

New insights into classification and evolution of the Lecanoromycetes (Pezizomycotina, Ascomycota) from phylogenetic analyses of three ribosomal RNA- and two protein-coding genes

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Abstract: The Lecanoromycetes includes most of the lichen-forming fungal species (>13 500) and is therefore one of the most diverse class of all Fungi in terms of phenotypic complexity. We report phylogenetic relationships within the Lecanoromycetes

resulting from Bayesian and maximum likelihood analyses with complementary posterior probabilities and bootstrap support values based on three combined multilocus datasets using a supermatrix approach. Nine of 10 orders and 43 of 64 families currently recognized in Eriksson's classification of the Lecanoromycetes (Outline of Ascomycota—2006 Myconet 12:1–82) were represented in this sampling. Our analyses strongly support the Acarosporomycetidae and Ostropomycetidae as monophyletic, whereas the delimitation of the largest subclass, the Lecanoromycetidae, remains uncertain. Independent of future delimitation of the Lecanoromycetidae, the Rhizocarpaceae and Umbilicariaceae should be elevated to the ordinal level. This study shows that recent classifications include several nonmonophyletic taxa at different ranks that need to be recircumscribed. Our phylogenies confirm that ascus morphology cannot be applied consistently to shape the classification of lichen-forming fungi. The increasing amount of missing data associated with the progressive addition of taxa resulted in some cases in the expected loss of support, but we also observed an improvement in statistical support for many internodes. We conclude that a phylogenetic synthesis for a chosen taxonomic group should include a comprehensive assessment of phylogenetic confidence based on multiple estimates using different methods and on a progressive taxon sampling with an increasing number of taxa, even if it involves an increasing amount of missing data.

Key words: Bayesian inference, Lecanoromycetes, lichen-forming ascomycetes, maximum likelihood, missing data, mitochondrial ribosomal small subunit (mitSSU), molecular phylogenetic classification, nuclear ribosomal large subunit (nuLSU), nuclear ribosomal small subunit (nuSSU), phenotypic characters, photobionts, phylogenetic confidence, phylogeny, RNA polymerase II largest subunit (*RPB1*), RNA polymerase II second largest subunit (*RPB2*)

INTRODUCTION

The Lecanoromycetes, as recognized in Eriksson's (2006) classification, is the largest class of Fungi. It includes the majority (about 90%) of all described lichen-forming Ascomycota (estimated to be > 13 500 species, Kirk et al 2001). A common character uniting members of this class is their ascohymental ascomatal ontogeny, with a predominance of apothecial fruiting bodies, although of diverse construction and shape. Perithecioid ascomata are known in only four of 64 families (Grube et al 2004, Schmitt et al 2005) of Eriksson's (2006) classification and in a few unclassified genera. In most lineages asci have a multilayered

ascal wall of which two layers are thick enough to be visible with light microscopy and display different types of dehiscence (predominantly rostrate but also semi-fissitunicate or bilabiate), however some members (calicioid lichen-forming fungi, such as *Calicium* and *Sphaerophorus*) produce asci with a single evanescent layer (Luttrell 1955; Eriksson 1981; Reynolds 1981, 1989; Tibell 1984; Hafellner 1988).

Members of the Lecanoromycetes form bipartite symbiotic associations with a broad range of photobionts, representing chlorococcalean algae (*Asterochloris*, *Coccomyxa s.l.*, *Dictyochloropsis s.l.* and *Trebouxia*, are the most frequent genera), filamentous algae (*Trentepohlia*, *Phycopeltis*) and cyanobacteria (*Calothrix*, *Nostoc*, *Scytonema* and *Stigonema*) (e.g. Tschermak-Woess 1988; Rikkinen 1995; Beck et al 1998, 2002; Rambold et al 1998; Peršoh et al 2004; Cordeiro et al 2005). Tripartite symbioses with cyanobacteria as the secondary photobiont (in terms of relative abundance in mature thalli) occur in several unrelated genera within the Lecanoromycetes, however they are particularly common in peltigeralean lichens (Peltigerales). Rambold et al (1998) suggested that photobionts associated with lichen-forming fungi could be used in lichen systematics. These authors detected a strong selectivity of mycobionts with respect to their photobionts at the rank of families and genera in the order Lecanorales.

Most members of the Lecanoromycetes are known to produce a wide variety of unique secondary compounds, especially polyketide derivatives (such as depsides and depsidones, anthraquinones and xanthenes) terpenes and pulvinic acid derivatives (e.g. Elix 1996). These chemical compounds are of biological and ecological importance (especially if present in the upper cortex of lichen thalli; e.g. Rundel 1978, Lawrey 1986, Solhaug and Gauslaa 1996, Pöykkö et al 2005) and of systematic (e.g. Elix 1993, Culberson and Culberson 1994, Schmitt and Lumbsch 2004) and evolutionary significance (e.g. Culberson 1986).

Circumscription and ranking of subgroups within the Lecanoromycetes varied in previous classifications, and the last major improvement before molecular phylogenetic studies was derived from the study of reproductive structures, in particular the apical structures of asci. These characters were used to delineate groups of lichen-forming fungi and resulted in a high number of families in the Lecanorales (Hafellner 1984). Because of controversy associated with the uniform implementation of these characters to circumscribe families across the Lecanorales (e.g. Timdal 1991) many families were redefined (e.g. Rambold and Triebel 1992, Hafellner 1993).

Molecular studies have substantially challenged

phenotypically based groupings applied to previous classifications, as well as resolved placement of many sterile taxa, and taxa with uncertain taxonomic affiliation. The Lecanoromycetes include a minimum of three subclasses, the Acarosporomycetidae, Ostropomycetidae and Lecanoromycetidae, according to Reeb et al (2004) and Lutzoni et al (2004). The Acarosporomycetidae encompasses a single family, the Acarosporaceae, defined in most cases by the presence of a crustose or squamulose thallus, a chlorococcoid photobiont (*Trebouxia*), apothecia of various structures, generally more than a hundred simple spores per ascus, and functionally unitunicate ascus with non- or slightly amyloid tholus and ocular chamber. The Ostropomycetidae includes lichenized and nonlichenized fungi (including lichenicolous taxa, Lücking et al 2005) with crustose, squamulose and filamentous thalli, trentepohlioid and chlorococcoid photobionts, ascomata of apothecial or perithecial type, eight or fewer spores per ascus and functionally unitunicate asci. Eriksson (2006) recognizes five orders in this subclass, Agyriales (two families), Gyalectales (two families), Ostropales (seven families), Pertusariales (three families) and Trichotheliales (two families). The subclass Lecanoromycetidae currently (Eriksson 2006) accommodates three recognized orders: Lecanorales (29 families), the most speciose group of the Lecanoromycetes; Peltigerales (seven families); and Teloschistales (three families). Six families (Brigantiaceae, Elixiaceae, Fuscideaceae, Phlyctidaceae, Umbilicariaceae and Vezdaeaceae) are of uncertain position within the Lecanoromycetidae and 30 genera could not be placed with certainty in any of the three existing subclasses of the Lecanoromycetes, according to Eriksson (2006). All members of this largest subclass within the Lecanoromycetes are discomycetes with apotheciate fruiting bodies and most species have chlorococcoid or cyanobacterial (in Peltigerales) primary photobionts. The lichenicolous living strategy (lichenized and nonlichenized fungi growing on lichens) is found in many groups of the Lecanoromycetidae, whose members also serve frequently as hosts for other such fungi (e.g. Clauzade et al 1989, Rambold and Triebel 1992, Kirk et al 2001, Lawrey and Diederich 2003).

Many recent phylogenetic studies have explored relationships within the Lecanoromycetes to evaluate delimitations of particular taxa and less frequently the validity of diagnostic features (especially ascomata and ascus characters) used to circumscribe taxa (e.g. Grube et al 2004, Schmitt et al 2005, Wedin et al 2005). Most of these studies were based on different combinations of two or three nuclear ribosomal genes (i.e. nucSSU, nucLSU and mitochondrial ribosomal

small subunit [mitSSU]) (e.g. Lumbsch et al 2001, 2004a; Lutzoni et al 2001; Ekman and Tønsberg 2002; Kauff and Lutzoni 2002; Lumbsch 2002; Lücking et al 2004; Wedin et al 2005) with only four phylogenetic studies using at least one protein coding gene (*RPB2*: Liu and Hall 2004, Lutzoni et al 2004 and Reeb et al 2004; *RPB1* and *RPB2*: Hofstetter et al 2007). Hofstetter et al (2007) evaluated the phylogenetic contribution (resolving power and statistical confidence) provided by protein-coding (*RPB1* and *RPB2*) and ribosomal RNA-coding (nucSSU, nucLSU and mitSSU) loci in a phylogenetic study of 82 members of the Lecanoromycetes. This study provided a robust phylogenetic framework and useful guidance for selecting loci in future multilocus studies on Lecanoromycetes and Pezizomycotina in general.

Two studies, Lumbsch et al (2004a) and Wedin et al (2005), were designed specifically to reconstruct phylogenetic relationships within the Lecanoromycetes at the family and higher levels as a framework for the evaluation of existing classifications. Although these studies, as well as Lutzoni et al (2004, 83 taxa using nucSSU+nucLSU), substantially increased taxon sampling compared to previously published two-gene phylogenies, many internodes including deep relationships among major groups in the Lecanoromycetes remained poorly supported when using ribosomal genes exclusively. Nevertheless they convincingly argued that ascus and ascoma characters should not be applied consistently to the same hierarchical levels across the Lecanoromycetes. Wedin et al (2005) also provided an overview of the recent major phylogenetic analyses of the Lecanoromycetes. A recent overview of coexisting classifications of the Lecanoromycetes at the order level also can be found in Lumbsch et al (2004a).

The main objectives of this study were to (i) increase significantly both taxon and character sampling to diminish phylogenetic uncertainty within the Lecanoromycetes, (ii) evaluate Eriksson's classification (2006) at the family and higher ranks, (iii) resolve the phylogenetic placement of taxa with unknown affinities and (iv) revisit the distribution and evolution of selected phenotypic characters (including photobionts and ascus structure) across the major groups within the Lecanoromycetes and their utility in lichen systematics.

Using a supermatrix approach we assembled three datasets with a progressively higher number of taxa and missing data. Internodal support estimated with maximum likelihood bootstrap (with RAxML and PHYML) and Bayesian posterior probabilities (with MrBayes) are compared and discussed in the context of missing data and phylogenetic reconstructions.

MATERIALS AND METHODS

Because of space limitation associated with this issue of *Mycologia*, this section is presented in SUPPLEMENT 1 (<http://www.mycologia.org>).

RESULTS AND DISCUSSION

Phylogenetic reconstructions and confidence.—Missing data in the 5+4-gene supermatrix (26%) and the 5+4+3-gene supermatrix (37%) datasets overall did not have a negative affect on phylogenetic resolution and support when using maximum likelihood (RAxML) and Bayesian methods (MrBayes) (see also Wiens 2006). However noticeably lower bootstrap values for several nodes were obtained from PHYML analyses on the 5+4-gene and 5+4+3-gene datasets (FIG. 1, second column vs. first and third columns of grid showing support for each internode). All phylogenies were concordant with the tree based on the most complete 5-gene dataset (the 5+4+3-gene tree is shown in FIG. 1). Only a few branches that were highly supported in the 5-gene phylogeny received no significant support (based on two or all three methods) in the 5+4-gene or 5+4+3-gene reconstructions (e.g. the monophyly of the group delimited by Parmeliaceae and Mycoblastaceae in the Lecanorales, FIG. 1). Adding taxa with missing data to the 5-gene and 5+4-gene datasets often improved phylogenetic confidence (e.g. the monophyly of the Collematineae and the Pertusariaceae). Comparing the three methods used to estimate phylogenetic confidence, we found that support provided by MrBayes generally was congruent with RAxML bootstrap values, whereas PHYML seems to require more data (less efficient) than the other two methods to provide significant support values and seems the least stable as the number of taxa and missing data increased.

Acarosporomycetidae/Acarosporales.—The phylogenetic distinctiveness of the Acarosporaceae was shown by Reeb et al (2004), who suggested recognizing this family at the subclass level (Acarosporomycetidae). This result was confirmed by Lutzoni et al (2004), Miadlikowska and Lutzoni (2004), Hofstetter et al (2007) and this study. In agreement with Reeb et al (2004) neither *Acarospora* nor *Sarcogyne* are monophyletic (FIG. 1). In our analyses *Polysporina* (*P. simplex*) diverged earlier than *Pleopsidium* and the remaining genera of the Acarosporales, a significant result based on all nine support values (but see Wedin et al 2005). *Pleopsidium* (FIG. 2), with *Lecanora*-type asci and ascospores that resemble those of *Lecanora*, was expected to be closely related to *Lecanora* (Hafellner 1993). The Acarosporales represent a strong case where taxa that appear phylogenetically

closely related have very different types of asci and differ considerably also in other characters such as hamathecium and secondary chemistry (including *Timdalia*, a member of the Acarosporaceae in Wedin et al 2005).

