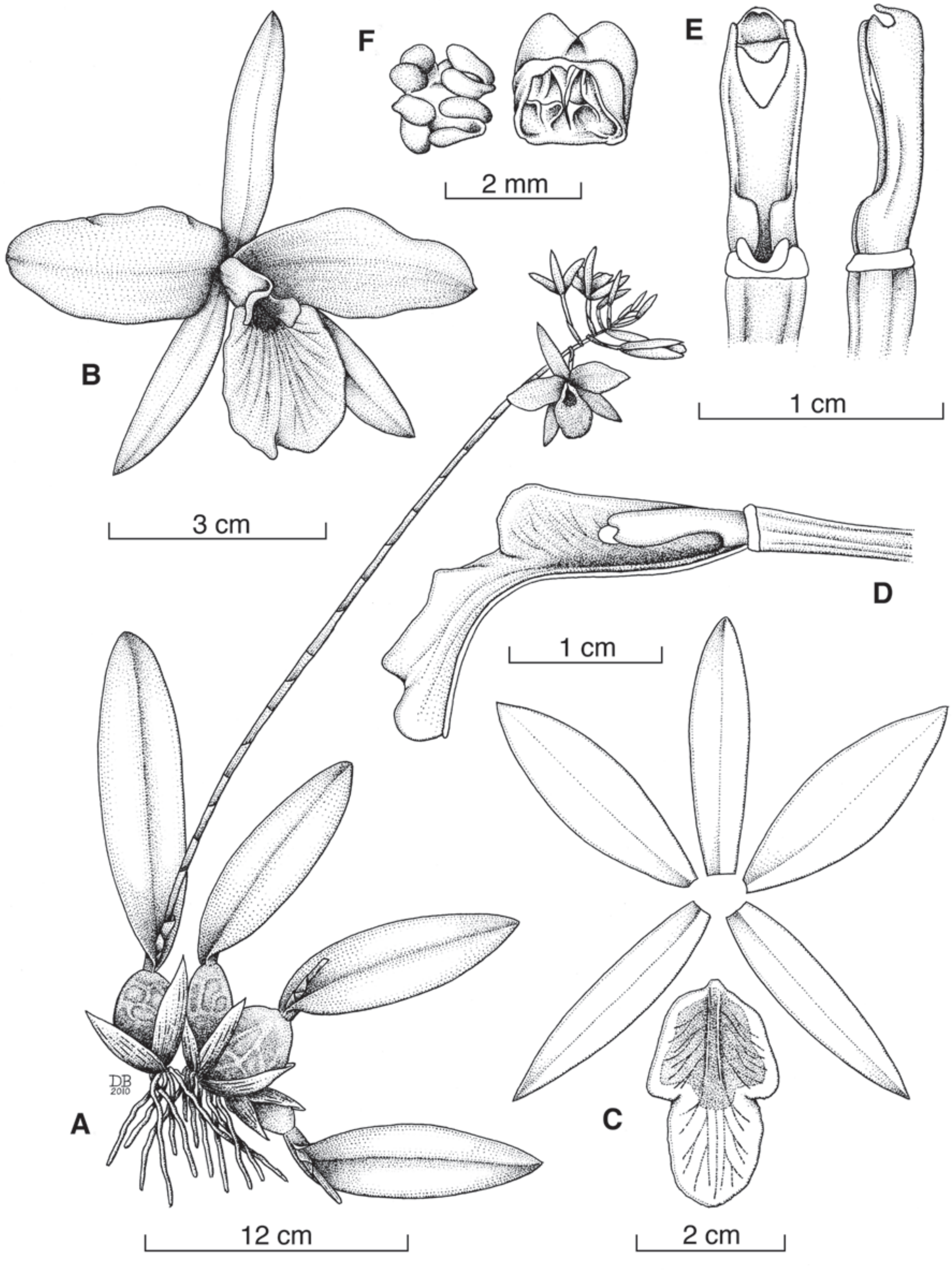

FIGURE 35. *Laelia rubescens* Lindl. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip (longitudinal section), side view. **E,** Pollinarium and anther cap. Drawn by D. Bogarín from *Bogarín 1666* (JBL).

FIGURE 36. *Laelia rubescens* flowering in situ at BHNP. Photograph by F. Pupulin.

terminal, elongated, terete, subcorymbose, successively flowered, the flowers arranged in a helical, subdistichous pattern, concealed by several tubular, acute, papyraceous bracts to 7 cm long, peduncle, 25–95 cm long, rachis to 6 cm long. *Floral bracts* oblong-lanceolate, obtuse to subacute, canaliculate, scarious, 1.5 × 0.2 cm. *Ovary* pedicellate, 2.3–4.5 cm long. *Flowers* rose-purple or rose-lavender, rarely white, with a dark purple or carmine blotch on the central portion of the lip surrounded by a white-cream stain at the base of the midlobe, spread, fragrant (grape-like). *Sepals* linear-elliptic or linear-lanceolate, obtuse to narrowly acute, somewhat oblique, slightly thickened apically, 3.2–4.3 × 0.4–0.7 cm. *Petals* free, spread, broadly elliptic, wider than sepals, obtuse to acute, somewhat undulate, 3.4–4.2 × 1.5–1.8 cm. *Lip* 3-lobed, 2.2–3.7 × 1.7–2.2 cm, lateral lobes rounded-obtuse, involute, folded over the column, midlobe oblong-quadrate to oblong-oval, subtruncate to acute or somewhat emarginate, basally puberulent, spread, wavy, 1.0–1.7 mm wide, with 2–3 parallel keels extending up to the base of the midlobe and several low keels radiating from the base toward the margins. *Column* semiterete, clavate, basally cuniculate in the entrance of a short nectary, somewhat broadened and tridentate apically, 7–13 mm long. *Stigma* ventral, entire. *Anther* incumbent, operculate, 4-celled. *Pollinia* 8, with caudicles.

Distribution: from Mexico to the northern and central Pacific of Costa Rica.

Distribution in the Park: it is a common epiphyte growing on several phorophytes such as *Bursera simarouba* and *Bursera permollis* (Burseraceae), *Spondias mombin*, *Cedrela odorata* (Meliaceae), *Brosimum aliscastrum* (Moraceae), and *Sideroxylum capiri* (Sapotaceae). It is found along Ceiba and El Mirador trails, toward Las Cascadas, Bosque de Piedra, Los Mesones, Las Delicias, and Cerros Quebrada Honda.

Etymology: from the Latin *rubescens*, "turning red, reddening," in allusion to the flowers' color.

Habitat and ecology: plants are common elements of the tropical seasonal or deciduous dry forest of northern Guanacaste and Puntarenas at elevations below 800 m. They grow in medium-shaded environments or exposed to full sunlight conditions, often forming large colonies on the host tree branches (Fig. 36).

Phenology: flowering season occurs from September to February, rarely to March.

Discussion: it is characterized by the aggregate, elliptic to orbicular, subglobose, flattened, ancipitous pseudobulbs having a single elliptical leaf and the long pedunculate apical inflorescence with several rose-purple flowers with the petals wider than the sepals and the lip involute, folded over the column with a dark purple center. The flower is similar in appearance to a small *Guarianthe skinneri*.

Additional specimens examined: BHNP, Sendero Ceiba, desviación hacia Las Cascadas, La Mantequilla, 10°10'37.0"N, 85°21'09.6"W, 415 m, bosque húmedo premontano transición a basal, epífita sobre Myrtaceae, en bosque secundario, 11 julio 2005, *D. Bogarín 1666 y F. Paniagua* (JBL-spirit). BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, al lado derecho, en dirección a La Mantequilla, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, epífita en *Plumeria rubra* (Apocynaceae), 21 febrero 2006, *D. Bogarín 2598* (JBL-spirit).

16. ***Lalexia*** Luer, Harvard Pap. Bot 16(2): 358. 2011.
TYPE: *Lalexia quadrifida* (Lex.) Luer.

Loddigesia Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 251 (2006), *nom. illeg*.

Plants epiphytic, caespitose. *Stems* erect, enclosed by tubular sheaths, with an annulus. *Leaf* coriaceous, elliptical to oblong, acute, sessile or petiolate. *Inflorescence* apical, racemose, distichous, subcongested, produced from a papery spathe, multiflowered and longer than the leaf. *Flowers* resupinate, yellow to yellow-green, secund. *Sepals* connate in an ovate, obtuse, subcarinate, concave synsepal, *Petals* ovate, acute, concave. *Lip* obovate-pandurate, slightly arcuate, the margins irregular, basally truncate, the basal lobes rounded and erect, the midlobe rounded, obtuse. *Column* terete, slightly arcuate, footed, apically denticulate with a prominent clinandrium. *Anther*, apical. *Stigma* ventral. *Pollinia* 2, obovate. *Anther cap*, cucullate, with 2 cells.

A genus of one or two species ranging from Mexico to northern South America and the Antilles. One species in Costa Rica and at BHNP.

Lalexia quadrifida (La Llave & Lex.) Luer, Harvard Pap. Bot. 16(2): 358. 2011. Fig. 12C, 37.

Basionym: *Dendrobium quadrifidum* La Llave & Lex., Nov. Veg. Descr. 2 (Orch. Opusc.): 40–41. 1825. TYPE: Habitat supra arbores versus Jesus del monte, propé Vallisoletum. Floret Septembri, *J. J. M. de Lexarza s.n.* (Holotype: G).

Homotypic synonyms: *Humboltia quadrifida* (La Llave & Lex.) Kuntze, Revis. Gen. Pl. 2: 668. 1891.

Loddigesia quadrifida (La Llave & Lex.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 251. 2006. *Pleurothallis quadrifida* (La Llave & Lex.) Lindl., Edwards's Bot. Reg. 28: Misc. 70. 1842.

Stelis quadrifida (La Llave & Lex.) R. Solano & Soto Arenas, Icon. Orchid. (Mexico) 5–6: xi. 2003. *Specklinia quadrifida* (La Llave & Lex.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 263. 2004.

Heterotypic synonyms*:* *Pleurothallis racemiflora* Lindl. ex Lodd. Bot. Cab. 10: t. 949. 1824 [1825], *nom. illeg*.

Pleurothallis lyroglossa Schltr., Repert.Spec. Nov. Regni Veg. 8(191–195): 566. 1910. TYPE: COSTA RICA. [Guanacaste]: in den Wäldern von Nicoya, blühend im Dez 1899, *A. Tonduz s.n.* (Museo Nacional de Costa Rica) 13731 (Holotype: B, destroyed; Lectotype: designated by Luer, 2000, tracings of the original drawing of the holotype made under Schlechter's supervision: AMES).

Plants epiphytic, caespitose, up to 16 cm tall. *Roots* slender, up to 1 mm in diam., white with green tips. *Ramicaul* cylindrical, erect, stout, 1-leaved, up to 5 cm long, covered by papyraceous, tubular bracts, appressed bracts to 7 cm long. *Leaf* erect, glossy, glaucous-translucent adaxially, light green abaxially, oblong-elliptic to elliptic-obovate, obtuse, conduplicate, thick, somewhat arcuate, the base cuneate into a petiole, 5.0–13.0 × 1.8–2.5 cm. *Inflorescence* apical, racemose, distichous, subcongested, with 5–30 secund, simultaneous flowers, to 28 cm long, peduncle to 8 cm long, produced from a papery spathe up to 1.5 cm long. *Floral bracts* oblique acute, to 5 mm long. *Pedicel* 5 mm long, persistent. *Ovary* cylindrical, basally arcuate, sulcate, up to 5 mm long. *Flowers* resupinate, yellow to yellow-green, secund. *Dorsal sepal* ovate, acute, concave, glabrous, subcarinate, 0.7–1.2 × 0.4–0.5 cm. *Lateral sepals* connate in an ovate, obtuse, subcarinate, concave synsepal, 0.7–1.3 × 0.4–1.2 cm. *Petals* ovate, acute, concave, parallel to the column, 0.5–0.9 × 0.3–0.4 cm. *Lip* obovate-pandurate, slightly arcuate, the margins irregular, basally truncate, the basal lobes rounded and erect, the midlobe rounded, obtuse, the disc with 2 low, thick, keels running from the base up to the middle third, sulcate between the keels, hinged to the column foot, 4–6 × 2–3 mm. *Column* 3.0 × 0.8 cm, terete, slightly arcuate, footed, apically denticulate with a prominent clinandrium. *Anther*, apical. *Stigma*, ventral. *Pollinia* 2, obovate. *Anther cap*, cucullate, with 2 cells.

Distribution: from Mexico to Colombia, Venezuela, and the Antilles.

Distribution in the Park: they are found growing on *Syderoxylum capiri* (Sapotaceae), *Brosimum aliscastrum* (Moraceae), and *Spondias mombin*, along the trails El Mirador and La Ceiba, and along Las Cascadas and Bosque de Piedra.

Etymology: from the Latin *quadrifidus*, "four-divided, split into four," in allusion to perianth parts.

Habitat and ecology: epiphytic in tropical dry forest and tropical moist forest along the Pacific coast around Península de Nicoya, Cordillera de Tilarán, and Valle Central toward Península de Osa, at elevations from 100 to 1200 m.

Phenology: from December to April.

Discussion: characterized by the caespitose, erect plants without pseudobulbs, the slender, elongate, cylindrical stems with 1 oblong, fleshy, coriaceous, glaucous, translucent adaxially leaf, producing a lax inflorescence with completely yellow secund flowers. The flowers have a distinct synsepal, and the lip is distinguished by its panduriform shape (Luer, 2011). According to phylogenetic studies, this species is related to *Pleurothallis* R. Br. rather than to *Stelis* Sw., but it can also be recognized as a distinct genus (*Lalexia* Luer) because it forms an independent clade apart from *Pleurothallis* s.s. (Pérez-Escobar et al., 2017). If

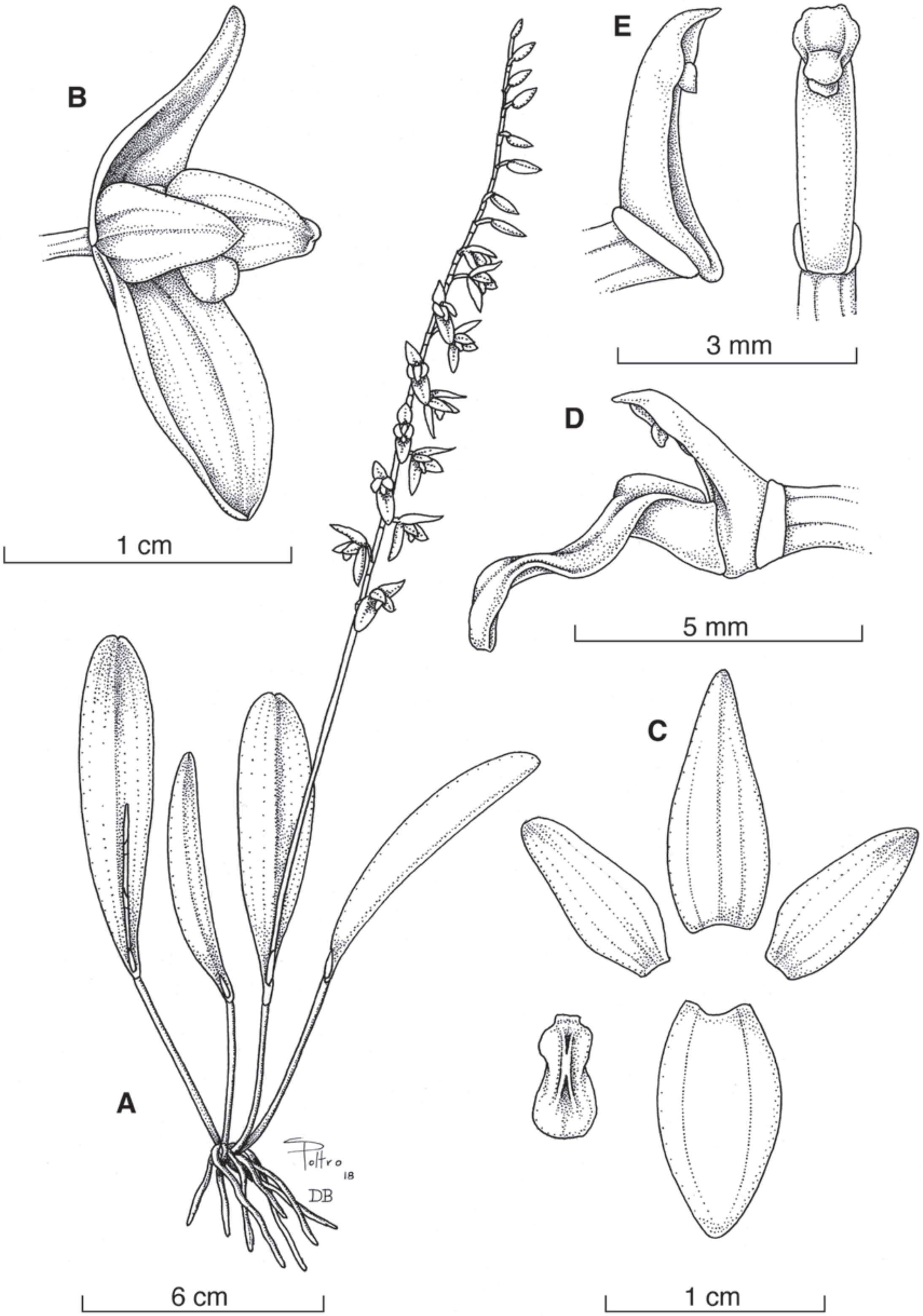

FIGURE 37. *Lalexia quadrifida* (La Llave & Lex.) Luer. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, side and ventral view. Drawn by D. Bogarín and S. Poltronieri from *Bogarín 1676* (JBL).

treated in *Pleurothallis*, it should be named as *Pleurothallis quadrifida* (Lex.) Lindl. The name *Pleurothallis racemiflora* (Sw.) Lindl. ex Hook. was applied to this species (Pupulin, 2002); however, it refers to a different species found in Cuba, the Dominican Republic, and Jamaica known as *Stelis multirostris* (Rchb.f.) Pridgeon & M.W. Chase. In addition, *Pleurothallis racemiflora* Lindl. ex Lodd. (=*Pleurothallis quadrifida* (Lex.) Lindl.) is illegitimate because *Pleurothallis racemiflora* (Sw.) Lindl. ex Hook. (=*Stelis multirostris*) has priority.

Additional specimens examined: Guanacaste: BHNP, Sendero Ceiba, sector de Las Cascadas, 10°11'15.0"N, 85°20'36.1"W, 210 m, bosque húmedo premontano transición a basal, epífitas en árbol caido de *Ficus* sp. (Moraceae), 11 julio 2005, *D. Bogarín 1676 y F. Paniagua* (JBL-spirit). BHNP, sector de Las Cascadas ingresando por Finca San Diego (Finca Los Trejos), 10°11'02.90"N, 85°20'20.02"W, 104 m, bosque húmedo premontano transición a basal, epífitas en árbol de Ojoche, *Brosimum alicastrum* (Moraceae), 7 noviembre 2011, *D. Bogarín 9406, Minor Díaz & Dorian Méndez* (JBL-spirit).

17. ***Leochilus*** Knowles & Westc., Fl. Cab. 2: 143. 1838.
TYPE: *Leochilus oncidioides* Knowles & Westc.

Plants small, caespitose, epiphytic herbs with short creeping rhizomes, often growing on twigs. *Pseudobulbs* ovoid, laterally compressed, more or less ancipitous, 1- to 2-foliate at apex, subtended by 1–2 foliaceous sheaths, often hidden. *Leaves* conduplicate, elliptic to oblong, subcoriaceous, articulate. *Inflorescence* lateral, a successively few- to many-flowered raceme or panicle. *Flowers* small, resupinate, greenish yellow usually striped with brown. *Sepals* and *petals* spreading, the lateral sepals variously connate. *Lip* simple or 3-lobed, oblong, the apex bilobed, provided near the base with a fleshy callus serving as an open nectary filled with oil. *Column* erect, nearly terete, footless, often provided with stigmatic arms. *Anther* terminal, operculate, incumbent. *Stigma* rounded, ventral. *Pollinarium* 2, waxy, yellow, pyriform. *Capsule* triangular, ellipsoid.

A Neotropical genus of about 12 species ranging from southern Florida through Mexico, Central America, the Antilles, and South America. Five species in Costa Rica and one at BHNP.

Leochilus scriptus (Scheidw.) Rchb. f., Xenia Orchid. 1(1): 15, t. 6. 1854. Fig. 12D, 38.

Basionym: *Cryptosanus scriptus* Scheidw., Allg. Gartenzeitung 11(13): 101. 1843. TYPE: [BRAZIL]. *Patria Brasilia. Dem habitus und der organisation der Blume nach würde diese Gattung ihre Stelle zwischen Maxillaria und Cymbidium finden* (Holotype: not stated).

Homotypic synonym: *Oncidium scriptum* (Scheidw.) Rchb. f., Ann. Bot. Syst. 6: 772. 1863.

Heterotypic synonym: *Leochilus retusus* Schltr., Repert. Spec. Nov. Regni Veg. Beih. 19: 256. 1923. TYPE: COSTA RICA. [Alajuela]. Arbres des haies au Maderal de San Mateo, alt. 400 m, Jan 1922; fleurs jaune-pâles, *A. M. Brenes 229* (Holotype: B, destroyed; Lectotype designated by Barringer,1986: CR-25897; Isolectotype: AMES).

Plant twig epiphyte, cespitose, to about 15 cm tall, with abbreviated rhizome. *Roots* fleshy, white with green vegetative apex, to 1 mm in diam. *Pseudobulbs* ovate to elliptic, laterally flattened, to 3.2 × 1.5 cm, basally covered by 2–3 leafy sheaths, monophyllous. Leaf linear to linear-elliptic, obtuse, conduplicate, slightly emarginate or unequally 2-lobed, coriaceous, contracted into a short petiole, to 10.0–12.0 × 1.2–2.0 cm. *Inflorescence* basal, to 16 cm long, 1- to many-flowered (mainly 3-flowered), arching, racemose or somewhat paniculate; peduncle terete; bracts triangular-lanceolate, acute, about 0.7 cm long. *Flowers* small, greenish yellow spotted with purple or reddish-brown markings on the petals and lip. *Dorsal sepal* elliptic-obovate, free, concave, acute, keeled on the reverse surface, to 5.5–6.0 × 0.3–0.4 mm. *Lateral sepals* obliquely elliptic-obovate, conduplicate, spreading and somewhat reflexed apically, acute to slightly apiculate, to 7.0 × 0.3 mm. *Petals* linear or ovate-oblong, somewhat conduplicate, apiculate, parallel to the column, to 6.0–7.0 × 3.0–3.5 mm. *Lip* obovate, obtuse, the apex somewhat retuse, flat, spreading or slightly concave, with a small, concave nectary at the base provided with pilose margins; callus trapezoidal, with a central papillose groove and 2 distinct parallel, fleshy, puberulent calli running up to the half of the lip; entire lip 9 × 5 mm. *Column* short, with a pair of triangular, acute, ligular, porrect stigmatic arms, to 2.5 mm long. *Pollinia* 2, subspherical, on a short, ligulate stipe; viscidium peltate, brown. *Anther cap* hemiglobose, 2-celled.

Distribution: from Mexico to northern South America and the Antilles.

Distribution in the Park: plants are easily found growing on insolated trees in pastures surrounding the Park, mostly on twigs of old calabash trees. A population was located between Millal and Caballito, on the eastern boundary of PBNH.

Etymology: from the Latin *scriptus*, "written," in allusion to the petals' marks.

Habitat and ecology: a twig epiphyte of tropical moist and tropical wet forest along the Caribbean and Pacific lowlands from 100 to 1200 m of elevation. It is commonly found on twigs of *Crescencia cujete*, *Codiaeum variegatum* (Euphorbiaceae), *Trichilia havanensis* (Meliaceae), or *Hibiscus* L. sp. (Malvaceae) fences in disturbed areas, gardens, or insolated trees. It is pollinated by two species of Polybiine wasps: *Stelopolybia areata* and *S. hamiltoni* (Chase, 1986).

Phenology: plants flower mostly from October to January, but may throughout the year.

Discussion: plants are distinguished by the monophyllous laterally flattened pseudobulbs, basally covered by 2–3 leafy sheaths and the racemose or paniculate inflorescences with small green-yellow flowers, spotted with red-brown. The seedlings are fan-shaped.

Additional specimens examined: Guanacaste: Nicoya, San Antonio, camino entre Millal y Caballito, en finca limítrofe al Parque Nacional Barra Honda, 10°13'11.27"N,

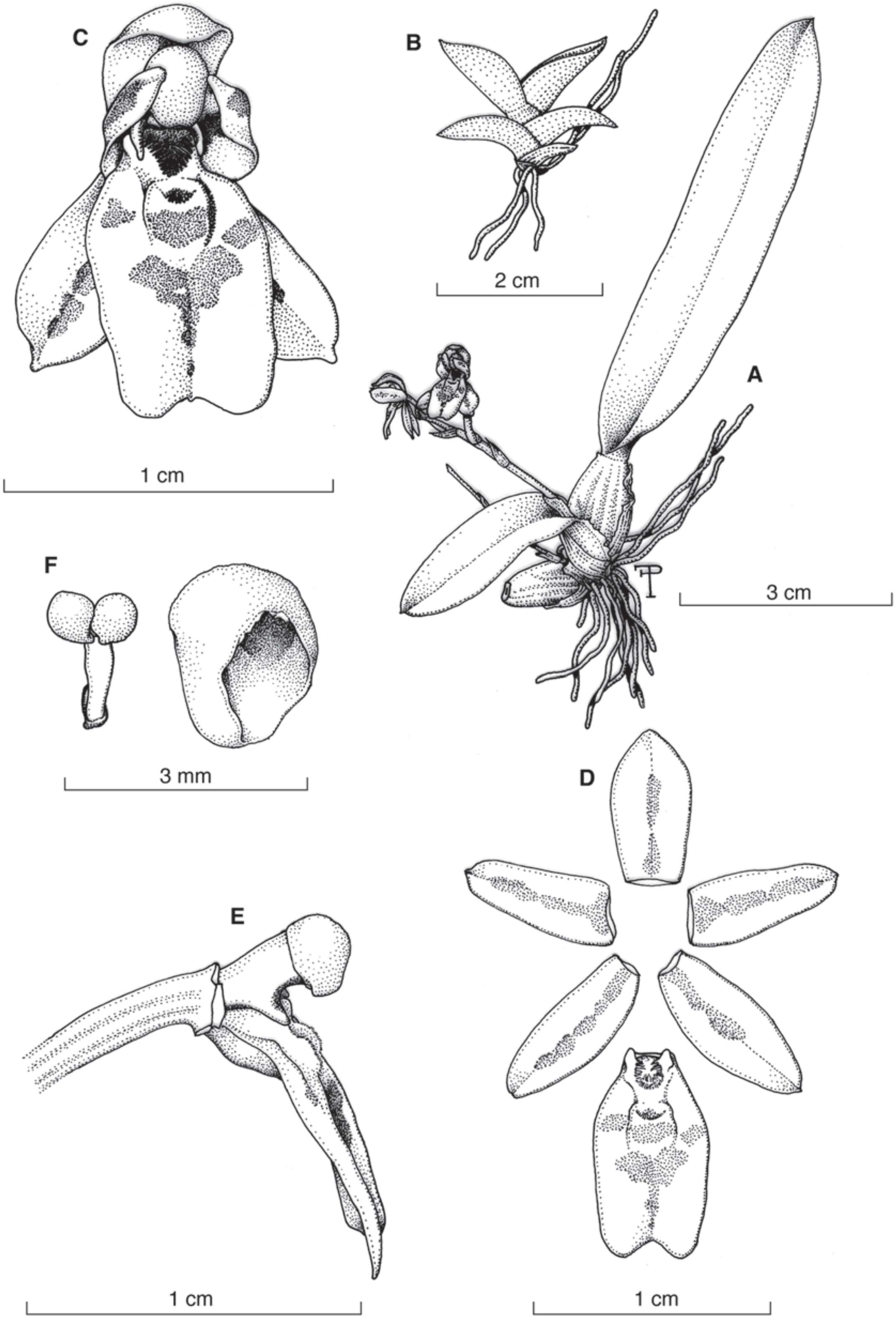

FIGURE 38. *Leochilus scriptus* (Scheidw.) Rchb.f. **A,** Habit. **B,** Juvenile plant. **C,** Flower. **D,** Perianth flattened. **E,** Column and lip, side view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 374* (JBL).

85°19'53.94"W, 16 m, epífita sobre ramitas de *Crescentia cujete* (Jícaro) en bosque húmedo premontano transición a basal, 4 noviembre 2011, *D. Bogarín 9385* (JBL-spirit).

18. ***Lophiaris*** Raf., Fl. Tellur. 4: 40–41. 1836[1838].
TYPE: *Lophiaris lanceana* (Lindl.) Braem.

Plants epiphytic or lithophytic caespitose herbs. *Pseudobulbs* short, subglobose, 1-leaved. *Leaf* conduplicate, fleshy, abaxially keeled, often spotted with red or purple, suberect, or pendant. *Inflorescences* lateral from the base of the pseudobulbs, paniculate or racemose. *Flowers* showy, resupinate, spreading, red, purple, yellow, or white with red or maroon spots or blotches. *Sepals* and *petals* subsimilar, clawed, often spotted with red-brown, crisped-undulate. *Lip* 3-lobed, the midlobe larger than the laterals with the callus made up of small teeth or protuberances, often spotted. *Column* short, cylindrical, the stigmatic surface suborbicular, usually with small horns or wings at each side and a tabula infrastigmatica. *Anther* terminal, operculate. *Pollinarium* 2, yellow, obpyriform, with stipe and viscidium.

A Neotropical genus of about 25 species distributed from Florida (USA) and Mexico to South America and the Antilles. One species in Costa Rica and BHNP.

Lophiaris oerstedii (Rchb. f.) R. Jiménez & Carnevali, Harvard Pap. Bot. 5(2): 423. 2001. Fig. 12E, 39.

Basionym: *Oncidium oerstedii* Rchb.f., Bonplandia (Hanover) 2(7): 91. 1854. *nom. cons. prop*. TYPE: Unzweifelhaft die schönste Entdeckung des Hrn. Dr. Oersted, *A. S. Oersted s.n.* (Holotype: W). *Oncidium carthagenense var. oerstedii* (Rchb. f.) Lindl., Fol. Orchid. Oncidium 40. 1855.

Homotypic synonyms: *Trichocentrum oerstedii* (Rchb. f.) R. Jiménez & Carnevali, Icon. Orchid. (Mexico) 5–6: ix. 2002 [2003].

Plants epiphytic, cespitose, pendent to suberect, up to 45 cm long with abbreviated rhizome. *Roots* up to 2 mm in diam., white with green tips. *Pseudobulbs* oblate to globose or broadly ovoid, short, 1.2 × 1.4 cm, unifoliate, enclosed by 4 imbricate, conduplicate papyraceous sheaths 2.5–4.5 × 2.0–2.8 cm. *Leaves* fleshy-coriaceous, elliptic-oblong to obovate, 37.2–42.3 × 7.4–7.7 cm, dark green matte, purple-spotted, conduplicate, abaxially keeled, acute, petiole to 4 cm. *Inflorescence* basal, lateral, racemose or paniculate, erect to arched, up to 120 cm long with 7 or more branches, the branches 3- to 7-flowered, peduncle bracts 6–8 × 3–5 mm, lanceolate, acute; bracts subtending the lateral branches similar, broadly lanceolate-ovate, acute, to 8 mm long; floral bracts 1.5–4.0 × 1.0–1.5 mm, triangular-ovate, acute. *Ovary* pedicellate, cylindric, to 25 mm long. *Flowers* resupinate, medium-sized for the genus, white-spotted and blotched with reddish purple, the lip white stained with reddish purple, basally tinged with yellow, the callus pink, the column stained with brown with the tabula infrastigmatica yellow, the wings white stained with pink. *Dorsal sepal* unguiculate, spathulate, suborbicular to ovate, obtuse, 11.7 × 9.2 mm. *Lateral sepals* unguiculate, ovate to oblong, subacute, 12.8 × 6.2 mm. *Petals* unguiculate, ovate to oblong, obtuse, undulated, 10.0 × 8.8 mm. *Lip* deeply 3-lobed, pandurate, 10.7 × 11.0 cm, the lateral lobes shorter than the midlobe, ovate, obtuse, the midlobe reniform, retuse, somewhat bilobate, undulate, the isthmus 3.5 × 4. 0 mm, the disc 4.5 × 3.7 mm, a callus made up by 4 tuberculate protuberances and a central tuberculate keel. *Column* to 5.7 mm long, thick basally, with 2 stigmatic, reniform wings, with a sulcate tabula infrastigmatica. *Pollinarium* 2, obpyriform, cleft, the stipe suborbicular with 2 pointed projections, viscidium rounded, yellow. *Anther cap* cucullate, operculate, papillose, white stained with purple.

Distribution: from Mexico to Costa Rica, perhaps ranging to western Panama.

Distribution in the Park: found at Las Cascadas in the humid gallery forest.

Eponymy: named after its discoverer and collector, the Danish botanist Anders Sandøe Ørsted (1816–1872).

Habitat and ecology: epiphytic on main tree trunks or in lower branches in the humid evergreen forest close to streams, lagoons, or rivers in shady conditions.

Phenology: plants flower from October to November.

Discussion: among the orchids of BHNP, *Lophiaris oerstedii* can be easily recognized even when not in flower by the large, conduplicate, thick-succulent leaves borne on a small, rudimentary pseudobulb. Fertile specimens are unmistakable by the long, paniculate inflorescences with several white, purple-speckled flowers.

Cetzal-Ix and Balam Narvaez (2012) and Cetzal-Ix and collaborators (2016) treated what they considered the only species of *Lophiaris* from Costa Rica as *L. crispiflora* (Schltr.) Balan & Cetzal, a taxon supposedly ranging from eastern Honduras through Caribbean Nicaragua and Costa Rica to northwest Panama (the type specimen from Panama City, Margin of the Pacific Ocean, *Powell 1*). On the other hand, they treated *L. oerstedii* (Rchb.f.) R. Jiménez, Carnevali & Dressler, originally described from a Nicaraguan collection by A. Oersted, as restricted to the countries north of Costa Rica, where it spans to northwestern Mexico.

We were tempted, following the Cetzal-Ix and Balam Narvaez (2012) and Cetzal-Ix et al. (2016) proposal, to treat the Caribbean populations as *Lophiaris crispiflora* (comparing them with the recorded distribution of this taxon in Caribbean Nicaragua and Honduras) and regarding those confined to the Pacific side of the continental divide as *L. oerstedii*. However, from a phytogeographic point of view, the Caribbean lowlands of Nicaragua, which drain into the San Juan River, are indistinguishable from the seasonal, Pacific plains of Guanacaste in northern Costa Rica, which are separated from the humid region of the Caribbean by a chain of high volcanoes that loses elevation toward the northwest. Also, from a morphological point of view, our observations do not support designating populations from the Pacific and the Caribbean watersheds as belonging to different species. If a single species alone of *Lophiaris* has to be named in the flora of Costa Rica, we favor the use of *L. oerstedii*, which is the oldest available name. The fine, colored illustration of a flower made by Oersted of his Nicaraguan collection of the type looks precisely the same as the flowers that we documented from populations found at BHNP.

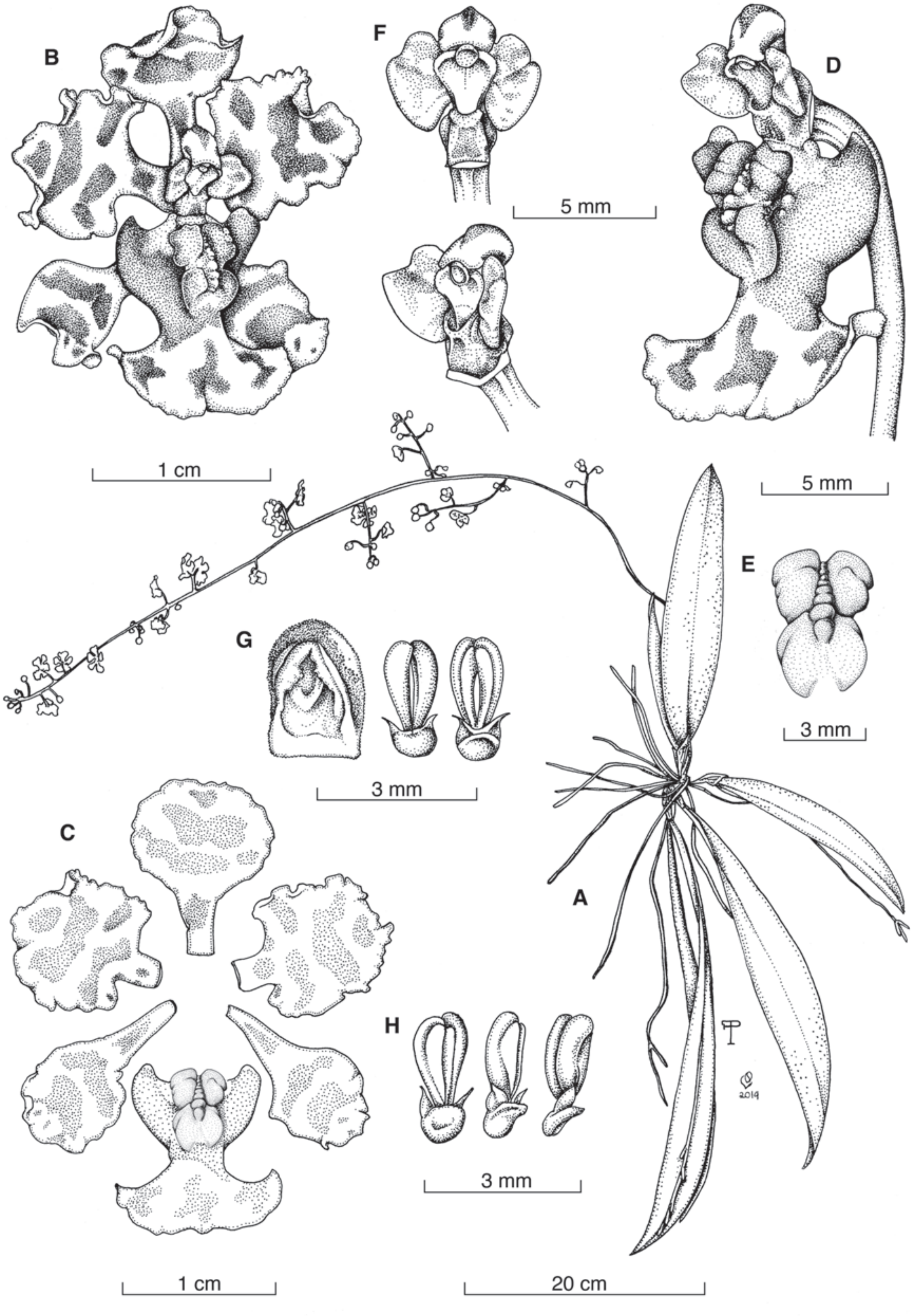

Figure 39. *Lophiaris oerstedii* (Rchb.f.) R. Jiménez, Carnevali & Dressler. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Lip callus, detail of tuberculate protuberances. **F,** Column, side and ventral view. **G,** Pollinarium and anther cap. Drawn by F. Pupulin, inked and rendered by L. Oses from *Pupulin 8189* (JBL).

Additional specimens examined: BHNP, Las Cascadas (the waterfalls), entering from Finca San Diego (Finca Los Trejos), 10°10'59.86"N, 85°20'17.41"W, 86 m, premontane moist, transition to tropical moist forest, epiphytic in gallery forest on *Brosimum alicastrum* "Ojoche" (Moraceae) close to a stream, 22 February 2012, *F. Pupulin 8189 & D. Bogarín* (JBL-spirit).

19. *Malaxis* Sol. ex Sw., Prodr. 8, 119. 1788.
TYPE: *Malaxis spicata* Sw.

Plants terrestrial or rarely epiphytic, rhizomatous, often creeping, or with globose corms or conic-ovoid pseudobulbs. *Leaves* 1–3, ovate, oblong or cordate, not articulated, petiolate, with the sheath embracing the base of the inflorescence. *Inflorescence* a few- to many-flowered subcorymbose, subumbellate or elongate raceme, terminal, erect, unbranched, with persistent floral bracts. *Flowers* inconspicuous, resupinate or not, generally green or brownish. *Sepals* free or with the lateral sepals connate, spreading, broader than petals. *Petals* narrowly linear to filiform. *Lip* sessile, usually on the upper part of the flower, erect or spreading, entire or lobed above and auriculate below, concave with a basal cavity. *Column* very short, terete, lacking a foot. *Anther* terminal, suberect or incumbent. *Pollinia* 4, without caudicles. *Capsule* small, ovoid.

A cosmopolitan genus of nearly 300 species, mostly in Asia and Oceania. About 20 species in Costa Rica, 1 in BHNP.

Malaxis aurea Ames, Schedul. Orch. 5: 3, f. 1. 1923. Fig. 12F, 40.
TYPE: COSTA RICA. Cartago. Las Cóncavas, flowers apricot-yellow, leaf and rachis yellowish oil-green, *C. Lankester 346* (Holotype: K).

Plants terrestrial, up to 22 cm high, with an underground monophyllous, deciduous, white corm, and abbreviated rhizome, 1.7 × 1.8 cm. *Roots* slender, filiform, up to 1 mm in diam., white to gray. *Pseudobulbs (corms)* hypogeous or among the organic litter, subglobose, ovoid, covered by leafy bracts, up to 1.0 × 1.2 cm; petiole tubular, up to 12 cm long. Leaf ovate, cordate to auriculate at the base where it clasps the peduncle, abaxially keeled, with a conspicuous midvein and several parallel secondary veins, entire, subacute to obtuse, 3.8–10.0 × 4.0–6.2 cm. *Inflorescence* apical, subumbellate, supported by a sulcate peduncle of 12 cm long, rachis 8 mm with several helical flowers, opening successively. *Floral bracts* to 1 mm long, green, shorter than the slender pedicels. *Ovary* to 1.3 mm long. *Flowers* small, not resupinate, to 5.1 mm long, light green to yellow with age. *Dorsal sepal* oblong-elliptic to linear-ovate, obtuse, with the margins recurved or strongly coiled in natural position, 2.6 × 1.3 mm. *Lateral sepals* subsimilar to the dorsal sepal, obovate-elliptic to oblong-elliptic, acute, with margins recurved, strongly coiled in natural position, 2.5 × 1.5 mm. *Petals* linear-filiform, oblong, obtuse to acute, strongly reflexed with the tips connivent, 2.0 × 0.2 cm. *Lip* thick, subcordate to broadly ovate, complanate-concave, inflexed, with a thick rostrate apicule to 0.6 mm long, and 2 holes at the base forming a groove in the center, 1.6 × 2.0 cm. *Column* small, inconspicuous, 0.5 × 0.6 mm. *Pollinia* 4, ovoid. *Anther cap* cucullate. *Capsule* ellipsoid, 6 × 3 mm, valved.

Distribution: from Mexico to Costa Rica.

Distribution in the Park: plants grow terrestrially among organic litter and dead leaves between calcareous rocks in the shade in the rocky cactus forest at Cerro Barra Honda and Las Delicias.

Etymology: from the Latin *aureus*, "golden yellow," in allusion to the color of the flowers.

Habitat and ecology: terrestrial in tropical wet and moist forest and premontane wet forest from 300 to 1500 m of elevation along the Cordilleras de Guanacaste and Tilarán, Reventazón Valley and Las Cóncavas, Cartago. Plants are deciduous during the dry season when the basal corms are still alive until the beginning of the wet season when they start to develop new leaves and inflorescences.

Phenology: plants flower from July to September.

Discussion: plants are terrestrial with ovoid, unifoliolate pseudobulbs hidden under the ground or organic litter, the leaf blade is cordate, and the inflorescence is apical, subumbellate, with green-yellow flowers opening successively. At BHNP, it is the only terrestrial species with unifoliolate pseudobulbs and apical inflorescences.

Additional specimens examined: BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, terrestres en sitio rocoso con hojarasca, 26 Julio 2005, *D. Bogarín 1755 y F. Paniagua*. BHNP, Cerro Corralillo, Sector Las Delicias, en bosque al final de las plantaciones de frijol, 10°11'11.82"N, 85°21'09.28"W, 481 m, terrestre entre rocas y materia orgánica en bosque húmedo premontano transición a basal, 5 noviembre 2011, *D. Bogarín 9397 & E. Artavia* (JBL-spirit). Same locality, *D. Bogarín 9398 & E. Artavia* (CR).

20. *Maxillariella* M.A.Blanco & Carnevali, Lankesteriana 7(3): 527–528. 2007.
TYPE: *Maxillariella diuturna* (Ames & C. Schweinf.) M.A. Blanco & Carnevali.

Plants epiphytic, rhizomatous, cespitose (rarely subcespitose), erect, suberect, or hanging. *Rhizome* elongated, covered by several bracts. *Pseudobulbs* ovoid, laterally flattened, rarely reduced or even absent, separated by the rhizome segments, sometimes covered by foliaceous sheaths and scarious bracts. *Leaves* 1–2, linear-elliptic to oblong, conduplicate, developed at the apex of the pseudobulbs. *Inflorescence* 1-flowered, produced from each leaf or bract axil. *Floral bract* shorter than the pedicel and ovary. *Flowers* small to medium size, resupinate, campanulate, white, red, yellow, or orange, sometimes spotted with purple or red. *Sepals* free, oblong, acute to obtuse. *Petals* oblong, acute. *Lip* simple or obscurely 3-lobed with a glossy callus. *Column* terete, with a very short column foot. *Anther* apical. *Pollinia* 2, with caudicles. *Capsule* small, ovoid with lateral dehiscence.

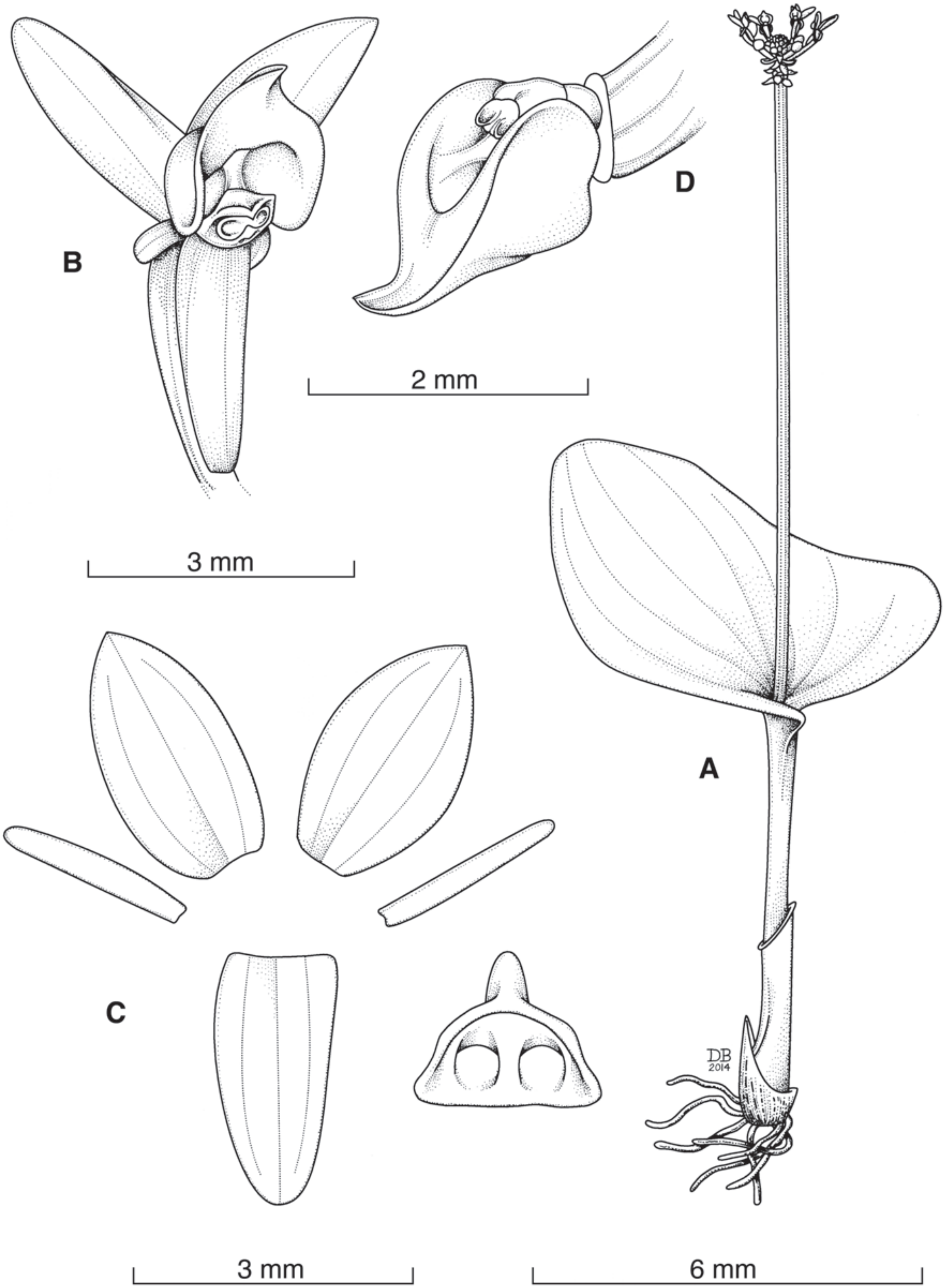

FIGURE 40. *Malaxis aurea* Ames. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. Drawn by D. Bogarín from *Bogarín 1755* (JBL).

A Neotropical genus of nearly 50 species, from Mexico and Central America to Peru and Brazil. About 15 species in Costa Rica, 1 in BHNP.

Maxillariella acervata (Rchb. f.) M.A. Blanco & Carnevali, Lankesteriana 7(3): 528. 2007. Fig. 12G, 41.

Basionym: *Maxillaria acervata* Rchb.f., Bonplandia 3:217.1855. TYPE: [COSTA RICA. Alajuela: San Mateo, Surubres]: Ad Surungnes in Costarica, *A. Oersted s.n.* (Holotype: W; Isotype: K).

Plants epiphytic, cespitose, pendent to suberect, straggly, to about 25 cm long. *Roots* filiform, slender, glabrous, emerging at the base of the plant or from the rhizome at the connection of old and new pseudobulbs, 0.5–1.0 mm in diam. *Pseudobulbs* unifoliate, ovoid, laterally flattened, separated by an elongate rhizome, 1.4–3.0 × 0.6–1.2 cm, rhizome internodes 1.5–2.0 cm long, covered by scarious, imbricate papyraceous, conduplicate sheaths 1.1 × 0.6 cm. *Leaves* 1 leaf at the apex of each pseudobulb, linear to narrowly oblong, obliquely retuse, conduplicate, subcoriaceous, 7.5–9.0 × 0.5–0.7 cm, basal leaves articulated with the sheaths surrounding the base of the pseudobulb, linear, 4.5–5.5 × 0.5–0.7 cm. *Inflorescence* 1-flowered, borne at the base of each pseudobulb. Pedicel to 7.5 mm long. *Ovary* pedicellate, linear, to 1 cm long. *Floral bracts* ovate-elliptic, acute, to 8 mm long. *Flowers* small, to 1.3 cm in diam., the sepals and petals creamy yellow rarely with pale red stains, the lip with a purple blotch at base, the apex yellow, the column yellowish with purple spots. *Dorsal sepal* oblong-elliptic, acute, conduplicate, slightly concave toward the apex, 11.0 × 3.5 mm. *Lateral sepals* free at base, elliptic, acute, conduplicate, subfalcate, 11.0 × 3.5 mm. *Petals* elliptic, acute, subfalcate, slightly conduplicate, 8.0 × 2.5 mm. *Lip* obscurely 3-lobed, ovate; lateral lobes rounded erect in natural position; midlobe oblong, obtuse to emarginate or somewhat truncate; the callus oblong, glossy, running just before the mid, entire lip 8.0 × 4.5 mm between the lateral lobes. *Column* terete, arcuate, dilated and ciliate at apex, to 6 mm long. *Pollinia* 2, ovoid, cleft, on a horseshoe-like stipe. *Anther cap* cucullate, rounded, ciliate at apex, 2-celled.

Distribution: known only from Costa Rica.

Distribution in the Park: found at Cerros de Jesús on a fallen branch, and likely found at Las Cascadas and Los Mesones in Barra Honda.

Etymology: from the Latin *acervatus*, “heaped,” in allusion to the cespitose habit with crowded pseudobulbs and short rhizomes.

Habitat and ecology: plants grow epiphytically in the canopy of tall trees in evergreen tropical moist forest and tropical dry forest, moist province transition along rivers and streams in the lowlands of the Pacific watershed. Common on *Anacardium excelsum* and *Pachira quinata*.

Phenology: plants flower mostly from May to October.

Discussion: easily distinguished by the crowded caespitose plants with ovoid, flattened pseudobulbs separated by short rhizomes. The pseudobulbs are unifoliate at apex, subtended by foliaceous sheaths at base; the leaves are linear-ligulate. The flowers are inconspicuous, cream with a yellow lip with purple at the base and acute sepals and petals.

Additional specimens examined: Guanacaste: Nicoya, Mansión, Zona Protectora Cerros de Jesús, 10°05'41.71"N, 85°18'59.58"W, 370 m, bosque húmedo premontano transición a basal, epífita en bosque secundario maduro sobre una quebrada estacional con árboles altos, 23 febrero 2012, *D. Bogarín 9520 y F. Pupulin* (CR).

21. *Oeceoclades* Lindl., Edwards’s Bot. Reg. 18: sub t. 1522. 1832; et Gen. et Sp. Orch. 235. 1833.

TYPE: *Oeceoclades maculata* (Lindl.) Lindl.

Plants terrestrial, caespitose, rarely lithophytic. *Roots* basal, thick. *Pseudobulbs* 1- to 3-leaved apically, heteroblastic, cylindrical, fusiform, conical, or ovoid. *Leaves* linear-lanceolate, ovate or elliptic, acute to acuminate, conduplicate, coriaceous or plicate, articulate at the base, usually petiolate, green, or maculate with light and dark green. *Inflorescence* lateral, usually exceeding leaves, simple or branching, bracts inconspicuous, persistent. *Ovary* cylindrical, grooved. *Flowers* spread, relatively small and showy, white, yellow, green, or brown, sometimes purple striped. *Sepals* free obovate, spathulate oblique at the base. *Petals* free, subequal to sepals, obovate to elliptic-oblong, often broader than sepals. *Lip* free to base, trilobed, basally spurred, the callus thickened at the spur entrance or with parallel ridges, lateral lobes free to base of column, midlobe flat, or convex. *Column* relatively short, with a distinct foot. *Pollinia* 2, ovoid or pyriform.

A genus of about 50 species native to Africa, Madagascar, and tropical Asia. *Oeceoclades maculata* is naturalized and widespread in the Neotropics, ranging from Florida to Brazil and the Antilles. One species in Costa Rica and BHNP.

Oeceoclades maculata (Lindl.) Lindl., Gen. Sp. Orchid. Pl. 237–238. 1833. Fig. 12H, 42.

Basionym: *Angraecum maculatum* Lindl., Coll. Bot. 3: pl. 15. 1821. TYPE: Messrs. Loddiges sent it to us in the middle of last December. Messrs. Loddiges informs us that they are uncertain from what quarter they received it, but they think from South America (Holotype: K).

Homotypic synonyms: *Limodorum maculatum* (Lindl.) Lodd., Bot. Cab. 5: t. 496. 1821.

Aerobion maculatum (Lindl.) Spreng., Syst. Veg. 3: 718. 1826.

Eulophia maculata (Lindl.) Rchb.f. in W.G.Walpers, Ann. Bot. Syst. 6: 647. 1863.

Eulophidium maculatum (Lindl.) Pfitzer, Entwurf. Anordn. Orch.: 87. 1887.

Graphorkis maculata (Lindl.) Kuntze, Revis. Gen. Pl. 2: 662. 1891.

Plants terrestrial, caespitose, up to 24 cm tall. *Roots* thick, up to 7 mm in diam., whitish with yellow tips, pilose. *Pseudobulbs* ovoid, sulcate, heteroblastic, covered by papyraceous bracts, evident in young pseudobulbs, eventually deciduous, with 1 at the apex, 4.0 × 2.2 cm. *Leaves* obovate to elliptical, dark green with conspicuous light green irregular macules, cuneate, petiolate, conduplicate, coriaceous, acute, entire, 10–32 × 4.5–5.2 cm. *Inflorescence* lateral, basal, racemose or rarely paniculate or branched, distichous, covered by tightly appressed tubular bracts, to

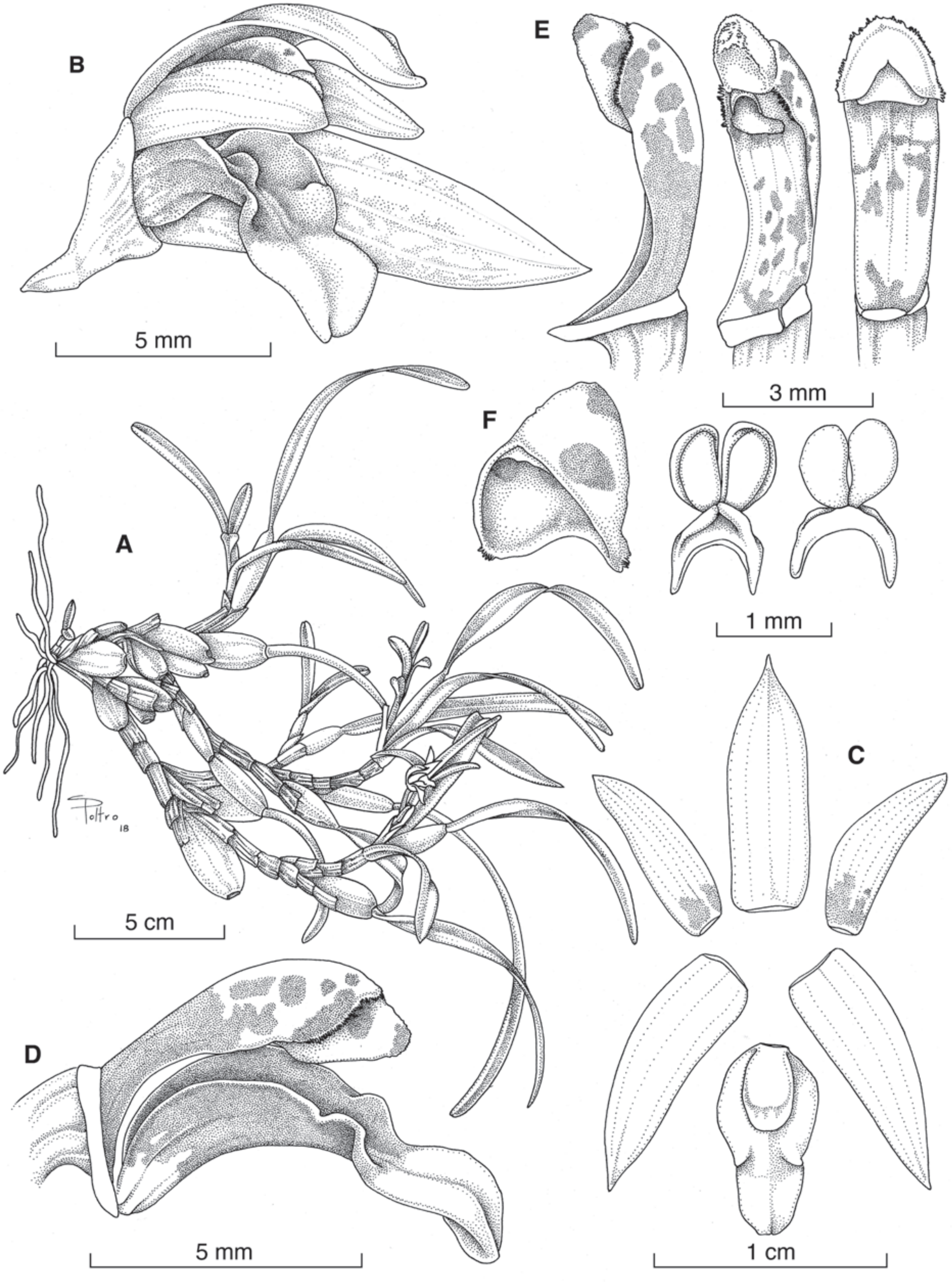

FIGURE 41. *Maxillariella acervata* (Rchb.f.) M.A. Blanco & Carnevali. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, side and ventral view. **F,** Pollinarium and anther cap. Drawn by D. Bogarín and rendered by S. Poltronieri from *Bogarín 9523* (JBL).

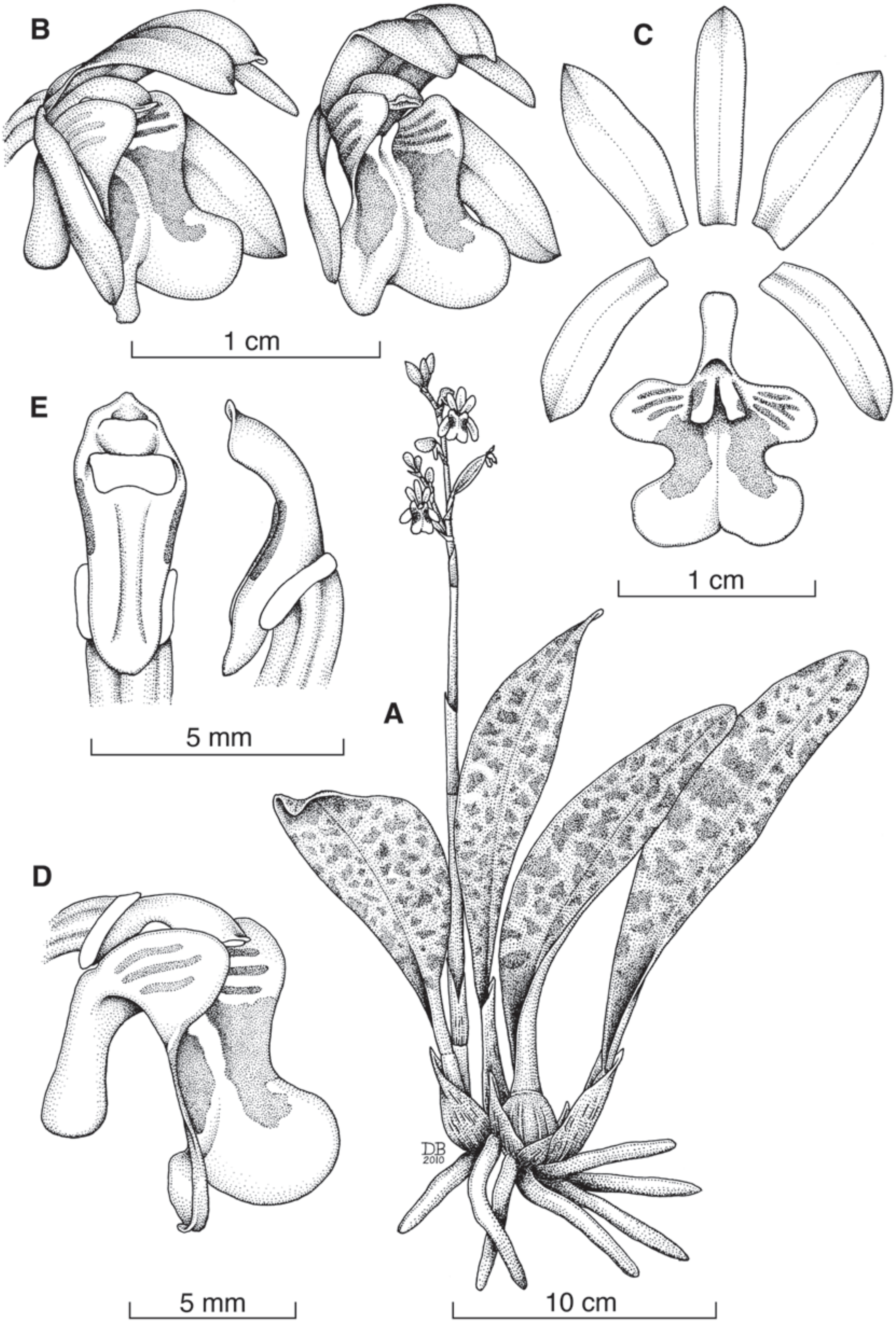

FIGURE 42. *Oeceoclades maculata* (Lindl.) Lindl. **A,** Habit. **B,** Flower, two views. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, side and ventral view. Drawn by D. Bogarín from *Bogarín 1729* (JBL).

11 flowers, up to 10–45 cm long, usually exceeding the leaves, with several flowers opening at once (rarely 1–2 open), rachis 7–14 cm. *Ovary* cylindrical, up to 0.5 cm long. *Flowers* small and rather showy, resupinate, up to 1.5 cm, white with the lip white with pink spots and stripes at the basal lobes, spurred. *Dorsal sepal* oblong-elliptic to spathulate, obtuse to acute, conduplicate, free, concave, and rather arcuate, 1.3 × 0.2 mm. *Lateral sepals* subfalcate oblong, acute, conduplicate, free, spread, 1.0 × 0.3 cm. *Petals* obovate, elliptic, acute, free, rather arcuate and connivent with the dorsal sepal, 1.0 × 0.4 cm. *Lip* 3-lobed or deeply panduriform, retuse, conduplicate, provided with a basal rounded, arcuate spur shorter than the blade, the basal lobes parallel and arching toward the column, the midlobe somewhat spread, with a bifid thickened forked callus at the base near the spur entrance, 1.3 × 1.0 cm. *Column* rostrate, concave, widened apically, arcuate, with the foot adnate to the lip, 5.6 × 2.0 mm. *Pollinia* 2, obovate. *Anther cap* cucullate. *Capsule* 3.0 × 1.5 cm, 6-valved.

Distribution: native to Africa but widespread in the Neotropics from Florida (USA) to Argentina and the Antilles. In Costa Rica, it is found along the humid, warm lowlands of the Pacific, Santa Rosa, Guanacaste to Corcovado, Puntarenas and Valle Central, and the Caribbean plains under 900 m.

Distribution in the Park: widespread and abundant at Cerro Barra Honda, Las Delicias, and Las Cascadas, and along the main trails of the Park.

Etymology: from the Latin *maculatus*, "spotted, blotched," in allusion to the conspicuously blotched leaves.

Habitat and ecology: plants grow terrestrially among organic litter and humus in shady conditions, mostly moist to wet understory forests. It is widespread in the Neotropics, where it is considered one of the most successful invasive orchid species (Cohen and Ackerman, 2009). Plants are autogamous and produce many capsules, thus explaining its success in colonizing many areas of the Neotropics. It was first recorded in Costa Rica around 2000.

Phenology: plants flower throughout the year but mostly from August to November. Capsules were observed from November to March.

Discussion: easily distinguished by the terrestrial plants with clustered pseudobulbs and one apical dark green leaf, irregularly maculated with light green. The inflorescences are racemose with small, white flowers stained with pink. They form large populations of several clustered individuals.

Additional specimens examined: BHNP, bifurcación del camino en Sendero Ceiba y Mirador, 10°10'25.4"N, 85°21'40.1"W, 410 m, bosque húmedo premontano transición a basal, terrestres a orillas del camino, bosque secundario, 23 julio 2005, *D. Bogarín 1729 y F. Paniagua* (JBL-spirit). BHNP, camino principal de la estación al Sendero Ceiba, parte alta antes de llegar al parqueo, 10°10'21.53"N, 85°21'42.50"W, 342 m, bosque húmedo premontano transición a basal, terrestres orillas del camino, bosque secundario, 7 noviembre 2011, *D. Bogarín 9422* (CR).

22. *Pelexia* Poit. ex Rich., De Orchid. Eur. 37. 1817 [Aug–Sep 1817]; preprint from Mém. Mus. Natl. Hist. Nat. 4: 59. 1818.
TYPE: *Pelexia adnata* (Sw.) Spreng.

Plants terrestrial, often epiphytic with abbreviated stems. *Roots* fleshy, fusiform, fasciculate. *Leaves* arranged in the basal rosette, petiolate, the petiole narrow, the leaves present at flowering but often deciduous. *Inflorescence* slender, erect, covered by several tight sheaths, the rachis loosely or densely few- to many-flowered. *Flowers* small to large, white or green, erect, arcuate, tubular basally forming a nectary adnate to the ovary, spurred, usually green to greenish or white-colored. *Sepals* connate in the lower part, usually pubescent or glandular, lateral sepals arcuate, decurrent with the ovary forming a spur. *Petals* linear, usually oblong-ovate to lanceolate, falcate. *Lip* clawed, arcuate apically, constricted below the apex, widest apically, with basal auricles, entire or crenulate, spurred. Spur adnate to the ovary, rounded or acute. *Column* part shorter than the anther, footed, cuniculate. *Anther* erect, flattened, 2-chambered. *Pollinia* 4, powdery.

A Neotropical genus of about 70 species ranging from Florida (USA) to Mexico, Central and South America, and the Antilles. About 4 species in Costa Rica and 1 in BHNP.

KEY TO THE COSTA RICAN SPECIES OF *PELEXIA*

1a. Flowers small, the lip <10 mm long . . . . *P. obliqua*
1b. Flowers large, the lip >20 mm long 2
2a. Spur subequal to the ovary length 3
2b. Spur up to half the length of the ovary 4
3a. Apex of spur obtuse to rounded; lip with a distinct isthmus between hypochile and epichile . . . . *P. barrahondaensis*
3b. Apex of spur acute; the apex of the hypochile reaching the base of the epichile or overlapping it . . . . . . *P. maculata* (doubtful in Costa Rica)
4a. Apex of spur rounded . . . . *Pelexia laxa*
4b. Apex of spur acute 5
5a. Spur ca. 10 mm . . . . *P. funkiana*
5b. Spur ca. 3 mm . . . . *P. congesta*

Pelexia barrahondaensis Bogarín & Pupulin, *sp. nov.* Fig. 12I, 43–44.
TYPE: COSTA RICA. Guanacaste: Nicoya, San Antonio, Parque Nacional Barra Honda, Cerro Corralillo, Sector Las Delicias, in the forest at the upper end of bean plantations and "jaragua" pastures, 10°11'11.19"N, 85°21'08.46"W, 438 m, terrestrial among rocks and organic materials in premontane moist, transition to tropical moist forest, 24 February 2012, *F. Pupulin 8198, D. Bogarín and S. Villagra* (Holotype: JBL-spirit; Isotype: CR).

Species floribus turpiter similis illis Pelexiae gutturosae (Rchb.f.) Garay *per labium isthmo rectangularis inter*

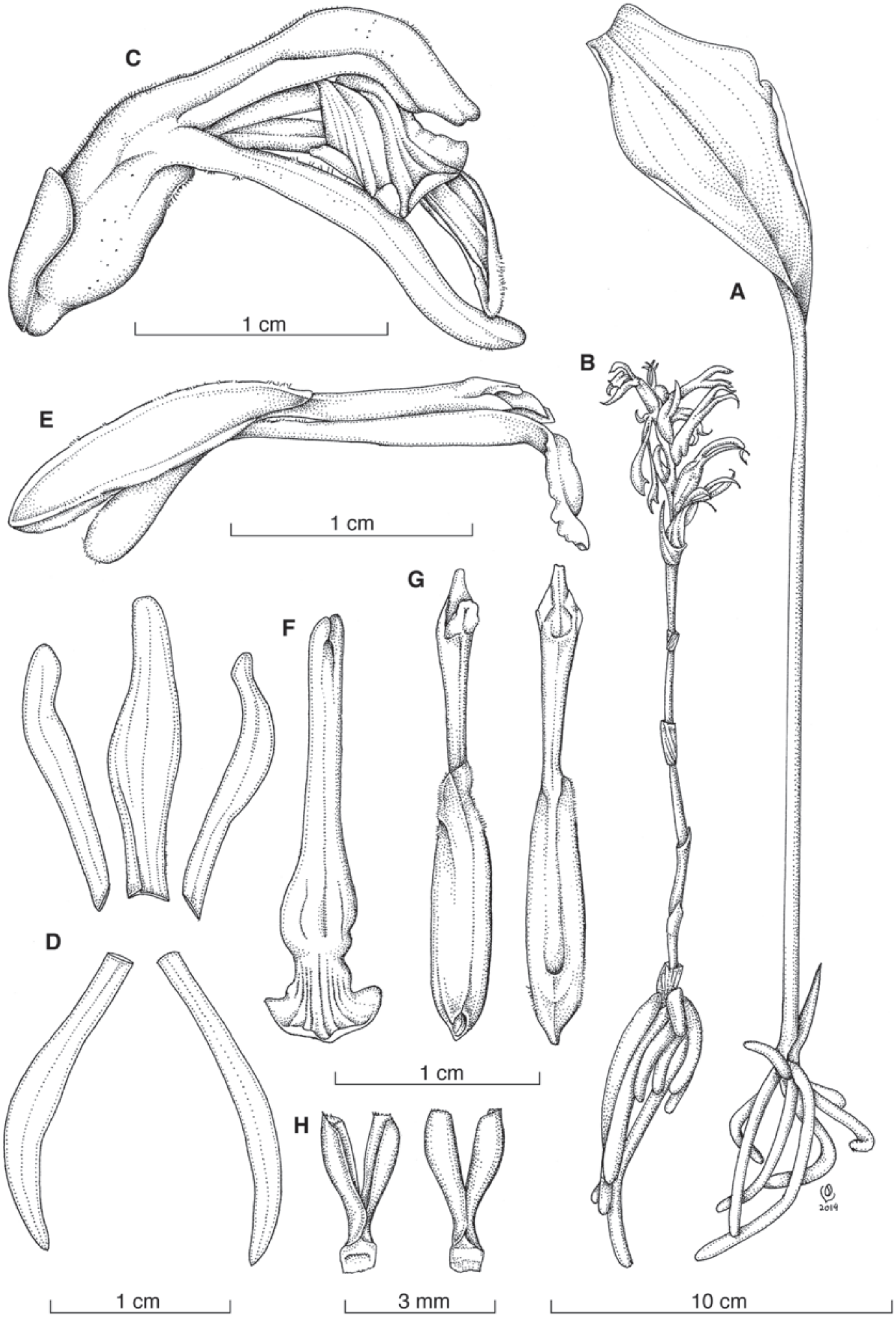

FIGURE 43. *Pelexia barrahondaensis* Bogarín & Pupulin. **A,** Leafy habit. **B,** Leafless habit. **C,** Flower. **D,** Perianth flattened. **E,** Column and lip, side view. **F,** Column, side and ventral view. **G,** Pollinarium and anther cap. Drawn by F. Pupulin, inked and rendered by L. Oses from *Pupulin 8189* (JBL).

FIGURE 44. *Pelexia barrahondaensis* flowering in situ at BHNP. Photograph by F. Pupulin.

epichilum et hypochilum munitum, sed pedunculo foliorum multo longiore, nectario duplo longiore et epichilo ecalloso recedit; a Pelexiae maculatae Rolfe *per labium ecallosum confert, sed foliis concoloribus viridibus, nectario multo longiore obtuso facile distinguitur*.

Plants terrestrial, up to 26 cm tall, deciduous during the dry season and at flowering. *Roots* thick, succulent, fusiform, fasciculate, 8–10 cm long, to 9 mm in diam., pubescent. *Leaves* 1-leaf, developed from the abbreviated stem, conspicuously petiolate, elliptic-ovate, acute, conduplicate, deciduous at flowering, 10–13 × 3.1–6.2 cm; petiole narrow, basally reddish-pinkish, 13–23 cm long. *Inflorescence* apical, erect, stout, racemose, subdense, produced from the center of the basal rosette when the plant is deciduous, helical or subdistichous, pubescent or densely glandular, with about 8 flowers opening in succession, scape 19.5–29.5 cm long, peduncle 13.5–23.0 cm long, rachis 5.5–6.5 cm long, with about 7 tightly appressed tubular, acute, somewhat glandular cauline bracts, to 1.7–3.0 × 0.5–0.6 cm. *Floral bracts* ovate, acute to acuminate, basally glandular, shorter, or as long as the ovary, 1.6 × 0.5 cm. *Ovary* glandular-pubescent, cylindrical, fusiform, ridged, to 1.1 × 0.3 cm. *Flowers* medium, up to 2 cm long, densely glandular-pubescent in the outer part of the floral parts, resupinate, basally tubular, arcuate toward the apex, brown-green, the lip white with the mesochile yellow, the epichile white with green stripes. *Dorsal sepal* oblong-elliptic, truncate, concave, arcuate, adaxially pubescent, 16.1 × 4.2 mm. *Lateral sepals* narrowly oblong, basally connate, subacute, falcate, arcuate, with the margins involute, the apexes touching each other, adaxially pubescent, 17.7 × 2.5 mm. *Petals* linear to narrowly oblong, falcate, subacute, connivent with the dorsal sepal forming a hood over the column, 14.7 × 2.0 mm. *Lip* clawed, oblong, arcuate, adnate to the lateral sepals, with 2 digitate basal auricles, canaliculate, the blade constricted basally and below the apex, the hypochile oblong, mesochile obovate, the isthmus subquadrate, the epichile reniform, undulate, crisped, curved downward, with 2 parallel keels from the apical constriction to the epichile apex and several veins radiating toward the margins, 23.0 × 6.5 mm. *Nectary* to 1 cm long. *Column* cylindrical, oblong, slightly wider at apex, dorsally sulcated beaked, 9.6 mm. *Pollinia* 2, narrowly ovoid to oblong, puberulent with a blackish rounded viscidium.

Distribution: known only from BHNP, Costa Rica.

Distribution in the Park: known only from Cerro Corralillo in the area of Las Delicias, in a patch of forest at the upper end of bean plantations and jaragua pastures.

Etymology: named for Barra Honda National park, where the species was discovered.

Habitat and ecology: terrestrial or lithophytic on rocky limestone areas among organic matter in a secondary forest. Plants grow in medium to full sunlight conditions.

Phenology: the plants studied flowered in February. Inflorescences start to develop in November, just before the beginning of the dry season.

Discussion: the *Pelexia* species found at Barra Honda shows a mix of morphological characters similar to several other species in the genus but combined in a unique way. The long spur, almost equaling the length of the ovary, is similar to that of *P. callosa* Ames, *P. hondurensis* Ames, and *P. saccata* Rolfe, three species restricted in distribution to northern Central America, as well as the mostly Andean *P. maculata* Rolfe. The latter has been recorded from Costa Rica by Szlachetko and collaborators (2005) on the basis of a collection from the northern, Caribbean foothills of the Talamanca mountain chain. Still, this species's occurrence north of the Panamanian isthmus is unlikely, as its distribution is restricted to South America, where it has been otherwise documented from Colombia to Bolivia and Brazil. The general outline of the lip of *P. barrahondaensis*, which presents a distinct rectangular isthmus between hypochile and epichile, is rare in *Pelexia*, and to our knowledge, it can only be observed in *P. gutturosa* (Rchb.f.) Garay, a species endemic to Honduras. However, the latter has very short leaves, a distinctly shorter spur, and an epichile with a strongly thickened keel along the midvein, while the epichile of *P. barrahondaensis* is ecallose. Also, the absence of callosities on the epichile and the apex of the hypochile is rarely found in *Pelexia* and probably limited to *P. funkiana* (A. Rich. & Gal.) Schltr., a species of broad distribution, and *P. maculata*. *Pelexia funkiana*, however, has a short spur (ca. 3 mm vs. ca. 10 mm), and in Costa Rica it is exclusively known from the wet forests of Caribbean Talamanca. From the wet Caribbean forest of the Tilarán Cordillera in northern Costa Rica is also known *P. congesta* Ames & C.Schweinf, which, however, has an acute spur and lip without an isthmus below the hypochile.

Pelexia barrahondaensis is a rare species at BHNP, where a single population was located on the summit of Cerro Corralillo. Here the plants grow terrestrially in the rocky soil's crevices, where some debris accumulates that helps them survive the very harsh and prolonged dry season of the central Nicoya peninsula.

Additional specimens examined: COSTA RICA. Guanacaste: Nicoya, San Antonio, BHNP, Cerro Corralillo, Sector Las Delicias, en bosque al final de las plantaciones de frijol, 10°11'11.82"N, 85°21'09.28"W, 481 m, terrestres entre rocas y materia orgánica en bosque húmedo premontano transición a basal, 5 noviembre 2011, *D. Bogarín 9395, E. Artavia & O. Cubero* (CR). Same locality, *D. Bogarín 9396, E. Artavia & O. Cubero* (CR). BHNP, Cerro Corralillo, Sector Las Delicias, in forest at the upper end of bean plantations and "jaragua" pastures, 10°11'11.19"N, 85°21'08.46"W, 438 m, terrestrial among rocks and organic materials in premontane moist, transition to tropical moist forest, 24 February 2012, *F. Pupulin 8199, D. Bogarín and Salomón Villagra* (JBL-spirit).

23. ***Sarcoglottis*** C. Presl., Reliq. Haenk., 1(2): 95. 1827.
TYPE: *Sarcoglottis speciosa* C. Presl.

Plants terrestrial, rarely epiphytic with abbreviated stems. *Roots* fleshy, fusiform, fasciculate. *Leaves* arranged in the basal rosette, sometimes cauline, subsessile or petiolate, and often deciduous before flowering. *Inflorescence* slender, erect, covered by several tight sheaths, the rachis loosely or densely few- to many-flowered. *Flowers* small to large, erect, arcuate, tubular basally forming a nectary adnate to the ovary, usually green to greenish or dull-colored. *Sepals* dissimilar, lateral sepals decurrent, connate in the lower part, usually pubescent or glandular. *Petals* linear, usually oblong ovate to lanceolate, falcate. *Lip* clawed, arcuate apically, constricted below the apex, widest apically, with basal auricles and prominent V-shaped thickenings, entire or crenulate, spurred. *Column* part shorter than the anther, footed, cuniculate. *Anther* erect, flattened, 2-chambered. *Pollinia* 4, powdery.

A genus of about 45 species ranging from Mexico, Central America, and the Antilles to Bolivia and Argentina. About 7 species in Costa Rica, 3 in BHNP.

Key to Species of *Sarcoglottis*

1a. Inflorescence congested; floral bracts short, less than half the length of the ovary; flowers small (the lip <2 cm long); the petals falcate; the base of midlobe rounded, with 2 keels converging at apex . . . . *S. calcicola*

1b. Inflorescence laxe to sublaxe; floral bracts long, more than three-fourths the length of the ovary; flowers large (the lip >3 cm long); the petals straight; the base of midlobe truncate, with a central thickening 2

2a. Floral bracts long-acuminate; flowers green; lateral sepals curved-arched, the free portion curved, the margins undulate; nectariferous horns curved, thin, 5 mm long, extending almost to the apex of the spur . . . . *S. sceptrodes*

2b. Floral bracts acute; flowers bronze; lateral sepals reflexed, the free portion falcate, the margins straight; nectariferous horns straight, stout, 7 mm long, reaching the middle of the spur . . . . *S. acaulis*

23a. ***Sarcoglottis acaulis*** (J.E.Sm.) Schltr., Repert. Sp. Nov. Regni Veg. 6: 53. 1919. Fig. 13A, 45.

Basionym: *Neottia acaulis* J.E. Sm., Exot. Bot. 2: 105. 1806. TYPE: TRINIDAD. Without specific locality, *A. Anderson s.n.* (Lectotype: designated by Rutkowski et al., 2008: S-Linn).

Homotypic synonym: *Spiranthes acaulis* (J.E. Sm.) Cogniaux, Martius Fl. Bras. 3(4): 221. 1895.

A terrestrial *herb* up to 54 cm high, deciduous during the dry season and at flowering. *Roots* thick, succulent, fusiform, fasciculate, 5–20 cm long, 0.5–1.5 cm in diam., pubescent. *Leaves* 3–5, arranged in a basal rosette, oblanceolate, elliptic-obovate to oblong, acute, somewhat petiolate, 20.4–32.6 × 4.1–5.2 cm; petiole narrow, to 10.2 cm long. *Inflorescence* apical, erect, stout, racemose, subdense or lax, produced from the center of the basal rosette when the plant is deciduous, helical, pubescent or densely glandular, with about 3–9 flowers opening in succession, scape to 26–51 cm long, peduncle 18–35 cm long, rachis 7.0–19.2 cm long, with 6–10 tightly appressed tubular, acute, somewhat glandular cauline bracts, to 5.5–6.5 cm long. *Floral bracts* ovate or oblong-lanceolate, acuminate, basally glandular, with red tips, longer or as long as the ovary, 3.0–4.5 × 0.5–1.0 cm. *Ovary* glandular-pubescent, cylindrical, widened basally, to 3.2 × 0.9 cm. *Flowers* medium, up to 1.5 cm long, densely glandular-pubescent in the outer part of the segments, resupinate, basally tubular, arcuate toward the apex, yellow-green, green, yellowish brownish, or reddish, the buds rostrate. *Dorsal sepal* elliptic to oblong, subacute, deeply concave, reflexed apically, adaxially pubescent, 3.0 × 0.4 cm. *Lateral sepals* subsimilar, narrowly oblong, connate basally, acute, the free portion strongly falcate, reflexed, adaxially pubescent, spreading and somewhat involute apically, 3.4 × 0.6 cm. *Petals* unguiculate, linear-ligulate, subacute, twisted, and slightly reflexed apically and connivent with the dorsal sepal forming a hood over the column, 2.8 × 0.3 cm. *Lip* clawed, strongly arcuate apically, adnate to the lateral sepals, with 2 digitate basal auricles, basally pubescent, canaliculate, the blade constricted basally and below the apex, the hypochile obovate, widened apically, the epichile ovate, with 2 parallel convergent V-shaped keels from the apical constriction to the epichile apex and several veins radiating toward the margins, emarginate, 4.1 × 1.0 cm. *Nectary* to 2.5 cm long. *Column* cylindrical and laterally flattened, basally papillose, somewhat 3-dentate or with 2 arms or projections, beaked at the apex, to 1.2 cm. *Pollinia* 2, narrowly ovoid to oblong, united basally, puberulent with a short black viscidium. *Anther cap* cucullate, rostrate, with 2 cells.

Distribution: broadly distributed from Mexico (type of *Sarcoglottis purpusiorum* Schltr.) to French Guyana, Brazil (type of *S. allemanii* Barb. Rodr.), and Peru in South America, and the West Indies.

Distribution in the Park: they grow on rocky areas among organic matter in the evergreen forest at Cerros de Jesús.

Etymology: from the Latin *acaulis,* “without a stem,” in allusion to the basal rosette of leaves, apparently stemless.

Habitat and ecology: terrestrial or lithophytic among organic litter in rocky areas or understory forest in shade. Plants are deciduous during the dry season when they are in bloom. After the dry season, the plants develop several leaves arranged in a basal rosette.

Phenology: plants flower from January to April, mainly in February.

Discussion: like other *Sarcoglottis* species at BHNP, *S. acaulis* is characterized by the terrestrial plants without pseudobulbs, the succulent fasciculate roots, and sessile leaves arranged into a basal rosette, deciduous during the blooming season. It differs from other species of *Sarcoglottis* by the combination of long floral bracts, apically acute (not long-acuminate), reflexed sepals (not simply recurved by bending) with their free portion falcate, and midlobe of the lip distinctly wider than long. Dressler (2003) excluded *S. acaulis* from Costa Rica, but it was recorded by Pupulin (2002). Also, Szlachetko et al. (2005) cited a voucher of this species from Guanacaste (*Kupper 391*, M). We provide here the first illustration of this species for the flora of Costa Rica.

Additional specimens examined: Guanacaste: Nicoya, San Antonio, Parque Nacional Barra Honda, alrededores de la caverna Pozo Hediondo, 10°10’08.3"N, 85°21'49.7"W, 423 m, bosque húmedo premontano transición a basal, terrestres entre piedras calizas, 3 octubre 2014, *D. Bogarín 11207, N. Belfort & A. Karremans* (JBL).

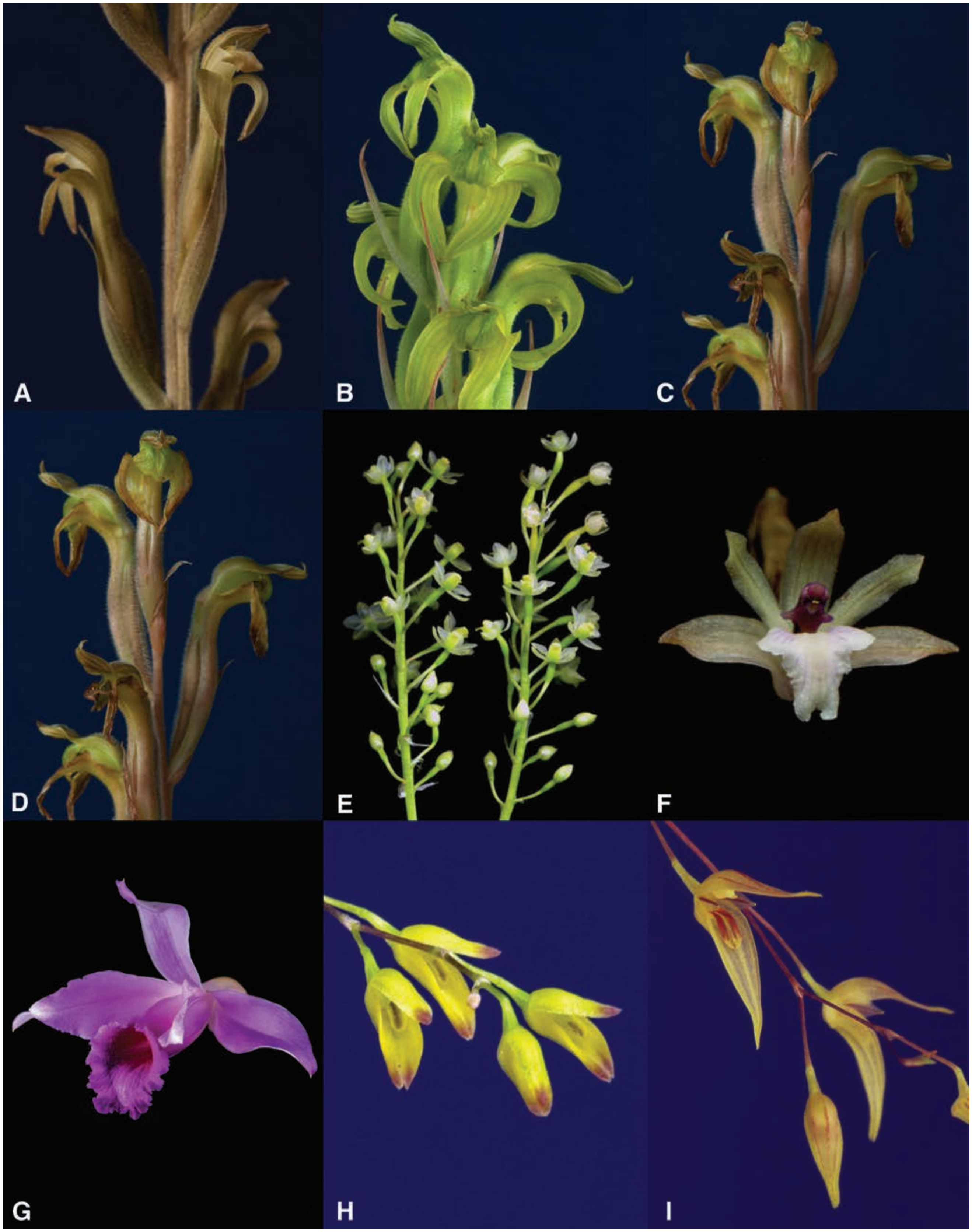

FIGURE 13. **A–I.** Orchid species found at Barra Honda National Park. **A,** *Sarcoglottis acaulis* (*Bogarín 11207*, JBL). **B,** *Sarcoglottis calcicola* (*Bogarín 11206*, JBL). **C,** *S. sceptrodes* (*Pupulin 8194*, JBL). **D,** *S. sceptrodes* (*Pupulin 8196*, JBL). **E,** *Scaphyglottis micrantha* (*Bogarín 1672*, JBL). **F,** *S. stellata* (*Bogarín 1673*, JBL). **G,** *Sobralia fenzliana* (*Bogarín 1693*, JBL). **H,** *Specklinia grobyi* (*Bogarín 1697*, JBL). **I,** *S. panamensis* (*Bogarín 1689*, JBL). Photographs by the authors.

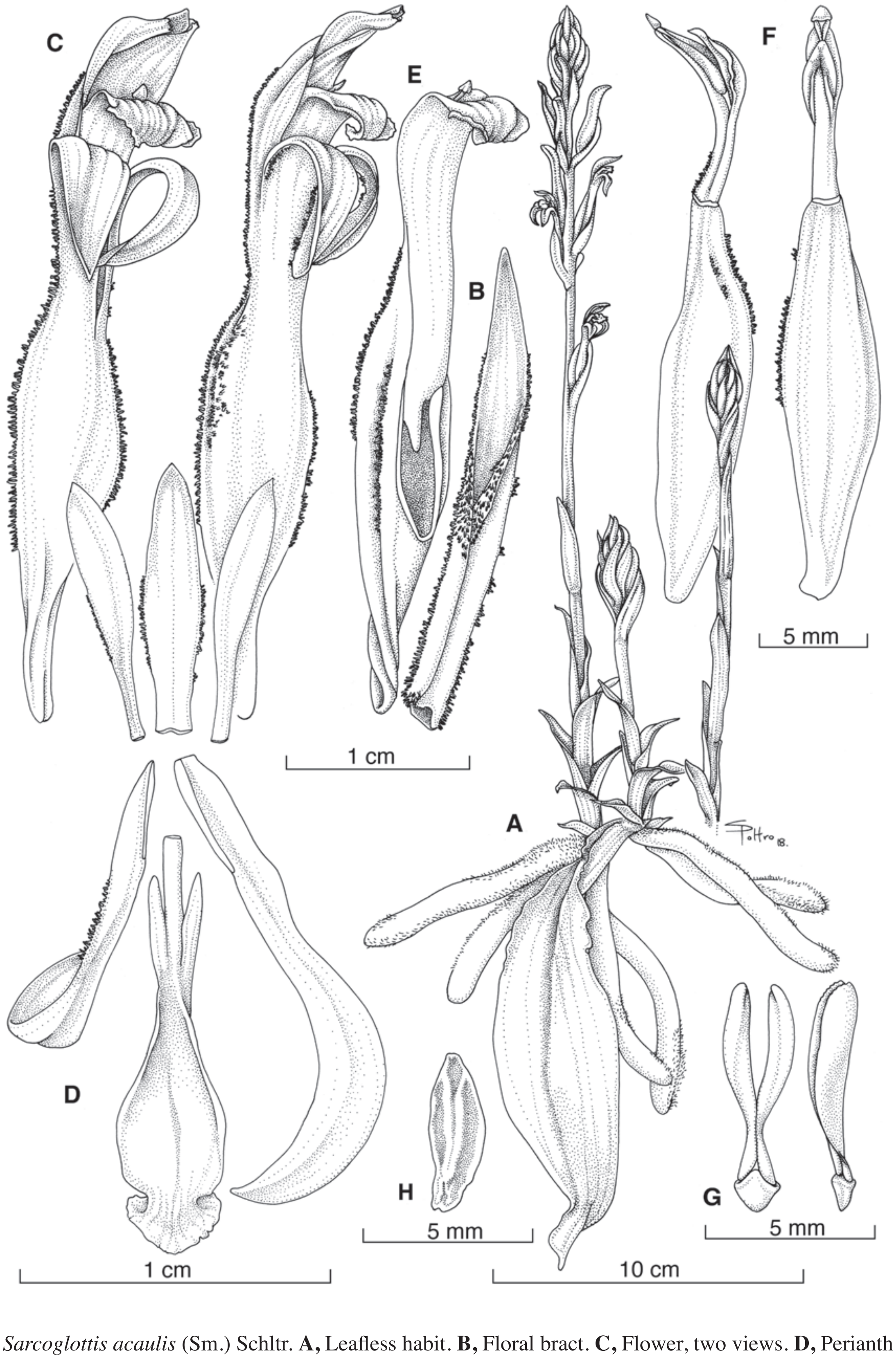

FIGURE 45. *Sarcoglottis acaulis* (Sm.) Schltr. **A,** Leafless habit. **B,** Floral bract. **C,** Flower, two views. **D,** Perianth flattened. **E,** Column and lip, side view. **F,** Column, side and ventral view. **G,** Pollinarium. **H,** Anther cap. Drawn by F. Pupulin, inked and rendered by L. Oses from *Bogarín 11207* (JBL).

23b. **Sarcoglottis calcicola** Bogarín & Pupulin, *sp. nov.* Fig. 13B, 46.
TYPE: COSTA RICA. Guanacaste: Nicoya, San Antonio, Parque Nacional Barra Honda, camino principal de la estación al Sendero Ceiba, parte alta antes de llegar al parqueo, 10°10'21.53"N, 85°21'42.50"W, 342 m, bosque húmedo premontano transición a basal, terrestres a orillas del camino, bosque secundario, 3 octubre 2014, *D. Bogarín 11206, N. Belfort & A. Karremans* (Holotype: CR; Isotype: JBL).

A Sarcoglotti hunteriana Schltr. *foliis concoloribus viridis, bracteis floralibus breviorbus mediam partem ovarii non assurgentibus, inflorescentia congesta, floribus multo parvioribus recedit.*

A terrestrial *herb* up to 50 cm high, deciduous during the dry season and at flowering. *Roots* thick, succulent, fusiform, fasciculate, 5–17 cm long, 0.5–1.2 cm in diam., pubescent. *Leaves* 3–7, arranged in a basal rosette, oblanceolate, elliptic-obovate to oblong, acute, somewhat petiolate, 13.0–46.0 × 4.9–7.6 cm; petiole narrow, 2.5–9.0 cm long. *Inflorescence* apical, erect, stout, racemose, subdense, produced from the center of the basal rosette when the plant is deciduous, helical, pubescent or densely glandular, with about 15 flowers opening in succession, scape to 28 cm long, peduncle 14–18 cm long, rachis 7–8 cm long, with 6–10 tightly appressed tubular, acute, somewhat glandular cauline bracts, to 1.5–2.0 × 0.6–0.8 cm. *Floral bracts* ovate or oblong-lanceolate, acute to acuminate, basally glandular, shorter than the ovary, 1.5 × 0.8 cm. *Ovary* glandular-pubescent, cylindrical, widened basally, to 1.4 × 0.5 cm. *Flowers* medium, up to 1.5 cm long, densely glandular-pubescent in the outer part of the floral parts, resupinate, basally tubular, arcuate toward the apex, yellow-green, green or yellowish brownish, the buds rostrate. *Dorsal sepal* ovate to elliptic, acute or subacute, deeply concave, reflexed apically, 1.3–1.5 × 0.4–0.5 cm. *Lateral sepals* subsimilar, narrowly oblong, connate basally, subacute, the free portion falcate, reflexed, spreading and somewhat involute apically, 2.2–2.3 × 0.3–0.4 cm. *Petals* linear-ligulate, falcate, obtuse to subacute, twisted and slightly reflexed apically and connivent with the dorsal sepal forming a hood over the column, 1.2 × 0.2 cm. *Lip* clawed, strongly arcuate apically, adnate to the lateral sepals, with two digitate basal auricles, canaliculate, the blade constricted basally and below the apex, the hypochile oblong-obovate, widened apically, the epichile reniform, undulate and somewhat crisped, with 2 convergent V-shaped keels from the apical constriction to the epichile apex and several veins radiating toward the margins, 1.9 × 0.6 cm. *Nectary* to 1.5 cm long. *Column* cylindrical and laterally flattened, basally papillose, somewhat 3-dentate, beaked, to 6 mm. *Pollinia* 2, narrowly ovoid to oblong, puberulent with a short viscidium. *Anther cap* cucullate, rostrate, with 2 cells.

Distribution: known only from Barra Honda National Park in northern Costa Rica.

Distribution in the Park: they grow on rocky areas among organic matter around cactus forests and along the paths La Ceiba, El Mirador, Las Cascadas, Bosque de Piedra, La Palma, and Las Delicias.

Etymology: from the Latin *calx*, "lime," and *cola*, "a dweller," in reference to the species growing on limestone outcrops at Barra Honda.

Habitat and ecology: terrestrial among organic litter in rocky areas or understory forest in shade at around 400 m of elevation. Plants are deciduous during the dry season when they are in bloom. After the dry season, the plants develop several leaves arranged in a basal rosette.

Phenology: from January to April.

Discussion: they are characterized by the terrestrial plants without pseudobulbs, the succulent fasciculate roots, and sessile leaves arranged into a basal rosette, deciduous during the blooming season. The size and shape of leaves vary, and some plants have white-spotted leaves. The flowers are arcuate, with the lateral sepals strongly falcate. Other *Sarcoglottis* species from the area are similar; however, *S. calcicola* differs in the congested inflorescence, floral bracts shorter than the ovary (rather than as long as or longer than the ovary), the small flowers with lip less than 2 cm long, the falcate petals and the base of midlobe rounded, with 2 keels converging at apex. These keels are similar to those of *S. hunteriana* Schltr., also known from Guanacaste, but the latter has leaves mostly marked with silvery stripes and blotches, floral bracts (distinctly exceeding the middle of the ovary), and much larger flowers on a laxly flowered raceme.

Plants of *Sarcoglottis* spp. can also be confused with *Beloglottis costaricensis* when they are not in flower, as both have basal leaves arranged in a rosette; however, in the latter, the leaves have waved margins, whereas in species of *Sarcoglottis* the margin is straight. When in flower, *Sarcoglottis calcicola* has bigger brown-green flowers, instead of the smaller flowers that are white with a green stripe of *B. costaricensis*.

Additional specimens examined: COSTA RICA. Guanacaste: Nicoya, San Antonio, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, terrestres en sitio rocoso con hojarasca, 21 febrero 2006, *D. Bogarín 2593* (JBL-spirit). BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, al lado derecho, en dirección a La Mantequilla, 10°10'34.6"N, 85°21'20.7"W, 421 m, bosque húmedo premontano transición a basal, 22 febrero 2006, *D. Bogarín 2614* (JBL-spirit). BHNP, camino principal de la estación al Sendero Ceiba, parte alta antes de llegar al parqueo, 10°10'21.53"N, 85°21'42.50"W, 342 m, bosque húmedo premontano transición a basal, terrestres orillas del camino, bosque secundario, 7 noviembre 2011, *D. Bogarín 9418* (CR).

23c. ***Sarcoglottis sceptrodes*** (Rchb.f.) Schltr., Beih. Bot. Centralbl. 37(2): 421. 1920. Fig. 13C–D, 47.

Basionym: *Spiranthes sceptrodes* Rchb.f., Bonplandia (Hannover) 3: 214. 1855. TYPE: NICARAGUA. Segovia: Guanacarta [Costa Rica: Guanacaste], *A. S. Oersted s.n.* (Holotype: W).

Homotypic synonyms: *Gyrostachys sceptrodes* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 664. 1891. *Gyrostachys sceptrodes* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 664. 1891.

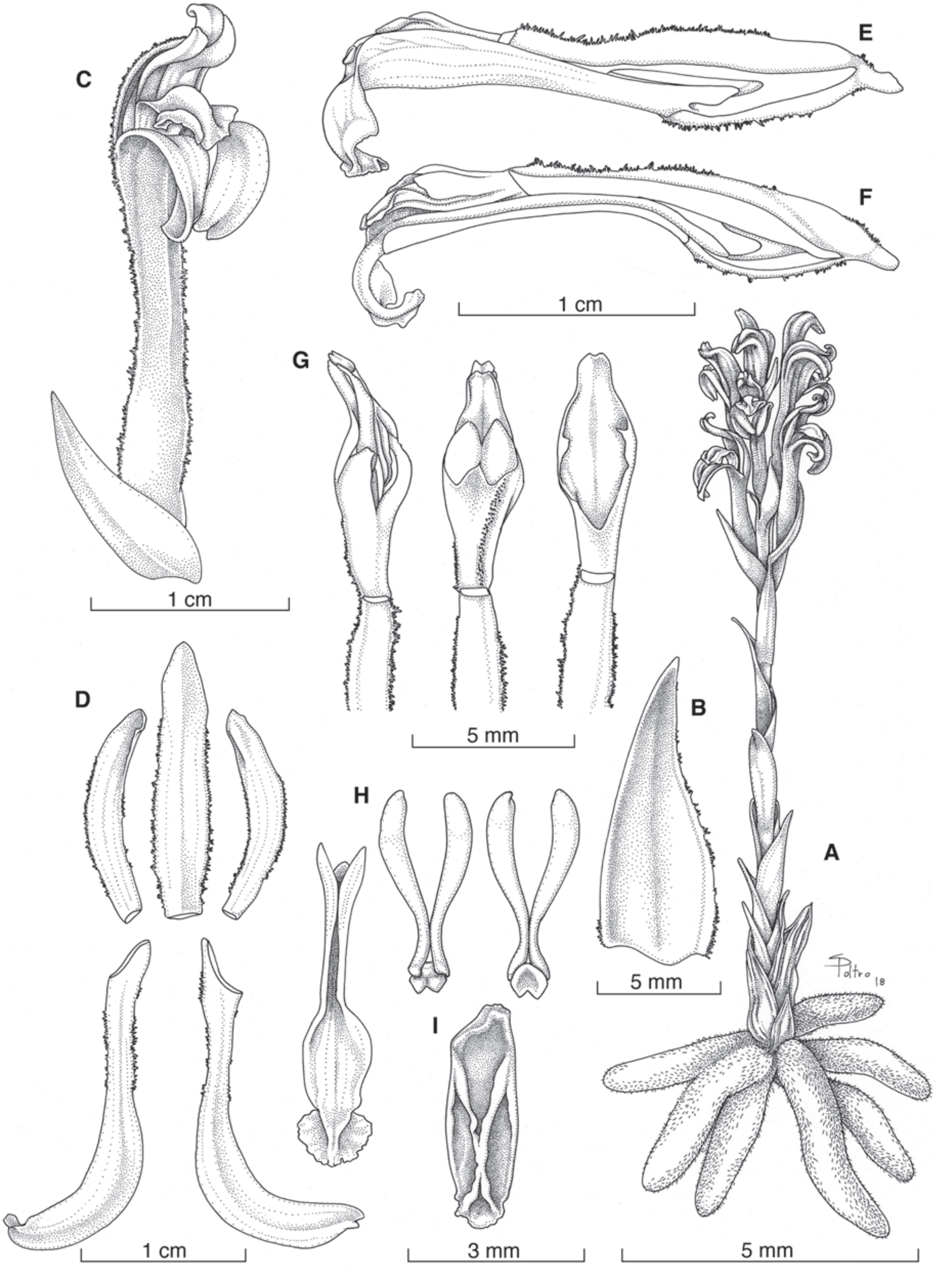

FIGURE 46. *Sarcoglottis calcicola* Bogarín & Pupulin. **A,** Leafless habit. **B,** Floral bract. **C,** Flower. **D,** Perianth flattened. **E,** Column and lip, side view. **F,** Column and lip (longitudinal section), side view. **G,** Column, side and ventral views. **H,** Pollinarium. **I,** Anther cap. Drawn by S. Poltronieri and F. Pupulin from *Bogarín 11206* (JBL).

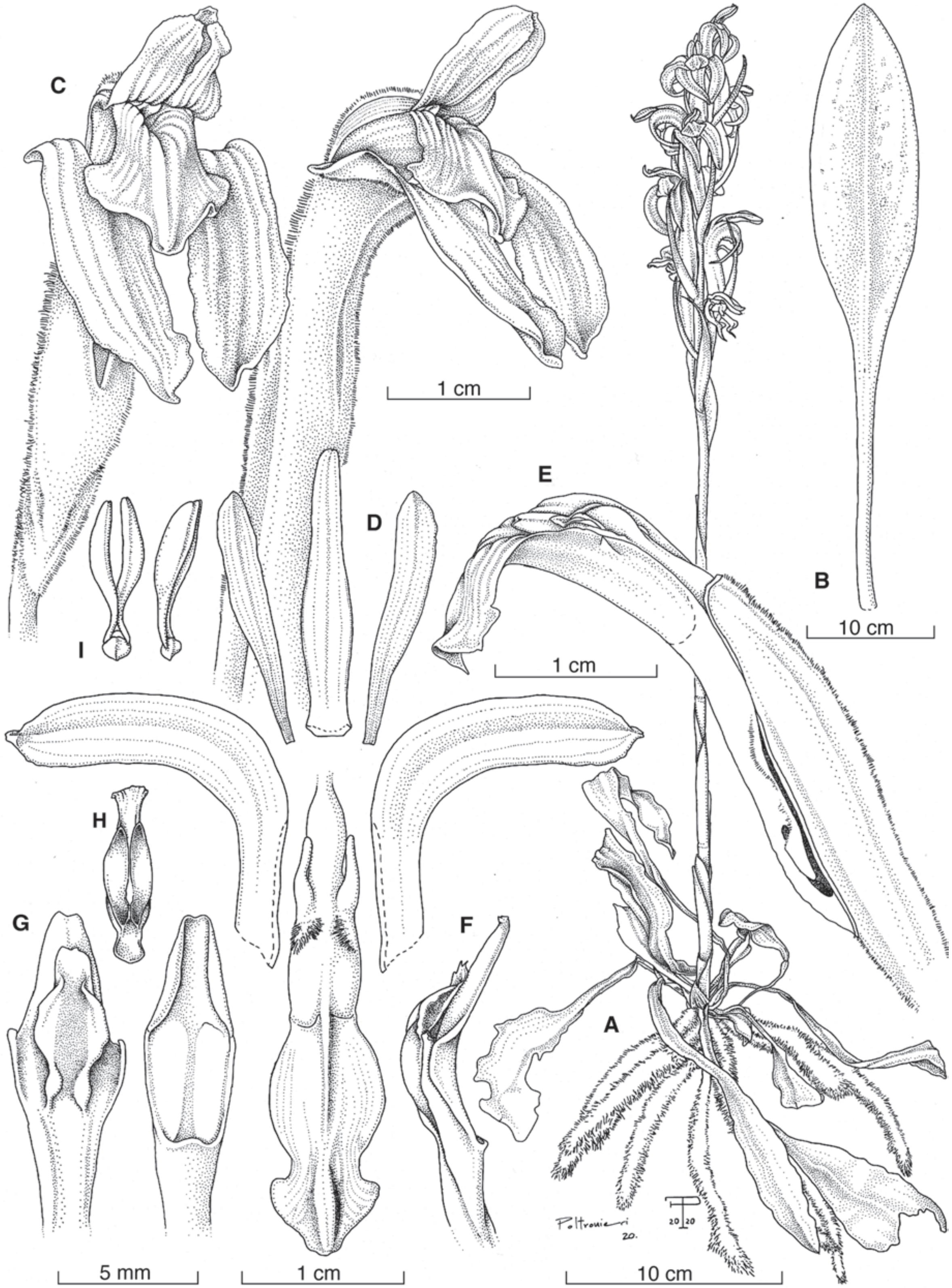

FIGURE 47. *Sarcoglottis sceptrodes* (Rchb.f.) Schltr. **A,** Habit with shredding leaves. **B,** Leaf. **C,** Flower, two views. **D,** Perianth flattened. **E,** Column and lip, side view (the nectary sectioned). **F,** Column, lateral view. **G,** Column, dorsal and ventral view. **H,** Anther cap. **I,** Pollinarium, two views. Drawn by F. Pupulin and rendered by S. Poltronieri from *Pupulin 8195* (JBL).

A terrestrial *herb*, up to 40 cm high, deciduous during the dry season and at flowering. *Roots* thick, succulent, fusiform, fasciculate, 5–20 cm long, 0.5–1.0 cm in diam., pubescent. *Leaves* 3–9, arranged in a basal rosette, distinctly petiolate, the petiole canaliculated, to 20 cm long, the blade elliptic, acute, 11–20 × 4.5–8.2 cm, green, occasionally marked with white spots and small blotches. *Inflorescence* apical, erect, stout, racemose, subdense, produced from the center of the basal rosette when the plant is deciduous, helical, densely glandular, with 5–11 flowers opening in succession, scape to 40 cm long, peduncle 18–25 cm long, rachis 7–8 cm long, with 8–10 tightly appressed tubular, acute, subglabrous caulinar bracts longer than the internodes, to 3.0 × 0.8 cm. *Floral bracts* narrowly lanceolate, long acuminate, basally glandular, subequalling or exceeding the length of the ovary, 3.7–4.6 × 0.7–1.0 cm. *Ovary* glandular-pubescent, cylindrical, to 3.2 × 0.5 cm. *Flowers* large, up to 3.5 cm long from the tips of dorsal and lateral sepals, densely glandular-pubescent in the outer part of the floral parts, resupinate, basally tubular, the dorsal sepal and the petals porrect, the lateral sepals gently bending, yellow-green to green. *Dorsal sepal* linear-lanceolate, subobtuse, concave, gently recurved apically, 1.7 × 0.3 cm. *Lateral sepals* subsimilar, oblong, connate basally, acute, abruptly subacuminate, the free portion curved, spreading, apically subconduplicate, the margins undulate, 2.5–2.7 × 0.4 cm. *Petals* ligulate-oblong, obtuse, abruptly subacute, twisted and slightly upturned from the middle point, apically connivent with the dorsal sepal forming a channel with the base of the lip, 1.70 × 0.26 cm. *Lip* clawed, clearly divided into hypochile and epichile, apically geniculate, extended over the claw into 2 digitate, sinuous, basally hirsute auricles, then canaliculate, the blade constricted basally and below the apex, the hypochile elliptic, widened apically, provided with a low keel above the middle, the epichile subtriangular, truncate at the base, undulate, with a central thickened, rounded keel running from the apical constriction to the epichile apex and several veins radiating toward the margins, 2.9 × 0.7 cm. *Nectary* to 2 cm long. *Column* hemicylindrical, dorsoventrally flattened, broadened in the middle, basally papillose, with 2 subelliptic, truncate wings, beaked, the rostellar apex excise, to 12 mm long. *Pollinia* 2, narrowly ovoid to oblong, sigmoid, puberulent, with a short rounded viscidium. *Anther cap* cucullate, rostrate, with 2 cells.

Distribution: from Mexico to northern Costa Rica.

Distribution in the Park: a large population of *S. acaulis* was located along a seasonal stream in the secondary, premontane moist forest of Zona Protectora Cerros de Jesús.

Etymology: from the Greek *skeptron, sceptrum*, "wand, shaft, or baton," and *odes*, "resembling," in allusion to the shape of the inflorescence.

Discussion: the plants found in this study match well the type specimen of *Sarcoglottis sceptrodes*, especially in the long-acuminate floral bracts and the base of the lip midlobe truncate. It is easily distinguished by other *Sarcoglottis* species at BHNP by the combination of mostly green flowers with lateral sepals nonreflexed, the free portion curved, and the margins wavy-undulated, and the midlobe of the lip basally truncate. Pupulin (2002) and Dressler (2003) did not include *S. sceptrodes* among the species of the genus in Costa Rica. However, the type of *Spiranthes sceptrodes* is undoubtedly from "Guanacarta" (Guanascaste) in Costa Rica, even though erroneously referred by the collector to the Nicaraguan region of Segovia.

Additional specimens examined: Guanacaste: Nicoya, Mansión, Zona Protectora Cerros de Jesús, 10°05'41.71"N, 85°18'59.58"W, 370 m, premontane moist, transition to tropical moist forest, terrestrial in secondary mature vegetation along a seasonal stream with high trees, 23 February 2012, *F. Pupulin 8193 & D. Bogarín* (JBL-spirit). Same locality, *F. Pupulin 8194 & D. Bogarín* (JBL-spirit), *F. Pupulin 8195 & D. Bogarín* (JBL-spirit), *F. Pupulin 8196 & D. Bogarín* (JBL-spirit).

24. *Scaphyglottis* Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 58. 1835[1836].
TYPE: *Scaphyglottis graminifolia* (Ruiz & Pav.) Poepp. & Endl.

Plants cespitose or repent, epiphytic herbs, with definite pseudobulbs or thickened, simply or distichous, superposed stems, often producing 1 to several new shoots at the apices of older shoots. *Leaves* 1–3, conduplicate to semiterete, thin to coriaceous, persistent. *Inflorescence* terminal racemose, or at the nodes of the stem, appearing fasciculate, 1- to few-flowered. *Flowers* small green, tan, red, or white. *Sepals* and *petals* subequal, spreading, the lateral sepals more or less adnate to the column foot. *Lip* articulated with the column foot, straight to geniculate, with or without a claw, entire or 3-lobed. *Column* short, provided with wings or auricles or wingless, usually with a short to prominent foot, usually a distinct nectary on the column foot. *Anther* terminal, operculate, incumbent. *Pollinia* 4 or 6, laterally compressed, ceraceous.

A Neotropical genus of about 55 species, distributed from Mexico to Brazil, Bolivia, and the West Indies. The majority of species occur in Costa Rica and Panama. About 35 species in Costa Rica, 2 in BHNP.

Key to Species of *Scaphyglottis*

1a. Pseudobulbs not prolific, inflorescence racemose elongate .... *S. micrantha*
1b. Pseudobulbs prolific, inflorescence shortly racemose appearing fasciculate .... *S. stellata*

24a. ***Scaphyglottis micrantha*** (Lindl.) Ames & Correll, Bot. Mus. Leafl. 10(4): 85. 1942. Fig. 13E, 48.

Basionym: *Hexadesmia micrantha* Lindl., Edwards's Bot. Reg. 30: Misc. 2. 1844. TYPE: GUATEMALA. Without locality, collected by Skinner and cultivated by *Messrs. Loddiges catalogue no. 389* (Holotype: K).

Homotypic synonyms: *Pseudohexadesmia micrantha* (Lindl.) Brieger, Die Orchideen 8(2932): 489. 1976. *nom. inval*.

Plants epiphytic, caespitose, erect, to about 16 cm tall, with abbreviated rhizome. *Roots* filiform, slender, glabrous, with green vegetative apex. *Pseudobulbs* fusiform, stipitate,

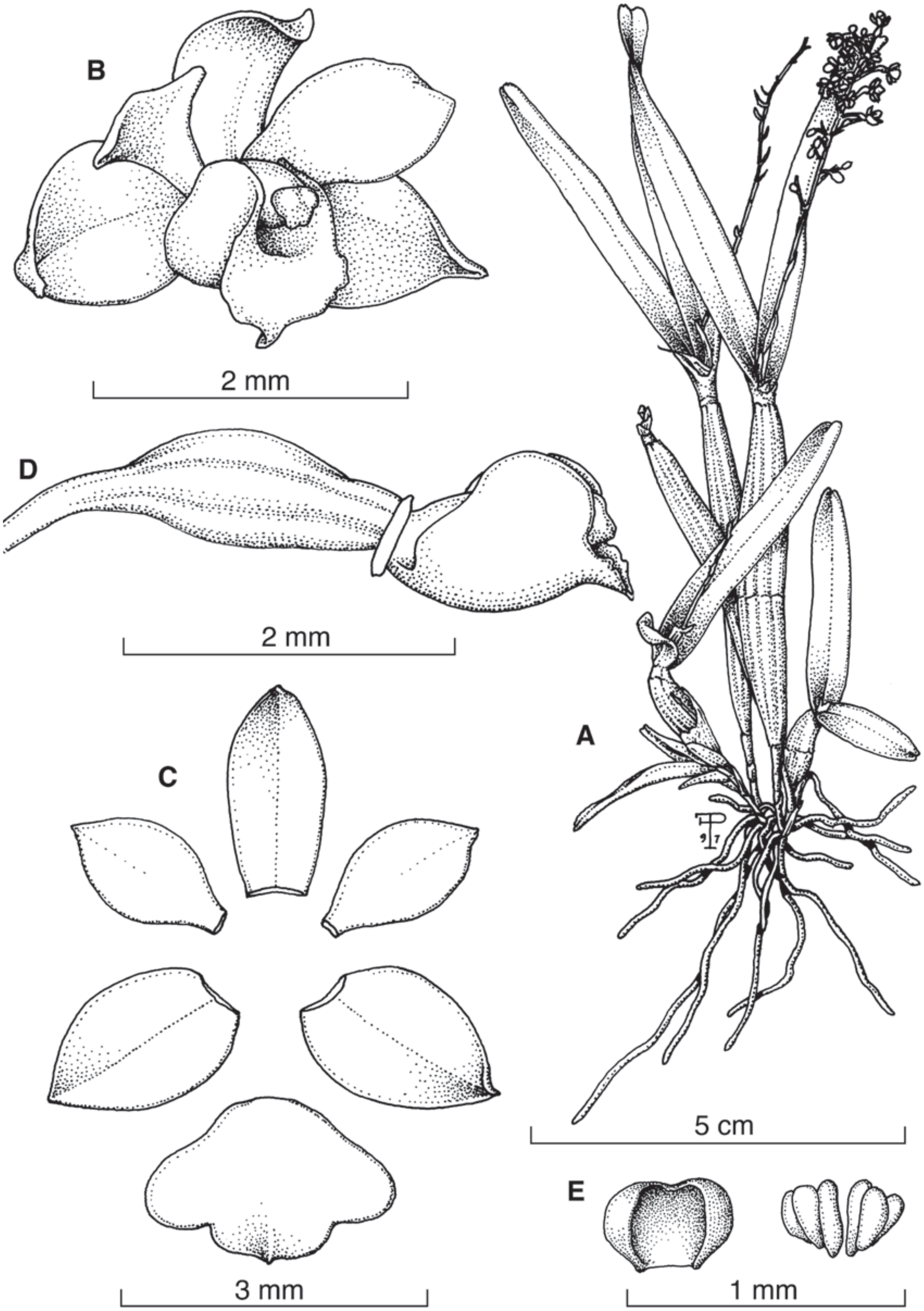

FIGURE 48. *Scaphyglottis micrantha* (Lindl.) Ames & Correll. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 377* (JBL).

somewhat curved, unbranched, diphyllus, subtended by many scarious, imbricating, whitish sheaths, sulcate, to 7 × 0.8 cm. *Leaves* linear, conduplicate, membranaceous, obliquely retuse, to 4.0–8.4 × 0.6–0.8 cm. *Inflorescence* apical, racemose, many-flowered, to 8.5 cm long; peduncle filiform, provided with several spreading sheaths, subtended by several scarious sheaths. *Ovary* pedicellate, linear, abruptly thickened at apex, 9 mm long, including the pedicel. *Floral bracts* linear-lanceolate, acuminate, scarious. *Flowers* very small, inconspicuous, hyaline, resupinate, with white sepals and petals, and green lip and column. *Dorsal sepal* elliptic-obovate, obtuse to slightly apiculate, concave, 2 × 1 mm. *Lateral sepals* obliquely broadly ovate-elliptic, apiculate, forming an inconspicuous mentum, 1.9 × 1.4 mm. *Petals* obliquely elliptic, rounded and apiculate at apex, slightly crenulate, 1.7 × 0.9 mm. *Lip* 3-lobed, subreniform-flabellate, 1.6 × 2.5 mm; the lateral lobes obliquely elliptic, broadly rounded at apex, erect and surrounding the column in natural position, attached to the column foot; the midlobe transversally elliptic to subquadrate, apiculate, with minutely crenulate margins. *Column* short, terete, slightly arcuate, 1.2 mm long. *Pollinia* 6, on a short caudicle. *Anther cap* subcordate, cucullate, 2-celled.

Distribution: from Guatemala to Panama.

Distribution in the Park: widespread along the main trails toward Bosque de Piedra, Cerro Barra Honda, Las Delicias, Las Cascadas, and La Palma, and pastures and secondary forest surrounding the park.

Etymology: from the Greek *micro*, "little, small," and *anthos*, "flower," in allusion to the tiny flowers.

Habitat and ecology: plants grow epiphytically in tropical moist and wet forest, seasonal warm lowlands along the Pacific coast, and the seasonal areas of Valle Central under 1500 m of elevation. It was observed on *Plumeria rubra* (Apocynaceae), *Spondias mombin*, *Syderoxylum capiri* (Sapotaceae), and *Brosimum aliscastrum* (Moraceae).

Phenology: from March to July.

Discussion: they are characterized by caespitose plants with fusiform, shortly stipitate, and not prolific pseudobulbs with 2 ligulate leaves at apex. The inflorescence is apical, racemose with several tiny white flowers less than 3 mm in diam. The other species of *Scaphyglottis* at BHNP, *S. stellata,* is distinguished by the larger, prolific plants and the larger, white-pink flowers in a shorter, racemose, few-flowered inflorescence.

Additional specimens examined: BHNP, Sendero Ceiba, sector de Las Cascadas, 10˚11'15.0"N, 85˚20'36.1"W, 210 m, bosque húmedo premontano transición a basal, epífitas en árbol caido de *Ficus* sp. (Moraceae), 11 julio 2005, *D. Bogarín 1672 y F. Paniagua* (JBL-spirit). BHNP, Cerros Barra Honda, Bosque de Cactus hacia una loma rocosa, al lado derecho, en dirección a La Mantequilla, 10˚10'34.6"N, 85˚21'20.7"W, 421 m, bosque húmedo premontano transición a basal, epífitas en *Plumeria rubra* (Apocynaceae), 21 febrero 2006, *D. Bogarín 2603* (JBL-spirit). BHNP, sendero hacia el Mirador Nacaome, 10˚09'56.7"N, 85˚21'39.3"W, 388 m, bosque húmedo premontano transición a basal, epífitas en bosque secundario a orillas del sendero, 20 marzo 2010, *D. Bogarín 7471* (JBL-spirit).

24b. ***Scaphyglottis stellata*** Lodd. ex Lindl., Edwards's Bot. Reg. 25: misc. 44. 1839. Fig. 13F, 49.

TYPE: [Guyana]. It is a native of Demerara, whence it was obtained by *Messrs. Loddiges* (Holotype: K).

Homotypic synonym: *Ponera stellata* (Lodd. ex Lindl.) Rchb. f., Ann. Bot. Syst. 6: 454. 1862.

Heterotypic synonyms: *Ponera amethystina* Rchb.f. in W.W. Saunders, Refug. Bot. 2(1): 93. 1872. TYPE: [PANAMA]. Sent from Santa Fé de Veraguas, by the late Mr. Skinner, to W. Wilson Saunders, *G. Skinner s.n.* (Holotype: W).

Scaphyglottis amethystina (Rchb.f.) Schltr., Beih. Bot. Centralbl. 36(2): 456. 1918.

Scaphyglottis brachiata Schltr., Repert. Spec. Nov. Regni Veg. 9: 432. 1911. TYPE: COSTA RICA. [Guanacaste]. In den Wäldern von Nicoya, blühend in Dezember 1899, *A. Tonduz* [s.n. (Herb. Instit. physico-geogr. nat. costaricensis] *13729* (Holotype: B, destroyed; Lectotype: designated by Pupulin et al., 2016: US).

Plants epiphytic, caespitose, erect or pendent, to about 40 cm tall, usually with superimposed pseudobulbs. *Roots* filiform, slender, glabrous, emerging from the rhizome, or at the connection of old and new pseudobulbs. *Pseudobulbs* fusiform, distinctly stipitate, to 12.0 × 0.5 cm, bearing 2 leaves (rarely 1-leaved), laterally flattened, each pseudobulb usually producing 1 to several new shoots at the apices of older shoots emerging from imbricating, papyraceous sheaths. *Leaves* linear-lanceolate to narrowly elliptic, obliquely retuse, conduplicate, subcoriaceous, to 12.0 × 0.8 cm. *Inflorescence* few-flowered, racemose, abbreviated, and appearing fasciculate, borne at the apex of each internode of the stem. *Ovary* pedicellate, linear, to 5 mm long. *Floral bracts* ovate-elliptic, acute, imbricate, scarious. *Flowers* small, with white sepals and petals, the lip rose-purple striped with purple; column and anther deep purple. *Dorsal sepal* lanceolate-elliptic, acute, slightly concave toward the apex, 7.0 × 2.5 mm. *Lateral sepals* connate at the base, forming a short mentum, obliquely linear-lanceolate, acute, 8.0 × 2.5 mm. *Petals* ligulate, slightly constricted toward the apex, then rounded and apiculate, 7.0 × 1.5 mm. *Lip* clawed, the blade 3-lobed, obovate-flabellate; lateral lobes large, rounded, erose at apex, inserted at the middle of the lip; midlobe subquadrate, obtuse to emarginate; entire lip 7 × 5 mm between the lateral lobes. *Column* terete, slightly arcuate, with 2 narrowly triangular stelidiar arms toward the apex, 3 mm long. *Pollinia* 4, on short bifid caudicles. *Anther cap* cucullate, rounded, 4-celled.

Distribution: Costa Rica to Bolivia and Brazil.

Distribution in the Park: common at Cerro Barra Honda, along the main trails and at Las Cascadas.

Etymology: from the Latin *stellatus*, "stellate, star-like, with spreading rays," in allusion to the spreading sepals and petals.

Habitat and ecology: epiphytic in tropical wet and moist forest from 0 to 1000 m of elevation along the Pacific lowlands from Península de Nicoya to Península de Osa. It was observed on *Brosimum aliscastrum, Ficus* sp. (Moraceae), and *Plumeria rubra*.

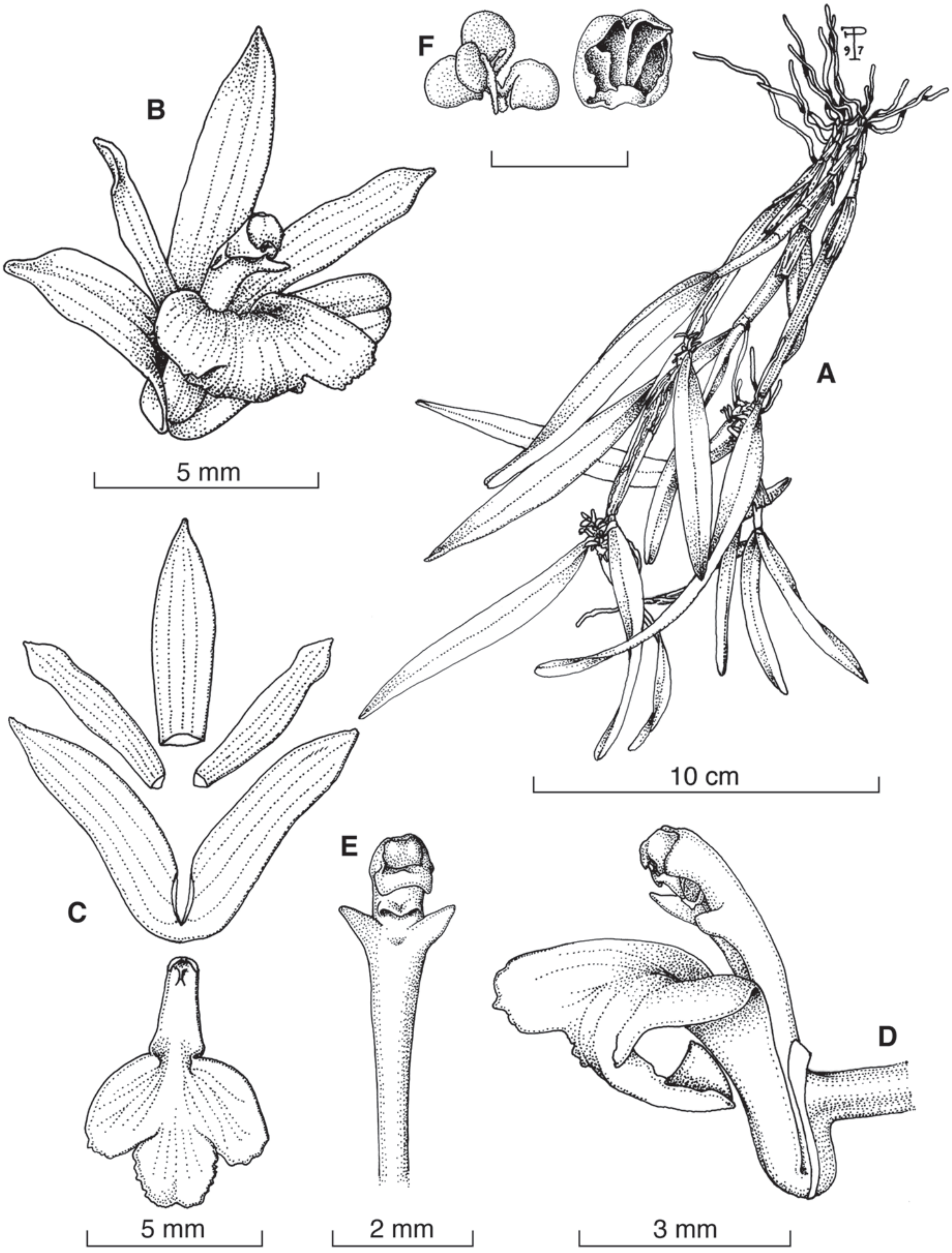

FIGURE 49. *Scaphyglottis stellata* Lodd. ex Lindl. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 300* (JBL).

Phenology: plants flower throughout the year but mostly from May to July.

Discussion: it is distinguished by the thick pseudobulbs produced in chains, the oblong leaves, the white-pink flowers in a short inflorescence developed at the base or at the apex of each pseudobulb, and the column with 2 stigmatic arms. *Scaphyglottis micrantha* has linear leaves, a nonprolific habit, and smaller white flowers produced apically in an elongate racemose inflorescence, and the plants are comparatively shorter than *S. stellata*.

Additional specimens examined: BHNP, Sendero Ceiba, sector de Las Cascadas, 10°11'15.0"N, 85°20'36.1"W, 210 m, bosque húmedo premontano transición a basal, epífitas en árbol caido de *Ficus* sp. (Moraceae), 11 julio 2005, *D. Bogarín 1673 y F. Paniagua* (JBL-spirit).

25. *Sobralia* Ruiz & Pav., Fl. Peruv. Prodr. 120. 1794.
TYPE: *Sobralia biflora* Ruiz & Pav.

Plants terrestrial or epiphytic, small or large herbs, with foliaceous, reed-like stem, rarely branching. *Leaves* distichous, sessile, pergameneous, plicate. *Inflorescence* a terminal raceme, often 1-flowered. *Flowers* showy, large, spread, fugacious, usually lasting 1 day or up to 3 days, often showing synchronous flowering in gregarious species. *Sepals* and *petals* subequal, sometimes shortly connivent at the base, spreading, the petals usually broader than sepals. Lip prominent, trumpet-like, not clawed, entire or 3-lobed, usually concave, the basal margins enfolding the column at the base, commonly retuse or bilobed, the disc smooth or lamellate, generally with an inconspicuous to conspicuous callus at the base made up of keels, toothed crests or bristles. *Column* elongate, fragile, usually ventrally provided with a strong keel, footless, often with a pair of falcate angles at the summit. *Anther* incumbent, 2-celled. *Pollinia* 8 or 4 in each cell, granular or subceraceous.

A Neotropical genus of about 130 species, widespread from Mexico to Peru, Bolivia, southern Brazil, and the West Indies. About 35 species in Costa Rica. One species recorded in BHNP.

