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The Journal of the Arnold Arboretum

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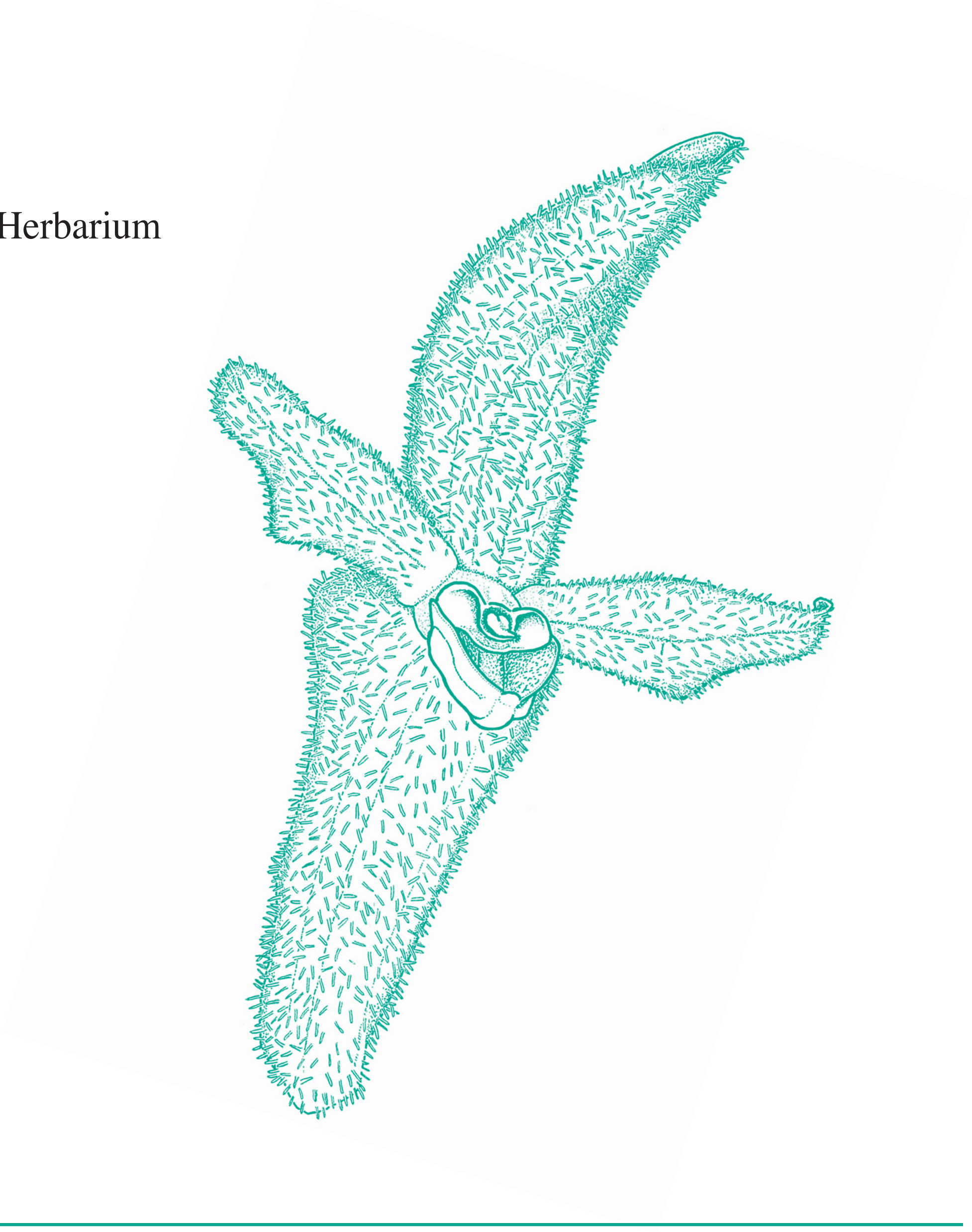

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Cover: *Pleurothallis rikseniana* Mark Wilson & B.T. Larsen (See page 209, Fig. 18A).
Drawn by Bruno Larsen.

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A NEW ANDEAN SPECIES OF *MAGNOLIA* (SECTION *TALAUMA*, MAGNOLIOIDEAE, MAGNOLIACEAE), AND A KEY TO THE SPECIES FOUND IN COLOMBIA

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Juan E. Carvajal-Cogollo,[1] and Gerardo A. Aymard-Corredor[2,3]

Abstract. *Magnolia pajarito*, a new species from the Andean slopes of the Eastern Cordillera of Colombia, is described and illustrated, and its morphological relationships with other similar *Magnolia* species are discussed. This new species is a tree between 9 and 30 m tall from montane forest remnants and pasture lands with dispersal trees (1500–1700 m), and it does not appear to be closely allied to any particular *Magnolia* species. This new species shares several features with four other species (M. *arcabucoana, M. caricifragans, M. santanderiana,* and *M. virolinensis*) in section *Talauma*. Morphologically it has some similarity to *M. arcabucoana*, but it differs in the length of the adaxial scar of the petiole, the size and shape of the leaf blade, the sepal and inner petal, and in the number of secondary veins, vaginal hypsophyl, and stamens. Additionally, habitat information, a distribution map, and data on *Magnolia* conservation status are included. An identification key of species of *Magnolia* found in Colombia is also provided. This new species elevates to 40 the number of *Magnolia* taxa for the flora of Colombia, of which 31 are endemic. Colombia has the highest diversity of the genus in the neotropics.

Keywords: Andean forests, Eastern Cordillera, Boyacá department, Colombia, *Magnolia*, Magnoliaceae

Resumen. *Magnolia pajarito* una nueva especie de las vertientes de la Cordillera Oriental de los Andes de Colombia, es descrita, ilustrada y se discuten sus relaciones morfológicas con otras especies similares. Esta nueva especie es un árbol entre 9 y 30 m de altura, que se encuentra en remanentes de bosques montanos y con árboles dispersos (1500–1700 m) y aparentemente no esta cercanamente relacionada con ninguna especie en particular de *Magnolia*. *M. pajarito* comparte algunos caracteres con cuatro especies (M. *arcabucoana, M. caricifragans, M. santanderiana* y *M. virolinensis*) de la sección *Talauma*. Sin embargo, morfológicamente, tiene cierta similaridad con *M. arcabucoana*, de la cual difiere en el largo de la cicatriz adaxial del pecíolo, en el tamaño y forma de la hoja, sépalos y pétalos internos y en el número de las venas secundarias, hipsófilos vaginales y estambres. Adicionalmente, se incluye información del hábitat, un mapa de distribución, datos acerca del estado de conservación de *Magnolia* y una clave para la identificación de las especies de *Magnolia* presentes en Colombia. Esta nueva especie eleva actualmente en 40 el número de especies para la flora de Colombia, 31 son endémicas. Colombia es el país con la mayor diversidad del género en el neotropico.

Palabras clave: Bosques andinos, Cordillera Oriental, departamento de Boyacá, Colombia, *Magnolia*, Magnoliaceae

Magnolia L. (Magnoliaceae) is a pantropical and temperate genus of between 345 and 350 species (World Checklist of Vascular Plants; kew.org; Vázquez-García et al., 2021a). The genus is disjunctly distributed from Southeastern North America, Mexico, Central America, Antilles, the Andes (Venezuela, Colombia, Ecuador, Peru, and Bolivia), along the Pacific Coast of Colombia and Ecuador to Southeastern Brazil (Frodin and Govaerts, 1996), and in Asia, from India, Sri Lanka, Vietnam, the Himalayas, China, Japan, Korea, Taiwan, and southeastward through the Malay Archipelago and New Guinea (Nooteboom, 1993; Azuma et al., 2001; Cicuzza et al., 2007; Sánchez-Velásquez et al., 2016). The genus is absent in Africa, Australia and Europe (World Checklist of Vascular Plants; kew.org). The main center of species diversity for Magnoliaceae is in China (Rivers et al., 2016). However, a second center of diversity is in the Neotropics, where a large number of new species have been described and published in the last two decades (see Literature Cited). According to Vázquez-García et al. (2015) and Sánchez-Velásquez et al. (2016), *Magnolia* includes nearly 160 species distributed in the Neotropics between sea level and 3200 m (Cicuzza et al., 2007). The neotropical countries with the highest number of species are Colombia (40 species) and Mexico and Ecuador (39 and 24 species, respectively). Neotropical *Magnolia* is most diverse throughout the Mexico, Central America and Andes (Venezuela, Colombia, Ecuador, Perú and Bolivia) bioregions, where species are found from lowland vegetation to montane forests. Additionally, several taxa are found along the Pacific Coast of Colombia and Ecuador (e.g., *M. mahechae* (Lozano) Govaerts; *M. mindoensis* A. Vázquez, D.A. Neill & Dahua) and the Amazon basin (e.g., *M. clementinana* F. Arroyo & M. Serna; *M. manuensis* F. Arrollo). A few species are found on rocky slopes and

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This contribution is a product of "Proyecto BPIN No. 2020000100003—Investigación de la biodiversidad de Boyacá: complementación y síntesis a través de gradientes altitudinales e implicaciones de su incorporación en proyectos de apropiación social de conocimiento y de efectos de cambio climático." The authors would like to thank Julio Betancur (COL) for his herbarium assistance, Ariadna Valenzuela Zúñiga for preparing the illustration, to Fredy Archila (BIGU) for his help locating current literature, Noralba Carvajal Cogollo for her help with the Colombian map, and, especially, J. Orlando Rangel-Ch. (COL) for his kind colaboration and for the use of his office and laboratory facilities. This work would not be possible without the International Plant Names Index, JSTOR Global Plants, Biodiversity Heritage Library, and Tropicos.

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oligotrophic soils derived from the Precambrian crystalline basement of the Guayana Shield (e.g., *M. chimantensis* Steyerm. & Maguire; *M. ptaritepuiana* Steyerm.; *sensu* Berry and Miller, 2001). Others are endemic to particular geographical areas, such as the Caribbean islands (e.g., *M. cristalensis* Bisse; *M. cubensis* Urban, *sensu* Ulloa Ulloa et al., 2018 onwards) or in Central to Southeast Brazil (e.g., *M. brasiliensis* C.O. Azevedo, A.F.P. Machado & A. Vázquez; *M. paranaensis* A. Vázquez, *sensu* Azevedo et al., 2018).

Classification within the Magnoliaceae is largely disputed, and authors are not in agreement about the number of taxa: subfamilies (0–2), genera (1–11), and sections (0–11) (Azuma et al., 2001, Li and Conran, 2003, Figlar and Nooteboom, 2004; Kim and Suh, 2013). A recent molecular study, based on phylogenetic, morphological, and geographic evidence, recognized two subfamilies in Magnoliaceae (Liriodendroideae and Magnolioideae) each with one genus, *Liriodendron* and *Magnolia* (Wang et al., 2020), respectively. In this work *Magnolia* was divided into 15 sections. In the Neotropics, most authors agree with Figlar and Nooteboom (2004) and Kim and Suh (2013), who consider the Neotropical Magnoliaceae to consist of a single genus, *Magnolia*, which is divided into three sections: sect. *Macrophylla* Figlar & Nooteboom, sect. *Magnolia* and sect. *Talauma* (Juss.) Baill. However, Wang et al. (2020) added a fourth section, sect. *Splendentes* Dandy ex J.A. Vázquez, based on whole plastid genome analysis, that strongly supports the *Talauma* clade as sister to the *Splendentes* clade. Their phylogenetic analyses sampled very few taxa of subsects. *Dugandiodendron* and *Splendentes*, and each of them, indeed, forms a subclade. Rather, they included taxa of subsect. *Dugandiodendron* and subsect. *Splendentes* in sect. *Splendentes*, and subsect. *Chocotalauma* A. Vázquez, J.A. Pérez & F. Arroyo in sect. *Talauma*.

In the past decade, 82 new species of Magnoliaceae have been described from the Neotropics (Vázquez-García et al., 2012a,b,c, 2013a,b,c,d, 2015a,b, 2016a,b, 2017a,b,c, 2018, 2019, 2020, 2021a,b, 2022a,b; Marcelo-Peña and Arroyo, 2013, Arroyo and Pérez, 2013, Arroyo et al., 2013, Arroyo, 2014; Molinari-Novoa, 2016; Pérez et al., 2016; Azevedo et al., 2018; Arrollo et al., 2019; Cogollo-Pacheco et al., 2019; Arrollo and Serna-González, 2020; Fernández-Hilario et al., 2020; Archila et al., 2022). This is the result of establishing permanent monitoring plots and from botanical exploration in unexplored tropical regions, and illustrates the need for further fieldwork for certain groups of neotropical plants (Vázquez-García et al., 2016a; 2017a).

The present work describes and illustrates a new species of *Magnolia* sect. *Talauma*, found in an isolated population composed of nine individuals located in disturbed and highly fragmented montane forest and pasture lands with dispersal trees. This discovery was made by a team of botanists from the project entitled: "Investigación de la biodiversidad de Boyacá: complementación y síntesis a través de gradientes altitudinales e implicaciones de su incorporación en proyectos de apropiación social de conocimiento y de efectos de cambio climático." Currently, the distribution of this new species is restricted to Pajarito Municipality, Boyacá department. However, a more detailed exploration is required in other forest remnants of neighboring municipalities in southeastern Boyacá and northern Santander departments, where additional populations of this species may occur. This contribution increases the number of *Magnolia* species known in Colombia, the country with the highest diversity of the genus in the neotropics, to forty. Of these 40 species, thirty-one are endemic. The department of Antioquia has the highest number of species (13) (Serna-González and Velásquez, 2016; Cogollo-Pacheco et al., 2019).

MATERIALS AND METHODS

We examined, in person, 300 herbarium specimens from South America deposited in the *Magnolia* collection in the "Herbario de la Universidad Nacional de Colombia (COL). In addition, all type specimens, as well as general collections, hosted by virtual herbaria, were consulted, including those maintained by the Field Museum (F; http://emuweb.fieldmuseum.org/botany/taxonomic.php), Instituto Nacional de Pesquisas da Amazônia (INPA; http://inct.florabrasil.net/en/), JSTOR Global Plants (http://plants.jstor.org), Museum of Natural History, Paris (P; http://www.mnhn.fr), Reflora Virtual Herbarium (http://reflora.jbrj.gov.br/reflora/), speciesLink (https://specieslink.net/), Smithsonian Institution (US; https://collections.si.edu/search/), Universidad de Antioquia, Colombia (HUA; http://www2.udea.edu.co/herbario/paginas/consultas/consultarEjemplares.iface), Universidad Nacional Autónoma de México (MEXU; https://datosabiertos.unam.mx/biodiversidad/), and the National Herbarium of The Netherlands (U; https://www.nationaalherbarium.nl/).

This work is based on morphological and herbarium studies. The species description was based on field observations (flower material was preserved in alcohol) and herbarium specimens. The flowers from herbarium specimens were rehydrated for three days before measuring using a 1:1 combination of glycerin and physiological solution.

The World Checklist of Vascular Plants (kew.org) and general taxonomic literature on *Magnolia* were consulted; in particular, Nooteboom (1993), Frodin and Govaerts (1996), Azuma et al. (2001), Li and Conran (2003), Figlar and Nooteboom (2004), Kim and Suh (2013), Sánchez-Velásquez et al. (2016), and Wang et al. (2020). In addition, neotropical bibliographic sources were analyzed; Lozano-Contreras (1983, 1994), Arroyo et al. and Vázquez-García et al. contributions (see Literature Cited). The *Catálogo de plantas y Líquenes de Colombia* (Serna-González and Velásquez, 2016) was also reviewed. Additionally, the International Plant Names Index (https://www.ipni.org/), the online botany collections of the Smithsonian National Museum of Natural History (https://naturalhistory.si.edu/research/botany), and Tropicos (http://legacy.tropicos.org/Home.aspx) were consulted to update the current nomenclature and geographical information.

Terminology for vegetative characters, inflorescences, flowers, and fruit morphology follow Lozano-Contreras (1983, 1994) and Font-Quer (2001). Conservation status (IUCN, 2020), the extent of occurrence (EOO), and area of occupancy (AOO) were calculated using the supporting Red List threat assessments with GeoCAT (Bachman et al., 2011; https://geocat.kew.org/)

TAXONOMY

Magnolia pajarito Aymard, Rodríguez-D. & M. Escobar, *sp. nov*. TYPE: COLOMBIA: Boyacá: Municipio Pajarito, Vereda Corinto, Finca el Porvenir, selva subandina muy intervenida del piedemonte llanero, 1669 m, 5°23'47.6"N, 72°43'34.8"W, 11 Noviembre, 2021 (fl), *Juan D. García-G., Dayro Rodríguez-D. & Magda Escobar-A. 2328* (Holotype: COL; Isotype: UPTC). Fig. 1–2.

Magnolia pajarito belongs in *M*. sect. *Talauma* and is similar to *M. arcabucoana*. It differs from the latter in having leaf blades 7–17 × 2.5–10 cm, oblanceolate or obovate-elliptic, midvein on the lower surface covered by erect and adpressed yellowish trichomes, more dense at the base, secondary veins 7–9; adaxial canaliculate scar along the entire lenght of the petiole, vaginal hypsophyl one, sepals widely ovate, 3.0–3.2 × ca. 2.0 cm, inner petals lanceolate, stamens 21–35 in 2 series, and 11–12 carpels (Table 1).

Evergreen trees, 9–30 m high, 38–62 cm DBH, branches and branchlets fragrant, glabrous; apical bud lanceolate, glabrous; twig internodes 0.8–1.8 × 0.5–0.8 cm, glabrous; stipules not seen, soon deciduous, adnate to the petioles, leaving a scar on both edges of the adaxial side of petioles and converging apically. *Leaf* blades obovate, oblanceolate or obovate-elliptic, 7–17 × 2.5–10 cm, discolorous, dull on the upper surface (when dried), shiny on the lower surface, glabrous on both sides, except along the midvein on the lower surface, which is covered by erect and adpressed yellowish trichomes, more dense at the base, glabrescent when mature, coriaceous; the base obtuse or cuneate, the apex rounded or obtuse, sometimes very short mucronate, margin entire, revolute, midvein canaliculate above, prominent beneath, venation brochidodromous, secondary veins, 7–9, prominent on both surfaces, veinlets strongly reticulate forming net venation on both surfaces. *Petioles* 1–4.5 cm long, 1–2 mm wide, 1–4 mm wide at the base, glabrous, with an adaxial canaliculate scar along the entire length of the petiole. *Floral peduncles* 3–6 cm long, glabrous, with 6–8 segments differentiated by anular scars, the major segment length ca. 1 cm, flower buds ellipsoid, 1.5–2 × 1–1.2 cm long, rostrate at the apex; spathaceous bract (vaginal hypsophyl) 2–2.5 × ca. 3 cm, orbicular, glabrous on both sides, rigid. *Flowers* 4–5 cm in diameter; *Sepals* 3, 3–3.2 × ca. 2 cm, widely ovate, gradually narrower basally (ca. 1.1 cm wide), concave, white, revolute and acute at the apex, truncate at the base; *Petals* 6, white, unequal, concave, glabrous, outer petals 3–3.2 × ca. 1.1 cm, obovate, gradually narrower basally (ca. 5 mm wide), acute at the apex, truncate at the base, inner petals 2.2–2.5 × 0.5–0.6, lanceolate, gradually narrower basally (3–3.5 cm wide), revolute and acute at the apex, truncate at the base; *Stamens* 21–35, 1.5–1.6 × ca. 0.25 cm, arranged in two series, short acute at the apex; *Gynoecium* ellipsoid, 1.5–2 × 0.6–1 cm, formed by 11–12 carpels, glabrous, without persistent styles; *Fruit* narrowly ellipsoid, ca. 2.8 × ca. 1.2 cm, follicles ca. 12, glabrous, costate, slightly gibbous.

Phenology: The type specimen with flowers and young fruits was collected in November, and with flowers in April (Fig. 2).

Etymology: *Magnolia pajarito* is named after Municipio Pajarito, Boyacá department, the type locality (Fig. 2–3). The Municipio Pajarito is located on the Andean slopes of the Eastern Cordillera of Colombia ("Cordillera Oriental") in the southeastern portion of Boyacá Department. This region is well-known as a geostrategic territory for access from the Andes to the foothills ("piedemonte llanero"). The epithet also honors the civilian rural societies of Pajarito, who resisted with courage and wisdom more than three decades of armed conflict in their region (for a review see Díaz-Bonilla, 2019).

Distribution and habitat: The species is known to occur in montane forest remmants and pasture lands with dispersal trees between 1500 and 1700 m. In the type locality, *M. pajarito* grows in forest consisting of medium to tall trees. Some dominate species in these forests are *Alchornea glandulosa* Poepp. (Euphorbiaceae)*, Vismia mandurr* Hierom. (Hypericaceae)*, Cecropia angustifolia* Trécul (Urticaceae), *Beilschmiedia* cf. *B. tovarensis* (Klotzsch & H. Karst. ex Meisn.) Sach Nishida (Lauraceae), *Guatteria hirsuta* Ruiz & Pav. (Annonaceae)*, Henriettea tuberculosa* (Donn. Sm.) L. O. Williams (Melastomataceae)*, Meriania haemantha* (Planch. & Lind.) H. Mend. & Fern. Alonso (Melastomataceae), *Vochysia megalophylla* Stafleu (Vochysiaceae), *Billia rosea* (Planch & Lind.) C. Ulloa & P. Jørg. (Sapindaceae), and *Geonoma undata* Klotzsch and *Wettinia praemorsa* (Willd.) Wes. Boer (Arecaceae).

Conservation status. Since this species is currently known only from the type locality, and from four additional collections made around the type locality, consisting of 9 individuals, it is reported here as a very rare species. Under IUCN (2020) guidelines, fewer localities are required in order to assess its conservation status as data deficient (DD). Nevertheless, it should be regarded as Endangered (EN) and Critically Endangered (CR) based on the criterion B1ab(iii)+2ab(iii), due to the low number of known localities (five), its estimated Area of Occupancy, 20,000 km², and its estimated Extent of Occurrence, 1698 km² (IUCN, 2020). Additionally, the Pajarito municipality has been highly deforested over the past six decades, especially in the years during the pre- and post-conflict period. The expansion of deforestation and degradation continues unregulated, with significantly greater agricultural use and pasture lands with dispersal trees, that will accelerate land cover change in the coming years (for a review see Murillo-Sandoval et al., 2021). Although conservation status assessments can be made for species with such small numbers of collections (Rivers et al., 2011), it may be difficult to determine whether the appearance of rarity in a species is due to the lack of, or outdated, data, or to its actual rarity. Furthermore, the area where *Magnolia pajarito* was found is not currently protected by the Colombian National Park service (*Parques Nacionales Naturales de Colombia*).

Notes about *Magnolia* conservation status. Most of the 50% of the species of *Magnolia* included in the Red List of Magnoliaceae are listed as threatened in their geographical distribution range (Cicuzza et al., 2007; Sánchez-Velásquez et al., 2016). It is estimated that 22% of *Magnolia* species are critically endangered (CR), 41% are endangered (EN), 16% are vulnerable (VU), 5% are near threatened (NT), 6% are of least concern (LC), and 6% are considered data deficient (DD). In Colombia, the situation is very similar; all species of this genus are threatened in some risk category (Calderón et al., 2007; Serna-González and Velásquez, 2016).

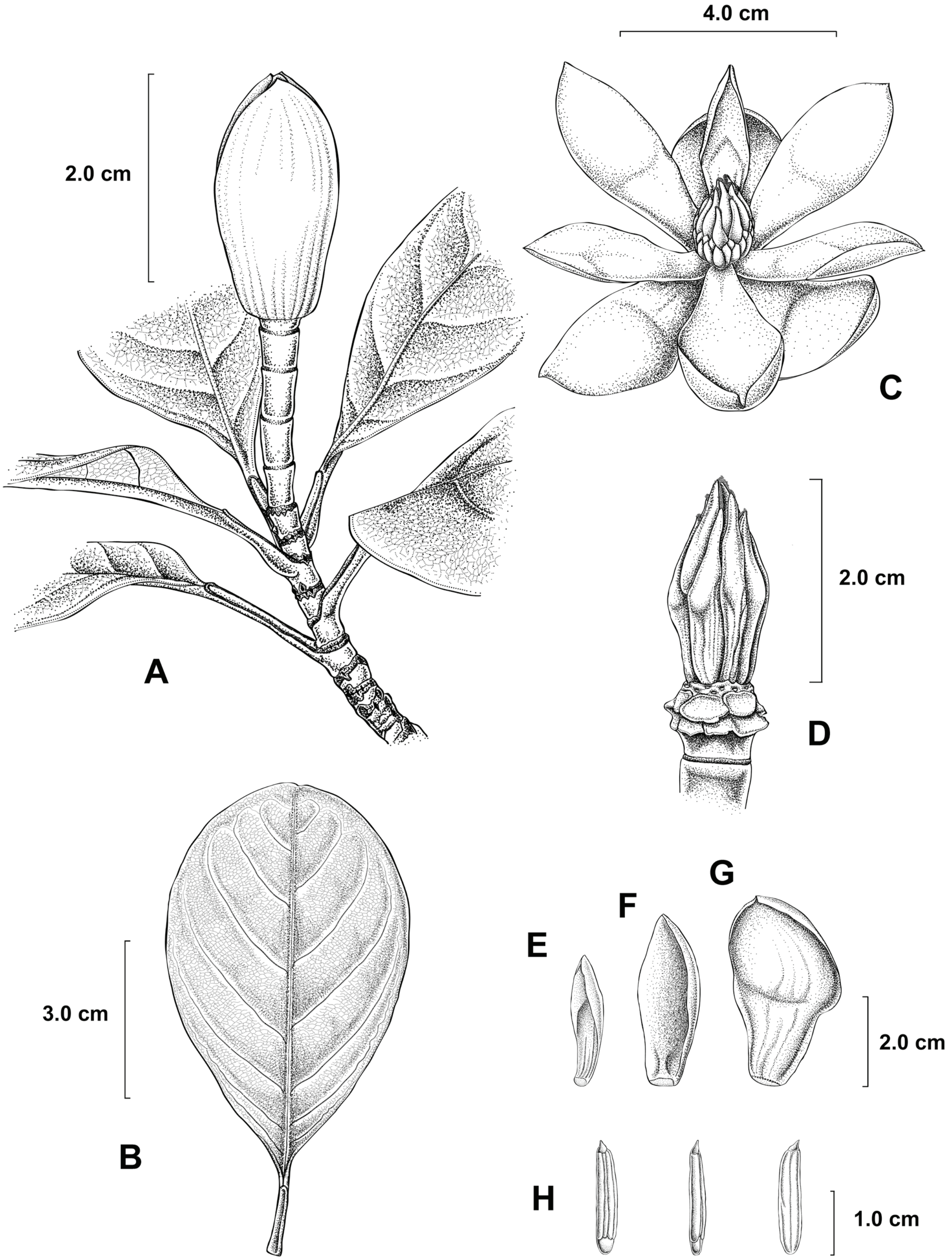

FIGURE 1. *Magnolia pajarito* Aymard, Rodríguez-D. & M. Escobar. **A**, Branch showing the spathaceous bract in bud flower; **B**, Leaf adaxial surface showing the canaliculate scar along the entire length of petiole; **C**, Flower; **D**, Gynoecium; **E**, Inner petal; **F**, Outer petal; **G**, Sepal; **H**, Stamens. Drawn by A. Valenzuela Zúñiga based on the holotype.

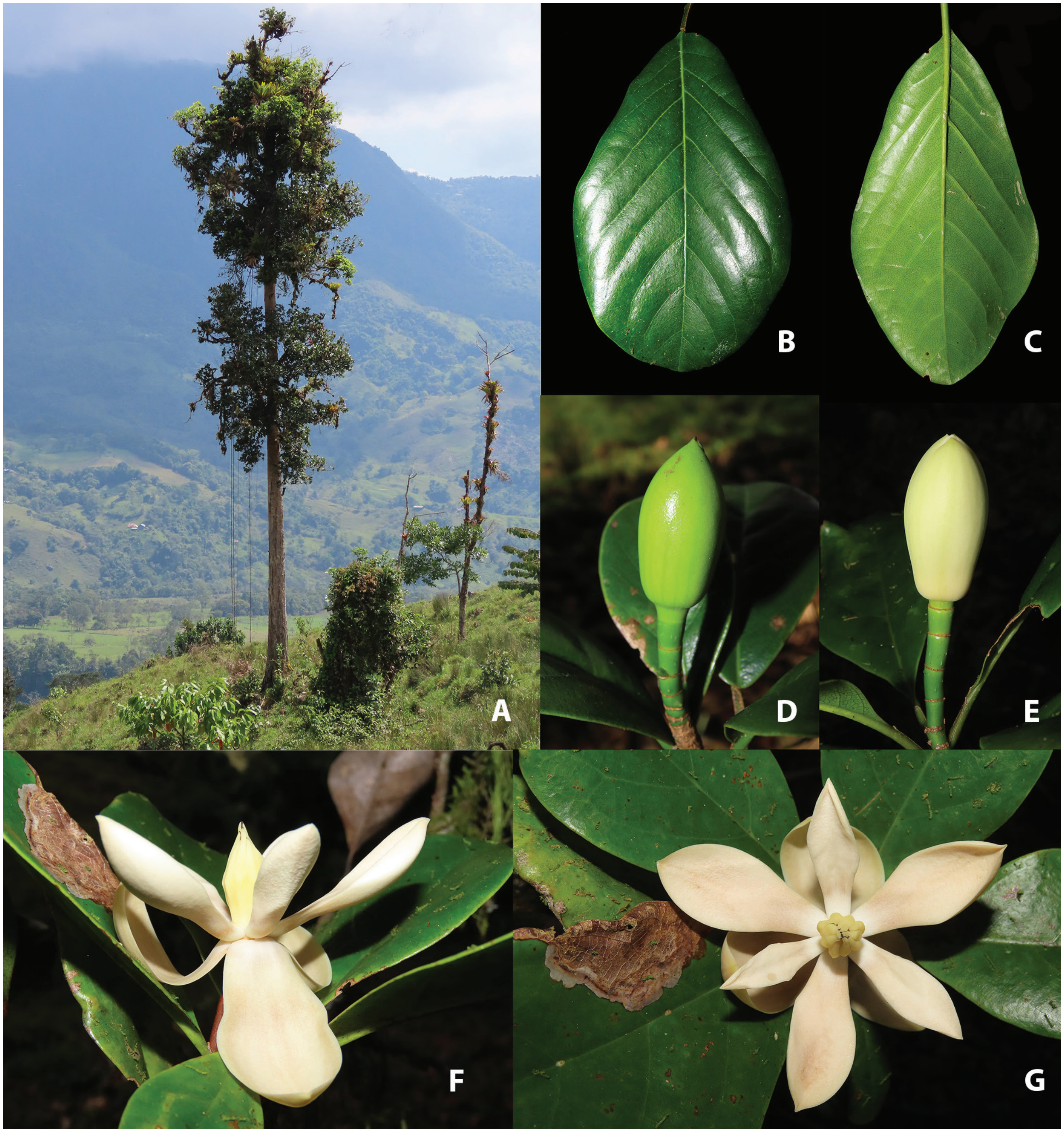

FIGURE 2. *Magnolia pajarito* Aymard, Rodríguez-D. & M. Escobar. **A**, Habit; **B**, Leaf adaxial size partially showing the canaliculate scar along the petiole; **C**, Leaf abaxial surface; **D**, Flower bud with spathaceous bract; **E**, Flower bud without spathaceous bract showing one of the sepals in the foreground; **F**, Flower, lateral view; **G**, Flower, upper view. Photographs by D. Rodríguez-D.

A new Red List of Magnoliaceae was published in 2016 (Rivers et al., 2016). This work contains conservation assessments for 304 Magnoliaceae species. All assessments were submitted for publication in the IUCN Red List of Threatened Species and reveal that a large proportion of Magnoliaceae species are threatened with extinction in the wild (at least 48%). Furthemore, nearly one third of all species are still too poorly known to make a conservation assessment. In an overall context, this analysis concluded that only one in five species of Magnoliaceae is considered not threatened, and that the neotropics has the highest proportion of threatened *Magnolia* species (75%). A recent study found that the vulnerability of *Magnolia* species to future climate change is negatively related to range size (Wang et al., 2022). Wang et al. (2022) concluded that narrow-ranged *Magnolia* species distributed in Asia are more vulnerable than those distributed in the Americas, and that protected area coverage is lower in Asia than in the Americas. Moreover, the conservation status

Table 1. Comparison of diagnostic morphological characters of *Magnolia pajarito* Aymard, Rodríguez-D. & M. Escobar and closely related species.

Character	*M. arcabucoana*	*M. caricifragrans*	*M. santanderiana*	*M. pajarito*	*M. virolinensis*
Internodes of the young branchlets	glabrous	tomentose	tomentose	glabrous	puberulent
Leaf blade	30–33 × 16–18 cm, obovate, glabrous on both surfaces	12–30 × 7–15 cm, obovate, pubescent on the lower surface	12–22 × 7–15 cm, oblong, pubescent on the lower surface, more dense along the midvein	7–17 × 2.5–10 cm, oblanceolate or obovate-elliptic, glabrous on both surfaces, except midvein on the lower surface which is covered by erect and adpressed yellowish trichomes	12–21 × 5–11 cm, obovate or elliptic, with sparse trichomes on the lower surface
Secondary veins	18–21	15–18	9–12	7–9	12–15
Adaxial canaliculate scar of petiole	covers ca. 75% length of petiole	along the entire length of petiole	along the entire length of petiole	along the entire length of petiole	covers ca. 60% length of petiole
Vaginal hypsophyl	2	3	(1–)2	1	2–3(–4)
Sepal	3, obovate, ca. 2.5 × ca. 1.3 cm	3, elliptic, 3.8–5.3 × 1.6–3 cm	3(–4), oblong, ca. 3.8 × ca. 1.4 cm	3, widely ovate, 3–3.2 × ca. 2 cm	3, obovate, ca. 2.9 × ca. 1.3 cm
Petal	6, outer obovate to ovate, ca. 2.5 × ca. 1 cm; inner rhomboid, ca. 2 × ca. 1 cm	6(–7), elliptic, outer 4–5.55 × 3.30–5.5 cm; inner ca. 4.2 × ca. 1.8 cm	7(–8), outer obovate, ca. 5 × ca. 1.8 cm; inner. lanceolate, ca 4.1 × ca. 1.3 cm	6, outer obovate, 3–3.2 × ca. 1.1 cm; inner lanceolate, 2.2–2.5 × 0.5–0.6	6, obovate, outer ca. 3.3 × ca. 1.60; inner ca. 3.1 × 1.1 cm
Stamens	40 in 3 series	35–51 in 3 series	25–28 in 2 series	21–35 in 2 series	29–31 in 2 series
Carpels	12	10–17	10–12	11–12	8–11

ranking of *Magnolia* species classified by the IUCN Red List will likely change as the climate continues to change. Some species classified as Near Threatened and of Least Concern were estimated to be more vulnerable to climate change than species currently classified as Endangered.

Magnolia has evoloved through allopatric speciation; i.e., new species evolve as a result of geographic isolation and new selection pressures. As a result, their presence in forests tends to be scanty (Sánchez-Velásquez et al., 2016). In tropical mountain landscapes of the Andes, changes in habitat suitability are expected to be of a mixed character, favorable for some tree species but not for others (Vázquez-García et al., 2021a). In the case of *Magnolia*, the narrow distribution ranges of most species may constitute a risk factor that could lead to the disappearance of suitable habitats due to climate change projected to the end of the 21st century (Vázquez-García et al., 2018).

Additional specimens examined: COLOMBIA. Boyacá: Municipio of Pajarito, aledaño a la quebrada Combita, bosque ripario intervenido, 5˚23'45.8"N, 72˚43'27.5"W, 1534 m, 04 Abril 2021 (fl), *M. Escobar-A., D. Rodríguez-D., M. L. Verdugo & P. Hernández-A. 382* (COL); Municipio Pajarito, Vereda Corinto, Finca El Porvenir, en potreros, 5˚24'01.9"N, 72˚43'39.5"W, 1551 m, 11 Septiembre 2021 (bud), *M. Escobar-A., Dayro Rodríguez-D., J. D. García-G. & J. Rodríguez-F. 713* (COL); Municipio Pajarito, Vereda Corinto, Finca El Porvenir, selva subandina muy intervenida del piedemonte llanero, 1710 m, 5˚23'45.4"N, 72˚43'44.4"W, 11 Noviembre 2021 (young fruit), *J. D. García-G., D. Rodríguez-D. & M. Escobar-A. 2332* (COL); Municipio Pajarito, Vereda Corinto, Finca El Porvenir, selva subandina muy intervenida del piedemonte llanero, 1605 m, 5˚23'50.4"N, 72˚43'28.3"W, 11 Noviembre 2021 (sterile), *J. D. García-G., D. Rodríguez-D. & M. Escobar-A. 2343* (COL).

The species described here is placed in sect. *Talauma* because it is an evergreen tree, the stipules are adnate to 40%–100% of the length of the petiole, caducous, and leave an adaxial canaliculate scar, and there is an absence of long filaments at the stamen connective (Figlar and Nooteboom, 2004; Wang et al., 2020). It is morphologically related to four other taxa in sect. *Talauma* (M. *arcabucoana* (Lozano) Govaerts*, M. caricifragans* (Lozano) Govaerts*, M. sandanderiana* (Lozano) Govaerts, and *M. virolinensis* (Lozano) Govaerts). However, it is roughly related to M. *arcabucoana* from the Andean forests of the Eastern Cordillera of Colombia (Lozano-Contreras, 1994). Both

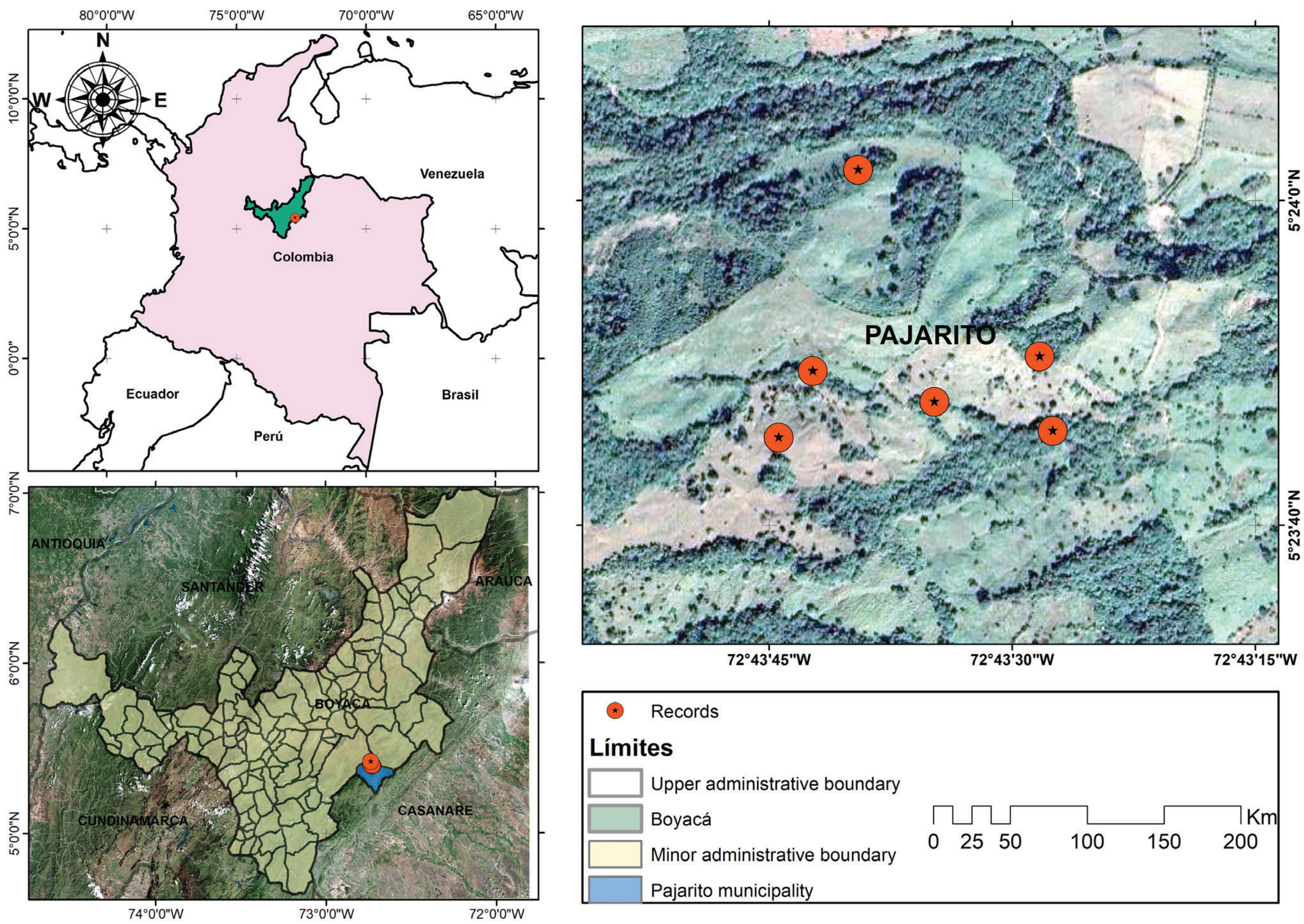

FIGURE 3. Geographical distribution of *Magnolia pajarito* Aymard, Rodríguez-D. & M. Escobar.

species have leaves that are dull on the upper surface, (when dried) shiny on the lower surface, have veinlets strongly reticulate forming net venation on both surfaces, the same shape in the outer petals, and have almost the same number of carpels. However, *M. pajarito* differs from *M. arcabucoana* and the other three species in the characters presented in diagnosis, Table 1, and in the key to the species presented below.

KEY TO THE SPECIES OF MAGNOLIA OF COLOMBIA

Modified from Lozano-Contreras, 1994; Species indicated with an asterisk (*) are endemic to Colombia

1a. Petioles without an adaxial canaliculate scar 2
1b. Petioles with an adaxial canaliculate scar 17
2a. Leaf blade elliptic 3
2b. Leaf blade obovate, widely obovate, ovate, suborbicular or orbicular 9
3a. Fruits globose, spheroid or ovoid 4
3b. Fruits ellipsoid 5
4a. Internodes of the young branchlets covered by dense yellow indument; leaf blade chartaceous . . . . . . *M. calophylla** (Colombia: Nariño)
4b. Internodes of the young branchlets glabrescent or with sparse cream trichomes; leaf blade membranaceous or papyraceous . . . . *M. striatifolia* (Colombia: Nariño; Ecuador)
5a. Leaf blade with base decurrent and revolute, fruits small, 1.17–2.9 cm long . . . . *M. frontinoensis** (Colombia: Antioquia)
5b. Leaf blade with base acute, attenuate, obtuse, truncate or cuneate, fruits larger than 3 cm 6
6a. Leaf blade on the lower surface glabrous or with few trichomes on the veins . . . . *M. urraoensis** (Colombia: Antioquia)
6b. Leaf blade on the lower surface pubescent 7
7a. Youngest internodes of the branches with a ring of woolly, golden pubescence . . . . *M. coronata** (Colombia: Antioquia)
7b. Youngest internodes of the branches without a ring of woolly, golden pubescence, but brown lanate or covered by a hispid indument 8
8a. Leaf blade on the lower surface with a short hispid indument; stamens 58–79 in 4 series . . . . *M. mahechae** (Colombia: Valle)
8b. Leaf blade on the lower surface with a large lanate indument; stamens ca. 144 in 6 series . . . . *M. calimaensis** (Colombia: Valle)
9a. Fruits globose, spheroid or ovoid . . . . *M. neomagnifolia* * (Colombia: Chocó, Valle)
9b. Fruits ellipsoid 10

Key to the species of Magnolia of Colombia cont.

Modified from Lozano-Contreras, 1994; Species indicated with an asterisk (*) are endemic to Colombia

10a. Leaf blades orbicular, suborbicular or widely obovate 11

10b. Leaf blades obovate or widely elliptic 12

11a. Internodes of the young branchlets tomentose, leaf blade suborbicular or widely obovate, 8–10 cm wide; petals 8; stamens 83–89 in 6 series . . . . *M. yarumalensis** (Colombia: Antioquia, Risaralda)

11b. Internodes of the young branchlets glabrous, leaf blade orbicular to suborbicular, 13–15 cm wide; petals 8–10; stamens ca. 155 in 5 series . . . . *M. argyrotricha** (Colombia: Boyacá, Santander)

12a. Leaf blade on the lower surface glabrous or with sparse trichomes . . . . *M. cararensis** (Colombia: Norte de Santander)

12b. Leaf blade on the lower surface densely pubescent 13

13a. Internodes of the young branchlets with a ring of woolly, golden pubescence. . . . . *M. coronata** (Colombia: Antioquia)

13b. Internodes of the young branchlets without a ring of woolly, golden pubescence, but glabrous, creamy lanate, densely gray villose or covered with adpressed yellow indument 14

14a. Internodes of the young branchlets glabrous; leaf blade 7–10 cm long, apex emarginate, lower surface covered by a short pilose indument . . . . *M. guatapensis** (Colombia: Antioquia)

14b. Internodes of the young branchlets pubescent; leaf blade 10–22 cm long, apex abruptly acuminate, lower surface covered with a lanate-lanuginous indument 15

15a. Bark, branches and branchlets strongly lenticellate; secondary nerves 27–25; petioles 2.8–4.5 cm long . . . . *M. lenticellata** (Colombia: Antioquia)

15b. Bark, branches and branchlets without lenticels or few; secondary nerves 8–24; petioles 1.2–2.6 cm long 16

16a. Leaf blade ca. 19–21 × 10–12, obovate to widely elliptic; stamens 106–120, fruit glabrous. . . . . *M. colombiana** (Colombia: Huila)

16b. Leaf blade 10–17 × 5–11 cm, obovate; stamens 42–49; fruit lanate. . . . . *M. betuliensis** (Santander)

17a. Fruits globose, spheroid or ovoid with more than 35 carpels 18

17b. Fruits ellipsoid, with fewer than 30 carpels, rarely more 26

18a. Adaxial canaliculate scar covering 40% to 75% length of petiole 19

18b. Adaxial canaliculate scar along the entire length of petiole 20

19a. Internodes of the young branchlets and petioles glabrous; leaf blade obovate, base decurrent; petiole ca. 2 cm long; vaginal hypsophyl one. . . . . *M. narinensis** (Colombia: Nariño)

19b. Internodes of the young branchlets; petioles densely pubescent; leaf blade elliptic, base attenuate; petiole 3–7 cm long; vaginal hypsophyl 4. . . . . *M. katiorum** (Colombia: Nariño)

20a. Internodes of the young branchlets; petioles densely pubescent; carpels 38 . . . . *M. neillii* (Colombia: Amazonas; Ecuador)

20b. Internodes of the young branchlets and petioles glabrous or petioles with scatered trichomes; carpels more than 50 21

21a. Petioles stout, ca. 5 mm diameter; leaf blade ovate; petals 8 . . . . *M. hernandezii** (Colombia: Antioquia, Quindío, Risaralda, Valle)

21b. Petioles thin, 2–4 mm diameter; leaf blade elliptic, narrowly elliptic, widely elliptic, obovate or trullate; petals 6, rarely 7 22

22a. Vaginal hypsophyl 6–9; stamens 252–375 . . . . *M. cespedesii** (Colombia: Cundinamarca)

22b. Vaginal hypsophyl 1–3; stamens 74–255 23

23a. Leaf blade elliptic, narrowly elliptic to widely elliptic, 6–11 cm wide; petiole 2–5.5 cm long 24

23b. Leaf blade obovate or trullate, 11–15 cm wide; petiole 4.5–8.5 cm 25

24a. Foliar bud glabrous; leaf blade on fruit branches not resupinate; vaginal hypsophyl two; outer petals 6.8–7.3 × 4.8–7.1 cm, inner petals 5.6–6.5 × 4–4.2 cm . . . . *M. sambuensis* (Colombia: Antioquia, Chocó, Córdoba; Panamá)

24b. Foliar bud sericeous; leaf blade on fruit branches resupinate (upside down due to twisting of the petiole); vaginal hypsophyl three; outer petals 5.8–6.2 × 2.8–4.2 cm, inner petals ca. 5.1 × 2.3 cm . . . . *M. resupinatifolia** (Colombia: Santander)

25a. Petiole glabrous; petals ca. 7.6 cm long; stamens 222–247; carpels more than 120. . . . . *M. silvioi** (Colombia: Antioquia)

25b. Petiole with large trichomes; petals 4–5.5 cm long; stamens 74; carpels less than 90 . . . . *M. wolfii** (Colombia: Risaralda)

26a. Adaxial canaliculate scar covering 40% to 80% length of petiole 27

26b. Adaxial canaliculate scar along the entire length of petiole 31

27a. Leaf blades elliptic, widely elliptic or (sub)elliptic, apex acute or acuminate 28

27b. Leaf blade obovate, apex obtuse 29

28a. Leaf blades elliptic or (sub)elliptic, 8–12 secondary nerves; petals 8, outer petals punctate . . . . *M. jardinensis** (Colombia: Antioquia)

28b. Leaf blade widely elliptic, 13–21 secondary nerves; petals 6, outer petals not punctate 30

29a. Internodes of the young branchlets 1.6–3.6 × 0.8–1.1 cm; leaf blades ca. 1.2 × 6.8 cm, secondary nerves 17–21; adaxial canaliculate scar covering 75% to 80% length of petiole; petals ca. 3.1 × ca. 1.1 cm; stamens 32–34, all entire . . . . *M. gilbertoi** (Colombia: Quindío, Risaralda, Valle)

29b. Internodes of the young branchlets ca.1 × ca. 0.5 cm; leaf blades (13–)15–32 × (7.5–)9–18, secondary nerves 13–17; adaxial canaliculate scar covering 40% to 60% length of petiole; petals 6.4–7.1 × 3.3–3.6 cm; stamens 84–86, several bifide and trifide . . . . *M. mindoensis* (Colombia: Nariño; Ecuador)

30a. Leaf blade 14–16 cm long, coriaceous, secondary nerves 12–15; petiole 2–2.5 cm long; stamens 32–34 . . . . *M. virolinensis** (Boyacá, Santander)

30b. Leaf blade 28–32 cm long, papyraceous, secondary nerves 18–21; petiole 3–4 cm long; stamens 40 . . . . *M. arcabucoana** (Colombia: Boyacá, Cundinamarca, Santander)

31a. Internodes of the young branchlets glabrous. 32

31b. Internodes of the young branchlets pubescent 36

Key to the species of Magnolia of Colombia cont.