Candelariomycetidae/Candelariales.—One of the most surprising outcomes of all three dataset studies (although the strongest support came from the 5-gene analyses) is the placement of *Candelariella* (FIG. 3) and *Candelaria* (former Candelariaceae, Hakulinen 1954) outside the Lecanorales and Lecanoromycetidae (FIG. 1). Owing to the ascus type these genera often were considered close relatives of the Lecanoraceae and currently are classified in this family (Eriksson 2006). This unexpected placement of Candelariaceae also was found and discussed by Wedin et al (2005) and Hofstetter et al (2007), although in the latter study the Candelariaceae is strongly supported as the first phylogenetic split before the divergence of the Acarosporomycetidae. We confirm that this group should be recognized as a major independent lineage within the Lecanoromycetes by classifying it in its own subclass (Candelariomycetidae) the same way it was done to accommodate the unique phylogenetic placement of the Acarosporaceae. No morphological features are known to confirm the separation of these two genera from the Lecanoraceae and the Lecanoromycetidae. A revision of the genera *Candelaria* and *Candelariella* is needed, given that *Candelaria concolor* was found nested within *Candelariella* (FIG. 1).

Ostropomycetidae.—As revealed from analyses on 5+4-gene and 5+4+3-gene datasets, the subclass Ostropomycetidae is well supported as monophyletic (except by PHYML-BS). The phylogenetic tree presented here includes members of these four of five orders part of the current classification of the Ascomycota (Eriksson 2006): Agryriales, Gyalectales, Ostropales and Pertusariales (FIG. 1). The Baecomyetales and Loxosporaceae need to be recognized as members of the Ostropomycetidae, based on our results.

The Ostropales and Gyalectales are treated usually as Ostropales *s.l.* (Kauff and Lutzoni 2002, Lücking et al 2004) due in part to the poor taxon sampling and support these relationships received in past studies. In this study we show that the order Ostropales as circumscribed by Eriksson (2006) is nonmonophyletic due to the inclusion of the Gyalectales. For this reason the Gyalectales should be subsumed within the Ostropales *s.l.* as proposed by Kauff and Lutzoni (2002) and Lücking et al (2004). Because *Ostropa* is classified within the Stictidaceae, the Ostropales *s.str.* could be restricted to this family (well supported in FIG. 1, Ostropales 1), which would allow the recogni-

No. of genes/ data set	No. of taxa	% of missing data	RAxML BP	PHYML BP	MrBayes PP
5	111	17	1	2	3
5+4	188	26	4	5	6
5+4+3	274	37	7	8	9

not applicable due to missing taxa
 RAxML-BP/PHYML-BP $\geq 70\%$ / MrBayes-PP $\geq 95\%$
 RAxML-BP/PHYML-BP $< 70\%$ / MrBayes-PP $< 95\%$ / node does not exist

Primary photobiont:

- Trebouxia* or *Asterochloris*
- Trebouxia*
- Asterochloris*
- Myrmecia*
- Cystococcus*
- Trentepohlia*
- Dictyochloropsis*
- Coccomyxa*
- Other chlorococcoid algae
- Cyanobacteria
- Non-lichenized

Secondary photobiont:

- S/Sc* *Stigonema* / *Scytonema*
- N* *Nostoc*
- C* *Calothrix*

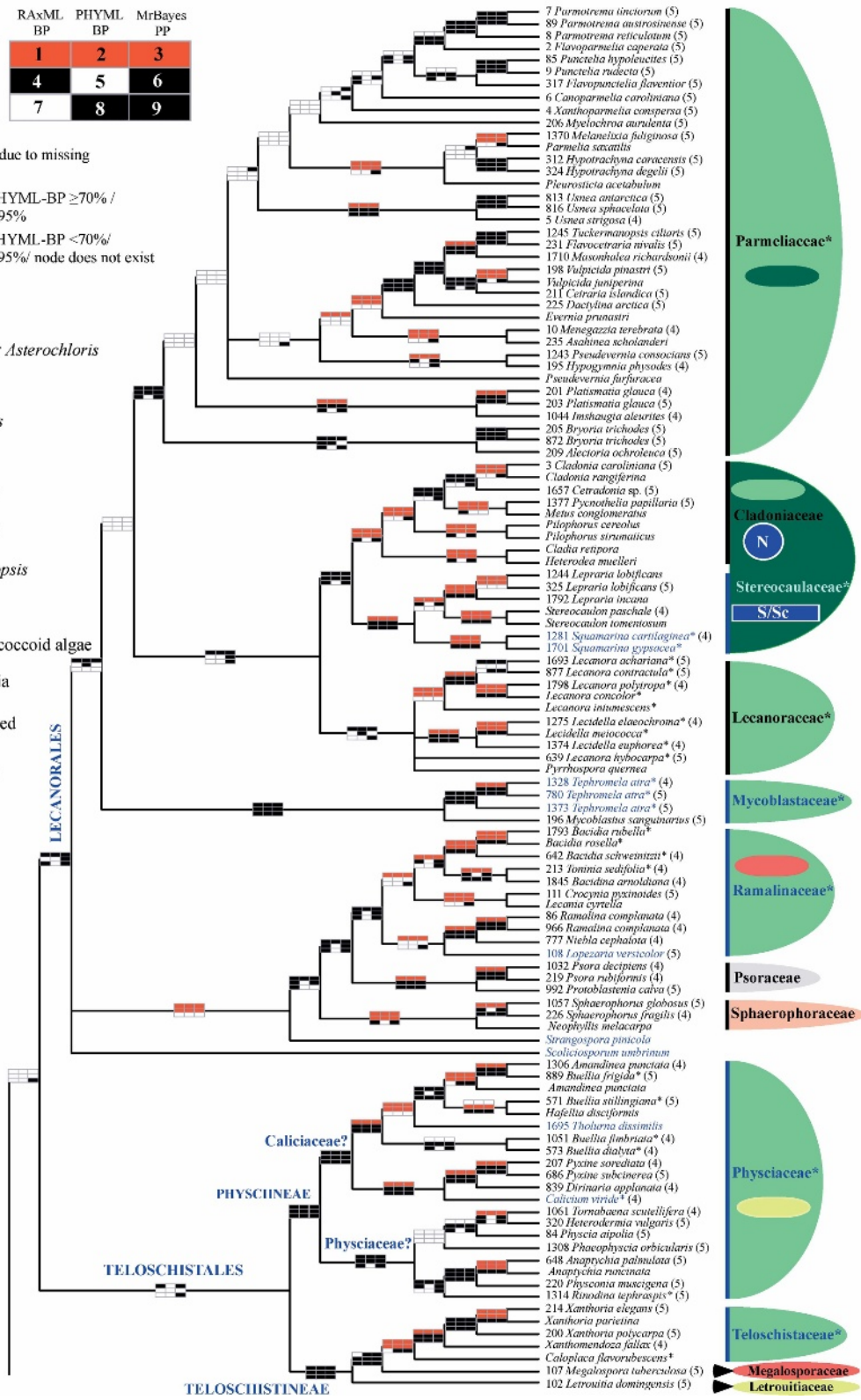


FIG. 1.

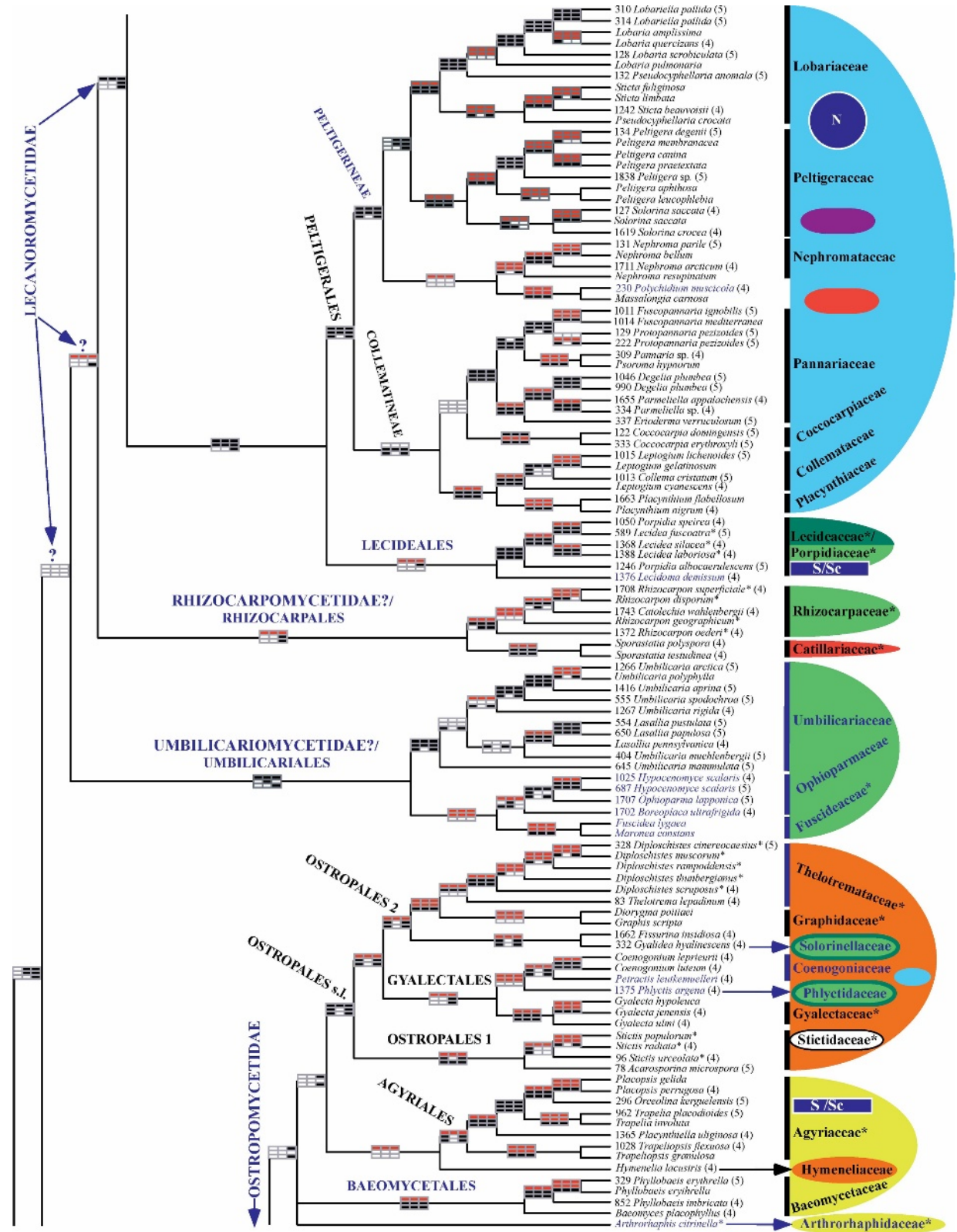


FIG. 1. Continued.

