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A NEW SPECIES OF *ANDINIA* (PLEUROTHALLIDINAE) FROM PERU AND AN UPDATED PHYLOGENETIC ANALYSIS OF THE GENUS WITH EMPHASIS ON SUBGENUS *AENIGMA*

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Abstract. A new species, *Andinia peruviana*, from Amazonas department, Peru, is described and illustrated. Updated phylogenetic analyses of nuclear internal transcribed spacer (nrITS) sequences in this study re-affirm the monophyletic nature of *Andinia sensu lato* and further support the previously proposed circumscription which incorporated genera *Lueranthos*, *Masdevalliantha*, *Neooreophilus,* and *Xenosia*. *Andinia* subgenus *Aenigma* was strongly supported in all analyses. The new species was determined phylogenetically to belong to subgenus *Aenigma*, along with *A. barbata*, *A. dalstroemii*, *A. hirtzii*, *A. pogonion*, *A. schizopogon,* and *A. uchucayensis*. The phylogenetically-confirmed representatives of subgenus *Aenigma* are illustrated with drawings and photographs, and their geographic distribution is discussed. The updated phylogenetic analyses also show the corrected phylogenetic positions of *A. vestigipetala*, as the sole representative of the clade corresponding to subgenus *Minuscula*, and *A. trimytera*, as a member of the clade corresponding to subgenus *Andinia*.

Resumen. Se describe e ilustra una nueva especie de *Andinia*, *A. peruviana*, procedente del departamento de Amazonas, Perú. Los análisis filogenéticos actualizados de las secuencias del espaciador transcrito interno nuclear (nrITS) en este estudio reafirman la naturaleza monofilética de *Andinia sensu lato* y apoyan aún más la circunscripción propuesta anteriormente que incorporaba los géneros *Lueranthos*, *Masdevalliantha*, *Neooreophilus* y *Xenosia*. El subgénero *Aenigma* de *Andinia* recibió un fuerte apoyo en todos los análisis. Se determinó que la nueva especie pertenece filogenéticamente al subgénero *Aenigma*, junto con *A. barbata*, *A. dalstroemii*, *A. hirtzii*, *A. pogonion*, *A. schizopogon* y *A. uchucayensis*. Los representantes del subgénero *Aenigma* confirmados filogenéticamente se ilustran con dibujos y fotografías y se discute su distribución geográfica. Los análisis filogenéticos actualizados también muestran las posiciones filogenéticas corregidas de *A. vestigipetala*, como único representante del clado correspondiente al subgénero *Minuscula*, y de *A. trimytera*, como miembro del clado correspondiente al subgénero *Andinia*.

Keywords/Palabras clave: *Aenigma* species, bosques montanos, endemic species, especies de *Aenigma*, especies endémicas, filogenia, montane forests, neotrópico, neotropics, phylogeny, taxonomía, taxonomy

Introduction. *Andinia* (Luer) Luer was re-circumscribed by Wilson *et al*. (2017) to reflect phylogenetic affinities and to reduce taxonomic confusion. The new circumscription incorporated species of uncertain affinity previously assigned to various different genera, including *Lueranthos* Szlach. & Marg., *Mas-*

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devalliantha (Luer) Szlach. & Marg., *Neooreophilus* Archila, *Pleurothallis* R.Br., *Stelis* Sw. and *Xenosia* Luer. Wilson *et al.* (2017) conducted the phylogenetic analyses based only on nuclear internal transcribed spacer (nrITS) sequences and the plastid *matK* gene. However, a study by Doucette (2017) incorporated the low-copy nuclear gene *phyC* and the plastid sequences *trnL-F* and *ycf1* and also found strong support for the clade representing *Andinia sensu* Wilson *et al*. (2017). While there are no rules for generic re-circumscription and the outcomes can sometimes be contentious, Wilson *et al*. (2017) circumscribed a genus representing a strongly supported monophyletic clade that encompassed similar phylogenetic depth to that occurring in the related genera *Dryadella* Luer, *Muscarella* Luer, *Platystele* Schltr., *Specklinia* Lindl., *Scaphosepalum* Pfitzer and *Teagueia* (Luer) Luer (Chumová *et al*. 2021, Doucette *et al*. 2017, Karremans 2016, Pérez-Escobar *et al*. 2017, Wilson *et al*. 2017).

A recent criticism of the genus as circumscribed by Wilson *et al*. (2017) was not the absence of a synapomorphy *per se*, but the lack of a consistent morphology for all members of *Andinia* (Szlachetko *et al*. 2022). In particular Szlachetko *et al.* (2022) contrasted the *Lepanthes*-like flowers and pendent vegetative morphology of species formerly assigned to *Neooreophilus*, currently assigned to subgenus *Brachycladium*, with the caespitose vegetative morphology of the species assigned to the other subgenera of *Andinia*. However, neither a synapomorphy nor a consistent vegetative or floral morphology are required in generic circumscriptions and they have not been employed in recent circumscriptions in Pleurothallidinae. Further, the circumscription by Wilson *et al*. (2017) appears to have general acceptance by the botanical community. Apart from the one species described by Szlachetko *et al*. (2022), most new pendent taxa have been described in *Andinia* rather than *Neooreophilus* (Karremans & Vieira-Uribe 2016, Karremans & Vieira-Uribe 2020, Ocupa-Horna *et al*. 2021) and *Neooreophilus* is listed as a synonym of the accepted genus *Andinia* in the World Checklist of Selected Plant Families (WCSP 2022).

Despite their preference for a broadly defined genus *Andinia*, Wilson *et al*. (2017) did suggest the recognition of five monophyletic subgenera: subgenus *Aenigma* (Luer) Karremans & Mark Wilson; subgenus *Andinia*; subgenus *Brachycladium* (Luer) Karremans & S.Vieira-Uribe; subgenus *Masdevalliantha* (Luer) Karremans & Mark Wilson; and subgenus *Minuscula* Karremans & Mark Wilson. However, although subgenera *Brachycladium* and *Masdevalliantha* were well sampled, subgenera *Andinia*, *Aenigma,* and *Minuscula* were less well sampled, and, therefore, several species were assigned to subgenera based on morphological similarity alone. In the current study additional species were sampled, primarily in subgenus *Aenigma*, to provide phylogenetic confirmation of subgeneric assignments of some of the taxa previously assigned solely based on morphology.

Luer (1986) originally created subgenus *Aenigma* in genus *Pleurothallis* to include *P. dalstroemii* Luer, *P. ibex* Luer, *P. schizopogon* Luer, *P. trimytera* Luer & R. Escobar and *P. vestigipetala* Luer. To these were added *P. hystricosa* Luer, *P. pentamytera* Luer and *P. pogonion* Luer (Luer 1994); *P. panica* Luer & Dalström (Luer 1996); and *P. lappacea* Luer (Luer 2000). At that time *Andinia* consisted of only two species, *A. pensilis* (Schltr.) Luer and *A. dielsii* (Mansf.) Luer (Luer 2000). However, following the inclusion of *P. lappacea* in their phylogeny, Pridgeon and Chase (2001) transferred all these species to the genus *Andinia*. With the addition of *A. hirtzii* Luer by Luer (2005), this brought the number of species in the genus to 13. However, neither Pridgeon (2005) nor Chase *et al*. (2015) proposed an infrageneric taxonomy.

Of the 13 species assigned to genus *Andinia* at that time, Wilson *et al*. (2017) sequenced all but *A. hystricosa*, *A. hirtzii*, *A. ibex*, *A. panica* and *A. pentamytera*. In their nrITS phylogeny, species *A. dalstroemii*, *A. pogonion* and *A. schizopogon* clustered with 100% bootstrap support. Since Luer (1986) designated *Pleurothallis schizopogon* as the type of subgenus *Aenigma*, this clade in *Andinia* was designated by Wilson *et al*. (2017) as subgenus *Aenigma*. Based on morphology, the subgenus was provisionally circumscribed to additionally include *A. ibex* and *A. pentamytera*, plus the newly described species *A. sunchubambensis* A.Doucette & Janovec and *A. uchucayensis* A.Doucette & J.Portilla.

In this study we describe and illustrate the new species *Andinia peruviana*, hypothesized to belong to subgenus *Aenigma* based on morphological similarity to *A. schizopogon*. The nrITS region of *A. peruviana* was sequenced and phylogenetic analyses performed to test this hypothesis. Furthermore, additional nrITS sequences of the previously described species *A. hirtzii* and *A. uchucayensis* were incorporated in these phylogenetic analyses to determine whether those species had been correctly assigned to subgenus *Aenigma*. And, additional nrITS sequences of *A. trimytera* and *A. vestigipetala*, each only represented by a single sample in the analyses of Wilson *et al.* (2017), were incorporated to determine whether their exclusion from subgenus *Aenigma*, in contradiction to the taxonomy of Luer (1986), was correct or not. To confirm or refute inclusion in subgenus *Aenigma,* these limited objectives are adequately achieved using nrITS sequencing alone and do not require the sequencing of multiple nuclear and plastid genes as would a complete re-assessment of the circumscription of the genus *Andinia*.

Materials and methods. *Phylogenetic methods.—* For genetic analysis, plant material was legally purchased from the commercial nurseries Ecuagenera, Gualaceo, Ecuador; Mundiflora, Cuenca, Ecuador; or EquaflorA, Cuenca, Ecuador. Genomic DNA of the *Andinia* plants grown in the Colorado College living collection was extracted, the nrITS region amplified by PCR, and the PCR product purified as described in Wilson *et al.* (2017). Purified PCR products were sequenced with primers 17SE, 26SE, ITS1 and ITS4 (Wilson *et al*. 2017) at Azenta/GeneWiz (New Jersey, USA). The two forward and two reverse sequences were aligned and a consensus generated using Geneious Prime v. 2022.1.1 (Dotmatics, USA). Consensus ITS sequences truncated in front of CGG GCG GTT at the 5’ end and after CCA CCC G at the 3’ end were uploaded to GenBank (Table 1). ITS sequences of these species, those sequenced by Wilson *et al*. (2017), and others available from GenBank (Table 1) were aligned using MUSCLE (Edgar 2004) with default parameters in MEGA 11 (Tamura *et al*. 2021).

