



Taxonomic and phylogenetic approach to some Antarctic lichenicolous fungi

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Abstract

This study was focused on lichenicolous fungi from the Antarctic region whose diversity is not yet well known. The sampling was carried out in the maritime Antarctica, South Shetland Islands, Livingston Island, during a trip in 2018. In total, more than one hundred species of lichenicolous fungi were collected, of which a selection has been studied here. The remaining species will be studied in future papers. As a result of our morphological and molecular studies (based on ITS rDNA, LSU rDNA, and mtSSU), three new species are proposed: *Arthonia olechiana* on *Steinera olechiana*, *Sphaeropezia neuropogonis* on *Usnea*, and *Sphinctrina sessilis* on *Pertusaria excludens*. Moreover, the new combinations *Bryostigma excentricum* on *Lepraria* and *Raesaenenia usneae* on *Usnea* are also proposed.

Keywords *Ascomycota* · *Acremonium* · *Arthonia* · *Bryostigma* · *Mycota* · *Protothelenella* · *Raesaenenia* · *Sphaeropezia* · *Sphinctrina*

Introduction

Less than 2% of the Antarctic continent is free of ice and thus capable to be colonized by terrestrial organisms. A large part of this ice-free area is located on the Antarctic Peninsula and adjacent islands, the region known as maritime Antarctica (Green et al. 2007; Terauds and Lee 2016). This region is favoured by a milder climate, which increases biodiversity and even supports the growth of the only vascular plants in Antarctica: the Antarctic hair grass, *Deschampsia antarctica* Desv., and the Antarctic pearlwort, *Colobanthus quitensis* (Kunth) Bartl. The tundra vegetation near the coast and in the nunataks (bare mountain peaks emerging from snow and ice) is

not only almost dominated by lichenized fungi and bryophytes, but also algae and cyanobacteria. Lichenized fungi are so far the most diverse component of the autotrophic Antarctic biota (Lewis Smith 1984; Ruisi et al. 2007; Bridge and Spooner 2012). More than 400 species of lichenized fungi can be found in the continent (Øvstedal and Lewis Smith 2001), which rises to more than 500 species when South Georgia is included (Øvstedal and Schaefer 2013). Lichenized fungi in turn support a great variety of fungi (U'Ren et al. 2012; Diederich et al. 2018), though these fungal communities have not been deeply studied in the Antarctic. Lichenicolous fungi are a polyphyletic group of fungi living on lichens as parasites, commensals, or saprotrophs (Hawksworth 2003, Diederich et al. 2018), considered an important source of undescribed fungal species (Hawksworth and Rossman 1997). Vainio (1903) and Spegazzini (1910) reported the first lichenicolous fungi from Antarctica. Afterwards, other authors recorded or described dozens of lichenicolous fungal species from this region (Hawksworth and Iturriaga 2006; Pérez-Ortega et al. 2015; Alstrup et al. 2018). The most recent catalogue of these fungi reported 96 species from South Shetland Islands (Alstrup et al. 2018). However, an exhaustive study is necessary to encompass and understand the diversity of lichenicolous fungi in this region. The first author of the present paper collected numerous species of lichenicolous fungi on Livingston Island between February and March 2018 (in a period of approximately

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1 month). The base of the collections was Juan Carlos I Base, situated in Hurd Peninsula. More than one hundred lichenized fungal species collected in that expedition have been identified, representing nearly one-fourth of the total lichen mycota to the continent. So far ca. 200 lichenized species have been reported from Livingston Islands (Sancho et al. 1999; Søchting et al. 2004), indicating that the lichenicolous mycota could reach one-half of the lichenized mycota in Antarctica. A comprehensive study of the flora of these organisms in the Antarctic is pending, but this study presents a set of species which have been selected for their special taxonomic or biogeographical interest. The study is based on both morphological and molecular analyses. A comparison between the species found and other morphologically similar ones, as well as other species reported from Antarctica, is provided.

Material and methods

Taxon sampling and morphological study

All the samples have been collected in Antarctica, South Shetlands Archipelago, Livingston Island. The localities sampled are listed under the studied material of each species. Samples were collected and gathered in envelopes, using the traditional method in lichenology. As soon as the boxes arrived at the lab, some samples were selected for molecular studies, conducted by R.P-B. The material was studied macro- and microscopically. Hand-cut sections or squash preparations were mounted in Congo red, Lugol's solution (I), and KOH 10% (K); or Lugol's solution with KOH pretreatment (KI) in order to study the hymenial and ascus reactions. Measurements were made in H₂O. Morphological studies were made using a Nikon Eclipse 80i microscope with a ProgRes CT1 camera. Only mature spores discharged from asci were measured. All the specimens are deposited in MAF herbarium as well as in J. Etayo's private herbarium unless otherwise specified.

DNA extractions, PCRs, and sequencing

Lichen thalli were cleaned with Milli-Q SP Ultra-Pure-Water, and ascomata or conidiomata were selected under a dissecting microscope. Genomic DNA was extracted using the E.Z.N.A. Forensic DNA Isolation Kit (Omega Bio-Tek). DNA was eluted in the final step in 70 µl of elution buffer provided by the manufacturer. The region ITS rDNA, the barcode of fungi (Schoch et al. 2012), was amplified for all the specimens. Additionally, other loci were amplified for some species. LSU rDNA was amplified for *Acremonium psychrophilum* C. Möller & W. Gams, *Sphinctrina sessilis* sp. nov., and *Protothenella* cf. *croceae* (Bagl. & Car.) Hafellner & Mayrh., and mtSSU was amplified for *P. cf. croceae*.

The following primers were used for the PCRs: ITS4 and ITS1F (Gardes and Bruns 1993; White et al. 1990) for ITS rDNA; LROR and LR5 (Vilgalys and Hester 1990; Vilgalys and Sun 1994) for LSU rDNA; and mtSSU1 and mtSSU3R (Zoller et al. 1999) for mtSSU. The PCR programs are described in Pino-Bodas et al. (2017). PCR products were cleaned with Illustra™ ExoProStar™ 1-step (GE Healthcare). The sequencing was performed at MacroGen Spain service (www.macrogen.com) with the same primers used for the PCRs.

Taxon sampling, alignment, and phylogenetic analyses

Sequencher 4.1.4 program (Gene Codes Corporation, Inc, Ann Arbor, Michigan, USA) was used to assemble the sequences. BLAST searches (Altschul et al. 1997, www.ncbi.nlm.nih.gov/BLAST) were done for each sequence in order to dismiss contaminations and to check closely related taxa. Alignments were carried out in MAFFT (<https://mafft.cbrc.jp/alignment/server/>) using the default parameters and improved manually in BIOEDIT 7.0 (Hall 1999). Regions ambiguously aligned were removed from the alignments with Gblocks 0.91b (Castresana 2000) using the less stringent option. Sampling was based on the BLAST searches and completed with recent phylogenetic and taxonomic studies of *Arthonia* (Frisch et al. 2014; Frisch and Holien 2018; Kondratyuk et al. 2019, 2020), *Bionectriaceae* (Summerbell et al. 2011; Giraldo et al. 2017; Voglmayr and Jaklitsch 2019), *Ostropales* (Schmitt et al. 2009; Miadlikowska et al. 2014; Pino-Bodas et al. 2017), and *Mycocaliciales* (Prieto et al. 2013; Tibell et al. 2014). The sequences used in the phylogenetic analyses are listed in Annexe 1. In total, five datasets were generated, named as follows: *Bryostigma* dataset, *Acremonium* dataset, *Raesaenenia* dataset, *Protothenella* dataset, and *Sphinctrina* dataset (Supplementary information).

For each single locus alignment, maximum likelihood analyses (ML) were carried out in RAxML 7.0.3 (Stamatakis et al. 2005), using the GTRGAMMA model and 1000 replicates of fast bootstrap in order to check conflicts among the loci, following Hillis and Bull (1993) criteria. No conflict was found, and the alignments were combined. ML analyses for the concatenated datasets were carried out with the same settings as in the ML for each alignment, considering each locus as a single partition.

The optimal substitution model for each locus was selected with jModeltest (Posada 2008), using Akaike information criterion. The models selected are listed in Table 1. Bayesian analyses were carried out for each concatenated dataset. They were run in MrBayes 3.2.6 (Ronquist et al. 2012) in CIPRES Science Gateway v. 3.1 (Miller et al. 2010). The posterior probabilities were approximated by sampling trees

Table 1 Features of the analyses of different datasets, including the number of positions in each alignment, model of evolution selected with jmodeltest, and likelihood values from ML and Bayesian analyses

| Dataset | Positions | Substitution models | -Lnl (ML analysis) | -Lnl (Bayesian analysis) |
|------------------------|-----------|--|--------------------|--------------------------|
| <i>Acremonium</i> | 1361 | ITS: SYM+I+G; LSU: TrNef+I+G | 10,461.2069 | 10,333.95 |
| <i>Bryostigma</i> | 1296 | ITS: SYM+G; mtSSU: SYM+I+G | 6970.5640 | 7345.291 |
| <i>Raesaenenia</i> | 467 | ITS: TrNef+G | 3575.017 | 3479.327 |
| <i>Protothelenella</i> | 2038 | ITS: SYM+I+G; LSU: SYM+I+G; mtSSU: SYM+I+G | 12,582.013 | 12,530.65 |
| <i>Sphinctrina</i> | 1696 | ITS: GTR+I+G; LSU: TrN+I+G | 8776.645 | 8778.527 |

using Markov Chain Monte Carlo (MCMC). Two simultaneous runs with 20,000,000 generations each were executed, starting with a random tree and employing 4 simultaneous chains. Every 1000th tree was saved into a file. The convergence was assessed in Tracer v. 1.7 (Rambaut et al. 2018) plotting the likelihood versus generation number and the average standard deviation of split frequencies (≤ 0.01). The first 50% trees were discarded as burn-in.

Results

The phylogenetic analyses based on five the different datasets were conducted in order to establish the phylogenetic relationships of the studied taxa, including nine new DNA sequences (five of ITS rDNA, GenBank accession numbers OP883926-OP883930; three of LSU rDNA, GenBank accession numbers OP883933-OP883935; and one of mtSSU, GenBank accession number OP895167) and sequences downloaded from GenBank (Annexe 1). Table 1 summarizes features of each analysis and substitution models used for each partition in the Bayesian analyses. The topologies from ML and Bayesian trees of the same dataset were highly consistent and only the trees from Bayesian analyses are shown (Figs. 1, 2, 3, 4, 5).

