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Research Article

A new *Ophidion* (Orchidaceae, Pleurothallidinae) from the Pacific lowlands of Colombia and the unresolved phylogenetic position of *Phloeophila* s.l.

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A species new to science of a miniature orchid, endemic to the humid Pacific lowland, Municipality of Buenaventura (Valle del Cauca, Colombia), is described and illustrated. *Ophidion erectilabrum* sp. nov. is morphologically similar to *O. alphonsianum*, but the new species is recognized by the orbicular leaves (vs. elliptic), the erect inflorescence, longer than the leaves (vs. descending, shorter than the leaves), and the abruptly upward curved epichile (vs. flat). Because of the different proposals in the circumscription of *Phloeophila* s.l., we performed a new phylogenetic analysis to assess the most appropriate genus to place the new species, and discuss the phylogenetic position of *Luerella*, *Ophidion*, and *Phloeophila* based on all currently available data from nrITS and *mat*K and recent studies using high-throughput sequencing. Although the three genera are supported as monophyletic groups, we recovered unresolved relationships and discordant topologies among them using only these two molecular markers. Therefore, we describe this species in *Ophidion* because of the morphological differences between *Luerella* and *Phloeophila* and because the grouping of *Phloeophila* s.l. lacks diagnostic features, and is yet to be supported by molecular analysis.

Key words: Chocó biodiversity hotspot, orchids, phylogenetics, plant systematics, taxonomy

Introduction

The Neotropical orchid subtribe Pleurothallidinae is counted as one of the megadiverse angiosperm groups on Earth, with nearly 5500 species described in 48 genera representing about 20% of total orchid diversity (Chumová et al., 2021; Karremans & Vieira Uribe, 2020). Due to its extraordinary number of species, morphological diversity, and complex ecological interactions with pollinators, Pleurothallidinae has been a model for studying the diversification of angiosperms. For example, Pérez-Escobar et al. (2017) found that the group displays one of the highest species diversification rates among angiosperms with accelerated diversification across elevational zones in Central America and montane environments in the Andes. Furthermore, other studies have shown that Pleurothallidinae is a model for studying genome evolution and its role in plant diversification (Chumová et al., 2021). However, even though hundreds of new species have been described for science, mainly in the last 40 years, the trend of describing new species continues at a constant rate, mainly in megadiverse countries such as Colombia (Restrepo et al., 2022). Therefore, we are still far from knowing an accurate estimate of the number of species of the subtribe (Karremans & Vieira Uribe, 2020).

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The genus *Ophidion* belongs to the Pleurothallidinae and was erected by Luer (1982) including four species previously treated under *Cryptophoranthus* by Barbosa Rodrigues (1881). The genus *Cryptophoranthus* was based on *C. fenestratus* (Barb. Rodr.) Barb.Rodr. (=*Acianthera fenestrata* (Barb. Rodr.) Pridgeon & M.W. Chase) a species now considered under *Acianthera* s.l. Scheidw (Pridgeon & Chase, 2001). Species of *Cryptophoranthus* were segregated into several genera of the Pleurothallidinae characterized by the apex of the dorsal sepal connate to the synsepal (Pridgeon et al., 2001). This feature is homoplastic and evolved independently in species of Pleurothallidinae included in *Acianthera*, *Luerella* Braas, *Ophidion*, *Phloeophila* Hoehne & Schltr., *Specklinia* Lindl., and *Zootrophion* Luer, among others (Bogarín et al., 2019).

Phloeophila was described by Hoehne and Schlechter (1926) and lectotypified by *Phloeophila paulensis* (=*Phloeophila echinantha* (Barb. Rodr.) Hoehne & Schltr.). Initially, Luer (1986) treated the genus under *Pleurothallis* subgenus *Acianthera* sect. *Phloeophilae*. Later, Pridgeon et al. (2001) assessed the phylogenetic relationships of the Pleurothallidinae including the phylogenetic position of *Luerella*, *Ophidion*, and *Phloeophila*. However, the relationships recovered among these genera were uncertain because of topological discordances between plastid and nuclear datasets and low bootstrap support attained in branches. Here, *Ophidion* was recovered as sister to *Pleurothallis*+*Stelis* clade in the combined *mat*K/*trn*L-F/nrITS analysis, whereas with the nrITS, *Ophidion* was sister to *Luerella* and *Phloeophila*. Notwithstanding the poorly supported relationships and topological incongruence, Pridgeon et al. (2001) proposed tentatively merging *Ophidion* and *Luerella* into *Phloeophila* based on the nrITS dataset alone. This proposal was followed by subsequent authors (Chiron et al., 2016; Matthews, 2018; Vierling, 2019), excluding Luer (2002), who argued that vegetative and reproductive morphology of these three groups are divergent enough to grant them the status of genera.

Although Pridgeon (2005) recognized vegetative and floral differences among the repent species of *Phloeophila* with the cespitose *Luerella* and *Ophidion* he decided to merge them under a broad concept of *Phloeophila* because the three genera formed a clade in their nrITS analysis. Again, Luer (2006) considered this a discordant, morphologically incompatible grouping and maintained *Luerella*, *Ophidion*, and *Phoeophila* as separate. Chiron et al. (2016) did not follow this proposal and maintained *Phloeophila* s.l. as circumscribed by Pridgeon et al. (2001). However, recent studies based on multilocus datasets indicate incongruences between nuclear and plastid data regarding the position of *Luerella* and *Ophidion*, although species of *Phloeophila* s.s. were not yet evaluated (Chumová et al., 2021). Therefore, Karremans and Vieira Uribe (2020) and Jiménez et al. (2021) followed Luer (2006) and treated the three genera as separate.

Ophidion is characterized by caespitose plants, with erect and short ramicauls with thin alternate spiral leaves. Inflorescences elongate, arcuate, successively flowered; the apical portion of the dorsal sepal is connate to the apical part of the synsepal, provided lateral openings of the flower. The most distinguishing features of *Ophidion* is the proportionately large lip, nearly filling the synsepal cavity, the blade-like epichile and concave hypochile with lateral lobes auriculate (Luer, 2004).

Luerella is a monotypic genus based on *Masdevallia pelecaniceps* Luer and established by Braas (1979). The single species, *L. pelecaniceps* (Luer) Braas is endemic to Panama and differs from *Masdevallia* and *Ophidion* in the thickened sepals with verrucose margins and corrugations in the adaxial surface not fused at the apex and the lip structure, which is elliptical, acute, geniculate, thickened at the apex with a pair of uncinate, small lobes. In contrast, plants of *Phloeophila* are creeping, repent, ramicauls with thick, prostrate, coriaceous, orbicular, verrucose, alternate distal leaves, and single small flowers, externally fleshy, proportionally as large or larger than the leaves. The lip is oblong, shorter than the synsepal, with erect margins below the middle (Jiménez et al., 2021; Karremans & Vieira Uribe, 2020; Luer, 2006). Inflorescences with pubescent sepals, and a dorsal sepal fused to the synsepal below the middle. *Phloeophila* includes about three species ranging from Mexico and the Antilles to Brazil (Luer, 2006).

