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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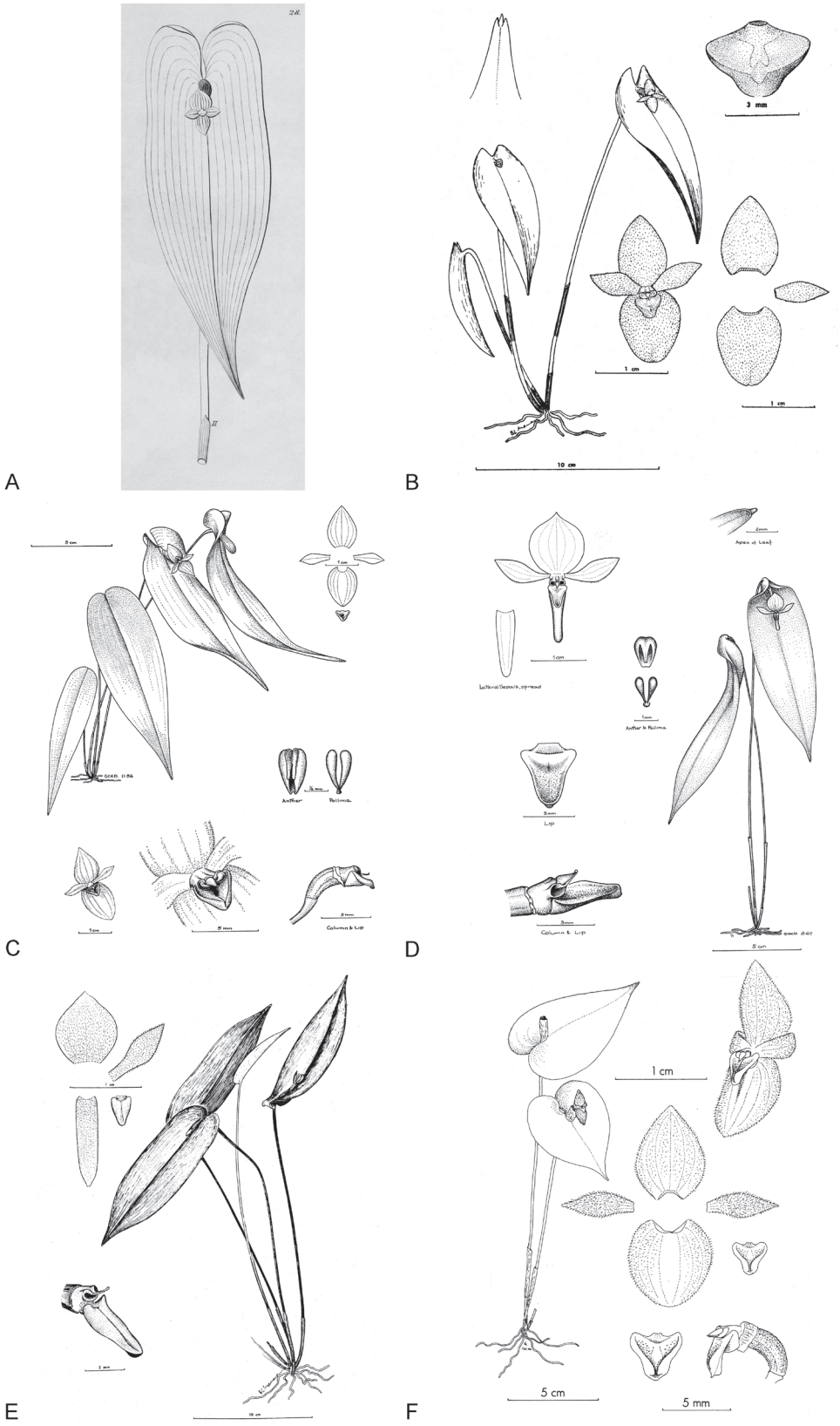

FIGURE 1. *Pleurothallis* species. **A**, *Pleurothallis cardiostola* Rchb.f. by Lindley (Reichenbach, [1858] 1854: Fig. 28II); **B**, *Pleurothallis cardiostola* from Foldats (1970: 229); **C**, *Pleurothallis cardiostola* from Garay and Dunsterville (1959: 387); **D**, *Pleurothallis lilijae* from 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.

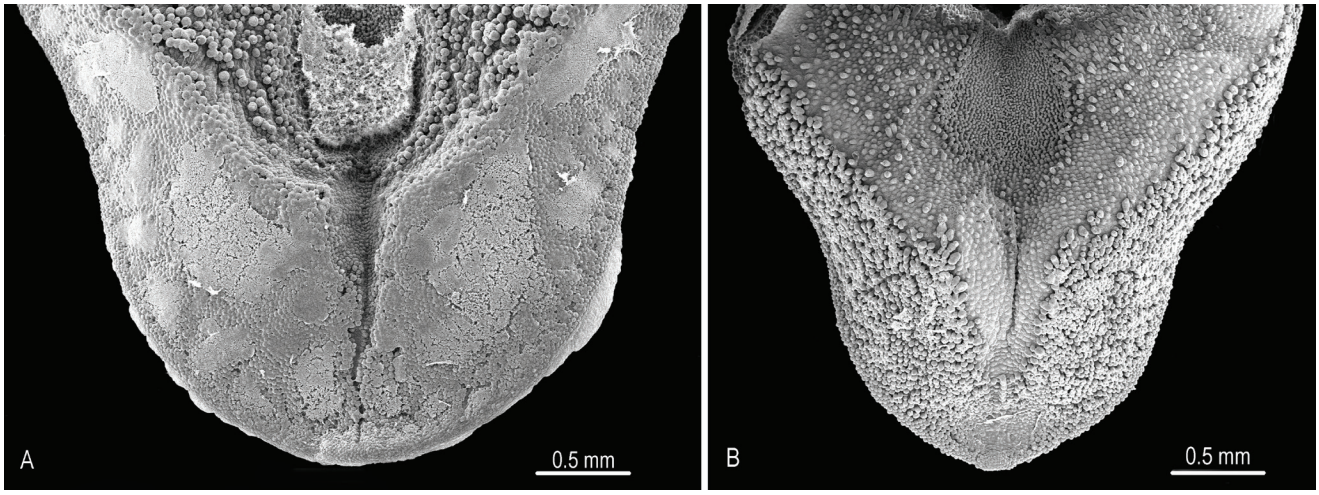

FIGURE 3. Scanning electron micrographs of labellum of **A**, *Pleurothallis cf. cardiostola* PL1228; **B**, *Pleurothallis lanigera* PL1229, by Mark Wilson.

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.

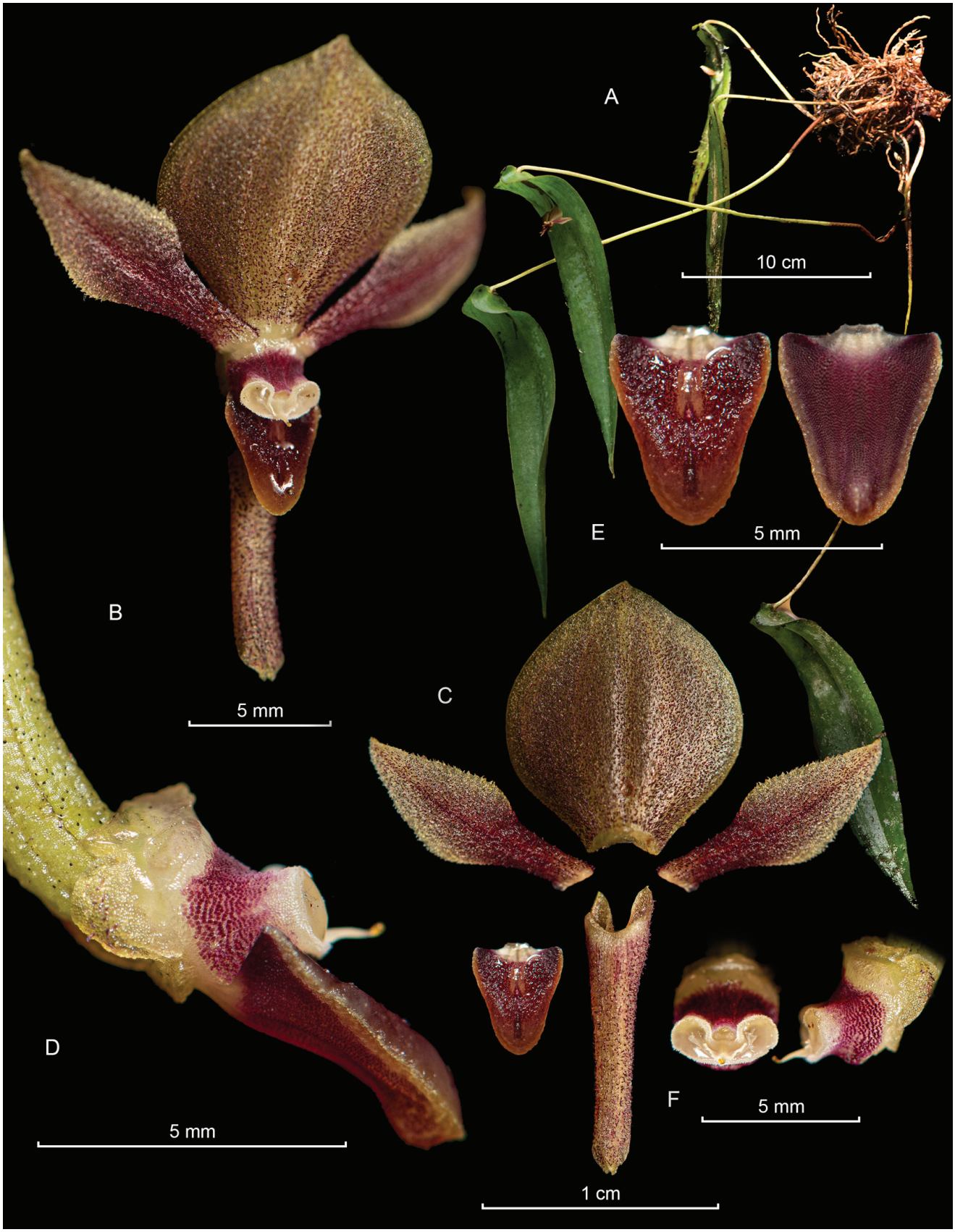

FIGURE 4. Composite digital plate of *Pleurothallis lilijae* from Boyacá, Colombia. **A**, Whole plant; **B**, Whole flower; **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal and ventral view); **F**, Column, stigmatic surfaces and rostellum (front and lateral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

