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## Phylogenetic analysis of *Andinia* (Pleurothallidinae; Orchidaceae) and a systematic re-circumscription of the genus

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### Abstract

Most of the species studied in this paper have previously been placed in either *Pleurothallis* or *Lepanthes*. However, at one time or another, members of the group have also been placed in the genera *Andinia*, *Brachycladium*, *Lueranthos*, *Masdevalliantha*, *Neooreophilus*, *Oreophilus*, *Penducella*, *Salpistele* and *Xenosia*. Phylogenetic analyses of nuclear ITS and plastid *matK* sequences indicate that these species form a strongly supported clade that is only distantly related to *Lepanthes* and is distinct from *Pleurothallis* and *Salpistele*. Since this clade includes the type species of *Andinia*, *A. dielsii*, and it has taxonomic precedence over all other generic names belonging to this group, *Andinia* is re-circumscribed and expanded to include 72 species segregated into five subgenera: *Aenigma*, *Andinia*, *Brachycladium*, *Masdevalliantha* and *Minuscula*. The required taxonomic transfers are made herein. We hypothesize that convergent evolution towards a similar pollinator syndrome involving deceit pollination via pseudocopulation by Diptera resulted in a similar floral morphology between species of subgenus *Brachycladium* and species of *Lepanthes*; hence the prior placement of the species of subgenus *Brachycladium* in *Lepanthes*. Species of the re-circumscribed *Andinia* are confined exclusively to the Andes, ranging from about 1,200 to 3,800 m, from Colombia south to Bolivia, making the generic name very apt. Elevational distributions of the individual clades are discussed in relation to the possible evolutionary diversification of the most species-rich clade, subgenus *Brachycladium*.

### Resumen

La mayoría de las especies aquí estudiadas han sido previamente incluidas ya sea en el género *Pleurothallis* o en *Lepanthes*. Sin embargo, en un momento u otro, miembros del grupo también han sido colocados en los géneros *Andinia*, *Brachycladium*, *Lueranthos*, *Masdevalliantha*, *Neooreophilus*, *Oreophilus*, *Penducella*, *Salpistele* y *Xenosia*. Análisis filogenéticos de secuencias de las regiones ITS y *matK* indican que estas especies forman un clado fuertemente soportado que está solo distantemente relacionado con *Lepanthes* y que es diferente de las especies de *Pleurothallis* y *Salpistele*. Ya que este clado incluye la especie tipo de *Andinia*, *A. dielsii* y que tiene precedencia taxonómica sobre los demás nombres genéricos que pertenecen al grupo, se re-circunscribe y expande el género *Andinia* para incluir 72 especies segregadas en cinco subgéneros: *Aenigma*, *Andinia*, *Brachycladium*, *Masdevalliantha* y *Minuscula* y se hacen las transferencias taxonómicas requeridas. Hipotetizamos que la evolución convergente hacia un síndrome de polinización similar que involucra la polinización por engaño por medio de la pseudocópula por Diptera, resultó en una morfología floral similar entre las especies del subgénero *Brachycladium* y las especies de *Lepanthes*; de ahí la ubicación previa de las especies del subgénero *Brachycladium* en *Lepanthes*. Las especies de *Andinia* están confinadas exclusivamente a los Andes, distribuidas aproximadamente desde 1200 m a 3800 m desde Colombia hasta Bolivia, haciendo del nombre genérico uno muy adecuado. Se discuten las distribuciones altitudinales de los clados individuales en relación a la posible diversificación evolutiva del clado con más especies, el cual corresponde al subgénero *Brachycladium*.

**Keywords:** molecular phylogeny; phylogenetics; taxonomy

## Introduction

The group of species addressed in this study, in subtribe Pleurothallidinae, have a complex and confusing taxonomic history. They have been placed at one time or another in the genera *Andinia* (Luer 1991: 123) Luer (2000: 5); *Brachycladium* (Luer 1986a: 31) Luer (2005: 307); *Lepanthes* Swartz (1799a: 85); *Lueranthos* Szlachetko & Margonska (2001: 117); *Masdevalliantha* (Luer 1986b: 44) Szlachetko & Margonska (2001: 117); *Neooreophilus* Archila (2009: 73); *Oreophilus* Higgins & Archila in Archila & Higgins (2008: 202); *Penducella* Luer & Thorerle (2010: 68); *Pleurothallis* Brown in Aiton (1813: 211); *Salpistele* Dressler (1979: 6); and *Xenosia* Luer (2004: 265).

Many of the species in consideration were originally placed in *Lepanthes*. Luer (1986a) transferred two species of *Lepanthes*, *Lepanthes dielsii* Mansfeld (1937: 72) and *L. pensilis* Schlechter (1921: 55) to *Salpistele*. Five years later, Luer (1991) subdivided *Salpistele* into *Salpistele* subgenus *Salpistele* and *Salpistele* subgenus *Andinia* Luer (1991: 123), based on differences between the species in growth habit and distributions. Subsequently, Luer recognized that the differences between these two subgenera were distinct enough to warrant elevation of subgenus *Andinia* to generic status (Luer 2000) as *Andinia* (Luer) Luer. At that time *Andinia* contained only the two species, *A. dielsii* (Mansf.) Luer (2000: 6) and *A. pensilis* (Schltr.) Luer (2000: 6), though this did not last long, as several more species were soon to be added from *Pleurothallis*.

Luer (1986b) created *Pleurothallis* subgenus *Aenigma* Luer (1986b: 26), to include the enigmatic species *P. dalstroemii* Luer (1994: 54), *P. ibex* Luer (1979: 168), *P. schizopogon* Luer (1979: 179), *P. trimytera* Luer & Escobar (1983: 34) and *P. vestigipetala* Luer (1977: 404). Luer (1994) added three more species to the subgenus: *P. hystricosa* Luer (1994: 54), *P. pentamytera* Luer (1994: 58) and *P. pogonion* Luer (1994: 61). Subsequently two more species, *P. panica* Luer & Dalström (1996: 6) and *P. lappacea* Luer (2000: 129) were added, bringing the number of species in *Pleurothallis* subgenus *Aenigma* to ten.

The first molecular phylogenetic study of the subtribe Pleurothallidinae (Pridgeon *et al.* 2001), based on a relatively small sampling of species from the different genera and subgenera and including only *A. pensilis* from *Andinia*, concluded that *Pleurothallis* was highly polyphyletic. Pridgeon & Chase (2001) added *P. lappacea* from subgenus *Aenigma* to their phylogenetic analyses and found that it was sister to *A. pensilis* with strong bootstrap support. This observation was evidence enough for them to expand the concept of *Andinia* to include all ten species of *Pleurothallis* subgenus *Aenigma*, bringing the total number of species in *Andinia* to twelve (Pridgeon & Chase 2001). Morphological similarities of the rhizome, ovaries, lip and column between *Andinia* and *Pleurothallis* subgenus *Aenigma*, as well as sympatric distributions in the Andes, supported this expansion of *Andinia* (Pridgeon & Chase 2001; Pridgeon 2005).

A more recent addition to *Andinia* came when Luer (2005) described the species *A. hirtzii* Luer (2005: 275), which he characterized as being morphologically similar to *A. schizopogon* (Luer) Pridgeon & Chase (2001: 251). This brought the number of species in *Andinia* to 13, the number recognized by Chase *et al.* (2015). The circumscription of *Andinia* preceding the current study, therefore, consisted of those species included by Pridgeon & Chase (2001), plus *A. hirtzii* (Luer 2005), as recognized by Chase *et al.* (2015). *Andinia*, hereafter, refers to this circumscription (Pridgeon & Chase 2001; Luer 2005; Chase *et al.* 2015).

*Pleurothallis* subgenus *Aenigma* was originally divided into section *Aenigmata* Luer (1986b: 26), with four species, and *Vestigipetalae* Luer (1986b: 26), containing only *P. vestigipetala*. Shortly after the expansion of *Andinia* to include the species of *Pleurothallis* subgenus *Aenigma* (Pridgeon & Chase 2001), Szlachetko & Margonska (2001) suggested that the floral morphology of *A. vestigipetala* (Luer) Pridgeon & Chase (2001: 252) was sufficiently distinct from the other species to create the monotypic genus *Lueranthos*, with *L. vestigipetalus* (Luer) Szlachetko & Margonska (2001: 117) as its sole member. However, neither Luer (2002) nor Pridgeon (2005) agreed with the transfer, Luer preferring to retain the species in *Pleurothallis* and Pridgeon to retain it in *Andinia*.

As was the case with *Andinia*, the first species assigned to *Neooreophilus* were also segregated from *Lepanthes*. When Reichenbach described *Lepanthes nummularia* Reichenbach (1858: 142), he recognized that, while all other species of *Lepanthes* had longer ramicauls than rhizomes, the reverse was true for *L. nummularia*. Reichenbach created two sections for *Lepanthes*, placing *L. nummularia* into *Lepanthes* section *Brachycladae* Reichenbach (1858: 142), meaning “short branches”, and the rest into *Lepanthes* section *Macrocladae* Reichenbach (1858: 143). Luer (1986a) elevated *Lepanthes* section *Brachycladae* to subgeneric status, giving it the name *Lepanthes* subgenus *Brachycladium* Luer (1986a: 31). Luer (1994) later described ten new species and delineated two new sections of the subgenus, which contained by that time 24 species. Subsequently, Luer (2005) elevated *Lepanthes* subgenus *Brachycladium* to generic status under the name *Brachycladium*, comprising by then 35 species. The name *Brachycladium*, however, was already occupied by a fungus, thereby rendering Luer’s name a posterior homonym and motivating Archila & Higgins

(2008) to propose *Oreophilus* as a substitute name. This name, however, was invalid as Archila & Higgins (2008) had included *A. dielsii*, the type species of *Andinia*, in their circumscription of *Oreophilus*. Realizing the mistake, Archila (2009) proposed a new name for the genus, *Neooreophilus*, this time validly. Just a few months later Luer & Thorerle (2010) published the name *Penducella* to replace *Brachycladium* and *Oreophilus*, unwittingly creating a synonym of *Neooreophilus*. Although *Neooreophilus* was validly proposed and some new species have been described under the genus (Ortíz 2011; Uribe & Thorerle 2011; Kolanowska 2013; Tobar & Archila 2012a; 2012b; Archila 2014; Vieira-Urbe & Jost 2015), the generic name has not been widely accepted by taxonomists, field botanists or hobbyists. Further, the genus was not even considered for acceptance by Chase *et al.* (2015) in their updated classification of the Orchidaceae.

Preliminary results of molecular phylogenetic analyses by Wilson & Jost (presented 2007; publ. 2009) using the nuclear internal transcribed spacer (ITS) region showed that *Neooreophilus* constituted a monophyletic group that was not closely related to *Lepanthes*. Instead, *Neooreophilus* was most closely related to *Andinia* as circumscribed by Pridgeon & Chase (2001), Luer (2005) and Chase *et al.* (2015). The connection between *Andinia* and *Neooreophilus* was confirmed following sequencing of additional species in a broadened analysis that also included species from *Xenosia* and *Masdevalliantha* because of vegetative morphological similarities to some species of *Andinia* (Wilson & Jost, presented 2009; publ. 2011).

*Xenosia* and *Masdevalliantha* were segregates from *Pleurothallis*. Luer & Escobar (1983) commented on the possible relatedness of *Pleurothallis xenion* Luer & Escobar (1983: 38) and *P. spiralis* (Ruiz & Pavón 1798: 237) Lindley (1830: 7) and Luer (1986b) went on to create *Pleurothallis* subgenus *Xenion* Luer (1986b: 96) for the two species. Luer even described these species as sharing a climbing growth habit and short ramicauls with members of *Pleurothallis* subgenus *Aenigma*, which Pridgeon & Chase (2001) would later add to *Andinia*. Luer (2004) elevated *Pleurothallis* subgenus *Xenion* to generic status, giving it the name *Xenosia*, with just two species *Xenosia spiralis* (Ruiz & Pav.) Luer (2004: 265) and *Xenosia xenion* (Luer & R.Escobar) Luer (2004: 265).

Luer & Escobar (1983) had recognized similarities in the growth habit of *P. xenion* and *P. longiserpens* Schweinfurth (1942: 183), however, Luer (1986b) did not place *P. longiserpens* in subgenus *Xenion*. Instead, in his earliest organization of *Pleurothallis*, Luer (1986b) created the subgenus *Masdevalliantha* Luer (1986b: 44) for the two species *P. longiserpens* and *P. masdevalliopsis* Luer (1979: 170). Later, Szlachetko & Margonska (2001) elevated the subgenus to generic status under the name *Masdevalliantha*, encompassing just the two species, *M. longiserpens* (C.Schweinf.) Szlachetko & Margonska (2001: 117) and *M. masdevalliopsis* (Luer) Szlachetko & Margonska (2001: 117). Neither of these generic names *Xenosia* or *Masdevalliantha* have entered common usage, nor have they been accepted by taxonomists (Pridgeon 2005; Chase *et al.* 2015) still being considered synonyms of *Pleurothallis*.

The pioneering molecular phylogenetic studies of Pridgeon *et al.* (2001) on Pleurothallidinae demonstrated that many of the genera recognized at that time were either polyphyletic or paraphyletic and that additional sampling and sequencing would need to be done in the different groups in order to characterize monophyletic genera. In the last decade and a half, a number of molecular phylogenetic studies have been published on multiple genera in Pleurothallidinae, including: *Acianthera* Scheidweiler (1842: 292) (Stenzel 2004; Chiron *et al.* 2012; Karremans & Rincón-González 2015; Karremans *et al.* 2016b); *Anathallis* Barbosa Rodrigues (1877: 23) (Chiron *et al.* 2012; Karremans 2014, 2015; Pessoa *et al.* 2014); *Masdevallia* Ruiz & Pavón (1794: 122) (Matuszkiewicz & Tukulalo, 2006; Abele 2007); *Pabstiella* Brieger & Senghas (1976: 195) (Chiron *et al.* 2012); *Phloeophila* (Chiron *et al.* 2016); *Specklinia* Lindley (1830: 8) (Bogarín *et al.* 2013; Karremans *et al.* 2013b; Karremans *et al.* 2015a; Karremans *et al.* 2015b; Karremans *et al.* 2016a); and *Stelis* Swartz (1799ba: 239) (Solano-Gomez 2005; Karremans 2010; Karremans *et al.* 2013a). Other molecular phylogenetic studies are in progress and preliminary reports have been published, including *Dracula* Luer (1978: 190) (Meyer & Cameron, 2009); *Masdevallia* (Doucette *et al.* 2014.); *Pleurothallis* (Wilson *et al.* 2011; 2013); *Porroglossum* Schlechter (1920: 82) (McDaniel & Cameron 2015); and *Scaphosepalum* Pfitzer (1888: 139) (Endara *et al.* 2011). Several of these studies have confirmed the occurrence of polyphyly and paraphyly in the genera circumscribed on the basis of morphology, necessitating the re-circumscription of the genera in the light of phylogenies based on molecular data.

The preliminary phylogenetic analyses by Pridgeon & Chase (2005) and Wilson & Jost (2009; 2011) suggested that species in the four genera *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia* were possibly related and perhaps *Andinia* should be re-circumscribed. The data were, however, based mostly upon nuclear ITS rDNA sequences from a relatively small number of species. In this more comprehensive study, we examine the phylogenetic relationships between species of *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia*, utilizing both nuclear ITS and plastid *matK* sequences, in order to determine whether these species form a monophyletic group.