Some authors still favoured *Phloeophila* s.l. as circumscribed by Pridgeon and Chase (2001). Matthews (2018) recently described two species under *Phloeophila*, one from Colombia and another from an unknown locality. Subsequently, Vierling (2019) added eight species in *Phloeophila*, unfortunately without citing a country of origin. These recently described species fit with Luer's concept of *Ophidion* and thereafter they were later transferred to the genus along with a new species by Moreno and Karremans (2020) based on preliminary molecular results by Chumová et al. (2021) and morphological differences pointed out by Luer (2006). *Ophidion*, as circumscribed by Luer (1982), currently includes 15 species ranging from south-eastern Panama to Colombia, Venezuela, Ecuador, Peru, and Bolivia. Five species have been recorded from Colombia (Betancur et al., 2015; Matthews, 2018). Members of *Ophidion* are found in humid lowland and high Andean forests in Colombia, where orchids stand as the most diverse component of the flora (Pérez-Escobar et al., 2022) and novelties in the Pleurothallidinae are discovered continuously (Hágsater et al., 2013; Pérez-Escobar et al., 2010, 2011; Reina-Rodríguez et al., 2019, 2020; Valdivieso et al., 2009). The discovery of new species to science is possible due to large areas that still remain unexplored such as the Pacific lowlands (Pérez-Escobar et al., 2019), where these miniature species occupy specialized niches in the forest canopy (Reina-Rodríguez et al., 2019). Recent species descriptions (Matthews, 2018; Moreno & Karremans, 2020; Vierling, 2019), suggest the genus diversity might expand when explorations in the Neotropical realm are conducted jointly with monographic work (Grace et al., 2021).

A morphologically distinct species of *Ophidion* was found while we worked with the ranger team and community members of the Escalerete and San Cipriano National Protective Forest Reserve, Valle del Cauca, Colombia. To assess whether this species should be assigned to *Ophidion* or *Phloeophila* s.l., in this study we conducted phylogenetic analyses with all current available data of these genera from nrITS and *mat*K in the NCBI GenBank database (https://www.ncbi.nlm.nih.gov/genbank/). Also, we evaluated the incongruence between plastid and nuclear datasets and describe and illustrate a new species of *Ophidion* currently endemic to Valle del Cauca, Colombia.

Materials and methods

During 2019 and 2020, a sampling of vascular epiphytes focused on Orchidaceae and Bromeliaceae was carried out within the Escalerete and San Cipriano National Protective Forest Reserve, in the lower basin of Dagua river, Buenaventura, Colombia. The type specimen *in situ* was photographed with an EOS 60 D® using a 60 mm macro lens. Morphometric data were obtained with Micro-Capture Software Ver. 2.0 (20×–200×). Dissections of the plant and flower were arranged according to LCDP format and were edited with Adobe Photoshop® CS4. The spirit material was used to prepare the line drawing. Plant material was preserved as a voucher in the herbarium (CUVC) at the Universidad del Valle in Cali. Location map was prepared with ArcGIS 10, module ArcMap ESRI®. The website http://es.climate-data.org was used to determine the weather. We used The International Plant Name Index IPNI (2020) (https://www.ipni.org), and Tropicos (http://www.tropicos.org) for accepted names.

Phylogenetic analyses

To test the phylogenetic position of *Luerella*, *Ophidion*, and *Phloeophila* and assess the most appropriate genus to describe the new species, we obtained nuclear (nrITS) and plastid (*mat*K) sequences of 248 selected accessions of Pleurothallidinae from NCBI GenBank. The datasets included four accessions of *Ophidion*, two *Phloeophila* s.s. and one *Luerella*. This is the first study in which several DNA sequences of *Phloeophila* s.l. are analyzed in a comparative phylogenetic framework (Table 1). Most of the sequences are from our ongoing research on the Pleurothallidinae (Bogarín et al., 2019; Pérez-Escobar et al., 2017) plus other sequences such as *O. carrilloi* not available at the time of our phylogenetic reconstruction of the subtribe. Phylogenetic analyses were performed for the nrITS and *mat*K datasets and for a combined nrITS+*mat*K dataset following the procedures described in Pérez-Escobar et al. (2017) and Bogarín et al. (2019). We performed Maximum likelihood (ML) analyses with RAxML-HPC2 on XSEDE (8.2.10) (Stamatakis et al., 2008) using 1,000 bootstrap iterations. We plotted the bootstrap percentages for ML (MLB) on the ML 50% majority-rule consensus tree and a comparison of the nrITS and *mat*K tree using the R packages ape and phytools (Paradis et al., 2004; R Core Team, 2017; Revell, 2012). Sequences and alignments were edited in Geneious © 8.1.7 (Biomatters Ltd). Final trees were edited in Adobe® Illustrator CS6 (Adobe Systems Inc., CA, USA). We evaluated the incongruence between plastid and nuclear datasets with the Procrustean Approach to Cophylogeny (PACo) application (Balbuena et al., 2013) in R (http://datadryad.org/review?doi=doi:10.5061/dryad.q6s1f) implemented by Pérez-Escobar et al. (2016). The test was executed on 1,000 nuclear and plastid bootstrap replicate trees derived from RAxML. The phylogenetic results were interpreted with available morphological data complemented with herbarium specimens (Luer, 1982, 2006).

Results

Phylogenetic position of Ophidion, Luerella, *and* Phloeophila

The three genera are supported as monophyletic groups, but their interrelationships are still uncertain because of the low bootstrap percentages and discordant topologies between plastid and nuclear datasets. In the nrITS phylogeny, *Ophidion*, *Luerella*, and *Phloeophila* were grouped together but with low support (Maximum likelihood bootstrap [MLB] = 45%) for *Ophidion* as sister to *Luerella*+*Phloeophila* and 78% for the grouping

Table 1. NCBI GenBank accession numbers and species of the two molecular markers analysed.

Species	Voucher	nrITS	*mat*K
Acianthera aberrans	FP7839	KY084268	KY218740
Acianthera atropurpurea	Zampin 25	KT599874	KT709633
Acianthera breedlovei	AK3962	KY084269	KY218743
Acianthera butcheri	FP8127	KY084270	KY218749
Acianthera cabiriae	AK5440	KY084272	KY218751
Acianthera cogniauxiana	AK5879	KR816545	KR816554
Acianthera crassilabia	AK5870	KY084273	KY218754
Acianthera decipiens	AK4229	KY084274	KR816555
Acianthera erinacea	AK5984	KY084293	KY218778
Acianthera erosa	AK7315	KY084290	KY218775
Acianthera fenestrata	MWC6798	AF262857	AF265468
Acianthera fenestrata	Rodrigues 506	JQ306353	KT709635
Acianthera geminicaulina	AK5209	KY084275	KY218756
Acianthera hamata	DB5114	KY084277	KY218759
Acianthera hatschbachii	Rodrigues 503	KT599876	KT709638
Acianthera hondurensis	DB9255	KY084280	KY218761
Acianthera hystrix	Rodrigues 507	KT599877	KT709639
Acianthera johnsonii	AK5720	KY084282	KY218762
Acianthera johnsonii	AK5727	JQ306378	KR816556
Acianthera josephensis	HBG120676	EF079371	EF079330
Acianthera lanceana	AK5452	KY084284	KY218765
Acianthera lepidota	AK5796	KY084285	KY218766
Acianthera lojae	AK2746	KR816549	KR816558
Acianthera luteola	Rodrigues 509	KX495754	KT709640
Acianthera mantiquyrana	Rodrigues 520	KT599878	KT709641
Acianthera octophrys	Rodrigues 521	KT599879	KT709643
Acianthera oscitans	AK5175	KY988806	KY988625
Acianthera prolifera	Rodrigues 513	KT763378	KT709644
Acianthera saurocephala	MWC5534	AF262851	AF265469
Acianthera sicaria	AK121	KY084286	KY218769
Acianthera sicaria	MWC5609	JQ995335	AF302648
Acianthera sp.	AK5432	JQ306359	KY218772
Acianthera teres	Rodrigues 519	KT763379	KT709649
Acianthera testifolia	AK4914	KR816551	KR816560
Acianthera tricarinata	AK5954	KY084289	KY218773
Anathallis anfracta	AK5499	KY084291	KY218777
Anathallis angustilabia	MWC5631	AF262868	AF302647
Anathallis burzlaffiana	AK4857	KC425727	KC425857
Anathallis funerea	DB10298	KY988807	KY988627
Anathallis lewisiae	DB1056	KC425733	KC425858
Anathallis linearifolia	MWC1104	MN551449	AF265473
Anathallis pabstii	AK4821	KC425737	KC425859
Andinia longiserpens	LO4515	AF262837	KP012520
Andinia nummularia	AN050	KR827583	KP012525
Andinia pensilis	AP200	KP01234	KP012517
Andinia schizopogon	AN069	KR827588	KR709295
Andinia xenion	AN074	KP012358	KP012522
Arpophyllum giganteum	s.n.	AF266742	AF263768
Barbosella australis	AK5758	MF669943	KY988628
Barbosella cucullata	MWC1334	AF262815	AF265483
Barbosella dolichorhiza	HBG123410	EF079370	EF079328
Brachionidium kirbyii	DB9045	KY988809	KY988629
Brachionidium valerioi	MWC1459	AF262913	AF265488
Coelia macrostachya	s.n.	AY008472	AY121743
Dilomilis montana	MWC206	AF262915	AY368404
Diodonopsis erinacea	MWC1106	AF262788	EU214180
Domingoa nodosa	s.n.	AY008565	AY425794
Draconanthes aberrans	AK5978	KC425741	KY988630
Dracula chimaera	MWC967	AF262766	AF265444
Dracula inexperata	DB7437	KY988811	KY988631
Dresslerella elvallensis	AK5741	AF262902	KY988632
Dresslerella hispida	AK5738	KY988813	KP012427