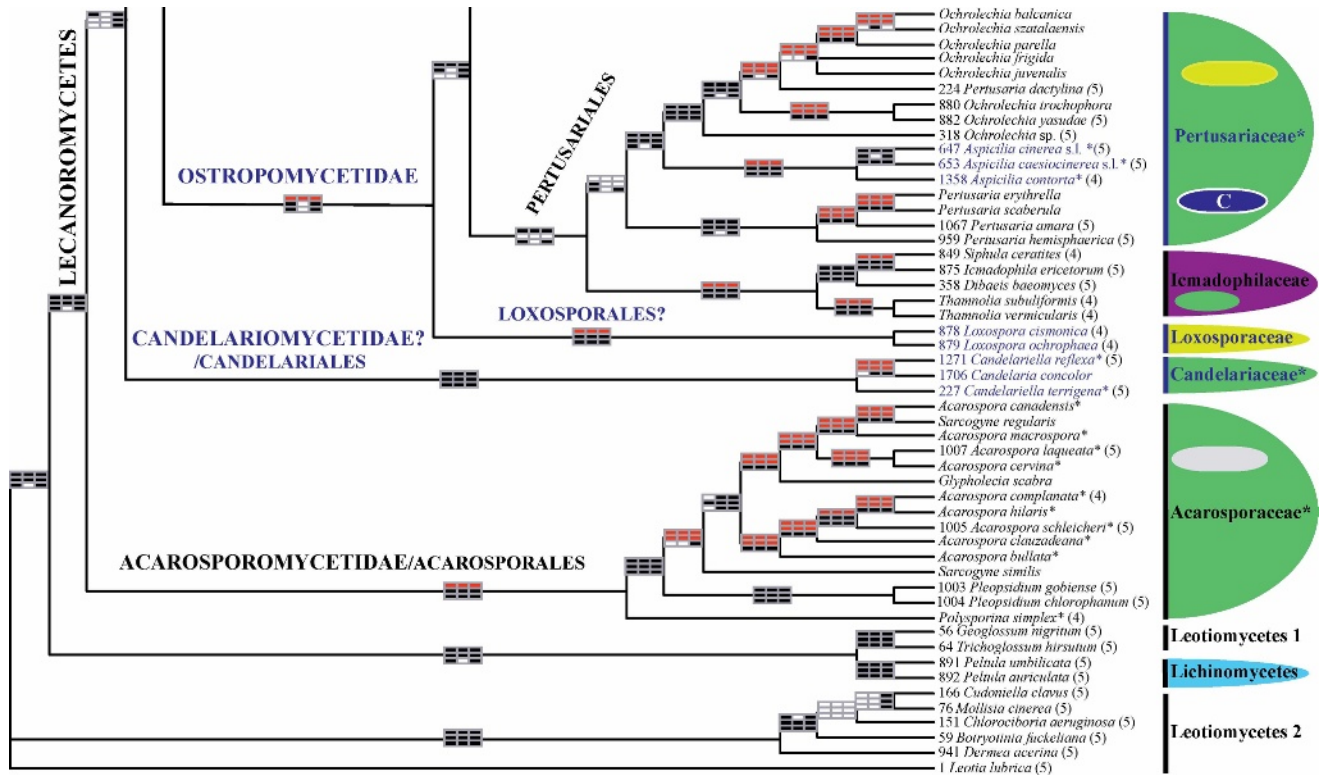


FIG. 1. Phylogenetic relationships among 264 putative members of the Lecanoromycetes based on Bayesian analyses of the combined nucSSU, nucLSU, mitSSU, *RPB1* and *RPB2* sequences (5+4+3-gene dataset) and 10 species used as outgroup (Geoglossaceae, Lichinomycetes and Leotiomycetes). This cladogram resulted from a 50% majority rule consensus of 30 000 trees sampled with Bayesian MCMCMC (SUPPLEMENT 1). Numbers in parentheses after taxon names indicate the dataset in which they were included: 5 refers to taxa present in the 5-, 5+4- and 5+4+3-gene datasets, and 4 refers to taxa present in the 5+4- and 5+4+3-gene datasets. When no numbers are found after names, taxa were included only in the 5+4+3-gene supermatrix. Stars indicate genera and families with lichenicolous members. Taxa at the tip of the tree shown in blue indicate phylogenetic placements that are newly revealed or significantly supported compared to previous studies. Taxa in blue at the family and higher levels indicate suggested changes in their circumscription and ranking that needs to be incorporated in future classifications of the Ascomycota. Names followed by a question mark indicate potential changes for future consideration. The nine-box grids on internodes indicate support with different phylogenetic methods (column 1 [boxes 1, 4, 7] = bootstrap values calculated with RAxML, column 2 [boxes 2, 5, 8] = bootstrap values calculated with PHYML, column 3 [boxes 3, 6, 9] = posterior probabilities calculated with MrBayes) based on different datasets (top row [boxes 1–3] being the smallest dataset [111 taxa] but with the least amount of missing data, and the bottom row [boxes 7–9] being the largest dataset [274 taxa] with the largest amount of missing data). Red boxes indicate cases where internodal support is not applicable due to at least one of the (usually two) immediately downstream branches being absent in the 188 or the 111 taxa datasets compared to the 274 taxa dataset. Black boxes indicate RAxML bootstrap values $\geq 70\%$ (column 1), PHYML bootstrap values $\geq 70\%$ (column 2) or MrBayes posterior probability values $\geq 95\%$ (column 3). White boxes indicate RAxML bootstrap values $< 70\%$, PHYML bootstrap values $< 70\%$ or MrBayes posterior probability values $< 95\%$. Colors on the right side of the figure indicate major types of primary photobionts associated with mycobionts within an order/family/monophyletic group based on available records for members classified in these taxa, even if not included in the tree. Presence of secondary photobionts (different genera of cyanobacteria) is indicated by a dark blue box (*Scytonema/Stigonema*), a circle (*Nostoc*) and an oval (*Calothrix*).

tion of the Graphidales (Ostropales 2; well supported monophyletic group including Graphidaceae, Asterothyriaceae [= Solorinellaceae; Henssen and Lücking 2002] and Thelotremaaceae in FIG. 1) and the Gyalectales (a poorly supported monophyletic group in FIG. 1, that would include the Coenogoniaceae, Gyalectaceae and Phlyctidaceae), thus partly reflecting the earlier classifications by Henssen and Jahns

(1974) and Sherwood (1977). However this three-order classification would remove the use of Ostropales *s.l.* for a well supported monophyletic group of lichen-forming fungi preferentially associated with *Trentepohlia*, (FIG. 1), which would leave this important internode and associated putative synapomorphy without a name and commonly used rank. An alternative solution to this problem would be the

use of suborders Graphidineae (Ostropales 2), Gyalectineae (Gyalectales) and Stictidineae (Ostropales 1) within the Ostropales *s.l.* as phylogenetically circumscribed here. Simultaneous inclusion of Odonotremataceae and Gomphillaceae in phylogenetic studies is necessary before any changes to the classification of the Ostropales *s.l.* are made.

The Ostropales *s.l.* includes morphologically and ecologically diverse lichens. Lücking et al (2004) demonstrated that the Gomphillaceae, with anastomosing paraphyses, are part of this group, and Grube et al (2004) have shown that the perithecial Porinaceae, with unitunicate asci and unbranched true paraphyses, also belongs to this clade. Lumbsch et al (2004b) confirmed that the mazaediate genus *Nad-vornikia* is a member of the Thelotremataceae and thus the Ostropales *s.l.* The genus *Phlyctis* was placed traditionally in the Lecanorales due to its amyloid hymenium and chlorococcoid photobiont; however its thallus and apothecial structure are more reminiscent of the Ostropales *s.l.* (RL unpublished) therefore supporting its placement in the latter group (Gyalectaceae).

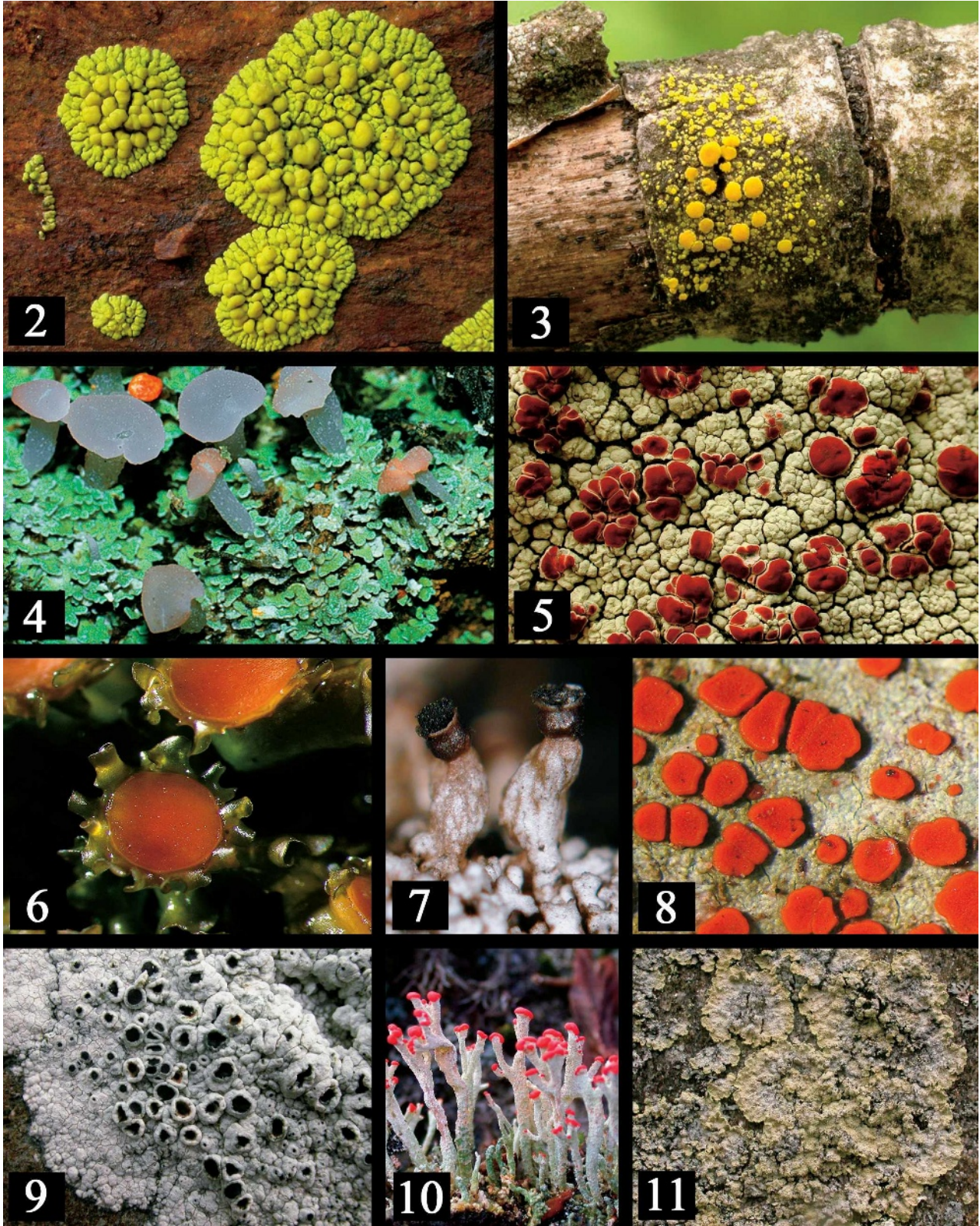
Our study shows a well supported sister clade relationship of Pertusariaceae (with nonmonophyletic *Ochrolechia* and *Pertusaria*) and Icmadophilaceae, to form the order Pertusariales (reconstructed as paraphyletic in Wedin et al [2005]) and the unexpected placement of *Aspicilia* (Hymeneliaceae) nested within the Pertusariaceae. Wedin et al (2005) and Hofstetter et al (2007) also suggested a close affinity among *Aspicilia* and members of the Pertusariaceae and Icmadophilaceae but without obtaining strong support for this relationship. *Aspicilia* was shown to be outside the family Hymeneliaceae more than 10 y ago based on morphological and isozyme data (Lutzoni and Brodo 1995). The current circumscription of the Hymeneliaceae and Pertusariaceae needs to be updated accordingly.

The Baeomycetaceae (with an uncertain placement in the Ascomycota according to Eriksson 2006) is delimited as monophyletic and a highly supported lineage (*Phyllobaeis* [FIG. 4] and *Baeomyces*) in our phylogeny (FIG. 1). *Arthrorhaphis* is also part of this subclass, although an accurate placement in the Ostropomycetidae remains unresolved. The latter is true for the Hymeneliaceae and Agryiales. Based on ribosomal genes Kauff and Lutzoni (2002) proposed an elevation of the Baeomycetaceae (represented in their tree by *Baeomyces placophyllus*) to the order level (Baeomycetales) in the Ostropomycetidae. This suggestion is confirmed by our study; however some putative close relatives of the Baeomycetaceae (*Ainoa* and *Anamylopsora*) were not included. The placement of *Arthrorhaphis citrinella* (a juvenile parasite of

Baeomyces) in the Ostropomycetidae, where two of its hosts belong, also was unexpected given the different ascomatal structures (see also Wedin et al 2005).

Our study also shows that *Loxospora* is part of the most basal divergence within the Ostropomycetidae (with significant support values, FIG. 1). Members of this genus have coccalean green algae and somewhat spirally arranged ascospores. This novel phylogenetic affinity revealed by this study is not surprising due to *Loxospora's* (Loxosporaceae) greater similarity (thallus structure) to Pertusariaceae than to Lecanorales, where this taxon is classified currently (Eriksson 2006). *Loxospora* was re-established as a genus by Hafellner (1984) and previously was classified in the Haematommataceae. Staiger and Kalb (1995) noticed anatomical characters that were not shared by other members of this family (e.g. the genus *Haematomma*) and created a separate family to accommodate *Loxospora*. Loose and thick paraphyses, predominance of elatinic acid and the presence of wide and grouped ascogenous hyphae in ascomatal primordia (cf. Brodo and Henssen 1995) are further characters that circumscribe this newly reconstructed lineage in the Ostropomycetidae. Because none of the members of the Haematommataceae has been included in phylogenetic analyses we cannot justify the exclusion of the Loxosporaceae from the Haematommataceae.

Lecanoromycetidae.—The delimitation of the Lecanoromycetidae is ambiguous due to a lack of support for the phylogenetic placement of the Catillariaceae (*Sporastatia*; Rambold and Triebel 1992, Eriksson 2006), Fuscideaceae, Ophioparmaceae, Rhizocarpaceae and Umbilicariaceae (FIG. 1). An early divergence of the Rhizocarpaceae as revealed here and in previous studies (Reeb et al 2004, Lutzoni et al 2004) was postulated by Honegger (1980) based on characters of the ascus tip. Our phylogeny confirms that the narrowest delimitation of the Lecanoromycetidae contains at least three main lineages (Miadlikowska and Lutzoni 2004, Hofstetter et al 2007): the Lecanorales, Peltigerales (and most closely related group, including the Lecideaceae and Porpidiaceae) and Teloschistales. If the current topology receives high support values in future studies, the Fuscideaceae-Ophioparmaceae-Umbilicariaceae and the Rhizocarpaceae-Catillariaceae monophyletic groups should be classified as separate orders (Umbilicariales and Rhizocarpales) within the Lecanoromycetidae. If future studies show that it is not possible to encompass these two new orders within a monophyletic Lecanoromycetidae it is likely that each group would have to be recognized at the subclass level



FIGS. 2–11. Lichen-forming members of the Lecanoromycetes. 2. *Pleopsidium chlorophanum*, Acarosporomycetidae, Acarosporales, Acarosporaceae (photo by E. Timdal). 3. *Candelariella lutella*, Candelariaceae (photo by E. Timdal). 4. *Phyllobaeis imbricata*. Close-up of fruiting bodies, Ostropomycetidae, Baeomycetaceae (photo by R. Lücking). 5. *Ophioparma ventosa*, Ophioparmaceae (photo by E. Timdal). 6. *Leptogium burgessii*. Close-up of fruiting bodies, Lecanoromycetidae,

(Umbilicariomycetidae and Rhizocarpomycetidae). Therefore no matter how these two monophyletic entities will be resolved in future studies, they both need to be recognized at least at the ordinal level, as proposed here.