Sobralia fenzliana Rchb.f., Bot. Zeitung (Berlin) 10: 714. 1852. Fig. 13G, 50.
TYPE: PANAMA. Chiriqui Cordilleren 1–2000', *J. Warszewicz s.n.* (Holotype: W).
Heterotypic synonyms: *Sobralia neglecta* Schltr., Repert. Sp. Nov. Regni. Veg. Beih. 19: 161. 1923. TYPE: COSTA RICA. Lisière des bois au Maderal de San Mateo, 450–500 m. 1922. *A. M. Brenes 279* (Holotype: B, destroyed; Isotype: AMES).

Plants epiphytic or rarely terrestrial, erect to pendent, to about 2 m tall. *Roots* fleshy, glabrous, to 5 mm in diam. Stem reed-like, slender, covered with amplexicaul, black-warty, hispidulous, tubular leaf sheaths, sometimes branched, lepidote. *Leaves* 3–7, distichous, plicate-veined, lanceolate to lanceolate-ovate, acuminate, coriaceous, to about 15–20 × 2.3–5.5 cm. *Inflorescence* apical, sessile, a 1-flowered raceme produced among several imbricating bracts. *Ovary* glabrous, to 3 cm long. *Flowers* large, fragile, fugacious often lasting 1 day, not wholly spreading, sepals and petals rose-purple with margins and tips white, the lip purple darker with the center red-purple and the base yellow, rarely white. *Dorsal sepal* lanceolate to oblong-elliptic, free, acute, slightly concave, conduplicate, recurved apically, about 4.5–6.0 × 1.6–1.9 cm. *Lateral sepals* obliquely lanceolate, acute, conduplicate, concave, and recurved toward the apex, 4.5–6.0 × 1.4–1.9 cm. *Petals* elliptic-lanceolate to elliptic-obovate, apically slightly conduplicate, acute, wider than sepals, 4.5–5.7 × 1.5–2.2 cm. *Lip* obovate, cuneate, obtuse to minutely retuse, deeply concave, trumpet-like, the basal margins tubular-involute, enclasping the column, the apex deflexed, spread, with slightly lacerate-crenulate margins, 6.5 × 3.6 cm; callus at the base of the lip formed by 2 low, slender, divergent carinae and numerous minute lamellae from the base toward the apex. *Column* elongated, subterete, slender, abaxially keeled, to 3.5 cm long, with a pair of falcate arms at the apex's sides, galeate in the middle. *Pollinia* 8, granular. *Anther cap* cucullate, bifid at the base, about 3 mm long.

Distribution: Nicaragua, Costa Rica, and Panama.

Distribution in the Park: a plant was found growing at La Jaralosa in Zona Protectora Cerros de Jesús, 6 km from BHNP in the humid evergreen forest. It is likely found at Los Mesones and Las Cascadas.

Eponymy: after the Austrian botanist Eduard Fenzl (1808–1879), professor of botany, director of the Imperial Botanical Cabinet, and member of the Vienna Academy of Sciences, who presented this species to H. G. Reichenbach.

Habitat and ecology: epiphytic in humid, warm, tropical moist and wet forest, premontane moist forest basal belt transition on both Caribbean and Pacific lowlands from 0 to 600 m of elevation. Plants were observed on *Syderoxylum capiri* (Sapotaceae).

Phenology: from January to July.

Discussion: distinguished by the epiphytic plants with branching, leafy, elongated stems bearing several plicate leaves and the rose-purple flowers with a trumpet-like lip, lasting 1 or 2 days.

Additional specimens examined: Guanacaste: Nicoya, Mansión, Zona Protectora Cerros de Jesús, ascenso por el sector de La Jaralosa, 10°05'58.1"N, 85°19'11.7"W, 436 m, bosque húmedo premontano transición a basal, epífitas en bosque secundario sobre un yurro con árboles altos, 14 julio 2005, *D. Bogarín 1693, F. Villalobos, C. Aguilar, O. Durán, F. Paniagua* (JBL-spirit).

26. *Specklinia* Lindl., Gen. Sp. Orchid. Pl. 8. 1830.
TYPE: *Specklinia lanceola* (Sw.) Lindl.

Plants epiphytic, rarely lithophytic, caespitose, or repent. *Stem* enclosed by tubular, imbricating sheaths, with an annulus. *Leaf* coriaceous, elliptic, oblong, orbicular to obovate, acute to obtuse, usually petiolate. *Inflorescence* racemose, sometimes flexuous. *Flowers* small, relatively inconspicuous, resupinate, rarely nonresupinate. *Sepals* triangular, ovate, acute or obtuse, elliptical, often caudate, or transversely ovate and cucullate, the lateral sepals free or variously connate to form a synsepal. *Petals* elliptical to

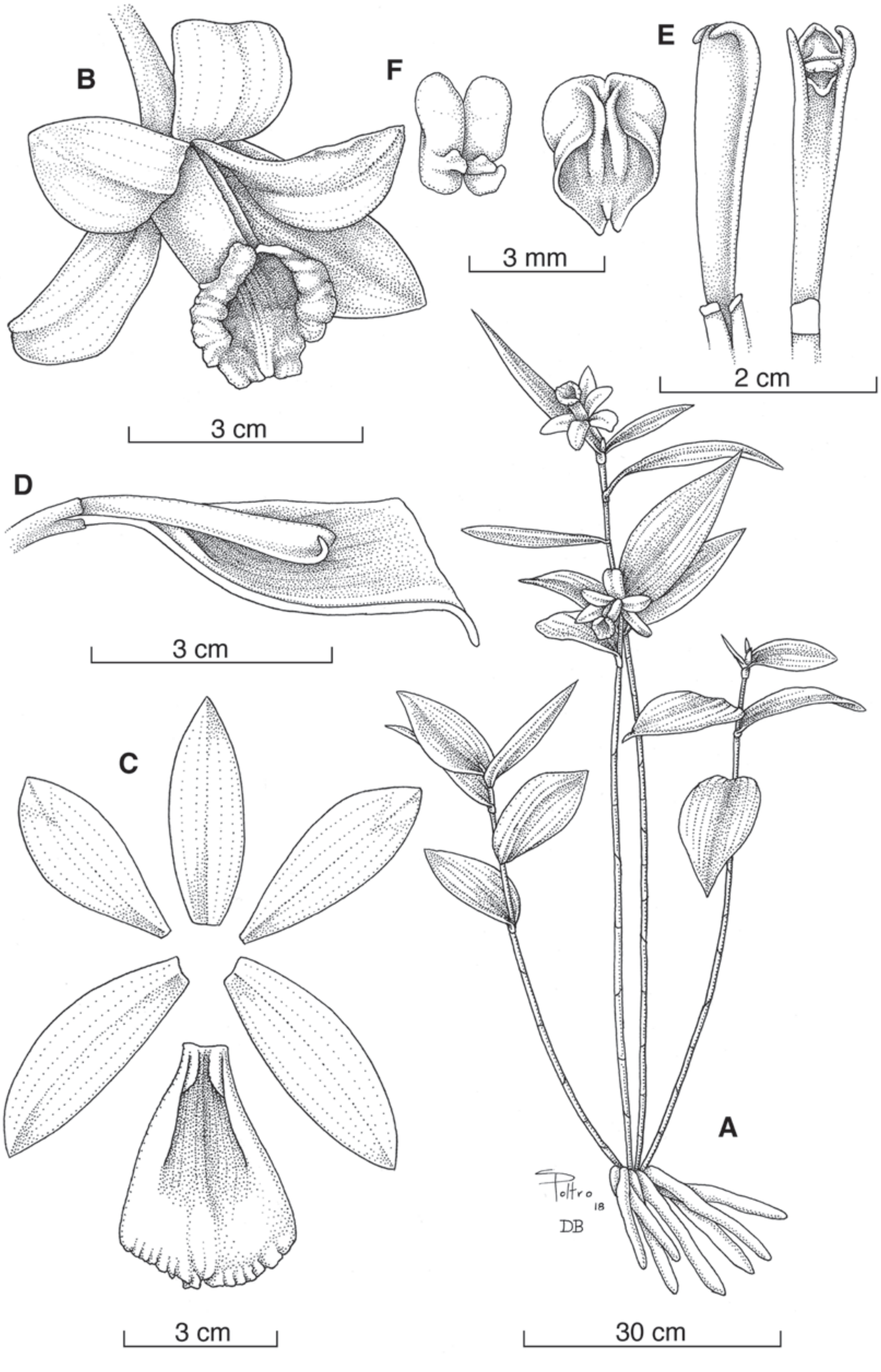

Figure 50. *Sobralia fenzliana* Rchb.f., **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip (longitudinal section), side view. **E,** Column, side and ventral view. **F,** Pollinarium and anther cap. Drawn by D. Bogarín and S. Poltronieri from *Bogarín 1693* (JBL).

oblong or spathulate, acute to obtuse, entire to fimbriate or lacerate. *Lip* simple or trilobed, elliptical to pyriform and subpandurate, acute to rounded, sometimes fimbriate, base usually hinged to column foot. *Column* semiterete, usually winged, with a foot. *Anther* apical, incumbent; *pollinia* 2; *stigma* entire. *Capsule* globose, elliptical to obovoid, sometimes verrucose or echinate.

A genus of nearly 200 species from Mexico to Bolivia, Brazil, and the West Indies. About 40 species in Costa Rica, 2 at BHNP.

KEY TO SPECIES OF *SPECKLINIA*

1a. Plants cespitose, erect, leaves smooth, not superposed .... *S. grobyi*

1b. Plants prostrate, creeping, appressed to the substrate, leaves granulose, superposed .... *S. panamensis*

26a. ***Specklinia grobyi*** (Bateman ex Lindl.) F. Barros, Hoehnea 10: 110. 1983 [1984]. Fig. 13H, 51.

Basionym: *Pleurothallis grobyi* Bateman ex Lindl., Edwards's Bot. Reg. 21: t. 1797. 1835. TYPE: [GUYANA. Demerara] "A native of Demerara, whence it was imported by Mr. Bateman," *J. Bateman s.n.* (Holotype: K). *Specklinia grobyi* (Bateman ex Lindl.) Pridgeon & M.W. Chase, Lindleyana 16(4): 258. 2001, isonym.

Plants epiphytic, caespitose, up to 3 cm high. *Roots* thin, to 1 mm in diam., grayish white with greenish-reddish tips. *Rhizome* distichous, covered by imbricate scarious bracts. *Ramicauls* slender, erect, to 1 cm long, enclosed by 2–3 whitish, imbricate, scarious, tubular sheaths. *Leaves* narrowly obovate-elliptic, oblong or suborbicular, erect, fleshy, coriaceous, lenticular, obtuse, conduplicate, emarginate with a small apicule beneath, stained with purple spots or lines on the underside, 1.0–2.2 × 0.6–1.1 cm, the base narrowly cuneate into a petiole 0.5–1.1 cm long. *Inflorescence* apical, racemose, distichous, lax, somewhat fractiflex, producing 3–7 flowers, longer than leaves, up to 6 cm long; peduncle filiform, to 3 cm long; rachis to 3 cm long. *Ovary* cylindrical, ridged, less than 2.0–2.5 mm; pedicel, 2.5–3.0 mm long. *Flowers* small, less than 5 mm in diam., resupinate, somewhat tubular, yellow, sometimes stained with red-purple at the apex of the sepals and striped with the same color along the lip and petals. *Dorsal sepal* ovate to elliptic, concave, conduplicate, acute, 4.8 × 1.8 mm. *Lateral sepals* connate up to the apex into an ovate synsepal forming a shallow mentum below the column foot, concave, conduplicate, subacute to obtuse, retuse, 4.7 × 2.5 cm. *Petals* oblanceolate-obovate, membranaceous, oblique, acute, 1.8 × 0.8 cm. *Lip* oblong, obtuse, somewhat arcuate basally, with a central depression and a callus with 2 light keels on both sides, the truncate base hinged to the column foot, 2.0 × 0.8 mm. *Column* oblong with 2 apical arms, the foot provided with 2 lobes on both sides at the base, the anther and stigma ventral, 2.0 × 0.7 mm. *Pollinia* 2, ovoid. *Anther cap* cucullate.

Distribution: widespread from Mexico to Brazil.

Distribution in the Park: found at Las Cascadas, BHNP, and La Jaralosa in Zona Protectora Cerros de Jesús, 6 km from BHNP in the humid evergreen forest.

Eponymy: Mr. Bateman named it in honor of Lord Grey of Groby, a British orchid enthusiast of the 19th century.

Habitat and ecology: epiphytic in seasonal tropical moist forest and premontane moist forest basal belt transition along the Caribbean and Pacific lowlands from 0 to 1000 m of elevation.

Phenology: from December to April.

Discussion: characterized by the caespitose, erect, small (less than 4 cm tall) plants without pseudobulbs, and the distichous inflorescences that produce tiny yellow flowers less than 6 mm long. The other species of *Specklinia* at BHNP have similar flower morphology. However, it could be easily distinguished by the creeping or repent plants, shorter petioles less than 5 mm long (vs. up to 1.1 cm long in *S. grobyi*) with prostrate, superposed, granulose-verrucose leaves (see description and discussion below).

Additional specimens examined: Guanacaste: Nicoya, Mansión, Zona Protectora Cerros de Jesús, ascenso por el sector de La Jaralosa, 10°05'58.1"N, 85°19'11.7"W, 436 m, bosque húmedo premontano transición a basal, epífitas en bosque secundario sobre un yurro con árboles altos, 14 Julio 2005, *D. Bogarín 1697, F. Villalobos, C. Aguilar, O. Durán, F. Paniagua* (JBL-spirit).

26b. **Specklinia panamensis** (Schltr.) Bogarín & Pupulin, *comb. nov.* Fig. 13I, 52.

Basionym: *Pleurothallis panamensis* Schltr., Repert. Spec. Nov. Regni Veg. 17(8–12): 140. 1921. TYPE: PANAMA. Auf Pampasbäumen in der Provinz Chiriqui und Veragua, blühend im Apr 1858, *M. Wagner 24* (Holotype: B, destroyed; Lectotype: designated here, tracings of Schlechter's drawings of the holotype: AMES 22755).

Plants epiphytic, creeping, prostrate, attached to the substrate, with overlapping leaves, forming large aggregations or mats on the branches and trunks. *Roots* thin, to 1 mm in diam., grayish white with green-reddish tips. *Rhizome* distichous, fractiflex, repent, covered by imbricate, scarious bracts. *Ramicauls* slender, horizontal, prostrate, to 5 mm long, enclosed by 2–3 imbricate, whitish, scarious tubular sheaths. *Leaves* oblong-elliptic, widely ovate or suborbicular, distichous, prostrate, verrucose or granulose in both sides, coriaceous, superposed, fleshy, lenticular, subacute, shallowly conduplicate, shallowly emarginate with a small apicule beneath, abaxially with purple spots on the verrucae, 1.0–2.2 × 0.6–1.1 cm, the base narrowly cuneate into a petiole less than 5 mm long. *Inflorescence* apical, racemose, distichous, lax, somewhat fractiflex, producing up to 5 flowers, longer than leaves, up to 8.5 cm long; peduncle filiform, to 4.0–4.5 cm long; rachis 3–4 cm long. *Ovary* cylindrical, widened apically, ridged, to 3 mm; pedicel, to 8 mm long. *Flowers* small, to 1 cm in diam., resupinate, somewhat tubular, yellow, the dorsal sepal striped with red-purple along the main veins, the petals with a red-purple stripe in the middle, the lip yellow stained with

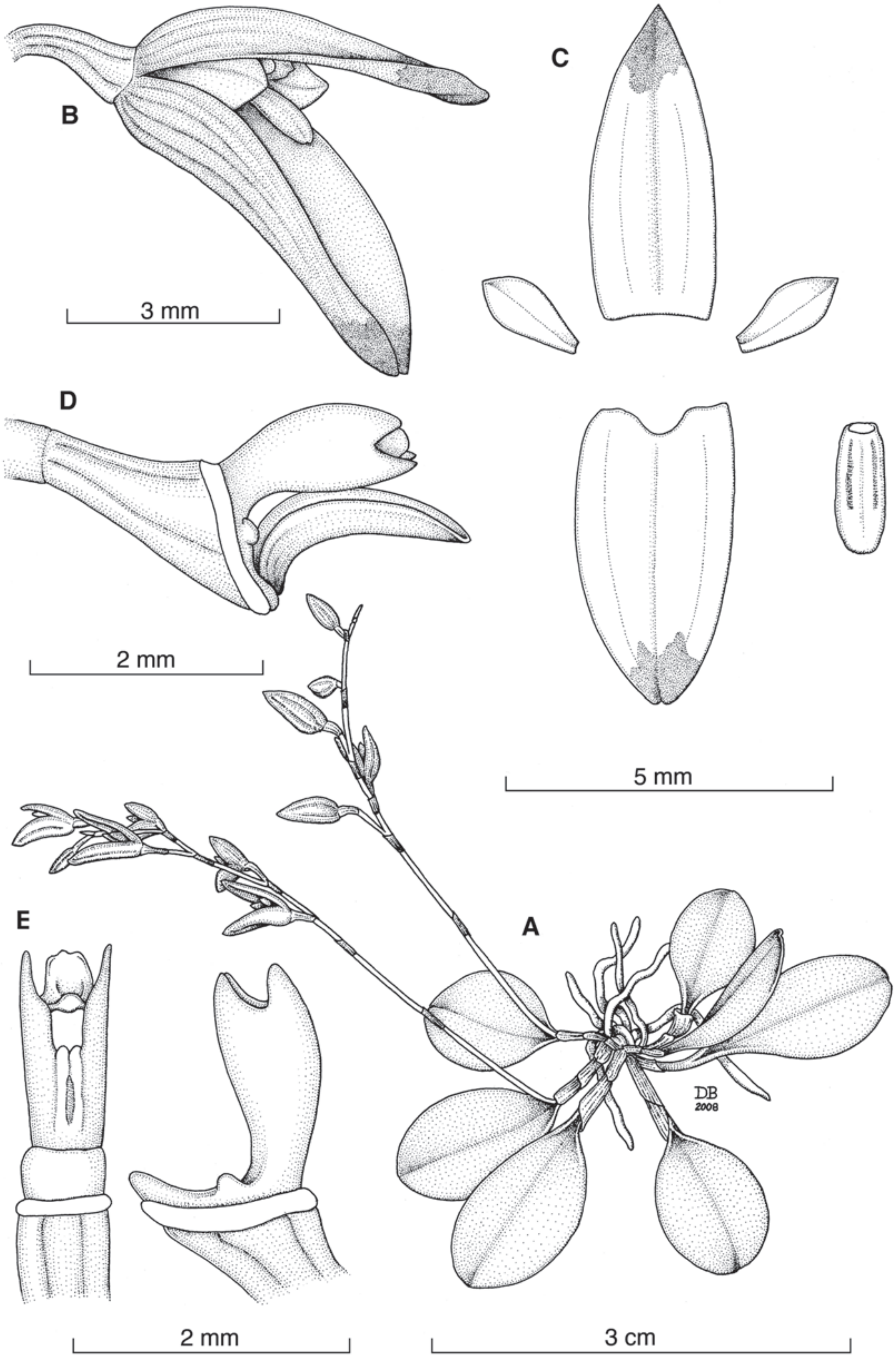

FIGURE 51. *Specklinia grobyi* (Bateman ex Lindl.) F. Barros. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, side and ventral view. Drawn by D. Bogarín from *Bogarín 1697* (JBL).

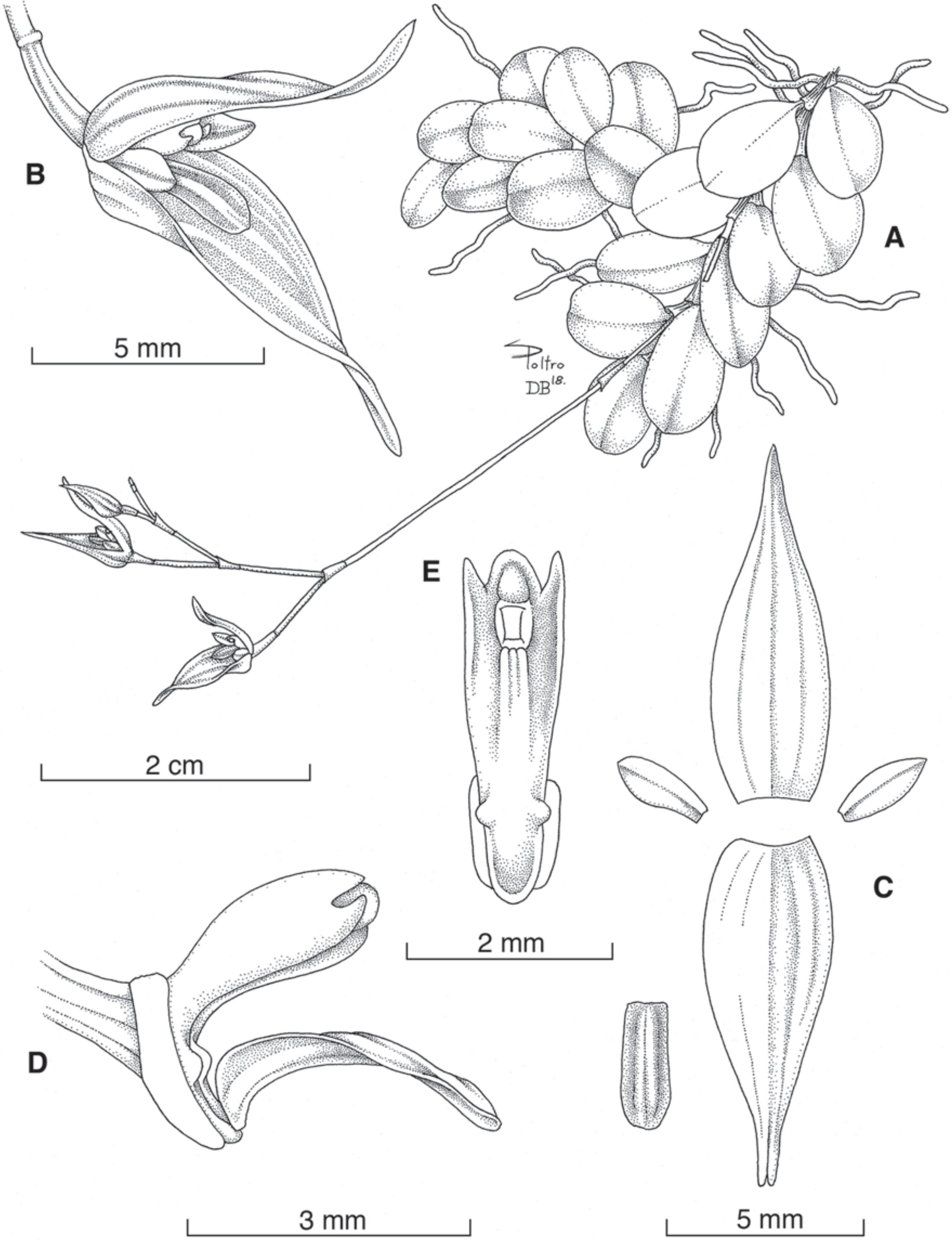

FIGURE 52. *Specklinia panamensis* (Schltr.) Bogarín & Pupulin. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. Drawn by D. Bogarín and inked by S. Poltronieri from *Bogarín 1688* (JBL).

red-purple on the keels, the column yellow. *Dorsal sepal* ovate, concave, conduplicate, acute to acuminate, 9.3 × 3.0 mm. *Lateral sepals* connate up to the apex into an ovate synsepal forming a shallow mentum below the column foot, concave, conduplicate, subacute to obtuse, bifid, 9.0 × 3.5 cm. *Petals* oblanceolate-obovate, membranaceous, oblique, acute, 2.5 × 1.0 cm. *Lip* oblong, obtuse, somewhat arcuate basally, with a central depression and a callus with 2 light keels on both sides, the truncate base hinged to the column foot, 3.0 × 1.5 mm. *Column* oblong with 2 apical arms, the foot provided with 2 lobes on both sides at the base, the anther and stigma ventral, widened apically, 3.1 × 0.9 mm. *Pollinia* 2, ovoid. *Anther cap* cucullate.

Distribution: known from Costa Rica and Panama.

Distribution in the Park: common around the main trails at Cerro Barra Honda, Las Cascadas, and Las Delicias, and on tall trees, branches, and main tree trunks.

Etymology: named after Panama, the country where Moritz Wagner collected the type specimen in 1858.

Habitat and ecology: epiphytic in tropical moist forest, premontane moist forest basal belt transition on branches or main tree trunks, mostly on exposed full sunlight.

Phenology: from March to June.

Discussion: the species complex around *Specklinia grobyi-microphylla* has been challenging to interpret because of the similar flower morphology and small size. We were unable to locate the type specimen of *S. microphylla*. However, a drawing of the type (AMES 57908) shows a plant with erect leaves and 2 flowers on each inflorescence, as noted in the protologue by Richard and Galeotti (1845). The specimens of BHNP differ from *S. microphylla* in the creeping plant habit (vs. caespitose), shorter petioles less than 5 mm long (vs. up to 1.1 cm long), prostrate, granulose-verrucose leaves (vs. erect, smooth), and inflorescences with up to 5 flowers (vs. 2). Among the synonyms assigned to *S. microphylla* (Luer, 2006), we found a species named by Schlechter (1921) as *Pleurothallis panamensis* that matches the specimens collected in BHNP. *Specklinia panamensis* is distinguished by the creeping, repent plants with prostrate, superposed, rounded, granulose-verrucose leaves with lax inflorescences. The flowers are yellow with red stripes on the dorsal sepal, the petals and lip are stained red-purple. Flower morphology of *S. panamensis* is similar to *S. grobyi*; however, it has rounded, prostrate, granulose-verrucose leaves (vs. pedicellate, smooth, elliptic), larger flowers up to 1 cm in diam. (vs. less than 5 mm), and the synsepal and the dorsal sepal acuminate and longer—up to 9 mm long (vs. acute and smaller—less than 5 mm long in *S. grobyi*). Inflorescences are also comparatively longer, with peduncles up to 4.5 cm long (vs. less than 3 mm) and pedicels up to 8 mm long (vs. 3 mm long). This species ranges from Costa Rica (Guanacaste, Alajuela, Puntarenas) up to Panama (Chiriquí). The specimens collected in BHNP and treated here as *S. panamensis* differ from the drawing published by Luer (2006) as *S. microphylla,* which shows a repent habit but erect, smooth leaves and different flower shape (i.e., pandurate lip vs. oblong). Specimens with those characteristics have been collected in the Caribbean lowlands of Costa Rica.

Additional specimens examined: BHNP, Sendero Ceiba y Mirador, 10°10'06.1"N, 85°21'47.4"W, 430 m, bosque húmedo premontano transición a basal, epífita sobre *Spondias mombin*, en bosque secundario, 12 julio 2005, *D. Bogarín 1688 y F. Paniagua* (JBL-spirit).

27. *Trichosalpinx* Luer, Phytologia 38: 393–394. 1983.
TYPE: *Trichosalpinx ciliaris* (Lindl.) Luer.

Plants epiphytic, rarely lithophytic or terrestrial, caespitose, ascending to long-repent, erect, or pendent. *Stem* enclosed by tubular or infundibular lepanthiform sheaths, often proliferating, with an annulus. *Leaf* coriaceous, elliptical, oblanceolate to obovate, acute to obtuse, petiolate, conduplicate, sometimes suffused with purple. *Inflorescence* racemose, rarely single-flowered. *Floral bracts* tubular or infundibular. *Flower* small, resupinate, or nonresupinate. *Sepals* elliptical to ovate, often caudate and pubescent, entire or ciliate, the lateral sepals free or connate into a synsepal. *Petals* smaller than sepals, elliptical to oblong or triangular, acute to rounded entire, dentate, pubescent. *Lip* simple and oblong or trilobed, ciliate, the base flexibly hinged to column foot. *Column* terete or semiterete, winged or hooded, with a foot. *Anther apical*, incumbent. *Pollinia* 2, ovoid with a granular caudicle. *Stigma* entire. *Capsule* ellipsoid or obovoid.

A genus of more than 100 species ranging from Mexico to the West Indies, Bolivia, Venezuela, and Brazil. About 25 species in Costa Rica, 1 at BHNP.

Trichosalpinx reflexa Mel. Fernández & Bogarín, Phytotaxa 38: 42. 2011. Fig. 14A, 53.
TYPE: COSTA RICA. Guanacaste: Nicoya, San Antonio, Barra Honda National Park, Ceiba trail, area of Las Cascadas, 10°11'15"N, 85°20'36.1"W, 210 m, basal transition to premontane wet forest, epiphytes in fallen *Ficus* sp. (Moraceae) tree, 11 July 2005, *D. Bogarín 1674 y F. Paniagua* (Holotype: JBL; Isotype: CR).

Plants epiphytic, caespitose, erect to suberect, up to 10 cm tall. *Roots* slender, flexuous, to 2 mm in diam. *Ramicauls* slender, pendulous, terete, 1.5–5.5 cm long, enclosed by 2–7 tubular bracts, adpressed at the base, ribbed, minutely ciliate at the margins, brown, 0.8–1.4 cm long. *Leaves* narrowly elliptical to narrowly obovate, apiculate, erect, fleshy, coriaceous, green suffused with purple beneath, 2.7–5.4 × 0.7–1.4 cm, the cuneate-attenuate base narrowing into a petiole up to 0.7 cm long. *Inflorescence* distichous, a successively 4- to 8-flowered raceme, 1.2–1.6 cm long including the peduncle 4 mm long, produced at the base of the leaf from a small, conduplicate, linear-ovate, acute spathe. *Floral bracts* cuneiform, conduplicate, 1 × 1 mm. *Pedicels* 1 mm long, persistent. *Ovary* cylindric, 1 mm long. *Flowers* with the sepals white suffused with dark purple toward the apex, petals translucent white, the lip blackish purple, the column, and anther white. *Dorsal sepal* erect, oblong, obtuse, convex toward the apex, 3.5–4.5 × 2.0–2.5 mm, 3-veined. *Lateral sepals* connate into an ovate-oblong, retuse, entire synsepal, concave at the base, and reflexed toward the apex, 3–4 × 2.0–2.5 mm, 3-veined. *Petals* oblong, acute, entire or minutely serrate, the apex

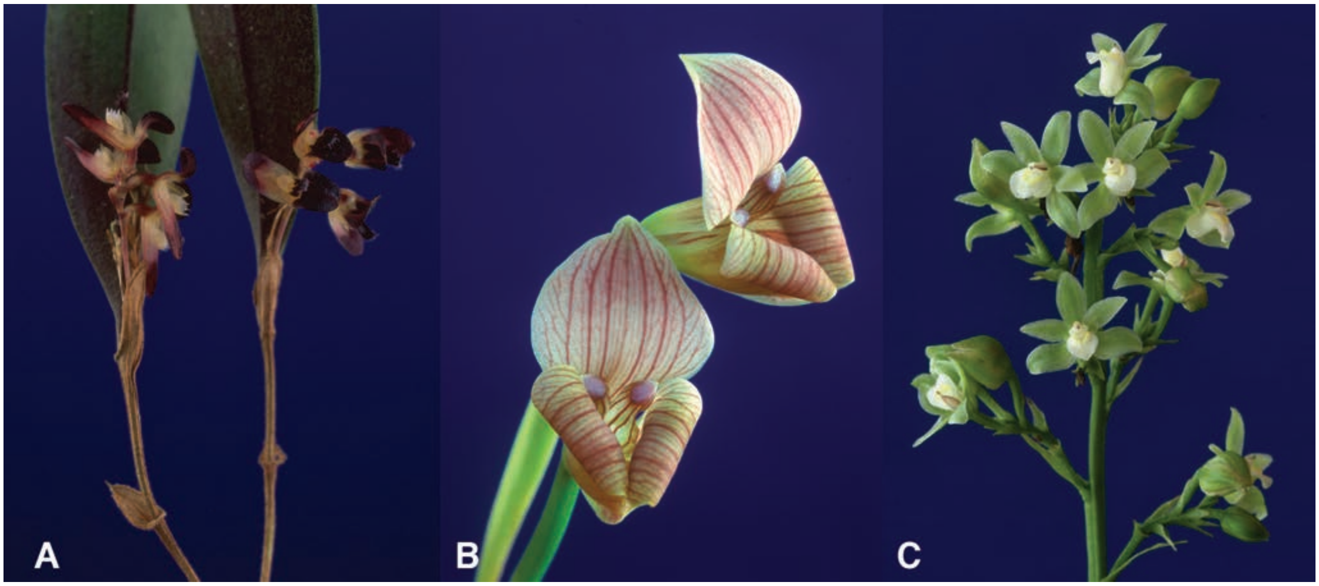

FIGURE 14. **A–C.** Orchid species found at Barra Honda National Park. **A,** *Trichosalpinx reflexa* (*Bogarín 1674*, JBL). **B,** *Trigonidium egertonianum* (*Pupulin 8200*, JBL). **C,** *Tropidia polystachya* (*Bogarín 11025*, JBL). Photographs by the authors.

erose, 1.8 × 1.0 mm. *Lip* oblong, obtuse, ciliate, 2.0–3.0 × 1.5 mm, the disc with a central carina in the basal third, divided into 2 low keels close to the second third, the basal lobes erect. *Column* short, semiterete, deeply erose-fimbriate at the apex, broadly winged near the apex, 2 mm long, the clinandrium apical, the stigma ventral. *Anther cap* incumbent, ovate, emarginate. *Pollinia* 2, pyriform, on a cellular, oval viscidium.

Distribution: known only from Costa Rica. It could be found in southwestern Nicaragua.

Distribution in the Park: found growing in the gallery forest at Las Cascadas.

Etymology: from the Latin *reflexus,* "reflexed," in reference to the characteristic reflexed synsepal of the flowers.

Habitat and ecology: it is restricted to the lowland semideciduous forests of the northern Pacific lowlands of Costa Rica. Plants inhabit tropical wet, very wet, and transitional premontane forests, between 100 and 500 m elevation. They were recorded growing on *Ficus* sp. (Moraceae) and the main tree trunks of *Anacardium excelsum*, mostly along riverbanks under shady conditions.

Phenology: plants flower from September to December.

Discussion: Plants are epiphytic without pseudobulbs, with stems covered by lepanthiform bracts and the leaves tinged with purple on the underside. The inflorescence comes under the leaf with several purple-white flowers. *Trichosalpinx reflexa* is similar to *T. memor* (Rchb.f.) Luer but differs mainly by the narrow elliptic-lanceolate leaves, glabrous sepals, the erect dorsal sepal, and the synsepal reflexed toward the apex (Fernández and Bogarín, 2011).

Additional specimens examined: BHNP, Ceiba trail, area of Las Cascadas, 10˚11'15"N, 85˚20'36.1"W, 210 m, basal transition to premontane wet forest, epiphytes in fallen *Ficus* sp. (Moraceae) tree, 11 July 2005, *D. Bogarín 1674 y F. Paniagua*.

28. *Trigonidium* Lindl., Edwards's Bot. Reg. 23: t. 1923. 1837.

TYPE: *Trigonidium obtusum* Lindl.

Plants epiphytic, caespitose, rhizomatous, erect to scandent herbs. *Pseudobulbs* sulcate, 2- to 5-foliate at the apex. *Leaves* conduplicate, linear or elliptic, subcoriaceous, acute, persistent. *Inflorescence* a simple, short to usually elongate, erect, raceme from the bases of pseudobulbs, 1-flowered. *Flowers* relatively large, tubular, erect, trigonous, yellow to greenish, or cream with purplish stripes. *Sepals* subequal, the bases connivent forming a tube that encloses the petals, labellum, and column, the apex spreading. *Petals* smaller and narrower than sepals, with an apical, glossy brown callus. *Lip* 3-lobed, the lateral lobes erect, the midlobe thickened, the disc with a ligular callus. *Column* short, semiterete, footless, with terminal, incumbent anther. *Pollinia* 4, waxy.

A Neotropical genus of some 12 species, ranging from Mexico to Brazil. Only 3 species in Costa Rica, 1 at BHNP.

Trigonidium egertonianum Bateman ex Lindl., Edwards's Bot. Reg. 24: misc. 73–74. 1838. Fig. 14B, 54.

TYPE: A native of the Bay of Dulce in Honduras, where it was discovered by *G. U. Skinner s.n.* (Holotype: K).

Plants epiphytic, caespitose, forming large clumps, to 50 cm long. *Roots* fleshy, glabrous, to 2 mm in diam. *Pseudobulbs* ovate, somewhat laterally compressed, sulcate, to 3.5–7.0 × 1.5–3.2 cm, basally covered by 2–3 papyraceous sheaths, bifoliate at the apex (rarely monophyllous). *Leaves* narrowly oblanceolate to linear, arching, acute, to about 28.4–38.0 × 1.7–2.4 cm. *Inflorescence*s basal, erect, slender, single-flowered scape to 20 cm long, covered by many closely appressed, tubular, papyraceous sheaths. *Flowers* rather showy, pale yellow to pale orange striped and reticulated with purple, the petals provided with metallic blue to mauve blotch near the apex. Sepals free, appressed

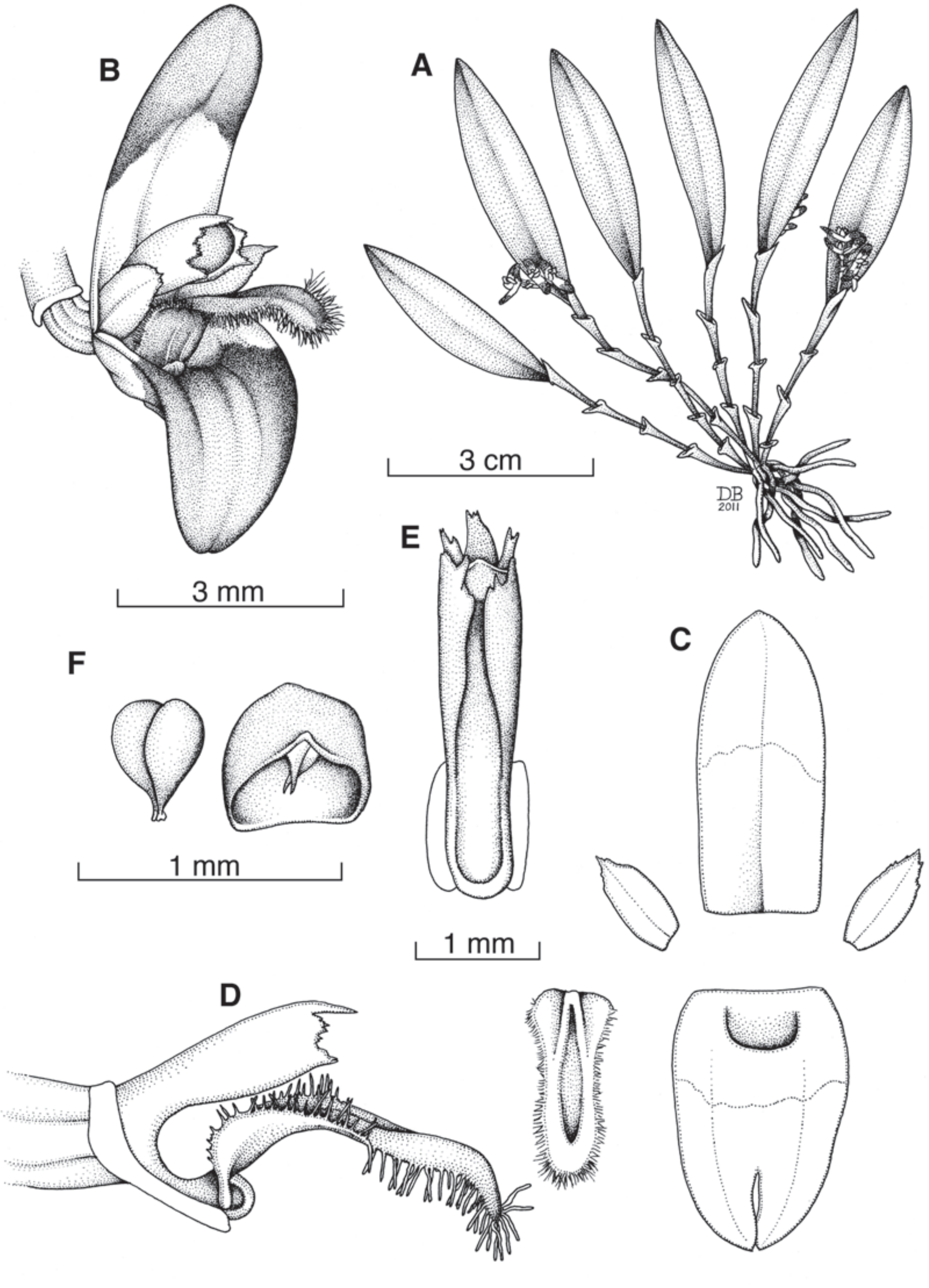

FIGURE 53. *Trichosalpinx reflexa* Mel. Fernández & Bogarín. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by D. Bogarín from *Bogarín 1674* (JBL).

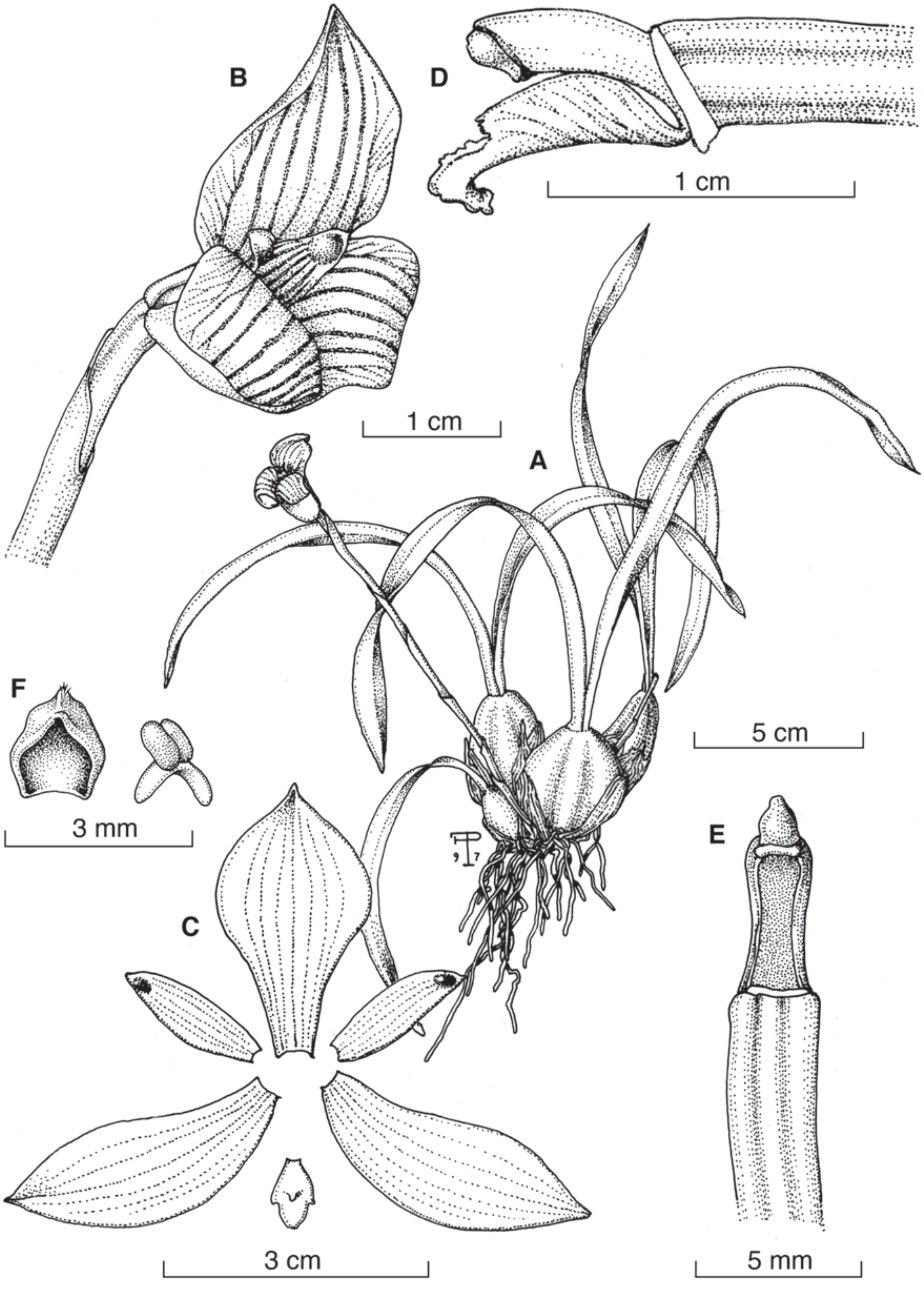

FIGURE 54. *Trigonidium egertonianum* Bateman ex Lindl. **A,** Habit. **B,** Flower. **C,** Perianth flattened. **D,** Column and lip, side view. **E,** Column, ventral view. **F,** Pollinarium and anther cap. Drawn by F. Pupulin from *Pupulin 368* (JBL).

toward the base forming a tube, then abruptly expanded and reflexed at the apex. *Dorsal sepal* shortly unguiculate, elliptic oblanceolate, acute, 3.3 × 1.8 cm. *Lateral sepals* obliquely elliptic-lanceolate, acute, 3.4 × 1.3 cm. *Petals* lanceolate, acute, about 1.8 × 0.6 cm. *Lip* 3-lobed, articulate with the base of the column; lateral lobes erect and parallel to the column, acute; the midlobe ovate, acute to obtuse, somewhat fleshy, verrucose; disc with a fleshy ligulate callus as long as the lateral lobes; entire lip 8 × 5 mm wide between lateral lobes. *Column* subterete, about 7 mm long. *Pollinia* 2, elliptic, on a saddle-shaped caudicle. *Anther cap* cucullate, keeled.

Distribution: from Mexico to Colombia and Venezuela.

Distribution in the Park: found at Las Cascadas and Los Mesones in the humid evergreen forest.

Eponymy: named after Sir Philip de Malpas Grey Egerton, 10th Baronet FRS (1806–1881), an English paleontologist who introduced many tropical plants to England.

Habitat and ecology: common at lowland elevations from 0 to 900 m in both Caribbean and Pacific watersheds, forming large populations in the forest canopy. Mostly found on *Anacardium excelsum*, *Pachira fendleri,* and *Syderoxylum capiri*.

Phenology: plants flower throughout the year but mostly from January to May.

Discussion: plants are easily distinguished by the abbreviated rhizome, the bifoliate pseudobulbs with narrow-linear leaves, and the 1-flowered, elongate inflorescence with campanulate upward-facing flowers produced at the base of mature pseudobulbs. The sepals hide the shorter petals, lip, and column.

Additional specimens examined: BHNP, sector de Las Cascadas ingresando por Finca San Diego (Finca Los Trejos), 10°10'59.86"N, 85°20'17.41"W, 86 m, bosque húmedo premontano transición a basal, epífitas en bosque de galería sobre *Brosimum alicastrum* "Ojoche" (Moraceae) cercano a un curso de agua, 22 febrero 2012, *D. Bogarín s.n.* (unvouchered).

29. *Tropidia* Lindl. in Wall., Cat. n. 7386. 1831; Lindl., Bot. Reg. 19: sub. t. 1618. 1833.
TYPE: *Tropidia curcugiloides* Lindl.

Plants terrestrial, perennial, erect, leafy herbs, palm-like. *Roots* fibrous pubescent developed from a short rhizome with several secondary rootlets, sometimes with swollen nodules. *Stems* erect, with several leaves at the apex, branching. *Leaves* distichous, oblong-lanceolate to elliptic-lanceolate, membranaceous or chartaceous, strongly plicate. *Inflorescence* apical, a densely paniculate raceme with several subulate floral bracts, rarely occurring also in the axils of the leaves along the stem. *Flowers* small, numerous, inconspicuous, often self-pollinated. *Sepals* and *petals* oblong-elliptic, acute, concave, the lateral sepals connate at the base forming an inconspicuous mentum, petals elliptic-lanceolate. *Lip* cymbiform, strongly concave-saccate with the basal margin involute, sessile, entire, oblong, canaliculate, parallel to and partly embracing the column in natural position. *Column* short, straight. *Anther* dorsal. *Stigma* apical. *Pollinia* 2, granulose, sectile. *Capsule* spreading, 6-ridged.

A Pantropical genus of about 40 species ranging from India to southeast Asia, northeast Australia, and the South Pacific Islands (Fiji and Samoa). *Tropidia polystachya* is the only species outside of Asia, ranging from Florida through the Antilles, Central America, Venezuela, and the Galapagos Islands. This is the first record in Costa Rica and BHNP.

Tropidia polystachya (Sw.) Ames, Orchidaceae 2: 262. 1908. Fig. 14C, 55.

Basionym: *Serapias polystachya* Sw., Prodr. 119. 1788.
TYPE: JAMAICA. Hispaniola, *O. Swartz s.n.* (Holotype: not located).

Homotypic synonyms: *Neottia polystachya* (Sw.) Sw., Fl. Ind. Occid. 3: 1415. 1806.

Stenorrhynchos polystachyon (Sw.) Spreng., Syst. Veg. 3: 710. 1826.

Tomotris polystachya (Sw.) Raf., Fl. Tellur. 2: 89. 1837.

Chloidia polystachya (Sw.) Rchb.f. in W.G. Walpers, Ann. Bot. Syst. 6: 644. 1863.

Corymborkis polystachya (Sw.) Kuntze, Revis. Gen. Pl. 2: 658. 1891.

Plants erect, leafy, palm-like, up to 45 tall, with a short rhizome. *Roots* slender, fibrous, coarse, pubescent, about 2 mm in diam. *Stems* often branched, with 3–4 lateral branches up to 30 cm long. *Leaves* several, distichous, oblong-elliptic to elliptic-lanceolate, acute to long-acuminate, 7-veined, 9.4–17.0 × 4.3–7.3 cm, thin, plicate, chartaceous, petiole 2.0–3.5 cm long, nervose, involving the stem. *Inflorescence* densely paniculate, with a slender, ridged peduncle, 3.8 cm long, flowers rarely occurring also in the axils of the leaves along the stem, rachis 9.5 cm long, about 14 lateral branches 0.2–1.3 cm long with 2–6 helicoid flowers on each branch. *Floral bracts* subulate to ovate-lanceolate, conduplicate, acute to acuminate, 3.0–3.5 × 2.0–2.5 mm, the bracts subtending each branch of the inflorescence much longer, narrowly lanceolate, acute or acuminate, peduncle bracts 1.7–3.0 × 0.2–0.3 cm, basal bracts of the lateral branches of rachis 1.7 × 0.2 cm. *Ovary* cylindrical, 9 mm long. *Flowers* greenish white, spread, self-pollinated. *Dorsal sepal* oblong-elliptic, strongly concave, acute, slightly apiculate, 7.6–2.6 mm. *Lateral sepals* obliquely oblong-elliptic to rarely linear-oblong, acute or subacute, conduplicate or concave at the apex, gibbous at the base, subfalcate, 7.2–2.5 mm. *Petals* elliptic-lanceolate, curved, acute, 6.7–2.1 mm. *Lip* cymbiform, strongly concave-saccate with the basal margins involute, thickened and with a median groove at the base, lightly constricted at about the middle, with the anterior half thin and somewhat expanded, broadly rounded and often retuse with an apicule in the sinus; disc pubescent at about the middle, with 2 intramarginal ridges that converge near the apex, 5.5 × 2.1 mm. *Column* terete, 3.5 × 1.2 mm, anther dorsal, stigma apical. *Anther cap* oblong, acute, dorsally keeled. *Capsule* oblong-ellipsoid, prominently 6-ribbed, becoming dark brown or black at maturity, about 1 cm long.

Distribution: from Florida to northern South America and the Antilles.

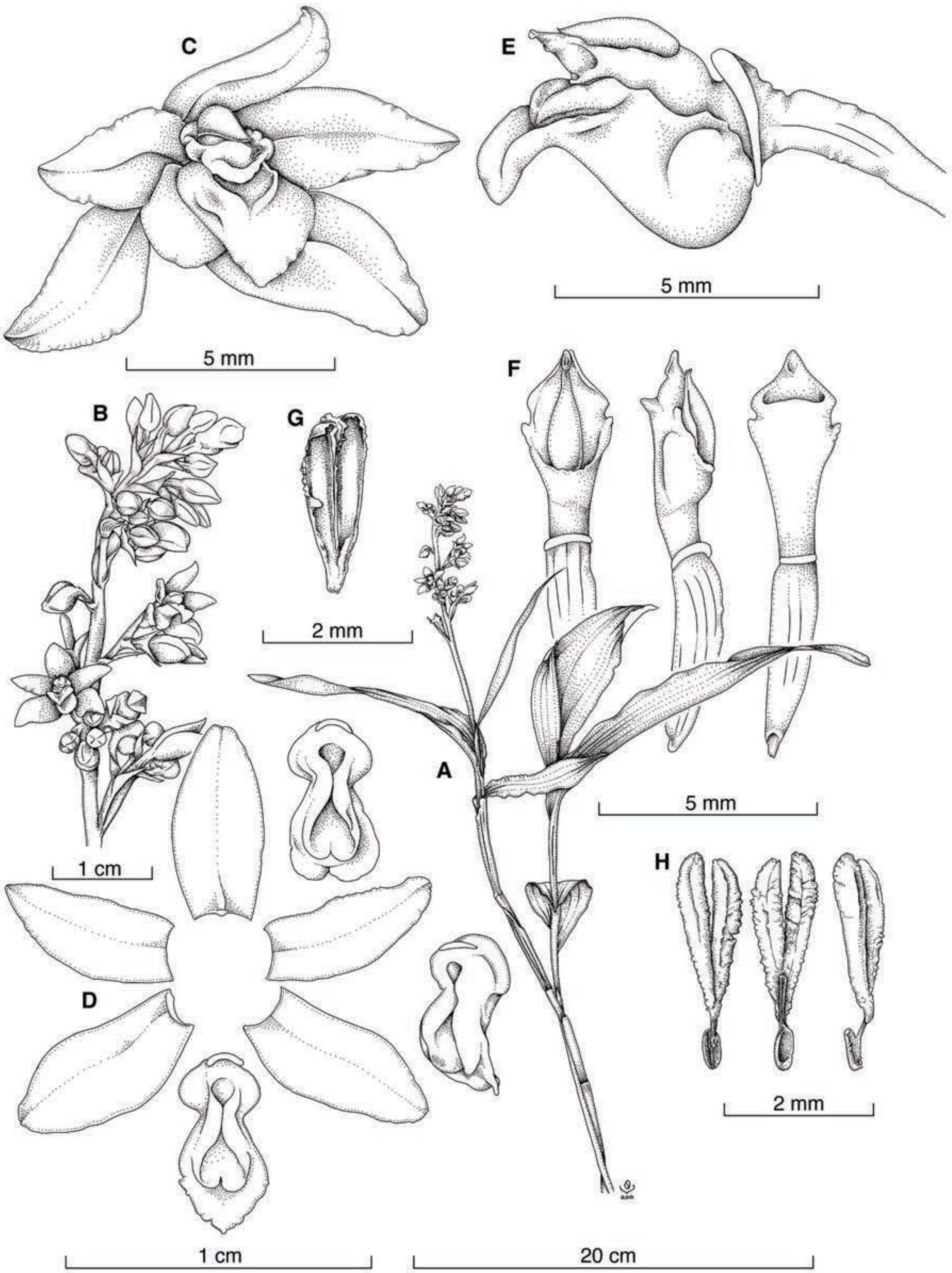

FIGURE 55. *Tropidia polystachya* (Sw.) Ames. **A,** Habit. **B,** Portion of the inflorescence. **C,** Flower. **D,** Perianth flattened. **E,** Column and lip, side view. **F,** Column, dorsal, lateral and ventral view. **G,** Anther cap. **H,** Pollinarium, front, ventral and side view. Drawn by F. Pupulin and L. Oses from *Bogarín 11205* (JBL).

Distribution in the Park: rare in the Park. We found only 1 population of 8 plants just before the beginning of Sendero Ceiba.

Etymology: from the Greek *poly*, "many," and *stachys*, "spike," referring to the several branches of the inflorescence.

Habitat and ecology: terrestrial in humus on shaded hills in secondary forest, premontane moist forest, basal belt transition in the lowlands of Península de Nicoya in Guanacaste, at around 350 m of elevation.

Phenology: September to November.

Discussion: plants are terrestrial with branching stems and plicate, chartaceous, dark-green leaves, similar to other species of *Corymborkis* Thouars and *Palmorchis* Barb. Rodr. The inflorescences are paniculate with somewhat inconspicuous greenish-white flowers, often self-pollinated. The lip is thickened, cymbiform, and concave-saccate. In the understory forest, they can be confused with small palms. Within BHNP, they are the only terrestrial species without pseudobulbs or corms bearing persistent plicate, chartaceous leaves and branching stems. This is the first record of the genus *Tropidia* in Costa Rica.

Additional specimens examined: BHNP, camino principal de la estación al Sendero Ceiba, parte alta antes de llegar al parqueo, 10°10'21.53"N, 85°21'42.50"W, 342 m, bosque húmedo premontano transición a basal, terrestres a orillas del camino, bosque secundario, 7 noviembre 2011, *D. Bogarín 9424* (CR). Same locality, *D. Bogarín 9426* (USJ); *D. Bogarín 9426 and 9427* (JBL-spirit). Same locality, 3 octubre 2014, *D. Bogarín 11205, N. Belfort & A. Karremans* (JBL).

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NOTES ON THE GENUS *CAPPARIDASTRUM* (CAPPARACEAE) AND THE DESCRIPTION OF *C. ESTRELLAE*, A NEW SPECIES FROM NORTHWESTERN ECUADOR

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Abstract. The genus *Capparidastrum* (Capparaceae) is discussed and *C. estrellae*, a new tree species endemic to northwestern Ecuador, is described and illustrated. Its conservation status is here assessed as endangered.

Keywords: Capparaceae, Ecuador, *Capparidastrum estrellae*, endemic

Resumen. Se comenta el género *Capparidastrum* (Capparaceae), y se describe e ilustra *Capparidastrum estrellae*, una nueva especie de árbol endémica del noroccidente de Ecuador. El estado de conservación de *Capparidastrum estrellae* aquí asignado es en peligro.

Palabras claves: Capparaceae, Ecuador, *Capparidastrum estrellae*, endémica

Capparidastrum (DC.) Hutch. (Capparaceae) is a Neotropical genus of shrubs and trees, comprising two subgenera, *Capparidastrum* and *Pulviniglans* Cornejo & Iltis, and 24 species. These range from western Mexico to Bolivia and the West Indies, in dry, moist, and wet forests from sea level to 1600 m (Cornejo and Iltis, 2008, 2016; Mercado et al., 2020; Cornejo and Vargas, 2020). In South America, where 22 of the 24 species of *Capparidastrum* are found, subgenus *Capparidastrum* is represented by two species: the Amazonian *C. sola* (J.F. Macbr.) Cornejo & Iltis and *C. frondosum* (Jacq.) Cornejo & Iltis, the latter being the nomenclatural type and the only widespread species in the genus that is distributed from the West Indies and Central America to northern Colombia, Venezuela, and Brazil and disjunct to the seasonally deciduous dry forests of coastal Ecuador (Cornejo and Iltis, 2008). In South America, the transandean and mostly allopatric pattern of distribution of members of subgenus *Capparidastrum* (Cornejo and Iltis, 2008, 2010; Mercado-Gómez et al., 2019) is correlated with its recent Pliocenic origin (Cardinal-McTeague et al., 2016), suggesting that *C. frondosum* and *C. sola* simultaneously diverged as separate lineages and arrived (in the case of *C. frondosum*) or evolved after the establishment of Amazonia (in the case of *C. sola*) as a consequence of the Andean uplift.

Subgenus *Pulviniglans* includes 10 species (9 Andean plus *C. megalospermum* Cornejo & Iltis from the lowlands of southern Chocó in southwestern Colombia to northwestern Ecuador) characterized by having relatively large, fleshy, cushion-shaped floral nectaries, 4–9 mm wide; they are the largest floral nectaries in the genus and among all Neotropical Capparaceae, hence the subgeneric name *Pulviniglans*, which was inspired by the impressive and distinctive massive floral nectaries of *C. petiolare*, the nomenclatural type (Cornejo and Iltis, 2008). The relatively high concentration of taxa in northwestern South America (Cornejo and Iltis, 2008, 2010; Cornejo et al., 2014; Mercado-Gómez et al., 2020; Cornejo and Vargas, 2020) suggests that the diversity was triggered by the Andean orogeny that drove the explosive formation of many local and regional endemics in wet, moist, and dry forests, as is the case for the regional evolution in Rubiaceae and many other taxa of Andean vascular plants (Antonelli et al., 2009). Sixteen species of subgenus *Pulviniglans* that produce medium- to large-sized pepo fruits, 4–8 cm in diam.—several of those eaten by wild mammals and sometimes also by humans, although not sold in local markets—are scattered throughout the northern and uppermost-central Andes (Cornejo and Iltis, 2005a,b), the center of diversity in this subgenus. From those 16 Andean species, *C. bonifaziana* (Cornejo & Iltis) Cornejo & Iltis, from western Ecuador to the lowlands of southwestern Colombia, and *C. petiolare* (Kunth) Hutch., from western and southern-central Ecuador and northwestern Peru, currently exhibit an allopatric pattern of distribution between the Andes and the Pacific coast (Cornejo and Iltis 2010, fig. 2). The fact that the fruits of both species are edible by extant medium- to large-sized mammals and humans, coupled with the several Andean autochthonous vernacular names of *C. petiolare* (X. Cornejo, unpubl. data), make it most likely that extinct megafauna played a role as dispersers and that domestication by Amerindian pre-Hispanic people may have driven the present pattern of distribution.

A new species in subgenus Pulviglans was detected during the elaboration of the treatment of Capparaceae for the *Flora of Ecuador*, and it is formally described herein.

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Taxonomy

1. Capparidastrum estrellae Cornejo & N. Mejía-Pazos, *sp. nov.* TYPE: ECUADOR. Pichincha: Cantón San Miguel de Los Bancos, Recinto Saloya, Reserva Choco Andés, secondary wet forest, ca. 0°01'07.7"N, 78°50'50.3"W, 1230 m, 10 Jan 2021 (fl, fr), *N. Mejía, W. Matango, I. Ortiz, and E. Vallejo 453* (Holotype: GUAY; Isotypes: to be distributed). Fig. 1.

Capparidastrum estrellae is a new species from northwestern Ecuador, which resembles *C. bonifazianum* (Cornejo & Iltis) Cornejo & Iltis from western Ecuador and southwestern Colombia but differs from the latter by the stipules linear-lanceolate, 0.3–0.5 mm wide (vs. narrowly triangular, 0.5–0.8 mm wide), flower buds globose (vs. obovoid or ellipsoid), petals snow-white or pinkish-white (vs. cream to greenish), ovary ovoid to sublanceoloid, 4–5 mm long (vs. ellipsoid to subcylindrical, 6–8 mm long); fruits globose, 7.0–7.5 cm wide (vs. cylindrical or ellipsoid, 2–4 cm wide). It is also similar to the disjunct *C. petiolare* (Kunth) Hutch., from the dry forests of coastal Ecuador to northwestern Peru, but differs from the latter by the mature leaves elliptic (vs. mostly oblong), inflorescences glabrous (vs. pilose), sepals 5–8 mm wide, observable at anthesis (vs. 2–3 mm wide, hidden by the nectary glands at anthesis), floral nectaries dorsiventrally compressed (vs. subglobose), stamens ca. 60 (vs. 22 to 44), and found in wet forests (vs. dry forests).

Trees ca. 15 m high, stem to at least 30 cm in diam.; glabrous. *Stipules* linear-lanceolate, 1.0–1.2 × 0.3–0.5 mm. *Leaves* near ends of branches, unequal in size; blades coriaceous, elliptic to obovate-elliptic, 14–25 × 7–15 cm, obtuse to rounded at base, acuminate to slightly acute or obtuse and often apiculate at apex, dark green above, pale green beneath; lateral veins 8–11 per side; petioles 0.5–15.0(–20.0) cm long, glabrous, the pulvinus 4–10 mm long, dark brown when dried. *Inflorescences* terminal, erect racemes 5–20 cm long, glabrous; floral bracts triangular, minute; pedicels 2.5–5.5 cm long, glabrous. *Sepals* broadly deltoid to semiorbicular, 4–7 × 5–8 mm, more or less reflexed at anthesis, greenish to greenish-white without, whitish and erose-ciliolate at margins. Floral nectaries 2.5–4.0 × 6–8 mm, dorsiventrally compressed, purple-red to pink or light-green, black to brown when dried. Flower buds globose, 13–20 × 15–20 mm. *Petals* ovate to ovate-elliptic, 17–20 × 15–16 mm, somewhat fleshy, ascending or divergent, forming a bowl-shaped corolla at anthesis, sessile at base, broadly rounded at apex, snow-white within, snow-white and sometimes pinkish-white without, more or less entire, minutely and irregularly erose-denticulate at margins, glabrous without. Stamens ca. 60; filaments 6.5–7.8 cm long; anthers ca. 4 mm long, dorsifixed in the basal third, white. *Gynophore* 7–9 cm long, white, glabrous. *Ovary* ovoid to sublanceoloid, 4–5 × 2–3 mm, green; stigma truncate to hemispherical. *Infructescences* with gynophores ca. 10 × 0.4–0.6 cm, green to yellow. Fruits globose or subglobose, ca. 7.0–7.5 × 7.0–7.5 cm, green and densely white lenticellate, at maturity turning yellow, longitudinally 4-sulcate, the grooves deep green when immature, glabrous; fruit wall coriaceous, flexible; pulp white. Seeds 10–25, ca. 10 × 8 mm.

The placement of this new taxon in *Capparidastrum* subgenus *Pulviniglans* is supported by morphological evidence, such as the presence of glabrous leaves, 4 fleshy cushion-shaped floral nectaries, and pepo fruits. *Capparidastrum estrellae* may resemble the also-Ecuadorian *C. bonifazianum*, which vegetatively is very similar but from which it differs by the characters in flowers and fruits as described in the diagnosis.

Etymology: the epithet *estrellae* of this taxonomic novelty honors Dr. Eduardo Estrella Aguirre (1941–1996), an Ecuadorian researcher, founder of the Ecuador National Museum of Medicine and the great discoverer and editor of the long-lost work *Flora Huayaquilensis* by Juan Tafalla, a botanical masterpiece and the first flora of present Ecuador from the colonial period, in which the most common species of Capparaceae from coastal Ecuador were documented with splendid handmade, natural-sized illustrations.

Habitat and distribution: known from the type in the vicinity of San Miguel de los Bancos toward Saloya, a lower montane secondary wet forest, in which individuals of *Capparidastrum estrellae* are scattered forest elements at 1230 m and may persist as solitary individuals in open areas. On the basis of field photographs sent by Jaime West to the first author, it is most likely that a second population of this taxonomic novelty occurs at 500 m on the same western side of Pichincha Province.

Conservation status: at present, the native vegetation of the area where *Capparidastrum estrellae* occurs is disturbed by selective timber cutting, deforestation, and forest fragmentation due to the advancing agricultural frontier and cattle farming. Therefore, the species is assigned the preliminary status of Endangered (EN B1ab[iii]) (IUCN, 2017).

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FIGURE 1. *Capparidastrum estrellae* Cornejo & N. Mejía-Pazos. **A,** raceme bearing globose, snow-white flower buds, lateral view; **B,** flower at anthesis, lateral view; **C,** calyx, corolla, fleshy compressed nectary glands and base of filaments, lateral view; **D,** fruit nearly at maturity; **E,** mature leaf blade, abaxial view; **F,** gray bark. Photographs of the holotype, *N. Mejía-Pazos s.n.* (GUAY). Photographs by Nicanor Mejía-Pazos.

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A NEW SPECIES OF *SIDA* SECTION *MALACROIDEAE* (MALVACEAE, MALVOIDEAE) FROM NORTHEASTERN BRAZIL

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Abstract. A new species of *Sida* section *Malacroideae* (Malvaceae), *Sida nordestinensis*, is described and illustrated. The new taxon is currently restricted to the State of Paraíba, Northeastern Brazil. This novelty is based on fieldwork and on the examination of relevant material from several herbaria. This study includes a taxonomic description, a distribution map, reproductive phenology data, and images for this new species.

Keywords: Caatinga, Malvales, Malveae, Neotropical flora, taxonomy

Sida Linnaeus is one of the most representative genera of Malvaceae s.l. worldwide, comprising ca. 200 species currently placed in subfamily Malvoideae (Fryxell, 1997; Krapovickas, 2003; Brandão, 2017). The genus is characterized by flowers bearing 10-ribbed calyces and schizocarps with 5–14 mericarps (Fryxell, 1997). Brazil is one of *Sida*'s main diversity centers, with more than half of its species recorded for the country (i.e., 103 out of 200 species; Flora do Brasil, 2020).

Sida section *Malacroideae* Don is one of the most diverse sections of this genus, occurring in Argentina, Brazil, Bolivia, Cuba, Ecuador, United States, Mexico, Uruguay, Paraguay, Peru, and Venezuela (Krapovickas, 2007, 2012). Brazil is the diversity center for this section, with 16 recorded species occurring in the Pampas, Pantanal, Cerrado, and Caatinga domains (Flora do Brasil, 2020; Krapovickas, 2007). This section comprises 23 species recognized by their herbaceous habit, axillary solitary and subsessile flowers/inflorescences (which are fused to the base of the stipules), staminal tube glabrous or with simple to stellate trichomes, calyx covered with stellate trichomes, and apiculate fruits bearing pubescent stellate trichomes (Krapovickas, 2007, 2012). Additionally, the Brazilian Caatinga (i.e., Seasonally Dry Tropical Forests) represents a secondary diversity center for this section (Krapovickas, 2007).

During work on a taxonomic treatment for *Sida* section *Malacroideae* (Figueiredo & Melo, in prep.) in the Caatinga biome of Northeastern Brazil, a new species of the section was found, which is here described and illustrated.

Materials and Methods

Morphological analyses were based on field observations of the specimens collected in the municipality of Arara, Paraíba, Northeastern Brazil, and on specimens from the CTES herbarium at the Instituto de Botánica del Nordeste (Corrientes, Argentina), where most type specimens of *Sida* section *Malacroideae* are deposited. Moreover, materials from the following herbaria were analyzed: ALCB, ASE, CSTR, EAN, FCQ, HACAM, HST, HUEFS, IPA, JPB, MAC, PEUFR, PY, SCP, UFP, and UFRN (acronyms according to Thiers, 2020, continuously updated). The terminology for vegetative and reproductive structures followed Harris and Harris (1994), Hickey (1973), Payne (1978), and Rizzini (1977). Conservation assessment follows the categories and criteria from the red list of IUCN (International Union for Conservation Nature, 2017).

Description

Sida nordestinensis S.S. Figueiredo & J.I.M. Melo, *sp. nov.* TYPE: BRAZIL. Paraíba: Arara, roadside, 6°51'07.3"S, 35°46'10.7"W, 646 m, 30 April 2019, *S. S. Figueiredo 60* (Holotype: HACAM; Isotype: JPB, to be distributed). Fig. 1–3.

Herbs erect. *Stems* covered with stellate trichomes, 7- to 8-branched. Stipules ca. 8 × 2 mm, spatulate, ciliate, cilia 1–2 mm long. *Petioles* 7–8 mm long, covered with stellate trichomes. *Leaf blades* 8–20 × 3–10 mm, lanceolate, base obtuse, margin proximally entire and dentate from the median region to the apex, apex acute, adaxial surface sericeous, trichomes stellate, 6- to 8-branched, appressed, abaxial surface sericeous, slightly floccose, trichomes stellate; secondary veins 8–9 pairs, conspicuous, abaxially raised, covered with stellate trichomes, 7- to 8-branched, 2 branches longer than others, 1.0–1.5 mm long. *Inflorescences* cymes, helicoidal, terminal. *Flowers* with pedicels ca. 2 mm long; ca. 13 mm long; *floral bud* 3–4 mm long; calyx ca. 7 × 5–6 mm, gamosepalous, 5-lobed, externally ciliate on apical lobes and base glabrous, internally tomentose, margin ciliate, with simple trichomes; *corolla* 6–7 mm long, dialypetalous, *petals* externally pale pink, base internally

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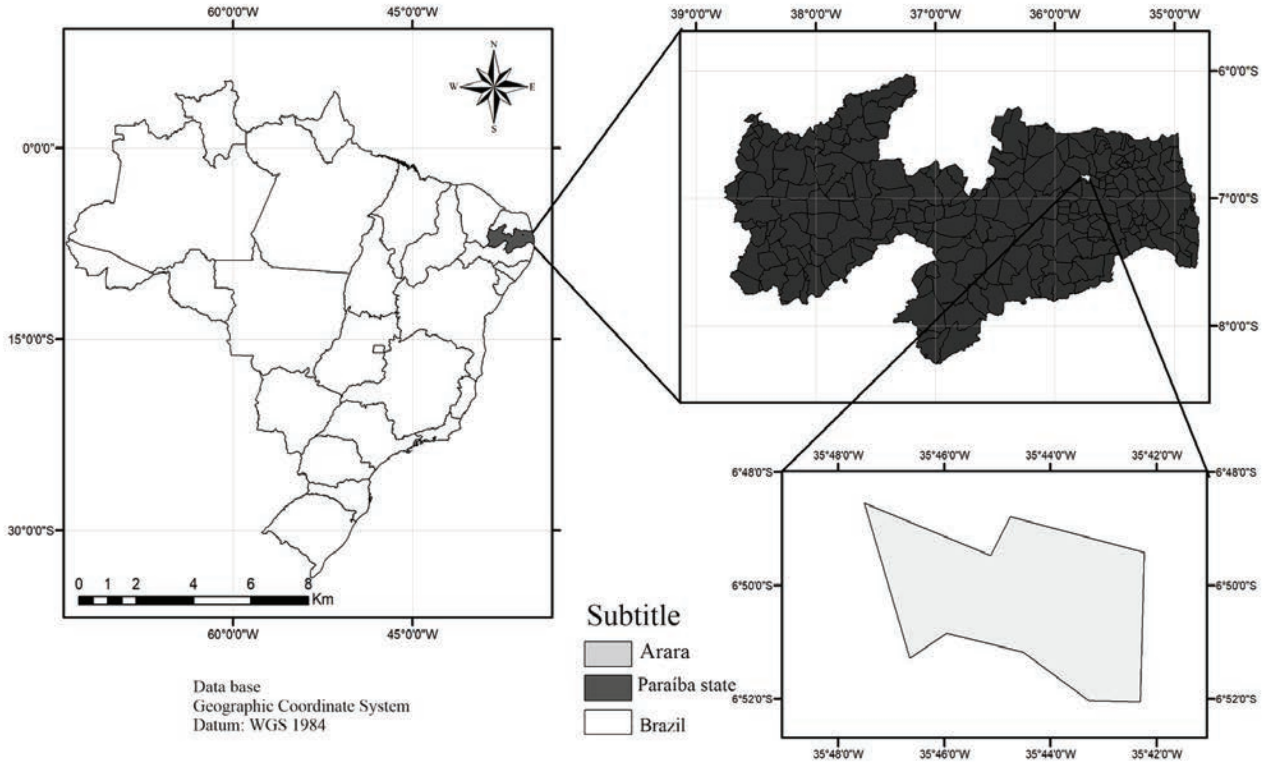

FIGURE 1. Distribution map of *Sida nordestinensis* S.S. Figueiredo & J.I.M. Melo.

yellow, with vinaceous longitudinal stripes from the middle portion to the apex; *staminal tube* 1.5–2.0 mm long, covered with stellate trichomes, the 5-branched, free portion of filaments ca. 1 mm long, anthers ca. 0.5 mm long; *ovary* ca. 1 × 1 mm, 5–8 locular, locules triangular. *Schizocarps* 4–5 × ca. 3 mm, with 5–8 mericarps, aristate, prominences covered with a mixture of radial stellate and glandular trichomes, sometimes glabrous, stellate trichomes 10- to 13-branched, glandular trichomes stipitate; mericarps 2–3 mm long, 2-aristate, aristae with radial stellate trichomes, 10- to 13-branched. *Seeds* 5–8 per schizocarp, ca. 2 mm long, pubescent, dark brown when dry.

Phenology: flowering and fruiting in April.

Etymology: the specific epithet refers to Northeastern Brazil, the region where this new taxon is recorded.

Conservation status: *Sida nordestinensis* was recorded only along the roadside in the municipality of Arara, State of Paraíba. For this reason, this species was categorized as data deficient (DD) because its complete distribution is currently unknown.

Distribution and habitat: *Sida nordestinensis* was recorded in the Caatinga domain within the municipality of Arara, Agreste mesoregion, State of Paraíba, Northeastern Brazil.

As mentioned above, Brazil is the diversity center of *Sida* section *Malacroideae*, with the Caatinga domain being its secondary diversity center (Krapovickas, 2007, 2012). The discovery of *S. nordestinensis* increases the total number of species of the section from 23 to 24 species, corroborating Krapovickas's assertion (2007, 2012) that this region is an important center of taxonomic diversity for the section.

Species from *Sida* section *Malacroideae* are morphologically very similar when analyzed with the naked eye, and this fact is responsible for the long-misapplied name *S. ciliaris* Linnaeus for practically all species in this section (Krapovickas, 2007). Despite the morphological similarities among these species, several morphological characters are key in differentiating the species from *S.* section *Malacroideae*, according to Krapovickas (2007): mostly herbaceous habit, roots generally adventitious, stems erect or prostrate; leaves spatulate to lanceolate, leaf blades with trichomes on both surfaces, simple to stellate; petioles with or without stellate trichomes; inflorescences or solitary flowers, subsessile, staminal tube glabrous or with simple to stellate trichomes; calyx covered with stellate or simple trichomes; mericarps apiculate, with pubescent, stellate trichomes; 1 seed per mericarp. In addition, the calyx is persistent, protecting the fruit.

In a detailed study, including all species of *Sida* section *Malacroideae*, we noticed that the species most similar to *S. nordestinensis* is *S. centuriata* Clement, but they differ in the characteristics listed in Table 1. In addition to the morphological features, it is worth mentioning that *S. centuriata* is a species restricted to the Pantanal domain, currently known only in the State of Mato Grosso do Sul, Brazil.

Sida nordestinensis shows pink corollas, a characteristic resembling several species in this section, such as *S. castanocarpa* Krapovickas. However, the latter is differentiated from this section's remaining species by the leaf blade's adaxial surface covered with stellate trichomes along the margins, simple trichomes in the middle portion, and the abaxial surface covered with stellate trichomes.

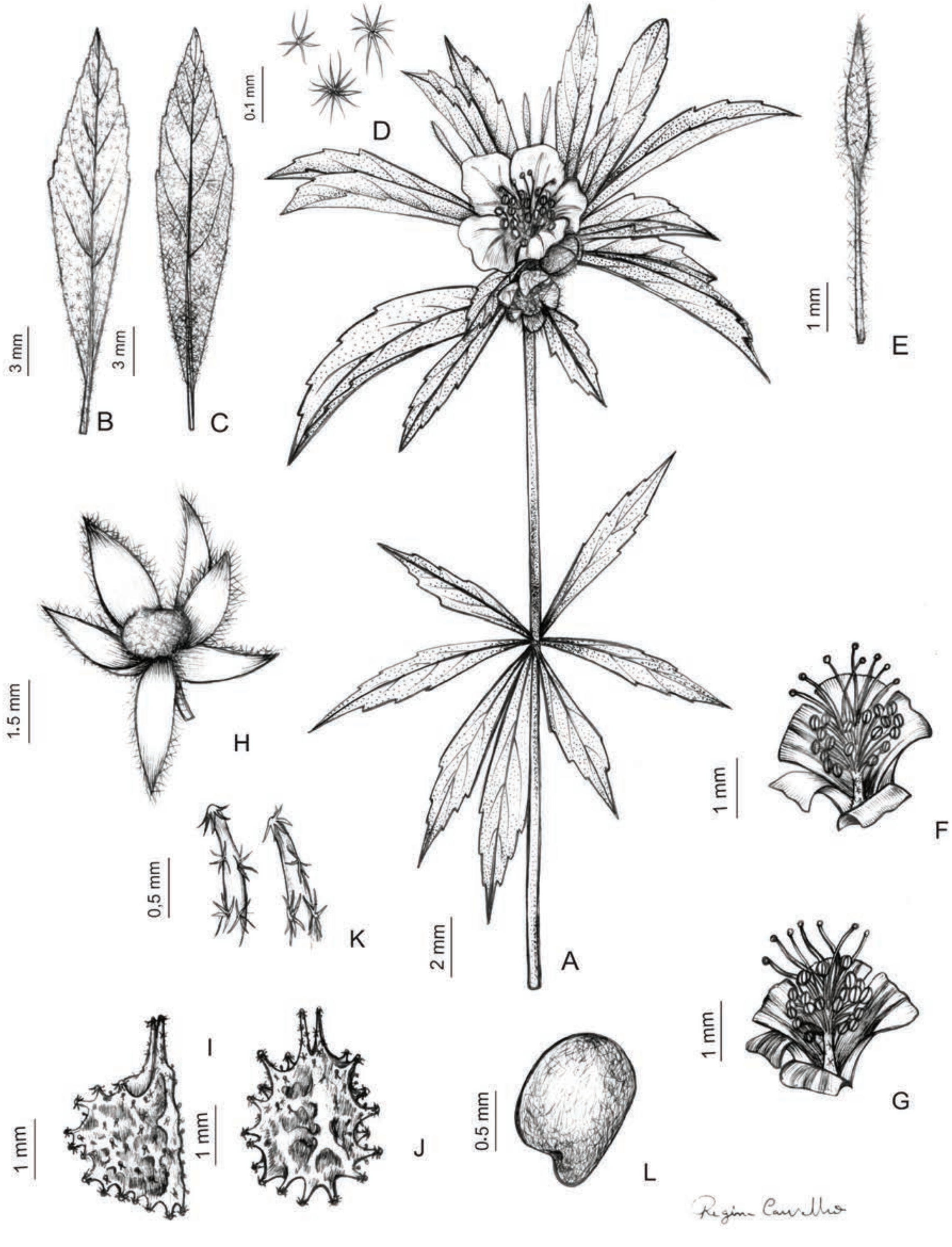

FIGURE 2. *Sida nordestinensis* S.S. Figueiredo & J.I.M. Melo. **A,** reproductive branch detaching flower with gynoecium showing 5 stigmas; **B,** adaxial surface of a leaf blade showing stellate trichomes; **C,** abaxial surface of a leaf blade showing stellate trichomes; **D,** stellate trichomes; **E,** stipule; **F,** gynoecium showing 8 stigmas; **G,** gynoecium showing 7 stigmas; **H,** ovary and persistent calyx; **I,** lateral surface of the mericarp with radial stellate trichomes and stipitate-glandular trichomes; **J,** dorsal surface of the mericarp; **K,** aristae with radial stellate trichomes; **L,** seed, side view. Based on *S. S. Figueiredo 60*.

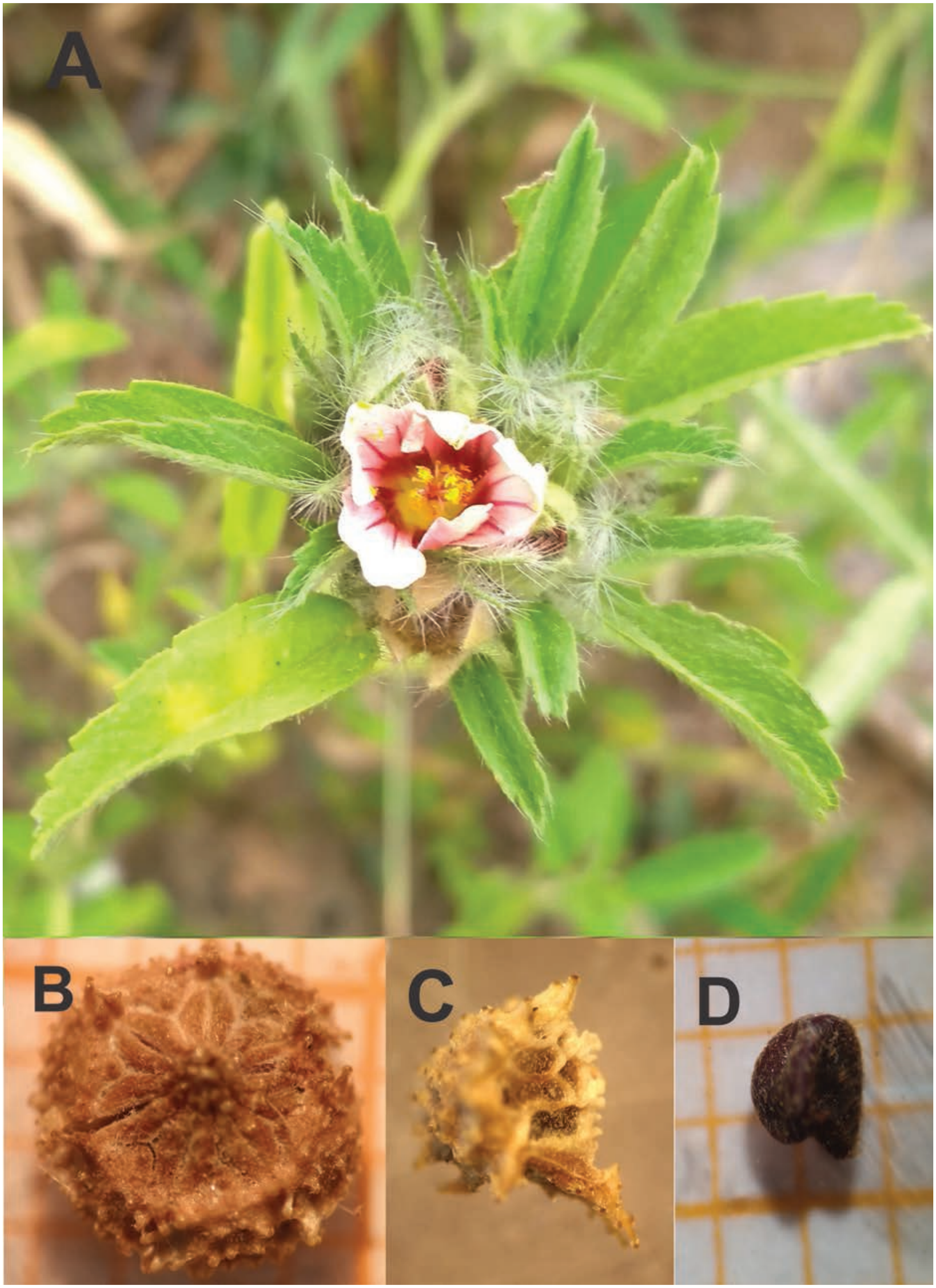

FIGURE 3. *Sida nordestinensis* S.S. Figueiredo & J.I.M. Melo. **A,** habit; **B,** fruit; **C,** bi-aristate mericarp, with radial stellate and pedicellate glandular trichomes; **D,** seed. Photographs by S. S. Figueiredo. Based on *S. S. Figueiredo 60*.

TABLE 1. Morphological comparison among *Sida nordestinensis* from *S. centuriata* and *S. castanocarpa*.

FEATURES	***S. CASTANOCARPA***	***S. CENTURIATA***	***S. NORDESTINENSIS***
Habit	Erect and/or prostrate herb	Prostrate herb	Erect herb
Shape of the stipules	Linear	Linear-lanceolate	Spatulate
Branching of the stellate trichomes of the stem	6–7–branched	4–branched	7–8–branched
Fruits indumentum	Presenting stellate trichomes and glandular trichomes	Always presenting glandular trichomes	Sometimes presenting glandular trichomes

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NOTE ON THE DISTRIBUTION OF *POLYCARPAEA CORYMBOSA* (CARYOPHYLLACEAE) IN BRAZIL

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Jailson Ferreira Moreira,[4] and Eduardo Bezerra de Almeida Jr.[5]

Abstract. This paper presents the distribution of *Polycarpaea corymbosa* in Brazil with particular attention to the state of Maranhão. *Polycarpaea corymbosa* is an herb with lanceolate leaves and capsular fruits. This paper provides data on area of distribution and taxonomy of the species.

Keywords: Cerrado, herbaceous, taxonomy, plant diversity

The family Caryophyllaceae has a cosmopolitan distribution (Bittrich, 1993; Harbaugh et al., 2010). It is common in Mediterranean and Asian regions and found less frequently in Africa, America, and Oceania (Dequan et al., 2001). It includes three subfamilies (Alsinoideae, Caryophylloideae, and Paronychioideae) with about 3,000 species and 88 genera (Rabeler and Hartman, 2005); ca. 42 species distributed among 17 genera are found in Brazil (Flora do Brasil, 2020).

Polycarpaea Lam. (Caryophyllaceae) has ca. 50 species that occur predominantly in the Old World (Dequan et al., 2001). *Polycarpaea corymbosa* (L.) Lam. is the only species found in Brazil (Flora do Brasil, 2020). This species is characterized by its herbaceous habit and opposite leaves, apparently verticillate, cymose inflorescences, and capsular fruits (Dequan et al., 2001). It is rare in Brazil and there are few collections from the Brazilian Northeast; the goal of this article is to increase knowledge of its distribution.

We wish to highlight the need to understand extinction threat levels in rare species located in critically endangered biomes like Cerrado. We also aim to reinforce the importance of floristic studies that contribute to the identification and distribution of species in forest fragments that need targeted actions for their conservation (Almeida et al., 2012). This paper contributes to expansion and reproductive phenology records for species in Brazil, mainly in the state of Maranhão in the Northeast region.

Materials and Methods

Our study was based on field collections in the main herbaria of Maranhão state (MAR, Herbarium of the Federal University of Maranhão), Bahia state (HUEFS, Herbarium of the State University of Feira de Santana), and Brasilia (CEN, Herbarium of EMBRAPA) (acronyms follow Thiers, continuously updated) and websites (Flora do Brasil, 2020; Tropicos, 2020). The websites for Flora do Brasil (2020) and Tropicos (2020) were consulted for geographic distributions and phytogeographic domains. Data on reproductive phenology were obtained from labels of the exsiccatae consulted. Two new occurrences of *Polycarpaea corymbosa* were detected for Maranhão state—in the city of Alto Parnaíba (09°11'39"S, 45°54'27"W) in southern Maranhão in the Cerrado biome, and in Tutoia (42°11'01"S, 2°43'55"W) in the northeast—and are reported for the first time. The collected specimens were deposited in the herbarium of Maranhão (MAR) in the Federal University of Maranhão.

The study of Dequan et al. (2001), together with the images of exsiccates in the database SpeciesLink (http://inct.splink.org.br/), were consulted to confirm the species. We used data from online records of 135 exsiccates, including records collected in Maranhão state, to draw up the distribution map (Fig. 1). The map was prepared using QGIS format and software (version 2.14) obtained from the Brazilian Institute of Geography and Statistics (IBGE, 2016).

Polycarpaea corymbosa (L.) Lam., Tabl. Encycl. 2: 129 (1797). Fig. 2A–D.

Annual *herb*, 0.4–0.5 m tall. *Stems* erect, cylindrical, branched from the base, pilose. *Leaves* 3.4–4.6 × 0.1–0.2 mm, filiform, apparently verticillate, chartaceous, attenuate base, acute apex, margin entire, pilose. *Bracts* 2.4–3.4 × 0.5–0.7 mm, paleaceous, hyaline, narrowly elliptic to

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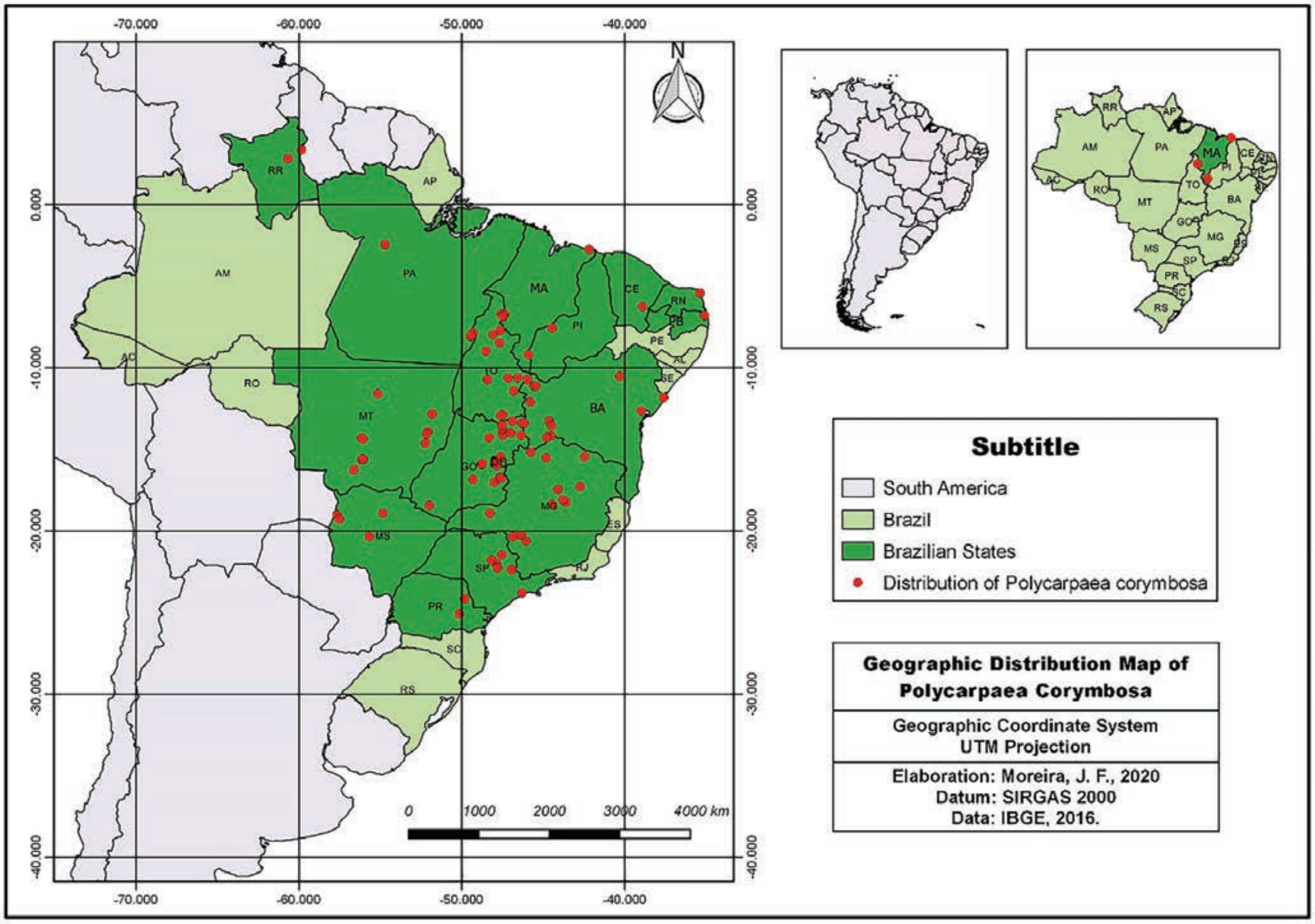

FIGURE 1. Map of the distribution of *Poycarpaea corymbosa* (L.) Lam in Brazil.

lanceolate, enfolding the inflorescence. *Inflorescence* axillary, pedunculate cymes (4–5 × 3.2–6.7 mm); paleaceous bracts 4–5 around at the base. Flowers translucent, 2.9–3.0 × 0.6–0.8 mm long. *Calyx* with bracts, *Calyx* with hyaline bracts, *sepals* hyaline, glabrous, lanceolate, acuminate, 2.2–3.2 × 0.4–0.9 mm, acute apex. *Corolla* with lobes slightly shorter than the calyx; petals 5, free, 0.36–0.57 × 0.18–0.36 mm, rose to red-brown, ovate. *Stamens* usually 5–6, free, 0.44 mm, *anthers* 0.08 mm, yellow. *Ovary* 0.5–1.2 × 0.1–0.7 mm long, super, l- locular, ovoid, glabrous, undivided style, *ovules* 3.

Distribution and habitat: Asia, Africa, and America. In Brazil, this species is located in Amazônia, caatinga, cerrado, Mata Atlântica, pampa, and Pantanal domains (Flora do Brasil, 2020), where it is found growing in humid, sandy soils (Dequan et al., 2001), mainly in campo de altitude, campo limpo, campo rupestre, savanna Amazonica, and rock fields (Flora do Brasil, 2020).

It occurs in the midwestern and southeastern regions of Brazil. There were few collections from the northeastern region, augmented with the ones reported herein from the state of Maranhão.

Phenology: flowering in and fruiting between January and July.

Additional specimens examined: BRAZIL. Maranhão: Alto do Parnaíba, 24 May 2014, fl., fr., *E. B. Almeida Jr. 1256* (MAR); BRAZIL. Bahia: Formosa do Rio Preto, 02 May 2009, fl., fr., *L. P. Queiroz 14457* (HUEFS); BRAZIL. Bahia: Inhaúmas, 28 April 1980, fl., fr., *Harley et al. 21899* (UEC); BRAZIL. Mato Grosso: Várzea Grande, 23 June 1995, fl., fr., *M. Macêdo 4253* (INPA); BRAZIL. Pará: Santarém, 11 July 1952, fl., fr., *G. A. Black 52-15625* (INPA); BRAZIL. Paraíba: Rio Tinto, 22 August 2002, *A. C. Sevilha 2335* (CEN 55359); BRAZIL. São Paulo: Mogi Guaçu, 09 January 2001, fl., fr., *M. C. E. Amaral, MCE and Bittrich V*2001/05 (UEC).

This species is easily distinguished by its filiform leaves, paleaceous and hyaline bracts enfolding a set of flowers, short style (0.1 mm long), and long ovary. Popularly known as “pallipoondu” in Tamil Nadu, it has ornamental and, in African communities, medicinal uses (Balamurugan et al., 2012).

FIGURE 2. *Polycarpaea corymbosa* (L) Lam. **A,** habit (scale bar = 1 cm); **B,** inflorescence, general view (scale bar = 1 mm); **C,** bracts, lateral view (scale bar = 1 mm); **D,** ovary and style, frontal view (scale bar = 1 mm). Based on *E. B. Almeida Jr. 1256* (MAR).

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CORRECTION OF DATE ERRORS IN THE PROTOLOGUES OF EIGHTEEN TAXON NAMES FROM CHINA

Yun Lin,[1] Yu-Lai Han[2] and Qian Sun[2,3]

Abstract. Following Article 9.2 of the *International Code of Nomenclature for algae, fungi, and plants* (*Shenzhen Code*, 2018), errors in the dates in the protologues of the names of eighteen taxa from China were corrected. They include *Aralia plumosa* (Araliaceae), *Berberis bergmaniae* var. *acanthophylla* (Berberidaceae), *Biondia parviurnula* (Asclepiadoideae, Apocynaceae), *Boottia heterophylla* (Hydrocharitacea), *Bredia hainanensis* (Melastomataceae), *Cornus yunnanensis* (Cornaceae), *Cotoneaster glabrata* (Rosaceae), *Dendropanax productus* (Araliaceae), *Dendropanax stellatus* (Araliaceae), *Hedyotis obliquinervis* (Rubiaceae), *Hypericum macrosepalum* (Clusiaceae), *Lonicera flavipes* (Caprifoliaceae), *Pandanus gressittii* (Pandanaceae), *Pedicularis membranacea* (Scrophulariaceae), *Phyllagathis setotheca* (Melastomataceae), *Phyllagathis xanthotricha* (Melastomataceae), *Plagiopetalum quadrangulum* (Melastomataceae), and *Tylophora nana* (Asclepiadoideae, Apocynaceae). The holotypes of all eighteen names are at the Harvard University Herbaria.

Keywords: Chinese plants, date citation errors, holotype, protologue

The Harvard University Herbaria include six integrated herbaria: the Herbarium of the Arnold Arboretum (A), Oakes Ames Orchid Herbarium (AMES), Economic Herbarium of Oakes Ames (ECON), Farlow Herbarium (FH), Gray Herbarium (GH), and New England Botanical Club Herbarium (NEBC). The combined collections contain more than 5 million specimens and over 100 thousand type specimens of vascular plants and mosses. Especially included are more than 10,000 type specimens of Chinese plants.

During a review and collation of type specimens of Chinese plants in the Harvard University Herbaria between 2018 and 2021 we discovered errors in the citation of collection dates that need to be corrected according to the International Code of Nomenclature for algae, fungi, and plants (ICN; Turland et al., 2018). This paper provides updates for those citations based on a review of the literature and examination of the digital images (https://kiki.huh.harvard.edu/databases/) of those specimens. Article 9.2 of the ICN states "If a designation of holotype made in the protologue of the name of a taxon is later found to contain errors (e.g. in locality, date, collector, collecting number, herbarium code, specimen identifier, or citation of an illustration), these errors are to be corrected provided that the intent of the original author(s) is not changed" (Turland et al., 2018). We herewith correct errors in the citation of dates in the protologues of eighteen names of taxa from China. The eighteen names subject to this study are arranged alphabetically by genus followed by a brief discussion on the need for correcting the date of collection. It should also be noted that the dates of collection for these specimens are cited correctly in the Harvard University Herbaria's online database of type specimens. Each of the bar codes cite below is an active link to the image it represents.

1. *Aralia plumosa* H. L. Li (Araliaceae), Sargentia 2: 114. 1942. TYPE: CHINA. Sichuan Province: Muli County, alt. 2300 m, 22 July 1937, *T. T. Yu 7337* (Holotype: A [00068040], image seen).

Li (1942) designated *T. T. Yu 7337* (A) as the holotype of *Aralia plumosa* and cited the date of collection as 1938 in the protologue. Although the date on the label of the holotype specimen is 1938, we found that label is incomplete. A label on an isotype specimen in the herbarium of the Institute of Botany, Chinese Academy of Sciences (PE) provides complete collection details and gives the date as July 22, 1937 (Fig. 1). The erroneous date of 1938 in the protologue should be corrected to 22 July 1937.

2. *Berberis bergmaniae* Schneid. var. ***acanthophylla*** C. K. Schneid. (Berberidaceae) in Sargent, Pl. Wilson. 1(3): 362. 1913. TYPE: CHINA. Sichuan Province: Wenchuan County, alt. 1525-1830 m, October 1910, *E. H. Wilson 4149* (Holotype: A [00057549], image seen).

Schneider (1913) cited the date of only one gathering, *E. H. Wilson 4149*, as "November 1910" in the protologue. However, we found that the date of collection on the label of the holotype gathering is written as "10/10". The date of collection should therefore be corrected to October 1910.

3. *Biondia parviurnula* M. G. Gilbert & P. T. Li (Asclepiadoideae, Apocynaceae), Novon 5: 2. 1995. TYPE: CHINA. Anhui Province: Jinzhai County, alt. 800 m, 16 May 1984, *K. Yao 8956* (Holotype: A [00273668], image seen).

The gathering *K. Yao 8956* (A) was designated the holotype of the name *Biondia parviurnula* and the date of collection was cited as "4 Mar. 1984" in the protologue (Gilbert et al., 1995). The date of collection on the label

We are very grateful to the China National Specimen Information Infrastructure (NSII) for providing images of the specimens cited. This work was supported by grants from the Plant Specimen Digitization and Chinese Virtual Herbarium Establishment (Grant No. 2005DKA21401) and the Natural Science Foundation of Top Talent of SZTU (Grant No. 2019010801010).

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FIGURE 1. Isotype of *Aralia plumose* H. L. Li (PE).

of the holotype specimen, however, is 16 May 1984. Thus, the date cited in the protologue is obviously erroneous and should be corrected to 16 May 1984.

4. *Boottia heterophylla* Merr. & F. P. Metcalf (Hydrocharitaceae), Lingnan Sci. J. 17: 568, 25. 1938. TYPE: CHINA. Hainan Province: Wenchang City, 4–25 August 1932, *H. Fung 20444* (Holotype: GH [00022879], image seen).

H. Fung 20444 (GH) was the only gathering cited in the protologue of the name *Boottia heterophylla*. The date of collection was cited as "August 3–25, 1932" (Merrill and Metcalf, 1938). We found that the date of collection on the label of the holotype is August 4–25, 1932. Thus, the date of collection cited in the protologue of this name should be corrected to 4–25 August 1932.

5. *Bredia hainanensis* Merr. & Chun (Melastomataceae), Sunyatsenia 5: 145. 1940. TYPE: CHINA. Hainan Province: Baoting County, alt. 2100 m, 22 June 1935, *F. C. How 72967* (Holotype: A [00055336], image seen).

The gathering *F. C. How 72967* was designated as the type of the name *Bredia hainanensis*. The date of collection was cited in the protologue as "June 22 1934" (Merrill and Chun, 1940). However, the date of collection on the label of the holotype specimen is June 22, 1935. The date of collection cited in the protologue should therefore be corrected to 22 June 1935.

6. *Cornus yunnanensis* H. L. Li (Cornaceae), J. Arnold Arbor. 25: 312. 1944. TYPE: CHINA. Yunnan Province: Chungtien (Zhongdian, now Xianggelila), alt. 2000 m, 20 November 1939, *K. M. Feng 3410* (Holotype: A [00368049], image seen).

Li (1944b) designated *K. M. Feng 3410* as the holotype of the name *Cornus yunnanensis*, and cited the date of collection as "Nov., 1930.". We found the date on the specimen label to be November 20, 1939. The date of collection cited in the protologue should be corrected to 20 November 1939.

7. *Cotoneaster glabratus* Rehder & E. H. Wilson (Rosaceae) in Sargent, Pl. Wilson. 1(2): 171. 1912. TYPE: CHINA. Sichuan Province: Ebian County, Wa Shan, alt. 1830–2593 m, July 1908, *E. H. Wilson 2185* (Holotype: A [00026240], image seen).

E. H. Wilson 2185 (A) was the only gathering cited in the protologue of the name *Cotoneaster glabratus*. The date of collection of this gathering was cited as "July 1906" (Rehder and Wilson, 1912). However, the date of collection on the label of this specimens is written 7/08. Thus, the date of collection cited in the protologue should be corrected to July 1908.

8. *Dendropanax productus* H. L. Li (Araliaceae), Sargentia 2: 44. 1942. TYPE: CHINA. Guangdong Province: Huiyang City, 1-19 October 1935, *W. T. Tsang 25945* (Holotype: A [00057983], image seen).

The gathering *W. T. Tsang 25945* (A) was designated as the type of the name *Dendropanax productus*, and the date of collection was cited as "Oct. 1–10, 1935" (Li, 1942). However, the date of collection on the type specimen is October 1–19, 1935. The date of collection cited in the protologue should be corrected to 1–19 October 1935.

9. *Dendropanax stellatus* H. L. Li (Araliaceae), Sargentia 2: 42. 1942. TYPE: CHINA. Guangxi Zhuangzu Zizhiqu: Sanjiang County, alt. 300 m, 12 September 1933, *A. N. Steward and H. C. Cheo 1054* (Holotype: A [00003481], image seen).

A. N. Steward and H. C. Cheo 1054 (A) was designated the type of the name *Dendropanax stellatus*. The date of collection was cited as "Sept. 12, 1935" in the protologue (Li, 1942). Upon checking *A. N. Steward and H. C. Cheo 1054* we found the date on the field label of the type specimen to be September 12, 1933. Therefore, the date of collection cited in the protologue should be corrected to 12 September 1933.

10. *Hedyotis obliquinervis* Merr. (Rubiaceae), Lingnan Sci. J. 14(1): 56. 1935. TYPE: CHINA. Hainan Province: Ngai (=Sanya city), 28 August 1932, *S. K. Lau 452* (Holotype: A [00097081], image seen).

S. K. Lau 452 (A) was the only gathering cited in the protologue of the name *Hedyotis obliquinervis* (Merrill, 1935). Merrill recorded the date of collection of this specimen as "August 8, 1932," but the date of collection on the label of the specimen is August 28, 1932. Thus, the date of collection as cited in the protologue should be corrected to 28 August 1932.

11. *Hypericum macrosepalum* Rehder (Hypericaceae) in Sargent, Pl. Wilson. 3: 451. 1917. TYPE: CHINA. Sichuan Province: Tatien Lu [Kangding], alt. 3050 m, 5 July 1909, *E. H. Wilson 2426* (Holotype: A [00139564], image seen).

Rehder (1917a) cited only one gathering, *E. H. Wilson 2426* (A), in the protologue of *Hypericum macrosepalum*, giving the date of collection as "July 5, 1908.". The date of collection on the specimen, however, is written 5/7/09. Wilson consistently wrote the date with the day first followed by the month and year. The date of collection cited in the protologue should therefore be corrected to 5 July 1909.

12. *Lonicera flavipes* Rehder (Caprifoliaceae) in Sargent, Pl. Wilson. 1: 132. 1911. TYPE: CHINA. Hubei Province: Xingshan County, alt. 2135-2440 m, 5 June 1907, *E. H. Wilson 1868* (Holotype: A [00056597], image seen).

Only one gathering, *E. H. Wilson 1868* (A), was cited in the protologue of the name *Lonicera flavipes*. The date of collection was cited as "June 5, 1908" (Rehder, 1911). We found the date of collection on the specimen label to be 5/7/07. As a result, the date of collection cited in the protologue should be corrected to 5 July1907.

13. ***Pandanus gressittii*** B. C. Stone (Pandanaceae), J. Arnold Arbor. 43(3): 348. 1962. TYPE: CHINA. Hainan Province: Liamui, alt. 405 m, 2 August 1935, *J. Linsley Gressitt 1185* (Holotype: A [00019922], image seen).

Stone (1962) designated *J. Linsley Gressitt 1185* in A as the holotype of *Pandanus gressittii* B. C. Stone and cited the date of collection as "June–July 1935.". However, the date of collection on the field label in the upper left of the sheet is VIII-2-1935. The date of collection cited in the protologue should therefore be corrected to 2 August 1935.

14. ***Pedicularis membranacea*** H. L. Li (Orobanchaceae), Proc. Acad. Nat. Sci. Philadelphia 101: 168. 1949. TYPE: China. Sichuan Province: Kangding County, alt. 2400 m, 7 August 1939, *C. Y. Chiao 1657* (Holotype: A [00097271], image seen).

C. Y. Chiao1657 deposited in A was designated the holotype of *Pedicularis membranacea*, with the date of collection given as "Aug. 7, 1937" (Li, 1949). We found the date of collection on the label of this specimen to be August 7, 1939. Thus, the date of collection cited in the protologue should be corrected to 7 August 1939.

15. ***Phyllagathis setotheca*** H. L. Li (Melastomataceae), J. Arnold Arbor. 25: 32. 1944. TYPE: CHINA. Guangxi Zhuangzu Zizhiqu: Shangsi County, Shiwan Dashan, 21 July 1937, *H. Y. Liang 69817* (Holotype: A [00055328], image seen).

Li (1944a) designated *H. Y. Liang 69817* (A) as holotype of the name *Phyllagathis setotheca*, and cited the date of collection as "July 21, 1931." However, the date of collection on the field label in the upper left corner of the sheet is July 21, 1937. Thus, the date of collection cited in the protologue should be corrected to 21 July 1937.

16. ***Phyllagathis xanthotricha*** Merr. & Chun (Melastomataceae), Sunyatsenia 5: 149. 1940. TYPE: CHINA. Hainan Province: Po-ting (=Baoting County), alt. 488 m, 31 May 1935, *F. C. How 72690* (Holotype: A [00055325], image seen).

F. C. How 72690 (A) was designated as type of the name *Phyllagathis xanthotricha*, with the date of collection cited as "May 21 1935" (Merrill and Chun, 1940). We examined this gathering and found the date of collection on the field label (in the upper left corner of the sheet) to be May 31, 1935. As a result, the date of collection cited in the protologue should be corrected to 31 May 1935.

17. ***Plagiopetalum quadrangulum*** Rehder (Melastomataceae) in Sargent, Pl. Wilson. 3: 453. 1917. TYPE: CHINA. Sichuan Province: Hongya County, alt. 610–915 m, 6 September 1908, *E. H. Wilson 3261* (Holotype: A [00073146], image seen).

E. H. Wilson 3261 is the only gathering cited in the protologue of *Plagiopetalum quadrangulum* (Rehder, 1917b). The date of collection is cited as "June 9, 1908." The date of collection on the field label of this gathering indicates 6/9/08. Thus, the date of collection cited in the protologue should be corrected to 6 September 1908, following Wilson's habit of indicating the day first followed by the month and year.

18. ***Tylophora nana*** C. K. Schneid. (Asclepiadoideae, Apocynaceae) in Sargent, Pl. Wilson. 3: 351. 1916. TYPE: CHINA. Sichuan Province: Wenchuan County, alt. 1220 m, 31 May 1908, *E. H. Wilson 2253* (Holotype: A [00076862], image seen).

Schneider (1916) cited only one gathering, *E. H. Wilson 2253*, in the protologue of *Tylophora nana*, and the date of collection as "May 3, 1908." The date of collection given on the label of this gathering is 31/5/08. Therefore, the date of collection in the protologue should be corrected to 31 May 1908.

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STUDIES IN NEOTROPICAL VOCHYSIACEAE: A NEW SPECIES OF *VOCHYSIA* (SECTION *CILIANTHA*) FROM A PLUVIAL FOREST OF WESTERN COLOMBIA

Luis B. Marcano-Berti[1,2] and Gerardo A. Aymard C.[3]

Abstract. *Vochysia carol-scottii* from the pluvial forests of "Chocó biogeográfico," a megadiverse region between the Pacific Ocean and the slopes of the Colombian Western Cordillera, Valle del Cauca department, is described and illustrated, and its morphological relationships with other similar *Vochysia* species are discussed. This new species is a small tree of 12 m tall and shares features with five species (*V. artantha, V. assua, V. calamana, V. cayennensis,* and *V. tomentosa*) of section *Ciliantha*. Morphologically, it is closest to *V. artantha*, but it differs in its leaves, inflorescences, spurred sepal, petals, and stamen size. A key and synopsis of the 44 species of *Vochysia* found in Colombia is provided. A brief note on the ethnobotany of *Vochysia* in the Amazon basin is presented in an appendix.

Keywords: pluvial forest, Flora of Colombia, Valle del Cauca, *Vochysia,* Vochysiaceae

Resumen. *Vochysia carol-scottii* de los bosques pluviales del "Chocó biogeográfico," una región megadiversa entre el Océano Pacifico y la vertientes de la cordillera occidental, departamento del Valle del Cauca, es descrita e ilustrada y sus relaciones morfológicas con sus especie afines son discutidas. Esta nueva especie es un árbol pequeño de 12 m de altura, que presenta similitudes morfológicas con cinco especies (*V. artantha, V. assua, V. calamana, V. cayennensis* y *V. tomentosa*) de la sección *Ciliantha*. Sin embargo, está más relacionada con *V. artantha*, de la cual difiere en sus hojas, inflorescencias, y en el tamaño del cáliz espolanado, los pétalos y el estambre. Se incluye una clave y una sinopsis de las 44 especies de *Vochysia* presentes en Colombia, y una nota breve sobre la etnobotánica de *Vochysia* en la cuenca Amazónica es presentada en un apéndice.

Palabras clave: bosques pluviales, Flora de Colombia, Valle del Cauca, *Vochysia,* Vochysiaceae

Vochysia Aublet (1775:18), encompassing 145 species, including the new species described herein, is the most diverse and representative genus in Vochysiaceae, a pantropical family (Kawasaki, 2007) of ca. 238 species and eight genera.[4]

Vochysia is a Neotropical genus found in southern Mexico (Chiapas, Oaxaca, Tabasco, and Veracruz states) through Central America, Colombia, Venezuela, Guianas, Ecuador, Peru, Brazil, Bolivia, and Paraguay (Marcano-Berti, 1998, 2005). It is represented by relatively few species in Mexico, Central America, the Andes, the Pacific region, and Southeast Brazil and has its highest diversity in the Amazon and Orinoco river basins and the Guayana Shield region (ca. 86 species; Marcano-Berti, 2014).

With regard to habit, some species of *Vochysia* are large trees that can be up to 50 m tall, with well-developed buttresses and wide crowns (e.g., *V. aurantiaca* Stafleu). However, several species are small trees, shrubs (e.g., *V. catingae* Ducke and *V. petraea* Warm.), or perennial herbs or undershrub (e.g., *V. herbacea* Pohl). The genus is characterized by its opposite or verticillate leaves, in whorls of 3, 4, or 5; stipules present, often deciduous, inflorescences thyrses or racemes, usually terminal; spurred calyx-lobe persistent; petals usually 3, yellow, sometimes 1–2 or absent; stamen in the plane of symmetry; stigma terminal or lateral; ovules 2 per locule, seeds 3, unilaterally winged (Stafleu, 1948; Marcano-Berti, 1998, 2005; Kawasaki, 2007).

Vochysia was monographed worldwide by Stafleu (1948),

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[4] Including the genus *Ruizterania* Marc.-Berti (Marcano-Berti, 1969), which in the past has been reduced to the synonymy of *Qualea* Aubl. (Litt, 1999; Sajo and Rudall, 2002; León, 2003; Kawasaki, 2007). However, anatomical and morphological evidence (Litt and Stevenson, 2003a,b) and a recent molecular phylogenetic study of Vochysiaceae (Gonçalves et al., 2020) showed that the monophyly of all genera was well supported, except for *Qualea*, which is divided into two monophyletic subclades, *Qualea* I and one that includes two equally monophyletic groups, with less support, *Qualea* II and *Ruizterania*, where *Qualea* II includes the type of the genus. On the basis of this phylogeny, the recognition of *Ruizterania* as a separate genus would render *Qualea* paraphyletic. These authors (Gonçalves et al., 2020) nonetheless indicated that "it is important to point out that not all species of *Ruizterania* and *Qualea* were sampled. Further investigation with expanded sampling is necessary to resolve their delimitation and monophyly." The authors fully understand that *Ruizterania* is not tenable until further phylogenetic information supporting both it and *Qualea* as monophyletic groups is available, or unless the clade *Qualea* I in Gonçalves et al. (2020) is described as a separate genus. Nonetheless, the senior author maintains, on the basis of five decades of research on Vochysiaceae, that these two genera, *Qualea* and *Ruizterania*, are coherent sister groups rather than a paraphyletic assemblage, and that *Ruizterania* is a natural group, morphologically and unambiguously easy to separate from *Qualea,* on the basis of its spur exerted in bud, the lateral sepals not imbricated (vs. spur hidden in the bud by the lateral sepals), petal elliptic to obovate (vs. obcordate), stamen pseudolaminal, the connective indistinguishable from the filament (vs. stamen laminal, the connective distinguishable from the filament), and ovules 7 in each locule (vs. 4–24).

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who divided the genus into three sections (*Ciliantha* Stafleu, *Pachyantha* Stafleu, and *Vochysiella* Stafleu) and eight subsections, recognizing 97 species and describing 14. Later, on the basis of vegetative and flower features, Marcano-Berti (2014) established the section *Apopetala*, to which he also transferred 9 species of section *Ciliantha* Stafleu.

Since F. A. Stafleu's contributions (1948, 1952a,b, 1954, 1955, 1957), 51 new species have been described, 1 has been reestablished, and 5 have been reduced to synonymy (for a review see Ulloa Ulloa et al., 2018 onward). The genus has been treated for the flora of the Guianas (Marcano-Berti, 1998), the flora of the Venezuelan Guayana (Marcano-Berti, 2005) and the *Manual de Plantas de Costa Rica* (Morales Quirós, 2015).

On the basis of our knowledge of this genus, we suspect that a new revision will reveal that several taxa described before and after Stafleu's last monograph (1948) could be relegated to synonymy or perhaps treated at a rank below species.

The present contribution increases to 44 the number of *Vochysia* species known from Colombia. In this geographical and political context, we treat *V. guatemalensis* Donn. Sm. as different from *V. macrophylla* Stafleu and *V. calamana* Stafleu from *V. vismifolia* Spruce ex Warm.; we reduce *V. columbiensis* Marc.-Berti to the synonymy of *V. laxiflora* Stafleu, *V. gigantea* Stafleu to that of *V. aurantiaca* Stafleu, *V. megalantha* Stafleu to that of *V. duquei* Pilger, and *V. lopezpalaciosii* Marc.-Berti to that of *V. megalophylla* Stafleu.

This new species was detected during research on Vochysiaceae conducted by the senior author in the herbarium of the New York Botanical Garden (NY).

Materials and Methods

This work is based on morphological (using a dissecting stereomicroscope) and herbarium studies in COAH, COL, GH, HUA, MER, MO, NY, PORT, and VEN (herbarium codes after Thiers, 2019). In addition, historical and current taxonomic literature on *Vochysia* was examined, in particular a monograph of the genus (Stafleu, 1948), the treatments of Vochysiaceae in the *Flora of Guianas* (Marcano-Berti, 1998) and the *Flora of the Venezuelan Guayana* (Marcano-Berti, 2005), and the checklist *Catálogo de plantas y líquenes de Colombia* (Marcano-Berti, 2016). Type specimens of *Vochysia* species involved in this study were examined using online images from JSTOR Global Plants (https://plants.jstor.org/). The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit morphology follow Font-Quer (2001) and Harris and Harris (2006).

Taxonomy

Vochysia carol-scottii Marc.-Berti & Aymard. *sp. nov.* TYPE: COLOMBIA. Valle del Cauca: Buenaventura. Corregimiento Bajo Calima, Vereda San Isidro, km 39 of road to Bahia Málaga, zona de explotación forestal (Cartón de Colombia), Frente B1 ("Canalete"), 4°02'N, 76°58'W. 30–50 m 16 May 1989 (fl). *Douglas C. Daly, Ricardo Callejas P. & Miryam Monsalve B. 5991* (Holotype: CUVC; Isotype: HUA, NY). Fig. 1–2.

Arbor plus minusve 12 m alta. Folia oposita; stipulae circa 2.4 mm longae; petioli 1–1.1 cm longi, glabri; lamina eliptica, circa 9 cm longa et circa 4 cm lata, glabra; venis lateralibus plus minusve 16 in utroque semilimbo, sub angulo cum vena media plus minusve 63□. Inflorescentiae circa 16 cm longae. Cincini 4-flori, circa 1.9 cm longi. Sepalo calcarato in anthesim 11–12 mm longo. Calcare circa 7.5 mm longo recto vel subincurvo. Petalis 3, inaequalibus; intermedia 2/3 minora stamini longitudini. Ovarium glabrum. Capsula glabra.

Trees 12 m high. *Leaves* opposite, glabrous to glabrescent above, loosely spread pubescent below with grayish appressed hairs, generally elliptic, ca. 9.2 × ca. 4.2 cm, apex obtuse-retuse; base acute, midvein impressed above, prominent below, main lateral veins ca. 16 on each side, subplane above, very slightly prominent above, slightly curved upward, at an angle of ca. 63° with the midvein; secondary lateral veins 0–1 between each pair of main secondary ones; remaining venation forms a network (reticule) with meshes of different forms and sizes; marginal vein present near apical fourth of blade, margin slightly revolute, stipules triangular acuminate, ca. 2.4 mm long, petiole 1.0–1.1 cm long, glabrous to glabrescent. *Inflorescence* terminal, ca. 16 cm long; cincinni 4-flowered, ca. 1.9 cm long, peduncle 6.5–7.5 mm long, pedicels 4.5–5.0 mm long. *Flower* bud near anthesis ca. 1.8 mm wide near apical third, obtuse at apex; spurred sepal, including the hypanthium, 11–12 mm long at anthesis, spur ca. 7.5 mm × ca. 0.9 mm toward the central part, ca. 2 mm wide near base, straight to very slightly incurved, at an angle of 35□–60□ with pedicel and 100□–130□ with spurred sepal, spur plus spurred sepal arched to C-shape, smaller sepals subequal, ca. 3.3 mm long; *petals* 3, central petal canal-shape 2/3 shorter than the stamen, ciliate at obtuse apex, throughout pubescent on the dorsum, lateral petals, slightly shorter than central petal, with a narrow line of appressed hairs (along central part) dorsally, ciliate at apex, at least one of them with a little notch near apex; stamen 1, subrounded at apex, totally pubescent on the convex (posterior) side, pubescent on the concave (anterior) surface, except the thecae glabrous, anther, ca. 3.5 times longer than the filament, staminodes ciliate at apex, subtriangular, ca. 0.7 × ca. 0.5 mm at base, ca. 0.2 mm wide at truncated apex; *ovary* glabrous, style ca. 0.5 mm wide at base, ca. 0.6 mm wide at middle, ca. 0.7 mm wide at truncated apex, stigma subterminal, slightly pointed. *Young fruit* 10.1–20.0 × 3–4 mm, glabrous, dried black in herbarium specimens.

Phenology: this new species had been collected with flowers in bud in May and June, with young fruits in July.

Etymology: *Vochysia carol-scottii* is named after Scott A. Mori (1941–2020) and his wife Carol Gracie. Scott was one of the most distinguished botanists of the 20th and 21st centuries. His outstanding, productive career as a tropical botanist at the New York Botanical Garden and his notable interpersonal skills earned him the admiration and respect of students and colleagues, and emphasize the broad range of his scientific pursuits and accomplishments. The vernacular name "Soroga" was recorded in the specimen *M. Monsalve B. 1515*.

THE NEW YORK BOTANICAL GARDEN
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No. 5991 Vochysiaceae

Qualea

Mun. Buenaventura, Crrgto. Bajo Calima, Vereda San Isidro, km 39 of road to Bahia Malaga (under construction). Zona de Explotación Forestal (Cartón de Colombia), Frente B1 ("Canalete"). Elev. 30-50m. 4°02'N, 76°58'W. Disturbed pluvial forest on dissected terrain. Material preserved in alcohol.

Tree 12m, (fallen), buds yellow. Rare.

NCI code nos. Q65T-1303-I, 1304-J.

D. C. Daly, R. Callejas, M. Monsalve 16 May, 1989
Field work supported by the National Cancer Institute

Figure 1. Holotype of *Vochysia carol-scottii* Marc.-Berti & Aymard (*Daly, Callejas and Monsalve B. 5991*, CUVC).

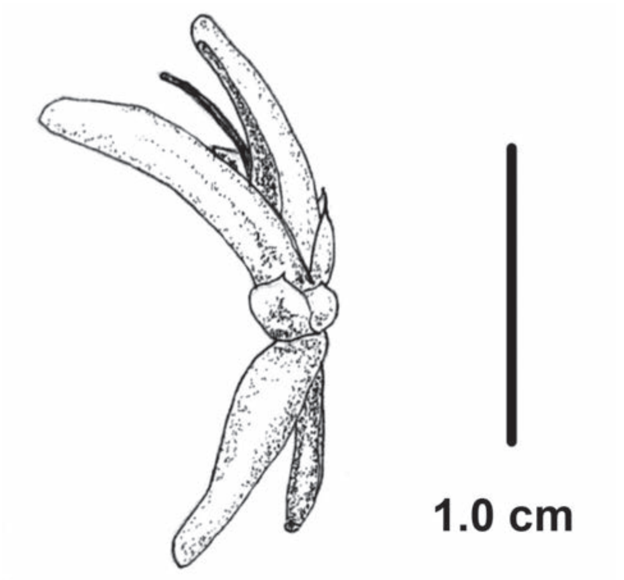

FIGURE 2. Sketch of a partial dissection of the flower of *Vochysia carol-scottii* Marc.-Berti & Aymard (drawn by Johanna Bakker Kalkman).

Distribution and ecology: the species is known to occur on primary or secondary pluvial forest on dissected terrain at 50–100 m elevation, in the type locality in the "Bajo Calima" region, Valle del Cauca department. These plant communities are common in the plains of western Colombia and northwestern Ecuador, areas that harbor some of the wettest forests in the world (Arellano-Peña and Rangel-Ch., 2004). This natural region is known as the biogeographical Chocó or "Chocó biogeográfico," a broad strip of land found between the Pacific Ocean and the slopes of the Colombian Western Cordillera (Cuatrecasas, 1989; Rangel-Ch., 2004). The area includes sections of five ecoregions (Olson et al., 2001), and its plant diversity and number of endemic species are among the highest on earth (Gentry, 1986; WWF, 2019). It is one of the world's biodiversity hotspots and yet is threatened by road building, degradation, and deforestation (Myers et al., 2000; WWF, 2019), as well as mining activities (Valois-Cuesta and Martínez-Ruiz, 2016).

Additional specimens examined: COLOMBIA. Valle del Cauca: Buenaventura. Corregimiento Bajo Calima, Concesión Pulpa Papel/Buenaventura, 3°55'N, 77°00'W. 100 m 03 June 1987 (fl). *Miryam Monsalve B. 1515* (CUVC); same locality: 27 July 1989 (fr). *Miryam Monsalve B. 3121* (CUVC).

Conservation status: currently, *Vochysia carol-scottii* is known only from three collections made at the type locality, and under IUCN (2017) guidelines that constitutes insufficient data to accurately determine its conservation status. Although conservation status assessments can still be carried out for species with such low numbers of collections (Rivers et al., 2011), it may be hard to determine whether an appearance of rarity in a species is due to the lack of data or to its actual rarity. Also, it is important to note that a species with such limited data actually can be endangered, and thus a reassessment will be needed when more data become available (Maas et al., 2019). Nonetheless, according to IUCN criteria (IUCN, 2017), this species would be ranked as Endangered (EN Alc) because the region of the type and additional specimens represents a small area where much of the forest has been removed in the last four decades.

Regardless, we expect this species to have a wider distribution along the wetter coastal forests of western Colombia and northwestern Ecuador, like numerous other taxa (e.g., *Cassipourea calimensis* Cuatr., *C. floribunda* Cuatr., and *Dacryodes granatensis* Cuatr.) that share the same habitats in the biogeographical Chocó natural region.

Because of its leaves opposite, petal pubescent on the abaxial side, stamen pubescent on both sides, staminodes ciliate, and ovary glabrous, *Vochysia carol-scottii* belongs in section *Ciliantha* subsection *Ferrugineae* (Stafleu, 1948; Marcano-Berti, 2016).

This new species is morphologically related to five other taxa of section *Ciliantha*—*Vochysia artantha* Stafleu, *V. assua* Stafleu, *V. calamana* Stafleu, *V. cayennensis* Warm., and *V. tomentosa* (G. F. W. Meyer) DC.—but it is most closely related to *V. artantha* from the middle Rio Vaupés basin of Colombia. Both species have stamen pubescent and glabrous ovary. However, *V. carol-scottii* differs from *V. artantha* and the other four species in the characters presented in Table 1 and in the key to the species below.

KEY TO THE COLOMBIAN SPECIES OF *VOCHYSIA*

1a. Ovary pubescent 2

1b. Ovary glabrous 9

2a. Corolla present 3

2b. Corolla absent 7

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

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

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

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

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

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

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

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

Key to the Colombian Species of *Vochysia* cont.

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

7b. Lower surface of leaf blade pubescent on the veins, trichomes 2-branched 8

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

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

9a. Corolla absent 10

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

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

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

11a. Petal 1 12

11b. Petals 3 16

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

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

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

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

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

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

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

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

16a. Stamen glabrous 17

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

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

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

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

18b. Stigma terminal, not 2-branched 19

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

19b. Apex of the leaf acute to acuminate 20

20a. Margin of the leaf flat; no marginal vein present; spurred sepal at anthesis ca. 17 mm long . . . . *V. guatemalensis*

20b. Margin of the leaf strongly revolute; marginal vein present; spurred sepal at anthesis ca. 7 mm long . . . . *V. parviflora*

21a. Leaves opposite 22

21b. Leaves 3- to 5-verticillate 37

22a. Spurred sepal (including the hypanthium or calyx tube) 6.0–10.8 cm long at anthesis 23

22b. Spurred sepal (including the hypanthium or calyx tube) 1.2–2.6 cm long at anthesis 32

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

23b. Spur straight or slightly curved; leaf on the lower surface glabrous or densely adpressed pubescent, with 2-branched sessile or subsessile trichomes; main lateral veins 15–20 24

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

24b. Leaf on the lower surface densely pubescent, with gray to pale golden trichomes 29

25a. Apex of the leaf truncate-emarginate to bilobulate . . . . *V. biloba*

25b. Apex of the leaf shortly acuminate, obtuse to obtuse-retuse 26

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

26b. Petals pubescent dorsally (at least the central one), leaf blade with 1 submarginal vein 27

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

27b. Inflorescence 9–13 cm long; central petal 1/4 to 1/2 shorter than the stamen 28

28a. Leaf blade 8–12 × 3.0–4.4 cm; inflorescence 5–10 cm long . . . . *V. vismiifolia*

28b. Leaf blade 12–18 × 5.0–7.5 cm; inflorescence ca. 15 cm long . . . . *V. casiquiarensis*

29a. Central petal 2/3 shorter than the stamen; lateral petals pubescent dorsally . . . . *V. carol-scottii*

29b. Central petal as long as the stamen or 1/3 shorter than it; lateral petals glabrous dorsally, sometimes ciliate at the margin 30

30a. Apex of the leaf blade obtuse-retuse to rounded-retuse . . . . *V. angustifolia*

30b. Apex of the leaf blade acute to acuminate 31

31a. Apex of the leaf blade acute; central petal as long as the stamen, sparsely pubescent dorsally . . . . *V. artantha*

31b. Apex of the leaf blade acuminate; central petal covers ca. 2/3 of the stamen, with a narrow strip of adpressed trichomes at the central portion dorsally, glabrous at the borders . . . . *V. calamana*

Key to the Colombian Species of *Vochysia* cont.

32a. Leaf blade glabrous on both surfaces; main lateral veins 24–26 33
32b. Leaf blade pubescent on lower surface; main lateral veins 13–18 34
33a. Spur sepal 2.4–2.6 cm long; central petal 4.7–5.8 mm long; staminodes ciliate at the base . . . . *V. garcia-barrigae*
33b. Spur sepal ca. 1.8 cm long; central petal ca. 3 mm long; staminodes glabrous . . . . *V. complicata*
34a. Spur inflate, almost as long as wide . . . . *V. densiflora*
34b. Spur not inflate, 4–7 times longer than wide 35
35a. Leaf blade 14–21 × 4.5–9.0 cm; inflorescence 30–60 cm long . . . . *V. saccata*
35b. Leaf blade 6.5–13.0 × 2.5–4.0 cm; inflorescence no longer than 26 cm 36
36a. Main lateral veins 10–15 . . . . *V. calamana*
36b. Main lateral veins 20–25 . . . . *V. allenii*
37a. Leaves 3-verticillate 38
37b. Leaves 4- to 5-verticillate 41
38a. Central petal glabrous, glabrous or ciliate dorsally, ciliate at the margin 39
38b. Central petal pubescent dorsally 40
39a. Leaf blade densely adpressed ferrugineous pubescent on the entire lower surface . . . . *V. elegans*
39b. Leaf blade densely sparsely gray pilose along the midrib on the lower surface . . . . *V. macrophylla*
40a. Leaf blade 1–2 times longer than wide; central petal spatulate, ca. 2/3 as long as the the stamen . . . . *V. braceliniae*
40b. Leaf blade 3–4 times longer than wide; central petal obovate, ca. 3/4 as long as the stamen . . . . *V. magna*
41a. Staminodes ciliate 42
41b. Staminodes glabrous 45
42a. Spur strongly incurved . . . . *V. spathiphylla*
42b. Spur straight to slightly recurved 43
43a. Leaf blade broadly obovate, 1–2 times longer than wide; central petal ca. 2/3 as long as the stamen . . . . *V. braceliniae*
43b. Leaf blade spathulate or obovate, ca. 4 times longer than wide; central petal as long as the stamen 44
44a. Main lateral veins 20–25; stipules ca. 2 mm long; inflorecence densiflorous, cincini 2-flowered . . . . *V. lomatophylla*
44b. Main lateral veins not more than 16; stipules 4–6 mm long; inflorecence laxiflorous, cincini 3-flowered . . . . *V. laxiflora*
45a. Cincini 1- to 2-flowered; central petal slightly to strongly cucullate . . . . *V. aurantiaca*
45b. Cincini 1-flowered; central petal not cucullate 46
46a. Young branchlets, stipules, and leaves on both surfaces glabrous . . . . *V. meridensis*
46b. Young branchlets and stipules piloses; leaves sparsely pilose on the lower surface, mainly on the venation . . . . *V. duquei*

Table 1. Comparison of diagnostic morphological characters of *Vochysia carol-scottii* and closely related species.

