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A novel, exclusively lichen-inhabiting lineage of hypocrealean fungi revealed in the *Sordariomycetes*

V. Darmostuk[1*], J. Etayo[2], P. Rodriguez-Flakus[1], M. Kukwa[3], R. Pino-Bodas[4,5], S. Pérez-Ortega[6], A. Flakus[1]

[1]W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, PL-31-512 Kraków, Poland
[2]Navarro Villoslada 16, 3º dcha, 31003 Pamplona, Navarra, Spain
[3]Department of Plant Taxonomy and Nature Conservation, Faculty of Biology, University of Gdańsk, Wita Stwosza 59, PL-80-308 Gdańsk, Poland
[4]Instituto de Investigación en Cambio Global (IICG-URJC), Universidad Rey Juan Carlos, Tulipán s/n, 28933 Móstoles, Spain
[5]Departamento de Biología y Geología, Física y Química Inorgánica, Rey Juan Carlos University, Tulipán s/n, 28933 Móstoles, Madrid, Spain
[6]Real Jardín Botánico, CSIC, Claudio Moyano 1, E-28014 Madrid, Spain

*Corresponding author: v.darmostuk@botany.pl

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Abstract: Lichen-inhabiting (lichenicolous) fungi comprise a considerable portion of the *Hypocreales* (*Sordariomycetes*), their placement and phylogenetic relationships within the order remain largely unknown due to a lack of available molecular data. This study focuses mainly on tropical lichenicolous hypocrealean fungi which were neglected for a long time. Increasing knowledge of this fungal group is crucial to better understanding the complex evolutionary histories and trophic strategies of the *Hypocreales*. Through an order-wide phylogeny based on multiple loci, we unveiled a novel lineage within the *Hypocreales*, composed exclusively of lichenicolous species from genera such as *Ovicuculispora* and *Paranectria*, along with *Nectriopsis lichenophila* and *Nectria byssophila*-like taxa. Beyond the strong phylogenetic support, the clade is also characterized by its distinct morphology. Here it is introduced as a new family *Paranectriaceae* characterized by yellow to orange sessile ascomata, featuring a distinct tomentum, and by pigment in ascomata walls that do not change colour in KOH solution. The delimitation of interspecific and generic boundaries within the novel family was based on molecular, morphological and ecological data. As a result, we established nine species and five genera, including two genera new to science (*Rossmaniella* and *Sphaeronectria*) and four new species (*Rossmaniella coenogonii*, *R. cryptica*, *R. filispora*, and *R. tylophori*). Additionally, we reinstated the genus *Ciliomyces*, with the type species *Ciliomyces oropensis*, from the synonyms of *Paranectria*. Our results also show that the genus *Neobaryopsis* is more closely related to the family *Calcarisporiaceae* than to the *Cordycepitaceae*, as originally described. A key to species determination within *Paranectriaceae* is provided. The present study suggests that neglected lichenicolous fungi are an important component that appears in *Hypocreales* several times during their evolution, and indicates that their considerable diversity can still be hidden.

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INTRODUCTION

Fungi represent one of the three major eukaryotic life forms on our planet, alongside plants and animals (Hawksworth 2001, Hawksworth & Lücking 2017, Burki *et al.* 2019). With 150000 known species (Phukhamsakda *et al.* 2022), fungi are essential components of all ecosystems, providing ecological functions ranging from beneficial symbionts through antagonistic pathogens to decomposers of organic matter and ecosystem services (Pringle *et al.* 2011). One of the largest groups of fungi are *Sordariomycetes* which are represented by 10500 species (Maharachchikumbura *et al.* 2016). This fungal class is characterized by perithecioid ascomata and unitunicate asci, and its large part consists of *Hypocreales*. All major nutritional modes, such as saprotrophs, endophytes, parasites of insects, plants, other fungi, and lichen, are represented in *Sordariomycetes* (e.g. Hyde *et al.* 2020). They are ubiquitous, with a cosmopolitan distribution, playing an important role as decomposers and in nutrient cycling (Zhang *et al.* 2006, Zhang & Wang 2015). However, they constitute one of the least understood groups of fungi (Maharachchikumbura *et al.* 2016). *Hypocreales* is comprised of more than 6000 species and 300 genera in several families and has become one of the most diverse orders in *Sordariomycetes* (Hyde *et al.* 2020). Members of *Hypocreales* are characterized by unitunicate asci produced within usually fleshy, lightly to brightly coloured (rarely blackish), uniloculate, typically ostiolate ascomata with various hyphomycetous asexual morphs (Rogerson 1970, Rehner & Samuels 1995). *Hypocreales* have been extensively studied in recent years, but their taxonomy, phylogeny, diversity, distribution, and ecology still require

thorough revision and are far from being well understood (Giraldo *et al.* 2015, Maharachchikumbura *et al.* 2015, 2016, Hongsanan *et al.* 2017, Gams *et al.* 2019, Hyde *et al.* 2020, Hou *et al.* 2023, Li *et al.* 2023, Perera *et al*. 2023, Sun *et al.* 2023, Yu *et al.* 2024). Currently, *Hypocreales* is comprised of 27 families: *Acremoniopsiaceae*, *Albomorchellophilaceae*, *Bionectriaceae*, *Calcarisporiaceae*, *Chrysonectriaceae*, *Clavicipitaceae*, *Cocoonihabitaceae*, *Cordycipitaceae*, *Flammocladiellaceae*, *Hypocreaceae*, *Ijuhyaceae*, *Myrotheciomycetaceae*, *Nectriaceae*, *Neoacremoniaceae*, *Niessliaceae*, *Nothoacremoniaceae*, *Ophiocordycipitaceae*, *Polycephalomycetaceae*, *Pseudoniessliaceae*, *Pseudodiploosporeaceae*, *Sarocladiaceae*, *Sedecimiellaceae*, *Stachybotryaceae*, *Stromatonectriaceae*, *Tilachlidiaceae*, *Valsonectriaceae* and *Xanthonectriaceae*.

The order has a long and complex taxonomical history and, due to its morphological diversity, several attempts have been made to circumscribe it. It was introduced by Lindau (1897) to accommodate the family *Hypocreaceae* with *Hypocrea* as the type genus. Subsequently, Seaver (1909) accepted two families, *Nectriaceae* and *Hypocreaceae*, in the order. His classification relied on morphological and anatomical features of ascomata, and this taxonomic hypothesis was supported by several researchers (Petch 1938, Kreisel 1969). The family *Hypocreaceae* includes the species with often disarticulating ascospores and yellow to orange, KOH+ perithecia that are mostly immersed in a stroma or sessile on a subiculum. In contrast, the *Nectriaceae* include fungi with red to dark purple, KOH+ ascomata, and non- to multiseptate and muriform ascospores. The most recent and comprehensive revision of *Nectriaceae* was published by Lombard *et al.* (2015), who, based on a multi-gene phylogeny, re-assessed the family and accepted 47 genera. Currently, *Nectriaceae* remains one of the best-studied families in *Hypocreales* and includes numerous species with wide practical applications (Lombard *et al.* 2015, Crous *et al.* 2021).

Niessliaceae was established to accommodate *Niesslia* species (Kirschstein 1939) and it was classified as *Ascomycota* incertae sedis for a long time. Based on hamathecium features, e.g., short paraphyses, periphysate ostiole, dark pigmented peridium and phialidic conidiogenous cells *Acremonium* or *Monocillium*-type, as well as molecular relationship, it was emplaced in the order *Hypocreales* (Samuels & Barr 1997, Jaklitsch & Voglmayr 2012, Maharachchikumbura *et al.* 2015, 2016, Hongsanan *et al.* 2017, Sun *et al*. 2017, Hyde *et al*. 2020). So far, the family includes 20 odd genera of saprobic, parasitic and lichenicolous fungi (Müller & von Arx 1962, Barr 1990, Samuels & Barr 1997, Hyde *et al.* 2020, Huang *et al.* 2021, Crous *et al.* 2023). However, DNA sequences are lacking for many genera of *Niessliaceae*, and a comprehensive phylogenetic study is needed to circumscribe it and establish the phylogenetic relationships within the family (Maharachchikumbura *et al.* 2016, Huang *et al.* 2021).

The family name *Clavicipitaceae* was initially used by Earle (1901) for a group previously treated as a subfamily within *Hypocreaceae*. Rogers (1979) revised the clavicipitalen fungi, i.e., species with cylindrical asci, thickened ascus apices and filiform ascospores, which often disarticulate into part-spores, and classified them in to separate order *Clavicipitales*. However, early phylogenetic analyses showed that the *Clavicipitaceae* belonged to the order *Hypocreales* (Spatafora & Blackwell 1993, Rehner & Samuels 1995). Sung *et al.* (2007) divided the *Clavicipitaceae* into three families based on the phylogenetic results and morphological features: *Clavicipitaceae* (with dark to bring-coloured solid ascomata), *Cordycipitaceae* (with immersed to superficial perithecia on the fleshy stroma or on pallid to bring coloured subiculum) and *Ophiocordycipitaceae* (with darkly pigmented stromata that are flexible to wiry). Recently, a new family, *Polycephalomycetaceae*, was described to accommodate genera *Polycephalomyces*, *Perennicordyceps*, and *Pleurocordyceps*, which were previously included in the family *Ophiocordycipitaceae* (Xiao *et al.* 2023). This family was separated based on morphological differences, such as stromatic ascomata with a thick peridium and cylindrical secondary spores, as well as the results of multi-locus phylogenetic analyses.

The *Bionectriaceae* was introduced by Rossman *et al.* (1999) to accommodate genera with immersed to superficial perithecioid ascomata that are white, yellow, orange to tan or brown, without colour reaction in KOH or lactic acid. These authors included 26 genera in *Bionectriaceae* which primarily consist of herbicolous, corticolous, lichenicolous or fungicolous species. Later, Rossman *et al.* (2001) conducted the first phylogenetic assessment of this family based on the LSU gene sequences, showing that the family forms a monophyletic lineage within *Hypocreales*.

In the last decade, molecular data has been used to comprehensively revise several groups within the *Hypocreales*, leading in updated classifications and a significant increase in the number of accepted families. Crous *et al.* (2014) established the *Stachybotryaceae* to accommodate the genera *Myrothecium*, *Peethambara* and *Stachybotrys*, which previously were classified as *Hypocreales* incertae sedis. Species of this family are characterized by a hyphomycetes asexual morphs with mononematous to sporodochial to synnematous conidiomata, with phialidic conidiogenous cells and 0–1-septate conidia in dark green to black slimy masses (Castlebury *et al*. 2004, Crous *et al.* 2014, Lombard *et al.* 2016). Another family, the *Tilachlidiaceae*, was introduced by Lombard *et al.* (2015) based on multi-gene phylogenetic analyses and it includes two genera with synnematous conidiomata, *Tilachlidium* and *Septofusidium*. Recently, *Psychronectria* was described (Pawłowska *et al.* 2017), representing the first sexual genus within *Tilachlidiaceae*.

Flammocladiellaceae (type genus *Flammocladiella*) was distinguished by Crous *et al.* (2015) based on the phylogenetic analyses of the LSU gene sequences and morphological characters, such as flame-like conidial masses formed in sporodochia. The genus *Flammocladiella* is represented by two fungicolous species, *Flammocladiella anomiae* and *F. decora* (Crous *et al*. 2015, Lechat & Fournier 2018). Sun *et al*. (2017) described *Calcarisporiaceae* (type genus *Calcarisporium*) based on multi-locus molecular data and the combination of the following morphological characters: hyaline, erect, verticillate conidiophores and sympodial, polyblastic conidiogenesis. Currently, this family includes the fungicolous genus *Calcarisporium* and the saprotrophic genus *Verticimonosporium* (Sun *et al.* 2017, Perera *et al.* 2023). In the same year, *Cocoonihabitaceae* was described by Zhuang & Zeng (2017) to accommodate the genus *Cocoonihabitus.* The genus formed a distinct clade in a multi-locus phylogeny and it is characterized by the following morphological features: asci with a thickened apical

cap penetrated by a narrow pore as well as on specific host preferences (Zhuang & Zeng 2017).

The family *Sarocladiaceae* was introduced by Crous *et al.* (2018a) to accommodate a distinctive lineage previously included within the *Bionectriaceae*. This lineage consists of the asexual genera with stained verrucous hyaline to brown phialidic conidiogenous cells and fusiform aseptate conidia, such as *Parasarocladium* and *Sarocladium*. *Myrotheciomycetaceae* was introduced by Crous *et al.* (2018b) with the type genus *Myrotheciomyces.* The family, which appeared as a monophyletic distinct lineage in a phylogeny based on LSU sequences, is characterized by the presence of phialidic conidiogenous cells, as well as 0–1-septate conidia aggregated in a slimy mass. These authors also included the asexual genera *Emericellopsis*, *Leucosphaerina*, and *Trichothecium* into this family, which previously classified as *Hypocreales* incertae sedis. However, recent phylogenetic studies conducted by Hou *et al.* (2023) placed the genus *Emericellopsis* in the *Bionectriaceae.*

In addition, several new families have been recently identified through mult-gene phylogenetic analyses and morphological features. These include *Ijuhyaceae*, *Stromatonectriaceae* and *Xanthonectriaceae*, which have been segregated from *Bionectriaceae* (Perera *et al.* 2023). Additionally, two families, *Albomorchellophilaceae* and *Pseudodiploosporeaceae*, which included fungal parasites were established (Sun *et al.* 2023, Yu *et al.* 2024). Furthermore, a comprehensive study of fungal isolates from mangrove sediments allowed to establish the families *Acremoniopsiaceae* and *Sedecimiellaceae* (Li *et al.* 2023). Moreover, a recent revision of Acremonium-like fungi in *Hypocreales*, based on multi-gene phylogeny, has revealed five new hypocrealean families: *Chrysonectriaceae*, *Neoacremoniaceae*, *Nothoacremoniaceae*, *Pseudoniessliaceae* and *Valsonectriaceae* (Hou *et al.* 2023). The family delimitation within the order *Hypocreales* remains unclear due to the morphological variability of species, particularly in their asexual morphs (e.g., Acremonium-like, Clonostachys-like species) and the lack of sampling from certain geographic regions.

Lichenicolous fungi form a distinct group of fungi that showed parasitic, parasymbiotic, or saprotrophic relationships with lichens, developing sporocarps on their thalli or reproductive structures. These fungi interact with lichens in various ways, ranging from symptomless associations to more aggressive parasitism, influencing the functionality of the lichen (Lawrey & Diederich 2003, Hafellner & Obermayer 2009, Diederich *et al.* 2018, 2022, Hafellner 2018). Over 2300 species of these fungi have been described, although it is estimated that the total number could be at least twice as high. These fungi primarily belong to *Ascomycota*, with a smaller portion classified under *Basidiomycota*, and they showed a high degree of specialization toward their lichen hosts (Diederich *et al.* 2018, 2022). However, uncertainties in species boundaries can obscure the full extent of host specificity.

The exploration of poorly known groups of *Hypocreales* and specific ecological niches led to the discovery of several novel lineages, which were formally described as the families and listed above. However, further studies in some still neglected groups, including lichen-inhabiting species, may substantially contribute to our knowledge of *Hypocreales*. Lichenicolous fungi constitute a significant part of *Hypocreales* with ca 180 currently known species, which is about 7.7 % of all known lichenicolous fungi (Lawrey & Diederich 2003, Diederich *et al.* 2018). Therefore, it is essential to include a broad sampling of lichenicolous fungi in further phylogenetic studies to clarify their systematics and gain a better understanding of the evolutionary patterns associated with lifestyles in *Hypocreales*. Based on morphological and anatomical features many lichenicolous fungi in the order *Hypocreales* were assigned to *Bionectriaceae*, *Nectriaceae* and *Niessliaceae* (Rossman *et al.* 1999, Diederich *et al.* 2018). Several of these fungi were classified into previously known genera, which include fungicolous or saprotrophic species. However, recent molecular studies have revealed that some of these taxa belong to other genera and families within *Hypocreales* (Lawrey *et al.* 2015, Flakus *et al.* 2019a, Haldeman & Darmostuk 2024).

In this study, we focused on determining the phylogenetic placement of lichenicolous fungi within *Hypocreales* using a five-loci phylogeny (nuSSU, ITS, LSU, *tef1* and *rpb1*). Most of them have previously been assigned to the family *Bionectriaceae*. To achieve this aim, we reconstructed the phylogeny of the *Hypocreales* using a representative dataset containing 228 taxa. Our specific goals were as follows: i) to reconstruct a more comprehensive phylogeny of *Hypocreales*; ii) to resolve the phylogenetic placement and clarify the taxonomy of lichenicolous species from the genera *Ovicuculispora*, *Paranectria*, *Nectriopsis lichenophila*, and *Nectria byssophila*-like species; and iii) to clarify the phylogenetic relationship between the new lichenicolous lineage and other families of the order *Hypocreales*.

MATERIALS AND METHODS

Taxon sampling and morphological studies

This study is based on freshly collected material of lichenicolous species belonging to *Hypocreales*, complemented by specimens deposited at K-M, KHER, KRAM, LPB, UGDA and UPS herbaria and personal herbarium of J. Etayo (hb. Etayo). Morphological and anatomical characters were examined using standard dissecting- and compound-microscopes (Nikon SMZ 800, Nikon Eclipse 80i DIC; and Leica S9i and S9D). Sections were prepared manually using a razor blade, or freezing sliding microtome Microm HM 430 (Thermo Fisher Scientific, USA) combined with a BFS-MP freezing stage and a BFS-3MP controller. Sections and squash mounts were examined in distilled water, 10 % KOH (K) or lactophenol cotton blue (LPCB; Fluka, no. 61335-100ML). 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). All measurements were made in distilled water or LPCB. Measurements are given as (min.–)x–SD–x+SD(–max.), where x is the average and SD is the standard deviation.

DNA extraction, PCR amplification, and DNA sequencing

Lichen thalli with ascomata of lichenicolous fungi were stored at -20 °C until processing. The ascomata 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. Genomic DNA was extracted from 4 to 10 clean ascomata or hymenia, depending on each specimen, using the QIAamp DNA Investigator Kit (Qiagen, Germany), the E.Z.N.A Forensic DNA Isolation kit (Omega Bio-Tek) or the DNeasy Plant Mini Kit following the manufacturer's instructions. We amplified and sequenced the small ribosomal subunit nuc rDNA (nuSSU) using primer pair N24 and NS1 (White *et al.* 1990, Gargas & Taylor 1992), nuc rDNA internal transcriber spacers (ITS = ITS1+5.8S+ITS2) and nuc rDNA large subunit (LSU) using the primer pairs ITS1F and LR5 or ITS1F/ITS4 and LROR/LR5 (White *et al.* 1990, Gardes & Bruns 1993), a fragment of the region coding for protein synthesis elongation factor 1 alpha (*tef1*) with the primer pair EF1-1983F and EF1-2228R (Rehner & Samuels 1995) and a fragment of the region coding for the RNA polymerase largest subunit (*rpb1*) using the primers pair RPB1cf and RPB1Af (Stiller & Hall 1997). The 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.* (2019a). The PCR amplicons were sequenced in both directions by Macrogen (Amsterdam, the Netherlands or Madrid, Spain). The newly generated sequences were carefully checked, assembled, and edited manually using Geneious Pro v. 8.0. (Biomatters Ltd) and deposited in GenBank. Detailed information on the sequences used in this study is provided in Table 1.

Phylogenetic analyses and taxon selection

All sequences generated were firstly checked by BLAST nucleotides searches (Altschul *et al.* 1990) to discard potential contaminations by any unrelated fungi. Alignments for each region were generated using MAFFT (Katoh & Standley 2013) implemented on the GUIDANCE2 Web server (Penn *et al.* 2010). We used the default cut-off score of 0.93 in all single gene alignments. The single-locus phylogenies for all loci were generated (results not shown) to detect topology incongruences. The intron regions of nuSSU were delimited and removed from the alignment manually. The coding domain sequence (CDS) of the protein-coding regions were detected by Augustus web-tool (Stanke *et al.* 2008). Two multi-locus datasets were assembled:

1) the *Hypocreales* order-wide matrix (LSU+*tef1*+*rpb1* +*rpb2*+*tub2*), to reveal the phylogenetic placement and relationship of target group of lichenicolous species with other *Hypocreales* fungi. The dataset includes representatives of all families of the order, e.g. 321 specimens of 228 species, with four species from the order *Sordariales* selected as outgroup taxa, e.g. *Achaetomium macrosporum*, *Chaetomium elatum*, *Neurospora crassa* and *N. tetrasperma* (available at https://doi.org/10.6084/m9.figshare.25324963);

2) the *Paranectriaceae* multi-gene matrix (5.8S+LSU +nuSSU+*tef1*+*rpb1*), to delimit species and elucidate their relationships within the *Paranectriaceae*. The dataset included target lichenicolous specimens (28 specimens of 9 species), as well as representatives of the *Cylindromonium-Trichonectria* clade (10 specimens of 6 species). Three specimens of the *Niessliaceae* selected as outgroup taxa (available at https://doi.org/10.6084/m9.figshare.25324936).

PartitionFinder 2 (Lanfear *et al.* 2017) was used to select the best partition scheme for our dataset and substitution models for each partition. The single substitution model was selected for each region for two datasets under a greedy search algorithm and the Akaike information criterion (AIC) (Lanfear *et al.* 2012). For the four protein-coding gene regions (*tef1*, *rpb1*, *rpb2* and *tub2*), each codon position was analysed as a distinct partition, the first, second and third codon position. The final partition scheme used in the analyses is presented in Table 2.

Maximum Likelihood (ML) analyses were carried out using a heuristic search as implemented in IQ-TREE v. 2.1.2 on the CIPRES Science Gateway (Ronquist *et al.* 2012) and 1000 ultrafast bootstrap replicates were selected to estimate branch support (Nguyen *et al.* 2015, Minh *et al.* 2020). The Bayesian inference (BI) phylogenetic tree was generated in MrBayes v. 3.2.6 on the CIPRES Science Gateway (Ronquist *et al.* 2012) using the partitions and substitution models obtained by PartitionFinder v. 2. The posterior probabilities were calculated by sampling trees using the Markov chain Monte Carlo (MCMC) approach. Two independent parallel runs were started each with four incrementally heated chains (temperature parameter for MCMC chains was 0.15). This MCMC was allowed to run for 100 million generations, sampling every 1000th tree and discarding the first 50 % of the sampled tree as a burn-in factor. The analysis was stopped when the standard deviation of split frequencies had dropped below 0.01. The resulting ML and BI phylogenetic trees were visualized in FigTree v. 1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/) and Inkscape v. 1.4 (https://inkscape.org/).

RESULTS

Phylogenetic relationship of *Hypocreales* at the family level

In this study, 115 new sequences from 35 specimens of lichenicolous fungi were generated (22 of nuSSU, 28 of ITS, 27 of LSU, 22 of *tef1* and 16 of *rpb1*). The combined *Hypocreales* order-wide matrix consisted of 4 584 characters (843 of LSU, 1065 of *tef1*, 669 of *rpb1*, 1101 of *rpb2*, 906 of *tub2*), of which 2053 are parsimony-informative sites, 392 singleton sites and 2139 constant sites. The order-level backbone tree of *Hypocreales* (Fig. 1) showed similar topology from ML and BI analyses and therefore the ML tree was selected to represent and discuss the phylogenetic relationships among taxa.

Our *Hypocreales* order-wide phylogenetic matrix based on five genomic regions showed high support (bootstrap, bp/posterior probability, pp – 100/1) for the ingroup of 228 *Hypocreales* species. This clade further consisted of 29 well-supported subclades, which corresponded to the 27 families previously recognized in the order (Hyde *et al.* 2020, Hou *et al.* 2023, Li *et al.* 2023, Perera *et al.* 2023, Xiao *et al.* 2023) and two of these subclades represent the *Cylindromonium-*

Table 1. GenBank accession numbers for Hypocrealaes sequences used in the phylogenetic analyses. Sequences newly generated in this study are shown in bold. The asterisk indicates type materials. Voucher specimen includes collector, collector number, herbarium or culture collection and isolation number.

