

TWO NEW ORCHID SPECIES (*CAMARIDIUM*: MAXILLARIINAE; *LEPANTHES*: PLEUROTHALLIDINAE) FROM THE PACIFIC SLOPE OF THE NORTHERN ANDES, COLOMBIA

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ABSTRACT. The Northern Andean Cordillera in Colombia hosts unique, megadiverse, and fragile ecosystems, including wet tropical lowland, cloud forest, and paramo that are essential for climate regulation and the subsistence of human settlements. The Serranía de Los Paraguas on the Pacific slope of the western range of the Northern Andes, Colombia, is an ecosystem that needs to be preserved in the face of a major threat due to rapid deforestation. However, there have been very few explorations surveying its plant diversity in the area. Here, we describe two new orchid species to science from the genera *Camaridium* (*C. antonellii*: Maxillariinae, Cymbidieae) and *Lepanthes* (*L. valerieae*: Pleurothallidinae, Epidendreae) discovered during a floristic survey conducted in the region. *Camaridium antonellii* is similar to *C. inauditum* but differs in the fractiflex, ovate-elliptic, acute leaves, the flowers with pink sepals and petals, the lip white, distinctly three-lobed, spotted with purple on the lateral lobes and yellow-cream towards the apex, the mid-lobe ovate to transverse ovate and lanceolate sepals. *Lepanthes valerieae*, which is similar to *L. antennata*, differs in the long apical lobes of the petals, surpassing the dorsal sepal, the longer connectives > 18 mm, rounded lobes of the lip, and the oblong, flattened appendix. Illustrations, distribution maps, and photographs are provided.

KEY WORDS/PALABRAS CLAVE: Andes, Chocó biogeographic region, Chocó biogeográfico, epiphyte diversity, diversidad de epífitas, Neotropical realm, región neotropical, new species, nuevas especies, Orchidaceae

Introduction. With *ca.* 30,000 plant species, the South American tropical Andes is the world's richest plant biodiversity hotspot (Myers *et al.* 2000, Mittermeier *et al.* 2011, Ulloa *et al.* 2017, Antonelli 2021, Pérez-Escobar *et al.* in press). For centuries, this hyper-diversity of the region has attracted the interest of botanists (Cuatrecasas 1958), geologists (Hoorn *et al.* 2010), naturalists (Humboldt 1820, Darwin 1846), and all range of scientists (Gentry 1982, Antonelli *et al.* 2009, Antonelli & Sanmartín, 2011, Pérez-Escobar *et al.* 2017a, 2019), yet knowledge gaps remain in understanding plant species diversity, its origin, and distribution (Antonelli *et*

al. 2018a). This lack of understanding stems from the scarcity of floristic studies and botanical exploration in the region (Orejuela 2005), an urgent task that is sorely needed because of the constant threat of climate change and anthropogenic pressures on Andean ecosystems (Pérez-Escobar *et al.* 2009, Parra-Sánchez *et al.* 2016, Helmer *et al.* 2019).

The Orchidaceae are one of the most prominent floristic elements of the tropical Andes (Gentry & Dodson 1987, Pérez-Escobar *et al.* 2017a, Pérez-Escobar *et al.* in press). In particular, the western slope of the western range in the Northern Andean cordil-

lera of Colombia and Ecuador exhibits higher levels of orchid endemism (Gentry 1982, Zotz 2013) and richness (Gentry & Dodson 1987) when compared with the rest of the tropical Andes. This high epiphyte diversity is attributed to the confluence of Andean and Chocóan landscapes at the Andean foothills (Richter *et al.* 2009), the high humidity at mid-range elevations (Küper *et al.* 2004), and rapid orchid diversifications boosted by biotic and abiotic factors such as Andean mountain building (Givnish *et al.* 2015, Pérez-Escobar *et al.* 2017a, 2019), migrant exchanges between biogeographical regions (Pérez-Escobar *et al.* 2017b, 2019, Antonelli *et al.* 2018b) and the evolution of plant-organism interactions (Ramírez *et al.* 2011, Givnish *et al.* 2015, Balbuena *et al.* 2020).

Despite the biological importance of the ecosystems nested in the western slope of the Northern Andes' western range (Amaya-Marquez & Marín-Gómez 2012), only a few floristic studies aimed at quantifying its orchid diversity have been conducted (Silverstone-Sopkin & Ramos-Pérez 1995, Misas-Urreta 2005, García-Ramírez & García-Revelo 2013). To date, 160 orchid species (of which five are endemic) in 37 genera have been recorded for selected protected areas in the region, including Serranía de los Paraguas and Cerro del Torrá. As an outcome of field expeditions conducted in 2018 in the Serranía del Paraguas (western slope of the western range in Northern Andes, Colombia, between Valle del Cauca and Chocó departments) aimed at expanding our knowledge on the orchid diversity of this locality. Populations of two morphologically distinctive species from the genera *Lepanthes* Sw. and *Camaridium* Lindl. were discovered, which we propose here as new.

Lepanthes Sw. is one of the most species-rich groups in the Neotropics with >1200 species and the third most diverse in Colombia with about 304 species. Most of the diversity of *Lepanthes* is recent and derived from rapid diversifications in the Andes and Central America (Pérez-Escobar *et al.* 2017a). In addition, most of the species have narrow distributions, restricted to specific mountain ranges. For example, ~98% of the species of Costa Rica and Panama (mainly in the Cordillera de Talamanca) are endemic and do not occur in the Andes or northern Central America. In Colombia, Moreno *et al.* (2019) identified the western range of the Northern Andes as one of the ten hotspots

for *Lepanthes* in the country. They pointed out the need for floristic studies in the region.

Camaridium comprises about 80 species ranging from southern Florida (USA) and Mexico to Peru and southeastern Brazil. Most of the diversity is concentrated in Costa Rica and Panama, with >80% of the species. There are 18 species in Colombia, but new species frequently appear with more botanical exploration and reliable herbarium identifications (Rodríguez-Martínez & Blanco 2015). Also, floristic similarities between southern Central America and Chocó suggest that the number of species discovered within the Maxillarinae in the Northern Andes' western range of Colombia could increase (Kirby 2011, Pérez-Escobar *et al.* 2019).

