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Phylogenetic placement within *Lecanoromycetes* of lichenicolous fungi associated with *Cladonia* and some other genera

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Key words

cladoniicolous species
Pilocarpaceae
Protothelenellaceae
Scutula cladoniicola
Stictidaceae
Stictis cladoniae

Abstract Though most of the lichenicolous fungi belong to the *Ascomycetes*, their phylogenetic placement based on molecular data is lacking for numerous species. In this study the phylogenetic placement of 19 species of lichenicolous fungi was determined using four loci (LSU rDNA, SSU rDNA, ITS rDNA and mtSSU). The phylogenetic analyses revealed that the studied lichenicolous fungi are widespread across the phylogeny of *Lecanoromycetes*. One species is placed in *Acarosporales*, *Sarcogyne sphaerospora*; five species in *Dactylosporaceae*, *Dactylospora ahtii*, *D. deminuta*, *D. glaucoides*, *D. parasitica* and *Dactylospora* sp.; four species belong to *Lecanorales*, *Lichenosticta alcicorniaria*, *Epicladonia simplex*, *E. stenospora* and *Scutula epiblastematica*. The genus *Epicladonia* is polyphyletic and the type *E. sandstedei* belongs to *Leotiomycetes*. *Phaeopyxis punctum* and *Bachmanniomyces uncialicola* form a well supported clade in the *Ostropomycetidae*. *Epigloea soleiformis* is related to *Arthrorhaphis* and *Anzina*. Four species are placed in *Ostropales*, *Corticifraga peltigerae*, *Cryptodiscus epicladonia*, *C. galaninae* and *C. cladoniicola* comb. nov. (= *Lettauia cladoniicola*). Three new species are described, *Dactylospora ahtii*, *Cryptodiscus epicladonia* and *C. galaninae*.

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INTRODUCTION

Lichenicolous fungi are a group of fungi specialized in living on lichens as parasites, commensals or saprotrophs (Hawksworth 2003, Lawrey & Diederich 2003). About 2 000 species of lichenicolous fungi have been described, 96 % of them belonging to the *Ascomycota* and the rest to the Basidiomycota (Lawrey & Diederich 2016). However, it is assumed that their species diversity is much greater (Hawksworth & Rossman 1997), the estimated total number of species lying between 3 000 and 4 000 (Hawksworth 2001, Lawrey & Diederich 2003). From approximately 15 % of the described species only the asexual stage is known (Lawrey & Diederich 2016) and the taxonomical affiliation of most of them is uncertain. The generic concepts of asexual fungi are still based on morphological characters and numerous changes are to be expected in the future. Just as in fungi with other lifestyles, phylogenetic studies have proved that many genera are polyphyletic (Verkley & Starink-Willemse 2004, Crous et al. 2007, Aveskamp et al. 2010, De Gruyter et al. 2010). The biology and ways of interaction of lichenicolous fungi with their hosts are still rather poorly known, although some anatomic studies have been carried out. Lichenicolous basidiomycetous fungi, most of which belong to the *Tremellomycetes*, generally induce the formation of galls. Both the host and the parasite hyphae take part in these galls, while the photobiont does not intervene in their production (Grube & De los Ríos 2001). The interaction of ascomycetous lichenicolous fungi with their hosts is more varied: some of them also induce galls, others produce necrotic areas on the lichen thallus, and others do not produce any morphological change in the thallus (Rambold & Triebel 1992). As for the connections with the host, often the lichenicolous fungus hyphae reach the algal layer, where they form haustoria with the photobiont, while some species establish connections with the mycobiont (Rambold & Triebel 1992, De los Ríos & Grube 2000, De los Ríos et al. 2000).

More than a decade ago DNA sequences began to be used in order to determine the phylogenetic placement of lichenicolous fungi (e.g., Peršoh & Rambold 2002, Hawksworth et al. 2010, Ruibal et al. 2011, Suija et al. 2015), but this work has been much slower than in other groups of fungi, essentially due to the small size of most lichenicolous fungi, the risk of a contamination with the host material and the difficulty of obtaining axenic cultures. The lichenicolous lifestyle is present in seven classes within the *Ascomycota* (Lawrey & Diederich 2016), but their abundance is not the same in all of them (Arnold et al. 2009). A high number of lichenicolous species belong to *Lecanoromycetes* (Rambold & Triebel 1992, Lawrey & Diederich 2003, Gams et al. 2004). The *Lecanoromycetes*, 95 % of which are lichenized fungi, are characterized by apothecioid ascomata (rarely perithecioid) with an ascohymenial ontogeny and a two-layered ascus wall with a rostrate dehiscence (Miadlikowska et al. 2014, Gueidan et. al. 2015). Recent phylogenetic studies divide *Lecanoromycetes* into five subclasses: *Lecanoromycetidae*, *Ostropomycetidae*, *Umbilicariomycetidae*, *Acarosporomycetidae* and *Candelariomycetidae* (Hofstetter et al. 2007, Miadlikowska et al. 2014). The subclass *Ostropomycetidae* comprises the highest number of species with a different lifestyle from the lichenized one (Baloch et al. 2010). Several authors have proposed different hypotheses to explain the evolution of the lichenicolous lifestyle. While Hawksworth (1988) proposed that this lifestyle is just one more type of nutrition within fungi, Lutzoni et al. (2001) put forward the idea that the lichenicolous lifestyle originated from lichenized fungi and that it is an intermediate stage towards other lifestyles, such

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Table 1 List of specimens sequenced in this study, voucher information and the GenBank accession numbers.

Taxa	Code	Host species	Voucher specimen	ITS rDNA	LSU rDNA	SSU rDNA	mtSSU
Bachmanniomyces uncialicola	RP352	*Cladonia stygia*	Finland, South Häme, *R. Pino-Bodas* s.n. (H)	KY661637	–	KY661702	–
	RP123	*Cladonia gracilis* subsp. *elongata*	USA, Alaska, Kodiak Island, *S.* & *S. Talbot* CHI017-56 (H)	KY661617	–	–	–
Corticifraga peltigerae	RP282	*Peltigera elisabethae*	India, Jammu and Kashmir State, *M.P. Zhurbenko* 1353 (LE 260537)	KY661634	KY661661	–	KY661684
Cryptodiscus cladoniicola	RP159	*Cladonia furcata*	Czech Republic, Western Bohemia, *J. Kocourková* (H)	KY661619	KY661652	KY661694	KY661674
(= *Lettauia cladoniicola*)	RP160	*Cladonia uncialis* subsp. *biuncialis*	Faroe Islands, Viðoy Island, *J. Kocourková et al.* s.n. (H)	KY661620	KY661653	KY661695	KY661675
Cryptodiscus epicladonia	RP208	*Cladonia mitis*	USA, Alaska, Unimak, *T. Ahti* 70348a & *S. Talbot* (H) **Holotype**	KY661628	–	–	KY661680
Cryptodiscus galaninae	RP314	*Cladonia rappii*	Canada, New Brunswick, *T. Ahti* 74421a & *S. Clayden* (H)	KY661636	–	KY661701	–
Dactylospora ahtii	RP127	*Cladonia gracilis*	USA, Alaska, Kodiak Island, *S.* & *S. Talbot* CHI017-63a (H) **Holotype**	KY661618	–	–	–
	RP182	*Cladonia rangiferina*	USA, Alaska, Kodiak Island, *S.* & *S. Talbot* CHI17-37a (H)	KY661622	–	–	KY661687
	RP23	*Cladonia uncialis* subsp. *biuncialis*	Iceland, Snæfellsnessýsla, *F. Högnabba* 1325a (H)	KY661630	KY661659	–	KY661686
Dactylospora deminuta	RP235	*Biatora vernalis*	Finland, Kuusamo Region, *J. Pykälä* 39390 (H)	KY661629	–	–	KY661681
Dactylospora glaucomarioides	RP275	*Ochrolechia akagiensis*	Russia, Jewish Autonomous Region, *M.P. Zhurbenko* 13107 (LE 261065)	KY661632	KY661660	–	KY661683
Dactylospora parasitica	RP422	*Ochrolechia* sp.	Russia, Khabarovsk Territory, *E.W. Tugi* (LE 260868)	KY661646	KY661666	–	KY661690
	RP423	*Ochrolechia* sp.	Russia, Karachaevo-Cherkessia, *M.P. Zhurbenko* 12135 (LE 261336)	–	–	–	KY661691
	RP424	*Ochrolechia* sp.	Finland, Kuusamo Region, *J. Pykälä* 39145 (H)	–	KY661667	–	KY661692
Dactylospora sp.	RP391	*Cladonia rangiferina*	Chile, Antártida chilena, *W.R. Buck* 60495a (H)	–	KY661664	–	KY661689
Epicladonia sandstedei	RP106	*Cladonia coniocraea*	Finland, South Häme, Heinola, *V. Haikonen* 27543a (H)	KY661614	KY661650	KY661693	KY661672
	RP263	*Cladonia* sp.	Russia, Republic of Adygeya, *M.P. Zhurbenko* 141 (LE 308482)	KY661631	–	–	KY661682
Epicladonia simplex	RP426	*Cladonia botrytes*	Russia, Krasnoyarsk Territory, *M.P. Zhurbenko* 1050 (LE308685)	KY661647	–	–	–
	RP427	*Cladonia botrytes*	Russia, Irkutsk Region, *M.P. Zhurbenko* 0563b (LE 309078)	KY661649	–	–	–
	RP428	*Cladonia coccifera*	Russia, Tyumen' Region, *S.S. Kholod* (LE 308573)	KY661648	–	–	–
Epicladonia stenospora	RP362	*Cladonia humilis* s. lat.	Spain, Toledo, *R. Pino-Bodas* (H)	–	KY661663	KY661703	–
	RP392	*Cladonia pyxidata*	Turkey, Kars, *M. Kocakoya* 485a (H)	–	–	KY661704	–
	RP68	*Cladonia rei*	Lithuania, Asveja Park, *F. Högnabba* 220911-15b (H)	KY661640	KY661668	–	–
	RP119	*Cladonia nana*	Portugal, Madeira, *P. v.d. Boom* 47938a (H)	KY661616	KY661651	–	KY661673
	RP189	*Cladonia chlorophaea*	USA, Alaska, Adak Island, *S.* & *S. Talbot* ADA 702a (H)	KY661623	KY661654	–	–
	RP190	*Cladonia pyxidata*	Turkey, Çankırı, *M. Kocakaya* 719b (H)	KY661624	KY661655	KY661697	–
Epigloea soleiformis	RP203	*Cladonia subcervicornis*	Faroe Islands, Streymoy Island, *J. Kocourková et al.* s.n. (H)	–	–	–	KY661677
	RP204	*Cladonia subcervicornis*	Faroe Islands, Streymoy Island, *J. Kocourková et al.* s.n. (H)	KY661625	KY661656	–	KY661678
Lichenosticta alcicorniaria	RP109	*Cladonia pyxidata*	Russia, Russian Far East, *J. Miadlikowska et al.*	KY661615	–	–	–
	RP168	*Cladonia arbuscula*	Finland, Uusimaa, *R. Pino-Bodas* s.n. (H)	KY661621	–	KY661696	KY661676
	RP395	*Cladonia tessellata*	Chile, Región de los Lagos, *U. Schiefelbein* (H)	KY661638	KY661665	–	–
Phaeopyxis punctum	RP43	*Cladonia ustulata*	New Zealand, *S. Stenroos* 6040a (H)	KY661639	–	–	–
	RP93	*Cladonia coniocraea*	Finland, South Häme, *V. Haikonen* 29409 (H)	KY661641	KY661669	–	–
	RP94	*Cladonia coniocraea*	Finland, North Karelia, *A. Launis* 2212 (H)	KY661642	–	–	–
	RP95	*Cladonia coniocraea*	Finland, North Karelia, *A. Launis* 2017 (H)	KY661643	KY661670	–	–
	RP96	*Cladonia coniocraea*	Finland, North Karelia, *A. Launis* 2213 (H)	KY661644	KY661671	–	–
	RP97	*Cladonia arbuscula*	Finland, Uusimaa, *R. Pino-Bodas* s.n. (H)	KY661645	–	KY661705	–
Protothelenella santessonii	RP205	*Cladonia subcervicornis*	Faroe Islands, Viðoy Island, *J. Kocourková et al.* s.n. (H)	KY661626	KY661657	KY661698	KY661679
	RP206	*Cladonia subcervicornis*	Faroe Islands, Streymoy Island, *J. Kocourková et al.* s.n. (H)	KY661627	KY661658	KY661699	–
Sarcogyne sphaerospora	RP301	*Candelariella* sp.	India, Jammu & Kashmir, Leh, *M.P. Zhurbenko* 1323 (LE 260996)	KY661635	KY661662	KY661700	KY661685
Scutula epiblastematica	RP276	*Peltigera* cf. *malacea*	Russia, Sakha Republic, *S.E. Vershinina* (LE 261003)	KY661633	–	–	KY661688

as saprophytism or parasitism. If the latter hypothesis was true, we would expect a greater number of lichenicolous fungi to belong to *Lecanoromycetes*. Moreover, it is worth pointing out that according to some studies the lichenicolous lifestyle is more flexible than was thought (Wedin et al. 2004). Many optionally lichenicolous species are known, such as several species of the genus *Chroodiscus* (Lücking & Grube 2002) or *Diploschistes muscorum*, which in the initial stages of development parasitizes *Cladonia* species and subsequently forms an independent lichenized thallus (Friedl 1987).

The present work mainly focuses on the lichenicolous fungi that live on *Cladonia* (*Lecanorales*, *Ascomycota*), a sub-cosmopolitan genus with 470 species (Ahti pers. comm.) characterized by a dimorphic thallus formed by a primary crustose or squamulose thallus and a fruticulose secondary thallus (Ahti 2000). Currently, 128 species of obligately lichenicolous fungi are known to live on *Cladonia*, which is one of the lichen host genera along with *Lecanora*, *Peltigera* and *Pseudocyphellaria* on which most species of lichenicolous fungi have been reported (Hawksworth & Miadlikowska 1997, Lawrey & Diederich 2016, Zhurbenko & Pino-Bodas 2017). Some authors proposed that certain genera, such as *Peltigera* or *Pseudocyphellaria* are suitable hosts for the development of lichenicolous fungi because they have large thalli and live in damp habitats (Etayo & Diederich 1996, Etayo & Sancho 2008). This explanation can also be applied to the genus *Cladonia* that can form wide mats and cover the soil in areas where humidity is rather high. The cladoniicolous species of *Lecanoromycetes* occur in the genera *Dactylospora*, *Diploschistes*, *Phaeopyxis*, *Protothelenella*, *Scutula* and *Stictis* (Lumbsch & Huhndorf 2011, Suija et al. 2015), the phylogenetic positions of which has been confirmed by molecular data only for the optionally lichenicolous *Diploschistes muscorum* and for *Phaeopyxis punctum* (Suija et al. 2015). The aim of this study was to determine the phylogenetic placement of 19 species of lichenicolous fungi, most of which live on species of the genus *Cladonia*, using four loci.

MATERIALS AND METHODS

Material studied and taxon sampling

Specimens of *Cladonia* species from the herbaria H and LE plus new collections (also deposited in H or LE) were screened in order to find lichenicolous fungi. In addition, lichenicolous fungi on other lichen genera were selected to complete the sampling. The morphology and anatomy of the specimens were examined and photographed using dissecting microscopes Stemi 2000-CS and Leica DFC490, and compound microscopes Axio Imager A1 (equipped with Nomarski differential interference contrast optics) and Leica DM2500. Microscopic examination was done in water, 10 % KOH (K), Meltzer, Lugol's iodine, directly (I) or after a KOH pre-treatment (K/I), or phloxine. The length, breadth and length/breadth ratio (l/b) of asci and ascospores are given (where n > 10) as: (minimum–) {X–SD}–{X+SD}(–maximum), where X is the arithmetic mean and SD the corresponding standard deviation, followed by the number of measurements.

For the molecular study 74 fresh specimens were selected. Unfortunately, for many specimens the amplifications were not successful, and DNA sequences were obtained only from 43 specimens, representing 19 species (Table 1). We tried to select at least two specimens per species studied, but only one specimen could be sequenced for some of the species (Table 1), owing to the difficulties of finding additional fresh material or to the amplification failure of additional specimens.

The DNA sequences were first included in the dataset of Schoch et al. (2009), allowing us to verify that all species in the present study belong to *Lecanoromycetes* (data not shown). For the phylogenetic analyses the sampling was completed with sequences downloaded from GenBank (Appendix 1), based on the results of Miadlikowska et al. (2014) plus sequences of lichenicolous fungi belonging to the *Lecanoromycetes* (Lawrey & Diederich 2016). The clades containing the species studied were sampled more intensively. *Leotia lubrica* was selected as outgroup. Several species were placed in the family *Stictidaceae*, and separate phylogenetic analyses were run for this family based on the phylogenies of Baloch et al. (2009, 2013).

DNA extraction, PCR and sequencing

Lichen thalli were cleaned by Milli-Q SP Ultra-Pure-Water, then 1–10 lichenicolous ascomata or conidiomata were removed using an insect needle size 00 (Imperial Karlsbad) and cleaned from the remaining lichen using a sterilized razor blade. Genomic DNA was extracted using E.Z.N.A. Forensic DNA Isolation Kit (Omega Bio-Tek). DNA was eluted in the final step in 100 µl of elution buffer provided by the manufacturer. Four loci were selected to infer the phylogeny: ITS rDNA, LSU rDNA, SSU rDNA and mtSSU. In addition, *RPB1* and *RPB2* were also tested, with different combinations of primers (gRPB1-Af/gRPB1-CR, RPB2-607F/RPB2-1554R, RPB2-5F/RPB2-7R, fRPB2-7cF/fRPB2-11aR) but the amplifications were not successful. The PCRs were carried out using Ready-to-Go-PCR Beads (GE Healthcare Life Sciences, UK), with 25 µl of final volume, 1 µl of each primer at 10 µM concentration and 3 µl of DNA. The primers used were: ITS1F/ITS4 (White et al. 1990, Gardes & Bruns 1993) for ITS rDNA; mrSSU1/mrSSU3R (Zoller et al. 1999) for mtSSU; LROR/LR5 or LR6 (Vilgalys & Hester 1990, Vilgalys & Sun 1994) for LSU rDNA; and NS1/NS22 or NS24 (White et al. 1990, Gargas & Taylor 1992) for SSU rDNA. Amplifications were performed using an Eppendorf Mastercycler ep Gradient S thermal cycler with the following programs: 95 °C 5 min; 5 cycles of 30 s at 95 °C, 30 s at 58 °C, 60 s at 72 °C; 30 cycles of 30 s at 95 °C, 30 s at 56 °C, 60 s at 72 °C; 7 min at 72 °C for ITS rDNA; 95 °C 5 min; 30 cycles of 30 s at 95 °C, 30 s at 55 °C, 60 s at 72 °C; 10 min at 72 °C for LSU rDNA; 95 °C 5 min; 40 cyles of 30 s at 95 °C, 40 s at 52 °C, 60 s at 72 °C; 10 min at 72 °C for SSU rDNA; 95 °C 5 min; 35 cycles of 30 s at 95 °C, 60 s at 50 °C, 60 s at 72 °C; 7 min at 72 °C for mtSSU. PCR products were cleaned with GFX PCR DNA and Gel Band Purification kit (GE Healthcare), E.Z.N.A. Ultra-Sep Gel Extraction Kit (Omega Bio-Tek), or Illustra TM ExoProStar TM 1-step (GE Healthcare). Sequencing was performed at Macrogen Europe service (www.macrogen.com).

Phylogenetic analyses

The sequences were assembled in Sequencher 4.1.4 program (Gene Codes Corporation, Inc, Ann Arbor, Michigan, USA). 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 which taxa are most similar to our sequences.

The sequences were aligned using MAFFT (Katoh & Standley 2013) with different algorithms depending on the input, then the alignments were improved manually in BIOEDIT 7.0 (Hall 1999). Introns and ambiguous regions were removed from the alignments with Gblock 0.91b (Castresana 2000) using the less stringent option.