Modified from Lozano-Contreras, 1994; Species indicated with an asterisk (*) are endemic to Colombia

32a. Leaf blade papyraceous, base attenuate; sepals panduriform (having rounds ends and a contracted center) . . . . . *M. henaoi** (Colombia: Huila)

32b. Leaf blade chartaceous or coriaceous, base obtuse, cuneate, rounded or acute; sepals obovate, ovate or widely ovate 33

33a. Leaf blade ovate; petals 8 . . . . *M. venezuelensis* (Colombia: Cesar, likely in Norte de Santander and Santander; Venezuela)

33. Leaf blade elliptic, obovate, oblanceolate or obovate-elliptic; petals 6 34

34a. Leaf blade 7–17 cm long, obovate, oblanceolate or obovate-elliptic, midvein on the lower surface covered with erect and adppresed yellowish trichomes, secondary veins 7–9; vaginal hypsophyl one; inner petals lanceolate . . . . *M. pajarito** (Colombia: Boyacá)

34b. Leaf blade 10–27 cm long, elliptic; midvein on the lower surface glabrous, secondary veins 11–16; vaginal hypsophyl 2–11; inner petals obovate 35

35a. Vaginal hypsophyl 8–11; stamens 30–43; carpels 9–14; fruit 6–7 cm long . . . . *M. polyhypsophylla** (Colombia: Antioquia)

35b. Vaginal hypsophyl 2; stamens 110–120; carpels 24–28; fruit ca. 4.5 cm long . . . . *M. gloriensis* (Colombia: Chocó; Nicaragua, Costa Rica, and Panamá)

36a. Leaf blade with apex obtuse or emarginate 37

36b. Leaf blade with apex acute or acuminate 38

37a. Leaf blade oblong, base obtuse; petiole 5–6 cm long; petals spathulate; stamens 25–28; fruits 4–5 cm long . . . . *M. santanderiana** (Colombia: Boyacá, Santander)

37b. Leaf blade elliptic or slightly obovate, base attenuate; petiole 2–3 cm long; petals obovate; stamens 29–41; fruits 8–9 cm long . . . . *M. georgii** (Colombia: Boyacá, Santander)

38a. Leaf blade elliptic 39

38b. Leaf blade obovate, oblong or ovate 40

39a. Leaf blade 11–13 cm wide; petiole pubescent; stamens 31–38. . . . . *M. chocoensis** (Colombia: Chocó; Risaralda)

39b. Leaf blade 5–10 cm wide; petiole glabrous or with sparse trichomes; stamens 81–87 . . . . *M. rimachii* (Colombia: Amazonas; Ecuador and Perú)

40a. Leaf blade 12–30 × 7–22 cm, obovate or oblong, base cuneate, pubescent on the lower surface; petiole 1.7–4.7 cm long; 35–51 stamens . . . . *M. caricifragrans** (Colombia: Arauca, Boyacá, Cundinamarca, Norte de Santander)

40b. Leaf blade 14–17 × 7–9 cm, ovate, base obtuse; glabrous or with sparse trichomes on the lower surface; petiole ca. 2 cm long; 50–52 stamens . . . . *M. espinalii** (Colombia: Antioquia)

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NOVELTIES IN *SECURIDACA* (POLYGALACEAE, POLYGALEAE) FOR THE FLORAS OF COLOMBIA AND VENEZUELA

Gerardo A. Aymard-Corredor[1]

Abstract. A new species and two new records of *Securidaca* were found during the preparation of an updated checklist of Polygalaceae for the *Nuevo Catálogo de la Flora de Venezuela* and *Catálogo de Plantas y Líquenes de Colombia*. *Securidaca aquae-nigrae* from the upper Rio Negro (northern/northwestern Amazon basin) and part of the adjacent southwestern Orinoco basins of Colombia and Venezuela, is described and illustrated, and its morphological relationships with an allied species are discussed. This new species is similar to *S. coriacea*, but it differs by its leaves, the size and shape of the outer and lateral enlarged sepals, the inflorescence and fruit size, and the keel petal without a well-developed apical crest. *Securidada fragilis* and *S. leiocarpa*, two species previously known from Ecuador and Peru, are reported here as new country records for the flora of Colombia. A lectotypification of *Securidaca schlimii* is also proposed. In a geographical and taxonomical context, *Securidaca amazonica* is considered different from *S. rivinifolia* and *S. volubilis*, while *S. densiflora* is treated here as a synonym of *S. pubescens*, and *S. dasycarpa* as a synonym of *S. diversifolia*. An updated key to the Colombian and Venezuelan species of *Securidaca* is presented.

Keywords: Rio Negro basin, Flora of Colombia and Venezuela, *Securidaca*, Polygalaceae

Resumen. Una nueva especie y dos nuevos registros del género *Securidaca* se encontraron durante la actualización de las listas de la familia Polygalaceae para el *Nuevo Catálogo de la Flora de Venezuela* y el *Catálogo de Plantas y Líquenes de Colombia*. *Securidaca aquae-nigrae* de la región del alto río Negro (norte/noroeste de la cuenca Amazónica) y parte de sector souroeste de la cuenca del río Orinoco de Colombia and Venezuela, es descrita, ilustrada y sus relaciones morfológicas con su especie afín son discutidas. Esta nueva especie es similar a *S. coriacea*, sin embargo, difiere por poseer las hojas, los sépalos externos y laterales desiguales en tamaño y forma, las inflorescencias y frutos de tamaño diferentes y la quilla (el pétalo inferior) sin una cresta bien desarrollada. *S. fragilis* y *S. leiocarpa*, dos especies previamente conocidas para Ecuador y Perú, se registran para la flora de Colombia. Se propone la leptotipificación de *Securidaca schlimii*. En un contexto geográfico y taxonómico, *S. amazonica* es considerada como una especie diferente de *S. rivinifolia* y *S. volubilis*. Igualmente, *S. densiflora* es tratada como un sinónimo de *S. pubescens* y *S. dasycarpa* de *S. diversifolia*. Se presenta una clave actualizada para diferenciar las especies del género *Securidaca* presentes en Colombia y Venezuela.

Palabras clave: Cuenca del río Negro, Floras de Colombia y Venezuela, *Securidaca*, Polygalaceae

Securidaca L., *nom. cons.*, is a pantropical genus of Polygalaceae encompassing about 66 species. The largest diversity (ca. 59 species) is found in the Neotropics (Eriksen et al., 2000; Aymard et al., 2004; Persson, 2004); a few species are found in Africa and Southeast Asia. The genus is absent in Australia (World Checklist of Vascular Plants; kew.org). *Securidaca* includes woody lianas and herbaceous vines, rarely shrubs or small trees (Eriksen and Persson, 2007).

Securidaca in the Neotropics is most diverse throughout the Amazon (Marques, 1996) and Andes bioregions, where the species are found in lowland ("terra firme") vegetation and montane forests. Several species are found on rocky slopes and oligotrophic soils derived from the Precambrian crystalline basement of the Guayana Shield (e.g., *S. cacumina* Wurdack, *S. marginata* Benth.), and drained by black water rivers (e.g., *S. savannarum* Wurdack) and on white sandy shrubby savannas and Caatinga forests (Aymard et al., 2004). The remaining species are found in more particular habitats, such as foothills in the low-medium to high altitude (500–2500 m) mountains of the Andes (e.g., *S. leiocarpa* S.F. Blake, *S. planchoniana* Killip & Dugand), along the Pacific Coast of Colombia and Ecuador (e.g., *S. calophylla* (Poepp.) S.F. Blake) and dry forests (e.g., *S. scandens* Jacq.). Several species have wide geographic distributions (e.g., *S. divaricata* Nees & Mart., *S. diversifolia* (L). S.F. Blake). Others are endemic to particular geographical areas, such as species found only on Caribbean islands (e.g., *S. lophosoma* Cheesman, *sensu* Ulloa Ulloa et al., 2018 Onwards), in Mesoamerica (e.g., *S. micheliana* Chodat, *sensu* Morales Quiros, 2014), or in Central to Southeast Brazil (e.g., *S. ovalifolia* A. St. Hil. & Moq., *S. tomentosa* A. St. Hil., *sensu* Marques, 1996).

Ethnobotanical information about neotropical species of *Securidaca* is not commonly found in the literature. The roots of several species of Polygalaceae are important sources of methyl salicylate (da Rocha et al., 2012), which is a compound used in traditional medicine, mainly as an anti-inflammatory, analgesic, expectorant or anti-rheumatic remedy (Effmert et al., 2005). This natural compound is

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widely used in flavoring for foods, candies, and beverages, and in the pharmaceutical industry for making topical ointments to treat muscle pains (Vitório et al., 2011). Aymard et al. (2004) reported that the bark and leaves of *Securidaca* ssp. (e.g., *S. pyramidalis* Sprague, *S. retusa* Benth) soaked in water produce a very good soap used in the upper Rio Orinoco basin and upper Rio Negro region of Colombia and Venezuela. These species are known locally as "Bejuco jabón". The roots of "African Violet tree" (*S. longipedunculata* Fresen.), have been used as a remedy to treat more that 24 diseases in Africa (Abubakar et al., 2019). The combination of the extracts of the roots, stems, and leaves of this taxon with artemether and lumefantrine exhibited effective antiplasmodial activity against *Plaspodium falciparum* welch strains (Ochora et al., 2022).

Polygalaceae is monophyletic and is currently divided into four tribes: *Carpolobieae* B. Eriksen, *Diclidanthereae* Reveal, *Polygaleae* Chodat and *Xanthophylleae* Chodat (Pastore et al., 2017; Mota et al., 2019). *Securidaca* is included in the tribe *Polygaleae* and is characterized by a 3-merous corolla (rarely also with two rudimentary lateral petals) and a bicarpellate gynoceium with one ovule per fertile locule (Eriksen, 1993a,b; Eriksen and Persson, 2007). *Securidaca* is further distinguished by the keel with a crest well-developed or obsolete, a one-seeded samara, and an unappendaged seed (Aymard and Campbell, 2008).

Like the subfamily Papilionoideae of the Fabaceae (Leguminosae), the subfamily *Polygaleae* has keel flowers that consist of three parts or a 3-merous corolla, a standard, two wings and a keel (Westerkamp and Weber, 1999; Prenner, 2004). However, several differences exist between the groups. The standard consists of a single median petal in Fabaceae, but is composed of two lateral sepals in Polygalaceae. The wings are formed by two petals in Papilionoideae, but are formed by two petaloid lateral sepals in Polygalaceae (Westerkamp and Weber, 1999). The keel is outlined by one or two fused lower lateral petals in legumes, but it comprises one median petal in Polygalaceae. The keel flowers consist of five petals in Polygalaceae, only three of which are fully developed, and the abaxial one forms an asymmetric keel (Persson, 2001; Castro et al., 2008). According to Aygören Uluer et al. (2022a,b), keel flowers in the two families represent a superficial functional and morphological convergence rather than a homologous similarity. Despite the fact that the flowers of these two Fabales lineages are not homologous, their similarity has led some authors to propose that this shared resemblance is more than convergance on a floral syndrome (Aygören Uluer et al. 2022a,b). These authors also noted that by the time keel flowers appeared in the Polygaleae (46.98–45.16 Ma), the subfamily, Papilionoideae, was already distributed almost globally.

Securidaca has never been monographed, and no formal infrageneric division has been proposed. Early contributions on this genus were made by De Candolle (1826), Sprengel (1826), Bennett (1874), Triana and Planchon (1862), Chodat (1895; 1896) and Wurdack (1957; 1972). Marques (1996) identified two taxonomically useful inflorescence characters that separate species: 1) flowers solitary or in short racemes 0.5–2.5 cm long, with 5–15(–20) flowers; and 2) inflorescences racemes or panicles, 2.5–45 cm long, with more than 15 flowers. Since the Wurdack (1972) and Marques (1996) publications, only four species have been described (Wallnöfer, 1998; Eriksen et al., 2000; Aymard and Campbell, 2007; Da Costa et al., 2013). In addition, the genus has been included in the Flora of Peru (Macbride, 1950), Flora of Panama (Woodson et al., 1969), Flora of Brazil (Marques, 1996), Flora of Ecuador (Eriksen et al., 2000), Flora of the Venezuelan Guayana (Aymard et al., 2004), and *Manual de Plantas de Costa Rica* (Morales Quiros, 2014).

While conducting herbarium research for an update of Polygalaceae in the *Nuevo Catálogo de la Flora de Venezuela* (Aymard and Campbell, 2008) and *Catálogo de Plantas y Líquenes de Colombia* (Aymard and Freire-Fierro, 2016), specimens of a morphologically distinct species of *Securidaca,* collected on the Upper Rio Negro southwestern Orinoco regions, were discovered. I have conducted floristic and phytogeographic studies in this area along the Colombian-Venezuelan border over the past four decades. This contribution increases to twenty-five the number of *Securidaca* species known from Colombia and twenty-seven from Venezuela. In a geographical and taxonomical context, *Securidaca amazonica* Chodat is treated here as distinct from *S. rivinifolia* A. St. Hil. and *S. volubilis* L., while *S. densiflora* Linden & Planchon is considered a synonym of *S. pubescens* DC., and *S. dasycarpa* Turcz. as a synonym of *S. diversifolia* (L.) S. F. Blake.

Materials and Methods

This work is based on morphological and herbarium studies in COAH, COL, GH, HUA, MO, NY, PORT, US and VEN (herbarium codes after Thiers, 2019). A 1:1 combination of glycerin and physiological solution was used over three days to hydrate and soften the dried flowers taken from herbarium specimens. The world checklist of vascular plants (WCVP) was consulted, and historical taxonomic literature on *Securidaca* was examined (http://www.biodiversitylibrary.org), primarily Bennett (1874), Triana and Planchon (1862), Linden and Planchon's Plantae Columbianae (see Sprague, 1926), and Chodat (1895; 1896). Current bibliographies were also reviewed: Wurdack (1957; 1972), Flora of Brazil (Marques, 1996), Flora of Ecuador (Eriksen et al., 2000), and the Flora of the Venezuelan Guayana (Aymard et al., 2004). The checklists *Nuevo Catálogo de la Flora de Venezuela* (Aymard and Campbell, 2008) and *Catálogo de Plantas y Líquenes de Colombia* (Aymard and Freire-Fierro, 2016) were also reviewed.

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

The specific terminology for vegetative characters, vestiture description, inflorescences, flowers, and fruit morphology follow Font-Quer (2001), Harris and Harris (2006), and Endress (2010). To determine the conservation status (according to IUCN categories and criteria; IUCN, 2017), the extent of occurrence (EOO) and area of occupancy (AOO) were calculated using the supporting Red List threat assessments with GeoCAT (Bachman et al., 2011), which is continually updated (https://geocat.kew.org/).

TAXONOMY

Securidaca aquae-nigrae Aymard, *sp. nov.* TYPE: VENEZUELA. Amazonas: Rio Guianía basin, along Pimichín-Yavita trail, ca. 1 km from Pimichín, aprox. 2°51'37"N, 67°32'8"W, 120–140 m, 10 October 1947 (fl), *B. Maguire, J. J. Wurdack & W. M. Keith 41787* (Holotype: VEN; Isotypes: COL, NY). (Fig. 1)

Securidaca aquae-nigrae is similar to *S. coriacea*, but morphologically it differs from the latter in having leaf blades on the main branches oblong to narrowly oblong or broadly ovate, charthaceus to subcoriaceous, puberulent to glabrous on the upper surface, short-pilose beneath, base rounded to slightly obtuse or acute, apex rounded, lateral veins 5–12, margins revolute, ciliate. Inflorescences 8–17 cm long; sepals of the outer whorl broadly oblong to slighty oblanceolate, adpressed pubescent at the middle outside, glabrous inside, margins ciliate, the outer sepals ca. 1.2 × ca. 1.0 mm, the inner sepal ca. 2 × ca. 1 mm, lateral enlarged sepals 5–6 × ca. 6 mm, broadly ovate with 14–16 major veins. The keel petal ca. 4 × 2.6–3 mm long, glabrous on both surfaces, without well-developed apical crest (ecristate), 0.25 mm long; fruit with spheroidal body ca. 5 × ca. 4 mm, dorsal secondary wing 0.4–0.5 mm long, oblong, primary wing 2.5–3 × 1–1.4 cm, sparsely pilose.

Liana or shrubby vine, lateral branches not forming sensitive hooks or looped tendrils. *Branches and branchlets* terete, dense short-pilose, sparsely pilose to glabrescent when mature, longitudinally striate, bark flaking off in small plates when mature; nodal glands at the base of the petioles, branchlets and pedicels conspicuous, circular, ca. 0.5–1.0 mm in diameter, glabrous, short-stalked at the middle. *Leaf blades* on main branches oblong to narrowly oblong or broadly ovate, 3–11 × 3–6 cm, shiny, puberulent to glabrous on the upper surface, short-pilose on the lower surface, more dense along the midvein and secondary veins, chartaceous to subcoriaceous; the base rounded to slightly obtuse or acute; the apex rounded, short mucronate; the margin entire, revolute, ciliate; the midvein canaliculate above, prominent beneath, venation brochidodromous, the secondary veins 5–12, very prominent on both surfaces, veinlets strongly reticulate forming a net nervation. *Petioles* 2–3 × ca. 1 mm, not canaliculate, densely short-pilose, transversely rugose when mature. *Leaf blades* on inflorescences broadly ovate, ca. 1.2 × ca. 1 cm, puberulent to glabrous on the upper surface, short-pilose on the lower surface, more dense along the midvein and secondary veins, subcoriaceus, the base and apex rounded, the margin entire, revolute, ciliate; venation brochidodromous, the midvein canaliculate above, prominent beneath, the secondary veins 5–6, very prominent on both surfaces, veinlets strongly reticulate forming a net nervation. *Racemes* terminal, unbranched or with 1 lateral branch, forming lax, paniculoid synflorescences, each raceme 8–17 cm long, with 10–25 flowers, rachis densely short-pilose, sparsely pilose when mature, bract early caducous, lanceolate, ca. 2 × 1 mm long, adpressed pubescent on both sides, margins ciliate, bracteoles 2, inserted pairwise at the base of pedicels, linear, ca. 1 × 0.3 mm, adpressed pubescent on both sides, margins ciliate, pedicels 3–4 mm long, densely adpressed pubescent. *Sepals* of the outer whorl unequal, broadly oblong to slighy oblanceolate, adpressed pubescent at the middle outside, glabrous inside, margins ciliate, the outer sepals ca. 1.2 × ca. 1 mm, the inner sepal ca. 2 × ca. 1 mm, lateral enlarged sepals (petal-like) purple-pink, broadly ovate, 5–6 × ca. 5 mm, claw 1–1.5 mm long, glabrous on both surfaces, strongly reticulate-veined, with 14–16 major veins, emarginate at the apex. *Corolla* purple-pink; keel petal oblong, ca. 4 × 2.6–3 mm, claw ca. 1 mm long, glabrous on both surfaces, strongly reticulate-veined, with ca. 10 major veins, without well-developed apical crest (ecristate), 0.25 mm long; adaxial petals 5–6 × 1–2 mm, oblong, glabrous on both sides, strongly reticulate-veined, with ca. 7 major veins. *Filament sheath* ca. 4 mm × ca. 4 mm, glabrous, margins short-pilose, free filaments 8, ca. 3 mm long, those of peripheral stamens short-geniculate just below the anthers; anthers oblong, ca. 0.5 mm long. *Ovary* ca. 1 mm long, glabrous; style 6–6.5 mm long, distally arcuate, glabrous; stigma capitate; nectary inconspicuous. *Samara* 3–4 × ca. 1 cm, body spheroidal ca. 5 × ca. 4 mm, densely pilose, strongly reticulate, dorsal secondary wing, obsolete, oblong, 4–5 mm long, sparsely pilose, primary wing 2.5–3 × 1–1.4 cm, entire, 12–20 veins, sparsely pilose. *Seed*, ca. 3 × ca. 2 mm, brown, glabrous, striate.

Phenology: This new species has been collected in flower in February, March, and October and in fruit in February, May, and October.

Etymology: The epithet *aquae-nigrae* refers to this species' habitat through black water drained systems located in the Upper Rio Negro and middle Orinoco basins. This region in the northern/northwestern Amazon basin portion of the Amazonas basin of Brazil, Colombia and Venezuela is known for its biodiversity.

Vernacular name: "Bejuco de jabón" (*Clark and Gomes 8051*; see additional specimens examined below).

Distribution and ecology: Known from primary wet forests, granitic outcrops and the borders of white sand shrubby savannas between 100–300 m. The type and additional collections of *Securidaca aquae-nigrae*, are from the upper Rio Negro (northern/northwestern Amazon basin) and part of the adjacent southwestern Orinoco basins. This region comprises the southwest of the Amazonas state of Venezuela, the southeast of the Guainía and Vaupés departments of Colombia, and the Roraima and northwest portion of the Amazonas state of Brazil. The Rio Negro watershed is characterized predominantly by black water tributaries that originate from habitats encompassing large

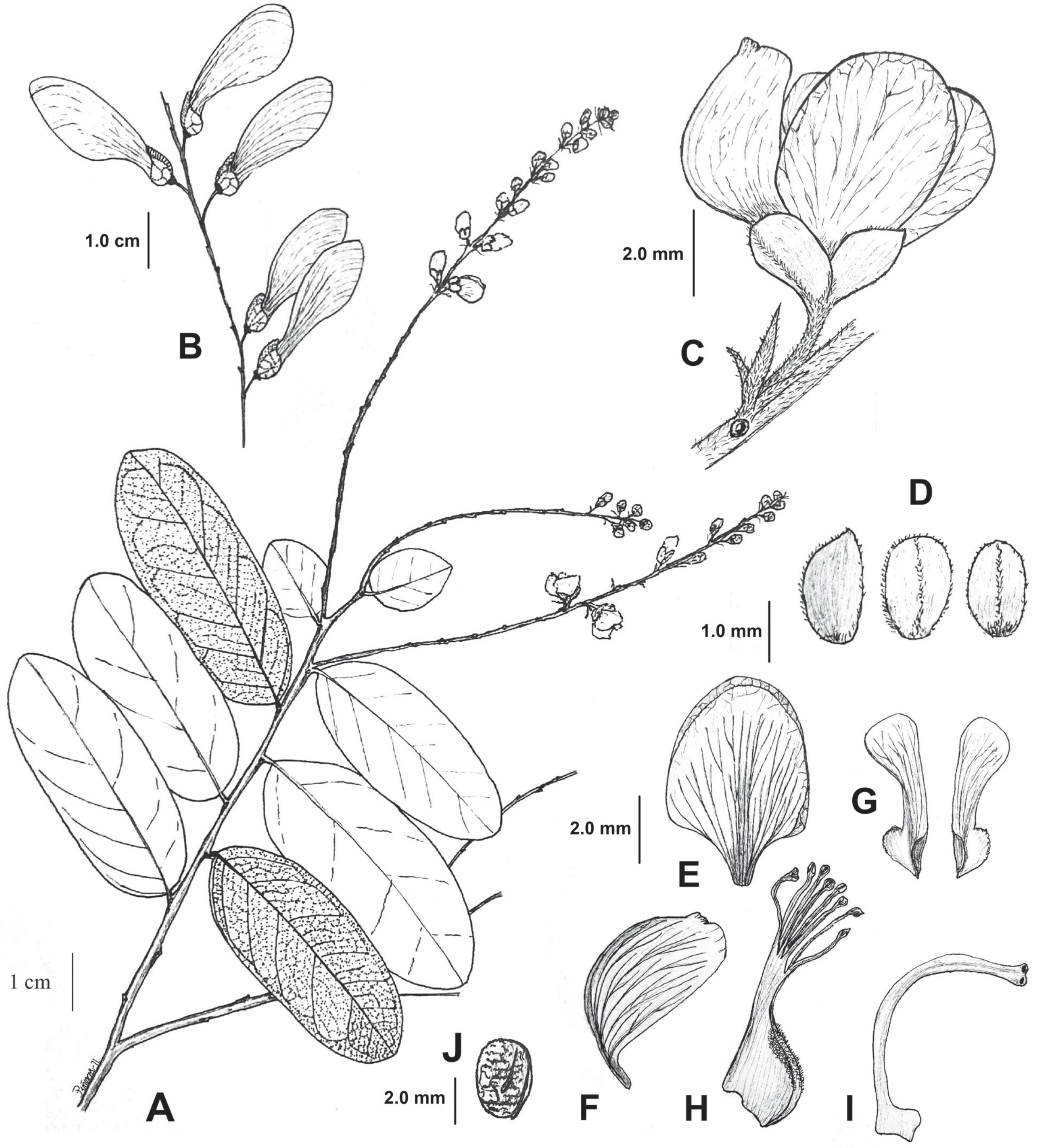

FIGURE 1. *Securidaca aquae-nigrae*. **A and B**, Branch showing the inflorescence and fruits; **C**, Lateral view of the flower showing the bract, bracteoles and the gland; **D**, Sepals of the outer whorl; **E**, Lateral enlarged sepals (petal-like); **F**, Keel petal without apical crest; **G**, Adaxial petals; **H**, filament-sheath; **I**, Gynoecium; **J**, Seed. A, C, D, E, F, G, H, and I from the holotype, *Maguire, Wurdack and Keith 41787*, COL; B, the fruit branch from *Clark and Gomes 8051*, COL.

areas covered by white sand soils (i.e., spodosols and quartzipsamments) formed from the erosion of Precambrian Guayana Shield sandstone rocks (Huber, 1995a). The middle Orinoco river basin does have a few minor black water tributaries, such as the Atabapo, Inírida (*via* the Guaviare), Ucata, and Sipapo rivers, among others, and a major one in its lower course, the Caroní river. These basins show considerable variation in floristic composition and forest structure along local and regional environmental gradients (Aymard et al., 2009). The region also comprises a large, low-altitude peneplain of ca. 165,000 km^2, where hydromorphic spodosols and quartzipsamments are frequent (Dubroeucq and Volkoff, 1998). The peneplain landscape comprises a mosaic of unique vegetation types; in particular, sclerophyllous forests on oligotrophic and acid soils known as “caatinga Amazónica” (Colombia, Venezuela), "caatinga Amazónica baja," "bosques de arena blanca" (Colombia), "campinarana forestada," "campina alta" (Brazil), "varillales" (Colombia), and "hamáliani" in Baniwa languages (Abraão et al. 2009). Additionally, these white sand forests are established across an ecological and floristic transition between terra firme forests commonly found on peneplain red-yellow clay soils and flooded forest communities on alluvial plains called "igapó" and "varzéa" (Aymard et al., 2009). The peneplain landscape also harbors unique extensive areas of savannas, shrubby savannas, and scrublands growing on white sand soils (Huber 1995b; Aymard et al., 2014).

Additional specimens examined: COLOMBIA. Guianía: Rio Inírida, Caranacoa, aprox. 3°50'N, 67°58'W, 03 March 1965 (fl), *A. Fernández-Pérez y R. Jaramillo-M. 7067* (COL). VENEZUELA. Amazonas: Upper Rio Negro basin, San Carlos de Río Negro, ca. 20 km S of confluence of Rio Negro and brazo Casiquiare, aprox. 1°56'N, 67°03'W, 119 m, 18 May 1981 (fr), *H. L. Clark & G. Gomes 8051* (COL, MO, NY, VEN). 1 km al sur de San Carlos de Río Negro, aprox. 1°49'N, 67°03'W, 119 m, 22 febrero 1989 (fl; fr), *G. Aymard, K. Kubitzki & B. Stergios 7360* (PORT, US). Guianía river, lower caño San Miguel, caño El Pavón, aprox. 1°41'N, 67°31'W, 127 m, 26 March 1942 (fr), *Ll. Williams 14909* (F, US, VEN). Río Pasimoni, Mamurividi, aprox. 1°32'N, 66°32'W, 125 m, 03 April 1984 (fl; fr), *R. Liesner 17191* (MO, US, VEN). Casiquiari, Vasiva et Pasimoni, 1853–54 (fr), *R. Spruce 1207* (US). Casiquiare cannel, Chapazón, between Casiquiare mouth and Solano, aprox. 1°58'N, 67°03'W, 120 m, 09 November 1987 (fr), *R. Liesner &. G. Carnevali 22951* (MO, US, VEN). Yatua river, Piedra Catipán, aprox. 1°22'N, 66°22'W, 100-150 m, 30 November 1953 (fr), *B. Maguire, J. J. Wurdack & G. Bunting 36492* (NY, US, VEN).

Conservation status: Currently, this species is only known from the type and paratypes, and it is reported here as a geograhical local taxon from the upper Rio Negro (northern/northwestern Amazon basin) and part of the adjacent southwestern Orinoco basins. According to IUCN (2017) guidelines, nine localities are required data to determine the conservation status of a taxon. Nevertheless, this taxon should be regarded as Endangered (EN) based on the criterion B1ab(iii)+2ab(iii), due to the smaller estimated Area of Occupancy (AOO), with just 32,000 km^2. Its Vulnerable (VU) status was determinated by its Extent of Occurrence (EOO) of 14,629.997 km^2 (IUCN, 2017) and the continual deforestation and degradation of the ecosystems of this región (e.g., "Cerro Yapacana"). These areas have been deforested and degraded over the past two decades because of the expansion of illegal mining (Fundaredes, 2022). Conservation status assessments can still be carried out for species with such low numbers of collections (Rivers et al., 2011). It may, however, be difficult to determine whether an appearance of rarity in a species is due to the lack of data or to its actual rarity (Verspagen et al., 2022).

This new species is similar to *Securidaca coriacea* Bonpland with its leaves of two different sizes, the ones on the inflorescence rachis smaller than ones on main branches, the abaxial surface of leaves short-pilose or densely appressed-pubescent, the presence of nodal glands at the base of the petiole, branchlets and pedicels, and inflorescences racemes or panicles, 2.5–45 cm long with more than 15 flowers. Herbarium specimens of *Securidaca aquae-nigrae* have often been annotated as *Securidaca coriacea* (Orinoco variant) by J. J. Wurdack. However, *S. aquae-nigrae* differs from *S. coriacea* in the vegetative and reproductive characters discussed in the diagnosis (Table 1) and from the Colombian and Venezuelan taxa in the key presented on pages 151–153.

New Records

Securidaca fragilis B. Ståhl & B. Eriksen, Flora of Ecuador 52: 122, 2000. TYPE. ECUADOR. Morona-Santiago: Mutintz and vicinity, about 15 km SW of Makuma, 700–800 m, 77°44'W, 02°12'S, 4 April 1996, *B. Ståhl, H. Navarrete, B. Øllgaard & E. Ternéus 3558* (Holotype: AAU; Isotypes: GB, QCA). Fig. 2

Liana 4–5 m long; branchlets terete, minutely puberulous, nodal glands rather inconspicuous. *Leaves* petiolate, gradually diminishing in size toward branch tips; blade narrowly ovate or oblong, 3–11 × 1.5–5 cm, herbaceous, glabrous, base truncate, apex acuminate with acumen 0.5–1.5 cm long, margins entire, midvein prominent beneath, impressed above, lateral veins 4–6 per side, prominent on both sides, veinlets rather conspicuous; petiole 0.2–0.5 cm long, subcanaliculate, sparsely puberulous. *Racemes* axillary, 1–3 cm long, with 5–15 (–20) flowers; rachis very sparsely strigulose; bracts not seen, very early caducous; *pedicels* 6–7 mm long, very thin, glabrous. *Sepals* of the outer whorl glabrous, ciliolate at margins, somewhat unequal, lower lobes ovate, ca. 2 × ca. 2 mm, upper lobe ovate, ca. 2.5 × ca. 1.5 mm; enlarged lateral sepals broadly oblong, ca. 8 × ca 5 mm including claw, ca. 1 mm long. with ca. 6 major veins. *Corolla* purple to pink, yellowish at base; carina ca. 6 mm long, ca. 1.5 mm deep, glabrous, without apical crest; lateral lobes oblong to subspathulate, ca.5 × ca. 2 mm, glabrous. *Filament sheath* ca. 5 mm long, ciliate at margins, free filaments 0.5–1 mm long; *anthers* ca. 1 mm long. *Ovary* square, ca. 0.7 mm long, glabrous; *style* ca.6 mm long, curved, glabrous; *stigma* truncate. *Fruit* glabrous, main body spheroidal, ca. 13 × ca. 8 mm, coarsely reticulate from prominent veins, dorsal lobe 3–4 mm wide, major wing 5–5.5 × 2–2.3 cm.

Colombian material studied: Antioquia. Anorí, 5 km al sur de la Estación Providencia, 500 m, 7°19'61"N, 75°03'407"W, 28 Marzo 1996 (fl), *R. Fonnegra, R. Callejas. F. J. Roldán, C. López & A. Idarraga 5971* (HUA, MO), det. A. Freire-Fierro-2006. Caquetá. La Montañita. Corregimiento El Santuario, vereda Las Iglesias, reserva natural privada de La Hacienda El Ceilán, aprox. 1°15'N, 75°10'W, ca. 280 m, 27–30 Junio 2005(fl, fr), *D. Giraldo-Cañas et al. 3938* (COL).

According to Eriksen et al. (2000), this species is distinguished by its thin leaves, short axillary inflorescences and thin, fragile pedicels. It was known from two collections made on the slopes of the "Cordillera de Cutucú" (Morona-Santiago). In Colombia, this species was

TABLE 1. Comparison of distinguishing characters of *Securidaca aquae-nigrae* and *S. coriacea*.

CHARACTER	*S. AQUAE-NIGRAE*	*S. CORIACEA*
Leaf blades on main branches	Oblong to narrowly oblong or broadly ovate, chartaceous to subcoriaceous, puberulent to glabrous above, short-pilose beneath, base rounded to slightly obtuse or acute; apex rounded, lateral veins 4–12, margins revolute, ciliate	Ovate to broadly ovate, coriaceous, sparsely pilulose to subglabrous above, densely pilose beneath, base cordate, truncate or short-attenuate at base, apex obtuse, lateral veins 4–6, margins somewhat revolute, not ciliate
Inflorescences	8–17 cm long	3–11(–13) cm long
Sepals of the outer whorl	Broadly oblong to slightly oblanceolate, adpressed pubescent at the middle outside, the outer sepals ca. 1.2 mm × ca. 1 mm, the inner sepal ca. 2 × ca 1 mm	Ovate, puberulent outside, the outer sepals ca. 2.5 × ca. 2 mm, the inner sepal ca. 3 × ca. 2.5 mm
Lateral enlarged sepals	Broadly orbicular, 5–6 × ca. 5 mm, with 14–16 major veins	Elliptic to ovate, ca. 7–11 × 6–8 mm, with 6–8 major veins
Keel petal	Ca. 4 × 2.6–3.0 mm, glabrous on both surfaces, without well-developed apical crest (ecristate), 0.25 mm long	7–8 × ca. 4 mm, densely tomentulose inside, with a well-developed apical crest, 10–12 mm long
Filament sheath	Ca. 4 mm long, glabrous on both sides, margins short-pilose, filament ca. 3 mm long	Ca. 6 mm long, pilulose on inside and along margins, filament 1–2 mm long
Fruit	Spheroidal body ca. 5 × ca. 4 mm, dorsal secondary wing 0.4–0.5 mm long, oblong, primary wing 2.5–3 × 1–1.4 cm, sparsely pilose	Spheroidal body 8–10 × 4–5 mm, dorsal seconday wing 1.2–1.4 cm long, acute, primary wing 3.5–4 × 1.2–1.4 cm, hirsute

collected in flower in March, and with flowers and fruits in June. It grows in wet forests located in the foothills on the east side of the Cordillera Central and Oriental at 280–500 m. The latter locality currently corresponds to the regional private conservation area known as “La Hacienda El Ceilán” in the La Montañita municipality in the department of Caquetá.

Securidaca leiocarpa S. F. Blake, Proc. Biol. Wash. 40: 52–53. (1927). TYPE: ECUADOR. El Oro: Vicinity of Portovelo, 6–15 October 1918, *J. N. Rose & G. 23385* (Holotype: US; Isotypes: GH, NY). Fig. 3

Liana; branchlets terete, hirsute to pilose, stipular glands prominent. *Leaves* petiolate, gradually diminishing in size towards branch tips; blade ovate, 2–4 × 1.2–2.7 cm, coriaceous or subcoriaceous, lower surface sparsely to densely hirsute, at least on the midvein, upper surface distinctly darkened when dried, deep green when fresh, ± nitidous, sparsely hirsute to glabrous, base truncate or sometimes short-attenuate, apex retuse or obtuse-retuse, margins usually somewhat revolute, at least towards the base, midvein prominent beneath, impressed above, lateral veins 4–6 per side, veinlets inconspicuous; petioles 0.1–0.2 cm long, densely hirsute. *Racemes* terminal, usually on short, lateral branches, 1–3 cm long with 8–20 flowers; *rachis* densely hirsute; *bracts* lanceolate, ca. 1 × 0.5 mm, early caducous; *bracteole*s not seen; *pedicels* 8–11 mm long, hirsute. *Sepals* of the outer whorl sparsely hirsute, unequal, lower lobes broadly ovate, ca. 4 × ca. 3.5 mm, upper lobe narrowly ovate, ca. 5 × ca. 3 mm; enlarged lateral sepals purple, almost circular, 9–10 mm long including claw 0.5–1 mm long, with 6–8 major veins. *Corolla* purple; *carina* 9–10 mm long, 4–5 mm deep, apically without, or with a poorly developed crest, margins somewhat puberulous; *lateral lobes* narrowly oblong, ca.5 × ca.3 mm. *Filament sheath* ca. 6 mm long, margins papillose-puberulous, *free filaments* ca. 3 mm long; *anthers* 0.8–1 mm long. *Ovary* ± square, ca. 1 mm long, glabrous; *style* 10–11 mm long, strongly curved; *stigma* subcapitate. *Fruit* glabrous, with central body ca. 5 × ca. 5 mm, dorsal lobe rounded, ca. 1 mm wide, major wing 25–30 × 12–15 mm.

Colombian material studied: Magdalena, Camino San Lorenzo-Sierra Nevada de Santa Marta, 2100 m, 14 Julio 1969 (fl, fr), *N. de López 292* (COL); Municipio Santa Marta, base del Cerro Quemado y Cerro San Lorenzo, aprox. 10°35'N, 73°56'W, 2000–2300 m, 22 Abril 1959 (fl, fr), *R. Romero-Castañeda 7844* (COL); Municipio Santa Marta, entre la Estación Forestal del INDERENA y el Cerro Quemado, 08 Agosto 1971 (fr), *R. Romero-Castañeda y S. Llinás 11258* (COL).

HERBARIO NACIONAL COLOMBIANO - COL

Securidaca fragilis B. Ståhl & B. Eriksen

Actualizó: G. Aymard - 2022

HERBARIO NACIONAL COLOMBIANO (COL)

Securidaca cf. fragilis Ståhl & B. Eriksen

Det.: M. A. Bello /06

HERBARIO NACIONAL COLOMBIANO
Flora de Colombia

POLYGALACEAE

Securidaca

Det.: D. Giraldo-Cañas/2005

Arbusto lianescente; corola lila; frutos verdes; ramas y follaje con olor a leguminosa. Localmente frecuente en las riberas de una pequeña quebrada de aguas transparentes, la cual corre en medio de un afloramiento rocoso, rodeado de un bosque típicamente amazónico de tierra firme.

COLOMBIA. **Caquetá**: Mun. La Montañita, corregimiento El Santuario, vereda Las Iglesias, reserva natural privada de la hacienda El Ceilán; ca. 280 m.

3938 *D. Giraldo-Cañas et al.* 27-30 de junio/2005

FIGURE 2. Specimen of *Securidaca fragilis* from El Santuario, vereda Las Iglesias, Caquetá, Colombia (*D. Giraldo Cañas et al. 3938* (COL 000217076).

FIGURE 3. Specimen of *Securidaca leiocarpa* from Municipio Santa Marta, base del Cerro Quemado y Cerro San Lorenzo, Madgalena, Colombia (*R. Romero-Castañeda 7844*, COL 000245596).

According to Eriksen et al. (2000), *Securidaca leiocarpa* has been rarely collected in the montane forests of southern Ecuador (El Oro, Loja, Morona-Santiago, Zamora-Chinchipe) and adjacent Peru (Cajamarca). lt is easily distinguished by the rather small leaves, the upper surfaces of which dry black-brown.

In Colombia, this species was collected in flower and fruit in April and July and in fruit in August. There it grows in montane wet forest located on the west side of "La Sierra Nevada de Santa Marta," at 2000–2300 m, Madgalena department.

LECTOTYPIFICATION

Securidaca schlimii Planch. & Linden ex Triana & Planch. Annales des Sciences Naturelles; Botanique, série 4, 17: 135. 1862. TYPE: COLOMBIA [Nouvelle-Grenade]. Agua Chica, prov. d'Ocaña (currently Norte de Santander department), 1624 m, 1846–1852, *Louis J. Schlim 513* (Lectotype: [designated here], MPU [15937]); Isolectotypes: G [00440395], K [000012903], P [00733667], US [00109085]).

Jóse Jéromino Triana and Jules Émile Planchon cited a general locality (Triana and Planchon, 1862), but they did not specify any particular herbarium specimen. In the current study, it was found that only a single collection was made by Louis J. Schlim (No. *513*) in the type locality region with five duplicates.

KEY TO THE SPECIES OF *SECURIDACA* OF COLOMBIA AND VENEZUELA

Modified from Aymard et al., 2004 and Aymard and Campbell, 2007;
(*) Species endemic to Colombia; (**+**) Species endemic to Venezuela

1a. Flowers solitary or in short racemes 0.5–2.5 cm long, with 5–15(-20) flowers 2

1b. Inflorescences racemes or panicles, 2.5–45 cm long, with more than 15 flowers 11

2a. Branchlets glabrous or minutely puberulous; samara wing glabrous 3

2b. Branchlets densely hirsute, pilose or sparsely strigulose to glabrescent when mature; samara wing pubescent, sparsely pilose to puberulent 7

3a. Leaves narrowly ovate to ovate, or oblong, inflorescences 5–15(–20)-flowered 4

3b. Leaves ovate to broadly-ovate or orbicular-ovate; flowers solitary or inflorescences with 2–6-flowered 5

4a. Branchlets glabrous; leaves 15–22 cm long; veinlets inconspicuous on both sides; flowers yellowish to green; enlarged lateral sepals subrotund, claw 2–3 mm long; pedicels 2–5 mm long; fruit with a broadly attached wing . . . . *S. calophylla* (Colombia: Antioquia, Boyacá, Caquetá, Nariño; Brazil, Ecuador Perú)

4b. Branchlets minutely puberulous; leaves 3–11 cm long; veinlets forming a strongly reticulate net nervation; flowers pink-purple; enlarged lateral sepals broadly oblong, claw ca. 1 mm long; pedicels 6–8 mm long; fruit with a narrowly attached, lateral wing . . . . *S. fragilis* (Colombia: Antioquia, Caquetá; Ecuador)

5a. Leaves ovate, 5–8 × 2–4.5 cm, puberulent on the abaxial surface, margins revolute, petiole 2–2.5 mm long; inflorescence with 1–3 flowers; keel petal without a crest . . . . *S. uniflora* (Colombia: Caquetá; Venezuela: Amazonas; Brazil, Guianas)

5b. Leaves ovate to broadly-ovate or orbicular-ovate, 5–15 × 4–11 cm, glabrous on abaxial surface margins not revolute, petiole 4–7 mm long; inflorescence with 3–6 flowers; keel petal crested 6

6a. Branchlets glabrous; leaves ovate to broadly-ovate, 5–15 × 4–11 cm; petiole 4–7 mm long, sparsely pilose, canaliculate; outer sepals ovate; main samara wing 7–8 cm long, secondary wing rhomboid, ca. 4 × 6–7 mm . . . . *S. fundacionensis* (Venezuela: Táchira+)

6b. Branchlets puberulous; leaves orbicular-ovate, 5–6 × 3–4 cm; petiole 3–4 mm long, glabrous, not canaliculate; outer sepals broad oblong; main samara wing ca. 4 cm long, secondary wing lanceolate, ca. 18 × ca. 2 mm . . . . . . *S. goudotiana* (Antioquia, Cundinamarca, Tolima, Valle*)

7a. Leaves ovate, 2–4 × 1–2 cm, drying black-brown on the upper surface, golden-green on the lower surface; major wing 2–3 cm long . . . . *S. leiocarpa* (Colombia: Magdalena; Ecuador, Perú)

7b. Leaves ovate-elliptic, elliptic, ovate-oblong or oblong-ovate, 5–11 × 3–6 cm, drying brown-green on the upper surface, light green on the lower surface; major wing longer than 5 cm 8

8a. Branchlets, petioles and pedicels with white pubescence; leaves ovate-elliptic or elliptic; margins revolute; ovary sparsely strigulose to glabrescent . . . . *S. savannarum* (Venezuela: Amazonas**+**; probably in Colombia: Guainía and Vaupés departments)

8b. Branchlets, petioles, and pedicels with golden pubescence; leaves ovate-oblong or oblong-ovate; margins not revolute; ovary glabrous 9

9a. Branchlets sparsely strigulose to glabrescent when mature with trichomes 0.05 mm long; petiolar glands elevated; leaves coriaceous, base obtuse or rotund; lateral petals abaxially glabrous . . . . *S. fruticans* (Venezuela: Amazonas**+**)

9b. Branchlets densely hirtellous with trichomes ca. 1 mm long; petiolar glands sessile; leaves chartaceous or subcriaceous; lateral petals abaxially sparsely ciliate 10

10a. Leaves elliptic to narrowly ovate, chartaceous, white-puberulent on the lower surface, base subcordate or truncate; inflorescences 0.5–1 cm long; outer sepals puberulent at the middle externally; flowers white-yellow or green, keel crest 8–14 mm long . . . . *S. prancei* (Venezuela: Amazonas, Bolívar; Brazil)

10b. Leaves ovate to broadly ovate or oblong, subcoriaceous, yellow-pubescent on the lower surface, base rounded to slighy obtuse; outer sepals glabrous or sparsely strigose externally; inflorescences 2–2.5 cm long; flowers pink-purple, keel crest 4–6 mm long. . . . . . *S. aff. S. purpurea* (Colombia: Norte de Santander; Venezuela: Mérida)

11a. Leaves completely glabrous on both surfaces 12

11b. Leaves sparsely hirtellous, strigulose, pilose, pilosulous, puberulent, or pubescent-hirsute to densely appressed-pubescent at least on one surface (more evident along the midrib and secondary veins) 16

Key to the species of *Securidaca* of Colombia and Venezuela cont.

