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## Article

# Taxonomy and Biogeography of *Andinia*-Complex (Orchidaceae)

Dariusz L. Szlachetko <sup>1</sup>, Magdalena Dudek <sup>1</sup> , Aleksandra Naczka <sup>2</sup>  and Marta Kolanowska <sup>3,4,\*</sup>

- <sup>1</sup> Department of Plant Taxonomy and Nature Conservation, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland; [dariusz.szlachetko@gmail.com](mailto:dariusz.szlachetko@gmail.com) (D.L.S.); [magdalena.dudek@ug.edu.pl](mailto:magdalena.dudek@ug.edu.pl) (M.D.)
- <sup>2</sup> Department of Evolutionary Genetics and Biosystematics, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland; [bioa.naczka@gmail.com](mailto:bioa.naczka@gmail.com)
- <sup>3</sup> Department of Geobotany and Plant Ecology, Faculty of Biology and Environmental Protection, University of Lodz, Banacha 12/16, 90-237 Lodz, Poland
- <sup>4</sup> Department of Biodiversity Research, Global Change Research Institute AS CR, Bělidla 4a, 603 00 Brno, Czech Republic
- \* Correspondence: [marta.a.kolanowska@gmail.com](mailto:marta.a.kolanowska@gmail.com)

**Abstract:** The results of a revision of the orchid genus *Andinia* are presented. The proposed classification is based on outcomes of morphological and molecular studies. Additionally, the similarity of the climatic niches occupied by representatives of the *Andinia*-complex was calculated and visualized. The highest number of *Andinia* representatives is found in the Eastern Cordillera real montane forests, while *Neooreophilus* species are found in two ecoregions—the Eastern Cordillera real montane forests, and the Northwestern Andes. According to the level of endemism, a very unique orchid flora was noted in the Guajira–Barranquilla xeric scrub ecoregion, as well as in the Isthmian-Pacific and the Ucayali moist forests, where single endemic species occur. In the proposed classification, nine genera are recognized within the *Andinia*-complex, three of which (*Xenosiella*, *Chicalia*, and *Minuscula*) are described in this paper. A key to the identification of all genera is provided. Additionally, sections *Amplectentes* and *Bilamellatae* of *Neooreophilus* are elevated to the subgeneric rank, and subgenus *Aenigma* is here considered as a separate genus. A complete list of representatives of each taxon is provided, and new combinations are proposed accordingly. A new species of *Neooreophilus* from Colombia is described.

**Keywords:** taxonomy; Pleurothallidinae; phylogeny; biogeography



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## 1. Introduction

The Neotropical subtribe Pleurothallidinae, comprising ca. 5000 species, is one of the largest groups within Orchidaceae [1,2]. The generic composition of this taxon has been studied for years [1,3–5], but the taxonomic concept of numerous genera is still debated [6–10] due to the enormous morphological diversity of pleurothallid orchids and the relatively poor molecular data which could be used to delineate well-defined taxa.

The genus *Lepanthes* described at the end of the XVIII century is one of several hyperdiverse genera within Pleurothallidinae [11]. In 1986, it was divided by Luer into four subgenera—*L.* subgen. *Brachycladium* Luer, *L.* subgen. *Draconanthes* Luer, *L.* subgen. *Lepanthes*, and *L.* subgen. *Marsipanthes* Luer. The former two were later considered as separated genera—*Brachycladium* Luer (Luer) [12] and *Draconanthes* Luer (Luer) [1], respectively. *Brachycladium* was, however, illegitimate, as the same name was previously used for a genus of fungus. For this reason, Archila and Higgins [13] proposed a substitute name, *Oreophilus* W.E. Higgins & Archila, for *Brachycladium*, but again, the authors made a nomenclatural mistake, and finally in 2009 a correct name, *Neooreophilus* Archila, was given to encompass pleurothallids characterized by long-repent, pendent habit, creeping rhizomes, leaves appearing alternating, and *Lepanthes*-like flowers [14]. The concept of *Neooreophilus* was accepted for eight years until Wilson et al. [15], based on phylogenetic analyses, proposed to group the genus representatives with *Andinia* (Luer) Luer, which in

the suggested broad concept included also *Masdevalliantha* (Luer) Szlach. & Marg., and *Xenosia* Luer. *Andinia* was initially recognized as a subgenus of *Salpistele* Dressler and encompassed plants with repent habit, echinate ovaries, abbreviated petals, presence of callus on the lip disc, and large, auriculate lip lateral lobes. Pridgeon and Chase [4] later transferred to this genus also a single representative of *Lueranthos* Szlach. & Marg.

In this broad concept, morphological variation of *Andinia* s.l. is significant in aspects of vegetative and floral characters. Representatives of this complex are caespitose or rhizomatous plants with variously developed rhizome. Their leaves of various shape are glabrous or with ciliate or denticulate margins, and in numerous species they appear alternating and often overlapping. The inflorescence of these plants is single-flowered to racemose, sometimes reclining. The ovary is glabrous to papillose, verrucose, echinate, or spiculate. Sepals are spiculate or glabrous, variously connate, while the petals vary in size (from microscopic to subequal to sepals) and form (suborbicular to variously lobed and trifurcate). In addition, the lip form significantly differs among the *Andinia*-complex. It is entire to variously lobed, sometimes with an appendix, with or without callus. The gynostemium is usually (but not always) footless, with elongated or reduced rostellum.

The discrepancy between the genetic and morphological and/or ecological data together with the question about the precision of using a barcoding approach were recognized as serious problems in taxonomy of numerous organisms [16,17]. As summarized by Wiens et al. [18], while the rates of genome sequencing increase, scientists should continue to construct classification systems using morphological data. A reason supporting morphological analyses is that DNA of many taxa, including numerous *Andinia* s.l., have not been sequenced, and many species remain known from a single specimen that was collected decades ago. Moreover, because various issues may result in the creation of false but statistically well-supported molecular phylogenies [18], it is still important to develop accurate, morphology-based phylogenies. Noteworthy, a typical set of morphological characters is information obtained from various unlinked genes, while a molecular dataset is often linked and inherited as a single unit [19].

The substantial differences in the morphology within *Andinia sensu* Wilson et al. [15] and the obvious discontinuum in numerous characters prompted us to revise the classification of species included in this genus. Moreover, we tested if species classified in *Andinia* s.l. exhibit any ecological differences. Based on the confrontation of morphological, molecular, and ecological data, we propose a new taxonomic concept of *Andinia* s.l.

## 2. Materials and Methods

### 2.1. Phylogenetic Analyses

For phylogenetic reconstruction, we applied the ITS sequences and the *matK* gene (70/40), representing taxa from six genera of the *Andinia*-complex: *Andinia* s.str., *Lueranthos*, *Masdevalliantha*, *Pleurothallis*, *Neoreophila*, and *Xenosia*. *Laelia* was used as an outgroup. All sequences were downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>, accessed on 1 June 2021), and the accession numbers were placed on the cladograms together with the names of the species. We performed three matrixes, two for single markers (ITS, *matK*), and combined both these markers as well. The sequences were automatically aligned by SeaView [20], choosing the MUSCLE algorithm [21]. The generated matrices were analyzed under maximum likelihood (ML) and Bayesian Inference (BI). The ML/Transfer bootstrap expectation workflow analysis was performed using RAXML-HPC2 [22] by searching for the best-scoring ML tree with the GTR+I+G as the best fit substitution model. The branch support values (BS) were calculated with RaxML by halting bootstrapping automatically under the autoMRE criterion. For bootstrap support levels, we considered the following percentage values of 50–70% as weak, 71–85% as moderate, and >85% as strong [23].

The BI was performed using MrBayes v. 3.2.7a [24] with GTR+I+G as the selected evolutive model for all matrices. An evolutionary model was determined with MrModeltest 2.2 [25] and selected according to the Akaike Information Criterion (AIC). Each analysis consisted of two independent runs of four chains, one hot and three cold chains, and were started from different random trees to ensure that individual runs had converged to the same result. We used 10 million generations per runs with a sampling frequency of 100. Split frequencies below 0.01 were used to check for convergence, and the effective sample size (ESS) for each run was checked in Tracer v. 1.7.1 [26]. Twenty-five percent of trees were excluded as burn-in. Saved trees were summarized in a majority rule consensus tree created with nodal confidence assessed by posterior probabilities (PP), which were considered strongly supported when equal to or higher than 0.95. The trees obtained in both methods were edited with FigTree v.1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/> accessed on 1 June 2021) and Inkscape (<https://inkscape.org/release/inkscape-1.0.2/> accessed on 1 June 2021).

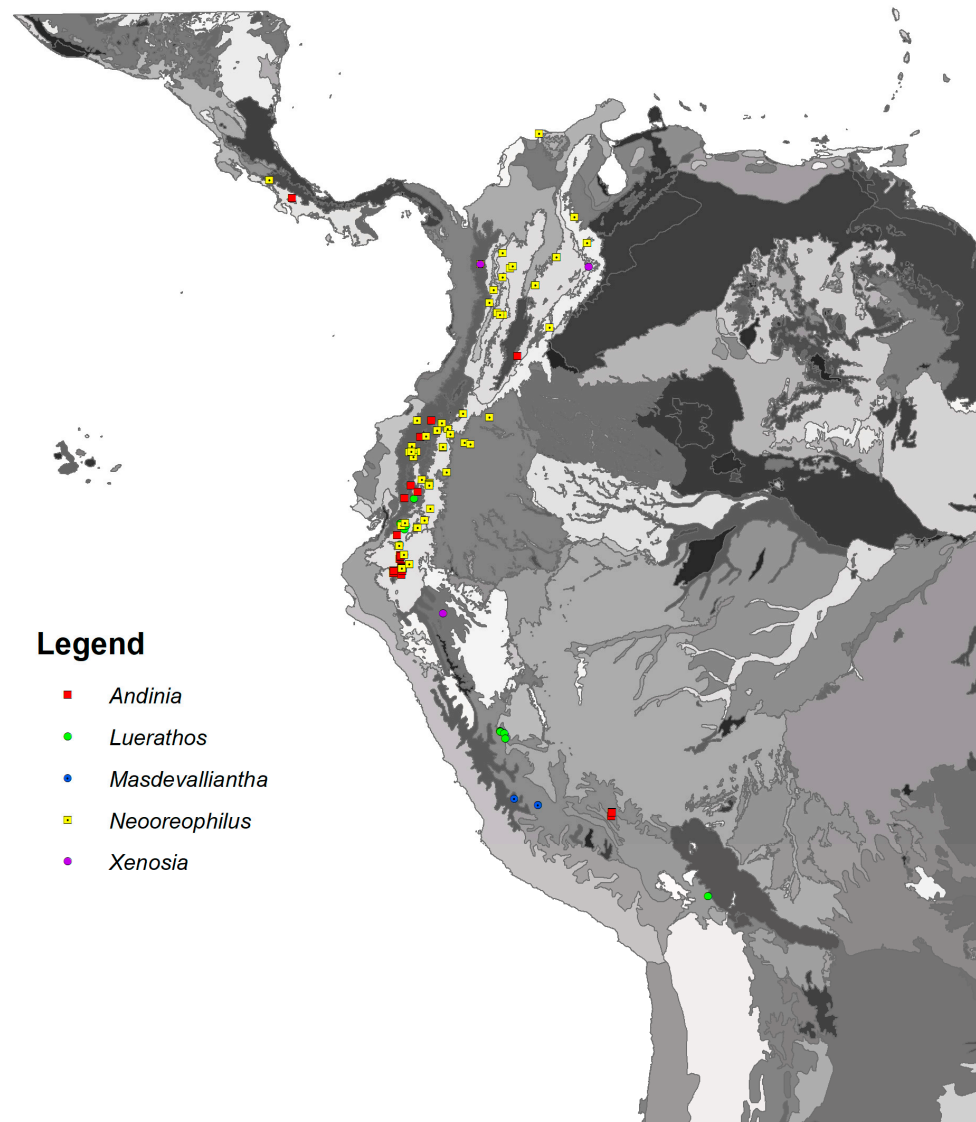
## 2.2. Taxonomic Studies

The database of diagnoses and original illustrations of 18 *Andinia* s.str., 52 *Neooreophilus*, 3 *Xenosia*, 2 *Masdevalliantha*, and single *Lueranthos* species was compiled. A total of over 300 herbarium specimens and liquid preserved flowers of orchids included by Wilson et al. [15] in *Andinia* deposited in AMES, BM, COL, JAUM, K, MO, NY, U, US, UGDA, and W [27] was examined according to the standard procedures. Additionally, plants cultivated in Ecuagenera, Mundiflora, Ecuaflorea, and the private collection of Ramiro Medina Trejo were analyzed. Every studied herbarium sheet was photographed, and the data from the labels were taken. Both vegetative and generative characters of each plant were examined. The form and surface of leaves were studied first. Then the construction of the inflorescence and the shape and size of the floral bracts were examined. The morphology of flowers was studied after their boiling using a stereomicroscope. The database of vegetative and floral characters of all species was compiled to facilitate comparison of *Andinia*-complex representatives (Annex S1).

