

# Biodiversity assessment of ascomycetes inhabiting *Lobariella* lichens in Andean cloud forests led to one new family, three new genera and 13 new species of lichenicolous fungi

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**Abstract.** Neotropical mountain forests are characterized by having hyperdiverse and unusual fungi inhabiting lichens. The great majority of these lichenicolous fungi (i.e., detectable by light microscopy) remain undescribed and their phylogenetic relationships are mostly unknown. This study focuses on lichenicolous fungi inhabiting the genus *Lobariella* (*Peltigerales*), one of the most important lichen hosts in the Andean cloud forests. Based on molecular and morphological data, three new genera are introduced: *Lawreyella* gen. nov. (*Cordieritidaceae*, for *Unguiculariopsis lobariella*), *Neobaryopsis* gen. nov. (*Cordycipitaceae*), and *Pseudodidymocyrtis* gen. nov. (*Didymosphaeriaceae*). Nine additional new species are described (*Abrothallus subhalei* sp. nov., *Atronectria lobariellae* sp. nov., *Corticifraga microspora* sp. nov., *Epithamnolia rugosopycnidata* sp. nov., *Lichenotubeufia cryptica* sp. nov., *Neobaryopsis andensis* sp. nov., *Pseudodidymocyrtis lobariellae* sp. nov., *Rhagadostomella hypolobariella* sp. nov., and *Xylaria lichenicola* sp. nov.). Phylogenetic placements of 13 lichenicolous species are reported here for *Abrothallus*, *Arthonia*, *Globonectria*, *Lawreyella*, *Monodictys*, *Neobaryopsis*, *Pseudodidymocyrtis*, *Sclerococcum*, *Trichonectria* and *Xylaria*. The name *Sclerococcum ricasoliae* comb. nov. is reestablished for the neotropical populations formerly named *S. lobariellum* (*Sclerococcales*). A key to sexual and asexual states of 40 species of lobariellicolous ascomycetous fungi is provided. Teleomorph-anamorph connections were established for several species using molecular methods and/or visual observations in nature. Additionally, we found that the anamorphic species *Cornutispora ophiurospora* inhabiting *Lobariella* was often accompanied by ascumata of *Spirographa*. Results of phylogenetic analyses, including newly generated sequences of several *Cornutispora* and *Spirographa* species inhabiting various host lichens, support the conclusion that *Cornutispora* is a synonym of *Spirographa*. Our Maximum Likelihood inference based on multiple loci show that all studied *Spirographa* (including *Cornutispora*) belong to a new lineage within *Ostropales*. Based on these highly supported phylogenetic placements and the distinct character states of their conidiomata, in comparison with other *Lecanoromycetes*, a new family is proposed – *Spirographaceae* fam. nov. This new lineage includes broadly distributed mycoparasites, inhabiting various lichen and fungal hosts, and representing an early diversification event preceding the lichen-forming clade of *Fissurinaeae*, *Gomphillaceae* and *Graphidaceae*. Two lichenicolous species, *Asteroglobulus giselae* and *Pleoscutula arsenii*, were found to be nested within the *Spirographa* clade, and their teleomorph-anamorph connections were confirmed based on genotypic and phenotypic data. This phylogenetic result is corroborated by their highly similar ascumata anatomy. Together these results strongly indicate that both species are congeneric with *Spirographa*. As a result, four new species (*S. aggregata* sp. nov., *S. galligena* sp. nov., *S. maroneae* sp. nov., and *S. parmotrematis* sp. nov.) and 15 new combinations are proposed (*Spirographa ascaridiella* comb. nov., *S. arsenii* comb. nov., *S. ciliata* comb. nov., *S. giselae* comb. nov., *S. herteliana* comb. nov., *S. hypotrachynae* comb. nov., *S. intermedia* comb. nov., *S. lichenicola* comb. nov., *S. limaciformis* comb. nov., *S. ophiurospora* comb. nov., *S. pittii*

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comb. nov., *S. pyramidalis* comb. nov., *S. triangularis* comb. nov., *S. tricupulata* comb. nov., and *S. vermiformis* comb. nov.). Species of the genus *Spirographa*, as outlined here, are strongly host-specific, mainly at the generic level of their host. Some host genera can harbour more than one *Spirographa* species.

**Key words:** Anamorph-teleomorph connection, *Asteroglobulus*, *Cornutispora*, lichenicolous fungi, Neotropics, Pezizomycotina, phylogenetics, *Pleoscutula*, *Spirographa*, systematics

## Introduction

The combination of high altitude and precipitation drastically increases the biodiversity of symptomatic lichen-inhabiting fungi detectable by light microscopy (i.e., lichenicolous fungi, reproducing sexually or asexually on their hosts) in neotropical forests. Consequently, a network of tropical and subtropical montane cloud forests along the Andean cordillera and the Mexican mountain ranges hosts very particular and hyperdiverse lichenicolous fungi (Diederich 1997; Etayo 2002, 2017; Flakus et al. 2019). *Lobariella* (*Peltigerales*) is endemic to neotropical cloud forests, and one of the most common lichen genera in this ecosystem. It is also known to host the largest numbers of lichenicolous fungi (Etayo 2002, 2017). The genus *Lobariella* is known from Mexico to southern Brazil, with the exception of one species – *L. crenulata*, which is known additionally from Hawaii (Moncada et al. 2013). According to Moncada et al. (2013), *Lobariella* is a monophyletic, species-rich genus within *Lobariaceae*, with about 26 recently accepted species.

Prior to our study, 19 species of lichenicolous Ascomycota and three species of Basidiomycota were described or reported from *Lobariella*, mainly from Colombian and Ecuadorian forests (Etayo 2002, 2010b, 2017; Flakus & Kukwa 2012a; Diederich et al. 2014). The main aims of this study were to: (i) describe previously unknown ascomycetous lichenicolous fungi growing on *Lobariella* in Bolivia, (ii) reveal their phylogenetic relationships within Pezizomycotina, and (iii) provide an identification key to facilitate future research on lichenicolous fungi. Moreover, during our study of *Cornutispora* and *Spirographa* inhabiting *Lobariella* in Bolivia, we discovered that they represent conidial and ascospore states of a single genus (*Spirographa*). Therefore, we included newly generated sequences from *Cornutispora* and *Spirographa* collected from other host genera to reveal their phylogenetic affinity and to establish species boundaries within the genus *Spirographa*.

## Materials and methods

**Taxon sampling and morphological studies.** Our results are based mainly on fresh material collected from Bolivia and Panama, and on specimens deposited at COL, DAOM, G, H, KRAM, LPB, M, PMA, UPS, UGDA, and VIT, as well as in the private herbarium of J.E. (Pamplona). Each type examined in this study is indicated by an exclamation mark (!). Specimens for this study were collected by J. Etayo (J.E.), A. Flakus (A.F.), M. Kukwa (M.K.), and P. Rodríguez-Flakus (P.R.F.). Morphological and anatomical characters were examined using standard

stereo- and compound-microscopes (Nikon SMZ 800, Nikon Eclipse 80i DIC, Japan). Sections were prepared manually using a razor blade, or a Thermo Fisher Scientific Microm HM430 (USA) freezing microtome combined with a BFS-MP freezing stage and a BFS-3MP controller. Sections and squash mounts were examined in distilled water, 10% KOH (K), Lactophenol Cotton Blue (LPCB; Fluka, no. 61335-100ML) or Congo Red. All photomicrographs showing anatomical characters were made using transmitted differential interference contrast (DIC) microscopy. Amyloid reactions of anatomical structures were tested using Lugol's solution (I) (Fluka, no. 62650-1L-F), or with Lugol's solution preceded by a 10% KOH treatment (K/I). The solubility of crystals was tested using K and a 50% nitric acid solution (N). All measurements were made in distilled water or LPCB. Ascospore measurements of several newly described taxa are presented as arithmetic mean ( $\bar{x}$ ) and standard deviation (s) (in brackets), flanked by the minimum and maximum observed values. Length/breadth ratios (l/b) are presented in the same way, followed by the number of measurements (n). Host lichen substances were investigated by thin layer chromatography (TLC) in solvents B' and C following the methods by Culberson and Kristinsson (1970) and Orange et al. (2001).

**DNA extraction, PCR amplification, and DNA sequencing.** We investigated 30 specimens of lichenicolous fungi inhabiting *Lobariella* species representing a broad phylogenetic array within the *Pezizomycotina*: *Abrothallales*, *Arthoniales*, *Cordieritidaceae* (*Helotiales*), *Cordycipitaceae* (*Hypocreales*), *Dactylosporaceae* (*Sclerococcales*), *Didymosphaeriaceae* (*Pleosporales*), *Nectriaceae* (*Hypocreales*), *Ostropales*, and *Xylariales*. Additionally, we studied 18 specimens of *Asteroglobulus*, *Cornutispora*, *Pleoscutula* and *Spirographa* (the *Spirographa* complex) and two additional collections of *Protounguicularia* from various lichen hosts (altogether 32 specimens). Ascomata or conidiomata of lichenicolous fungi, still on their lichen host, were stored at  $-20^{\circ}\text{C}$ . They were removed from the host thallus and carefully cleaned in double distilled water on a microscope slide under sterile conditions to remove host tissues and other visible impurities using ultra-thin tweezers and a razor blade. DNA was extracted from 3 to 20 clean ascomata, conidiomata, or hymenia, depending on each specimen, using either the DNeasy™ Plant Mini Kit or QIAamp DNA Investigator Kit (Qiagen, Germany) following the manufacturer's instructions. Primers used for PCR and sequencing are provided in Table 1, whereas the

**Table 1.** Sequence data acquisition (e.g., primers used, original source of sequences), assembled datasets (e.g., loci) and phylogenetic analyses (e.g., loci) and phylogenetic analyses (e.g., substitution models and partitions) used for this study.

Systematic group	Figure no.	Loci	Primer pairs + sequencing primers	Substitution models and partitions	Outgroup	References
<i>Abrothallus</i> ( <i>Abrothallales</i> )	Figure 1	nrITS + nrLSU + mrSSU	ITS1F-ITS4, mrSSU1-mrSSU3R, LROR-LR7, LR5	HKY+G (ITS1, ITS2), SYM+I+G (5.8S), SYM+G (mrSSU), GTR+I+G (LSU)	<i>Pateallaria atrata-Jahmala bipilcata</i> clade	Pérez-Ortega et al. 2014; Suijja et al. 2015
<i>Arthonia</i> ( <i>Arthoniales</i> )	Figure 2	nrLSU + mrSSU + <i>RPB2</i>	mrSSU1-mrSSU3R, LROR, LR3, LR5	GTR+I+G (mrSSU), GTR+I+G (LSU, <i>RPB2</i> -1), SYM+G ( <i>RPB2</i> -2), GTR+I+G ( <i>RPB2</i> -3)	<i>Opegrapha lithyrga-O. vulgata</i> clade	Frisch et al. 2014
<i>Globonetria</i> and <i>Trichonetria</i> ( <i>Hypocreales</i> )	Figure 3	nrLSU + <i>RPB1</i> + <i>RPB2</i> + <i>TEFI</i>	ITS1F-LR5, ITS5	GTR+I+G ( <i>RPB2</i> -2, <i>RPB2</i> -3, <i>RPB1</i> -1, <i>RPB1</i> -2, TEF1-2, TEF1-3, LSU), GTR+G ( <i>RPB2</i> -1, <i>RPB1</i> -3)	<i>Rosasphaeria moravica-Niesslia exilis</i> clade	Voglmayr & Jaklitsch 2019
<i>Neobaryopsis</i> ( <i>Hypocreales</i> )	Figure 4	nrSSU + nrLSU + <i>RPB1</i> + <i>RPB2</i> + <i>TEFI</i>	ITS1F-LR5, ITS5, LR3	GTR+I+G (LSU), K80+I+G (SSU), SYM+I+G ( <i>RPB1</i> , <i>RPB2</i> ), GTR+I+G (TEF1)	<i>Hypocrea lactea-H. rufa</i> clade	Lawrey et al. 2015; Kepler et al. 2017
<i>Pseudodidymomyces</i> ( <i>Pleosporales</i> )	Figure 5	nrSSU + nrITS + nrLSU	ITS1F-LR5, NS1-nssu1088	GTR+I+G (LSU), TVM+I+G (5.8S, SSU), SYM+G (ITS1), TVM+I+G (ITS2)	<i>Lenithecium fluviatile-Stagonospora paludosa</i> clade	Ariyawansa et al. 2014
<i>Lawreyella</i> ( <i>Helotiales</i> )	Figure 6	nrSSU + nr5.8S + nrLSU	ITS1F-ITS4, ITS1F-LR5, LIC15R-LR6, LROR-LR7, NS1-NS24, NS1-nssu1088, ITS5, LROR, LR5, nssu131, SRS7,	SYM+I+G (SSU, 5.8S), GTR+I+G (LSU)	<i>Chlorociboria glauca-Encoelia furfuracea</i> clade	Suijja et al. 2015; Fryar et al. 2019
<i>Sclerococcium</i> ( <i>Sclerococcales</i> )	Figure 7	nrITS + nrLSU + mrSSU	ITS1F-ITS4, mrSSU1-mrSSU3R, LROR-LR7, LR5	HKY+G (mrSSU), K80+G (ITS1, ITS2), K80+I (5.8S), SYM+I+G (LSU)	<i>Fusichalara minuta-Rhopalophora clavispora</i> clade	Diederich et al. 2018; Olariaga et al. 2019
<i>Xylaria</i> ( <i>Xylariales</i> )	Figure 8	nrITS + <i>RPB2</i> + beta-tub	ITS1F-LR5, <i>RPB2</i> -5F- <i>RPB2</i> -7cf, BT3LM5-BT10LM3	GTR+I+G (ITS1, ITS2, Beta-tub), GTR+I+G ( <i>RPB2</i> ), JC (5.8S)	<i>Poronia pileiformis-Podosordaria multi</i> clade	URen et al. 2016
<i>Spirographaceae</i> within <i>Ostropales</i>	Figure 23	nrLSU, mrSSU, <i>RPB1</i> , <i>RPB2</i> ,	ITS1F-LR5, mrSSU1-mrSSU3R, <i>RPB1</i> af- <i>RPB1</i> cf	GTR+G ( <i>RPB1</i> -1, <i>RPB2</i> -1, mrSSU, <i>RPB1</i> -2, <i>RPB2</i> -2) (LSU, SSU) ( <i>RPB2</i> -3, <i>RPB1</i> -3)	<i>Arctomia interfixa-Gregorella humida</i> clade	Baloch et al. 2013; Miadlikowska et al. 2014; Pino-Bodas et al. 2017; Carbone et al. 2018
<i>Spirographa</i> within <i>Graphidaceae</i> s.l.	Figure 24A	nrLSU, mrSSU, <i>RPB2</i>	ITS1F-LR5, mrSSU1-mrSSU3R	GTR+G (mrSSU) (LSU, <i>RPB1</i> -1, <i>RPB1</i> -2) ( <i>RPB1</i> -3)	<i>Coenogonium luteum-Gyallecta jenensis</i> clade	Lücking et al. 2004; Lumbsch et al. 2014; Miadlikowska et al. 2014; Carbone et al. 2017, 2019; Suijja et al. 2018
<i>Spirographa</i> complex (species level relationships)	Figure 24B	nrITS, nrLSU, mrSSU, <i>RPB1</i>	ITS1F-ITS4, ITS1F-LR5, mrSSU1-mrSSU3R, <i>RPB1</i> af- <i>RPB1</i> cf	GTR+G (ITS) ( <i>RPB1</i> -1, <i>RPB1</i> -2, mrSSU) (LSU) ( <i>RPB1</i> -3)	<i>Fissurina nigrolabiata-F. aggregatula</i> clade	This study

amplification parameters and additional detailed information on PCR, visualization of amplicons, and preparation of samples can be found in Rodriguez-Flakus & Printzen (2014) and Flakus et al. (2019). PCR amplicons were sequenced by Macrogen (Amsterdam, the Netherlands). The newly generated sequences were carefully checked, assembled and edited manually using Geneious Pro 8.0. (Biomatters Ltd) and deposited in GenBank. Information about all OTUs used in this study including sequences downloaded from GenBank and newly obtained accession numbers are provided in Table S1.

**Phylogenetic analyses of *Lobariella*-inhabiting fungi, excluding the *Spirographa* complex.** All sequences generated were subjected to BLAST (Altschul et al. 1990) and/or T-BAS Evolutionary Placement Algorithm (EPA) as implemented in the Tree-Based Alignment Selector toolkit (T-BAS version 2.1; Carbone et al. 2017, 2019) to verify potential fungal contamination and to reveal their general phylogenetic placement within *Pezizomycotina*. Alignments were generated for each locus using MAFFT (Katoh et al. 2005) as implemented in Geneious Pro. We removed ambiguously aligned regions using Gblocks version 0.91b (Castresana 2000) with default settings but allowing gaps in 50% of the sequences. All phylogenetic analyses were performed in the CIPRES Scientific Gateway (<http://www.phylo.org/portal2/>) (Miller et al. 2010). PartitionFinder 2 (Lanfear et al. 2016) was used to select the best partitioning scheme and substitution models under a greedy search algorithm and the Akaike information criterion (AICc) (Lanfear et al. 2012). Details about each partition and the substitution model selected are included in Table 1. Maximum likelihood (ML) analyses were carried out using a heuristic search as implemented in RAxML-HPC2 on XSEDE (Stamatakis 2006) with the GTRGAMMAI or GTRCAT model and 1000 bootstrap replicates to estimate branch support. Bayesian inference (BI) of phylogenetic relationships was implemented in MrBayes 3.2.6 on XSEDE (Ronquist et al. 2012) using the partitions and substitution models obtained with PartitionFinder 2. Two independent parallel runs were implemented, each with four incrementally heated (0.15) chains. This analysis was allowed to run for 20M generations, sampling every 1000<sup>th</sup> tree and discarding the first 50% of the sampled trees as part of the burn-in. The resulting ML and BI phylogenetic trees were visualized with Figtree 1.3.1 (Rambaut 2009).

**Datasets and phylogenetic analyses of the *Spirographa* complex.** Although inconclusive because of low similarity (up to 80%) compared to available sequences, the BLAST results indicated a putative placement of 18 individuals morphologically identified as *Asteroglobulus*, *Cornutispora*, *Pleoscutula*, and *Spirographa* (i.e., the *Spirographa* complex) (Table S1) in *Ostropomycetidae*. We applied the Evolutionary Placement Algorithm (EPA) as implemented in T-BAS (version 2.1; Carbone et al. 2017, 2019) using the *Lecanoromycetes* reference tree (Miadlikowska et al. 2014; Carbone et al. 2019) based on each individual locus separately (mrSSU, nrLSU, and *RPB1* A-F) and on these datasets combined. For each

analysis we used the GTRGAMMA substitution model and calculated likelihood weights with a placement cutoff distance of 10. Based on the EPA analyses, which show a sister relationship of the *Spirographa* clade with *Graphidaceae* (results not presented), we selected a larger clade containing *Arctomiales*, *Baeomycetales*, *Hymeneliales*, *Trapeliales* and *Ostropales* from the *Lecanoromycetes* tree for a more thorough RAxML search and bootstrap analyses (1000 replicates) as implemented in T-BAS v. 2.1 based on the mrSSU, nrLSU and *RPB1* A-F combined dataset. The following options were selected: do not include unknown duplicates, realign sequences in clade with MAFFT, GTRGAMMA substitution model, and *Arctomiales* to root the tree.

Based on the resulting RAxML phylogeny (where the *Spirographa* complex remained sister to *Graphidaceae* with strong bootstrap support; results not shown), we selected *Ostropales* and *Arctomiales* clades (the latter was used to root the tree) containing 195 OTUs, combining 177 reference taxa and 18 individuals from the *Spirographa* complex. The single-locus alignments for three ribosomal loci: mrSSU, nrLSU, nrSSU; and two protein coding genes: *RPB1* (two amplicons: *RPB1* A-F, *RPB1* F-G) and *RPB2* (two amplicons: *RPB2* 5-7 and *RPB2* 7-11) were downloaded from T-BAS v. 2.1 (files associated with the *Lecanoromycetes* reference tree; Carbone et al. 2017, 2019). We supplemented this dataset with 13 additional taxa including members of three lichenicolous genera: *Corticifraga*, *Sphaeropezia*, *Taitaia* (Baloch et al. 2013; Pino-Bodas et al. 2017; Suija et al. 2018) and the genus *Epigloea*, potentially belonging to *Ostropales* (Pino-Bodas et al. 2017). All single-loci alignments were manually adjusted using Mesquite v.3.11 (Madison & Madison 2015) with the option ‘Nucleotide with AA color’ for guiding all alignments of protein-coding genes. Ambiguously-aligned regions (sensu Lutzoni et al. 2000) were delimited manually to be excluded from subsequent analyses. The combined 195-taxon dataset (with 177 reference taxa) included five taxa with one locus, 113 taxa with two loci, 39 taxa with three loci, eleven taxa with four loci, and nine taxa with five loci. It represented eight families currently classified in *Ostropales*: *Coenogoniaceae*, *Gomphillaceae*, *Graphidaceae*, *Gyalectaceae*, *Protothelenellaceae*, *Sagiolechiaceae*, *Stictidaceae*, *Thelenellaceae* (Lücking et al. 2017), and other lineages, e.g. *Epigloeaceae* and *Thrombium epigaeum*, both potentially affiliated with *Ostropales* (Pino-Bodas et al. 2017; Carbone et al. 2019).

Based on the resulting sister relationship between the *Spirographa* and *Graphidaceae* clades, we assembled a 144-taxon dataset restricted to *Graphidaceae* s.lat. using mrSSU, nrLSU and *RPB2* 7-11 sequences and a 104-taxon dataset from Lumbsch et al. (2014; sequence data received from the last author upon request) to confirm this relationship. The initial single-locus alignments were reajusted manually (using Mesquite v.3.11), the *RPB2* sequences were reverse complemented to reflect the 5’-3’ direction, the option ‘Nucleotide with AA color’ was used for guiding the alignment of this protein-coding gene, and the ambiguous regions were re-delimited. Because published

phylogenies (e.g., Miadlikowska et al 2014) and the 195-taxon phylogeny from the current study (Fig. 23) strongly supported the sister relationship of the subfamilies *Fissurinoideae* and *Gomphilloideae* (currently recognized as *Gomphillaceae*; Lücking et al. 2017), which represent the first evolutionary split in *Graphidaceae*, we supplemented the alignments with ten additional members from both subfamilies (part of the *Ostropales* 195-taxon dataset) and twelve members of *Gomphillaceae* from Lücking et al. (2004) for a total of 144 taxa. Our *Graphidaceae* 144-taxon dataset includes all four subfamilies currently recognized in *Graphidaceae* (*Fissurinoideae*, *Rodonographoideae*, *Graphidoideae*, and *Gomphilloideae*=*Gomphillaceae*) and all tribes within *Graphidoideae*. The reference data for *Graphidaceae* included 20 taxa with one locus, 65 taxa with two genes, and 42 taxa with three genes.

For the reconstruction of species level relationships within the *Spirographa* complex, we assembled a combined dataset of four loci (nrITS, nrLSU, mrSSU, and *RPB1A-F*) for all taxa with available sequence data, and two *Fissurina* species to root the tree (Table S1).

ML analyses using RAXMLHPC-MPI-SSE3 (RAXMLHPC2 on XSEDE (8.2.10); Stamatakis 2006; Stamatakis et al. 2008) were performed (at the nucleotide level) on each locus separately and on each concatenated dataset (*Ostropales* 195-taxon dataset, *Graphidaceae* 144-taxon dataset, *Spirographa* complex 20-taxon dataset; Table S1). Optimal tree and bootstrap searches were conducted with the rapid hill-climbing algorithm for 1000 replicates with the GTR substitution model (Rodríguez et al. 1990) and gamma distribution parameter as implemented in CIPRES Science Gateway V 3.3 (Miller et al. 2010). For the concatenated analyses, each dataset was partitioned into subsets using PartitionFinder2 on XSEDE (Lanfear et al. 2012) as implemented in the CIPRES portal, with greedy search and using the AICc (Akaike Information Criterion) for model selection (Table 1). Relationships receiving bootstrap support above 70% were considered well supported.

## Results

### Phylogenetic relationships of *Lobariella*-inhabiting fungi, excluding the *Spirographa* complex

The BLAST and EPA results for 32 specimens (61 newly generated sequences for eight loci) of lichenicolous fungi inhabiting *Lobariella* in Bolivia using the *Pezizomycotina* tree in T-BAS (Table S1), revealed that they are spread across five classes within this subphylum (*Arthoniomycetes*, *Dothideomycetes*, *Eurotiomycetes*, *Leotiomycetes* and *Sordariomycetes*). Phylogenetic analyses were implemented on datasets restricted to eight taxonomic groups with more inclusive sampling for a finer resolution of their affinities: *Abrothallus*, *Abrothallales* (including *Abrothallaceae*, *Aliquandostipitaceae*, *Hysteriaceae*, and *Patellariaceae*; nrITS: 479 bp, nrLSU: 1265 bp, and mrSSU: 666 bp for 58 OTUs; Fig. 1), *Arthonia*, *Arthoniales* (including *Arthoniaceae*, *Bryostigma* clade, and *Opegraphaceae*; nrLSU: 1124 bp, mrSSU: 643 bp, and *RPB2*: 864 bp

for 27 OTUs; Fig. 2), *Globonectria* and *Trichonectria*, *Hypocreales* (including *Bionectriaceae*, *Flammocladaceae*, *Nectriaceae*, *Niessliaceae*, and *Stachybotriaceae*; nrLSU: 853 bp, *RPB1*: 708 bp, *RPB2*: 1074 bp, and *TEF1*: 960 bp for 106 OTUs; Fig. 3), *Neobaryopsis*, *Hypocreales* (including *Clavicipitaceae*, *Cordycipitaceae*, *Hypocreaceae*, and *Ophiocordycipitaceae*; nrSSU: 1032 bp, nrLSU: 823 bp, *RPB1*: 700 bp, *RPB2*: 945 bp, and *TEF1*: 984 bp for 50 OTUs; Fig. 4), *Pseudodidymocyrtis*, *Pleosporales* (including *Didymosphaeriaceae*, *Lentitheciaceae*, and *Massarinaceae*; nrSSU: 987 bp, nrITS: 400 bp, and nrLSU: 875 bp for 65 OTUs; Fig. 5), *Lawreyella*, *Helotiales* (including *Chlorociboriaceae*, *Cordieritidaceae*, *Helotiaceae*, and *Sclerotiniaceae*; nrSSU: 1451 bp, nr5.8S: 456 bp, and nrLSU: 1130 bp for 50 OTUs; Fig. 6), *Sclerococcum*, *Sclerococcales* (including *Dactylosporaceae*; nrITS: 427 bp, nrLSU: 854 bp, and mrSSU: 656 bp for 44 OTUs; Fig. 7), and *Xylaria*, *Xylariales* (including *Xylariaceae*; nrITS: 383 bp, *RPB2*: 1149 bp, and *beta-tub*: 1103 bp for 20 OTUs; Fig. 8). The ML and BI analyses yielded similar topologies for each dataset. The trees are mostly congruent with recently published phylogenies (see Table 1).

*Abrothallus macrosporus* and *A. subhalei* were found to be related to a single specimen of *A. secedens*, and part of a clade also containing *A. sp.*, *A. nephromatis*, *A. cladoniae*, and a specimen of *A. suecicus*, however, with low phylogenetic confidence (Fig. 1). *Abrothallus subhalei* forms a well-supported clade (together with their anamorph: J.E. 44-1) distinct from *A. macrosporus*. Another anamorphic specimen, *A. aff. ertzii* (J.E. 5-1) seems to be closely related to the sexual state of *A. ertzii* s.str., but this relationship received low support. The large phylogenetic distance separating these two asexual morphs suggests that they may represent two distinct species (Fig. 1).

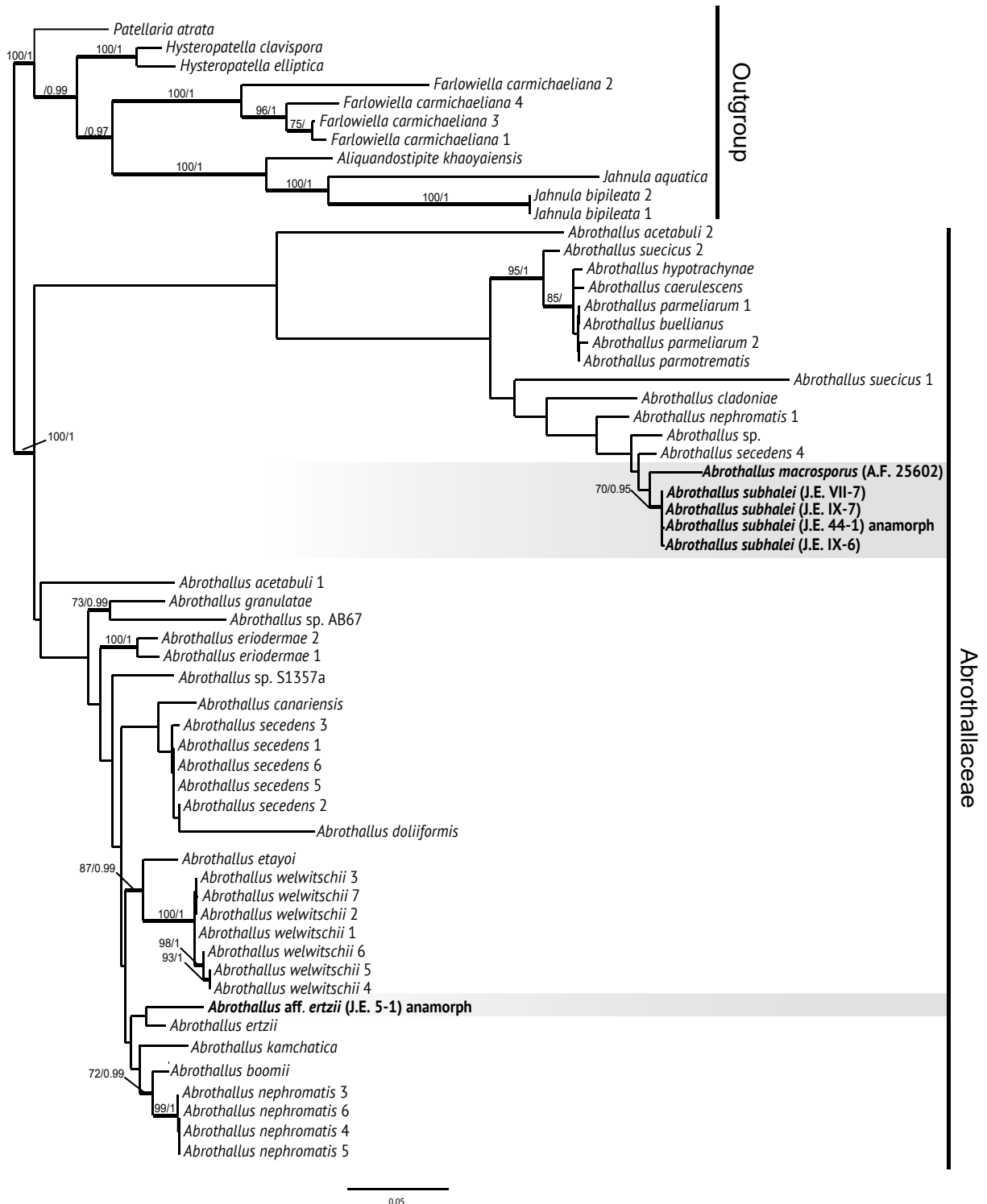
*Arthonia lobariellae* is closely related to *Arthonia 'lobariicola'* (highly supported relationship), an undescribed species from Japan (Fig. 2), which is part of the *Bryostigma* clade discussed by Frisch et al. (2014).

Because our preliminary analyses (results not shown) revealed that four species from *Hypocreales* were split into two groups belonging to *Nectriaceae* and *Cordycipitaceae*, we performed two separate phylogenetic analyses to establish their relationships within each family. *Globonectria cochensis* and *Trichonectria setadpressa* are nested within *Nectriaceae* (Fig. 3), shown to be not monophyletic because of the inclusion of *Stachybotryaceae*, a relationship that is poorly supported. *Globonectria* forms a monophyletic group together with an unidentified *Acremonium*-like a sexual state (*G. cochensis* J.E. 33-20) growing on the same host lichen. The placement of *Globonectria cochensis* is uncertain in our phylogeny, but the genus appears to be closely related to members of the *Nectriaceae*. *Globonectria* is shown to be only distantly related to other lichenicolous genera, such as *Pronectria*. *Trichonectria setadpressa* was resolved in a well-supported clade together with the mycoparasitic *T. rectipila* (Fig. 3). Additionally, anamorph-teleomorph connections are established for *Trichonectria setadpressa* (sexual state)

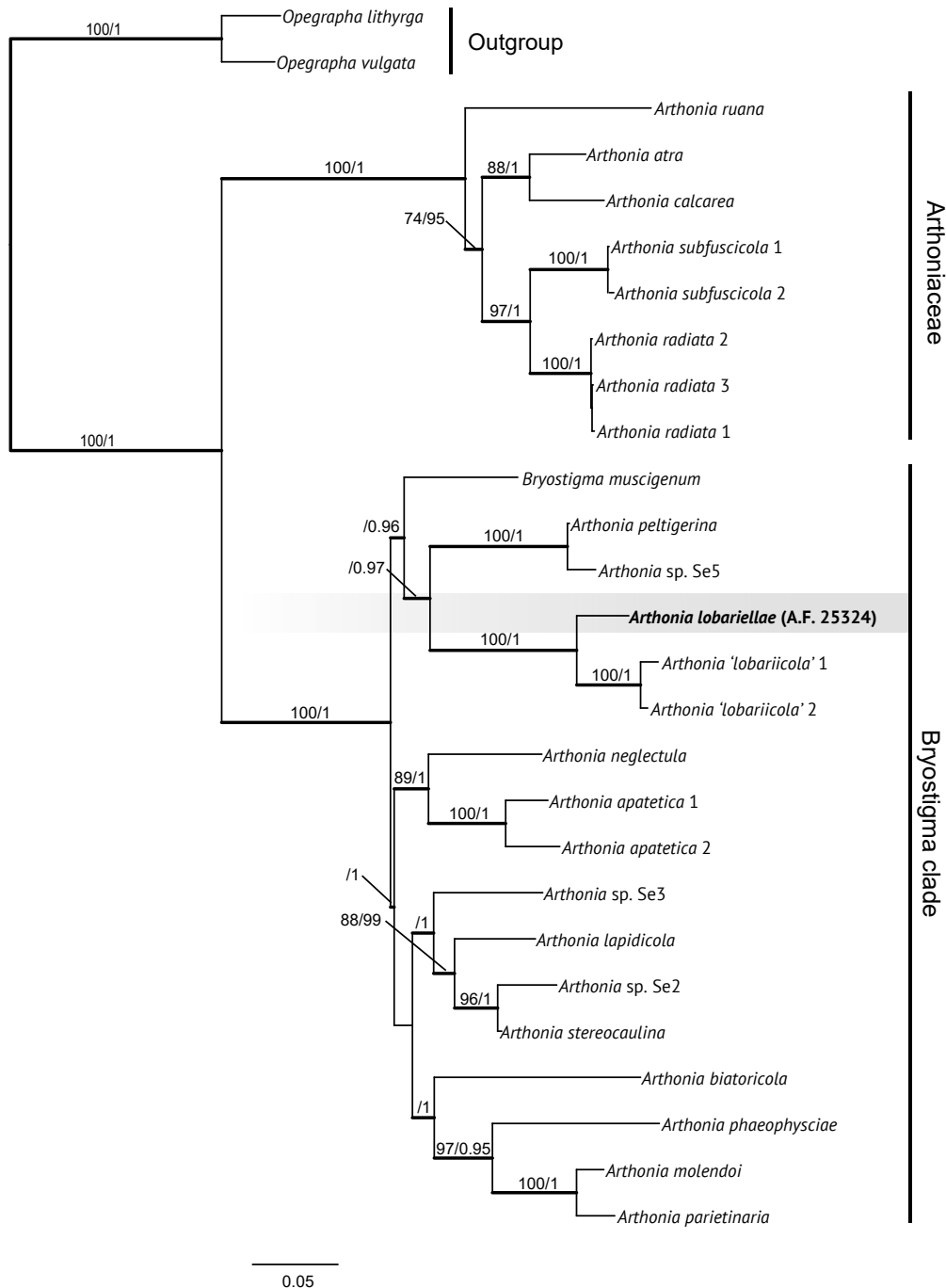
and an *Acremonium*-like asexual state (A.F. 29612 and J.E. 20-13), which together form a well-supported monophyletic group (Fig. 3).

The new genus *Neobaryopsis* (A.F. 25976-1 and J.E. 20-11) represents, together with the genus *Simplicillium*, the first lineage to split from the rest of the *Cordycipitaceae* (a result well-supported by bootstrap

and Bayesian analyses, Fig. 4). The type species of the genera *Lichenobarya* (*L. usneae*) and *Neobarya* (*N. parasitica*) are resolved in different families (*Hypocreaceae* and *Clavicipitaceae*, respectively). Their relatively distant relationship to *Neobaryopsis*, confirms the results by Lawrey et al. (2015). An anamorphic specimen of *Neobaryopsis andensis* (A.F. 25967-2) is nested within



**Figure 1.** Phylogenetic relationship of *Abrothallus* (specimens on *Lobariella* highlighted) within *Abrothallales* (including *Abrothallaceae*, *Aliquandostipitaceae*, *Hysteriaceae*, and *Patellariaceae*) inferred with ML analyses of combined nrITS, nrLSU and mrSSU dataset for 58 OTUs. Thick branches represent bootstrap values  $\geq 70\%$  and/or Bayesian posterior probabilities  $\geq 0.95$ . The *Abrothallus* species inhabiting *Lobariella* are bolded. The scale bar represents number of nucleotide substitutions per site.



**Figure 2.** Phylogenetic relationships of *Arthonia lobariellae* within *Arthoniales* (including *Arthoniaceae*, *Bryostigma* clade, and *Opegraphaceae*) inferred with ML analyses of combined nrLSU, mrSSU and *RPB2* dataset for 27 OTUs. Thick branches represent bootstrap values  $\geq 70\%$  and/or Bayesian posterior probabilities  $\geq 0.95$ . The *Arthonia* species inhabiting *Lobariella* is bolded and highlighted. The scale bar represents number of nucleotide substitutions per site.

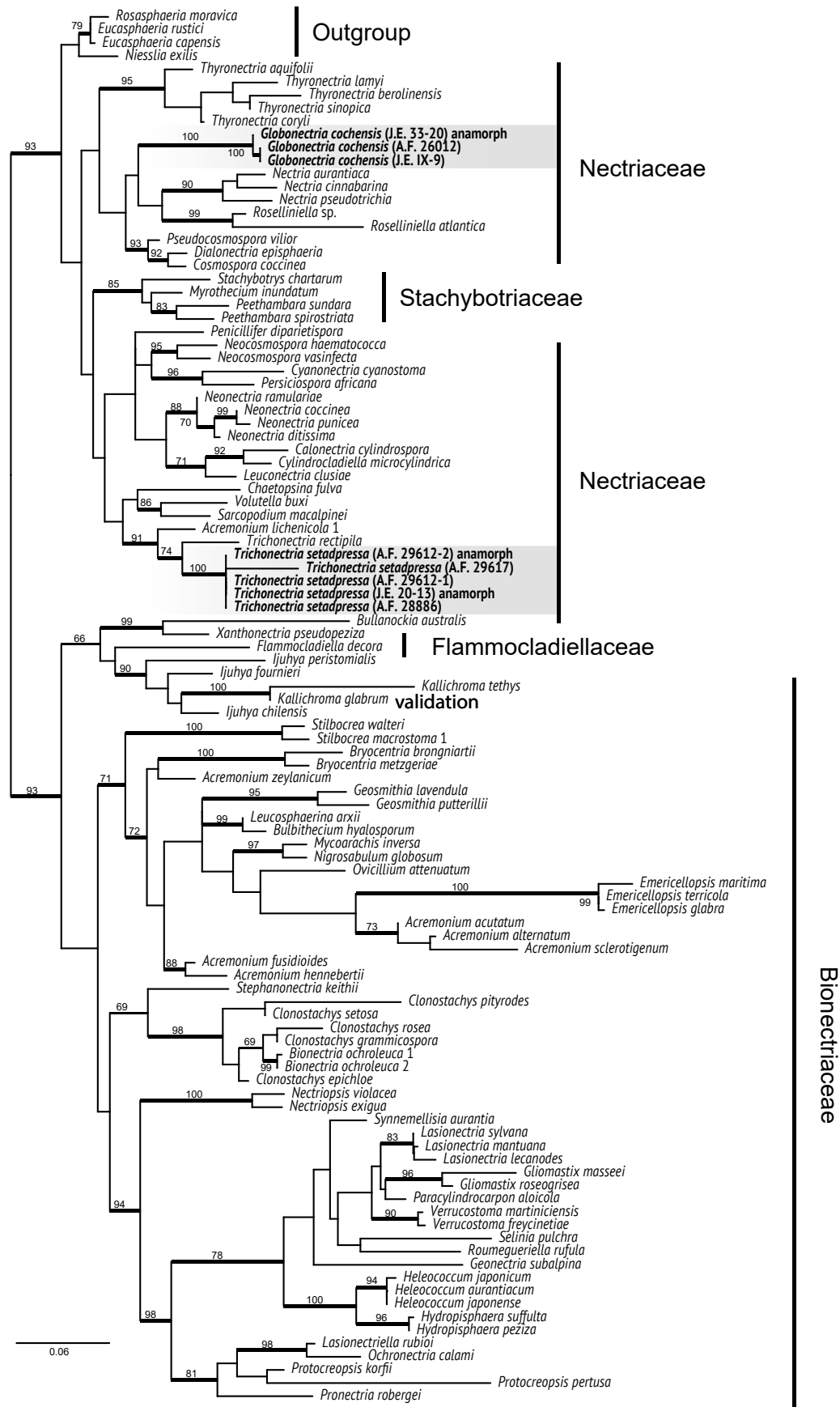
the clade represented by specimens in the sexual state of this species (Fig. 4).

A specimen morphologically very similar to members of *Didymocyrtis* (*Phaeosphaeriaceae*) is shown in our phylogeny to represent a new genus *Pseudodidymocyrtis* (*P. lobariellae* A.F. 25130), sister to the saprobic genus *Kalmusia* (highly supported relationship, Fig. 5).

Our phylogenetic analysis placed *Lawreyella lobariella* (= *Unguiculariopsis lobariella*) within *Cordieritidaceae* (encoelioid-clade according to Suija et al. 2015a) together with several lichenicolous *Helotiales* (Fig. 6). This species is well-supported within a clade that includes

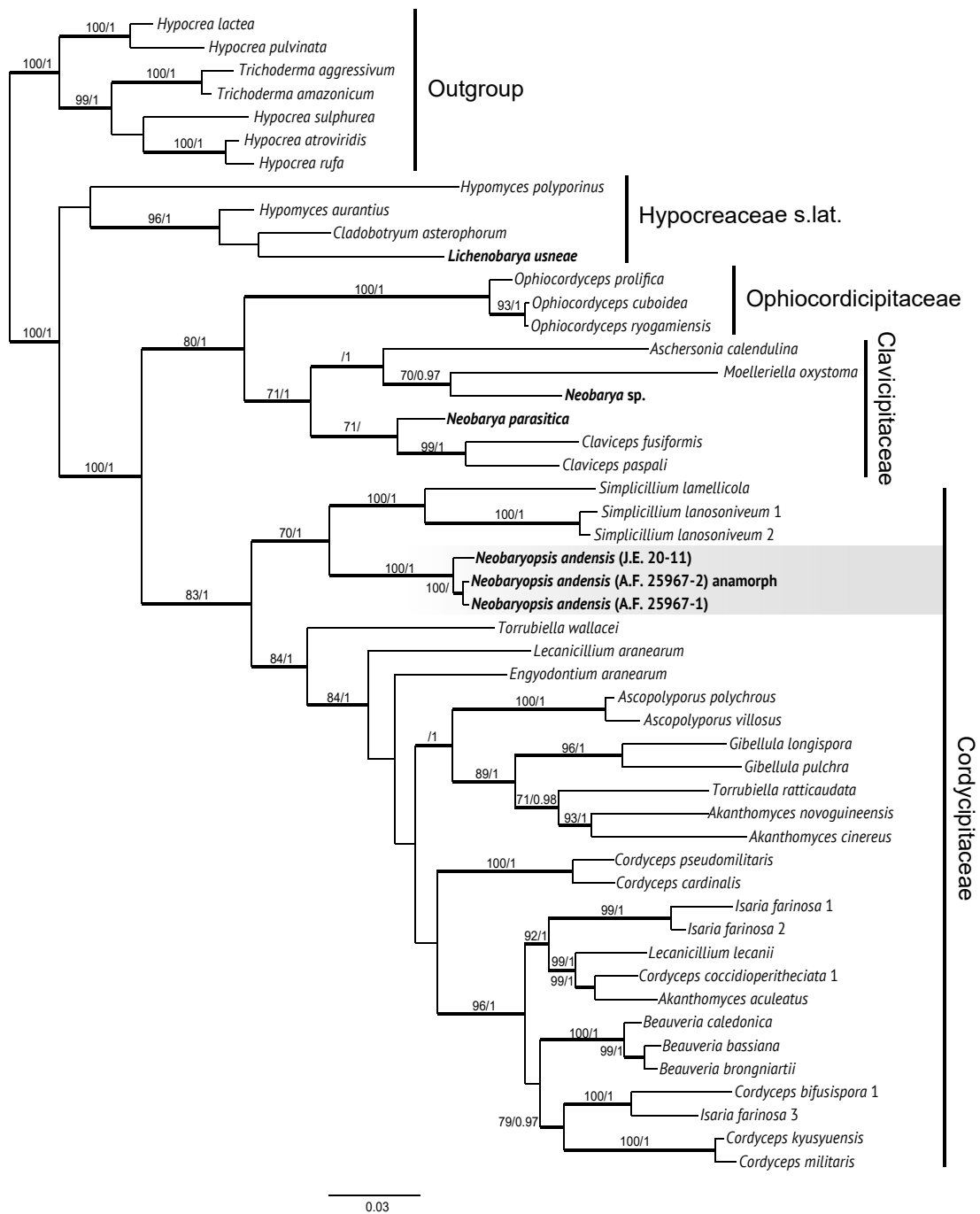
*Diplolaeviopsis ranula*, *Macroskyttea parmotremitis*, and *Protounguicularia nephromatis*. This is the first time that *P. nephromatis* is included in a phylogenetic analysis (based on newly generated sequences from Bolivia). *Unguiculariopsis*, represented in our tree by *U. lettai* and *U. thallophila*, is distantly related to *L. lobariella* within *Cordieritidaceae*. Therefore, a new genus, *Lawreyella* is proposed here to accommodate *U. lobariella*.

As previously demonstrated by Diederich et al. (2018), *Sclerococcum lobariellum* is classified within the family *Dactylosporaceae*, *Sclerococcales*. The neotropical populations represented by four Bolivian collections growing



**Figure 3.** Phylogenetic relationships of *Globonectria* and *Trichonectria* within *Hypocreales* (including *Bionectriaceae*, *Flammocladiaceae*, *Nectriaceae*, and *Stachybotriaceae*) inferred with ML analyses of combined nrLSU, *RPB1*, *RPB2* and *TEF1* dataset for 106 OTUs. Thick branches represent bootstrap values  $\geq 70\%$ . The *Globonectria* and *Trichonectria* species inhabiting *Lobariella* are bolded and highlighted. The scale bar represents number of nucleotide substitutions per site.