Modified from Aymard et al., 2004 and Aymard and Campbell, 2007;
(∗) Species endemic to Colombia; (**+**) Species endemic to Venezuela

12a. Inflorescences compound by 1-2-to several racemes, sometimes paniculate 13

12b. Inflorescences unbranched racemes 15

13a. Inflorescences compound by more than 3 lateral racemes (paniculate); major fruit wing ca. 1.5 cm long . . . . *S. paniculata s.l.* (Colombia: Amazonas, Antioquia, Chocó, Putumayo, Vaupés; Venezuela: Amazonas, Bolívar, Delta Amacuro, Distrito Capital, Mérida; Brazil, Guianas, Perú)

13b. Inflorescences compound by 1 or 2 lateral racemes; major fruit wing longer than 2 cm long 14

14a. Leaf margins crenate and strongly thickened . . . . *S. marginata* (Venezuela: Bolívar, Monagas; Brazil, Guyana)

14b. Leaf margins entire and not thickened 15

15a. Leaves ovate to broadly ovate, shiny on the upper surface; racemes 3–5 cm long; pedicels 8–10 mm long; samara wings glabrous, secondary wing nearly fully confluent with the primary wing; deciduous dry forests . . . . *S. scandens* (Colombia: Antioquia, Bolívar, Cesar, Magdalena, Santander, Valle; widespread in north Venezuela)

15b. Leaves elliptic or ovate; racemes 4–12 cm long, dull on the upper surface; pedicels 5–6 mm long; samara wings basally puberulent, sometimes sparsely so; secondary wing noticeably cleft from primary wing, acute; wet forest . . . . *S. retusa* (Colombia: Amazonas, Vaupés: Venezuela: Amazonas, Bolívar; Brazil, French Guiana, Guyana)

16a. Secondary wing of the samara well-developed (samaras 2-winged) 17

16b. Secondary wing of the samara weakly developed or obsolete (samaras 1-winged) 20

17a. Racemes 10–30 cm long; samara wings ca. 1 cm long . . . . *S. pendula* (Colombia: Meta, Vichada; Venezuela: Amazonas, Anzoátegui, Apure, Bolívar, Guárico; Brazil, Guyana)

17b. Racemes 4–10 cm long; samara wings 1.5–3.5 cm long 18

18a. Leaves oblong, sometimes elliptic or obovate; inflorescences compound (panicle); flowers 5–7 cm long; ovary glabrous . . . . *S. paniculata* Rich. *s. l.* (Colombia: Amazonas, Antioquia, Chocó, Putumayo, Vaupés; Venezuela: Amazonas, Bolívar, Delta Amacuro, Distrito Capital, Mérida; Brazil, Guianas, Perú)

18b. Leaves ovate, lanceolate, or lanceolate-ovate; inflorescences unbranched racemes; flowers 8–16 cm long; ovary pubescent 19

19a. Leaves coriaceous; outer sepals symmetric, abaxially glabrescent; keel petal crest 1.2–2 mm long; samara 2–2.5 cm long, wings glabrescent . . . . *S. bialata* (Colombia: Amazonas, Guianía, Vichada; Venezuela: Amazonas, Bolívar, Delta Amacuro, Falcón, Guárico; Brazil)

19b. Leaves chartaceous to subcoriaceous; outer sepals asymmetric, abaxially pilose; keel petal crest 0.5–0.7 mm long; samara 1.5–1.8 cm long, wings densely strigulose . . . . *S. longifolia* (Colombia: Amazonas; Venezuela: Amazonas; Brazil, Guyana, Perú, Bolivia)

20a. Abaxial surface of the leaves puberulent, sparsely hirtellous, strigulose or pilosulous, more evident along the midrib and secondary veins 21

20b. Abaxial surface of leaves hirsute, shortly-pilose, densely appressed-pubescent or velutine, not pilosulous to glabrescent 27

21a. Keel petal without a crest or crest reduced, 0.5–4 mm long, not reflexed 21

21b. Keel petal crested well developed; crest 6–15 mm long, reflexed 25

22a. Leaves chartaceous or subcoriaceous, margins not revolute, pilosulous on the adaxial surface 23

22b. Leaves coriaceous, margins revolute, glabrous on the adaxial surface; outer sepals ovate-orbicular, 2–3.5 mm wide; keel petal ciliate on the margins 24

23a. Branches and branchlets densely hirsute; leaf blades oblong to narrowly elliptic or broadly oblong, 1–2(–3) cm wide, pilosule on both sides; inflorescences unbranched, keel petal glabrous on both sides; lateral wings glabrous . . . . *S. divaricata* (Colombia: Amazonas, Caquetá, Cundinamarca, Meta, Vaupés; Venezuela: Amazonas, Anzoátegui, Aragua, Miranda; Brazil, Guianas, Ecuador, Perú, Bolivia)

23a. Branches and branchlets sparsely strigulose; leaf blades ovate or oblong-ovate, sparsely strigulose on both sides; inflorescences with 2 lateral racemes; keel petal sparsely fine- setulose outside; lateral wings covered by golden trichomes outside . . . . *S. schlimii* (Colombia: Bolívar, Norte de Santander*; probably in Venezuela: Táchira and Mérida states)

24a. Branchlets, petioles, rachis of inflorescence, and pedicels hirsute; petioles 5–7 mm long; basal cleft of samara well-developed . . . . *S. cacumina* (Venezuela: Amazonas, Bolívar**+**)

24b. Branchlets, petioles, rachis of inflorescence, and pedicels velutinous-pubescent; petioles 1–2 mm long; secondary wing of samara minute . . . . *S. warmingiana* (Colombia: Guianía, Vaupés; Venezuela: Amazonas, Mérida; Brazil, Guyana, Perú, Bolivia)

25a. Leaves all one size; outer sepals glabrous abaxially; samara wing 1–1.5 cm long . . . . *S. paniculata s. l.* (Colombia: Amazonas, Antioquia, Chocó, Putumayo, Vaupés; Venezuela: Amazonas, Bolívar, Delta Amacuro, Distrito Capital, Mérida; Brazil, Guianas, Perú)

25b. Leaves two different sizes, the ones on inflorescence rachis smaller than the ones on main branches; outer sepals strigulose abaxially; samara wing 2–4 cm long 26

26a. Leaves elliptic-ovate, obtuse or subcordate at the base, sparsely hirtellous to glabrescent on the adaxial surface; inflorescences 8–45 cm long; keel petal 10–11 mm long . . . . *S. speciosa* (Colombia: Guianía; Amazonas, Bolívar)

26b. Leaves ovate-oblong, sometimes ovate, acute or short-attenuate at the base, strigulose on the abaxial surface; inflorescences 4–12 cm long; keel petal ca. 8 mm long . . . . *S. diversifolia* (widespread in Colombia and Venezuela: SE U.S.A. to Argentina)

27a. Young branchlets, petioles, inflorescences, and pedicels densely white-pubescent; petioles 10–15 mm long; ovary puberulent . . . . *S. maguirei* (Venezuela: Amazonas; Brazil)

27b. Young branchlets, petioles, inflorescences, and pedicels not white-pubescent; petioles 1–7 mm long; ovary glabrous or densely hirsute 28

Key to the species of *Securidaca* of Colombia and Venezuela cont.

Modified from Aymard et al., 2004 and Aymard and Campbell, 2007;
(*) Species endemic to Colombia; (**+**) Species endemic to Venezuela

28a. Leaves two different sizes, the ones on the inflorescence rachis smaller than ones on main branches, with long trichomes (0.7–1.5 mm long) on the abaxial surface 29

28b. Leaves all one size, trichomes ca. 0.5 mm long on the abaxial surface 30

29a. Leaf blades on main branches ovate to broadly ovate, coriaceous, sparsely pilulose to glabrous on the upper surface, lateral veins 4–6; enlarged lateral sepals ca. 8 × 6–8 mm, with 6–8 major veins; keel ca. 8 mm long, densely tomentose inside, with a well-developed apical crest, 8–14 mm long; samara primary wing 3.5–4 cm long, hirsute . . . .*S. coriacea* (widespread in Colombia and Venezuela; Panamá, Brazil, Guyana, Surinam, Ecuador, Perú, Bolivia)

29b. Leaf blades on main branches oblong to narrowly oblong or broadly ovate, subcoriaceous, puberulent to glabrous on the upper surface, lateral veins 5–12; enlarged lateral sepals 5–6 × ca. 6 mm, with 14–16 major veins; keel 4–5 mm long, glabrous outside, without well developed apical crest (ecristate), 0.25 mm long; samara primary wing 2.5–3 cm long, sparsely pilose . . . .*S. aquae-nigrae* (Colombia: Guianía; Venezuela: Amazonas)

30a. Leaves coriaceous; branches and branchlets furfuraceous-pilose . . . . *S. pyramidalis* (Venezuela: Amazonas, Bolívar; Guyana)

30b. Leaves chartaceous or subcoriaceous; branches and branchlets tomentose, densely pilose or densely pubescent. 31

31a. Leaves glabrescent, puberulent, short pilose or sparsely pilose on the adaxial surface 32

31b. Leaves dense pubescent or densely puberulent on the adaxial surface. 34

32a. Leaves subcoriaceous; flowers 6–8 mm long; outer sepals densely pubescent . . . . *S. planchoniana* (Colombia: Antioquia, Boyacá, Cundinamarca, Guaviare, Magdalena, Norte de Santander, Putumayo, Valle; Venezuela: Carabobo, Lara, Mérida, Táchira, Zulia)

32b. Leaves herbaceous to chartaceous; flowers 9–12 mm long; outer sepals glabrous or puberulent 33

33a. Leaves ovate to broadly ovate or oblong, shiny on the upper surface, yellow-pubescent on the lower surface; outer sepals glabrous or sparsely strigose externally . . . . *S. purpurea* (Colombia: Antioquia, Cauca, Vaupés; Venezuela: Distrito Capital, Mérida, Miranda)

33b. Leaves elliptic or ovate-elliptic, dull on the upper surface, velutinous on the lower surface; outer sepals puberulent externally .*S. amazonica* (Colombia: Putumayo; Brazil, very probably in Ecuador and Perú)

34a. Leaves densely puberulent on the abaxial surface; petioles 5–9 mm long; ovary glabrous; samara wing ca. 4 cm long. . . . . *S. pubescens* (widespread in Colombia and Venezuela; Brazil, Guianas, Perú)

34b. Leaves densely pubescent or velvety-pilose on the abaxial surface, especially along the vein; petioles 2–4 mm long; ovary pubescent; samara wing 3–7 cm long 35

35a. Leaves ovate to broadly ovate or oblong-ovate, margins not revolute, sparsely pilose to glabrous on the adaxial surface. 36

35b. Leaves elliptic to ovate, margins revolute, densely pubescent or strigose on the adaxial surface 37

36a. Scandent shrubs or herbaceous vines; branchlets soft pilose, leaves oval, oblong-ovate or narrowly ovate, densely velvety-pilose on the abaxial surface; outer sepals densely pilose outside . . . . *S. tenuifolia* (Colombia: Antioquia, Bolívar, Cundinamarca, Magdalena; Venezuela: Aragua, Bolívar, Distrito Capital, Mérida, Miranda, Portuguesa, Táchira; Panamá, Trinidad and Tobago)

36b. Woody lianas, branchlets densely hirsute, leaves ovate to broadly ovate, pubescent on the abaxial surface; outer sepals sparsely puberulent to glabrous except the margin outside. . . . . *S. trianae* (Colombia: Boyacá, Cundinamarca; Venezuela: Aragua, Carabobo, Distrito Capital, Falcón, Miranda, Táchira; Ecuador)

37a. Leaves densely pubescent on the adaxial surface; pedicel 4–6 mm long; outer sepals puberulous; keel petal spatulate-ovate, obtuse. . . . . *S. volubilis* (Colombia: Putumayo; Amazonas, Bolívar, Mérida, Zulia; Costa Rica, Panamá, Puerto Rico, Brazil, Guianas, Ecuador, Perú, Bolivia)

37b. Leaves strigose on the adaxial surface; pedicel 6–8 mm long; outer sepals densely pubescent; keel petal obovate, acute. . . . . *S. planchoniana* (Colombia: Antioquia, Boyacá, Cundinamarca, Guaviare, Magdalena, Norte de Santander, Putumayo, Valle; Venezuela: Carabobo, Lara, Mérida, Táchira, Zulia)

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HOMONYMY: LEGITIMACY VS. ILLEGITIMACY

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Abstract. Homonyms, if based on different types and recognized at the same rank, may be created either unintentionally or deliberately. Identical infrageneric names of the same genus or identical infraspecific names of the same species may be homonyms, even if they differ in rank. Although later homonymy usually causes illegitimacy, the provisions on homonymy do not apply to infrafamilial names, such as tribes. Simultaneously published homonyms may be legitimate.

Keywords: *Epidendrum*, homonymy, infrafamilial names, infrageneric names, infraspecific names, *Lemanea*, *Ludwigia*, *Mora*, *Morus*, *Sacheria*, *Scenedesmus*

According to the Glossary of the Shenzhen Code, a homonym is "A name spelled exactly like another name published for a taxon at the same rank based on a different type…names of subdivisions of the same genus or of infraspecific taxa within the same species that are based on different types and have the same final epithet are homonyms, even if they differ in rank… because the rank-denoting term is not part of the name…" (Turland et al., 2018).

In this regard, we add that homonyms may be created either unintentionally or deliberately. Although later homonymy usually causes illegitimacy, the provisions on homonymy do not apply to infrafamilial names, such as tribes and simultaneously published homonyms may be legitimate. We illustrate the concepts with a few examples.

Regarding the homonymy at the same rank, we provide two examples here. The first example, belonging to the family Onagraceae, explains how *Ludwigia* DC. (Prodr. 3: 58. 1828) became a later homonym of *Ludwigia* L. (Sp. Pl. 1: 118. 1753) by exclusion of the type of *Ludwigia* L. The second example, in Orchidaceae, explains how *Epidendrum* L. (Sp. Pl. 2: 952. 1753) and *Epidendrum* L. (Sp. Pl., ed. 2. 2: 1347. 1763) became homonyms because of the provisions of the Code on conservation of names from later usage with conserved types and rejection of identical earlier names with different types.

The case of *Ludwigia* might be considered as an example of "genuine" homonyms, whereas that of *Epidendrum* as an example of "artificial" homonyms.

LUDWIGIA L. (SP. PL. 1: 118. 1753) AND LUDWIGIA DC. (PRODR. 3: 58. 1828)

Britton and Brown (1913) were the first to typify the genus name *Ludwigia* L. (Sp. Pl. 1: 118. 1753). They cited *L. alternifolia* L., one of the original species of the genus, as the lectotype. Subsequently, Hitchcock (1929) also selected *L. alternifolia* as the type of the genus name.

Prior to the Shenzhen Code, any generic name typification done by the practitioners of the then existing American Code, such as the typifications done by Britton, was rejected as a mechanical process (see Melbourne Code Art. 10 Ex. 7, McNeill et al., 2012). In such cases, the next typification done by a non-practitioner of the American Code was accepted. Since Hitchcock's typification (1929: 125) was the next one, he was considered as the designator of the type for *Ludwigia* L. (see The Linnaean Plant Name Typification Project at https://www.nhm.ac.uk/our-science/data/linnaean-typification/search/index.dsml; accessed on August 30, 2022).

However, in the Shenzhen Code a provision was made to accept mechanical designations as outlined in Art. 10.5 (Turland et al., 2018): "…A type chosen using a largely mechanical method of selection is superseded by any later choice of a different type not made using such a method, unless, in the interval, the supersedable choice has been affirmed by its adoption in a publication that did not use a mechanical method of selection." Since Hitchcock's (1929) selection of *L. alternifolia* as the "type species" for *Ludwigia* affirms the selection done by Britton and Brown (1913), their designation is accepted (see Index Nominum Genericorm-Plantarum at https://naturalhistory2.si.edu/botany/ing/; accessed on August 30, 2022). The lectotype (Habitat in Virginia, Kalm, Herb. Linn. No. 154.1 (LINN [image]) of *L. alternifolia* L. was designated by Reveal (1993).

De Candolle (1828) recognized "*Ludwigia* Roxb. fl. Ind. I. p. 440 [1820]" as an accepted genus and included 10 species. De Candolle (1828: 59) treated *Isnardia* L. as an accepted genus and listed *Ludwigia* L. as a synonym, and included 16 species, such as *I. alternifolia* (L.) DC. (based on *L. alternifolia*). The Linnaean *Ludwigia* originally included two species, i.e., *L. alternifolia* and *L. perennis*. De Candolle (1828) included *L. alternifolia* within *Isnardia* and seems to have doubtfully included "*L? perennis* (Linn. spec. ed. 2. p.

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173.)… Confer *Jussiæam Burmanni* [= *Jussiaea burmanni* DC.]?” in his usage of “*Ludwigia* Roxb.” Because of the “retention” of *L. perennis* within “*Ludwigia* Roxb.,” one may argue that De Candolle’s usage of “*Ludwigia* Roxb.” includes one of the original Linnaean species, and that he did not create a later homonym. However, it is emphasized here that in his treatment of *Isnardia*, De Candolle cited “*Ludwigia* Lin. gen. n. … 153” [= Gen., Pl., ed. 6: 60, no. 153. 1762] … non Roxb.” as a synonym, and that within his treatment of “*Ludwigia* Roxb.,” de Candolle mentioned that “*Ludwigia* Linnæi sit eadem ac *Isnardia*” (= *Ludwigia* of Linnaeus is the same as *Isnardia*). Based on these facts, it is evident that De Candolle’s usage of “*Ludwigia* Roxb.” did create a later homonym (non L.,1753). K. N. Gandhi (pers. comm.) confirmed that Werner Greuter (B), John Wiersema (US), and John McNeill (E) agree with this assessment and that the next Madrid Code might include De Candolle’s usage of *Ludwigia* as an example.

Since Roxburgh (1820) cited *Ludwigia*. ‘Schreb. Gen. No. 204,’ he indirectly referred to Linnaeus, and it is ascertained here that he did not publish *Ludwigia* as a new genus name. However, since De Candolle treated the Roxburghian usage of *Ludwigia* as different from that of Linnaeus’ *Ludwigia*, it is construed here that De Candolle (page 58) inadvertently created *Ludwigia* DC. as a later homonym (non L., 1753), that De Candolle alone is the author, and that *Ludwigia* DC. remains untypified. Although *Ludwigia* L. is typified by *L. alternifolia* and *Ludwigia* has 10 “syntypes,” in the present taxonomy, they are the same and thus *Ludwigia* L. and *Ludwigia* DC. are now to be considered as homonyms applying to the same taxon. This is evident from the treatment of Wagner et al. (2007: 32, 34, 36), who assigned the original species of *Ludwigia* DC. to *Ludwigia* L. It is emphasized here that except for the International Plant Name Index (see https://www.ipni.org/n/60440057-2; accessed on September 19, 2022), no other published work on *Ludwigia* classification has hitherto addressed the issue discussed here.

Epidendrum L. (Sp. Pl. 2: 952. 1753) and Epidendrum L. (Sp. Pl., ed. 2. 2: 1347. 1763)

In contrast to *Ludwigia* L. (1753) and *Ludwigia* DC. (1828), the case for *Epidendrum* L. (1753) and *Epidendrum* L. (1763) is different. Linnaeus did not either deliberately or inadvertently publish *Epidendrum* (1763) as a new genus name. It was automatically created when *Epidendrum* was conserved from the Linnaean 1763 usage and typified with a type different from that of *Epidendrum* (1753), nom. rej.

So far as *Epidendrum* L. (1753) is concerned, the first lectotypification was by Britton and Wilson (1924), and this selection was affirmed by Green (1929). Following Rec. 10A.2 of the Shenzhen Code (Turland et al., 2018), it is, therefore, to be cited as “*Epidendrum* L., Sp. Pl.: 952. 1753, nom. rej. Type: *E. nodosum* L.” (designated by Britton and Wilson, 1924; affirmed by Green, 1929). The lectotype of *E. nodosum* L. is [icon] “Orchidi affinis Epidendron Corassavicum folio crasso Sulcato” in Hermann, Parad. Bat. t. 187 (bis). 1698: designated by Jones (1967). A lectotype was superfluously designated by Cribb (1999). The current name of *E. nodosum* is *Brassavola nodosa* (L.) Lindl.

Epidendrum nocturnum Jacq. (Enum. Syst. Pl.: 29. 1760) is the conserved type of *Epidendrum* L. (1763). It was listed as “standard species” [equivalent to type—see Art. 7 voted *Ex. 16 of the Shenzhen Code (Turland et al., 2018)] when the name was first proposed for conservation (Sprague, 1929) and was recognized as being a conserved type by Rickett and Stafleu, 1959. The lectotype of *E. nocturnum* Jacq. is Jacquin, Select. Strip. Amer. Hist. 225, t. 139. 1763, designated by Garay and Sweet (1974).

It is emphasized here that Linnaeus did not alter or emend his circumscription of *Epidendrum* between 1753 and 1763. His descriptions of *Epidendrum* given in “Genera Plantarum, ed. 5: 408. 1754 and ed. 6: 464. 1764” are almost the same; in 1763, he merely added 10 additional species, including *E. nocturnum*, that became the conserved type (see Sprague, 1929: 69 and Green, 1929: 186 for discussion).

In summary, prior to the acceptance of Sprague’s (1929) proposal for conservation of *Epidendrum* L. (1763) and rejection of *Epidendrum* L (1753) in 1930, only *Epidendrum* L. (1753) existed with *E. nodosum* L. as the lectotype. Since1930, two *Epidendrum* homonyms have existed. Unlike the situation of the homonyms *Ludwigia* L. and *Ludwigia* DC., which pertain to the same taxon, the homonyms *Epidendrum* L. (1753) and *Epidendrum* L. (1763) are taxonomically different and now refer to two different genera. Additionally, unlike most homonyms, *Epidendrum* (1753) and *Epidendrum* (1763) have the same author, i.e., Linnaeus.

Regarding homonymy of identical subdivisional names at different ranks, an example is mentioned here. The names *Scenedesmus armatus* f. *brevicaudatus* L. S. Péterfi (in Stud. Cercet. Biol. (Bucharest), Ser. Biol. Veg. 15: 25. 1963) and *S. armatus* var. *brevicaudatus* (Hortob.) Pankow (in Arch. Protistenk. 132: 153. 1986) are based on different types, and, although the latter name is at a different rank, it is a later homonym and illegitimate. (see Art. 53.3; Turland et al., 2018). Homonymy at infrageneric ranks within the same genus is rare.

The homonymy of infrafamilial names is addressed here with an example; the derivation of the name tr. Moreae Britton & Rose (in Britton, N. Amer. Fl. 23: 201, 217. 1930) from the genus name *Mora* Benth. (in Trans. Linn. Soc. London 18: 210. 1839) [genitive form: morae; Fabaceae] and the name tr. Moreae Dumort. (Anal. Fam. Pl.: 17. 1829) from *Morus* L. (Sp. Pl. 2: 986. 1753), [genitive form: mori; Moraceae]. The concept of illegitimacy due to homonymy does not apply to infrafamilial names, and the later homonym tr. Moreae Britton & Rose is legitimate (see Art. 53.1 Ex. 5, Turland et al., 2018).

As in the above case, simultaneously published homonyms, which have equal priority, may be legitimate; e.g., *Mimosa cinerea* (Sp. Pl. 1: 517 [sp. no. 10]. 1753) and *M. cinerea* (Sp. Pl. 1: 520 [sp. no. 25]. 1753) are homonyms and legitimate (see Art. 53.5; Turland et al., 2018).

In contrast to the above, “When an author adopts an existing name but definitely excludes its type, a later homonym that must be attributed solely to that author is considered to have been published" (see Art. 48.1; Turland et al., 2018). Two examples are mentioned here. *Lemanea corallina* Bory (in Ann. Mus. Natl. Hist. Nat. 12: 183, t. 21, f. 2. 1808) is the type of *Lemanea* Bory (Ann. Mus. Natl. Hist. Nat. 12: 178. 1808). In the new genus *Sacheria* Sirodot (Ann. Sci. Nat., Bot., ser. 5, 16: 69. 1872), Sirodot included *L. corallina*, and at the same time, recognized *Lemanea* as a genus distinct from his *Sacheria*. In this case, *Lemanea*, as treated by Sirodot, is cited as *Lemanea* Sirodot (1872), non Bory (1808).

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ON THE NOMENCLATURE OF *ALOCASIA ODORA* (ARACEAE)

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Abstract. A nomenclatural revision of the vascular plant taxon *Alocasia odora* is presented. Issues associated with the valid publication of its basionym, *Arum odorum*, and the arguments for the accepted name are addressed here. The correct epithet of *Caladium odoratum*, a confusing synonym, is clarified and the name is lectotypified. A determined attempt is made to clarify the nomenclature of *Alocasia odora* and related nomenclatural entities and to provide the correct citations for them.

Keywords: *Arum*; *Caladium odoratum*; homonym; valid publication; William Roxburgh.

Alocasia odora (Roxb.) K. Koch (Araceae) is a species common to tropical Asia and Oceania and is a popular ornamental plant in the horticultural industry. It is widely known as "海芋" (hai yu) or "滴水观音" (di shui guan yin) in the Chinese market. The discovery of species of *Alocasia* (Schott) G. Don can be traced back to the Linnean era. As early as Roxburgh's time, a few names (e.g. *Arum cucullatum* Lour., *Arum odorum* Roxb., *nom. nud.*, *Arum fornicatum* Roxb., *nom. nud.* and *Arum macrorrhizon* L.) had been proposed. During a revision of *Alocasia* in China, we noticed that the correct name and typification of *Alocasia odora* and its related nomenclatural entities are unclear in the literature (sensu Boyce, 2008; Engler, 1920: 97; Govaerts et al., 2021; IPNI, 2021; Li, 1979: 76; Li and Boyce, 2010: 76; Schott, 1860: 149; The Plant List, 2013; Tropicos, 2019). In this paper we discuss the nomenclature history of *Alocasia odora* and its relationship with related names and address the validation of its basionym, citations, and typifications.

MATERIALS AND METHODS

Literature concerning the nomenclature of *Alocasia odora* and related names was obtained from Biodiversity Heritage Library (BHL) and HathiTrust Digital Library and examined in terms of effectiveness of publication, validity, and legitimacy in accordance with the *International Code of Nomenclature for algae, fungi, and plants* (Turland et al., 2018). The libraries of the Royal Botanic Gardens, Kew, and the Calcutta Botanical Garden, as well as twenty herbarium databases (CAL, BM, BR, E, G, K, LIV, A, B, C, FC, FI, GLAS, LINN, NY, OXF, P, PH, TCD, and UPS) were examined in an attempt to locate original material, including specimens and illustrations.

RESULTS

Validation and typification of the basionym *Arum odorum*

Roxburgh (1814: 65) first used the name *Arum odorum*, but without a diagnosis or description. Loddiges et al. (1820) later provided a detailed description with an illustration and cited Roxburgh's *Hortus Bengalensis*, thereby validly publishing the name, *Arum odorum* Roxb. ex Lodd., G.Lodd. & W.Lodd. (Art. 35.1). In 1832, the name *Arum odorum* Roxb. was published with detailed descriptions in Roxburgh's *Flora Indica*. Since the name with description was prepared before Roxburgh's death in 1815, it cannot be an emended description of *Arum odorum* Roxb. ex Lodd. et al. (1820) and should be considered a nomenclatural novelty attributed to Roxburgh. *Arum odorum* Roxb. was spelled exactly the same as *Arum odorum* Roxb. ex Lodd. et al., but it was based on a different type. Therefore, we consider the name *Arum odorum* Roxb. a separate name from, and a later homonym to, *Arum odorum* Roxb. ex Lodd. et al. (Art. 53.1).

Turner (2016) designated the illustration in the *Botanical Cabinet* 7: t. 641. 1820 as the lectotype of *Arum odorum*, although that citation needs to be corrected to Bot. Cab. 5: t. 416. 1820; since the illustration in the former is *Aristolochia tomentosa* Sims. We consider Turner's citation to be an amendable error that does not match the context of "serious conflict with the protologue" in the Code (sensu Art. 9.19c, Ex. 16). Consequently, this lectotypification must be accepted with correction (Art. 9.19).

The correct epithet of *Caladium odoratum*

Two years after the valid publication of *Arum odorum*, Gawler (1822) published a page from Roxburgh's manuscript with the name *Caladium odorum* (sensu Boyce 2008; IPNI 2021; Li,1979: 76; Li and Boyce, 2010: 76; The Plant List, 2013; Tropicos, 2019). The two epithets are not orthographical variants and cannot be used interchangeably

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because they are derived from different Latin words, *odorum* from the noun *odor*, while *odoratum* from the adjective *odoratus* (Art. 61.2 ex. 2). An errata at the beginning of the volume where *Caladium odorum* was published that reads: "Vol. 8. fol. 641. l. 2. pro 'CALADIUM odorum' lege 'CALADIUM odoratum'" (Gawler 1822); *Caladium odoratum*, but not *Caladium odorum*, is the only legitimate name published here. In fact, Hooker (1842) adopted the former as the basionym for his new combination *Colocasia odorata* Hook.

Furthermore, the name *Caladium odoratum* should be adopted as a name of a new taxon, ascribed to Gawler, the volume editor. Although Roxburgh's contribution was acknowledged at the end of the text as "Roxburgh MSS," whether it was Roxburgh's intention to use the name *Caladium odoratum* is still doubtful (Art. 46.2. Note 1. Ex. 11). Therefore, *Caladium odoratum* Roxb. ex Ker Gawl. should be the correct name (Art. 46.5).

To maintain the stability of these names, *Caladium odoratum* is lectotypified here. After consulting the online databases of major herbaria in the world (see Materials and Methods), we have not found any specimens traceable to Gawler, or any specimens collected by Roxburgh identified as either *Arum odorum* or *Caladium odoratum*. Therefore, we choose the illustration associated with the protologue as the type for *Caladium odoratum*, which clearly indicates its synonymy with *Arum odorum*.

The correct name of *Alocasia odora*

Brongniart (1834) proposed a new combination, *Colocasia odora*, without reference to a basionym or a previously published diagnosis or description. We presume it was his intention to make a new combination based on an existing basionym (Art. 41.4). Hence, we consider the earliest validly published name, *Arum odorum* Roxb. ex Lodd. G. Lodd., & W. Lodd., to be the basionym for the combination *Colocasia odora* (Roxb. ex Lodd., G.Lodd. & W.Lodd.) Brongniart.

The combination *Alocasia odora* was first proposed by Spach (1846) in his *Histoire Naturelle des Végétaux. Phanérogames Vol. 12*. The French common name, Alocase odorante, precedes the name accepted by Spach (1846, Page 46), *Alocasia odora*, which is attributed to Kunth. We believe the new combination, *Alocasia odora*, should not be ascribed to Kunth, since Kunth (1841, Page 39) followed Brogniart's treatment by placing the species in *Colocasia* sect. *Alocasia* Schott without proposing a new combination.

The basionym of *Alocasia odora* is also worth discussion. Although it was not directly indicated in the protologue, both Spach (1846: 46) and Kunth (1841: 39) cited most of the synonyms back to Roxburgh's time and paraphrased the description from Brongniart (1834). We, therefore, believe the basionym of *Alocasia odora* should be *Arum odorum*, the same basionym as that of *Colocasia odora*, due to the presence of an indirect reference (Art. 38.14 & 41.3).

Subsequently, Koch published the later homonym, *Alocasia odora* K. Koch, 1854, *non auct*. (Roxb. ex Lodd., G. Lodd. & W. Lodd.) Spach, 1846, citing only *Arum odorum* Roxb., 1832, *non auct*. Roxb. ex Lodd. G. Lodd. & W. Lodd., 1820. (The latter's illegitimacy precludes its potential of being a basionym). This nomenclatural entity, therefore, should be solely ascribed to Koch himself as a name of a new taxon despite being illegitimate (Art. 53.1). In conclusion, the correct name for this taxon should be *Alocasia odora* (Roxb. ex Lodd. G. Lodd. & W. Lodd.) Spach.

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LECTOTYPIFICATION OF *CAREX AESTIVALIS* (CYPERACEAE SECT. *HYMENOCHLAENAE*)

Allen W. Milby[1]

Abstract: A lectotype for *Carex aestivalis* (Cyperaceae; sect. *Hymenochlaenae*), a sedge from the Appalachian Mountains, U.S.A., is designated. The authorship of the name, hitherto cited as M.A. Curtis ex A. Gray, is revised to show that M.A. Curtis, alone, is the author of the species name and the original description.

Keywords: *Carex*, Cyperaceae, lectotypification, Asa Gray, M.A. Curtis

The name *Carex aestivalis* (Cyperaceae; sect. *Hymenochlaenae*), a sedge ranging through the Appalachian Mountains from northern Georgia to Vermont and northeastern New York (Smith and Waterway, 2008), was published by Asa Gray (1842) following a collecting trip in the summer of 1841 to the mountains of North Carolina with John Carey and James Constable. Gray (1842: 28) attributed the name, *C. aestivalis*, to its discoverer, the Rev. Moses A. Curtis, who used it on the labels of specimens he distributed before its formal publication. In the description, Gray (1842) commented, "A species of *Carex*, nearly allied to *C. gracillima*, occurs in the greatest abundance on all the higher mountains of North Carolina, forming tufts on the earth or on rocks, and flowering throughout the summer. On this account it is called *C. aestivalis* by Mr. Curtis, who discovered it several years since, and pointed out its characters.[†]" The preceding sign pertains to a formal Latin description of "[†]*C. aestivalis* (M.A. Curtis, ined. [sic])" given in the footnote in which Gray wrote "Hab. in montibus altioribus Carolinae Septentrionalis ubique. Julio–Augusto floret…"

Regarding the authorship of the name *Carex aestivalis*, it may be debatable whether it is "M.A. Curtis ex A. Gray" or "M.A. Curtis" alone. In this regard, it is noted here that whenever Asa Gray mentioned a description from another author *verbatim*, he placed the relevant description within double quotes (e.g., *C, sullivantii* Boott; Gray mentioned "… I trust I may be allowed to publish the notes of this sedulous caricographer unchanged …"). In contrast, for *C. aestivalis*, although Gray did mention that Curtis "pointed out the characters," the given description is not in double quotes. Therefore, it is evident that Gray did not use Curtis's description *verbatim* and most likely edited it. Perhaps for this reason, many works in the past accepted "M.A. Curtis ex A. Gray" for the authorship. However, it is emphasized here that Curtis provided the characters, that Gray acted as an editor, that Gray's editing is comparable to any other reviewer's editing, and, therefore, Curtis alone is the author. Kanchi N. Gandhi (GH, pers. comm.), reported that Werner Greuter (B) agreed with the preceding analysis. Thus, the authorship should be attributed solely to Curtis as *Carex aestivalis* M.A. Curtis (in Gray 1842: 28).

In a comprehensive taxonomic treatment of the globally rare *Carex roanensis* F.J. Herm. and its allies (including *C. aestivalis*), Smith and Waterway (2008) provided keys to the species and type specimen information for each of the species included in their study. For *C. aestivalis* they stated "TYPE: U.S.A. North Carolina: Burke Co. Table Mountain, [s.d.], *Curtis s.n.* (Holotype: MO [scanned image]; Isotype: GH)." It is noted here that except for mentioning the locality and phenology (as "*Hab. in montibus altioribus Carolinae Septentrionalis ubiquo. Julio-Augusto floret*"), no other collection information was associated with this name. Nevertheless, since Curtis was the discoverer of this species and is the author of the species name, his own collections are relevant for the typification of this name. Therefore, Smith and Waterway (2008) were correct in mentioning a Curtis collection as the type, but their choice of the term "holotype," which implies that the description was based on a single specimen, is not acceptable as discussed below.

Although the concept of the term 'type' was known even in the 1830s, neither Curtis nor Gray used this term. Besides Smith and Waterway's (2008) mention of two specimens (GH, MO), from the available evidence it is certain that Curtis's "original description" was based on several collections, viz., Mts. of N. C., without date, *M. A. Curtis s.n.* (MO [357136]). North Carolina: Mts. of N. C., without date, *M. A. Curtis s.n.* (MO [357137]). North Carolina: Mts. of N. Car., without date, *M. A. Curtis s.n.* (K000907946). North Carolina: Table Mt., without date, *M. A. Curtis s.n.* (NY [00025085]). North Carolina: N. Carolina, without date, *M. A. Curtis s.n.* (NY [00025086]). North Carolina: Table Mt., without date, *M. A. Curtis s.n.* (PH [00208806]). North Carolina: Mts. of N.C., without date, *M. A. Curtis s.n.* (BRU [00019374]). North Carolina: Mts. of N.C., without date, *M. A. Curtis s.n.* (GH [01640677]). North Carolina: Table Mt., without date, *M. A. Curtis s.n.* (GH [00221767]).

With the above facts in mind, the need to designate a lectotype for *C. aestivalis* from among the specimens used by Curtis at the time of his publication is apparent. These nine specimens were likely available prior to the publication of the name, *Carex aestivalis,* and are, therefore, to be considered original material.

Although Smith and Waterway's (2008) usage of the

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FIGURE 1. Lectotype of *Carex aestivalis* M.A. Curtis (specimen on the right). Image courtesy of the Gray Herbarium, Harvard University Herbaria.

terms "holotype" and "isotype" are correctable to lectotype and isolectotype, respectively (Shenzhen Code Art. 9.10), and that their type citation could be construed as an inadvertent act of lectotypification, they did not use the phrase "designated here," which is required for the purpose of priority of typification (vide Art. 7.11). Also, there are two collections at MO (357136 and 357137), but it is uncertain whether these two specimens belong to the same collection or whether the GH specimen belongs to one of them. In other words, Smith and Waterway did not typify the name, and a lectotype needs to be designated. The next question is whether to choose one of the two specimens at MO or some other original specimen as the lectotype. It should be noted that one of the GH specimens (00221767) is mounted on the same sheet with a collection of *C. aestivalis* that Gray and J. Carey collected on their trip to North Carolina (Fig. 1). It was on this trip that Curtis pointed out the plant to Gray, and during which Curtis could have given the collection to Gray, prior to publication of the name. With this in mind, and due to the uncertainty about the total number of collections, as well as to avoid any ambiguity, I have chosen the aforementioned GH specimen (00221767) as the lectotype and designate it here.

Carex aestivalis M.A. Curtis, Amer. J. Sci. Arts 42: 28. 1842. TYPE: UNITED STATES OF AMERICA. North Carolina: Table Mountain. *M. A. Curtis s. n.* (Lectotype: [designated here]: GH [00221767]).

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NOTES ON SOME MALESIAN ORCHIDACEAE IV

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

Abstract. Continuing literature and herbarium studies of the Malesian orchid flora reveal the need for four transfers, viz. *Aeridostachya bancana, Bryobium consanguineum, Phreatia microscopica,* and *Zeuxine zollingeri*. Two taxa, *Dendrobium lancifolium* and *Eria stellata* are reinstated. Furthermore, aside from lectotypifications, nine new synonyms are proposed in the genera *Bulbophyllum, Dendrobium, Eria, Gastrochilus,* and *Habenaria*.

Keywords: Malesia, Orchids, *Aeridostachya, Bryobium, Phreatia, Zeuxine*.

This paper is a continuation of our studies (e.g. Ormerod and Juswara, 2021) that are intended as an effort to update the knowledge of Malesian orchids. Most of the taxa dealt with here occur in Indonesia, but two, *Dendrobium papilio* Loher and *Eria cochleata* Lindl., are so far only found in the Philippines.

Aeridostachya (J.D. Hook.) Brieger, in Schltr., Die Orchideen ed. 3, 1 (11–12): 714. 1981.

Basionym: *Eria* Lindl. section *Aeridostachya* J.D. Hook., Fl. Brit. Ind. 5: 786, 809. 1890 as *Acridostachya*.

Type species: *Eria aeridostachya* Rchb.f. ex Lindl.

Homotypic synonym: *Pinalia* Lindl. section *Aeridostachya* (J.D. Hook.) O. Kuntze, in Post & Kuntze, Lex. Gen. Phan.: 439. 1904 as *Acridostachya*.

Heterotypic synonym: *Dendrolirium* Blume section *Brachystomium* Blume, Bijdr.: 346. 1825; Bijdr.: Clav. Gen. Orch. Jav. 1825.

Lectotype species: [designated here]: *Dendrolirium robustum* Blume

A genus of Subtribe Eriinae with about 20 species distributed from Thailand to Fiji. Most of the species (14) are to be found in Indonesia. The plants are pseudobulbous epiphytic herbs with dense, pubescent racemes of small (sepals 2–3 mm long) flowers. The flowers have a mentum formed by the lateral sepals and column foot, a simple labellum, and a short column bearing eight pollinia. The different taxa are difficult to identify due to the great similarity of their flowers.

Aeridostachya bancana (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Eria bancana* J.J. Sm., Bull. Jard. Bot. Buitenz. s. 3, 2: 53. 1920.

TYPE: INDONESIA. Bangka, without locality, *leg. H.A.B. Bunnemeijer 69, cult. Hort. Bogor. XIB, IX, 104* (Holotype: BO [0064934]).

Distribution: Malaysia (Sabah); Indonesia (Bangka).

Wood (2011) first proposed this combination but, unfortunately, omitted the year of publication for the basionym, making the new binomial invalid. The transfer of *Eria bancana* to *Aeridostachya* is validated here. The holotype consists of a single dried inflorescence.

Bryobium Lindl., Intr. Nat. Syst. Bot. ed. 2: 446. 1836.

Type species: *Bryobium pubescens* Lindl.

A genus of Subtribe Eriinae with about 25 species distributed from Thailand to the Solomon Islands. It is a cryptic genus that is especially difficult to distinguish from *Pinalia* Lindl. using floral morphology. The molecular studies of Ng et al. (2018) show that *Bryobium* is more closely related to *Ceratostylis* Blume than to *Pinalia*.

Bryobium consanguineum (J.J. Sm.) Ormerod & Juswara, *comb. nov.*

Basionym: *Eria consanguinea* J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 3, 11: 131. 1932.

TYPE: INDONESIA. Kalimantan, West Koetei, Gunung Kemoel, 1600 m, 18 October 1925, *F. H. Endert 4315* (Holotype: L [0058745] [image seen]).

Homotypic synonym: *Pinalia consanguinea* (J.J. Sm.) Schuit., Y.P. Ng & H.A. Pedersen, Bot. J. Linn. Soc. 186: 197. 2018.

Distribution: Indonesia (Kalimantan).

In the protologue, Smith compared this taxon to the species now known as *Bryobium bicristatum* (Blume) Schuit., Y.P. Ng & H.A. Pedersen and *B. hyacinthoides* (Blume) Y.P. Ng & Cribb. We believe Smith's observations are correct on the relationships of *Eria consanguinea* and accordingly transfer it to *Bryobium*.

Bulbophyllum Thouars, Hist. Part. Orch. Iles Austral. Afr.: Trois. Tabl. Esp., tt. 93–110. 1822 *nom. cons*.

Lectotype: *Bulbophyllum nutans* Thouars

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A genus of over 2000 species distributed throughout the warm tropics of the world, but also extending to mildly temperate regions such as part of Japan and New Zealand. They may be recognized by their one to two (rarely more) apically-leaved pseudobulbs, basal inflorescences, and flowers quite often bearing a hinged, usually motile labellum.

Bulbophyllum gibbosum (Blume) Lindl., Gen. Sp. Orch. Pl.: 54. 1830.
TYPE: INDONESIA. Java, high altitudes of Mt. Salak, fl. June, *C. L. Blume 1873* (Lectotype: [J. J. Verm. 1992: 57, as holotype]: L [0058196] [image seen]).
Basionym: *Diphyes gibbosa* Blume, Bijdr.: 312. 1825.
Homotypic synonym: *Phyllorkis gibbosa* (Blume) O. Kuntze, Rev. Gen. Pl. 2: 677. 1891.
Heterotypic synonyms: *Dendrobium javanicum* Swartz, Kongl. Vetensk. Acad. Nya Handl. 21, 3: 247. 1800 *syn. nov.* TYPE: INDONESIA. Java, *C. P. Thunberg s.n.* (Neotype: [designated here]: UPS-Thunb. [21478] [image seen]).
Eria javanica (Swartz) Blume, Rumphia 2: 23. 1839.
Not *Bulbophyllum javanicum* Miquel 1859
Not *Bulbophyllum javanicum* (Blume) J.J. Sm. 1918.

Distribution: Malaysia; Brunei; Indonesia.

Select specimens examined: INDONESIA. West Java Prov., Preanger, Cadas Malang, Cidadap, Cibeber, 1000 m, 21 October 1916, *R. C. Bakhuizen van den Brink 942* (BO); same area, Cibeber, July 1917, *W. F. Winckel 589B* (BO); Mt. Cikuray, E of Mt. Gede, 1450 m, 30 March 1914, *C. A. Backer 12868* (BO).

Lindley (1825) questionably treated *Dendrobium javanicum* as a synonym of his *Eria stellata*. Blume later transferred the former to *Eria*. However, this tentative synonymy wasn't accepted until Ames (1908) formally united the two taxa. Since then the identity of *Dendrobium javanicum* has not been questioned even though the type has not been located. The protologue of *D. javanicum* reads “caule radicante, foliis petiolatis erectis lato-lanceolatis obtusis, scapis e basi vaginarum petiolorum multifloris. E Java. Thunberg”. *Eria stellata* has acute (not obtuse) leaves, and its inflorescence is axillary (not basal). Furthermore, Swartz does not mention any pubescence on the scape or flowers such as is found in *Eria stellata*.

No specimens annotated with the name *Dendrobium javanicum* by Swartz have been found. However, in UPS we found in Thunberg's herbarium a collection from Java annotated with the names *“Orchis monophylla*” and *“Dendrobium monophylla*”. Both annotations are by Thunberg (Hjertson, pers. comm.). This specimen fits very well with the diagnosis of Swartz, for it has a rooting stem (actually the rhizome, but the minute pseudobulbs wouldn't have been recognised at the time), petiolate, erect, obtuse leaves, and a scape and leaf petiole enveloped by a basal sheath. We believe this collection is the actual holotype of *Dendrobium javanicum*, but since it is not annotated with the specific epithet we have chosen it as the neotype.

The consequences of this discovery are that *Dendrobium javanicum* becomes a synonym of *Bulbophyllum gibbosum* (see Vermeulen,1992, for further synonymy) and that *Eria stellata* (see below) must be reinstated.

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

A genus of 1520–1530 species distributed from India and Sri Lanka to Tahiti. The plants are primarily epiphytes, though a few terrestrial taxa are known, especially from New Caledonia. Many species and artificial hybrids are popular horticultural subjects. Some of the artificial hybrids are commercially used in the cut-flower market. *Dendrobium* is the largest orchid genus in Indonesia, comprising about 690 species. With the exception of *D. papilio,* all of the species discussed here occur in Indonesia.

Dendrobium lancifolium A. Rich., Sert. Astrol., Atlas: t.8. 1833; Sert. Astrol.: 20. 1834.
TYPE: INDONESIA. Maluku Prov., Buru Island, June to July 1828, *A. Lesson s.n.* (Holotype: [not found]).
Homotypic synonym: *Callista lancifolia* (A. Rich.) O. Kuntze, Rev. Gen. Pl. 2: 655. 1891.
Heterotypic synonyms: *Dendrobium lanceolatum* Gaud., Voy. Uranie: 423. 1829 *nom. illeg., non* Pers. 1807. TYPE: INDONESIA. Papua Prov., Waigeo [as Rawak] Island, *C. Gaudichaud s.n.* (Holotype: P [00328856] [image seen]).
Dendrobium lilacinum Teijsm. & Binn., Natuurk. Tijdschr. Ned. Ind. 27: 18. 1864. TYPE: INDONESIA. “Java, Mt. Salak” [prob. ex Maluku Prov.], *J. E. Teijsmann s.n.* (Holotype: L [0059502] [image seen]).
Dendrobium huttonii Rchb.f., Gard. Chron.: 686. 1869. TYPE: “MALAYAN ARCHIPELAGO”. Without locality, *leg. H. Hutton, cult. Messrs. Veitch s.n.* (Holotype: W-R [21007] [image seen]).
Callista huttonii (Rchb.f.) O. Kuntze, Rev. Gen. Pl. 2: 654. 1891.
Eurycaulis huttonii (Rchb.f.) M.A. Clem., Telopea 10, 1: 286. 2003.
Dendrobium vulcanicum Schltr., Bull. Herb. Boiss. s. 2, 6: 459. 1906. TYPE: INDONESIA. Maluku Prov., Banda Islands, Pulau Gunung Api, upper half of active peak, October 1901, *R. Schlechter 13660* (Holotype: B [destroyed]).
Dendrobium lancifolium A. Rich. var. *papuanum* J.J. Sm., Nova Guin. 12, 4: 325. 1916. TYPE: INDONESIA. Papua Prov., Arfak Range, 1900 m, 26 April 1912, *K. Gjellerup 1065* (Holotype: BO [0062961]).

Distribution: Indonesia (Sulawesi, N Maluku, Maluku, Papua).

Select specimens examined: INDONESIA. Sulawesi, without precise locality, *cult. Hort. Bogor. s.n.* (AMES); without precise locality, *leg. L. van Vuuren 92, cult. Hort.*

Bogor. s.n. (BO). South Sulawesi Prov., Enrekang, *leg. L. van Vuuren 285, cult. Hort. Bogor. s.n.* (BO; L [1502235] [image seen]); Kalosi, 600 m, 16 May 1929, *G. Kjellberg 1434* (BO). North Sulawesi Prov., Talaud Islands, Karakelong Island, E slope Mt. Piapi, 350 m, 31 May 1926, *H. J. Lam 3242* (BO; L [1502211] [image seen]). North Maluku Prov., Ternate, W Sulamadaha, 25 m, 8 October 1920, *V. M. A. Beguin 880* (BO; L [1502224] [image seen]). Papua Prov., Biak Island, 20 m, 30 June 1961, *W. Vink BW 12027* (A); Cyclop Mountains, 350 m, 29 June 1938, *E. Meijer Drees 130* (BO).

