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, Neoreorphilus, Oreoophilus, 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 sub-genus 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, Neoreorphilus, Oreoophilus, 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 distan-temente relacionado con Pleurothallis 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 pseudócúpula 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 (2005: 220); Penducella Luer & Thoerle (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 (Schlr.) Luer (2000: 6), though this did not last long, as several more species were soon to be added from Pleurothallis.


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. vestigipetal. 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. vestigipetal (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 Brachycladidae Reichenbach (1858: 142), meaning “short branches”, and the rest into Lepanthes section Macrocladae Reichenbach (1858: 143). Luer (1986a) elevated Lepanthes section Brachycladidae 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
Phytotaxa 2013a). 

The pioneering molecular phylogenetic studies of Pridgeon (2005) and Wilson & Jost (2009; 2011) 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 ramiicals 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 Masdevallanthia, 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 & Tukallo, 2006; Abele 2007); Pabstiella Brieger & Senghas (1976: 195) (Chiron et al. 2012); Phloeophila (Chiron et al. 2016); Specklinia Lindley (1830: 8) (Bogarin 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 Pfizter (1888: 139) (Endara et al. 2011). Several of these studies have confirmed the occurrence of polyplyphy and paraplyly 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.**

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Collection – Voucher</th>
<th>ITS</th>
<th>matK</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Andinia dalstroemii</em> (Luer) Pridgeon &amp; M.W.Chase (1)</td>
<td>Wilson AN005</td>
<td>KP012339</td>
<td>KR709284</td>
<td>This Study</td>
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<td>KP012343</td>
<td>KP012516</td>
<td>This Study</td>
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<td>KC425837</td>
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<td>Pridgeon &amp; Chase 2002</td>
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<td>KP012345</td>
<td>KR709288</td>
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<td>AF261955</td>
<td>Pridgeon et al. 2001</td>
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<td>KP012514</td>
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<td>KP012344</td>
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<td>This Study</td>
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<td>O’Shaughnessy 03688</td>
<td>KP012377</td>
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</table>

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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 λ 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 μL 2× PCR Master Mix (Promega), 1 μL 17SE (25 μM), 1 μL 26SE (25 μM), 1 μL dimethyl sulfoxide (DMSO), and 4.5 μL molecular biology grade water per reaction, for a total of 20 μL per reaction. In a 0.2 mL PCR tube, 5 μL containing approximately 10 ng template DNA was added to 20 μL 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 μL 2× PCR Master Mix (Promega), 1 μL 390f (25 μM), 1 μL 1326r (25 μM), and 0.5 μL molecular biology grade water per reaction, for a total of 15 μL. In a 0.2 mL PCR tube, 10 μL containing approximately 2.5 ng template DNA was added to 15 μL 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\textsubscript{260}/A\textsubscript{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 \textit{et al}. 1994) and ITS1 and ITS4 (White \textit{et al}. 1990).

The \textit{matK} PCR products were sequenced with the primers 390F and 1326R (Cuénoud \textit{et al}. 2002) and Nina-matK-F (GCGATTGTTTTCACGAAAT) and Nina-matK-R (TCCGCTCTGTATAAGCAAA) (Sheade 2012).

A small number of samples were processed in Leiden, The Netherlands by AK using procedures described previously (Karremans \textit{et al}. 2013a). The ITS region was amplified and sequenced using the primers 17SE and 26SE (Sun \textit{et al}. 1994) and the plastid gene \textit{matK} was amplified and sequenced using the primers 2.1aF and 5R (Karremans \textit{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 \textit{et al}. 2013a). All ITS and \textit{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 \textit{Andinia} (as defined above [Pridgeon \& Chase 2001; Luer 2005; Chase \textit{et al}. 2015]) and species from the genera \textit{Masdevalliantha}, \textit{Neooreophilus} and \textit{Xenosia}, considered possibly related to \textit{Andinia} (Table 1). The analysis additionally included the pleurothallid genera \textit{Anathallis}, \textit{Dryadella} Luer (1978: 207), \textit{Lankesteriana} Karremans (2014: 321), \textit{Lepanthes}, \textit{Pabstiella}, \textit{Phloeophila} (Hoehne \& Schlechter 1926: 199), \textit{Platystele} Schlechter (1910: 565), \textit{Pleurothallis}, \textit{Scaphosepalum}, \textit{Specklinia}, \textit{Stelis} (including three species of the former \textit{Salpistele}), \textit{Trichosalpinx} Luer (1983: 393), and \textit{Zootrophion} Luer (1982: 80) (Table 2).