Each dataset was analyzed with maximum likelihood (ML) analysis in RAxML 7.0.3 (Stamatakis et al. 2005), using the GTRGAMMA model and with 500 replicates of fast bootstrap in order to check conflicts among the datasets, following Hillis & Bull (1993) criteria. No incongruence was found and the datasets were combined. The optimal substitution model for each locus (Table 2) was selected with jModeltest (Posada 2008)

Table 2 Features of each dataset analyzed, including number of sequences aligned (N), number of positions in each aligment (bp), number of variable positions (NV), number of parsimony informative positions (NP), consistence index (CI), retention index (RI), model of evolution selected with jmodeltest and likelihood from ML analysis.

	N	bp	NV	NP	CI/RI	Model	-Lnl
Lecanoromycetes							
LSU rDNA	226	1270	837	592	0.1838/0.5391	GTR+I+G	39343.844280
SSU rDNA	184	1019	386	305	0.2672/0.5578	GTR+I+G	15289.101485
ITS rDNA	156	379	297	248	0.1632/0.5057	HKY+I+G	16141.468421
mtSSU	227	596	484	414	0.1563/0.5991	GTR+I+G	31424.666287
Stictidaceae							
LSU rDNA	27	870	288	200	0.6167/0.7235	GTR+I+G	4373.206559
ITS rDNA	20	477	262	195	0.5711/0.5942	GTR+I+G	3916.270036
mtSSU	28	702	325	267	0.5366/0.7100	GTR+I+G	5234.960566

using the Akaike Information Criterion (AIC). The combined dataset was analyzed with ML and Bayesian inference (BI). The ML analysis was run in RAxML considering each locus as different partition with the GTRGAMMA model and 1 000 replicates of fast bootstrap to assess the node support. The Bayesian analysis was 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 using Markov Chain Monte Carlo (MCMC). Two simultaneous runs with 90 000 000 generations each, starting with a random tree and employing 6 simultaneous chains, were executed. Every 2 000th tree was saved into a file. The convergence was assessed in Tracer v. 1.5 (Rambaut & Drummond 2009) 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 and the consensus tree was calculated with the remaining 22 500 trees.

Additionally, a phylogeny of the family *Stictidaceae*, based on LSU rDNA, mtSSU and ITS rDNA, was constructed to study more accurately the relationship of *Lettauia* and *Cryptodiscus* species. *Trapeliopsis flexuosa* and *Xylographa parallela* were used as outgroup. For every dataset an ML analysis was run according to the options above. The datasets were congruent and they were combined. The combined dataset was analyzed with ML, considering each locus as different partition with the GTRGAMMA model and 1 000 replicates of fast bootstrap to assess the node support. The optimal substitution model for each locus was selected with jModeltest, these models are listed in Table 2. The Bayesian analysis was run with two simultaneous runs of 10 000 000 generations each, starting with a random tree and employing 4 simultaneous chains. The convergence was assessed with the same method as in the previous analysis. The initial 50 % trees were discarded as burn-in and the consensus tree was calculated.

Topological hypothesis tests

The phylogenetic analyses revealed placements or taxa circumscriptions incongruent with the current classifications, whereby alternative phylogenetic topologies were tested: a) the monophyly of the genus *Epicladonia*; b) the genus *Lettauia* belongs to the family *Fuscidiaceae*. First, the optimal ML trees were estimated in RAxML using the GTRGAMMA model and considering each locus as a different partition. Shimodaira-Hasegawa test (SH, Shimodaira & Hasegawa 1999) and expected likelihood weight (ELW, Strimmer & Rambaut 2002) were conducted in TREE-PUZZLE 5.2 (Schmidt et al. 2002), using the GTR+I+G model with four-category approximation to the gamma distribution for substitution rate among sites and using 1 000 RELL bootstrap replicates.

RESULTS

In this study, 92 new sequences were generated (36 of ITS rDNA, 22 of LSU rDNA, 21 of mtSSU and 13 of SSU rDNA). Members of the genera *Bachmanniomyces*, *Corticifraga*, *Epicladonia*, *Epigloea*, *Lettauia* and *Lichenosticta* were sequenced for the first time in this study.

BLAST searches revealed a similarity between the sequences generated here and the ones deposited in GenBank. The results are listed in Appendix 2. The most similar sequences corresponded to *Lecanoromycetes* sequences or, in some cases, to sequences coming from non-identified environmental fungi. BLAST searches revealed that the sequences most similar to *Epicladonia sandstedei* corresponded to sequences of the *Leotiomycetes*. The mtSSU sequence of *Dactylospora deminuta* showed an 85 % similarity with one sequence of the *Chaetothyriales*. The BLAST searches did not generate similarity with sequences of the genus *Cladonia* or with any other host genus. Therefore we can maintain that none of the sequences included in the analyses corresponds to the host.

Table 2 summarizes the data for single loci datasets. The concatenated dataset included 285 sequences and 3 264 characters. The ML analysis yielded a tree with -LnL = 106201.732, while the Bayesian analyses yielded a consensus tree with -LnL = 102147.35 (arithmetic mean). The ML tree and the Bayesian consensus had a similar topology. The Bayesian consensus tree is shown in Fig. 1. The general topology agreed with the recently published phylogenies of the *Lecanoromycetes* (Miadlikowska et al. 2006, 2014), showing the same main clades (although some of them were not supported). According to our phylogenetic analyses one lichenicolous species belonged to the *Acarosporales*, *Sarcogyne sphaerospora* (Fig. 1); it was phylogenetically related to *Polysporina subfuscescens* with high support. Four species were included in the order *Ostropales*, *Corticifraga peltigerae*, *Cryptodiscu*s *epicladonia*, *Cryptodiscus galaninae* and *Lettauia cladoniicola*, (Fig. 1). *Corticifraga peltigerae* is closely related to *Actinoplaca strigulacea* in the family *Graphidaceae*, subfamily *Gomphilloideae* (Fig. 1). *Lettauia cladoniicola* and the two new species of *Cryptodiscu*s were placed in the *Stictidaceae* (Fig. 1). Four species were placed in the order *Lecanorales*, *Epicladonia simplex*, *E. stenospora*, *Lichenosticta alcicorniaria* and *Scutula epiblastematica* (Fig. 1). The three specimens of *Lichenosticta alcicorniaria* formed a well-supported clade. This clade turned out to be phylogenetically related to *Gypsoplaca macrophylla*, but the relationship lacked support in all the analyses. The genus *Epicladonia* was polyphyletic, the type species *E. sandstedei* was monophyletic (two specimens studied) but it fell outside the class *Lecanoromycetes*. The other two species, *E. stenospora* and *E. simplex* formed a well-supported clade inside the family *Pilocarpaceae*, possibly related to the genus *Micarea* (low statistical support).

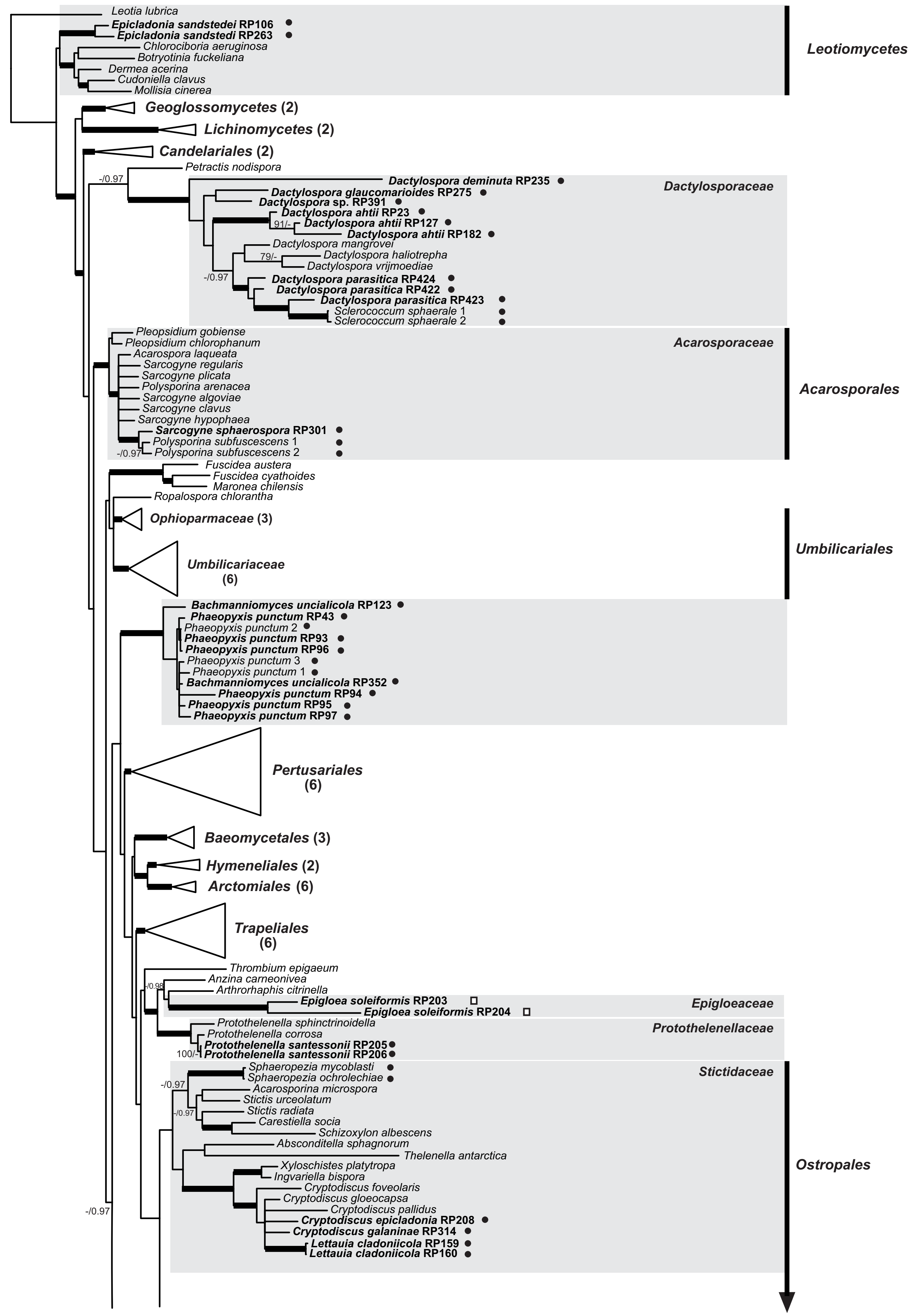

Fig. 1 This is the 50 %-majority-rule consensus tree of Bayesian analysis of *Lecanoromycetes* based on nLSU, nSSU, mtSSU and ITS rDNA. Branches supported with posterior probability ≥ 0.95 and bootstrap ≥ 70 % are indicated in **bold**. Grey rectangles show the groups where lichenicolous fungi studied were placed. Lichenicolous fungi are marked with a black circle. The black triangles indicate lichenicolous lichens. The squares mark the facultative lichenicolous species. The **bold** names indicate the newly sequence specimens (extraction codes are indicated). Classification according to Miadlikowska et al. (2014).

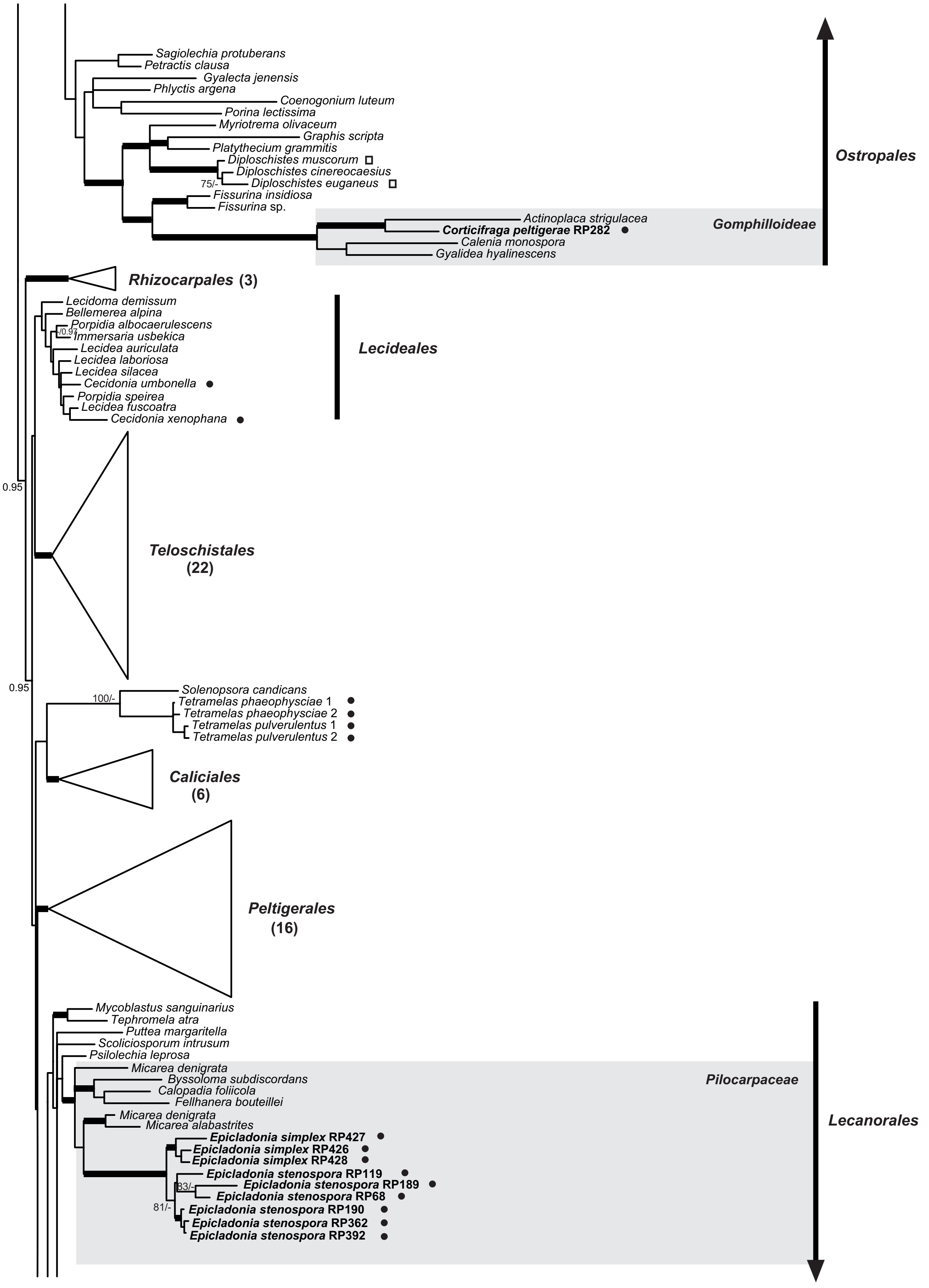
Sagiolechia protuberans
Petractis clausa
Gyalecta jenensis
Phlyctis argena
Coenogonium luteum
Porina lectissima
Myriotrema olivaceum
Graphis scripta
Platythecium grammitis
Diploschistes muscorum ☐
Diploschistes cinereocaesius
75/-
Diploschistes euganeus ☐
Fissurina insidiosa
Fissurina sp.
Actinoplaca strigulacea
Corticifraga peltigerae RP282 ●
Calenia monospora
Gyalidea hyalinescens
Gomphilloideae
Ostropales
Rhizocarpales (3)
Lecidoma demissum
Bellemerea alpina
Porpidia albocaerulescens
-/0.97
Immersaria usbekica
Lecidea auriculata
Lecidea laboriosa
Lecidea silacea
Cecidonia umbonella ●
Porpidia speirea
Lecidea fuscoatra
Cecidonia xenophana ●
Lecideales
0.95
Teloschistales (22)
0.95
100/-
Solenopsora candicans
Tetramelas phaeophysciae 1 ●
Tetramelas phaeophysciae 2 ●
Tetramelas pulverulentus 1 ●
Tetramelas pulverulentus 2 ●
Caliciales (6)
Peltigerales (16)
Mycoblastus sanguinarius
Tephromela atra
Puttea margaritella
Scoliciosporum intrusum
Psilolechia leprosa
Micarea denigrata
Byssoloma subdiscordans
Calopadia foliicola
Fellhanera bouteillei
Micarea denigrata
Micarea alabastrites
Epicladonia simplex RP427 ●
Epicladonia simplex RP426 ●
Epicladonia simplex RP428 ●
Epicladonia stenospora RP119 ●
83/-
Epicladonia stenospora RP189 ●
Epicladonia stenospora RP68 ●
81/-
Epicladonia stenospora RP190 ●
Epicladonia stenospora RP362 ●
Epicladonia stenospora RP392 ●
Pilocarpaceae
Lecanorales

Fig. 1 (cont.)

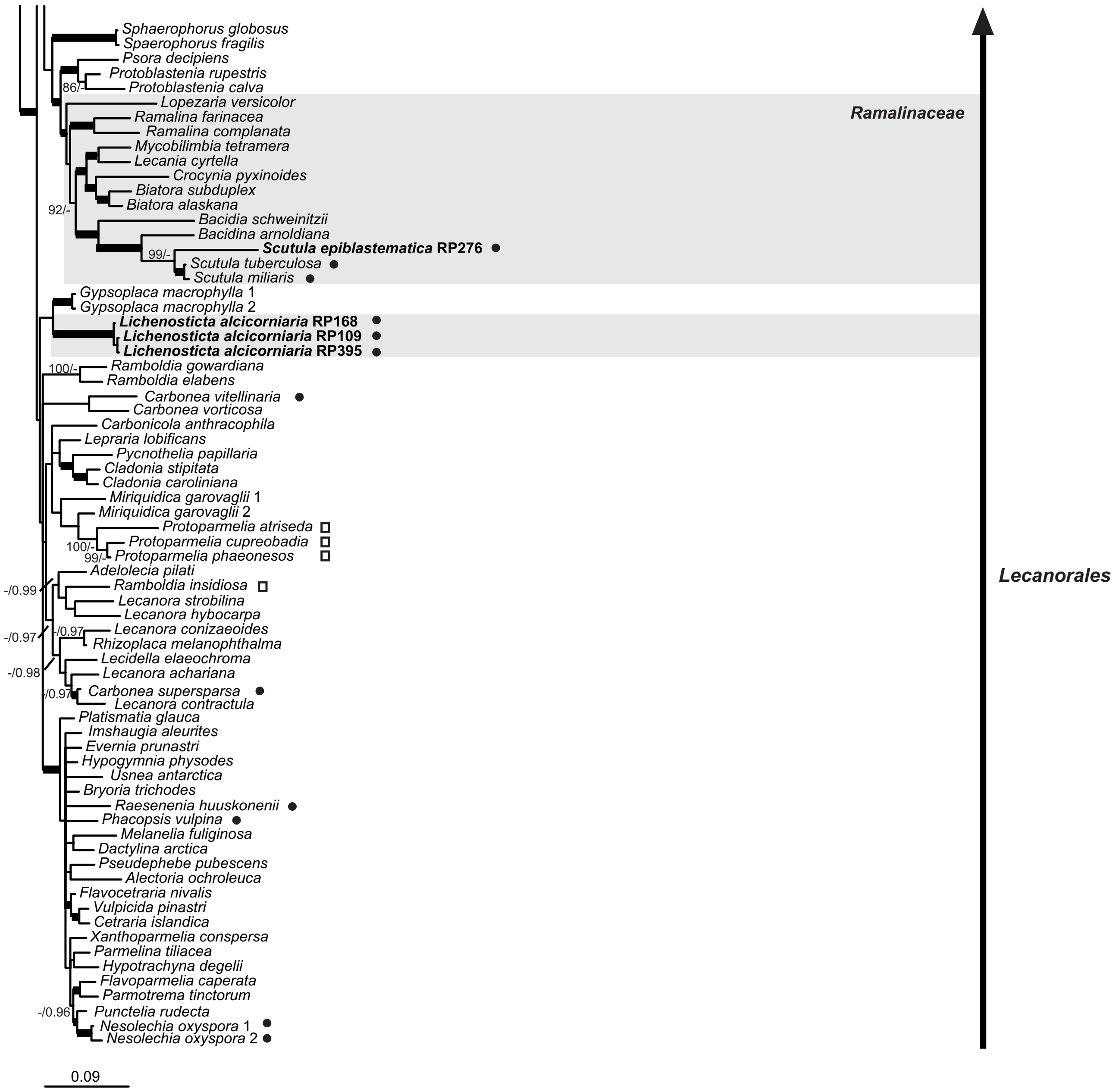

Fig. 1 (cont.)