(*continued*)

Table 1. Continued.

Species	Voucher	nrITS	*mat*K
Dresslerella hispida	DB10001	KY988817	KP012428
Dresslerella pilosissima	DB6243	KY988818	KP012446
Dryadella albicans	AK4861	KC425742	KC425863
Dryadella edwallii	MWC305	AF262824	AF265454
Dryadella fuchsii	AK6180	KY988820	KY988636
Dryadella hirtzii	HBG123364	EF079367	EF079327
Dryadella simula	MWC1095	AF262825	AF265453
Dryadella yupanki	AK4858	KC425748	KP012498
Earina autumnalis	s.n.	AF260149	AF263656
Earina valida	C296	AF521077	EU214340
Echinosepala aspasicensis	MWC971	AF262905	AF302645
Echinosepala pan	DB1913	KP012471	KP012429
Echinosepala sempergemmata	DB5775	KP012473	KY988637
Echinosepala shuarii	AK5498	KP012475	KP012437
Echinosepala uncinata	MWC1321	AF262904	AF265478
Epibator ximenae	AK6502	KY989001	KY988805
Frondaria caulescens	MWC5928	AF262914	AF265471
Helleriella guerrerensis	s.n.	AF260142	AF263761
Isochilus amparoanus	s.n.	AF260143	AF263762
Lankesteriana casualis	AK6190	KY988821	KY988638
Lepanthes ankistra	AK6147	KY988822	KY988639
Lepanthes atrata	DB11053	KY988823	KY988640
Lepanthes blephariglossa	DB9604	KY988824	KY988641
Lepanthes blepharistes	DB11465	KY988826	KY988643
Lepanthes calliope	DB11873	KY988832	KY988649
Lepanthes calodyction	DB11872	KY988833	KY988650
Lepanthes caprimulgus	DB11874	KY988835	KY988652
Lepanthes dubbeldamii	AK6464	KY988849	KY988665
Lepanthes elata	DB10554	KY988850	KY988666
Lepanthes kleinii	FP7999	KY988862	KY988678
Lepanthes latisepala	DB11102	KY988863	KY988679
Lepanthes wendlandii	DB11827	KY988894	KY988710
Lepanthopsis astrophora	MWC5613	KY988897	AF265487
Lepanthopsis floripecten	DB7795	MK306369	KY988714
Luerella pelecaniceps	MWC1128	DQ923793	AF265450
Masdevallia calura	DB8888	KY988900	KY988716
Masdevallia eburnea	AK6360	KY988901	KY988717
Masdevallia floribunda	MWC296	AF262776	AY368416
Masdevallia fulvescens	DB9316	KY988903	KY988719
Masdevallia lata	AK5290	KY988905	KY988721
Masdevallia molossus	AK6465	DQ923769	KY988722
Masdevallia pinocchio	MWC976	AF262778	AF265445
Masdevallia smallmaniana	DB10767	KY988907	KY988723
Masdevallia zahlbruckneri	AK6495	KY988911	KY988727
Muscarella cabellensis	AK5712	KF747794	KP012396
Muscarella catoxys	AK6488	KY988912	KY988728
Muscarella furcatipetala	AK6489	KY988913	KY988729
Muscarella hastata	DB4910	KF747773	KR816553
Muscarella schudelii	AK6493	KY988914	KY988730
Muscarella semperflorens	AK6492	KY988915	KY988731
Myoxanthus exasperatus	AK5952	KY988918	KP012439
Myoxanthus hirsuticaulis	DB5875	KY988919	KP012442
Myoxanthus parahybunensis	AK5953	KY988922	KP012440
Myoxanthus punctatus	MWC1324	AF262885	AF265479
Myoxanthus scandens	AK1322	KY988921	KP012443
Myoxanthus serripetalus	HBG124228	EF079369	EF065600
Nemaconia striata	C6168	KY239236	KY239496
Neocogniauxia hexaptera	C244	AF260148	AF263766
Octomeria costaricensis	DB8920	KY988924	KY988733
Octomeria gracilis	MWC977	AF262911	AF265484
Octomeria valerioi	DB10504	KY988925	KY988734

(*continued*)

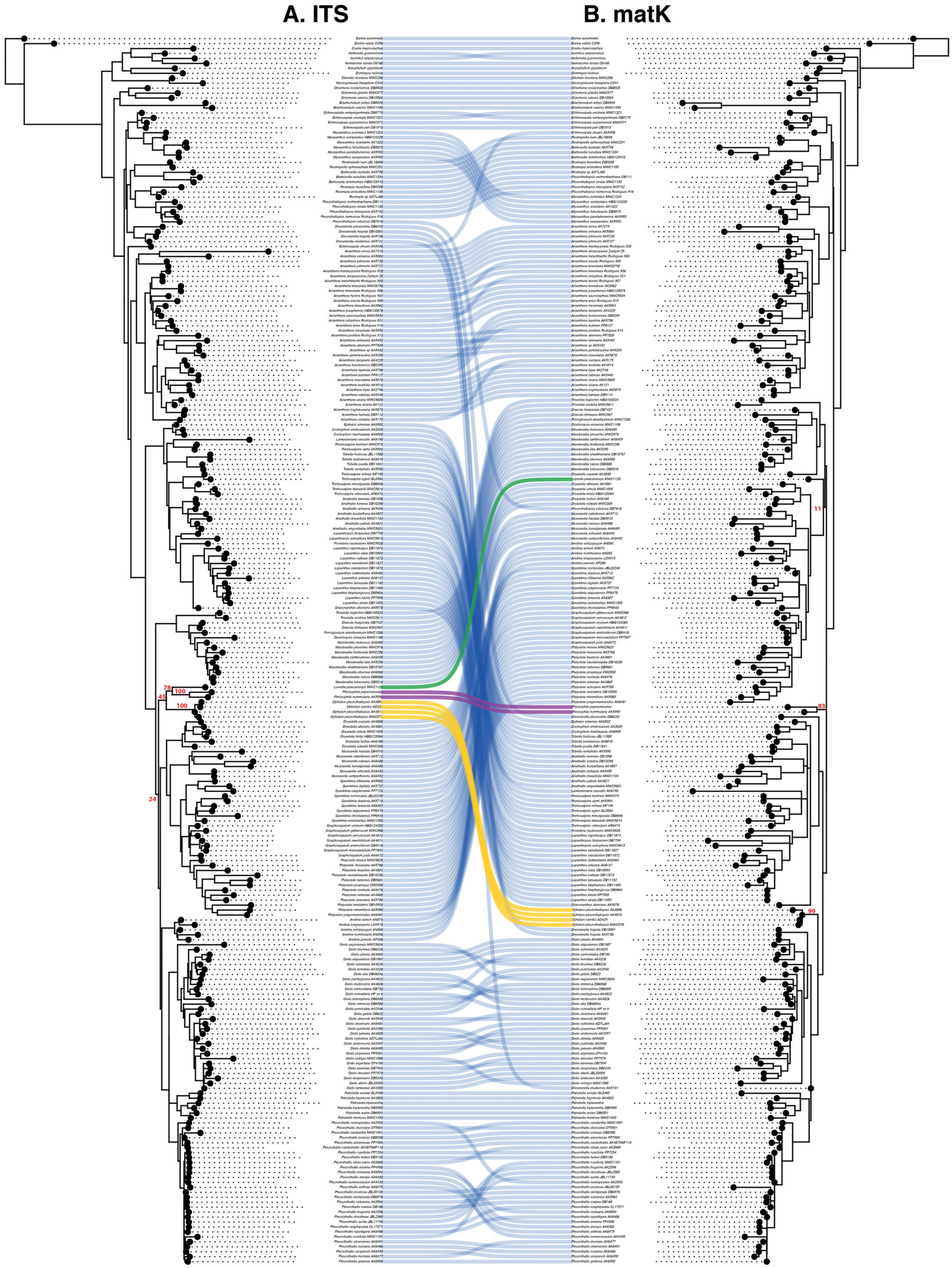
Table 1. Continued.