Umbilicariomycetidae?/Umbilicariales.—Some novel and interesting relationships are found in the group containing the Umbilicariaceae. Placement of the Fuscideaceae outside Teloschistaceae was suggested by Lutzoni et al (2004), Reeb et al (2004) and Wedin et al (2005) and is confirmed in this study. We found it interesting that *Fuscidea* and *Maronea*, despite striking differences in ascocarp anatomy and spore number per ascus, share a unique ascus type and a distinctive type of epihymenial pigmentation, which led Hafellner (1984) to the description of the family Fuscideaceae. Therefore similarities in the ascus structure between Teloschistales and Fuscideaceae were misleading and turned out to be homoplastic.

Three other groups of lichen-forming fungi fall within the Fuscideaceae-Umbilicariaceae clade: Ophioparmaceae (represented by *Ophioparma* [FIG. 5], *Boreoplaca* [Lecanoromycetes genera *inc. sed.*] and *Hypocenomyce* [Lecideaceae] [FIG. 1]). Presence of an amyloid ascus with a tholus exhibiting a strongly amyloid dome in these otherwise morphologically and anatomically distinct genera was used by Wedin et al (2005) to support the monophyly (strong PP support) of *Boreoplaca*, *Hypocenomyce* and *Ophioparma* to form the extended family Ophioparmaceae. Lumbsch et al (2004a) found in their study based on nuLSU and mitSSU data that the family Elixiaaceae (with a single species *Elixia flexella*, not included in this study) formed a well supported monophyletic group within the family Umbilicariaceae and that the former family circumscription including species with foliose (umbilicate) thalli, possibly comprised a sister group of crustose species.

Rhizocarpomycetidae?/Rhizocarpaceae.—This order proposed here includes Rhizocarpaceae and *Sporastatia*. While excluding *Sporastatia* from the family Acarosporaceae, Hafellner (1995) already questioned its placement in the Catillariaceae, which could not be tested here. A close affiliation between *Sporastatia* and *Rhizocarpon* first was shown by Reeb et al (2004)

and corroborated by Buschbom and Mueller (2004) and Lutzoni et al (2004). Both taxa are strictly crustose and distinctly areolate. While members of the Rhizocarpaceae often form large, hyaline to brown, transversely septate to distinctly muriform ascospores, *Sporastatia* develops multiple, hyaline ascospores. The placement of *Catolechia* within *Rhizocarpon* (FIG. 1) is interesting because this genus, with thick squamulose thalli, reveals a strong pigmentation of the spore wall around the septum of mature ascospores (torus) but lacks the typical gelatinous perispore (“halo”). A closer relationship of *Catolechia* and *Rhizocarpon* rather than with *Buellia* was assumed by Hafellner (1978). Noteworthy in this group is also the tendency toward lichenicolous growth (e.g. in *Rhizocarpon* and *Epilichen*; Hafellner and Poelt 1976, Lawrey and Diederich 2003, Santesson et al 2004) in several parallel lineages however in none of them is the lichenization lost completely.

Peltigerales.—Strongly supported as monophyletic in all analyses, the order Peltigerales comprises two suborders, the Peltigerineae and Collematineae, as defined by Miadlikowska and Lutzoni (2004) based on ribosomal genes and confirmed by Hofstetter et al (2007) based on a five-locus analysis. Peltigerineae, which differs from the Collematineae by the development of conspicuous heteromerous thalli, the common occurrence of tripartite symbioses with *Nostoc* as a secondary photobiont (cephalodia), the presence of bipartite associations with green algae (*Coccomyxa*) and the production of diverse secondary compounds (mostly triterpenoids), includes Lobariaceae, Peltigeraceae and Nephromataceae. For the first time the monophyly of *Solorina* (FIG. 1) is shown here to receive high bootstrap values. We found that *Polychidium*, a member of the Placynthiaceae (classified in the Collematineae), belongs to the Peltigerineae and we confirm that *Massalongia* is placed also in this suborder; however their sister relationship and phylogenetic placement within the Peltigerineae remains uncertain. The monophyly of the Collematineae, the second suborder within the Peltigerales, became significantly supported only when more members from each family were incorporated in the phylogenetic analyses (10 taxa in the 5-gene dataset

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Peltigerales, Collemataceae (photo by R. Lücking). 7. *Tholurna dissimilis*. Close-up of fruiting bodies, Lecanoromycetidae, Teloschistales, Caliciaceae (photo by E. Timdal). 8. *Pyrrhospora russula*, Lecanoromycetidae, Lecanorales, Lecanoraceae (photo by R. Lücking). 9. *Tephromela atra*, Lecanoromycetidae, Mycoblastaceae (photo by E. Timdal). 10. *Cladonia floerkeana*, Lecanoromycetidae, Lecanorales, Cladoniaceae (photo by E. Timdal). 11. *Lepraria membranacea*, Lecanoromycetidae, Lecanorales, Stereocaulaceae (photo by E. Timdal). All photographs by E. Timdal are available at http://www.toyen.uio.no/botanisk/lav/Photo_Gallery/PG_index.html.

vs. 19 in the 5+4+3-gene dataset). Collematineae as defined here includes the monophyletic Pannariaceae (*Degelia*, *Erioderma*, *Fuscopannaria*, *Parmeliella*, *Protopannaria* and *Psoroma*), Coccocarpiaceae (only *Coccocarpia* was sampled), Collemataceae (*Collema* and nonmonophyletic *Leptogium* [FIG. 6]) and Placynthiaceae (excluding *Polychidium*).

Lecideales.—Lecideaceae, intermixed with Porpidiaceae (*Porpidia*), appeared as a sister group of the Peltigerales (strongly supported in FIG. 1). This is surprising because the Lecideaceae seem to share no common features with members of the Peltigerales. Moreover the placement of *Porpidia* intermixed with *Lecidea* in the Lecideaceae, detected also by Buschbom and Mueller (2004), questions the recognition of the entire family Porpidiaceae based on ascus structures. A basal position of *Lecidoma* (former *Lecidea*) to Lecideaceae received only PP support in the 5+4-gene analysis. Both *Lecidoma* and *Porpidia* have asci with amyloid tube structures but of different features (Hafellner 1984), whereas in *Lecidea* this tube seems to be reduced to a minute structure in the tholus tip. These three genera have brown to dark ascospores, crustose to adpressed squamulose thalli with coccalean green algae, (*Asterochloris* and *Trebouxia*, Rambold et al 1998). In contrast to *Lecidea*, *Porpidia* species have prominent dark parathecial margins, halonate ascospores and intensely anastomosing paraphyses, while a carbonization of portions of the apothecia as in these two genera is not found in *Lecidoma*. Furthermore *Porpidia* and *Lecidea* are strictly saxicolous whereas *Lecidoma* grows on soil. Hafellner (1984) had introduced the monotypic family Lecidomataceae to accommodate the relatively unique genus *Lecidoma*.

Teloschistales.—The Letrouitiaceae, Megalosporaceae and Teloschistaceae forming a monophyletic group sister of the monophyletic Physciaceae is confirmed here for the first time (FIG. 1). These families differ considerably in the cortical pigmentation of their thallus. While the Physciaceae are diverse in their cortical pigmentation (mostly atranorin), predominance of anthraquinones is characteristic for the Teloschistaceae. Most representatives of the Teloschistaceae and Physciaceae are characterized by polar diblastic ascospores, which often display conspicuous endospore thickenings. *Letrouitia* (Letrouitiaceae) diverged earlier than *Megalospora* (Megalosporaceae) and Teloschistaceae. *Megalospora* is phenotypically different from the Teloschistales, especially in its peculiar ascus type (i.e. without any teloschistalean features, ascospores without internal thickenings, thallus chemistry and the lack of quinoid substances). *Caloplaca* is represented only by one

species here, and this phenotypically diverse genus and its relatives, *Fulgensia*, *Teloschistes* (both not included in this study) and *Xanthoria*, are all nonmonophyletic genera (Kasalicky et al 2000, Gaya et al 2003, Søchting and Lutzoni 2003, Gaya 2006).

Our results also confirm that the Caliciaceae, here represented by *Tholurna* (FIG. 7) and *Calicium*, are nested in the buellioid branch (*Buellia* and related genera) of the Physciaceae (Wedin et al 2002) and are not supported as a monophyletic group. Loss of active ascospore dispersal (i.e. evanescent asci) and evolution of mazaedial ascomata evidently occurred several times (e.g. Mycocaliciales shown to be sister of the Eurotiomycetes by Geiser et al [2006]), including in the buellioid clade. Placement of *Amandinea* within *Buellia* (see also Helms et al [2003]) raises doubts about the validity of the former genus, which is distinguished only by spermatial characters; however *Amandinea* species included in the analysis is not the generic type (*A. conioops*). Although the genus *Buellia* s.l. is extremely diverse (e.g. Marbach 2000) and pending a proper sampling in phylogenetic study, we propose to maintain the current classification. A close relationship between the genus *Pyxine* and *Dirinaria* was mentioned by Scheidegger et al 2001 and demonstrated in a phylogenetic study by Helms et al (2003). Both taxa have delayed ascospore septum formation, shared with the genus *Hafellia*, which is nested in the buellioid clade.

We propose here to establish two suborders within the Teloschistales, Physciineae and Teloschistineae. The phylogeny presented here (FIG. 1) shows two main lineages within the Physciineae, a predominantly buellioid clade (Caliciaceae) and a rinodinoide clade (*Rinodina* and related genera, Physciaceae).

Lecanorales.—The order Lecanorales includes eight families (FIG. 1), Cladoniaceae, Lecanoraceae, Mycoblastaceae, Parmeliaceae, Psoraceae, Ramalinaceae, Sphaerophoraceae and Stereocaulaceae. At least one further large family, the emended Pilocarpaceae (not sampled for this study), which also includes members of the Micareaceae and Ectolechiaceae (Eriksson 2006), was found to be closely related to Ramalinaceae by Andersen and Ekman (2004, 2005) and therefore is part of the Lecanorales.

The well supported Parmeliaceae is the most speciose family within the Lecanorales and comprises mostly foliose to fruticose lichens associated exclusively with coccalean green algae (predominantly *Trebouxia*, Rambold et al 1998). A diagnostic character for this family is the presence of a cupula in the ascospores, a well differentiated cup-shaped hyphal structure beneath the hypothecium (Henssen and Jahns 1974). All members also share a similar type of

ascus with a broadly shaped nonamyloid masse axiale. A series of papers recently reviewed the previously controversial classification within this family (e.g. Crespo et al 2001; Blanco et al 2004a, b, 2005, 2006; Thell et al 2004). Blanco et al (2006) recently demonstrated that the taxonomic value of key characters (presence of usnic acid and atranorin in the cortex of the thallus, occurrence of pseudocyphellae and pored epicortex) traditionally used to classify members of the Parmeliaceae at generic and suprageneric levels has been overemphasized in previous classifications. Most of the cetrarioid genera are grouped together, sister of *Dactylina* (FIG. 1). Another well supported monophyletic group includes *Alectoria* and *Bryoria*, both with fruticose, pendent to shrubby thalli and distinguished by cortical compounds (usnic acid vs. amorphous melanin-like substances) and hymenial characters including ascospore pigmentation (pigmented vs. hyaline). The lack of support for most deep internodes within the Parmeliaceae is due to the little divergence recorded within this strongly supported monophyletic group. ITS can be aligned across members of this family for example. Therefore the fastest evolving sites of the nucLSU, nucSSU and mitSSU, which would be most appropriate to increase phylogenetic confidence in this portion of the tree, had to be excluded from these analyses due to the presence of indels rendering positional homology too uncertain in these regions (a typical problem of broad selection of taxa that also include a large group of closely related taxa).

The Lecanoraceae comprise *Lecanora*, *Lecidella* and *Pyrrhospora* (FIG. 8) in our tree. This relationship is supported by tholus amyloidity in the ascus and the presence of a broad masse axiale, common features in all three genera. The sister relationship of *Mycoblastus* and *Tephromela* (FIG. 9), as also found by Wedin et al (2005), is unexpected. Both genera were classified in separate families by Hafellner (1984). They differ considerably in their ascospores (large and thick-walled in *Mycoblastus* vs. small and thin-walled in *Tephromela*) and secondary chemistry (*Mycoblastus* partly with chinoid substances vs. *Tephromela* partly with the rare α -collatolic acid) but share the tar-black pigmentation of the epihymenium, which can extend downward into the hymenium. The inclusion of further taxa will show whether two separate families, Tephromelataceae and Mycoblastaceae, are needed.

The monophyletic Psoraceae, Ramalinaceae and Sphaerophoraceae as well as their interfamilial relationships are all well supported. Our analyses support the Ramalinaceae to include the Bacidiaceae, as outlined by Ekman (2001, but see Andersen and Ekman 2005). *Lopezaria*, considered to be a genus of uncertain position within the Lecanoromycetes

(Eriksson 2006), is shown here to be a member of the Ramalinaceae. *Lopezaria* is similar in ascospore type and ecology to *Megalospora* but apparently not closely related to the latter, and its large, thick-walled ascospores thus have evolved independently. Apothecial features are otherwise similar to those of certain tropical *Bacidia* species and support its placement in the Ramalinaceae. Except for *Lopezaria*, asci in this group are of similar type, but diverse growth forms include crustose, squamulose and fruticose thalli. Hafellner (1988) regarded Lecaniaceae (as an available family name for crustose bacidioid lichens with lecanorine apothecia) and Ramalinaceae as members of the same evolutionary lineage in term of thallus evolution. *Scoliciosporum*, currently classified within the Lecanoraceae and *Strangospora*, currently with an uncertain placement in the Lecanoromycetes (Eriksson 2006), are shown here as members of the Lecanorales. Hafellner (1984) had introduced the family Scoliciosporaceae and later (Hafellner 1995) discussed a possible closer relationship of *Strangospora* and *Scoliciosporum*, both with similar ascomata and *Lecanora*-type asci, but the type species of these genera have different ascospores (polyspored one-celled vs. eight-spored phragmospore). The addition of more taxa from these genera is needed to resolve their affiliation within the Lecanorales.