Both species of *Epicladonia* (*E. simplex* and *E. stenospora*) were monophyletic. *Scutula epiblastemica* was placed in the *Ramalinaceae*, it was related to *S. miliaris* and *S. tuberculosa.*

Other species were included in different families with uncertain phylogenetic placement in the *Lecanoromycetes* (*Dactylosporaceae*, *Epigloeaceae* and *Protothenellaceae*). Five species were placed in the family *Dactylosporaceae* (Fig. 1), *Dactylospora ahtii*, *D. deminuta*, *D. glaucomarioides*, *D. parasitica* (the generic type) and *Dactylospora* sp. Three specimens of *D. parasitica* formed a well-supported clade together with *Sclerococcum sphaerale.* The three specimens of the new species *Dactylospora ahtii* were monophyletic. *Dactylospora glaucomarioides* grouped with *Dactylospora* sp. *Protothelenella santessonii* was monophyletic and formed a well-supported clade with the other species of *Protothelenella* (Fig. 1). *Epigloea soleiformis* was placed in the *Ostropomycetidae* and is related to the genera *Arthrorhaphis* and *Anzina* (Fig. 1). *Phaeopyxis punctum* and *Bachmanniomyces uncialicola* were included in the *Ostropomycetidae* but their relationships within this subclass were not resolved.

The combined dataset of the *Stictidaceae* contained 2 049 characters, the ML analysis yielded a tree with a likelihood value of -LnL = 13788.449, while the arithmetic mean likelihood of Bayesian analysis was -LnL = 14304.77. The topology of both trees was the same and so only the Bayesian 50 % consensus majority tree is shown (Fig. 2). The genus *Lettauia* and two newly described species clustered in the genus *Cryptodiscus*, with high support (100 % of bootstrap/1.00 of posterior probability). The *Cryptodiscus* clade is closely related to a clade formed by *Ingvariella bispora* and *Xyloschistes platytropa*. *Acarosporina microspora*, *Carestiella sociata*, *Ostropa barbata*, *Schizoxylon albescens*, *Stictis confusa* and *S. populorum* formed another well-supported clade. The genus *Stictis* was polyphyletic. The genera *Absconditella*, *Geisleria* and *Sphaeropezia* turned out to be closely related. The SH and ELW tests rejected both alternative hypothesis tested (Table 3).

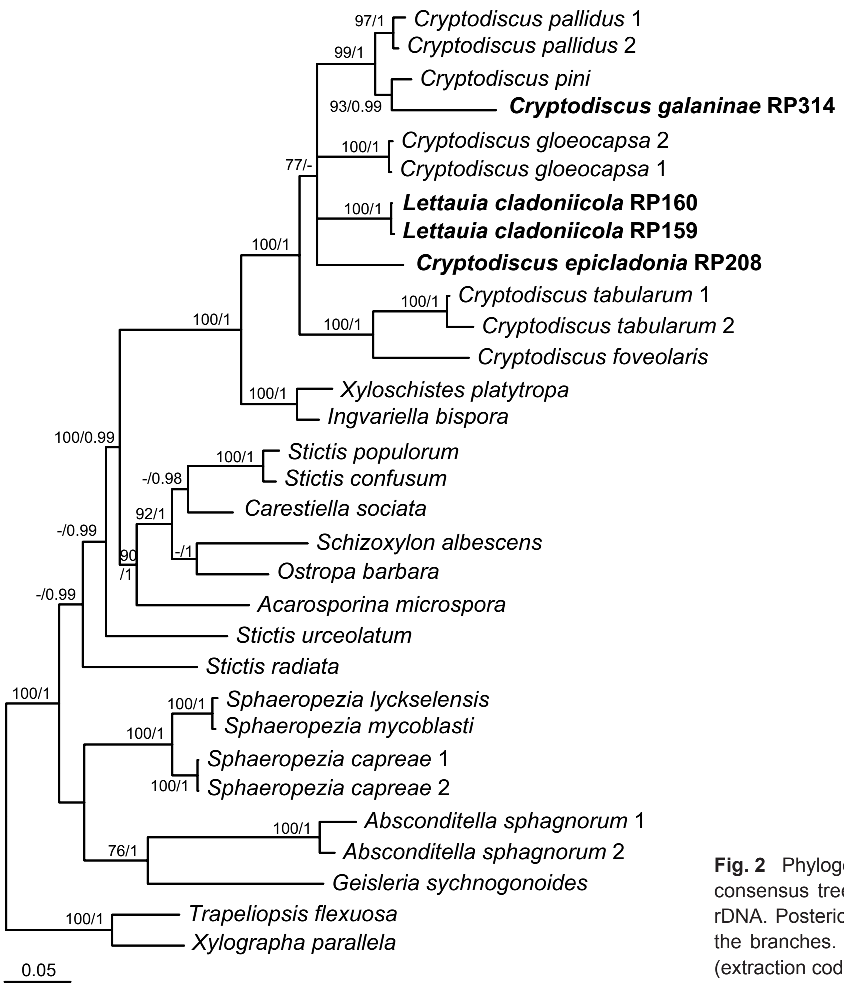

Fig. 2 Phylogeny of the family *Stictidaceae*. This is the 50 %-majority-rule consensus tree of a Bayesian anlysis based on nLSU, mtSSU and ITS rDNA. Posterior probability ≥ 0.95 and bootstrap ≥ 70 % are indicated on the branches. The **bold** names indicate the newly sequence specimens (extraction codes are indicated).

TAXONOMY

Cryptodiscus cladoniicola (D. Hawksw. & R. Sant.) Pino-Bodas, Zhurb. & S. Stenroos, *comb. nov.* — MycoBank MB820201; Fig. 3

Basionym. *Lettauia cladoniicola* D. Hawksw. & R. Sant., Biblioth. Lichenol. 38: 138. 1990.

Type. GERMANY, Baden, Schwarzwald, Feldberg-Gipfels, Nordseite, elev. 1400 m, on *Cladonia amaurocraea* (podetia), 14 July 1912, *G. Lettau*, holotype B 7700.

Ascomata apothecia, soon sessile, more or less round in surface view, slightly constricted at the base, 180–300(–430) μm diam, disc initially plane, pale yellow/orange yellow, becoming convex (up to hemispherical) and light to moderate orange under aging, epruinose, margin initially slightly raised, white, 20–40(–60) μm wide, becoming lacerated, reduced or even excluded under aging; dispersed or occasionally aggregated to contiguous. *Proper exciple* composed of round or tangentially elongated cells c. 2.5–6 × 2–3 μm with walls 0.5–1 μm thick, without embedded crystals; *lateral exciple* hyaline except for the light orange yellow outermost part, 25–40 μm thick; *lower exciple* (hypothecium) hyaline, 15–40 μm thick. *Periphysoids* absent. *Epihymenium* light orange yellow, c. 5 μm tall. *Hymenium* hyaline, 30–50 μm tall, I+ fleetingly blue then immediately yellow green (mainly due to yellow colouration of ascal plasma) with some remnants of blue colouration, K/I+ blue or partly red due to colouration of ascal walls. *Subhymenium* hyaline, c. 10 μm tall. *Paraphyses* filiform, often di- or occasionally trichotomically branched, mainly above, 1.2–1.7(–3.0) μm diam, frequently septate, often somewhat constricted at the septa and strangulated, particularly near the apices, which are occasionally slightly swollen. *Asci* narrowly clavate to subcylindrical, with short foot, (43–)44–48(–50) × 6.5–9(–10) μm (n = 16, in water, I or K/I), tholus up to 5 μm tall, I–, K/I–, apical structures not observed, wall/periascal gel I+ fleetingly blue, K/I+ blue or partly red, 8-spored. *Ascospores* hyaline, cylindrical to slightly fusiform, the apices rounded or occasionally acute, (13.5–) 16.8–22.8(–26.0) × (2.0–)2.3–2.9(–3.5) μm, l/b = (4.9–) 6.3–8.9(–12.2) (n = 54, in water, I or K), (2–)3(–4)-septate, not constricted at the septa, wall smooth, without a gelatinous sheath, with conspicuous guttules, arranged in the ascus in a bundle, diagonally or overlappingly 2–4 seriate. *Anamorph* not found.

Table 3 Results of topological tests Shimodaira-Hasegawa (SH) and likelihood weight test (ELW).

Hypothesis	-Lnl	SH	ELW
Monophyly of *Epicladonia*	111117.04	0.0010*	0.0000*
Lettauia belongs to *Fuscidiaceae*	111260.55	0.0000*	0.0000*

* indicate significant results.

Distribution & Hosts — The species is known from Austria, the British Isles, Canada, the Czech Republic, Denmark, Finland, Germany, Norway, Russia, Slovenia, Sweden and the USA, growing on podetia of *Cladonia amaurocraea*, *C. arbuscula*, *C. furcata*, *C. gracilis*, *C. mitis*, *C. portentosa*, *C. rangiferina*, *C. stellaris*, *C. stygia* and *C. uncialis* (Hawksworth & Santesson 1990, Alstrup 1993, Coppins 1998, Diederich 2003, Santesson et al. 2004, Kocourková & Van den Boom 2005, Hafellner 2008, present paper). *Cladonia uncialis* is a new host species. Pathogenicity not observed.

Specimens examined. CZECH REPUBLIC, Western Bohemia, distr. Karlovy Vary, Bečov nad Teplou, 1 km E of the town, Psí skála hill, on *Cladonia furcata* (podetia), 2 Aug. 2014, *J. Kocourková*, H. – DENMARK, Faroe Islands, Viðoy

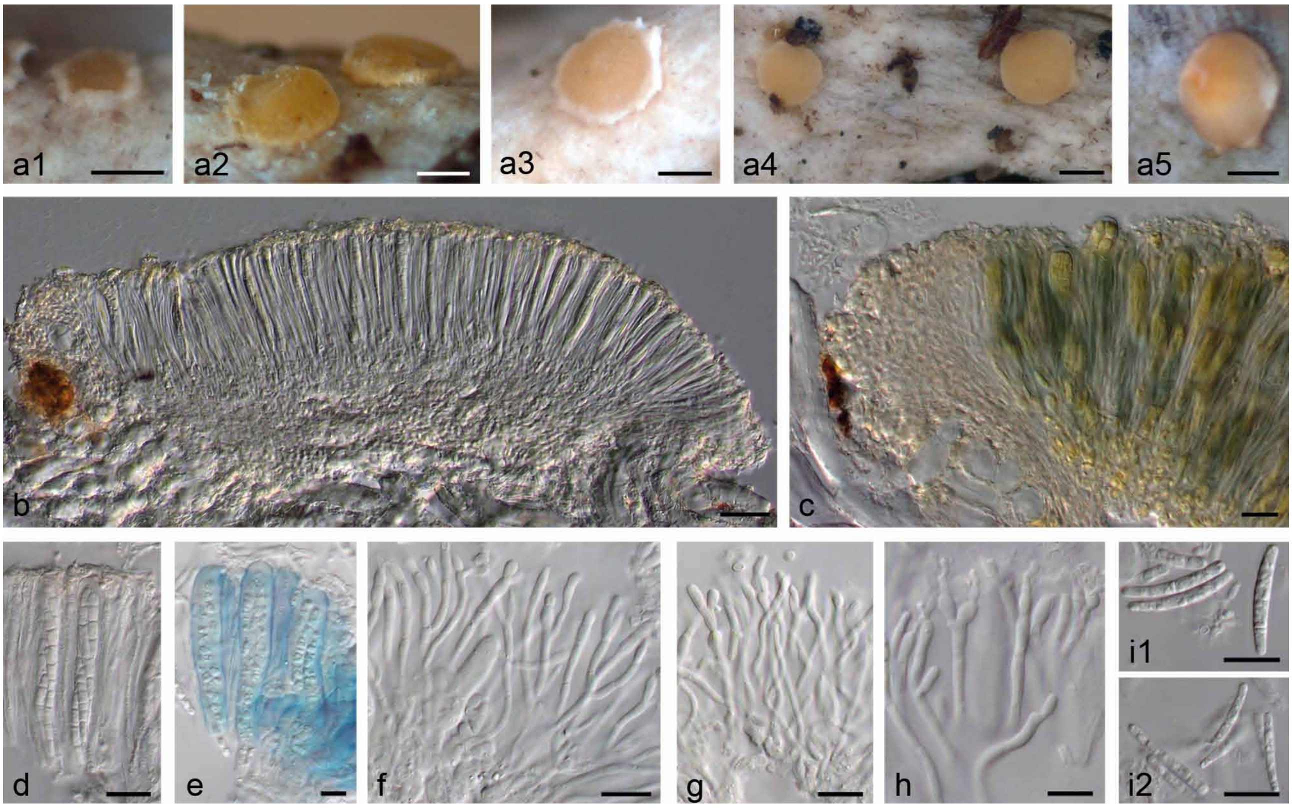

Fig. 3 *Cryptodiscus cladoniicola*. a. Appearance of apothecia: a1–a3 from LE 308679, a4 from LE 308798, a5 f from LE 308695; b. apothecial section in water from LE 308798; c. exciple and hymenium in cross section in I from LE 308798; d. asci in water from LE 308696; e. asci in K/I from LE 308695; f–g. paraphyses in K from LE 308679; h. paraphyses in K from LE 308695; i. ascospores in K, i1 from LE 308679, i2 from LE 308695. — Scale bars: a = 200 µm; b = 20 µm; c–i = 10 µm.

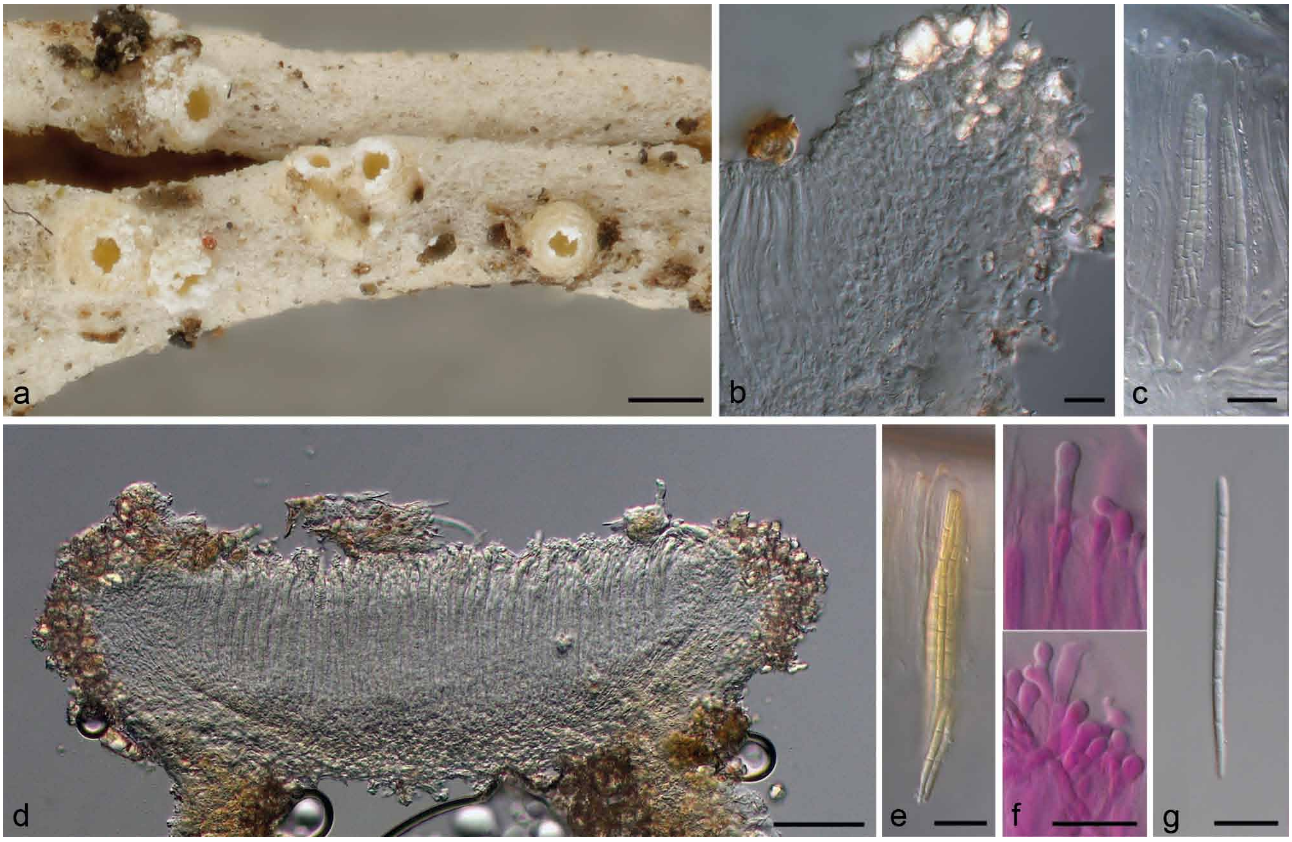

Fig. 4 *Cryptodiscus epicladonia*. a. Appearance of apothecia from the holotype; b. lateral exciple in cross section in K from LE 338773a; c. asci in water from the holotype; d. apothecial section in water from LE 308773a; e. ascus in I from the holotype; f. paraphyses in phloxine from LE 308498; g. ascospore in water from LE 308498. — Scale bars: a = 500 µm; b–c, e–g = 10 µm; d = 50 µm.

Table 4 Main morphological differences among the cladoniicolous species of the genus *Cryptodiscus* and *Stictis cladoniae* (based on original data).

Characters	*C. cladoniicola*	*C. epicladonia*	*C. galaninae*	*Stictis cladoniae*
Apothecia	plane to convex disc pale yellow, orange-yellow or orange margin white epruinose	urceolate disc light orange-yellow margin orange-yellow white pruinose rim	urceolate disc pale to yellow or yellowish white margin subhyaline or yellowish white epruinose	urceolate disc blackish margin brownish black epruinose
Lateral exciple (thickness)	25–40 µm	40–100 µm	15–40 µm	20–70 µm
Epihymenium	light orange yellow	indistinct	indistinct	indistinct
Hymenium	30–50 µm tall I+ fleetingly blue then immediately yellow green, K/I+ blue or partly	70–100 µm tall I–, K/I–	30–45 µm tall I+ blue then quickly orange to red K/I+ blue with occasional reddish stripes	50–70 µm tall I+ red, K/I+ blue
Asci (mainly)	44–48 × 6.5–9 µm	73–93 × 7–9 µm	28–38 × 5–6.5 µm	57–71 × 8–10 µm
Ascospores	cylindrical to slightly fusiform 7–23 × 2.5–3 µm (2–)3(–4)-septate	filiform to cylindrical 50–73 × 1.5–2 µm (5–)7–11-septate	fusiform, slightly clavate or bacilliform 9.5–12.5 × 1.5–2 µm (0–)1(–2)-septate	filiform to cylindrical, c. 40–60 × 1.5–2 µm at least 4–5-septate

Island, Viðareiðy, Mýrnafjall Mt, 3 km SE of the town, Bergshálsur plateau on north end of the mountain crest, on *C. uncialis* (podetia), 13 Aug. 2013, *J. Kocourková*, *W.J. Halda* & *I. Sommerová*, H. – Russia, Krasnoyarsk Territory, Putorana Plateau, Kapchuk Lake, on *C. arbuscula* (podetia), 18 Aug. 1983, *M.P. Zhurbenko* 83236, LE 308897; Krasnoyarsk Territory, Western Sayan Mts, Ergaki Nature Park, Olen'ya River, on *C. arbuscula* (podetia), 11 July 2010, *M.P. Zhurbenko* 1041, LE 308679; ibid., on *C. mitis* (podetia), 11 July 2010, *M.P. Zhurbenko* 1053, LE 308684; Republic of Sakha (Yakutia), Indigirka River, Silyapskii Range, on *C. rangiferina* (bases of podetia), 24 June 1976, *I.I. Makarova*, LE 308798; Primorye Territory, Sikhote-Alin' Range, Mt Glukhomanka, on *C. uncialis* (podetia), 21 Aug. 2003, *K.S. Podlubnaya*, LE 308695.