Species	Voucher	nrITS	*mat*K
Ophidion carrilloi	AD425	MK294817	MK258045
Ophidion pleurothallopsis	AK4818	KC425746	KP012495
Ophidion pleurothallopsis	AK4856	KC425747	KP012496
Ophidion pleurothallopsis	MWC978	MK306372	AF265451
Pabstiella aryter	DB6501	MN551424	JF934876
Pabstiella hypnicola	AK4803	JQ995333	KY988735
Pabstiella mentosa	MWC1453	AF262864	AF265486
Pabstiella seriata	GL0460	KJ472381	KJ472337
Pabstiella tripterantha	s.n.	AF262834	AF302649
Pabstiella tripterantha	DB5905	JF934815	JF934875
Pendusalpinx berlineri	MWC975	AF262900	AF265475
Pendusalpinx sijmii	AK5994	KY988993	KY988801
Phloeophila nummularia	AK5959	KF747839	KP012380
Phloeophila peperomioides	s.n.	AF275690	AF291103
Platystele acicularis	AK5785	KF747778	KP012383
Platystele beatricis	AK4801	KC425749	KP012499
Platystele catiensis	DB9661	KP012491	KP012384
Platystele caudatisepala	DB10230	KP012492	KP012385
Platystele jungermannioides	AK6461	KY988926	KY988736
Platystele lancilabris	DB10593	KP012493	KP012386
Platystele minimiflora	AK5980	KF747782	KP012387
Platystele misasiana	AK5768	KF747783	KP012388
Platystele misera	MWC5625	AF262823	AF265470
Platystele propinqua	CMS500	KF747785	KP012390
Platystele resimula	AK6476	KY988927	KY988737
Platystele ximenae	AK4865	KC425760	KP012502
Pleurothallis adventurae	FP7904	KY988929	KY988738
Pleurothallis anceps	AK6483	KY988930	KY988739
Pleurothallis anthrax	AK6475	KY988931	KY988740
Pleurothallis arietina	FP4500	KY988932	KY988741
Pleurothallis aurita	JBL11749	KY988933	KY988742
Pleurothallis bogarinii	AK2396	KY988934	KY988743
Pleurothallis cardiantha	MWC1091	AF262832	AF265462
Pleurothallis cardiothallis	AK4879	KY988936	KY988744
Pleurothallis cypelligera	AK6486	KY988937	KY988745
Pleurothallis dentipetala	DB6976	KY988938	KY988746
Pleurothallis discoidea	OT5901	KJ472423	KJ472364
Pleurothallis dorotheae	JBL2369	KY988940	KY988748
Pleurothallis eumecocaulon	AK4435	KY988941	KY988749
Pleurothallis gratiosa	AK6500	KY988942	KY988750
Pleurothallis helleri	DB5130	KY988943	KY988751
Pleurothallis inornata	AK6477	KY988944	KY988752
Pleurothallis pruinosa	JBL00135	KY988946	KY988753
Pleurothallis renieana	AK6504	KY988947	KY988754
Pleurothallis restrepioides	AK2953	JF934795	FR837536
Pleurothallis rowleei	DB168	KY988949	KY988756
Pleurothallis ruscaria	AK6466	KY988950	KY988757
Pleurothallis ruscifolia	FP7254	JF934814	JF934874
Pleurothallis ruscifolia	MWC1101	AF262836	AF265463
Pleurothallis scaphipetala	CL17371	KY988951	KY988758
Pleurothallis scoparum	AK6499	KY988952	KY988759
Pleurothallis silvae-pacis	AK3069	JQ995337	KY988760
Pleurothallis silverstonei	AK6491	KY988953	KY988761
Pleurothallis tonduzii	DB8358	KY988956	KY988763
Pleurothallis volcanica	AK3564	KY988957	KY988764
Pleurothallopsis microptera	AK5742	KY988958	KY988765
Pleurothallopsis nemorosa	Rodrigues 516	KT599880	KT709650
Pleurothallopsis reichenbachiana	DB111	KY988959	KY988766
Pleurothallopsis striata	MWC1103	JF934800	AF265480
Pleurothallopsis tubulosa	DB7618	KY988961	KY988768
Porroglossum amethystinum	MWC1336	AF262804	AF265448
Restrepia aristulifera	MWC1109	AF262907	AF265481

(*continued*)

Table 1. Continued.