To propose the comprehensive classification of *Andinia* s.l., we used morphological data gathered in this research as well as outcomes of the phylogenetic analyses conducted for the sequences downloaded from GenBank.

## 2.3. Variation of Climatic Preferences and Biogeographical Analyses

The database of localities for species representing the *Andinia*-complex was compiled. Only localities which should be localized based on information included in herbarium specimen labels were included in the distribution maps (Figure 1) created using ArcGis 10.6 (Esri, Redlands, CA, USA). We were able to obtain precise (precision of 10 km) coordinates for 93 various locations and assign 122 records to specific terrestrial ecoregions [28]. The datasets are presented as Annexes S2 and S3. To visualize climatic niches of the studied taxa, multivariate analyses were performed. A preliminary Detrended Correspondence Analysis (DCA) showed relatively low values of gradient length (<3 SD units). Therefore, a principal component analysis (PCA) was used as the most appropriate method for examine species variation within different climatic spaces and to account for the multicollinearity nature of the initial variables. Analysis was carried out based on 12 of the 19 available bioclimatic variables (Table 1 [29]), also used in ENM analysis.



**Figure 1.** Distribution of studied genera. Base map of ecoregions developed by Olson [28].

**Table 1.** Codes of climatic variables used in this study.

Code	Description
bio1	Annual Mean Temperature
bio2	Mean Diurnal Range = Mean of Monthly (max temp – min temp)
bio3	Isothermality ( $\text{bio2}/\text{bio7} \times 100$ )
bio4	Temperature Seasonality (standard deviation $\times 100$ )
bio5	Max Temperature of Warmest Month
bio8	Mean Temperature of Wettest Quarter
bio12	Annual Precipitation
bio13	Precipitation of Wettest Month
bio14	Precipitation of Driest Month
bio15	Precipitation Seasonality (Coefficient of Variation)
bio18	Precipitation of Warmest Quarter
bio19	Precipitation of Coldest Quarter

The analyses were carried out with the division into studied genera and species, where more than one record was recorded. For each vector, the determination coefficient  $R^2$  and  $p$ -value were calculated using a permutation test with 999 iterations. To determine the bioclimatic variables which differentiate the studied orchids the most, canonical variate analysis (CVA) was applied in order to reduce the dataset by selecting only the factors that showed the strongest discrimination. The significance of bioclimatic differences between the studied taxa was evaluated using Wilk's  $\lambda$  with 10,000 permutations. In turn, the Bray–Curtis similarity between samples was calculated to classify the terrestrial ecoregions, in which species occur at sites, and the resulting matrix was then used in the cluster analysis UPGMA (unweighted pair-group average method). The Shannon–Wiener index was calculated to compare species diversity between terrestrial ecoregions. All analyses were performed using PAST v. 3.20 software [30].

### 3. Results

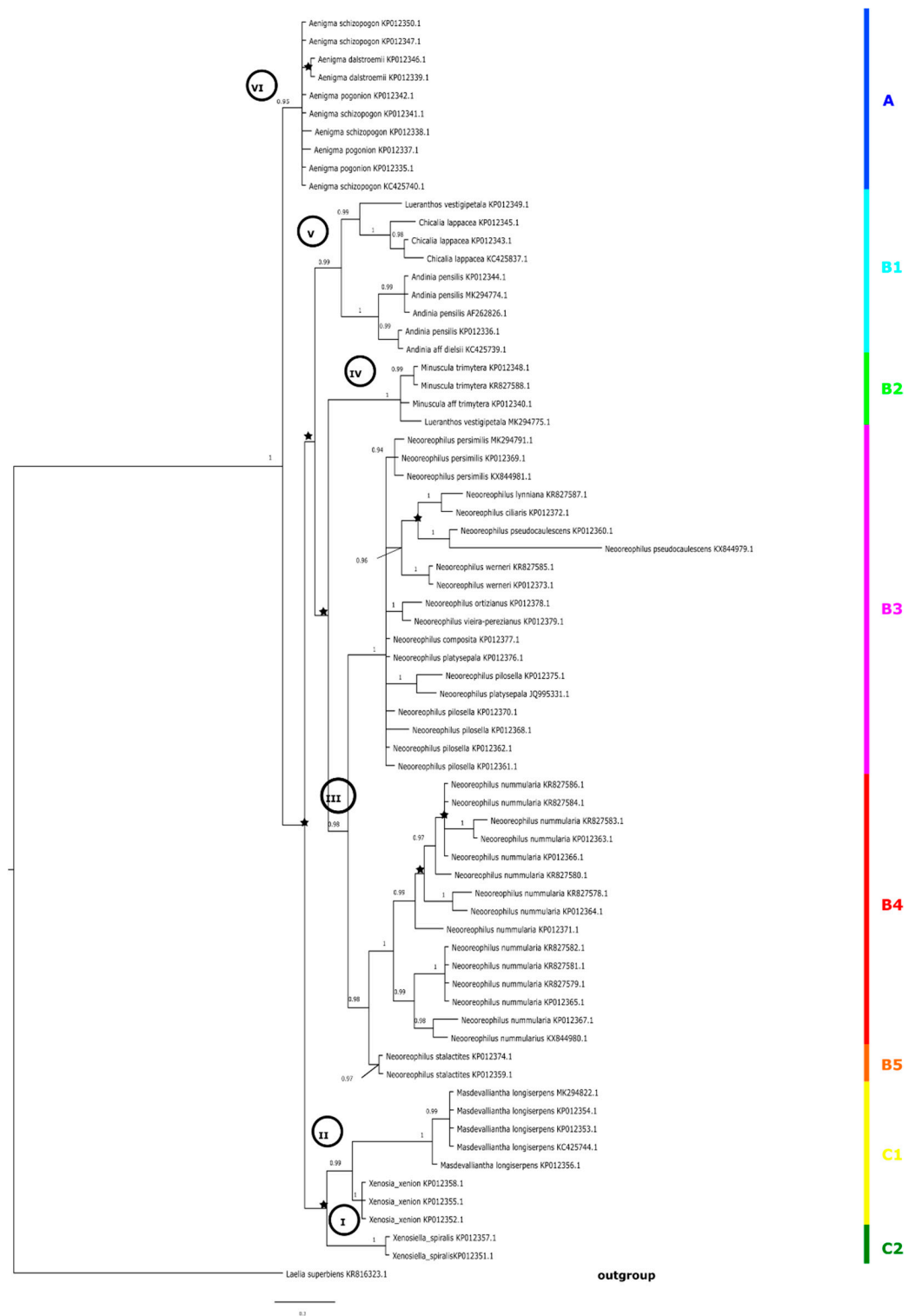
#### 3.1. Phylogeny

##### 3.1.1. ITS Matrix

On the tree obtained by Bayesian inference for the ITS marker, we could distinguish six main and strongly supported phylogenetic groups (Figure 2, clades I–VI).

Clade I (pp = 1.00) was represented by only one species, *Andinia spiralis*, whereas the second group (clade II, Figure 2) included samples of representatives of *Andinia longiserpens*, combined with *Andinia xenion* (pp = 0.99). Clade III, also with a high value of posterior probability (pp = 0.98), was represented by members of *Neooreophilus*, and according to the results of analysis of the ITS sequence, this clade was fragmented into three suballiances. The following three groups (clades IV–VI, Figure 2) included representatives of *Andinia* s.l. with a high value of probability. The first one (clade IV) included *A. trimytera* and *A. vestigipetala*, while clade V encompassed *A. vestigipetala*, *A. lappacea*, *A. pensilis*, and *A. cf. dielsii*. *A. vestigipetala* was sampled by two sequences (KP012349.1 and MK294775.1) placed in two different clades. Probably it could be the result of an incorrectly labelled sample, misidentification, or contamination of the sample. The last clade with high pp value comprised three species: *A. schizopogon*, *A. dalstroemii*, and *A. pogonion*.

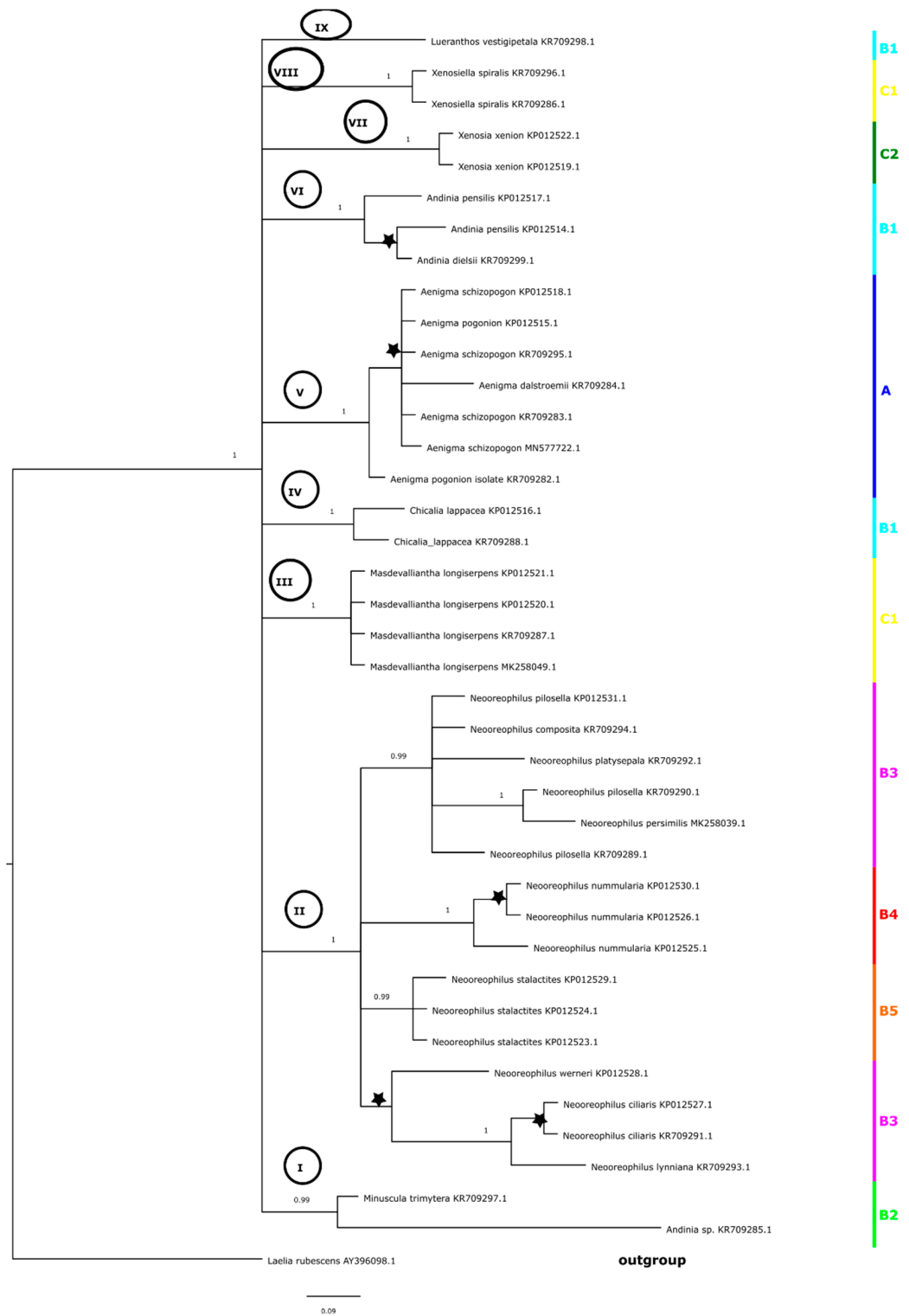
The topology of the tree (Figure 3) obtained for the same marker but based on the ML method was slightly different. Samples representing the following species did not form a consistent clade: *A. schizopogon*, *A. dalstroemii*, and *A. pogonion*. *A. spiralis* (clade a), *A. longiserpens*, and *A. xenion* (clade b) clustered together in a strongly supported group (clade I, BS = 89). On the ML tree, we could distinguish three better supported groups of taxa (clades II–IV). Clade II (BS = 90) included *A. vestigipetala*, *A. lappacea*, *A. pensilis*, and *A. cf. dielsii* and overlapped with clade V on the BI tree (Figure 2). Group III (Figure 3) was formed by the same taxa as clade V on the Bayesian inference tree (Figure 2). Clade IV (Figure 3) corresponded as well to the results based on the BI method (Figure 2, clade III), and included representatives of *Neooreophilus*.