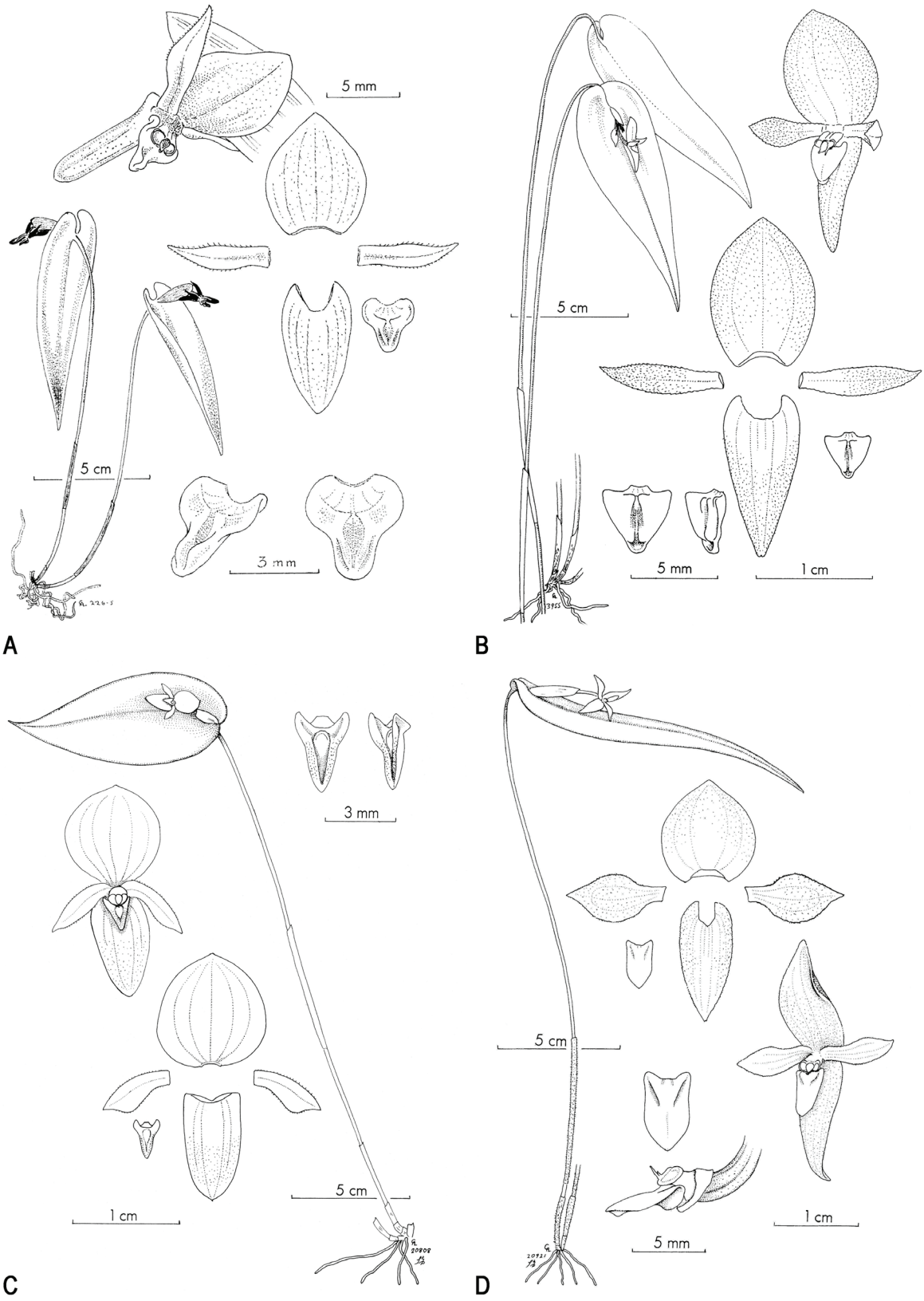

FIGURE 5. Drawings of species morphologically similar to *Pleurothallis lilijae*. **A**, *Pleurothallis alopex* from Luer (2005: 210, Fig. 7); **B**, *Pleurothallis apopsis* from Luer (2005: 211, Fig. 12); **C**, *Pleurothallis diazii* from Luer (2005: 230, Fig. 73); **D**, *Pleurothallis tobarii* from 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 *synsepal*, 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).

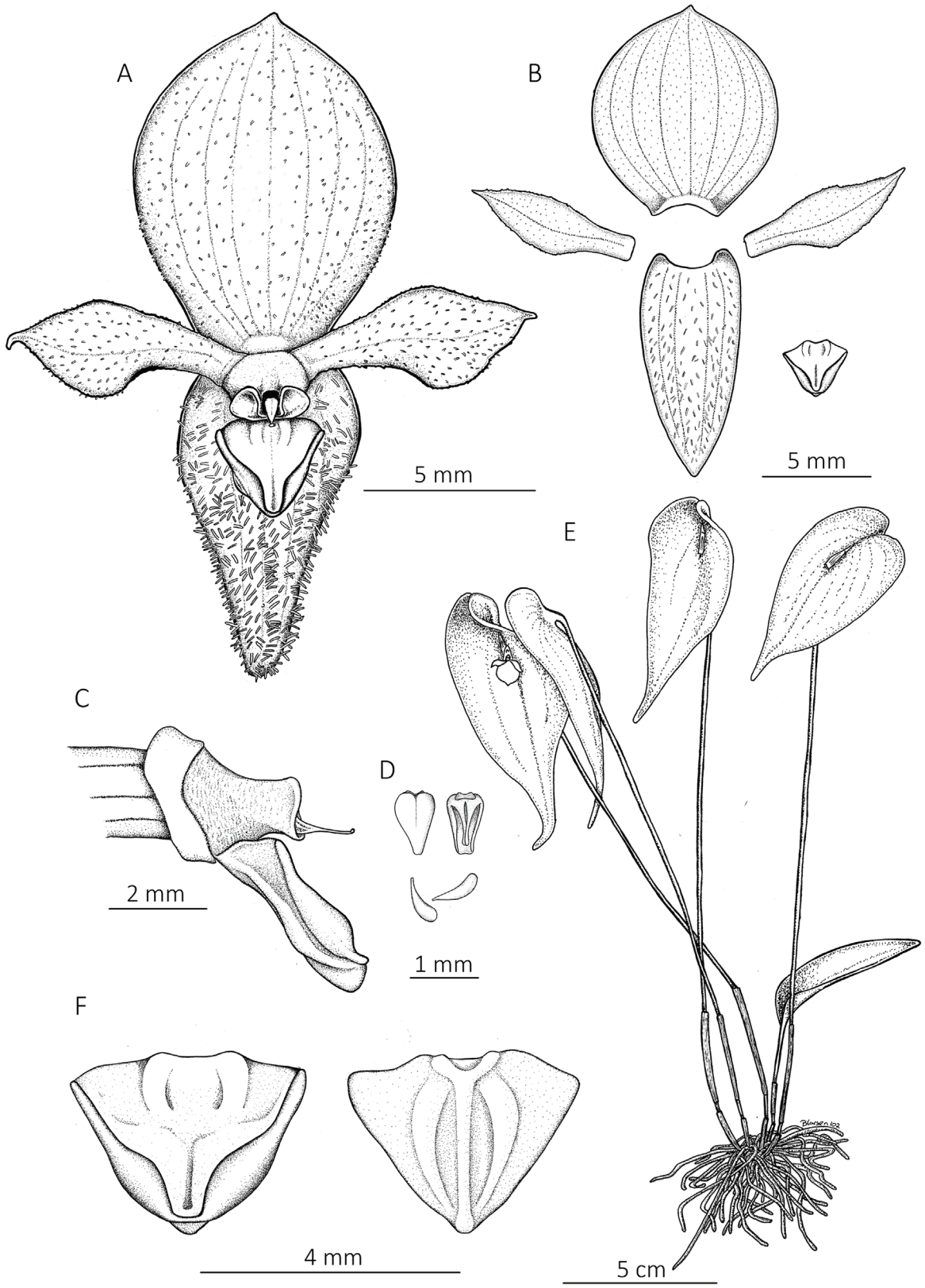

FIGURE 7. Drawing of *Pleurothallis andreaskayi*. **A**, Whole flower (front view); **B**, Floral dissection; **C**, Column and lip (lateral view); **D**, Anther cap and pollinarium; **E**, Whole plant; **F**, Lip (dorsal and ventral views). Prepared from paratype PL1142 by Bruno Larsen.

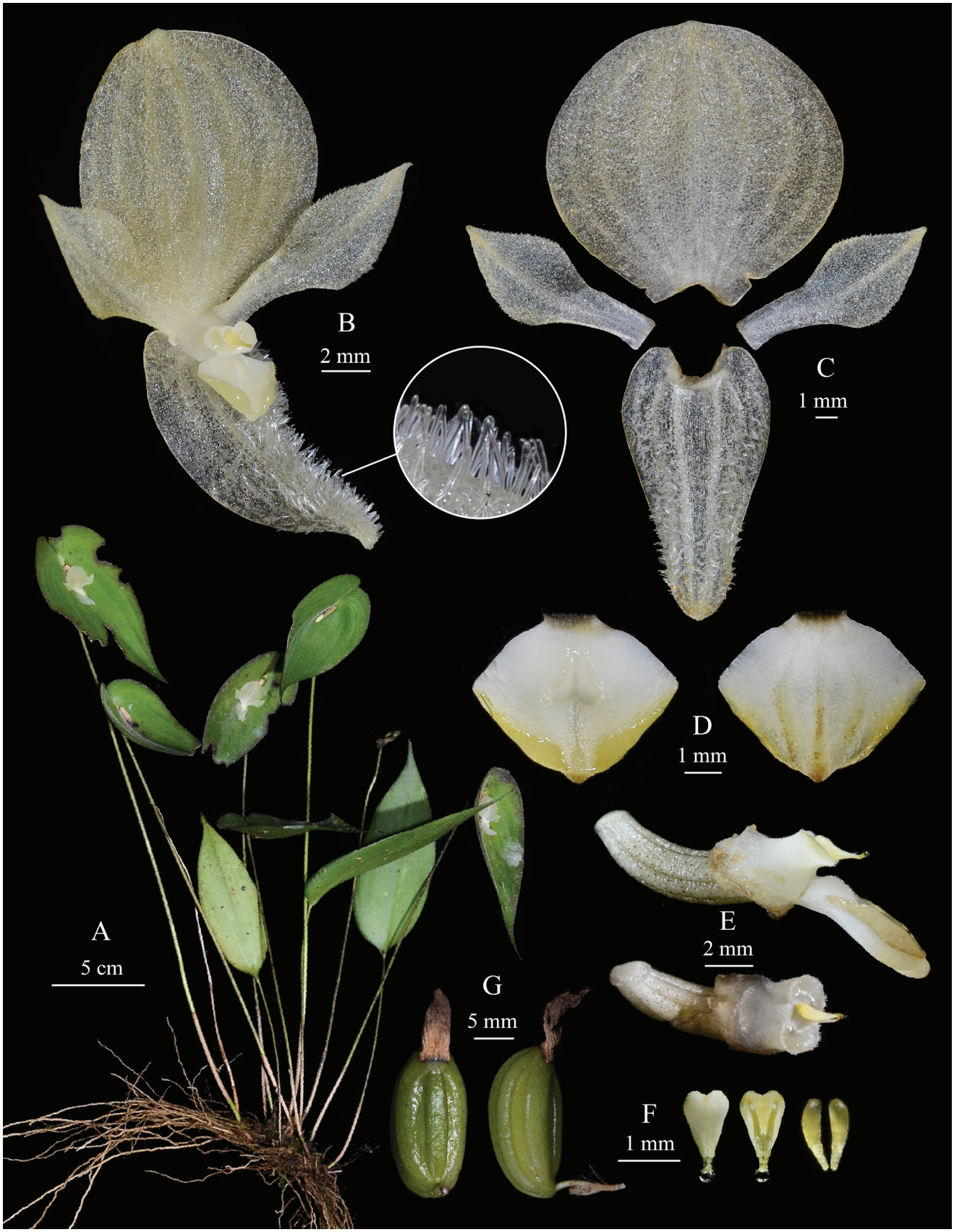

FIGURE 8. Composite digital plate of *Pleurothallis andreaskayi*. **A**, Whole plant; **B**, Whole flower (3/4 view); **C**, Floral dissection; **D**, Lip dorsal and ventral views; **E**, Column and lip; **F**, Pollinarium and anther cap; **G**, capsule. Prepared from the holotype by Henry Garzón Suárez.