Species	Voucher	nrITS	*mat*K
Restrepia muscifera	DB9208	KY988965	KP012449
Restrepia sp.	AD7LJ60	MF349131	MF349936
Restrepiella lueri	JBL18696	KY988966	KY988769
Restrepiella ophiocephala	MWC291	AF262909	AF265482
Scaphosepalum anchoriferum	DB5418	KP012459	KP012392
Scaphosepalum gibberosum	MWC968	AF262817	AF265458
Scaphosepalum jostii	AK6472	KY988967	KY988770
Scaphosepalum microdactylum	FP7897	KP012460	KP012393
Scaphosepalum swertiifolium	AK4811	KC425765	KP012504
Scaphosepalum ursinum	HBG124283	EF079365	EF079325
Scaphosepalum verrucosum	AK4812	KC425767	KP012505
Specklinia alajuelensis	FP8470	KY988968	KY988771
Specklinia calyptrostele	FP7724	KF747798	KP012398
Specklinia cfliliacina	AK5962	KF747828	KP012421
Specklinia chontalensis	FP6543	KF747799	KP012399
Specklinia corniculata	JBL02240	AF262862	KP012401
Specklinia digitalis	AK5737	KF747806	KP012404
Specklinia displosa	AK5713	KF747808	KP012405
Specklinia endotrachys	MWC1303	AF262859	AF265456
Specklinia lanceola	AK6307	KC425845	KY988777
Stelis alajuelensis	DB1987	JF934810	JF934870
Stelis allenii	JBL03905	JQ995342	KY988780
Stelis alta	DB4604a	JF934804	JF934865
Stelis anderssonii	AK2957	JF934777	JF934841
Stelis argentata	OT4104	AF262879	KJ472346
Stelis atwoodii	AK3540	JQ995343	KY988781
Stelis brunnea	DB6226	JF934798	JF934859
Stelis carnosilabia	DB730	JF934807	JF934868
Stelis convallaria	HF sn	JF934792	JF934852
Stelis cylindrata	AK4025	JQ995345	KY988784
Stelis cylindrica	AD7LJ64	MF349139	MF349928
Stelis despectans	DB5249	JF934762	JF934832
Stelis dimidia	AK6485	KY988977	KY988785
Stelis divaricans	AK6481	KY988939	KY988747
Stelis dressleri	FP7579	JQ306410	JF934830
Stelis ferrelliae	AK4326	JQ995347	KY988786
Stelis galeata	AK4800	JQ995348	KY988787
Stelis gelida	DB622	JF934778	JF934842
Stelis immersa	DB6588	JQ306502	JF934850
Stelis kareniae	DB7594	JF934769	JF934834
Stelis lankesteri	AK4269	JQ995353	KY988788
Stelis listerophora	DB6000	JF934785	JF934846
Stelis multirostris	AK4826	JQ995354	KY988789
Stelis pachyglossa	AK4822	JQ995359	KC425865
Stelis pileata	AK4604	JQ995329	KC425861
Stelis poasensis	FP5301	KF747836	JF934839
Stelis pulchella	AK2480	JF934772	JF934836
Stelis punctulata	AK2946	JF934783	JF934845
Stelis rodrigoi	MWC1088	AF262829	AF265460
Stelis segoviensis	MWC5634	AF262866	AF276313
Trichosalpinx blaisdellii	MWC5614	MK306385	AF265474
Trichosalpinx egleri	GL0584	KJ472384	KJ472357
Trichosalpinx minutipetala	DB8696	KY988987	KY988795
Trichosalpinx orbicularis	AR6474	MK306391	KY988797
Trichosalpinx reflexa	MF195	MK306394	KY988800
Trisetella scobina	MWC5611	AF262808	AF265449
Trisetella triglochin	HBG103324	EF079368	EF065592
Tubella cedralensis	AK6010	KY988985	KY988793
Tubella fruticosa	JBL11580	KY988986	KY988794
Tubella nymphalis	AK5950	KY988988	KY988796
Tubella pusilla	DB11841	KY988990	KY988798
Zootrophion endresianum	AK3035	KY988994	KY988802
Zootrophion machaqway	AK6505	KY988998	KY988803


A. ITS
B. matK

Luerella+*Phloeophila* (Fig. 1). The four accessions of *Ophidion* and the two *Phloeophila* accessions constituted two independent monophyletic groups with maximum statistical support (MLB = 100%). *Luerella* with only one accession, did not cluster within any of the accessions of *Ophidion* and *Phloeophila*. The phylogenetic analysis derived from the *mat*K dataset recovered *Ophidion* as a monophyletic group with strong support (MLB = 99%), whereas the clustering of the two accessions of *Phloeophila* received moderate support (MLB = 83%). In contrast, *Luerella* clustered with the *Specklinia* clade with low support (MLB = 11%). The relationships of the three genera within the Pleurothallidinae were uncertain with the analyses inferred from the *mat*K dataset. Incongruences were detected with PACo analysis, but they were all linked to unsupported branches (MLB = <70%). Thus, in the combined analysis the results were similar to the tree inferred with nrITS. *Ophidion*, *Luerella*, and *Phloeophila* were grouped together but with low support (MLB = 39% for *Ophidion* as sister to *Luerella*+*Phloeophila* and 59% for *Luerella*+*Phloeophila*) (Fig. 1).

Systematic treatment

Ophidion erectilabrum Reina-Rodr., Ó.Pérez & Bogarín sp. nov. (Fig. 2)

Type. COLOMBIA. Valle del Cauca: Municipio de Buenaventura, Reserva Forestal Protectora Nacional de los ríos Escalerete y San Cipriano, Bosque muy húmedo tropical. 184 m, 19 de septiembre 2019, Epífita miniatura, creciendo sobre bejuco "chicao", *Guillermo Reina-Rodríguez, Isabel Nicholls, Yerlin Hernández, Enrique Payán, Jose Einer Murillo Rivas 3044* (holotype CUVC!).

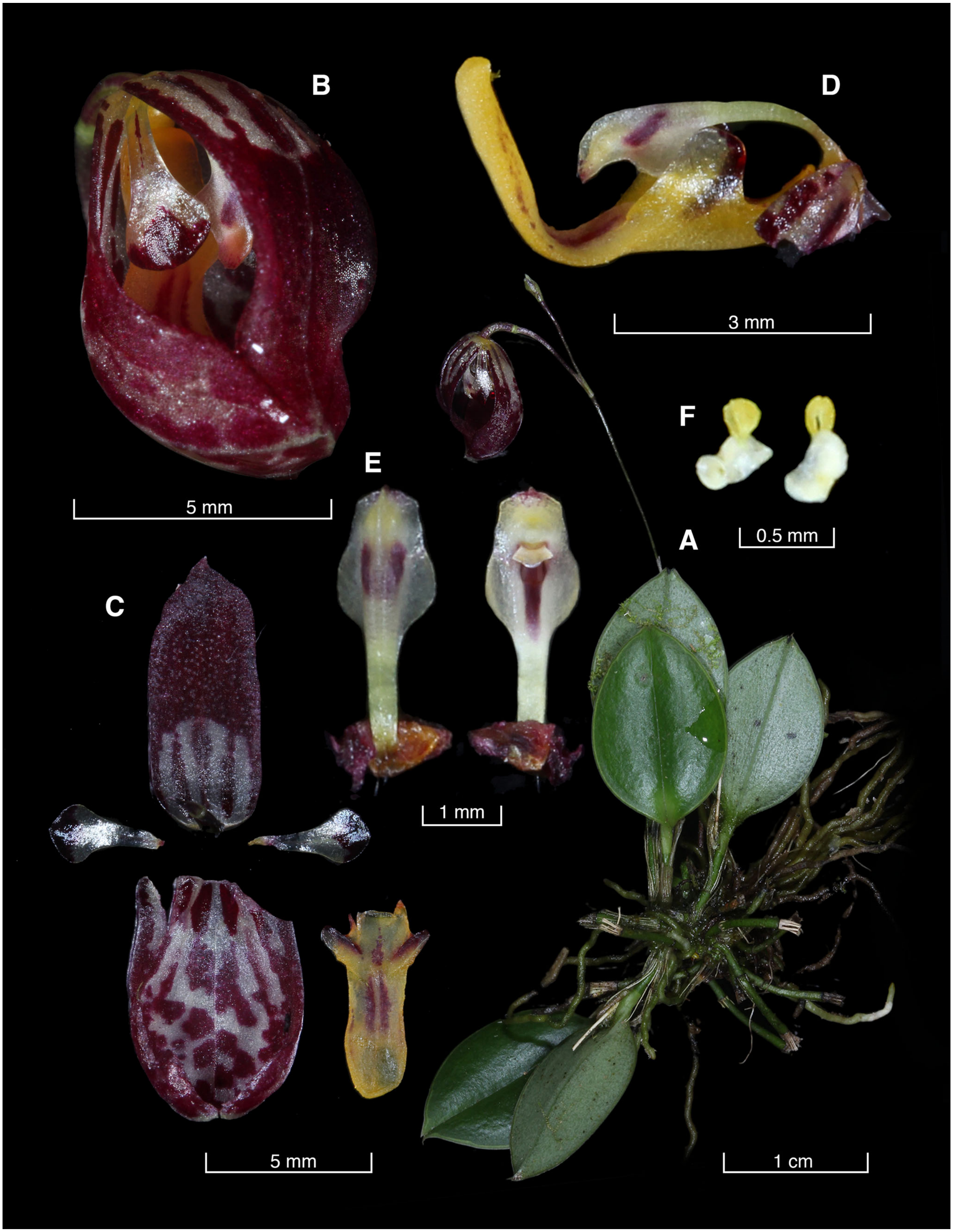
Diagnosis. *Ophidion erectilabrum* Reina-Rodr., Ó.Pérez & Bogarín is similar to *O. alphonsianum* (L.E.Matthews ex Doucette) Karremans & J.S.Moreno, but it differs in the smaller leaf blade, the erect, lax inflorescence and the smaller, narrowly oblong lip with ascending epichile.

