

*ANASTROPHYLLUM ASTORGAE* (ANASTROPHYLLACEAE, MARCHANTIOPHYTA),  
A NEW SPECIES FROM CHILE

*ANASTROPHYLLUM ASTORGAE* (ANASTROPHYLLACEAE, MARCHANTIOPHYTA),  
НОВЫЙ ВИД ИЗ ЧИЛИ

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Abstract

A new species of the genus *Anastrophyllum* (Spruce) Steph. is described from the Los Lagos Region, Chile using integrative taxonomic approach. The new species differs from all members of the genus by the very small size and *Cephaloziella*-like habit, deeply bilobed and entire-margined leaves, and the equally thickened walls of leaf cells.

Резюме

Новый для науки вид рода *Anastrophyllum* (Spruce) Steph. описан из области Лос-Лагос Республики Чили на основе интегративного подхода. Новый вид отличается от всех видов рода мелкими размерами, обликом побегов сходным с видами рода *Cephaloziella* (Spruce) Schiffn., а также глубоко вырезанными цельнокрайными листьями и равноутолщенными стенками клеток листьев.

KEYWORDS: ITS1-2, integrative approach, liverworts, Patagonia, taxonomy, *trnL*-F, *trnG*-intron

INTRODUCTION

The modern diversity of the genus *Anastrophyllum* (Spruce) Steph. s.l. (including *Schizophyllopsis* Váňa & L.Söderstr. and *Zantenia* (S.Hatt.) Váňa & J.J.Engel, but without *Anastrophyllopsis* (R.M.Schust.) Váňa & L.Söderstr.) remains an open question due to the limited molecular phylogenetic data and unresolved taxonomic issues connected with the narrow or broad concepts of several taxa. According to Söderström *et al.* (2015), there are 26 species in *Anastrophyllum* s.l., including five species of *Schizophyllopsis* and four of *Zantenia*. However, many of these species have numerous synonyms; for example, the Patagonian *Anastrophyllum crebrifolium* (Taylor & Hook.f.) Steph., *A. crenulatum* R.M.Schust., *A. semifissum* Steph., and the New Zealand *A. novazelandiae* R.M.Schust. have been synonymized with *A. auritum* (Lehm.) Steph. in Váňa *et al.* (2013a) and are not cited in Söderström *et al.* (2015). In general, *A. auritum* includes 32 synonyms (according to Tropicos database), however the conspecificity of some synonyms may be called into question. Resolving of the taxonomic issues in *Anastrophyllum* s.l. is complicated since the only fragmentary data concerning 14 species of the genus with different composition of DNA markers are available from early studies of Jungermanniales (Schill *et al.*, 2004; de Roo *et al.*, 2007; Vilnet *et al.*, 2010; Mamontov & Vilnet,

2013; Feldberg *et al.*, 2013). The aim of the presented study is to compete the nucleotide sequence data on *Anastrophyllum* species recently gathered in the Aysén and Los Lagos Regions of Chile, to reveal their phylogenetic affinity and morphological divergence, and to provide description of a new species *A. astorgae* sp. nov. discovered with the use of an integrative taxonomic approach.

MATERIAL AND METHODS

**Morphological study.** Plant material was studied and photographed using a Leitz Wetzlar Orthoplan light microscope equipped with digital cameras Canon EOS 1100D (Fig. 4B, G; 5D, E, I, M, N) and Nikon D700 (all the other photographs). In order to better illustrate the three-dimensional objects, photomicrographs were combined from several optical sections using the stacking software Helicon Focus 8 (Kozub *et al.*, 2008). SEM photographs were obtained with a Quattro S microscope (Thermo Fisher Scientific) in the mode of «natural environment» (pressure of 800 Pa, temperature of 4° C, humidity of 90%), without sputtering of metal coatings.

**Taxa sampling.** Two specimens determined as *A. crebrifolium* and one specimen identified as a probable new species *A. astorgae*, were selected for molecular phylogenetic estimation. Considering nucleotide sequence data for *Anastrophyllum* in GenBank, the ITS1-2 nrDNA, *trnL*-F locus and *trnG*-intron of cpDNA were selected as

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appropriate molecular markers. The previously published accessions from 27 *Anastrophyllum* specimens and 25 specimens of the allied genera of the family Anastrophyllaceae were downloaded from GenBank; additionally, the ingroup includes newly generated nucleotide data from seven specimens. Two *Scapania* species, one for each of the two created datasets, were selected as outgroup taxa according with commonly accepted phylogenetic schema of the suborder Jungermanniineae. The voucher details and GenBank accession numbers are provided in Appendix 1 (Supplementary material).

**DNA isolation, PCR amplification and DNA sequencing.** DNA was extracted from dried liverwort shoots with DNeasy Plant Mini Kit (Qiagen, Germany) according to the manufacturer's protocol. The ITS1-2, *trnL*-F and *trnG*-intron sequence data were amplified and sequenced with primers previously described (White *et al.*, 1990; Taberlet *et al.*, 1991; Shaw *et al.*, 2005). PCR was carried out in 20 µl volumes with the following amplification cycles: 3 min at 94°C, 30 cycles [30 s 94°C, 40 s 56°C (for ITS1-2 and *trnL*-F) or 64°C (for *trnG*-intron) 60 s 72°C] and 2 min of final extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the Cleanup Mini Kit (Evrogen, Russia), and used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

**Phylogenetic analysis.** The program BioEdit 7.0.1 (Hall, 1999) was used to assemble the newly generated sequence data and align the datasets. The incorporated ClustalW option was used to produce automatic alignments, which later were manually corrected. Since the previously studied species and specimens in Genbank have different compositions of the sequenced loci, two datasets (ITS1-2+*trnL*-F and *trnG*-intron) were produced to include the maximum number of taxa in analyzes. Each dataset combines 10 species of *Anastrophyllum*, including undescribed taxa. In total, 13 species of the genus were involved in the current estimation, although their sampling in each dataset is different. All positions were taken into account and absent data were coded as missing.

The ITS1-2+*trnL*-F and *trnG*-intron alignments were tested with two analytical procedures. The maximum likelihood analysis (ML) was performed with RAxML v. 7.2.6 (Stamatakis, 2006), the Bayesian analysis (BA) – with MrBayes v. 3.2.1 (Ronquist *et al.*, 2012). The incorporated options of RAxML v. 7.2.6 determined the GTR+I+Å model as the best-fit evolutionary model of nucleotide substitutions, four rate categories of gamma distribution and 200 replicates of resampling for ML analysis of each dataset. For the Bayesian analysis both datasets were assigned the GTR+I+G model as recommended by the program's developers; gamma distribu-

tions were approximated with four rate categories. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated chain, and the two starting trees were chosen randomly. The number of generations for both calculations was one million, trees were saved every 100th generation. The average standard deviation of split frequencies between two runs for the ITS1-2+*trnL*-F analysis was 0.003582 and 0.009521 for the *trnG*-intron analysis. The first 2500 (25%) trees in both analyses were discarded in each run, and 15000 trees from both runs were sampled after burning. Bayesian posterior probabilities were calculated from trees sampled after burn-in.

The infraspecific and interspecific sequence variability was estimated as the average pairwise *p*-distances for ITS1-2, *trnL*-F and *trnG*-intron in Mega 11 (Tamura *et al.*, 2021) using the pairwise deletion option for counting gaps.

## RESULTS

ITS1-2 and *trnL*-F nucleotide sequence data were obtained for ten specimens, *trnG*-intron – for three specimens. Newly generated data were deposited into GenBank. The ITS1-2+*trnL*-F alignment included nucleotide sequences from 40 specimens belonging to 29 taxa with total length of 1378 positions. Among them, 897 positions belong to ITS1-2 and 481 – to *trnL*-F. The *trnG*-intron alignment included data from 37 specimens of 25 taxa with total length of 656 positions.