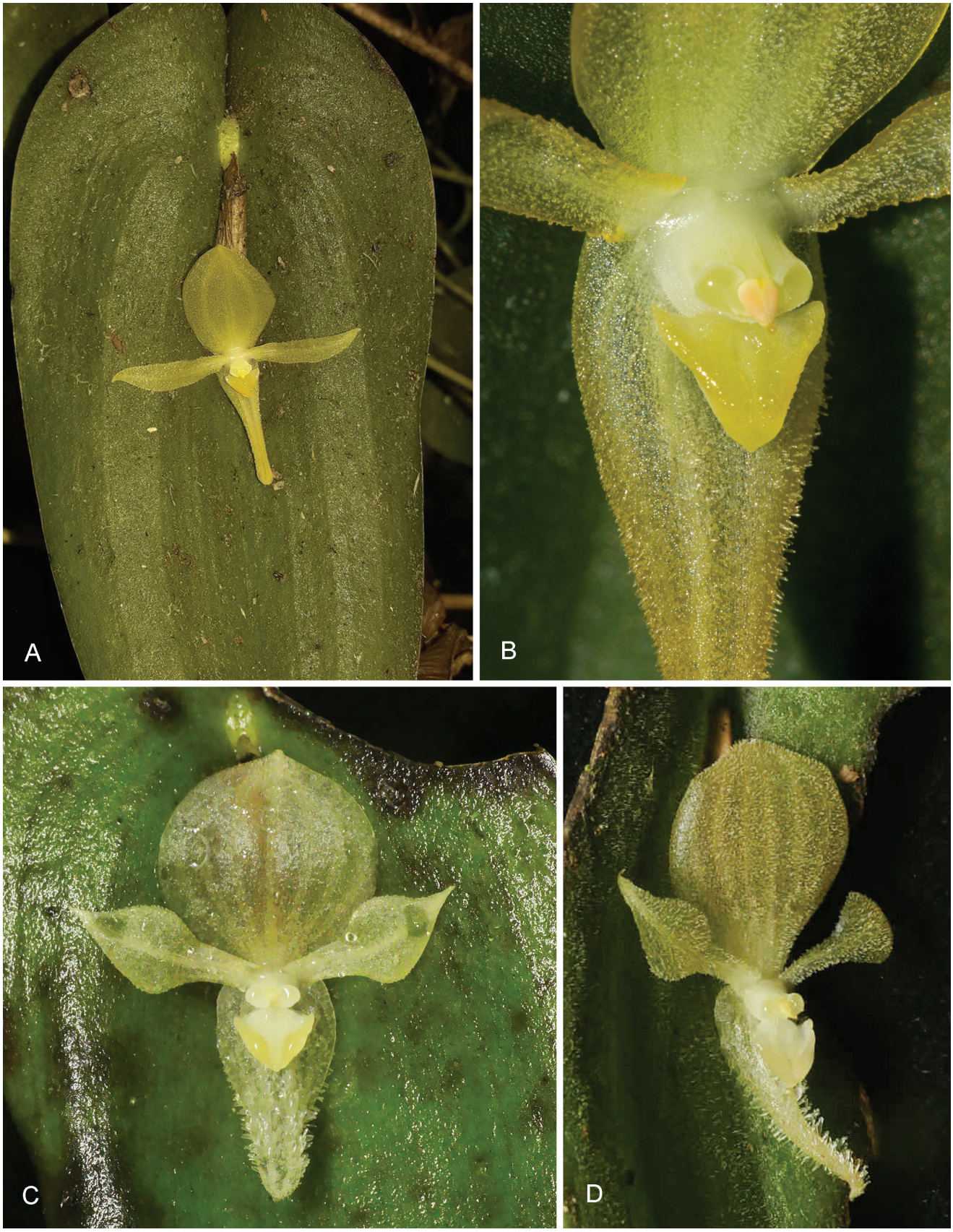

FIGURE 9. **A**, Photograph of *Pleurothallis apopsis* leaf and flower, courtesy of David Torres; **B**, Photograph of flower of *P. apopsis*, courtesy of Kilian Zuchan; **C**, **D**, *Pleurothallis andreaskayi in situ* in Morona Santiago, Ecuador, by Marco Jiménez.

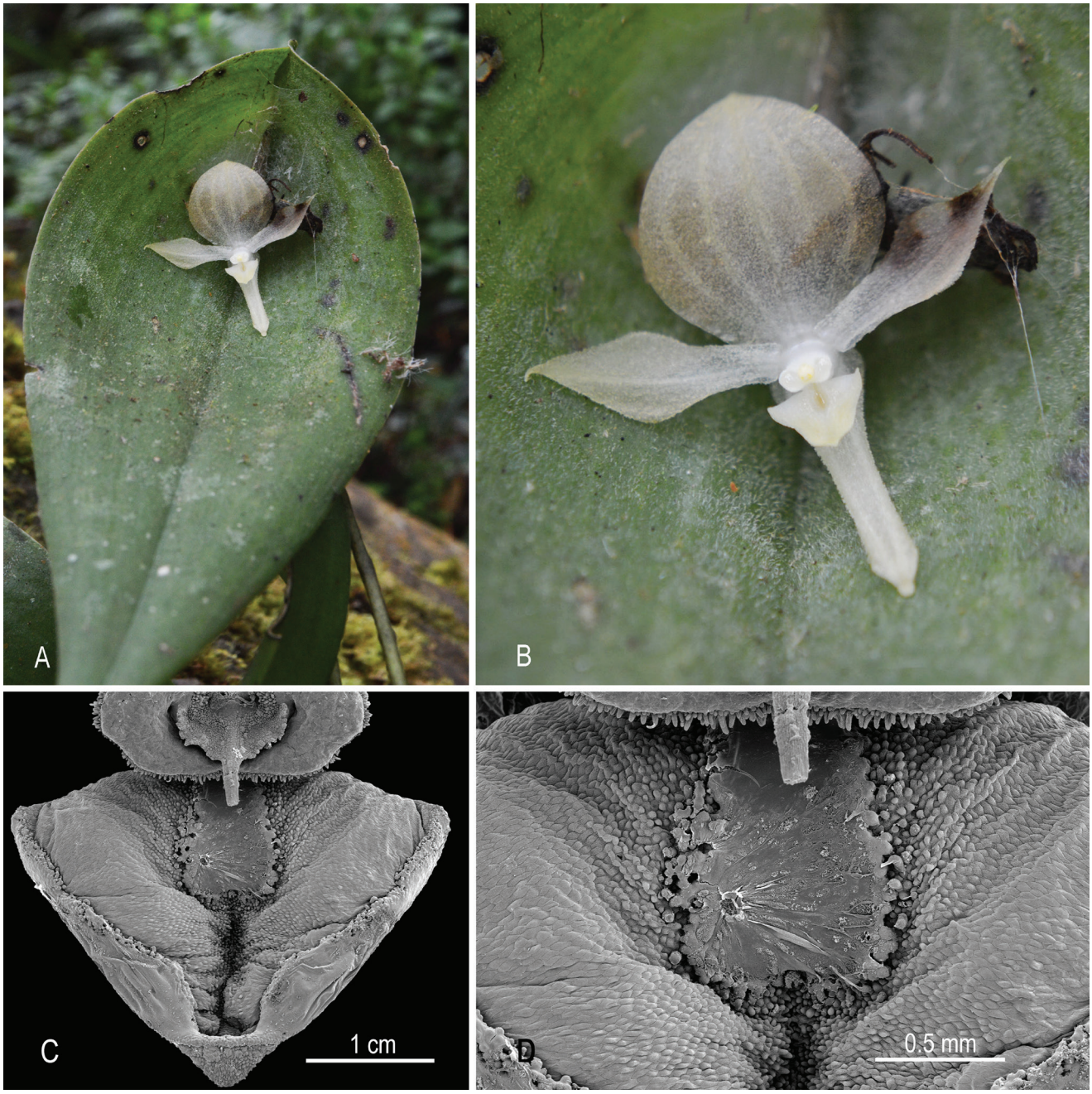

FIGURE 10. **A**, **B**, Photograph of *Pleurothallis andreaskayi in situ* in Cerro el Tablazo, Subachoque, Cundinamarca, Colombia at ca. 2800–3500 m, courtesy of Karen Gil; **C**, **D**, Scanning electron micrographs of *Pleurothallis andreaskayi* **C**, Lip, stigmatic surfaces and rostellum; **D**, 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

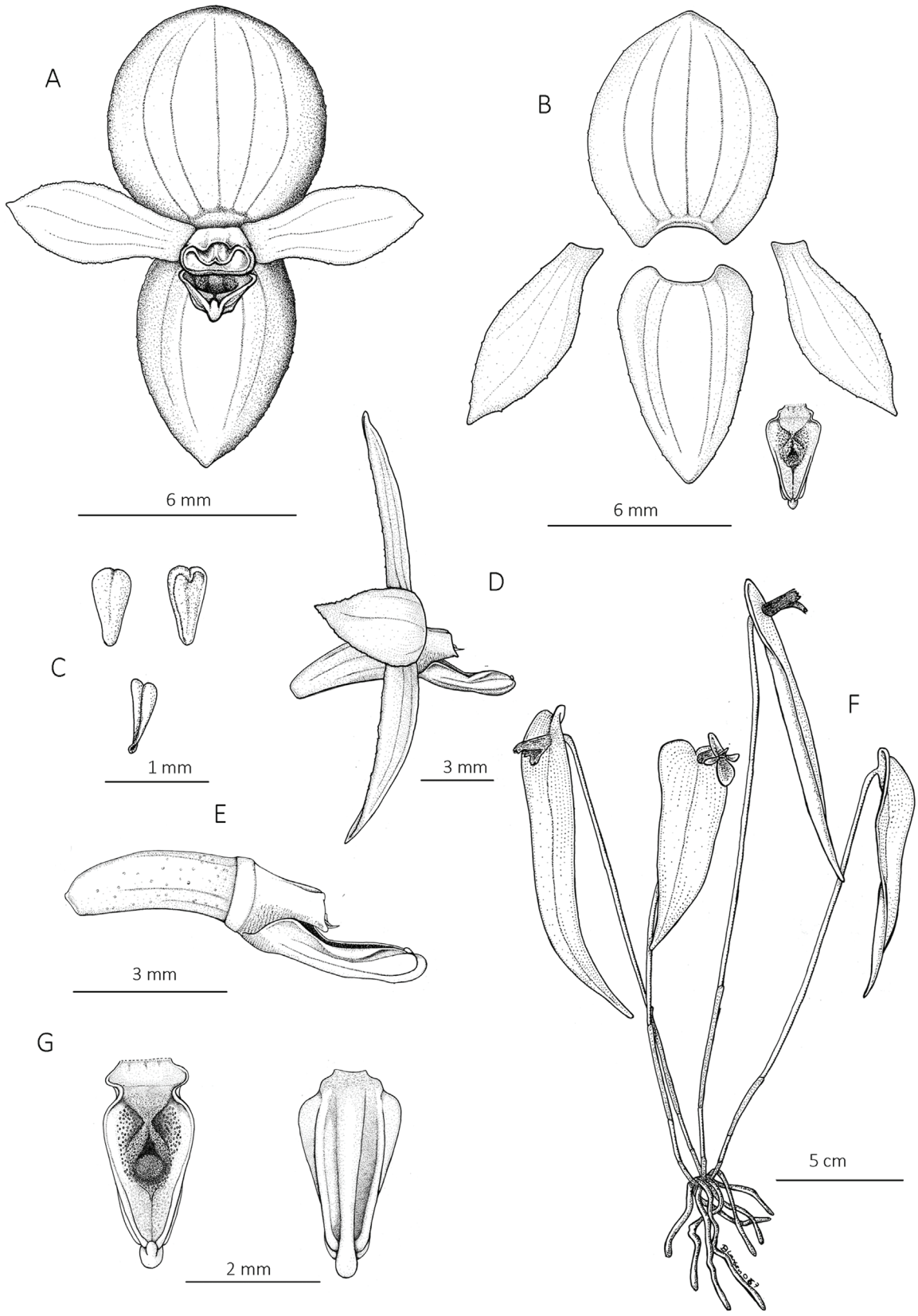

FIGURE 11. Drawing of *Pleurothallis whitteniana*. **A**, Whole flower (front view); **B**, Floral dissection; **C**, Anther cap and pollinarium; **D**, Whole flower (lateral view); **E**, Ovary, column and lip (lateral view); **F**, Whole plant; **G**, Lip (dorsal and ventral views). Prepared from holotype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