## Materials and Methods

### Plant Material

The following study was conducted between 2005 and 2015. Plant material for analysis by MW and GSF in the U.S. was obtained from multiple sources including Lou Jost (with all appropriate permits) and Ecuagenera in Ecuador; Andy's Orchids and Lynn O'Shaughnessy in the U.S.; and Orquideas del Valle in Colombia (Table 1). Accessions are vouchered at Colorado College (COCO) or in Baños, Ecuador with flowers in spirits and/or by photographs of flowers. Plant material for analysis by AK in the Netherlands was obtained from various collections in that country (Table 1). Spirit vouchers were deposited at the Jardín Botánico Lankester (JBL), Costa Rica and in Leiden (L), The Netherlands. Nomenclature and authorities for plant names follow the International Plant Names Index (IPNI 2016).

**TABLE 1. List of all ingroup taxa; collection/voucher numbers; ITS and *matK* DNA sequences from this study.**

Taxon	Collection – Voucher	ITS	<i>matK</i>	Source
<i>Andinia dalstroemii</i> (Luer) Pridgeon & M.W.Chase (1)	Wilson AN005	KP012339	KR709284	This Study
<i>Andinia dalstroemii</i> (Luer) Pridgeon & M.W.Chase (2)	Wilson AN068	KP012346	-	This Study
<i>Andinia dielsii</i> (Mansf.) Luer <i>aff.</i>	Karremans 5429	KC425739	-	This Study
<i>Andinia lappacea</i> (Luer) Pridgeon & M.W.Chase (1)	O'Shaughnessy 01428	KP012343	KP012516	This Study
<i>Andinia lappacea</i> (Luer) Pridgeon & M.W.Chase (2)	Pridgeon 108	KC425837	-	Pridgeon & Chase 2002
<i>Andinia lappacea</i> (Luer) Pridgeon & M.W.Chase (3)	Wilson AN022	KP012345	KR709288	This Study
<i>Andinia pensilis</i> (Schltr.) Luer (1)	Chase 8007	AF262826	AF265455	Pridgeon <i>et al.</i> 2001
<i>Andinia pensilis</i> (Schltr.) Luer (2)	Wilson AN002	KP012336	KP012514	This Study
<i>Andinia pensilis</i> (Schltr.) Luer (3)	Pridgeon 200	KP012517	KP012344	This Study
<i>Andinia pogonion</i> (Luer) Pridgeon & M.W.Chase (1)	Jost 8293	KP012335	KR709282	This Study
<i>Andinia pogonion</i> (Luer) Pridgeon & M.W.Chase (2)	Wilson AN003	KP012337	KP012515	This Study
<i>Andinia pogonion</i> (Luer) Pridgeon & M.W.Chase (3)	O'Shaughnessy 03845	KP012342	-	This Study
<i>Andinia schizopogon</i> (Luer) Pridgeon & M.W.Chase (1)	Wilson AN004	KP012338	KR709283	This Study
<i>Andinia schizopogon</i> (Luer) Pridgeon & M.W.Chase (2)	O'Shaughnessy 02004	KP012341	-	This Study
<i>Andinia schizopogon</i> (Luer) Pridgeon & M.W.Chase (3)	Karremans 5783	KC425740	-	This Study
<i>Andinia schizopogon</i> (Luer) Pridgeon & M.W.Chase (4)	Wilson AN069	KP012347	KR709295	This Study
<i>Andinia schizopogon</i> (Luer) Pridgeon & M.W.Chase (5)	Wilson AN076	KP012350	KP012518	This Study
<i>Andinia trimytera</i> (Luer & R.Escobar) Pridgeon & M.W.Chase	Wilson AN073	KR827588	KR709297	This Study
<i>Andinia</i> sp.	Wilson AN006	KP012340	KR709285	This Study
<i>Andinia vestigipetala</i> (Luer) Pridgeon & M.W.Chase	Wilson AN075	KP012349	KR709298	This Study
<i>Masdevalliantha longiserpens</i> (C.Schweinf.) Szlachetko & Margonska (1)	O'Shaughnessy 04515	KP012353	KP012520	This Study
<i>Masdevalliantha longiserpens</i> (C.Schweinf.) Szlachetko & Margonska (2)	O'Shaughnessy 01755	KP012354	KR709287	This Study
<i>Masdevalliantha longiserpens</i> (C.Schweinf.) Szlachetko & Margonska (3)	Karremans 5724	KC425744	-	This Study
<i>Masdevalliantha longiserpens</i> (C.Schweinf.) Szlachetko & Margonska (4)	Wilson AN021	KP012356	KP012521	This Study
<i>Neoreophilus ciliaris</i> (Luer & Hirtz) Archila	O'Shaughnessy 01380	KP012372	KR709291	This Study
<i>Neoreophilus compositus</i> (Luer & R.Escobar) Archila	O'Shaughnessy 03688	KP012377	KR709294	This Study

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TABLE 1. (Continued)

Taxon	Collection – Voucher	ITS	matK	Source
<i>Neoreophilus lynnianus</i> (Luer) Archila	O'Shaughnessy 02869	KR827587	KR709293	This study
<i>Neoreophilus nummularius</i> (Rchb. f.) Archila (1)	O'Shaughnessy 00096	KR827583	KP012525	This Study
<i>Neoreophilus nummularius</i> (Rchb. f.) Archila (2)	O'Shaughnessy 00125	KR827584	KP012526	This Study
<i>Neoreophilus nummularius</i> (Rchb. f.) Archila (3)	O'Shaughnessy 02359	KR827586	KP012530	This Study
<i>Neoreophilus nummularius</i> (Rchb. f.) Archila (4)	Jost #8316	KP012365	-	This Study
<i>Neoreophilus nummularius</i> (Rchb. f.) Archila (5)	Jost #8320	KP012367	-	This Study
<i>Neoreophilus persimilis</i> (Luer & Sijm) Archila	O'Shaughnessy 982	KP012369	-	This Study
<i>Neoreophilus pilosellus</i> (Rchb. f.) Archila (1)	O'Shaughnessy 01008	KP012370	KR709290	This Study
<i>Neoreophilus pilosellus</i> (Rchb. f.) Archila (2)	O'Shaughnessy 00146	KP012368	KR709289	This Study
<i>Neoreophilus pilosellus</i> (Rchb. f.) Archila (3)	O'Shaughnessy 02624	KP012375	KP012531	This Study
<i>Neoreophilus platysepalus</i> (Luer & R.Escobar) Archila (1)	Karremans 4847	JQ995331	KC425864	This Study
<i>Neoreophilus platysepalus</i> (Luer & R.Escobar) Archila (2)	O'Shaughnessy 02625	KP012376	KR709292	This Study
<i>Neoreophilus pseudocaulescens</i> (L.B.Sm. & S.K.Harris) Archila	Jost 5444	KP012360	-	This Study
<i>Neoreophilus stalactites</i> (Luer & Hirtz) Archila (1)	Wilson AN024	KP012359	KP012523	This Study
<i>Neoreophilus stalactites</i> (Luer & Hirtz) Archila (2)	O'Shaughnessy 02248	KP012374	KP012529	This Study
<i>Neoreophilus wernerii</i> (Luer) Archila (1)	O'Shaughnessy 01492	KP012373	KP012528	This Study
<i>Neoreophilus wernerii</i> (Luer) Archila (2)	O'Shaughnessy 00508	KR827585	-	
<i>Xenosia spiralis</i> (Ruiz & Pav.) Luer (1)	Wilson AN007	KP012351	KR709286	This Study
<i>Xenosia spiralis</i> (Ruiz & Pav.) Luer (2)	Wilson AN070	KP012357	KR709296	This Study
<i>Xenosia xenion</i> (Luer & R.Escobar) Luer (1)	Wilson AN008	KP012352	KP012519	This Study
<i>Xenosia xenion</i> (Luer & R.Escobar) Luer (2)	Pridgeon 250	KP012355	-	This Study
<i>Xenosia xenion</i> (Luer & R.Escobar) Luer (3)	Wilson AN074	KP012358	KP012522	This Study

### DNA Extraction, PCR and Sequencing

The majority of the accessions were processed by MW and GSF in the U.S. using the following procedures. Genomic DNA was extracted from frozen leaf tissue using a DNeasy Plant Mini Kit (Qiagen). Genomic DNA concentrations were estimated by running samples on gels against known quantities of  $\lambda$  DNA.

The primer pair 17SE and 26SE (Sun *et al.* (1994) was used to amplify the nuclear internally transcribed spacer (ITS) region of rDNA. A master mix was created using 12.5  $\mu$ L 2 $\times$  PCR Master Mix (Promega), 1  $\mu$ L 17SE (25  $\mu$ M), 1  $\mu$ L 26SE (25  $\mu$ M), 1  $\mu$ L dimethyl sulfoxide (DMSO), and 4.5  $\mu$ L molecular biology grade water per reaction, for a total of 20  $\mu$ L per reaction. In a 0.2 mL PCR tube, 5  $\mu$ L containing approximately 10 ng template DNA was added to 20  $\mu$ L mastermix. PCR amplification was performed using an iCycler (Bio-Rad Laboratories, Inc.) with the following program: 1 cycle of 94°C 5 min; 5 cycles of 94°C 1 min, 60°C 1 min, 72°C 3 min; 30 cycles of 94°C 1 min, 58°C 1 min, 72°C 3 min; 1 cycle of 72°C 15 min; 4°C hold.

The primer pair 390F and 1326R (Cuénoud *et al.* 2002) was used to amplify the plastid *matK* gene. A master mix was created using 12.5  $\mu$ L 2 $\times$  PCR Master Mix (Promega), 1  $\mu$ L 390f (25  $\mu$ M), 1  $\mu$ L 1326r (25  $\mu$ M), and 0.5  $\mu$ L molecular biology grade water per reaction, for a total of 15  $\mu$ L. In a 0.2 mL PCR tube, 10  $\mu$ L containing approximately 2.5 ng template DNA was added to 15  $\mu$ L mastermix. PCR amplification was performed using an iCycler (Bio-Rad

Laboratories, Inc.) with the following program: 30 cycles of 94°C 1 min, 48°C 30 s, 72°C 1 min; 1 cycle of 72°C 7 min; 4°C hold.

PCR products were extracted from gels and purified using a QIAquick Gel Extraction Kit (Qiagen) according to the protocol provided. Concentration (ng/μL) and purity ( $A_{260}/A_{280}$ ) of purified DNA were estimated on a NanoDrop 2000 Spectrophotometer (Thermo Scientific) or Biophotometer (Eppendorf). Purified PCR products were sequenced commercially by either GeneWiz or University of Michigan DNA Sequencing Core (UM). ITS PCR products were sequenced with primers 17SE and 26SE (Sun *et al.* 1994) and ITS1 and ITS4 (White *et al.* 1990). The *matK* PCR products were sequenced with the primers 390F and 1326R (Cuénoud *et al.* 2002) and Nina-matK-F (GCGATTGTTTTTCCACGAAT) and Nina-matK-R (TCCGCTGTGATAACGACAAA) (Sheade 2012).

A small number of samples were processed in Leiden, The Netherlands by AK using procedures described previously (Karremans *et al.* 2013a). The ITS region was amplified and sequenced using the primers 17SE and 26SE (Sun *et al.* 1994) and the plastid gene *matK* was amplified and sequenced using the primers 2.1aF and 5R (Karremans *et al.* 2013a).

### Sequence Analysis

Sequence trace files generated by MW and GSF from either GeneWiz or UM were examined and edited as necessary in FinchTV v. 1.4 (Geospiza). Multiple sequences (usually two forward and two reverse sequences) were manually aligned using the freeware Se-Al v. 2.0a11 or BioEdit v. 7.2.5 to create a consensus sequence for each accession. When the consensus contained ambiguous nucleotides additional sequences were obtained in order to resolve ambiguities. When abnormalities could not be resolved Unicode nomenclature was employed. Sequence trace files generated by AK were processed as described previously (Karremans *et al.* 2013a). All ITS and *matK* sequences generated in this study were deposited in GenBank (Table 1).

### Phylogenetic analysis of *Andinia* and related genera in the context of subtribe *Pleurothallidinae*

A phylogenetic analysis was conducted with representative species from *Andinia* (as defined above [Pridgeon & Chase 2001; Luer 2005; Chase *et al.* 2015]) and species from the genera *Masdevalliantha*, *Neooreophilus* and *Xenosia*, considered possibly related to *Andinia* (Table 1). The analysis additionally included the pleurothallid genera *Anathallis*, *Dryadella* Luer (1978: 207), *Lankesteriana* Karremans (2014: 321), *Lepanthes*, *Pabstiella*, *Phloeophila* (Hoehne & Schlechter 1926: 199), *Platystele* Schlechter (1910: 565), *Pleurothallis*, *Scaphosepalum*, *Specklinia*, *Stelis* (including three species of the former *Salpistele*), *Trichosalpinx* Luer (1983: 393), and *Zootrophion* Luer (1982: 80) (Table 2).

**TABLE 2.** List of all outgroup taxa used for the overview phylogeny; collection/voucher numbers; ITS and *matK* DNA sequences from GenBank. Collection, voucher or sequence not available (NA).