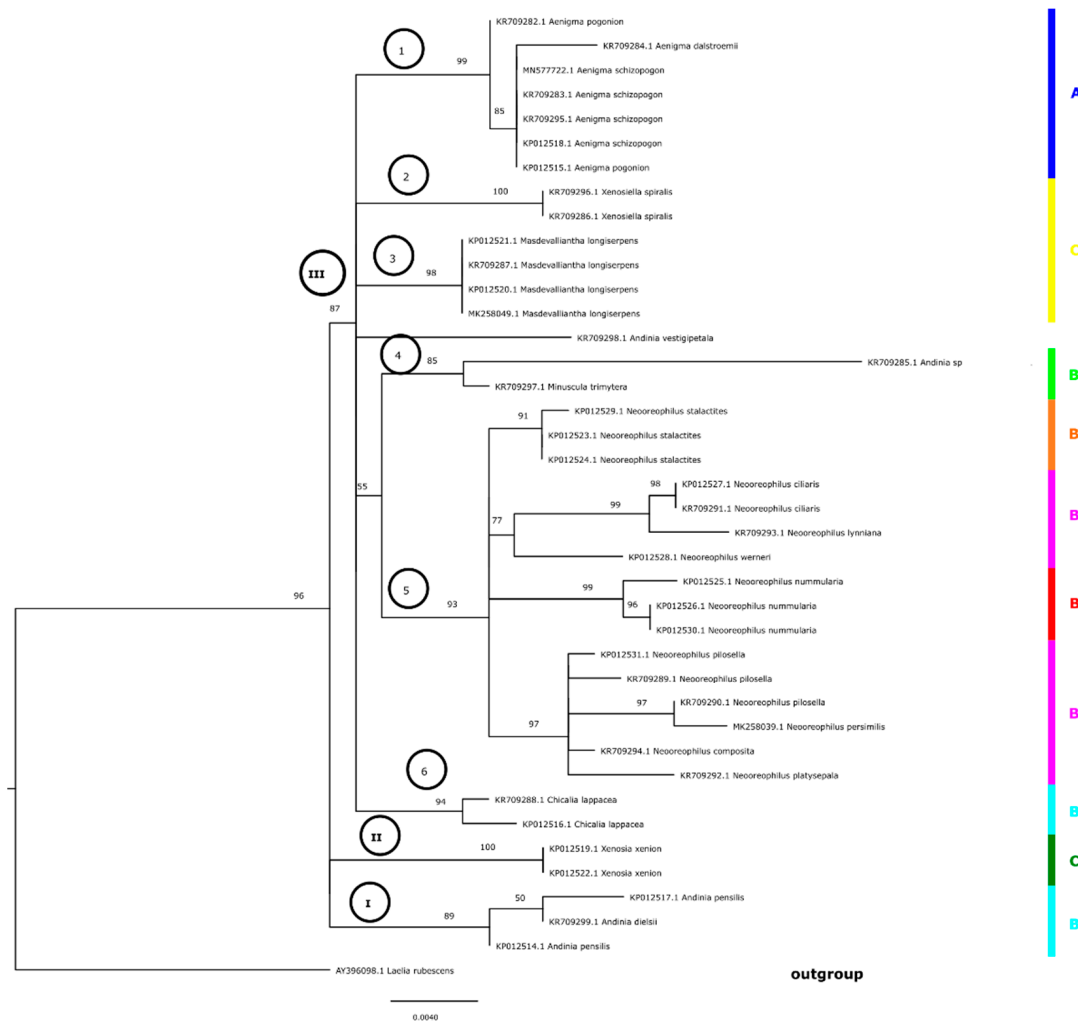
**Figure 2.** Majority-rule consensus tree for *Andinia* s.l. obtained in Bayesian analysis from ITS1-5.8S-ITS2 sequences. Values above branches represent posteriori probabilities; values with pp < 0.9 are indicated with an asterisk. The main and strong supported clades on the tree are marked with the numbers I–VI. Discussed groups of species are marked as A–C2.







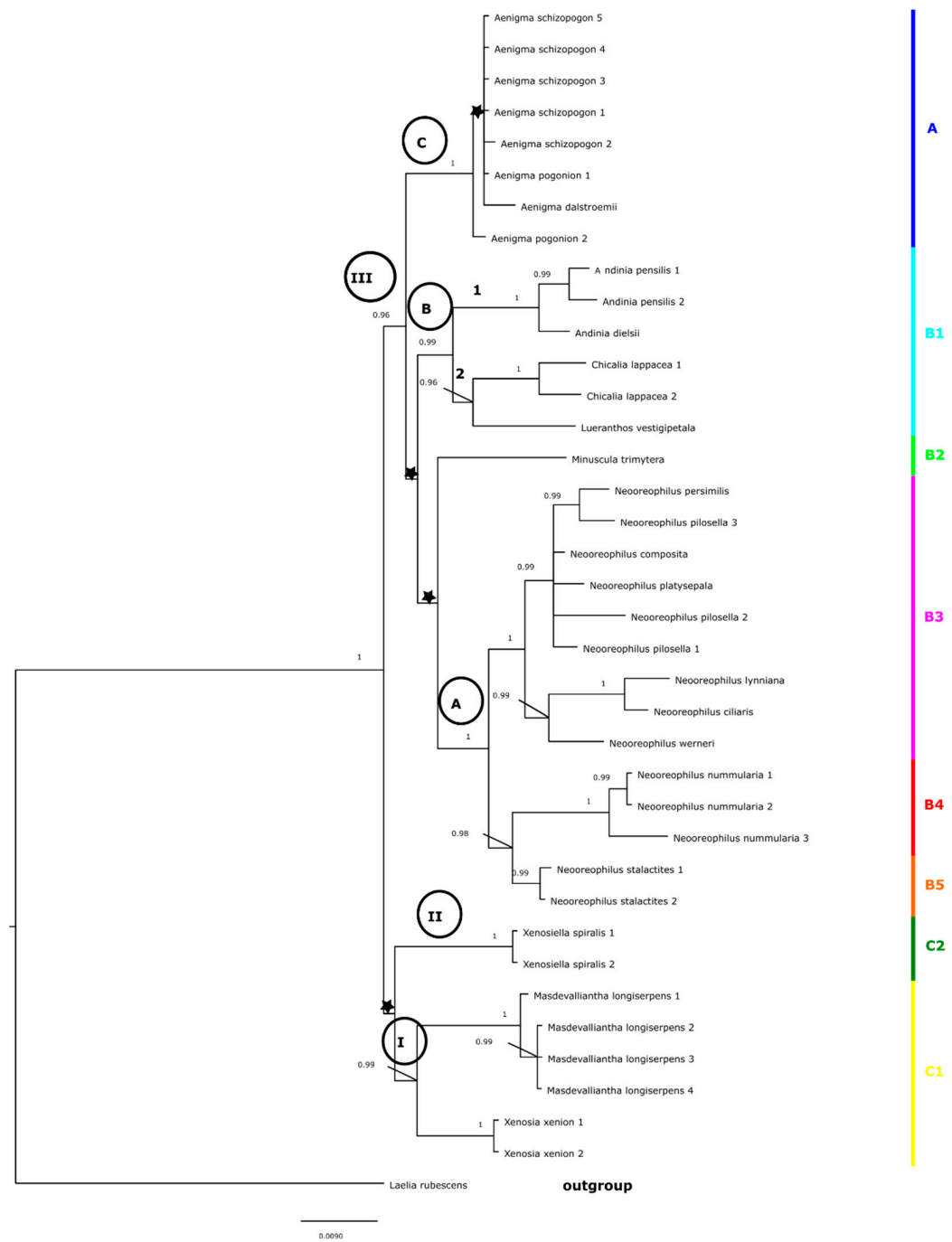
**Figure 4.** Majority-rule consensus tree obtained in Bayesian analysis of part of *matK* gene for *Andinia* s.l. Values above branches represent posteriori probabilities; values with pp < 0.9 are indicated with an asterisk. The main and strong supported clades on the tree are marked with the numbers I–IX. Discussed groups of species are marked as A–C2.



**Figure 5.** Phylogenetic tree performed based on maximum likelihood analysis inferred from the *matK* matrix using ML/Transfer bootstrap expectation with 1000 bootstrap replicates in RaxML. Values at each node represent percent bootstrap support; bootstrap percentages less than 50% are not shown. The main and strong supported clades on the tree are marked with the numbers I–III. The subclades are tagged as 1–6. Discussed groups of species are marked as A–C1.

### 3.1.3. Combined Matrix

The topology of trees obtained for the combined matrix (ITS + *matK*) (Figures 6 and 7) was similar to that based on the ITS marker. We could distinguish three main clades (I–III, Figures 6 and 7). Two of these included representatives of *A. xenion* and *A. longiserpens* (clade I), and the other was represented by *A. spiralis* (clade II). However, within the last one (clade III, Figure 6), on the tree based on BI analysis, we could recognize the following three subgroups: A, B, and C. The first one (A) included representatives of *Neoreophilius* ( $pp = 1.00$ ), and the next one (B, Figure 6) included samples of *A. pensilis*, *A. dielsii*, *A. lappacea*, and *A. vestigipetala*. The last group—C—with *A. schizopogon*, *A. pogonion*, and *A. dalstroemii* has also a high value of probability (Figure 6,  $pp = 1.00$ ). On the maximum likelihood tree, clade III (Figure 7) split into two subgroups: A and B. Within the first of these (A) we could also distinguish two subclades (C and D) with strong bootstrap support. Subclade C included *Neoreophilius* representatives ( $BS = 100$ ), and subclade D included *A. pensilis*, *A. dielsii*, *A. lappacea*, and *A. vestigipetala* ( $BS = 93$ ). *A. trimytera* was also placed in group A (Figure 7) as a sister to subclade D. The second group—B—with *A. schizopogon*, *A. pogonion*, and *A. dalstroemii* also had strong bootstrap support (Figure 7,  $BS = 1.00$ ).



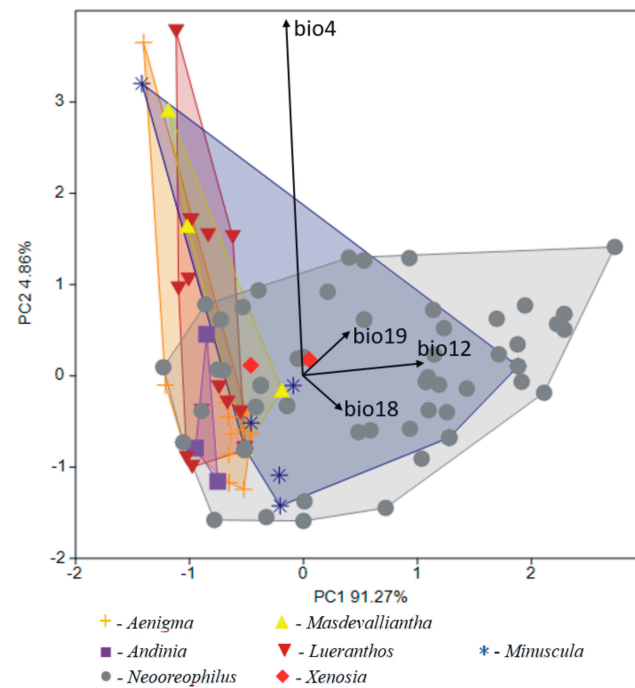
**Figure 6.** Majority-rule consensus tree for *Andinia* s.l. obtained in Bayesian analysis from combined matrix (ITS + *matK*). Values above branches represent posteriori probabilities; values with pp < 0.9 are indicated with an asterisk. The main and strong supported clades on the tree are marked with the numbers I–III. The subclades are tagged as capitals A–C. Discussed groups of species are marked as A–C2.