Materials and methods. We collected living plants in field in March 2018 at Valle del Cauca, El Cairo municipality, Colombia. The descriptions and drawings were based on living specimens and herbarium material, following the terminology by Christenson (2013) and Luer (2011). Digital images were taken with a Nikon D7100 with a Nikon AF-D 50 mm f/1.8 lens. Sketches were prepared with a Leica® MZ7.5 stereomicroscope with a drawing tube and digitalized. A draft composite template was designed in Adobe Photoshop® CS6 and exported as a JPEG file. Then, we made the digital composite-line drawing (lines and stippling), uploading the template in Procreate illustration applications for iPad Pro tablet computer (Apple Inc.). The resulting drawing was exported as TIFF file at 800 dpi. The *Camaridium* species was prepared and inked in paper.

TAXONOMIC TREATMENT

Camaridium antonellii* O.Pérez & Bogarín, *sp. nov.

TYPE: Colombia. Valle del Cauca: El Cairo municipality, Cerro El Inglés, "Santicos" locality, epiphyte in disturbed forest, 2330 m, 25 March 2018, O. Pérez-Escobar & A. Zuluaga 1987 (Holotype: CUVU). Fig. 1–2.

DIAGNOSIS: *Camaridium antonellii* is similar to the Central American *C. inauditum* (Rchb.f.) M.A.Blanco, but differs in the fractiflex leaf-sheaths, ovate-elliptic, acute leaves, the flowers with dark pink to purple se-

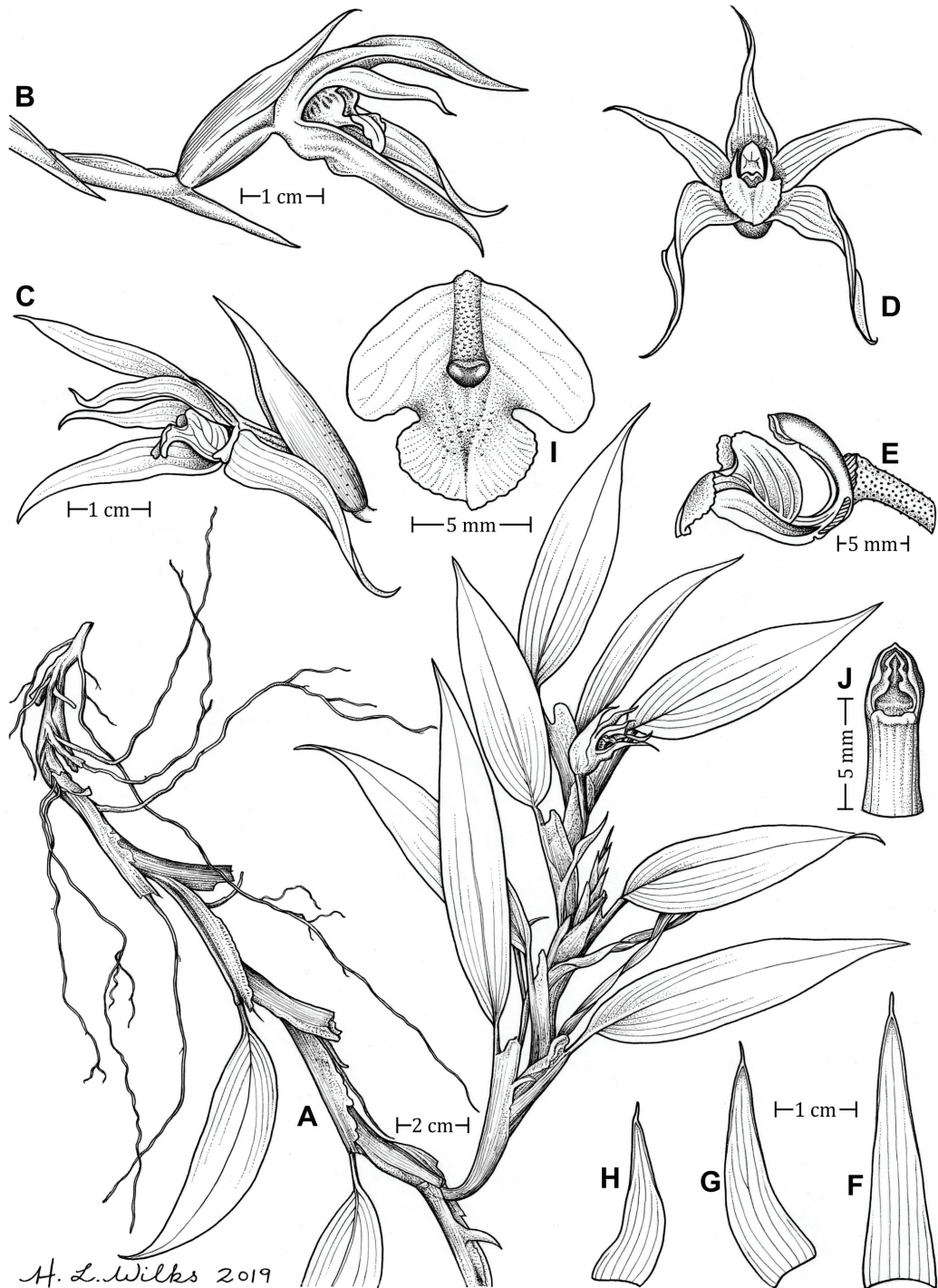


FIGURE 1. *Camaridium antonellii*. A. Habit. B. Flower in lateral position. C. Flower in lateral position, exposing the lip. D. Flower in frontal position. E. Ovary, column and lip, lateral view. F-G. Dorsal, lateral sepal and petal in ventral position, respectively. I. Lip (ventral position). J. Column (ventral position). Drawn from the holotype by H. Wilks.