Maximum parsimony (MP) and maximum likelihood (ML) analyses of the nrITS matrix were conducted in MEGA 11 using default parameters and 1000 bootstrap replicates (Tamura *et al.* 2021). The nrITS matrix was then analyzed by Bayesian inference (BI) using MrBayes (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck, 2003) on XSEDE v. 3.2.7a through the CIPRES Science Gateway v. 3.3. (Miller *et al*. 2010) using the GTR+G+I evolutionary model (Ponert *et al*. 2020; Szlachetko *et al*. 2022). Two parallel runs of four chains were run, with 10 million generations per run and a sampling frequency of 1000 trees. The first 25% of trees were discarded as burn-in. Effective sample size (ESS) was checked in Tracer v. 1.7.1 in BEAST 2 and found to be sufficient. The trees were imported into Geneious Prime v. 2022.1.1 and a consensus tree generated. Nodes with less than 0.60 posterior probability were collapsed. The resulting tree was exported as a Newick file and imported into MEGA v. 11 to allow formatting consistent with the MP and ML trees.

Taxonomic methods.— The type specimen was collected in northern Peru under permit RDG N° 247-2016-SERFOR/DGGSPFFS and the extension Resol. 430-2017-SERFOR/DGGSPFFS. Vouchers were dried as herbarium material and were deposited in the HUT and USM herbaria. Living and preserved specimens were examined for morphological and taxonomic comparisons. In addition, original descriptions of related species were reviewed and compared, and specimens from the following herbaria were consulted online: HA, MO, PRC and SEL, and no additional material of the new species was found.

The description and drawings were prepared from dissected living specimens. Floral and vegetative structures of living plants were photographed with a Canon® Rebel 80D camera equipped with a Canon EF 100mm f/2.8L Macro USM lens and a pressurized Raynox DCR-250 mm super-macro lens. The images were used to create a Lankester composite digital plate (LCDP) using Adobe Photoshop® CC 2020. In addition, a digital composite line drawing was made in the Procreate illustration application with an iPad 8th generation tablet. The botanical terminology used in the manuscript was consulted in Beentje (2016) and Stearn (2004).

Preparation of species occurrence map.— A map showing the occurrence of species of the subgenus *Aenigma* was prepared using QGIS 3.10 software (Development Team 2022), using as reference the protologues and the localities of the species vouchers in the online databases (GBIF.org 2022, Tropicos 2022).

TABLE 1. List of ingroup taxa; collection/voucher numbers; and GenBank accession numbers for nuclear ITS sequences; and origin of sequences.

Taxon	**Collection-Voucher**	**GenBank Accession Number**	**Source**
Andinia barbata J.Ponert, M.Portilla, Chumová & P.Trávn.	P998	MT249823	Ponert *et al.* (2020)
Andinia dalstroemii (Luer) Pridgeon & M.W.Chase	AN005	KP012339	Wilson *et al.* (2017)
Andinia dalstroemii (Luer) Pridgeon & M.W.Chase	AN068	KP012339	Wilson *et al.* (2017)
Andinia aff. dielsii	AK5429	KC425739	Karremans *et al.* (2012) unpubd.
Andinia hirtzii Luer	AN097	ON391672	This study
Andinia lappacea (Luer) Pridgeon & M.W.Chase	AN022	KP012345	Wilson *et al.* (2017)
Andinia lappacea (Luer) Pridgeon & M.W.Chase	AP108	KC425837	Pridgeon & Chase (2001)
Andinia lappacea (Luer) Pridgeon & M.W.Chase	LO1428	KP012343	Wilson *et al.* (2017)
Andinia longiserpens (C.Schweinf.) Karremans & Mark Wilson	AK5724	KC425744	Karremans *et al.* (2012) unpubd.
Andinia longiserpens (C.Schweinf.) Karremans & Mark Wilson	AN013	KP012354	Wilson *et al.* (2017)
Andinia longiserpens (C.Schweinf.) Karremans & Mark Wilson	AN021	KP012356	Wilson *et al.* (2017)
Andinia longiserpens (C.Schweinf.) Karremans & Mark Wilson	LO4515	KP012353	Wilson *et al.* (2017)
Andinia longiserpens (C.Schweinf.) Karremans & Mark Wilson	---	MK294822	Doucette (2017)
Andinia lynniana (Luer) Karremans & S.Vieira-Uribe	AN065	KR827587	Wilson *et al.* (2017)
Andinia nummularia (Rchb.f.) Karremans & S.Vieira-Uribe	AN042	KR827578	Wilson *et al.* (2017)
Andinia nummularia (Rchb.f.) Karremans & S.Vieira-Uribe	AN044	KR827579	Wilson *et al.* (2017)
Andinia nummularia (Rchb.f.) Karremans & S.Vieira-Uribe	AN045	KR827580	Wilson *et al.* (2017)
Andinia nummularia (Rchb.f.) Karremans & S.Vieira-Uribe	AN048	KR827581	Wilson *et al.* (2017)
Andinia nummularia (Rchb.f.) Karremans & S.Vieira-Uribe	AN051	KR827584	Wilson *et al.* (2017)
Andinia ortiziana (S.Vieira-Uribe & Thoerle) Karremans & S.Vieira-Uribe	AN071	KP012378	Wilson *et al.* (2017)
Andinia pensilis (Schltr.) Luer	AN002	KP012336	Wilson *et al.* (2017)
Andinia pensilis (Schltr.) Luer	AP200	KP012344	Pridgeon *et al.* (2001)
Andinia pensilis (Schltr.) Luer	---	MK294774	Doucette (2017)
Andinia pensilis (Schltr.) Luer	MWC8007	AF262826	Pridgeon *et al.* (2001)
Andinia peruviana Ocupa, S.Vieira-Uribe & Mark Wilson	AN135	ON391673	This study
Andinia pilosella (Rchb.f.) Karremans & S.Vieira-Uribe	AN063	KP012375	Wilson *et al.* (2017)
Andinia pogonion (Luer) Pridgeon & M.W.Chase	AN003	KP012337	Wilson *et al.* (2017)

Table 1. continues...

Andinia pogonion (Luer) Pridgeon & M.W.Chase	AN110	ON391674	This study
Andinia pogonion (Luer) Pridgeon & M.W.Chase	AN117	ON391675	This study
Andinia pogonion (Luer) Pridgeon & M.W.Chase	LO3845	KP012342	Wilson *et al.* (2017)
Andinia pogonion (Luer) Pridgeon & M.W.Chase	LJ8293	KP012335	Wilson *et al.* (2017)
Andinia schizopogon (Luer) Pridgeon & M.W.Chase	AK5783	KC425740	Karremans *et al.* (2012) unpubd.
Andinia schizopogon (Luer) Pridgeon & M.W.Chase	AN004	KP012338	Wilson *et al.* (2017)
Andinia schizopogon (Luer) Pridgeon & M.W.Chase	AN069	KP012347	Wilson *et al.* (2017)
Andinia schizopogon (Luer) Pridgeon & M.W.Chase	AN076	KP012350	Wilson *et al.* (2017)
Andinia schizopogon (Luer) Pridgeon & M.W.Chase	DCI610	MN551415	Gutiérrez Morales *et al.* (2020)
Andinia schizopogon (Luer) Pridgeon & M.W.Chase	LO2004	KP012341	Wilson et al. (2017)
Andinia sp.	AN006	KP012340	Wilson *et al.* (2017)
Andinia spiralis (Ruiz & Pav.) Karremans & Mark Wilson	AN007	KP012351	Wilson *et al.* (2017)
Andinia spiralis (Ruiz & Pav.) Karremans & Mark Wilson	AN070	KP012357	Wilson *et al.* (2017)
Andinia stalactites (Luer & Hirtz) Karremans & S.Vieira-Uribe	AN024	KP012359	Wilson *et al.* (2017)
Andinia stalactites (Luer & Hirtz) Karremans & S.Vieira-Uribe	LO2248	KP012374	Wilson et al. (2017)
Andinia trimytera (Luer & R.Escobar) Pridgeon & M.W.Chase	AN073	KP012349	Wilson *et al.* (2017)
Andinia trimytera (Luer & R.Escobar) Pridgeon & M.W.Chase	AN136	ON391676	This study
Andinia uchucayensis A.Doucette & J.Portilla	AN132	ON391677	This study
Andinia vestigipetala (Luer) Pridgeon & M.W.Chase	AN075	KR827588	Wilson *et al.* (2017)
Andinia vestigipetala (Luer) Pridgeon & M.W.Chase	---	MK294775	Doucette (2017)
Andinia vestigipetala (Luer) Pridgeon & M.W.Chase	AN093	ON391678	This study
Andinia vieira-pereziana (P.Ortiz) Karremans & S.Vieira-Uribe	AN072	KP012379	Wilson *et al.* (2017)
Andinia werneri (Luer) Karremans & S.Vieira-Uribe	AN053	KR827585	Wilson *et al.* (2017)
Andinia xenion (Luer & R.Escobar) Karremans & Mark Wilson	AN008	KP012352	Wilson *et al.* (2017)
Andinia xenion (Luer & R.Escobar) Karremans & Mark Wilson	AN074	KP012358	Wilson *et al.* (2017)
Andinia xenion (Luer & R.Escobar) Karremans & Mark Wilson	AP250	KP012355	Wilson *et al.* (2017)