Epiphytic, caespitose, erect, plant up to 4.5–5.0 cm tall, including the inflorescence. Roots basal, swollen, and sinuous up to 6 mm long. Ramicauls 4–8 mm long, short, with two internodes enclosed by sheaths. Sheaths (3) 2.0–5.0 × 1.0–2.0 mm funnel-shaped, papery-fibrous, enclosed by ribbed, successively longer sheaths. Leaf 12.0–13.9 × 8.0–9.7 mm, orbicular, glossy, rigid, conduplicate, basally truncate, cuneate, margin entire with a double vein, apex bicuspid. Apiculus 0.6 mm, protruding. Inflorescence including peduncle 43.0 × 0.3 mm, borne in the apex of ramicaul, unique, infrafoliar or lateral with annulus, filiform and terete, three times longer than blade. Pedicels 5.0–7.0 mm, curved, dichotomic, terete, with one flower produced at a time by pedicel. Inflorescence bracts (3), 2.0 mm long, cylindrical, brown, attached to the peduncle, spaced 12–14 mm. Ovary 1.5 mm long, green with red wine stains, basally white, curved with ribs. Flower 9.0 mm × 4.0 mm, cymbiform, petals and synsepal whitish with dark red wine spots, the lip yellowish with reddish stains at the base of the lateral lobes and in the centre. Dorsal sepal 8.0–8.5 × 4.0–4.5 mm, oblong-acute, basally truncate, abaxially papillose, red wine colouration apically, basally whitish with three dark red wine colour lines. Synsepal 9.0–9.2 × 3.2–3.5 mm cymbiform, entire, whitish with red wine stains. Petals 4.0 × 1.7 mm, spathulate, basally translucent, apically dark red wine, entire. Lip 4.5 × 1.5 mm, trilobed, the lateral lobes 1 mm long, curved forward, rounded towards the apex, obtuse, entire, the central lobe oblong, epichile ascending, obtuse, with a thickened and erose margin, the callus narrowly elongated towards the centre of the lip, parallel, yellow with reddish stains on the lateral lobes and at the base of the midlobe along the central keel. Column 3 mm long, curved, basally narrow, distally widened, whitish, dorsally with elongated dark red wine spots. Anther and stigma ventral. Anther cap 0.4 × 0.5 cucullated, whitish. Pollinarium 0.2 mm long. Pollinia two, yellow, laterally flattened. Fruits not seen.

Eponymy. From the Latin *erectus* "erect" and *labrum* "labellum, lip", referring to the lip's ascending epichile (Fig. 3).

Ecology, distribution, and phenology. *Ophidion erectilabrum* is only known from the type specimen. It was found growing in the lower part of the Dagua river basin, in the Valle del Cauca department of Colombia, on the Chocó biogeographic region (Fig. 4). The area has been classified as a tropical rain forest (Holdridge, 1987) and reports annual precipitation between 7,000 and 7,500 mm, and the local relative humidity is near

Fig. 1. Comparison between Maximum likelihood trees derived from (A) nrITS dataset and (B) *mat*K showing links between the tips (248) using the R packages APE (Paradis et al., 2004) and phytools (Revell, 2012), showing topological discordances between both datasets. Green line represents *Luerella*, yellow *Ophidion*, and purple *Phloeophila*. Likelihood bootstrap percentages are shown in red for the nodes involving these genera.


B
D
3 mm
F
E
5 mm
0.5 mm
A
C
1 mm
5 mm
1 cm

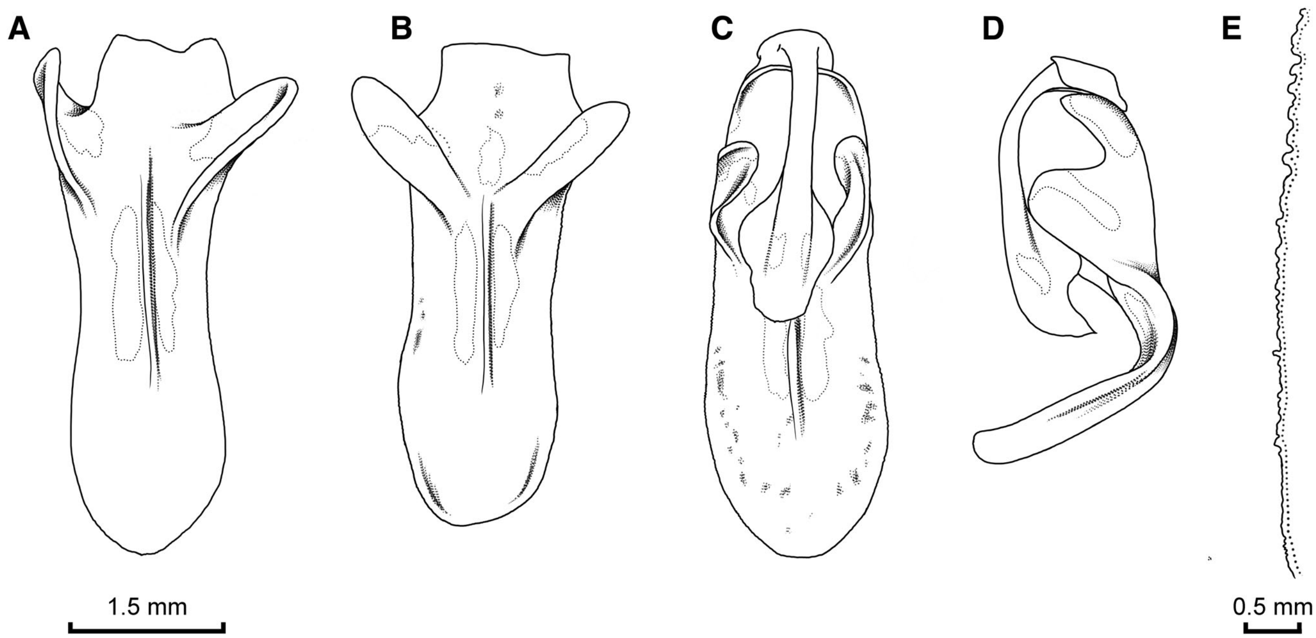


Fig. 3. Morphology of the lip of *Ophidion erectilabrum*. (A) Front view with lateral lobes in natural position showing the central keel. (B) Front view with lateral lobes flattened. (C) Column and lip, front view. (D) Column and lip, lateral view showing the erect apex of the lip and lateral lobes. (E) Detail of the margin of the lip.