The ML analysis of the ITS1-2+*trnL*-F dataset produced a single tree with the arithmetic mean of Log likelihood -6515.989753. The means of Log likelihood for both sampled runs in the BA analysis were -6473.72 and -6473.55, respectively. The obtained tree revealed similar topologies, thus in Fig. 1 the ML tree from ITS1-2+*trnL*-F calculation was depicted with indication of bootstrap support (BS) and posterior probabilities (PP) values. The ML analysis of the *trnG*-intron dataset resulted in a single tree with the arithmetic mean of Log likelihood -2587.771367. The means of Log likelihood for both sampled runs in the BA analysis were -2622.67 and -2622.95. The topologies in both calculations became similar, so that Fig. 2 also illustrates ML topology with BS and PP values indicated at nodes.

On the topologies reconstructed from different DNA markers sets, all specimens belonging to the genus *Anastrophyllum* compose a group robustly supported only from ITS1-2+*trnL*-F (BS=99, PP=1.00 or 99/1.00). On the ITS1-2+*trnL*-F topology (Fig. 1), the three Chilean specimens group together: two specimens of *A. crebrifolium* in one clade (100/1.00) and one specimen of *A. astorgae* in a sister relation to them (96/1.00). This group is placed in affinity to the multiply sampled clade of *A. assimile* (Mitt.) Steph. with insufficient support (62/0.88).

In *trnG*-intron analysis (Fig. 2), the specimen of *A.*

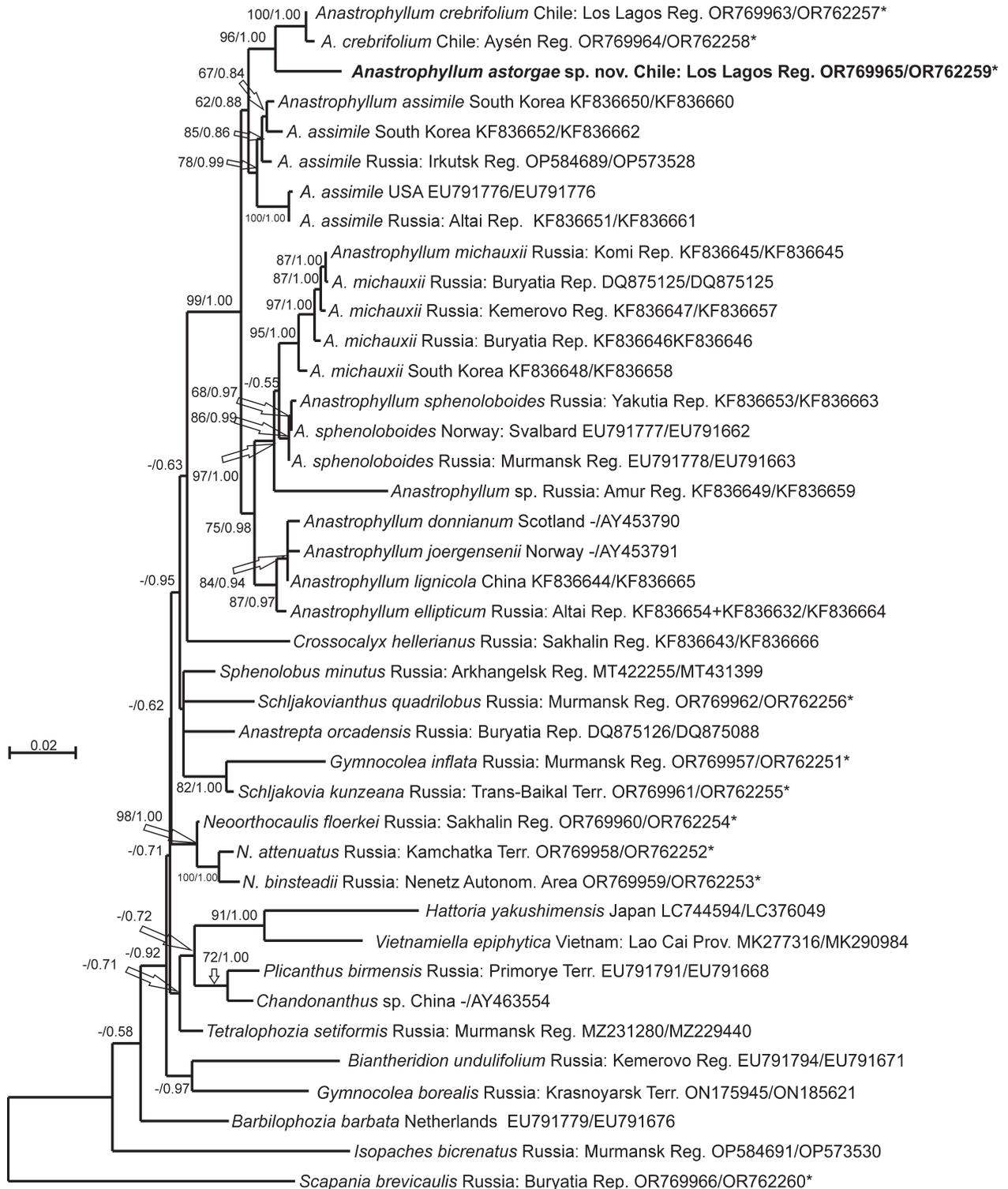


Fig. 1. The ML phylogram for the family Anastrophyllaceae reconstructed from ITS1-2+trnL-F of 40 specimens. Bootstrap supports from maximum likelihood and Bayesian posterior probabilities greater than 50% (0.50) are indicated. The newly obtained accessions are marked by an asterisk.