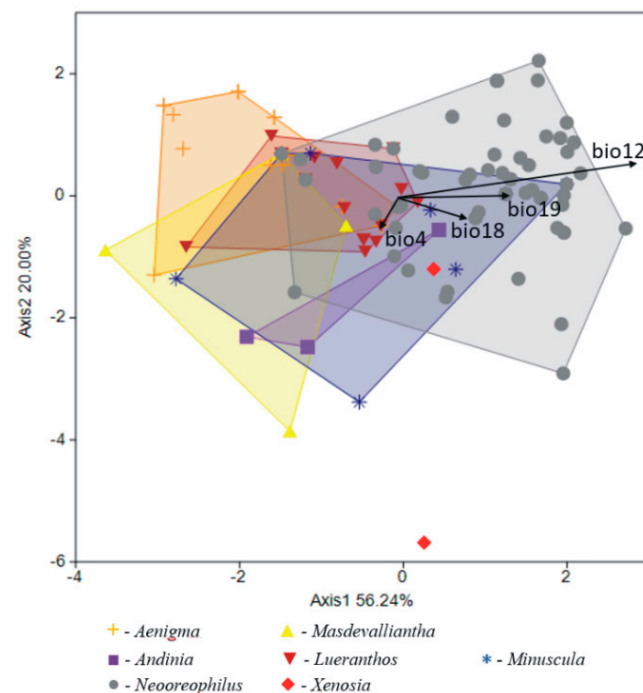
**Figure 7.** Phylogenetic tree performed based on maximum likelihood analysis inferred from the combined ITS-*matK* dataset using ML/Transfer bootstrap expectation with 1000 bootstrap replicates in RaxML. Values at each node represent percent bootstrap support; bootstrap percentages less than 50% are not shown. The main and strong supported clades on the tree are marked with the numbers I–III. However, the subclades are tagged as capitals A–D. Discussed groups of species are marked as A–C2.

### 3.2. Climatic Niche Similarity

The general similarity of the climatic niches occupied by genera within the *Andinia*-complex is visible in the PCA graph (Figure 8) and explained 96.13% of variance. Variables with the greatest contributions enhanced in the overall analysis were: the temperature seasonality (bio4); the annual precipitation (bio12); the precipitation of the warmest quarter (bio18); and the precipitation of the coldest quarter (bio19). The main shift in differentiation of climatic niches was along the PCA axis 2, where *Andinia*, *Aenigma*, *Masdevalliantha*, and *Lueranthos* were separated on the left side of the diagram. However, the climatic niches for all genera overlapped in this plot. There were no clear boundaries between the studied genera in terms of their preferred climatic conditions. In turn, the canonical variate analysis (CVA) showed a highly statistically significant differential value for the studied genera with respect to the bioclimatic variables (Wilks  $\lambda = 0.200$ ;  $F_{(72;577)} = 2.762$ ;  $p < 0.001$ ). The canonical variate axes (56.24 and 20.00% of explained variance, respectively) distinguished specimens from each other along the environmental gradient derived from bioclimatic variables, similar to the PCA analysis (Figure 9).



**Figure 8.** Principal component analysis (PCA) of the climatic variables present in the studied genera among the *Andinia*-complex. Variables with the greatest contributions are presented as vectors.



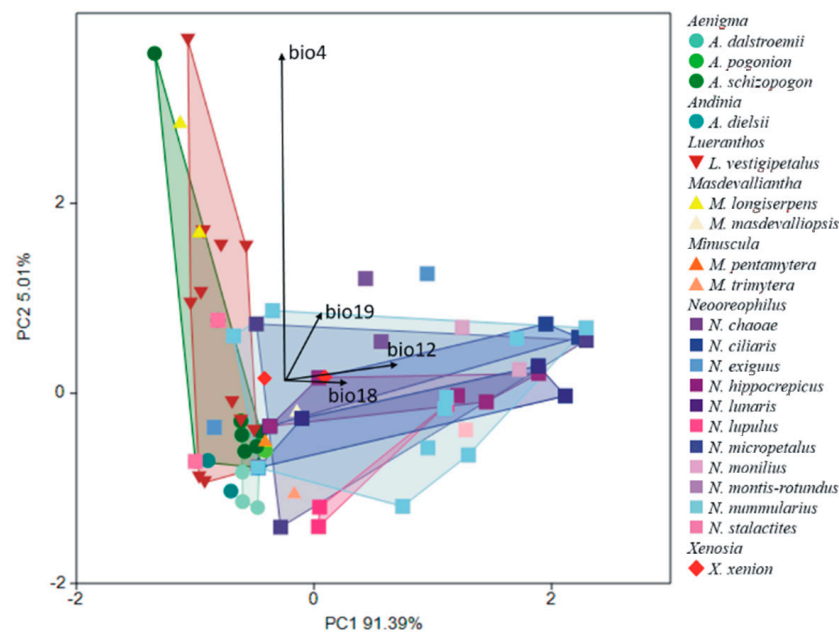
**Figure 9.** Canonical variate analysis (CVA) of the studied genera among the *Andinia*-complex along the climatic gradient. The relative contributions of bioclimatic factors are shown as vectors. Variables with low discriminating impact are omitted.

In the next PCA analysis including species within the *Andinia*-complex, the first axis distinguished *Masdevalliantha longiserpens*, *Neoreophilus chaoae*, *N. monilius*, *N. montis-rotundus*, and *Xenosia xenion* (above the axis) from *Andinia dielsii*, *A. dalstroemii*, *A. pogonion*, *A. pentamytera*, and *N. lupulus* (below the axis). Furthermore, the second axis separated *Aenigma schizopogon*, *Lueranthos vestigipetalus*, *Masdevalliantha longiserpens*, *M. masdevalliopsis*, and *N. stalactites* on the left side of the diagram (Figure 10). Variables with the

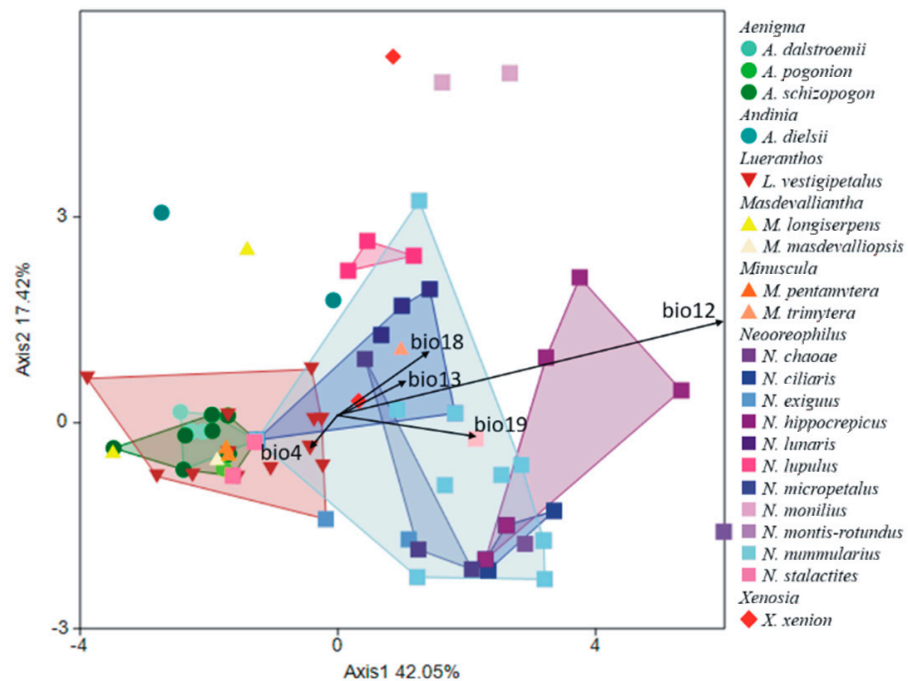
greatest contributions enhanced in the analysis were: the annual precipitation (bio12); the precipitation of the wettest month (bio13); the precipitation of the warmest quarter (bio18); and the precipitation of the coldest quarter (bio19); and also the temperature seasonality (bio4) (Table 2). The same variables indicated in the above analysis were significant contributions to the discrimination of the studied species. This analysis distinguished most species of *Neoreophilus* (e.g., *N. chaoae*, *N. ciliaris*, *N. hippocrepicus*, *N. lunaris*, *N. lupulus*, *N. micropetalus*, *N. montis-rotundus*, *N. nummularius*) on the right side of the diagram (Figure 11). The described shift in discrimination of climatic niches was along Axis 2 (Wilks  $\lambda = 0.002$ ;  $F_{(240;651)} = 2.295$ ;  $p < 0.001$ ).

**Table 2.** Variables fitted to the PCA analysis focusing on climatic niche similarity of the studied species and determination coefficients ( $R^2$ ), where level of significance is marked (ns—not significant; \*— $p < 0.05$ ; \*\*— $p < 0.01$ ; \*\*\*— $p < 0.001$ ).

Variables	PC1	PC2	$R^2$
bio1	0.034	−0.009	0.019 ns
bio2	−0.009	0.034	0.019 ***
bio3	0.001	−0.015	0.112 ***
bio4	−0.061	0.992	0.046 ns
bio5	0.029	0.014	0.960 ***
bio8	0.032	−0.005	0.996 ***
bio12	0.910	0.030	0.435 ns
bio13	0.104	−0.017	0.451 ns
bio14	0.044	0.011	0.310 ns
bio15	−0.066	0.011	0.026 ns
bio18	0.221	−0.006	0.201 ns
bio19	0.322	0.112	0.412 **



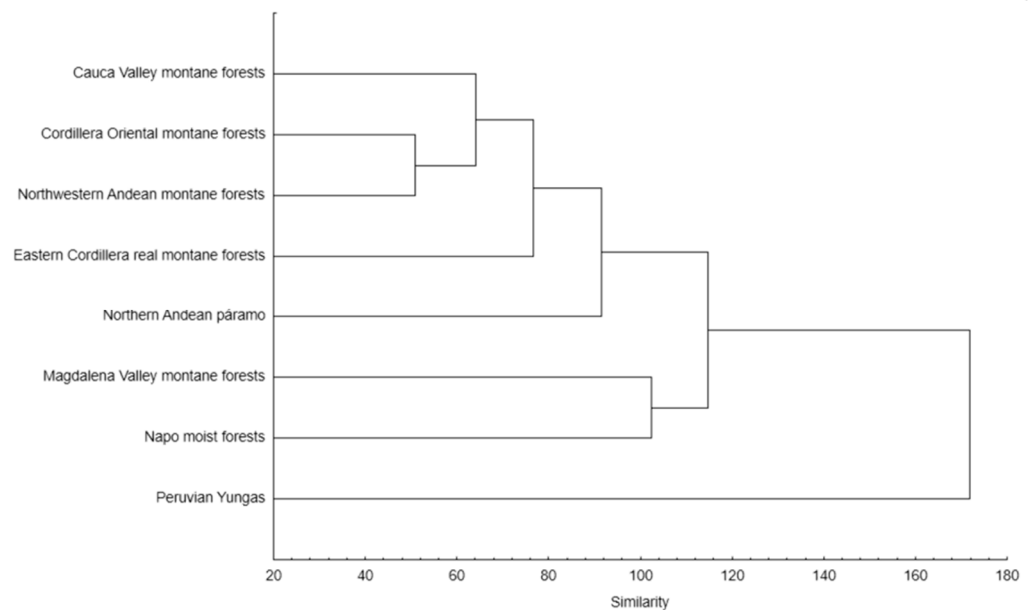
**Figure 10.** Principal component analysis (PCA) of the climatic variables present in the studied species. Variables with the greatest contributions are presented as vectors.



**Figure 11.** Canonical variate analysis (CVA) of the studied species along the climatic gradient. The relative contributions of bioclimatic factors are shown as vectors. Variables with low discriminating impact are omitted.

### 3.3. Biogeography

Two main groups were recognized in the UPGMA dendrogram illustrating the similarity between analyzed ecoregions in the occupied climatic niches (Figure 12). One of them included mountain forests of the Eastern and Oriental Cordillera, the Northwestern Andean montane forests, the Northern Andean páramo, and the Cauca Valley montane forests ecoregions. The second group was comprised of the Magdalena Valley montane forests and the Napo moist forests. The Peruvian Yungas remained separate.