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
Achroiostachys humicola	CBS 868.73*	Turkey	soil	—	—	KU845819	KU845854	—	KU845837	KU845760
	DAOM 226830	Canada	soil	—	—	KU845822	KU845857	—	KU845838	KU845763
Acremoniopsis suttonii	CBS 138708*	Spain	soil	—	—	MH877666	OQ470733	—	OQ453831	—
Acremonium rutilum	CBS 396.66*	Germany	moist greenhouse wall	—	—	HQ232124	OQ471142	—	—	—
	CBS 229.70	Germany	moist greenhouse wall	—	—	MH871348	OQ471141	—	—	—
Akanthomyces lecanii	CBS 101247	West Indies	*Coccus viridis*	—	—	KM283794	—	DQ522407	KM283859	—
Akanthomyces tuberculatus	OSC 111002	n/a	*Lepidoptera*	—	—	DQ518767	DQ522338	DQ522384	DQ522435	DQ522499
Albomorchellophila morchellae	KUNCC21-10005*	China	*Morchella* sp.	—	—	OP580862	OP585424	—	—	—
	KUNCC21-10100	China	*Morchella* sp.	—	—	OR420021	OR420838	—	—	—
Albonectria rigidiuscula	CBS 315.73	Malaysia	*Theobroma cacao*	—	—	KM231677	KM231938	KM232229	KM232378	KM232071
	CBS 122570	Cameroon	bark	—	—	KM231676	KM231937	KM232228	KM232377	KM232070
Allantonectria miltina	CBS 121121	Italy	*Agave americana*	—	—	HM484572	HM484524	HM484587	KM232409	HM484609
	CBS 474.69	Spain	*Agave americana*	—	—	KM231716	KM231973	KM232269	KM232408	—
Aquanectria penicillioides	CBS 257.54	USA	*Acer* sp., leaf	—	—	MH868856	KM231865	KM232135	KM232299	—
Aquanectria submersus	CBS 394.62*	UK	unknown	—	—	KM231612	—	KM232134	HQ897728	KM231999
Aschersonia calendulina	SM 00186.01	Thailand	leaves	—	—	JN940909	—	JN987887	—	—
Balansia claviceps	CBS 501.70	India	*Cyrtococcum oxyphyllum*	—	—	MH871588	—	—	—	—
Balansia pilulaeformis	AEG 94-2	n/a	n/a	—	—	AF543788	DQ522319	DQ522365	DQ522414	—
Beauveria brongniartii	ARSEF 617*	France	*Melolontha melolontha*	—	—	—	HQ880991	HQ880854	HQ880926	—
	BCC 16585	n/a	*Anomala cuprea*	—	—	JF415967	JF416009	JN049885	JF415991	—
Beauveria scarabaeidicola	ARSEF 5689	n/a	*Scarabaeidae*	—	—	AF339524	DQ522335	DQ522380	DQ522431	DQ522496
Bisifusarium dimerum	CBS 108944*	Netherlands	human	—	—	JQ434514	KR673912	KM232212	KM231919	EU926400
Bisifusarium nectrioides	CBS 176.31	Honduras	humus	—	—	EU926245	EU926312	JX171477	JX171591	EU926378
Brevistachys subsimplex	ATCC 32888	USA	water hyacinth	—	—	AY489711	AY489606	AY489639	EF692519	—
Bullanockia australis	CPC 28976	Australia	*Kingia australis*	—	—	KY173506	OQ470804	—	OQ451835	—
Caespitomonium euphorbiae	CBS 147075*	Namibia	*Euphorbia* sp.	—	—	OK663737	OK651197	—	OK651157	OK651201
Caespitomonium hyalinulum	CBS 271.36	USA	air in hospital	—	—	HQ232045	—	—	—	—
Calcarisporium arbuscula	CBS 144.52	UK	*Russula* sp.	—	—	MH868488	—	—	—	—
	CBS 518.66	Netherlands	*Boletus* sp.	—	—	MH870517	—	—	—	—

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
	CBS 900.68	Germany	decayed agaric fungi	—	—	KX442598	KX442596	—	KX442597	—
Calcarisporium cordycipiticola	CGMCC 3.17904	China	*Cordyceps militaris*	—	—	KX442604	KX442605	—	KX442607	—
	CGMCC 3.17905*	China	*Cordyceps militaris*	—	—	KX442599	KX442593	—	KX442594	—
Calcarisporium xylariicola	HMAS 276836*	Italy	*Xylaria* sp.	—	—	KX442601	KX442595	—	KX442600	—
Calonectria brassicae	CBS 111869	Indonesia	*Argyreia splendens*	—	—	GQ280698	FJ918567	KM232181	KM232308	AF232857
Calonectria daldiniana	CBS 749.70*	Netherlands	*Ilex aquifolium*, leaf litter	—	—	GQ280706	GQ267312	—	—	—
Calostilbe striispora	CBS 133491	French Guiana	bark	—	—	KM231653	KM231918	KM232204	KM232361	KM232048
Campylocarpon fasciculare	CBS 112613*	South Africa	*Vitis vinifera*	—	—	HM364313	JF735691	HM364331	KM232322	AY677221
Campylocarpon pseudofasciculare	CBS 112679*	South Africa	*Vitis vinifera*	—	—	HM364314	JF735692	HM364332	KM232323	AY677214
Capitofimbria compacta	CBS 111739*	Brazil	rotten leaf	—	—	MH874460	KU846378	-	KU846349	KU846404
Chaetomium elatum	CBS 374.66	USA	decomposing leaf	—	—	MH870466	KF001730	KF001775	KF001820	KC109776
Chaetopsina fulva	CBS 142.56*	Italy	*Cedrus deodara*	—	—	KM231637	KM231902	KM232188	—	—
	CBS 137301	Spain	dead leaves	—	—	KY853492	—	—	—	—
Chrysonectria crystallifera	CBS 102567*	Japan	*Monstera* sp.	—	—	OQ055444	OQ470825	—	OQ453920	—
Chrysonectria finisterrensis	JPP17021*	France	*Quercus* sp.	—	—	MF611689	—	—	—	—
Ciliomyces oropensis	**Darmostuk 957**	**Ukraine**	***Lecania croatica***	—	**PP513162**	**PP513187**	**PP583632**	—	—	—
	Etayo 29106	**Spain**	***Parmelina tiliacea***	**PP513209**	**PP513163**	**PP513188**	—	**PP594991**	—	—
	Flakus 26387	**Bolivia**	***Normandina pulchella***	**PP513210**	**PP513164**	**PP513189**	**PP583633**	**PP594992**	—	—
	Etayo 31139	**Spain**	***Physconia perisediosa***	—	**PP513224**	**PP513228**	**PQ031220**	—	—	—
	Etayo 31593	**Spain**	***Anaptychia ciliaris***	—	**PP513225**	**PP513229**	—	—	—	—
	Etayo 31861	**Spain**	***Hypotrachyna revoluta***	—	**PQ012595**	**PQ012597**	—	—	—	—
Cladobotryum asterophorum	CBS 676.77*	Japan	agaric	—	—	AJ583469	FN868712	FN868776	FN868649	—
Cladobotryum penicillatum	CBS 407.80*	Netherlands	*Sebacina effusa*	—	—	MH873046	FN868725	FN868788	FN868661	—
Claviceps fusiformis	ATCC 26019	n/a	*Poaceae*	—	—	U17402	DQ522320	DQ522366	—	DQ522477
Claviceps paspali	ATCC 13892	n/a	*Poaceae*	—	—	U47826	DQ522321	DQ522367	DQ522416	—
Clonostachys miodochialis	CBS 997.69*	Netherlands	agricultural soil	—	—	MH871287	OQ944658	—	OQ927715	OQ982677
Clonostachys rosea	CBS 114056	Venezuela	bark	—	—	AY489176	AY489611	—	DQ522415	DQ522476
Coccinonectria pachysandricola	CBS 501.63*	Germany	*Pachysandra terminalis*	—	—	KM231640	KM231905	KM232190	KM232350	KM232033

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
	CBS 476.92	Netherlands	*Pachysandra terminalis*	—	—	KM231641	KM231906	KM232191	MH936693	KM232034
Cocoonihabitus sinensis	voucher 8039*	China	cocoon of *Saturniidae*	—	—	KY924869	—	—	—	—
	voucher 9880	China	cocoon of *Saturniidae*	—	—	MF687396	—	—	—	—
Collarina aurantiaca	CBS 138274*	Spain	sediments	—	—	MH877656	—	—	OQ560707	—
	CBS 110646	Netherlands	Reed sandy soil	—	—	OQ055447	OQ470828	—	—	—
Corallocytostroma ornithocopreoides	WAC 8705	Australia	*Astrebla pectinata*	—	—	—	LT216546	—	LT216598	FJ711476
Corallonectria jatrophae	CBS 913.96*	Puerto Rico	tree	—	—	KM231611	KM231863	KM232132	KM232298	KC479787
Cordyceps militaris	YFCC 6587	China	n/a	—	—	MN576818	MN576988	MN576878	MN576932	—
Cordyceps subtenuipes	YFCC 6051*	China	*Lepidoptera*	—	—	MN576775	MN576945	MN576835	MN576891	—
Cosmospora arxii	CBS 748.69	Germany	*Hypoxylon* sp.	—	—	KM231694	KM231950	KM232245	—	—
Cosmospora coccinea	CBS 343.70	Germany	*Inonotus radiatus*	—	—	MH871456	—	—	—	—
	CBS 341.70	Germany	*Inonotus nodulosus*	—	—	KM231692	KM231947	KM232242	HQ897777	KM232086
Cosmospora khandalensis	AR 4770	Argentina	*Annulohypoxylon* sp.	—	—	KJ676180	—	KJ676217	—	KJ676256
Cosmosporella cavisperma	CBS 172.31*	Norway	*Pinus sylvestris*	—	—	MW827645	—	JX171465	MW834000	—
Curvicladiella cignea	CBS 109167*	French Guiana	leaf litter	—	—	—	KM231867	KM232142	KM232311	KM232002
Cyanonectria buxi	CBS 130.97	France	*Buxus sempervirens*	—	—	KM231679	HQ728150	KM232233	HM626690	KM232075
Cyanonectria cyanostoma	CBS 115512*	France	*Buxus sempervirens*	—	—	MH874353	HM626647	GQ506017	HQ897759	HM484611
Cylindrocladiella camelliae	CPC 234	South Africa	*Eucalyptus grandis*	—	—	JN099249	JN099087	KM232139	KM232304	AY793471
Cylindrocladiella lageniformis	CBS 340.92*	Brazil	*Eucalyptus* sp	—	—	JN099165	JN099003	JN989491	KM232303	—
Cylindromonium eugeniicola	CBS 146075*	South Africa	*Eugenia capensis*	—	MN562142	MN567649	OQ470832	—	OQ560710	—
Cylindromonium everniae	CPC 40760*	Netherlands	*Evernia prunastri*	—	OK664736	OK663775	OK651192	—	OK651171	—
Cylindromonium lichenicola	CBS 303.70	Germany	*Alnus glutinosa*, on bark	—	MH859675	MH871429	OQ470833	—	OQ453927	—
	CBS 415.70A	Netherlands	*Desmococcus* sp., on bark	—	MH859774	MH871536	—	—	—	—
Cylindromonium rhabdosporum	CBS 438.66*	Austria	old *Cladonia furcata*	—	MH858850	HQ232120	OQ470835	—	OQ453929	—
Dactylonectria macrodidyma	CBS 112615*	South Africa	*Vitis vinifera*	—	—	KM515900	JF268750	HM364333	JF268710	AY677233
Didymostilbe aurantiospora	CBS 616.85*	Japan	*Arenga tremula*, petioles	—	—	MH873595	—	—	—	—
Elaphocordyceps fracta	OSC 110990	n/a	n/a	—	—	DQ518759	DQ522328	DQ522373	DQ522425	DQ522487

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
Elaphocordyceps japonica	OSC 110991	n/a	n/a	—	—	DQ518761	DQ522330	DQ522375	DQ522428	DQ522490
Eucasphaeria capensis	CBS 120028*	South Africa	*Eucalyptus* sp., living leaves	—	—	MH874626	OQ470896	—	OQ453986	—
	CBS 120027	South Africa	*Eucalyptus* sp., living leaves	—	—	MH874625	OQ470897	—	OQ453987	—
Eucasphaeria protea	CBS 146815*	South Africa	*Protea neriifolia*	—	—	MW175397	MW173129	—	MW173116	—
Eucasphaeria rustici	CBS 142085*	Australia	*Eucalyptus creta*, leaves	—	—	KY173501	OQ470898	—	OQ453988	—
Flammocladiella anomiae	CBS 142775	Bulgaria	*Massaria anomia*	—	—	MN597426	MW890089	—	MW890062	MW890128
	CBS 144256*	France	*Massaria anomia*	—	—	MN597425	MW890090	—	MW890090	MW890129
	SOMF 30203	Bulgaria	*Massaria anomia*	—	—	MN597424	—	—	—	—
Flammocladiella decora	CLL16020	France	*Massaria inquinans*	—	—	MF614949	OQ470901	—	—	—
	CBS 138906	Germany	*Acer platanoides*, twigs	—	—	KR611901	MW890088	—	MW890061	MW890127
Fusariella atrovirens	CBS 311.73	Algeria	desert soil	—	—	MH872395	OQ470904	—	OQ453993	—
Fusariella hughesii	CBS 435.70	Netherlands	agricultural soil	—	—	MH871547	OQ470906	—	OQ453995	—
Fusicolla melogrammae	CBS 141092*	UK	*Melogramma campylosporum*	—	—	KY092489	—	—	—	MW834305
Fusicolla violacea	CBS 634.76*	Iran	*Diaspidiotus perniciosus*	—	—	KM231700	KM231956	KM232251	HQ897696	KM232095
Geejayessia atrofusca	CBS 125482	Canada	*Staphylea trifolia*, twigs	—	—	MH875066	MW834282	MW834196	HQ897775	—
Geejayessia celtidicola	CBS 125502*	Canada	*Celtis occidentalis*, twigs	—	—	HM626669	HM626638	KM232232	HM626685	KM232074
Gelasinospora tetrasperma	CBS 178.33	Canada	dung of *Lagopus* sp., grouse	—	—	DQ470980	—	DQ471178	DQ470932	—
Gliomastix murorum	CBS 154.25*	n/a	*Malus sylvestris*	—	—	HQ232063	OQ470923	—	OQ454012	—
	CBS 127397	USA	n/a	—	—	MH876020	—	—	—	—
Gliomastix tumulicola	CBS 127532*	Japan	white salt-like masses on painting	—	—	OQ055547	OQ470950	—	OQ454039	—
	K5916-10-3	Japan	viscous substances on the stone wall	—	—	AB540476	—	—	—	—
Grandibotrys hyalinus	MFLUCC 17-1076*	Thailand	decaying wood	—	—	MF346064	—	—	—	—
Grandibotrys pseudotheobromae	CBS 136170*	Nepal	decaying wood	—	—	KU846161	KU846216	—	KU846188	KU846241
Grandibotrys xylophila	CBS 136179*	Nepal	decaying wood	—	—	KU846163	KU846217	—	KU846190	—
Gregatothecium humicola	CBS 205.96*	Papua New Guinea	soil	—	—	KU846347	KU846402	—	KU846376	KU846432

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
Heleococcum aurantiacum	CBS 201.35	n/a	mushroom compost	—	—	JX158441	JX158397	—	JX158463	—
Heteroacremonium album	CGMCC 3.22405*	China	sediment	—	—	OQ758137	OQ809041	—	OQ809001	—
	CGMCC 3.22409	China	sediment	—	—	OQ758138	OQ809042	—	OQ809002	—
Heteroacremonium rugosum	CGMCC 3.22520*	China	sediment	—	—	OQ758139	OQ809043	—	OQ809003	—
Hevansia novoguineensis	NHJ 11923	n/a	Spider (*Arachnida*)	—	—	EU369032	EU369013	EU369052	EU369072	—
Hirsutella thompsonii	ARSEF 2800	USA	*Acari*	—	—	KM652142	KM652023	KM652058	—	—
	ARSEF 3323	Costa Rica	*Dolichotetranychus floridanus*	—	—	KM652143	KM652024	KM652059	—	—
Hydropisphaera peziza	BPI 802846	USA	bark	—	—	AY489730	AY489625	AY489661	DQ522444	—
	CBS 123792	Netherlands	n/a	—	—	MH874857	—	—	—	—
Hypocrella discoidea	BCC 8237	n/a	n/a	—	—	DQ384937	DQ384977	DQ385000	DQ452461	—
Hypomyces semitranslucens	CBS 458.71	Russia	*Lentinus* sp.	—	—	MH871985	—	—	—	—
Ijuhya chilensis	CBS 102803	USA	*Nolina micrantha*	—	—	KY607553	—	KY607579	—	KY684187
Ijuhya paraparilis	MAFF241404	Japan	n/a	—	—	GQ506012	—	GQ506041	—	—
Ilyonectria capensis	CBS 132815*	South Africa	*Protea* sp.	—	—	KM515908	JX231119	KM232171	KM232336	JX231103
Ilyonectria destructans	CBS 264.65	Sweden	*Cyclamen persicum*	—	—	KM515927	JF735695	KM232169	KM232334	—
Lasionectria lecanodes	CBS 139482	France	*Peltigera* sp.	—	—	KP899119	—	—	—	—
Lasionectria mantuana	A.R. 4029	Finland	n/a	—	—	GQ505994	HM484844	GQ506024	—	—
	CBS 114291*	Finland	decortivated wood	—	—	OQ055596	OQ471001	—	OQ454092	—
Lichenobarya usneae	Buck 61451	Canada	dead *Usnea*	—	—	KP899625	—	—	—	—
Macroconia leptosphaeriae	CBS 717.74	France	*Sordariomycetes* sp.	—	—	KM231707	—	KM232257	KM232390	KM232099
Macroconia papilionacearum	CBS 125495	USA	*Ascomycota* sp.	—	—	KM231704	KM231958	KM232254	HQ897776	KM232096
Mariannaea humicola	CBS 740.95*	Brazil	soil	—	—	KM231619	KM231880	KM232153	KM232328	KM232012
Mariannaea elegans	HU0029*	Netherlands	*Pinus sylvestris*, decayed bark	—	—	KX986139	—	—	—	KX986145
Melanopsamma pomiformis	BPI843533	UK	*Ulmus* sp.	—	—	AY489709	AY489604	AY489637	EF692511	—
	UAMH 10484	Canada	dead twig	—	—	—	DQ676611	—	DQ676598	—
	CBS 101322*	Czech Republic	*Fagus sylvatica*	—	—	KU846068	—	—	KU846078	—
Memnoniella echinata	CBS 216.32*	UK	cotton yarn	—	—	KU846169	KU846222	—	KU846196	KU846245
Metapochonia bulbillosa	CBS 145.70*	Denmark	*Picea abies*, root 7.5 mm thick	—	—	AF339542	EF468796	EF468902	EF468943	—
Metapochonia goniodes	CBS 891.72*	Germany	*Pulcherricium caeruleum*	—	—	AF339550	DQ522354	DQ522458	DQ522401	DQ522521

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
Metarhizium blattodeae	MY 00896	Thailand	*Blattodea*	—	—	HQ165719	HQ165678	HQ165739	HQ165638	—
Metarhizium ellipsoideum	BCC 49285*	Thailand	*Hemiptera* adult	—	—	MN781858	MN781713	MN781759	MN781808	—
Microcera coccophila	CBS 310.34	Italy	scale insect	—	—	KM231703	JF740692	JX171462	HQ897705	—
Microcera larvarum	CBS 738.79*	Iran	*Diaspidiotus perniciosus*	—	—	KM231701	KM231957	KM232252	KM232387	—
Microcera physciae	CPC 41038*	Netherlands	*Physcia tenella*	—	—	OK663767	OK651191	OK651154	OK651169	OK651209
Microcera rubra	CBS 638.76*	Iran	*Diaspidiotus perniciosus*	—	—	KM231702	JF740696	KM232253	HQ897767	EU860019
Moelleriella oxystoma	BCC 8406	n/a	n/a	—	—	DQ384943	DQ384978	DQ384993	DQ452468	—
Mycogone rosea	YBM050	China	*Agaricus bisporus*	—	—	MW475168	MW014059	—	MW486042	MW397569
Myrotheciomyces corymbiae	CPC 33206*	Australia	*Corymbia variegata*	—	—	MH327837	OQ471031	—	—	—
Myrothecium cylindrosporum	MFLU 14-0823*	Thailand	*Bambusae*	—	—	KP744491	—	—	—	—
Myrothecium inundatum	CBS 616.70	Canada	leaf litter	—	—	MH871662	—	—	—	KU846534
	BPI843536	UK	*Russula nigricans*	—	—	AY489731	AY489626	—	—	—
Myxospora masonii	CBS 174.73*	UK	*Glyceria* sp.	—	—	KU846484	KU846523	—	KU846500	KU846543
Nectria cinnabarina	CBS 125165*	France	*Aesculus* sp.	—	—	KM231715	HM484527	HM484577	KM232402	HM484606
Nectria mariae	CBS 125294*	France	*Buxus sempervirens*	—	—	JF832684	JF832542	JF832789	KM232404	JF832899
Nectria nigrescens	CBS 125148	USA	dicotyledonous tree	—	—	HM484720	HM484672	HM484781	KM232403	HM484806
Nectriopsis exigua	BPI 748377	Puerto Rico	myxomicetes	—	—	GQ505986	HM484852	GQ506014	—	HM484883
Nectriopsis lindauiana	CBS 839.70	Germany	*Fuligo septica*	—	—	KU382229	—	—	—	—
	CBS 897.70*	Germany	*Fuligo septica*	—	—	OQ055629	OQ471042	—	OQ454132	—
Nectriopsis violacea	CBS 849.70	Germany	*Fuligo septica*	—	—	MH871773	OQ471047	—	OQ454137	—
	CBS 914.70*	Germany	*Fuligo septica*	—	—	OQ055632	OQ471048	—	OQ454138	—
Neoacremonium distortum	CBS 314.72*	Netherlands	soil under *Phragmites australis*	—	—	OQ055634	OQ471050	—	OQ454140	—
	CBS 665.75	Netherlands	aerial contaminant	—	—	OQ055635	OQ471051	—	OQ454141	—
Neoacremonium flavum	CBS 398.70	Netherlands	*Chamaerops humilis*	—	—	OQ055641	OQ471058	—	OQ454148	—
	CBS 452.70*	Netherlands	*Musa* sp.	—	—	OQ055640	OQ471057	—	OQ454147	—
Neoacremonium vitellinum	CBS 792.69*	Netherlands	*Phoenix dactylifera*	—	—	OQ055643	OQ471060	—	OQ454150	—
	CBS 793.69	Netherlands	*Phoenix dactylifera*	—	—	OQ055644	OQ471061	—	OQ454151	—
Neobarya parasitica	Marson s/n	Luxembourg	*Bertia*	—	—	KP899626	—	—	—	—
Neobarya sp.	Buck 26786 (F)	Brazil	*Bertia*	—	—	AY346293	—	—	—	—
Neobaryopsis andensis	Flakus 25967.1*	Bolivia	*Lobariella pallida*	—	MT153956	MT153985	**PP583634**	**PP594993**	—	—

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
	Flakus 25967.2*	Bolivia	*Lobariella pallida*	—	MT153957	MT153986	—	—	—	—
	Etayo 20-11 (LPB)	Bolivia	*Lobariella pallida*	—	MT153958	MT153987	—	—	—	—
Neocosmospora ambrosia	CBS 571.94*	India	*Camellia sinensis*	—	—	KM231668	KM231929	KM232220	KM232368	KM232063
Neocosmospora illudens	CBS 147303	n/a	n/a	—	—	AF178362	AF178326	JX171488	JX171601	—
Neocosmospora vasinfecta	CBS 325.54	South Africa	soil	—	—	AF178381	AF178348	JX171497	JX171610	KM232065
Neoeucasphaeria eucalypti	CBS 145075*	Australia	*Eucalyptus* sp.	—	—	MK047495	—	—	OQ454152	—
Neonectria faginata	CBS 217.67*	Canada	*Fagus grandifolia*	—	—	HQ840382	JF268746	—	DQ789797	JF268730
Neonectria neomacrospora	CBS 118984	Canada	*Abies balsamea*	—	—	HQ840379	JF268754	HQ840401	DQ789810	DQ789882
Neonectria ramulariae	CBS 151.29	UK	*Malus sylvestris*, fruit	—	—	AY677333	JN131772	HQ840403	DQ789792	JF735438
Neurospora crassa	ICMP 6360	n/a	n/a	—	—	AY681158	—	—	—	AY681226
Niesslia cladoniicola	CBS 960.73*	UK	*Cladonia rangiformis*	—	—	MG826850	MG896370	—	—	—
Niesslia constricta	CBS 760.69*	Netherlands	bark of *Pinus sylvestris*	—	—	MG826839	MG896401	—	—	—
Niesslia exilis	CBS 357.70	Germany	bark of *Picea abies*	—	—	MG826775	MG896368	—	OQ454154	—
	CBS 560.74	UK	*Pinus sylvestris*, needle	—	—	MG826806	MG896434	—	—	—
Niesslia nordinii	CBS 101.63*	Canada	*Pinus contorta*	—	—	MG826720	MG896398	—	—	—
	CBS 116.70	Canada	*Pinus contorta*, wood	—	—	MG826731	MG896399	—	—	MG896231
Nothoacremoniopsis sedimenticola	CGMCC 3.22383*	China	sediment	—	—	OQ758148	OQ809050	—	OQ809012	—
	CGMCC 3.22385	China	sediment	—	—	OQ758149	OQ809051	—	OQ809013	—
Nothoacremonium exiguum	CBS 587.73*	Sri Lanka	*Tubulicium dussii* on *Dicksonia antarctica*	—	—	OQ055647	OQ471073	—	OQ454159	—
Nothoacremonium subcylindricum	CBS 416.68*	Netherlands	skin and nail of man	—	—	OQ055648	OQ471074	—	OQ454160	—
	CBS 781.69	USA	deformed toe nail	—	—	OQ055649	OQ471075	—	OQ454161	—
	CBS 190.70	Germany	decaying wood	—	—	OQ055651	OQ471077	—	OQ454163	—
Nothoacremonium vesiculophorum	CBS 397.70B*	Netherlands	*Cladium mariscus*	—	—	OQ055652	OQ471078	—	OQ454164	—
Ochronectria calami	ATCC46692	USA	n/a	—	—	AF193243	—	—	—	—
	CBS 445.96	Puerto Rico	palm	—	—	OQ055653	OQ471079	—	OQ454165	—
Ochronectria thailandica	MFLUCC 15-0140*	Thailand	wood in the water	—	—	KU564069	—	—	—	—
Ophiocordyceps heteropoda	EFCC 10125	n/a	*Paraisaria heteropoda*	—	—	EF468812	EF468752	EF468860	EF468914	—
	OSC 106404	Australia	*Paraisaria heteropoda*	—	—	AY489722	AY489617	AY489651	-	—
Ophiocordyceps lanpingensis	YHOS0705	China	*Hepialidae* larva	—	—	KC417460	KC417462	KC417464	KC456333	—