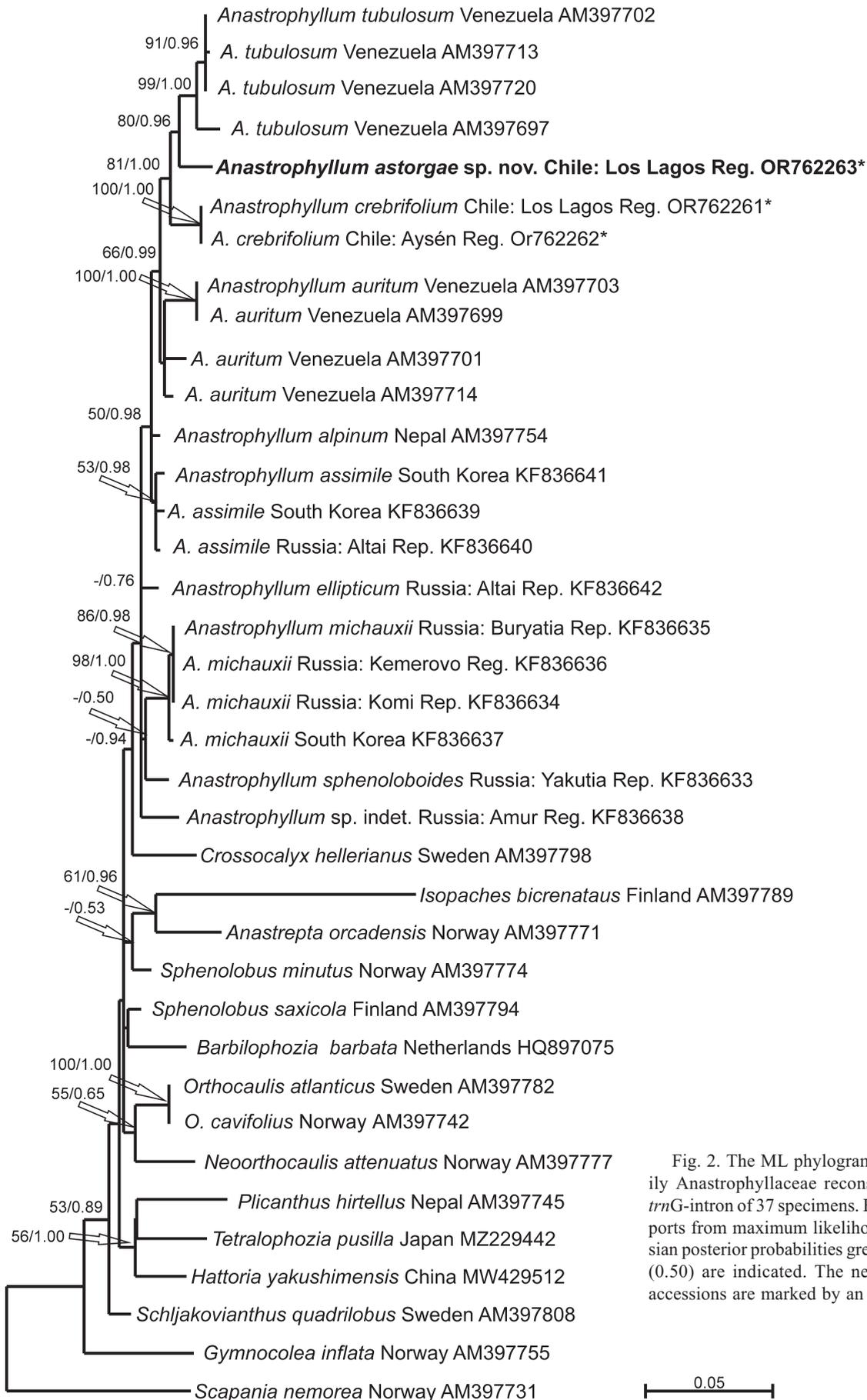


Fig. 2. The ML phylogram for the family Anastrophyllaceae reconstructed from *trnG*-intron of 37 specimens. Bootstrap supports from maximum likelihood and Bayesian posterior probabilities greater than 50% (0.50) are indicated. The newly obtained accessions are marked by an asterisk.

Table 1. The infra- and interspecific *p*-distances for the selected taxa of the genus *Anastrophyllum*.

a) ITS1-2 and <i>trnL-F</i>										
Taxon	Intraspecific	1	2	3	4	5	6	7	8	9
1 <i>A. crebrifolium</i>	0.4/0.0									
2 <i>A. astorgae</i>	n/c/ n/c	2.3/3.6								
3 <i>A. assimile</i>	1.3/0.6	2.5/2.5	3.3/3.2							
4 <i>A. michauxii</i>	1.0/0.0	4.5/2.5	4.9/2.9	4.1/1.3						
5 <i>A. sphenoloboides</i>	0.1/0.3	3.3/3.1	3.6/3.4	2.9/1.4	2.0/0.8					
6 <i>Anastrophyllum</i> sp.	n/c/ n/c	6.6/3.2	6.6/3.6	6.4/1.2	6.1/0.6	5.0/1.0				
7 <i>A. donnianum</i>	n/c/ n/c	-2.6	-2.6	-1.1	-1.1	-1.2	-1.4			
8 <i>A. joergensenii</i>	n/c/ n/c	-2.6	-2.6	-1.1	-1.1	-1.2	-1.4	-0.6		
9 <i>A. lignicola</i>	n/c/ n/c	3.0/3.2	3.5/2.7	2.9/1.4	3.3/1.1	2.1/1.0	5.9/1.3	-0.3	-0.3	
10 <i>A. ellipticum</i>	n/c/ n/c	3.9/2.7	4.9/3.1	3.7/1.0	4.3/0.6	3.0/0.9	7.8/0.8	-0.9	-0.9	0.8/0.4

b) <i>trnG</i> -intron										
Taxon	Intraspecific	1	2	3	4	5	6	7	8	9
1 <i>A. tubulosum</i>	0.6									
2 <i>A. astorgae</i>	n/c	2.1								
3 <i>A. crebrifolium</i>	0.0	2.6	2.6							
4 <i>A. auritum</i>	1.3	2.7	2.3	2.5						
5 <i>A. alpinum</i>	n/c	2.3	2.3	2.0	1.7					
6 <i>A. assimile</i>	0.5	2.5	2.6	2.2	1.8	0.8				
7 <i>A. ellipticum</i>	n/c	2.9	3.1	2.8	2.2	1.0	1.3			
8 <i>A. michauxii</i>	0.2	3.2	3.4	2.9	2.6	1.8	1.9	1.8		
9 <i>A. sphenoloboides</i>	n/c	2.8	3.3	2.8	2.2	1.7	1.8	1.7	1.8	
10 <i>Anastrophyllum</i> sp.	n/c	3.2	3.3	3.0	2.4	2.0	2.1	2.0	2.5	2.0

*astorgae* became sister related to a clade of *A. tubulosum* (Nees) Grolle from Venezuela (80/0.96). This latter clade appears as sister to an *A. crebrifolium*-clade (81/1.00). An *A. auritum*-clade from Venezuela in *trnG*-intron analysis shows a intraspecific divergence, meaning that one subclade in this clade stands out with a high support (100/1.00). Whereas, the *A. auritum*-clade itself is unsupported on the tree (Fig. 2). Analogously, the accessions of *A. assimile* in *trnG*-intron analysis form a clade, which has only weak bootstrap support (BS=53). These results show a possible specific or subspecific diversity within the clades of *A. assimile* and *A. auritum*, as too indicated by the supported divergence within *A. assimile*-clade in the ITS1-2+*trnL-F* topology (Fig. 1).

In the *trnG*-intron topology, the South American taxa compose its own group, although not highly supported (66/0.99), where the relation of *A. tubulosum* and *A. auritum* has previously been suggested in De Roo *et al.* (2007). Multiply sampled clades of *A. michauxii* (F.Weber) H.Buch and *A. sphenoloboides* R.M.Schust. kept their sister relation on both topologies with low supports (PP=0.55 in ITS1-2+*trnL-F*, and PP=0.50 in *trnG*-intron) as was achieved in Mamontov & Vilnet (2013). The specimens of *A. donnianum* (Hook.) Steph., *A. joergensenii* Schiffl., *A. lignicola* D.B. Schill & D.G. Long and *A. ellipticum* Inoue form a group (87/0.97) that is sister related (75/0.98) to the group of *A. michauxii* and *A. sphenoloboides* in ITS1-2+*trnL-F* topology. The specimen of *Anastrophyllum* sp. indet. from Amur Region, Russia kept its separate position, as shown in Mamontov & Vilnet (2013); this specimen possibly represents a new

taxon and needs additional study.

The intraspecific variability among two *A. crebrifolium* specimens gathered in different regions of Chile is 0.4% in ITS1-2 and is absent in *trnL-F* and *trnG*-intron; such level of variability is smaller than that in other multiply sampled species, for example *A. assimile* (1.3/0.6/0.5) and *A. michauxii* (1.0/0.0/0.2) in all three loci, or *A. tubulosum* (0.6) and *A. auritum* (1.3) in *trnG*-intron only (Table 1a,b). The *p*-distances between *A. crebrifolium* and *A. astorgae* are 2.3% in ITS1-2, 3.6% in *trnL-F*, and 2.6% in *trnG*-intron, which is similar with the level of differentiation among other related species: *A. assimile*, *A. tubulosum* and *A. auritum*. The lower level of divergence is between *A. michauxii* and *A. sphenoloboides* (2.0/0.8/1.8). The specimen *Anastrophyllum* sp. indet. from Amur Region of Russia shows the highest level of divergence in ITS1-2 (up to 7.8%) and also quite variable values of divergence in *trnL-F* (0.6–3.6%), while the values in *trnG*-intron (2.0–3.3%) are similar to differentiation among other species. Such level of the divergence between this specimen and other *Anastrophyllum* species also shows a possibility of a distinct taxon.