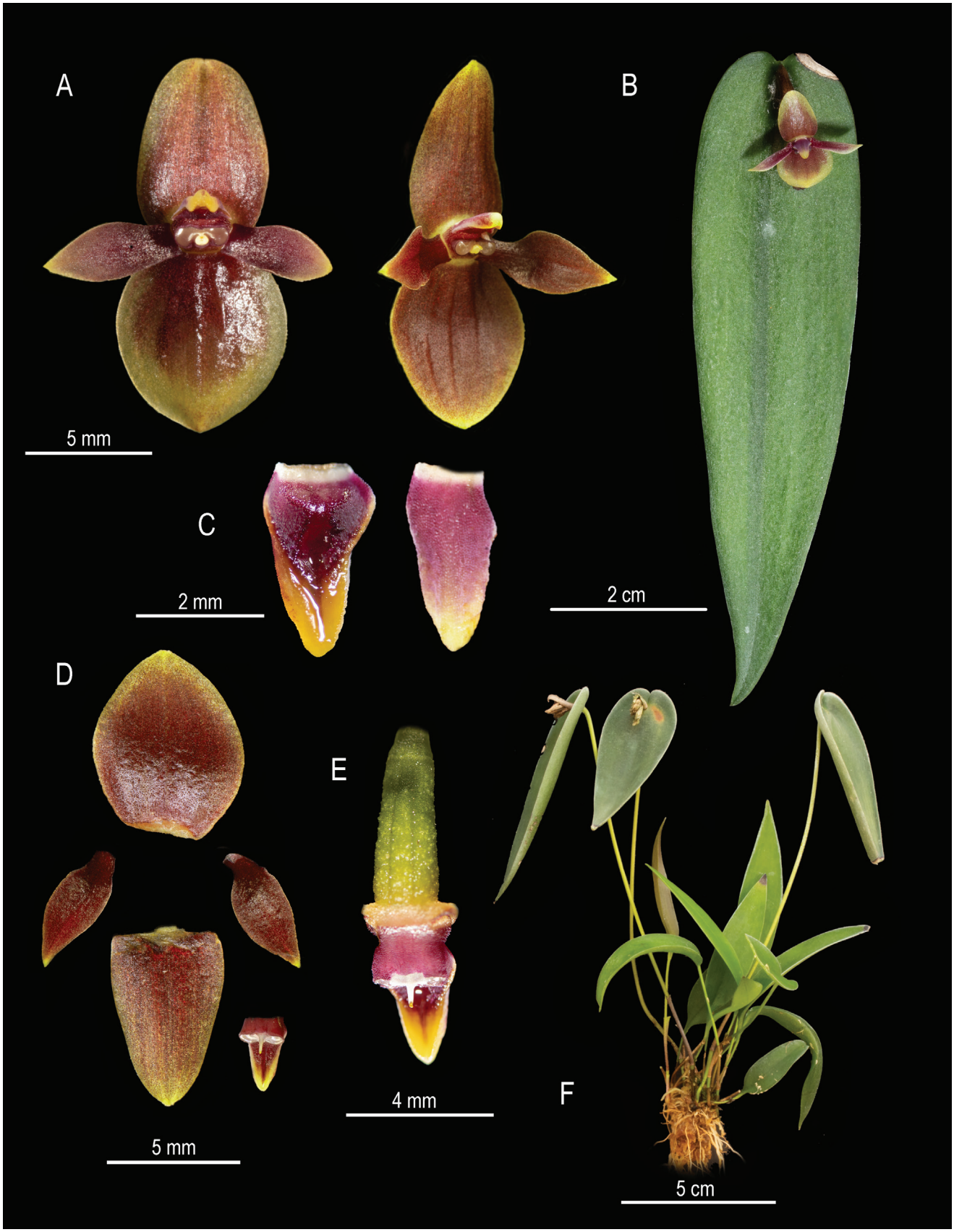

FIGURE 12. Composite digital plate of *Pleurothallis whitteniana*. **A**, Whole flower (front view and 3/4 view); **B**, Leaf and flower; **C**, Lip (dorsal and ventral views); **D**, Floral dissection; **E**, Ovary, column and lip (dorsal view); **F**, Whole plant. Prepared from holotype PL1049 by Mark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

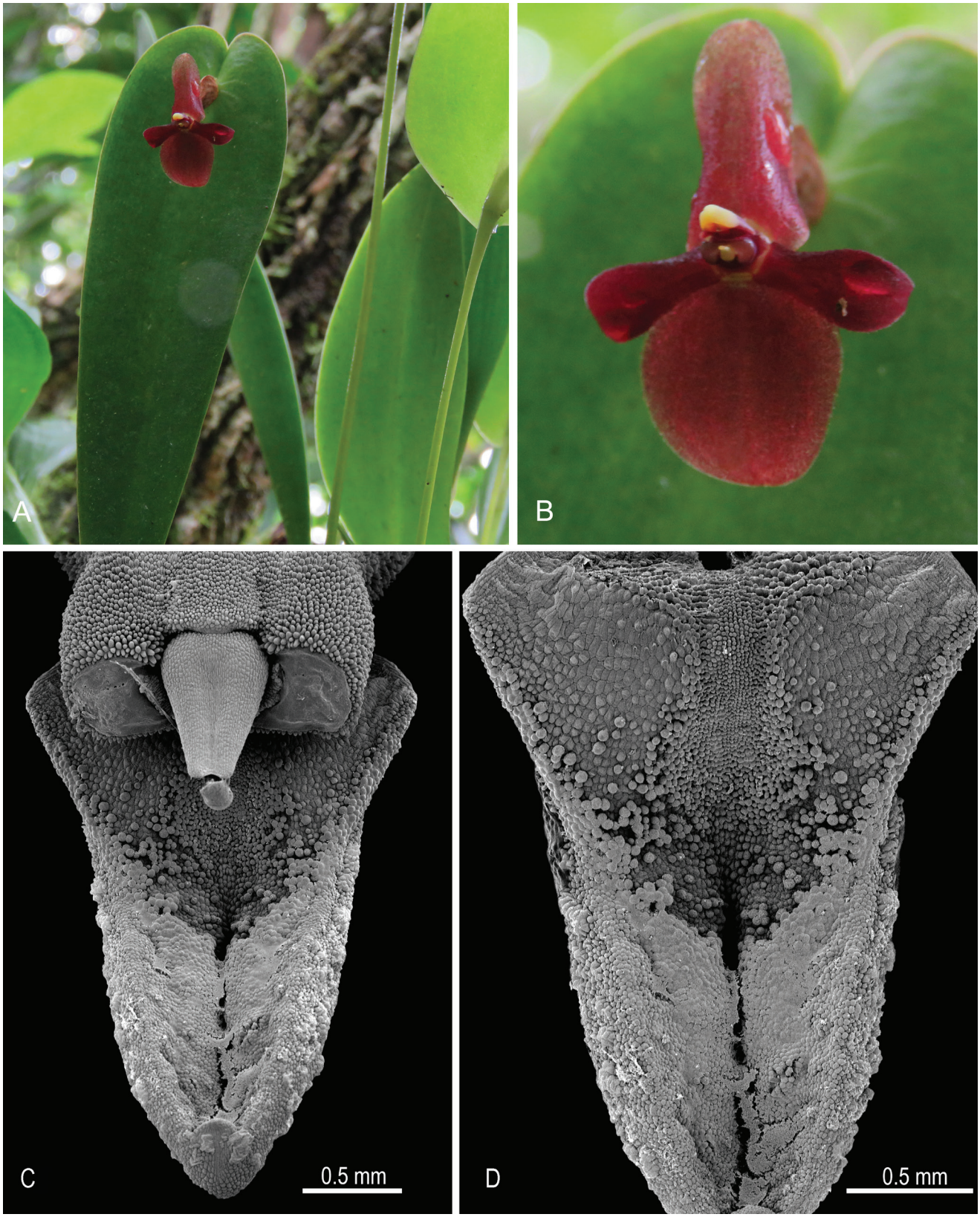

FIGURE 13. **A**, **B**, *Pleurothallis whitteniana in situ* at 1750 m in Huambo, Rodríguez de Mendoza, Amazonas, Peru, the first record of this species for the country, A, Flower and leaf; B, Flower. Courtesy of Génderson Arbildo Lopez. **C**, **D**, Scanning electron micrographs of *Pleurothallis whitteniana*.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