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
Ophiocordyceps sinensis	EFCC 7287	n/a	Lepidopteran pupa	—	—	EF468827	EF468767	EF468874	EF468924	—
Ovicuculispora* cf. *macrospora	**Flakus 29171**	**Bolivia**	**sterile lichen**	**PP513212**	**PP513166**	**PP513191**	—	—	—	—
	Flakus 29165	**Bolivia**	**sterile lichen**	**PP513211**	**PP513165**	**PP513190**	**PP583635**	—	—	—
Ovicuculispora parmeliae	**LE261143**	**Russia**	***Heterodermia* cf. *obscura***	—	**PP513226**	**PP513230**	—	—	—	—
	Flakus 27067	**Bolivia**	***Remototrachyna* cf. *costaricensis***	—	**PP513172**	**PP513195**	**PP583638**	—	—	—
	Flakus 26009	**Bolivia**	***Sticta* sp.**	**PP513213**	**PP513167**	**PP513192**	—	**PP594994**	—	—
	Flakus 26252	**Bolivia**	***Hypotrachyna* sp.**	**PP513214**	**PP513170**	**PP513193**	**PP583636**	**PP594995**	—	—
	Flakus 27025	**Bolivia**	***Crocodia aurea***	**PP513215**	**PP513171**	**PP513194**	**PP583637**	**PP594996**	—	—
	Flakus 26011	**Bolivia**	***Sticta* sp.**	—	**PP513169**	—	—	—	—	—
	Flakus 26010	**Bolivia**	***Sticta* sp.**	—	**PP513168**	—	—	—	—	—
Paracremonium apiculatum	CGMCC3.19309*	China	soil	—	—	MK329028	MK336058	—	—	MK336136
Paracremonium inflatum	CBS 485.77*	India	human	—	—	HQ232113	KM231964	KM232260	KM232394	KM232101
Paracylindrocarpon aloicola	CBS 141300*	South Africa	*Aloe* sp., leaves	—	—	KX228328	OQ471089	—	OQ454174	—
Paracylindrocarpon nabanheensis	KUMCC 16-0147*	China	*Pandanaceae*	—	—	MH376730	MH388392	—	—	—
Paracylindrocarpon pandanicola	KUMCC 17-0272*	Hong Kong	*Pandanaceae*	—	—	MH376731	MH388393	—	—	—
Paranectria affinis	**K-M 253675**	**UK**	***Ephebe lanata***	**PP508343**	**PP513227**	**PP513231**	**PQ449050**	—	—	—
	UPS F-561663	**Sweden**	***Ephebe lanata***	—	**PP513173**	**PP513196**	—	—	—	—
Parasarocladium debruynii	CBS 144942*	Netherlands	soil	—	—	MK069416	MK069410	—	OQ454197	MK069407
Parasarocladium radiatum	CBS 142.62*	India	soil	—	—	HQ232104	OQ471308	—	OQ454200	—
Parasarocladium tasmanniae	CPC 38162*	Australia	*Tasmannia insipida*	—	—	MW175380	MW173121	—	—	MW173134
Parvothecium terrestre	CBS 198.89*	Brazil	soil	—	—	MH873856	KU846528	—	KU846506	KU846548
Peethambara spirostriata	CBS 110115	Ecuador	*Theobroma cacao*	—	—	AY489724	AY489619	AY489654	KU847293	KU847334
Peethambara sundara	CBS 646.77*	India	*Macaranga indica*, twig	—	—	MH872865	KU846531	—	KU846509	KU846551
Polycephalomyces formosus	CGMCC 5.2205	n/a	n/a	—	—	MN586841	MN598056	MN598047	MN598063	—
	NBRC 100686	Japan	n/a	—	—	AB925959	—	—	—	—
	CGMCC 5.2206	n/a	n/a	—	—	MN586842	MN598057	MN598048	MN598064	—
Pronectria robergei	CBS 128021	Luxembourg	*Peltigera* sp.	—	—	MH876199	—	—	—	—
Protocrea farinosa	TFC 97-168	n/a	n/a	—	—	EU754022	EU703896	—	EU703941	—
Protocrea pallida	TFC 99-209	n/a	n/a	—	—	EU710769	EU703902	—	EU703949	—

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
Protocreopsis freycinetiae	CBS 573.76*	New Zealand	*Freycinetia banksii*, leaves	—	—	MH872776	OQ471132	—	OQ451837	—
Pseudocosmospora eutypellae	CBS 133966*	USA	*Eutypella* sp.	—	—	KC291757	—	KC291871	—	KC291912
	G.J.S. 10-294	USA	*Eutypella* sp.	—	—	KC291773	—	KC291873	—	KC291910
Pseudodiploospora longispora	CGMCC 3.23771	China	*Morchella* sp.	—	—	OP231751	OP265139	—	OP243573	—
	KUNCC21-10026	China	*Morchella* sp.	—	—	OP580848	OP585410	—	—	—
	KUNCC21-10027	China	*Morchella* sp.	—	—	OP580849	OP585411	—	—	—
	KUNCC21-10020	China	*Morchella* sp.	—	—	OP580844	OP585406	—	—	—
Pseudohyaloseta pandanicola	MFLUCC 16-0316*	Thailand	*Pandanaceae*	—	—	MH376737	MH388398	—	MH412733	—
Pseudoniesslia minutispora	CBS 246.82*	Netherlands	agricultural soil	—	—	MG826759	MG896429	—	OQ454216	—
	CBS 148.70	Netherlands	*Fagus sylvatica*	—	—	OR052114	OQ471149	—	OQ454219	—
	CBS 735.69	Germany	*Fraxinus excelsior*	—	—	OR052115	OQ471148	—	OQ454218	—
	CBS 267.89	Belgium	*Salix cinerea*	—	—	OQ430081	OQ471147	—	OQ454217	—
Rectifusarium robinianum	CBS 430.91*	Germany	*Robinia pseudoacacia*	—	—	KM231657	KM231923	JX171520	JX171633	KM232053
Rectifusarium ventricosum	CBS 748.79*	Germany	soil	—	—	KM231658	KM231924	KM232208	HQ897761	KM232054
Rosasphaeria moravica	CBS 124270*	Austria	*Rosa* sp., dead twigs	—	—	JF440985	JF440987	—	—	—
Roselliniella atlantica	E-235007	UK	*Melanohalea exasperata*	—	—	GQ888763	—	—	—	—
Roselliniella euparmeliicola	BM-920346*	UK	*Parmelia meiophora*	—	—	GQ888764	—	—	—	—
Rossmaniella coenogonii	**Kukwa 15078a***	**Bolivia**	***Coenogonium* sp.**	—	**PP513174**	**PP513197**	—	—	—	—
Rossmaniella cryptica	**Flakus 26967**	**Bolivia**	***Hypotrachyna* sp.**	**PP513216**	**PP513175**	**PP513198**	**PP583639**	**PP594997**	—	—
Rossmaniella fusispora	**Etayo 30600a**	**Bolivia**	***Peltigera didactyla***	**PP513217**	**PP513176**	**PP513199**	**PP583640**	**PP594998**	—	—
	Etayo 30600b	**Bolivia**	***Peltigera didactyla***	—	**PP513177**	**PP513200**	—	—	—	—
	Etayo 31862a	**Spain**	***Hypotrachyna revoluta***	**PP513218**	**PP513178**	**PP513201**	**PP583641**	**PP594999**	—	—
	Etayo 31862b	**Spain**	***Hypotrachyna revoluta***	**PP513219**	**PP513179**	**PP513202**	**PP583642**	—	—	—
	Flakus 27468	**Bolivia**	***Phyllopsora* sp.**	**PP513220**	**PP513181**	**PP513204**	**PP583644**	**PP595001**	—	—
	Flakus 26556*	**Bolivia**	***Punctelia* sp.**	—	**PP513180**	**PP513203**	**PP583643**	**PP595000**	—	—
Rossmaniella tylophori	**Flakus 26805***	**Bolivia**	***Tylophoron protrudens***	—	**PP513182**	**PP513205**	**PP583645**	**PP595002**	—	—
Roumegueriella rufula	CBS 346.85	Switzerland	*Globodera rostochiensis*	—	—	DQ518776	DQ522355	DQ522403	DQ522461	DQ522524

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
	G.J.S. 91-164	n/a	*Globodera rostochiensis*	—	—	EF469082	EF469070	EF469099	EF469116	EF469150
Rugonectria rugulosa	CBS 126565	Venezuela	dead wood	—	—	MH877897	KM231873	MW834261	KM232320	KM232007
	CBS 129158	USA	twig	—	—	JF832761	—	JF832836	KM232319	JF832911
Samsoniella inthanonensis	TBRC 7915*	Thailand	*Lepidoptera*	—	—	MF140725	MF140849	MF140815	MF140790	—
Sarcopodium circinatum	CBS 587.92*	Costa Rica	soil	—	—	KM231651	—	KM232202	KM232360	KM232046
	CBS 100998	Brazil	leaf litter	—	—	KM231650	KM231917	KM232201	KM232359	KM232045
Sarocladium ochraceum	CBS 428.67*	Kenya	*Zea mays*, cob	—	—	HQ232070	OQ471176	—	OQ454245	—
Sarocladium oryzae	CBS 180.74*	India	*Oryza sativa*	—	—	HG965047	OQ471177	—	OQ454246	—
Sarocladium strictum	CBS 346.70*	Germany	*Triticum aestivum*, old leaf	—	—	HQ232141	OQ471184	—	OQ454252	—
Sedecimiella funiculosa	CGMCC 3.22348*	China	sediment	—	—	OQ758168	OQ809062	—	OQ809028	—
	CGMCC 3.22356	China	sediment	—	—	OQ758169	OQ809063	—	OQ809029	—
Sedecimiella taiwanensis	CY5100*	China	mangrove wood	—	—	HM451496	—	—	—	—
Septomyrothecium uniseptatum	MUCL 52942	Japan	n/a	—	—	KY389351	KY769918	—	KY389369	KY366464
Simplicillium lamellicola	CBS 116.25*	UK	*Agaricus bisporus*	—	—	AF339552	DQ522356	DQ522404	DQ522462	DQ522525
Simplicillium lanosoniveum	CBS 704.86	Venezuela	*Hemileia vastatrix*	—	—	AF339553	DQ522358	DQ522406	DQ522464	DQ522527
	CBS 101267	Jamaica	*Hemileia vastatrix*	—	—	AF339554	DQ522357	DQ522405	DQ522463	DQ522526
Sirastachys phaeospora	CBS 100155*	Cuba	decaying leaf	—	—	KU846779	KU846995	—	KU846891	KU847102
Sphaeronectria lichenophila	**Flakus 27086**	**Bolivia**	***Heterodermia* sp.**	**PP513223**	**PP513184**	**PP513208**	**PP583647**	**PP595004**	—	—
	Flakus 27650	**Bolivia**	***Heterodermia comosa***	**PP513221**	**PP513186**	—	—	**PP595006**	—	—
	Flakus 26977	**Bolivia**	***Leucodermia* sp.**	**PP513222**	**PP513183**	**PP513207**	**PP583646**	**PP595003**	—	—
	Flakus 27360	**Bolivia**	***Heterodermia japonica***	—	**PP513185**	**PP513206**	**PP583648**	**PP595005**	—	—
Stachybotrys chartarum	CBS 182.80*	Netherlands	cheese wrapping	—	—	KU846792	—	—	—	—
Stachybotrys chlorohalonata	UAMH 6417	Namibia	desert sand	—	—	AY489712	AY489607	AY489640	—	—
Stephanonectria keithii	BPI 802669	France	*Eleagnus*, bark	—	—	AY489727	AY489622	AY489657	—	—
Striatibotrys eucylindrospora	CBS 203.61*	Canada	bog soil	—	—	MH869586	DQ676605	—	DQ676581	KU847189
Stromatonectria caraganae	CBS 125579	Austria	*Colutea arborescens*, branches	—	—	MH875179	HQ112286	—	HQ112290	HQ112289
	CBS 127387*	Austria	*Caragana* sp., branch	—	—	HQ112285	HQ112285	—	OQ454274	—
Synnemellisia aurantia	COAD:2070*	Brazil	*Passiflora edulis*	—	—	KX866396	—	—	—	—

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
Synnemellisia urenae	BRIP 71652*	Australia	*Acacia* sp.	—	—	OK342134	—	—	—	—
Syspastospora parasitica	IMI255607	n/a	*Paecilomyces*	—	—	AY015634	—	—	—	—
Thelonectria discophora	CBS 125153	New Zealand	*Pinus radiata*	—	—	HM364307	KM231897	HM364326	KM232344	HM352860
Thelonectria olida	CBS 215.67*	Germany	*Asparagus officinalis*	—	—	MH870642	HM364345	HM364334	KM232342	KM232024
Thelonectria veuillotiana	MAFF 241544	Japan	n/a	—	—	JQ403378	—	JQ403415	—	JQ394729
Thyronectria caudata	CBS 136003*	Greece	*Berberis cretica*	—	—	MH877604	KJ570762	KJ570719	KJ570743	KJ570642
Thyronectria lamyi	CBS 417.89	Germany	*Berberis vulgaris*	—	—	KM231718	JF832580	JF832830	KM232413	KM232108
Thyronectria quercicola	CBS 128976*	Spain	*Quercus ilex*	—	—	JF832743	JF832581	JF832831	KM232411	HM484595
Tilachlidium brachiatum	CBS 363.97	France	*Agaricus* sp.	—	—	KM231719	KM231975	KM232271	KM232414	KM232110
	CBS 505.67	Poland	old *Hypholoma fasciculare*	—	—	MH870764	KM231976	KM232272	KM232415	KM232109
	CBS 506.67	Poland	old *Mycena galericulata*	—	—	HQ232177	—	—	—	—
Trichoderma viride	CBS 757.71	Finland	soil	—	—	MH872090	—	—	—	—
	CBS 127113	New Zealand	n/a	—	—	MH875860	—	—	—	—
Trichonectria setadpressa	A.F. 28886	Bolivia	*Lobariella pallida*	OR510622	MT153965	MT154012	OR525301	—	—	—
	A.F. 29612-1	Bolivia	*Lobariella pallida*	OR510623	MT153966	MT154013	—	—	—	—
	A.F. 29612-2	Bolivia	*Lobariella pallida*	OR510624	MT153967	MT154014	OR525300	—	—	—
	A.F. 29617	Bolivia	*Lobariella pallida*	OR510625	MT153968	MT154015	OR525299	OR529404	—	—
	J.E. 20-13	Bolivia	*Lobariella pallida*	—	MT153969	MT154016	—	—	—	—
Trichothecium crotocinigenum	CBS 129.64*	Hungary	*Trametes versicolor*	—	—	MH870018	OQ471217	—	—	—
Trichothecium hongkongense	CBS 102186	Ecuador	*Marasmius* sp.	—	—	OQ430138	OQ471218	—	OQ454287	—
	CBS 101444	China	living leaves	—	—	OQ430139	OQ471219	—	OQ454288	—
Trichothecium roseum	DAOM 208997	n/a	n/a	—	—	JN938864	—	JN985147	—	—
	PG	n/a	n/a	—	—	JQ237687	—	—	—	—
	DAOM 57205	n/a	n/a	—	—	—	DQ676610	—	DQ676586	—
	KUNCC 21-10015	China	*Morchella* sp.	—	—	OP580876	OP585438	—	—	—
	UAMH 7839	Canada	honeybee facility	—	—	—	DQ676623	—	DQ676599	—
	LCP 50.627	n/a	n/a	—	—	JQ434510	—	—	—	JQ434527
	PH6	Russia	*Linaria vulgaris*	—	—	KY234151	—	—	—	KY273921
	RiT1	China	*Ricinus communis*	—	—	MW478330	—	—	—	MW493379
Trichothecium sympodiale	CBS 227.76*	France	silage of cereal	—	—	MH872742	—	—	—	-

Table 1. (Continued).

Taxa	Herbarium/Strain number	Country	Substrate/host	nuSSU	ITS	LSU	*tef-1*	*rpb1*	*rpb2*	*tub2*
	ATCC 36477	n/a	n/a	—	—	U69891	—	—	—	-
Valsonectria inflata	CBS 212.69	UK	intertidal salt marsh mud	—	—	HQ232050	OQ471228	—	OQ560706	-
	CBS 604.68	Germany	soil	—	—	OQ430149	OQ471229	—	OQ454295	-
	CBS 497.82	Netherlands	agricultural soil	—	—	OQ430150	OQ471230	—	OQ454296	-
Valsonectria roseola	CBS 416.81	UK	*Dianthus caryophyllus*	—	—	OQ430151	OQ471231	—	OQ454297	-
	CBS 289.62*	UK	*Dactylis glomerata*	—	—	OQ430152	OQ471232	—	OQ454298	-
Valsonectria soli	CBS 770.69*	France	agricultural soil	—	—	OQ430158	OQ471306	—	OQ454304	-
	CBS 106.70	Netherlands	agricultural soil	—	—	MH878244	OQ471237	—	OQ454303	-
Verrucostoma freycinetiae	MAFF 240100*	Japan	*Freucinetia boninensis*, dead leaves	—	—	GQ506013	HM484853	GQ506018	—	HM484885
Verrucostoma martinicensis	CBS 138731*	Martinique	*Danaea elliptica*, dead stem	—	—	MH877668	—	—	—	—
Virgatospora echinofibrosa	AR2824	Mexico	litter	—	—	AY489706	AY489601	AY489634	—	—
Xanthonectria pseudopeziza	CBS 140160	France	*Suaeda vera*	—	—	KU593583	OQ471291	—	OQ454358	—
	CBS 141245	France	*Smyrnium olusatrum*	—	—	KU946964	OQ471290	—	OQ454357	—
	CBS 126104	France	*Buxus sempervirens*	—	—	MH875476	—	—	—	—
	MFLU 16-0513	Italy	*Robinia pseudoacacia*	—	—	ON230061	ON238005	—	—	—
Xenoacremonium falcatus	CBS 400.85*	New Zealand	*Pinus radiata*	—	—	KM231712	KM231967	KM232263	OQ454359	KM232104
Xenoacremonium recifei	CBS 137.35*	Brazil	human	—	—	HQ232106	KP012646	KM232264	KM232397	KM232105
Xenocylindrocladium guianense	CBS 112179*	French Guiana	plant litter	—	—	JQ666073	KM231895	KM232166	KM232314	AF320197
Xenocylindrocladium serpens	CBS 128439	Ecuador	bark	—	—	KM231688	KM231894	KM232165	—	—
Xenogliocladiopsis cypellocarpa	CBS 133814*	Australia	*Eucalyptus cypellocarpa*	—	—	KM231623	KM231885	KM232158	KM232332	KM232017
	CPC 17153	Australia	*Eucalyptus* sp.	—	—	KM231624	KM231884	KM232159	KM232333	KM232018
Xepicula leucotricha	BPI 843408	USA	decaying grass leaf	—	—	AY489707	AY489602	AY489635	—	—

Fig. 1. Phylogenetic relationships within the order *Hypocreales* inferred from a Maximum likelihood analysis (ML) of a combined LSU, *tef-1, rpb1, rpb2* and *tub2* data set. *Achaetomium macrosporum*, *Chaetomium elatum*, *Neurospora crassa* and *N. tetrasperma* were used as the outgroup. Lichenicolous fungi are highlighted in blue. Bootstrap support value from ML/posterior probability from Bayesian analyses at branches. Thickened branches represent either bootstrap support values ≥ 70 % and/or Bayesian posterior probabilities ≥ 0.97, lower values inducated by '-'. The asterisk indicates type materials.

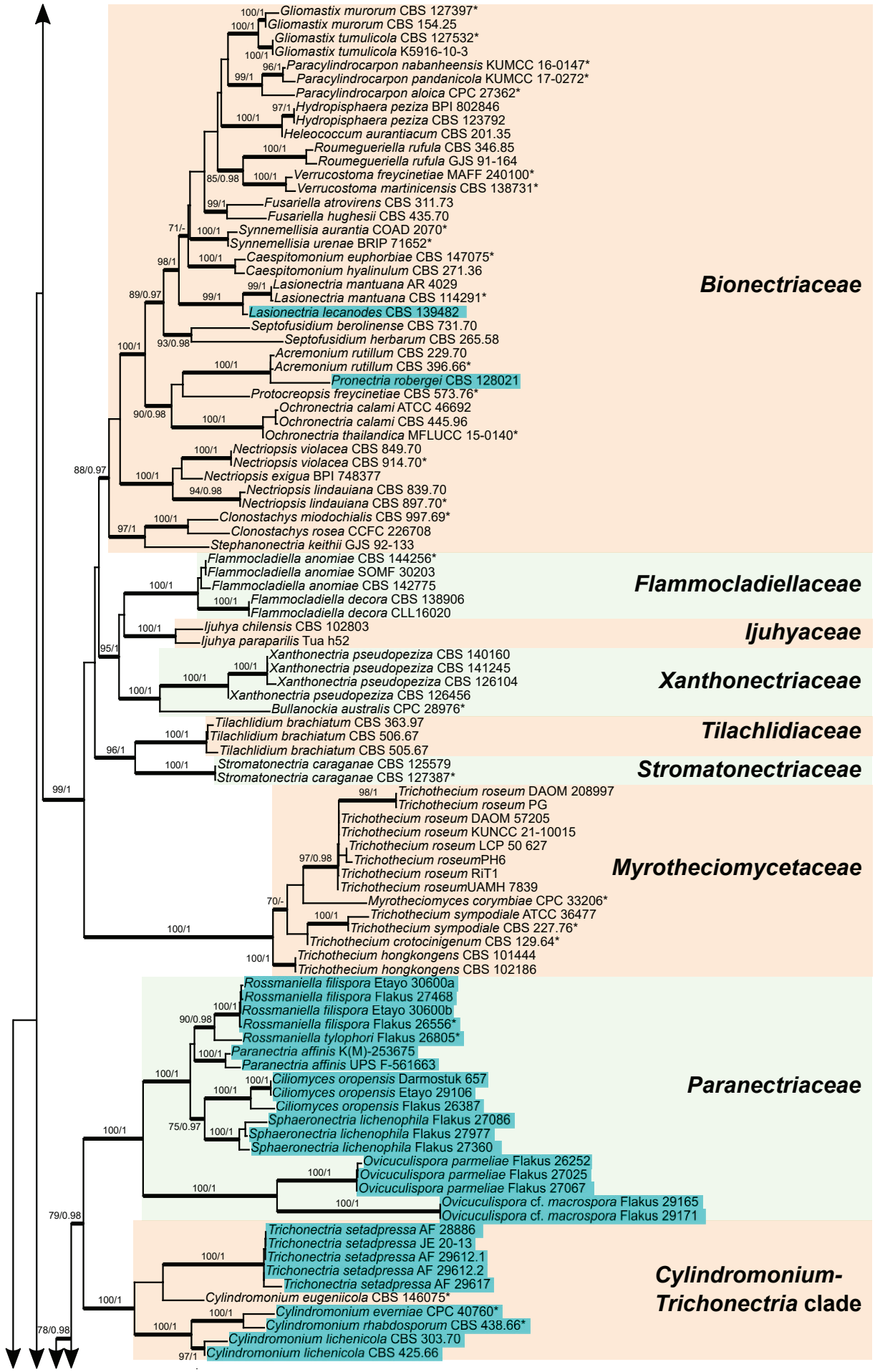

Fig. 1. (continued)

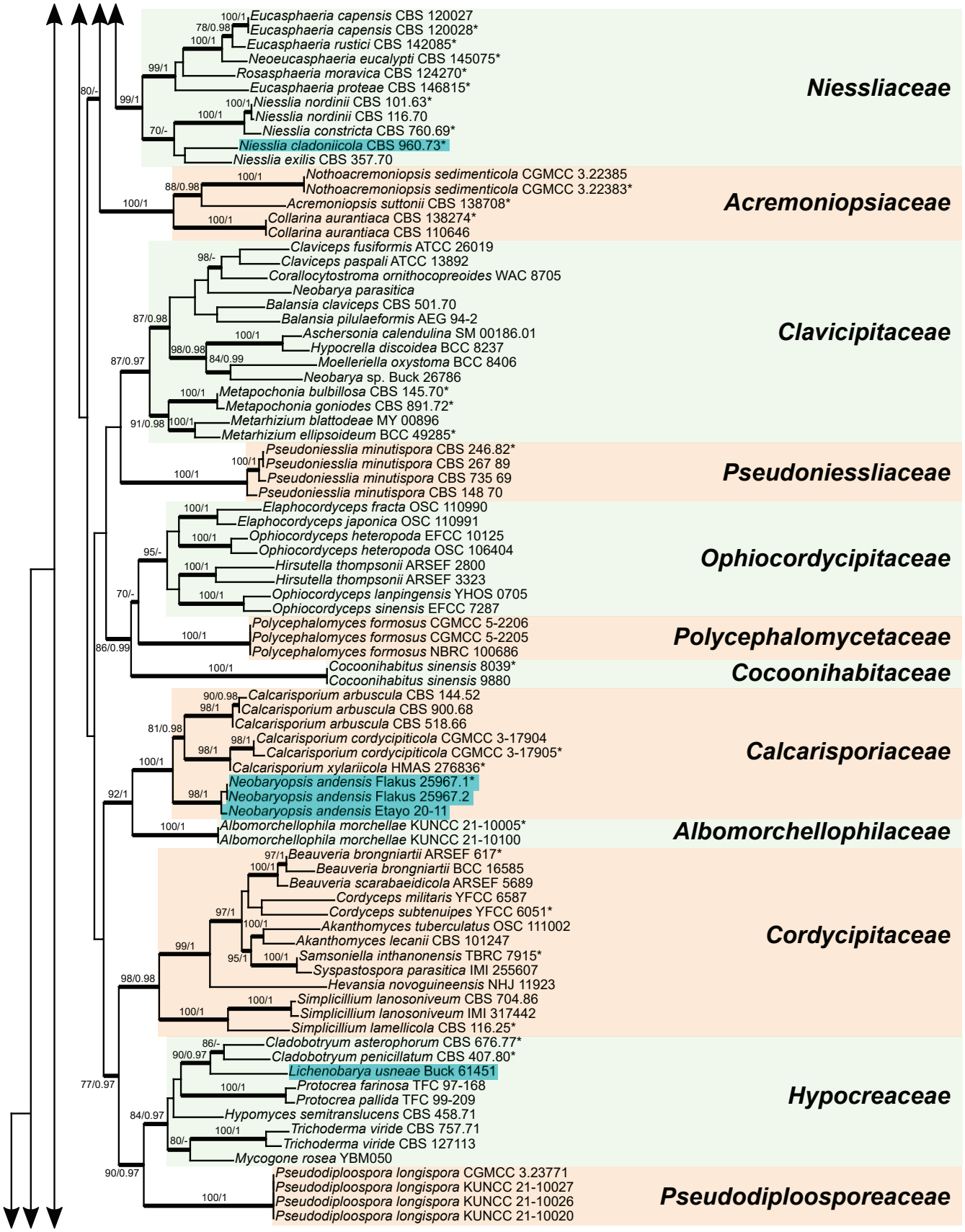

Fig. 1. (continued)