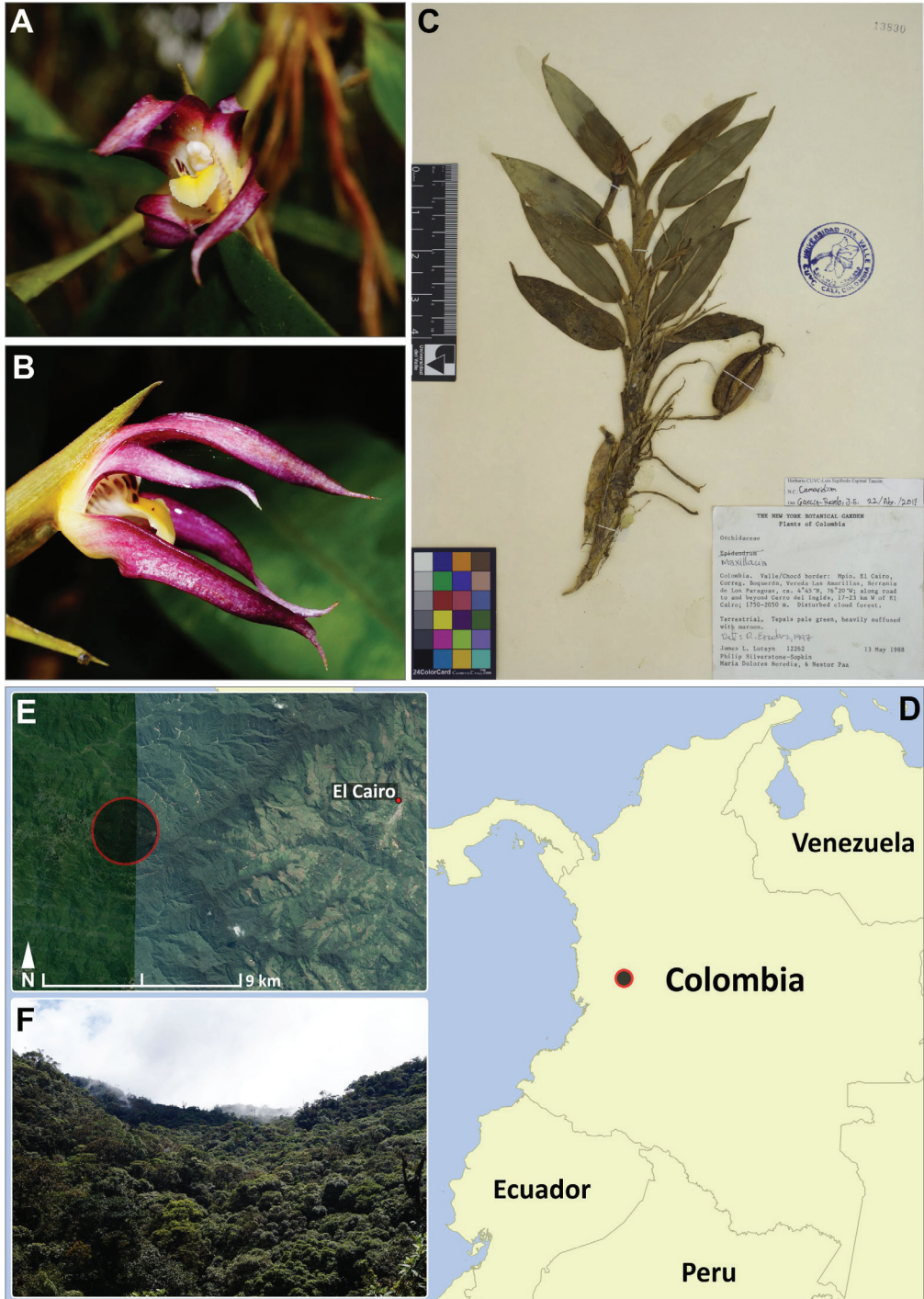


FIGURE 2. **A-B.** Flowers of *Camaridium antonellii* in Frontal and lateral position, respectively. **C** Pressed plant of *C. antonellii* bearing a dehiscent fruit (*Luteyn 12262* CUVCI). **D-E.** Type locality of *C. antonellii* and *Lepanthes valerieae* (enclosed in the black circle). **F.** Canopy view of cloud forests in Serranía del Paraguas (type locality). Photos: O. Pérez & Google Earth.

pals and petals, the distinctly three-lobed lip, white, spotted with purple on the lateral lobes and yellow-cream towards the apex, the mid-lobe ovate to transverse ovate, and lanceolate sepals.

Plant epiphyte, up to 44 cm tall. *Roots* white, 1 mm thick, lateral, profuse, produced from the base of the leaves and sprouting from the leaf sheaths. *Stems* sympodial canes, decumbent, flattened, with fractiflex leaf-sheaths, rarely branching towards the apex, without evident pseudobulbs. 22–26 cm long, 0.8–1.5 cm wide, entirely covered by the leaf sheaths. *Leaves* distichous, 5–11, monomorphic, the blade ovate-elliptic, coriaceous, deciduous, green, acute, minutely mucronate, the base invaginate, with a clear abscission line, pseudopetiolate, 7–12 × 2 cm; the petiole conduplicate and articulated with the leaf, coriaceous, cordate, winged, persistent on the stem after leaf's abscission. *Inflorescences* single-flowered, produced from the apical leaf sheath's axils, 1-many per axil, with flowers opening successively. *Peduncle* 16 mm long, with 2–4 distichous, conduplicate, acute, yellow-green pale, papyraceous bracts (including the floral bract), slightly verrucous towards the apex, the papillae pale brown, 31.1–32.2 × 12 mm, the floral bract extending over basal 1/3 of the dorsal sepal with the midrib stained with purple. *Ovary* pedicellate, 14 mm long (including the pedicel), markedly verrucose in the distal half. *Flowers* resupinate; sepals and petals pink towards the distal two thirds, the margin slightly darker, the base white to pale yellow, immaculate; lip white with transverse purple blotches on the lateral lobes extending to the margins, pale yellow towards the apex, with a yellow callus; column white. *Sepals* narrowly triangular to lanceolate, acute, mucronate, fleshy; the dorsal sepal 36.7 × 9.0 mm, 7-veined, the lateral sepals falcate, 30.4 × 7.6 mm, 7-veined. *Petals* lanceolate, falcate, acute, mucronate, 22.2 × 7.1 cm, 6-veined. *Lip* sub-rhombic, three-lobed, slightly truncate at the base, with a prominent oblong, apically projected bifid callus extending from the base of the lip to the apical portion of the disc, 10.1 × 10.3 mm; lateral lobes obliquely elliptic, obtuse, erect, entire, 6.1 × 4.0 mm; mid-lobe broadly ovate to transverse ovate, subtruncate, obtuse with a small mucron, margin sub-crenate, fleshy, 5.0 × 5.9 mm. *Column* arcuate, hemicylindrical, 7.8 × 2.8 mm.

Anther apical, *stigma* ventral. *Pollinia* not seen. *Fruit* oblong, 47 mm long.

EPONYMY: This new species honours Prof. Alexandre Antonelli, Director of Science at the Royal Botanic Gardens, Kew (UK) and mentor of the lead authors of this paper. Prof. Antonelli is one of the most prominent tropical plant biogeographers of the 21st century, whose contributions have revolutionized the understanding of the spatio-temporal dynamics of plant diversification in the American tropics, including orchids.

PHENOLOGY: Flowering was recorded from March to July. Fruits were recorded in May.

HABITAT AND ECOLOGY: Epiphyte, growing in primary forest, humid tropical forest (cloud forest), at 1700–2300 m elevation. Dense populations of *C. antonellii* of 15 or more individuals were reported growing on isolated trees. *Camaridium antonelli* is the only known representative of the genus growing in the type locality.

