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Phylogenetic affiliations of members of the heterogeneous lichen-forming fungi of the genus *Lecidea* sensu Zahlbruckner (Lecanoromycetes, Ascomycota)

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Abstract: The genus *Lecidea* Ach. sensu lato (sensu Zahlbruckner) includes almost 1200 species, out of which only 100 species represent *Lecidea* sensu stricto (sensu Hertel). The systematic position of the remaining species is mostly unsettled but anticipated to represent several unrelated lineages within Lecanoromycetes. This study attempts to elucidate the phylogenetic placement of members of this heterogeneous group of lichen-forming fungi and to improve the classification and phylogeny of Lecanoromycetes. Twenty-five taxa of *Lecidea* sensu lato and 22 putatively allied species were studied in a broad selection of 268 taxa, representing 48 families of Lecanoromycetes. Six loci, including four ribosomal and two protein-coding genes for 315- and 209-OTU datasets were subjected to maximum likelihood and Bayesian analyses. The resulting well supported phylogenetic relationships within Lecanoromycetes are in agreement with published phylogenies, but the addition of new taxa revealed putative rearrangements of several families (e.g. Catillariaceae, Lecanoraceae, Lecideaceae, Megalariaceae, Pilocarpaceae and Ramalinaceae). As expected, species of *Lecidea* sensu lato and putatively related taxa are scattered within Lecanoromycetidae and beyond, with several species nested in Lecanoraceae and Pilocarpaceae and others placed outside currently recognized families in Lecanorales and orders in Lecanoromycetidae. The phylogenetic affiliations of *Schaereria* and *Strangospora* are outside Lecanoromycetidae, probably with Ostropomycetidae. All species referred to as *Lecidea* sensu stricto based on morphology (including the type species, *Lecidea fuscoatra* [L.] Ach.) form, with *Porpidia* species, a monophyletic group with high posterior probability outside Lecanorales, Peltigerales and Teloschistales, in Lecanoromycetidae, supporting the recognition of order Lecideales Vain. in this subclass. The genus name *Lecidea* must be redefined to apply only to *Lecidea* sensu stricto and to include at least some members of the genus *Porpidia*. Based on morphological and chemical similarities, as well as the phylogenetic relationship of *Lecidea pullata* sister to *Frutidella caesioatra*, the new combination *Frutidella pullata* is proposed here.

Key words: ascus type, Lecanoromycetidae, Lecideaceae, Lecideales, lichen-forming ascomycetes, mitochondrial ribosomal small subunit (mtSSU), molecular phylogenetic classification, nuclear ribosomal large subunit (nucLSU), nuclear ribosomal small subunit (nucSSU), photobiont, phylogeny, ribosomal internal transcribed spacers (ITS) and 5.8S nuclear

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ribosomal DNA, RNA polymerase II largest subunit (*RPB1*), RNA polymerase II second largest subunit (*RPB2*), *Schaereria*, secondary metabolites

INTRODUCTION

Traditional classification of lichen-forming ascomycetes often had suffered from using easily observed characters to delimit taxa, frequently resulting in artificial assemblages of species. A prominent example of a highly polyphyletic group resulting from such taxonomic practice is the genus *Lecidea* Ach. Originally described by Acharius (1803), *Lecidea* has been, in the sense of Zahlbruckner, one of the largest lichen genera and included about 1200 species (Zahlbruckner 1925, 1932). Zahlbruckner's concept was the most influential during the first half of the 20th century, although in the 1850s the Massalongo-Körber school attempted to circumscribe smaller, more homogeneous genera based on microscopic characters (Hale 1984). Studies based on morphological and chemical characters demonstrated that *Lecidea* sensu Zahlbruckner is artificial (e.g. Hertel 1983, 1984; Hertel and Rambold 1985; Santesson 1952) because it was based on the use of a few homoplasious, sometimes plesiomorphic, character states (crustose thallus, biatorine or lecideine apothecia and simple ascospores).