Bryostigma dataset

The dataset included 24 sequences representing 24 species and 358 parsimony informative characters. Three well-supported clades were obtained, one of them included *Arthonia apotheciorum* (A. Massal.) Almq. and *A. subfuscicola* (Linds.) Triebel, and another included *A. didyma* Körb. and *A. physidiicola* Frisch & G. Thor, while the third one represents the clade *Bryostigma*, according to Frisch et al. (2014). *Arthonia excentrica* was included in the *Bryostigma* clade. It formed a clade with *B. dokdoensis* (S. Y. Kondr., L. Lököš, B. G. Lee, J.-J. Woo et J.-S. Hur) S. Y. Kondr. et J.-S. Hur and *B. molendoi* (Heufl. ex Arnold) S.Y. Kondr. & Hur, supported only in the ML analysis (Fig. 1).

Acremonium dataset

The dataset included 39 sequences, representing 38 species, 20 of which belong to *Acremonium*, and 382 parsimony informative characters. The phylogenetic tree included eleven well-supported clades (Fig. 2), nine of them included *Acremonium* taxa. The specimen of *Acremonium psychrophilum* on *Mastodia* was closely related to *A. rutilum* W. Gams, a species also previously collected in Antarctica. These two species were included in a clade with *Protocreopsis phormiicola* (Samuels) Samuels & Rossman and *Beauveria bassiana* (Bals.-Criv.) Vuill.

Raesaenenia dataset

The dataset included 31 sequences, representing 24 species of *Parmeliaceae*, four of which were lichenicolous fungi belonging to the genera *Nesolechia*, *Phacopsis*, and *Raesaenenia*. *Raesaenenia huuskonenii* (Räsänen) D. Hawksw., Boluda & H. Lindgr., *Phacopsis vulpina* Tul. and *Nesolechia oxyspora* (Tul.) A. Massal. were included. The alignment included 71 parsimony informative characters. The phylogenetic placement of lichenicolous fungi is concordant with the results of Divakar et al. (2015) (Fig. 3), *Nesolechia oxyspora* was related to *Punctelia borreri* (Turner ex Sm.) Krog, *Phacopsis vulpina* was related to a clade including *Protousnea magellanica* (Mont.) Krog, *Phacopsis usneae* C.W. Dodge, and *Raesaenenia huuskonenii*. *Phacopsis usneae* was more closely related to *R. huuskonenii* than *P. vulpina*. Therefore, a new combination is proposed.

Protothelenella dataset

The dataset included 20 sequences, representing 19 species and 617 parsimony informative characters. Three *Protothelenella* species were included in the phylogenetic analyses (Fig. 4), *P. corrossa* (Körb.) H. Mayrhofer & Poelt, *P. santessonii* H. Mayrhofer, and *P. sphinctrinoidella* (Nyl.) H. Mayrhofer & Poelt. *Protothelenella* was monophyletic and closely related to *Anzina carneonivea* (Anzi) Scheid. (Fig. 4). The specimen of *Protothelenella* collected on *Psoroma*, identified as *P. cf. croceae*, was related to a clade including

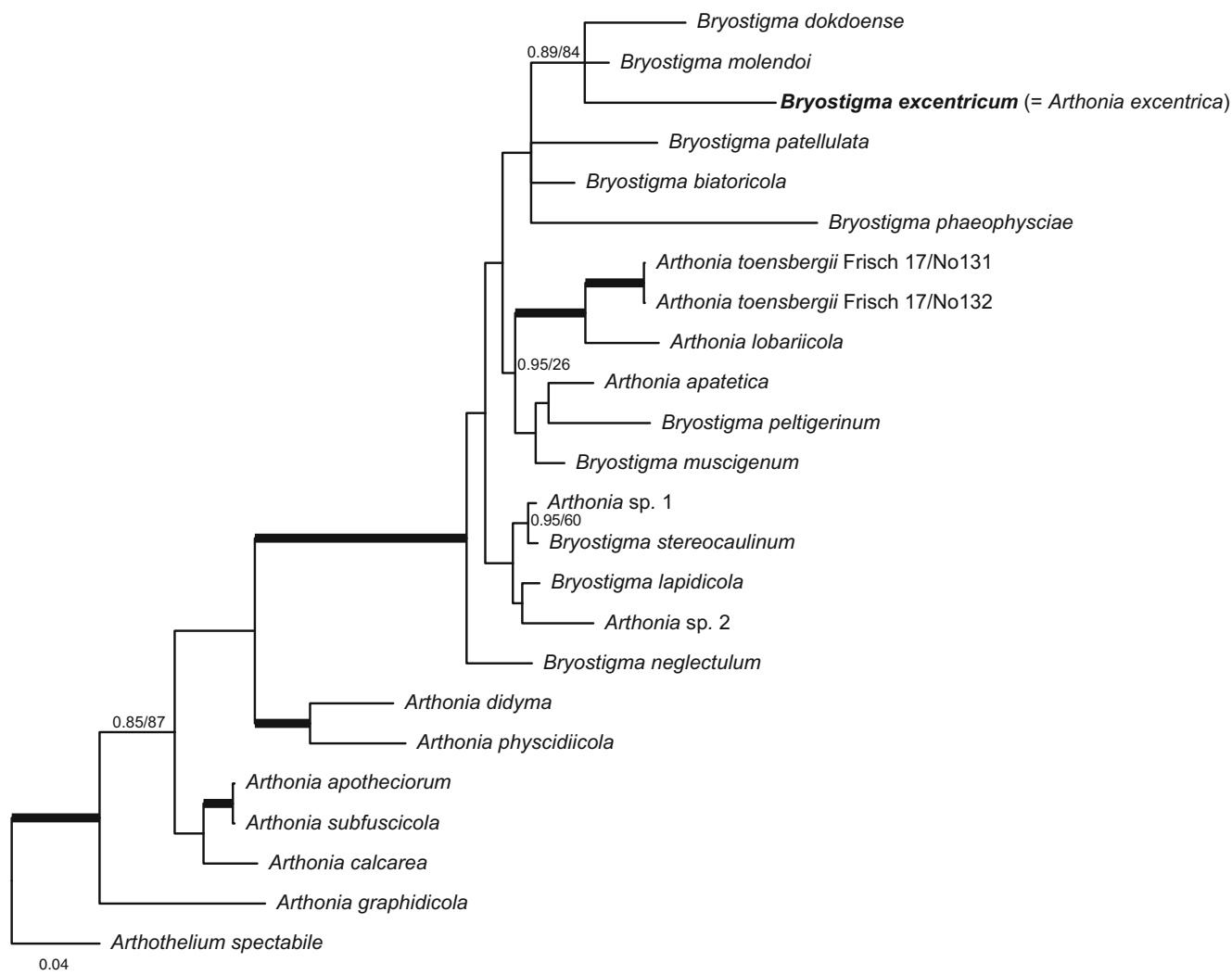


Fig. 1 Phylogeny of *Bryostigma*-clade based on ITS rDNA and mtSSU. This is the 50%-majority-rule consensus tree of a Bayesian analysis. *Arthonia excentrica* is shown in bold. Branches supported with posterior probability ≥ 0.95 and bootstrap $\geq 70\%$ are indicated in bold.

P. corrosa and *P. sphinctrinoidella*, but this relationship was not supported. The analyses based on ITS rDNA and LSU rDNA clearly show that this species is different from *P. sphinctrinoidella*.

Sphinctrina dataset

The dataset included 26 sequences, representing 23 species, four of them belonging to *Sphinctrina*. The alignment included 372 parsimony informative characters. *Sphinctrina* was polyphyletic (Fig. 5); *S. intermedia* Tibell was related to *Chaenothecopsis savonica* (Räsänen) Tibell, although this relation was not supported. The other species of *Sphinctrina* formed a well-supported clade, related to a clade including *Chaenothecopsis khayensis* Rikkinen & Tuovila and *C. resinophila* Rikkinen & Tuovila. The new species, *Sphinctrina sessilis*, was closely related to *S. leucopoda* Nyl.

Bootstrap and posterior probability values are indicated for the branches supported only in one of the analyses (posterior probability ≥ 0.95 or bootstrap $\geq 70\%$)

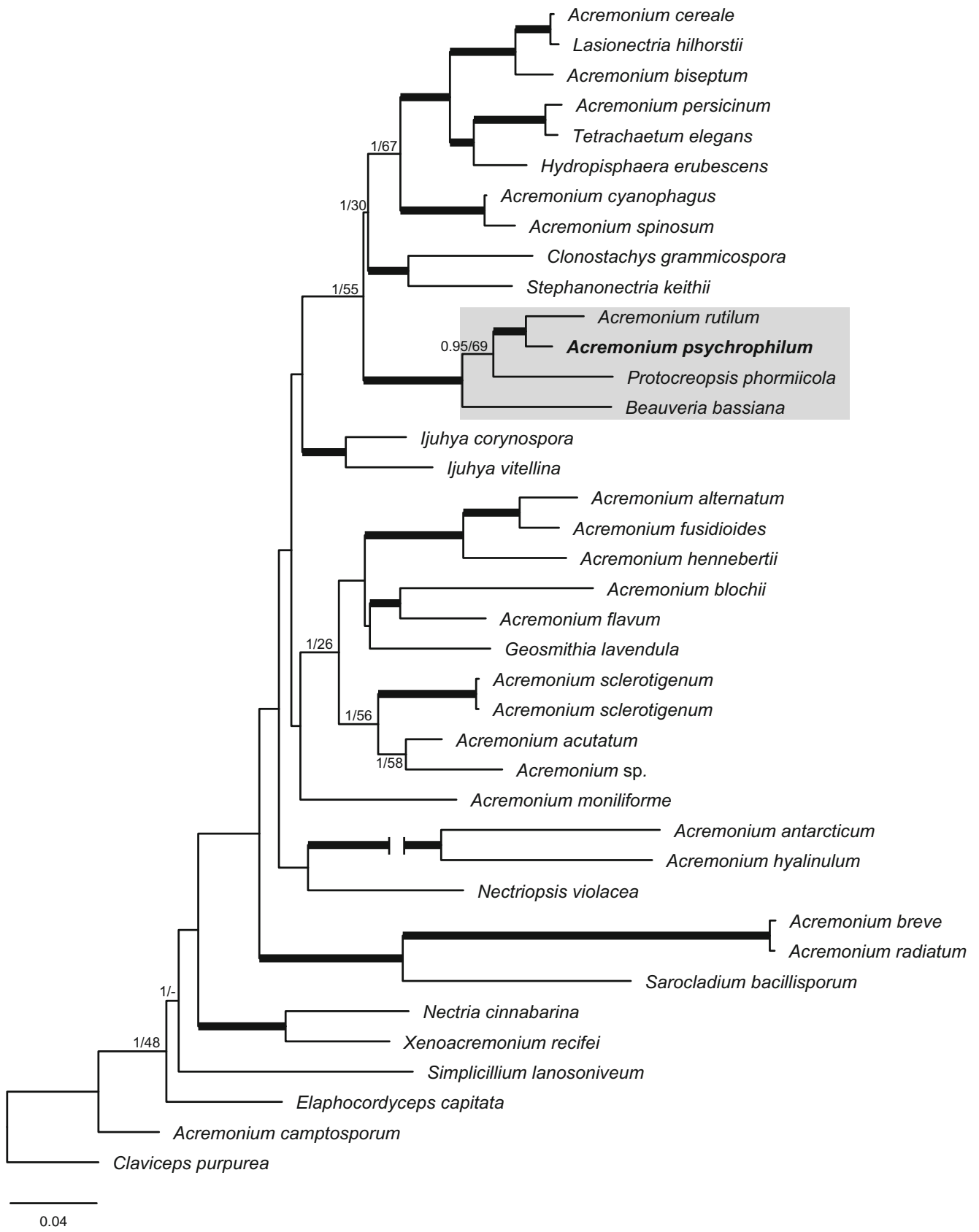
(Fig. 5), but based on morphological and molecular results we consider it to represent an undescribed species.