Trichonectria clade as well as a newly described family (Fig. 1).The families *Albomorchellophilaceae*, *Bionectriaceae*, *Chrysonectriaceae*, *Clavicipitaceae*, *Flammocladiellaceae*, *Ijuhyaceae*, *Nectriaceae*, *Neoacremoniaceae*, *Ophiocordycipitaceae*, *Polychephalomycetaceae*, *Pseudodiploosporeaceae*, *Sedecimiellaceae*, *Stachybotriaceae*, *Stromatonectriaceae*, *Tilachlidiaceae* and *Xanthonectriaceae* formed well-supported clades and phylogenetic relationships between them are consistent with those found in previous studies (Hou *et al.* 2023, Li *et al.* 2023, Perera *et al.* 2023,

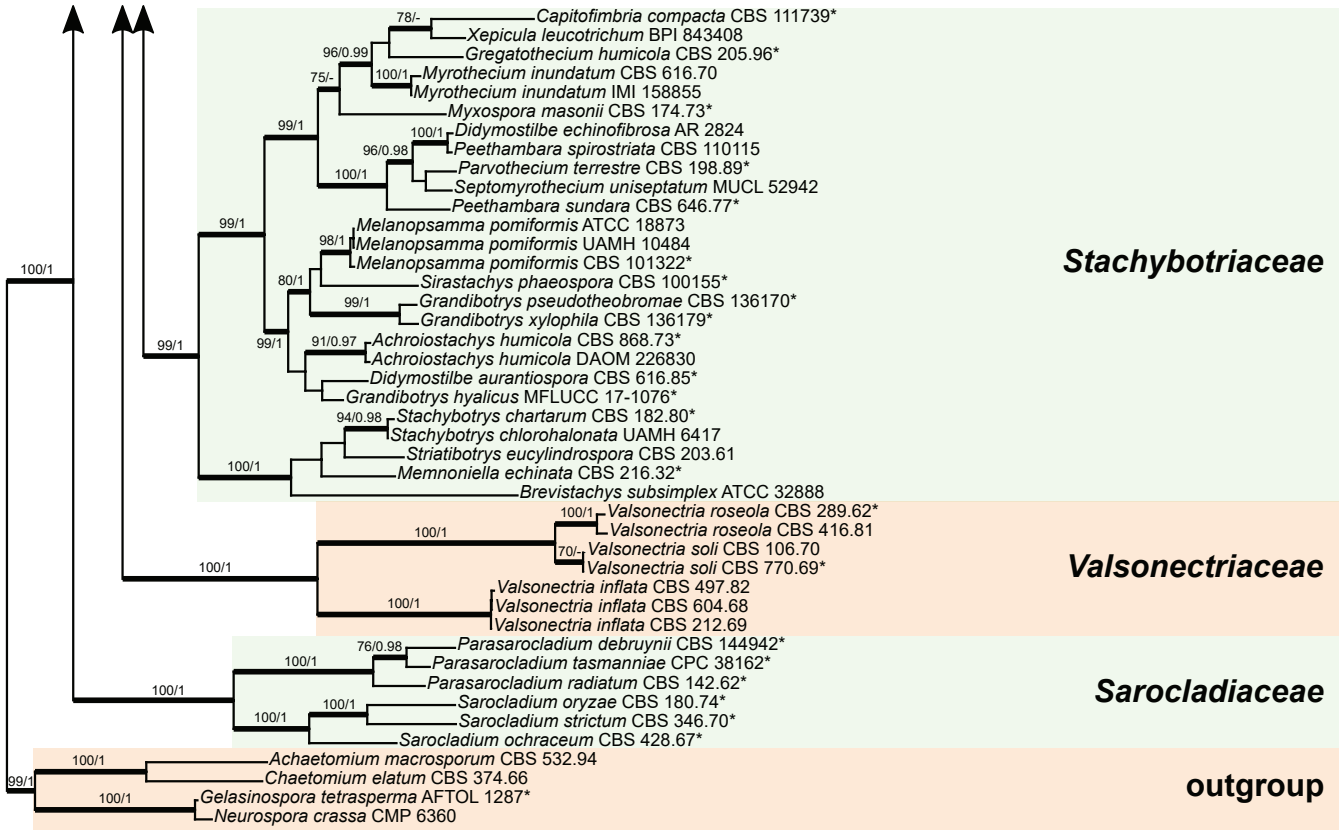

Fig. 1. (continued)

Xiao *et al.* 2023). Details of the phylogenetic relationships of targeted lichenicolous species are given in the next section.

In our phylogeny, the 66 species of the family *Nectriaceae* formed a well-supported clade (95/1). Additionally, two specimens of the genus *Roselliniella*, formed a well-supported clade (100/1) within *Nectriaceae*. This genus was previously classified as *Hypocreales* insertae sedis; however, as the generic type of *Roselliniella* (*R. nephromatis*) has not been sequenced yet, the inclusion within *Nectriaceae* is tentative.

The species of the family *Myrotheciomycetaceae* formed a well-supported clade (100/1). *Myrotheciomycetaceae* showed a close relationship to the clade comprising families *Bionectriaceae*, *Flammocladiellaceae*, *Stromatonectriaceae*, *Tilachlidiaceae* and *Xanthonectriaceae*, with strong statistical support (99/1). The genera *Calcarisporium* (with three species, including the generic type *C. arbuscula*) and the monotypic *Neobaryopsis*, which previously has been placed within the *Cordycipitaceae* by Flakus *et al.* (2019a), formed a well-supported clade (100/1) corresponding to the family *Calcarisporiaceae*. This clade showed a highly supported (92/1) sister relationship to the family *Albomorchellophilaceae*.

Similar to previous studies, the phylogenetic relationship between the families *Cocoonihabitaceae*, *Cordycipitaceae*, *Hypocreaceae*, *Polychephalomycetaceae* and *Pseudoniessliaceae* received moderate or low statistical support (Hou *et al.* 2023, Perera *et al.* 2023, Xiao *et al.* 2023). The species previously assigned to the family *Cordycipitaceae* and *Hypocreaceae* were placed in a well-supported clade (98/0.98 and 84/0.97 respectively). Members of the recently established *Pseudodiploosporeaceae* were resolved in the well-supported clade (100/1) and showed a sister relationship to the family *Hypocreaceae*. *Pseudoniessliaceae* is represented in our analyses by four specimens of *Pseudoniesslia minutispora*, which showed a low-supported sister relationship to the family *Clavicipitaceae*. Two specimens of *Cocoonihabitus* species (*Cocoonihabitaceae*) are resolved in a well-supported clade and showed a sister relationship (86/0.99) to the clade comprised by families *Ophiocordycipitaceae* and *Polychephalomycetaceae*.

Specimens of the family *Nothoacremoniaceae* clustered in a highly supported clade (100/1) and it was closely related to the clade (80/0.97) comprising families *Chrysonectriaceae*, *Neoacremoniaceae* and *Sedecimiellaceae*. The *Valsonectriaceae* is represented by three species of *Valsonectria* in our data set, forming a distinct and well-supported clade (100/1). The family *Sarocladiaceae* (100/1) showed a sister relationship to the remaining families of the order *Hypocreales*.

This is the first phylogenetic study that includes a wide sampling of lichenicolous species of the genera *Ovicuculispora* and *Paranectria*, as well as *Nectriopsis lichenophila*, and *Nectria byssophila*-like species, which in our phylogenetic analyses are nested together in a monophyletic highly supported clade (100/1). This new lichenicolous clade demonstrates a well-supported sister relationship (79/0.98) to the clade consisting of species from the asexual morph genus *Cylindromonium* (generic type *C. eugeniicola*) and a few species from the sexual genus *Trichonectria* (generic type *T. hirta*, but not sequenced so far). This clade represents an independent lineage with strong statistical support (100/1), and perhaps needs to be uploaded to the family level. However, *Trichonectria* appears to be a polyphyletic assemblage and no sequences of *T. hirta,* which is the type species of the genus, are available. Because of this, we decided not to introduce any nomenclature changes until further studies resolve the phylogenetic placement of *T. hirta*.

Our analyses included sequences of 9 specimens of the family *Niessliaceae* which were resolved as a monophyletic clade with a high support (99/1). The family *Niessliaceae*

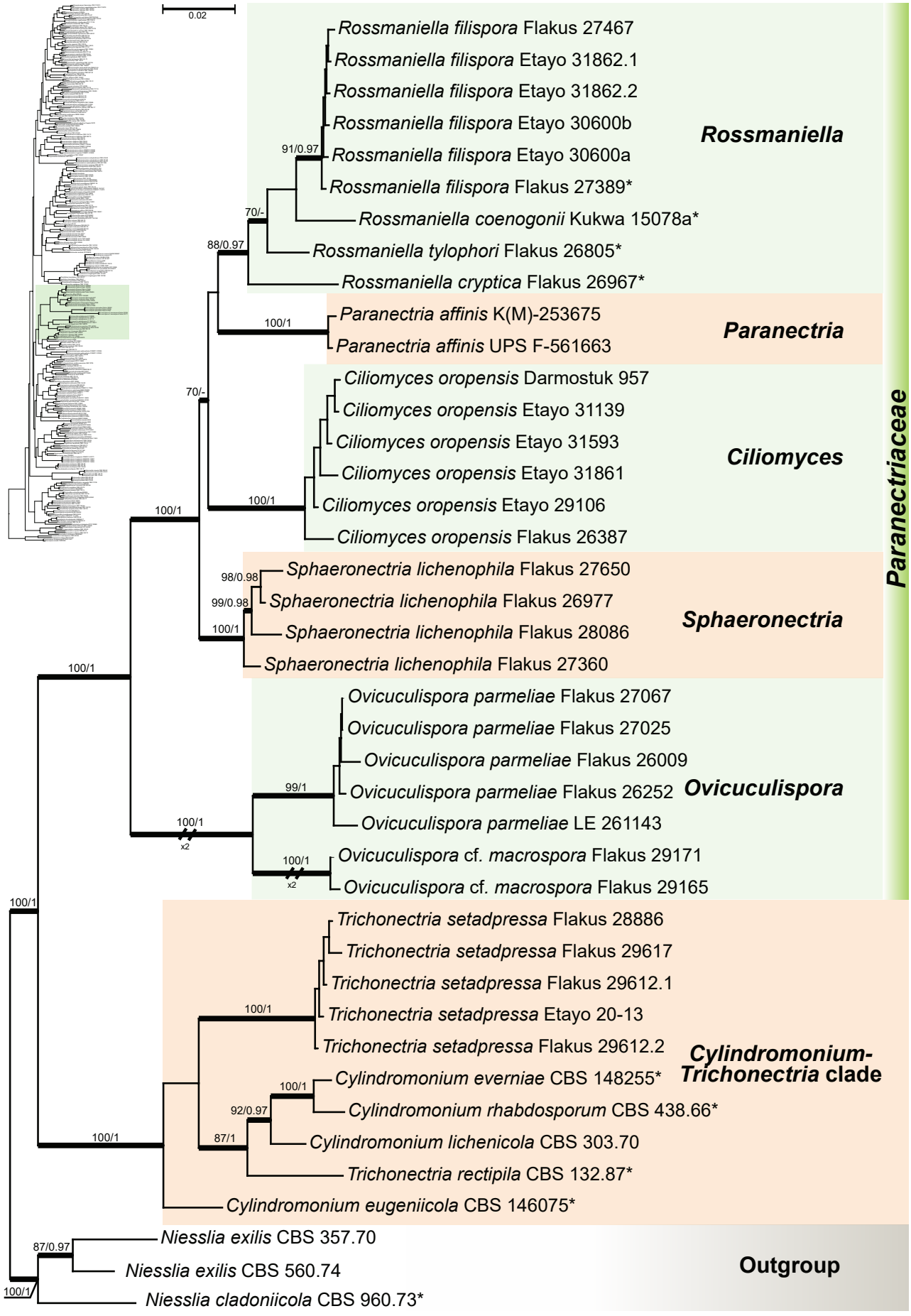

Fig. 2. Phylogenetic relationships within the family *Paranectriaceae* and sister *Cylindromonium-Trichonectria* clade inferred from a Bayesian Inference analysis (BI) of a combined 5.8S, LSU, nuSSU, *tef-1* and *rpb1* data set. *Niesslia* spp. were used as the outgroup. Bootstrap value from ML/posterior probability from Bayesian analyses at branches. Thickened branches represent either bootstrap support values ≥ 70 % and/or Bayesian posterior probabilities ≥ 0.97, lower values inducated by '-'. The asterisk indicates type materials.

Table 2. Partition scheme used in the phylogenetic analyses.

Dataset	Region	Codon position	Model
Hypocreales dataset	LSU	—	GTR+I+G
	tef-1	The first codon position	TVM+I+G
	tef-1	The second codon position	TVM+I+G
	tef-1	The third codon position	GTR+I+G
	rpb1	The first codon position	GTR+I+G
	rpb1	The second codon position	TVM+I+G
	rpb1	The third codon position	TVM+I+G
	rpb2	The first codon position	GTR+I+G
	rpb2	The second codon position	TVMEF+I+G
	rpb2	The third codon position	GTR+I+G
	tub2	The first codon position	GTR+I+G
	tub2	The second codon position	TRNEF+G
	tub2	The third codon position	SYM+I+G
Paranectriaceae dataset	5.8S	—	TRNEF+I+G
	LSU	—	TRNEF+I+G
	nuSSU	—	K80-I
	tef-1	The first codon position	TIM+I+G
	tef-1	The second codon position	TIM+I+G
	tef-1	The third codon position	GTR+G
	rpb1	The first codon position	TIM+I+G
	rpb1	The second codon position	TRNEF+I+G
	rpb1	The third codon position	TVM+G

showed a sister relationship to the clade comprising the new family *Paranectriaceae* and *Cylindromonium-Trichonectria* clade. The members of the family *Acremoniopsiaceae* clustered in a well-supported clade (100/1) and showed moderately supported sister relationships to the aforementioned families.

Phylogenetic relationships within the new family

The *Paranectriaceae* multi-gene dataset was analysed to determinate the interspecific relationships among genera representing the target lichenicolous lineage of the order *Hypocreales.* This dataset consisted of 42 specimens with sequences of the 5.8S, LSU, nuSSU, *tef-1*, *rpb1* regions. This five-locus alignment contained 4209 characters (158 5.8S, 886 LSU, 1 631 nuSSU, 960 *tef-1*, 594 *rpb1*), of which 640 were parsimony-informative, 257 singleton sites, and 3312 constant sites. The tree topology of ML and Bayesian analysis was the same and only the 50 % majority rule consensus tree is shown in Fig. 2.

The new lineage of lichenicolous fungi, proposed here as a new family *Paranectriaceae*, formed a strongly supported clade (100/1), showing a sister relationship to the *Cylindromonium-Trichonectria* clade. The new family consists of five genera represented by lichenicolous species. The nine lichenicolous specimens characterized by having filiform ascospores formed a well-supported clade of *Rossmaniella* genus (88/0.97). Morphologically, due to byssoid ascomata grouped on a distinct subiculum and long filiform ascospores, the specimens resemble such lichenicolous fungi as *Lichenobarya*, *Nectria byssophila* and *Neobaryopsis*, but they are phylogenetically not related. Therefore, the new genus *Rossmaniella*, with four newly recognized species is introduced for this group. This clade shows a sister relationship to the morphologically different genus *Paranectria*, although without significant statistical support.

The phylogeny revealed the species of the genus *Paranectria* clustered in two separate clades. Two specimens of *P. affinis*, the generic type of *Paranectria*, growing on *Ephebe lanata* formed a separate, highly supported (100/1) clade (Fig. 2) and showed a relationship to the genus *Rossmaniella*, but with low support. In contrast, six specimens of *Paranectria oropensis* (under the name *Ciliomyces oropensis* in the Fig. 2) formed a separate and well-supported clade (100/1), which seems to be not related to the sequences of *P. affinis*; however, the relationships are not well resolved. Due to differences in morphology of those two species and together with phylogenetic placement, the genus *Ciliomyces* is reinstated for this species.

The four specimens of the tropical species *Nectriopsis lichenophila* clustered in a well-supported (100/1) clade sister to the larger clade consisting of *Ciliomyces*, *Paranectria* and *Rossmaniella*. This fungus appears to be not related to the genus *Nectriopsis* s. str. (generic type *N. violaceae* growing on *Fuligo septica*) which belongs to the family *Bionectriaceae* (see Fig. 1). Thereby, based on the phylogenetic and morphological differences between *Nectriopsis lichenophila* and other species in *Nectriopsis* s. str., the new monotypic genus *Sphaeronectria* is described here.

The genus *Ovicuculispora* is represented by two species in our phylogeny, *O. parmeliae* (generic type, represented by five specimens) and *O.* cf. *macrospora* (two specimens). They both cluster in a well-supported monophyletic clade (100/1) showing a sister relationship to the remaining taxa of the new family. The sequenced specimens of *O. parmeliae* were collected on different host species (see Table 1)

belonging to the families *Parmeliaceae* (*Lecanorales*) and *Lobariaceae* (*Peltigerales*). However, all the specimens grouped in a single well-supported clade (99/1), indicating a non-specific phylogenetic correlation with the host type. Despite growing on several unrelated host genera, the genetic variation among loci seems to be low and indicates that all examined specimens belong to the same lichenicolous species. Additional specimens of *Ovicuculispora parmeliae* (Flakus 26010, 26011) collected on *Sticta* sp. from Bolivia were not included in the tree, due to the fact that only ITS sequences were obtained. However, we have tried to use morphological data and the ITS region (not included here) to place this species within the new family circumscription and it showed 100 % similarity with a sequence obtained from the specimen on *Sticta* sp. (KRAM L-74677), as well as 99 % similarity to sequences for specimens on other hosts (*Crocodia*, *Heterodermia* and *Hypotrachyna s.lat*).

TAXONOMY

Paranectriaceae Darmostuk, Etayo & Flakus, ***fam. nov.*** MycoBank MB 858383.

Etymology: Referring to the name of the type genus.

Type genus: *Paranectria* Sacc.

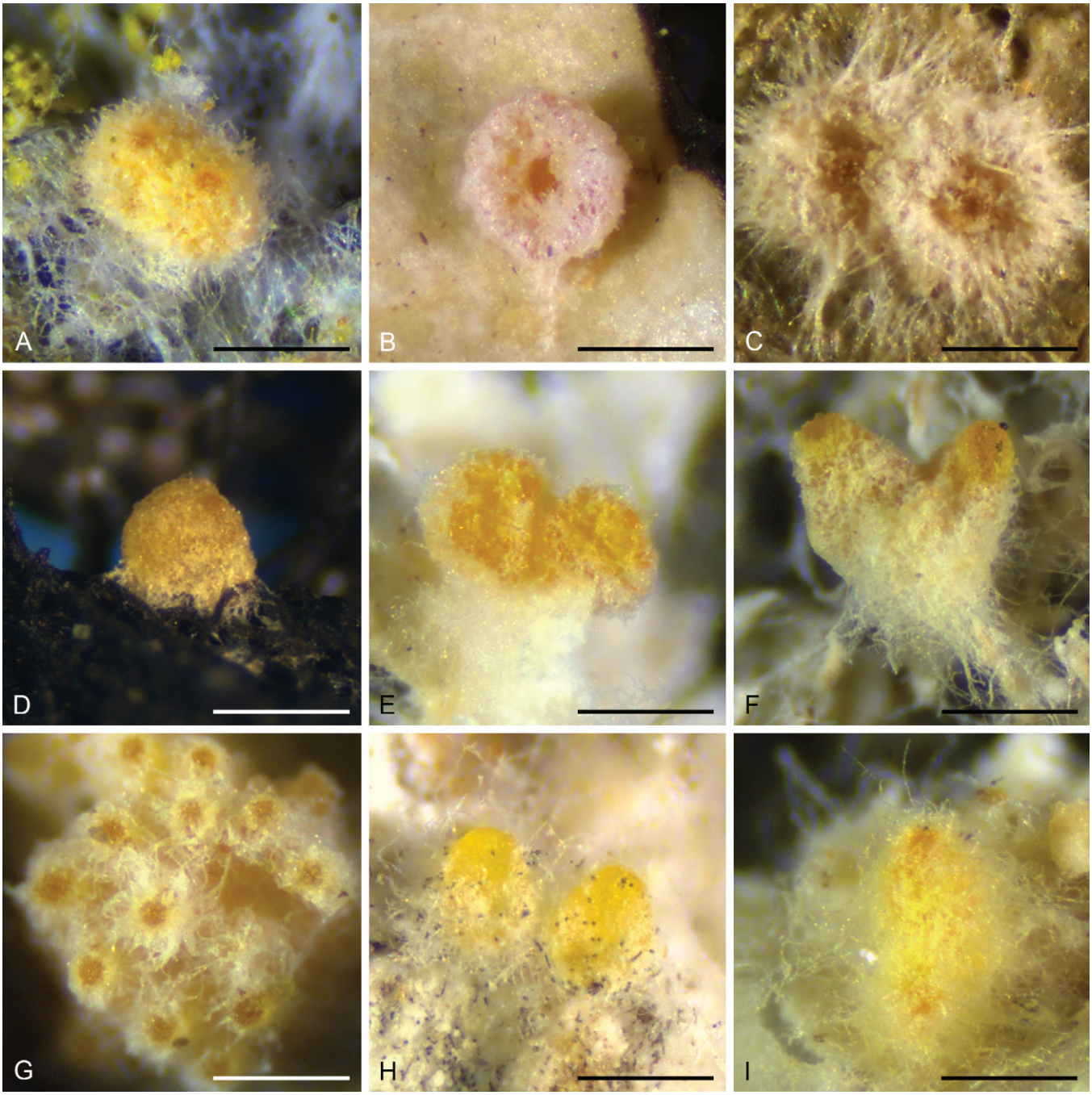

Fig. 3. Ascomata morphology of the family *Paranectriaceae*. **A.** *Ciliomyces oropensis* (Darmostuk 957). **B.** *Ovicuculispora parmeliae* (Etayo 32636). **C.** *Ovicuculispora* cf. *macrospora* (Flakus 29165). **D.** *Paranectria affinis* (UPS F-561663). **E.** *Sphaeronectria lichenophila* (Flakus 26997). **F.** *Rossmaniella filispora* (Flakus 27467). **G.** *Rossmaniella filispora* (Etayo 30600); **H.** *Rossmaniella tylophori* (Flakus 26805). **I.** *Rossmaniella cryptica* (Flakus 26967). Scale bars = 250 µm.

Ascomata perithecioid, superficial, globose to pyriform, yellow to bright orange, scattered or forming groups, with more or less developed whitish subiculum in the lower part of ascomata. *Ascomatal wall* composed of several layers of irregular cells, hyaline to yellowish, not changing colour in KOH. *Asci* unitunicate, cylindrical to subclavate, 4–8-spored. *Ascospores* hyaline, ellipsoid to filiform, 1–3-septate to muriform, also two types (macro- and microspores) can occur in the same ascus. All the genera included in this family are lichenicolous species.

Included genera: *Ciliomyces*, *Ovicuculispora*, *Paranectria*, *Rossmaniella*, *Sphaeronectria.*

Ciliomyces Höhn., *Sber. Akad. Wiss. Wien, Math.-naturw. Kl.*, Abt. 1 **115**: 673. 1906. MycoBank MB 1057.

Type species: *Ciliomyces oropensis* (Ces.) Höhn.

Ascomata perithecioid, globose to ovoid, superficial, scattered, totally covered by whitish tomentum, with visible ostiole. *Ascomatal wall* up to 35 µm thick, composed of pseudoparenchymatous thick-walled cells. *Asci* clavate, short-stalked, 8-spored (rarely 4-spored). *Ascospores* hyaline, ovoid to narrowly ellipsoid, with elongate appendages at each end, submuriform to muriform. *Asexual morph* acremonium-like with 1–3-septate, hyaline, ellipsoid to subcylindrical conidia.

Notes: Our phylogeny shows that the sequences of *Paranectria oropensis* clustered in a well-supported monophyletic clade are only distinctly related to the type of the genus *Paranectria*, *P. affinis*. Furthermore, we observed morphological differences in ascomata and ascospores of both species. Therefore *Ciliomyces*, with the type species *Ciliomyces oropensis*, is reinstated here from the synonyms of *Paranectria*.