Taxon	Collection - Voucher	ITS	<i>matK</i>
<i>Anathallis lewisiae</i> (Ames) Solano & Soto Arenas	DB1056	KC425733	KC425858
<i>Anathallis obovata</i> (Lindl.) Pridgeon & M.W.Chase	AK4796	KF747797	NA
<i>Anathallis sertularioides</i> (Sw.) Pridgeon & M.W.Chase	HS483	KC425840	NA
<i>Dryadella albicans</i> (Luer) Luer	AK4861	KC425742	KC425863
<i>Dryadella edwallii</i> (Cogn.) Luer	MWC305	AF262824	AF265454
<i>Dryadella hirtzii</i> Luer	NA	EF079367	EF079327
<i>Laelia anceps</i> Lindley	MWC1209	AY008576	NA
<i>Laelia anceps</i> Lindley	MWC998	NA	AF263794
<i>Laelia gouldiana</i> Reichenbach f.	MWC6408	AY008577	NA
<i>Laelia gouldiana</i> Reichenbach f.	LG156	NA	EF079315
<i>Laelia rubescens</i> Lindley	MWC284	AY429391	AY396098
<i>Lankesteriana barbulata</i> (Lindl.) Karremans	DB8606	KC425726	NA
<i>Lankesteriana duplooyi</i> (Luer & Sayers) Karremans	AK488	KJ472363	NA
<i>Lankesteriana fractiflexa</i> (Ames & C.Schweinf.) Karremans	DB8998b	KC425729	NA

...continued on the next page

TABLE 2. (Continued)

Taxon	Collection - Voucher	ITS	matK
<i>Lepanthes elata</i> Reichenbach f.	DB2663	NA	EU214374
<i>Lepanthes steyermarkii</i> Foldats	MWC980	AF262889	NA
<i>Lepanthes turialvae</i> Reichenbach f.	DB977	NA	EU214376
<i>Lepanthes vestigialis</i> Bogarín & Pupulin	MF585	KP012489	NA
<i>Lepanthes woodburyana</i> Stimson	MWC1094	AF262890	AF265472
<i>Octomeria gracilis</i> Loddiges ex Lindley	MWC977	AF262911	AF265484
<i>Octomeria gracilis</i> Loddiges ex Lindley	NA	NA	AY368421
<i>Octomeria lithophila</i> Barbosa Rodrigues	MWC5533	AF262912	NA
<i>Octomeria</i> sp. "Heidelberg"	BG125079	NA	EF079352
<i>Pabstiella aryter</i> (Luer) F.Barros	DB6501	JF934816	JF934876
<i>Pabstiella tripterantha</i> (Rchb.f.) F.Barros	NA	AF275694	AF302649
<i>Phloeophila pelecanceps</i> (Luer) Pridgeon & M.W.Chase	MWC1128	AF262810	AF265450
<i>Phloeophila peperomioides</i> (Ames) Garay	NA	AF275690	AF291103
<i>Phloeophila pleurothallopsis</i> (Kraenzl.) Pridgeon & M.W.Chase	MWC978	AF262812	AF265451
<i>Platystele stenostachya</i> (Rchb.f.) Garay	AK4250a	KC425757	NA
<i>Platystele stenostachya</i> (Rchb.f.) Garay	1745	NA	JQ771571
<i>Pleurothallis quadrifida</i> (Lex. ) Lindley	PL295	Wilson unpubd.	Wilson unpubd.
<i>Pleurothallis ruscifolia</i> R.Brown	PL003	Wilson unpubd.	Wilson unpubd.
<i>Pleurothallis sandemanii</i> Luer	PL206	Wilson unpubd.	Wilson unpubd.
<i>Scaphosepalum gibberosum</i> Rolfe	MWC968	AF262817	AF265458
<i>Scaphosepalum rapax</i> Luer	NA	NA	EU490705
<i>Scaphosepalum swertiifolium</i> Rolfe	MWC1383	AF262818	NA
<i>Scaphosepalum ursinum</i> Luer	NA	EF079365	EF079325
<i>Specklinia calyptrostele</i> (Schltr.) Pridgeon & M.W.Chase	FP7724	KF747798	NA
<i>Specklinia costaricensis</i> (Rolfe) Pridgeon & Chase	MWC3656	AF262863	AF265459
<i>Specklinia microphylla</i> (A.Rich & Galeotti) Pridgeon & M.W. Chase	DB9394	KC425808	NA
<i>Specklinia microphylla</i> (A.Rich & Galeotti) Pridgeon & M.W. Chase	DB1688	NA	EU214488
<i>Stelis deutroadrianae</i> J.M.H. Shaw (syn. <i>Salpistele adrianae</i> Luer & Sijm)	DB5917a	JF934799	JF934860
<i>Stelis argentata</i> Lindley	OT4043	KJ472399	KJ472363
<i>Stelis brunnea</i> (Dressler) Pridgeon & M.W.Chase (syn. <i>Salpistele brunnea</i> Dressler)	DB6226	JF934798	JF934859
<i>Stelis carnosilabia</i> (A.H.Heller & A.D.Hawkes) Pridgeon & M.W.Chase	DB730a	JF934807	JF934868
<i>Stelis maculata</i> Pridgeon & M.W.Chase (syn. <i>Salpistele lutea</i> Dressler)	MWC6802	AF262827	NA
<i>Stelis sclerophylla</i> (Lindl.) Karremans	AK4791	JQ995326	NA
<i>Trichosalpinx blaisdellii</i> (S.Watson) Luer	MWC5614	AF262887	AF265474
<i>Trichosalpinx egeri</i> (Pabst) Luer	GLO584	KJ472384	KJ472357
<i>Trichosalpinx orbicularis</i> (Lindl.) Luer	MWC1300	AF262886	AF265476
<i>Zootrophion atropurpureum</i> (Lindl.) Luer	MWC5624	AF262898	NA
<i>Zootrophion dayanum</i> (Rchb.f.) Luer	MWC1096	AF262895	AF265452
<i>Zootrophion hirtzii</i> Luer	MWC972	AF262897	NA

Concatenated ITS-*matK* sequences for four species of *Andinia* and one species each of *Masdevalliantha*, *Neooreophilus* and *Xenosia* were aligned with concatenated ITS-*matK* sequences of the other genera from GenBank (Table 2). Where possible, the ITS and *matK* sequences were derived from the same collection of a species, but some were from two different collections of the same species. For some taxa only ITS or *matK* was available. Alignments were generated in the software suite MEGA 6 v.6.06 (Tamura *et al.* 2013) using MUSCLE (Edgar 2004) with default parameters. The ITS-*matK* matrix, which included 59 taxa and a total of 1,637 positions, was analyzed by maximum parsimony (MP) and maximum likelihood (ML) in MEGA 6 with 1000 bootstrap replicates (Hall 2011; 2013). MP analyses were conducted using the Subtree-Pruning-Regrafting algorithm (Nei & Kumar 2000) with search level 1 in which the initial trees were obtained by the random addition of sequences (10 replicates). ML analyses were conducted using the model of Tamura & Nei (1993). Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pair-wise distances estimated using the maximum composite likelihood approach, and then selecting the topology with superior log likelihood value (Tamura *et al.* 2013). All trees were rooted with four outgroup sequences of *Laelia* species (Laeliinae; Orchidaceae). For assessment of bootstrap percentages in MP and ML analyses, we considered 85–100% as “strong” support, 75–84% as “moderate” support, 50–74% as “weak” support and <50% as “no support”.

### **Phylogenetic analysis within the clade containing *Andinia* and related genera: ITS; *matK*; and ITS-*matK***

In order to examine relationships within the clade containing *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia*, ITS and *matK* sequences of representative species (Table 1) were analyzed separately. The ITS sequences were 762–764 bp when truncated at: 5’ end CGGGCGGTT; and 3’ end GGCCACCCG. The aligned ITS matrix, which consisted of 65 taxa with 802 positions, was analyzed by MP and ML in MEGA 6 with 1,000 bootstrap replicates. The *matK* sequences were 821 bp long when truncated at: 5’ end ATCTACTAA; and 3’ end TCCTCAAAG. The aligned *matK* matrix, which consisted of 53 taxa with 821 positions, was analyzed by MP and ML in MEGA 6 with 1,000 bootstrap replicates. Plastid *matK* sequences were analyzed as both coding and non-coding sequence, since there is still some debate as to whether *matK* is a pseudogene in Orchidaceae (Barthet *et al.* 2015).

While the *matK* tree exhibited less resolution than the ITS tree, there were no hard incongruencies. The decision was therefore made to concatenate the ITS and *matK* data. The ITS-*matK* matrix, which included 55 taxa and a total of 1,621 positions, was analyzed by MP and ML in MEGA 6 with 1,000 bootstrap replicates.

### **Distribution Maps and Elevation Data**

Species collection localities were downloaded from Tropicos (2016). The program ArcMap in ArcGIS (ESRI) was used to generate maps for the distribution of the subgroups within the clade containing the species of *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia*. Species collection elevation data were downloaded from Tropicos and used to calculate elevational ranges and mean collection elevations for each of the clades in the phylogenetic analyses.

## **Results**

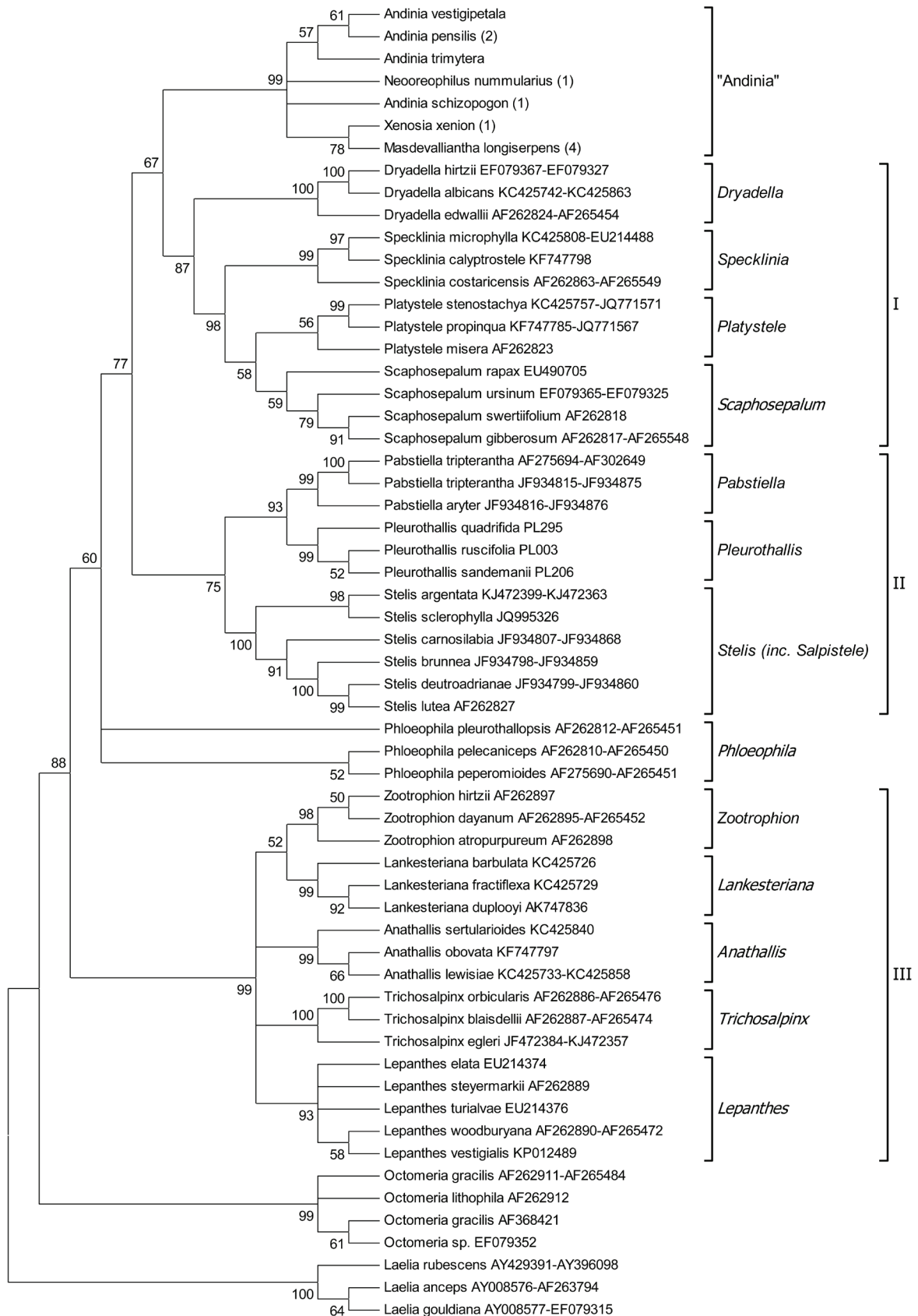
### **Phylogenetic analysis of *Andinia* and related genera in the context of subtribe Pleurothallidinae**

The MP analysis produced a single most parsimonious tree. In the bootstrap consensus tree (Fig. 1) the clade “*Andinia*” containing the genera *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia*, was strongly supported. This clade was sister with weak support to the strongly supported clade I, containing the genera *Dryadella*, *Platystele*, *Scaphosepalum* and *Specklinia*. The combined clade containing “*Andinia*” and clade I, was sister with moderate support to the moderately supported clade II, containing the genera *Pabstiella*, *Pleurothallis* and *Stelis* (including *Salpistele*). The genus *Phloeophila* was basal to the clade containing clades “*Andinia*”, I and II. The strongly supported clade III, containing the genera *Anathallis*, *Lankesteriana*, *Lepanthes*, *Trichosalpinx* and *Zootrophion*, was basal to the clades “*Andinia*”, I, II and genus *Phloeophila*.

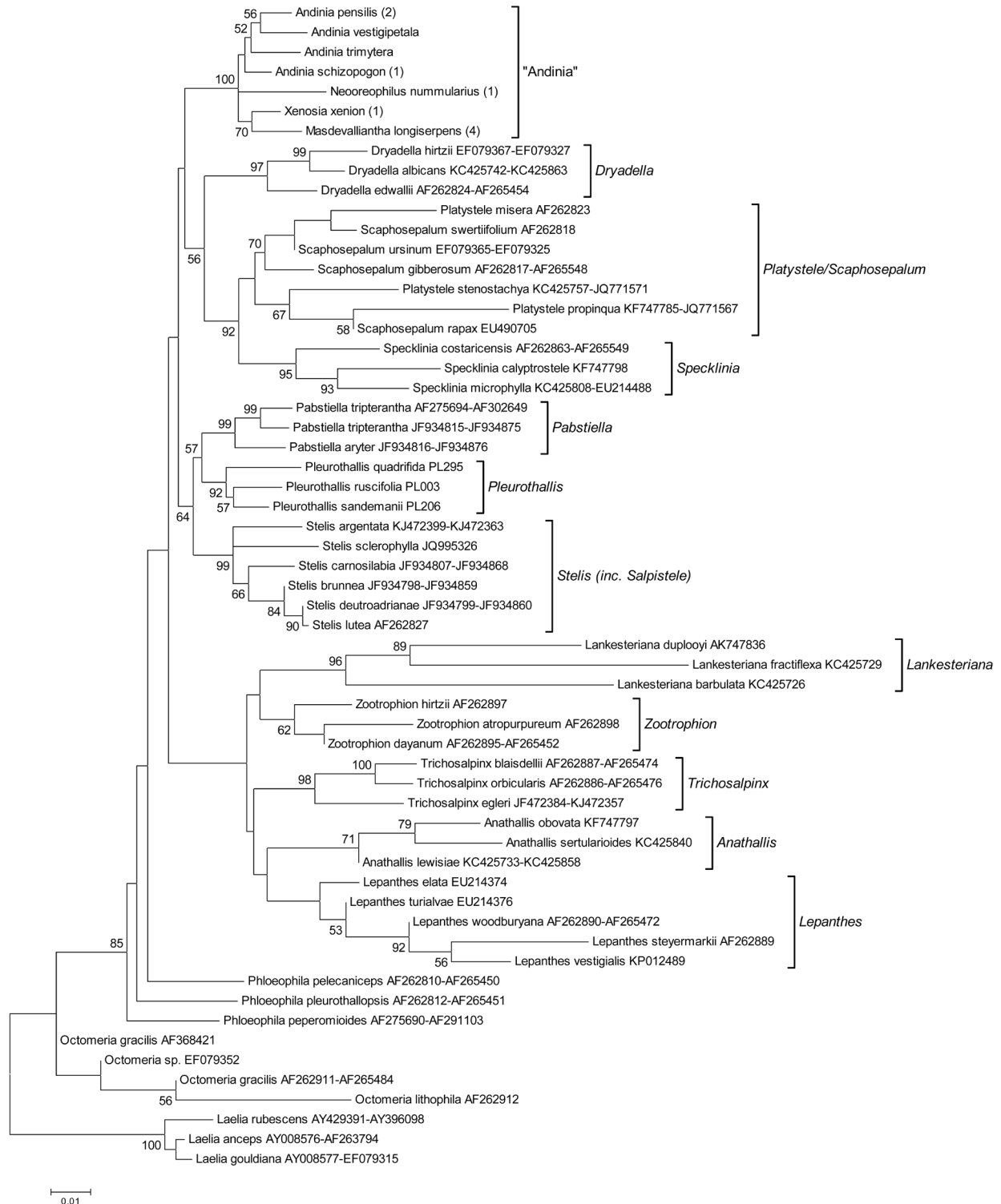
The tree with maximum log likelihood from ML analysis (Fig. 2) is drawn to scale, with branch lengths measured in the number of substitutions per site. The scaled tree is included to allow comparisons of relative phylogenetic depth for accepted genera in the Pleurothallidinae (Chase *et al.* 2015) and the proposed genus *Andinia*, representing the clade labeled “*Andinia*”. The tree topology was largely the same as the bootstrap consensus tree from MP analysis (Fig. 1). In this tree the “*Andinia*” clade was also strongly supported. The ML analysis did not support a closer relationship of clade “*Andinia*” with clade I (*Dryadella*-*Platystele*-*Scaphosepalum*-*Specklinia*), than with clade II



(*Pabstiella*-*Pleurothallis*-*Stelis*). Interestingly, *Platystele* and *Scaphosepalum* were not resolved into distinct clades in this analysis, perhaps because of limited sampling.