Results from this study do not support previous subordinal circumscriptions within the Lecanorales (Hafellner et al 1993). Cladoniineae as shown here includes Cladoniaceae (*Cetradonia*, *Cladonia* [FIG. 10] and *Pycnothelia*) and Stereocaulaceae (*Lepraria* [FIG. 11], *Stereocaulon* and *Squamarina*). Both families share the same main photobiont type identified as *Asterochloris* (Rambold et al 1998) and, with the exception of *Squamarina*, asci with tholi provided with amyloid tube structures. Discovered for the first time by Ekman and Tønsberg (2002) the close relationship of *Lepraria* and *Stereocaulon* was supported only in the 5+4-gene phylogeny. For the first time *Squamarina* is well supported as being related to the Stereocaulaceae (shown by Stenroos and DePriest 1998 but not supported). However the inclusion of *Squamarina* in Stereocaulaceae is incongruent with morpho-anatomical characters, such as ascomatal and ecological attributes (e.g. all *Squamarina* grow on calcareous substrates). While the Cladoniaceae and Stereocaulaceae previously were placed in the informal *Micarea* group owing to ascus characters, Squamarinaceae was recognized as a separate group (Hafellner et al 1993). Ekman and Tønsberg (2002) demonstrated that the Lecanoraceae are more closely related to the Cladoniaceae and Stereocaulaceae than suggested by Hafellner et al (1993), who included the Lecanoraceae together with

the Parmeliaceae in the suborder Lecanorineae. Thus in our analysis the Cladoniineae are nested within the Lecanorineae using the previous subordinal concept (Poelt 1974). It is too early to propose a revised subordinal classification within the Lecanorales.

Photobiont selectivity as a taxonomic character.—Although photobiont relationships and life strategy characters were mainly disregarded in previous taxonomic treatments of the lichen-forming fungi, photobiont associations are highly structured across the Lecanoromycetes phylogeny (FIG. 1, similar to what was anticipated for the Lecanorales by Rambold et al 1998) suggesting that these symbiotic interactions are the result of a highly selective process and where shifts from one main type of photobiont to another were rare during the evolution of the lichen symbiosis. Large monophyletic groups of the Lecanoromycetes have preferences for certain types of photobionts (FIG. 1). For example members of the Ostropales *s.l.*, with mostly crustose thalli and high species diversity in wet tropical habitats, are predominantly associated with photobionts of the Trentepohliaceae, which do not occur as photobionts in the Acarosporomycetidae, Candelariomycetidae, Lecanoromycetidae, Rhizocarpaceae and Umbilicariales. Only a few lineages in this order, including Gomphillaceae, Asterothyriaceae (with *Gyalidea*), *Diploschistes*, *Phlyctis*, and *Stictis*, were able to switch from filamentous to chlorococcalean green algae or in rare cases (*Petractis*) to cyanobacteria (*Scytonema*) as their photosynthetic partner. Mycobionts of the Peltigerales (Lecanoromycetidae) have strong preferences for cyanobacteria (mostly *Nostoc*). In the Peltigerales bipartite associations with cyanobacteria seem to be the ancestral state, which either is maintained or switched repeatedly to coccalean green algae (*Coccomyxa* and *Dictyochloropsis* in *Peltigera*, *Lobaria* and *Sticta*), resulting either in phycosymbiodemes, tripartite symbioses or bipartite species that associate only with green algae in the later stage of development (Miadlikowska and Lutzoni 2004).

Photobiont-mycobiont patterns of associations can greatly contribute to our understanding of relationships and evolution of lichen-forming fungi, as already suggested by Rambold et al (1998). However this will require a re-examination of existing records of green algae and cyanobacteria reported to be associated with lichen-forming taxa based on recent phylogenetic treatments of these photobionts.

Ascomatal features as taxonomic characters.—As already reported by Reeb et al (2004), highly polyspor-

ous asci (i.e. > 100 spores/ascus) evolved independently in several lineages of the Lecanoromycetes (e.g. in *Acarosporaceae*, *Biatorella*, *Maronea*, *Sporastatia*, *Strangospora* and *Thelocarpon*). Less pronounced polyspory is found in many other groups throughout the Lecanoromycetes (e.g. in *Candelariella*, *Gyalidea* [species formerly assigned to *Solorinella*], *Gyalideopsis*, members of *Buellia*, *Caloplaca*, *Catillaria*, *Lecanora*, *Rinodina* and other genera). Unusually large ascospores (e.g. in *Asterothyrium*, *Megalospora*, *Mycoblastus*, *Pertusaria*, *Psorotheciopsis* and *Solorina*) or long-filiform ascospores (e.g. in *Bacidina*, *Bapalmuia*, *Stictis* and *Gomphillus*) also have evolved independently many times within the Lecanoromycetes.

Our study confirms that different types of asci can occur in a single lineage of closely related taxa or that the same ascus type can be found in distinct lineages (homoplasy). The widespread occurrence of the *Lecanora* type ascus (in Candelariaceae, *Lecanora*, Parmeliaceae, *Physcia*, *Pleopsidium*, *Scoliciosporum* and *Strangospora*) suggests that this type of ascus could be ancestral (Chadefaud et al 1968) as discussed by Wedin et al (2005) and therefore residual in many lineages of the Lecanoromycetes.

Characters of ascomatal architecture and pigmentation are also of varying significance for classification in the Lecanoromycetes. While a cupula structure in the ascomata of the Parmeliaceae is a characteristic feature of the whole group, such structures also occur intermittently in other Lecanoromycetes and can be found in species of *Caloplaca*, *Collema*, *Lecanora* and *Rinodina*. Although perithecioid ascomata characterize the large family Porinaceae, such ascomata also are found in smaller unrelated genera in the Ostropomycetidae (e.g. *Belonia*, *Protothelenella*, *Thelenella* or *Topelia*).

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SUPPLEMENT 1

MATERIALS AND METHODS

Gene and taxon sampling.—We collected molecular data for five different loci: nucSSU, nucLSU, mitSSU, *RPB1* and *RPB2*. Three different taxon sets (according to the availability of sequence data for these five genetic loci) were used for phylogenetic analyses (TABLE I). Taxa with all five genes complete or partially available (139) were retrieved from the AFTOL WASABI database (<http://ocid.nacse.org/research/aftol>) to form the 5-gene dataset. For the 5+4-gene dataset, the 5-gene dataset was extended with taxa for which at least four of the 5 genes were available, resulting in a total of 198 taxa: 174 taxa from AFTOL and 24 taxa from GenBank. The 5+4+3-gene dataset was generated by adding to the 5+4-gene dataset all available taxa with at least three of the five targeted genes, resulting in a total of 284 taxa: 180 taxa from AFTOL and 104 taxa from GenBank. GenBank sequences shorter than 100 base pairs were not included in our datasets. After performing congruence tests (see phylogenetic analyses), the resulting three datasets contained 111 taxa with five genes, 188 taxa with five and four genes, and 274 taxa with five, four and three genes.

Our largest 5+4+3-gene dataset (274 taxa) includes 261 members from three recognized subclasses within the Lecanoromycetes: Acarosporomycetidae (15 taxa), Ostropomycetidae (50 taxa) and Lecanoromycetidae (192 taxa); three genera (*Boreoplaca*, *Lopezaria* and *Strangospora*) with unknown placement in the Lecanoromycetes; four representatives of the family *Baeomycetaceae*, a family of uncertain position within the Ascomycota according to Eriksson

(2006); and 10 outgroup genera selected from the Lichinomycetes (Peltulaceae) and Leotiomycetes (including Geoglossaceae). Our choice of outgroup taxa was based on Spatafora et al (2006) showing a sister relationship between the Lecanoromycetes and Geoglossaceae + Peltulaceae. Within the Acarosporomycetidae we sampled five of seven genera. For the Ostropomycetidae, taxa from all orders, except the Trichotheliales, were included, representing nine of 14 recognized families and 22 of 128 genera classified in orders Agyriales, Gyalectales, Ostropales and Pertusariales. We also included two members of the family Hymeneliaceae (*Aspicilia* and *Hymenelia*) with uncertain placement in the Ostropomycetidae according to Eriksson (2006). Our sampling for the Lecanoromycetidae encompasses 19 of 29 families from the order Lecanorales; all families recognized in the order Peltigerales including suborders Collematineae (four families) and Peltigerineae (three families); and the order Teloschistales (three families). Three families of uncertain positions in the Lecanoromycetidae (Eriksson 2006), the Fuscideaceae, Phlyctidaceae and Umbilicariaceae, also were sampled (TABLE II).

Molecular data and phylogenetic analyses.—From a total of 1210 sequences included in this study 436 (36%) are published here for the first time. Sources for laboratory protocols and primers used for generating these new sequences, as well as information about alignments can be found in Lutzoni et al (2004) and Hofstetter et al (2007).

TABLE I. Summary of datasets including number of taxa, length of alignments and number of analyzed characters for each gene separately and when combined after removal of conflicting taxa. The 5-gene dataset includes taxa for which complete or partial data from all five loci (nucSSU, nucLSU, mitSSU, *RPB1* and *RPB2*) were available. The 5+4-gene and 5+4+3-gene datasets include taxa for which at least four or three genes were sequenced, respectively.

Dataset/taxa+alignment		5-gene dataset	5+4-gene dataset	5+4+3-gene dataset
Number of taxa	Number of taxa before testing for congruence	139	198	284
	Number of taxa after testing for congruence	111	188	274
nucSSU	Alignment length	7445	7228	7215
	Characters included	1125	1085	1071
nucLSU	Alignment length	5162	5151	5096
	Characters included	1141	1121	1122
mitSSU	Alignment length	2635	2691	2862
	Characters included	471	437	445
<i>RPB1</i>	Alignment length	3159	3243	3229
	Characters included	2688	2676	2673
<i>RPB2</i>	Alignment length	2291	2349	2409
	Characters included	1932	1851	1803
Combined data	Alignment length	20 692	20 662	20 811
	Characters included	7357	7170	7114
	percent of missing data	17	26	37

TABLE II. Taxa included in this study according to the classification by Eriksson 2006 (Outline of Ascomycota, <http://www.fildmuseum.org/myconet/outline.asp>) and sequence source information. GenBank identification numbers are provided for sequences obtained from GenBank, and accession numbers are provided for new sequences generated as part of the Assembling the Fungal Tree of Life project (AFTOL). Sequences of *RPBI* and *RPB2* are divided into two amplicons (A-F, F-G and 5-7, 7-11, respectively) to indicate parts for these two genes that were included in this study. In the source column GB refers to GenBank as a source of all sequences for particular taxon, whereas numbers refer to the AFTOL database. For each family number of genera included in this study is shown before the slash and a total number of recognized genera based on Eriksson (2006) is shown after the slash. ? = the position of the taxon is uncertain in Eriksson's classification (2006).

Classification (Eriksson 2006)		Taxon	Source	nucSSU	nuLSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Lecanoromycetes										
Lecanoromycetidae										
Acarosporales										
Acarosporaceae 5/7										
		<i>Acarospora bullata</i>	GB	52699728	52699687	—	—	—	52699767	52699767
		<i>Acarospora canadensis</i>	GB	52699729	52699688	—	—	—	52699769	52699769
		<i>Acarospora cervina</i>	GB	52699730	52699689	—	—	—	52699771	52699771
		<i>Acarospora clauzadeana</i>	GB	52699735	52699694	—	—	—	52699787	52699787
		<i>Acarospora complanata</i>	GB	15216664	15216665	46411448	—	—	52699773	52699773
		<i>Acarospora hilaris</i>	GB	52699731	52699690	—	—	—	52699775	52699775
		<i>Acarospora laqueata</i>	1007	52699732	52699691	DQ991757	DQ782860	DQ782860	52699777	52699777
		<i>Acarospora macrospora</i>	GB	52699733	52699692	—	—	—	52699779	52699779
		<i>Acarospora schlaicheri</i>	1005	52699734	52699693	46411449	DQ782859	—	52699773	52699773
			345							
		<i>Glypholecia scabra</i>	GB	52699739	52699699	—	—	—	52699811	52699811
		<i>Pleopsidium</i>	1004	DQ525541	DQ842017	DQ991756	DQ782858	DQ782858	DQ525474	DQ525474
		<i>chlorophanum</i>								
		<i>Pleopsidium gobiense</i>	1003	DQ525573	DQ883698	DQ991755	DQ883746	DQ883746	DQ525452	DQ525452
		<i>Polysporina simplex</i>	GB	52699748	52699709	62005392	—	—	52699858	52699858
		<i>Sarcogyne regularis</i>	GB	52699751	52699712	—	—	—	52699869	52699869
		<i>Sarcogyne similis</i>	GB	52699753	52699714	—	—	—	52699871	52699871
Lecanoromycetes										
Lecanoromycetidae										
Lecanorales										
		? <i>Arthrorhaphidaceae</i> 1/1	GB	12025058	12025059	62005365	—	—	—	—
		<i>Calicium viride</i>	GB	15216680	44903359	33304586	—	—	52699791	52699791
		<i>Thoburnia dissimilis</i>	1695	DQ973002	—	DQ972974	—	—	DQ973086	—
		<i>Sporastatia polyspora</i>	GB	52699756	52699716	46411479	—	—	52699879	52699879
		<i>Sporastatia testudinea</i>	GB	52699757	52699717	46411480	—	—	52699881	52699881
		<i>Cetradonia</i> sp.	1657	DQ973003	DQ973026	DQ972975	DQ973050	DQ973050	DQ973087	—