90%. The average annual temperature is 26.1 °C. The protected area spans over 8,269 ha of the National Forest Reserve of the Escalerete and San Cipriano rivers. *Ophidion erectilabrum* was found on the lowland dense forest corridor (at 184 m) (see Table 2). Growing on the woody vine "Chicao". The tree flora of the type collection area is dominated by *Otoba lehmannii* (A.C. Sm.) A.H. Gentry, *Huberodendron patinoi* Cuatrec, Subdosel species (10–20 m) *Brosimum utile* (Kunth) Oken, *Minquartia guianensis* Aubl., Shrub vegetation (<10 m) *Eschweilera sclerophylla* Cuatrec, *Ryania pyrifera* (Rich.) Uittien & Sleumer. The palms community *Welfia regia* Moore & Mast, *Socratea exorrhiza* (Mart.) H. Wendl., *Wettinia aequalis* (O.F. Cook & Doyle) R.Bernal. Also, there is a community of epiphytes dominated by *Aechmea germinyana* (Carrière) Baker, *Guzmania musaica* (Linden & André) Mez, *Guzmania scherzeriana* Mez, and *Guzmania sprucei* (André) L.B. Sm.

Ophidion erectilabrum was registered in flower during February and October *in situ*, coinciding with rainy periods.

Conservation status. The species was found within a protected area; however, we cannot provide a conservation status assessment because only one specimen was found. Hence, this taxon must be classified tentatively as data deficient (DD) (IUCN, 2012).

Discussion

The phylogenetic analyses performed to assess the most appropriate genus to describe the new species based on *mat*K and nrITS supports the recognition of *Luerella*, *Ophidion*, and *Phloeophila* (Fig. 1, 5, 6) as monophyletic groups; however, their relationships within the subtribe remain unresolved. Recent preliminary molecular analyses based on target enrichment hybrid capture combined with a high-throughput sequencing approach suggest that *Ophidion* is sister to the *Pleurothallis*+*Stelis* clade. In contrast, *Luerella* is sister to the *Dracula*+*Masdevallia*+*Trisetella* clade (Chumová et al., 2021). Although unsupported, these results agree with the plastid (*mat*K) tree better than the nuclear (nr*ITS*) tree. Interestingly, the conflicting positions observed between the Sanger sequence datasets remain unresolved when multiple markers are analysed. For example, Chumová et al. (2021) did not assign *Luerella* and *Ophidion* to a clade within the Pleurothallidinae because

Fig. 2. *Ophidion erectilabrum.* Reina-Rodríguez, O. Pérez & Bogarín. (A) Habit. (B) Flower. (C) Dissected perianth. (D) Column and lip, lateral view. (E) Columns dorsal and ventral views. (F) Pollinarium and anther cap. LCDP by D. Bogarín based on photographs by G. Reina-Rodríguez of the plant that served as type.

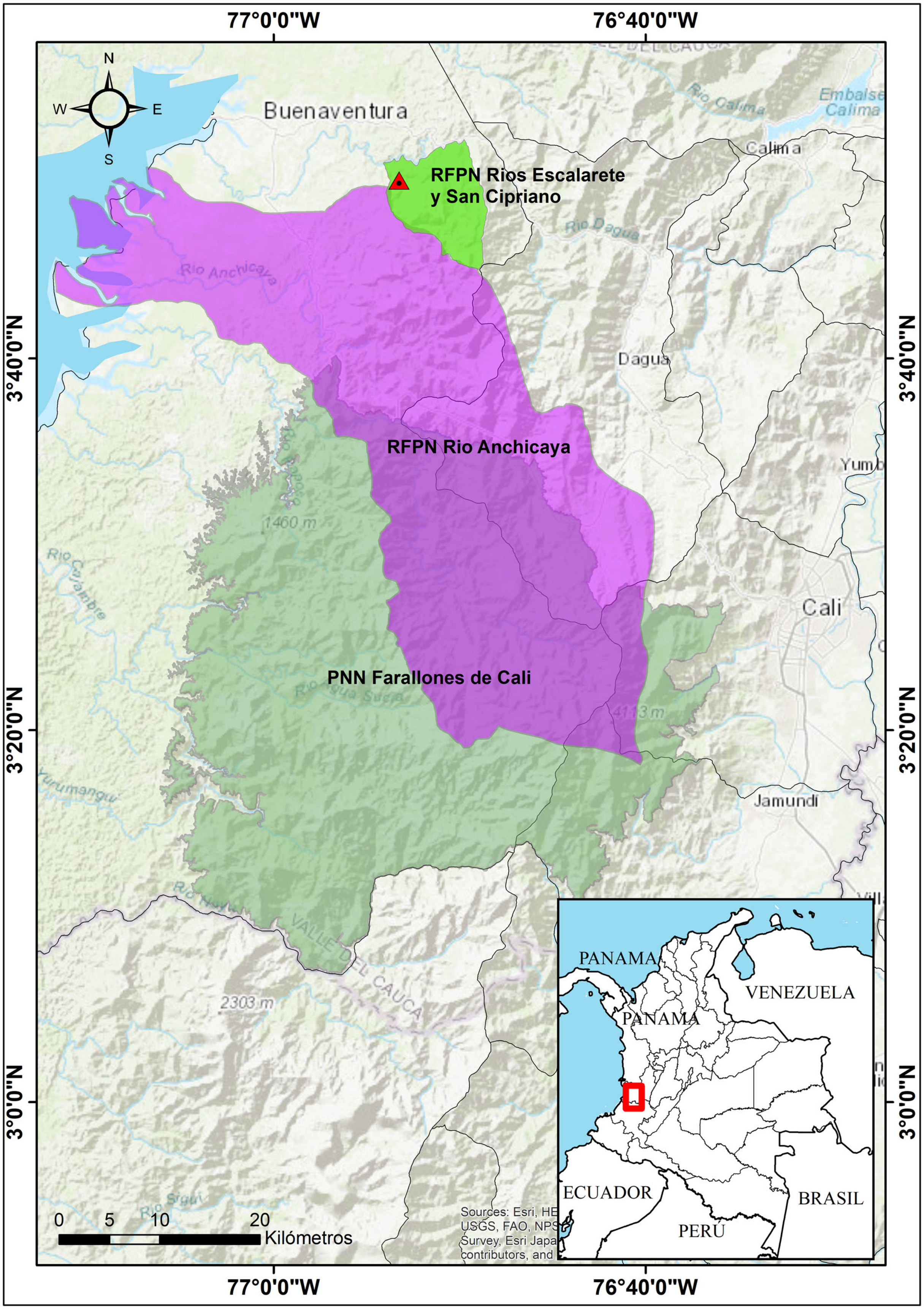


Fig. 4. Location where the type specimen of *Ophidion erectilabrum* was collected.

Table 2. Differences between *Ophidion erectilabrum* and related taxa in terms of biotic conditions and morphology.

Traits	*Ophidion erectilabrum*	*Ophidion alphonsianum*	*Ophidion cunabulum*	*Ophidion carrilloi*
Distributional and abiotic conditions				
Distributional range	Valle del Cauca (Dagua basin)	Colombia unknown place	Antioquia (Atrato basin)	Cundinamarca (Eastern high Andes)
Life zone (*sensu* Holdridge, 1987)	Tropical rain forest	No date	Tropical rain forest	Lower montane moist forest
Habitat	Primary rain forest	No date	Fragmented rain forest	Fragmented montane forest
Elevation range (m)	120–250	No date	170–443	2500–2700
Mean annual rainfall (mm)	7500	No date	4541	800
Annual mean temperature (°C)	26.1	No date	27.0	13.7
Morphological and/phenological conditions				
Habit	Epiphytic	Epiphytic	Epiphytic	Epiphytic/Terrestrial
Flowering period	October, February	February	October, November, April	October
Plant size (mm)	40–45	29–76	80–170	50–60
Sheaths size (mm)	2.0–5.0 × 1.0–2.0	4.0–20.0 × 1.5–2.0	30.0–35.0 × 7.0–10.0	10.0–20.0 × 0.25–0.35
Leaf blade size (mm)	12.0–13.9 × 8.0–9.7	24.0–66.0 × 11.0–17.0	60.0–130.0 × 1.5–2.3	30.0 × 1.5
Leaf blade form	Orbicular	Elliptic	Elliptic, acute, petiolate	Ovate-lanceolate
Apex	Bicuspid with awl	No date	acute	acute
Inflorescence condition	Erect	Descending, flexuous	Creeping or Pendent	Erect
Inflorescence length/diameter (mm)	43.0/0.3	20.0 / 1.0	30.0–80.0/No data	50.0/0.5
Dorsal sepal size (mm)	8.5 × 4.5	16.0 × 6.0	20.0 × 6.0	17.0 × 3.0
Petal size (mm)	4.0 × 1.7	10.0 × 4.5	8.0 × 3.0	5.0 × 2.0
Lip form	Narrowly–oblong	Elliptic, subacute	Obovate, obtuse	Oblong
Lip size (mm)	4.5 × 1.5	11.0 × 4.0	15.0 × 3.5	7.0 × 0.25
Lip margins	Erose	Cellular, papillose	Cellular, glandular	Ciliated
Epichile (central lobe)	Curved apically	Flat	Flat	Flat