Species and taxonomy

Acremonium psychrophilum C. Möller & W. Gams

This species was described from King George Island (Möller and Gams 1993) forming tufts on *Mastodia tessellata*

Fig. 2 Phylogeny of *Hypocreales* based on ITS rDNA and LSU rDNA. This is the 50%-majority-rule consensus tree of a Bayesian analysis. *Acremonium psychrophilum* on *Mastodia* is shown in bold. Branches supported with posterior probability ≥ 0.95 and bootstrap $\geq 70\%$ are indicated in bold. Bootstrap and posterior probability values are indicated for the branches supported only in one of the analyses (posterior probability ≥ 0.95 or bootstrap $\geq 70\%$)



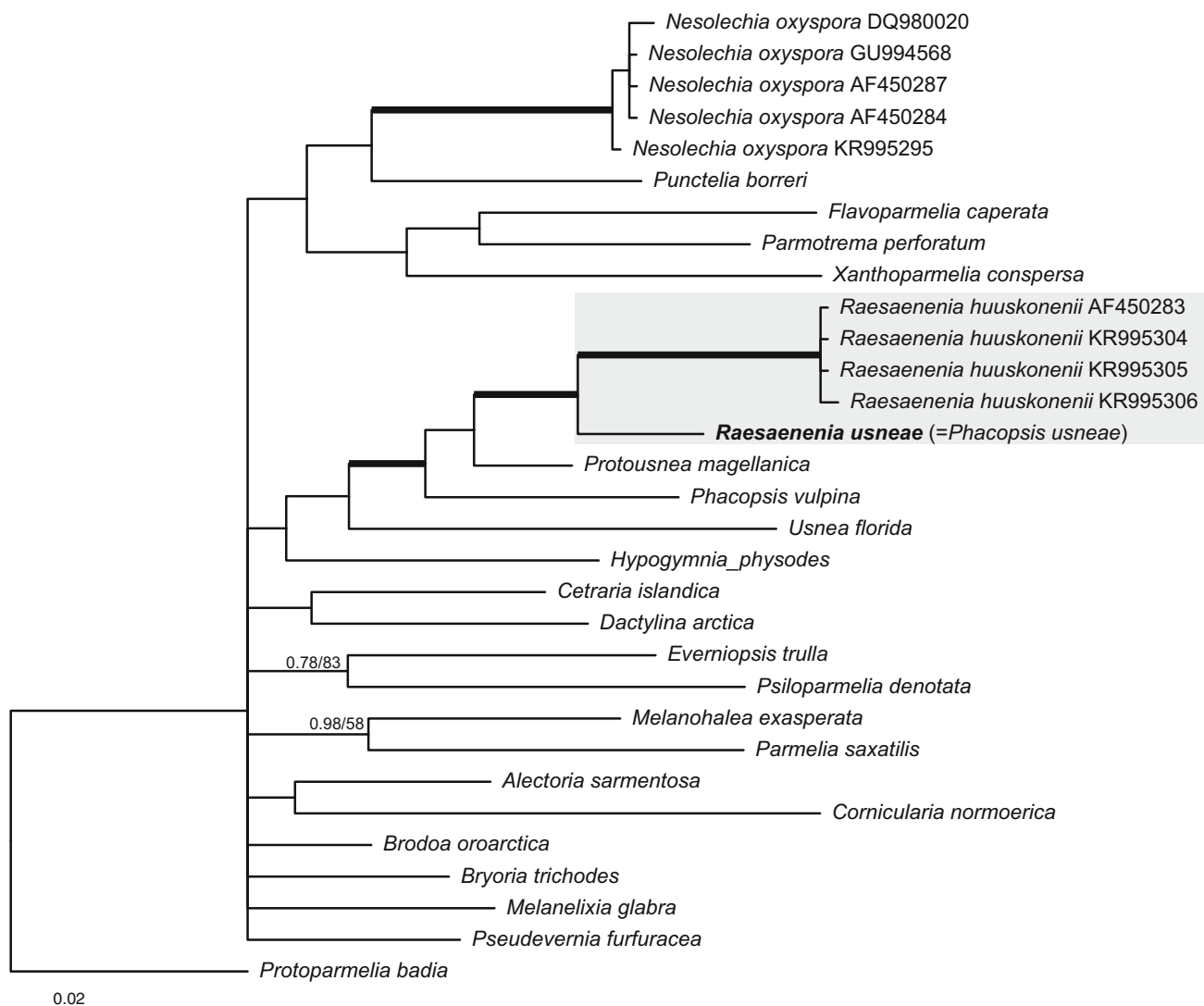


Fig. 3 Phylogeny of *Phacopsis* within *Parmeliaceae*, based on ITS rDNA. *Phacopsis usneae* is shown in bold. This is the 50%-majority-rule consensus tree of a Bayesian analysis. Branches supported with posterior probability ≥ 0.95 and bootstrap $\geq 70\%$ are indicated in bold.

Bootstrap and posterior probability values are indicated for the branches supported only in one of the analyses (posterior probability ≥ 0.95 or bootstrap $\geq 70\%$)

(Hook f. & Harv.) Hook f. & Harv. (*Turgidosculum complicatulum* (Nyl.) Kohlm. & E. Kohlm. in that paper). The description of *A. psychrophilum* indicates that this species has vegetative chondroid hyphae, phialides straight or slightly curved, thick-walled, $20\text{--}70 \times 1.8\text{--}2.8 \mu\text{m}$ (base), tapering towards the apex, $0.8\text{--}2 \mu\text{m}$ wide, and conidia cylindrical to ellipsoid, hyaline, smooth-walled, $5\text{--}13.5 \times 2\text{--}2.5 \mu\text{m}$. The specimen studied fits well the original description, forming white dots on *Mastodia*, with unbranched conidiophores, conidiogenous cells $30\text{--}58 \times 2\text{--}3 \mu\text{m}$ (in base), $1\text{--}2 \mu\text{m}$ in apex, sometimes septate, and conidia ellipsoidal, straight $0\text{--}1$ septate, $5\text{--}9(12) \times 1.5\text{--}2.5 \mu\text{m}$.

Material examined: Antarctica: Livingston Island, South Bay, Caleta Argentina, rocks to the East of the beach, $62^{\circ}40'11''\text{S}$, $60^{\circ}24'13''\text{W}$, $0\text{--}10 \text{ m}$, on *M. tessellata* on a rock, 23 February 2018, *J. Etayo* 31294 (hb. Etayo).

Arthonia olechiana Etayo, sp. nov. (Fig. 6)

Mycobank: MB 846737

Type: Antarctica: Livingston Island, cliffs and rocks around lab in Base Española Juan Carlos I, 15 m, $62^{\circ}39'45.4''\text{S}$, $60^{\circ}23'09.2''\text{W}$, 6 March 2018, on *Steinera olechiana* on the soil between rocks, *J. Etayo* 31620 (MAF-Lich.-holotype).

Diagnosis: It differs from *Arthonia epifarinoso* in having larger ascomata, $200\text{--}600 \mu\text{m}$ diam., simple, not formed by coalescence of other smaller ones; hyaline hymenium, KI+ blue; epihymenium brown and generally larger ascospores, $10.5\text{--}16 \times 3.8\text{--}5.5 \mu\text{m}$.

Etymology: This species is named in honour of Maria Olech, a Polish researcher of lichens and lichenicolous fungi from Antarctica.

Description: Ascomata apothecia, effuse, black, matt, first fly flat, then convex, $200\text{--}600 \mu\text{m}$ diam. Proper exciple