**Figure 12.** The cluster analysis UPGMA of the studied biogeographical ecoregions in terms of bioclimatic variables.

The highest values of the Shannon–Wiener index for taxa belonging to the *Andinia*-complex were obtained in montane forests of the Eastern Cordillera ( $H' = 1.26$ ) and the Northwestern Andean montane forests ( $H' = 1.08$ ). The highest number of *Andinia* representatives was found in the Eastern Cordillera real montane forests (29 species), while *Neooreophilus* species were found in two ecoregions—the Eastern Cordillera real montane forests, and the Northwestern Andean montane forest (20 and 8 species, respectively). According to the level of endemism, a very unique orchid flora was noted in the Guajira–Barranquilla xeric scrub ecoregion, as well as in the Isthmian-Pacific and the Ucayali moist forests, where single endemic species occur (*N. triangularis*, *A. lappacea*, *A. tingomariana*, respectively).

#### 4. Discussion

##### 4.1. Total Evidence Classification

The problem of non-monophyletic taxa is rather common in plant classification, and still numerous recognized genera are not monophyletic [31–34]. Paraphyletic groups are often acknowledged as separated genera mostly because their morphological and ecological characters prevented taxonomist from lumping them into larger, monophyletic taxa. Ideally, a “good” genus should be recognizable in molecular, morphological, and also ecological attributes. Unfortunately, the availability of data on various molecular markers in orchids is still relatively poor and most phylogenetic studies rely on just several barcode loci—ITS, *trnL*, *rbcL*, *matK*, *psbA-trnH*, and *psbK* [35–37]. Incompatibilities between classification systems derived from morphological and molecular analyses, and between phylogenetic trees based on various subsets of molecular sequences has become widespread [38,39]. Tree topology conflicts can be explained either by hybridization or incomplete lineage sorting [40]. The incongruencies between morphological and molecular data were observed in numerous orchids, e.g., with the complex *Erycina–Stacyella–Psycmorchis* [41], genus *Otoglossum* [42], numerous oncidoid orchids [43], and pleurothallids [8,44]. Hopefully, the development and availability of more advanced techniques of DNA analyses will bring some conclusions into Orchidaceae taxonomy [45].

##### 4.2. Classification of *Andinia*

The genus *Andinia* has been recently revised and re-circumscribed by Wilson et al. [15]. The authors described the genus as follows: “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”. We decided to cite expressis verbis Wilson’s et al. [15] definition of *Andinia* s.l. to make evident the problem in identification the unique combination of characters of this genus in its widest concept.

The habit detected in *Andinia* s.l. is not unique at all, as was previously suggested by the authors. There can be distinguished two main habit types. The first one includes species with dangling rhizome, with short, pendulous ramicaul enclosed in typical, lepanthiform sheath(s) with ciliate or echinate margins. They produce orbicular to elliptic leaves, often with ciliate margins and/or upper surface. All of them have lepanthiform flowers with more or less connate sepals, and altered petals covered by various kinds of ciliae or hairs. The lip is simple in form, ecallose, canaliculated, and enclaspings the gynostemium. The gynostemium is also lepanthiform, i.e., footless, terete, with erect anther lying on the dorsal surface of the column, and elongate, subulate rostellum. The stigmatic surface is subapical, horizontal, which facilitates grabbing the pollen mass. As thus can be seen, species of this group are similar to the representatives of *Lepanthes*, and in fact for a long time all



of them have been accommodated in this genus. Archila and Higgins [13] were the first who emphasized differences between this group of species versus other *Lepanthes*, giving them a rank of a separate genus (*Oreophilus* W. Higgins & Archila), but for nomenclatural reason changing it soon to *Neooreophilus* [14]. Except for morphological background, the genus is supported by phylogenetic analyses in which all species belonging here create a monophyletic clade, although with various degrees of support.

Lepanthiform sheaths can be found also in *Lepanthes* and *Trichosalpinx*. Moreover, flowers of *Lepanthes* and *Neooreophilus* are similar in having basally connate sepals which are often widely spread and forming a kind of triangle, modified petals, and surface of various flower segments covered by ciliae or other protuberances. According to Wilson et al.'s [15] phylogenetic analyses, however, these genera and *Neooreophilus* are only distantly related. It is interesting to note that flowers of *Lepanthes–Trichosalpinx* are borne below, whereas in *Neooreophilus* they are above or upon the leaf blade. Phylogenetic studies can suggest independent origin of similar sheaths and other characters in both *Neooreophilus* and *Lepanthes–Trichosalpinx*. In our opinion it is necessary to consider as well a hybrid origin of the genus *Neooreophilus*. The putative parents could be *Lepanthes* and *Andinia* species. It would be interesting to study sequences of other markers than *matK*, ITS, or *rbcL* in a wide spectrum of Pleurothallidinae.

While *Neooreophilus* was not well-sampled, several morphologically consistent groups can be recognized in the phylogenetic tree. The first subclade (B3) (Figures 2–7) includes samples of species with ascending inflorescence borne above the leaf surface. Closely related *N. compositus*, *N. persimilis*, *N. pilosellus*, and *N. platysepalus* are characterized by hirsute or ciliate–denticulate leaves and cucullate dorsal sepal. The group composed by *N. ciliaris* and *N. lynnianius*, which are characterized by glabrous leaves, is sister to *N. wernerii*, which has hirsute or ciliate–denticulate leaves and not cucullate dorsal sepals. The generitype of *Neooreophilus*, *N. nummularius* (B4) (Figures 2, 3, 6 and 7), characterized by transversely ovate to trapeziform lip without an appendix, is sister to *N. stalactites* (B5) (Figures 2, 3, 6 and 7), which is the only representative of the genus having a bilaminate lip with an appendix.

The second large group of species is relatively uniform as the habit is considered and completely different from the aforementioned one. The plants are usually small to even tiny with short, creeping, or ascending rhizome. A short, erect ramicaul is enclosed in tight sheaths. Leaf is narrow, oblong to oblanceolate, always glabrous. Usually the few-flowered inflorescence is erect, rarely reclining, and longer than leaf. Both flower segments and reproductive structures are much more diversified than in *Neooreophilus*, and it is difficult to detect a common character to all of the species belonging here. This is not surprising, as according to the results of molecular analyses, they are paraphyletic, unlike *Neooreophilus*, which is monophyletic and strongly supported.

The clade B1 (Figures 2, 3, 6 and 7) is much more complicated. It is represented in our study by *A. pensilis*, *A. dielsii*, *A. lappacea*, and *A. vestigipetala*. This clade is strongly supported on the trees obtained based on both ITS and combined matrices (Figures 2, 3, 6 and 7), while on the cladograms performed for the *matK* matrix, the relation between these taxa are unsolved (Figures 4 and 5). In fact, it is very difficult to find a common character for such set of species. The only one we could detect are relatively small or even rudimentary petals. It is much easier to single out features characterized for each of them separately. *A. pensilis*, to which we can also classified morphologically very similar *A. dielsii* (a generitype of *Andinia*) and the recently described *A. tingomariana*, have a very peculiar gynostemium form, which can be compared to that found in *Neooreophilus* and which could be described as lepanthiform, i.e., footless, erect, terete, with erect anther lying on its upper surface. The erect rostellum is much elongated, elliptic to oblong, and much exceeding the anther. The stigma is ventral. In all aforementioned species, the lip is basally (or even subapically in *A. tingomariana*) connate with the gynostemium, more or less 3-lobed with both lateral lobes being upcurved and enclaspings the gynostemium.

The subclade 1 (Figures 6 and 7), including *A. pensilis* and *A. dielsii*, is sister to the pair of sample representatives *A. lappacea* and *A. vestigipetala* (Figures 6 and 7), and it has both high value of probability (pp = 0.99) and bootstrap support (BS = 93). A similar situation we observed also on the trees performed on the ITS marker (clade V, Figures 2 and 3).

*Andinia vestigipetala* is unique in Pleurothallidinae in having erect, terete gynostemium, which is connate with rudimentary petals combined with simple, canalculated lip, glabrous, free sepals, and glabrous ovary. *A. lappacea* is characterized by connate lateral sepals, and a subquadrate, ciliate lip, which is basally reflexed and apically emarginated. Sepals are densely ciliate–papillate. The gynostemium is short, clavate, slightly sigmoid, and basally enclaspd by the lip. The ovary is echinate. We cannot find any mutual character for this pair except vestigial petals. The subclade *A. pensilis*, *A. vestigipetala*, and *A. lappacea* is weakly supported with *Neoreophilus* and *A. trimytera*.

However, based on the similarity in morphology of the flowers, the following species can be classified here as well: *A. hystricosa*, *A. panica*, *A. sunchubambensis*, and *A. wayqechensis*. All of them can be characterized by subsimilar sepals, of which both lateral ones are connate together in the lower half, prominent petals (except *A. trimytera*, where they are obscure), and peculiar lip. The lip is sessile, strongly reflexed near the middle, with its basal part enclaspd the gynostemium. Its apical part is deeply 3-lobed, with all lobes being subsimilar, more or less elongate. The central part of the lip is adorned by an elevated callus. The gynostemium is also uniform, i.e., footless, elongate, clavate, apically somewhat bent forward, and the apical clinandrium is obscure, the anther is apical and bent forward, and the rostellum is triangular–ligulate and bent over the stigmatic surface, which is ventral. The ovary is always hispid or muricate. All of these characters are shared by two additional species, *A. pentamytera* and *A. ibex*, despite some differences in their lip morphology (e.g., additional lobules in the sinus between middle and lateral lobes in the former, and two minute calli on the lip with widely spread lateral lobes in the latter one).

The taxa of group A (clade IV Figure 2 and clade C Figure 6) is represented by *A. pogonion*, *A. schizopogon*, and *A. dalstroemii*. In our opinion, two other species should be classified with them, i.e., *A. hirtzii* and *A. uchucayensis*, as they share many common characters. In all of them the ovary is echinate, lateral sepals are basally connate, petals are prominent, linear–lanceolate, acute to long–acuminate or even caudate, and the lip is sessile, gently reflexed near the middle, enclaspd the gynostemium. The lip is suborbicular to elliptic–cordate, apically apiculate, or acute with central thickening. Its upper surface is more or less glandular or warty. The gynostemium is footless, rather short, clavate, somewhat sigmoid, the anther is suberect, the rostellum is short, suberect, and obtuse at the apex, and the ventral stigma is deeply concave. In all species of this group, inflorescence is few-flowered and usually longer than leaf, which is of course not a unique character, as it can be found elsewhere in *Andinia*.

*Andinia spiralis* and *A. xenion* have been classified to the genus *Xenosia* by Luer (2004), and *A. longiserpens* to *Masdevalliantha* by Szlachetko and Margońska [46]. *Xenosia* as originally described included three species, with *Pleurothallis xenion* as the generitype. *Masdevalliantha* included *M. masdevalliopsis* and *M. longiserpens* only. *Xenosia* as proposed by Luer [47] appears to be a paraphyletic taxon in the light of molecular analyses. This impression is intensified by morphology. In the case of this clade we have been dealt a kind of puzzle. The genus *Xenosia* can be characterized by a gynostemium structure, which is elongate, slender, clavate, slightly arcuate, with narrow apical clinandrium, apical, ventral anther, ligulate, incumbent rostellum, and short, baton-like column foot. This is the only mutual characteristic for the species of this genus, as they are different in other aspects of the flower structure. Inflorescence of *X. spiralis*–*X. macrorrhiza* is a few-flowered raceme, longer than leaf, with obtuse sepals, lateral sepals connate almost to the apex, sagittate lip apically papillate, with oblong, central callus. Inflorescence of *X. xenion* is single-flowered, shorter than leaf, the sepals are caudate, free to the base, and the lip is basally 3-lobed with an oblong central callus. Its apical half is densely hairy. The gynostemium morphology and especially the connection between lip and column foot recall the situation found in other

*Xenosia* species. The common character of *Masdevalliantha* is a unique gynostemium morphology, which is short, massive, with long column foot and shelf-like, and massive process elevating rostellum. Especially interesting is the connection between lip and column foot, as the lip is attached on the ventral surface of the column foot, the apex of which is free and becoming accommodated by the basal lip cavity. We have not found such characteristics elsewhere in *Andinia* s.l. species. Flower segments are similar to those found in *X. xenion*, except lateral sepals, which in both *Masdevalliantha* species are basally shortly connate.