The name *Dendrobium lanceolatum* Gaud. was used by the first author (Ormerod, 2017) for this species, but, unfortunately, further literature research has shown there is an earlier *D. lanceolatum* (= *Specklinia lanceola* (Sw.) Lindl.). We have, therefore, adopted the next available binomial, viz. *D. lancifolium*.

Dendrobium macfarlanei F. Muell., Descr. Notes Papuan Pl. 1: 29. 1876. TYPE: PAPUA NEW GUINEA. Baxter River, *Rev. S. Macfarlane s.n.* (Holotype: MEL [0544736]).

Homotypic synonyms: *Aporum macfarlanei* (F. Muell.) Rauschert, Rep. Sp. Nov. Regni Veg. 94, 7-8: 440. 1983.

Aporopsis macfarlanei (F. Muell.) M.A. Clem. & D.L. Jones, Orchadian 13, 11: 485. 2002.

Ceraia macfarlanei (F. Muell.) M.A. Clem., Telopea 10, 1: 292. 2003.

Heterotypic synonyms: *Dendrobium litorale* Schltr., Rep. Sp. Nov. Regni Veg., Beih. 1: 567. 1912, *syn. nov.* TYPE: PAPUA NEW GUINEA [as KAISER WILHELMSLAND]. Morowe (Adolfhafen), 10 m, April 1909, *R. Schlechter 19214* (Syntype: B [destroyed]); Waria River mouth, 15 m, July 1909, *R. Schlechter 19958* (Syntype: B [destroyed]; Isosyntypes: NSW [926674]; AD [96608145]; G [00165429]; S [1937] [images seen]).

Aporum litorale (Schltr.) Rauschert, Rep. Sp. Nov. Regni Veg. 94, 7–8: 440. 1983.

Aporopsis litoralis (Schltr.) M.A. Clem. & D.L. Jones, Orchadian 13, 11: 485. 2002.

Ceraia litoralis (Schltr.) M.A. Clem., Telopea 10, 1: 292. 2003.

Dendrobium platybasis Ridl., Trans. Linn. Soc. ser. 2, Bot. 9: 168. 1916 *syn. nov.* TYPE: INDONESIA. Papua Prov., Launch Camp, 0 m, 13 March 1913, *C. B. Kloss s.n.* (Holotype: BM [000017528]).

Ceraia platybasis (Ridl.) M.A. Clem., Telopea 10, 1: 293. 2003.

Distribution: Indonesia (Papua); Papua New Guinea; Australia (Torres Strait).

Select specimens examined: INDONESIA. Papua Prov., Idenburg River, Bernhard Camp, 50 m, April 1939, *L. J. Brass 13783* (BRI). PAPUA NEW GUINEA. Western Prov., Oriomo River, Dagwa, February to March 1934, *L. J. Brass 5924* (AMES); Oriomo River, Dagwa, February to March 1934, *L. J. Brass 5981* (AMES).

The type of *D. macfarlanei* was collected by the Reverend Samuel Macfarlane somewhere on the Baxter (now Mai-Kassa) River on 31 May 1875 (van Steenis-Kruseman, 1950). The Mai-Kassa River is a lowland waterway that empties into the Torres Strait, not too far from Dauan Island from where *D. macfarlanei* was recorded for the first time in Australian territory under the later synonym *D. litorale* (Jones, in Lavarack, 1989).

Study of type material of *D. macfarlanei* and *D. litorale* showed these two taxa to be conspecific. Both entities agree in having an 8–10 mm long mentum, and a cuneate, apically trilobulate to quadrilobulate labellum bearing three low keels. *Dendrobium platybasis,* based on material collected in coastal West New Guinea, proved to have the same features, and it is also reduced to synonymy.

The reason that *D. macfarlanei* and *D. litorale* have not been previously considered conspecific is due to Schlechter's (1912) influential account of *D. macfarlanei* and its allies. Schlechter's concept of *D. macfarlanei* differs in having a very low median, narrowly sulcate thickening (vs. three distinct keels) on the labellum. It is probably an undescribed taxon, but we have not been able to obtain any material of it.

Dendrobium papilio Loher, Gard. Chron. ser. 3, 21: 416. 1897. TYPE: NOT CITED. (Holotype: [not found]). Neotype: [designated here]: Philippines, Luzon, Tonglon, and Benguet, Galou, *A. Loher 477* (Neotype: K [001085101] [image seen]).

Homotypic synonym: *Aporum papilio* (Loher) Rauschert, Rep. Sp. Nov. Regni Veg. 94, 7–8: 441. 1983.

Heterotypic synonym: *Dendrobium greatrixianum* Hort. Sander ex H. J. Veitch, Gard. Chron. ser. 3, 22: 222. 1897, *syn. nov.* TYPE: "NEW GUINEA". Exhibited at the R.H.S. 21 September 1897, *cult. Messrs. F. Sander & Co. s.n.* (Holotype: [lost]).

Dendrobium vanoverberghii Ames, Philipp. J. Sci. 8, C: 425. 1914. TYPE: PHILIPPINES. Luzon, Bontoc Subprov., 19 July 1911, *M. Vanoverbergh 1345* (Holotype: AMES [00090243] [image seen]; Isotypes: GH [02336763], K [001085076], K [001085077], L [0059396] [images seen]).

Distribution: Philippines.

The description of *D. greatrixianum* mentions that it is a pretty, slender species, bearing white flowers with a large ovate labellum, which has a purple blotch at the base and apex. No such *Dendrobium* has been found in New Guinea, but the sparse details given indicate that *D. greatrixianum* is a synonym of *D. papilio*. It is likely that Sander saw the description given by Loher of his *Dendrobium* with butterfly-like flowers and ordered his collectors to bring it back from the Philippines for commercial sale in Europe and Britain. Thus, the locality, New Guinea, is likely a deliberate error to throw off commercial rivals.

Loher cited no type in the protologue of *D. papilio*, so we have chosen a collection of his in Kew as the neotype.

Dendrobium pseudocalceolum J.J. Sm., Bull. Dep. Agr. Ind. Neerl. 5: 34. 1907. TYPE: INDONESIA. Papua Prov., between Geelvink Bay and MacCleur Gulf, 1906, *leg. W. den Berger, cult. Hort. Bogor. s.n.* (Lectotype: BO [0061600]) [designated here]; same data, *leg. W. den Berger, cult. Hort. Bogor. s.n.* (Syntype: BO [0061425])

Homotypic synonyms: *Aporum pseudocalceolum* (J.J. Sm.) Rauschert, Rep. Sp. Nov. Regni Veg. 94, 7-8: 441. 1983.

Ceraia pseudocalceola (J.J. Sm.) M.A. Clem., Telopea 10, 1: 293. 2003.

Heterotypic synonyms: *Dendrobium ferdinandii* Kraenzl., in Engl., Pflanzenr. IV. 50, II, B. 21, 45: 209. 1910 *syn. nov.* TYPE: PAPUA NEW GUINEA. Southeast part, *leg. F. M. Bailey, cult. Bot. Gard. Melbourne s.n.* (Holotype: [not found]). Neotype: [designated here]: *Sine loc. et coll. s.n.* (Neotype: HBG [501569] [image seen], as *"Aporum muellerianum"*).

Ceraia ferdinandii (Kraenzl.) M.A. Clem., Telopea 10, 1: 295. 2003.

Distribution: Indonesia (Papua); Papua New Guinea.

This species is a common and widespread plant in lowland regions of New Guinea. It has the smallest flowers of section *Aporum* in New Guinea. The dorsal sepal is about 4 mm long, and the mentum formed by the lateral sepals is slightly shorter. All other species with ensiform leaves in New Guinea have a mentum at least twice as long as the dorsal sepal.

Kraenzlin's description of *D. ferdinandii* is rather lacking in precise floral measurements, mentioning that the flowers are about one cm long, the lip the same length and three mm wide. These details fit with the single flower remaining on the specimen in Hamburg. We believe this specimen is the actual type (or part of it) of *D. ferdinandii*, but, unfortunately, it lacks any collecting details, so we have chosen it as the neotype. The specimen is representative of *D. pseudocalceolum*, and we have reduced *D. ferdinandii* to its synonymy.

Two sheets in BO are treated as type material of *D. pseudocalceolum*. One (BO 0061600) is annotated in the year 1906 in J. J. Smith's hand. We have chosen this as the lectotype. The other sheet (BO 0061425) is annotated in a different, neater hand as *"det. J.J. Smith 1906,"* with the collector's name misspelled as "den Bergher". We have treated the latter as a syntype.

Dendrobium recurvatum (Blume) J.J. Sm., Nova Guin. 8, 1: 52. 1909. TYPE: NEW GUINEA. Collector not cited (Holotype: [not found]). Neotype: [designated here]: Indonesia, Papua Prov., without locality, *A. Zippel 22* (Neotype: L [1495643] [image seen]).

Basionym: *Cadetia recurvata* Blume, Mus. Bot. Lugd.-Bat. 1, 2: 30. 1849.

Heterotypic synonyms: *Dendrobium transversilobum* J.J. Sm., Bull. Dep. Agr. Ind. Neerl. 39: 11. 1910, *syn. nov.* TYPE: INDONESIA. Papua Prov., upper Digul River, 1909, *leg. B. Branderhorst, cult. Hort. Bogor. 203B* (Syntype: BO [not found]; Isosyntype: K [000943769] [image seen]); Noord River, October 1909, *L. S. A. M. von Roemer 661* (Syntype: BO [not found]).

Cadetia transversiloba (J.J. Sm.) Schltr., Rep. Sp. Nov. Regni Veg., Beih. 1: 424. 1912.

Cadetia heterochroma Schltr., Rep. Sp. Nov. Regni Veg., Beih. 1: 437. 1912. TYPE: PAPUA NEW GUINEA. Eitape District, Garup River, 50 m, September 1909, *R. Schlechter 20014* (Holotype: B [destroyed]; Isotype: L [0064680] [image seen]).

Dendrobium heterochromum (Schltr.) J.J. Sm., Bull. Jard. Bot. Buitenz. ser. 2, 8: 18. 1912.

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

This species may be recognised by its broadly oblong leaves, colorful red and yellow flowers, recurved, medially bent mentum, and trilobed labellum with a broadly ovate epichile. The short diagnosis of *Cadetia recurvata* mentions all of these features (except the flower color) leading us to believe that a matching specimen in L, collected by Alexander Zippel from New Guinea, represents the long lost type of this taxon. It is, however, not annotated with the name *Cadetia recurvata,* so we have chosen the collection as the neotype.

Among the unidentified *Cadetia* Gaud. in Leiden is another Zippel collection (L [1495598] [image seen]) with lanceolate leaves 8–10 cm long. We believe this specimen could be the lost type of *Cadetia biloba* Blume (= *Dendrobium cadetia* J.J. Sm. 1909). This taxon may prove to be the earlier name for *Dendrobium versteegii* J.J. Sm., or at least closely allied to it.

Eria Lindl., Bot. Reg. 11: t. 904. 1825.

Type species: *Eria stellata* Lindl.

A genus of about 20 species in the sense of Ng et al. (2018), distributed from India to the Solomon Islands. From the other genera of Eriinae, it may be distinguished by having convolute (versus conduplicate) leaves in the developing state. The second species discussed here is widespread and has been known for about the last hundred years as *E. javanica* (Swartz) Blume, but, as shown above, the latter name must be treated as a synonym of *Bulbophyllum gibbosum*.

Eria cochleata Lindl., Edwards's Bot. Reg. 30: misc. 14, no. 23. 1844. TYPE: PHILIPPINES. Luzon, Manila, *imp. & cult. Messrs. Loddiges s.n.* (Holotype: K-L [not seen]). Fig. 1C–D

Heterotypic synonym: *Eria merrillii* Ames, Philipp. J. Sci. 2, C: 331. 1907, *syn. nov.* TYPE: PHILIPPINES. Mindoro, Alag River, 380 m, 12 November 1906, *E. D. Merrill 5519* (Holotype: PNH [destroyed]; Isotypes: AMES [9643]; K [000827458] [image seen]).

Distribution: Philippines.

Additional specimens examined: PHILIPPINES. Luzon, Rizal Prov., without precise locality, cult. in Manila, December 1908, *W. S. Lyon BS 5625* (AMES); Rizal Prov., without precise locality, September 1909, *A. Loher 14742*

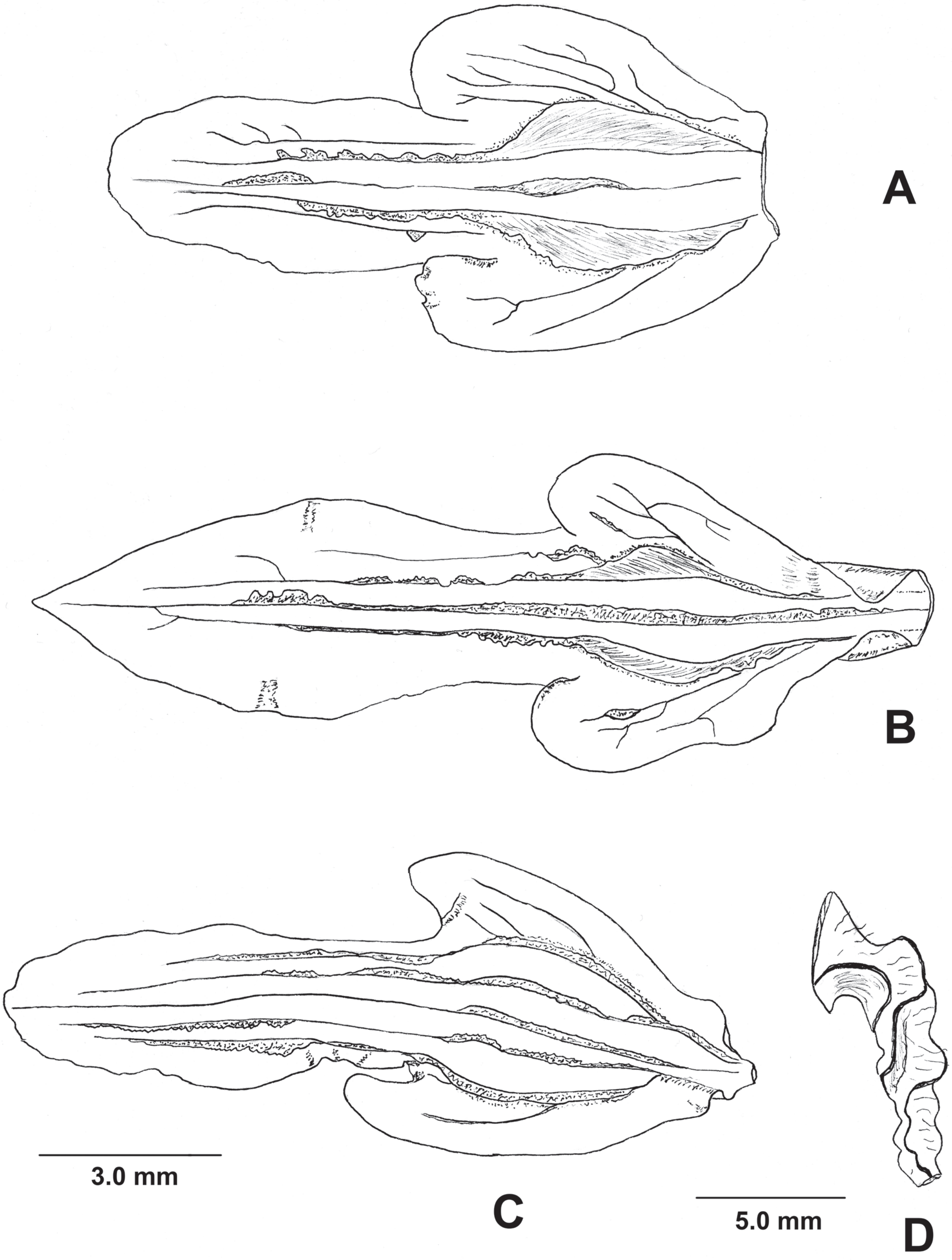

FIGURE 1. *Eria stellata* Lindl. **A–B**, labellum variation. *Eria cochleata* Lindl. **C**, labellum; **D**, pedicel plus ovary. A from *Hort. Bogor. s.n.* (AMES). B from *C. A. Wenzel 100* (AMES). C–D from AMES, isotype of *Eria merrillii* Ames.

(AMES); same data, *A. Loher 14615* (AMES); Rizal Prov., Montalban, January 1914, *A. Loher 13771* (AMES); Rizal Prov., Mt. Irid, 610 m, November 1926, *M. Ramos & G. E. Edano BS 48446* (AMES); Sorsogon Prov., Irosin, Mt. Bulusan, December 1915, *A. D. E. Elmer 15552* (AMES); same data, April 1916, *A. D. E. Elmer 15552* (AMES). Mindoro, S slopes of Mt. Yagaw, 660 m, 5 August 1953, *H. C. Conklin 317 (= PNH18621)* (AMES). Samar, Catubig River, Mt. Capotoan, 120 m, 20 February 1916, *M. Ramos BS 24395* (AMES). Leyte, Jaro, Canpagal, 800 m, 24 November 1914, *C. A. Wenzel 0717* (AMES). Mindanao, Surigao, no date, *W. S. Lyon 116* (AMES, 4 sheets).

This species has been listed in the synonymy of *E. javanica* (i.e., *E. stellata*) in some online databases (e.g., World Checklist of Selected Plant Families = WCSP), but differs from that taxon in having spiral laminate (vs. straight, low rounded) ribs on the pedicellate ovary. In the WCSP, *Eria merrillii* is listed as a synonym of *Pinalia ovata* (Lindl.) W. Suarez & Cootes. This is an error arising from a mistake in Garay and Sweet (1974), where *E. merrillii* was cited in synonymy with *Eria ovata* Lindl. var. *retroflexa* (Lindl.) Garay & Sweet, instead of citing the similar and simultaneously proposed name *E. merrittii* Ames.

Another species that shares the spiral laminate ribs on the ovary is *E. sessilifolia* (J. Fraser) D.L. Roberts & Sayers from Sulawesi, Indonesia. This Indonesian taxon also has a very similarly shaped lip but differs in the pseudobulbs that bear only two almost sessile leaves. In *E. cochleata*, the pseudobulbs usually bear four distinctly petiolate leaves. There is a Philippine specimen from Bohol Island (*M. Ramos s.n.* [AMES]) called *E. merrillii* that has bifoliate pseudobulbs. Further study may show it to be *E. sessilifolia*.

Eria stellata Lindl., Bot. Reg. 11: t. 904. 1825. TYPE: INDONESIA. Java, fl. in cult. February, *W. Cattley s.n.* (Holotype: K-L [not seen]). Fig. 1A–B

Homotypic synonyms: *Octomeria stellata* (Lindl.) Spreng., Syst. Veg. ed. 16, 4 (2, Cur. Post): 310. 1827.

Tainia stellata (Lindl.) Pfitz., in Engl., Nat. Pflanzenfam. 2, 6: 153. 1888.

Pinalia stellata (Lindl.) O. Kuntze, Rev. Gen. Pl. 2: 679. 1891.

Heterotypic synonyms: *Dendrolirium rugosum* Blume, Bijdr. Fl. Ned. Ind. 7: 345. 1825. TYPE: INDONESIA. Java, Mt. Salak, fl. September to October, *C. L. Blume 313* (Syntypes: L [0063890], L [0063891], L [0063892] [images seen]).

Eria rugosa (Blume) Lindl., Gen. Sp. Orch. Pl.: 66. 1830.

Pinalia rugosa (Blume) O. Kuntze, Rev. Gen. Pl. 2: 679. 1891.

Octomeria vaginata Breda, Gen. Sp. Orch. Asclep. [fasc. 1]: [t.5]. 1828. TYPE: INDONESIA. Java, Tjiminjak, fl. October, *H. Kuhl & J. C. van Hasselt 2* (Lectotype: L [1511129] [designated here] [image seen]); Bantam, *H. Kuhl & J. C. van Hasselt 16* (possible Syntype: L [1511128] [image seen]).

Eria vaginata (Breda) Benth. ex B.D. Jackson, Index Kew. Suppl. 1: 864. 1893.

Eria fragrans Rchb.f., Bot. Zeitung (Berlin) 22: 415. 1864. TYPE: MYANMAR. Moulmein, *Messrs. Low's coll. s.n.* (Holotype: W-R [19965], [43705] [not seen]).

Pinalia fragrans (Rchb.f.) O. Kuntze, Rev. Gen. Pl. 2: 679. 1891.

Eria striolata Rchb.f., Gard. Chron. ser. 3, 3: 554. 1888. TYPE: NEW GUINEA? Without precise locality, *imp. Messrs. Linden s.n.* (Holotype: W-R [not seen]).

Dendrobium perakense J.D. Hook., Fl. Brit. Ind. 5: 712. 1890. TYPE: MALAYSIA. Perak, without specific locality, *B. Scortechini 1969* (Holotype: K [000827356] [image seen]; Isotype: CAL [0000000128] [image seen]).

Callista perakensis (J.D. Hook.) O. Kuntze, Rev. Gen. Pl. 2: 655. 1891.

Sarcopodium perakense (J.D. Hook.) Kraenzl., in Engl., Pflanzenr. IV. 50, II, B. 21, 45: 328. 1910.

Katherinea perakensis (J.D. Hook.) A.D. Hawkes, Lloydia 19: 97. 1956.

Eria micholitzii Kraenzl., Oesterr. Bot. Zeitschr. 44: 459. 1894. TYPE: PAPUA NEW GUINEA [as KAISER WILHELMS-LAND]. Friedrich-Wilhelmshafen [= Madang], September 1893, *W. Micholitz s.n.* (Lectotype [Christenson, 1994: 349 as Holotype]): HBG [501670] [image seen]; possible Isolectotype: HBG [501669], dated September 1895 [image seen], both as *E. papuana*).

Eria papuana Kraenzl., in Engl., Pflanzenr. IV. 50, II, B. 21, 50: 25. 1911 *nom. illeg.* (non J.J. Sm. 1908).

Eria pseudostellata Schltr., in Schum. & Laut., Fl. Deutsch. Schutzgeb. Sudsee, Nachtr. 2: 182. 1905. TYPE: PAPUA NEW GUINEA [as KAISER WILHELMS-LAND]. New Ireland, near Karu, 0 m, June 1902, *R. Schlechter 14625* (Holotype: B [destroyed]).

Eria inamoena Schltr., Bot. Jahrb. Syst. 45, Beibl. 104: 32. 1911. TYPE: INDONESIA. Sumatra, near Padang Pandjang, *J. H. G. Wichers s.n.* (Syntype: B [destroyed]); Gunung Merapi, 1200 m, 24 January 1907, *R. Schlechter 15941* (Syntype: B [destroyed]; Isosyntypes: AMES [11914]; K [000827325], P [00360311] [images seen]).

Eria javanica (Swartz) Blume var. *philippinensis* Kraenzl., in Engl., Pflanzenr. IV. 50, II, B. 21, 50: 26, f. 15E-F. 1911 *nom. inval.* [no description].

Basis for name: PHILIPPINES. Luzon, Albay Prov., fl. in Manila 6 June 1905, *A. Loher 6003* (AMES); Rizal Prov., without precise locality, 31 July 1907, *M. Ramos 3036* (AMES). Mindanao, Lake Lanao, Camp Keithley, September to October 1907, *M. S. Clemens s.n.* (AMES, 2 sheets).

Distribution: Myanmar; Thailand; Malaysia; Philippines; Indonesia; Papua New Guinea.

Select specimens examined: PHILIPPINES. Luzon. Laguna Prov., Mt. Maquiling, May 1913, *W. H. Brown BS 17905* (AMES). Leyte, Dagami, Panda, 20 May 1913, *C. A. Wenzel 100* (AMES). INDONESIA. Java, without precise locality, *cult. Hort. Bogor. s.n.* (AMES). Papua Prov., Waigeo Island, Warmaserim Creek, E of Kabare, 7 m, 2 February 1955, *P. van Royen 5434* (A). PAPUA NEW GUINEA. New Britain, Talasea Subdistr., Wasissi Village, 25 April 1959, *K. J. White NGF 10924* (AMES, BRI, LAE, spirit).

This widespread taxon is well-represented in herbaria, so we have just cited a few specimens of it. Our illustration depicts a labellum of a Philippine plant and a labellum of a plant from the type locality of Java. Despite the differences between the two (hypochile and epichile ratios), we found that intermediates exist and varieties cannot, so far, be justified in *E. stellata*.

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

An Aeridinae genus of about 65–70 species distributed from Sri Lanka and India to Sulawesi in Indonesia, north to Japan. There are four recorded species in Indonesia, one of which we believe is based on wrongly localised material.

Gastrochilus obliquus (Lindl.) O. Kuntze, Rev. Gen. Pl. 2: 661. 1891. TYPE: MYANMAR [as "India Orientalis"]. Toong Dong, November 1826, *N. Wallich Catal. No. 7304* (Lectotype: [Tsi, 1996: 140 as type]: K-L [not seen]; Isolectotypes: CAL [0000075019] [image seen]; K-W [not seen]); *icon N. Wallich 1314* (Syntype: K [not seen]).

Basionym: *Saccolabium obliquum* Lindl., Gen. Sp. Orch. Pl.: 223. 1833.

Heterotypic synonyms: *Saccolabium bigibbum* Rchb.f. ex J.D. Hook., Curtis's Bot. Mag. 95: t. 5767. 1869. TYPE: MYANMAR. Rangoon or Arrakan, *leg. R. Benson,* fl. in cult. November 1868, *Messrs. Veitch 40* (Lectotype: [Seidenf. 1988: 298 as type]: W-R [42844] [not seen]; drawings W-R [42843] [not seen]).

Gastrochilus bigibbus (Rchb.f. ex J.D. Hook.) O. Kuntze, Rev. Gen. Pl. 2: 661. 1891.

Gastrochilus suavis Seidenf., Opera Bot. 95: 298. 1988. TYPE: THAILAND. NW of Pang Mapha, 600–820 m, 27 February 1968, fl. in cult. 19 October 1968, *G. Seidenfaden & T. Smitinand GT 7162* (Holotype: C [10024087], spirit [image seen]).

Gastrochilus obliquus (Lindl.) O. Kuntze var. *suavis* (Seidenf.) Z.H. Tsi, Guihaia 16, 2: 141. 1996.

Gastrochilus puncticulatus Cavestro, Orchidophile (Asnieres) 141: 53. 2000, *syn. nov.* TYPE: INDONESIA. Sulawesi. Pays Toraja (Tanatoraja), near Rantepao, 400 m, July 1992, fl. in cult. November 1999, *J. L. Martin 120* (Holotype: P [00546578] [image seen]).

Distribution: India; Bhutan; China; Myanmar; Laos; Thailand.

Careful examination of the protologue, as well as images of the type of *G. puncticulatus*, convinces us that it is a synonym of *G. obliquus*, in particular, the variety with rich spotting on the sepals and petals known as var. *suavis*. We believe that some kind of mix-up happened, and that a plant thought to be from Sulawesi probably came from Thailand. *Gastrochilus obliquus,* in our opinion, does not occur in Indonesia.

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 generally terrestrial herbs, growing in a variety of habitats such as grassland, open forest, and rainforest. Kolanowksa et al. (2021) provided a review of the genus in New Guinea and nearby islands. They found 27 species in the study region, but, as noted below, one of these must be relegated to synonymy.

Habenaria trichaete Schltr., Rep. Sp. Nov. Regni Veg., Beih. 1: 14. 1911. TYPE: PAPUA NEW GUINEA. Umbili District, Djamu River, 400 m, August 1907, *R. Schlechter 16383* (Holotype: B [destroyed]). Neotype: (Kolan. et al. 2021: 65): Papua New Guinea, Morobe Prov., Wampit, Buru Village, 1310 m, 13 July 1967, *A. N. Millar NGF 22945* (Neotype: LAE [image seen]; Isoneotypes: L [1516332], RENZ [12256.1], RENZ [14488.1] [images seen]).

Heterotypic synonym: *Habenaria devogeliana* Kolan., Szlach., Kras. & S. Nowak, Peer J. 9 (e 12011): 60. 2021, *syn. nov.* TYPE: PAPUA NEW GUINEA. Eastern Highlands Prov., Crater Mountain Wildlife Management Area, near "wara oh" base camp, 600 m, 6 July 1996, *G. D. Weiblin 807* (Holotype: A).

Distribution: Indonesia (Papua); Papua New Guinea.

Habenaria devogeliana seems at first easily distinguished from *H. trichaete* in a number of characters, such as untailed sepals and deeply bilobed petals. However, these differentiating features have arisen through a mix-up in the descriptive process, whereby a mislabelled flower of another species has been mistakenly identified as belonging to *Weiblin 807*. The authors' own image of the type of *H. devogeliana* shows the distinctive tailed sepals in contrast to the description and analytical drawing. Furthermore, we have studied the type of *H. devogeliana*, and all of its features are identical to *H. trichaete*.

Phreatia Lindl., Gen. Sp. Orch. Pl.: 63. 1830.
Type species: *Phreatia elegans* Lindl.

A member of subtribe Thelasinae with about 215 species distributed from Sri Lanka and India to Tahiti. In general, the plants are small epiphytic herbs with racemes of small (sepals 1.00–2.75 mm long), often white, flowers. The taxon transferred here comes from Indonesia, where 75 species have so far been recorded.

Phreatia microscopica (Kraenzl.) Ormerod & Juswara, *comb. nov.*

Basionym: *Sarcochilus microscopicus* Kraenzl., Bot. Jahrb. Syst. 17: 487. 1893.

TYPE: INDONESIA. Sumatra, near Padang, 610–915 m, February 1892, *W. Micholitz s.n.* (Holotype: B [destroyed]).

Distribution: Indonesia (Sumatra).

No later collections of this species have been identified, but due to its small size, the plants are probably easily overlooked in the field. It belongs to section *Rhizophyllum* (Blume) J.J. Sm., a group characterised by having very short stems on which the leaf sheaths closely overlap.

Zeuxine Lindl., Coll. Bot. (Lindley): Append. [no. 18]. 1826 (as *Zeuxina*) *orth. cons.*

Type species: *Pterygodium sulcatum* Roxb.

A Goodyerinae genus of about 90 species distributed from India and Sri Lanka to Samoa in the Pacific. The taxonomy of species in the genus is hampered by the superficial similarity of a number of taxa, thus leading to misidentifications (Ormerod, 2018).

Zeuxine zollingeri (Rchb.f.) Ormerod & Juswara, *comb. nov.*

Basionym: *Monochilus zollingeri* Rchb.f., Xenia Orch. 1: 215. 1856.

TYPE: INDONESIA. Java, near the waterfall between Tjudruk and Tjigalin, 4 September 1842, *H. Zollinger 592* (Lectotype: [designated here] P [1802230] [image seen]; drawing W-R [1199] [image seen]).

Distribution: Indonesia (Java).

Smith (1927) reduced this species to *Z. gracilis* (Breda) Blume based on Reichenbach's simplified floral sketches in Wien, but it differs in habit (stem slender, leaves persistent with broad white median zone at the time of capsule formation vs. stem swelling, leaves wilted and plain at the time of capsule formation) and in having a denser inflorescence. It may well prove to be an earlier name for *Z. tjiampeana* J.J. Sm., or at least closely related to it.

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ADDITIONAL NOTES ON SOME INDIAN ORCHIDACEAE

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Abstract. Nomenclatural and taxonomic notes are provided for some Indian orchids, with additional synonymy provided for *Cleisostoma tenuifolium, Dendrobium tsangianum,* and *Vanda tessellata*. The identities of *Eria clarkei* (= *Pinalia rimannii*) and *Nephelaphyllum nudum* are elucidated. *Habenaria modesta* is reinstated over *H. ovalifolia* due to nomenclatural priority. Two taxa are excluded from the Indian flora, namely *Dendrobium fargesii* (misidentified) and *D. versicolor* (= Philippine *D. ionopus*).

Keywords: additions, India, lectotypifications, Orchidaceae, synonymy

Schuiteman et al. (2022) recently published a checklist of the Orchidaceae of India, providing a handy base reference for studies of the Indian orchid flora. We add here a few additional synonyms, elucidate the identities of some obscure taxa, and provide some nomenclatural notes on other entities.

Cleisostoma Blume, Bijdr. Fl. Ned. Ind. 8: 362. 1825.
Type species: *Cleisostoma sagittatum* Blume

A genus of about 100 monopodial orchids distributed from India to Fiji. It was long known as *Sarcanthus* until Garay (1972) showed that *Cleisostoma* was the correct name. The flowers are small (sepals usually 5–8 mm long) and bear a complex, spurred labellum. About 22 species are recorded from India, but some of these require further study to ascertain their identities and correct names.

Cleisostoma tenuifolium (L.) Garay, Bot. Mus. Leafl. Harv. Uni. 23, 4: 175. 1972.
Basionym: *Epidendrum tenuifolium* L., Sp. Pl. 2: 952. 1753. Lectotype (Majumdar and Bakshi, 1979: 353): t. 5 of *Tsjerou-mau-maravara* in Rheede, Hort. Malab. 12: 11. 1692.
Homotypic synonyms: *Cymbidium tenuifolium* (L.) Willd., Sp. Pl. ed. 4, 1: 103. 1805.
Aerides tenuifolia (L.) Moon, Catal. Pl. Ceylon: 60. 1824.
Luisia tenuifolia (L.) Blume, Mus. Bot. Lugd.-Bat. 1: 64. 1849.
Sarcochilus tenuifolius (L.) Naves, Noviss. App. 238. 1880.
Saccolabium tenuifolium (L.) Alston, Ann. Roy. Bot. Gard. Peradeniya 11: 205. 1929.
Sarcanthus tenuifolius (L.) Seidenf., Dan. Bot. Ark. 27, 4: 37. 1971.
Heterotypic synonym: *Sarcochilus tenuifolius* (L.) Naves var. *majus* Naves, Noviss. App. 238. 1880. TYPE: t. 6 of *Kolli-Tsjerou-Mau-Maravara* in Rheede, Hort. Malab. 12: 13. 1692.

Distribution: Sri Lanka; India; Myanmar; Thailand.

We have added *Sarcochilus tenuifolius* var. *majus* to the synonymy. In our opinion, the type illustration depicts a sterile plant of this species. *Epidendrum tenuifolium* has long been confused with a species of *Luisia*, although the original illustration clearly depicts a species of *Cleisostoma*. That species of *Luisia* cannot be known as *L. tenuifolia*. The correct name is *L. birchea* (see below for discussion).

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

A genus of about 1520–1530 species distributed from India and Sri Lanka to Tahiti. Approximately 124 species are recorded for India (Schuiteman et al., 2022). As discussed below, we do not think that *D. versicolor* Cogn. actually came from India, but that it is really a Philippine taxon. We also think that *D. fargesii* Finet does not occur in India due to confusion with *D. tsangianum*.

Dendrobium ionopus Rchb.f., Gard. Chron. n.s., 18: 808. 1882. TYPE: MYANMAR [as "Birmah"]. Without locality, *cult. H. Low & Co. s.n.* (Holotype: W-R [image seen]).
Homotypic synonyms: *Callista ionopus* (Rchb.f.) O.Kuntze, Rev. Gen. Pl. 2: 655. 1891 as *ionopus*.
Eurycaulis ionopus (Rchb.f.) M.A. Clem., Telopea 10, 1: 287. 2003.
Heterotypic synonyms: *Dendrobium versicolor* Cogn., J. Orchidees 6: 153. 1895, *syn. nov.* TYPE: INDIA. Assam, introduced by *L'Horticulture Internationale,* fl. first half of July 1895, *cult. in the garden of la Societe Bruxelloise s.n.* (Holotype: [lost]).
Dendrobium epidendropsis Kraenzl., Orchis 2: 79. 1908. TYPE: PHILIPPINES. Without locality, *leg. A. Loher, cult. Bot. Gart. Erlangen s.n.* (Holotype: HBG [500397] [image seen]).

Distribution: Philippines.

We have carefully analyzed the description of *D. versicolor* and believe it matches the characters of

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D. ionopus. Both taxa have had their identities obscured due to erroneous locality data. Among the species of section *Pedilonum* Blume, *D. ionopus* may be recognized by its pendulous inflorescences bearing up to 20 flowers, yellowish (often purple suffused) flowers with sepals 10–13 mm long, a long mentum (ca. 20–25 mm), and long- clawed lip with a subquadrate midlobe.

Dendrobium tsangianum (Ormerod) Schuit. & Peter B. Adams, Muelleria 29, 1: 66. 2011.

Basionym: *Epigeneium tsangianum* Ormerod, Taiwania 49, 2: 97. 2004. TYPE: CHINA. Guangxi, near Guangdong border, Shap Man Tai Shan, Nam She Village, 19 November 1934, *W. T. Tsang 24684* (Holotype: AMES [56278]; Isotypes: AMES [111361]; US [00503293] [not seen]). Fig. 1

Heterotypic synonyms: *Epigeneium chapaense* Gagnep., Bull. Mus. Natl. Hist. Nat. (Paris) s. 2, 4: 596. 1932, *syn. nov.* TYPE: VIETNAM. Tonkin, Col de Lo qui Ho, KM 9 near Chapa, 1800 m, 28 July 1926, *E. Poilane 12605* (Lectotype [Seidenf. 1980: 70, 1st step] [designated here]; 2nd step: P [00387205] [image seen]; Isolectotype: P [000387204] [image seen]); Col de Lo qui Ho, near Chapa, 28 July 1926, *E. Poilane 12607bis* (Syntype: P [00387206] [image seen]).

Sarcopodium chapaense (Gagnep.) T. Tang & F.T. Wang, Acta Phytotax. Sin. 1, 1: 83. 1951.

Dendrobium brunneum Schuit. & Peter B. Adams, Muelleria 29, 1: 65. 2011.

Epigeneium clemensiae Gagnep., Bull. Mus. Natl. Hist. Nat. (Paris) s. 2, 4: 595. 1932, *syn. nov.* TYPE: VIETNAM. Annam, Mt. Bani summit, 25 km from Tourane, 17 August 1927, *J. Clemens & M. S. Clemens 4327* (Holotype: P [00387199] [image seen]; Isotype: NY [8819] [image seen]).

Sarcopodium clemensiae (Gagnep.) T. Tang & F.T. Wang, Acta Phytotax. Sin. 1, 1: 83. 1951.

Dendrobium mariae Schuit. & Peter B. Adams, Muelleria 29, 1: 66. 2011.

Epigeneium delacourii Gagnep., Bull. Mus. Natl. Hist. Nat. (Paris) s. 2, 4: 595. 1932. TYPE: LAOS. Environs of Nape, *M. Delacour s.n.* (Holotype: P [00387200] [image seen]).

Epigeneium arunachalense A.N. Rao, Bull. Arunachal For. Res. 25, 1–2: 3. 2010. TYPE: INDIA. Arunachal Pradesh, Lower Subansiri District, Hakhetari to Rizampak, 1200 m, April 1965, *A. R. K. Sastry 44804* (Holotype: ASSAM [not seen]).

Dendrobium subansiriense D.Verma & Barbhuiya, Phytotaxa 167, 1: 150. 5 May 2014.

Dendrobium deuteroarunachalense J.M.H. Shaw, Orch. Review 122 (1306, Suppl.): 38. June 2014, *nom. illeg*.

Dendrobium nageswarayanum Chowlu, Natl. Acad. Sci. Lett. 43, 7: 659. 2020. TYPE: INDIA. Arunachal Pradesh, Kurung Kumey District, Koloriang Hill, 823 m, 11 November 2016, *K. Chowlu 40066* (Holotype: CAL [not seen]).

Epigeneium nageswarayanum (Chowlu) Agrawala, C. Deori, Aazhiv. & Chowlu, Fl. Pl. India Annot. Checkl. Monocot.: 50. 2020, *nom. inval*.

Usage synonym: *Epigeneium fargesii auct. non* (Finet) Gagnep., N.P. Balakr. & Sud. Chowdhury, Bull. Bot. Surv. India 8, 3–4: 313, Pl. 1. 1966.

Not *Dendrobium arunachalense* C. Deori, S.K. Sarma, Phukan & A.A. Mao 2006 (Section *Formosae*).

Not *Dendrobium chapaense* Aver. 2006 (Section *Formosae*).

Not *Dendrobium clemensiae* Ames 1912 (Section *Diplocaulobium*).

Not *Dendrobium delacourii* Guill. 1924 (Section *Stachyobium*).

Distribution: India; Bhutan; China; Laos; Vietnam.

Additional specimens examined: INDIA. Arunachal Pradesh, Subansiri Division, SW corner of Apu Tani Valley, 1615 m, 13 April 1965, *P. A. Cox & P. Hutchison 370* (K). VIETNAM. Ha Giang Province, Yen Minh District, Lao Va Chai Municipality, to W of Ngan Chai Village, 1380–1450 m, 25 November 2004, *S. K. Wu et al. WP 617* (A).

The above taxa have been distinguished on leaf length, lateral sepal width, labellum hypochile and epichile width, and the type of calli on the hypochile. A renewed investigation into these features was sparked by material excellently photographed by Ba Vuong Truong in Vietnam. Our review of the differentiating features previously used shows that leaf length is essentially continuous, lateral sepal width is not different among any of the taxa (depending on where one measures width), labellum hypochile and epichile width is variable, but the epichile is always slightly wider than the hypochile. The epichile shape is also variable, and the calli shape is often misinterpreted in herbarium material due to artefacts arising from the drying process. Thus, the calli in some cases may appear as well-separated narrow lamellae due to the inner parts failing to rehydrating. The calli are broad, cuneiform in cross-section (outer margin thickest) in fresh flowers and gently convergent apically.

We have not been able to verify any records of *D. fargesii* Finet from India. It differs from *D. tsangianum* in its flowers having a longer mentum (20–24 versus 12–15 mm), broader, ovate-lanceolate to oblong-lanceolate (versus ligulate to ligulate-lanceolate) petals, and a white (versus brown) labellum epichile that is distinctly wider than long (versus slightly wider than long to longer than broad, i.e., broadly obovate to trapeziform).

We illustrate here a north Vietnamese specimen collected just northwest of the type locality of *Epigeneium chapaense*. This shows the well-separated lamellae artifact discussed above, a feature also evident in the protologue figure of *E. arunachalense*.

The earliest available epithet in *Dendrobium* is *Epigeneium tsangianum*, since all of the others are already in use.

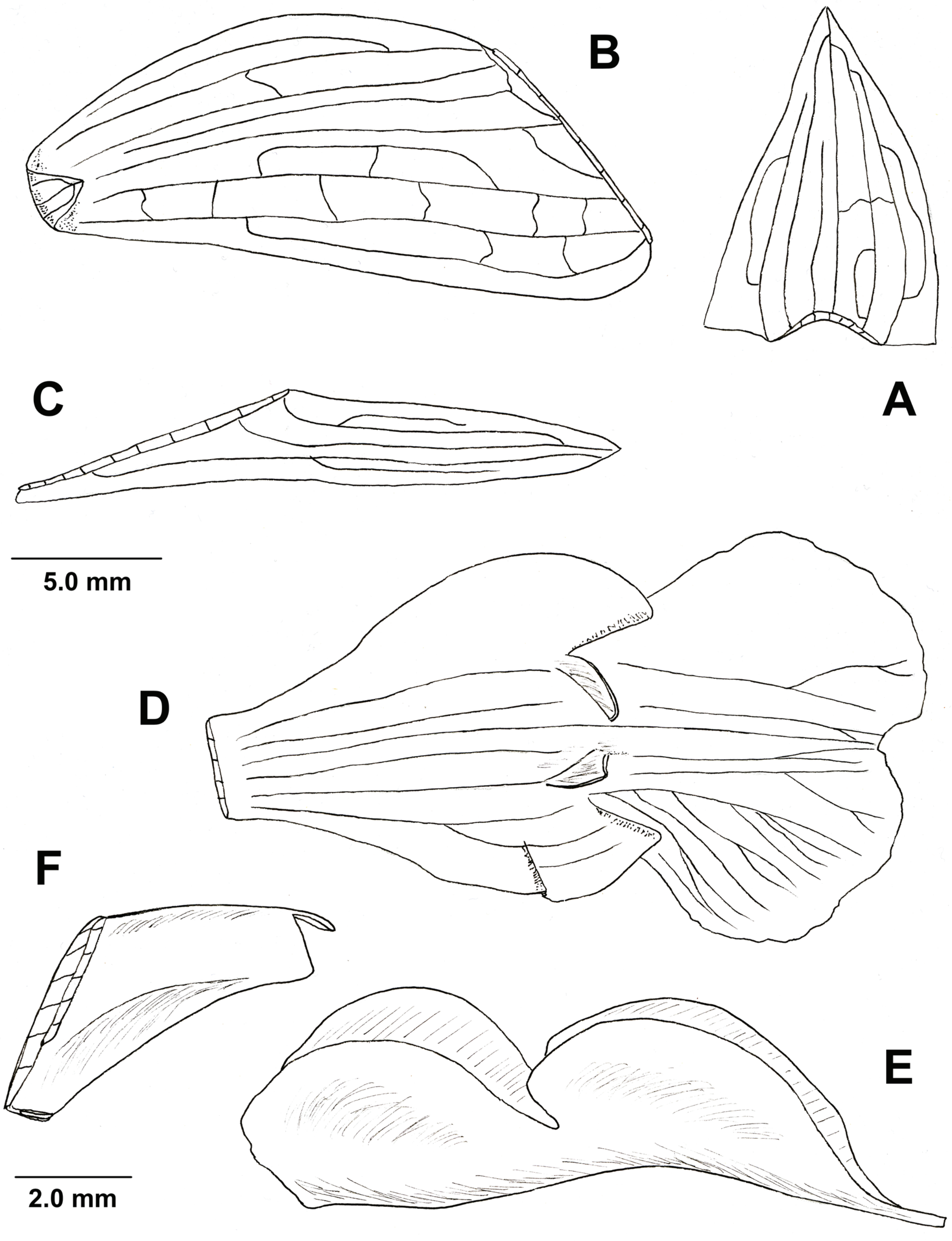

FIGURE 1. *Dendrobium tsangianum* (Ormerod) Schuit. & Peter B. Adams. **A**, dorsal sepal; **B**, lateral sepal; **C**, petal; **D**, labellum from above; **E**, labellum from side; **F**, column. Drawn from *S. K. Wu et al. WP 617* (A).

Habenaria Willd., Sp. Pl. ed. 4: 5, 44. 1805.
Type species: *Habenaria macroceratitis* Willd. (= *Orchis habenaria* L.).

About 900 species of mostly terrestrial herbs distributed worldwide. They have terminal racemes of flowers that are usually in shades of white or green. About 67 species (Schuiteman et al. 2022) have been recorded from India.

Habenaria modesta Dalzell, Hooker's J. Bot. Kew Gard. Misc. 2: 262. 1850. TYPE: INDIA. Mumbai District, Salsette Island, fl. August, *N. A. Dalzell s.n.* (Holotype: [not found]).

Heterotypic synonyms: *Habenaria ovalifolia* Wight, Icon. Pl. Ind. Orient. 5, 1: 13, t. 1708. 1851. TYPE: INDIA. Malabar and Anamally Hills, fl. July to August, *R. Wight s.n.* (Holotype: K [00247464] [image seen]).

Habenaria platantheropsis Kraenzl., Bot. Jahrb. Syst. 28: 172. 1900. TYPE: INDIA. Nilgiri and Coorg Hills, *25. Platanthera, G. Thomson s.n.* (Holotype: B: [destroyed]; Lectotype: P [0043654] [designated here] [image seen]).

Distribution: India.

Schuiteman et al. (2022) listed this taxon as *H. ovalifolia* with the older *H. modesta* in synonymy. Naturally, the older name has priority and should be utilized. There is no apparent surviving type material of *H. modesta*, but we are aware that other Indian researchers have discovered drawings of the species by Nicholas Dalzell that may be used in a future typification proposal.

No type material of *H. platantheropsis* can be found at Kew (Schuiteman, pers. comm.) or HBG, so we have chosen a collection located in P as the lectotype.

Luisia Gaud., Voy. Uranie, Bot.: 426. 1829.
Type species: *Luisia teretifolia* Gaud.

A genus of Aeridinae with about 50 species, 22 of which are reported for India (Schuiteman et al., 2022). The genus is distributed from India and Sri Lanka to Fiji and Samoa. The plants are outwardly recognized by their monopodial stems bearing terete leaves, very short inflorescences, and one to few relatively fleshy flowers. The flowers often have yellow sepals and petals contrasted by a labellum with dark purple to maroon coloring. Unlike many Aeridinae, *Luisia* has a rather simple labellum that is divided into a shallow, unspurred hypochile and an often larger epichile.

Luisia birchea Blume, Mus. Bot. Lugd.-Bat. 1: 64. 1849.