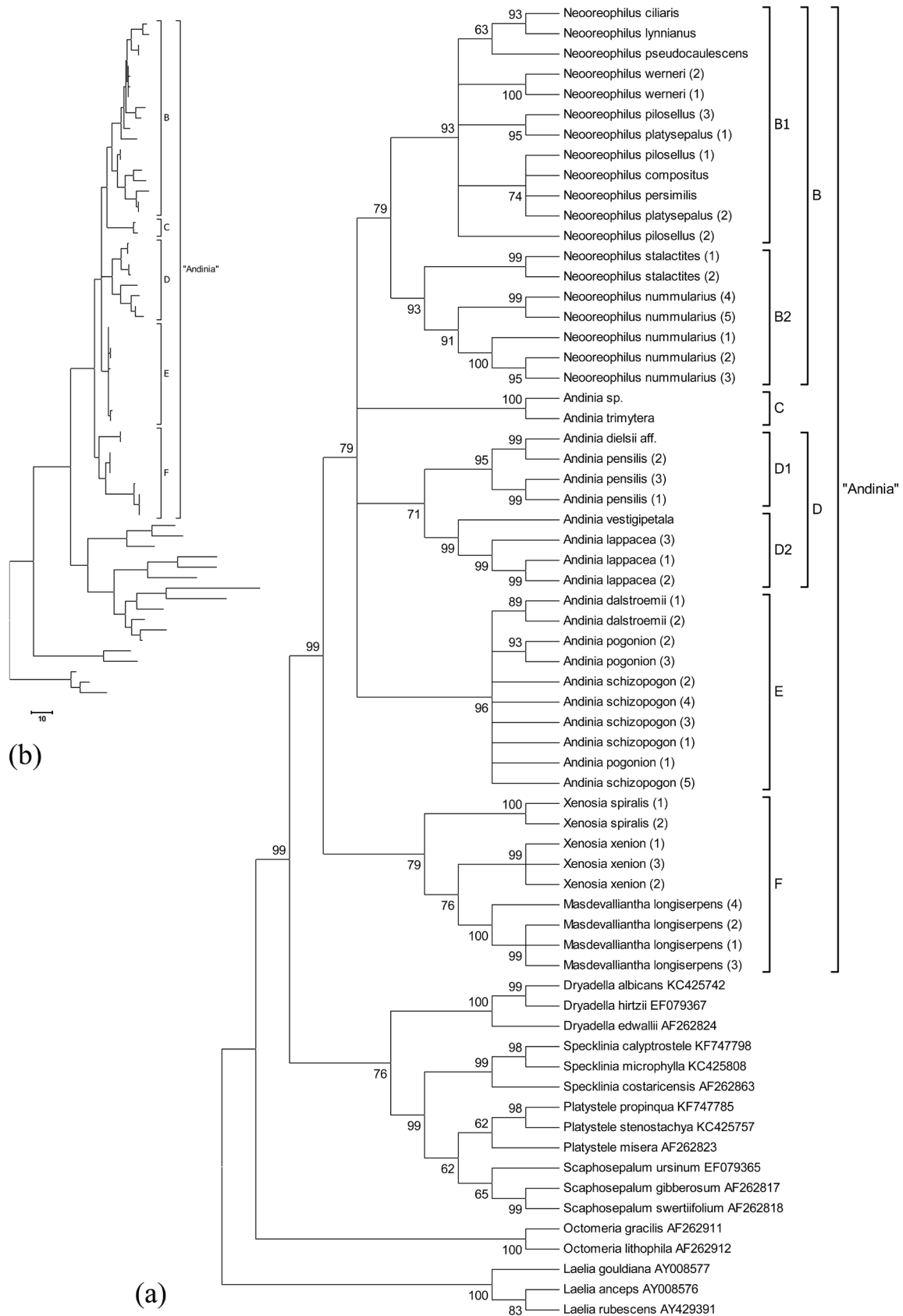
**FIGURE 1.** Bootstrap consensus phylogenetic tree inferred from the concatenated ITS-*matK* data set using MP analysis with 1000 bootstrap replicates in MEGA 6. Values at each node represent percent bootstrap support; bootstrap percentages less than 50% are not shown.



**FIGURE 2.** Phylogenetic tree with maximum log likelihood inferred from the concatenated ITS-*matK* data set using ML analysis with 1000 bootstrap replicates in MEGA 6. Values at each node represent percent bootstrap support; bootstrap percentages less than 50% are not shown.

### ***Phylogenetic analysis within the clade containing Andinia and related genera: nuclear ITS***

The MP analysis of ITS sequence data produced three equally parsimonious trees. In the MP bootstrap consensus tree (Fig. 3), the "Andinia" clade, containing species of *Andinia*, *Masdevalliantha*, *Neoreophilus* and *Xenosia*, was strongly supported. The moderately supported clade B contained all the species of *Neoreophilus*; the strongly supported clade B2 contained the species *N. nummularius* and *N. stalactites*; and the strongly supported sister clade B1 contained the



**FIGURE 3.** (a) Bootstrap consensus phylogenetic tree inferred from the ITS data set using MP analysis with 1000 bootstrap replicates in MEGA 6. Values at each node reflect percent bootstrap support; bootstrap percentages less than 50% are not shown. (b) One of five the most parsimonious trees scaled for branch length.

remaining *Neooreophilus* species. Clade C contained *A. trimytera* and an unidentified, unflowered plant presumed to be *A. trimytera* based on the ITS sequence. The weakly supported clade D consisted of two strongly supported sister clades, D1 containing *A. dielsii* and *A. pensilis* and D2 containing *A. vestigipetala* and *A. lappacea* (Luer) Pridgeon & Chase (2001: 251). The strongly supported clade E contained *A. dalstroemii* (Luer) Pridgeon & Chase (2001: 251), *A. pogonion* (Luer) Pridgeon & Chase (2001: 251) and *A. schizopogon* (Luer) Pridgeon & Chase (2001: 251). The moderately supported clade F, which was basal to clades B-E, contained *M. longiserpens*, *X. spiralis* and *X. xenion*.

In the ML analysis (data not shown) the “Andinia” clade, containing species of *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia* was also strongly supported (BP 98%). The topology of the bootstrap consensus tree was almost identical to that of the MP bootstrap consensus tree. Support for the clades was as follows: clade B (BP 69%); clade B1 (BP 89%); clade B2 (BP 83%); clade C (BP 100%); clade D (BP 74%); clade D1 (BP 97%); clade D2 (BP 96%); clade E (BP 93%); and clade F (BP 77%).

#### **Phylogenetic analysis within the clade containing *Andinia* and related genera: plastid *matK***

The MP analysis of *matK* sequence data produced four equally parsimonious trees. The MP bootstrap consensus tree (Fig. 4) exhibited less resolution than the ITS tree, as has been observed in other studies in Pleurothallidinae (Pridgeon *et al.* 2001; Karremans *et al.* 2013b). The “Andinia” clade, containing species of *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia* was strongly supported. Clade B, containing all species of *Neooreophilus* was also strongly supported. Additional strongly supported clades included, clade D1 containing *A. dielsii* and *A. pensilis* and clade E containing *A. dalstroemii*, *A. pogonion* and *A. schizopogon*. The remaining clades, which represented multiple accessions of the same species, and other taxa, formed a polytomy with clades B, D1 and E.

In the ML analysis (data not shown) the “Andinia” clade, containing species of *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia* was moderately supported (BP 85%). As in the MP analysis, the only strongly supported clades were: clade B (BP 93%); D1 (BP 87%); and E (BP 99%).

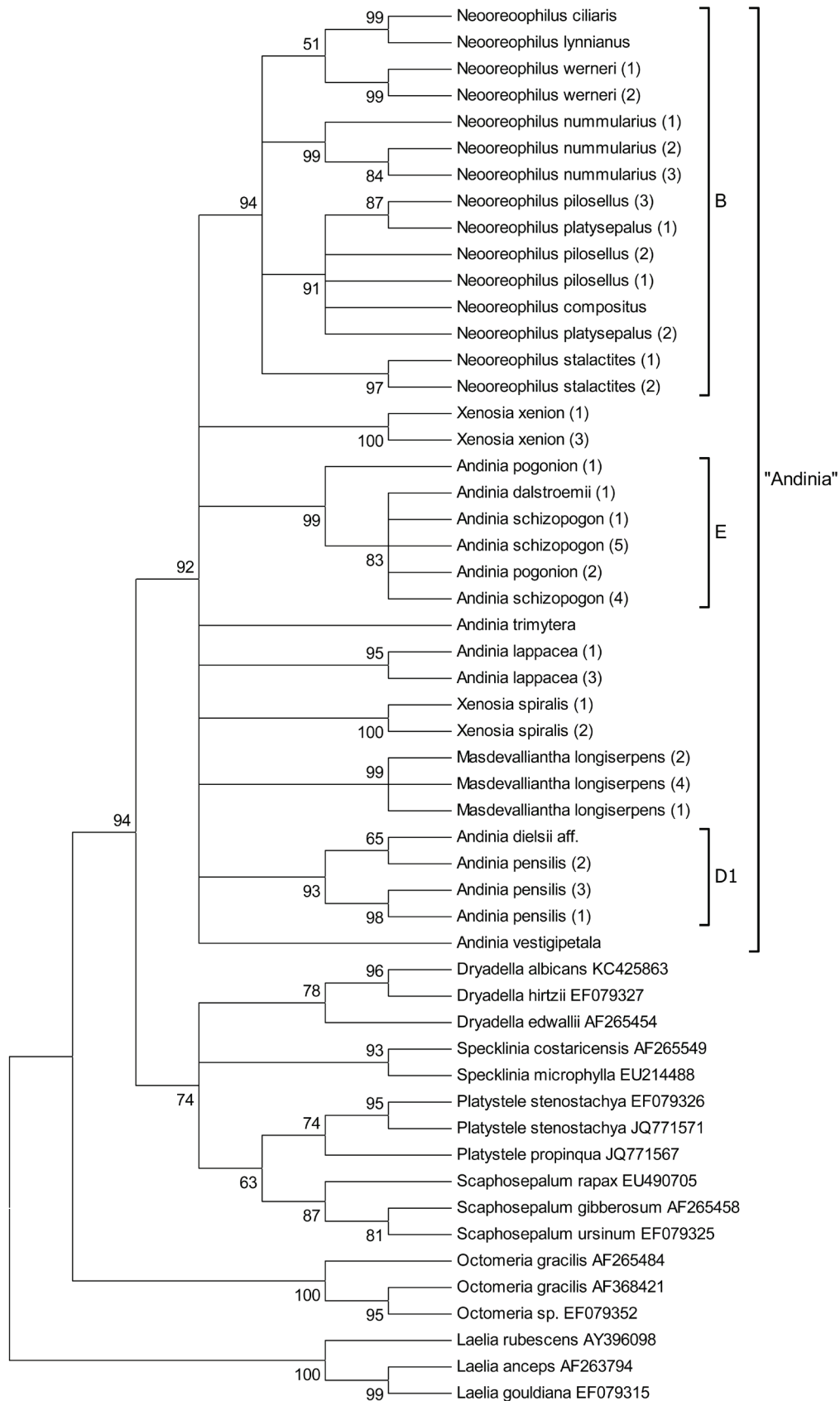
#### **Phylogenetic analysis within the clade containing *Andinia* and related genera: concatenated ITS-*matK***

The MP analysis of ITS-*matK* sequence data produced two equally parsimonious trees. In the MP bootstrap consensus tree (Fig. 5), the “Andinia”, containing species of *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia*, was strongly supported. The strongly supported clade B contained all the species of *Neooreophilus*: the strongly supported clade B2 contained the species *N. nummularius* and *N. stalactites* and the strongly supported sister clade B1 contained the remaining *Neooreophilus* species. Clade C contained *A. trimytera* and the accession presumed to be *A. trimytera*. The moderately supported clade D consisted of two strongly supported sister clades, D1 containing *A. pensilis* accessions and D2 containing *A. vestigipetala* and *A. lappacea*. The strongly supported clade E contained *A. dalstroemii*, *A. pogonion* and *A. schizopogon*. Clade F, which exhibited low support, was basal to clades B-E and contained the species *M. longiserpens*, *X. spiralis* and *X. xenion*.