DISTRIBUTION: Endemic to the Chocó, Colombia, where it is only known from the type locality (Fig. 2D, E).

Discussion. *Camaridium antonellii* is similar to the Central American *C. inauditum* but differs in the fractiflex leaf-sheaths, ovate-elliptic, acute leaves (*vs.* two-ranked, oblong, obtuse), the flowers with pink sepals and petals (*vs.* ivory white), the distinctly three-lobed lip (*vs.* obscurely three-lobed), white, spotted with purple on the lateral lobes and yellow-cream towards the apex (*vs.* yellow and also light stained with brownish to the apex), the mid-lobe broadly ovate to transverse ovate (*vs.* ovate to elliptical), and the lanceolate sepals (*vs.* linear).

Some species of *Camaridium* and *Maxillaria* Ruiz & Pav., as defined by Whitten *et al.* (2007) but its current generic boundaries and relationships have long been regarded as artificial. Phylogenetic relationships within subtribe Maxillariinae *sensu* Dressler (1993), can be confused mostly because of the generalized plant habit. However, plants of *Camaridium* typically lack pseudobulbs in contrast to *Maxillaria s.s.*, which shows well-developed pseudobulbs with one

apical, spatulate leaf. Nevertheless, some of these traits evolved several times across the Maxillariinae (in *Ornithidium* Salisb. ex R.Br., *Maxillaria* s.s., and the *M. variabilis* clades), their taxonomic value in generic delimitations is not useful. Therefore, Whitten *et al.* (2007) but its current generic boundaries and relationships have long been regarded as artificial. Phylogenetic relationships within subtribe Maxillariinae sensu Dressler (1993 suggested the combination of apical fruit dehiscence, absence of fibers in floral segments, and a floral bract that often exceeds the ovary to separate *Camaridium* from *Maxillaria*. Vegetatively, some species of *Maxillaria* s.s., such as *Maxillaria caveroi* D.E.Benn. & Christenson, *M. floribunda* Lindl., *M. platyloba* Schltr. and *M. sibundoyensis* Szlach., Kolan., Lipińska & Medina Tr. (Bennett & Christenson 1998, Bentham 1839, Schlechter 1921, Szlachetko *et al.* 2017) are similar to *C. antonellii*, mainly in plant habit and general flower appearance. However, plants of these species have traits typical of *Maxillaria* s.s. such as the tough perianth fibers, crested or ornamented anther cap (Blanco *et al.* 2007). If the broad generic concept of *Maxillaria* proposed by Schuiteman & Chase (2015) is accepted, then *C. antonellii* also differs from the species of the *M. platyloba* group (Christenson 2013) mainly by the pink sepals and petals, yellow-cream lip (*vs.* yellow or brown sepals and petals), lanceolate dorsal sepal (*vs.* linear, oblong) and the ovate to transverse ovate, acute lip (*vs.* ovate to elliptical, truncate, emarginate or obtuse).

Lepanthes valerieae O.Pérez, Jaramillo & Bogarín, *sp. nov.*

TYPE: Colombia. Valle del Cauca, El Cairo municipality, Cerro El Inglés, 2300 m, 25 March 2018, O.A. Pérez *et al.* 1981 (holotype: CUVC). Fig. 3–4.

DIAGNOSIS: *Lepanthes valerieae* is most similar to *L. silverstonei* Luer, but it differs in the narrowly-elliptic to narrowly ovate leaves, < 1 cm wide, the filiform upper lobe of the petals surpassing the dorsal sepal length and the rudimentary ovate, sub-triangular lower lobe, and the triangular, concave appendix with a subcylindric, retuse almost glabrous apex. It is also similar to *L. antennata* Luer & Escobar; however, it is distinguished

by the long apical lobes of petals, surpassing the dorsal sepal, the longer connectives > 18 mm, rounded lobes of the lip, and the oblong, flattened appendix.

Plant epiphytic, pendent, or suberect, up to 20 cm tall. *Roots* slender, flexuous, to 1 mm in diameter. *Ram-icauls* slender, suberect, when young, mostly pendent at maturity, to 12 cm long, enclosed by 6–11 brownish, adpressed lepanthiform sheaths, the ostia minutely ciliate, acute. *Leaves* narrowly-elliptic to narrowly lanceolate, coriaceous, attenuate-acuminate, with recurved margins, 8.0 × 1.0 cm, the attenuate base narrowing into a petiole less than 3 mm long. *Inflorescence* racemose, distichous, glabrous, successively flowered, developed above the leaf, shorter than the leaves, up to 3.0 cm, long, peduncle 2.5 mm long, rachis 5 mm long. *Floral bracts* ovate, acuminate, 1 mm long. *Pedicels* 2 mm long, persistent. *Ovary* to 3 mm long, glabrous. *Flowers* with red sepals, the dorsal sepal yellowish tinted red, the lateral sepals with a yellow mid-vein, and light-yellow petals basally tinted red with reddish tips and yellow lip and column. *Dorsal sepal*, ovate, acute, concave, denticulate, abaxially with three ciliate keels, connate to the lateral sepals for about 1 mm, 4.8 × 2.5 mm. *Lateral sepals* oblong-ovate, acute, denticulate, abaxially with two ciliate keels, oblique, connate for about 3 mm, 5.0 × 3.2 mm. *Petals* transversally bilobed, minutely ciliate, 0.8 × 11.4 mm, the upper lobe filiform ovate at the base, filiform, 10.8 × 0.8 mm, the lower lobe introrse, ovate, sub-triangular, about 0.5 mm long. *Lip* bilobed, minutely pubescent, adnate to the column at the base, exceeding the column length, with oblong blades and rounded ends, embracing the column, 1.5 × 3.2 mm, with cylindrical connectives, 1.8 mm long, the narrow body, laminar, connate to the base of the column, appendix triangular, concave, with a subcylindric retuse, almost glabrous apex. *Column* cylindrical to 2.2 mm long, with a prominent, orbicular stigma with the margins papillose, anther apical, and stigma ventral. *Pollinia* two, obovoid. *Anther cap*, cucullate. *Fruit* not seen.