**Figure 4.** Phylogenetic placement of *Neobaryopsis* (highlighted) within *Hypocreales* (including *Clavicipitaceae*, *Cordycipitaceae*, *Hypocreaceae* and *Ophiocordicipitaceae*) inferred with ML analyses of combined nrSSU, nrLSU, *RPB1*, *RPB2* and *TEF1* dataset for 50 OTUs. Thick branches represent bootstrap values  $\geq 70\%$  and/or Bayesian posterior probabilities  $\geq 0.95$ . The lichenicolous species are bolded. The scale bar represents number of nucleotide substitutions per site.

on *Lobariella pallida*, together with the anamorphic fungus *Monodictys* cf. *fuliginosa* (sample A.F. 27774), form a well-supported clade (Fig. 7) sister to *S. lobariellum* s.str., the latter growing on *Lobaria pulmonaria* and represented in our tree by four samples collected in Europe (Austria, Canary Islands and France). Our results revealed that *S. lobariellum* s.lat. as delimited by Hafellner (1979) is an assemblage of at least two cryptic species (*S. lobariellum* and *S. ricasoliae*).

An undescribed asexual state of a lichenicolous *Xylaria* was revealed, with strong phylogenetic support, to be a member of *Xylaria*, subgenus *Pseudoxylaria* sensu

Hsieh et al. (2010) (Fig. 8). This lichenicolous species is sister to an endolichenic *Xylaria* species (FL0491) isolated in pure culture from *Cladonia didyma* in Florida (U'Ren et al. 2016).

Taxonomy of *Lobariella*-inhabiting species excluding the *Spirographa* complex

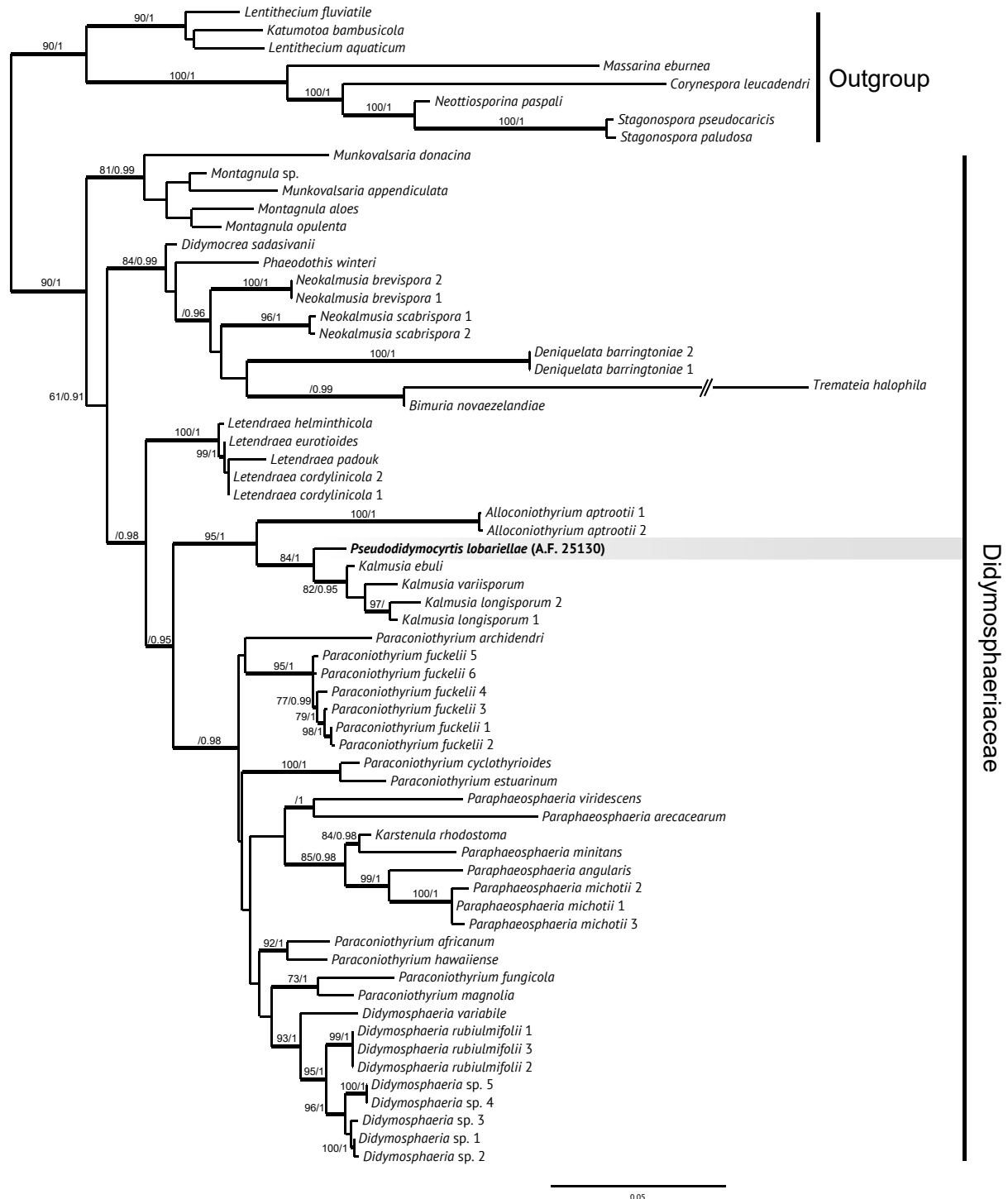
***Abrothallus* aff. *ertzii*** Suija & Pérez-Ortega

**Note.** This anamorph is characterized by having 1-septate, truncate, brown, verruculose conidia, (12.5–)14–18(–19)  $\times$  8.5–11  $\mu\text{m}$ , produced in large, sessile conidiomata,

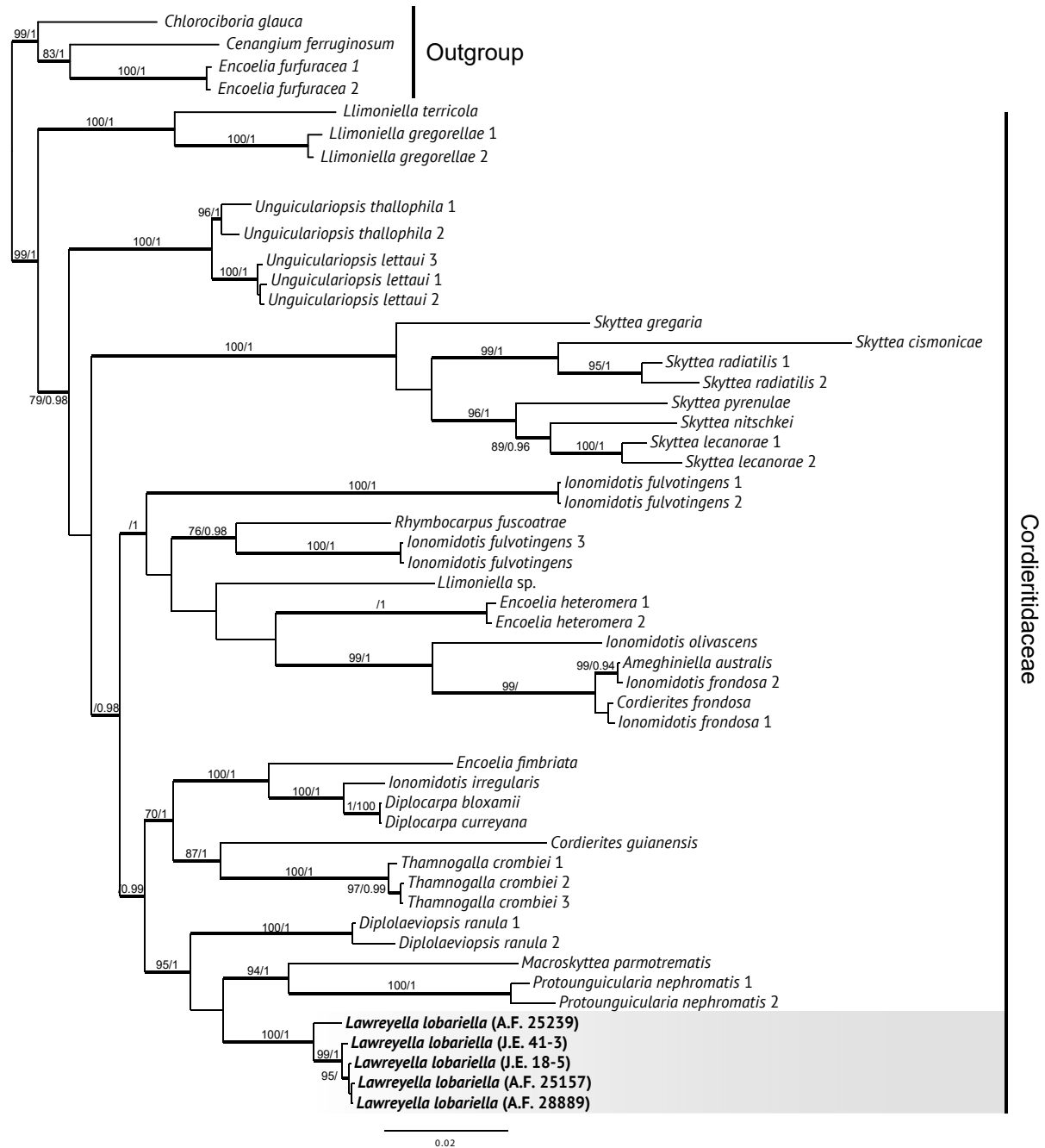
0.2–0.3 mm diam., with green and purple pigments (K+ bright-green). It represents very likely an undescribed species, that seems to be phylogenetically related (Fig. 1) to *A. ertzii* s.str. (but not conspecific) and unrelated to the sexual states of *A. subhalei* and *A. macrosporus* known from *Lobariella* (Fig. 1). A similar conidial state considered as a possible anamorph of *A. macrosporus* was described and illustrated by Etayo (2017).

*Abrothallus ertzii* was described based on telomorphic specimens from Canada (Suija et al. 2015b). This

species inhabits *Lobaria pulmonaria* and is characterized by having 1-septate ascospores [ $9-(10.3)-11.5 \times 3-(3.6)-4.5 \mu\text{m}$  according to Suija et al. 2015b], that easily break into part-spores. Its asexual state is unknown, but the species was reported by the authors as growing together with *Phoma lobariae*, a common coleomycetous fungus inhabiting *Lobaria pulmonaria*. Later, Diederich et al. (2018) assumed that *P. lobariae* is an anamorphic state of *Abrothallus*. Potentially, *A. ertzii* and *A. lobariae* may represent sexual and asexual states of a single



**Figure 5.** Phylogenetic placement of *Pseudodidymocyrtis* (shown in bold and highlighted) within *Pleosporales* (including *Didymosphaeriaceae*, *Lentitheciaceae*, and *Massarinaceae*) inferred with ML analyses of combined nrSSU, nrITS and nrLSU dataset for 65 OTUs. Thick branches represent bootstrap values  $\geq 70\%$  and/or Bayesian posterior probabilities  $\geq 0.95$ . The scale bar represents number of nucleotide substitutions per site.



**Figure 6.** Phylogenetic relationships of *Lawreyella* (shown in bold and highlighted) within *Helotiales* (including *Chlorociboriaceae*, *Cordieritiaceae*, *Helotiaceae*, and *Sclerotiniaceae*) inferred with ML analyses of combined nr SSU, nr5.8 and nrLSU dataset for 50 OTUs. Thick branches represent bootstrap values  $\geq 70\%$  and/or Bayesian posterior probabilities  $\geq 0.95$ . The scale bar represents number of nucleotide substitutions per site.

species, however, this connection was not confirmed using molecular tools (as no sequences are available recently). *Abrothallus lobariae* is very different from our material as it develops aseptate, hyaline, smooth-walled conidia of a smaller size ( $3\text{--}4 \times 2.5\text{--}3 \mu\text{m}$ ) (Etayo & Diederich 1996b).

**Ecology and distribution.** Known so far from epiphytic *Lobariella auriculata* and *L. exornata* in Bolivia and Ecuador (Etayo 2017).

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Muñecas: Área Natural de Manejo Integrado Nacional Apolobamba, above Camata, close to Charazani-Paujeyuyo road, open area with shrubs, on *Lobariella auriculata*,  $15^{\circ}14'35''\text{S}$ ,

$68^{\circ}45'09''\text{W}$ , 1900 m, J.E. 5-1 (LPB, hb. Etayo). ECUADOR. Prov. Imbabura. Otavalo, Reserva bosque nublado INTAG, La delicia, bosque nublado con *Gunnera* y helechos arborescentes, sobre *L. subexornata*, corticícola, 2700 m, J.E. 25627 y Z. Palice (QCA, hb. Etayo).

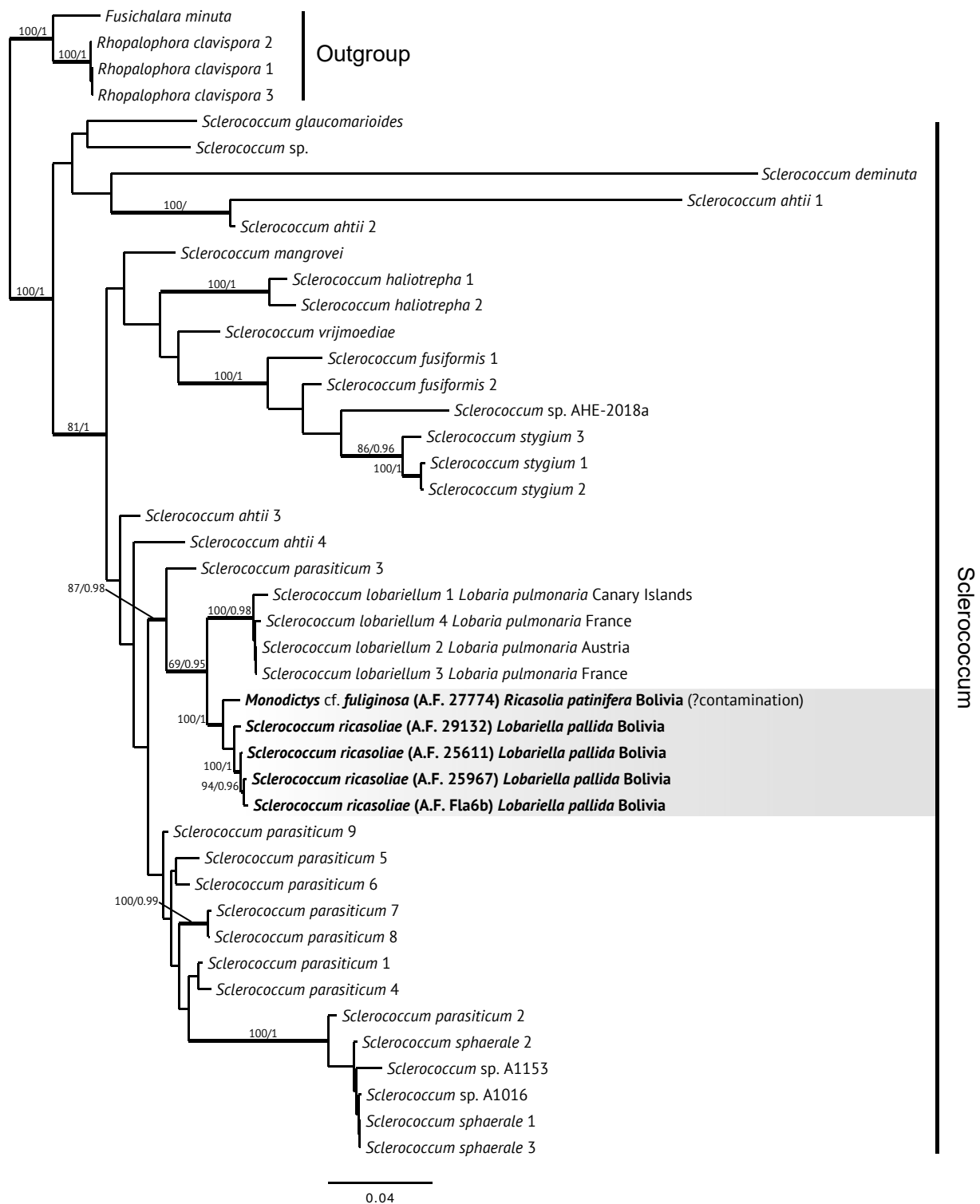
***Abrothallus macrosporus*** Etayo & R. Sant.

**Notes.** This species was described by Etayo (2010b) from *Lobariella crenulata* specimens collected in Colombia and Peru. It is characterized by having large, epruinose ascomata and 3-septate ascospores of  $18.5\text{--}24 \times 7\text{--}9 \mu\text{m}$ . The Bolivian samples fit the original description, but some specimens have slightly larger ascospores,  $19\text{--}27 \times 7\text{--}10 \mu\text{m}$ .

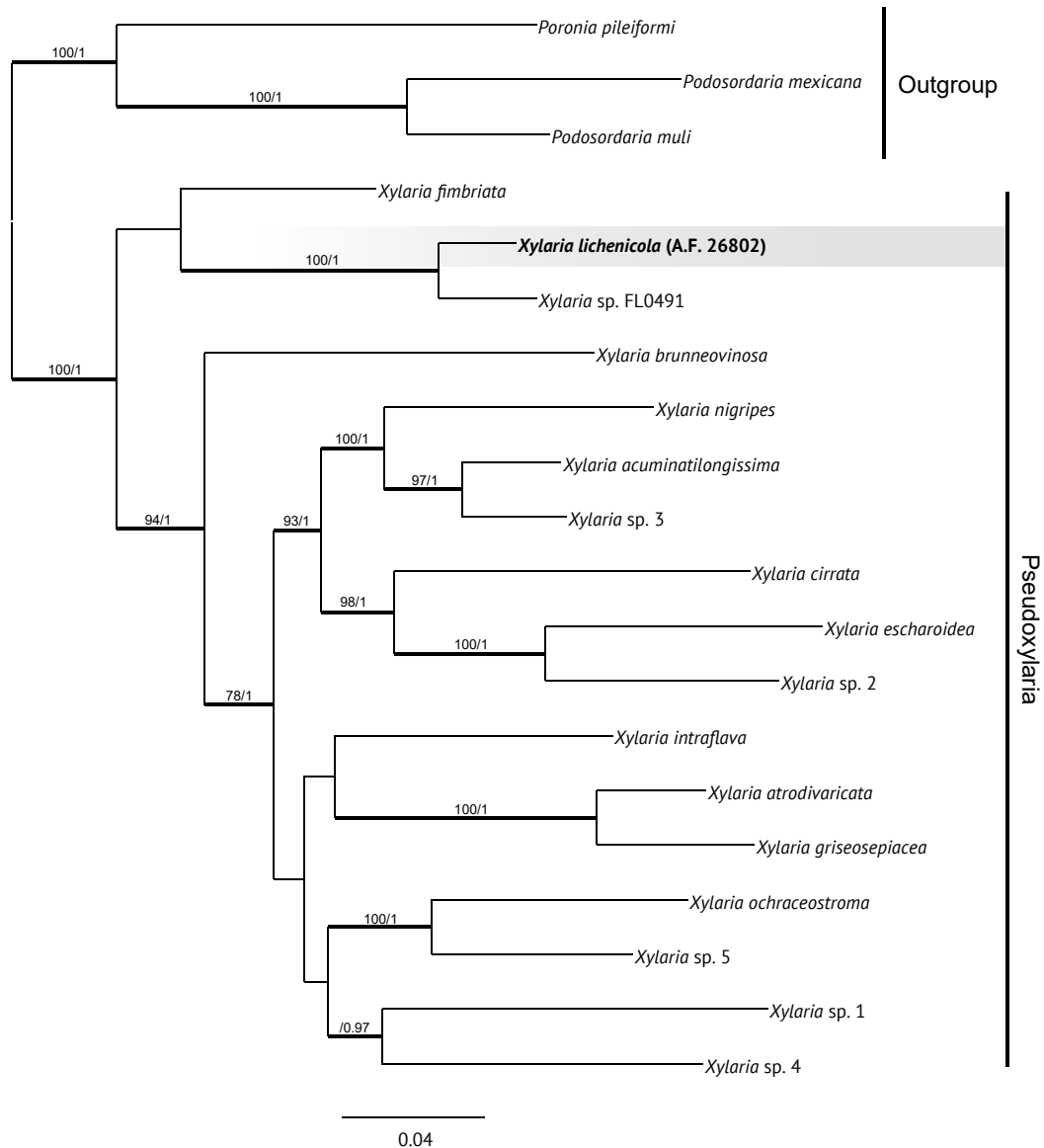
**Ecology and distribution.** Known from Bolivia, Colombia and Peru (Etayo 2010b), and Ecuador (Etayo 2017) from epiphytic *Lobariella crenulata* and *L. pallida*.

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Meruvia close to Monte Punku, 17°35'06"S, 65°14'54"W, 3283 m, *Podocarpus-Polyplepis* forest, on corticolous *Lobariella* sp., M.K. 15043b; on *L. pallida*, A.F. 25602 (KRAM, LPB), on *L. pallida*, A.F. 25592;

between Meruvia and Monte Punku, 17°34'43"S, 65°15'25"W, 3082 m, *Podocarpus* forest, corticolous, on *L. pallida*, A.F. 25615 (KRAM, LPB); Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, corticolous, on *L. pallida*, A.F. 24708, on *Lobariella* sp., A.F. 24705 (KRAM, LPB), on *L. cf. pallida*, J.E. 29501 (LPB, hb. Etayo); Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado Nacional Apolobamba, near Rio Pelechuco, below Pelechuco close to new road to Apolo,



**Figure 7.** Phylogenetic relationships of *Sclerococcum ricasoliae* and *Monodictys cf. fuliginosa* (shown in bold and highlighted) within *Sclerococcales* (including *Dactylosporaceae*) inferred with BI analyses of combined nrITS, nrLSU and mrSSU dataset for 44 OTUs. Thick branches represent bootstrap values  $\geq 70\%$  and/or Bayesian posterior probabilities  $\geq 0.95$ . The scale bar represents number of nucleotide substitutions per site.



**Figure 8.** Phylogenetic relationships of *Xylaria lichenicola* within *Xylariaceae* [including *Pseudoxyllaria* ‘TE’ clade (according to U’Ren et al. 2016), and also *Poronia* and *Podosordaria*] inferred with ML analyses of combined nrITS, *RPB2* and *beta-tub* dataset for 20 OTUs. Thick branches represent bootstrap values  $\geq 70\%$  and/or Bayesian posterior probabilities  $\geq 0.95$ . The lichenicolous species is bolded and highlighted. The scale bar represents number of nucleotide substitutions per site.

14°47'28"S, 69°01'32"W, 2860 m, open area with scattered trees, on corticolous *L. pallida*, M.K. 14824 (LPB); Prov. Nor Yungas: km 62 on the road Coroico–La Paz, 16°14'30"S, 67°49'58"W, 2848 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27650 (LPB); near Nogalani village, on the road Coroico–La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27960, 27980 (LPB, hb. Etayo). Prov. Bautista Saavedra: km 202 on the road from Apolo to Charazani villages, 20 km from Charazani, 15°12'35"S, 68°51'30"W, 2259 m, transition Yungas montane forest-cloud forest, on apothecia of *L. pallida*, J.E. 27420 (LPB, hb. Etayo).

***Abrothallus subhalei*** Etayo, Flakus & Kukwa, sp. nov. (Fig. 9)

Mycobank MB 833328

Diagnosis: Differs from *A. halei* in having smaller ascospores, 9–13  $\times$  3–5  $\mu\text{m}$ , which remain entire in ascus, yellowish green pruinose to almost black acomata, 0.22–0.45 mm diam., immersed black conidiomata, 100–160  $\mu\text{m}$  diam., and hyaline,

bacilliform to ellipsoid conidia, 2.5–7  $\times$  1–2.5  $\mu\text{m}$ , borne on large conidiogenous cells, 10–15  $\times$  1.5–2.5  $\mu\text{m}$ , and by the host selection (*Lobariella*).

Type: Dept. Tarija, Prov. Burnet O’Connor, Sandiego Sur, campamento de los bomberos, old road between Tarija and Entrerios, 21°28'10"S, 64°12'37"W, 1912 m, disturbed Boliviano-Tucumano forest, on *Lobariella crenulata*, 30 July 2015, Javier Etayo IX-6 (LPB – holotype!).

**Description.** Mycelium immersed, K/I–. Ascomata apothecioid, superficial on the thallus of the host, plane then convex to subsphaerical, covered by a yellowish green pruina and with age devoid of pruina and then almost black, 0.22–0.45 mm diam., constricted at the base, sessile. Epitecium brownish, covered by small yellow crystals and brown pigments dissolving in K, ~5  $\mu\text{m}$  tall. Hymenium 60–80  $\mu\text{m}$  tall, hyaline or with greenish and purple pigments in the upper part, K+ aeruginose, N± violet, hyaline in the lower part. Interascal filaments 1–1.5  $\mu\text{m}$

wide, dichotomously branched but strongly anastomosing in the upper part, the tips slightly widened, up to 2 µm wide. Subhymenium hyaline, indistinct, 15–25 µm tall. Hypothecium hyaline to pale brown, ~60–70 µm tall, of isodiametric to enlarged cells, 3–13 × 2–6 µm. Exciple evident but disappearing in older ascomata, 20–30 µm wide, composed of radially arranged hyphae in the upper part, and of isodiametric cells below. Asci bitunicate, clavate, with an apical apparatus when young, 40–63 × 7–10 µm, 8-spored. Ascospores brown, (1–)3-septate, 9–( $\bar{x}$ =11 s=1)–13 × 3–( $\bar{x}$ =4 s=0.5)–5 µm, l/b ratio 2.2–( $\bar{x}$ =2.8 s=0.3)–4 (n=80), asymmetrical, constricted at the middle septum, usually not breaking into part-spores, verruculose. Anamorph pycnidial. Conidiomata black, *Vouauxiomyces*-like, immersed to slightly erumpent, 100–160 µm diam., usually with a white mass of conidia at the top. Pycnidial wall dark brown, 10–13 µm wide, of isodiametric cells, 2–6 µm diam. Conidiogenous cells emerging from the inner part of the wall, long, phialidic, 10–15 × 1.5–2.5 µm, sometimes with 1(–2) pseudoseptata. Conidia bacilliform to narrowly ellipsoidal, hyaline, with both ends obtuse, 2.5–( $\bar{x}$ =4.6 s=1.1)–7 × 1–( $\bar{x}$ =1.8 s=0.3)–2.5 µm, l/b ratio 1.2–( $\bar{x}$ =2.7 s=1)–6 (n=74).

**Etymology.** Epithet refers to the morphologically similar *Abrothallus halei*.

**Ecology and distribution.** Grows on epiphytic *Lobariella auriculata*, *L. crenulata* and *L. pallida* in Bolivia.

**Notes.** *Abrothallus subhalei* is characterized by having small, (1–)3-septate ascospores, which remain unbroken in the ascus, and medium-sized apothecia that are usually yellow pruinose. The asexual state is characterized by having immersed conidiomata producing bacillar to narrowly ellipsoidal (2.5–6 × 1.5–2 µm) conidia, borne on large conidiogenous cells. The most similar taxon, *A. halei* was described from *Lobaria pulmonaria* and *Ricasolia quercizans* collected in Norway and the USA (Suija et al. 2011, 2015b). It is characterized by having ascospores breaking into two part-spores within the ascus when mature, 9–(10.7)–14 × 3.0–(4.0)–5.0 µm (according to Suija et al. 2011), and ascomata of 200–500 µm diam. (Suija et al. 2011). The asexual state of that species is unknown. Another species known only from its anamorphic state is *A. lobariae*, but conidia in this species have a different shape and size (3–4 × 2.5–3 µm in Etayo & Diederich 1996b).

**Specimens examined (sexual state).** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Koricaza, 17°33'21"S, 65°16'29"W, 2950 m, Páramo Yungueño, on trees, on *Lobariella* sp., J.E. 29323 (LPB, hb. Etayo); between Meruvia and Monte Punku, 17°34'43"S, 65°15'25"W, 3082 m, *Podocarpus* forest, corticolous on *L. crenulata*, A.F. 25617 (KRAM, LPB); Meruvia close to Monte Punku, 17°35'06"S, 65°14'54"W, 3283 m, *Podocarpus-Polylepis* forest, corticolous, on *L. crenulata*, A.F. 25587, on *Lobariella* sp., A.F. 25562 (KRAM, LPB); Wayra Mayu close to Monte Punku, 17°33'30"S, 65°16'08"W, 2750 m, lower montane Yungas cloud forest, corticolous, on *L. auriculata*, A.F. 25847 (KRAM, LPB); Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi: Pukara between Keara and Keara Bajo,

14°42'09"S, 69°05'17"W, 3420 m, open area with shrubs, Ceja de Monte Inferior (Altimontano), on corticolous *L. reticulata*, M.K. 14934 (LPB), corticolous, on *L. crenulata*, A.F. 25337 (KRAM, LPB); near Keara Bajo, 14°41'59"S, 69°04'34"W, 3290 m, open area with shrubs and scattered trees, corticolous, on *L. crenulata*, A.F. 25250 (KRAM, LPB); Prov. Larecaja: Jocollone village and 1 km further, Paramo Yungeño vegetation, open anthropogenic area, much *Berberis*, NE oriented slope, on *Lobariella* sp., 15°37'35"S, 68°41'21"W, 3545 m, 14 May 2011, J.E. 27212 (LPB, hb. Etayo); Prov. Muñecas: Área Natural de Manejo Integrado Nacional Apolobamba, above Camata, close to Charazani–Paujeyuyo road, 15°14'35"S, 68°45'09"W, 1900 m, open area with shrubs, corticolous, on *L. crenulata*, A.F. 24941 (KRAM, LPB); Prov. Nor Yungas: carretera Coroico-La Paz, bosque nublado yungas, sendero que parte de la Estación de servicio, on *L. pallida*, 3220–3250 m, S16°17'09", W67°51'00", J.E. 26712 (LPB, hb. Etayo); below Unduavi village, on the road La Paz–Chulumani, 16°18'27"S, 67°53'48"W, 3210 m, Yungas cloud forest, on *L. pallida*, A.F. 22187 (KRAM, LPB). Dept. Tarija. Prov. Burnet O'Connor: old road between Tarija and Enterrios, on *Lobariella* sp., 21°27'35"S, 64°13'28"W, 1917 m, Boliviano-Tucumano forest with *Podocarpus*, J.E. VII-7 (LPB, hb. Etayo).

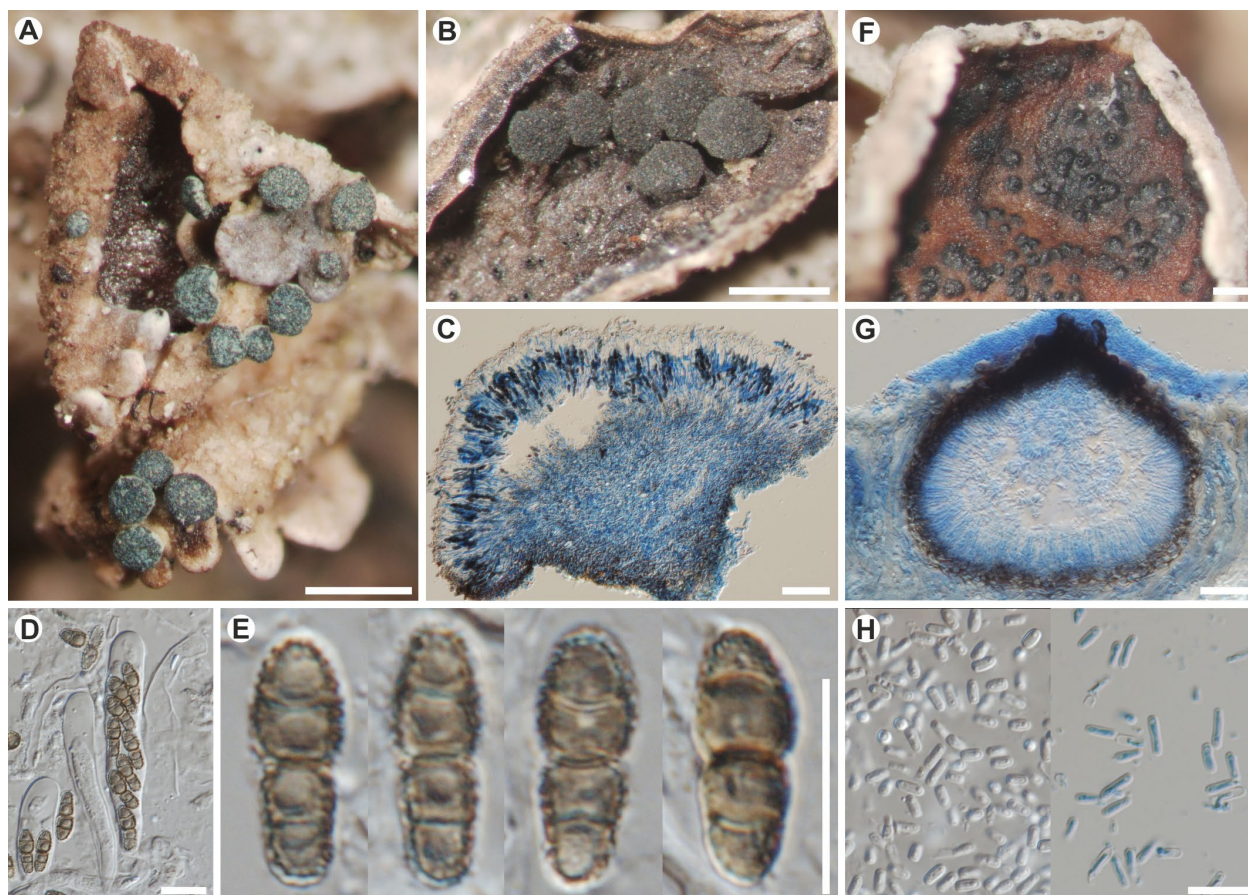
**Specimens examined (asexual state).** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Koricaza, 17°33'21"S, 65°16'29"W, 2950 m, Páramo Yungueño, on trees, on *Lobariella* sp. J.E. 29323 (LPB, hb. Etayo). Prov. Tiraque: Parque Nacional Carrasco, old guard's camp close to T7, open area with shrubs, on *L. pallida*, 17°18'23"S, 65°45'60"W, 3360 m, J.E. s.n. (44-1) (LPB, hb. Etayo). Dept. La Paz. Prov. Nor Yungas: carretera Coroico-La Paz, bosque nublado yungas, sendero que parte de la Estación de servicio, on *L. pallida*, 3220–3250 m, S16°17'09", W67°51'00", J.E. 26712 (LPB, hb. Etayo). ECUADOR. Dept. Otavalo. Prov. Imbabura: Lago Cuicocha, bosque arbustivo (2–3 m altura) con *Puya hamata*, taludes cerca del restaurante, on *L. pallida*, 17N 0795589, 0033416, 3100 m, J.E. 25554 (hb. Etayo).

#### *Arthonia lobariellae* Etayo

**Notes.** This recently described species (Etayo 2017) is characterized by having pale orange-brown to dark brown, large, irregular ascomata (flat when young and resembling galls of *Tremella* when well developed), 1-septate, hyaline ascospores, 6–11 × 3.5–5 µm and/or 1-septate conidia, 11–14 × 2.5–3.5 µm. In Bolivia its *Bachmanniomyces*-like anamorphic state seems to be relatively abundant. *Bachmanniomyces santessonii* (potential anamorph of *Arthonia digitispora*, fide Etayo 2002) described from Peru on *Sticta* has similar conidiomata that differ in having smaller conidia 9–10.5 × 2.5–3 µm (Etayo 2010b).

**Ecology and distribution.** Known from Bolivia, Colombia and Ecuador (Etayo 2017) from epiphytic *Lobariella crenulata* and *L. pallida*.

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Meruvia close to Monte Punku, 17°35'06"S, 65°14'54"W, 3283 m, *Podocarpus-Polylepis* forest, corticolous, on *Lobariella* sp. growing on bark, M.K. 15036d (LPB); on *L. crenulata*, M.K. 15046a (LPB); on *L. crenulata*, A.F. 25558, 25559 (KRAM, LPB); between Meruvia and Monte Punku, 17°34'43"S, 65°15'25"W, 3082 m, *Podocarpus* forest, on corticolous *L. crenulata*, M.K. 15051b (LPB); near Río Batea Mayu close to Monte Punku, 17°31'33"S, 65°16'21"W, 2430 m, lower montane Yungas cloud forest, corticolous, on



**Figure 9.** *Abrothallus subhalei* (A–E, teleomorph on *Lobariella crenulata*, based on J.E. IX-6, holotype; F–H, anamorph on *L. pallida*, based on J.E. 44-1). A – pruinose apothecial ascomata on apothecial margin of the host; B – epruinose ascomata on apothecial disc of the host; C – section of ascomata in LPCB; D – asci in KOH; E – ascospores in water; F – pycnidial conidiomata immersed in apothecial hymenium of the host; G – section of conidiomata in LPCB; H – conidia in water (left) and LPCB (right). Scales: A–B = 500  $\mu$ m; C = 50  $\mu$ m; D, E, H = 10  $\mu$ m; F = 250  $\mu$ m; G = 25  $\mu$ m.

*L. pallida*, A.F. 25815 (KRAM, LPB); Wayra Mayu close to Monte Punku, 17°33'30"S, 65°16'08"W, 2750 m, lower montane Yungas cloud forest, corticolous, on *L. pallida*, A.F. 25858 (KRAM, LPB); on *Lobariella* sp., M.K. 15175b (LPB); Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, corticolous, *L. pallida*, A.F. 24715 (KRAM, LPB); Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *L. cf. pallida*, J.E. 29499 (LPB, hb. Etayo); on *L. pallida*, J.E. 29500 (LPB, hb. Etayo). Prov. Tiraque: Parque Nacional Carrasco, Camino de los Nubes, Antenas Sillar-Villa Tunari old road, 17°12'32"S, 65°41'52"W, 3520 m, upper montane Yungas cloud forest, corticolous, on *L. crenulata*, A.F. 25986 (KRAM, LPB); Dept. La Paz. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, near Keara Bajo, 14°41'59"S, 69°04'34"W, 3290 m, open area with shrubs and scattered trees, corticolous, on *L. pallida*, A.F. 25217, 25246 (KRAM, LPB), on *L. crenulata*, A.F. 25245 (KRAM, LPB); on *L. pallida*, M.K. 14861b, 14868 (LPB, UGDA); below Keara Bajo, 14°41'47"S, 69°04'10"W, 3160 m, open area with shrubs and scattered trees, corticolous, on *L. pallida*, A.F. 25292, 25293, 25301 (KRAM, LPB); Pukara between Keara and Keara Bajo, 14°42'09"S, 69°05'17"W, 3420 m, open area with shrubs, corticolous, on *L. pallida*, A.F. 25323, 25324, 25325, M.K. 14918, 14919, 14920, 14923, 14929, 14932 (KRAM, LPB, UGDA); Área Natural de Manejo Integrado Nacional Apolobamba, below Pelechuco, 14°49'08"S, 69°03'50"W, 3560 m, open area with shrubs and *Polylepis* trees, corticolous, on *L. pallida*, A.F. 25459 (KRAM, LPB); Dept. La Paz. Prov. Murillo: Sainani, Valle del Zongo,

16°07'03"S, 68°04'42"W, 2170 m, open area with shrubs and scattered trees, corticolous, on *L. pallida*, A.F. 26277 (KRAM, LPB); Valle del Zongo, páramo yungueño, rocas sueltas entre pastos con arbustos, on *Lobariella* sp., 3375 m, S16°10'15", W68°08'02", J.E. 26796, (LPB, hb. Etayo); Valle del Zongo, bosque yungas nublado, on *L. pallida* on bryophytes, 2900 m, 16°08'38"S, 68°06'59"W, J.E. 26811 (LPB, hb. Etayo). Prov. Nor Yungas: Desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, bosque nublado; on *L. pallida*, 3210 m, S16°18'27", W67°53'48", J.E. 26915, 26936, (LPB, hb. Etayo). Dept. Santa Cruz. Prov. Manuel María Caballero: close to Siberia, 17°48'13"S, 64°40'45"W, 2550 m, in closed forest, on *L. pallida* on branches, J.E. 29450 (LPB, hb. Etayo).

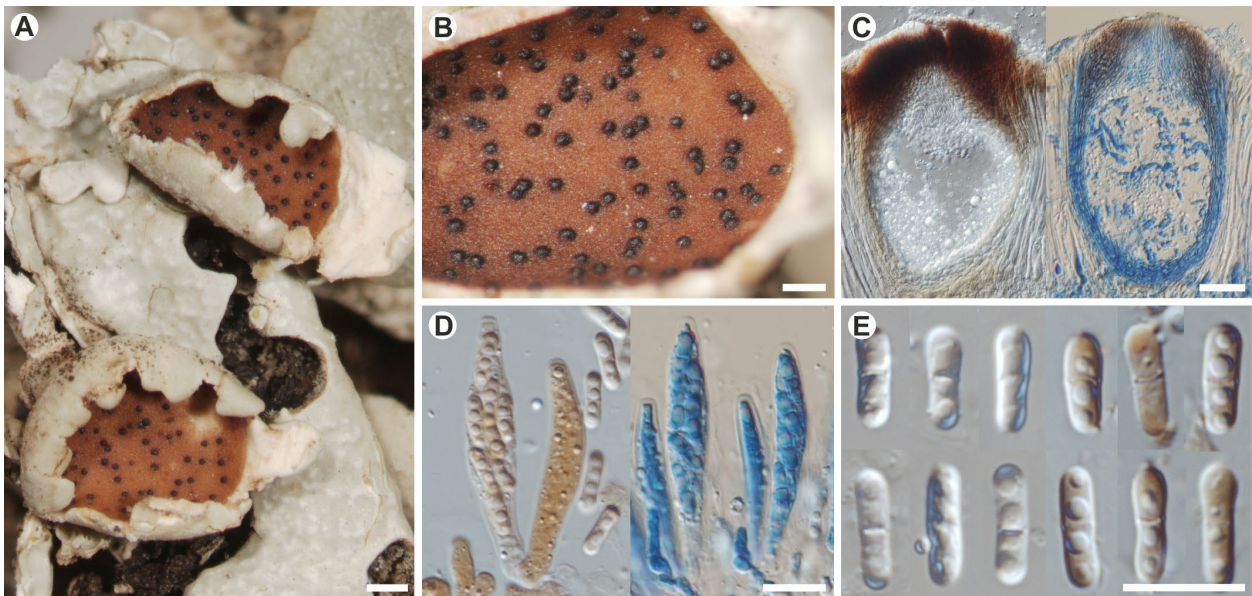
***Atronectria lobariellae* Etayo & Flakus, sp. nov. (Fig. 10)**

MycoBank MB 833329

Diagnosis: Differs from *A. magellanica* by smaller ascomata, 70–90  $\mu$ m wide and 90–130  $\mu$ m tall, the presence of oil guttules in the peridium, the absence of papillae, and its ecological preferences (growing on apothecial hymenia of *Lobariella crenulata*).

Type: Bolivia: Dept. La Paz, Prov. Bautita Saavedra, 28 km from Charazani village, on the road Charazani–Apolo, 15°12'43"S, 68°47'25"W, 1650–1775 m, Yungas montane forest, open area with boulders or. SW, on *L. crenulata*, 18 May 2011, Javier Etayo 27343 (LPB – holotype!; hb. Etayo – isotype!).

**Description.** Mycelium hyaline, immersed. Ascomata perithecioid dispersed, black, almost completely



**Figure 10.** *Atronectria lobariellae* (on *Lobariella crenulata*, based on A.F. 24939). A–B – perithecioid ascomata immersed in apothecial hymenium of the host; C – section of ascomata in water (left) and LPCB (right); D – asci in Congo Red (left) and LPCB (right); E – ascospores in water (left) and Congo Red (right). Scales: A = 500  $\mu\text{m}$ ; B = 250  $\mu\text{m}$ ; C = 25  $\mu\text{m}$ ; D–E = 10  $\mu\text{m}$ .

immersed in the hymenium of the host (only the apical part of the peridium is slightly above the hymenium surface), subsphaerical to widely pyriform, 70–90  $\mu\text{m}$  wide and 90–130  $\mu\text{m}$  tall, without papilla. Peridium 7–12  $\mu\text{m}$  thick, hyaline, composed of several rows of thick-walled, isodiametric to elongated cells, 2–12  $\times$  1.5–3  $\mu\text{m}$ , thicker in the upper part, up to 20–30  $\mu\text{m}$  wide, with dark orange-brown to almost black color, K+ slightly purplish, N+ bright orange-brown, with yellowish orange oil guttules located in lower part of peridium, 4–7  $\mu\text{m}$  diam. Hymenium I+ orangish, KI–, composed of simple to sparsely branched, septate paraphyses, 4–7  $\mu\text{m}$  wide, strongly constricted near septa, and soon disappearing. Peryphyses thin, abundant around ostiolum, simple to septate, thinner at the apical part, 10–17  $\times$  0.5–1.5  $\mu\text{m}$ . Asci unitunicate, 8-spored, elongate clavate, obtuse (in water) to truncate (in K), slightly thickened apically (K/I–), with many small oil droplets (even in mature ascomata), 35–55  $\times$  7–10  $\mu\text{m}$ . Ascospores cylindrical, rarely ellipsoidal, straight, with a thin wall, hyaline, 1-septate, usually with two or more oil guttules per cell, not constricted at the septum, 6–( $\bar{x}$ =9 s=1.2)–11  $\times$  2.5–( $\bar{x}$ =2.8 s=0.3)–3.5  $\mu\text{m}$ , l/b ratio 2–( $\bar{x}$ =3.3 s=0.5)–4 (n=76), without a perispore.

**Etymology.** The epithet refers to the host genus.

**Ecology and distribution.** This species is known from four localities in Bolivia where it grows in the apothecial disks of *Lobariella crenulata*.

**Notes.** This hypocrealean fungus is a member of the previously monotypic genus *Atronectria* with *A. magellanica* known in southern South America from *Nephroma antarcticum*, *Pseudocyphellaria coriifolia* and *P. hillii* (Etayo & Sancho 2008). The new species, *A. lobariellae*, was found in the apothecial hymenia of *Lobariella crenulata*. *Atronectria magellanica*, which grows on the thallus of different hosts (not on the hymenium), clearly

differs by having bigger ascomata (120–170  $\mu\text{m}$  diam.), the absence of oil guttules in the peridium, the presence of prominent papillae, and ascospores containing refringent oil guttules (Etayo & Sancho 2008).

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado de Apolobamba, near Río Pelechuco, below Pelechuco close to new road to Apolo, 14°46'39"S, 69°00'35"W, 2550 m, on *L. pallida*, J.E. 13-3 (LPB, hb. Etayo). Dept. La Paz. Prov. Muñecas: Área Natural de Manejo Integrado Nacional Apolobamba, above Camata, close to Charazani-Paujeyuyo road, 15°14'35"S, 68°45'09"W, 1900 m, open area with shrubs, corticolous, on discs of *L. crenulata*, A.F. 24939 (KRAM, LPB). Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, bosque nublado; 3210 m, 16°18'27"S, 67°53'48"W, on disk of *L. crenulata*, J.E. 26925 (LPB, hb. Etayo).

***Capronia epilobarina*** S. Y. Kondr. & D. J. Galloway

**Notes.** The species was described by Kondratyuk and Galloway (1995b) from a species of *Lobaria* that has recently been shown to belong to *Lobariella* (Etayo 2017). *Capronia epilobarina* is characterized by having submuri-form ascospores with (0–)3–5 transverse and 0–1 longitudinal septa, (20–)21.5–25.5(–29)  $\times$  (4.5–)5.5–7  $\mu\text{m}$ , and ascomata up to 250  $\mu\text{m}$  diam. and covered by curved hairs, 45–54  $\times$  3.5–4  $\mu\text{m}$  (Kondratyuk & Galloway 1995b; Etayo 2017). It is probably a rare species as it was not re-collected during lichen explorations of Bolivia, Colombia and Ecuador.

**Ecology and distribution.** Known only from the type collection in Ecuador on *Lobariella* sp. (Kondratyuk & Galloway 1995b; Etayo 2017).