The genus *Ciliomyces* was established by Höhnel (Höhnel & Litschauer 1906) to accommodate the lichenicolous species *Ciliomyces oropensis* and was later accepted by Keissler (1930) and Samuels (1976) as a separate genus. However, referring to the presence of elongate appendages at each end of ascospores in both genera, Hawksworth & Pirozynski (1977) considered *Ciliomyces* to be a heterotypic synonym of *Paranectria*. Nevertheless, the generic type of *Paranectria*, *P. affinis*, is characterized by white to pale luteous ascomata with arachnoid hyphae appearing only at their lower part and ascospores with transverse septa only. In contrast, the reinstated *Ciliomyces* is characterized by yellow orange ascomata fully covered by whitish tomentum and submuriform to muriform ascospores (Hawksworth 1982, Rossman 1983, Rossman *et al.* 1999, Zhurbenko 2009). Although these differences have been briefly discussed in several works, not considered to have enough taxonomic value to separate both genera (Rossman 1983, Rossman *et al.* 1999). No molecular data are available for *Paranectria alstrupii* and *P. superba*. However, based on their similar muriform ascospores to *C. oropensis* and lichenicolous lifestyle, we consider that these species can be affiliated with *Ciliomyces* (Hawksworth 1982, Zhurbenko 2009, Zhurbenko & Dillman 2010). We are awaiting further data before proposing formal changes.

Ciliomyces oropensis (Ces.) Höhn., *Sber. Akad. Wiss. Wien, Math.-naturw. Kl.*, Abt. 1 **115**: 673. 1906. MycoBank MB 232256. Figs 3A, 4C.

Basionym: *Sphaeria (Nectria) oropensis* Ces., in Rabenhorst, *Klotzschii Herb. Viv. Mycol., Edn Nov, Ser. Sec., Cent*. **6**: no. 524. 1857.

Synonyms: *Cucurbitaria oropensis* (Ces.) Kuntze, *Revis. gen. pl. (Leipzig)* **3**(3): 461. 1898.

Dialonectria oropensis (Ces.) Cooke, *Grevillea* **12**(64): 111. 1884.

Nectria oropensis (Ces.) Sacc., *Syll. Fung. (Abellini)* **2**: 511. 1883.

Paranectria oropensis subsp. *parviseptata* M.S. Cole & D. Hawksw., *Mycotaxon* **77**: 324. 2001.

Paranectria oropensis (Ces.) D. Hawksw. & Piroz., *Canad. J. Bot.* **55**(19): 2555. 1977. *Typus*: **Italy**, Province of Biella, Piedmont, near the great Sanctuary of the Blessed Virgin Maria on Mount Oropa, Sep. 1856, *V. Cesati* (M, not examined).

Nectria lichenicola P. Crouan & H. Crouan, *Florule de Finistère (Paris)*: 256. 1867.

Dialonectria lichenicola (P. Crouan & H. Crouan) Cooke, *Grevillea* **12**(64): 111. 1884.

Pleonectria lichenicola (P. Crouan & H. Crouan) Sacc., *Michelia* **1** (3): 325. 1878. *Typus*: **France**, Finistère, on the granular thallus of a lichen, on the trunk of a beech tree (type not located).

Pleonectria appendiculata Vouaux, *Bulletin de la Société Mycologique de France* **28**: 193. 1912. *Typus*: **France**,France, on a thin unidentified thallus, on an old oak near Docelles in the Vosges, J. Harmand *J. Harmand* (type not located).

For detailed description see Hafellner & Obermayer (2009) and Navarro-Rosinés & Llimona (2018).

Distribution, habitat and host range: This is a common generalist species in the northern hemisphere, with scattered records from the southern hemisphere. It has been reported on many unrelated corticolous lichens (Diederich 2003, Hafellner & Obermayer 2009, Brackel 2014) and rarely on saxicolous ones (Navarro-Rosinés & Llimona 2018).

Specimens examined: **Bolivia**, Chuquisaca Department Chuquisaca, Zudañez Province, El Palmar Integrated Management Natural Area, Salviatójo near Lomán,, 18º45’51”S, 64º50’09”W, 2836 m a.s.l., disturbed Boliviano-Tucumano forest with *Podocarpus* and shrubs, on *Normandina pulchella*, 14 Jul. 2015, *A. Flakus* 26387 (KRAM L-74672; LPB). **Spain**, Cáceres, Monfragüe National Park, Saltos del Torrejón, near Tres Caños, Quercus ilex ssp. ballota wood pasture with quartzite stones.39º50’39”N, 06º00’05”W, 230 m a.s.l., on *Parmelina tiliacea* on *Quercus ilex*, 9 May 2015, *J. Etayo* 29106 (hb. Etayo); Guipúzcoa, Peñas de Aia, Lesakako Bidea road, just before the tunnel 43º16’25”N, 1º47’35.5”W, 500 m a.s.l., on *Hypotrachyna revoluta* on *Fagus sylvatica*, 31 Aug. 2019, *J. Etayo* 31862 (hb. Etayo, sub *Rossmaniella filispora*); Navarra, Basaburúa Mayor valley, between Aizároz and Arrarás, track to Bergañe, 550 m a.s.l., on unidentified lichen and bryophytes on *Fagus*, 20 Nov. 1994, *J. Etayo* 35899 (hb. Etayo); Lizarrusti pass, between Etxarri Aranaz and Beasain, 42º57’20”N, 2º05’00”W, 565 m a.s.l., on *Physconia*

perisidiosa growing on *Quercus robur*, 5 Jan. 2017, *J. Etayo* 31139 (hb. Etayo); Ciaúrriz, track a few meters before the junction of the N-411 with the entrance to the town, oak grove with wet boxwood, 42º55'49"N, 1º37'18"W, 625 m a.s.l., on *Anaptychia ciliaris* on *Quercus faginea*, 25 Nov. 2018, *J. Etayo* 31593 (hb. Etayo); Teruel, between Albarracín and Bezas, 40º22'52"N, 1º24'02"W, 1350 m a.s.l., on *Physconia grisea* on sandstones under *Pinus pinaster*, 16 Aug. 2020, *J. Etayo* 32605 (hb. Etayo). **Ukraine**, Ternopil region, Ternopil district, vicinity of the Posukhiv village, 49.41122 N, 24.93305 E, on thallus of *Lecania croatica*, on *Fagus* bark, 5 Sept. 2020, *V. Darmostuk 957 & O. Sira* (KRAM L-74673).

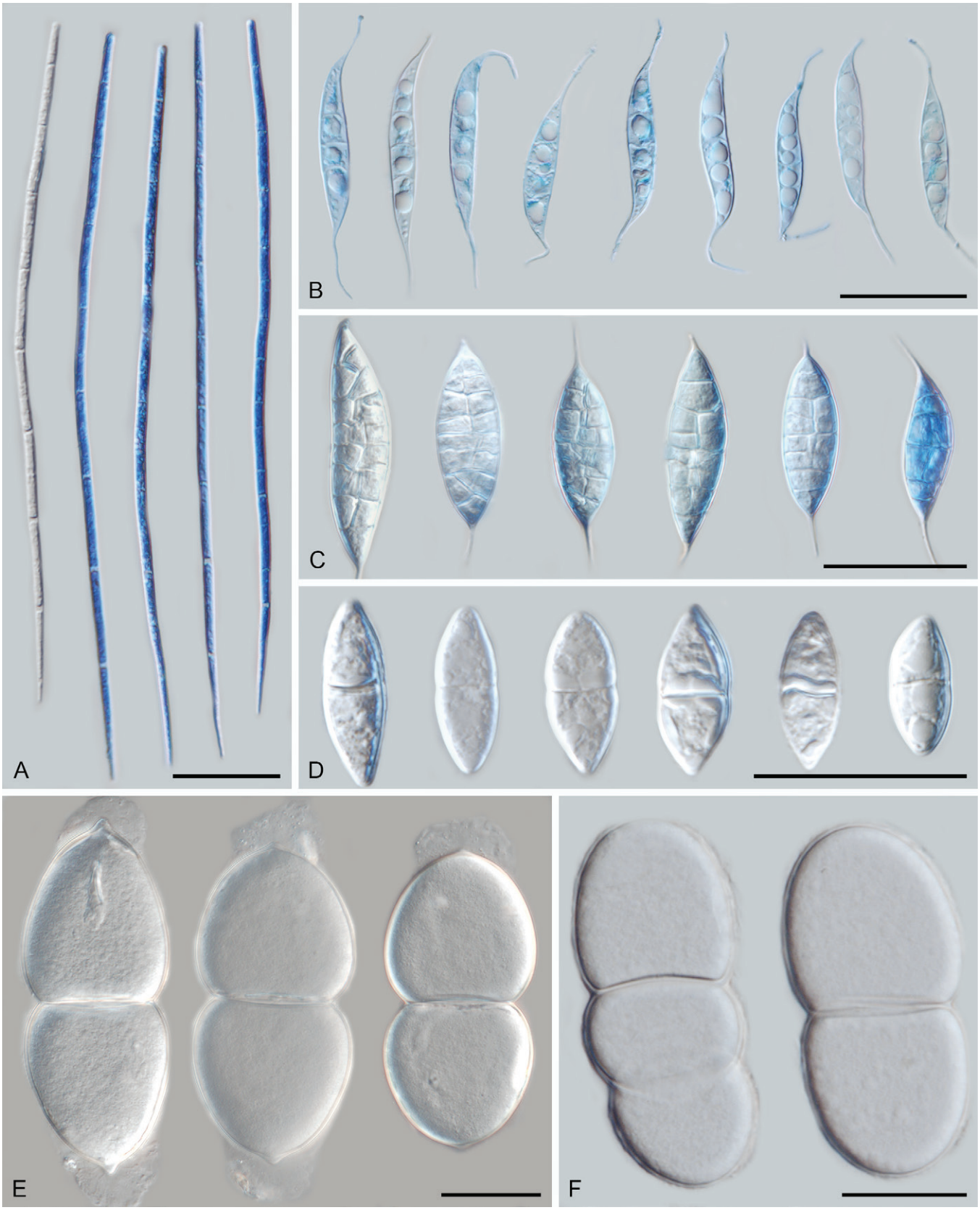

Fig. 4. Ascospores morphology of the family *Paranectriaceae*. **A.** *Rossmaniella cryptica* (Flakus 26967). **B.** *Paranectria affinis* (UPS F-561663). **C.** *Ciliomyces oropensis* (Darmostuk 957). **D.** *Sphaeronectria lichenophila* (Kukwa 16271). **E.** Macrospores of *Ovicuculispora* cf. *macrospora* (Flakus 29165). **F.** Macrospores of *Ovicuculispora parmeliae* (Flakus 26011). Scale bars = 25 µm.

Notes: *Ciliomyces oropensis* is a widely distributed and locally common species of lichenicolous *Hypocreales*. It plays an essential role in the dynamics of some corticolous lichen communities due to its ability to grow on various lichen hosts (Hafellner & Obermayer 2009). It has been collected on a wide range of hosts and exhibits significant variability in terms of ascospore size and septation. Discussions regarding the species boundaries of *C. oropensis* have arisen due to the variation found in spores of specimens from Scotland [(22–)25–32(–36) × (9–)11–14(–15) µm, Hawksworth 1982] and from Spain [(21–)25–30.8–37.5(–45) × (7–)8–9.8–12(–14) µm, Navarro-Rosinés & Llimona 2018]. This has led to discussions regarding the species boundaries of *Paranectria oropensis*. Cole & Hawksworth (2001) described a new subspecies, *P. oropensis* subsp. *parviseptata*, based on specimens from Taiwan, the USA, and Great Britain. This subspecies was characterized by shorter ascospores with fewer septa compared to the type subspecies. However, this taxonomic decision did not receive support in other studies that were based on larger sampling, indicating that differences in ascospore septation and size may be due to variations in ascus maturations (Diederich 2003, Brackel 2008, Navarro-Rosinés & Llimona 2018).

So far, *Ciliomyces oropensis* is the only known species of the family *Paranectriaceae* in which the asexual morph is known. The asexual morph is acremonium-like with 1–3-septate, hyaline ellipsoid conidia measuring 20–22 × 4–6 µm, arising from long conidiogenous cells (70–80 µm long) forming on whitish tomentum generally alone, rarely between the ascomata of the fungus. This asexual morph was reported based on a few specimens from Italy (Brackel 2015) and also found in our collections from Spain (hb. Etayo 31862). However, we were unable to obtain DNA sequences directly from the asexual morph and cannot confirm this connection by molecular data.

Ovicuculispora Etayo, *Bull. Soc. linn. Provence* **61**: 110. 2010. MycoBank MB 565893.

Type species: *Ovicuculispora parmeliae* (Berk. & M.A. Curtis) Etayo

Ascomata perithecioid, superficial, single to rarely in groups of 2–5, globose to subglobose at first, collapsing and becoming cupulate when dry, pinkish to orange, the lower part covered by frequently dense white mycelium. *Ascomatal wall* composed of 5–7 layers of radially compressed pseudoparenchymatous thick-walled cells, KOH–. Interascal filaments absent. *Asci* unitunicate, subcylindrical to clavate, with 1–2 smooth to ornamentated macrospores and 4–5 verruculous microspores. *Ascospores* two types, macrospores and microspores, 1-septate, ellipsoid, hyaline. *Conidiomata* unknown.

Notes: The genus *Ovicuculispora* is characterized by a unique feature in the order *Hypocreales*, the presence of two types of ascospores in the same ascus, i.e. macrospores and microspores. The genus comprises two species, *Ovicuculispora macrospora* and *O. parmeliae* (generic type).

Ovicuculispora* cf. *macrospora Etayo, *Bull. Soc. linn. Provence* **61**: 111. 2010. Figs 3C, 4E, 5.

Typus: **Peru**, San Martín, Prov. San Martín, Cerro Escalera (NE of Tarapoto), NW of the tunnel, 6°26'S, 76°15'W, ca 1000 m a.s.l., on saxicolous sterile crust, 15 Mar. 1981, *R. Santesson & G. Thor* P74:80 (**holotype** UPS).

Ascomata globose to cupulate when dry, scattered or in groups of 2–5 ascomata, saffron to more orange, 0.3–0.5 mm in diam, ascomata fully covered by whitish hyphae which formed the arachnoid tomentum at basal part of the ascomata; tomentum formed by a dense network of long, simple to branched, hyaline, septate, thin-walled, verruculous hyphae, 4–5 µm thick. Ostiole well developed, 35–45 µm in diam, with short hyaline 0–1-septate periphyses. *Ascomatal wall* 25–40 µm thick, hyaline to pale yellow, composed 3–5 layers of elongated, thick-walled cells, 9–12 × 2–3 µm, cells wall 1.0–1.5 µm, KOH–. *Asci* broadly clavate, normally with 1 macrospore, and (2–)4(–5) microspores, 80–105 × 25–35 µm (n = 10). *Macrospores* hyaline, broadly ellipsoid, 1-septate, constricted at the septum, with pointed to slightly attenuated ends, perisporium well-developed and forming hair-like surface in mature macrospores, (53.0–)56.4–66.2(–75.8) × (23.0–)25.2–31.6(–35.0) µm (n = 30), 1/b (1.8–)2.0–2.3(–2.5); *microspores* hyaline, ellipsoid, 1-septate, with rounded ends, not constricted at the septum, verruculose, (8.0–)9.2–10.4(–11.4) × (4.8–)5.3–6.0(–6.6) µm (n = 60), 1/b (1.4–)1.5–1.9(–2.1).

Distribution, habitat and host range: Examined specimens have only been reported from a few localities in the Yungas cloud forest (2200–3000 m a.s.l.) and a single location in Boliviano-Tucumano forests (940 m. a.s.l.). It grows on sterile corticolous lichens and the infection does not cause visible damage to the host.

Specimens examined: **Bolivia**, La Paz Department, Nor Yungas Province, Chuspipata station, old road Coroico-La Paz, 16º18'18"S, 67º48'55"W, 3009 m a.s.l., disturbed Yungas cloud forest with shrubs and small trees, on sterile crustose lichen, 23 Nov. 2016, *A. Flakus* 28844 (KRAM L-74674, LPB); Santa Cruz Department, Comarapa Province, Amboró National Park, Remate 17°51'39"S, 64°21'15"W, 2270 m a.s.l., natural Yungas forest with big trees, on sterile crustose lichen, 15 May 2017, *A. Flakus* 29165 (KRAM L-74675, LPB), ibid., 29171 (KRAM L-74676, LPB); Tarija Department, Aniceto Arce Province, close to Coyambuyo, between Padcaya and Bermejo, 22º17'23"S, 64º28'50"W, 942 m a.s.l., Sub-Andean Tucumano-Boliviano forest with bryophytes, *Lauraceae* and *Meristomataceae*, on sterile crustose lichen, 26 Jul. 2015, *M. Kukwa* 16732 (LPB).

Notes: This lichenicolous fungus is morphologically similar to *Ovicuculispora macrospora* described from saxicolous sterile lichens from Peru (Etayo 2010). However, examined material differences from the protologue by somewhat smaller macrospores [56.4–66.2(–75.8) × (23.0–)25.2–31.6(–35.0) µm in *Ovicuculispora* cf. *macrospora* vs 67–105 × 32–40 µm in *Ovicuculispora macrospora*], broader microspores [(4.8–)5.3–6.0(–6.6) µm in *Ovicuculispora* cf. *macrospora* vs 4.5–5 µm in *Ovicuculispora macrospora*] and hair-like surface of macrospores (Etayo 2010). We were not able to include *Ovicuculispora macrospora* into our phylogenetic analyses as this species is known so far only from the type locality in Peru. However, *O. macrospora* can also show the

variability of ascospores size and shape as it was reported to *O. parmeliae* (see notes below). Therefore, based on morphological differences between our specimens and type description, we tentatively referred our materials to *O.* cf. *macrospora* before more samples will be collected.

Ovicuculispora parmeliae (Berk. & M.A. Curtis) Etayo, *Bull. Soc. Linn. Provence* **61**: 112. 2010. MycoBank MB 565895. Figs 3B, 4F.

Basionym: *Diplodia parmeliae* Berk. & M.A. Curtis, in Berkeley, *Grevillea* **3**(25): 3. 1874.

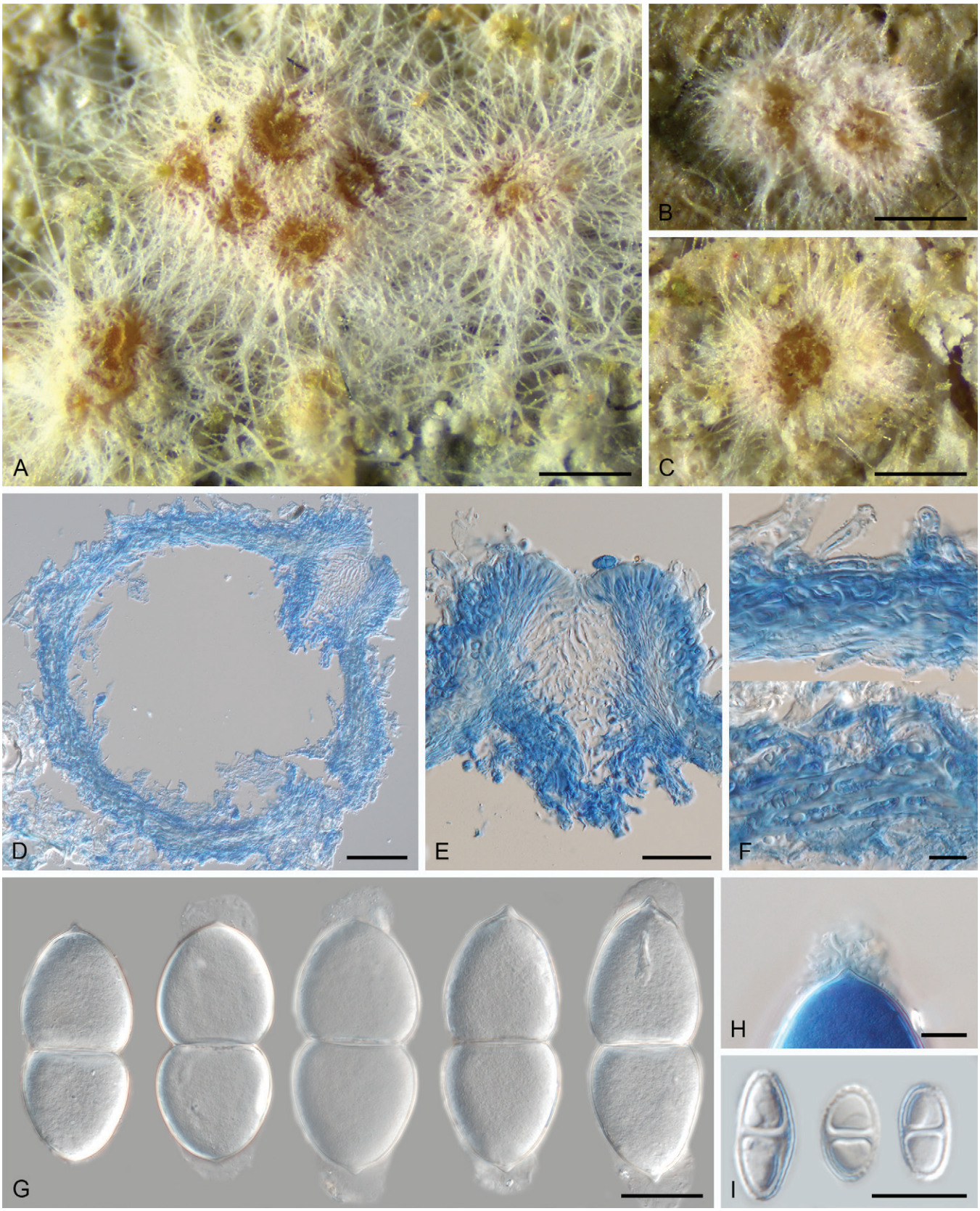

Fig. 5. *Ovicuculispora* cf. *macrospora* (Flakus 29171). **A–C.** Ascomata on the host thallus. **D.** Section of the ascomata (in LPCB). **E.** Section of the ostiole part (in LPCB). **F.** Ascomatal wall (in LPCB). **G.** Macrospores (in water). **H.** Macrospores hair-like surface (in LPCB). **I.** Microspores (in water). Scale bars: A–C = 250 µm; D = 50 µm; E, G = 25 µm; F, H, I = 10 µm.

Synonyms: *Diplodina parmeliae* (Berk. & M.A. Curtis) Sacc., *Syll. Fung. (Abellini)* **3**: 413. 1884.
Nectria parmeliae (Berk. & M.A. Curtis) D. Hawksw., *Bull. Br. Mus. Nat. Hist., Bot*. **9**(1): 76. 1981.
Nectriopsis parmeliae (Berk. & M.A. Curtis) M.S. Cole & D. Hawksw., *Mycotaxon* **77**: 321. 2001.*Typus*: **USA**, South Carolina, on *Parmelia* cf. *rudecta* Ach., *M.A. Curtis* Car. Inf. 1278 (**holotype** K, not examined)
Nectria heterospora Speg., *Boln Acad. nac. Cienc. Córdoba* **11**(4): 523. 1889.
Cucurbitaria heterospora (Speg.) Kuntze, *Revis. gen. pl. (Leipzig)* **3**(3): 461. 1898.*Typus*: **Brazil**, Apiahy, on *Lobaria* sp., 1881/86, *J. Puiggari* 126 (**lectotype** LPS 1.585ª, not examined).
Nectria diplocarpa Ellis & Everh., *Proc. Acad. nat. Sci. Philad*. **42**: 244. 1890.
Cucurbitaria diplocarpa (Ellis & Everh.) Kuntze, *Revisio generum plantarum* **3**(3): 461. 1898.

Typus: **USA**, New York, Farmington, on *Physcia* cf. *aipolia*, Dec. 1888, *E. Brown* 17 (**holotype** NY, not examined).

Ascomata perithecioid, globose, scattered or in group 2–5 ascomata, pale to medium pink to orange, mostly covered by hyphae, which produce a whitish to pinkish tomentum at the lower part, collapsed when dry, 200–350 µm in diam. *Ascomatal wall* composed of 5–7 layers of radially compressed pseudoparenchymatous thick-walled cells, KOH–. *Asci* broadly clavate, normally with 1 macrospore, and 3–4 microspores, 50–70 × 10–15 µm (n = 8). *Macrospores* hyaline, broadly ellipsoid to ellipsoid, 1-septate, rarely 2-septate, not constricted to constricted at the septa, with round ends, smooth-walled, (40.0–)44.2–56.5(–64.0) × (16.5–)19.0–25.2(–29.5) µm (n = 50), 1/b (1.7–)1.9–2.5(–3.2); *microspores* ellipsoid, hyaline, 1-septate, not constricted at the septa, verruculose, (8.5–)9.2–12.2(–13.8) × (3.8–)4.2–5.4(–6.2) µm (n = 80), 1/b (1.5–)1.9–2.3(–2.7).

Distribution, habitat and host range: *Ovicuculispora parmeliae* seems to be a cosmopolitan generalist species found on various distantly related lichen genera from families *Candelariaceae*, *Cladoniaceae*, *Graphidaceae*, *Lecanoraceae*, *Pannariaceae*, *Parmeliaceae*, *Physciaceae* and *Teloschistaceae* (e.g. Etayo 2010, Tadome & Ohmura 2021).