Notes — There are some discrepancies with the detailed species description in Hawksworth & Santesson (1990) who reported more or less plane apothecia up to 250 µm diam, an I+ blue hymenium up to 65 µm tall, sometimes anastomosed paraphyses and (1–)3-septate ascospores, measuring 19–25(–31) × 2.5–3 µm. The species was formerly reported in Russia from Bol'shezemel'skaya tundra in Nenets Autonomous Area (LE 210357, Zhurbenko 2008), the Northern Ural Mts in Komi Republic (LE 308521, Zhurbenko 2004) and Putorana Plateau in Krasnoyarsk Territory (LE 207133, Zhurbenko 2000). We confirm the identification of LE 308521, while LE 210357 belongs to *Cryptodiscus galaninae*; the identification of LE 207133 is uncertain due to scanty material.

Cryptodiscus epicladonia Zhurb. & Pino-Bodas, *sp. nov.* — MycoBank MB820198; Fig. 4

Etymology. Referring to its occurrence on *Cladonia*.

Type. USA, Alaska, Aleutian Islands, Unimak Is., False Pass, 3 km SW of airstrip, N54.837° E163.417°, elev. 160 m, on *Cladonia mitis* (podetia), 25 Aug. 2011, *T. Ahti* & *S. Talbot* 70348a, holotype H.

Diagnosis — Lichenicolous fungus. Differs from *Stictis cladoniae* mainly in the light orange yellow with white pruinose rim vs brownish black and epruinose ascomata, the hyaline to very pale orange yellow vs mainly medium to dark brown proper exciple, the I–, K/I– vs I+ red, K/I+ blue hymenium, the longer asci, mainly 73–93 × 7–9 µm and the longer, (5–)7–11-septate ascospores, mainly 50–73 × 1.5–2 µm.

Ascomata apothecioid, more or less superficial, initially almost closed, later widely urceolate, roundish, hemispherical, broader or narrower at the base, 100–500 µm diam, 50–160 µm tall, laterally light orange-yellow, above usually with a white, coarsely granulose, sometimes outwardly extending crystalline rim 20–80 µm wide; disc concolorous with lateral parts, sometimes slightly more intensively coloured, rounded to elongated in surface view, 50–100 µm lengthways; scattered to aggregated, sometimes adjacent. *Proper exciple* composed of thick-walled, rounded or somewhat elongated cells c. 2–6 µm lengthways; *lateral exciple* 40–100 µm thick, hyaline, outwardly usually covered by 10–40 µm thick layer of colourless crystals 2–12 µm across; *lower exciple* (hypothecium) 20–30 µm thick, hyaline to very pale orange yellow at the base. *Periphysoids* absent. *Epihymenium* indistinct. *Hymenium* hyaline, 70–100 µm tall, I–, K/I–. *Subhymenium* hyaline, 10–30 µm thick, composed of thin-walled more or less isodiametric cells c. 2–4 µm diam, hardly distinct from lower exciple. *Paraphyses* filiform, septate, 0.8–1.5 µm diam, apices usually spathulate or capitate, occasionally shortly forked, 1.5–3.0 µm diam, sometimes protruding above the hymenium. *Asci* subcylindrical to elongate clavate, with short foot, apex rounded, tholus 1–3(–9) µm thick, sometimes with a narrow apical beak to 2 µm tall, (71–)73–93(–97) × (6–)7–9 µm (n = 13, in water, phloxine, I or K/I), I–, K/I–, 8-spored. *Ascospores* hyaline, filiform to cylindrical, slightly tapering towards the apices, (37.0–)50.0–72.5(–87.0) × (1.3–)1.5–1.9(–2.2) µm, l/b = (22–)28–46(–55) (n = 81, in water, phloxine, I or K/I), (5–)7–11-septate (septa sometimes indistinct), not constricted at the septa, smooth-walled, lacking a gelatinous sheath, with many small, hardly conspicuous guttules, arranged in the ascus in a bundle. *Anamorph* not found.

Distribution & Hosts — The species is known from tundra (mainly) and taiga biomes of Asia and North America, growing on podetia and rarely basal squamules of *Cladonia amaurocraea*, *C. arbuscula*, *C. mitis* and *C. uncialis*. Pathogenicity not observed.

Additional specimens examined. Canada, Newfoundland & Labrador, Labrador Straits, L' Anse Amour, on *Cladonia arbuscula* (podetia), 10 Sept. 2015, *T. Ahti* 75728a & *J.M. McCarthy*, H. – Russia, Krasnoyarsk Territory, Taimyr Peninsula, Osipovka, on *C. arbuscula* (podetia), 18 July 1990, *M.P. Zhurbenko* 901105, LE 308498; same peninsula, Levinson-Lessing Lake, on *C. arbuscula* (moribund bases of podetia), 27 Aug. 1995, *M.P. Zhurbenko* 95598, LE 308913; Chukotka Autonomous Area, Provideniya, on *C. uncialis* (bases of podetia), 3 July 1969, *Safronov*, LE 308789; Chukotka Autonomous Area, lower Bol'shoi Anyui River, on *C. amaurocraea* (bases of podetia), 11 July 1951, *V.N. Andreev*, LE 308795; Chukotka Autonomous Area, headwaters of Utesiki River, on *C. amaurocraea* (podetia), 21 July 1948, *M.N. Avramchik*, LE 308773a.

Notes — With respect to the other cladoniicolous fungi, *Cryptodiscus epicladonia* morphologically resembles *C. cladoniicola*, *C. galaninae* and *Stictis cladoniae*, which are compared in Table 4.

Cryptodiscus galaninae Zhurb. & Pino-Bodas, *sp. nov.* — MycoBank MB820199; Fig. 5

Etymology. The species is named after the Russian lichenologist Irina A. Galanina, who collected the type.

Type. Russia, Magadan Region, Ol'skii District, km 82 of road Magadan-Talon, near Magtur field station, N59°45'27" W149°39'56", elev. 26 m, on *Cladonia* sp. (moribund podetia), 7 Aug. 2013, *I.A. Galanina*, holotype LE 308693.

Diagnosis — Lichenicolous fungus. Differs from *Cryptodiscus foveolaris* in the I+ red and shorter hymenium 30–45 µm vs

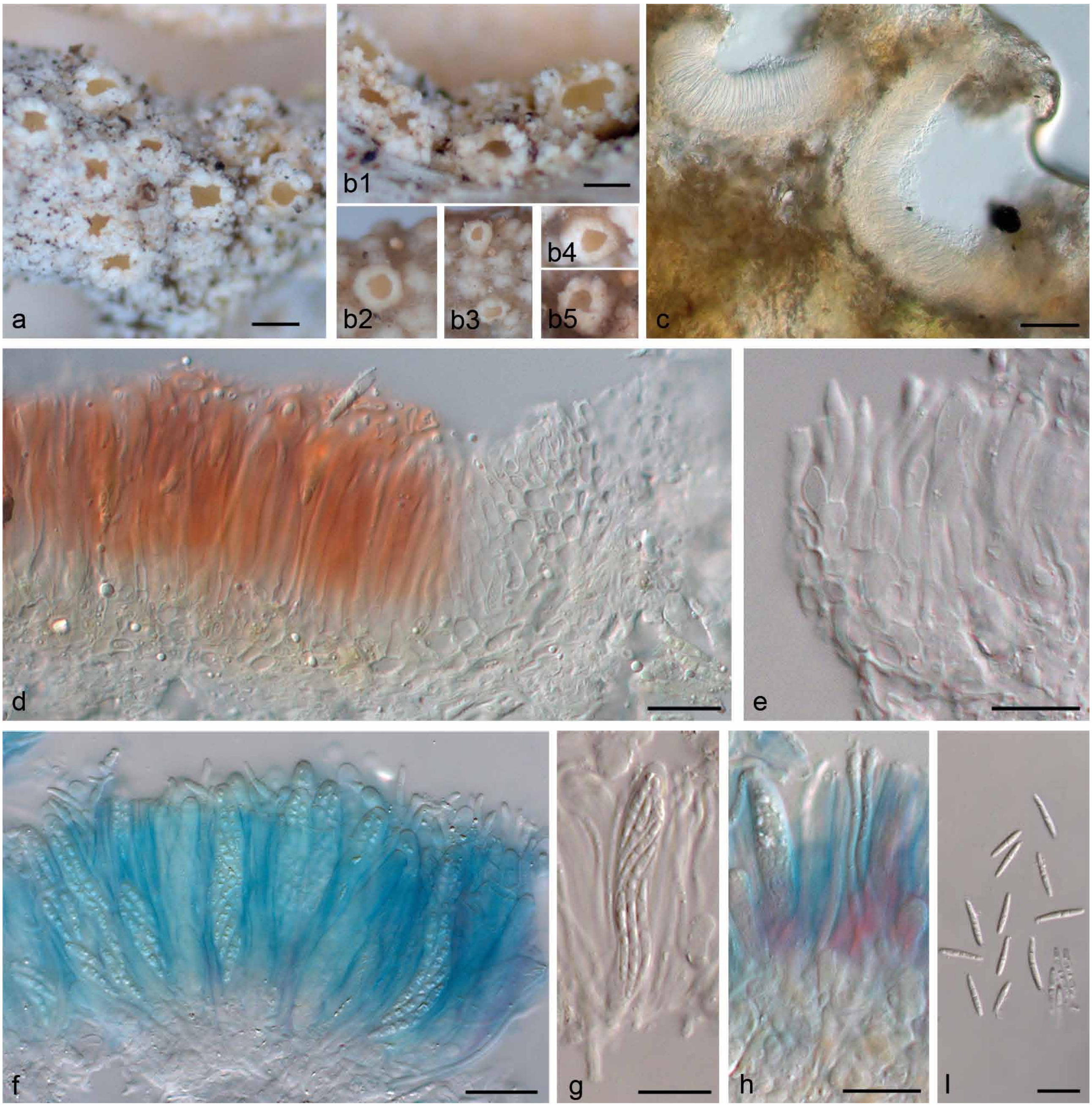

Fig. 5 *Cryptodiscus galaninae*. a. Appearance of apothecia from the holotype; b. apothecia, b1 from the holotype, b2–b5 from LE 380730; c. apothecial section in water from LE 308741; d. apothecial section in I from the holotype; e. short-celled hyphae on the inner side of lateral exciple in K from LE 309139; f. asci in K/I from LE 309139; g. ascus in K from the holotype; h. asci in K/I from the holotype; i. ascospores in K from the holotype. — Scale bars: a–b = 200 µm; c = 50 µm; d–i = 10 µm.

50–80 µm tall, the shorter asci 27–42 µm vs 50–65 µm long, the longer and narrower ascospores 7–14.5 × 1.5–2 µm vs 6–9 × 2.5–3 µm and in the lichenicolous life habit.

Ascomata apothecioid, initially immersed in the host thallus then erumpent and eventually superficial, cupulate, round to ellipsoid in surface view, sometimes constricted at the base, widely urceolate, epruinose, up to 330 µm diam, up to 150 µm tall; margin subhyaline or yellow-white, up to 40 µm thick; disc deeply concave, pale to moderate yellow or yellow-white, translucent, glossy; usually aggregated to contiguous. *Proper exciple* composed of isodiametric or tangentially elongated cells 2–6 × 1–4 µm with walls 0.5–2 µm thick, hyaline, not differentiated into layers, without embedded crystals, 15–40 µm thick laterally, 5–10 µm thick below the hymenium. *Periphysoids* absent, but short-celled hyphae reminiscent of those mentioned in Baloch et al. (2009: 60) have been observed on the inner side of lateral exciple (Fig. 5d). *Epihymenium* indistinct. *Hymenium* hyaline, 30–45 µm tall, I+ blue then quickly orange to red, K/I+ blue with occasional reddish stripes. *Subhymenium* hyaline, c. 5 µm tall. *Paraphyses* filiform, septate, mainly 1.2–1.5 µm diam, up to 2.5 µm diam at the base and up to 2 µm diam at the apices, which are sometimes slightly clavate, rarely with short branchlets or forked in the upper part. *Asci* subcylindrical to elongate clavate, with short foot, apex rounded, tholus up to 2.5 µm thick, apical structures not observed, (27–)28–38(–42) × (4.5–)5–6.5(–7) µm (n = 20, in water, I, K or K/I), I–, periascal gel K/I+ blue, 8-spored. *Ascospores* hyaline, slightly fusiform or slightly clavate (tapering down), occasionally almost bacilliform, straight, (7.1–)9.6–12.4(–14.5) × (1.3–)1.6–2.0(–2.2) µm, l/b = (4.2–)5.0–7.4(–9.7) (n = 140, in water, I, K or K/I), (0–)1(–2)-septate, not constricted at the septa, with thin and smooth wall, lacking a gelatinous sheath, sometimes with conspicuous guttules, diagonally or overlappingly 2–4-seriate in the ascus. *Anamorph* not found.

Distribution & Hosts — The species is known from tundra and taiga biomes of Europe, Asia and North America, growing on aged or moribund podetia or rarely basal squamules of *Cladonia gracilis*, *C. rangiferina*, *C. rappii* s.lat., *C. umbricola* and *Cladonia* sp. Pathogenicity not observed.

Additional specimens examined. Canada, British Columbia, Columbia Mts, Beaver River, on *Cladonia umbricola* (basal squamules), 17 July 2002, *M.P. Zhurbenko* 02100c, LE 308741; British Columbia, Wells Gray Provincial Park, Mt Raft, on *C. rangiferina* (podetia), 3 Aug. 2002, *M.P. Zhurbenko* 02309, LE 308730; New Brunswick, Charlotte Co., 1.5 km NNW of Chance Harbour along power line corridor W of Route 790, on *C. rappii* s.lat. (moribund podetia), 6 Sept. 2014, *T. Ahti* 74421a & *S.R. Clayden*, H. – Russia, Nenets Autonomous Area, Bol'shezemel'skaya tundra, Khar'yaga oilfield, on *C. rangiferina* (podetia), 25 July 2007, *M.P. Zhurbenko* 0735, LE 210357 (formerly erroneously identified and published as *Lettauia cladoniicola* (Zhurbenko 2008)). – USA, Alaska, Kotzebue, on *C. gracilis* (moribund podetia), 19 Aug. 2000, *M.P. Zhurbenko* 00239, LE 309139.

Notes — *Cryptodiscus galaninae* is quite distinct from the other species of the genus with 1-septate ascospores, viz. *C. foveolaris* and *C. pini* (Baloch et al. 2009). Both of these species are saprotrophs on wood, the former one can be distinguished by its I– and taller hymenium 50–80 µm tall, longer asci 50–65 × 4–5 µm and shorter and wider ascospores 6–9 × 2.5–3 µm; the latter one differs in its larger ascomata 0.3–0.6 mm diam with dark reddish brown outer layer of the exciple, I– and taller hymenium 60–80 µm tall and larger asci 40–60 × 6–7 µm. The other known species of *Cryptodiscus* also growing on *Cladonia* are *C. cladoniicola* and *C. epicladonia* described here in detail. The differences among these species are presented in Table 4. The other lichenicolous fungi with urceolate apothecia and hyaline ascospores growing on *Cladonia* are *Biazrovia stereocaulicola*, *Spirographa fusisporella* and *Stictis cladoniae*. *Biazrovia stereocaulicola* can easily be distinguished from *Cryptodiscus galaninae* by its vinaceous, cinnamon or orange-brown apothecia and ellipsoid, 3-septate, larger ascospores measuring (12–)15–20(–28) × (4–)4.5–5.5(–6.5) µm (Zhurbenko & Etayo 2013). *Spirographa fusisporella* is distinct by its 16–32-spored asci and helicoid, longer ascospores 22–31 × 1–2.5 µm (Diederich 2004). The differences from *Stictis cladoniae* can be found in Table 4.

Dactylospora ahtii Zhurb. & Pino-Bodas, *sp. nov.* — MycoBank MB820200; Fig. 6

Etymology. The species is named after the Finnish lichenologist, our friend Prof. Teuvo Ahti.

Type. USA, Alaska, Kodiak Archipelago, Chirikof Island, N55.77095° W155.63464°, elev. 174 m, on *Cladonia gracilis* subsp. *vulnerata* (podetia), 19 July 2013, *S.* & *S. Talbot* CHI017-67a, holotype H.

Diagnosis — Lichenicolous fungus. Differs from *Dactylospora aeruginosa* mainly in the stipitate ascomata, the shorter hymenium, 40–60 µm tall, somewhat smaller ascospores, (7.6–)10.4–13.0(–16.3) × (3.0–)3.5–4.3(–5.5) µm vs (9–)11–14.5 (–16) × (3–)3.5–5.5(–7) µm and in the disparate hosts.

Ascomata apothecia, more or less scattered, composed of a disc usually sitting on a distinct stipe (in LE 264407 stipe poorly developed); disc shiny, dark brown to almost black when dry, medium brown and somewhat translucent when wet, epruinose, round, plane to somewhat concave, occasionally urceolate in senescent overmature apothecia with disintegrated hymenium, (80–)130–250(–600) µm diam (n = 103), surrounded by a usually slightly elevated, often darker (particularly when wet) distinct margin, in side view forming a sharply delimited marginal flange 15–40 µm thick protruting from the stipe for 20–40 µm; stipe usually somewhat tapering towards the base, typically 80–230 µm wide, 40–100 µm tall, pale to medium brown, much paler than the disc or occasionally concolorous. *Proper exciple* 15–30(–70) µm thick laterally, up to 150 µm tall basally, where it forms a stipe; consists of a cupulate, medium red-brown or orange-brown inner layer and of a subhyaline or pale red-brown to orange-brown outer layer with a darker red-brown to orange-brown outermost edge c. 5 µm thick; the outer layer composed of comparatively large isodiametric to tangentially elongated cells c. 5–11 µm lengthways, with walls 1–2 µm thick; the upper lateral part of the exciple usually contains deep purple to dark violet, K+ dark green to blue-green blotches (not observed in LE 264407). *Epihymenium* unevenly pale to medium red-brown to orange-brown, pigmentation amorphous, 5(–10) µm tall, sometimes rather indistinct. *Hymenium* hyaline to pale red or orange-brown, 40–60 µm tall, I+ blue above, red below or I+ blue throughout (in LE 308774), K/I+ blue with red patches. Apothecial section K– (except for the blotches) or becomes less red. *Paraphyses* septate, somewhat constricted at the septa, particularly above, occasionally with ramifications above, 1.5–2 µm diam, apical cells usually medium red or orange-brown, more or less capitate, 3–4(–5.5) µm diam, sometimes not pigmented and only slightly enlarged. *Asci* elongate clavate, c. 40–55 × 9–12 µm, 8-spored, with I+ blue, K/I+ blue external gelatinous cap, 8-spored. *Ascospores* hyaline or rarely light brown, homopolar to somewhat heteropolar, ellipsoid to slightly obovate (with a wider upper cell), occasionally oblong, straight or occasionally slightly curved, (7.6–)10.4–13.0(–16.3) × (3.0–)3.5–4.3(–5.5) µm, l/b = (1.8–)2.6–3.4(–4.3) (n = 302, in water, K, I or K/I), (0–)1-septate, not or occasionally slightly constricted at the septum, guttulate, wall c. 0.5 µm thick, smooth, without internal thickenings, non-halonate, arranged irregularly 2–3-seriate in the ascus. *Anamorph* not found.