***Capronia* cf. *solitaria*** Etayo

**Notes.** This species was originally described from *Heterodermia* sp. in Ecuador, but also reported from



*Lobaria pulmonaria*, *Rinodina* sp. and *Sticta* sp. (Etayo 2017). It is characterized by having small ascospores, 50–100 µm diam., and submuriform, fusiform ascospores with (0–3–)4–5 transverse and 0–(2) longitudinal septa, 13–16 × 4–6 µm, and aseptate, straight setae, 21–42 × 2.5–5 µm, developing close to the ostiole (Etayo 2017).

Our Bolivian sample, growing on *Lobariella pallida*, differs from the original description in having 3-septate, ascospores, 15–16 × 4.5–5 µm, and most probably represents an undescribed species that deserves further studies. See also comments under *C. solitaria* in Etayo (2017).

**Ecology and distribution.** The species has been reported from Ecuador and Spain on *Lobaria pulmonaria*, *Rinodina* sp. and *Sticta* sp. (Etayo 2017). As lichenicolous on *Lobariella* (*L. pallida*, *L. subexornata*) it is known only from two localities in Bolivia and Ecuador (Etayo 2017).

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Nor Yungas: near Siniari colony, km 74 on the road Coroico-La Paz, 16°13'20"S, 67°50'37"W, 2090–2186 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27637 (LPB, hb. Etayo).

#### *Ceratosporium* sp.

**Notes.** *Ceratosporium* is an anamorphic state of the cosmopolitan, saprobic genus *Iodosphaeria*, *Xylariales* (Samuels et al. 1987; Hsieh et al. 1997). Although we found in Bolivia a fungus morphologically similar to *Ceratosporium* growing on *Lobariella pallida*, we decided to postpone any taxonomic conclusions, as the material is sparse and the genus has never been reported from lichens. Our sample is characterized by having dark brown, smooth conidia with three arms, each one 130–147 × 16–19 µm, tapering towards the apex, with 13–14 distoseptate cells, and large, dark brown, 4–5 µm thick conidiophores.

**Ecology and distribution.** Known from a single sample growing on epiphytic *L. pallida* in Bolivia.

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Murillo: Valle del Zongo, bosque Yungas nublado, 2900 m, 16°08'38"S, 68°06'59"W, on *L. pallida* on bryophytes, J.E. 26811 (LPB, hb. Etayo).

#### *Cladophialophora parmeliae* (Etayo & Diederich) Diederich & Unter.

**Notes.** This species was originally described as a member of *Sclerococcum* inhabiting *Parmelia saxatilis* (Etayo & Diederich 1996a) and recently transferred to *Cladophialophora* based on DNA sequences obtained from two strains growing on *Hypotrachyna* (Diederich et al. 2013). It is characterized by having 50–120 µm diam. sporodochia with a greyish conidial mass, and distinctly verrucose, greyish brown, ellipsoidal, (0–)1–(2)-septate, catenate conidia, 6–9 × 4–4.5 µm (Etayo & Diederich 1996a). *Cladophialophora parmeliae* is a typical generalist and was reported from a wide range of hosts. Further molecular studies are necessary to confirm its broad host preferences, or alternatively, the presence of multiple cryptic species. Because the Bolivian samples growing

on *Lobariella* spp. fit well with the original description, we decided to treat them as a single species.

**Ecology and distribution.** The species is cosmopolitan and was reported from *Hypotrachyna*, *Lobaria*, *Normandina*, *Pannaria*, *Parmelia*, *Punctelia* and *Sticta*. In Bolivia it grows on epiphytic *Lobariella crenulata*, *L. exornata*, *L. reticulata* and *L. subexornata*.

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Murillo: Valle del Zongo, bosque nublado, near bridge, 2450 m, 16°07'41"S, 68°05'55"W, on *Lobariella exornata* on twigs, J.E. 26738 (LPB). Prov. Nor Yungas: carretera Coroico-La Paz, bosque nublado yungas, sendero que parte de la Estación de servicio, 3220–3250 m, 16°17'09"S, 67°51'00"W, J on *L. cf. reticulata* on twigs, E. 27700 (LPB, hb. Etayo); desviación de La Paz a Coroico hacia Unduavi, camino a Chulumani, bosque nublado, 3210 m, 16°18'27"S, 67°53'48"W, on *L. subexornata* on twigs, J.E. 26933 (LPB, hb. Etayo). Dept. Santa Cruz. Prov. Manuel María Caballero: near Siberia, 17°49'38"S, 64°44'45"W, 3950 m, open Yungas cloud forest, on *L. cf. crenulata*, J.E. 29593 (LPB, hb. Etayo).

#### *Corticifraga microspora* Etayo & Flakus, sp. nov. (Fig. 11)

MycoBank MB 833330

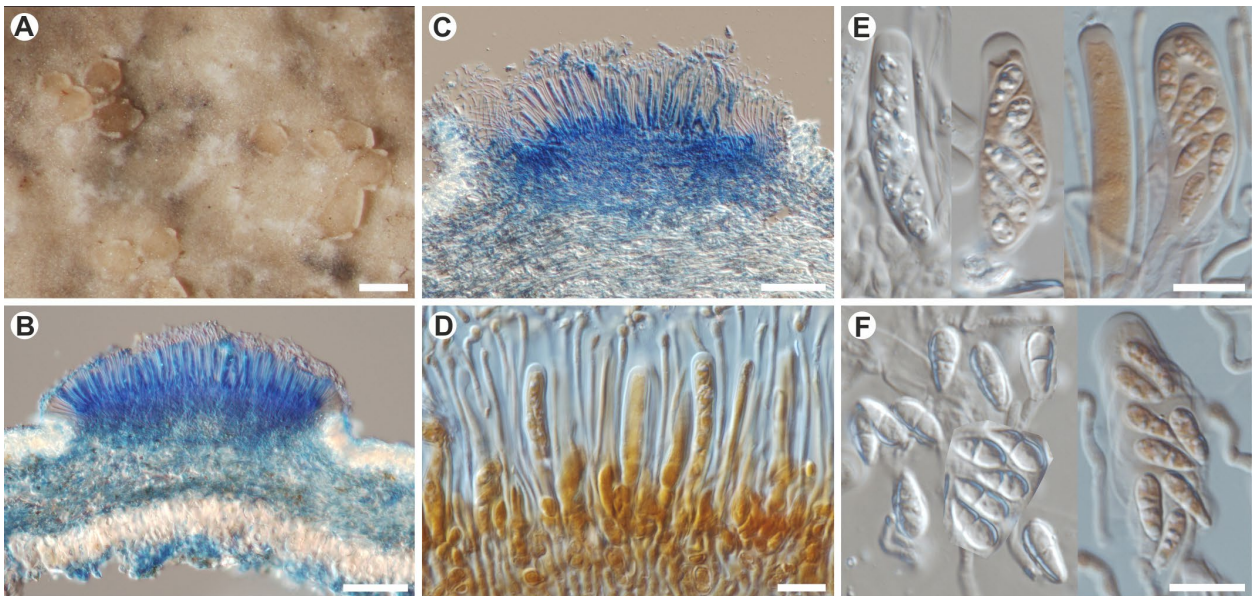
Diagnosis: Differs from *C. fuckelii* by smaller, pyriform ascospores, 7–10 × 2.5–4 µm, and a different host selection (*Lobariella pallida*).

Type: Bolivia: Dept. La Paz, Prov. Larecaja, Jocollone vilage and 1 km further, Paramo Yungeño vegetation, open anthropogenic area, with *Berberis*, NE oriented slope 15°37'35"S, 68°41'21"W, 3545 m, 14 May 2011, on *Lobariella pallida*, Javier Etayo 27205 (LPB – holotype!; hb. Etayo – isotype!).

**Description.** Mycelium hyaline. Apothecia breaking through the host cortex, single to slightly aggregated, not arranged concentrically, flat, not raised above the thallus level, rounded, angular or elongated, 150–280 µm diam., marginate. Margin thin, slightly elevated, incised, concolorous with the disc, 20–30 µm thick. Disc translucent, epruinose, yellowish to cream, finally brownish, flat. Epithemium hyaline to pale brown, indistinct. Hymenium colorless, 30–50 µm tall, I–, KI–. Paraphyses straight, simple, 1–1.5 µm thick, not or rarely slightly capitate and with apices up to 2–3 µm wide. Hypothecium colorless, ~20–25 µm thick, K–, I–, of textura intricata, cells 1.5–2.5 µm wide. Exciple hyaline to yellowish brown, 30–80 µm thick, paraplectenchymatous, composed of isodiametric cells, 4–9 µm diam., K–, I–. Asci bitunicate, narrowly clavate, with markedly thickened apices, I–, KI–, 30–43 × 6–10 µm, 8–spored, endoascus K/I+ orange. Ascospores pyriform to widely ellipsoid, straight to slightly curved, 1-septate, not constricted at the septa, colorless, with a thin wall, with several small oil droplets inside, 7–( $\bar{x}$  = 8.3 s = 0.9)–10 × 2.5–( $\bar{x}$  = 3.4 s = 0.4)–4 µm, l/b ratio 1.8–( $\bar{x}$  = 2.5 s = 0.3)–3.2 (n = 46).

**Etymology.** The epithet reflects the small size of the ascospores observed in this species.

**Ecology and distribution.** *Corticifraga microspora* is known only from two localities at a high altitude in the Yungas forest where it grows on *Lobariella pallida*.



**Figure 11.** *Corticifraga microspora* (on *Lobariella pallida*, based on J.E. 27205, holotype). A – ascomata erumpent from the host thallus; B–C – section of ascomata in LPCB; D – hymenium in Congo Red; E – asci in K/I (left) and Congo Red (right); F – ascospores in water (left) and Congo Red (right). Scales: A = 250  $\mu\text{m}$ , B–C = 50  $\mu\text{m}$ ; D–F = 10  $\mu\text{m}$ .

**Notes.** *Corticifraga microspora* has 1-septate ascospores similar to those of *C. fuckelii*, *C. pseudocyphellariae* and *C. scrobiculatae*. All those species can be separated by ascospore dimensions, which are (12–)13–17(–19)  $\times$  (4–)4.5–6  $\mu\text{m}$ , 12–15.5  $\times$  3.5–4  $\mu\text{m}$ , and (8.5–)10–11.5(–14)  $\times$  (4.5–)5–6(–7.5)  $\mu\text{m}$ , respectively (Hawksworth & Santesson 1990; Zhurbenko 2007). Additionally, they differ in their host preferences: *C. fuckelii* is a common species growing on *Peltigera* (Hawksworth & Santesson 1990; Zhurbenko 2007); while the two other species occur on *Pseudocyphellaria freycinetii* in Chile (Etayo & Sancho 2008) and on *Lobarina scrobiculata* in Alaska, respectively (Spribille et al. 2010).

**Specimens examined.** BOLIVIA Dept. La Paz. Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, bosque nublado; on *L. pallida*, 3210 m, 16°18'27"S, 67°53'48"W, J.E. 26946 (LPB, hb. Etayo).

***Ellisembia* cf. *lichenicola*** Heuchert & U. Braun

**Notes.** *Ellisembia* currently comprises about 40 species that are mainly saprobic, growing on wood, plants and dead culms of grasses and bamboos (Wu & Zhuang 2005). However, *E. asterinum* (Shoemaker & Hambleton 2001) is fungicolous on *Sphaeropsis* and *Macrophoma*, and *E. lichenicola* is lichenicolous on *Pertusaria* and *Physconia distorta* (Heuchert & Braun 2006). Our specimen of *Ellisembia* inhabiting *Lobariella* in Bolivia fits very well within the genus description and is somewhat similar to *E. lichenicola* s.str. However, the Bolivian material differs in having shorter conidiophores [32–55  $\times$  4–6  $\mu\text{m}$ ; vs. 20–60(–95)  $\times$  5–8  $\mu\text{m}$  in *E. lichenicola*] and in conidia size [33–55  $\times$  7–9  $\mu\text{m}$ ; vs. (19–)25–107  $\times$  8–10  $\mu\text{m}$  in *E. lichenicola*]. Although the range of conidial size included in the protologue is quite large, the observed differences suggest that the Bolivian material collected from *Lobariella* most probably represents a second, undescribed lichenicolous species within the genus. The

small size of the sample and the lack of DNA sequences withheld us from its formal description.

**Ecology and distribution.** Known only from a single specimen growing on epiphytic *Lobariella* sp. in Bolivia.

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Larecaja: Jocollone village, Paramo Yungeño vegetation, open anthropogenic area with *Berberis*, NE oriented slope, on *Lobariella* sp., 15°37'35"S, 68°41'21"W, 3545 m, J.E. 27212 (LPB, hb. Etayo).

***Endophragmiella* cf. *hughesii*** D. Hawksw.

**Notes.** *Endophragmiella hughesii* was described by Hawksworth (1979) from *Lobaria pulmonaria* in the British Isles. The Bolivian samples causes bleaching or necrosis on the host thallus, and conidiophores develop on the apothecial margin (*Lobariella pallida*) or on the top of isidia (*L. exornata*). Our material is characterized by having 6–7-septate conidiophores of a similar size to that in the protologue (120–140  $\times$  5–7  $\mu\text{m}$ ; vs. 80–150  $\times$  5–8  $\mu\text{m}$  in *E. hughesii*), but develop a widened base (to 9  $\mu\text{m}$ ), and slightly smaller 2-septate conidia (20–25  $\times$  9–13  $\mu\text{m}$ ; vs. 25–30(–40)  $\times$  11–13  $\mu\text{m}$  in *E. hughesii*), with the medium cell slightly darker than the terminal cells. Further studies on a broader sampling are necessary to confirm whether populations of this fungus growing on *Lobariella* are conspecific with individuals inhabiting *Lobaria pulmonaria*.

**Ecology and distribution.** The species is known from Europe (from *Lobaria pulmonaria*) and Bolivia (from *Lobariella exornata* and *L. pallida*).

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Nor Yungas: near Siniari colony, km 74 on the road Coroico-La Paz, 16°13'20"S, 67°50'37"W, 2090–2186 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27645 (LPB, hb. Etayo); on *L. exornata*, J.E. 27647 (LPB).

***Epithamnolia rugosopycnidiata*** Etayo & Flakus, sp. nov.  
(Fig. 12)

Mycobank MB 833331

**Diagnosis:** Differs from *E. rangiferina* by pyriform, grey-brown to blackish conidiomata (K+ violet), 150–350 µm tall, 140–250 µm wide, and smaller, bacilliform, conidia, 2–3 × 1–1.5 µm.

**Type:** Bolivia, Dept. Santa Cruz, Provincia Caballero, near Siberia, 17°49'38"S, 64°44'45"W, 3950 m, on open yungas cloud forest, on unhealthy *Lobariella* sp. on twigs, 16 August 2012, Javier Etayo 29601 (LPB – holotype!; hb. Etayo – isotype!).

**Description.** Mycelium indistinct. Conidiomata superficial, pyriform, grey brown to blackish, glabrous, with rugose surface, apiculate, 150–350 µm tall, 140–250 µm wide, dispersed to loosely aggregated in small groups. Peridium wall brown to greenish brown, K+ violet, 15–20 µm thick, of isodiametric to elongate cells, 2–10 × 1–4 µm, with dark and irregularly thickened walls. Conidiophores hyaline, arising from the base of the conidioma and sometimes acting as conidiogenous cells, simple to composed of 2–3 cells, straight or curved, 5–9 × 1.5–2 µm. Conidiogenous cells hyaline, enteroblastic, phialidic, determinate, integrated, acropleurogenous, habitually growing verticillately from a conidiophore, smooth-walled, lageniform, 7–12(–20) × 1–2 µm, with a thin apex, ~1 µm. Conidia hyaline, bacilliform, straight, with a base more or less truncate and a rounded apex, aseptate, smooth-walled, 2–( $\bar{x}$ =2.5 s=0.4)–3 × 1–( $\bar{x}$ =1.2 s=0.3)–1.5 µm, l/b ratio 1.4–( $\bar{x}$ =2.1 s=0.6)–3 (n=32).

**Etymology.** The epithet highlights the strongly corrugated pycnidial wall of the conidiomata in dry conditions.

**Ecology and distribution.** Similar to several other species in the genus (Suija et al. 2017), *Epithamnolia rugosopycnidiata* does not seem to be a host-specific fungus. It was observed on *Lobariella pallida* and *Lopezaria versicolor* in Bolivia and Ecuador. The sample

from Ecuador also grows on twigs around remnants of crustose lichens.

**Notes.** The genus *Epithamnolia* was described by Zhurbenko (2012) for *E. karatyginii* growing on *Thamnolia vermicularis*. Recently, Suija et al. (2017) revealed the phylogenetic placement of *Epithamnolia* in *Leotiomyces* and suggested that lichenicolous species of *Hainesia* also belong to this genus.

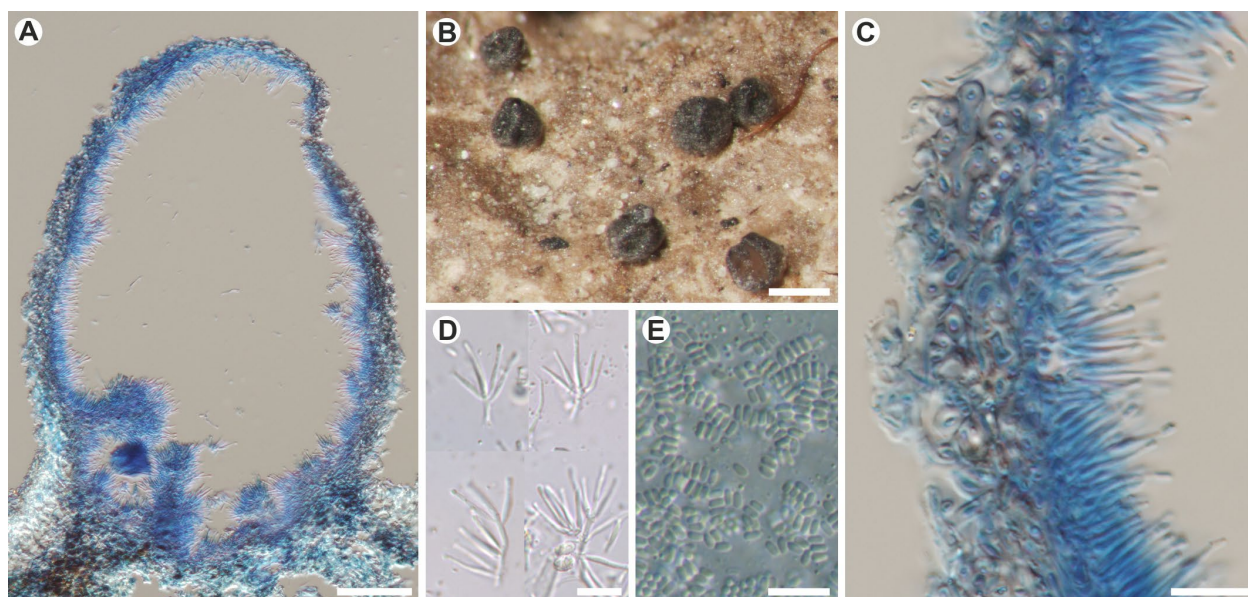
*Epithamnolia rugosopycnidiata* is very similar to *E. rangiferinae* growing on *Cladonia rangiferina* by having similar simple and very short conidia. *Epithamnolia rangiferinae* can be distinguished by its larger conidia (4.5–5 × 1.4–1.5 µm) and cupulate, pale to dark brown conidiomata (K–) (Suija et al. 2017). This is the second known species of the genus with short, aseptate conidia.

**Specimens examined.** BOLIVIA. Dept. Santa Cruz. Prov. Manuel María Caballero: near Siberia, open Yungas cloud forest, on *Lopezaria versicolor*, 17°49'38"S, 64°44'45"W, 3950 m, J.E. 29608 (LPB, hb. Etayo). ECUADOR. Dep. Nariño. Prov. Pasto: corregimiento El Encano, vereda Sta. Isabel, S lago La Cocha (guamues), páramo azonal con *Blechnum*, *Weimannia*, *Esperomeles*, etc., 0.59N 77.09W, 2700 m, on *Lobariella pallida*, J.E. 16596 (hb. Etayo).

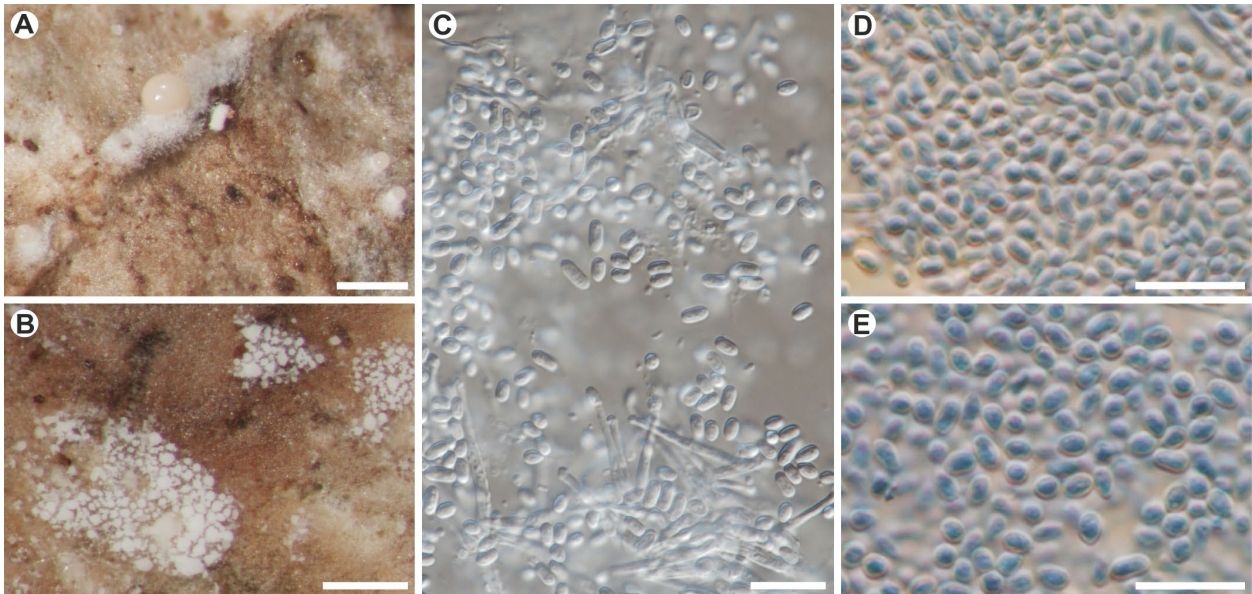
***Globonectria cochensis*** Etayo (Fig. 13)

**Description of the asexual state.** Conidiomata sporodochia-like agglomerated conidiophores, developing on an arachnoid subiculum on the upper side of the host thallus, white, fused in groups resembling droplets. Conidiogenous cells hyaline, aseptate, straight to slightly curved, wider at the base and tapering towards the apex, 15–30 × 1–2 µm. Conidia hyaline, aseptate, subglobose to broadly ellipsoidal, not truncate, 2–( $\bar{x}$ =3.3 s=0.8)–5 × 1.5–( $\bar{x}$ =1.9 s=0.3)–2.5 µm, l/b ratio 1–( $\bar{x}$ =1.8 s=0.5)–2.7 (n=57).

**Notes.** *Globonectria cochensis* was described from specimens collected in Colombia, and is characterized by



**Figure 12.** *Epithamnolia rugosopycnidiata* (on *Lobariella* sp., based on J.E. 29601, holotype). A – section of pycnidial conidiomata in LPCB; B – conidiomata on the host thallus; C – section of conidiomata wall in LPCB; D – conidiogenous cells in water; E – conidia in water. Scales: A = 50 µm; B = 250 µm; C–D = 10 µm.



**Figure 13.** *Globonectria cochensis* anamorph (A, E, on *Lobariella crenulata*, based on A.F. 22184; B–D on *Lobariella* sp., based on J.E. 33-20). A–B – sporodochia-like conidiomata growing on the host thallus; C – conidia mixed with conidiogenous cells in water; D–E – conidia in LPCB. Scales: A–B = 250  $\mu$ m; C–E = 10  $\mu$ m.

having a colorless peridium bordered by an external portion of orange color, cylindrical, 8-spored asci with an apical thickening, and subspherical ascospores (Etayo 2002). Later studies showed that this taxon produces 4-spored asci with ascospores that are first 1-septate, but very soon break into two subspherical half-spores (Etayo 2017). It is very similar to species of *Pronectria*, but our phylogenetic analysis confirmed its identity as a distinct genus (Fig 3).

We have found an *Acremonium*-like anamorph growing intermixed with the sexual state of *G. cochensis* (J.E. 33-20) which, according to our phylogenetic analyses (Fig. 3), may represent the asexual state of the species.

**Ecology and distribution.** This species is known from Bolivia and Colombia (Etayo 2002) where it grows on epiphytic *Lobariella crenulata* and *L. pallida*.

**Specimens examined (sexual state).** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *L. cf. pallida* on trees, J.E. 29527 (LPB, hb. Etayo); near Lago Corani, 17°13'44"S, 65°53'39"W, 3260 m, open area with shrubs, on *L. crenulata*, J.E. IX-9 (LPB, hb. Etayo). Prov. Tiraque: Parque Nacional Carrasco, Camino de los Nubes, Antenas Sillar–Villa Tunari old road, 17°12'29"S, 65°41'24"W, 3591 m, open area with shrubs, corticolous, on *L. crenulata*, A.F. 26012 (KRAM, LPB). Dept. La Paz. Prov. Nor Yungas: below Unduavi village, on the road La Paz – Chulumani, Yungas cloud forest, 3210 m, 16°18'27"S, 67°53'48"W, on *L. crenulata*, J.E. 26942 (LPB, hb. Etayo), on *L. crenulata*, A.F. 22184, 22194 (KRAM, LPB); carretera La Paz a Pando, desviación hacia Hunduavi, orilla río Hunduabi, bosque nublado secundario, valle orientado al E, 3135 m, 16°18'50"S, 067°54'35"W, *L. pallida*, J.E. 26966 (LPB); near Nogalani village, on the road Coroico–La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *L. crenulata* and *L. pallida*, J.E. 27969 (LPB, hb. Etayo).

**Specimens with Acremonium-like anamorph examined.** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional

Carrasco, near Río Batea Mayu close to Monte Punku, lower montane Yungas cloud forest, 17°31'33"S, 65°16'21"W, 2430 m, on *Lobariella* sp., J.E. 33-13, 33-20 (LPB, hb. Etayo). Dept. La Paz. Prov. Nor Yungas: below Unduavi village, on the road La Paz – Chulumani, Yungas cloud forest, 3210 m, 16°18'27"S, 67°53'48"W, on *L. crenulata*, A.F. 22184 (LPB).

***Intralichen lichenum*** (Diederich) Hawksworth & Cole

**Notes.** *Intralichen lichenum* is a widely distributed species reported from various lichen hosts in Europe, USA, New Guinea and Antarctica (Hawksworth 1979; Brackel 2014; Diederich et al. 2018). It is easily distinguished by its poorly differentiated conidiophores developing in the host hymenium, and pale-brown, smooth-walled, aseptate conidia (3–4.5  $\times$  2.5–4  $\mu$ m) produced in basipetal chains. We found this species as a hyperparasite in the hymenium of *Lawreyella lobariella* growing on *Lobariella crenulata* in Colombia. Previously it has been reported as a hyperparasite of two other lichenicolous fungi: *Opegrapha plectocarpoidea* and *Tremella ramalinae* (Brackel 2014).

**Ecology and distribution.** A cosmopolitan species reported from several host lichens and as a hyperparasite on some lichenicolous fungi (Hawksworth 1979; Brackel 2014; Diederich 2018).

**Specimens examined.** COLOMBIA. Dept. Nariño. Prov. Pasto: Serranía de Morasurco, 1.16N, 77.13W, 3000–3300 m, preramo arbustivo with *Macleania*, *Oreopanax*, *Weimannia* and *Espeletia pycnophylla*, *Puya*, on *Lawreyella lobariella* growing on *Lobariella crenulata* on twigs, J.E. 15917 (LPB, hb. Etayo).

***Lawreyella*** Flakus, Etayo, Kukwa & Rodr. Flakus, gen. nov. (Fig. 14)

Mycobank MB 833332

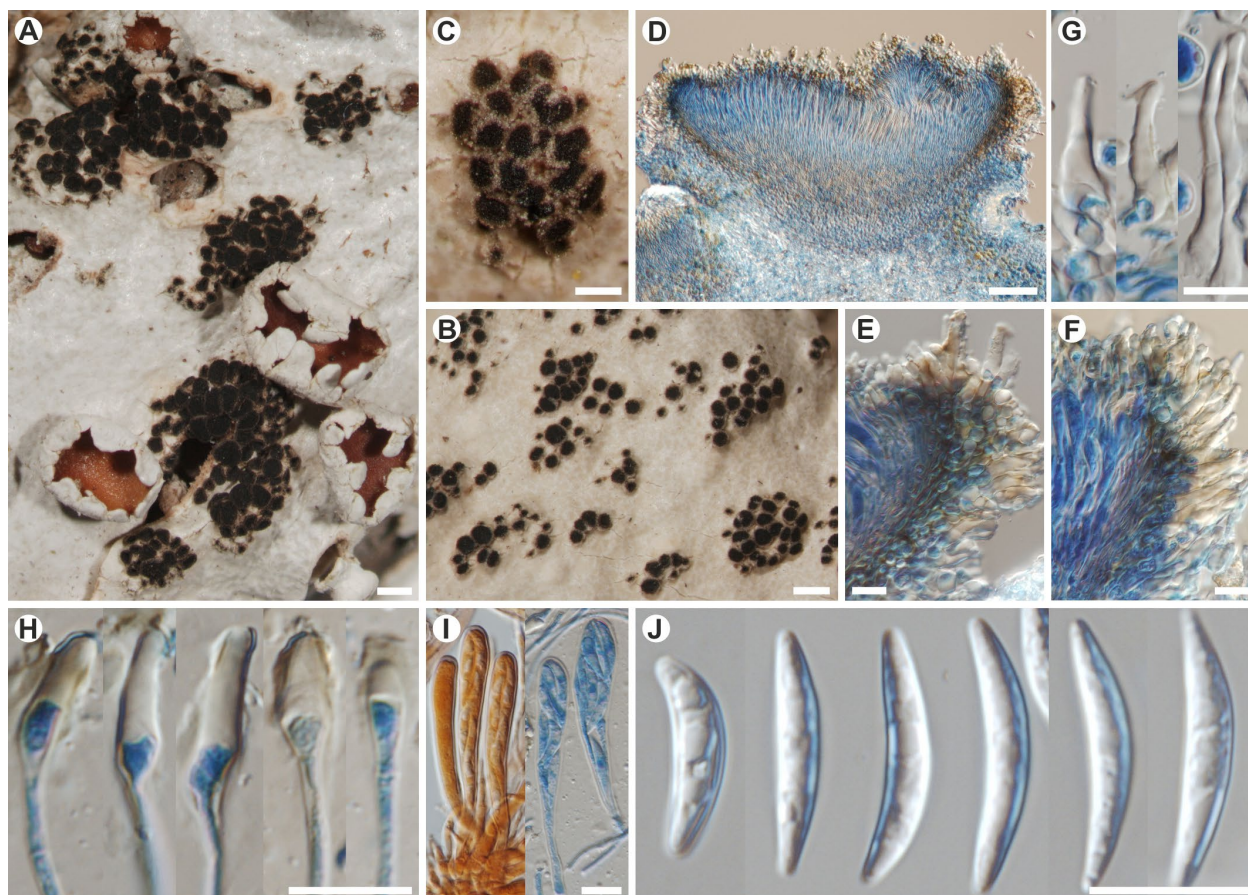
Diagnosis: Differs from *Diplolaeviopsis*, *Macroskyttea*, *Protounguicularia* and *Unguiculariopsis* by having black, aggregate

ascomata, containing a greenish pigment (K+ reddish brown, N+ bright green) in the hymenium and an additional orange-brown pigment in the exciple and epithecium (K+ purple then dark-brown, N+ purplish then orange-brown), short, aseptate, acute excipular hairs, that are wide at the base and solid along almost the entire length, and paraphyses with a large, swollen, tapering apical cell with a solid upper part.

Generic type: *Lawreyella lobariella* (S. Y. Kondr. & D. J. Galloway) Flakus, Etayo, Kukwa & Rodr. Flakus, comb. nov., MycoBank MB 833333 (Basonym: *Unguiculariopsis lobariella* [as '*lobariellum*'] S. Y. Kondr. & D. J. Galloway, Bibliotheca Lichenologica 58: 238. 1995a).

**Description.** Lichenicolous on *Lobariaceae*. Ascomata apothecia, 0.5–5 mm diam., dark brown to black, matte, immersed and interrupting the cortex of the host when young, sessile when mature, arranged in circular groups; groups of apothecia 0.5–3.5 mm diam., composed of ~10–60 apothecia. Disc exposed almost from the beginning, black, matte, slightly concave to flat (strongly concave when young and slightly convex when overmature). Margin greyish to blackish, paler than disc, hairy. Exciple well developed, pale to dark-brown, K+ purple then dark-brown, N+ slightly purplish then orange-brown, hyaline in the lower part, 40–60  $\mu\text{m}$  wide laterally (without hairs 10–30  $\mu\text{m}$  wide), paraplectenchymatous,

consisting of thick-walled, elongated to subspherical cells, 3–10  $\times$  1–5  $\mu\text{m}$ ; inner exciple composed of more elongated cells, outermost part composed of cells protruding into excipular hairs. Excipular hairs 10–40  $\times$  3–7  $\mu\text{m}$ , simple, aseptate, smooth-walled, hyaline to brownish, with wide base or cylindrical, with tapering apex, solid almost along the entire length, composed of glassy material, and with small, rounded lumen at the base. Epithymenium brown, with granular K+ soluble pigments, KI–, K+ purple then dark brown, N+ slightly purplish then orange-brown, 10–20  $\mu\text{m}$  tall. Hymenium hyaline to greenish, pigments K+ reddish brown, N+ yellowish green, 60–80  $\mu\text{m}$  tall. Hypothecium brownish, up to 20–90  $\mu\text{m}$  tall. Paraphyses not conglutinated, simple to sparsely branched, 1–2  $\mu\text{m}$  wide, with a large apical cell; apical cell hyaline to pale brown, usually covered by a gel, 12–20  $\times$  3–7  $\mu\text{m}$ , with tapering apex, solid in the upper part (solid part 3–15  $\mu\text{m}$  tall) and with a small lumen at the base. Asci 8-spored, functionally unitunicate, clavate with a long stem, 50–70  $\times$  6–10  $\mu\text{m}$ , with wall apically slightly thickened. Ascospores hyaline, simple, straight to curved, narrowly ellipsoidal with acute ends, without perispore, in the type species 10–( $\bar{x}$ =14.9 s=2.7)–20  $\times$  2.5–( $\bar{x}$ =2.9 s=0.3)–3.5  $\mu\text{m}$ , l/b ratio 3.3–( $\bar{x}$ =5.1 s=1.1)–7.6 (n=49).



**Figure 14.** *Lawreyella lobariella* (on *Lobariella pallida*; A, D–J based on J.E. 41-3; B–C based on A.F. 25157). A – aggregated apothecial ascomata on the host thallus; B – dispersed apothecial ascomata; C – apothecial ascomata with paler, hairy margins; D – section of ascomata in LPCB; E–F – section of exciple showing paraplectenchymatous tissue and outermost excipular cells protruding into hairs in LPCB; G – excipular cells with solid, glassy material and small lumen at the base in LPCB; H – enlarged apical cells of paraphyses with solid, glassy material in the apical part in LPCB; I – asci in Congo Red (left) and LPCB (right); J – ascospores in water. Scales: A–B = 500  $\mu\text{m}$ ; C = 250  $\mu\text{m}$ ; D = 50  $\mu\text{m}$ ; E–J = 10  $\mu\text{m}$ .

**Etymology.** *Lawreyella* is named in honor of American lichenologist, Dr. James D. Lawrey, for on the occasion of 70<sup>th</sup> birthday.

**Ecology and distribution.** *Lawreyella lobariella* was described from *Ricasolia* cf. *erosa* in Venezuela (Konratyuk & Galloway 1995a). It is a very common species in neotropical cloud forests growing mainly on *Lobariella crenulata* and *L. pallida*, and rarely on *Ricasolia* in Bolivia, Colombia, Ecuador and Peru (Etayo 2002, 2010b, 2017).

**Notes.** *Lawreyella lobariella* is phylogenetically unrelated to *Unguiculariopsis* (Fig. 6), the genus under which this species was initially described. *Unguiculariopsis* differs from *Lawreyella* by aseptate and strongly hook-shaped excipular hairs with characteristically swollen base, reddish brown to brown ascomata (K+ reddish to purplish, N–) and paraphyses that are apically not widened (Diederich & Etayo 2000). Although the new genus is closely related to *Diplolaeviopsis*, *Macroskyttea*, and *Protounguicularia*, it is easily distinguished by several anatomical characters. *Diplolaeviopsis* and *Macroskyttea* have aseptate, long, cylindrical or tapering excipular hairs, urceolate ascomata with a narrow pore when young and paraphyses that are apically not thickened (Diederich & Coppins 2014; Etayo et al. 2015; Suija et al. 2015a). *Protounguicularia* can be separated by its white to pale brownish ascomata, septate, cylindrical to slightly tapering excipular hairs and paraphyses that are apically not swollen (Huhtinen et al. 2008). We also collected other morphologically very similar fungi growing on *Ricasolia casarettiana*, but further molecular phylogenetic investigations are needed to confirm whether they represent *Lawreyella lobariella*.

**Specimens examined (on *Lobariella*).** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Korikaza, 17°33'21"S, 65°16'29"W, 2950 m, Páramo Yungueño, on *Lobariella* on trees, J.E. 29322, 29331, 29324 (LPB, hb. Etayo); Korikaza close to Monte Punku, 17°33'30"S, 65°16'32"W, 2880 m, lower montane Yungas cloud forest, corticolous, on *L. pallida*, A.F. 25752, 25754, M.K. 15106a (KRAM, LPB, UGDA); Meruvia close to Monte Punku, 17°35'06"S, 65°14'54"W, 3283 m, *Podocarpus-Polylepis* forest, corticolous, on *L. auriculata*, A.F. 25565, M.K. 15036c, 15042d, on *L. pallida*, A.F. 25566, M.K. 15042e (KRAM, LPB, UGDA); Wayra Mayu close to Monte Punku, 17°33'30"S, 65°16'08"W, 2750 m, lower montane Yungas cloud forest, on corticolous *L. auriculata*, M.K. 15175a, on *L. pallida* M.K. 15175, A.F. 25864 (KRAM, LPB, UGDA); near Lago Corani, close to Villa Tunari-Cochabamba road, 17°13'24"S, 65°53'31"W, 3271 m, open area with shrubs, on corticolous *L. crenulata*, M.K. 15420 (LPB, UGDA). Prov. Tiraque: Parque Nacional Carrasco, old guard's camp, 17°18'23"S, 65°45'60"W, 3360 m, open area with shrubs, on corticolous *Lobariella* sp., M.K. 15290 (LPB, UGDA); Camino de los Nubes, Antenas Sillar-Villa Tunari old road, 17°12'32"S, 65°41'52"W, 3520 m, upper montane Yungas cloud forest, corticolous, on *L. pallida* A.F. 25977, 25982, M.K. 15249 (KRAM, LPB, UGDA); ibidem, 17°12'29"S, 65°41'24"W, 3591 m, open area with shrubs, corticolous, on *L. pallida* A.F. 26008 (KRAM, LPB), J.E. 41-3 (LPB, hb. Etayo); old guard's camp close to T7, 17°18'23"S, 65°45'60"W, 3360 m, open area with shrubs, corticolous, on

*L. pallida*, A.F. 26032, on *L. crenulata*, A.F. 26041 (KRAM, LPB). Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *L. pallida* on trees, J.E. 29500 (LPB, hb. Etayo). Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara Bajo, 14°41'47"S, 69°04'10"W, 3160 m, open area with shrubs and scattered trees, corticolous, on *L. pallida* A.F. 25284, 25290, M.K. 14898 (KRAM, LPB, UGDA); below Pelechuco, 14°49'08"S, 69°03'50"W, 3560 m, open area with shrubs and *Polylepis* trees, on corticolous *L. pallida*, M.K. 14974 (LPB, UGDA); near Keara Bajo, 14°41'59"S, 69°04'34"W, 3290 m, open area with shrubs and scattered trees, on corticolous *L. pallida*, M.K. 14870, A.F. 25239/1, J.E. 18-5 (KRAM, LPB, UGDA, hb. Etayo); Pukara between Keara and Keara Bajo, 14°42'09"S, 69°05'17"W, 3420 m, open area with shrubs, on corticolous *Lobariella* sp., M.K. 14924, on *L. pallida* A.F. 25326 (KRAM, LPB, UGDA); Chuñuna above Keara, 14°41'11"S, 69°05'30"W, 4053 m, *Polylepis pepeii* forest, corticolous, on *L. soredians* A.F. 25439 (KRAM, LPB); Área Natural de Manejo Integrado Nacional Apolobamba, near Rio Pelechuco, below Pelechuco close to new road to Apolo, 14°46'22"S, 69°00'11"W, 2480 m, lower montane Yungas cloud forest, corticolous, on *Lobariella* sp., A.F. 25070 (KRAM, LPB); ibid. 14°47'28"S, 69°01'32"W, 2860 m, open area with scattered trees, corticolous, on *L. pallida* A.F. 25157 (KRAM, LPB); below Pelechuco, 14°49'08"S, 69°03'50"W, 3560 m, open area with shrubs and *Polylepis* trees, corticolous, on *L. pallida* A.F. 25466, 25467 (KRAM, LPB). Prov. Larecaja: Jocollone village and 1 km further, Paramo Yungueño vegetation, open anthropogenic area, much *Berberis*, NE oriented slope, 15°37'35"S, 68°41'21"W, 3545 m, J.E. 27202, 27205, 27290, 27355 (LPB, hb. Etayo). Prov. Murillo: Valle del Zongo, páramo yungueño, rocas sueltas entre pastos con arbustos, 3375 m, 16°10'15"S, 68°08'02"W, on *L. crenulata* on bushes, J.E. 26767 (LPB); Valle del Zongo, bosque yungas nublado, 2900 m, 16°08'38"S, 68°06'59"W, on *L. pallida* on bryophytes, J.E. 26811 (LPB, hb. Etayo); Sainani, Valle del Zongo, 16°07'20"S, 68°05'09"W, 2220 m, open area with shrubs and scattered trees, corticolous, on *L. pallida*, A.F. 26252, on *Lobariella* sp. A.F. 26253, 26262 (KRAM, LPB). Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unduavi, camino a Chulumani, bosque nublado, 3210 m, 16°18'27"S, 67°53'48"W, on *L. subexornata*, J.E. 26912 (LPB, hb. Etayo); on road La Paz -Chulumani, cloud forest, 3210 m, 16°18'27"S, 67°53'48"W, on *L. crenulata*, J.E. 26925 (LPB, hb. Etayo); Chuspipata station, old road Coroico-La Paz, 16°18'18"S, 67°48'55"W, 3009 m, disturbed Yungas cloud forest with shrubs and small trees, on *L. pallida* A.F. 28889 (KRAM, LPB); Coroico, Uchumachi footpath, 16°11'36"S, 67°43'21"W, 1897 m, disturbed Yungas cloud forest with shrubs and small trees, on *L. pallida* A.F. 28844 (KRAM, LPB). Dept. Santa Cruz. Prov. Manuel María Caballero: near Siberia, 17°49'34"S, 64°43'14"W, 2800 m, Yungas cloud forest with outcrops, on *Lobariella* sp., J.E. 28765 (LPB, hb. Etayo). Dept. Tarija. Prov. Burnet O'Connor: near Soledad, 21°39'52"S, 64°07'22"W, 1700 m, Tucumano-Boliviano montano forest, on *Lobariella* sp., J.E. 28792 (LPB).

**Specimens on *Ricasolia* examined.** BOLIVIA. Dept. Chuquisaca. Prov. Belisario Boeto: between Nuevo Mundo and Villa Cerrano, 19°00'49.5"S, 64°20'08.8"W, 2555 m, Boliviano-Tucumano forest with *Podocarpus* and *Polylepis*, on *R. casarettiana* on branch, J.E. 29790 (LPB, hb. Etayo). Dept. Tarija. Prov. Burnet O'Connor: old road between Tarija and Enterrios, 21°27'50"S, 64°12'51"W, 1924 m, Boliviano-Tucumano forest with epiphytes exposed, on *R. casarettiana* on branch, J.E. 29918 (LPB, hb. Etayo).

*Lichenopeltella santessonii* (P. M. Kirk & Spooner) R. Sant.

**Notes.** The Bolivian samples differ from the original description by having slightly larger ascospores ( $16\text{--}18 \times 3.5\text{--}4.5 \mu\text{m}$ ) and the presence of ascospores with three pairs of setulae.

**Ecology and distribution.** The species is known from a few countries in the Northern Hemisphere (Spooner & Kirk 1990; Brackel 2011b), and from Bolivia, where it grows on species of *Peltigera*, *Lobariella auriculata*, and *L. subexornata*.

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, Incachaca,  $17^{\circ}14'59''\text{S}$ ,  $65^{\circ}49'36''\text{W}$ , 2560 m, Yungas cloud forest, on *L. auriculata*, A.F. 24725-1 (KRAM, LPB). Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado Nacional Apolobamba, near Río Pelechuco, below Pelechuco close to new road to Apolo,  $14^{\circ}46'59''\text{S}$ ,  $69^{\circ}01'08''\text{W}$ , 2750 m, open area with scattered small trees, corticolous, on *L. auriculata*, A.F. 25117 (KRAM, LPB); Prov. Murillo: Valle del Zongo, bosque Yungas nublado, on *L. subexornata*, 2900 m,  $16^{\circ}08'38''\text{S}$ ,  $68^{\circ}06'59''\text{W}$ , J.E. 26798 (LPB, hb. Etayo).

*Lichenotubeufia cryptica* Etayo & Flakus, sp. nov.  
(Fig. 15)

Mycobank MB 833334

**Diagnosis:** Differs from *L. boomiana* by having shorter ascospores,  $100\text{--}150 \times 2\text{--}3.5 \mu\text{m}$ , and a different ecology (growing on the lower side of thalli of *Lobariella pallida*).

**Type:** Bolivia: Dept. Cochabamba. Prov. Carrasco: PN Carrasco, Koricaza,  $17^{\circ}33'21''\text{S}$ ,  $65^{\circ}16'29''\text{W}$ , 2950 m, Páramo Yungueño, 18 Aug. 2012, on *Lobariella pallida* growing on trees, Javier Etayo 29331 (LPB – holotype!; hb. Etayo – isotype!, microscopic slide).