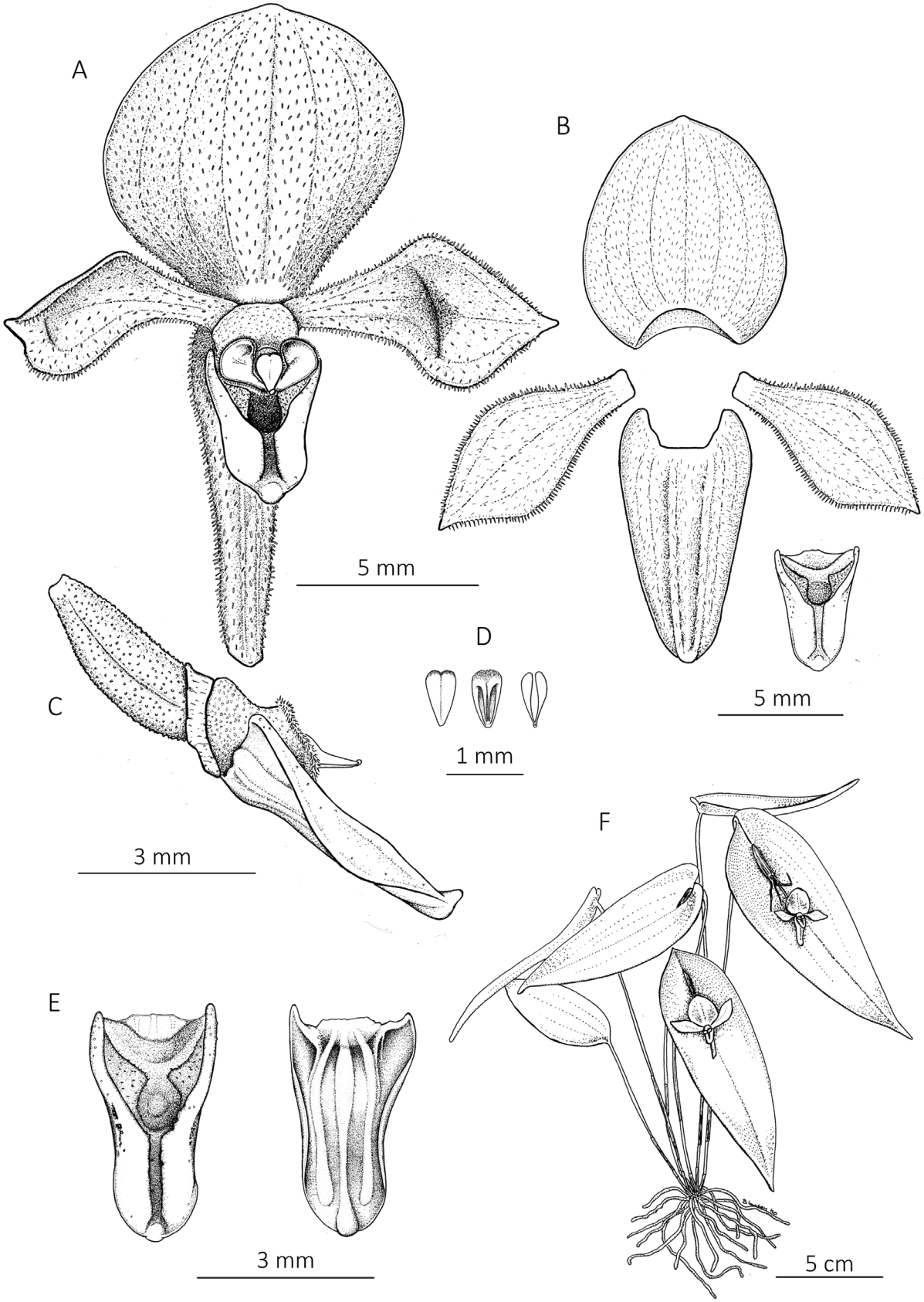

FIGURE 14. Drawing of *Pleurothallis carmensotoana*. **A**, Whole flower; **B**, Floral dissection; **C**, Ovary, column and lip (lateral view); **D**, Anther cap and pollinarium; **E**, Lip (dorsal and ventral views); **F**, Whole plant. Prepared from the paratype PL1154 by Bruno Larsen.

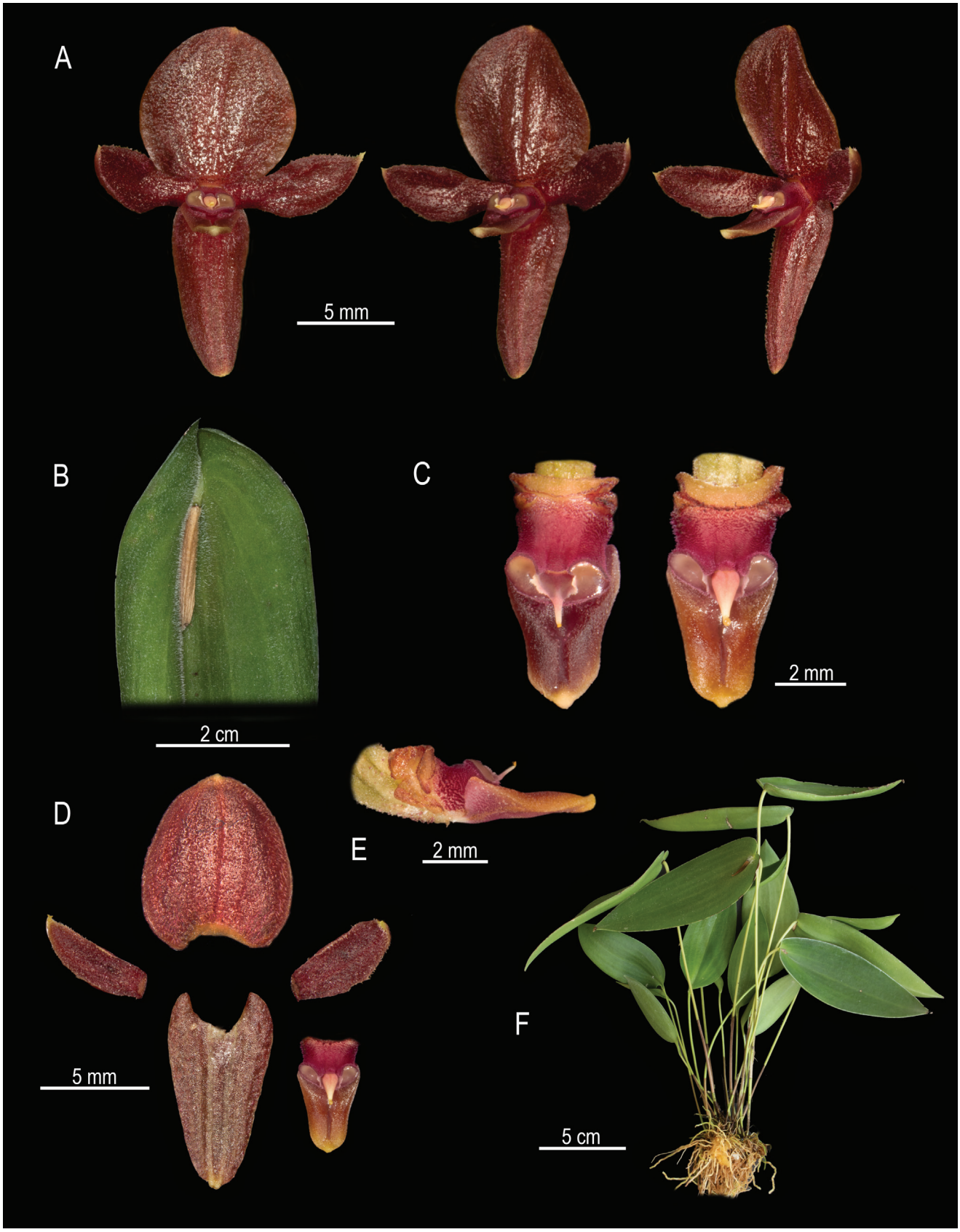

FIGURE 15. Composite digital plate of *Pleurothallis carmensotoana*. **A**, Whole flower (front, 2/3 and 3/4 views); **B**, Leaf base and spathaceous bract; **C**, Column and lip with and without anther cap and pollinarium; **D**, Floral dissection; **E**, Column and lip (lateral view); **F**, Whole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

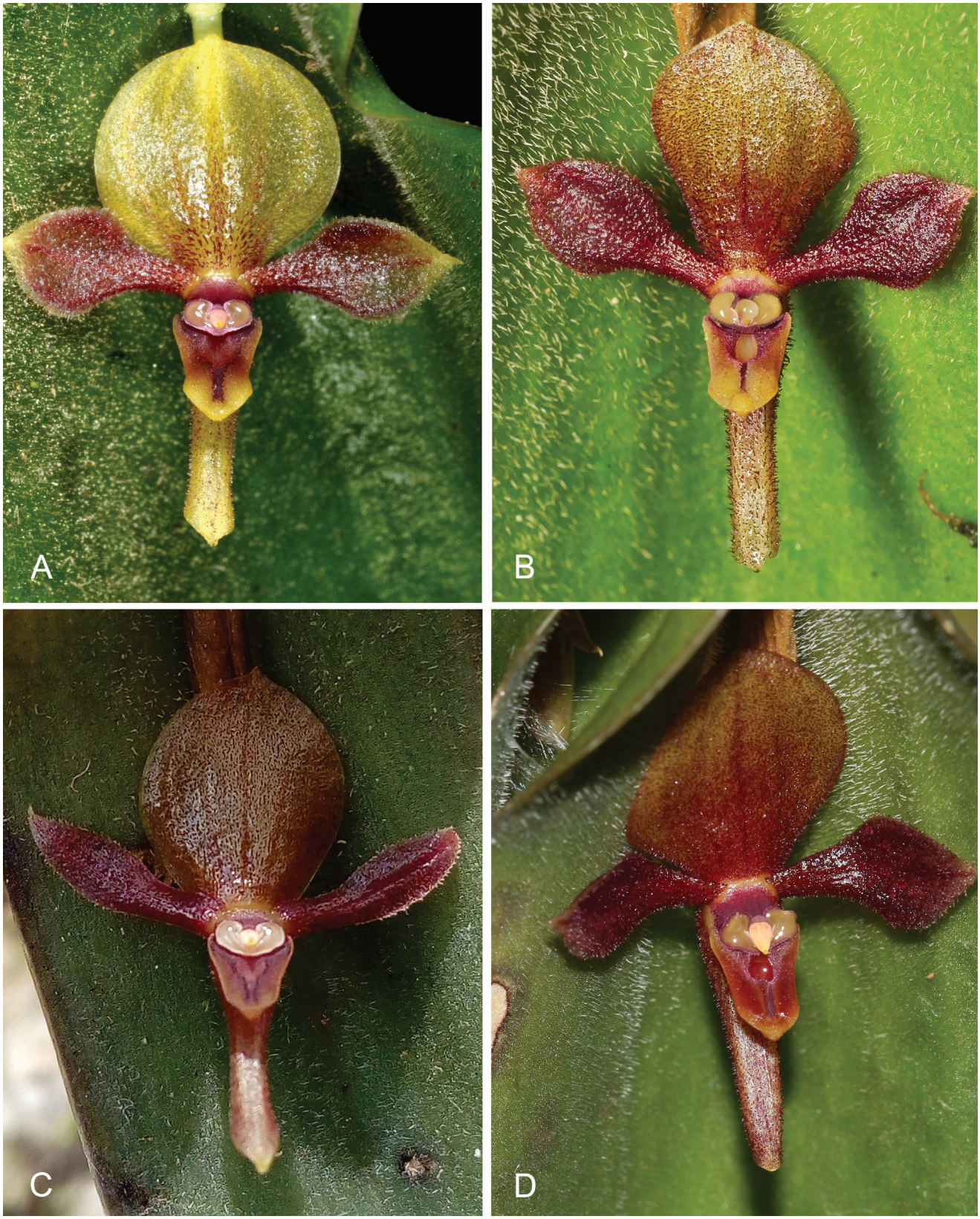

Figure 16. Photographs of *Pleurothallis carmensotoana*. **A**, Flower *in situ* in Parque Nacional Podocarpus, Zamora Chinchipe, Ecuador, courtesy of Ron Parsons; **B**, Flower *in situ* in Reserva Tapichalaca, Zamora Chinchipe, Ecuador, by Marco Jiménez; **C**, Flower from Oxapampa, Peru, courtesy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