Basionym: *Birchea teretifolia* A. Rich., Ann. Sci. Nat., Bot., ser. 2, 15: 67. 1841. TYPE: INDIA. Nilgiri Hills, near Avalanchy, *G. Perrottet s.n.* (Holotype: P [00324112] [image seen]).

Homotypic synonyms: *Birchea nilgherrensis* D. Dietr., Syn. Pl. 5: 118. 1852, *nom. illeg.*

Luisia laurifolia M.R. Almeida, Fl. Maharashtra 5A: 66. 2009, *nom. illeg.*

Usage synonyms: *Cymbidium tenuifolium auct. non* (L.) Willd., Lindl., Gen. Sp. Orch. Pl.: 167. 1833.

Luisia tenuifolia auct. non (L.) Blume, Blume, Mus. Bot. Lugd.-Bat. 1: 64. 1849.

Distribution: India; Sri Lanka.

Schuiteman et al. (2022) used the name *Luisia tenuifolia* Blume for this species. The nomenclatural situation regarding the name *Luisia tenuifolia* was clearly explained by Seidenfaden (1971): this binomial must be treated as a homotypic synonym of *Cleisostoma tenuifolium* (L.) Garay. The recently proposed *Luisia laurifolia* had a non-existent *Cymbidium laurifolium* Lindl. as its basis, but the authors also cited *Luisia birchea* in synonymy. *Luisia laurifolia* is, therefore, a superfluous and illegitimate name for *L. birchea*.

Nephelaphyllum Blume, Bijdr. Fl. Ned. Ind. 8: 372. 1825.
Type species: *Nephelaphyllum pulchrum* Blume

A genus of about twelve species distributed from India to Indonesia. They are sympodial plants with creeping rhizomes bearing unifoliate pseudobulbs, the latter topped with a single cordate to deltate, often maculated leaf. The flowers have a spurred, entire to trilobed labellum, that is usually adorned with various keels and processes. India has three species of *Nephelaphyllum,* two of which have an intertwined history which we discuss below.

Nephelaphyllum cordifolium (Lindl.) Rchb.f., Xenia Orch. 1: 216. 1856.

Basionym: *Cytheris cordifolia* Lindl., Gen. Sp. Orch. Pl.: 129. 1831. TYPE: INDIA. Mountains of Sylhet [Bangladesh], August 1822, *leg. F. De Silva 1135, in N. Wallich Catal. No. 3750* (Holotype: K-L [image seen]; Isotype: K-W [not seen]).

Homotypic synonym: *Tainia cordifolia* (Lindl.) Gagnep., Bull. Mus. Natl. Hist. Mus. (Paris) ser. 2, 4: 706. 1932, *nom. illeg.* (*non* J.D. Hook. 1889).

Distribution: India; Bangladesh?; Myanmar.

The transfer of this taxon to *Nephelaphyllum* is often attributed to Lindley (1858) or Blume (1858), but we found that Reichenbach was the first in 1856 (now updated in IPNI). The holotype of the species was illustrated by Pearce and Cribb (2002). The illustration shows the labellum to have three keels with forward-pointing, extended apices.

Nephelaphyllum nudum J.D. Hook., Fl. Brit. Ind. 6: 192. 1890. TYPE: INDIA. Sikkim, without precise locality, 1874-1875, *G. King 500* (Lectotype: CAL [0000000307[[designated here] [inflorescence only]).

Usage synonym: *Nephelaphyllum cordifolium auct. non* (Lindl.) Rchb.f., Blume, Fl. Jav. Ins. Adj. n.s. 1: 145–146, t. 61, f. 3. 1858; Coll. Orch. Arch. Ind.: 172, t. 61, f. 3. 1858.

Distribution: India.

Specimens examined: INDIA. Meghalaya, Churra, 14 October 1835, *W. Griffith s.n.* (CAL [454006]); Khasia Hills, "1844," *W. Griffith s.n.* (L [0940466] [image seen]).

The type of this species consists of an inflorescence mounted on top of a three-leaved stem belonging to a species of Goodyerinae (possibly a *Goodyera* or *Zeuxine*). This mixture led to Hooker's misleading diagnosis that mentions a stout four inch stem. We have, therefore, selected the inflorescence as the lectotype. The species is very similar to *N. cordifolium* but differs in the labellum having a single high-lamellate keel (versus three raised, acute, forward-pointing keels) on the midlobe.

Pinalia Lindl., Orch. Scelet.: 14, 21, 23, t. 71. 1826.
Lectotype species: *Pinalia alba* Buch.-Ham. ex Lindl.

A genus of Eriinae with about 210 species distributed from India and Sri Lanka to Tahiti. Most of the species are found in Indonesia, but other tropical Asian countries such as Malaysia and the Philippines also have a significant number of taxa. About 22 species are found in India.

Pinalia rimannii (Rchb.f.) O. Kuntze, Rev. Gen. Pl. 2: 679. 1891.

Basionym: *Eria rimannii* Rchb.f., Gard. Chron. n.s., 24: 712. 1885. TYPE: MYANMAR [as "Burmah"]. Without locality, *E. Rimann s.n.* (Holotype: W-R).

Heterotypic synonym: *Eria clarkei* J. Fraser, Gard. World 11: 758. 27 July 1895 as *clarkii;* H.J. Veitch, Gard. Chron. ser. 3, 18: 49. 13 July 1895 as *clarkei, nom. inval.*; Hort., The Garden (1871-1927) 48: 30. 13 July 1895 as *clarki, nom. inval., syn. nov.* TYPE: WITHOUT ORIGIN. Exhibited at the R.H.S. 9 July 1895, *cult. W. Lewis & Co. s.n.* (Holotype: [lost]).

Distribution: Myanmar.

We decided to investigate the overlooked name *Eria clarkei* on the presumption that it could be named after C. B. Clarke, who did so much work for the flora of India and made extensive collections there. The description of this taxon provided by Fraser in *The Gardening World Illustrated* mentions the dark brown, apically two- to three-leaved, ovoid pseudobulbs, leathery leaves, and the dense arching raceme of straw-colored flowers with a trilobed, clear yellow lip. Our analysis of this description leaves us in no doubt this taxon is a synonym of the Myanmar endemic *Pinalia rimannii.*

We have adopted Veitch's spelling of "*clarkei"* since he first used the epithet, although he gave no clue to who Clarke was. Veitch's description is wholly inadequate for valid publication since he only says "… with small greenish-white flowers". The description in *The Garden* is equally inadequate, giving only "… dull yellow species with dense spikes of blooms".

Vanda W. Jones ex R. Br., Bot. Reg. 6: t. 506. 1820.
Type species: *Vanda roxburghii* R. Br.

A genus of Aeridiinae with about 85 species distributed from Sri Lanka and India to the Solomon Islands. The plants are monopodial epiphytes (occasionally lithophytes) that are quite popular in the horticultural trade, so many are endangered from over-collection. The genus was recently the subject of a popular monograph by Motes (2021). About 15 or 16 species, and perhaps two natural hybrids, are found in India.

Vanda peetersiana (Cogn.) Andre, Rev. Hort. (Paris) 70: 50. 1898.

Basionym: *Vanda coerulea* Griff. ex Lindl. var. *peetersiana* Cogn., Gard. Chron. s. 3, 22: 394. 1897. TYPE: INDIA. Khasia Mountains, November 1896, *imp. & cult. A. A. Peeters s.n.* (Holotype: [lost]).

Distribution: India.

Additional specimens examined: INDIA. Nagaland, Kohima, Naga Hills, 1525 m, 22 September 1950, *W. Koelz 26250* (K); Kohima, Naga Hills, 1525 m, 20 September 1950, *W. Koelz 26205* (K). WITHOUT ORIGIN. January 1899, *cult. J. W. Moore s.n.* (K).

Vanda peetersiana seems to be a natural hybrid between *V. coerulea* Griff. ex Lindl. and *V. coerulescens* Griff. A color painting of the original plant can be found in Cogniaux (1897), depicting its basically white flowers that are tinted lilac-pink, especially towards the tips of the tepals. The two Indian specimens cited above have darker flowers, and were said by the collector to be lavender-violet, darkest on the lip and spur.

Vanda tessellata (Roxb.) Lodd. ex G. Don, Hort. Brit. (Loudon): 372. 1830.

Basionym: *Epidendrum tessellatum* Roxb., Pl. Coromandel 1, 2: 34. 1795. TYPE: INDIA. Circar Mountains, *W. Roxburgh s.n.* (Holotype: [lost]); Lectotype: [designated here]): t. 42 in Roxb., Pl. Coromandel 1, 2. 1795.

Homotypic synonyms: *Cymbidium tessellatum* (Roxb.) Sw., Nova Acta Regiae Soc. Sci. Upsal. 6: 75. 1799.

Aerides tessellata (Roxb.) Wight ex Lindl., Gen. Sp. Orch. Pl.: 240. 1833.

Heterotypic synonyms: *Vanda roxburghii* R. Br., Bot. Reg. 6: t. 506. 1820. TYPE: INDIA. Bengal, *W. Roxburgh s.n.* (Lectotype: BM [000538864] [designated here] [image seen]); Bengal, *imp. J. Banks, cult. D. Banks s.n.* (Syntype: [lost]. Represented by t. 506 in Bot. Reg. 6, 1820); description of *Vanda* W. Jones, Asiat. Res. 4: 311–312. 1799.

Cymbidium tesselloides Roxb., Fl. Indica ed. 2, 3: 463. 1832, *nom. illeg.*

Vanda tesselloides (Roxb.) Rchb.f., Ann. Bot. Syst. 6, 6: 864. 1864, *nom. illeg.*

Vanda tessellata (Roxb.) Lodd. ex G. Don subsp. *tesselloides* Motes, Natural Gen. Vanda: 42. 2021.

Vanda roxburghii R. Br. var. *wrightiana* Rchb.f., Gard. Chron. n.s., 20: 262. 1883. TYPE: WITHOUT ORIGIN. *Cult. J. Hodges s.n.* (Holotype: W-R [not seen]).

Vanda roxburghii R. Br. var. *rubra* Rodigas, Illustr. Hortic. (Belge) 32: 185, t.579. 1885. TYPE: WITHOUT ORIGIN. *Imp. Compagnie Continentale Horticulture [Messrs. Linden] s.n.* (Holotype: [lost]).

Vanda suavis Lindl. var. *rubra* (Rodigas) B.S. Williams, Orch. Grow. Man. ed. 7: 749. 1894.

Vanda roxburghii R. Br. var. *coerulea* Hort. ex Stein, Orchideenb.: 585. 1892. TYPE: Not cited.

Vanda roxburghii R. Br. var. *spooneri* Gammie, J. Bombay Nat. Hist. Soc. 19: 625. 1909. TYPE: INDIA.

Southern Mahratta Country, common between Londa and Tinai Ghat, fl. October to January, *T. J. Spooner s.n.* (Syntype: [not found]); Wynaad, *R. L. Proudlock s.n.* (Syntype: [not found]).

Distribution: Sri Lanka; India; Nepal; Bangladesh; Myanmar.

Motes (2021) divided this species into two subspecies based on distribution and flower size. We have not been able to discern any distinct taxa based on these parameters. Distribution appears continuous, as does flower size. The variety *spooneri* was distinguished by its smaller plant size (stems 20 cm versus 60 cm long) and white (versus violet) labellum. Despite our efforts, it has not been possible to locate type material of this variety. Plant size and labellum color are quite variable, and we agree with Schuiteman et al. (2022), who reduced this variety to synonymy. However, it is possible that var. *spooneri* is a mixed concept because white-lipped plants in the Wynaad region could be *V. sathishii* Motes, which is found here and has a predominantly white labellum (see Ratheesh Narayanan et al., 2013).

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A NEW NAME FOR *CRYPTERONIA GRIFFITHII* C.B. CLARKE (CRYPTERONIACEAE)

Paul Ormerod[1]

Abstract. An overlooked binomial *Henslowia rubiflora* is found to be an earlier name for *Crypteronia griffithii*, thus requiring one new combination, viz. *Crypteronia rubiflora*.

Keywords: *Crypteronia, Henslowia,* priority, new combination.

The tree genus *Crypteronia* Blume (Crypteroniaceae) comprises seven species distributed from northern India to Papua New Guinea. Six of the seven species can be found on the island of Borneo. They may grow to 60 metres tall and are occasionally used for timber, but never grow in large stands so are not a commercially viable commodity. *Crypteronia* was monographed by van Beusekom-Osinga (1977) who recognised four species. Pereira and Wong (1995) subsequently added another three taxa from Borneo.

During unrelated literature research for studies in the Orchidaceae, the name *Henslowia rubiflora* was noted and found not to be indexed in IPNI (International Plant Names Index). Subsequent studies reveal that *Henslowia rubiflora* is the earlier name for *Crypteronia griffithii*.

Crypteronia rubiflora (Griff.) Ormerod, *comb. nov.*

Basionym: *Henslowia rubiflora* Griff., Itin. Pl. Khasyah Mts.: 371. 1848 as *Henslovia rubiflora*.

TYPE: MALAYSIA. Malacca, Ayer Punnus [= Air Panas], Ching, Byhass Jungle, October 1842, *W. Griffith s.n.* (Holotype: [lost]). Neotype: [designated here]: MALAYSIA, Malacca, *W. Griffith s.n.* (K [000674035] [image seen]; possible Isoneotype: CGE [image seen]).

Heterotypic synonym: *Crypteronia griffithii* C.B. Clarke, in J.D. Hook., Fl. Brit. Ind. 2, 6: 574. 1879, *syn. nov.*

TYPE: MALAYSIA. Malacca, *W. Griffith (Kew Distr.) 2513* (Lectotype: K [000674034] [designated here]: [image seen]; Isolectotypes: CAL [0000212252] [image seen]; GH [00974041] [image seen]; P [05088408] [image seen]); Malacca, 1845, *W. Griffith s.n.* (Syntype: K [000566434] [image seen]); Malacca, *W. Griffith s.n.* (Syntypes: K [000674035]; CGE [image seen]); Malaya, without locality, 1867–1868, *A. C. Maingay 2429 (= Kew Distr. 651)* (Syntype: K [000566432] [image seen]; Isosyntypes: CAL [0000212251] [image seen]; L [0614165] [image seen]).

Usage synonym: *Henslowia* sp.: Griff., Notul. Pl. Asiat. 4: 406–407. 1854 as *Hensloviae sp.*; Icon. Pl. Asiat. 4: t. 564, fig. 1. 1854 as *Henslovia*.

Distribution: Myanmar; Malaysia; Singapore; Brunei; Indonesia (Sumatra, Kalimantan).

Griffith collected this species in the Ayer Punnus region (now Air Panas, literally 'hot water,' in reference to the hot springs there) near Malacca in October 1842. He was supposedly in Calcutta, India from August 1842 to August 1844 before returning to Malacca on the Malay Peninsula. There are two other Griffith collections with the same collection date, namely *Durio oxleyanus* Griff. and *Mangifera odorata* Griff., so it seems possible that he returned briefly to Malacca in October 1842. No material has been found that is annotated with the original locality data, although it is likely that Griffith annotated all of his material from the Malacca region as simply "Malacca". Therefore, one of his Malacca specimens is chosen as the neotype.

Clarke (1879) cited *Griffith 2513* and *Maingay* as types for his *Crypteronia griffithii*. It is evident that he had three of Griffith's collections (two of which were unnumbered) at his disposal at Kew, and one specimen collected by Maingay. *Griffith (Kew Distr.) 2513* is chosen as the lectotype. Previously, van Beusekom-Osinga and van Beusekom (1975) had inadvertently indicated *Griffith 2513* as the type but cited two herbaria ("K, L") for that collection even though no duplicate has been found in L. Their typification is therefore invalid. One of the Kew syntypes is attributed to *H. Cover* (K [000566434]), but this is a misinterpretation of a label on that sheet saying *Henslovia sp. nov.*

Griffith (Kew Distr.) 2513/1 (A [00068535] [image seen]; CAL [0000212250] [image seen]) from East Bengal (India) is not a syntype of *C. griffithii*, because the material is from a different locality and belongs to *C. paniculata* Blume.

Crypteronia rubiflora has only been recorded once from Myanmar (*H. Falconer s.n.*; L [2491060] [image seen]). It was collected from near Moulmein during January to March 1849 when Hugh Falconer went there to inspect the teak forests. The species should occur in Peninsular Thailand but has not been found there yet. The one specimen identified as *C. griffithii* from Thailand (*T. Smitinand & A. S. Cheke 10815*; C, P [images seen]) appears to represent *C. paniculata* Blume.

A specimen from Penang Island, Malaysia (*C. Curtis s.n.*; P [image seen]) differs in having narrowly oblong leaves with a narrow base (vs. elliptic to ovate-elliptic, base rounded). Further studies of the Penang Island population are needed to show if this variation is significant.

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A NOMENCLATURAL ASSESSMENT AND A NEW COMBINATION IN NORTH AMERICAN *OENOTHERA* (ONAGRACEAE)

Warren L. Wagner[1,2] and Kanchi Gandhi[3]

Abstract. *Oenothera californica* (S. Watson) S. Watson is here replaced by *O. avita* (W.M. Klein) W.M. Klein. Consequently, the associated taxa names *O. californica* (S. Watson) S. Watson subsp. *californica*, *O. californica* subsp. *avita* W.M. Klein, and *O. californica* subsp. *eurekensis* (Munz & J.C. Roos) W.M. Klein are replaced with *O. avita* (W.M. Klein) W.M. Klein subsp. *avita, O. avita* subsp. *californica* (S. Watson) W.L. Wagner & Gandhi, and *O. avita* subsp. *eurekensis* (Munz & J.C. Roos) W.M. Klein.

Keywords: *Oenothera albicaulis* var. *melanosperma*, *O. avita*, *O. californica*, *O. deltolides* subsp. *eurekensis*

Oenothera L., the second largest genus in Onagraceae with about 150 species, is widely distributed in the New World, and a number of species are widely naturalized worldwide with a center of phylogenetic diversity in western North America (Wagner et al., 2007; Wagner, 2021). *Oenothera* sect. *Anogra* consists of eight species (17 taxa) native to western North America, found usually in dry, sandy soil in a wide variety of habitats in the Chihuahuan, Great Basin, Mojave, and Sonoran deserts, to grasslands and open sites in montane forest, at 50 to 3300 m.

One of the complexes in the section has previously been subdivided into two species, *Oenothera californica* (S. Watson) S. Watson and *O. avita* (W.M. Klein) W.M. Klein (Munz, 1965; Klein, 1964). In recent studies for regional floras, the basic taxonomy of Klein (1964, 1970) and Munz (1965) has been maintained, except for the recent elevation of one of Klein's subspecies of *O. avita* to species-level as *O. arizonica* (Munz) W.L. Wagner (Wagner, 1998) and the inclusion of the autotetraploid, *O. californica* with its diploid relatives, in one species. This resulted in *O. avita* and treated as a subspecies under the presumed older and legitimate name *O. californica* (Wagner et al., 1993).

With the realization that the combination *Oenothera californica* (S. Watson) S. Watson is a later homonym, we here adopt the oldest validly published and legitimate name at the species level, *O. avita* for the complex. The one new combination needed is provided. Current names that should be adopted for the other taxa are also provided.

Oenothera avita (W.M. Klein) W.M. Klein, N. Amer. Fl. ser. 2, 5: 116. 1965.

Basionym: *Oenothera californica* (S. Watson) S. Watson subsp. *avita* W. M. Klein, Aliso 5: 179. 1962. TYPE: U.S.A. Utah: Washington Co., along U.S. Highway 91 about 0.5 miles northeast of Leeds, 3400 ft, 21 May 1959, *W. M. Klein 1049* (Holotype: RSA-145518; Isotypes: GH, UC).

Homotypic synonym: *Oenothera californica* S. Watson var. *avita* (W.M. Klein) S.L. Welsh & N. D. Atwood, Utah Fl., ed. 4. 538. 2008.

Neither of the specimens cited by Klein as isotypes could be located; however, another collection, *Klein 1060,* is at GH and labelled incorrectly by Klein as an isotype.

Oenothera avita **subsp.** ***avita***

Oenothera avita (W.M. Klein) W.M. Klein subsp. ***californica*** (S. Watson) W.L. Wagner & Gandhi, *comb. nov*.

Basionym: *Oenothera albicaulis* Pursh var. *californica* S. Watson, Proc. Amer. Acad. Arts 8: 582. 1872. TYPE: U.S.A. California: Los Angeles vicinity, *W. T. Wallace s.n*. (Lectotype: GH, designated by Munz, 1931).

Homotypic synonyms: *Oenothera californica* (S. Watson) S. Watson, in Brewer & S. Watson, Bot. Calif. 1: 223. 1876, *non* D. Dietr., Syn. Pl. [D. Dietrich] ii. 1288 (1840), *nom. illeg., nom. superfl.*

Anogra californica (S. Watson) Small, Bull. Torrey Club 23: 176. 1896.

Oenothera pallida Lindl. var. *californica* (S. Watson) Jepson, Man. FI. PI. Calif. 681. 1925.

Heterotypic synonyms: *Oenothera albicaulis* Pursh var. *melanosperma* H. Léveillé, Bull. Acad. Int. Géogr. Bot. sér. 3, 19(241–242): 302, 305. 1910. TYPE: U.S.A. California: San Bernardino Co., San Bernardino Mountains, Bear Valley, 6500 ft, 18 June 1894, *S. B. Parish 3147* (Syntypes: CAS, US [2 sheets]).

Oenothera californica (S. Watson) S. Watson var. *glabrata* Munz, Amer. J. Bot. 18: 327. 1931. TYPE: U.S.A. California: San Bernardino Co., San Bernardino, 1000–1500 ft, 1 June 1896, *S. B. Parish 4177* (Holotype: GH; Isotypes: K [not seen], UC [not seen], US [2 sheets]).

Oenothera avita (W. M. Klein) W. M. Klein subsp. ***eurekensis*** (Munz & J. C. Roos) W.M. Klein, N. Amer. FI. ser. II, 5: 116. 1965.

Basionym: *Oenothera deltoides* Torrey & Frémont subsp. *eurekensis* Munz & J. C. Roos, Aliso 3: 118, fig. 7. 1955. TYPE: California, Inyo Co., deep sand at north end of dunes in southeast part of Eureka Valley, east

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of the Inyo Mts., 3100 ft, 18 September 1954, *P. A. Munz & F. C. Roos 20158* (Holotype: RSA; Isotypes: CAS [not seen], DS [not seen], COLO [not seen], GH, K [not seen], NY [not seen], RM [not seen], UC [not seen], US, WTU [not seen]).

Homotypic synonym: *Oenothera californica* (S. Watson) S. Watson subsp. *eurekensis* (Munz & J.C. Roos) W.M. Klein, Aliso 5: 179. 1962.

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NEW SPECIES OF *PLEUROTHALLIS* (ORCHIDACEAE: PLEUROTHALLIDINAE), A NEW COUNTRY RECORD, AND LABELLAR MORPHOLOGY IN THE *P. CARDIOSTOLA-P. LILIJAE* COMPLEX OF SUBSECTION *MACROPHYLLAE-FASCICULATAE*

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Abstract. *Pleurothallis* subsection *Macrophyllae-Fasciculatae* is the most species-rich infrageneric grouping within this genus. Within this subsection, based on floral and vegetative morphology, we recognize the *P. cardiostola-P. lilijae* complex, an expansion of Luer's previously proposed subsection *Cardiostolae*. The nature of the two species *P. cardiostola* and *P. lilijae* is clarified here to allow comparison to an additional 24 possible members of the complex. Recognizing *P. lanigera* as distinct from *P. cardiostola*, and the other putative species as distinct from each other, brings the complex of previously described species to 26. In the process of reviewing living material and photographs of these species, as well as of the many plants misidentified as *P. lilijae*, it quickly became apparent that there are multiple undescribed species in this group. Six new species from Colombia, Ecuador and Peru are described herein. Each species is typified, described and illustrated, in most cases with a drawing, a composite digital plate, photos to show floral variability, and a scanning electron micrograph of the lip. Including these additional 6 species brings the *P. cardiostola-P. lilijae* complex to 32 members, which is both more numerous and more widely distributed than the *P. cardiothallis-P. titan* complex. One characteristic of species in this group is the copious production of nectar-like liquid on the lip and a prominent glenion.

Keywords: New species, *Pleurothallis cardiostola*, *Pleurothallis lilijae*, species complex

Within *Pleurothallis* (Orchidaceae, Pleurothallidinae), subsection *Macrophyllae-Fasciculatae* is the most species-rich infrageneric grouping with ca. 247–317 described species, depending on synonymy, and many more yet to be described. Despite the large number of species, to date no phylogenetic lineages within the group have been defined. As with other recently evolved Neotropical genera, sequence variation within the subsection is low (Wilson, 2011). And, while several phylogenetic studies have included species of *Macrophyllae-Fasciculatae* (Pridgeon et al., 2001; Chiron et al., 2012; Wilson et al., 2013; Karremans et al., 2013; Pérez-Escobar et al., 2017; Guttiérez Morales et al., 2020), to date, there have been no studies with both sufficient taxonomic breadth and genomic depth to reveal phylogenetic affinities within the subsection. Nevertheless, botanists familiar with the subsection have been able to recognize some groupings based on shared morphological traits that *may* represent lineages with phylogenetic affinity, such as the *P. cardiothallis* complex (Pupulin et al., 2017, Pupulin et al., 2021). Within subsection *Macrophyllae-Fasciculatae* exists an even larger, more widely distributed group of species than the *P. cardiothallis* complex, with a unifying set of morphological characteristics represented by *P. cardiostola* Rchb.f. and *P. lilijae* Foldats.

Pleurothallis cardiostola Rchb.f. was described (Reichenbach, 1854) and illustrated (Reichenbach, [1858] 1854) from a specimen collected by Wagener from Caracas, Venezuela. The illustration (Fig. 1A) shows a lanceolate leaf with a deeply cordate base, with the basal lobes somewhat incurved, and a non-resupinate flower borne from a spathaceous bract at the base of the leaf. More recent illustrations of *P. cardiostola* from Venezuela by Foldats (1970) (Fig. 1B) and Dunsterville and Garay (1959) (Fig. 1C) are consistent with, but more detailed than that of Reichenbach ([1858] 1854; Fig. 1A). These illustrations reveal two more important characteristics, retention of leaves of juvenile morphology, lanceolate but with a cuneate rather than cordate base, referred to as "paedomorphic form" by Pupulin et al. (2021), on a mature flowering plant; and a concave lip with raised apical and lateral edges.

Pleurothallis lilijae Foldats was described and illustrated using a specimen collected by Steyermark and Dunsterville

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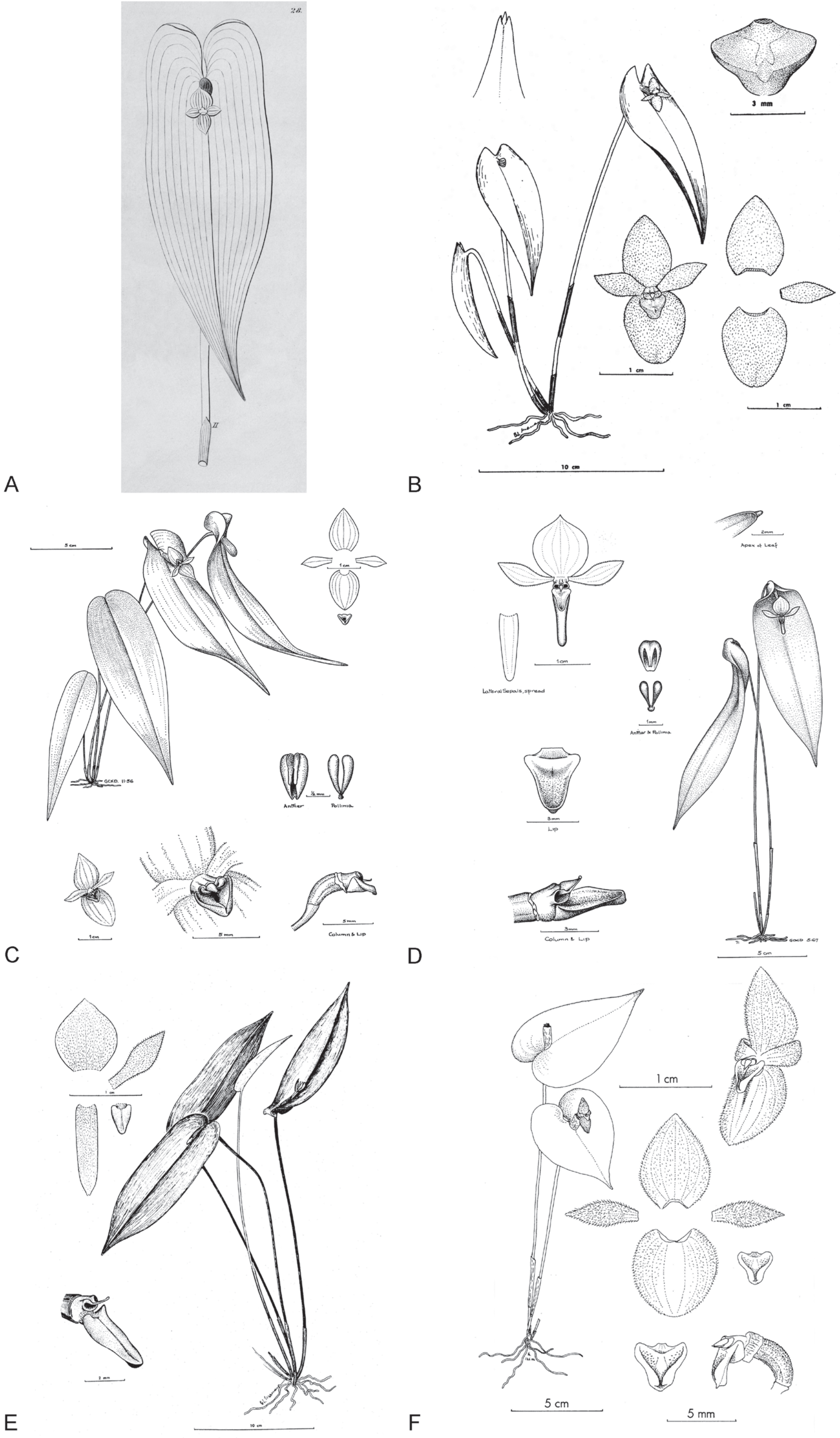

FIGURE 1. *Pleurothallis* species. **A**, *Pleurothallis cardiostola* Rchb.f. by Lindley (Reichenbach, [1858] 1854: Fig. 28II); **B**, *Pleurothallis cardiostola* from Foldats (1970: 229); **C**, *Pleurothallis cardiostola* from Garay and Dunsterville (1959: 387); **D**, *Pleurothallis lilijae* from Dunsterville and Garay (1976: 785); **E**, *Pleurothallis lilijae* from Foldats (1970: 330); **F**, *Pleurothallis lanigera* from Luer (2005: 220, Fig. 38B, as *Acronia cardiostola*). B, E courtesy of Fundación Instituto Botánico de Venezuela Dr. Tobías Lasser; C–D courtesy of the Orchid Herbarium of Oakes Ames; F courtesy of the Missouri Botanic Gardens Press.

from Tachira, Venezuela (Foldats, 1968). Foldats (1968) described the leaves as ovate-lanceolate with a cordate base with incurved edges, though the latter characteristic is not reflected in the illustration by Foldats (1970) (Fig. 1E). A more detailed illustration provided by Dunsterville and Garay (1976) (Fig. 1D), however, clearly shows the cordate leaf base with incurved basal lobes. While not mentioned in the description or illustrated in either drawing, the paratype herbarium sheet exhibits a leaf of juvenile or paedomorphic form, with a cuneate base, alongside a mature leaf with cordate base and incurved basal lobes.

It was Lindley (1859) who originally created an infrageneric grouping called "section" *Macrophyllae-Fasciculatae*. He included *Pleurothallis cardiostola* of Reichenbach f., but not *P. lilijae*, since that species was yet to be described. In his organization of the genus, Luer (1986) retained Lindley's *Macrophyllae-Fasciculatae*, creating a section within subgenus *Pleurothallis*, but did not recognize any subdivision of the group. Two years later, Luer (1988) went a step further and proposed dividing section *Macrophyllae-Fasciculatae* into two subsections, *Macrophyllae-Fasciculatae* and *Cardiostolae*. Subsection *Cardiostolae* was described as having "deflexed, cordate leaves more or less conduplicate at the base as typified by *Pleurothallis cardiostola* Rchb.f.". Later, Luer (1998) relegated section *Macrophyllae-Fasciculatae* to the level of subsection to be at the same taxonomic level as *Acroniae*, but he did not address consequences of this for the taxonomic group *Cardiostolae*. Luer (2005), however, reduced *Pleurothallis* subsection *Cardiostolae* to synonymy with *Acronia* section *Macrophyllae-Fasciculatae*. Despite having effectively dropped the taxonomic group *Cardiostolae*, in the same volume Luer (2005) states that "*A. cardiostola* forms a perplexing complex of varying shapes and sizes of the leaves and floral parts and is closely related to *A. lilijae*". Mentioning *P. lanigera* and *P. alopex* in the same paragraph, this is as close as Luer comes to acknowledging the continued existence of a grouping morphologically related to *P. cardiostola* and *P. lilijae* that he formerly referred to as subsection *Cardiostolae*.

In a recent publication on the *Pleurothallis* flora of Costa Rica, Pupulin et al. (2021) introduced a list of species within subsection *Macrophyllae-Fasciculatae* that they referred to as the *P. phyllocardia* group. From that group, *P. peculiaris* is very likely related to *P. cardiostola* and *P. lilijae*, and *P. compressa* is probably related to those species. We do not believe, however, that any of the other members of the *P. phyllocardia* group are close affiliates of *P. cardiostola* and *P. lilijae*, despite the presence of some of the characteristics of those two species, such as an erect spathaceous bract and foliage of paedomorphic form. In this regard, in our opinion, the eponymous *P. phyllocardia*, which is grown in the Colorado College living collection, is quite different from *P. cardiostola* and *P. lilijae* and, therefore, is not included in our list of morphologically similar species.

Acknowledging that in the absence of a robust phylogeny of the entire subsection *Macrophyllae-Fasciculatae*, utilizing at a minimum multiple nuclear and plastid regions, which we still do not have, opinions of affinities in the subsection are subjective, we nevertheless recognize an additional 24 species (Table 1) that each exhibit a majority of the defining set of characteristics observed in *Pleurothallis cardiostola* and *P. lilijae*. These characteristics are: a mature leaf that is deflexed, highly coriaceous, ovate-to-lanceolate, somewhat conduplicate in the basal portion, with a cordate base where the edges of the basal lobes are incurved; persistent leaves of juvenile or paedomorphic form that are erect, less coriaceous, lanceolate, with a cuneate rather than cordate base, of similar size to mature leaves; an erect, papery spathaceous bract; non-resupinate flowers that are concolorous and microscopically papillose-to-trichomatous; spathulate petals that are reflexed behind sepals; a lip that is concave with elevated apical and lateral edges, with a prominent glenion; and secretion of nectar-like liquid from the apical and lateral edges of the lip as well as from the glenion. Henceforth, we refer to this list of 26 species (Table 1) as the *P. cardiostola-P. lilijae* complex.

The *Pleurothallis cardiostola-P. lilijae* complex as recognized here is widely distributed, from Costa Rica in the north, represented by *P. peculiaris* (Pupulin, 2021), to Paraguay in the south, represented by *P. alopex* (Luer 2005). Despite the wide distribution of the complex as a whole, *P. cardiostola* itself is probably restricted to Venezuela, Ecuador and, presumably, the intervening country of Colombia. *P. lanigera* Luer & Hirtz (Luer 1988), considered by Luer (2005) to be a synonym of *Acronia cardiostola* (Rchb.f.) Luer, is here considered to be a separate species. The spreading, flat, ovate leaves of *P. lanigera* (Fig. 1F) are very distinct from the lanceolate leaves of *P. cardiostola* (Fig. 1A–1C), as originally noted by Luer (1988). Further, the flowers of *P. cardiostola* (Fig. 2A–2B) are also distinct from those of *P. lanigera* (Fig. 2C–2D). As are the lips when examined by scanning electron microscopy (Fig. 3A–3B). Unfortunately, in his monograph on *Macrophyllae-Fasciculatae* Luer (2005) uses a drawing of *P. lanigera* to represent *A. cardiostola*, thereby creating confusion regarding the identity of these two species, which, hopefully, is clarified here. *P. lanigera* was previously known only from southeast Ecuador, in the province of Zamora Chinchipe, but is here recorded from 1750 m in Huambo, Rodríguez de Mendoza, Amazonas, Peru for the first time (Fig. 2D).

Pleurothallis lilijae is also probably restricted to Venezuela, Colombia and Ecuador—a Colombian form from Boyacá is illustrated here (Fig. 4). However, determining an accurate distribution is very difficult since it is the most frequently misidentified species in the *P. cardiostola-P. lilijae* complex. Part of the problem is that there are a number of other species superficially similar to *Pleurothallis lilijae* (Fig. 5–6), that are often misidentified as that species, such as *P. alopex* Luer (Fig. 5A), *P. apopsis* Luer (Fig. 5B), *P. culpameae* (Luer) J.M.H. Shaw, *P. diazii* (Luer & Endara) J.M.H. Shaw (Fig. 5C) and *P. tobarii* (Luer & Hirtz) Pfahl (Fig. 5D and 6). The misidentification problem is further exacerbated by the two drawings of *Acronia lilijae* in the widely used monograph on *Macrophyllae-Fasciculatae* (Luer, 2005), neither of which appears to correspond to typical *P. lilijae* as illustrated by Foldats (Fig. 1D) or Dunsterville (Fig. 1E). This study was initiated partially in response to this confusion, to clarify the nature of *P. cardiostola* and *P. lilijae*; to confirm the distinction of the morphologically-similar species *P. apopsis*, *P. alopex*, *P. culpameae*, *P. diazii* and *P. tobarii*; to draw attention to these other morphologically similar species; to circumscribe the *P. cardiostola-P. lilijae* complex; and to start the process of description of new species in the complex.

TABLE 1. Species of the *Pleurothallis cardiostola-Pleurothallis lilijae* complex described prior to this study.

SPECIES AND SYNONYMS
***Pleurothallis adelphe* Luer & Hirtz**, Lindleyana 11(3): 142–143, f. 2. (1996) Homotypic synonyms: *Acronia adelphe* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 84 (2005); *Zosterophyllanthos adelphe* (Luer & Hirtz) Szlach. & Kulak, Heterotypic synonym: *Pleurothallis perforata* Luer & Hirtz, Lindleyana 11: 178 (1996).
***Pleurothallis alopex* Luer**, Selbyana 3(1–2): 46 (1976). Homotypic synonyms: *Zosterophyllanthos alopex* (Luer) Szlach. & Marg., Polish Bot. J. 46: 118 (2001); *Acronia alopex* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 86 (2005).
***Pleurothallis apopsis* Luer**, Selbyana 5(2): 160. (1979). *Zosterophyllanthos apopsis* (Luer) Szlach. & Marg., Polish Bot. J. 46: 118 (2001); *Acronia apopsis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 88 (2005).
***Pleurothallis barrowii* Schuit.**, Orchideen Journal 25(2): 55–57 (2018). Heterotypic synonym: *Pleurothallis cardiostola* fo. *magnidraba* A. Doucette & J. Portilla, Phytotaxa 257(3): 235–238, f. 5A–G, 11G (2016).
***Pleurothallis bilobulata* M.M.Jiménez, Ocupa & Vélez-Abarca**, Phytotaxa 518(1): 079–086 (2021).
***Pleurothallis cardiostola* Rchb.f.**, Bonplandia (Hannover) 2: 26 (1854). Homotypic synonyms: *Humboltia cardiostola* (Rchb.f.) Kuntze, Revis. Gen. Pl. 2: 667 (1891): *Acronia cardiostola* (Rchb.f.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 104 (2005): *Zosterophyllanthos cardiostola* (Rchb.f.) Szlach. & Kulak, Richardiana 6: 187 (2006). Heterotypic synonyms: *Pleurothallis choroniensis* Schnee, Revista Fac. Agron. (Maracay) 1: 116 (1952).
***Pleurothallis carrenoi* Carnevali & I. Ramírez**, Ernstia no. 44: 18 (-20), fig (1987). Homotypic synonyms: *Acronia carrenoi* (Carnevali & I.Ramírez) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 108 (2005); *Zosterophyllanthos carrenoi* (Carnevali & I.Ramírez) Szlach. & Kulak, Richardiana 6: 187 (2006).
***Pleurothallis castanea* Mark Wilson, G. Merino & J. D. Werner**, Lankesteriana 16(3): 358, fig. 2A, 9–10 (2016).
Pleurothallis compressa Luer, Lindleyana 11: 75 (1996). Homotypic Names: *Acronia compressa* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 112 (2005); *Zosterophyllanthos compressus* (Luer) Szlach. & Kulak, Richardiana 6: 188 (2006).
***Pleurothallis culpameae* (Luer) J.M.H.Shaw**, Orchid Rev. 122: 76 (2014). Basionym: *Acronia culpameae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 122 (2005). Heterotypic synonym: *Pleurothallis privigna* Luer & Hirtz, Revista Soc. Boliv. Bot. 3: 59 (2001), nom. illeg.
***Pleurothallis diabolica* Luer & R. Escobar**, Orquideología 14(2): 142 (1981). Homotypic synonyms: *Zosterophyllanthos diabolicus* (Luer & R.Escobar) Szlach. & Marg., Polish Bot. J. 46: 118 (2001); *Acronia diabolica* (Luer & R.Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 125 (2005). Heterotypic synonym: *Pleurothallis exserta* Luer & Hirtz, Lindleyana 3: 143 (1988).
***Pleurothallis diazii* (Luer & Endara) J.M.H.Shaw**, Orchid Rev. 122: 76 (2014). Basionym: *Acronia diazii* Luer & Endara, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 126 (2005).
***Pleurothallis dilemma* Luer**, Revista Soc. Boliv. Bot. 3: 45 (2001). Homotypic synonyms: *Acronia dilemma* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 127 (2005); *Zosterophyllanthos dilemma* (Luer) Szlach. & Kulak, Richardiana 6: 189 (2006).

TABLE 1 CONT. Species of the *Pleurothallis cardiostola-Pleurothallis lilijae* complex described prior to this study.

SPECIES AND SYNONYMS
***Pleurothallis lanigera* Luer & Hirtz**, Lindleyana 3(3): 146 (145, fig.) (1988).
***Pleurothallis lilijae* Foldats**, Acta Bot. Venez. 3: 379 (1968). Homotypic synonyms: *Zosterophyllanthos lilijae* (Foldats) Szlach. & Marg., Polish Bot. J. 46: 119 (2001); *Acronia lilijae* (Foldats) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 150 (2005).
Pleurothallis neobarbosae J.M.H.Shaw, Orchid Rev. 122: 77 (2014). Basionym: *Acronia barbosae* Luer & Thoerle, Selbyana 30: 3 (2009).
***Pleurothallis ortegae* Luer & Hirtz**, Lindleyana 11: 174 (1996). Homotypic synonyms: *Acronia ortegae* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 166 (2005); *Zosterophyllanthos ortegae* (Luer & Hirtz) Szlach. & Kulak, Richardiana 6: 191 (2006).
***Pleurothallis peculiaris* Luer**, Selbyana 3: 158 (1976). Homotypic synonyms: *Zosterophyllanthos peculiaris* (Luer) Szlach. & Marg., Polish Bot. J. 46: 120 (2001); *Acronia peculiaris* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 170 (2005).
***Pleurothallis penelops* Luer**, Selbyana 2: 387 (1978). Homotypic synonyms: *Acronia penelops* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 171 (2005); *Zosterophyllanthos penelops* (Luer) Szlach. & Kulak, Richardiana 6: 191 (2006).
***Pleurothallis perijaensis* Dunst.**, Selbyana 2: 210 (1978). Homotypic synonyms: *Zosterophyllanthos perijaensis* (Dunst.) Szlach. & Marg., Polish Bot. J. 46: 120 (2001); *Acronia perijaensis* (Dunst.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 171 (2005).
***Pleurothallis perryi* Luer**, Selbyana 5: 174 (1979). Homotypic synonyms: *Acronia perryi* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 172 (2005); *Zosterophyllanthos perryi* (Luer) Szlach. & Kulak, Richardiana 6: 191 (2006).
***Pleurothallis ramiromedinae* Thoerle & Hirtz**, OrchideenJ. 6(1): 6 (2018).
***Pleurothallis troglodytes* Luer**, Selbyana 7: 125 (1982). Homotypic synonyms: *Acronia troglodytes* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 201 (2005); *Zosterophyllanthos troglodytes* (Luer) Szlach. & Kulak, Richardiana 6: 194 (2006).
Pleurothallis tobarii (Luer & Hirtz) Pfahl, Internet Orchid Sp. Photo Encycl. Nomencl. Notes 1(3a): 1 (2012). Basionym: *Acronia tobarii* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 105: 247 (2006).
***Pleurothallis valladolidensis* Luer**, Phytologia 54: 388 (1983). Homotypic synonyms: *Acronia valladolidensis* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 204 (2005); *Zosterophyllanthos valladolidensis* (Luer) Szlach. & Kulak, Richardiana 6: 194 (2006).
Pleurothallis volans Luer & Hirtz, Lindleyana 11: 195 (1996). Homotypic Names: *Acronia volans* (Luer & Hirtz) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 205 (2005); *Zosterophyllanthos volans* (Luer & Hirtz) Szlach. & Kulak, Richardiana 6: 194 (2006).

FIGURE 2. Photographs of flowers of **A**, *Pleurothallis cardiostola*, courtesy of Gerrit Verhellen; **B**, *P. cardiostola*, courtesy of Alan Gregg; **C**, *Pleurothallis lanigera*, courtesy of Kevin Holcomb; **D**, *P. lanigera in situ* at 1750 m in Huambo, Rodríguez de Mendoza, Amazonas, Peru, the first record of this species for the country, courtesy of Génderson Arbildo Lopez.

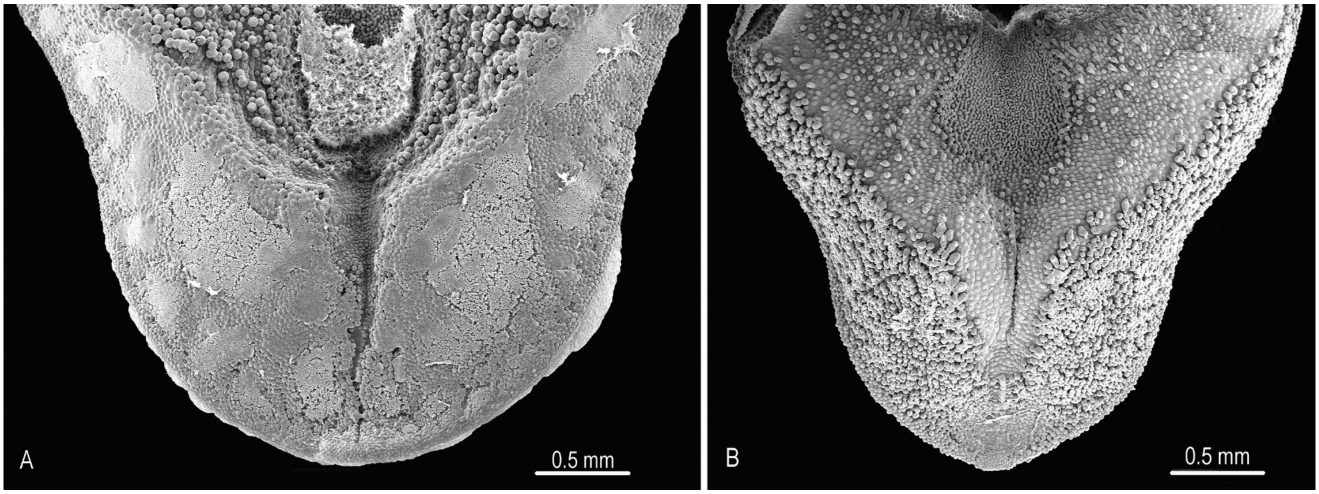

FIGURE 3. Scanning electron micrographs of labellum of **A**, *Pleurothallis cf. cardiostola* PL1228; **B**, *Pleurothallis lanigera* PL1229, by Mark Wilson.

MATERIALS AND METHODS

Plant material

Specimens of *Pleurothallis gonzaloi* and *P. mahechae* were collected *in situ* in Colombia under the following collection permits. *P. gonzaloi*: Milton Rincón, "Permiso Marco de Recolección de Especímenes de Especies Silvestres de la Diversidad Biológica con fines no comerciales a nivel Nacional otorgado mediante Resolución 2191 de 2018 por la Autoridad Nacional de Licencias Ambientales (ANLA);" Robinson Galindo-Tarazona, "1070 of August 28th of 2015, modified by permit 01004 of 07 June 7th of 2019." *P. mahechae*: Laura Suarez Romero, "Resolución 0198 del 2016 modificada por la resolución 1470 de 2017 permiso marco de recolección de especímenes silvestres de la biodiversidad para investigación científica no comercial, emitido por la autoridad nacional de licencias ambientales;" Sebastian Vieira Uribe, "Resolución No. 01711." Specimens of *P. andreaskayi* and *P. carmensotoana* were collected *in situ* in Ecuador under collection permit MAATE-DBI-CM-2022-0248 issued to Marco Jiménez.