TABLE II. Continued

Classification (Eriksson 2006)	Taxon	Source	nucSSU	nuclSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Cladoniaceae 6/15	<i>Cladia retipora</i>	GB	3360250	34148718	34148561	—	—	—	—
	<i>Cladonia caroliniana</i>	3	46411405	46411429	46411379	DQ782816	DQ782816	46451691	46451691
	<i>Cladonia rangiferina</i>	GB	10441368	46852258	32141054	—	—	—	—
	<i>Heterodea muelleri</i>	GB	10441369	34148723	34148568	—	—	—	—
	<i>Metus conglomeratus</i>	GB	10441370	34148733	34148584	—	—	—	—
	<i>Pilophorus cereolus</i>	GB	10441371	34148737	34148590	—	—	—	—
	<i>Pilophorus strumaticus</i>	GB	10441373	34148738	34148591	—	—	—	—
	<i>Pycnothelia papillaria</i>	1377	DQ983481	DQ986800	DQ986783	DQ986856	—	DQ992473	DQ992473
	<i>Crocymia pyxinoidea</i>	111	46411418	46411442	46411380	DQ883735	—	DQ883748	DQ883748
	<i>Candelaria concolor</i>	1706	—	DQ986791	DQ986806	—	—	DQ992419	DQ992419
Crocyiaceae 1/1	<i>Candelariella reflexa</i>	1271	DQ912309	DQ912331	DQ912272	DQ912354	DQ912354	DQ912380	DQ912380
	<i>Candelariella terrigena</i>	227	DQ986730	DQ986745	DQ986884	DQ986816	—	DQ992427	DQ992427
	<i>Lecanora achamana</i>	1693	DQ973004	DQ973027	DQ972976	DQ973051	DQ973088	—	—
	<i>Lecanora concolor</i>	GB	52699741	52699702	—	—	52699826	52699826	52699826
	<i>Lecanora contractula</i>	877	DQ986741	DQ986746	DQ986898	DQ986817	—	DQ992428	DQ992428
	<i>Lecanora hybocarpa</i>	639	DQ782883	DQ782910	DQ912273	DQ782829	DQ782871	DQ782871	DQ782871
	<i>Lecanora intumescens</i>	GB	9828144	37960800	32141065	—	—	—	—
	<i>Lecanora polytropa</i>	1798	DQ986701	DQ986792	DQ986807	—	DQ992418	DQ992418	DQ992418
	<i>Lecidella elaeochroma</i>	1275	DQ986719	DQ986747	—	DQ986818	—	DQ992429	DQ992429
	<i>Lecidella euphorea</i>	1374	DQ983482	—	DQ986784	DQ986857	—	DQ992479	—
Lecideaceae 2/9	<i>Lecidella meiococca</i>	GB	9828141	37960801	32141066	—	—	—	—
	<i>Pyrrhospora quercea</i>	GB	9828142	37960817	32141081	—	—	—	—
	<i>Scoliciosporum umbrinum</i>	GB	9828145	52699715	32141084	—	—	—	—
	<i>Hypocenomyce scalaris 1</i>	687	DQ782886	DQ782914	DQ912274	DQ782854	DQ782854	DQ782875	DQ782875
	<i>Hypocenomyce scalaris 2</i>	1025	—	DQ986748	DQ986861	DQ986819	—	DQ992430	DQ992430
	<i>Lecidea fuscoatra</i>	589	DQ912310	DQ912332	DQ912275	DQ912355	DQ912381	DQ912381	DQ912381
	<i>Lecidea laboriosa</i>	1388	DQ986727	—	DQ986882	DQ986821	—	DQ992432	DQ992432
	<i>Lecidea silacea</i>	1368	DQ986723	—	DQ986878	DQ986820	—	DQ992431	DQ992431
	<i>Loxospora cismonica</i>	878	DQ986742	DQ986749	DQ986899	—	—	DQ992433	DQ992433
	<i>Loxospora ochrophaea</i>	879	—	DQ986750	DQ986900	DQ986822	DQ986822	DQ992434	DQ992434
Mycoblastaceae 1/1	<i>Mycoblastus sanguinariis</i>	196	DQ782879	DQ912333	DQ912276	DQ782827	DQ782827	DQ782867	DQ782867
	<i>Ophioparma lapponica</i>	1707	DQ973005	DQ973028	DQ972977	DQ973052	DQ973052	DQ973089	—

TABLE II. Continued

Classification (Eriksson 2006)		Source	nucSSU	nuLSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Parmeliaceae 27/89									
	<i>Alectoria ochroleuca</i>	209	DQ983483	DQ986801	DQ986785	DQ986858	DQ986858	DQ992474	DQ992474
	<i>Asahinea scholanderi</i>	235	—	DQ973029	—	DQ973053	DQ973053	DQ973090	DQ973090
	<i>Bryoria trichodes</i> 1	205	DQ986728	DQ986751	DQ986883	DQ986823	—	DQ992438	DQ992438
	<i>Bryoria trichodes</i> 2	872	DQ986740	DQ986752	DQ986896	DQ986824	—	DQ992439	—
	<i>Canoparmelia caroliniana</i>	6	46411399	46411423	46411378	DQ782817	DQ782817	46451690	46451690
	<i>Cetraria islandica</i>	211	DQ912311	DQ912334	DQ912277	DQ912356	DQ912356	DQ912382	DQ912382
	<i>Dactylina arctica</i>	225	DQ983484	DQ986802	DQ986786	DQ986859	—	DQ992475	DQ992475
	<i>Evernia prunastri</i>	GB	6684446	6318536	15987426	—	—	—	—
	<i>Flavocetraria nivalis</i>	231	DQ883786	DQ883795	DQ912278	DQ883758	DQ883751	DQ883751	DQ883751
	<i>Flavoparmelia caperata</i>	2	464114043	46411428	46411382	DQ883778	46411493	46411493	46411493
	<i>Flavopunctelia flaventior</i>	317	DQ912312	DQ912335	DQ912279	DQ912357	—	—	DQ912383
	<i>Hypogymnia physodes</i>	195	DQ973006	DQ973030	DQ972978	—	—	DQ973091	DQ973091
	<i>Hypotrachyna caracensis</i>	312	DQ912313	DQ912336	DQ912280	DQ912358	DQ912358	DQ912384	DQ912384
	<i>Hypotrachyna degelii</i>	324	DQ912314	DQ912337	DQ912281	DQ912359	DQ912359	DQ912385	DQ912385
	<i>Imshaugia aleurites</i>	1044	—	DQ986753	DQ986864	DQ986825	—	DQ992440	DQ992440
	<i>Masonhalea richardsonii</i>	1710	—	DQ973031	DQ972979	DQ973054	DQ973054	DQ973092	DQ973092
	<i>Melanelixia fuliginosa</i>	1370	DQ983485	DQ986803	DQ986787	DQ986860	—	DQ992476	DQ992476
	<i>Menegazzia terebrata</i>	10	46411402	46411426	46411389	—	—	DQ973093	—
	<i>Myelochroa aurulenta</i>	206	DQ973001	DQ973025	DQ972972	DQ973049	DQ973049	DQ973070	DQ973070
	<i>Parmelia saxatilis</i>	GB	6684444	37960808	34148588	—	—	—	—
	<i>Parmotrema austrosinense</i>	89	DQ912315	DQ912338	DQ912282	DQ912360	DQ912360	DQ912386	DQ912386
	<i>Parmotrema reticulatum</i>	8	DQ912316	DQ912339	DQ912283	DQ912361	—	DQ912387	DQ912387
	<i>Parmotrema tinctorum</i>	7	46411400	46411424	46411392	DQ912362	—	46411497	46411497
	<i>Platismatia glauca</i> 1	201	DQ973007	DQ973032	DQ972980	DQ973055	—	—	DQ973094
	<i>Platismatia glauca</i> 2	203	DQ912317	DQ912340	DQ912284	DQ912363	DQ912363	DQ912388	DQ912388
	<i>Pleurosticta acetabulum</i>	GB	6684450	50953143	50953258	—	—	—	—
	<i>Pseudevernia consocians</i>	1243	DQ986714	DQ986754	DQ986868	DQ986826	—	DQ992441	—
	<i>Pseudevernia furfuracea</i>	GB	46254373	50953329	119633194	—	—	—	—
	<i>Punctelia hypoleucites</i>	85	46411411	46411435	46411394	DQ912364	—	46411501	46411501
	<i>Punctelia rudecta</i>	9	46411401	46411425	46411395	DQ912365	—	DQ912389	DQ912389
	<i>Tuckermannopsis ciliaris</i>	1245	DQ986715	DQ986755	DQ986870	DQ986827	—	DQ992442	—
	<i>Usnea antarctica</i>	813	DQ883702	DQ883692	DQ990920	DQ883721	—	DQ883709	DQ883709
	<i>Usnea sphacelata</i>	816	DQ883703	DQ883693	DQ990919	DQ883722	—	DQ883710	DQ883710
	<i>Usnea strigosa</i>	5	DQ973008	DQ973033	DQ972981	—	—	DQ973095	DQ973095
	<i>Vulpicida juniperina</i>	GB	6684449	34148753	34148609	—	—	—	—
	<i>Vulpicida pinastri</i>	198	DQ912318	DQ912341	DQ912285	DQ912366	DQ912366	DQ912390	DQ912390
	<i>Xanthoparmelia conspersa</i>	4	46411406	46411430	46411398	DQ912367	DQ912367	46488901	46488901

TABLE II. Continued

Classification (Eriksson 2006)		Taxon	Source	nucSSU	nuLSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Physciaceae 12/34		<i>Amandinea punctata</i> 1	GB	45433320	54873375	33304583	—	—	—	—
		<i>Amandinea punctata</i> 2	1306	DQ986721	DQ986756	DQ986873	—	—	DQ992435	DQ992435
		<i>Anaptychia palmulata</i>	648	DQ883792	DQ883801	DQ912286	DQ883744	DQ883744	DQ883757	DQ883757
		<i>Anaptychia runcinata</i>	GB	21955817	54873376	44307549	—	—	—	—
		<i>Buellia diabyta</i>	573	DQ973009	—	DQ972982	DQ973056	DQ973056	DQ973096	DQ973096
		<i>Buellia fimbriata</i>	1051	DQ973010	DQ973034	—	DQ973057	—	DQ973097	DQ973097
		<i>Buellia frigida</i>	889	DQ883699	DQ883695	DQ986903	DQ883724	—	DQ883712	DQ883712
		<i>Buellia stilingiana</i>	571	DQ912319	DQ912342	DQ912287	DQ912368	DQ912368	DQ912391	DQ912391
		<i>Dirinaria appianata</i>	839	DQ973011	DQ973035	DQ972983	—	—	DQ973098	DQ973098
		<i>Hafellia discoformis</i>	GB	10998394	34148715	33304585	—	—	—	—
		<i>Heteroderma vulgare</i>	320	DQ883789	DQ883798	DQ912288	DQ883741	DQ883741	DQ883754	DQ883754
		<i>Phaeophyscia orbicularis</i>	1308	DQ912320	DQ912343	DQ912289	DQ912369	—	DQ912392	DQ912392
		<i>Physcia aipolia</i>	84	DQ782876	DQ782904	DQ912290	DQ782820	—	DQ782862	DQ782862
		<i>Physconia muscigena</i>	220	DQ912321	DQ912344	DQ912291	DQ912370	—	DQ912393	DQ912393
	Porpidiaceae 1/16		<i>Pyxine soredata</i>	207	DQ973012	DQ973036	DQ972984	—	—	DQ973071
		<i>Pyxine subcinerea</i>	686	DQ883793	DQ883802	DQ912292	DQ883745	DQ883745	DQ883758	DQ883758
		<i>Rinodina tephraspis</i>	1314	DQ912322	DQ912345	DQ912293	DQ912371	—	DQ912394	DQ912394
		<i>Tornabaea scutellifera</i>	1061	DQ973013	DQ973037	DQ972985	DQ973058	—	—	—
		<i>Porpidia arborescens</i>	1246	DQ986716	DQ986757	DQ986871	DQ986828	—	DQ992443	DQ992443
		<i>Porpidia spetrea</i>	1050	DQ986711	DQ986758	DQ986865	DQ986829	DQ986829	DQ992444	DQ992444
		? <i>Lecidoma demissum</i>	1376	DQ986726	DQ986759	DQ986881	—	—	DQ992445	DQ992445
		<i>Protoblastenia calva</i>	992	34148570	46852266	DQ986904	DQ986830	—	DQ992446	DQ992446
		<i>Psora decipiens</i>	GB	DQ986710	DQ986760	DQ986863	—	—	DQ992447	—
		<i>Psora rubiformis</i>	219	DQ986729	DQ986761	—	DQ986831	DQ986831	DQ992448	DQ992448
Ramalinaceae 8/36		<i>Bacidia rosella</i>	GB	9828143	37960788	32141050	—	—	—	—
		<i>Bacidia rubella</i>	1793	—	DQ986793	DQ986808	—	—	DQ992422	DQ992422
		<i>Bacidia schweinitzii</i>	642	—	DQ782911	DQ972998	—	—	DQ782872	DQ782872
		<i>Bacidina arnoldiana</i>	1845	DQ986702	DQ986798	DQ986810	DQ782830	DQ782830	DQ992423	DQ992423
		<i>Lecania cyrtella</i>	GB	9828147	37960799	32141064	—	—	—	—
		<i>Niebla cephalota</i>	777	—	DQ986762	DQ986893	DQ986832	—	DQ992436	—
		<i>Ramatina complanata</i> 1	86	—	DQ973038	DQ972986	DQ973059	DQ973059	DQ973072	DQ973072
		<i>Ramatina complanata</i> 2	966	—	DQ883783	DQ972986	DQ883782	DQ883782	DQ883762	DQ883762
		? <i>Squammarina cartilaginea</i>	1281	DQ986720	DQ986763	—	DQ986833	—	DQ992449	DQ992449
		? <i>Squammarina gypsacea</i>	1701	DQ986703	—	—	DQ986853	—	DQ992420	DQ992420
Psoraceae 3/7		<i>Tephromela atra</i> 1	780	DQ986737	DQ986764	DQ986894	DQ986834	—	DQ992450	DQ992450
		<i>Tephromela atra</i> 2	1328	DQ986722	DQ986765	DQ986875	—	—	DQ992451	DQ992451
		<i>Tephromela atra</i> 3	1373	DQ986724	DQ986766	DQ986879	DQ986835	DQ986835	DQ992452	DQ992452
		<i>Tominia sedifolia</i>	213	DQ973014	DQ973039	DQ972987	—	—	DQ973073	—