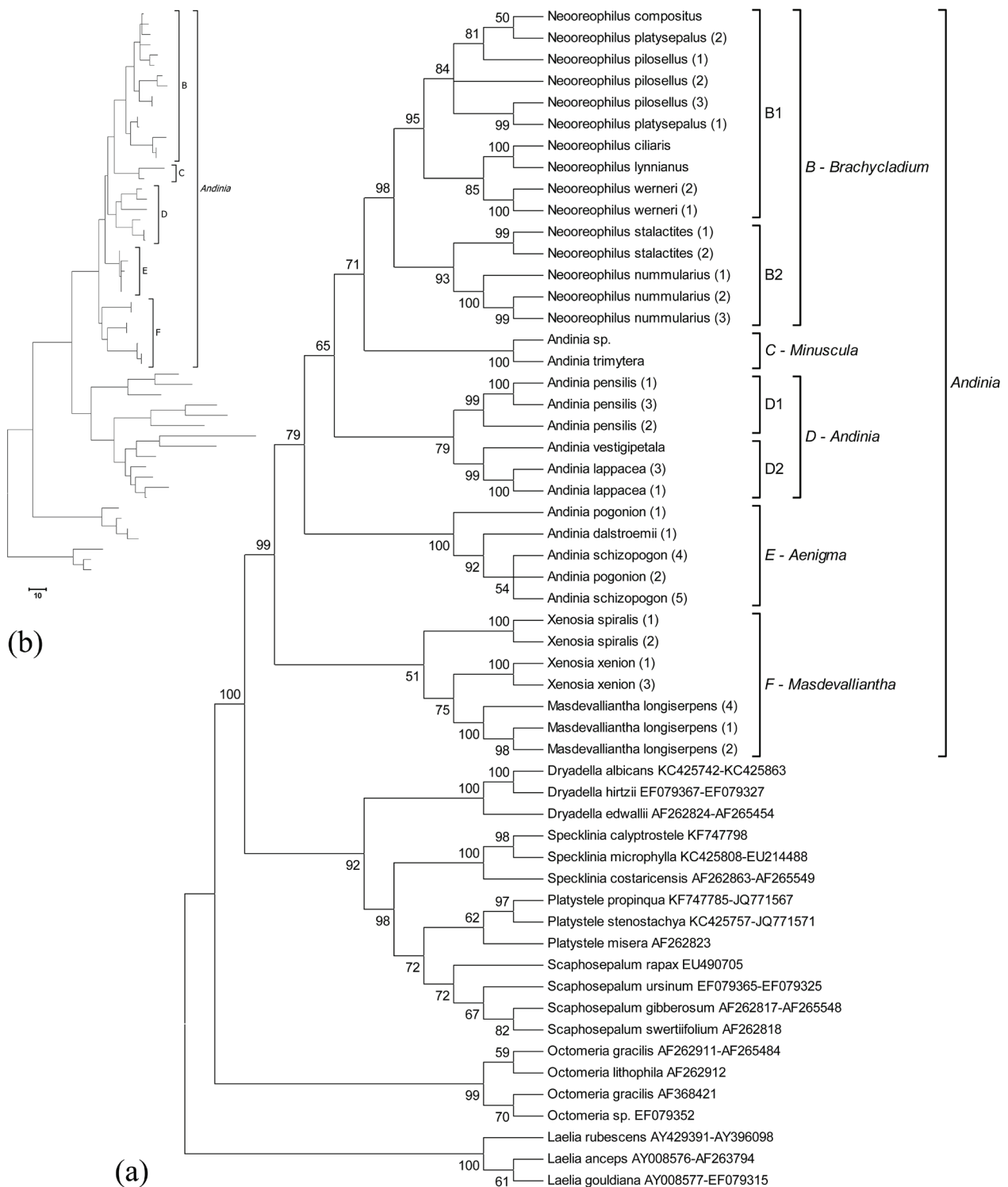
In the ML analysis (data not shown) the “Andinia” clade was again strongly supported (BP 100%). The topology of the bootstrap consensus tree was almost identical to that of the MP bootstrap consensus tree. Support for the clades was as follows: clade B (BP 98%); clade B1 (BP 96%); clade B2 (BP 86%); clade C (BP 100%); clade D (BP 74%); clade D1 (BP 99%); clade D2 (BP 95%); clade E (BP 99%); and clade F (BP 68%).

#### **Distribution maps and elevation data**

Distribution maps of species in the “Andinia” clade are presented by subgroup, or proposed subgenus: *Aenigma* (Fig. 5 clade E), *Andinia* (Fig. 5 clade D), *Masdevalliantha* (Fig. 5 clade F) and *Minuscula* (Fig. 5 clade C) (Fig. 6) and *Brachycladium* (Fig. 5 clade B) (Fig. 7). The species exhibit an exclusively Andean distribution in Colombia, Ecuador, Peru and Bolivia. Collection data from Tropicos were also used to determine the mean elevation of the collections and the range of elevations of the collections for each proposed infrageneric taxon or clade (Table 3). Although the elevational ranges overlap, species of subgenus *Brachycladium* (clade B) exhibited a significantly lower ( $P < 0.0001$ ) mean collection elevation (2,108 m) than the mean collection elevation of the other subgenera (2,883 m) (Fig. 8).



**FIGURE 4.** Bootstrap consensus phylogenetic tree inferred from the *matK* data set using MP analysis with 1000 bootstrap replicates in MEGA 6. Values at each node represent percent bootstrap support; bootstrap percentages less than 50% are not shown. Clade lettering as per clades in the ITS MP analysis (Fig. 3).



**FIGURE 5.** (a) Bootstrap consensus phylogenetic tree inferred from the concatenated ITS-*matK* data set using MP analysis with 1000 bootstrap replicates. Values at each node represent percent bootstrap support; bootstrap percentages less than 50% are not shown. Clade lettering as per clades in the ITS MP analysis (Fig. 3). (b) One of five the most parsimonius trees scaled for branch length.

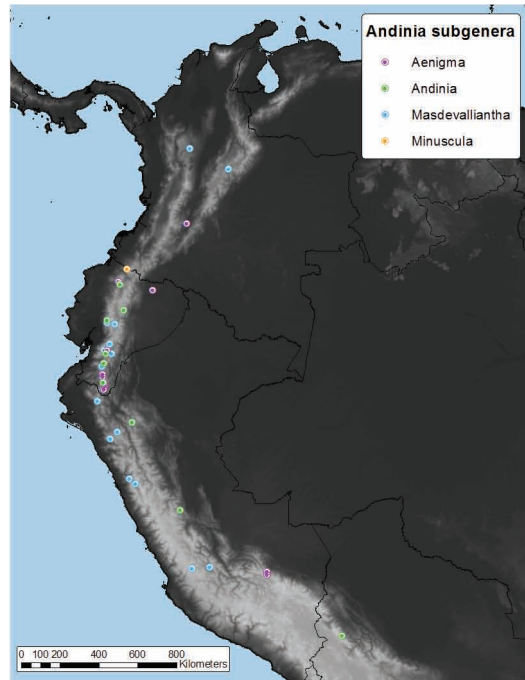


FIGURE 6. Distributions of clades or proposed subgenera *Aenigma*, *Andinia*, *Masdevalliantha* and *Minuscula*.

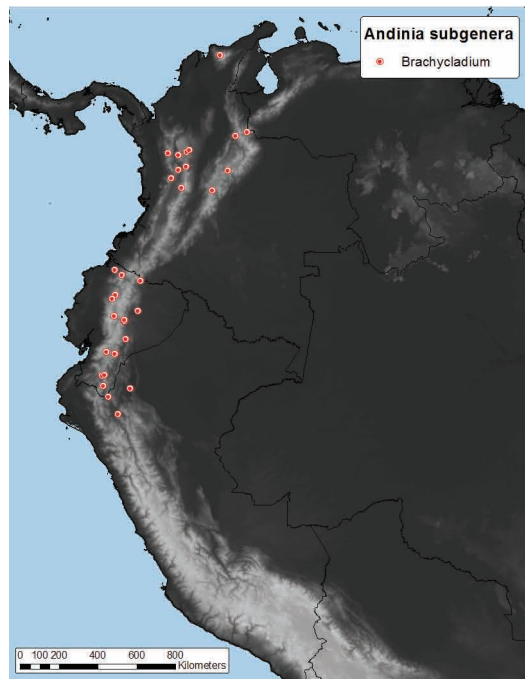
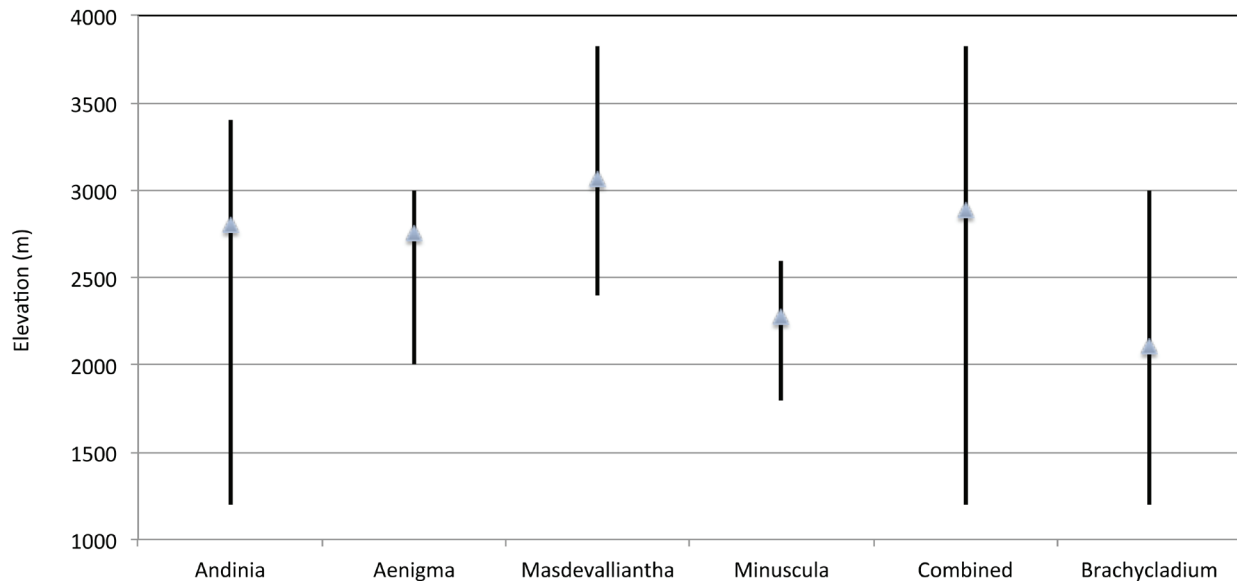


FIGURE 7. Distributions of clade or proposed subgenus *Brachycladium*.



**FIGURE 8.** Mean elevations and elevational ranges of collections from Tropicos for proposed subgenera *Andinia*; *Aenigma*; *Masdevalliantha*; *Minuscula*; all four subgenera combined (i.e. excluding *Brachycladium*); and *Brachycladium*. Blue triangles represent mean collection elevation (m) and black bar represents elevational range of collections.

## Discussion

Analyses of the ITS, *matK* and combined ITS-*matK* datasets, using maximum parsimony and maximum likelihood, all exhibit strong support for the monophyletic group “Andinia” (Figs. 1–5), containing species previously assigned to the genera *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia*. This is consistent with the preliminary findings based solely upon ITS sequence analysis reported by Wilson & Jost (2009; 2011). Although the relationship between *Andinia* and *Neooreophilus* was noticed by Pridgeon & Chase (2005), apart from the preliminary results of Wilson & Jost (2011), no published analyses have reported that these five groups are closely related. As the name *Andinia* has taxonomic priority over the other three genera we propose that the circumscription of *Andinia* be expanded to include the species currently assigned to *Masdevalliantha*, *Neooreophilus* and *Xenosia*, thereby increasing the size of the genus from 13 to 72 described species. Although concern has been expressed about the similarity of the generic names *Andinia* (Luer) Luer (Orchidaceae) and *Andina* Jiménez & Cano (2012: 296) (Pottiaceae) (Freitas & Tonini 2014), *Andinia* has taxonomic priority over *Andina*, hence this re-circumscription is unaffected by any nomenclatural ruling.

There are no universally agreed-upon criteria for the circumscription of genera in Orchidaceae. Indeed, absence of such criteria has resulted in inconsistent generic circumscriptions and hence, considerable disagreement in estimates of the number of genera in Pleurothallidinae (Higgins 2009). The only widely accepted criterion for generic circumscription is phylogenetic monophyly. The four genera *Andinia*, *Masdevalliantha*, *Neooreophilus* and *Xenosia* form a strongly supported monophyletic group. *Andinia*, as circumscribed prior to this study (Pridgeon & Chase 2001; Luer 2005; Chase *et al.* 2015), is not monophyletic, with species distributed across three clades, C, D and E. Although there are other strongly supported clades within clade “Andinia”, retention of generic status for some of these clades would not only necessitate splitting the existing circumscription of *Andinia* but also the creation of at least one additional genus.

Monophyly itself, however, gives no indication of the phylogenetic depth at which generic limits should be established. While it has been suggested that it would be desirable to have consistency in the phylogenetic depth at which genera in Pleurothallidinae are circumscribed, the importance of this criterion relative to other considerations has not been widely discussed. Salazar & Jost (2012) used phylogenetic depth as one criterion for establishing *Quechua* (Spiranthinae); however, consistency of phylogenetic depth *per se* was not invoked as a significant criterion in recent generic re-circumscriptions of Pleurothallidinae (Pridgeon *et al.* 2001; Pridgeon & Chase 2001). Further, generic circumscriptions based upon phylogenetic depth would be affected by variable rates of evolution across different



lineages of Pleurothallidinae. Nevertheless, it would be undesirable to have genera circumscribed at significantly different depths among related genera in Pleurothallidinae; otherwise, genera would be meaningless as guides for conservation actions, or as surrogates for more quantitative measures of phylogenetic diversity (Chao *et al.* 2010). In this regard, the genetic distance between the clade containing the species in the proposed circumscription of *Andinia* and nearby taxa, *Dryadella*, *Platystele*, *Scaphosepalum* and *Specklinia* is comparable to the genetic distance between *Dryadella* and *Specklinia*, or between *Specklinia* and *Platystele/Scaphosepalum*, but is greater than the genetic distance between *Platystele* and *Scaphosepalum* (Fig. 2).

Other possible considerations in generic circumscription in addition to monophyly and genetic distance or phylogenetic depth include how informative the circumscription will be for users, the stability of the new taxonomy created, and the morphological recognizability of the genus. The proposed inclusion of *Masdevalliantha*, *Neooreophilus* and *Xenosia* in an expanded *Andinia* conveys the relatedness of the species that would be lost in a taxonomic model retaining multiple genera and conveys the Andean distribution of the group. A more broadly circumscribed *Andinia* would also bring taxonomic stability and simplification to a group of species that have been assigned to no fewer than 11 different generic names in the past: *Andinia*, *Brachycladium*, *Lepanthes*, *Lueranthos*, *Masdevalliantha*, *Neooreophilus*, *Oreophilus*, *Penducella*, *Pleurothallis*, *Salpistele*, and *Xenosia*. While morphological recognizability of a genus is certainly desirable for field botanists, morphological similarities do not necessarily indicate relatedness. After all, morphological homoplasies were responsible for the original inclusion of *Neooreophilus* species in *Lepanthes*, to which they are only distantly related. So, although the species of the proposed circumscription of *Andinia* are morphologically variable, inclusion of *Masdevalliantha*, *Neooreophilus* and *Xenosia* in an expanded *Andinia* seems preferable on balance because of monophyly, comparable phylogenetic depth, recognizability and taxonomic stability.

The “*Andinia*” clade, proposed genus *Andinia*, is phylogenetically distinct from genera in which some of these species have been placed previously, namely *Lepanthes*, *Pleurothallis* and *Salpistele* (now included in *Stelis*). In fact, *Andinia* is only distantly related to *Lepanthes* in which *Neooreophilus* species were originally placed (Fig. 1). In the phylogenetic analysis of concatenated ITS-*matK* sequences from multiple pleurothallid genera (Fig. 1), *Andinia* was sister not to *Lepanthes*, but to a clade containing *Dryadella*, *Platystele*, *Scaphosepalum*, and *Specklinia*, though the bootstrap support was weak. In their combined ITS-*matK-trnLF* phylogeny of Pridgeon *et al.* (2001) found *A. pensilis* to be sister with moderate support to *Dryadella*, *Platystele*, *Scaphosepalum*, and several species now considered part of *Specklinia*. In a preliminary analysis of pleurothallid genera based on 9 gene regions (Whitten & Pridgeon, unpubl.) *A. pensilis* and *X. xenion* were more closely related to a clade that included *Dryadella*, *Platystele* and *Specklinia*, rather than *Pleurothallis*. The data presented here (Fig. 1), as well as the data of Pridgeon *et al.* (2001) and (Whitten & Pridgeon, unpubl.), suggest that *Andinia* is more closely related to the clade containing *Dryadella*, *Platystele*, *Scaphosepalum* and *Specklinia*, than it is to the clade containing *Pabstiella*, *Pleurothallis*, and *Stelis*. However, other studies in progress (Karremans unpubl.) suggest the opposite relationship, therefore, identification of the group closest to *Andinia* must await further study.