## DISCUSSION

The newly obtained nucleotide sequence data did not change one of the results published in Mamontov & Vilnet (2013), in the sense that the Holarctic *A. sphenoloboides* maintains its position within the genus *Anastrophyllum* in a close affinity with *A. michauxii* (Fig. 1). The former species is the type of *A.* subg. *Schizophyllum* R.M. Schust., which has been raised to a separate genus *Schizophyllopsis* in Vána *et al.* (2013b). Due to the discovered

affinity between *A. sphenoloboides* and other species of *Anastrophyllum* s.str. (Fig. 1), the necessity of separation of *Schizophyllopsis* is challenging. The possible solutions of this taxonomic difficulty are: (1) the treatment of *Schizophyllopsis* as a synonym of *Anastrophyllum*; (2) the treatment of *Schizophyllopsis* as a subgenus within the genus *Anastrophyllum* and a separation of one more subgenus of *Anastrophyllum* according to the results of the obtained phylogeny (Fig. 1); (3) the transfer of *A. michauxii* to the genus *Schizophyllopsis* and further separation of the group composed by *A. alpinum*, *A. assimile*, *A. auritum*, *A. crebrifolium* and *A. tubulosum* as a distinct genus (probably based on *A. sect. Assimilia* R.M. Schust.). The latter possibility needs further consideration on the base of expanded sampling of species involved in molecular phylogenetic studies, including the other species presently treated as members of *Schizophyllopsis*, besides *A. sphenoloboides*. However, based on the available data, *A. sphenoloboides* and other species of *Schizophyllopsis* are treated here as members of the genus *Anastrophyllum* s.str.

Concerning the South American taxa, it should be noted that the plants determined as *A. astorgae* represent a reduced morphological type, compared with the majority of species of the genus. Indeed, *A. auritum*, *A. crebrifolium*, and *A. tubulosum*, the taxa phylogenetically most closely related to *A. astorgae*, represent much larger robust plants bearing bulging trigones in leaf cells, as opposed to *A. astorgae* with its *Cephaloziella*-like habit and the absence of nodular thickenings in leaf cells. A little admixture of *A. astorgae* among the mat of *A. crebrifolium* in one of the studied specimens, as well as the absence of *Anastrophyllum* species characterized by such reduced morphology in southern South America and New Zealand (Schuster, 2002; Engel & Glenny, 2008; Hässel de Menéndez & Rubies, 2009) has resulted in questions whether *A. astorgae* represents merely underdeveloped plants of *A. crebrifolium*. However, the close phylogenetic distance between the Los Lagos and Aysén specimens of *A. crebrifolium* (the collecting points were at a distance of ca. 400 km from each other), more than to the Los Lagos specimen of *A. astorgae*, showed that the latter may be considered as a separate species. Moreover, the topology of phylogenetic trees and the *p*-distances between specimens determined as *A. auritum*, *A. astorgae*, *A. crebrifolium* and *A. tubulosum* support the recognition of all these taxa as separate species.

The morphological similarity between *A. auritum* and *A. crebrifolium* was grounds for the placement of the latter into the synonymy of the former (Váňa *et al.*, 2013a). However, the phylogeny obtained here shows a close affinity of the Chilean *A. crebrifolium* to the Venezuelan *A. tubulosum* (which has never been synonymized with *A. auritum*), more than to the Venezuelan *A. auritum* (Fig. 2). This phylogenetic affinity gives rise to a taxonomic difficulty, which could be resolved by the following ways:

(1) the placement of *A. tubulosum* into the synonymy of *A. auritum*, along with *A. crebrifolium*; (2) the recognition of *A. astorgae*, *A. crebrifolium* and *A. tubulosum* as infraspecific taxa (subspecies) within the broadly treated *A. auritum*; (3) the resurrection of *A. crebrifolium* as a distinct species and the separation of *A. astorgae* as a new one. The level of *p*-distances (*trnG*-intron) between the Venezuelan specimens of *A. auritum* and *A. tubulosum* is 2.7%, while it is 2.5% between *A. auritum* and *A. crebrifolium*; these *p*-distances distinctly exceed those between *A. michauxii* and *A. sphenoloboides* (1.8%) and between *A. assimile* and *A. auritum* (1.8%). It argues for the third possibility, namely the recognition of all the discussed taxa as separate species. The morphological differences between Venezuelan *A. auritum* (as it was described and illustrated in Schuster, 2002), *A. astorgae*, *A. crebrifolium* and *A. tubulosum* (based on the studied specimen Schäfer-Vervimp 9603, MHA 9090674 from Brazil), in our opinion, also argues for the specific level of the latter three taxa (see also the key below). Therefore, *A. astorgae* and *A. crebrifolium* are considered here as separate species. The description and photomicrographs of the former are provided below.

#### TAXONOMY

**Anastrophyllum astorgae** Mamontov & Vilnet, sp. nov. Fig. 2–6.

**Type:** CHILE, Los Lagos Region, Palena Province, Chaitén Commune, Sendero Ventisquero Yelcho, 43°16'32.5" S, 72°25'31.0" W, 155 m a.s.l., evergreen-coniferous-bamboo-fern-moss forest, on tree, 29.XI.2021, Mamontov 928-3 (MHA-9088477 – holotype, CONC, G, KPABG, MO – isotypes).

**Etymology.** The species is named for Dr. Anna Beatrice Astorga Roine (Center for Research on Patagonia Ecosystems) for her great help in our study of bryophytes in southern Chile.

**Diagnosis.** A transversely to succubously foliated *Cephaloziella*-like liverwort with deeply bilobed leaves, differs from all species of *Cephaloziella* by the shape of mature sterile leaves and the larger ratio of their size to the stem diameter, from the similar *Anastrophyllum crenulatum* and *A. novazelandiae* by the more deeply bilobed leaves and the absence of nodular thickenings in leaf cells, from the similar *Sphenolobopsis pearsonii* (Spruce) R.M. Schust. by the absence of underleaves.

**Description.** In thin, depressed, yellowish to bluish brown mats; stems intricately interwoven or creeping as isolated stems among other bryophytes. Shoots 1–5 mm long, 160–610 µm wide, filiform, brittle when dry, prostrate, with shoot apices often attenuate. Stems 48–90 µm in diameter, 4–5 cells high in cross section (Fig. 5M, N), remotely furcate, branches intercalary, from leaf axils (Fig. 4D, K) or postical stem face (Fig. 3I, 4D, I, 5I); cortical cells 17–30 µm long, 13–18 µm wide, 1.0–2.3× as long as wide, rectangular, mostly thick-walled, in cross