Specimens examined: **Bolivia**, Cochabamba Department, Tiraque Province, Carrasco National Park, Camino de los Nubes, Antenas Sillar-Villa Tunari old road, 17º12’29”S, 65º41’24”W, 3591 m a.s.l., open area with shrubs, on *Sticta* sp., 30 Nov. 2014, *A. Flakus* 26009 (KRAM L-74677, LPB), ibid., on *Sticta* sp., *A. Flakus* 26010 (KRAM L-74678, LPB); ibid., on *Sticta* sp., *A. Flakus* 26011 (KRAM L-74679, LPB); La Paz Department, Murillo Province, Sainani, Valle del Zongo, 16º07’20”S, 68º05’09”W, 2220 m a.s.l., open area with shrubs and scattered trees, on *Hypotrachyna* sp., 7 Dec. 2014, *A. Flakus* 26252 (LPB); Tarija Department, Aniceto Arce Province, Tariquía Flora and Fauna National Reserve, between la Cumbre and camamento los Alisos, 22º01’02”S, 64º34’51”W, 2135 m a.s.l., Boliviano-Tucumano forest with *Alnus acuminata* and *Polylepis*, on *Remototrachyna* cf. *costaricensis*, 22 July 2015, *A. Flakus* 27067 (KRAM L-74680, LPB); ibid., 22º02’38”S, 64º35’47”W, 2460 m a.s.l., on *Crocodia aurea*, 22 July 2015, *A. Flakus* 27025 (LPB); ibid., 21º59’21”S, 64º36’52”W, 3040 m a.s.l., open area with shrubs and rocks, on *Heterodermia* sp., 25 July 2015, *A. Flakus* 27227 (KRAM L-74682, LPB); Burnet O’Connor Province, Sandiego Sur, top of the hill on old road between Tarija and Entre Ríos, 21º27’04”S, 64º13’59”W, 1812 m a.s.l., Boliviano-Tucumano forest, on *Punctelia* sp., 30 July 2015, *J. Etayo* 32636 (hb. Etayo, LPB).

Notes: *Ovicuculispora parmeliae* is a quite variable species regarding to ascospore shape and host selection. Additionally, considerable variation in the size of macrospores has been reported (Hawksworth & Booth 1976, Etayo 2010, Zhurbenko 2014), even within a single specimen or population. This has raised many concerns about the species circumscription and the taxonomy based on macrospore features, distribution data and host selection (Hawksworth 1981, Flakus *et al.* 2006, Etayo 2010, Etayo & van den Boom 2013, Zhurbenko 2014, Tadome & Ohmura 2021).

During this study, we observed a huge variability within three specimens of *Ovicuculispora parmeliae* collected on *Sticta* sp. from the same locality. The macrospores exhibit a range of shapes and sizes, including: ellipsoid, 1-septate, not constricted at the septum, (41.0–)43.5–53.2(–61.0) × (16.5–)17.8–20.6(–22.8) µm (n = 25) in KRAM L-74677; ellipsoid, 1-septate, not constricted at the septum, (26.3–)30.8–42.3(–48.2) × (12.2–)13.0–18.4(–23.8) (n = 25) in KRAM L-74678; broadly ellipsoid, 1(–2)-septate, constricted at the septum, (57.2–)65.5–80.8(–85.0) × (27.2–)32.2–36.6(–41.0) µm (n = 25) in KRAM L-74679. However, the ITS sequences generated for these abovementioned specimens showed 100 % identity and 99 % of similarity to other specimens growing on different hosts. Similar results were found in multi-gene phylogeny (Fig. 2), where the specimens on different hosts formed a single well-supported clade. However, to better understand the intraspecific variability of the species a larger sampling is needed.

Paranectria Sacc., *Michelia* **1**(3): 317. 1878. MycoBank MB 3707.

Type species: *Paranectria affinis* Sacc.

For a detailed description see Rossman (1983).

Notes: This genus is characterized by globose luteous ascomata, with indistinct tomentum at the base, 8-spored clavate asci and 3-septate hyaline ascospores with elongate appendages. Two specimens of the generic type *P. affinis* formed a well-supported monophyletic clade which showed a sister relationship to the *Rossmaniella* clade.

The genus *Paranectria* has been known to include only lichenicolous species (Rossman *et al.* 1999), but recently *Paranectria longiappendiculata* was described as a fungicolous species on *Meliola* sp. (Bermúdez-Cova *et al.* 2023). However, this species required further studies to confirm its relationship to the generic type of *Paranectria*.

Paranectria affinis Sacc., *Michelia* **1**(3): 317. 1878. MycoBank MB 236721. Figs 3D, 4B.
Basionym: *Sphaeria affinis* Grev., *Scott. crypt. fl. (Edinburgh)* **4**: 186. 1825.

Synonyms: *Cucurbitaria affinis* (Sacc.) Kuntze, *Revis. gen. pl. (Leipzig)* **3**(3): 460. 1898.
Dialonectria affinis (Sacc.) Cooke, *Grevillea* **12**(64): 110. 1884.
Nectria affinis (Sacc.) Cooke, *Grevillea* **7**(41): 9. 1878.

Typus: **Great Britain**, Appin, on branches of *Bangia atrovirens* (*Ephebe lanata*), 10 Oct. 1824, *Carmichael* (slide from **holotype** K-M000293541 = IMI 123655).

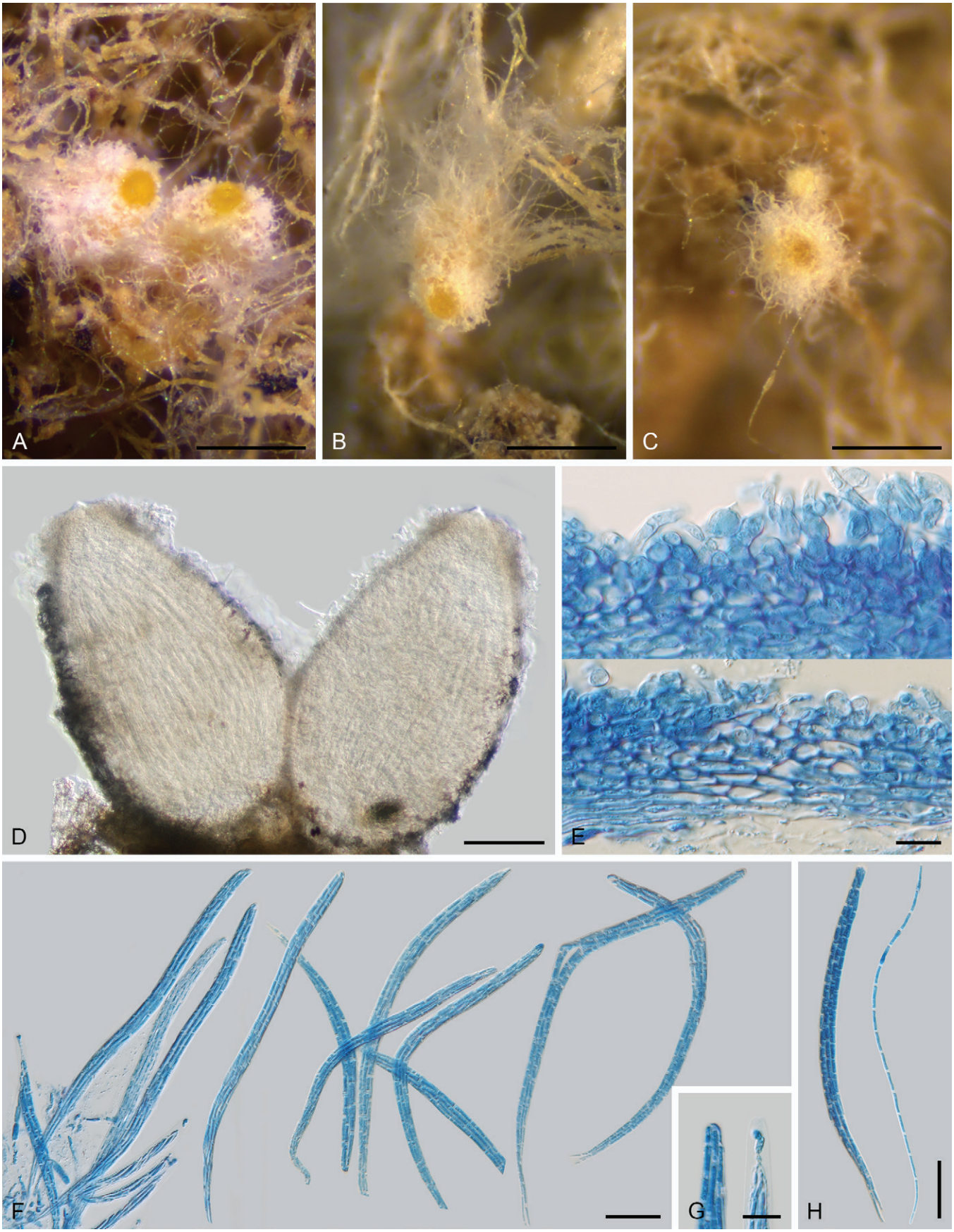

Fig. 6. *Rossmaniella coenogonii* (holotype Kukwa 15078a). **A–C.** Ascomata on the host thallus. **D.** Squashed ascomata (in water). **E.** Ascomatal wall (in LPCB). **F.** Asci (in LPCB). **G.** Mature (left) and young (right) ascus apex (in LPCB). **H.** Ascus and ascospore (in LPCB). Scale bars: A–C = 250 µm; D = 100 µm; E, G = 10 µm; F, H = 25 µm.

The examined slides from the holotype contain narrowly ellipsoid to fusiform, 3-septate ascospores with elongate appendages at each end, (24.0–)24.8–29.2(–30.0) × (5.0–)6.2–7.8(–9.0) µm (n = 25). For a detailed description see (Rossman 1983).

Distribution, habitat and host range: *Paranectria affinis* seems to be a host-specific taxon since is only known to grow on *Ephebe lanata* (*Lichinaceae*). However, Rossman (1983) recorded this fungus also on *Pseudephebe pubesces* (*Parmeliaceae*) based on a specimen from Fontainebleau (France). An examined specimen from the same region in France (UPS F-522124) confirmed that the species grows on *Ephebe lanata* and therefore we assume that the host species was erroneously reported as *Pseudephebe*. This lichenicolous fungus has been rarely collected but is locally abundant and it was reported from Great Britain, France, Norway and Sweden (e.g. Rossman 1983, Rossman *et al.* 1999, Westberg *et al.* 2021).

Specimens examined: **France**, Fontainebleau, on *Ephebe* sp., 10 Mar. 1859, *Du Cuvier* (slide, K-M000629348 = IMI 52294); Île-de-France, Fontainblau, on *Ephebe lanata*, 6 Apr. 1860, collector unknown (UPS F-522124). **Great Britain**, Scotland, Glen Lethnot, Stoneycroft, on *Ephebe lanata,* 6 Sep. 2017, *P.F. Cannon* 3349 (K-M000253675). **Sweden**, Dalarna, Storön in Bysjön, 9 km south of Nås church, on the thallus of Ephebe lanata on a boulder in the shoreline zone on the north side of the island, 60.3827 N 14.51433 E, 220 m a.s.l., 4 Apr. 2005, *J. Hermansson* 14368 (UPS F-561663)

Rossmaniella Darmostuk, Etayo & Flakus, ***gen. nov.*** MycoBank MB 858384.

Etymology: Named to honour Dr. Amy Y. Rossman, who made an enormous contribution to the taxonomy of *Hypocreales*.

Type species: *Rossmaniella filispora* Darmostuk, Etayo & Flakus (introduced below).

Ascomata perithecioid, ovoid to obpyriform, clustered in groups of 3–12 ascomata, rarely scattered, yellowish to bright orange, with well-developed tomentum at the lower part of ascomata, not collapsing when dry, superficially covered by a net of hyphae. *Ascomatal wall* 25–35 µm thick, composed of 7–10 layers of compressed irregular cells. *Asci* narrowly cylindrical, without apical thickness, up to 300 µm long, 8-spored. *Ascospores* hyaline, filiform, straight to slightly curved, with rounded to pointed ends, 8–16-septate, smooth-walled, parallel to twisted in the ascus.

Notes: The newly described genus *Rossmaniella* corresponds to the so-called *Nectria byssophila* group, which includes species with distinct tomentum, obpyriform ascomata, long filiform multiseptate ascospores and characterized by lichenicolous lifestyle (Etayo 2003, 2017, Etayo & Sancho 2008, Flakus *et al.* 2019a). It differs from other similar lichenicolous genera with long filiform ascospores by its morphological features of ascomata. The genus *Neobaryopsis* can be distinguished by having bigger ascomata, up to 500–700 µm, not covered by tomentum, long asci with thickened apex, 50–90 septate ascospores and synnematous asexual morph (Flakus *et al.* 2019a). Another genus, *Lichenobarya*, differs from *Rossmaniella* by having solitary brownish ascomata and longer filiform ascospores (Etayo 2002). Despite their morphological similarities, these genera are phylogenetically distant.

The newly established genus *Rossmaniella* consists of four novel species.

Rossmaniella coenogonii Darmostuk, Kukwa & Flakus, ***sp. nov.*** MycoBank MB 858385. Fig 6.

Etymology: Named after the host lichen genus, *Coenogonium*.

Typus: **Bolivia**, Cochabamba Department, Carrasco Province, Parque Nacional Carrasco, near Río López Mendoza, 2248 m a.s.l., lower montane Yungas cloud forest, Andino montano (Montano), on corticolous *Coenogonium* sp., 27 Nov. 2014, *M. Kukwa* 15078a (**holotype** LPB).

Ascomata perithecioid, ovoid to pyriform, not collapsed when dry, superficial, solitary, pale orange, 300–430 × 185–240 µm (n = 7), ascomata surface fully covered by not dense, whitish, arachnoid tomentum, composed of hyaline, septate, thin-walled, verruculose hyphae, 4–5 µm thick, without papilla in ostiolar region. *Ascomatal wall* 25–40 µm wide, slightly thicker at the upper part than in the lower part, hyaline to pale yellow, composed of two layers of flattened cells: external layer composed of 3–5 layers of isodiametric, thin-walled cells, 6–8 × 5–6 µm; an inner region with 2–4 layers of elongated thin-walled cells, 9–12 × 2–3 µm, KOH–. *Asci* narrowly cylindrical, without apical thickness, 8-spored, (175–)180–200(–220) × (8.0–)8.4–10.0(–10.4) µm (n = 10). *Ascospores* hyaline, (12–)14–16-septate, filiform, mostly curved to sigmoid, parallel to spirally twisted in the ascus, proximal ends rounded, distal end pointed, (170–)180–200(–210) × (1.8–)2.0–2.6(–3.0) µm (n = 25), individual cells (6.4–)8.0–12.2(–12.8) µm (n = 30) long. *Conidiomata* not observed.

Distribution, habitat and host range: This lichenicolous fungus is only known from the type locality in the Yungas cloud forest (2200 m a.s.l.) growing on the thallus of corticolous *Coenogonium* sp. This species likely causes a strong pathogenic effect on the host, forming discoloured infected areas up to 1 cm in size, covered by a whitish, arachnoid tomentum.

Specimen examined of Nectria byssophila: **Ceylon**, Nuwara Eliya, on mosses on the tree trunk, 19 Jun. 1927, *T. Petch* (K-M001434927)

Notes: *Nectria byssophila* s. str. is a poorly known species originally described from Ceylon where was growing on epiphytic mosses (Petch 1944). Subsequently, this name was commonly used for hypocrealean lichenicolous fungi growing on different hosts with long filiform ascospores and ovoid to pyriform yellow orange ascomata (Etayo 2003, 2017, Etayo & Sancho 2008). The type specimen (Fig. 7, K-M001434927) was examined by us and it has a pale orange ovoid ascomata (only seven ascomata observed), mainly scattered, totally covered by whitish tomentum, 300–350 × 200–250 µm (n = 7). Unfortunately, asci and ascospores

were not observed. Following the description by Rossman (1983) and macroscopic features, *Nectria byssophila* exhibits a greater resemblance to *Rossmaniella coenogonii* than to other species within the genus *Rossmaniella*. However, a fresh collection is from the type locality in Ceylon is needed to reveal the real relationship of this species to the genus *Rossmaniella*.

Only two lichenicolous species of the order *Hypocreales* were previously reported on *Coenogonium* and both were from tropical regions. The first, *Nectriopsis mindoensis*, was reported on an undetermined lichen host from Colombia (Samuels 1988) and the second, *Niesslia coenogonii*, was described as lichenicolous fungus from Panama on *Coenogonium luteum* (van den Boom *et al.* 2017).

Rossmaniella cryptica Darmostuk, Etayo & Flakus, ***sp. nov.*** MycoBank MB 858386. Figs 3I, 4A, 8.

Etymology: Named after morphological similarity to *Rossmaniella filispora*.

Typus: **Bolivia**, Tarija Department, Aniceto Arce Province, Reserva Nacional de Flora y Fauna Tariquía, between la Cumbre and camamento los Alisos, 22º00'41"S, 64º36'02"W, 2560 m a.s.l., Boliviano-Tucumano forest with *Alnus acuminata* and *Polylepis*, on *Hypotrachyna* sp., 22 Jul. 2015, *A. Flakus* 26967 (**holotype** KRAM L-74683, **isotype** LPB).

Ascomata perithecioid, ovoid to pyriform, not collapsed when dry, superficial, solitary to clustered in groups of 3–4(–7) ascomata, vivid orange, with brighter ostiole part, (330–)350–390(–450) × (220–)235–260(–280) µm (n = 10), lower half to entire ascomata covered by dense yellowish-orange tomentum, composed of hyaline, septate, thin-walled, verruculose hyphae, 4–5 µm thick. *Ascomatal wall* 28–35 µm thick, slightly thicker at the upper part, hyaline to pale yellow, composed of two layers of cells: external layer composed of 3–5 layers of isodiametric, thin-walled cells, 5–6 µm in diam; an inner region with 3–5 layers of elongated thin-walled cells, 8–10 × 2–3 µm, K–. *Asci* narrowly cylindrical, without apical thickness, 8-spored, (160–)175–180(–195) × (8.5–)9.0–11.2(–12.0) µm (n = 10). *Ascospores* hyaline, 8–12(–13)-septate, septa often hardly visible, filiform, straight or slightly curved, parallel to spirally twisted in the ascus, proximal ends rounded, distal end pointed, (160–)165–175(–180) × (2.4–)2.5–2.8(–3.0) µm (n = 25), individual cells (13.2–)15.2–21.0(–23.8) µm (n = 30) long. *Conidiomata* not observed.

Distribution, habitat and host range: The species is known from the Boliviano-Tucumano forest (2500 m a.s.l.) in Bolivia on corticolous *Hypotrachyna* species. Moreover, a specimen from New Zealand on *Thelotrema* species (reported as *Thelotrema clathroporina*) was reported (K-M000454728). This specimen was previously published under the name *Nectria byssophyla* by Rossman (1983). The examined specimen from Bolivia on *Hypotrachyna* sp. showed a strong pathogenic effect, forming discoloured infection spots.

Specimens examined: **Bolivia**, Tarija Department, Aniceto Arce Province, Tariquía Flora and Fauna National Reserve, between la Cumbre and camamento los Alisos, 22º00'40.9"S, 64º35'48.9"W, 2485 m a.s.l., Boliviano-Tucumano forest with *Alnus acuminata* and cactus, on apothecial disk of *Hypotrachyna* sp. on trunk, 22 Jul. 2015, *J. Etayo* 32974 (hb. Etayo); 22º00'50.4"S, 64º36'24.3"W, on *Leucodermia fertilis*, 27 Jul. 2015, *J. Etayo* 29713 (LPB); ibid., on dead *Hypotrachyna* sp. on twig of *Polylepis*, 27 Jul. 2015, *J. Etayo* 29712 (hb. Etayo); ibid., *J. Etayo* 29822 (LPB). **New Zealand**, Waiwera Scenic Reserve, 20 m N of Auokland, on *Thelotrema 'chathroporina'* on bark of *Rhopalostylis sapida*, 30 Oct. 1981, *J.K. Barthy* H1275/81/YN2 (K-M000454728 = IMI 263194a).

Fig. 7. *Nectria byssophyla* (holotype K-M001434927). **A.** Original label. **B.** Ascomata on the host thallus. **C.** Squashed ascomata (in water). Scale bars: B = 250 µm; C = 100 µm.

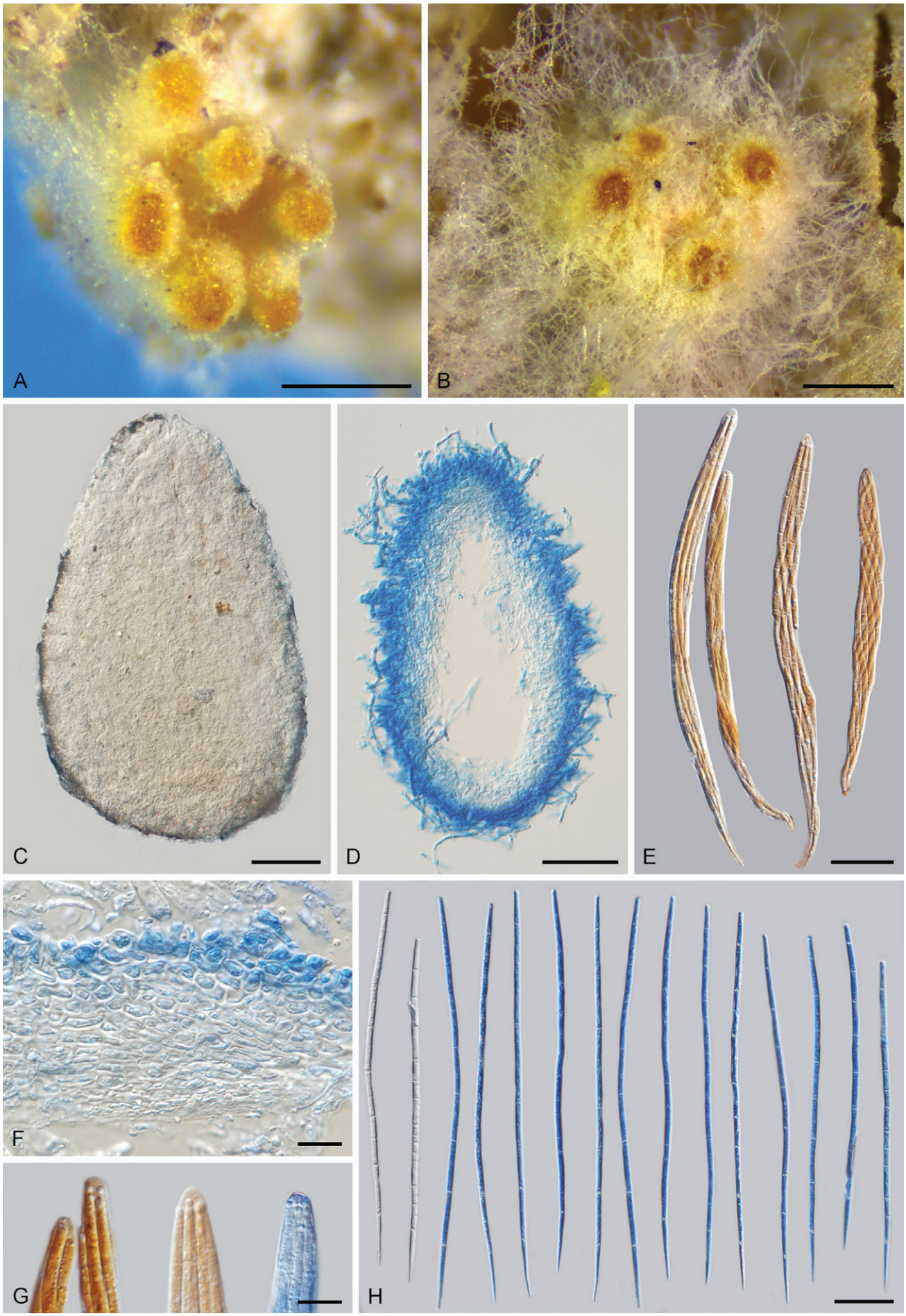

Fig. 8. *Rossmaniella cryptica* (holotype Flakus 26967, except B from K-M000454728). **A, B.** Ascomata on the host thallus. **C.** Squashed ascomata (in water). **D.** Section of the ascomata (in LPCB). **E.** Asci (in Congo Red). **F.** Ascomatal wall (in LPCB). **G.** Asci apex (in Congo Red and LPCB). **H.** Ascospores (first and second in water, other in LPCB). Scale bars: A, B = 250 µm; C, D = 50 µm; E, H = 25 µm; F, G = 10 µm.

Notes: This species is morphologically very similar to *Rossmaniella filispora*, but can be distinguished by the combination of morphological features and phylogenetic position. *Rossmaniella cryptica* has somewhat bigger, vivid orange ascomata, mostly in a group up to 4(–7) [in *R. filispora* (5–)7–12 ascomata in a group], bright orange ostiolate part without distinct hairs (distinct hairs present in *R. filispora*), somewhat shorter ascospores (160–)165–175(–180) µm [in *R. filispora* (165–)180–200(–210) µm] with longer, (13.2–)15.2–21.0(–23.8) µm, individual cells [in *R. filispora* (11.0–)11.5–13.7(–14.5) µm].