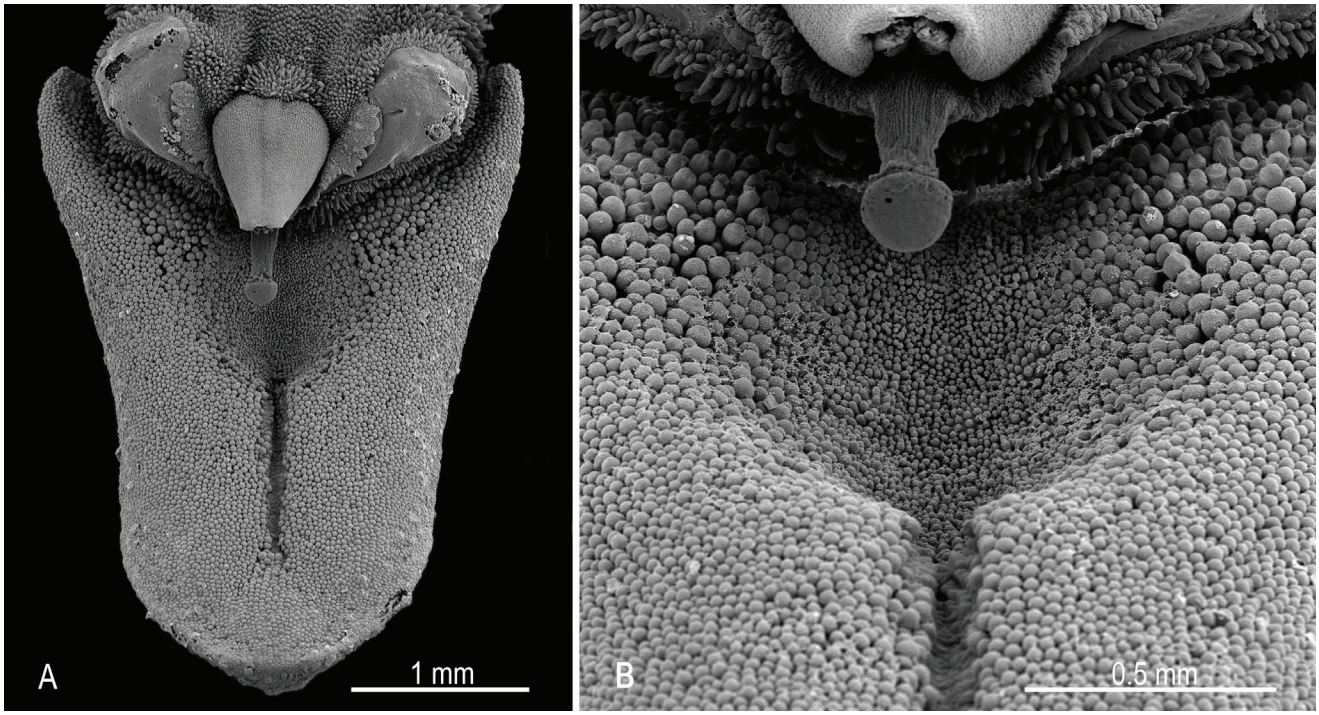

FIGURE 17. Scanning electron micrographs of *Pleurothallis carmensotoana*. **A**, Column, stigmatic surfaces, anther and lip; **B**, Lip base and glenion. Prepared from paratype PL1154 by Raven Ward.

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

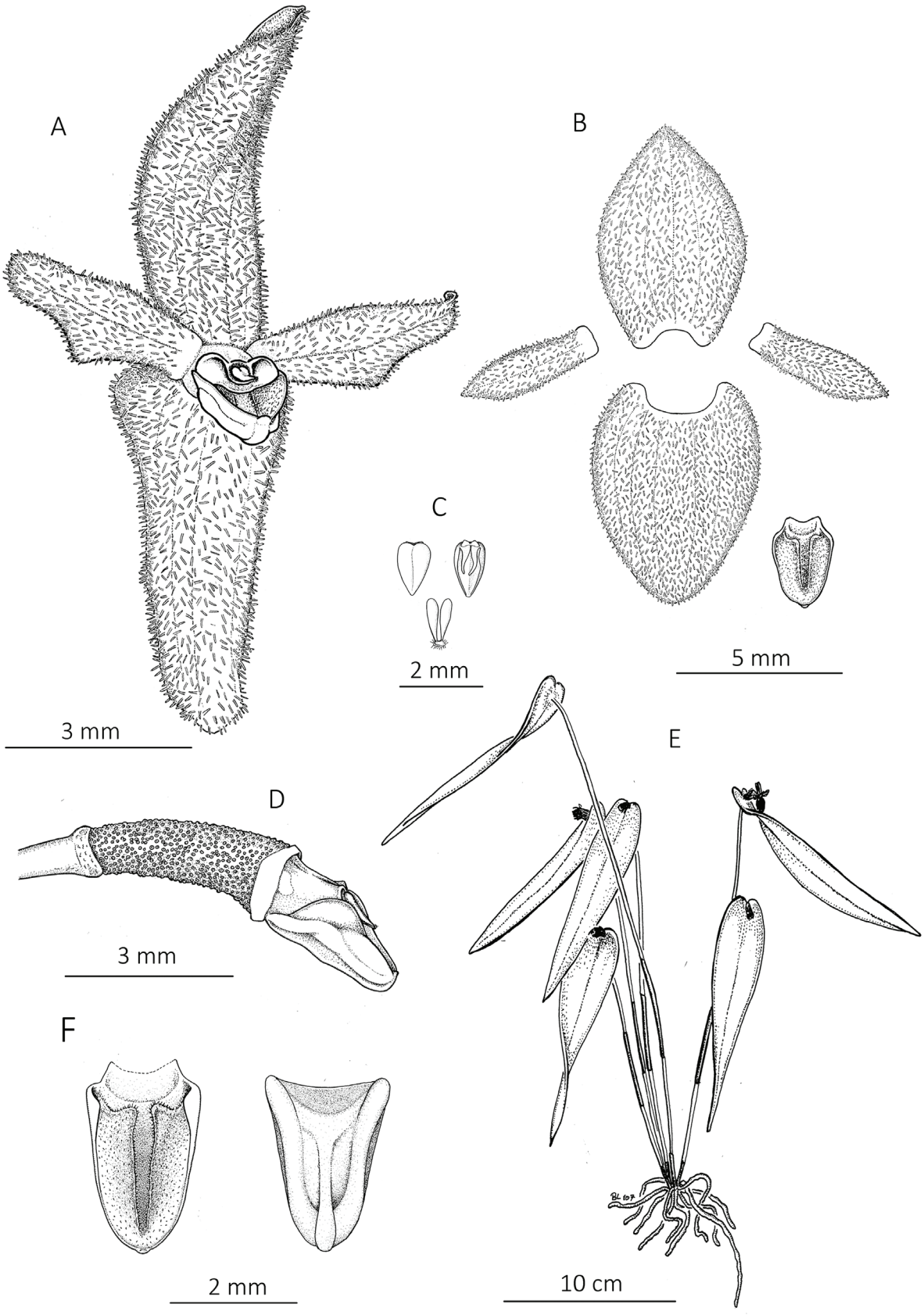

FIGURE 18. Drawing of *Pleurothallis rikseniana*. **A**, Whole flower (2/3 view); **B**, Floral dissection; **C**, Anther cap and pollinarium; **D**, Ovary, column and lip (lateral view); **E**, Whole plant; **F**, Lip (dorsal and ventral view). Prepared from the holotype PL1174 by Bruno Larsen.

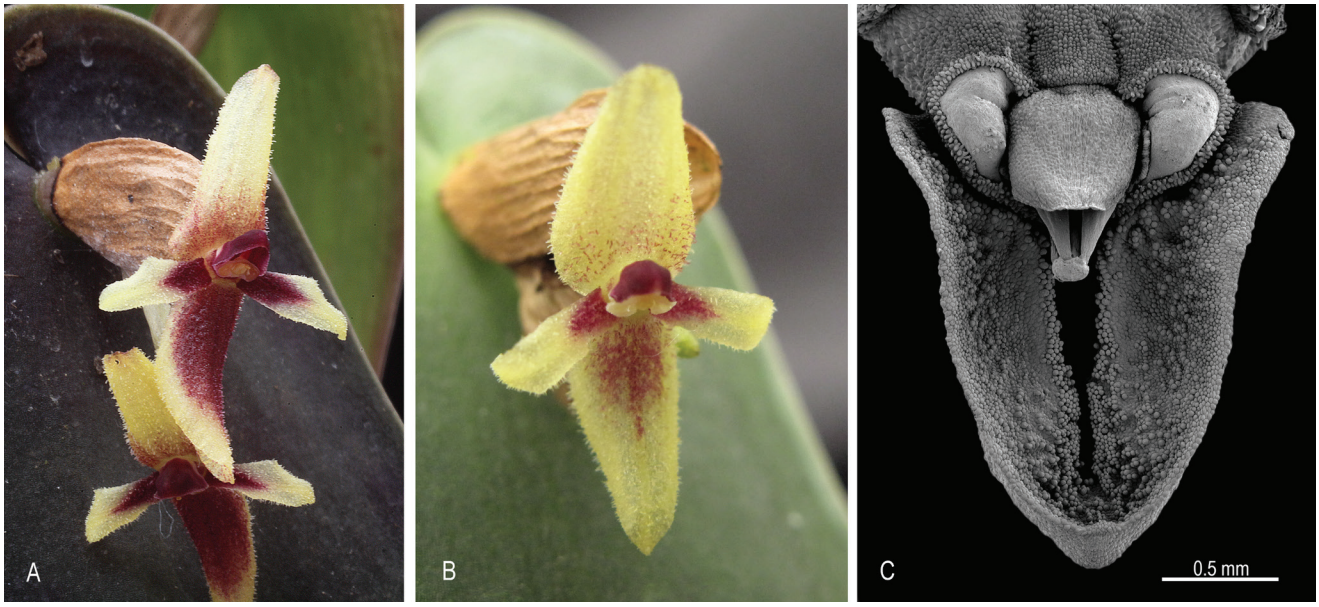

FIGURE 19. **A**, Photograph of flower of *Pleurothallis rikseniana*, prepared from the holotype PL1174 by Joost Riksen; **B**, Photograph of flower of a different color form of *P. rikseniana* in collection of Ecuagenera, by Mark Wilson; **C**, Scanning electron micrograph of column, stigmatic surfaces,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

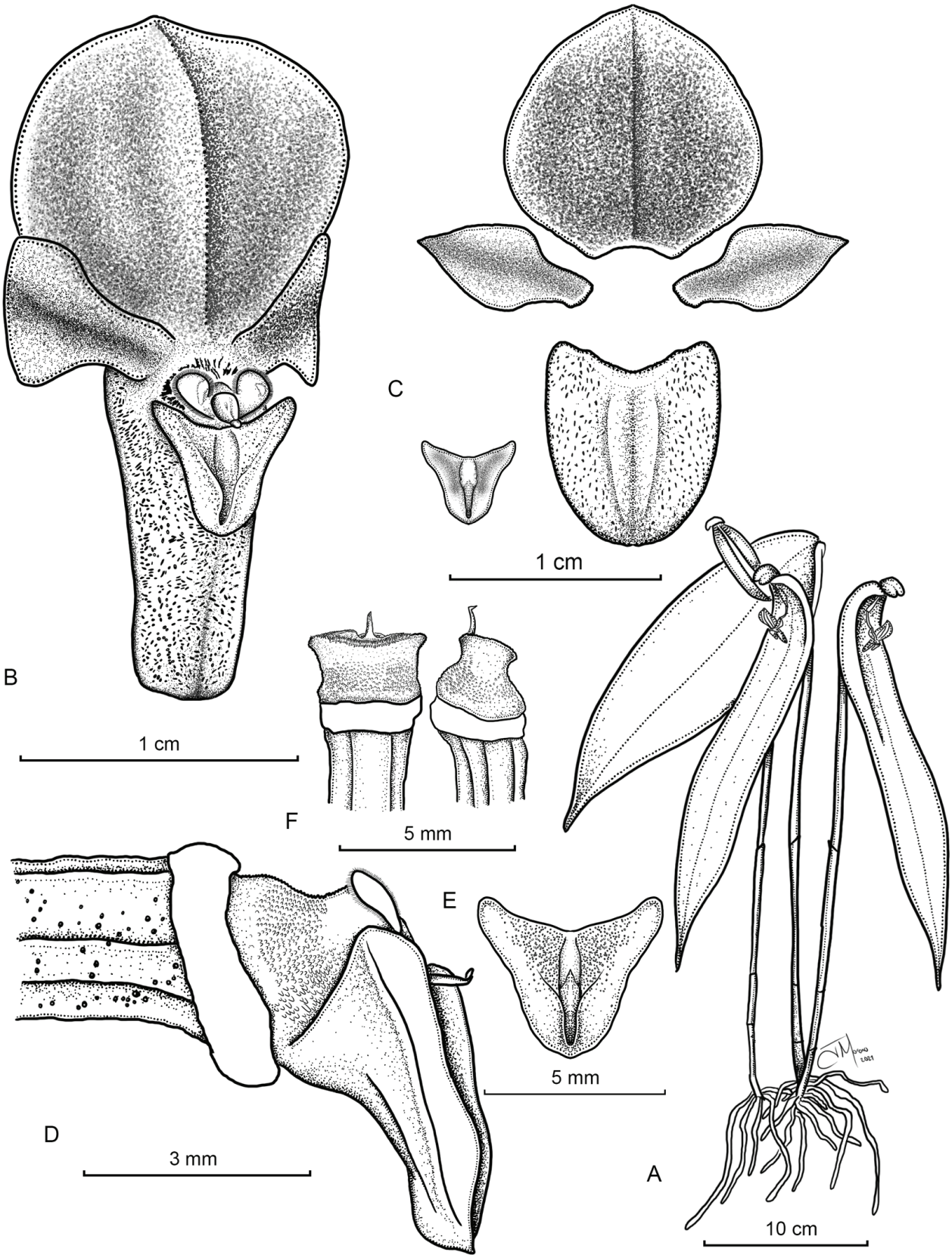

FIGURE 20. Drawing of *Pleurothallis gonzaloi*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view); **F**, Column (dorsal and lateral views). Prepared from holotype by Sebastián Moreno.