Additionally, *Pleurothallis andreaskayi* (sold as *P. lilijae* "white") was purchased from Mundiflora, Cuenca, Ecuador; and *P. whitteniana* (sold as *P. culpameae*) and *P. carmensotoana* (sold as *P. crateriformis*) were purchased from Ecuagenera, Gualaceo, Ecuador. Purchase of *Pleurothallis* species in US from Ecuadorian commercial vendors does not require the purchaser (Wilson) to have phytosanitary, collection, or CITES permits, since under CITES and Ecuadorian law, all permitting is the responsibility of the commercial vendor. The plants from Ecuagenera and Mundiflora were grown and flowered in the living collection at Colorado College where the misidentifications became apparent. *Pleurothallis rikseniana* (sold as *Pleurothallis* "ligiae") was purchased from Jacky Orchiflora, Belgium, by W.G. Riksen in 2011 and has been grown in a private collection in Bunde, The Netherlands since that time.

Herbarium specimens were prepared using standard procedures and deposited in herbaria in the country of origin or in the Colorado College (COCO) herbarium. Flowers were preserved in Kew Mix (5% formalin [37.6% formaldehyde], 53% methanol, 5% glycerol, and 37% deionized water) for inclusion in the COCO spirit collection. Each species was illustrated with a drawing and a composite digital plate. Putative new species were compared with types and drawings of the 26 previously described species (Table 1) to confirm uniqueness.

Scanning electron microscopy

For scanning electron microscopy (S.E.M.), fresh flowers or flowers preserved in Kew Mix were dehydrated in successively higher concentrations of ethanol (80%, 95%, 100%, 100%) for 15–30 min each before being placed in 100% ethanol from a freshly-opened container. For flowers of those species, such as *Pleurothallis andreaskayi*, with copious quantities of nectar-like liquid on the lip, flowers were washed by shaking in deionized water for 2 min to remove the fluid on the lip prior to alcohol dehydration. Specimens were dried in a critical point dryer (EMS 850) prior to mounting on aluminum stubs and sputter coating with gold (Cressington 108 manual sputter coater, Ted Pella). Specimens were imaged with a scanning electron microscope (Jeol JSM-6390LV) at an accelerating voltage of 10-15 kV.

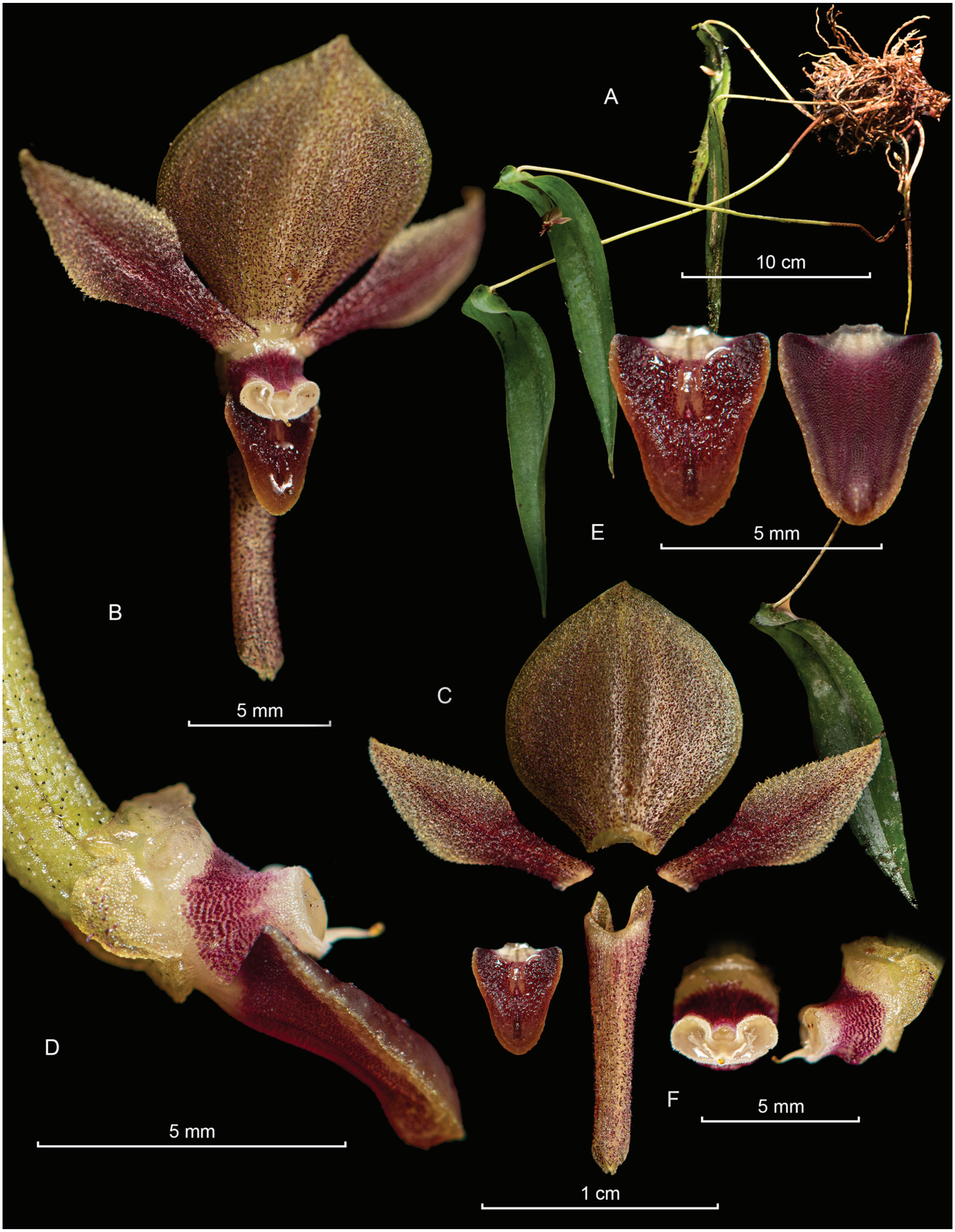

FIGURE 4. Composite digital plate of *Pleurothallis lilijae* from Boyacá, Colombia. **A**, Whole plant; **B**, Whole flower; **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal and ventral view); **F**, Column, stigmatic surfaces and rostellum (front and lateral views). Prepared by J. Sebastián Moreno.

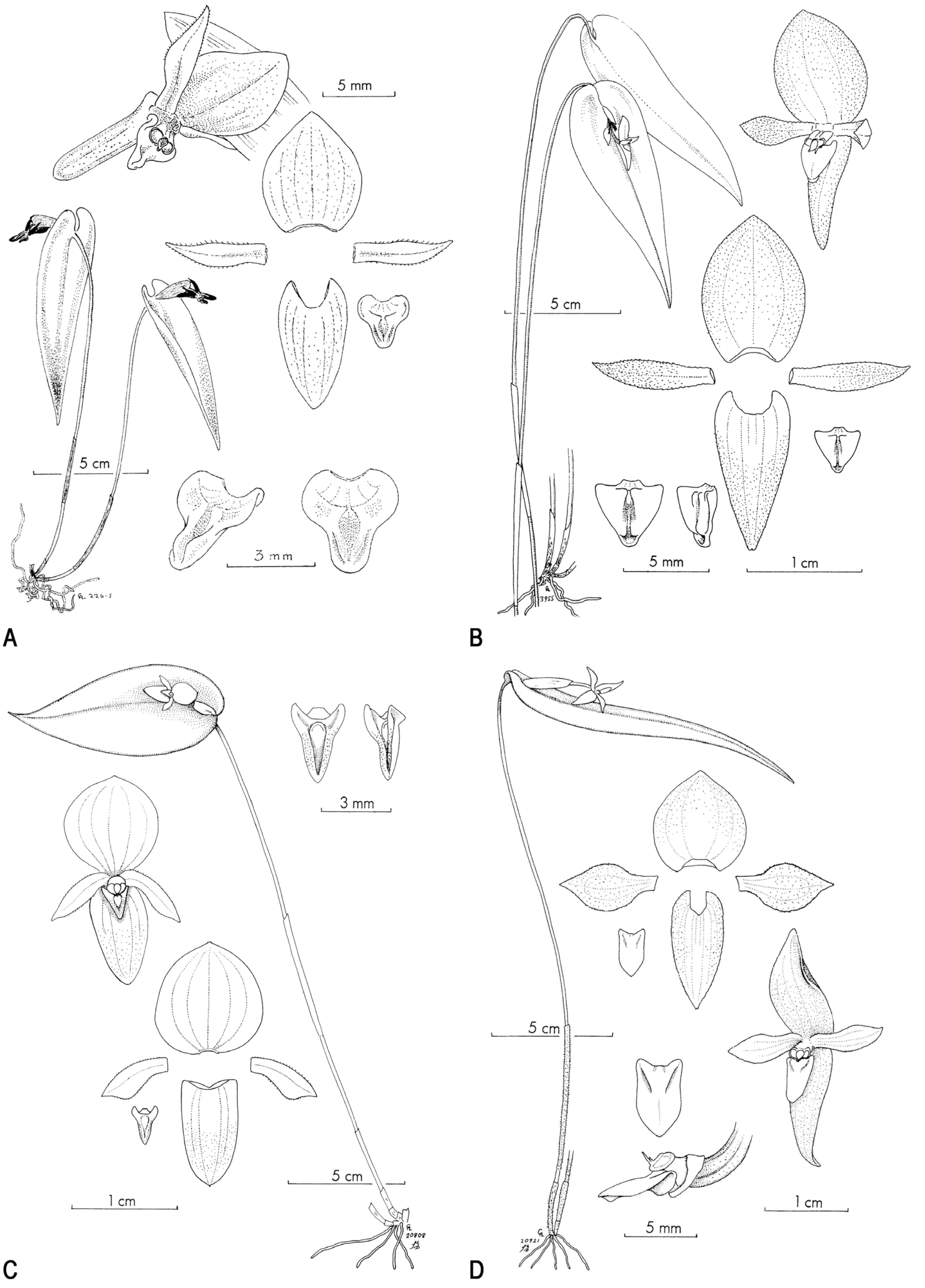

FIGURE 5. Drawings of species morphologically similar to *Pleurothallis lilijae*. **A**, *Pleurothallis alopex* from Luer (2005: 210, Fig. 7); **B**, *Pleurothallis apopsis* from Luer (2005: 211, Fig. 12); **C**, *Pleurothallis diazii* from Luer (2005: 230, Fig. 73); **D**, *Pleurothallis tobarii* from Luer (2006: 256, Fig. 4, as *Acronia tobarii*). A–C from Luer (2005) and D from Luer (2006), courtesy of Missouri Botanic Gardens Press.

FIGURE 6. Photographs of *Pleurothallis tobarii* from the type locality, near Guamote, Chimborazo Province, Ecuador. **A**, Flower (3/4 view). **B**, Flower (lateral view). Courtesy of Francisco Tobar.

TAXONOMIC TREATMENT

Pleurothallis andreaskayi Mark Wilson & B.T. Larsen, *sp. nov*.

TYPE: ECUADOR. Morona Santiago: Municipal Conservation Ecological Area Tinajillas–Río Gualaceño, between Limón and Gualaceo, 6 September 2022, 2336 m, M. Jiménez & H. Garzón 1410 (Holotype: HUTPL 14634). Fig. 7–8, 9C–9D and 10.

Pleurothallis andreaskayi is most similar to *P. apopsis* (Fig. 9A–9B) but can be easily distinguished by the color (cream-colored in *P. andreaskayi* versus yellow in *P. apopsis*); the number of veins in the dorsal sepal (7-veined in *P. andreaskayi* versus 3-veined in *P. apopsis*); and the lip morphology and size (lip base with rounded "shoulders," significantly wider than column in *P. andreaskayi* versus lip base straight, slightly wider than column in *P. apopsis*).

Epiphytic, caespitose *herb*, up to 27 cm tall; *Roots* slender, flexuous, ca. 1 mm in diameter; *Ramicauls* slender, terete, ca. 1.3 mm in diameter, erect, 23.5–26.0 cm long, with a tubular, 0.8–1.5 cm long papery basal sheath, and a 3.5–4.6 cm long, tightly adpressed, tubular sheath below the middle; *Leaves* deflexed, coriaceous, sessile, cordate-ovate, acute, 9.0–11.4 × 4.7–5.4 cm; *Inflorescence* a fascicle of solitary, successive flowers, rarely in pairs, borne from a reclined spathaceous, 9.0–10.0 mm long bract; pedicel 3.8–4.3 mm long; ovary terete, rounded in section, 3.3 mm long; *flowers* resupinate to non-resupinate, with the sepals, petals and lip pale yellow to white; *Dorsal sepal* broadly ovate, acute, minutely pubescent, 10.2–11.2 × 8.4–8.7 mm, 7-veined, the margins smooth; *Lateral sepals* completely connate into an ovate, acute s*ynsepal*, 8.7–9.5 × 5.1–5.6 mm, 4-veined, long-pubescent-spiculate, the margins smooth, lightly reflexed; *Petals*, ovate-spathulate, acute, 6.2–6.7 × 2.6–2.7 mm, 1-veined, microscopically pubescent, the margins denticulate; *Labellum* triangular, obtuse, 2.8–3.1 × 3.5–3.7 mm, hinged to the base of the column, lightly sulcate along the middle above the glenion, the apex truncate, the lateral margins covered with a thick, sticky secretion, the glenion recessed between two, parallel, longitudinal small calli above the base, the base concave, the abaxial surface with, three, longitudinal calli, the median callus with the base bifurcate and the apex rounded, projecting above the truncate apex, the lateral calli oblique; *Column* transversely subrectangular, dorsally complanate, 2.5–2.8 × 2.4–2.8 mm, the anther apical, the stigma apical, bilobed; *Pollinarium* two, narrowly oblong-pyriform pollinia 1.0 × 0.3 mm; Anther cap cucullate, ovate, subcordate, truncate, two-celled, 1.0 × 0.6 mm; *Capsule* not seen.

Additional specimen examined: ECUADOR. Purchased from Mundiflora, Cuenca, Ecuador, without collection data, as *Pleurothallis lilijae* "white" and flowered in cultivation at Colorado College, February 2021, *M. Wilson PL1142* (COCO).

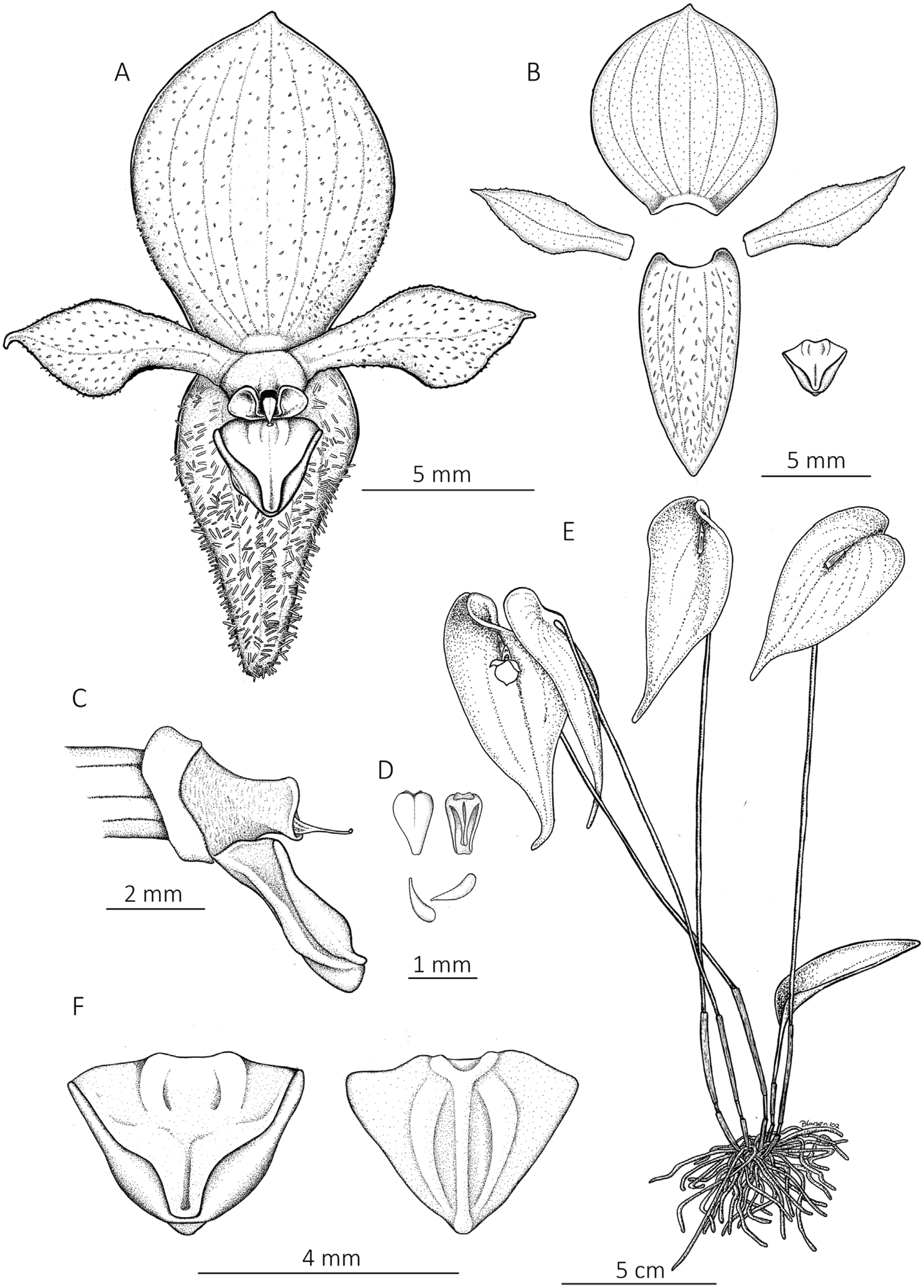

FIGURE 7. Drawing of *Pleurothallis andreaskayi*. **A**, Whole flower (front view); **B**, Floral dissection; **C**, Column and lip (lateral view); **D**, Anther cap and pollinarium; **E**, Whole plant; **F**, Lip (dorsal and ventral views). Prepared from paratype PL1142 by Bruno Larsen.

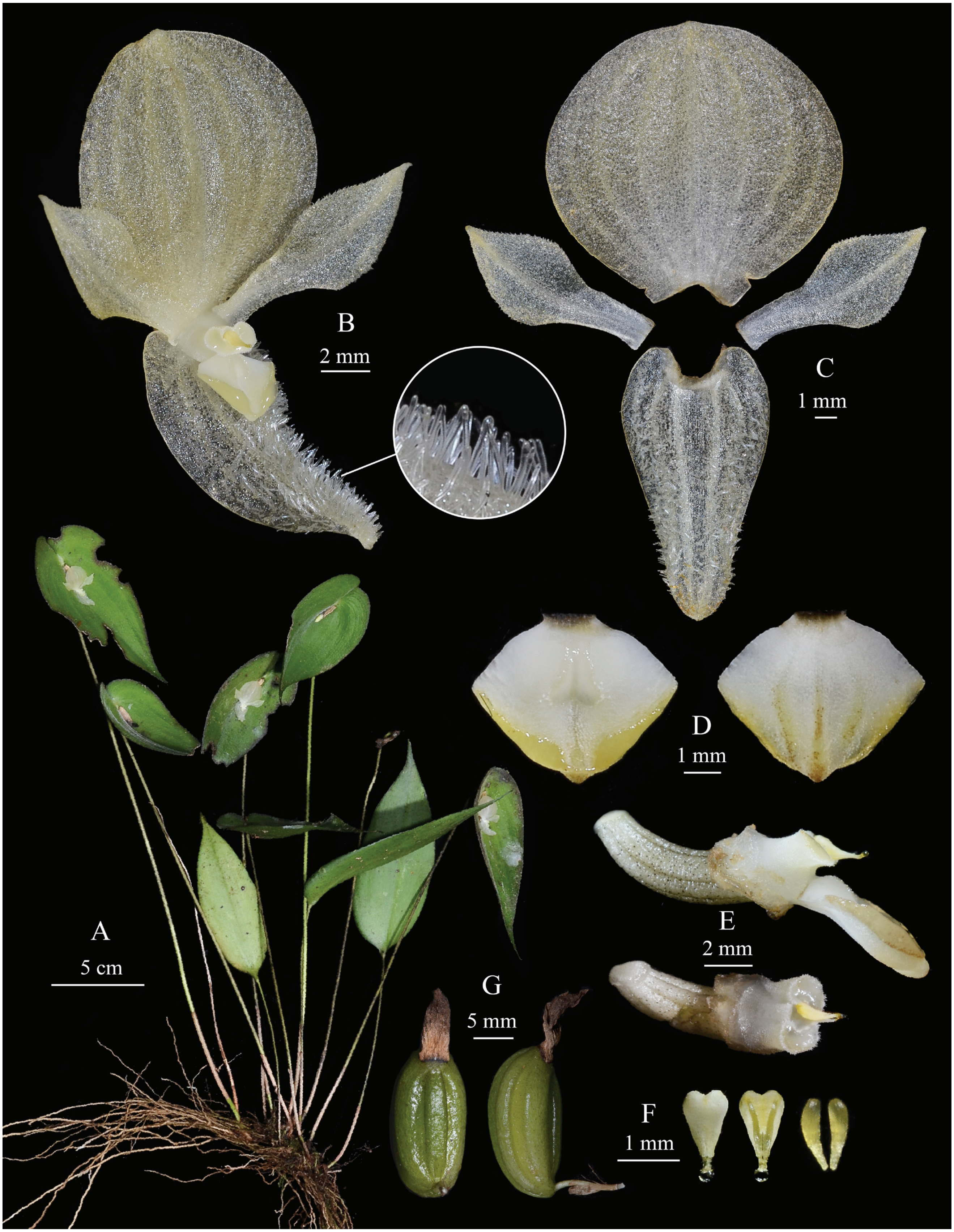

FIGURE 8. Composite digital plate of *Pleurothallis andreaskayi*. **A**, Whole plant; **B**, Whole flower (3/4 view); **C**, Floral dissection; **D**, Lip dorsal and ventral views; **E**, Column and lip; **F**, Pollinarium and anther cap; **G**, capsule. Prepared from the holotype by Henry Garzón Suárez.

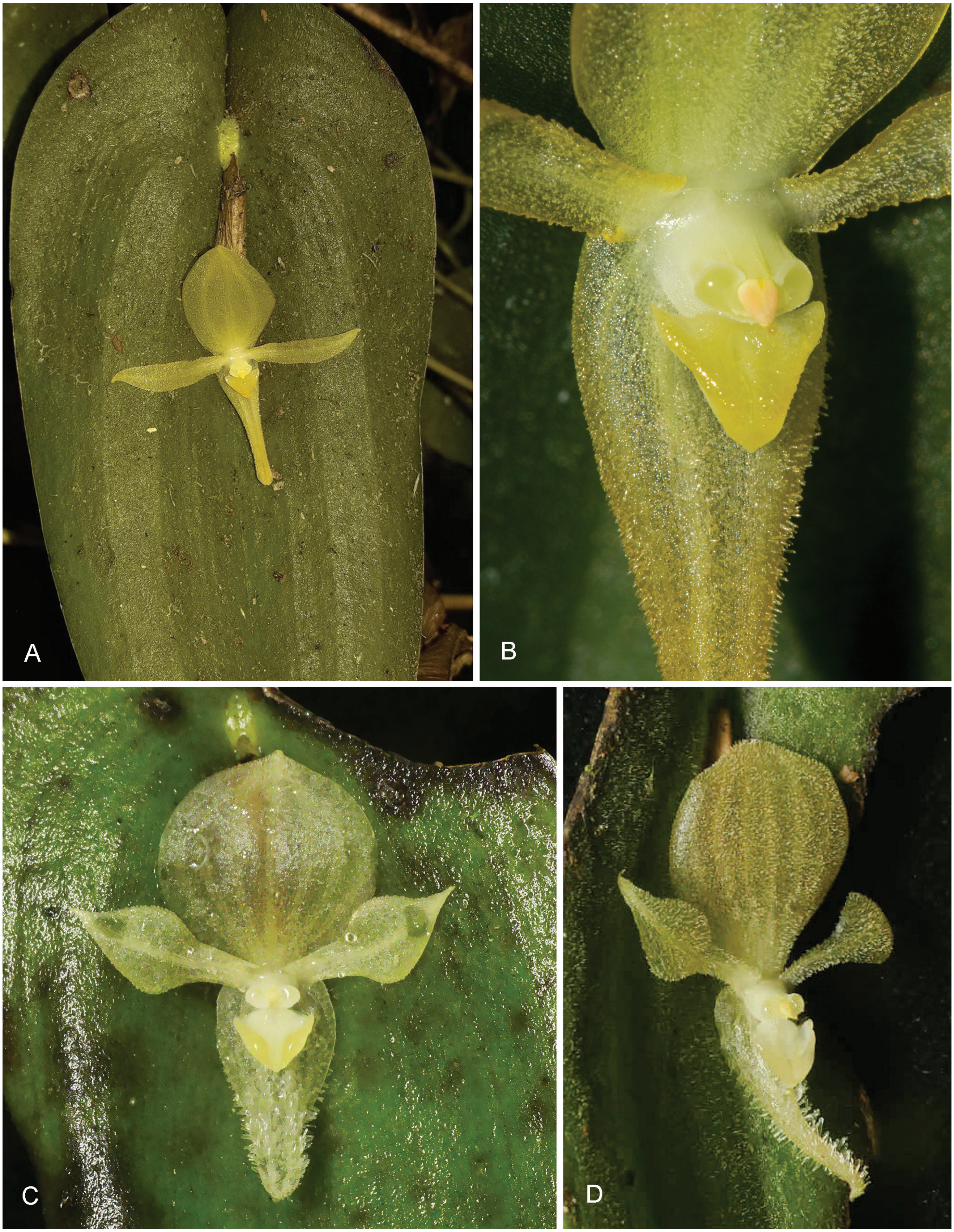

FIGURE 9. **A**, Photograph of *Pleurothallis apopsis* leaf and flower, courtesy of David Torres; **B**, Photograph of flower of *P. apopsis*, courtesy of Kilian Zuchan; **C**, **D**, *Pleurothallis andreaskayi in situ* in Morona Santiago, Ecuador, by Marco Jiménez.

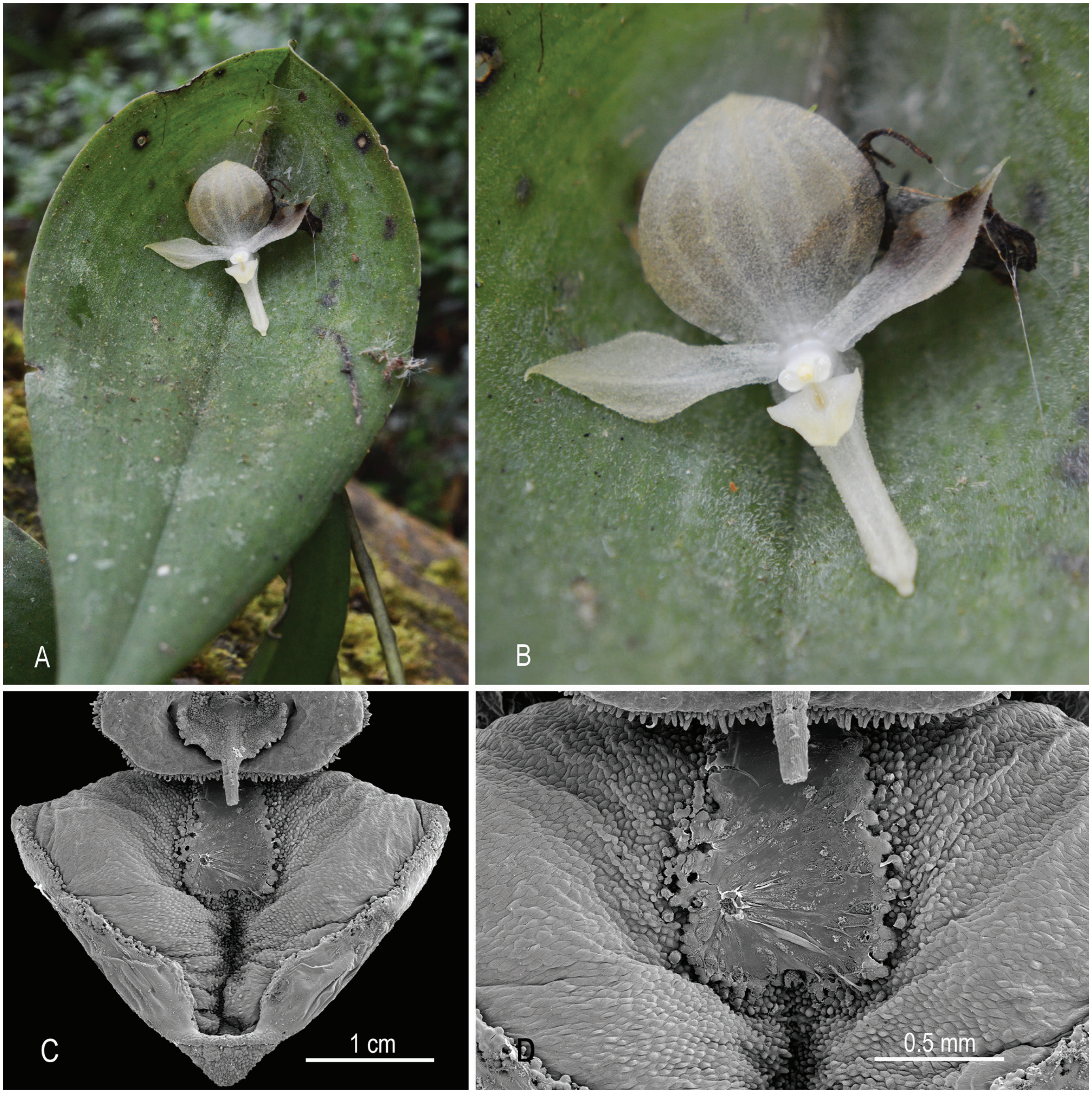

Figure 10. **A**, **B**, Photograph of *Pleurothallis andreaskayi in situ* in Cerro el Tablazo, Subachoque, Cundinamarca, Colombia at ca. 2800–3500 m, courtesy of Karen Gil; **C**, **D**, Scanning electron micrographs of *Pleurothallis andreaskayi* **C**, Lip, stigmatic surfaces and rostellum; **D**, Glenion at base of lip. Prepared from paratype PL1142 by Raven Ward.

Etymology: Named in honor of Andreas Kay (1963–2019) (https://andreaskay.org/), accomplished physicist-turned-photographer of Ecuadorian natural history who documented the diverse *Pleurothallis* flora of northwestern Ecuador (https://www.flickr.com/photos/andreaskay).

Distribution and conservation status: This species has been photographed *in situ* in Morona Santiago, Ecuador by Marco Jiménez (Fig. 9C–9D) and also in Cerro el Tablazo, Subachoque, Cundinamarca, Colombia by Karen Gil (Fig. 10A–10B), so the distribution appears to be from southeast Ecuador to north central Colombia. According to IUCN criteria the species should be considered Data Deficient, however, the paucity of *in situ* observations suggests that it is a vulnerable species.

In most species of *Pleurothallis* subsection *Macrophyllae-Fasciculatae*, the nectar-like liquid on the lips is largely water-soluble and can mostly be removed through rinsing in deionized water prior to SEM. In contrast, the liquid on the lateral edges of *P. andreaskayi* appeared mucilaginous in consistency under the light microscope, resisted washing, and persisted on the edges of the lip, obscuring the cells below in scanning electron micrographs (Fig. 10C–10D).

Pleurothallis whitteniana Mark Wilson & B.T. Larsen, *sp. nov.*

TYPE: ECUADOR. Purchased from Ecuagenera, Gualaceo, Ecuador, without collection data, as *Pleurothallis culpameae* and flowered in cultivation at Colorado College, Feb 2021, *M. Wilson PL1049* (Holotype: COCO). Fig. 11–13.

Pleurothallis whitteniana is most similar in floral and particularly labellar morphology to *P. diazii* but it is easily distinguished from this species by the plant size (~15 cm tall in *P. whitteniana* versus ~30 cm tall in *P. diazii*); leaf shape (lanceolate in *P. whitteniana* versus ovate in *P. diazii*); and the flower orientation (non-resupinate in *P. whitteniana* versus resupinate in *P. diazii*).

Epiphytic, caespitose *herb*, up to 15 cm tall; *Roots* slender, flexuous, ca. 0.8 mm in diameter; *Ramicauls* slender, terete, ca. 1.2 mm in diameter, erect, 10.5–15.0 cm long, with a tubular, 7 mm long papery basal sheath, and a longer, tightly adpressed, tubular sheath below the middle, 2.3–2.9 cm long; *Leaves* subpendent, thinly coriaceous, sessile, lanceolate, acute, cordate, 6.5–8.9 × 1.9–2.8 cm; *Inflorescence* a fascicle of solitary, successive flowers, rarely in pairs, borne from an erect spathaceous bract, 1.0–1.1 cm long; peduncle 2 mm long; pedicel 4.5 mm long; ovary terete, rounded in section, 1.8–2.0 mm long; *flowers* non-resupinate, with the sepals and petals and lip dark purple to pale pink; *Dorsal sepal* broadly ovate, acute, 7.2–7.4 × 4.5–4.8 mm, the margins microscopically denticulate, lightly reflexed, 5-veined; Lateral sepals completely connate into an ovate, acute s*ynsepal*, 7.3–7.6 × 7.0–7.2 mm, the margins microscopically denticulate, lightly reflexed, 4-veined; *Petals*, ovate-spathulate, acute, 6.9–7.0 × 2.5–2.6 mm, the margins microscopically denticulate, 3-veined; *Labellum* triangular, obtuse, 3.7–3.8 mm long, 1.6–1.7 mm wide across the base, adnate to the base of the column by a membranous claw, lightly sulcate along the middle above the glenion the apex rounded, with a minute, vertical conical callus, the margins thickened, the glenion recessed between the basal lobes, densely verrucose, the basal lobes rounded, each with a triangular, verrucose callus above the base, the base concave, the abaxial surface with, three, oblique, longitudinal calli; *Column* short, transversely subrectangular, dorsally complanate, 3.4–3.5 × 1.1–1.2 mm, the anther apical, the stigma apical, bilobed; *Pollinarium* two, narrowly oblong-pyriform pollinia, 0.6 × 0.13 mm, attached to an spherical viscidium through a short, cylindrical caudicle; Anther cap obtriangular, cucullate, 0.75 × 0.4 mm; *Capsule* not seen.

Additional specimens examined: ECUADOR. Purchased from Ecuagenera, Gualaceo, Ecuador, without collection data, as *Pleurothallis culpameae* and flowered in cultivation at Colorado College, *M. Wilson PL0503, PL0667, PL1041* (flowers in spirits, COCO).

Etymology: Named in honor of William “Mark” Whitten (1954–2019) prolific author in the areas of orchid pollination biology and systematics (Blanco et al., 2019).

Distribution and conservation status: While we assume that this species was collected in Ecuador either by Padre Angel Andreetta or the Portilla family, it has not been photographed *in situ* in Ecuador to our knowledge. This species has, however, been photographed *in situ* by Génderson Arbildo López in Huambo District, Province Rodríguez de Mendoza, Region Amazonas, Peru (Fig. 13A–13B). The contiguous forests of Zamora Chinchipe, Ecuador and Amazonas, Peru share many species in common, so the presumed distribution is SE Ecuador and NE Peru. According to IUCN criteria the species should be considered Data Deficient, however, the paucity of *in situ* observations suggests that it is a vulnerable species.

This species has been cultivated by Ecuagenera, Gualaceo, Ecuador, misidentified as *Pleurothallis culpameae* and sold under that incorrect name. While both are relatively small plants, *P. whitteniana* is easily distinguished from *P. culpameae* by the leaf shape (lanceolate in *P. whitteniana* versus ovate in *P. culpameae*); spathaceous bract from which the inflorescence emerges (erect in *P. whitteniana* versus reclining in *P. culpameae*); the orientation of the flower (non-resupinate in *P. whitteniana* versus resupinate in *P. culpameae*); and the position of the lip (projecting from synsepal at ca. 90 degrees in *P. whitteniana* versus flat against the synsepal in *P. culpameae*).

In scanning electron micrographs (Fig. 13C–13D) the lip is deeply convex, with an elongated glenion and evidence of residual nectar on the lateral edges of the apical region or epichile.

Pleurothallis carmensotoana Mark Wilson & B.T. Larsen, *sp. nov.*

TYPE: ECUADOR. Loja: Near Yangana, 7 September 2022, 2546 m, *M. Jiménez 1433* (Holotype: HUTPL 14645). Fig. 14–17.

Pleurothallis carmensotoana is most similar to *P. lilijae* but can be easily distinguished by the lip morphology, including: shape of the lip apex (oblong in *P. carmensotoana* versus triangular in *P. lilijae*); the edges of the mid lip (reflexed in *P. carmensotoana* versus erect in *P. lilijae*); and the interior of the lip apex (partially filled by two raised calli, separated by a distinct apical channel in *P. carmensotoana* versus concave without distinct calli or apical channel in *P. lilijae*).

Epiphytic, caespitose *herb* up to 23 cm tall; *Roots* slender, flexuous, ca. 1 mm in diameter; *Ramicauls* slender, terete, ca. 1.8 mm in diameter, erect, 6.4–22.6 cm long, with a tubular, 0.8–1.6 cm long papery basal sheath, and a 2.8–4.6 cm long, tightly adpressed, tubular sheath below the middle; *Leaves* erect, coriaceous, ovate, acute, 5.7–12.5 × 1.6–3.9 cm, the base sessile, deeply cordate; *Inflorescence* a fascicle of solitary, successive flowers, rarely in pairs, borne from a reclining spathaceous, 0.9–1.7 cm long bract; peduncle 2 mm long; floral bract 1 mm long; pedicel 1.7 mm long; ovary terete, densely verrucose, rounded in section, 3.5–4.7 × 1.4–1.8 mm; *flowers* resupinate, with the sepals and petals densely pubescent; *Dorsal sepal* yellow to purple, ovate to sub-orbicular, obtuse, 8.7–9.2 × 7.8–8.0 mm, 7-veined, lightly convex; *Lateral sepals* yellow to purple, completely connate into a ovate, obtuse, 8.8–9.9 × 5.2–5.6 mm, 6-veined s*ynsepal* with acutely reflexed margins; *Petals* purple with yellow margins to completely purple, ovate-subfalcate, acute, densely pubescent, the margins ciliate, 6.9–9.2 × 2.4–3.6 mm, 1-veined; *Labellum* purple, suffused with yellow at the apex, triangular-oblong, obtuse, with

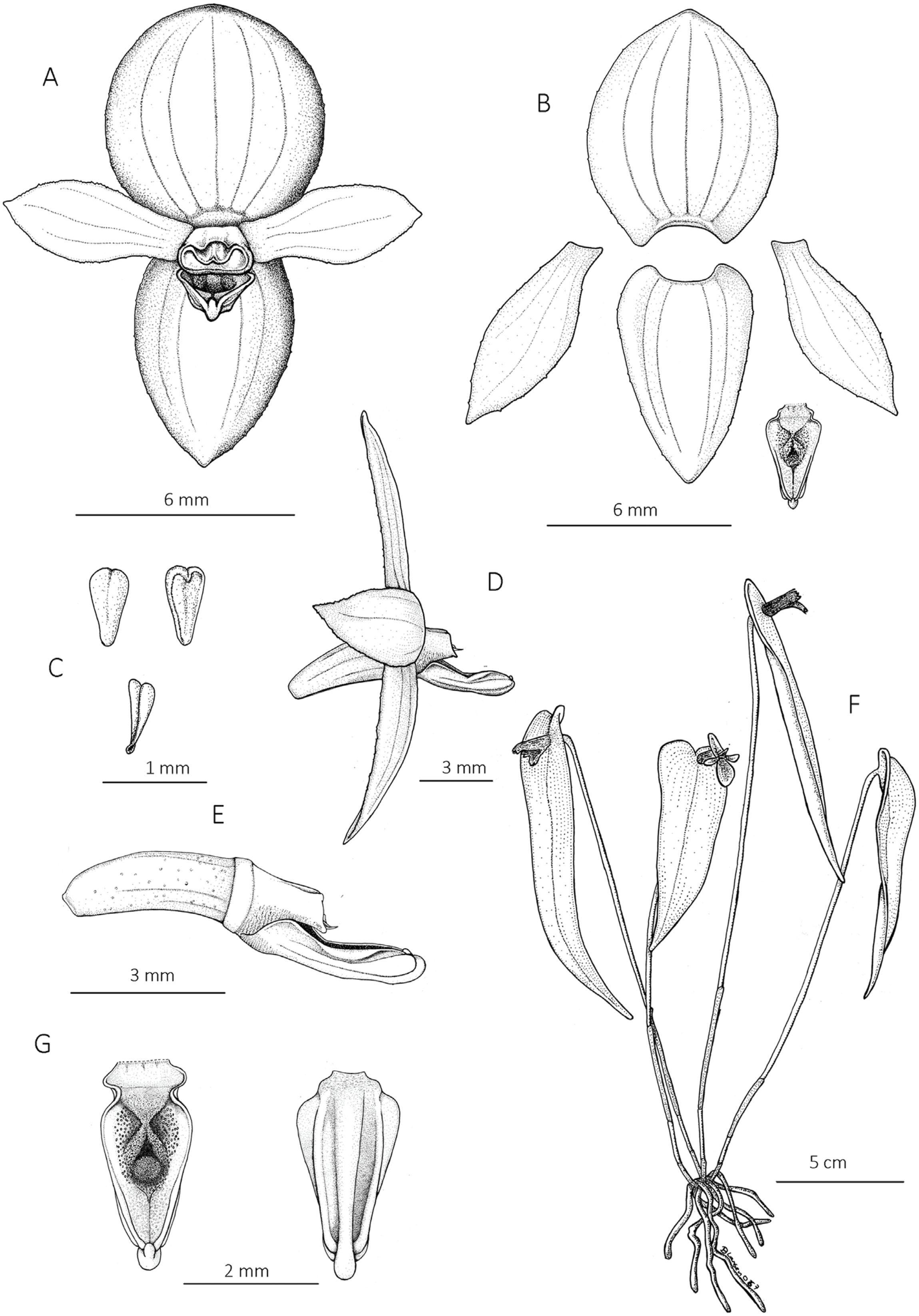

FIGURE 11. Drawing of *Pleurothallis whitteniana*. **A**, Whole flower (front view); **B**, Floral dissection; **C**, Anther cap and pollinarium; **D**, Whole flower (lateral view); **E**, Ovary, column and lip (lateral view); **F**, Whole plant; **G**, Lip (dorsal and ventral views). Prepared from holotype PL1049 by Bruno Larsen.

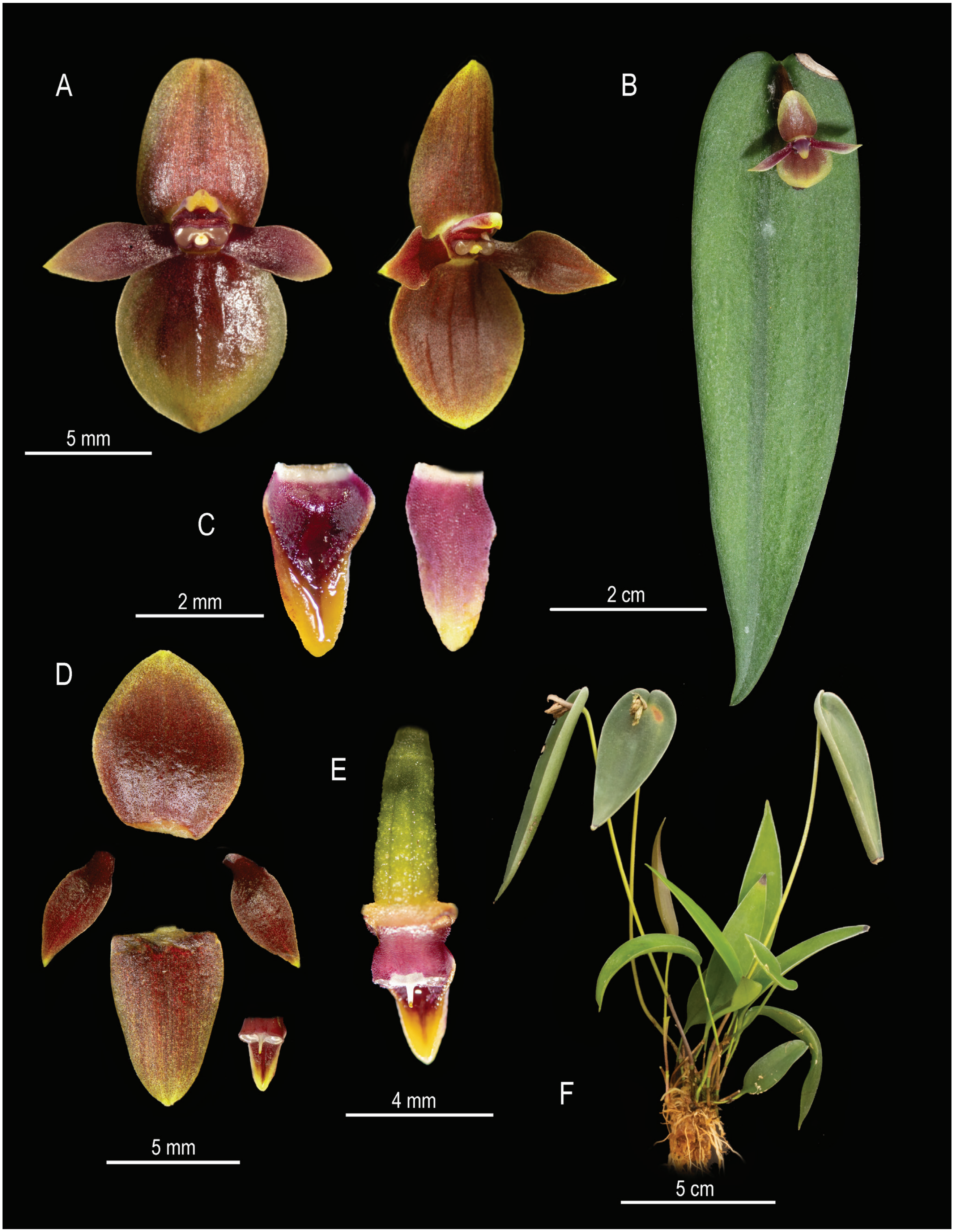

FIGURE 12. Composite digital plate of *Pleurothallis whitteniana*. **A**, Whole flower (front view and 3/4 view); **B**, Leaf and flower; **C**, Lip (dorsal and ventral views); **D**, Floral dissection; **E**, Ovary, column and lip (dorsal view); **F**, Whole plant. Prepared from holotype PL1049 by Mark Wilson.