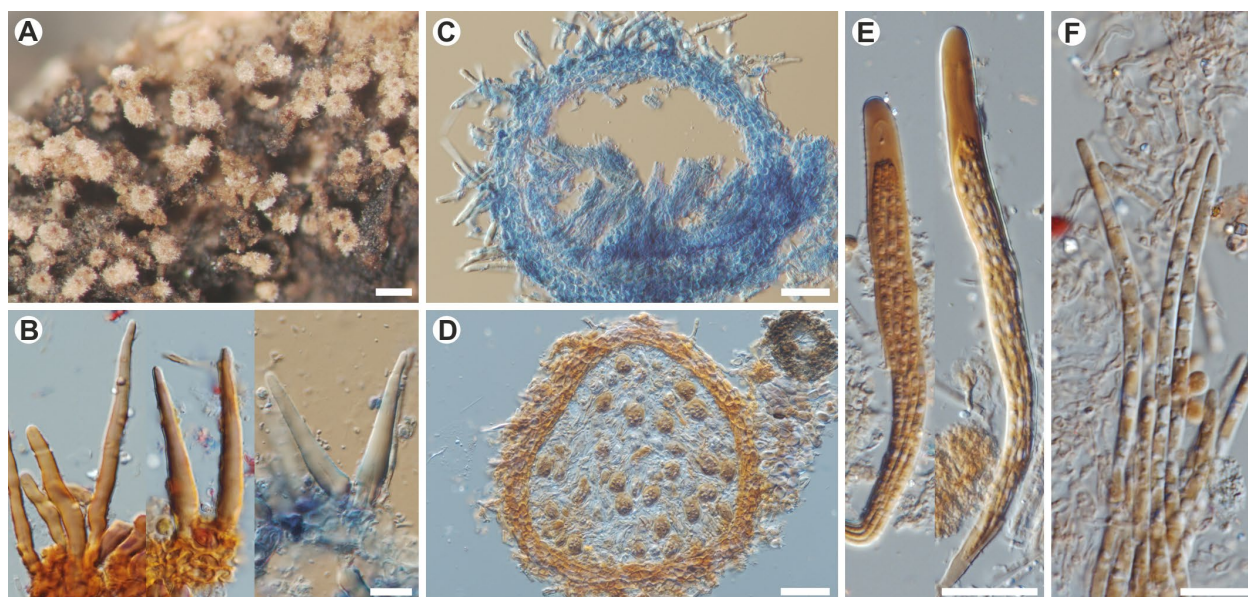
**Description.** Ascomata perithecia,  $130\text{--}200 \mu\text{m}$  diam., superficial, solitary, scattered or in groups, subglobose to pyriform, beige to cream colored, hairy around the whole

surface, not cupulate, not papillate, with a slightly darker spot around the ostiole. Peridium  $15\text{--}20 \mu\text{m}$  wide, composed of several layers, hyaline to creamy colored, K+ slightly yellowish green, with isodiametric, thin-walled cells,  $2\text{--}6 \mu\text{m}$  diam. Hairs hyaline, simple to septate, not branched, with acute apex,  $35\text{--}80 \times 3\text{--}8 \mu\text{m}$ , straight, thick-walled (with very thin lumen along the entire length) or solid in the apical part (with lumen only at the base). Hamathecium I–, KI–, composed of persistent, branched and anastomosed paraphysoids,  $0.5\text{--}1 \mu\text{m}$  wide. Asci bitunicate, long cylindrical, with a short foot, with thickened apex,  $105\text{--}165 \times 9\text{--}13 \mu\text{m}$ , 8–spored, K/I–, endoascus K/I+ orange. Ascospores needle-shaped, acicular, with acute ends, multiseptate, hyaline,  $100\text{--}(x=106.9 s=13.9)\text{--}150 \times 2\text{--}(x=2.7 s=0.4)\text{--}3.5 \mu\text{m}$ , l/b ratio  $33.3\text{--}(x=40.9 s=6.1)\text{--}50$  ( $n=26$ ).

**Etymology.** The epithet emphasizes the extreme difficulty of finding this fungus because it occurs on the lower side of thalli of *Lobariella*, where it is intermixed with host rhizines of the same color as the ascomata of the fungus.

**Ecology and distribution.** It was found in two localities in Bolivia on *Lobariella pallida* near 3000 m and seems to be a very rare species.

**Notes.** The genus *Lichenotubeufia* was introduced by Etayo (2017) to accommodate *Tubeufia*-like fungi occurring on lichens, and currently contains five species. Three of them grow on lichens from *Peltigerales*: *L. boomiana* (on *Sticta*), *L. eriodermiae* (on *Erioderma*) and *L. tafallae* (on *Leptogium*). *Lichenotubeufia boomiana* is characterized by having shorter ascospores,  $95\text{--}112 \times 3\text{--}4 \mu\text{m}$ , and grows on the upper side of a different host thallus (Etayo 2017). *Lichenotubeufia eriodermiae* clearly differs in having larger perithecia (reaching  $200\text{--}300 \mu\text{m}$  diam.), larger aggregated hairs ( $100\text{--}150 \times 2.5\text{--}3.5 \mu\text{m}$ ), and thicker ascospores ( $4\text{--}5 \mu\text{m}$  wide) (Etayo 2002), whereas



**Figure 15.** *Lichenotubeufia cryptica* (on *Lobariella pallida*, based on A.F. 25145). A – perithecioid ascomata mixed with rhizines on the underside of the host thallus; B – excipular hairs in Congo Red (left) and LPCB (right); C–D – section of ascomata in LPCB (C) and Congo Red (D); E – asci in Congo Red; F – ascospores in Congo Red. Scales: A = 250  $\mu\text{m}$ ; B, F = 10  $\mu\text{m}$ ; C–E = 25  $\mu\text{m}$ .

*L. tafallae* has much larger hairs (200–250 × 20–30 µm), which grow in groups near the ostiole. Other species from the genus can be identified using the key provided by Etayo (2017).

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado Nacional Apolobamba, near Río Pelechuco, below Pelechuco close to new road to Apolo, 14°47'28"S, 69°01'32"W, 2860 m, open area with scattered trees, corticolous, on *Lobariella pallida*, A.F. 25145 (KRAM, LPB).

*Nanostictis pluriseptatum* Etayo

**Notes.** This rare species was described from specimens collected in Colombia (Etayo 2002) and has recently been found in Bolivia. It is characterized by having marginate ascomata (0.25–0.35 mm diam.) with a pale yellowish disc and acicular 15–27-septate ascospores (64–105 × 3.5–4.5 µm).

**Ecology and distribution.** Known from Bolivia and Colombia from *Lobariella pallida* and *L. subexornata* (Etayo 2002).

**Specimen examined.** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *Lobariella subexornata* on bushes, J.E. 29621 (LPB).

*Nectriopsis curtiseta* Etayo

(Fig. 16)

**Notes.** This species was recently described from Ecuador (Etayo 2017) and is characterized by having relatively large ascomata (120–200 µm diam.) and hyaline, verrucose ascospores, 7–10 × 3–3.5 µm.

In some samples of *N. curtiseta*, chalk-white sporodochia-like agglomerated conidiophores mainly covering the apothecial margin of the host were observed. This anamorph is characterized by having colonies 0.2–0.8 mm diam., simple to branched, colorless conidiophores (5–6 ×

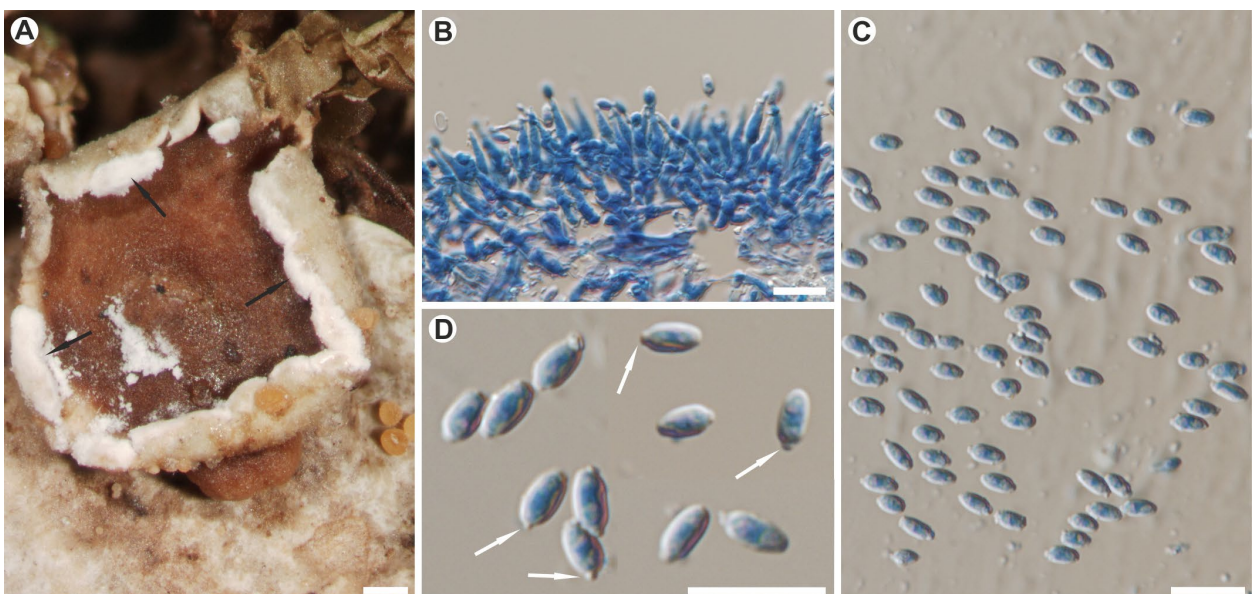
3–3.5 µm), hyaline, aseptate, conidiogenous cells (8–17 × 1.5–2.5 µm) that are wider at the base and tapering at the apex, and narrowly ellipsoidal, slightly tapering and evidently truncate, hyaline conidia 3.5–(x̄=4.8 s=0.7)–6 × 2–(x̄=2.3 s=0.3)–3 µm, l/b ratio 1.3–(x̄=2.1 s=0.5)–3 (n=29). It was also characterized and illustrated by Etayo (2017; Fig. 9 as *Acremonium* sp.) based on a sample from Ecuador (J.E. 25430). It is most probable that this *Acremonium*-like anamorph is the asexual state of *N. curtiseta*, a hypothesis that needs, however, molecular confirmation.

**Ecology and distribution.** A relatively common species known from several localities in Bolivia and Ecuador, where it grows on *Lobariella crenulata*, *L. pallida* and *Ricasolia patinifera*.

**Specimens on *Lobariella* examined (sexual state).** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *Lobariella* sp., J.E. 29503 (LPB, hb. Etayo); near Río Batea Mayu close to Monte Punku, 17°31'33"S, 65°16'21"W, 2430 m, corticolous, on *Lobariella* sp., A.F. 25810 (KRAM, LPB). Dept. La Paz. Prov. Murillo: Sainani, Valle del Zongo, 16°07'20"S, 68°05'09"W, 2220 m, open area with shrubs and scattered trees, corticolous, on *L. pallida*, A.F. 26258 (KRAM, LPB). Prov. Nor Yungas: near Nogalani village, on the road Coroico–La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *L. pallida*, 23 May 2011, J.E. 27960 (LPB, hb. Etayo); carretera Coroico–La Paz, bosque nublado yungas, sendero que parte de la Estación de servicio, 3220–3250 m, 16°17'09"S, 67°51'00"W, on *L. pallida*, J.E. 27682 (LPB, hb. Etayo).

**Specimens on *Ricasolia* examined (sexual state).** Dept. Tarija. Prov. O'Connor: 26 km from Entre Ríos, near Soledad, 21°39'52"S, 64°07'22"W, 1700 m, Tucumano-Boliviano montano forest, on dead and brown *R. patinifera*, J.E. 28778 (LPB, hb. Etayo).

**Specimens of *Acremonium*-like anamorph examined (possible asexual state of *N. curtiseta*).** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, near Río Batea



**Figure 16.** *Nectriopsis curtiseta* anamorph (on *Lobariella* sp., based on A.F. 25810). A – white colonies of sporodochia growing in apothecial margin of the host; B – conidiogenous cells in LPCB; C – conidia in LPCB; D – evidently truncated conidia in LPCB. Scales: A = 250 µm; B–D = 10 µm.



Mayu close to Monte Punku, 17°31'33"S, 65°16'21"W, 2430 m, corticolous, on *Lobariella* sp., A.F. 25810 (KRAM, LPB). Dept. La Paz. Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, bosque nublado 3210 m, 16°18'27"S, 67°53'48"W, on *L. pallida*, J.E. 26936 (LPB, hb. Etayo). ECUADOR. Prov. Imbabura. Reserva Ecológica Regional Cotacachi-Cayapas, desde Irunguicho a Lagunas de Piñán, bosque nublado or. N, on *L. crenulata*, 2700–3100 m, 17N 0803255, 0048059, J.E. & Z. Palice 25430 (hb. Etayo).

***Neobaryopsis andensis*** Flakus, Etayo, Kukwa & Rodr. Flakus, gen. et sp. nov. (Fig. 17)

Mycobank MB 833335 (genus), MB 833336 (species)

Diagnosis: Lichenicolous fungus characterized by having narrowly pyriform, yellowish to orange perithecioid ascomata, 500–700 µm high, 250–300 µm wide, developing on reduced white arachnoid subiculum, large, 50–90-septate, needle-shaped ascospores, 225–430 × 1.5–2.5 µm, and a synnematosus asexual state, 100–400 µm tall, with a white stipe and a hyaline, pink to yellowish orange conidial mass, branched conidiophores, large phialides, 20–47 × 1.5–2 µm, and hyaline, ellipsoidal to obovoid conidia, 4–7 × 2–2.5 µm.

Type: Bolivia, Dept. Cochabamba, Pov. Tiraque, Parque Nacional Carrasco, Camino de los Nubes, Antenas Sillar–Villa Tunari old road, 17°12'32"S, 65°41'52"W, 3520 m, upper montane Youngas cloud forest, corticolous, on *Lobariella pallida*, Adam Flakus 25967 (KRAM – holotype!; LPB – isotype!).

**Description.** Ascomata perithecioid, distributed on the thallus of *Lobariella*, in small groups, growing on a poorly developed, white arachnoid subiculum not developing stromata, pyriform to elongate pyriform, 500–700 µm high, 250–300 µm wide, apex acute, smooth, yellowish orange to orange. Peridium 30–45 wide, hyaline to golden-orange, K<sup>+</sup> pink then hyaline, composed of two layers of tangentially flattened cells; external layer of isodiametric, thick-walled cells, 2–4 × 2–3 µm; inner region of thin-walled cells, 3–12 × 1–2 µm. Hamathecium not seen. Asci linear, 8-spored, 340–450 × 5–7 µm, apex thickened with a conspicuous cap, 8-spored. Ascospores thread-like, 50–90-septate, 225–( $\bar{x}$ =319.1 s=64)–430 × 1.5–( $\bar{x}$ =1.9 s=0.4)–2.5 µm, l/b ratio 128–( $\bar{x}$ =169.2 s=29.8)–215 (n=22). Anamorph synnematosus. Synnemata unbranched, solitary or in small groups, 100–400 µm tall, capitate; stipe 50–150 µm wide, cylindrical, white, of intricately arranged hyphae, 1.5–3 µm wide; conidial mass 50–300 µm diam., globose, hemispherical, hyaline, pink to yellowish orange, smooth, opaque to slightly translucent. Conidiophores 50–90 µm large, branched, bi- or ter-verticillate, hyaline, 2–2.5 µm wide. Phialides developing terminally or intercalarily, cylindrical to slightly tapering, straight to slightly curved, 20–47 × 1.5–2 µm. Conidia ellipsoidal, bacilliform-ellipsoidal to obovoid, at one end wider, sometimes slightly constricted in the middle, hyaline, aseptate, smooth, without a gelatinous sheath or perispore, slightly truncated, 4–( $\bar{x}$ =6 s=1)–7 × 2–( $\bar{x}$ =2.3 s=0.3)–2.5 µm, l/b ratio 2–( $\bar{x}$ =2.7 s=0.5)–3.5 (n=39).

**Etymology.** The genus name refers to its morphological similarity with *Neobarya*, and the epithet reflects its occurrence in the Andes.

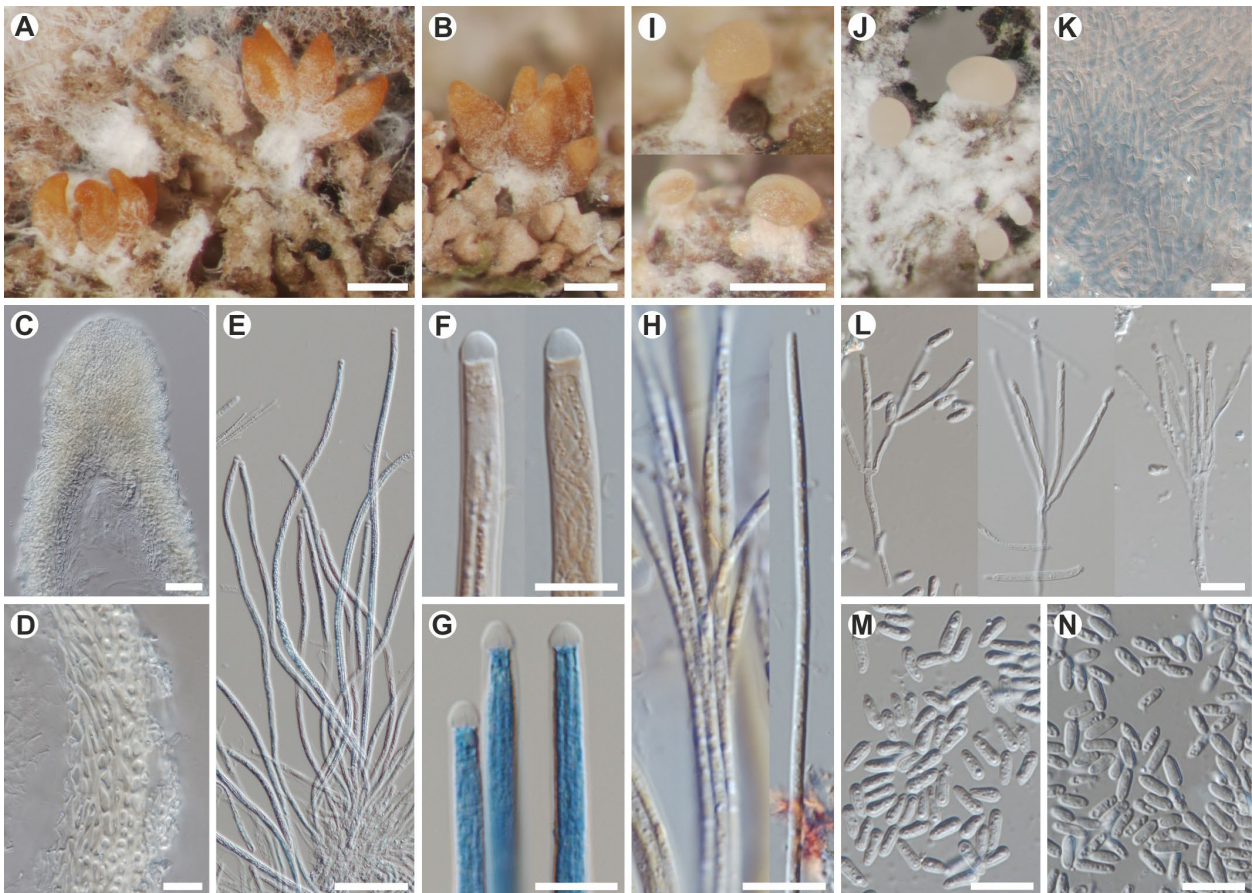
**Ecology and distribution.** The species is known from several localities in the Bolivian Andes where it grows on *Lobariella auriculata*, *L. crenulata* and *L. pallida* in Yungas and Boliviano-Tucumanos forests at a high altitude.

**Notes.** Phylogenetic analyses revealed a strongly supported placement of *Neobaryopsis* in *Cordycipitaceae* (Fig. 4) and its recognition as a distinct genus within the group of *Neobarya*-like lichenicolous fungi. *Neobaryopsis andensis* occurs on *Lobariella* and is characterized by having very particular narrowly pyriform, yellowish to orange ascomata developing on a reduced white arachnoid subiculum, and large, multiseptate needle-like ascospores. Its asexual state produces short synnematosus conidiomata with pale yellowish to pink conidial mass at the top. The morphology of ascomata makes it very similar to *Nectria byssophila* (Rossman 1979, 1983), *Lichenobarya* (Lawrey et al. 2015) and *Neobarya* s.str. (Candoussau et al. 2007). *Nectria byssophila* was originally described from bryophytes and frequently reported from various lichens. It develops a different asexual state, its ascomata are almost entirely immersed in abundant white subiculum (byssoid stroma), and its ascospores are considerably thicker (Rossman 1983). Unfortunately, the phylogenetic position of *Nectria byssophila* is still unknown. *Lichenobarya* and *Neobarya* differ in their host selection (pyrenomycetes and *Usnea*, respectively) and the color of the ascomata (brown in *Lichenobarya usneae* vs. yellowish green in *Neobarya parasitica*). *Neobarya parasitica* (type species of the genus) is additionally characterized by having a different asexual state abundantly surrounding the perithecia of the species (Candoussau et al. 2007; Lawrey et al. 2015).

South American material of *Nectria byssophila* has a variable morphology and it was reported from various lichens, e.g., *Hypotrachyna*, *Normandina*, *Parmotrema*, *Stereocaulon* and *Teloschistes* (Etayo 2002, 2017, Etayo & Sancho 2008). We have not studied specimens growing on hosts other than *Lobariella*, but probably some of them may also represent *Neobaryopsis andensis*.

**Specimens examined (sexual state).** BOLIVIA. Dept. Cochabamba. Prov. Tiraque: Parque Nacional Carrasco, Camino de los Nubes, Antenas Sillar–Villa Tunari old road, 17°12'32"S, 65°41'52"W, 3520 m, upper montane Youngas cloud forest, on corticolous *L. pallida*, M.K. 15254 (LPB), on *Lobariella* sp., M.K. 15240 (LBP, UGDA). Dept. Chuquisaca. Prov. Belisario Boeto: close to Padilla, between Nuevo Mundo and Santa Rosa, slope or. W-NW, 18°57'11.9"S, 64°16'36.3"W, 1830 m, transition between Boliviano-Tucumano forest and dry interandean vegetation, bushy forest with Acacia and a large compositeae, on *L. cf. pallida* on branches, J.E. 29446 (LPB, hb. Etayo). Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara Bajo, open area with shrubs and scattered trees, 14°41'47"S, 69°04'10"W, 3160 m, on *L. auriculata*, J.E. 20-11 (LPB, hb. Etayo). Prov. Murillo: Valle del Zongo, páramo yungueño, rocas sueltas entre pastos con arbustos, 3375 m, 16°10'15"S, 68°08'02"W, on *L. crenulata* on bushes, J.E. 26771, 26788 (LPB, hb. Etayo).

**Specimens examined (asexual state).** BOLIVIA. Dept. Cochabamba. Prov. Tiraque: Parque Nacional Carrasco, Camino



**Figure 17.** *Neobaryopsis andensis* teleomorph (A–H) and anamorph (I–N) (A, C–I on *Lobariella pallida*, based on A.F. 25967, holotype; B, on *L. auriculata*, based on J.E. 20-11; J, N on *L. cf. auriculata*, based on J.E. 20-2). A – perithecioid ascomata on the host thallus; B – ascomata on the host isidia; C – section of the apical part of peridium in water; D – section of the lateral peridium in water; E – asci in water; F–G – ascus apex in Congo Red (F) and LPCB (G); H – ascospores in Congo Red; I–J – capitate synnemata growing on the host thallus; K – section of synnemata stem showing hyphal cells in LPCB; L – conidiogenous cells; M–N – conidia in water. Scales: A–B, I–J = 250  $\mu$ m; C = 25  $\mu$ m; E = 50  $\mu$ m; D, F–H, K–N = 10  $\mu$ m.

de los Nubes, Antenas Sillar-Villa Tunari old road, 17°12'32"S, 65°41'52"W, 3520 m, upper montane Yungas cloud forest, on corticolous *L. pallida*, M.K. 15248 (LPB, UGDA). Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara Bajo, open area with shrubs and scattered trees, 14°41'47"S, 69°04'10"W, 3160 m, on *L. cf. auriculata*, J.E. 20-2 (LPB, hb. Etayo).

#### *Niesslia cf. lobariae* Etayo & Diederich

**Notes.** *Niesslia lobariae* was described by Etayo & Diederich (1996b) from *Lobaria pulmonaria*, and it is characterized by having 50–150  $\mu$ m diam., black ascomata, large setae (50–85  $\times$  5–7  $\mu$ m) and small, 1-septate, hyaline ascospores (4.5–8.5  $\times$  1.5–2.5  $\mu$ m).

*Niesslia cf. lobariae* collected in Bolivia and Ecuador on *Lobariella* and *Ricasolia* partly fits the original description but develops shorter, 10–37  $\times$  4–6  $\mu$ m (base up to 6  $\mu$ m wide) setae. Similar material was reported also from Ecuador on *Sticta humboldtii* and *S. weigelii* (Etayo 2017). The *Monocillium*-like anamorph growing on the thallus or directly on the ascomata of *Niesslia cf. lobariae* is characterized by having hyaline phialides, 2–4-septate, 42–75  $\times$  3–4  $\mu$ m, slightly wider at the base and in the upper part. A molecular phylogenetic evaluation of this complex is needed to establish species boundaries.

**Ecology and distribution.** The species is known from Bolivia, France, Spain, and Papua New Guinea when it grows on *Lobaria pulmonaria*, *Lobaria* sp., *Lobariella* and *Sticta* (Etayo & Diederich 1996; Etayo 2017).

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, near Lago Corani, close to Villa Tunari–Cochabamba road, 17°13'24"S, 65°53'31"W, 3271 m, open area with shrubs, on corticolous *Lobariella* sp., M.K. 15427 (LPB); Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *L. cf. pallida* on trees, J.E. 29527 (LPB, hb. Etayo). Prov. Carrasco: Parque Nacional Carrasco, Koricaza, 17°33'21"S, 65°16'29"W, 2950 m, Páramo Yungueño, on disk of *L. cf. pallida* on trees, J.E. 29333 (LPB, hb. Etayo). Dept. La Paz. Prov. Nor Yungas: near Nogalani village, on the road Coroico-La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27981 (LPB, hb. Etayo).

#### *Niesslia schizospora* Etayo

**Notes.** *Niesslia schizospora* was originally described from specimens from Colombia colonizing *Hypotrachyna*, and is characterized by having ascospores measuring 5–8  $\times$  1.5–2  $\mu$ m and breaking into half-spores in asci, and setae with short secondary branches (Etayo 2002). It was also reported from *Dichosporidium* and *Lobariella crenulata* in Ecuador (Etayo 2017) and seems

to be able to colonize different lichen hosts. According to Gams et al. (2019) the branched perithecial setae and fragmenting ascospores suggest that *N. schizospora* is not a member of *Niesslia* and might be more related to *Valetioniella*. Further phylogenetic studies are necessary to confirm this hypothesis.

**Ecology and distribution.** In addition to being found on *Hypotrachyna* in Colombia (Etayo 2002) it was later reported from *Dichosporidium* sp. and *Lobariella crenulata* in Ecuador (Etayo 2017).

*Niesslia stictarum* (Nannf. & R. Sant.) Tretiach & R. Sant. var. *stictarum*

**Notes.** This taxon is characterized by having short setae (10–26 µm long) with a widened base (7–13 µm wide), giving the appearance of shark teeth, and 6–7 × 1.5–2 µm ascospores (Tretiach 2002; Etayo 2017).

**Ecology and distribution.** Originally described from *Sticta ambavillaria* in Tanzania (Tretiach 2002), but also known from Ecuador on *Sticta* and *Lobariella pallida* (Etayo 2017), and from Bolivia on *L. pallida*.

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, bosque nublado, 3210 m, 16°18'27"S, 67°53'48"W, on *L. pallida*, J.E. 26940 (LPB, hb. Etayo).

*Niesslia stictarum* var. *nuda* Etayo

**Notes.** This variety was described from Ecuador (Etayo 2017) on *Lobariella pallida*, and characterized by having ascomata covered only by hyaline setae 34–45 × 4–5 µm, and 7.5–10.5 × 2–3 µm ascospores. It is somewhat similar to saprobic *N. waitemataensis* described by Gams et al. (2019) from New Zealand, due to the absence of dark-brown setae and a subiculum, but it can be distinguished by larger ascomata (200–300 µm) and ascospores (10–13 × 3–3.5 µm).

**Ecology and distribution.** Known from Bolivia and Ecuador on *Lobariella pallida*.

**Specimens examined.** BOLIVIA. Dept. Santa Cruz. Prov. Manuel María Caballero: near Siberia, km 23, 217°49'13"S, 64°40'45"W, 2550 m, Yungas cloud forest, on *Lobariella* sp., J.E. 29453 (LPB).

*Ovicuculispora parmeliae* (Berk. & Curt.) Etayo s.lat.

**Notes.** The genus *Ovicuculispora* was introduced by Etayo (2010) to accommodate two lichenicolous species, *O. macrospora* and *O. parmeliae*. It is characterized by having orange perithecia developing on a white arachnoid mycelium, and by the production of 1–2 macrospores together with 4 microspores in the same ascus. *Ovicuculispora parmeliae* s.lat. was shown to have a huge variation in size of macrospores and has been reported from many hosts (e.g., Lawrey et al. 1994; Cole & Hawksworth 2001; Diederich 2003; Flakus et al. 2006; Etayo 2010). It is very likely that it represents a species complex. Samples growing on *Lobariella* are characterized by having ascospores measuring (60–)73–94(–99) × 24–34 µm and

having reticulate walls, and may represent another undescribed species.

**Ecology and distribution.** Widely distributed and known from various lichen genera, including *Candelariella*, *Cladonia*, *Erioderma*, *Graphis*, *Heterodermia*, *Lobariella*, *Parmelia*, *Pertusaria*, *Physcia*, *Punctelia* and *Sticta* (Etayo 2010).

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Nor Yungas: below Unduavi village, near Río Unduavi, 16°18'50"S, 67°54'35"W, 3135 m, Yungas cloud forest, on *Lobariella* sp., J.E. 26963 (LPB, hb. Etayo); near Siniari colony, km 74 on the road Coroico–La Paz, 16°13'20"S, 67°50'37"W, 2090–2186 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27645 (LPB, hb. Etayo). PANAMA. Prov. Chiriquí. Parque Nacional Volcán Barú, Sendero Volcán, W slope, 08°48'49"N, 82°33'50"W, 2444 m, montane forest close to open rocks, on *Lobariella* sp. and *Hypotrachyna* sp., A.F. Baru-0-C1-P1-Fla1 (KRAM, PMA).

*Pronectria microspora* Etayo

**Notes.** This species was described from specimens collected in Colombia and is characterized by having very small, yellowish to orange, immersed ascomata (60–85 µm diam.) and hyaline, smooth-walled ascospores, 5–6.5(–7.5) × 3–4.5 µm (Etayo 2002).

**Ecology and distribution.** Known from *Lobariella crenulata*, *L. exornata* and *L. pallida* from Bolivia and Colombia (Etayo 2002).

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *Lobariella* sp., J.E. 29504 (LPB), on *L. exornata*, J.E. 29520 (LPB, hb. Etayo). Dept. La Paz. Prov. Larecaja: Jocollone village and 1 km further, 15°37'35"S, 68°41'21"W, 3545 m, Paramo Yungeño vegetation, open anthropogenic area, much *Berberis*, NE oriented slope, on *L. crenulata*, J.E. 27206 (LPB, hb. Etayo). Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unduavi, camino a Chulumani, S16°18'27", W67°53'48", 3210 m, bosque nublado, on *L. pallida*, J.E. 26940 (LPB, hb. Etayo).

*Pseudocercospora* cf. *lichenum* (Keissl.) D. Hawksw.

**Notes.** This species was described from specimens found on *Loxospora cismonica* and later reported from other lichens (Hawksworth 1979; Etayo & Diederich 1996; Etayo 2002). Our material is characterized by having the following features: conidiophores scattered or loosely grouped, well differentiated, brown, 3–5 septate, smooth, conidiogenous cells, 3.5–5 µm wide, sympodial, conidiogenous loci difficult to see, and pale brown, 1–3-euseptate conidia, 10–17 × 3–4 µm.

**Ecology and distribution.** This species is widely distributed and has been reported from several lichen genera (*Cladonia*, *Phyllospora*, *Lobaria*, *Sticta*; Hawksworth 1979; Etayo & Diederich 1996; Etayo 2002) including the Bolivian *Lobariella pallida*.

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Larecaja: Jocollone village and 1 km further, Paramo yungeño vegetation, 15°37'35"S, 68°41'21"W, 3545 m, on *L. pallida* on schrubs, J.E. 27202 (LPB, hb. Etayo). Prov. Nor Yungas: desviación de

La Paz a Coroico hacia Unduavi, camino a Chulumani, bosque nublado, 3210 m, 16°18'27"S, 67°53'48"W, on *L. pallida*, J.E. 26946 (LPB, hb. Etayo).

*Pseudodidymocyrtis lobariellae* Flakus, Rodr. Flakus & Etayo, gen. et sp. nov. (Fig. 18)

Mycobank MB 833337 (genus), MB 833338 (species)

Diagnosis: Differs from species of *Kalmusia* by its the lichenicolous life style, asci with a much shorter pedicel and a strongly thickened apical apparatus and an evident apical cushion, and paler, golden-brown to brown ascospores, K+ dark olivaceous-brown.

Type: Bolivia: Dept. La Paz, Prov. Franz Tamayo, Área Natural de Manejo Integrado Nacional Apolobamba, near Rio Pelechuco, below Pelechuco close to new road to Apolo, 14°46'59"S, 69°01'08"W, 2750 m, open area with scattered small trees, on corticolous *Lobariella pallida*, Adam Flakus 25130 (KRAM – holotype!; LPB – isotype!).

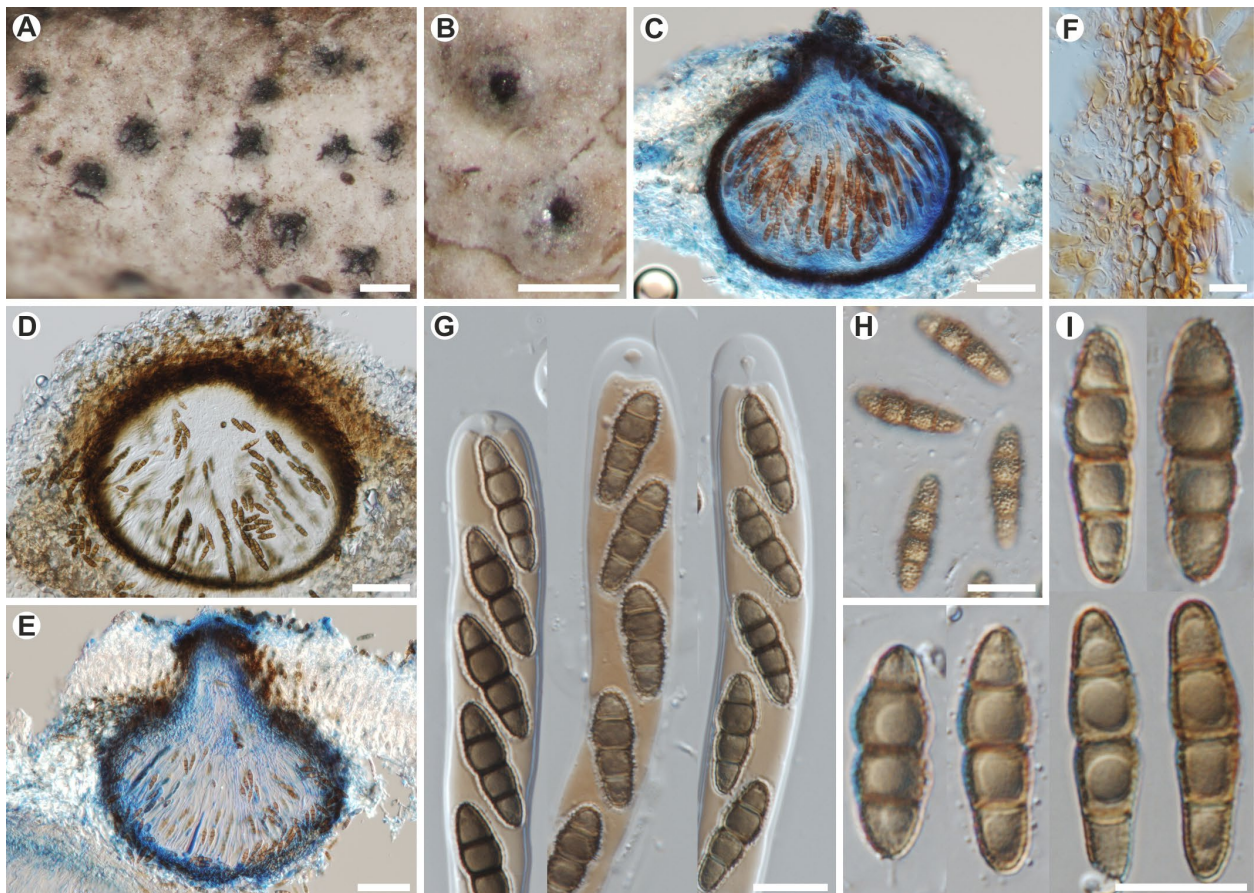
**Description.** Ascomata perithecioid, 200–250 µm high, 200–300 µm wide, subspherical to pyriform, dispersed, fully immersed in the host thallus and apothecial margins or breaking the cortex of the host thallus when older, visible as black dots, not causing gall formation. Peridium dark brown, covered by an indistinct clypeus, in the upper part usually developing a short beak, laterally 15–23 µm diam., consisting of 4–6 layers of cells, cell size 3–13 × 2–8 µm, inner part of thin-walled, hyaline to

pale brown cells, outer layer of thin- to thick-walled, dark-brown cells. Pseudoparaphyses branched and anastomosing, 1.5–3 µm wide. Asci bitunicate, 90–130 × 10–12 µm, narrowly cylindrical, with a short pedicel, 10–15 µm, I–, K/I–, endoascus KI+ orange, with strongly thickened apical apparatus (2–7 µm tall) and an evident apical cushion (when seen in K/I), 8-spored. Ascospores uniseriate to half-overlapping, golden-brown to brown, K+ dark olivaceous-brown, 3-septate, strongly verruculose, strongly constricted, especially near median septum, the second cell from above wider, with a 1–3 µm thick gelatine coat when young, 15–( $\bar{x}$  = 18.9 s = 1.9)–22 × 5–( $\bar{x}$  = 5.8 s = 0.4)–6.5 µm, l/b ratio 2.6–( $\bar{x}$  = 3.3 s = 0.4)–4 (n = 35).

**Etymology.** The generic name emphasizes the morphological similarities with the lichenicolous genus *Didymocyrtis*. The epithet refers to the host genus.

**Ecology and distribution.** Known only from the type locality where it grows on *Lobariella pallida*.

**Notes.** As shown by our phylogenetic analyses (Fig. 5), *Pseudodidymocyrtis lobariellae* is placed in *Didymosphaeriaeae* close to the genus *Kalmusia*. In addition to the saprobic life style, *Kalmusia* differs from *Pseudodidymocyrtis* by asci with a long furcate pedicel and darker ascospores (Ariyawansa et al. 2014; Zhang et al. 2014). *Pseudodidymocyrtis lobariellae* also has a morphology



**Figure 18.** *Pseudodidymocyrtis lobariellae* (on *Lobariella pallida*, based on A.F. 25130, holotype). A–B – perithecioid ascomata immersed in the host thallus; C–E – section of ascoma showing hymenium (C in LPCB), indistinct clypeus forming by projecting hyphae (D in water), and short apical beak (E in LPCB); F – section of lateral peridium in Congo Red; G – asci with evident apical apparatus in K/I; H – ascospores ornamentation in water; I – ascospores in water. Scales: A–B = 250 µm; C–E = 50 µm; F–I = 10 µm.

very similar to some lichenicolous fungi, such as *Didymocyrtis ramalinae* (on *Ramalina*; Ertz et al. 2015), *Leptosphaeria clarkii* (on *Peltigera*; Hawksworth 1980), *L. protousneae* (on *Protousnea*; Etayo & Sancho 2008), and *Leptosphaerulina peltigerae* (on *Peltigera*; Hawksworth 1980). The morphologically most similar species are *Didymocyrtis ramalinae* (*Phaeosphaeriaceae*) and *Leptosphaeria protousneae*, but both differ by their asci having strongly thickened apical apparatus with a poorly developed structure (observed in K/I), uniform and thinner pseudoparaphyses, different pigments (in peridium and ascospores) changing colors in K to dark olivaceous-brown, not constricted ascospores and *Phoma*-like asexual state (Ertz et al. 2015). *Leptosphaeria clarkii* has ascospores [ $19\text{--}21\text{--}(22) \times 4.5\text{--}6\text{--}(6.5) \mu\text{m}$ ] and pseudoparaphyses ( $2.5\text{--}4 \mu\text{m}$  thick) very similar to *P. lobariellae* and may represent another species in the genus. However, sequence data are presently not available to confirm this relationship. *Leptosphaeria clarkii* differs by its host selection, smooth-walled ascospores, and smaller ascomata ( $75\text{--}125 \mu\text{m}$  diam.) (Hawksworth 1980). *Leptosphaerulina peltigerae* may easily be separated from the new species by the gelatinized hamathecium (lack of paraphyses), and hyaline to very pale brown, smooth-walled and thicker [ $(4\text{--})6.5\text{--}7.5 \mu\text{m}$  wide] ascospores, with  $(3\text{--})4\text{--}(5)$  transverse septa and  $0\text{--}1$  vertical septum (Hawksworth 1980).

#### *Pyrenidium* sp. ined.

**Notes.** *Pyrenidium* is a member of the recently established family *Pyrenidiaceae*, *Pleosporales* (Huanraluek et al. 2019). A description of the new species discussed in this study will be included in the forthcoming taxonomic revision of the genus *Pyrenidium* (Navarro-Rosenés et al. in press). The species causes gall formation ( $0.2\text{--}0.3 \text{ mm}$  diam.) on the host thallus, has immersed, aggregated perithecia,  $130\text{--}150 \mu\text{m}$  diam., 8-spored asci, and dark brown 3-septate,  $18\text{--}22 \times 6.5\text{--}9 \mu\text{m}$  ascospores.

**Ecology and distribution.** In Bolivia this species usually occurs on *Lobariella*, but similar morphotypes were also observed on *Yoshimurella subdissecta* and *Ricasolia patinifera*. It is uncertain if the individuals growing on different lichen hosts represent the same species.

**Specimens examined (on *Lobariella*).** BOLIVIA. Dept. La Paz. Prov. Muñecas: Área Natural de Manejo Integrado Nacional Apolobamba, above Camata, close to Charazani-Paujeyuyo road,  $15^{\circ}14'35''\text{S}$ ,  $68^{\circ}45'09''\text{W}$ , 1900 m, open area with shrubs, corticolous, on *L. crenulata*, A.F. 24935 (KRAM, LPB). Prov. Murillo: Valle del Zongo, 2450 m,  $S16^{\circ}07'41''$ ,  $W68^{\circ}05'55''$ , -bosque nublado, near bridge, on *L. exornata* on trees, J.E. 26739 (LPB); Sainani, Valle del Zongo,  $16^{\circ}07'20''\text{S}$ ,  $68^{\circ}05'09''\text{W}$ , 2220 m, open area with shrubs and scattered trees, corticolous, on *Lobariella* sp., A.F. 26255 (KRAM, LPB). Prov. Nor Yungas: near Nogalani village, on the road Coroico-La Paz (casa azul de Alejo),  $16^{\circ}12'57''\text{S}$ ,  $67^{\circ}49'15''\text{W}$ , 2168 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27968 (LPB, hb. Etayo). Prov. Bautista Saavedra: 28 km from Charazani village, on the road Charazani-Apolo,  $15^{\circ}12'43''\text{S}$ ,  $68^{\circ}47'25''\text{W}$ , 1650–1775 m, Yungas montane forest, open area with boulders on SW, on *L. crenulata*, J.E. 27324 (LPB, hb. Etayo).

**Specimens examined (on *Ricasolia* and *Yoshimurella*).** BOLIVIA. Dept. La Paz. Prov. Nor Yungas: Parque Nacional Cotapata, between Tunkini and Chairo villages, above Tunkini, even Biologic station,  $16^{\circ}11'\text{S}$ ,  $67^{\circ}52'\text{W}$ , 1300–1600 m, Yungas montane forest, on *Y. subdissecta*, J.E. 27708, 27725, (LPB, hb. Etayo). Dept. Tarija. Burnet O'Connor: 28 km from Entre Ríos, near Soledad,  $21^{\circ}41'00''\text{S}$ ,  $64^{\circ}07'29''\text{W}$ , 1500 m, Tucumano-Boliviano montano forest, corticolous, on *R. patinifera*, A.F. 24225-1 (LPB); 26 km from Entre Ríos, near Soledad,  $21^{\circ}39'52''\text{S}$ ,  $64^{\circ}07'22''\text{W}$ , 1700 m, Tucumano-Boliviano montano forest, on dead and brown *Ricasolia* sp., J.E. 28783, 28787 (LPB, hb. Etayo).

#### *Rhagadostomella hypolobariella* Etayo & Flakus, sp. nov. (Fig. 19)

MycoBank MB 833339

**Diagnosis:** Differs from *R. gregaria* by having 4-spored asci,  $22\text{--}31 \times 6\text{--}8 \mu\text{m}$ ,  $(0\text{--})2$ -septate ascospores,  $10\text{--}17 \times 1.5\text{--}3 \mu\text{m}$ , with acute ends, and the host selection, inhabiting the lower thallus surface of *Lobariella pallida*.

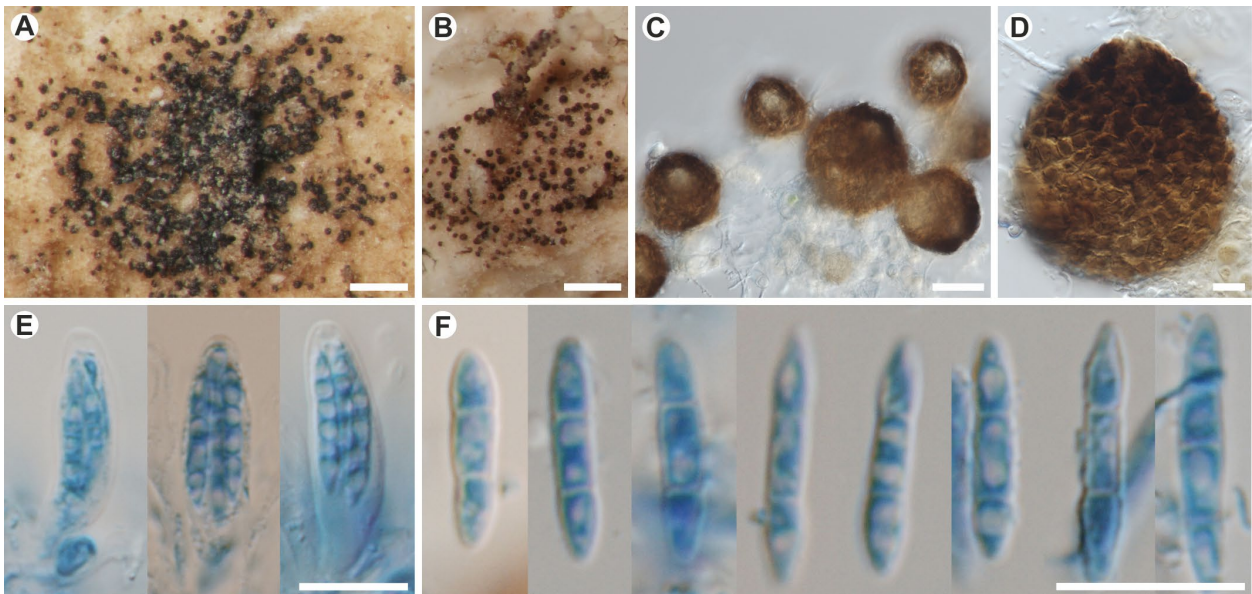
**Type:** Bolivia, Dept. La Paz, Prov. Nor Yungas, near Siniari colony, km 74 on the road Coroico-La Paz,  $16^{\circ}13'20''\text{S}$ ,  $67^{\circ}50'37''\text{W}$ , 2090–2186 m, Yungas secondary cloud forest, on *Lobariella pallida*, 24 May 2011, Javier Etayo 27636 (LPB – holotype!; hb. Etayo – isotype!).