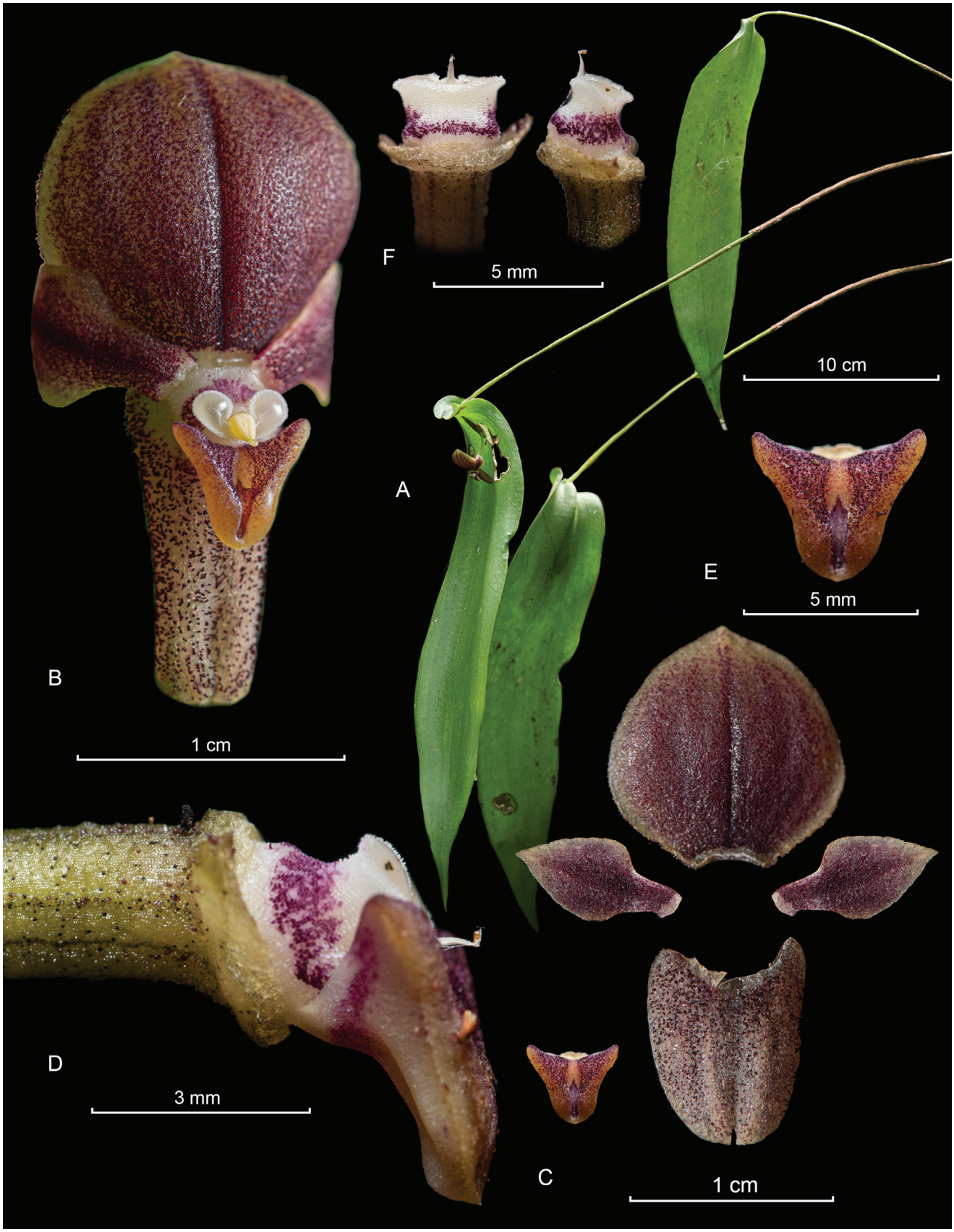

FIGURE 21. Composite digital plate of *Pleurothallis gonzaloi*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view); **F**, Column (dorsal and lateral views). Prepared from holotype by Sebastián Moreno.

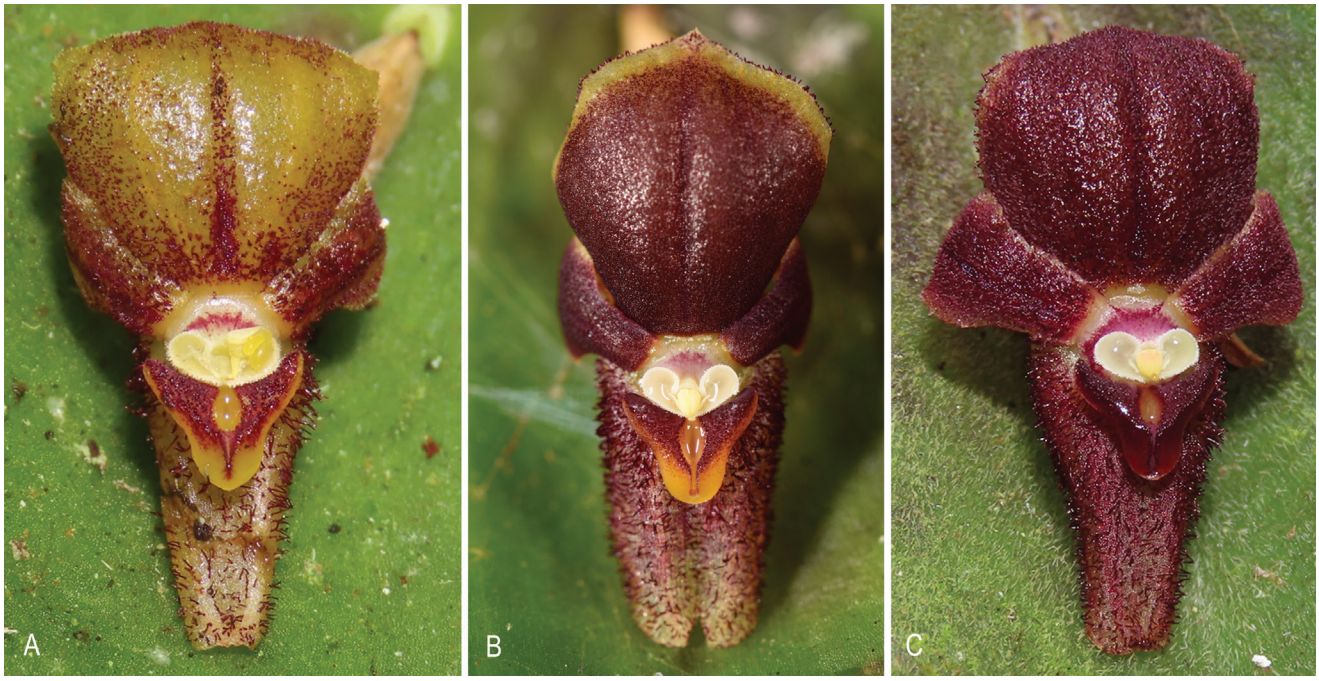

FIGURE 22. Photographs of flowers of *Pleurothallis gonzaloi* illustrating different color forms. **A**, **C**, Courtesy of Sebastián Arango; **B**, By David Haelterman.

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

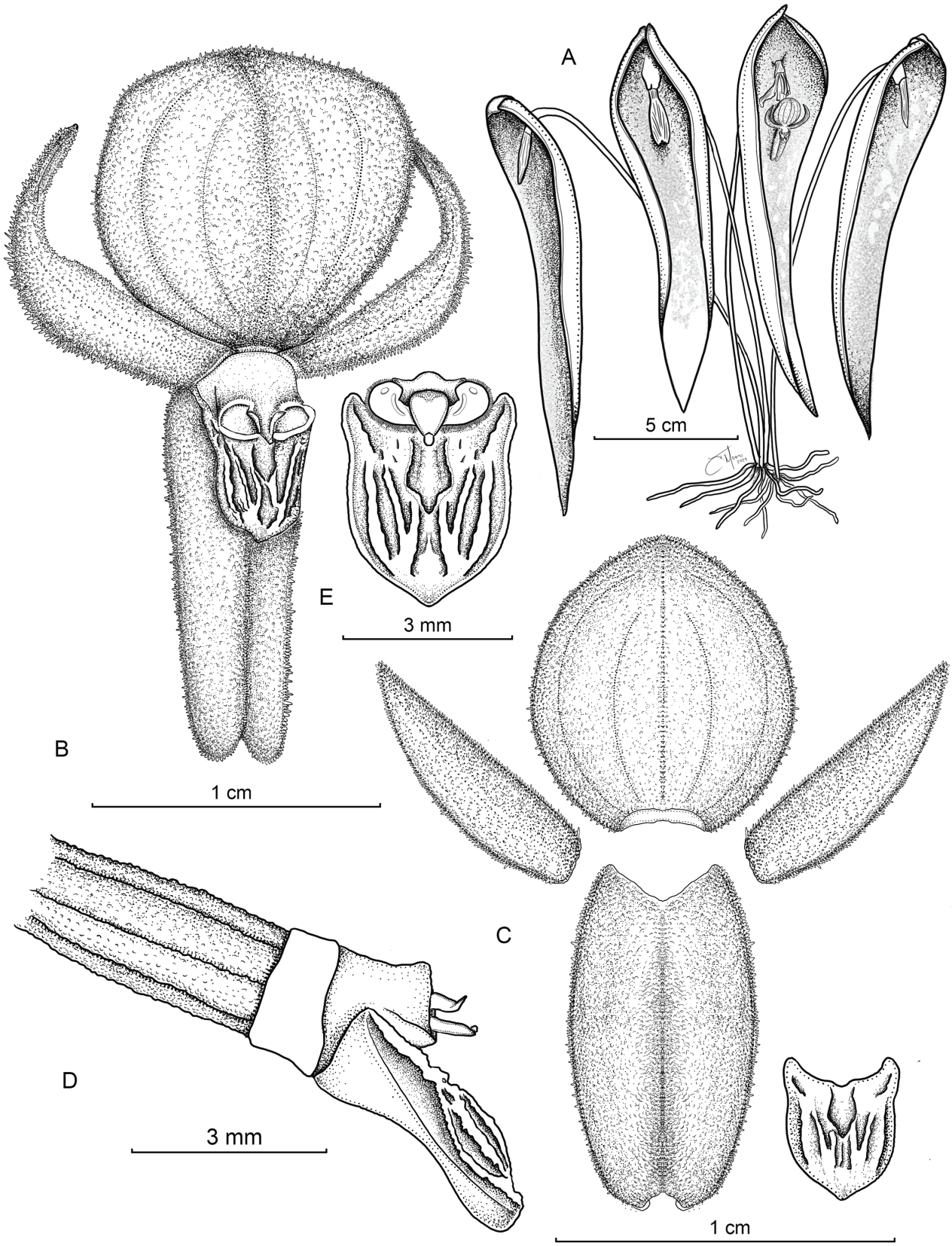

FIGURE 23. Drawing of *Pleurothallis mahechae*. **A**, Whole plant; **B**, Whole flower; **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view). Prepared from holotype by Sebastián Moreno.