All analyses provide moderate to strong support for the monophyly of clade B (Fig. 3–5), containing species of *Neooreophilus*. The overview phylogeny (Fig. 1) demonstrated clearly that *Neooreophilus* is not closely related to *Lepanthes* in which the species of this group were originally placed. Based on our phylogeny of multiple genera in Pleurothallidinae (Fig. 1), the study of Freudenstein & Chase (2015) and that of Whitten & Pridgeon (unpubl.), *Lepanthes* falls in a clade unrelated to *Andinia*, with *Anathallis*, *Lankesteriana*, *Trichosalpinx* and *Zootrophion*. Our analyses unequivocally support the segregation of the species originally described in *Lepanthes* subgenus *Brachycladium* from *Lepanthes*. And the data could support the creation of a separate genus, as proposed by Luer (2005), Archila & Higgins (2008), Archila (2009) and Luer & Thorerle (2010). However, we contend that the group is best placed within *Andinia* under the proposed subgenus *Brachycladium*. The alternative, retaining generic status for clade B as *Neooreophilus*, would necessitate the splitting of *Andinia*; the creation of two additional genera for clades C and E; and the re-circumscription and continued use of either *Xenosia* or *Masdevalliantha*, neither of which are regularly utilized, for clade F. This would create a situation of 5 different genera, *Neooreophilus*, “clade C”, *Andinia*, “clade E” and *Xenosia/Masdevalliantha*, which would convey no information about the phylogenetic relatedness of the species in these genera. Therefore, we propose the incorporation of *Neooreophilus* in the new circumscription of *Andinia* under subgenus *Brachycladium*: (i) to convey that these are a group of phylogenetically related species; (ii) to avoid splitting the widely accepted genus *Andinia*; (iii) to avoid taxonomic inflation and the creation of two additional pleurothallid genera; and (iv) to reduce the nomenclatural confusion surrounding the group of species due to successive illegitimate names, from genus *Brachycladium* (Luer 2005) to *Oreophilus* (Archila & Higgins 2008) and almost simultaneously to *Neooreophilus* (Archila 2009) and *Penducella* (Luer & Thorerle 2010).

The prior placement of *Neooreophilus* species in *Lepanthes* was the result of not only similar floral morphology

but the presence of the so-called “lepanthiform sheath” in both groups. In floral morphology at least, homoplasy is common in Pleurothallidinae (Luer 1986a; Pridgeon & Chase 2001). *Lepanthes* species are believed to be deceit-pollinated by pseudocopulation by Diptera; in some species these dipteran pollinators are sciarid fungus gnats (Blanco & Barboza 2005). At least one *Neooreophilus* species, *N. pendens* (Garay 1956) Archila (2009: 84), has also been observed to be pollinated by pseudocopulation by Sciaridae (Álvarez 2011). One might speculate then, that homoplasy in floral characteristics between *Lepanthes* and *Neooreophilus* is the result of convergent evolution to deceit-pollination by pseudocopulation involving similar taxa of dipteran pollinators. Such pollination syndromes are common in Orchidaceae and emphasize the importance of a taxonomy based on both phylogenetic relationships and morphological similarity, not on morphology alone (Karremans *et al.* 2015c).

Our ITS (Fig. 3) and combined ITS-*matK* (Fig. 5) analyses show strong support for two internal clades, clade B2 containing *Neooreophilus nummularius* and *N. stalactites*, and clade B1 containing all other *Neooreophilus* species. These parallel Luer’s *Lepanthes* subgenus *Brachycladium* sections *Brachycladae* and *Bilamellatae* Luer (1994: 3, clade B2) and *Amplectentes* (Luer 1994: 3, clade B1) based on floral and vegetative morphology; hence we propose retaining two sections of this group of species. There appears to be significant genetic variation among collections of the species *N. nummularius*, as reported previously (Wilson & Jost 2009), and *N. pilosellus* (Reichenbach 1886: 556) Archila (2009: 85), probably indicating the presence of unrecognized or ‘cryptic’ species. Analyses in progress (Jost, Wilson & Vieira-Urbe unpubl.) indicate there may be five or more species in our current concept of *N. nummularius*.

*Andinia* as previously circumscribed, containing 13 species (Pridgeon & Chase 2001; Luer 2005; Chase *et al.* 2015) does not form a single clade, but is instead split into three moderately to strongly supported monophyletic groups, clades C, D and E (Figs. 3 and 5). Clade C includes just two collections, *A. trimytera* (Luer & R. Escobar) Pridgeon & Chase (2001: 252) and an unflowered plant designated as *Andinia* sp., but presumed to be *A. trimytera* based on the ITS sequence. For this clade we propose the subgenus *Minuscula* to include, in addition to *A. trimytera*, the species *A. hystricosa* (Luer) Pridgeon & Chase (2001: 251) and *A. panica* (Luer & Dalström) Pridgeon & Chase (2001: 251). The name *Minuscula* reflecting the small size of the flowers and plants of these three species (Fig. 10). Although the placement of *A. hystricosa* and *A. panica* in the proposed subgenus *Minuscula* cannot be confirmed until material becomes available for sequencing, Luer (1994) indicated that *A. hystricosa* “is closely allied to” *A. trimytera* and Luer (1996) stated that *A. panica* is close to *A. hystricosa*.

Clade D includes *A. dielsii*, *A. pensilis*, *A. lappacea* and *A. vestigipetala* for which we propose the subgenus *Andinia*, because the clade contains the type species *A. dielsii*. Clade E includes *A. dalstroemii*, *A. pogonion* and *A. schizopogon*, for which we propose resurrecting the subgeneric name *Aenigma*.

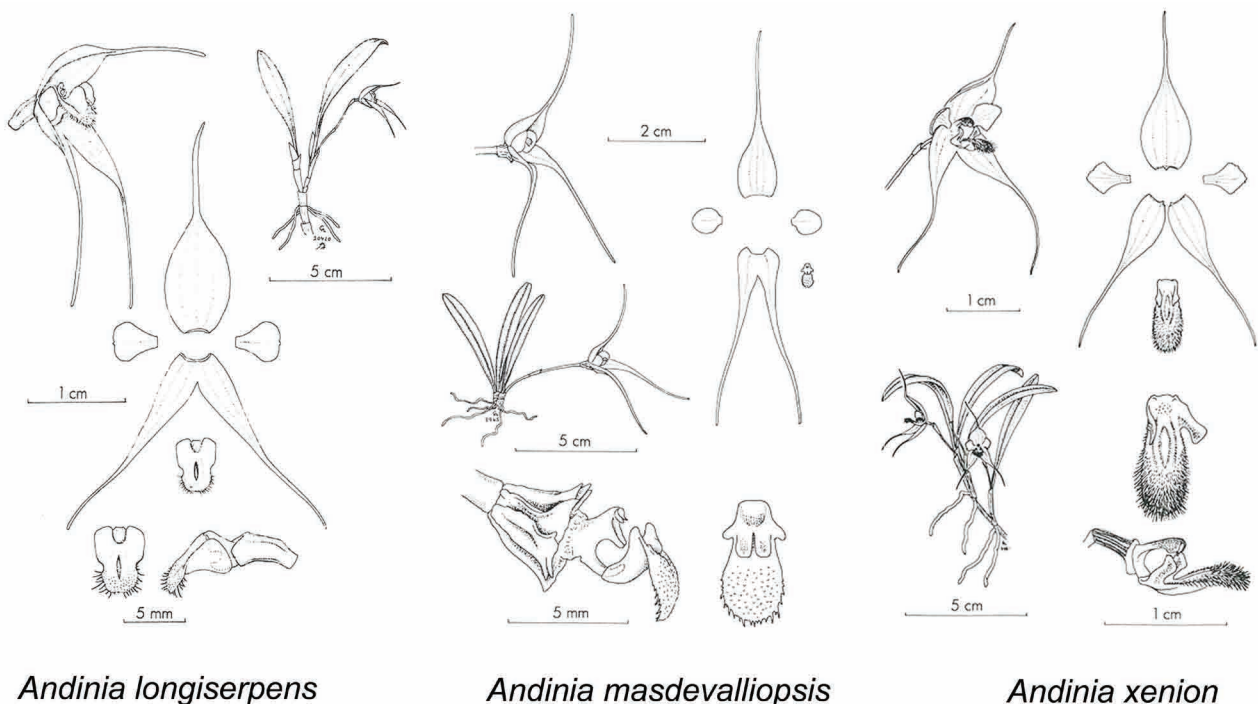
The taxonomic placement of *A. vestigipetala* requires further mention. The species has an unusual floral morphology with vestigial petals and a labellum tightly adherent to the column. Consequently, different authors have recommended inclusion of the species in *Pleurothallis* (Luer 2002), *Andinia* (Pridgeon & Chase 2001) or *Lueranthos* (Szlachetko & Margonska 2001). Although in the analysis of ITS sequences (Fig. 3) and combined ITS-*matK* sequences (Fig. 5) this species is placed with *A. dielsii*, *A. pensilis* and *A. lappacea*, in the *matK* analysis (Fig. 4) it occurs in a polytomy with other members of *Andinia*. Unfortunately, in our study this species is represented by only a single collection. Despite this, the data indicate that *A. vestigipetala* should be retained in *Andinia*, but the infrageneric placement has to be considered preliminary pending the inclusion of additional collections of the species.

In the ITS analysis (Fig. 3) the moderately supported clade F contains *Masdevalliantha longiserpens*, *Xenosia xenion* and *X. spiralis*, which is basal to the other clades of *Andinia*. However, these species do not group together in the *matK* analysis (Fig. 4), and in the combined analysis (Fig. 5) support for clade F is weak. We nevertheless propose tentatively combining the genera *Xenosia* and *Masdevalliantha* into the subgenus *Masdevalliantha* within *Andinia*. This subgenus would be comprised of the 4 species *Andinia longiserpens*, *A. masdevalliopsis* and *A. xenion*, the flowers of which exhibit striking morphological similarity (Fig. 9), and *A. spiralis*. The alternative would be to combine *X. xenion* and *M. longiserpens*, splitting *X. spiralis* into its own subgenus. However, this would conflict with the strong support for the group of three species in the ITS analysis (Fig. 3) and the clear vegetative morphological similarities between *X. spiralis*, *X. xenion* and *M. longiserpens*.

There is considerable interest in the drivers of evolutionary diversification in tropical Orchidaceae. Among drivers of diversification are the evolution of CAM; the adoption of epiphytism; distribution in tropical cordilleras; and pollination by Diptera (Freudenstein & Chase 2015; Givnish *et al.* 2015). Species of *Andinia* occur in the Andean regions of Colombia, Ecuador, Peru and Bolivia (Figs. 6 and 7); range in elevation from 1,200 to 3,825 m (Fig. 8); include lithophytic and epiphytic species; and include some species that appear to be deceit-pollinated via pseudocopulation by Diptera (Álvarez 2011), whereas other species, based on the presence of a glenion, may offer a reward or exhibit reward-deception. In our analyses, clade F, proposed subgenus *Masdevalliantha*, is basal to clades B–E. These three

species, *M. longiserpens*, *X. macrorhiza*, and *X. xenion*, are primarily lithophytic, whereas the majority of species in clades B-E are epiphytic; this might indicate that lithophytic growth is ancestral to epiphytism in *Andinia* and that epiphytism may have contributed to diversification within this group.

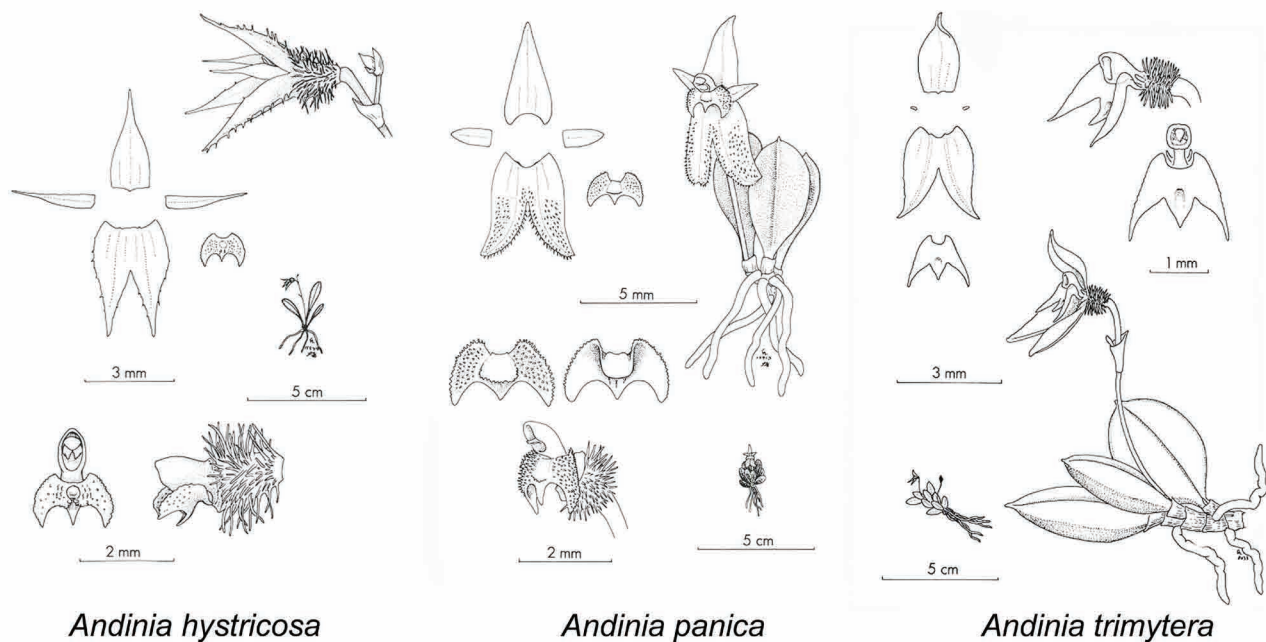
Among the clades of the proposed circumscription of *Andinia*, the most diverse or species rich is *Andinia* subgenus *Brachycladium* with approximately 53 species, depending on synonymy. From data in Tropicos we determined that although the elevational distributions overlap, collections of species in the derived clade B, proposed *Andinia* subgenus *Brachycladium*, have a mean collection elevation of 2,108 m, whereas collections of the species from the more basal clades, proposed *Andinia* subgenera *Aenigma*, *Andinia* and *Masdevalliantha*, have a statistically significantly higher mean collection elevation of 2883 m (Fig. 8). One might speculate, therefore, that the basal clades of *Andinia* diversified at higher elevations during or following the Andean uplift, whereas the more derived *Andinia* subgenus *Brachycladium* diversified as species migrated down to lower elevations and encountered new ecological niches. A similar radiation occurred with the high-elevation pleurothallid genus *Teagueia* (Jost 2004); in both *Andinia* subgenus *Brachycladium* and *Teagueia*, identifying the variable(s) in the ecological niche (pollinator, mycobiont, micro-environmental variations etc.) that promoted allowing such radiations is difficult.