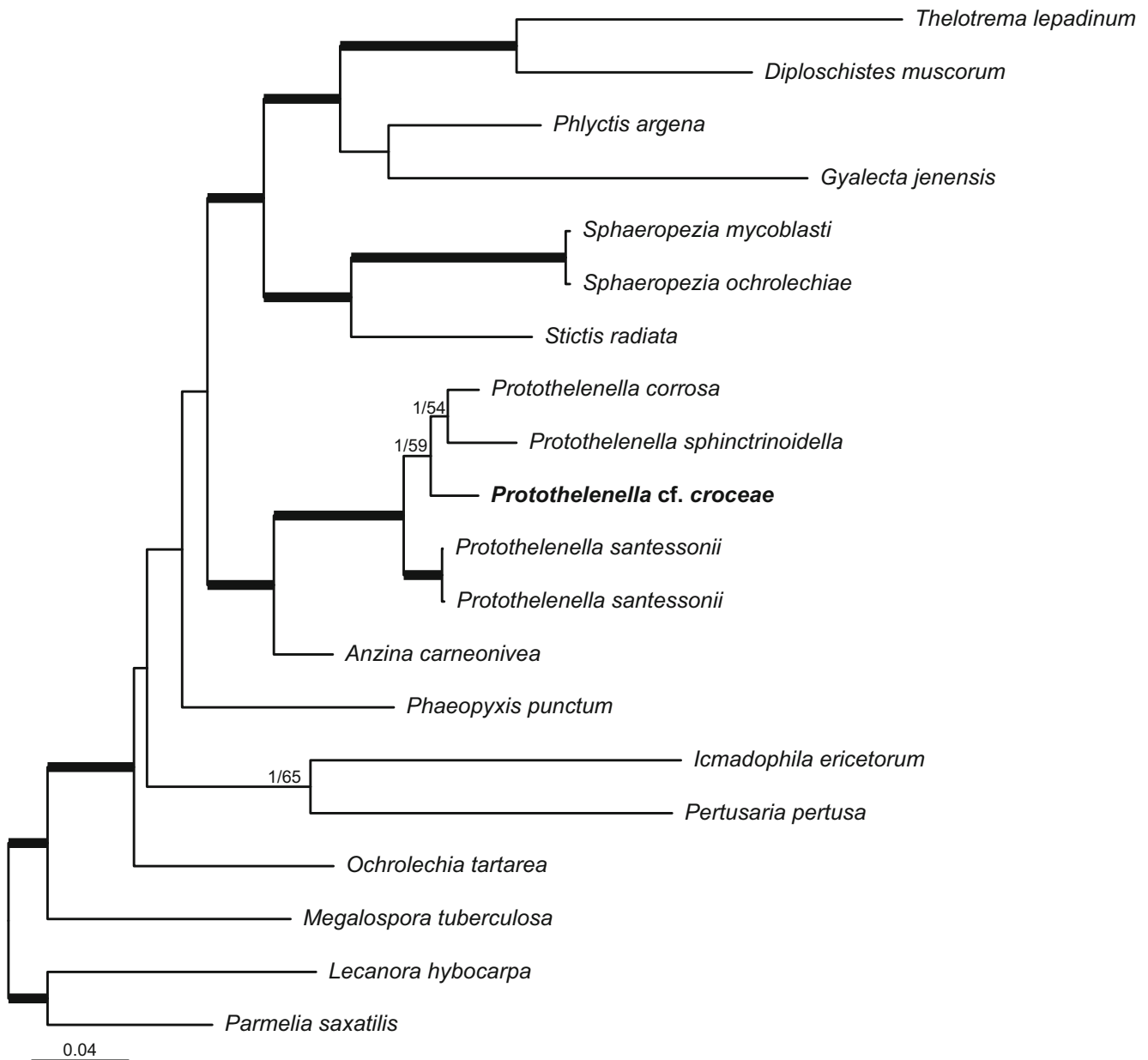


Fig. 4 Phylogeny of *Ostropales* based on ITS rDNA, LSU rDNA, and mtSSU. *Protothelenella cf. croceae* is shown in bold. This is the 50%-majority-rule consensus tree of a Bayesian analysis. Branches supported with posterior probability ≥ 0.95 and bootstrap $\geq 70\%$ are indicated in

bold. Bootstrap and posterior probability values are indicated for the branches supported only in one of the analyses (posterior probability ≥ 0.95 or bootstrap $\geq 70\%$)

present, thin, formed by a net of hyphae similar to paraphyses, septate, 2–2.5 μm wide. Epithymenium greenish brown, K+ intensifying. Hymenium hyaline, I+ reddish, KI+ blue, 40–50 μm tall, composed by abundant paraphysoids, septate, branched-anastomosed, 2–2.5 μm wide, apically capitate, 3–7 μm wide, with thin wall. Hypothecium hyaline. Asci widely clavate, semi-fissitunicate, with large apical dome and distinct ocular chamber, *Arthonia*-type, 8-spored, externally KI+ blue, showing a small apical ring more intensely blue, 26–45 \times 13–19 μm ($n = 14$). Ascospores hyaline, (0–)1-septate, ellipsoidal, straight, not constricted at the septum, upper cell slightly

wider, with obtuse ends, with many small oil guttules inside, 10.5–16 \times 3.8–5.5 μm ($n = 40$).

Distribution: It is known from King George Island and Livingston Island, living on the thallus of *Steinera*.

Remarks: This species forms large, black structures similar to galls but showing hymenial structures with many asci and ascospores when cut. Sometimes hyphae of a probably fungicolous hyphomycetes are present too. It seems not to be present on other similar species sometimes living together with the host, such as *Massalongia carnosae* (Dicks.) K rb. No other species of *Arthonia* is known to live on *Steinera* or

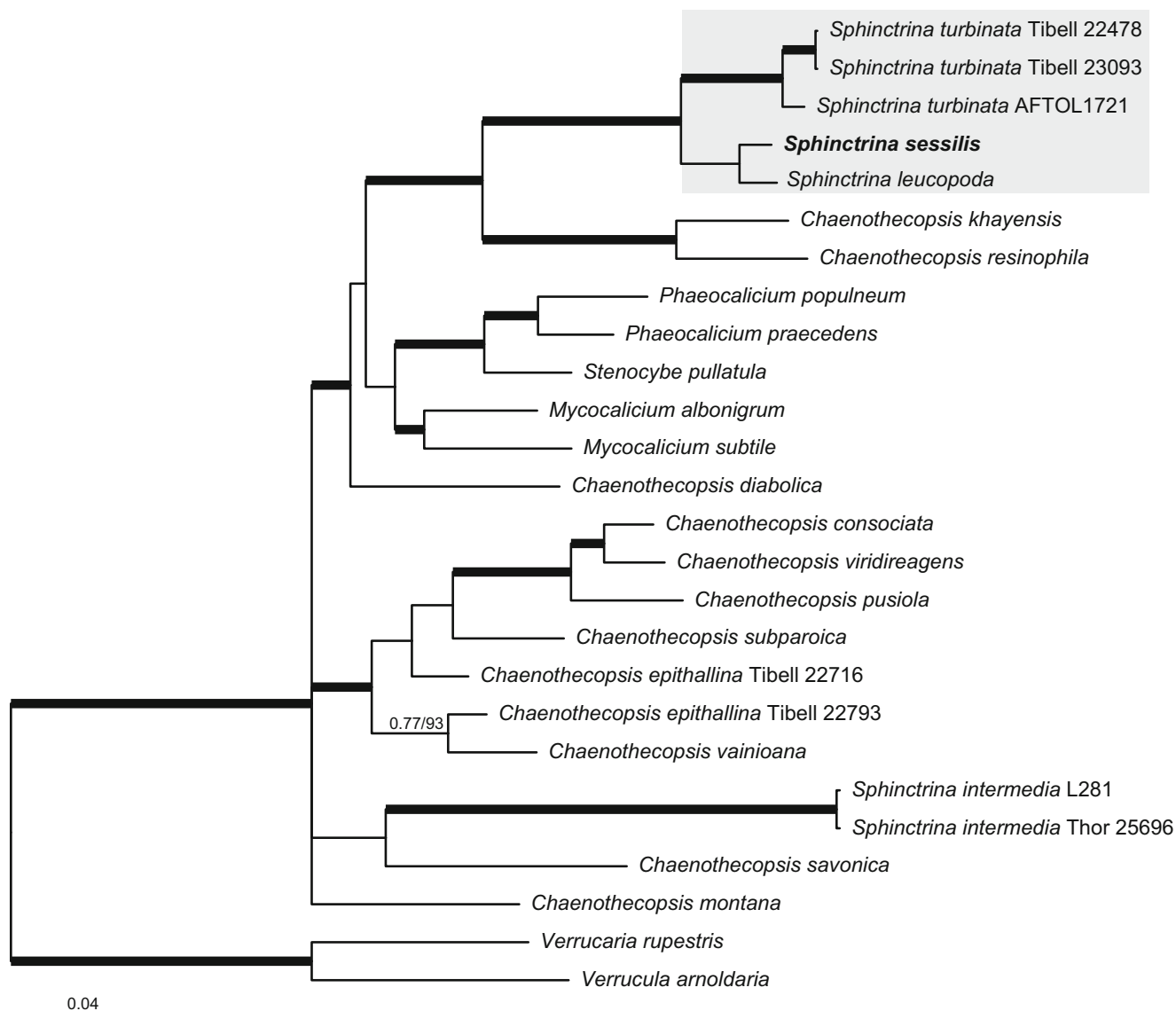


Fig. 5 Phylogeny of *Mycocaliciales* based on ITS rDNA, LSU rDNA and mtSSU. *Sphinctrina sessilis* sp. nov. is shown in bold. This is the 50%-majority-rule consensus tree of a Bayesian analysis. Bootstrap and

posterior probability values are indicated on the branches. Branches supported with posterior probability ≥ 0.95 and bootstrap $\geq 70\%$ are indicated in bold

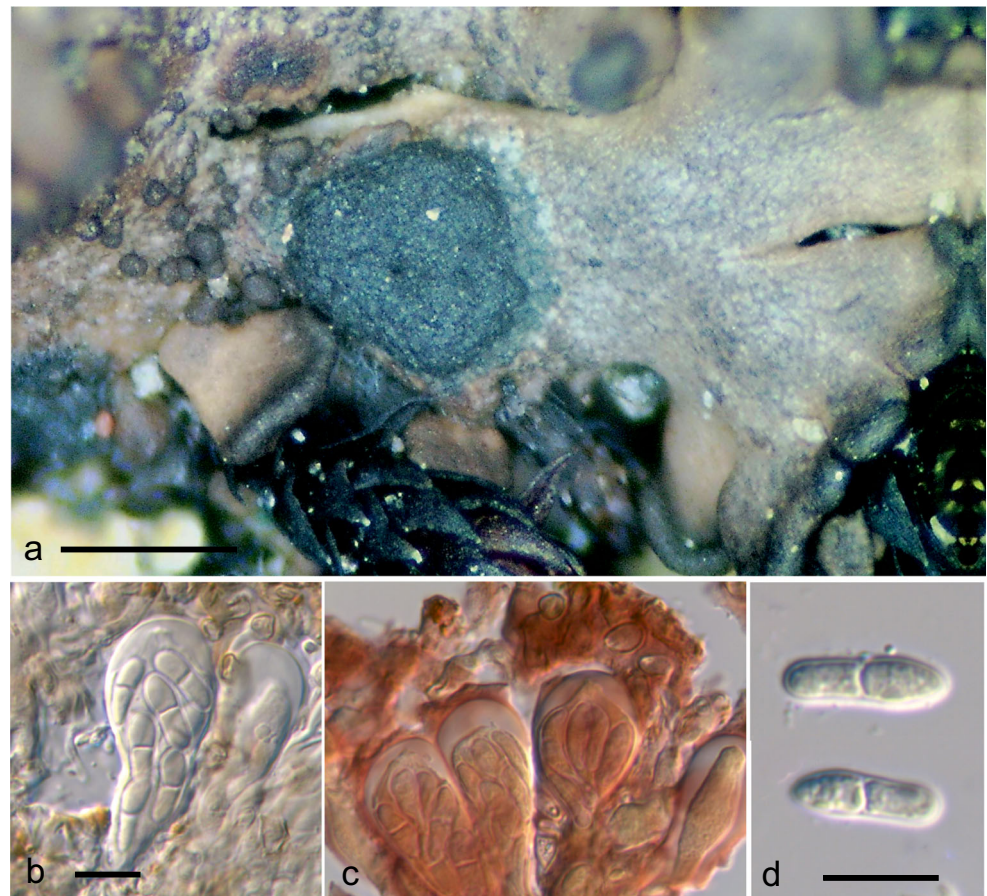
Massalongia. Another species described on a related genus is *A. epifarinoso* Etayo (Etayo and Sancho 2008). This species grows on *Pannaria farinosa* Elvebakk & Fritt-Rasm. and is known from Navarino Island (South Chile). It differs from *A. olechiana* in its smaller ascospores (50–250 μm diam.), normally grouped forming tuberculiform structures, greenish hymenium, KI+ red, green epihymenium, and generally smaller spores, 11.5–13 \times 4–4.5 μm . This species also resembles *A. peltigerea* Th. Fr. which has larger ascospores (15–19 \times 5–6(–7) μm) and different hosts (*Peltigera* and *Soralina*).