Distribution & Hosts — The species is known from polar desert, tundra (mainly) and taiga biomes of Europe, Asia and North America, growing on podetia of *Cladonia arbuscula*,

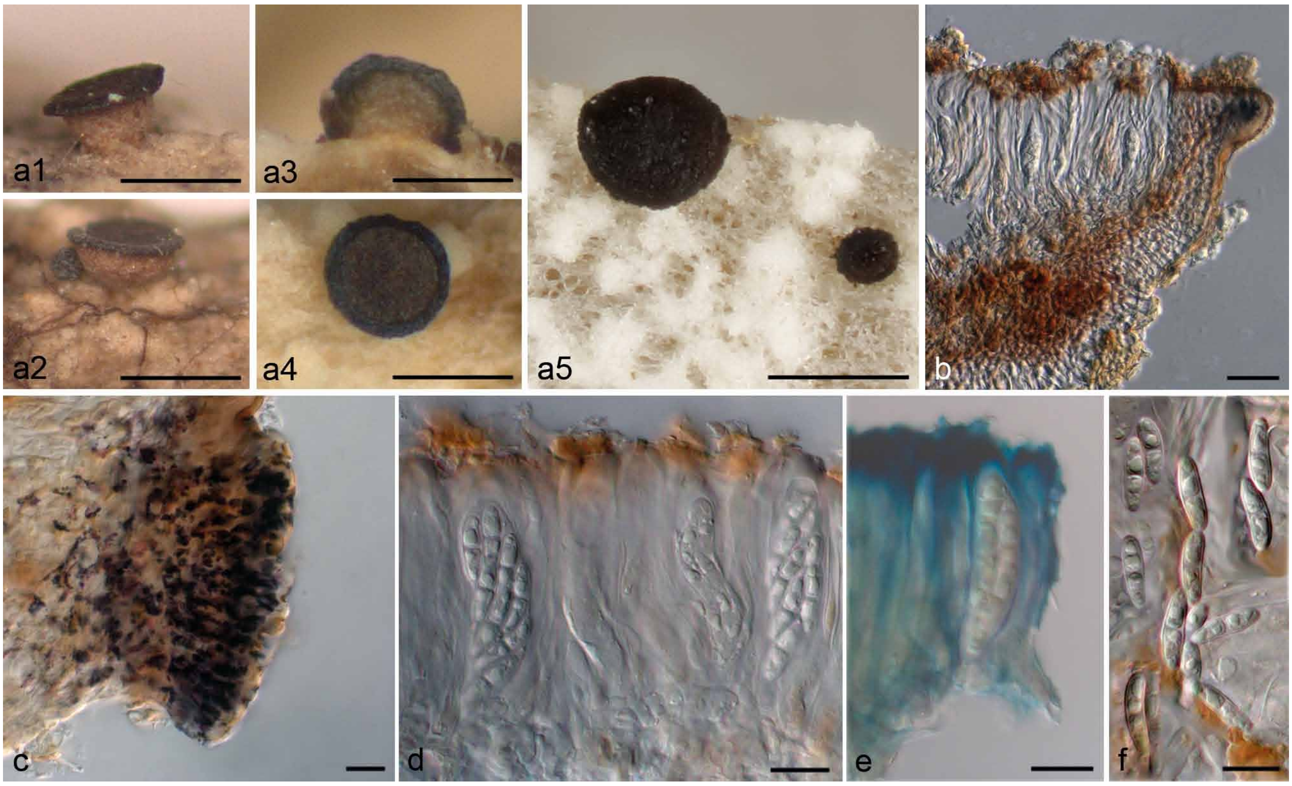

Fig. 6 *Dactylospora ahtii*. a. Appearance of apothecia, a1–a2 from LE207408, a3–a4 from LE 207407, a5 from the holotype; b. apothecial section in water from LE 207408; c. dark purple excipular blotches in water from LE 207407; d. hymenium in K from the holotype; e. asci in K/I from the holotype; f. ascospores in K from the holotype. — Scale bars: a = 200 μm; b = 20 μm; c–f = 10 μm.

C. gracilis subsp. *vulnerata*, *C. mitis*, *C. portentosa* subsp. *pacifica*, *C. rangiferina* (most finds) and *C. uncialis*. Often grows on aged parts of host podetia, visible damage to the host not observed.

Additional specimens examined. Greenland, Frederikshåbs Isblink, on *Cladonia rangiferina* (podetia), 7 July 2009, *E.S. Hansen*, Lichenes Groenlandici Exsiccati 1092a, H; Siorapaluk, on *C. rangiferina* (podetia), 25 July 2009, *E.S. Hansen*, H. – Iceland, Snæfellsnessýsla, Fróðárheiði pass, between Mt Miðfell and Mt Knarrarfjall, on *C. rangiferina* and *C. uncialis* (podetia), 22 July 2009, *F. Högnabba* 1325c, H. – Norway, Svalbard, Aldegondabreen glacier, on *C. rangiferina* (podetia), 16 July 2003, *M.P. Zhurbenko* 03211, LE 264407. – Russia, Murmansk Region, Khibiny Mts, Mt Kukisvumchorr, on *C. rangiferina* (base of podetia), 9 Aug. 1997, *M.P. Zhurbenko* 971, LE 207408 (formerly erroneously reported as *Scutula epicladonia* in Zhurbenko 2001); Krasnoyarsk Territory, Severnaya Zemlya Archipelago, Bol'shevik Is., Mt Bol'shaya, on *C. rangiferina* (podetia), 27 Aug. 1998, *N.V. Matveeva*, LE 308885; Krasnoyarsk Territory, Taimyr Peninsula, mouth of Pyasina River, on *C. rangiferina* (base of podetia), 6 Aug. 1993, *V.B. Kuvaev* 2184, LE 207407 (formerly erroneously reported as *Scutula epicladonia* in Zhurbenko & Santesson 1996); same peninsula, Levinson-Lessinga Lake, on *C. rangiferina* (moribund bases of podetia), 28 July 1995, *M.P. Zhurbenko* 95592, LE 308880; same peninsula, Kotui River, Kayak, on *C. rangiferina* (podetia), 24 July 1996, *I.Yu. Kirtsideli*, LE 308937; Republic of Sakha (Yakutia), Indigirka River, Ust'-Nera, on *C. rangiferina* (podetia), 11 July 1992, *M.P. Zhurbenko* 92568, LE 308922; Chukotka Autonomous Area, Innepinkuliveem River, on *C. mitis* (podetia), 10 Aug. 1951, *Ababkov*, LE 308796; Chukotka Autonomous Area, Lorino, on *C. arbuscula* (bases of podetia), 16 Aug. 1972, *I.I. Makarova*, LE 308781. – USA, Alaska, Seward Peninsula, 7 km ESE of Nome, on *C. rangiferina* (moribund podetia), 1 Sept. 2001, *M.P. Zhurbenko* 0142c, LE 308589c, *M.P. Zhurbenko* 0171, LE 308516; Mause Creek, on *C. rangiferina* (podetia), 22 July 2000, *D.A. Walker*, LE 309135; Kotzebue, on *C. rangiferina* (podetia), 19 Aug. 2000, *M.P. Zhurbenko* 00232, LE 309138; Kobuk Valley Wilderness, Waring Mts, on *C. arbuscula* (podetia), 31 July 2000, *M.P. Zhurbenko* 00139, LE 309137; Kodiak Archipelago, Chirikof Is., on *C. rangiferina* (podetia), 19 July 2013, *S.* & *S. Talbot* CHI017-65a, H; Aleutian Islands, Carlisle Is., on *C. gracilis* subsp. *vulnerata* (podetia), 28 July 2013, *S.* & *S. Talbot* CAR001-23b, H; same islands, northwest corner of Amalia Is., on *C. gracilis* subsp. *vulnerata* (podetia), 2 Aug. 2013, *S.* & *S. Talbot* AML305a, H; same islands, Adak Is., northern side of Finger Bay, on *C. rangiferina* (podetia), 26 Aug. 2013, *S.* & *S. Talbot* ADA717a, H; Wosnesenski Is., Port Moller, on *C. portentosa* subsp. *pacifica* (podetia), 31 June 2009, *S. Talbot* WOS019-19a, H.

Notes — Compared to the *Dactylospora* species with 1-septate ascospores produced in 8-spored asci *D. ahtii* is most similar to *Dactylospora* sp. (presented below), *D. aeruginosa* and *D. protothallina*. The *Dactylospora* sp. differs from *D. ahtii* in having only occasionally stipitate ascomata with a much shorter stipe, a completely dark reddish orange or brown upper part of the exciple, more intensively red tinge of epihymenium and proper exciple and K+ aeruginose blotches sometimes located in the hypothecium. Further, *Dactylospora* sp. differs in its ascospores, which are constantly pale to medium pigmented, somewhat larger, (8.9–)10.9–14.9(–18.3) × (3.4–)4.5–5.9(–7.6) μm, exceptionally also 2-septate and sometimes distinctly constricted at the septum. *Dactylospora aeruginosa* differs from the new species in having non-stipitate apothecia, a much thicker hymenium mainly 70–120 μm thick, violet-blue, K+ aeruginose blotches occurring not only in the lateral exciple, but also in the epihymenium and hymenium, a light brown hypothecium and somewhat larger ascospores, (9–)11–14.5(–16) × (3–)3.5–5.5(–7) μm, with a perispore up to 2 μm thick (Ihlen et al. 2004). This species have been reported from the coastal forests of Norway, Alaska and from the Arctic, growing on thalli of various epiphytic crustose lichens from the genera *Biatora*, *Japewia*, *Lopadium* and *Micarea* or directly on wood and bark of *Picea* and *Juniperus* and on terricolous crustose lichens *Lecidea epiphaea* (Zhurbenko & Von Brackel 2013) and *Biatora subduplex* (as 'cf.'; Zhurbenko 2009). *Dactylospora protothallina* differs from *D. ahtii* in the absence of K+ aeruginose blotches, a brown epihymenium, a somewhat taller hymenium of 65–80 μm and somewhat wider, brown ascospores (9–)10–15 × 4.5–7.5 μm (Hafellner 1979, Nimis 1993, Alstrup & Ahti 2007, Spribille et al. 2010). So far, *D. prothallina* has been reported from the lichen species of *Fuscopannaria*, *Massalongia*, *Parmeliella*, *Protopannaria* and from adjacent biofilms. The other *Dactylospora* species reported on *Cladonia* are *D. cladoniicola*, so far known only from the holotype on *Cladonia macrophyllodes* collected in Svalbard (Alstrup & Olech 1993) and *D. deminuta*, a widely distributed species recorded from many unrelated host genera. Both of them have brown mature ascospores. In addition, *D. cladoniicola* has much larger ascospores measuring 33–37 × 12–14 µm and *D. deminuta* has (3–)5–7(–8)-transseptate ascospores. Another similar species is *Scutula cladoniicola*, which differs from *Dactylospora ahtii* in the following characters:

1. apothecial stipe usually absent or, if present, shorter than 40 µm and concolorous with the disc;
2. apothecial disc blackish and not translucent when wet;
3. lateral exciple medium brown throughout, with hyaline outermost edge;
4. epihymenium indistinct;
5. hymenium hyaline to olive grey below;
6. violet, K+ aeruginose blotches occur also in the hymenium;
7. apices of paraphyses usually medium reddish orange-brown, more or less capitate, 3–4(–5.5) µm diam;
8. amyloid external gelatinous cap of the asci not observed;
9. ascospores hyaline, usually homopolar, larger, 13.0–16.4 × 5.5–6.7, (0–)1(–3)-septate, with granulate wall 0.5–1 µm thick.

Dactylospora **sp.** — Fig. 7

Apothecia blackish, glossy, 0.2–0.6 mm diam, sessile, without a stipe or with a short paler stipe up to 40 µm tall (in LE 308774), disc plane to convex, margin thin, prominent, concolorous with the disc, not translucent when wet. *Epihymenium* medium red-brown, to 10 µm tall. *Paraphyses* with somewhat swollen apices 3–4 µm diam. *Hymenium* more or less colourless, 40–60 µm tall. *Proper exciple* red-orange or orange-brown, dark and 25–50 µm thick laterally and pale (but with darker marginal rim), 40–50 µm thick below the hymenium, where it is composed of much larger, mainly isodiametric cells up to 16 µm across with relatively thin wall. *Lower exciple* (hypothecium) medium to dark red-brown, up to 100 µm tall, with dark, indistinctly coloured, K+ aeruginose blotches or without them (in LE 308809). Apothecial section becomes less reddish in K. *Asci* 8-spored. *Ascospores* pale yellow-gray-olive-brown to medium brown, slightly obovate (with wider upper cell) to occasionally ellipsoid, (0–)1(–2)-septate (only exceptionally aseptate or 2-septate), sometimes distinctly constricted at the septum, (8.9–)10.9–14.9(–18.3) × (3.4–)4.5–5.9(–7.6) µm, l/b = (1.6–)2.1–2.9(–3.9) (n = 256, in water, I or K), smooth, non-halonate.

Distribution & Hosts — The species is known from tundra and taiga biomes of Asia and from the subantarctic part of South America. Mainly found on moribund parts of *Cladonia amaurocraea*, *C. cariosa*, *C. rangiferina* and *C. symphycarpa*, but also occur on adjacent biofilms and plant remnants and thus probably somewhat saprobic.

Specimens examined. Chile, Antártida Chilena, Comuna Cabo de Hornos, Alberto de Agostini National Park, Hoste Is., on *Cladonia rangiferina* (podetia), 16 Jan. 2013, *W.R. Buck* 60495a, H (specimens sequenced). – Russia, Krasnoyarsk Territory, Eastern Sayan Mts, Kryzhina Range, Belyi Kitat River, on *C. symphycarpa* (moribund basal squamules) and biofilms over terricolous mosses, 14 July 2009, *M.P. Zhurbenko* 0956, LE 308658; Republic of Sakha (Yakutia), Olenek Region, Siibikte River basin, on *C. cariosa* (basal squamules) and occasionally on adjacent plant remnants, 11 Aug. 1957, *A.N. Lukicheva*, LE 308809; Chukotka Autonomous Area, Pekul'nei Range, on *C. amaurocraea* (moribund base of podetia), 4 July 1950, *M.N. Avramchik*, LE 308774.

Notes — The examined material resembles *Dactylospora ahtii*, *D. aeruginosa* and *D. protothallina*. *Dactylospora aeruginosa* can be distinguished by its much taller hymenium (up to 120 µm), a light brown hypothecium and halonate ascospores (Ihlen et al. 2004). *Dactylospora protothallina* differs in the absence of K+ aeruginose blotches and a brown epihymenium (Hafellner 1979). The differences with *D. ahtii* have been discussed above under the latter species. The studied specimens might represent a new species of *Dactylospora*, but it is not formally described, pending the discovery of additional material.

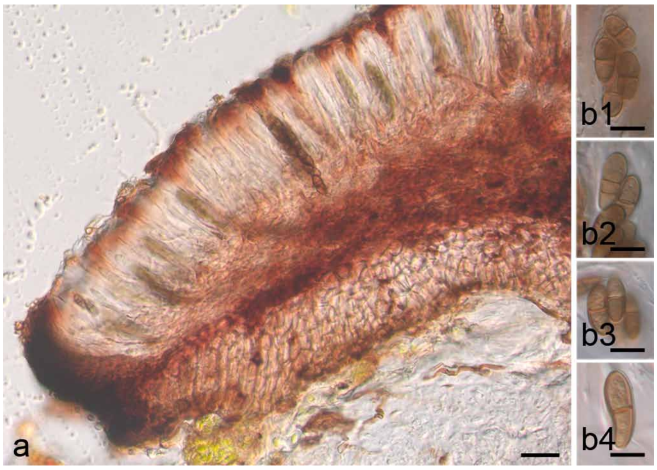

Fig. 7 *Dactylospora* sp. (LE 308658) a. Apothecial section in water; b. variation of ascospores in water. — Scale bars: a = 20 µm; b = 10 µm.

Scutula cladoniicola Alstrup & D. Hawksw., Meddel. Gronland, Biosci. 31: 65. 1990 — Fig. 8

Type. Greenland, Near Ivigtut, N61°14', elev. 0–50 m, on the ground in dwarf shrub heath, on *Cladonia stricta* (podetia), 9 July 1946, *M.S. Christiansen* 5504, holotype herb. Christiansen, C (?), isotype IMI 331024! The type host is apparently *Cladonia trassii*, not *C. stricta*, which was misused in 1946.

Ascomata apothecial, sessile, black throughout, not translucent when wet, epruinose, glossy, rounded, strongly constricted at the base to short stipitate, 150–800 µm diam, up to 450 µm tall, disc plane, somewhat convex or concave, margin slightly raised or flush with the disc. *Lateral exciple* 40–60(–100) µm thick, moderate brown, K+ brown-orange, with hyaline outermost layer c. 5 µm thick, in cross section composed of radially elongated cells c. 5.5–17 × 4–9 µm, with walls 1–3 µm thick. *Lower exciple* (hypothecium) up to 350 µm tall, merging with lateral exciple, moderate brown, K+ brownish orange, in cross section composed of rounded cells with walls 1.5–4 µm thick. *Epihymenium* indistinct. *Hymenium* (40–)50–70 µm tall, hyaline throughout or olive grey below, with scattered orange yellow crystalline granules on the surface, I+ blue, K/I+ blue with occasional red patches. K+ blue-green blotches are scattered in lateral exciple (mainly), lower exciple and hymenium. *Paraphyses* 1.8–2.9 µm diam, apices reddish orange-brown, slightly clavate, 2.5–3.2 µm diam, septate, sometimes slightly constricted at the septa (particularly in K), occasionally branched and anastomosed. *Asci* narrowly clavate, c. 40–65 × 8–11 µm, staining of tholus with I and K/I not observed, but periascal gel I and K/I+ blue, 8-spored. *Ascospores* hyaline, usually homopolar, ellipsoid, occasionally oblong or rarely obovate, (10.0–)13.0–16.4(–19.0) × (4.5–)5.5–6.7(–7.5) µm, l/b = (1.7–)2.0–2.8(–3.6) (n = 152, in water, I, K or K/I), (0–)1(–2 or exceptionally –3)-septate, not constricted at the septum, wall 0.5–1 µm thick, granulate, lacking a gelatinous sheath, overlappingly uniseriate to irregularly biseriate in the ascus.

Distribution & Hosts — The species was reported from the Arctic Canada, Greenland, Iceland and Turkey (Alstrup & Hawksworth 1990, Hansen & Alstrup 1995, Von Brackel 2010, Zhurbenko 2013, Kocakaya et al. 2016), growing on *Cladonia monomorpha*, *C. pyxidata*, *C. rangiferina* and *C. stricta*.

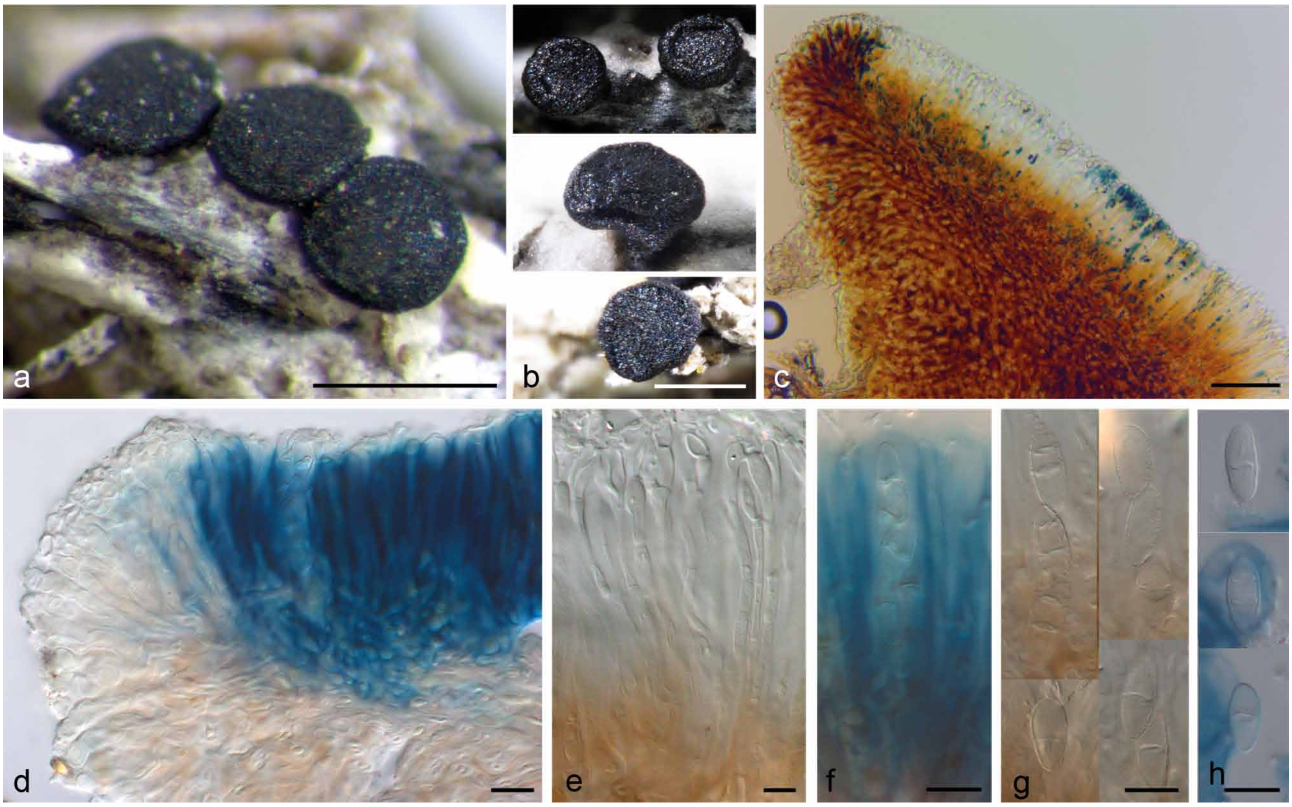

Fig. 8 *Scutula cladoniicola* (isotype). a. Apothecia on host surface; b. appearance of apothecia; c. apothecial section in K; d. ascomatal section in K/I; e. paraphyses in K; f. ascus in K/I; g. ascospores in K; h. ascospores in K/I. — Scale bars: a–b = 0.5 mm; c = 50 µm; d = 20 µm; e–g = 10 µm.