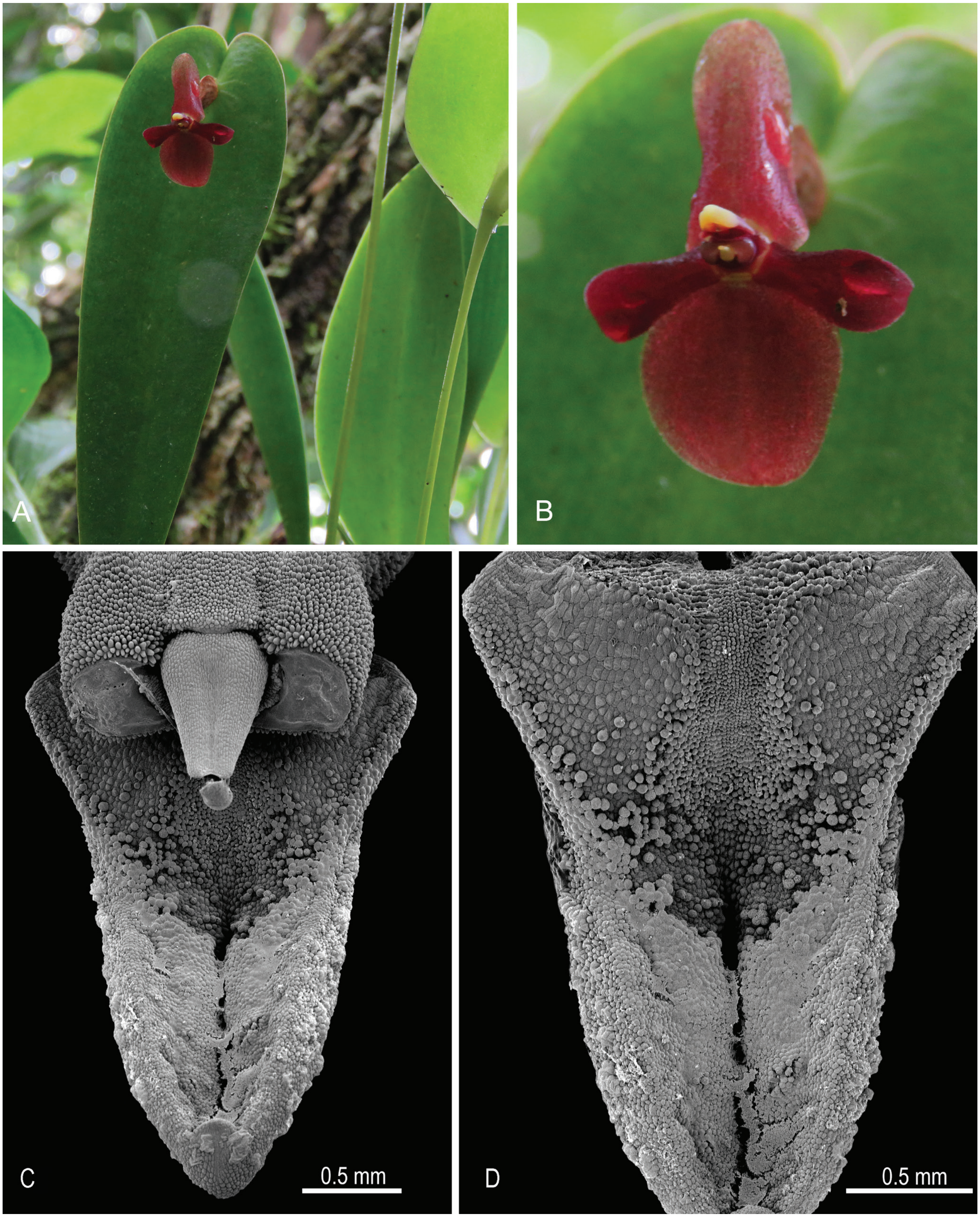

FIGURE 13. **A**, **B**, *Pleurothallis whitteniana in situ* at 1750 m in Huambo, Rodríguez de Mendoza, Amazonas, Peru, the first record of this species for the country, A, Flower and leaf; B, Flower. Courtesy of Génderson Arbildo Lopez. **C**, **D**, Scanning electron micrographs of *Pleurothallis whitteniana*. **C**, Lip, stigmatic surfaces and anther; **D**, Lip and glenion. Prepared from holotype PL1049 by Raven Ward.

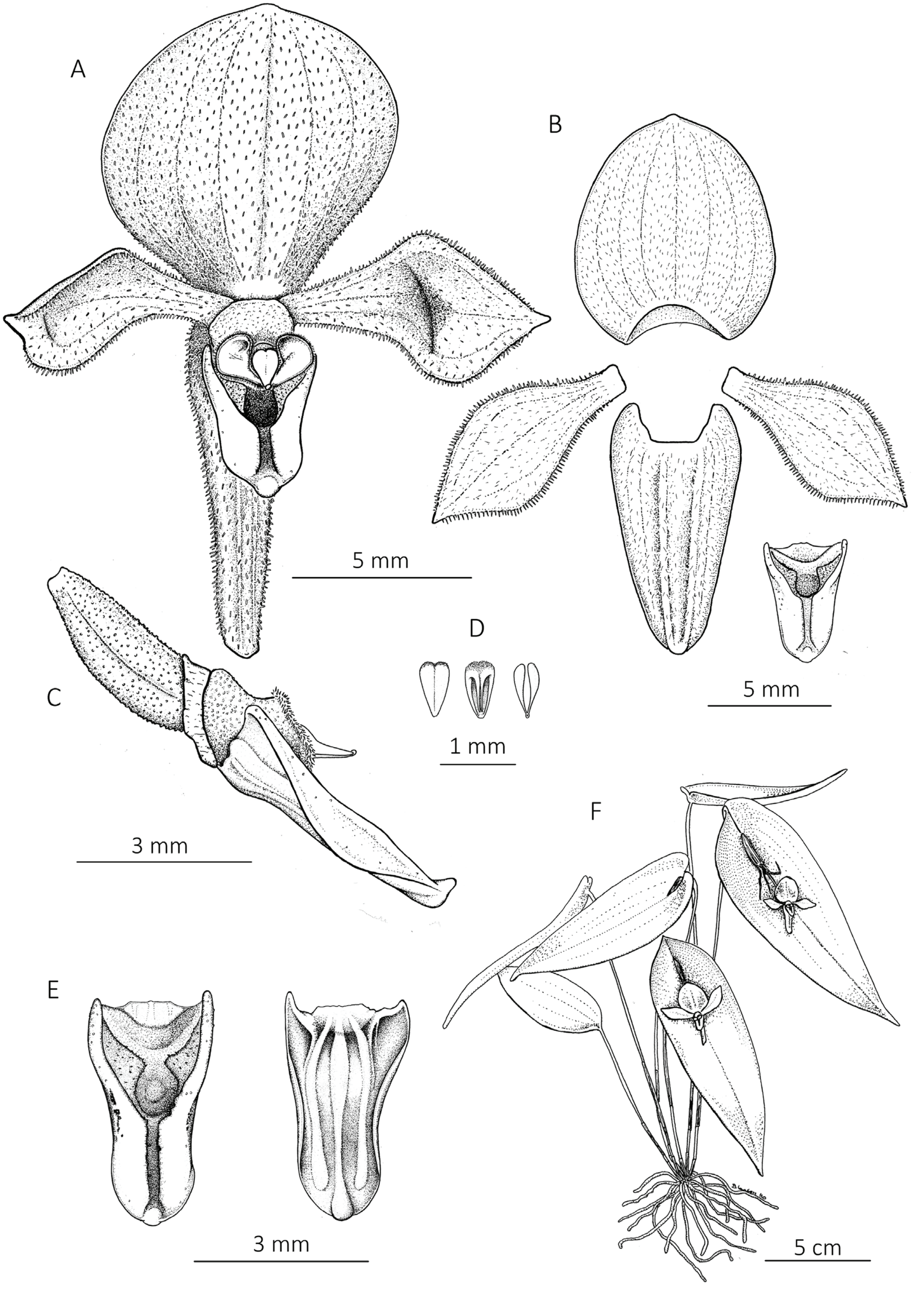

FIGURE 14. Drawing of *Pleurothallis carmensotoana*. **A**, Whole flower; **B**, Floral dissection; **C**, Ovary, column and lip (lateral view); **D**, Anther cap and pollinarium; **E**, Lip (dorsal and ventral views); **F**, Whole plant. Prepared from the paratype PL1154 by Bruno Larsen.

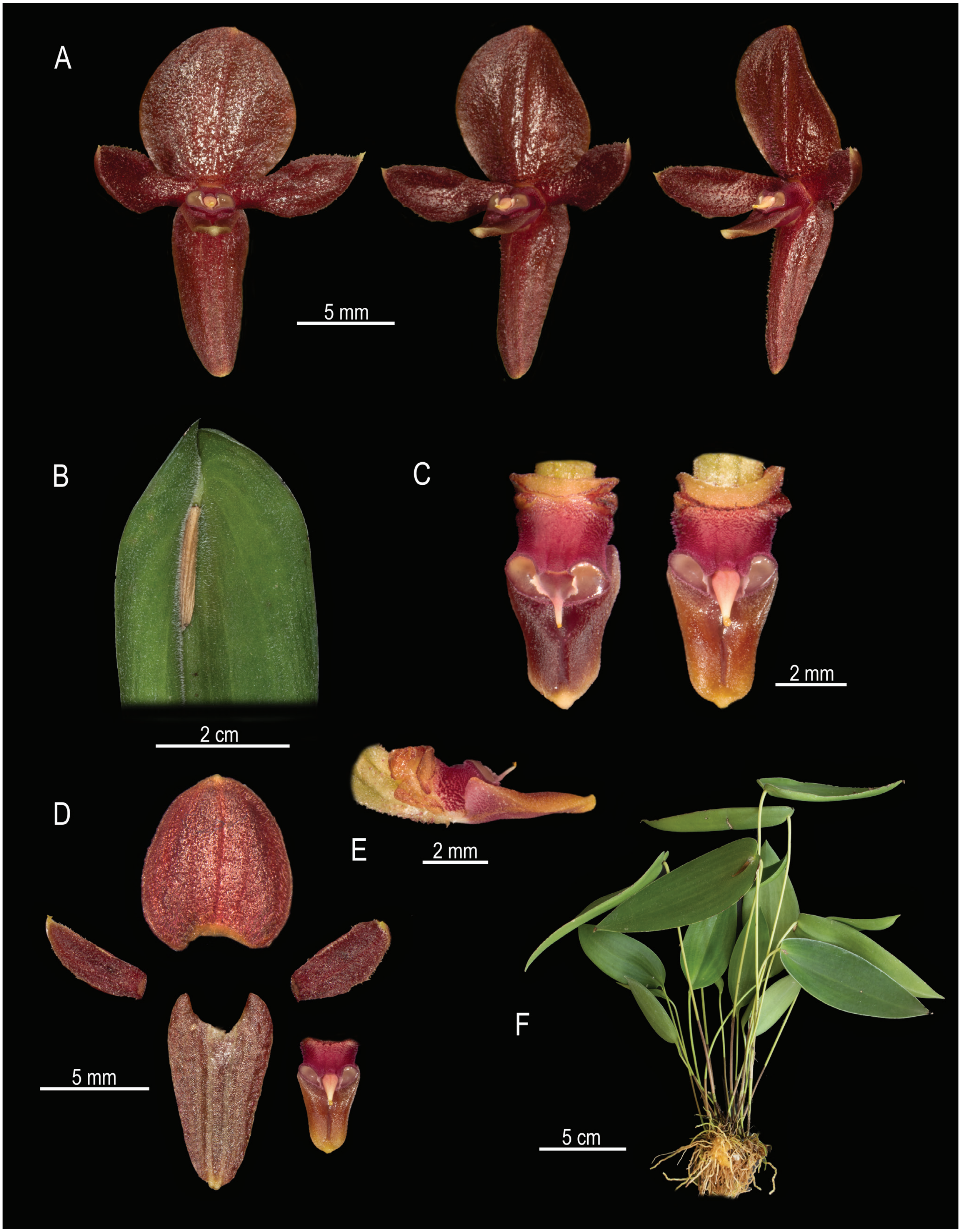

FIGURE 15. Composite digital plate of *Pleurothallis carmensotoana*. **A**, Whole flower (front, 2/3 and 3/4 views); **B**, Leaf base and spathaceous bract; **C**, Column and lip with and without anther cap and pollinarium; **D**, Floral dissection; **E**, Column and lip (lateral view); **F**, Whole plant. Prepared from the paratype PL1154 by Mark Wilson.

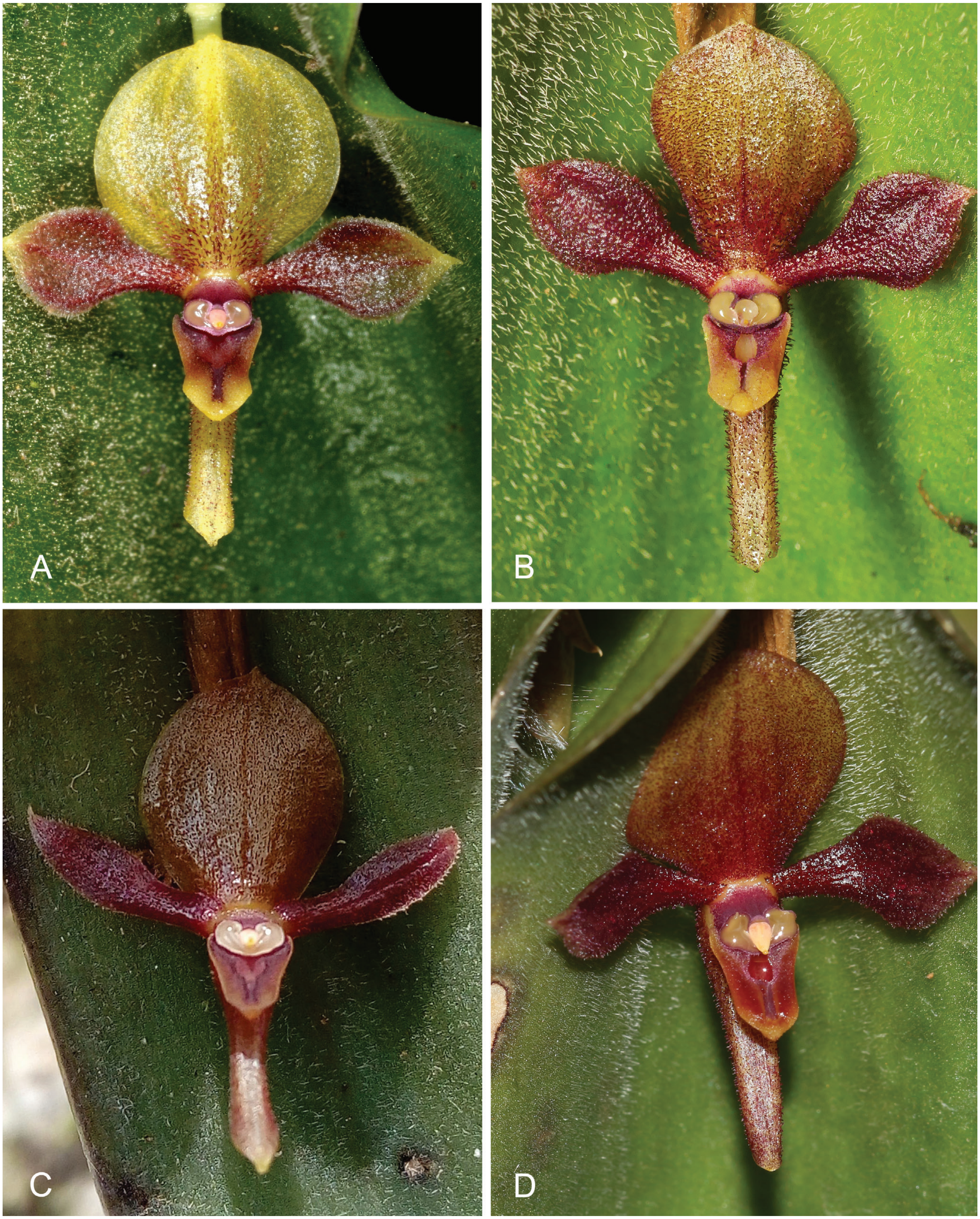

Figure 16. Photographs of *Pleurothallis carmensotoana*. **A**, Flower *in situ* in Parque Nacional Podocarpus, Zamora Chinchipe, Ecuador, courtesy of Ron Parsons; **B**, Flower *in situ* in Reserva Tapichalaca, Zamora Chinchipe, Ecuador, by Marco Jiménez; **C**, Flower from Oxapampa, Peru, courtesy of Abel Huayta Baltazar; **D**, Flower *ex situ* showing nectar-like liquid on lip calli and in glenion, courtesy of Fabian Kulka.

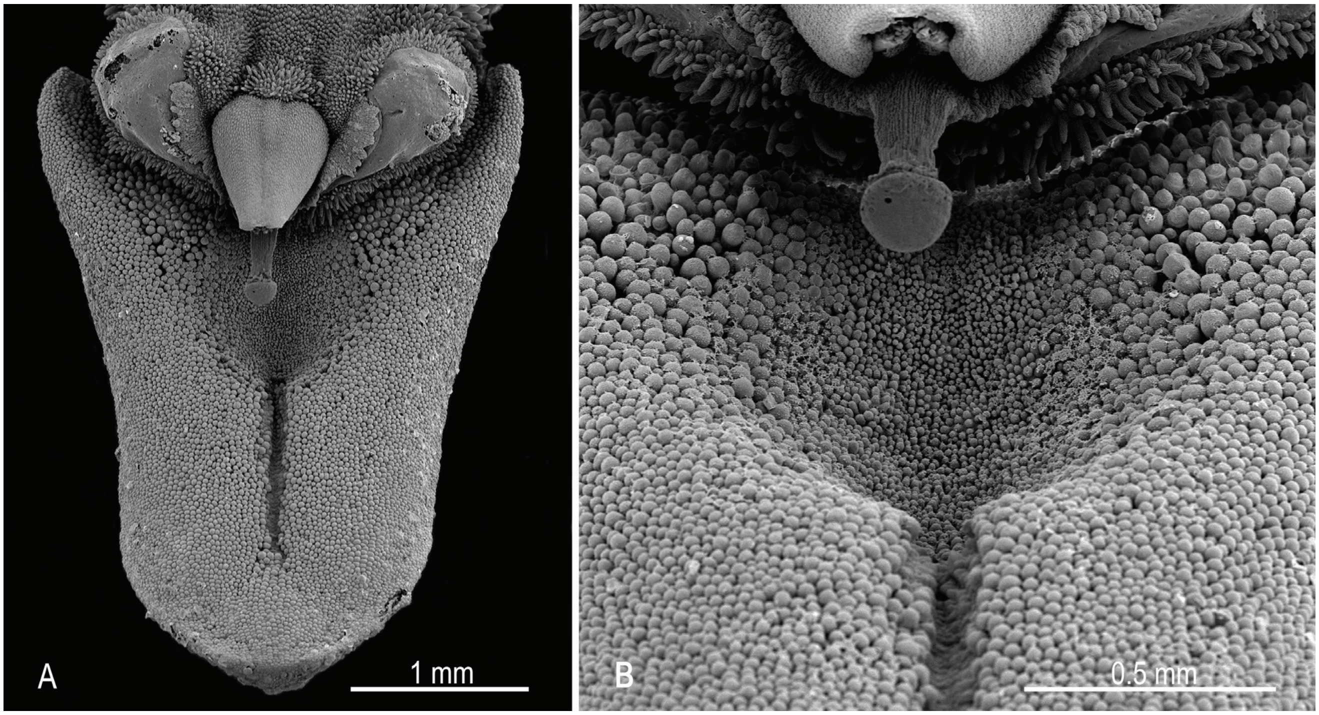

FIGURE 17. Scanning electron micrographs of *Pleurothallis carmensotoana*. **A**, Column, stigmatic surfaces, anther and lip; **B**, Lip base and glenion. Prepared from paratype PL1154 by Raven Ward.

revolute margins, 4.5–5.3 × 2.2–2.7 mm, adaxially with the mesochile channeled centrally, with a prominent circular depression bellow the middle, the base truncate, with a pair of auriculate, oblique, horizontal, minutely pubescent calli, connate to the base of the column, the apex rounded, obtuse, with a minute, erect, rounded callus, the margins deflexed, the abaxial surface with three, longitudinal parallel calli with the apices rounded; *Column* transversely subrectangular, dorsally complanate, microscopically pubescent, 2.8 × 2.1 mm, the anther apical, the stigma apical, bilobed with minutely ciliate margins; *Pollinarium* two, narrowly oblong-pyriform pollinia 1.1 × 0.2 mm attached to a discoid viscidium; Anther cap cucullate, ovate, subcordate, truncate, two-celled, 1.3 × 0.6 mm; *Capsule* not seen.

Additional specimens examined: ECUADOR. Purchased from Ecuagenera, Gualaceo, Ecuador, without collection data, as *Pleurothallis crateriformis* and flowered in cultivation at Colorado College, *M. Wilson PL1055* and *PL1154* (COCO).

Etymology: Named in honor of Carmen Rosa Soto Vargas (1964–2021) orchid specialist at Inkaterra Machu Picchu Pueblo Hotel, Cusco, Peru (Mirenda 2021). The given name is included along with the family name to avoid confusion with other individuals of the name Soto.

Distribution and conservation status: This species has been photographed *in situ* in Ecuador in Podocarpus National Park by Ron Parsons (Fig. 16A), in Reserva Tapichalaca by Marco Jiménez (Fig. 16B) and near Valladolid by Rudy Gelis. It has also been photographed much further south in Oxapampa, Peru by Abel Huayta Baltazar (Fig. 16C) and Huancayo Province, Junín Region, Peru by Wilder Quispe. These observations suggest that the species is widely distributed throughout the southern Andes from southern Ecuador to central Peru. While according to IUCN criteria the species must be considered Data Deficient, the breadth of distribution and the occurrence in two Ecuadorian protected areas suggests that it is not a vulnerable species.

This species, misidentified as *Pleurothallis lilijae*, is represented in Orchids of Ecuador volume IV (Dodson 2003: 778, photo #1794, by Alexander Hirtz).

Pleurothallis rikseniana Mark Wilson & B.T. Larsen, *sp. nov.*

TYPE: ECUADOR. Purchased from Jacky Orchiflora, Belgium, without collection data, flowered in cultivation by W.G. Riksen in Bunde, The Netherlands, 2021, *M. Wilson & J. Riksen*, PL1174 (Holotype: flowers in spirits COCO). Fig. 18–19.

Pleurothallis rikseniana is most similar to *P. lilijae* but can be easily distinguished by the lip length (2.5–2.7 mm long in *P. rikseniana* versus ca. 3.8 mm long in *P. lilijae*); shape (ovate-short triangular in *P. rikseniana* versus narrowly ovate [“*anguste ovato*”] in *P. lilijae*; concavity (deeply concave in *P. rikseniana* versus shallowly concave in *P. lilijae*); and presence/absence of labellar sulcus (glenion continuous with deep, linear sulcus in *P. rikseniana* versus distinct, circular glenion and no sulcus).

Epiphytic, caespitose *herb*, up to 28 cm tall; *Roots* slender, flexuous, ca. 1 mm in diameter; *Ramicauls* slender, terete, ca. 1.2 mm in diameter, erect, 18.5–24.0 cm long, with a tubular, 1.2–2.2 cm long papery basal sheath, and a 4.0–4.5 cm long, tightly adpressed, tubular sheath below the middle; *Leaves* horizontal to acutely deflexed, coriaceous, narrowly-ovate, acute, 12.0–13.8 × 2.3–2.8 cm, the base sessile, deeply cordate; *Inflorescence* a fascicle of solitary, successive flowers, rarely in pairs, borne from an oblique

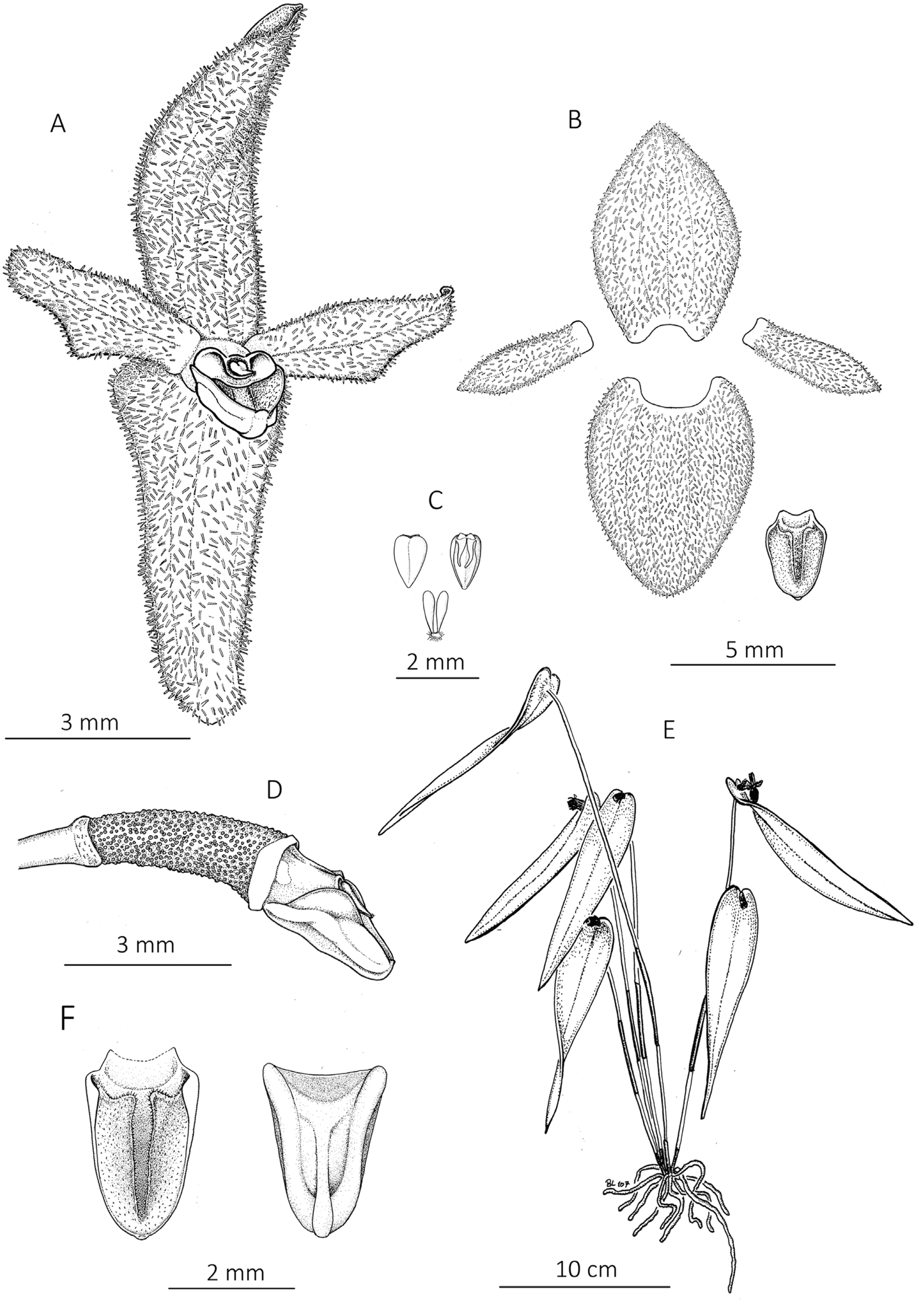

FIGURE 18. Drawing of *Pleurothallis rikseniana*. **A**, Whole flower (2/3 view); **B**, Floral dissection; **C**, Anther cap and pollinarium; **D**, Ovary, column and lip (lateral view); **E**, Whole plant; **F**, Lip (dorsal and ventral view). Prepared from the holotype PL1174 by Bruno Larsen.

FIGURE 19. **A**, Photograph of flower of *Pleurothallis rikseniana*, prepared from the holotype PL1174 by Joost Riksen; **B**, Photograph of flower of a different color form of *P. rikseniana* in collection of Ecuagenera, by Mark Wilson; **C**, Scanning electron micrograph of column, stigmatic surfaces, anther and lip of *P. rikseniana*, prepared from holotype PL1174 by Raven Ward.

spathaceous, 1.1–1.4 cm long bract; peduncle 2 mm long; floral bract 1 mm long; pedicel 1.7 mm long; ovary terete, densely verrucose, rounded in section, 3.2 × 1.4 mm; *flowers* non-resupinate, with the sepals and petals long-pubescent-spiculate; *Dorsal sepal* translucent yellow, purple centrally, ovate, acute, 6.2–6.6 × 4.4–4.7 mm, 5-veined, the margins reflexed; *Lateral sepals* translucent yellow-white, sparsely purple at the base, completely connate into a ovate, obtuse, 5.5–5.7 × 5.1–5.4 mm, 6-veined s*ynsepal* with reflexed margins; *Petals* translucent yellow-white, purple to bellow the middle, oblong, acute, 4.4–4.6 × 1.0–1.2 mm, 1-veined; *Labellum* triangular-ovate, obtuse, 2.5–2.7 × 2.0–2.2 mm, adaxially microscopically pubescent, with a pair of auriculate, longitudinally oblique, horizontal calli, the disc channeled centrally, the base truncate, concave, horizontally connate to the base of the column, the apex rounded, obtuse, with a minute, rounded callus, the margins thickened, deflexed, the abaxial surface with three, longitudinal calli, the median callus bifurcate at the base, with the apex rounded, the lateral calli oblique; *Column* transversely subrectangular, dorsally complanate, 1.2 × 1.6 mm, the anther apical, the stigma apical, bilobed; *Pollinarium* two, narrowly oblong-pyriform pollinia 0.9 × 0.3 mm attached to a circular, ciliate viscidium; Anther cap cucullate, ovate, subcordate, truncate, two-celled, 1.0 × 0.7 mm; *Capsule* not seen.

Etymology: Named in honor of Wil G. Riksen (1938–) from Bunde, The Netherlands, enthusiastic collector of orchids for almost 38 years, who cultivated this species.

Distribution and conservation status: This species has been photographed in the collection of Ecuagenera by Wilson and it is morphologically similar to a species from southeastern Ecuador (Jiménez unpubd.), suggesting that *P. rikseniana* may originate from that area. Efforts to locate *in situ* populations to determine the distribution are ongoing. Without additional information, *P. rikseniana* must be considered Data Deficient according to IUCN criteria.

Pleurothallis gonzaloi J.S. Moreno, Rinc.-González & Gal.-Tar., *sp. nov*.
TYPE: COLOMBIA, Tolima: Roncesvalles, Vereda San Miguel, Finca Villa Uva, 3100 m, July 2019, *M. Rincón-González and J.S. Moreno 1354* (Holotype: TOLI). Fig. 20–22.

Pleurothallis gonzaloi is most similar to *P. lanigera* but is easily distinguished by the leaf shape (oblong-lanceolate versus broadly ovate in *P. lanigera*); leaf base (cordate, with basal lobes deeply reflexed in *P. gonzaloi* versus cordate, with basal lobes flat or occasionally slightly reflexed); the spathaceous bract (reclining in *P. gonzaloi* versus erect in *P. lanigera*); the position of the flower (resupinate in *P. gonzaloi* versus predominantly non-resupinate in *P. lanigera*); and the synsepal (glabrous in *P. gonzaloi* versus pubescent in *P. lanigera*).

Epiphytic, caespitose *herb*, suberect, up to 35 cm tall. *Roots* slender, ca. 1.3 mm in diameter. *Ramicauls* terete, slender, 15–30 cm long, 1.8–2.8 mm in diameter, yellowish green, provided with a tubular, truncated sheath up to 4 cm long at the base, and a tubular, narrow, truncate sheath below the middle, to 8–12 cm long, the bracts pale brown, papyraceous, fibrous. *Leaf* borne horizontally at the apex of the ramicaul, acutely deflexed, strongly coriaceous, rigid, sessile, oblong, acuminate, curved up above the middle to the base, 16–21 × 3–4.3 cm, slightly cordate, forming two imbricate lobes at the base. *Inflorescence* a solitary flower, usually produced singly, from a reclined, prominent, lanceolate spathaceous bract, 1.5 mm long, dark brown, papyraceous and fibrous when mature, eventually dissolving with age. *Pedicel* terete, 15 mm long. *Ovary* straight, striate, verrucose, with black dots and reddish pustules, 8–12 mm long, pale green. *Flowers* white with many purple dots, which darken its color, especially on the dorsal sepal and petals, the lip is yellowish, the texture very vesiculose, less on the margins and lateral sepals. *Dorsal*

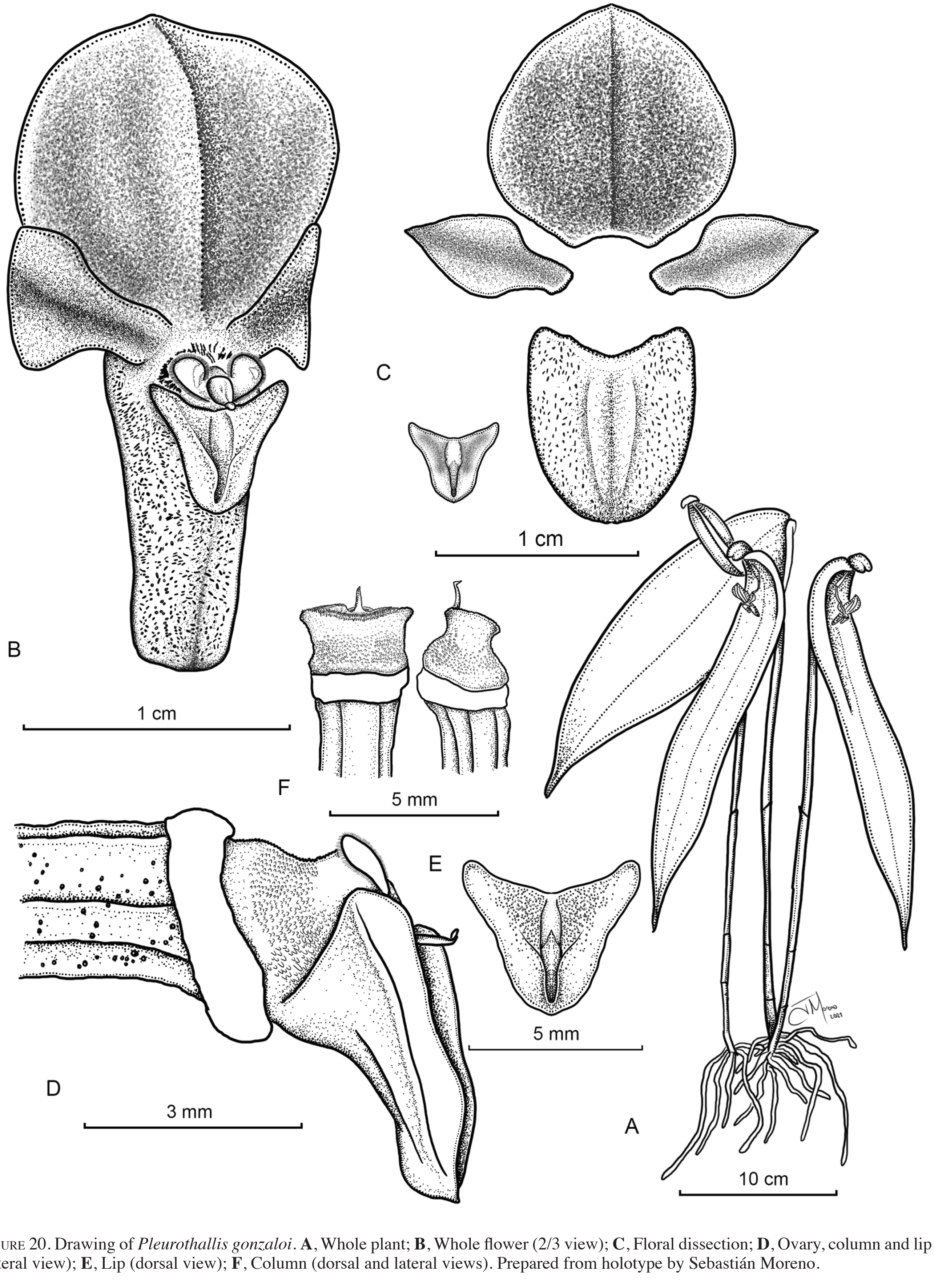

FIGURE 20. Drawing of *Pleurothallis gonzaloi*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view); **F**, Column (dorsal and lateral views). Prepared from holotype by Sebastián Moreno.

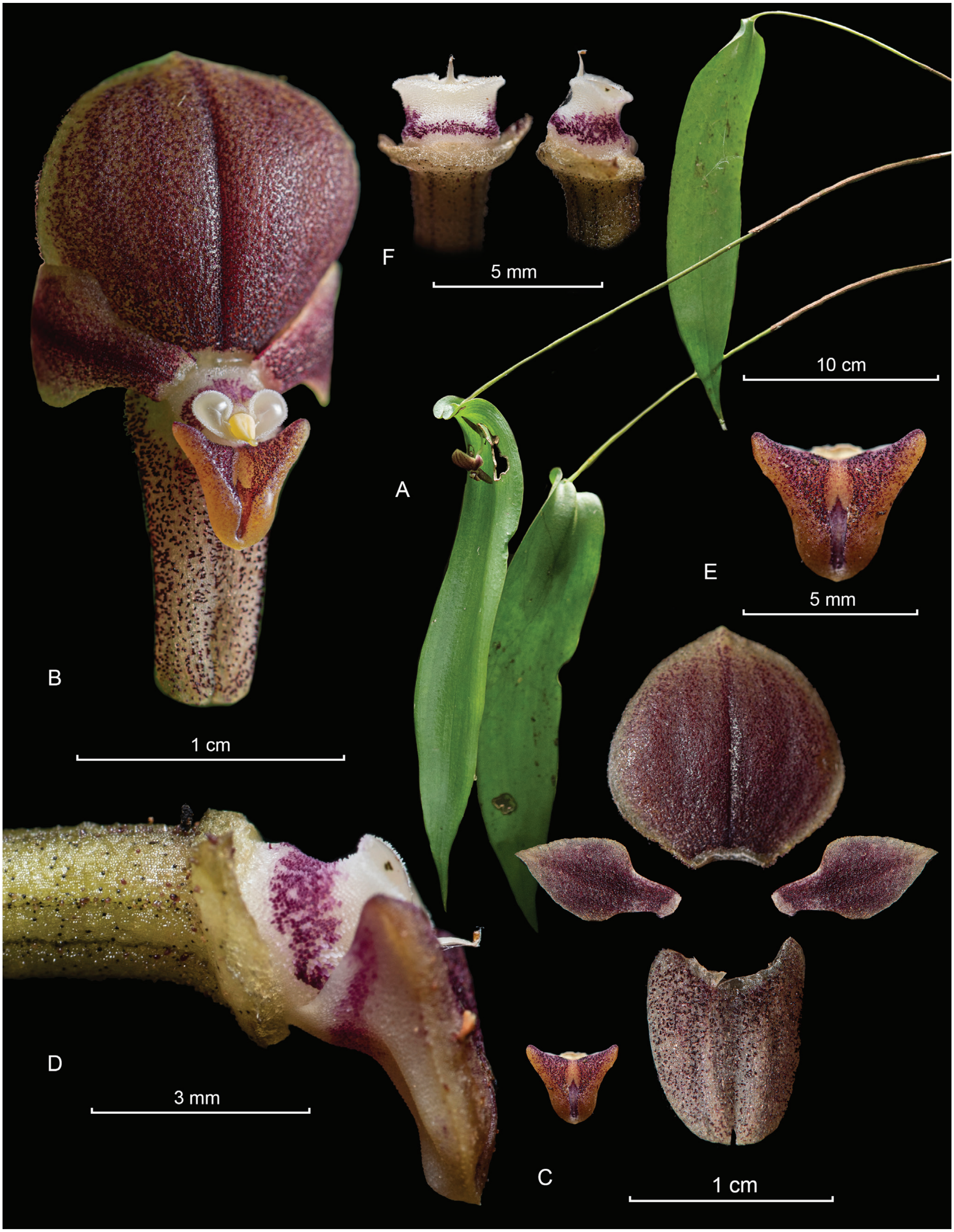

FIGURE 21. Composite digital plate of *Pleurothallis gonzaloi*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view); **F**, Column (dorsal and lateral views). Prepared from holotype by Sebastián Moreno.

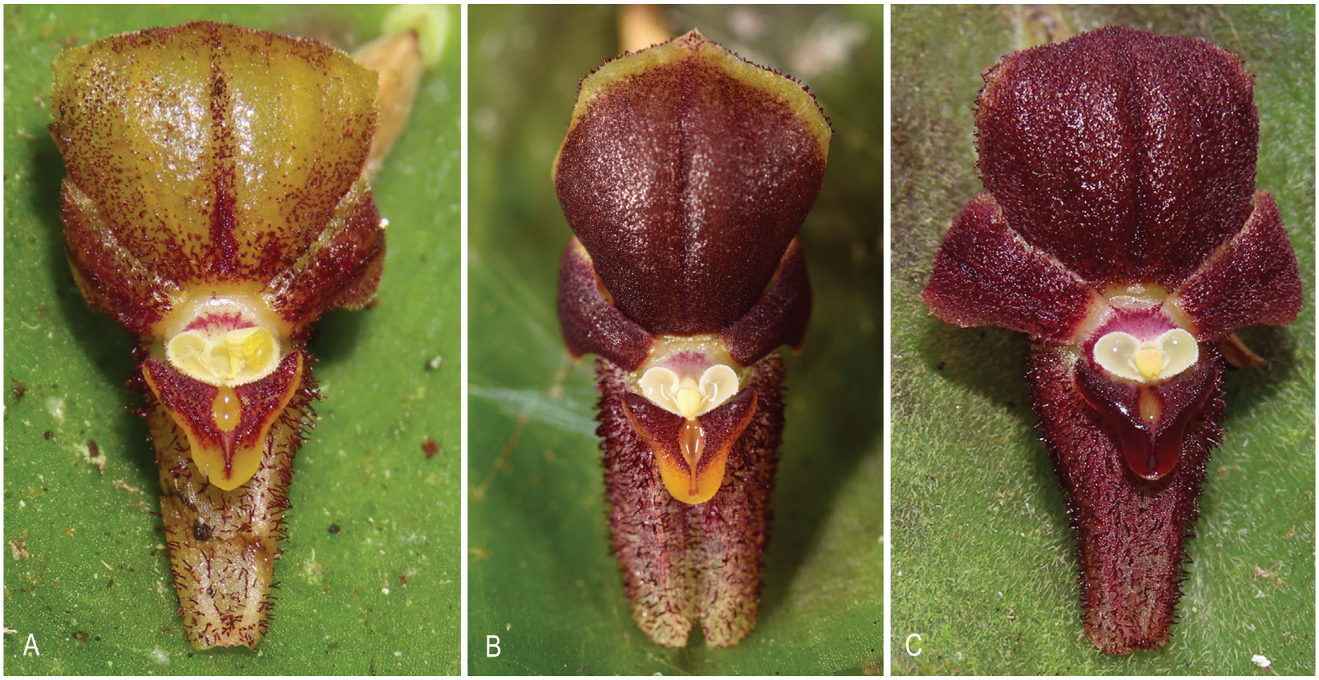

FIGURE 22. Photographs of flowers of *Pleurothallis gonzaloi* illustrating different color forms. **A**, **C**, Courtesy of Sebastián Arango; **B**, By David Haelterman.

sepal suborbicular, rounded, 11–13 × 10–13 mm, 7-veined. *Lateral sepals* connate into a broadly ovate to suborbicular, emarginate synsepal, l0–12 × 7-9 mm, 5-veined. *Petals* elliptical-lanceolate, acute, the cuneate base 8–9 × 3.5–4.2 mm, 3 veined. *Lip* articulated at the column foot, broadly ovate, basally truncate with rounded angles, concave to conduplicate, fleshy, vesiculose, thick margins, rounded to acute, 3.8–4.2 × 4.7–5.2 mm; the center shallowly channeled from base to apex above a basal glenion, the glenion deep, elliptic, ca. 1.7 mm long. *Column* white with a purple stripe towards the base, short, transversely subcuadrate, dorsiventrally complanate, very papillate, ca. 3 × 4 mm, steep margins *Anther cap* ovate, pale yellow, acute, 2-celled, ca. 1.3 × 0.8 mm. *Pollinia* two, narrowly oblong, pyriform, 1.4 mm long, attached to an elliptic viscidium, viscous. *Capsule* not seen.

Additional specimen examined: COLOMBIA, Valle del Cauca: Cali, Trail to Minas del Socorro from Peñas Blancas, PNN Farallones, 2873 m, June 29, 2020, *R. Galindo-Tarazona, A. Fierro, G. Rodriguez and M. Espitia 1475* (CUVC).

Etymology: Named to honor Gonzalo Cardona Molina "Burro, Burrito" (1966–2021), an environmental leader and lover of his hometown Roncesvalles, the municipality where the new species was found. He was a defender of the wax palm (*Ceroxylon quindiuense* (H. Karst.) H. Wendl.), the national tree of Colombia, and the yellow-eared parrot (*Ognorhynchus icterotis*), both species at risk of extinction. His labor went further and he tried to connect the local people with conservation, where he taught them the importance of preserving the environment and respect for all ecosystems. Gonzalo was an innate and empirical scientist who gave all his efforts for his people and hometown Roncesvalles.

Distribution and conservation status: *Pleurothallis gonzaloi* appears to be widely distributed in central-southwest Colombia having been observed and collected or photographed in the five geographically adjacent departments of: Tolima by Milton Rincón; Valle del Cauca by David Haelterman and Robinson Galindo; Quindío by Pedro Cardona; Caldas by Sebastián Arango; and Huila by Juan David Medina. So, although according to IUCN criteria it must be considered Data Deficient, *P. gonzaloi* is probably not vulnerable at the present time.

Pleurothallis mahechae J.S. Moreno, Sierra-Ariza & L.C. Pina, *sp. nov.*

TYPE: COLOMBIA, Caldas: Alongside road between Manizales, Caldas and Herveo, Tolima, 2700–2800 m, 29 March 2022, *Clara Santafé Millán y Laura Suarez Romero* (Holotype: HUEB TRA-3855). Fig. 23–26.

Pleurothallis mahechae is most similar to *P. lanigera* but is easily distinguished by the leaf shape (oblong-lanceolate in *P. mahechae* versus broadly ovate in *P. lanigera*); leaf base (cordate, with basal lobes deeply reflexed in *P. mahechae* versus cordate, with basal lobes flat or occasionally slightly reflexed in *P. lanigera*); the position of the flower (resupinate in *P. mahechae* versus predominantly non-resupinate in *P. lanigera*); and the lip morphology (planar to convex, with two V-shaped calli in *P. mahechae* versus concave with thickened lateral edges in *P. lanigera*).

Epiphytic, caespitose *herb*, erect to suberect, medium-sized herb to 17 cm tall. *Roots* slender, ca. 1 mm in diameter. *Ramicauls* terete, slender, bowed, 7–15 cm long, 1–1.8 mm in diameter, yellowish green, provided with a tubular, truncate sheath to 2.8–3.5 cm long at the base, whitish to brown, papyraceous. *Leaf* borne transversally at the apex of the ramicaul, parallel to the stem, strongly coriaceous, rigid, sessile, oblong-lanceolate, acute to acuminate, concave, with involute margins, 8–16 × 2.3–3 cm, deeply cordate, forming two slightly imbricate lobes at the base, the surface

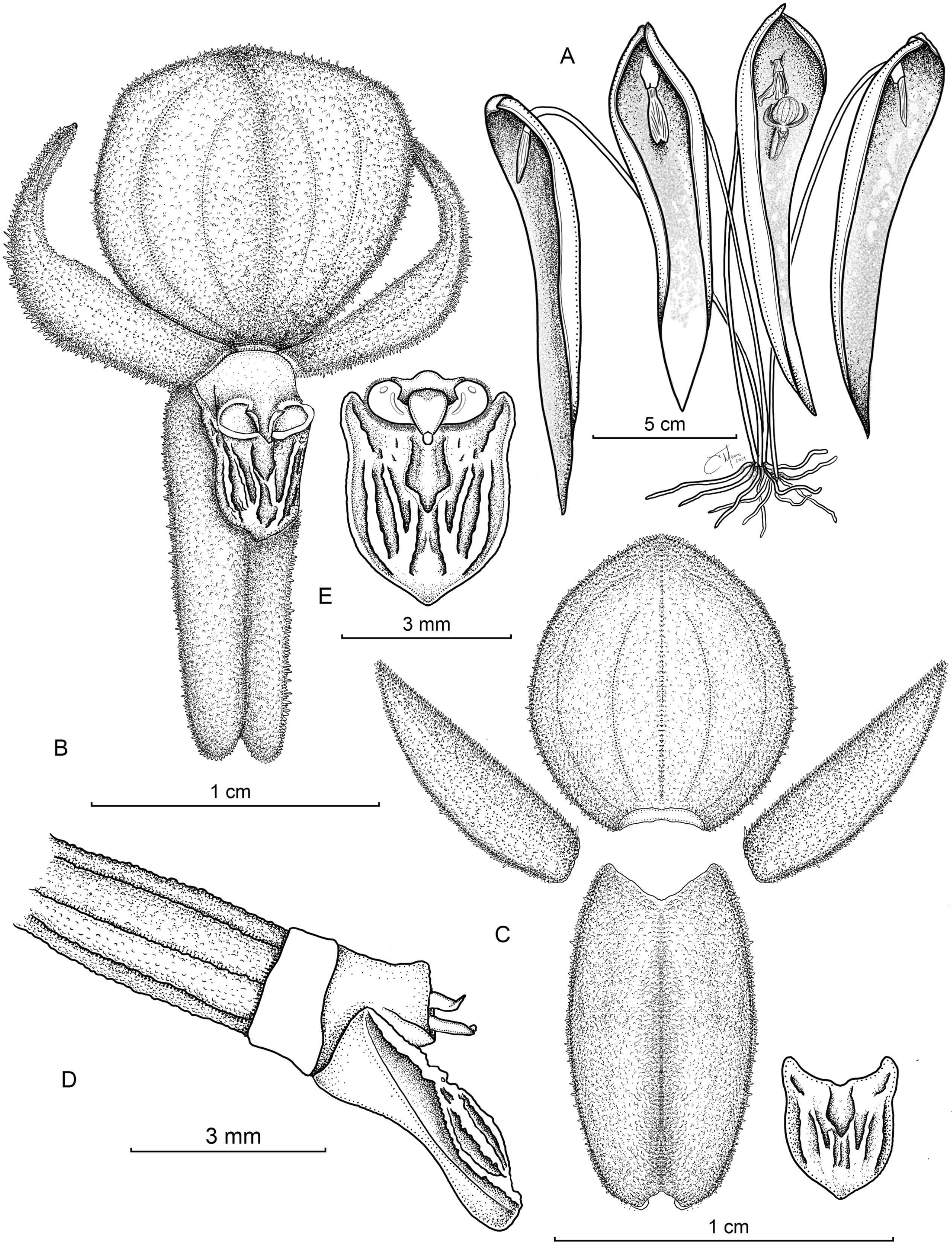

FIGURE 23. Drawing of *Pleurothallis mahechae*. **A**, Whole plant; **B**, Whole flower; **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view). Prepared from holotype by Sebastián Moreno.