TABLE II. Continued

Classification (Eriksson 2006)	Taxon	Source	nucSSU	nuLSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Rhizocarpaceae 2/4	<i>?Catelechia wahlenbergii</i>	1743	DQ986704	DQ986794	DQ986811	—	—	DQ992424	DQ992424
	<i>Rhizocarpon dispersum</i>	GB	15216688	15216689	—	—	—	52699865	52699865
	<i>Rhizocarpon geographicum</i>	GB	4731136	62005347	29837334	—	—	—	—
Sphaerophoraceae 2/5	<i>Rhizocarpon oederi</i>	1372	DQ983486	DQ986804	DQ986788	—	—	DQ992477	DQ992477
	<i>Rhizocarpon superficiale</i>	1708	DQ973015	—	DQ972988	DQ973060	DQ973060	DQ973074	DQ973074
	<i>Neophyllis melacarpa</i>	GB	6690342	34148734	34148585	—	—	—	—
Stereocaulaceae 2/4	<i>Sphaerophorus fragilis</i>	226	DQ983487	DQ986805	DQ986789	—	—	—	DQ995360
	<i>Sphaerophorus globosus</i>	1057	DQ986712	DQ986767	DQ986866	DQ986836	DQ986836	DQ992453	DQ992453
	<i>Lepraria incana</i>	1792	—	DQ986795	DQ986812	—	—	—	DQ995361
Peltigerales	<i>Lepraria lobificans</i> 1	325	DQ986733	DQ986768	DQ986887	DQ986837	DQ986837	DQ992454	DQ992454
	<i>Lepraria lobificans</i> 2	1244	—	—	DQ986869	DQ986838	DQ986838	DQ992455	—
	<i>Stereocaulon paschale</i>	GB	8163581	12025096	34148599	—	—	52699883	52699883
	<i>Stereocaulon tomentosum</i>	GB	70779661	34148745	34148600	—	—	—	—
Coccocarpiaceae 1/5	<i>Coccocarpia erythroxyli</i>	333	DQ883791	DQ883800	DQ912294	DQ883743	DQ883743	DQ883756	DQ883756
	<i>Coccocarpia domingensis</i>	122	DQ912323	DQ912346	DQ912295	—	—	DQ912395	DQ912395
Collemataceae 2/8	<i>Collema cristatum</i>	1013	DQ917410	DQ917408	DQ917409	—	DQ923121	—	DQ917411
	<i>Leptogium cyanescens</i>	GB	15216682	15216683	34148570	—	—	52699830	52699830
Lobariaceae 3/4	<i>Leptogium gelatinosum</i>	GB	40557685	40557700	34148571	—	—	—	—
	<i>Leptogium lichenoides</i>	1015	DQ917413	DQ917412	DQ923120	DQ917414	—	DQ917415	DQ917415
	<i>Lobaria amplissima</i>	GB	40557669	40557694	34148574	—	—	—	—
	<i>Lobaria pubmonaria</i>	GB	6739627	8476003	34148578	—	—	—	—
	<i>Lobaria quercizans</i>	GB	12025079	12025080	46411465	—	—	—	—
Nephromataceae 1/1	<i>Lobaria scrobiculata</i>	128	46411420	46411444	46411386	DQ883736	DQ883736	52699832	52699832
	<i>Lobariella pallida</i> 1	310	DQ883787	DQ883796	DQ912296	DQ883739	DQ883739	DQ883749	DQ883752
	<i>Lobariella pallida</i> 2	314	DQ883788	DQ883797	DQ912297	DQ883740	DQ883740	DQ883753	DQ883753
	<i>Pseudocyphellaria anomala</i>	132	DQ833785	DQ883794	DQ912298	DQ883737	DQ883737	DQ883750	DQ883750
	<i>Pseudocyphellaria crocata</i>	GB	40557672	15293979	34148595	—	—	—	—
Nephromataceae 1/1	<i>Sticta beauvoisii</i>	1242	DQ986713	DQ986769	DQ986867	—	—	DQ992456	DQ992456
	<i>Sticta fuliginosa</i>	GB	40557674	14423025	22213559	—	—	—	—
	<i>Sticta limbata</i>	GB	40557673	40557695	34148605	—	—	—	—
	<i>Nephroma arcticum</i>	1711	DQ973016	DQ973040	DQ972989	—	—	DQ973076	—
	<i>Nephroma bellum</i>	GB	40557682	40557699	22213576	—	—	—	—
Nephromataceae 1/1	<i>Nephroma parile</i>	131	46411445	46411421	46411390	DQ973061	DQ973061	DQ973075	—
	<i>Nephroma resupinatum</i>	GB	40557683	14423030	22213566	—	—	—	—

TABLE II. Continued

Classification (Eriksson 2006)	Taxon	Source	nucSSU	nuclSU	miSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Pannariaceae 7/17	<i>Degelia plumbea</i> 1	990	DQ912324	DQ912347	DQ912299	DQ912373	DQ912373	DQ912396	DQ912396
	<i>Degelia plumbea</i> 2	1046	DQ912325	DQ912348	DQ912300	DQ912374	DQ912374	DQ912396	DQ912396
Pannariaceae 3/12	<i>Erioderma verruculosum</i>	337	DQ973017	DQ973041	DQ972990	DQ973062	DQ973062	DQ973077	—
	<i>Fuscopannaria ignobilis</i>	1011	DQ986708	DQ917417	DQ917416	DQ986839	—	—	DQ992457
	<i>Pannaria mediterranea</i>	1014	—	DQ917419	DQ917418	—	—	DQ992437	DQ992437
	<i>Pannaria</i> sp.	309	DQ973018	—	DQ972991	DQ973063	—	DQ973078	DQ973078
	<i>Parmeliella appalachensis</i>	1655	DQ973019	—	DQ972992	DQ973064	—	DQ973079	DQ973079
	<i>Parmeliella</i> sp.	334	—	DQ973042	DQ972993	DQ973065	DQ973065	DQ973080	DQ973080
	<i>Protopannaria pezizoides</i>	129	DQ912327	DQ912349	DQ912302	DQ912376	—	—	DQ912397
	<i>Protopannaria pezizoides</i> ¹	222	DQ912326	DQ912350	DQ912301	DQ912375	DQ912375	DQ912397	—
	<i>Psoroma hypnorum</i>	GB	40557680	40557698	34148597	—	—	—	—
	<i>Peltigera aphthosa</i>	GB	40557644	14422959	22213560	—	—	—	—
Peltigeraceae 2/2	<i>Peltigera canina</i>	GB	15216692	14423022	—	—	—	52699840	52699840
	<i>Peltigera degenii</i>	134	46411422	46411446	46411393	DQ782826	DQ782826	46411499	46411499
	<i>Peltigera leucophlebia</i>	GB	40557647	14422953	22213564	—	—	—	—
	<i>Peltigera membranacea</i>	GB	40557655	32364274	—	—	—	45545340	45545340
	<i>Peltigera praetextata</i>	GB	40557656	14423014	22213565	—	—	—	—
	<i>Peltigera</i> sp.	1838	DQ986705	DQ986796	DQ986809	DQ986854	—	DQ992425	DQ992425
	<i>Solorina crocea</i>	1619	DQ973020	DQ973043	—	DQ973066	—	DQ973081	DQ973081
	<i>Solorina saccata</i> 1	127	DQ973021	DQ973044	DQ972994	—	—	—	—
	<i>Solorina saccata</i> 2	GB	40557639	40557688	34148598	—	—	—	—
	<i>Placynthium flabelliforme</i>	1663	DQ973024	DQ973047	DQ972999	—	—	—	—
Placynthiaceae 2/7	<i>Placynthium nigrum</i>	GB	15216684	15216685	46411472	—	—	52699852	52699852
	<i>Polychidium muscicola</i>	230	DQ986731	DQ986770	DQ986885	—	—	DQ992426	DQ992426
	<i>Massalongia carnosia</i>	GB	40557684	14423027	34148583	—	—	—	—
?									
Teloschistales									
Letroitiaceae 1/1	<i>Letroitia domingensis</i>	102	46411437	46411413	46411384	DQ883734	DQ883734	DQ883747	DQ883747
	<i>Megalospora tuberculosa</i>	107	46411439	46411415	46411388	DQ883781	—	DQ883761	DQ883761
Teloschistaceae 3/12	<i>Caloplaca flavorubescens</i>	GB	10998391	13810817	33304587	—	—	—	—
	<i>Xanthomendoza fallax</i>	GB	52699766	52699727	46411486	—	—	52699907	52699907
	<i>Xanthoria elegans</i>	214	DQ912329	DQ912352	DQ912304	DQ912378	DQ912378	DQ912400	DQ912400
	<i>Xanthoria parietina</i>	GB	10998392	13810818	33304592	—	—	—	—
<i>Xanthoria polycarpa</i>	200	DQ912328	DQ912351	DQ912303	DQ912377	DQ912377	DQ912399	DQ912399	

TABLE II. Continued

Classification (Eriksson 2006)		Taxon	Source	nucSSU	nuclSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Lecanoromycetidae										
?	?Fuscideaceae 2/3	<i>Fuscidea bygaea</i>	GB	52699738	52699698	—	—	—	52699809	52699809
		? <i>Maronea chilensis</i>	GB	52699742	52699703	—	—	—	52699834	52699834
	Phlyctidaceae 1/2	<i>Phlyctis argena</i>	1375	DQ986725	DQ986771	DQ986880	—	—	DQ992458	DQ992458
	Umbilicariaceae 2/2	<i>Lasallia papulosa</i>	650	DQ883701	DB883691	DQ986891	DQ883720	DQ883708	DQ883708	DQ883708
		<i>Lasallia pennsylvanica</i>	GB	50659896	15216676	48773785	—	—	52699824	52699824
		<i>Lasallia pustulata</i>	554	DQ883700	DB883690	DQ986889	DQ883719	DQ883707	DQ883707	DQ883707
		<i>Umbilicaria aprina</i>	1416	DQ986706	DQ986799	DQ986814	DQ986840	DQ992459	DQ992459	DQ992459
		<i>Umbilicaria arctica</i>	1266	DQ986717	DQ986772	DQ986872	DQ986841	—	DQ992460	DQ992460
		<i>Umbilicaria mammulata</i>	645	50659902	DQ782912	DQ912305	DQ782831	DQ782873	DQ782873	DQ782873
		<i>Umbilicaria muehlenbergii</i>	GB	52699764	52699725	46411484	—	—	52699903	52699903
		<i>Umbilicaria polyphylla</i>	404	10644715	62005358	62005405	—	—	—	—
		<i>Umbilicaria rigida</i>	GB	DQ986718	—	DQ986873	DQ986843	DQ992461	DQ992461	DQ992461
		<i>Umbilicaria spodochoa</i>	1267	DQ986707	DQ986773	DQ986815	DQ986844	DQ992462	DQ992462	DQ992462
			555	DQ986707	DQ986773	DQ986815	DQ986844	DQ992462	DQ992462	DQ992462
Lecanoromycetes										
Ostropomycetidae										
Agyriales										
Agyriaceae 5/16										
		<i>Orceolina kerguelensis</i>	296	90103012	28916540	14318290	91717263	91717263	91717264	91717264
		<i>Placopsis gelida</i>	GB	7105704	28916546	28916569	—	—	—	—
		<i>Placopsis perrugosa</i>	GB	15216670	15216671	46411471	—	—	52699854	52699854
		<i>Placynthiella uliginosa</i>	1365	—	DQ986774	DQ986877	DQ986845	—	DQ992463	—
		<i>Trapelia involuta</i>	GB	7105701	8926420	14318297	—	—	—	—
		<i>Trapelia placodioides</i>	962	7105702	8926425	20334369	91717261	—	91717265	91717265
		<i>Trapeliopsis flexuosa</i>	1028	DQ986709	8926440	DQ986862	DQ986846	—	—	—
		<i>Trapeliopsis granulosa</i>	GB	12025097	12025098	14318296	—	—	—	—
			GB	12025097	12025098	14318296	—	—	—	—
Gyalectales										
	Coenogoniaceae 1/2	<i>Coenogonium lepreurii</i>	GB	19171992	19171977	46411453	—	—	52699793	52699793
		<i>Coenogonium luteum</i>	GB	12025069	12025070	46411454	—	—	52699805	52699805
	Gyalectaceae 1/7	<i>Gyalecta hypoleuca</i>	GB	19171995	19171988	—	—	—	52699848	52699848
		<i>Gyalecta jenensis</i>	GB	12025073	12025074	34148567	—	—	52699815	52699815
		<i>Gyalecta ulmi</i>	GB	4731127	18481692	32141061	—	—	52699817	52699817