Notes — There are some discrepancies between the examined isotype of the species and its protologue (Alstrup & Hawksworth 1990), where anastomoses of the paraphyses and violet blotches in the proper exciple and hymenium were not mentioned, the epihymenium was reported being greyish brown and interspersed with greenish granules, the apical cells of paraphyses bearing a brown gelatinous coat, the asci with I+ structures in the tholus (Alstrup & Hawksworth 1990: f. 38C) and the ascospores 1(–2)-septate, (12.5–)13–15(–16) × 5–6.5 µm. Morphologically, *Scutula cladoniicola* recalls *Dactylospora ahtii*, their distinguishing characters being summarized under the latter species.

Stictis cladoniae (Rehm) Sacc., Syll. Fung. (Abellini) 8: 692. 1889 — Fig. 9

Type. Austria, Tyrol, Piztal valley, near the Taschach glacier, elev. c. 2000 m, on *Cladonia gracilis* s.l. (podetia), Aug. 1875, *H. Rehm*, holotype S! The type host is apparently *Cladonia macroceras*, since *C. gracilis* should not occur in Tyrol.

Ascomata apothecioid, initially immersed and almost or possibly completely closed, later superficial and deeply urceolate, up to 530 µm diam and up to 190 µm tall, brown-black, epruinose, with blackish disc, scattered. *Proper exciple* cupulate, 20–70 µm thick laterally, 15–25 µm thick basally, uniformly medium to dark brown except for the pale brown to hyaline internal lateral parts, composed of thick-walled, tangentially more or less elongated cells. *Periphysoids* absent. *Epihymenium* indistinct. *Hymenium* hyaline, 50–70 µm tall, I+ red, K/I+ blue. *Subhymenium* hyaline, composed of thin-walled isodiametric cells, up to 10 µm tall. *Paraphyses* filiform, unbranched, septate, 1.5–1.7 µm diam, apices somewhat enlarged, to 2.4 µm diam. *Asci* subcylindrical, with short foot, endoascus thickened at the apex to 2.5 µm, apical beak not observed, (55–)57–71(–78) × (7–)8–10 µm (n = 17, in K/I), periascal gel I+ red, K/I+ blue, staining of apical structures in K/I not observed, 8-spored. *Ascospores* hyaline, filiform/cylindrical, slightly tapering towards the apices, c. 40–60 × 1.5–2 µm (n = 13, in K/I), septation was obscure, but 4–5-septate spores were observed, smooth-walled, without a perispore, guttulate, arranged in the ascus in a bundle.

Notes — So far the species was known only from the type collection in the Austrian Alps (Rehm 1882) and from Lappland in Sweden (Santesson et al. 2004), growing on *Cladonia gracilis* s.lat. We revised its holotype, as the former descriptions of the species (Saccardo 1889, Rehm 1912, Sherwood 1977) essentially recapitulate the protologue (Rehm 1882), where its ascospores were described as being aseptate and much shorter, c. 36 × 1.5–2 µm, and asci shorter, c. 48–50 × 8 µm.

DISCUSSION

Prior studies have proved that the lichenicolous lifestyle arose multiple times along biological evolution (Arnold et al. 2009, Diederich et al. 2013, Suija et al. 2015). Within *Lecanoromycetes*, Divakar et al. (2015) showed that the lichenicolous lifestyle originated at least three times in the family *Parmeliaceae*. The results presented here confirm manifold independent origins of the lichenicolous lifestyle in the class *Lecanoromycetes*. The richest order as for lichenicolous fungi is the *Lecanorales*, followed by the *Ostropales* (Fig. 1). In addition, the latter comprises the greatest number of species with a different lifestyle from the lichenized one within *Lecanoromycetes* (Schoch et al. 2009, Baloch et al. 2010).

The family *Dactylosporaceae* was introduced by Bellemere & Hafellner (1982) to fit the genus *Dactylospora*. The species of this genus are characterized by a type of asci with an I– tholus covered by an I+ blue external gelatinous cap (Hafellner 1979, Bellemere & Hafellner 1982). Molecular studies have shown different phylogenetic positions for this family, while in the phylogenies published by Schoch et al. (2009) and Diederich et al. (2013) it was placed in the *Eurotiomycetes*. Miadlikowska et al.

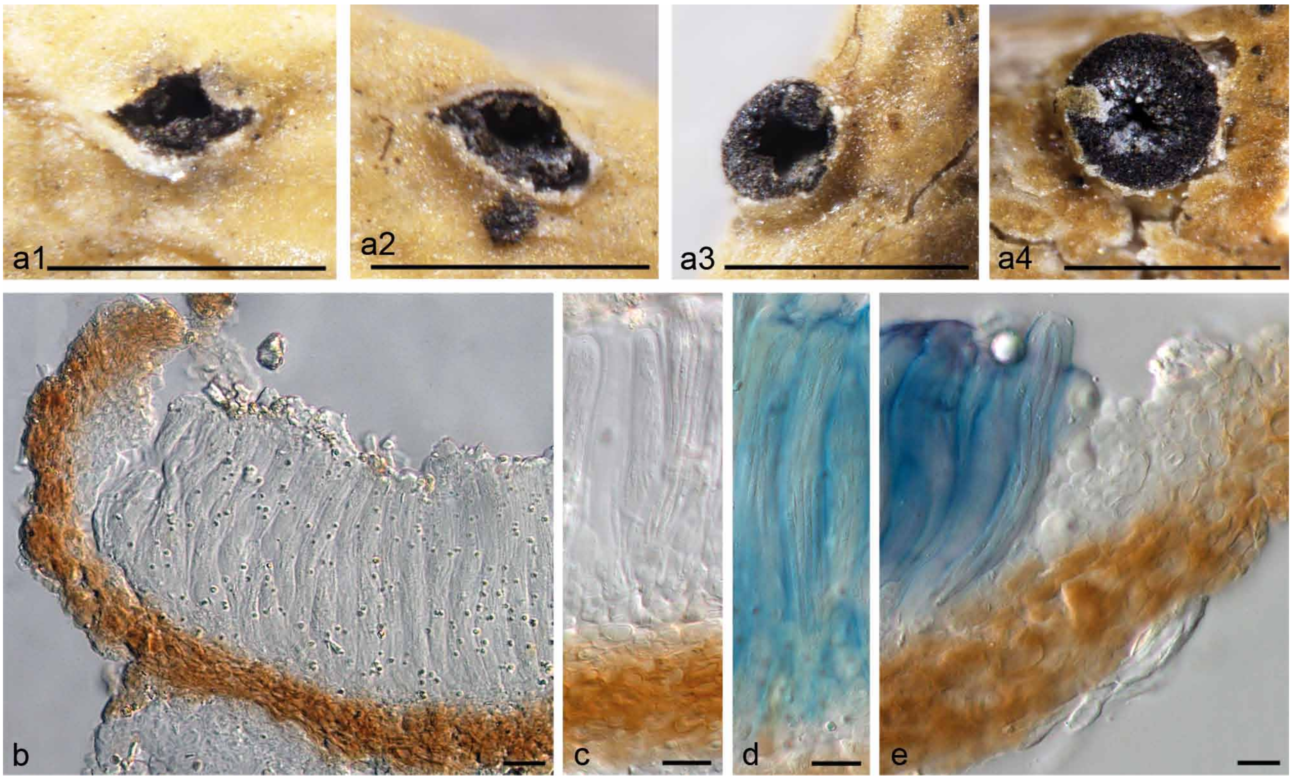

Fig. 9 *Stictis cladoniae* (holotype). a. Appearance of apothecia; b. apothecial section in K; c. hymenium and basal exciple in K; d. asci with spores in K/I; e. asci with spores and lateral exciple in K/I. — Scale bars: a = 0.5 mm; b = 20 µm; c–e = 10 µm.

(2014) suggested that the family belongs to *Lecanoromycetes*, a more consistent result with the morphological characters of the genus, and confirmed in our analyses. These authors recommend using more than six loci to obtain a well-founded result about the phylogenetic position of the family. Since we have not sequenced additional genes we do not discuss the phylogenetic position of the family and limit ourselves to describe the relationships between the species. Schoch et al. (2009) found that the genus *Dactylospora* was polyphyletic, and that the determination of which of the two clades represented *Dactylospora* s.str. was still pending. In the present work three specimens of the generic type species, *D. parasitica*, were included and we confirmed that this species belongs to the clade formed by *D. haliotrepha* and *D. mangrovei* in the phylogeny of Schoch et al. (2009). *Dactylospora parasitica*, formed a well-supported monophyletic group with the sporodochial hyphomycete *Sclerococcum sphaerale* (Hawksworth 1975, Diederich et al. 2013). Both species mainly grow on species of the genus *Pertusaria*. Excluding this relationship, the species with the same lichen host genera were not phylogenetically related. *Dactylospora ahtii* and *Dactylospora* sp., both growing on the genus *Cladonia*, are not closely related. *Dactylospora* sp. is related to *D. glaucomarioides* growing on *Ochrolechia*. *Dactylospora glaucomarioides* morphologically resembles *D. parasitica* (Hafellner 1979), while *Dactylospora* sp., is more similar to *D. aeruginosa* (species not studied here). *Dactylospora ahtii* resembles *D. aeruginosa* and *D. protothallina* (see above). *Dactylospora deminuta* represents an early-diverging lineage in the genus, apparently with a very long branch. This could be due to the fact that we only achieved sequencing two loci (ITS rDNA and mtSSU). The ancestor of the family could have a lichenicolous lifestyle and the switch to saprobic lifestyle have occurred in the lineage formed by *D. mangrovei*, *D. haliotrepha* and *D. vrijmoediae*. But this hypothesis must be proved with more loci and more species, since in our phylogenetic analyses most of the relationships among species are not supported.

Sarcogyne sphaerospora was placed in the family *Acarosporaceae*, related with *Polysporina subfuscescens* (Fig. 1). This result agrees with its current classification based on morphology (Hafellner 1995). The genera *Sarcogyne* and *Polysporina* differ in the presence of a carbonized epihymenium in the latter (Vězda 1978). Lendemer et al. (2009) pointed out that this character could be insufficient to keep these genera apart. The recent phylogenetic analyses of the family *Acarosporaceae* (Reeb et al. 2004, Westberg et al. 2015) indicate that both genera are polyphyletic and that a carbonized epihymenium is not restricted to a unique phylogenetic lineage (Westberg et al. 2015). In turn it has been shown that *Polysporina subfuscescens* is a polyphyletic species (Westberg et al. 2015). On the basis of morphology, it has been considered that *S. sphaerospora* could be related to *Acarospora stapfiana* and *A. succedens* (Lendemer et al. 2009). These two species share with *S. sphaerospora* the presence of spherical ascospores with a perispore. This relationship is highly probable since other species of *Sarcogyne* and *Acarospora* have been shown to be closely related (Westberg et al. 2015). The family *Acarosporaceae* needs an exhaustive taxonomical study in order to delimit the genera and the species.

In the phylogenetic analysis presented by Suija et al. (2015) a common cladoniicolous fungus, *Phaeopyxis punctum* (type species of the genus) was placed in the *Lecanoromycetes*, subclass *Ostropomycetidae*, but its relationships within this subclass was not resolved. Our results, based on the sequences of six new specimens, confirm the placement of *P. punctum* in the *Lecanoromycetes* but do not solve either the relationship of the species within *Ostropomycetidae*. Our phylogenetic analyses showed that *P. punctum* along with the coelomycete *Bachmanniomyces uncialicola* (also confined to species of *Cladonia*) form a well-supported clade on the base of the *Ostropomycetidae* (Fig. 1). *Phaeopyxis punctum* frequently grows on both podetia and basal squamules of *Cladonia* and usually does not induce galls, while *Bachmanniomyces uncialicola* mostly grows on podetia, only rarely on basal squamules and almost always induces galls (Zhurbenko & Pino-Bodas 2017). However, gall formation has also been reported for *Phaeopyxis punctum* (Grummann 1960, Rambold & Triebel 1990, Zhurbenko & Pino-Bodas 2017), and occasionally both species grow together (Motiejūnaitė et al. 2011, our own specimens on *Cladonia stygia*, Finland, *R. Pino-Bodas* s.n., H). The two binomials may refer to the same species, as indicated by our phylogenetic analyses, and *B. uncialicola* may be an anamorph of *Phaeopyxis punctum*.

So far the phylogenetic placement of the genus *Epigloea* was uncertain in the *Ascomycota*. Davis (1987) created the family *Epigloeaceae*, exclusively containing the genus *Epigloea*. The features peculiar to *Epigloea* are gelatinous perithecioid ascomata, non-fissitunicate, 8- to multispored asci with an I+ wall and colourless septate ascospores sometimes with terminal apiculae (Döbbeler 1984, Davis 1987, Pérez-Ortega & Barreno 2006). Originally the genus was considered as lichenized (Zukal 1890), but later Döbbeler (1984) showed it to be a highly specialized parasite of algae. One species, *Epigloea urosperma*, is exclusively lichenicolous, and two other species, *E. bactrospora* and *E. soleiformis*, occasionally grow on lichens (Döbbeler 1994, Zhurbenko 2010, Czarnota & Hernik 2013). No author has found morphological characters that permit to place this genus in some of the groups of the *Ascomycota*. Our phylogenetic analyses show that *E. soleiformis* belongs to the subclass *Ostropomycetidae*, close to *Anzina carneonivea* and *Arthrorhaphis citrinella*. The placement of *Epigloea* in the *Ostropomycetidae* is not particularly surprising, because this class comprises species with different types of ascomata (Grube et al. 2004, Schmitt et al. 2005, 2009). Nevertheless, no morphological character suggested beforehand that this genus could be related to the genera *Anzina* or *Arthrorhaphis*. However, the confirmation of the phylogenetic position of the genus *Epigloea* will require the inclusion of the type species, *E. bactrospora*, in a phylogenetic study.

The family *Protothelenellaceae* was first placed in the *Ostropomycetidae* by Schmitt et al. (2005). We have sequenced for the first time one of the three known lichenicolous species of the genus, namely *P. santessonii*, confirming that it belongs to the genus *Protothelenella*. *Protothelenella santessonii* is the only species of the genus likely to be confined to the genus *Cladonia*. It is characterized by black perithecia, subcylindrical asci and hyaline, submuriform ascospores often with an apiculus (Mayrhofer 1987, Zhurbenko & Alstrup 2004). The phylogenetic position of the genus *Protothelenella* and the family *Protothelenellaceae* remains uncertain within the *Ostropomycetidae*. Schmitt et al. (2005) found that this family was basal to the order *Ostropales*, but could not fit it in any order. In the recent phylogeny of the *Lecanoromycetes* (Miadlikowska et al. 2014) no member of the family was included. Several phylogenetic studies have found that *Protothelenella* forms a well-supported clade with *Anzina* (Lumbsch et al. 2007, 2012, Aptroot et al. 2014, Resl et al. 2015), a result similar to what we found here.

The genus *Lettauia* was first placed in the family *Fuscidiaceae* (Hawksworth & Santesson 1990) on the basis of the ascus type, similar to that of the genus *Ropalospora*. However, our results placed *Lettauia cladoniicola*, the type species of the genus, in the genus *Cryptodiscus*, family *Stictidaceae*, rejecting the hypothesis that *Lettauia* belonged to the family *Fuscidiaceae* (Table 3). So far the family *Stictidaceae* comprised fungi with saprophytic, lichenized and lichenicolous lifestyles characterized by a crystalline ascoma margin and long, filiform ascospores (Wedin et al. 2005, Baloch et al. 2009, 2013). *Lettauia cladoniicola* differs from the genus *Cryptodiscus* basically by its non-urceolate apothecia, although also *C. pini* presents superficial apothecia (Baloch et al. 2009) and by its lichenicolous lifestyle. However, the presence of a more or less hyaline proper exciple without embedded crystals, the absence of periphysoids and the comparatively short, few-celled ascospores are consistent with the genus *Cryptodiscus* (Baloch et al. 2009). Therefore we propose to combine *Lettauia cladoniicola* in *Cryptodiscus*.

The phylogenetic analyses unequivocally support that the two newly described species, *C. epicladonia* and *C. galaninae* belong to the genus *Cryptodiscus*. Morphologically, *C. epicladonia* differs from *Cryptodiscus* in the presence of more or less superficial ascomata with a crystalline rim, asci with a narrow internal apical beak, a K/I– hymenium and asci and a lichenicolous lifestyle. This species slightly resembles the genus *Nanostictis*, a small genus of lichenicolous fungi whose hosts mostly belong to the order *Peltigerales* (Christiansen 1954, Etayo 2002, Etayo & Sancho 2008). *Cryptodiscus*, however, differs from *Nanostictis* species in several ascomatal characters. The monophyly and phylogenetic relationship of *Nanostictis* within the family *Stictidaceae* remain unstudied. *Cryptodiscus galaninae* fits well the current concept of *Cryptodiscus* (Baloch et al. 2009) except for the lichenicolous lifestyle. The placement of these three species in the genus *Cryptodiscus* broadens the generic concept presented by Baloch et al. (2009). Another lichenicolous fungus from *Stictidaceae* that grows on *Cladonia* is *Stictis cladoniae*. We have revised the type material of this species and confirmed that it is morphologically very different from the other species inhabiting *Cladonia* (see above). Several authors doubted that this species belongs to the genus *Stictis* (Christiansen 1954, Sherwood 1977), however, no fresh material was available to solve this doubt by means of molecular data.

The genus *Corticifraga* was described by Hawksworth & Santesson (1990) as an obligately lichenicolous genus growing on species of *Peltigerales*, with C. *peltigerae* as type species. Currently, the genus comprises seven species and is characterized by initially immersed almost perithecioid or lens-shaped, finally apothecioid ascomata, an often rather reduced exciple, paraphyses with gradually thicked or capitate apices, clavate, non-amyloid, 8-spored asci, and ellipsoid, soleiform, fusiform or subcylindrical, transseptate ascospores (Hawksworth & Santesson 1990, Zhurbenko 2007, Etayo & Sancho 2008, Spribille et al. 2010). Hawksworth & Santensson (1990) suggested that this genus could belong to the order *Ostropales* because of the presence of non-amyloid asci. The phylogenetic analyses showed that *C. peltigerae* belongs to the family *Graphidaceae* subfamily *Gomphilloidae*, closely related to *Actinoplaca strigulacea*. The species included in *Gomphilloidae* have rounded to elongate, immersed to sessile apothecia, anastomosed paraphyses, non amyloid asci, ascospores with transversal to muriform septa and a special kind of conidiomata called hyphopores (Vězda & Poelt 1987, Lücking et al. 2004). It is noteworthy that anastomosed paraphyses and hyphopores (important characters of *Gomphilloidae*) have never been observed in species of *Corticifraga*. The current circumscription of this subfamily includes 23 genera (Rivas-Plata et al. 2012), most of which are lichenized and live in tropical areas (Vězda & Poelt 1987, Lücking et al. 2004). However, it also includes species with a lichenicolous lifestyle, such as *Gyalideopsis cochlearifera*, *G. epithallina*, *G. floridae*, *G. parvula*, *G. stereocaulicola* and *Aulaxina aggregata* (Lücking 1997, Lücking & Sérusiaux 1998, Etayo & Diederich 2001, Lücking & Kalb 2002, Etayo 2010).