This species was already recorded and described by Alstrup et al. (2018) as *A. massalongiae* Alstrup and Olech on *Massalongia olechiana* Alstrup and Söchting from King George Island and Livingston Island. The species name, as

well as others published by Alstrup et al. (2018), is invalid since it was not registered in Mycobank, which is a mandatory requirement under International Code of Nomenclature for algae, fungi, and plant (ICN) after 2013. Furthermore, the host, *Massalongia olechiana*, is correctly named now *Steinera olechiana* (Alstrup & Söchting) Ertz & Söchting (Ertz et al. 2017).

Material examined: Antarctica: Livingston Island, rocks over Punta Polaca, 60–70 m, 62°39'49.4"S, 60°23'51.5"W, 5 March 2018, on *Steinera olechiana*, on soil, *J. Etayo* 31611, 31613 (hb. Etayo); Punta Barnard, boulders near a great beach and in a promontory near it, 0–5 m, 62°45'07.8" S, 60°19'43.1"W, 9 March 2018, on *S. olechiana* on soil crevices, *J. Etayo* 31689 (hb. Etayo).

Fig. 6 *Arthonia olechiana* (holotype, hb. Etayo 31620): **a** ascomatal habit of *Arthonia* growing on *Steinera olechiana*, **b** hymenium showing asci in water, **c** hymenium with asci in I, **d** ascospores in water. Scales: **a** = 500 μm ; **b**, **c**, **d** = 10 μm



Bryostigma excentricum (Th. Fr.) Etayo & Pino-Bodas, comb. nov.

Mycobank: MB 846740

Basionym: *Arthonia excentrica* Th. Fr., *K. svenska Vetensk-Akad. Handl., ny följd* 7(no. 2): 46 (1867).

Type: Supra muscos parce lecta in Lovéns berg et verisimiler quoque ad Brandewijnebay (Chyd.), A.J. Malmgren (UPS-L-085577–holotype, not seen).

Allarthonia excentrica (Th. Fr.) Zahlbr., *Cat. Lich. Univers.* 2: 109 (1922)

Description: Ascomata apothecia, black, small, firstly sunken on the host and flat, then generally convex, 60–170 μm diam. Proper exciple thin and reduced. Hymenium brownish with some greenish hue, 35–40 μm tall, I+ red, KI+ blue. Epithymenium light brown, formed by subhorizontal apical zones of branched paraphysoides anastomosed and apically capitate, 3–4 μm , with intracellular pigment. Hypothecium concolourous with hymenium or slightly darker, 7–10 μm tall. Asci widely obpyriform, 8-spored, apically thickened, 32–43 \times 18–21 μm ($n = 12$). Ascospores hyaline, ellipsoidal to oblong, 1-septate, upper cell a bit larger than lower one, without a sheath, not constricted in the septum, wall I+ red, 11–13(–15) \times 4.5–5.5 μm ($n = 25$).

Distribution: This species is widely distributed in the northern Holarctic (reported for instance by Alstrup and Elvebakk 1996; Alstrup and Hawksworth 1990; Santesson 1993; Ihlen and Wedin 2008; Zhurbenko 2010) and is also known from Chile (Etayo and Sancho 2008), Malaysia (Zhurbenko and Ohmura 2019), and also recorded on *Lepraria* from Antarctica, in King George Island, Livingston Island and Penguin Island (Alstrup et al. 2018). We have found that it is a common species on *Lepraria* in Livingston Island, particularly on the yellowish *L. straminea* Vain., and we also give a record from Ardley Island.

Remarks: *Arthonia excentrica* Th. Fr. was described as a lichen with a verrucous to farinaceous thallus (Fries 1867), which in fact corresponded to the host, some species of *Lepraria* and *Leprocaulon*. Not many recent and detailed descriptions of this species exist. In the specimens studied here, the spore wall is I+ red. Some authors (e.g. Ihlen and Wedin 2008) recorded brown hypothecium and spores of similar size to ours (11–13 \times 5–6 μm) but they did not mention the spore reaction with I.

Material examined: Antarctica: Livingston Island, slope from Base Española to the antenna of Reina Sofía, 62°39' 59"S, 60°23'13"W, 60–100 m, 22 Feb. 2018, on

L. straminea on soil, *J. Etayo* 31256 (hb. Etayo); Punta Polaca, rocks and soil in an esplanade, 20–50 m, 62°39'48" S, 60°23'39"W, 26 Feb. 2018, on *Lepraria alpina* and *L. straminea* on soil, *J. Etayo* 31352 (hb. Etayo); Punta Polaca, rocks near the shore, 0–10 m, 62°39'42"S, 60°23'36"O, 26 Feb. 2018, on white *Lepraria* sp. on bryophytes, *J. Etayo* 31376 (hb. Etayo); Caleta Argentina beach and boulders and soil far ahead on the beach, 62°40'20"S, 60°24'43"O, 0–10 m, 2 March 2018, on *L. straminea* on soil, *J. Etayo* 31524, 31530 (hb. Etayo, MAF-Lich.abundant and well developed); outcrops on Punta Polaca, 20–50 m, 62°39'48.8"S, 60°23'40"W, 5 March 2018, on *L. straminea* on soil, *J. Etayo* 31589 (hb. Etayo); track to Reina Sofia mountain, boulders and rocks in the way, 50–120 m, 62°40'07"S, 60°22'48"W, 26 Feb. 2018, on *Lepraria alpina* on soil, *J. Etayo* 31431 (hb. Etayo); outcrops on Punta Polaca, 60–70 m, 62°39'49.4"S, 60°23'51.5"W, 5 March 2018, on *Lepraria* sp. (white) on soil, *J. Etayo* 31615 (hb. Etayo); outcrops and walls surrounding the Spanish Base laboratory, 15 m, 62°39'45.4"S, 60°23'09.2" W, 6 March 2018, on *L. straminea* on bryophytes on boulder, *J. Etayo* 31629, 31639 (hb. Etayo, MAF-Lich.); Juan Carlos I Spanish Base, outcrops behind zodiak hangar 13–20 m, 62°39'40"S, 60°22'57"W, 7 March 2018, on *L. straminea* on bryophytes, *J. Etayo* 31669 (hb. Etayo); Punta Barnard, boulders near a great beach and in a promontory near it, 0–5 m, 62°45'07.8"S, 60°19'43"S, 1°W, 9 March 2018, on *Lepraria alpina* on bryophytes, *J. Etayo* 31699 (MAF-Lich.). South Shetland archipelago. Ardley Island, "Ardley", on *Lepraria alpina* on soil, c. 20 m, 62°12'46"S, 58°55'53W, J. Boy, 1 Feb. 2015, *Schiefelbein* 4284, 4285, 4289 (hb. Schiefelbein).

Protothelenella* cf. *croceae (Bagl. & Car.) Hafellner & Mayrh.

Description: Ascomata perithecia, firstly semi-immersed then sessile, obpyriform, black, round and papillate, 170–350 µm diam., growing on whitish, dead squamules of the hosts. Ascomatal wall orange brownish in the external part, with *textura intricata* superficially, formed by a net of thin hyphae, hyaline in the inner part, thickness of wall 60–75 µm in the upper part around the ostiole, thinner in the lateral and basal parts, to 15–30 µm thick. Furthermore, with a hyaline gel layer covering the perithecia, 5–10 µm thick. Paraphyses abundant, filiform, branched, very thin, 0.5–1 µm thick. Asci cylindrical to clavate, widened apically and I+ blue, 90–135 × 16–18 µm ($n = 5$), firstly with 8 young spores, sometimes lately with only 4 mature spores. Ascospores first simple, then 3–4-septate, finally muriform, ellipsoidal, sometimes with apiculate ends, (17–)22–35(–40) × (8–)10–13(–14) µm ($n=37$).

Ecology and distribution: Found especially not only on unhealthy *Psoroma cinnamomeum* Malme but also on *Steinera*, living only on decolored and dead areas of host squamules, never on healthy thalli. *Cladonia* and *Lepraria*

are also questionable hosts. Due to the bad health condition of the host thalli, showing generally white and thin squamules, we firstly considered the species to be a saprophyte, but the study of several findings in different development stages rather points to a parasitic behaviour.

Remarks: This species is morphologically very similar to *P. croceae*. *Protothelenella croceae* s.s. has spores 28–40 × 9–13 µm (Mayrhofer 1987) and has been reported on *Peltigera* sp. pl. and *Solorina crocea* (L.) Ach. (type) from Northern Europe and the Alps. Zhurbenko and Brackel (2013) described a specimen collected from Svalbard, whose paraphyses are clearly thicker, (1–)2 µm, but similar for the rest of features to the Antarctic specimens. Several species of *Protothelenella*, lichenicolous and humicolous, are hardly distinguishable, and further studies are required to clarify the taxonomy of this group. *Protothelenella sphintrinoidella* was considered a muscicolous lichen with membrane-like to evanescent thallus by Orange et al. (2009). However, Zhurbenko (2010) reported *P. sphintrinoidella* in the Arctic, growing on soil, mosses, *Cladonia*, *Peltigera*, *Stereocaulon*, etc. Our Antarctic specimens of *P. cf. croceae* are also similar to Zhurbenko (2010) diagnosis of *P. sphintrinoidella*, except for larger ascospores, (23–)25–30(–32) × (8–)8.5–10.5(–14) µm, l/b = (2.1–)2.5–3.3(–3.6). *Protothelenella santessonii* Mayrh. is also similar, but the host of the type specimen was *Cladonia squamosa* Hoffm. (Mayrhofer 1987). Later, *P. santessonii* was also recorded from Antarctica (Alstrup and Cole 1998; Alstrup et al. 2018) on *Cladonia pyxidata* (L.) Hoffm. According to Mayrhofer (1987), *P. santessonii* has smaller ascomata, 0.1–0.2 mm diam. and also smaller submuriform, ellipsoid spores, 18–24 × 10–12 µm. As our specimens growing on *Cladonia* are indistinguishable from others recorded from different hosts in Livingston Island, we think they belong to the same species and are provisionally named here *P. cf. croceae*.