Character	*V. artantha*	*V. assua*	*V. calamana*	*V. carol-scottii*	*V. cayennensis*	*V. tomentosa*
Leaves	Elliptic or sub-oblanceolate, 10–12 × 3–4 cm	Elliptic or elliptic-lanceolate, 7–10 × 2.5–3.5 cm	Elliptic, 8–10 × 3–4 cm	Elliptic, ca. 9.2 × ca. 4.2 cm	Elliptic or oblong 6.0–7.5 × 2.5–3.5 cm	Elliptic, 6–8 × 2–3 cm
Lateral nerves	Ca. 10; angle with the midrib 40°–50°	14–20; angle with the midrib ca. 70°	10–15; angle with the midrib 45°–60°	Ca. 16; angle with the midrib ca. 63°	14–18; angle with the midrib ca. 60°	9–13; angle with the midrib 50°–60°
Cincinni	1- to 2-flowered	1- to 2-flowered	1- to 2-flowered	4-flowered	1- to 2-flowered	1- to 2-flowered
Spurred sepal (including the hypanthium or calyx tube) at anthesis	Ca. 1.4 cm long	1.4–1.5 cm long	Ca. 1.3 cm long	1.1–1.2 cm long	1.6–1.9 cm long	Ca. 1.2 cm long
Central petal	As long as the stamen, sparsely pilose dorsally, not ciliate at the apex	1/5 shorter than stamen, glabrous, ciliate at the apex	1/2 as long as stamen or 1/3 shorter, with a narrow band of appressed hairs dorsally, ciliate at the apex	1/3 shorter than stamen, densely pubescent on back, with a narrow band of appressed hairs dorsally, ciliate at the apex	1/5 shorter than stamen, glabrous	Elliptic-oblong, as long as the stamen or 1/3 shorter, pilose

Synopsis of the Colombian Species of *Vochysia*

Vochysia allenii Standl. & L.O. Williams, Ceiba 3(2): 119. 1952. TYPE: COSTA RICA. Puntarenas: pastures near Esquinas, 80 m, 15 June 1951, *Paul H. Allen 6256* (Holotype: US; Isotypes: EAP, F, GH).

Habitat and ecology: tree up to 25 m tall; pluvial lowland to montane forests. At elevations of 50–1000 m.

Distribution: Colombia (Chocó, Valle), Nicaragua, Costa Rica, and Panamá.

Vochysia angustifolia Ducke, Bull. Mus. Hist. Nat. (Paris) sér 2, 4: 738. 1932. TYPE: BRAZIL. Amazonas: Ad ripas fluminis Curicuriary affl. Rio Negro superioris, 20 November 1929, *Walter A. Ducke s.n.* (Holotype: RB [RG2499]; Isotypes: G, K, NY, P, S, U, US).

Heterotypic synonym: *Vochysia javitensis* Stafleu, Recueil Trav. Bot. Néerl. 41: 509. 1948. TYPE: VENEZUELA. Amazonas: Yavita, along río Temi, 31 January 1931, *Llewelyn Williams 14118* (Holotype: F; Isotypes: G, NY, RB, US).

Habitat and ecology: tree 3–20 m tall; evergreen riparian forests and high Amazon Caatinga forests. At elevations of 100–200 m.

Distribution: Colombia (Amazonas, Caquetá, Guianía), Venezuela, and Brazil.

Vochysia antioquiae Sanoja & Marc.-Berti, Acta Bot. Venez. 29(2): 258–261. 2006. TYPE: COLOMBIA. Antioquia: San Carlos, alto de Samaná, Vereda Miraflores, finca "El Desespero," en el camino a Jardín, 6°05'N, 74°50'W, *Ricardo Callejas P., Francisco J. Roldán & Iván D. Castaño 8585* (Holotype: HUA; Isotype: NY).

Habitat and ecology: tree 15–30 m tall; evergreen montane forests. At elevations of 750–890 m.

Distribution: Colombia (Antioquia). Endemic.

Vochysia artantha Stafleu, Acta Bot. Neerl. 6: 342. 1957. TYPE: COLOMBIA. Vaupés: Vicinity of Mitú, 21 March 1945, *Paul H. Allen 3347* (Holotype: US; Isotypes: MO, NY)

Habitat and ecology: tree up to 30 m tall; evergreen nonflooded forests. At elevations of 50–150 m.

Distribution: Colombia (Vaupés). Endemic.

Vochysia aurantiaca Stafleu, Recueil Trav. Bot. Néerl. 41: 487. 1948. TYPE: COLOMBIA. Magdalena: Santa Marta, near Valparaiso, 5°46'30"N, 74°20'30"W, 1200 m, 1898–1901, *Herbert H. Smith 1877* (Holotype: NY; Isotypes: BM, BR, G. GH, K, L, MO, P, S).

Heterotypic synonym: *Vochysia gigantea* Stafleu, Recueil Trav. Bot. Néerl. 41: 489.1948. TYPE: COLOMBIA. Boyacá. Mt. Chapón, 1200 m, *Alexander E. Lawrance 275* (Holotype: NY; Isotypes: A, BM, E, F, G, K, MO, S, US).

Habitat and ecology: tree 15–30 m tall; evergreen montane forests. At elevations of 1000–2200 m.

Distribution: Colombia (Boyacá, Cundinamarca, Magdalena, Meta, Putumayo), Venezuela, Ecuador, Perú, and Bolivia.

Vochysia biloba Ducke, Arq. Inst. Biol. Veg. 2(1): 52. 1935. TYPE: BRAZIL. Amazonas: Sao Paulo de Olivença, 30 November 1934, *Walter A. Ducke 24080* (Holotype: RB; Isotypes: K, NY, P, S, U, US).

Habitat and ecology: tree up to 30 m tall; evergreen nonflooded to montane forests. At elevations of 50–1120 m.

Distribution: Colombia (Amazonas, Putumayo), Brazil, Ecuador, Perú, and Bolivia.

Vochysia braceliniae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 149. 1940. TYPE: PERÚ. Loreto: near Yurimaguas, trail to San Ramón, 180 m 25 October 1931, *Ynés E. J. Mexía 6081* (Holotype: F; Isotypes: BM, FI, G, GB, GH, K, LA, MICH, MO, NY, PH, RSA, S, TEX, U, UC, US).

Habitat and ecology: tree up to 25 m tall; evergreen nonflooded to montane forests. At elevations of 100–1300 m.

Distribution: Colombia (Antioquia, Caquetá, Guaviare, Meta, Putumayo), Ecuador, and Perú.

Vochysia calamana Stafleu, Rec. Trav. Bot. Neerl. 41: 498. 1948. TYPE: BRAZIL. Amazonas: Rio Madeira near Calama, 01 January 1931, *Boris A. Krukoff 1299* (Holotype: BM; Isotypes: A, G, K, NY, P, S, U).

Habitat and ecology: tree up to 20 m tall; evergreen nonflooded forests. At elevations of 100–200 m.

Distribution: Colombia (Amazonas), Brazil.

Vochysia calophylla Spruce ex Warm. In Mart., Fl. Bras. 13(2): 98, t. 18, fig 1. 1875. TYPE: COLOMBIA or VENEZUELA. Amazonas: Along the Guainia river, above the mouth of the Casiquiare. 01 January 1854, *Richard Spruce 3538*, Holotype: K; Isotypes: BM, BR, F, G, GH, GOET, LD, NY, P, W).

Habitat and ecology: tree 3–15 m tall; seasonally flooded forests along black-water rivers. At elevations of 50–200 m.

Distribution: Colombia (Guianía), Brazil, and Venezuela.

Vochysia carol-scottii Marc. Berti & Aymard. TYPE: COLOMBIA. Valle del Cauca: Buenaventura, corregimiento Bajo Calima, vereda San Isidro, km. 39 of road to Bahia Málaga, zona de explotación forestal (Cartón de Colombia), Frente B1 ("Canalete"), 4°02'N, 76°58'W. 30–50 m 16 May 1989, *D. C. Daly, Ricardo Callejas & Miryam Monsalve 5991* (Holotype: CUVC; Isotype: HUA, NY).

Habitat and ecology: tree 12 m tall; pluvial lowland forests. At elevations of 30–100 m.

Distribution: Colombia (Valle). Endemic.

Vochysia casiquiarensis (as "*cassiquiarensis*") Stafleu, Acta Bot. Neerl. 3: 405. 1954. TYPE: VENEZUELA. Amazonas: San Jose do Cassiquiare, 12 December 1945, *Ricardo de L. Froes 21503* (Holotype: K; Isotypes: F, K, NY, US).

The epithet of *Vochysia cassiquiarensis* Stafleu is misspelled, with a double "s". This spelling is corrected here according to Art. 60.7 of the current International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018).

Habitat and ecology: tree 3–15 m tall; seasonally flooded forests. At elevations of 50–200 m.

Distribution: Colombia (Caquetá, Guianía?), Brazil?, and Venezuela.

Vochysia catingae Ducke, Arq. Inst. Biol. Veg. 4: 33. 1938. TYPE: BRAZIL. Amazonas: Ad ripas fluminis Curicuriary affl. Rio Negro superioris, 26 February 1936, *Walter A. Ducke s.n.* (Holotype: RB [RG34651]; Isotypes: G, K, U, US).

Habitat and ecology: shrub or tree 3–10 m tall; seasonally flooded margins of black-water rivers, scrub savannas on granitic outcrops. At elevations 50–200 m

Distribution: Colombia (Guianía, Vichada), Brazil, and Venezuela.

Vochysia complicata Ducke, Bull. Mus. Hist. Nat. (Paris) sér 2, 4: 738. 1932. TYPE: BRAZIL. Amazonas: Manaos, 29 October 1929, *Walter A. Ducke s.n.* (Holotype: BR [RB23498]; Isotypes: G, K, P, S, U, US).

Habitat and ecology: tree 15–30 m tall; seasonally flooded forests along black-water rivers. At elevations of 100–200 m.

Distribution: Colombia (Guainía, Vaupés), Brazil, and Venezuela.

Vochysia densiflora Spruce ex Warm., In Mart., Fl. Bras. 13(2): 101. 1875. TYPE: BRAZIL. Amazonas: Panure, ad Rio Uaupes, 1852–1853, *Richard Spruce 2627* (Holotype: K; Isotypes; BM, BR, C, G, GH, K, NY, OXF, P, US, W).

Habitat and ecology: tree up to 30 m tall; unflooded and high Amazon Caatinga forests. At elevations of 100–300 m.

Distribution: Colombia (Amazonas, Vaupés), Brazil, and the Guianas.

Vochysia diversa J.F. Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 67. 1931. TYPE: PERÚ. Loreto: Mishuyacu, near Iquitos, December 1929, *Guillermo Klug 685* (Holotype: F; Isotypes: G, NY, US).

Habitat and ecology: tree up to 30 m tall; lowland to submontane evergreen forests. At elevations of 100–550 m.

Distribution: Colombia (Caquetá), Brazil, and Perú.

Vochysia duquei Pilg. in Burret, Notizbl. Bot. Gart. Berlin-Dahlem 13: 498. 1937. TYPE: COLOMBIA. Valle: Cuenca del río Cali, 1600 m, August 1936, *J. M. Duque Jaramillo 55* (Holotype B?; Isotype: US).

Heterotypic synonym: *Vochysia megalantha* Stafleu, Recueil Trav. Bot. Néerl. 41: 485 1948. TYPE: COLOMBIA. Santander [“Cauca” in the protologue]: Portachuelo, 1851, *José J. Triana 3783* (Holotype; G; Isotypes: BM, K, P, W).

The protologue specimen citation includes a misspelling in the main locality (which should be Portachuelo, not Portachueto) and the wrong department (which should be Santander, not Cauca), both corrected here. With regard to the latter, Acuña (2011) reported that in 1851 José J. Triana collected in Santander department, not in Cauca.

Habitat and ecology: tree up to 30 m tall; evergreen montane forests. At elevations of 1100–2400 m.

Distribution: Colombia (Antioquia, Bolívar, Cundinamarca, Huila, La Guajira, Norte de Santander, Santander, Valle), Ecuador, and Perú.

Vochysia elegans Stafleu, Acta Bot. Neerl. 3: 405, fig. 1c–d. 1954. TYPE: BRAZIL. Amazonas: Rio Negro, Uarurá, acima de Uananacá, 03 March 1936, *Walter A. Ducke s.n.* (Holotype: U; Isotypes: RB [RB34656], G, K, P, S, U, US).

Habitat and ecology: tree up to 25 m tall; evergreen lowland forests. At elevations of 100–200 m.

Distribution: Colombia (Caquetá, Guianía?), Brazil, and Venezuela.

Vochysia expansa Ducke, Arq. Inst. Biol. Veg. 4(1): 32. 1938. TYPE: BRAZIL. Amazonas: Ad ripas fluminis Curicuriary affl. Rio Negro superioris, 23 February 1936, *Walter A. Ducke s.n.* (Holotype: RB [RG34655]; Isotypes: G, K, NY, P, S, U, US).

Habitat and ecology: tree up to 18 m tall; high Amazon Caatinga forests. At elevations of 100–200 m.

Distribution: Colombia (probably in Guianía department), Venezuela (San Carlos de Río Negro, Amazonas state), and Brazil.

Vochysia ferruginea Mart., Nov. Gen. Sp. Pl. 1: 151. 1824 [1826]. TYPE: BRAZIL. Amazonas: Provinciae Rio Negro, Sylvis at Pagum ad Coari, November 1819, *Carl F. P. von Martius 2861* (Holotype: M; Isotypes: K, L).

Homotypic synonyms: *Cucullaria ferruginea* (Mart.) Spreng., Syst Veg. 4(cur. post.): 9. 1827.
Vochya ferruginea (Mart.) Standl. in Britton & Rose, N. Amer. Fl. 25: 302. 1924.

Habitat and ecology: tree 6–22 m tall; evergreen lowland to montane forests, riparian forests, secondary forests-savannas border. At elevations of 50–1600 m.

Distribution: Colombia (Amazonas, Antioquia, Chocó, Cundinamarca, Guainía, Guaviare, Meta, Nariño, Norte de Santander, Santander, Tolima, Valle, Vaupés, Vichada), Honduras, Nicaragua, Costa Rica, Panamá, Venezuela, Guyana, Ecuador, Perú, Brazil, and Bolivia.

Vochysia garcia-barrigae Marc.-Berti, Pittieria 1: 2. 1967. TYPE: COLOMBIA. Vaupés: Río Kananarí y Cerro Isibukuri, 250 m, 29–30 Noviembre 1951, *Hernando García-Barriga 13781* (Holotype: MER; Isotype: COL).

Habitat and ecology: tree up to 30 m tall; evergreen lowland forests. At elevations of 100–250 m.

Distribution: Colombia (Caquetá, Vaupés). Endemic.

Vochysia gentryi Marc.-Berti, Pittieria 20: 113. 1993. TYPE: COLOMBIA. Chocó: lower slopes of Serranía del Darién, west of Ungría, 600–800 m, 17 July 1975, *Alwyn H. Gentry & Luis E. Aguirre 15241* (Holotype: MER; Isotypes: COL, MO).

Habitat and ecology: tree up to 30 m tall; evergreen montane forests. At elevations of 600–800 m.

Distribution: Colombia (Chocó), Costa Rica, and Panamá.

Vochysia grandis Mart. var. ***uaupensis*** Warm. in Mart. Fl. Bras. (Martius) 13(2): 75. 1875. TYPE: BRAZIL. Amazonas: Rio Uaupes near Panure, 01 October 1852, *Richard Spruce 2657* (Holotype: K; Isotypes: BM, BR, C, G-BOIS, GH, K, NY, OXF, P, W).

Habitat and ecology: tree up to 35 m tall; evergreen lowland forests and high Amazon Caatingas. At elevations of 100–200 m.

Distribution: Colombia (Guianía, Vaupés), Brazil, and Venezuela.

Vochysia guatemalensis Donn.Sm., Bot. Gaz. 12: 131; 13: 299. 1887. TYPE: GUATEMALA. Alta Verapaz: in the mountain forests of Pansamala, 1200 m, June 1886, *Hans von Türckheim 943* (Holotype: US; Isotypes: A, F, G, GH, K, M, MO, NY, P, PH).

Habitat and ecology: tree up to 25 m tall; evergreen lowland to montane forests. At elevations of 5–1600 m.

Distribution: Colombia (Chocó), México, Belice, Guatemala, Honduras, Nicaragua, Costa Rica, Panamá, and Ecuador.

Vochysia jefensis A. Robyns Ann. Missouri Bot. Gard. 54(2): 188–189. 1967. TYPE: PANAMA. Panamá: Cerro Jefe (summit), 9°14'02"N, 79°22'30"W, 900 m, 12 March 1967, *John D. Dwyer, G. W. Gauger & Richard K. Baker 7269* (Holotype: MO; Isotype: US).

Habitat and ecology: shrub or tree up to 25 m tall; evergreen montane forests. At elevations of 700–1600 m.

Distribution: Colombia (probably in Chocó department), Panamá (just along the Colombian-Panamanian border, in Cerro Mali, Darién).

Vochysia laxiflora Stafleu, Acta Bot. Neerl. 3: 407, 1954. TYPE: COLOMBIA. Vaupés: Río Apaporis, entre los ríos Kananarí y Pacoa, 250 m, 1–15 December 1951, *Hernando García Barriga 13841* (Holotype: US; Isotypes: COL, ECON).

Heterotypic synonym: *Vochysia columbiensis* Marc.-Berti, Pittieria 1: 8. 1967. TYPE: COLOMBIA. Vaupés: Río Kananari (affluent of Río Apaporis), Cerro Isibukuri, 04 December 1951, *Richard E. Schultes & Isodoro Cabrera 14704a* (Holotype: MER; Isotypes: COL, GH).

Habitat and ecology: tree 9–25 m tall; evergreen forests. At elevations ca. 250 m.

Distribution: Colombia (Caquetá, Guianía, Vaupés), Venezuela.

Vochysia lehmannii Hieron., Bot. Jahrb. Syst. 20(3, Beibl. 49): 38. 1895. TYPE: COLOMBIA. Tolima: prope El Carmén, Purificación, Cundai et Dolores, 500–1000 m, without date, *Friedrich C. Lehmann 7427* (Holotype K; Isotype: F).

Habitat and ecology: tree 5–35 m tall; deciduous to evergreen lowland and montane forests, along the rivers and streams (gallery forests) and savannas-forests border. At elevations of 20–1700 m.

Distribution: Colombia (Arauca, Bolívar, Casanare, Cundinamarca, Guaviare, Magdalena, Meta, Norte de Santander, Santander, Tolima), Brazil, Venezuela, and Perú.

Vochysia lomatophylla Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 150. 1940. TYPE: PERÚ. Loreto: Gamitanacocha, Río Mazán, 100–125 m, 13 January 1935, *José M. Schunke V. 14* (Holotype F; Isotype: US).

Habitat and ecology: tree 5–25 m tall; evergreen lowland riverine and "terra firme" forests. At elevations of 100–1000 m.

Distribution: Colombia (Amazonas, Caquetá, Guaviare, Putumayo, Vaupés), Ecuador, Perú, Brazil, and Bolivia.

Vochysia macrophylla Stafleu, Recueil Trav. Bot. Néerl. 41: 469. 1948. TYPE: COLOMBIA. Chocó: Quibdó, río Atrato, 60 m, April-May 1931, *William R. Archer 1889* (Holotype: US; Isotype: NY).

Habitat and ecology: tree ca. 15 m tall; pluvial lowland forests. At elevations of 60–100 m.

Distribution: Colombia (Chocó). Endemic.

Vochysia magna Stafleu, Recueil Trav. Bot. Néerl. 41: 502. 1948. TYPE: COLOMBIA. Boyacá: El Humbo, 130 miles North of Bogotá, 5°35'55"N, 74°16'15"W, 1300 m, 12 April 1933, *Alexander E. Lawrence 747* (Holotype: G; Isotypes: F, K, S).

Habitat and ecology: tree 20–50 m tall; evergreen montane forests. At elevations of ca. 1300 m.

Distribution: Colombia (Boyacá). Endemic.

Vochysia megalophylla Stafleu, Acta Bot. Neerl. 3(3): 407. 1954. TYPE: COLOMBIA. Santander: Mesa de los Santos, 1500 m, 11–15 December 1926, *Ellsworth P. Killip & Albert C. Smith 15276* (Holotype: NY; Isotypes: A, GH).

Heterotypic synonym: *Vochysia lopezpalaciosii* Marc.-Berti Pittieria 20: 112–113. 1993. TYPE: COLOMBIA. Santander: Mesa de los Santos, 6°52'00"N, 73°03'00"W, 1100–1300 m, 06 August 1968, *Lorenzo Uribe-Uribe 6156* (Holotype: MER; Isotype: NY).

Habitat and ecology: tree up 25 m tall; evergreen montane forests. At elevations of 1000–1500 m.

Distribution: Colombia (Santander), Costa Rica, Panamá, and Venezuela.

Vochysia meridensis Marc.-Berti, Pittieria 10: 11. 1982. TYPE: VENEZUELA. Mérida: La Carbonera, carretera Mérida–La Azulita, *Luis B. Marcano-Berti 1188* (Holotype: MER).

Habitat and ecology: tree up 30 m tall; evergreen montane forests. At elevations of 1900–2600 m.

Distribution: Colombia (Cundinamarca, Norte de Santander), Venezuela, Ecuador, and Perú.

Vochysia moskovitsiana Huamantupa, Phytotaxa 277(3): 293. 2016. TYPE: ECUADOR. Pastaza: Pozo petrolero "Moretecocha" de Arco, río Landayacu, 75 km al este de Puyo, 1°34'S, 77°25'W, 580 m, 4 December 1990, *Edgar Gudiño 1190* (Holotype: QCNE; Isotype: MO).

Habitat and ecology: tree up 40 m tall; evergreen submontane and montane forests. At elevations of 400–1000 m.

Distribution: Colombia (Putumayo), Ecuador, and Perú.

Vochysia obscura Warm. in Mart., Fl. Bras. 13(2): 73. 1875. TYPE: VENEZUELA. Amazonas: San Carlos, ad Rio Negro, October 1853, *Richard Spruce 3700* (Holotype: K; Isotypes: BM, E, P).

Habitat and ecology: tree 5–25 m tall; evergreen lowland, submontane and montane forests. At elevations of 50–1200 m.

Distribution: Colombia (Amazonas, Caquetá, Guainía, Guaviare, Meta, Vaupés, Vichada), Venezuela, Brazil, and Perú.

Vochysia pachyantha Ducke, Arq. Inst. Biol. Veg. 4(1): 36 1938. TYPE: BRAZIL. Amazonas: Ad ripas fluminis Curicuriary affl. Rio Negro superioris, 21 February 1936, *Walter A. Ducke s.n.* (Holotype [RG34653]: RB; Isotypes: G, K, NY, P, RB, S, U, US).

Habitat and ecology: tree up to 25 m tall; evergreen submontane forests. At elevations of ca. 600 m.

Distribution: Colombia (Putumayo), Brazil.

Vochysia pacifica Cuatrec., Revista Acad. Colomb. Ci. Exact. 6: 548. 1946. TYPE: COLOMBIA. Valle: Río Cajambre, 10 m, 09 May 1944, *José Cuatrecasas 17468* (Holotype: VALLE; Isotypes: F, U, US).

Habitat and ecology: tree 25–30 m tall; pluvial lowland forests. At elevations of 10–50 m.

Distribution: Colombia (Valle). Endemic.

Vochysia parviflora Spruce ex Warm. Flora Brasiliensis 13(2): 75. 1875. TYPE: BRAZIL. Amazonas: Rio Negro, inter Barcellos and Sta. Isabel, December 1851, *Richard Spruce 1974* (Holotype: K; Isotypes: BM, C, E, F, FI, G-BOIS, GH, K, LD, M, NY, OXF, P, RB, W).

Habitat and ecology: tree ca. 20 m tall; evergreen nonflooded forests. At elevations of 100–300 m.

Distribution: Colombia (Vaupés), Brazil.

Vochysia pinkusii A.C. Sm., Bull. Torrey Bot. Club 67: 288. 1940. TYPE: BRAZIL. Roraima: Maurukow Creek (tributary of Rio Cotinga), near Venezuelan boundary, 1350 m, 22 February 1939, *Albert S. Pinkus 167* (Holotype: NY; Isotypes: G, GH, IFI, K, NY, S, US).

Habitat and ecology: tree ca. 20 m tall; evergreen lowland to montane forests. At elevations of 100–1400 m.

Distribution: Colombia (Caquetá, Guianía), Venezuela, and Brazil (along the Venezuelan-Brazilian border in Roraima state).

Vochysia punctata Spruce ex Warm. In Mart., Fl. Bras. 13(2): 102. 1875. TYPE: BRAZIL. Amazonas: Rio Uaupes near Panure, 01 October 1852, *Richard Spruce 2675* (Holotype: K; Isotypes: BM, BR, G-BOIS, GH, NY, OXF, P, W).

Habitat and ecology: tree 15–30 m tall; evergreen lowland to submontane forests. At elevations of 100–450 m.

Distribution: Colombia (Amazonas, Caquetá, Guianía, Vaupés), Venezuela, Ecuador, and Brazil.

Vochysia saccata Stafleu, Recueil Trav. Bot Néerl. 41: 508. 1948. TYPE: BRAZIL. Amazonas: Ad ripas fluminis Curicuriary affl. Rio Negro superioris, 23 November 1936, *Walter A. Ducke s.n.* – RG34654 (Holotype: U; Isotypes: G, K, P, S, U, US).

Habitat and ecology: tree up to 25 m tall; evergreen lowland to montane forests. At elevations of 100–1200 m.

Distribution: Colombia (Caquetá), Venezuela, and Brazil.

Vochysia spathiphylla Stafleu, Acta Bot. Neerl. 6: 341. 1957. TYPE: COLOMBIA. Vaupés: Cabeceras del río Cubiyu, 08 December 1943, *Paul H. Allen 3248* (Holotype: US).

Habitat and ecology: tree 15–30 m tall; evergreen lowland to montane forests. At elevations of 100–1700 m.

Distribution: Colombia (Vaupés), Venezuela, and Brazil.

Vochysia splendens Spruce ex Warm. In Mart., Fl. Bras. 13(2): 101. 1875. TYPE: BRAZIL. Amazonas: Rio Uaupes near Panure, 01 October 1852, *Richard Spruce 2697* (Holotype: K; Isotypes: BM, BR, G-BOIS, GH, NY, OXF, P, W).

Habitat and ecology: tree 15–30 m tall; evergreen riparian and "terra firme" lowland forests. At elevations of 100–200 m.

Distribution: Colombia (Amazonas, Caquetá, Guianía, Vaupés), Venezuela, and Brazil.

Vochysia steyermarkiana Marc.-Berti, Pittieria 13: 10. 1986. TYPE: VENEZUELA. Amazonas: Yavita, 110 m, *Llewelyn Williams 14162* (Holotype: MER; Isotypes: G, NY, VEN).

Habitat and ecology: tree 15–25 m tall; evergreen "terra firme" lowland forests and high Amazon Cattinga. At elevations of 100–200 m.

Distribution: Colombia (Guianía), Venezuela.

Vochysia venezuelana Stafleu, Recueil Trav. Bot. Néerl. 41: 437. 1948. TYPE: VENEZUELA. Bolívar: Lower Caura river, 50–80 m, 07 February 1939, *Llewelyn Williams 11200* (Holotype: F; Isotypes: S, US).

Habitat and ecology: tree 5–20 m tall; deciduous to evergreen lowland and montane forests, along the rivers and streams (gallery forests) and savannas-forests border. At elevations of 20–1200 m.

Distribution: Colombia (Arauca, Bolívar, Casanare, Cundinamarca, Guaviare, Meta, Vichada), Venezuela.

Vochysia vismiifolia Spruce ex Warm. In Mart., Fl. Bras. 13(2): 99. 1875. TYPE: BRAZIL. Amazonas: Manaos, 1851, *Richard Spruce 1823* (Holotype: K; Isotypes: BM, C, G, GH, NY, OXF, P, W).

Habitat and ecology: tree 15–30 m tall; evergreen lowland to montane forests. At elevations of 100–1300 m.

Distribution: Colombia (Caquetá, Chocó, Guaviare, Guianía, Putumayo, Valle, Vaupés, Vichada), Venezuela, Brazil, Ecuador, Perú, and Bolivia.

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Appendix

The ethnobotany of *Vochysia* has been largely ignored in monographs and recent nomenclatural contributions. However, information on this topic is relatively well known due to R. E. Schultes's research from the 1950s to the 1970s. Schultes (1977) reported that, along the Piriparaná River (Vaupés, Colombia), members of the Maku nation prepare poison for arrows from the bark of *V. columbiensis* Marc.-Berti (treated here as a a synonym of *V. laxiflora* Stafleu) as a curare substitute. He also recorded use of the decoction of the bark of *V. ferruginea* Mart. by the Kubeo people from the Querarí River (Vaupés, Colombia) to wash ulcering sores on the legs, and their use of the dried and powdered leaves added to coca (*Erythroxylon coca* Lam.) in the belief that they are beneficial for sores of the mucous membrane of the mouth and gums. The Puinave Indians call *V. laxiflora* by the same name ("Po-ho-glo") that they use for *V. ferruginea*, although they easily recognize the two as different; they do not use it medicinally (Schultes, 1977). The several Indian tribes (Taiwanos, Barasanas, and Makunas) residing in the middle Apaporis River region (Vaupés, Colombia), on the contrary, value *Vochysia laxiflora* for several therapeutic purposes: its leaves are boiled with the leaves of coca (*E. coca*) to prepare a tea "when urination is painful or impossible"; and the bark, dried and finely powdered, is rubbed into skin sores that will not react to more common treatments with various washes. The bark is also thrown on fires and the acrid smoke thus produced is vigorously inhaled to relieve asthmatic and other respiratory ailments (Schultes, 1977).

Finally, Schultes (1977) also reported that the Barasana Indians from the Pacoa River (Vaupés, Colombia) gave the pulverized leaves and bark of a tree called "ka-kwee-gaw-ya" (*V. lomatophylla*) to pregnant women in warm *chicha* as an abortifacient, and that it "was formerly used for this purpose."

A TAXONOMIC REVISION OF *ESPELETIA* (ASTERACEAE). II. UPDATED LIST OF TAXA, NOMENCLATURE, AND CONSERVATION STATUS IN THE COLOMBIAN RADIATION

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Abstract. In this work a taxonomic revision is made of the nomenclature, distribution, and conservation status for the 84 species in the Colombian clade of *Espeletia*. Taxonomic changes include five new combinations for taxa at the species level that are transferred to *Espeletia*. Seventy-three species are endemic to the Colombian Cordillera Oriental (including four extending into the Venezuelan side of Páramo de Tamá), six are found in the Colombian Cordillera Central (four endemic to this range, one extending into Ecuador, and one shared with the Colombian Cordillera Occidental), three are endemic to the Colombian Cordillera Occidental, and two are endemic to Sierra de Perijá (including one yet to be found within Colombian borders). Geographic distributions at the páramo massif level are given for all species and subspecies. The IUCN Red List category is listed for each species, with suggestions for recategorization of some species with small distribution areas, low number of populations, and threats to their habitat extent and quality. In all, about 60 species in the Colombian *Espeletia* clade must be classified within a threatened category. When species belonging to the Venezuelan *Espeletia* clade that are found within Colombian borders are included, the current estimate of total diversity of *Espeletia* in this country is 90 species.

Keywords: Andes, caulescent rosette, Compositae, frailejón, páramo, Colombia

Asteraceae subtribe Espeletiinae (Cuatrecasas, 1976) are rapidly becoming a model for studies of ecology and evolution in páramos, particularly with regard to population and community ecology (Mora et al., 2019), ecophysiology (Rada, 2016), climate change (Mavárez et al., 2019), diversification and adaptive radiation (Pouchon et al., 2018, 2021) and, of course, taxonomy (Diazgranados, 2012; Cuatrecasas, 2013; Mavárez, 2019). Taxonomic research in particular started more than two centuries ago with the formal publication of *Espeletia* Mutis ex Bonpl., and the Colombian species *E. grandiflora* Bonpl., *E. argentea* Bonpl., and *E. corymbosa* Bonpl. (Humboldt and Bonpland, 1809). The genus *Espeletia* was attributed by Humboldt and Bonpland to José Celestino Mutis, director of the Expedición Botánica del Nuevo Reino de Granada, who first named it at the end of the 18th century (see the detailed chronological account of systematic studies in Cuatrecasas, 2013). Another species from Venezuela described as *Trixis neriifolia* Bonpl. ex Humb. (Humboldt, 1814), was renamed *Baillieria? neriifolia* (Bonpl. ex Humb.) Kunth (Humboldt et al., 1820), later as *Clibadium? neriifolium* (Bonpl. ex Humb.) DC (De Candolle, 1836), and finally as *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd. (Weddell, 1855). The genus remained undivided in almost all subsequent taxonomic treatments of the group—namely, Standley, 1915; Smith and Koch, 1935; Cuatrecasas, 1949; and Aristeguieta, 1964—with the only exception of Ernst (1870), who unaware of Weddell's work renamed *T. neriifolia* in a new genus as *Libanothamnus neriifolius* (Bonpl. ex Humb.) Ernst. Cuatrecasas (1976) raised the 124 *Espeletia* species known at that time to subtribe Espeletiinae and divided it into seven genera defined mainly according to plant habitus and the position and structure of the capitulescence: *Carramboa* Cuatrec., *Coespeletia* Cuatrec., *Espeletia* Mutis ex Bonpl., *Espeletiopsis* Cuatrec., *Libanothamnus* Ernst, *Ruilopezia* Cuatrec., and *Tamania* Cuatrec. An additional genus, *Paramiflos* Cuatrec., was segregated from *Espeletiopsis* and added to the subtribe in Cuatrecasas (1995). The eight-genera system was subsequently used in biodiversity catalogues, for example, Rangel-Churio, 2000, and Hokche et al., 2008, and in taxonomic treatments of the group, for example, Diazgranados, 2012, and Cuatrecasas, 2013. The latter work, unfortunately published posthumously in an unfinished state (one genus with ca. 20 species missing), represents an impressive monographic masterpiece of the subtribe. Therein, Cuatrecasas fully developed the classification and nomenclatural system of this group sketched in his 1976 work, among many other topics.

It should be noted that, contrary to some common belief, Cuatrecasas's classification system was far from being unanimously accepted. Indeed, several workers on the ecology and physiology of these plants did not agree with this multigeneric system, and a number of very influential studies were published after 1976 using only *Espeletia,* for example, Baruch and Smith, 1979; Smith, 1981; Goldstein et al., 1984, 1985; Monasterio, 1986; Berry et al., 1988; Guariguata and Azócar, 1988; Berry and Calvo, 1989, 1994; Monasterio and Sarmiento, 1991; and Silva et al., 2000. Further doubts about the validity of Espeletiinae genera were raised when their relationships started to be analyzed with molecular phylogenetic methods—for example, Rauscher, 2002; Madriñán et al., 2013; Diazgranados and Barber, 2017—and

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have been confirmed with the advent of metabolombics (Padilla-González et al., 2017) and phylogenomic approaches (Pouchon et al., 2018, 2021). These studies have provided unequivocal phylogenetic evidence supporting patterns in clear contradiction to previous ideas on the evolution and systematics of this group:

1. There have been two geographically delimited and mostly disconnected radiations in the Venezuelan and Colombian Andes, respectively, instead of an initial radiation in Venezuela followed by multiple colonizations of Colombia, as proposed by Smith and Koch (1935) and Cuatrecasas (1986b, 2013). The "Venezuelan clade" (Fig. 1A), with 54 species, includes all taxa distributed in the Venezuelan Cordillera de Mérida, plus a few lineages that colonized the northern areas in the Colombian Cordillera Oriental, Sierra de Perijá, and Sierra Nevada de Santa Marta. The "Colombian clade" (Fig. 1B, 2), with 84 species, comprises all remaining taxa distributed in the Colombian Andes, Sierra de Perijá, and northern Ecuador (see Mavárez, 2019).

2. As currently circumscribed, most genera in the classification system of Espeletiinae proposed by Cuatrecasas (1976, 1995) are poly- or paraphyletic (Fig. 3). For instance, the phylogenomic analysis by Pouchon et al. (2021), based on 9880 fragments covering > 4 million bp of the nuclear genome, has shown that the three largest genera in the subtribe—*Espeletia*, *Espeletiopsis*, and *Ruilopezia*—representing ca. 85% of the species, are clearly polyphyletic. Each of the former two genera comprises at least two distantly related clades, one in Venezuela and one in Colombia, a number that could increase upon analysis of more taxa from the latter country. The polyphyly of *Ruilopezia* is even greater, since it embraces at least three unrelated clades in Venezuela plus one species nested within *Libanothamnus*. *Espeletia semiglobulata* Cuatrec. is nested within *Coespeletia*. The monotypic *Tamania* is nested within a clade of *Ruilopezia*, whereas the phylogenetic affinities of the monotypic *Paramiflos* are still unclear. Only *Carramboa* appeared to be monophyletic.

These patterns of extensive polyphyly/paraphyly among genera of Espeletiinae indicated that the classification system proposed by Cuatrecasas (1976, 1995) is largely artificial and must be modified. Mavárez (2019) proposed a modification adopting the view that only *Espeletia* should be recognized in the subtribe, with the other seven genera considered as heterotypic synonyms. Thus, *Espeletia* recovered its original definition, encompassing the ensemble of the subtribe Espeletiinae. An obvious advantage of this system is that since the majority of the species were already placed in the genus *Espeletia* (72 species), the proposed change to the classification system implied essentially the restoration of 54 species originally named under *Espeletia* but transfered later to other genera by Cuatrecasas (1976, 1995), and 12 new combinations for some species described after 1976: 2 in *Coespeletia* (Cuatrecasas, 2013; Diazgranados and Morillo, 2013), 2 in *Libanothamnus* (Cuatrecasas, 1980), 3 in *Ruilopezia* (Cuatrecasas, 1986a), and 5 in *Espeletiopsis* (Díaz-Piedrahita and Obando, 2004; Díaz-Piedrahita et al., 2006; Díaz-Piedrahita and Rodríguez-Cabeza, 2008, 2010; and Diazgranados and Sánchez, 2013). Mavárez (2019) formally applied the proposed nomenclatural changes to the taxa in the Venezuelan clade, which led to 38 species recovering their original name under *Espeletia*, while another 7 were transferred to this genus with new combinations.

Continuing with the taxonomic revision started in Mavárez (2019), in this work I present an updated list of species and nomenclatural changes in the Colombian clade of *Espeletia*. A review of distribution information is also given, in the form of presence of species and subspecies in the recognized páramo complexes in Colombia and nearby areas in northern Ecuador and western Venezuela. However, contrary to the revision in Mavárez (2019), no maps or morphological descriptions of taxa will be given here, to maintain this work's length within reasonable limits. That information will be provided in future publications.

MATERIALS AND METHODS

The taxonomy of the Colombian clade of *Espeletia* was reexamined, with an emphasis on the nomenclatural changes proposed by Mavárez (2019). A list of valid names is provided, with all known homotypic and heterotypic synonyms, and with basionyms for new combinations (*comb. nov.*). Taxa below the rank of species are also given, that is, subspecies (subsp.), variety (var.), and forma (f.), although the validity of most of these infraspecific ranks remains to be verified. Autonyms are provided as well for databasing purposes. Over 300 specimens were analyzed, of which 145 corresponded to type specimens. Analyzed samples are deposited in herbaria AMD, B, BC, BM, BR, CAS, COL, CM, E, F, FI, G, GB, GH, HUA, K, L, LD, MA, MO, MY, NY, P, PRC, S, U, US, W, and WIS (acronyms according to Thiers, 2020).

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

Valid name, followed by the appropriate reference or *status*. TYPE: whenever possible given as: COUNTRY. Department: Locality, elevation, coordinates, collection date, *collection number* (herbaria acronyms).

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

Distribution: retrieved exclusively from herbarium samples and provided here as confirmed presence of the species and subspecies in the main geographic units of páramo officially considered for Colombia (Morales et al., 2007) and neighboring areas in Venezuela and Ecuador (Fig. 4–6). At least one representative collection number per páramo unit is given, with preference for samples available in online databases.

Conservation status: IUCN threat category, followed by suggestions for recategorization in species that may deserve a change in their current conservation status.

A list of interspecific hybrid taxa in the Colombian clade of *Espeletia* and the reference supporting their hybrid status are provided at the end of the Taxonomy section. Parents in hybrid formulae are provided in alphabetical order.

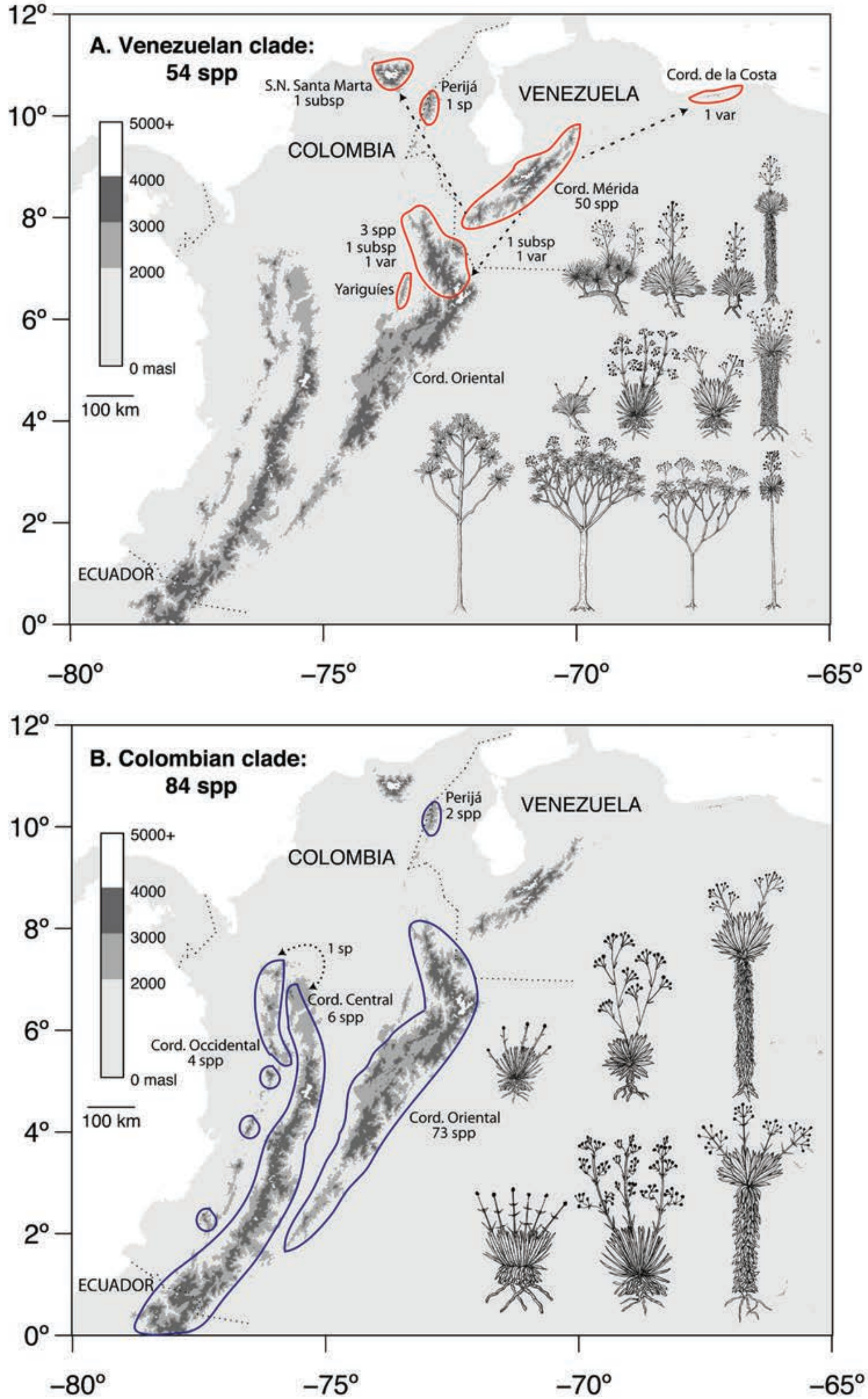


FIGURE 1. **A,** Species diversity and distribution in the Venezuelan clade of *Espeletia*. Upper row—examples of monocarpic rosette plants with monochasial inflorescences; middle row—examples of polycarpic rosette plants with monocephalous (left), dichasial (2nd), or monochasial (3rd, right) capitulescences; lower row—examples of trees with branched and unbranched stems. **B,** Species diversity and distribution in the Colombian clade of *Espeletia*. Upper row—examples of polycarpic rosette plants with monochasial capitulescences; lower row—examples of polycarpic rosette plants with dichasial capitulescences. Arrows indicate shared species between regions. (Plant drawings by C. Perrier, SAJF).

FIGURE 2. Examples of species diversity in the Colombian *Espeletia* clade. Top row, left to right: *E. garciae* Cuatrec., *E. guacharaca* S. Díaz, *E. conglomerata* A.C. Sm., and *E. incana* Cuatrec. Second row, left to right: *E. murilloi* Cuatrec., *E. brachyaxiantha* S. Diaz, *E. barclayana* Cuatrec., and *E. ramosa* Mavárez & M.T. Becerra. Third row, left to right: *E. muiska* Cuatrec., *E. jaramilloi* S. Díaz., and *E. santanderensis* A.C. Sm. Bottom row, left to right: *E. congestiflora* Cuatrec., *E. jimenezquesadae* Cuatrec., and *E. curialensis* Cuatrec.

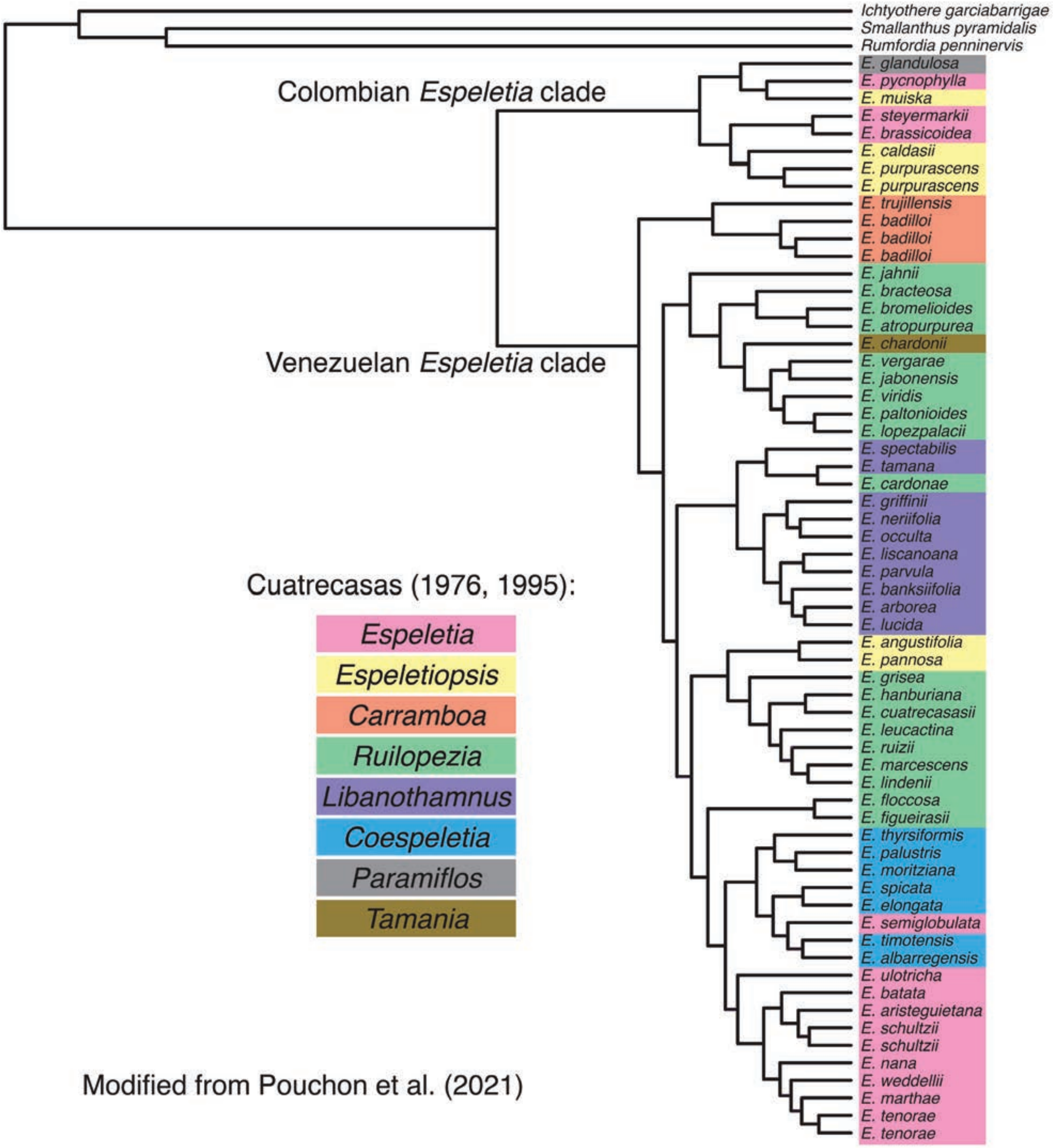


FIGURE 3. Molecular phylogenomic analysis of species in subtribe Espeletiinae based on maximum likelihood. Color shades highlight genera according to Cuatrecasas (1976, 1995). See Pouchon *et al*. (2021) for details on phylogenomic reconstructions.

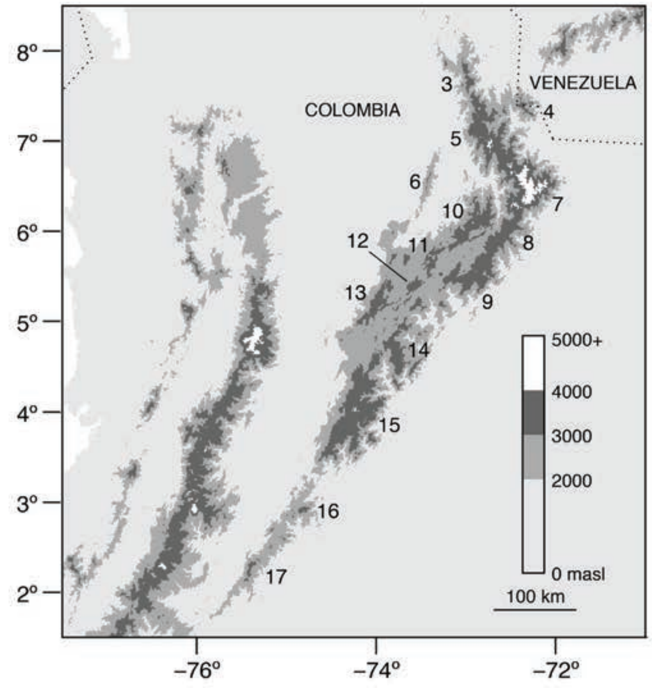
RESULTS

Taxonomic Changes

Five new combinations are proposed for taxa at the species level transferred to *Espeletia*.

Diversity

The Colombian clade of *Espeletia* currently contains valid names for 84 species, which, together with 6 others phylogenetically affiliated with the Venezuelan *Espeletia* clade but found within Colombia's political borders, elevate the total diversity of the genus in this country to 90 species. However, it's important to note that the biological validity of these taxa was not evaluated in this work, and this number should therefore be considered approximate. A better estimate of the diversity in the Colombian *Espeletia* clade will require thorough morphological and genetic analyses, which will likely lead to the detection of previously overlooked taxa (e.g., Alzate and Giraldo-Gómez, 2020) but also to the removal of others that may not represent good biological entities, such as hybrids and poorly described taxa. With regard to the latter, seven species are known only from the type specimens, that is,



Geographic area: spp COL (spp VEN)

Cordillera Oriental: 73 (+5) spp

3. Jurisdicciones-Santurbán: 10, 13, 14, 21, 24, 31, 69, 71, 72, 76, 82 (+2)
4. Tamá: 10, 21, 63, 77 (+4)
5. Almorzadero: 21, 26, 28, 39, 57, 61, 74, 76 (+2)
6. Yariguíes: 38? (+1)
7. S.N. Cocuy: 1, 18, 19, 23, 41, 44, 48, 57 (+1)
8. Pisba: 4, 7, 8, 19, 20, 23, 27, 29, 35, 40, 44, 46, 50, 57, 58, 59, 62, 75
9. Tota-Bijagual-Mamapacha: 1, 2, 8, 15, 20, 35, 38?, 44, 48, 49, 53, 56, 66 80, 83
10. Guantiva-La Rusia: 1, 2, 5, 6, 8, 9, 12, 17, 20, 25, 33, 34, 35, 38, 43, 48 49, 51, 59, 70, 83
11. Iguaque-Merchán: 2, 6, 8, 32, 33, 35, 48, 49, 51, 54, 59, 83
12. Rabanal-Río Bogotá: 6, 8, 16, 22, 49, 65, 67
13. Guerrero: 3, 6, 15, 16, 22, 34
14. Chingaza: 3, 22, 34, 42, 84
15. Cruz Verde-Sumapaz: 3, 11, 22, 34, 42, 47, 59, 78, 79
16. Picachos: ?
17. Miraflores: ?

FIGURE 4. Distribution of species in the Colombian *Espeletia* clade along the main páramo complexes of the Colombian Cordillera Oriental and nearby areas in Western Venezuela. (Numbers within parentheses indicate additional species belonging to the Venezuelan *Espeletia* clade). **1.** *Espeletia annemariana* Cuatrec. **2.** *Espeletia arbelaezii* Cuatrec. **3.** *Espeletia argentea* Bonpl. **4.** *Espeletia ariana* Rodríguez-Cabeza & S. Díaz. **5.** *Espeletia azucarina* Cuatrec. **6.** *Espeletia barclayana* Cuatrec. **7.** *Espeletia betancurii* (Rodríguez-Cabeza, S. Díaz & Gal.-Tar.) Mavárez. **8.** *Espeletia boyacensis* Cuatrec. **9.** *Espeletia brachyaxiantha* S. Díaz. **10.** *Espeletia brassicoidea* Cuatrec. **11.** *Espeletia cabrerensis* Cuatrec. **12.** *Espeletia cachaluensis* Rodríguez-Cabeza & S. Díaz. **13.** *Espeletia caldasii* Cuatrec. **14.** *Espeletia canescens* A.C. Sm. **15.** *Espeletia cayetana* (Cuatrec.) Cuatrec. **16.** *Espeletia chocontana* Cuatrec. **17.** *Espeletia chontalensis* Rodríguez-Cabeza & S. Díaz. **18.** *Espeletia cleefii* Cuatrec. **19.** *Espeletia colombiana* Cuatrec. **20.** *Espeletia congestiflora* Cuatrec. **21.** *Espeletia conglomerata* A.C. Sm. **22.** *Espeletia corymbosa* Bonpl. **23.** *Espeletia curialensis* Cuatrec. **24.** *Espeletia diazii* (Diazgr. & L.R. Sánchez) Mavárez. **25.** *Espeletia discoidea* Cuatrec. **26.** *Espeletia dugandii* Cuatrec. **27.** *Espeletia episcopalis* Rodríguez-Cabeza & S. Díaz. **28.** *Espeletia estanislana* Cuatrec. **29.** *Espeletia formosa* S. Díaz & Rodríguez-Cabeza. **31.** *Espeletia funckii* Sch. Bip. ex Wedd. **32.** *Espeletia garciae* Cuatrec. **33.** *Espeletia glandulosa* Cuatrec. **34.** *Espeletia grandiflora* Bonpl. **35.** *Espeletia guacharaca* S. Díaz. **38.** *Espeletia incana* Cuatrec. **39.** *Espeletia insignis* Cuatrec. **40.** *Espeletia jaramilloi* S. Díaz. **41.** *Espeletia jimenezquesadae* Cuatrec. **42.** *Espeletia killipii* Cuatrec. **43.** *Espeletia laxiflora* (S. Díaz & Rodríguez-Cabeza) Mavárez. **44.** *Espeletia lopezii* Cuatrec. **46.** *Espeletia mirabilis* S. Díaz & Rodríguez-Cabeza. **47.** *Espeletia miradorensis* (Cuatrec.) Cuatrec. **48.** *Espeletia muiska* Cuatrec. **49.** *Espeletia murilloi* Cuatrec. **50.** *Espeletia mutabilis* S. Díaz & Rodríguez-Cabeza. **51.** *Espeletia nemekenei* Cuatrec. **53.** *Espeletia oswaldiana* S. Díaz. **54.** *Espeletia paipana* S. Díaz & Pedraza. **56.** *Espeletia pescana* (S. Díaz) S. Díaz. **57.** *Espeletia petiolata* Cuatrec. **58.** *Espeletia pisbana* S. Díaz & Rodríguez-Cabeza. **59.** *Espeletia pleiochasia* Cuatrec. **61.** *Espeletia praesidentis* Diazgr. & L.R. Sánchez. **62.** *Espeletia pulcherrima* Rodríguez-Cabeza & S. Díaz. **63.** *Espeletia purpurascens* Cuatrec. **65.** *Espeletia rabanalensis* (S. Díaz & Rodríguez-Cabeza) Mavárez. **66.** *Espeletia ramosa* Mavárez & M.T. Becerra. **67.** *Espeletia raquirensis* Rodríguez-Cabeza & S. Díaz. **69.** *Espeletia roberti* Cuatrec. **70.** *Espeletia rositae* Cuatrec. **71.** *Espeletia sanchezii* (S. Díaz & Obando) Mavárez. **72.** *Espeletia santanderensis* A.C. Sm. **74.** *Espeletia sclerophylla* Cuatrec. **75.** *Espeletia soroca* S. Díaz & Rodríguez-Cabeza. **76.** *Espeletia standleyana* A.C. Sm. **77.** *Espeletia steyermarkii* Cuatrec. **78.** *Espeletia summapacis* Cuatrec. **79.** *Espeletia tapirophila* Cuatrec. **80.** *Espeletia tibamoensis* Rodríguez-Cabeza & S. Díaz. **82.** *Espeletia trianae* Cuatrec. **83.** *Espeletia tunjana* Cuatrec. **84.** *Espeletia uribei* Cuatrec.

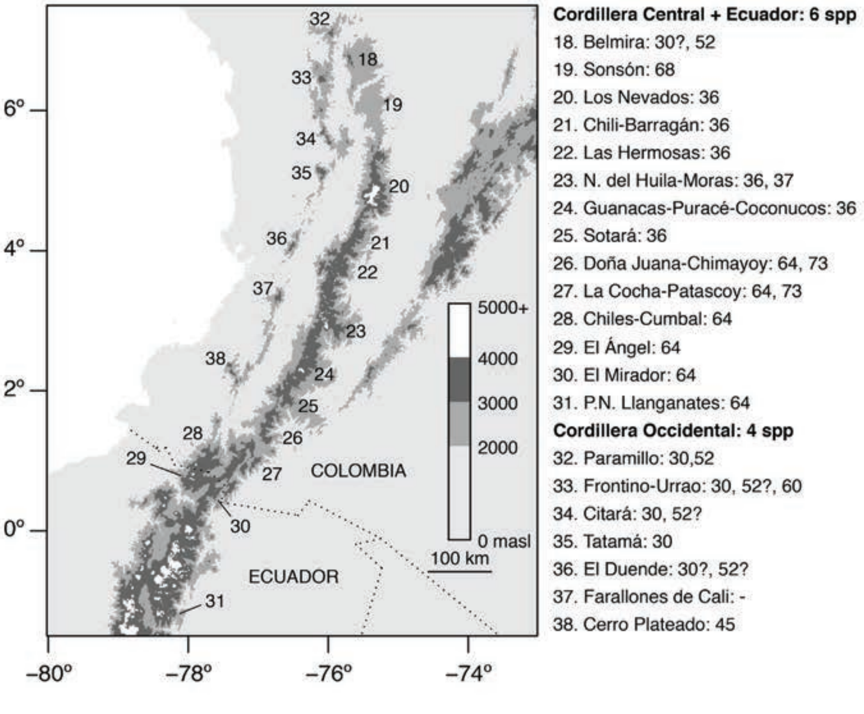
E. chontalensis Rodríguez-Cabeza & S. Díaz, *E. marnixiana* S. Díaz & Pedraza, *E. mirabilis* S. Díaz & Rodríguez-Cabeza, *E. miradorensis* (Cuatrec.) Cuatrec., *E. tapirophila* Cuatrec., *E. tillettii* Cuatrec., and *E. trianae* Cuatrec. The validity of these and other taxa known from a handful of samples needs to be reviewed.

Distribution

Of the 84 species currently recognized in the Colombian *Espeletia* clade, 73 are endemic to the Colombian Cordillera Oriental (including 4 extending into the Venezuelan side of Páramo de Tamá) (Fig. 4), 6 are found in the Colombian Cordillera Central (4 endemic to this range, 1 extending into Ecuador, and 1 also found in the Colombian Cordillera Occidental) (Fig. 5), 3 are endemic to Colombian Cordillera Occidental, and 2 are endemic to Perijá (1 of which is known so far only from the Venezuelan side but very close to the border with Colombia) (Fig. 6).

Among the 73 species in the Colombian *Espeletia* clade located in the Cordillera Oriental, 19 are found in the north section (Tamá, Jurisdicciones-Santurbán, and Almorzadero), 29 in the east-central section (S.N. Cocuy, Pisba, and Tota-Bijagual-Mamapacha), 29 in the west-central section (Yariguíes, Guantiva-La Rusia, Iguaque-Merchán, Rabanal-Río Bogotá, and Guerrero), and 10 in the south section (Chingaza, Cruz Verde-Sumapaz, Picachos, and Miraflores) (Fig. 7). No species in the Colombian *Espeletia* clade is shared between the north and west-central sections of Cordillera Oriental, although these sections share a species belonging to the Venezuelan clade, *E. chardonii* A.C. Sm. North and east-central sections share 2 species, *E. petiolata* Cuatrec. (Colombian clade) and *E. tamana* Cuatrec. (Venezuelan clade). The two central sections share 10 species: *E. boyacensis* (Cuatrec.) Cuatrec., *E. congestiflora* Cuatrec., *E. guacharaca* S. Díaz, *E. muiska* Cuatrec., *E. murilloi* Cuatrec., *E. pleiochasia* Cuatrec., *E. tunjana* Cuatrec., *E. annemariana* Cuatrec., and *E. arbelaezii* Cuatrec., although the case for the latter 2 may be based on misdentifications. Finally, east-central and south sections share 4 species—*E. argentea*, *E. corymbosa*, *E. grandiflora*, and *E. pleiochasia*—the latter being the only species found in three sections of the Cordillera Oriental.

At the páramo level, *Espeletia* is absent from P.N.N. Farallones de Cali (Fig. 5), and the only species found in S.N. Santa Marta is a tree belonging to the Venezuelan clade, *E. occulta* S.F. Blake subsp. *glossophylla* (Matff.) Mavárez (Fig. 6). In general, most páramos in the Cordillera Oriental are home to 5 or more *Espeletia* species, with the largest numbers found in Guantiva–La Rusia (21 spp.) and Pisba (18 spp.) (Fig. 4). Only three relatively small and isolated páramos in Cordillera Oriental contain 1–2 species: P.N.N. Serranía de los Yariguíes, P.N.N. Los Picachos, and P.N.R. Miraflores (the identity of the *Espeletia* species in the latter two páramos remains to be verified). In sharp contrast, the majority of páramos in Cordillera Central contain a single and widespread species, *E. hartwegiana* Sch. Bip ex Cuatrec., with 2 coexisting species found only in páramos around Laguna La Cocha, in páramo de Moras, and possibly in Belmira (Fig. 5). The distribution of species in Cordillera Occidental seems to follow the pattern of a single species in



Cordillera Central + Ecuador: 6 spp
18. Belmira: 30?, 52
19. Sonsón: 68
20. Los Nevados: 36
21. Chili-Barragán: 36
22. Las Hermosas: 36
23. N. del Huila-Moras: 36, 37
24. Guanacas-Puracé-Coconucos: 36
25. Sotará: 36
26. Doña Juana-Chimayoy: 64, 73
27. La Cocha-Patascoy: 64, 73
28. Chiles-Cumbal: 64
29. El Ángel: 64
30. El Mirador: 64
31. P.N. Llanganates: 64

Cordillera Occidental: 4 spp
32. Paramillo: 30,52
33. Frontino-Urrao: 30, 52?, 60
34. Citará: 30, 52?
35. Tatamá: 30
36. El Duende: 30?, 52?
37. Farallones de Cali: -
38. Cerro Plateado: 45

FIGURE 5. Distribution of species in the Colombian *Espeletia* clade along the main páramo complexes of the Colombian Cordillera Central, Colombian Cordillera Occidental, and nearby areas in Northern Ecuador. **30.** *Espeletia frontinoensis* Cuatrec. **36.** *Espeletia hartwegiana* Sch. Bip. ex Cuatrec. **37.** *Espeletia idroboi* Cuatrec. **45.** *Espeletia marnixiana* S. Díaz & Pedraza. **52.** *Espeletia occidentalis* A.C. Sm. **60.** *Espeletia praefrontina* Cuatrec. **64.** *Espeletia pycnophylla* Cuatrec. **68.** *Espeletia restricta* Alzate & S. Giraldo. **73.** *Espeletia schultesiana* Cuatrec.

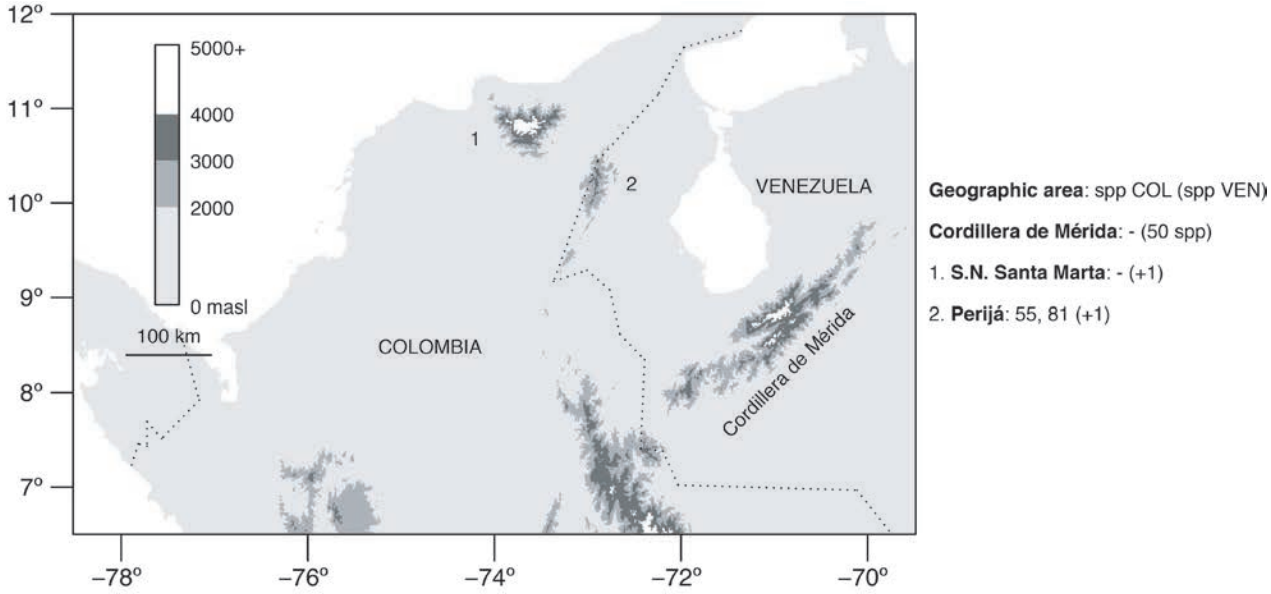


FIGURE 6. Distribution of species in the Colombian *Espeletia* clade along the páramo complexes of Sierra Nevada de Santa Marta, Perijá, and nearby areas in Western Venezuela. Numbers within parentheses indicate additional species belonging to the Venezuelan *Espeletia* clade: *E. occulta* S.F. Blake subsp. *glossophylla* (Matff.) Mavárez in Santa Marta and *E. divisoriensis* (Cuatrec.) Mavárez in Perijá. **55.** *Espeletia perijaensis* Cuatrec. **81.** *Espeletia tillettii* Cuatrec.

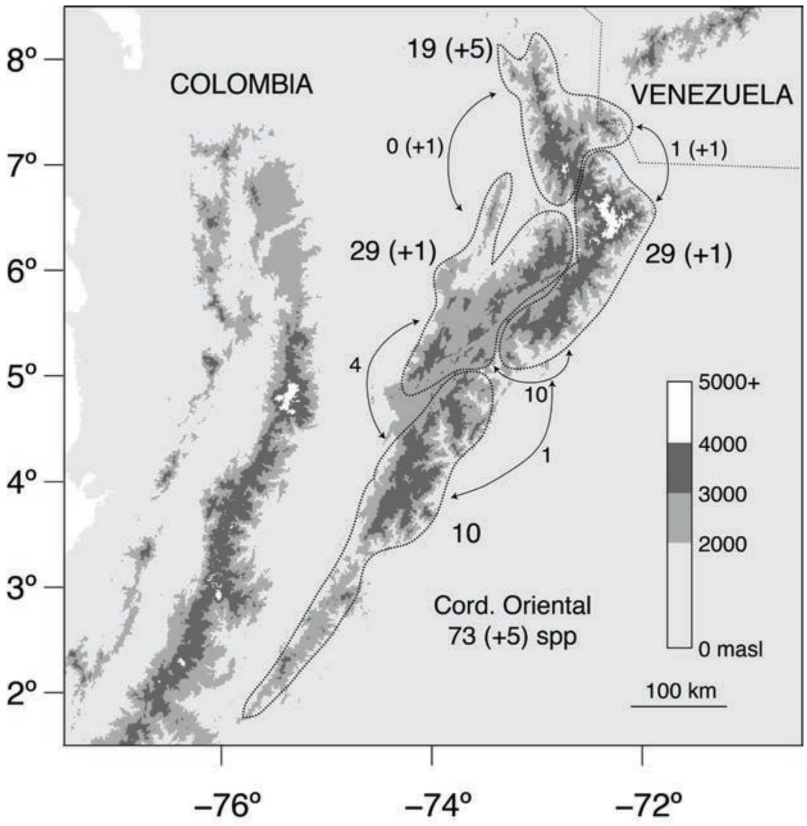


FIGURE 7. Diversity of species in the Colombian *Espeletia* clade along the four major geographic regions of the Cordillera Oriental. Arrows give the number of shared species between regions. (Numbers within parentheses indicate additional species belonging to the Venezuelan *Espeletia* clade).

small and isolated páramos, with the exception of Frontino-Urrao and perhaps Paramillo, both in the extreme north (Fig. 5). However, it is important to note that knowledge about distribution patterns of *Espeletia* at the páramo level in Colombia may be subject to change. On the one hand, as mentioned above, the presence of some species must be confirmed in some páramos, and the validity of several species must even be verified. On the other hand, scientific explorations in poorly sampled or remote areas will certainly lead to updates in the distribution of some species, and perhaps also to the discovery of others that have remained so far unknown or overlooked.

Conservation

Out of 84 species in the Colombian *Espeletia* clade, the conservation status of 3 have not been formally evaluated following IUCN critera (*E. ramosa* Mavárez & M.T. Becerra, *E. restricta* Alzate & S. Giraldo, and *E. tillettii* Cuatrec.), 4 remain Data Deficient (*E. chontalensis*, *E. marnixiana*, *E. tapirophila*, and *E. trianae*), and 77 have been categorized in one of the six IUCN risk categories. Among the latter, 25 species fall within the "lower risk" categories—20 Least Concern (LC) and 5 Near Threatened (NT); and 52 species fall within "threatened" categories—14 Vulnerable (VU), 23 Endangered (EN), and 15 Critically Endangered (CR). Unfortunately, the current number of threatened species could indeed represent an underestimate, since 2 species categorized as Not Evaluated (NE) were considered Critically Endangered by their authors—*E. ramosa* (Mavárez and Becerra, 2019) and *E. restricta* (Alzate and Giraldo-Gómez, 2020). Furthermore, some species currently categorized in lower-risk categories—for example, *E. pisbana* S. Díaz & Rodríguez-Cabeza (LC), *E. praefrontina* Cuatrec. (LC), and *E. mutabilis* S. Díaz & Rodríguez-Cabeza (NT)—are known from a single páramo unit, and in some cases even from a single locality. These and other species likely need to be reclassified as Endangered according to the IUCN critera Extent of Occurrence (< 5000 km^2), Area of Occupancy (< 500 km^2), number of known locations (≤ 5), and continuing future decline projected in Extent of Occurrence (IUCN, 2019). In all, the number of threatened species in the Colombian *Espeletia* clade is probably ca. 60, of which ca. 47 are likely in the Endangered or Critically Endangered categories. This means that out of 90 *Espeletia* species in Colombia, nearly 66% are threatened and about 50% are in the two extreme categories. Whatever the final number and appropriate threat category for this genus in Colombia, it is clear that some urgent measures are required to guarantee their conservation.

Hybrid Taxa

Eight interspecific hybrids in the Colombian *Espeletia* clade have received binomial names in the past. In all cases, at least one parental species is geographically widespread and demographically very abundant—that is, *E. argentea*, *E. corymbosa*, *E. grandiflora,* and *E. petiolata*—which increases the chance for pollen transfer between different taxa by unspecific pollinators such as bees and bumblebees. This observation also casts some doubts on the taxonomic status of certain taxa that are geographically very restricted and known from a handful of samples (e.g., *E. miradorensis* and *E. tapirophila*), morphologically very close to another sympatric and abundant species (e.g., *E. killipii* Cuatrec. var. *chisacana* Cuatrec.), or morphologically variable (e.g., *E. rositae* Cuatrec. and *E. mutabilis* S. Díaz & Rodríguez-Cabeza).

Common Names

The common name *frailejón* (plural: *frailejones*) appears frequently in the herbarium samples examined. It is without doubt the most common name used for *Espeletia*, although it is also applied to some species of *Senecio*. As noted by Diazgranados (2012) and Cuatrecasas (2013), there are some common names that appear relatively more specific within *Espeletia*, but they are never or rarely used bi-univocally, and tend to be relatively local. For instance, *frailejón (f.) plateado* is used interchangeably for *Espeletia argentea* and *E. boyacensis*. Species with glabrous leaves such as *E. corymbosa* and *E. pleiochasia* are sometimes known as *f. verde* or *f. liso* (the latter also used for *E. argentea*). Several species with white indumentum—for example, *E. brachyaxiantha* S. Díaz*, E. incana* Cuatrec., and *E. pescana* (S. Díaz) S. Díaz—are sometimes given the name *f. blanco*. A notable exception to this tendency is *f. guacharaco*, a name frequently and exclusively used for *E. guacharaca* S. Díaz. Common names therefore seem rare or inconsistent in this plant group and will not be provided in this work. New common names will not be proposed either. As mentioned in Mavárez (2019), I do share the view expressed in Diazgranados (2012) that giving common names helps in "socializing the knowledge of these species and instilling a feeling of responsibility among local inhabitants to protect these resources," but I also believe that these names must be chosen by or in agreement with local communities so that they can be accepted and used.

TAXONOMY

Espeletia Mutis ex Bonpl., Plant. Aeq. 2: 10. 1808(1809). Type species: *Espeletia grandiflora* Bonpl., Plant. Aeq. 2: 11. 1808(1809). TYPE: COLOMBIA. Santa Fe de Bogotá i Quindio, *Herbier de l'Amérique équatoriale, donné par M. A. Bonpland s.n.* (Holotype: P [MNHN-P-P00320272]; Isotypes: P [MNHN-P-P00320273, MNHN-P-P00307378, MNHN-P-P00680447]).

Synonyms: *Carramboa* Cuatrec., Phytologia 35(1): 54. 1976. Type species: *Espeletia pittieri* Cuatrec., Ciencia (México) 6(7–9): 262. 1945. TYPE: VENEZUELA. Mérida: forest between El Molino and ridge above San Isidro Alto, 2430–2895 masl, 14 May 1944, *J. Steyermark 56532* (Holotype: VEN [not seen]; Isotypes: F, NY, US).

Coespeletia Cuatrec., Phytologia 35(1): 56. 1976. Type species: *Espeletia spicata* Sch. Bip. ex Wedd., Chlor. Andina 1: 65. 1855(1856). TYPE: VENEZUELA. Mérida: Sierra Nevada de Mérida, 14,000 pieds, August 1842, *J. Linden 400* (Holotype: P; Isotypes: F, FI, K, P).

Espeletiopsis Cuatrec., Phytologia 35(1): 54. 1976. Type species: *Espeletia jimenezquesadae* Cuatrec., Rev. Acad. Col. Ci. Exact. 3(11): 247. 1940. TYPE: COLOMBIA. Boyacá: Cordillera Oriental, Nevado del Cocuy, hacia la Cueva, en la Zanja, 3700 masl, 13 September 1938, *J. Cuatrecasas & H. García-Barriga 1635* (Holotype: COL; Isotype: US).

Libanothamnus Ernst, Vargasia 7: 186. 1870. Type species: *Espeletia neriifolia* (Bonpl. ex Humb.) Sch. Bip. ex Wedd., Chlor. Andina 1: 67. 1855(1856). TYPE: VENEZUELA. Caracas: Silla de Caracas, [3 January] 1800, *Herbier donné par M. Bonpland en 1833 No. 652* (Lectotype: P [MNHN-P-P04086343]; Isolectotype: P [MNHN-P-P04086342]).

Ruilopezia Cuatrec., Phytologia 35(1): 51. 1976. Type species: *Espeletia figueirasii* Cuatrec., Phytologia 20(8): 475. 1971. TYPE: VENEZUELA. Mérida: Sierra Nevada de Santo Domingo, Páramo de los Granates, Loma de Paja, las Escaleras, 3240 masl, 11 October 1969, *J. Cuatrecasas*, *L. Ruiz-Terán & M. López-Figueiras 28068* (Holotype: US; Isotypes: F, IVIC, MERF, U, US).

Paramiflos Cuatrec., Proc. Biol. Soc. Wash. 108(4): 748. 1995. Type species: *Espeletia glandulosa* Cuatrec., Rev. Acad. Col. Ci. Exact. 3(12): 434. 1940. TYPE: COLOMBIA. Boyacá: Cordillera Oriental, Páramo de Guantiva, Alto de Canutos, vertiente sur, 3200–3400 masl, *J. Cuatrecasas 10360* (Holotype: COL; Isotypes: BC, COL, F, G, K, NY, P, U, US).

Tamania Cuatrec., Phytologia 35(1): 53, 1976. Type species: *Espeletia chardonii* A.C. Sm., Bol. Soc. Ven. Ci. Nat. 7: 237. 1942. TYPE: VENEZUELA. Táchira: Páramo de Tamá, El Paramito, 2550 masl, 15 August 1939, *C. E. Chardon 78* (Holotype: US; Isotypes: NY, VEN [not seen]).

1. *Espeletia annemariana* Cuatrec. Phytologia 32(4): 315. 1975. TYPE: COLOMBIA. Boyacá: Carretera Vadohondo-Labranzagrande, Alto de Mogotes, subpáramo con gramíneas y muchas hierbas sobre suelos arenosos, 3300 masl, 2 April 1973, *A. M. Cleef 9296* (Holotype: US; Isotypes: COL, F, GB, K, MO, NY, P, S, U, US).

Distribution: COLOMBIA. Tota-Bijagual-Mamapacha (*A. M. Cleef 9556*, US; *A. M. Cleef 9466*, US), Sierra Nevada del Cocuy (*A. M. Cleef 9900*, US), Guantiva–La Rusia (*A. M. Cleef 9735*, US; *A. M. Cleef 7397*, US). The taxonomic status of populations in Guantiva–La Rusia needs to be reviewed.

Conservation status: Endangered.

1.1 *Espeletia annemariana* Cuatrec. var. ***annemariana***.

1.2. *Espeletia annemariana* Cuatrec. var. ***rupicola*** Cuatrec. Phytologia 32(4): 317. 1975. TYPE: COLOMBIA. Boyacá: Peña del Arnical, N. de Vadohondo, crece en grietas de roca, 3600 masl, 6 April 1973, *A. M. Cleef 9466* (Holotype: US; Isotypes: COL, L).

2. *Espeletia arbelaezii* Cuatrec. Revista Acad. Colomb. Ci. Exact. 3(11): 247. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Huinas, 3300 masl, 19 September 1938, *J. Cuatrecasas & H. García-Barriga 1964* (Holotype: COL; Isotypes: BC, COL, F, US).

Distribution: COLOMBIA. Guantiva–La Rusia (*A. M. Cleef 9837*, US), Iguaque-Merchán (*R. Jaramillo-Mejía 96*, COL), Tota-Bijagual-Mamapacha (*S. Díaz 62*, COL). The taxonomic status of populations in Iguaque-Merchán and Tota-Bijagual-Mamapacha needs to be reviewed.

Conservation status: Vulnerable. According to IUCN data, this species is known from about 10 localities with Extent of Occurrence (EOO) = 4725 km^2, although with a continuous decline in habitat extent and quality since 1960. However, the number of populations and their EOO would be significantly reduced if populations in Iguaque-Merchán and Tota-Bijagual-Mamapacha are not cospecific with *E. arbelaezii*. If that is the case, this species would very likely need to be reclassified in the Endangered category, as in García et al. (2005).

3. *Espeletia argentea* Bonpl., Plant. Aeq. 2: 14. 1808 (1809). TYPE: COLOMBIA. Cundinamarca: "Nous avons trouvé l'*Espeletia argentea* dans les environs de la petite ville de Zypaquira, distante de dix lieues au nord-nord-ouest de Santa-Fe. Elle croît à une élévation de 1300 mètres au-dessus du niveau de la mer" [We have found *Espeletia argentea* nearby the small town of Zipaquirá, ten leagues NNW of Bogotá. It grows at 1300 masl], 1801 [**1**], *Herbier de l'Amérique équatoriale, donné par M. A. Bonpland s.n.* (Holotype: P [MNHN-P-P00320277]; Isotypes: P [MNHN-P-P02441487, MNHN-P-P02441488], F [fragment, catalog number 972210]).

[**1**]: Humboldt and Bonpland visited Bogotá and its surroundings between 7 July and 8 September 1801. The type must have been collected or received from collectors during this time.

Nomen nudum: *Espeletia nivea* Moritz ex Wedd., Chlor. Andina 1: 65. 1855(1856). As synonym of *E. argentea*.

Distribution: COLOMBIA. Chingaza (*J. Cuatrecasas 28260*, US; *H. García-Barriga 11466*, US), Guerrero (*A. Fernández-Pérez & R. Jaramillo-Mejía 439*, US; *A. M. Cleef 4201*, US), Cruz Verde–Sumapaz (*S. Díaz 2388*, US; *J. Cuatrecasas 10476*, US; *A. M. Cleef 906*, US).

Conservation status: Least Concern.

3.1. *Espeleta argentea* Bonpl. f. ***argentea***.

3.2. ***Espeletia argentea*** Bonpl. f. ***phaneractis*** (S.F. Blake) Cuatrec., Phytologia 27(3): 179. 1973. TYPE: COLOMBIA. Cundinamarca: Dry páramo on Mt. Águila west of Z. [Zipaquirá], 3100–3200 masl, 20–24 October 1917, *F. W. Pennell 2522* (Holotype: US; Isotypes: F, GH, MO, NY).

Homotypic synonyms: *Espeletia argentea* Bonpl. subsp. *phaneractis* S.F. Blake, Contr. U.S. Natl. Herb. 22(8): 603. 1924.

Espeletia phaneractis (S.F. Blake) A.C. Sm., Brittonia 1(7): 525. 1935.

4. ***Espeletia ariana*** Rodríguez-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 30(116): 343. 2006. TYPE: COLOMBIA. Boyacá: Municipio de Socotá, Vereda Comezabao [**1**], sector Pantano Hondo, lado izquierdo arriba de la quebrada Pantano Hondo, 3600 masl, 5°55'34.1"N, 72°37'19"W, 19 October 2005, *B. V. Rodríguez-Cabeza, L. Velasco & E. Benítez 1454* (Holotype: COL; Isotype: UIS [not seen]).

[**1**]: Type locality given as "Comeza Hoyada" in Diazgranados (2012).

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza, L. Velasco & E. Benítez 1454*, COL).

Conservation status: Vulnerable. According to IUCN data, this species is known from a single locality with a population < 1000 adult individuals and Area of Occupancy = 8 km^2. Farming and ranching threaten its habitat. It would very likely need to be reclassified in the Endangered category.

5. ***Espeletia azucarina*** Cuatrec., Phytologia 47(1): 12. 1980. TYPE: COLOMBIA. Boyacá: Municipio Tutazá, Macizo alto N. de Belén, Cerro Pan de Azúcar y vecindades, páramo pedregoso y seco, vertiente E. del Cerro, 4000 masl, 7 May 1973, *A. M. Cleef 9835* (Holotype: US; Isotypes: COL, HUA [not seen], L, US).

Distribution: COLOMBIA. Guantiva–La Rusia (*A. M. Cleef 9835*, US).

Conservation status: Critically Endangered.

6. ***Espeletia barclayana*** Cuatrec., Phytologia 38(1): 10. 1977. TYPE: COLOMBIA. Cundinamarca: Represa de Neusa y alrededores, cerro al NW. del embalse, en las cercanías de la estación Telecom, páramo seco, 3650 masl, 26 May 1972, *A. M. Cleef & R. Jaramillo-Mejía 4174* (Holotype: US; Isotypes: COL, L, US). Fig. 2.

Distribution: COLOMBIA. Guerrero (*S. Díaz & A. M. Cleef 804*, US), Rabanal-Río Bogotá (*J. C. Arias-G. et al. 3688*, COL), Iguaque-Merchán (*G. Huertas 6763*, COL), Guantiva–La Rusia (*J. L. Fernández-Alonso et al. 11924*, MA).

Conservation status: Near Threatened.

7. Espeletia betancurii (Rodríguez-Cabeza, S. Díaz & Gal.-Tar.) Mavárez, *comb. nov*.

Basionym: *Espeletiopsis betancurii* Rodríguez-Cabeza, S. Díaz & Gal.-Tar., Revista Acad. Colomb. Ci. Exact. 30(116): 349. 2006. TYPE: COLOMBIA. Boyacá: Municipio Chita, Vereda Minas, Páramo de Los Venados, carretera hacia Sácama, km 86 desvío a Chita, 06°03'15.8"N, 72°26'20.0"W, 3300 masl, 23 October 2005, *B. V. Rodríguez-Cabeza & L. Velasco BVR-1515* (Holotype: COL).

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza & R. Galindo-Tarazona BVR-2189*, COL).

Conservation status: Critically Endangered.

8. ***Espeletia boyacensis*** Cuatrec., Phytologia 27(3): 176. 1973. TYPE: COLOMBIA. Boyacá: Vereda El Bosque, vertiente sur del Alto de Canutos, loma paramuna, 3350 masl, 13 September 1969, *J. Cuatrecasas & L. Rodríguez 27759* (Holotype: US; Isotypes: COL, U, US).

Heterotypic synonym: *Espeletia phaneractis* (S.F. Blake) A.C. Sm. subsp. *boyacensis* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 167. 1941. TYPE: COLOMBIA. Boyacá: Páramo de Guantiva, cerca de Las Gaitas, 3300 masl, 3 August 1940, *J. Cuatrecasas 10364-A* (Holotype: COL).

Distribution: COLOMBIA. Pisba (*H. Dueñas & J. Robles 81*, COL), Tota-Bijagual-Mamapacha (*G. Huertas & L. Camargo 6839*, US), Iguaque-Merchán (*S. Madriñán SM-2086*, COL), Guantiva–La Rusia (*H. Barclay & P. Juajibioy 7556*, US), Rabanal–Río Bogotá (*L. Camargo 7189*, COL).

Conservation status: Least Concern.

9. ***Espeletia brachyaxiantha*** S. Díaz, Mutisia 37: 5. 1972. TYPE: COLOMBIA. Boyacá: Páramos al NW. de Belén, Vereda San José de la Montaña, Alto de las Cruces y alrededores, 3800 masl, 6 March 1972, *A. M. Cleef 2326* (Holotype: COL; Isotypes: B, COL, F, MO, NY, U, US, WIS). Fig. 2.

Distribution: COLOMBIA. Guantiva–La Rusia (*J. Cuatrecasas & R. Jaramillo-Mejía 28723*, US).

Conservation status: Endangered.

10. ***Espeletia brassicoidea*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(15–16): 337. 1941. TYPE: COLOMBIA. Norte de Santander: Páramo de Fontibón, 2700 masl, 21 July 1940, *J. Cuatrecasas & H. García-Barriga 10096* (Holotype: COL; Isotypes: COL, F, US).

Nomen nudum: *Espeletia brassicoidea* Cuatrec. f. *pamplonensis* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(15–16): 338. 1941 [**1**].

[**1**]: Reference given as "Revista Acad. Colomb. Ci. Exact. 5(17): 338. 1942" in Diazgranados (2012).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*J. Cuatrecasas, R. E. Schultes & E. Smith 12306*, US; *J. Cuatrecasas & R. Jaramillo-Mejía 28754*, US; *J. Cuatrecasas & R. Jaramillo-Mejía 28755*, US). COLOMBIA-VENEZUELA. Tamá (*J. Cuatrecasas, R. E. Schultes & E. Smith 12653*, US; *J. Cuatrecasas, L. Ruíz-Terán & M. López-Figueiras 28354*, US).

Conservation status: Vulnerable.

10.1. ***Espeletia brassicoidea*** Cuatrec. subsp. ***brassicoidea***.

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*J. Cuatrecasas, R. E. Schultes & E. Smith 12306*, US).

10.2. ***Espeletia brassicoidea*** Cuatrec. subsp. ***angusta*** Cuatrec., Phytologia 47(1): 13. 1980. TYPE: COLOMBIA. Norte de Santander: Entre Pamplona y Berlín, lado izquierdo carretera, abajo, km 89, 3050 masl, 23 September 1969, *J. Cuatrecasas & L. Rodríguez 27916* (Holotype: US; Isotypes: COL, U, US).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*J. Cuatrecasas & R. Jaramillo-Mejía 28755*, US).

10.3. ***Espeletia brassicoidea*** Cuatrec. subsp. ***constricta*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 324. 2013. TYPE: COLOMBIA. Norte de Santander: Páramo de Tamá, alrededores de la Cueva, 3000–3200 masl, 28 October 1941, *J. Cuatrecasas, R. E. Schultes & E. Smith 12653-A* (Syntype: COL; Isosyntypes: GH, U, US), and *J. Cuatrecasas, R. E. Schultes & E. Smith 12653-B* (Syntype: COL; Isosyntypes: COL, F, U, US).

Homotypic synonym: *Espeletia brassicoidea* Cuatrec. f. *constricta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942.

Heterotypic synonym: *Espeletia brassicoidea* Cuatrec. f. *minorifolia* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942. TYPE: COLOMBIA. Norte de Santander: Páramo de Tamá, alrededores de la Cueva, 3000–3200 m, 28 October 1941, *J. Cuatrecasas, R. E. Schultes & E. Smith 12653* (Syntype: COL; Isosyntypes: F, US) and *J. Cuatrecasas, R. E. Schultes & E. Smith 12653-C* (Syntype: COL; Isosyntypes: GH, U, US).

Distribution: COLOMBIA-VENEZUELA. Tamá (*J. Cuatrecasas, L. Ruíz-Terán & M. López-Figueiras 28354*, US).

11. ***Espeletia cabrerensis*** Cuatrec., Phytologia 32(4): 318. 1975. TYPE: COLOMBIA. Cundinamarca: Cabrera, subida al Alto de Sumapaz, planada paramuna de Hoyerías, 3200 masl, 23 February 1970, *L. Uribe-Uribe 6400* (Holotype: US; Isotype: COL).

Distribution: COLOMBIA. Cruz Verde–Sumapaz (*L. Uribe-Uribe 6400*, US).

Conservation status: Vulnerable. According to IUCN data, this species is known from a single locality with Area of Occupancy = 4 km^2. Furthermore, its habitat is threatened by farming and ranching. Under these conditions, this species would very likely need to be reclassified in the Endangered category.

12. ***Espeletia cachaluensis*** Rodríguez-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 33(125): 459. 2008. TYPE: COLOMBIA. Santander: Santuario de Fauna y Flora Guanentá Alto Río Fonce, Municipio de Encino, Vereda Avendaños, sector Los Cuadros, 3744 masl, 05°49'N, 73°06'W, [**1**], 12 October 2007, *B. V. Rodríguez-Cabeza, H. Palacios, R. Rivero, J. Velasco BVR-1897* (Holotype: COL; Isotypes: COL, UIS [not seen]).

[**1**]: Geographic coordinates provided with the holotypus do not match type locality.

Distribution: COLOMBIA. Guantiva–La Rusia (*B. V. Rodríguez-Cabeza, H. Palacios, S. Estepa BVR-1976*, COL).

Conservation status: Critically Endangered.

13. ***Espeletia caldasii*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 431. 1940. TYPE: COLOMBIA. Norte de Santander: Páramo de Santurbán entre Cuesta Boba y el extremo oeste, 3400 masl, 27 July 1940, *J. Cuatrecasas & H. Garcia-Barriga 10317* (Holotype: COL; Isotypes: BC, COL, F, GH, US).

Homotypic synonym: *Espeletiopsis caldasii* (Cuatrec.) Cuatrec., Phytologia 35(1): 55 (1976).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*A. M. Cleef 10189*, US).

Conservation status: Critically Endangered.

14. ***Espeletia canescens*** A.C. Sm., Brittonia 1(7): 516. 1935. TYPE: COLOMBIA. Norte de Santander: Páramo del Romeral, 3800–4200 masl, 30 January 1927, *E. P. Killip & A. C. Smith 18624* (Holotype: NY; Isotypes: GH, PH [not seen], US).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*E. P. Killip & A.C. Smith 18624*, US).

Conservation status: Endangered.

15. ***Espeletia cayetana*** (Cuatrec.) Cuatrec., Phytologia 52(3): 159. 1982. TYPE: COLOMBIA. Cundinamarca: Páramo entre Cogua y San Cayetano, cercanías de la Laguna Seca, vertiente E del filo de El Santuario, valle abrigado unos 2 km S de la Laguna Seca, 3650 masl, 17 November 1972, *A. M. Cleef 6508* (Holotype: US; Isotypes: COL, K, L, NY, S, U, US).

Homotypic synonym: *Espeletia grandiflora* Bonpl. var. *cayetana* Cuatrec., Phytologia 32(4): 323. 1975.

Distribution: COLOMBIA. Guerrero (*S. Díaz & A. M. Cleef 805*, US), Tota-Bijagual-Mamapacha (*P. A. Gil-Leguizamón 2603*, UPTC).

Conservation status: Endangered.

16. ***Espeletia chocontana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 164. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Chocontá, 2760–2830 m, *J. Cuatrecasas 9658* (Holotype: COL; Isotypes: F, US)

Distribution: COLOMBIA. Guerrero (*A. M. Cleef 4202*, US), Rabanal–Río Bogotá (*J. Cuatrecasas 9646*, US).

Conservation status: Endangered.

17. ***Espeletia chontalensis*** Rodríguez-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 33(125): 462. 2008. TYPE: COLOMBIA. Santander: Santuario de Fauna y Flora Guanentá Alto Río Fonce, Municipio de Encino, Vereda Río Negro, camino sector Chontales-Páramo de La Rusia. 28 June 2007, *B. V. Rodríguez-Cabeza & H. Palacios BVR-1874* (Holotype: COL [not seen]; Isotypes: COL, UIS [not seen]).

Distribution: COLOMBIA. Guantiva–La Rusia (*B. V. Rodríguez-Cabeza, H. Palacios, S. Estepa BVR-1976*, COL).

Known only from the type specimen. The validity of this species needs to be reviewed.

Conservation status: Data Deficient.

18. ***Espeletia cleefii*** Cuatrec., Phytologia 32(4): 312. 1975. TYPE: COLOMBIA. Boyacá: Sierra Nevada del Cocuy, Boquerón de Cusirí, vertiente W, superpáramo (cerca límite con páramo prop. dicho), 4300 masl, 6 October 1972, *A. M. Cleef & P. A. Florschutz 5922* (Holotype: US; Isotypes: COL, K, MY, MO, NY, S, U, US).

Distribution: COLOMBIA. Sierra Nevada del Cocuy (*A. M. Cleef 9100*, US).

Conservation status: Endangered.

19. ***Espeletia colombiana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(11): 249. 1940. TYPE: COLOMBIA. Boyacá: Nevado del Cocuy, las Lagunillas, Pozo Azul, 4110 masl, 11 September 1938, *J. Cuatrecasas & H. García-Barriga 1432* (Holotype: COL; Isotypes: BC, F, US).

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

Distribution: COLOMBIA. Sierra Nevada del Cocuy (*A. M. Cleef & P. A. Florschutz 5924*, US), Pisba (*J. Cuatrecasas & R. Jaramillo-Mejía 28739*, US).

Conservation status: Least Concern.

20. ***Espeletia congestiflora*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 434. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Guantiva, cerca de Las Gaitas, 3300 masl, 3 August 1940, *J. Cuatrecasas 10366* (Holotype: COL; Isotypes: BC, COL, F, US). Fig. 2.

Distribution: COLOMBIA. Guantiva–La Rusia (*A. M. Cleef 7521*, US), Tota-Bijagual-Mamapacha (*A. M. Cleef 9556*, US), Pisba (*A. M. Cleef 4758*, US).

Conservation status: Least Concern.

21. ***Espeletia conglomerata*** A.C. Sm., Brittonia 1(7): 515 (1935). TYPE: COLOMBIA. Norte de Santander: Páramo del Romeral, 3800–4200 masl, 30 January 1927, *E. P. Killip & A. C. Smith 18635* (Holotype: NY; Isotypes: F, GH, K, PH [not seen], S, US). Fig. 2.

Heterotypic synonym: *Espeletia brassicoidea* Cuatrec. f. *contracta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942. TYPE: COLOMBIA. Norte de Santander: Páramo de Tamá, alrededores de la Cueva, 3000–3200 m, 28 October 1941, *J. Cuatrecasas, R. E. Schultes & E. Smith 12653-D* (Holotype: COL; Isotypes: F, GH)

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*J. Cuatrecasas & R Jaramillo-Mejía 28749*, US), Almorzadero (*J. Cuatrecasas, R. E. Schultes & E. Smith 12052*, US). COLOMBIA-VENEZUELA. Tamá (*L. Ruíz-Terán & M. López-Figueiras 8886*, US).

Conservation status: Vulnerable.

22. ***Espeletia corymbosa*** Bonpl., Plant. Aeq. 2: 16 1808(1809). TYPE: COLOMBIA. Cundinamarca [**1**]: "*Habitat in Peruviæ frigidis, juxta urbem Almaguer*" [lives in Peruvian cold areas, near the city of Almaguer]. Also, "*Nous avons trouvé l'Espeletia corymbosa dans la Cordillère des Andes, près de la ville d'Almaguer, à 1163 toises (2268 m) d'élévation au-dessus du niveau de l'Océan*" [We have found *Espeletia corymbosa* in the Andes, near the town of Almaguer, at 1163 toises (2268 m) above sea level], 1801 [**2**], *Herbier de l'Amérique équatoriale, donné par M. A. Bonpland s.n.* (Holotype: P [MNHN-P-P00320274, MNHN-P-P00320275, MNHN-P-P00320276]; Isotypes: P [MNHN-P-P00660025], F [fragment]).

[**1**]: *Espeletia corymbosa* grows only in páramos around Bogotá, Cundinamarca department, Colombia. Both country (Peru) and locality (Almaguer) were therefore incorrectly given in the original description. The country was later changed to "*Crescit in frigidis Andium Novo Granatensium, juxta urbem Almaguer*" [Grows in cold areas in the Andes of New Granada, near the town of Almaguer] in Humboldt et al. (1820), while the correct distribution was given for the first time in Smith and Koch (1935).

[**2**]: Humboldt and Bonpland visited Bogotá and its surroundings between 7 July and 8 September 1801. The type must have been collected or received from collectors during this time.

Homotypic synonym. *Espeletiopsis corymbosa* (Bonpl.) Cuatrec., Phytologia 35(1): 55. 1976.

Heterotypic synonyms. *Espeletia corymbosa* Bonpl. var. *foliosa* Duse, Nuovo Giorn. Bot. Ital. n.s. 12: 284. 1905. TYPE: COLOMBIA. Bogota, locis frigidis, March 1844, *Goudot s.n.* (Lectotype: P?) [**3**].

[**3**]: A specimen in P ("Bogota, locis frigidis, marzo 1844, *Goudot s.n.*," MNHN-P-P04086355) corresponds exactly with the protologue of *Espeletia corymbosa* Bonpl. var. *foliosa* Duse and might be designated as lectotypus.

Nomen nudum: *Espeletia rigida* Bonpl., Plant. Aeq. 2: Planche 72. 1808 (1809).

Espeletia platylepis Sch. Bip. ex Wedd., Chlor. Andina 1: 64. 1855(1856). TYPE: COLOMBIA. Cundinamarca: "Nouvelle-Grenade, Cordillères de Bogotá, hauteur 2250 mètres," *Goudot s.n.* (Syntype: P), *J. J. Linden 1291* (Syntype: P) [**4**]. As synonym of *Espeletia corymbosa* Bonpl.

[**4**]: Syntypes of *Espeletia platylepis* given as a single collection "*Goudot & J. J. Linden 1291*" in Diazgranados (2012).

Distribution: COLOMBIA. Chingaza (*W. S. Hodge 6492*, US; *J. Cuatrecasas 5643*, US), Guerrero (*O. Haught 5971*, US; *J. Cuatrecasas 9564*, US), Rabanal–Río Bogotá (*D. Stancik 449*, COL; *H. García-Barriga, R. E. Schultes & R. Jaramillo-Mejía 13618*, US), Cruz Verde–Sumapaz (*D. D. Soejarto 403*, US).

Conservation status: Least Concern.

22.1. ***Espeletia corymbosa*** Bonpl. subsp. ***corymbosa***.

Distribution: COLOMBIA. According to Cuatrecasas (1941), this subspecies is abundant in Chingaza and Cruz Verde–Sumapaz.

22.2. ***Espeletia corymbosa*** Bonpl. subsp. ***zipaquirana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 168. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Zipaquirá, entre Zipaquirá y Pacho, 3100–3200 masl. 16 June 1940 [**1**], *J. Cuatrecasas 9564* (Holotype: COL? [**2**]; Isotypes: BC, COL, F, US).

[**1**]: Collection date given as "16 January 1940" in Diazgranados (2012) and Cuatrecasas (1941).

[**2**]: *J. Cuatrecasas 9564* is labelled as isotypus in all herbaria consulted. If no holotypus reappears, an exsiccata in COL must be relabelled as holotypus for *E. corymbosa* Bonpl. subsp. *zipaquirana* Cuatrec.

Distribution: COLOMBIA. Chingaza (*J. Cuatrecasas 5643*, US), Guerrero (*J. Cuatrecasas 9564*, US), Rabanal–Río Bogotá (*H. García-Barriga, R. E. Schultes & R. Jaramillo-Mejía 13618*, US).

23. ***Espeletia curialensis*** Cuatrec., Phytologia 20(8): 473. 1971. TYPE: COLOMBIA. Boyacá: Páramo entre Chita y Sacama, vertiente oriental de la cordillera, quebrada del Curial (la Porquera), 3550 masl, 15 September 1969, *J. Cuatrecasas & L. Rodríguez 27790* (Holotype: US; Isotypes: F, U). Fig. 2.

Distribution: COLOMBIA. Sierra Nevada del Cocuy (*A. M. Cleef 9171*, US; *B. V. Rodríguez-Cabeza, J. M. Valderrama & O. E. López 1537*, COL), Pisba (*J. Cuatrecasas & R. Jaramillo Mejía 28740*, US).

Conservation status: Least Concern. According to IUCN data, this species has Extent of Occurrence (EOO) = 294 km^2. No significant threats are signaled, although the species is usually found in relatively dry subpáramo habitats that are prone to fires, particularly in Pisba. Given the relatively small EOO of this species and the environmental threats to the habitat in its southern range, it would very likely need to be reclassified at least in the Vulnerable category.

23.1. ***Espeletia curialensis*** Cuatrec. var. ***curialensis***.

23.2. ***Espeletia curialensis*** Cuatrec. var. ***exigua*** Rodríguez-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 30(116): 347. 2006. TYPE: COLOMBIA. Casanare: Parque Nacional Natural El Cocuy, Municipio de La Salina, sector El Ahogadero, 3200 masl, 03°18'49.583"N, 72°23'36.726"W, [**1**], 12 December 2005, *B. V. Rodríguez-Cabeza, J. M. Valderrama & O. E. López 1537* (Holotype COL; Isotypes: COL, UIS [not seen]).

[**1**]: Geographic coordinates provided with the holotypus do not match type locality.

24. Espeletia diazii (Diazgr. & L.R. Sánchez) Mavárez, *comb. nov*.

Basionym: *Espeletiopsis diazii* Diazgr. & L.R. Sánchez, PhytoKeys 32: 39. 2013. TYPE: COLOMBIA. Norte de Santander: Municipio de Cáchira, Páramo de Cáchira o de Guerrero, vía Alto Chiquito (desde Villa Caro) a Cáchira, alto del páramo, a los lados de la vía antes de comenzar el descenso a Cáchira, 3394 masl, 73.00173°W, 7.7655°N, *M. Diazgranados & L. R. Sánchez 3898* (Holotype: COL [not seen]; Isotypes: COL [not seen], HECASA [not seen]).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*M. Diazgranados & L.R. Sánchez 3898*, COL).

Conservation status: Critically Endangered.

25. ***Espeletia discoidea*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 437. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Guantiva, Alto de Canutos, vertiente sur, 3200–3400 masl, 3 August 1940, *J. Cuatrecasas 10358* (Holotype: COL; Isotypes: BC, COL, F, P, US)

Distribution: COLOMBIA. Guantiva–La Rusia (*S. Díaz 51*, US; *H. G. Barclay & P. Juajibioy 7680*, US; *A. M. Cleef 9782*, US).

Conservation status: Endangered.

25.1. ***Espeletia discoidea*** Cuatrec. var. ***discoidea***.

25.2. ***Espeletia discoidea*** Cuatrec. var. ***brevis*** Cuatrec., Mem. New York Bot. Gard. 107: 293. 2013 [**1**]. TYPE: COLOMBIA. Boyacá: Páramos al NW de Belén, cabeceras Q[uebrada] Laguna Grande, vertiente NW (ca. 30° inclinación) del filo divisorio, 3830 masl, 6 May 1973, *A. M. Cleef 9774* (Holotype: US; Isotypes: COL, U).

[**1**]: Reference given as "Revista Acad. Colomb. Ci. Exact. 3(12): 437. 1940" in Diazgranados (2012).

26. ***Espeletia dugandii*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 163. 1941. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, extremo sur, Peralonso, 3200 masl, 19 July 1940, *J. Cuatrecasas & H. García-Barriga 9889* (Holotype: COL; Isotypes: F, US).

Distribution: COLOMBIA. Almorzadero (*A. H. G. Alston 7380*, US).

Conservation status: Critically Endangered.

27. ***Espeletia episcopalis*** Rodríguez-Cabeza & S. Díaz [**1**], Revista Acad. Colomb. Ci. Exact. 30(116): 341. 2006. TYPE: COLOMBIA. Boyacá: Municipio Socotá, Vereda Comeza Hoyada, sector río Arzobispo, parte alta, Los Corazones, alrededores de las lagunas Larga y Peña Negra, 3700 masl, 05°55'47"N, 72°35'51"W, 21 October 2005, *B. V. Rodríguez-Cabeza, L. Velasco & E. Benitez BVR-1498* (Holotype: COL, Isotype: UIS [not seen]).

[**1**]: Author given as "S. Díaz & Rodríguez-Cabeza" in Diazgranados (2012).

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza & L. Velasco BVR-1514,* COL).

Conservation status: Vulnerable. According to IUCN data, this species is known from a single locality with a population < 1000 adult individuals and Area of Occupancy (AOO) = 16 km^2. Its habitat is supposed to be a relatively well-conserved area without significant threats within PNN Pisba. However, the low number of populations and their small AOO suggest that this species would very likely need to be reclassified in the Endangered category.

28. ***Espeletia estanislana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 429. 1940. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, 3700–3800 masl, 28 May 1940, *Hno. Antonio Miguel s.n.* (Holotype: COL [**1**]).

[**1**]: The holotypus is deposited in COL, not US as stated in Diazgranados (2012) and Cuatrecasas (2013).

Distribution: COLOMBIA. Almorzadero (*A. M. Cleef 10187,* US).

Conservation status: Endangered.

29. ***Espeletia formosa*** S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 30(116): 336. 2006. TYPE: COLOMBIA. Boyacá: PNN Pisba, Municipio Socotá, Vereda Chipa Viejo, ruta libertadora, sector El Santuario, 3414 masl, 06˚08'49.963"N, 72˚45'33.672"W, [**1**], 16 June 2005, *B. V. Rodríguez-Cabeza & L. Velasco BVR-1407* (Holotype: COL; Isotype: COL, HUA, UIS [not seen]).

[**1**]: Geographic coordinates provided with the holotypus do not match type locality.

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza & L. Velasco BVR-1407,* COL).

Conservation status: Endangered.

30. ***Espeletia frontinoensis*** Cuatrec., Phytologia 38(1): 15. 1977. TYPE: COLOMBIA. Antioquia: Páramo Frontino, near Llano Grande, 3450 masl, 25 October 1976, *J. D. Boeke & J. B. McElroy 234* (Holotype: US; Isotype: GH, MEDEL [not seen], NY, U).

Distribution: COLOMBIA. Paramillo (*H. Cuadros 5004,* MO), Frontino-Urrao (*J. M. MacDougal, F. J. Roldán & J. Betancur 4317*, US), Citará (*W. D. Rodríguez et al. 6517*, COL), Tatamá (*J. H. Torres et al. 1778*, COL). Apparently found as well in Belmira (e.g., *R. Callejas 10069*, US) and El Duende (e.g., *W. Vargas 4854*, COL), but these records need to be confirmed.

Conservation status: Least Concern.

31. ***Espeletia funckii*** Sch. Bip. ex Wedd., Chlor. Andina 1: 64. 1855(1856). TYPE: COLOMBIA. Norte de Santander: Province de Pamplona, paramos de La Baja, 10.500 pieds, January 1847, *N. Funck & L. J. Schlim 1290* [**1**] (Holotype: P [**2**]; Isotypes: BR, F, G, GH, KW [not seen], P, US [photograph], W).

[**1**]: Collectors given as "*V. A. Funck & L. J. Schlim*" in Diazgranados (2012).

[**2**]: The holotypus in P needs status label.

Homotypic synonym. *Espeletiopsis funckii* (Sch. Bip. ex Wedd.) Cuatrec., Phytologia 35(1): 55. 1976.

Heterotypic synonym [**3**]: *Espeletia smithiana* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(15–16): 339. 1941. TYPE. COLOMBIA. Santander: Páramo de Santurbán, entre Cuesta Boba y el extremo oeste, 3400 masl, 27 July 1940, *J. Cuatrecasas & H. García-Barriga 10315* (Holotype: COL; Isotypes: F, P, US).

[**3**]: Synonym status given in Diazgranados (2012).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*E. P. Killip & A. C. Smith 18425*, US).

Conservation status: Endangered.

32. ***Espeletia garciae*** Cuatrec., Phytologia 23(4): 358. 1972. TYPE: COLOMBIA. Boyacá: Villa de Leyva, vereda de capilla, encima del km 21, en el monte, 2640 masl, 2 January 1940, *L. Uribe-Uribe 6491* (Holotype: US; Isotypes: COL, MA, MO, NY, US). Fig. 2.

Homotypic synonym. *Espeletiopsis garciae* (Cuatrec.) Cuatrec., Phytologia 35(1): 55. 1976.

Distribution: COLOMBIA. Iguaque-Merchán (*J. Cuatrecasas, H. García-Barriga, & R. Jaramillo-Mejía 28660*, US).

Conservation status: Vulnerable. According to IUCN data, this species is known from at least 10 localities with Extent of Occurrence (EOO) = 342 km^2, including a large and abundant population supposedly found in Cundinamarca, Guerrero. However, no verifiable herbarium records of this species have been found for that páramo. *Espeletia garciae* is in fact known only from some upper Andean forests and subpáramos in Iguaque-Merchán, some of which are threatened by agriculture and frequent fires. This species would very likely need to be reclassified in the Endangered category, as in García et al. (2005).

33. ***Espeletia glandulosa*** Cuatrec., Revista. Acad. Colomb. Ci. Exact. 3(12): 434. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Guantiva, Alto de Canutos, vertiente sur, 3200–3400 masl, 3 August 1940, *J. Cuatrecasas 10360* (Holotype: COL; Isotypes: BC, COL, F, G, K, NY, P, U, US).

Homotypic synonyms. *Paramiflos glandulosus* (Cuatrec.) Cuatrec., Proc. Biol. Soc. Wash. 108(4): 749. 1995. *Espeletiopsis glandulosa* (Cuatrec.) Cuatrec., Phytologia 35(1): 55. 1976.

Heterotypic synonym: *Espeletia glandulosa* Cuatrec. var. *scaberrima* Cuatrec., Brittonia 8(3): 185. 1956. TYPE: COLOMBIA. Norte de Santander: Andes de Pamplona, 2800 masl, June 1851, *J. Triana 1327* (Holotype: P; Isotypes: COL [= *J. Triana 2476*], P).

Distribution: COLOMBIA. Iguaque-Merchán (*J. Cuatrecasas & R. Jaramillo-Mejía 28760*, US), Guantiva–La Rusia (*H. G. Barclay & P. Juajibioy 7196*, US).

Conservation status: Vulnerable.

34. ***Espeletia grandiflora*** Bonpl., Plant. Aeq. 2: 11. 1808(1809). TYPE: COLOMBIA. Cundinamarca: Santa Fe de Bogotá i Quindio, *Herbier de l'Amérique équatoriale, donné par M. A. Bonpland s.n.* (Holotype: P [MNHN-P-P00320272]; Isotypes: P [MNHN-P-P00320273, MNHN-P-P00307378, MNHN-P-P00680447]).

Heterotypic synonyms: *Espeletia grandiflora* Bonpl. f. *longiligulata* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 169. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Cruz Verde, 3400–3500 masl, 15 September 1940, *J. Cuatrecasas 10467* (Holotype: COL; Isotypes: CM, F, US).

Espeletia grandiflora Bonpl. f. *multiflora* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 169. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Zipaquirá, entre Zipaquirá y Pacho, 3100–3200 masl, 16 June 1940, *J. Cuatrecasas 9527* (Holotype: COL; Isotypes: F, US).

Espeletia grandiflora Bonpl. f. *reducta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 169. 1941. TYPE. COLOMBIA: Cundinamarca: Páramo de Zipaquirá, 3100–3200 masl, 16 June 1940, *J. Cuatrecasas 9527-A* (Holotype: COL; Isotypes: F, US).

Distribution: COLOMBIA. Guerrero (*R. E. Schultes, R. T. Martin & T. C. Plowman 43*, US), Chingaza (*H. G. Barclay, P. Juajibioy & J. Gama 3259*, US; *H. García-Barriga 8103*, US; *G. Huertas & L. Camargo 5957*, US), Cruz Verde–Sumapaz (*H. García-Barriga 10440*, US; *S. Díaz 2360*, US; *A. M. Cleef 1115*, US; *A. M. Cleef 8054*, US), Guantiva–La Rusia (*B. V. Rodríguez Cabeza, H. Palacios & S. Estepa BVR-1977*, COL; *R. Jaramillo-Mejía, J. Hernandez-Camacho & Th. Van der Hammen 942*, US).

Conservation status: Least Concern.

34.1. ***Espeletia grandiflora*** Bonpl. subsp. ***grandiflora***.

Distribution: COLOMBIA. Chingaza (*H. G. Barclay, P. Juajibioy & J. Gama 3259*, US), Cruz Verde–Sumapaz (*H. García-Barriga 10440*, US), Guerrero (*R. E. Schultes, R. Martin & T. C. Plowman 43*, US).

34.1.1. ***Espeletia grandiflora*** Bonpl. subsp. ***grandiflora*** var. ***grandiflora***.

34.1.2. ***Espeletia grandiflora*** Bonpl. subsp. ***grandiflora*** var. ***attenuata*** Cuatrec., Phytologia 32(4): 325. 1975. TYPE: COLOMBIA. Cundinamarca: Macizo de Bogotá, Páramo de Chisacá, around the Laguna de Chisacá, 3650–3700 masl, 29 December 1959, *J. Cuatrecasas & R. Jaramillo-Mejía 25748* (Holotype: US; Isotypes: BC, COL, F).

34.2. ***Espeletia grandiflora*** Bonpl. subsp. ***boyacana*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 194 (2013). TYPE: COLOMBIA. Boyacá: Páramo de La Rusia, NW-N de Duitama, Serranía Negra, vertiente sur, ca. 3900 masl, 10 December 1972, *A. M. Cleef 6955* (Holotype: US; Isotypes: COL, K, MO, S, U, VEN [not seen]).

Homotypic synonym: *Espeletia grandiflora* Bonpl. var. *boyacana* Cuatrec., Phytologia 32(4): 322. 1975.

Distribution: COLOMBIA. Guantiva–La Rusia (*R. Jaramillo-Mejía, J. Hernandez-Camacho & Th. Van der Hammen 942*, US).

34.3. ***Espeletia grandiflora*** Bonpl. subsp. ***subnivalis*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 193. 2013. TYPE: COLOMBIA. Meta: Páramo de Sumapaz, Cerro Nevado del Sumapaz, vertiente SW hacia el Alto del Buque, 3650 masl, 29 January 1972, *A. M. Cleef 1372* (Holotype: US; Isotypes: COL, K, U, VEN [not seen]).

Homotypic synonym: *Espeletia grandiflora* Bonpl. var. *subnivalis* Cuatrec., Phytologia 32(4): 324. 1975.

Distribution: COLOMBIA. Cruz Verde–Sumapaz (*A. M. Cleef 8054*, US).

35. ***Espeletia guacharaca*** S. Díaz, Caldasia 11(53): 19. 1975. TYPE: COLOMBIA. Boyacá: Páramo de La Rusia, cerca a la cima, carretera Duitama-Charalá, 3500 masl, 13 May 1968, *S. Díaz 42* (Holotype: COL; Isotype: US). Fig. 2.

Homotypic synonyms: *Espeletiopsis guacharaca* (S. Díaz) Cuatrec., Phytologia 35(1): 55. 1976.

Espeletiopsis jimenezquesadae var. *guacharaca* (S. Díaz) Cuatrec., Anales Jard. Bot. Madrid 54(1): 374. 1996.

Distribution: COLOMBIA. Guantiva–La Rusia (*L. Uribe-Uribe 5213*, US), Iguaque-Merchán (*M. Melampy 1325*, US), Tota-Bijagual-Mamapacha (*J. Cuatrecasas, R. Jaramillo-Mejía & A. Kleef 28699*, US), Pisba (*D. Stancik & S. Medina 2441*, COL).

Conservation status: Near Threatened.

36. ***Espeletia hartwegiana*** Sch. Bip. ex Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 26: 17. 1933. TYPE: COLOMBIA. Cauca: Páramo de Guanacas, Andes de Popayán, 1843, *C. T. Hartweg 1137* (Lectotype: G; Isolectotypes: BM, E, FI, G, K, LD, P, W).

Homotypic synonym: *Espeletia grandiflora* Bonpl. var. *hartwegiana* (Cuatrec.) Benoist, Bull. Soc. Bot. France 92: 139. 1945.

Nomen nudum: *Espeletia hartwegiana* Sch. Bip. ex Wedd., Chlor. Andina 1: 62. 1855(1856). As a synonym of *Espeletia grandiflora* Bonpl.

Distribution: COLOMBIA. Los Nevados (*J. Cuatrecasas 23129*, US), Chili-Barragán (*J. L. Luteyn, J. Fuertes & O. Rangel 12946*, US), Las Hermosas (*W. Devia & F. Prado 1881*, US; *J. Cuatrecasas & H. Cuadros 28893*, US), Nevado del Huila-Moras (*J. Cuatrecasas 28783*, US; *J. Cuatrecasas 27440*, US), Guanacas-Puracé-Coconucos (*J. Cuatrecasas & L. Willard 26333*, US; *H. Pittier 1116*, US), Sotará (*J. Cuatrecasas & F. C. Lehmann 27387*, US; *J.M. Idrobo 4025*, US).

Conservation status: Least Concern.

36.1. ***Espeletia hartwegiana*** Sch. Bip. ex Cuatrec. subsp. ***hartwegiana***.

Distribution: COLOMBIA. Las Hermosas (*W. Devia & F. Prado 1881*, US), Nevado del Huila-Moras (*J. Cuatrecasas 27440*, US), Guanacas-Puracé-Coconucos (*J. Cuatrecasas & L. Willard 26333*, US), Sotará (*J. Cuatrecasas & F. C. Lehmann 27387*, US).

36.1.1. ***Espeletia hartwegiana*** Sch. Bip. ex Cuatrec. subsp. ***hartwegiana*** var. ***hartwegiana***.

36.1.2. ***Espeletia hartwegiana*** Sch. Bip. ex Cuatrec. subsp. ***hartwegiana*** var. ***morarum*** Cuatrec., Phytologia 45(1): 25. 1980. TYPE. COLOMBIA: Cauca: Cordillera Central, vertiente occidental, Páramo de Moras, 3600 masl, 19 March 1973, *J. Cuatrecasas & C. Lehmann 28638* (Holotype: US; Isotypes: COL, U, US).

36.1.3. ***Espeletia hartwegiana*** Sch. Bip. ex Cuatrec. subsp. ***hartwegiana*** var. ***vegasana*** Cuatrec., Phytologia 45(1): 24. 1980. TYPE. COLOMBIA. Valle del Cauca: Cordillera Central, vertiente occidental, cabeceras de los ríos Tuluá y Bugalagrande: Páramo de las Vegas, 3600–3800 masl, 22 March 1946, *J. Cuatrecasas 20285* (Holotype: US; Isotypes: COL, F).

36.2. ***Espeletia hartwegiana*** Sch. Bip. ex Cuatrec. subsp. ***barragensis*** Cuatrec., Phytologia 45(1): 23. 1980. TYPE. COLOMBIA. Valle del Cauca: Cordillera Central, vertiente occidental, hoya del río Bugalagrande, Barragán: Páramo de Bavaya, 3600–3680 masl, 16–17 March 1946, *J. Cuatrecasas 20076* (Holotype: COL; Isotypes: BC, F, US).

36.3. ***Espeletia hartwegiana*** Sch. Bip. ex Cuatrec. subsp. ***centroandina*** Cuatrec., Phytologia 45(1): 21. 1980. TYPE. COLOMBIA. Caldas: Cordillera Central, vertiente occidental, vertiente sudoeste del [Nevado] del Ruiz, El Aprisco, páramos, 3600 masl, 5 May 1940, *J. Cuatrecasas 9312* (Holotype: COL; Isotypes: COL, US).

Nomen nudum: *Espeletia centroandina* Cuatrec., Trab. Mus. Nac. Ci. Nat., Ser. Bot. 26: 17. 1933. As synonym of *Espeletia hartwegiana* Sch. Bip. ex Cuatrec.

Distribution: COLOMBIA. Los Nevados (*J. Cuatrecasas 23129*, US), Chili-Barragán (*J. L. Luteyn, J. Fuertes & O. Rangel 12946*, US).

37. ***Espeletia idroboi*** Cuatrec., Phytologia 38(1): 12. 1977. TYPE: COLOMBIA. Cauca: Macizo Colombiano, Valle de las Papas, alrededores de Valencia, 2910 masl, 11 September - 1 October 1958, *J. M. Idrobo, P. Pinto & H. Bischler 3212* [**1**] (Holotype: COL; Isotypes: COL, P).

[**1**]: Type collection number given as "*Idrobo, Pinto & Bischler 3372*" in Diazgranados (2012).

Distribution: COLOMBIA. Nevado del Huila-Moras (*H. G. Barclay & P. Juajibioy 6083*, US).

Conservation status: Endangered.

38. ***Espeletia incana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 435. 1940. TYPE: COLOMBIA. Santander: Páramo de La Rusia, vertiente noroeste, 3300–3500 masl, 4 August 1940, *J. Cuatrecasas 10430* (Holotype: COL; Isotypes: BC, COL, F, US). Fig. 2.

Distribution: COLOMBIA. Guantiva–La Rusia (*J. Cuatrecasas & R. Jaramillo-Mejía 28728*, US; *J. H. Langenheim 3511*, US). Records of this species from Yariguíes and páramo de Siscunsí-Ocetá (Tota-Bijagual-Mamapacha complex) need to be verified. The latter probably represent confusions with *Espeletia pescana* (S. Díaz) S. Díaz.

Conservation status: Vulnerable. According to IUCN data, this species has Extent of Occurrence (EOO) = 1920 km^2, with 6 to 10 localities distributed in two main areas: Guantiva–La Rusia and Siscunsí-Oceta (part of the Tota-Bijagual-Mamapacha complex). However, herbarium records from the latter probably belong to *Espeletia pescana*. The real EOO and number of localities of *E. incana* are probably much smaller than shown in current IUCN analyses, and this species would very likely need to be reclassified in the Endangered category.

38.1. ***Espeletia incana*** Cuatrec. f. ***incana***.

38.2. ***Espeletia incana*** Cuatrec. f. ***prolificens*** Cuatrec., Mem. New York Bot. Gard. 107: 276. 2013. TYPE: COLOMBIA. Boyacá: Páramo de La Rusia, NW-N de Duitama, Serranía Peña Negra, cerca de las torres transmisoras del ejército nacional, pedregales de la peña, 2900 masl, 12 December 1972, *A. M. Cleef 7124* (Holotype: US; Isotypes: COL, U).

39. ***Espeletia insignis*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 432. 1940. TYPE: COLOMBIA. Norte de Santander: Hoya del río Chitagá, en "Vega Colombia," abajo de Presidente, 2880–3000 masl, 21 July 1940, *J. Cuatrecasas & H. García-Barriga 10071* (Holotype: COL; Isotypes: BC, COL, F, US).

Homotypic synonym: *Espeletiopsis insignis* (Cuatrec.) Cuatrec., Phytologia 35(1): 55. 1976.

Distribution: COLOMBIA. Almorzadero (*J. Cuatrecasas 13476*, US).

Conservation status: Endangered.

40. ***Espeletia jaramilloi*** S. Díaz, Mutisia 37: 1. 1972. TYPE: COLOMBIA. Boyacá: por la carretera entre Socha y Sácama en el páramo de Pisba (o Socha), 3550–3650 masl, 9 October 1971, *R. Jaramillo-Mejía, G. Lozano & S. Díaz 5047* (Holotype: COL; Isotype: US). Fig. 2.

Distribution: COLOMBIA. Pisba (*J. Cuatrecasas & R. Jaramillo-Mejía 28738*, US).

Conservation status: Vulnerable.

41. ***Espeletia jimenezquesadae*** Cuatrec. [**1**], Rev. Acad. Col. Ci. Exact. 3(11): 247. 1940. TYPE: COLOMBIA. Boyacá: Cordillera Oriental, Nevado del Cocuy, hacia la Cueva, en la Zanja, 3700 masl, 13 September 1938, *J. Cuatrecasas & H. García-Barriga 1635* (Holotype: COL; Isotype: BC, F, P, US). Fig. 2.

[**1**]: According to Art. 60.11 of the International Code of Nomenclature for algae, fungi, and plants (Turland et al., 2018), the correct spelling for the derived substantival epithet is "*jimenezquesadae*" (instead of "*jimenez-quesadae*").

Homotypic synonym: *Espeletiopsis jimenezquesadae* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976.

Distribution: COLOMBIA. Sierra Nevada del Cocuy (*J. Cuatrecasas & L. Rodríguez 27835*, US).

Conservation status: Vulnerable.

42. ***Espeletia killipii*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 425. 1940. TYPE: COLOMBIA. Cundinamarca: Municipio de Guasca, Páramo de Guasca, vertiente oriental, 3000–3500 masl, 11 October 1939, *H. García-Barriga 8117* (Holotype: COL; Isotypes: COL, US).

Distribution: COLOMBIA. Chingaza (*J. H. G. Barclay & P. Juajibioy 6527*, US; *J. Cuatrecasas 13543*, US), Cruz Verde-Sumapaz (*H. G. Barclay & P. Juajibioy 6472*, US).

Conservation status: Least Concern. According to IUCN data, this species has Extent of Occurrence (EOO) = 1993 km^2, with several localities distributed in two main areas: Chingaza and the north area of Cruz Verde–Sumapaz. However, inspection of herbarium records indicates that individuals from Cruz Verde–Sumapaz could indeed be hybrids between *Espeletia grandiflora* Bonpl. and *E. summapacis* Cuatrec., and that in Chingaza *E. killipii* is frequently confounded with the much more broadly distributed *E. grandiflora* (pers. obs.). Thus, the real EOO, AOO, and number of localities of *E. killipii* are certainly significantly smaller than shown in current IUCN analyses, and this species would very likely need to be reclassified at least in the Vulnerable category.

42.1. ***Espeletia killipii*** Cuatrec. var. ***killipii***.

42.2. ***Espeletia killipii*** Cuatrec. var. ***chisacana*** Cuatrec., Phytologia 32(4): 326. 1975. TYPE: COLOMBIA. Cundinamarca: Macizo de Bogotá, Páramo de Chisacá, open hill at the left side of the road, 3680–3700 masl, 16 September 1961, *J. Cuatrecasas & R. Jaramillo-Mejía 25986* (Holotype: US; Isotypes: BC, COL, F, US).

43. Espeletia laxiflora (S. Díaz & Rodríguez-Cabeza) Mavárez, *comb. nov*.

Basionym: *Espeletiopsis laxiflora* S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 34(133): 442. 2010. TYPE: COLOMBIA. Santander: Santuario de Fauna y Flora Guanentá Alto Río Fonce, Municipio de Encino, Vereda Avendaños Tres, sector Páramo de las Playas, 19 October 2008, *B. V. Rodríguez-Cabeza, H. Palacios, R. Rivero & S. Estepa BVR-1993* (Holotype: COL; Isotypes: COL, HUA [not seen], UIS [not seen], UPTC [not seen]).

Homotypic synonym: *Coespeletia laxiflora* (S. Díaz & Rodríguez-Cabeza) S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 35(137): 422. 2011.

Distribution: COLOMBIA. Guantiva–La Rusia (*B. V. Rodríguez-Cabeza, H. Palacios, R. Rivero & S. Estepa BVR-1993*, COL).

Conservation status: Critically Endangered.

44. ***Espeletia lopezii*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(11): 248. 1940. TYPE: COLOMBIA. Boyacá: Nevado del Cocuy, alto valle de Las Lagunillas, 4000–4300 masl, 12 September 1938, *J. Cuatrecasas & H. García-Barriga 1540* (Holotype: COL; Isotypes: BC, F, P, U, US).

Distribution: COLOMBIA. Sierra Nevada del Cocuy (*H. G. Barclay & P. Juajibioy 7444*, US; *H. G. Barclay & P. Juajibioy 7397*, US; *M. Villarreal 3*, US; *J. Cuatrecasas & L. Rodríguez 27826*, US; *A. M. Cleef & T. van der Hammen 10345*, U), Pisba (*A. M. Cleef 4759*, US), Tota-Bijagual-Mamapacha (*J. Cuatrecasas, R. Jaramillo-Mejía & A. Kleef 28696*, US).

Conservation status: Least Concern.

44.1. ***Espeletia lopezii*** Cuatrec. subsp. ***lopezii***.

Distribution: COLOMBIA. Sierra Nevada del Cocuy (*H. G. Barclay & P. Juajibioy 7397*, US; *H. G. Barclay & P. Juajibioy 7444*, US; *M. Villarreal 3*, US; *J. Cuatrecasas & L. Rodríguez 27826*, US), Pisba (*A. M. Cleef 4759*, US), Tota-Bijagual-Mamapacha (*J. Cuatrecasas, R. Jaramillo-Mejía & A. Kleef 28696*, US).

44.1.1. ***Espeletia lopezii*** Cuatrec. subsp. ***lopezii*** var. ***lopezii***.

44.1.1.1 ***Espeletia lopezii*** Cuatrec. subsp. ***lopezii*** var. ***lopezii*** f. ***lopezii***.

44.1.1.2 ***Espeletia lopezii*** Cuatrec. subsp. ***lopezii*** var. ***lopezii*** f. ***alticola*** Cuatrec., Phytologia 31(4): 327. 1975. TYPE: COLOMBIA. Boyacá: Sierra Nevada del Cocuy, Páramo Co´ncavo, valle abrigado y pantanoso entre morrenas peladas, límite páramo-superpáramo, 4335 masl, 26 February 1973, *A. M. Cleef 8547* (Holotype: US; Isotypes: COL, GB, NY, S, U, US, VEN [not seen]).

44.1.2. ***Espeletia lopezii*** Cuatrec. subsp. ***lopezii*** var. ***escobalensis*** Cuatrec., Phytologia 45(1): 21. 1980. TYPE: COLOMBIA. Boyacá: Between Soatá and Cocuy, páramo del Alto del Escobal, 3750 masl, 8 September 1938, *J. Cuatrecasas & H. García-Barriga 1236* (Holotype: US; Isotypes: COL, F).

44.1.3. ***Espeletia lopezii*** Cuatrec. subsp. ***lopezii*** var. ***major*** Cuatrec., Phytologia 31(4): 325. 1975. TYPE: COLOMBIA. Boyacá: Páramo entre Chita y Sácama, vertiente oriental de la cordillera, Quebrada del Curial (La Porquera), 3350 masl, 15 September 1969, *J. Cuatrecasas & L. Rodríguez 27791* (Holotype: COL; Isotype: US).