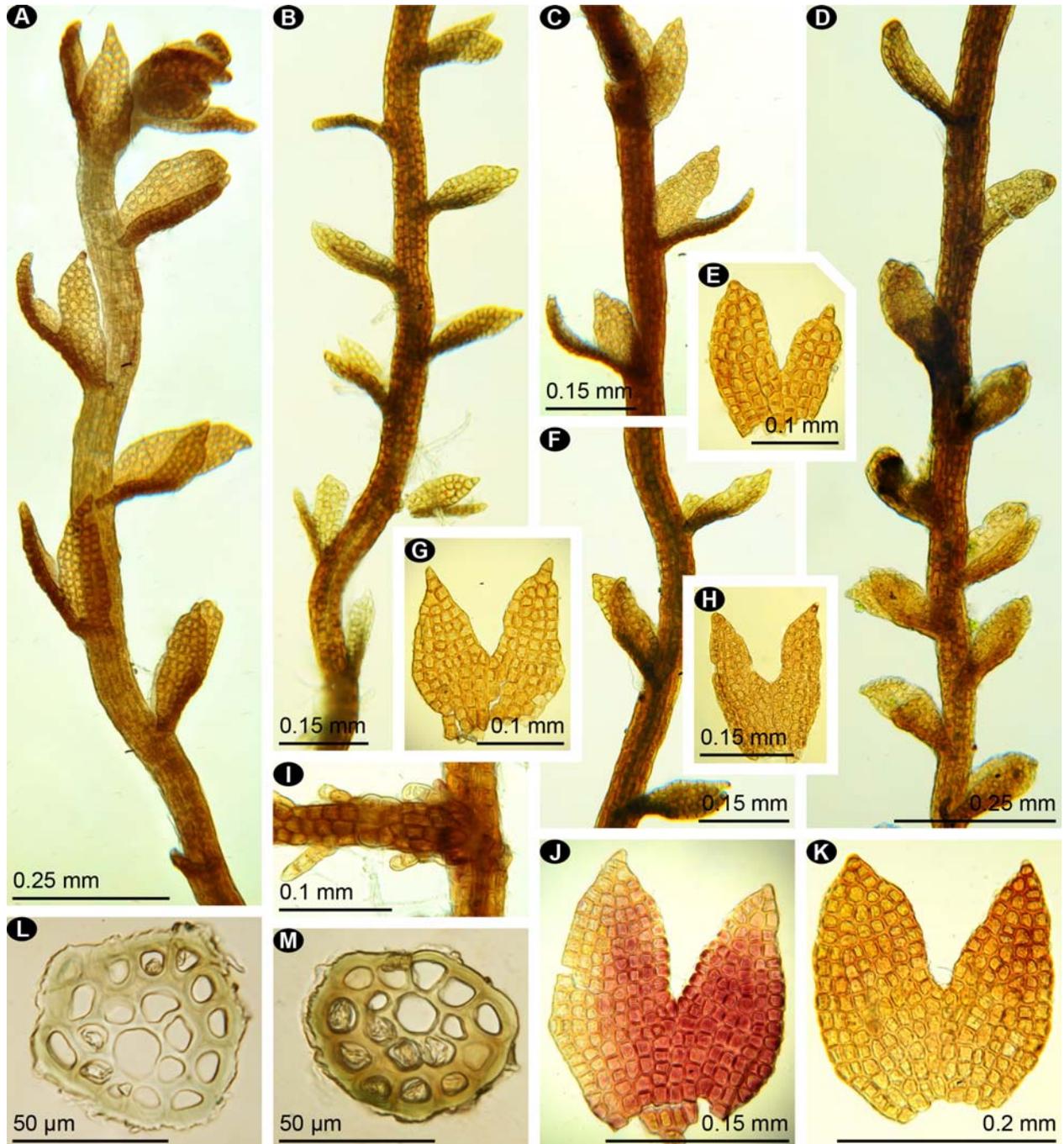


Fig. 3. *Anastrophyllum astorgae* (A–I, K–M from holotype; J from MHA-9088479): A, C, D, F: fragments of the same shoot (dorsal view); B: shoot fragment (ventral view); E, G, H, J, K: leaves; I: an intercalary branch base (ventral view); L, M: stem cross sections.

section almost equal in shape and size with that of medulla. Rhizoids sparse, scattered. Leaves remote, 180–355  $\mu\text{m}$  long, 155–270  $\mu\text{m}$  wide, (0.94–)1.0–1.4 $\times$  as long as wide, spreading or erect-spreading or squarrose (Fig. 4D, 5I) at base, concave (Fig. 5B) to conduplicate (Fig. 5F), lobes suberect or often nearly erect and parallel to stem, the lobe tips often incurved (Fig. 5B, D); leaves transversely to slightly succubously inserted, oblong-ovate to obovate or subquadrate, sinus descending to 0.35–0.58 of the leaf length, V-shaped, at base acute to obtuse; lobes

mostly subequal, rarely almost equal, divergent to suberect, narrowly triangular-ovate, acute to acuminate, (4–)5–8(–10) cells broad at base, margins entire or  $\pm$  sinuous; lobes often terminated by 1–2 superposed cells. Cells equally thick-walled, at lobe bases 14–23  $\mu\text{m}$  long, 10–15  $\mu\text{m}$  wide, 1.0–1.5(–1.9) $\times$  as long as wide, subquadrate to rectangular; cuticle papillose with relatively small (in comparison with the size of the cell lumen), rounded to elongated papillae (Fig. 6). Underleaves absent. Asexual reproduction not observed. Dioecious (?).

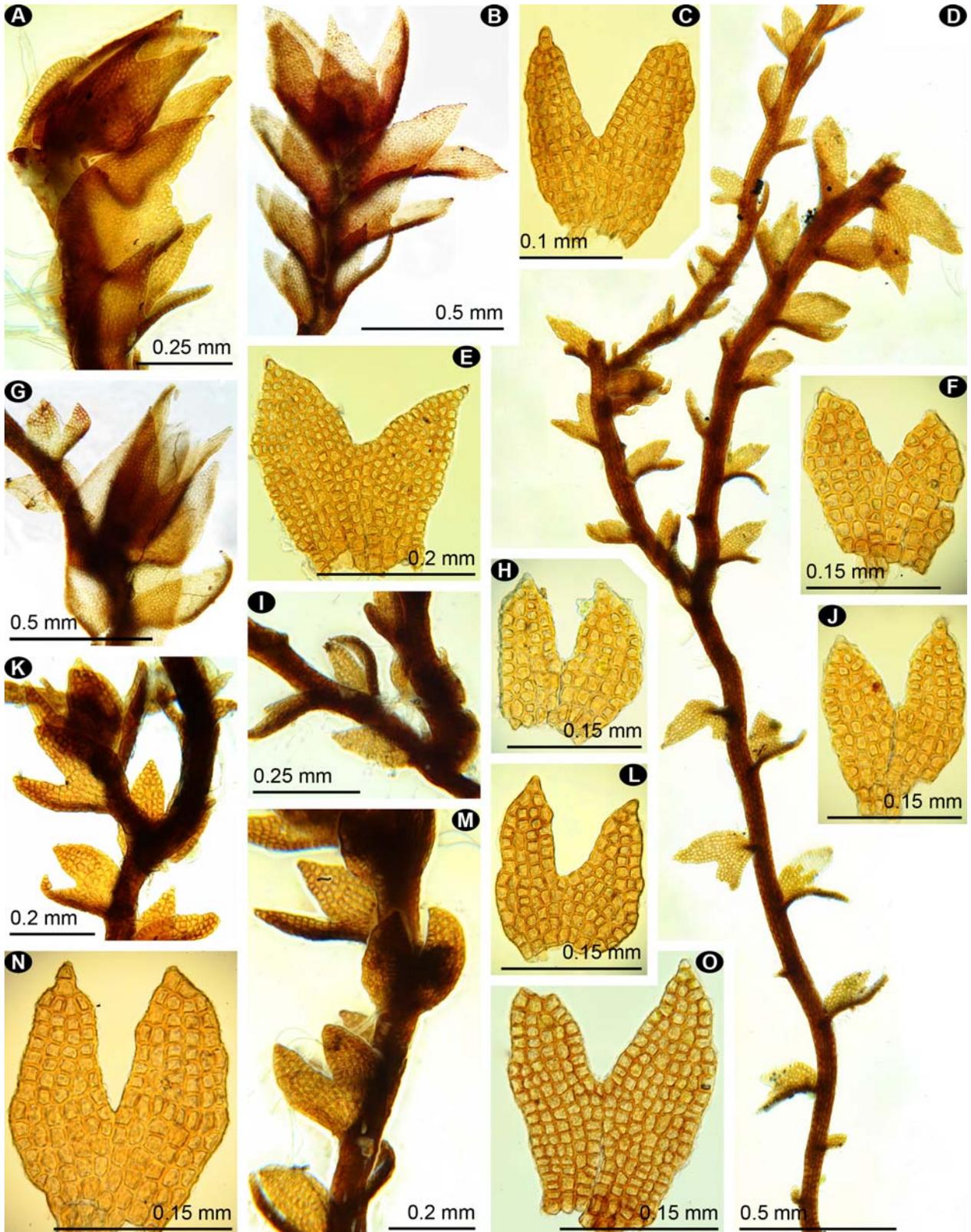


Fig. 4. *Anastrophyllum astorgae* (A from MHA-9088479; B, G from MHA-9088478; C–F, H–O from holotype): A, G: gynoecial shoots apices (lateral view); B: gynoecial shoot apex (dorsal view); C, E, F, H, J, L, N, O: leaves; D: sterile shoot fragment (dorsal view); I, K: shoot fragments showing intercalary branching (ventral view); M: sterile shoot fragment (lateral view).