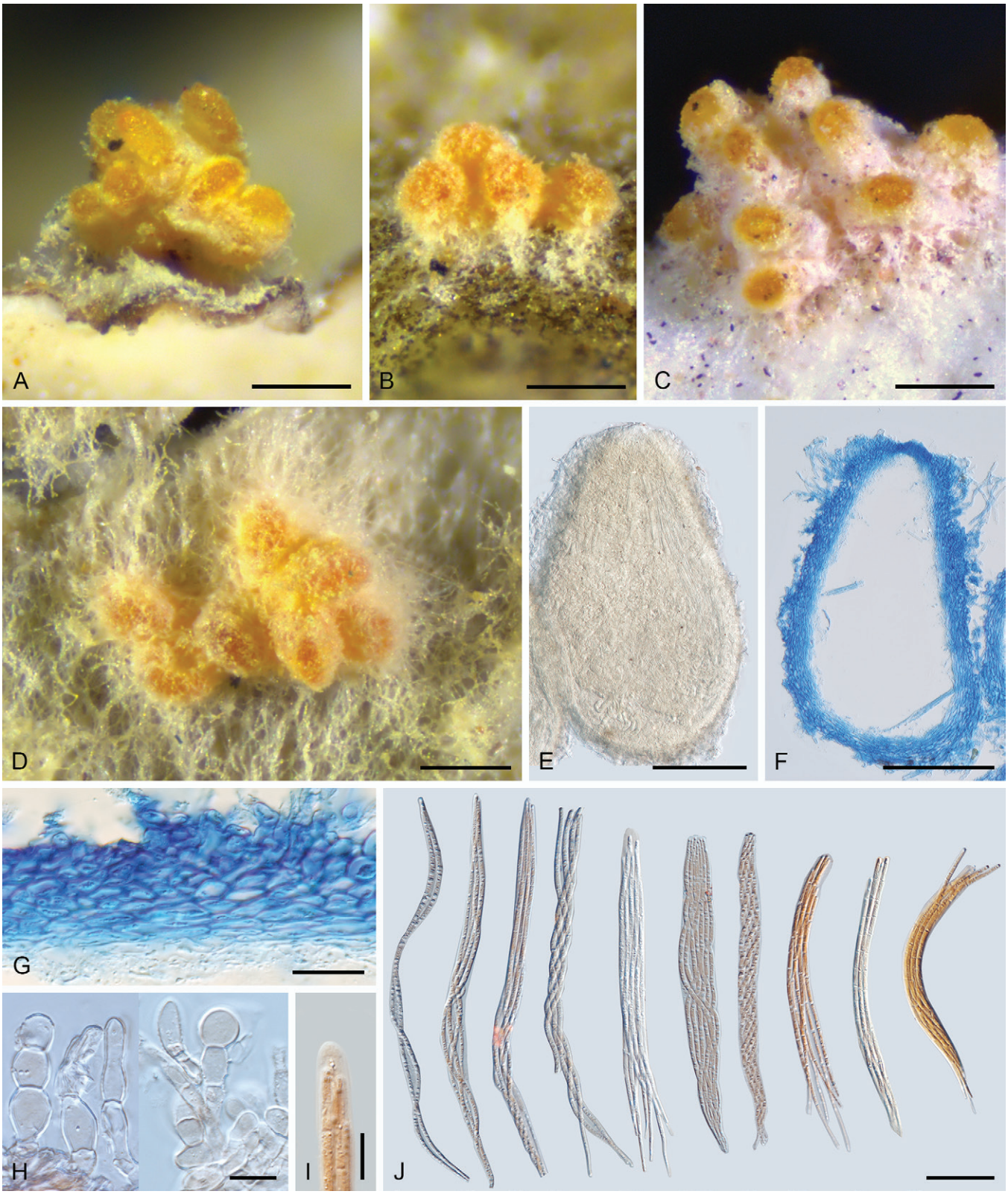

Fig. 9. *Rossmaniella filispora* (holotype Flakus 26556, except B from Flakus 29557). **A–D.** Ascomata on the host thallus. **E.** Squashed ascomata (in water). **F.** Section of the ascomata (in LPCB). **G.** Ascomata wall (in LPCB). **H.** Hairs (in Congo Red). **I.** Ascus apex (in Congo Red). **J.** Asci with ascospores (in Congo Red). Scale bars: A–D = 250 µm; E, F =100 µm; G, H, I = 10 µm; J = 25 µm.

Rossmaniella filispora Darmostuk, Etayo & Flakus, ***sp. nov.*** MycoBank MB 858387. Figs 3F, 3G, 9.

Etymology: Named after the filiform ascospores.

Typus: **Bolivia**, Chuquisaca Department, Belisario Boeto Province, close to Padilla between Nuevo Mundo and Santa Rosa, 18º57'12"S, 64º16'37"W, 1790 m a.s.l., transition between Boliviano-Tucumano forests and dry interandean vegetation, on corticolous *Punctelia* sp., 16 Jul. 2015, *A. Flakus* 26556 (**holotype** KRAM L-74684, **isotype** LPB).

Ascomata perithecioid, ovoid to pyriform, not collapsed when dry, superficial, clustered in dense groups of (5–)7–12 ascomata, pale to bring orange, ostiolate part the same colour as ascomatal surface, the lover part covered by hyaline tomentum, becoming more compact towards the top of ascomata, (220–)270–340(–365) × (190–)200–235(–270) µm (n = 20), sometimes individual ascomata has irregular form in the group due to compression by other ascomata. Ascomatal surface near the ostiole with short, cylindric, hyaline, 1–2-septate hairs, sometimes with inflated tips, 20–55 × 5–7 µm. *Ascomatal wall* 20–35 µm thick, thicker at the upper part, hyaline to pale yellow, composed of two layers of cells: external layer composed of 3–5 layers of isodiametric to irregular, thin-walled cells, 5–7 µm in diam; an inner region with 3–5 layers of elongated thin-walled cells, 10–15 × 3–4.5 µm, KOH–. *Asci* narrowly cylindrical, without apical thickness, 8-spored, (164–)180–210(–230) × (8.5–)9.0–13.0(–14.4) µm (n = 15). *Ascospores* hyaline, 8–12-septate, septa often hardly visible, filiform, straight or curved, parallel to twisted in the ascus proximal ends rounded, distal end pointed, (165–)180–200(–210) × (2.8–)3.0–3.4(–3.8) µm (n = 30), individual cells (11.0–)11.5–13.7(–14.5) µm (n = 30) long. *Conidiomata* not observed.

Distribution, habitat and host range: This species was reported from scattered localities in Europe (Spain) and South America (Bolivia). *Rossmaniella filispora* is probably not a host-specific taxon as it was found on several lichen hosts belonging to the *Parmeliaceae* (*Flavopunctelia*, *Parmotrema, Hypotrachyna*), *Peltigeraceae* (*Peltigera*) and *Ramalinaceae* (*Phyllopsora*). This species did not show any pathogenic effect on the host.

Specimens examined: **Bolivia**, Chuquisaca Department, Belisario Boeto Province, close to Padilla between Nuevo Mundo and Santa Rosa, 18º57'06"S, 64º16'14"W, 1936 m a.s.l., transition between Boliviano-Tucumano forests and dry interandean vegetation, on *Flavopunctelia* sp., 16 Jul. 2015, *A. Flakus* 26594 (LPB); ibid., 18º57'12"S, 64º16'37"W, 1790 m a.s.l., transition between Boliviano-Tucumano forests and dry interandean vegetation, on corticolous *Flavopunctelia* sp., 16 Jul. 2015, *A. Flakus* 26557 (LPB); Cochabamba Department, Carrasco Province, Carrasco National Park, Korikaza close to Monte Punku, 17º33'30"S, 65º16'32"W, 2880 m a.s.l., lower montane Yungas cloud forest, on corticolous *Parmotrema* sp., 27 Nov. 2014, *J. Etayo* 29951 (LPB); Tarija Department, Burnet O'Connor Province, close to los Pinos, old road between Entre Ríos and Tarija, 21º24'50"S, 64º18'33"W, 2149 m a.s.l., Boliviano-Tucumano forest dominated by shrubs, with *Alnus acuminata*, *Podocarpus* and *Ericaceae*, on *Phyllopsora* sp., 29 Jul. 2015, *A. Flakus* 27468 (KRAM L-74686, LPB); ibid., on *Parmotrema* sp., *M. Kukwa* 16861a (UGDA L, LPB); ibid., 21º27'48"S, 64º13'24"W, 1943 m a.s.l., Boliviano-Tucumano forest with *Podocarpus*, on corticolous *Punctelia* sp., 28 Jul. 2015, *A. Flakus* 27389a (LPB); ibid., 21º25'07"S, 64º18'50"W, 2190 m a.s.l., Boliviano-Tucumano forest dominated by shrubs, Andino Montano belt, on *Peltigera didactyla*, 29 Jul. 2015, *J. Etayo* 30600 (LPB); ibid., 112 km from Tarija on the way to Entre Ríos, near San Diego, 21°26'28"S, 64°14'37"W, 1620 m a.s.l., Tucumano-Boliviano montano forest, on *Parmotrema* sp. on twig, 9 Aug. 2012, *J. Etayo* 28594 (hb. Etayo); near Soledad, 21°39'52"S, 64°07'22"W, 1700 m, Tucumano-Boliviano montano forest, on *Parmotrema reticulatum* on twig, 11 Aug. 2012, *J. Etayo* 28777 (LPB). **Spain**, Guipuzcoa, Peñass de Aia, Lesakako Bidea, antes del tunel, 43 16'25"N, 1 47'35.5"W, 500 m a.s.l., on *Hypotrachyna revoluta* on *Fagus sylvatica*, 31 Aug. 2019, *J. Etayo* 31862 (hb. Etayo).

Notes: The species is morphologically very similar to *Rossmaniella cryptica*, but it can be distinguished by specific morphological features and its phylogenetic position. However, *R. filispora* does not seem to be a rare species in the tropical forests of Bolivia and is known from several localities.

Rossmaniella tylophori Darmostuk & Flakus, ***sp. nov.*** MycoBank MB 858388. Figs 3H, 10.

Etymology: Named after the host lichen genus, *Tylophoron*.

Typus: **Bolivia**, Chuquisaca Department, Luis Calvo Province, Iñao National Park and Integrated Management Natural Area, between Ticucha and Entre Ríos, 19º31'09"S, 63º53'31"W, 1373 m a.s.l., disturbed area with shrubs, on corticolous *Tylophoron protrudens*, 19 Jul. 2015, *A. Flakus* 26805 (**holotype** KRAM L-74687, **isotype** LPB)

Ascomata perithecioid, ovoid to pyriform, superficial, solitary, lemon yellow, (200–)230–270(–300) × (150–)160–175(–185) µm (n = 15), covered by not dense whitish tomentum, composed of simple to branched, hyaline, septate, thin-walled, verruculose hyphae, 4–5 µm thick. Ascomata surface evenly coloured, without hairs near ostiole part. *Ascomatal wall* 18–25 µm thick, slightly thicker at the upper part, hyaline to pale yellow, composed of two layers: an external layer of globose, thin-walled cells, 2–4 × 2–3 µm; an inner region of flattened, thin-walled cells, 3–12 × 1–2 µm, KOH–. *Asci* cylindrical, without apical thickness, 8-spored, (170–)175–180(–200) × (12.6–)13.0–13.8(–14.2) µm (n = 15). *Ascospores* hyaline, 8–12-septate, filiform, straight or rarely slightly curved, parallel to rarely twisted in the ascus, both ends rounded, (125–)140–155(–180) × (2.8–)3.4–4.4(–4.6) µm (n = 30), individual cells (10.0–)12.0–15.6(–16.8) µm (n = 30) long. *Conidiomata* not observed.

Distribution, habitat and host range: This species is known only from the type locality in Bolivia. This fungus grows on corticolous *Tylophoron protrudens* and the infection does not cause visible damage to the host thallus.

Notes: *Rossmaniella tylophori* can be distinguished from other *Rossmaniella* species by solitary lemon-yellow ascomata, shorter and wider ascospores and host specificity. However, since the species is known only from a single collection, the host range is unknown. Previously only two lichenicolous species were reported on *Tylophoron* species, i.e. *Taeniolella serusiauxii* reported from Europe and tropical regions (Heuchert *et al.* 2018) and *Chaenothecopsis pilosa* described from Tanzania (Tibell & Ryman 1995).

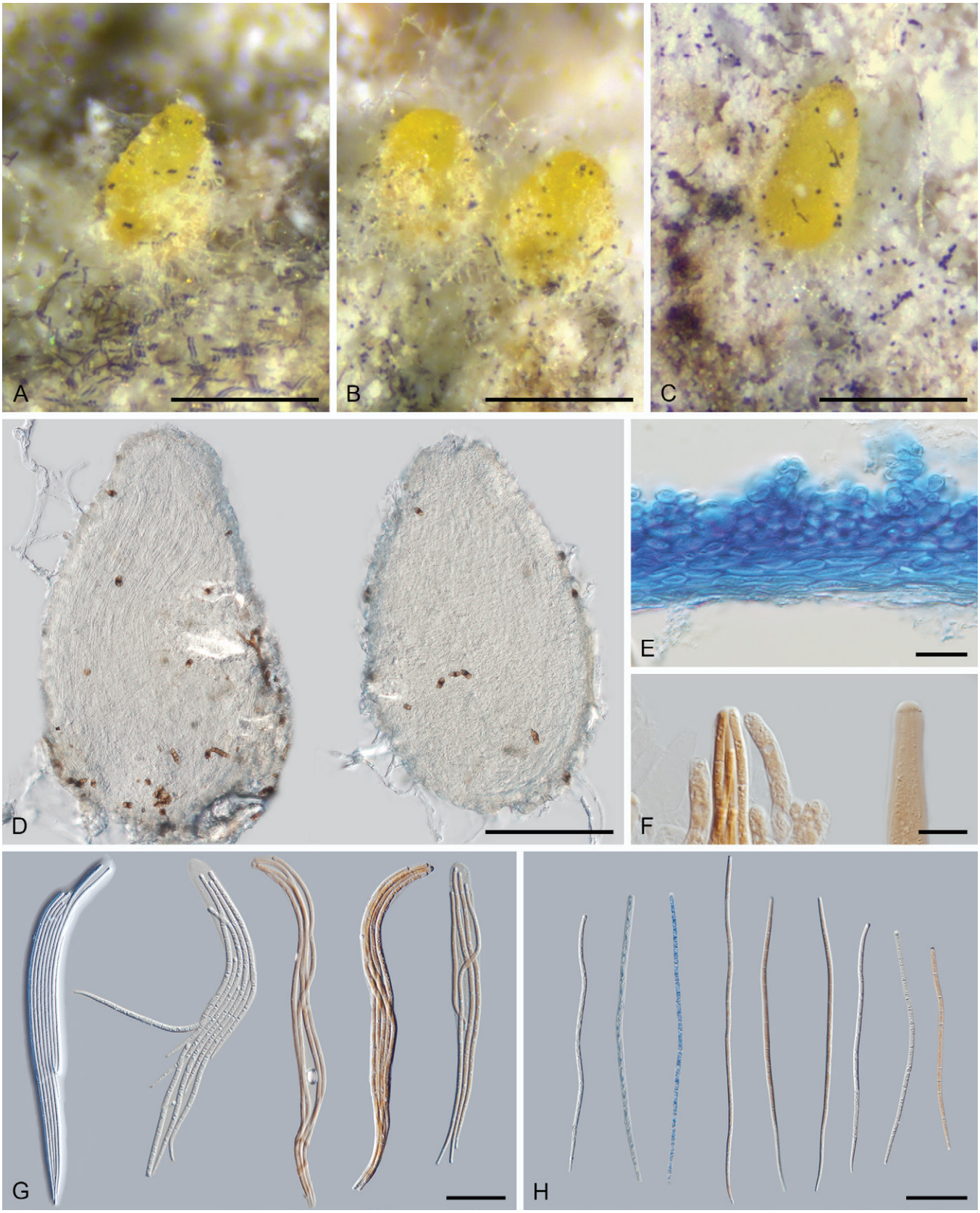

Fig. 10. *Rossmaniella tylophori* (holotype Flakus 26805). **A–C.** Ascomata on the host thallus. **D.** Squashed ascomata (in water). **E.** Ascomatal wall (in LPCB). **F.** Asci apex (in Congo Red). **G.** Asci (in Congo Red). **H.** Ascospores (in Congo Red and LPCB). Scale bars: A–C = 250 µm; D = 100 µm; E, F = 10 µm; G, H = 25 µm.

Sphaeronectria Darmostuk, Etayo & Flakus, ***gen. nov.*** MycoBank MB 858389.

Etymology: Referring to the globose ascomata.

Type species: *Sphaeronectria lichenophila* (Speg.) Darmostuk, Etayo & Flakus

Ascomata perithecioid, superficial, globose to subglobose, constricted laterally or apically, yellowish to orange, with tiny tomentum on the lower part of ascomata, 150–250 µm diam., covered by abundant septate hyaline hyphae, 50–100 µm long. *Ascomatal wall* formed by several layers of cells, hyaline to pale yellowish in the outer part, up to 20 µm thick, superficially paraplectenchymatous, KOH–. *Asci* unitunicate, subcylindrical, 4-spored, without apical thickness. *Ascospores* hyaline, 1-septate, ellipsoid, with pointed ends, slightly constricted at the septa, smooth-walled. *Conidiomata* not observed.

Notes: Previously the type species of *Sphaeronectria* (*S. lichenophila*) was included in the genus *Nectriopsis*, typified by *N. violacea*, but based on our phylogenetic results, *S. lichenophila* showed a different phylogenetic position in *Paranectriaceae*, whereas *Nectriopsis* is a member of *Bionectriaceae*. Currently, the genus is monotypic.

Sphaeronectria lichenophila (Speg.) Darmostuk, Etayo & Flakus, ***comb. nov.*** MycoBank MB 858390. Figs 3E, 4D.
Basionym: *Nectria lichenophila* Speg., *Boln Acad. Nac. Cienc. Córdoba* **11**(4): 525. 1889.
Synonyms: *Nectria spegazzinii* Vouaux, *Bull. Soc. Mycol. Fr.* **28**: 189. 1912.
Nectriopsis lichenophila (Speg.) Etayo, *Bibliotheca Lichenologica* **84**: 71. 2002.*Typus*: **Brazil**, Apiahy, on *Anaptychia* cf. *podocarpa*, 1881, *J. Puiggari* (**holotype** LPS-1587).
Solenopezia [*Solenopeziza*] *tetraspora* Henn., in Engler, *Pflanzenw. Ost-Afrikas Nachbarg., Teil C*: 30. 1895. *Typus*: **Tanzania**, on thallus of *Physcia integrata* Nyl., unknown collection date, *Holst* n. 795 (type not located).

Ascomata perithecioid, superficial, globose to subglobose, yellow to orange, collapsed when dry, with tiny subiculum on the lower part of ascomata, covered by abundant septate hyaline hairs, 150–250 µm diam. *Ascomatal wall* formed by several layers of cells, yellowish externally, up to 20 µm thick, inner hyaline, 10–12 µm, KOH–. *Asci* unitunicate, subcylindrical, 4-spored, 70–80 × 7–10 µm (n = 20). *Ascospores* hyaline, 1-septate, ellipsoid, with pointed and sometimes apiculate ends, slightly constricted at the septa, smooth-walled, without perisporium, (16.8–)19.4–24.4(–26.6) × (5.9–)6.2–7.5(–8.4) µm (n = 50). *Conidiomata* not observed.

Distribution, habitat and host range: This species is known from numerous localities from South America and Africa (Tanzania), growing on several species of *Heterodermia* s. lat. (Etayo 2002, 2017). However, the record from Tanzania needs revision as we were not able to locate the specimen in the collection of P.C. Hennings stored at B.

Specimens examined: **Bolivia**, Chuquisaca Department, Belisario Boeto Province, close to Padilla between Nuevo Mundo and Santa Rosa, 18º57’12”S, 64º16’37”W, 1790 m a.s.l., transition between Boliviano-Tucumano forests and dry interandean vegetation, on *Heterodermia* cf. *spinigera*, 16 Jul. 2015, *A. Flakus* 26552 (LPB), ibid., on *Heterodermia comosa*, *M. Kukwa* 16271 (UGDA L, LPB); Luis Calvo Province, Iñao National Park and Integrated Management Natural Area close to Ticucha, between Tranqua and Monte Agudo, 19º39’50”S, 63º49’14”W, 1022 m a.s.l., disturbed area with shrabs, on lower and upper part of *Heterodermia* cf. *comosa* on twigs, 18 Jul. 2015, *J. Etayo* 32702, 32709 (hb. Etayo, LPB); Santa Cruz Department, Manuel María Caballero Province, Monte Empalme near Siberia, 17º50’05”S, 64º42’09”W, 2439 m a.s.l., partly grazed Yungas cloud forest near stream, on *Heterodermia podocarpa*, 8 Nov. 2016, *A. Flakus* 28086 (KRAM L-74693, LPB); Tarija Department, Aniceto Arce Province, Tariquía Flora and Fauna National Reserve between la Cumbre and camamento los Alisos, 22º02’38”S, 64º35’47”W, 2460 m a.s.l., Boliviano-Tucumano forest with *Alnus acuminata* and *Polylepis*, on *Leucodermia* sp., 22 Jul. 2015, *A. Flakus* 26977 (KRAM L-74690, LPB); *ibid*., 22º01’02”S, 64º34’51”W, 2135 m a.s.l., on *Heterodermia* cf. *comosa*, 22 Jul. 2015, *A. Flakus* 27056 (KRAM L-74691, LPB); ibid., close to los Alisos camp, 22º01’25”S, 64º34’06”W, 1900 m a.s.l., disturbed Boliviano-Tucumano forest with *Alnus acuminata, Podocarpus* and *Solanaceae*, on *Heterodermia* sp. growing on twig, 24 Jul. 2015, *A. Flakus* 27086 (KRAM-L, LPB), *M. Kukwa* 16600 (UGDA L, LPB); ibid., on *Leucodermia fertilis*, 24 Jul. 2015, *A. Flakus* 27087 (KRAM L-74693, LPB); ibid., close to Coyambuyo, between Padcaya and Bermejo, 22º17’23”S, 64º28’50”W, 942 m a.s.l., Tucumano-Boliviano forest with bryophytes, *Lauraceae* and *Meristomataceae*, on corticolous *Heterodermia* cf. *spinigera*, 26 Jul. 2015, *M. Kukwa* 16726 (LPB); Burnet O’Connor Province, close to Entre Ríos, new road between Tarija and Entre Ríos, 21º30’47”S, 64º11’49”W, 1338 m a.s.l., disturbed Tucumano-Boliviano forest with shrubs and *Tillandsia*, on *Heterodermia japonica*, 28 Jul. 2015, *A. Flakus* 27360 (KRAM L-74694, LPB), ibid., on *Heterodermia* sp., *M. Kukwa* 16812, 16821 (UGDA L, LPB); la Cumbre close to Entre Ríos, old road between Entre Ríos and Tarija, 21º27’48”S, 64º13’24”W, 1943 m, Boliviano-Tucumano forest with *Podocarpus*, on *Heterodermia comosa*, 28 Jul. 2015, *A. Flakus* 27392 (KRAM L-74695, LPB), ibid., *M. Kukwa* 16833a (LPB); ibid., on *Heterodermia* cf. *comosa*, 28 Jul. 2015, *A. Flakus* 27383 (LPB); ibid., on *Leucodermia* sp., 28 Jul. 2015, *A. Flakus* 27400 (KRAM L-74696, LPB); ibid., 21º27’50”S, 64º12’51”W, 1924 m a.s.l., Boliviano-Tucumano forest with epiphytes exposed NW, on *Heterodermia comosa*, 30 Jul. 2015, *A. Flakus* 27650 (KRAM L-74698, LPB); ibid., 21º25’57”S, 64º19’17”W, 2178 m a.s.l., Boliviano-Tucumano forest close to small river dominated by shrubs, on *Leucodermia* cf. *fertilis*, 31 Jul. 2015, *A. Flakus* 27780 (LPB); ibid., on *Leucodermia leucomelos* on twigs, *J. Etayo* 32928 (LPB); ibid., close to los Pinos, 90 km from Tarija on old road between Entre Ríos and Tarija, 21º25’30”S, 64º19’07”W, 2265 m a.s.l., Boliviano-Tucumano forest dominated by shrubs, with *Alnus acuminata*, *Podocarpus* and *Ericaceae*, on *Leucodermia leucomelos*, 29 Jul. 2015, *A. Flakus* 27419

(KRAM L-74697, LPB); ibid., 21º24’50”S, 64º18’33”W, 2149 m a.s.l., on corticolous *Leucodermia leucomelos*, 29 Jul. 2015, *M. Kukwa* 16865b (LPB); ibid., close to Soledad, old road between Entrerios and Chuquiaca, 21º39’45”S, 64º07’22”W, 1750 m, Boliviano-Tucumano forest with shrubs and *Alnus acuminata*, on *Leucodermia leucomelos*, 31 Jul. 2015, *J. Etayo* XI-7 (LPB)

Notes: Etayo (2002) discussed the morphological similarity of the ascomata of *Sphaeronectria lichenophila* to the genus *Paranectria* and pointed out the differences between this species and other fungi of *Nectriopsis*. These differences are supported by resulting phylogenetic analyses which showed a close relationship between *Sphaeronectria* and *Paranectria* rather than *Nectriopsis*.