44.2. ***Espeletia lopezii*** Cuatrec. subsp. ***ursina*** Cuatrec., Mem. New York Bot. Gard. 107: 303 (2013). TYPE: COLOMBIA. Arauca: Sierra Nevada del Cocuy, cabeceras de Q[uebrada] Los Osos, 3800 masl, 25 March 1977, *A. Cleef & T. van der Hammen 10345* (Holotype: US? [**1**]; Isotypes: AMD, U).

[**1**]: According to Cuatrecasas (2013), the holotypus is located in US, but it does not appear in online databases.

Distribution: COLOMBIA. Sierra Nevada del Cocuy (*A. M. Cleef & T. van der Hammen 10345*, U).

45. ***Espeletia marnixiana*** S. Díaz & Pedraza, Revista Acad. Colomb. Ci. Exact. 25(94): 12. 2001. TYPE: COLOMBIA. Cauca: Municipio de Argelia, Vereda el Naranjal, Cordillera Occidental, Río Plateado, nacimiento del río Micay, Páramo de La Soledad, 3250 masl, 19 June 1993, *M. L. Becking 1042* (Holotype: COL).

Distribution: COLOMBIA. Cerro Plateado (*M. L. Becking 1042*, COL).

Known only from the type specimen. The validity of this species needs to be reviewed.

Conservation status: Data Deficient.

46. ***Espeletia mirabilis*** S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 34(133): 449. 2010. TYPE: COLOMBIA. Boyacá: Parque Nacional Natural Pisba, Municipio Socotá, vereda Corral de Piedra, sector río Arzobispo, parte alta de Los Estupendos, 3550 masl, 5°58'33"N, 72°33'47"W, 14 September 2008, *B. V. Rodríguez-Cabeza & L. Velasco 2001* (Holotype: COL; Isotypes: COL, HUA, UIS [not seen], UPTC [not seen]).

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza & L. Velasco 2001*, COL).

Known only from the type specimen. The validity of this species needs to be reviewed.

Conservation status: Critically Endangered. Given the lack of information this taxon would likely need to be reclassified as Data Deficient.

47. ***Espeletia miradorensis*** (Cuatrec.) Cuatrec., Phytologia 52(3): 158. 1982. TYPE: COLOMBIA. Cundinamarca: Páramo de Sumapaz, Alto de Lagunitas, El Mirador, 5 km al S de San Juan, 3560 masl, 28 January 1973, *A. M. Cleef 8421* (Holotype: COL; Isotypes: COL, K, MO, U, US, VEN [not seen]).

Homotypic synonym: *Espeletia grandiflora* Bonpl. var. *miradorensis* Cuatrec., Phytologia 32(4): 324. 1975.

Distribution: COLOMBIA. Cruz Verde–Sumapaz (*A. M. Cleef 8421*, US).

Known only from the type specimen. The validity of this species needs to be reviewed.

Conservation status: Critically Endangered. Given the lack of information this taxon would likely need to be reclassified as Data Deficient.

48. ***Espeletia muiska*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 429. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Guantiva, Alto de Canutos, vertiente sur, 3200–3400 masl, 3 August 1940, *J. Cuatrecasas 10359* (Holotype: COL; Isotypes: F, US). Fig. 2.

Homotypic synonym: *Espeletiopsis muiska* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976.

Distribution: COLOMBIA. Guantiva–La Rusia (*J. Cuatrecasas 10409*, US), Iguaque-Merchán (*J. Cuatrecasas 10440*, US), Tota-Bijagual-Mamapacha (*F. O. Zuloaga & X. Landono 4158*, COL), Sierra Nevada del Cocuy (*J. Cuatrecasas & L. Rodríguez 27806*, US).

Conservation status: Least Concern.

49. ***Espeletia murilloi*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 425. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Arcabuco, 2800 masl, 24 February 1940 [**1**], *E. Pérez-Arbeláez & J. Cuatrecasas 8098* (Holotype: COL; Isotypes: F, US). Fig. 2.

[**1**]: Collection date given as "22 February 1940" in Diazgranados (2012) and Cuatrecasas (2013).

Distribution: COLOMBIA. Guantiva–La Rusia (*A. M. Cleef 7184*, US; *J. Cuatrecasas 10429*, US; *J. Cuatrecasas 10411*, US), Iguaque-Merchán (*H. García-Barriga 20371*, US), Tota-Bijagual-Mamapacha (*A. M. Cleef* 9540, US), Rabanal–Río Bogotá (*D. Stancik 1282*, COL).

Conservation status: Least Concern.

49.1. ***Espeletia murilloi*** Cuatrec. var. ***murilloi***.

49.2. ***Espeletia murilloi*** Cuatrec. var. ***rusiana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 168. 1941. TYPE: COLOMBIA. Santander [**1**]: Páramo de La Rusia, vertiente noroeste, 3300–3500 masl, 4 August 1940, *J. Cuatrecasas 10429* (Holotype: COL; Isotypes: F, US).

[**1**]: Department given as "Boyacá" in Diazgranados (2012).

49.3. ***Espeletia murilloi*** Cuatrec. var. ***subcoriacea*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 168. 1941. TYPE: COLOMBIA. Boyacá: Páramo de La Rusia, vertiente sudeste, Boca del Monte, 3300–3400 m, 4 August 1940, *J. Cuatrecasas 10411* (Holotype: COL; Isotype: US).

Nomen nudum: *Espeletia murilloi* Cuatrec. subsp. *subcoriacea* Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(14): 168. 1941 [**1**].

[**1**]: Cuatrecasas never validly published *Espeletia murilloi* subsp. *subcoriacea*. The name with subsp. rank appeared in the legend of the figure depicting *E. murilloi* var. *subcoriacea*, probably by mistake, and has never been used again.

50. ***Espeletia mutabilis*** S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 30(16): 345. 2006. TYPE: COLOMBIA. Boyacá: Municipio de Socha, Vereda El Mortiñal (parte alta), sector El Alizal, sitio El Frailejonal, finca de la Alcaldía, 3700 masl, 28 July 2006, *B. V. Rodríguez & P. Velasco BVR-1675* (Holotype: COL; Isotypes: COL, UIS [not seen]).

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez & P. Velasco BVR-1675*, US).

Conservation status: Near Threatened. According to IUCN data, this species has Area of Occupancy (AOO) = 12–20 km^2, with three to five localities distributed within a single páramo nearby Socha, Boyacá, and with ca. 1000–1500 adult individuals. Its habitat is described as relatively well conserved so far but surrounded by areas with active farming, ranching, and coal mining. Under these conditions, this species would very likely need to be reclassified at least in the Vulnerable category.

51. ***Espeletia nemekenei*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 430. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Guantiva, Alto de Canutos, vertiente sur, 3200–3400 masl, 3 August 1940, *J. Cuatrecasas 10348* (Holotype: COL; Isotypes: BC, COL, F, US).

Distribution: COLOMBIA. Guantiva–La Rusia (*J. Cuatrecasas & L. Rodríguez 27749*, US), Iguaque-Merchán (*L. Uribe-Uribe 6604*, US).

Conservation status: Endangered.

52. ***Espeletia occidentalis*** A.C. Sm., Brittonia 1(7): 520. 1935. TYPE: COLOMBIA. Border Antioquia-Bolívar [currently Antioquia-Córdoba]: Páramo de Chaquiro, 3000–3200 masl, 23 February 1918, *F. W. Pennell 4266* (Holotype: NY; Isotypes: GH, US).

Distribution: COLOMBIA. Paramillo (*E. L. Core 544*, US), Belmira (*R. Fonnegra & D. Tuberquia 4605*, US). Apparently found as well in Frontino-Urrao (*E. Rentería 5125*, HUA), Citará (*F. Alzate 4733*, HUA), and El Duende (*Vargas 4855*, HUA), but these records need to be confirmed.

Conservation status: Near Threatened.

52.1. ***Espeletia occidentalis*** A.C. Sm. subsp. ***occidentalis***.

Distribution: COLOMBIA. Paramillo (*E. L. Core 544*, US).

52.2. ***Espeletia occidentalis*** A.C. Sm. subsp. ***antioquensis*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 216. 2013. TYPE: COLOMBIA. Antioquia: Entre Yarumal y Santa Rosa, páramo en Llanos de Cuiba, 2700 masl, 20 February 1942, *J. Cuatrecasas & R. D. Metcalf 30163* (Holotype: COL; Isotypes: BC, F, G, GH, LIL [not seen], US).

Homotypic synonym: *Espeletia occidentalis* A.C. Sm. var. *antioquensis* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 24.1942.

Distribution: COLOMBIA. Belmira (*R. Fonnegra & D. Tuberquia 4605*, US).

53. ***Espeletia oswaldiana*** S. Díaz, Mutisia 32: 1. 1970. TYPE: COLOMBIA. Boyacá: Carretera Sogamoso-Pajarito, 2 km adelante de Vadohondo, valle del Río Cusiana, 2 July 1968, *S. Díaz-Piedrahita 74* (Holotype: COL; Isotypes: ENCB [not seen], NY, US, VEN [not seen]).

Distribution: COLOMBIA. Tota-Bijagual-Mamapacha (*J. Cuatrecasas* & *R. Jaramillo-Mejía 28703*, US).

Conservation status: Critically Endangered.

54. ***Espeletia paipana*** S. Díaz & Pedraza, Revista Acad. Colomb. Ci. Exact. 25(94): 12. 2001. TYPE: COLOMBIA. Boyacá: Municipio Paipa, Cuchilla "El Páramo," 3300 masl, 3–4 December 1998, *D. Stancik 1507* (Holotype: COL; Isotypes: COL, PRC).

Distribution: COLOMBIA. Iguaque-Merchán (*B. V. Rodríguez-Cabeza et al. 1918*, COL).

Conservation status: Critically Endangered.

55. ***Espeletia perijaensis*** Cuatrec., Phytologia 38: 17. 1977. TYPE: COLOMBIA. Magdalena: Sierra de Perijá, east of Manaure, Quebrada de Floridablanca, 2700–2800 masl, 10 November 1959, *J. Cuatrecasas & R. Romero-Castañeda 25192* (Holotype: US; Isotype: COL).

Distribution: COLOMBIA-VENEZUELA. Perijá (*J. Cuatrecasas & R. Romero-Castañeda 25032,* US).

Conservation status: Endangered.

56. ***Espeletia pescana*** (S. Díaz) S. Díaz, Revista Acad. Colomb. Ci. Exact. 33(125): 459. 2008. TYPE: COLOMBIA. Boyacá: Municipio de Pesca, Páramo de la Cortadera, Vereda la Peña, 3750 masl, 21 August 1982, *M. Bejarano 257* (Holotype: COL; Isotypes: COL, US).

Homotypic synonym: *Espeletia brachyaxiantha* S. Díaz subsp. *pescana* S. Díaz, Mutisia 61: 8. 1985.

Distribution: COLOMBIA. Tota-Bijagual-Mamapacha (*M. Bejarano 335,* US).

Conservation status: Vulnerable.

57. ***Espeletia petiolata*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(15–16): 338. 1941. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, región media, 3500–3700 masl, 20 July 1940, *J. Cuatrecasas & H. García-Barriga 9973* (Holotype: COL; Isotypes: BC, F, US).

Homotypic synonyms: *Espeletiopsis petiolata* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976.

Nom. Illeg.: *Espeletia petiolata* Cuatrec. f. *paniculata* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 22 (1942).

Distribution: COLOMBIA. Almorzadero (*J. Cuatrecasas & L. Rodríguez 27877*, US), Sierra Nevada del Cocuy (*D. Stancik & J. R. Carvajal 1813*, COL), Pisba (*R. Jaramillo-Mejía, G. Lozano-Contreras & S. Díaz-Piedrahita 5058*, US). The status of populations in Pisba must be reviewed.

Conservation status: Least Concern.

57.1. ***Espeletia petiolata*** Cuatrec. var. ***petiolata***.

57.1.1. ***Espeletia petiolata*** Cuatrec. var. ***petiolata*** f. ***petiolata***.

57.1.2. ***Espeletia petiolata*** Cuatrec. var. ***petiolata*** f. ***corymbosa*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 22. 1942. TYPE: COLOMBIA. Norte de Santander: Quebrada de Presidente en la alta hoya del Río Chitagá, 3100 masl, 28 November 1941, *J. Cuatrecasas 13479* (Holotype: COL; Isotype: COL).

Homotypic synonym: *Espeletiopsis petiolata* Cuatrec. f. *corymbosa* (Cuatrec.) Diazgr., PhytoKeys 16: 31. 2012.

57.1.2. ***Espeletia petiolata*** Cuatrec. var. ***petiolata*** f. ***media*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 22. 1942. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, vertiente norte, 3600–3800 masl, 28 November 1941, *J. Cuatrecasas 13497* [**1**] (Holotype: COL; Isotype: US).

[**1**]: Collection date given as "28 November 1931" in Diazgranados (2012).

Homotypic synonym: *Espeletiopsis petiolata* Cuatrec. f. *media* (Cuatrec.) Diazgr., PhytoKeys 16: 32. 2012.

57.1.3. ***Espeletia petiolata*** Cuatrec. var. ***petiolata*** f. ***reducta*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4(15–16): 338. 1941. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, vertiente norte, 3500–3700 masl, 20 July 1940, *J. Cuatrecasas & H. García-Barriga 9987-A* (Holotype: COL).

Homotypic synonym: ***Espeletiopsis petiolata*** Cuatrec. var. ***petiolata*** f. ***reducta*** (Cuatrec.) Diazgr., PhytoKeys 16: 32. 2012.

57.2. ***Espeletia petiolata*** Cuatrec. var. ***escobensis*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 22. 1942. TYPE: COLOMBIA. Boyacá: Between Soatá and Cocuy, Páramo del Alto del Escobal, 3800–3900 masl, 15 September 1938, *J. Cuatrecasas & H. García-Barriga 1760* (Holotype: COL; Isotypes: F, US).

Homotypic synonym: *Espeletiopsis petiolata* Cuatrec. var. *escobensis* (Cuatrec.) Diazgr., PhytoKeys 16: 31. 2012.

58. ***Espeletia pisbana*** S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 30(116): 332. 2006. TYPE: COLOMBIA. Boyacá: PNN Pisba, Municipio Socotá, Vereda Pueblo Viejo, ruta Libertadora, Sector La Australia, sitio El Alto del Almorzadero, 3406 masl, 6°09'57.229"N, 72°46'11.615"W, [**1**], 16 June 2005, *B. V. Rodríguez-Cabeza & L. Velasco 1389* (Holotype: COL; Isotypes: COL, UIS [not seen]).

[**1**]: Geographic coordinates provided with the holotypus do not match type locality.

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza & L. Velasco 1402*, COL).

Conservation status: Least Concern. According to IUCN data, this species has EOO = 62 km^2, Area of Occupancy (AOO) = 12 km^2, with all localities distributed within the Páramo de Pisba. Its populations are described as locally abundant (up to 300 mature indiviuals), in habitats considered well conserved and without major threats. However, given the small known distribution of this species, it would very likely need to be reclassified at least in the Vulnerable category.

59. ***Espeletia pleiochasia*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 432. 1940. TYPE: COLOMBIA. Boyacá: Quebrada de Becerra al noroeste de Duitama, páramos entre bosque, 2970–3300 masl, 4 August 1940, *J. Cuarecasas 10399* (Holotype: COL; Isotypes: BC, COL, F, P, US).

Homotypic synonym: *Espeletiopsis pleiochasia* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976.

Distribution: COLOMBIA. Guantiva–La Rusia (*H. García-Barriga & R. Jaramillo-Mejía 20279*, US), Pisba (*R. Jaramillo-Mejía, G. Lozano-Contreras & S. Díaz-Piedrahita 5017*, US), Iguaque-Merchán (*D. Stancik 1680*, COL), Cruz Verde–Sumapaz (*G. Huertas & R. Jaramillo-Mejía 6087*, COL).

Conservation status: Near threatened.

59.1. ***Espeletia pleiochasia*** Cuatrec. var. ***pleiochasia***.

59.2. ***Espeletia pleiochasia*** Cuatrec. var. ***socotana*** Cuatrec., Phytologia 31: 328. 1975. TYPE: COLOMBIA. Boyacá: Carretera Socha–Los Pinos, km 40, 2 km al N. del Alto Las Pilas y 4 km al E-NE de Socha, 2970 masl, 22 May 1973, *A. M. Cleef 9870* (Holotype: US; Isotypes: COL, U, US).

Homotypic synonym: *Espeletiopsis pleiochasia* Cuatrec. var. *socotana* (Cuatrec.) Diazgr., PhytoKeys 16: 32. 2012.

60. ***Espeletia praefrontina*** Cuatrec., Phytologia 47(1): 10. 1980. TYPE: COLOMBIA. Antioquia: Páramo Frontino, near Llano Grande, 3450 masl, 25 October 1976, *J. D. Boeke & J. B. McElroy 273* (Holotype: US; Isotypes: MEDEL [not seen], NY, U).

Distribution: COLOMBIA. Frontino-Urrao (*J. D. Boeke & J. B. McElroy 309*, US). Apparently found as well in Paramillo (e.g., *H. Cuadros 5004*, US), but these records need to be confimed.

Conservation status: Least Concern. According to IUCN data, this species has Extent of Occurrence (EOO) = 1100 km^2, with three localities distributed in Paramillo, Frontino-Urrao, and El Duende. However, there are no confirmed records of *Espeletia praefrontina* in the latter. Furthermore, this species is sometimes confounded with the more broadly distributed *E. frontinoensis* and *E. occidentalis* (obs. pers.). Indeed, when only confirmed *E. praefrontina* occurrences are used in the analysis, its EOO = 43 km^2 and its AOO = 24 km^2, with only two localities (data not shown). This species would very likely need to be reclassified in the Endangered category.

61. ***Espeletia praesidentis*** Diazgr. & L.R. Sánchez, PhytoKeys 76: 3. 2017. TYPE: COLOMBIA. Norte de Santander: Páramo de Presidente, en vía a Chitagá, llegando al páramo, 3503 masl, -72°40.8828'W, 6°59.8362'N, 3 October 2009, *M. Diazgranados & L. R. Sánchez 3865* (Holotype: COL; Isotype: HECASA [not seen]).

Distribution: COLOMBIA. Almorzadero (*M. Diazgranados & L. R. Sánchez 386*, COL).

Conservation status: Least Concern. According to IUCN data, this species has Area of Occupancy (AOO) = 8 km^2, with only one locality in Páramo de Presidente. The species is described as locally abundant, with several hundred individuals in a habitat that, although currently not threatened, is not formally protected. Given its extremely small distribution, low number of known populations, and absence of conservation actions, this species would very likely need to be reclassified in the Critically Endangered category, as originally in Diazgranados and Sánchez (2017).

62. ***Espeletia pulcherrima*** Rodríguez-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 30(116): 339. 2006. TYPE: COLOMBIA. Boyacá: Municipio Chita, Vereda Minas, Páramo de Los Venados, carretera hacia Sácama, km 86 - desvío a Chita, 3300 masl, 6°03'0.65"N, 72°25'40.7"W, 23 October 2005, *B. V. Rodríguez-Cabeza & L. Velasco 1520* (Holotype: COL; Isotype: UIS [not seen]).

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza & L. Velasco 1520*, COL).

Conservation status: Endangered.

63. ***Espeletia purpurascens*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 16. 1942. TYPE: COLOMBIA. Norte de Santander: Páramo de Tamá, alrededores de La Cueva, 3000–3200 masl, 28 October 1941, *J. Cuatrecasas, R. E. Schultes & E. Smith 12689* (Holotype: COL; Isotypes: BC, COL, F, GH, U, US).

Homotypic synonym: *Espeletiopsis purpurascens* (Cuatrec.) Cuatrec., Phytologia 35(1): 56 (1976).

Distribution: COLOMBIA-VENEZUELA. Tamá (*L. Ruíz-Terán & M.* López-*Figueiras 8926*, US).

Conservation status: Endangered.

64. ***Espeletia pycnophylla*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 24. 1942. TYPE: COLOMBIA. Nariño-Putumayo: Alta cuenca del Río Putumayo, filo de la cordillera entre El Encano y Sibundoy, Páramo de San Antonio del Bordoncillo, 3250 masl, 4 January 1941, *J. Cuatrecasas 11736* (Holotype: COL; Isotypes: BC, F, US).

Distribution: COLOMBIA. La Cocha–Patascoy (*J. Cuatrecasas, E. Hernández & A. Estrada 28652*, US; *J. Cuatrecasas 11820*, US), Doña Juana–Chimayoy (*S. L. Díaz-Ibarra 2311*, US), Chiles-Cumbal (*J. L. Luteyn, J. Fuertes & J. O. Rangel-Ch. 12881*, US). ECUADOR: Páramo del Angel (*H. G. Barclay & P. Juajibioy 9411*, US), Páramo El Mirador (*V. A. Funk & M. Gavilanes 11049*, US), P.N. Llanganates (*H. Vargas, J. C. Ronquillo & N. Granda 2713*, US).

Conservation status: Least Concern.

64.1. ***Espeletia pycnophylla*** Cuatrec. subsp. ***pycnophylla***.

Distribution: COLOMBIA. La Cocha–Patascoy (*J. Cuatrecasas, E. Hernández & A. Estrada 28652*, US), Doña Juana-Chimayoy (*S. L. Díaz-Ibarra 2311*, US).

64.1.1. ***Espeletia pycnophylla*** Cuatrec. subsp. ***pycnophylla*** var. ***pycnophylla***.

64.1.2. ***Espeletia pycnophylla*** Cuatrec. subsp. ***pycnophylla*** var. ***galerana*** Cuatrec., Phytologia 45(1): 17. 1980. TYPE: COLOMBIA. Nariño: Macizo del Volcán Galeras, eastern slopes, páramo bushes, 3900 masl, 7 February 1960, *J. Cuatrecasas & L. E. Mora 26931* (Holotype: COL; Isotype: US).

64.1.3. ***Espeletia pycnophylla*** Cuatrec. subsp. ***pycnophylla*** var. ***lacinulata*** Cuatrec., Phytologia 45(1): 17. 1980. TYPE: COLOMBIA. Nariño-Putumayo: Filo de la cordillera, Páramo de Quilinchayaco, lado oriental, 3200–3250 masl, 21 March 1973, *J. Cuatrecasas, E. Hernández & A. Estrada 28643* (Holotype: US; Isotypes: COL, U, US).

64.2. ***Espeletia pycnophylla*** Cuatrec. subsp. ***angelensis*** Cuatrec., Phytologia 45(1): 18. 1980. TYPE: ECUADOR. Carchi: Páramo del Angel, 3400 masl, 21 June 1939, *E. Asplund 7078* (Holotype: S; Isotypes: CAS, G, US).

Heterotypic synonym: *Espeletia cochensis* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 25. 1942. TYPE. COLOMBIA: Putumayo: Lado sur de la Laguna de La Cocha, Quebrada de Santa Lucía, bosque, 2850 masl, 8 January 1941, *J. Cuatrecasas 11820* (Holotype: COL; Isotypes: F, US).

Distribution: COLOMBIA. Chiles-Cumbal (*J. L. Luteyn, J. Fuertes & J. O. Rangel-Ch. 12881*, US), La Cocha–Patascoy (*J. Cuatrecasas 11820*, US). ECUADOR. Páramo del Angel (*H. G. Barclay & P. Juajibioy 9411*, US), Páramo El Mirador (*V. A. Funk & M. Gavilanes 11049*, US).

64.3. ***Espeletia pycnophylla*** Cuatrec. subsp. ***llanganatensis*** Cuatrec., Phytologia 45(1): 20. 1980. TYPE: ECUADOR. Tungurahua: Cordillera de Llanganates, near Las Torres, páramo, 3700–3800 masl, 23 November 1939, *E. Asplund 9944* (Holotype: S; Isotype: S).

Distribution: ECUADOR. P.N. Llanganates (*H. Vargas, J. C. Ronquillo & N. Granda 2713*, US).

65. Espeletia rabanalensis (S. Díaz & Rodríguez-Cabeza) Mavárez, *comb. nov*.

Basionym: *Espeletiopsis rabanalensis* S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 33(125): 456. 2008. TYPE: COLOMBIA. Boyacá: Municipio de Samacá, Páramo del Rabanal, 3412 masl, 05°44'N, 73°35'W, 3–5 October 2007, *B. V. Rodríguez-Cabeza & F. Márquez 1895* (Holotype: COL; Isotypes: COL, UIS [not seen]).

Distribution: COLOMBIA. Rabanal–Río Bogotá (*J. C. Arias-G. et al. 3704*, COL).

Conservation status: Endangered.

66. ***Espeletia ramosa*** Mavárez & M.T. Becerra, Phytologia 101(4): 223. 2019. TYPE: COLOMBIA. Boyacá: near El Alto, about 4.5 km in the road Pesca-Tota, 3060 masl, 5.546853 N 73.031896 W, 17 August 2019, *M. T. Becerra, J. Mavárez & J. Aguirre 35* (Holotype: COL; Isotype: COL). Fig. 2.

Distribution: COLOMBIA. Tota-Bijagual-Mamapacha (*M. T. Becerra, J. Mavárez & J. Aguirre 35*, COL).

Conservation status: Not Evaluated. Critically Endangered according to Mavárez and Becerra (2019).

67. ***Espeletia raquirensis*** Rodríguez-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 34(133): 446. 2010. TYPE: COLOMBIA. Boyacá: Municipio de Ráquira, Vereda Firita, Peña Arriba, Páramo de Rabanal, en límites con el municipio de Guachetá, vereda San Antonio (Cundinamarca), 3260 masl, 5°24'35.7"N, 73°36'33.0"W, 12 August 2008, *B. V. Rodríguez-Cabeza, R. Galindo-T. & I. Cortez BVR-1973* (Holotype: COL; Isotypes: COL, HUA, UIS [not seen], UPTC [not seen]).

Distribution: COLOMBIA. Rabanal–Río Bogotá (*B. V. Rodríguez-Cabeza, R. Galindo-T. & I. Cortez BVR-1973*, HUA).

Conservation status: Critically Endangered.

68. ***Espeletia restricta*** Alzate & S. Giraldo, Phytotaxa 433(4): 289. 2020. Type: COLOMBIA. Antioquia: Municipio Sonsón, Vereda La Paloma, Páramo de Sonsón, Cerro de Las Palomas, 3370 masl, 5°43'3"N, 75°14'58"W, 7 January 2016, *F. Alzate 5220* (Holotype: HUA [not seen]; Isotypes: COL [not seen]).

Distribution: COLOMBIA. Sonsón (*J. Betancur & S. P. Churchill 5868*, COL).

Conservation status: Not Evaluated. Critically Endangered according to Alzate and Giraldo (2020).

69. ***Espeletia roberti*** Cuatrec., Phytologia 38(1): 7. 1977. TYPE: COLOMBIA. Norte de Santander-Cesar: límites entre los departamentos de Norte de Santander y Cesar, Cerro de Oroque (Las Jurisdicciones), 3700–3900 masl, 22–27 July 1974, *H. García-Barriga & R. Jaramillo-Mejía 20648* (Holotype: US; Isotype: COL).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*H. García-Barriga & R. Jaramillo-Mejía 20662*, US).

Conservation status: Endangered. According to IUCN data, this species has Extent of Occurrence (EOO) = 216 km^2, with three to five localities distributed in two main areas: Cerro de Oroque and around Vetas, both within the Jurisdicciones-Santurbán complex. However, no confirmed records of the species in the latter area have been found. Indeed, all confirmed records are located within an area with EOO < 20 km^2, with the largest population occupying a patch with ca. 5 ha of páramo habitat (García et al., 2005). Furthermore, the area is severely affected by farming and ranching, with no formal protection. Given its extremely small distribution, low number of known populations, and absence of conservation actions, this species would very likely need to be reclassified in the Critically Endangered category, as originally in García et al. (2005).

70. ***Espeletia rositae*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 4: 164. 1941. TYPE: COLOMBIA. Boyacá: Páramo de Güina - Santa Rosita, 3300–3400 masl, 3 August 1940, *J. Cuatrecasas 10371* (Holotype: COL; Isotypes: BC, COL, F, U, US).

Distribution: COLOMBIA. Guantiva–La Rusia (*J. Cuatrecasas 10371*, US; *A. M. Cleef 9824*, US).

Conservation status: Endangered.

70.1. ***Espeletia rositae*** Cuatrec. subsp. ***rositae***.

Distribution: COLOMBIA. Guantiva–La Rusia (*J. Cuatrecasas 10371*, US).

70.2. ***Espeletia rositae*** Cuatrec. subsp. ***macrocephala*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 264. 2013. TYPE: COLOMBIA. Boyacá: Gran páramo entre Santa Rosita y Gonzaga [Onzaga], extreme NW, 3300 masl, 6 April 1973, *J. Cuatrecasas & R. Jaramillo-Mejía 28743* (Holotype: US; Isotypes: COL, F, U, US).

Homotypic synonym: *Espeletia rositae* Cuatrec. var. *macrocephala* Cuatrec., Phytologia 31(4): 329. 1975.

Distribution: COLOMBIA. Guantiva–La Rusia (*A. M. Cleef 9824*, US).

71. Espeletia sanchezii (S. Díaz & Obando) Mavárez, *comb. nov*.

Basionym: *Espeletiopsis sanchezii* S. Díaz & Obando, Revista Acad. Colomb. Ci. Exact. 28(108): 324. 2004. TYPE: COLOMBIA. Norte de Santander: Pamplona, sector de La Lejía, páramo de Tierranegra, 3200–3300 masl, 23 November 2002, *L. R. Sánchez, M. A. Murcia & W. Valencia 7281* (Holotype: COL; Isotypes: COL, HECASA [not seen]).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*L. R. Sánchez, M. A. Murcia & W. Valencia 7281*, COL).

Conservation status: Endangered.

72. ***Espeletia santanderensis*** A.C. Sm., Brittonia 1(7): 527. 1935. TYPE: COLOMBIA. Santander: Páramo de Vetas, 3400–3700 masl, 16 January 1927, *E. P. Killip & A. C. Smith 17422* (Holotype: NY; Isotypes: F, GH, K, PH [not seen], S, US). Fig. 2.

Homotypic synonym: *Espeletiopsis santanderensis* (A.C. Sm.) Cuatrec., Phytologia 35(1): 56. 1976.

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*H. G. Barclay & P. Juajibioy 10439*, US).

Conservation status: Least Concern.

73. ***Espeletia schultesiana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 26. 1942. TYPE: COLOMBIA. Putumayo: Páramo del Tambillo, northwest of the Valle de Sibundoy, ca. 8400 ft [2560 masl], 13–14 December 1941, *R. E. Schultes & C. E. Smith 3096* (Holotype: COL; Isotypes: BR, CAS, F, FI, G [not seen], GH, MO [not seen], NY, P, US).

Distribution: COLOMBIA. La Cocha–Patascoy (*J. Cuatrecasas & E. Hernández 28656*, US), Doña Juana–Chimayoy (*S. Garzón 42*, COL).

Conservation status: Vulnerable. According to IUCN data, this species has Extent of Occurrence (EOO) = 254 km^2, with eight to ten localities distributed in two main areas to the East and Northeast of Laguna La Cocha. However, although this species can be locally abundant, it inhabits low-elevation and azonal páramos that are threatened by agriculture and fires, most of which are not formally protected. This species would very likely need to be reclassified in the Endangered category.

73.1. ***Espeletia schultesiana*** Cuatrec. f. ***schultesiana***.

73.2. ***Espeletia schultesiana*** Cuatrec. f. ***alternifolia*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 236. 2013. TYPE: COLOMBIA. Nariño-Putumayo: Páramo de San Antonio, entre Santiago y El Encano, 3500 masl, 10 February 1942, *F. Miguel-de-Ipiales 42* (Holotype: COL?; Isotypes: US).

Homotypic synonym: *Espeletia alternifolia* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 27. 1942.

74. ***Espeletia sclerophylla*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 436. 1940. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, extremo sur, Peralonso, 3200 masl, 19 July 1940, *J. Cuatrecasas & H. García-Barriga*

9929 (Holotype: COL; Isotypes: F, US).

Homotypic synonym: *Espeletiopsis sclerophylla* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976.

Distribution: COLOMBIA. Almorzadero (*J. Cuatrecasas & L. Rodríguez 27868*, US).

Conservation status: Endangered.

75. ***Espeletia soroca*** S. Díaz & Rodríguez-Cabeza, Revista Acad. Colomb. Ci. Exact. 30(116): 334. 2006. TYPE: COLOMBIA. Boyacá: Municipio de Chita, Vereda Minas, Páramo de Los Venados, carretera hacia Sácama, km. 86, desvío a Chita, 3200 masl, 6°02'26.1"N, 72°24'45.5"W, 23 October 2005, *B. V. Rodríguez-Cabeza & L. Velasco BVR-1509* [**1**] (Holotype: COL; Isotypes: COL, HUA [not seen], UIS [not seen]).

[**1**]: Collection number given as " *B. V. Rodríguez-Cabeza & L. Velasco BVR-150*" in Díaz-Piedrahita et al., (2006) and Diazgranados (2012).

Distribution: COLOMBIA. Pisba (*B. V. Rodríguez-Cabeza & L. Velasco BVR-2013*, COL).

Conservation status: Critically Endangered.

76. ***Espeletia standleyana*** A.C. Sm., Brittonia 1(7): 514. 1935. TYPE: COLOMBIA. Santander: Páramo de Santurbán, en route from Tona to Mutiscua, 3800–4300 masl, 18 February 1827, *E. P. Killip & A. C. Smith 19558* (Holotype: NY; Isotypes: F, GH, K, PH [not seen], US).

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*J. Cuatrecasas & H. García-Barriga 10290*, US; *S. Díaz-Piedrahita 78*, US), Almorzadero (*J. Cuatrecasas & L. Rodríguez 27894*, US).

Conservation status: Vulnerable.

76.1. ***Espeletia standleyana*** A.C. Sm. subsp. ***standleyana***.

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*J. Cuatrecasas & H. García-Barriga 10290*, US).

76.2. ***Espeletia standleyana*** A.C. Sm. subsp. ***ampla*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 205. 2013. TYPE: COLOMBIA. Santander: Páramo de Santurbán, vertiente oeste, matorrales-bosque, bajando hacia Bucaramanga, 3100 masl, 27 July 1940, *J. Cuatrecasas & H. García-Barriga 10323* (Holotype: COL; Isotypes: F, US).

Homotypic synonym: *Espeletia standleyana* A.C. Sm. var. *ampla* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 22. 1942.

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*S. Díaz-Piedrahita 78*, US).

76.3. ***Espeletia standleyana*** A.C. Sm. subsp. ***laxior*** (Cuatrec.) Cuatrec., Mem. New York Bot. Gard. 107: 205. 2013. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, vertiente norte, 3600–3800 masl, 28 November 1941, *J. Cuatrecasas 13515* (Holotype: COL; Isotypes: BC, GH, US).

Homotypic synonym: *Espeletia standleyana* A.C. Sm. var. *laxior* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5: 23. 1942.

Distribution: COLOMBIA. Almorzadero (*J. Cuatrecasas & L. Rodríguez 27894*, US).

77. ***Espeletia steyermarkii*** Cuatrec., Ciencia (Mexico) 6: 265. 1945. TYPE: VENEZUELA. Táchira: Swampy meadow in Paramito, between Quebrada de Palmar and Quebrada de Paramito, at base of Páramo de Tamá, 2 km above Betania and 7 km above Villapaez, 2500 masl, 14 July 1944, *J. A. Steyermark 57217* (Holotype: VEN [not seen]; Isotypes: F, NY, US).

Homotypic synonym: *Espeletia brassicoidea* Cuatrec. var. *contracta* Aristeg., Fl. Venez. 10(1): 449. 1964.

Distribution: COLOMBIA-VENEZUELA. Tamá (*J. Cuatrecasas, L. Ruíz-Terán & M. López-Figueiras 28324*, US). According to Diazgranados and Sánchez (2017), *Espeletia steyermarkii* is apparently also found in Colombia, Santander, Páramo del Almorzadero.

Conservation status: Critically Endangered.

78. ***Espeletia summapacis*** Cuatrec., Phytologia 31(4): 331. 1975. TYPE: COLOMBIA. Cundinamarca: Macizo de Sumapaz, adelante de Andabobos, cerca al Pico de San Mateo, 3950–4000 masl, 7 February 1975, *L. Uribe-Uribe & R. Jaramillo-Mejía 6895* (Holotype: US; Isotypes: COL, G, NY, US).

Distribution: COLOMBIA. Cruz Verde–Sumapaz (*A. M. Cleef 1574*, US).

Conservation status: Endangered.

79. ***Espeletia tapirophila*** Cuatrec., Phytologia 32(4): 320. 1975. TYPE: COLOMBIA. Meta: Páramo de Sumapaz, Hoya Río Nevado, Puerta de Las Dantas, ca. 3400 masl, 25 January 1973, *A. M. Cleef 8301* (Holotype: US; Isotypes: COL, K, MO, U, US, VEN [not seen]).

Distribution: COLOMBIA. Cruz Verde–Sumapaz (*A. M. Cleef 8301*, US).

Known only from the type specimen. The validity of this species needs to be reviewed.

Conservation status: Data Deficient.

80. ***Espeletia tibamoensis*** Rodríguez-Cabeza & S. Díaz, Revista Acad. Colomb. Ci. Exact. 34(133): 451. 2010. TYPE: COLOMBIA. Boyacá: Limites entre los municipios de Siachoque y Toca, veredas Cormechoque arriba y Tubenecos, Páramo La Cortadera, sector Alto Tibamoa, 3600 masl, 16 May 2008, *B. V. Rodríguez-Cabeza & A. Burgos BVR-1959* (Holotype: COL; Isotypes: COL, HUA, UIS [not seen], UPTC [not seen]).

Distribution: COLOMBIA. Tota-Bijagual-Mamapacha (*B. V. Rodríguez-Cabeza & A. Burgos BVR-1959*, HUA).

Conservation status: Critically Endangered.

81. ***Espeletia tillettii*** Cuatrec., Phytologia 47(1): 8. 1980. TYPE: VENEZUELA. Zulia: Distrito Maracaibo, Campamento "Monte Viruela," on tepui-like limestone massif 5 x 2.5 km, on international boundary, Sierra de Perijá, Serranía de Valledupar, ca. 3100 masl, 10˚25'13"N, 72˚52'42"W, 21–28 July 1974, *S. Tillett 747-1126* (Holotype: US; Isotypes: US, VEN [not seen]).

Distribution: VENEZUELA. Perijá (*S. Tillett 747-1126*, US). *Espeletia tillettii* is likely to be found on the Colombian side of Perijá.

Known only from the type specimen. The validity of this species needs to be reviewed.

Conservation status: Not Evaluated.

82. ***Espeletia trianae*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 18. 1942. TYPE: COLOMBIA. Norte de Santander: Páramos de Pamplona, 3000 masl, June 1851, *J. Triana 2476–5* (Holotype: COL; Isotypes: P).

Homotypic synonym: *Espeletiopsis trianae* (Cuatrec.) Cuatrec., Phytologia 35(1): 56. 1976.

Distribution: COLOMBIA. Jurisdicciones-Santurbán (*J. Triana 2476–5*, COL).

Known only from the type specimen. The validity of this species needs to be reviewed.

Conservation status: Data Deficient.

83. ***Espeletia tunjana*** Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 433. 1940. TYPE: COLOMBIA. Boyacá: Páramo de Santa Rosa, entre Santa Rosa y Cerinza, El Portachuelo, 3000 masl, 3 August 1940, *J. Cuatrecasas 10338* (Lectotype: COL; Isolectotype: F, US).

Heterotypic synonym: *Espeletia tunjana* Cuatrec. f. *reducta* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 433. 1940. TYPE: COLOMBIA. Boyacá: Páramos de Tunja, 3100 masl, 5 August 1940, *J. Cuatrecasas 10445* (Holotype: US; Isotype: COL).

Nom. Illeg.: *Espeletia tunjana* Cuatrec. f. *magnificens* Cuatrec., Revista Acad. Colomb. Ci. Exact. 3(12): 433. 1940.

Distribution: COLOMBIA. Guantiva–La Rusia (*J. Cuatrecasas & R. Jaramillo-Mejía 28714*, US), Tota-Bijagual-Mamapacha (*X. Londoño & F. O. Zuluaga 443*, US), Iguaque-Merchán (*G. Huertas & L. Camargo 6306*, US).

Conservation status: Endangered.

84. ***Espeletia uribei*** Cuatrec., Mutisia 16: 1. 1953. TYPE: COLOMBIA. Cundinamarca: Municipio de La Calera, Páramo de Siberia, 3500 masl, 25 October 1952, *L. Uribe-Uribe 2475* (Holotype: F; Isotypes: BC, COL, LP [not seen]).

Distribution: COLOMBIA. Chingaza (*A. M. Cleef 5120*, US).

Conservation status: Least Concern. According to IUCN data, this species has Extent of Occurrence (EOO) = 582 km^2, with all known localities distributed in the Chingaza complex. The species can be locally abundant, and most of its known populations are found within protected areas. However, its relatively small distribution concentrated within a single páramo unit indicates that species would very likely need to be reclassified in the Near Threatened or Vulnerable categories.

Hybrid Taxa

H1. *Espeletia* × *garcibarrigae* Cuatrec. (= *Espeletia argentea* Bonpl. f. *phaneractis* (S.F. Blake) Cuatrec. × *E. grandiflora* Bonpl.), Revista Acad. Colomb. Ci. Exact. 3(12): 426. 1940. TYPE: COLOMBIA. Cundinamarca: Páramo de Guasca, 3000–3500 masl, 11 October 1939, *H. García-Barriga 08108* (Holotype: COL). Cuatrecasas suggested the hybrid combination in the original publication. Hybrid status in Diazgranados (2012).

H2. *Espeletia* × *pachoana* Cuatrec. (= *Espeletia argentea* Bonpl. f. *phaneractis* (S.F. Blake) Cuatrec. × *E. grandiflora* Bonpl.), Revista Acad. Colomb. Ci. Exact. 4(14): 165. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Zipaquirá, entre Zipaquirá y Pacho, 3100–3200 masl, 16 June 1940, *J. Cuatrecasas 9563* (Holotype: COL; Isotypes: F, US). Hybrid status in the original publication.

Heterotypic synonym: *Espeletia* × *pachoana* Cuatrec. f. *brevifolia* Cuatrec. (= *Espeletia argentea* Bonpl. f. *phaneractis* (S.F. Blake) Cuatrec. × *E. grandiflora* Bonpl.), Revista Acad. Colomb. Ci. Exact. 4(14): 166. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Zipaquirá, entre Zipaquirá y Pacho, 3100–3200 masl, 16 June 1940, *J. Cuatrecasas 9561* (Holotype: COL; Isotype: US). Hybrid status in the original publication.

H3. *Espeletia* × *verdeana* Cuatrec. (= *Espeletia argentea* Bonpl. × *E. grandiflora* Bonpl.), Revista Acad. Colomb. Ci. Exact. 4(14): 166. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Cruz Verde, 3400–3500 masl, 15 September 1940, *J. Cuatrecasas 10477* (Holotype: COL; Isotypes: F, US). Hybrid status in the original publication.

H4. *Espeletia* × *guascensis* Cuatrec. (= *Espeletia argentea* Bonpl. f. *phaneractis* (S.F. Blake) Cuatrec. × *E. killipii* Cuatrec.), Revista Acad. Colomb. Ci. Exact. 4(14): 166. 1941. TYPE: COLOMBIA. Cundinamarca: Páramo de Guasca, 3200–3300 masl, 2 June 1940, *J. Cuatrecasas 9493* (Holotype: COL; Isotypes: BC, F, US). Hybrid status in the original publication.

H5. *Espeletia* × *conglomerata* A.C. Sm. var. *macroclada* Cuatrec. (= *E. brassicoidea* Cuatrec. × *Espeletia conglomerata* Cuatrec.), Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942. TYPE. COLOMBIA: Santander: Páramo del Almorzadero, northern slopes, 3600–3800 masl, 28 November 1941, *J. Cuatrecasas 13494A* (Holotype: COL; Isotypes: BC, F, US). Hybrid status in Cuatrecasas (2013).

H6. *Espeletia* × *conglomerata* A.C. Sm. var. *pedunculata* Cuatrec. (= *E. brassicoidea* Cuatrec. × *Espeletia conglomerata* Cuatrec. Revista Acad. Colomb. Ci. Exact. 5(17): 23. 1942. TYPE. COLOMBIA: Santander: Páramo del Almorzadero, eastern slopes, 3600–3800 m, 28 November 1941, *J. Cuatrecasas 13494* (Holotype: COL; Isotypes: BC, F, US). Hybrid status in Cuatrecasas (2013).

H7. *Espeletia* × *almorzana* Cuatrec. (=*Espeletia sclerophylla* Cuatrec. × *Espeletia petiolata* Cuatrec.), Revista Acad. Colomb. Ci. Exact. 4(14): 340. 1941. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, región media, 3500 masl, 20 July 1940, *J. Cuatrecasas & H. García-Barriga 9987* (Holotype: US). Hybrid status in the original publication.

Homotypic synonym: *Espeletiopsis* × *almorzana* (Cuatrec.) Diazgr., Phytokeys 16: 34. (2012).

Heterotypic synonym: *Espeletia* × *almorzana* Cuatrec. f. *latifolia* Cuatrec., Revista Acad. Colomb. Ci. Exact. 5(17): 22. 1942 [**1**]. TYPE: COLOMBIA. Santander: Páramo del Almorzadero, vertiente norte, 3600–3800 masl, 28 November 1941, *J. Cuatrecasas 13503* (Holotype: COL). Hybrid status in the original publication.

[**1**]: Reference given as "Revista Acad. Colomb. Ci. Exact. 4(14): 340. 1941" in Diazgranados (2012).

H8. *Espeletia* × *bogotensis* Cuatrec. (= *Espeletia corymbosa* Bonpl. × *Espeletia grandiflora* Bonpl.), Revista Acad. Colomb. Ci. Exact. 3(12): 427. 1940. TYPE: COLOMBIA. Cundinamarca: Macizo de Bogota en Cerro de Monserrate, vert. oriental, 3000 masl, 28 January 1940, *J. Cuatrecasas 7998* (Holotype: COL; Isotypes: COL, US). Hybrid status in the original publication.

Homotypic synonym: *Espeletiopsis* × *bogotensis* (Cuatrec.) Cuatrec., Phytologia 35(1): 55 (1976).

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LEAF VENATION OF BRAZILIAN SPECIES OF *CRYPTOCARYA* R. BR. (LAURACEAE)

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Abstract. With the aim of recognizing and identifying both fertile and sterile specimens of *Cryptocarya* from Brazil, we analyzed the leaf venation pattern of 14 taxa, 6 of them being described and illustrated for the first time. A dichotomous identification key was built from a matrix of 12 leaf venation characters and 30 character states, which distinguishes among taxa.

Keywords: Laurales, leaf venation, morphology, Neotropics, taxonomy

The genus *Cryptocarya* (Lauraceae) was described by Robert Brown (1810: 402), with three species from Australia: *C. glaucescens* R. Br., *C. obovata* R. Br., and *C. triplinervis* R. Br., of which Kostermans (1939: 112) designated *C. glaucescens* as lectotype. It is a pantropical genus of monoecious trees, present in Central and South America, East Africa (Tanzania, Zimbabwe, Malawi, Mozambique), South Africa, Madagascar, Asia, Australia, and Oceania (van der Werff, 1992; Rohwer, 1993; Diniz, 1996; Moraes, 2007; Moraes and van der Werff, 2010). The number of known species is uncertain, since the genus has never been revised in full (de Kok, 2015, 2016). Regardless, some estimates have been proposed, but they are inconsistent among authors: a more conservative one ranges from 200 to 250 species, which is the one most usually cited (e.g., Kostermans, 1957b, 1995; Vattimo-Gil, 1966, 1979; Klucking, 1987; Mabberley, 1987; Rohwer and Richter, 1987; Hyland, 1989; Tressens, 1997; Le Cussan et al., 2007; Li Xiwen et al., 2008; Cooper, 2013; de Kok, 2015, 2016), whereas more liberal ones assume ca. 300 (e.g., Mabberley, 2017; Fasila et al., 2020), more than 300 (e.g., van der Werff, 2001; Gangopadhyay and Chakrabarty, 2005; Nishida et al., 2016), 300–350 (Moraes, 2007), 250–350 (Carter, 2017), or ca. 350 species (Kostermans, 1974; Rohwer, 1993; Moraes et al., 2007; van der Werff, 2008; Moraes and van der Werff, 2010; Morden et al., 2015; Munzinger and McPherson, 2016; Moraes and Vergne, 2018), the latter considered to be too high (Rohwer et al., 2014; Morden et al., 2015; van der Merwe et al., 2016). Several of the previous estimates did not consider another 30 Malagasy species originally named under *Ravensara* Sonnerat (1782), the latter being sunk in synonymy of *Cryptocarya* (see Kostermans, 1958; van der Werff, 1992, 2008, 2013, 2017; Rohwer et al., 2014; Kottaimuthu and Rajendran, 2018). This difference in estimates of about 100 species may reflect different opinions on the more than 500 specific binomials of *Cryptocarya* enumerated in Index Kewensis (e.g., Kostermans, 1937, 1964, 1968, 1990; Vattimo-Gil, 1966; Frodin, 1976; Kochummen, 1989; Ng, 2005; Moraes, 2007; de Kok, 2016), since there is no list of currently accepted names encompassing the homotypic and heterotypic synonyms. Therefore, *Cryptocarya* is in need of a comprehensive taxonomic revision (Rohwer, 1993; van der Werff, 2017). However, its large size and widespread distribution make revision of the genus difficult to accomplish, being beyond the scope of most botanists.

The increase in knowledge of *Cryptocarya* diversity over the last 210 years can be summarized as follows: in *Systema laurinarum*, the first general monograph of all known Lauraceae, Nees von Esenbeck (1836) recognized 13 species, of which 7 are currently accepted, 4 are heterotypic synonyms, and 2 belong to other genera. In Meissner's treatment (1864), the second complete monograph of the family, 37 species were recognized, of which currently 25 are accepted, 7 are heterotypic synonyms, and 5 belong to other genera; in addition, 3 species listed in *species exclusæ* are also currently accepted, thus totalling 28 species. Gamble (1912) reported ca. 40 species, Lecomte (1914) ca. 55 species, and Liou (1932) ca. 173 species. Kostermans (1957b) noted the existence of 303 (318) binomials, whereas in 1964 he listed 327 binomials (with several homonyms), from the literature through 1962. At present, the Tropicos database lists 519 taxa, whereas 544 are listed in the International Plant Name Index (IPNI) database.

There are several modern regional treatments (or accounts) of the genus, which help in understanding its variability and distribution and also provide evidence of a relatively high level of endemism for most of the analyzed regions and territories: 48 Australian species are accepted (Hyland, 1989; Le Cussan et al., 2007; Cooper, 2013), of which 39–40 (81–83%) are considered to be endemic; 21 species are recognized from the Indian subcontinent (Gangopadhyay and Chakrabarty, 2005; Gangopadhyay, 2006, 2008; Bachan et al., 2018; Fasila et al., 2020), of

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which 16 (76%) are considered to be endemic; 21 Chinese taxa have been revised by Li Xiwen et al. (2008), of which 15 (71%) are considered to be endemic; 22 endemic species (100%) are recognized from New Caledonia (Morat et al., 2012; Munzinger and McPherson, 2016); 17 species have been recognized from Thailand and Indochina (Laos, Cambodia, and Vietnam), with 14 recorded (3 endemic) from Thailand, 10 (1 endemic) from Vietnam, 8 from Laos, and 5 from Cambodia, of which 7 species (41%) are endemic for the region as a whole (de Kok, 2015; Zhang et al., 2020); among the 17 taxa currently recognized from Peninsular Malaysia, only three (18%) are endemic (de Kok, 2016); about 40 Malagasy species are recognized, of which 39 (97%) are endemic (van der Werff, 2017); and 31 species are recognized from the Philippines, of which 16 (52%) are endemic (Collantes and Pelser, 2020).

In his monograph on the American Lauraceae, Mez (1889) recognized 9 species of *Cryptocarya*. He accepted all species treated by Meissner except *C. dubia* Kunth [= *Aiouea dubia* (Kunth) Mez] and *C. emarginata* [= *Beilschmiedia emarginata* (Meisn.) Mez]. He also described *C. aschersoniana* Mez and *C. saligna* Mez, and reduced *Aydendron floribundum* Meisn. to the synonymy of *C. minima* Mez. Later, Mez (1892, 1893, 1902, 1907) and described another five Brazilian taxa as new: *Cryptocarya hypoleuca* Mez, *C. longistyla* Mez, *C. minutiflora* Mez, *C. schwackeana* Mez, and *C. subcorymbosa* Mez. Kostermans (1937) revised the American species and recognized 7 of them, including the Chilean *C. alba* (Molina) Looser [= *C. rubra* (Molina) Skeels]. More recently, Moraes (2005b) lectotypified the names of Brazilian *Cryptocarya*, accepting 8 species, which were further revised by Moraes (2007), then recognizing 13 species, 5 of them being newly described and 11 being endemic (85%). Another 2 species were described by Moraes and van der Werff (2010), increasing to 16 the number of currently accepted species to the Americas. Furthermore, extra Brazilian specimens collected in Costa Rica, Ecuador, Peru, Venezuela, and Bolivia likely represent undescribed species, but they still lack flowering herbarium material for a proper description (Moraes, 2007; Moraes and van der Werff, 2010).

Cryptocarya can be easily distinguished from other laurel genera by its bisexual and invariably trimerous flowers, which are very typical in shape, with six equal to subequal tepals, nine fertile stamens with disporangiate anthers, staminal glands only in the third androecial whorl, three relatively big cordate to sagittate staminodes, a usually slender, deeply urceolate, apically narrowed receptacular tube and immersed ovary. Its characteristic fruit is completely enclosed in the receptacular tissue and appears to be inferior, hence its etymology: from Greek *κρυπτός*, "kruptós," hidden, and *κάρυον*, "káruon," nut, that is, the fruit is covered by the accrescent flower tube (Kostermans, 1957b; Ng, 2005; Moraes, 2007; Nishida et al., 2016). Its leaves generally do not bear domatia, which are only found in a few Australian and Papuasian species (e.g., *C. alleniana* C.T. White, *C. erythroxylon* Maiden & Betche ex Maiden, *C. foveolata* C.T. White & Francis, *C. rigida* Meisn., and *C. triplinervis*; Brouwer and Clifford, 1990). It is placed in tribe Cryptocaryeae Nees sensu van der Werff and Richter (1996), as bearing "paniculate-± cymose inflorescences," or as "paniculate" in van der Werff (2001); however, according to Endress and Lorence (2020), botryoids, thyrsoids, and compound botryoids and thyrsoids are the most common forms. This tribe is also known as the *Cryptocarya* group (Rohwer, 1993), which was first recognized by Richter (1981) on the basis of wood and bark anatomy and which currently encompasses the genera *Aspidostemon* Rohwer & H.G. Richt., *Beilschmiedia* Nees, *Endiandra* R.Br., *Eusideroxylon* Teijsm. & Binn., *Dahlgrenodendron* J.J.M. van der Merwe & A.E. van Wyk, *Potameia* Thouars, *Potoxylon* Kosterm., *Sinopora* J. Li, N.H. Xia & H.W. Li, *Triadodaphne* Kosterm., and *Yasunia* van der Werff (Chanderbali et al., 2001; Rohwer et al., 2014; Rohwer, 2017).

A molecular phylogenetic study by Rohwer et al. (2014) supported the monophyly of *Cryptocarya*, although based on only 20 species sampled from the genus. Within *Cryptocarya*, their results showed a split between a group comprising *C. alba*, *C. oubatchensis* Schltr. (see below), and *C. pluricostata* Kosterm. (the latter two from New Caledonia) and all the remaining species. Among the latter, three major well-supported clades were retrieved: the Asian-Australian clade, the southeastern Brazilian (including all Brazilian *Cryptocarya* species investigated, *C.* aff. *aschersoniana* Mez, *C. botelhensis* P.L.R. Moraes, *C. citriformis* [Vell.] P.L.R. Moraes, *C. mandioccana* Meisn., *C. moschata* Nees & Mart., *C. saligna* Mez, and *C. wiedensis* P.L.R. Moraes), and the two Malagasy species, *C. subtriplinervia* (Kosterm.) van der Werff and *Ravensara elliptica* Kosterm. (≡ *Cryptocarya rigidifolia* van der Werff). Therefore, the origin of *C. alba* has been shown to be different from that of the other South American species, indicating two independent colonization events. In the phylogenetic study by van der Merwe et al. (2016), which was focused on Australian species, *C. alba* was found as sister to five Australian species not included in Rohwer's study (*C. erythroxylon*, *C. oblata* F.M. Bailey, *C. onoprienkoana* B. Hyland, *C. rhodosperma* B. Hyland, and *C. rigida*), thus indicating that this lineage is present also in Australia. Moreover, the phylogenetic study by Carter (2017), focused on New Caledonian species, indicated that at least another New Caledonian species, *C. aristata* Kosterm., would belong to that lineage. However, Carter's work also suggests the possibility that the sample of *C. oubatchensis* used by Rohwer et al. (2014; and later by Morden et al., 2015), *McPherson 19131* (MO-398160; as determined by the collector in 2004), actually belongs to *C. aristata*, or is closely related to it, as determined by J. Munzinger & G. McPherson in March 2018 on a duplicate at the Paris Herbarium (P02033187). Another sample of *C. oubatchensis* used by Carter (2017), *Munzinger 7078* (MPU026704, NOU082910, P00806970), formed a strongly supported clade with *C. phyllostemon* Kosterm., which in turn was sister to a clade formed by *C. chinensis* (Hance) Hemsl. and *C. densiflora* Blume., which all together were sister to a clade formed by *C. subtriplinervia* and *Ravensara elliptica*.

As pointed out by van der Merwe et al. (2016), although molecular phylogenies have supported the monophyly of the Cryptocaryeae and the genus *Cryptocarya*, there has been little success in finding morphological characters that can elucidate subgeneric or species-level relationships (Chanderbali et al., 2001; Rohwer et al., 2014). With regard to the Australian *Cryptocarya*, two attempts to arrange species into morphologically distinguishable groups have been made by Hyland (1989) and by Christophel and Rowett (1996), who evaluated relationships among species on the basis of morphological similarity. However, the molecular phylogenetic study by van der Merwe et al. (2016) has shown that just a few of Hyland's (1989) morphology-based groups reflected the phylogenetic relationships, whereas none of the groups proposed by Christophel and Rowett (1996), based on leaf and epidermal characters, has been congruent with the evolutionary relationships assessed by molecular data. For instance, *Cryptocarya* species with triplinerved leaves, which is a much smaller group than the one having pinnately veined leaves (the great majority), have a convergent origin as evidenced for *C. densiflora*, *C. subtriplinervia*, and *C. triplinervis* (Rohwer et al., 2014; Carter, 2017) and reinforced by van der Merwe et al. (2016), as exemplified by the placement of *C. grandis* B. Hyland, *C. pleurosperma* C.T. White & Francis, and *C. triplinervis*, which did not form a clade. Nevertheless, de Kok (2016) assembled the *Cryptocarya* species of Peninsular Malaysia in three groups on the basis of a single morphological character (i.e., leaf venation: pinnate vs. acrodromous) and their geographical distribution. The first two groupings comprise (i) a bigger group of species with pinnately veined leaves and (ii) a smaller group of species with triplinerved leaves (i.e., *C. densiflora*, *C. laevigata* Blume, and *C. wrayi* Gamble).

As for the Brazilian *Cryptocarya*, Moraes (2007) was unable to arrange species into morphologically clearly distinguishable groups (de Kok, 2016; Nishida et al., 2016), because of their morphological homogeneity. Regardless, Moraes (2005a) evaluated isozymic data in combination with morphological criteria for classifying Brazilian species of *Cryptocarya*. Through the analysis of 19 enzyme systems, 41 putative isozyme loci (polymorphic in at least one population), 124 alleles were recorded from 739 adult trees of 35 natural populations of 10 species of *Cryptocarya* native to the southeastern Atlantic rain forest. Results demonstrated that discriminant analysis of isozymic data can be used for efficient marker-based allocation of individual trees into predefined groups of populations and species of *Cryptocarya*, complementing and/or confirming information obtained from traditional taxonomic studies; as pointed out by Moraes (2007), unsupervised classification through cluster analysis revealed that *C. mandioccana* and *C. moschata*, as well as *C. citriformis* and *C. saligna*, are closely related species, corroborating morphological evidence and a former indication by Moraes et al. (2002).

Despite the apparent morphological uniformity of Brazilian *Cryptocarya*, which makes their circumscription a difficult task, particularly because of the lack of exclusive diagnostic characters, several studies have demonstrated their diversity and variability through characters other than those traditionally used. For instance, Flörsheim and Barbosa (1983–1985) studied the wood anatomy of samples of *Cryptocarya aschersoniana*, *C. mandioccana*, *C. moschata*, and *C. saligna* collected at Serra da Cantareira, São Paulo. Whether or not the variability they found, among the three different taxa considered (*C. aschersoniana*, *C. mandioccana*, and *C. moschata*, which may actually represent just *C. mandioccana*), was caused by adaptive responses to different environment conditions and/or by different cambial age is a matter awaiting further evaluation. Moraes and Alves (2002) studied the biometry of mature fruits of *C. mandioccana* ($N = 1892$, from 27 trees of 1 population) and *C. moschata* ($N = 1487$, from 37 trees of 11 populations). Despite their differences in shapes and sizes, fruits of *C. moschata* showed a tendency to positive allometry, that is, greater increase of the equatorial radius than of the polar radius when increasing in size, whereas fruits of *C. mandioccana* from all trees investigated have shown a tendency to isometry, that is, a constancy of shape for both small and large fruits. For 12 natural populations (267 individuals) of *C. moschata*, genetic structure, differentiation, and diversity were determined by Moraes and Derbyshire (2002, 2003) by analyzing 39 polymorphic isozyme loci. Those results indicated that individuals within populations might be panmitic and that the diversity among populations was fairly high, being superior to what would be expected for groups of plants having a full-sib family structure, suggesting the existence of significant genetic drift and/or natural selection effects between populations. The within-sample gene diversity accounted for 66.12% of overall gene diversity, indicating a greater variability occurring within populations than among them. Similarly, Moraes and Derbyshire (2004) published results of the genetic structure of 11 natural populations (335 individuals) of *C. mandioccana* from southeastern Brazilian Atlantic rain forest. Results indicated that individuals within populations must be panmitic and that the diversity among populations is fairly high, being superior to what would be expected for groups of plants having a full-sib family structure in a single generation. In addition, the pronounced populational differentiation might be more related to drift and founder effects than to selection.

Phytochemical studies are another important source of information for around 40 *Cryptocarya* species, which have isolated and provided structural identification of more than 140 secondary metabolites. With regard to the Brazilian species, studies were conducted on *C. botelhensis*, *C. mandioccana*, *C. moschata*, and *C. saligna* and included intraspecific variability of secondary metabolites from *C. mandioccana* and *C. moschata*. In earlier phytochemical investigations of the essential oils of these species, the presence of linalool was reported in leaf oil of *C. moschata* and *C. aschersoniana* (current status: *C. mandioccana* and *C. moschata*, respectively; Moraes, 2005b), although the latter also contained β-myrcene, 1,8-cineol, and stereoisomeric linalool oxides (Naves et al., 1963). Detailed composition of essential oil from leaves of *C. mandioccana* has been determined by Telascrea et al. (2007), yielding the identification of 64 compounds with a predominance of isomeric sesquiterpenes with molecular weight of 204. The intraspecific chemical variability of essential oil obtained by steam distillation was evaluated within populations of trees growing at three separate locations in the state of São Paulo, Brazil. Three distinct chemical groups could be characterized on the basis of differences in the relative percentages of the three main sesquiterpenes from essential oil: CGB, BCG, and GCB (i.e., with a predominance of β-caryophyllene [C], germacrene-D [G], and bicyclogermacrene [B], respectively). Individuals from groups CGB and BCG were found more frequently in southern locations, while group GCB, with a predominance of germacrene, occurred more frequently in the northern region of the Atlantic rain forest. A comparison of essential oils from leaves of four species of *Cryptocarya* was reported by Telascrea et al. (2008). Monoterpenes were found to be the main constituents of essential oils from *C. moschata* and *C. botelhensis,* with a predominance of acyclic and menthane monoterpene skeletons in the former and pinane monoterpene skeletons in the latter. However, the major sesquiterpenes identified in essential oil from leaves of *C. mandioccana* belong to two main classes, from distinct sesquiterpene synthases, each associated with a different mode of cyclization of the C15-precursor, while the main constituents of essential oil from *C. saligna* were formed by C1-C11 cyclization, which is indicative of a preferential cyclization way of farnesyl diphosphate precursor in this species.

Phytochemical studies of the bark of *Cryptocarya mandioccana* have shown that styrylpyrones are the typical secondary metabolites present in this species (Cavalheiro and Yoshida, 2000), whereas flavonoid glycosides, as well as styrylpyrones, have been detected in leaves and fruits. The qualitative and quantitative intraspecific variability of these secondary metabolites has been determined by Nehme at al. (2002). A more detailed study on the polar chemical variability of flavonoids and styrylpyrones was undertaken by Nehme et al. (2008), who analyzed leaves of 57 trees of *C. mandioccana* from three sites of Atlantic rain forest in São Paulo state. The flavonoid glycosides profiles were very conservative in all individuals, with a predominance of quercetin. In addition, four chemotypes were recognized by qualitative and quantitative differences in the styrylpyrone composition. Chemotype F could be characterized by a predominance of flavonoid glycosides (F1–F6) and low content of styrylpyrones. Chemotypes FS1, FS2, and FS3 each presented at least one intense peak attributed to styrylpyrones, while differing from each other in the number of acetate units in their polyketides: in chemotype FS1, the most intense peak was attributed to deacetylcryptocaryalactone (S5); in chemotype FS2 there were three intense styrylpyrone peaks, which were attributed to cryptomoschatone E3 (S1), cryptomoschatone F1 (S4), and cryptomoschatone E1 (S6); and in chemotype FS3, the most intense peak was attributed to cryptomoschatone D1 (S2). The distribution of these chemotypes revealed inter- and intrapopulational chemical variability, with a predominance of trees with higher levels of styrylpyrones in southern regions with soils of higher K^+, Ca^{2+}, and Mg^{2+} content. The northern population of Ubatuba showed trees with a clear predominance of flavonoids (chemotype F) and a good correlation with lower levels of Mg^{2+}, K^+ and Ca^{2+}, suggesting some possible influence of soil nutrients on styrylpyrone profiles of *C. mandioccana*. However, evidence that chemical variability would also be under genetic control has been provided by some pairs of trees that presented different chemical profiles, in spite of being located just a few meters apart from each other. Moreover, the genetic studies by Moraes and Derbyshire (2004) and Moraes et al. (2007) have demonstrated that individuals of *C. madioccana* from different populations formed distinct genetic groups (among them the north and south groups) closely related to geographical origin. Furthermore, locus Skdh-2 was significantly related to production of quercetin-3-*O*-β-D-glucopyranoside (F2) and the diastereoisomers cryptofolione and cryptomoschatone E2 (S6/S7), indicating that shikimate dehydrogenase could affect differential regulation on these chemotypes of *C. mandioccana*. Moraes and Derbyshire (2004) have shown relatively weak genetic differentiation among large areas of sampled populations, which indicated no significant differences in genetic structure among different regions. Since the greatest environmental differences are related to the different regions, it is probable that selective differences were of little or no importance and that the fixation indexes were essentially measures of random drift due to endogamous mating in populations, and probably accidental differences in the founding individuals among the populations (Wahlund effect), which are largely smoothed out in the regions.

According to Wilf et al. (2016), understanding the extremely variable and complex angiosperm leaf architecture (shape and venation characters) is one of the most challenging problems in botany. Nevertheless, leaf features of the Lauraceae have long been reported and demonstrated to be helpful for identification of taxa, being used as taxonomic descriptors (Christophel and Rowett, 1996). This type of information is relatively scarce for the Brazilian species of the family, however, and therefore for the species of *Cryptocarya*.

Data on leaf venation of *Cryptocarya* species can be found in treatments of local floras or florulas, being usually restricted to information on the venation pattern of secondary veins and the "number of pairs of secondaries." Concerning the species treated here, such information has been recorded by Vattimo-Gil (1957) for collections from Monte Sinai and by Quinet and Andreata (2002) for collections from Nova Friburgo, Rio de Janeiro state; Pedralli (1987) for collections from Rio Grande do Sul state; Brotto et al. (2009) for collections from Paraná state; Gomes-Bezerra et al. (2011), for collections of the Federal District (Brasília); Barbosa et al. (2012), for collections from Santa Teresa, Espírito Santo state; and Poszkus Borrero et al. (2016), for collections from Misiones, Argentina. From these reports, it is possible to verify how constant these features are across a wider geographical range for each species and in different populations and/or environments.

Material and Methods

This study is based on the Brazilian species of *Cryptocarya* recognized in Moraes (2007), where a more detailed account on the species and specimens analyzed can be consulted. In that publication, narrow species concepts were used in order to maintain the boundaries among species. Nevertheless, in the particular case of *C. aschersoniana*, Moraes's concept has been more inclusive, since he had not evaluated in the field all the variability detected in herbarium collections, especially from the south of Brazil. Here, we kept discriminating specimens of the "true" *C. aschersoniana* from southern Brazil, Uruguay, and Argentina, from those determined by Moraes (2007) as *C.* aff. *aschersoniana* from some populations of São Paulo state (e.g., Base Ecológica da Serra do Japi [*Moraes 2243*] and Parque Estadual de Campos do Jordão [*Moraes 2403*, *Robim 588*]) and from Espírito Santo state (e.g., Linhares [*Moraes 2543*] and Santa Teresa [*Moraes 3242*]). Whenever available, herbarium leaf samples of at least four specimens of each species were used for this study, which are listed in Table 1. Most specimens are deposited in herbarium HRCB, and just a few are from samples taken from ALCB, CEPEC, HUEFS, MG, MO, NY, and RB (acronyms according to Thiers, 2020 [continuously updated]).

For description of basic venation patterns—that is, the major secondary vein framework—samples of entire leaves of all *Cryptocarya* species from Brazil were digitally X-rayed in a Faxitron® LX-60 cabinet X-ray system coupled to a computer with the software Faxitron DX version 1.0, where the images were captured using an X-ray exposure time of 19 seconds at a voltage of 30 kV. For illustration and description of the reticulation, closed-up images of the former leaves were captured with a magnification of about 10x by placing the leaves very close to the X-ray source.

For description of minor venation patterns—that is, the patterns of higher-order veins, areolations, and veinlets—we employed the following clearing technique. Leaf samples of 1 cm^2 were taken from the middle part of the lamina of mature leaves. To rehydrate the herbarized, dry leaf, the samples were boiled in water for about 10 min. Afterward, samples were soaked in a 20% solution of NaOH at room

Table 1. *Cryptocarya* species and voucher specimens analyzed in this study.

Species[a]	Voucher[b]
C. aff. *aschersoniana* Mez	*Moraes 2243, 2403* (HRCB)/SP, *Moraes 2543, 2544, 3242, 3696, 3735* (HRCB)/ES, *Robim 588* (HRCB)/SP
C. aschersoniana Mez	*Brotto 2547, 2550* (HRCB)/PR, *Klein 3187* (HRCB)/SC, *Moraes 2295, 2297* (HRCB)/SP, *Moraes 5362* (HRCB)/RS, *Moraes 5402* (HRCB)/PR
C. botelhensis P.L.R. Moraes	*Moraes 1252, 1254, 1264, 3349* (HRCB)/SP
C. citriformis (Vell.) P.L.R. Moraes	*Barreto 1784* (HRCB)/MG, *Folli 320, 6123* (HRCB)/ES, *Moraes 2154, 2456* (HRCB)/RJ, *Moraes 3199, 3712, 3746* (HRCB)/ES, *Paixão 17* (CEPEC)/BA
C. guianensis Meisn.	*Bondar 65* (RB)/BA, *Goulding 1117 (MG)/RO, Jardim 1263* (MO)/BA, *Pires s.n.* (NY 51511)/AP, *Prance 25443* (MG)/PA, *Thomas 4752* (MG)/MT
C. mandioccana Meisn.	*Moraes 2505, 4099* (HRCB)/SP, *Moraes 3509* (HRCB)/MG, *Santos 2811* (CEPEC)/BA
C. micrantha Meisn.	*Moraes 2155, 2458, 2468, 2469* (HRCB)/RJ, *Moraes 2449* (HRCB)/SP
C. moschata Nees & Mart.	*Bertoni 425* (HRCB)/SP, *Hoehne s.n.* (MO 3600631)/SP, *Moraes 2237, 2257, 2259, 2264, 3491* (HRCB)/SP, *Moraes 2277* (HRCB)/MG, *Pereira PCD 1753* (CEPEC)/BA
C. riedeliana P.L.R. Moraes	*Braga s.n.* (RB 358589)/RJ, *Farias 80* (RB)/RJ, *Jardim 2104* (ALCB)/BA, *Kollmann 4413* (HRCB)/ES, *Moraes 3126* (HRCB)/BA, *Moraes 4716* (HRCB)/ES
C. saligna Mez	*Folli 88* (ESA)/ES, *Magnago 1471* (HRCB)/ES, *Moraes 3182, 3226, 3682* (HRCB)/ES
C. sellowiana P.L.R. Moraes	*Luz 196* (HRCB)/MG
C. subcorymbosa Mez	*Moraes 5161* (HRCB)/SP
C. velloziana P.L.R. Moraes	*Braga s.n.* (RB 358585)/RJ, *Lombardi 7150* (HRCB)/BA, *Lombardi 8950* (HRCB)/MG, *Moraes 2621* (HUEFS)/ES, *Moraes 3227* (HRCB)/ES
C. wiedensis P.L.R. Moraes	*Kollmann 2464* (HRCB)/ES

a) Species determination by the first author, according to Moraes (2007).

b) Samples from vouchers deposited in several herbaria, acronyms indicated in parentheses, followed by abbreviations of Brazilian states: AP, Amapá; BA, Bahia; ES, Espírito Santo; MG, Minas Gerais; MT, Mato Grosso; PA, Pará; PR, Paraná; RJ, Rio de Janeiro; RO, Rondônia; RS, Rio Grande do Sul; SC, Santa Catarina; SP, São Paulo.

temperature for 12–24 hours, then rinsed three times with tap water. The samples were decolorized with household bleach (50%) for 12 hours, then thoroughly washed (3 times) with distilled water. Dehydration of the cleared samples was done in alcohol series before staining them in 1% safranin in 50% ethanol for 1 min. They were mounted on microscope slides in Entellan.® Photomicrographs were obtained with a photomicroscope (Leica DM500) coupled with a camera (Leica ICC50), using the software LAS (Leica Application Suite) EZ v.3.0.0.

An interactive multiple-entry key was created using the program *Lucid* 3 v3.5 (https://www.lucidcentral.org/), based on a matrix of 12 leaf venation characters, with a total of 30 states and 14 taxa (Table 2). A dichotomous key was built from this matrix.

Terminology

Two basic venation patterns occur within the Lauraceae (Christophel and Rowett, 1996): (1) pinnate (Hickey, 1973, 1979; Dilcher, 1974) or penninerved (Hyland, 1989), in which there is a central midvein (primary vein) from which arise lateral veins; and (2) acrodromous (Hickey, 1973, 1979; Dilcher, 1974) or triplinerved (Hyland, 1989), in which a basal pair of veins is strengthened to the point of being similar in size to the midvein. For convenience of comparison with other works on the Lauraceae, we have used Hyland's terminology. The nature of the midvein course can be monopodial, where its trunk is not deflected by lateral veins, or sympodial, where the midvein axis is deflected at each branch point (Ellis et al., 2009).

For the pattern of secondary veins, Hickey's classification (1973, 1979) is adopted here. For Lauraceae leaves, the relevant categories include (1) brochidodromous, in which the secondaries join together in a series of prominent arches; and (2) eucamptodromous, in which the secondaries are upturned, gradually diminish apically inside the margin, and are connected to the superadjacent secondaries by a series of cross veins without forming prominent marginal loops. Cases in which proximal secondaries are eucamptodromous but distal secondaries form loops of secondary gauge (subcategory "Eucamptodromous becoming brochidodromous distally"; Ellis et al., 2009) are termed here eucamptodromous-brochidodromous. An additional category was described by Pole (1991) and labelled by Christophel and Rowett (1996) as pseudobrochidodromous, in which the leaf appears brochidodromous but the loops are formed by strengthened tertiary veins and not by the secondary veins themselves.

The number of secondary veins per side of the midvein is recorded for each species, rather than the "number of pairs of secondary veins," as some species have different numbers of veins on either side of the midvein; moreover, when counting secondary veins, the apical 10% of the lamina is excluded, since veins there are generally so much smaller as to make determining relative orders difficult (Christophel and Rowett, 1996). The major features of secondary venation proposed by Klucking (1987) are adopted here; we list only the subcategories observed from the analyzed material: (1) the nature of the course of the secondary vein: (a) straight—the secondary vein extends laterally in an essentially straight line; or (b) curved—the secondary vein curves gently apically as it extends laterally from the midvein; (2) the spacing of the secondary veins along the midvein: (a) broad—secondary veins are noticeably spaced more than 1/10 the length of the leaf apart; (b) medium—secondary veins are spaced about 1/10th the length of the leaf apart; or (c) narrow—secondary veins are noticeably less than 1/10th the length of the leaf apart; and (3) the angle between the secondary course and the midvein: (a) high—most of the lateral course of the secondary veins is oriented at 55 degrees or more to the midvein; (b) moderate—most of the lateral course of the secondary veins is oriented at about 45 degrees to the midvein; or (c) low—most of the lateral course of the secondary veins is oriented at 40 degrees or less to the midvein. The angle of secondary courses usually varies from the apex to the base of the leaf, but it is more or less constant in the middle region of the leaf, for each species (Coe-Teixeira, 1980). For this reason, in the present study the angles of secondary courses are recorded from the middle part of the lamina.

Regarding tertiary-order veins, Christophel and Rowett (1996) recognized two major types for the Lauraceae: (1) percurrent, in which the tertiary veins directly connect two adjacent secondary veins; this category can be divided into two further categories: (a) strongly percurrent, having a ladder-like appearance; and (b) weakly percurrent, appearing to meander or arch in their course; and (2) reticulate, in which a pattern of tertiary veins anastomoses with other tertiary or secondary veins and does not directly connect two secondary veins; reticulate tertiary veins can be (a) orthogonal, forming mainly right-angled anastomoses; or (b) random, in which they are either curved or form a variety of anastomoses.

As for higher-order venation patterns, the discriminating character is the number and relative size of vein orders in the reticulum, and the veinlet pattern (Nishida and Christophel, 1999). According to Christophel and Rowett (1996), "veins of leaves keep dividing into smaller, higher orders, until ultimately they form small enclosed areas called areoles which fairly uniformly cover the lamina surface in a pattern often referred to as the reticulum." The areoles themselves are described in terms of (1) development: (a) well developed, forming meshes of relatively consistent size and shape; (b) imperfect, with meshes of irregular shape, more or less variable in size; or (c) incompletely closed meshes, in which one or more sides of the mesh is not bounded by a vein, giving rise to anomalously large meshes of highly irregular shape; (2) arrangement: (a) random, areoles showing no preferred orientation; or (b) oriented, areoles having a similar alignment or pattern of arrangement within blocks or domains; (3) shape: (a) quadrangular, or (b) polygonal, here defined as having more than 4 sides; (4) size: (a) very large, > 2 mm; (b) large, 1–2 mm; (c) medium, 0.3–1.0 mm; or (d) small, < 0.3 mm (Hickey, 1973, 1979; Dilcher, 1974). With regard to the development and size of the areoles, the appearance of the minor venation pattern can be divided into two categories: (1) fine—the highest vein order is sixth or more, and areoles are usually less than 0.5–0.7 mm diam.; and (2) coarse—the highest vein order is less than fifth, with larger areoles over 1.0 mm diam. In Hickey's terminology (1973, 1979), the veinlets

TABLE 2. Leaf venation features of Brazilian *Cryptocarya*.

SPECIES	NUMBER 2RY VEINS	VENATION PATTERN^a	MIDVEIN^b	NATURE 2RY COURSE^c	SPACING 2RY VEINS^d	ANGLE 2RY COURSE^e	3RY VEINS^f	RETICULUM^g	DEVELOPMENT^h	AREOLE SHAPE^i	SIZE^j	VEINLET^k	FIGURE
C. aff. *aschersoniana*	5–12	BRO/PB	MON	STR	BRO/MED	HIG	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/BON	4A–H
C. aschersoniana	5–12	EU-BRO/PB	MON/SYM	STR/CUR	BRO/MED	HIG/MOD	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/BON	1A, 2A, 4I–N
C. botelhensis	4–8	EU-BRO/BRO	MON/SYM	STR/CUR	BRO/MED	HIG/MOD	RET, RAN	FIN	IMP/INC	POL	MED/LAR	BON/BTW/DEN	1B, 2B, 4O–P
C. citriformis	6–9	EU-BRO/PB	MON/SYM	CUR/STR	BRO	HIG/MOD	RET, RAN/ PER, weakly	FIN	WDE	POL/QUA	SMA	ABS/[LIN]	1C, 2C, 4Q–T
C. guianensis	6–12	EU-BRO/ BRO/PB	MON	CUR/STR	BRO	HIG/MOD	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/BON	1D, 2D, 4U–X
C. mandioccana	5–9	EU-BRO	MON/SYM	CUR/STR	BRO/MED	HIG-[LOW]	RET, RAN/ PER, weakly	FIN	WDE/IMP	POL/QUA	SMA	LIN/BON/BTW/DEN	1E, 2E, 4Y–B’
C. micrantha	7–12	EU-BRO/PB	MON/SYM	STR/CUR	BRO-NAR	HIG/MOD	RET, RAN	FIN	IMP/WDE	POL/QUA	MED/SMA	ABS/LIN/BON/BTW/DEN	1F, 2F, 5A–H
C. moschata	5–12	EU-BRO/ BRO/PB	MON/SYM	STR/CUR	BRO/MED	HIG	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN/CUR/BON/BTW	1G, 2G, 5I–L
C. riedeliana	5–11	EU-BRO/PB	MON/SYM	CUR/STR	BRO-NAR	MOD/LOW	RET, RAN	FIN	WDE/IMP	POL/QUA	SMA/MED	LIN/BON/DEN	1H, 2H, 5M–P
C. saligna	4–14	EU-BRO/PB/ BRO	MON/SYM	STR/CUR	BRO/MED	HIG	RET, RAN	FIN	WDE	POL/QUA	MED/SMA	ABS/LIN/BTW/DEN	1I, 2I, 5Q–T
C. sellowiana	6–10	EU-BRO	MON/SYM	CUR	BRO	HIG/MOD	RET, RAN	FIN	WDE/IMP	POL	SMA/MED	DEN	1J, 2J, 5U–V
C. subcorymbosa	4–10	BRO/PB	MON/SYM	STR/CUR	BRO/MED	HIG	RET, RAN	FIN	WDE	QUA/POL	SMA	ABS/LIN	1K, 2K, 5W–X
C. velloziana	6–11	EU-BRO/PB/ BRO	MON/SYM	CUR/STR	BRO	HIG/MOD	RET, RAN	FIN	WDE	POL	SMA	ABS/LIN/BON/DEN	1L, 2L, 5Y–B’
C. wiedensis	4–7	BRO	MON/SYM	STR/CUR	BRO	HIG	RET, RAN	FIN	WDE	POL/QUA	SMA	ABS/LIN	1M, 3A–C

a) Venation pattern (major secondary vein framework): EU-BRO, mixed eucamptodromous-brochidodromous; BRO, brochidodromous; PB, pseudobrochidodromous.

b) Nature of the midvein course: MON, monopodial; SYM, sympodial.

c) Nature of the secondary course: STR, straight; CUR, curved.

d) Spacing of secondary veins along the midrib: BRO, broad (> 1/10th the length); MED, medium (≈ 1/10th the length); NAR, narrow (< 1/10th the length).

e) Angle secondary course makes with the midrib: HIG, high (≥ 55°); MOD, moderate (≈ 45°); LOW, low (≤ 40°).

f) Tertiary veins: RET, RAN, random reticulate; PER, percurrent reticulate.

g) Reticulum (minor venation pattern—pattern of higher-order veins): FIN, fine (the highest vein order is sixth or more, and areoles are usually less than 0.5–0.7 mm diam.); COA, coarse (the highest vein order is less than fifth with larger areoles over 1.0 mm diam.).

h) Areole development: WDE, well developed; IMP, imperfect; INC, incomplete.

i) Areole shape: QUA, quadrangular; POL, polygonal.

j) Areole size: LAR, large (1–2 mm); MED, medium (0.3–1.0 mm); SMA, small (< 0.3 mm).

k) Veinlet: ABS, absent; LIN, linear; CUR, curved; BON, branched once; BTW, branched twice; DEN, dendritic.

are freely ending ultimate veins (FEV; i.e., the veins of the finest gauge) of the leaf and veins of the same order, which occasionally cross areoles to become connected distally. They can be classed as (1) veinlets none; (2) simple, without branches, either (a) linear or (b) curved; or (3) branched, giving rise to ramifications by dichotomizing (a) once, (b) twice, (c) thrice, etc. (= dendritic, i.e., branching unequally) (Hickey, 1973, 1979; LAWG, 1999; Ellis et al., 2009).

RESULTS

All leaf venation characters and states are summarized in Table 2, with respective figures for each taxon indicated. Fig. 1 shows X-ray images of an entire leaf of each species, and Fig. 2–3 show closed up images of the intercostal region from the middle part of the leaf. Fig. 3–5 show photomicrographs of the reticulum and areoles from cleared leaves of each taxon.

All species show leaves with the secondary veins forming marginal loops variously prominent, which fall into the various categories of brochidodromous venation. Most species present leaves predominantly with proximal secondaries eucamptodromous becoming brochidodromous distally. Only *Cryptocarya wiedensis* (Fig. 1M) presents leaves strictly brochidodromous; they

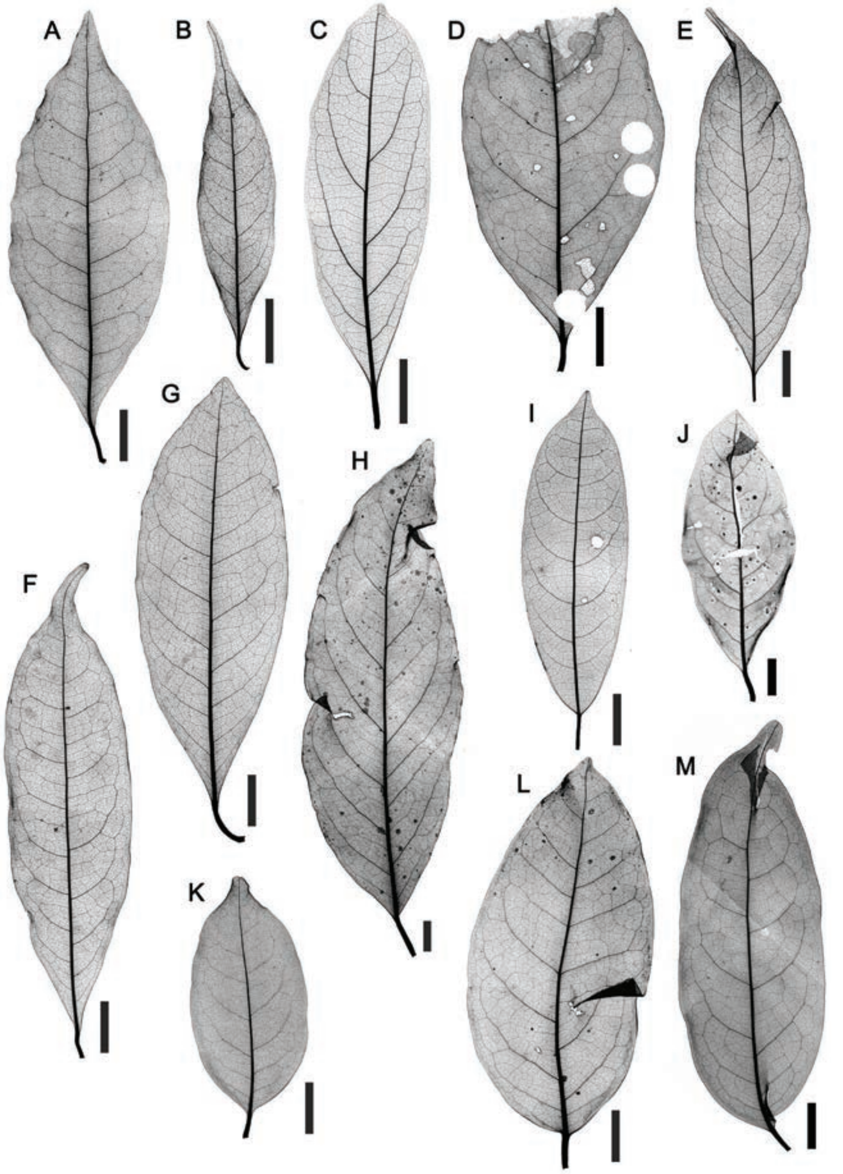

FIGURE 1. X-ray images of *Cryptocarya* leaves. **A,** *C. aschersoniana* Mez (*Moraes 5362*); **B,** *C. botelhensis* P.L.R. Moraes (*Moraes 1254*); **C,** *C. citriformis* (Vell.) P.L.R. Moraes (*Moraes 2456*); **D,** *C. guianensis* Meisn. (*Prance 25443*); **E,** *C. mandioccana* Meisn. (*Moraes 4099*); **F,** *C. micrantha* Meisn. (*Moraes 2155*); **G,** *C. moschata* Nees & Mart. (*Moraes 2259*); **H,** *C. riedeliana* P.L.R. Moraes (*Kollmann 4413*); **I,** *C. saligna* Mez (*Magnago 1471*); **J,** *C. sellowiana* P.L.R. Moraes (*Luz 196*); **K,** *C. subcorymbosa* Mez (*Moraes 5161*); **L,** *C. velloziana* P.L.R. Moraes (*Lombardi 8950*); **M,** *C. wiedensis* P.L.R. Moraes (*Kollmann 2464*). Bars = 1 cm.

are mixed brochidodromous and pseudobrochidodromous in *C.* aff. *aschersoniana* and *C. subcorymbosa* (Fig. 1K). Monopodial midveins are constant only in *Cryptocarya* aff. *aschersoniana* and *C. guianensis* (Fig. 1D), while in the remaining species the midveins are slightly sympodial mainly from the middle part of the leaf toward the apex, at least in some leaves (e.g. Fig. 1A,B,J,M).

The number of secondary veins per side of the midvein varies between species with a relatively small number (up to 7 [*Cryptocarya wiedensis*] or 8 [*C. botelhensis*]), and those with 9 to as many as 14 secondaries, as in *C. saligna*. Only *C. sellowiana* (Fig. 1J) has leaves with secondary veins strictly curved, whereas they are strictly straight in *C.* aff. *aschersoniana*. Another five species have leaves with mainly curved secondaries mixed with straight ones (Fig. 1C,D,E,H,L), while in another seven species they are mainly straight mixed with curved ones (Fig. 1A,B,F,G,I,K,M).

Five species (*Cryptocarya citriformis*, *C. guianensis*, *C. sellowiana*, *C. velloziana*, and *C. wiedensis*) have leaves with the secondary veins broadly spaced, whereas they are mixed broadly and medium-spaced in another seven species, or mixed broadly, medium-, and narrowly spaced in *C. micrantha* and *C. riedeliana*. Five species (*Cryptocarya* aff. *aschersoniana*, *C. moschata*, *C. saligna*, *C. subcorymbosa*, and *C. wiedensis*) have leaves with secondary veins diverging at strictly high angles to the midvein, whereas in *C. riedeliana* (Fig. 1H) their courses run at moderate and low angles, and in the remaining species the courses are mainly highly to moderately angled.

The tertiary veins are randomly reticulate in all species (e.g., Fig. 2A,B,D,F–L; 3A), except for *Cryptocarya citriformis* (Fig. 2C) and *C. mandioccana* (Fig. 2E), whose tertiary veins vary from randomly reticulate to weakly percurrent. All species have a fine reticulum. Areoles vary

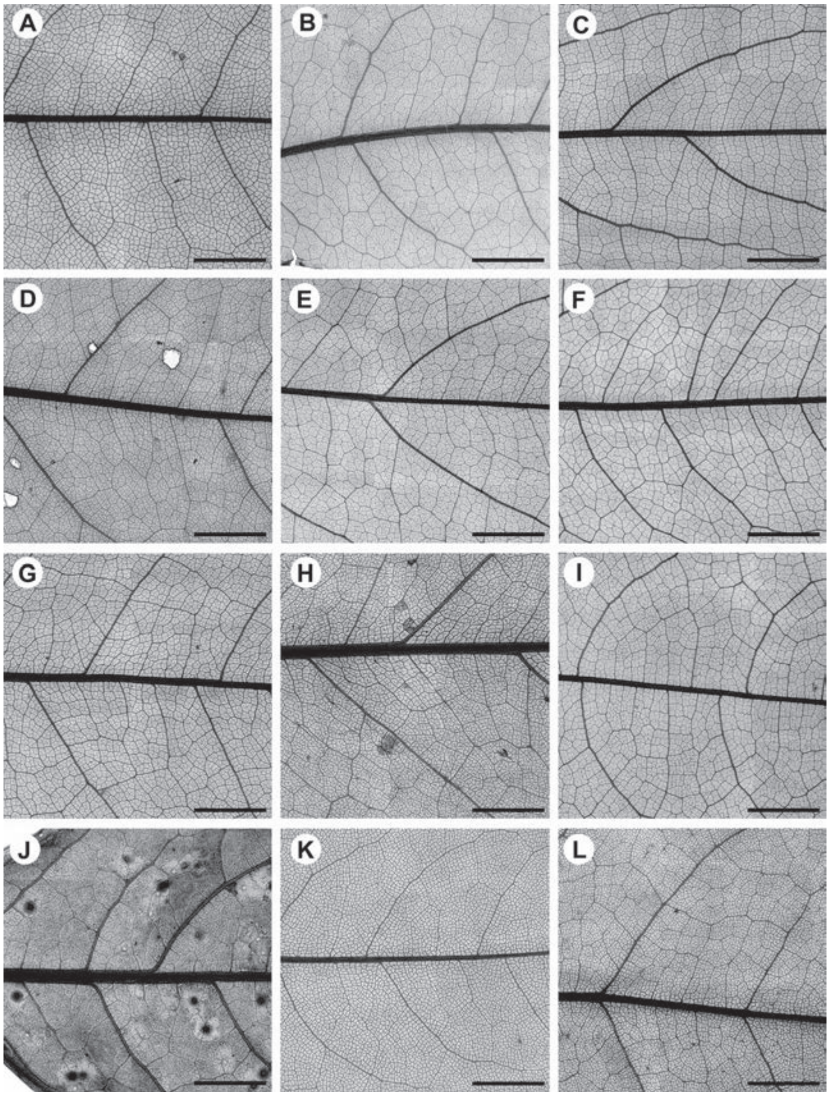

FIGURE 2. X-ray images (closed up) of the leaf venation of *Cryptocarya*. **A,** *C. aschersoniana* Mez (*Moraes 5362*); **B,** *C. botelhensis* P.L.R. Moraes (*Moraes 3349*); **C,** *C. citriformis* (Vell.) P.L.R. Moraes (*Moraes 2456*); **D,** *C. guianensis* Meisn. (*Prance 25443*); **E,** *C. mandioccana* Meisn. (*Moraes 4099*); **F,** *C. micrantha* Meisn. (*Moraes 2458*); **G,** *C. moschata* Nees & Mart. (*Moraes 2259*); **H,** *C. riedeliana* P.L.R. Moraes (*Kollmann 4413*); **I,** *C. saligna* Mez (*Magnago 1471*); **J,** *C. sellowiana* P.L.R. Moraes (*Luz 196*); **K,** *C. subcorymbosa* Mez (*Moraes 5161*); **L,** *C. velloziana* P.L.R. Moraes (*Lombardi 8950*). Bars = 5 mm.

among and within taxa in terms of development and size. Nine species have areoles strictly well developed (Fig. 2A,C,D,G,I,K,L; 3A–C; 4A–N,Q–X; 5I–L,Q–T,W–B'), whereas the other species present areoles with two types of development, with the one indicated first in Table 2 being predominant (Fig. 2B,E,F,H,J; 4O,P,Y–B'; 5A–H,M–P,U,V). Areoles strictly small are present in nine species, whereas they are mixed medium and small in *Cryptocarya micrantha* (Fig. 2F; 5A–H), *C. riedeliana* (Fig. 2H; 5M–P), *C. saligna* (Fig. 2I; 5Q–T), and *C. sellowiana* (Fig. 2J; 5U,V), or mixed medium and large in *C. botelhensis* (Fig. 2B; 4O,P). Areoles strictly or predominantly polygonal are found in all species, except for *C. subcorymbosa* (Fig. 2K; 5W–X), whose areoles are predominantly quadrangular.

With regard to veinlets, *Cryptocarya citriformis* (Fig. 2C; 4Q–T), *C. subcorymbosa* (Fig. 2K; 5W–X) and *C. wiedensis* (Fig. 3A–C) present areoles with mixed absent and simple linear veinlets, while only *C. sellowiana* (Fig. 2J; 5U,V) presents veinlets strictly dendritic. In the remaining species, areoles have mixed veinlets of several sorts, involving absent, linear, curved, branched once and/or twice, and/or dendritic ones (Fig. 4A–P,U–B'; 5A–T,Y–B').

Altogether, these characters and states allow recognition of the studied taxa, which can be determined through the following dichotomous identification key.

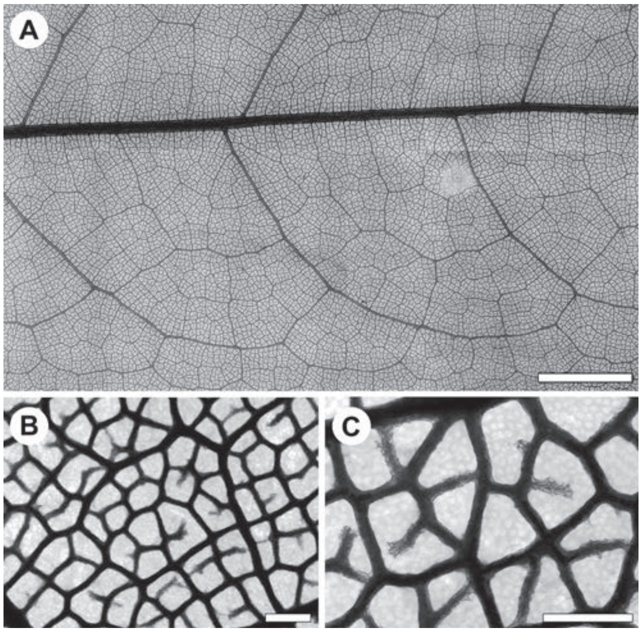

FIGURE 3. X-ray image (close up) and photomicrographs of *Cryptocarya wiedensis* P.L.R. Moraes (*Kollmann 2464*). Bars = 5 mm (A), 250 µm (B–C).

Key to the Brazilian Species of *Cryptocarya*, Based on Leaf Venation Characters

1a. Veinlets strictly dendritic . . . *C. sellowiana*
1b. Veinlets other . . . 2
2a. Veinlets mixed absent and linear . . . 3
2b. Veinlets other . . . 5
3a. Venation eucamptodromous-brochidodromous to pseudobrochidodromous, 6–9 secondary veins per side of the midvein, course of secondary veins predominantly curved, spacing of secondary veins broad, angle of secondary courses mixed high and moderate, tertiary veins mixed randomly reticulate and weakly percurrent . . . *C. citriformis*
3b. Venation strictly brochidodromous to mixed brochidodromous and pseudobrochidodromous . . . 4
4a. 4–10 secondary veins per side of the midvein, spacing of secondary veins mixed broad and medium, shape of areoles predominantly quadrangular . . . *C. subcorymbosa*
4b. 4–7 secondary veins per side of the midvein, spacing of secondary veins broad, shape of areoles predominantly polygonal . . . *C. wiedensis*
5a. Areoles strictly small (< 0.3 mm) . . . 6
5b. Areoles other . . . 11
6a. Areoles strictly well developed . . . 7
6b. Areoles mixed well developed and imperfect . . . *C. mandioccana*
7a. Midvein strictly monopodial . . . 8
7b. Midvein sympodial toward the apex, at least in some leaves . . . 9
8a. Venation brochidodromous to pseudobrochidodromous, course of secondary veins strictly straight, spacing of secondary veins mixed broad and medium, angle of secondary veins strictly high . . . *C.* aff. *aschersoniana*
8b. Venation eucamptodromous-brochidodromous to brochidodromous to pseudobrochidodromous, course of secondary veins predominantly curved, spacing of secondary veins broad, angle of secondary veins mixed high and moderate . . . *C. guianensis*
9a. Course of secondary veins predominantly curved, spacing of secondary veins broad, areoles polygonal . . . *C. velloziana*
9b. Course of secondary veins predominantly straight, spacing of secondary veins mixed broad and medium, areoles mixed polygonal and quadrangular . . . 10
10a. Venation eucamptodromous-brochidodromous to pseudobrochidodromous, angle of secondary veins mixed high and moderate, veinlets mixed absent and linear and branched once . . . *C. aschersoniana*
10b. Venation eucamptodromous-brochidodromous to brochidodromous to pseudobrochidodromous, angle of secondary veins strictly high, veinlets mixed absent and linear and curved and branched once and twice . . . *C. moschata*
11a. Areoles mixed medium (0.3–1.0 mm) and large (1–2 mm) . . . *C. botelhensis*
11b. Areoles mixed medium (0.3–1.0 mm) and small (< 0.3 mm) . . . 12
12a. Areoles strictly well developed . . . *C. saligna*
12b. Areoles mixed well developed and imperfect . . . 13
13a. 7–12 secondary veins per side of the midvein, course of secondary veins predominantly straight, angle of secondary veins mixed high and moderate . . . *C. micrantha*
13b. 5–8(–11) secondary veins per side of the midvein, course of secondary veins predominantly curved, angle of secondary veins mixed moderate and low . . . *C. riedeliana*

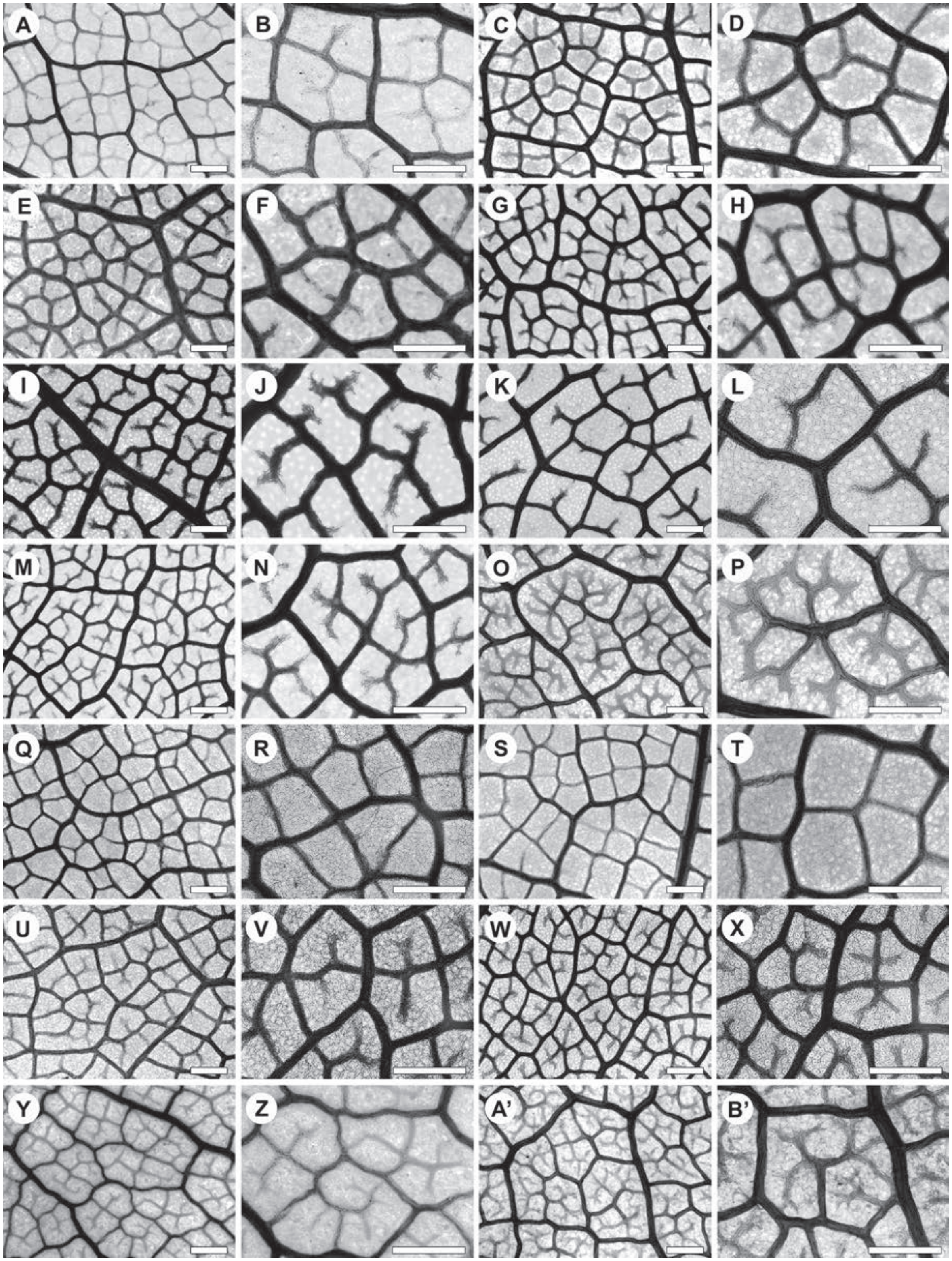

FIGURE 4. Photomicrographs of *Cryptocarya* leaves. **A–B,** *C*. aff. *aschersoniana* Mez (*Moraes 2243*); **C–D,** *C*. aff. *aschersoniana* Mez (*Moraes 2543*); **E–F,** *C*. aff. *aschersoniana* Mez (*Moraes 3242*); **G–H,** *C*. aff. *aschersoniana* Mez (*Robim 588*); **I–J,** *C*. *aschersoniana* Mez (*Moraes 2295*); **K–L,** *C*. *aschersoniana* Mez (*Moraes 5362*); **M–N,** *C*. *aschersoniana* Mez (*Moraes 5402*); **O–P,** *C*. *botelhensis* P.L.R. Moraes (*Moraes 3349*); **Q–R,** *C*. *citriformis* (Vell.) P.L.R. Moraes (*Moraes 2154*); **S–T,** *C*. *citriformis* (Vell.) P.L.R. Moraes (*Moraes 3199*); **U–V,** *C*. *guianensis* Meisn. (*Prance 25443*); **W–X,** *C*. *guianensis* Meisn. (*Thomas 4752*); **Y–Z,** *C*. *mandioccana* Meisn. (*Moraes 3509*). **A’–B’,** *C*. *mandioccana* Meisn. (*Moraes 4099*). Bars = 250 µm.

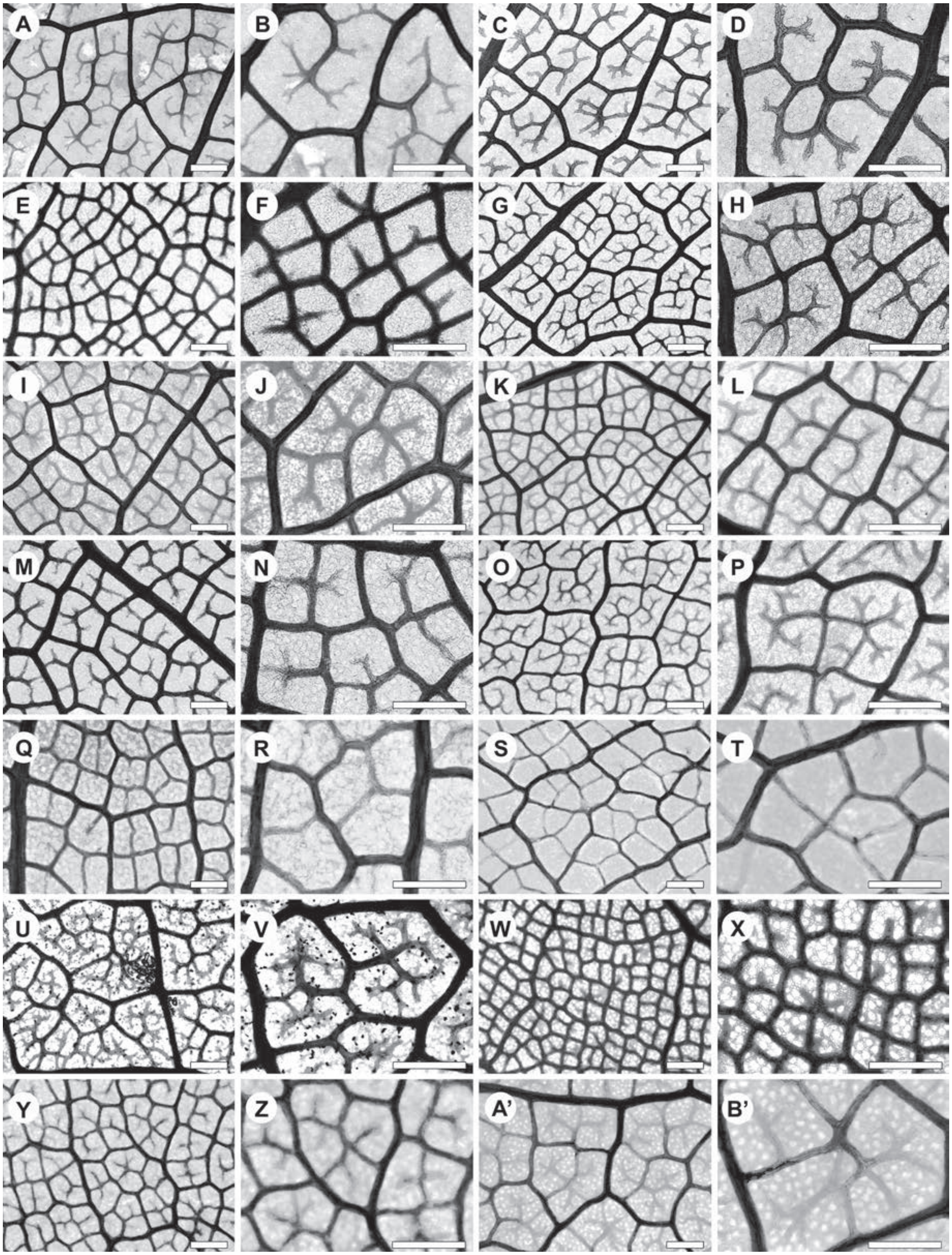

FIGURE 5. Photomicrographs of *Cryptocarya* leaves. **A–B,** *C. micrantha* Meisn. (*Moraes 2155*); **C–D,** *C. micrantha* Meisn. (*Moraes 2449*); **E–F,** *C. micrantha* Meisn. (*Moraes 2458*); **G–H,** *C. micrantha* Meisn. (*Moraes 2468*); **I–J,** *C. moschata* Nees & Mart. (*Moraes 2259*); **K–L,** *C. moschata* Nees & Mart. (*Moraes 2264*); **M–N,** *C. riedeliana* P.L.R. Moraes (*Kollmann 4413*); **O–P,** *C. riedeliana* P.L.R. Moraes (*Moraes 4716*); **Q–R,** *C. saligna* Mez (*Magnago 1471*); **S–T,** *C. saligna* Mez (*Moraes 3226*); **U–V,** *C. sellowiana* P.L.R. Moraes (*Luz 196*); **W–X,** *C. subcorymbosa* Mez (*Moraes 5161*); **Y–Z,** *C. velloziana* P.L.R. Moraes (*Lombardi 8950*). **A'–B',** *C. velloziana* P.L.R. Moraes (*Moraes 3227*). Bars = 250 µm.

Discussion

The most comprehensive study on leaf venation of Lauraceae has been undertaken by Klucking (1987), in the second volume of his series of leaf architectural atlases. According to Klucking, since many individual leaves may have one kind of venation in the basal part of the leaf, another kind in the middle part of the leaf, and a third kind in the upper part, each of these types of venation—the basal, middle, and apical—have different characteristics and are distinct. These kinds of venation are distinguished by the nature of the secondary venation and the type of intercostal venation, as the secondary venation of a leaf begins to form in the basal part of the leaf and develops progressively apically or acropetally. Consequently, each of these types of venation is formed during a different phase of development, with the venation in the basal part of the leaf formed first (Early Phase Venation), that in the middle part of the leaf next (Middle Phase Venation), and that in the apical part last (Late Phase Venation). Since the three types of venation are usually not present on a leaf in equal amounts, the venation pattern for the leaf has been named by Klucking after the dominant type of venation (i.e., presence on half the leaf or more).

For species of *Cryptocarya*, Klucking (1987) examined leaves of 245 species, from which specimens of 49 species were cleared for description. Leaves of another 13 species of *Ravensara* were also examined, from which specimens of 6 species were cleared for description. From Brazil, only *C. aschersoniana* was cleared from the collection of "*L. B. Smith and R. Klein 7528*, Santa Catarina, Brazil, UC M080142; plate 44, fig. 1" (also B 10 0002525, F, R, RB00128594, US01350763), being classified as having the "Predominant Venation Pattern," that is, "Early Phase Pinnate Venation dominant with small amounts of Middle Phase and Late Phase Venation present in the apical part of the leaf... most leaves with 8 to 10 pairs of secondary veins, courses curved or geniculate, curving sharply distally at closure and merging into a marginal looping; secondary courses running at low or moderate angles, spacing broad, narrow or a mixture of broad and narrow." Pedralli (1987) reported the leaves as brochidodromous, with secondary veins oriented at 45–60 degrees to the midvein (from specimens treated by him as *C. aschersoniana*) or with secondary veins oriented at 30–60 degrees to the midvein (from specimens treated by him as *C. moschata*). In Moraes (2007, thus including specimens of *C.* aff. *aschersoniana*), leaves were described as having camptodromous-brochidodromous venation, 5–12 secondary veins per side of the midvein, but in Brotto et al. (2009) as having 6–10 pairs of secondaries. Poszkus Borrero et al. (2016) recorded the leaves as brochidodromous, 7–11 pairs of secondary veins (vs. 6–12 pairs in Tressens, 1997), areoles quadrangular to polygonal, and veinlets linear to branched once. Here, our results corroborate the findings of Moraes et al. (2021), which showed that specimens from Linhares (*C.* aff. *aschersoniana*), despite their morphological similarity with those from southern Brazil (*C. aschersoniana*), partially match these former descriptions of the latter taxon, mainly disagreeing with the nature of the secondary veins (courses, angles, and spacing) as indicated by Klucking (1987). Evidence provided by DNA sequences prepared by Suganuma (2012), Rohwer et al. (2014), and Bolson et al. (2015) further indicates that at least the specimens from Espírito Santo, which have been formerly treated by Moraes (2007) as *C.* aff. *aschersoniana*, actually belong to *C. wiedensis*, according to the phylogenies inferred by Rohwer et al. (2014) and Carter (2017). Moreover, evidence provided by discriminant and cluster analyses based on isozymic data (Moraes, 2005a; P. L. R. Moraes, unpubl.) have shown that the populations of Serra do Japi and Campos do Jordão had genetic support to be treated as *C.* aff. *aschersoniana* (by Moraes, 2007), since they were clearly different from those belonging to *C. botelhensis*, *C. mandioccana*, and *C. moschata* (later also corroborated by the DNA sequences prepared by Suganuma, 2012).

With regard to *Cryptocarya botelhensis*, leaves were originally described by Moraes (2007) as having a brochidodromous venation pattern. However, they are better classified here as having mixed eucamptodromous-brochidodromous and brochidodromous venation.

Leaves of *Cryptocarya citriformis* were described by Kostermans (1937) (as *C. minima* Mez) and by Moraes (2007) as having camptodromous-brochidodromous venation, with 6–9 secondary veins per side of the midvein. Leaves of Bahian specimens are slightly different from those studied by Moraes et al. (2021) from specimens of Linhares. The leaves in the former have secondary veins broadly to narrowly spaced (vs. broadly), and courses highly to moderately angled (vs. highly) to the midvein. Nevertheless, the species remains poorly collected, which undermines the evaluation of its real variability. Regardless, it is the only American species of *Cryptocarya*, along with *C. mandioccana*, that shows some leaves with tertiary venation with a weakly defined percurrency. However, it is quite different from the degree of percurrency presented by many species of the genus, which often exhibit clearly scalariform tertiary venation. This organization of the tertiary venation has been used in *Cryptocarya* species identification (de Kok, 2016) in a number of studies: Christophel and Rowett (1996) described the leaf venation of 48 species of *Cryptocarya* from Australia (46 or 47 species respectively treatened by Hyland [1989] and Le Cussan et al. [2007], and 1 undescribed species), from which 32 species presented tertiary veins percurrent; and 14 out of 22 New Caledonian species of *Cryptocarya* have leaves with tertiary veins percurrent (Kostermans, 1974; Munzinger and McPherson, 2016). Leaves with tertiary veins percurrent to scalariform were found in 21 species from the Indian subcontinent (Gangopadhyay and Chakrabarty, 2005; Gangopadhyay, 2006, 2008; Bachan et al., 2018; Fasila et al., 2020); 14 out of 17 species from Thailand and Indochina (de Kok, 2015; Zhang et al., 2020); 16 out of 17 species from Peninsular Malaysia, where only 2 species feature a tertiary venation that could be classified as reticulate (i.e., *C. enervis* Hook.f. and *C. malayana* de Kok; Kostermans, 1975; de Kok, 2016); 12 out of 40 species from Madagascar (Kostermans, 1939, 1950, 1957a, 1958; van der Werff, 2008, 2013, 2017); 2 out of 7 species from South Africa and the Flora Zambesiaca area (Kostermans, 1938; Diniz, 1996); and most of the species from Papua New Guinea (e.g., Teschner, 1923; Allen, 1942; Kostermans, 1988, 1990).

With regard to leaves of *Cryptocarya guianensis*, Kostermans (1937) described them as having 6–10 secondary veins per side, whereas Moraes (2007) reported them as brochidodromous, with 6–12 secondary veins per side. Here, after a more thorough investigation on the leaf venation, the classification of leaves as varying from eucamptodromous-brochidodromous to brochidodromous to pseudobrochidodromous is seen to be more accurate.

Leaves of *Cryptocarya mandioccana* were studied by Moraes and Paoli (1999) (as *C. moschata* Nees & Mart.; see Moraes, 2005b, 2007) and reported as camptodromous-brochidodromous, with (4–)5–8(–9) pairs of secondary veins (7–9 in Coe-Teixeira, 1965), courses curved to geniculate, running at moderate to high angles to the midvein, spacing broad to narrow, areoles mostly imperfect to well developed, small, with random arrangement, shape irregular, and intrusive veinlets mostly multibranched or multiforked (dendritic). The minor venation of *C. mandioccana* varied among different individuals of the population analyzed from Carlos Botelho State Park. Both perfect and imperfect reticulation were found, composed of subrotund or polygonal areoles, with low to highly ramified veinlet terminations. Genetical, environmental, and/or ontogenetical variation would explain the variability at this level, which has been shown to be present in different collections from different populations. It is worth noting that the cleared leaf of an unnamed species of *Cryptocarya* from tropical America, presented by Ettingshausen (1861: 45–46, fig. 14), mainly resembles the major venation pattern of eophylls of *C. mandioccana* but also of some of its nomophylls.

Quinet and Andreata (2002) reported the leaves of *Cryptocarya micrantha* as brochidodromous, with 7–12 pairs of almost-straight secondary veins, diverging at 30–35 degrees from the midvein. In Moraes (2007), leaves were described as camptodromous-brochidodromous, with 7–12 secondary veins per side of the midvein, rather patent, arcuate toward margin, whereas Barbosa et al. (2012) reported 10–12 pairs of secondaries. Here, leaves are better classified as eucamptodromous-brochidodromous to pseudobrochidodromous, differing from the former description by Quinet and Andreata (2002) in the angle mixed high and moderate to the midvein, and course of secondary veins predominantly straight to curved.

Cryptocarya moschata was reported by Moraes (2007) as bearing leaves camptodromous-brochidodromous, with 5–11 secondary veins per side. In Gomes-Bezerra et al. (2011), from specimen *Ratter 3887* (UB) (as *C. aschersoniana* Mez), leaves were given as brochidodromous, with 8–11 pairs of secondary veins, areoles quadrangular to polygonal, and veinlets linear to branched. Specimens from Bahia differ from the former descriptions and other collections in the venation pseudobrochidodromous, up to 12 secondary veins per side, and veinlets mixed curved and branched once and twice.

Leaves of *Cryptocarya riedeliana* were described by Moraes (2007) as camptodromous-brochidodromous, with 5–8 secondary veins per side, whereas Barbosa et al. (2012) reported 8–10 pairs of secondary veins. The Bahian specimens slightly surpass the number of secondary veins (up to 11) and their leaves are pseudobrochidodromous.

As for *Cryptocarya saligna*, Kostermans (1937) and Vattimo-Gil (1957) reported leaves with 8–14 secondary veins per side of the midvein. Coe-Teixeira (1965) described the course of secondary veins as oriented at 50–85 degrees to the midvein. Moraes (2007) reported leaves with camptodromous-brochidodromous venation, 4–14 secondary veins per side, whereas Barbosa et al. (2012) with 8–11 pairs of secondaries. The venation pattern described by Moraes et al. (2021), from specimens of Linhares, is virtually the same as that found in other populations from different regions. In Bahia, the collection by *Monteiro 23556* (ESA, HST, HUEFS—2 sheets, PEUFR) is the only one known so far, differing in the course of secondary veins curved (vs. predominantly straight), and broadly spaced (vs. broadly to medium-spaced).

Since its description by Moraes (2007), *Cryptocarya sellowiana* remains known only from the type and two other collections from the region of Rio Piracicaba, Minas Gerais state. Its leaf venation pattern has been shown to fall within the variability found in leaves of *C. mandioccana*, corroborating the assertion by Moraes (2007) that it could be a local variation of the latter species. However, the species was evaluated here from only one collection, and further collections and study are needed to clarify the relationships between these taxa (including in terms of their leaf venation).

Leaves of *Cryptocarya subcorymbosa* were described by Moraes (2007) as brochidodromous, with 4–10 secondary veins per side of the midvein. The species remains poorly collected and is known only from a few collections from Rio de Janeiro, São Paulo, and Paraná states. Regardless, the species presents leaves usually small, being the smallest among the Brazilian species, and also with the smallest areoles, thus giving the tightest mesh.

Cryptocarya velloziana was described by Moraes (2007), on the basis of a few collections from Estação Biológica de Santa Lúcia, in Santa Teresa, Espírito Santo. Its leaves were described as having camptodromous-brochidodromous venation, with 6–10 secondary veins per side of the leaf. Some Bahian specimens show leaves better classified here as having pseudobrochidodromous to brochidodromous venation, and they can present up to 11 secondaries per side of the leaf.

Cryptocarya wiedensis was described by Moraes (2007), on the basis of four collections from the region of Santa Maria de Jetibá and Santa Teresa, Espírito Santo. Here, although only a sample of the type collection was analyzed, its leaf venation pattern is shown to be quite similar to that presented by other espírito-santense samples previously determined as *C.* aff. *aschersoniana*.

The leaf venation patterns of species, much less genera, cannot be accurately described because they must be generalized from the patterns of a large number of individuals (Klucking, 1987). Variation in venation patterns can be seen in individual leaves from the base of the leaf to the apex, as well as among individual leaves from different specimens of a species and among the different species of a genus. Another source of variability in observed patterns arises when leaves from the same collection are formed during different periods of secondary venation development, which is seen in several taxa of the present study. Although this variability adds additional difficulty to the intrinsic complexity of the venation patterns, it is not an impediment for describing and using them in a taxonomic sense, as an additional tool for discriminating taxa. Here, the major venation pattern has been demonstrated to be more conservative and, along with minor leaf venation, has proved to be useful for detecting possible misidentifications between taxa that are alike in their leaf venation characters.

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THREE NEW SPECIES OF *LEPANTHES* (ORCHIDACEAE: PLEUROTHALLIDINAE) FROM SAN JOSÉ DEL SALADO, VALLE DEL CAUCA, IN SOUTHWESTERN COLOMBIA

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Abstract. Three new species of *Lepanthes* from the Western Cordillera of the Colombian Andes are described and illustrated. The new species were found during several botanical expeditions to the mountains in San José del Salado, department of Valle del Cauca, Colombia.

Keywords: taxonomy, Andes, Western Cordillera, Neotropics, systematics, Pleurothallidinae

Resumen. Tres especies nuevas de *Lepanthes* de la Cordillera Occidental de los Andes Colombianos son descritas e ilustradas. Las nuevas especies se encontraron durante varias expediciones botánicas a las montañas en San José del Salado en el Departamento del Valle del Cauca, Colombia.

Palabras claves: taxonomía, Andes, Cordillera Occidental, Neotropico, sistemática, Pleurothallidinae

Lepanthes Sw. is one of the most diverse genera in Orchidaceae, representing 23% of subtribe Pleurothallidinae with 1158 described species (Karremans and Vieira, 2020). In Colombia, since the publications by Carlyle A. Luer (1953–2019) and Rodrigo Escobar (1935–2009), where they described 208 species (Moreno et al., 2018), several new species have been found and described recently (Vieira-Uribe and Larsen, 2014a,b; Moreno et al., 2017, 2018; Vieira-Uribe and Moreno, 2018, 2019, 2020; Moreno, Baquero, et al., 2020; Moreno, Pisso-Florez, et al., 2020; Gutiérrez et al., 2021), and the number keeps increasing year by year as more expeditions to unexplored areas are carried out.

Between the years of 2015 and 2017, eight new species of orchids were described from the mountains of San José del Salado, department of Valle del Cauca, in southwestern Colombia, including species from the genera *Epidendrum* L., *Camaridium* Lindl., *Pleurothallis* R.Br., and *Lepanthes* (Rodríguez-Martínez and Blanco, 2015; Hágsater et al., 2015, 2016; Rodríguez-Martínez et al., 2015; Karremans et al., 2017; Moreno et al., 2017). This area in the Western Cordillera of Colombia includes the confluence of the Chocó Biogeographic Region and the Tropical Andes, two of world's most biodiverse hotspots, whose great variety of microhabitats promote species richness and endemism within the Orchidaceae family (Karremans et al., 2017).

Here we describe three new species of *Lepanthes* from the mountains of San José del Salado, an orchid biodiversity hotspot.

MATERIALS AND METHODS

Descriptions and Drawings

The descriptions were prepared from living specimens. Specimens were preserved in alcohol and dissected under a stereo microscope (AmScope SM-1TNZ-144A-3M). Digital images were taken with a Nikon D750 with a Nikkor 105 mm f/2.8 macro lens. Sketches from living and preserved specimens were digitalized, and the images were used for diagramming draft composite templates in Adobe Photoshop® CS6. Then, digital drawings were prepared (using lines and stippling) in Procreate for Apple iPad (6th generation) (Bogarín et al., 2019).

Lepanthes specimens in the following herbaria—AMES, CAUP, ICESI, JAUM, HPUJ, HUA, FMB, VALLE, JBB, CUVC, SEL, MO (online), TOLI, and COL (online)—were consulted, but no additional material was found in these collections to include in the protologues of the new species described herein.

We thank Humberto Dominguez Escobar from El Carare Natural Reserve for allowing us to explore his property in San José del Salado (Dagua) and Argemiro Vargas Rodriguez for providing access to his territory in El Limonar (Dagua, Valle del Cauca). We wish to acknowledge the National Natural Parks of Colombia, especially Luis Carlos Mamian and Alvaro Fierro from the Farallones de Cali National Natural Park. We also thank Mr. Alvaro José Ortiz from Finca Montañita and Martin Cortez from Finca San Martin in the Cerro Tokio locality, as well as the Fundación Grupo Conserva for its logistical support. Finally, the authors are very grateful to José Otocar Reina and his son Juan Fernando Reina for their company and hospitality in the Altos of San José del Salado.

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TAXONOMY

Lepanthes irmae Gal.–Tar., Zuluaga, J.S. Moreno & Mora-Aguilar, *sp. nov*. TYPE: COLOMBIA, Valle del Cauca: municipio de Dagua, corregimiento de San José del Salado, predio El Almorzadero, 1732 m, 15 Sept 2020. *R. Galindo-Tarazona and D.L. Mora 1504* (Holotype: CUVC). Fig. 1–2.

Lepanthes irmae is most similar to *L. licrophora* Luer & B.T. Larsen, by its leaves and habit, but is distinguished by its triangular trilobed petals, lip blades obovate with rounded ends, and oblong pubescent appendix.

Plant medium in size, epiphytic, caespitose, 4.1–5.9 cm tall. *Roots*, slender, flexuous, filiform, 0.8–1.0 mm in diam. *Ramicauls* slender, suberect to horizontal, 2.9–4.4 cm long, enclosed by 8–14 acuminate, furrowed and microscopically pubescent lepanthiform sheaths, with a dilated and ciliate ostia. *Leaves* dark green, more or less horizontal, coriaceous, reticulate-veined, with 8 main veins, corrugate, lanceolate, acute, 3.5–3.6 × 1.0–1.4 cm, the apex emarginate with an abaxial apiculum in the middle, 3.5–3.6 × 1.0–1.4 cm, the base cuneate contracted into a petiole 2.0–3.2 mm long. *Inflorescence* a congested, distichous raceme, 6–12, successively several flowered, shorter than the leaf, up to 1.4–2.1 cm long including the peduncle, borne on top of the leaf by a filiform, terete peduncle 0.9–1.2 cm long, from near the apex of the ramicauls; *floral bracts* acuminate, 1.0–1.5 mm long; *pedicels* terete, longer than the floral bracts, 2.1 mm long. *Ovary* costate, 2.3 mm long. *Flowers*: *sepals* saffron yellow orange; *petals* fulvous yellow, tawny with ferruginous-rust color in the middle; *lip* ferruginous-rust colored. *Sepals* glabrous, shortly ciliate along the margins, similar in size. *Dorsal sepal* ovate, acute, 3-veined, 3.5–4.0 × 2.3–2.5 mm, connate at the base to the lateral sepals for ca. 0.9 mm. *Lateral sepals* ovate, oblique, acuminate, 2-veined, 3.5–4.2 × 1.5–2.2 mm, connate for 1.5 mm. *Petals* microscopically pubescent, transversely trilobed, 3-veined, 2.0 × 3.2–3.5 mm; the upper lobe oblong, sharply truncate, triangular in the exterior angle; the middle lobe linear, arcuate, triangular; the lower lobe narrowly triangular, acute. *Lip* bilaminate, the blades obovate with rounded ends, glabrous, 1.44 × 0.57 mm long, the connectives short, cuneate, the body broad, connate to the base of the column, the sinus obtuse, with an oblong, pubescence at the tip and narrowly elliptical appendix. *Column* scarlet, thin, terete, slender, 1.4 mm long, the anther dorsal and the stigma ventral; *stigma* trilobed with smaller and apiculate central lobe. *Anther cap* pink, cordate, cucullate, 0.5 mm wide. *Pollinia* yellow, 2, pyriform, 0.5 mm long.

Eponymy: the name honors Irma Tarazona Rubio, mother of Robinson Galindo-Tarazona.

Habitat and ecology: *Lepanthes irmae* was found in a very humid area in a secondary forest, growing close to the ground in a small creek that flows into the Quebrada Española (Map 1), sharing habitat with *L. aciculifolia* Luer, *L.* aff. *carunculigera*, *L. lycocephala* Luer & R. Escobar, *L. posadae* Luer & R. Escobar, and *L. satyrica* Luer & Hirtz.

Conservation status: *Lepanthes irmae*, *L. fimbriatilabia*, and *L. pogonochila* are known only from their type locality (Map 1). *Lepanthes fimbriatilabia* is the only species that was found in a protected area, the National Natural Park Farallones de Cali. The IUCN classification is data deficient (DD) because we lack adequate distribution and population information to make an assessment (IUCN Standards and Petitions Subcommittee, 2017; IUCN, 2021).

Lepanthes irmae resembles a group of species with similar habit and reticulate leaves, such as *L. licrophora* (Fig. 3), *L. silverstonei* Luer, and *L. antennata* Luer & R. Escobar, but the flower is entirely different from the last species and does not resemble any other described species so far. It can be easily recognized by the combination of dark green reticulate and corrugate leaves, transversely bilobed petals with a middle lobe, and the ovate blades of the bilaminate lip.

Lepanthes fimbriatilabia J.S. Moreno, Gal.–Tar., Zuluaga, *sp. nov*. TYPE: Colombia. Valle del Cauca: municipio de Dagua, corregimiento de San José del Salado, en proximadades de un pequeño afluente que da a la Quebrada La Española, 1776 m,10 Jan 2021. *R. Galindo-T and D. L. Mora 1548* (Holotype: CUVC). Fig. 4–6.

Lepanthes fimbriatilabia resembles *L. pecunialis* Luer & Hirtz, but it can be recognized by the transversely bilobed petals with the lower lobe pubescent and fimbriate, as well as the bilaminate lip strongly fimbriate along the margins with the blades oblong and falcate.

Plant small in size, epiphytic, caespitose, up to 14.8 cm tall. *Roots* slender, flexuous, 0.6 mm in diam. Ramicauls slender, erect to suberect, 10.8 cm long, enclosed by 10 dark brown, tightly fitting, lepanthiform sheaths, with a minutely acuminate, ciliated ostia. *Leaves* coppery, erect, thickly coriaceous, ovate, obtuse, 3.4–3.6 × 2.3–2.7 cm, the base rounded and contracted into a petiole 1.0–1.5 cm long. *Inflorescence* a very congested, successively, distichous, long-pedicellate, many-flowered raceme, up to 2.5 cm long including the peduncle, borne beneath the leaf by a filiform peduncle 1.8–2.5 cm long; *floral bract* acuminate, scabrous, 1.3 mm long; *pedicel* terete, persistent, longer than the floral bract, 1.0–1.7 mm long. *Ovary* costate, 2.4 mm long. *Flowers: sepals* beige, very pale creamy brown with fawn, light yellowish brown, similar in shape and size. Glabrous, ovate, obtuse. *Dorsal sepal* 3-veined, 3.0–3.1 × 2.1–2.3 mm, connate to the lateral sepals for 0.5 mm. *Lateral sepals* oblique, 2-veined, 2.6 × 1.4 mm, connate for 1.5 mm. *Petals* saffron, yellow-orange with maroon, dark red margins, transversely bilobed, 1-veined, 1.6 × 4.1–4.2 mm, the upper lobe larger than the lower lobe, ovate, obtuse, the lower lobe narrowly triangular, obtuse, pubescent, fimbriate. *Lip* peach, light pink, strongly fimbriate, bilaminate, the blades oblong, falcate with rounded ends, 1.5–1.8 × 0.5 mm long, the connectives cuneate, connate to the base of the column, the appendix bisegmented, the apical portion subquadrate, pubescent. *Column* buff, dull yellow-brown, terete, 1.2 mm long, the anther dorsal and stigma ventral. *Anther cap* not seen. *Pollinia* not seen.