EPONYMY: This species honors Valerie Anders for her passion for supporting science projects that celebrate the Anders' family legacy of exploring and expanding human knowledge. Her generosity has helped generations of paleobiologists worldwide, especially Latin

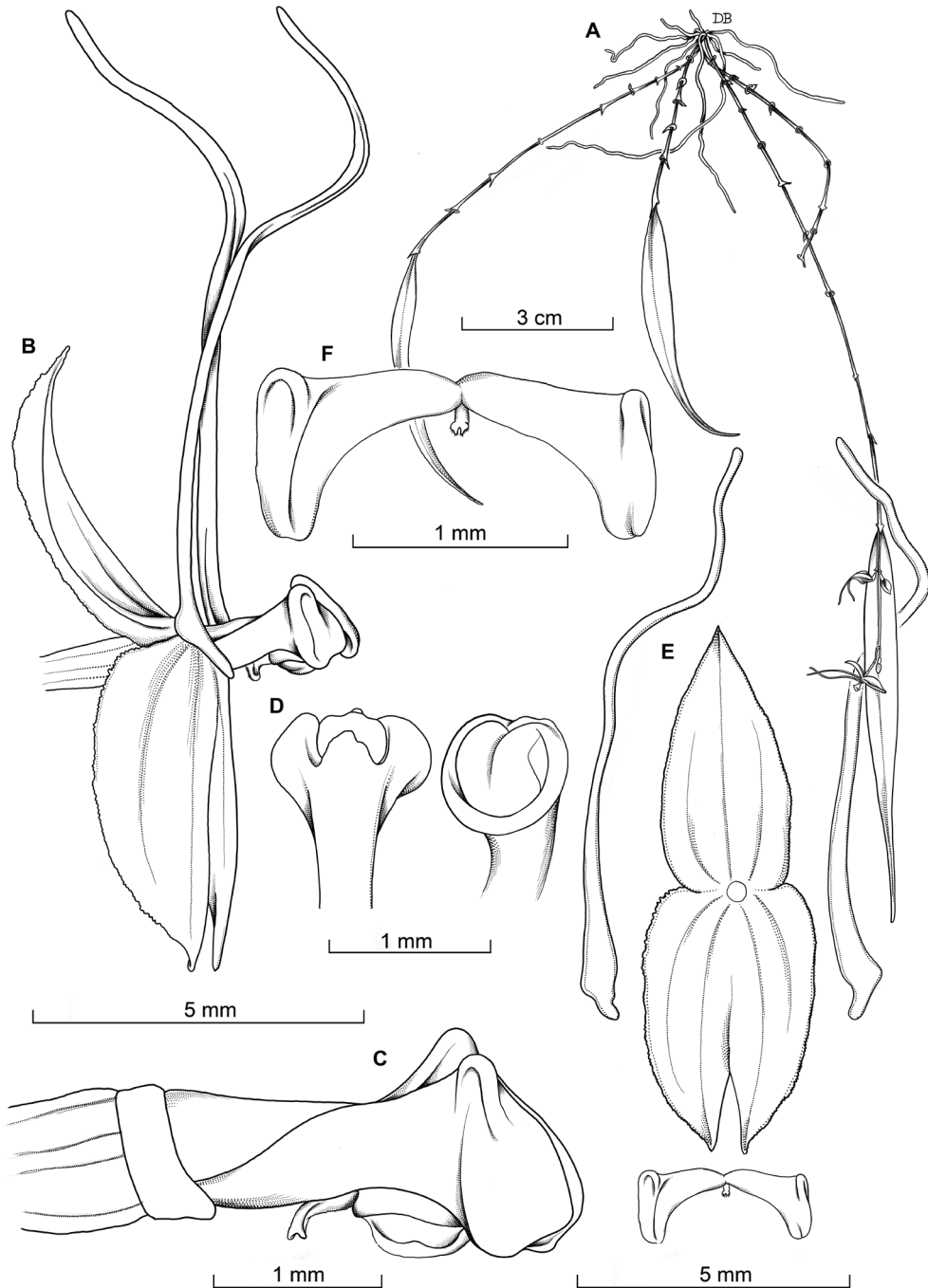


FIGURE 3. *Lepanthes valerieae*. A. Habit. B. Flower in natural position. C. Ovary, column and lip, lateral view. D. Column. E. Dissected perianth, flattened. F. Lip spread, adaxial view. Drawn from the holotype by D. Bogarín.