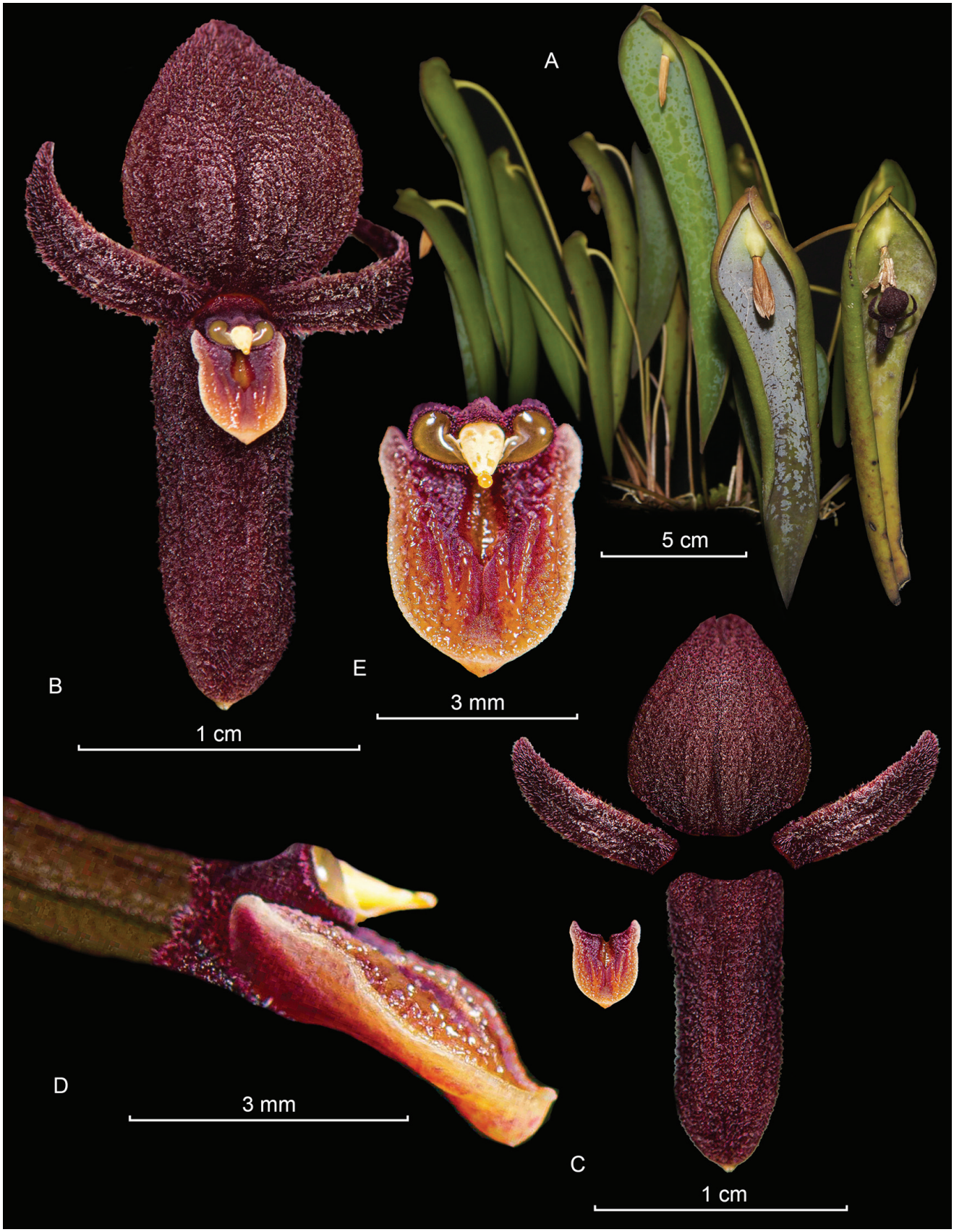

FIGURE 24. Composite digital plate of *Pleurothallis mahechae*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view). Prepared from holotype by Sebastián Moreno.

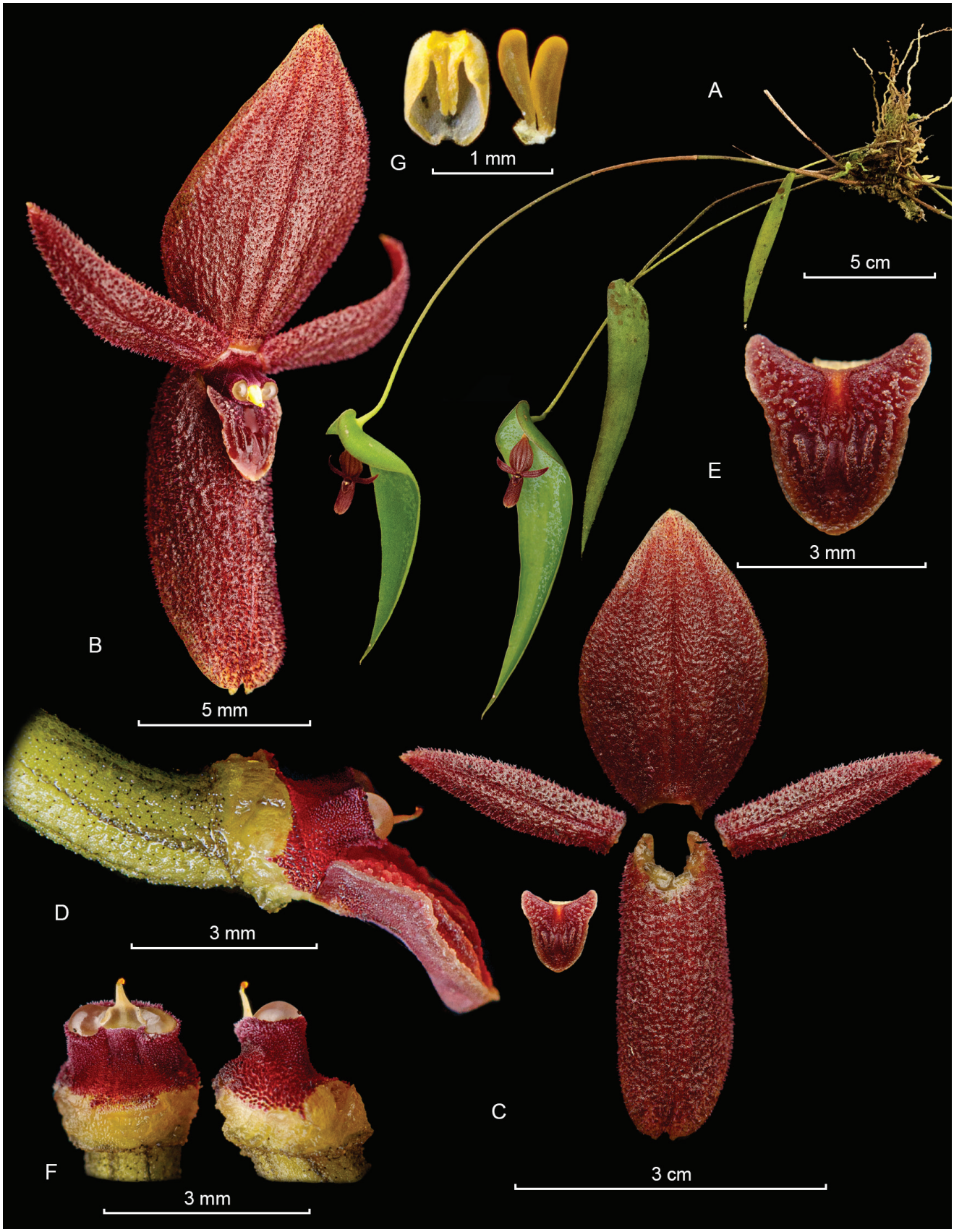

FIGURE 25. Composite digital plate of different morphotype of *Pleurothallis mahechae*. **A**, Whole plant; **B**, Whole flower (2/3 view); **C**, Floral dissection; **D**, Ovary, column and lip (lateral view); **E**, Lip (dorsal view); **F**, Column (dorsal and lateral views). Prepared from paratype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

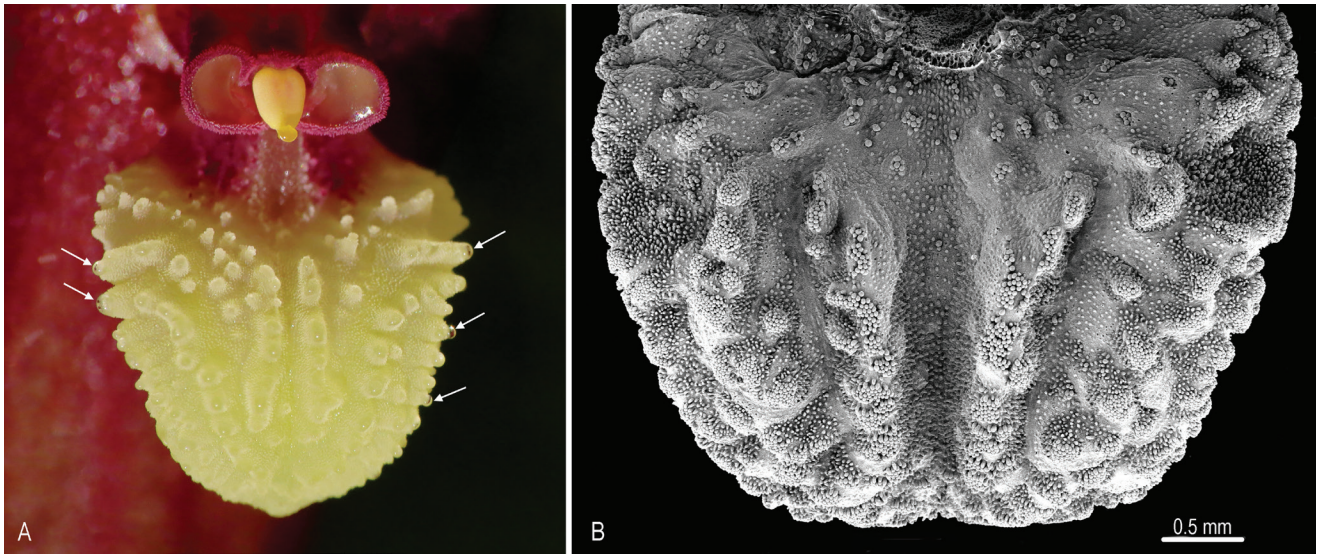

FIGURE 27. **A**, Lip of *Pleurothallis perijaensis* showing columnar calli and drops of nectar-like liquid (arrows). By David Haelterman; **B**, Scanning electron micrograph of lip of *P. perijaensis*, prepared by Mark Wilson.

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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