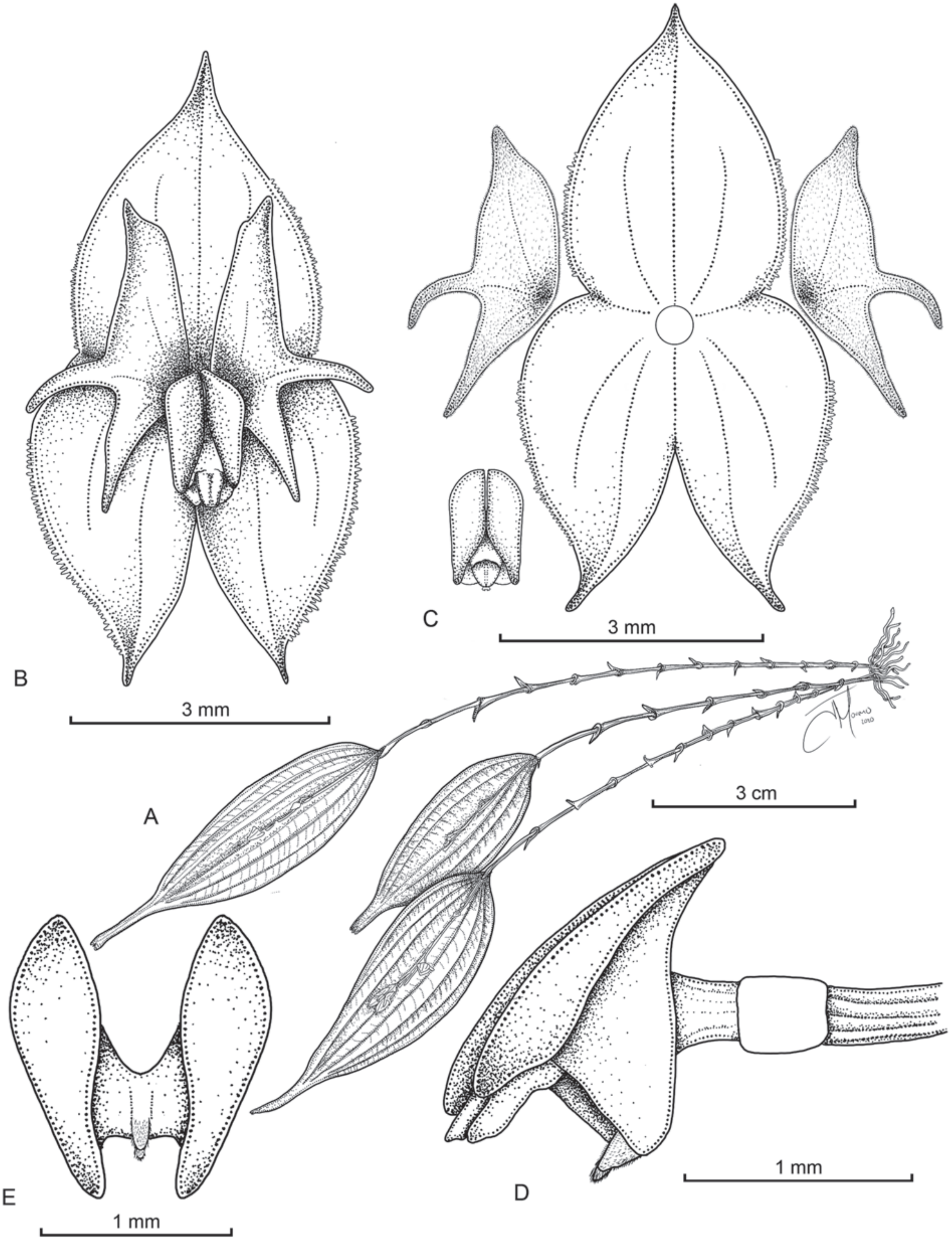


FIGURE 1. Illustration of *Lepanthes irmae* Gal.–Tar., Zuluaga, J.S. Moreno & Mora-Aguilar. **A,** habit; **B, f**lower; **C,** dissected perianth; **D,** colum and lip, lateral view; **E,** lip. Drawn by J. S. Moreno, based on *R. Galindo-T. & D. L. Mora 1504*.

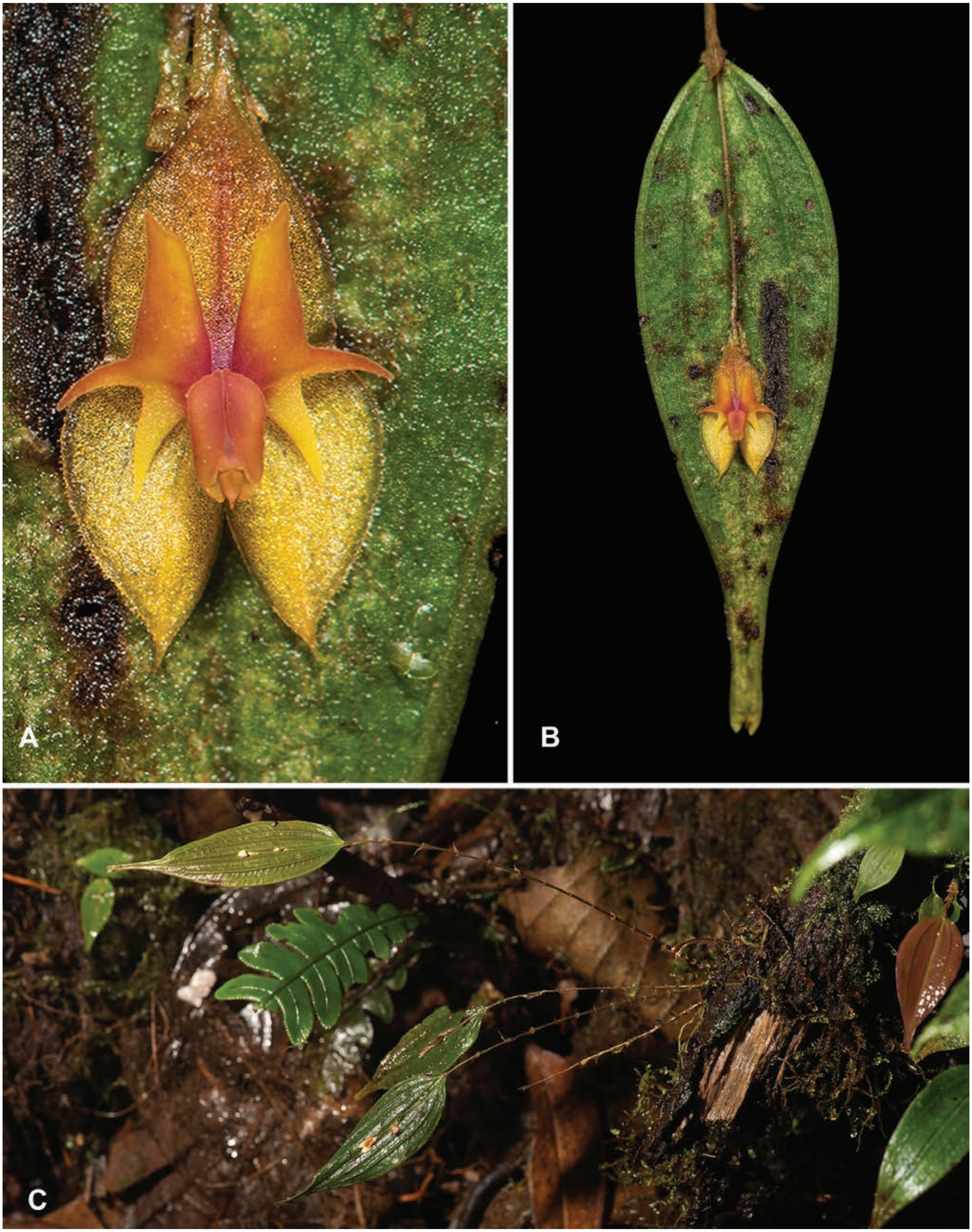
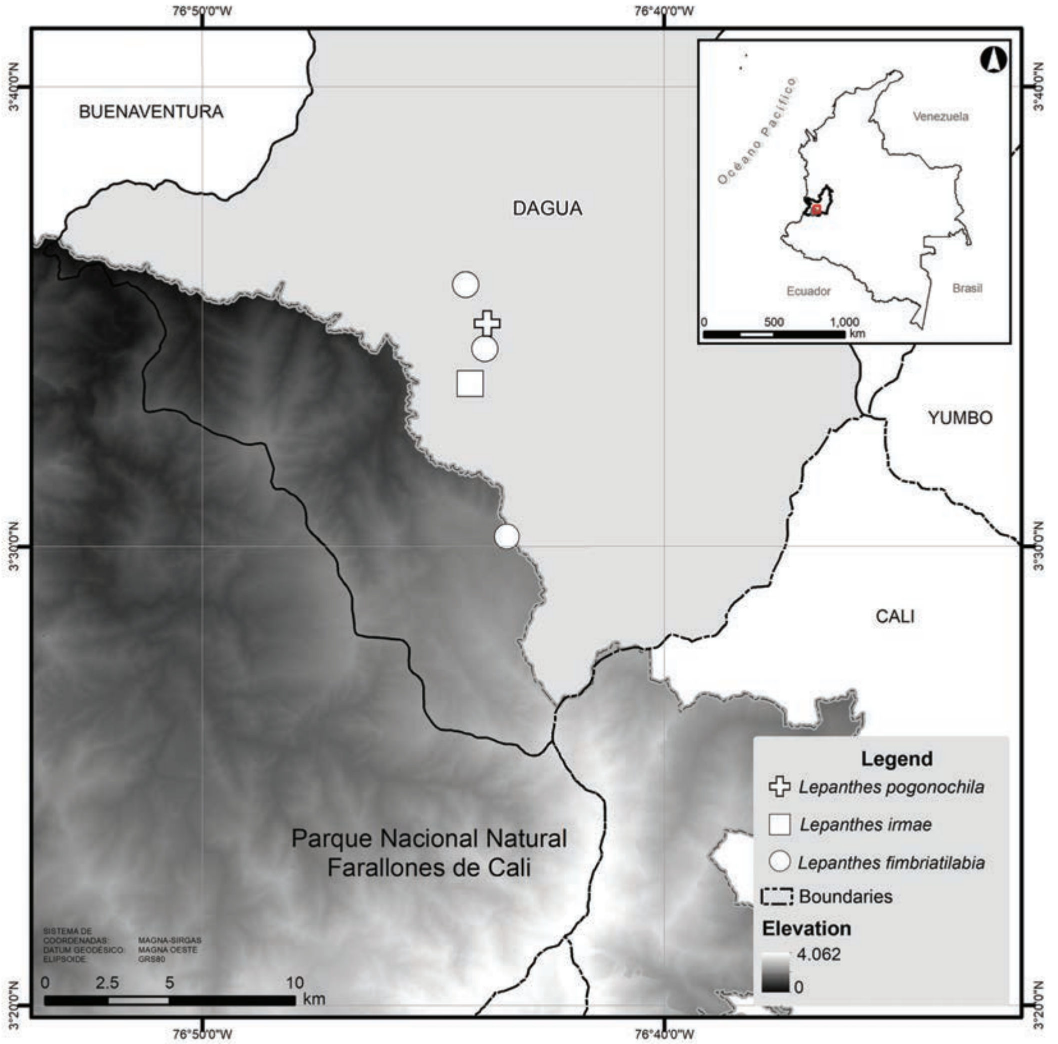


FIGURE 2. Photographs of *Lepanthes irmae* Gal.–Tar., Zuluaga, J.S. Moreno & Mora-Aguilar. **A,** flower; **B,** leaf and inflorescence; **C,** plant and habit, in-situ. (Photos: R. Galindo-T. from the type specimen).



MAP 1. Distribution map of *Lepanthes irmae* Gal.–Tar., Zuluaga, J.S. Moreno & Mora-Aguilar (square); *L. fimbriatilabia* J.S. Moreno, Gal.–Tar., Zuluaga (circle); and *L. pogonochila* Zuluaga, Alegria-Valencia., J.S. Moreno & Gal.–Tar. (cross) in the Department of Valle del Cauca, Colombia.

Additional specimen examined: COLOMBIA. Valle del Cauca: Corregimiento El Queremal, Parque Nacional Natural Farallones de Cali, Cerro Tokio, en cercanias de la Finca del Sr. Alvaro, Municipio de Dagua, 1800 m, 8 Dec 2020, *R. Galindo-T, V. Varón,* and *D. L. Mora 1536* (CUVC). Municipio de Dagua, Corregimiento de San Jose´ *del Salado, Altos de San José del Salado, Finca* Totogol, 1860 m, 20 Nov 2021, *J. S. Moreno and A. L. Erazo 525* (CAUP).

Etymology: from the Latin *fimbriatus,* “fringed,” and *labium,* “lip, labellum,” in reference to the fringed margins of the lip in the new species.

Habitat and ecology: plants were found growing as epiphytes in *Andesanthus lepidotu*s (Bonpl.) P.J.F. Guim. & Michelang Baill. (Melastomataceae) trees along the edge of a pasture in close proximity to a very well preserved forest. It shares habitat with *Lepanthes elata* Rchb.f. and *L. agglutinata* Luer.

Conservation status: see *Lepanthes irmae*.

Lepanthes pogonochila Zuluaga, Alegria-Valencia., J.S. Moreno & Gal.–Tar., *sp. nov*. TYPE: Colombia. Valle del Cauca: municipio de Dagua, corregimiento El Limonar, Quebrada La Española, 1700 m, 27 Sept 2020. *R. Galindo-T, V. Varón and D. L. Mora 1523* (Holotype: CUVC). Fig. 7–9.

Lepanthes pogonochila is most similar to *L. impotens* Luer & R. Escobar from Colombia, but it can be recognized mainly by its lip’s obovate blades, with the apex of each blade provided with conspicuous, dense bristles and a subquadrate, bilobed, concave appendix.

Plant medium in size, epiphytic, weak, caespitose, 4.3–6.7(–9.9) cm tall. *Roots* slender, flexuous 0.5–0.7 mm in diam. *Ramicauls* slender, suberect, 2.2–6.0 cm long, enclosed by 7–10 lepanthiform sheaths, furrowed, with a dilated, ciliated, ostia long acuminate. *Leaves* pendent, thinly coriaceous, ovate, acute, long acuminate, the apex emarginate with an abaxial apiculum in the middle, 1.7–3.6 × 0.8–1.1 cm, the base cuneate contracted into a petiole

FIGURE 3. Leaves and habit of *Lepanthes licrophora* Luer & B.T. Larsen, the species most similar to *Lepanthes irmae* Gal.–Tar., Zuluaga, J.S. Moreno & Mora-Aguilar.

4.9–8.4 mm long. *Inflorescence* a congested, successively flowered raceme, up to 1.7–2.0 cm long including the peduncle, borne on top of the leaf by a filiform peduncle 4.4–7.0 mm long; floral bract acuminate, 0.7–1.1 mm long; pedicel terete, persistent, longer than floral bract, 1.1–2.2 mm long. *Ovary* costate, 1.1 mm long. *Flowers: sepals* khaki, dull brownish yellow, similar in shape and size; *petals* russet, reddish brown with cinnabar, vermilion, blood-red in the middle; *lip* russet, reddish brown. *Sepals* convex, glabrous, ciliate along the margins, similar in size. *Dorsal sepal* ovate, acute, 3.3 × 2.5 mm, 3-veined, connate to the lateral sepals for 0.6 mm. *Lateral sepals* ovate, oblique, acute, 3.1–3.2 × 1.6 mm, 2-veined, connate for 1.4 mm. *Petals* transversely bilobed, 3-veined, 0.9–1.0 × 4.4–4.5 mm, the upper lobe subquadrate, obliquely truncate, short pubescent in the base; the lower lobe longer than the upper lobe, narrowly triangular, acute, attenuate, long pubescent from the base toward the apices. *Lip* glabrous, bilaminate, the blades obovate, with rounded ends, the apex of each lobe provided with conspicuous bristles, 1.6 × 0.6 mm, the connectives short, broadly cuneate, the body thick, rounded, connate to the base of the column, the sinus obtuse, the appendix bisegmented, the apical portion thick, subquadrate, bilobed, the basal portion concave, pubescent. *Column* terete, slender, 0.9 mm long, the anther dorsal and stigma ventral. *Anther cap* pink, cordate, cucullate, 0.5 mm wide. *Pollinia* yellow, 2, pyriform, 0.3 mm long.

Etymology: from the Greek words *pṓgōn,* "beard," and *kheîlos,* "lip," in reference to the long bristles found at the apex of the lip blade.

Conservation status: see *Lepanthes irmae*.

Lepanthes pogonochila (Fig. 7A) shares many traits with *L. impotens* (Fig. 7B). Both species have caespitose and weak habit with the ramicauls slender to suberect; the leaves ovate, pendent, coriaceous with an apex long acuminate, like most of the species in the series *Mucronatae* proposed by Luer and Thoerle in 2011. The new species could be distinguished from the latter by its lip's obovate blades covered by numerous dense, conspicuous bristles at the apex, a pubescent bisegmented appendix with the apical portion subquadrate and bilobed, and the basal portion concave (vs. the lip blades elliptical, with short trichomes, and an appendix reduced to a ciliate margin of the body of the lip) (Luer and Thoerle, 2012). Finally, the new species is also similar to *L. oscillifera* Luer & R. Escobar (Fig. 7C), but the apex of the blades are minutely ciliate (vs. covered by numerous dense and conspicuous bristles at the apex), the appendix broadly hinged from the center, flap-like, and the apical portion concave and ciliate with a minutely bilobed apex (vs. appendix with the apical portion subquadrate, bilobed, and the basal portion concave).

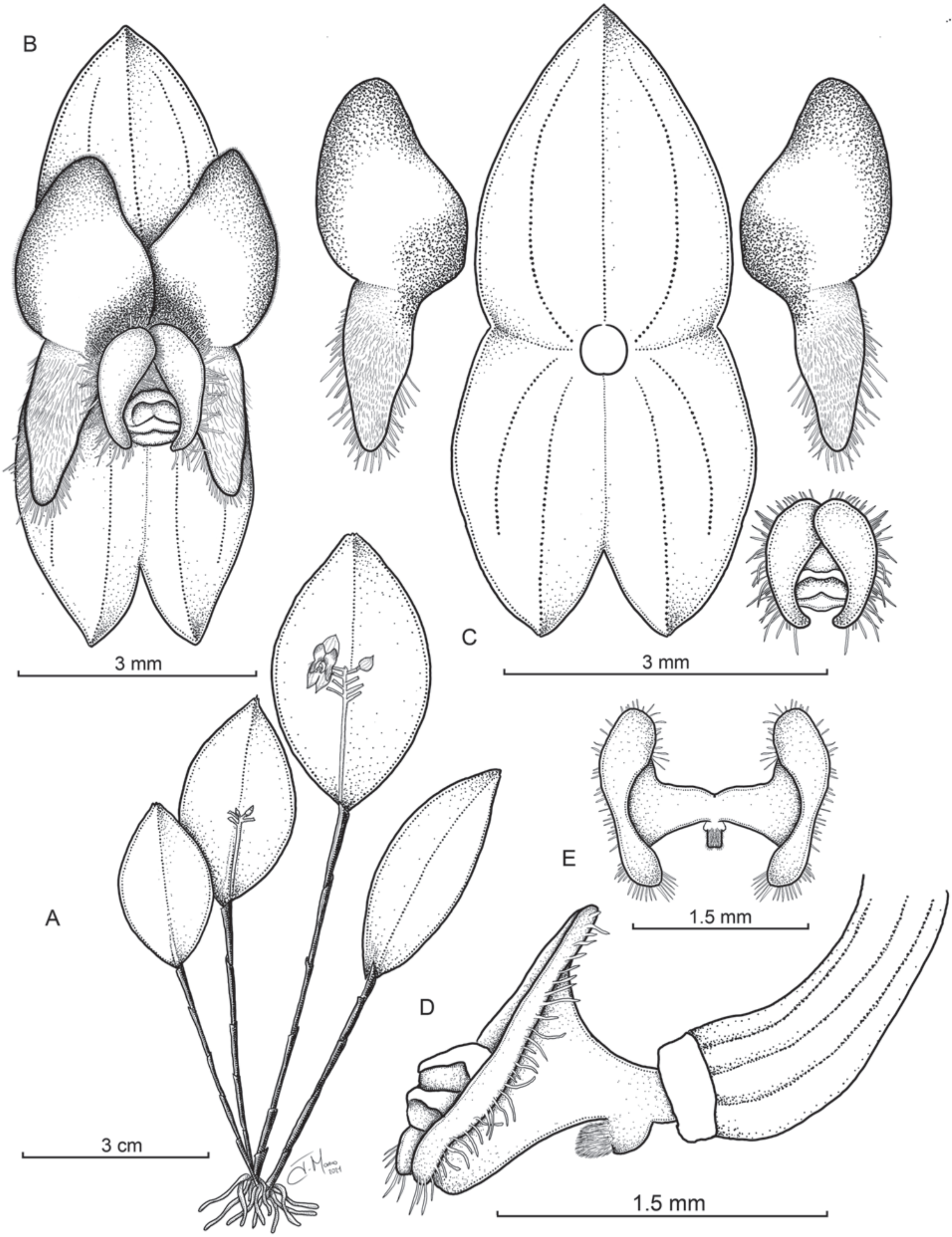


FIGURE 4. Illustration of *Lepanthes fimbriatilabia* J.S. Moreno, Gal.–Tar., Zuluaga. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** column and lip, lateral view; **E,** lip. Drawn by J. S. Moreno, based on *R.Galindo-T. & D. L. Mora 1548*.

FIGURE 5. Photographs of *Lepanthes fimbriatilabia* J.S. Moreno, Gal.–Tar., Zuluaga. **A,** flower, frontal view; **B,** leaf and inflorescence; **C,** plant and habit, in-situ. (Photos: J. S. Moreno from the type specimen).

FIGURE 6. Comparison of the most similar species. **A,** *Lepanthes fimbriatilabia* J.S. Moreno, Gal.–Tar., Zuluaga; **B,** *Lepanthes pecunialis* Luer & Hirtz.

FIGURE 7. Comparison of the most similar species. **A,** *Lepanthes pogonochila* Zuluaga, Alegria-Valencia., J.S. Moreno & Gal.–Tar.; **B,** *Lepanthes impotens* Luer & R. Escobar; **C,** *Lepanthes oscillifera* Luer & R. Escobar.

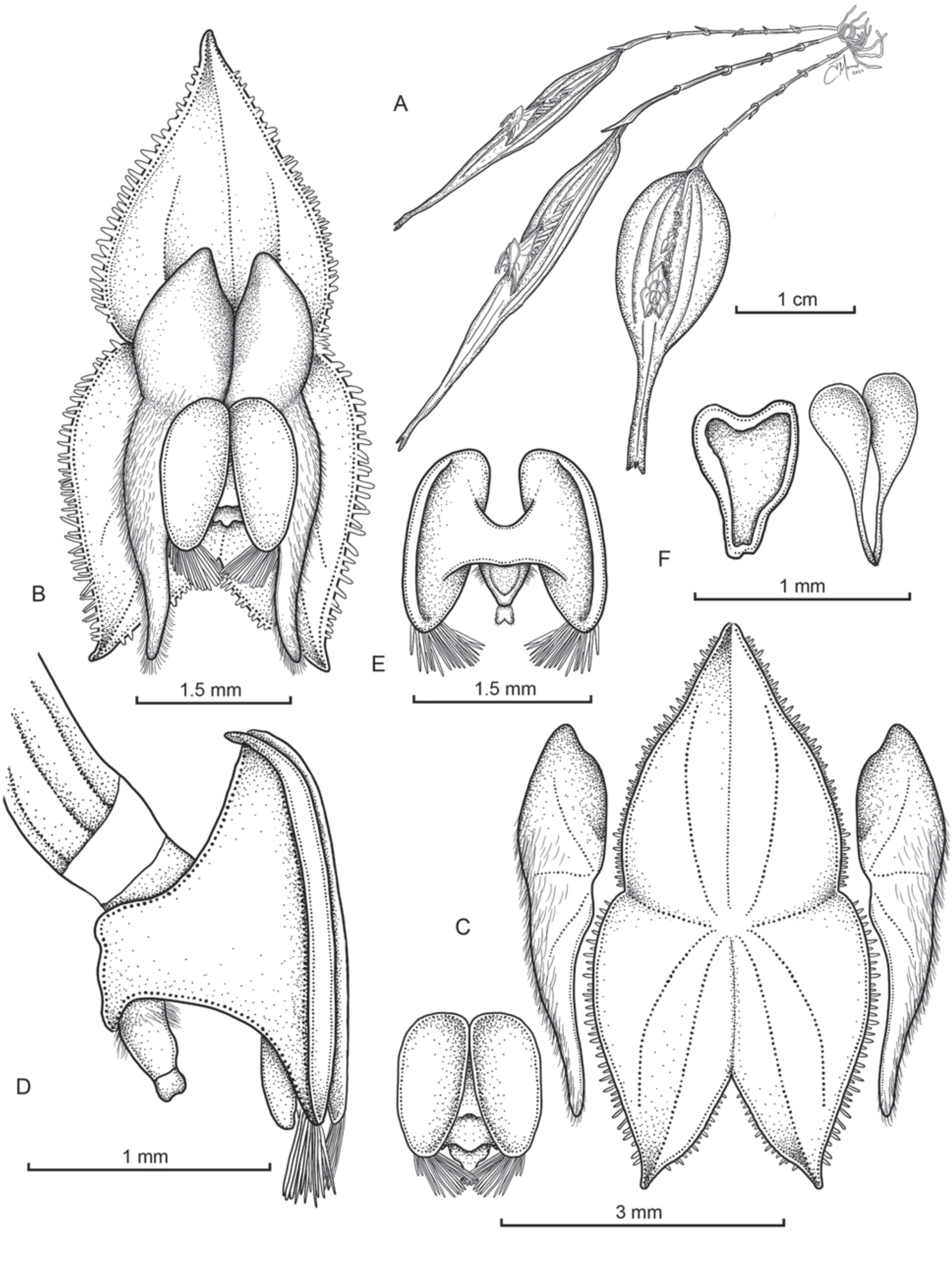


FIGURE 8. Illustration of *Lepanthes pogonochila* Zuluaga, Alegria-Valencia., J.S. Moreno & Gal.–Tar. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** column and lip, lateral view, **E,** lip; **F,** anther cap and pollinia. Drawn by J. S. Moreno, based on *R.Galindo-T., V. Varón & D. L. Mora 1523*.

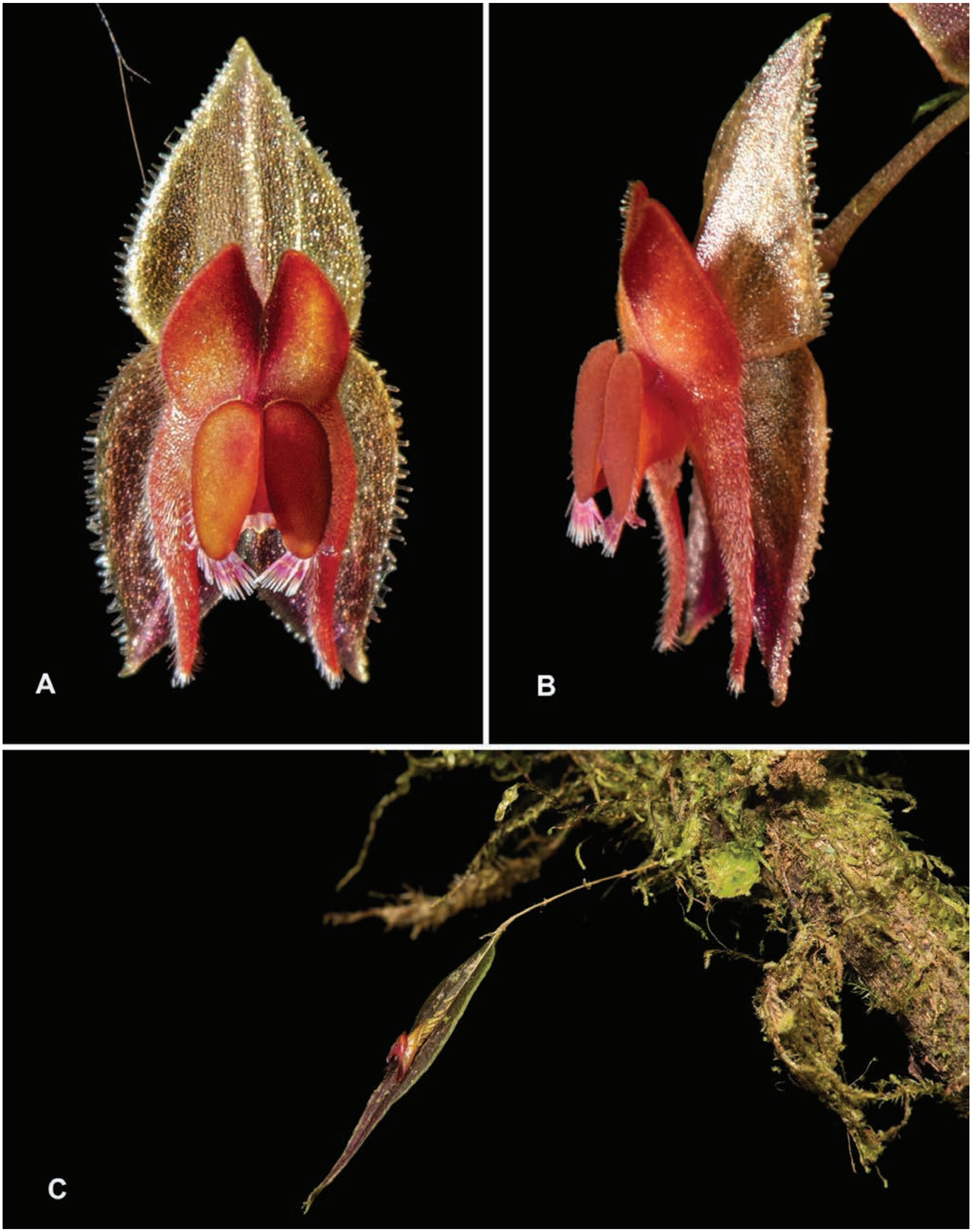


FIGURE 9. Photographs of *Lepanthes pogonochila* Zuluaga, Alegria-Valencia., J.S. Moreno & Gal.–Tar. **A,** flower, frontal view; **B,** flower, 3/4 view; **C,** plant and habit, in-situ. (Photos: R. Galindo-T. from the type specimen).

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DRABA (BRASSICACEAE) OF CANADA AND ALASKA

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Abstract. Four new arctic species of *Draba* are described here. Of these, *D. airdii*, *D. shehbazii*, and *D. darbyshireii* are from Canada, and *D. catlingii* is from both Canada and Alaska. Two new species described by others, *D. adamsii* and *D. macrocarpa,* are also added. The chromosome numbers $n = 19$ and $2n = 36$ should be attributed to *D. grandis*, and $n = 8$ for *D. lonchocarpa* var. *kamtschatica* to *D. chamissonis*. *Draba kluanei* is now known to occur at a second location in Yukon. The six new *Draba* species added in this study bring the total number in Canada and Alaska to 65. A key to all of these species is presented.

Keywords: Alaska, Brassicaceae, Canada, *Draba*

Recent publications have added many new species and other information about the genus *Draba* L. (Brassicaceae) in Canada and Alaska (Al-Shehbaz, 2009, 2012, 2016; Al-Shehbaz and Mulligan, 2013; Elven and Al-Shehbaz, 2008; Mulligan, 1971a,b, 1974a,b, 1976, 1979, 2002; Mulligan and Findlay, 1970). The present study adds four new species and two described but unrecognized species. *Draba airdii* G.A. Mulligan, *D. shehbazii* G.A. Mulligan, *D. catlingii* G.A. Mulligan, and *D. darbyshireii* G.A. Mulligan are new and described here. The names *Draba adamsii* Ledebour and *D. macrocarpa* Adams were described by others but have not been used for plants of Canada and Alaska. The following key contains all 65 species presently known to occur in Canada and Alaska and some recent information about *D. bruce-bennettii* Al-Shehbaz, *D. chamissonis* G. Don, *D. grandis* Langsd. Ex DC., *D. mulliganii* Al-Shehbaz, and *D. novolympica* Payson & H. St. John.

NEW SPECIES

1. Draba airdii G.A. Mulligan, *sp. nov.* TYPE: CANADA. Yukon, near Porcupine River, approx. 66˚02'N, 138˚44'W. Occasionally around ground squirrel burrows on uppermost ridge at about 3500 ft [1069 m]; flowers white, 29 June 1960 *J. A. Calder & J. M. Gillett 26104* (Holotype: DAO).

Perennial, cespitose herbs with a compacted *caudex*. *Stems* erect, few to many, 6–14 cm, with 2–4 cauline leaves; *basal leaves* persistent, abaxially with sparse to dense, fine, subsessile, 0.1- to 0.25-mm-wide, stellate trichomes. Petals white.

Eponymy: this species is named after Dr. Paul Leet Aird, born January 11, 1930, Professor Emeritus of forest conservation, University of Toronto, Canada.

Additional specimen examined: CANADA. Yukon, Almost Lake: 60˚28'N, 131˚05'W, 28 July–2 August 1984, Catherine Kennedy A-7 (DAO).

This is the only species of *Draba* in North America that has a minute sparse to dense, up to 0.15 mm, simple to few-branched puberulence on the surface of the fruit.

2. Draba catlingii G.A. Mulligan, *sp. nov.* TYPE: CANADA. Northwest Territories, Mackenzie District, Alvar A3, 37.77 km W of Enterprise, site 208, 60.7894˚N, 116.5913˚W, *P. M. Catling & B. Kostiuk 2007-08-07* (Holotype: DAO).

Perennial, cespitose, often pulvinate *herbs*; *caudex* compacted, covered with the persistent remains of previous seasons. Both surfaces of basal leaves pubescent with divergently rayed, short-stalked, less than 10-rayed, stellate trichomes 0.2–0.3(–0.4) mm. Stems 1–4(6), 10–30 cm high with (4–)7–10 cauline leaves. *Petals* white, 2–2.5 × 0.75 × 1.0 mm; *sepals* 1.5–2.0 mm. *Anthers* cordate to orbiculate, 0.15–0.20(–0.25) mm. *Stigmas* broadly ovate 0.3–0.4 mm. *Styles* (0.1–)0.2–0.3 mm long. Most fruiting pedicels appressed to rachis. Fruiting racemes subumbellate with apical flower buds usually aborting. Some of lower pedicels bracteate. *Fruit* elliptic to narrowly elliptic, surfaces with fine, divergently few-branched, substellate trichomes; fruit inflated proximally, some asymmetrical, none twisted. *Seeds* oval, brown, 0.75 × 0.05 mm.

Eponymy: this species is named after Dr. Paul M. Catling, a taxonomist with Agriculture Canada and a collector of the type material.

Additional specimens examined: UNITED STATES. Alaska: Valdez Quad. Chitina, confluence of China and Copper Rivers. Bluff on W bank of Copper River, 61˚30'N, 144˚25'W, 214 m, 8 July 1981, *A. P. Khokhryakov, B. A. Yurtsev, & D. F. Murray 6192* (DAO). CANADA. Yukon, 4 mi. E of junction of Kaskawulsh and Degadeash Rivers & ca. 8 mi. WSW of Haines Jct., in community dominated by *Artemisia* sp.; aspect S25E: slope 2%, 2000 ft [610 m]. *G. W. & G. G. Douglas 67C1.* (DAO). Mackenzie District, Northwest Territories. Reindeer Grazing Preserve: Campbell Lake 68˚08'N, 133˚27'W, rock outcrop, 3 August 1966, *G. W. Scotter 10335* (DAO): Reindeer Grazing Preserve, Eskimo Lakes 68˚54'N, 132˚41'W. Small knoll with moist depressions, 1 August 1966, *G. W. Scotter 10334* (DAO).

Draba catlingii seems most closely related to *D. cana* Rydberg, which usually has an open caudex; lower fruiting pedicels appressed to rachis, none genticulate; anthers (0.25–)0.30–0.40 mm; fruiting racemes elongated, with few or no apical flower buds aborting, the fruit not inflated and is often twisted. *D. catlingii* has a very compacted, pulvinate, caudex; most fruiting pedicels appressed to rachis, many genticulate; the fruiting racemes usually subumbellate with many apical flower buds aborting, fruit inflated proximally and not twisted; anthers 0.15–20 mm.

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3. Draba darbyshireii G.A. Mulligan, *sp. nov*. TYPE: CANADA. Northwest Territories, Mackenzie District, Melville Hills Region, Bluenose Lake area, site 7, 68˚33'N, 120˚46'W, 490 m, 25 July 1990, *G. W. Scotter & S. Zoltai 90-263* (Holotype: DAO).

Stoloniferous basal leaves subopposite, not rosulate *herbs*. Abaxial surfaces of *basal leaves* pubescent with mostly fine, flaccid, short-stalked, symmetrical, 5- to 10(–12)-rayed stellate trichomes 0.1–0.2(–0.3) mm wide; fewer simple trichomes are present proximally and subdendritic ones distally and marginally. *Stems* 10–20 mm, erect, with 0–2 cauline leaves. *Petals* white 3–4 mm, 2 × length and width of *sepals*; *anthers* truncate, 0.3–0.4 mm. *Styles* terete, (0.30–)0.50–0.75 mm. *Fruit* not inflated, surfaces with fine, short-stalked, 4- to 8-rayed stellate trichomes 0.1–0.2 mm wide. *Fruiting raceme* open, 2- to 7(–9)-fruited; pedicels spreading-ascending to ascending, basally ebracteate. *Seeds* brown, 1.1–1.3 mm.

Eponymy: this species is named after a former colleague, Stephen Darbyshire.

Additional specimens examined: CANADA. Yukon, Useful Lake: 50 km SSW of Old Crow, 67˚11'N, 140˚26'W, limestone ridge, 12 July 1975, *L. C. Cwynar 262* (DAO). All Mackenzie District, Northwest Territories. Site 14:m. Dryas tundra polygonal community, 69˚20'N, 125˚54'W, 275 m, July 20, 1978, *G. W. Scotter & S. Zoltai 25903* (DAO). Site 9, 68˚39'N, 121˚15'W, 730 m, 6 July 1990, *G. W. Scotter & S. Zoltai 90-315* (DAO); Site 2, Hornaday Lake, 68˚42'N, 120˚48'W, 513 m, *G. W. Scotter 90-34*, *90-138*, and *90-152A*, 24 July 1990 (DAO); Site 7, 68˚33'N, 120˚46'W, 490 m, *G. W. Scotter & S. Zoltai 90-262*, 25 July 1990 (DAO); Croker River Canyon, 69˚06'N, 119˚30'W, 340 m, *G. W. Scotter & S. Zoltai 90-378*, 27 July 1990 (DAO); Site 17, 69˚18'N, 119˚56'W, 180 m, *G. W. Scotter & S. Zoltai 90-464*, 27 July 1990 (DAO); Site 26, 68˚23'N, 120˚06'W, 480 m, 30 July 1990, *G. W. Scotter & S. Zoltai 90-602* and *90-602a* (DAO); Site 37, 68˚33'N, 121˚05'W, 1 August 1990, *G. W. Scotter & S. Zoltai 90-745B* (DAO).

Draba darbyshireii is the only stoloniferous perennial in North America with mostly fine, flaccid, short-stalked, symmetrical, 5- to 10(–12)-rayed stellate trichomes.

4. Draba shehbazii G.A. Mulligan, *sp. nov*. TYPE: CANADA. Northwest Territories, Mackenzie District, Mackenzie River Delta: northeast side of Richards Island; Kidluit Bay, 69˚31'N, 133˚48'W, localized on moist sandy slope by small lake, 32 July 1957, *W. J. Cody & D. H. Ferguson 10186* (Holotype: DAO).

Perennial, cespitose, not pulvinate *herbs*; *caudex* loosely to tightly branched with the remains of previous seasons. Stems with 1–3(–4) cauline leaves, lowest 1–2 cm wide. *Caudex leaves* abaxially with short-stalked, asymmetrical, substellate trichomes (0.25–)0.30–0.40 mm wide. Petals white; proximally narrow, broad distally. Anthers orbiculate to broadly cordate, 0.20–0.25(–0.30) mm long. Fruit inflated, narrowly to broadly elliptic. Stigmas suborbiculate to ovate. *Fruit, racemes, and stems* sparely to densely pubescent with fine, short-stalked, divergent, few- to >10-rayed substellate trichomes 0.2–0.3 mm wide. *Fruiting pedicels* strongly ascending. *Fruit* often aborted or asymmetrical; basally with very prominent protruding and fused remnants of nectar glands. Possibly allogamous.

Eponymy: this species is named after Dr. Ihsan A. Al-Shehbaz, an authority on the systematics of plants of the family Brassicaceae.

Additional specimens examined: CANADA. Mackenzie District, Northwest Territories: Mackenzie River Delta: northeast side of Richards Island; Kidluit Bay, 69˚31'N, 133˚48'W, localized on moist sandy slope by small lake, flowers white, 32 July 1957, *W. J. Cody & D. H. Ferguson 10187* (Holotype: DAO). Mackenzie River Delta: North Point Richards Island, west of Hansen Harbour, 69˚38'N, 134˚20'W, lake bank, 12 July 1963, *W. J. Cody 12636* (DAO). Campbell Lake, 10 miles southeast of Inuvik, 68˚14'N, 133˚28'W, rare, shallow soil crevice of limestone talus slope, 14 July 1963, *W. J. Cody & F. Kehoe 12676* (DAO), *n* = 24 by G. A. Mulligan on plants grown from seeds taken from this collection. Reindeer Grazing Preserve, Bird Refuge, South Boundary Marker, west bank of Anderson River, few, July 17, 1965, *G. W. Scotter 7189* (DAO); *n* = 24 by *G. A. Mulligan* on plants grown from seeds taken from this collection. "BB" Lake, 3 miles SE of Indian Mountain Lake, 63˚02'N, 110˚57'W, very shallow soil over igneous rocky slope, 8 August 1966, *W. J. Cody 16017* (DAO). Pethei Peninsula, S of Talthrilei Narrows, 62˚28'N, 111˚37'W. Great Slave Lake. Very shallow soil on cliff ledges. 10 August 1966, *W. J. Cody 16058* (DAO), *n* = 24 by *G. A. Mulligan* on plants grown from seeds taken from this collection. Bluenose Lake Area, Melville Hills Region, 510 m, 68˚17'N, 121˚14'W, 26 July 1990, *G. W. Scotter & S. Zoltai 90-366* (DAO). Bluenose Lake Area, La Ronciere Falls, 215–275 m, 69˚08'N, 122˚52'W, 31 July 1990, *G. W. Scotter & S. Zoltai 90-691* (DAO).

Miscellaneous New Records And Information

1. *Draba adamsii* Ledebour, Fl. Ross. 1:147. 1871, *non Draba pauciflora* R. Brown, Chlor. Melvill., 266. 1823.

In Canada, *Draba adamsii* is a plant of the high arctic islands of Franklin District, from 73˚ to 81˚ N and in Alaska at 71˚ N. The name *D. pauciflora* is based on plant material collected by Parry on Iglooik Island that was deposited in K. However, Reider Elven searched in vain for material of the high arctic species in K in the 1990s and in 2006. He was only able to find Parry specimens of *D. microcarpa*. I have seen it and other material of *D. microcarpa* from Iglooik Island but no specimens of the high arctic plant that I call *D. adamsii*. I do not think that *D. adamsii* is present on Iglooik Island. I believe that *D. pauciflora* should be considered a synonym of *D. microcarpa*.

2. The chromosome numbers in Taylor and Mulligan (1968) of $n = 19$ and $2n = 36$ for *Draba hyperborea* should be attributed to *D. grandis* Langsdorff and the number $n = 8$ for *D. lonchocarpa* var. *kamtschatica* to *D. chamissonis* G. Don.

3. *Draba kluanei* G.A. Mulligan was previously known only from the holotype collection: Canada, Yukon, Kluane

National Park, Hoge Creek, ca. 31 km SSW of Burwass Landing on rocky alpine slope: aspect SW, slope 25%, elev. ca. 1980 m, 61°17'N, 139°35'W, 8 July 1976, *G. W. Scotter, G. G. Douglas & L. Freese 9845* (DAO). It is now known to also occur at a nearby location: Canada, Yukon, Kluane National Park, Wade Mountain, 61°18'N, 139°33'W, alpine tundra, W-facing slope of 5 degrees, 100% vegetative cover, organic soil in seep, 28 June 2002, *P. Caswell 251* (DAO).

4. ***Draba macrocarpa*** Adams has been considered a synonym of *D. corymbosa* Brown *ex* DC (Al-Shehbaz et al. (2010). However, I feel that *D. macrocarpa* is a separate species quite distinct from *D. corymbos*a. The stigmas of *D. macrocarpa* are capitate to semicapitate, 0.40.5–(0.5) mm wide; styles are truncate and never winged; petals are gradually narrowed from above the middle; nectar glands are large, and fruit frequently abort and/or are asymmetrical. *Draba macrocarpa* may be allogamous. Both *D. macrocarpa* and *D. corymbosa* are cespitose perennials with rosettes of the year above old rosettes and rosette remnants. These form a long, closely subtended series in *D. macrocarpa* but not in *D. corymbosa*. The stigmas of *D. corymbosa* are (0.50–)0.65–0.90 mm wide and compressed parallel to septum; styles are broadly winged; petals are broadly obovate except for a short stalk proximally; nectar glands are smaller, and fruit are usually symmetrical and well formed. *Draba corymbosa*, like many species of *Draba*, is probably autogamous.

5. Al-Shehbaz et al. (2010) correctly pointed out that the *Draba paysonii* of Mulligan (1971b) should be attributed to *D. novolympica* Payson & St. John.

6. Two collections of a new species were discovered by Ihsan A. Al-Shehbaz during a study of specimens of Canadian *Draba* sent to him for determination. He named the new species *Draba bruce-bennettii* after one of the collectors (Al-Shehbaz, 2016). The two collections, both from southwestern Yukon, Canada, are: Langham Mountain, 19 July 2012, 62.25057°N, 138.04092°W, 1898 m, *B. A. Bennett & S. G. Cunnings 12-0195* (Holotype: MO 6598201; Isotype: BABY 8349); and Triptop Mountain, 62.21593°N, 137.51984°W, 1836 m, 19 July 2012, *B. A. Bennett & S. G. Cannings 12-0205* (MO 6598200).

KEY TO *DRABA* OF CANADA AND ALASKA

1a. Annuals, winter annuals, biennials, or short-lived perennials (lacking rosette remnants of previous years) 2
1b. Long-lived perennials 7
2a. Annuals or winter annuals 3
2b. Biennials or short-lived perennials 5
3a. Stems scapose or with a single cauline leaf 4
3b. Stems with 3 or more cauline leaves. Sporadically naturalized . . . . ***Draba nemorosa*** **L.**
4a. Petals white, deeply lobed. Fruit less than 3 × as long as wide . . . . ***Draba verna*** **L.**
4b. Petals yellow, entire or slightly emarginated at apex. Fruit more than 4 × as long as wide . . . . ***Draba reptans*** **(Lamark) Fernald**
5a. Surfaces of fruit with stellate and/or substellate trichomes. Fruit nearly terete. Petals white . . . . ***Draba yukonensis*** **A.E. Porsild**
5b. Surfaces of fruit glabrous or with sparse simple trichomes. Fruit flattened. Petals yellow 6
6a. Abaxial surfaces of basal leaves with short-stalked 3- and 4-rayed trichomes 0.25–0.35 mm wide; occasionally glabrous. Petals yellow, often purple-tinged . . . . ***Draba albertina*** **Greene**
6b. Abaxial surfaces of basal leaves glabrous or ciliate with soft, mostly simple trichomes up to 0.5 mm long. Petals pale yellow, not purple-tinged . . . . ***Draba crassifolia*** **Graham**
7a. Plants stoloniferous 8
7b. Cespitose perennials 11
8a. Surfaces of fruit glabrous or with short, simple or few-branched trichomes 9
8b. Surfaces of leaves glabrous or pubescent with simple and/or few-branched trichomes; rayed trichomes absent . . . ***Draba oligiviensis*** **Hultén**
9a. Leaves abaxially with short-stalked cruciform trichomes . . . . ***Draba juvenilis*** **Komarov**
9b. Leaves abaxially with stellate and/or substellate trichomes 10
10a. Leaves abaxially with substellate and few-branched trichomes . . . . ***Draba ventosa*** **A. Gray**
10b. Leaves abaxially mostly with fine flaccid, short-stalked, symmetrical, 5- to 10(–12)-rayed stellate trichomes; with fewer simple ones proximally and subdendritic ones distally and marginally . . . . ***Draba darbyshireii*** **G.A. Mulligan**
11a. Abaxial surfaces of caudex leaves glabrous. Cauline leaves absent 12
11b. Abaxial surfaces of caudex leaves sparsely to densely pubescent. Cauline leaves none to many 15
12a. Midveins on abaxial surfaces of caudex leaves prominent, raised, and long-persisting 13
12b. Midveins on abaxial surfaces of caudex leaves neither prominent nor long-persisting 14
13a. Petals white. Abaxial midveins thick . . . . ***Draba lactea*** **Adams**
13b. Petals yellow. Abaxial midveins long-lanceolate . . . . ***Draba pilosa*** **DC.**
14a. Short-lived perennial; remnants of old rosettes few or lacking . . . . ***Draba crassifolia*** **Graham**
14b. Cespitose perennial with a compacted caudex of stemmed and stemless new rosettes above old rosettes and rosette remnants . . . . ***Draba cayouettei*** **G.A. Mulligan & Al-Shehbaz**
15a. Pubescence on abaxial surfaces of caudex leaves distinctly crisped 16
15b. Pubescence on abaxial surfaces of caudex leaves not crisped 17

Key to *Draba* of Canada and Alaska cont.

16a. Not pulvinate. Petals white. Anthers dehiscent . . . . *Draba puvirnituqii* **G.A. Mulligan & Al-Shehbaz**

16b. Pulvinate. Petals pale yellow. Anthers indehiscent . . . . *Draba taylori* **G.A. Mulligan & Al-Shehbaz**

17a. Perennial with fleshy caudex. Fruit (6–)10–25 mm long . . . . *Draba grandis* **Langsdorff**

17b. Perennials, caudexes not fleshy. Fruit mostly less than 10 mm long, often much smaller 18

18a. Fruit mostly with rayed and/or subrayed trichomes 19

18b. Fruit glabrous or with simple and/or branched trichomes; stellate and/or substellate trichomes rare or absent 32

19a. Petals yellow. Styles over 0.5 mm long 20

19b. Petals white. Styles up to 0.5 mm long 22

20a. Anthers dehiscent. Abaxial surfaces of caudex leaves pubescent with short-stalked, 4-rayed (cruciform) trichomes. Stems with 10 or more cauline leaves . . . . *Draba aurea* **Vahl *ex* Hornemann**

20b. Anthers indehiscent. Stems scapose or nearly so 21

21a. Abaxial surfaces of caudex leaves with long-stalked (3–)4(–5)-rayed stellate trichomes. Stems scapose . . . . *Draba paysonii* **J.F. Macbr.**

21b. Abaxial surfaces of caudex leaves densely pubescent with tangle of medium to very long stalked 2- to 6(–9)-rayed stellate and substellate trichomes. Stems scapose or nearly so . . . . *Draba ventosa* **A. Gray**

22a. Abaxial surfaces of basal leaves pubescent with simple and/or branched trichomes, at least marginally and distally; symmetrical stellate trichomes few or absent 23

22b. Abaxial surfaces of basal leaves pubescent with stellate and/or substellate trichomes; simple or branched trichomes very few or absent . 25

23a. Short-lived perennial with 2–4 cauline leaves. Abaxial surfaces of caudex leaves pubescent with simple trichomes to 1 mm long or slightly longer. Fruit nearly terete . . . . *Draba yukonensis* **A.E. Porsild**

23b. Long-lived perennials, stems with (0–)1 cauline leaf. Abaxial surfaces of caudex leaves pubescent with coarse, simple and/or branched trichomes, at least distally and marginally. Fruit flattened 24

24a. Abaxial surfaces of caudex leaves pubescent with coarse, simple and/or branched trichomes distally and marginally; elsewhere with stalked, divergently branched, substellate trichomes. Anthers broadly cordate. Fruit pubescent with (2–)5- to 12-rayed trichomes . . . . *Draba oblongata* **R.Br. *ex* DC**.

24b. Abaxial surfaces of caudex leaves pubescent with coarse, simple and forked trichomes; rayed trichomes few or absent. Anthers broadly truncate. Fruit pubescent with mostly 3- and 4-rayed trichomes . . . . *Draba arctogena* **(E. Ekman) E. Ekman**

25a. Perennial with (15–)22–54(–75) densely overlapping cauline leaves . . . . *Draba incana* **L.**

25b. Perennials with 0–8(–16) cauline leaves; cauline leaves not overlapping 26

26a. Stems with (3–)4–8(–16) cauline leaves. Fruiting pedicels strongly ascending or appressed to rachis 27

26b. Stems with 0–3(–4) cauline leaves. Fruiting pedicels spreading, ascending to strongly ascending; none appressed to rachis 28

27a. Perennial, cespitose, often pulvinate. Fruiting raceme short; apical flower buds usually aborting. Fruit elliptic to narrowly elliptic, some asymmetrical; none twisted. Anthers broadly cordate to orbiculate, 0.15–0.20(–0.25) mm long . . . . *Draba catlingii* **G.A. Mulligan**

27b. Perennial, rarely cespitose, never pulvinate. Fruiting raceme elongated; apical flower buds rarely aborting. Fruit lanceolate to broadly lanceolate, symmetrical; often twisted. Anthers broadly cordate, (0.25–)0.30–0.40 mm long . . . . *Draba cana* **Rydberg**

28a. Stellate or substellate trichomes on abaxial surfaces of basal leaves mostly less than 3.0 mm wide 29

28b. Stellate or substellate trichomes on abaxial surface of basal leaves mostly 3.0 mm wide or wider 30

29a. Stoloniferous. Basal leaves subopposite; pubescent with fine, flaccid, short-stalked, symmetrical, 5- to 10(–12)-rayed stellate trichomes 0.1–0.2(–0.3) mm wide, fewer subdendritic ones marginally and distally . . . . *Draba darbyshirei* **G.A. Mulligan**

29b. Not stoloniferous. Basal leaves rosulate. Fruit with a minute, sparse to dense, simple to few-branched puberulence. Abaxial surfaces of leaves with sessile substellate trichomes less than 0.25 mm wide . . . . *Draba airdii* **G.A. Mulligan**

30a. Fruit inflated, narrowly to broadly elliptic. Fruit, racemes, and stems canescent with fine, short-stalked, divergent, few to more than 10-rayed substellate trichomes 0.2–0.3 mm wide. Fruit often aborted or asymmetrical, allogamous? Stigmas suborbiculate to ovate. Abaxial surfaces of caudex leaves with asymmetrical substellate trichomes (0.25–)0.30–0.40 mm wide. Possibly stoloniferous . . . . *Draba shehbazii* **G.A. Mulligan**

30b. Fruit flattened 31

31a. Fruit trichomes coarse, cruciform to branched cruciform with spreading rays. Anthers truncate, 0.4–0.5 mm long. Abaxial surfaces of basal leaves with coarse, subsessile, spreading-rayed stellate trichomes . . . . *Draba arctica* **J. Vahl s. l.**

31b. Fruit trichomes fine, substellate and asymmetrical. Anthers broadly cordate. Abaxial surfaces of basal leaves with short- to medium-stalked, divergently ascending, stellate trichomes . . . . *Draba cinerea* **Adams s. l.**

32a. Abaxial surfaces of caudex leaves pubescent with symmetrical or asymmetrical stellate trichomes 33

32b. Abaxial surfaces and/or margins of caudex leaves pubescent with simple and/or branched trichomes 63

33a. Abaxial surfaces of caudex leaves predominantly with symmetrical stellate trichomes 34

33b. Abaxial surfaces of caudex leaves predominantly with asymmetrical substellate trichomes 59

34a. Symmetrical stellate trichomes on abaxial surfaces of caudex leaves stalkless (sessile) 35

34b. Symmetrical stellate trichomes on abaxial surfaces of caudex leaves stalked 36

35a. Perennial, cespitose; subpulvinate. Stems scapose. Petals yellow. Anthers indehiscent . . . . *Draba oligosperma* **Hooker**

35b. Perennial, not cespitose. Stems with 4–10 cauline leaves. Petals white. Anthers dehiscent . . . . *Draba arabisans* **Michaux**

36a. Symmetrical stellate trichomes on abaxial surfaces of caudex leaves predominantly long to very long stalked 37

36b. Symmetrical stellate trichomes on abaxial surfaces of caudex leaves predominately short- and/or medium-stalked 38

Key to *Draba* of Canada and Alaska cont.

37a. Cespitose perennial; densely pulvinate. Rosette leaves 0.5–1.5 mm wide. Anthers usually indehiscent. Possibly apomictic . . . . *Draba novolympica* **Payson & H. St. John**

37b. Cespitose perennial; not pulvinate. Rosette leaves 1.5–4.5 mm wide. Anthers dehiscent . . . . *Draba ruaxes* **Payson & H. St. John**

38a. Symmetrical stellate trichomes on abaxial surfaces of caudex leaves 3- and/or 4-rayed 39

38b. Symmetrical stellate trichomes on abaxial surfaces of caudex leaves mostly 5- or more rayed. 46

39a. Cespitose perennials 40

39b. Biennials and/or noncespitose perennials 42

40a. Pulvinate. Trichomes on abaxial surfaces of basal leaves 3- and 4-rayed. Valves of fruit inflated basally into pouch. Petals bright yellow . . . . *Draba bruce-bennettii* **Al-Shehbaz**

40b. Not pulvinate. Trichomes on abaxial surfaces of basal leaves 4-rayed (cruciform). Valves of fruit flat. Petals white or, if yellow, often tinged with purple 41

41a. Stems 9–30 cm tall with 1–3(–6) cauline leaves. Petals white, 3–5 mm long; styles 0.75–2.00 mm long, Fruit linear-lanceolate to narrowly elliptic. Racemes usually 10- or more fruited . . . . *Draba murrayi* **G.A. Mulligan**

41b. Stems (0.5–)1.0–8.0 cm tall, scapose. Petals yellow, often purple-tinged; styles less than 0.25 mm long. Fruit elliptic to broadly elliptic. Racemes (2–)3- to 9-fruited . . . . *Draba adamsii* **Ledebour**.

42a. Stems with more than 10 cauline leaves. Racemes proximally bracteate . . . . *Draba aurea* **Vahl *ex* Hornemann**

42b. Stems with less than 10 cauline leaves. Racemes not bracteate 43

43a. Petals white, 4–8 mm long. Fruit often twisted, some aborted. Cruciform trichomes on abaxial surfaces of caudex leaves often 1- to few-spurred . . . . *Draba borealis* **DC.**

43b. Petals yellow, 2–4 mm long. Fruit neither twisted nor aborted. Cruciform trichomes on abaxial surfaces of caudex leaves never spurred . 44

44a. Caudex loosely branched. Styles 0.25–0.70 mm long. Basal leaves with very short stalked cruciform trichomes 0.25-0.50 mm wide. Anthers 0.4–0.5 mm long . . . . *Draba juvenilis* **Komarov**

44b. Caudex not loosely branched. Styles shorter than 0.25 mm. Basal leaves with cruciform trichomes 0.20–0.35 mm wide. Anthers 0.15–0.40 mm long 45

45a. Short-lived perennial. Abaxial surfaces of basal leaves glabrous or with 3- and 4-rayed trichomes 0.25 to 0.35 mm wide. Petals yellow, often purple-tinged, 2.0–2.5(–3.0) mm long . . . . *Draba albertina* **Greene**

45b. Perennial with compacted caudex. Abaxial surfaces of rosette leaves with 3- and 4-rayed trichomes up to 0.2 mm wide. Petals yellow, (2.5–)3.5–4.0 mm long . . . . *Draba stenoloba* **Ledebour**

46a. Biennial or short-leaved perennial, frequently lacking remnants of caudex leaves of previous years. Anthers less than 0.25 mm long. Petals creamy yellow, often fading to white . . . . *Draba praealta* **Greene**

46b. Perennials with many remnants of caudex leaves of previous years. Anthers more than 0.25 mm long. Petals yellow or white 47

47a. Symmetrical stellate trichomes on abaxial surfaces of basal leaves mostly more than 0.4 mm wide 48

47b. Symmetrical stellate trichomes on abaxial surfaces of basal leaves mostly less than 0.4 mm wide. 51

48a. Petals white. Stems with (1–)2–17(–25) cauline leaves 49

48b. Petals yellow. Stems usually scapose . . . . *Draba incerta* **Payson**

49a. Symmetrical stellate trichomes on abaxial surfaces of basal leaves stalked. Fruit not twisted. Racemes rarely basally bracteate 50

49b. Symmetrical stellate trichomes on abaxial surfaces of basal leaves sessile or nearly so. Fruit often twisted. Racemes usually basally bracteate. . . . . *Draba arabisans* **Michaux**

50a. Fruit flattened. Stems 15–25(–45) cm tall. Stellate trichomes on surfaces of basal leaves mostly 8- or more rayed, many with longer axes; cruciform trichomes rare or absent . . . . *Draba glabella* **Pursh**

50b. Fruit strongly inflated. Stems 5–10 cm tall. Stellate trichomes on surfaces of basal leaves mostly 4-rayed (cruciform). . . . . *Draba pycnocarpa* **Fernald & Knowlton**

51a. Stigmas 0.1 mm wide, markedly narrowed perpendicularly to septum and extending decurrently to base of style. Leaves, rachis, and stems pubescent with very flaccid symmetrical stellate trichomes . . . . *Draba caswellii* **G.A. Mulligan & Al-Shehbaz**

51b. Stigmas much wider than 0.1 mm; not markedly narrowed perpendicularly to septum. Leaves rachis and stem lack flaccid stellate trichomes 52

52a. Styles 0.50–0.75(–1.00) mm long. Petals yellow (at least proximally) 53

52b. Styles less than 0.5 mm long. Petals white 54

53a. Petals yellow. Fruit lanceolate to narrowly ovate, symmetrical, not aborting. Symmetrical stellate trichomes on abaxial surfaces of basal leaves (0.25–)0.30–0.40 mm wide . . . . *Draba scotteri* **G.A. Mulligan**

53b. Petals white, usually tinged yellow proximally. Fruit narrowly elliptic, often aborting or asymmetrical. Symmetrical stellate trichomes on abaxial surfaces of basal leaves 0.15–0.35 wide . . . . *Draba palanderiana* **Kjellman**

54a. Sepals, petals, and stamens long-persisting. . . . . *Draba franktonii* **G.A. Mulligan & Al-Shehbaz**

54b. Sepals, petals, and stamens caducous 55

55a. Fruit not twisted. 56

55b. Some fruit twisted 57

56a. Rachis, stems, and surfaces of rosette leaves densely pubescent with short-stalked, symmetrical, stellate trichomes 0.05–0.20 mm wide . . . . *Draba nivalis* **Liljeblad**

56b. Rachis glabrous. Stems glabrous or sparsely pubescent proximally. Petiolar bases and proximal margins of rosette leaves ciliate with stiff, subsetiform, simple trichomes 0.3–0.6 mm long. Abaxial surfaces of rosette leaves pubescent with short-stalked 9- to 12-rayed stellate trichomes; rarely glabrous with trichomes confined to margins. Alaska: 300–1600 m . . . . *Draba mulliganii* **Al-Shehbaz**

Key to *Draba* of Canada and Alaska cont.

57a. Fruit narrowly linear to linear, some twisted; fruiting pedicels appressed to rachis . . . . ***Draba chamissonis* G. Don**

57b. Fruit linear, lanceolate, or oblong, mostly twisted; fruiting pedicels not appressed to rachis 58

58a. Fruit linear to lanceolate, mostly less than 1 mm wide. Stigmas 0.35–0.45 mm wide; styles rarely slightly wider than stigmas . . . . ***Draba lonchocarpa* Rydberg**

58b. Fruit oblong, 2.5–3.0 mm wide. Stigmas to 0.3 mm wide, often much narrower; styles usually much broader than stigmas . . . . ***Draba thompsonii* (C.L. Hitchc.) G.A. Mulligan & Al-Shehbaz**

59a. Asymmetrical substellate trichomes on abaxial surfaces of caudex leaves setaceous. Filaments greatly expanded below middle. Petals bright yellow . . . . ***Draba healyi* G.A. Mulligan & Al-Shehbaz**

59b. Asymmetrical substellate trichomes on abaxial surfaces of caudex leaves not setaceous. Filaments not greatly expanded below middle. Petals either white or yellow 60

60a. Petals yellow, narrowly spatulate with nearly parallel sides. Stigmas flat-capitate . . . . ***Draba micropetala* Hooker**

60b. Petals white, without parallel sides. Stigmas not capitate 61

61a. Biennial or short-lived perennial. Stems with (15–)22–54(–75) densely overlapping cauline leaves . . . . ***Draba incana* L.**

61b. Cespitose perennials with fewer than 6 cauline leaves, these not overlapping 62

62a. Stems with (0–)1–3(–5) cauline leaves. Abaxial midveins of caudex leaves not thickened, raised, or long-persisting . . . . ***Draba norvegica* Gunnerus**

62b. Stems with 0(–1) cauline leaves. Abaxial midveins of caudex leaves proximally thickened, raised, and long-persisting . . . . ***Draba porsildii* G.A. Mulligan**

63a. Simple and/or branched trichomes on abaxial surfaces of caudex leaves distinctly crooked or crispated 64

63b. Simple and/or branched trichomes on abaxial surfaces of basal leaves neither crispated nor crooked 66

64a. Abaxial surfaces of basal leaves pubescent with crooked, simple or branched trichomes. Stems with 1–2(–3) cauline leaves . . . . ***Draba kluanei* G.A. Mulligan**

64b. Abaxial surfaces of basal leaves sparsely to densely pubescent with crispated, simple or branched trichomes. Stems scapose 65

65a. Stems and rachis densely pubescent with simple and branched crispated trichomes. Petals white. Anthers 0.3–0.4 mm long, dehiscent . . . . ***Draba puvirnituqui* G.A. Mulligan & Al-Shehbaz**

65b. Stems and rachis glabrous or nearly so. Petals pale yellow. Anthers 0.5–0.75 mm long, indehiscent (possibly apomictic) . . . . ***Draba taylori* G.A. Mulligan & Al-Shehbaz**

66a. Stigmas 0.1–0.3 mm wide 67

66b. Stigmas at least 0.4 mm in diam.; often much wider 73

67a. Stems, rachis, and pedicels densely pubescent with soft, spreading, simple trichomes 0.75–1.00 mm long . . . . ***Draba bennettii* G.A. Mulligan & Al-Shehbaz**

67b. Trichomes on stems, rachis, and pedicels neither spreading nor more than 0.5 cm long 68

68a. Cespitose perennials. Midveins on abaxial surfaces of caudex leaves raised, long-persisting, thickened to apex 69

68b. Biennial and/or perennial species. Midveins on abaxial surfaces of basal leaves not thickened to apex 71

69a. Plants pulvinate-cespitose. Stems scapose 70

69b. Plants delicate, never pulvinate; Stems with (0–)1–2 cauline leaves . . . . ***Draba fladnizensis* Wulfen**

70a. Petals yellow. Anthers indehiscent (possibly apomictic). Stigmas capitate . . . . ***Draba densifolia* Nuttall *ex* Torrey & Gray**

70b. Petals white. Anthers dehiscent. Stigmas compressed parallel to septum . . . . ***Draba subcapitata* Simmons**

71a. Biennial or short-lived perennial. Basal leaves few or are lacking . . . . ***Draba crassifolia* Graham**

71b. Cespitose perennials with persistent caudex leaves and remnants of leaves of many previous years 72

72a. Anthers broadly deltate, 0.25–0.35 mm long. Fruit ovate to elliptic, inflated proximally, 4–8 mm long . . . . ***Draba macounii* O.E.Schulz**

72b. Anthers narrowly deltate, 0.4–0.5 mm long. Fruit lanceolate, 5.5—9.0(–11.0) mm long; slightly flattened . . . . ***Draba simmonsii* Elven & Al-Shehbaz**

73a. Petals white. 4- to 12-branched subdendritic trichomes present on distal surfaces of basal leaves . . . . ***Draba lactea* Adams**

73b. Petal yellow. 4- to 12-branched subdendritic trichomes on basal leaves lacking 74

74a. Stigmas and styles slightly to extremely compressed parallel to septum; styles winged. Petals broadly obovate distally and abruptly narrowed to a short blade proximally . . . . ***Draba corymbosa* R. Br. *ex* DC.**

74b. Stigmas and styles capitate or only slightly compressed parallel to septum. Styles narrower than stigmas, never winged 75

75a. Cespitose perennials, pulvinate 76

75b. Cespitose perennials, never pulvinate 77

76a. Fruit suborbicular, flattened distally; glabrous or with sparse pubescence. Stigmas globose or dome-shaped, 0.50–0.75 mm. Petals yellow, purple-tinged, narrowly linear, 2.5–5.0 mm long; much narrower than sepals. Anthers deltoid, 0.40–0.65 mm long . . . . ***Draba stenopetala* Trautvetter**

76b. Fruit broadly obovoid, subglobose, or suborbicular; strongly inflated; glabrous or puberulent. Petals yellow-green to pale yellow; linear-oblanceolate, 3–4 mm long. Anthers oblong, 0.3–0.5 mm long . . . . ***Draba aleutica* Ekman**

77a. Rosettes of the present year, old rosettes, and rosette remnants all closely subtended. Fruit often aborting or asymmetrical . . . . ***Draba macrocarpa Adams***

77b. Rosettes of present year, old rosettes, and rosette remnants not closely subtended. Fruit neither aborting nor asymmetrical 78

78a. Fruiting racemes elongated. Rosette leaves oblanceolate to oblong. Abaxial leaf midveins obscure, not thickened . . . . ***Draba alpina* L.**

78b. Fruiting racemes semiracemose or semicorymbose. Rosette leaves linear. Abaxial leaf midveins thick, long-lanceolate, raised, and persistent . . . . ***Draba pilosa* DC.**

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NOTES ON SOME MALESIAN ORCHIDACEAE III

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Abstract. Eleven new combinations are proposed in the recently established genus *Blepharoglossum*. Further, six names are found to be synonyms of earlier taxa in other genera and are here reduced to synonymy. Five names are also lectotypified, namely *Dendrobium hastilabium, Eria dura, E. gracilicaulis, Habenaria zollingeri,* and *Trichotosia microbambusa*.

This paper is a continuation of previous efforts (Ormerod et al., 2019; Ormerod and Juswara, 2019; Ormerod and Kurzweil, 2019) to update the knowledge of Malesian orchids. The basic Malesian area extends from the Malaysian peninsula to the Solomon Islands, an area dominated by large tropical islands such as Borneo, Sumatra, Java, Sulawesi, and New Guinea.

Here we again deal with some former members of the genus *Liparis* L.C. Rich. (490–500 species in the broad sense) by transferring them to the recently established concept *Blepharoglossum*. Another problem that besets taxonomists is rather ambiguously described species for which types do not seem to exist, and of which no published illustrations are available either. Fortunately we have been able to resolve six such cases here, of which three taxa disappear into synonymy.

Bambuseria Schuit., Y.P. Ng & H.A. Pedersen, Bot. J. Linn. Soc. 186: 193. 2018.

Basionym: *Eria* Lindl. section *Bambusifolia* J.D. Hook., Fl. Brit. Ind. 5: 786. 1890.

Type species: *Eria bambusifolia* Lindl.

Homotypic synonym: *Pinalia* Lindl. section *Bambusifolia* (J.D. Hook.) O. Kuntze, Lexicon Gen. Phan.: 439. 1904.

Distribution: two species found from northern India to Thailand.

Though this genus does not occur in the Malesian region, one species erroneously accredited to New Guinea does belong here.

Bambuseria crassicaulis (J.D. Hook.) Schuit., Y.P. Ng & H.A. Pedersen, Bot. J. Linn. Soc. 186: 193. 2018.

Basionym: *Eria crassicaulis* J.D. Hook., Fl. Brit. Ind. 5: 805. 1890. TYPE: INDIA. Khasia Mountains, Pomrang and *Hort. Cave*, 1220–1525 m, 13 November 1850, *J. D. Hooker & T. Thomson s.n.* (Syntypes: K, K-L, images seen); fl. in cult. December 1866, *cult. Hort. Kew. s.n.* (Syntype: K, not seen); drawing in *Herb. Calcutta* (Syntype: CAL).

Homotypic synonyms: *Pinalia crassicaulis* (J.D. Hook.) O. Kuntze, Rev. Gen. Pl. 2: 679. 1891.

Trichotosia crassicaulis (J.D. Hook.) Kraenzl., Bot. Jahrb. Syst. 44, Beibl. 101: 22. 1910.

Cylindrolobus crassicaulis (J.D. Hook.) Brieger, in Schltr., Die Orchideen ed. 3, 1: 664. 1981.

Heterotypic synonyms: *Eria micholitziana* Kraenzl., Notizbl. Konigl. Bot. Gard. Berl. 3: 21. 1900 *syn. nov.* TYPE: “NEW GUINEA.” *Leg. W. Micholitz, imp. Messrs. Sander & Co.,* fl. in cult. November 1899, *cult. Berlin Bot. Gart. s.n.* (Holotype: B, destroyed; Isotype: HBG, image and drawing seen).

Pinalia micholitziana (Kraenzl.) O. Kuntze, Deutsch. Bot. Monatschr. 21: 173. 1903.

Usage synonym: *Eria clavicaulis auct. non* Wall. ex Lindl.: Lindl., J. Proc. Linn. Soc., Bot. 3: 59. 1858.

Distribution: India; Myanmar (?).

Eria micholitziana was supposedly collected by Wilhelm Micholitz for Messrs. Sander in New Guinea. A specimen obtained by the Berlin Botanic Garden flowered there in November 1899. However, the protologue of *E. micholitziana* describes a glabrous plant with pubescent inflorescence and flowers, reflexed floral bracts, and a circular lip. This combination of features is unknown among Malesian Eriinae but agrees fully with *Bambuseria crassicaulis*. The critical floral features were also confirmed in a sketch of the isotype of *E. micholitziana* kindly supplied by Dariusz Szlachetko.

Eria crassicaulis was based on three elements, namely, flowerless plants collected by Hooker and Thomson, a plant cultivated at Kew, and a drawing from the Calcutta Botanic Garden. The latter drawing was partly published by Hooker (1892) and shows various floral features, such as a strongly trilobed lip with a thick basal callus that extends as a medial line of hairs that ends in a papillose band on the upper half of the midlobe. In the cultivated Kew specimen, however, the lip is circular and weakly trilobed and the keels are mealy and papillose, with the midlobe totally mealy-papillose.

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Blepharoglossum (Schltr.) L. Li, Pl. Syst. Evol. 306:54: 6. 2020.

Basionym: *Liparis* L.C. Rich. section *Blepharoglossum* Schltr., Rep. Sp. Nov. Regni Veg., Beih. 1: 199. 1911.

Type species (van Royen 1979: 697): *Liparis latifolia* Lindl.

Homotypic synonyms: *Cestichis* Pfitz. section *Blepharoglossum* (Schltr.) M.A. Clem. & D.L. Jones, Orchadian 15, 1: 40. 2005.

Cestichis Pfitz. section *Laxiflorae* Pfitz., in Engl. & Prantl., Naturl. Pflanzenfam. 2, 6: 131. 1889.

Type species: *Liparis latifolia* Lindl.

Distribution: about 39 species distributed from China to Fiji.

The genus *Blepharoglossum* was recently proposed by Lin Li (in Li et al., 2020) after molecular studies showed that species belonging to *Liparis* L.C. Rich section *Blepharoglossum* Schltr. formed a phylogenetically distinct group more closely related to *Oberonia* Lindl. than *Cestichis* Pfitz. Previously it had been supposed that section *Blepharoglossum* belonged in the genus *Cestichis* Pfitz. because both groups are pseudobulbous epiphytes with conduplicate leaves, have similar-sized flowers, and possess similar floral structures (slender column and basal callus or calli usually present on the labellum).

Li et al. (2020) included 26 species in *Blepharoglossum*, of which we exclude *Liparis werneri* Schltr. from Papua New Guinea. This species has nonarticulate leaves, unlike all other *Blepharoglossum,* which have the leaves articulate with the pseudobulbs.

Blepharoglossum beccarii (Ridl.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis beccarii* Ridl., J. Linn. Soc., Bot. 22: 284. 1886. TYPE: INDONESIA. Sumatra, Padang Highlands, Mt. Singgalang, 1700 m, June to July 1878, *O. Beccari 380* (Holotype: K, image seen; Isotype: FI 013472, image seen).

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

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

Distribution: Indonesia (Sumatra).

Additional specimen examined: INDONESIA. Sumatra, Mt. Sago, N slope, 1800–2000 m, 19 August 1956, *J. Jacobs 4662* (A).

Blepharoglossum bleyi (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis bleyi* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 9: 485. 1928. TYPE: INDONESIA. Java, Semarang, *leg. G. Bley, cult. Hort. Bogor. s.n.* (Holotype: BO, not found).

Usage synonym: *Liparis dendrochilum* auct. non Rchb.f.: J.J. Sm., Orch. Java: 274. 1905.

Distribution: Indonesia (Java).

Blepharoglossum firmum (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis firma* J.J. Sm., Bull. Jard. Bot. Buitenz. s.2, 13: 7. 1914. TYPE: INDONESIA. Sulawesi, Kampoeng Masawa, Polewal, *L. van Vuuren Exped., cult. Hort. Bogor. 423* (Holotype: BO, not found; possible Isotype: L 0061550, image seen).

Distribution: Indonesia (Sulawesi).

Blepharoglossum fulgens (Rolfe) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis fulgens* Rolfe, Gard. Chron. s.3, 6: 620. 1889. TYPE: PHILIPPINES (?). Without locality, *cult. Messrs. F. Horsman & Co. s.n.* (Holotype: K).

Distribution: Philippines?

This species is treated as a synonym of *Liparis latifolia* Lindl. on the World Checklist of Seed Plants (WCSP) website. However, it differs from *Blepharoglossum latifolium* (Lindl.) L. Li et al. in having bifoliate (vs. unifoliate) pseudobulbs, a lip with oblong-elliptic (vs. subquadrate to cuneate), entire (vs. dentate to scalloped) lobules, and fleshier (not thinly lamellate) calli. Its origin was speculated to be the Philippines, but we have examined no matching material from there. We have seen a somewhat similar collection from Sulawesi (*M. Mendum et al. 0019* [A]), but it has trifoliate pseudobulbs and the lip has more rounded (vs. quadrangular) calli.

Blepharoglossum lauterbachii (Schltr.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis lauterbachii* Schltr., Bull. Herb. Boiss. s.2, 6: 308. 1906. TYPE: INDONESIA. Java, Mt. Ardjuno, near Tretes, 900 m, February 1890, *K. Lauterbach 4197* (Holotype: B, destroyed; Isotype: WRSL, not seen).

Distribution: Indonesia (Java).

Blepharoglossum longissimum (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis longissima* J.J. Sm., Bull. Jard. Bot. Buitenz. s.2, 13: 6. 1914. TYPE: INDONESIA. Kalimantan, Gunung Labang, *leg. Amdjah, cult. Hort. Bogor. 18* (Syntype: BO, not found; Isosyntypes: L 0061569, U 1470347, images seen); Gunung Djempanga, *leg. Amdjah, cult. Hort. Bogor. 70* (Syntype: BO, not found).

Homotypic synonym: *Stichorkis longissima* (J.J. Sm.) Marg., Szlach. & Kulak, Acta Soc. Bot. Polon. 77, 1: 38. 2008.

Distribution: Malaysia (Sarawak); Indonesia (Kalimantan).

Blepharoglossum maotiense (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis maotiensis* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 10: 125. 1928. TYPE: INDONESIA. Maluku Prov., Seram, Maoti Pass, 1200–1300 m, 30 January 1929, *L. Rutten 1978* (Syntype: BO;

Isosyntype: L, image seen); Hatoemeten Pass, S of Manosela, 500–600 m, 29 October 1917, *leg. Kornasi, L. Rutten 618* (Syntype: BO; Isosyntype: L, image seen).

Distribution: Indonesia (Maluku).

Blepharoglossum minahassae (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis minahassae* J.J. Sm., Icon. Bogor. 2: 43, t.109A. 1903. TYPE: INDONESIA. Sulawesi, Minahassa Peninsula, *leg. S. H. Koorders, cult. Hort. Bogor. s.n.* (Holotype: BO, not found).

Distribution: Indonesia (Sulawesi, North Maluku).

Additional specimens examined: INDONESIA. Sulawesi, Minahassa Prov., 19 January 1895, *S. H. Koorders 29533B* (L 1522509, image seen); Without locality data, [treated with soda sublimate December 1910], *cult. Hort. Bogor. 482* (AMES).

This species was described from living material collected by S. H. Koorders on the Minahassa Peninsula, Sulawesi. As with a number of orchids described from live collections by Smith in Icones Bogoriensis, it seems he did not preserve a type specimen. The dried Koorders collection in L was not seen by Smith until 1919; it had been earlier identified by Rolfe as *Liparis latifolia* Lindl. We do not believe the plant in AMES (*Hort. Bogor. 482*) is an isotype because of the date (December 1910) it was treated with soda sublimate (= mercuric chloride). It is our belief the insect treatment of Bogor specimens usually occurred shortly after preservation.

Blepharoglossum riparium (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis riparia* J.J. Sm., Rep. Sp. Nov. Regni Veg. 11: 557. 1913. TYPE: INDONESIA. Papua Prov., Noord River, May 1907, *G. M. Versteeg 1089* (Syntype: BO); foot of Nepenthes Hill, July 1907, *G. M. Versteeg 1348* (Syntype: BO); Reiger River mouth, *leg. Djibdja, cult. Hort. Bogor. 273* (Syntype: BO).

Usage synonym: *Liparis parviflora auct. non* (Blume) Lindl.: J.J. Sm., Nova Guinea 8, 1: 38. 1909.

Distribution: Indonesia (Papua).

Blepharoglossum tenellum (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis tenella* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 12: 149. 1932. TYPE: INDONESIA. Kalimantan, West Koetei, Long Liang Leng, 300 m, 1 September 1925, *F. H. Endert 3078* (Holotype: L, image seen; Isotype: BO).

Homotypic synonym: *Liparis tenuis* J.J. Sm., Bull. Jard. Bot. Buitenz. s.3, 11: 121. 1931 *nom. illeg.* (non Rolfe ex Downie 1925).

Distribution: Indonesia (Kalimantan).

Blepharoglossum trifoliatum (J.J. Wood & Ormerod) Ormerod & Juswara, *comb. nov.*

Basionym: *Liparis trifoliata* J.J. Wood & Ormerod, Males. Orch. J. 2: 117. 2008. TYPE: MALAYSIA. Sabah, Mt. Kinabalu, Bambangan River, 1500 m, 25 February 1964, *W. L. Chew & E. J. H. Corner RSNB 4529* (Holotype: K).

Distribution: Malaysia (Sabah).

Additional specimens examined: MALAYSIA. Sabah, Mt. Kinabalu, Tenompok, 1525 m, 16 July 1933, *C. E. Carr SFN 27820* (AMES, 2 sheets); Tenompok, 1370 m, 22 August 1931, *J. & M. S. Clemens 26123* (AMES).

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

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

A genus of 1600–1800 species distributed from Sri Lanka and India to Tahiti. Two of the species discussed below belong to section *Grastidium* Blume, the largest group in the genus. There are about 225 species of section *Grastidium,* 159 of which are so far found on New Guinea and nearby islands. The plants are caulescent and leafy, and bear short axillary inflorescences with paired flowers that emerge from two pairs of sheaths. In most taxa the flowers are ephemeral and have usually wilted by midday.

The other species discussed (*Dendrobium curvum* Ridl.) belongs to section *Pedilonum* Blume, a group of about 85 horticulturally attractive species. This section is primarily confined to southeast Asia and western Malesia, with one species (*D. platygastrium* Rchb.f.) reaching Fiji.

Dendrobium angraecifolium Schltr., in Schum. & Laut., Fl. Deutsch. Schutzgeb. Sudsee, Nachtr. 2: 169. 1905. TYPE: PAPUA NEW GUINEA. Foot of Bismarck Range, 200 m, January 1902, *R. Schlechter 14089* (Holotype: B, destroyed).

Heterotypic synonyms: *Dendrobium branderhorstii* J.J. Sm., Bull. Dep. Agr. Ind. Neerl. 39: 8. 1910. TYPE: INDONESIA. Papua Prov., upper Digul River, 1909, *leg. B. Branderhorst, cult. Hort. Bogor. 34B* (Syntype: BO, not found); 1909 Lorentz Exped., *leg. Rachmat, cult. Hort. Bogor. 171R* (Syntype: BO, not found); Papua border [with Papua New Guinea], 240 m, October 1909, *L. S. A. M. von Roemer 407* (Syntype: BO, not found).

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

Trichotosia microbambusa Kraenzl., Bot. Jahrb. Syst. 44, Beibl. 101: 22. 1910 *syn. nov.* TYPE: INDONESIA. Papua Prov., Andai, 29 August 1872, *O. Beccari 669* (Lectotype, here designated: FI 018921, image seen).

Eria microbambusa (Kraenzl.) Ormerod, Harvard Pap. Bot. 19, 1: 88. 2014.

Cylindrolobus microbambusa (Kraenzl.) Schuit., Y.P. Ng & H.A. Pedersen, Bot. J. Linn. Soc. 186: 195. 2018.

Distribution: Indonesia (Papua); Papua New Guinea.

Additional specimens examined: INDONESIA. Papua Prov., Waigeo Island, Radjah Ampat, Lupintol, on SW coast of Majalibit Bay, 8 February 1955, *P. van Royen 5457* (A). PAPUA NEW GUINEA. East New Britain Prov., Gazelle Peninsula, Warangoi area, Ilugi Creek, 60 m, 14 October 1955, *J. S. Womersley & M. Kazakof NGF 7923* (LAE); without locality [probably Gazelle Peninsula], 1886, *R. Parkinson 44* (MEL). New Ireland Prov., Danfu River area, 245 m, 15 February 1970, *M. J. E. Coode NGF 46132* (LAE).

The type of *Trichotosia microbambusa* was found among unidentified *Dendrobium* specimens in FI. The specimen is clearly a member of *Dendrobium* section *Grastidium* and identical in habit to the relatively common lowland species *D. angraecifolium*. Floral features described by Kraenzlin also match this taxon, and therefore we have no hesitation in reducing *T. microbambusa* to synonymy.

Dendrobium curvum Ridl., J. Fed. Mal. St. Mus. 8, 4: 91. 1917. TYPE: INDONESIA. Sumatra, W side of Barisan Range, Barong Bharu, Tapan, 1220 m, 10 June 1914, *H. C. Robinson & C. B. Kloss 179* (Lectotype [Ormerod and Kurzweil, 2019: 279]: BM 000038209, image seen).

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

Heterotypic synonyms: *Dendrobium rappardii* J.J. Sm., Blumea 5: 308. 1943. TYPE: INDONESIA. Sumatra, Bengkulu, Air Sablat Lebong, 650 m, 8 September 1938, *F. W. Rappard 172* (Holotype: L 0059462, image seen).

Eurycaulis rappardii (J.J. Sm.) M.A. Clem., Telopea 10, 1: 287. 2003.

Dendrobium nafisae Cavestro, Orchideen J. (Internet) 7, 2: 3. 2019 *syn. nov.* TYPE: INDONESIA. Sumatra, Bukit Barisan, Mount Dempo, fl. in cult. by *A. Marup,* 10 December 2018, *W. Cavestro & A. Marup s.n.* (Holotype: ANDA, not seen).

Distribution: Indonesia (Sumatra).

The protologue of *Dendromium nafisae* describes and shows all the features of *D. curvum,* including its laxly flowered rachis and large colorful flowers with a prominent, curved, narrowly conical mentum. We therefore reduce it to synonymy.

Dendrobium hastilabium Kraenzl., in Engl., Pflanzenr. IV 50, II, B. 21, 45: 52. 1910. TYPE: INDONESIA. Papua Prov., Andai, 29 August 1872, *O. Beccari 617* (Lectotype, here designated: FI 018928, image seen; Isolectotype: HBG, image seen).

Distribution: Indonesia (Papua).

Kraenzlin (1911) placed this taxon among species of section *Aquea* Kraenzl. (= section *Dendrobium*), thereby misleading later authors about its true relationships. The isolectotype in HBG is a floral fragment derived from the previously unrecognized specimen in FI.

Habenaria Willd., Sp. Pl. ed. 4, 4: 5, 44. 1805.

Type species: *Habenaria macroceratitis* Willd. (= *Orchis habenaria* L.).

A worldwide genus of about 900 species. The plants are mostly terrestrial herbs, growing in a variety of habitats such as grasslands, open forest, and rainforest. Previously, the species discussed below had been dealt with as *H. undatifolia* (Ormerod and Juswara, 2019), but we now find it must be reduced to *H. zollingeri*. The latter had become an obscure species due to a simple error in the protologue.

Habenaria zollingeri Rchb.f., Bonplandia 5: 35. 1857. TYPE: INDONESIA. Java, Idjin, 760–1065 m, 29 May 1845, *H. Zollinger 695 [as "495"]* (Lectotype, here designated: P 00352838, image seen; Isolectotypes: BM, L, images seen).

Heterotypic synonyms: *Platanthera undulata* J.J. Sm., Orch. Java: 27. 1905 *syn. nov.* TYPE: INDONESIA. Java, Mt. Salak, *C. L. Blume 2303* (Syntype: L 903, 16-221, image seen); Slamat, near Djedjek, collector not cited (Syntype: BO, not found); Idjin, 760–1065 m, 29 May 1845, *H. Zollinger 695* (Syntype: L 904, 44-151, image seen; Isosyntypes: BM, P, images seen).

Habenaria undulata (J.J. Sm.) J.J. Sm., Bull. Jard. Bot. Buitenz. s.2, 14: 10. 1914 *nom. illeg.* (non Frapp. Ex Cordem. 1895).

Pecteilis undulata (J.J. Sm.) Schltr., Rep. Sp. Nov. Regni Veg. 21: 120. 1925.

Habenaria undatifolia Ormerod & Juswara, Harvard Pap. Bot. 24, 1: 29. 2019.

Distribution: Indonesia (Java).

In describing this plant from Zollinger's collection Reichenbach (1857) quoted the type as "In sylvis Idjeng 2500–3500'. 29 V. 45 Nr. 495." He also quoted Zollinger's note on the flower color: "Flores virescentes." In P the specimen *Zollinger 695* has all these details and matches Reichenbach's description in the protologue, therefore it is obvious an error occurred in citing the type number. The specimen in P is chosen as lectotype of the name since the other duplicates lack label data (other than the collector and number), and no material could be found in W. Material of *Zollinger 495* in P does not have matching details and is referrable to three non-orchidaceous plants (*Euonymus, Tetrastigma,* and *Vitis*). Smith (1905) proposed *Platanthera undulata*, unaware that the syntype *Zollinger 695* (L) was actually an isotype of *Habenaria zollingeri* due to Reichenbach's erroneous citation, and the specimen did not have any specific locality data.

Pinalia Lindl., Orch. Scelet.: 14, 21, 23, t.71. 1826.

Type species (Ormerod et al., 2019: 286): *Pinalia alba*

Buch.-Ham. ex Lindl.

A genus of Eriinae with about 210 species distributed from India and Sri Lanka to Tahiti. The center of speciation is Indonesia, where 73 species are so far known.

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

Basionym: *Eria dura* Kraenzl., Bot. Jahrb. Syst. 44, Beibl. 101: 23. 1910. TYPE: INDONESIA. Sumatra, Padang Highlands, Mt. Singgalang, 1700 m, June to July 1878, *O. Beccari s.n.* (Lectotype, here designated): FI 008203, image seen, as "*Eria sclerophylla* Kraenzl.").

Heterotypic synonyms: *Eria merapiensis* Schltr., Bot. Jahrb. Syst. 45, Beibl. 104: 41. 1911 *syn. nov.* TYPE: INDONESIA. Sumatra, Mt. Merapi, 2500 m, 25 January 1907, *R. Schlechter 15957* (Holotype: B, destroyed).

Urostachya merapiensis (Schltr.) Rauschert, Rep. Sp. Nov. Regni Veg. 94: 471. 1983.

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

Eria chrysantha Schltr., Bot. Jahrb. Syst. 45, Beibl. 104: 42. 1911. TYPE: INDONESIA. Sumatra, Bukit Djarat, 1300 m, 1 February 1907, *R. Schlechter 15996* (Holotype: B, destroyed; Isotype: BO).

Urostachya chrysantha (Schltr.) Brieger, in Schltr., Die Orchideen ed. 3, 1: 716. 1981.

Eria lutea J.J. Sm., Bull. Dep. Agr. Ind. Neerl. 45: 18. Mar. 1911. TYPE: INDONESIA. Sumatra, Padang Highlands, Bukit Gompong, *M. C. Piepers s.n.* (Holotype: BO, not found).

Eria chrysostachys Ridl., J. Fed. Mal. St. Mus. 8, 4: 101. 1917. TYPE: INDONESIA. Sumatra, Sungei Kumbang, 1370 m, 17 April 1914, *H. C. Robinson & C. B. Kloss s.n.* (Syntype: BM, not seen; Isosyntypes: K, SING, images seen); Barong Baru, W side of Barisan Range, 1220 m, 4 June 1914, *H. C. Robinson & C. B. Kloss s.n.* (Syntype: BM, not seen; Isosyntype: K, image seen); Sungei Penoh, 820 m, *H. C. Robinson & C. B. Kloss s.n.* (Syntype: BM, not seen).

Usage synonym: *Eria lamonganensis auct. non* Rchb.f.: Kraenzl., in Engl., Pflanzenr. IV 50, II, B. 21, 50: 80, f.16A-D. 1911 [figure only, not description].

Distribution: Indonesia (Sumatra).

Kraenzlin originally intended to name this species *Eria sclerophylla*, but the epithet had already been used by Lindley for another taxon (now *Mycaranthes oblitterata* Blume). He therefore chose another name with a similar meaning, also referring to the rather rigid leaves. The following year another calamity arose to hide the identity of the species when his illustration (Kraenzlin,1911) of it was erroneously published under the name of the unrelated *E. lamonganensis* Rchb.f. Schlechter studied the type of *E. dura* without realizing it and determined the specimen as *E. chrysantha*. We agree with his identification, which means that *E. dura* must be adopted as the earliest available name for this beautiful species, noteworthy for its golden yellow flowers and prominent inflated mentum.

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

Basionym: *Eria gracilicaulis* Kraenzl., Bot. Jahrb. Syst. 44, Beibl. 101: 24. 1910. TYPE: INDONESIA. Sumatra, Padang Prov., near Ayer Mantjoer, 360 m, August 1878, *O. Beccari s.n.* (Holotype: FI 008198, image seen).

Heterotypic synonyms: *Eria euryloba* Schltr., Bot. Jahrb. Syst. 45, Beibl. 104: 45. 1911 *syn. nov.* TYPE: INDONESIA. Sumatra, near Padang Pandjang, 800 m, 20 January 1907, *R. Schlechter 15915* (Holotype: B, destroyed).

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

Distribution: Indonesia (Sumatra).

Schlechter examined the type of *Eria gracilicaulis* and found his *E. euryloba* to be conspecific, but he never published the reduction. We agree with his view and reduce the latter to synonymy here.

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FLORAE COSTARICENSIS SUBTRIBUI PLEUROTHALLIDINIS (ORCHIDACEAE) PRODROMUS II. SYSTEMATICS OF THE *PLEUROTHALLIS CARDIOTHALLIS* AND *P. PHYLLOCARDIA* GROUPS, AND OTHER RELATED GROUPS OF *PLEUROTHALLIS* WITH LARGE VEGETATIVE HABIT

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Abstract. We discuss a group of *Pleurothallis* species mostly characterized by plants relatively tall for the genus, with stems more than 20 cm long and fasciculate inflorescences produced above the leaf from a spathaceous, sometimes erect bract. We recognize 26 species and 4 natural hybrids in Costa Rica in this group of *Pleurothallis*, belonging to 4 informal assemblages of species, each one characterized by a unique set of vegetative, floral, and ecological features. This group, as well as its component units, is discussed as to its salient characteristics and internal relationships, underlying possible evolutionary trends. Diversity, general and floral ecology, color dimorphism, and natural hybridization are examined to address their systematic significance. We present a dichotomic key to the groups and the species discussed in this study, together with descriptions based on Costa Rican materials, and one or more line drawings or a Lankester Composite Dissection Plate when required for improved clarity. Also, we discuss their taxonomy and provide information on etymology, habitat, distribution, distinguishing features, and Costa Rican collections. Three species (*P. callosa, P. longipetala*, and *P. mesopotamica*), and three nothospecies (*P.* ×*karremansiana*, *P.* ×*subversa,* and *P.* ×*parentis-certa*) are described as new to science, discussed as to their affinities, and illustrated with photographs, composite digital plates, and ink drawings. *Pleurothallis triangulabia* is removed from the synonymy of *P. phyllocardia*, treated as a distinct species, and lectotypified. *Pleurothallis anthurioides* and *P. maduroi* are first recorded and documented for the flora of Costa Rica.

Keywords: flora of Costa Rica, floral activity, lectotypification, natural hybridization, new species, new nothospecies, orchid diversity, Pleurothallidinae

In a previous publication we presented a general overview of the work in progress aimed at completion of the Orchidaceae treatment for *Flora Costaricensis*, as well as the rationale behind the series of precursors to this floristic treatise, in particular relative to large and taxonomically complex groups of species in the Pleurothallidinae (Pupulin et al., 2020).

Orchid diversity in the subtribe Pleurothallidinae is far from being thoroughly understood. The recent work by Carl Luer and collaborators, aimed at producing a formal treatment of *Stelis sensu stricto* in Ecuador (Luer, 2002, 2004, 2007, 2009) well exemplify how much our appreciation of a genus's diversity can vary in a short lapse of time. While the monograph of *Stelis* by Óscar Duque Hernández was waiting to be published, figuring out a total of 363 recognized species in the genus (Duque Hernández 2008), a first century of new species from Ecuador was published by Luer (2002). In the next 7 years, Luer went to press with three more centuries of new *Stelis* species from Ecuador (Luer 2004, 2007, 2009). In his catalog of the Orchidaceae of Ecuador, Dodson (2004) recorded 448 species of *Stelis*. Today the genus exceeds, in Ecuador alone, 850 species. This means that a great collection effort focused on a particular group, access to a large amount of material for study, and a better understanding of species circumscriptions and their relationships produced an increase of almost 100% in the known diversity in a single large genus of Pleurothallids, in a single country, in just 5 years. According to Duque Hernández (2008), this significant number of new species of *Stelis* "will require a new systematics of the genus." And this does not take into account, of course, the broadening of the generic circumscription of *Stelis*, as proposed by Pridgeon and Chase (2001) and now broadly accepted (see in particular the general overview of the genus proposed

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by Karremans, 2019), which would require the inclusion of hundreds of other species in the "new systematics of the genus."

This argument is also true for groups that have received considerable attention relative to their phylogenetic placement within the subtribe, like *Pleurothallis* R. Br., but that have been less studied as to their diversity through broad comparative analysis. This paper deals with one such largely neglected group, the species of *Pleurothallis* R. Br. related to *Humboltia cordata* Ruiz & Pavón (1798) (= *Pleurothallis cordata* [Ruiz & Pav.] Lindl.), which represents one of the largest assemblages of phylogenetically related taxa within the genus (Luer, 2005). The importance of a valid modern taxonomic treatment of *Pleurothallis*, in which all taxa are carefully illustrated, transcends the limits of systematic botany, as has been recently shown by Mo and Cetzal-Ix (2015). They recorded the use of *Pleurothallis* species as remedies in traditional q'eqchi (quekchí) medicine in Guatemala, reporting the difficulty younger members of the q'eqchi communities had in distinguishing *Pleurothallis cardiothallis* from other morphologically similar species that did not have the same pharmaceutical properties.

In reconstructions of the evolutionary history of the Pleurothallidinae (Pridgeon and Chase, 2001; Pridgeon et al., 2001), this assemblage was shown to be closely related to the group of species that includes the type of *Pleurothallis*, *P. ruscifolia* (Jacq.) R. Br., within a clade that also includes *Stelis* Sw. *Pleurothallis sensu stricto* is nested within a clade that includes *Specklinia* Lindl., sister to the clade of *Masdevallia*/*Dracula* and related genera. The affinities among the species of the group of *P. cordata* were first recognized by John Lindley (1859), who created *Pleurothallis* sect. *Macrophyllae-Fasciculatae* to gather those species within the genus provided with terete-angulate stems, cordate leaves, and fasciculate flowers. The section was typified by Luer (1988) with *P. grandiflora* Lindl., an Andean species ranging from Venezuela to Bolivia. Several attempts have been made by contemporary authors to nomenclaturally recognize this large assemblage of species, raising generic concepts to accommodate them, but none has gained consensus (Pridgeon, 2005; Karremans, 2016). *Pleurothallis* section *Macrophyllae-Fasciculatae* has been treated at the generic rank by Szlachetko and Margońska (2001), who created *Zosterophyllanthos*. More recently, Luer (2005) reconsidered the validity of the monotypic *Acronia* C. Presl (1827), broadening the original circumscription of the genus to embrace not only those species with flowers produced in racemes, for example, *A. phalangifera* C. Presl (*typus generis*) and the taxa assigned by Lindley (1859) to section *Macrophyllae-Racemosae*, but also the species provided with fasciculate inflorescences, previously assigned to section *Macrophyllae-Fasciculatae* (Lindley, 1859). According to Luer's circumscription, the group today includes some 170 species of *Pleurothallis*, not all formally recombined in *Acronia*. Neither the treatment by Szlachetko and Margońska (2001) nor that by Luer (2005) received substantial recognition in botanical works.

Molecular analyses showed that *Pleurothallis* is sister to *Stelis sensu lato* and consecutive sister to *Pabstiella* Brieger & Senghas (Pridgeon et al., 2001; Pérez-Escobar et al., 2017). Within this clade, the sampled species with fasciculate inflorescences (i.e., *P. cardiantha* Rchb.f., *P. cardiothallis* Rchb.f., *P. teaguei* Luer, and *P. truncata* Lindl.) are not strictly related to species of *Macrophyllae-Racemosae* (e.g., *P. allenii* L.O. Williams and *P. rowleei* Ames), which would make the use of *Acronia* sensu Luer (2005) incorrect. Phylogenetic analyses by Pridgeon and Chase (2001) suggested that species of *Pleurothallis* with fasciculate versus racemose inflorescences clustered on different clades within the genus. Further expanded phylogenetic analyses (Wilson et al., 2011; Pérez-Escobar et al., 2017) based on nuclear *nrITS* and plastid *matK* datasets, including some of the species treated here (*P. adventurae*, *P. cardiothallis*, *P. fantastica*, *P.* ×*silvae-pacis*, and *P. tonduzii*), showed relationships similar to those found by Pridgeon and Chase (2001). However, these relationships within *Pleurothallis* are uncertain because phylogenies based on traditional Sanger sequencing datasets still yield poor resolution and low statistical support for the inference of infrageneric relationships in the Pleurothallidinae. This is mainly because of the limited number of informative characters in the loci analyzed that could be linked to the recent and rapid diversification of the genus (inferred to have occurred around 5 Ma) (Pérez-Escobar et al., 2017). Moreover, biological phenomena such as the high degree of natural hybridization (notably documented herein) and potential introgression can lead to poorly resolved phylogenies, lack of statistical support, and discordant inferences between nuclear and plastid datasets. These issues can be addressed by multi-locus approaches involving the three different plant genomes, as demonstrated in Pleurothallidinae for a clade of *Lepanthes* (Bogarín et al., 2018). Therefore, the relationships of the *Pleurothallis* species treated here remain uncertain as a result of limited available molecular information (including our unpublished Sanger sequences of species of the *P. cardiothallis* and *P. phyllocardia* groups). Also, for the same reason, a phylogenetic-based infrageneric classification of *Pleurothallis* is not yet possible to propose; thus we prefer to treat these species in four informal assemblages on the basis of morphological similarities rather than on unresolved phylogenies.

This study therefore deals with the taxonomy of the species of *Pleurothallis* with fasciculate inflorescences produced above the leaf from a spathaceous bract (largely corresponding to *P.* section *Macrophyllae-Fasciculatae* Lindl., or *Zosterophyllanthos* Szlach. & Margońska but excludes the group that Wilson, Belle, et al. (2013) and Wilson, Pupulin, et al. (2013) characterized as the "Mesoamerican clade" of *Pleurothallis*, made up of fairly small plants and mostly nonresupinate flowers, with a deeply concave lip without a basal glenion (Pupulin et al., in prep.). So circumscribed, the group includes at least 40 taxa in Costa Rica, but this figure has to be considered highly speculative as it also encompasses the taxonomically difficult *P. discoidea* Lindl. complex. These taxa, the so-called "frogs," comprise mostly miniature plants with small flowers, and several have complicated taxonomic histories. The complex is likely grossly underestimated as to its real diversity (Pupulin et al., in prep.). The present work focuses therefore on those taxa that are mainly characterized by large vegetative habit, that is, by mature plants with secondary stems (ramicauls) significantly longer than 20 cm. The division is obviously artificial, and some overlapping occurs between small or juvenile individuals of the group treated in the present paper and large individuals of the "frog" group of species. Nevertheless, both in the field and in cultivation, *Pleurothallis* species with large habits are easily spotted and equally easy to distinguish from the group of species with smaller habit close to *P. discoidea* Lindl. (Fig. 1). Even when arbitrarily split into large versus small members of the *Macrophyllae-Fasciculatae* group, the assemblage still embraces several quite different sets of species, each one with unique suites of morphological and ecological characteristics. We discuss these in the Results section of the present paper.

FIGURE 1. **A–V.** Comparison among *Pleurothallis* species with large habit treated in this paper (A–K) and other species of *Pleurothallis* in the *Macrophyllae-Fasciculatae* group with habit of reduced size (L–V). **A,** *P. phyllocardia* (*JBL-01967*); **B,** *P. scotinantha* (*Bogarín 7455*); **C,** *P. oncoglossa* (*Bogarín 5686*); **D,** *P. navisepala* (*JBL-33356*); **E,** *P. cardiothallis* (*Pupulin 6414*); **F,** *P. rectipetala* (*Bogarín 574*); **G,** *P. radula* (*Pupulin 8129*); **H,** *P. angusta* (*Karremans 6175*); **I,** *P. compressa* (*Bogarín 7839*); **J,** *P. luna-crescens* (*Zúñiga 178*); **K,** *P. pudica* (*Karremans 6249*); **L,** *Pleurothallis* sp. (*Karremans 7805*); **M,** *P.* cf. *rhodoglossa* (*Bogarín 6628*); **N,** *Pleurothallis* sp. (*Bogarín 9886*); **O,** *Pleurothallis bothros* (*Karremans 7494*); **P,** *Pleurothallis* sp. (*Pupulin* 7563); **Q,** *P. correllii* (*JBL-02482*); **R,** *P.* cf. *phyllocardioides* (*Serrano 155*); **S,** *P. rhodoglossa* (*Pupulin 5039*); **T,** *P. correllii* (*JBL-00484*); **U,** *P. vide-vallis* (*Calderón 96*); **V,** *P.* cf. *rhodoglossa* (*Bogarín 7291*). Scale bar = 20 cm. All the vouchers at JBL.

MATERIALS AND METHODS

Plants intended for this study were collected between 2001 and 2018 in suitable areas throughout Costa Rica and brought back to Lankester Botanical Garden (JBL, its acronym in Spanish) for cultivation and successive documentation. Whenever possible, type localities and other critical sites from which rare and/or unique species records were previously reported were visited for plant collecting and subsequent study. At least five specimens per morphospecies were collected at any given locality when possible. Field notes were taken during collections, including GPS and political data, elevation, ecological zones, and main types of vegetation. At JBL, plants were mostly cultivated in individual pots but also on hardwood planks when they seemed intolerant of pot culture; field data were recorded on individual labels affixed to the pots and plaques; and relevant information was stored in the general databases of JBL. Each plant belonging to this group that reached flowering in cultivation was documented by a high-resolution image of at least the flower with a scale bar and frequently of the whole plant and floral details with relative scales. Photographs were mostly taken with Nikon cameras (D5200, D7100, D810) mounted on Manfrotto tripods, fitted with macro lenses (Micro Nikkor 60mm f/2.8, Micro Nikkor 105mm AF f/2.8, Micro Nikkor 105mm AF/ED f/2.8, Sigma

DG Macro HSM 105mm f/2.8). Floral details were captured with a Micro-Nikkor 60mm f.2.8 mounted on a Nikon PB6 bellow or on extension tubes (12, 20, 36 mm), and/or with microscopes (Leica dissecting stereo microscopes MZ9.5 and M60, and Leica macroscope 16APO) fitted with Leica DFC420 digital color microscope cameras. Images were optimized through post-processing with Adobe® Photoshop CS5 and CS6, and comparative plates of flowers and/or relevant floral details were also prepared using the same software. Drawings of flowers and floral details were prepared using dissecting stereo microscopes Leica MZ9.5 and M60, fitted with Leica ApoPlanar lenses and drawing tubes. Whenever possible, Lankester Composite Dissection Plates (LCDP) and ink illustrations were prepared from individuals showing average characteristics for the portrayed species. Line drawings were done mostly with Rotring Rapidograph technical drawing pens with line widths of 0.1 or 0.2 mm on Fabriano, acid-free, smooth paper of 240g/m^2. For some ink plates, the line drawing was prepared using an Apple® iPad and Procreate® digital drawing application, the electronic drawing successively printed on Fabriano paper with a HP Color Laser Jet Pro M452nw, and the printed drawing hand-dotted with a Rotring Rapidograph technical drawing pen. One or more vouchers for each specimen were conserved in the liquid collection of JBL. Individual plants intended for the description of new species were also preserved as dried specimens to be deposited in national herbaria. To assess individual variability in flower morphology and size through time, several plants belonging to most morphospecies were documented in different years/flowerings, including photographs and dissections of successive flowers during the same flowering season, and vouchers in spirit were prepared for any individual flower, associated with the time of flowering. Notes on floral ecology were taken through direct observation of the plants under the semiartificial conditions of open greenhouses. The aging of individual flowers was documented with the same techniques and equipment described above for general flower documentation. Measurements were mostly taken under a dissecting stereoscope or with the aid of electronic scale bars inserted in the high-definition images of floral details. The major herbaria of the country, as well as relevant herbaria that allow digital access to their collections, were utilized to study specimens of the taxa intended for this study, and specimens were annotated when required. Source information on the taxonomy of these taxa, including at least the original protologues, nomenclatural types, type materials, and associated elements, were digitized and stored in the JBL databases, where they are available to the public upon request.

RESULTS

Species of *Pleurothallis* with fasciculate inflorescence produced from a spathaceous bract at the base of the leaf (exerted from the apex of the stem) and provided with a tall or relatively tall vegetative habit present several sets of diagnosable features—both morphological and ecological—that allow them to be put into four artificial groups (Fig. 2). The artificiality of these groups largely depends on the presence of taxa that, in several cases, seem to fill the gaps between groups for one or another of the key features used to characterize them. While the existence of these intermediate forms actually prevents our using of these groups as a formal proposal of classification—which would also be unnecessary—evidence suggests that the taxa included in each group do share some common features that, at least in some cases, could be hypothesized as indicating a shared lineage instead of convergent evolution. It is, perhaps, not fortuitous that most of the species with taller habit and larger flowers also show temporal activity of the perianth that is unknown in *Pleurothallis* outside the *P. cardiothallis* group, and it seems reasonable to see a link between the erect orientation of the spathe—which is unique to species in the *P. phyllocardia* group—and the orientation of the flower facing down toward the leaf, somewhat limiting access of pollinators to the perianth, which is also unique to this group. So, our use of the term "artificial" with respect to the systematic frame presented in this paper should be interpreted not as a simple and convenient way to gather species into an identification key but as a way to preliminarily recognize evolutionary paths and trends within the genus, without the limits of formal recognition.

The first group includes only three species diagnosable on a morphological basis, plus two nothospecies described hereafter that are likely the result of the natural cross of *P. tonduzii* with species of *Pleurothallis* from other groups in the *Macrophyllae-Fasciculatae* clade. The species close to *P. tonduzii* are vegetatively different from other taxa with tall habit in the very long and narrow leaves with lateral margins often slighting curling underside to increase rigidity of the leaf. The leaves are distinctly coriaceous, dark green, and shiny on the upper surface. The ramicauls are often tinged with blackish brown toward the apex. These characteristics made the species of the group easy to recognize both in the field and in herbaria. The flowers do not show temporal activity of the perianth and flowering is relatively long-lasting, with individual flowers remaining in full anthesis up to eight days. The flowers of *P. angusta* are rigid and someway shiny, while those of *P. grandilingua* and *P. tonduzii*—as well as those of the hybrids created with the latter species—are membranous and matte. In the three species, the lip of the flower presents a constriction toward the apex, where a small midlobe is inserted; this is less pronounced in *P. angusta*, but clearly distinguishable in several individuals (Fig. 3). The putative hybrids of *P. tonduzii* also present a distinct terminal lobe of the lip, even if it can be somewhat obscure. The lip of *P. angusta* is shiny, while those of the other two species are matte and distinctly verrucose. The warts may be quite protruding on the apical lobe of *P. tonduzii*, which could be sometimes described as subechinate. In both *P. grandilingua* and *P. tonduzii*, but to a greater extent in the latter, the lip is complexly folded. In *P. grandilingua* it is slightly conduplicate, with the two longitudinal halves becoming convex and flushing toward the apex, where the lamina presents a constriction and where an apical short lobe, in turn biconvex, is inserted. The lip of *P. tonduzii* is three-dimensionally still more complex, and variable within individual plants (Fig. 4). When extended,

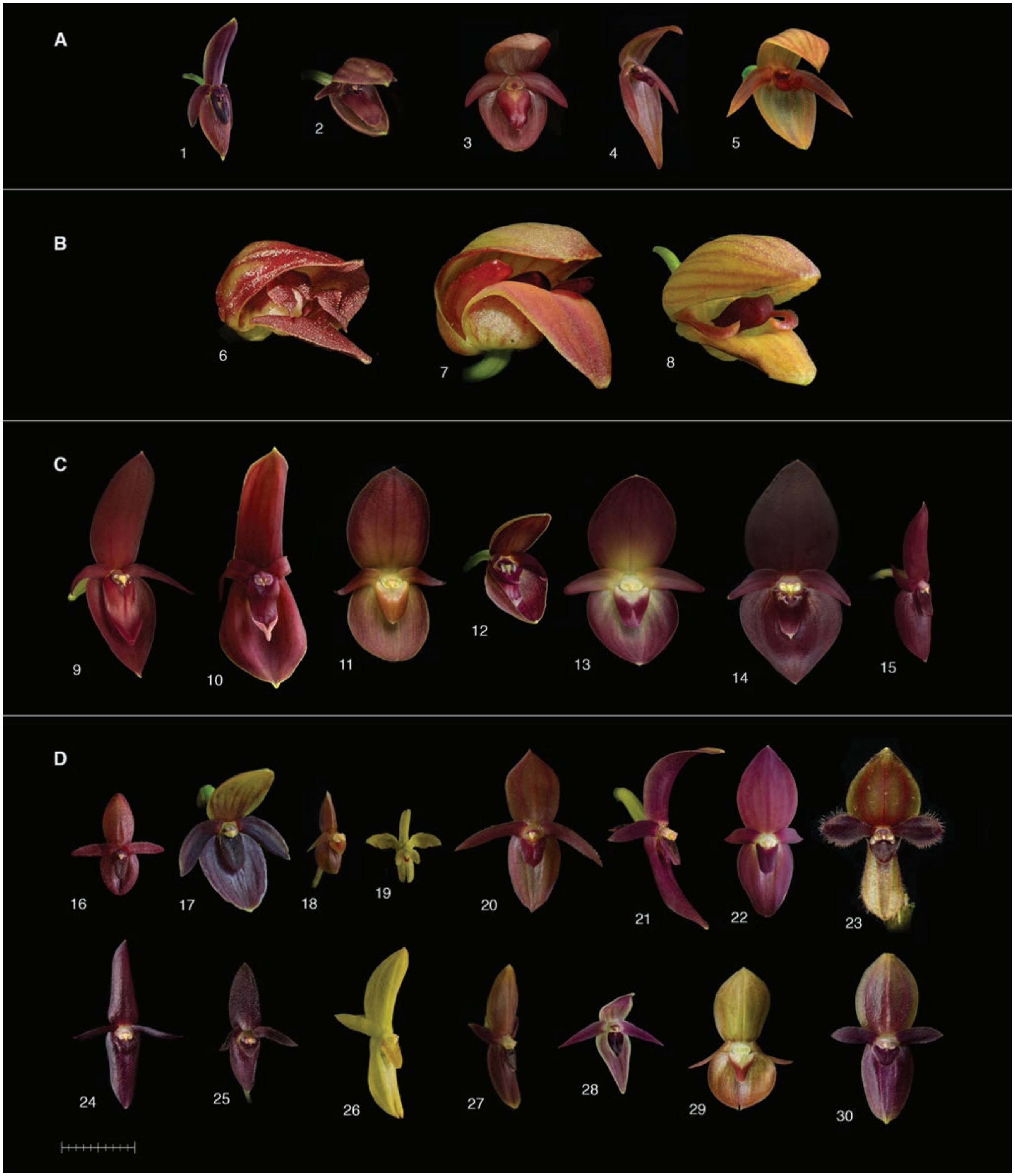


Figure 2. Synopsis of the flowers in different groups and species of *Pleurothallis*. **A,** *Pleurothallis tonduzii* group. 1. *P. angusta*. 2. *P. grandilingua*. 3. *P.* ×*karremansiana*. 4. *P.* ×*parentis-certa*. 5. *P. tonduzii*; **B,** *Pleurothallis palliolata* group. 6. *P. chavezii*. 7. *P. maduroi*. 8. *P. palliolata*; **C,** *Pleurothallis cardiothallis* group. 9. *P. callosa*. 10. *P. cardiothallis*. 11. *P. gonzaleziorum*. 12. *P. navisepala*. 13. *P. oncoglossa*. 14. *P. scotinantha*. 15. *P. tapantiensis*; **D,** *Pleurothallis phyllocardia* group. 16. *P. adventurae*. 17. *P. anthurioides*. 18. *P. compressa*. 19. *P. fantastica*. 20. *P. longipetala*. 21. *P. luna-crescens*. 22. *P. mesopotamica*. 23. *P. peculiaris*. 24. *P. phyllocardia*. 25. *P. pudica*. 26. *P. radula*. 27. *P. rectipetala*. 28. *P.* ×*silvae-pacis*. 29. *P.* ×*subversa*. 30. *P. triangulabia*. Scale bar = 1 cm. All the flowers pictured as resupinate to facilitate comparison, including those that are nonresupinate in natural position (18, 23, 25, 29). Photographs by F. Pupulin, except 6 (R. Joyce), 7 (E. Klaes), 9 (M. Díaz), 20, 26, 30 (D. Bogarín), and 25 (A. P. Karremans).

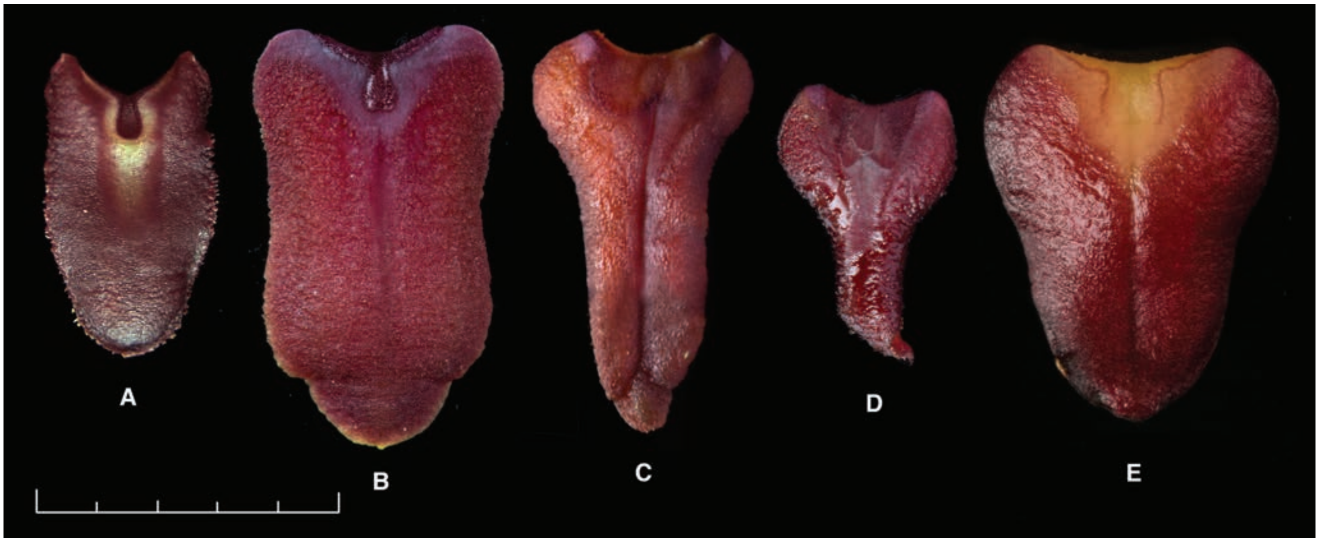


FIGURE 3. Lips of the species and nothospecies in the *Pleurothallis tonduzii* group. **A,** *P. angusta* (*Karremans 6175*); **B,** *P. grandilingua* (*Bogarín 5638*); **C,** *P. tonduzii* (*Karremans 5840*). **D,** *P.* ×*parentis-certa* (*Bogarín 11802*); **E,** *P.* ×*karremansiana* (*Díaz 270*). Scale bar = 5 mm. All the vouchers at JBL. Photographs by F. Pupulin (A–C, E) and D. Bogarín (D).

the lip is arrow-shaped, with the basal angles rounded, strongly conduplicate below the area of the glenion, with the two longitudinal halves slightly convex; close to the apex the blade is constricted into a small, elliptic, rounded, convex midlobe, inserted where the convex halves flush into the blade. During anthesis, whereas the base of the lip becomes slightly convex, the lateral margins fold under to touch themselves behind the lip, the blade becomes strongly geniculate at about two-thirds of its length, and the folded-down apex twists on one side. The final shape of the lip of *P. tonduzii* represents a real challenge in conveying its complexity through descriptive terminology. According to our observations, the torsions of the lip of *P. tonduzii* are transmitted in varying degrees to its progeny. Thus, in *P.* ×*karremansiana*, likely a cross with a species of the *P. cardiothallis* group, the lip is conduplicate with a central depression, the margins are convex and slightly folded under, and the lamina presents a subterminal constriction with a terminal lobule. In *P.* ×*parentis-certa*, which we interpret as a nothospecies formed by *P. tonduzii* with a species of the *P. phyllocardia* group, the morphology of the lip is very similar to that of the putative parent except for the much more distinct glenion, and the size that is roughly half that of the lip of *P. tonduzii*.

The species of the *Pleurothallis palliolata* group are vegetatively indistinguishable from several other medium-sized taxa with ovate leaves, which is the predominant shape in the large assemblage of species treated in this paper. The flowers of *P. palliolata* and the other morphologically similar species are, however, unique in the genus for their conspicuous, inflated, deeply concave-cucullate dorsal sepal, which is much wider than the synsepal and forms a hood over the gynostemium. In *P. maduroi*, which ostensibly has one of the larger flowers in the genus as far as the flora of Central America is concerned, the dorsal sepal is almost 3 cm wide, with 16–18 veins, and in *P. palliolata* it reaches 2 cm in width. However, notwithstanding a visual similarity in the general shape of the flowers, the three Costa Rican species in the *P. palliolata* group strongly differ in most of their floral details. *Pleurothallis maduroi* is likely the single representative in the American isthmus of a group of species mostly Andean in distribution, which we hypothesize are phylogenetically closely related, including *P. gargantua* Luer, *P. imperialis* Luer, *P. marthae* Luer & Escobar, and *P. teaguei* Luer. In all these species, the flowers are large if not gargantuan, provided with a rounded and comparatively large lip and wide, rectangular, twisted petals, which probably play a specific role in their pollination syndrome. *Pleurothallis palliolata* also has large flowers and a rounded lip, but the petals are narrow and incurved, more similar in structure to those of the South American *P. corysta* Luer, *P. hoeijeri* Luer & Hirtz, and *P. quitu-cara* Carrera & Baquero, to which it is perhaps related. Finally, *P. chavezii* has much smaller flowers, a long and narrow lip, and long, lanceolate petals that are borne erect and then bend abruptly, which is completely different morphologically from other species in the group and is perhaps comparable to the Ecuadorean *P. megalotis* Luer & Hirtz. The broad, cucullate dorsal sepal reclined over the column is functionally analogous, but not homologous, to the deeply cymbiform synsepal, which is frequent in many unrelated species of *Pleurothallis* with nonresupinate flowers, not only in the *Macrophyllae-Fasciculatae* group. We do not have a phylogenetic tree of *Pleurothallis* with sufficient resolution to allow plotting the systematic and evolutionary occurrence of the "cowled flowers" in the genus, but we strongly suspect that this character evolved independently several times in the entire subtribe.

Another group discussed in the present treatment is that of *Pleurothallis cardiothallis* Rchb.f. and its relatives, of which we recognize seven species. *Pleurothallis cardiothallis* is the oldest name referrable in Costa Rica to the species of this group. It was originally described from a plant without specific locality acquired in England and

FIGURE 4. **A–H.** Morphology of the lip in *Pleurothallis tonduzii*. **A,** *Bogarín 10434*; **B,** *JBL-04789*; **C,** *Serrano 154*; **D,** *Karremans 4575*; **E,** *Bogarín 3808*; **F,** *Pupulin 4389*; **G,** *Karremans 5158*; **H,** *JBL-04793*. Scale bar = 5 mm. All the vouchers at JBL. Photographs by F. Pupulin.

cultivated in Hamburg by Consul Gustav Wilhelm Schiller (Reichenbach, 1857). Plants of the *P. cardiothallis* group are among the largest Pleurothallid orchids in the flora of Costa Rica: they have large, ovate, flexible leaves, deeply cordate at the base and with the basal margins mostly overlapping at maturity. The adaxial surface of the leaves is distinctly matte, often with the main veins slightly protruding. The flowers of species belonging to this group are unique among Costa Rican Pleurothallidinae in their delicate and usually large flowers with distinct temporal activity. The perianth reaches incomplete anthesis during the first day, and then it closes before night, to re-open the next morning when it almost completely spreads. Complete anthesis is usually reached during the third or fourth day of flowering, when in some species the sepals and petals become fully reflexed. At the end of the fifth to eighth day of intermittent anthesis, the flower withers and detaches from the pedicel (Fig. 5).

A fourth group of species is mostly characterized by the inflorescence produced from an erect to suberect spathaceous bract, with flowers that do not exhibit temporal activity. *Pleurothallis phyllocardia* Rchb.f. represents the oldest name in this group, and it was proposed from a plant collected by Herman Wendland in Costa Rica (Reichenbach, 1866). The group is treated here as encompassing 11 species in Costa Rica. Most of the species of the *P. phyllocardia* group present an erect or suberect spathaceous bract at the base of the leaf that protects the developing inflorescences, and even though this character is not consistent throughout all the species, the erect spathe has not been recorded outside this group. In most species of the *P. phyllocardia* group, the margins of the sepals are completely reflexed at maturity; in several species the petals strongly curve back immediately after the flower opens. Anthesis of individual flowers in the group spans 6 to 8 days. Furthermore, some of the species are unique in *Pleurothallis* in the fact that, after anthesis, the pedicel becomes strongly geniculate, forcing the flowers to face down toward the leaf. So, even when the flowers open erect once exerted from the spathaceous bract, they eventually recline over the leaf, leaving a relatively small space open between the column and the leaf surface. It may be that this particular arrangement of the flowers, which is unique to this group and which we documented

Figure 5. Temporal activity on flower of *Pleurothallis cardiothallis* (from Pupulin, Díaz-Morales, Aguilar, et al., 2017). Flower in the foreground is at the third day of anthesis on 01.09.2017; it partially opens and closes during the next six days, until it fades on 01.18. Flower in the background begins anthesis on 01.10 and opens and closes during the next 10 days until it fades on 01.20. A new floral bud is partially developed on 01.13; it begins anthesis on 01.20 and reaches its fully spread shape on 01.21, then partially closes on 01.22. All the photographs taken approximately at 9:00 AM. Voucher*: F. Pupulin 6414* (JBL). Photographs by J. Aguilar. Reproduced with permission from the Editor of *Lankesteriana*.

in three species in Costa Rica, affects potential pollinators approaching the flowers, but we have no direct observations of pollinator behavior on the flowers to support this hypothesis. In most species of the *P. phyllocardia* group, juvenile leaves are cuneate or rounded at the base, and basally deeply cordate leaves are associated with mature, flowering stems. We interpret the cuneate leaves on fertile stems of *P. fantastica* as a retention of the paedomorphic form, which is otherwise characteristic of the juvenile stage within the group.

The *Pleurothallis phyllocardia* group also includes some species of *Pleurothallis* that do not fit well in it or in any of the artificial groups defined by particular features. Nonetheless, they are closer to the assemblage of species discussed here than to any other group within the genus, at least in the flora of Costa Rica. They are tall species of *Pleurothallis*, with terete stems and fasciculate flowers produced above the leaf from a spathe, but they have narrow, acuminate leaves, a prostrate spathe, erect flowers without temporal activity, a flat dorsal sepal similar in size to the synsepal, and a somewhat bizarre floral morphology as compared with other Costa Rican taxa in this large group of *Pleurothallis*. The deeply three-lobed lip of *P. fantastica*, with the erect lateral lobes much larger than the reduced, almost vestigial midlobe, is highly anomalous in *Pleurothallis*. *Pleurothallis fantastica* is also the only species treated here in which leaves are cuneate—instead of cordate—at the base. We suggested above that this represents the retention of a paedomorphic character, which is common in immature leaves throughout the other sampled taxa of the *P. phyllocardia* group. *Pleurothallis adventurae* and *P. peculiaris* apparently represent misfits in this treatment, but nonetheless they most firmly belong in the *P. phyllocardia* group. This affinity is difficult to visualize when arranging the species of Costa Rica in discrete groups on the basis of shared morphological characteristics, but it becomes boldly apparent when other taxa from South American floras are added to the analysis. Two of us (MD, FP) had the opportunity to revise in depth a very large sample of Andean taxa morphologically close to *P. adventurae* and *P. peculiaris* (virtually including all the hitherto known species). When the entire series is taken into account, it becomes apparent that species with erect spathes—close to *P. phyllocardia*—blend via *P. peculiaris* and other similar taxa into a group of South American species with both erect and supine spathes, glaucous, dark green, narrow leaves, and dark red-purple flowers frequently with scabrous to hirsute indumenta, which are morphologically very similar to *P. adventurae*. Such a broad comparison is, nonetheless, outside the scope of the present work. The inclusion of *P. adventurae* and *P. peculiaris* in the Costa Rican group of species close to *P. phyllocardia* is based therefore on a broader understanding of the genus, even though it makes it more difficult to characterize the group based on any possible sets of shared features.

Diversity

In the present systematic treatment, we recognize 30 taxa in a group that had traditionally included 14 species recorded for the flora of Costa Rica with a similar circumscription of taxa. This increase in recorded diversity, more than doubling the number of taxa in the assemblage of species as defined in this study, is the direct result of research initiated by our group almost 10 years ago (Karremans and Bogarín, 2011; Karremans and Muñoz García, 2011; Pupulin, Díaz-Morales, Aguilar, et al., 2017; Pupulin, Díaz-Morales, Fernández, et al., 2017; Pridgeon, 2020), as well as of the methodology employed in this study.

The oldest taxa in the group were described by Reichenbach (1857, 1866), on the basis of dried specimens and sometimes without specific locality data. Several morphological details that are critical to fully understanding individual characteristics and species circumscriptions are for the most part impossible to be interpreted in pressed and distorted material. Floral features that are likely a response to environmental factors, like the temporal activity of the perianth and its shape at maturity, cannot be observed, of course, in conserved flowers. This traditional way of studying pressed *Pleurothallis* specimens collected by others continued with the work of Schlechter (1918) and Ames and collaborators, who added a few more species to the group (Ames, 1922, 1936; Ames and Schweinfurth, 1925). It was not until the seminal works by Luer on the Pleurothallidinae, however, that the diversity of *Pleurothallis* in this large and complex group of species could be studied for the first time through the analysis of living specimens, fresh flowers, and pickled vouchers kept in alcohol to preserve their tridimensionality. Luer thereby significantly increased our knowledge of *Pleurothallis* species native to Costa Rica and produced much more detailed and truthful descriptions and accurate illustrations, but he was nonetheless limited by the relatively sparse botanical sampling he was able to do personally during his visits to the country (Luer, 1979, 1996, 1997).

In the last 15 years or so, we have amassed in the living collections of JBL a large number of specimens of *Pleurothallis* from a broad range of localities, spanning most of the geographical, altitudinal, and ecological regions of Costa Rica. When plants flowered, most of them were fully documented in LCDPs, and they were photographed at maximal development to record floral shape, dimensions, and colors. Hundreds of vouchers were conserved in the ancillary spirit and DNA collections of the center. Data on phenology and floral behavior were collected and sometimes photographically recorded over several years, and observations and measurements of vegetative and floral parts were made under uniform greenhouse conditions to reduce to a minimum those individual variations produced by environmental factors. There is probably no other way to attain a sound preliminary framework of diversity in a given group that could take into account the variation expected in nature within and among populations of the studied species, independent of nomenclature matters. It is, of course, a method that can be applied only to a local flora, with the support of legal permits that allow collecting a certain number of specimens of any morphospecies or working taxonomic unit, and a permanent place for cultivation.