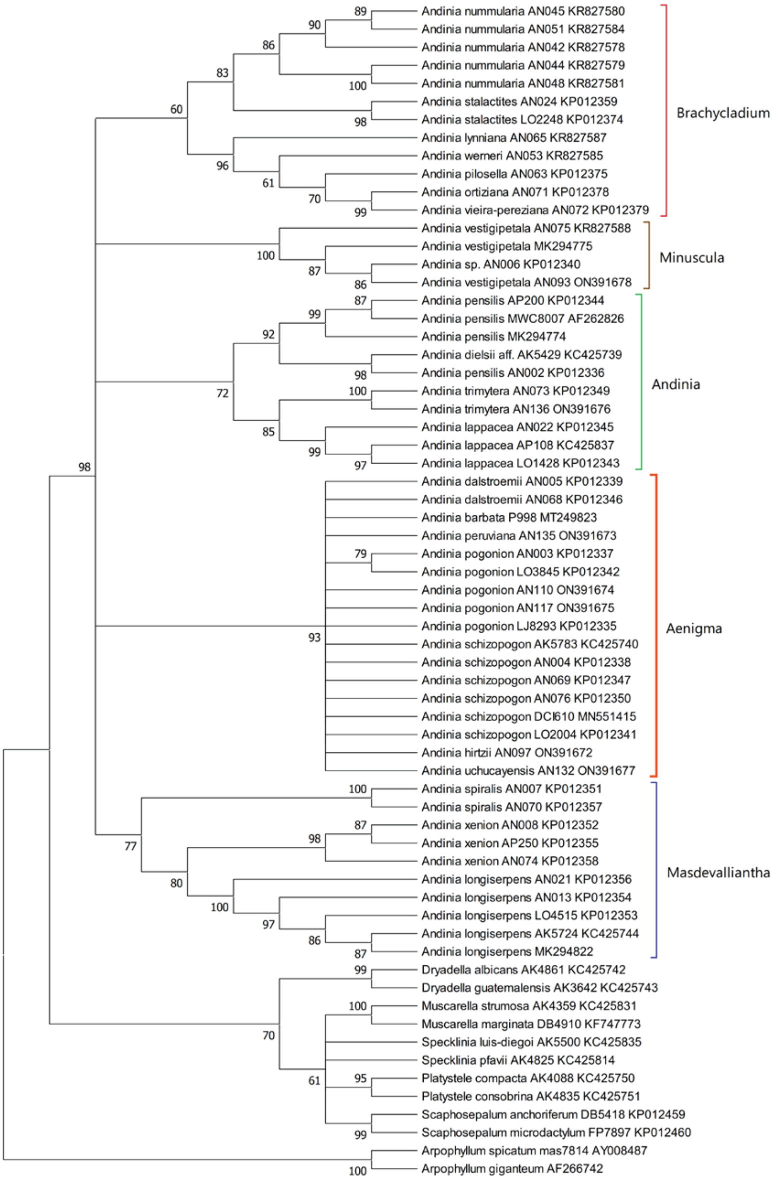

Figure 1. Bootstrap consensus phylogenetic tree inferred from nrITS sequence data set using maximum parsimony analysis with 1000 bootstrap replicates in MEGA 11 using default parameters. Values at each node represent percent bootstrap support. Nodes with less than 60% bootstrap support are collapsed. Clades corresponding to subgenera proposed by Wilson *et al*. (2017) are labeled.

Results. *Phylogenetic analysis.*— The clade corresponding to genus *Andinia,* as circumscribed by Wilson *et al*. (2017), was strongly supported in all three analyses of nrITS sequence data: MP = 98% (Fig. 1); ML = 93% (Fig. 2); and BI = 0.96 (Fig. 3). Within *Andinia*, all three analyses recovered the same 6 clades as those previously reported by Wilson *et al*. (2017), with one exception (see below). As expected, these clades correspond to the five subgenera and two sections circumscribed by Wilson *et al*. (2017): *Aenigma*, *Andinia, Brachycladium* section *Amplectentes, Brachycladium* section

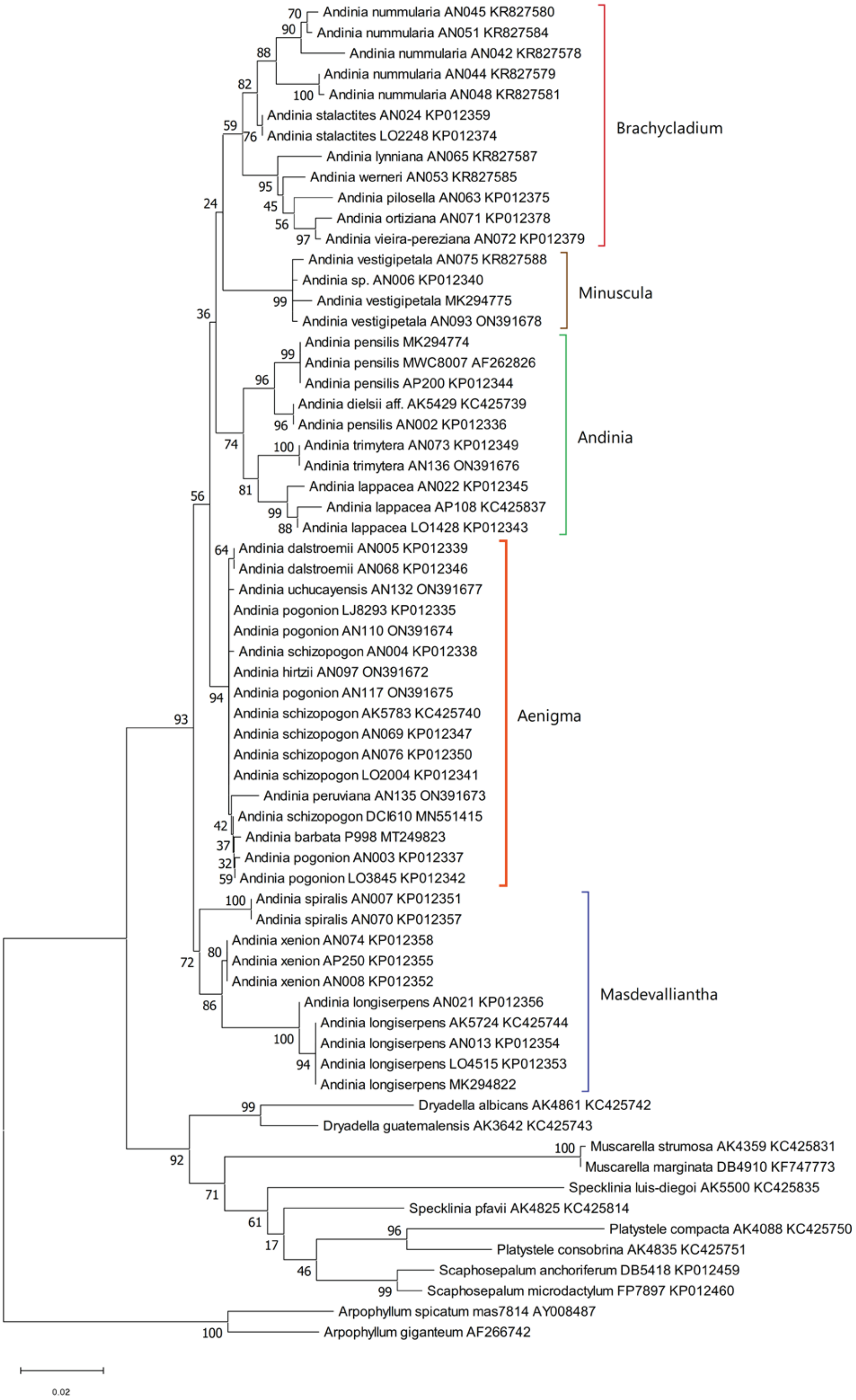

FIGURE 2. Phylogenetic tree inferred from the nrITS sequence data set using maximum likelihood analysis with 1000 bootstrap replicates in MEGA 11 using default parameters. The tree with the highest log likelihood is shown. Values at each node represent percent bootstrap support. Clades corresponding to subgenera proposed by Wilson *et al*. (2017) are labeled.

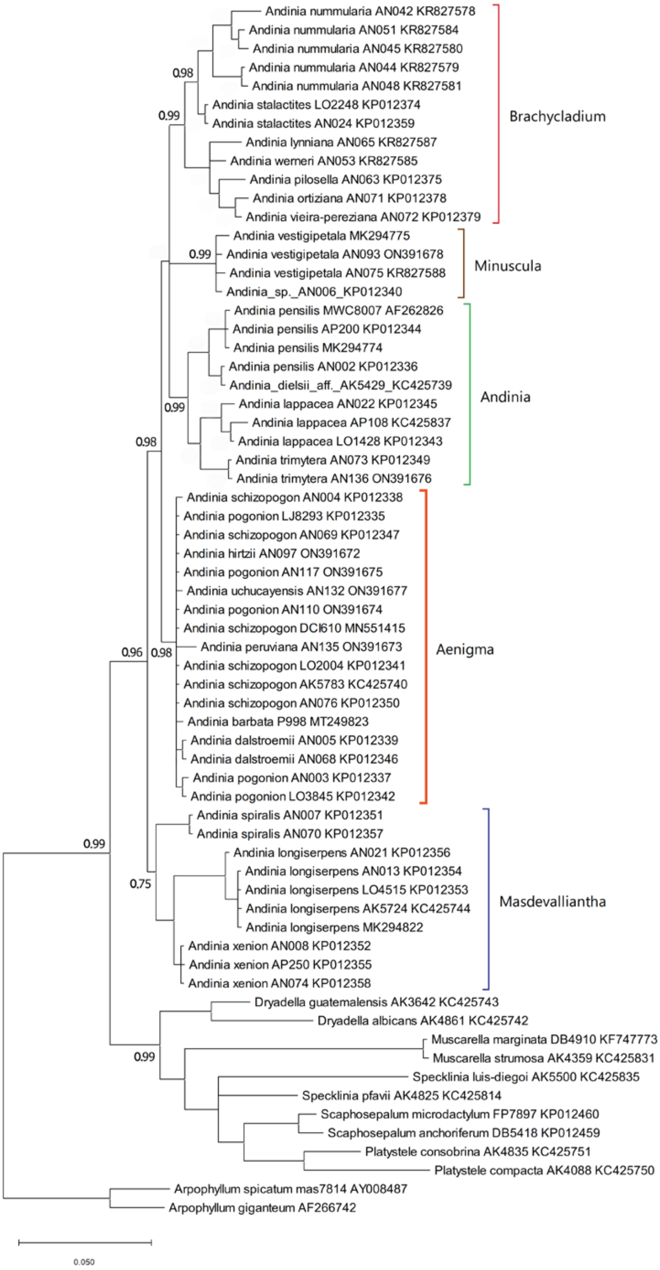

FIGURE 3. Consensus phylogenetic tree inferred from nrITS sequence data using MrBayes. Values at nodes represent posterior probabilities of pertinent clades. Nodes with less than 0.6 posterior probability are collapsed. Clades corresponding to subgenera proposed by Wilson *et al*. (2017) are labeled.