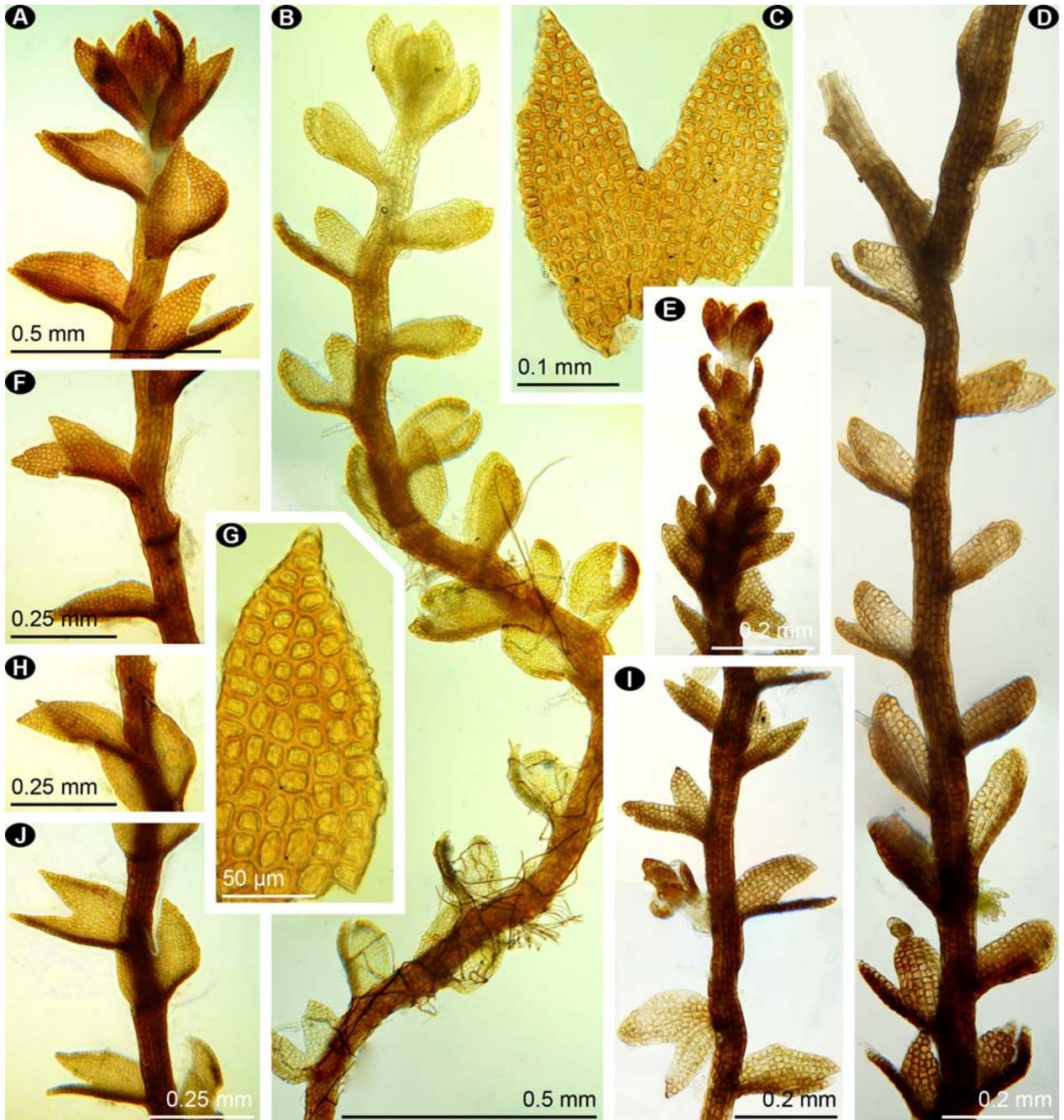


Fig. 5. *Anastrophyllum astorgae* (A, B, F, H, J from MHA-9088479; C, G, I from holotype; D, E – from MHA-9088478): A, F, H, J: fragments of the same shoot (dorsal view); B, D: sterile shoots (dorsal and ventral view, respectively); C: leaf; E, I: fragments of the same shoot (dorsal view); G: leaf lobe.

Androecia not found, unfertilized gynoecia terminal on leading axis, always with innovations. Gynoecial bracts in 3 pairs, becoming gradually larger, the innermost bracts much larger than leaves but somewhat less deeply bifid (sinus descending to 0.39–0.52 of the bract length), leaf-like, elliptic to ovate, 490–580 µm long, 320–470 µm wide, 1.24–1.52× as long as wide, sheathing at base, with acute and erect, lanceolate lobes; the margins entire or with 1–2 blunt teeth and/or a short appendage near anti-cal base; bracteole vanishing.

**Differentiation.** *Anastrophyllum astorgae* is one of the most small-sized species of the genus; its *Cephalozella*-like habit easily distinguishes it from all other species of *Anastrophyllum*. The underdeveloped minute shoots of *A. crebrifolium* can be confused with *A. astorgae*, however they are distinguished from the latter by the leaf margins crenulate via dilated septa between marginal cells (in *A. astorgae* the septae between marginal cells are not dilated, and the leaf margins are entire or somewhat sinuous). The distinctions between *A. astor-*

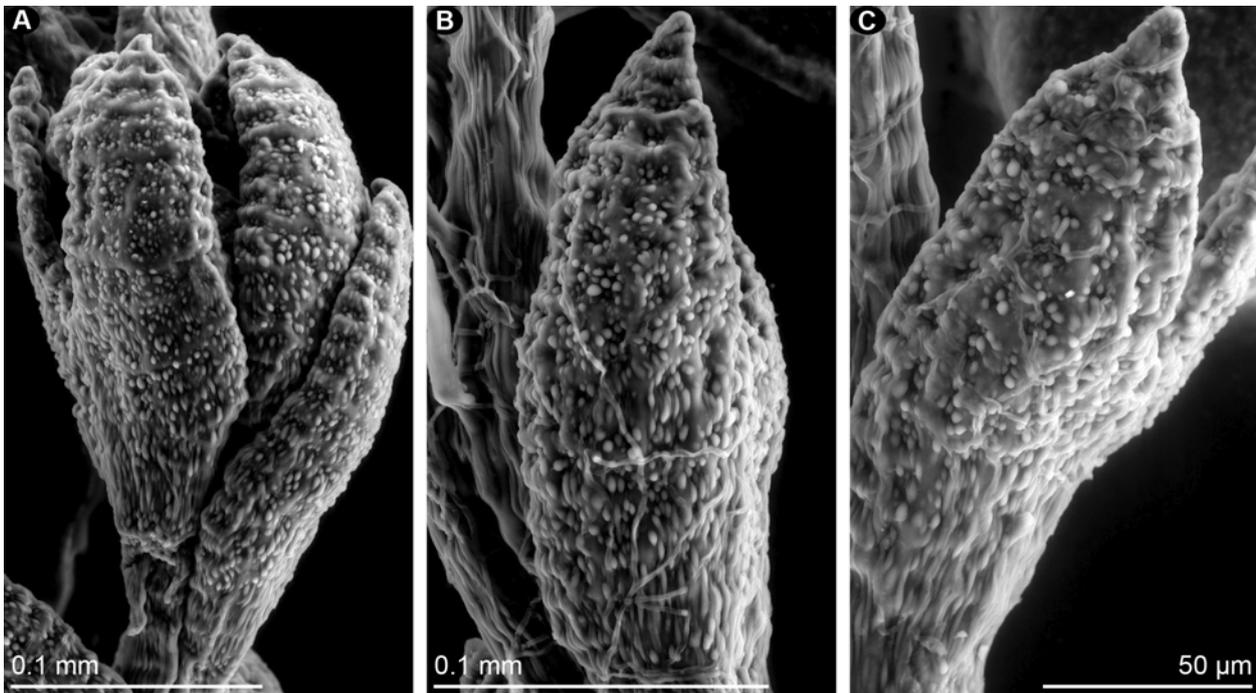


Fig. 6. *Anastrophyllum astorgae* (all from MHA-9088478): A–C: surface of leaves showing cuticular papillae.