Systematic work in groups as large and complex as *Pleurothallis* benefits from the identification of smaller taxonomic units, whose diversity can be more easily investigated piecemeal. Even if these taxonomic units do not in any way represent an attempt to be recognized in a formal hierarchical system, nevertheless, they do not even constitute a simple artificial grouping scheme. They correspond in fact to a selective profile made on the basis of taxonomically significant characters and, in many cases, of synapomorphic characters that are unique and specific for each unit. As such, they underline the possible belonging of the species included in each group to a particular lineage according to a phylogenetic perspective.

Given the increasing diversity in the group revealed by our study, and the relatively restricted geographical distributions known for some of the taxa—which are endemic to one or a few mountain ranges—it is possible that our horizontal sampling over the entire country of Costa Rica was less complete than desirable. We are nonetheless confident that our sampling in favorable habitats was robust and that the number of specimens studied and documented for this paper offer future students a valuable comparative basis for the recognition of possible novelties in the group and for placing them into a correct systematic and phylogenetic frame.

Ecology

With their narrow stems and soft, subcoriaceous leaves, most species in the group inhabit the premontane and lower montane forests along all the major Costa Rican cordilleras, where the mild to cool climate and humid environmental conditions that prevail throughout the year prevent desiccation of the plants in their epiphytic habitat. With the notable exception of *Pleurothallis cardiothallis*, whose populations may be found as low as 350 m above sea level (a.s.l.), all taxa are restricted in vertical distribution above 700 m. Species diversity significantly increases above 1000 m, reaching a peak at the elevational gradient of 1300–1400 m, where 60% of the taxa (18 species) are found (Fig. 6). Diversity decreases over 2000 m, and only a single species (*P. longipetala*) may be found above 2400 m in elevation. No species of this group have been found over 2800 m.

The highest concentration of species in Costa Rica is found along the Cordillera de Talamanca, which spans from the Chiriquí region in Panama to the eastern end of the Central Valley in Costa Rica. Here the spine of the Continental Divide transforms into the young mountain system of the Cordillera Volcánica Central and, northward, into the relatively low Cordillera de Tilarán and the northern Cordillera Volcánica de Guanacaste. Species diversity in

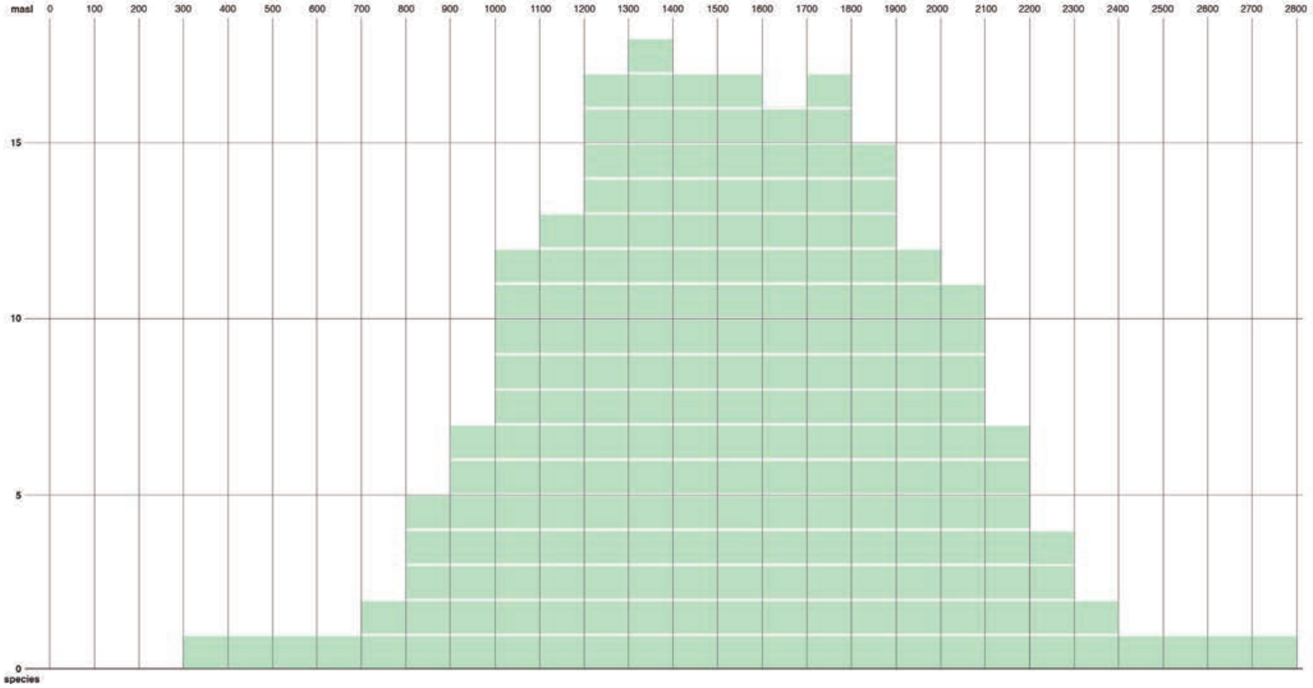


FIGURE 6. Elevational distribution of taxa in the *Pleurothallis cardiothallis* group. x-axis = elevation; y-axis = number of species.

the study group progressively diminishes toward the north, likely reflecting an ancient Andean origin of the group and its immigration from northern South America via the Panamanian isthmus.

While populations of *Pleurothallis cardiothallis*, *P. longipetala, P. phyllocardia*, and *P. tonduzii* are known from both watersheds of the Continental Divide, most species in the group are restricted to only one side of the mountain chains that longitudinally cross the country, with a majority of taxa confined to the wetter environments of the Caribbean watershed. Interestingly, except for the species close to *P. palliolata*, which are exclusively Caribbean in distribution, all the other groups treated here present "sister" species on both sides of the continental divide. So, *P. angusta, P. callosa, P. compressa, P. chavezii, P. gonzaleziorum, P. ×karremansiana, P. maduroi, P. navisepala, P. oncoglossa, P. palliolata*, and *P. tapantiensis* are exclusively found along the slopes of the Costa Rican chain that face the Caribbean Sea, while populations of *P. grandiflora* and *P. scotinantha* are seemingly restricted to the Pacific side. The apparently rare *P. anthurioides* has been collected in Costa Rica so far only on the Pacific watershed of the Cordillera de Talamanca, but the type specimen was allegedly found on the Caribbean side of the same mountain chain in Panama. Concerning life zones, most of the species (20 spp. = 66%) are found in the moist and wet premontane forests, followed by the wet lower montane forests (18 spp. = 60%), the montane forest at elevations higher than 2000 m (7 spp. = 23%), and the tropical forest of the basal belt (only a single species = 3%).

Phenologically, the species of the group present flowers most of the year. However, a graph that shows the number of species in flower by month (Table 1) clearly reveals that the flowering of these taxa is mostly associated with seasonality. Flowering shows a peak in the wettest month, November, when 65% of the taxa are in flower (19 species), and a progressive diminishing of flowering during the driest months to a low of only 5 species in flower (ca. 17%) during April, at the end of the dry season.

Floral Ecology

The floral ecology of species in the *Pleurothallis cardiothallis* group was first addressed by Pupulin, Díaz-Morales, Aguilar, et al. (2017), who tentatively associated flower longevity and periodicity in species belonging to the group with reduction of transpirational water loss. While flower lifespan in the Pleurothallidinae may be extremely short (1–2 days in *Specklinia colombiana* [Garay] Pridgeon & W.M. Chase) or unusually long (to 30 days in *Diodonopsis erinacea* [Rchb.f.] Pridgeon & M.W. Chase and, according to literature, up to 3 months in *Lepanthes escobariana* Garay [di Vita, 2017]), most genera and species in the subtribe have anthesis periods of 7–15 days (pers. observ.). The lifespan of flowers in species close to *P. cardiothallis* is usually 7–10 days, which is about average in both the subtribe and the genus. As the glenion at the base of the lip likely acts as a deceptive lure for potential pollinators, a relatively long flower lifespan may effectively increase the chances of visitation, and this trait has been effectively associated with deceit-pollination species (Internicola and Harder, 2012).

Unlike other species of *Pleurothallis*, taxa in the *P. cardiothallis* group are invariably characterized by short daily activity in the flowers. To date, we have observed only temporal activity in flowers of this group, and we consider that this trait has taxonomic significance. In the flowers of most species in the *P. cardiothallis* group, the two

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1. *P. angusta*	■									■	■	■
2. *P. grandilingua*	■						■					
3. *P.* × *karremansiana*					■	■	■	■	■	■	■	■
4. *P.* × *parentis-certa*							■					
5. *P. tonduzii*	■	■	■	■	■	■	■	■	■	■	■	■
6. *P. chavezii*	■									■	■	■
7. *P. maduroi*											■	
8. *P. palliolata*										■	■	
9. *P. callosa*								■				
10. *P. cardiothallis*	■			■	■	■	■	■	■	■	■	■
11. *P. gonzaleziorum*			■					■				■
12. *P. navisepala*	■	■							■	■	■	■
13. *P. oncoglossa*	■	■							■	■	■	■
14. *P. scotinantha*	■				■	■	■				■	■
15. *P. tapantiensis*			■									
16. *P. anthurioides*	■											■
17. *P. compressa*	■	■				■				■	■	■
18. *P. longipetala*	■	■	■						■	■	■	■
19. *P. luna-crescens*		■	■			■	■	■				
20. *P. mesopotamica*					■							
21. *P. phyllocardia*	■	■			■	■	■			■	■	
22. *P. pudica*							■	■				
23. *P. radula*				■	■	■			■	■	■	■
24. *P. rectipetala*				■	■	■					■	
25. *P.* × *silvae-pacis*	■	■	■						■	■	■	■
26. *P.* × *subversa*		▨									■	
27. *P. triangulabia*			■		■	■	■	■	■		■	
28. *P. adventurae*						■				■	■	■
29. *P. fantastica*	■	■		■	■				■			
30. *P. peculiaris*								■	■	■		■

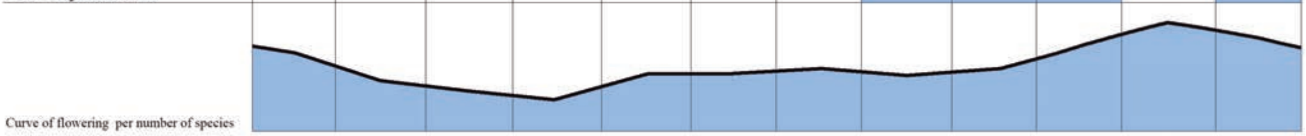


TABLE 1. Phenological records relatives to the species of *Pleurothallis* discussed in this paper. Data from field observations and plants grown at the Lankester Botanical Garden.

labia formed by the sepals are slightly to deeply concave at maturity, while the petals are completely extended and straight. In *P. cardiothallis* and *P. tapantiensis*, however, the lateral margins of the sepals and the apex of the petals continue extending backward until they are completely reflexed. In all the species of the group, during the late hours of the morning and at noon, likely as a response to the decreasing humidity of the environment, the tip of the petals begins curving toward the column, while the dorsal sepal and synsepal progressively approach each other until the perianth completely closes. This activity of the perianth repeats daily, even though on particularly hot and dry days the flowers may not spread out completely. At evening, they are regularly closed, at least partially. During rainy days, the flowers remain active for longer periods, and on several occasions, the closure of the perianth is not complete. Intermittent anthesis of individual flowers can continue for up to 8 days, after which the flowers definitively closes and, unless pollinated, the perianth plus the ovary detach from the pedicel. Floral activity in *P. cardiothallis* has been photographically documented in Pupulin, Díaz-Morales, Aguilar, et al. (2017) (Fig. 5).

Intermittent anthesis has never been observed in taxa belonging to the so-called "frog" group of *Pleurothallis*, which are phylogenetically close. Species of the latter group invariably have distinctly smaller flowers, however, and this seems to support the hypothesis that temporal activity of the perianth in larger flowers is aimed at reducing water loss in delicate floral tissues. We have not encountered floral scents perceivable by the human nose, but we cannot exclude the possibility that particular regions of the perianth can produce volatile substances to which visitors are attracted. In this case, shorter periods of flower activity during the total time of potential anthesis could also reduce metabolic costs.

Santos and Presley (2010) and Aguiar et al. (2013) have suggested that short flower activity may represent a temporal niche, aimed at reducing competition with other species that occupy the same habitat, rely on the same pollinators, and are active at different times. This scenario is however unlike that observed in our study group. According to Karremans and Díaz-Morales (2019), Pleurothallidinae is the largest fly-pollinated group in Orchidaceae, with at least 15 genera presenting a myophilous pollination syndrome. Within *Pleurothallis*, 11 different families of Diptera have been recorded as flower visitors, with a majority of species belonging to Sciaridae (recorded in 11 species of *Pleurothallis*) and Drosophilidae (in 6 species) (Karremans and Díaz-Morales, 2019). Potential pollinators have been observed for only 8 species of *Pleurothallis* of the *Macrophyllae-Fasciculatae* group (including 2 of the species treated in this paper, *P. navisepala* and *P. phyllocardia*), and they also mostly belong to the families Sciaridae and Drosophilidae. Flowers are visited by several different flies, which apparently attempt to reach the rounded glenion at the base of the lip. When the insect touches the viscidium placed above the glenion, the pollinia are removed and adhere to the head (more rarely to the leg) of the visitor. Even though it is still unclear if this simple mechanism makes *Pleurothallis* a truly generalist group in terms of pollination, it is nonetheless clear that the interaction between glenion and apical anther/stigma allows for the pollinator group to be less specific than in genera in which a more precise fit is required between insect and flower (Karremans and Díaz-Morales, 2019). Furthermore, small flies are active during most of the day, often irrespective of the weather conditions, and pollination of *Pleurothallis* by Mycetophilidae and Sciaridae has been documented to be even nocturnal (Duque-Buitrago et al., 2014), which makes it hard to interpret intermittent anthesis in terms of a temporal pollination niche.

Color Dimorphism

In the group of *Pleurothallis* species discussed here, the flowers are mostly purple, sometimes with an orange-purple background and darker purple stripes around the veins. The purple color is often very dark, in some of the taxa almost blackish, and the lip is often very dark, including in those species that have lighter-colored sepals and petals. As the flowers of this group of species do not emit any fragrance that is perceivable by the human nose, the widespread occurrence of this dull color throughout the entire group is perhaps suggesting that this particular tone is in some way associated with visual preferences of pollinators, which could be lured to visit the flowers through a visual signal. Noteworthy, however, is the relative frequency of entirely yellow flowers in individuals of several typically purple-flowered species treated in this study. Species dimorphism in flower color, with the frequent occurrence of entirely yellow flowers among typically purple-colored populations, has been documented in other advanced orchid groups as well (Pupulin, 2003; Pupulin and Rojas, 2006). In those groups, however, the yellow phase is likely associated with a specific pollination syndrome. In the species close to *Oncidium guatemalenoides* M.W. Chase & N.H. Williams (in the *Sigmatostalix* group), which have flowers normally boldly blotched with purple, all the taxa also present individuals with concolorous, bright yellow flowers. As these flowers are pollinated by bees foraging for nectar and oils, this color shift may represent an advantage in terms of attracting possible visitors. Papadopulos et al. (2013) have shown that yellow-flowered species in the Oncidiinae occupy a distinct portion of color space in the color vision of Hymenopterans when the insects approach floral communities, and that floral reflectance of yellow Oncidiinae flowers closely mimics the floral signals of rewarding Malpighiaceae. While this suggests that a shift toward concolorous yellow flowers likely represents an enhancement of the mimic model syndrome in the Oncidiinae, no evidence allows us to extrapolate this phenomenon to *Pleurothallis* since the species of this genus are mostly visited by Dipterans, which perceive visual signals in a very different way than Hymenopterans. Nonetheless, the color dimorphism associated with several species of the group treated here is noteworthy. Such dimorphism is not unique to this group and is quite widespread in the genus: we observed it as a frequent variation throughout the *Macrophyllae-Fasciculatae* group, as well as in the "Mesoamerican group" of species sensu Wilson, Belle, et al. (2013) and Wilson, Pupulin, et al. (2013) (Pupulin et al., unpubl. data). In our species group, all the taxa close to *P. cardiothallis* exhibit a yellow phase together with the typical purple one. Among species of the *P. phyllocardia* group, which are invariably purple to blackish purple, a single species, *P. radula*, has concolorous yellow flowers. In this species, we also documented a form with rose apices of the sepals, which seem to clearly indicate the presence of unexpressed anthocyanins in the flowers (Fig. 7). Flowers with yellow sepals are also known among the mostly light- to dark-purple flowers in *P. tonduzii* (Fig. 8). The frequency of the yellow phase among populations with mostly dark-purple flowers, as well as the production of capsules in a wild population of *P. radula* with flowers of the rose phase, suggests that these variations are equally visited by their pollinators and reproductively functional.

Natural Hybridization

It seems of particular interest that 4 out of 30 taxa (= 13%) of the group studied for this monograph are most surely of hybrid origin, while others (like *P. grandilingua*) present some features that are somewhat intermediate between species of the group and perhaps represent vestigial characters of ancient hybridization processes. Considering the highly random possibility of finding and collecting a hybrid plant in the field, as well as the highly scattered spatial distribution of hybrid individuals that could be reproductively nonfunctional, the percentage of natural hybrids documented for this study suggests that their occurrence, in the midst of parent populations, could be much more frequent than expected. It is not fortuitous that two of the four nothospecies recorded in our study were originally described from Bosque de Paz Biological Reserve. Long-term studies carried out at the reserve (Kirby, 2003; Kirby and Muñoz, 2007; Muñoz and Kirby, 2007; Karremans and Muñoz García, 2011; Bogarín et al., 2015; Díaz-Morales and Karremans, 2015; Belfort-Oconitrillo, in prep.), documenting not only species diversity but also phenotypic and individual variations between and within populations, have increased the probability of coming across scattered individuals of putative hybrid origin. The case of Bosque de Paz shows how vertical and thorough local sampling is likely the only viable strategy that can allow us to understand the possible role of hybridization in shaping the extraordinary variability of some characters in *Pleurothallis* and correctly distinguish between good species and the products of hybridization with successive introgressions.

The relatively high number of natural hybrids we documented for this study also raises the question of how much gene flow between species may have contributed to the actual diversity of the *Pleurothallis* group and perhaps to the overall diversity of the genus. The apparently unspecialized pollination system of *Pleurothallis* probably results in the

FIGURE 7. Color variation in flowers of *Pleurothallis radula*. **A,** *Pupulin 8130*; **B,** *Pupulin 7796*; **C,** *Díaz 385*; **D,** *Karremans 5161*; **E,** *Pupulin 8129*; **F,** *Belfort-Oconitrillo569*. All the flowers at the same scale. Vouchers at JBL. Photographs by F. Pupulin (A–E) and N. Belfort-Oconitrillo (F).

FIGURE 8. Color variation in flowers of *P. tonduzii*. **A,** *Pupulin 549*; **B,** *JBL-02515*; **C,** *JBL-02455*; **D,** *Bogarín 10434*; **E,** *Karremans 5840*. All the flowers at the same scale. Vouchers at JBL. Photographs by F. Pupulin.

occasional deposition of pollen on the "wrong" stigma. Karremans and Díaz-Morales's 2019 review of pollination in the Pleurothallidinae records no fewer than 11 families of flies (Diptera) as visitors of *Pleurothallis* flowers, with members of 8 families observed removing pollinaria. In the subgroup of species belonging to our study group, flowers are visited by various fly species of the families Calyptratae, Drosophilidae, Phoridae, Sciaridae, and Tephritidae (Karremans and Díaz-Morales, 2019), which remove flower pollinaria while walking on the flowers. The apical position of the anther and the rostellum pointing forward at the apex of a short column favor the placement of the droplike viscidium on the head (more rarely on the legs) of the fly, while the frontal position of the broad stigmatic cavity, filled with abundant fluid, makes the deposition of pollinaria easy even during short and occasional visits. Karremans and Díaz-Morales (2019) speculated that this relatively unspecialized but efficient mechanism allows the pollinator group to be less delimited in this genus than in other Pleurothallid genera, which require a more precise mechanical interaction between the flower and the insect body, suggesting that *Pleurothallis* species may be true generalists in their pollination system. Such hypothetical generalism would also favor the occasional transference of pollen between species that present the same "open system" of pollination because of the relative facility for the opportunist visitor to enter in contact with the viscidium of the pollinarium and to deposit it on the broad and prominent stigmatic surfaces.

TAXONOMIC TREATMENT

KEY TO THE SPECIES OF THE *PLEUROTHALLIS CARDIOTHALLIS* AND *P. PHYLLOCARDIA* GROUPS AND OTHER RELATED GROUPS IN COSTA RICA

1a. Leaves thick-coriaceous, rigid, with a distinctly protruding midvein abaxially, shiny on the upper surface, narrowly oblong-lanceolate, usually more than 6 times longer than broad . . . . (*P. tonduzii* group) 2

1b. Leaves soft-coriaceous, elastic, without distinctly protruding midvein, matte on upper surface, ovate to lanceolate, usually less than 4 times longer than broad. 6

2a. Lip with the lateral margins strongly revolute, particularly in the midportion, so appearing pandurate in outline 3

2b. Lip with the lateral margins straight; the apex not bent downward 4

3a. Apex of lip abruptly bent upward, then strongly geniculate, twisted on one side . . . . ***P. tonduzii***

3b. Apex of lip bent downward, straight. . . . . ***P. ×parentis-certa***

Key to the Species of the *Pleurothallis cardiothallis* and *P. phyllocardia* Groups and Other Related Groups in Costa Rica cont.

4a. Flowers small, the dorsal sepal <11 mm long, mostly oriented laterally along the margin of the leaf . . . . . ***P. angusta***
4b. Flowers comparatively large, the dorsal sepal >12 mm, opening along the leaf midvein 5
5a. Leaves thick, coriaceous; margins of petals denticulate; lip rectangular-subpandurate . . . . . ***P. grandilingua***
5b. Leaves soft, flexible; margins of petals entire; lip peltate . . . . . ***P. ×karremansiana***
6a. Dorsal sepal deeply concave, reclined over the column, much broader than the synsepal . . . . . (*P. palliolata* group) 7
6b. Dorsal sepal flat or slightly concave, erect, narrower than the synsepal 9
7a. Lip lanceolate-pandurate, much longer than wide . . . . . ***P. chavezii***
7b. Lip suborbicular or reniform, wider than long 8
8a. Lip suborbicular; petals ligulate, falcate . . . . . ***P. palliolata***
8b. Lip reniform; petals subrectangular . . . . . ***P. maduroi***
9a. Leaves large, >5 cm wide; spathaceous bract always prostrate; flowers membranaceous, with distinct temporal activity, opening and closing several times . . . . . (*P. cardiothallis* group) 10
9b. Leaves narrow, <4 cm wide; spathaceous bract erect to suberect, not prostrate (except in *P. adventurae*); flowers coriaceous, remaining open after anthesis . . . . . (*P. phyllocardia* group) 16
10a. Lip triangular 11
10b. Lip peltate 13
11a. Flower solid dark purple, lip spread at apex . . . . . ***P. scotinantha***
11b. Flower pale purple, with the center yellowish white or entirely yellow 12
12a. Apex of lip hooked . . . . . ***P. oncoglossa***
12b. Apex of lip straight . . . . . ***P. gonzaleziorum***
13a. Flowers large, sepals >10 mm long 14
13b. Flowers small, sepals <7 mm long 15
14a. Lip distinctly wider at the base, <9 mm long . . . . . ***P. cardiothallis***
14b. Lip wider in the middle the base, >11 mm long . . . . . ***P. callosa***
15a. Ramicauls with sheaths only at the base; flowers solitary; the synsepal slightly concave; dorsal sepal ≥10 mm long . . . . . ***P. tapantiensis***
15b. Ramicauls with basal sheaths and a sheath close to the middle; flowers 1–3 simultaneously; the synsepal concave to almost saccate at the base; dorsal sepal ≤7 mm long . . . . . ***P. navisepala***
16a. Mature leaves cuneate at the base . . . . . ***P. fantastica***
16b. Mature leaves cordate to deeply cordate at the base (immature leaves maybe cuneate), the basal margins frequently overlapping 17
17a. Ramicaul ancipitous . . . . . ***P. compressa***
17b. Ramicaul terete 18
18a. Spathe prostrate 19
18b. Spathe erect or suberect, not prostrate; flowers glabrous or covered with soft, white hairs within 20
19a. Flowers resupinate, dark purple, the adaxial surface completely covered with short, stiff, pointed tubercles . . . . . ***P. adventurae***
19b. Flowers non-resupinate, bronze, the lip white apically red, the adaxial surface smooth . . . . . ***P. ×subversa***
20a. Flowers reclinate, facing the leaf 21
20b. Flowers erect 23
21a. Flowers with the inner surface tomentose-hirsute . . . . . ***P. pudica***
21b. Flowers glabrous 22
22a. Mature plant large, usually >30 cm tall; dorsal sepal narrowly ovate; petals oblong; lip longer than wide . . . . . ***P. phyllocardia***
22b. Mature plant small, usually <20 cm tall; dorsal sepal elliptic-suborbicular; petals elliptic-lanceolate; lip wider than long . . . ***P. triangulabia***
23a. Flowers hairy, the dorsal sepal subcircular, the lip rhombic, with pointed lateral lobes . . . . . ***P. peculiaris***
23b. Flowers glabrous, the dorsal sepal lanceolate to elliptic, the lip triangular, without pointed lateral lobes 24
24a. Sepals concave 25
24b. Sepals reflexed 27
25a. Petals subfalcate, entire, pointing downward . . . . . ***P. anthurioides***
25b. Petals linear-acuminate, serrulate, held horizontally 26
26a. Flowers with purple or dull purplish yellow, striped dark purple, >10 mm long; petals purple, falcate; lip erect, pointing forward; glenion of the lip transversely rectangular . . . . . ***P. longipetala***
26b. Flowers with white sepals striped rose-purple, <8 mm long; petals rose-purple, straight; lip reclinate, pointing downward; glenion of the lip rectangular . . . . . ***P. ×silvae-pacis***
27a. Flowers concolorous yellow . . . . . ***P. radula***
27b. Flowers dark purple, sometimes with subhyalinous dorsal sepal 28
28a. Petals >3 times longer than broad, with dentate margins . . . . . ***P. luna-crescens***
28b. Petals <3 times longer than broad, with entire to minutely denticulate margins 29
29a. Petals linear-lanceolate to linear-oblong, with minutely denticulate margins; the flowers dull purple on a yellow base; the lip papillose . . . . . ***P. rectipetala***
29b. Petals subfalcate, with entire margins; the flowers dark-purple color; the lip verrucose . . . . . ***P. mesopotamica***

A. The *Pleurothallis tonduzii* group

1. ***Pleurothallis angusta*** Ames & C. Schweinf., Schedul. Orchid. 8: 23. 1925. TYPE: Costa Rica. [Cartago]. In cultivation at Las Concavas, May 1924, probably native of Cachí, *C. H. Lankester 850* (Holotype: AMES). Fig. 9 (Voucher, *Pupulin 4767*, JBL).

Epiphytic, caespitose, erect to suberect *herb*, to 50 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 24–35 cm long, 2–3 mm in diam., green suffused with dark red, provided with a tubular, short, truncate sheath to 2.5 cm long at the base, and a longer, tubular, tightly adpressed, obtuse sheath below the middle, to 5–7 cm long. *Leaf* borne erect at the apex of the ramicaul, becoming horizontal and revolute along the margins in the basal half with age, coriaceous, sessile, lanceolate, acute, 8.0–16.5 × 2–3 cm, cordate at the base, the midvein channeled on the adaxial surface, prominent on the abaxial surface, grass to dark green. *Inflorescence* a fascicle of 1–2(–7) simultaneous flowers, from a prostrate spathaceous bract ca. 1 cm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, pale green, 11–14 mm long, bending toward the margin of the leaf. *Ovary* subclavate, terete, 5–7 mm long. *Flowers* dark purple, suffused with yellow on the margins of the sepals and petals. *Dorsal sepal* ovate, acute, 10.5–11.0 × 4.5–5.0 mm, 3-veined. *Lateral sepals* connate into a broadly ovate, acute synsepal, 9–10 × 5–6 mm, 5-veined. *Petals* falcate to subovate, obtuse, 6.3–7.0 × 1.5–2.0 mm, 1-veined. *Lip* unguiculate, hinged to the column foot, geniculate, thick, ligulate, minutely ciliate, basally bilobed, obtuse, 4–5 × 3 mm; glenion deeply recessed between the basal lobes of the lip, ca. 0.51 mm long. *Column* short, transversely subrectangular, dorsoventrally complanate, ca. 1.2–1.8 × 1.8 mm, the anther apical, the stigma apical, bilobed. *Anther cap* obtriangular, truncate, bilobed at the base, 2-celled. *Pollinia* 2, narrowly oblong-pyriform, attached to an elliptic viscidium through a short, cylindric caudicula. (Fig. 10A–B).

Etymology: from the Latin *angustus*, "narrow," probably in reference to the narrow, oblong leaves of the species.

Distribution: Costa Rica and Panama.

Ecology: a large, suberect epiphyte spanning a broad altitudinal range, *P. angusta* has been recorded from 750 to about 2100 m of elevation. It is restricted to the Caribbean watershed of the Cordillera Volcánica Central and the Cordillera de Talamanca, where populations have been found in lower montane rain forests to wet montane forests. Flowering occurs from October to February, which generally corresponds to the end of the rainy season and the beginning of the dry season in Costa Rica.

Distinguishing features: the narrow, oblong, coriaceous leaf and the mostly dark-purple flowers usually facing a margin of the leaf, with a bright, shiny, ligulate lip that is ciliate along the margins, are diagnostic of the species.

Pleurothallis angusta was described from an incomplete specimen without original locality data (maybe collected in Cachí), cultivated at Las Cóncavas by Charles Lankester, and the holotype consists only of a single, sterile leaf and a portion of the subtending stem. The narrow, coriaceous leaf, as well as Ames's description of the flower (in Ames and Schweinfurth, 1925) and Lankester's notes on flower color and his crude sketch of the lip (AMES74048), unmistakably indicates the species as treated and illustrated here. Costa Rican and Panamanian populations of *P. angusta* have been sometimes treated as *P. bivalvis* Lindl. (e.g. Bogarín et al., 2014; Monro et al., 2017), but that species from northern South America (the type, Venezuela, *J. Linden 1480*, K) has broadly ovate leaves, and the bilabiate flowers have much broader sepals and petals with distinctly denticulate margins. Luer (2003) stated that *P. angusta* is apparently rare in Costa Rica, while it is quite common at high elevations in the Andes, but none of the materials that we had the opportunity to study from South America bear even a superficial resemblance with the true *P. angusta*, and we suspect that the records from Colombia to the south probably refer to one or more distantly related taxa.

Costa Rican material examined: Alajuela: Carrizal, Concordia, entre Los Cartagos y Cinco Esquinas, bosque pluvial montano bajo, en potreros arbolados y bosque secundario, 10°08'16.8"N, 84°09'49.8"W, 2027 m, 17 junio 2009, *D. Bogarín 7319, R. L. Dressler, F. Pupulin & R. Trejos* (JBL). **Cartago:** Jiménez, Pejibaye, Parque Nacional Tapantí, sector Taus, Selva, entre Quebrada Selva y Río Taus, 9.7875000, -83.7569444, 900–1200 m, v13 Jun 2006, *J. F. Morales Quirós 14014* (CR). Jiménez, Pejibaye, Tausito, ca. 3.8 km después del cruce de Kiri, 9°46'37.8"N, 83°46'30.4"W, 1281 m, bosque pluvial premontano, epífitas en bosque secundario alterado a orillas del camino, 30 abril 2009, *D. Bogarín 6990, M. Fernández, R. Gómez, Y. Kisel, F. Pupulin, P. Renshaw & R. Trejos* (JBL). Jiménez-Turrialba, La Suiza, La Suiza, Pejivalle, road to Esperanza, on hills close to Quebrada Puente, premontane wet forest, epiphytic in secondary vegetation along the sugar cane plantations, 9°48'46,0"N, 83°39'10,0"W, 750 m, 5 Feb 2007, *F. Pupulin 6498, D. Bogarín & R. L. Dressler* (JBL). Turrialba, Tayutic, Moravia de Chirripó. On the road to Platanillo, in remaining forest on the side of the road. Humid montane forest. 9°49'26.07"N, 83°25'27.30"W, 1160 m, 15 December 2013, *A. Karremans 6175 & M. Contreras Fernández* (JBL); Tayutic, Jicotea, Finca La Pradera, epífitas en vegetación madura a orillas de una quebrada, 9°47'06.79"N, 83°32'49.48"W, 1073 m, 22 Sep 2016, *A. P. Karremans 7347, I. Chinchilla, M. Díaz & G. Rojas-Alvarado* (JBL). Turrialba, Moravia de Chirripó, hills north of Moravia across the plain with pasture, premontane wet forest, secondary mature vegetation and remnants of secondary vegetation in pastures, 9°50'18"N, 83°26'45"W, 1135 m, 12 Jun 2002, *F. Pupulin 3895, M. Bonilla, R. Gómez, H. León-Páez & W. Schug* (JBL); Turrialba, La Suiza, Llanos del Quetzal, ca. 1 km sobre el camino detrás de la Escuela de Kabébata (Alto Quetzal), 9°46'43.6"N, 83°24'41.6"W, 1449 m, epífitas en bosque primario y secundario, bosque muy húmedo premontano "supra arbores in nemoribus Llanos del Quetzal ad Turrialba in Cartago," 17 Junio 2011, *D. Bogarín 8860, M. Fernández & A. Karremans* (JBL); same collecting data, *D. Bogarín 8863, M. Fernández & A. Karremans* (JBL); Turrialba: Tuís, Cien Manzanas, 9°51'25"N, 83°33'47"W, ca. 950 m, along a minor tributary of Río Pacuare, premontane wet forest, secondary vegetation and remnants of primary, 26 May 2003, *F. Pupulin 4767 R. Dressler, K. Dressler, J.*

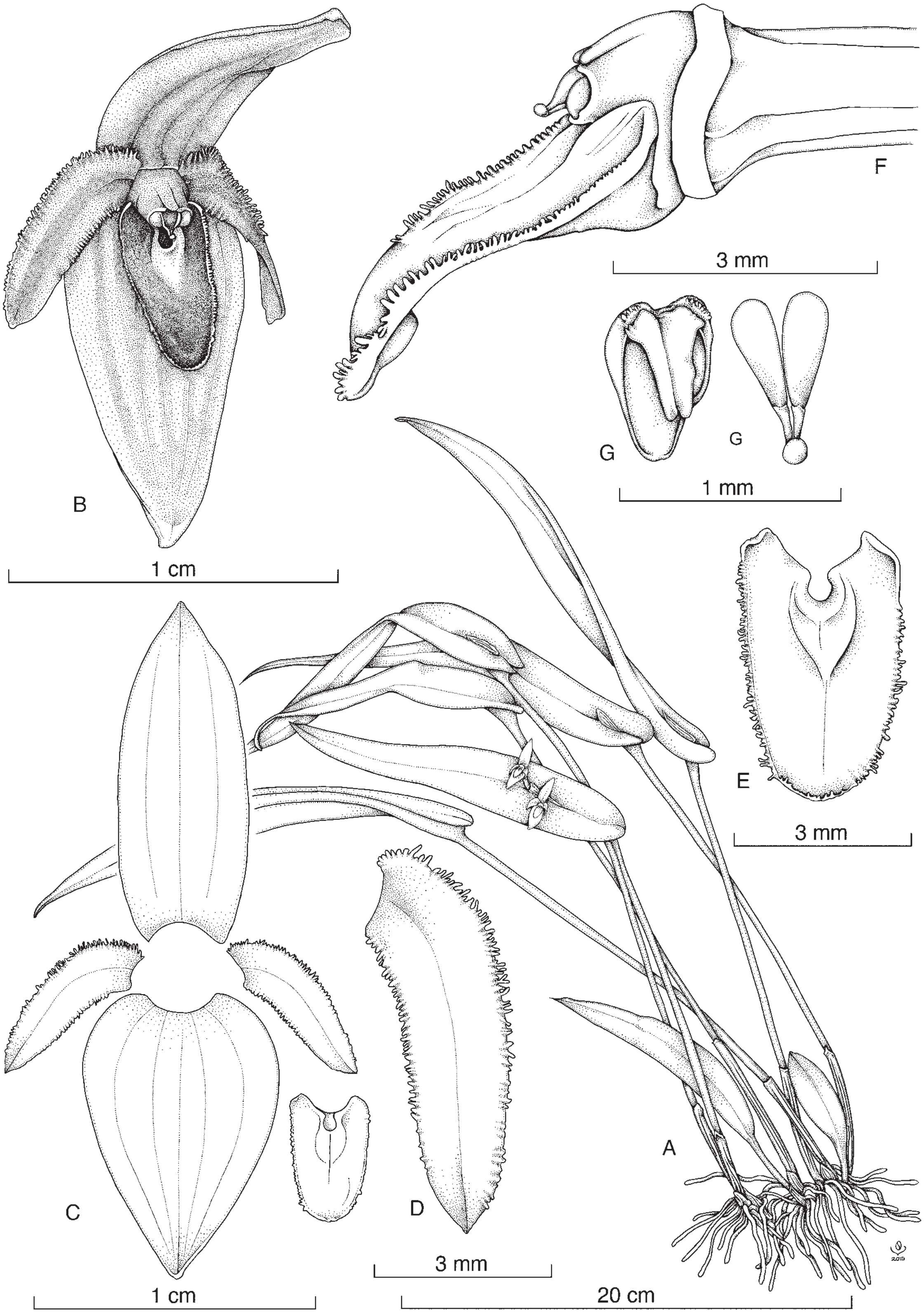


FIGURE 9. *Pleurothallis angusta* Ames & C. Schweinf. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** petal (left); **E,** lip, adaxial view; **F,** apex of ovary, column, and lip in lateral view; **G,** anther cap and pollinarium. Drawn by L. Oses from *Pupulin 4767* (JBL).

FIGURE 10. Flowers of *Pleurothallis* species from Costa Rica in the *P. tonduzii* group. **A–B,** *P. angusta* (*Bogarín 8863*; *Pupulin 1350*); **C–D,** *P. grandilingua* (*Bogarín 5638*; *Bogarín 8358*); **E,** *P.* ×*karremansiana* (*Díaz 270*); **F,** *P.* ×*parentis-certa* (*Bogarín 11802*); **G–I,** *P. tonduzii* (*Serrano154*; *Karremans 4575*; *Karremans 5840*). Not at the same scale. All the vouchers at JBL. Photographs by F. Pupulin (A–E, G–I) and D. Bogarín (F).

Aguilar, G. Gerlach, P. Kindlmann, H. León-Paéz, S. Pugh-Jones & E. Serrano (JBL). **Limón:** Talamanca, Bratsi, en el Valle del Silencio, Atlantic slope, Valle de Silencio, area just N of Cerro Hoffman, 4 1/2 airline km W of the Costa Rica-Panama, 9.1333333, -82.9666667, 2300–2450 m, 24 Jun 2003, *E. Alfaro 4683, R. Delgado & M. Alfaro* (CR). Talamanca, Bratsi, P.N. La Amistad, Atlantic slope, Valle de Silencio, area just N of Cerro Hoffman, 4 1/2 airline km W of the Costa Rica-Panama, 1333333, -82.9666667, 2300–2450 m, 24 Jun 2003, *E. Alfaro 4683, R. Delgado & M. Alfaro* (CR). Talamanca, Bratsi, P.N. La Amistad Caribe, Reserva Indigena Bribri, 1.7 km de Alto Lari. In primary forest with heavy epiphyte density, 9.3958333, -83.0944444, 1500–1530 m, 27 Feb 1992, *H. Schmidt 627* (CR). Talamanca, Bratsi, R.I. Talamanca Caribe, Amubri, Alto Lari, Kivut, 9.4041667, -83.0875000, 1300 m, 7 Mar 1992, *G. Herrera 5199* (CR). Talamanca, Bratsi, Area protegida: R.I. Talamanca Caribe, Amubri, Alto Lari, siguiendo la fila entre los Ríos Dapari y Lari, 9.4041667, -83.0819444, 1300 m, 19 Jun 2007, *G. Herrera 5099* (CR). **Without specific locality:** flowered in cultivation at Jardín Botánico Lankester, 23 Feb 1999, *F. Pupulin 1350* (JBL); flowered in cultivation at Jardín Botánico Lankester, 3 Dec 2005, *F. Pupulin s.n.* (JBL-photo). In cultivation at Las Concavas, probably native of Cachí, *C. H. Lankester 850* (AMES). Map 1.

2. ***Pleurothallis grandilingua*** Pupulin, M. Díaz & Pridgeon, Vanishing Beauty. Vol. 2: 851–853. 2020. TYPE: Costa Rica. Costa Rica. San José: Tarrazú, San Lorenzo, ca. 4 km southeast of Santa Marta, road to Bajo Reyes, 9˚36''38.2"N, 84˚00'52.1"W, 1475 m, wet premontane forest, epiphytic on pastures' fences on the roadside, 20 November 2008, flowered in cultivation at Lankester Botanical Garden, 22 Jul 2016, *D. Bogarín 5638, R. L. Dressler, M. Fernández, R. Gómez & R. Trejos* (Holotype: JBL). Fig. 11 (Voucher, *Bogarín 5638*, JBL).

Epiphytic, tall, caespitose *herb*, to 30 cm tall. *Roots* slender, flexuous, ca. 1.5 mm in diam. *Ramicauls* 11–18 cm long, enclosed by 1–3 tubular, obtuse, tightly adpressed, papyraceous, brown sheaths, the first one basal, ca. 2 cm long, the second inserted in the lower third of the ramicaul, 4–5 cm long. *Leaves* coriaceous, dark green, paler on the underside, narrowly lanceolate, acute to subacuminate, 9–12 × 2–3 cm, rounded at the conduplicate base, the midvein protruding abaxially into a rounded keel, slightly decurring on the stem. *Inflorescence* a single flower, exerted from a narrow triangular, acute, brown, papery, prostrate spathaceous bract 1.5 cm long; peduncle filiform, ca. 2 cm long. *Floral bract* triangular-ovate, subacute, glumaceous, to 2 mm long. *Pedicel* terete, 2 cm long. *Ovary* terete-subclavate, rounded, stout, ca. 2 cm long. *Flowers* not completely spreading, with the sepals purple-red on a yellowish ground, paler between veins, the apex green, the petals purple, marked with green along the margins, the lip concolorous purple, the column dark purple, the anther pink. *Dorsal sepal* elliptic, acute, with a rounded apicule, 13 × 8 mm, 5-veined. *Lateral sepals* fused into an ovate, acute, rounded-apiculate, 5-veined synsepal, 12 × 9 mm, yellow-hyaline at the base. *Petals* narrowly lanceolate-ligulate, subacuminate, 7–8 × 2 mm, irregularly denticulate-erose along the margins, the base thickened into a pad-like callus. *Lip* three-lobed, subrectangular-subpandurate, convex, with a shallow median groove, 7 × 4 mm, the geniculate base cordiform, the lateral lobes elliptic, minutely erose, apically slightly inflated-convex, the midlobe transversely hemielliptic, rounded, ca. 1 × 2 mm, provided with a minute apicule and a hemispherical, papillose callus underneath. *Column* short, thick, dorsiventrally flattened-cylindrical, with a median keel toward the apex, 2 mm long, with the anther apical, bent, and the stigma apical, bilobed. *Anther cap* ovate, cucullate, 2-celled. *Pollinia* 2, pyriform, apically attenuate-recurved, on a rounded viscidium. (Fig. 10C–D).

Etymology: from the Latin *grande*, "large," and *lingua*, "tongue," in allusion to the large size of the lip in relation to other parts of the flower, uncommon in species of *Pleurothallis*.

Distribution: known only from Costa Rica.

Ecology: the species is known to inhabit wet premontane and lower montane forests of the Talamanca mountain range, where it is apparently restricted to the Pacific watershed at elevations of 1450–2000 m. The only phenological records show that *P. grandilingua* flowers at least in January and July.

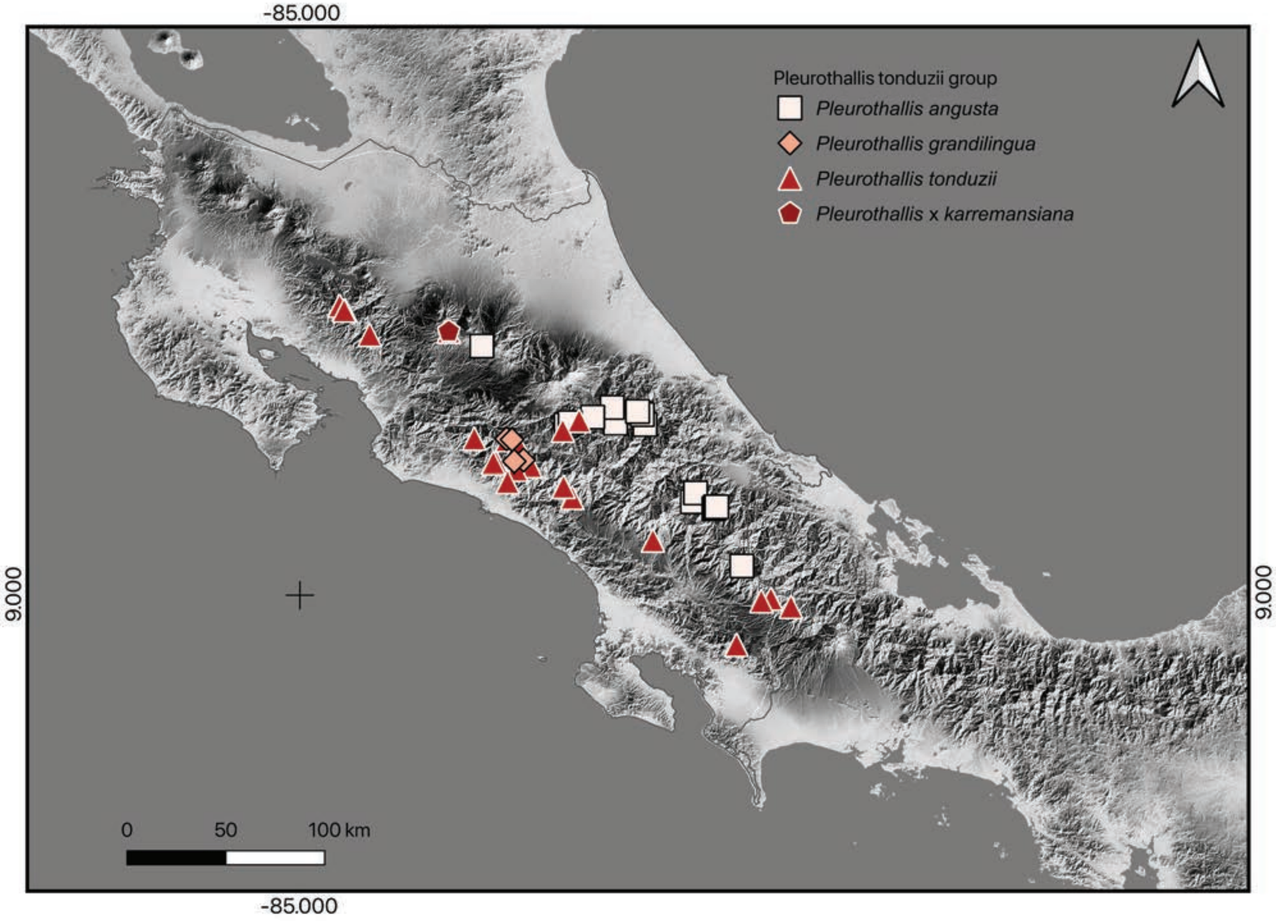
Distinguishing features: *Pleurothallis grandilingua* is allied to the Costa Rican and western Panamanian endemic *P. tonduzii* Schltr., from which it can be distinguished by the broader leaves, the mostly purple flowers (the sepals greenish yellow to pink, the petals rose in *P. tonduzii*), the narrower synsepal, the ligulate petals (vs. falcate), and the subrectangular, slightly convex lip with the apex extended (vs. sagittate, the apex abruptly bent upward and then strongly geniculate).

Costa Rican material examined: San José: León Cortés, San Pablo, 9˚42'35.87"N, 84˚01'28.77"W, ca. 2000 m, secondary wood on the old dump of San Pablo de León Cortés, road to the telecommunication towers, *legit* Daniel Matamoros, flowered in cultivation at Lankester Botanical Garden, 20 January 2011, *D. Bogarín 8358* (JBL). León Cortés, San Antonio, ca. 1 km después de San Antonio camino a San Pablo, ladera noroeste del Cerro Abejonal, 9˚42'49.91"N, 84˚3'0.92"W, 1917.8 m, bosque muy húmedo montano bajo, epífitas en bosque secundario, 25 febrero 2020, *D. Bogarín 12800*, *I. Chinchilla & R. Parra* (JBL). Map 1.

3. **Pleurothallis ×karremansiana** Pupulin, J. Aguilar & M. Díaz, ***nothosp. nov***.

TYPE: Costa Rica. Alajuela: Zarcero, Palmira, Reserva Biológica Bosque de Paz, creciendo en el jardín de orquídeas, 10˚12'15.70"N, 84˚19'00.02"W, 1534 m, bosque pluvial montano bajo, 20 agosto 2016, *M. Díaz 270, N. Belfort-Oconitrillo & A. P. Karremans* (Holotype: JBL). Fig. 10E, 12, 13 (Voucher, *Díaz 270*, JBL).

Pleurothallis nothospecie nova inter P. tonduzii Schltr. *et P. gonzaleziorum* Pupulin, M. Díaz & Pridgeon, *a consimilis*



MAP 1. Map of collection sites for the species of *Pleurothallis tonduzii* group.

foliis cordatis anguste ovatis tenuiter coriaceis, floribus purpureis sepalis late ovatis obtusis vel subacutis, petalis anguste triangulari-subfalcatis acutis, labello pandurato purpureo dignoscenda.

Epiphytic, caespitose, erect to suberect, large *herb* to 35 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 12.5–16.5 cm long, 1.5–2.0 mm in diam., yellowish green, provided with a tubular, truncate sheath to 2.6 cm long at the base, and a longer, tubular, tightly adpressed, broadly obtuse sheath below the middle, to 5.5 cm long, the bracts glumaceous, pale green with minute purple warts when young, becoming brown, dry-papyraceous with age. *Leaf* erect, thinly coriaceous, flexible, sessile, narrowly ovate, acuminate, 12.5–16.5 × 3.5–4.2 cm, cordate at the base, grass green, matte. *Inflorescence* a fascicle of 1–2 flower, usually produced singly, from a prostrate spathaceous bract 1.3–1.6 cm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, pale green, 15–17 mm long. *Ovary* clavate, terete, 7–9 mm long. *Flowers* glabrous, sepals and petals pale red becoming dark red toward the margins, lip dark red with yellow glenion, short-lived. *Dorsal sepal* ovate, obtuse, 12.5–18.5 × 8–13 mm, 7-veined. *Lateral sepals* connate into a broadly ovate, obtuse to subacute synsepal, 10.5–15.0 × 8.5–14.0 mm, 7- to 8-veined. *Petals* narrowly triangular-subfalcate, subacute, 7.5–11.0 × 2.0–2.5 mm, 3-veined. *Lip* hinged to the column foot, geniculate, pandurate, basally truncate with rounded angles, abruptly acuminate, 6–7 × 4–5 mm, the apical margins thickened; glenion recessed between the basal lobes of the lip, ca. 1.5 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 2.5 × 2 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* obtriangular, acute, bilobed at the base, 2-celled, ca. 1.0 × 0.8 mm. *Pollinia* 2, narrowly oblong-pyriform, ca. 0.7 mm long, attached to an elliptic viscidium through a short, cylindric caudicula. *Fruit* not seen.

Eponymy: named after Adam P. Karremans, a world-recognized botanist with a strong interest in Pleurothallidinae orchids, who first collected the nothospecies.

Distribution: endemic to Costa Rica.

Ecology: this nothospecies grows as an epiphyte in the premontane and lower montane forests of the Cordillera Volcánica Central, where it is apparently restricted to the Caribbean watershed at elevations of 1400–1600 m. Blooming has been recorded at least from May to December, according to the long-term phenological records of the Orchid Conservation Project at Bosque de Paz Biological Reserve.

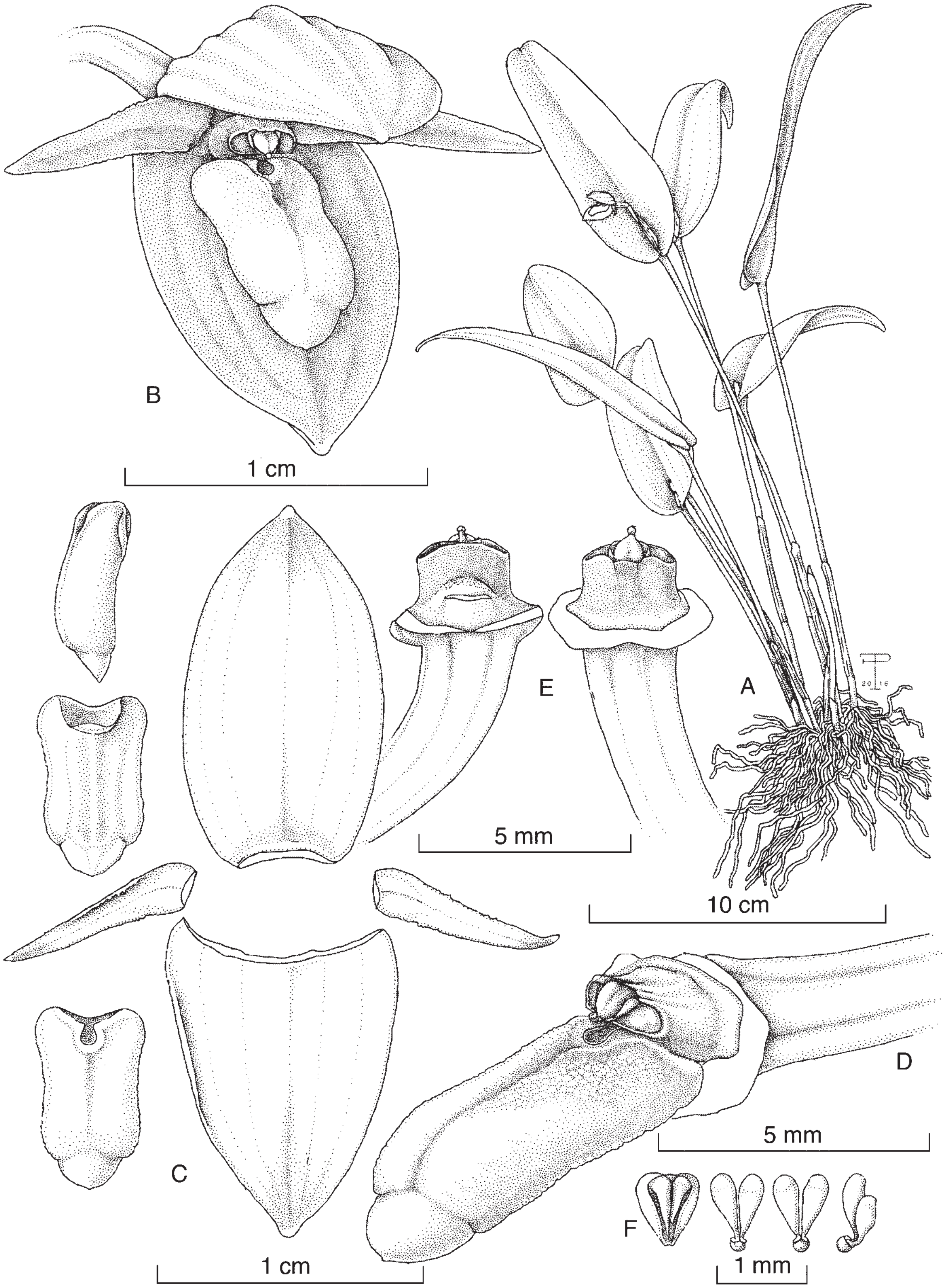


FIGURE 11. *Pleurothallis grandilingua* Pupulin, M. Díaz & Pridgeon. **A,** habit; **B,** flower; **C,** dissected perianth (the lip in lateral, abaxial, and adaxial views); **D,** apex of ovary, column, and lip in three-quarter view; **E,** column, ventral and dorsal views; **F,** anther cap and pollinarium (three views). Drawn by F. Pupulin and S. Díaz Poltronieri from *Bogarín 5638* (JBL). From Pupulin, 2020.

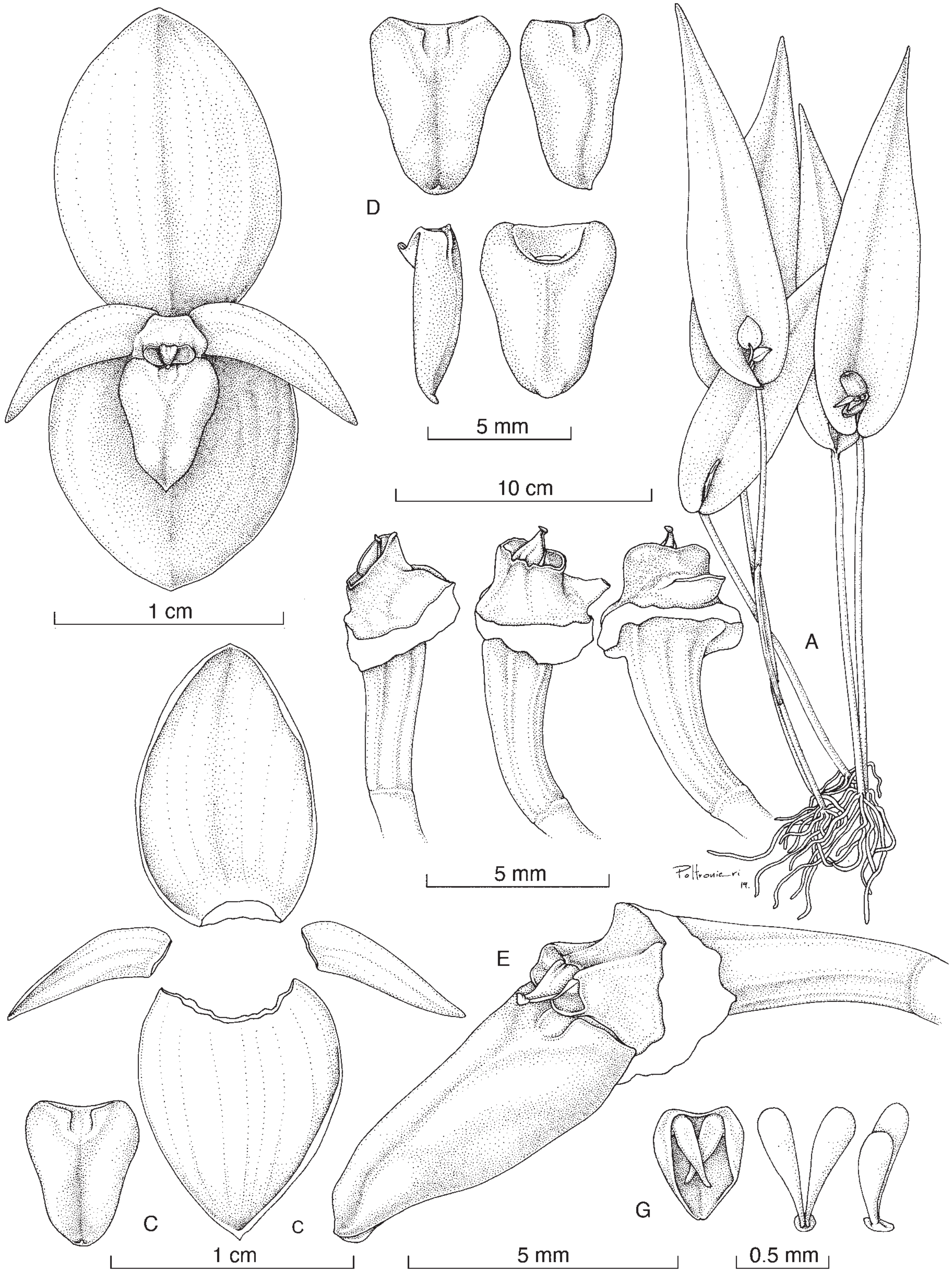


FIGURE 12. *Pleurothallis* ×*karremansiana* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, in adaxial, three-quarter, lateral, and abaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** column in lateral, dorsal, and ventral views; **G,** anther cap and pollinarium (two views). Drawn by S. Díaz Poltronieri from *Díaz 270* (JBL).

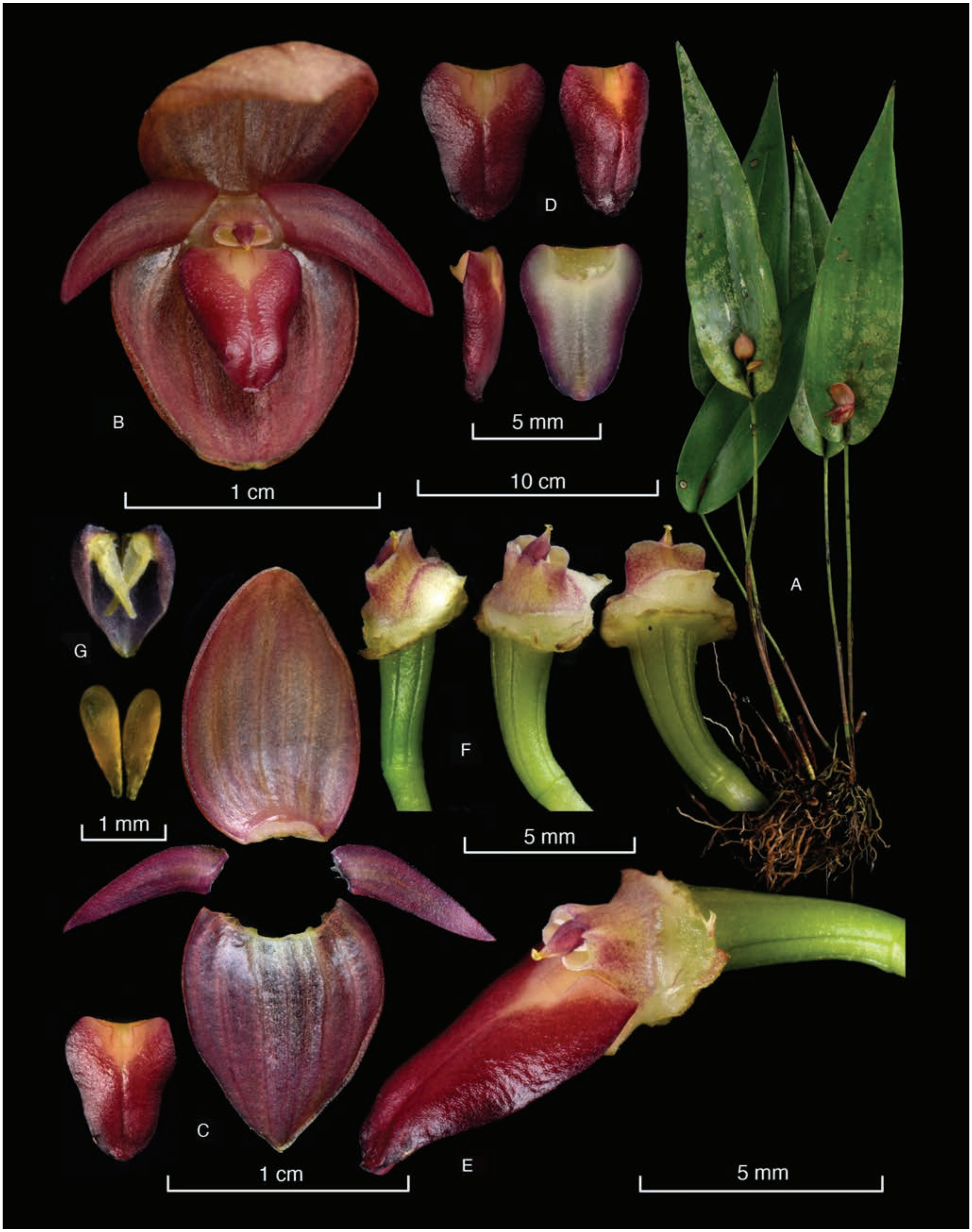


FIGURE 13. *Pleurothallis ×karremansiana* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, in adaxial, three-quarter, lateral, and abaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** column in lateral, dorsal, and ventral views; **G,** anther cap and pollinarium (two views). Lankester Composite Dissection Plate prepared by M. Díaz from *Díaz 270* (JBL).

Distinguishing features: the cordate, narrowly ovate, thinly coriaceous, matte leaves and the purple flowers with broadly ovate, arched, inflexed, obtuse to subacute sepals, narrowly triangular-subfalcate, subacute petals, and pandurate lip allow the determination of this natural hybrid.

We interpret the plant that served as the type as a new natural hybrid between *Pleurothallis tonduzii* and the recently described *P. gonzaleziorum* (Fig. 14), both species recorded for the orchid flora at Bosque de Paz Reserve, where Adam P. Karremans first noted this nothospecies while it was blooming at the Stephen Kirby Orchid Garden. Vegetatively, it shows long acuminate leaves like those of *P. tonduzii*, which are narrowly ovate, cordate, thinly coriaceous and matte like in *P. gonzaleziorum* (the leaves are distinctly coriaceous in *P. tonduzii*, with the adaxial surface shiny). At bloom, the flower is similar to *P. tonduzii* in color, its position on the leaf (closer to the base than *P. gonzaleziorum*), and in the arched, kind of inflexed concave sepals (but wider than in *P. tonduzii*). However, it resembles *P. gonzaleziorum* in the narrowly triangular-subfalcate, subacute petals with entire margin (vs. narrowly linear-lanceolate, acuminate, minutely denticulate in *P. tonduzii*). The lip also shows an interesting combination of features, as it is pandurate and slightly recurved on the apical third like in *P. tonduzii*, but it is not revolute on the distal half and it is glabrous, with the glenion deeply recessed between the thickened basal lobes of the lip, which makes it look more similar to the lip of *P. gonzaleziorum* (Fig. 14). Recently, another individual of the nothospecies was found growing in the wild in the forest of the Bosque de Paz Reserve, which allows us to discard the possibility that it represents a garden hybrid.

Costa Rican material examined: Alajuela: Valverde Vega, Bajos del Toro, Reserva Biológica Bosque de Paz, sendero Jaulares, 10°12'19.25"N, 84°18'58"W, 1540 m, bosque premontano en regeneración, ceciendo *in situ* a una altura de 1.50 m, 25 enero 2020, *N. Belfort-Oconitrillo 568, Juan López* (JBL, eVoucher). Map 1.

4. **Pleurothallis ×parentis-certa** Pupulin & Bogarín, ***nothosp. nov.***

TYPE: Costa Rica. Without collecting data, flowered in cultivation with G. Villalobos in San Miguel de Santo Domingo de Heredia, 20 July 2015, *D. Bogarín 11802* (Holotype: JBL). Fig. 10F, 15–16 (Voucher, *Bogarín 11802*, JBL).

Pleurothallis nothospecie nova inter P. tonduzii Schltr. *et quemquam speciem Pleurothallidi infloreseen-tibus fasciculatissuccessivis, forsan speciem Pleurothalliditurm-aephyllocardiae Luer affinem, intermedia, foliis coriaceis longis anugustibusque, labello sagittato angulis basalis rotundatis figura valde complexeque torta P. tonduzii similis, indumento labelli papillato-verrucoso et petalis deflexis alium genitorem reminiscens.*

Epiphytic, caespitose, spreading to subpendent *herb*, up to 25 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 6–12 cm long, 1.3–2.0 mm in diam., greenish brown, with 2 basal, tubular, tightening, obtuse-truncate sheaths, the lowest one much shorter, the upper one to 3.3 cm long, glumaceous, grayish brown when developing, dry-papyraceous, brown when mature. *Leaf* borne at the apex of the ramicaul, subpendent to pendent, slightly arched, coriaceous, flexible, sessile, oblong-ligulate, acuminate, 14.0–16.5 × 1.1–1.3 cm, rounded to subcordate at the base, the basal lobes suberect, not overlapping, the margin flat, dark green. *Inflorescence* a solitary flower, subtended by a spathaceous, supine, brown, dry-papyraceous, bract ca. 10 mm long, dissolving with age. *Peduncle* terete,

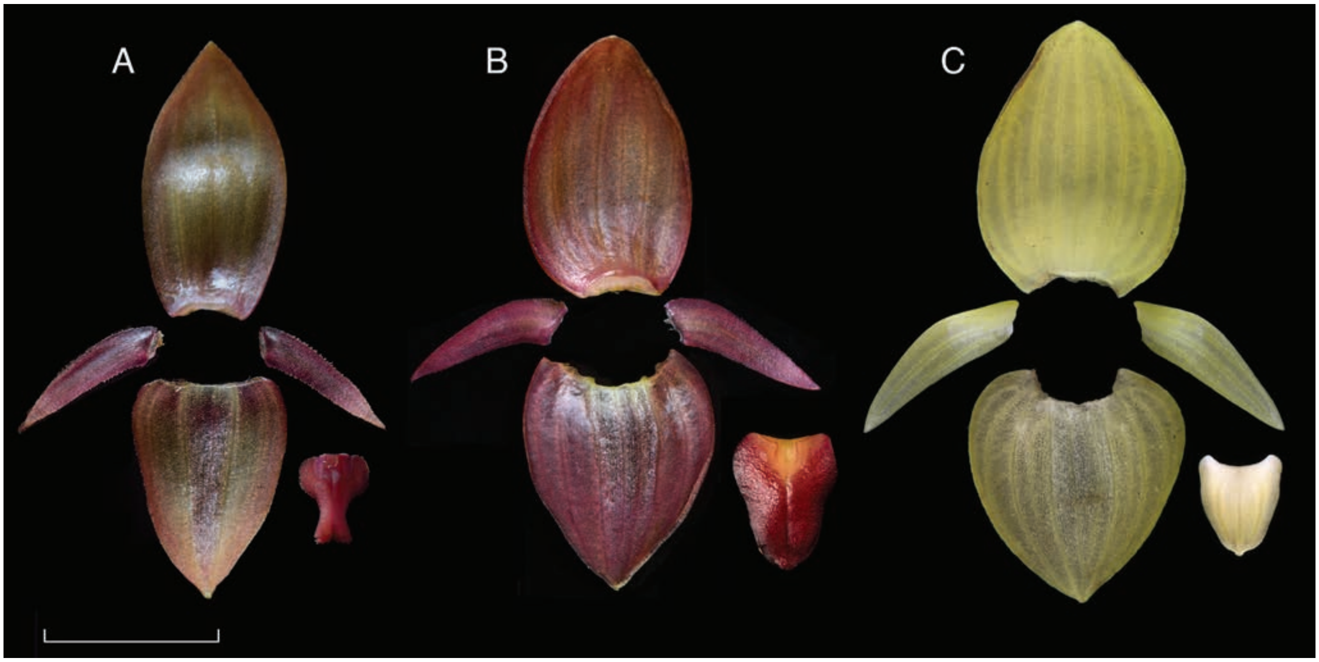


FIGURE 14. Comparison of the perianths of *Pleurothallis ×karremansiana* and the putative parents. **A,** *P. tonduzii* (*JBL-02455*); **B,** *P. ×karremansiana* (*Díaz 270*); **C,** *P. gonzaleziorum* (*Díaz 281*). Scale bar = 1 cm. All the vouchers at JBL. Photographs by F. Pupulin.

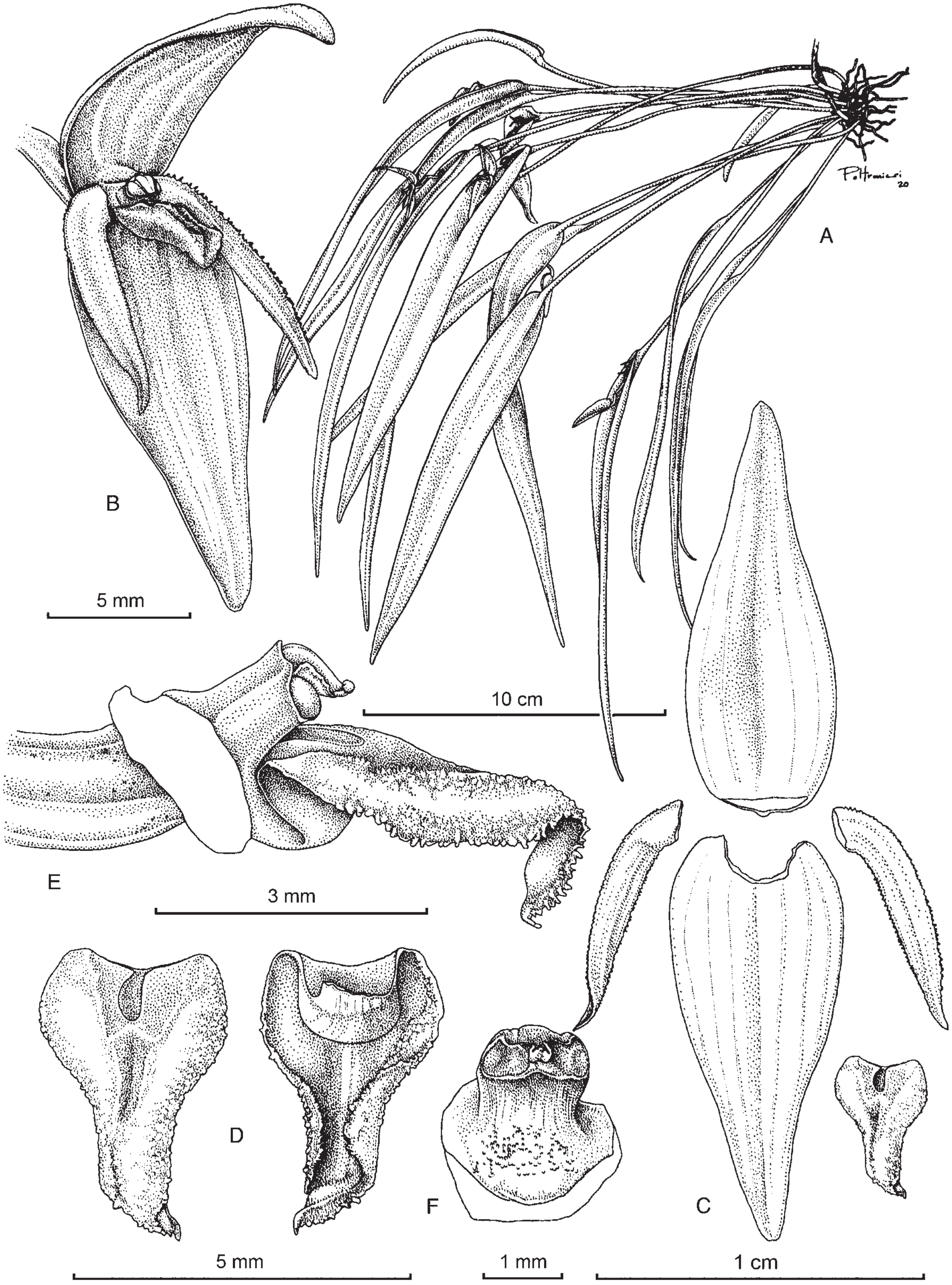


FIGURE 15. *Pleurothallis* ×*parentis-certa* Pupulin & Bogarín. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, in adaxial and abaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** column, ventral view. Drawn by S. Díaz Poltronieri from *Bogarín 11802* (JBL).

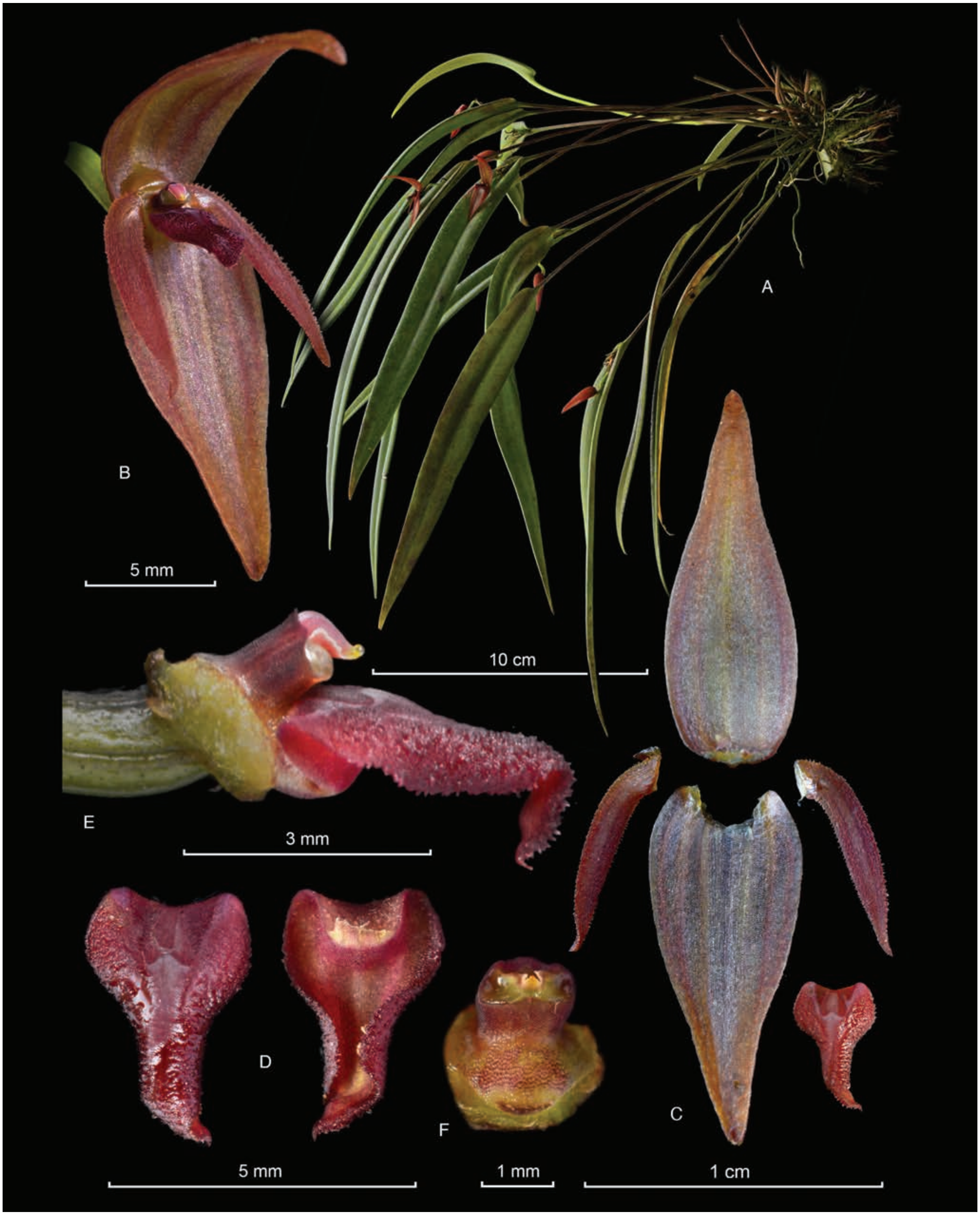


FIGURE 16. *Pleurothallis* ×*parentis-certa* Pupulin & Bogarín. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, in adaxial and abaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** column, ventral view. Lankester Composite Dissection Plate prepared by D. Bogarín and F. Pupulin from *Bogarín 11802* (JBL).

slender, 10–11 mm long. *Pedicel* terete, green, 6 mm long. *Ovary* terete-subclavate, upcurved, 5.5 mm long. *Flowers* spreading-inflexed, the sepals rose-purple with purple stripes, the petals purple red, the lip dark magenta-purple, the column purple. *Dorsal sepal* arched over the column, concave, lanceolate, acuminate, 12.5 × 4.2 mm, 5-veined. *Lateral sepals* connate into a lanceolate, abruptly acuminate, basally concave synsepal, 12 × 5 mm, each half 3-veined. *Petals* narrowly linear, falcate, acuminate, minutely serrulate, deflexed, 7.5 × 1.5 mm, single-veined. *Lip* unguiculate, hinged to the column foot, thick, fleshy, erect, lanceolate-pandurate, basally truncate-subcordate with rounded angles, abruptly recurved toward the apex, acute, the margins denticulate, revolute on the distal half, 4.0 × 2.6 mm when spread, minutely papillous-verrucose throughout; glenion recessed within a conic, glabrous, apical bilobed cavity at the base, 1.2 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, with a thick, densely papillose foot ca. 1 mm long, 1.4 × 1.3 mm, the anther apical, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subtruncate, 2-celled. *Pollinia* 2, claviform, 1.0 mm long, attached to a globose viscidium.

Etymology: from the Latin *parens, parentis,* "a parent," and *certus*, *-a*, "certain, sure, trusty," in reference to the possibility of determining with certainty only one of the two putative parents of the nothospecies.

Distribution: know only from Costa Rica.

Ecology: nothing is known of the ecology of this putative natural hybrid.

Distinguishing features: the long and narrow, coriaceous leaves and the small rose-purple flowers with lanceolate, acuminate sepals and an erect, highly torsioned magenta-purple lip are characteristic of the nothospecies.

We interpret this peculiar finding as a new natural hybrid of *Pleurothallis*, involving *P. tonduzii* as one of the putative parents. The habit of the plant, with long and narrow, coriaceous, ligulate-oblong leaves and a highly complex three-dimensional lip held almost perpendicularly to the flower and subject to several different torsions both longitudinally and transversally, is unmistakably associated with *P. tonduzii*, which we postulate to be one of the parents of the new nothospecies. Apart from the shape and orientation of the lip, however, the flowers of *P. parentis-certa* have only a superficial resemblance to those of *P. tonduzii* as to their dimensions and morphology. Both the dorsal sepal and the synsepal of the nothospecies are lanceolate and subacuminate, while in *P. tonduzii* they are ovate-elliptic and subacute to acute; they are distinctly shorter than in *P. tonduzii* and about half the width. The size of the flower, which is roughly half those of *P. tonduzii* (Fig. 17), the papillate-verrucose indumentum of the lip, and the falcate-pending, denticulate petals, are suggesting a parentage with a species of the *Pleurothallis phyllocardia* group.

5. ***Pleurothallis tonduzii*** Schltr., Beih. Bot. Centralbl., Abt. 2 36(3): 397. 1918. *Acronia tonduzii* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 199, f. 200. 2005. *Zosterophyllanthos tonduzii* (Schltr.) Szlach. & Kulak, Richardiana 6(4): 193. 2006. TYPE: Costa Rica. [Alajuela:] Forêts de San Ramón, 1500–1600 m, May 1913, *A. Tonduz s.n.* (Herb. Nac. Costa Rica 17646) (Holotype: B, destroyed; Lectotype, designated by Pupulin et al., 2016, tracings of the original drawing of the holotype, made under Schlechter's supervision: AMES 23680/barcode 00074808). Fig. 18–19 (Vouchers, *Karremans 5840* and *JBL-02455*, JBL).

Epiphytic, caespitose, erect *herb*, up to 35 cm tall. *Roots* slender, flexuous, 1–2 mm in diam. *Ramicauls* terete, slender, 4–23 cm long, 1.0–2.5 mm in diam., dark green, with 2–3 basal, tubular, obtuse sheaths, the lowest ones much shorter, 2.5–5.3 cm long, dry-papyraceous, brown when mature. *Leaf* borne at the apex of the ramicaul, erect, slightly or notably arched toward the apex, coriaceous, flexible, sessile, narrowly elliptic, acute, becoming sometimes uncinate toward the apex, 5.0–16.0 × 1.3–3.2 cm, obtuse to cordate at the base, the basal lobes inflexed to suberect, not overlapping, the margin flat, dark green. *Inflorescence* a successive, solitary flower, subtended by a spathaceous bract ca. 1 mm long, green, becoming brown, dry-papyraceous when mature. *Pedicel* terete, green, 13 mm long. *Ovary* terete, curved, 7 mm long. *Flowers* spreading-inflexed, the sepals yellowish green or yellow stained light purple, usually adaxially brownish and abaxially vinous along veins, the petals yellowish green or vinous, the lip dark fuchsia, lustrous, the column light to bright fuchsia. *Dorsal sepal* arched, concave, ovate, acute, 12.3–15.5 × 7.2–8.2 mm, abaxially sulcate, the margins inflexed, 7-veined. *Lateral sepals* connate into an ovate, acute synsepal, the margins inflexed, 10.3–12.5 × 8.8–9.0 mm, each half 4-veined. *Petals* narrowly linear-lanceolate, acuminate, minutely denticulate, apically somewhat inflexed at maturity, 7.5–9.0 × 2.1–2.5 mm, single-veined. *Lip* unguiculate, hinged to the column foot, thick, fleshy, almost porrect, pandurate, basally truncate-subcordate with rounded angles, abruptly recurved on the apical third, subacute, the sides denticulate, revolute on the distal half, when spread out 6.4–7.0 × 3.9–4.8 mm, minutely verrucose; glenion raised on a minute, dull callus on the disc, 0.5–0.7 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, with a thick foot 1.2–1.5 mm long, 1.3–2.3 × 1.0–2.2 mm, the anther apical, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subtruncate, 2-celled. *Pollinia* 2, claviform, 1.0–1.4 × 0.35–0.37 mm, attached to a globose viscidium. (Fig. 10G–I).

Eponymy: named after the Swiss botanist Adolphe Tonduz, who discovered the species.

Distribution: endemic to Costa Rica and western Panama.

Ecology: a widespread but uncommon epiphyte of the premontane and low montane forests on both watersheds of the Continental Divide, from 800 to 1800 m in elevation. Flowering occurs throughout the year, with a peak in the rainy season between May and November.

Distinguishing features: the thick, narrowly lanceolate leaves subequal in length to the stem, often strongly recurved toward the apex, and the subspreading flower with a complicated lip (Fig. 4), which is basally straight and abruptly raised-geniculate apically made this species unmistakable.

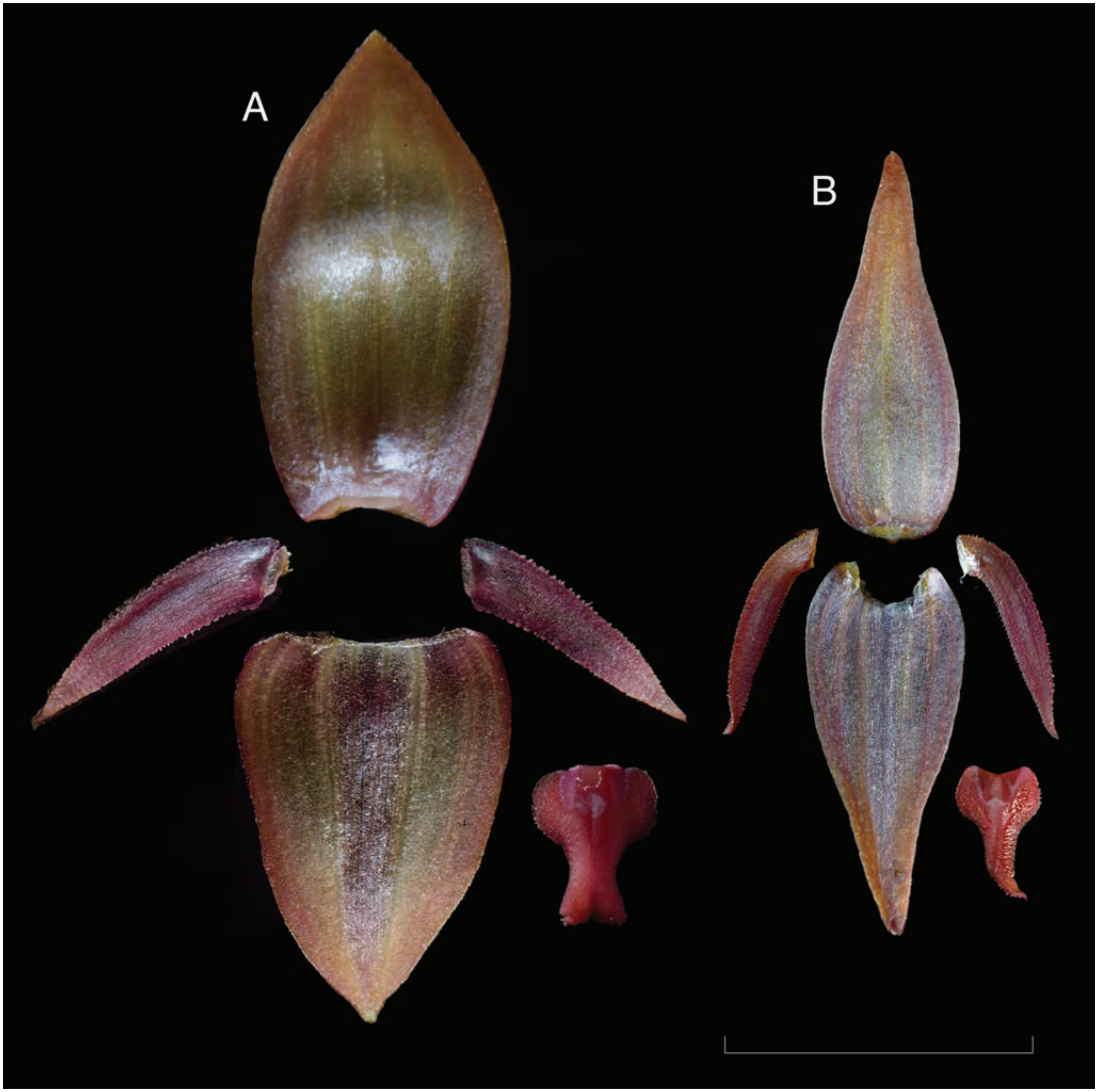


FIGURE 17. Comparison of the perianths of *Pleurothallis* ×*parentis-certa* and the putative parent *P. tonduzii*. **A,** *P. tonduzii* (*JBL-02455*); **B,** *P.* ×*parentis-certa* (*Bogarín 11802*). Scale bar = 1 cm. Vouchers at JBL. Photographs by F. Pupulin.

No actual material of the original collection by Tonduz has been located, and for this reason Pupulin et al. (2016) designated the tracings made in Berlin of the original drawings of the holotype, prepared by Schlechter and made under his supervision, as the species's lectotype. These tracings clearly show the characteristic, tall habit of the plant with narrow, erect leaves, slightly cordate at the base. The sketches of the flower illustrate the denticulate petals and the lip with strongly revolute margins, appearing pandurate in outline, that Schlechter mentioned in the protologue. The same analysis of the flower prepared by Schlechter was posthumously published by Mansfeld (1931: flower analysis no. 44).

Costa Rican material examined: Alajuela: Bajos del Toro, Cataratas, without collector, December 1999, flowered in cultivation at Jardín Botánico Lankester, 11 Jun 2019, *JBL-02455* (JBL). Alfaro Ruiz, Palmira, Reserva Biológica Bosque de Paz, orillas del sendero Jaulares, 10°12'17.00"N, 84°19'02.10"W, 1541 m, bosque muy húmedo montano bajo, 11 agosto 2011, *A. P. Karremans 4575, D. Bogarín & M. Muñoz* (JBL). **Cartago:** Paraíso, Orosi, P.N. Tapantí-Macizo de La Muerte, Sendero

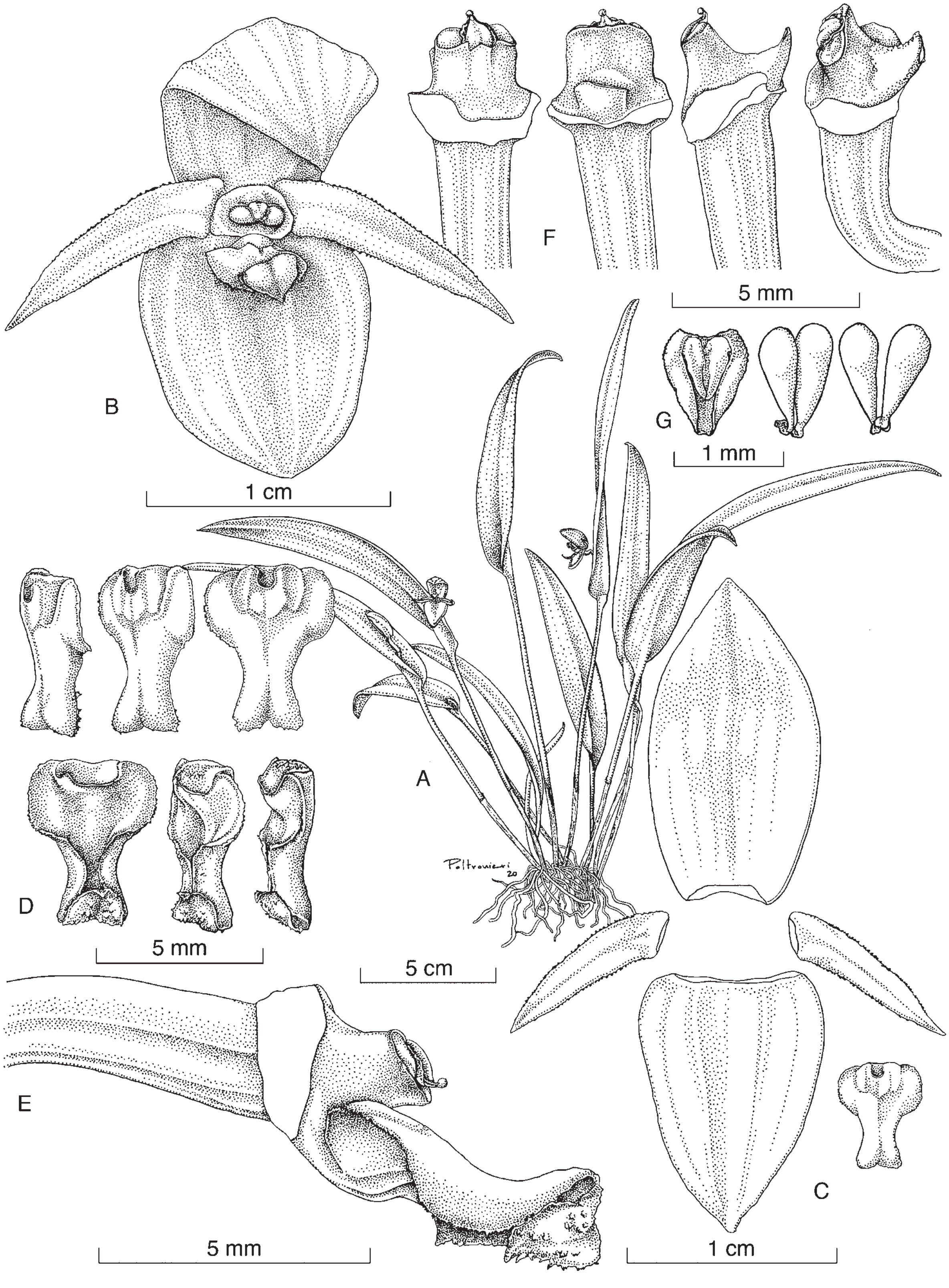


FIGURE 18. *Pleurothallis tonduzii* Schltr. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, several views; **E,** apex of ovary, column, and lip in lateral view; **F,** column in several views; **G,** anther cap and pollinarium (two views). Drawn by S. Díaz Poltronieri from *JBL-02455*(JBL).

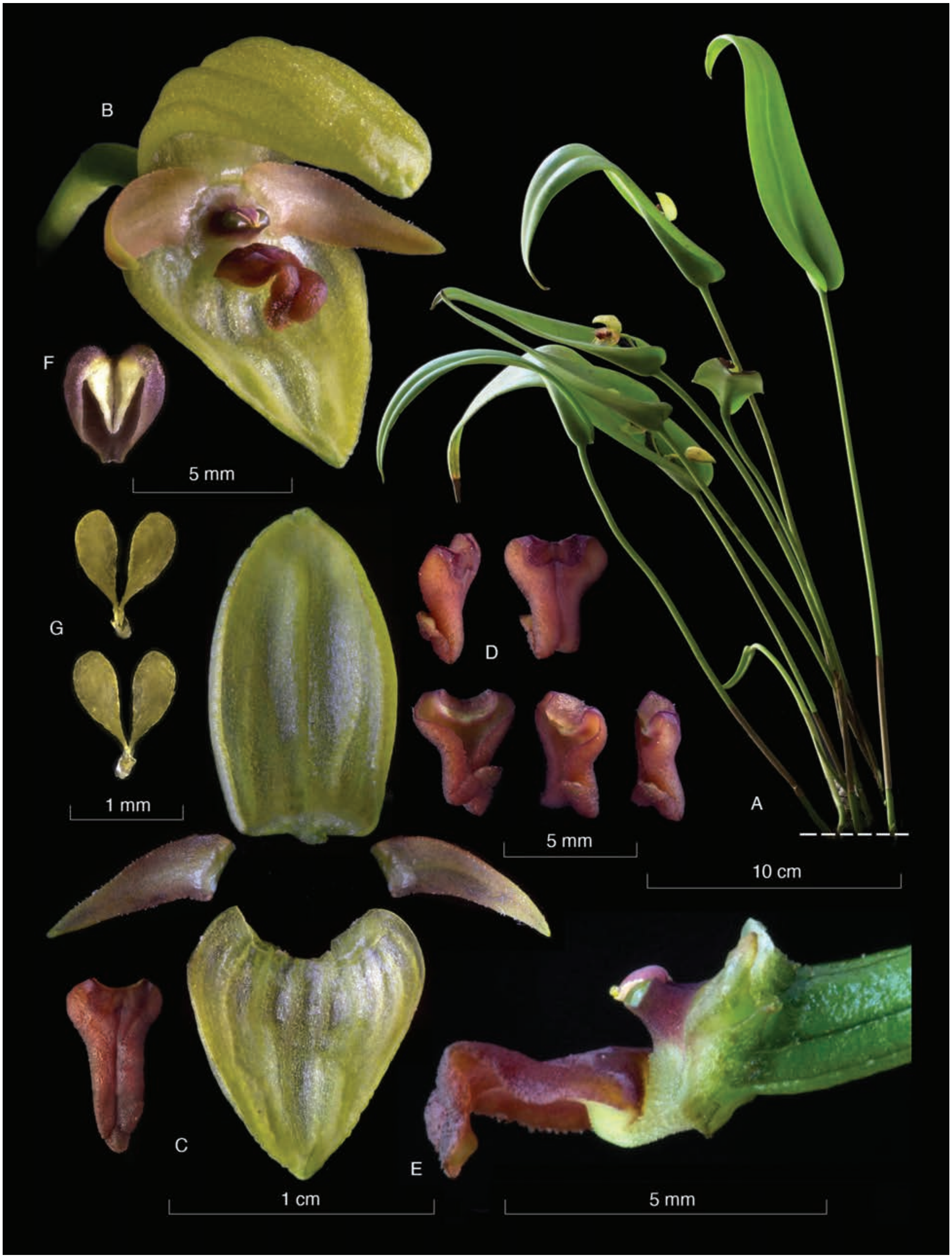


FIGURE 19. *Pleurothallis tonduzii* Schltr. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, several views; **E,** apex of ovary, column, and lip in lateral view; **F,** anther cap; **G,** pollinarium (two views). Lankester Composite Dissection Plate prepared by F. Pupulin from *Karremans 5840* (JBL).

Oropendola. Bosque secundario, 9.7516667, -83.7908333, 1300 m, 20 Aug 1992, *J. F. Morales Quirós 415* (CR). **Puntarenas:** Buenos Aires, Buenos Aires, entre Santa Rosa y Convento, orillas de la Quebrada Santa María, afluente del Río Cañas, 9°15'3.797"N, 83°22'33.968"W, 824 m, bosque muy húmedo premontano epífita en árboles a orillas de la quebrada, 20 marzo 2013, *A. Karremans 5840, D. Bogarín, J. Cambronero & F. Pupulin* (JBL). Coto Brus, Las Alturas de Cotón, Fila Cedro, unpaved road to Río Cedro, 8°58'20"N, 82°52'40"W–8°59'03"N, 82°54'20"W, 1670–1240 m, lower montane moist forest, primary vegetation, 20 March 2003, *F. Pupulin 4389, H. Léon-Páez & A. C. Rodríguez* (JBL). Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, 8°56'46.1"N, 82°44'30.9"W, 1778 m, finca "El Capricho" de Miguel Sandí, principalmente en árboles de *Quercus* en las lomas y potreros al margen del río Sutú, bosque muy húmedo premontano, 6 octubre 2010, *M. Fernández 381, R. L. Dressler, D. Bogarín & F. Pupulin* (JBL). Coto Brus, Sabalito, Las Alturas de Cotón, Zona Protectora Las Tablas, Estación Biológica Las Alturas, camino al Cerro Chai, 8°59'00.9"N, 82°50'01.5"W, 1650 m, bosque muy húmedo premontano, en bosque secundario a orillas del camino, 26 Octubre 2005, *D. Bogarín 2100, R. L. Dressler, R. Gómez, F. Pupulin, A. y S. Rambelli* (JBL). Coto Brus, Limoncito, Fila Cruces, camino al Cerro Paraguas, ca. 10 km al oeste del Jardín Botánico R. & C. Wilson sobre el camino a Río Claro de Golfito, 8°46'22.4"N, 82°59'33.1"W, 1367 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del camino, 5 Junio 2010, *D. Bogarín 7789, A. Karremans* (JBL). Montes de Oro, Unión, camino entre Palmital y Cedral, ca. 1.5 km al noreste del cruce de Palmital, finca de la familia Elizondo, 10°11'20.80"N, 84°40'54.15"W, 1376 m, bosque pluvial premontano, epífitas en bosque secundario y potreros, 26 Octubre 2013, *D. Bogarín 10434* (JBL). Monteverde, Sendero Tranquilo, 1.5 km SE of Cerro Amigos. Lower montane wet forest. Disturbed primary forest, 10.3000000, -84.8000067, 1500 m, 5 May 1995, *D. Penneys 425* (CR). **San José:** Acosta, Sabanillas, Hda. Tiquires. Los Ayarales, bosque primario y potreros en la Fila innominada al S. del Río Tiquires, 9.7152778, -84.1986111, 1400 m, 4 Jun 1995, *J. F. Morales Quirós 4333* (CR). Dota, San Joaquín, 1 km después de la escuela de San Joaquín yendo hacia Quepos, 09°34'32.88"N, 84°00'18.06"W, en árboles esparcidos en potreros, 20 de febrero 2012, *A. Karremans 5158* (JBL). León Cortés, San Antonio, Cuenca del Pirrís - Damas. San Pablo de León Cortéz, Cerro Abejonal, 9.7083333, -84.0472222, 12 Oct 2003, *J. F. Morales Quirós 10022* (CR). Pérez Zeledón, R.F. Los Santos, Los Angeles, Páramo, 9.4975000, -83.7872222, 7 Mar 2001, *A. Quesada Hernández 540* (CR). Tarrazú, San Marcos, Carretera hacia San Carlos de Tarrrazú. Remanentes de Bosque a la orilla de la carretera. Plantas epífitas. 09°36'24"N, 84°05'53"O, 1607 m.s.n.m., 24 Setiembre 2004, *E. Serrano 154* (JBL). Tarrazú, San Lorenzo, Faja Costena Quepos. Cerro San Isidro, Falda Sur en el camino hacia Esquipulas, 9.5191667, -84.0450000, 400–600 m, 18 Nov 2010, *J. F. Morales Quirós 19291, F. A. González Brenes & D. Santamaría* (CR). Tarrazú, San Carlos, Cerro Cura, camino a San Marcos, Bosque remanente en la orilla de la carretera a San Jerónimo de Tarrazú, 9.6047222, -84.1108333, 21 Sep 2004, *S. Lobo Cabezas 736 & A. F. Rojas Alvarado* (CR.). Tarrazú, San Marcos, Cerro San Pedro, 9.6847222, -83.9966667, 28 Sep 2000, *S. Lobo Cabezas 209, A. Cascante & J. Sánchez* (CR). **Without specific locality data:** flowered in cultivation at Jardín Botánico Lankester, 28 Apr 1998, *F. Pupulin 548* (JBL); flowered in cultivation at Jardín Botánico Lankester, 31 May 2016, JBL-02428 (JBL); flowered in cultivation at Jardín Botánico Lankester, 21 Nov 2016, *JBL-02458* (JBL); flowered in cultivation at Jardín Botánico Lankester, 12 Jun 2019, *JBL-02515* (JBL); flowered in cultivation at Jardín Botánico Lankester, 27 May 2016, *JBL-04793* (JBL); flowered in cultivation at Jardín Botánico Lankester, 13 June 2016, *JBL-04794* (JBL); flowered in cultivation at Jardín Botánico Lankester, 3 Aug 2016, *JBL-04795* (JBL); flowered in cultivation at Jardín Botánico Lankester, 8 Jul 2016, *JBL-29983* (JBL). Map 1.

B. The *Pleurothallis palliolata* group

6. ***Pleurothallis chavezii*** Luer, Lindleyana 11(2): 72. 1996. TYPE: Costa Rica: Guanacaste: epiphytic in Parque Nacional Guanacaste, Estación Biológica Volcán Cacao, Estación Pitilla, 10°55'45"N, 85°28'15"W, 1100 m, 24 October 1990, *C. Chávez 438* (Holotype, K; Isotypes: CR, MO). Fig. 20 (Vouchers, *C. Chávez 438*, *R. Joyce s.n.*-photograph).

Epiphytic, caespitose, erect *herb*, up to 25 cm tall. *Roots* slender, flexuous, 1 mm in diam. *Ramicauls* terete, slender, 15–26 cm long, ca. 3 mm in diam., pale green, with 2–3 basal, short, tubular, obtuse sheaths, and a longer sheath below the middle to 4.5 cm long, pale green, glumaceous, aging dry-papyraceous, brown. *Leaf* borne at the apex of the ramicaul and clasping the stem, suberect to a right angle with the stem, convex, coriaceous, flexible, sessile, ovate, acute, abruptly short-acuminate, medium green, 8.0–12.2 × 4.0–6.5 cm, cordate at the base, the basal lobes not overlapping. *Inflorescence* fascicle-like, bearing 1–3 flowers, subtended by a spathaceous, ovate, complanate, obliquely truncate bract ca. 11–13 mm long, green, becoming brown, dry-papyraceous when mature. *Peduncle* terete, 1–3 mm long. *Pedicel* terete, green, 12–15 mm long. *Ovary* terete, green, round in section, 4 mm long. *Flowers* bilabiate, ringent, red, the base of the sepals white, the dorsal sepal yellowish white with red stripes along the vein, the base of the lip white. *Dorsal sepal* cucullate with the apex bent upward, reclinate over the column, broadly elliptical to ovate when spread, obtuse, much wider than the synsepal, 8.5 × 6.5 mm, 5-veined. *Lateral sepals* connate into an oblong, acute synsepal, the base concave and then convex toward the apex, the apex and margins spreading, 8.5 × 3 mm, each half 6-veined. *Petals* narrowly elliptical-oblong, acute, narrowed above the base, with a basal lobule lying adjacent to the column, geniculate at the middle, the margins minutely denticulate, thickened along the midvein, 6.5 × 1.5 mm, single-veined. *Lip* lanceolate to narrowly subpandurate, acute, hinged to the column foot, fleshy, basally subtruncate with obtuse angles, the apex acute, 4.25 × 1.5 mm, narrowed to 0.75 mm above the base and geniculate with a minute

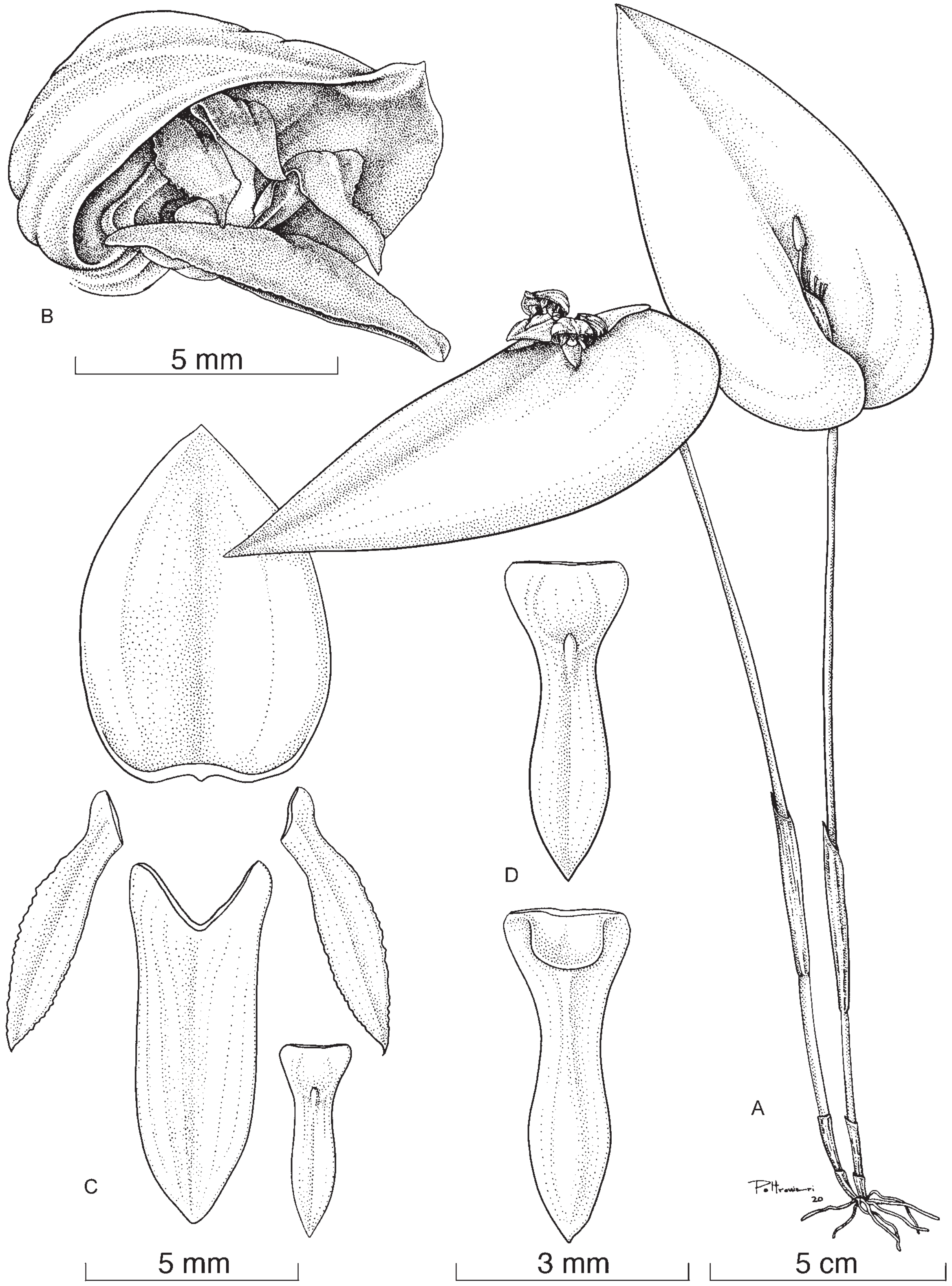


FIGURE 20. *Pleurothallis chavezii* Luer. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial and lateral views. A–B, drawn by S. Díaz Poltronieri from *Joyce s.n.* (JBL–photograph); C–D, modified by S. Díaz Poltronieri from Luer (1996) on the basis of *Chávez 438* (MO).

callus on the anterior margin, truncate, with a deflexed claw, the undersurface with a thickening along the midvein greatest above the middle. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, 1 mm long, 1.5 mm wide, with a thick, broad foot ca. 1.5 mm long, the anther apical, the stigma apical, bilobed. *Anther cap* and *pollinia* not seen. (Fig. 21A)

Eponymy: named after Carlos Chávez who discovered this species.

Distribution: known only from Costa Rica.

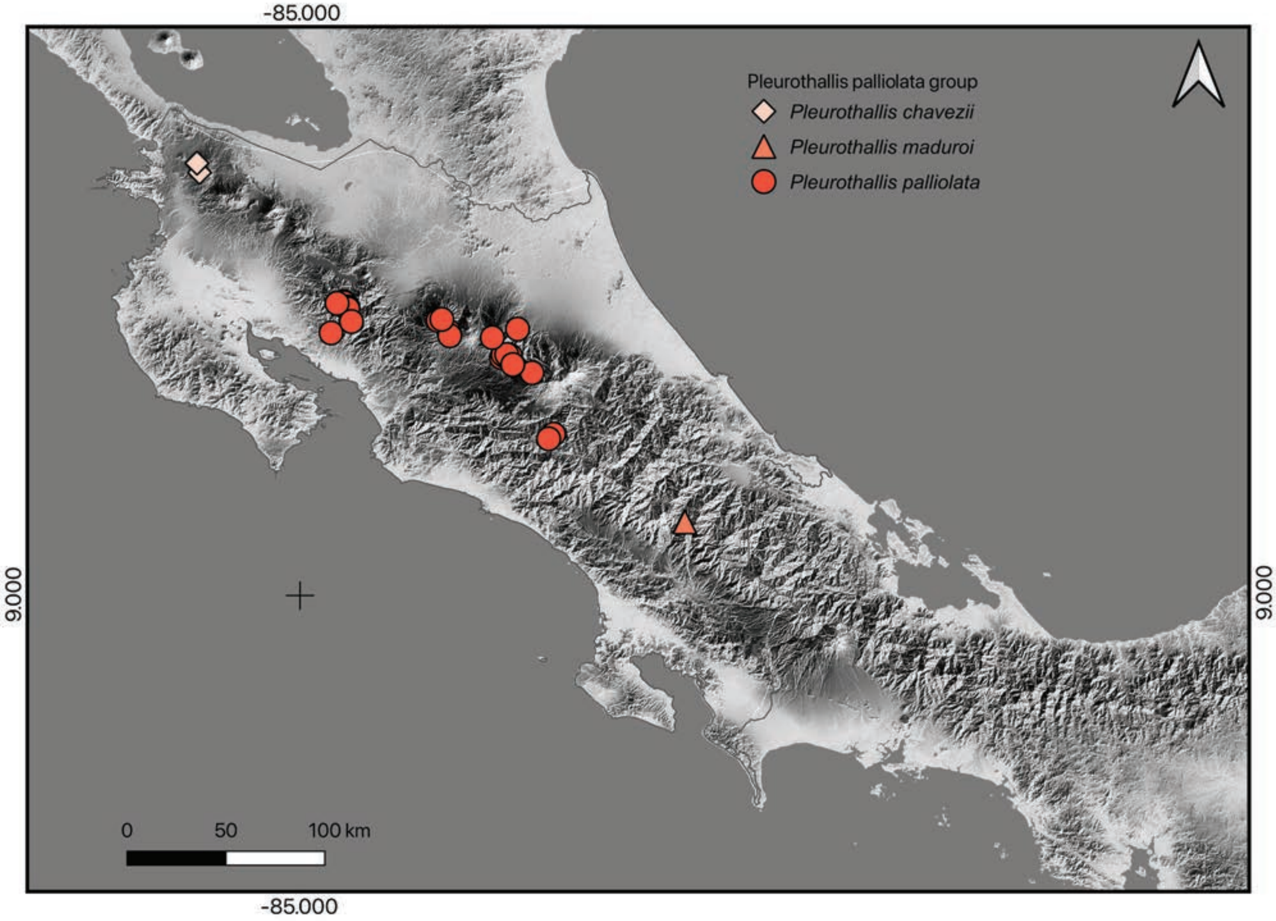
Ecology: epiphytic in premontane wet forest around 900–1100 m of elevation in the slopes of Volcán Cacao and Volcán Orosí in the Cordillera de Guanacaste, northwestern Costa Rica. Flowering was recorded in January and October.

Distinguishing features: this species is morphologically similar to *Pleurothallis maduroi* and *P. palliolata* mainly because of the hood-shaped flowers, having the dorsal sepal deeply concave, reclined over the column and much broader than the synsepal. However, *P. chavezii* differs by the red flowers, with a lanceolate-pandurate, geniculate lip and the petals narrowly elliptical-oblong, acute and geniculate. Luer (1996) described this species on the basis of herbarium material. Therefore, the illustration of the type shows the petals and lip flattened. However, in living specimens, the petals and lip are geniculated at its narrowest point, a diagnostic feature of this species.

Costa Rican material examined: Guanacaste: Liberia, Mayorga, P.N. Guanacaste. Estación Biológica Volcán Cacao. Estación Pitilla, 10.9291667, -85.4708333, 24 Oct 1990, *C. Chávez 438 & Curso II de Parataxónomos* (CR). La Cruz, Santa Elena, southwestern slopes of Volcán Orosí, east of Sitio Pedregalito, ca. 10°58'18.86"N, 85°28'58.48"W, ca. 913 m, photographed *in situ* by Richard Joyce and submitted to the iNaturalist website (https://www.inaturalist.org/taxa/140436-Pleurothallis-chavezii). Map 2.

7. ***Pleurothallis maduroi*** Luer, Lindleyana 12(1): 51, f. 12. 1997. *Acronia maduroi* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 156. 2005. TYPE: Panama. Chiriquí: Guadalupe area, March 1985, *A. Maduro 18-M* (Holotype: MO). Fig. 21B, 22 (Vouchers, *Kaes s.n.*, JBL; *Maduro 18-M*, MO).

Epiphytic, caespitose, erect to suberect *herb*, up to 25 cm tall. *Roots* slender, flexuous, 1 mm in diam. *Ramicauls* terete, slender, 13–17 cm long, ca. 2 mm in diam., brownish green, with a basal, tubular, tighten, obtuse sheath 3.5–5.0 cm long, pale green, glumaceous when developing, aging dry-papyraceous, brown. *Leaf* borne at the apex of the ramicaul, sessile, erect to curved toward the ramicaul, soft-coriaceous to coriaceous, lanceolate to narrowly ovate, acute, abruptly subacuminate, the base deeply cordate, the basal lobes not overlapping, the margins sometimes



Map 2. Map of collection sites for the species of *Pleurothallis palliolata* group.

FIGURE 21. Flowers of *Pleurothallis* species from Costa Rica in the *P. palliolata* (A–C) and *P. cardiothallis* (D–I) groups. **A,** *P. chavezii* (*Joyce s.n.*); **B,** *P. maduroi* (*Kaes s.n.*); **C,** *P. palliolata* (*Bogarín 7303*); **D,** *P. callosa* (*Rojas-Alvarado 258*);. **E–F,** *P. cardiothallis* (*Blanco 2813*; *Pupulin 6414*); **G–H,** *P. gonzaleziorum* (*Díaz 281*; *Díaz 269*); **I,** *P. navisepala* (*Pupulin 8846*). Not at the same scale. All the vouchers at JBL except A, not conserved. Photographs by F. Pupulin except A (R. Joyce), B (E. Kaes), and D (M. Díaz).

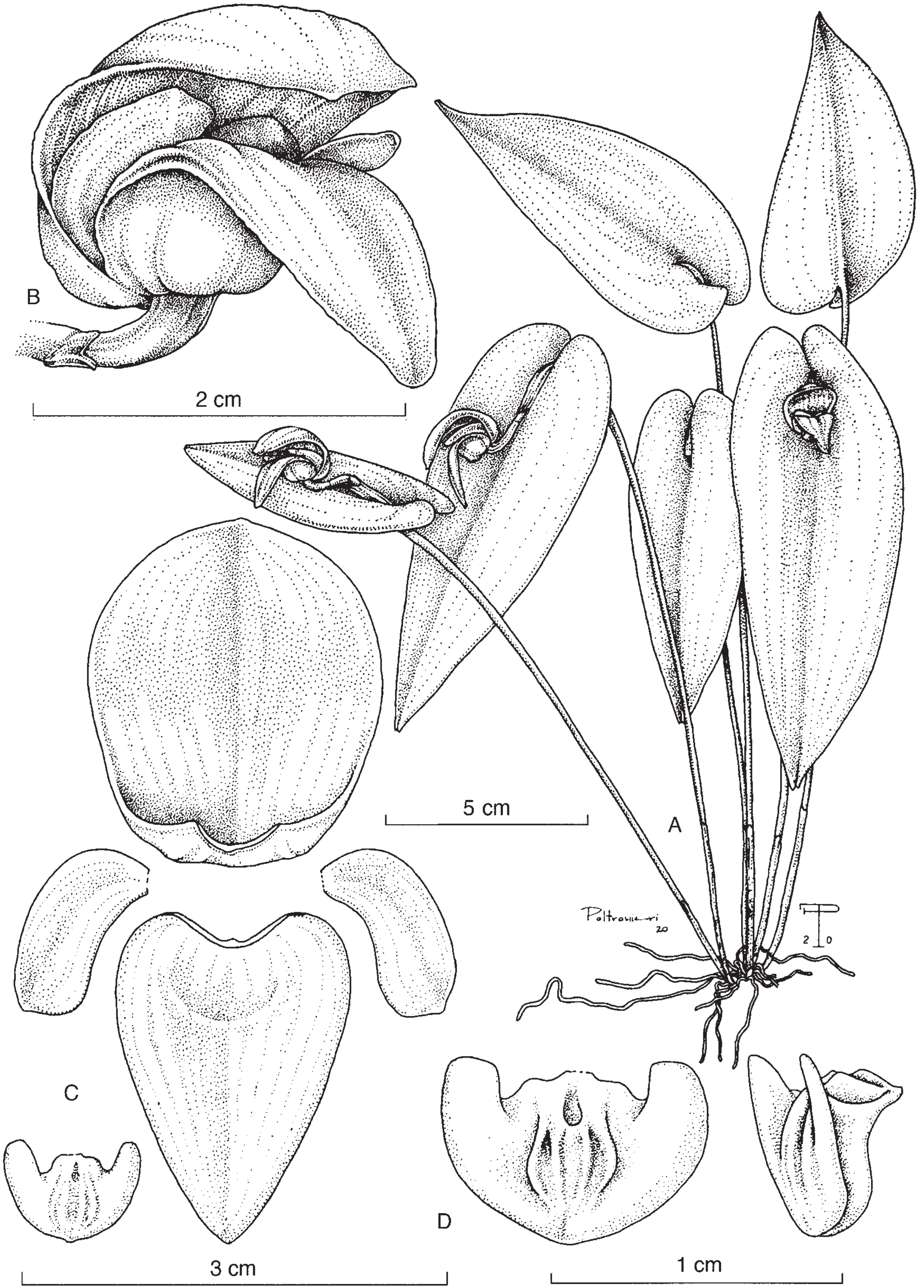


FIGURE 22. *Pleurothallis maduroi* Luer. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial and lateral views; A–B, drawn by S. Díaz Poltronieri from *Kaes s.n.* (JBL); C–D, modified by S. Díaz Poltronieri from Luer (1997) on the basis of *Maduro 18* (MO).

undulate toward the base, 6.0–12.2 × 3.2–5.6 cm, grass green, the adaxial surface shiny. *Inflorescence* a single flower, subtended by a spathaceous, oblong, complanate, acute bract 11–12 mm long, green, becoming brown, dry-papyraceous when mature. *Peduncle* terete, shorter than the spathe, ca. 10 mm long. *Pedicel* terete, green, 5–7 mm long. *Ovary* terete, sigmoid, green, round in section, 10 mm long. *Flowers* bilabiate, ringent, the sepals pale rose-purple on a creamish yellow background, flushed and striped pinkish red toward the apices, the petals red, the lip dark purple, the column white. *Dorsal sepal* deeply cucullate, almost completely reclinate over the column, broadly obovate-suborbicular when spread, obtuse-rounded, with a rounded apicule, distinctly wider than the synsepal, 2.7 × 2.3 cm, 17-veined. *Lateral sepals* connate into a lanceolate, subacute synsepal, the base deeply concave, forming a short chin, the apex and margins spreading, geniculate at the middle, 2.5 × 1.8 cm, each half 6-veined. *Petals* oblong, falcate, broadly obtuse, decurrent, entire, the thickened apex provided with a short, rounded, adaxial keel, ca. 13 × 7 mm, 5-veined. *Lip* unguiculate, hinged to the column foot, fleshy, geniculate at the base, 3-lobed, transversely rheniform-semilunate, basally with 2 lateral, rectangular, rounded-truncate, retrorse lobes, the apex broadly obtuse to subrounded, thick, flat to slightly convex, 6 × 9 mm, with 4 prominent, thickened veins running from the disc toward the apex and flushing into the blade before the margin, the glenion elliptic, on a low, rounded thickening at the base of the disc, ca. 1.5 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, 1.5 mm long, with a thick foot, the anther apical, the stigma apical, bilobed. *Anther cap* and *pollinia* not seen.

Eponymy: named after Andrés Maduro of Panama City, Panama, who discovered the species.

Distribution: Costa Rica and Panama.

Ecology: terrestrial among organic litter, inhabiting the lower montane wet forest of the Continental Divide in the Cordillera de Talamanca. Flowering has been recorded in the field in November.

Distinguishing features: the large flower with deeply hooded dorsal sepal, distinctly broader than the synsepal and almost completely reclined over the column; the synsepal geniculate at the middle with the distal portion extended; the falcate, oblong petals; and the 3-lobed lip with retrorse auricles are diagnostic of *P. maduroi*.

Costa Rican material examined: Limón: Talamanca, Telire, sendero entre Cerro Arbolado y San José Cabécar, Cerro Casma, entre Quebrada Kuisa y Río Lori, 9°20'11.40"N, 83°13'47.90"W, 2192 m, bosque pluvial montano bajo, terrestre entre hojarasca en bosque primario, 11 noviembre 2016, *E. Kaes s.n., M. Acuña & O. Zúñiga* (JBL e-voucher). Map 2.

8. ***Pleurothallis palliolata*** Ames, Proc. Biol. Soc. Wash. 35: 86. 1922. *Acronia palliolata* (Ames) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 168. 2005. *Zosterophyllanthos palliolatus* (Ames) Szlach. & Kulak, Richardiana 6(4): 191. 2006. TYPE: Costa Rica. *C. H. Lankester 192/1920* (Holotype: K). Fig. 21C, 23 (Voucher, *Bogarín 6106*, JBL).

Epiphytic, caespitose, erect to suberect *herb*, up to 15 cm tall. *Roots* slender, flexuous, 1 mm in diam. *Ramicauls* terete, slender, 10–16 cm long, ca. 2 mm in diam., pale green, with 2–3 basal, short, tubular, obtuse sheaths, and a longer sheath below the middle to 4 cm long, pale green, glumaceous, aging dry-papyraceous, brown. *Leaf* borne at the apex of the ramicaul and clasping the stem, suberect to a right angle with the stem, coriaceous, flexible, sessile, ovate-lanceolate, acute, abruptly short-acuminate, medium green, sometimes flushed with purple, 7–10 × 2.8–4.0 cm, cordate at the base, the basal lobes not overlapping; juvenile leaves rounded at the base, the margin flat. *Inflorescence* a fascicle of 1–3 flowers, subtended by a spathaceous, oblong, complanate, obliquely truncate bract ca. 8 mm long, green, becoming brown, dry-papyraceous when mature. *Peduncle* terete, slightly exceeding the spathe, ca. 20 mm long. *Pedicel* terete, green, 6–7 mm long. *Ovary* terete, green, round in section, 5 mm long. *Flowers* bilabiate, ringent, the sepals pale yellow, flushed and striped reddish brown to red toward the apices, the petal white, becoming rose-red at apex, the lip dark purple, the column yellowish white. *Dorsal sepal* cucullate, reclinate over the column, broadly ovate to suborbicular when spread, obtuse, much wider than the synsepal, 1.9–2.0 × 1.8 cm, 9–13-veined. *Lateral sepals* connate into a triangular-ovate, obtuse to subacute synsepal, the base deeply concave, the apex and margins spreading, 1.3 × 1.3 cm, each half 3-veined. *Petals* narrowly linear-falcate, acuminate, the base boldly thickened, apically subuncinate, the margins minutely serrate, thickened along the midvein, 7–10 × 2 mm, single–veined. *Lip* unguiculate, hinged to the column foot, fleshy, broadly obovate to rounded, basally subtruncate with obtuse angles, the apex rounded, concave, 5 × 6 mm, with 2 lateral, thickened keels flushing into the middle of the blade, and 2 small, triangular calli at the base. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, 2 mm long, with a thick foot ca. 1.5 mm long, the anther apical, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subcordate, 2-celled, 1.2 × 0.7 mm. *Pollinia* 2, claviform, 2.3 × 0.5 mm, attached to a round viscidium through 2 short, cylindrical caudicles.

Etymology: from the Latin *palliolatus*, "covered with a cloak-cape or hood" (the *pallĭŏlum* was a small Greek mantle), in reference to the hooded dorsal sepal.

Distribution: Costa Rica and Panama.

Ecology: epiphytic, inhabiting the premontane and lower montane wet and cloud forests of the main Costa Rican mountain chains, where it is restricted to the Caribbean watershed at elevations of 1000–2100 m. Flowering has been recorded mostly in October and November.

Distinguishing features: the large flower with the dorsal sepal cucullate, much broader than the synsepal, and the falcate petals apically tinged with red, falcate-uncinate at apex toward the rounded, concave lip easily distinguish *P. palliolata*.

Costa Rican material examined: Alajuela: Carrizal, Concordia, entre Los Cartagos y Cinco Esquinas, 10°08'16.8"N, 84°09'49.8"W, 2027 m, 2027 m, bosque

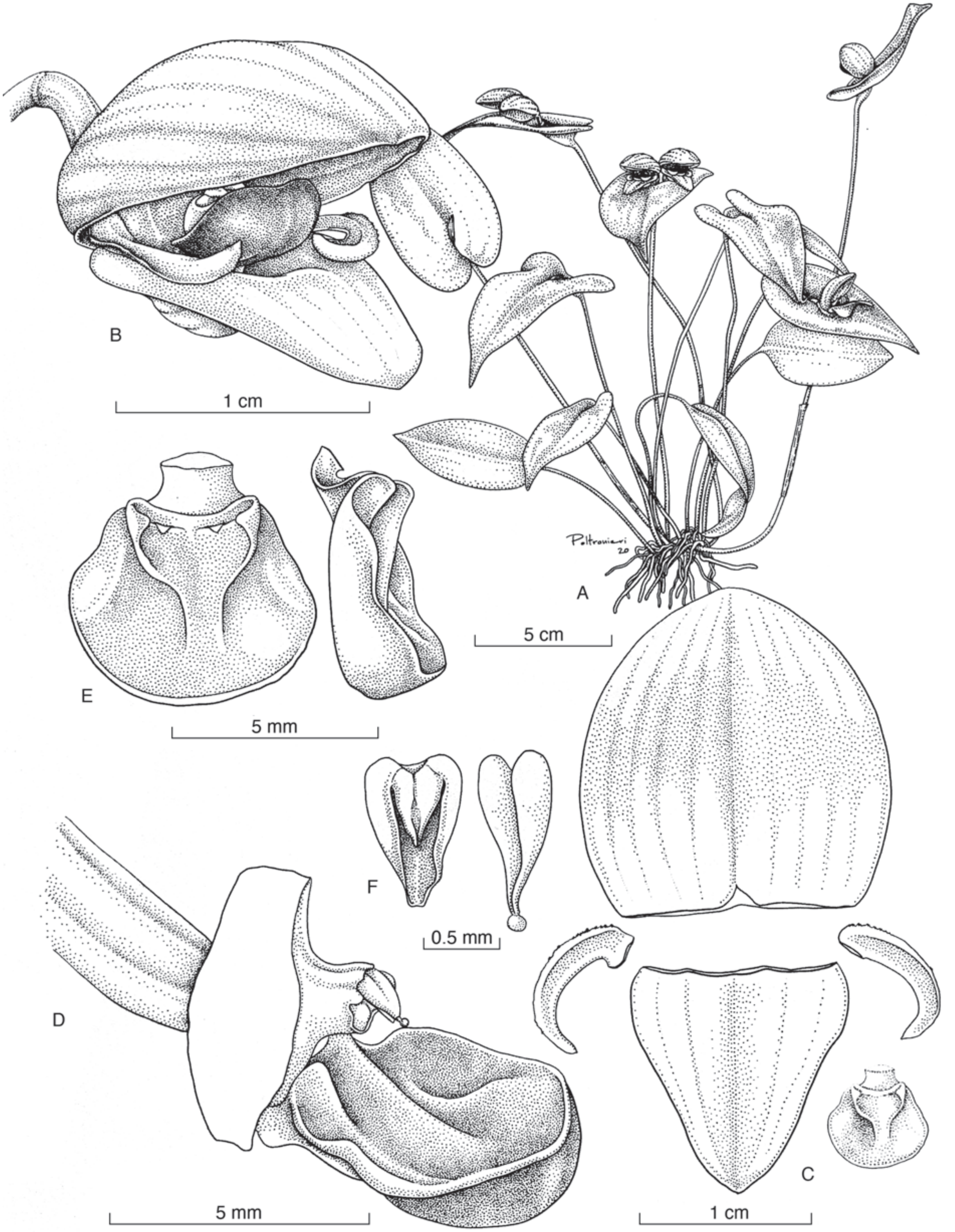


FIGURE 23. *Pleurothallis palliolata* Ames. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in abaxial and lateral views; **E,** apex of ovary, column, and lip, three-quarter view; **F,** anther cap and pollinarium. Drawn by S. Díaz Poltronieri from *Bogarín 7303* (JBL).

pluvial montano bajo, en potreros arbolados y bosque secundario, 17 junio 2009, *D. Bogarín 7303, R. L. Dressler, F. Pupulin & R. Trejos* (JBL). San Ramón, Peñas Blancas, R.B. Monteverde. Río Caño Negro, Monteverde Cerro Negro y Cabeceras, Río San Gerardo, trail leading to Cerro Amigos, 10.3166667, -84.7833333, 7 Oct 1987, *W. Haber 7538 & E. Bello* (CR). San Ramón, Peñas Blancas, Z.P. Arenal-Monteverde (Caribe), Sendero Pantanoso, Valle Torre, 10.3083333, -84.7833333, 1600–1700 m, 15 Nov 1991, *E. Bello 4255* (CR). **Cartago:** El Guarco, San Isidro, Paso Macho (Macho Gaff), después del puesto de guardaparques del Parque Nacional Tapantí-Macizo de La Muerte, cuenca del Río Macho, camino a Queverí, 9°42'53.2"N, 83°51'25.1"W, 2242 m, epífitas en bosque pluvial montano, 5 Diciembre 2013, *D. Bogarín 10530, F. Carbonell & D. Jiménez* (JBL). **Guanacaste:** Abangares, Sierra, Monteverde, R.B. Monteverde. Chomogo, trail to Chomogo peak, Pacific slope and continental divide, cloud forest, 10.3333333, -84.8333333, 9 Nov 1985, *W. Haber 3323 & E. Bello* (CR). Abangares, Sierra, Monteverde, Monteverde reserve, Pacific slope, lower montane wet forest, 10.3333333, -84.8333333, 30 Nov 1985, *W. Haber 3647& E. Bello* (CR). Volcán Tenorio, without more specific data, flowered in cultivation at Jardín Botánico Lankester, 23 Feb 1999, *F. Pupulin 1361* (JBL). Volcán Tenorio (?). Recolector desconocido, sin fecha de recolecta en campo. Floreció en cultivo en Jardín Botánico Lankester el 28 de diciembre de 1999. Sépalos amarillo verdoso translúcido con venas rojizas y teñidos de rojo hacia las puntas. Sépalo dorsal muy cóncavo y cerrado sobre el resto de la flor. Pétalos rojos, verde claro en la base. Labelo rojo sangre. Columna verde claro. *M. Blanco 1062* (USJ). **Heredia:** Heredia, Vara Blanca, Refugio de Vida Silvestre Cerro Dantas, orillas del Río Nuevo, 10°5'40.3"N, 84°3'31.4"W, 1927 m, bosque pluvial premontano, epífitas en bosque secundario, 28 diciembre 2008, *D. Bogarín 6106 & W. Salazar* (JBL). Heredia, Varablanca, RVS Cerro Dantas, Bosque nuboso en refugio Cerro Dantas, sobre ladera caribe a 2 km después de Cerro Chompipe (entrada a torres del ICE), 10.0937222, -84.0590556, 22 Nov 2009, *A. Cascante Marín 2145 & J. Solano Zárate* (CR). Heredia, Varablanca, El Gallito, above and west of Wet secondary forest about 15 m high, with many epiphytes, with frequent wind and rain from the Caribbean. Río Vueltas, (upper río Patria), eastern slope of Volcán Barva near the Continental Divide, 10.1000000, -84.0666667, about 2000 m, 22 Nov 1969, *W. C. Burger 6396 & R. L. Liesner* (CR). Heredia, Varablanca, P.N. Braulio Carrillo. Lower montane rain forest formations and open pastures with frequent wind and rain from the Caribbean on the eastern slopes of Volcan Barva between the Río Las Vueltas and Río Nuevo (upper Río Nuevo) (upper Río Patria), 10.1000000, -84.0500000, 25 Oct 1975, *W. C. Burger 9453 & A. Baker* (CR). San Isidro, 10°13'N, 084°00'W, 1700 m, 6 Nov 1991, Á. Fernández 157 (CR). Heredia, Vara Blanca, P.N. Braulio Carrillo, Park Refugio at 2050 m in 1 forest 0.5–1 km NE of Refugio, 10.1777778, -84.1166667, 2100 m, 4 Nov 1990, *S. Ingram 660* (CR). San Rafael, camino del Monte de La Cruz hacia el Refugio de Vida Silvestre Cerro Dantas, a orillas del Río Nuevo y la Quebrada Cabra, Reserva Forestal Cordillera Volcánica Central, 1800 m, 10°5'45"N, 84°02'02"W, bosque pluvial premontano, epífitas en bosque secundario, 7 enero 2004, *D. Bogarín 580, D. Lobo & A. Vargas* (JBL). **Puntarenas:** Puntarenas, Guacimal, R.B. Monteverde. Ojo de Agua, finca de Leonel Hernández, bosque pantanoso semiachaparrado, lado Pacífico de la reserve, 10.2500000, -84.7666667, 18 Nov 1997, *W. Haber 7805 & E. Bello* (CR). Puntarenas, Guacimal, Z.P. Arenal-Monteverde, Ojo de Agua, Finca de Leonel Hernández, Bosque pantanoso semiachaparrado. Lado Pacífico de la reserva,10.2500000, -84.7666667, 1600 m, 18 Nov 1987, *W. Haber 7792* (CR). **San José:** Moravia, San Jerónimo, Cerro de Zurquí, open pasture and remnants of lower montane rain forest formations on ridges and steep slopes along the Río Para Blanca (Pacific drainage), 10.0500000, -84.0166667, 21 Oct 1975, *W. C. Burger 9316, K. Burt-Utley, J. F. Utley, R. A. Baker & R. Bakes* (CR). Vázquez de Coronado, Cascajal, P.N. Braulio Carrillo. Bajo de la Hondura, Wood on ridge above río Cascajal, 10.0166667, -83.9333333, 1 Jan 1977, *R. W. Lent 4026* (CR). Limit between **San Jose-Heredia:** Moravia, San Jerónimo, P.N. Braulio Carrillo, Sitio Mojón de Cooper, entrando por Calle Zurquí, 10.0541667, -84.0222222, 1700 m, 6 Nov 1991, *A. Fernández 157* (CR). **Without specific locality data:** *C. H. Lankester 192/1920* (K). Map 2.