**FIGURE 9.** Drawings of *Andinia longiserpens* (from Luer 2006) and *A. masdevalliopsis* (from Luer 1986b) and *A. xenion* (from Luer 1986). Courtesy of Missouri Botanical Garden Press.

## Conclusions

Considerable taxonomic confusion has surrounded this group of approximately 72 species, with species being described variously in *Andinia*, *Brachycladium*, *Lepanthes*, *Lueranthos*, *Masdevalliantha*, *Neooreophilus*, *Oreophilus*, *Penducella*, *Pleurothallis*, *Salpistele*, and *Xenosia*. We show here that the species of *Andinia*, *Neooreophilus*, *Masdevalliantha* and *Xenosia* form a strongly supported monophyletic group distinct from *Pleurothallis* and only distantly related to *Lepanthes* and that the phylogenetic depth of the clade is similar to the depths of many widely-recognized pleurothallid genera. Therefore, we propose *Andinia* be re-circumscribed to additionally encompass the species currently described in *Masdevalliantha*, *Neooreophilus* and *Xenosia*. Additionally, we propose an infrageneric taxonomy for *Andinia*, including subgenera *Aenigma*, *Andinia*, *Brachycladium*, *Masdevalliantha* and *Minuscula*.



**FIGURE 10.** Drawings of *Andinia hystricosa* and *A. trimytera* from Luer (1994) and *A. panica* from Luer (1996). Courtesy of Missouri Botanical Garden Press.

*Andinia* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 5. 2000. Bas. *Salpistele* subgen. *Andinia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 39: 124. 1991. Type: *Lepanthes dielsii* Mansf., Biblioth. Bot. 29 (Heft 116): 72. 1937.

Syn. *Brachycladium* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 307. 2005.

Syn. *Lueranthos* Szlach. & Marg., Polish Bot. J. 46(2): 117. 2002.

Syn. *Masdevalliantha* (Luer) Szlach. & Marg., Polish Bot. J. 46(2): 117. 2002.

Syn. *Neooreophilus* Archila, Revista Guatemalensis 12(2): 73. 2009.

Syn. *Oreophilus* W.E.Higgins & Archila, Selbyana 29(2): 202. 2009.

Syn. *Penducella* Luer & Thorerle, Orchid Digest 74(2): 68. 2010.

Syn. *Xenosia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

**Description:** Plants caespitose or rhizomatous in habit; in the latter the rhizome repent, creeping or pendulous (similar to species of *Brachionidium*). The inflorescence mostly successively multi-flowered, with only one flower open at a time. Ovaries glabrous to echinate. The flowers of some species similar to those of *Lepanthes*. The petals mostly very much abbreviated compared to the sepals. The lip three-lobed (very shallowly in a few species), with the mid-lobe modified into an appendix in many species, and the lateral lobes frequently surrounding the column. Only a couple of species do not have an apical anther and stigma, but all have drop-like pollinaria, with a bubble-like viscidium.

**Distribution and Ecology:** *Andinia* currently includes 72 species confined to the northern Andean countries of Colombia, Ecuador, Peru and Bolivia (Fig. 6 and 7), where they are found in very humid forests, at elevations from 1,200 to 3,825 m (Fig. 8), growing mostly under shady conditions.

## Taxonomic Treatment

We propose a subgeneric classification of *Andinia*, based on both DNA and morphological data, and a dichotomous key based upon floral and vegetative morphology.

- 1a. Mid-lobe of the lip obtuse, conspicuously larger than the lateral lobes. Column foot present .... *Andinia* subgen. *Masdevalliantha*
- 1b. Mid-lobe of the lip absent or when present acute to apiculate or transformed into an appendix, subequal to lateral lobes. Column

	foot absent .....	2
2a.	Mid-lobe of the lip acute to apiculate, petals subequal to the sepals, anther incumbent .....	<i>Andinia</i> subgen. <i>Aenigma</i>
2b.	Mid-lobe of the lip transformed into an appendix or appendix-like structure, petals much reduced, anther apical .....	3
3a.	Plants ascending (except sometimes in <i>A. trimytera</i> ). Leaves and bracts glabrous .....	4
4a.	Leaf herbaceous to coriaceous, lateral lobes of lip subtending the column .....	<i>Andinia</i> subgen. <i>Andinia</i>
4b.	Leaf thickly coriaceous, lateral lobes of the lip frontal .....	<i>Andinia</i> subgen. <i>Minuscula</i>
3b.	Plants strictly pendent. Leaves and bracts frequently hirsute.....	5
5a.	Leaves thinly coriaceous, glabrous with margins entire. Flower borne on short pedicels, placed close to the leaf surface. Mid-lobe of the lip transformed into an appendix, much shorter than the column, rostellum reduced, inconspicuous .....	<i>Andinia</i> subgen. <i>Brachycladium</i> sect. <i>Brachycladium</i>
5b.	Leaves fleshy, mostly hirsute with margins sparsely denticulate-fimbriate. Flower borne from elongate pedicels, placed well above the leaf surface. Mid-lobe of the lip not transformed into an appendix, subequal to longer than the column, rostellum elongate, conspicuous .....	<i>Andinia</i> subgen. <i>Brachycladium</i> sect. <i>Amplectentes</i>

*Andinia* subgen. ***Aenigma*** (Luer) Karremans & Mark Wilson, comb. nov. Bas. *Pleurothallis* subgen. *Aenigma* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 26. 1986. Type. *Pleurothallis schizopogon* Luer, Selbyana 5(2):179. 1979.

Syn. *Pleurothallis* subgen. *Aenigma* sect. *Aenigmata* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 26. 1986. Type. *Pleurothallis schizopogon* Luer, Selbyana 5(2):179. 1979.

Plant ascending. Inflorescence loose, successively flowered. Ovary papillose or spiculate (hirsute). Petals conspicuous (not vestigial), subequal to the sepals in most species. Lip three-lobed, with the midlobe reduced and acute-acuminate. Column foot absent. Anther incumbent. Pollinaria with drop-like viscidium. Eight species distributed through the Andean regions of Colombia, Ecuador and Peru (Fig. 6), with an elevational range of 2,000 to 3,000 m (Fig. 8). An example, *Andinia schizopogon* (Luer) Pridgeon & M.W.Chase, is illustrated (Fig. 11b).

*Andinia dalstroemii* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Bas. *Pleurothallis dalstroemii* Luer, Orchideer 5: 52. 1984.

*Andinia hirtzii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 275. 2005.

*Andinia ibex* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Bas. *Pleurothallis ibex* Luer, Selbyana 5(2): 168. 1979.

*Andinia pentamytera* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Bas. *Pleurothallis pentamytera* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 58. 1994.

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

Bas. *Pleurothallis pogonion* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 61. 1994.

*Andinia schizopogon* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Bas. *Pleurothallis schizopogon* Luer, Selbyana 5(2): 179. 1979.

*Andinia sunchubambensis* A.Doucette & Janovec, IOSPE Aug 5, 2016.

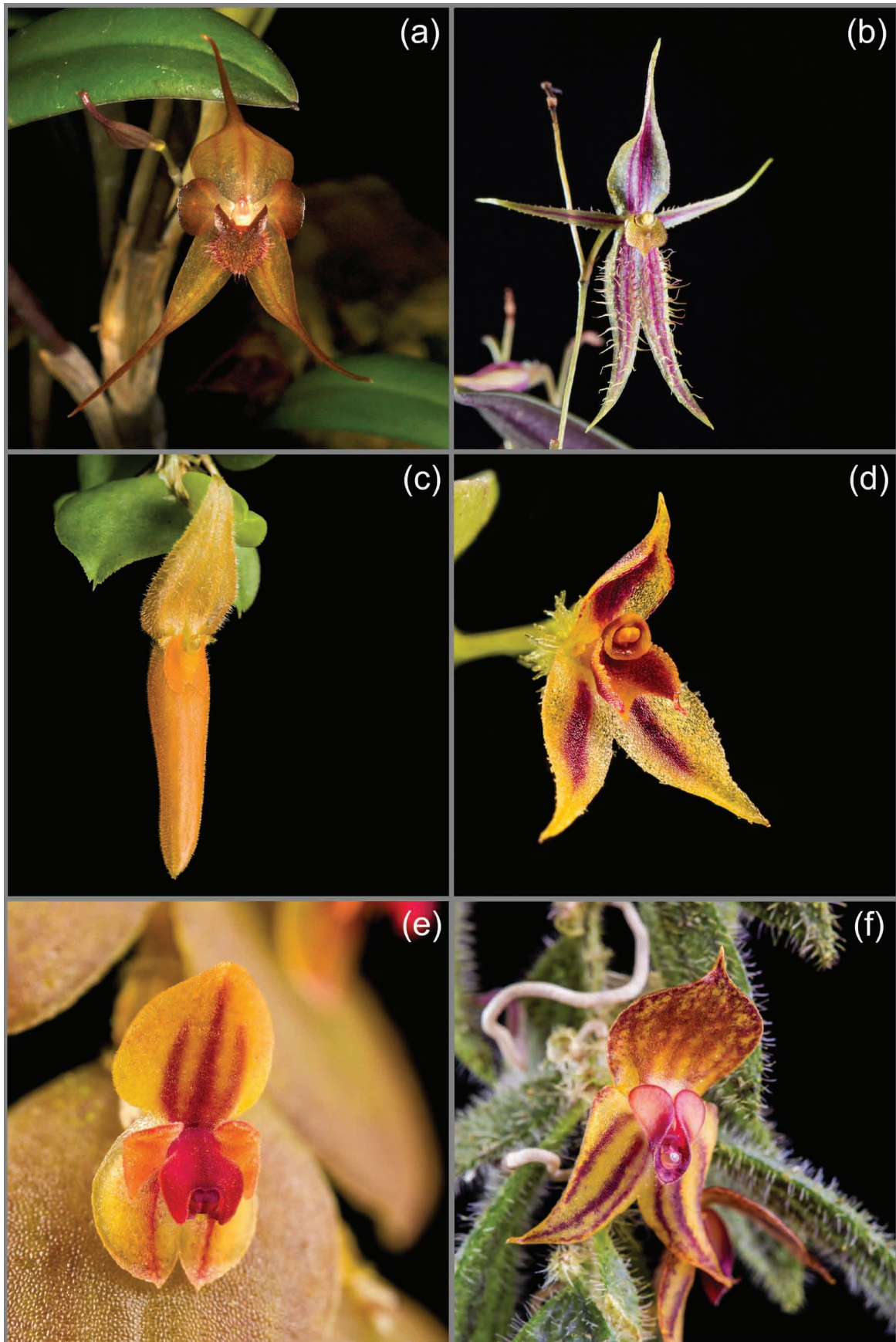
*Andinia uchucayensis* A.Doucette & J.Portilla, Orchids (Lindleyana) 86(1): 72. 2017.

*Andinia* subgen. ***Andinia***. Type: *Lepanthes dielsii* Mansfeld, Biblioth. Bot. 29 (Heft 116): 72. 1937.

Syn. *Salpistele* subgen. *Andinia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 39: 124. 1991.

Syn. *Pleurothallis* subgen. *Aenigma* sect. *Vestigipetalae* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 26. 1986. Type: *Pleurothallis vestigipetala* Luer, Selbyana 3(3,4): 404. 1977.

Plant repent, ascending or descending. Inflorescence loose, successively flowered or successively single-flowered. Ovary papillose or spiculate, glabrous in one species. Lip three-lobed (sometimes inconspicuously), a few species with the midlobe transformed into what is possibly performing the same function as the appendix in *Lepanthes*. Anther and stigma apical. Column foot absent. Pollinaria with a drop-like viscidium. Four species, distributed through the Andean regions of Colombia, Ecuador, Peru and Bolivia (Fig. 6), with an elevation range of 2,400 to 3,825 m (Fig. 8). An example, *Andinia lappacea* (Luer) Pridgeon & M.W.Chase, is illustrated (Fig. 11c).



**FIGURE 11.** Representatives of the proposed infrageneric taxa: (a) subgenus *Masdevalliantha* - *Andinia longiserpens* (photo credit: Ron Parsons); (b) subgenus *Aenigma* - *Andinia schizopogon*; (c) subgenus *Andinia* - *Andinia lappacea*; (d) subgenus *Minuscula* - *Andinia trimytera*; (e) subgenus *Brachycladium* section *Brachycladae* - *Andinia nummularia*; and (f) subgenus *Brachycladium* section *Amplectentes* - *Andinia montis-rotundi*.

*Andinia dielsii* (Mansf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 6. 2000.  
Bas. *Lepanthes dielsii* Mansfeld, Biblioth. Bot. 29 (Heft 116): 72. 1937.  
*Andinia lappacea* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.  
Bas. *Pleurothallis lappacea* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 129. 2000.  
*Andinia pensilis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 6. 2000.  
Bas. *Lepanthes pensilis* Schltr., Repert. Spec. Nov. Regni Veg. 8: 55. 1921.  
*Andinia vestigipetala* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 252. 2001.  
Bas. *Pleurothallis vestigipetala* Luer, Selbyana 3(3,4): 404. 1977.

*Andinia* subgen. ***Brachycladium*** (Luer) Karremans & S.Vieira-Uribe, *comb. nov.* Bas. *Lepanthes* subgen. *Brachycladium* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 31. 1986. Type: *Lepanthes nummularia* Reichenbach f., *Xenia Orchid.* 1: 142. 1856.

Syn. *Lepanthes* sect. *Brachycladae* Reichenbach f., *Xenia Orchid.* 1: 142, 1856. Type: *Lepanthes nummularia* Reichenbach f., *Xenia Orchid.* 1: 142. 1856. Syn. *Lepanthes* sect. *Caulescentes* Garay, *Canad. J. Bot.* 34: 252, 1956. *Nom. nud.* Syn. *Brachycladium* (Luer) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 103: 307. 2005. *Nom. illeg. hom. syn. Oreophilus* W.E.Higgins & Archila, *Selbyana* 29(2): 202. 2009. *Nom. illeg. superfl. syn. Neooreophilus* Archila, *Revista Guatemal.* 12(2): 73. 2009. Syn. *Penducella* Luer & Thoerle, *Orchid Digest* 74(2): 68. 2010.

*Andinia* subgen. ***Brachycladium*** sect. ***Brachycladae*** (Rchb.f.) Karremans & S.Vieira-Uribe, *comb. nov.* Bas. *Lepanthes* subgen. *Brachycladium* sect. *Brachycladae* Rchb. f., *Syst. Bot. Missouri Bot. Gard.* 52: 3. 1994. Type: *Lepanthes nummularia* Reichenbach f., *Xenia Orchid.* 1: 142. 1856.

Syn. *Lepanthes* subgen. *Brachycladium* sect. *Bilamellatae* Luer, *Syst. Bot. Missouri Bot. Gard.* 52: 3. 1994. Type: *Lepanthes stalactites* Luer & Hirtz, *Lindleyana* 2(2): 105. 1987.

Plants repent, pendent. Leaves glabrous with margins entire. Ovary glabrous. Lip at least obscurely trilobate, with the midlobe transformed into an appendix-like structure, prominently hirsute, much shorter than the column. Column foot absent. Anther apical, stigma ventral, rostellum inconspicuous. Pollinaria with a drop-like viscidium. Two species distributed through the Andean regions of Colombia, Ecuador and Peru (Fig. 7), an elevational range of 1,690 to 3,000 m (Fig. 8). An example, *Andinia nummularia* (Rchb.f.) Karremans & S.Vieira-Uribe, is illustrated (Fig. 11e).