*gae* and other species of the genera *Anastrophylopsis* and *Anastrophyllum* listed for Patagonia in Hässel de Menéndez & Rubies (2009) are generalized in the key below. The key is based on the studied specimens of *A. astorgae* and *A. crebrifolium*, also the descriptions and illustrations of other species in literature: for *Anastrophylopsis involulifolia* (Mont. ex Gottsche, Lindenb. & Nees) Vána & L. Söderstr. in De Notaris (1855) and Engel (1978), for *A. subcomplicata* (Lehm. & Lindenb.) Vána & L. Söderstr. [as *Anastrophyllum schismoides* (Mont.) Steph.] in Schuster (2002) and Engel & Glenn (2008), for *Anastrophyllum ciliatum* Steph. in Stephani (1893), Gola (1923, sub *A. pampaninii* Gola) and Engel (1978), for *A. crenulatum* R.M. Schust. and Venezuelan *A. auritum* in Schuster (2002), and for *A. semifissum* Steph. in Stephani (1911).

KEY TO SPECIES OF *ANASTROPHYLOPSIS* AND *ANASTROPHYLLUM* IN PATAGONIA

- |  |  |
|--|--|
| <p>1. Plants medium-sized to robust. Leaves slightly to strongly anticlyally secund, often with teeth, laciniae or appendages at the base ..... 2</p> <p>1. Plants minute to small. Leaves not anticlyally secund, margins entire or crenulate via dilated septa between marginal cells ..... 7</p> <p>2. Leaf lobes acute to apiculate, ending in an apiculum of (1–)2–5(–7) cells long ..... 3</p> <p>2. Leaf lobes blunt or subacute or apiculate with an apiculum of 1–2 cells long ..... 6</p> <p>3. Leaves, distinctly to strongly asymmetric, the dorsal lobe clearly smaller and narrower than the ventral ..... 4</p> | <p>3. Leaves weakly asymmetric or more or less symmetric, the leaf lobes subequal ..... 5</p> <p>4. Leafless lateral-intercalary stolons rather common. Leaves falcate, bilobed to 0.3–0.45 the length, the sinus base not or slightly reflexed, dorsal leaf margins entire or toothed by 1–several, blunt to rather narrow sharp teeth. Gemmae rather common. Perianths deeply plicate in distal 0.5–0.75, at times almost to the perianth base .....<br/>..... <i>Anastrophylopsis subcomplicata</i><br/>(incl. <i>Anastrophyllum schismoides</i>)</p> <p>4. Leafless lateral-intercalary stolons absent. Leaves not falcate, bilobed to 0.4–0.6 the length, the sinus base usually distinctly reflexed to form an anticlyally incurved fold, dorsal leaf margins without teeth in upper two thirds, at base often with 1–2 teeth or a rather large (up to 0.3(–0.4) of leaf length), entire or toothed or bilobed lacinium, or an appendage. Gemmae unknown. Perianths loosely plicate in distal 0.25–0.4 .....<br/>..... <i>Anastrophyllum crebrifolium</i></p> <p>5. Leaf keel strongly arced, leaf margins dentate-ciliate at base, then entire ... <i>Anastrophyllum ciliatum</i></p> <p>5. Leaf keel not arced, leaf margins entire(?) .....<br/>..... <i>Anastrophyllum semifissum</i></p> <p>6. Leaves subhorizontal and distichous, slightly anticlyally secund, subfalcate, retuse or shallowly bilobed. Leaf margins entire, usually incurved to involuted near the apex ..... <i>Anastrophylopsis involulifolia</i></p> <p>6. Leaves strongly anticlyally secund, not falcate, bilobed up to 0.45 of the length. Leaf margins plane, usually with an appendage of antical base .....<br/>.....</p> |
|--|--|

- .....*Anastrophyllum auritum*
7. Leaves bilobed to 0.2–0.35 of the length, leaf cells with bulging trigones, leaf margins crenulate via dilated septa between marginal cells. *Frullania*-type branching present ..... *Anastrophyllum crenulatum*
7. Leaves bilobed to 0.35–0.58 of the length, leaf cells with equally thickened walls, without nodulose thickenings, leaf margins entire. *Frullania*-type branching absent ..... *Anastrophyllum astorgae*

Due to its small size and reduced morphology, *A. astorgae* can be confused with some species of the genera *Andrewsianthus* R.M. Schust. and *Cephaloziella* known in Patagonia and occurring in the same or similar habitats. The new species differs from *Andrewsianthus australis* J.J. Engel and *A. scabrellus* (C. Massal.) R.M. Schust. ex J.J. Engel by the absence of flagelliform shoots and underleaves, from *A. australis* also by the equally thick-walled leaf cells and the absence of nodular thickenings, while from *A. scabrellus* (as much as from all species of *Cephaloziella*) by the larger ratio of the size of mature sterile leaves to the stem diameter, and by the leaves broadest in the middle or in upper third and gradually tapering to the base (Fig. 3H, 4E, N, O). The Amphiatlantic plant *Sphenolobopsis pearsonii* (Spruce) R.M. Schust. reported from Tristan da Cunha (Schuster, 2002) is greatly similar to *Anastrophyllum astorgae* by the shape and size of shoots, also the shape of leaves and leaf cells. However, Schuster (1980: 10) noted for *Sphenolobopsis pearsonii* that “quite different from *Anastrophyllum* ... is the large, free bracteole in the gynoeceum, as well as the conspicuous, ± lanceolate underleaves of gynoeceal shoots”.

**Ecology-Distribution.** The new species is known only from a single locality in southern Chile, where it was collected in a humid evergreen-coniferous-bamboo-fern-moss forest. The plants were gathered from bark of living trees at a height of ca. 1.0–1.5 m, together with *Anastrophyllum crebrifolium*, *Cephaloziella hispidissima* R.M. Schust., *Harpalejeunea* sp., *Lepidozia* sp., *Lepidoscyphus cuneifolius* subsp. *fragilis* (J.B. Jack & Steph.) Grolle, *L. expansus* (Lehm.) Grolle, and *Temnoma quadripartitum* (Hook.) Mitt., also from rotten log within the mats of *Anastrophyllum crebrifolium*, with an admixture of *Cephaloziella heterophylla* Reimers, *Clasmatocolea gayana* (Mont.) Grolle, *Lepicolea ochroleuca* (Spreng.) Spruce and *Syzygiella colorata* (Lehm.) K. Feldberg, Vána, Hentschel & Heinrichs.

**Other studied specimens (paratypes).** CHILE, Los Lagos Region, Palena Province, Chaitén Commune, Sendero Ventisquero Yelcho, 43°16'32.5" S, 72°25'31.0" W, 155 m a.s.l., evergreen-coniferous-bamboo-fern-moss forest, on tree, 29.XI.2021, Mamontov 928-3-7468 (MHA-9088480), 928-3-7469 (MHA-9088478); *ibid.*, on rotten log, 29.XI.2021, Mamontov 928-4-7467 (MHA-9088479).

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Appendix 1. The list of specimens included in phylogenetic estimation with vouchers and GenBank accession numbers. Accessions obtained in current study are in bold.