**Description.** Ascomata perithecioid, with a central ostiole, in large groups of hundreds of perithecia on the lower surface of the thallus and rhizines of *Lobariella*, dark brown to black, subsphaerical to obpyriform, slightly flattened when dry, sessile,  $30\text{--}60 \mu\text{m}$  diam. Peridium in upper part orange-brown, K+ olivaceous-brown, BCr+ blue, almost hyaline to pale brown below, paraplectenchymatous, with external cells thick-walled in the upper part,  $4\text{--}8 \mu\text{m}$  diam., almost hyaline and with a very thin wall in the lower part. Paraphysoids soon disappearing. Paraphyses  $\sim 1 \mu\text{m}$  wide, surrounded by a gel layer. Asci bitunicate, clavate, apex obtuse slightly flattened, wall slightly thickened at the apex, with a small ring in upper part easily visible in BCr, I–, KI–, epiplasm K/I+ orange, 4-spored,  $22\text{--}31 \times 6\text{--}8 \mu\text{m}$ . Ascospores present in the upper part of the ascus, narrowly ellipsoidal to fusiform, with acute ends and small constrictions in the middle, hyaline,  $(0\text{--})2$ -septate, with 3–4 oil guttules, without a perispore, BCr+ blue,  $10\text{--}(\bar{x}=14.3 \text{ s}=1.6)\text{--}17 \times 1.5\text{--}(\bar{x}=2.3 \text{ s}=0.4)\text{--}3 \mu\text{m}$ , l/b ratio  $4.8\text{--}(\bar{x}=6.4 \text{ s}=1.1)\text{--}9.3$  ( $n=29$ ).

**Etymology.** The epithet refers to the ecology of the new species inhabiting the lower thallus surface of *Lobariella*.

**Ecology and distribution.** The species is known from several localities in Bolivian Yungas forest where it is always found on the lower surface of the thallus of *Lobariella pallida*.

**Notes.** The monospecific genus *Rhagadostomella* was introduced by Etayo (2002) for *R. gregaria* growing on *Sticta weigeli* in Colombia. Etayo (2002) suggested that it belongs to the *Nitschkiaceae* (*Coronophorales*) but its phylogenetic position remains unknown. *Rhagadostomella gregaria* differs from the new species by its narrower and 1-septate ascospores ( $14\text{--}16.5 \times 1.5\text{--}2 \mu\text{m}$ ) that never develop acute apices.



**Figure 19.** *Rhagadostomella hypolobariella* (on *Lobariella pallida*; A, based on J.E. 27636, holotype; B–F, based on A.F. 25157-1). A–B – perithecioid ascomata on the underside of the host thallus; C – ostiolate, perithecioid ascomata in water; D – ascomata showing isodiametric cells of peridium in water; E – asci in LPCB; F – ascospores in LPCB. Scales: A = 200  $\mu$ m; B = 250  $\mu$ m; C = 25  $\mu$ m; D–F = 10  $\mu$ m.

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Manuel María Caballero: cerca Siberia, 17°45'54"S, 64°48'47"W, 2570 m, open Yungas cloud forest, on *Lobariella* sp., J.E. 28826 (LPB, hb. Etayo), on *L. pallida*, J.E. 29324 (LPB, hb. Etayo). Prov. Carrasco: Parque Nacional Carrasco, near Río Batea Mayu close to Monte Punku, 17°31'33"S, 65°16'21"W, 2430 m, lower montane Yungas cloud forest, corticolous, on *Lobariella* sp., A.F. 25827 (LPB). Dept. La Paz. Prov. Franz Tamayo; Área Natural de Manejo Integrado Nacional Apolobamba, near Río Pelechuco, below Pelechuco close to new road to Apolo, 14°47'28"S, 69°01'32"W, 2860 m, open area with scattered trees, corticolous, on *L. pallida*, A.F. 25157/1 (KRAM, LPB). Prov. Nor Yungas: near Nogalani village, on the road Coroico-La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27956 (LPB, hb. Etayo).

#### *Roselliniella ramirezii* Etayo

**Notes.** The species is characterized by having black perithecioid ascomata (250–400  $\mu$ m diam.) immersed in the host thallus and breaking through the thallus cortex with age, a dark brown mycelium, and aseptate, hyaline to pale brown ascospores (16–25  $\times$  8–12  $\mu$ m in Bolivian samples). The Bolivian samples are characterized by having slightly larger ascospores than those observed in Colombian and Ecuadorian populations, which measured 16–23  $\times$  6–9  $\mu$ m (Etayo 2002, 2017).

**Ecology and distribution.** Known from Bolivia, Colombia (Etayo 2002) and Ecuador (Etayo 2017) from different species of *Lobariella*.

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, near Río Lopez Mendoza, 17°30'25"S, 65°16'51"W, 2248 m, lower montane Yungas cloud forest, corticolous, on *Lobariella* sp., A.F. 25690 (KRAM, LPB); Wayra Mayu close to Monte Punku, 17°32'27"S, 65°16'14"W, 2553 m, lower montane Yungas cloud forest, on saxicolous *Lobariella* sp., M.K. 15162 (LPB, UGDA); near Río Ibirisu, close to Sajtarumi, 17°27'09"S, 65°16'29"W, 2059 m, lower montane Yungas cloud forest, on corticolous *Lobariella* sp.,

M.K. 15144c (LPB). Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, oncorticolous, *L. auriculata*, A.F. 24711, 24724, 24725, on *L. pallida*, A.F. 24723 (KRAM, LPB), on *L. exornata* J.E. 29494, 29621, 29495 (LPB, hb. Etayo); near Río Batea Mayu close to Monte Punku, 17°31'33"S, 65°16'21"W, 2430 m, lower montane Yungas cloud forest, corticolous, on *Lobariella* sp. A.F. 25828 (KRAM, LPB); San Jacinto, cose to Villa Tunari-Lago Corani road, 17°10'26"S, 65°45'13"W, 1877 m, open area with shrubs and scattered trees, on corticolous *Lobariella* sp., M.K. 15407 (LPB, UGDA). Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara Bajo, 14°41'40"S, 69°03'51"W, 3060 m, open area with shrubs and scattered trees, on corticolous *Lobariella* sp., M.K. 14882c, on *L. crenulata*, M.K. 14914 (LPB, UGDA); near Keara Bajo, 14°41'59"S, 69°04'34"W, 3290 m, open area with shrubs and scattered trees, corticolous, on *L. pallida*, A.F. 25243, 25247, *L. crenulata*, M.K. 14873b (KRAM, LPB, UGDA); Pukara between Keara and Keara Bajo, 14°42'09"S, 69°05'17"W, 3420 m, open area with shrubs, on corticolous *L. pallida*, M.K. 14936 (LPB); Área Natural de Manejo Integrado Nacional Apolobamba, near Río Pelechuco, below Pelechuco close to new road to Apolo, 14°47'28"S, 69°01'32"W, 2860 m, open area with scattered trees, corticolous, on *L. pallida*, A.F. 25142, on *L. auriculata*, A.F. 25149 (KRAM, LPB). Prov. Nor Yungas: Desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, 3210 m, S16°18'27", W67°53'48", bosque nublado, on *L. pallida*, J.E. 26937 (LPB, hb. Etayo). Prov. Bautista Saavedra: km 202 on the road from Apolo to Charazani villages, 20 km from Charazani, 15°12'35"S, 68°51'30"W, 2259 m, transition Yungas montane forest-cloud forest, on *L. pallida*, J.E. 27416 (LPB); near Charazani village, 15°10'39"S, 68°56'36"W, 2237 m, Yungas montane forest with outcrops, on *Lobariella* sp., J.E. 15-3 (LPB, hb. Etayo). Dept. Santa Cruz. Prov. Manuel María Caballero: near Siberia, km 232, 17°49'13"S, 64°40'45"W, 2550 m, Yungas cloud forest, on *L. subexornata* on trees, J.E. 29441 (LPB, hb. Etayo). Dept. Tarija. Prov. O'Connor: 26 km from Entre Ríos, near Soledad, 21°39'52"S, 64°07'22"W, 1700 m, Tucumano-Boliviano montano forest, on *Lobariella* cf. *reticulata*, J.E. 54-2 (LPB, hb. Etayo).

*Sclerococcum ricasoliae* (Vouaux) Flakus, Rodr. Flakus & Etayo, comb. nov. (Fig. 20)

Mycobank MB 833340

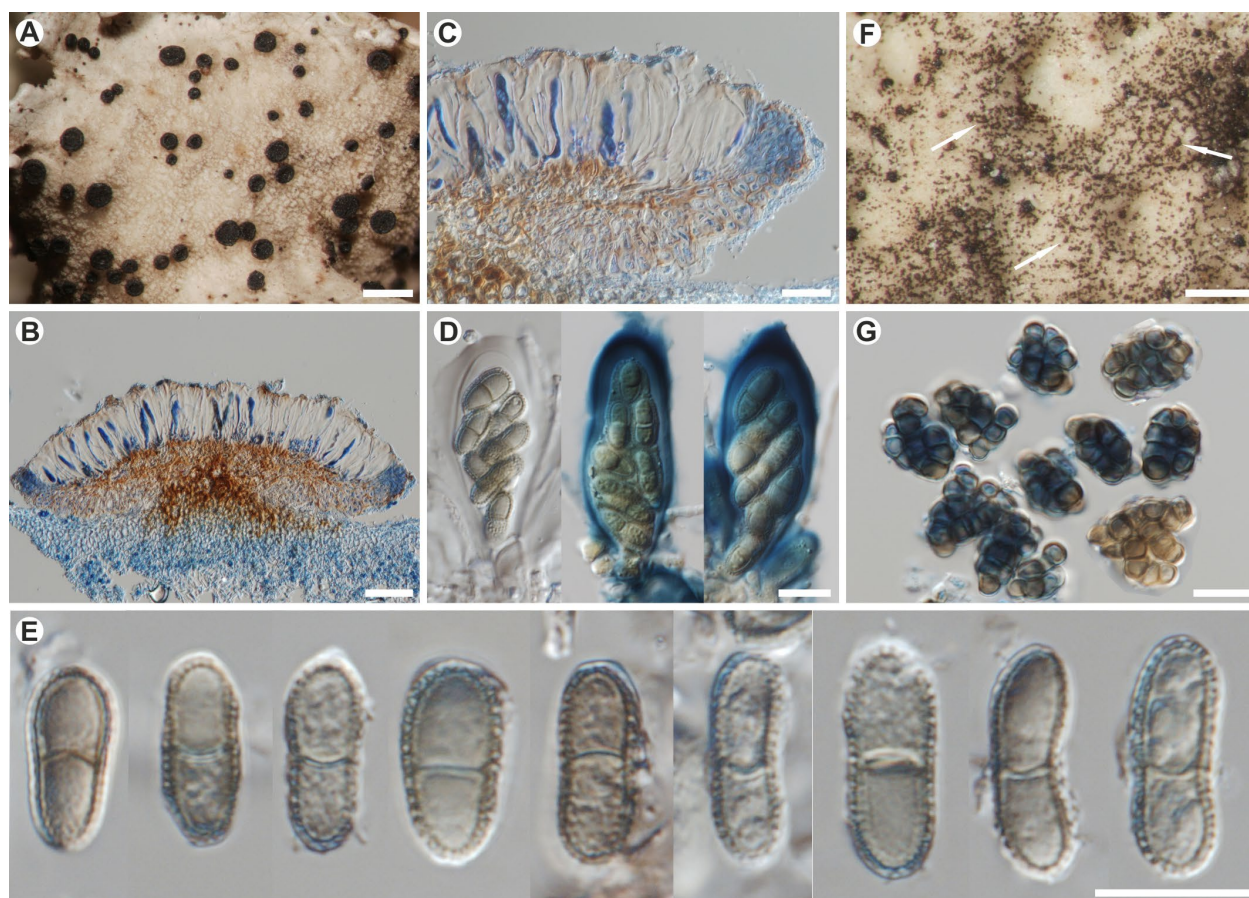
Basionym: *Karschia ricasoliae* Vouaux, Bulletin de la Société Mycologique de France 29: 448. 1913.

Type: Mexico, Morelia, Cerro Azul, 2300 m, 10 March 1910, Brouard (Y. Rondon, MARSSJ – lectotype!, selected by Hafellner 1979).

**Description.** Ascomata apothecioid, rounded, 0.15–0.6 mm diam., dispersed or in small groups, black, matte. Disc flat, black. Margin distinct, persistent, concolorous with the disc. Exciple orange- to dark-brown, paraplectenchymatous, composed of thick-walled cells, laterally 20–40  $\mu\text{m}$  wide, basally 25–50  $\mu\text{m}$  wide, in the upper part composed of small cells, 2–6  $\times$  2–4  $\mu\text{m}$ , in the lower part of large cells, 5–15  $\times$  4–11  $\mu\text{m}$ . Epithymenium hyaline to light brown. Hymenium hyaline to light orange-brown, 45–70  $\mu\text{m}$  high, strongly gelatinized. Paraphyses slightly branched and anastomosing, 1–2  $\mu\text{m}$  wide, sometimes with swollen and pigmented apices, up to  $\sim$ 4  $\mu\text{m}$  wide. Hypothecium dark orange-brown. Asci with a K/I+ dark blue outer layer, 8-spored, 35–50  $\times$  10–15  $\mu\text{m}$ . Ascospores light to dark greyish brown to brown, ellipsoidal, verruculose, 1-septate, without a gelatine coat, 8–( $\bar{x}$ =11.6  $s$ =1.7)–15  $\times$  4–( $\bar{x}$ =5.2  $s$ =0.7)–6  $\mu\text{m}$ , l/b ratio 1.5–( $\bar{x}$ =2.2  $s$ =0.4)–3.5 ( $n$ =94).

**Ecology and distribution.** The species is known from Bolivia, Ecuador, Mexico and Panama (also as *Dactylospora lobariella*) where it grows on various species of *Lobariella*, *Ricasolia* and *Yoshimuriella* (Flakus & Kukwa 2011; Etayo 2017).

**Notes.** *Dactylospora lobariella* as circumscribed by Hafellner (1979) was reported from several host species from the order *Peltigerales* (*Lobaria erosa*, *L. pulmonaria*, *Lobariella pallida*, *Pseudocyphellaria coppinsii*, *Ricasolia amplissima*, *R. patinifera*, *R. quercizans*, *R. virens* and *Yoshimuriella dissecta*) in Bolivia, Canada, Chile, Ecuador, Europe, Macaronesia, Mexico and USA (Vouaux 1913; Hafellner 1979; Kondratyuk & Galloway 1995; Etayo & Diederich 1996; Galloway & Quilhot 1998; Diederich 2003; Spribille et al. 2010; Flakus & Kukwa 2012; Etayo 2017). Recently Diederich et al. (2018) confirmed its placement in *Sclerococcales* and transferred it to genus *Sclerococcum*. According to our analyses (Fig. 7) *S. lobariellum* s.lat. represents two semicryptic species: (i) neotropical populations growing on *Lobariella pallida* and *Ricasolia patinifera* and (ii) European populations of *S. lobariellum* s.str. growing on *Lobaria pulmonaria*. Because we observed additional small differences between the two taxa, mainly in ascospores size [8–( $\bar{x}$ =11.6)–15  $\times$  4–( $\bar{x}$ =5.2)–6  $\mu\text{m}$  (l/b ratio 2.2) in *S. ricasoliae* vs. 12–( $\bar{x}$ =14)–17  $\times$  4.5–( $\bar{x}$ =5.2)–6.5  $\mu\text{m}$  (l/b ratio 2.7) in



**Figure 20.** *Sclerococcum ricasoliae* (A–E, on *Lobariella pallida*, based on A.F. 25967-3) and *Monodyctis cf. fuliginosa* (F–G, on *Ricasolia patinifera*, based on A.F. 27774). A – apothecial ascomata on the host thallus; B – section of ascomata in LPCB; C – section of exciple in LPCB; D – asci in water (left) and K/I (right); E – ascospores in water; F – simple conidia dispersed on the host thallus; G – muriform conidia in LPCB. Scales: A, F = 250  $\mu\text{m}$ ; B = 50  $\mu\text{m}$ ; C = 25  $\mu\text{m}$ ; D–E, G = 10  $\mu\text{m}$ .

*S. lobariellum*], but also in the exciple and hymenium dimensions (already mentioned by Etayo 2017), we support the taxonomic distinctiveness of the neotropical populations from *S. lobariellum* s.str. *Karschia ricasoliae* described by Vouaux (1913) on *Ricasolia* (the type is small and in a poor condition, making it difficult to choose between *Lobariella* or *Ricasolia*) from mountain forest in Mexico seems to be the only available name.

During our examination of several *Ricasolia patinifera* collections from Bolivia, we found an additional anamorphic fungus (A.F. 27774) growing intermixed with ascomata of *Sclerococcum ricasoliae*. The fungus is characterized by having dark brown, muriform conidia measuring 10–25 µm diam. (composed of cells of 4–6 µm diam.) and arising solitarily on the surface of the host from short conidiogenous cells. The fungus is very similar to *Monodictys fuliginosa* described and illustrated by Etayo & Diederich (1996) from *Lobaria pulmonaria*. Molecular data obtained from this individual (extracted directly from conidia) support its affiliation with *Sclerococcum ricasoliae* (Fig. 7). Because all known anamorphic states of *Sclerococcum* develop sporodochia while the conidia of the Bolivian *Monodictys* cf. *fuliginosa* (A.F. 27774) arise individually, we suspect that the sequence may be a result of a contamination from the sexual state of *S. ricasoliae* co-occurring on the same sample. On the other hand, in Europe we frequently observed *M. fuliginosa*-like anamorphs intermixed with *S. lobariellum* suggesting a possibility that our fungus represents a second type of anamorphic state of *Sclerococcum*, but this putative teleomorph-anamorph connection needs to be confirmed on a larger number of samples.

**Specimens on *Lobariella* examined.** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Meruvia close to Monte Punku, 17°35'06"S, 65°14'54"W, 3283 m, *Podocarpus-Polylepis* forest, corticolous, on *L. pallida*, A.F. 25590, on *Lobariella* sp. A.F. 25591, M.K. 15034 (KRAM, LPB, UGDA), on *L. auriculata*, M.K. 15029c (LPB), on *Lobariella* sp., J.E. 27-4 (LPB, hb. Etayo); between Meruvia and Monte Punku, 17°34'43"S, 65°15'25"W, 3082 m, *Podocarpus* forest, corticolous, on *L. pallida*, A.F. 25611, 25620 (KRAM, LPB). Prov. Tiraque: Parque Nacional Carrasco, Camino de los Nubes, Antenas Sillar-Villa Tunari old road, 17°12'32"S, 65°41'52"W, 3520 m, upper montane Yungas cloud forest, corticolous, on *L. pallida*, A.F. 25967; (KRAM, LPB) 17°12'29"S, 65°41'24"W, 3590 m, on *Lobariella pallida*, J.E. 41-2 (LPB, hb. Etayo); old guard's camp, 17°18'23"S, 65°45'60"W, 3360 m, open area with shrubs, on *L. pallida*, A.F. 26039, 26044 (KRAM, LPB), on *Lobariella* sp. J.E. 44-3 (LPB, hb. Etayo); Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado Nacional Apolobamba, near Rio Pelechuco, below Pelechuco close to new road to Apolo, 14°46'22"S, 69°00'11"W, 2480 m, lower montane Yungas cloud forest, corticolous, on *L. pallida*, A.F. 25068 (KRAM, LPB); near Rio Pelechuco, below Pelechuco close to new road to Apolo, 14°46'59"S, 69°01'08"W, 2750 m, open area with scattered small trees, on corticolous *Lobariella* sp., M.K. 14787b (LPB). Prov. Larecaja: near Chumisa, close to Sorata-Consata road, 15°36'18"S, 68°39'28"W, 3337 m, open area with shrubs, corticolous, on *L. pallida*, A.F. 26303 (KRAM, LPB); above Sorata, close to Sorata-Mapiri road, 15°44'11"S, 68°38'41"W, 3706 m, open area with shrubs including *Ericaceae*, on *Lobariella* sp., J.E. II-1 (LPB, hb. Etayo). Prov. Murillo:

Valle del Zongo, páramo yungueño, rocas sueltas entre pastos con arbustos, 3375 m, 16°10'15"S, 68°08'02"W, on *L. crenulata*, J.E. 26765 (LPB, hb. Etayo). Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, bosque nublado, 3210 m, 16°18'27"S, 67°53'48"W, on *L. pallida*, J.E. 26936 (LPB, hb. Etayo); near Nogalani village, on the road Coroico-La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27960 (LPB, hb. Etayo); Coroico village, 16°11'10"S, 67°43'16"W, 1550 m, Yungas montane forest, on *L. pallida*, A.F. 16420-2 (KRAM, LPB); below Unduavi village, on the road La Paz-Chulumani, 16°18'27"S, 67°53'48"W, 3210 m, Yungas cloud forest, corticolous, on *L. pallida*, A.F. 22200 (KRAM, LPB). Dept. Santa Cruz. Prov. Comarapa: Remate, 17°52'11"S, 64°20'53"W, 2250, Yungas forest with big trees, partly grazed, corticolous, on *L. pallida*, A.F. 29132 (KRAM, LPB). PAN-AMA. Prov. Chiriquí. Parque Nacional Volcán Barú, Sendero Volcán, W slope, 08°48'49"N, 82°33'50"W, 2444 m, montane forest close to open rocks, on *L. cf. pallida*, A.F. Fla6/B (PMA).

**Specimens on *Ricasolia patinifera* examined.** BOLIVIA. Dept. Chuquisaca. Prov. Belisario Boeto: between Nuevo Mundo and Villa Cerrano, 19°00'52"S, 64°20'17"W, 2569 m, Boliviano-Tucumano forest with *Podocarpus* and *Polylepis*, corticolous, A.F. 26632 (KRAM, LPB). Dept. Tarija. Prov. Burnet O'Connor: 26 km from Entré Ríos, near Soledad, 21°39'52"S, 64°07'22"W, 1690 m, Tucumano-Boliviano montano forest, corticolous, A.F. 24225 (KRAM, LPB); 60 km from Tarija, new road between Tarija and Entrerios, 21°28'52"S, 64°17'41"W, 1837, Boliviano-Tucumano forest with *Podocarpus*, corticolous, A.F. 27635 (KRAM, LPB); 112 km from Tarija on the way to Entre Ríos, near San Diego, 21°26'28"S, 64°14'37"W, 1620 m, Tucumano-Boliviano montano forest, J.E. 28595 (LPB, hb. Etayo).

**Specimen of *Monodictys* cf. *fuliginosa* examined.** BOLIVIA. Dept. Tarija. Prov. Burnet O'Connor: close to los Pinos, old road between Entrerios and Tarija, 21°25'57"S, 64°19'17"W, 2178, Boliviano-Tucumano forest close to small river dominated by shrubs, on corticolous *Ricasolia patinifera*, A.F. 27774 (KRAM, LPB).

#### *Stigmatidium disconeophromeum* Etayo

**Notes.** *Stigmatidium disconeophromeum* has characteristic perithecioid ascomata (60–70 µm diam.), that are almost entirely immersed in the hymenium of the host apothecia, and small bacilliform, hyaline ascospores (10–13.5 × 3–3.5 µm), and was originally described from *Nephroma antarcticum* in Chile (Etayo & Sancho 2008). Later the species was reported from Ecuador as a parasite of *Lobariella pallida* (Etayo 2017). Although *Stigmatidium* is considered strongly host-specific (Roux & Triebel 1994; Diederich et al. 2018) and the specimen growing on *Lobariella* may represent an additional species, further studies on a larger material are needed to reveal its taxonomic identity.

There is one additional species, *Stigmatidium lobariae*, described from *Lobariaceae* (*Lobaria pulmonaria*) and known from Alaska and Spain (Zhurbenko & Etayo 2012). This species is easily distinguished by its smaller ascomata (40–70 µm) and larger ascospores [(9.5–)12.5–15(–16.5) × (3–)3.5–4(–4.5) µm] of a different shape and color (olive-brown when mature). Other species growing on *Peltigerales*, such as *S. croceae*, *S. cupulare*, *S. peltideae*, *S. pseudopeltideae*, *S. schaeereri*, *S. solorinarium*, and *S. spegazzinii*, apart from their distinct host preferences



(inhabiting *Peltigera*, *Pseudocyphellaria*, *Sticta* or *Solorina*) can also be differentiated by the ascospore and/or ascomata characters as discussed in detail by Zhurbenko & Etayo (2012).

**Ecology and distribution.** The species is known from Chile (Etayo & Sancho 2008) and Ecuador (Etayo 2017) where it grows in the apothecial hymenium of *Nephroma antarcticum* and *Lobariella pallida*.

**Specimens examined.** ECUADOR. Prov. Imbabura. Otavalo, Reserva bosque nublado INTAG, La delicia, bosque nublado con *Gunnera* y helechos arborescentes, 2700 m, corticícola, sobre *L. pallida*, J.E. 25618 y Z. Palice (hb. Etayo).

*Trichonectria setadpressa* Etayo (Fig. 21)

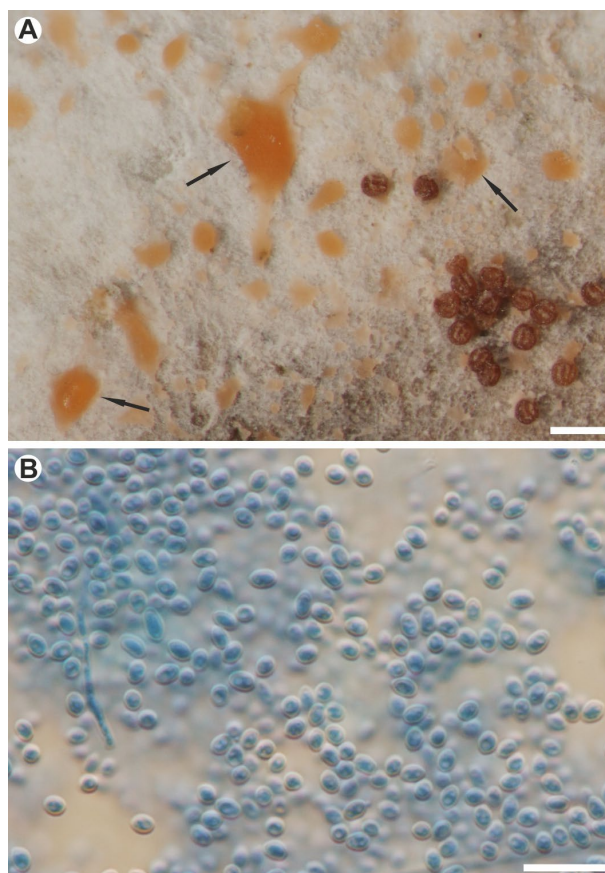
**Description of asexual state.** Conidiomata sporodochia-like aggregated conidiophorus, developing on an arachnoid subiculum on the upper side of the host thallus, pinkish, fused in groups resembling droplets. Conidiogenous cells hyaline, aseptate, straight to bent or twisted, wider at the base and tapering at the apex,  $10\text{--}30 \times 1\text{--}2.5 \mu\text{m}$ . Conidia hyaline, aseptate, subglobose to broadly ellipsoidal, not truncate,  $2\text{--}(\bar{x}=3.1 \text{ s}=0.7)\text{--}4.5 \times 2\text{--}(\bar{x}=2.3 \text{ s}=0.3)\text{--}3 \mu\text{m}$ , l/b ratio  $0.7\text{--}(\bar{x}=1.4 \text{ s}=0.4)\text{--}2.3$  (n=47).

**Notes.** This species was described from Colombia (Etayo 2002) and is characterized by having orange to brown, sessile ascomata (100–130  $\mu\text{m}$  diam.), covered by short, adpressed, branched setae, and hyaline ascospores of  $6\text{--}8 \times 2\text{--}3 \mu\text{m}$ .

We found two samples of *T. setadpressa* in Bolivia accompanied by an *Acremonium*-like anamorph representing its asexual state, as confirmed by our phylogenetic analysis (Fig. 3)

**Ecology and distribution.** Known from Bolivia, Colombia (Etayo 2002) and Ecuador (Etayo 2017) from different species of *Lobariella*.

**Specimens examined (sexual state).** BOLIVIA. Dept. Cochabamba. Prov. Chapare: PN Carrasco, Incachaca,  $17^{\circ}14'59''\text{S}$ ,  $65^{\circ}49'36''\text{W}$ , 2560 m, Yungas cloud forest, on *Lobariella subexornata* on bushes, J.E. 29621 (LPB). Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara Bajo, open area with shrubs and scattered trees,  $14^{\circ}41'47''\text{S}$ ,  $69^{\circ}04'10''\text{W}$ , 3160 mm, on *L. pallida*, J.E. 20-13 (LPB, hb. Etayo). Prov. Larecaja: Jocollone village and 1 km further, Paramo Yungueño vegetation, open anthropogenic area, with *Berberis*,  $15^{\circ}37'35''\text{S}$ ,  $68^{\circ}41'21''\text{W}$ , 3545 m, NE oriented slope, on *L. pallida*, J.E. 27199 (LPB, hb. Etayo). Prov. Murillo: Valle del Zongo, 3375 m,  $S16^{\circ}10'15''$ ,  $W68^{\circ}08'02''$ , páramo yungueño, rocas sueltas entre pastos con arbustos, on *L. crenulata* on bushes, J.E. 26776 (LPB, hb. Etayo). Prov. Nor Yungas: desviación de La Paz a Coroico hacia Unduavi, camino a Chulumani, bosque nublado, 3210 m,  $16^{\circ}18'27''\text{S}$ ,  $67^{\circ}53'48''\text{W}$ , on *L. crenulata*, J.E. 26939 (LPB, hb. Etayo); near Siniari colony, km 74 on the road Coroico-La Paz,  $16^{\circ}13'20''\text{S}$ ,  $67^{\circ}50'37''\text{W}$ , 2090–2186 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27645 (LPB, hb. Etayo); near Nogalani village, on the road Coroico-La Paz (casa azul de Alejo),  $16^{\circ}12'57''\text{S}$ ,  $67^{\circ}49'15''\text{W}$ , 2168 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27958 (LPB, hb. Etayo); Parque Nacional Cotapata, la Cumbre de Sillu Tincara,  $16^{\circ}17'22''\text{S}$ ,  $67^{\circ}53'29''\text{W}$ , 3518, Páramo Yungueño, corticolous, on *L. pallida*, A.F. 29612, 29617 (KRAM, LPB); Chus-



**Figure 21.** *Trichonectria setadpressa* anamorph (on *Lobariella pallida*, based on A.F. 29612-2). A – sporodochia-like conidiomata growing on the host thallus; B – conidia in LPCB. Scales: A = 250  $\mu\text{m}$ ; B = 10  $\mu\text{m}$ .

pipata station, old road Coroico-La Paz,  $16^{\circ}18'18''\text{S}$ ,  $67^{\circ}48'55''\text{W}$ , 3009, disturbed Yungas cloud forest with shrubs and small trees, on *L. crenulata*, A.F. 28886 (KRAM, LPB).

**Specimens examined (Acremonium-like asexual state).** BOLIVIA. Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, below Keara Bajo,  $14^{\circ}41'47''\text{S}$ ,  $69^{\circ}04'10''\text{W}$ , 3160 m, open area with shrubs and scattered trees, on *L. pallida*, J.E. 20-13 (LPB, hb. Etayo). Prov. Nor Yungas: Parque Nacional Cotapata, la Cumbre de Sillu Tincara,  $16^{\circ}17'22''\text{S}$ ,  $67^{\circ}53'29''\text{W}$ , 3518, Páramo Yungueño, on corticolous *L. pallida*, A.F. 29612 (KRAM, LPB).

*Xenonectriella coppinsiana* Etayo

**Notes.** This species was described by Etayo (2017) as having red, K+ violet ascomata (120–200  $\mu\text{m}$  diam.), with large, concolorous papillae, and verruculose ascospores ( $8.5\text{--}10.5 \times 5.5\text{--}8 \mu\text{m}$ ).

**Ecology and distribution.** Known from Bolivia and Ecuador on *Lobariella pallida* (Etayo 2017).

**Specimens examined.** BOLIVIA. Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, near Keara Bajo,  $14^{\circ}41'59''\text{S}$ ,  $69^{\circ}04'34''\text{W}$ , 3290 m, open area with shrubs and scattered trees, on corticolous *L. pallida*, M.K. 14873a (LPB). Prov. Nor Yungas: Desviación de La Paz a Coroico hacia Unchuavi, camino a Chulumani, bosque nublado, 3210 m,  $S16^{\circ}18'27''$ ,  $W67^{\circ}53'48''$ , on *L. pallida*, J.E. 26930 (LPB, hb. Etayo); below Unduavi village, on the road La Paz – Chulumani,  $16^{\circ}18'27''\text{S}$ ,  $67^{\circ}53'48''\text{W}$ , 3210 m, Yungas cloud forest, on *L. pallida*, A.F. 22202 (KRAM, LPB).

*Xenonectriella rugulatispora* Etayo

**Description of the asexual state.** *Fusarium*-like aggregated conidiophores yellowish to orange (sometimes violet) (K–), conidiophores hyaline, simple to branched, 3–4 µm thick, conidiogenous cells straight, hyaline, 15–18 × 2–3 µm, conidia hyaline, acicular, curved to sigmoid, simple (when young) to multi-septe, (60–)65–120(–130) × 2–3 µm.

**Notes.** The sexual state of the species is characterized by having brown or black ascomata with a reddish tinge (250–500 µm diam.), with large papillae (up to 100 µm long), and rugulose ascospores (11–14.5 × 9–10 µm) (Etayo 2017). A *Fusarium*-like asexual state was observed growing close to *X. rugulatispora* on the same host in two Bolivian samples (J.E. 27314, 29592). Because *Fusarium*-like fungi were reported as an asexual state of several hypocrealean genera (Booth 1971; Gerlach & Nirenberg 1982; Nelson et al. 1983; Rossman et al. 1999), we speculate that this state in our specimens belongs to *X. rugulatispora*.

**Ecology and distribution.** Known from Bolivia, Colombia and Ecuador (Etayo 2017) on *Lobariella auriculata*, *L. crenulata* and *L. pallida*. In Bolivia the species is more frequent than *X. coppinsiana*.

**Specimens examined (sexual state).** BOLIVIA Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Meruvia close to Monte Punku, 17°35'06"S, 65°14'54"W, 3283 m, *Podocarpus* – *Polylepis* forest, on corticolous *L. pallida*, M.K. 15043a (LPB). Prov. Chapare: PN Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *L. pallida*, J.E. 29520 (LPB, hb. Etayo); Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *L. auriculata*, A.F. 24734 (KRAM, LPB). Dept. La Paz. Prov. Franz Tamayo: Parque Nacional y Área Natural de Manejo Integrado Madidi, Pukara between Keara and Keara Bajo, 14°42'09"S, 69°05'17"W, 3420 m, open area with shrubs, on corticolous *L. pallida*, M.K. 14922 (LPB, UGDA). Prov. Larecaja: Jocollone village and 1 km further, Paramo Yungeño vegetation, open anthropogenic area, with *Berberis*, NE oriented slope, 15°37'35"S, 68°41'21"W, 3545 m, on *L. pallida*, J.E. 27199 (LPB, hb. Etayo). Prov. Murillo: Valle del Zongo, bosque nublado, near metal bridge, 2450 m, 16°07'41"S, 68°05'55"W, on *L. exornata* on trees, J.E. 26739 (LPB). Prov. Nor Yungas: carretera Coroico – La Paz, sendero que parte de la Estación de servicio, 3220–3250 m, S16°17'09", W67°51'00", bosque nublado yungas, on *Lobariella* sp., J.E. 26698, 27682. (LPB, hb. Etayo), on *L. cf. reticulata*, J.E. 27700 (LPB, hb. Etayo); desviación de La Paz a Coroico hacia Unduavi, camino a Chulumani, 3210 m, 16°18'27"S, 67°53'48"W, bosque nublado, on *L. pallida*, J.E. 26918 (LPB, hb. Etayo); Parque Nacional Cotapata, between Tunkini and Chairi villages, above Tunkini, even Biologic station, 16°11'S, 67°52'W, 1300–1600 m, Yungas montane forest, on *L. crenulata*, J.E. 27773 (LPB, hb. Etayo); near Nogalani village, on the road Coroico–La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *L. pallida*, J.E. 27981 (LPB, hb. Etayo). Prov. Bautista Saavedra: 28 km from Charazani village, on the road Charazani–Apolo, 15°12'43"S, 68°47'25"W, 1650–1775 m, Yungas montane forest, open area with boulders SW, on *L. crenulata*, J.E. 27319 (LPB, hb. Etayo). Dept. Santa Cruz. Prov. Manuel María Caballero: near Siberia, 17°49'34"S, 64°43'14"W, 2800 m, Yungas cloud forest with outcrops, on *Lobariella* sp., J.E. 28762 (LPB); near Siberia, 17°49'38"S, 64°44'45"W, 3950 m, open Yungas cloud forest, on *L. cf. pallida*, J.E. 29599 (LPB), on *Lobariella* sp., J.E. 29601 (LPB, hb. Etayo); near Siberia,

17°49'38"S, 64°44'45"W, 3950 m, open Yungas cloud forest, on *L. pallida*, J.E. 29577 (LPB, hb. Etayo).

**Specimens of a *Fusarium*-like asexual state examined.** BOLIVIA. Dept. La Paz. Prov. Bautista Saavedra: 28 km from Charazani village, on the road Charazani–Apolo, 15°12'43"S, 68°47'25"W, 1650–1775 m, Yungas montane forest, open area with boulders, on *L. exornata*, J.E. 27314 (LPB, hb. Etayo). Dept. Santa Cruz. Prov. Manuel María Caballero: near Siberia, 17°49'38"S, 64°44'45"W, 3950 m, open Yungas cloud forest, on apothecial disk of *L. cf. pallida*, J.E. 29592 (LPB, hb. Etayo).

*Xylaria lichenicola* Flakus, Rodr. Flakus & Etayo, sp. nov. (Fig. 22)

MycoBank MB 833341

**Diagnosis:** Lichenicolous fungus characterized by having dark brown sclerotia, 0.2–1.0 × 0.1–0.3 mm, with a rough surface, developing on a white arachnoid mycelium or directly on the host thallus, internally composed of hyaline, thick-walled, interwoven hyphae, 4–10 µm thick, with lumina 0.5–3 µm thick, surrounded by a cortical layer composed of dark-brown, isodiametric, thin-walled hyphae, with cells 4–17 µm diam.

**Type:** Bolivia: Dept. Chuquisaca, Prov. Luis Calvo, Parque Nacional y Área Natural de Manejo Integrado Serranía del Iñao, between Ticucha and Entre Ríos, 19°31'09"S, 63°53'31"W, 1373, disturbed area with shrubs, corticolous, on *Lobariella* sp., Adam Flakus 26802 (KRAM – holotype!; LPB – isotype!).

**Description.** Ascospores or conidia unknown. Colonies appearing as dispersed sclerotia with a white arachnoid mycelium, growing on the host thallus and causing bleaching. Mycelium hyaline, arachnoid, composed of branched and septate, hyaline hyphae, of two types, one with large, straight, cells, 30–150 × 2–10 µm, usually aggregated in compacted bunches, and a second of loosely arranged, short cells, 7–15 × 4–9 µm. Sclerotia dark brown, borne on a mycelium or directly on the host thallus, not immersed, narrowly ellipsoidal with acute ends to subglobose, 0.2–1.0 × 0.1–0.3 mm, usually in groups, dark brown, not translucent, shiny, with a rough surface, covered by short, dark brown hairs; internally composed of a mass of hyaline, thick-walled, interwoven hyphae, 4–10 µm thick, with lumina 0.5–3 µm thick, surrounded by a dark-brown, cortical layer composed of isodiametric, thin-walled hyphae, with cells 4–17 µm diam.

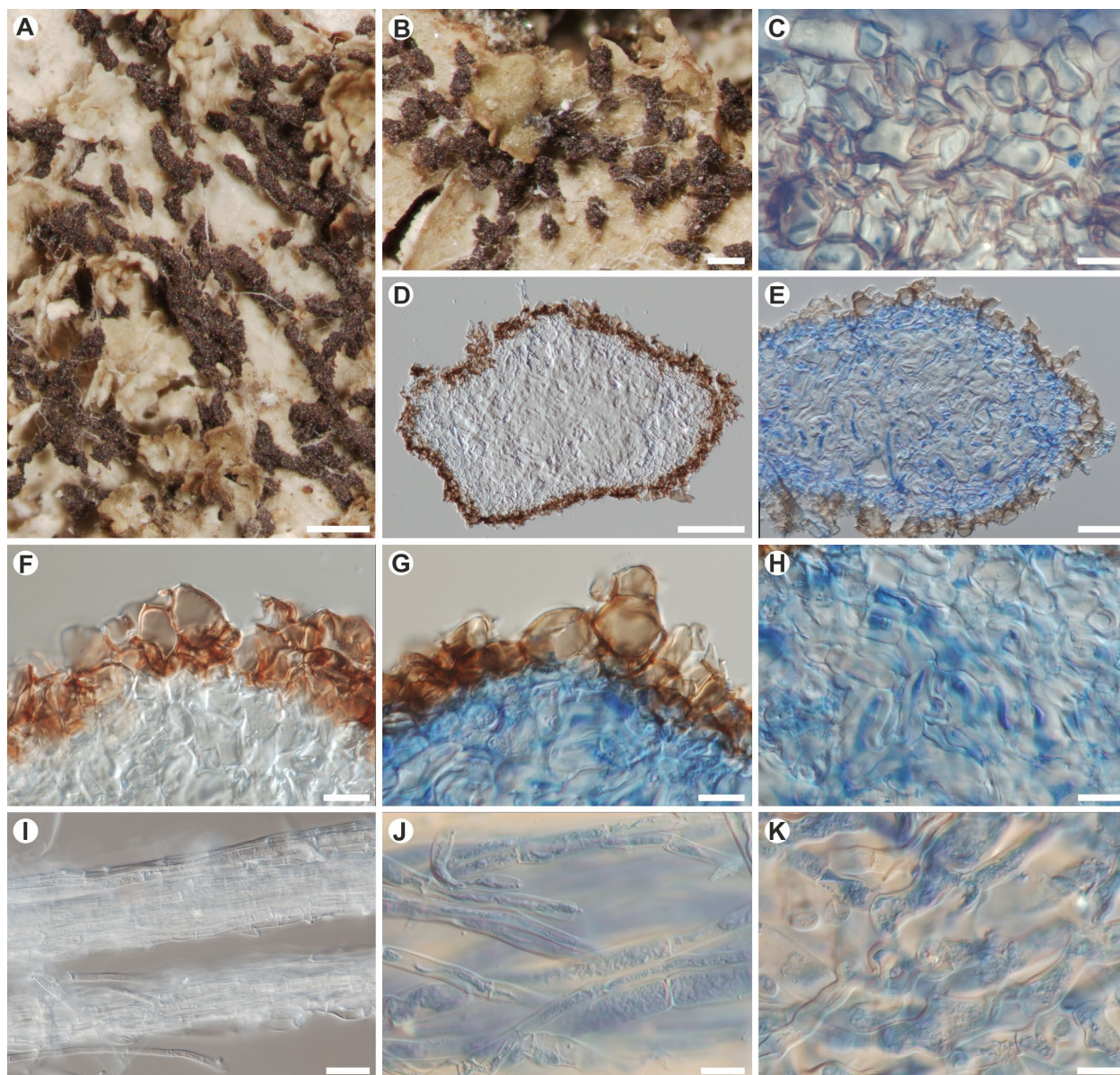
**Etymology.** The epithet refers to the lichenicolous habitat.

**Ecology and distribution.** Known only from the locus classicus in Bolivia on *Lobariella* sp.

**Notes.** *Xylaria lichenicola* was revealed as a member of *Xylaria* subgenus *Pseudoxylaria* and was shown to be closely related to an endolichenic strain of *Xylaria* sp. (FL0491) known from *Cladonia didyma*. Based on the differences in host selection, we decided to formally describe the lichenicolous species (Fig. 8), although, the endophyte may also belongs to it.

Phylogenetic study of the *Spirographa* complex

We gathered multilocus sequence data (nrITS, mrSSU, nrLSU, *RPB1* A–F) from 18 individuals morphologically representing *Spirographa* and related taxa (the



**Figure 22.** *Xylaria lichenicola* (on *Lobariella* sp., based on A.F. 26802, holotype). A–B – sclerotia growing on host thallus; C – paraplactenchymatous tissue of the cortical layer in LPCB; D–E – section of the sclerotium in water (D) and LPCB (E); F–G – section of the brown-pigmented cortical layer in water (F) and LPCB (G); H – section of the hyaline, inner part of sclerotia in LPCB; I – compacted bunches of mycelial tissue in water; J – mycelium composed of large-celled straight hyphae in LPCB; K – mycelium composed of short-celled curved hyphae in LPCB. Scales: A = 500  $\mu$ m; B = 250  $\mu$ m; C, F–K = 10  $\mu$ m; D = 50  $\mu$ m; E = 25  $\mu$ m.

*Spirographa* complex) (Table S1). All 18 individuals were consistently monophyletic with strong bootstrap support (Figs 23–24A) forming an independent lineage sister to a highly supported clade encompassing *Fissurinaceae* + *Gomphillaceae* (sister relationship with 77% bootstrap support) + *Graphidaceae* (with 99% bootstrap support) in *Ostropales* (Fig. 23). Deep relationships representing the early evolutionary splits in the *Ostropales* are poorly supported, however, the overall topology (Fig. 23) is in agreement with the relationships revealed by multiple multilocus phylogenies for the class *Lecanoromycetes* (Miadlikowska et al. 2014; Pino-Bodas et al. 2017; Carbone et al. 2019; but see an alternative phylogeny and classification in Kraichak et al. 2019). Our phylogeny for *Graphidaceae* s.lat. (Fig. 24A) confirms overall the topology (e.g., delimitations and relationships

among the subfamilies and tribes) revealed previously by Lumbsch et al. (2014). Based on the robust phylogenetic placement (above 75% bootstrap support) and phenotypic characteristics of all collections examined, we propose to recognize the *Spirographa* clade at the family level within the order *Ostropales*. Twenty-two species including four newly described (*Spirographa aggregata*, *S. galligena*, *S. maroneae*, and *S. parmotremitis*) are currently recognized in this monogeneric family. This discovery of another non-lichenized (lichenicolous and fungicolous) lineage in the *Ostropales* (Fig. 23) adds to the current understanding that multiple trophic transitions occurred in the *Ostropomycetidae*, including multiple putative losses of lichenization in this lichen dominated clade (Lutzoni et al. 2001; Spribille et al. 2014; Resl et al. 2018).

Taxonomy of the genus *Spirographa****Spirographaceae*** Flakus, Etayo & Miadlikowska, fam. nov.

Mycobank MB 833342

Diagnosis: A monotypic family of lichenicolous and fungicolous fungi belonging to the *Ostropales* (*Lecanoromycetes*). The sexual state characterized by having apothecioid or perithecioid, cleistohymenial ascomata, immersed or sessile on the host thalli or hymenia, single or aggregated on a stroma, with honey-brown, dark-brown or black pigments, a persistent exciple, I– and K/I– hymenium, simple to branched paraphyses, functionally unitunicate asci, ~16–32-spored, and 1-septate, hyaline, narrowly ellipsoidal to fusiform, curved or sigmoid ascospores. The asexual state characterized by having immersed, pycnidial conidiomata, hyaline to yellowish brown or dark brown, disintegrating irregularly at the top to release conidia; hyaline, septate, branched conidiophores, holoblastic, synchronous or sympodial conidiogenous cells, and hyaline, Y-shaped, with a main axis and two diverging arms, or triangular, or tetra- to polyhedral conidia.

Type genus: *Spirographa* Zahlbr.

**Description.** Ascomata apothecioid or perithecioid, developing in the host thallus or hymenia, cleistohymenial, single or aggregated in stromata, immersed in the host or rarely sessile. Disc hidden (covered by the exciple at maturity) or, if visible, concave, orange-brown, dark-brown or black. Exciple honey-brown, dark-brown or black, K–, N–, prominent, composed of isodiametric to elongate cells, without hairs. Hymenium K/I–, I–, composed of hyaline, simple, slightly branched paraphyses, 1.5–4.0 µm thick, usually apically thickened, covered by gel and granular pigments. Epihymenium with honey-brown, orange brown or black, pigments granular, K–, N–. Asci clavate to cylindrical, functionally unitunicate, wall apically not thickened, K/I–, I–, ~16–32-spored. Ascospores 1-septate, hyaline, narrowly ellipsoidal to fusiform, spirally arranged in asci (except in short-spored species), with rounded or pointed ends, sometimes with large cilia developed on both ends, not constricted at the septa, straight to curved or sigmoid, smooth, without a gelatinous cover. Conidiomata immersed in the host thallus or hymenia, pycnidial, globose to pyriform, hyaline to yellowish brown or dark brown. Pycnidial wall composed of isodiametric to slightly elongated cells, disintegrating irregularly at the top to release a colorless to pale-pink mass of agglutinated conidia. Conidiophores hyaline, septate, thin-walled, arising from the innermost cells of the pycnidial walls, branched. Conidiogenous cells holoblastic, synchronous or sympodial, integrated, terminal to lateral, thin-walled, producing few conidia from minute loci. Conidia hyaline, truncate, aseptate, either Y-shaped, with a main axis and two diverging arms, or triangular, or tetra- to polyhedral.