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

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Collection - Voucher</th>
<th>ITS</th>
<th>\textit{matK}</th>
</tr>
</thead>
<tbody>
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<td>\textit{Anathallis lewisiae} (Ames) Solano &amp; Soto Arenas</td>
<td>DB1056</td>
<td>KC425733</td>
<td>KC425858</td>
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<tr>
<td>\textit{Anathallis obovata} (Lindl.) Pridgeon &amp; M.W.Chase</td>
<td>AK4796</td>
<td>KF747797</td>
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<tr>
<td>\textit{Anathallis sertularioides} (Sw.) Pridgeon &amp; M.W.Chase</td>
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<td>KC425840</td>
<td>NA</td>
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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 1,000 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.
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, Neoeoreophilus and Xenosia, was strongly supported. The moderately supported clade B contained all the species of Neoeoreophilus; 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) that 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, Oreopilus, 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-trnL 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 & Thoerle (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 Oreopilus (Archila & Higgins 2008) and almost simultaneously to Neooreophilus (Archila 2009) and Penducella (Luer & Thoerle 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 *Neoreorchis* 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 *Neoreorchis* 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 *Neoreorchis nummularius* and *N. stalactites*, and clade B1 containing all other *Neoreorchis* species. These parallel Luer’s *Lepanthes* subgenus Brachycladium sections Brachycladus 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 for 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-Uribe unpublished) 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. hystroica* (Luer) Pridgeon & Chase (2001: 251) and *A. panic* (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. hystroica* and *A. panic* in the proposed subgenus *Minuscula* cannot be confirmed until material becomes available for sequencing, Luer (1994) indicated that *A. hystroica* “is closely allied to” *A. trimytera* and Luer (1996) stated that *A. panic* is close to *A. hystroica*.

Clade D includes *A. dielsii*, *A. pensilis*, *A. lappacea* and *A. vestigipetalata* 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. vestigipetalata* 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. vestigipetalata* 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 *Masdevallianthia longiserpens*, *Xenosis 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 *Xenosis* 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 (Freudentstein & 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](image)

**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, Neoooreophilus, Oreophilus, Penducella, Pleurothallis, Salpistele*, and *Xenosia*. We show here that the species of *Andinia, Neoooreophilus, 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, Neoooreophilus* and *Xenosia*. Additionally, we propose an infrageneric taxonomy for *Andinia*, including subgenera *Aenigma, Andinia, Brachycladium, Masdevalliantha* and *Minuscula*. 


**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


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 transformed into what is possibly performing the same function as the appendix in Lepanthes. Anther and stigma apical. Column foot absent. Pollinia with a 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).


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. Pollinia 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*.


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), with 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).


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 apical, stigma ventral, rostellum inconspicuous. 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 chelosepala (Luer & Hirtz) Karremans & S.Vieira-Uribe, comb. nov.

Andinia chilopsis (Luer & Hirtz) Karremans & S.Vieira-Uribe, comb. nov.

Andinia ciliaris (Luer & Hirtz) Karremans & S.Vieira-Uribe, comb. nov.


Andinia cordilabia (Luer) S.Vieira-Uribe & Karremans, comb. nov.


Andinia erepsis (Luer & Hirtz) Karremans & S.Vieira-Uribe, comb. nov.

Andinia exigua (Luer & L.Jost) Karremans & S.Vieira-Uribe, comb. nov.


Andinia lueri S.Vieira-Uribe & Karremans, comb. nov.

Andinia lunaris (Luer) Karremans & S.Vieira-Uribe, comb. nov.

Andinia lunatocheila (Tobar & Archila) Karremans & S.Vieira-Uribe, comb. nov.

Andinia lupula (Luer & Hirtz) Karremans & S.Vieira-Uribe, comb. nov.

Andinia lynni (Luer) Karremans & S.Vieira-Uribe, comb. nov.

Andinia macrotricha (Luer & Dalström) Karremans & S.Vieira-Uribe, comb. nov.

Andinia micropetala (L.O.Williams) Karremans & S.Vieira-Uribe, comb. nov.

Andinia mongei (Tobar & Archila) Karremans & S.Vieira-Uribe, comb. nov.


Andinia montis-rotundi (P.Ortiz) Karremans & S.Vieira-Uribe, comb. nov.

Andinia octocornuta (Luer) Karremans & S.Vieira-Uribe, comb. nov.

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


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* 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 macrochiza* (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 longiserpen*s (C.Schweinf.) Karremans & Mark Wilson, *comb. nov.*

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

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

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


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).


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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.