Analysis of the distribution of all samples in the climatic space was carried out, where *Andinia*, *Aenigma*, *Masdevalliantha*, and *Lueranthos* were separated. The distribution of all observations in the two-dimensional climatic space indicates that the samples are widespread across the whole climatic space defined by the annual precipitation (bio12) and the temperature seasonality (bio4).

The question arises, what is the sense in creating genera which although monophyletic in terms of sequence of two molecular markers, are impossible to define in terms of morphology? The partial answer can be found in Chase et al. [48]. The authors stated that their “general philosophy in developing the classification of Orchidaceae has been to minimize the number of tribes in order to make the system as simple as possible”. The next question is why they wish to minimize the number of tribes and other taxa? The answer is dumbfounding. They argued that “five is a reasonable number of subfamilies and is easily remembered by everyone”. This argument is difficult to challenge, but we dare to assume that if anyone is not able to remember six or seven subfamilies, that five is also too much to learn. Therefore Chase et al. [48] “have tended to reduce well-supported sister tribes to a single tribe”. We can add that even such taxa are ill-defined. From the other papers they published, we can guess that it is a general rule they try to implement into the orchid classification on various taxonomic levels and is followed by other authors. In this case, it is less important whether the group can be defined in terms of morphology or not. Much more important is whether they are monophyletic in terms of one or another molecular marker, and it is completely unimportant whether it is possible to propose a key to determination of taxa distinguished in such an odd manner. Moreover, Górniak et al. [39] was trying to prove that the topology of phylogenetic tree depends on the number of markers used in analyses and different taxonomic units could be proposed based on different tree topologies obtained.

To the best of our knowledge, the molecular marker used in analysis shows the phylogeny of this particular marker, and its extrapolation to the pattern of phylogeny of the entire organisms seems to be malfeasance. Furthermore, different markers can show different evolutionary paths which quite often are incongruent. In this case, which marker is more important?

Because all the above-mentioned morphologically uniform species groups form separated clades according to the results of phylogenetic analyses conducted by Wilson et al. [15], we propose to split *Andinia* s.l. into several genera, easily definable in terms of morphology and hence recognizable: *Aenigma*, *Andinia*, *Chicalia*, *Lueranthos*, *Masdevalliantha*, *Minuscula*, *Neooreophilus*, *Xenosia*, and *Xenosiella*. Most of these taxa were previously considered as valid genera, and we believe that there is no reason to lump them into a single ill-defined genus. The taxonomic decisions presented here were made primarily on the basis of morphology, with DNA data demonstrating congruence with the morphological distinctions.

#### 4.3. Taxonomic Treatment

##### Key to genera of *Andinia*-complex

1. Gynostemium footless or foot rudimentary . . . 2
- 1\* Gynostemium with prominent column-foot . . . 6
2. Plants pendent, leaves appearing alternating and often overlapping . . . 1. *Neooreophilus*
- 2\* Plants ascending or caespitose, leaves not appearing alternating and overlapping . . . 3
3. Inflorescence single-flowered . . . 4. *Chicalia*
- 3\* Inflorescence few-flowered . . . 4

4. Petals prominent . . . 2. *Aenigma*
- 4\* Petals much smaller than sepals . . . 5
5. Lip erect, canaliculate, petals rudimentary, minutely papillate along margins, fused with the base of the column part and tightly adnate to it . . . 5. *Lueranthos*
- 5\* Lip and petals not as above . . . 3. *Andinia*
6. Ovary muricate . . . 6. *Minuscula*
- 6\* Ovary glabrous . . . 7
7. Inflorescence few-flowered . . . 9. *Xenosiella*
- 7\* Inflorescence single-flowered . . . 8
8. Lip motile, base with prominent cavity accommodating free apex of the column foot . . . 7. *Masdevalliantha*
- 8\* Lip deeply 3-lobed at the base, firmly fixed on the apex of the column foot . . . 8. *Xenosia*

#### 1. *Neoreophilus* Archila

Revista Guatemalensis 12(2): 73. 2009; Generitype: *Neoreophilus nummularius* (Rchb.f.) Archila [= *Lepanthes nummularia* Rchb. f.]. ≡ *Lepanthes* sect. *Brachycladae* Rchb. f., Xenia Orchid. 1: 142. 1856. ≡ *Lepanthes* subgen. *Brachycladium* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 15: 31. 1986. ≡ *Oreophilus* W. E. Higgins & Archila, Revista Guatemal. 12(2): 73. 2009, *nom. illeg.* ≡ *Penducella* Luer & Thoerle, Orchid Digest 74(2): 68. 2010, *nom. illeg.*

Plants pendent, delicate, with rarely branching rhizome, rooting occasionally. Ramicaul obscure, terete, enclosed in 1–2 lepanthiform sheaths. Leaf much longer than ramicaul, elliptic to suborbicular, hispid to ciliate all over, all glabrous, with prominent venation. Few-flowered inflorescence usually shorter than leaf. Flowers typically lepanthiform, with sepals dissimilar or subsimilar in form and size, variously connate, lateral ones sometimes almost completely united together, more or less papillate or ciliate. Petals distinctly smaller than sepals, sometimes rudimentary, variously formed, longer than wide, or wider than long, entire or lobed, ciliate, papillate or with other protuberances. Lip shortly clawed to sessile, ecallose, with more or less auriculate base, lateral lobes upcurved, enveloping the gynostemium, ciliate or papillate. Gynostemium short, erect, terete, column foot missing, stigma subapical, horizontal, rostellum elongate, subulate or digitate, much exceeding the anther, erect or upcurved, anther erect, dorsal, ellipsoid, pollinia clavate, viscidium large, plate-like.

Three clearly separated assemblages in *Neoreophilus* can be distinguished based on morphological data and outcomes of molecular analyses, and these groups are presented here as subgenera. To facilitate identification of representatives within the largest subgenus, *Amplectentes*, this taxon was further divided into sections. However, it is important to emphasize the poor sampling of *Neoreophilus* that complicates comparison of morphological data with phylogenetic relationships. Based on similarity of related species, the more complicated division of the genus could be conducted based, for example, on petal form. More comprehensive molecular study is required to propose formal sectional division of the largest subgenus of *Neoreophilus*.

#### Key to subgenera of *Neoreophilus*

1. Inflorescence reclining, borne upon the leaf surface . . . 2
- 1\* Inflorescence ascending, borne above the leaf surface . . . 1.1. *Neoreophilus* subgen. *Amplectentes*
2. Lip bilaminar with an appendix . . . 1.2. *Neoreophilus* subgen. *Bilamellatae*
- 2\* Lip transversely ovate to trapeziform in outline, without an appendix . . . 1.3. *Neoreophilus* subgen. *Neoreophilus*

##### 1.1. Subgenus *Amplectentes* (Luer) Kolan. & Szlach., *stat. et comb. nov.*

Basionym: *Lepanthes* sect. *Amplectentes* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 52: 3. 1994. ≡ *Andinia* sect. *Amplectentes* (Luer) Karremans & S. Vieira-Urbe, Phytotaxa 295(2): 123. 2017. Type: *Lepanthes pilosella* Rchb. f., Flora 69: 556. 1886.

This is the largest subgenus of *Neoreophilus*. Three species groups can be distinguished within this subgenus.

***Neoreophilus ciliaris*-group**

This group is characterized by glabrous leaves. Species included in this group:

- *Neoreophilus ariasianus* (Luer & L.Jost) Archila, *Revista Guatemalensis* 12(2): 73 (-74). 2009.
- *Neoreophilus bifidus* Tobar & Archila, *Revista Guatemalensis* 15(2): 2, Figures 1 and 2. 2012.
- *Neoreophilus chaoae* S.V.Uribe & L.Jost, *Lankesteriana* 15(3): 213. 2015.
- *Neoreophilus chelosepalus* (Luer & Hirtz) Archila, *Revista Guatemalensis* 12(2): 76. 2009.
- *Neoreophilus ciliaris* (Luer & Hirtz) Archila, *Revista Guatemalensis* 12(2): 76. 2009.
- *Neoreophilus cordilabius* (Luer) Archila, *Revista Guatemalensis* 12(2): 77. 2009.
- *Neoreophilus dentatus* Archila, *Revista Guatemal.*, 17(1): 41. 2014.
- *Neoreophilus destitutus* (Luer & R.Escobar) Archila, *Revista Guatemalensis* 12(2): 78. 2009.
- *Neoreophilus lunaris* (Luer) Archila, *Revista Guatemalensis* 12(2): 81. 2009.
- *Neoreophilus lynnianus* (Luer) Archila, *Revista Guatemalensis* 12(2): 81. 2009.
- *Neoreophilus macroticus* (Luer & Dalström) Archila, *Revista Guatemalensis* 12(2): 82. 2009.
- *Neoreophilus ortizianus* S.V.Uribe & Thoerle, *Orquideologia* 28(2): 135 (-139; fig.; photogr.). 2011.
- *Neoreophilus pendens* (Garay) Archila, *Revista Guatemalensis* 12(2): 84. 2009.
- *Neoreophilus pholeter* (Luer) Archila, *Revista Guatemalensis* 12(2): 85.
- *Neoreophilus ricii* (Luer & R.Vásquez) Archila, *Revista Guatemalensis* 12(2): 86. 2009.
- *Neoreophilus triangularis* (Luer) Archila, *Revista Guatemalensis* 12(2): 87. 2009.
- *Neoreophilus vieira-perezianus* P.Ortiz, *Orquideologia* 28(1): 7 (-10; Figure 1; photogr.). 2011.

**1.1.2. *Neoreophilus pilosellus* group**

This group is characterized by hirsute or ciliate–denticulate leaves and cucullate dorsal sepal. It includes:

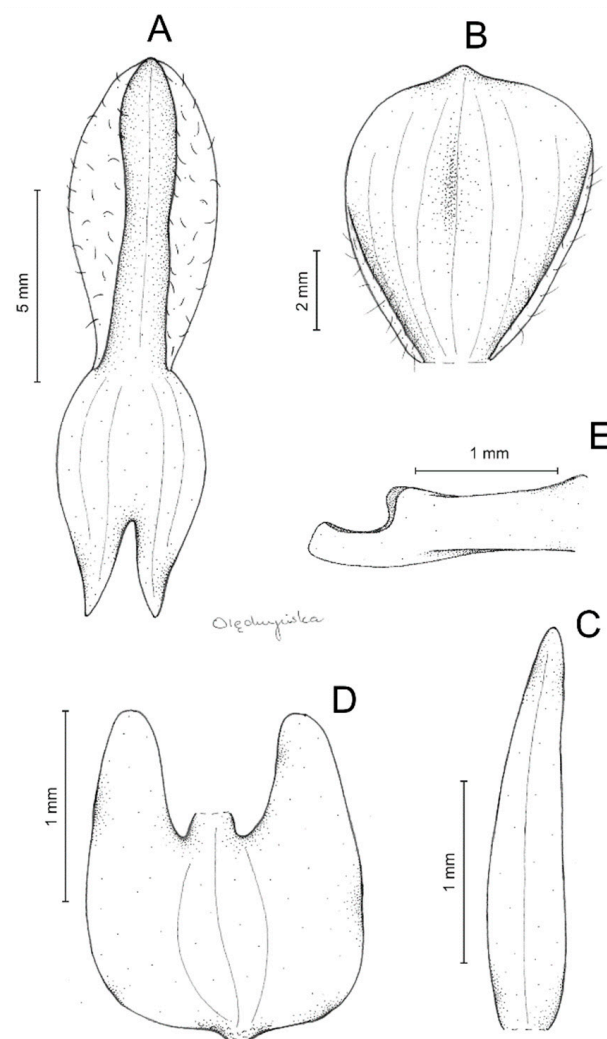
- *Neoreophilus cardiochilus* (Luer & R.Escobar) Archila, *Revista Guatemalensis* 12(2): 75. 2009.
- *Neoreophilus chilopsis* (Luer & Hirtz) Archila, *Revista Guatemalensis* 12(2): 76. 2009.
- *Neoreophilus compositus* (Luer & R.Escobar) Archila, *Revista Guatemalensis* 12(2): 77. 2009.
- *Neoreophilus erepsis* (Luer & Hirtz) Archila, *Revista Guatemalensis* 12(2): 78. 2009.
- *Neoreophilus lunatocheillus* Tobar & Archila, *Revista Guatemalensis* 15(2): 26, Figure 3. 2012.
- *Neoreophilus mongei* Tobar & Archila, *Revista Guatemalensis* 15(2): 23, Figure 2. 2012.
- *Neoreophilus octocornutus* (Luer) Archila, *Revista Guatemalensis* 12(2): 84. 2009.
- *Neoreophilus persimilis* (Luer & Sijm) Archila, *Revista Guatemalensis* 12(2): 84. 2009.
- *Neoreophilus phalicus* Tobar & Archila, *Revista Guatemalensis* 15(2): 20, Figure 1. 2012.
- *Neoreophilus pilosellus* (Rchb.f.) Archila, *Revista Guatemalensis* 12(2): 85. 2009.
- *Neoreophilus platysepalus* (Luer & R.Escobar) Archila, *Revista Guatemalensis* 12(2): 85. 2009.
- *Neoreophilus tridactylus* (Luer) Archila, *Revista Guatemalensis* 12(2): 88. 2009.
- *Neoreophilus ursulus* (Luer & R.Escobar) Archila, *Revista Guatemalensis* 12(2): 88. 2009.
- *Neoreophilus viebrockianus* (Luer & L.Jost) Archila, *Revista Guatemalensis* 12(2): 89. 2009.
- *Neoreophilus villosus* (Løjtnant) Archila, *Revista Guatemalensis* 12(2): 89. 2009.