**Notes.** The genus *Spirographa* was introduced by Zahlbruckner (1907) and later classified by Hawksworth and Sherwood (1982) in the family *Odontotremataceae* in *Ostropales*. Diederich & Etayo (2000) suggested a placement in *Helotiales* close to *Skyttea*. However, Diederich (2004) confirmed that ascomata in the young state are cleistohymenial and maintained the systematic position

proposed by Hawksworth and Sherwood (1982). For a long time, the species concept in *Spirographa* was misunderstood and all known species were incorporated into *S. fusisporella* s.lat. (Kocourková 2000; Diederich 2004; Santesson et al. 2004; Ihlen & Wedin 2008; Brackel 2014). However, Etayo (2002, 2017) and Diederich (2004) mentioned high morphological variability of *S. fusisporella* and suggested that further taxonomic studies may split the taxon in several species. An additional two species of *Spirographa* were described from *Usnea* (*S. usneae*) and *Sticta* (*S. longispora*) (Flakus & Kukwa 2012b; Etayo 2017) based on morphological characters.

Based on our multilocus phylogenetic analyses (Fig. 23, 24B), we demonstrated that *Spirographa* forms an independent lineage (recognized as *Spirographaceae*) within *Ostropales*, sister to the clade containing *Fissurinaceae*, *Gomphillaceae* and *Graphidaceae*. We also revealed that *Cornutispora* (Pirozynski 1973), a conidial genus of previously unknown phylogenetic position, represents an asexual state of *Spirographa*, and that *Asteroglobulus* (Brackel 2011) together with *Pleoscutula* (Vouaux 1913; Hafellner 1982) are congeneric with *Spirographa* (Fig. 24B). Our comprehensive assessment based on molecular, anatomical and ecological data, reveal that species of the re-circumscribed genus *Spirographa* are strongly host-specific, mainly at the generic level.

***Spirographa*** Zahlbr.

(Figs 25–30)

Generic type: *Spirographa spiralis* (Müll. Arg.) Zahlbr.= *Asteroglobulus* Brackel, *Herzogia* 24(1): 69. 2011., syn. nov. Type: *Asteroglobulus giselae* Brackel= *Cornutispora* Piroz., *Mycologia* 65(4): 763. 1973., syn. nov. Type: *Cornutispora limaciformis* Piroz.= *Graphinella* Zahlbr., *Cat. Lich. Univers.* 2: 285. 1923. Type: *Graphinella fusisporella* (Nyl.) Zahlbr.= *Pleoscutula* Vouaux, *Bull. Soc. Mycol. Fr.* 29: 434. 1913., syn. nov. Type: *Pleoscutula arsenii* Vouaux= *Pleospilis* Clem., *Gen. Fung. (Minneapolis)*: 69. 1909. Type: *Pleospilis vermiformis* (Leight.) Clem.= *Spilomela* (Sacc. & D. Sacc.) Keissl., *Beih. Bot. Zbl.*, Abt. 2 37: 272. 1920. ≡ *Melaspilea* subgen. *Spilomela* Sacc. & D. Sacc., *Syll. Fung. (Abellini)* 18: 179. 1906. Type: *Spilomela vermifera* (Leight.) Keissl.= *Spirographomyces* Cif. & Tomas., *Atti Ist. bot. Univ. Lab. Crittog. Pavia* 10(1): 43, 69. 1953. Type: *Spirographomyces spiralis* (Müll. Arg.) Cif. & Tomas.

**Description of the sexual state.** Ascomata apothecioid or perithecioid, cleistohymenial, arising singly or aggregated in stromata, immersed in the host or sessile. When hymenium exposed at maturity then disc concave, dark-brown, orange-brown or black, usually concolorous with the margin or paler. Exciple honey-brown, dark-brown or black, K–, N–, prominent, without hairs, composed of isodiametric cells. Hymenium hyaline, K/I–, I–. Subhymenium indistinct. Epihymenium with honey-brown, orange brown or black, granular pigments, K–, N–. Paraphyses 1.5–4 µm thick, hyaline, simple, septate, sometimes slightly branched in the upper part, usually apically thickened and covered by granular pigment. Asci clavate

to cylindrical, functionally unitunicate, wall apically not thickened, K/I–, I– (only endoascus I+ slightly orange), ~16–32-spored. Ascospores 1-septate, hyaline, narrowly ellipsoidal to fusiform, usually spirally arranged in the ascus, with rounded- or pointed-ends, sometimes with large cilia developed on both apices, not constricted at the septum, straight to curved or sigmoid, multiguttulate, smooth, without perispore,  $7\text{--}48 \times 1\text{--}4 \mu\text{m}$ .

**Description of the asexual state.** Conidiomata immersed in the host thallus or hymenia, pycnidial, globose to pyriform, hyaline to yellowish brown or dark brown. Pycnidial wall composed of thin- to thick-walled isodiametric cells, disintegrating irregularly around the top to release a colorless to pale-pink mass of agglutinated conidia. Conidiophores hyaline, septate, thin-walled, arising from the innermost cells of the pycnidial walls, branched. Conidiogenous cells holoblastic, synchronous or sympodial, integrated, terminal to lateral, thin-walled, producing 1–3 conidia from minute loci. Conidia hyaline, truncate, aseptate, either Y-shaped, with a main axis and two diverging arms, or triangular, or tetra- to polyhedral,  $3\text{--}35 \mu\text{m}$  diam. For a detailed description see Pirozynski (1973), Hawksworth (1976) and Punithalingam (2003).

**Notes.** Members of the cosmopolitan genus *Spirographa* (especially its asexual *Cornutispora*-like states) were previously treated as generalists and reported from a broad variety of host lichens and also from non-lichenized fungi (e.g., Punithalingam 2003; Santesson et al. 2004; Ihlen & Wedin 2008; Brackel 2014). Our phylogenetic analyses showed that species in the genus are strongly host-specific, as the individuals collected from the same host genus clustered together (Fig. 24B). Future examination of a larger material may reveal additional undescribed species and could also help to understand the species boundaries, distribution, and host range in *Spirographa*.

Our results clearly show that asexual states of *Spirographa* with very similar characteristics of conidia may be not related phylogenetically (e.g. *S. giselae*, *S. pyramidalis* and *S. macropyramidalis*) and their sexual states strongly differ in ascospore size ( $11\text{--}20 \times 2\text{--}3.5 \mu\text{m}$ ,  $7\text{--}10 \times 2\text{--}3 \mu\text{m}$ , and  $9\text{--}13 \times 2.5\text{--}3 \mu\text{m}$ , respectively). Keys for the identification of the majority of described *Cornutispora*-like anamorphs are available (Punithalingam 2003; Etayo 2017; Diederich et al. 2019).

**Ecology and distribution.** *Spirographa* is a cosmopolitan genus known from a variety of lichen hosts and non-lichenized fungi. However, the distribution of the majority of the species is poorly known.

***Spirographa aggregata*** Flakus, Etayo & Miadlikowska, sp. nov. (Figs 25A, 26A, B, 27A)

Mycobank MB 833343

Diagnosis: Differs from *Spirographa arsenii* in having longer, ciliate ascospores,  $30\text{--}48 \times 2.5\text{--}4 \mu\text{m}$ , apothecia of  $250\text{--}450 \mu\text{m}$  diam. developing on black stromata,  $1\text{--}8 \text{mm}$  diam., and in the host selection (*Polyblastidium corallophorum*).

Type: Bolivia. Dept. La Paz. Prov. Murillo: below Potosí near campamento de los mineros, on the road La Paz – Valle

del Zongo,  $16^{\circ}17'43''\text{S}$ ,  $68^{\circ}07'42''\text{W}$ , 4716 m, high Andean vegetation, on *Polyblastidium corallophorum*, Javier Etayo 34-5 (LPB – holotype!; hb. Etayo – isotype!).

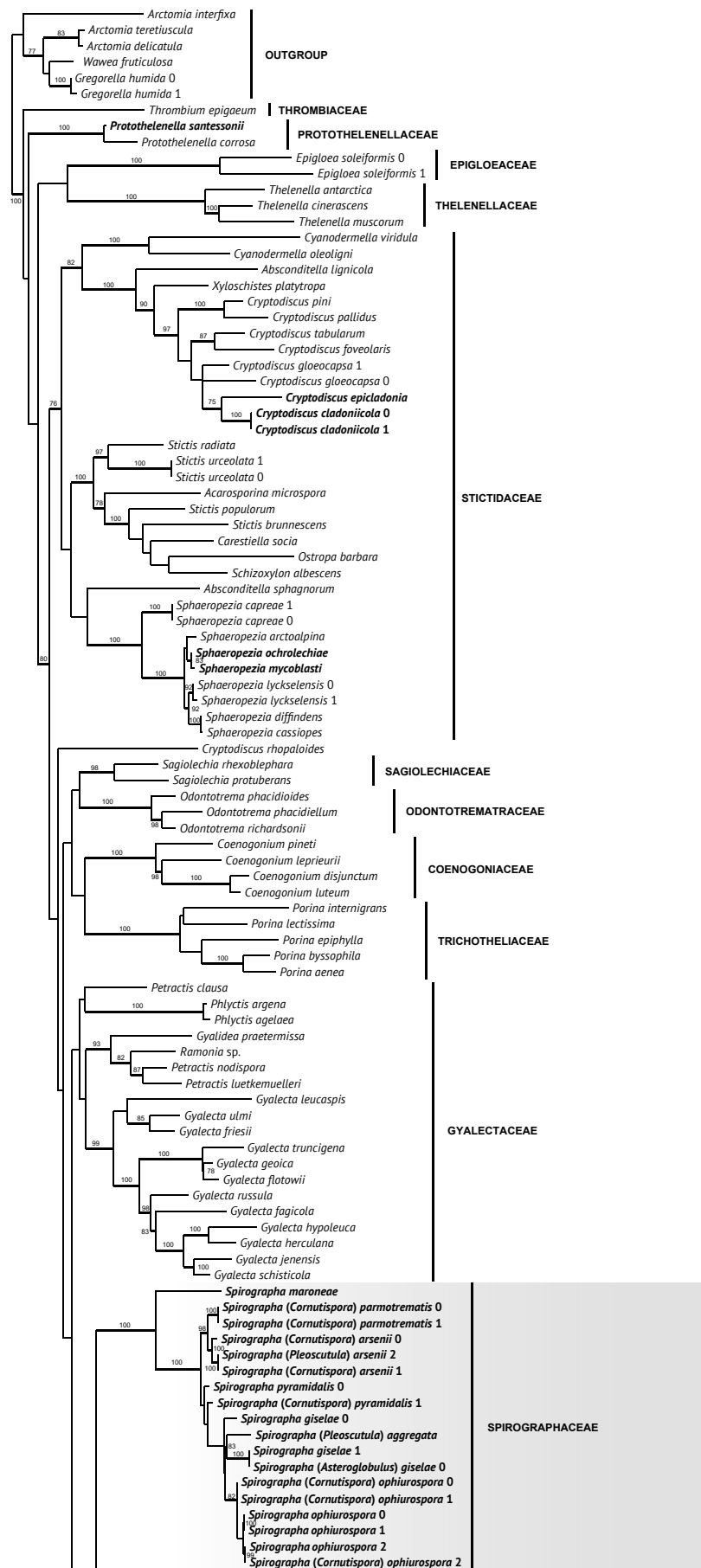
**Description.** Ascomata arranged in black, convex, matte, stromata,  $1\text{--}8 \text{mm}$  diam. Ascomata  $250\text{--}450 \mu\text{m}$  diam., apothecioid, black, strongly concave, matte, cleistohymenial. Disc exposed when mature, strongly concave, black, matte. Margin black, prominent, thick, with a rough surface, without hairs, concolorous with the disc. Exciple laterally  $60\text{--}100 \mu\text{m}$  wide, of irregular outline, irregularly pigmented, paraplectenchymatous, composed of thick-walled, isodiametric cells,  $2\text{--}6 \mu\text{m}$  diam., dark brown, olivaceous-brown to orange-brown, with additional yellowish green pigment (K+ intensifying yellowish green), with thin hyaline to yellowish green inner layer,  $10\text{--}15 \mu\text{m}$  wide, composed of narrow, thin-walled hyphae. Epithemium with orange-brown to dark-brown granular pigments. Hymenium  $100\text{--}150 \mu\text{m}$ , hyaline. Subhymenium hyaline to yellowish green,  $\sim 20 \mu\text{m}$  tall. Paraphyses simples to sparsely branched, septate,  $1.5\text{--}3.5 \mu\text{m}$ , usually with a widened apical cell, up to  $4\text{--}6 \mu\text{m}$ , with pigmented gel cover. Asci functionally unitunicate, widely clavate, with obtuse apex, about 32-spored, I–, KI–,  $8\text{--}100 \times 10\text{--}20 \mu\text{m}$ . Ascospores long fusiform, and apically ciliate, hyaline, straight to curved, 1-septate,  $30\text{--}(\bar{x}=37.9 \text{ s}=3.9)\text{--}48 \times 2.5\text{--}(\bar{x}=3.7 \text{ s}=0.4)\text{--}4 \mu\text{m}$ , l/b ratio  $7.5\text{--}(\bar{x}=10.5 \text{ s}=1.8)\text{--}14$  (n=27). Asexual state unknown.

**Etymology.** The epithet refers to ascomata that are aggregated in stromata.

**Notes.** The species is the only one in *Spirographa* developing ascomata aggregated on a stroma. It is characterized by having apothecioid ascomata, a strongly pigmented and large exciple, the presence of an additional yellowish green pigment in the exciple, and large, distinctly ciliate ascospores. The only other species of *Spirographa* having ciliate ascospores of a similar size is *S. maroneae*, which differs by single, perithecioid ascomata that are immersed in the host thallus, and by a different host selection (*Maronea constans*). The new species can be also confused with *Spirographa arsenii* and *S. hypotrachynae*, members of the former genus *Pleoscotula*, because of having similarly dark pigmented ascomata. Both, however, can be differentiated by their non-aggregated ascomata, shorter ascospores ( $9\text{--}13 \times 2.5\text{--}4 \mu\text{m}$  in *S. arsenii* and  $13\text{--}19 \times 2\text{--}2.5 \mu\text{m}$  in *S. hypotrachynae*), and a different host selection (*Heterodermia* spp., *Polyblastidium japonicum*, and *Lichenopeltella* growing on *Hypotrachyna*, respectively) (Hafellner 1982; Etayo 2002).

**Ecology and distribution.** It is known only from two localities in Bolivia where it grows on saxicolous *Polyblastidium corallophorum*. It seems to be a very rare species.

**Additional specimen examined.** BOLIVIA. Dept. Cochabamba. Prov. Carrasco: Carrasco National Park, Wayra Mayu close to Monte Punku,  $17^{\circ}32'27''\text{S}$ ,  $65^{\circ}16'14''\text{W}$ , 2550 m, Yungas cloud forest, on *Polyblastidium corallophorum* on rock, J.E 31907 (LPB, hb. Etayo).



**Figure 23.** Phylogenetic placement of *Spirographaceae* (highlighted) within *Ostropales* inferred from ML analyses based on a combined nrLSU, mrSSU, *RPB1* and *RPB2* dataset for 195 OTUs. Thick branches represent bootstrap values  $\geq 70\%$ . The lichenicolous species are bolded. The scale bar represents number of nucleotide substitutions per site.

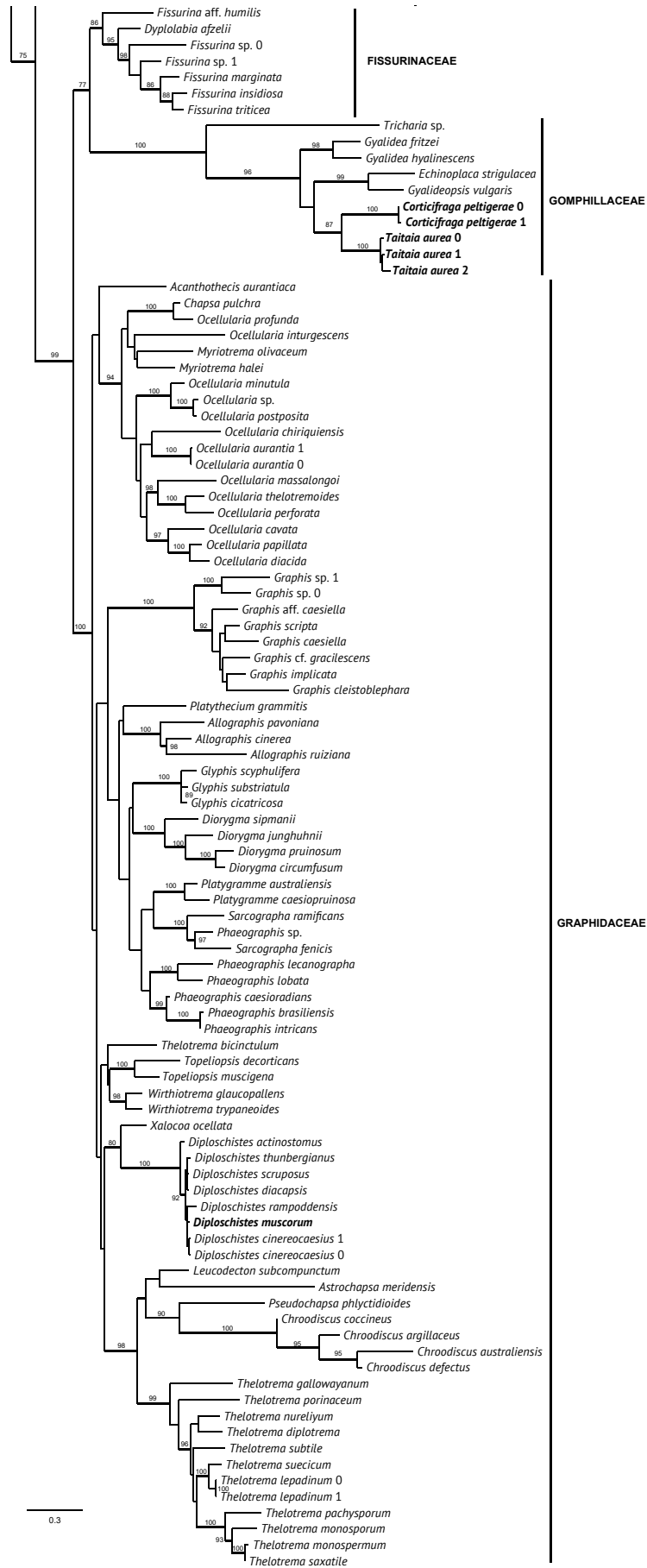


Figure 23. Continued.

*Spirographa arsenii* (Vouaux) Flakus, Etayo & Miadlikowska, comb. nov. (Figs 25B, 26C, 27B, 28A, 29A, 30A)

Mycobank MB 833344

Basionym: *Pleoscutula arsenii* Vouaux, Bull. Soc. Mycol. Fr. 29: 435. 1913.

**Notes.** The species was described by Vouaux (1913) and, as shown by Hafellner (1982), is characterized by having black, usually aggregated apothecia and small, narrowly ellipsoidal and slightly curved ascospores (9–13 × 2.5–4 µm). In the Bolivian material it was accompanied by a *Cornutispora*-like asexual state with triangular conidia (5–6.5 µm diam.).

**Ecology and distribution.** The species is known from Bolivia and Mexico where it grows on different species of *Heterodermia* s.lat., including *H. flabellata*, *H. galactophylla* and *Polyblastidium japonicum*.

**Specimens examined (sexual state).** BOLIVIA. Dept. Chuquisaca. Prov. Belisario Boeto: between Nuevo Mundo and Villa Cerrano, 19°00'49.5"S, 64°20'08.8"W, 2555 m, Boliviano-Tucumano forest with *Podocarpus* and *Polylepis*, on *Heterodermia* sp. on trunk, J.E. 29823 (LPB, hb. Etayo). Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, La Cumbre, El Camino de las Nubes, 17°17'46"S, 64°43'56"W, 4100 m, Páramo Yungueño with outcrops, on *H. flabellata*, J.E. 33-3 (LPB, hb. Etayo). Dept. La Paz. Prov. Franz Tamayo: between Apollo and Mapiro, 14°38'51"S, 68°24'44"W, 1521 m, savanna with shrubs and some trees, on *Polyblastidium japonicum*, A.F. 28238 (KRAM, LPB). Dpt. Tarija. Prov. Aniceto Arce: Reserva Nacional Flora y Fauna de Tariquía, between La Cumbre and guard station Los Alisos, 22°01'18.9"S, 64°34'22.5"W, 1950 m, upper montano Tucumano-boliviano cloud forest, on *Heterodermia* sp. on tree, J.E. 29840 (LPB, hb. Etayo); near La Mamora between Tarija and Bermejo, 22°09'51"S, 64°40'03"W, 1320 m, disturbed Tucumano-Boliviano forest, on *Heterodermia* sp. on trunk, J.E. 30409 (LPB). Prov. Burnet O'Connor: 60 km from Tarija, new road between Tarija and Entrerios, 21°28'52"S, 64°17'41"W, 1837 m, Boliviano-Tucumano forest with *Podocarpus* and small epiphytic orchids exposed SE, on *Heterodermia* sp. on branches, J.E. 30667 (LPB, hb. Etayo).

**Specimens examined (asexual state).** BOLIVIA. Dept. Chuquisaca. Prov. Belisario Boeto: close to Padilla between Nuevo Mundo and Santa Rosa, 18°57'06"S, 64°16'14"W, 1936 m, transition between Boliviano-Tucumano forests and dry interandean vegetation, on *Heterodermia* sp. on trunk, J.E. 30583 (LPB, hb. Etayo). Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, near Sehuencas, 17°29'48"S, 65°16'22"W, 2250 m, vegetation with *Alnus* sp. along the river near Yungas cloud forest, on *Heterodermia* sp., J.E. 28238 (LPB, hb. Etayo). Dept. La Paz. Prov. Murillo: Sainani, Valle del Zongo, 16°07'03"S, 68°04'42"W, 2170 m, open area with shrubs and scattered trees, on *H. galactophylla*, A.F. 26271 (KRAM); Sainani, Valle del Zongo, 16°07'20"S, 68°05'09"W, 2220 m, open area with shrubs and scattered trees, on *P. cf. japonicum*, A.F. 26253 (LPB). Prov. Nor Yungas: Parque Nacional Cotapata, Santa Catalina village, above Tunkini, 16°11'12"S, 67°52'07"W, 1600–1840 m, Yungas montane forest, on *P. japonicum*, J.E. 27387 (LPB, hb. Etayo). Dept. Santa Cruz. Prov. Manuel María Caballero: El Camino de las Orquideas, 17°49'50"S, 64°42'11"W, 2415 m, Yungas cloud forest, on *Heterodermia* sp., J.E. 28811, (LPB, hb. Etayo); 17°49'20"S, 64°42'31"W, 2340 m, Yungas cloud

forest, on *H. galactophylla*, J.E. 28847 (hb. Etayo); near Siberia, 17°50'15"S, 64°42'36"W, 2700 m, Yungas cloud forest, on *Heterodermia* sp., J.E. 29181 (LPB, hb. Etayo). Dept. Tarija. Prov. Aniceto Arce: Papachacra, 21°41'52"S, 64°29'15"W, 1900 m, Tucumano-Boliviano altimontano forest, on *Heterodermia* sp. growing on tree, J.E. 28369 (hb. Etayo). Prov. Burnet O'Connor: old road between Tarija and Entrerios, 21°27'50"S, 64°12'51"W, 1924 m, Boliviano-Tucumano forest with epiphytes, on *H. flabellata*, J.E. 29-2, J.E. 29932 (LPB, hb. Etayo); Sandiego Sur, top of the hill on old road between Tarija and Entrerios, 21°27'04"S, 64°13'59"W, 1812 m, Boliviano-Tucumano forest, on *H. flabellata*, A.F. 27724 (KRAM); 60 km from Tarija, new road between Tarija and Entrerios, 21°28'52"S, 64°17'41"W, 1837 m, Boliviano-Tucumano forest with *Podocarpus* and small epiphytic orchids exposed SE, on *Heterodermia* sp., J.E. 30668 (LPB, hb. Etayo); near Soledad, 21°40'49"S, 64°07'33"W, 1600 m, Tucumano-Boliviano montano forest, on *Heterodermia* sp. on tree, J. E. 28406 (LPB); RN de Flora y Fauna Tariquía, near Salinas, 21°49'15"S, 64°12'44"W, 1430 m, Tucumano-Boliviano montano forest, on *Heterodermia* sp., J.E. 28152 (LPB).

*Spirographa ascaridiella* (Nyl.) Flakus, Etayo & Miadlikowska, comb. nov. (Fig. 25C, 26C, 27C)

Mycobank MB 833345

Basionym: *Lecidea ascaridiella* Nyl. Nyl., Flora 51: 162. 1868.

Type: [Ireland] Ad saxa calcarea prope Killarney in Hibernia, Carroll, (H-Nyl-21874 – lectotype!, selected by Holien & Triebel 1996; BM, isolectotype, non vidi).

**Notes.** *Spirographa ascaridiella* was originally described in *Lecidea* (Nylander 1868) and later placed in *Spilomela* and *Pleopsis* (Hawksworth 1980, 1983; Sherwood-Pike 1987). Here we propose to place it in the genus *Spirographa* based on its similar anatomical characters. The species is known only from its sexual state and is characterized by having medium sized vermiform ascospores (22–36 × 2–2.5 µm) and by its host preference (*Porpidia* spp.). Ascospores from the holotype (H-Nyl-21874; Fig. 27C) were also pictured by Hawksworth (1980; Fig. 5A).

**Ecology and distribution.** The type material is known from Ireland and grows on sterile cf. *Porpidia* sp. (containing confluent acid) (Hawksworth 1980).

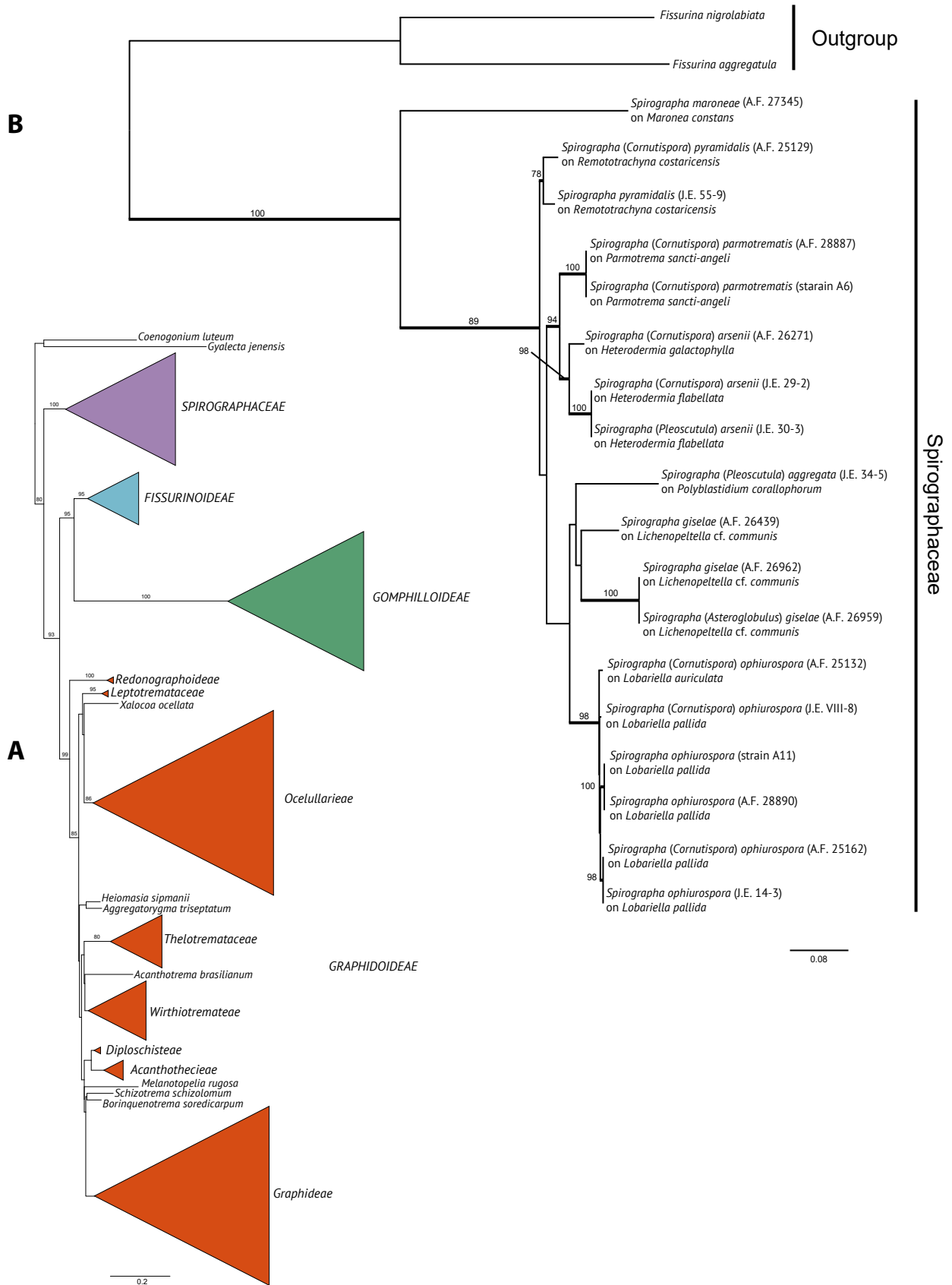
*Spirographa ciliata* (Kalb) Flakus, Etayo & Miadlikowska, comb. nov.

Mycobank MB 833346

Basionym: *Cornutispora ciliata* Kalb, in Gierl & Kalb, Herzogia 9: 632. 1993.

**Notes.** The species was described from *Dibaeis cretacea* and is characterized by having Y-shaped conidia (~10 × 7 µm), composed of strongly swollen (at the base) and apically ciliate arms, with non-evident main axis (6.5–9 × 2–2.5 µm) (Gierl & Kalb 1993). Punithalingam (2003) included into the species more *Cornutispora* specimens with a similar kind of conidia, but having various sizes and growing on different hosts, thereby broadening the species concept. We observed *ciliata*-like conidia on different hosts, however, only further molecular studies can





**Figure 24.** Phylogenetic placement of the *Spirographa* complex (*Spirographaceae*) within *Graphidaceae* s.lat. (A, based on nrLSU, mrSSU and *RPB1*) and relationships within the *Spirographa* complex (B, based on nrITS, nrLSU, mrSSU and *RPB1*), inferred from ML analyses of combined dataset for 144 OTUs and 20 OTUs, respectively. Thick branches represent bootstrap values  $\geq 70\%$ . The scale bars represent number of nucleotide substitutions per site.

determine if they belong to single generalistic fungus or, more likely, to several host-specific species.

**Ecology and distribution.** The type specimen was described from *Dibaeis cretacea* from Tasmania (Gierl & Kalb 1993), but the species has been reported from a number of other hosts.

*Spirographa fusisporella* (Nyl.) Zahlbr.  
(Figs 25D, 26D–F, 27D)

≡ *Graphis fusisporella* Nyl., Flora (Regensburg) 49: 292. 1866. ≡ *Graphinella fusisporella* (Nyl.) Zahlbr., Cat. Lich. Univers. 2: 285. 1923.

Type: CUBA. On trees in the Harallones M.V., coll. C. Wright 27, 14 Sept. (Nyl. 17) (M0086813 – lectotype! designated here, MBT389635).

= *Opegrapha spiralis* Müll. Arg. Flora, Regensburg 63: 43. 1880. ≡ *Spirographa spiralis* (Müll. Arg.) Zahlbr., Cat. Lich. Univers. 2: 267. 1923, syn. nov.

Type: BRAZIL. Coll. J. I. Puiggari, s.n., 1879 (G00294262 – lectotype!, selected by Holien & Triebel 1996).

=? *Spirographa antillarum* Vain., Ann. Acad. Sci. Fenn., Ser. A 6(7): 164. 1915.

**Notes.** *Graphis fusisporella* was described from Cuba (Nylander 1866) and the holotype is characterized by having hyaline, perithecioid ascomata (150–220 µm wide and 180–230 µm high) immersed in hymenia of corticolous *Fissurina* sp., and acicular, vermiform ascospores with ciliate ends (25–35 × 2–3 µm, n=17). The lectotype of *Opegrapha spiralis* (Müller 1880) has very similar ascomata immersed in hymenia of a corticolous *Graphis* sp. and very similar, ciliate ascospores (17–35 × 2–3 µm, n=7). As both taxa have very distinct ascomata of a similar kind, growing immersed in hymenia of corticolous members of *Graphidaceae* and similar ciliate ascospores, we suggest considering *Opegrapha spiralis* as a synonym of *Graphis fusisporella*. Based on examination of a specimen of '*Cornutispora* cf. *limaciformis*' growing on *Graphidales* in Brazil, we conclude that the conidia of *S. fusisporella* are *limaciformis*-like but of a larger size (Etayo in prep.).

Following the original description of *S. antillarum*, this species is likely to be a synonym of *S. fusisporella*, but the type has not yet been examined.

**Ecology and distribution.** The species is known from Brazil and Cuba where it grows in hymenia of corticolous *Graphidaceae* (*Fissurina* sp. and *Graphis* sp.), whereas in Europe it is reported here on *Graphis* from Cantabri (northern Spain).

**Additional specimens examined.** CUBA. Coll. A. Krempelhuber, s.n., 1883, (G00291639). SPAIN. Cantabria, valle de Villaverde, Mollinedo, Monte Tejea, sendero de las Fuentes del Agüera, 43°13'0.08"N, 3°16'15.5"W, 260–350 m, bosque mixto, on *Graphis* on *Alnus*, J.E. 28511 (hb. Etayo).

*Spirographa galligena* Flakus, Etayo & Miadlikowska, sp. nov. (Figs 28B, 29B–C, 30B)

Mycobank MB 833347

Diagnosis: Differs from other species of *Spirographa* by the triangular, or tetra- to polyhedral to almost Y-shaped conidia,

5–13 × 4–9 µm, galls formation on the host thallus, and the host preference (*Erioderma* sp.).

Type: PANAMA. Prov. Chiriquí. Parque Nacional Volcán Barú, Sendero Volcán, W slope, montane forest close to open rocks, 08°48'49"N, 82°33'50"W, 2444 m, on epiphytic *Erioderma* sp., Adam Flakus Fla39B (PMA – holotype!).

**Description.** Lichenicolous fungus causing galls formation on the host thallus; galls beige to pale brown, sometimes with pink tinge, 0.4–1.5 mm diam, internally hyaline to slightly yellowish, paraplectenchymatous, composed of thick-walled cells, 3–10 µm diam. Ascomata unknown. Conidiomata pycnidial, forming groups of 2–30, immersed inside galls induced on the host thallus, erumpent and sometimes partly exposed, subglobose to pyriform, 70–130 µm diam. Pycnidial wall hyaline to yellowish brown, 5–10 µm wide, composed of 5–10 layers of thin-walled hyphae, cells 3–10 × 1–3 µm, disintegrating by irregular opening around the top. Conidiophores hyaline, septate, thin-walled, arising from the innermost cells of the pycnidial walls, branched. Conidiogenous cells 10–13 × 1–2 µm, holoblastic, synchronous or sympodial, integrated, terminal to lateral, thin-walled, producing few conidia from minute loci. Conidia hyaline, aseptate, triangular, polyhedral or branched (almost Y-shaped), if branched then composed of thick main axis (5–8 × 5–6 µm) and two cylindrical to acute, short (1–3 × 1–2 µm) arms; entire measuring 5–(x̄=8.7 s=2.5)–13 × 4–(x̄=7.1 s=1.7)–9 µm (n=22). Sexual state unknown.

**Etymology.** The epithet refers to the gall induction on the host thallus.

**Ecology and distribution.** Known from the type locality in Panama where it occurs on epiphytic *Erioderma* sp.

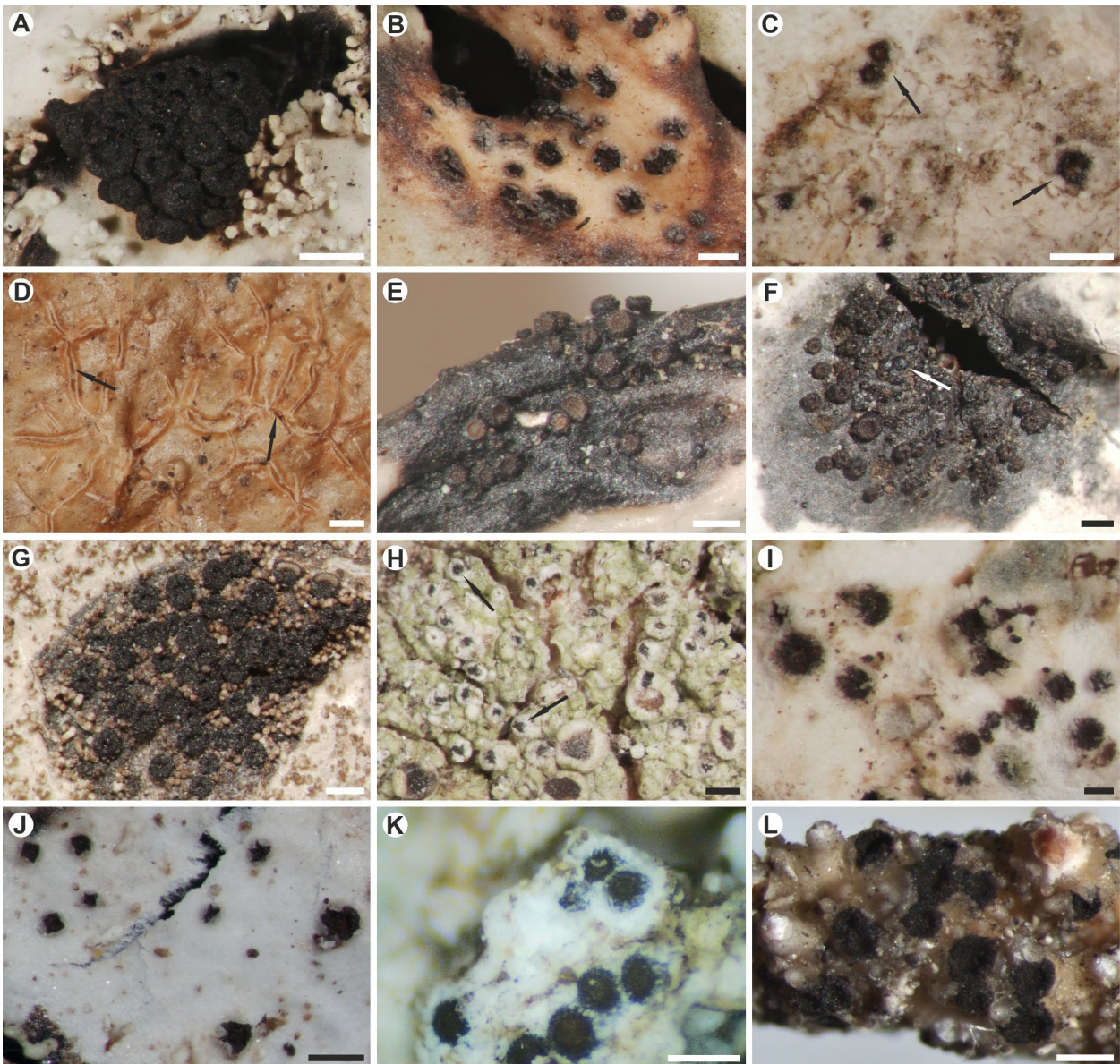
**Notes.** *Spirographa galligena* can easily be differentiated from other anamorphic states of *Spirographa* species by its unique characters, such as the induction of galls on the host thallus, and conidia that are intermediate between *triangularis*-like and *limaciformis*-like and measure 6–13 × 4–9 µm in total.

*Spirographa giselae* (Brackel) Flakus, Etayo & Miadlikowska, comb. nov. (Figs 25E, F, 26G, 27E, 28C, 29D, 30C)

Mycobank MB 833348

Basionym: *Asteroglobulus giselae* Brackel, Herzogia 24(1): 69. 2011.

**Description of the sexual state.** Ascomata cleistohymenial, sessile since young on the host thallus, rounded, with dark brown color, 100–200 µm diam. Margin distinct, dark-brown to black. Disk orange-brown. Exciple laterally 20–60 µm thick, basally 35–40 µm thick, with olivaceous-brown to brown pigments, composed of isodiametric cells. Hymenium hyaline, I–, KI–, 60–80 µm tall. Paraphyses hyaline, filiform, simple to slightly branched in upper part, septate, 1.5–2 µm wide, not or slightly capitate (to 2.5 µm) and covered by a yellow to orange-brown pigment. Epithymenium with an orange-brown pigment. Hypothecium hyaline, 15–20 µm tall. Asci clavate, not thickened apically, ~32-spored, 48–90 ×



**Figure 25.** Morphological diversity of ascomata in *Spirographa*. A – *S. aggregata* on *Polyblastidium coralloporum* (J.E. 34-5, holotype); B – *S. arsenii* on *Heterodermia flabellata* (J.E. 30-3); C – *S. ascaridiella* on *Porpidia* sp. (H-Nyl-21874, lectotype); D – *S. fusisporella* on *Fissurina* sp. (M0086813, lectotype); E – *S. giselae* on *Lichenopeltella* cf. *ramalinae* growing on *Ramalina farinacea* (J.E. 30112); F – *S. giselae* on *Lichenopeltella* cf. *communis* (white arrow showing catathecium of *Lichenopeltella*) growing on *Parmotrema crinitum* (A.F. 26962); G – *S. hypotrachynae* on *Hypotrachyna* sp. (A.F. 19896); H – *S. maroneae* (perithecioid ascomata) in *Maronea constans* (A.F. 27345, holotype); I – *S. ophiurospora* on *Lobariella* cf. *pallida* (A.F. 28890); J – *S. pyramidalis* on *Remototrachyna costaricensis* (J.E. 55-1); K – *S. triangularis* on *Pertusaria pertusa* (J.E. 30859); L – *S. usneae* on *Usnea* sp. (A.F. 8176-2, holotype). Scales: A, D = 500  $\mu$ m; B–C, E–H, J = 250  $\mu$ m; I = 100  $\mu$ m; K = 300  $\mu$ m; L = 200  $\mu$ m.

9–20  $\mu$ m. Ascospores hyaline, acicular, curved to helicoid, with acute ends, 1-septate, not constricted at the septum, smooth, with several small oil guttules inside, without gelatin perispore, 11–( $\bar{x}$  = 16.7 s = 2.2)–20  $\times$  1.5–( $\bar{x}$  = 2.6 s = 0.6)–3.5  $\mu$ m, l/b ratio 4–( $\bar{x}$  = 6.8 s = 1.7)–12 (n = 71).

**Description of the asexual state.** See Brackel (2011).

**Notes.** The genus *Asteroglobulus* was introduced by Brackel (2011) for the conidial fungus *A. giselae* from Italy. It was characterized by having black conidiomata developing on blackish areas on *Ramalina farinacea* thalli and small triangular to tetrahedral conidia, 6–8(–10)  $\mu$ m diam. Later Diederich (2018) transferred *Cornutispora pyramidalis* (Etayo 2010) to the genus *Asteroglobulus* based on a similar anatomy of conidiomata and conidia.

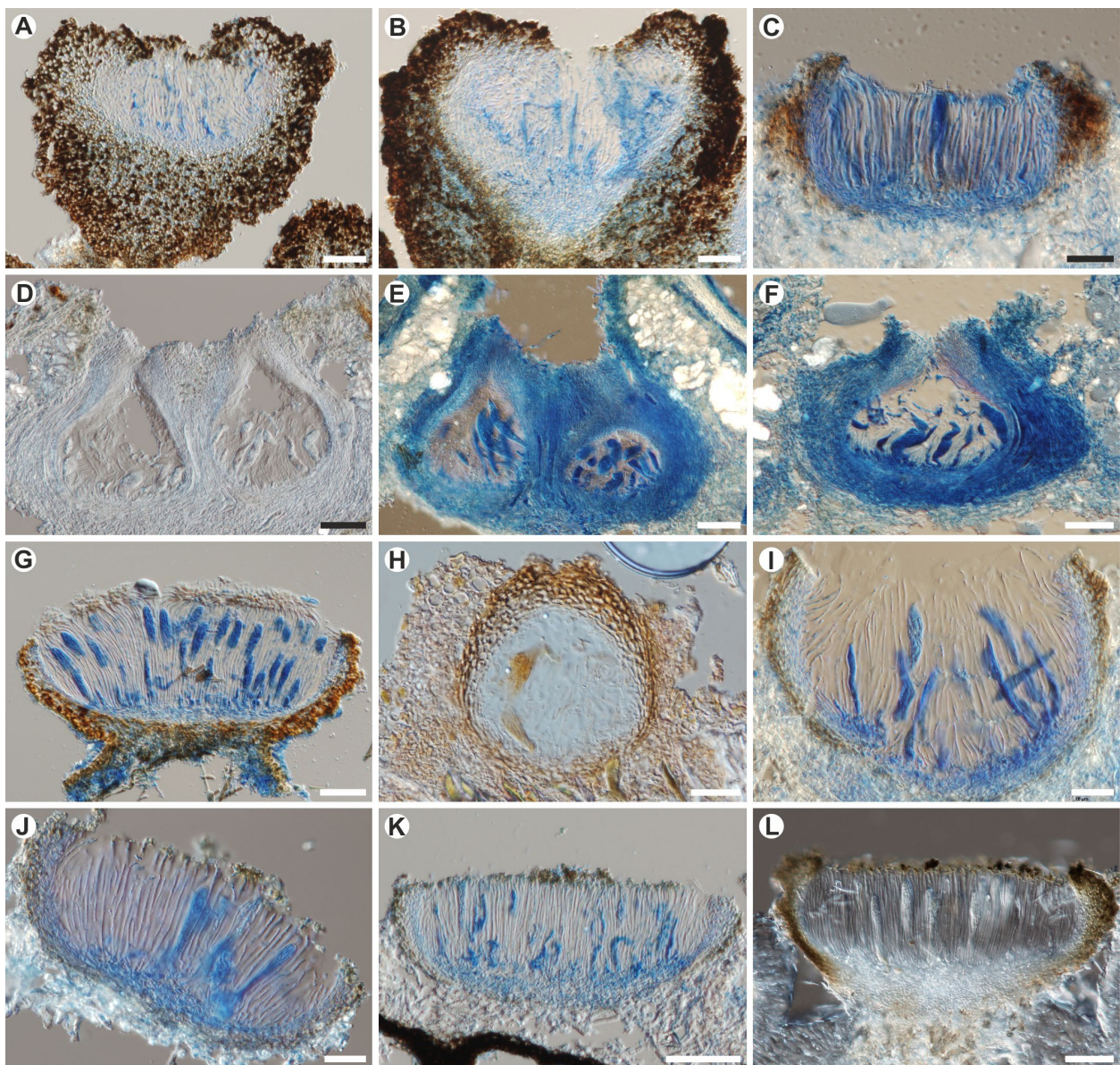
Our phylogenetic analyses (Fig. 24B) placed the Bolivian samples of *A. giselae* in a clade together with members of *Cornutispora* and *Spirographa*. We also observed the conidial state and *Spirographa*-like sexual state growing together on the same host thalli. All together, this convinced us that *Asteroglobulus* is another synonym of *Spirographa*.