Key of the lichenicolous species included in the family *Paranectriaceae*

1a. Asci with two types of ascospores (macro- and microspores) 2
1b. Asci with one type of ascospores 4

2a. Macrospores with pointed ends, mostly > 50 µm in length, ascomata with dense arachnoid tomentum at the lower part 3
2b. Macrospores with rounded ends, mostly 40–60 µm in length, ascomata rarely with arachnoid tomentum at the lower part ..... ***Ovicuculispora parmeliae***

3a. Macrospores with hair-like surface, (53.0–)56.4–66.2(–75.8) µm in length ..... ***Ovicuculispora* cf. *macrospora***
3b. Macrospores with smooth surface, 67–105 µm in length ..... ***Ovicuculispora macrospora***

4a. Ascospores filiform, (8–)10–15-septate 5
4b. Ascospores ellipsoid to ovoid, 1–3-septate to muriform 8

5a. Ascomata solitary, lemon yellow, ascospores (125–)140–155(–180) × (2.8–)3.4–4.4(–4.6) µm, on *Tylophoron* ..... ***Rossmaniella tylophori***
5b. Ascomata in group of 3–12, pale to bright orange, on other hosts 6

6a. Ascomata entirely covered by whitish tomentum, ascospores (12–)14–16-septate, individual cells (6.4–)8.0–12.2 (–12.8) µm, on *Coenogonium* ..... ***Rossmaniella coenogonii***
6b. Ascomata covered by yellowish tomentum in the lower half, ascospores 8–12-septate, individual cells > 12 µm, on various hosts except *Coenogonium* 7

7a. Ascomata in group of 3–5(–7), without distinct hairs near the ostiolate part, ascospores (160–)165–175(–180) × (2.4–)2.5–2.8(–3.0) µm, individual cells (13.2–)15.2–21.0(–23.8) µm ..... ***Rossmaniella cryptica***
7b. Ascomata in group (5–)7–12, with distinct hairs near the ostiolate part, ascospores (165–)180–200(–210) × (2.8–)3.0–3.4(–3.8) µm, individual cells (11.0–)11.5–13.7(–14.5) µm ..... ***Rossmaniella filispora***

8a. Ascospores muriform 9
8b. Ascospores 1–3-septate 11

9a. Ascomata 200–400 µm, asci < 140 µm in length, ascospores 25–45 µm in length 10
9b. Ascomata 400–750 µm, asci 140–220 µm in length, ascospores (45–)54–75(–92) µm in length ..... ***Paranectria alstrupii***

10a. Ascomata globose, 300–400 µm, asci 2–4-spored, ascospores (10–)13–18(–23) µm in width ..... ***Paranectria superba***
10b. Ascomata ovoid to pyriform, 140–260(–300) µm, asci (4–)8-spored, ascospores (7–)8–12(–14) µm in width ..... ***Ciliomyces oropensis***

11a. Asci 4-spored, ascospores 1-septate, on *Physciaceae* ..... ***Sphaeronectria lichenophila***
11b. Asci 8-spored, ascospores 3-septate, on *Ephebe* ..... ***Paranectria affinis***

DISCUSSION

Phylogenetic relationships in the order *Hypocreales*

Hypocreales is an order within the *Sordariomycetes* that includes a diverse range of species with many potential applications (Hyde *et al.* 2020, Hou *et al.* 2023). The main research efforts have focused on species with practical applications, while groups without such importance have received little attention. Consequently, the taxonomic system of *Hypocreales* seems to be incomplete (Hyde *et al.* 2020). For instance, the connection between their asexual and sexual stages is often unclear, most researchers have focused primarily on the phylogeny within individual families, rather than extensively exploring the relationships between the families themselves and more comprehensive studies

have shown contrasting results regarding the phylogenetic relationships within the order *Hypocreales* (e.g. Chaverri *et al.* 2011, Hirooka *et al.* 2012, Quandt *et al.* 2014, Giraldo *et al.* 2015, Lombard *et al.* 2015, 2016, Crous *et al.* 2021, Hou *et al.* 2023, Li *et al.* 2023, Perera *et al.* 2023, Sun *et al.* 2023, Xiao *et al.* 2023, Yu *et al.* 2024). Therefore, our study has considerably broadened the sampling, including several poorly known lichenicolous taxa to reconstruct a comprehensive multi-locus phylogeny of *Hypocreales*. As a result, this study has successfully established a phylogenetic framework for *Hypocreales*, revealing a new lineage associated with lichens. To accommodate the genera *Ovicuculispora*, *Paranectria*, as well as *Nectriopsis lichenophila* and *Nectria byssophila*-like species, this lineage is described as a new family named *Paranectriaceae*.

Several studies reported similar topologies for the family *Bionectriaceae* and related families, which were previously considered part of a broader concept of *Bionectriaceae* (Maharachchikumbura *et al.* 2016, Hongsanan *et al.* 2017, Hyde *et al.* 2020, Perera *et al.* 2023). The family *Tilachlidiaceae* consistently exhibits a highly supported sister relationship with the *Bionectriaceae* clade in multiple studies (Maharachchikumbura *et al.* 2016, Hongsanan *et al.* 2017, Hyde *et al.* 2020). Perera *et al.* (2023) introduced a new family *Stromatonectriaceae*, which showed a well-supported sister relationship with *Tilachlidiaceae*. The resulting comprehensive phylogeny of the order further confirms the relationship between these families (*Stromatonectriaceae* and *Tilachlidiaceae*) rather than exclusively with *Bionectriaceae*. The family *Myrotheciomycetaceae*, consisting of a few hyphomycetous genera, has only recently been described although its phylogenetic relationships were still unclear (Crous *et al.* 2018). Our phylogenetic analyses have revealed that this family forms a well-supported clade related to the clade comprised of *Bionectriaceae*, *Flammocladiellaceae*, *Stromatonectriaceae*, *Tilachlidiaceae* and *Xanthonectriaceae*. However, the relationship of the family *Myrotheciomycetaceae* with other families of *Hypocreales* is still being elucidated, but our analyses and previous studies suggest its association with the *Bionectriaceae* and related families (Hou *et al.* 2023, Perera *et al.* 2023).

The phylogenetic placement of the family *Flammocladiellaceae* has been unclear, but some studies suggested possible phylogenetic relationships to *Cordycipitaceae*, *Ophiocordycipitaceae*, or even *Clavicipitaceae* (Maharachchikumbura *et al.* 2016, Crous *et al.* 2018). In other studies, it appeared as a sister clade to *Sarocladiaceae*, *Tilachlidiaceae* or *Myrotheciomycetaceae* (Hyde *et al.* 2020, Li *et al.* 2024). Our study found that *Flammocladiellaceae* formed a sister clade to the family *Ijuhyaceae* with a strong support, which is congruent the results found by Perera *et al.* (2023). Those two families share similar morphological features, such as globose pale yellow to orange ascomata and ellipsoid 1–3(–5)-septate ascospores, which are quite different from representatives of *Cordycipitaceae* (Crous *et al.* 2015, Lechat & Fournier 2018).

According to our phylogeny, the family *Valsonectriaceae* forms a distinct lineage, while Hou *et al.* (2023) and Yu *et al.* (2024) indicated it as a well-supported clade sister to the *Bionectriaceae* and related families. Another inconsistency with the phylogenetic results of Hou *et al.* (2023) is the phylogenetic placement of *Pseudoniessliaceae*, while the authors find it as a sister clade to the *Chrysonectriaceae*, *Nectriaceae* and *Neoacremoniaceaea*, but our analyses reveal it to be as a sister clade to the *Clavicipitaceae*, but without statistical support.

The family *Nectriaceae* is indeed one of the most extensively studied groups within the order *Hypocreales*. It was broadly sampled and included in several multi-gene phylogenetic studies, leading to the development of a robust taxonomy for the family (Lombard *et al.* 2014, 2015, Crous *et al.* 2021). However, the relationship of the *Nectriaceae* to other groups within *Hypocreales* has shown some inconsistencies across different studies. Phylogenetic analyses conducted by Maharachchikumbura *et al.* (2016) and Hongsanan *et al.* (2017) suggested that the *Nectriaceae* forms a sister clade to the *Stachybotriaceae*, but with low statistical support in both studies. In more recent studies, *Nectriaceae* was found to be the sister group to a few sequences of *Niesslia* species (*Niessliaceae*) or as a sister to the *Chrysonectriaceae* and *Neoacremoniaceae* (Perera *et al.* 2023, Hou *et al.* 2023). In our phylogeny, *Nectriaceae* is monophyletic with high support and similarly to the results by Hou *et al.* (2023) is closely related to *Neoacremoniaceae*.

Sedecimiella taiwanensis, the type species for *Sedecimella*, was described based on limited material, and LSU (HM451496) as well as nuSSU (HM451495) sequences are available (Pang *et al.* 2010). This species was transferred to the genus *Neoacremonium* (*Neoacremoniaceae*) and suggested as the first sexual species in this genus (Hou *et al.* 2023). Simultaneously, other authors described three new asexual *Sedecimiella* species and together with the genus *Heteroacremonium*, established the new family *Sedecimiellaceae* (Li *et al.* 2023). Our phylogenetic results showed that both families, *Neoacremoniaceae* and *Sedecimiellaceae*, formed well-supported clades with strongly supported sister relationships. However, further investigation, including more sequences of both families, especially for sexual taxa, is required to evaluate their circumscriptions.

The families *Hypocreaceae*, *Cordycipitaceae*, *Clavicipitaceae*, and *Ophiocordycipithaceae* form distinct clades within the order *Hypocreales*, as supported by multiple previous studies (Maharachchikumbura *et al.* 2016, Hongsanan *et al.* 2017, Hyde *et al.* 2020, Perera *et al.* 2023), as well as in our phylogeny. However, the specific relationships between these families and the circumscriptions are not yet clear. In addition, some species or genera have undergone recent changes regarding their placements, moving from one family to another. These taxonomic changes are often a result of sampling bias, and in response to this, several new lineages at the family level (*Polychephalomycetacea*, *Pseudoniessliaceae*, *Pseudodiploosporeaceae*) have been described recently (Hou *et al.* 2023, Sun *et al.* 2023, Xiao *et al.* 2023). The family *Calcarisporaceae* was established to accommodate the species of the genus *Calcarisporium*, which was previously classified as *Hypocreales* insertae sedis (Sun *et al.* 2017). The authors demonstrated the relationship of the new family with the *Cordycipitaceae*, *Clavicipitaceae*, and *Ophiocordycipithaceae* subclade, which has been further supported by subsequent research (Hyde *et al.* 2020, Hou *et al.* 2023, Perera *et al.* 2023,). Based on our phylogenetic analyses *Calcarisporaceae* showed a strongly supported sister relationship to the family *Albomorchellophilaceae* as it was reported by Yu *et al.* (2024).

Another recently described family within *Hypocreales* is *Cocoonihabitaceae*, which currently includes only one known species, *Cocoonihabitus sinensis* (Zhuang & Zeng 2017). However, only a few sequences of this species are available and therefore the phylogenetic relationships of *Cocoonihabitaceae* are not resolved well. Previous studies showed the low or moderately supported sister relationship of *Cocoonihabitaceae* with families *Hypocreaceae*, *Cordycipitaceae* or *Pseudoniessliaceae* (Zhuang & Zeng 2017, Hou *et al*. 2023, Perera *et al*. 2023 Yu *et al.* 2024). In our multigene phylogenetic analyses, we find *Cocoonihabitaceae* to be a sister clade comprised of *Ophiocordycipithaceae* and *Polychephalomycetaceae* with strong statistical support.

The phylogenetic position of the genus *Trichonectria* was unstable in different studies, and the genus was classified as *Hypocreales* incertae sedis (Perera *et al.* 2023) or clustered inside the *Niessliaceae* clade (Hou *et al.* 2023). Our phylogenetic analyses reveal that the asexual genus *Cylindromonium*, with sexual *Trichonectria*, forms a well-supported clade sister to the newly described family *Paranectriaceae*. *Cylindromonium-Trichonectria* clade is not formally described here due to the absence of sequences from the type species *Trichonectria hirta* and will be treated by us in the future.

Our research focused on filling the sampling gaps within hypocrealen fungi represented by lichenicolous species, which are highly specialized and their practical applications are largely unknown. Previously, none of treated here species were included in larger phylogenetic studies and this is the first study that addresses their phylogenetic position based on freshly collected specimens. Therefore, this investigation enhances our comprehension of the evolutionary histories of *Hypocreales* and provides a solid phylogenetic backbone for improving the systematics of this order.

Phylogenetic relationships within the family *Paranectriaceae*

The newly described family *Paranectriaceae* consists of species characterized by yellow to orange superficial ascomata, scattered or grouped, with distinct whitish tomentum, KOH not reacting ascomata wall and 1-septate to multiseptate or muriform ascospores. The family members are lichenicolous and can infect many unrelated lichen hosts without showing a strict host specificity. Due to the limited molecular data available, the genera *Ovicuculispora* and *Paranectria* were classified as members of *Bionectriaceae* based on morphological features and the lack of KOH reaction in the ascomata (Rossman *et al.* 1999, Diederich *et al.* 2018). However, this relationship was never confirmed through further phylogenetic analyses (Perera *et al.* 2023). The species *Ovicuculispora parmeliae* was sequenced by Sikaroodi *et al.* (2001) and the authors demonstrated the phylogenetic placement of this species in *Hypocreales* without affiliation to the family level. Subsequent phylogenetic studies of *Hypocreales* did not include this species and therefore its phylogenetic position was unresolved. Later, Telfer *et al.* (2015) in their biodiversity inventory based on a DNA barcoding approach obtained a sequence of the ITS region for *Ovicuculispora parmeliae*. This genus is characterized by huge morphological variability especially in terms of macrospore sizes and their ornamentation. This variability together with the wide host spectrum and quite limited molecular data provoked a lot of discussion about the circumscription of this species (Flakus *et al.* 2006, Etayo 2010, Etayo & van den Boom 2013, Zhurbenko 2014, Tadome & Ohmura 2021, Zhurbenko 2023). During this study, we were able to generate new sequence data from seven specimens of *Ovicuculispora parmeliae* from South America and Eurasia, which all cluster in a well-supported monophyletic clade (Fig. 2). These specimens showed considerable morphological variation, but because of a lack of strong phylogenetic signal distinguishing them as separate species was impossible at this moment. More specimens from other regions and different hosts are needed to evaluate the morphological variability of this species and the species concept. Another two specimens of *Ovicuculispora* cf. *macrospora* were resolved as a highly supported clade sister to *O. parmeliae*. Those specimens are characterized by slight morphological differences from the protologue of *O. macrospora* (Etayo 2012). We suggest that those differences can be an intraspecific variation, but more samples are needed to test this hypothesis.

The genus *Paranectria* was included in the *Bionectriaceae* by Rossman *et. al.* (1999) based on morphological features. So far, only one sequence of the generic type, *Paranectria affinis*, was available in public repositories (MZ159749). In our study, six specimens of *Paranectria oropenis* and two specimens of *P. affinis* were sequenced and included in the phylogenetic analyses. The resulting phylogeny showed the genus *Paranectia* to be polyphyletic due to the separate position of the generic type and *P. oropensis*. These results are also congruent with the morphological differences in ascospores between *Paranectria affinis* (3-septate ascospores) and other lichenicolous species of the genus, e.g. *P. alstrupii*, *P. oropensis* and *P. superba* (muriform ascospores). Thereby, we reinstated the old genus *Ciliomyces*, which currently included one species. *Ciliomyces oropensis* (=*Paranectria oropensis*) also presents morphological variation and a broad host spectrum. However, the taxonomical value of ascospores variation found in this species has been questioned, as many authors considered it to be dependent on the maturity stage of collected specimens (Diederich 2003, Brackel 2008, Hafellner & Obermayer 2009, Navarro-Rosinés & Llimona 2018). We included in our phylogenetic analyses six specimens of *Ciliomyces oropensis* collected from different regions and on various hosts, and they all were clustered in a well-supported clade (Fig. 2).

Nectriopsis lichenophila was previously placed in *Bionectriaceae*, but in our phylogenetic analyses, it formed a well-supported monophyletic clade in the family *Paranectriaceae*. As a result we proposed a new monotypic genus *Sphaeronectria* to accommodate *N. lichenophila*. The four sequenced specimens of *N. lichenophila* included in this study showed phylogenetic differences, but their morphological features are identical. We suggest that these phylogenetic differences reflect intraspecific variability across studied loci. However, the genus *Nectriopsis* including more than 70 fungicolous and lichenicolous species which are characterized by pale, superficial ascomata, not reacting in KOH (or being rarely violaceous), thin-walled setae and 1-septate ascospores (Samuels 1988, Rossman *et al.* 1999, Diederich *et al.* 2018). The case of *Nectriopsis lichenophila* suggests that *Nectriopsis* needs a critical taxonomic revision with additional sampling because its morphology may represent several homoplasies.

The new genus *Rossmaniella* is placed in a new family

Paranectriaceae. The genus is characterized by the yellowish to bright orange, ovoid to obpyriform ascomata, and clustered in groups, with a well-developed tomentum at the lower part of ascomata and filiform ascospores. At least part of previous records applying the name *Nectria byssophila* on different lichen hosts refers to the species of the genus *Rossmaniella* (Etayo & Sancho 2008, Etayo 2003, 2017). We obtained the sequences from eight specimens of the genus *Rossmaniella* and they represented four species clustered in a well-supported clade in our phylogeny.

Lichenicolous species in other lineages of *Hypocreales*

Lichenicolous fungi represent a highly diverse ecological group of fungi related to lichens and comprising more than 2300 described species (Diederich *et al.* 2018). The lichenicolous lifestyle evolved multiple times in fungi, most of them belonging to *Ascomycota*. The *Hypocreales* is a group of fungi that is particularly rich in lichenicolous fungi, with a total of 180 species described (Diederich *et al.* 2018). However, phylogenetic studies have given little attention to hypocrealean lichenicolous species, resulting in DNA sequences being available for only about 10 % (18 species) of the taxa (Crous *et al.* 2019, Flakus *et al.* 2019a, Berger *et al.* 2020, Darmostuk 2021, Berger & Zimmermann 2022, Crous *et al*. 2023a, b, Ohmaki *et al*. 2023). Traditionally, lichenicolous fungi were described based on morphological data, the host specificity, and frequently included in genera described for fungi with other lifestyles. That situation was widely extended in the order *Hypocreales*. Therefore, the circumscription of many lichenicolous genera remain to tentative taxonomical changes when more lichenicolous taxa are included in phylogenetic analyses. One such example is *Neobarya* (*Clavicipitaceae*), which was established to accommodate host-specific parasites of fungi or lichens (Candoussau *et al.* 2007). Lawrey *et al.* (2015) conducted the first phylogenetic assessment (based on ITS and LSU region) of several *Neobarya* species, demonstrating that the lichenicolous *Neobarya usneae* (Etayo 2002) was not phylogenetically related to the generic type (*Neobarya parasitica*). As a result, the new lichenicolous genus, *Lichenobarya*, was described and placed in *Hypocreaceae*. However, the phylogenetic position of other lichenicolous species within the genus *Neobarya* (*N. ciliaris, N. darwiniana, N. lichenophila* and *N. peltigerae*) remains unclear due to a lack of molecular data. Another example is *Neobaryopsis* a new monotypic genus described to accommodate a *Neobarya*-like species growing on *Lobariella* (Flakus *et al.* 2019a). It was suggested that this genus belongs to *Cordycipitaceae*, marking the first record of a lichenicolous lifestyle in this family.

Our phylogenetic results revealed that lichenicolous taxa belong at least to seven lineages of *Hypocreales*, i.e. the families *Bionectriaceae* (*Lasionectria lecanodes* and *Pronectria robergei*), *Nectriaceae* (*Microcera physciae* and *Roselliniella* spp.), *Hypocreaceae* (*Lichenobarya usneae*), *Calcarisporaceae* (*Neobaryopsis andensis*), *Paranectriaceae* (*Ciliomyces oropensis*, *Paranectria affinis*, *Ovicuculispora* spp., *Rossmaniella* spp., *Sphaeronectria lichenophila*), *Niessliaceae* (*Niesslia cladoniicola*) as well as the *Cylindromonium-Trichonectria* clade. However, many lichenicolous fungi still require further study to enhance our understanding of the evolution of this lifestyle in *Hypocreales*. Additionally, data on facultatively lichenicolous, such as *Sarocladium strictum* (*Sarocladiaceae*), are necessary to have a more complete picture of the changes in the lifestyle in *Hypocreales* (Hawksworth 1979, Diederich *et al.* 2018).

The *Cylindromonium-Trichonectria* clade included several sequences of the asexual genus *Cylindromonium* (generic type *C. eugenicola*) and sexual genus *Trichonectria* (generic type *T. hirta*) and forming a well-supported clade in our phylogeny. The relationship between both genera has been long discussed in the literature. An *acremonium*-like asexual morph has been suggested for several *Trichonectria* species, but has never been confirmed by molecular data (Lowen & Hawksworth 1986, Lowen 1989, 1995). Lowen (1995) and later Glenn *et al.* (1997) proposed that *C. rhabdosporum* (as *Acremonium rhabdosporum*) corresponds to the asexual morph of *Trichonectria rubefaciens* (as *Nectria rubefaciens*) and this statement was used for a long time to indicate the asexual-sexual relationship in *Trichonectria*. Recently, Ohmaki *et al.* (2023) described *Cylindromonium dirinariae* and confirmed the relationship between a trichonectria-like sexual morph and a *Cylindromonium* asexual morph by multigene phylogenetic analyses. The phylogenetic affinities of both genera have been challenging, e.g. *Cylindromonium* was classified as a member of *Nectriaceae* based on phylogenetic analyses (Crous *et al.* 2019), but *Trichonectria* was suggested to belong to the *Bionectriaceae* based on morphological data, although it was placed as *Hypocrelaes* incertae sedis (Rossman *et al.* 1999, Perera *et al.* 2023). In addition, the relationship between *Cylindromonium* and *Trichonectria* raised a nomenclatural problem. However, *Cylindromonium eugeniicola*, a generic type of *Cylindromonium*, is associated with leaf litter and is not closely related (Figs 1, 2) to lichenicolous species of this genus (Crous *et al.* 2023b). The generic type of *Trichonectria* is *T. hirta*, known from several collections across Europe but for which no molecular data is available. As *T. hirta* is characterized by quite different morphology, e.g. multiseptate vs 1-septate ascospores from other species classified currently in the genus, the rest of lichenicolous species may belong to another genus. The fresh collections, culture and molecular data for this species are crucial to further clarify the genus circumscription and phylogenetic position of the other species placed in *Trichonectria*.

The genus *Roselliniella* is characterized by erumpent, brownish perithecioid ascomata, thin-walled asci without apical apparatus, filamentous interascal filaments and brown, aseptate ascospores (Hoffman & Hafellner 2000). The genus originally was classified as a member of the order *Sordariales* by morphological data (Hoffmann & Hafellner 2000). Later, Hawksworth *et al.* (2010) obtained the LSU sequences data for two species of *Roselliniella* and resolved the genus in the order *Hypocreales* rather than *Sordariales*, but without indicating the family placement. Our phylogenetic results indicated that *Roselliniella* is closely related to *Nectria* and would belong to *Nectriaceae*. These results do not fit with the features of the family *Nectriaceae,* which is characterized by unilocular, white, yellow, orange-red or purple ascomata and phialidic asexual morphs (Lombard *et al.* 2015). Therefore, it is crucial to evaluate the phylogenetic placement of the genus *Roselliniella* by conducting a wide sampling of taxa, including the generic type.

The recently described genus *Neobaryopsis* is characterized by very particular narrowly pyriform, yellowish to orange ascomata developing on a reduced white arachnoid subiculum, and large, multiseptate needle-like ascospores and short synnematous conidiomata and was originally placed on *Cordycipitaceae* (Flakus *et al.* 2019a). This is incongruent with our results , based on a larger number of loci, which supported that *Neobaryopsis andensis* belong to *Calcarisporiaceae*, closely related to the asexual genus *Calcarisporium*. Therefore, we suggest, that *Neobaryopsis* belongs to the family *Calcarisporaceae* instead of *Cordycipitaceae*. *Neobaryopsis* belongs to the so-called group of Neobarya-like lichenicolous fungi to which *Neobarya*, *Leptobarya* and *Lichenobarya* also belong (Candoussau *et al.* 2007; Lawrey *et al.* 2015, Flakus *et al.* 2019a). Despite the high level of morphological similarity among those genera, they belong to different phylogenetic lineages of the order *Hypocreales*, i.e. *Lichenobarya* to *Hypocreaceae*, *Neobarya* to *Clavicipitaceae*, *Neobaryopsis* to *Calcarisporaceae* and the new *Rossmaniella* to *Paranectriaceae*. This pattern can indicate that Neobarya-like habits have evolved separately in *Hypocreales*. However, future studies including a wider sampling of the abovementioned genera and other neobarya-like genera will improve our knowledge on the evolution of cryptic speciation in *Hypocreales*.

Tropical ecosystems harbour a significant fraction of the known mycobiota, including the highest diversity of lichen species (Hawksworth 2012). However, the number of known lichenicolous fungi in these regions has remained relatively small. This has led to the discovery of numerous lichenicolous species from South America in previous years years (e.g., Flakus *et al*. 2014, 2019a, Etayo *et al*. 2015, Etayo 2010, 2017, Darmostuk & Flakus 2024) The tropical cloud forests of Bolivia, one of the world's biodiversity hotspots, appear to be extremely diverse and particularly rich in undescribed species, especially within the order *Hypocreales* (Flakus *et al.* 2019a, b, Crous *et al.* 2023a, b, Etayo *et al.* 2024). In this study, we demonstrated that extensive sampling of tropical fungi can help clarify their phylogenetic position and influence order-wide systematics. We provide new distribution and phylogenetic data for the monotypic genus *Sphaeronectria*, an exclusively tropical genus, as well as *Rossmaniella* and *Ovicuculisopora*, which are widely distributed in tropical regions.

The lichenicolous lifestyle has evolved multiple times from different ancestors throughout the evolutionary history of *Ascomycota* (e.g., Divakar *et al.* 2015, Suija *et al.* 2015). Our phylogenetic results suggest that lichenicolous taxa belong at least to seven lineages of *Hypocreales,* revealing relationships with species with different lifestyles. However, some lichenicolous species within the *Hypocreales* are related to saprotrophs, known from plant debris (*Lasionectria* and *Pronectria* in *Bionectriaceae*, *Niesslia* in *Niessliaceae*). Additionally, other taxa, such as *Lichenobarya* in *Hypocreaceae* and *Neobaryopsis* in *Calcarisporaceae*, are nested within clades comprised of fungicolous species. Furthermore, a few lichenicolous species are related to insect pathogens, such as *Microcera* in *Nectriaceae*. Further evolutionary studies of *Hypocreales* should include data on lichenicolous species, as they are widely distributed within the order, and this lifestyle is supposed to have undergone gains or losses multiple times throughout evolutionary history.

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