The coelomycetous genus *Lichenosticta* currently comprises five lichenicolous species (Hawksworth 1981, Lawrey & Diederich 2016). It is characterized by uniloculate, subglobose to broadly pyriform, translucent brown to black, erumpent pycnidia; branched conidiophores; enteroblastic, phialidic, acropleurogenous conidiogenous cells integrated into chains; and hyaline, aseptate, smooth-walled conidia (Hawksworth 1981). Its relationship with *Lecanorales* was previously suggested, since similar catenate conidiogenous cells and an enteroblastic conidiogenesis had been found in lichenized species (Hawksworth 1981, Vobis & Hawksworth 1981). In this study, its phylogenetic placement in *Lecanorales* is confirmed by molecular data. However, our analyses do not clarify to which family this genus belongs, because its relation with *Gypsoplaca macrophylla* was not supported. With regard to morphological similarities, the genus *Gypsoplaca* has branched conidiophores (Timdal 1990), such as those found in *Lichenosticta*, but the production of conidia is always apical, while in *Lichenosticta* it is both lateral and terminal.

The lichenicolous coelomycetous genus *Epicladonia* includes four species (Hawksworth 1981, Ihlen & Wedin 2005), three of which have been included in the study. This genus was resolved as polyphyletic, forming two clades, one of which is exclusively constituted by the type species *E. sandstedei* and another formed by the other two monophyletic species, *E. simplex* and *E. stenospora*. *Epicladonia simplex* and *E. stenospora* were placed in the family *Pilocarpaceae* and *E. sandstedei* was placed in the class *Leotiomycetes*. The polyphyly of the genus *Epicladonia* is hardly surprising, since the studies based on molecular data have proved that many anamorphic fungi, for example *Phoma* (Lawrey et al. 2012), are polyphyletic. On the other hand, it is unexpected for *E. sandstedei* to be phylogenetically so far from *E. simplex* and *E. stenospora*. Furthermore, there are very few anamorphic fungi known in the class *Leotiomycetes* (Wang et al. 2006), although several genera of hyphomycetes have recently been placed in it (Campbell et al. 2006, Réblová et al. 2011). *Epicladonia simplex* and *E. stenospora* seldom induce the formation of galls and their conidia are almost always aseptate, while *E. sandstedei* usually induces galls and its conidia generally have one septum (Hawksworth 1981, Zhurbenko & Pino-Bodas 2017). The family *Pilocarpaceae* is mostly formed by lichenized fungi, although some species of the genus *Micarea* are lichenicolous (Coppins 2009, Van den Boom & Ertz 2014). The pycnidia of some species, such as *Fellhanera gyrophorica* which has a gaping ostiole (Sérusiaux et al. 2001), are similar to the pycnidia of *Epicladonia* (Hawksworth 1981). The conidiogenous cells of the genus *Micarea* are ampulliform to cylindrical, similar to those of *Epicladonia.* However, their conidiogenesis is enteroblastic (Coppins 1983), while in *Epicladonia* it is holoblastic (Hawksworth 1981).

The genus *Scutula* is closely related to *Bacidia* (Fig. 1), a result already found by Andersen & Ekman (2005). *Scutula epiblastematica* was related to the clade formed by *S. miliaris* and *S. tuberculosa*. These three species together with *S. heeri* and *S. dedicata* form *Scutula* s.str. (Wedin et al. 2007). Several authors have pointed out that *Scutula* is heterogeneous (Santesson 1960, Triebel et al. 1997, Hawksworth 2003, Wedin et al. 2007) and they agreed on the necessity of a revision. According to Triebel et al. (1997) and Wedin et al. (2007), *Scutula* s.str. is distinguished by its lichenicolous lifestyle, lecideine apothecia, an 8-spored asci with amyloid tholus and a diffuse non-amyloid axial body, hyaline, mainly 1-septate, smooth-walled ascospores and mitospores of different types. One species of this genus, *S. cladoniicola*, has been described living on species of *Cladonia*. We have studied the isotype of this species (see the description above) and according to our observations the reactions of asci with I and K/I are neither suggestive of *Scutula* nor of *Dactylospora*, therefore this species may belong to a different genus. However, we have not obtained any fresh material to test its phylogenetic position.

Several lichenicolous fungi, so far unclassified in any class of *Ascomycota* (*Bachmanniomyces uncialicola*, *Epicladonia stenospora*, *E. sandstedei*, *E. simplex*, *Epigloea soleiformis*, *Lichenosticta alcicorniaria*) have been placed within *Lecanoromycetes* in this study. The phylogenetic positions of other lichenicolous fungi have been confirmed or sharpened (*Corticifraga peltigerae*, *Dactylospora deminuta*, *D. glaucomarioides*, *D. parasitica*, *Protothelenella santessonii* and *Sarcogyne sphaerospora*). Our results offer a new approach to the family *Stictidaceae*, extending the generic concept of *Cryptodiscus*, which now includes species with a lichenicolous life-style. Nevertheless, additional sampling will be necessary in order to understand the evolution of the lichenicolous lifestyle in this class. On the basis of the morphological characters it has been maintained that the genera *Aabaarnia*, *Biazrovia*, *Caliciella*, *Catillaria*, *Corticiruptor*, *Endohyalina*, *Epilichen*, *Nimisiostella*, *Normanogalla*, *Paralethariicola*, *Piccolia*, *Raesaenenia*, *Scoliciosporum*, *Spirographa*, *Umbilithecium* and *Umushamyces* belong to the *Lecanoromycetes* (Lawrey & Diederich 2016), but there are no molecular studies yet that confirm this assertion. As we have found here, more anamorphic lichenicolous fungi might belong to *Lecanoromycetes*.

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Appendix 1 List of sequences downloaded from GenBank.

Taxa	ID	LSU rDNA	SSU rDNA	mtSSU	ITS rDNA
Absconditella sphagnorum 1	AFTOL-ID 2315	AY300824	–	AY300872	–
Absconditella sphagnorum 2	M24	EU940095	–	EU940247	JX298897
Acarospora laqueata	AFTOL-ID 1007	AY640943	AY640984	DQ991757	DQ842014
Acarosporina microspora	AFTOL-ID 78	AY584643	AY584667	AY584612	DQ782834
Actinoplaca strigulacea	AFTOL-ID 106	DQ782905	DQ782878	–	–
Adelolecia pilati	Ekman 3373	AY300826	–	AY300874	–
Alectoria ochroleuca	AFTOL-ID 209	DQ986801	DQ983483	DQ986785	HQ650597
Anaptychia palmulata	AFTOL-ID 648	DQ883801	DQ883792	DQ912286	HQ650702
Anzina carneonivea	Palize 4168	AY212829	–	AY212851	AF274077
Arctomia delicatula	Palice s.n. (F)	AY853355	–	AY853307	–
Arthrorhaphis citrinella	AFTOL-ID 2341	AY853356	–	AY853308	–
Aspicilia caesiocinerea	AFTOL-ID 653	DQ986778	DQ986736	DQ986892	HQ650636
Aspicilia cinerea	AFTOL-ID 647	DQ986779	DQ986735	DQ986890	HQ650637
Bacidia schweinitzii	AFTOL-ID 642	DQ782911	DQ782884	DQ972998	DQ782850
Bacidina arnoldiana	AFTOL-ID 1845	DQ986798	DQ986702	DQ986810	HQ650650
Baeomyces placophyllus	AFTOL-ID 347	AF356658	AF356657	AY584695	–
Bellemerea alpina	Buschbom 23.8.2000-22	AY532982	AY456692	–	–
Biatora alaskana	G. Thor 24732	–	–	KF662405	KF650958
Biatora subduplex	AFTOL-ID 4912	KJ766533	KJ766693	KJ766360	–
Botryotinia fuckeliana	AFTOL-ID 59	AY544651	AY544695	AY544732	DQ491491
Brigantiaea fuscolutea	Gaya 65	JQ301544	JQ301604	JQ301478	–
Bryoria trichodes	AFTOL-ID 872	DQ986752	DQ986740	DQ986896	HQ650610
Byssoloma subdiscordans	Tonsberg 25968	–	–	AY567779	–
Calenia monospora	Lücking 032h	KF833327	–	KF833339	–
Calopadia foliicola	Lücking 16011	–	–	AY567782	–
Caloplaca arnoldii	Gaya 5	JQ301547	JQ301606	JQ301481	JQ301657
Caloplaca chalybaea	Gaya 38	JQ301550	JQ301607	JQ301484	JQ301659
Caloplaca chilensis	Gaya 68	JQ301551	JQ301608	JQ301485	JQ301660
Caloplaca cinnamomea	Gaya 24	JQ301552	JQ301609	JQ301487	–
Caloplaca gloriae	Gaya 59	JQ301555	JQ301613	JQ301491	–
Caloplaca saxicola	Soechting 7451	AJ535282	AJ535269	–	–
Caloplaca scoriophila	Gaya 47	JQ301560	JQ301617	JQ301496	JQ301664
Caloplaca scotoplaca	Gaya 40	JQ301561	JQ301618	JQ301497	JQ301665
Candelariella reflexa	AFTOL-ID 1271	DQ912331	DQ912331	DQ912272	–
Carbonea supersparsa	AFTOL-ID 3696	–	–	–	–
Carbonea vitellinaria	R. Tuerk 32321	–	–	–	AY541239
Carbonea vorticosa	Tuerk 44642	–	–	–	JN873871
Carbonicola anthracophila	Timdal 11027	KF360456	–	KF360424	KF360379
Carestiella socia	Gilenstam 2437a	AY661682	–	AY661678	AY661682
Catolechia wahlenbergii 1	AFTOL-ID 1667	KJ766542	KJ766697	KJ766370	–
Catolechia wahlenbergii 2	AFTOL-ID 1743	DQ986794	DQ986704	DQ986811	HQ650649
Cecidonia umbonella	Buschbom 21.08.2001-9b	AY532990	–	–	–
Cecidonia xenophana	Buschbom 26.08.2001-9	AY532991	–	–	–
Cetraria islandica	AFTOL-ID 211	DQ912334	DQ912311	DQ912277	JQ301699
Chlorociboria aeruginosa	AFTOL-ID 151	AY544669	AY544713	AY544734	DQ491501
Cladonia caroliniana	AFTOL-ID 3	AY584640	AY584664	AY584614	DQ782832
Cladonia stipitata	AFTOL-ID 1657	DQ973003	DQ973026	DQ972975	–
Coccocarpia domingensis	AFTOL-ID 122	DQ912346	DQ912323	–	–
Coccocarpia erythroxyli	AFTOL-ID 333	DQ883800	DQ883791	DQ912294	HQ650691
Coccocarpia palmicola	AFTOL-ID 1636	KJ766545	KJ766700	KJ766375	–
Coenogonium luteum	AFTOL-ID 352	AF279387	AF279386	AY584699	HQ650710
Collema cristatum	AFTOL-ID 1013	DQ917408	DQ917410	DQ917409	–
Crocynia pyxinoides	AFTOL-ID 111	AY584653	AY584677	AY584615	–
Cryptodiscus foveolaris	EB88	FJ904671	–	FJ904693	–
Cryptodiscus gloeocapsa 1	AFTOL-ID 2367	AF465440	AF465456	AY300880	–
Cryptodiscus gloeocapsa 2	EB93	FJ904674	–	FJ904696	–
Cryptodiscus pallidus 1	EB152	FJ904679	–	FJ904701	FJ904679
Cryptodiscus pallidus 2	EB173	–	–	–	FJ904680
Cryptodiscus pini	EB178	FJ904683	–	FJ904705	FJ904683
Cryptodiscus tabularum 1	Baloch SW073	FJ904688	–	FJ904710	–
Cryptodiscus tabularum 2	EB77	FJ904687	–	FJ904709	FJ904687
Cudoniella clavus	AFTOL-ID 166	DQ470944	DQ470992	FJ713604	DQ491502
Dactylina arctica	AFTOL-ID 225	DQ986802	HQ650598	DQ986786	HQ650598
Dactylospora haliotrepha	AFTOL-ID 758	FJ176855	FJ176802	KJ766382	–
Dactylospora lobariella	AFTOL-ID 2137	FJ176891	FJ176837	–	–
Dactylospora mangrovei	AFTOL-ID 2108	FJ176890	FJ176836	KJ766382	–
Dactylospora vrijmoediae	NTOU4002	–	–	–	KJ958534
Degelia plumbea	AFTOL-ID 990	DQ912347	DQ912324	DQ912299	–
Dermea acerina	AFTOL-ID 941	DQ247801	DQ247809	DQ976373	–
Diploschistes cinereocaesius	AFTOL-ID 328	DQ883799	DQ883790	DQ912306	HQ650715
Diploschistes euganeus	DNA6795	KF688507	–	KF688507	KF688485
Diploschistes muscorum	SFB 3	KC167077	KC167077	KC167055	KC167004
Erioderma verruculosum	AFTOL-ID 337	DQ973041	DQ973017	DQ972990	–
Evernia prunastri	AFTOL-ID 1272	KJ766557	KJ766713	KJ766389	HQ650611
Fellhanera bouteillei	AFTOL-ID 4917	KJ766559	KJ766716	KJ766392	–
Fissurina insidiosa	AFTOL-ID 1662	DQ973045	DQ973022	DQ972995	–
Fissurina sp.	AFTOL-ID 2101	KJ766560	KJ766717	KJ766393	–
Flavocetraria nivalis	AFTOL-ID 231	DQ883795	DQ883786	DQ912278	–

Appendix 1 (cont.)

Taxa	ID	LSU rDNA	SSU rDNA	mtSSU	ITS rDNA
Flavoparmelia caperata	AFTOL-ID 2	AY584639	AY584663	AY584617	HQ650680
Fuscidea austera	AFTOL-ID 1671	KJ766562	KJ766719	KJ766395	–
Fuscidea cyathoides	AFTOL-ID 1672	KJ766563	–	KJ766396	–
Fuscopannaria ignobilis	AFTOL-ID 1011	DQ917417	DQ986708	DQ917416	HQ650673
Geoglossum nigritum	AFTOL-ID 56	AY544650	AY544694	AY544740	DQ491490
Graphis scripta	AFTOL-ID 2091	KJ440899	AF038878	KJ440959	–
Gyalecta jenensis	AFTOL-ID 361	AF279391	AF279390	AY584705	HQ650712
Gyalidea hyalinescens	AFTOL-ID 332	DQ973046	DQ973023	DQ972996	–
Gypsoplaca macrophylla 1	AFTOL-ID 1703	–	KJ766722	–	–
Gypsoplaca macrophylla 2	AFTOL-ID 3810	–	KJ766722	–	–
Hymenelia epulotica 1	AFTOL-ID 1829	KJ766569	KJ766405	KJ766405	–
Hymenelia epulotica 2	AFTOL-ID 1844	KJ766569	KJ766404	KJ766404	–
Hypocenomyce scalaris	AFTOL-ID 687	DQ782914	DQ782886	DQ912274	DQ782852
Hypogymnia physodes	AFTOL-ID 1966	JQ301600	JQ301651	JQ301541	JQ301700
Hypotrachyna degelii	AFTOL-ID 324	DQ912337	DQ912314	DQ912281	–
Icmadophila ericetorum	AFTOL-ID 875	DQ883694	DQ883704	DQ986897	–
Immersaria usbekica	Roux 1.09.2000.5	AY532985	–	–	–
Imshaugia aleurites	AFTOL-ID 1044	DQ986753	JQ301652	DQ986864	HQ650612
Ingvariella bispora	BCNLich 17183	HQ659185	–	HQ659174	–
Lasallia papulosa	AFTOL-ID 650	DQ883691	DQ883701	DQ986891	HQ650603
Lasallia pustulata	AFTOL-ID 554	DQ883690	DQ883700	DQ986889	HM161456
Lecania cyrtella	AFTOL-ID 1791	KJ766577	KJ766732	KJ766412	HQ650645
Lecanora achariana	AFTOL-ID 1693	DQ973027	DQ973004	DQ972976	–
Lecanora conizaeoides	AFTOL-ID 1858	–	KJ766736	KJ766418	–
Lecanora contractula	AFTOL-ID 877	DQ986746	DQ986741	DQ986898	HQ650604
Lecanora hybocarpa	AFTOL-ID 639	DQ782910	DQ782883	DQ912273	DQ782849
Lecanora strobilina	AFTOL-ID 1794	KJ766583	KJ766739	KJ766420	–
Lecidea auriculata	Lay 07-0075	HQ660536	HQ660520	GU074500	–
Lecidea fuscoatra	AFTOL-ID 589	DQ912332	DQ912310	DQ912275	HQ650707
Lecidea laboriosa	AFTOL-ID 1388	KJ766586	DQ986727	DQ986882	–
Lecidea silacea	AFTOL-ID 1368	–	DQ986723	DQ986878	HQ650629
Lecidella elaeochroma	AFTOL-ID 1275	DQ986747	–	–	HQ650605
Lecidoma demissum	AFTOL-ID 1376	DQ986759	DQ986726	DQ986881	HQ650630
Leotia lubrica	AFTOL-ID 1	AY544644	AY544687	AY544746	DQ491484
Lepraria lobificans	AFTOL-ID 325	DQ986768	DQ986733	DQ986887	–
Leptogium lichenoides	AFTOL-ID 1015	DQ917412	DQ917413	DQ923120	HQ650672
Letrouitia domingensis	Gaya 55	JQ301569	JQ301625	JQ301505	–
Letrouitia vulpina	Gaya 72	JQ301571	JQ301627	JQ301509	–
Lithographa tesserata	P95	KJ462346	KR017261	KR017340	KJ462269
Lobaria scrobiculata	AFTOL-ID 128	AY584655	AY584679	AY584621	–
Lobariella palliola	AFTOL-ID 310	DQ883796	DQ883787	DQ912296	HQ650695
Lobothallia radiosa	AFTOL-ID 1860	KJ766596	KJ766746	KJ766430	–
Lopezaria versicolor	AFTOL-ID 108	DQ912353	DQ912330	AY584622	–
Maronea chilensis	AFTOL-ID 370	AY640955	AY640994	KJ766432	–
Massjukiella candelaria	AFTOL-ID 4377	JQ301587	JQ301639	JQ301528	–
Megalospora sulphurata	Gaya 73	JQ301573	–	JQ301514	–
Megalospora tuberculosa	AFTOL-ID 107	AY584650	AY584674	AY584623	HQ650701
Melanelia fuliginosa	AFTOL-ID 1370	DQ986803	DQ983485	DQ986787	HQ650599
Micarea alabastrites	Andersen 17	AY756327	–	AY567764	AY756469
Micarea denigrata	AFTOL-ID 4923	KJ766598	KJ766750	KJ766437	–
Miriquidica garovaglii 1	Szczepanska 538	KF562180	–	KR995350	KF562188
Miriquidica garovaglii 2	AFTOL-ID 2688	–	–	AY567711	–
Mollisia cinerea	AFTOL-ID 76	DQ470942	DQ470990	DQ976372	DQ491498
Mycobilimbia lurida	AFTOL-ID 1859	KJ766653	KJ766789	KJ766486	–
Mycobilimbia tetramera	AFTOL-ID 1637	KJ766600	–	KJ766439	–
Mycoblastus sanguinarius	AFTOL-ID 196	DQ912333	DQ782879	DQ912276	DQ782842
Myriotrema olivaceum	Lumbsch 19113f & Mangold	EU075627	–	EU075579	–
Nephroma parile	AFTOL-ID 131	AY584656	AY584680	AY584625	HQ650698
Nesolechia oxyspora 1	Wedin 7890	GU994613	–	GU994659	GU994568
Nesolechia oxyspora 2	Ertz 16840 (BR)	KR995417	–	–	KR995295
Ochrolechia trochophora	AFTOL-ID 880	KJ766609	DQ986743	DQ986901	–
Ochrolechia yasudae	AFTOL-ID 882	DQ986776	DQ986744	DQ986902	–
Ophioparma lapponica	AFTOL-ID 1707	DQ973028	DQ973005	DQ972977	–
Ophioparma ventosa	AFTOL-ID 1694	KJ766610	–	KJ766447	–
Orceolina kerguelensis	AFTOL-ID 296	AF274116	DQ366257	AY212830	–
Ostropa barbara	EB85	–	–	–	HM244773
Parmelina tiliacea	AFTOL-ID 1307	KJ766616	KJ766759	KJ766451	–
Parmotrema tinctorum	AFTOL-ID 7	AY584635	AY584659	AY584627	HQ650684
Peltigera degenii	AFTOL-ID 134	AY584657	AY584681	AY584628	–
Peltigera sp.	AFTOL-ID 1838	DQ986796	DQ986705	DQ986809	HQ650648
Peltula auriculata	AFTOL-ID 892	DQ832330	DQ832332	DQ922953	DQ832329
Peltula umbilicata	AFTOL-ID 891	DQ832334	DQ782887	DQ922954	DQ832333
Pertusaria amara	AFTOL-ID 1067	AF274101	AF274104	AY584713	HQ650677
Pertusaria hemisphaerica	AFTOL-ID 959	AF381556	DQ902340	DQ973000	HQ650676
Petractis clausa	Hafellner A 1	AF356662	AF356661	–	–
Petractis nodispora	AFTOL-ID 7804	FJ588713	FJ588712	–	–
Phacopsis vulpina	D132	–	–	–	AF450285
Phaeophyscia orbicularis	AFTOL-ID 1308	DQ912343	DQ912320	DQ912289	JQ301694

Appendix 1 (cont.)