***Neoreophilus medinae* Kolan. & Szlach., sp. nov.** TYPE: Colombia. Dept. Putumayo. Vereda Balsayaco, near San Andres. Alt. 1984 m. 7 September 2016. R. Medina T. S14/28 (holotype, JAUM!; MEDEL!—photos).

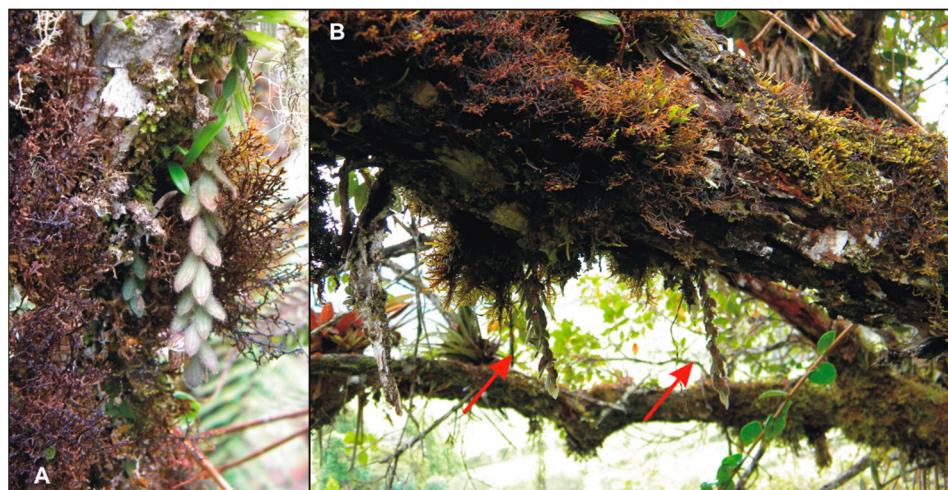
[urn:lsid:ipni.org:names:xxxxxxx-x]

*Species similar to N. platysepalus, N. ursulus, and N. pilosellus, distinguished by relatively shortly connate lateral sepals and prominent lip auricles. Moreover, from N. platysepalus and N. pilosellus, the new entity differs additionally by the lip and externally densely ciliate dorsal sepal.*

Epiphytic plant, up to 15 cm long in total; ramicauls spaced 4–5 mm, each segment enclosed by two imbricating, membranaceous, infundibular sheaths, ciliate along the ribs, with dilated, ciliated ostia. Ramicauls 0.8–1.1 mm long, enclosed by a single membranaceous, infundibular sheath ciliate along the ribs, with dilated, ciliate ostia. Leaves shortly petiolate; petiole 0.7–1 mm long; blade 9–10 mm long, 3.5–4 mm wide, elliptic to ovate-elliptic, subacute to acute, densely ciliate, 3-nerved, lateral veins sometimes dichotomous. Inflorescence borne upon the surface of leaf, single-flowered; floral bract about 0.5 mm long, infundibular, oblique, acuminate, membranaceous; pedicel slender, persistent, 1.5–2 mm long; ovary ciliate, about 1 mm long. Flower small, sepals light yellow with dark red stripes, dorsal sepal mottled with purple along veins, petals light yellow with purple stripe, lip light yellow with 3 purple veins. Dorsal sepal concave in the natural position,  $7.5 \times 6$  mm when expanded, broadly obovate, with a small, obtuse apiculus, 5- or 7-veined, externally densely ciliate. Lateral sepals  $7 \times 4$  mm, connate for about 4 mm, narrowly ovate, obtuse, 2-veined, externally glabrous. Petals  $2-2.1 \times 0.4$  mm, oblong-lanceolate to linear-lanceolate, basally cuneate, obtuse, 1-veined, glabrous. Lip embracing the column in the natural position,  $1.7 \times 1.5$  mm when expanded, subsessile, lamina subrectangular with prominent basal projections  $0.7 \times 0.5$  mm, apical part truncate with a small, obtuse apiculus and here glandular-ciliate, margin glabrous, disc 3-veined, glabrous. Gynostemium about 2 mm long, terete, anther and stigma apical (Figures 13 and 14).



**Figure 13.** *Neoreophilus medinae* Kolan. & Szlach.—dissected perianth. (A)—sepals, (B)—dorsal sepal, (C)—petal, (D)—lip, (E)—gynostemium. Drawn by N. Olędrzyńska from the holotype.



**Figure 14.** *Neoreophilus medinae* Kolan. & Szlach.—plant in situ. (A)—plant habit, (B)—plants hanging on a branch covered by mosses in natural habitat.

**Etymology:** Dedicated to Ramiro Medina Trejo, an orchid enthusiast who collected and cultivated new species.

**Distribution, habitat and ecology:** So far, *Neoreophilus medinae* is known only from the type locality in southern Colombia, where it was found on the mossy trunk and large branches of the tree in the pasture at the altitude of almost 2000 m. The population consists of about 50 specimens and its individuals grow sympatrically with specimens of *N. pseudocaulescens*. Flowering occurs in September.

**Notes.** *Neoreophilus medinae* resembles Colombian *N. platysepalus*, *N. pilosellus*, and *N. ursulus*, but the prominent basal projections of the lip allow one to easily distinguish it from the aforementioned species. In both *N. pilosellus* and *N. ursulus*, the lateral sepals are long-connate, free only at the apices. The most similar species is *N. platysepalus* known from the Colombian department of Antioquia, which is characterized by the glabrous sepals and small lip that is wider than long (1–1.25 × 1.5 mm), subquadrate to transversely subcordate, rounded to subtruncate at the apex, and minute basal projections. The lateral sepals of this species are connate in the basal 3/4–4/5.

**Conservation status.** Considering that about 50 specimens were found, the threat category according to IUCN [49] criterion D swings between Critically Endangered (CR) and Endangered (EN), while for the definition of the category according to criterion B data are missing on possible decline and fluctuations. Therefore, more in field research would be useful for the definition of distribution, population size, locations (*sensu* IUCN) and threats. In fact, new described species with a restricted distribution could be attributed to different IUCN categories, as Critically Endangered (CR) according to criterion B [50], or Vulnerable (VU) under criterion D [51,52].

### 1.1.3. *Neoreophilus weneri*-group

This group is characterized by hirsute or ciliate–denticulate leaves, not cucullate dorsal sepal, and variously connate, spreading lateral sepals. It includes:

- *Neoreophilus catellus* (Luer & R.Escobar) Archila, Revista Guatemalensis 12(2): 75. 2009.
- *Neoreophilus dactylus* (Garay) Archila, Revista Guatemalensis 12(2): 78. 2009.
- *Neoreophilus exiguus* (Luer & Hirtz) Archila, Revista Guatemalensis 12(2): 79. 2009.
- *Neoreophilus geminipetalus* (Luer & J.Portilla) Archila, Revista Guatemalensis 12(2): 79. 2009.
- *Neoreophilus hippocrepicus* (Luer & R.Escobar) Archila, Revista Guatemalensis 12(2): 80. 2009.
- *Neoreophilus irrasus* (Luer & R.Escobar) Archila, Revista Guatemalensis 12(2): 80. 2009.
- *Neoreophilus lueri* (S.V.Uribe & Karremans) Kolan. & Szlach., *comb. nov.*

- Basionym: *Andinia lueri* S.V.Uribe & Karremans, *Orquideologia* 33: 116. 2016.
- *Neoreophilus lupulus* (Luer & Hirtz) Archila, *Revista Guatemalensis* 12(2): 81. 2009.
- *Neoreophilus micropetalus* (L.O.Williams) Archila, *Revista Guatemalensis* 12(2): 82. 2009.
- *Neoreophilus monilius* (Luer & R.Escobar) Archila, *Revista Guatemalensis* 12(2): 83. 2009.
- *Neoreophilus montis-rotundus* (P.Ortiz) Archila, *Revista Guatemalensis* 12(2): 83. 2009.
- *Neoreophilus pseudocaulescens* (L.B.Sm. & S.K.Harris) Archila, *Revista Guatemalensis* 12(2): 86. 2009.
- *Neoreophilus rotundus* Archila, *Revista Guatemal.* 17(1): 42. 2014.
- *Neoreophilus sibundoyensis* Kolan., *Ann. Bot. Fenn.* 50(3): 170. 2013.
- *Neoreophilus sudamericanus* Archila, *Revista Guatemal.*, 17(1): 40. 2014.
- *Neoreophilus wernerii* (Luer) Archila, *Revista Guatemalensis* 12(2): 89. 2009.

#### *Incertæ sedis*

Due to the lack of sufficient information about morphological characters of the following species we were not able to assign them into any of the groups listed above:

- *Neoreophilus auriculatus* Archila, *Revista Guatemal.* 17(1): 44. 2014.
- *Neoreophilus caveroi* (D.E. Benn. & Christenson) Archila, *Revista Guatemal.* 12(2): 76. 2009.
- *Neoreophilus roseus* Archila, *Revista Guatemal.* 17(1): 43. 2014.

#### 1.2. **Subgenus *Bilamellatae*** (Luer) Kolan. & Szlach., *stat. et comb. nov.*

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

This group is characterized by the inflorescence reclining, borne upon the leaf surface and bilaminate lip with an appendix.

- *Neoreophilus stalactites* (Luer & Hirtz) Archila, *Revista Guatemalensis* 12(2): 87. 2009.

#### 1.3. **Subgenus *Neoreophilus***

This group is characterized by the inflorescence reclining, borne upon the leaf surface and transversely ovate to trapeziform lip without an appendix.

- *Neoreophilus nummularius* (Rchb.f.) Archila, *Revista Guatemalensis* 12(2): 83. 2009.
- *Neoreophilus obesus* (S.V.Uribe & Karremans) Kolan. & Szlach., *comb. nov.*

Basionym: *Andinia obesa* S.V.Uribe & Karremans, *Lankesteriana* 17: 311.2017.

#### 2. ***Aenigma*** (Luer) Szlach. & Kolan., *stat. et comb. nov.*

Basionym: *Pleurothallis* subgen. *Aenigma* Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 20: 26. 1986. ≡ *Andinia* subgen. *Aenigma* (Luer) Karremans & M. Wilson, *Phytotaxa* 295(2): 121. 2017. Generitype: *Aenigma schizopogon* (Luer). Szlach. & Kolan. [≡ *Pleurothallis schizopogon* Luer].

All species small, with somewhat elongate and ascending rhizome, producing ramicauls in short distance. Ramicaul short, terete, enveloped in 1 tight sheath. Leaf oblong, glabrous. Inflorescence longer than leaf, few-flowered, with flowers opening in succession. Ovary muricate, pedicel glabrous. Lateral sepals connate in the lower half, more or less acuminate, glabrous, or hispid. Petals prominent, linear-lanceolate, acuminate, as long as sepals, but distinctly narrower. Lip sessile, firmly connate with the column foot, more or less reflexed just above the base, enveloping the gynostemium, with prominent calli in the center, suborbicular to pentagonal in outline, shortly apiculate in the apex. Gynostemium erect to somewhat arcuate, clavate, column foot rudimentary, stigma subapical, rostellum blunt, short, rounded at the apex, anther subapical to subventral, suberect, ovoid-ellipsoid. The genus includes:

- *Aenigma dalstroemii* (Luer) Szlach. & Kolan., *comb. nov.*  
Basionym: *Pleurothallis dalstroemii* Luer, *Orchideer* 5: 52. 1984.
- *Aenigma hirtzii* (Luer) Szlach. & Kolan., *comb. nov.*  
Basionym: *Andinia hirtzii* Luer, *Monogr. Syst. Bot. Missouri Bot. Gard.* 103: 275. 2005.
- *Aenigma pogonion* (Luer) Szlach. & Kolan., *comb. nov.*



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

- *Aenigma schizopogon* (Luer) Szlach. & Kolan., comb. nov.