Material examined: Antarctica: Livingston Island, slope from Spanish Base to the antenna of Reina Sofia, 62°39'59" S, 60°23'13"W, 60–100 m, 22 Feb. 2018, on *Psoroma cinnamomeum* on soil, *J. Etayo* 31248 (hb. Etayo, MAF-Lich.); Punta Polaca, rocks and soil in an esplanade, 20–50 m, 62°39'48"S, 60°23'39"W, 26 Feb. 2018, on white patches of *Ps. cinnamomeum* (?) on soil, *J. Etayo* 31347 (hb. Etayo); Punta Polaca, rocks near the shore, 0–10 m, 62°39'42"S, 60°23'36"W, 26 Feb. 2018, on white lobules of *Pannariaceae* on bryophytes, *J. Etayo* 31376 (hb. Etayo); track to Reina Sofia mountain, boulders and rocks in the way, 50–120 m, 62°40'07"S, 60°22'48"W, 26 Feb. 2018, on dead *Pannariaceae* on soil, *J. Etayo* 31390 (hb. Etayo, MAF-Lich.); sally rocks, big rocks near the shore at both ends of a small beach, 62°42'07"S, 60°25'44"W, 1–5 m, 27 Feb. 2018, on *Ps. cinnamomeum* on soil, *J. Etayo* 31433 (hb. Etayo); Punta Polaca, boulders near the sea, 62°39'43"S, 60°23'36" W, 2 March 2018, on *Steinera* on soil, *J. Etayo* 31549, 31553

(hb. Etayo); outcrops on Punta Polaca, 20–50 m, 62°39'48.8" S, 60°23'40"W, 5 March 2018, on *Psoroma* on soil and bryophytes, *J. Etayo* 31579 (hb. Etayo, MAF-Lich.); outcrops and walls surrounding the Spanish Base laboratory, 15 m, 62°39'45.4"S, 60°23'09.2"W, 6 March 2018, on bryophytes, but also on *Psoroma* and *Cladonia* on boulder, *J. Etayo* 31629 (hb. Etayo); Pico Radio located over the Spanish Base, 130 m, 62°39'55.3"S, 60°23'51.4"W, 5 March 2018, on thallus of a white grey *Lepraria* on crevices, *J. Etayo* 31666 (hb. Etayo); ibidem, on squamules of *Cladonia* sp. and soil, *J. Etayo* 31667 (hb. Etayo); ibidem, on squamules of *Psoroma* sp. on soil in crevices, *J. Etayo* 31689 (hb. Etayo); Punta Barnard, boulders near a great beach and in a promontory near it, 0–5 m, 62°45'07.8"S, 60°19'43.1"W, 9 March 2018, on *Psoroma hypnorum* on soil, *J. Etayo* 31690 (hb. Etayo).

Raesaenienia usneae (C.W. Dodge) Etayo & Pino-Bodas, comb. nov.

Mycobank: MB 846761

Basionym: *Phacopsis usneae* C.W. Dodge, B.A.N.Z. Antarct. Res. Exped. Rep., Ser. B 7: 264 (1948).

Type: Antarctica: Kerguelen, Mount Wyville Thompson, 1000–1500 ft, on *Usnea trachycarpa*, Banzare B246–21 (holotype not located. FH–neotype, not seen).

The complete description of this species can be found in recent publications (Etayo and Sancho 2006; Hawksworth and Iturriaga 2006), so we do not repeat it here. It is one of the most morphologically variable lichenicolous fungi in Antarctica. According to our observations, the apothecia can be flat to hemispherical, shiny or rugose (then similar under a dissecting microscope to a *Plectocarpon*), dispersed to confluent and even forming large bunches of apothecia, etc. Some laciniae of *Usnea* are covered by abundant and conspicuous infections, with many apothecia in every lacinia, however, *Usnea* seems to survive relatively well in extreme cases like this. Sometimes small pycnidia appear inside the hymenium. Conidiogenous cells are more or less cylindrical, 6–11(–16) × 2–3(–3.5) µm and conidia straight to slightly curved, bacilar, with obtuse end, narrowing at the point of insertion with the conidiogenous cell (6–)8–10(–14) × 2–2.5 µm. Conidiomata on *Phacopsis* have been recorded as immersed in host thallus, with phialidic conidiogenous cells and bacilliform conidia (Triebel et al. 1995), features that fit well with those of *R. usneae*. Triebel and Rambold (1988) described the conidia of *R. huuskonenii* as bacilar, straight to slightly curved, and smaller, 6–7 × 1.5–2 µm, with similar size range of those studied here. According to the type of conidia and conidiogenous cells, the conidiomata observed most likely belong to *R. usneae*.

Distribution: It is known from Kerguelen, Melchior Archipelago, King George Island, Livingston Island, Penguin Island and Tierra de Fuego on different species of *Usnea*, particularly on *U. antarctica* Du Rietz (Hawksworth

and Iturriaga 2006; Etayo and Sancho 2006; Alstrup et al. 2018). It is a very common species in Livingston Island, reported from several additional localities by Etayo and Sancho (2006). A specimen with uncertain identification was reported from Northwest Caucasus in the Northern Hemisphere (Zhurbenko and Kobzeva 2014).

Remarks: This species, described by Dodge (1948) from Kerguelen, was studied by Etayo and Sancho (2006) and Hawksworth and Iturriaga (2006). Other species of *Phacopsis* has been described on *Usnea*, *P. falcispora* Triebel & Rambold, but according to Hawksworth and Iturriaga (2006) it is morphologically clearly distinct from *P. usneae*. Diederich et al. (2018) transferred it to *Nesolechia*.

Material examined: Antarctica: Livingston Island, slope from Base Española to the antenna of Reina Sofia, 62°39'59"S, 60°23'13"W, 60–100 m, 22 Feb. 2018, on *U. aurantiaco-atra* on rock, *J. Etayo* 31257 (hb. Etayo); German Cove, stones close to the west of the beach, 62°40'02"S, 60°24'07"W, 15 m, 23 Feb. 2018, on *Usnea antarctica* on soil stones, *J. Etayo* 31261, 31262, 31259 (hb. Etayo); on the base of *U. antarctica* on rock, *J. Etayo* 31365 (hb. Etayo). German Cove, stones at the East of the beach, 62°40'11.2"S, 60°24'09.1"W, 0–10 m, 23 Feb. 2018, on *U. antarctica* and *U. aurantiaco-atra*, *J. Etayo* 317174 (hb. Etayo); ibidem, on *U. antarctica* on boulder, *J. Etayo* 31309 (hb. Etayo); small glacier located at the SE of the base, outcrops, 62°39'56"S, 60°22'56"W, 110 m, 24 Feb. 2018, on thallus of *U. aurantiaco-atra* on rocks, *J. Etayo* 31322 (hb. Etayo), *J. Etayo* 31324 (MAF-Lich.); Punta Polaca, rocks near the shore, 0–10 m, 62°39'42"S, 60°23'36"W, 26 Feb. 2018, on *U. aurantiaco-atra* on rock, *J. Etayo* 31377 (hb. Etayo, MAF-Lich.); track to Reina Sofia mountain, boulders and rocks in the way, 50–120 m, 62°40'07"S, 60°22'48"W, 26 Feb. 2018, on *U. aurantiaco-atra* on stones, *J. Etayo* 31386 (hb. Etayo); Argentine Cove beach, boulders and soil far ahead of the beach, 62°40'20"S, 60°24'43"W, 0–10 m, 2 March 2018, on small almost death *Usnea* on pebbles, *J. Etayo* 31520, 31545 (hb. Etayo, MAF-Lich.); Punta Polaca, boulders near the sea, 62°39'43"S, 60°23'36"W, 2 March 2018, on *U. aurantiaco-atra* on rock, *J. Etayo* 31555, 31556 (hb. Etayo), *J. Etayo* 31557 (MAF-Lich.); Pico Moores, nunatak, scree on the cold and very windy peaks, c. 300 m, 62°40'51"S, 60°20'37"W, 3 March 2018, on *Usnea antarctica*, *J. Etayo* 31567 (MAF-Lich.); ibidem, on *U. aurantiaco-atra*, *J. Etayo* 31570 (hb. Etayo); outcrops and walls surrounding the Spanish Base laboratory, 15 m, 62°39'45.4"S, 60°23'09.2"W, 6 March 2018, on *U. antarctica* on rocks, *J. Etayo* 31618 (hb. Etayo, MAF-Lich.); ibidem, on *U. antarctica* on rocks, *J. Etayo* 31622 (hb. Etayo); outcrops and walls surrounding the Spanish Base laboratory, 15 m, 62°39'45.4"S, 60°23'09.2"W, 6 March 2018, on *U. antarctica* on boulder, *J. Etayo* 31630, 31637 (hb. Etayo); Hespérides Point, near Bulgarian base, 50–55 m, 62°08'35.3"S, 60°22'21"W, 6 March 2018, very common on

Usnea antarctica on stones near soil, *J. Etayo* 31652 (hb. Etayo); Pico Radio located over the Spanish Base, 130 m, 62°39'55.3"S, 60°23'51.4"W, 5 March 2018, on *Usnea aurantiaco-atra* on rock, *J. Etayo* 31661, 31663 (hb. Etayo); Juan Carlos I Spanish Base, outcrops behind zodiak hangar, 13–20 m, 62°39'40"S, 60°22'57"W, 7 March 2018, on *U. antarctica* on boulder, *J. Etayo* 31681 (hb. Etayo); Punta Barnard, boulders near a great beach and in a promontory near it, 0–5 m, 62°45'07.8"S, 60°19'43.1"W, 9 March 2018 on *Usnea aurantiaco-atra* and *U. antarctica*, on boulder, *J. Etayo* 31688 (hb. Etayo); ibidem, in *U. antarctica*, *J. Etayo* 31695, 31696 (MAF-Lich.); Punta Barnard, boulders near a great beach and in a promontory near it, 0–5 m, 62°45'07.8"S, 60°19'43.1"W, 9 March 2018, on healthy *U. antarctica*, *J. Etayo* 31706 (hb. Etayo).