*Spirographa giselae* was originally described from blackish areas on *Ramalina farinacea* from Italy (Brackel 2011). Our studies of material from Portugal and Spain (on *R. farinacea* and *R. fraxinea*) have shown that *S. giselae* is a hyperparasite and the black areas are caused by mycelia of the lichenicolous fungus *Lichenopeltella* cf. *ramalinae*. In Bolivia the species is also associated with members of *Lichenopeltella* (most

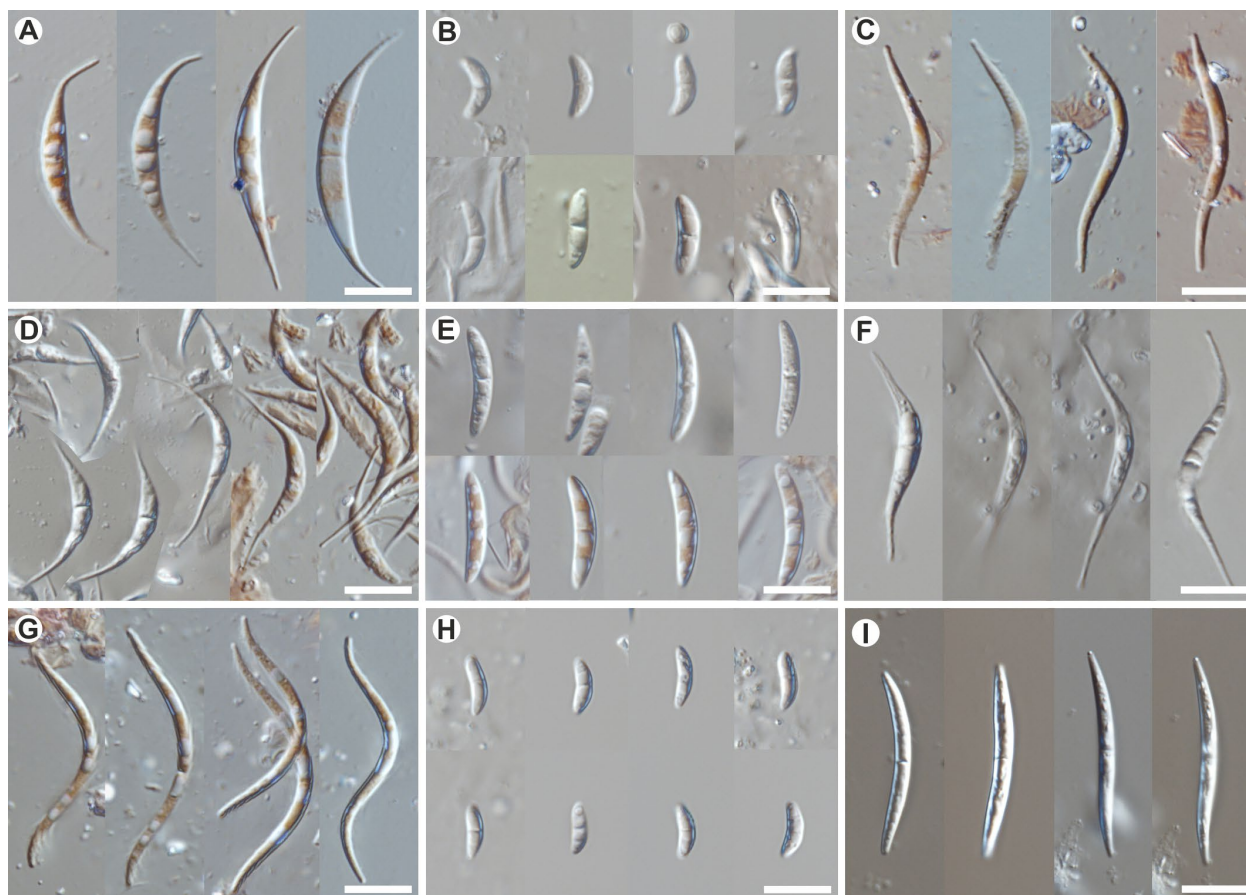
probably *L. cf. communis*) but growing on *Parmotrema crinitum* and *P. reticulatum*. Because the morphology of *Spirographa giselae* is very unique, i.e. sessile ascomata (not immersed from the early developmental stages) with orange-brown discs (Fig. 25E, F) and small triangular to tetrahedral conidia (Fig. 30C), and also because it is always associated with species of *Lichenopeltella*, we recognized the Bolivian and European material as a single species. However, the two populations differ slightly in ascospore shape and size [on *Ramalina*:  $11-(\bar{x}=16.2\ s=2.5)-20 \times 1.5-(\bar{x}=2\ s=0.3)-2.5\ \mu\text{m}$ , l/b ratio  $5.5-(\bar{x}=8.1\ s=1.6)-12$  ( $n=32$ )] vs. on *Parmotrema*:  $12-(\bar{x}=17.2\ s=1.7)-20 \times 2.5-(\bar{x}=3\ s=0.3)-3.5\ \mu\text{m}$ , l/b ratio  $4-(\bar{x}=5.8\ s=0.9)-7.6$  ( $n=39$ )], and the species boundaries need to be tested in the future on a larger material from its whole distribution range.

**Ecology and distribution.** *Spirographa giselae* is known from Bolivia, Italy (Brackel 2011), Portugal and Spain, where it occurs as a hyperparasite of *Lichenopeltella* (*L. cf. communis*, and *L. cf. ramalinae*) growing on *Ramalina farinacea* (type material), *R. fraxinea*, *Parmotrema crinitum*, and *P. reticulatum*.

**Specimens examined (sexual state).** BOLIVIA. Dept. Tarija. Prov. Aniceto Arce: Reserva Nacional de Flora y Fauna Tariquiá, between la Cumbre and campamento los Alisos,  $22^{\circ}00'41''\text{S}$ ,  $64^{\circ}36'02''\text{W}$ , 2560 m, Boliviano-Tucumano forest with *Alnus acuminata* and *Polylepis*, on *Lichenopeltella cf. communis* growing on *Parmotrema crinitum* and *P. reticulatum*, A.F. 26962, 26963 (LPB, KRAM). Dept. Chuquisaca, Prov. Zudañez, Área Natural de Manejo Integrado El Palmar, segunda villa de presto, Lomán, Salviatójo,  $18^{\circ}45'53''\text{S}$ ,  $64^{\circ}49'57''\text{W}$ , 2875 m, Boliviano-Tucumano forest with *Podocarpus*, on *L. cf. communis*



**Figure 26.** Sections of ascomata in selected species of *Spirographa* (A–C, E–G, I–K in LPCB; D, L in water; H in Congo Red). A–B – *S. aggregata* on *Polyblastidium corallophorum* (J.E. 34-5, holotype); C – *S. arsenii* on *Heterodermia flabellata* (J.E. 30-3); D–F – *S. fusisporella* (perithecioid ascomata) in hymenia of *Fissurina* sp. (M0086813, lectotype); G – *S. giselae* on *Lichenopeltella cf. communis* growing on *Parmotrema crinitum* (A.F. 26962); H–I – *S. maroneae* (perithecioid ascomata) in thallus of *Maronea constans* (A.F. 27345, holotype); J – *S. ophiurosora* on *Lobariella cf. pallida* (A.F. 28890); K – *S. pyramidalis* on *Remototrachyna costaricensis* (J.E. 55-1); L – *S. usneae* on *Usnea* sp. (A.F. 8176-2, holotype). Scales: A–B, D–G, K–L = 50  $\mu\text{m}$ ; C, H–J = 25  $\mu\text{m}$ .



**Figure 27.** Morphological variability of ascospores in *Spirographa*. A – *S. aggregata* on *Polyblastidium corallophorum* (J.E. 34-5, holotype, in Congo Red); B – *S. arsenii* on *Heterodermia flabellata* (J.E. 30-3, in water); C – *S. ascaridiella* on *Porpidia* sp. (H-Nyl-21874, lectotype, in Congo Red); D – *S. fusisporella* in hymenia of *Fissurina* sp. [(M0086813, lectotype, in water (left) and Congo Red (right)]; E – *S. giselae* on *Lichenopeltella* cf. *communis* growing on *Parmotrema crinitum* [A.F. 26962, in water (up) and Congo Red (down)]; F – *S. maroneae* (perithecioid ascomata) in thallus of *Maronea constans* (A.F. 27345, holotype, in water); G – *S. ophiurospora* on *Lobariella* cf. *pallida* (A.F. 28890, in Congo Red); H – *S. pyramidalis* on *Remototrachyna costaricensis* (J.E. 55-1, in water); I – *S. usneae* on *Usnea* sp. (A.F. 8176-2, holotype, in water). Scales: A–I = 10  $\mu$ m.

growing on *P. reticulatum*, A.F. 26439 (KRAM, LPB). PORTUGAL. Distr. Bragança. Tas-os-Montes, Parque Natural Montesinho, camino de Soeira a Fresulfe, bosquetes de *Quercus pyrenaica*, 850 m, 41°52'51"N, 6°54'48"W, on *L. cf. ramalinae* growing on *Ramalina farinacea*, J.E. 30112 & E. Ros (hb. Etayo). SPAIN. Madrid. Rascafría, Las Presillas del Lozoya, travesía del Río, bosque en galería, 40°52'50"N, 3°52'58"E, 1160 m, on *R. fraxinea* on *Q. pyrenaica*, J.E. 31796 (hb. Etayo).

**Specimens examined (asexual state).** BOLIVIA. Dept. Tarija. Prov. Aniceto Arce: Reserva Nacional de Flora y Fauna Tariquía, between la Cumbre and camamento los Alisos, 22°00'41"S, 64°36'02"W, 2560 m, Boliviano-Tucumano forest with *Alnus acuminata* and *Polylepis*, on *Lichenopeltella* cf. *communis* growing on *Parmotrema* sp., A.F. 26959 (KRAM). Prov. Burnet O'Connor: close to los Pinos, 90 km from Tarija on old road between Entre Ríos and Tarija, 21°25'30"S, 64°19'07"W, 2265 m, on *Lichenopeltella* cf. *communis* growing on *Parmotrema*, J.E. 30601 (LPB, hb. Etayo). PORTUGAL. Distr. Bragança. Tas-os-Montes, Parque Natural Montesinho, camino de Soeira a Fresulfe, bosquetes de *Quercus pyrenaica*, 850 m, 41°52'51"N, 6°54'48"W, on *L. cf. ramalinae* growing on *R. farinacea*, J.E. 30112 & E. Ros hb. Etayo). SPAIN. Cáceres. P.N. de Monfragüe, alrededores de la Fuente del Francés, ~300 m, 39°49'46"N, 06°02'08"W, on *L. cf. ramalinae* growing on *Ramalina* sp. on *Fraxinus*, J.E. 29094 (hb. Etayo).

*Spirographa herteliana* (Knoph.) Flakus, Etayo & Miadlikowska, comb. nov.

Mycobank MB 833349

Basionym: *Cornutispora herteliana* Knoph, Biblioth. Lichenol. 88: 346. 2004.

**Notes.** *Cornutispora herteliana* was described by Knoph (2004) from Japan. This species is characterized by having Y-shaped conidia (10.5–15.5  $\times$  ~7  $\mu$ m) composed of the main axis (~10–11  $\times$  2–3  $\mu$ m) and 3–5  $\mu$ m long conidial arms.

**Ecology and distribution.** The species is known only from the type locality where it grows on *Lecidella* cf. *elaeochroma* (Knoph 2004).

*Spirographa hypotrachynae* (Etayo) Flakus, Etayo & Miadlikowska, comb. nov. (Fig. 25G)

Mycobank MB 833350

Basionym: *Pleoscutula hypotrachynae* Etayo, Biblioth. Lichenol. 84: 94. 2002.

Type: Colombia. Dept. Cundinamarca. Munic. Villapizón: Páramo La Calavera, 3300 m, on *Hypotrachyna* sp., Javier Etayo 16305, E. Linares & J. Muñoz (COL – holotype!; hb. Etayo – isotype!).

**Notes.** *Spirographa hypotrachynae* was originally described by Etayo (2002) from Colombia growing on *Hypotrachyna*. This species is characterized by having black, partly immersed, apothecioid ascomata inhabiting *Lichenopeltella* growing on *Hypotrachyna* and medium sized ascospores ( $13\text{--}19 \times 2\text{--}2.5 \mu\text{m}$ ) (Etayo 2002). *Spirographa pyramidalis*, another species of this genus growing on *Hypotrachyna* can be easily separated by its shorter ascospores,  $7\text{--}10 \times 2\text{--}3 \mu\text{m}$ , with obtuse ends. *S. gise-lae* is also known as a hyperparasite on *Lichenopeltella* (growing on *Parmotrema* and *Ramalina*), but has slightly larger ascospores ( $12\text{--}20 \times 2\text{--}3.5 \mu\text{m}$ ) and usually an orange-brown pigmented discs. Further studies of fresh material are needed to confirm whether *S. hypotrachynae* and *S. giselae* represent separate species.

**Ecology and distribution.** The species is known from Bolivia (Flakus & Kukwa 2012a), Colombia and Ecuador and occurs on *Hypotrachyna* (Etayo 2002, 2017).

**Specimens examined.** BOLIVIA. Dept. Santa Cruz, Prov. Caballero, El Lago, Cochabamba-Santa Cruz road,  $17^{\circ}50'16''\text{S}$ ,  $64^{\circ}43'56''\text{W}$ , 2960 m, open Yungas moosy cloud forest, on *Hypotrachyna* sp. on twigs, J.E. 28375 (LPB); near Siberia,  $17^{\circ}49'38''\text{S}$ ,  $64^{\circ}44'45''\text{W}$ , 3950 m, open Yungas cloud forest, on *Hypotrachyna* sp. on branches, J.E. 29412 (hb. Etayo, LPB). Dept. Tarija. Prov. Aniceto Arce: Papachacra,  $21^{\circ}41'36''\text{S}$ ,  $64^{\circ}29'33''\text{W}$ , 2195 m, Tucumano-Boliviano montane forest with *Alnus acuminata*, on thallus of *Hypotrachyna* sp., A.F. 19896 & J. Quisbert (KRAM, LPB).

***Spirographa intermedia*** (Punith. & D. Hawksw.) Flakus, Etayo & Miadlikowska, comb. nov.

Mycobank MB 833351

Basionym: *Cornutispora intermedia* Punith. & D. Hawksw., in Punithalingam, Mycol. Res. 107(8): 920. 2003.

**Notes.** The species is known only from the asexual state described on *Ochrolechia* sp. from the USA and it is characterized by having Y-shaped conidia ( $15\text{--}25 \times 8\text{--}20 \mu\text{m}$ ) composed of an axis of somewhat similar size [main axis ( $7\text{--}8\text{--}11\text{--}12.5$ )  $\times 2\text{--}2.5 \mu\text{m}$ ] (Punithalingam 2003, Fig. 11).

**Ecology and distribution.** The type was described from epiphytic *Ochrolechia* sp. in the USA (Punithalingam 2003). Specimens with similar conidia and growing on the same host are known from Bolivia, Norway and Spain.

**Other material on *Ochrolechia* studied (asexual state).** BOLIVIA. Dept. Chuquisaca, Prov. Belisario Boeto, close to Padilla, between Nuevo Mundo and Santa Rosa, W-NW,  $18^{\circ}57'11.9''\text{S}$ ,  $64^{\circ}16'36.3''\text{W}$ , on *O. africana*, J.E. 29861 (hb. Etayo). NORWAY: Kinsarvik, Handargervidda N.P., Tveita-fossen galls, Pinus wood, on *O. tartarea* on rock,  $60^{\circ}21'04''\text{N}$ ,  $6^{\circ}45'34''\text{E}$ , 200 m, J.E. 29553 (hb. Etayo). SPAIN. Navarra, valle del Baztán, puerto de Izpegui, cumbre, roquedo entre hayas, ~700 m, on *O. tartarea* on rock, J.E. 14241 (hb. Etayo).

***Spirographa lichenicola*** (D. Hawksw. & Sutton) Flakus, Etayo & Miadlikowska, comb. nov.

Mycobank MB 833352

Basionym: *Cornutispora lichenicola* D. Hawksw. & B. Sutton, in Hawksworth, Trans. Br. Mycol. Soc. 67(1): 51. 1976.

**Notes.** The species was originally described from *Parmelia sulcata* in the UK as the first licheniculous member of *Cornutispora* (Hawksworth 1976). It is known only from its anamorphic state characterized by having Y-shaped, conidia ( $10\text{--}14 \times 7\text{--}9 \mu\text{m}$ ) composed of a larger main axis ( $6\text{--}11.5 \times 1.5\text{--}2 \mu\text{m}$ ) and two smaller arms ( $2.5\text{--}6 \times 0.5 \mu\text{m}$ ). It was reported from several unrelated host genera and may represent an assemblage of cryptic species.

**Ecology and distribution.** The type was collected in the UK on *Parmelia sulcata* (Hawksworth 1976). Additional collections were reported from several lichens (e.g., Brackel 2014).

***Spirographa limaciformis*** (Piroz.) Flakus, Etayo & Miadlikowska, comb. nov. (Figs 28D, 30D)

Mycobank MB 833353

Basionym: *Cornutispora limaciformis* Piroz., Mycologia 65(4): 763. 1973.

Type: Canada. Midhurst Nursery, Lake Simcoe Dist., Ontario, on *Therrya fuckelii* on *Pinus resinosa*, 27 May 1971, leg. R. L. Bowser & P. E. Buchan (DAOM 138360 – holotype!).

**Notes.** *Spirographa limaciformis*, the type species of *Cornutispora*, was described as hyperparasite on *Therrya fuckelii* growing on *Pinus resinosa* from Canada (Pirozynski 1973). The species is characterized by having large Y-shaped conidia, composed of a main axis ( $12\text{--}22 \times 2.5\text{--}3.5 \mu\text{m}$ ) and two smaller arms ( $7\text{--}9.5 \times 0.5 \mu\text{m}$ ).

**Ecology and distribution.** The type collection is known from Canada where it occurs on *Therrya fuckelii* growing on *Pinus resinosa* (Pirozynski 1973).

***Spirographa longispora*** Etayo

**Notes.** This species was recently introduced by Etayo (2017) to accommodate specimens growing on *Sticta* and characterized by having brownish ascomata, partly immersed in the host thallus, and large, vermiform ascospores ( $35\text{--}45 \times 2\text{--}2.5 \mu\text{m}$ ). An asexual state of the species is unknown.

**Ecology and distribution.** The species is known only from the type locality in Ecuador where it grows on *Sticta humboldtii* (Etayo 2017).

**Specimen examined.** ECUADOR. Prov. Carchi. Tulcán, Páramo El Ángel, de Tufiño a Maldonado ~km 10, zona de las Lagunas Verdes, páramo con frailejones, 4000 m,  $00^{\circ}47'49''\text{S}$ ,  $77^{\circ}52'26''\text{E}$ , on *Sticta humboldtii* en arbustos, Javier Etayo 26984 & Z. Palice (QCA – holotype!; hb. Etayo – isotype!).

***Spirographa maroneae*** Flakus, Etayo & Miadlikowska, sp. nov. (Figs 25H, 26H–I, 27F)

Mycobank MB 833354

Diagnosis: Differs from *S. fusisporella* by having dark brown pigmented perithecioid ascomata, 100–160  $\mu\text{m}$  diam., larger ascospores,  $30\text{--}40 \times 2.5\text{--}3.5 \mu\text{m}$ , and the host selection (*Maronea constans*).

Type: BOLIVIA. Dept. Tarija. Prov. Aniceto Arce: colese to la Mamora between Tarija and Bermejo,  $22^{\circ}09'51''\text{S}$ ,  $64^{\circ}40'03''\text{W}$ , 1320 m, disturbed Tucumano-Boliviano forest,

on corticolous *Maronea constans*, Adam Flakus 27345 (LPB – holotype!).

**Description.** Ascomata perithecioid, subglobose, 100–160  $\mu\text{m}$  diam., dark brown to black, immersed in the host thallus, erumpent and partly exposed when mature, causing bleaching of the host. Exciple wall laterally 10–25  $\mu\text{m}$  thick, with olivaceous-brown to brown pigment, K–, N–, paraplectenchymatous, composed of isodiametric to elongate cells, with hyaline inlayer of thin-walled cells, 3–7  $\times$  1–3  $\mu\text{m}$ , and pigmented outerlayer of thick-walled cells, 3–10  $\times$  2–4  $\mu\text{m}$ . Hymenium hyaline, I–, KI–, composed of adglutinate paraphyses. Paraphyses hyaline, filiform, simple to slightly branched, septate, 1.5–2  $\mu\text{m}$  wide, not or slightly capitate at the apex. Subhymenium indistinct. Asci clavate, not thickened apically,  $\sim$ 32-spored, 55–80  $\times$  12–25  $\mu\text{m}$ . Ascospores hyaline, acicular, curved to helicoid, with ciliate ends, 1-septate, not constricted at the septum, smooth, 30–( $\bar{x}$ =36.3  $s$ =3.3)–40  $\times$  2.5–( $\bar{x}$ =3  $s$ =0.3)–3.5  $\mu\text{m}$ , l/b ratio 9.1–( $\bar{x}$ =12.2  $s$ =1.5)–15.2 ( $n$ =24). Anamorphic state unknown.

**Etymology.** The epithet refers to the host of the new species.

**Ecology and distribution.** The species is known from the type locality in Tucumano-Boliviano forest and inhabits corticolous *Maronea constans*.

**Notes.** *Spirographa maroneae* is the second species in the genus with perithecioid ascomata. *Spirographa fusisporella*, which also has perithecioid ascomata, differs in having having hyaline perithecia, immersed in hymenia of lichens of the family *Graphidaceae*, and smaller ascospores (25–35  $\times$  2–3  $\mu\text{m}$ ). *Spirographa aggregata* has ciliate ascospores of similar in size, but apothecioid ascomata are aggregated in stromata and grow on *Polyblastidium corallophorum*.

***Spirographa ophiurospora*** (Etayo) Flakus, Etayo & Miadlikowska, comb. nov. (Figs 25I, 26J, 27G, 28E, 29E, 30E)

Mycobank MB 833355

Basionym: *Cornutispora ophiurospora* Etayo, Opera Lilloana 50: 148. 2017.

Type: Ecuador. Prov. Loja. Sierra sur, Loja, Cajanuma, Parque Nacional Podocarpus, 2750–3000 m, bosque nublado y páramo, montañas ‘nudo de Sabanilla’, sobre *Lobariella crenulata*, Javier Etayo 20127 & Z. Palice (QCA – holotype!; hb. Etayo – isotype!).

**Description of sexual state.** Ascomata 100–200 mm diam., cleistohymenial, sometimes aggregated, initially immersed in the host thallus, then breaking through the thallus cortex of the host and almost sessile when mature. Disc exposed, concave, concolorous with the margin or paler, dark brown, matte. Margin brown to black, prominent, thick, without hairs. Exciple paraplectenchymatous, laterally 35–45 mm wide, with a honey-brown to olive-brown pigment, K–, N–. Hymenium hyaline, 90–10  $\mu\text{m}$  tall, I–, K/ I–. Subhymenium hyaline, indistinct. Epihymenium with honey-brown to orange brown, granular pigments, K–, N–. Paraphyses hyaline, simple, septate,

sometimes slightly branched in the upper part, 1.5–2.5  $\mu\text{m}$  thick, apically slightly thicker (up to 3.5  $\mu\text{m}$ ) and covered by a granular pigment. Asci clavate to cylindrical, functionally unitunicate, wall apically not thickened, K/I–, I– (only endoascus slightly orange),  $\sim$ 32-spored, 55–70  $\times$  10–15  $\mu\text{m}$ . Ascospores hyaline, spirally arranged in ascus 1-septate with pointed ends, not constricted at the septum, fusiform, straight to curved or slightly sigmoid, smooth, without perispore, 30–( $\bar{x}$ =35.4  $s$ =2.9)–40  $\times$  1.5–( $\bar{x}$ =1.8  $s$ =0.3)–2.5  $\mu\text{m}$  ( $n$ =26).

**Description of asexual state.** See Etayo (2017).

**Notes.** The species was only recently described by Etayo (2017) from Ecuador based on its *Cornutispora*-like asexual state, producing conidia composed of three, large arms of equal size, and inhabiting *Lobariella crenulata*. The sexual state was first reported from Colombia (Etayo 2002) and Peru (Etayo 2010) as *Spirographa fusisporella* on *Lobariella pallida*, but its connection to *Cornutispora* was never observed. Our phylogenetic analyses clearly confirm that both reproductive states represent a single species (Fig. 24B).

**Ecology and distribution.** The species seems to be very common in Andean cloud forests, and is known from *Lobariella crenulata*, *L. pallida* and *L. subexornata* in Bolivia, Colombia (Etayo 2002), Ecuador (Etayo 2017) and Peru (Etayo 2010).

**Specimens examined (sexual state).** BOLIVIA. Dept. Cochabamba. Prov. Tiraque: Parque Nacional Carrasco, Camino de los Nubes, Antenas old road between Sillar and Villa Tunari, 17°12'32"S, 65°41'52"W, 3520 m, upper montane Youngas cloud forest, on corticolous *L. pallida*, M.K. 15249 (LPB, in specimen of *Lawreyella lobariella*). Dept. La Paz. Prov. Nor Yungas: Chuspipata station, old road Coroico-La Paz, 16°18'18"S, 67°48'55"W, 3009 m, disturbed Yungas cloud forest with shrubs and small trees, on *Lobariella* cf. *pallida*, A.F. 28890 (KRAM, LPB). Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado de Apolobamba, near Rio Pelechuco, below Pelechuco close to new road to Apolo, open area with scattered small trees 14°46'59"S, 69°01'08"W, 2750 m, J.E. 14-3 (LPB, hb. Etayo). COLOMBIA. Dept. Cundinamarca. Munic. Villapizón: Paramo La Calavera, 3200–3400 m, on *L. pallida*, JE 16401 (hb. Etayo). PERU. Dept. Cuzco. Prov. Paucartambo: road Paucartambo – Pillcopata, just SW of Paso de Tres Cruces, 13°8'S, 71°38'W, 3450 m, on *L. pallida*, R. Santesson, A. Tehler & G. Thor P96:18 (UPS).

**Specimens examined (asexual state).** BOLIVIA. Dept. Chuquisaca. Prov. Zudañez: Área Natural de Manejo Integrado El Palmar, segunda villa de presto, Lomán, Salviatójo, 18°45'51"S, 64°50'09"W, 2836 m, on *L. pallida* on trees, J.E. 29577 (LPB, hb. Etayo). Dept. Cochabamba. Prov. Carrasco: Parque Nacional Carrasco, Koricaza, 17°33'21"S, 65°16'29"W, 2950 m, Páramo Yungueño, on *L. pallida* on trees, J.E. 29324 (LPB, hb. Etayo); Meruvia close to Monte Punku, 17°35'06"S, 65°14'54"W, 3283 m, *Podocarpus -Polylepis* forest, on corticolous *L. pallida*, M.K. 15029b, A.F. 25567 (KRAM, LPB, UGDA). Prov. Chapare: Parque Nacional Carrasco, Incachaca, 17°14'59"S, 65°49'36"W, 2560 m, Yungas cloud forest, on *L. subexornata* on bushes, J.E. 29621 (LPB); near Lago Corani, close to Villa Tunari-Cochabamba road, 17°13'24"S, 65°53'31"W, 3271 m, open area with shrubs, on corticolous

*L. crenulata* M.K. 15420 (LPB, UGDA, specimen of *Lawreyella lobariella*); Prov. Tiraque, Parque Nacional Carrasco, old gurd's camp, 17°18'23"S, 65°45'60"W, elev. 3360 m, open area with shrubs, on corticolous *Lobariella* sp., M.K. 15291 (LPB, UGDA). Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado Nacional Apolobamba, below Pelechuco, 14°49'08"S, 69°03'50"W, 3560 m, open area with shrubs and *Polylepis* trees, on corticolous *L. pallida*, M.K. 14970, 14963 (LBP, UGDA); below Keara Bajo, 14°41'47"S, 69°04'10"W, 3160 m, open area with shrubs and scattered trees, on corticolous *L. pallida*, M.K. 14898b (LPB, UGDA); near Keara Bajo, 14°41'59"S, 69°04'34"W, 3290 m, open area with shrubs and scattered trees, corticolous, A.F. 25232 (KRAM, LPB); Área Natural de Manejo Integrado Nacional Apolobamba, near Río Pelechuco, below Pelechuco close to new road to Apolo, 14°47'28"S, 69°01'32"W, 2860 m, open area with scattered trees, on corticolous *Lobariella* sp., M.K. 14824a, A.F. 25162 (KRAM, LPB, UGDA); ibidem, 14°46'59"S, 69°01'08"W, 2750 m, open area with scattered small trees, corticolous, on A.F. 25132 (KRAM, LPB). Prov. Murillo: Valle del Zongo, bosque yungas nublado 2900 m, 16°08'38"S, 68°06'59"W, on *L. subexornata*, J.E. 26803 (LPB); Valle de Zongo, 3375 m, S16°10'15", W68°08'02", páramo yungueño, rocas sueltas entre pastos con arbustos, on *L. crenulata* on bushes, J.E. 26776 (LPB, hb. Etayo); Sainani, Valle del Zongo, 16°07'20"S, 68°05'09"W, 2220 m, open area with shrubs and scattered trees, corticolous, on *Lobariella* sp., A.F. 26260 (KRAM, LPB). Prov. Nor. Yungas: Desviación de La Paz a Coroico hacia Unchuvavi, camino a Chulumani, 3210 m, S16°18'27", W67°53'48", bosque nublado, on *L. pallida* and *L. crenulata*, J.E. 26919 (LPB, hb. Etayo); Parque Nacional Cotapata, Santa Catalina village, above Tunkini, 16°11'12"S, 67°52'07"W, 1600–1840 m, Yungas montane forest, on *L. pallida*, J.E. 27400 (LPB); near Nogalani village, on the road Coroico–La Paz (casa azul de Alejo), 16°12'57"S, 67°49'15"W, 2168 m, Yungas secondary cloud forest, on *Lobariella* sp., J.E. 27968 (LPB, hb. Etayo). Prov. Saavedra: 28 km from Charazani village, on the road Charazani – Apolo, 15°12'43"S, 68°47'25"W, 1650–1775 m, Yungas montane forest, open area with boulders SW, on *L. crenulata*, J.E. 27319 (LPB, hb. Etayo). Dept. Santa Cruz. Prov. Caballero: near Siberia, 17°49'38"S, 64°44'45"W, 3950 m, open Yungas cloud forest, on *Lobariella pallida*, J.E. 28607 (LPB). COLOMBIA. Dept. Nariño. Munic. de Pasto: corregimiento El Encano, Parque Natural Tunguragua, SE lago La Cocha (Guamués), en *Lobariella* sp., 2700 m, páramo azonal sobre turbera, J.E. 15780 (LPB, hb. Etayo). ECUADOR. Prov. Loja. sierra sur, Loja, Cajanuma, Parque Nacional Podocarpus, bosque nublado y páramo, bajada hacia la salida, taludes y árboles de cuneta, 2500–2700 m, sobre *L. pallida*, J.E. 20171 (hb. Etayo).

***Spirographa parmotrematis*** Flakus, Etayo & Miadlikowska, sp. nov. (Figs 28F, 29F, 30F)

Mycobank MB 833356

Diagnosis: Differs from *S. pyramidalis* by a different phylogenetical position, the smaller conidia 3–4.5 µm diam., and the host selection (*Parmotrema*).

Type: Bolivia. Dept. La Paz. Prov. Nor Yungas: Chuspipata station, old road Coroico–La Paz, 16°18'18"S, 67°48'55"W, 3009 m, disturbed Yungas cloud forest with shrubs and small trees, on epiphytic *Parmotrema sancti-angeli*, 23 Nov. 2016, Adam Flakus 28887 (LPB – holotype!).

**Description.** Lichenicolous fungus causing characteristic circular bleaching of the host thallus surrounded by dark-brown necrotic layer, ~0.3–1.2 mm diam. Ascomata

unknown. Conidiomata pycnidial, dispersed, immersed inside of the host thallus, finally erumpent and sometimes partly exposed, subglobose to pyriform, 110–150 µm diam. Pycnidial wall hyaline to yellowish brown, 5–8 µm wide, composed of 3–6 layers of thin-walled hyphae, cells 1–4 × 0.5–2 µm, desintegrating by an irregular opening around the top. Conidiophores hyaline, septate, thin-walled, arising from the innermost cells of the pycnidial walls, branched. Conidiogenous cells ~2–4 × 1–2 µm, holoblastic, synchronous or sympodial, integrated, terminal to lateral, thin-walled, producing few conidia from minute loci. Conidia hyaline, aseptate, triangular to tetrahedral, 3–(x̄=4 s=0.5)–4.5 (n=54) diam. Sexual state unknown.

**Etymology.** The epithet refers to the host of the species.

**Ecology and distribution.** Known from Bolivia and Portugal where it grows on *Parmotrema*.

**Notes.** Originally Etayo (2010) described *S. pyramidalis* (in *Cornutispora*) from *Hypotrachyna revoluta* and *Parmotrema* sp. occurring in oceanic forests in Spain and the Azores. This species was recognized from its small triangular conidia and bleaching of the host thalli. Our phylogenetic analyses however revealed that specimens growing on *Remototrachyna* (closely related to *Hypotrachyna*) are not related phylogenetically to those on *Parmotrema* (Fig. 24B). Further analyses also revealed that conidia of *S. pyramidalis* s.str. (growing on *Hypotrachyna* and *Remototrachyna*) are slightly but consistently larger (4–5 µm diam.) than those growing on *Parmotrema* (3–4.5 µm diam.). Therefore, we introduce a new species, *Spirographa parmotrematis*, for the specimens growing on *Parmotrema*.

**Additional specimens examined.** BOLIVIA. Dept. Chuquisaca. Belisario Boeto: close to Padilla between Nuevo Mundo and Santa Rosa, 18°57'06"S, 64°16'14"W, 1936 m, transition between Boliviano-Tucumano forests and dry interandean vegetation, on *Parmotrema* sp., A.F. 26593 (LPB). Dept. Tarija. Prov. Aniceto Arce: close to Limal between Cayambuyo and Bermejo, 22°19'36"S, 64°29'51"W, 860 m, disturbed Sub-Andean Tucumano-Boliviano forest close to orange plantation, on *P. sancti-angeli*, A.F. 27283 (KRAM); Reserva Nacional de Flora y Fauna Tariquíá, between la Cumbre and campamento los Alisos, 22°00'52"S, 64°36'24"W, 2796 m, forest with *Polylepis*, on thallus of corticolous *P. cetratum*, M.K. 16653 (LPB, UGDA). PORTUGAL. Azores. S. Miguel, Sete Cidades, Lagoa verde, on *Parmotrema* sp., on *Cryptomeria japonica*, 140 m, 37°50'N, 25°47'W, J.E. 24103 (hb. Etayo).

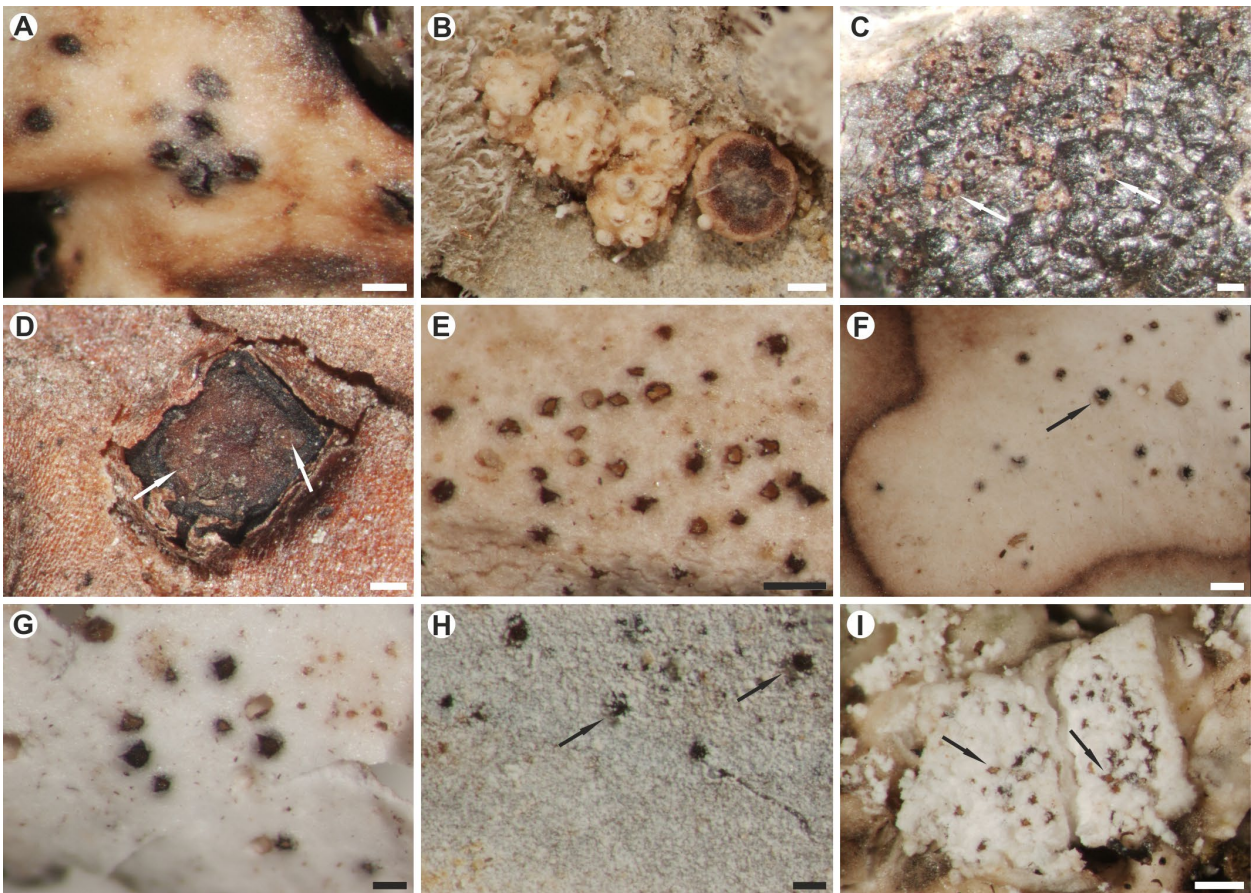
***Spirographa pittii*** (D. Hawksw. & Punith.) Flakus, Etayo & Miadlikowska, comb. nov.

Mycobank MB 833357

Basionym: *Cornutispora pittii* D. Hawksw. & Punith., in Punithalingam, Mycol. Res. 107(8): 925. 2003.

**Notes.** The species is known only from its asexual state described from Australian species of *Hypotrachyna* and is characterized by having small (~6–7 × 5–7 µm), Y-shaped conidia, composed of the main axis (3–3.5 × 1–1.5 µm) and two arms [2–2.5 × 1–1.5(–2) µm]





**Figure 28.** Morphological diversity of conidiomata in *Spirographa*. A – *S. arsenii* on *Heterodermia flabellata* (J.E. 29-2); B – *S. galligena* on *Erioderma* sp. (A.F. Fla39B, holotype); C – *S. giselae* on *Lichenopeltella* cf. *communis* growing on *Parmotrema crinitum* (A.F.26959); D – *S. limaciformis* on *Therrya fuckelii* (DAOM138360, holotype); E – *S. ophiurospora* on *Lobariella pallida* (A.F. 25162); F – *S. parmotremitis* on *Parmotrema sancti-angeli* (A.F. 28887, holotype); G – *S. pyramidalis* on *Remototrachyna costaricensis* (A.F. 25129); H – *S. usneae* on *Usnea* sp. (A.F. 26545); I – *S. vermiformis* on *Lepra amara* (A.F. s.n.). Scales: A, C, E, G–H = 100  $\mu$ m; B, D, F, I = 250  $\mu$ m.

(Punithalingam 2003). The asexual states of *Spirographa hypotrachynae* and *S. pyramidalis*, another two species of *Spirographa* growing on *Hypotrachyna*, can easily be distinguished by their smaller and triangular conidia with reduced arms.

**Ecology and distribution.** It is known only from *Hypotrachyna formosana* (?*H. osseoalba*) growing in Australia (Punithalingam 2003). The Bolivian record from *Canoparmelia amazonica* may represent other species (Flakus & Kukwa 2012a).

***Spirographa pyramidalis*** (Etayo) Flakus, Etayo & Miadlikowska, comb. nov. (Figs 25J, 26K, 27H, 28G, 29G, 30G)

MycoBank MB 833358

Basionym: *Cornutispora pyramidalis* Etayo, *Opuscula Philolichenum* 8: 134. 2010.

= *Asteroglobulus pyramidalis* (Etayo) Diederich, in Diederich, Lawrey & Ertz, *Bryologist* 121(3): 392. 2018.

Type: Spain. Guipuzkoa. Peñas de Aia, way to Bianditz, 400–600 m, 43°16'N, 1°47'W, on *Hypotrachyna revoluta* on *Larix*, Javier Etayo 24739 (VIT – holotype!; hb. Etayo – isotype!).

**Description of the sexual state.** Ascospores 100–200  $\mu$ m diam., cleistohymenial, dispersed, initially immersed in the host thallus, then breaking through the thallus cortex of

the host and almost sessile when mature; bleaching thallus of the host. Disc exposed, concave, concolorous with the margin or paler, dark brown, matte. Margin brown, prominent, thick, without hairs. Exciple paraplectenchymatous, laterally 15–25  $\mu$ m wide, with pale-brown pigment, K–, N–. Hymenium hyaline, 45–65  $\mu$ m tall, I–, K/I–. Subhymenium hyaline, ~10  $\mu$ m tall. Epithymenium with honey-brown to orange brown, granular pigments, K–, N– (dissolving in K), 5–10  $\mu$ m tall. Paraphyses hyaline, simple, septate, 1–1.5  $\mu$ m thick, sometimes slightly branched in the upper part, apically slightly thicker (up to 2.5 mm). Asci clavate to cylindrical, functionally unitunicate, wall apically not thickened, K/I–, I– (only endoascus slightly orange), ~32-spored, 40–50  $\times$  10–15  $\mu$ m. Ascospores hyaline, 1-septate, not constricted at the septum, narrowly ellipsoid to almost fusiform, straight to curved or slightly sigmoid, smooth, without perispore, 7–( $\bar{x}$ =8.7 s=0.8)–10  $\times$  2–( $\bar{x}$ =2.3 s=0.3)–3  $\mu$ m (n=94).

**Description of the asexual state.** See Etayo (2010).

**Notes.** So far *Spirographa pyramidalis* was known only in asexual state. The species, growing on closely related *Hypotrachyna* and *Remototrachyna*, is characterized by having small triangular, *pyramidalis*-like conidia (4–5  $\mu$ m diam.) and medium size ascospores (7–10  $\times$  2–3  $\mu$ m).

**Ecology and distribution.** The species is known from Bolivia, Ecuador and Spain (Etayo 2010) as a parasite of *Hypotrachyna revoluta* (host of the type), *Hypotrachyna* sp. and *Remototrachyna costaricensis*.

**Specimens examined.** BOLIVIA. Dept. Cochabamba. Prov. Chapare: Parque Nacional Carrasco, San Jacinto, cose to Villa Tunari-Lago Corani road, 17°10'26"S, 65°45'13"W, 1877 m, open area with shrubs and scattered trees, on epiphytic *Remototrachyna costaricensis*, A.F. 26238 (KRAM, LPB). Dept. La Paz. Prov. Franz Tamayo: Área Natural de Manejo Integrado Nacional APOLOBAMB A near Rio Pelechuco, below Pelechuco close to new road to Apolo, 14°46'59"S, 69°01'08"W, 2750 m, open area with scattered small trees, on epiphytic *R. costaricensis*, A.F. 25129 (KRAM, LPB). Dept. Tarija. Prov. Aniceto Arce: Reserva Nacional de Flora y Fauna Tariquia, between la Cumbre and camamento los Alisos, 22°02'38"S, 64°35'47"W, 2460 m, Boliviano-Tucumano forest with *Alnus acuminata* and *Polylepis*, on corticolous *Hypotrachyna* sp., M.K. 16563 (LPB). Prov. Murillo: Sainani, Valle del Zongo, open area with shrubs and scattered trees, 16°07'03"S, 68°04'42"W, 2170 m, on *R. costaricensis*, J.E. 55-9 (LPB, hb. Etayo). ECUADOR. Prov. Imbabura. R. E. R. Cotacachi-Cayapas, desde Irunguichoa Lagunas de Piñán, bosque

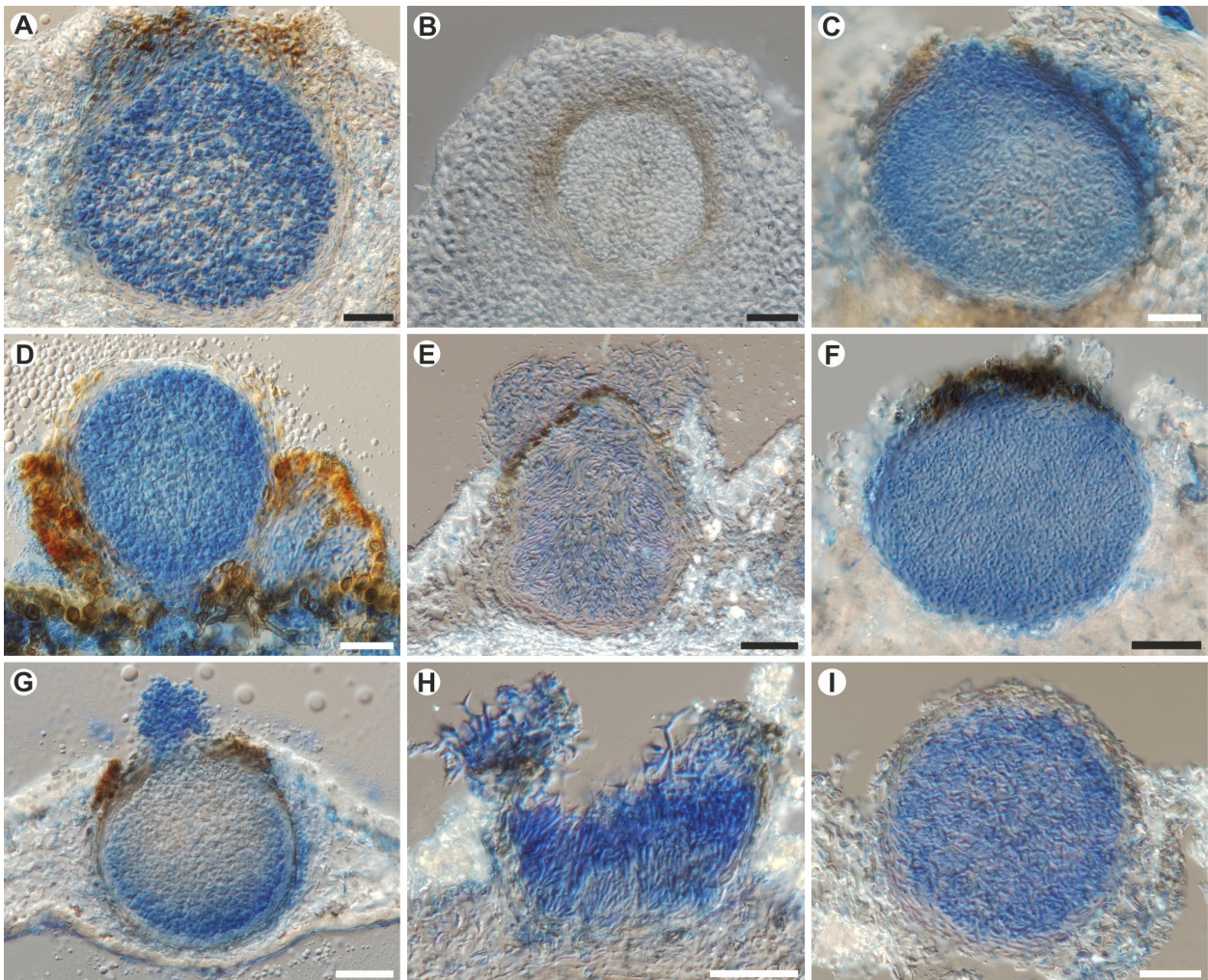
nublado, 2700–3100 m, en *Hypotrachyna* sp., J.E. 25483, J.E. 25495 (QCA, hb. Etayo).