Taxon	Specimen voucher	GenBank accession number		
		ITS1-2	trnL-F	trnG-intron
<i>Anastrepta orcadensis</i>	Norway, Söderström 2003/017 (BOL)			AM397771
<i>A. orcadensis</i>	Russia: Buryatia Rep., Konstantinova 59-1-01 (KPABG 102486)	DQ875126	DQ875088	
<i>Anastrophyllum alpinum</i>	Nepal, Long 30460 (E)			AM397754
<i>A. assimile</i>	Canada: British Columbia, Konstantinova A137-18-95 (KPABG 125159)	EU791776	EU791664	
<i>A. assimile</i>	Russia: Altai Rep., Ignatov 4/1 (KPABG)	KF836651	KF836661	KF836640
<i>A. assimile</i>	Russia: Irkutsk Reg., Mamontov 468-1-5a (KPABG 120896)	OP584689	OP573528	
<i>A. assimile</i>	South Korea, Choi, Hepaticae Korea Exsiccatae, Fasc. II, No. 51 (KPABG 115517)	KF836650	KF836660	KF836639
<i>A. assimile</i>	South Korea, Bakalin Kor-5-12-11 (VBGI, KPABG 115596)	KF836652	KF836662	KF836641
<i>A. astorgae</i>	Chile: ALos Lagos Reg., Mamontov 928-3 (MHA)	<b>OR769965</b>	<b>OR762259</b>	<b>OR762263</b>
<i>A. auritum</i>	Venezuela, Söderström 2004/029 (BOL)			AM397703
<i>A. auritum</i>	Venezuela, Söderström 2004/065 (BOL)			AM397699
<i>A. auritum</i>	Venezuela, Söderström 2004/110 (BOL)			AM397701
<i>A. auritum</i>	Venezuela, Söderström 2004/111 (BOL)			AM397714
<i>A. crebrifolium</i>	Chile: Aysén Reg., Mamontov 951-1-7477 (MHA)	<b>OR769964</b>	<b>OR762258</b>	<b>OR762262</b>
<i>A. crebrifolium</i>	Chile: Los Lagos Reg., Mamontov 929-3-7474 (MHA)	<b>OR769963</b>	<b>OR762257</b>	<b>OR762261</b>
<i>A. donnianum</i>	United Kingdom: Scotland, Long, 29876 (?)		AY453790	
<i>A. ellipticum</i>	Russia: Altai Rep., Mamontov 330/2 (KPABG)	KF836654/	KF836664	KF836642
		KF836632		
<i>A. joergensenii</i>	Norway, Long & Schill 31400 (?)		AY453791	
<i>A. lignicola</i>	China, Long 24067 (KPABG)	KF836644	KF836665	
<i>A. michauxii</i>	Russia: Buryatia Rep., Konstantinova 17-1-02 (KPABG 121605)	DQ875125	DQ875125	
<i>A. michauxii</i>	Russia: Buryatia Rep., Bakalin 22-1...27 (KPABG 102860)	KF836646	KF836646	KF836635
<i>A. michauxii</i>	Russia: Kemerovo Reg., Konstantinova 35-1a-00 (KPABG 101837)	KF836647	KF836657	KF836636
<i>A. michauxii</i>	Russia: Komi Rep., Dulin G109820 (KPABG 109820)	KF836645	KF836645	KF836634
<i>A. michauxii</i>	South Korea: Gangwon-do, Choi 54-09 (KPABG 115520)	KF836648	KF836658	KF836637
<i>A. sp. indet.</i>	Russia: Amur Reg., Bakalin 15-20-00 (KPABG101577)	KF836649	KF836659	KF836638
<i>A. sphenoloboides</i>	Russia: Murmansk Reg., Bakalin 23-3-01 (KPABG 8831)	EU791778	EU791663	
<i>A. sphenoloboides</i>	Russia: Yakutia Rep., Bakalin 19-4-00 (KPABG 101592)	KF836653	KF836663	KF836633
<i>A. sphenoloboides</i>	Norway: Svalbard, Konstantinova K50-3-06 (KPABG)	EU791663	EU791662	
<i>A. tubulosum</i>	Venezuela, Söderström 2004/030 (BOL)			AM397697
<i>A. tubulosum</i>	Venezuela, Söderström 2004/064 (BOL)			AM397713
<i>A. tubulosum</i>	Venezuela, Söderström 2004/066 (BOL)			AM397702
<i>A. tubulosum</i>	Venezuela, Söderström 2004/120 (BOL)			AM397720
<i>Barbilophozia barbata</i>	Netherlands, Konstantinova 3b-5-99 (KPABG102106)	EU791779	EU791676	HQ897075
<i>Biantheridion undulifolium</i>	Russia: Kemerovo Reg., Konstantinova 56-1-00 (KPABG 101859)	EU791794	EU791671	
<i>Chandonanthus sp.</i>	China, He-Nyngren 492 (?)		AY463554	
<i>Crossocalyx hellerianus</i>	Russia: Sakhalin Reg., Bakalin Exsiccatae, No. 82 (VLA, KPABG)	KF836643	KF836666	
<i>C. hellerianus</i>	Sweden, Söderström 2003/081 (BOL)			AM397798
<i>Gymnocolea inflata</i>	Norway, Söderström 2004/223 (BOL)			AM397755
<i>G. inflata</i>	Russia: Murmansk Reg., Konstantinova 193-1-02 (KPABG 9512)	<b>OR769957</b>	<b>OR762251</b>	
<i>Hattoria yakushimensis</i>	Japan: Kagoshima, Yakushima Island, Katagiri 428 (NICH)	LC744594	LC376049	W429512

<i>Isopaches bicrenatus</i>	Finland, <i>Söderström</i> 2003/100 (BOL)		AM397789
<i>I. bicrenatus</i>	Russia: Murmansk Reg., <i>Konstantinova K129-1-19</i> (KPABG 124358)	OP584691 OP573530	
<i>Neoorthocaulis attenuatus</i>	Norway, <i>Söderström</i> 2003/020 (BOL)		AM397777
<i>N. attenuatus</i>	Russia: Kamchatka Terr., <i>Bakalin 66-1-01-VB</i> (KPABG 103759)	<b>OR769958 OR762252</b>	
<i>N. binsteadii</i>	Russia: Nenetzky Autonom. Area, <i>Lavrinenko s.n.</i> (KPABG 100333)	<b>OR769959 OR762253</b>	
<i>N. floerkei</i>	Russia: Sakhalin Reg., Paramushir I., <i>Bakalin K-96-10-04</i> (KPABG 107496)	<b>OR769960 OR762254</b>	
<i>Orthocaulis atlanticus</i>	Sweden, <i>Söderström</i> 2003/057 (BOL)		AM397782
<i>O. cavifolius</i>	Norway, <i>Söderström</i> 2004/233 (BOL)		AM397742
<i>Plicanthus birmensis</i>	Russia: Primorsky Terr., <i>Bakalin P-76-5-05</i> (KPABG 123309)	EU791791 EU791668	
<i>P. hirtellus</i>	Nepal, <i>Long 30335</i> (E)		AM397745
<i>Rudolgaea borealis</i>	Russia: Krasnoyarsk Terr., <i>Lapshina 04354</i> (KPABG 125157)	ON175945 ON185621	
<i>Scapania brevicaulis</i>	Russia: Buryatia Rep., <i>Mamontov 397-1-3</i> (MHA)	<b>OR769966 OR762260</b>	
<i>S. nemorea</i>	Norway, <i>Söderström</i> 2004/200 (BOL)		AM397731
<i>Schljakovia kunzeana</i>	Russia: Trans-Baikal Terr., <i>Bakalin 38-1-00</i> (KPABG 101737)	<b>OR769961 OR762255</b>	
<i>Schljakovianthus quadrilobus</i>	Russia: Murmansk Reg., <i>Mamontov 412-3-1</i> (INEP 400334)	<b>OR769962 OR762256</b>	
<i>S. quadrilobus</i>	Sweden, <i>Söderström</i> 2003/061 (BOL)		AM397808
<i>Sphenolobus minutus</i>	Norway, <i>Söderström</i> 2003/316 (BOL)		AM397774
<i>S. minutus</i>	Russia: Arkhangelsk Reg., <i>Savchenko CA-19-29</i> (KPABG 122709)	MT422255 MT431399	
<i>S. saxicola</i>	Finland, <i>Söderström</i> 2003/099 (BOL)		AM397794
<i>Tetralophozia pusilla</i>	Japan: Yamanashi Pref. <i>Bakalin J-88-40-15</i> (VBGI 5796, KPABG123441)		MZ229442
<i>T. setiformis</i>	Russia: Murmansk Reg., <i>Konstantinova K201-1-07</i> (KPABG 18022)	MZ231280 MZ229440	
<i>Vietnamiella epiphytica</i>	Vietnam: Lao Cai Prov., <i>Bakalin V-9-7-17</i> (KPABG 122594)	MK277316 MK290984	

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