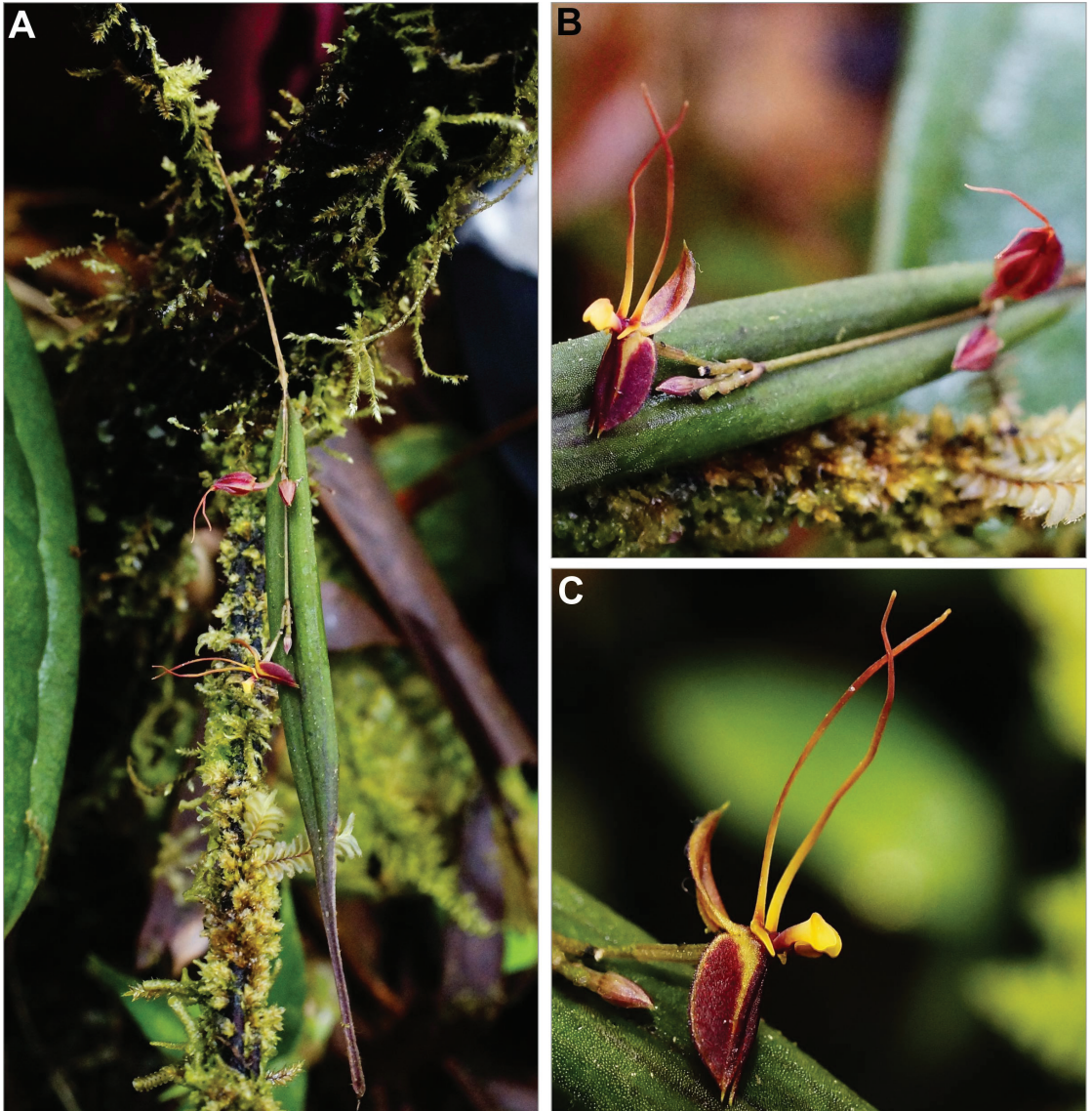


FIGURE 4. *Lepanthes valerieae*. A. Detail of ramicaul and leaf, bearing two inflorescences. B. Side position of a flower and flowers buds in development. C. Detailed view of the flower in lateral position. Photos: O. Pérez.

America, that seek to understand the evolution of life and landscapes in the Tropics.

PHENOLOGY: Flowering was recorded in March and April.

HABITAT AND ECOLOGY: Epiphyte, growing in primary humid tropical (cloud) forest on branches and twigs in the forest floor at 1700 m elevation. Two populations growing in bushes and distanced each other by about five meters were further reported. The type locality

seems to be highly diverse in *Lepanthes* orchids. Here, at least ten different species (including *L. antennata*) were recorded in adjacent branches.

DISTRIBUTION: Endemic to the Chocó, Colombia, only known from the type locality (Fig. 2D, E).

Discussion. *Lepanthes valerieae* is also most similar to *L. silverstonei*, but it differs in the narrowly-elliptic to narrowly ovate leaves, < 1 cm wide (vs. ovate, > 2 cm wide), the filiform upper lobe of the petals surpassing

the dorsal sepal length (*vs.* anguste-linear, shorter than the dorsal sepal) and the rudimentary ovate, sub-triangular lower lobe (*vs.* anguste-triangular, falcate) and the triangular, concave appendix with a subcylindric, retuse almost glabrous apex (*vs.* convex, with a pubescent, flabellate apex). *Lepanthes valerieae* also resembles *L. antennata* mostly in its filiform, long upper lobes of the lip; however, it is distinguished by the long apical lobes of petals, surpassing the dorsal sepal (*vs.* shorter or as long as the dorsal sepal), the longer connectives > 18 mm (*vs.* <1 mm long), rounded lobes of the lip and the oblong, flattened appendix (*vs.* triangular, concave).

Morphological variation in *Lepanthes silverstonei* has been documented in several other localities near the *locus typus* (Sebastian Vieira, *pers. com.* November 2020). Apparently, the petals of that species vary from filiform to bifid and shorter to more prolonged than the sepals. In addition, the phylogenetic relationships of *L. valerieae* with other morphologically similar species, including *L. antennata* and *L. licrophora* Luer & B.T.Larsen, remains to be tested. Thus, the description of *L. valerieae*, in addition to *L. antennata*, *L. licrophora*, and *L. silverstonei* (and its possible variations), provides new morphometrical resources to test hypothesis on *Lepanthes* species complexes (Bogarín *et al.* 2018). Such data, in combination with different lines of evidence such as DNA sequences will further enable the conduc-

tion of future integrated monographic work in the genus (Grace *et al.* 2021) but also comparative studies focusing on generic delimitations in the lineage and Pleurothallidinae overall (Bogarín *et al.* 2019). Also, given the intricate vegetative and reproductive morphology (Luer 2011, Bogarín *et al.* 2018) and rapid speciations characteristic of the genus (Pérez-Escobar *et al.* 2017a), phylogenomic (Bogarín *et al.* 2018, Pérez-Escobar *et al.* 2020, Peakall *et al.* 2021, Pérez-Escobar *et al.* 2021, Serna-Sánchez *et al.* 2021) and statistical morphometric approaches (Bateman *et al.* 2018, 2021) are needed to sort such species complexes.

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LITERATURE CITED

- Amaya-Marquez, M. & Marín-Gómez, O. H. (2012). *Columnea rangellii* (Gesneriaceae), a new species from the Serranía de los Paraguas in the Colombian Andes. *Caldasia*, 34, 69–74.
- Antonelli, A. (2021). The rise and fall of Neotropical biodiversity. *Botanical Journal of the Linnean Society*, 20, 1–17. doi.org/10.1093/botlinnean/boab061.
- Antonelli, A., Ariza, M., Albert, J., Andermann, T., Azevedo, J., Bacon, C., Faurby, S., Guedes, T., Hoorn, C., Lohmann, L. G., Matos-Maraví, P., Ritter, C. D., Sanmartín, I., Silvestro, D., Tejedor, M., terSteege, H., Tuomisto, H., Werneck, F. P., Zizka, A., & Edwards, S. V. (2018a). Conceptual and empirical advances in Neotropical biodiversity research. *PeerJ*, 6, e5644.
- Antonelli, A., Nylander, J.A.A., Persson, C., & Sanmartín I. (2009). Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 9749–9754.
- Antonelli, A. & Sanmartín, I. (2011). Why are there so many plant species in the Neotropics? *Taxon*, 60, 403–414.
- Antonelli, A., Zizka, A., Carvalho, F. A., Scharn, R., Bacon, C. D., Silvestro, D., & Condamine, F. L. (2018b). Amazonia is the primary source of Neotropical biodiversity. *Proceedings of the National Academy of Sciences*, 115, 6034–6039. doi.org/10.1073/pnas.1713819115.
- Balbuena, J. A., Pérez-Escobar, O. A., Llopis-Belenguer, C., Blasco-Costa, I. (2020). Random Tanglegram Partitions (Random TaPas): an Alexandrian approach to the cophylogenetic Godian knot. *Systematic Biology*, 69, 1212–1230.
- Bateman, R. M., Murphy, A. R. M., Hollingsworth, P. M., Hart, M. L., Denholm, I., Rudall, P. (2018). Molecular and morphological phylogenetics of the digitate-tubered clade within subtribe Orchidinae s.s. (Orchidaceae: Orchideae). *Kew Bulletin*, 73, 1–30.