Brachycladae, Masdevalliantha and *Minuscula*. The only significant topological difference between the phylogenies was the relationships among the clades (Fig. 1–3).

Unexpectedly, adding two new sequences of *Andinia vestigipetala* and one new sequence of *A. trimytera* revealed an unfortunate error in the prior analyses by Wilson *et al*. (2017), which was the accidental switch of the sequences for *A. trimytera* AN073 and *A. vestigipetala* AN075. The error is corrected in the current analyses (Fig. 1–3). Consequently, the position of each of these species in the clade is different than in the prior study.

The clade corresponding to subgenus *Aenigma*, the focus of this study, is strongly supported in all three analyses: MP = 93% (Fig. 1); ML = 94% (Fig. 2); and BI = 0.98 (Fig. 3). The clade includes the seven species *Andinia barbata*, *A. dalstroemii*, *A. hirtzii*, the new species *A. peruviana*, *A. pogonion*, *A. schizopogon* and *A. uchucayensis*.

The clade corresponding to subgenus *Andinia* is moderately-to-strongly supported in the three analyses: MP = 72% (Fig. 1); ML = 74% (Fig. 2); and BI = 0.99 (Fig. 3). The clade includes the *A. dielsii*, *A. lappacea*, *A. pensilis* and now, additionally, *A. trimytera*.

The clade corresponding to subgenus *Brachycladium* section *Brachycladae*, including *Andinia nummularia* (Rchb.f.) Karremans & S.Vieira-Uribe and *A. stalactites* (Luer & Hirtz) Karremans & S.Vieira-Uribe, is moderately-to-strongly supported: MP = 83% (Fig. 1); ML = 82% (Fig. 2); and BI = 0.98. The clade corresponding to subgenus *Brachycladium* section *Amplectentes*, includes all species previously assigned to *Neooreophilus* other than *A. nummularia* and *A. stalactites*, is strongly supported in all three analyses: MP = 96% (Fig. 1); ML = 95% (Fig. 2); and BI = 0.99 (Fig. 3).

The clade corresponding to subgenus *Masdevalliantha* has low-to-moderate support: MP = 77% (Fig. 1); ML = 72% (Fig. 3); and BI = 0.75 (Fig. 3). The clade includes the species *Andinia longiserpens* (C.Schweinf.) Karremans & Mark Wilson, *A. spiralis* (Ruiz & Pav.) Karremans & Mark Wilson and *A. xenion* (Luer & R.Escobar) Karremans & Mark Wilson.

The clade corresponding to subgenus *Minuscula* has high support in all three analyses: MP = 100% (Fig. 1); ML = 99% (Fig. 2); and BI = 0.99 (Fig. 3). The clade includes only *A. vestigipetala* and an unflowered and now deceased *Andinia*, accession AN006, presumed initially to be *A. trimytera* based solely on its position in the phylogeny of Wilson *et al.* (2017), but which was probably *A. vestigipetala*.

The only topological difference between these analyses is that in a consensus tree, MP and ML analyses recover a polytomy of five clades corresponding to the five subgenera. In comparison, BI recovers a polytomy of four clades corresponding to subgenera *Aenigma*, *Andinia*, *Brachycladium,* and *Minuscula*, which is found to be sister to the clade corresponding to subgenus *Masdevalliantha*.

Taxonomic treatment

Andinia peruviana Ocupa, S.Vieira-Uribe & Mark Wilson, ***sp. nov.*** (Fig. 4–5)

TYPE: PERU. Amazonas: Prov. Bongará, Distrito Florida, comunidad campesina San Lucas de Pomacochas, camino de San Lorenzo a Yambrasbamba, 3130 m, 23 October 2020, *L. Ocupa 267* (Holotype: HUT!).

Diagnosis: *Andinia peruviana* is most similar to *Andinia schizopogon* (Luer) Pridgeon & M.W.Chase (Fig. 6) but differs in the lateral sepals connate for ca. ⅔ of its length (*vs*. connate to less than ½ of their length), covered with hairs up to 5 mm long (*vs*. long-pubescent-spiculate), with strongly revolute sides (*vs*. revolute sides), petals with tortuous cilia on the margins (*vs*. microscopically irregular margins), the apical mid-lobe of the lip with lacerate to filiform-papillose margins (*vs*. shortly muriculate), basal lobes of the lip with papillose margins (*vs*. entire margins).

Epiphytic *herb*, caespitose, repent or ascending, up to 11 cm tall. *Roots* white, thick, flexuous, fleshy, 1.5 mm diameter. *Rhizome* stout, up to 8 mm between ramicauls. *Ramicauls* abbreviated, terete, ascending, unifoliate, 3–7 mm long, enclosed by 1–2 tubular, membranaceous, semi-translucent, ribbed sheaths. *Leaf* suberect to inclined, obovate to narrowly obovate, coriaceous, foveolate on both sides, adaxially green, occasionally with dark-purple lines parallel to the mid-vein, abaxially very pale green with purple splashing, adaxially canaliculate in the central vein, margin irregularly crenulate, marginate, apex obtuse to rounded, tridenticulate, 16–35 × 8.5–9.5 mm, the base cuneate to attenuate into a canaliculate petiole 10 mm long. *Inflorescence* a loose, successively 1–2 flowered raceme, to 4–6 cm long including a very slender filiform peduncle, borne from the apex of the ramicaul; floral bract infundibuliform, acuminate, membranous, 1 × 2 mm. *Ovary* pedicellate, greenish-yellow, terete, densely villose, *ca*. 3–7 mm

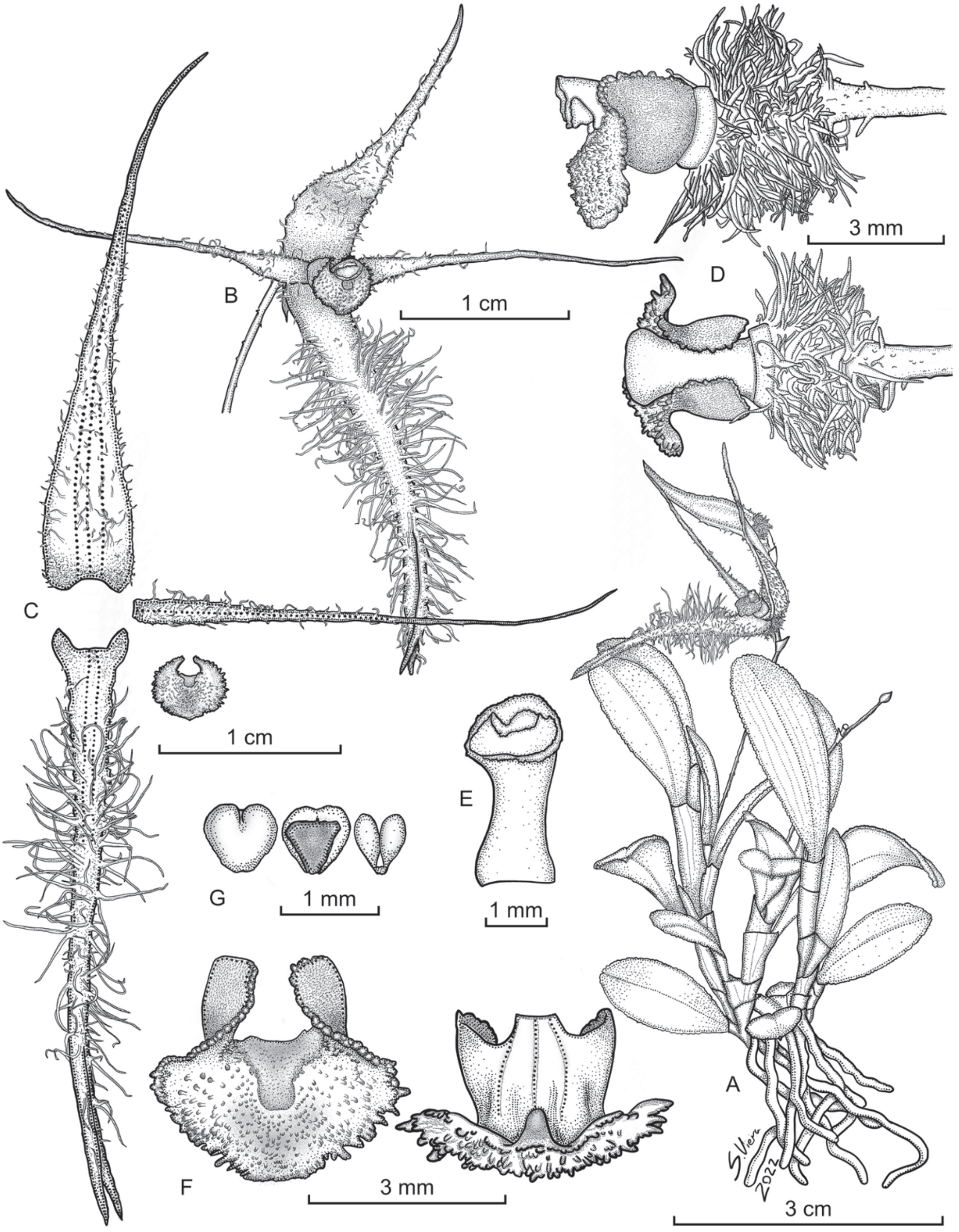

Figure 4. Illustration of *Andinia peruviana* Ocupa, S.Vieira-Uribe & Mark Wilson. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Lip, column and ovary, lateral and dorsal view. **E**. Column, ¾ view. **F**. Lip, adaxial (left) and abaxial (right) views. **G**. Anther cap and pollinia. Prepared by S. Vieira-Uribe from the plant that served as type.