Taxa	ID	LSU rDNA	SSU rDNA	mtSSU	ITS rDNA
Phaeopyxis punctum 1	TU65586	KJ559567	KJ559587	–	–
Phaeopyxis punctum 2	TU68298	KJ559568	KJ559588	–	–
Phaeopyxis punctum 3	Diederich 17303	–	KJ559591	–	KJ559551
Phlyctis argena	AFTOL-ID 1375	–	–	DQ986880	–
Phyllobaeis erythrella	AFTOL-ID 329	DQ986780	DQ986734	DQ986888	–
Phyllobaeis imbricata	AFTOL-ID 852	DQ986781	DQ986739	DQ986895	HQ650635
Physcia aipolia	AFTOL-ID 84	DQ782904	DQ782876	DQ912290	DQ782836
Physconia muscigena	AFTOL-ID 220	DQ912344	DQ912321	DQ912291	JQ301696
Placynthiella oligotropha	AFTOL-ID 1797	–	KJ766766	KJ766458	–
Platismatia glauca	AFTOL-ID 201	DQ973032	DQ973007	DQ972980	–
Platythecium grammitis	AFTOL-ID 2095	KJ766627	KJ766769	KJ766461	–
Pleopsidium chlorophanum	AFTOL-ID 1004	DQ842017	DQ525541	DQ991756	–
Pleopsidium gobiense	AFTOL-ID 1003	DQ883698	DQ525573	DQ991755	HQ650723
Polychidium muscicola	AFTOL-ID 230	DQ986770	DQ986731	DQ986885	HQ650626
Polysporina arenacea	SAR275	LN810814	–	LN810939	LN810814
Polysporina subfuscescens 1	CR26058	–	–	KM879329	KM879334
Polysporina subfuscescens 2	CR26059	–	–	KM879330	KM879333
Porina lectissima	Arup & Baloch SW152	HM244774	–	HM244756	–
Porpidia albocaerulescens	AFTOL-ID 1246	DQ986757	DQ986716	DQ986871	–
Porpidia speirea	AFTOL-ID 1050	DQ986758	DQ986711	DQ986865	DQ986711
Protoblastenia calva	AFTOL-ID 992	JQ301601	JQ301653	DQ986904	HQ650618
Protoblastenia rupestris	AFTOL-ID 4911	KJ766631	KJ766771	–	–
Protopannaria pezizoides	AFTOL-ID 222	DQ912350	DQ912326	DQ912301	HQ650693
Protoparmelia atriseda	Ponzetti 26046	KF562182	–	–	KF562190
Protoparmelia cupreobadia	Fryday 863	KF562184	–	–	KF562192
Protoparmelia phaeonesos	Timdal 11000	KF562185	–	–	KF562193
Protothelenella corrosa	Palice 2002	AY607734	–	AY607746	–
Protothelenella sphinctrinoidella	Lumbsch 19031d	AY607735	–	AY607747	–
Pseudephebe pubescens	AFTOL-ID 1775	KJ766635	KJ766773	KJ766467	–
Pseudocyphellaria anomala	AFTOL-ID 132	DQ883794	DQ883785	DQ912298	HQ650697
Psilolechia leprosa	Tonsberg & Botnen 27362	AY756333	–	AY567730	AY756496
Psora decipiens	AFTOL-ID 4857	KJ766640	KJ766778	KJ766474	–
Punctelia rudecta	AFTOL-ID 9	AY584636	AY584660	AY584630	HQ650686
Puttea margaritella	M149	EU940038	EU940111	EU940261	EU940187
Pycnothelia papillaria	AFTOL-ID 1377	DQ986800	DQ983481	DQ986783	HQ650595
Pyxine subcinerea	AFTOL-ID 686	DQ883802	DQ883793	DQ912292	HQ650705
Raesenenia huuskonenii	Myllys 040811-53	KR995426	AF450289	–	KR995306
Ramalina complanata	AFTOL-ID 966	DQ883783	DQ883784	DQ972986	HQ650720
Ramalina farinacea	AFTOL-ID 1965	KJ766646	KJ766783	KJ766480	–
Ramboldia elabens	AFTOL-ID 4996	KJ766648	KJ766784	KJ766482	–
Ramboldia gowardiana	AFTOL-ID 4913	KJ766649	KJ766785	–	–
Ramboldia insidiosa	AFTOL-ID 1756	KJ766650	KJ766786	–	–
Rhizocarpon oederi	AFTOL-ID 1372	DQ986804	DQ983486	DQ986788	–
Rhizoplaca melanophthalma	AFTOL-ID 2383/2384	DQ787351	–	DQ787352	–
Rimularia limborina	isolate 1062	KJ462349	KR017277	KJ462404	KJ462273
Rinodina tephraspis	AFTOL-ID 1314	DQ912345	DQ912322	DQ912293	–
Ropalospora chlorantha	AFTOL-ID 884	–	–	KJ766487	–
Sagiolechia protuberans	AFTOL-ID 7896	KJ766655	–	HM244757	–
Sarcogyne algoviae	SAR37	LN810849	–	LN810975	LN810849
Sarcogyne clavus	SAR220	LN810853	–	–	LN810853
Sarcogyne hypophaea	Pykala 23561	LN810857	–	–	LN810857
Sarcogyne plicata	AFTOL-ID 4830	KJ766657	KJ766791	–	–
Sarcogyne regularis	AFTOL-ID 3292	–	–	AY853343	–
Schizoxylon albescens 1	AFTOL-ID 4193	–	–	DQ401142	–
Schizoxylon albescens 2	Gilenstam 2696a	DQ401144	–	–	HQ287353
Sclerococcum sphaerale 1	Diederich 17283	JX081673	–	JX081678	–
Sclerococcum sphaerale 2	Ertz 17425	JX081674	–	JX081676	–
Scoliciosporum intrusum	Ekman s. n.	AY756329	–	AY567767	–
Scutula krempelhuberi	Wedin 6356	–	–	AY567789	–
Scutula miliaris	Wedin 6850	–	–	AY567790	–
Solenopsora candicans	AFTOL-ID 1277	KJ766660	KJ766795	KJ766493	–
Spaerophorus fragilis	AFTOL-ID 226	DQ986805	DQ983487	DQ986805	HQ650600
Sphaeropezia capreae 1	EB-2010	–	–	HM244751	–
Sphaeropezia capreae 2	HM244772	AY661684	–	AY661674	–
Sphaeropezia mycoblasti	EB-2012b	JX266159	–	JX266157	–
Sphaeropezia sp. 2	EB-2012c	JX266160	–	–	–
Sphaeropezia yckselensis	EB-2012a	JX266159	–	JX266156	–
Sphaerophorus globosus	AFTOL-ID 1057	DQ986767	DQ986712	DQ986866	HQ650622
Stictis confusum	Wedin 7070	DQ401143	–	DQ401141	DQ401143
Stictis populorum	Gilenstam 2610a	AY527327	–	AY527356	AY527327
Stictis radiata	AFTOL-ID 398	AF356663	U20610	AY584727	DQ782846
Stictis urceolatum	AFTOL-ID 96	DQ986790	–	DQ986790	HQ650601
Strangospora pinicola	AFTOL-ID 4980	KJ766664	KJ766803	KJ766500	–
Teloschistes exilis	AFTOL-ID 87	AY584647	AY584671	FJ772245	–
Teloschistes flavicans	AFTOL-ID 315	JQ301578	JQ301631	JQ301520	JQ301685
Tephromela atra	AFTOL-ID 780	–	DQ986737	DQ986894	HQ650606

Appendix 1 (cont.)

Taxa	ID	LSU rDNA	SSU rDNA	mtSSU	ITS rDNA
Tetramelas phaeophysciae 1	Nordin 4922	–	–	–	DQ198359
Tetramelas phaeophysciae 2	Nordin 5663	–	–	–	DQ201951
Tetramelas pulverulentus 1	Nordin 4417	–	–	–	DQ201952
Tetramelas pulverulentus 2	Nordin 4427	–	–	–	DQ201953
Thamnolia vermicularis	AFTOL-ID 2071	AY853395	AF085472	AY853345	–
Thelenella antarctica	Lumbsch 19006a	AY607739	–	AY607749	–
Thelotrema lepadinum	AFTOL-ID 83	–	–	DQ972997	HQ650717
Thrombium epigaeum	Lumbsch 11179	AY607741	–	AY607751	–
Trapelia placodioides	AFTOL-ID 962	AF274103	AF119500	AF431962	–
Trapeliopsis flexuosa	AFTOL-ID 1825	KJ766668	KJ766807	KJ766505	–
Trichoglossum hirsutum	AFTOL-ID 64	AY544653	AY544697	AY544758	DQ491494
Umbilicaria aprina	AFTOL-ID 1416	DQ986799	DQ986706	DQ986814	HM161480
Umbilicaria arctica	AFTOL-ID 1266	DQ986772	DQ986717	DQ986872	HM161454
Umbilicaria muelhenbergii	AFTOL-ID 404	AY640977	AY641016	AY584729	–
Umbilicaria spodochroa	AFTOL-ID 555	DQ986773	DQ986707	DQ986815	HM161481
Usnea antarctica	AFTOL-ID 813	DQ883692	DQ883702	DQ990920	HQ650616
Vulpicida pinastri	AFTOL-ID 198	DQ912285	–	–	–
Wawea fruticulosa	AFTOL-ID 3401	DQ007347	–	DQ871023	–
Xanthomendoza fallax	Gaya 33	JQ301580	JQ301633	JQ301522	–
Xanthomendoza poeltii	Gaya 7	JQ301583	JQ301636	JQ301525	–
Xanthoparmelia conspersa	AFTOL-ID 4	AY584641	AY584665	AY584633	HQ650688
Xanthoria aureola	Gaya 9	JQ301585	JQ301637	JQ301526	–
Xanthoria elegans	AFTOL-ID 214	DQ912352	DQ912329	DQ912304	–
Xanthoria parietina	Gaya 8	JQ301589	JQ301641	JQ301530	–
Xanthoria polycarpa	AFTOL-ID 200	DQ912351	DQ912328	DQ912303	–
Xylographa parallela	AFTOL-ID 4895	KJ766679	–	KJ766516	–
Xyloschistes platytropa	AFTOL-ID 4891	KJ766680	–	KJ766517	–

Appendix 2 Results of BLAST searches for each new sequences generated in this study, bp represent the covertage in pairs of bases.

	ITS rDNA			LSU rDNA			SSU rDNA			mtSSU		
Code	Best BLAST hit	% Similarity/bp	E-value	Best BLAST hit	% Similarity/bp	E-value	Best BLAST hit	% Similarity/bp	E-value	Best BLAST hit	% Similarity/bp	E-value
RP43 *P. punctum*	*Phaeopyxis punctum*, KJ559545	98 %/525	0.0	–	–	–	–	–	–	–	–	–
RP68 *E. stenospora*	Uncultured fungus, KC965887	86 %/370	2e-102	*Micarea adnata*, AY756326	83 %/445	3e-136	–	–	–	–	–	–
RP93 *P. punctum*	*Phaeopyxis punctum*, KJ559545	95 %/525	0.0	*Phaeopyxis punctum*, KJ559568	100 %/850	0.0	–	–	–	–	–	–
RP94 *P. punctum*	*Phaeopyxis punctum*, KJ559551	92 %/529	0.0	–	–	–	–	–	–	–	–	–
RP95 *P. punctum*	*Phaeopyxis punctum*, KJ559551	95 %/509	0.0	*Phaeopyxis punctum*, KJ559567	99 %/738	0.0	–	–	–	–	–	–
RP96 *P. punctum*	*Phaeopyxis punctum*, KJ559545	100 %/525	0.0	*Phaeopyxis punctum*, KJ559568	99 %/996	0.0	–	–	–	–	–	–
RP97 *P. punctum*	*Phaeopyxis punctum*, KJ559551	97 %/528	0.0	–	–	–	*Phaeopyxis punctum*, KJ559588	99 %/924	0.0	–	–	–
RP106 *E. sandstedei*	Uncultured fungus, KF617768	99 %/498	0.0	Fungal sp., KT289722	98 %/355	2e-175	*Helotiales* sp., LN901162	99 %/308	1e-157	*Leotiomycetes* sp., KT263275	99 %/782	0.0
RP109 *L. alcicorniaria*	*Rhizoplaca macleanii*, JX036152	83 %/468	6e-128	–	–	–	–	–	–	–	–	–
RP119 *E. stenospora*	*Squamarina gypsacea*	87 %/324	1e-93	*Psilolechia leprosa*, AY756333	90 %/911	0.0	–	–	–	*Micarea micrococca*, EF453683	93 %/762	0.0
RP123 *B. uncialicola*	*Phaeopyxis punctum*, KJ559551	93 %/529	0.0	–	–	–	–	–	–	–	–	–
RP127 *D. ahtii*	Uncultured fungus, KC965673	98 %/478	0.0	–	–	–	–	–	–	–	–	–
RP159 *L. cladoniicola*	Uncultured *Cryptodiscus*, KP323396	89 %/520	1e-174	*Bryophagus gloeocapsa*, AF465440	95 %/773	0.0	*Teloschistes flavicans*, JQ301631	96 %/398	0.0	*Bryophagus gloeocapsa*, AY300880	90 %/638	0.0
RP160 *L. cladoniicola*	Uncultured *Cryptodiscus*, KP323396	89 %/520	1e-174	*Bryophagus gloeocapsa*, AF465440	95 %/773	0.0	*Bryophagus gloeocapsa*, AF465456	98 %/349	7e-174	*Bryophagus gloeocapsa*, AY300880	90 %/741	0.0
RP168 *L. cladoniicola*	*Rhizoplaca macleanii*, JX036152	84 %/542	2e-133	–	–	–	*Gypsoplaca macrophylla*, KJ66722	98 %/936	0.0	*Lecanora hybocarpa*, EF105417	90 %/723	0.0
RP182 *D. ahtii*	Uncultured fungus, KC965673	98 %/477	0.0	–	–	–	–	–	–	*Porina lucida*, FJ11132	85 %/100	1e-23
RP189 *E. stenospora*	Uncultured fungus, KC965887	86 %/370	1e-105	*Palicella glaucopa*, KJ152458	81 %/592	3e-162	–	–	–	–	–	–
RP190 *E. stenospora*	*Lecidella* aff. *euphorea*, KT453756	83 %/363	1e-100	*Pisolechia leprosa*, AY756333	90 %/737	0.0	*Micarea adnata*, AF455134	96 %/1538	0.0	–	–	–
RP203 *E. soleiformis*	–	–	–	–	–	–	–	–	–	*Anzina carneonivea*, AY212851	88 %/561	0.0
RP204 *E. soleiformis*	Uncultured fungus, KF617618	92 %/196	4e-68	*Xylographa hians*, KJ462359	84 %/846	0.0	–	–	–	*Thrombium epigaeum*, AY607750	83 %/590	4e-167

RP205 *P. santessonii*	Uncultured soil fungus, KC965473	89 %/523	3e-180	*Prototelenella sphinctrinoidella*, AY607735	97 %/898	0.0	*Rhizoplaca chrysoleuca*, AY530883	94 %/740	0.0	*Protothelenella corrosa*, AY607746	98 %/780	0.0
RP206 *P. santessonii*	Uncultured soil fungus, KC965473	89 %/523	3e-180	*Prototelenella sphinctrinoidella*, AY607735	97 %/895	0.0	*Rhizoplaca chrysoleuca*, AY530883	94 %/668	0.0	–	–	–
RP208 *C. epicladonia*	Uncultured fungus, KF617267	92 %/508	0.0	–	–	–	–	–	–	*Cryptodiscus faveolaris*, AY661673	88 %/664	0.0
RP23 *D. ahtii*	Uncultured fungus, KC965673	98 %/477	0.0	Uncultured fungus, KP889692	87 %/557	0.0	–	–	–	*Dactylospora mangrovei*, KJ766383	88 %/549	0.0
RP235 *D. deminuta*	Uncultured fungus, KC966342	99 %/460	0.0	–	–	–	–	–	–	*Chaetothryales*, KT263240	85 %/502	2e-159
RP263 *E. sandstedei*	Fungal endophyte, HQ335298	93 %/304	0.0	–	–	–	–	–	–	Leotiomycetes sp., KT263275	96 %/499	0.0
RP275 *D. glaucomarioides*	Uncultured fungus, KC965719	85 %/467	1e-119	*Dactylospora mangrovei*, FJ176890	95 %/949	0.0	–	–	–	*Dactylospora mangrovei*, KJ766383	88 %/617	0.0
RP276 *S. epiblastematica*	*Bacidia circumspecta*, AF282124	94 %/482	0.0	–	–	–	–	–	–	*Scutula krempelhuberi*, AY567789	91 %/165	5e-60
RP282 *C. peltigerae*	Uncultured soil fungus, GU211937	87 %/380	9e-112	*Monilinia fructicola*, AY544683	83 %/714	0.0	–	–	–	*Calenia monospora*, KF833339	85 %/583	0.0
RP301 *S. sphaerospora*	Uncultured soil fungus, GU211937	87 %/380	9e-112	*Acarospora umbilicata*, LN810808	96 %/1031	0.0	–	–	–	*Polysporina subfuscescens*, LN10967	99 %/739	0.0
RP314 *C. galaninae*	*Cryptodiscus pini*, FJ904682	89 %/523	4e-174	–	–	–	*Xylographa vitiligo*, AY779284	97 %/865	0.0	–	–	–
RP352 *B. uncialicola*	*Phaeopyxis punctum*, KJ559551	97 %/528	0.0	–	–	–	*Phaeopyxis punctum*, KJ55959	99 %/1482	0.0	–	–	–
RP362 *E. stenospora*	–	–	–	*Psilolechia leprosa*, AY756333	92 %/943	0.0	*Micarea adnata*, AF455134	96 %/1534	0.0	–	–	–
RP391 *Dactylospora* sp.	–	–	–	*Dactylospora mangrovei*, FJ176890	94 %/926	0.0	–	–	–	*Dactylospora mangrovei*, KJ766383	91 %/591	0.0
RP392 *E. stenospora*	–	–	–				*Biatora subduplex*, KJ766693	96 %/1078	0.0	–	–	–
RP395 *L. cladoniicola*	*Rhizoplaca macleanii*, JX036152	83 %/545	5e-129	*Porpidia glaucophaea*, AY532950	93 %/975	0.0	–	–	–	–	–	–
RP422 *D. parasitica*	Ascomycete sp., EF210107	95 %/480	0.0	Ascomycete sp., EF210108	97 %/1028	0.0	–	–	–	*Dactylospora mangrovei*, KJ766383	95 %/656	0.0
RP423 *D. parasitica*	–	–	–	–	–	–	–	–	–	*Dactylospora mangrovei*, KJ766383	90 %/604	0.0
RP424 *D. parasitica*	–	–	–	Ascomycete sp., EF210108	97 %/538	0.0	–	–	–	*Dactylospora mangrovei*, KJ766383	95 %/614	0.0
RP426 *E. simplex*	*Biatora alaskana*, KF650958	87 %/304	6e-88	–	–	–	–	–	–	–	–	–
RP427 *E. simplex*	*Biatora alaskana*, KF650958	87 %/304	1e-89	–	–	–	–	–	–	–	–	–
RP428 *E. simplex*	*Biatora alaskana*, KF650958	84 %/304	3e-71	–	–	–	–	–	–	–	–	–