- Bateman, R. M., Rudall, P., Murphy, A. R. M., Cowan, R., Devey, D. S., Pérez-Escobar, O. A. (2021). Whole plastomes are not enough: phylogenomic and morphometric exploration at multiple demographic levels of the bee orchid clade *Ophrys* sect. *Sphogodes*. *Journal of Experimental Botany*, 72, 654–681.
- Bennett, D.E., & Christenson, E.A. (1998). New species of Peruvian Orchidaceae VI. *Lindleyana*, 13(2), 64–96.
- Bentham, G. (1839). *Plantas Hartwegianas: imprimis mexicanas adjectis nonnullis Grahamianis enumerat novasque*. Londini : [G. Pamplin.]. 393.pp.
- Blanco, M. A., Carnevali, G., Whitten, W. M., Singer, R. B., Koehler, S., Williams, N. H., Ojeda, I., Neubig, K. & Endara, L. (2007). Generic realignments in Maxillariinae (Orchidaceae). *Lankesteriana*, 7(3), 515–537.
- Bogarín, D., Pérez-Escobar, O. A., Groenenberg, D., Holland, S. D., Karremans, A. P., Lemmon, E., Lemmon, A., Pupulin, F., Smets, E., Gravendeel, B. (2018). Anchored hybrid enrichment generated nuclear, plastid and mitochondrial markers resolve the *Lepanthes horrida* (Orchidaceae: Pleurothallidinae) species complex. *Molecular Phylogenetics and Evolution*, 129, 27–47.
- Bogarín, D., Pérez-Escobar, O. A., Karremans, A. P., Fernández, M., Kruizinga, J., Pupulin, F., Smets, E., Gravendeel, B. (2019). Phylogenetic compaative methods improve the selection of characters for generic delimitatons in a hypediverse Neotropical orchid clade. *Scientific Reports*, 9, 1-17.
- Christenson, E. A. (2013). *Maxillaria; An unfinished monograph*. 2 vols. Published for Robert Christenson by Patricia Ann Harding, Lebanon OR, USA.
- Cuatrecasas, J. (1958). Aspectos de la vegetación natural de Colombia. *Revista académica Colombiana de Ciencias Exactas*, 10, 221–264.
- Darwin, C. (1846). *Geological observations of South America*. London: Smith, Elder and CO.
- García-Ramírez, D. A. & García-Revelo, J. S. (2013) Diversidad de orquídeas de los bosques altos de la Serranía de los Paraguas, Chocó Biogeográfico, Colombia. *Lankesteriana*, 13, 132–133.
- Gentry, A. H. (1982). Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Annals of the Missouri Botanical Garden*, 69, 557–593.
- Gentry, A.H. & Dodson, C.H. (1987). Diversity and Biogeography of Neotropical Vascular Epiphytes. *Annals of the Missouri Botanical Garden*, 74, 205–233.
- Givnish, T. J., Spalink D., Ames, M., Lyon, S. P., Hunter, Z., Zuluaga, A., Iles, W., Clements, M. A., Arroyo, M. T., Leebens-Mack, J., Endara, L., Kriebel, R., Neubig, K. M., Whitten, W. M., Williams, N. H. & Cameron, K. M. (2015). Orchid phylogenomics and multiple drivers of their extraordinary diversification. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20151553.
- Grace, O. M., Pérez-Escobar, O. A., Lucas, E. J., Vorontsova, M. S., Lewis, G. P., Walker, B. E., Lohman, L. G., Knapp, S., Wilkie, P., Sarkinen, T., Darbyshire, I., Lughadha, E. N., Monro, A., Woudstra, Y., Demissew, S., Muasya, A. M., Díaz, S., Baker, W. J., Antonelli, A. (2021). Botanical monograph in the Anthropocene. *Trends in Plant Science*, 26, 433–441.
- Helmer, E. H., Gerson, E. A., Scott Baggett, L., Bird, B. J., Ruzycki, T. S. & Voggeser, S. M. (2019). Neotropical cloud forests and páramo to contract and dry from declines in cloud immersion and frost. *PLoS ONE*, 14, 1–34. doi.org/10.1371/journal.pone.0213155
- Hoorn, C., Wesselingh, F. P., Steege, H., Bermudez, M. A., Mora, A., Sevink, J., Sanmartín, I., Anderson, C. L., Figueiredo, J. P., Jaramillo, C., & Riff, D. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, 330, 927–931.
- Humboldt, A. (1820). *Voyage aux régions équinoxiales du Nouveau Continent*. Paris: N. Mazé.
- Kirby, S. (2011). Active mountain building and the distribution of “core” Maxillariinae species in tropical Mexico and Central America. *Lankesteriana*, 11(3), 275–291.
- Küper, W., Krefth, H., Nieder, J., Köster, N. & Barthlott, W. (2004). Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. *Journal of Biogeography*, 31, 1477–1487.
- Luer, C. (2011). Miscellaneous new species in the Pleurothallidinae (Orchidaceae) excluding species from Brazil. *Harvard Papers in Botany*, 16(2), 311–310.
- Misas-Urreta, U. G. (2005). Orquídeas de la Serranía del Baudó, Chocó, Colombia. Bogota: Corporación Capitalina de Orquideología.
- Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M. & Gascon, C. (2011). Global Biodiversity Conservation: the Critical Role of Hotspots. In: F.E. Zachos & J.C. Habel (eds.), *Biodiversity Hotspots* (pp. 3–22). Berlin: Springer-Verlag.
- Myers N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