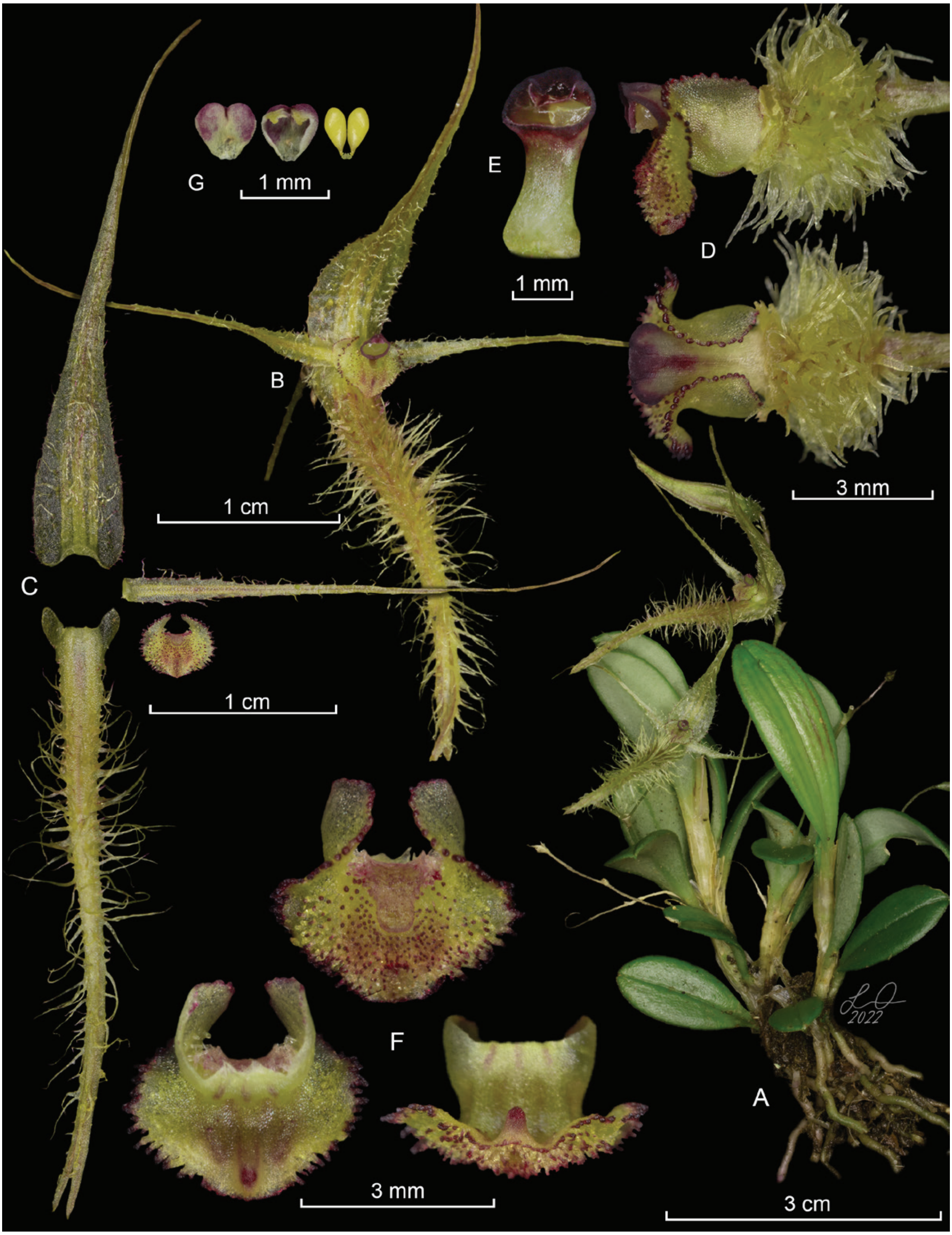

Figure 5. LCDP of *Andinia peruviana* Ocupa, S.Vieira-Uribe & Mark Wilson. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Lip, column and ovary, lateral and dorsal views. **E**. Column, ¾ view. **F**. Lip, adaxial (above) and abaxial (two views, below). **G**. Anther cap and pollinia. Prepared by L. Ocupa Horna from the plant that served as type.

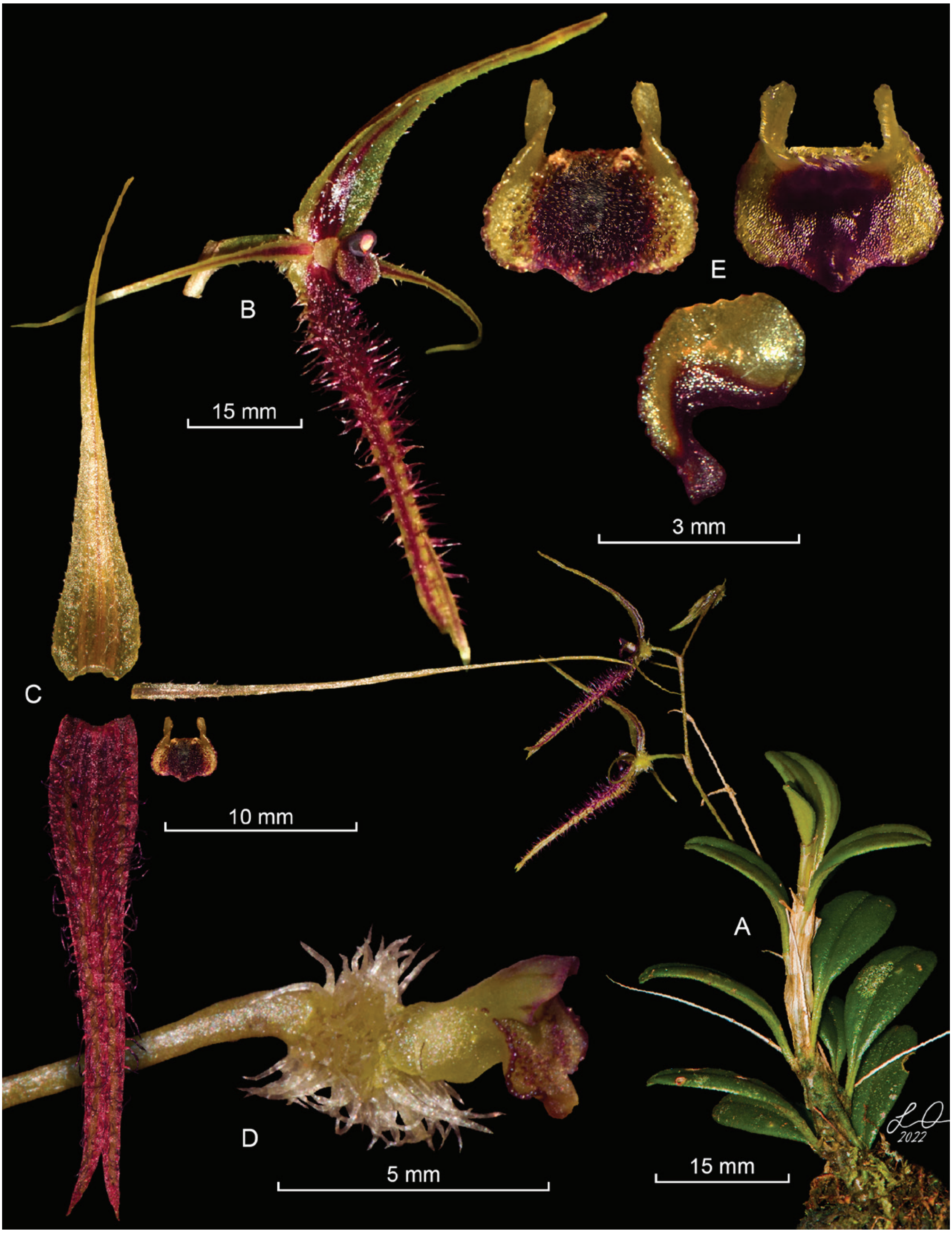

FIGURE 6. LCDP of *Andinia schizopogon* (Luer) Pridgeon & M.W.Chase. **A**. Habit. **B**. Flower. **C**. Dissected perianth. **D**. Lip, column and ovary, lateral view. **E**. Lip, adaxial (above, left), abaxial (above, right) and lateral (below) views. Prepared by L. Ocupa Horna using photos from A. Diaz (*A. Diaz s.n.* [HUT]).

long, including the pedicel. *Flowers* semi-translucent, with sepals and petals greenish yellow; lip greenish yellow with burgundy papillae; column greenish yellow, becoming vinaceous towards the apex. *Dorsal sepal* ovate, apex long-acuminate, arched forward, shallowly concave and subcordate at the base, margins irregular and sparsely ciliated, 3-veined, abaxially tricarinate, adaxially sparsely villose, 27–28 × 4.4–4.7 mm. *Lateral sepals* connate for *ca*. ⅔ of their length into a narrowly ovate, bifid synsepal, apex long-acuminate, cordate at the base, 4-veined, adaxially covered with hairs up to 5 mm long, abaxially bicarinate, with the sides strongly revolute, 30–32 × 5–7 mm. *Petals* spreading, oblong, apex gradually long-acuminate, 1-veined, with tortuous cilia on the margins, 26 × 1.3 mm. *Lip* 3-lobed, thick, adnate to the base of the column, 2.6 × 4.1 mm unexpanded, deflexed 90 degrees near the middle, 3-veined; the central, basal part sub-quadrate, concave, extending into the apical lobe as an orbicular depression, 1.4 × 1.5 mm; the apical mid-lobe widely ovate, the apex broadly rounded, minimally obtuse, cellular-papillose, with lacerate to filiform-papillose margins, with a shallow rounded central depression, 3.56 × 1.8 mm, 3-carinae along the veins on the abaxial surface, with a high, bell-shaped callus on the abaxial surface at the apex of the mid-vein; the basal lobes sub-circular, broadly rounded, erect, with papillose margins, surrounding the column. *Column* semi-terete, arched, dilated at base and apex, 4.5 mm long; stigma sub-apical, transversely elliptic, rostellum crescent-shaped, apical, acuminate, antrorse. *Anther* apical, sub-orbicular, cream purple tinged. *Pollinia* two, yellow, narrowly pyriform. *Capsule* not seen.