Sphaeropeziza neuropogonis Etayo & Pino-Bodas, sp. nov. (Fig. 7)

Mycobank: MB 846738

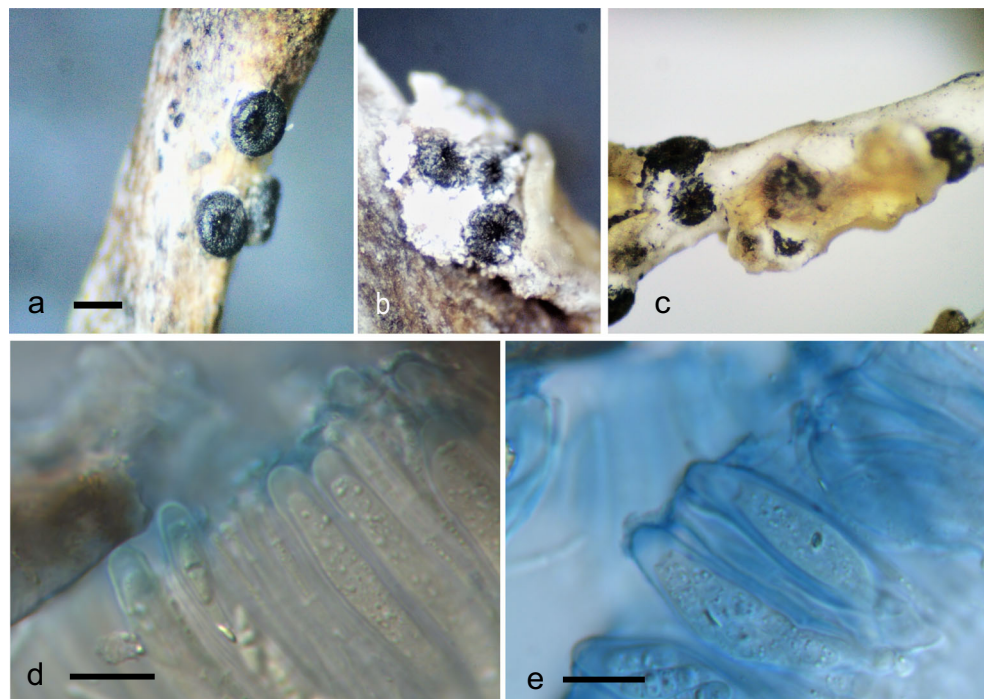
Type: Antarctica: Isla Livingston, rocks and walls surrounding the laboratory of the Spanish Base, on apothecia of *R. usneae* on dead *U. antarctica* on a rock, 15 m, 62°39'45.4" S, 60°23'09.2"W, 6 March 2018, *J. Etayo* 31618 (holotype—MAF-Lich., hb. Etayo—isotype).

Diagnosis: It differs from *Sphaeropeziza intermedia*, which lives on a very different host (*Thamnolia vermicularis*), by having smaller ascomata, 150–320 µm diam., with thinner lateral exciple, 40–50 µm thick and smaller asci, 40–68 × 6–10 µm.

Description: Ascomata apothecia, black, first immersed, apparently growing on the medulla of the host, finally emergent, breaking the cortex of the host, urceolate, 150–320 µm diam. Pore 70–100 µm diam. Ascomatal margin striate to smooth (only when directly on medulla), 50–100 µm wide. Proper exciple basal brown, 15–25 µm thick. Proper exciple lateral brown, 40–50 µm thick, with inner hyaline cells forming a paraplectenchymatic tissue with cells 4–9 µm wide. Outer exciple covered by thick layer with brown pigmented gel 4–15 × 2–10 µm. Epithecium not distinguishable. Hymenium hyaline, I+ blue, KI+ blue, especially upper gelatinous part, variable in thickness, 40–70 µm thick. Paraphyses simple, rarely branched at base, septated, filiform, 1.5–2 µm diam., sometimes slightly swollen at apex to 2–2.5 µm, embedded in a gelatinous coat particularly in apex part. Subhymenium hyaline, 10–15 µm tall. Asci fissitunicate, thickened apically with a distinct ocular chamber and a homogeneous reaction in KI+ blue, cylindrical to clavate, 8-spored, 40–68 × 6–10 µm (n = 17). Ascospores biseriolate inside the ascus, very small, (1–2)–3-septate, 8–11.5 × 3–4 µm (n = 42), l/w ratio 2.25–3.1.

Ecology and distribution: On *Usnea antarctica* growing intermixed with *Raesaenenia usneae*, even on the apothecia of the fungus in some samples, then difficult to see due to the dark colour of host and parasite; normally in older basal thallus parts, where it induces a brownish colouration. In thallus parts devoid of cortex, also observed growing on the medulla. It shares host with several lichenicolous fungi and it has been collected in several localities in Livingston Island.

Fig. 7 *Sphaeropeziza neuropogonis* (hb. Etayo 31622): **a, b, c** ascomatal habit on laciniae of *Usnea*; **a** in an *Usnea* thallus that lacks a cortex; **d, e**, hymenium showing asci and some ascospores inside (left-down of the figures), in KI. Scales: **a, b, c** = 200 µm; **d, e** = 10 µm



Remarks: The genus *Sphaeropezia* Sacc. was resurrected by Baloch et al. (2013) to include the lichenicolous species previously treated in the genus *Odontotrema* (Diederich et al. 2002). In their key, the authors considered *S. intermedia* to be the most similar species, occurring on a different host (*Thamnolia*) and it was only reported from the type locality, which is in Alaska (Diederich et al. 2002). Morphologically, *S. intermedia* has larger ascospores, (225–)320–460(–540) µm diam., wider margin, (110–)130–180(–210) µm, wider lateral exciple, 100–110 µm thick, and larger asci 60–75 × 6.5–7.5 µm. But the spores of both species are similar, although slightly larger in *S. intermedia*, of (10–)10.6–12.5(–13.5) × (3–)3.4–4.1(–4.5) µm, l/w ratio 2.7–3.5 and with l/w ratio smaller in *Sphaeropezia neuropogonis*. It differs also from *Odontotrema* sp. 2, growing on *Usnea* and only known from New Guinea (Diederich et al. 2002), in the latter having a larger hymenium, 65–85 µm thick, that does not react with I and KI, and also bigger spores, (12.9–)13.2–16.1(–18) × (4.8–)4.9–5.8 (–6.5) µm.

Material examined: Antarctica: Isla Livingston, German Cove, stones close to the West of the Beach, on *Usnea antarctica* on soil stones, 62°40'02"S, 60°24'07"W, 15 m, 23 Feb. 2018, *J. Etayo* et al. 31262 (hb. Etayo); German Cove, rocks to the East of the beach, on the base of *U. antarctica* on rock, 62°40'11.2"S, 60°24'09.1"W, 0–10 m, 23 Feb. 2018, *J. Etayo* et al. 31365 (hb. Etayo); about 500 m from the base in a Northeast direction, beach cliffs, on *U. antarctica* on boulder, 5–25 m alt., 62°39'36"S, 60°22'50"W, 0–25 m, 24 Feb. 2018, *J. Etayo* et al. 31309 (hb. Etayo); Sally Rocks, mountain slope with many large stones between soil ledges, on *U. antarctica* on rocks in the slope, 62°42'04"S, 60°24'59"W, 60–70 m, 27 Feb. 2018, *J. Etayo* 31457 (hb. Etayo); Argentine Cove beach and boulders and soil far ahead on the beach, on apothecia of *Phacopsis usneae* on *U. antarctica* on rock, 62°40'20"S, 60°24'43"W, 0–10 m, 2 March 2018, *J. Etayo* 31541 (hb. Etayo, MAF-Lich.); outcrops and walls surrounding the Spanish Base laboratory, on apothecia of *Ph. Usneae* on dead *U. antarctica* on rock, 15 m, 62°39'45.4"S, 60°23'09.2"W, 6 March 2018, *J. Etayo* 31618 (hb. Etayo, MAF-Lich.); ibidem, on *U. antarctica* on rocks, *J. Etayo* 31622 (hb. Etayo, MAF-Lich.); ibidem, on *U. antarctica* on boulder, *J. Etayo* 31630 (hb. Etayo); Juan Carlos I Spanish base, outcrops behind zodiac hangar, on *U. antarctica* on boulder, 13–20 m, 62°39'40"S, 60°22'57"W, 7 March 2018, *J. Etayo* 31681 (hb. Etayo); Barnard Point, boulders near a great beach and in a promontory near it, on *Usnea aurantiaco-atra* laciniae and medulla and also on *Phacopsis usneae* apothecia, 0–5 m, 62°45'07.8"S, 60°19'43.1"W, 9 March 2018, *J. Etayo* 31687 (hb. Etayo); ibidem, on *U. antarctica* in boulder, *J. Etayo* 31710 (hb. Etayo); Punta Barnard, boulders near a great beach and in a promontory near it, in *Phacopsis usneae* on *U. antarctica* and on lacinia of *U. antarctica*, 0–5 m,

62°45'07.8"S, 60°19'43.1"W, 9 March 2018, *J. Etayo* 31695 (MAF-Lich., hb. Etayo).

Sphinctrina sessilis Etayo & Pino-Bodas, sp. nov. (Fig. 8)

Mycobank: MB 846739

Type: Antarctica: Livingston Island, Caleta Argentina, low stones near the beach, 62°40'02"S, 60°24'07"W, 15 m, on *Pertusaria excludens* (sensu Øvstedal & Lewis Smith 2009), *J. Etayo* 31263 (MAF-Lich.–Holotype, hb. Etayo–Isotype).

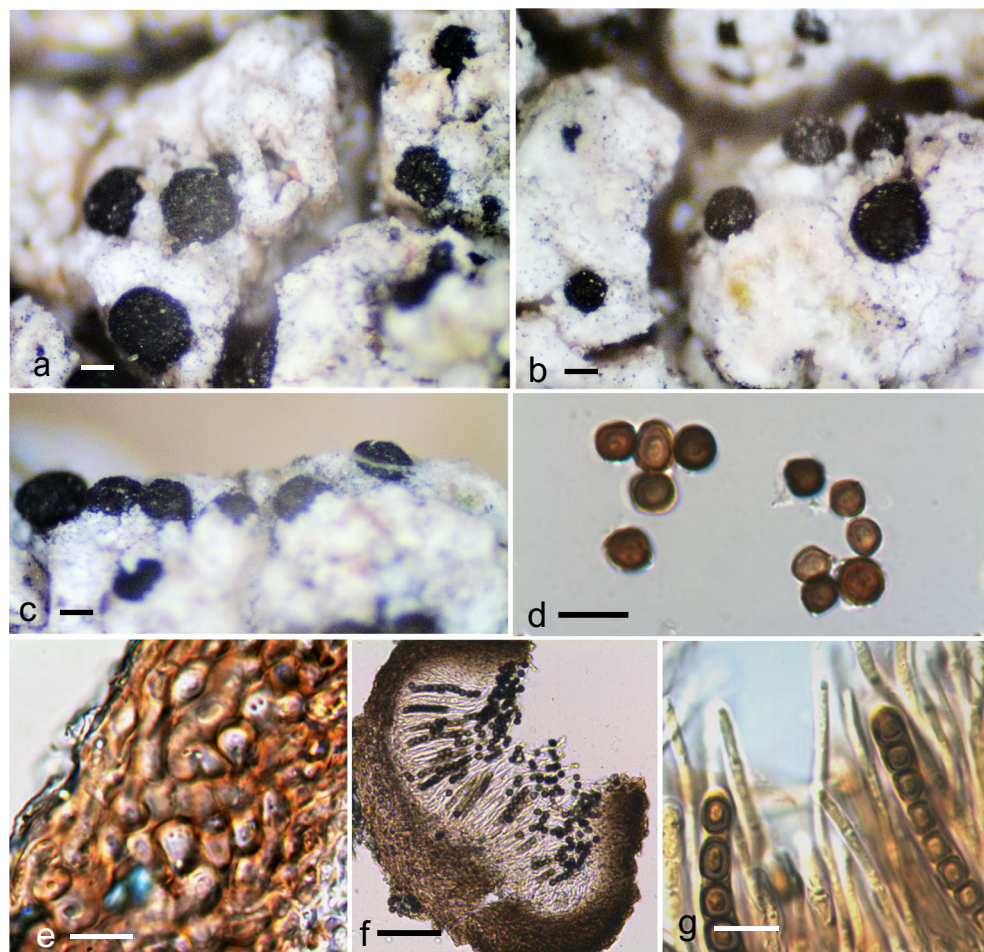
Diagnosis: Species growing on *Pertusaria excludens* with sessile ascospores, the only species of the genus with I+ red, KI+ blue hymenium and ascospores subspherical, smooth, with a thin gelatinous coat, 5–7.5 × 4.5–5.5 µm. Furthermore, it also differs from the similar *Sphinctrina turbinata* by lack of purplish to reddish-brown pigment in exciple and stalk.