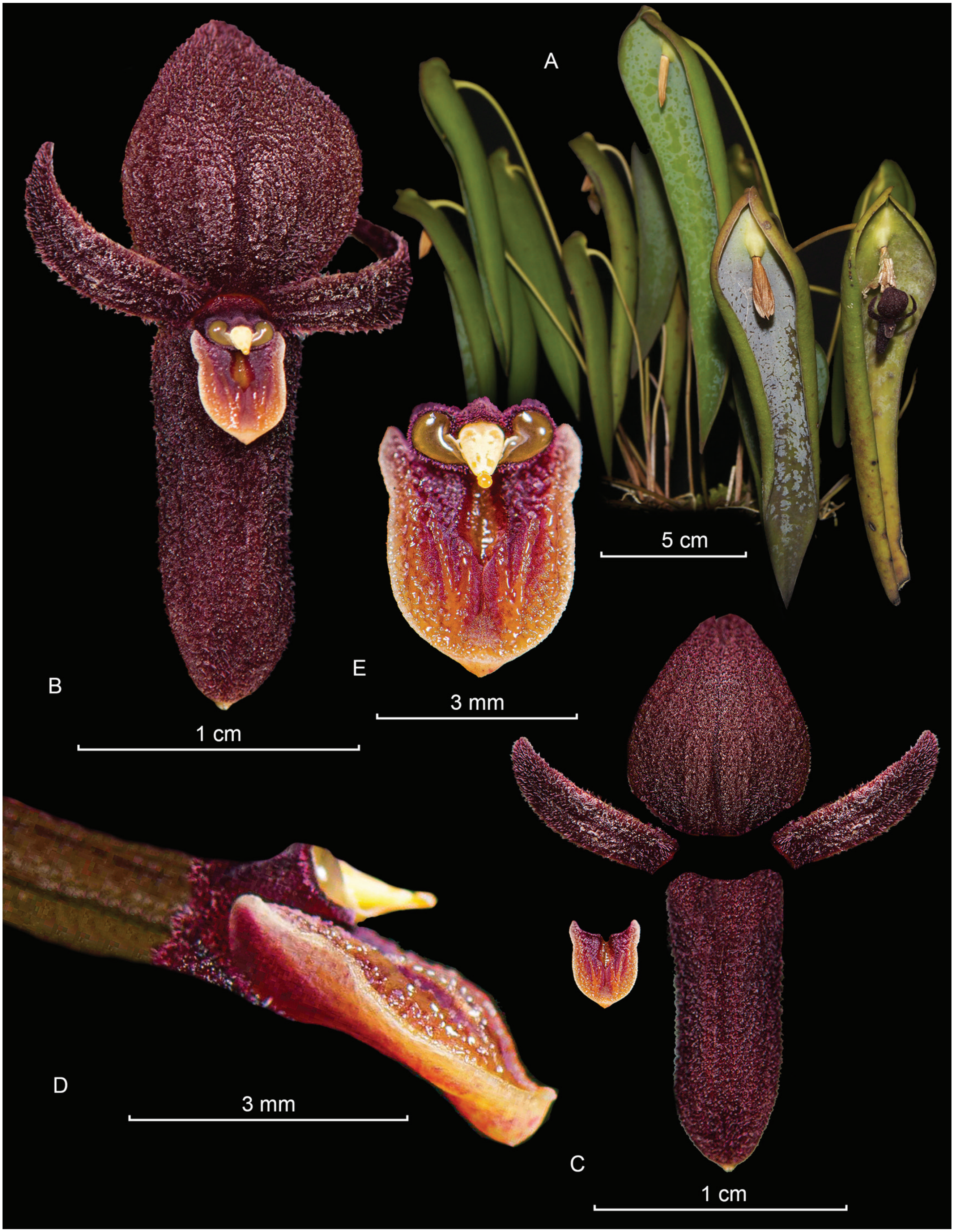

FIGURE 24. Composite digital plate of *Pleurothallis mahechae*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view). Prepared from holotype by Sebastián Moreno.

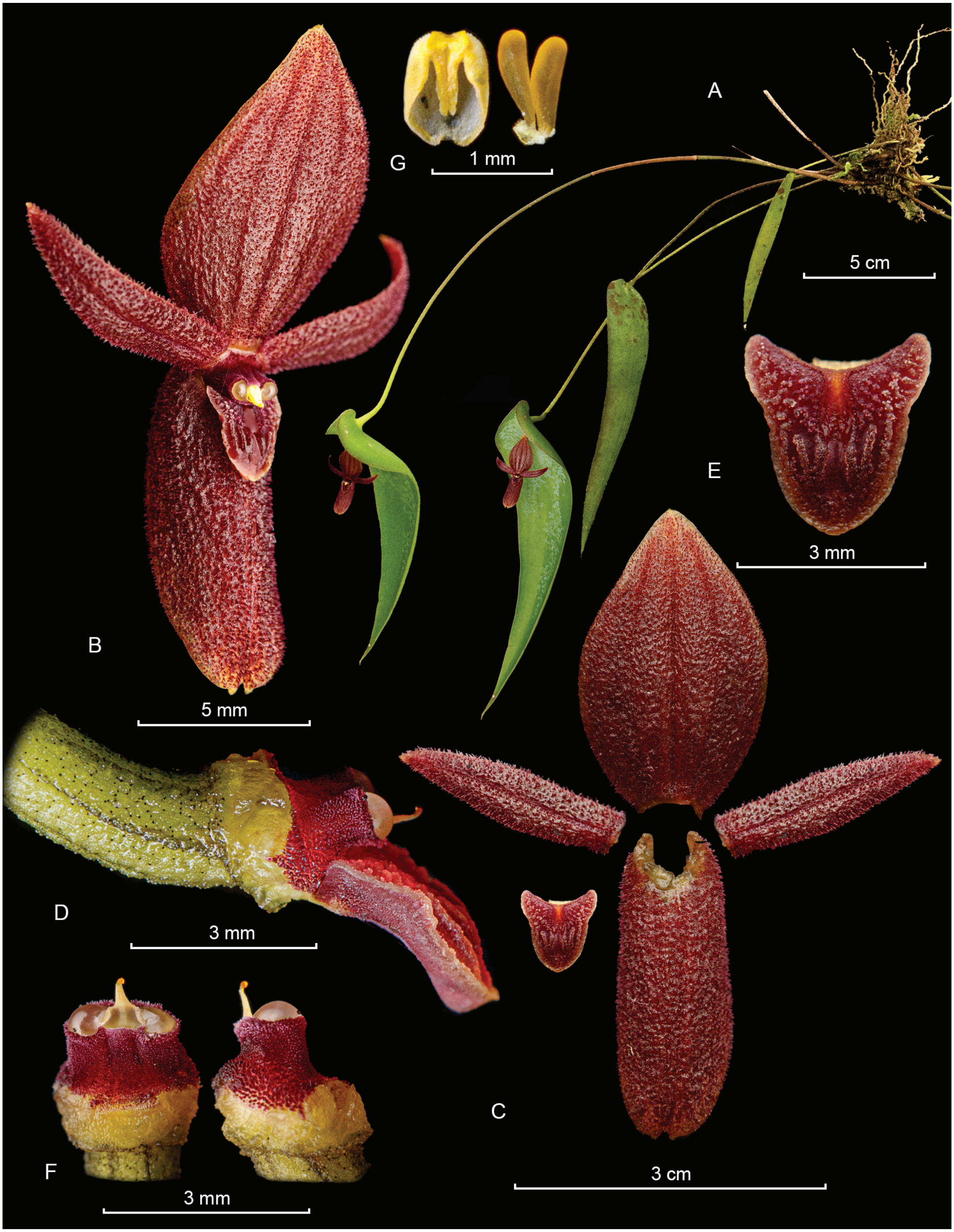

FIGURE 25. Composite digital plate of different morphotype of *Pleurothallis mahechae*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view); **F**, Column (dorsal and lateral views). Prepared from paratype by S. Vieira and J. Sebastián Moreno.

FIGURE 26. **A–B**, Lips of *Pleurothallis mahechae* showing pair of V-shaped calli and nectar-like liquid. A, By J. Sebastián Moreno; B, Courtesy of Esteban Domínguez Vargas; **C–D**, Scanning electron micrographs of lip of *P. mahechae*. C, Whole lip; D, Glenion, prepared from paratype PL1245 by Mark Wilson.

waxy. *Inflorescence* a solitary flower, usually produced singly, from a prominent, reclined spathaceous bract, 2–2.5 mm long, brown, papyraceous and fibrous when mature, eventually disintegrating with age. *Pedicel* terete, 5 mm long. *Ovary* straight, striate, 4–6 mm long, dark green; *flowers* dark purple, lip slightly yellow, the sepals and petals strongly papillose and pilose, the slightly fimbriated to ciliated margin. *Dorsal sepal* suborbicular, rounded, 8–10 × 7–9 mm, 5 veined. *Lateral sepals* connate into an oblong, obtuse synsepal, 11–12 × 4.5–5.5 mm, 5-veined. *Petals* oblong, rounded, 7.5–8.5 × 2.8–3.5 mm, 3-veined. *Lip* articulated at the foot of the column, suboval, basally truncate with acute angles, concave, fleshy, cellular-papillose to vesiculose, steep margins, rounded to acute, 3–3.5 × 3.5–4 mm; the basal callus, purple, broad, surrounding the glenion, that branches towards the apex forming 6 ridges, the lateral and central ridges longer than the others, glenion deep, obovate, ca. 1.5 mm long. *Column* short and wide, transversely suboval, dorsiventrally complanate, papillate, ca. 1.5 × 2.8 mm. *Anther cap* ovate, pale yellow, acute, 2-celled, ca. 1 × 0.6 mm. *Pollinia* two, narrowly oblong, pyriform, 1.1 mm long, attached to an elliptic viscidium, viscous. *Capsule* not seen.

Additional specimens examined: COLOMBIA, Antioquia. El Retiro, Alto del Escobero. Epiphytic in tree alongside a path in Ecological Reserve San Sebastián De La Castellana. *S. Vieira-Uribe and L. Pérez-Arcila 148* (JAUM). UKNOWN. Flowered in cultivation, Hanging

Gardens, San Francisco, USA, Jan 2022, *M. Wilson and D. Newman PL1245* (flowers in spirits COCO).

Etymology: Named to honor Gilberto Emilio Mahecha (deceased 2021), known as the father of Colombian dendrology or "the man who talked to trees". Gilberto was a Forest Engineer, professor, ecologist and the founder and former director of the "Forest Herbarium" of Universidad Distrital, being the main collector of most of the specimens in the collection. Nowadays the herbarium bears his name in his honor "Herbario Forestal Gilberto Emilio Mahecha Vega". In the past year four species have been dedicated to him, two species of Magnoliaceae, *Magnolia gilbertoi* (G. Lozano C.) Govaerts and *Magnolia mahechae* (G. Lozano C.) Govaerts, and one species of Malvaceae, *Spirotheca mahechae* Fern. Alonso.

Distribution and conservation status: This species has been collected or observed in the three contiguous Colombian departments of Antioquia, Caldas and Cundinamarca. While according to IUCN criteria it should be considered Data Deficient, the low frequency of observation and our inability to confirm the species grows in any protected areas, suggests that the species may be vulnerable.

Discussion

Using the aforementioned morphological criteria, we recognize 32 distinct species in the *Pleurothallis cardiostola-P. lilijae* complex, an expansion of Luer's (1988) taxonomic concept of subsection *Cardiostolae*. This is a grouping of significant size, including approximately 10-13% of described species in subsection *Macrophyllae-Fasciculatae*. As such, the *P. cardiostola-P. lilijae* complex is both more numerous and more widely distributed than the *P. cardiothallis* complex (Pupulin et al., 2017; Pupulin et al., 2021), which is itself part of what might be more broadly considered the *P. cardiothallis-P. titan* complex (Sierra-Ariza et al., 2022). It is important to restate in this context, however, that we do not claim that these 32 species are phylogenetically more closely related to each other than they are to any other member of *Macrophyllae-Fasciculatae*. While there have been phylogenetic studies incorporating species of the subsection, none have produced a well-supported phylogeny of the group. Until such a phylogeny is generated, expert recognition of morphologically-defined groupings is the best that can be achieved. So, while we assume that the majority of the 32 species in the complex are phylogenetically related, we acknowledge that the wide geographic distribution of species in the complex raises the possibility of either erroneous exclusion of phylogenetic relatives with divergent morphologies, or erroneous inclusion of phylogenetically unrelated species with similar morphology due to convergent evolution.

So, what is the benefit of recognizing a taxonomic group within subsection *Macrophyllae-Fasciculatae* if the group has not been demonstrated to be phylogenetically related? First, recognition of a group of morphologically-related species draws attention among botanists to the fact that there are several species similar to *P. cardiostola* and to *P. lilijae* among which they need to distinguish when identifying a plant in the field. And further, that botanists should be aware of the aforementioned misleading aspects of Icones Pleurothallidinarum XXVII (Luer, 2005) and that this should not be the sole source used to identify these species. Second, recognition of this group should prompt re-examination of non-type specimens in herbaria labeled "*P. cardiostola*" and "*P. lilijae*," since several are likely misidentified. Together with contemporary field observations, such as those recorded in iNaturalist, these data would then allow accurate distributions for the species to be developed. Thirdly, recognition of the group and characterization of its members allows the diagnosis of new morphologically-related species, of which there appear to be several more in addition to those described here. Lastly, recognition of the group prompts an examination of the morphological and ecological factors that may have contributed to the relative success of the group both in terms of numbers (10–13% of the subsection) and in its wide distribution.

Species of *Pleurothallis* in subsection *Macrophyllae-Fasciculatae* display a wide range of lip morphologies (Wilson et al. 2018). Among these, a large proportion display relatively open flowers in which the lip, glenion, anther, and stigmatic surfaces are fully exposed on a relatively planar flower. Karremans and Díaz-Morales (2019) have proposed the term "steliform" for such flowers, referring to the morphology of flowers of *Stelis sensu stricto* (e.g. *Stelis argentata* Lindl.) and the manner in which the pollinators interact with the reproductive structures. All of the *P. cardiostola-P. lilijae* complex exhibit flowers with such "steliform" morphology, but within the group there exists substantial variation in lip morphology that undoubtedly reflects different pollinator species and behaviors yet to be elucidated. Lip morphologies include predominantly concave structures, for example in *P. lilijae* (Fig. 1D–1E and 4), *P. rikseniana* (Fig. 18F and 19C) and, taken to the extreme, in *P. valladolidensis*; concave structures with lateral and apical thickening of the lip, for example in *P. cardiostola* (Fig. 1B–1C, 2A–2B and 3A), *P. lanigera* (Fig. 1F and 2C–2D), *P. andreaskayi* (Fig. 8D, 9C–9D and 10) and *P. gonzaloi* (Fig. 21E and 22); and lips with internal calli which partially or almost completely fill the concavity, for example in *P. carmensotoana* (Fig. 15C, 16 and 17) and, taken to the extreme, in *P. mahechae* (Fig. 24E, 25E and 26) and *P. perijaensis* (Fig. 27). These lips all produce nectar-like liquid along the lateral and apical edges of the lips (Fig. 2C, 3A, 4B, 8D, 9B–9C, 16D and 22) and/or on the apices of the calli (Fig. 24E and 26A–26B). Another attribute displayed by the flowers of this group is a distinct and relatively prominent glenion that itself often glistens with nectar-like liquid (Fig. 2C–2D, 3, 4E, 10C–10D, 13D, 16–17, 22 and 26). We hypothesize that these open, so-called "steliform" (Karremans and Díaz-Morales, 2019), rewarding flowers exhibit low pollinator specificity and are likely pollinated by multiple pollinators. Could this contribute to greater ecological flexibility and the ability to colonize new niches than in species of *Macrophyllae-Fasciculatae* with less open flowers or those producing lower amounts of nectar and, therefore, contribute to the success of the group? Or could

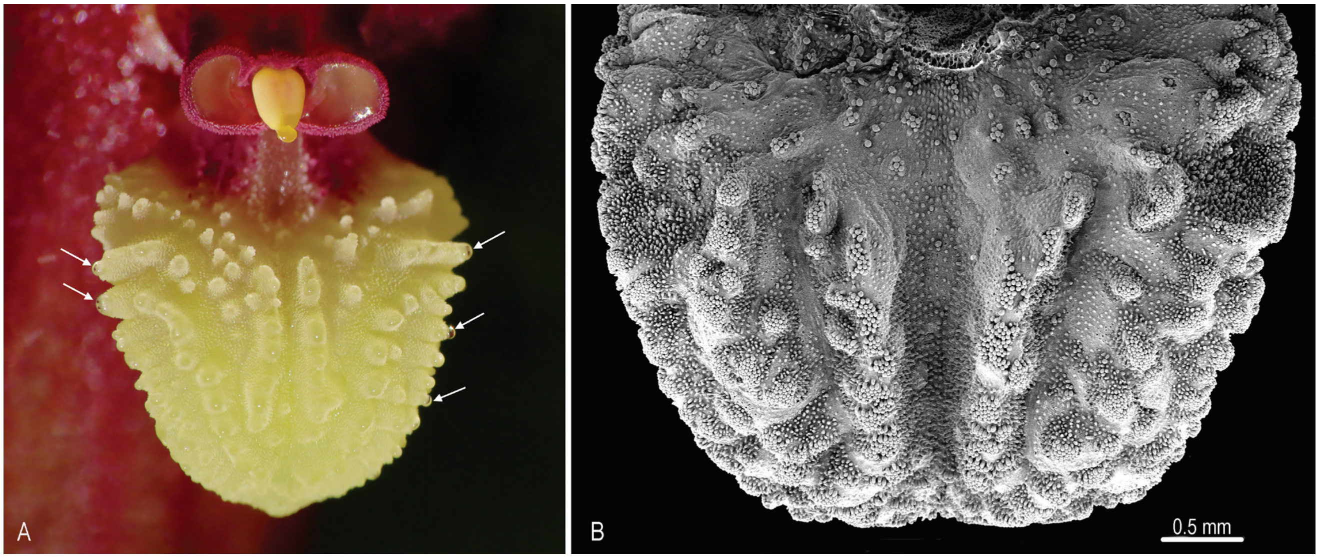

Figure 27. **A**, Lip of *Pleurothallis perijaensis* showing columnar calli and drops of nectar-like liquid (arrows). By David Haelterman; **B**, Scanning electron micrograph of lip of *P. perijaensis*, prepared by Mark Wilson.

the hypothesized low pollinator specificity lead to a higher frequency of cross-pollination and greater speciation through hybridization? To date, the possible role of hybridization as driver of rapid diversification in Neotropical floras has been understudied (Givnish et al., 2015; Schley et al., 2022). It is quite possible, however, that hybridization has played a significant role in speciation in *Pleurothallis* and indeed, botanists are starting to recognize and describe specimens in *Macrophyllae-Fasciculatae* as probable natural hybrids (Pupulin et al., 2021).

Future studies in this group include a description of several additional new species in the *Pleurothallis cardiostola-P. lilijae* complex; biogeographic analyses of distribution of the entire species complex; sequencing the nuclear internal transcribed spacer (nrITS) region of these species; analyses of the sugar composition of the nectar-like liquid on the lip and the glenion using liquid chromatography-mass spectrometry; and analyses of the floral volatiles by gas chromatography-mass spectrometry.

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MOLECULAR ANALYSES PLACE THE GENUS *KERAUNEA* OUTSIDE CONVOLVULACEAE

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Abstract. The genus *Keraunea* was recently described in the Convolvulaceae Juss. family. Two species are currently recognised, both from Brazil. Molecular sequence data using three commonly applied DNA markers (*matK*, *rbcL* and the *nuclear ribosomal Internal Transcribed Spacer*) show that neither species is correctly placed in Convolvulaceae but indicates that the type, *K. brasiliensis*, should be placed in Malpighiaceae despite several morphological anomalies. The second species, *K. capixaba*, should be placed in Ehretiaceae. Given the surprising nature of these results, further studies are recommended before formal reclassification of these two taxa is made.

Keywords: Brazil, Convolvulaceae, Ehretiaceae, Malpighiaceae, Neotropics, systematics

Keraunea Cheek & Sim.-Bianch. is a genus endemic to Brazil initially described in the family Convolvulaceae (Cheek and Simão-Bianchini, 2013). The genus includes two accepted species: *Keraunea brasiliensis* Cheek & Sim.-Bianch., the type species described from the Brazilian state of Bahía with a paratype from Minas Gerais (Cheek and Simão-Bianchini 2013), and *K. capixaba* Lombardi described from Espirito Santo (Lombardi, 2014). A few additional specimens have subsequently been ascribed to these two species, all of them from the same states where the species were first collected (see, e.g., records in GBIF: https://doi.org/10.15468/dl.e9wrys). In this article, we report the results of our study of images and herbarium specimens together with phylogenetic analyses of DNA sequence data sampled from type specimens of both species, which demonstrate the genus is misplaced in Convolvulaceae.

As part of our ongoing investigations of American Convolvulaceae (Wood, 2013; Wood et al., 2015; Muñoz-Rodríguez et al., 2019; Wood et al., 2020; Wood and Clegg, 2021), we came across high-resolution images of the type specimens of both *Keraunea brasiliensis* (K000979156) and *K. capixaba* (SP003725) available via JSTOR plants, as well as images of additional specimens available via the Reflora portal (http://reflora.jbrj.gov.br/reflora/herbarioVirtual). These specimens immediately attracted our attention because they did not resemble any American Convolvulaceae we have studied to date. The drawings and photographs in the original publications (Cheek and Simão-Bianchini, 2013, fig. 1; Lombardi 2014, fig. 1 and 2) are not an especially good fit with the morphology of Convolvulaceae, and there are some discrepancies between our observations of the types and the original descriptions and illustrations. Moreover, as indicated in the original publication (Cheek and Simão-Bianchini 2013), *Keraunea brasiliensis* resembles the Convolvulaceae genus *Neuropeltis* Wall., and that is the reason why *Keraunea* was originally placed in Convolvulaceae. However, *Neuropeltis* is restricted to the Palaeotropics, with a disjunct distribution in East Tropical Africa (ca. 9 species) and South East Asia and India (4 species). (Breteler, 2010; POWO 2020). Further, preliminary molecular analyses using DNA barcodes (see below) confirmed the position of *Neuropeltis* in Convolvulaceae but placed the *Keraunea* specimens outside this family (Fig. 1).

To further explore this question, we studied all *Keraunea brasiliensis* collections cited in the original publication: *L. Passos 5263* (isotype K000979156), *J. A. Lombardi 1819*, and *J. A. Lombardi 2107*. We studied these collections directly at the Kew herbarium or via high-resolution images in virtual herbaria. Similarly, we studied three *K. capixaba* collections listed in the original publication: *G. S. Siqueira 891* (isotype SP476897), *D. A. Folli 7117*, and *G. S. Siqueira 893*. To the best of our knowledge, the *Keraunea* species had not yet been sequenced when we began our study, or the sequences had not been made available (cf. Simões et al., 2022). Thus, in addition to our morphological studies, we also sampled and sequenced three of these collections to incorporate them in the Convolvulaceae phylogenies generated as part of our ongoing systematic studies of the family (Muñoz-Rodríguez et al., 2019).

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[7] Supplementary files at: https://figshare.com/projects/Ipomoea_Project_-_Oxford_University_-_Keraunea_Data/153432.

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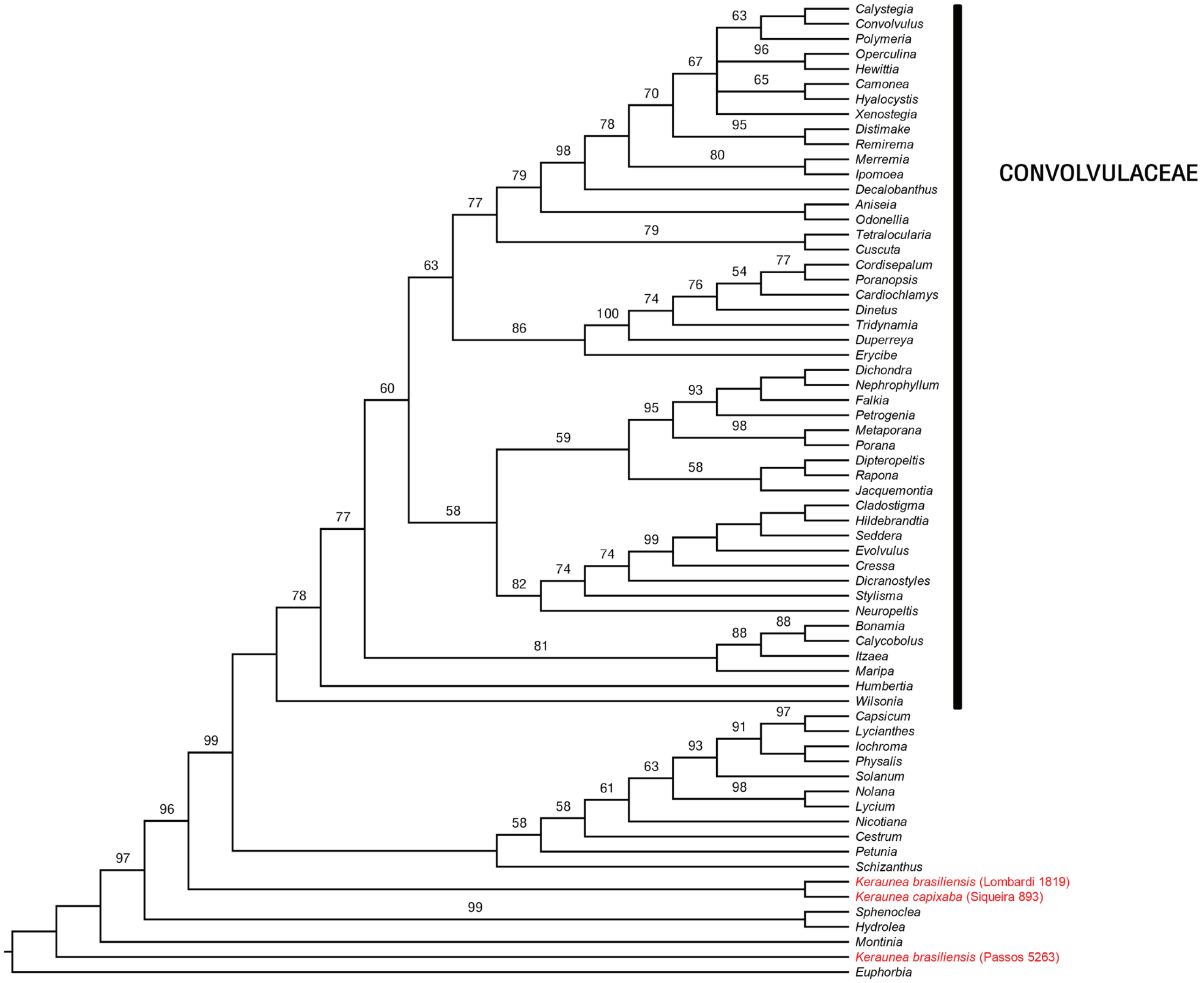

FIGURE 1. Maximum Likelihood phylogeny showing the position of the three specimens newly sequenced in this study (in red) outside Convolvulaceae. Phylogeny inferred using the chloroplast *rbcL+matK* regions; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. The black bar indicates the position of Convolvulaceae.

MATERIALS AND METHODS

We sequenced two *Keraunea brasiliensis* specimens (the isotype *Passos 5263* and the paratype *Lombardi 1819*) and one *K. capixaba* specimen (the paratype *G. S. Siqueira 893*). We sequenced three DNA markers: the *nuclear ribosomal Internal Transcribed Spacer* (*nrITS*) (*Passos 5263* and *Lombardi 1819*), and the chloroplast *matK* (all specimens) and *rbcL* regions (*Passos 5263*). We extracted total genomic DNA using the Qiagen DNEasy extraction kit, and used primers AB101 and AB102 for *nrITS* amplification (Douzery et al., 1999); 413f-1 and 1227r-3 for *matK* amplification (Heckenhauer, Barfuss, and Samuel, 2016); and rbcL-1F and rbcL-1460R for *rbcL* amplification (Fay et al., 1998; Olmstead et al., 1992). In all cases, we used a reagent volume of 15 μl (7.3 μl H_2O, 3 μl buffer, 0.7 μl $MgCl_2$, 0.3 μl of each primer, 0.5 μl dNTPs, 1 μl BSA, 0.4 μl Taq polymerase, 1.5 μl sample DNA) for PCR amplification and standard PCR conditions (5' at 80˚C; 30 cycles of 1' at 95˚C, 1' at 50˚C, and 4' at 65˚C and a final stage of 4' at 65˚C). We cleaned the PCR reactions using the GeneJET PCR purification kit. We sequenced the samples using Sanger sequencing at Source Biosciences in Cambridge, United Kingdom, with the same primers used in the PCR. Furthermore, in light of our results we repeated both DNA extractions and amplifications in a different laboratory, with identical results. *nrITS* samples generated in this study are available on GenBank (OP034980, OP034981); *rbcL* and *matK* sequences are available as supplementary material.

To place the *Keraunea* samples in a phylogenetic context, we first queried all our sequences against the NCBI database using BLAST (Madden, 2002) and inferred an *rbcL+matK* phylogeny (TVM+F+G4) including representatives of all genera in Convolvulaceae as well as several other genera in Solanales. In light of our results (see below), we also inferred a *matK* Angiosperm phylogeny using DNA sequence data previously published from across the Angiosperm diversity (Baldwin et al., 1995; Hilu et al., 2003). All phylogenies inferred in this study followed the same methodology, detailed next, with substitution models indicated in each case. We aligned the sequences using MAFFT v.7.310 (Katoh and Standley, 2013, 2016) and used Geneious v.9.1.8 to remove all columns in the alignments with 90% or more gaps. We then inferred a Maximum Likelihood phylogeny using IQ-Tree (Nguyen et al., 2015) with automatic model selection using ModelFinder (Kalyaanamoorthy et al., 2017) and 1,000 bootstrap replicates (-czb -bb 1000 -alrt 1000). The substitution model was selected based on the Bayesian Information Criterion. In the resulting phylogenies we collapsed all nodes with less than 50% bootstrap support (-minsup 0.5).

Results and Discussion

Both BLAST and phylogenetic analysis indicate the two *Keraunea brasiliensis* specimens and the one *K. capixaba* specimen sequenced do not belong in Convolvulaceae (Fig. 2). Furthermore, the Angiosperm phylogenies including most orders in Angiosperms (TVM+F+I+G4) indicate that the two *Keraunea* species are not closely related to each other: *K. brasiliensis* is nested within Malpighiaceae Juss. (order Malpighiales) and *K. capixaba* is nested within Ehretiaceae Mart. (order Boraginales). In other words, the genus *Keraunea* is polyphyletic with its two constituent species apparently belonging to Malpighiaceae and Ehretiaceae rather than Convolvulaceae as originally classified. The sequences we obtained were of high quality and showed no evidence of contamination, as would be expected since the labs where the DNA was processed had not sequenced any material of these families. We subsequently inferred densely-sampled phylogenies of the two families where these specimens were nested, Malpighiaceae and Ehretiaceae, and the results for each specimen are described below.

Passos 5263, the isotype of Keraunea Brasiliensis

All three regions (*matK*, *rbcL* and *nrITS*) amplified for *Passos 5263*, the isotype of *Keraunea brasiliensis*, indicate it is nested within the family Malpighiaceae (Fig. 2). To further explore its position within the family, we inferred three species-level Malpighiaceae phylogenies—*matK* (TVM+F+G4), *matK*+*rbcL* (TVM+F+I+G4), and *nrITS* (TIM2+F+I+G)—with GenBank data and including representatives of all genera accepted in the most recent review of the family (Davis and Anderson, 2010) (Supplementary File 1). We used specimens of several genera as outgroups following Davis and Chase (2004), Wurdack and Davis (2009) and Cai et al. (2019): *Bergia* L. (Elatinaceae), *Elatine* L. (Elatinaceae), *Bhesa* Buch.-Ham. ex Arn. (Centroplacaceae), and *Euphorbia maculata* L. (Euphorbiaceae), with *E. maculata* used to root the phylogenies. The *matK* phylogeny places *Passos 5263* in a clade with *Mascagnia affinis* W.R. Anderson & C. Davis, *M. cordifolia* (A. Juss.) Griseb., and *M. dissimilis* C.V. Morton & Moldenke, all three species also present in Brazil[8] (Fig. 3a) and corresponding to the core/true *Mascagnia* rather than the many recent segregates of this former polyphyletic genus (Anderson and Davis, 2005a, 2005b, 2007, 2012, 2013). This clade of three species is also retrieved, with higher support, in Davis and Anderson (2010), a phylogeny based on *matK* and *rbcL* plus two additional regions not sequenced in our study, chloroplast *ndhF* and nuclear *PHYC*.

The *nrITS* phylogeny (Fig. 3b) places *Passos 5263* in a clade with three *Mascagnia* species widely distributed in South America: *M. australis* C.E. Anderson, *M. divaricata* (Kunth) Nied. and *M. sepium* (A. Juss.) Griseb. Again, *M. australis* and *M. divaricata* are within the same *Mascagnia* clade in Davis and Anderson (2010), whereas *M. sepium* was not included in that study but is also taxonomically recognised as a member of core/true *Mascagnia*.

In summary, our molecular results strongly suggest *Passos 5263* is a Malpighiaceae, most likely a *Mascagnia*, and would therefore justify transferring the species *Keraunea brasiliensis*—and therefore the genus *Keraunea pro parte*—to this family. However, these molecular results are particularly surprising because *K. brasiliensis* does not exhibit the canonical "Malpighiaceae morphology". Members of Malpighiaceae usually present simple, opposite leaves with T-shaped, unicellular trichomes and often inter-petiolar stipules, oil glands present on the sepals and/or extra-floral glands on the petiole or leaf blade, and five free, usually clawed petals (Davis, Anderson, and Donoghue, 2001; Anderson, 2004). In contrast, leaves in *Passos 5263* seem to be alternate, and oil glands cannot be readily observed on this specimen's sepals. Moreover, this specimen seems to have a sympetalous perianth, the branching of the inflorescence is alternate, and the fruit is very peculiar if Malpighiaceae. In addition, although the molecular results reported here are robust, considering the strong morphological differences between *K. brasiliensis* and the members of Malpighiaceae we hesitate to formally propose this taxonomic change. We think further study is advisable before *Keraunea brasiliensis* can be re-classified. An additional trait to explore is the three carpellate ovary with a single locule per ovule as is found in Malpighiaceae. Finally, we have not seen the holotype (deposited at Sao Paulo herbarium (SP) and not yet digitised) and it may be different in whole or in part from the isotype at Kew. In conclusion, it seems clear that *Keraunea brasiliensis* is not a Convolvulaceae and future studies should be able to determine its generic placement within Malpighiaceae.

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[8] Adding the chloroplast *rbcL* region slightly improves phylogenetic resolution, but the only two *Mascagnia* (Bertero ex DC.) Bertero species (*M. adamsii* and *M. sepium*) that have data available for both *matK* and *rbcL* seem to be only distantly related to *Passos 5263*. See Supplementary File 3.

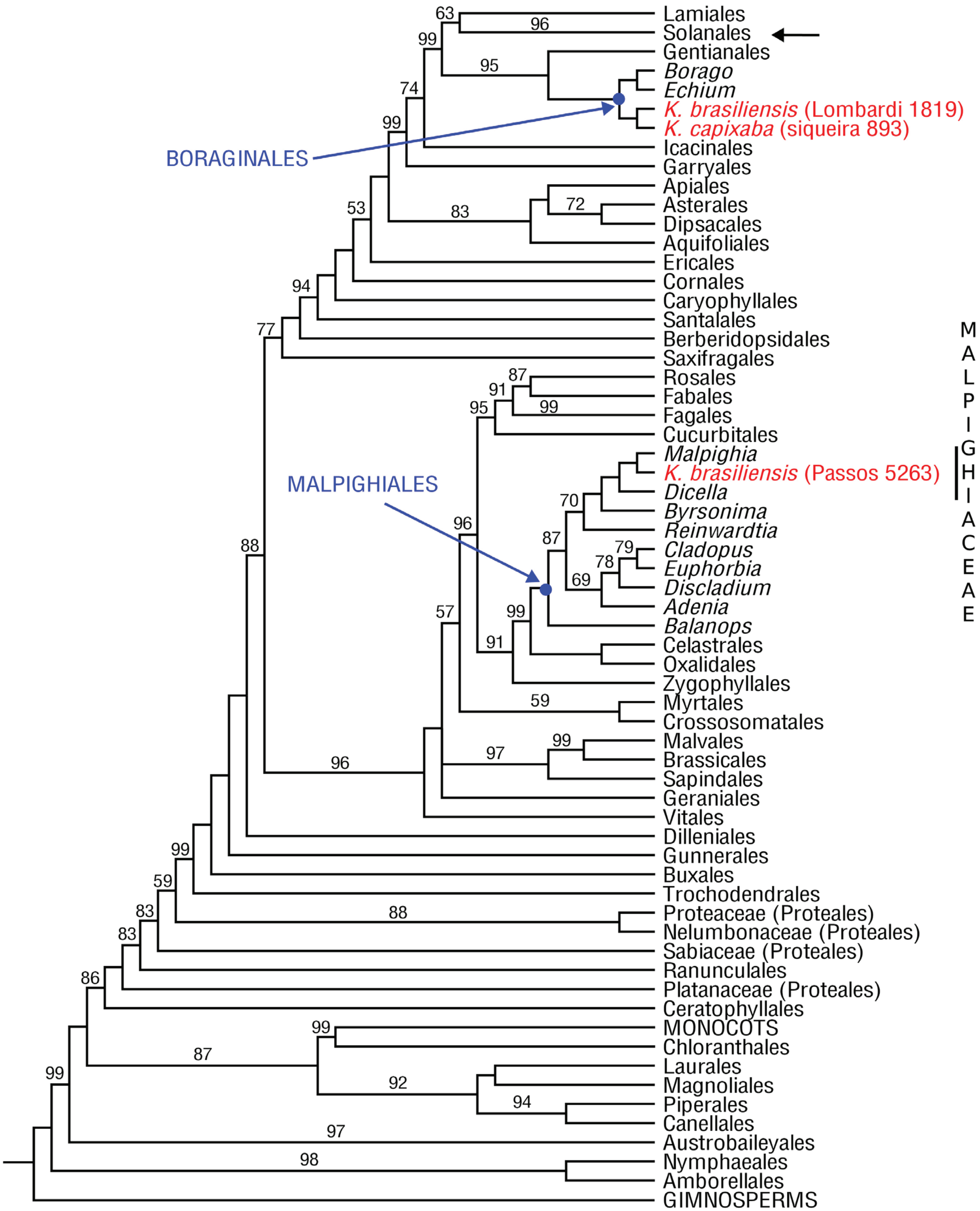

FIGURE 2. Summary Maximum Likelihood Angiosperm phylogeny showing the position of the three specimens newly sequenced in this study (in red). Phylogeny inferred using the chloroplast *matK* region; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. *Passos 5263* (*Keraunea brasiliensis*) is nested in Malpighiales; *Lombardi 1819* (*K. brasiliensis* Cheek & Sim.-Bianch.) and Siqueira 893 (*K. capixaba* Lombardi) are nested in Boraginales. The blue arrows indicate the position of Malpighiales and Boraginales; the black arrow indicates the position of Solanales, where the family Convolvulaceae belongs. See complete phylogeny in Supplementary File 2.

FIGURE 3. **A–B**. Summary Maximum Likelihood Malpighiaceae phylogenies showing the position of the *Passos 5263* specimen of *Keraunea brasiliensis* Cheek & Sim.-Bianch. (in red). Phylogenies inferred using A. the chloroplast *matK* region and B. the *nrITS* region; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. Passos 5263 (*Keraunea brasiliensis*) is nested in *Mascagnia* (Bertero ex DC.) Bertero in both phylogenies. See complete phylogenies in Supplementary File 3.

Lombardi 1819 and Siqueira 893 specimens

We also sequenced a paratype of *Keraunea brasiliensis*—*Lombardi 1819* (K) and one of *K. capixaba*—*Siqueira 893* (K). We sequenced *matK* and *nrITS* for *Lombardi 1819* and *matK* for *Siqueira 893*. We first checked our sequences against the GenBank database using BLAST and incorporated the *matK* sequences to the Angiosperm phylogenies aforementioned (Fig. 2). Interestingly, these two paratype specimens are nested in Boraginales and appear to be closely related to *Ehretia* P. Browne, *Halgania* Gaudich. and other genera in the family Ehretiaceae, recently segregated from Boraginaceae Juss. (Luebert et al., 2016). This was confirmed with a *matK* (TVM+F+G4) phylogeny of all accepted genera in Ehretiaceae (cf. Gottschling and Hilger 2004; Gottschling et al. 2014) and the other families in the order (Fig. 4a). In this *matK* phylogeny, both *Keraunea* specimens (*Lombardi 1819* and *Siqueira 893*) are most closely related to each other, and sister to a monophyletic genus *Ehretia*, with high support. The close relationship between *Lombardi 1819* and *Siqueira 893* is not surprising as these two specimens are remarkably similar morphologically.

A densely sampled *nrITS* phylogeny of Ehretiaceae (GTR+F+I+G4) places *Lombardi 1819* sister to monophyletic *Cortesia cuneifolia* Cav. (= *Ehretia cortesia* Gottschling), a genus recently segregated by Gottschling et al. (2014). This clade is sister to a monophyletic *Halgania* Gaudich., also with moderately high support (Fig. 4b). It is important to note that *Cortesia* Cav. and *Halgania* have not been sequenced for *matK* and therefore they are not included in the *matK* phylogeny.

The results of both *nrITS* and *matK* phylogenies presented here are congruent and show the two *Keraunea* collections *Lombardi 1819* and *Siqueira 893* are most closely related to *Cortesia, Halgania* and *Ehretia* P. Browne. Again, although our molecular results are robust, we think a comprehensive, complete study of *Keraunea* is needed before *Keraunea capixaba* and at least one of the *K. brasiliensis* paratypes can be re-classified. It seems clear that *K. capixaba* is also not a Convolvulaceae, and future studies should be able to confirm its placement in the right family, most likely Ehretiaceae.

Here, we have shown that *Keraunea brasiliensis* and *K. capixaba* comprise a mixture of specimens from different Angiosperm families not Convolvulaceae. We have refrained from proposing formal taxonomic changes as we think a comprehensive study of all material assigned to *Keraunea* is necessary, including the broader context of the respective families where the two species belong. It is unlikely that the mere addition of more molecular data will clarify the position of these two species, at least for their family designations, unless such a study is accompanied by a comprehensive taxonomic study of herbarium and living material. The results of our study highlight several important aspects of contemporary plant systematics. First, the inadequate role of gross morphology in placing some material in the correct family. Second, the ability of molecular sequence data to quickly place difficult specimens in the correct family. Third, the large fraction of taxa that still remain to be classified and fully understood.

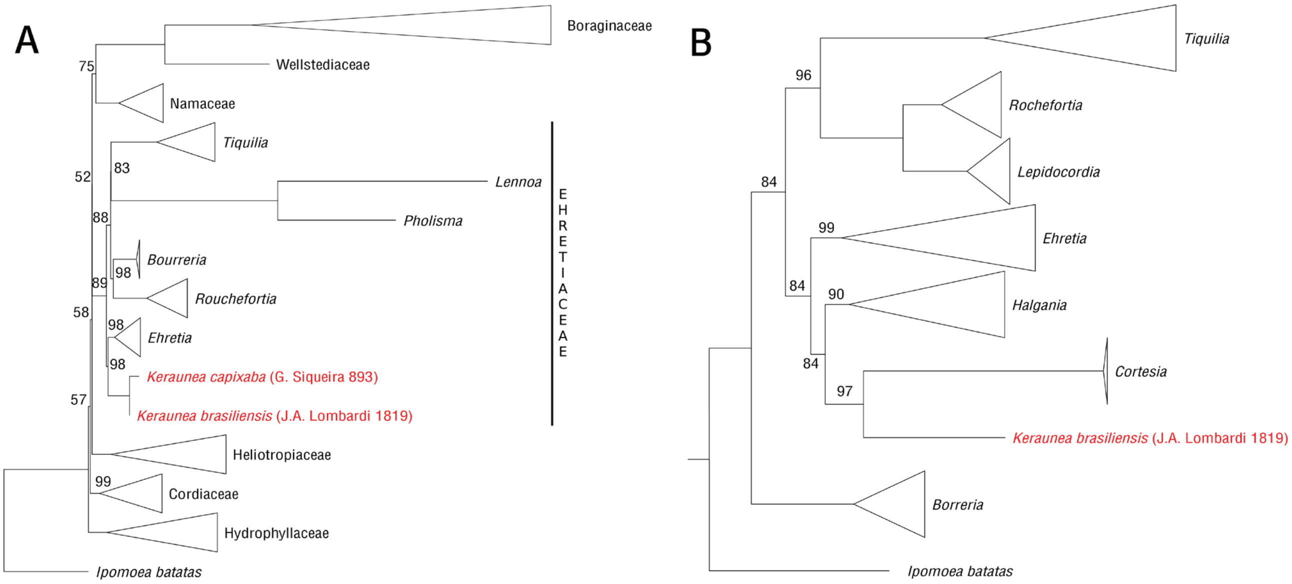

FIGURE 4. **A–B**. Summary Maximum Likelihood phylogenies showing the position of *Keraunea brasiliensis* Cheek & Sim.-Bianch. specimen *J.A. Lombardi 1819* and *K. capixaba* Lombardi specimen *G. Siqueira 893* in Ehretiaceae. A. Boraginales phylogeny inferred using the chloroplast *matK* region. B. Ehretiaceae phylogeny inferred using the *nrITS* regions. Triangles represent monophyletic family and/or genera with multiple specimens; numbers on the branches represent IQ-Tree Ultrafast Bootstrap support values; branches without numbers received 100% support. In A., the two specimens newly sequenced in this study, *Lombardi 1819* and *Siqueira 893*, are most closely related to each other and sister to a monophyletic genus *Ehretia* P. Browne, with high support. In B., *Lombardi 1819* is most closely related to a monophyletic genus *Cortesia* Cav., which is not included in A. See complete phylogenies in Supplementary file 4.

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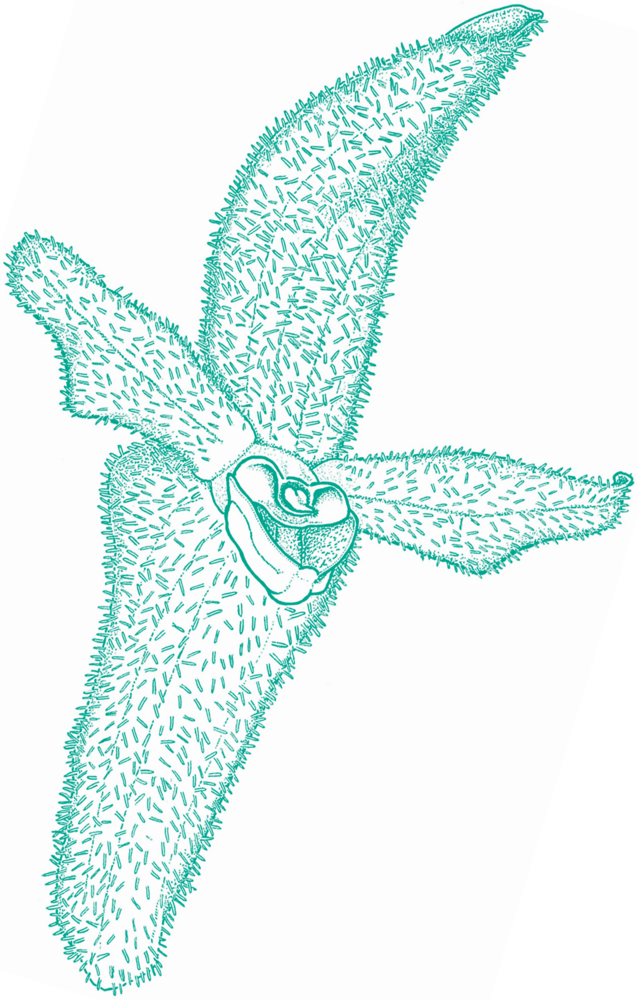

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