Additional material examined: **Ecuador**. Legally purchased from Mundiflora, Cuenca, Ecuador, as *Andinia schizopogon* "xanthina", without collection information, flowered in cultivation in Colorado. *M. Wilson & I. Acaro AN135* (COCO-spirit!). **Peru**. Amazonas: Prov. Bongará, Distrito Florida, ruta de San José a Nuevo Horizonte, en un bosque montano, 2720 m, 20 November 2021, *L. Ocupa 270* (USM!).

Etymology: The specific name is in reference to the country where the type was first collected, Peru.

Distribution and habitat: To date *Andinia peruviana* is only known from a small area located on the eastern side of the northern branch of the Andes, in the department of Amazonas, northern Peru (Fig. 7), at an elevation of ~3100–3200 m. The type specimen was found in a very humid secondary forest, growing as an epiphyte on the branches of *Weinmannia ovata* Cav. (Cunoniaceae) at ~1.5 m above the ground, on a trail on the way to Yambrasbamba (Fig. 8). The flowering of this species occurs at the beginning of the rainy season, between October and November.

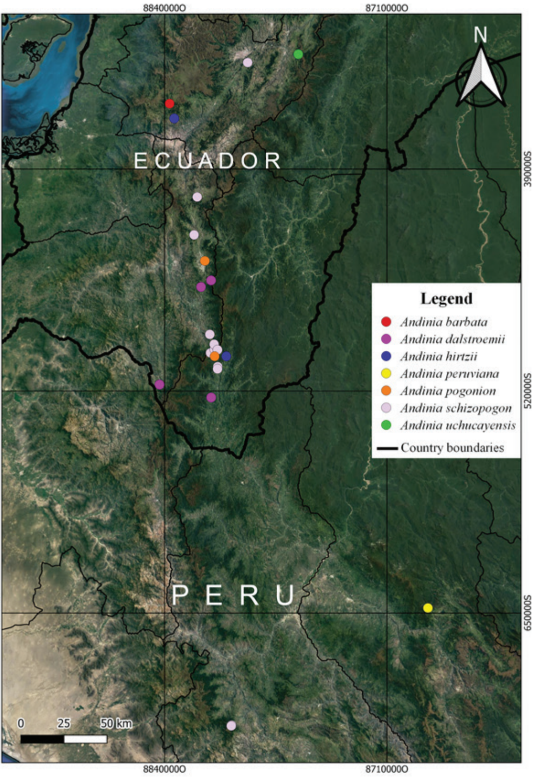

Figure 7. Map of occurrence of species of *Andinia* subgenus *Aenigma*. Prepared by L. Ocupa Horna.

Conservation status: This species is currently known from a single area in northern Peru. While the population occurs within the San Lorenzo Private Conservation Area, district of Florida, province of Bongará, Amazonas department, anthropogenic activities, such as deforestation and the expansion of crops, may endanger its small population. Therefore, according to the IUCN Red List (IUCN 2012), it may be listed as critically endangered (CR, criteria B1/extent of occurrence and C1/small population size and decline).

Figure 8. *Andinia peruviana* Ocupa, S.Vieira-Uribe & Mark Wilson *in situ*. **A**. Close-up of the flower. **B**. Detail of the plant growing on moss-covered tree trunk. **C**. Habitat. Prepared by L. Ocupa Horna.

Taxonomic comments: Among the species of subgenus *Aenigma*, *Andinia peruviana* is most similar to *A. schizopogon* (Fig. 6), sharing characteristics such as: obovate to narrowly obovate leaves, sepals ovate with long acuminate apices, petals oblong and long acuminate, lip 3-lobed, deflexed 90° near the middle, the central, basal part sub-quadrate with a cellular-papillose mesochile, the apical lobes broadly ovate, callus on the under surface, the basal lobes erect, surrounding the column. However, *A. peruviana* has smaller leaves

Table 2. Comparison of *Andinia peruviana* with closely related species.

	Andinia hirtzii	***Andinia peruviana***	***Andinia pogonion***	***Andinia schizopogon***	***Andinia uchucayensis***
Dorsal sepal size	18 × 3 mm	27.0–28.0 × 4.4–4.7 mm	7–8 × 2 mm	20–30 × 6–8 mm	11 × 2.9 mm
Synsepal size	18 × 5 mm	30–32 × 5–7 mm	7.0–8.0 x 2.5 mm	20–30 × 6–7 mm	12.0 × 1.9 mm
Connation of synsepal	13 mm	22 mm	2.5 mm	9–10 mm	2 mm
Synsepal ornamentation	minutely papillose	hairs up to 5 mm long	long-pubescent-spiculate	long-pubescent-spiculate	spiculate
Synsepal sides	revolute	strongly revolute	-	revolute	-
Petals (mm)	15 × 1	26 × 1.3	6–8 × 0.6–1.0	20–25 × 1.5–2.0	9.3 × 0.4
Lip (mm)	3 x 3	4 × 4	1.5 × 1.5	3 x 3	1.5 × 1.1
Column (mm)	3	4.5	1.5	3	1.2

(16–35 mm long *vs*. 25–65 mm long), a shorter petiole (10 mm *vs*. 25 mm long), inflorescences up to 6 cm long (*vs*. 15 cm long) laterals sepals connate to 22 mm (*vs*. connate to 10 mm), column up to 4.5 mm long (*vs*. 3 mm long). *A. peruviana* is easily distinguished from the other species of the subgenus *Aenigma* by the characteristics shown in Table 2.

It is important to mention that the leaves of *A. peruviana* are foveolate on both sides, are whitish-green with purple splashes on the abaxial side, have irregularly crenulate and marginate margins, the apex is obtuse-to-rounded, tridenticulate, and the base is cuneate-to-attenuate into a canaliculate petiole (Fig. 9), additional characteristics that could be useful to distinguish among species in subgenus *Aenigma*.

Discussion. As in previous studies (Doucette *et al.* 2017, Pérez-Escobar *et al.* 2017, Wilson *et al.* 2017), the species of *Andinia* analyzed here by MP, ML and BI form a strongly supported, monophyletic clade. Although a thorough re-evaluation of the circumscription of genus *Andinia* and infrageneric groupings is beyond the scope of this study and the nrITS data therein, we are not in agreement with the proposal of Szlachetko *et al*. (2022) to divide *Andinia* into 9 separate genera. We prefer to retain the five subgenera and two subsections previously proposed by Wilson *et al*. (2017) pending a far more comprehensive genetic analysis. In the future, with additional data from multiple nuclear genes (Chumová *et al*. 2021, Eserman *et al.* 2021, Pérez-Escobar *et al*. 2021); with plastid genomes (Chumová *et al.* 2021, Mauad *et al*. 2021, Pérez-Escobar *et al*. 2021, Serna-Sánchez *et al*. 2021); and with greater taxon sampling (including pertinent missing species, such as *A. barba-caprina*, *A. condorensis*, *A. hystricosa*, *A. ibex*, *A. panica*, *A. pentamytera*, *A. sunchubambensis,* and *A. tingomariana*), it may, at that time, be appropriate to propose alternate generic circumscriptions if indicated by the data.

This study was focused on one of those five subgenera, *Andinia* subgenus *Aenigma*. This clade was strongly supported in all three analyses by MP, ML and BI (Fig. 1–3). The clade corresponding to subgenus *Aenigma* in each case was found to include seven species: *Andinia barbata*, *A. dalstroemii*, *A. hirtzii*, the new species *A. peruviana*, *A. pogonion*, *A. schizopogon* and *A. uchucayensis*. While *A. hirtzii*, *A. peruviana,* and *A. uchucayensis* were previously presumed to be members of this subgenus based on morphology, this is the first confirmation of their phylogenetic inclusion in the *Aenigma* clade. Furthermore, *A. barbata*, described and sequenced recently by Ponert *et al*. (2020), is also confirmed to belong to subgenus *Aenigma*. Therefore, at this time, the phylogenetically-confirmed members of subgenus *Aenigma* are: *Andinia barbata*, *A. dalstroemii*, *A. hirtzii*, *A. peruviana*, *A. pogonion*, *A. schizopogon* and *A. uchucayensis* (Fig. 10–11). However, we disagree with Szlatchetko *et al.* (2022) that subgenus *Aenigma* should be segregated from *Andinia* as genus *Aenigma* (Luer) Szlach. & Kolan. at this time, so species in that genus are here listed as synonyms (see list below).

Species of *Andinia* subgenus *Aenigma* (Fig. 10–11) are distributed from southern Ecuador (which includes the provinces of Azuay, Loja, and Zamora-Chinchipe) to the montane forests located between southwestern