Basionym: *Pleurothallis schizopogon* Luer, Lindleyana 16(4): 251. 2001.

- *Aenigma uchucayensis* (A.Doucette & J.Portilla) Szlach. & Kolan., comb. nov.

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

### 3. *Andinia* (Luer) Luer

Monogr. Syst. Bot. Missouri Bot. Gard. 79: 5. 2000. ≡ *Salpistele* subgen. *Andinia* Luer, (Monogr. Syst. Bot. Missouri Bot. Gard. 39: 124. 1991; Generitype: *Andinia dielsii* (Mansf.) Luer [≡ *Lepanthes dielsii* Mansf.].

Plants with elongate rhizome, producing ramicauls in prominent intervals. Ramicaul short, terete, enclosed in 1–2 tight sheaths. Leaf oblong elliptic, glabrous. Multiflowered inflorescence much longer than leaf. The flowers produced in succession, broadly opened. Ovary muricate, or glabrous, pedicellate. Sepals subsimilar in size and form, shortly acuminate, mucronate, ciliate, or glabrous along margins, lateral sepals connate in the lower half or free to the base. Petals much smaller than sepals. Lip simple, 3-lobed, basally or subapically united with the gynostemium, lateral lobes upcurved, enveloping the gynostemium, with prominent callus in the center or ecallose. Gynostemium erect, slender, terete, column foot missing, stigma ventral, emarginate, anther subdorsal, erect, ovoid, rostellum elongate, ligulate, erect, much exceeding the anther.

The genus includes:

- *Andinia dielsii* (Mansf.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 6. 2000.
- *Andinia pensilis* (Schltr.) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 6. 2000.
- *Andinia tingomariana* A.G. Diaz & Mark Wilson, Phytotaxa 361(2): 223–227. 2018.

### 4. *Chicalia* Szlach. & Kolan., gen. nov.

Generitype: *Chicalia lappacea* (Luer) Szlach. & Kolan. [≡ *Pleurothallis lappacea* Luer]

Etymology: In reference to Chical, Carchi, Ecuador, where the type specimen of *P. lappacea* was collected.

Plants very small, subcaespitose. Ramicaul obscure, enclosed in 1 tight sheath. Leaf elliptic, glabrous. Single-flowered inflorescence longer than leaf, produces relatively large, broadly opened flower. Ovary densely muricate, pedicellate. Sepals subsimilar in size, papillate all over except central and basal parts, lateral sepals connate together almost to the apex forming a kind of platform, supporting lip. Petals rudimentary, with ciliate margins. Lip sessile, subquadrate in outline, reflexed just above the base, enveloping partially the gynostemium, with prominently emarginate apex. Its surface ciliate–glandular, except the central and apical portions. Gynostemium rather short, clavate, subsigmoid, with obscure column foot, anther apical, incubment ellipsoid, rostellum subapical, short, obscure, stigma subapical.

The genus includes:

- *Chicalia lappacea* (Luer) Szlach. & Kolan., comb. nov.

Basionym: *Pleurothallis lappacea* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 79: 129, f. 5. 2000.

### 5. *Lueranthos* Szlach. & Marg.

Polish Bot. J. 46(2): 117. 2001 [2002]; Generitype: *Lueranthos vestigipetalus* (Luer) Szlach. & Marg. [≡ *Pleurothallis vestigipetala* Luer].

Plants with elongate, ascending rhizome. Ramicaul short, terete, enclosed in tight sheath. Inflorescence few-flowered, somewhat longer than leaf. Flowers produced in succession with glabrous ovary and broadly opened sepals free to the base. Sepals similar in size and form. Petals rudimentary, minutely papillate along margins, fused with the base of the column part and tightly adnate to it. Lip erect, canaliculate, oblong–elliptic, ecallose, simple, more or less papillate all over. Gynostemium erect, terete, slender, elongate,

footless, with subapical, incumbent anther and short rostellum. Anther oblong ovoid. Stigma apical, horizontal.

This monotypic taxon includes:

- *Lueranthos vestigipetalus* (Luer) Szlach. & Marg., Polish Bot. J. 46(2): 117. 2001 [2002].

#### 6. *Minuscula* Szlach. & Kolan., *gen. nov.*

Generitype: *Minuscula trimytera* (Luer & R. Escobar) Szlach. & Kolan. [≡ *Pleurothallis trimytera* Luer & R. Escobar].

Etymology: From *minusculus* (Lat.)—small, tiny. An allusion to the size of species of this group.

Plants miniature, with very short, creeping rhizome or caespitose. Ramicaul obscure, terete, enclosed in 1 tight sheath. Leaf elliptic, shortly apiculate, glabrous. The inflorescence longer than leaf; 1-(2)-flowered. Flower broadly opened. Ovary muricate, pedicellate. Sepals subsimilar in form and size, glabrous, papillate or glandular in the basal part or all over, lateral sepals connate in the lower half, occasionally free. Petals shorter and narrower than sepals, occasionally rudimentary. Lip shortly clawed, transversely elliptic, deeply 3-lobed at the apex, geniculately bent forward, thickened in the center, concave below, rarely calli obscure. Gynostemium slightly sigmoid, clavate, column foot short, apical clinandrium obscure, anther apical, incumbent, oblong ovoid, stigma ventral, rostellum ventral, triangular, more or less incumbent.

The genus includes:

- *Minuscula hystricosa* (Luer) Szlach. & Kolan., *comb. nov.*

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

- *Minuscula ibex* (Luer) Szlach. & Kolan., *comb. nov.*

Basionym: *Pleurothallis ibex* Luer, Selbyana 5(2): 168 (–169). 1979.

- *Minuscula panica* (Luer) Szlach. & Kolan., *comb. nov.*

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

- *Minuscula pentamytera* (Luer) Szlach. & Kolan., *comb. nov.*

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

- *Minuscula sunchubambensis* (A. Doucette & Janovec) Szlach. & Kolan., *comb. nov.*

Basionym: *Andinia sunchubambensis* A. Doucette & Janovec, Internet Orchid Sp. Photo Encycl. Nomencl. Notes 2016: f. 1A–G, 2–3. 2016.

- *Minuscula trimytera* (Luer & R. Escobar) Szlach. & Kolan., *comb. nov.*

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

#### 7. *Masdevalliantha* (Luer) Szlach. & Marg.

Polish Bot. J. 46(2): 117. 2001. ≡ *Pleurothallis* subgen. *Masdevalliantha* Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 20: 44. 1986. ≡ *Andinia* subgen. *Masdevalliantha* (Luer) Karremans & M. Wilson, Phytotaxa 295(2): 125. 2017; Generitype: *Masdevalliantha masdevalliopsis* (Luer) Szlach. & Marg. [≡ *Pleurothallis masdevalliopsis* Luer].

Subcaespitose plant, with 1-flowered inflorescence longer than leaf. Ramicaul short, terete, with tight sheath. Flowers broadly opened. Sepals subsimilar in form and size, long-caudate, lateral sepals connate basally. Petals orbicular to obtriangular, much smaller than sepals. Lip motile, more or less 3-lobed, base with prominent cavity accommodating free apex of the column foot, apical part of the middle lobe hairy or hispid, callus single, oblong, or bifid. Gynostemium short, massive, suberect, rostellum elongate, oblong–triangular, perpendicular to the column axis, column foot long, upcurved with the lip attached below its apex, which is placed in the cavity at the lip base. Anther subapical, suberect, ovoid, relatively small. Stigma ventral.

The genus includes:

- *Masdevalliantha longiserpens* (C. Schweinf.) Szlach. & Marg., Polish Bot. J. 46(2): 117. 2001.
- *Masdevalliantha masdevalliopsis* (Luer) Szlach. & Marg., Polish Bot. J. 46(2): 117. 2001.

#### 8. *Xenosia* Luer

Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004; Generitype: *Xenosia xenion* (Luer & R. Escobar) Luer [= *Pleurothallis xenion* Luer & R. Escobar].

Etymology: In reference to the similarity to the genus *Xenosia*.

Plants miniature. Rhizome shortly repent. Ramicaul filiform, tightly enclosed in 1 sheath. Leaf linear-lanceolate, glabrous. Inflorescence shorter than leaf, single-flowered. Flowers broadly opened. Ovary glabrous, pedicellate. Sepals subsimilar in form and size, free to the base, long-caudate. Petals deltoid, prominently smaller than sepals. Lip deeply 3-lobed at the base, firmly fixed on the apex of the column foot, with basal lateral lobes obliquely rhombic, and oblong callus in the center, the middle lobe densely pubescent. Gynostemium slender, elongate, terete, apically somewhat arcuate. Apical clinandrium narrow. Column foot elongate, robust. Anther apical, incumbent, ovoid. Rostellum ventral, ligulate, incumbent. Stigma ventral.

The genus includes one species:

- *Xenosia xenion* (Luer & R. Escobar) Luer, Monogr. Syst. Bot. Missouri Bot. Gard. 95: 265. 2004.

#### 9. *Xenosiella* Szlach. & Kolan., *gen nov.*

Generitype: *Xenosiella spiralis* (Ruiz & Pav.) Szlach. & Kolan. [= *Humboltia spiralis* Ruiz & Pav.]

Plants with elongate, ascending rhizome. Pseudobulbs terete, short, enclosed in tight sheath. Leaf ligulate, glabrous. Inflorescence shorter than leaf, few-flowered. Flowers tubular borne in succession. Ovary glabrous, pedicellate. Sepals subsimilar in size and form, obtuse, glabrous, lateral sepals connate together in the basal 2/3, forming a kind of platform below lip. Petals oblong-ovate, much smaller than sepals. Lip firmly attached to the column foot, deltoid-ovate in outline, canaliculate, obscurely 3-lobed, with oblong callus in the center and papillate apical lobe. Gynostemium elongate, slender, clavate, with prominent, slightly upcurved column foot. Anther ventral, ellipsoid, pollinia 2, ovoid. Rostellum ligulate, obtuse, incumbent. Viscidium plate-like. Stigma ventral.

The two species classified in this genus are probably synonymic as the only noticeable difference between them is the lip base (cuneate in *X. spiralis* and rounded-broadly cuneate in *X. macrorhiza*). The genus includes:

- *Xenosiella macrorhiza* (Lindl.) Szlach. & Kolan., *comb. nov.*

Basionym: *Pleurothallis macrorhiza* Lindl., Monogr. Syst. Bot. Missouri Bot. Gard. 105: 233–234, f. 185. 2006.

- *Xenosiella spiralis* (Ruiz & Pav.) Szlach. & Kolan., *comb. nov.*

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

## 5. Conclusions

Molecular analyses clearly show a monophyly of the genus *Andinia* s.l. The genus is intangible, however, in morphological terms. High diversity in the flower and gynostemium structure can be interpreted as an adaptation to various pollination systems. We do not have sufficient information on pollination strategy of the species of the *Andinia*-complex, but we can assume that multifarious structure of the flowers can be attractive to different species of insects. The differences in the temperature seasonality, the annual precipitation, and the precipitation of the warmest and the coldest quarters, which differentiate species of the *Andinia*-complex, can also affect a species composition of potential pollinators. In our opinion, separation of monophyletic, smaller, but morphologically well-supported genera is unreservedly legitimate. It appeared that they represents closely related taxa which were

derived from a common ancestor. Unfortunately, it is difficult to define the relationship between these groups. It is likely that each evolved independently from the other. Perhaps this was due to climatic factors or the result of adaptation to different habitats.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d14050372/s1>, Annex S1: Morphological characters of *Andinia*-complex representatives; Annex S2: List of localities of *Andinia*-complex representatives with bioclimes values for each record; Annex S3: Ecoregions corresponding to localities of *Andinia*-complex representatives.

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