***Spirographa triangularis*** (Diederich & Etayo) Flakus, Etayo & Miadlikowska, comb. nov. (Fig. 25K)

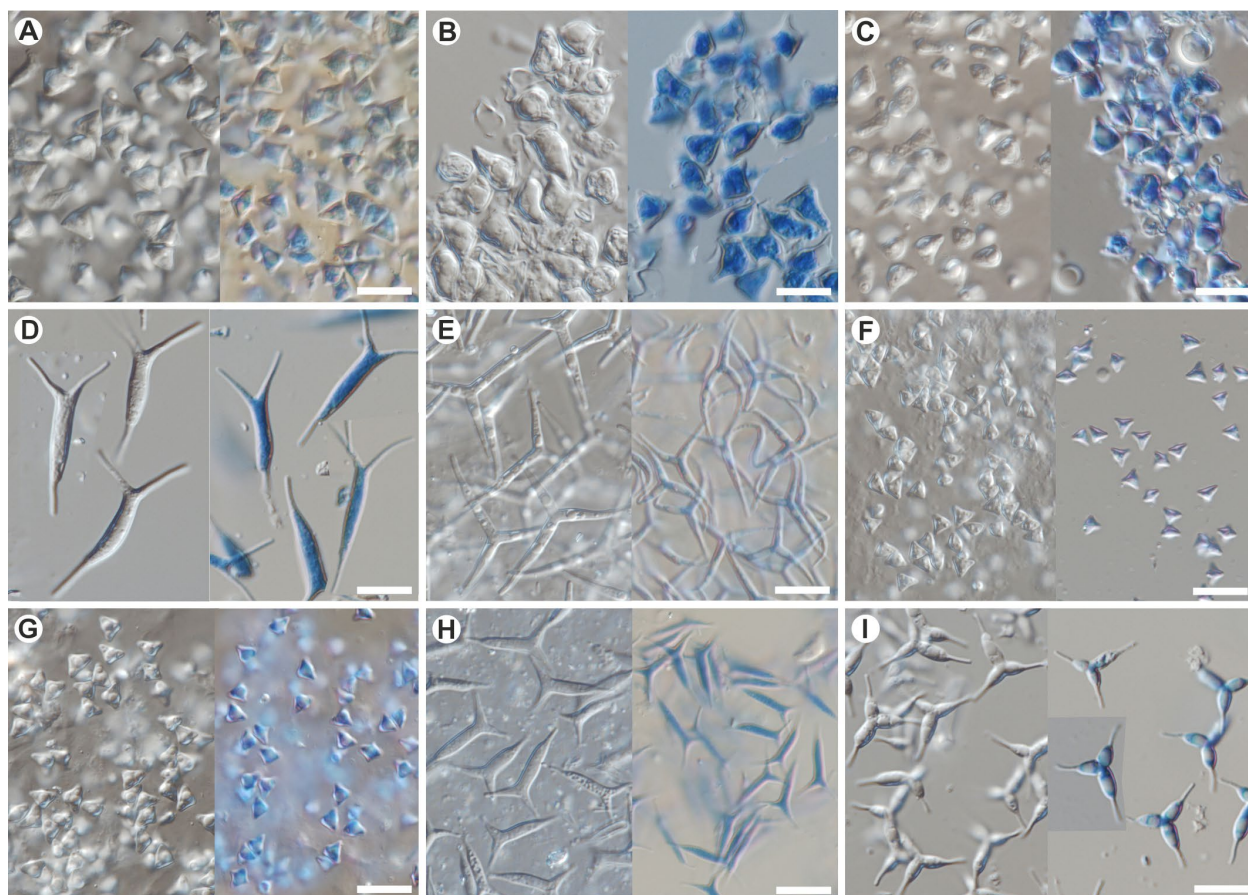
Mycobank MB 833359

Basionym: *Cornutispora triangularis* Diederich & Etayo, in Etayo & Diederich, Flechten Follmann, Contributions to Lichenology in Honour of Gerhard Follmann (Cologne): 209. 1995.

**Description of the sexual state.** Ascomata 100–170 µm diam., cleistohymenial, initially immersed and covered in part by the host thallus, then fully breaking the thallus cortex and almost sessile when mature. Disc exposed, concave, concolorous with margin, dark brown to black, matte. Margin dark brown, prominent, thick, without hairs. Exciple paraplectenchymatous, of 6–7 rows of cells, laterally 10–50 µm wide, brown to olivaceous brown, K–, N–, basally 15–20 µm thick. Hymenium hyaline, 60–90 µm tall, K/I–, I–. Subhymenium hyaline, indistinct. Epihymenium with orange-brown, granular pigments, K–, N–. Paraphyses 1–3 µm thick, simple to slightly branched



**Figure 29.** Sections of conidiomata in selected species of *Spirographa* (A, C–I in LPCB; B in water). A – *S. arsenii* in *Heterodermia flabellata* (J.E. 29-2); B–C – *S. galligena* in *Erioderma* sp. (A.F. Fla39B, holotype); D – *S. giselae* in *Lichenopeltella* cf. *communis* growing on *Parmotrema crinitum* (A.F.26959); E – *S. ophiurospora* in *Lobariella pallida* (A.F. 25162); F – *S. parmotrematis* in *Parmotrema sancti-angeli* (A.F. 28887, holotype); G – *S. pyramidalis* in *Remototrachyna costaricensis* (A.F. 25129); H – *S. usneae* in *Usnea* sp. (A.F. 26545); I – *S. vermiformis* in *Lepra amara* (A.F. s.n.). Scales: A–I = 25 µm.



**Figure 30.** Morphological variability of conidia in *Spirographa* [all in water (left) and LPCB (right)]. A – *S. arsenii* in *Heterodermia flabellata* (J.E. 29-2); B – *S. galligena* in *Erioderma* sp. (A.F. Fla39B, holotype); C – *S. giselae* in *Lichenopeltella* cf. *communis* growing on *Parmotrema crinitum* (A.F.26959); D – *S. limaciformis* on *Therrya fuckelii* (DAOM138360, holotype); E – *S. ophiurospora* in *Lobariella pallida* (A.F. 25162); F – *S. parmotremitis* in *Parmotrema sancti-angeli* (A.F. 28887, holotype); G – *S. pyramidalis* in *Remototrachyna costaricensis* (A.F. 25129); H – *S. usneae* in *Usnea* sp. (A.F. 26545); I – *S. vermiformis* in *Lepra amara* (A.F. s.n.). Scales: A–I = 10  $\mu$ m.

in the upper part, septate, apically not thickened. Asci clavate to cylindrical,  $50\text{--}90 \times 14\text{--}21 \mu\text{m}$ , functionally unitunicate, apically not thickened, K/I–, I– (only endoascus slightly orange),  $\sim 32$ -spored. Ascospores, hyaline, 1-septate with pointed ends, not constricted at the septum, fusiform, straight to curved or slightly sigmoid, smooth, without perispor,  $30\text{--}48 \times 1.5\text{--}2.5 \mu\text{m}$  ( $n=20$ ).

**Description of the asexual state.** See Etayo & Diederich (1995).

**Notes.** *Spirographa triangularis* was introduced by Etayo & Diederich (1995) based on a specimen of *Cornutispora* growing on epiphytic *Pertusaria pertusa* in Spain. It inhabits various species of *Pertusaria* and has conidia unique in the genus ( $11\text{--}17 \mu\text{m}$  diam.) composed of three segments of equal size ( $3\text{--}4 \mu\text{m}$  long), which are angular in shape and form distinctly triangular arms with cilia (Etayo & Diederich 1995; Fig. 3A). Based on a sample from Denmark growing on *Pertusaria hymenea* (IMI 233298), a possibly teleomorphic state of *S. triangularis* was illustrated by Hawksworth (1980; Fig. 5B as *Spilomela ascaridiella*) and by Sherwood-Pike (1987; Fig. 15 as *Pleopsilis ascaridiella*). In addition, in well preserved forests with *Fagus* and *Abies* in the Pyrenees, the *Spirographa triangularis* anamorph (*Cornutispora*) was observed growing intermixed with specimens of

*Spirographa* on *Pertusaria pertusa*. However, samples we examined were characterized by having larger ascospores ( $30\text{--}48 \times 1.5\text{--}2.5 \mu\text{m}$ ) than those discussed by Hawksworth (1980) and Sherwood-Pike (1987) ( $22\text{--}35 \times 1.5\text{--}2 \mu\text{m}$ ). Although we were not able to confirm this anamorph-teleomorph connection based on molecular data, it is possible that the specimens of *Spirographa* growing on members of *Pertusaria* s.str. represent the sexual state of *S. triangularis*.

**Ecology and distribution.** The species is known from Europe where it has been reported from epiphytic members of *Pertusaria* (*P. flavida*, *P. hymenea* and *P. pertusa*) (Hawksworth 1980; Sherwood-Pike 1987; Etayo & Diederich 1995).

**Specimens examined (sexual state).** SPAIN. Huesca. Refugio de Linza, subida hacia Aztaparreta, hayedo–abetal,  $42^{\circ}51'12''\text{N}$ ,  $0^{\circ}48'07''\text{W}$ , 1500 m, on *P. flavida*, J.E. 30861 (hb. Etayo). Álava. Ascensión al monte Gorbea por sendero desde Zárata, hayedo hiperhúmedo,  $43^{\circ}00'05.5''\text{N}$ ,  $2^{\circ}46'15.8''\text{W}$ , 1050 m, on *P. pertusa* on *Fagus*, J.E. 31601 (hb. Etayo). S. Miguel de Aralar, carretera de ascenso NA–7510, entre Km 8–9, hayedo entre roquedos calizos,  $42^{\circ}58'05''\text{N}$ ,  $1^{\circ}58'16.0''\text{W}$ , 940 m., on *P. hymenea* on *Fagus*, J.E. 31721 (hb. Etayo).

**Specimens examined (asexual state).** SPAIN. Navarra. S. Miguel de Aralar: sendero desde el aparcamiento casa forestal,  $42^{\circ}57'31''\text{N}$ ,  $2^{\circ}02'57.4''\text{W}$ , 1000 m., on *P. pertusa* on

*Fagus*, J.E. 31721 hb. Etayo); S. Miguel de Aralar, carretera de ascenso NA-7510, entre Km 8-9, hayedo entre roquedos calizos, 42°58'05"N, 1°58'16.0"W, 940 m, on *P. pertusa* on *Fagus*, J.E. 31764 (hb. Etayo). Leiza: Leizalarrea, robledal en ladera de *Quercus robur*, 600 m, on *P. pertusa* on *Q. robur*, J.E. 28685 (hb. Etayo). País Vasco. Guipúzcoa: SA de Aralar, Lizarrusti, Lareo, sendero y alrededores del lago, hayedo, 720–775 m, 42°58'43"N, 2°6'15"W, on *P. pertusa* on *Fagus*, J.E. 25973 (hb. Etayo); Oiartzun, camino a Artikutza, hayedo de Oieleku, 43°14'S, 1°49'W, on *P. pertusa* on *Fagus*, J.E. 23507 (hb. Etayo); 1 km después linde con Atallu (NA), área recreativa de Añi, cañón en pared or. S, 200–300 m, 43°04'30"N, 2°0'56"W, on *P. pertusa* on *Fagus*, J.E. 26556 (hb. Etayo).

***Spirographa tricupulata*** (F. Berger & E. Zimm.) Flakus, Etayo & Miadlikowska, comb. nov.

Mycobank MB 833360

Basionym: *Cornutispora tricupulata* F. Berger & Er. Zimm., in Zimmermann & Berger, Herzogia 31: 738. 2018.

**Notes.** *Spirographa tricupulata* was recently described by Zimmermann and Berger (2018) for a *Cornutispora*-like conidial fungus growing on *Physcia stellaris*. The species is characterized by having conidia composed of three equal arms ( $4\text{--}5.2 \times 2.4\text{--}3 \mu\text{m}$ ), which are strongly swollen at the base and develop cilia ( $1.2\text{--}1.5 \mu\text{m}$  long) at the ends. Conidia produced by the species are of an intermediate size as compared to *S. ciliata* and *S. triangularis*.

**Ecology and distribution.** It is known from a single locality in Austria from *Physcia stellaris*.

***Spirographa usneae*** Flakus, Kukwa & Etayo  
(Figs 25L, 26K, 27I, 28H, 29H, 30H)

Type: Bolivia. Dept. Cochabamba. Prov. Chapare: near Incachaca village, 17°14'13"S, 65°49'02"W, 2294 m, Yungas montane cloud forest, on thallus of *Usnea* sp., Adam Flakus 8176.2 (LPB – holotype!).

**Notes.** The species is characterized by having black, immersed ascogonia, 100–250  $\mu\text{m}$  diam., with the disc concolorous with the margin, and fusiform, straight to curved or slightly sigmoid, mainly 1-septate ascospores with pointed ends,  $15\text{--}32 \times 2\text{--}3 \mu\text{m}$  (Flakus & Kukwa 2012b). We found its potential asexual state on the apothecial disc of *Usnea* in Bolivia (A.F. 26545) causing slight necrosis. The specimen is characterized by having Y-shaped, *limaciformis*-like conidia, 14–19  $\mu\text{m}$  large, with the main axis of  $7\text{--}15 \times 1.5\text{--}2.5 \mu\text{m}$  and arms of  $4\text{--}5 \times 0.5\text{--}1 \mu\text{m}$ . However, the two states were never observed co-occurring, and molecular data should be used to confirm their identity.

**Ecology and distribution.** The species is known from Bolivia and Ecuador on *Usnea* species.

**Specimens examined (sexual state).** BOLIVIA: Dept. Cochabamba. Prov. Carrasco, Parque Nacional Carrasco, Korikaza close to Monte Punku, 17°33'30"S, 65°16'32"W, 2880 m, lower montane Yungas cloud forest, on corticolous *Usnea* sp., M.K. 15112a (LPB). Dept. La Paz, Prov. Franz Tamayo, Área Natural de Manejo Integrado Nacional Apolobamba, near Río Pelchucu, below Pelechucu, 14°47'28"S, 69°01'32"W, 2860 m, open area with scattered trees, on corticolous *Usnea* sp., M.K.

14822 (LPB, UGDA); Prov. Muñecas, Área Natural de Manejo Integrado Nacional Apolobamba, above Camata, 15°14'35"S, 68°45'09"W, 1900, open area with shrubs, on *Usnea* sp. growing on shrubs, M.K. 14588 (LPB). ECUADOR: Prov. Tungurahua. Camino Baños a Puyo, confluencia de ríos Verde y Pastaza, Pailón del Diablo, en *Usnea* de color rojizo, 1600 m, J.E. 19937 (hb. Etayo).

**Specimens examined (asexual state).** BOLIVIA. Dept. Chuquisaca. Prov. Belisario Boeto: close to Padilla between Nuevo Mundo and Santa Rosa, 18°57'12"S, 64°16'37"W, 1790 m, transition between Boliviano-Tucumano forests and dry interandean vegetation, on disc of corticolous *Usnea* sp., A.F. 26545 (LPB).

***Spirographa vermiformis*** (Leight.) Flakus, Etayo & Miadlikowska, comb. nov. (Figs 28H, 29I, 30I)

Mycobank MB 833361

Basionym: *Melaspilea vermiformis* Leighton, Grevillea 3: 114. 1875.

**Notes.** *Melaspilea vermiformis* was described by Leighton (1875) from Wales based on material growing on *Lepra albescens*. Hawksworth (1980) considered the species to be similar to *Lecidea ascaridiella* and included both of them under name *Spilomela ascaridiella*. Later the species was moved to the genus *Pleopsis* by Sharwood-Pike (1987) but the same species concept was maintained. For a long time *Melaspilea vermiformis* was treated as a later synonym of *Spilomela ascaridiella*, and some authors even considered those names as being synonyms of *Spirographa fusisporella* (eg. Holien & Triebel 1996; Diederich 2004; Etayo 2017). Because *Melaspilea vermiformis* and *Cornutispora triangularis* were described from rather similar hosts belonging to *Pertusaria* s.lat. (incl. *Pertusaria* s.str. and *Lepra*) we considered the possibility that they represent different sexual states of the same species. If so, it would mean that *C. triangularis* is a later synonym of *M. vermiformis*. However, we observed that samples of *Cornutispora* growing on *Pertusaria* s.str. (eg. *P. flavicans*, *P. hymenea*, *P. pertusa*) are characterized by having *triangularis*-like conidia (Etayo & Diederich 1995; Fig. 3A) while those growing on *Lepra* develop *ciliata*-like conidia (Fig. 30I). Together with the fact that the genus *Lepra* has recently been separated from *Pertusaria* based on phylogenetic results (Wei et al. 2017) it is likely that *Cornutispora triangularis* and *Melaspilea vermiformis* represent different species. In Europe at least two species of *Spirographa* can be distinguished on *Pertusaria* s.lat., especially by the conidia and host identity: (i) *S. triangularis* growing usually on *Pertusaria pertusa* and sporadically on *P. flavida* and *P. hymenea*, and (ii) *S. vermiformis* has conidia more similar to *C. ciliata* growing on *Lepra* (including *L. albescens*).

**Ecology and distribution.** The species was described from Wales on *Lepra albescens* growing on *Quercus* (Hawksworth 1980) and a possible anamorphic state was observed in France and Spain.

**Additional material of *S. cf. vermiformis* examined (asexual state).** FRANCE. Arette. La Pierre St. Martin le Braca,

hayedo-abetal cerca de carretera D-132, 42°59'06"N, 0°44'38"W, 1480 m, on *Fagus*, on *Lepra albescens*, J.E. 31218 (hb. Etayo). SPAIN: Navarra. Lezáun, robledal detrás del hotel abandonado de la carr. Na-120, 42°47'08"N, 2°00'30"E, 930 m, on *L. amara* on *Quercus pubescens*, J.E. 31429 (hb. Etayo); alto de Belate, sendero hacia el antiguo Monasterio hospital Nuestra Señora de Belate, 43°02'23"N, 1°36'43"W, 890 m, on *L. albescens* on *Fagus*, J.E. 31242 (hb. Etayo); Quinto Real, carretera Eugui-Irurita, hayedo cerca aparcamiento setero, 43°01'22"N, 1°30'35"W, 1050 m, on *L. albescens* on *Fagus*, J.E. 27823 (hb. Etayo); Ciaúrriz, pista unos metros antes del cruce de la N-411 con la entrada al pueblo, robledal con boj húmedo, 42°55'49"N, 1°37'18"W, 625 m, on *L. albescens* on *Q. faginea*, J.E. 31596 (hb. Etayo); Baraibar, Sierra de Aralar, carretera, cerca del Santuario, on *L. multipuncta* on *Fagus*, J.E. 663 & O. Breuss (hb. Etayo); S. Miguel de Aralar, carretera de ascenso NA-7510, entre Km 8-9, hayedo entre roquedos calizos, 42°58'05"N, 1°58'16"W, 940 m, on *L. albescens* var. *corallina* on *Fagus*, J.E. 31732 (hb. Etayo); ibidem, on *L. multipuncta* on *Fagus*, J.E. 31762 (hb. Etayo); Aldatz way to Beruete, pista por el NW hacia Aiztondo, hayedo y fresnedas, 43°01'10"N, 1°50'21"W, 880 m, on *Lepra* sp., J.E. 30634 (VIT). Álava: Álava, SA Entzia, puerto de Opacua, camino de Legaire, 940 m, on *L. multipuncta* on *Fagus*, J.E. 30071 (hb. Etayo).

### Key to lichenicolous ascomycetes growing on *Lobariella*

- 1 Sclerotia dark brown, with rough surface, 0.2–1.0 × 0.1–0.3 mm, internally composed of mass of hyaline, thick-walled, interwoven hyphae, 4–10 µm thick, surrounded by a dark-brown, cortical layer composed of isodiametric, thin-walled hyphae, of cells 4–17 µm diam; usually associated with superficial white mycelium; ascospores or conidia absent. . . . . *Xylaria lichenicola*  
Sclerotia absent, ascospores or conidia present . . . . . 2
- 2(1) Spores produced in asci . . . . . 3  
Spores not produced in asci . . . . . 32
- 3(2) Ascomata apothecioid or arthonioid; hymenium exposed at maturity . . . . . 4  
Ascomata perithecioid or catathecioid, hymenium not exposed at maturity . . . . . 11
- 4(3) Ascospores hyaline . . . . . 5  
Ascospores pale to dark brown . . . . . 9
- 5(4) Ascospores simple, straight to curved, narrowly ellipsoidal with acute ends, 10–20 × 2.5–3.5 µm, ascomata black, hairy, aggregated . . . . . *Lawreyella lobariella*  
Ascospores 1- to multiseptate . . . . . 6
- 6(5) Ascospores 15–27-septate, acicular, 64–105 × 3.5–4.5 µm, ascomata marginate, immersed, 0.25–0.35 mm diam., disc pale yellowish . . . . . *Nanostictis pluriseptatum*  
Ascospores 1-septate . . . . . 7
- 7(6) Ascospores fusiform, with pointed ends, slightly curved or sigmoid, 30–40 × 1.5–2.5 µm, asci multi-spored, ascomata immersed to sessile, dark brown, marginate . . . . . *Spirographa ophiurospora*  
Ascospores ellipsoidal with rounded ends, 7.5–11 × 3–5 µm, asci 8-spored . . . . . 8
- 8(7) Ascomata arthonioid, emarginate, sessile, slightly elevated and irregular, pale orange-brown to dark brown, resembling galls of *Tremella* when well developed, ascospores 6–11 × 3.5–5 µm, constricted at the septa, sometimes with one cell larger . . . . . *Arthonia lobariellae*  
Ascomata, originating from splits in the host cortex, then angular to rounded when mature, surrounded by a thin incised margin, 150–280 µm diam., pale yellowish to pale brown, ascospores not constricted at the septa, 7–10 × 2.5–4 µm . . . . . *Corticifraga microspora*
- 9(4) Ascospores constantly 1-septate, 8–15 × 4–6 µm, apothecia with elevated margin, shiny, epruinose . . . . . *Sclerococcum ricasoliae*  
Ascospores mainly 3-septate, apothecia emarginate, matte, epruinose or green-pruinose . . . . . 10
- 10(9) Ascospores 9–13 × 3–5 µm, ascomata usually green-pruinose . . . . . *Abrothallus subhalei*  
Ascospores 18.5–27 × 7–10 µm, ascomata epruinose . . . . . *Abrothallus macrosporus*
- 11(3) Ascomata catathecioid, composed of radially arranged quadrangular cells, with convergent ostiolar setae, asci 8-spored, ascospores hyaline, 16–18 × 3.5–4.5 µm, usually with setulae . . . . . *Lichenopeltella* cf. *santessonii*  
Ascomata perithecioid . . . . . 12
- 12(11) Ascomata pale pink, orange or red–violet . . . . . 13  
Ascomata dark brown or black . . . . . 21
- 13(12) Asci producing one single macrospore together with 4 microspores; macrospores hyaline, 1-septate, slightly reticulate, (60–)73–94(–99) × 24–34 µm; microspores verrucose, 8–12 × 5–6 µm, ascomata orange, 250–400 µm diam., sessile, developed on white arachnoid mycelium . . . . . *Oviculispora parmeliae* s.lat.  
Asci producing spores of similar size . . . . . 14
- 14(13) Ascospores multi-septate . . . . . 15  
Ascospores 0–1-septate . . . . . 16
- 15(14) Ascomata orange, elongate, pear-shaped, sessile on reduced white arachnoid mycelium, single or in small groups, 500–700 µm high, 250–300 µm wide, without hairs hamathecium absent, ascospores acicular, hyaline, 225–430 × 1.5–2.5 µm . . . . . *Neobaryopsis andensis*  
Ascomata beige to yellowish (intermixed with host rhizines on the lower side of the thallus), single, 130–200 µm diam., covered by thick-walled hairs, 35–80 × 3–8 µm, hamathecium with branched-anastomosed filaments, ascospores hyaline, acicular, 100–150 × 2–3.5 µm . . . . . *Lichenotubeufia cryptica*
- 16(14) Asci 4-spored. Ascospores 1-septate, breaking inside the ascus into two subglobose cells, hyaline, verrucose, 6–7.5 µm diam., ascomata orange, K–, 120–200 µm diam. . . . . *Globonectria cochensis*  
Asci 8-spored. Ascospores 1-septate not breaking inside the asci . . . . . 17
- 17(16) Ascospores finally yellowish brown, ascomata dark colored (red, reddish brown or reddish black), peridium K+ reddish violet . . . . . 18  
Ascospores hyaline, ascomata pale colored (salmon pink, yellowish orange or orange–brown), peridium K– . . . . . 19
- 18(17) Ascomata red with large, concolorous papillae, 120–200 µm in diam, ascospores verruculose, 8.5–10.5 × 5.5–8 µm . . . . . *Xenonectriella coppinsiana*

- Ascomata brown or black with reddish tinge, without red papillae, 250–500 µm diam., ascospores rugulose, 11–14.5 × 9–10 µm . . . . *Xenonectriella rugulatispora*
- 19(17) Ascomata large, 120–200 µm diam., salmon colored, subspherical, flattened in the apex, sessile, ascospores hyaline, verrucose, 7–10 × 3–3.5 µm . . . . *Nectriopsis curtiseta*  
Ascomata smaller 60–130 µm diam., yellowish to orange-brown, ascospores smooth-walled . . . . . 20
- 20(19) Ascomata yellowish to orange, immersed in the host thallus, 60–85 µm diam., ascospores 5–7.5 × 3–4.5 µm . . . . . *Pronectria microspora*  
Ascomata orange to brown, sessile, 100–130 µm diam., covered by short setae, ascospores 6–9 × 2–3 µm . . . . . *Trichonectria setadpressa*
- 21(12) Ascospores aseptate, hyaline to pale brown, 16–25 × 8–12 µm; ascomata black, 200–400 µm diam., breaking the thallus, at least immersed in part, mycelium dark brown . . . . . *Roselliniella ramirezii*  
Ascospores 1-septate, transversely septate or submuriform . . . . . 22
- 22(21) Ascospores grey-brown, yellow-brown or dark brown at maturity . . . . . 23  
Ascospores colorless at maturity, rarely brownish when overmatured . . . . . 26
- 23(22) Ascomata immersed in the host thallus at least in young stage, without setae, ascospores golden-brown to dark-brown . . . . . 24  
Ascomata sessile, covered by black setae, ascospores dark-brown . . . . . 25
- 24(23) Ascomata 200–300 µm wide, solitary, fully immersed or breaking when older, not causing gall formation, ascospores 3-septate, golden-brown to brown, 15–22 × 5–6.5, strongly verrucose . . . *Pseudodidymocyrtis lobariella*  
Ascomata 130–150 µm wide, in groups, fully immersed, causing galls formation, gall constricted at the base when older, of size 0.2–0.3 mm diam., ascospores 3-septate, dark-brown, 18–22 × 6.5–9 µm, smooth-walled . . . . . *Pyrenidium sp.*
- 25(23) Ascospores 3-septate, 15–16 × 4.5–5 µm . . . . . *Capronia cf. solitaria*  
Ascospores with with (0–)3–5 transverse and 0–1 longitudinal septa, 20–29 × 4.5–7 µm . . . . . *Capronia epilobarina*
- 26(22) Ascomata without setae, immersed to sessile on the host thallus, ascospores 0–2-septate . . . . . 27  
Ascomata covered by black or hyaline setae, sessile, ascospores 1-septate . . . . . 29
- 27(26) Ascomata pyriform, immersed in the apothecial hymenia of the host, 70–90 µm wide, single, dark orange-brown to almost black, K+ slightly purplish, ascospores 1-septate, 6–11 × 2.5–3.5 µm . . . . . *Atronectria lobariellae*  
Ascomata sub-globose, not breaking the host, very small, 25–70 µm wide, aggregated, dark brown to black, K–, ascospores 0–2-septate, at least in part >11 µm long . . . . . 28
- 28(27) Ascomata 25–40 µm diam., aggregated on the lower surface, asci 4-spored, ascospores fusiform, 0–2-septate, 10–17 × 1.5–3 µm . . . . *Rhagadostomella hypolobariella*
- Ascomata 60–70 µm diam., aggregated on apothecial disc, asci 8-spored, ascospores bacilliform, 1-septate, 10–13.5 × 3–3.5 µm . . . *Stigmatidium disconeophromeum*
- 29(26) Ascomata covered only by hyaline setae 34–45 × 4–5 µm, ascospores 7.5–10.5 × 2–3 µm . . . . . *Niesslia stictarum var. nuda*  
Ascomata covered by black setae . . . . . 30
- 30(29) Ascomata covered by medium sized setae with widened base, 10–37 × 4–6 µm (base up to 6 µm wide), ascospores 4.5–8.5 × 1.5–2.5 µm . . . . . *Niesslia cf. lobariae*  
Ascomata covered by shorter (8–26 × 5–13 µm long) or branched setae . . . . . 31
- 31(30) Ascospores breaking in ascus, 5–8 × 1.5–2 µm, setae usually with short branches . . . . *Niesslia schizospora*  
Ascospores not breaking, 6–7 × 1.5–2 µm, setae not branched, widened base (7–13 µm wide, shark-tooth shaped) . . . . . *Niesslia stictarum var. stictarum*
- 32(2) Conidia arising within pycnidial conidiomata . . . . . 33  
Conidia not arising within pycnidial conidiomata . . . . . 37
- 33(32) Conidia branched, Y-shaped, hyaline, 20–31 µm diam.; arms aseptate of the same size, 9–18 × 1.5–2.5 µm; conidiomata yellowish brown, peridium K–, immersed in the host thallus . . . *Spirographa ophiurospora* (anamorph)  
Conidia not branched . . . . . 34
- 34(33) Conidia brown, verrucose, 1-septate, 12.5–19 × 8.5–11 µm, conidiomata 200–300 µm diam. with green and purple pigments, K+ bright-green . . . . . *Abrothallus aff. ertzii* (anamorph)  
Conidia hyaline, smooth-walled, aseptate or 1-septate . . . . . 35
- 35(34) Conidia 1-septate, hyaline, constricted at the septum, 11–14 × 2.5–3.5 µm, conidiomata immersed in irregular, flat, orange to brown gall-resembling ascomata . . . . . *Arthonia lobariellae* (anamorph)  
Conidia aseptate . . . . . 36
- 36(35) Conidiomata sessile, 150–350 µm tall, 140–250 µm wide, grey brown to blackish, with rugose surface (in section brown to greenish brown, K+ violet), conidia bacilliform, 2–3 × 1–1.5 µm . . . . *Epithamnia rugosopycniata*  
Conidiomata immersed to erumpent, 100–160 µm diam., black with a white mass of conidia on the top, conidia bacilliform to narrowly ellipsoidal, 2.5–7 × 1.5–2.5 µm . . . . . *Abrothallus subhalei* (anamorph)
- 37(32) Conidiophores tightly aggregated in sporodochia or synnemata; conidia hyaline to greyish brown . . . . . 38  
Conidiophores scattered or loosely grouped, conidia brown . . . . . 40
- 38(37) Conidia produced on unbranched synnemata, 100–400 µm tall, developing on white arachnoid mycelium, conidial mass 50–300 µm diam., hemispherical, hyaline, pink to yellowish orange, conidia bacilliform-ellipsoidal to obovoid, aseptate, without perispore, delicately truncate, 4–7 × 2–2.5 µm . . . . . *Neobaryopsis andensis* (anamorph)  
Conidial mass forming sporodochial structures. . . . . 39
- 39(38) Sporodochia yellowish to orange, conidia acicular, simple to multiseptate, 60–130 × 2–3 µm . . . . *Fusarium sp.* (possibly anamorph of *X. rugulatispora*)

- Sporodochia brown to greyish, 50–120 µm diam., conidia ellipsoidal, distinctly verrucose, catenate, greyish brown, 0–2-septate, 6–9 × 4–4.5 µm . . . . . *Cladophialophora parmeliae*
- 40(37) Conidia branched, with three axes of similar size, 13–14-septate, single arm 130–147 × 16–19 µm developing directly on black, superficial, hyphae . . . . . *Ceratosporium* sp.  
Conidia not branched, not developing on superficial hyphae . . . . . 41
- 41(40) Conidia brown . . . . . 42  
Conidia hyaline . . . . . 46
- 42(41) Conidiophores poorly differentiated. . . . . 43  
Conidiophores well differentiated . . . . . 44
- 43(42) Conidiophores immersed in host apothecial hymenia, pale-brown, conidia in basipetal chains, smooth-walled, aseptate, 3–4.5 × 2.5–4 µm; hyperparasitic on *Lawreyella lobariella* . . . . . *Intralichen lichenum*  
Conidiophores developing on the host thallus, conidia muriform, subglobose to ellipsoidal, 10–25 µm diam., composed of cells 4–6 µm diam., arising singly on short, hyaline to pale brown conidiophores. . . . . *Monodictys* cf. *fuliginosa*
- 44(42) Conidia even in color, pale- to dark-brown, 1–3-septate, 10–17 × 3–4 µm . . . . *Pseudocercospora* cf. *lichenum*  
Conidia >20 µm long and wider, with basal or terminal cells paler . . . . . 45
- 45(44) Conidiophores 120–140 × 5–7 µm, conidia 2-septate, 20–25 × 9–13 µm, constricted at the septum, clavate, the basal cell paler, thin-walled . . . . . *Endophragmiella* aff. *hughesii*  
Conidiophores 32–55 × 4–6 µm, conidia 5–10-septate, not constricted at the septum, 33–55 × 7–9 µm, obclavate-subcylindrical, paler at the top, thick-walled . . . . . *Ellisembia* aff. *lichenicola*
- 46(41) Conidia narrowly ellipsoidal, slightly tapering and evidently truncate, 3.5–6 × 2–3 µm, l/b ratio average 2.1; growing in aggregated colonies covering large areas on apothecial margin of the host . . . . . *Acremonium* sp. (possibly anamorph of *Nectriopsis curtisetia*)  
Conidia subglobose to broadly ellipsoidal, not evidently truncate; growing together forming white or pinkish droplets and developing on white, arachnoid subiculum on upper side of the host thallus . . . . . 47
- 47(46) Conidial mass pinkish, conidia 2–4.5 × 2–3 µm, l/b ratio average 1.4 . . . . *Trichonectria setadpressa* (anamorph)  
Conidial mass white, conidia 2.5–5 × 1.5–2.5 µm, l/b ratio average 1.8 . . . . *Globonectria cochensis* (anamorph)

## Discussion

The genus *Abrothallus* inhabiting *Lobariella* is represented by three species including one new to science, *A. subhalei* (Fig. 1). The sister species *Abrothallus macrosporus* was previously described from Peru and seems to be a common parasite of *Lobariella* in Andean forests. Its potential anamorph, discussed previously by Etayo (2017), is thought to be *A.* aff. *ertzii*. However, in our phylogeny the latter is unrelated to *A. macrosporus* and

most probably represents an undescribed species or else the potential anamorph of *A. ertzii* s.str. (Fig. 1), which is known from *Lobaria pulmonaria* in Canada (Suija et al. 2015b).

As revealed in our analyses, *Arthonia lobariellae* is closely related to the undescribed *Arthonia* ‘*lobariicola*’ from Japan (Fig. 2). It is a member of the *Bryostigma* clade discovered by Frisch et al. (2014). The *Bryostigma* clade includes mainly lichenicolous fungi in addition to the bryophilous *Bryostigma muscigenum* and a few lichen-forming fungi. This clade forms a distinct early diverging lineage in the *Arthoniaceae* as shown by Frisch et al. (2014). Arthonioid species included in this clade are morphologically different from the core *Arthoniaceae* (Frisch et al. 2014). They are characterized by having blackish and convex ascomata, *Arthonia*-type asci, small, hyaline and 1-septate ascospores with an enlarged upper cell, and a dark brown epithecium. The ascospores and ascus anatomy of *Arthonia lobariellae* fit this description. However, the species has rather different large orange-brown ascomata resembling *Tremella*-like galls (Etayo 2017) and frequently develop into the asexual state.

*Globonectria cochensis* and *Trichonectria setadpressa* were for the first time revealed as members of *Nectriaceae*, however, their phylogenetic placement within the family is not well-supported and needs further work. *Globonectria* was shown to be distantly related to other lichenicolous genera in the family (especially to the most morphologically similar *Pronectria*) and connected with its potential anamorph. Therefore, its recognition at the genus level introduced by Etayo (2002) is justified (Fig. 3). *Trichonectria setadpressa* was resolved sister to *T. rectipila* (Fig. 3), a mycoparasitic member of the genus growing on *Diatrype stigma* (*Xylariales*) in North America (Rossman et al. 1999) and connected for the first time with its asexual morph. The co-occurrence of both the asexual and sexual states of *C. cochensis* and *T. setadpressa* was also observed a few times on the same host thalli.

A previous study of *Neobarya* s.lat. by Lawrey et al. (2015) showed that the genus is polyphyletic. *Neobarya* s.str. belongs to *Clavicipitaceae*. Therefore, the new genus *Lichenobarya* (member of *Hypocreaceae* s.lat.; Fig. 4) was established for *N. usneae*. We confirm the polyphyly of *Neobarya* s.lat. (Lawrey et al. 2015) and introduced *Neobaryopsis*, another genus in the *Neobarya*-like lichenicolous species group inhabiting *Lobariella* (Fig. 4). *Neobaryopsis andensis* is well supported within *Cordycipitaceae* and is characterized by having very particular narrowly pyriform yellowish to orange ascomata developing on reduced white arachnoid subiculum, large multiseptate needle-like ascospores, and an asexual state consisting of short synnemata with pale yellowish to pink conidial mass at the top.

Recently it was shown that pleosporalean lichenicolous fungi represent a polyphyletic assemblage (Ertz et al. 2015), with only some genera belonging to *Pleosporales*. Mycoparasites (including lichenicolous fungi) are rare in *Pleosporales*, an order that contains mainly

saprobic fungi and plant pathogens (Hyde et al. 2013; Ariyawansa et al. 2014). Therefore, it was surprising to find yet another lichenicolous species, *Pseudodidymocyrtis lobariellae* (*Didymosphaeriaceae*), in this group. This species is closely related to the saprobic genus *Kalmusia* (Fig. 5). In addition to its saprobic life style, *Kalmusia* clearly differs from *Pseudodidymocyrtis* by its asci developing long furcate pedicel and darker ascospores. *Pseudodidymocyrtis lobariellae* has a very similar morphology to some lichenicolous fungi inhabiting different lichen genera, especially *Didymocyrtis ramalinae* (on *Ramalina*; Ertz et al. 2015). The most morphologically similar species, *Didymocyrtis ramalinae* is a member of the recently reestablished genus *Didymocyrtis* (*Phaeosphaeriaceae*), accommodating several lichenicolous species (Ertz et al. 2015). It is characterized by its asci having a strongly thickened apical apparatus with a poorly developed structure (observed in K/I), uniform and thin pseudoparaphyses, pigments (in peridium and ascospores) changing colors in KOH to dark olivaceous-brown, not constricted ascospores and a *Phoma*-like asexual state (Ertz et al. 2015). In addition to the anatomical characters it differs from *Pseudodidymocyrtis lobariellae* in its phylogenetic placement in *Phaeosphaeriaceae*.

*Lawreyella lobariella*, originally described as a member of *Unguiculariopsis* (Kondratyuk & Galloway 1995a), was revealed as a member of *Cordieritidaceae*, *Helotiales* (Fig. 6). It is closely related to the lichenicolous genera *Diplolaeviopsis*, *Macroskyttea*, and *Protounguicularia*. However, these genera strongly differ anatomically from *Lawreyella*, which is characterized by having black ascomata containing greenish pigment (K+reddish brown, N+ bright green) in its hymenium and an additional orange-brown pigment in the exciple and epithecium (K+ purple then dark-brown, N+ purplish then orange-brown), short excipular hairs, wide and slightly acute, and paraphyses strongly swollen apically with evident triangular gel sheaths. *Diplolaeviopsis* and *Macroskyttea* differ from *Lawreyella* by having mainly aseptate large cylindrical to tapering excipular hairs, urceolate ascomata with a narrow pore when young, apically not thickened paraphyses and coelomycete anamorph with hyaline, 1-septate conidia of unequal cells (Giralt & Hawksworth 1991; Diederich & Coppins 2014; Etayo et al. 2015; Suija et al. 2015a). *Protounguicularia* can be distinguished from *Lawreyella* by its white to pale brownish ascomata; septate, cylindrical to slightly tapering excipular setae, and paraphyses not swollen apically (Huhtinen et al. 2008). The distantly related genus *Unguiculariopsis* (type species – *U. ilicincola*) has also a very different morphology and differs from the new genus mainly its very characteristic excipular hairs, which are aseptate, with swollen bases, narrow to pointed, and strongly hook-shaped (including in the type species), its reddish to brown ascomata with orange brown pigment (K+ reddish to purplish, N–), and paraphyses that are not swollen (Diederich & Etayo 2000).

*Dactylospora lobariella*, as circumscribed by Hafellner (1979), was reported from several host species (*Lobaria erosa*, *L. pulmonaria*, *Lobariella pallida*, *Pseudocyphellaria coppinsii*, *Ricasolia amplissima*, *R. patinifera*,

*R. quercizans*, *R. virens* and *Yoshimuriella dissecta*) in Bolivia, Canada, Chile, Ecuador, Europe, Macaronesia, Mexico and USA (Vouaux 1913; Hafellner 1979; Kondratyuk & Galloway 1995b; Etayo & Diederich 1996b; Galloway & Quilhot 1998; Diederich 2003; Spribille et al. 2010; Flakus & Kukwa 2012a; Etayo 2017). Recently, Diederich et al. (2018) established its position in *Sclerococcales* and showed that *Dactylospora* and *Sclerococcum* represent sexual and asexual states, respectively, of the same genus. Consequently, the new combination *Sclerococcum lobariellum* has been introduced. According to our analyses (Fig. 7), neotropical populations of *Sclerococcum lobariellum* (growing on *Lobariella pallida* and *Ricasolia patinifera*) form a well-supported clade within *Dactylosporaceae*, but distinct from European populations of *S. lobariellum* s.str. (growing on *Lobaria pulmonaria*). Our results suggest that *S. lobariella* s.lat. represents a complex of two cryptic species. In Bolivia and Ecuador, *S. lobariella* s.lat. grows not only on *L. pallida* but also sporadically on *Ricasolia patinifera* and has very similar morphology to *Karschia ricasoliae* described by Vouaux (1913) from mountain forests in Mexico (growing on *Ricasolia*). Therefore, we reestablished the name of *Sclerococcum ricasoliae* to accommodate the neotropical populations of *S. lobariellum* s.lat.

*Xylaria lichenicola*, which forms dark brown sclerotia usually associated with a superficial white mycelium and causing bleaching of the thallus of *Lobariella*, was revealed as a member of *Xylaria* subgenus *Pseudoxylaria* (Fig. 8). According to Hsieh et al. (2010), *Pseudoxylaria* is a monophyletic group that includes species associated with termite nests. Later studies by U'Ren et al. (2016) demonstrated that this clade also includes endolichenic fungi. Our lichenicolous *Xylaria* species forms a clade together with endolichenic *Xylaria* sp. (FL0491) and species associated with termite nests *X. fimbriata*. The endolichenic strain, most closely related to lichenicolous *Xylaria* inhabiting *Lobariella*, was isolated from *Cladonia didyma*. As was shown by Thomas et al. (2016), *Xylaria lichenicola* in Ecuadorian tropical cloud forest may develop different life strategies: they can grow in the forest canopy as endophytic fungi, or as decomposers on decaying wood. Therefore, it is possible that the asymptomatic endolichenic fungus from *Cladonia didyma*, and the lichenicolous fungus causing symptoms on *Lobariella*, represent the same species.

We discovered that the anamorphic species *Cornutispora ophiurospora* inhabiting *Lobariella*, and the undescribed teleomorphic species of *Spirographa*, represent a single species. Subsequently, extensive phylogenetic analyses, including newly generated sequences of several *Cornutispora* and *Spirographa* species inhabiting nine different host species were carried out to reveal phylogenetic affiliation of those fungi (Figs 23, 24A, B). Based on these resulting phylogenies, we established anamorph-teleomorph connections within the genus *Spirographa* for the four-following species: *Cornutispora pyramidalis*+*Spirographa pyramidalis*, *Cornutispora arsenii*+*Pleoscutula arsenii*, *Asteroglobulus giselae*+*Spirographa giselae*, *Cornutispora ophiurospora*+*Spirographa ophiurospora*



(Fig. 24B). The sexual and asexual states of several species were observed growing together on the same host. These multiple evidences of teleomorph-anamorph connections confirmed that *Cornutispora* and *Spirographa* are congeneric.

The teleomorphs of *Spirographa* are morphologically similar (Figs 25, 26) but can be classified into a few phenotypic groups, including: (i) perithecioid, hyaline to pale-brown ascomata immersed in host hymenia (*S. fusisporella*), (ii) perithecioid, dark-brown to black ascomata immersed in host thalli (*S. maroneae*), (iii) pale to dark-brown ascomata immersed in the host thalli (e.g., *S. ophiurospora*, *S. pyramidalis*, *S. usneae*), (iv) dark-brown to black ascomata sitting on the host thalli (*S. giselae*, *S. hypotrachyna*), and (v) dark-brown to black ascomata grouped on black stromata (*S. aggregata*). *Cornutispora*-like anamorphs are even more uniform across species (Figs 28, 29) and are characterized by having immersed to rarely sessile, honey-, orange- to dark-brown pycnidial conidiomata. However, microscopic characters, including ascospores (Fig. 27) and conidia shape and size (Fig. 30), can be helpful in taxonomic studies of this genus. Conidia are highly variable among and within species. Nevertheless, they can be divided into five main morphological groups: (i) *ciliata*-like with strongly swollen (at the base), rounded in shape arms, and apical cilia (Fig. 30J; Gierl & Kalb 1993; Punithalingam 2003), (ii) *intermedia*-like with arms of almost equal sizes, gradually tapering (without swollen base) (Fig. 30F; Punithalingam 2003), (iii) *limaciformis*-like with evident, larger main axis and two shorter arms (Fig. 30E; Pirozynski 1973), (iv) *pyramidalis*-like with triangular, or tetra- to polyhedral, to stellate, with reduced arms (Fig. 30G; Etayo 2010a), and (v) *triangularis*-like with distinctly triangular arms of equal size, and angular in shape (Fig. 3A in Etayo & Diederich 1995).

Determination of *Cornutispora* species using the key by Punithalingam (2003) was challenging and many of our samples did not fit well within the species descriptions. We often found intermediate morphotypes between species. We detected a slight difference in the size of conidia for the specimens inhabiting different hosts within the *C. pyramidalis* complex, corresponding to the relationships reported here (Fig. 24B). We concluded that the *C. pyramidalis* complex is composed of multiple species growing on different hosts: *S. arsenii* (on *Heterodermia*), *S. giselae* (on *Lichenopeltella* growing on *Parmotrema* and *Ramalina*), *S. parmotrematis* (on *Parmotrema*), and *S. pyramidalis* (on *Hypotrachyna* and closely related *Remototrachyna*). Moreover, each species is circumscribed by small but consistent differences in conidial size, and in the cases of *S. arsenii*, *S. giselae*, and *S. pyramidalis* by ascospores of different sizes ( $9\text{--}13 \times 2.5\text{--}4 \mu\text{m}$ ,  $7\text{--}10 \times 2\text{--}3 \mu\text{m}$  and  $12\text{--}20 \times 2\text{--}3.5 \mu\text{m}$ , respectively). This is convincing evidence that conidia size is an important taxonomic character supporting the separation of host-specific species, and that it may indicate that some specimens deviating from the original description and growing on another host, may represent previously overlooked species.

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## Supplementary electronic material

**Table S1.** Voucher data and GenBank accession numbers for the sequences included in this study. Newly generated sequences are shown in bold. [Download file](#)

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