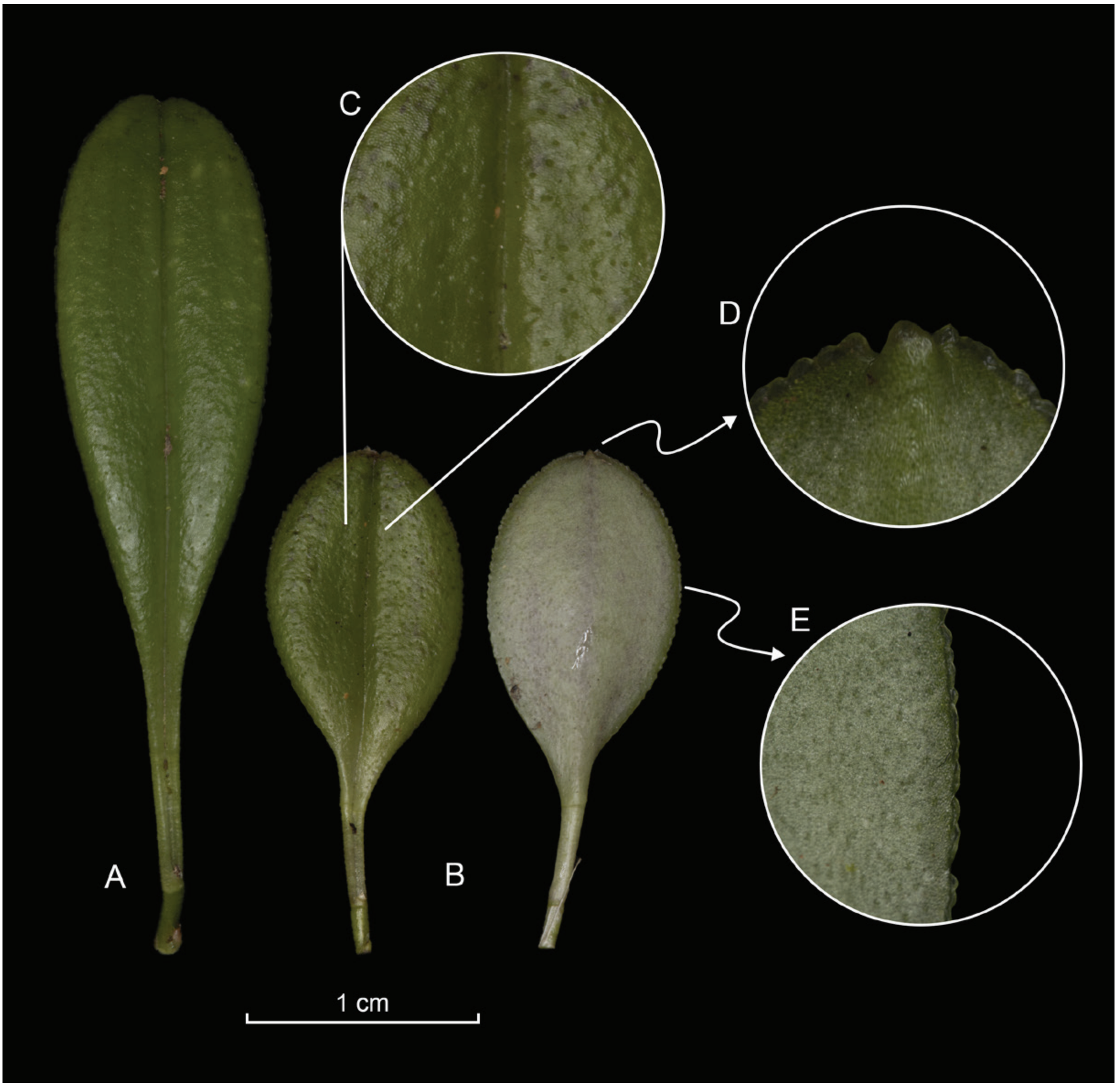

FIGURE 9. Detail of the leaves of *Andinia peruviana* Ocupa, S.Vieira-Uribe & Mark Wilson. **A**. Mature leaf. **B**. Young leaf, adaxial and abaxial view. **C**. Close-up of the blade surface. **D**. Close-up of the apex. **E**. Close-up of the margin. Photos by L. Ocupa Horna.

Cajamarca and northern Amazonas, in northern Peru (Fig. 7). Apparently, the center of richness for these species is southeastern Ecuador, in the provinces of Loja and Zamora-Chinchipe, with only two species occurring in Peru. Why this group of species exhibits such a relatively narrow distribution, at least in comparison to subgenus *Brachycladium* which ranges from Colombia to Peru, is unknown. Biogeographic studies by Szlachetko *et al*. (2022) did not reveal a unique ecological niche for these species, but the sampling in that study may not have been adequate. Perhaps the distribution is constrained by either pollinator or mycorrhizal symbiont availability.

There remains a question as to whether the sympatric *Andinia schizopogon* and *A. pogonion* are distinct species. In the description of *Pleurothallis pogonion*, Luer (1994) says, "*because* P. schizopogon *is variable in size, this species was at first thought to be merely a small form, but in retrospect the two taxa appear distinct. Except for size, the floral morphology of the two are similar.*" Despite the inclusion of multiple accessions of both species in this study, no consistent sequence differences in nrITS were observed, suggesting either that *A. schizopogon* and *A. pogonion* are the same species with a wide variation in floral dimensions or that they are sympatric sister species and that nrITS is not sufficiently variable to distinguish between them. Only sequencing of more variable nuclear and plastid genes/regions, accompanied by a floral morphometric study, will resolve this question with certainty. For now, they are retained as distinct species following Luer (1994).

Since only one accession each of *Andinia trimytera* and *A. vestigipetala* were included in the analyses of Wilson *et al*. (2017), a second sample of both species was included in this analysis to confirm the previously reported phylogenetic affinities and that the species were not part of subgenus *Aenigma* as originally circumscribed by Luer (1986). A third sequence of *A. vestigipetala* was obtained from GenBank (Doucette 2017). The analyses in this study revealed the very unfortunate switching of the sequences for *A. trimytera* AN073 and *A. vestigipetala* AN075 in Wilson *et al*. (2017). In the current corrected analyses, *A. vestigipetala* is now the sole representative of the clade corresponding to subgenus *Minuscula* and *A. trimytera* is recovered as a member of the clade corresponding to subgenus *Andinia*. Most unfortunately, this mistake impacted the proposed alternate taxonomy of Szlachetko *et al*. (2022), which those authors may now wish to revise.

Given the unusual floral morphology of *A. vestigipetala*, recognized by Luer (1994) when he segregated *Pleurothallis vestigipetala* from other members of subgenus *Aenigma* with the creation of section *Vestigipetalae*, the recovery of a clade consisting of this species alone is not surprising. However, we do not agree with Szlachetko & Margonska (2001) and Szlachetko *et al*. (2022) that *A. vestigipetala* should be segregated from *Andinia* in the monotypic genus *Lueranthos* Szlach & Marg. The species is embedded phylogenetically in *Andinia*; the vegetative morphology of *A. vestigipetala* is very similar to that of subgenus *Aenigma*; and the unique floral morphology likely reflects adaptation to a unique pollination syndrome.

The recovery of *Andinia trimytera* as sister to *A. lappacea* in the clade corresponding to subgenus *Andinia*, suggests the possibility that the other species with tri-lobed lips, including *A. hystricosa*, *A. ibex*, *A. panica*, *A. pentamytera* and *A. sunchubambensis* (syn. *A. wayqechensis*) (Fig. 12) also belong in subgenus *Andinia.* This would be different than their provisional infrageneric assignments by Wilson *et al*. (2017). Szlachetko *et al*. (2022) also noted the affinity of *A. hystricosa*, *A. ibex*, *A. panica*, *A. pentamytera* and *A. sunchubambensis* with *A. trimytera*. However, we are not in agreement with their proposal that these six species (Fig. 12) should be segregated from genus *Andinia* until their phylogenetic relationships with the other members of subgenus *Andinia* (i.e. *A. dielsii*, *A. pensilis* and *A. lappacea*) can be unequivocally determined. Sequencing of duplicate accessions of each of these difficult to acquire species will be required to confirm their infrageneric phylogenetic affinities prior to any taxonomic re-assignments.

Two additional species described since Wilson *et al*. (2017), *Andinia tingomariana* (Diaz-Hernández *et al*. 2018) and *A. barba-caprina* (Ocupa-Horna *et al*. 2021) have been hypothesized to be members of subgenus *Andinia*. Both *A. tingomariana* and *A. barba-caprina* exhibit unique floral morphologies reminiscent of the *Stelis* species formerly attributed to genus *Salpistele*. Further sequencing will allow the determination of their phylogenetic affinities and whether they belong in subgenus *Andinia* or not.

PHYLOGENY-CONFIRMED MEMBERS OF *ANDINIA* SUBGENUS *AENIGMA*

Andinia subgen. *Aenigma* (Luer) Karremans & Mark Wilson, Phytotaxa 295(2): 121. 2017.

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Andinia peruviana Ocupa, S.Vieira-Uribe & Mark Wilson, Lankesteriana 22(3): 249. 2022.

Andinia pogonion (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001. Basionym: *Pleuro-*

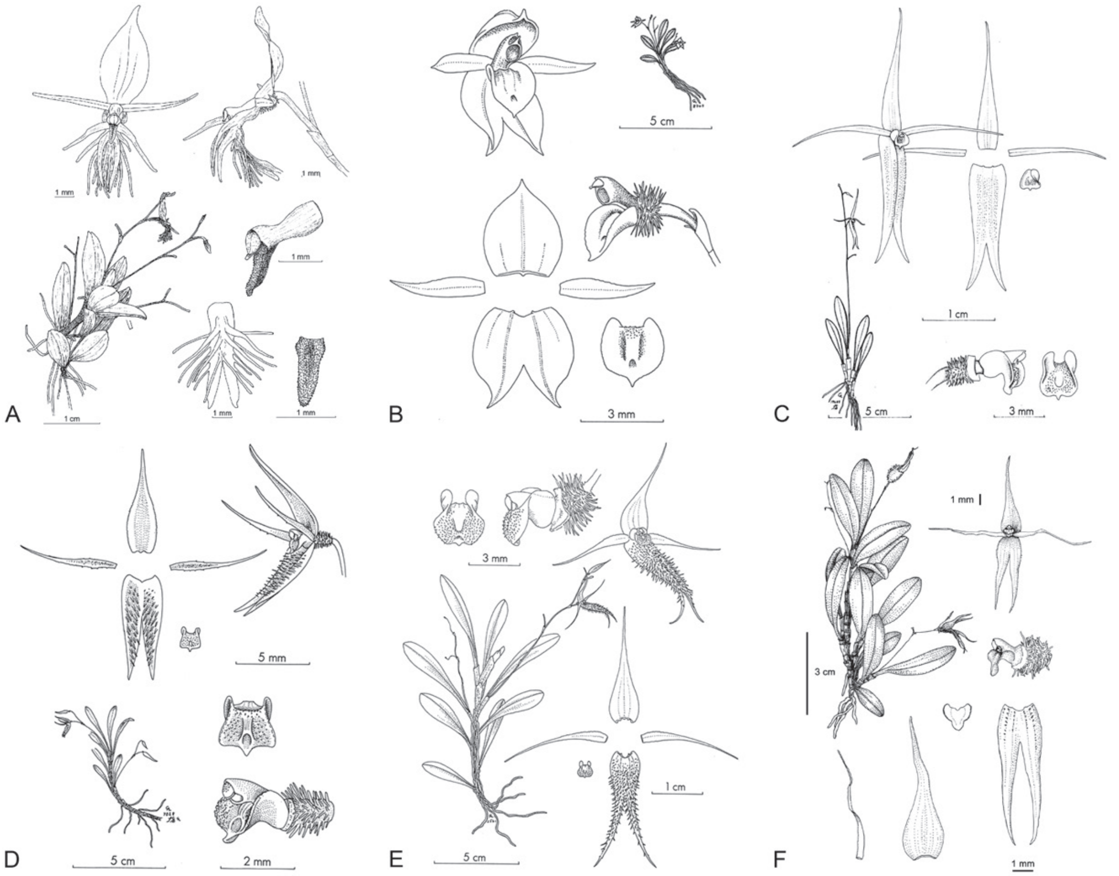

Figure 10. Drawings of the *Andinia* species subgenus *Aenigma*. **A**. *A. barbata*. **B**. *A. dalstroemii*. **C**. *A. hirtzii*. **D**. *A. pogonion*. **E**. *A. schizopogon*. **F**. *A. uchucayensis*. Drawings A (reproduced with permission of the author and the journal), B–E (reproduced with permission of Missouri Botanical Garden Press, St. Louis) and F (reproduced with permission of the author and Phytotaxa).

thallis pogonion Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 61. 1994. Synonym: *Aenigma pogonion* (Luer) Szlach. & Kolan., Diversity 14. 2022.