C. The *Pleurothallis cardiothallis* group

9. **Pleurothallis callosa** M. Díaz & Pupulin, ***sp. nov.***

TYPE: Costa Rica. Cartago: Turrialba, Chirripó, El Seis (Damaris), 9°48'14.10"N, 83°26'38.70"O, 1200 m, epiphytic on threes on the side of El Seis river, wet lower montane forest, 19 December 2018, *G. Rojas-Alvarado 258, M. Cedeño, A. Karremans & I. Chinchilla* (Holotype: JBL). Fig. 21D, 24, 25 (Voucher, *Rojas-Alvarado 258*, JBL).

A Pleurothallide cardiothallide Rchb. *f. similis, floribus concoloribus atrorubentis, labello conduplicato duobus calls prominentis in basi munito recedit.*

Epiphytic, caespitose, erect *herb* to 30 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 9.7–26.4 cm long, 1–2 mm in diam., grass green, provided with a tubular, truncate sheath to 2 cm long at the base, and a tubular, tightly adpressed, truncate sheath below the middle, to 5.1 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming subpendent with age, thinly coriaceous, sessile, narrowly ovate, acuminate, 10.5–13.5 × 3.0–5.5 cm, deeply cordate at the base, grass green, matte. *Inflorescence* a solitary flower, from a prostrate spathaceous bract ca. 1.5 cm long, green, dry-papyraceous when mature, eventually dissolving with age. *Peduncle* terete, slender, ca. 13 mm long. *Pedicel* terete, pale green, ca. 6 mm long. *Ovary* subclavate, terete, 7.5 mm long. *Flowers* solid dark red. *Dorsal sepal* erect, elliptic, acute, reflex, 17 × 8–9 mm, 5-veined. *Lateral sepals* connate into a broadly ovate, acute, concave synsepal, 13–15 × 10–11 mm, 8-veined. *Petals* falcate to lanceolate, acute, 11.5 × 1.0–1.5 mm, 1-veined.

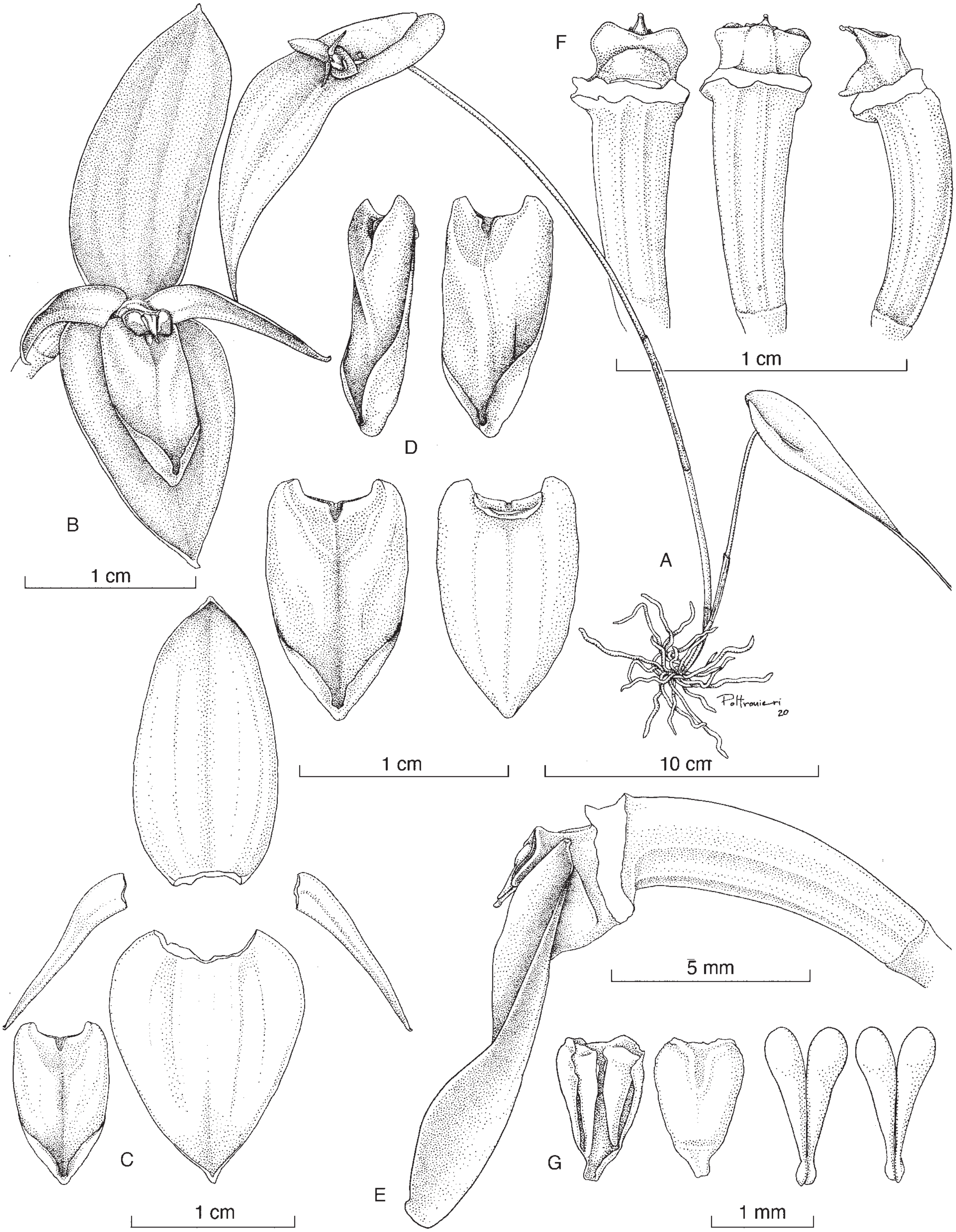


FIGURE 24. *Pleurothallis callosa* M. Díaz & Pupulin. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in lateral, three-quarter, adaxial, and abaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** column in ventral, dorsal, and lateral views; **G,** anther cap (two views) and pollinarium (two views). Drawn by S. Díaz Poltronieri from *Rojas-Alvarado 258* (JBL).

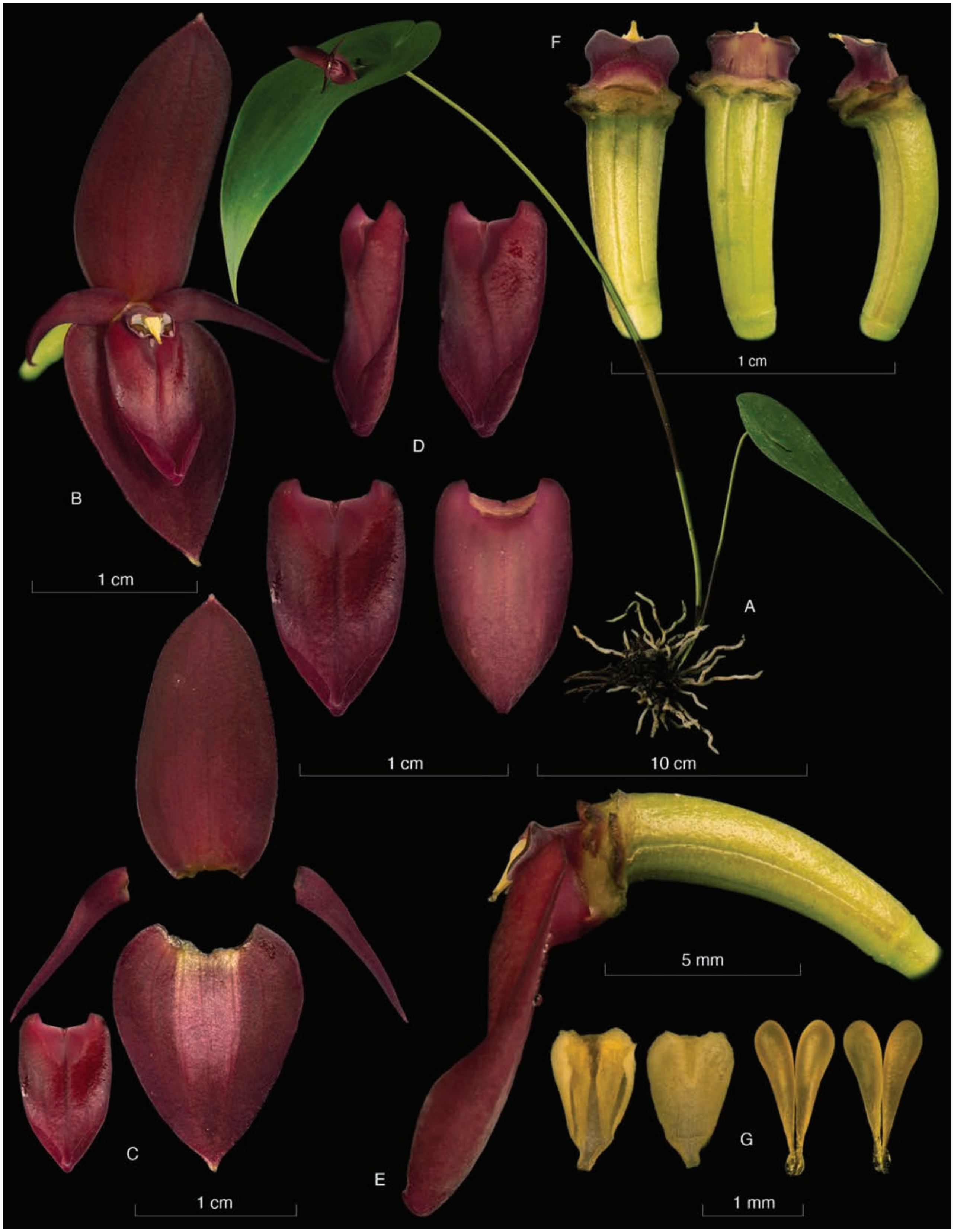


FIGURE 25. *Pleurothallis callosa* M. Díaz & Pupulin. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in lateral, three-quarter, adaxial, and abaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** column in ventral, dorsal, and lateral views; **G,** anther cap (two views) and pollinarium (two views). Lankester Composite Dissection Plate prepared by M. Díaz from *Rojas-Alvarado 258* (JBL).

Lip unguiculate, hinged to the column foot, geniculate, peltate, basally truncate, conduplicate, obtuse, the margins involute in the apical half, 10.0–10.5 × 6.5–7.0 mm; glenion triangular, deeply recessed between 2 calli that extent to the basal half of the lip, 0.8 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 2.5–3.0 × 2.0 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* ovate, truncate, bilobed at the base, 2-celled, 1.4 × 0.7 mm. *Pollinia* 2, narrowly oblong-pyriform, 1.5 × 0.5 mm, attached to an elliptic viscidium through 2 short, cylindric caudiculae.

Etymology: from the Latin *callosus*, "callose," in reference to the 2 prominent calli at the base of the lip that distinguish the species from its close relatives.

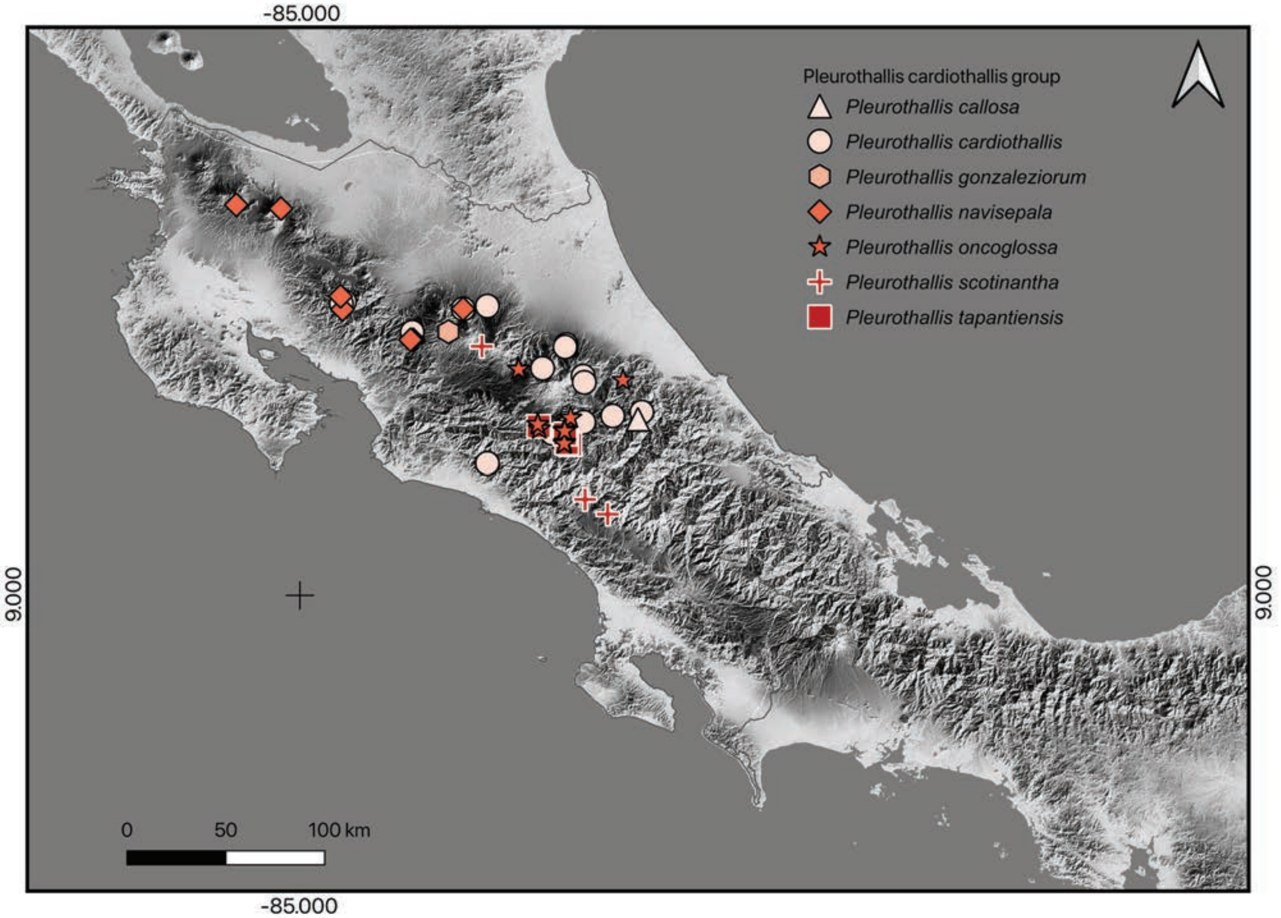
Distribution: known only from Costa Rica.

Ecology: the plants of the only population of *Pleurothallis callosa* known so far grow epiphytically in riparian forests at intermediate elevations (around 1200 m) in the Caribbean watershed of the Cordillera de Talamanca, in a region characterized by high humidity and frequent precipitation. The species bloomed in cultivation in June.

Distinguishing features: the species is differentiated from other species of the *P. cardiothallis* group by the solid dark-red flowers and the prominent calli on the basal half of the conduplicate lip. *Pleurothallis callosa* has the general, peltate outline of the lip that can be found in several of the species close to *P. cardiothallis*, but it is comparatively larger and provided with 2 large, elliptic, rounded calli at the base that embrace the area of the glenion. The concolorous, dark-red flower is superficially similar to that of *P. scotinantha*, but in the latter the lip is triangular, it is ecallose, and the flower is better described as dark purple in color instead of red.

Costa Rican material examined: Cartago: Turrialba, Chirripó, El Seis (Damaris), 9°48'14.10"N, 83°26'38.70"O, 1200 m, epiphytic on threes on the side of El Seis river, wet lower montane forest, 19 December 2018, flowered in cultivation al Lankester Botanical Garden, 19 June 2020, *G. Rojas-Alvarado 259, M. Cedeño, A. Karremans & I. Chinchilla* (voucher not preserved). Same locality data and collection date, flowered in cultivation al Lankester Botanical Garden, 19 June 2020, *G. Rojas-Alvarado 260, M. Cedeño, A. Karremans & I. Chinchilla* (voucher not preserved). Same locality data and collection date, flowered in cultivation al Lankester Botanical Garden, 30 June 2020, *G. Rojas-Alvarado 261, M. Cedeño, A. Karremans & I. Chinchilla* (voucher not preserved). Map 3.

10. ***Pleurothallis cardiothallis*** Rchb.f., Bot. Zeitung (Berlin) 15: 158. 1857. *Humboltia cardiothallis* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 667. 1891. *Acronia cardiothallis* (Rchb.f.) Luer Monogr. Syst. Bot. Missouri Bot. Gard.



Map 3. Map of collection sites for the species of *Pleurothallis cardiothallis* group.

103: 106. 2005. *Zosterophyllanthos cardiothallis* (Rchb.f.) Szlach. & Kulak, Richardiana 6(4): 187. 2006. TYPE: Ex Anglia in hortum Schillerianum introducta, *G. W. Schiller s.n.* (Holotype: W). *Pleurothallis subulata* Rolfe, Bull. Misc. Inform. Kew 1892 (65–66): 137–138. 1892. TYPE: Without locality, "flowered in the collection of Baron Hruby, of Peckau, Bohemia, and was sent to Kew for determination through Messrs. F. Sander & co., of St. Albans," *T. Hruby s.n.* (Holotype: K). Fig. 26 (Voucher, *Pupulin 6414*, JBL).

Epiphytic, caespitose, erect to suberect, large *herb* to 60 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 15–50 cm long, 1.5–4.5 mm in diam., yellowish green, sometimes spotted with brown basally, provided with 2 tubular, short, broadly obtuse-truncate sheaths to 4.5 cm long at the base, and a longer, tubular, tightly adpressed, obtuse-truncate sheath below the middle, to 7.5 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming subpendent with age, thinly coriaceous, flexible, sessile, ovate, acute to acuminate, 9–23 × 4–11 cm, deeply cordate at the base, grass green, matte. *Inflorescence* a solitary flower, usually produced singly, rarely in pairs, from a reclined spathaceous bract 9–27 mm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, green, 7–10 long. *Ovary* terete-subclavate, rounded in section, 5–9 mm long. *Flowers* mostly solid purple or solid yellow in Costa Rican populations, rarely with the dorsal sepals apically fading dull yellow, short-lived (usually 5, rarely 6, days), with distinct temporary activity, becoming reflexed at anthesis completion. *Dorsal sepal* broadly ovate, subacute, 10–14 × 7.5–9.0 mm, 7- to 11-veined. *Lateral sepals* connate into a broadly ovate-subrounded, obtuse to subacute synsepal, 10–15 × 9–12 mm, 9- to 15-veined. *Petals* narrowly triangular-subfalcate, rarely subsygmoid, acuminate, 8–11 × 2.5–3.5 mm, 3- to 5-veined. *Lip* unguiculate, hinged to the column foot, geniculate, peltate-subrectangular, basally truncate with rounded angles, obtuse, 5–8 × 3.5–5.0 mm, strongly conduplicate at the base, the apical margins thickened, inrolled, finely pubescent abaxially; glenion deeply recessed between the thickened basal lobes of the lip, ca. 0.8 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 1.0 × 2.5 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* obtriangular, acute, bilobed at the base, 2-celled, ca. 1.0 × 0.7 mm. *Pollinia* 2, narrowly oblong-pyriform, 1 mm long, attached to an elliptic viscidium through a short, cylindric caudicula. Figures 21E–F).

Etymology: from the Greek κᾰ́ρδῐ́ᾱ (kardíā), "hearth," and θαλλός (thallós), "stem," in reference to the heart-shaped leaf borne at the apex of the secondary stem, or ramicaul.

Distribution: ranging from Mexico to Ecuador. In Costa Rica it has been recorded from both watersheds of the Continental Divide.

Ecology: growing as an epiphyte, both in primary and secondary forests, as well as in open areas in premontane and low montane wet forests, between 350 and 2000 m. In Costa Rica, populations are known from both the Caribbean and Pacific drainages of the main mountain ranges. Plants have been found in bloom at least from April to January.

Distinguishing features: *Pleurothallis cardiothallis* can be recognized by the fully reflexed sepals and petals when anthesis is complete, and the peltate lip with the apical margins thickened and folded inward, revealing the papillose abaxial surface. It is similar to *P. oncoglossa*, from which it differs in the peltate lip (vs. distinctly triangular, with the apex thickened into a conical callus bent up as a hook), and *P. navisepala*, from which it differs in the much larger flowers (almost double the size) produced singly, very rarely in pairs (vs. 2–4 inflorescences at once), reflexed at maturity (vs. subringent at maturity).

Costa Rican material examined: Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, ca. 2 km después del Río Humo, 9°41'28.0"N, 83°45'43.1"W, 1564 m, epífitas en árboles a orillas del camino en bosque pluvial premontano, 24 Marzo 2006, *D. Bogarín 2667, G. Gigot & J. Warner* (JBL). 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, *D. Bogarín 3843, M. Bonilla, R. Gómez, R. Trejos & J.D. Zúñiga* (JBL). Turrialba, Santa Cruz, Las Abras, ladera sureste del Volcán Turrialba, cerca de Río Guayabo, 9°58'56"N, 83°44'46"W, 1946 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en potreros, 7 mayo 2007, *D. Bogarín 3739, A. Karremans* (JBL). Jiménez, Pejivalle, La Marta, shores of Río Gato, 9°47'27.2"N, 83°41'37.2"W, 750 m, premontane wet forest, on trees along pastures edges and overhanging the river, 3 November 2006, *F. Pupulin 6414, R. L. Dressler, R. Gómez, A. Karremans & G. Rojas* (JBL). Turrialba, Tayutic, Platanillo, laderas del Río Platanillo, 9°49'11"N, 83°33'37"W, 700–900 m, 20 de febrero 2004, *A. Karremans 139* (JBL). Turrialba, Tayutic, Moravia, 5 Kilometros al oeste del centro de Moravia, sobre sendero al lado de la calle que va a Platanillo, 9°50'12"N, 83°25'35"W, 1000–1200 m, 22 de enero 2005, *A. Karremans 659, D. Karremans y P. Ferreira* (JBL). Paraíso, Hacienda Queverí de la familia Fernández Estrada, 1.5 km por el sendero hacia bosque primario, 9°44'23.14"N, 83°50'18.42"W, 1790 m, bosque pluvial montano bajo, en troncos caídos, 28 Enero 2014, *M. Fernández 903, D. Bogarín & M. Díaz* (JBL). Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'50"N, 83°54'21"W, 1500 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 22 julio 2010, *M. Fernández 110, D. Bogarín, R. Trejos & C. Smith* (JBL). Turrialba, Santa Teresita, Guayabo, Monumento Nacional Guayabo, alrededores de los senderos principales, 9°58'23.31"N, 83°41'28.73"W, 1128 m, bosque muy húmedo, epífitas, 26 mayo 2015, *A. Karremans 6580, D. Bogarín & F. Pupulin* (JBL). Paraíso, Orosi, Purisil, orillas del Río Jaular, camino a Alto Jaular, ca. 1.5 km al sur de Purisil, 9°44'47.3"N, 83°48'43.8"W, 1406 m, bosque muy húmedo premontano, epífitas en bosque secundario y potreros, 30 abril 2009, *D. Bogarín 7005, M. Fernández, R. Gómez, Y. Kisel, F. Pupulin, P. Renshaw & R. Trejos* (JBL). Turrialba,

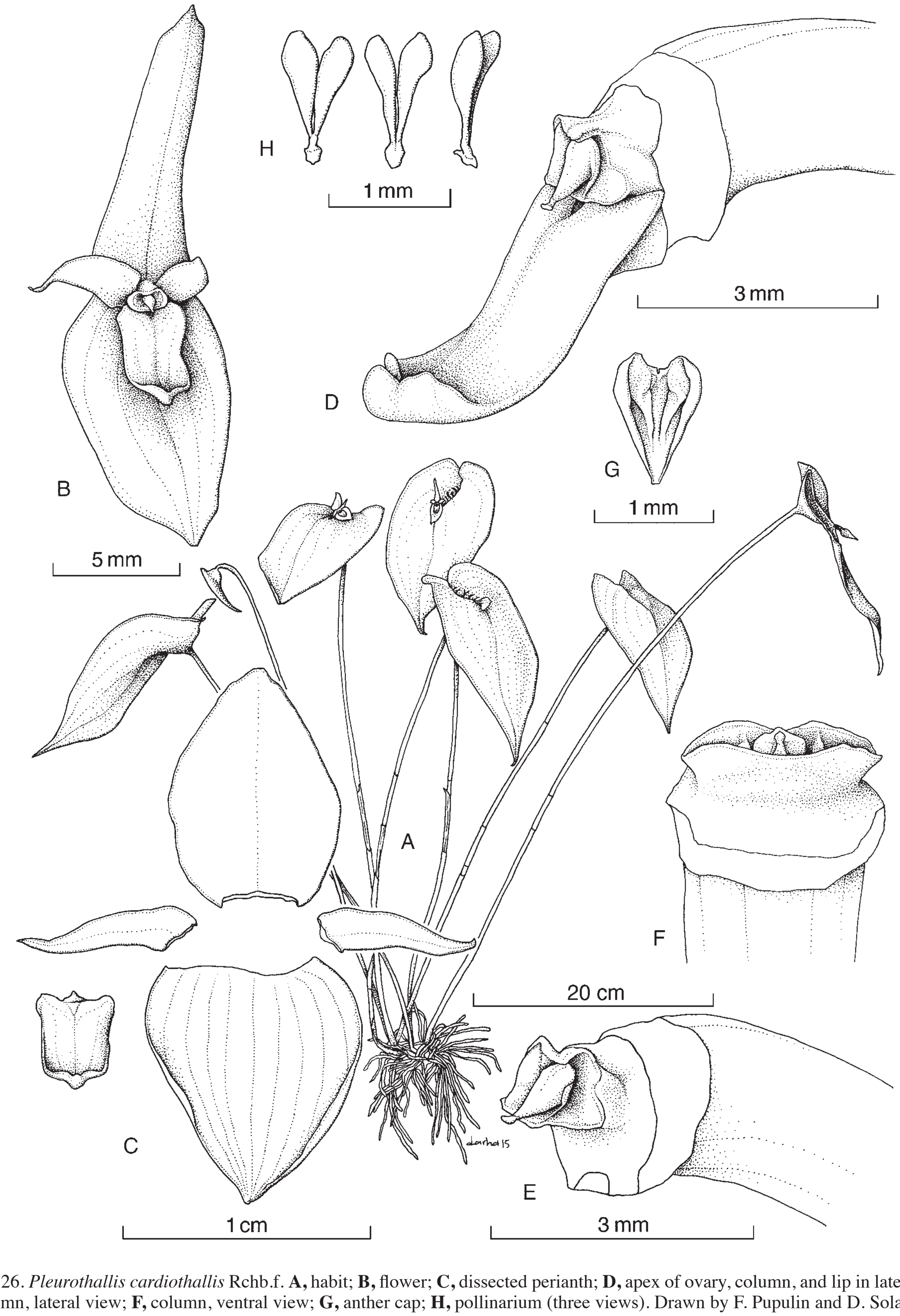


FIGURE 26. *Pleurothallis cardiothallis* Rchb.f. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** apex of ovary, column, and lip in lateral view; **E,** column, lateral view; **F,** column, ventral view; **G,** anther cap; **H,** pollinarium (three views). Drawn by F. Pupulin and D. Solano Ulate from *Pupulin 6414* (JBL).

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 de Diciembre 2010, *A. Karremas 3196, M. Contreras Fernandez* (JBL). **Heredia:** Sarapiquí, La Virgen, Colonia Carvajal, Poza Azul, shores of Río Poza Azul, 10°19'21.3"N, 84°08'19.1"W, 662 m, tropical wet, transition to premontane wet forest, epiphytic in secondary vegetation, flowers concolorous yellow, 13 May 2010, *F. Pupulin 7843, D. Bogarín, M. Fernández, A. Karremans & C. Smith* (JBL). San Rafael, camino del Monte de La Cruz hacia el Refugio de Vida Silvestre Cerro Dantas, a orillas del Río Nuevo y la Quebrada Cabra, Reserva Forestal Cordillera Volcánica Central, 1800 m, 10°5'45"N, 84°02'02"W, bosque pluvial premontano, epífitas en bosque secundario, 7 Enero 2004, *D. Bogarín 590, D. Lobo & A. Vargas* (JBL). **Limón:** Pococí, Guápiles, Pocora, La Argentina Sur, márgenes del río Dos Novillos, sendero Las Cataratas, 500–700 m, bosque premontano muy húmedo, vegetación primaria madura, 12 de Setiembre 2004, *R. Valverde 1341, E. & D. Arias, J. Vásquez, G. Hidalgo & P. Víquez* (JBL). Pococí, Guápiles, Hacianda La Cuenca, bosque pluvial premontano, falda norte del Volcán Turrialba, 10°8'7.81"N, 83°46'46.2"W, 611 m, 01 enero 2005, *M. A. Blanco 2813, A. Cháves, L. du Toit & C. Ugalde* (JBL). Pococí, Guápiles. 5 km al sur de la carretera; fin del camino paralelo con el Río Blanco, cerca de la Finca Tintoreras; 10°02'16.2"N, 83°53'02.1"W, 350–400 m, bosque muy húmedo tropical, 15 junio 2006, *R. L. Dressler 6762, D. Bogarín, J. Gómez-Laurito, F. Pupulin* (JBL). **Without specific locality data:** flowered in cultivation at Jardín Botánico Lankester, 21 Jun 2007, *JBL-02638* (JBL). Map 3.

11. ***Pleurothallis gonzaleziorum*** Pupulin, M. Díaz & Pridgeon, Vanishing Beauty. Vol. 2: 855–857. TYPE: Costa Rica. Alajuela: Zarcero, Palmira, Reserva Biológica Bosque de Paz, creciendo en el jardín de orquídeas, 10°12'15.70"N, 84°19'00.02"W, 1534 m, bosque pluvial montano bajo, 20 agosto 2016, *M. Díaz 269, N. Belfort-Oconitrillo & A. Karremans* (Holotype: JBL). Fig. 27 (Voucher, *Díaz 269*, JBL).

Epiphytic, caespitose, erect to suberect, large *herb* to 60 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 25–40 cm long, 2.5–3.0 mm in diam., yellowish green, provided with 2 tubular, short, truncate sheaths to 3.8 cm long at the base, and a longer, tubular, tightly adpressed, broadly obtuse sheath below the middle, to 7.6 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming subpendent with age, thinly coriaceous, flexible, sessile, ovate, acuminate, 12.5–16.6 × 6.5–8.3 cm, deeply cordate at the base, grass green, matte. *Inflorescence* a solitary flower, usually produced singly, rarely in pairs, from a prostrate spathaceous bract 2.0–2.6 cm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, pale green, 17–22 mm long. *Ovary* clavate, terete, 8.5–9.0 mm long. *Flowers* glabrous, mostly solid pale yellow, sometimes red with the center fading yellow, with distinct temporary activity. *Dorsal sepal* broadly ovate, obtuse, 15.5–18.5 × 12.5–16.0 mm, 9- to 11-veined. *Lateral sepals* connate into a broadly ovate, obtuse to subacute synsepal, 14.5–16.0 × 13–16 mm, 10-veined. *Petals* narrowly triangular-falcate, acute, 11.5–12.0 × 3.0–3.5 mm, 3-veined. *Lip* unguiculate, hinged to the column foot, geniculate, peltate, basally truncate with rounded angles, obtuse, 5.5–6.2 × 4.7–5.2 mm, conduplicate at the base, the apical margins thickened; glenion deeply recessed between the thickened basal lobes of the lip, ca. 1 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 2.5 × 3.0 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* obtriangular, acute, bilobed at the base, 2-celled, ca. 1.3 × 1.0 mm. *Pollinia* 2, narrowly oblong-pyriform, ca. 1.2 mm long, attached to an elliptic viscidium through a short, cylindric caudicula. *Fruit* an ellipsoid-clavate capsule, 5.1 × 0.8 cm long.

Eponymy: the name honors Federico González's family from Bosque de Paz Biological Reserve where the species was found, and who has avidly supported orchid research in the reserve since 2004.

Distribution: known only from Costa Rica, at 1500–1600 m in elevation.

Ecology: epiphytic in lower montane rain forest along the Caribbean slopes of the Cordillera Volcánica Central in Costa Rica.

Distinguishing features: *Pleurothallis gonzaleziorum* differs from *P. cardiothallis* by its distinctly triangular lip (vs. peltate), glabrous on the underside (vs. papillose), with the apical margins non involute. The lip is more similar to that of *P. oncoglossa*, but in the latter species the lip apex is thickened into a conical callus, bent back as a hook, whereas in *P. gonzaleziorum* it is straight and thin. By its triangular lip it is also similar to *P. scotinantha*, which however has much smaller, concolorous dark purple flowers.

As with other allied taxa close to *Pleurothallis cardiothallis*, *P. gonzaleziorum* also presents 2 different color morphs, one red and the other yellow (Fig. 21G–H), which grows sympatrically at the type locality.

Costa Rican material examined: Alajuela: Zarcero, Palmira, Bosque de Paz Biological Reserve, Gallery trail, 10°12'18.01"N, 84°19'5.09"W, 1585 m, flowers red, fading yellow in center, 19 November 2016, *M. Díaz 281, N. Belfort & M. Kolanowska* (JBL). **Guanacaste:** Tilarán, Quebrada Grande, road to Selvatura Adventure Park and Santa Elena Reserve, 10°20'23.5"N, 84°48'34.5"W, 1563 m, wet lower montane forest, epiphytic in secondary forest on the side of the river, 6 March 2015, *M. Fernández 1028, D. Bogarín, M. Díaz, F. Pupulin & A. Salazar* (JBL). Tilarán, Quebrada Grande, road to Selvatura Adventure Park and Santa Elena Reserve, 10°20'23.5"N, 84°48'34.5"W, 1563 m, wet lower montane forest, epiphytic in secondary forest on the side of the river, 6 March 2015, *M. Fernández 1035, D. Bogarín, M. Díaz, F. Pupulin & A. Salazar* (JBL). Map 3.

12. ***Pleurothallis navisepala*** Pupulin, J. Aguilar & M. Díaz, Lankesteriana 17(2): 344. 2017.
TYPE: Costa Rica. Alajuela: San Ramón, Ángeles, Balsa, road between San Ramón and La Fortuna de San Carlos,

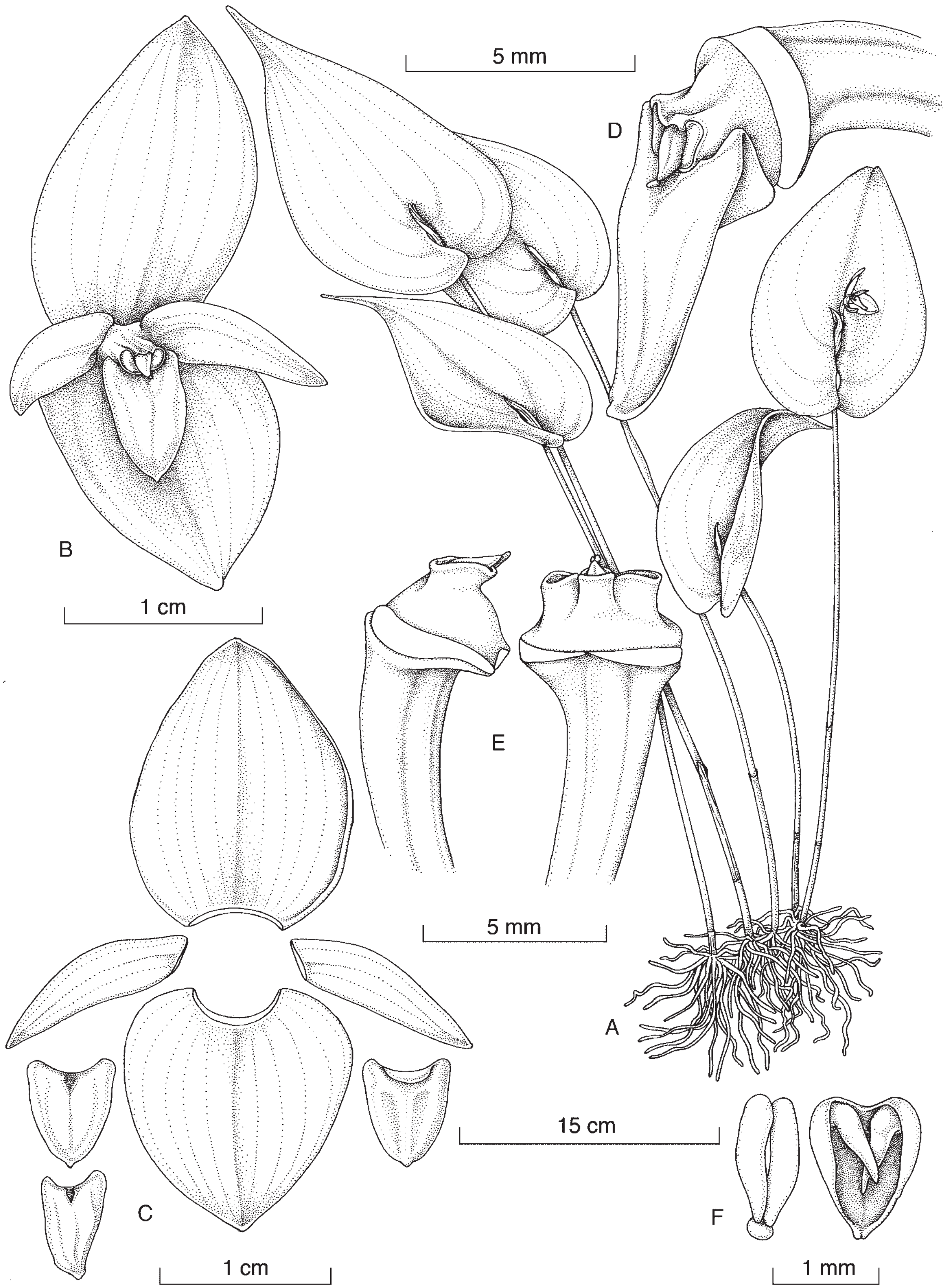


FIGURE 27. *Pleurothallis gonzaleziorum* Pupulin, M. Díaz & Pridgeon. **A,** habit; **B,** flower; **C,** dissected perianth (the lip in adaxial, three-quarter, and abaxial views); **D,** apex of ovary, column, and lip in three-quarter view; **E,** column in lateral and dorsal views; **F,** anther cap and pollinarium (two views). Drawn by S. Díaz Poltronieri from *M. Díaz 269* (JBL). From Pupulin, 2020.

10°10'03.6"N, 84°29'35.7"W, 1150 m, epiphytic on trees in pastures close to Río Balsa, premontane rain forest, 29 May 2013, *F. Pupulin 8435, D. Bogarín, M. Díaz, & M. Fernández* (Holotype: JBL). Fig. 28–30 (Vouchers, *Pupulin 8028*, *Pupulin 8435* and *Zúñiga 174*, all at JBL).

Epiphytic, caespitose, erect to suberect, large *herb* to 25 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 15–23 cm long, 0.2–0.3 cm in diam., yellowish green, provided with 2 tubular, short, obtuse sheaths to 1.5 cm long at the base, and a longer, tubular, tightly adpressed, subobtuse to truncate sheath below the middle, to 3.8 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming curved-subpendent with age, thinly coriaceous, flexible, sessile, ovate, narrowly acute to acuminate, 5.5–14.0 × 3.0–7.5 cm, deeply cordate at the base, grass green, matte. *Inflorescence* a solitary flower, usually produced singly, rarely in pairs, from a reclined spathaceous bract to 11 mm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, green, 5–8 mm long. *Ovary* terete-subclavate, curved, rounded in section, 5–8 mm long. *Flowers* not completely spreading, with distinct temporary activity, short-lived (to 5 days), the sepals purple, sparklingly pale reddish and microscopically pubescent-glandulous abaxially, the synsepal with a large, basal, pale greenish yellow, hyaline blotch, the petals purple, the lip purple-magenta, or the entire flower concolorous bright yellow. *Dorsal sepal* erect, ovate, acute, 5.0–6.5 × 3.5–4.0 mm, the margins microscopically glandulose, 7- to 9-veined. *Lateral sepals* connate into a broadly ovate, obtuse, deeply cymbiform synsepal, the margins microscopically glandulose, 5.5–6.0 × 6.5–7.5 mm when spread, 9- to 11-veined. *Petals* narrowly triangular-subfalcate, subsygmoid, acuminate, 4.0–4.5 × 1.2–1.4 mm, correct, apically incurved, 3-veined. *Lip* unguiculate, hinged to the column foot, strongly geniculate, peltate, basally truncate with rounded angles, acute, apiculate, infolded, 5–8 × 3.5–5.0 mm, strongly conduplicate at the base, the apical margins thickened, inrolled, finely pubescent abaxially; glenion recessed between the thickened basal lobes of the lip, ca. 0.8 mm long, the front of the glenion with a line of short papillae extending to the margins of the lip. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 1.0 × 2.5 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* oblong, acute, bilobed at the base, 2-celled, ca. 1.0 × 0.5 mm. *Pollinia* 2, narrowly oblong-pyriform, 1 mm long, attached to an elliptic viscidium through a short, cylindric caudicula. Fig. 21I, 31A.

Etymology: from the Latin *navis*, “ship,” and *sepala*, “sepals,” in reference to the boat-shaped synsepal that is characteristic of the species.

Distribution: known only from northwestern Costa Rica.

Ecology: epiphytic on branches of the lower canopy in premontane moist and premontane wet forest along the Caribbean watershed of the Cordillera de Tilarán and the Cordillera Volcánica de Guanacaste, at 850–1150 m in elevation. Flowering occurs between October and February.

Distinguishing features: the deeply concave shape of the synsepal, which is almost saccate at the base, prevents the perianth from spreading out completely at anthesis, and the bilabiate flower remains therefore somewhat cupped. This relatively small flower on a large-sized plant and the flower shape with the lip enclosed within the erect margins of the sysnsepal are unique within the group and easily recognizable.

Most of the known specimens of *Pleurothallis navisepala* come from a quite restricted area along the Caribbean drainage of the Cordillera de Tilarán southern end, where it is apparently frequent. It was first collected and illustrated around 1867 by August R. Endrés in a locality called “Legua” de San Ramón, likely one of the localities crossed by the new road that the Costa Rican government was building from San Ramón toward the northern San Carlos plains, where the species is still fairly common.

Costa Rican material examined: Alajuela: [San Ramón, Ángeles], Legua, Endres Pleurothallis no. 52, *A. R. Endrés s.n.* (W 0020259). San Ramón, Ángeles, Balsa, road between San Ramón and La Fortuna de San Carlos, 10°10'03.6"N, 84°29'35.7"W, 1150 m, epiphytic on trees in pastures close to Río Balsa, premontane rain forest, 29 May 2013, *F. Pupulin 8434, D. Bogarín, M. Díaz, & M. Fernández* (JBL); same collecting data, *F. Pupulin 8446, D. Bogarín, M. Díaz, & M. Fernández* (JBL). Balsa, Reserva Biológica A.M. Brenes, 800–1000 m, 19 June 1995, flowered in cultivation at the Lankester Botanical Garden, 25 Sept. 2002, *G. Carnevali & A. C. Rodríguez s.n.* under *JBL-00787* (JBL). San Ramón, Balsa, Reserva Biológica A.M. Brenes, 10 Dec. 1991, flowered in cultivation at the Lankester Botanical Garden, flowers yellow, 8 Sept. 2008, *M. Freiberg s.n.* under *JBL-02746* (JBL). Without specific locality, collected by D. Matamoros, 2010, flowered in cultivation at Jardín Botánico Lankester, 10 January 2011, *F. Pupulin 8028* (JBL). Without collecting data, flowered in cultivation at Jardín Botánico Lankester, 20 Feb. 1999, *F. Pupulin 1342* (JBL).Upala, Bijagua, Zapote, Finca La Escondida, ca. 5 km de la entrada de la finca hacia la ladera noreste del Volcán Miravalles, 10°46’00.8"N, 85°05'35.7"W, 900–1000 m, bosque pluvial premontano, epífitas en bosque secundario, 3 Feb. 2006, *Bogarín 2501, J. Barrantes, R. L. Dressler, R. Gómez & A. Rojas* (JBL). Without specific locality, flowered in cultivation at Lankester Botanical Garden, 20 Dec. 2016, *JBL-33356* (JBL). **Guanacaste**: Liberia, Liberia, Parque Nacional Rincón de la Vieja, the SE slopes of Volcán Santa María, above Estación Hacienda Santa María. Evergreen montane forest, 10.7833333, -85.3000000, 27 Jan 1983, *G. Davidse 23418 et al.* (CR). Tilarán, Tronadora, R.B. Monteverde. 5 km n of Santa Elena on road to Las Nubes, Finca San Bosco road, Río Negro, Atlantic slope, 10.3666667, -84.8166667, 10 Nov 1988, *W. Haber 8755 & W. Zuchowski* (CR). Map 3.

13. ***Pleurothallis oncoglossa*** Luer, Lindleyana 1: 86. 1996. *Acronia oncoglossa* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 166, f. 142. 2005. *Zosterophyllanthos oncoglossus* (Luer) Szlach. & Kulak, Richardiana 6: 191. 2006. TYPE: Costa Rica. Without collection data, collected by Leon Glicenstein, flowered in

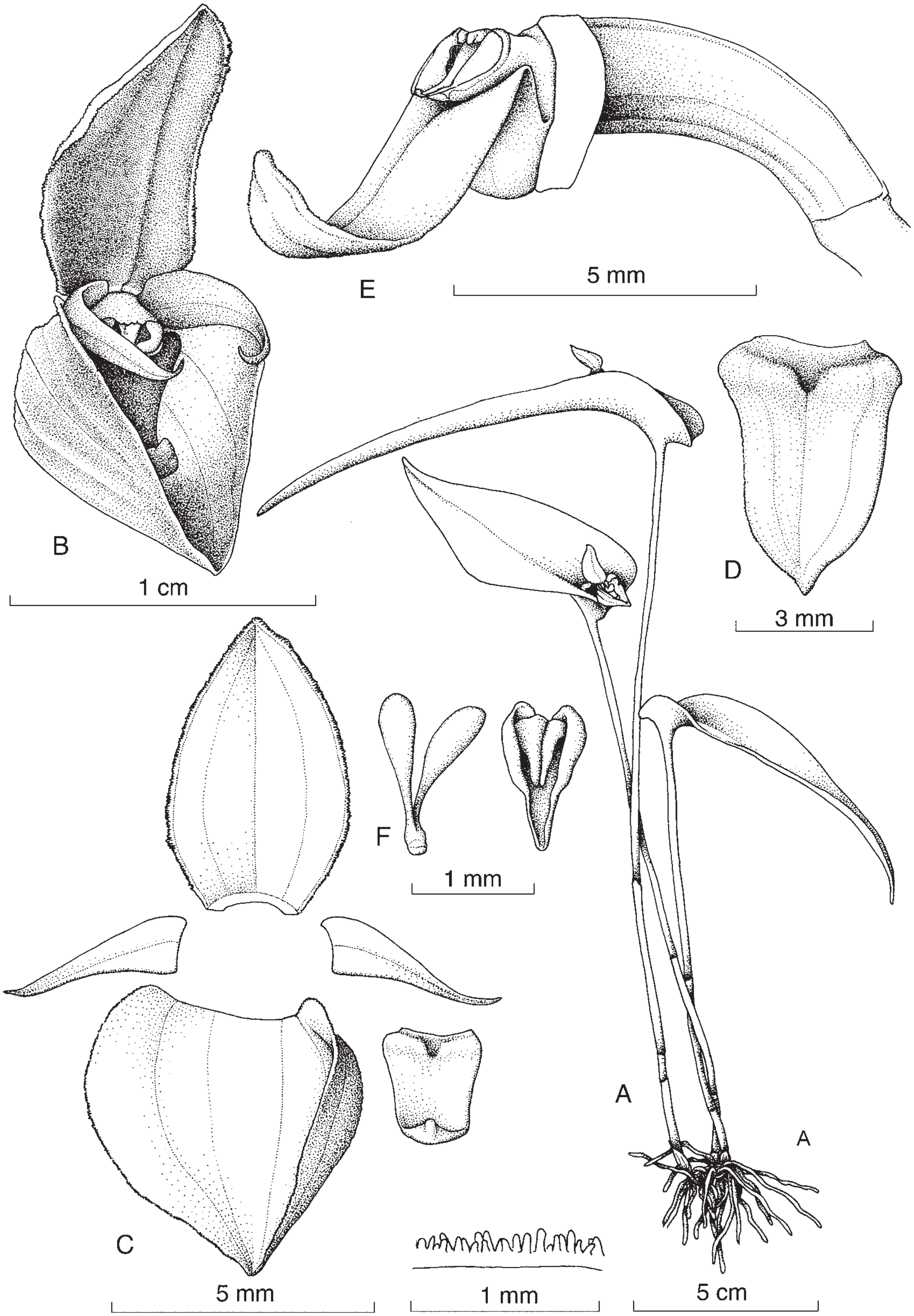


FIGURE 28. *Pleurothallis navisepala* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** apex of ovary, column, and lip in lateral view; **F,** pollinarium and anther cap. Drawn by F. Pupulin and D. Solano Ulate from *Pupulin 8028* (JBL). Reproduced with permission from the Editor of *Lankesteriana*.

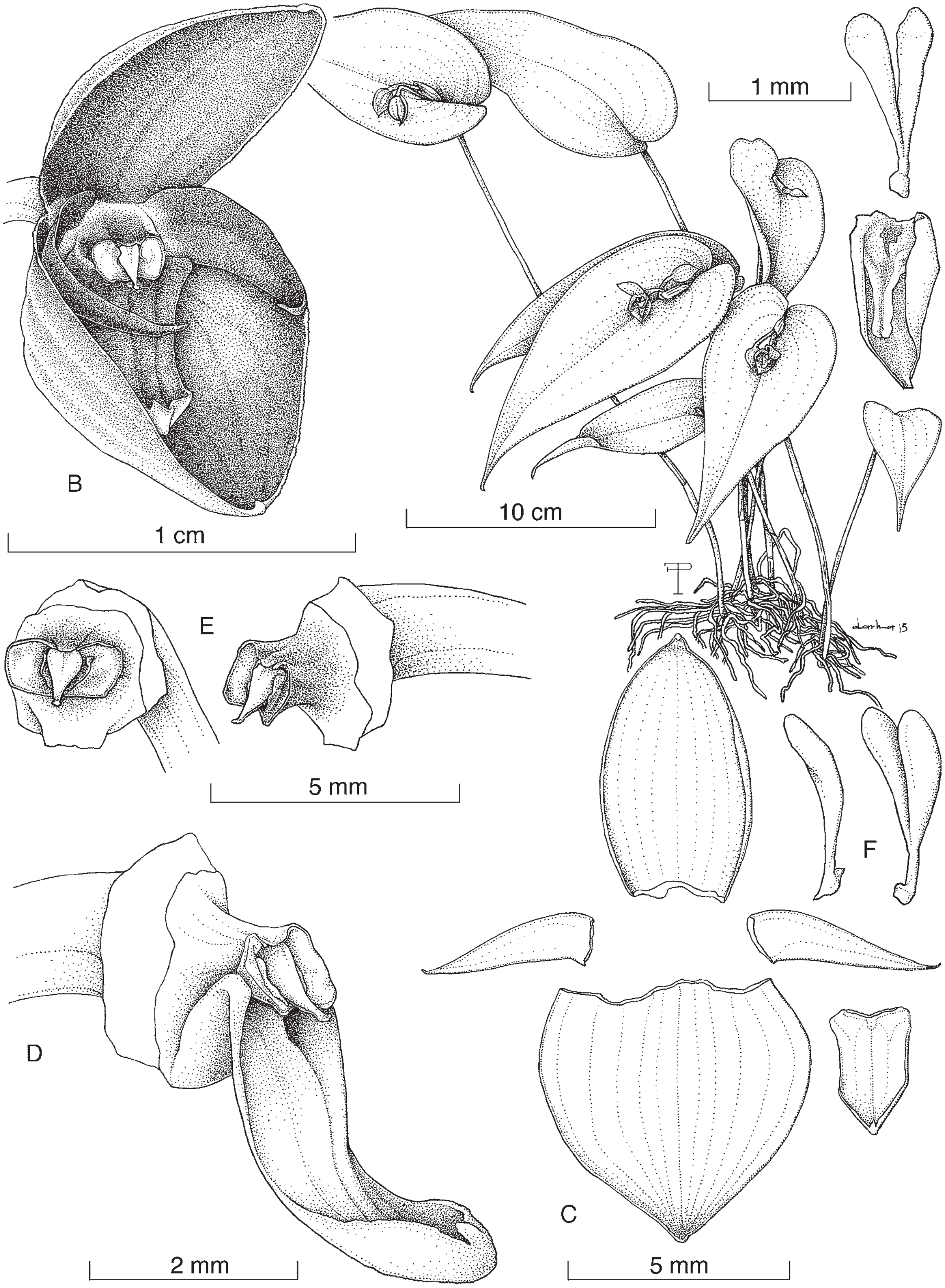


FIGURE 29. *Pleurothallis navisepala* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** apex of ovary, column, and lip in lateral view; **E,** column in front and lateral views; **F,** pollinarium, lateral and three quarters views. Drawn by F. Pupulin and D. Solano Ulate from *Pupulin 8435* (JBL).

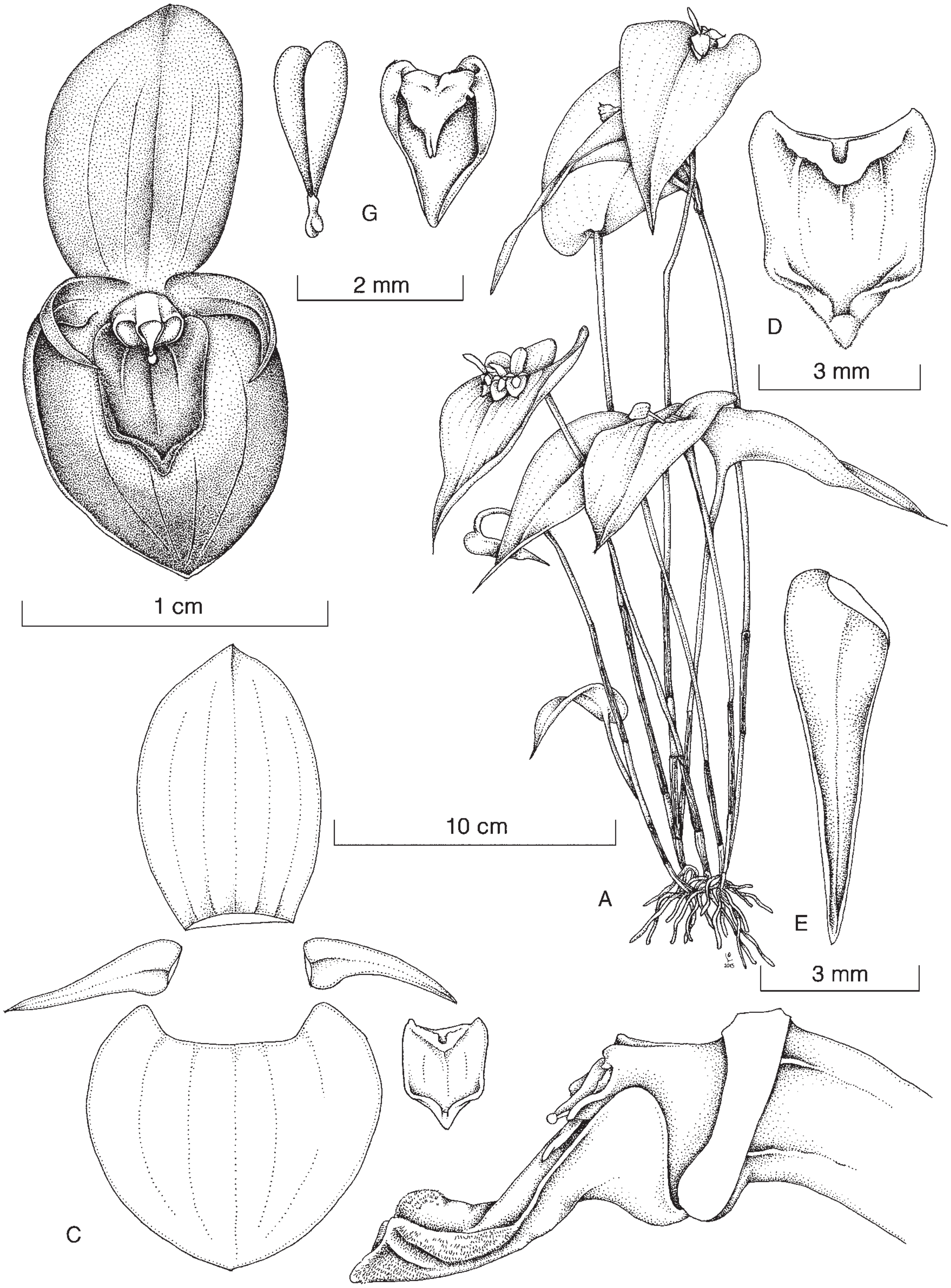


FIGURE 30. *Pleurothallis navisepala* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** right petal; **F,** apex of ovary, column, and lip in lateral view; **G,** pollinarium and anther cap. Drawn by L. Oses from *Zúñiga 174* (JBL).

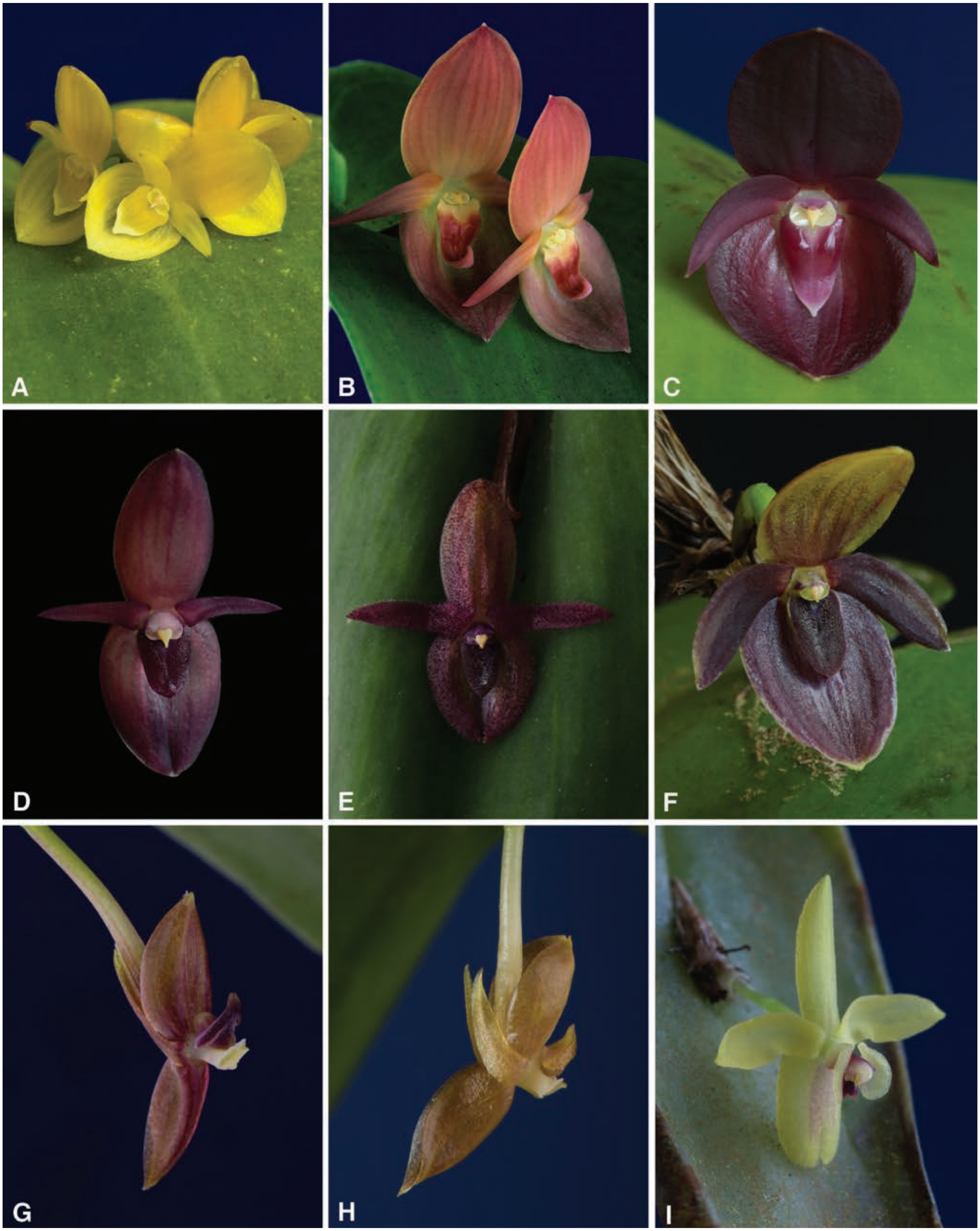


FIGURE 31. Flowers of *Pleurothallis* species from Costa Rica in the *P. cardiothallis* (A–C) and *P. phyllocardia* (D–I) groups. **A,** *P. navisepala* (*Bogarín 2501*); **B,** *P. oncoglossa* (*JBL-01976*); **C,** *P. scotinantha* (*Bogarín 7355*); **D,** *P. tapantiensis* (*Bogarín 11273*); **E,** *P. adventurae* (*Bogarín 7696*); **F,** *P. anthurioides* (*Bogarín 10649*); **G–H,** *P. compressa* (*Bogarín 7839*; *Karremans 2503*); **I,** *P. fantastica* (*Blanco 5087*). Not at the same scale. All the vouchers at JBL. Photographs by F. Pupulin.

cultivation by P. & A. Jesup in Bristol, CT, 10 Dec. 1988, *C. Luer 13833* (Holotype: MO). Fig. 32 (Voucher, *Bogarín 5686*, JBL).

Epiphytic, caespitose, erect *herb*, to 38 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 12–31 cm long, 1–3 mm in diam., yellowish green, provided with a tubular, short, truncate sheath, 1.0–2.5 cm long at the base, and a longer, tubular, tightly adpressed, truncate sheath below the middle, to 5–11 cm long, the bracts brown, dry-papyraceous. *Leaf* borne suberect at the apex of the ramicaul, becoming subpendent with age, thinly coriaceous, flexible, sessile, ovate, acuminate, 10.5–14.5 × 4.5–5.5 cm, deeply cordate at the base, matte green. *Inflorescence* a solitary flower, from a prostrate spathaceous bract 1–2 cm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, pale green, ca. 12 mm long. *Ovary* subclavate, terete, ca. 11.5 mm long. *Flowers* dark red on a pale-yellow background visible on the base of the petals, sepals, and lip. *Dorsal sepal* broadly ovate, obtuse, 15–17 × 12–15 mm, 9-veined. *Lateral sepals* connate into a broadly ovate, obtuse synsepal, 14–16 × 14–16 mm, 9- to 10-veined. *Petals* narrowly ovate-falcate, acute, 11–12 × 3–4 mm, 3-veined. *Lip* unguiculate, hinged to the column foot, geniculate, triangular, basally truncate with rounded angles, acute, 7–8 × 4–5 mm, the apex thickened into a conical callus bended up as a hook; glenion recessed in the middle of the base of the lip, slender, ca. 1 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 3 × 4 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* cordate, acute, bilobed at the base, bent up at the apex, 2-celled. *Pollinia* 2, narrowly oblong-pyriform, bent up at the apex, attached to an elliptic viscidium through a short, cylindric caudicula. Fig. 31B.

Etymology: from the Greek words ὄγϰος (ónkos), “topknot on the masks of classic tragedy,” and γλῶσσᾰ (*glôssa*), “tongue,” in reference to the callous projection at the apex of the lip.

Distribution: known only from Costa Rica.

Ecology: epiphytic in premontane wet forests of the northern Cordillera Volcánica Central and Cordillera de Talamanca foothills, apparently restricted to the Caribbean watershed between 1250 and 2100 m. Flowering has been recorded from October to February.

Distinguishing features: *Pleurothallis oncoglossa* is similar to *P. cardiothallis*, from which it differs in the distinctly triangular lip with the apex thickened into a conical callus, bent up as a hook (vs. peltate). *Pleurothallis oncoglossa* is also similar to *P. scotinantha*, but in the latter the lip is not hooked and the perianth is solid dark purple instead of dark red on a pale-yellow background.

Costa Rican material studied: Cartago: Cartago, San Francisco, Muñeco, Navarro, ca. 5 km al sur de la iglesia de Navarro, entre Río Sombrero y Quebrada Patarrá, camino a Alto Belén, bosque pluvial premontano, 9°45'38.28"N, 83°53'56.81"W, 1808 m, 3 feb. 2017, *D. Bogarín 12227, M. Cedeño, M. Fernández & E. Kaes* (JBL). 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, *D. Bogarín 3843, M. Bonilla, R. Gómez, Rafael Trejos & J. D. Zúñiga* (JBL). Cartago: Cartago, San Francisco, Muñeco, Finca Loma Verde y Jilguero, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'50"N, 83°54'21"W, 1500 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 22 Jul 2010, *M. Fernández 110. D. Bogarín, R. Trejos & C. Smith* (JBL). Jiménez, Pejibaye, Tucurrique, Bajos del Humo, between the rivers Humo and Vueltas, east side of Cerros Duán, 9°48'36.7"N, 83°45'16.2"W, 1396 m, rainy low montane forest, epiphytic on trees in paddocks and forest borders, 24 Nov 2008, *D. Bogarín 5686, R. L. Dressler, R. Gómez & R. Trejos* (JBL). 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 5711, R. L. Dressler, R. Gómez & R. Trejos* (JBL); same collecting data, *D. Bogarín 5712, R. L. Dressler, R. Gómez & R. Trejos* (JBL); same collecting data, *D. Bogarín 5723, R. L. Dressler, R. Gómez & R. Trejos* (JBL); same collecting data, *D. Bogarín 5726, R. L. Dressler, R. Gómez & R. Trejos* (JBL); same collecting data, *D. Bogarín 5728, R. L. Dressler, R. Gómez & R. Trejos* (JBL); Paraíso, Orosi, Purisil, ca. 1450 m, epiphytic in lower montane wet forest, secondary forest, 18 Oct 2001, *F. Pupulin 3342* (JBL). Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, entre Río Villegas y Río Dos Amigos, 9°41'32.9"N, 83°47'03.2"W, 1650 m, epífitas en árboles a orillas del camino en bosque pluvial premontano, 3 Mar 2009, *D. Bogarín 6323, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Turrialba, Torito, road to Santa Teresa, along a small creek, wet premontane forest, on scattered trees in a pasture, 31 July 1998, *F. Pupulin 973, R. L. Dressler, D. E. Mora, K. Dressler & M. Retana* (JBL); same collecting data, *F. Pupulin 977, R. L. Dressler, D. E. Mora, K. Dressler & M. Retana* (JBL). Turrialba, Santa Cruz, Las Abras, ladera sureste del Volcán Turrialba, cerca de Río Guayabo, 9°58'56"N, 83°30'46"W, 2100–1700 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en potreros, 7 mayo 2007, *D. Bogarín 3739 & A. Karremans* (JBL). Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, final del sendero Oropéndola, epífitas a orillas de la calle principal, 50–300 m antes de la entrada a sendero Oropéndola, 9,749669507 -83,78184389 1286 m bosque pluvial premontano, 28 de enero de 2019, *Fernández 1320 & D. Bogarín* (JBL). **Limón:** Siquirres, Florida, Destierro, cabeceras Río Destierro, cerca de Roca, 10.0561111, -83.6961111, 1400–1500 m, 9 diciembre 2008, *J. F. Morales Quirós 17256* (CR). **Without collecting data:** flowered in cultivation at Jardín Botánico Lankester, 30 Dec. 1999, *F. Pupulin 1903* (JBL); flowered in cultivation at Jardín Botánico Lankester, 21 Jan. 1999, *JBL-01976* (JBL). Map 3.

14. ***Pleurothallis scotinantha*** Pupulin, J. Aguilar & M. Díaz, Lankesteriana 17(2): 337. 2017. TYPE: Costa Rica. San José: Pérez Zeledón, Cajón, Montecarlo, 3.5 km al noreste de Montecarlo, orillas del Río Peña Blanquita,

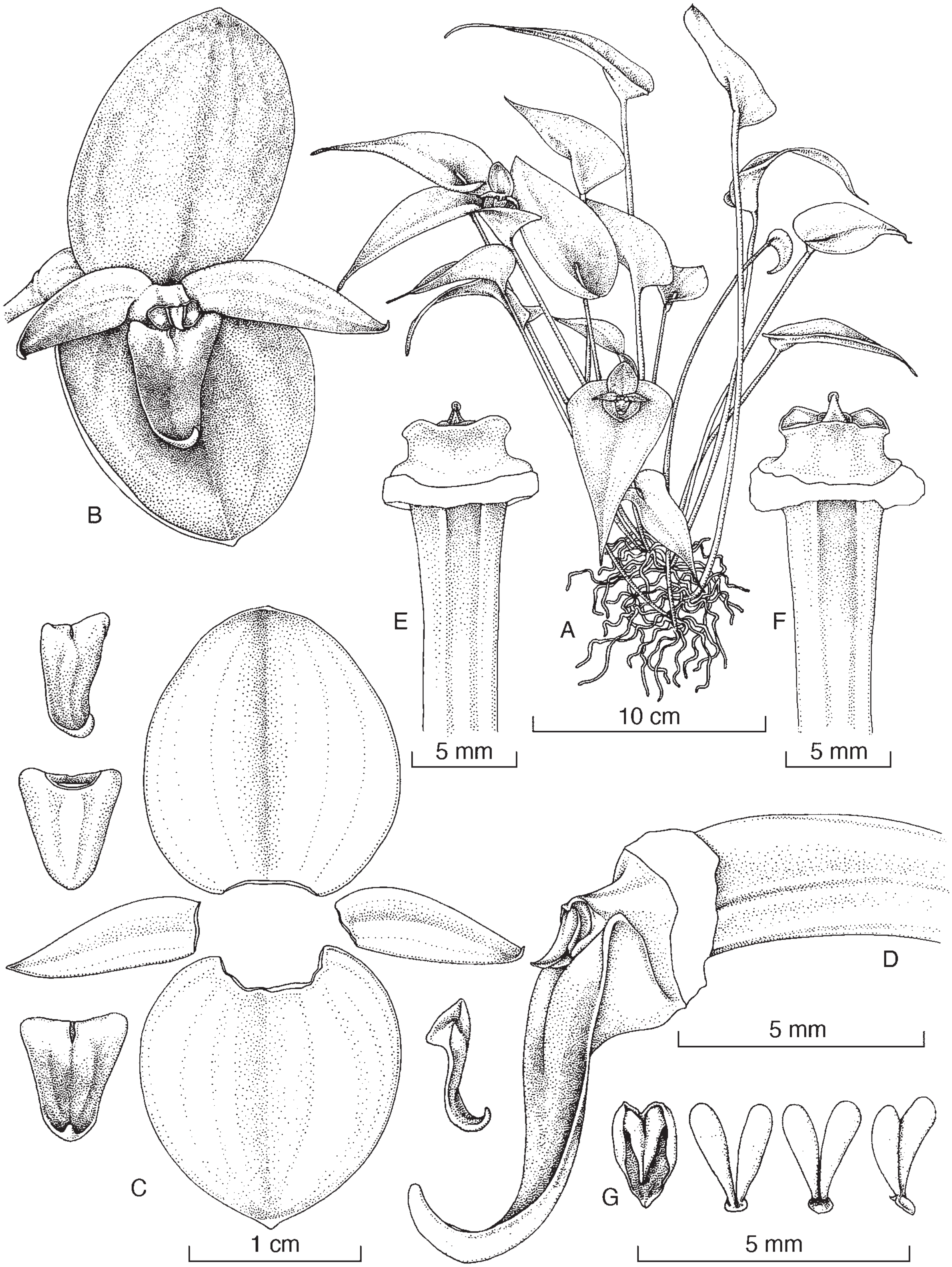


FIGURE 32. *Pleurothallis oncoglossa* Luer. **A,** habit; **B,** flower; **C,** dissected perianth (the lip in three-quarter, abaxial, adaxial and lateral views); **D,** apex of ovary, column, and lip in lateral view; **E,** column, dorsal view; **F,** column, ventral view; **G,** anther cap and pollinarium (three views). Drawn by S. Díaz Poltronieri from *Bogarín 5686* (JBL).

9°22'20.3"N, 83°35'01.8"W, 1261 m, bosque pluvial premontano, en bosque secundario remanente a orillas del río, 28 Julio 2009, *D. Bogarín 7355 & F. Pupulin* (Holotype: JBL; Isotype: JBL). Fig. 33–34 (Vouchers, *Bogarín 7355*, *Bogarín 7455*, JBL).

Epiphytic, caespitose, erect to suberect, large *herb* to 50 cm tall. *Roots* slender, flexuous, ca. 1.5 mm in diam. *Ramicauls* terete, slender, 29.0–43.5 cm long, 2.5–4.0 mm in diam., yellowish green, provided with a tubular, short, truncate sheath to 3.5–4.0 cm long at the base, and a longer, tubular, tightly adpressed, truncate sheath below the middle, to 4–6 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming subpendent with age, thinly coriaceous, flexible, sessile, ovate, acute to acuminate, 16–19 × 7.5–8.0 cm, deeply cordate, forming 2 slightly imbricate lobes at the base, grass green, matte. *Inflorescence* a solitary flower, usually produced singly, rarely in pairs, from a reclined spathaceous bract 10–15 mm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, pale green, 22–26 mm long. *Ovary* clavate, rounded in section, 4–8 mm long. *Flowers* solid dark purple with pale yellow tips on sepals, petals and lip, with distinct temporary activity, short-lived (usually 5, rarely 6, days). *Dorsal sepal* broadly ovate, subacute, 14–18 × 11–19 mm, 9- to 11-veined. *Lateral sepals* connate into a broadly ovate-subrounded, subacute synsepal, 11–20 × 15–20 mm, 9- to 11-veined. *Petals* subfalcate, acute, 14 × 3.5 mm, 3- to 5-veined. *Lip* unguiculate, hinged to the column foot, triangular, basally truncate with rounded angles, acuminate, 9–10 × 5–6 mm, strongly conduplicate at the base, apex with the margin finely pubescent; glenion deeply recessed between the basal lobes of the lip, ca. 1.2 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 1.3 × 4.0 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* obtriangular, acute, bilobed at the base, 2-celled, ca. 1.8 × 1.2 mm. *Pollinia* 2, narrowly oblong-pyriform, 2 mm long, attached to an elliptic viscidium through a short, cylindric caudicula. *Fruit* not seen. Fig. 31C.

Etymology: from the Greek words σκοτεινός (skotinós), “dark,” and άνθος (ánthos), “flower,” in reference to the solid, dark-purple flower of the species, uncommon in this group.

Distribution: exclusively known from the Cordillera Volcánica Central y Cordillera de Talamanca in Costa Rica, at 1200–2000 m in elevation.

Ecology: an epiphyte of wet premontane and lower montane forests, at mid-elevations on the Pacific watershed of both the Central and the Talamanca Cordilleras, *P. scotinantha* is associated with forest remnants close to riverbanks, forest edges, or isolated trees in pastures. Flowering, both in the field and in cultivation, has been recorded from May to July, and November to January.

Distinguishing features: the dark purple, blackish, glossy color of the flower and the triangular, flat, dark-purple lip fading into a small white region toward the apex, whitish on the underside, are useful characters to distinguish it from its closest relative, *P. oncoglossa*, which has light purple-red flowers on a greenish-yellow background, the sepals fading yellow green toward the base, and a characteristic, callose hook at the apex of the lip.

Costa Rican material examined: Alajuela: Carrizal, Concordia, entre Los Cartagos y Cinco Esquinas, 10°08'16.8"N, 84°09'49.8"W, 2027 m, 2027 m, bosque pluvial montano bajo, en potreros arbolados y bosque secundario, 17 junio 2009, floreció en cultivo en el Jardín Botánico Lankester, 8 enero 2010, *D. Bogarín 7455, R. L. Dressler, F. Pupulin & R. Trejos* (JBL). **San José:** Pérez Zeledón, Cajón, Montecarlo, 3.5 km al noreste de Montecarlo, orillas del Río Peña Blanquita, 9°22'20.3"N, 83°35'01.8"W, 1261 m, bosque pluvial premontano, en bosque secundario remanente a orillas del río, 28 julio 2009, *D. Bogarín 7355 & F. Pupulin* (JBL). Map 3.

15. ***Pleurothallis tapantiensis*** Pupulin, M. Díaz & Pridgeon, Vanishing Beauty. Vol. 2: 853–855. TYPE: Costa Rica. Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, Sendero Oropéndola, orillas del Río Grande de Orosi, 9°44'13.5"N, 83°46'49.6"W, 1376 m, epífitas en sitio sombreado en bosque secundario alrededor del sendero, bosque pluvial premontano, 11 diciembre 2014, *D. Bogarín 11273, M. Fernández, L. Taylor & J. Sharma* (Holotype: JBL). Fig. 35 (Voucher, *Bogarín 11273*, JBL).

Epiphytic, caespitose, erect to suberect, large *herb* to 23 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 15–22 cm long, 0.15–0.20 cm in diam., yellowish green, provided with 2 basal, tubular, obtuse sheaths 1.7–6.0 cm long, the bracts glumaceous, pale green with minute purple warts when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming curved-subpendent with age, thinly coriaceous, flexible, sessile, ovate, narrowly acute, acuminate, 7.3–11.7 × 4.5–5.5 cm, deeply cordate at the base, grass green, matte. *Inflorescence* a solitary flower, from a reclined, rectangular, acute, spathaceous bract to 1.7 cm long, brown, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, green, 8–12 mm long. *Ovary* terete-subclavate, curved, rounded in section, 3–5 mm long. *Flowers* spreading, with distinct temporary activity, short-lived (to 5 days), the sepals reflexed, solid purple. *Dorsal sepal* erect, ovate, obtuse, 10–11 × 7.0–7.5 mm, 7- to 9-veined. *Lateral sepals* connate into a broadly ovate, obtuse synsepal, 9.0–9.5 × 8.0–8.5 mm when spread, 9- to 11-veined. *Petals* narrowly triangular-subfalcate, acute, 6.0–7.0 × 0.9–1.1 mm, 3-veined. *Lip* unguiculate, hinged to the column foot, peltate, basally truncate with rounded angles, obtuse, with the apex slightly infolded, 6–7 × 3.0–3.5 mm, conduplicate at the base, the apical margins thickened; glenion recessed between the thickened basal lobes of the lip, ca. 0.8 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 1.2 × 2.5 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* obtriangular, acute, bilobed at the base, 2-celled, ca. 0.5 × 0.3 mm. *Pollinia* 2, narrowly oblong-pyriform, 0.5 mm long, attached to an elliptic viscidium through a short, cylindric caudicula. Fig. 31D.

Etymology: named after the Tapantí National Park, in the northern region of the Cordillera de Talamanca where the species was originally found. In the indigenous Cabécar

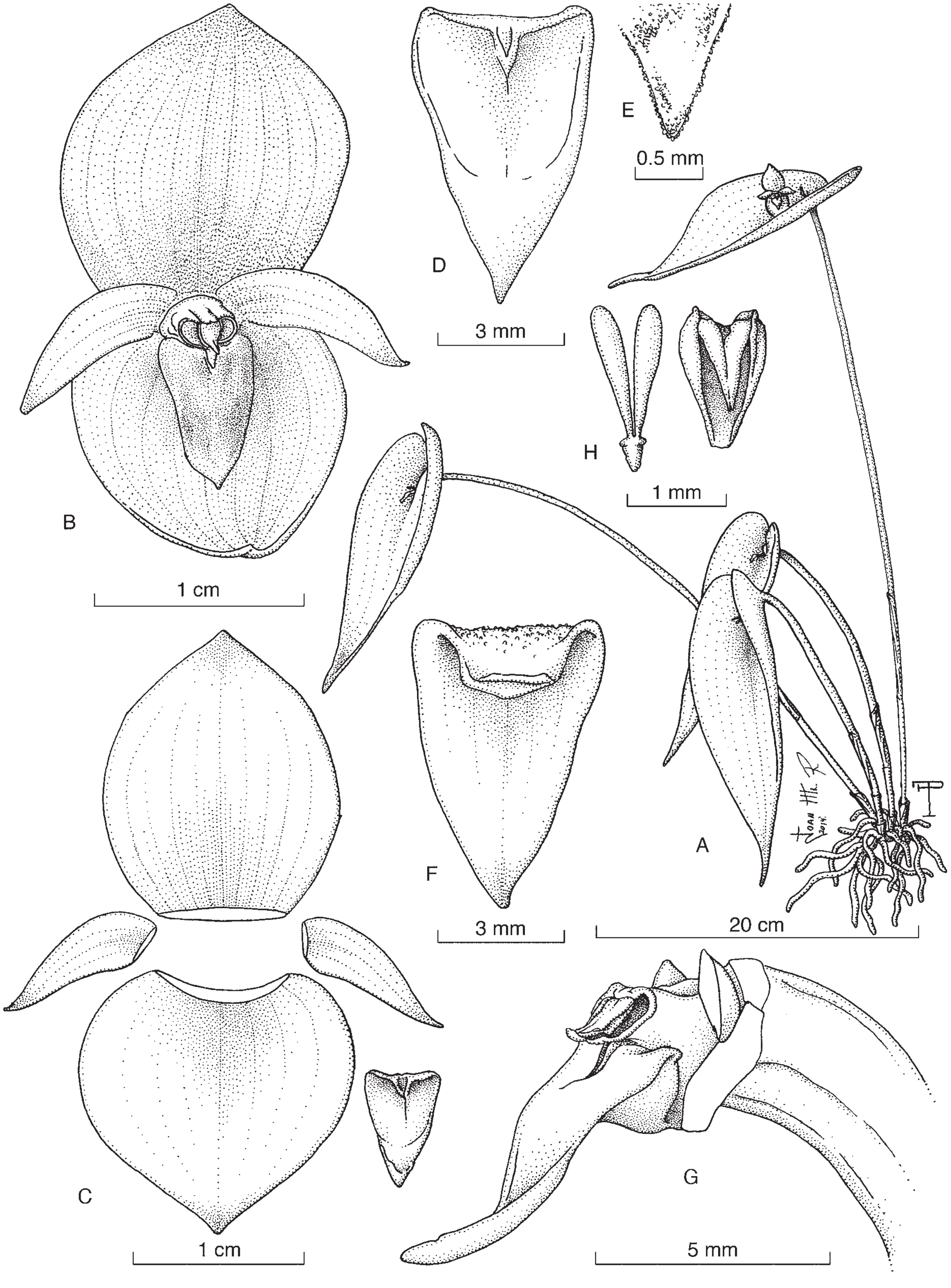


FIGURE 33. *Pleurothallis scotinantha* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** detail of the lip apex; **F,** lip, abaxial view; **G,** apex of ovary, column, and lip in lateral view; **H,** pollinarium and anther cap. Drawn by J. M. Ramírez from *Bogarín 7355* (JBL). Reproduced with permission from the Editor of *Lankesteriana*.

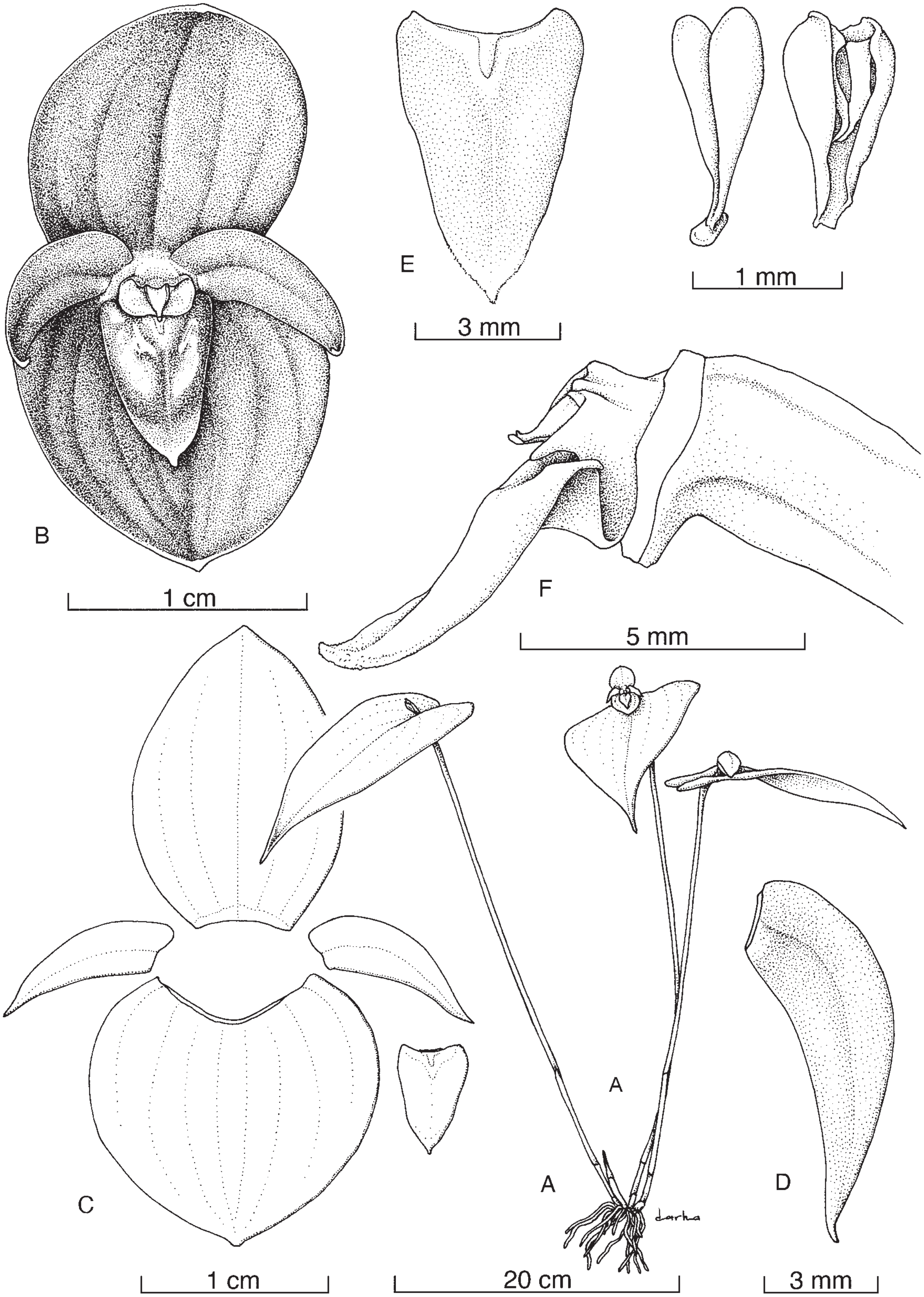


FIGURE 34. *Pleurothallis scotinantha* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** left petal; **E,** lip, adaxial view; **F,** apex of ovary, column, and lip in lateral view; **G,** pollinarium and anther cap. Drawn by F. Pupulin and D. Solano Ulate from *Bogarín 7455* (JBL).

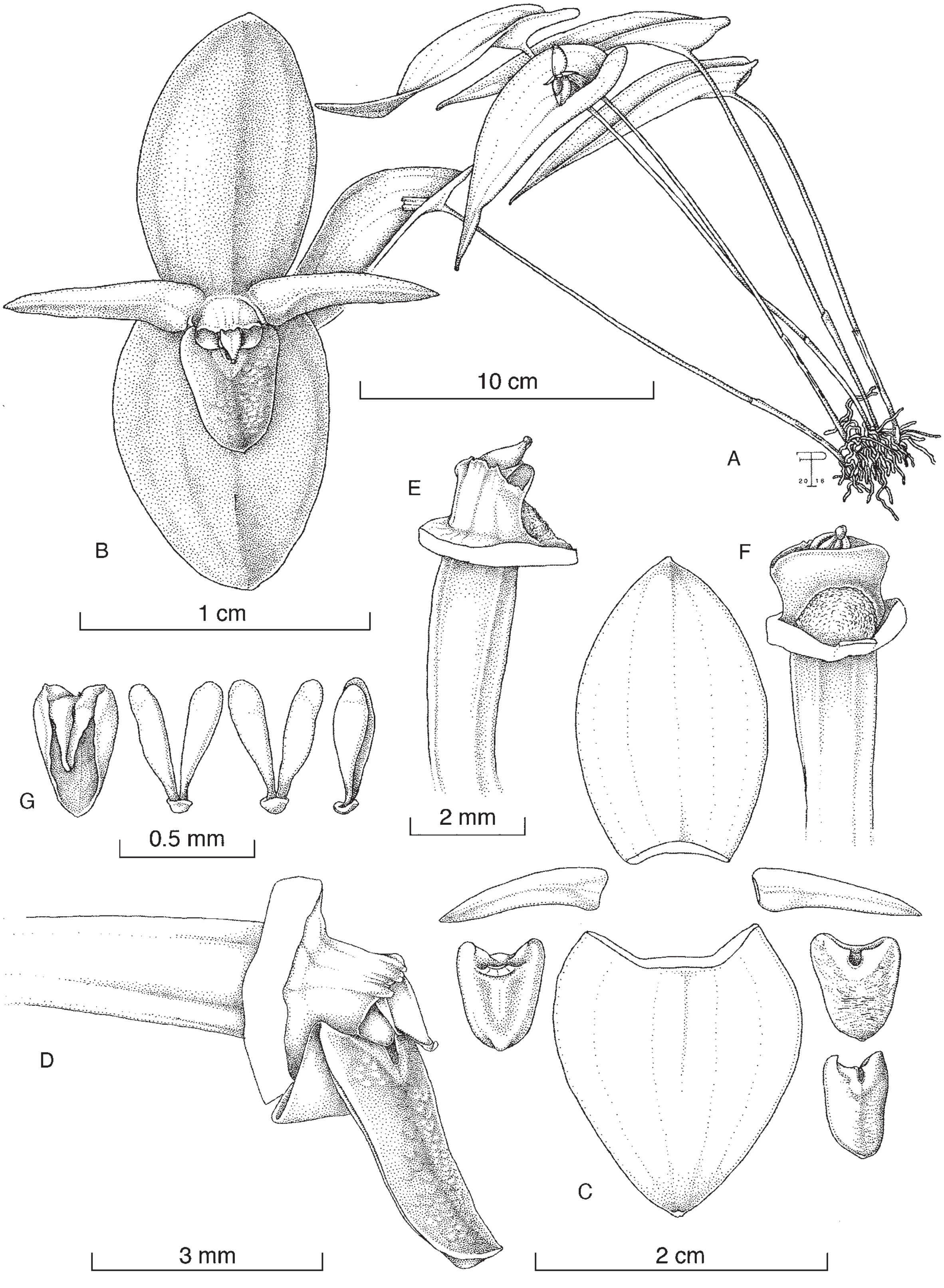


FIGURE 35. *Pleurothallis tapantiensis* Pupulin, M. Díaz & Pridgeon. **A,** habit; **B,** flower; **C,** dissected perianth (the lip in abaxial, adaxial, and three quarters views); **D,** apex of ovary, column, and lip in lateral view; **E,** column, three-quarter view; **F,** column, ventral view; **G,** anther cap and pollinarium (three views). Drawn by F. Pupulin and S. Díaz Poltronieri from *Bogarín 11273* (JBL). From Pupulin, 2020.

language, the word *tapantí* has several meanings, mostly related to water: "clear water," "a zone of many waters," "torrent from the heavens."

Distribution: known only from Costa Rica.

Ecology: epiphytic in premontane wet forest on the Caribbean slopes of the Cordillera de Talamanca, Costa Rica, where populations have been found in damp and shady places at elevations between 1300 and 1800 m. Flowering in cultivation has been recorded at least in March.

Distinguishing features: among the species of *Pleurothallis* close to *P. cardiothallis* provided with a peltate lip, which besides *P. cardiothallis* also includes in Costa Rica *P. navisepala*. *Pleurothallis tapantiensis* may be easily recognized by the lip that is glabrous and concolorous purple underneath (vs. papillose, whitish), with the apical margins straight (vs. involute, forming a pseudoapicule), provided for all its length with thin, irregular, transverse grooves.

Like most other species in this group, the flowers of *Pleurothallis tapantiensis* are temporarily active, likely in response to the levels of light and environmental humidity (Pupulin, Díaz-Morales, Aguilar, et al., 2017). The flowers open early in the morning and usually remain fully spread until noon, when the petals incurve and the lateral sepals lose turgor and fold over each other. The process repeats for 4 to 6 days, after which the flower fades and detaches from the pedicel.

Costa Rican material examined: Cartago: Paraíso, Orosi, Tapantí, Parque Nacional Tapantí, Sendero Oropéndola, orillas del Río Grande de Orosi, 9°44'13.5"N, 83°46'49.6"W, 1376 m, epífitas en sitio sombreado en bosque secundario alrededor del sendero, bosque pluvial premontano, 11 diciembre 2014, *D. Bogarín 11273, M. Fernández, L. Taylor & J. Sharma* (Holotype: JBL). Cartago, San Francisco, Muñeco, Navarro, ca. 5 km south of the Navarro church, between Río Sombrero and Quebrada Patarrá, road to Alto Belén, 9°45'38.28"N, 83°53'56.81"W, 1808 m, 3 Feb. 2017, flowered in cultivation at Lankester Botanical Garden, 31 Jan 2018, *D. Bogarín 12228, M. Cedeño, M. Fernández & E. Kaes* (JBL). Cartago, Aguacaliente, Navarro de Muñeco, 9°46'18.00"N, 83°54'08.40"W, 1526 m, bosque muy húmedo montano bajo, 13 Jul 2018, *M. Díaz 331, M. Fernández & D. Villalobos* (JBL). Map 3.

D. The *P. phyllocardia* group

16. ***Pleurothallis adventurae*** Karremans & Bogarín, Orchideen J. 18(3): 112. 2011. TYPE: Costa Rica. Puntarenas: Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1"N, 82°44'30.9"W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 6 junio 2010, *D. Bogarín 7696 & A. Karremans* (Holotype: CR; Isotypes: JBL-spirit, USJ). Fig. 36 (Voucher, *Bogarín 7696*, CR).

Epiphytic, caespitose, erect to suberect *herb* to 25 cm tall. *Roots* slender, flexuous, white, ca. 1 mm in diam. *Ramicauls* terete, slender, to 25 cm long, pale green, provided with 3–4 tubular, dry-papyraceous, brown sheaths in the basal third of the stem, the uppermost tightly clasping, 2.0–2.5 cm long. *Leaf* borne at the apex of the ramicaul, hanging, almost parallel to the stem, thinly coriaceous, flexible, narrowly lanceolate, acute, the margins frequently revolute, 8–12 × 2–3 cm, deeply cordate at the base, the basal lobes not overlapping, grayish-green, matte. *Inflorescence* fasciculate, with solitary flower borne in succession from a reclined, rectangular, truncate, spathaceous, dry-papyraceous, grayish-brown bract to 1.2 cm long. *Pedicel* terete, green, to 2 cm long. *Ovary* terete, 2 mm long. *Flowers* spreading, resupinate, the sepals purple red, the petals and lip dark purple, pubescent-tomentose. *Dorsal sepal* erect, elliptic, acute, 6.5–7.0 × 4.5–5.0 mm, 3-veined, pubescent-tomentose, more densely so toward the apex. *Lateral sepals* connate into an ovate-orbicular, subacute synsepal, pubescent-tomentose, 5.7–5.9 × 5.0–5.2 mm, 4-veined. *Petals* narrowly oblong, acute, denticulate, 5.6–5.7 × 1.2–1.3 mm, 1-veined. *Lip* unguiculate, hinged to the column foot, strongly geniculate at the base, triangular, basally truncate with obtuse angles, acute, minutely apiculate, the margins glandulose, the basal margins erect, 2.7–2.8 × 2.2–2.3 mm, papillose; glenion raised on a thick callus on the disc ca. 0.8 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, ca. 1.2 × 1.0 mm, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, truncate, 2-celled, ca. 0.8 × 0.5 mm. *Pollinia* 2, ovate-pyriform, 0.8 mm long, attached to an orbicular viscidium. *Fruit* not seen. Fig. 31E.

Etymology: from the Latin *adventura*, adventure, in reference to the adventurous circumstances under which the type plant was found.

Distribution: known only from southeastern Costa Rica but expected from nearby Panama as the type locality is less than 2 km from the boundary between the two countries.

Ecology: epiphytic in lower montane rain forest, in primary oak forest or on trees in pastures, at 1700–1800 m in elevation. Flowering has been recorded from June to December.

Distinguishing features: among Costa Rican specimens, *Pleurothallis adventurae* is easily distinguished by the grayish-green, matte leaves with revolute margins, and the purple-red flowers adaxially completely covered with short, stiff, pointed tubercles.

Notwithstanding its highly atypical morphological characteristics when studied in the framework of the Costa Rican flora, *Pleurothallis adventurae* surely belongs morphologically to the *P. phyllocardia* group. The apparent deviancy of this species with respect to the other taxa of the group is, in fact, just an artifact of the strictly local species sample targeted in this study. When a broader view of the group is adopted, including the highest species diversity shown in the northern Andes, it is evident that the *P. phyllocardia* group blends, via *P. peculiaris* Luer/*P. cardiostola* Rchb.f./*P. lilijae* Foldats, into the group of *P. dibolia* Luer/*P. diabolica* Luer & R. Escobar/*P. portillae* Luer, with both erect and supine spathes. More strictly, the affinities of *P. adventurae* are with a small group of mostly South American species that exhibit glaucous, dark green, flexible, usually long, narrowly lanceolate and deeply cordate leaves with revolute margins, provided with dark red-purple flowers often presenting scabrous to hirsute indumenta. It is most closely related to the Ecuadorian

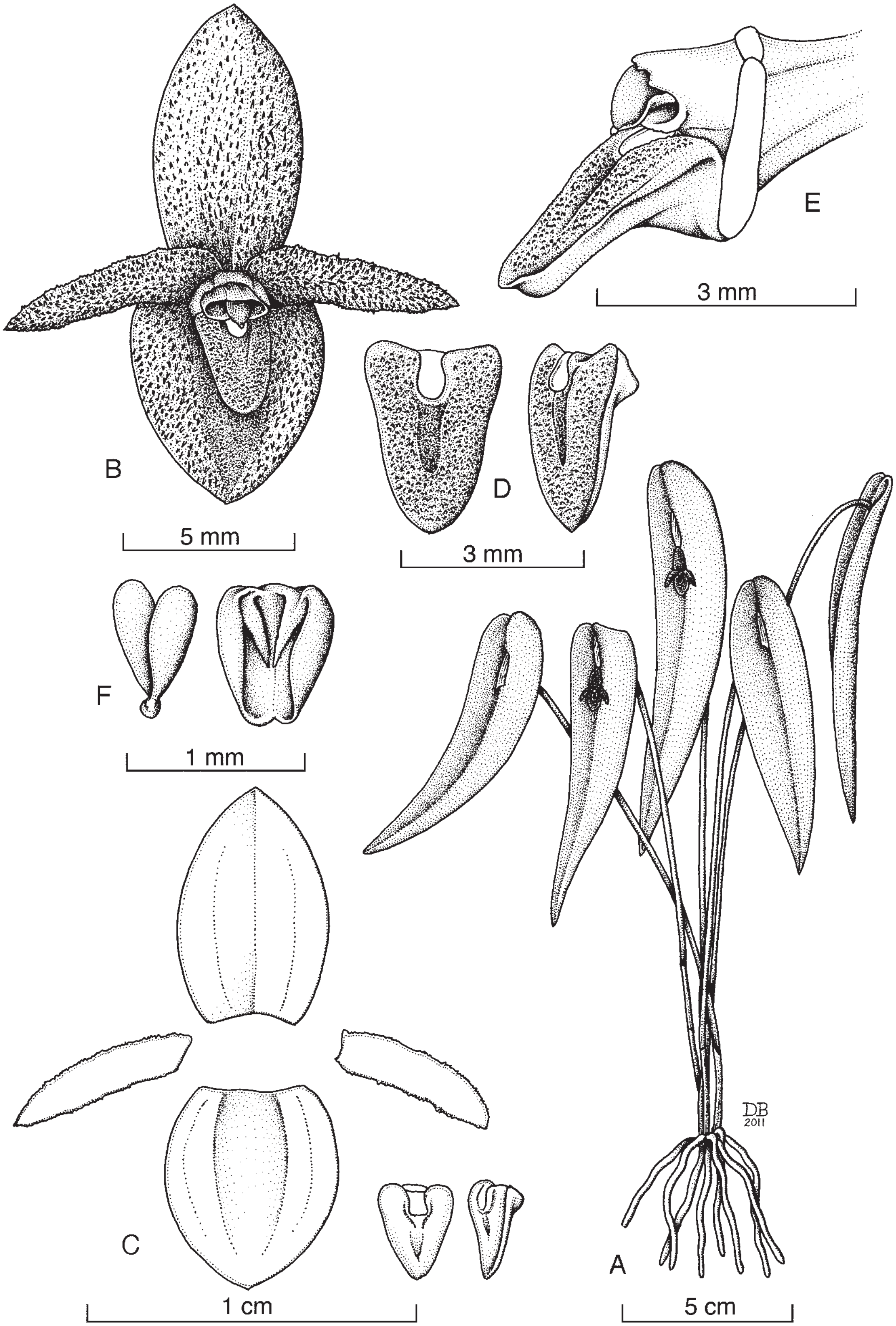


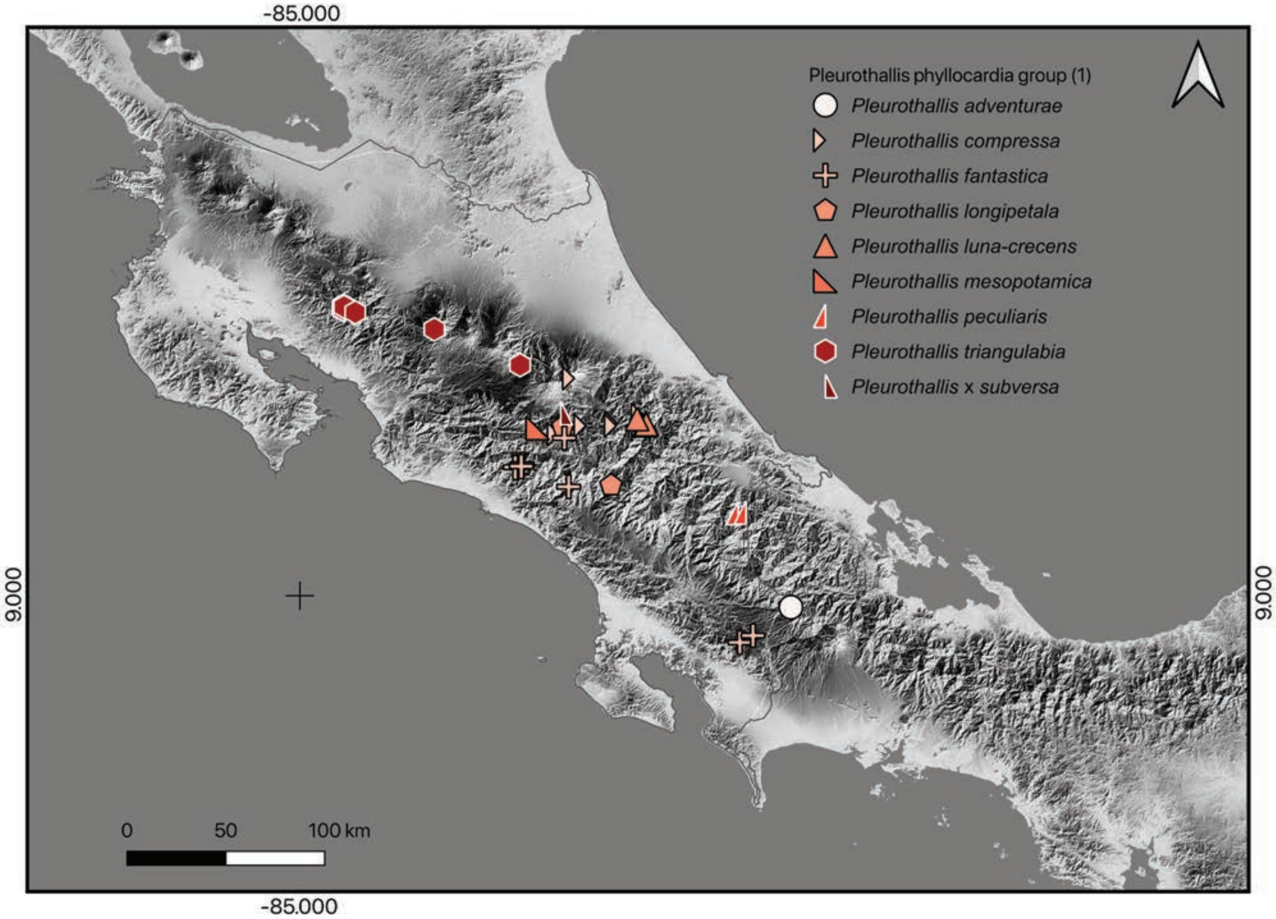
FIGURE 36. *Pleurothallis adventurae* Karremans & Bogarín. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in adaxial and three-quarter views; **E,** apex of ovary, column, and lip in lateral view; **F,** pollinarium and anther cap. Drawn by D. Bogarín from *Bogarín 7696* (CR).

P. portillae, from which it can be distinguished by the shape of the leaf, the color and indumentum of the flowers, and the width of the petals. It also resembles *P. calamifolia* Luer & R. Escobar, *P. omoglossa* Luer and *P. sigynes* Luer. In Costa Rica, it is known exclusively from the southern, Pacific extension of the Cordillera de Talamanca, close to the border with Panama, where the species must be also expected.

Costa Rican material examined: Puntarenas: Coto Brus, Sabalito, Zona Protectora Las Tablas, 13 km NE of Lucha, Sitio Coto Brus, finca Sandí "El Capricho," epiphytic on *Quercus* sp. in pastures and along the river Sutú, wet premontane forest, 8°56'46.1"N, 82°44'30.9"W, 1778 m, 6 oct. 2010, *F. Pupulin 7904, D. Bogarín, R. L. Dressler & M. Fernández* (JBL); Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1"N, 82°44'30.9"W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 6 junio 2010, *D. Bogarín 7697 & A. Karremans* (JBL); Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, Finca de Miguel Sandí, "*ad ager Sandiorum 'El Capricho,' supra arbores praecipue quercinis in collibus montibusque et ad margines pascuibus inter flumen Sutú*," bosque muy húmedo premontano, 8°56'46.1"N, 82°44'30.9"W, 1780 m, 6 Oct. 2010, *D. Bogarín 8093, R. L. Dressler, M. Fernández & F. Pupulin* (JBL); same locality, 6 Oct. 2011, *D. Bogarín 9253, R. L. Dressler, M. Fernández* (JBL); Zona Protectora Las Tablas, 13 km al noreste de Lucha, Sitio Coto Brus, entre Río Surá y Quebrada Sutú, Finca de Miguel Sandí, 8°56'46.1"N, 82°44'30.9"W, 1778 m, bosque pluvial montano bajo, epífitas en potreros arbolados, 10 dec. 2013, *A. Karremans 6125, D. Bogarín, M. Fernández & L. Sandoval* (JBL). Map 4.

17. ***Pleurothallis anthurioides*** A. Doucette, Orquideología 33(2): 126. 2016. TYPE. Panama. Bocas del Toro: Culebra, 800 m.a.s.l., flowered in cultivation at Finca Dracula, Guadalupe, Panama, 11 Jan 2012, *A. Doucette 3998* (Holotype: PMA). Fig. 37 (Voucher, *Bogarín 10649*, JBL).

Epiphytic, caespitose, large erect *herb* to 30 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 16–30 cm long, 0.3–0.4 cm in diam., pale green, provided with 2–3 basal, tubular, obtuse sheaths of different sizes, to 7 cm long, dry-papyraceous, brown when mature. *Leaf* borne at the apex of the ramicaul, held horizontally to facing down ca. 45°, thinly coriaceous, flexible, sessile, ovate, tridenticulate, 7–11 × 3.8–7.0 cm, deeply cordate at the base, green, matte. *Inflorescence* fasciculate, of several solitary flowers produced in succession from an erect, rectangular-subclavate, truncate, spathaceous bract to 2 cm long, glumaceous, green, becoming brown, dry-papyraceous when mature. *Pedicel* terete, green, subgeniculate at the



MAP 4. Map of collection sites for the species of *Pleurothallis phyllocardia* group.

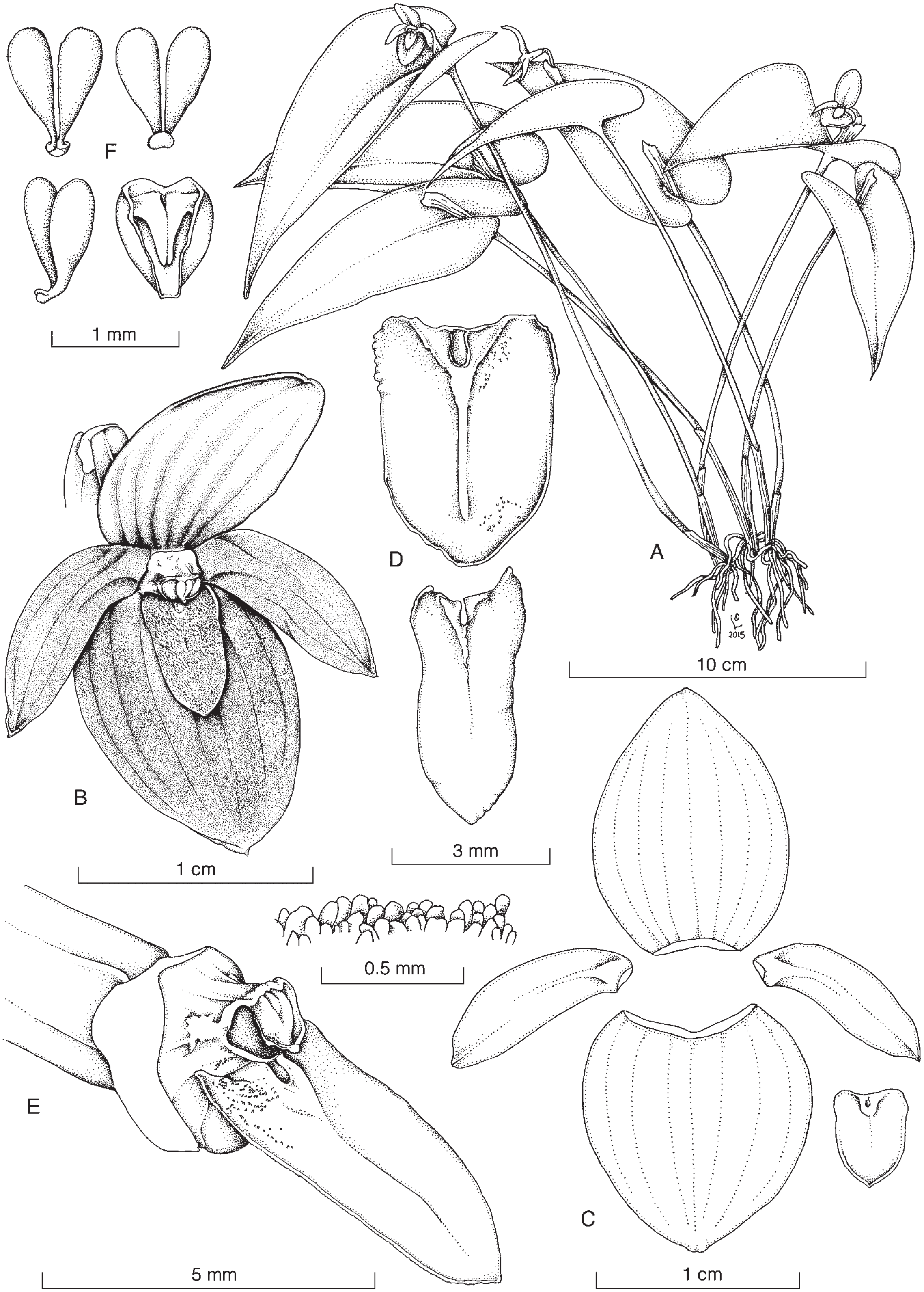


FIGURE 37. *Pleurothallis anthurioides* A. Doucette. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in adaxial and three-quarter views; **E,** apex of ovary, column, and lip in three-quarter view; **F,** pollinarium (three views) and anther cap. Drawn by L. Oses from *Bogarín 10649* (JBL).

joining point with the ovary, to 2 cm long. *Ovary* terete-subclavate, ca. 5 mm long. *Flowers* spreading, resupinate, with the dorsal sepal yellow, blotched with purple at the base and striated along the veins, the synsepal suffused with purple on a yellow background, the petals purple with yellow margins, the lip dark vinaceous purple. *Dorsal sepal* slightly reclined, broadly ovate-elliptic, acute, 15–19 × 8–10 mm, 7-veined. *Lateral sepals* connate into a broadly ovate-suborbicular, obtuse, slightly concave synsepal, 12–18 × 10–12 mm, 7-veined. *Petals* oblong, subfalcate, inserted at 45°, acute, ciliate, 10–13 × 3–4 mm, 1-veined, the vein body thickened at the base forming a low keel. *Lip* oblong-peltate, thick, hinged to the column foot, basally concave, truncate-emarginate with rounded angles, obtuse, 5–6 × 3–4 mm, rugulose adaxially; glenion raised on a thick callus on the disc ca. 0.5 mm long. *Column* short, stout, conical, dorsiventrally compressed, ca. 2 × 3 mm, with a distinct foot, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, 2-celled, ca. 0.8 × 0.6 mm. *Pollinia* 2, narrowly ovate, 0.8 mm long, attached to a rounded-subrheniform viscidium. Fig. 31F.

Etymology: named in allusion to the similarity of the vegetative shoots to the inflorescence of *Anthurium* species.

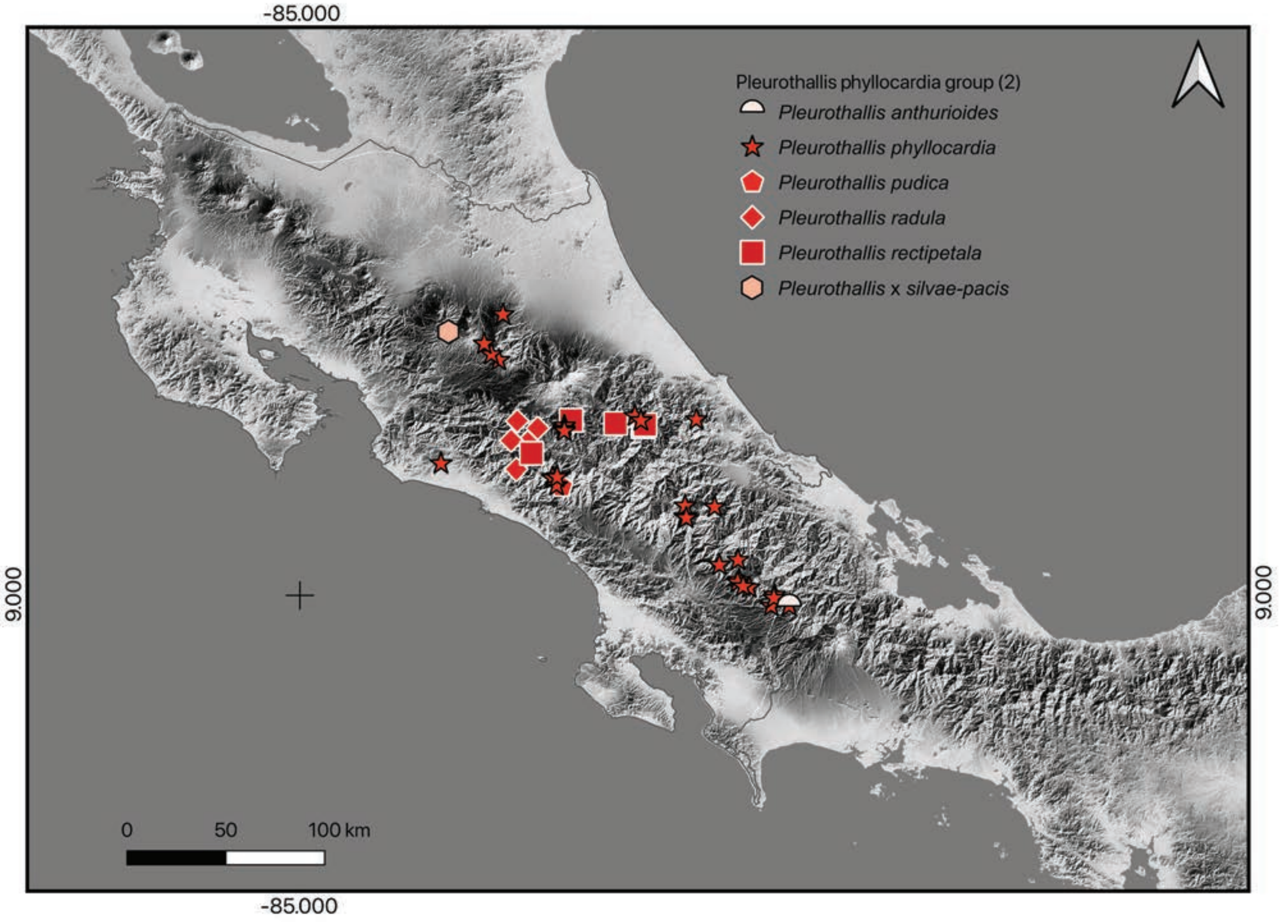
Distribution: known only from western Panama and southern Costa Rica.

Ecology: an epiphyte of the middle-elevation regions of southern Cordillera de Talamanca, where populations have been found on both the Caribbean (in Panama) and Pacific (in Costa Rica) watersheds of the chain. Phenological data are scanty, but the species apparently flowers at the beginning of the dry season in the region, with blooming specimens documented in the months of January and March.

Distinguishing features: the erect spathe and the comparatively large flowers, striped and suffused with dull purple on a yellow background with the lip dark vinaceous purple, concave sepals, and subfalcate, entire petals pointing downward and provided with a basal, callous keel, distinguish the species.

Florally, *Pleurothallis anthurioides* is superficially similar to species of the *P. cardiothallis* group, with large tepals and a slightly concave, bilabiate perianth, but the inflorescence is exerted from an erect bract and the lip of the flower is much more reminiscent, both in shape and indumentum, of those of species close to *P. phillocardia*. The comparatively very large petals, with a distinct, thickened keel at the base, held obliquely and pointing downward, are unique to *P. anthurioides*.

Costa Rican material examined: Puntarenas: Coto Brus, Sabalito, Zona Protectora Las Tablas, 15 km al noreste de Lucha, Sitio Tablas, Finca Sandí-Hartmann "El Capricho," camino a El Surá, 8°57'0.63"N, 82°44'59.72"W, 2017 m, bosque pluvial montano bajo, 10 diciembre 2013, *D. Bogarín 10649, A. Karremans, M. Fernández & L. Sandoval* (Holotype: JBL). Map 5.



Map 5. Map of collection sites for the species of *Pleurothallis phyllocardia* group.

18. ***Pleurothallis compressa*** Luer, Lindleyana 11(2): 75. 1996. *Acronia compressa* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 112. 2005. *Zosterophyllanthos compressus* (Luer) Szlach. & Kulak, Richardiana 6(4): 188. 2006., as *Z. compressa*. TYPE: Costa Rica. Cartago: Turrialba, flowered in cultivation at the Lankester Botanical Garden, Cartago, 7 March 1995, peduncle flat, flower light brown, column white, *C. Luer 17380* (Holotype: CR; Isotype: MO). Fig. 38 (Voucher, *Bogarín 7839*, JBL).

Epiphytic, caespitose, curved to pendent *herb*, to 30 cm tall. *Roots* slender, flexuous, 1–2 mm in diam. *Ramicauls* terete at the base becoming strongly ancipitous at apex, slender, 14–30 cm long, 2–5 mm in diam., yellowish green, provided with a tubular, short, truncate sheath to 2 cm long at the base, and a longer, tubular, tightly adpressed, truncate sheath below the middle, to 6 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* reclined, so the lower surface facing the pendent-curved stem, thinly coriaceous, flexible, sessile, narrowly lanceolate-ovate, acuminate, 11–18 × 4–6 cm, deeply cordate at the base, the basal lobes adpressed but not overlapping, grass green, matte. *Inflorescence* a solitary flower, borne pendent from a suberect, spathaceous, diagonally truncate bract 10 mm long, brown, dry-papyraceous when mature; peduncle terete, facing down, to 15 mm long. *Pedicel* terete, to 7 mm long. *Ovary* suclavate, curved rounded in section, reddish brown, 5–6 mm long. *Flowers* mostly nonresupinate, the sepals reddish brown, the petals light ocher-brown, the lip dull orange, the column white. *Dorsal sepal* ovate, acute, 6 × 4 mm, 3-veined. *Lateral sepals* connate into a subrounded, apically deeply excised synsepal, 6 × 5 mm, the apices free for 2 mm, acute, abruptly apiculate, each half 2-veined. *Petals* narrowly triangular-falcate, acuminate, 10 × 1 mm, 1-veined. *Lip* hinged to the column foot, broadly triangular-reniform, basally truncate with rounded angles, broadly obtuse, apiculate, sparsely verrucose, 2 × 3 mm, strongly conduplicate at the base, the margins slightly reflexed; glenion raised on a cushion-like callus between the basal lobes of the lip, less than 1 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 2 × 2 mm, apically diagonally truncate seen from the side, the anther apical, bent, the stigma apical, bilobed. *Anther cap* cucullate, narrowly ovate-triangular, cordate, 2-celled. *Pollinia* 2, narrowly oblong-pyriform, attached to a peltate-subrounded viscidium through 2 short, cylindrical caudicles. Fig. 31G–H.

Etymology: from the Latin *compressus*, “compressed, flattened,” in reference to the laterally compressed ramicaul.

Distribution: known only from Costa Rica, along the Caribbean watershed of the northern Cordillera de Talamanca.

Ecology: growing as an epiphyte in secondary forests and open areas of premontane pluvial forests along the Caribbean watershed of the Continental Divide, at 1150–1850 m in elevation. Blooming has been recorded in cultivation from October to February, and in July.

Distinguishing features: the curved to pendent plants, provided with ancipitous ramicauls, narrowly lanceolate-ovate, acuminate leaves deeply cordate at the base, and the small brown flower borne pendently beneath the leaf, completely reflexed (or laterally “compressed”), easily distinguish *Pleurothallis compressa* from any other species in the genus.

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, 1542 m, bosque pluvial premontano, epífitas en bosque secundario y árboles en zonas abiertas, 22 Jul 2010, *D. Bogarín 7839, M. Fernández, R. Trejos & C. Smith* (JBL). Paraíso. Orosi, Purisil, camino a Alto Jaular, entre los ríos Jaular y Purisil, Finca La Ponderosa, bosque muy húmedo premontano, epífitas en bosque secundario, 9˚44'13.9"N, 83˚48'26.9"W, 1606 m, 14 Oct 2008, *D. Bogarín 5378*, *R. Gómez, R. Trejos & J. Warner* (JBL). Turrialba. Santa Cruz, Más o menos 4–5 km de la Iglesia de Santa Cruz, en el camino a las Abras, después de Calle Vargas, cerca de Buenos Aires, en el punto del cruce entre Las Abras, Calle Vargas y Las Virtudes, al lado de la calle en un potrero pantanoso, 9˚59'32"N, 83˚44'13"W, 1750–1850 m, 5 Aug 2008, *A. P. Karremans 1370 & Karremans* (JBL). Turrialba, Torito, road to Santa Teresa, along a small creek, on insolate tree in pasture, 31 Jul 1999, flowered in cultivation at Jardín Botánico Lankester, 25 Feb 2000, *F. Pupulin 962, R. L. Dressler, K. Dressler, D. E. Mora & M. Retana* (JBL). Turrialba, Moravia de Chirripó, hills north of Moravia across the plain with pasture, premontane wet forest, secondary mature vegetation and remnants of secondary vegetation in pastures, 9˚50'18"N, 83˚26'45"W, 1135 m 12 Jun 2002, flowered in cultivation at Jardín Botánico Lankester, 11 Oct 2005, *F. Pupulin 3935, M. Bonilla, R. Gómez, H. León-Páez & W. Schug* (JBL). Turrialba, Tayutic, Moravia de Chirripó, 5 Kilómetros al oeste del centro de Moravia. Cerca de Tsipiri. Sobre sendero al lado de la calle que va a Platanillo, 9˚49'28"N, 83˚25'16"W, 1220 m, 4 Dec 2010, *A. P. Karremans 1220 & M. Contreras Fernández* (JBL). Turrialba. Valle del Reventazón, Jicotea, Finca La Pradera, 9˚47'15"N, 83˚32'35"W, 1000 m, 22 Jun 1995, *G. Rivera 2525 & A. Rojas* (CR). Turrialba, Tayutic, Finca La Pradera, Jicotea, 100–1200 m, 9.7875000, -83.5430556, 22 Jun 1995, *G. Rivera 2512* (CR); same collecting data, *G. Rivera 2519* (CR). Turrialba, Tayutic, Vereh. Siguiendo la fila entre Ríos Vereh y Jicotea, 9.7750000, -83.5444444, 26 Jul 1995, *A. Cascante Marín 8126 & G. Herrera* (CR). Turrialba, en cultivo en el Jardín Botánico Lankester, legit C. Luer 17380, planta sobre la cual se basó la descripción original (clonotypus), 16 Jan 2004, *D. Bogarín 642* (JBL). **Without specific locality data**: flowered in cultivation at Jardín Botánico Lankester, 11 Jun 2007, *D. Bogarín 3938* (JBL). Map 4.

19. ***Pleurothallis fantastica*** Ames, Bot. Mus. Leafl. 4(4): 45. 1936. *Acronia fantastica* (Ames) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 134. 2005. TYPE: Costa Rica: San José: vicinity of El General. Epiphyte on trees by a river, 830 m, Jan. 1936. Flowers yellow. *A. F. Skutch 2391* (Holotype: AMES; Isotype: AMES). *Pleurothallis horichii* Luer, Orchidee (Hamburg) 36(1): 23. 1985. TYPE: Costa Rica. Cordillera Brunquena, between Pacuarito - El Alto de San Juan, 1100 m, 26 May 1982, collected by C. Horich,

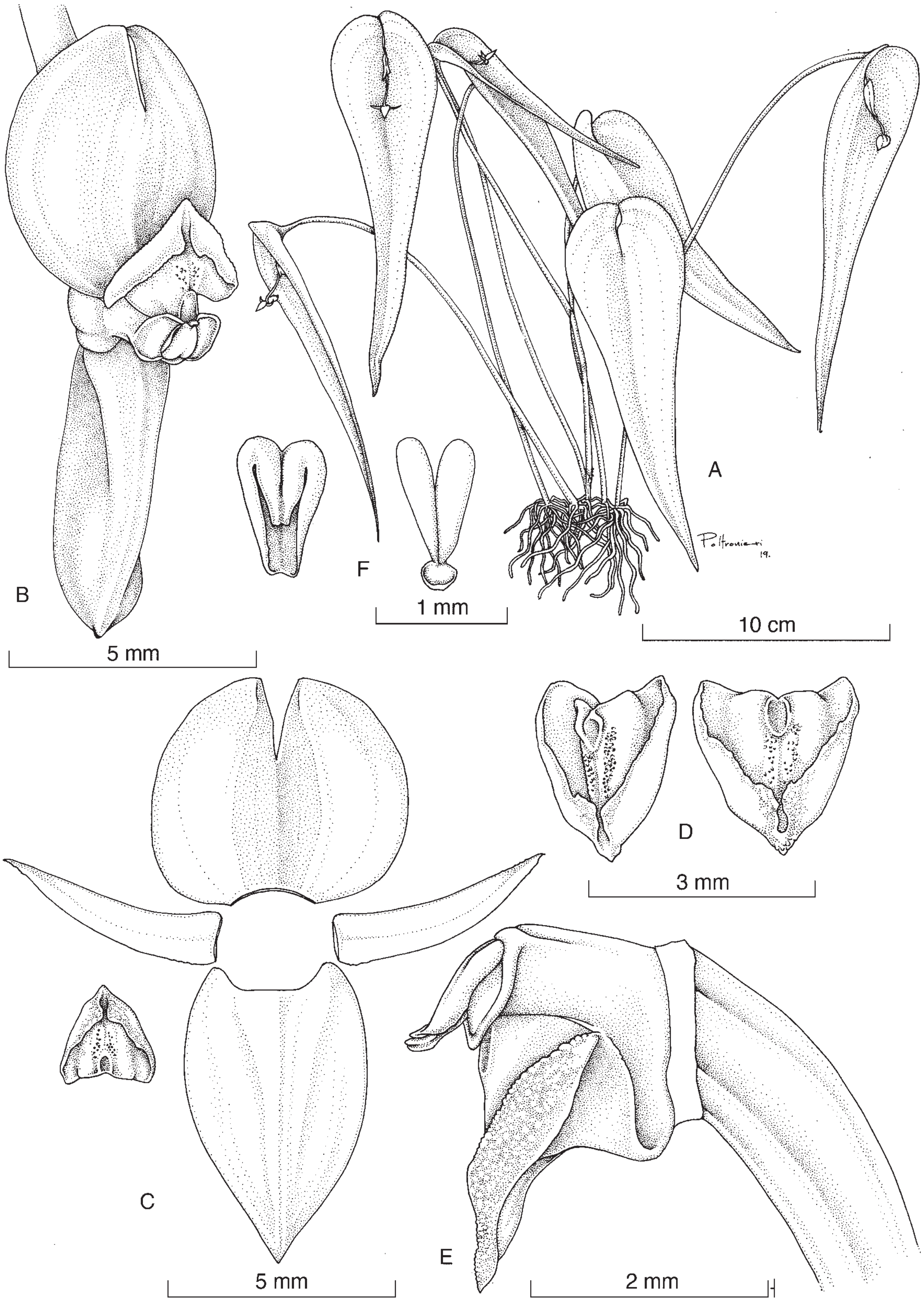


FIGURE 38. *Pleurothallis compressa* Luer. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in three quarters and adaxial views; **E,** apex of ovary, column, and lip in lateral view; **F,** anther cap and pollinarium. Drawn by S. Díaz Poltronieri from *Bogarín 7839* (JBL).

flowered in cultivation in Bern, Switzerland, *R. Jenny P-113* (Holotype: MO). Fig. 39 (Voucher, *Blanco 5087*, JBL).