the number of concordant gene tree quartets was lower than the number of conflicting quartets. In addition, the phylogenetic placement of *Phloeophila* is yet to be evaluated using nuclear targeted enrichment datasets, and its inclusion is critical for a proper comparison with the results found by Chumová et al. (2021). Another potential solution to the conflicting topologies and low support of these groups is the assessment of other genomic regions that have proved effective in resolving recalcitrant relationships within the Pleurothallidinae (Bogarín et al., 2018).

Although results from the nr*ITS* and *mat*K datasets yield phylogenies with low support to confidently discern the relationships of these genera within the subtribe, their placement as individual monophyletic groups in Pleurothallidinae is supported. The monophyly of these genera is further supported by morphological characters (Luer, 1976, 1982, 2004, 2006), but a broader concept of *Phloeophila* s.l. lacks diagnostic morphological features (Moreno & Karremans, 2020). Therefore, we decided to assign the species here proposed as new to science to the genus *Ophidion*.

Among species of *Ophidion*, *O. erectilabrum* differs in the inflorescences surpassing the leaves and the abruptly ascending epichile of the lip almost perpendicular to the centre of the lip. The most similar species is *O. alphonsianum* (see photographs in Matthews 2018: 8), but *O. erectilabrum* differs in the smaller leaf blade (12.0–13.9 vs. 24.0–66.0 mm long), the erect, lax inflorescence, longer than the leaves (vs. descending, flexuous, shorter than the leaf), the smaller (4.5 × 1.5 vs. 11.0 × 4.0 mm), narrowly oblong lip (vs. elliptic, subacute lip) with an ascending epichile (vs. flat). Also, *O. erectilabrum* differs from the variable and widely distributed *O. pleurothallopsis* (Kraenzl.) Luer in the shorter ramicauls <8 mm long (vs. 1–6 cm long), the smaller leaf blade <1.5 cm (vs. 3–9 cm) with inflorescences surpassing the leaves (vs. shorter than the leaves) and the smaller lip 4.5 × 1.5 mm, yellowish with reddish stains and ascending epichile (vs. maroon, 14 × 3.5 mm and flat or suberect epichile).

With the description of *O. erectilabrum*, the genus now comprises 16 species, 11 of which have been described in the last five years (Moreno & Karremans, 2020). This shows that alpha-taxonomy is key to better understanding the circumscription of genera in megadiverse groups and can potentially change interpretations about the diversification and distribution ranges of

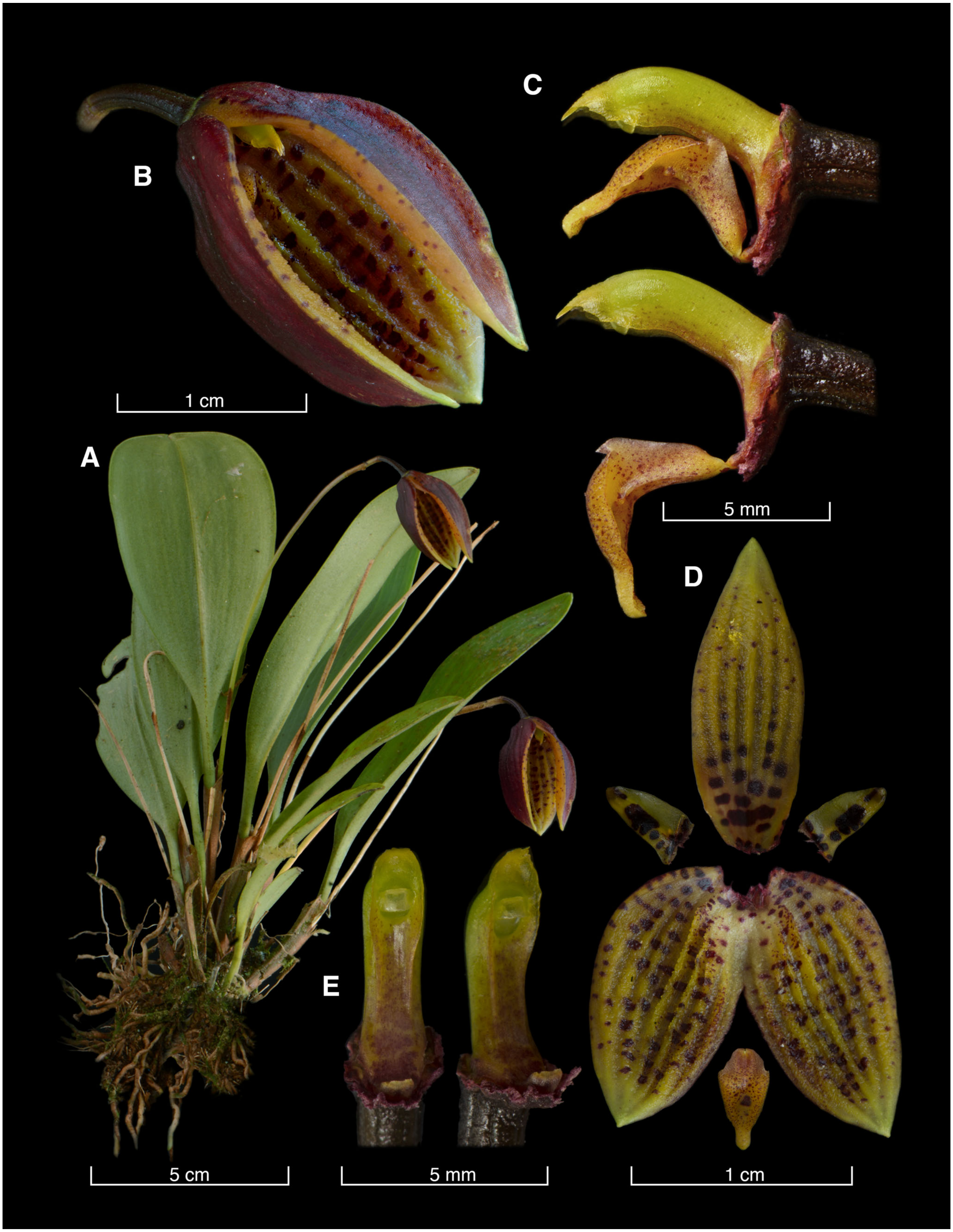


Fig. 5. *Luerella pelecaniceps* (Luer) Braas. (A) Habit. (B) Flower. (C) Dissected perianth. (D) Column and lip, lateral view. (E) Columns ventral and lateral views. LCDP by D. Bogarín 11577 (UCH).

Fig. 6. *Phloeophila peperomioides* (Ames) Garay. *In situ* photograph in Costa Rica by Y. Kisel.

species in the Neotropics, mainly in clades that were traditionally thought to have less species diversity.

Acknowledgements

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