Andinia schizopogon (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001. Basionym: *Pleurothallis schizopogon* Luer, Selbyana 5(2): 179. 1979. Synonym: *Aenigma schizopogon* (Luer) Szlach. & Kolan., Diversity 14. 2022.

Andinia uchucayensis A.Doucette & J. Portilla, Orchids (Lindleyana), 86(1): 72. 2017. Synonym: *Aenigma uchucayensis* (A.Doucette & J.Portilla) Szlach. & Kolan., Diversity 14. 2022.

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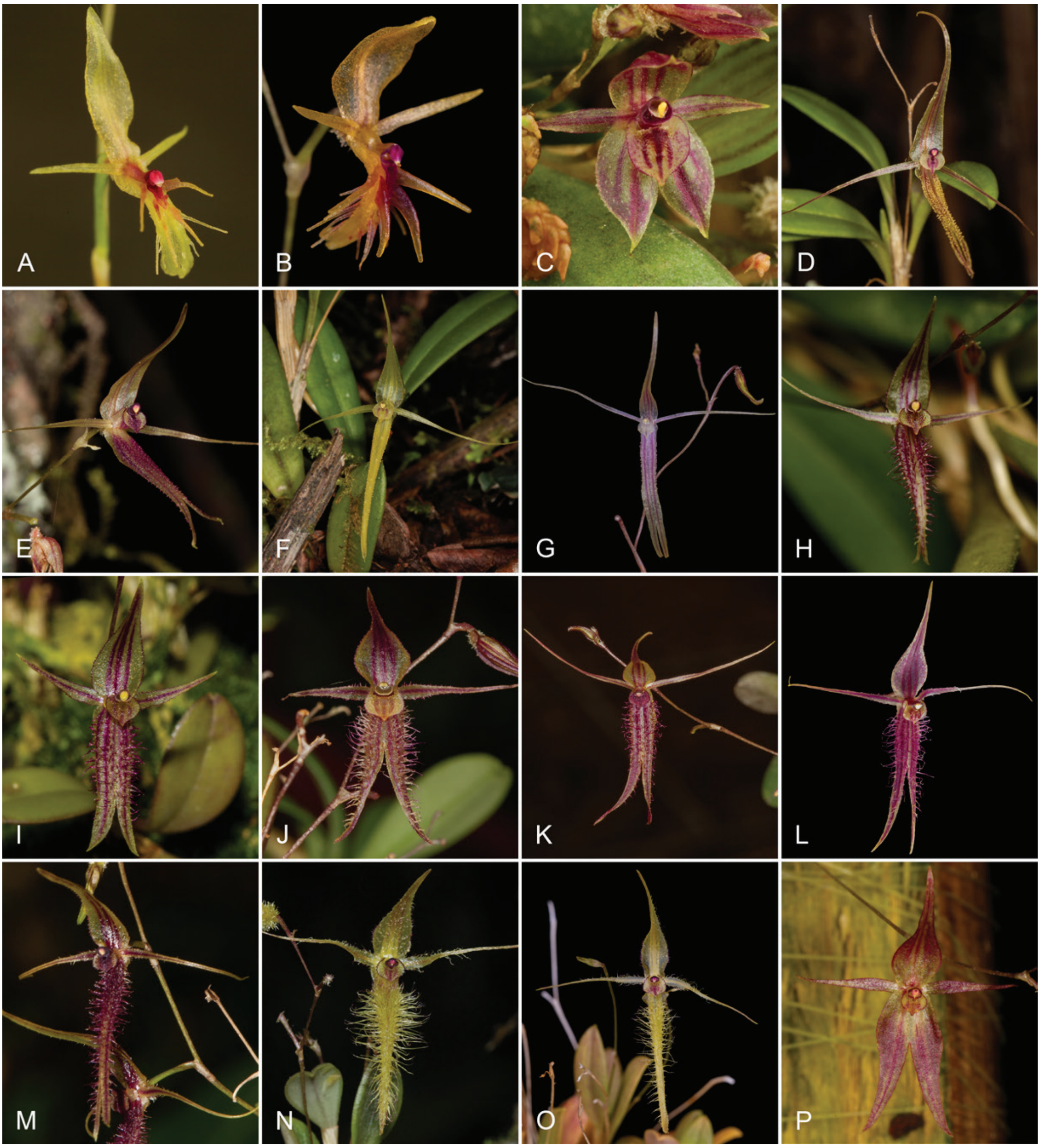

Figure 11. Photographs of the *Andinia* species subgenus *Aenigma*. **A–B**. *A. barbata*. **C**. *A. dalstroemii*. **D–G**. *A. hirtzii*. **H–J**. *A. pogonion*. **K–M**. *A. schizopogon*. **N–O**. *A. peruviana*. **P**. *A. uchucayensis*. Photographs by J.M. Pallandre (A), J. Ponert (B, G, O), Y. Dewèvre (C), M. Wilson (D, E, F, J, K, L, P), K. Olszowski (H), Kilian Zuchan (I), A. Diaz (M), L. Ocupa (N).

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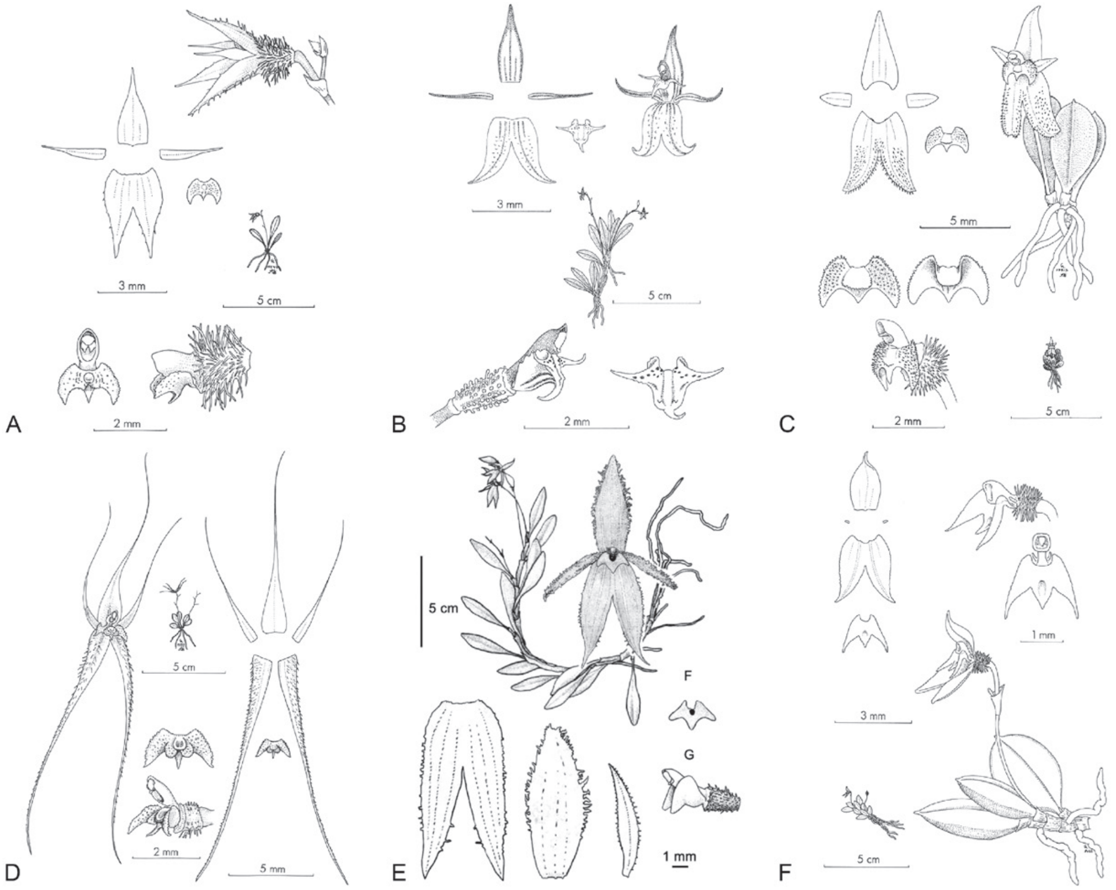

Figure 12. Drawings of the *Andinia* species with a tri-lobed lip. **A**. *A. hystricosa*. **B**. *A. ibex*. **C**. *A. panica*. **D**. *A. pentamytera*. **E**. *A. sunchubambensis*. **F**. *A. trimytera*. Drawings A, B, C, D and F (reproduced with permission of Missouri Botanical Garden Press, St. Louis) and E (reproduced with permission of the author and Internet Orchid Sp. Photo Encycl. Nomencl. Notes).

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