- Moreno, S., Rincón, M., Gutiérrez, N., Gil, K., Vieira-Urbe, S., Domínguez, E. & Hazzi N. (2019). *Lepanthes* of Colombia: areas of endemism, richness, and distribution. In A. M. Pridgeon & A. R. Arosemena (Eds.), *Proceedings of the 22nd World Orchid Conference*, vol. 1 (pp. 308–375). Guayaquil, Ecuador: Asociación Ecuatoriana de Orquideología.
- Orejuela, J. (2005). An integrated approach to orchid conservation in Colombia: what do orchids, hummingbirds, bears, potable water, and indigenous land rights have in common? *Selbyana*, 26, 32–45.
- Parra-Sánchez, E., Retana, J., & Centre, C. (2016). Edge influence on diversity of orchids in Andean Cloud Forests. *Forests*, 7, 1–13.
- Peakall, R., Wong, D. C., Phillips, R. D., Ruibal, M., Eyles, R., Rodríguez-Delgado, C. & Linde, C. (2021). A multi-tiered sequence capture strategy spanning broad evolutionary scales: applications for phylogenetic and phylogeographic studies of orchids. *Molecular Ecology Resources*, 21(4), 1118–1140. doi.org/10.1111/1755-0998.13327.
- Pérez-Escobar, O. A., Parra-Sánchez, E. & Valdivieso, P.O. (2009). Inventario orquideológico de la Reserva Bosque de Yotoco, Valle del Cauca. *Acta Agronómica*, 58, 189–196.
- Pérez-Escobar, O.A., Chomicki, G., Condamine, F.L., Karremans, A.P., Bogarín D., Matzke, N.J., Silvestro, D. & Antonelli, A. (2017a). Recent origin and rapid speciation of Neotropical orchids in the world's richest plant biodiversity hotspot. *New Phytologist*, 215, 891–905.
- Pérez-Escobar, O.A., Gottschling, M., Chomicki, G., Condamine, F.L., Klitgård, B.B., Pansarin, E., & Gerlach, G. (2017b). Andean Mountain building did not preclude dispersal of lowland epiphytic orchids in the Neotropics. *Scientific Reports*, 7, 4919, 1–10.
- Pérez-Escobar, O. A., Lucas, E. J., Jaramillo, C., Monro, A., Morris, S. K., Bogarín, D., Greer, D., Dodsworth, S., Aguilar-Cano, J., Meseguer, A. S. & Antonelli, A. (2019). The origin and diversification of the hyperdiverse flora in the Chocó biogeographic region. *Frontiers in Plant Science*, 10, 1328.
- Pérez-Escobar, O. A., Bogarín, D., Schley, R., Bateman, R. M., Gerlach, G., Harpke, D., Brassac, J., Fernández-Mazuuecos, M., Dodsworth, S., Hágater, E., Blanco, M. A., Gottschling, M. & Blattner, F. (2020). Resolving relationships in an exceedingly young Neotropical orchid lineage using Genotyping-by-Sequencing data. *Molecular Phylogenetics and Evolution*, 144, 106672.
- Pérez-Escobar, O. A., Dodsworth, S., Bogarín, D., Bellot, S., Balbuena, J. A., Schley, R., Kikuchi, I., Morris, S. K., Epitawalage, N., Cowan, R., Maurin, O., Zuntini, A., Arias, T., Serna, A., Gravendeel, B., Torres, M. F., Nargarm K., Chomicki, G., Chase, M. W., Leitch, I. J., Forest, F., & Baker, W.J. (2021). Hundreds of nuclear and plastid loci yield insights into orchid relationships. *American Journal of Botany*, 108(7), 1166–1180. https://doi.org/10.1002/ajb2.1702.
- Pérez-Escobar, O. A., Zizka, A., Bermúdez, M., Meseguer, A. S., Condamine, F. L., Hoorn, C., Hooghiemstra, H., Pu, Y., Bogarín, D., Boschman, L. M., Pennington, R. T., Antonelli, A., Chomicki, G. *In press*. The Andes through time and the evolution and distribution of Andean floras. *Trends in Plant Science*.
- Ramírez, S. R., Eltz, T., Fujiwara, M. K., Gerlach, G., Goldman-Huertas, B., Tsutsui, N. D. & Pierce, N. E. (2011). Asynchronous diversification in a specialized plant-pollinator mutualism. *Science*, 333, 1742–1746.
- Richter, M., Diertl, K., Emck, P., Peters, T. & Beck, E. (2009). Reasons for an outstanding plant diversity in the tropical Andes of Southern Ecuador. *Landscape Online*, 12, 1–35.
- Rodríguez-Martínez, L. & Blanco, M. A. (2015). A new species of *Camardium* (Orchidaceae: Maxillariinae) from the cloud forests of Colombia. *Phytotaxa*, 222(1), 61–66. https://doi.org/10.11646/phytotaxa.222.1.6
- Schlechter, R. (1921). Die Orchideenfloren der südamerikanischen Kordillerenstaaten. IV. Peru. *Repertorium Specierum Novarum Regni Vegetabilis, Beihefte*, 6–10, 1–900.
- Schuiteman, A. & Chase, M. (2015). A reappraisal of *Maxillaria* (Orchidaceae). *Phytotaxa*, 225(1), 1–78.
- Serna-Sánchez, M., Pérez-Escobar, O. A., Bogarín, D., Torres-Jimenez, M. F., Alvarez-Yela, A. C., Arcila-Galvis, J. E., Hall, C., de Barros, F., Pinheiro, F., Dodsworth, S., Chase, M. W., Antonelli, A., Arias, T. (2021). Plastid phylogenomics resolves ambiguous relationships within the orchid family and provides a solid timeframe for biogeography and macroevolution. *Scientific Reports*, 11, 6858.
- Silverstone-Sopkin, P. A. & Ramos-Pérez, J. E. (1995). Floristic exploration and phytogeography of the Cerro del Torra, Chocó, Colombia. *Biodiversity and conservation of Neotropical montane forests. Proc. symposium, New York Botanical Garden, 1993*.
- Szlachetko, D. L., Kolanowska, M., Medina Trejo, R. & Lipińska, M. (2017). New species of *Maxillaria* (Orchidaceae) from the Sibundoy valley, Colombia. *Botany Letters*, 164(2), 159–170. https://doi.org/10.1080/23818107.2017.1318091
- Ulloa, C. U., Acevedo-Rodríguez, P., Beck S., Belgrano, M. J., Bernal, R., Berry, P. E., Brako, L., Celis, M., Davidse, G., León-Yáñez, S., Magill, R. E., Neill, D. A., Nee, M., Raven, P. H., Stimmel, H., Strong, M. T., Villaseñor, J. L., Za-

- Lucchi, J. L., Zuloaga, F. O. & Jørgensen, P. M. (2017). An integrated assessment of the vascular plant species of the Americas. *Science*, 358, 1–5.
- Whitten, W., Blanco, M., Williams, N., Koehler, S., Carnevali, G., Singer, R., Endara, L. & Neubig, K. (2007). Molecular phylogenetics of *Maxillaria* and related genera (Orchidaceae: Cymbidieae) based on combined molecular data sets. *American Journal of Botany*, 94(11), 1860–1889. <https://doi.org/10.3732/ajb.94.11.1860>
- Zotz, G. (2013). The systematic distribution of vascular epiphytes – a critical update. *Botanical Journal of the Linnean Society*, 171, 453–481.