*Andinia nummularia* (Rchb.f.) Karremans & S.Vieira-Uribe, *comb. nov.*  
Bas. *Lepanthes nummularia* Rchb.f., *Xenia Orchid.* 1: 142. 1856.  
*Andinia stalactites* (Luer & Hirtz) Karremans & S.Vieira-Uribe, *comb. nov.*  
Bas. *Lepanthes stalactites* Luer & Hirtz, *Lindleyana* 2(2): 105. 1987.

*Andinia* subgen. ***Brachycladium*** sect. ***Amplectentes*** (Luer) Karremans & S.Vieira-Uribe, *comb. nov.* Bas. *Lepanthes* subgen. *Brachycladium* sect. *Amplectentes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 3. 1994. Type: *Lepanthes pilosella* Reichenbach f., *Flora* 69: 556, 1886.

Plants repent and pendent. Leaves mostly with margins denticulate-fimbriate, sometimes hirsute. The ovary glabrous to hirsute or spiculate. The lip variously lobed but always lacks the midlobe transformed into appendix and always surrounding or embracing the column. Anther and stigma apical, rostellum elongate, antrorse, pollinaria with a drop-like viscidium. Fifty one species distributed through the Andean regions of Colombia, Ecuador, Peru and Bolivia (Fig. 7), with an elevational range of 1,200 to 2,660 m (Fig. 8). An example, *Andinia montis-rotundi* (Ortiz 1997: 318) Karremans & S.Vieira-Uribe, is illustrated (Fig. 11f).

*Andinia ariasiana* (Luer & L.Jost) Karremans & S.Vieira-Uribe, *comb. nov.*  
Bas. *Lepanthes ariasiana* Luer & L.Jost, Monogr. Syst. Bot. Missouri Bot. Gard. 72: 104. 1998.  
*Andinia auriculata* (Archila) Karremans & S.Vieira-Uribe, *comb. nov.*  
Bas. *Neooreophilus auriculatus* Archila, *Revista Guatemal.* 17(1): 44. 2014.  
*Andinia bifida* (Tobar & Archila) Karremans & S.Vieira-Uribe, *comb. nov.*  
Bas. *Neooreophilus bifidus* Tobar & Archila, *Revista Guatemal.* 15(2): 2. 2012.  
*Andinia cardiocheila* (Luer & R.Escobar) Karremans & S.Vieira-Uribe, *comb. nov.*  
Bas. *Lepanthes cardiocheila* Luer & R.Escobar, *Orquideología* 19(2): 86. 1994.

*Andinia catella* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes catella* Luer & R.Escobar, Orquideología 16(1): 10. 1983.

*Andinia caveroi* (D.E.Benn. & Christenson) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes caveroi* D.E.Bennett & Christenson, Icon. Orchid. Peruv.: t. 670. 2001.

*Andinia chaoae* (S.Vieira-Urbe & L.Jost) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophila chaoae* S.Vieira-Urbe & L.Jost, Lankesteriana 15(3): 213. 2015.

*Andinia chelosepala* (Luer & Hirtz) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Oreophilus chelosepalus* Luer & Hirtz, Selbyana 30(1): 16. 2009.

*Andinia chilopsis* (Luer & Hirtz) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes chilopsis* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 88. 2002.

*Andinia ciliaris* (Luer & Hirtz) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes ciliaris* Luer & Hirtz, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 8. 1994.

*Andinia composita* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes composita* Luer & R.Escobar, Orquideología 19(2): 88. 1994.

*Andinia cordilabia* (Luer) S.Vieira-Urbe & Karremans, *comb. nov.*  
 Bas. *Lepanthes cordilabia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 88. 2002.

*Andinia dactyla* (Garay) Karremans & S.Vieira-Urbe, Orquideología 33(2): 114. 2016.  
 Bas. *Lepanthes dactyla* Garay, Orquideología 6(1): 13. 1971.

*Andinia dentata* (Archila) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophila dentatus* Archila, Revista Guatemal., 17(1): 41. 2014.

*Andinia destituta* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes destituta* Luer & R.Escobar, Orquideología 17(3): 179. 1988.

*Andinia erepsis* (Luer & Hirtz) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes erepsis* Luer & Hirtz, Die Orchidee 37(5): 215. 1986.

*Andinia exigua* (Luer & L.Jost) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes exigua* Luer & L.Jost, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 89. 2002.

*Andinia geminipetala* (Luer & J.Portilla) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes geminipetala* Luer & J.Portilla, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 89. 2002.

*Andinia hippocrepica* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes hippocrepica* Luer & R.Escobar, Orquideología 18(1): 54. 1991.

*Andinia irrasa* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes irrasa* Luer & R.Escobar, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 18. 1994.

*Andinia lueri* S.Vieira-Urbe & Karremans, Orquideología 33(2): 116. 2016.

*Andinia lunaris* (Luer) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes lunaris* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 21. 1994.

*Andinia lunatocheila* (Tobar & Archila) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophila lunatocheillus* Tobar & Archila, Revista Guatemal. 15(2): 26. 2012.

*Andinia lupula* (Luer & Hirtz) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes lupula* Luer & Hirtz, Amer. Orchid Soc. Bull. 53(11): 1162. 1984.

*Andinia lynniana* (Luer) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes lynniana* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 91. 2002.

*Andinia macrotica* (Luer & Dalström) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes macrotica* Luer & Dalström, Monogr. Syst. Bot. Missouri Bot. Gard. 61(4): 3. 1996.

*Andinia micropetala* (L.O.Williams) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes micropetala* L.O.Williams, Bot. Mus. Leafl. 9: 4. 1940.

*Andinia mongei* (Tobar & Archila) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophila mongeei* Tobar & Archila, Revista Guatemal. 15(2): 23. 2012.

*Andinia monilia* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes monilia* Luer & R.Escobar, Orquideología 16(1): 12. 1983.

*Andinia montis-rotundi* (P.Ortiz) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes montis-rotundi* P.Ortiz, Orquideología 20(3): 318. 1997.

*Andinia octocornuta* (Luer) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes octocornuta* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 91. 2002.

*Andinia ortiziana* (S.V.Urbe & Thoerle) Karremans & S.Vieira-Urbe, *comb. nov.*



Bas. *Neoreophilus ortizianus* S.V.Uribe & Thoele, Orquideología 28(2): 135. 2011.  
*Andinia pendens* (Garay) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes pendens* Garay, Can. J. Bot. 34: 252. 1956.  
*Andinia persimilis* (Luer & Sijm) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes persimilis* Luer & Sijm, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 92. 2002.  
*Andinia phallica* (Tobar & Archila) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophilus phalicus* Tobar & Archila, Revista Guatemal. 15(2): 20. 2012.  
*Andinia pholeter* (Luer) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes pholeter* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 33. 1994.  
*Andinia pilosella* (Rchb.f.) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes pilosella* Reichenbach f., Flora 69: 556. 1886.  
*Andinia platysepala* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes platysepala* Luer & R.Escobar, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 36. 1994.  
*Andinia pseudocaulescens* (L.B.Sm. & S.K.Harris) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes pseudocaulescens* L.B.Sm. & S.K.Harris, Bot. Mus. Leafl. 2(3): 33. 1934.  
*Andinia ricii* (Luer & R.Vásquez) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes ricii* Luer & R.Vásquez, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 40. 1994.  
*Andinia rosea* (Archila) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophilus roseus* Archila, Revista Guatemal. 17(1): 43. 2014.  
*Andinia rotunda* (Archila) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophilus rotundus* Archila, Revista Guatemal. 17(1): 42. 2014.  
*Andinia sibundoyensis* (Kolan.) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophilus sibundoyensis* Kolan., Ann. Bot. Fennici 50: 169. 2014  
*Andinia sudamericana* (Archila) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophilus sudamericanus* Archila, Revista Guatemal., 17(1): 40. 2014.  
*Andinia triangularis* (Luer) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes triangularis* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 43. 1994.  
*Andinia tridactyla* (Luer) S.Vieira-Urbe & Karremans, *comb. nov.*  
 Bas. *Lepanthes tridactyla* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 92. 2002.  
*Andinia ursula* (Luer & R.Escobar) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes ursula* Luer & R.Escobar, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 46. 1994.  
*Andinia viebrockiana* (Luer & L.Jost) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes viebrockiana* Luer & L.Jost, Monogr. Syst. Bot. Missouri Bot. Gard. 72: 108. 1998.  
*Andinia vieira-pereziana* (P.Ortiz) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Neoreophilus vieira-perezianus* P.Ortiz, Orquideología 28(1): 7. 2011.  
*Andinia villosa* (Løjtant) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes villosa* Løjtant, Bot. Not. 130(4): 419. 1977.  
*Andinia wernerii* (Luer) Karremans & S.Vieira-Urbe, *comb. nov.*  
 Bas. *Lepanthes wernerii* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 88: 93. 2002.

*Andinia* subgen. *Masdevalliantha* (Luer) Karremans & Mark Wilson, *comb. nov.* Bas. *Pleurothallis* subgen. *Masdevalliantha* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 44. 1986. Type. *Pleurothallis masdevalliopsis* Luer, Phytologia 44(3): 170. 1979.  
 Syn. *Pleurothallis* subgen. *Xenion* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 96. 1986.  
 Syn. *Masdevalliantha* (Luer) Szlachetko & Margonska., Polish Bot. J. 46(2): 117. 2001.  
 Syn. *Xenosia* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

Plant repent, ascending or caespitose. Inflorescence single-flowered. Lip three-lobed, with a midlobe prominent and obtuse, not transformed into appendix. Lip winged, not involving the relatively much shorter column. Column foot present. The subgenus includes the species previously assigned to the genera *Masdevalliantha* and *Xenosia*. Four species distributed through the Andean regions of Colombia, Ecuador and Peru (Fig. 6), with an elevational range of 2,400 to 3,825 m (Fig. 8). The three most similar species are illustrated to aid identification (Fig. 9) and a photograph of an example, *Andinia longiserpens* (C.Schweinf.) Karremans & Mark Wilson, is provided (Fig. 11a).

There has been some confusion regarding the generic affinity of the species *Humboltia spiralis* Ruiz & Pavón

(1798: 237) and its relationship to *Pleurothallis macrorhiza* Lindley (1834: 9). Persoon (1807) erroneously transferred *H. spiralis* to *Stelis*. *Stelis spiralis* (Ruiz & Pav.) Persoon (1807: 524) was subsequently declared a synonym of *Stelis purpurea* (Ruiz & Pav.) Willdenow (1805: pl. 4, 140). Hence, *Humboltia spiralis*, *Pleurothallis spiralis*, *Stelis spiralis* and *Xenosia spiralis* are all currently listed as synonyms of *Stelis purpurea* in the World Checklist of Selected Plant Families (WCSP 2016). To further compound the confusion, Luer (2006) transferred *P. macrorhiza* to *Xenosia*, as *Xenosia macrorhiza* (Lindl.) Luer (2006: 233), listing the previously described *X. spiralis* as a synonym. And in the World Checklist of Selected Plant Families *Pleurothallis macrorhiza*, *Humboltia macrorhiza* (Lindl.) Kuntze (1891: 667) and *Xenosia macrorhiza* are also listed as synonyms of *S. purpurea*. We have determined, however, that the type of *H. spiralis* is an *Andinia*, not a *Stelis*, and that *H. spiralis* and *P. macrorhiza* are likely the same species. Because *H. spiralis* Ruiz & Pavón (1798) has taxonomic priority over *P. macrorhiza* Lindley (1834), the appropriate combination under *Andinia* is *Andinia spiralis* (Ruiz & Pav.) Karremans & Mark Wilson. All of these names, except *S. purpurea*, are therefore reduced to synonymy with *A. spiralis*.

*Andinia longiserpens* (C.Schweinf.) Karremans & Mark Wilson, *comb. nov.*

Bas. *Pleurothallis longiserpens* C.Schweinf., Bot. Mus. Leafl. 10: 183. 1942.

*Andinia masdevalliopsis* (Luer) Karremans & Mark Wilson, *comb. nov.*

Bas. *Pleurothallis masdevalliopsis* Luer, Phytologia 44(3): 170. 1979.

*Andinia spiralis* (Ruiz & Pav.) Karremans & Mark Wilson, *comb. nov.*

Bas. *Humboltia spiralis* Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1: 237. 1798.

*Andinia xenion* (Luer & R.Escobar) Karremans & Mark Wilson, *comb. nov.*

Bas. *Pleurothallis xenion* Luer & R.Escobar, Orquideología 16(1): 38. 1983.

*Andinia* subgen. *Minuscula* Karremans & Mark Wilson, *subgen. nov.* Type. *Pleurothallis trimytera* Luer & R. Escobar, Orquideología 16: 34, 1983.

Plant repent-ascending, leaves coriaceous, inflorescence loose, successively flowered, ovary papillose, lip three-lobed, with lobes triangular, conspicuous, apical, anther and stigma apical, column foot absent.

**Etymology:** The name refers to the minuscule size of the plants and flowers of this subgenus compared to the other subgenera.

Three species distributed through Andean regions of Ecuador and Colombia (Fig. 6), with an elevational range of 1,800 to 2,590 m (Fig. 8). The three species are illustrated (Fig. 10) and a photograph of an example, *Andinia trimytera* (Luer & R.Escobar) Pridgeon & M.W.Chase, is provided (Fig. 11d).

*Andinia hystricosa* (Luer) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Bas. *Pleurothallis hystricosa* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 54. 1994.

*Andinia panica* (Luer & Dalström) Pridgeon & M.W.Chase, Lindleyana 16(4): 251. 2001.

Bas. *Pleurothallis panica* Luer & Dalström, Monogr. Syst. Bot. Missouri Bot. Gard. 61(3): 6. 1996.

*Andinia trimytera* (Luer & R.Escobar) Pridgeon & M.W.Chase, Lindleyana 16(4): 252. 2001.

Bas. *Pleurothallis trimytera* Luer & R.Escobar, Orquideología 16: 34. 1983.

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#### Author Contributions Statement

MW initiated the study of *L. nummularia* variation with LJ and expanded the project to the phylogeny of *Andinia*; generated most of the ITS sequences; and wrote the majority of this version of the manuscript, excluding the taxonomic treatment. GSF generated all the *matK* sequences, some ITS sequences and the GIS maps; uploaded some of the sequences to Genbank; and contributed extensively to this version of the manuscript through the completion of an undergraduate Senior Thesis upon which this manuscript is based. APK generated sequences for 4 taxa; uploaded the majority of the sequences to Genbank; prepared the taxonomic treatment; prepared an earlier version of a manuscript; and contributed extensively to this version of the manuscript. LJ initiated the study of *L. nummularia* variation; provided multiple samples; and contributed extensively to the discussion of phylogenetic depth in relation to generic delimitation. AP provided sequences for 4 taxa; made the earliest presentation of the relationships between *Andinia* and related taxa; and contributed edits to this version of the manuscript. SVU assisted in the preparation of the taxonomic treatment; provided the photographic plate; and contributed edits to this version of the manuscript.