TABLE II. Continued

Classification (Eriksson 2006)	Taxon	Source	nucSSU	nuLSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Ostropales									
Graphidaceae 3/20	<i>Fissurina insidiosa</i>	1662	DQ973022	DQ973045	DQ972995	—	—	DQ973083	DQ973083
	<i>Graphina poitiaei</i>	GB	19171994	19171982	—	—	—	52699813	52699813
Solorinellaceae 1/2	<i>Graphis scripta</i>	GB	3004976	55139924	62005378	—	—	—	—
	<i>Gyalidea hyalinus</i>	332	DQ973023	DQ973046	DQ972996	—	—	DQ973084	DQ973084
Stictidaceae 3/19	<i>Acarosporina microspora</i>	78	46411408	46411432	46411377	—	—	46411489	46411489
	? <i>Petractis luetkemuelleri</i>	GB	19171996	19171989	46411469	—	—	52699850	52699850
	<i>Stictis populorum</i>	GB	3885423	48995464	34148564	—	—	—	—
	<i>Stictis radiata</i>	GB	669005	15216674	32141087	—	—	52699885	52699885
	<i>Stictis urceolatum</i>	96	DQ983488	51945063	DQ986790	—	—	DQ992478	DQ992478
		GB							
Thelotremaataceae 2/15	<i>Diploschistes</i>	328	DQ883790	DQ883799	DQ912306	—	—	DQ883755	DQ883755
	<i>cineneocoesius</i>								
	<i>Diploschistes muscorum</i>	GB	—	37960795	32141059	—	—	45545328	45545328
	<i>Diploschistes</i>	GB	8926433	8926416	20334361	—	—	—	—
	<i>rampoddensis</i>								
	<i>Diploschistes scruposus</i>	GB	12025071	12025072	46411447	—	—	52699807	52699807
	<i>Diploschistes</i>	GB	8926434	8926417	20334362	—	—	—	—
	<i>thunbergianus</i>								
	<i>Thelotrema lepadinum</i>	83	—	37960825	DQ972997	—	—	DQ973085	DQ973085
		GB							
Pertusariales									
Icmadophilaceae 4/6	<i>Dibaeis baeomyces</i>	358	6502558	12025068	46411459	—	—	52699803	52699803
		GB							
	<i>Icmadophila ericetorum</i>	875	DQ883704	DQ883694	DQ986897	—	—	DQ883711	DQ883711
	<i>Siphula ceratites</i>	849	DQ986738	DQ986775	62005399	—	—	DQ992464	—
		GB							
	<i>Thamnomia subuliformis</i>	GB	6502560	15216690	46411483	—	—	52699897	52699897
	<i>Thamnomia vermicularis</i>	GB	714613	62005353	62005400	—	—	45545350	45545350

TABLE II. Continued

Classification (Eriksson 2006)	Taxon	Source	nuclSSU	nuclLSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)	
Pertusariaceae 2/5	<i>Ochrolechia balcanica</i>	GB	56555556	13241947	13241946	—	—	—	—	
	<i>Ochrolechia frigida</i>	GB	12025085	12025086	32141071	—	—	—	—	
	<i>Ochrolechia juvenalis</i>	GB	52699745	52699705	—	—	52699838	52699838	—	
	<i>Ochrolechia parella</i>	GB	8926431	8926419	13241949	—	—	—	—	
	<i>Ochrolechia szatalaensis</i>	GB	8926430	8926424	45643390	—	—	—	—	
	<i>Ochrolechia trochophora</i>	880	DQ986743	—	DQ986901	—	—	—	DQ992465	
	<i>Ochrolechia yasudae</i>	882	DQ986744	DQ986776	DQ986902	DQ986848	—	DQ992466	DQ992466	
	<i>Ochrolechia</i> sp.	318	DQ986732	DQ986777	DQ986886	DQ986849	—	DQ992467	DQ992467	
	<i>Pertusaria amara</i>	1067	8926426	8926423	32141073	DQ973048	—	DQ973069	DQ973069	
	<i>Pertusaria dactylina</i>	224	DQ782880	DQ782907	DQ972973	DQ782828	DQ782828	DQ782868	DQ782868	
	<i>Pertusaria erythrella</i>	GB	8926428	8926422	20334365	—	—	—	—	
	<i>Pertusaria hemisphaerica</i>	959	DQ902340	AF381556	DQ973000	DQ902341	—	DQ902342	DQ902342	
	<i>Pertusaria scaberrula</i>	GB	8926427	8926421	20334366	—	—	—	—	
	Ostropomycetidae									
	?									
Hymeneliaceae	<i>Aspicilia caesiocinerea</i> s.l.	653	DQ986736	DQ986778	DQ986892	DQ986851	DQ986851	DQ992469	DQ992469	
	<i>Aspicilia cinerea</i> s.l.	647	DQ986735	DQ986779	DQ986890	DQ986850	DQ986850	—	DQ992468	
	<i>Aspicilia contorta</i>	1358	—	DQ986782	DQ986876	DQ986852	—	DQ992470	—	
	<i>Hymelia lacustris</i>	GB	52699740	52699701	46411463	—	—	52699823	52699823	
Lecanoromycetes										
?										
?										
Boreoplaca ultrafrigida		1702	—	DQ986797	DQ986813	DQ986855	—	DQ992421	DQ992421	
	<i>Lopezaria versicolor</i>	108	DQ912330	DQ912353	DQ912308	DQ912379	—	DQ912401	DQ912401	
	<i>Strangospora pinicola</i>	GB	52699758	52699718	—	—	—	52699718	52699718	
Ascomycota										
?										
?										
Baecomycetaceae	<i>Baeomyces placophyllus</i>	GB	15216668	15216669	32141051	—	—	52699785	52699785	
	<i>Phyllobaëis erythrella</i> 1	GB	23451995	62005341	62005389	—	—	—	—	
	<i>Phyllobaëis erythrella</i> 2	329	DQ986734	DQ986780	DQ986888	DQ990921	—	DQ992471	DQ992471	
	<i>Phyllobaëis imbricata</i>	852	DQ986739	DQ986781	DQ986895	—	—	DQ992472	DQ992472	

TABLE II. Continued

Classification (Eriksson 2006)	Taxon	Source	nucSSU	nuLSU	mitSSU	RPBI (A-F)	RPBI (F-G)	RPB2 (5-7)	RPB2 (7-11)
Leotiomycetes (outgroup)									
Helotiales									
Dermataceae	<i>Dermea acerina</i>	941	DQ247809	DQ247801	DQ976373	DQ471164	—	DQ247791	DQ247791
	<i>Modisia cinerea</i>	76	DQ470990	DQ470942	DQ976372	DQ471122	—	DQ470883	DQ470883
Geoglossaceae	<i>Geoglossum nigrinum</i>	56	45775623	45775579	45775669	DQ471115	—	DQ470879	DQ470879
	<i>Trichoglossum hirsutum</i>	64	45775626	45775582	45775687	DQ471119	—	DQ470881	DQ470881
Helotiaceae	<i>Chlorociboria aeruginosa</i>	151	45775642	45775598	45775663	DQ471125	—	DQ470886	DQ470886
	<i>Cudoniella clavus</i>	166	DQ470992	DQ470944	DQ471056	DQ471128	—	DQ470888	DQ470888
Leotiaceae	<i>Leotia lubrica</i>	1	45775616	45775573	45775676	DQ471113	DQ471113	34369059	34369059
Sclerotiniaceae	<i>Botryotinia fucheliana</i>	59	45775624	45775580	45775661	DQ471116	—	DQ247786	DQ247786
Lichinomycetes (outgroup)									
Lichinales									
Peltulaceae	<i>Peltula auriculata</i>	892	DQ832332	DQ832330	DQ922953	DQ782856	DQ782856	DQ832331	DQ832331
	<i>Peltula umbilicata</i>	891	DQ782887	DQ832334	DQ922954	DQ782855	DQ782855	DQ832335	DQ832335

Models of evolution for all analyses were estimated with the hierarchical likelihood ratio test as implemented in Modeltest v3.5 (Posada and Crandall 1998). Bayesian Metropolis coupled Markov chain Monte Carlo analyses (B-MCMCMC) were conducted with MrBayes v3.1.1 (Huelsenbeck and Ronquist 2001). The combined dataset was divided into nine partitions (nucSSU, nuLSU, mitSSU, *RPB1* 1st/2nd/3rd and *RPB2* 1st/2nd/3rd). All Bayesian analyses were run with four independent chains for 20 000 000 generations, sampling every 500th tree, using a six-parameter model for nucleotide substitution (GTR, Rodríguez et al 1990) with a gamma distribution approximated with four categories, and a proportion of invariable sites. All model parameters were unlinked. Four independent B-MCMCMC runs were conducted to ensure that all runs reached stationarity and converged at the same log-likelihood level (verified by eye and with AWYT option, Wilgenbusch et al 2004). After discarding the burn-in, the last 10 000 trees of each run were pooled to calculate a 50% majority rule consensus tree.

Phylogenetic confidence was estimated for each dataset (5-gene, 5+4-gene and 5+4+3-gene) with Bayesian posterior probabilities (PP) obtained from MrBayes, and maximum likelihood bootstrap proportions. Bootstrap proportions were calculated with 250 bootstrap replicates using both PHYML v2.4.4 (PHYML-BS, Guindon and Gascuel 2003) implementing a GTR model with gamma distribution, approximated with four categories, and proportion of invariable sites, and RAxML version VI (RAxML-BS, Stamatakis et al 2005) implementing a GTR model with gamma distribution, approximated with four categories. Bootstrap proportions $\geq 70\%$, and posterior probabilities $\geq 95\%$, were considered significant. Internodes with at least one bootstrap value $\geq 70\%$ from RAxML or PHYML and at least one posterior probability $\geq 95\%$ for any of the three-taxon samplings (i.e. a minimum of one black box in the last column and one black box in one of the first two columns of the internodal grids of Fig. 1) were considered strongly supported. Internodes with at least one bootstrap value $\geq 70\%$ without a posterior probability $\geq 95\%$ also were interpreted as well supported (see Lutzoni et al 2004 and Alfaro et al 2003 for a discussion on the interpretation of support values).

To detect topological incongruences among single gene datasets, a reciprocal 70% neighbor joining bootstrap support criterion (NJ-BS) was implemented (Mason-Gamer and Kellogg 1996, Reeb et al 2004). A conflict was assumed to be significant if a group of taxa was supported ($\geq 70\%$ NJ-BS) as monophyletic in one tree but supported as nonmonophyletic in another. NJ-BS trees were obtained in PAUP v4b10 (Swofford 2002) with ML distances. The program compat.py (written by FK and available at www.lutzonilab.net) was used to detect conflicts among data partitions. Each pairwise combination of the five genetic loci was subjected to this screening for conflicts. For the *RPB1* and *RPB2* loci, this criterion was applied on each amplicon separately (two amplicons per locus). Taxa in conflict were removed from further analyses, and the test was repeated until no conflict was detected. The nexus 5+4+3-gene dataset is available on the AFTOL Website and

in TreeBASE (www.treebase.org) under accession number SN3062.

Alignments.—A summary of alignment lengths and number of included sites for each dataset after removal of conflicting taxa is provided (TABLE I). Due to detected incongruence when using our reciprocal 70% NJ-BS criterion, 28 taxa were removed from the initial 5-gene alignment for 139 taxa, resulting in a total number of 111 taxa included in the 5-gene dataset analyses. Ten taxa were removed from both the 5+4-gene and the 5+4+3-gene datasets for the final number of 188 and 274 taxa, respectively. The *RPB1* and *RPB2* loci provided the largest number of characters included in phylogenetic analyses. Compared to ribosomal loci these two genes contained the lowest proportion of ambiguously aligned characters (15–25% vs. 78–85%), which had to be excluded from the analyses. The proportion of missing data increased from 17% in the 5-gene alignment to 26% in the 5+4-gene alignment and 37% in the 5+4+3-gene alignment, mostly due to the missing *RPB1* and *RPB2* sequences (132 *RPB1* [A–F], 210 *RPB1* [F–G], 67 *RPB2* [5–7] and 84 *RPB2* [7–11] missing sequences in the 5+4+3-gene dataset). The number of characters for taxa part of the dataset with the greatest frequency of missing sequences (5+4+3-gene dataset) varied from 7114 characters for taxa with all genes included to 2638 characters for taxa with only nucSSU, nuLSU and mitSSU present.

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