Epiphytic, caespitose, arching to pendent *herb* up to 40 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* slender, 10–23 cm long, 1–2 mm in diam., terete at the base, becoming slightly ancipitous distally, pale green, with 2 basal, short, tubular, obtuse sheaths, and another tubular, cylindrical, tightly adpressed sheath below the middle, the lower ones 8–14 mm long, the upper to 40 mm long, the sheaths dry-papyraceous, brown. *Leaf* borne at the apex of the ramicaul, pendent, rigidly coriaceous, sessile, narrowly ovate, acute, tapering to a subacuminate, mucronate apex, concave at the base, green, matte, 10–14 cm long, 1.7–2.2 cm wide, the basal lobes suberect, decurrent on the ramicaul for about 15 mm. *Inflorescence* a fascicle of solitary flowers, produced in succession from a prostrate, rectangular, obliquely truncate, glumaceous, green, spathaceous bract emerging above the base of the leaf, 5–7 mm long, becoming brown, dry-papyraceous when mature and eventually fugacious; the peduncle terete, mostly adnate to the leaf, to 2 cm long. *Pedicel* terete, green, 5–6 mm long. *Ovary* terete, subclavate, ca. 5 mm long. *Flowers* spreading to slightly reflexed, concolorous pale yellow to greenish yellow, the midlobe and the disc of the lip reddish brown. *Dorsal sepal* erect, elliptic, subacute, the margins reflexed, 6–7 × 4 mm, 5-veined. *Lateral sepals* connate into a broadly elliptic, obtuse, minutely emarginate synsepal, the margins reflexed, 5 × 4 mm, each half 4-veined. *Petals* broadly asymmetrically lanceolate, subfalcate, acute, glandulose, the margins cellular 5–6 × 3 mm, 3-veined. *Lip* fleshy, adnate to the base of the column, transversely 3-lobed, 3 × 4 mm when spread, the lateral lobes transversely elliptic-rheniform, obliquely erect, minutely glandulose, the midlobe elliptic-subquadrate, bilobulate-retuse, distinctly glandulose, with a minute abaxial apiculum, ca. 1 × 1 mm, the disc with a low, bilobed callus. *Column* terete, stout, distinctly dilated distally, minutely glandulose, ca. 3 × 2 mm, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subcordate, truncate, 2-celled. *Pollinia* 2, narrowly ovoid, attached to an elliptic viscidium. Fig. 31I.

Etymology: from medieval Latin *fantasticus*, “imaginary,” but also “wonderful, marvelous,” in allusion to the shape of the flowers in this species, which do not resemble any other *Pleurothallis* in the American tropics.

Distribution: known only from Costa Rica.

Ecology: growing as an epiphyte in secondary vegetation along rivers, in premontane moist forest between 950 and 1400 m in elevation, on both the Caribbean and Pacific watersheds of the Continental Divide. Flowering has been recorded from January to June, and in September.

Distinguishing features: it is easy to distinguish *Pleurothallis fantastica* from any other species in the genus by the long, narrow, pendent leaves borne on a distally ancipitous ramicaul, which are cuneate (not cordate) at the base, and the flower showing a distinctly 3-lobed lip, the lateral lobes broad, elliptic, spread out, and the midlobe small, excised.

Pleurothallis fantastica could seem an obvious misfit here. Morphologically, it has no close relatives either in the flora of Costa Rica or in any other floras of the American tropics. Vegetatively, however, it more closely resembles species of the *P. phyllocardia* group, and particularly *P. compressa*, than any other *Pleurothallis* taxa known in Central America. In the other species of the group, mature, flowering stems end into a leaf that is basally deeply cordate, while juvenile leaves are mostly cuneate or rounded at the base. We interpret here the cuneate leaves on fertile stems of *P. fantastica* as a retention of the paedomorphic form, which is otherwise characteristic of the juvenile stage within the group.

Both the photograph and the drawing of *Pleurothallis horichii* published by Luer (1985) leave no doubt about the fact that this species, also native from the mountains surrounding the El General Valley in southern Costa Rica, is conspecific with *P. fantastica*.

Costa Rican material examined: Cartago: Paraíso, Orosi, P.N. Tapantí-Macizo de La Muerte, entre Quebrada Salto y Río Humo, 9.7194444, -83.7833333, 1200–1350 m, 27 Jun 2004, *J. F. Morales Quirós 10842 & L. Muñoz* (CR). **Puntarenas:** Coto Brus, San Vito, Estación Biológica Las Cruces, Reserva Biológica, Río Java, Sendero Ridge, 1340 m, 8.7856˚N, 82.9772˚W, epífita en árbol caído, 6 Oct 2018, *M. Blanco 5087, N. Jiménez, O. Alvarado, M. Cedeño, K. Gil & M. J. Mata* (JBL). Coto Brus, Sabalito, ca. 8˚49'N, 82˚55'W, 1020 m, collected by M. Flores, flowered in cultivation at Gaia Botanical Garden, 2 Sept 2001, *F. Pupulin 3329* (JBL). **San José:** Pérez Zeledón, San Ramón, unpaved road to Las Pegas, Páramo, Los Angeles, shore of Río División, 9˚29'58"N, 83˚45'49"W, 1390 m, premontane moist forest, epiphytic in secondary vegetation along the river, 20 april 2003, *F. Pupulin 4667, J. Cambronero, H. Leon-Paéz, M. Powell, E. Salas & V. Savolainen* (JBL). Dota, Santa María, San Joaquín. Río San Joaquín. Sobre un árbol caído al lado del río. 955 m, 09˚35'10"N, 84˚00'36"W 20 de febrero 2012, *A. P. Karremans 5120* (JBL). Dota, Santa María, entre San Joaquín y La Guaria, Desamparados, R.F. Los Santos, San Rafael Arriba, casa de Ana Morales, 9.6000000, -83.9777778, 1400–1700 m, 11 Jul 2004, *J. F. Morales Quirós 10892 & L. Muñoz* (CR). Dota, Santa María, R.F. Los Santos, San Joaquín, Quebrada Pirranga. 9.590277, -83.9819444, 1300–1500 m, 22 Nov 2003, *J. F. Morales Quirós 10135* (CR). Map 4.

20. **Pleurothallis longipetala** Bogarín & Belfort, ***sp. nov***. TYPE: Costa Rica. Cartago: Paraíso, Orosi, Tapantí, camino entre Tapantí y Tausito, cerca del Restaurante Tejos, 9˚46'16.5"N, 83˚47'24.6"W, 1453 m, bosque pluvial premontano, recolectada por Daniel Jiménez, 8 noviembre 2005, *D. Bogarín 9428* (Holotype: JBL-Spirit). Fig. 40 (Voucher, *Bogarín 9428,* JBL).

Species affinis Pleurothallis luna-crescente Pupulin, J.Aguilar *et* Mel.Fernández, *P. radula* Luer *et P. rectipetala* Ames *et* C. Schweinf., *sepalibus non reflexis quando perfectis, labello erecto, petalis distincte longioribus, glenione transverse rectangularis ab omnibus differt; floribus purpureis vel sordide flavis purpureo striatis a P. radula facile recedit; floribus planis a illis forma lunae-crescentis P. luna-cescente distinguitur; petalis quam sepalis longis a P. rectipetala expedite noscitur.*

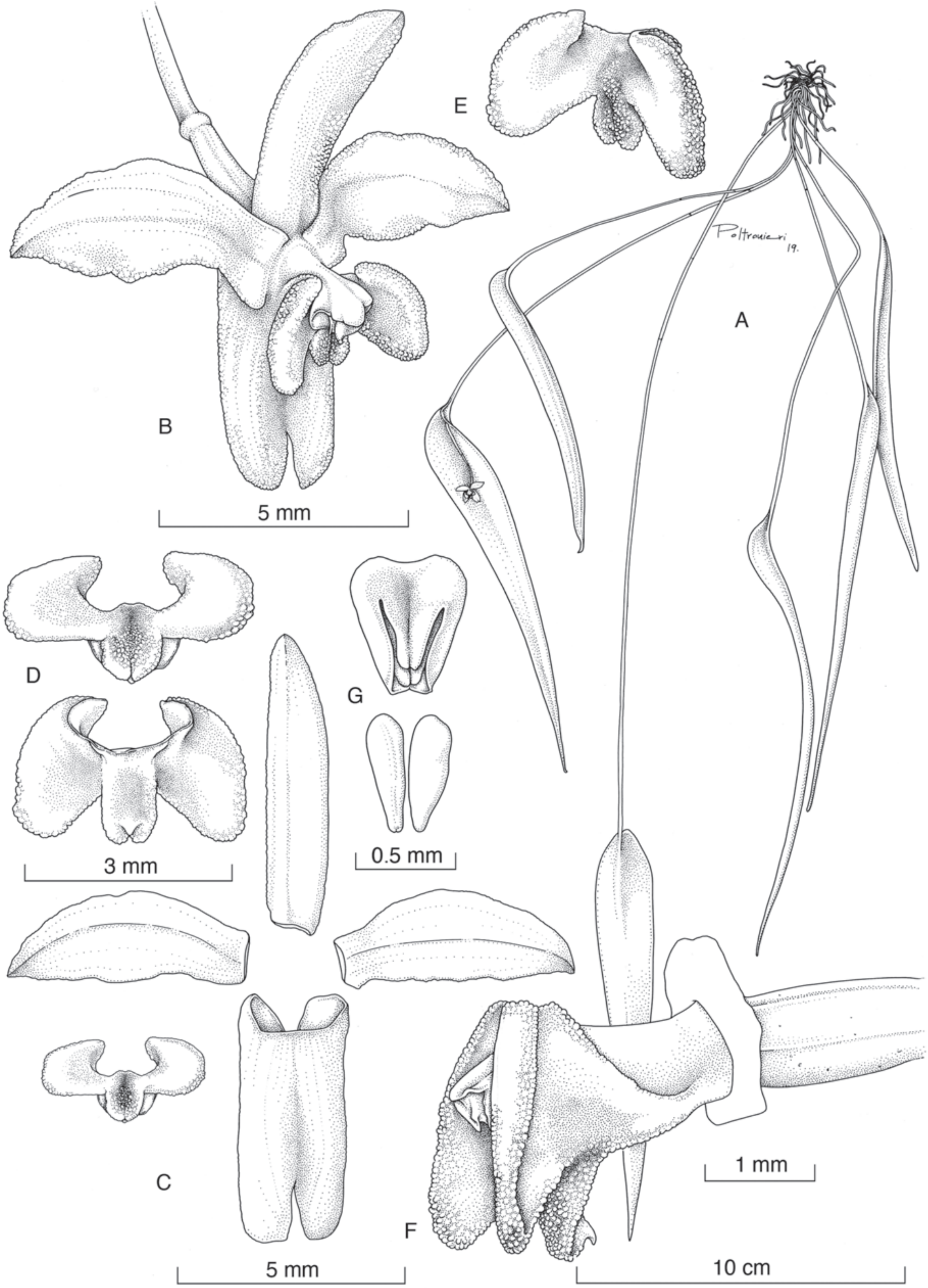


FIGURE 39. *Pleurothallis fantastica* Ames. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in adaxial and abaxial views; **E,** lip, three quarters view; **F,** apex of ovary, column, and lip, lateral view; **G,** anther cap and pollinarium. Drawn by S. Díaz Poltronieri from *Blanco 5087* (JBL).

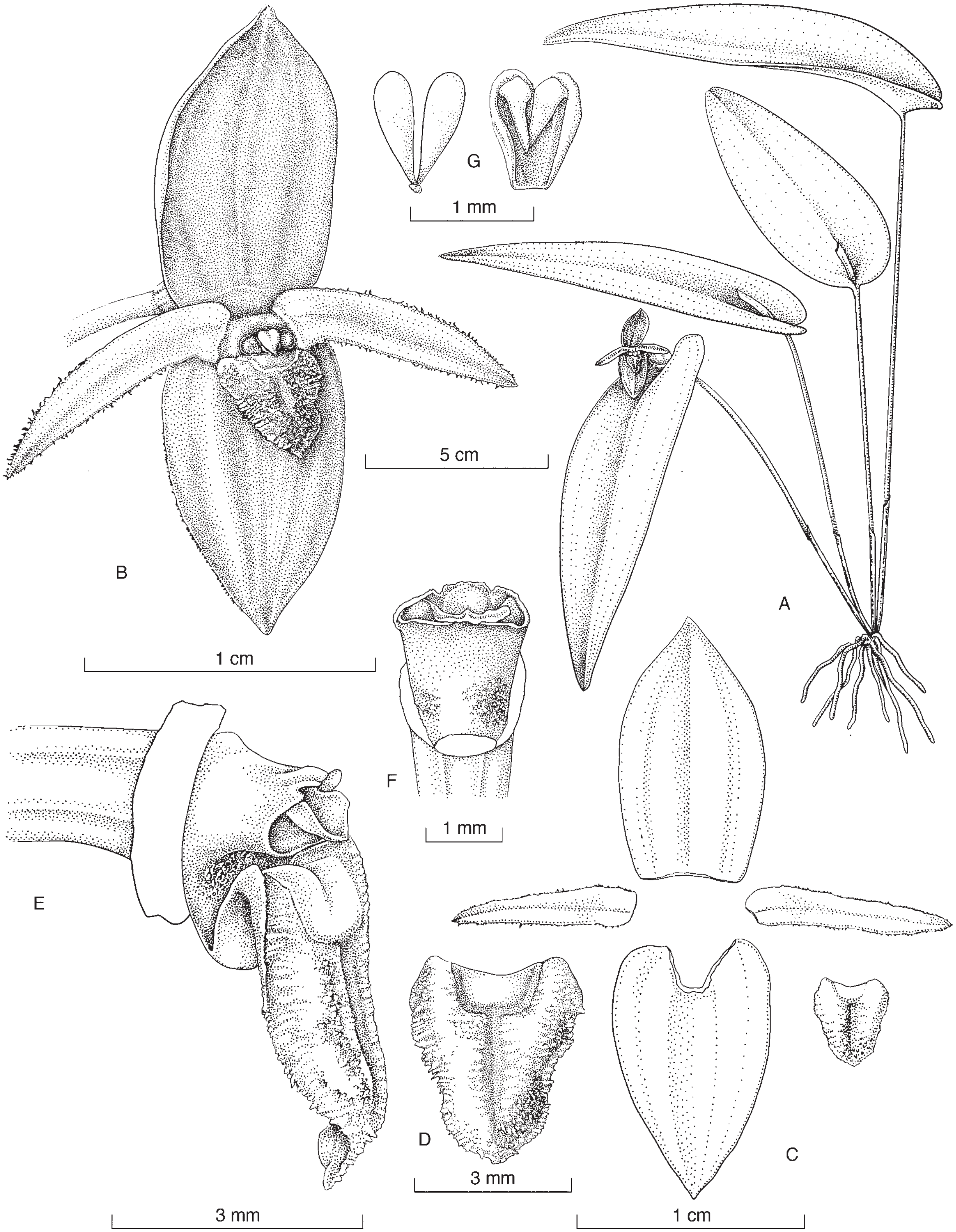


FIGURE 40. *Pleurothallis longipetala* Bogarín & Belfort. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** apex of ovary, column, and lip in three-quarter view; **F,** column, ventral view; **G,** pollinarium and anther cap. Drawn by S. Díaz Poltronieri from *Bogarín 9428* (JBL).

Epiphytic, caespitose, erect to suberect *herb* up to 20 cm tall. *Roots* slender, flexuous, less than 1 mm in diam. *Ramicaul* terete, slender, erect to suberect, up to 15 cm long, enclosed by 1 closely adpressed, tubular, long, acuminate sheath, which covers the first third of the ramicaul, pale green, aging dry-papyraceous, brown. *Leaf* horizontal to subhorizontal, soft coriaceous, narrowly ovate-lanceolate, 9–11 × 2.8–3.1 cm, the base sessile, deeply cordate, the basal margins not overlapping. *Inflorescence* single-flowered, produced in succession and emerging from a papyraceous, suberect spathe, 15–16 mm long, eventually disintegrating with age. *Peduncle* terete, ca. 15 mm long. *Pedicel* ca. 10 mm long. *Ovary* cylindrical, *ca*. 2 mm long. *Flowers* erect, resupinate, with purple sepals, veins dark purple, the petals and lip dark purple, the column whitish green suffused with dark purple in the apical portion. *Dorsal sepal* erect, slightly concave, narrowly ovate-acuminate, acute, 11 × 6 mm, 3-veined. *Lateral sepals* connate into an ovate-acuminate, basally slightly concave synsepal, 11 × 7 mm, the margins slightly reflexed, 5-veined. *Petals* linear-acuminate, acute, serrulate, held horizontally, 7.9–8.6 × 1.6–1.7 mm, 1-veined. *Lip* unguiculate, hinged to the column foot, geniculate, basally bilobulate, thick, fleshy, obtuse, 3.7–3.9 × 3.3 mm, densely verrucose on the adaxial surface, the lamina provided with a basal transversely rectangular glenion, ca. 1 mm long, recessed between the basal lobes of the lip. *Column* short, stout, transversely subrectangular, 2.3–2.5 mm long, the foot ca. 1.5 mm, densely papillose; stigma and anther apical. *Pollinia* 2, narrowly obpyriform, 0.9 mm long, provided with inconspicuous caudicles, and a hard, bubble-like viscidium. Fig. 41A.

Etymology: from the Latin *longipetalus*, “with long petals,” in allusion to the length of the petals, subequal to that of the sepals, which is uncommon in this group of *Pleurothallis* species.

Distribution: known only from Costa Rica, in the Pacific and Caribbean watershed foothills of the north-central Cordillera de Talamanca.

Ecology: epiphytic in premontane rain forest between 1400–2800 m in elevation. The plant has been recorded in flower from September to March.

Distinguishing features: the flat flower, with the sepals not swept back at maturity, the long petals, and the erect lip provided with a transversely rectangular glenion are diagnostic of *P. longipetala*.

Pleurothallis longipetala is similar to *P. luna-crescens*, *P. radula*, and *P. rectipetala*, but it is distinguished from those species by the margins of the sepals not swept back at maturity, the erect lip (instead of reclinate over the synsepal), the distinctly longer petals, and the transversely rectangular glenion of the lip, which is unique to it. The purple or dull-purplish-yellow flowers boldly striped with purple easily separates it from *P. radula*, whose flowers are concolorous yellow, while the almost flat flower (except for the erect lip) distinguishes it at first glance from the crescent moon-shaped flowers of *P. luna-cescens*. The long petals, almost equal in length to the sepals, cannot be mistaken for those of *P. rectipetala*, which are distinctly shorter than the sepals.

Costa Rican material examined: San José: Pérez Zeledón, Rivas, Herradura, Fila Palmito Morado, 9°30'21.74"N, 83°34'05.52"W, 2788 m, colectada por Denis Elizondo, floreció en cultivo en el Jardín Botánico Lankester, 3 Setiembre 2011, *D. Bogarín 9253* (JBL). Map 4.

21. ***Pleurothallis luna-crescens*** Pupulin, J. Aguilar & Mel. Fernández, Lankesteriana 17(2): 158–163. 2017. TYPE: Costa Rica. Cartago: Turrialba, Tayutic, Grano de Oro. On the road to the premontane forest, next to the road between Grano de Oro and Llanos del Quetzal, 2 km after crossing a river with a broken bridge. 9°48'23"N, 83°26'53"W, 1000–1200 m, 30 July 2005, *A. P. Karremans 881 & P. Ferreira* (Holotype: CR; Isotypes: JBL). Fig. 42 (Voucher, *Karremans 881*, JBL).

Epiphytic, caespitose, erect *herb* up to 30 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 7.5–28.0 cm long, ca. 3 mm in diam., pale green, with a basal, tubular, truncate sheath, 2.5–4.2 cm long, and a sub-basal, tubular, obtuse, tight sheath 2.3–5.2 cm long, dry-papyraceous, brown when mature. *Leaf* borne erect at the apex of the ramicaul, becoming subpendent with age, thinly coriaceous, flexible, sessile, lanceolate, acute, shortly subacuminate, 6.5–12.5 × 3.0–5.5 cm, deeply cordate at the base, green, sometimes irregularly mottled with purple along the margins, matte. *Inflorescence* a solitary flower from an erect, rectangular-subclavate, truncate, spathaceous bract 2.2–2.6 cm long, glumaceous, green, becoming brown, dry-papyraceous with age. *Peduncle* terete, ca. 10 mm long, completely hidden by the spathe. *Pedicel* terete, green, to 2.2 cm long. *Ovary* terete, subclavate, 6–7 mm long. *Flowers* spreading, the sepals and petals purple red, the lip dark purple. *Dorsal sepal* incurved, lanceolate, acute, 15.0–16.5 × 6.5–7.0 mm, the margins reflexed, 3-veined. *Lateral sepals* connate into an ovate, obtuse synsepal, the margins slightly reflexed, incurved, 14.8–15.3 × 8.0–8.5 mm, 5-veined. *Petals* narrowly ovate, acute, dentate, 8.7–9.0 × 2.8–3.0 mm, single-veined. *Lip* unguiculate, hinged to the column foot, ovate, basally truncate with obtuse angles, obtuse, minutely apiculate, 4.0–4.5 × 2.2–2.8 mm, minutely papillate; glenion raised on a thick callus on the disc, ca. 0.6 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, ca. 2.0 × 1.3 mm, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subcordate, truncate, 2-celled, ca. 0.9 × 0.7 mm. *Pollinia* 2, narrowly ovate-pyriform, 0.8 mm long, attached to an elliptic viscidium. Fig. 41B–C.

Etymology: from the Latin *luna crescens*, “crescent moon,” in reference to the characteristic shape of the flower seen in profile, due to the strongly reflexed-incurved sepals.

Distribution: known only from the Caribbean slopes of the northern Cordillera de Talamanca, in central Costa Rica.

Ecology: epiphytic on branches in the partial shade of the lower canopy, in lower montane and premontane rain to wet forest at 1000–1650 m in elevation. The species mostly flowers in June–August, with early flowering recorded in February–March.

Distinguishing features: the crescent-shaped, purple flowers with a finely rugulose lip, and the long, strongly dentate petals are distinctive of *P. luna-crescens*.

FIGURE 41. Flowers of *Pleurothallis* species from Costa Rica in the *P. phyllocardia* group. **A,** *P. longipetala* (*Bogarín 9428*); **B–C,** *P. luna-crescens* (*Zúñiga 178*; *Karremans 881*); **D,** *P. mesopotamica* (*Bogarín 8811*); **E,** *P. peculiaris* (*Bogarín 5972*); **F–H,** *P. phyllocardia* (*Bogarín 10664*; *Bogarín 7709*; *Chinchilla 3407*); **I,** *P. pudica* (*Karremans 6249*). Not at the same scale. All the vouchers at JBL. Photographs by F. Pupulin except D–E (D. Bogarín).

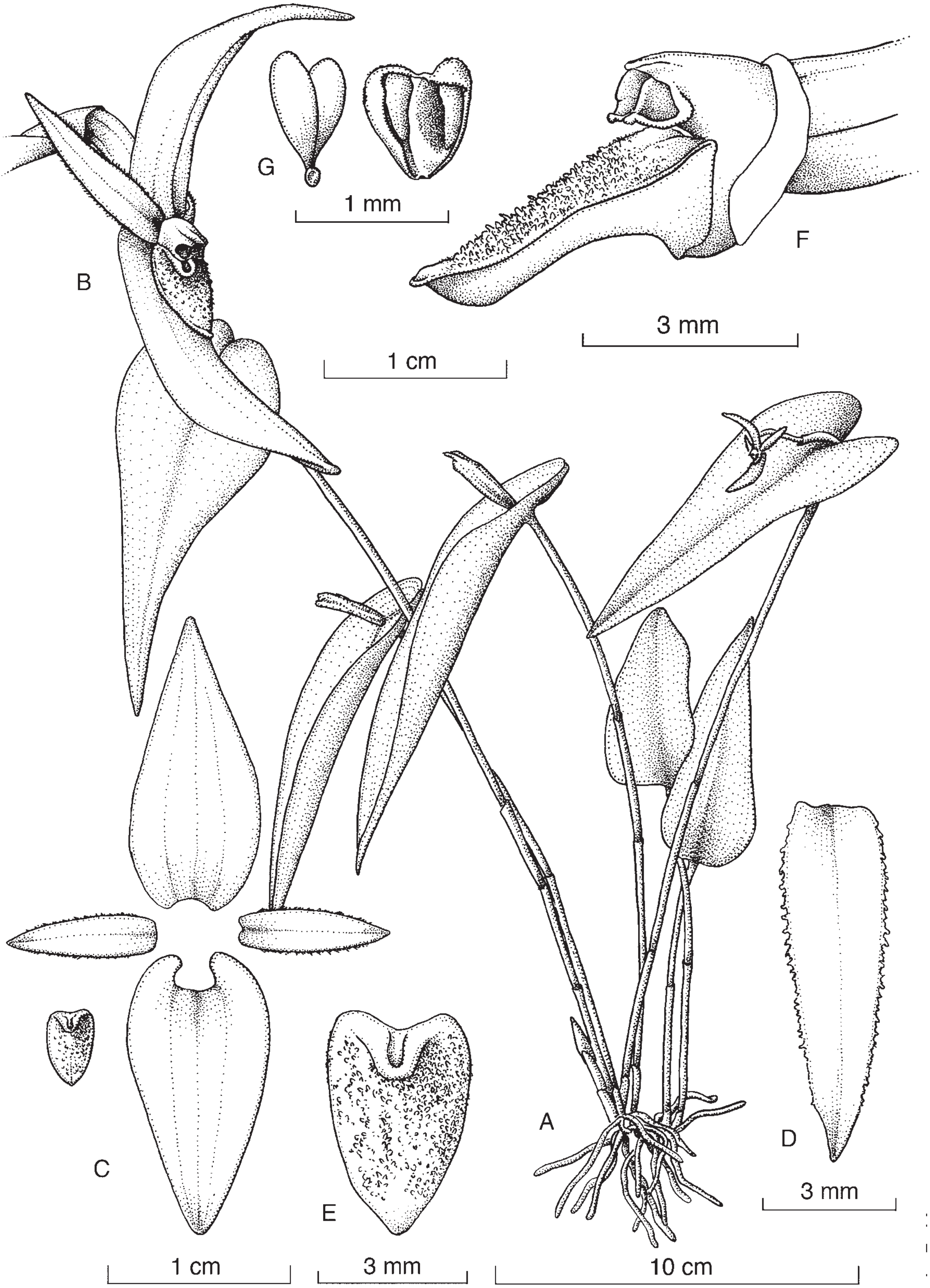


FIGURE 42. *Pleurothallis luna-crescens* Pupulin, J. Aguilar & Mel. Fernández. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** left petal; **E,** lip, adaxial view; **F,** apex of ovary, column, and lip in lateral view; **G,** pollinarium and anther cap. Drawn by S. Díaz Poltronieri from *Karremans 881* (JBL).

Costa Rican material examined: Cartago: Cartago, San Francisco, Navarro, Muñeco, Fincas Loma Verde y Jilguero, road to Alto Belén, between Río Sombrero and Quebrada Patarrá, 9˚46'50.3"N, 83˚54'21.1"O, 1430–1620 m, premontane rain forest, secondary woods and margins of the road, 23 May 2007, *J. D. Züñiga 178, D. Bogarín, M. Bonilla, R. Gómez, R. L. Dressler & R. Trejos* (JBL). Orosi, Tapantí, Parque Nacional Tapantí, sendero Árboles Caídos, 1280 m, epiphytc on low trunks in primary wet submontane forest, 6 Feb. 2000, *F. Pupulin 1981* (USJ). Turrialba, La Suiza, Llanos del Quetzal, ca. 1 km sobre el camino detrás de la Escuela de Kabébata (Alto Quetzal), epífitas en vegetación secundaria, bosque muy húmedo premontano, 9˚46'39.53"N, 83˚24'45.80"W, 1449 m. 22 setiembre 2016, *M. Díaz 279, I. Chinchilla, A. Karremans y G. Rojas-Alvarado* (JBL). Turrialba, La Suiza, Llanos del Quetzal, ca. 1 km on the road behind the School of Kabébata (Alto Quetzal), epiphytic in primary and secondary vegetation, premontane wet forest, 9˚46'43.6"N, 83˚24'41.6"W, 1450 m, 17 Jun. 2011, *A. P. Karremans 4262, M. Fernández & D. Bogarín* (JBL). Turrialba, La Suiza, Llanos del Quetzal, road to Chirripó Abajo, 9˚46'55.4"N, 83˚24'21.0"W, 1411 m, epiphytic in secondary vegetation around the road, premontane wet forest, 17 Jun. 2011, *M. Fernández 461, A. Karremans & D. Bogarín* (JBL). Turrialba, Tayutic, Platanillo. Hillside of the Platanillo River, 9˚49'11"N, 83˚33'37"W, 700–900 m, 30 April 2005, *A. Karremans 801* (JBL). [Turrialba,] Alto Pacuare, epiphyte, purple flowers, alt. 100 m, 21 July 1978, *R. A. Ocampo S. 2363* (CR).

22. **Pleurothallis mesopotamica** Bogarín & Belfort, ***sp. nov.***

TYPE: Costa Rica. Cartago: Cartago, San Francisco, Muñeco, Navarro, 3 km al sur de la iglesia de Navarro, entre Río Sombrero y Quebrada Patarrá, 9˚45'54.84"N, 83˚54'22.51"W, 1579 m, bosque pluvial premontano, “ad sylva secundaria et primaria prope oppidum Navarro ad margines viam ubi Standley probabiliter *Trichosalpinx navarrensis*, *Eurystyles standleyi* et *Coccineorchis navarrensis* invenit,” 12 Mayo 2011, *D. Bogarín 8811, M. Fernández, R. Gómez, A. Karremans & C. Smith* (Holotype: JBL). Fig. 43 (Voucher, Bogarín 8811, JBL). Map 4.

Pleurothallide rectipetala Ames *et* C. Schweinf. *plerumque similis, bractea spathacea suberecta, flore atropurpureo, petalis subfalcatis marginibus integris labelloque verrucoso recedit; a Pleurothallide radula* Luer *etiam confert, flore arropurpureo labello paulo verrucoso dignoscenda*.

Epiphytic, caespitose, erect *herb*, up to 25 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 8–25 cm long, 2.5–3.0 mm in diam., pale green, with 2 basal, tubular, obtuse, dry-papyraceous sheaths,17.5–42.5 mm long, the second longer than the basal one, brown. *Leaf* borne at the apex of the ramicaul, horizontal to subreclinate toward the stem, thinly coriaceous, flexible, sessile, narrowly ovate, acuminate, 12–16 × 3.5–5.0 cm, cordate at the base, the basal lobes overlapping, pale green with scattered purple spots, matte. *Inflorescence* a solitary flower, born from a suberect, oblanceolate, rounded to subtruncate, spathaceous bract to 11 mm long, becoming brown, dry-papyraceous with age. *Pedicel* terete, green, to ca. 15 cm long, completely hidden within the spathe. *Ovary* terete, curved, less than 5 mm long and 2 mm wide. *Flowers* erect, spreading-reflexed; the sepals purple becoming darker to the distal portion, with whitish margins and tip; the petals dark purple; the lip dark purple with light-purple glenion; the column white, with the margins of the clinandrium light purple, the anther cap light yellow. *Dorsal sepal* erect, broadly ovate, obtuse to subacute, 1.2–1.3 × 0.9 cm, the margins reflexed, 7-veined. *Lateral sepals* connate into a broadly ovate, obtuse to subacute, synsepal, the margins reflexed, 1.1 × 0.9 cm, each half 4-veined. *Petals* subfalcate, acute, with entire margins, reflexed at complete anthesis, 6–7 × 2 mm, 1-veined. *Lip* unguiculate, hinged to the column foot, thick and fleshy, ovate-peltate, basally truncate with obtuse angles, obtuse-rounded,the sides smooth, 4 × 3 mm, slightly verrucose throughout; glenion raised on a thick callus on the disc, less than 1 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, 2.4 × 1.3 mm, with a short foot, ca. 1 mm long; the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subcordate, subtruncate, two-celled, 0.9 × 0.7 mm. *Pollinia* 2, narrowly ovate, attached to an elliptic viscidium. Fig. 41D.

Etymology: from the Greek μέσος, “mésos,” meaning between or in the middle of, and ποταμός (potamós), “river,” alluding to the region where the type specimen was collected, between the Sombrero and Patarrá rivers in central Costa Rica.

Distribution: known only from Costa Rica.

Ecology: the only specimen known was found growing as an epiphyte in premontane moist forest at an elevation of 1579 m. The flowering has been recorded in January and February.

Distinguishing features: *Pleurothallis mesopotamica* is very similar to *P. rectipetala* but can be distinguished by the suberect spathe (vs. erect), the dark purple flowers (vs. dull purple flowers with yellow near the margins), the subfalcate petals with entire margins (vs. linear-lanceolate, minutely denticulate petals), and the verrucose lip (vs. irregularly papillose lip). It could be also compared with *P. radula*, from which it differs in the dark purple flowers (vs. yellow, rarely suffused with pink) and the slightly verrucose lip (vs. densely packed with shortly tuberculate-dentate, irregular projections).

23. ***Pleurothallis peculiaris*** Luer, Selbyana 3(1–2): 158–159. 1976. TYPE: Panama: Veraguas: epiphytic in the cloud forest near the continental divide above Santa Fé, alt. ca. 700 m, Sept 1976, *C. Luer & R. L. Dressler 1142* (Holotype: SEL). Fig. 44 (Vouchers, *Solís 25* and *Bogarín 5972*, CR, JBL).

Epiphytic, caespitose, arching to pendent *herb* up to 40 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 15–40 cm long, ca. 2 mm in diam., pale green, with 2 basal, short, tubular, obtuse sheaths, and

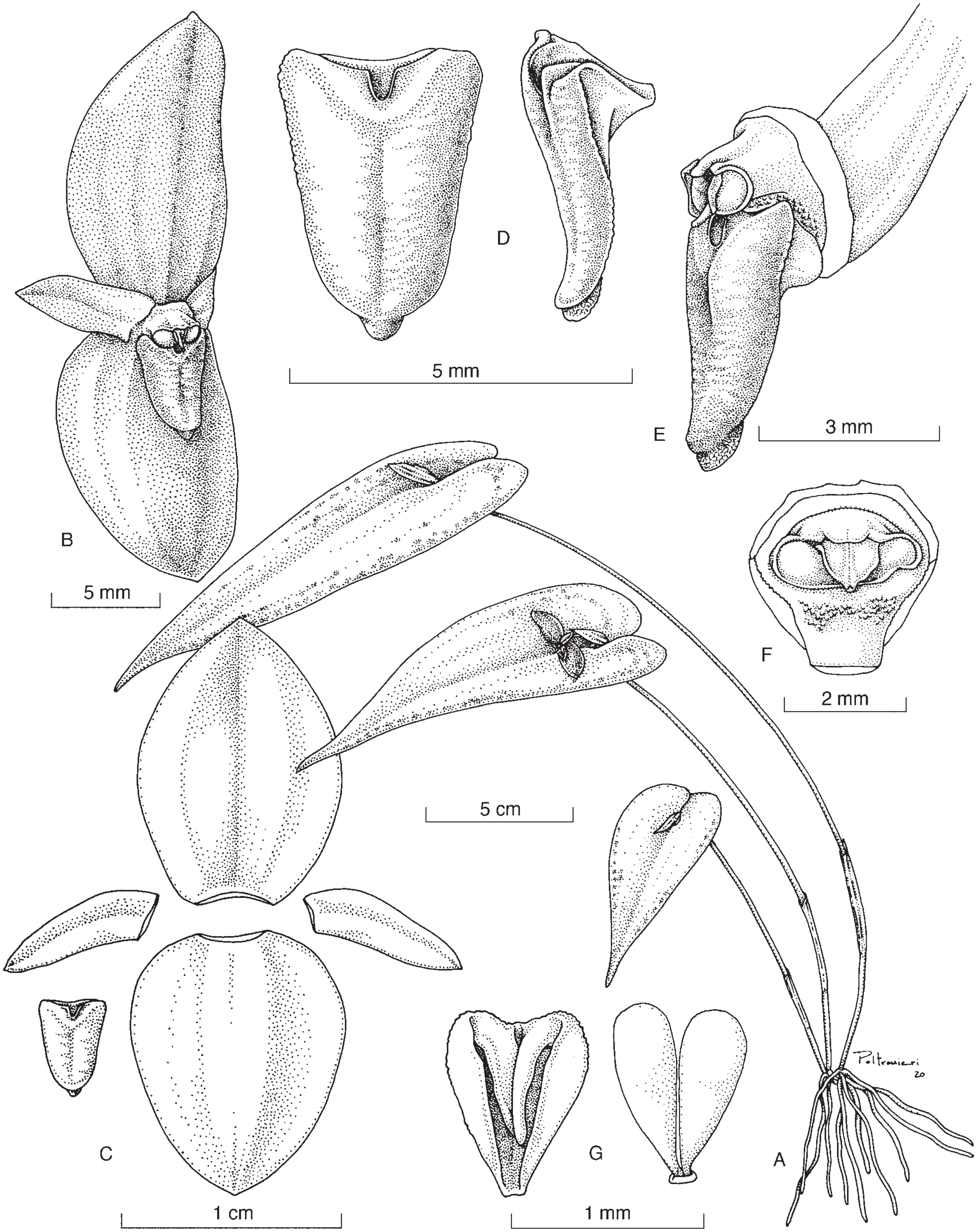


FIGURE 43. *Pleurothallis mesopotamica* Bogarín & Belfort. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip in adaxial and lateral views; **E,** apex of ovary, column, and lip, lateral view; **F,** column, frontal view; **G,** anther cap and pollinarium. Drawn by S. Díaz Poltronieri from *Bogarín 8811* (JBL).

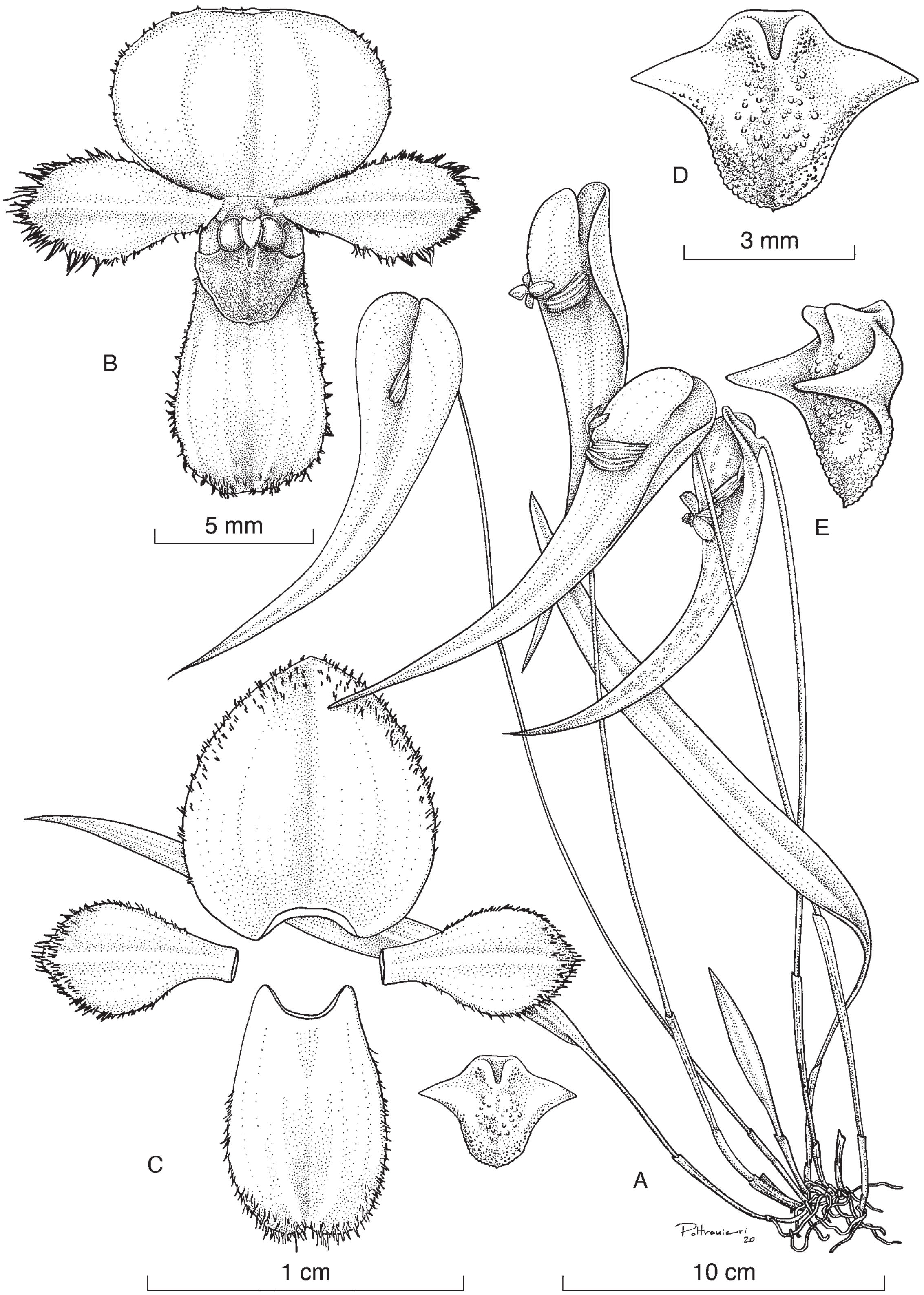


FIGURE 44. *Pleurothallis peculiaris* Luer. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** lip, three quarters view. Drawn by S. Díaz Poltronieri from *Solís 25* and *Bogarín 5972* (CR, JBL).

another tubular, tightly adpressed sheath below the middle, the lower ones 7–16 mm long, the upper one to 55 mm long, the sheaths dry-papyraceous, brown. *Leaf* borne at the apex of the ramicaul, sessile, deflexed, rigidly coriaceous, concave, incurved, narrowly ovate, attenuate, tapering to an acuminate, tri-denticulate apex, the base deeply cordate with the lobes suberect, overlapping, green to sparsely blotched with purple, matte, 12–15 × 3–3 cm. *Inflorescence* a fascicle with a solitary flower, produced from an erect, subrrectangular, obliquely truncate, spathaceous bract emerging at the base of the leaf, ca. 10 mm long, brown, dry-papyraceous; the peduncle terete, to 15 mm long. *Pedicel* terete, green, 12 mm long, completely hidden by the spathe. *Ovary* terete, to 7 mm long. *Flowers* nonresupinate, spreading, the margins of the synsepal reflexed, the sepals translucent yellow, striped and boldly suffused with red along the veins, the petals purple, with white hairs along the margins, the lip dark purple, the column rose-purple. *Dorsal sepal* erect, broadly ovate to suborbicular, obtuse to subrounded, the margins and the apical part pilose-hirsute, 9 × 8 mm, 3-veined. *Lateral sepals* connate into an oblong to narrowly obovate, rounded, minutely emarginate-retuse synsepal, the margins pilose, reflexed at the middle, 8 × 5 mm, each half 2-veined. *Petals* obovate-spatulate, obtuse, glandulose-papillose, the margins long-hirsute, with a thickened, rounded, low keel along the vein, 6.0 × 3.5 mm, 1-veined. *Lip* fleshy, adnate to the base of the column, subrhombic to trapezoidal-sagittate, 3-lobed, obtuse to rounded, the margins minutely erose, 3.5 × 5.0 mm when spread, the lateral lobes digitate, acuminate, inserted below or at the middle, spreading to retrorse, the midlobe triangular, verrucose, with a minute apiculum, the disc with two mamillate, erect callosities flanking the glenion. *Column* rectangular in section, stout, dilated distally, dorsoventrally flattened, ca. 2.5 × 4 mm, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, narrowly ovate, 2-celled. *Pollinia* 2, narrowly ovoid, attached to an elliptic viscidium. Fig. 41E.

Etymology: from the Latin *peculiaris*, "special, unusual, out of the ordinary," in reference to the several features that this species does not share with other close species of *Pleurothallis*.

Distribution: Costa Rica and Panama.

Ecology: epiphytic in primary forest in the very wet region of the lower Cordillera de Talamanca, at 700–900 (1300) m in elevation, on the low and medium Caribbean watershed of the Cordillera de Talamanca. Flowering was recorded from July to December.

Distinguishing features: the long, narrow, acuminate leaves, the erect spathe and the nonresupinate flower with the margins of the sepals pilose, the rounded dorsal sepal much broader than the synsepal, and the spathulate petals with very long, white hairs along the margins make this species unmistakable.

Florally, *Pleurothallis peculiaris* is highly anomalous in the Pleurothallid flora of Costa Rica. The long-pilose margins of the sepals and petals on a nonresupinate flower, the suborbicular dorsal sepals that largely exceed in width the synsepal, the spathulate petals, and the rhombic lip have apparently no close relatives in the flora of the country. Vegetatively, however, *P. peculiaris* is close to other species of the *Pleurothallis phyllocardia* group, with lanceolate leaves reclinate toward the stems, deeply cordate at the base, without prominent midvein and matte on the upper surface, provided with an erect spathaceous bract to protect the developing bud. Evidently, the treatment of a flora delimited by political boundaries is not the best strategy to understand the continuum of variation in morphological features that link the taxa to each other in a coherent picture that reflects evolutionary trends in a given group of plants. Comparing it with the much broader range of morphological variations that the *P. phyllocardia* group presents in the Andes, where it is most diverse, we have no doubts that *P. peculiaris* is a South American component of the group in our flora. Such a relationship is nevertheless difficult to envision when this peculiar species is compared, strictly, only with members of the group in the flora of Costa Rica.

Costa Rican material examined: Limón: Talamanca, Fila de exploración minera entre Río Sukut y Río Carbri. Muragubishi. 9°22'50"N, 82°56'50"W, 700 m, 14 Jul 1989, *F. Solís 25, G. Herrera & A. Chacón* (CR). Talamanca, R. I. [Indigenous Reserve] Talamanca. Cordillera de Talamanca. Alto Urén. Casa de don Gabriel el Sukia. 9°22'40"N, 82°59'00"W, 700–900 m, 21 Sep 1994, *G. Gallardo 275 & E. Lépiz* (CR). Map 4.

24. ***Pleurothallis phyllocardia*** Rchb.f., Beitr. Orchid.-K. C. Amer. 97. 1866. *Humboltia phyllocardia* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 668. 1891. *Zosterophyllanthos phyllocardius* (Rchb.f.) Szlach. & Marg., Polish Bot. J. 46(2): 120. 2001. *Acronia phyllocardia* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 173. 2005. TYPE: Costa Rica. Desengaño, 31 May 1858, *H. Wendland s.n.* (Holotype: W; drawing of type: AMES). Fig. 45 (Voucher, *JBL-01967*, JBL).

Epiphytic, caespitose, erect to suberect *herb* to 30 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 16–30 cm long, 1–2 mm in diam., yellowish green, provided with a tubular, short, truncate sheath to 2.5 cm long at the base, and a longer, tubular, tightly adpressed, obtuse sheath below the middle, to 3.7–4.5 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming subpendent with age, coriaceous, sessile, ovate, acute, 9.0–13.5 × 3.5–7.0 cm, deeply cordate at the base, grass green, matte, becoming dull green with age. *Inflorescence* a solitary flower, from an erect spathaceous bract 1.4–1.6 cm long, green, dry-papyraceous when mature, eventually dissolving with age. *Pedicel* terete, pale green, bending down throughout anthesis, 13–16 mm long. *Ovary* subclavate, terete, 4–6 mm long. *Flowers* solid dark purple. *Dorsal sepal* narrowly ovate, acute, minutely papillose on the adaxial surface, reflexed, 13–14 × 5–7 mm, 5-veined. *Lateral sepals* connate into a narrowly ovate, acute synsepal, minutely papillose on the adaxial surface, reflexed, 10–13 × 4–5 mm, 5-veined. *Petals* linear-oblong,

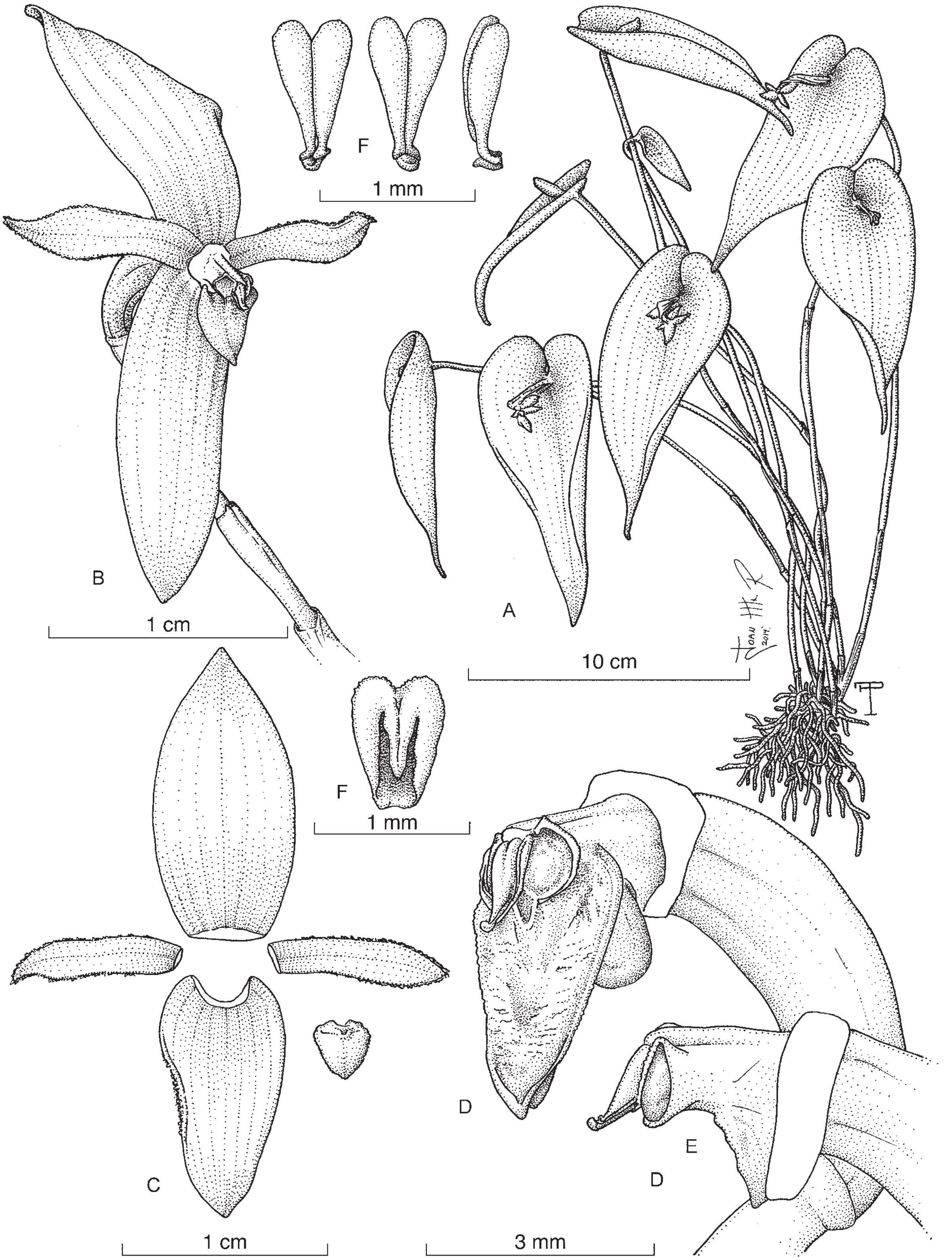


Figure 45. *Pleurothallis phyllocardia* Rchb.f. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** apex of ovary, column, and lip in three-quarter view; **E,** column, lateral view; **F,** anther cap; **G,** pollinarium (three views). Drawn by F. Pupulin and J. M. Ramírez from *Bogarín 7355* (JBL).

subfalcate, acute, bent backward throughout anthesis, the margins ciliate, 8–9 × 1–2 mm, 3-veined. *Lip* unguiculate, hinged to the column foot, geniculate, deltoid, basally bilobulate, obtuse, 3.5 × 2.5 mm, verrucose on the adaxial surface of the apical half, minutely papilose on the margins and around the glenion; glenion recessed between the basal lobes of the lip, ca. 1 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 2 × 1 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* obcordate, truncate, bilobed at the base, 2-celled. *Pollinia* 2, narrowly oblong-pyriform, attached to an elliptic viscidium through a short, cylindric caudicula. Fig. 41F–H.

Etymology: from the Greek words φῠ́λλον (*phúllon*), “leaf,” and κᾰρδῐ́ᾱ (*kardíā*), “heart,” in reference to the heart-shaped leaves of the species.

Distribution: known from southern Costa Rica and western Panama at 1300–2500 m in elevation.

Ecology: in Costa Rica, populations of *Pleurothallis phyllocardia* have been recorded from the premontane and lower montane wet forest of the Cordillera Volcánica Central and Cordillera de Talamanca, where the species inhabits both watersheds at elevations of 1200 to 2300 m. Plants have been recorded in flower from October to February, and from April to June.

Distinguishing features: *Pleurothallis phyllocardia* is recognized by the glabrous flowers born from an erect bract with the peduncle bent downward, reclining the flowers toward the leaves, and the linear-oblong petals. The most similar species are *P. pudica* and *P. triangulabia*, but the former has a much smaller habit, rounder, flat flowers with the dorsal sepal subequal to narrower than the synsepal, shorter, elliptic petals, and a transversely rectangular lip, while the latter has pubescent-hirsute flowers, with reflexed margins of the sepals, and angulate deflexed shape of the petals.

Costa Rican material examined: Cartago: Jiménez, Pejibaye, Fila Alto Velo de Novia, 9.7736111, -83.7833333, 1300–1700 m, 22 Apr 2006, *J. F. Morales Quirós 13806 & D. Santamaría* (CR). Jiménez, Pejibaye, Fila Alto Velo de Novia, 9.7736111, -83.7833333, 1300–1700 m, 22 Apr 2006, *J. F. Morales Quirós 13806 & D. Santamaría* (CR). Paraíso, Orosi, P. N. Tapantí, entre Quebrada Segundo y Patillos, 9.7583333, -83.7861111, 1300–1400 m, 17 June 2005, *J. F. Morales Quirós 13188* (CR). Paraíso, Orosi, P.N. Tapantí-Macizo Cerro de la Muerte. Camino principal que conduce a las instalaciones del ICE. Bosque húmedo premontano, 9.7500000, -83.7833333, ca. 1400 m, 27 Apr 2007, *A. Quesada Hernández 141* (CR). Orosi, Parque Nacional Tapantí, en árboles caídos en sendero, 1280 m, 6 Feb. 2000, *F. Pupulin 1981* (JBL). Turrialba, Tayutic, Vereh, siguiendo la fila entre Ríos Vereh y Jicotea, 9.7750000, -83.5444444, 26 Jul 1995, *G. Herrera 8121 & A. Cascante Marín* (CR). Turrialba, Tayutic, Grano de Oro. Moravia de Chirripo, 9.8194444, -83.4583333, 1110 m, 29 Jun 1993, *P. Campos 87* (CR). Turrialba, Tayutic, La Laguna, Quetzal. Grano de Oro. Moravia de Chirripó, Area protegida R.I. Chirripó, 9.7972222, -83.4305556, 1400 m, 20 Jun 2007, *P. Campos 119* (CR). **Heredia:** Barva, San José de la Montaña, Forêts du Rancho Flores. Massif du Barva, 10.1012950, -84.1199790, 22 Feb 1890, *H. F. Pittier 3055* (CR). San Rafael, camino al Monte de La Cruz, desviación al Residencial El Tirol, orillas del Río Segundo, 10˚04'27"N, 84˚05'08"W, 1800 m, 17 Apr. 2003, *D. Bogarín 169* (JBL). Santa Bárbara, Santo Domingo, Pasture above Los Cartagos, slopes of Barva Volcano, 10.1497750, -84.1529560, 31 Aug 1969, *R. W. Lent 1775* (CR). Sarapiquí, La Virgen, P.N. Braulio Carrillo, Primary forest between Río Peje and Río Sardinalito. Atlantic slope of Río Volcán Barva, 10.2833333, -84.0666667, 5 Apr 1986, *M. H. Grayum 6791 & A. C. Jermy* (CR). **Limón:** Talamanca, Bratsi, Amubri, Alto Lari, Kivut. Cuenca superior del Rio Dapari. R.I. Talamanca. 9.4041667, -83.0916667, 1200 m, 9 mar 1992, *G. Herrera 5252* (CR). Talamanca, Bratsi, P.N. La Amistad Caribe, Sector La Fila, 300 m antes de union Quebrada Kuisa con R. Lori. Entre Ujarras-San Jose Cabecar, 9.3597222, -83.2291667, 1800–1843 m, 21 Feb 2007, *D. Solano 3916 & A. Rodríguez G.* (CR). Talamanca, Bratsi, P.N. La Amistad Caribe, Valle del Silencio, dentro del jardín. Colectado en bosque, 9.1608333, -82.9844444, 2500–2600 m, 25 Jun 2003, *E. Alfaro 4687, M. Alfaro & R. Delgado* (CR). Talamanca, Parque Internacional La Amistad (PILA), sector Altamira, Valle del Silencio, entre cerro Quemado y la División Continental, epífitas en bosque primario, bosque pluvial montano, 2200–2500 m, 17 Sept. 2014, *M. Fernández 936, M. Díaz, C. Godínez, A. P. Karremans, L. Oses, J. Ramírez & D. Villalobos* (JBL). Talamanca, Telire, P.I. La Amistad. Cordillera de Talamanca. Fila arriba unión de ríos Lori y Coén. Entre Ujarrás y San José Cabécar, en sotobosque, 9.4097222, -83.2277778, 29 Mar 1993, *A. Fernández 914 & W. Gamboa* (CR). Talamanca, Telire, P. I. La Amistad. Cuenca del Sixaola. Bratsi, sendero Transtalamanca. Entre Ujarrás y San José Cabécar. Alrededores del Río Lori, 9.3537800, -83.2220000, 25 Feb 2007, *A. Rodríguez González 10810 et al.* (CR). Valle La Estrella, Fila Matama. Ca. 11 km SW del Pueblo de Aguas Zarcas, 9.8018056, -83.1747992, 1300–1400 m, 27 Oct 2007, *A. Rodríguez G. et al. 11538* (CR). **Puntarenas:** Biolley. Parque Internacional La Amistad-Pacífico, sendero hacia Valle del Silencio, después del Cerro Quemado, bosque pluvial montano bajo, bosque primario. Terrestre, a media luz, en suelo drenado, pedregoso, 9˚04'10.88"N, 82˚58'45.77"O, 2220 M, 30 Jan 2018, *I. Chinchilla 3546, J. E. Jiménez Vargas, J. Porras Quirós & M. Cedeño Fonseca* (JBL). Buenos Aires, Potrero Grande, Tres Colinas. 2–3 km de Tres Colinas. Cercanías del sendero a Cerro Kámuk, Herbazal arbolado de 5–15 m, 9.1381597, -83.0701089, 2000–2100 m, 28 Feb 2008, *D. Solano 5224, D. Santamaría & N. Veas Ayala* (CR). Buenos Aires, Potrero Grande, Altamira, Parque Internacional La Amistad, Sector Altamira, Sendero al Valle del Silencio, Cerro Frantzius, bosque pluvial montano bajo, 9˚03'31.8"N, 82˚59'10.6"W, 2081 m, 30 Aug. 2011, *D. Bogarín & A. Karremans 9090* (JBL); same locality and date, *D. Bogarín & A. Karremans 9134* (JBL). Coto Brus, Parque Pittier, June 1995, *G. Carnevali s.n.* (JBL). Coto Brus, Pittier, Z.P. Las Tablas, Fila del Cerro Gemelo, cerca Finca Chinchilla, 9.0347222, -82.9336111, 2100 m, 17 Sep 1996, *J. F. Morales Quirós 5813* (CR). Coto Brus, Parque Pittier, June 1995, *G. Carnevali s.n.* (JBL). Coto Brus, P.N. La Amistad Pacifico, Estación Pittier, 9.0401286, -82.9610786, 1550–1900 m, 8 Jun 1995, *A. Angulo 337* (CR). Coto Brus, Sabalito, P.I. La Amistad, Z. P. las Tablas, E.B. Las Alturas de Coton, 8.9500000, -82.8325000, 8 Jul 1994, *W. J. Kress 94-3891 & R. Calderón* (CR). Coto Brus, Sabalito, P.I. La Amistad, Z. P. Las Tablas, forested upper slopes of Cerro Burú, Oak forest with *Chusquea* understory, near Quebrada, 9.0000000, -82.8166667, 20 Aug 1983, *G. Davidse 23793 et al.* (CR). Coto Brus, Sabalito, Z.P. Las Tablas, Sendero a Cerro Echandi. Bosque primario, 8.9864814, -82.8199911, 2180–2230 m, 19 Nov 1997, *B. Gamboa R. 1955* (CR). Parrita, Sector El Chayote, entrando por Lourdes, Chirraca Abajo, de Chirraca Abajo 1 km SO, 9.6010836, -84.3522081, 2050 m, 16 Aug 2000, *A. Rodríguez G. 6185 & V. Ramirez* (CR). **San José:** Dota, Copey, R. F. Los Santos Pacífico, Providencia. Zapotal. Camino principal a la casa, 9.5372222, -83.8383333, 21 Aug 2003, *S. Lobo Cabezas 558 & A. Ruiz-Boyer* (CR). Pérez Zeledón, R.F. Los Santos, Páramo, 9.5038889, -83.8194444, 1700–1800 m, 8 Mar 2001, *A. Quesada 557* (CR). Pérez Zeledón, R.F. Los Santos, Páramo, Río Savegre, sendero a Catarata Escondida, 9.5416667, -83.8166667, 2100–2200 m, 22 Jun 2004, *J. F. Morales Quirós 10828* (CR). **Without collecting data:** *JBL-08730* (JBL). Map 5.

25. ***Pleurothallis pudica*** Pupulin, J. Aguilar & M. Díaz, Lankesteriana 17(2): 154. 2017. TYPE: Costa Rica. San José: Pérez Zeledón, Paramo, Los Ángeles, sobre el camino a San Gerardo de Dota, montañas al norte del río División, en línea con el centro de Los Ángeles, 1700 m, 9˚29'55"N, 83˚47'46"W, bosque pluvial premontano, terrestre a orillas del camino dentro del bosque, con 29 mayo 2014, *A. P. Karremans 6249, G. Meza y L. Oses* (Holotype: JBL; Isotypes: JBL). Fig. 46 (Voucher, *Karremans 6249*, JBL).

Epiphytic, caespitose, erect *herb* to 27 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 16.0–26.5 cm long, 0.15–0.20 cm in diam., pale green, provided with 2 basal, tubular, obtuse sheaths of different size, the lower one loose, the upper tightly clasping, 1.2–1.3 and 1.5–2.0 cm long, and a sub-basal, tubular, obtuse, tight sheath 3.8–4.5 cm long, the sheaths dry-papyraceous, brown. *Leaf* borne at the apex of the ramicaul, reclinate toward the stem, thinly coriaceous, flexible, sessile, ovate, acute, shortly subacuminate, 5.3–8.2 × 3.3–5.0 cm, deeply cordate at the base, the basal lobes sometimes overlapping, green, matte. *Inflorescence* a solitary flower, from an erect, rectangular-clavate, truncate, spathaceous bract 1.1–2.2 cm long, glumaceous, green, becoming brown, dry-papyraceous when mature. *Pedicel* terete, green, to 2.2 cm long. *Ovary* terete, curved-geniculate, 6–7 mm long. *Flowers* spreading, reclined toward the leaf, nonresupinate, the sepals purple red, the petals and lip dark purple, pubescent-tomentose abaxially. *Dorsal sepal* erect, elliptic-lanceolate, acute, 9–10 × 4.5–5.0 mm, 3-veined, pubescent-tomentose, more densely so toward the apex, the trichomes white, translucent. *Lateral sepals* connate into an ovate, subobtuse synsepal, the margins slightly reflexed, pubescent-tomentose, distinctly shorter than the dorsal sepal, 7.0 × 4.5 mm, 5-veined. *Petals* narrowly lanceolate-ligulate, subporrect, acute, ciliate, 7.0 × 1.8–2.0 mm, 1-veined. *Lip* unguiculate, hinged to the column foot, strongly geniculate, broadly ovate-triangular, basally truncate with obtuse angles, broadly obtuse, minutely apiculate, the margins glandulose, the basal margins erect, 2.3 × 3.0 mm, covered with coarse papillae at the base; glenion raised on a thick callus on the disc ca. 0.4 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, ca. 3.5 × 3.0 mm, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subcordate, truncate, 2-celled, ca. 0.8 × 0.6 mm. *Pollinia* 2, narrowly ovate-pyriform, 0.8 mm long, attached to an elliptic viscidium. Fig. 41I.

Etymology: from the Latin *pudicus*, "chaste, modest, shamefaced," in reference to the habit of turning the face of the flower toward the leaf, hiding it from the view of the observer.

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

Ecology: the only known specimen was found growing among mosses on a road cut within a montane forest at about 1700 m in elevation. Flowering occurs at least in June and July.

Distinguishing features: *Pleurothallis pudica* is easily recognized among the species of the group by the tomentose flowers facing down and reclinate over the leaf.

Pleurothalis pudica is close to *P. scitula* from Panama, another member of the *P. phyllocardia* group that is currently known only from the slopes of Cerro Hornito, in the western region of Chiriquí. Luer (1977) compared *P. scitula* with *P. phyllocardia*, noting that the flowers are pubescent and not deflexed, but facing straight outward. *Pleurothalis scitula* mainly differs from *P. pudica* for the resupinate flower (vs. nonresupinate) facing outward (vs. facing the leaf), yellow with bold red stripes (vs. concolorous dark purple), the shorter and broader sepals, and the ovate lip (vs. triangular-sagittate).

26. ***Pleurothallis radula*** Luer, Selbyana 5(2): 177–178. 1979. *Zosterophyllanthos radula* (Luer) Szlach. & Marg, Polish Bot. J. 46(2): 120. 2001[2002]. *Acronia radula* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 179. 2005. TYPE: Costa Rica. [Cartago]: terrestrial and epiphytic in cloud forest south of Cartago near San Cristobal, alt. ca. 1900 m, 22 Sept. 1979, *C. Luer 4251, J. Luer & K.S. Walter* (Holotype: SEL). Fig. 47 (Voucher, *Pupulin 8129*, JBL).

Epiphytic, rarely terrestrial, caespitose, erect *herb*, up to 50 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 6–50 cm long, 1–3 mm in diam., pale green, with 2 basal, tubular, obtuse sheaths, 0.5–2.5 cm long, and a longer, sub-basal, tubular, obtuse, tight sheath to 6.5 cm long, glumaceous, pale green, sometimes spotted purple when young, aging dry-papyraceous, brown. *Leaf* borne at the apex of the ramicaul, horizontal to deflexed toward the stem, thinly coriaceous, flexible, sessile, lanceolate to ovate, acute to shortly acuminate, 8–19 × 4–6

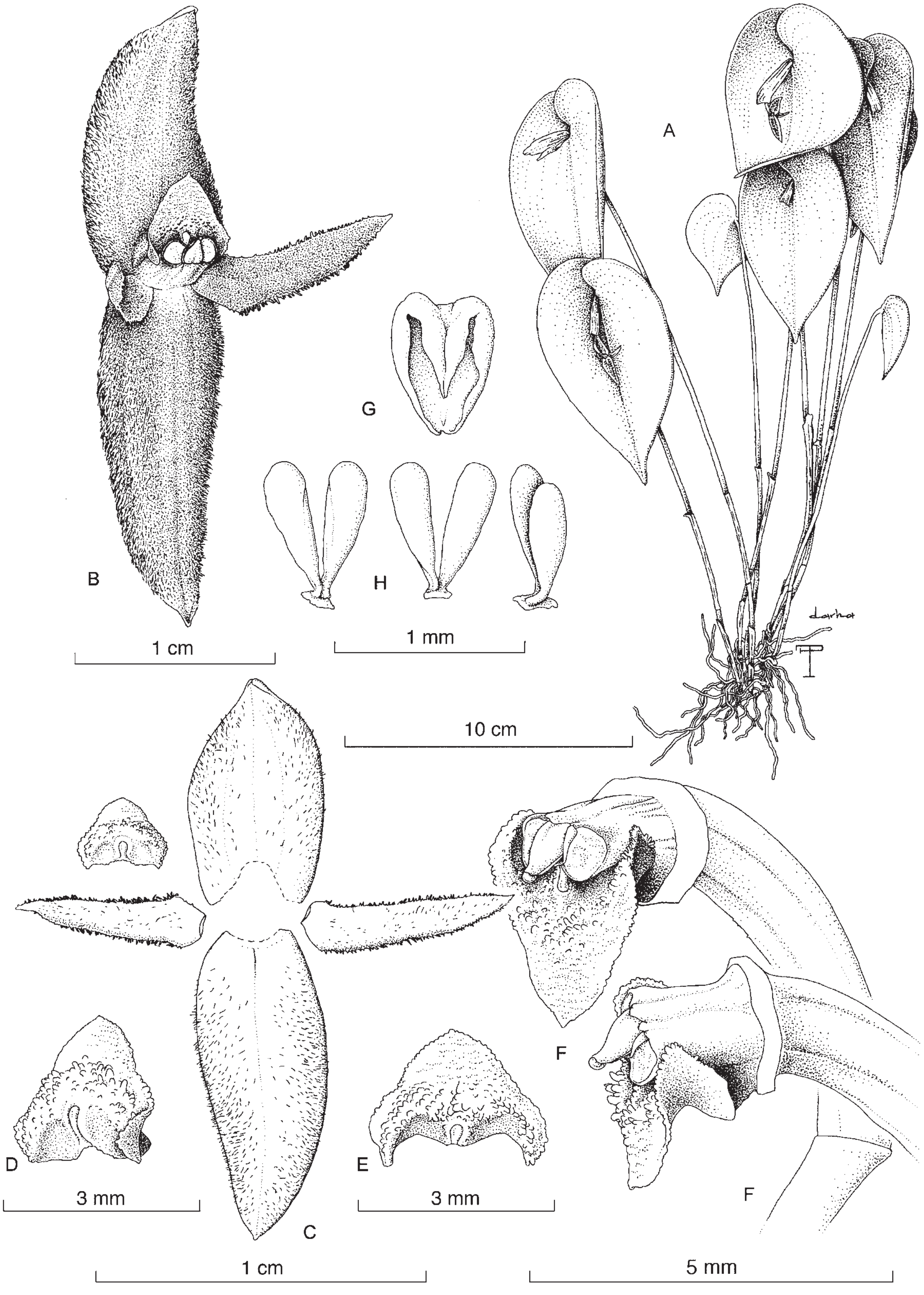


FIGURE 46. *Pleurothallis pudica* Pupulin, J. Aguilar & M. Díaz. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, three-quarter view; **E,** lip, adaxial view; **F,** apex of ovary, column, and lip in three-quarter and lateral views; **G,** anther cap; **H,** pollinarium (three views). Drawn by F. Pupulin and D. Solano Ulate from *Karremans 6249* (JBL). Reproduced with permission from the Editor of *Lankesteriana*.

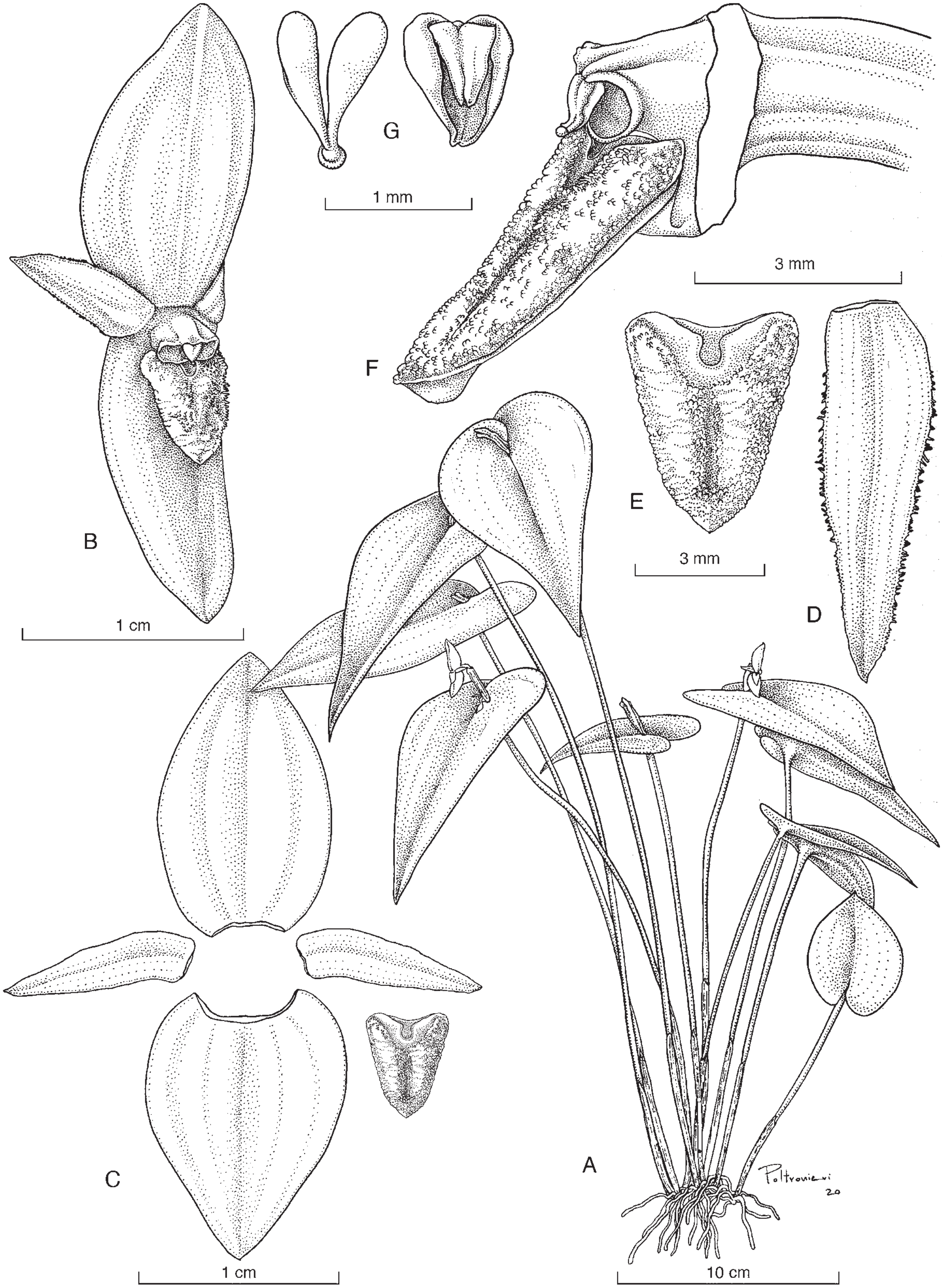


FIGURE 47. *Pleurothallis radula* Luer. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** left petal; **E,** lip, adaxial view; **F,** apex of ovary, column, and lip in lateral view; **G,** pollinarium and anther cap. Drawn by F. Pupulin and S. Díaz Poltronieri from *Pupulin 8129* (JBL).

cm, deeply cordate at the base, the basal lobes overlapping or not, the margins incurved, matte, green, sometimes sparsely spotted to boldly blotched purple along the margins; immature leaf narrowly elliptic-lanceolate, the base cuneate. *Inflorescence* a solitary flower, born from an erect, oblanceolate, subtruncate, spathaceous bract at the base of the leaf, to 27 × 8 mm, glumaceous, green, sometimes finely flecked with purple, becoming brown, dry-papyraceous with age, concealing peduncle, pedicel and floral bract. *Peduncle* terete, 6–8 mm long. *Floral bract* triangular, 3–5 mm long. *Pedicel* terete, green, 8–14 mm long, completely hidden within the spathe. *Ovary* terete-subclavate, curved, 4–6 mm long. *Flowers* spreading-reflexed, yellow, rarely with the sepals tinged rose toward the apices, the lip pale orange, the column greenish white. *Dorsal sepal* erect, ovate to ovate-elliptic, subacute to acute, 12–14 × 6–8 mm, the margins revolute, 3-veined. *Lateral sepals* connate into a narrowly ovate-lanceolate to ovate, subobtuse to acute, synsepal, sometimes shortly bifid at apex, the margins reflexed, 12–14 × 7 mm, each half 2-veined. *Petals* narrowly lanceolate, acute, serrate, reflexed, 8.0–9.5 × 2.0 mm, single-veined. *Lip* unguiculate, hinged to the column foot, thick and fleshy, peltate, basally cordate with rounded angles, acute, 4.5 × 3.2 mm, densely long papillose-verruculose except for the area around the glenion, the papillae irregularly coarse, the abaxial side smooth; glenion slowly raised on a glabrous callus on the disc, 1 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, ca. 2 × 2 mm, with a foot 1.8 mm long, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subcordate, 2-celled, 0.8 × 0.6 mm. *Pollinia* 2, ovate-complanate, apically attenuate into cylindrical caudicules, 0.8 mm long, attached to a round viscidium. Fig. 48A–C.

Etymology: from the Latin *radula*, “a rasp,” in allusion to the markedly verrucose lip.

Distribution: endemic to Central Costa Rica.

Ecology: epiphytic or terrestrial in lower montane wet forest of the Pacific watershed between 1900 and 2150 m. Flowering has been recorded from March to May, and from August to November.

Distinguishing features: *Pleurothallis radula* can be distinguished by the concolorous yellow flower borne at the apex of an erect spathe, with the margins of the sepals revolute and the serrate petals strongly reflexed.

Interestingly, the color dimorphism that is fairly common in species of *Pleurothallis* with tall vegetative habit, which frequently presents both solid purple and solid yellow forms, and sometimes a spectrum of intermediate color forms with both purple and yellow coloration, often intermixed in the same populations, is unknown in the group of *P. phyllocardia*. In this group, almost all the species have solid purple flowers to boldly purple, except for *P. radula*, whose flowers are concolorous yellow (rarely with the sepals tinged rose toward the apices). This makes the species unmistakable.

Costa Rican material examined: Cartago: near San Cristóbal, ca. 1900 m, 22 Sep 1979, *C. Luer 4251, J. Luer & K. S. Walter* (SEL). 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 May 2007, *D. Bogarín 3872, M. Bonilla, R. Gómez, Rafael Trejos & J. D. Zúñiga* (JBL). Jiménez, Pejibaye, Estación Biológica Copal, Instalaciones, en el sendero Ron Ron y hacia el albergue, 9.7834072, -83.7519294, 1000–1100 m, 10 June 2005, *D. Solano 2506* (CR). Jiménez, Pejibaye, Alto del Humo, 23 mayo 2005, *R. L. Dressler 6565* (JBL). San Francisco, Navarro, Muñeco, Fincas Loma Verde y Jilguero, camino a Alto Belén, entre Río Sombrero y Quebrada Patarrá, 9°46'50.3"N, 83°54'21.1"O, 1430–1620 m, bosque pluvial premontano, bosque secundario y orillas de caminos, 23 May 2007, *J. D. Zúñiga 178, D. Bogarín, M. Bonilla, R. Gómez, R. L. Dressler y R. Trejos* (JBL). Jiménez, Pejibaye, entre Tausito y Selva, alrededores de la Reserva Biológica El Copal, orillas del Río Taus y Quebrada Selva, 9°47'5.22"N, 83°45'46.1"W, 1197 m, bosque pluvial premontano, epífitas en bosque secundario a orillas del camino, 1 May 2008, *D. Bogarín 4767, A. Karremans, Y. Kisel & R. Phillips* (JBL). 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 5710, R. L. Dressler, R. Gómez & R. Trejos* (JBL); same collecting data, *D. Bogarín 5716, R. L. Dressler, R. Gómez & R. Trejos* (JBL). San Francisco, Muñeco, Navarro, from the square 7 km toward Alto Belén, 9°45'50.3"N, 83°54'21.1"W, 1900 m, premontane rain forest, epiphytic in altered vegetation, collected by Daniel Jiménez, 31 Oct 2008, flowered in cultivation at Lankester Botanical Garden, 15 Nov 2011, *F. Pupulin 8130* (JBL). El Guarco, Patio de Agua, Finca Integral Fractal, 9°47'48"N, 84°00'02"W, 2048 m, bosque pluvial montano bajo, en rama caída dentro de un parche de bosque maduro, con flores amarillas teñidas de rosado, 7 Aug 2020, *N. Belfort-Oconitrillo 569 & W. Calderón* (JBL). **San José**: León Cortés, Santa Cruz, 9°42'29"N, 84°01'38"W, 2145 m, terrestre, en bosque muy húmedo montano bajo, legit M. L. Gamboa, 26 mayo 2019, *M. Díaz 385* (JBL). León Cortés, Santa Cruz, 9°42'26"N, 84°01'44"W, 2140 m, epífita, en rama caída en bosque muy húmedo montano bajo, legit M. L. Gamboa, 26 mayo 2019, *M. Díaz 386* (JBL). Map 5.

27. ***Pleurothallis rectipetala*** Ames & C. Schweinf., Sched. Orch. 8: 32. 1925. *Acronia rectipetala* (Ames & C. Schweinf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 180. 2005. *Zosterophyllanthos rectipetalus* (Ames & C. Schweinf.) Szlach. & Kulak, Richardiana 6: 192. 2006. TYPE: Costa Rica. [Cartago:] Cachí, cultivated at Cartago and flowered in Jun 1924, *C. H. Lankester 915* (Holotype: AMES). Fig. 49–50 (Vouchers, *Bogarín 5743*, *Bogarín 8855*, JBL).

Epiphytic, caespitose, erect *herb*, up to 30 cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 18–29 cm long, 1–2 mm in diam., pale green, with 2 basal, tubular, obtuse sheaths, 1–2 cm long, and a longer, sub-basal, tubular, obtuse, tight sheath 6–7 cm long, the sheaths dry-papyraceous, brown. *Leaf* borne at the apex of

FIGURE 48. **A–I,** Flowers of *Pleurothallis* species from Costa Rica in the *P. phyllocardia* group. **A–C,** *P. radula* (*Pupulin 7796*; *Karremans 5162*; *Belfort-Oconitrillo 569*); **D–E,** *P. rectipetala* (*Dressler 6565*; *Bogarín 5743*); **F,** *P.* ×*silvae-pacis* (*Karremans 3069*); **G,** *P.* ×*subversa* (*Pupulin 8817*); **H–I,** *P. triangulabia* (*Pupulin 8739*; *Pupulin 8743*). Not at the same scale. All the vouchers at JBL. Photographs by F. Pupulin except C (N. Belfort-Oconitrillo) and E (D. Bogarín).

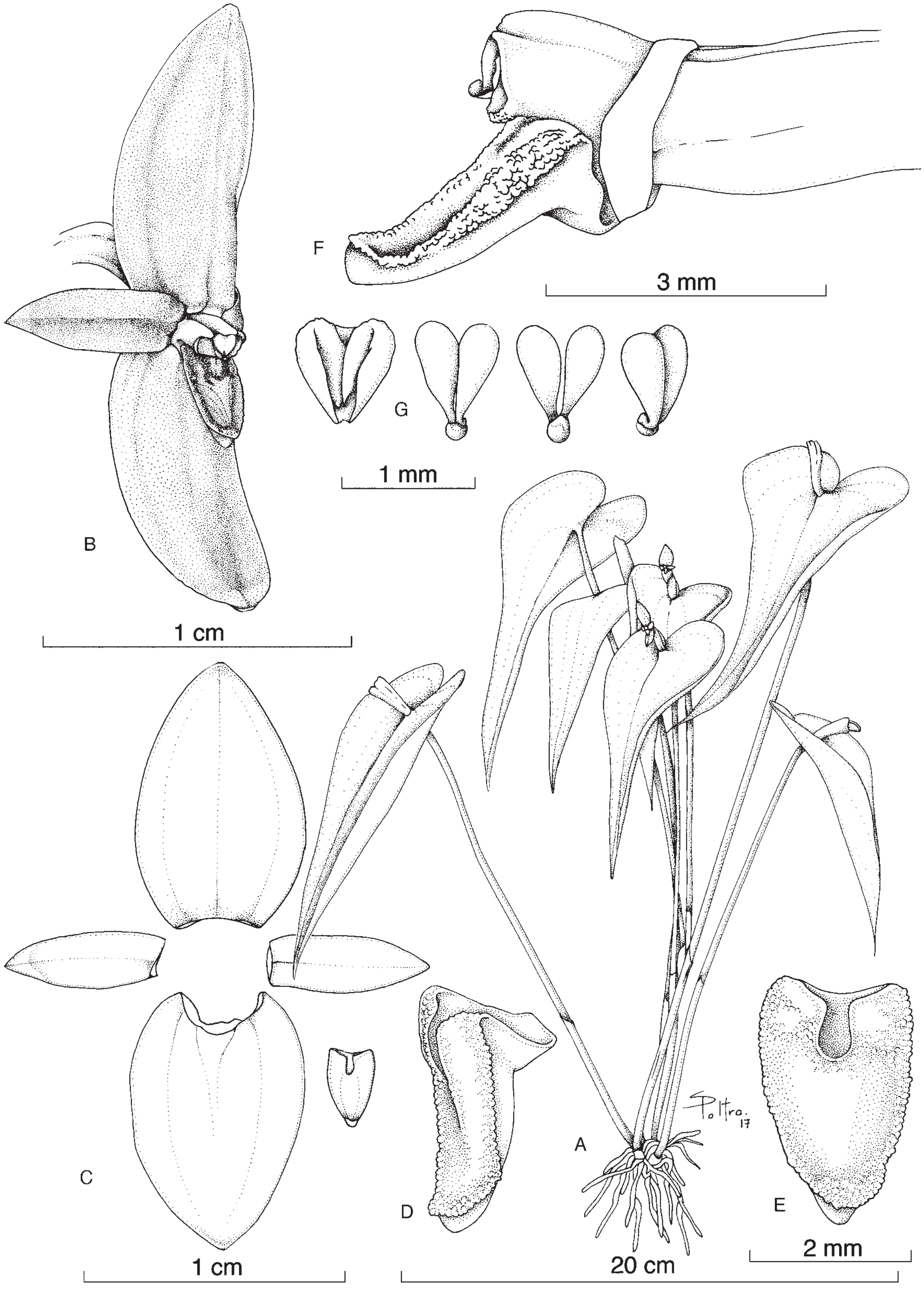


FIGURE 49. *Pleurothallis rectipetala* Luer. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, lateral view; **E,** lip, adaxial view; **F,** apex of ovary, column, and lip in lateral view; **G,** anther cap and pollinarium (three views). Drawn by F. Pupulin and S. Poltronieri from *Bogarín 8855* (JBL).

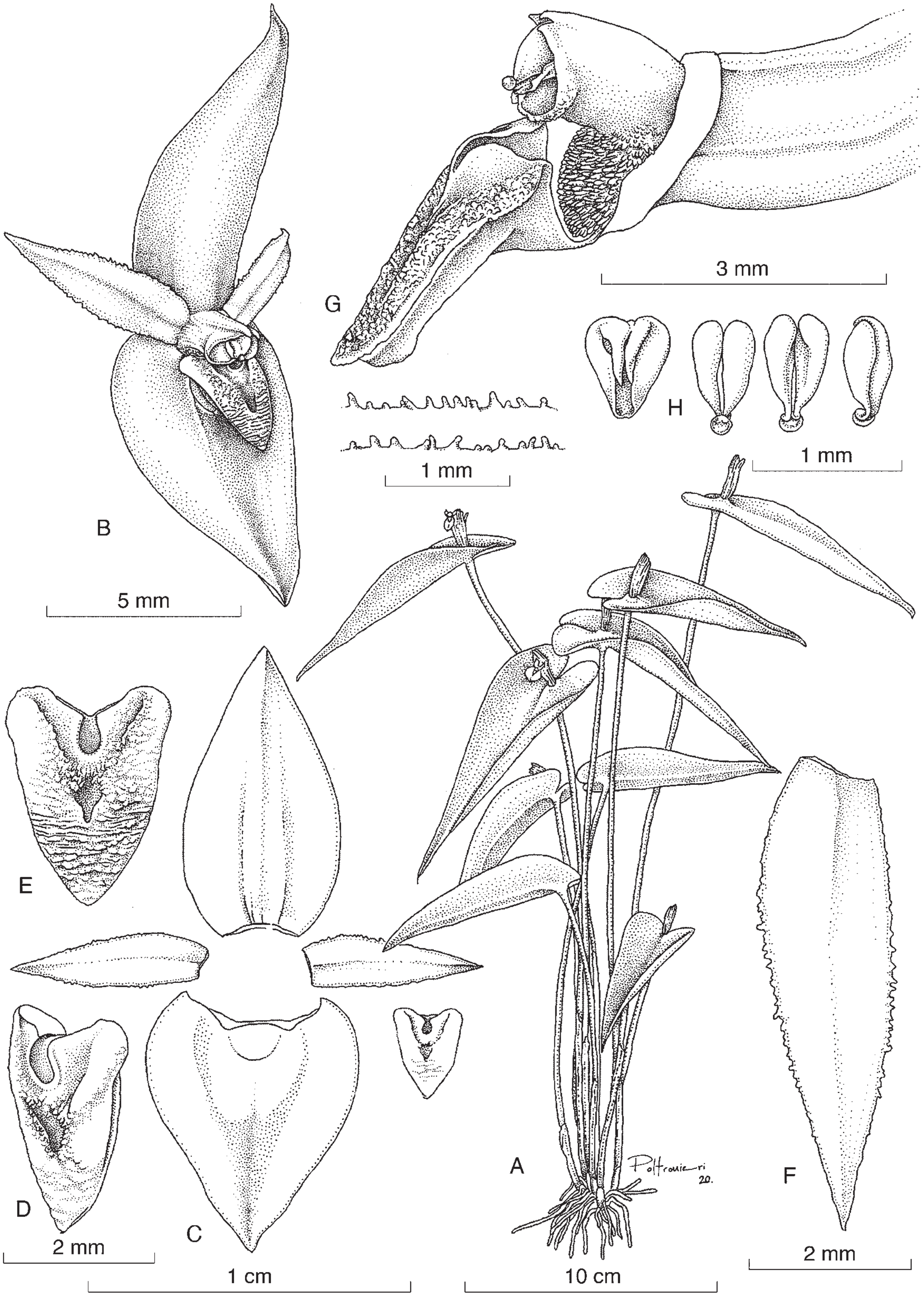


FIGURE 50. *Pleurothallis rectipetala* Luer. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, three-quarter view; **E,** lip, adaxial view; **F,** right petal; **G,** apex of ovary, column, and lip in lateral view; **H,** anther cap and pollinarium (three views). Drawn by F. Pupulin and S. Díaz Poltronieri from *Bogarín 5743* (JBL).

the ramicaul, horizontal to subreclinate toward the stem, thinly coriaceous, flexible, sessile, ovate, acute, shortly subacuminate, 11–14 × 4–7 cm, deeply cordate at the base, the basal lobes not overlapping, the margins incurved, green, matte. *Inflorescence* a solitary flower, borne from an erect, oblanceolate, rounded to subtruncate, spathaceous bract to 15 mm long, glumaceous, green, becoming brown, dry-papyraceous when mature. *Pedicel* terete, green, to ca. 15 cm long, completely hidden within the spathe. *Ovary* terete, curved, 5 mm long. *Flowers* spreading-reflexed, the sepals dull brownish purple, the dorsal sepal fading greenish yellow toward the margins, the petals purple tinged with yellow apically, the lip purple, the column white. *Dorsal sepal* erect, broadly elliptic-lanceolate, obtuse, 6–7 × 4 mm, the margins reflexed, 5-veined. *Lateral sepals* connate into an ovate, subobtuse, apically subexcise synsepal, the margins reflexed, 12 × 8 mm, each half four-veined. *Petals* linear-lanceolate to linear-oblong, acute, minutely apiculate, denticulate in the distal third, reflexed at maturity, 5–6 × 2 mm, single-veined. *Lip* unguiculate, hinged to the column foot, thick and fleshy, ovate-peltate, basally truncate with obtuse angles, obtuse-rounded, the sides smooth, 3 × 2 mm, densely papillose throughout, the papillae coarser at the base; glenion raised on a thick, velutine callus on the disc, less than 1 mm long. *Column* short, stout, transversely subrectangular, dorsiventrally complanate, with a short foot, ca. 2 × 2 mm, the anther apical, incumbent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, subcordate, subtruncate, 2-celled. *Pollinia* 2, narrowly ovate, apically attenuate, attached to an elliptic viscidium. Fig. 48D–E.

Etymology: from the Latin *rectus*, “straight,” in reference to the shape of the petals, which are linear-lanceolate to linear-oblong, reflexed, and pointing upward.

Distribution: known only from Costa Rica, where it is apparently restricted to the Caribbean watershed in the northern Cordillera de Talamanca.

Ecology: this species has been found growing in primary and secondary forests, as well as on scattered trees in paddocks and forest edges, in premontane and low montane forests, between 1300 and 1450 m in elevation. Blooming has been recorded in cultivation at least from May to June and in November.

Distinguishing features: *Pleurothallis rectipetala* can be distinguished by the combination of the comparatively large, cordate leaves, the erect spathe with the flowers barely exerted from it, the dull purple flowers with linear-oblong, reflexed petals, and the very thick, ovate-peltate lip. It is most similar to *P. radula*, which has yellow flowers and an irregularly crestate lip, and to *P. luna-crescens*, which has a moon crescent-shaped flower with much longer, narrow petals.

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 5743, R. L. Dressler, R. Gómez & R. Trejos* (JBL). Turrialba, La Suiza, Llanos del Quetzal, ca. 1 km sobre el camino detrás de la Escuela de Kabébata (Alto Quetzal), 9°46'43.6"N, 83°24'41.6"W, 1449 m, epífitas en bosque primario y secundario, bosque muy húmedo premontano “*supra arbores in nemoribus Llanos del Quetzal ad Turrialba in Cartago*,” 17 junio 2011, *D. Bogarín 8855, M. Fernández & A. Karremans* (JBL). Map 5.

28. ***Pleurothallis* ×*silvae-pacis*** Karremans, Orch. Rev. 121: 156. 2011. (*pro sp*.). TYPE: Costa Rica. Alajuela: Valverde Vega, Bajos del Toro, Hacienda Río Toro, Bosque de Paz Biological Reserve, 1500–2000 m. Flowered in cultivation in the orchid garden, 25 November 2010, *A. P. Karremans 3069* (Holotype: CR; Isotype: JBL-spirit). Fig. 51 (Voucher, *Karremans 3069*, CR).

Epiphytic, caespitose, erect *herb* up to 20 cm tall. *Roots* slender. *Ramicaul* cylindric, erect to suberect, up to 18 cm long, enclosed by a closely adpressed sheath that covers the first third of the ramicaul, with a few sheaths at the base. *Leaf* horizontal to subhorizontal, coriaceous, narrowly ovate to acuminate, 8–10 × 2.5 cm, the base sessile, cordate. *Inflorescence* single-flowered, produced in succession and emerging from a papyraceous, semierect spathe, 14–16 mm long, forming a fascicle of old inflorescences with time. *Floral bract* 3–4 mm long. *Pedicel* 8–9 mm long. *Ovary* cylindrical, 3–4 mm long. *Flowers* with greenish-rose sepals, veins rose, the petals and lip dark rose, the column whitish green. *Dorsal sepal* ovate-acuminate, obtuse, 9.2 × 4 mm, 3-veined. *Lateral sepals* connate into an ovate-acuminate synsepal, 7.5 × 3.7 wide, 4-veined. *Petals* linear-acuminate, somewhat falcate, acute, margins serrulate, 6.7–6.9 × 1.4–1.5 mm, 1-veined. *Lip* thick, ovate, acute, 3.0–3.2 × 1.7 mm, the base reflexed as a claw, hinged to the column foot, the lamina provided with a basal glenion, below it rises a conspicuous peak, the apical third of the lamina provided with shallow lateral sinuses. *Column* thick, 1.2–1.3 mm long, the foot thick-bulbous, papillose; stigma and anther apical. *Pollinia* 2, 0.75 mm long, provided with inconspicuous caudicles, and a hard, bubble-like viscidium. Fig. 48F.

Etymology: from the Latin *silva,* “forest,” and *pax-pacis,* “peace,” honoring the Bosque de Paz (Forest of Peace) Biological Reserve, where the type specimen was collected.

Distribution: known only from Costa Rica, on the Caribbean watershed of the Cordillera Volcánica Central, just north of the Central Valley.

Ecology: in the wild, *Pleurothallis* ×*silvae-pacis* grows as an epiphyte in premontane, very humid cloud forests at elevations of 1500–2000 m. The plant has been recorded in flower from September to March.

Distinguishing features: the combination of rather short and narrowly lanceolate, dark green leaves, the flower born on a long peduncle, the sepals and petals tinged with rose on a white background, and the narrowly ovate lip with an imperfect basal glenion distinguishes the nothospecies. The inflorescence with the long pedicel, the orientation of the flowers, the shape of the lip, and the structure of pollinaria suggest an affinity with *Pleurothallis eumecocaulon*, a species belonging to the group of *Pleurothallis* “Ancipitia” that has been recorded at the collection locality of the putative hybrid. The larger plant habit, the serrulate petals,

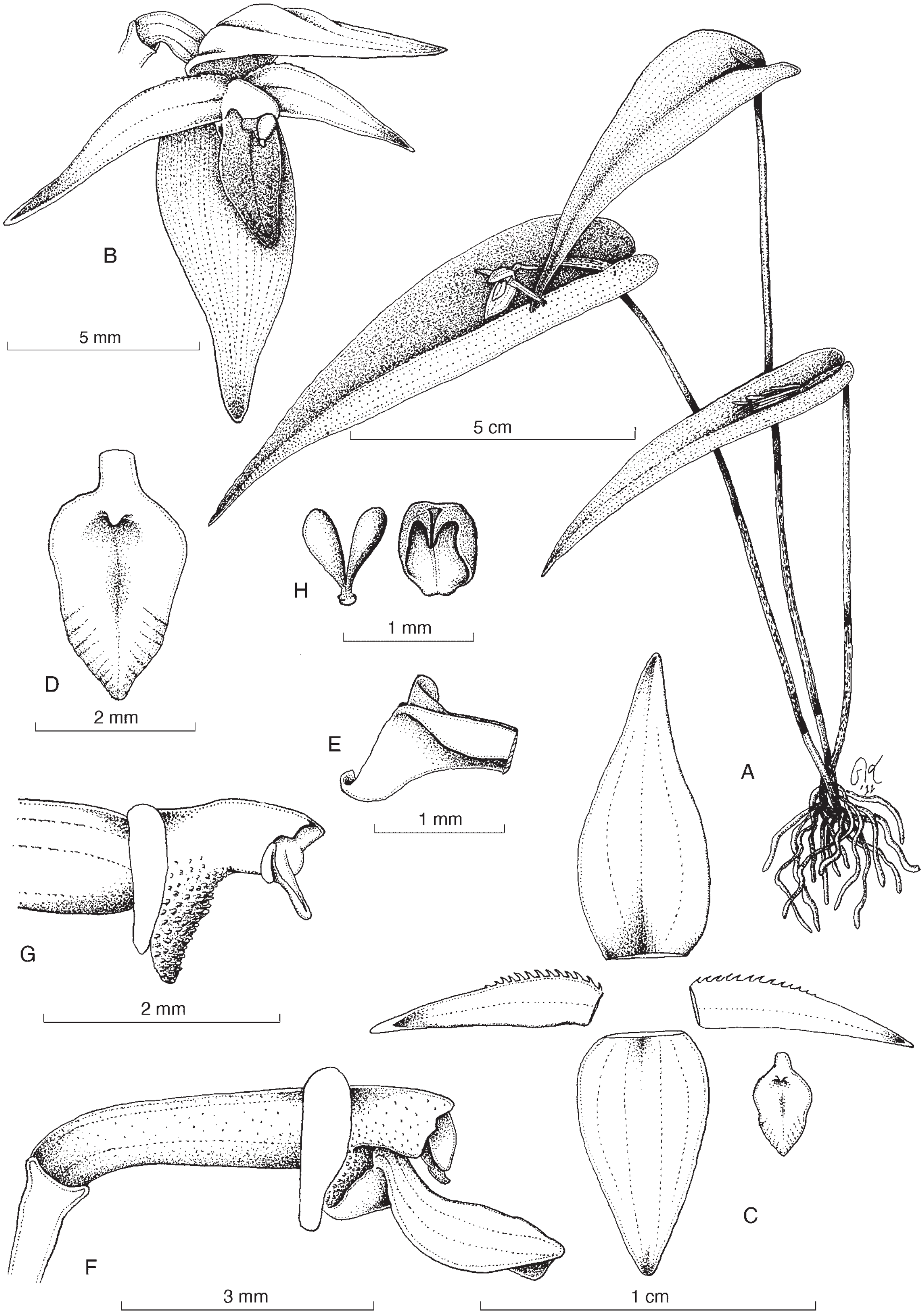


FIGURE 51. *Pleurothallis* ×*silvae-pacis* Karremans. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** base of the lip, lateral view; **F,** ovary, column, and lip in lateral view; **G,** column, lateral view; **H,** pollinarium and anther cap. Drawn by A. P. Karremans from *Karremans 3069* (CR). From Karremans & Muñoz García, 2011.

the lip distinctly geniculate at the base, and the presence of an imperfect glenion at the base of the disc would seem derived from the genetic influence of a species of the *Macrophyllae-Fasciculate* group, but at our current state of knowledge we cannot speculate about its identity.

We treat here *Pleurothallis* ×*silvae-pacis* as a probable nothospecies, from the natural cross between *P. eumecocaulon* and *P. phyllocardia*. Both species have been recorded at the type locality of *P.* ×*silvae-pacis*, and they are the only members of the *P.* "Ancipitia" (sensu Luer 1986) and *P. phyllocardia* groups (the latter defined in this paper), respectively, that form natural populations at Bosque de Paz. It has features of the group of *Pleurothallis* species treated like members of "Ancipitia," such as the size of the plant with long acuminate leaves, as well as the presence and accumulation of the senescent pedicels on the leaf, but it shares the unguiculate, purple lip that is typical of taxa belonging to the *P. phyllocardia* group.

Costa Rican material examined: **Alajuela**: Valverde Vega, Bajos del Toro, Hacienda Río Toro, Bosque de Paz Biological Reserve, 1500–2000 m, *BdP 06-242* (BdP, BdP-spirit). Map 5.

29. **Pleurothallis ×subversa** Pupulin & Bogarín**, *nothosp. nov.***

TYPE: Costa Rica. Cartago: Paraíso, Cachí, ca. 9°50'N, 83°48'W, 1300 m, collected by D. Jiménez, flowered in cultivation 9 November 2011, *F. Pupulin 8817* (Holotype: JBL). Fig. 52 (Voucher, *Pupulin 8817*, JBL). Map 4.

Pleurothallis nothospecie nova inter P. compressam Luer *et quemquam Pleurothallidem turmae cardiothallidis* Rchb.*f. affinem, fortasse Pleurothallidem oncoglossam* Luer, *intermedia, folio anguste ovato flore subverso synsepalo orbiculare labello bene triangulo P. compressa similis, ramicaulibus teretibus floribus dimensione alium genitorem reminiscens*.

Epiphytic, caespitose, suberect to curved *herb*, to 30 cm tall. *Roots* slender, flexuous, 1–2 mm in diam. *Ramicauls* terete throughout, slender, 9–31 cm long, 1.5–2.5 mm in diam., yellowish green, provided with 2 tubular, short, truncate sheath to 2 cm long at the base, glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* suberect to reclined toward the stem, thinly coriaceous, flexible, sessile, narrowly ovate-lanceolate, acuminate, 11–15.2 × 4.0–5.4 cm, deeply cordate at the base, the basal lobes not overlapping, sometimes upcurved, grass green, matte. *Inflorescence* a solitary flower, borne pendent from a suberect, spathaceous, diagonally truncate bract 14 mm long, brown, dry-papyraceous when mature; peduncle terete, facing down, 9–11 mm long. *Pedicel* terete, to 5 mm long. *Ovary* suclavate, curved, rounded in section, greento bronze-green, 7 mm long. *Flowers* nonresupinate, partially reflexed, the sepals reddish yellow to bronze, the petals brownish red, the lip white, flushed bright red toward the apex and the margins, the column white. *Dorsal sepal* broadly ovate, obtuse, 11 × 9 mm, 5-veined. *Lateral sepals* connate into a rounded, obtuse to subtruncate synsepal, 9.5 × 10.0 mm, each half 2-veined. *Petals* narrowly triangular-falcate, acuminate, 8.0 × 1.5 mm, 1-veined. *Lip* hinged to the column foot, triangular, basally truncate with acute angles, obtuse, sparsely verrucose around the glenion, 4 × 4 mm, thickened at the base; glenion raised on a cushion-like callus between the basal lobes of the lip, 1 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, ca. 2 × 2 mm, apically diagonally truncate, the anther apical, bent, the stigma apical, bilobed. *Anther cap* cucullate, ovate, cordate, 2-celled. *Pollinia* 2, narrowly oblong-pyriform, attached to a small. elliptic viscidium through two abbreviate caudicles. Fig. 48G.

Etymology: from the Latin *subversus* (present perfect of *subverto*), "subverted, inverted, turned upside down," in reference to the nonresupinate orientation of the flower.

Distribution: known only from the type specimen, collected in Costa Rica (Map 4).

Ecology: epiphytic in premontane rain forest along the Caribbean watershed of the Cordillera de Talamanca, just south of the Central Valley in Costa Rica. The plant has been recorded in flower in November.

Distinguishing features: the relatively large plants with narrowly ovate-lanceolate leaves, cordate at the base, and the large, truly pendent, partially reflexed, nonresupinate flowers with bronze sepals and red petals, provided with a white lip flushed bright red toward the apex and the margins, are diagnostic of *Pleuothallis* ×*subversa*.

The thinly coriaceous, narrowly ovate-lanceolate, apically long-acuminate leaves, with the basal margins often slightly incurved, as well as the nonresupinated flower borne at the apex of a truly pendent pedicel and the ovary curved 90°, with the sepals and petals partially reflexed, are strongly reminiscent of *P. compressa*, which we propose here as one of the putative parents of the natural hybrid. The ramicauls, however, are terete throughout, unlike those of *P. compressa*, which become strongly ancipitous toward the apex. The size of the flower is also different, almost double, that of *P. compressa*, and we hypothesize that it is inherited from the other putative parent, likely a large-flowered species close to *P. cardiothallis*. As both *P. cardiothallis* and *P. oncoglossa*, with flowers over 3 cm tall, form natural populations in the region where *P.* ×*subversa* was found, they both should be considered possible parents of the new nothospecies. However, the almost flat sepals are most likely inherited from *P. oncoglossa*, which is common around Cachí where the hybrid was found, and whose flowers remain spread during anthesis, while the sepals of *P. cardiothallis* have strongly swept back margins at maturity.

30. ***Pleurothallis triangulabia*** C. Schweinf., Ann. Missouri Bot. Gard. 24(2): 183. 1937.

SYNTYPES: Costa Rica. [Alajuela: Quesada,] arbres des paturages a Palmira de Alfaro Ruiz, 840 m, 4 Jul 1925, fleurs rouge-vineux foncé, *A. M. Brenes (138a) 1341* (AMES 43761, **selected here as the lectotype**). Panama. Chiriquí: valley of the upper Río Chiriquí Viejo, vicinity of Monte Lirio, 1300–1900 m, flowers dark reddish purple, June 27–July 13, 1935, *R. J. Sibert 269* (MO, not seen]. Fig. 53–54 (Voucher, *Pupulin 8739* and *Pupulin 8743*, both at JBL).

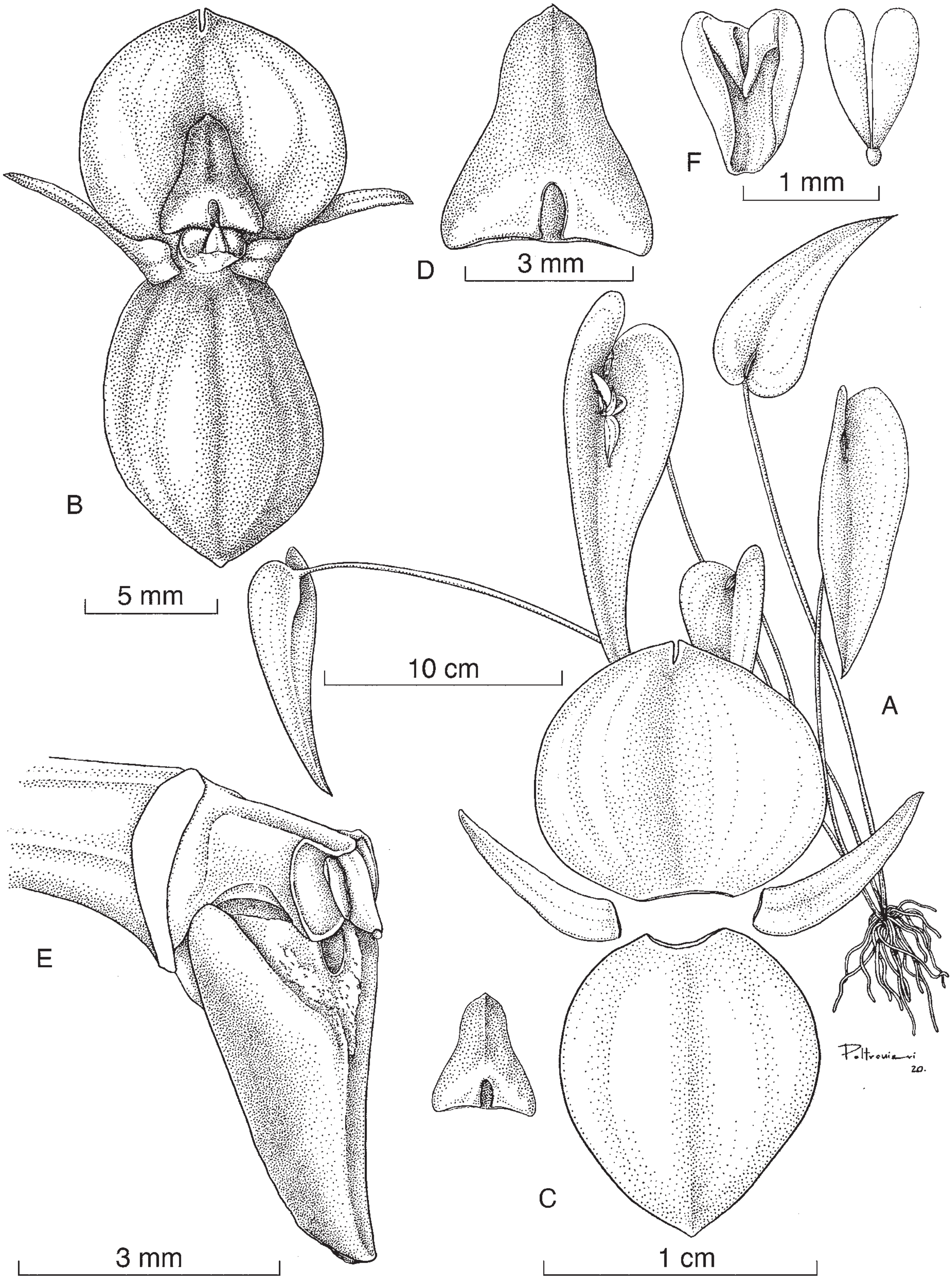


FIGURE 52. *Pleurothallis* ×*subversa* Pupulin & Bogarín. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, adaxial view; **E,** ovary, column, and lip in lateral view; **F,** anther cap and pollinarium. Drawn by S. Díaz Poltronieri from *Pupulin 8817* (JBL).

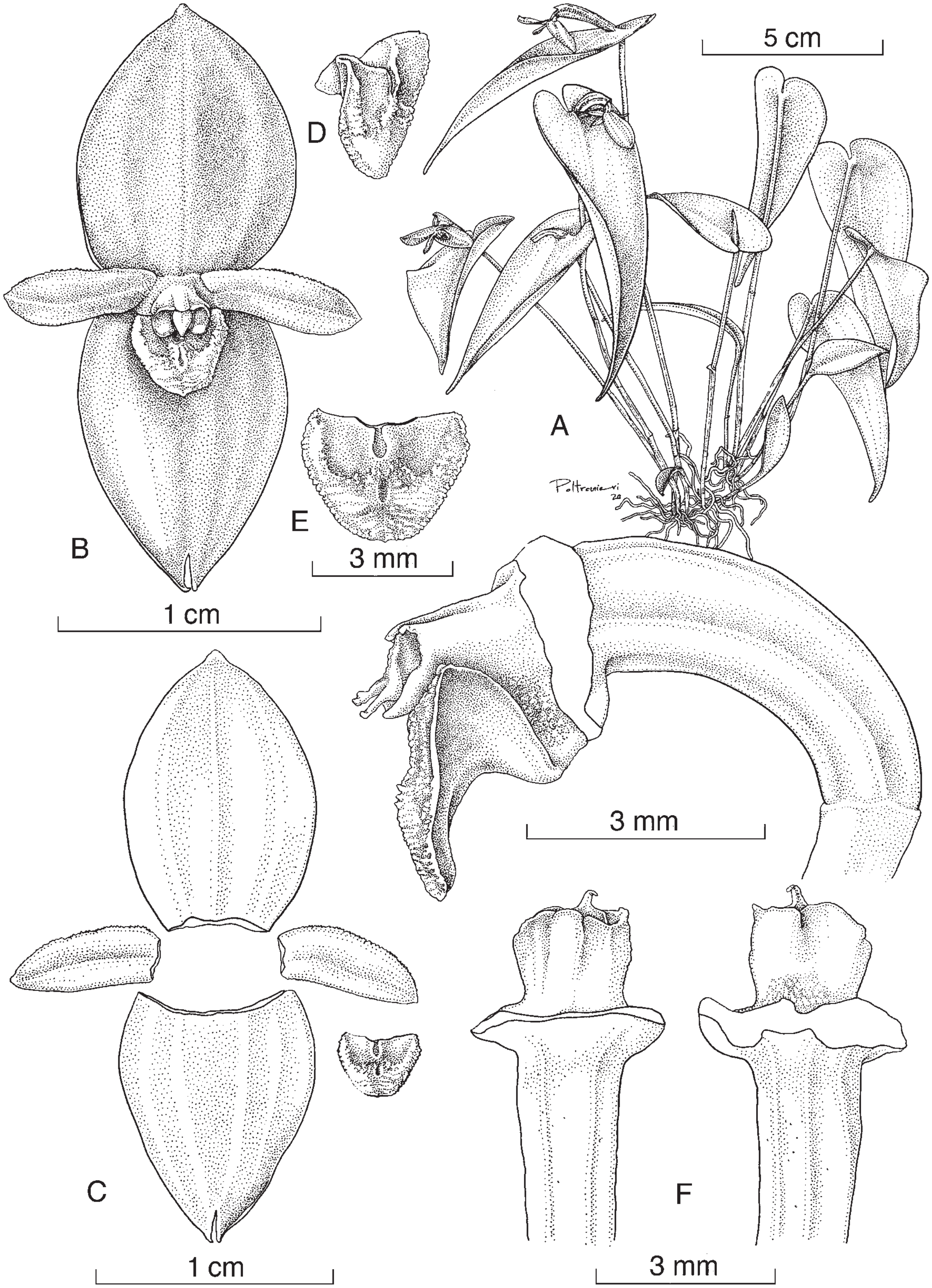


FIGURE 53. *Pleurothallis triangulabia* C. Schweinf. **A,** habit; **B,** flower; **C,** dissected perianth; **D,** lip, three quarters view; **E,** lip, adaxial view; **F,** ovary, column, and lip in lateral view; **G,** column in dorsal and ventral views. Drawn by S. Díaz Poltronieri from *Pupulin 8739* (JBL).

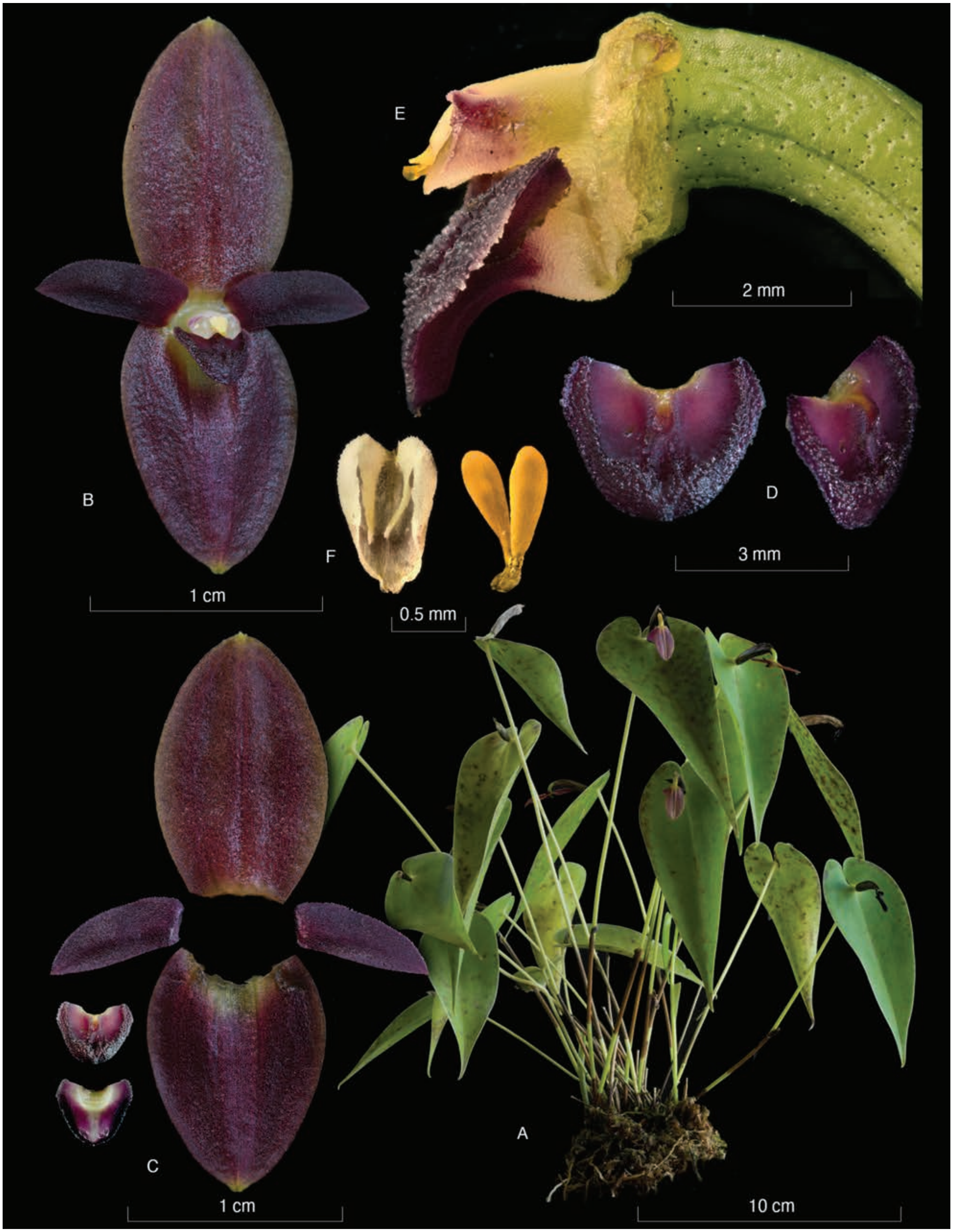


FIGURE 54. *Pleurothallis triangulabia* C. Schweinf. **A,** habit; **B,** flower; **C,** dissected perianth (lip in adaxial and abaxial views); **D,** lip, adaxial and three-quarter views; **E,** ovary, column, and lip in lateral view; **F,** anther cap and pollinarium. Lankester Composite Dissection Plate prepared by F. Pupulin from *Pupulin 8743* (JBL).

Epiphytic, caespitose, erect *herb* to 19(27) cm tall. *Roots* slender, flexuous, ca. 1 mm in diam. *Ramicauls* terete, slender, 8–19(–27) cm long, 1–2 mm in diam., yellowish green, provided with a tubular, short, truncate sheath to 3 cm long at the base, and a longer, tubular, tightly adpressed, obtuse sheath below the middle, to 4.5 cm long, the bracts glumaceous, pale green when young, becoming brown, dry-papyraceous with age. *Leaf* borne horizontally at the apex of the ramicaul, becoming subpendent with age, coriaceous, sessile, ovate, subacuminate, 5.6–10.0 × 3.0–5.9 cm, deeply cordate at the base with overlapping auricles, grass green, sometimes sparsely dotted with purple, matte. *Inflorescence* a solitary flower, from an erect spathaceous bract 1.7–3.0 cm long, green, dry-papyraceous when mature, eventually dissolving with age. *Peduncle* terete, slender, to 12 mm long. *Pedicel* terete, pale green, curving down throughout anthesis, 7–8 mm long. *Ovary* subclavate, terete, to 4 mm long. *Flowers* flushed with purple on a yellowish green background, often with darker purple stripes along the main veins, rarely solid dark purple. *Dorsal sepal* erect, elliptic to broadly ovate, obtuse to subacute, apiculate, flat, 12.0–12.5 × 8.0–9.8 mm, 3-veined. *Lateral sepals* connate into an ovate, acute synsepal, 10–12 × 8–9 mm, each half 2-veined. *Petals* elliptic-lanceolate, subfalcate, acute, spreading, the margins minutely denticulate, 6.5–7.3 × 2.2–3.0 mm, 3-veined. *Lip* unguiculate, hinged to the column foot, geniculate, transversely triangular, basally subcordate, obtuse, obscurely apiculate, 2.9–3.4 × 3.6–4.0 mm, verruculose on the adaxial surface of the apical half and along the margins, minutely papillose in front to the glenion; glenion on a cushion-like, convex callus recessed between the basal lobes of the lip, 0.7 mm long. *Column* short, transversely subrectangular, dorsiventrally complanate, apically obliquely truncate, ca. 2 × 1 mm, the anther apical, bent, the stigma apical, bilobed. *Anther cap* ovate, truncate, bilobed at the base, 2-celled, 1.0 × 0.6 mm. *Pollinia* 2, narrowly oblong-pyriform, 0.8 × 0.3 mm, attached to an elliptic viscidium through 2 short, cylindric caudiculae. Fig. 48H–I, 55.

Etymology: from the Latin *triangulus*, “triangle,” and *labium*, “lip,” in allusion to the shape of the labellum.

Distribution: Costa Rica and western Panama.

Ecology: populations of *P. triangulabia* were found growing epiphytically in secondary forests, as well as on scattered trees along pastures, in the premontane forest of the Cordillera Volcánica Central and Cordillera de Tilarán, at elevations of 1700–2400 m. Due to their proximity to the watershed of the Continental Divide, the collecting localities of the species are constantly windy, with perennial intermittent rains and fogs that allow the establishment of a particularly rich epiphytic flora. The species flowers at least from February to November.

Distinguishing features: the relatively small plants, with stems mostly around 15–20 long, and the glabrous, flat flowers facing the leaf, with the dorsal sepal subequal in width to the synsepal, the petals elliptic-lanceolate, and the lip transversely rectangular, are diagnostic of the species.

Pleurothallis triangulabia is superficially similar to *P. phyllocardia*, with which it shares the shape of the ovate, acute leaves, deeply cordate at the base, the erect spathe, and the mostly dark purple flower that faces the surface of the leaf. Vegetatively, however, plants of *P. triangulabia* are usually distinctly smaller—a habit that the plants maintain also in cultivation—with mature stems around 15–20 cm long (vs. 30[–33] cm) and leaves to 10 × 4 cm (vs. 12 × 7 cm). The flowers are proportionately rounder, flat (vs. reflexed), often flushed with purple on a greenish yellow background (vs. solid purple in *P. phylllocardia*), with the dorsal sepal broadly ovate-suborbicular (vs. narrowly ovate), subequal to the synsepal (vs. distinctly wider), the petals shorter, elliptic-lanceolate (vs. oblong), and the transversely rectangular lip that is wider than long (vs. longer than wide).

Pleurothallis triangulabia has been traditionally treated as a synonym of *P. phyllocardia* (e.g., Pupulin, 2002; Luer, 2003; Bogarín et al., 2014; Kolanowska, 2014), which it superficially resembles, but the type specimen at AMES that we chose as the lectotype (Fig. 55) clearly shows the large synsepal, the elliptic-lanceolate and comparatively short petals, and the transversely rectangular lip that Schweinfurth described and illustrated on the type sheet (Fig. 56). Our recent collections from the western end of the Cordillera Volcánica Central and the Cordillera de Tilarán in Costa Rica correspond well to Schweinfurth’s concept, and for this reason, we treat *P. triangulabia* here as a good species.

We have not seen the Panamanian syntype of *Pleurothallis triangulabia* from the Herbarium of the Missouri Botanical Garden, where the primary specimen is conserved according to the protologue (Schweinfurth, 1937). An isosyntype at NY shows a particularly large plant, likely over the upper dimensions that we have observed in *P. triangulabia*. Bogarín and co-workers (2014) treated the syntype collection (*Seibert 269*) from Chiriquí as conspecific with *P. phyllocardia*, a species that is effectively common in the same area, which is documented by several collections (e.g., *Croat 26312, Croat & Porter 16168, Allen 1468, Gentry 5882, Folsom 6024, Hammel 1425, Hammel et al. 7036, Liesner 315*, and others, all at MO) and a photograph, which can be seen at RENZ (*W. Löderbusch s.n.*, Slide no. 2040026, Swiss Orchid Foundation, 2016). The specimen that Schweinfurth (1937) designated as “cotype” might belong to a different taxon.

Costa Rican material examined: **Alajuela**: Alajuela: Alfaro Ruiz, Palmira, 2200 m, 9 Feb 1938, *A. P. Smith H1167* (AMES). Same locality, 11 Jun 1938, *A. P. Smith H1338* (AMES); 21 Sept 1938, *A. P. Smith H1226* (AMES). Alfaro Ruiz, Palmira, 2400 m, 16 May 1938, *A. P. Smith H592* (AMES). Same locality, 2000 m, 27 May 1938, *A. P. Smith H667* (AMES); 2300 m, Jul 1938, *A. P. Smith H932* (AMES).Alfaro Ruiz, vecindad de Palmira, en bosque sobre colina, 1900 m, 13 Nov 1964, *A. Jiménez M. 2560* (AMES). Carrizal, Concordia, entre Los Cartagos y Cinco Esquinas, bosque pluvial montano bajo, en potreros arbolados y bosque secundario, 10˚08'16.8"N, 84˚09'49.8"W, 2027 m, 17 Junio 2009, en cultivo en el Jardín Botánico Lankester, May 2011, *D. Bogarín 7308, R. L. Dressler, F. Pupulin & R. Trejos* (JBL); same locality and data, *D. Bogarín 7456, R. L. Dressler, F. Pupulin & R. Trejos* (JBL). Quesada, arbres des

FIGURE 55. Lectotype of *Pleurothallis triangulabia*, a specimen collected in Costa Rica by A. M. Brenes *(138a) 1341* (AMES 43761). Reproduced with kind permission from the Keeper, Oakes Ames Orchid Herbarium, Harvard University Herbaria.

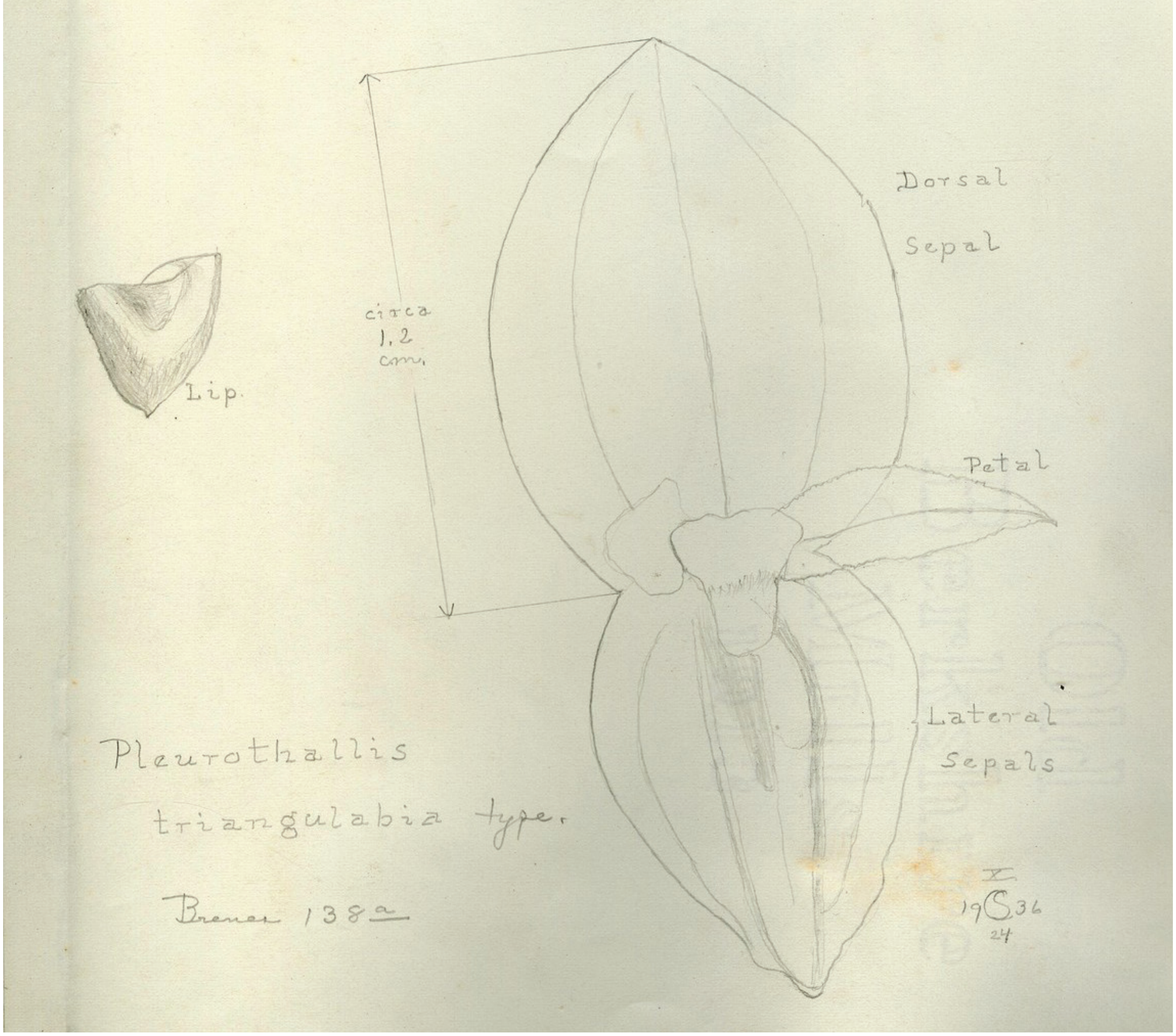


FIGURE 56. Charles Schweinfurth's sketch of the flower from the lectotype of *Pleurothallis triangulabia*, mounted on the type sheet (AMES 43761). Reproduced with kind permission from the Keeper, Oakes Ames Orchid Herbarium, Harvard University Herbaria.

paturages a Palmira de Alfaro Ruiz, [ca. 10°13'N, 84°23'W], 840 m, 4 Jul 1925*A. M. Brenes (138a) 1341* (AMES). San Ramón, Angeles, Monteverde, road to TV Tower, Z.P. Arenal-Monteverde Caribe, 10.2944444, -84.7500003, 1700 m, 24 Aug 1985, *W. Haber 2360* (CR). **Guanacaste**: Abangares, Sierra, R.B. Monteverde. Cerro Dos Amigos in area TV towers, cloud forest, 10.3333333, -84.8333333, 10 Oct 1985, *W. Haber 3466 & E. Bello* (CR). **Heredia**: Vara Blanca, 7 Feb 1936, *R. Valerio R. 361* (AMES). **Puntarenas**: Puntarenas, Monteverde, main road toward the summit of Cerro Amigos, 10°19'08.6"N, 84°48'01.0"W, 1750 m, wet lower montane forest, epiphytic in secondary vegetation, 6 March 2015, *F. Pupulin 8743, D. Bogarín, M. Díaz & M. Fernández* (JBL). Puntarenas, Monteverde, sendero hacia la cumbre del Cerro Amigos entrando por la estación del CIEE, 10°19'20"N, 84°48'27"W, 1600 m, bosque nuboso, epífitas en bosque secundario maduro, 11 junio 2016, floreció en cultivo en el Jardín Botánico Lankester, 3 Aug 2016, *M. Diaz 247, M. Fernández & L. Oses* (JBL). Puntarenas, Monteverde, sendero hacia la cumbre del Cerro Amigos, 10°19'17.00"N, 84°47'55.30"W, 1722 m, bosque pluvial montano bajo, epífitas en bosque secundario, 5 Marzo 2015, floreció en cultivo en el Jardín Botánico Lankester, 12 Jul 2016, *M.Fernández 1019, D. Bogarín, M. Díaz, F. Pupulin & A. Salazar* (JBL). Puntarenas: Puntarenas, Monteverde, main road toward the summit of Cerro Amigos, 10°19'08.6"N, 84°48'01.0"W, 1750 m, wet lower montane forest, epiphytic in secondary vegetation, 6 March 2015, flowered in cultivation at Jardín Botánico Lankester, 12 Jul 2016, *F. Pupulin 8735, D. Bogarín, M. Díaz & M. Fernández* (JBL). Same locality data, flowered in cultivation at Jardín Botánico Lankester, 1 Jul 2020, *F. Pupulin 8758, D. Bogarín, M. Díaz & M. Fernández* (JBL). Map 4.

Excluded species

Pleurothallis scitula Luer, Selbyana 3(3–4): 384. 1977. TYPE: Panama. Chiriquí: epiphytic in cloud forest on Cerro Hornito, alt. ca. 1700 m, 15 Dec 1976, *C. Luer 1361, A. Luer, R. L. Dressler, N. H. Williams & F. L. Stevenson* (Holotype: SEL).

Pupulin (2002) cited a voucher for *Pleurothallis scitula* from the rain montane forest of cerro Chomogo in the Cordillera de Tilarán (*Boyle 75-89, USJ*), but a recent re-examination of that collection revealed that it belongs instead to *P. triangulabia*, a species occurring relatively frequently around Monteverde. *Boyle 75-89* has narrowly ovate leves (vs. broadly ovate in *P. scitula*), concolorous purple flowers (vs. yellow striped with red) facing the leaf (vs. erect), with the synsepal smaller than the dorsal sepal (vs. larger), and relatively short, elliptic petals (vs. narrowly lanceolate). Another Costa Rican voucher was cited by Grayum et al. (2008), based on a specimen collected in 2005 from the Pacific slope of the Cordillera de Talamanca near the Panamanian border, and flowered in cultivation in 2007 (*J. F. Morales 15793*, then at INB, later at CR). With the help of CR curator Silvia Lobo, we searched for this specimen that is included in the National Museum database, but unfruitfully, as among the collection of CR the folder of *P. scitula* is missing.Without having been able to observe a sure voucher of this species in Costa Rica, we are not in a position to provide a description and illustration of *P. scitula* for this article, and we have no other option for the moment but to exclude it from treatment.

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