Description: Ascospores apothecia, sessile, black, without pruina; head globose when young, finally nearly flat, 150–300 µm diam. Proper exciple well developed c. 40–50 µm thick (lateral), arising above the disk, consisting of dark brown, periclinally arranged and interwoven hyphae, 2–3 µm wide, and with a more paraplectenchymatic tissue below hymenium, with gelatinized cells 5–10 × 2–4 µm; structures similar to periphysoids present on the inner excipular layer, thin, c. 1 µm thick; stalk very short, immersed in the host thallus, 50–75 µm long. Hymenium 55–60 µm tall, I+ red, KI+ blue. Paraphyses simple, 1–2 µm thick, not capitated. Epithecium not distinctly colored. Hypothecium hyaline 10–15 µm tall. Asci cylindrical, apically obtuse, with a single functional wall layer, KI+ blue, disintegrating at a rather late stage, 8-spored, 45–55 × 5–6 µm (n = 10). Ascospores cubic when young, subspherical when adult, 5–6 µm diam., to widely ellipsoidal, 5–7.5 × 4.5–5.5 µm (n = 33), simple, black, with a thin gelatinous coat, smooth or with undulate appearance, uniseriately arranged in asci; wall irregularly thickened, accumulating in a black spore mass. Conidiomata unknown.

Ecology and distribution: It only inhabits *Pertusaria excludens* Nyl., a species with crateriform soralia and norstictic acid, and has been found only in a single locality on Livingston Island. Although several lichenicolous species can colonize species of *Pertusaria* in Antarctica, especially *P. corallophora* Vain., this is the only species of lichenicolous fungi found on the sorediate *P. excludens* and no one has been found on the common isidiate species *P. signyae* Øvstedal. The fungus is parasitic; the infected zones of the host thallus change colour to grey.

Remarks: All species of *Sphinctrina* seem to have a hymenium I–, KI– but the hymenium of *S. sessilis* reacts I+ red, KI+ blue. *Sphinctrina turbinata* (Pers. ex Fr.) De Not. has also subspherical spores and apothecia sessile or with a very short stalk. However, this species differs from *S. sessilis* in having a purplish to reddish-brown pigment, K+ red, in exciple and stalk, hymenium KI–, and inhabits preferently corticolous

Fig. 8 *Sphinctrina sessilis* (holotype, hb. Etayo 31623); **a, b, c** ascomatal habit of *S. sessilis* growing on the thallus of *Pertusaria*, almost sessile; **d** simple, brown, subspherical ascospores; **e** exciple in section showing paraplechtenquimatic structure; **f** section of an apothecium; **g** hymenium portion in I, showing paraphyses and asci. Scales: **a, b, c** = 100 μm ; **d, e, g** = 10 μm ; **f** = 50 μm



Pertusaria. *Sphinctrina leucopoda* Nyl. is also similar but usually has a visible stalk slightly longer than the capitulum, sclerotized exciple consisting of isodiametric to irregular cells in the upper part, hymenium KI-, and grows in similar substrates to *S. turbinata* (Tibell 2004). The phylogenetic analyses showed that both differ from *S. sessilis*. *Sphinctrina intermedia* Tibell shows intermediate characters between *S. leucopoda* and *S. turbinata* (Tibell et al. 2004) and differs from *S. sessilis* in its visible black stalk and a K+ red pigment in the exciple. The recently described *S. paramerae* Muñiz & Hladun has an exciple that reacts K+ reddish brown, larger spores, $(7.9)8.9\text{--}11.7(14.4) \times (6.5)7.8\text{--}9.3(10.7) \mu\text{m}$, and lacks an outer gelatinous spore coat (Muñiz et al. 2013).

Discussion

The Antarctic region supports a great diversity in fungi (Bridge and Spooner 2012; Rosa et al. 2019). The vegetation is clearly dominated by lichenized fungi and bryophytes (Øvstedal and Lewis 2001; Sancho et al., 2007; Peat et al. 2007). Therefore, the biota of lichenicolous fungi is expected

to be also diverse. However, its diversity is not yet completely known (Hawksworth and Iturriaga 2006; Alstrup et al. 2018). In this study, new data from some lichenicolous taxa are gathered. Wherever possible, DNA sequences were used to provide a robust and updated taxonomy, allowing us to confirm the phylogenetic placement of the studied taxa and to propose taxonomic changes.

Acremonium is a polyphyletic genus (Glenn et al. 1996; Summerbell et al. 2011; Giraldo et al. 2012, 2014, 2017) that represents the anamorphic stage of different genera. However, the anamorph-teleomorph connection remains unknown for most *Acremonium* lichenicolous species. *Acremonium psychrophilum* is phylogenetically related to the *Gliomastix/Bionectria* clade (Summerbell et al. 2011), which includes numerous species with chondroid hyphae. Our phylogenetic results showed that *A. psychrophilum* is phylogenetically closely related to *A. rutilum*, a species recorded by Möller and Dreyfuss (1996) on three lichen specimens (without species identification) from Antarctica.

Arthoniaceae form a large family of fungi, including ca. 700 species of lichenized (Lücking et al. 2016) and ca. 140 species of lichenicolous fungi (Diederich et al. 2018), and the

amount of species it encompasses keeps increasing. Several phylogenetic studies proved that the genus *Arthonia* is polyphyletic (Ertz and Tehler 2011; Frisch et al. 2014; Van den Broeck and Ertz 2016). Therefore, *Arthonia* s. l. was segregated into eight genera, one of which is *Bryostigma*. This genus was placed in a clade related to *Arthoniaceae* (Frisch et al. 2014), although its phylogenetic position is unresolved (Lücking et al. 2016) and the relationships among the members need more study (Cannon et al. 2020). Recently, most of the species of this clade were transferred to the genus *Bryostigma* (Kondratyuk 2020), but several errors were introduced, according to Cannon et al. (2020). Our phylogenetic analyses based on ITS rDNA and LSU rDNA showed the placement of *Arthonia excentrica* from Antarctica in the *Bryostigma* clade. This clade includes mainly parasitic species characterized by black and convex ascomata, frequently adnate (Frisch et al. 2014). Morphological similarities of *A. excentrica* Th. Fr. to species of this clade were previously noted (Frisch & Holien 2018).

The genus *Protothelenella* includes lichenized, lichenicolous, or facultative lichenicolous species. Three species have been reported with lichenicolous habit (Diederich et al. 2018), but only DNA sequences for *P. santessonii* are available (Pino-Bodas et al. 2017). *Protothelenella sphinctrinoidella* and *P. sphinctrinoides* occasionally grow on terricolous lichens, *Cetrariella* and *Peltigera* (Zhurbenko and Brackel 2013). However, the species studied here grows specifically on *Psoroma*. The phylogenetic analyses based on ITS rDNA, LSU rDNA, and mtSSU clearly show that this species is genetically different from *P. sphinctrinoidella*. Unfortunately, no fresh material of *P. sphinctrinoides* was available to compare this species with the specimens growing on *Psoroma*, *Steinera*, and probably other genera. However, based on the morphology and in the disparate hosts, we considered that it is a different species from *P. sphinctrinoides*. No molecular data for boreal specimens of *P. croceae* are available to compare, and since this species has not previously been reported from Antarctica, we prefer to keep our specimen as *P. cf. croceae* awaiting further study, both morphological and molecular, of boreal specimens.

The circumscription of the lichenicolous genus *Phacopsis* was controversial for a long time (Triebel and Rambold 1988; Eriksson and Hawksworth 1989; Triebel et al. 1995). Phylogenetic studies showed that it was polyphyletic, and one species was transferred to the genus *Raesaenenia* (Peřsoh and Rambold 2002; Divakar et al. 2015). However, the generic placement within *Parmeliaceae* of eight species of *Phacopsis* still remains uncertain. In this study, an ITS rDNA sequence of *Phacopsis usneae* has been newly generated and the phylogenetic analyses show that it is more closely related to *R. huuskonenii* than to *P. vulpina*, the type species of the

genus. *Raesaenenia* has been synonymized to *Protousnea* using temporal banding criterium (Divakar et al. 2017). However, this change was not accepted by some authors (Diederich et al. 2018; Lücking 2019). We agree with the arguments presented by Lücking (2019) and keep the genus *Raesaenenia*. Therefore, we have proposed to combine *P. usneae* in *Raesaenenia*. Our studies showed that sometimes the apothecia of *R. usneae* are infected by *Sphaeropezia neuropogonis*. Interestingly, in such infected thalli, *S. neuropogonis* prefers colonizing the parasite fungus *R. usneae* and it is not found on *Usnea*. It is an unusual hyperparasitism behavior, similar to that of *Tremella huuskonenii* Diederich, Myllys, Goward & Lindgren, which parasitizes *R. huuskonenii* (Lindgren et al. 2015). This behaviour could indicate that *S. neuropogonis* was previously a parasite of the lichenicolous *Raesaenenia usneae*, finally extending to the host (*Usnea*).

Sphinctrina comprises five species widely distributed, although in regression, in temperate and tropical areas of both hemispheres (Giavarini and Purvis 2009). Our phylogenetic analyses based on ITS rDNA and LSU rDNA indicated that *Sphinctrina* is polyphyletic. *Sphinctrina intermedia* is more closely related to *Chaenothecopsis savonica* than to *Sphinctrina*. The new species *S. sessilis* belongs to *Sphinctrina* s.s. and it is closely related to *S. leucopoda*, from which it differs morphologically. Additionally, the ITS rDNA sequence of *S. sessilis* differs by 5% from *S. leucopoda*, indicating that they belong to different species.

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Author Contribution JE collected specimens and conducted the morphological study. RPB conducted the molecular analyses. JE, RPB, and LS wrote the manuscript. All the authors read and approved the manuscript.

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Data availability All DNA sequences have been submitted to GenBank. The alignments can be downloaded from the [supplementary material](#).

Declarations

Competing interests The authors declare no competing interests.

Animal research (ethics) This research does not involve animals

Consent to participate (ethics) This research does not involve humans.

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