Within the past 40 y research by several lichenologists has resulted in a clearer delimitation of *Lecidea* sensu lato (s.l. sensu Zahlbruckner) by moving many taxa to new genera (such as *Fuscidea* V. Wirth & Vězda, *Myochroidea* Printzen, T. Sprib. & Tønsberg and *Puttea* S. Stenroos & Huhtinen [Printzen et al. 2008, Stenroos et al. 2009]) or by placing them into existing genera (such as *Amygdalaria* Noman, *Biatora* Fr., *Huilia* Zahlbr. [synonym of *Porpidia* Körb.], *Lecidella* Körb., *Micarea* Fr., *Phyllopsora* Müll. Arg., *Porpidia*, *Psora* Hoffm., *Schaereria* Körb., and *Toninia* A. Massal.) subsequently recognizing morphologically homogenous groups (e.g. Hertel 1967, 1969, 1977, 1984, 1995; Poelt 1973; Vězda and Wirth 1976; Poelt and Vězda 1977, 1981; Schneider 1979; Hawksworth et al. 1980; Inoue 1981, 1982, 1983, 1984; Swinscow and Krog 1981; Coppins 1983; Hafellner 1984; Oberhollenzer and Wirth 1984; Timdal 1984a, b, 1991; Hertel and Rambold 1985; Rambold 1989; Printzen 1995; Andreev et al. 1998; Schmull and Spribille 2005). To date more than 160 genera from various families include species previously classified within *Lecidea* s.l. The classification of the remaining species still included in the genus *Lecidea* is uncertain for the most part. Currently 427 species are included in *Lecidea* s.l. (Kirk et al. 2008), but only about 100 of these (all saxicolous) are recognized in the genus *Lecidea* sensu stricto (s.s. sensu Hertel) based on differences in anatomical characters, such as excipulum, paraphyses and apical ascus structures (Hertel 1977, Hertel and Printzen 2004).

Nearly all taxonomic studies on the genus *Lecidea*, including the most recent published work (e.g. Leuckert and Hertel 2003, Printzen et al. 2008), have been based solely on comparisons of morphological features and secondary compounds. Only two recent molecular phylogenetic studies focused on *Lecidea* s.l. (Stenroos et al. 2009, Sérusiaux et al. 2010), and only a few other molecular phylogenetic studies included representatives from mainly *Lecidea* s.s. as a context for the groups being studied (Buschbom and Mueller 2004, Lutzoni et al. 2004, Peršoh et al. 2004, Reeb et al. 2004, Andersen and Ekman 2005, Wedin et al. 2005, Miadlikowska et al. 2006, Ekman et al. 2008). The genus *Lecidea* s.l. is in great need of a taxonomic revision, including a comprehensive phylogenetic treatment. Furthermore, the addition of members from *Lecidea* s.l. to a broad phylogeny of the Lecanoromycetes will play an important role in our understanding of the relationships and evolutionary patterns within the third largest class of Fungi.

Twenty-five taxa of *Lecidea* s.l. and 22 potentially closely-related species were selected for this phylogenetic study (SUPPLEMENTAL TABLE I). A sixth gene (5.8S) and a total of 43 species (44 taxa) were added to the five-gene supermatrix assembled by Miadlikowska et al. (2006), broadly representing the Lecanoromycetes, to infer the phylogenetic placement of members of *Lecidea* s.l. within this class. Maximum likelihood and Bayesian analyses were ultimately carried out on six combined single-locus datasets, including four nuclear ribosomal loci (the small and large subunits [nucSSU and nucLSU, respectively], the 5.8S gene of the ITS region, and the mitochondrial small subunit [mtSSU]); and two single copy protein-coding loci (the RNA polymerase II largest subunit [*RPB1*] and the RNA polymerase II second largest subunit [*RPB2*]). Important diagnostic characters used for delimitation of taxonomically controversial taxa (including *Lecidea* s.l.), such as morphological traits (e.g. Hertel 1977, 1984; Arvidsson 1982; Coppins 1983; Hafellner 1984; Hertel and Rambold 1988; Triebel and Rambold 1988; Timdal 1991; Rambold and Triebel 1992; Rambold et al. 1998; Peršoh et al. 2004; Schmitt et al. 2005; Wedin et al. 2005), secondary compounds (e.g. Leuckert and Hertel 1967, 1969; Culberson and Culberson 1968; Brodo and Hawksworth 1977; Hertel and Rambold 1985), photobiont identity (e.g. Rambold et al. 1998, Helms et al. 2001, Beck 2002, Peršoh et al. 2004, Hauck et al. 2007) and ecology (e.g. Rambold 1989) are discussed here in the context of inferred

relationships and newly delimited groups within the Lecanoromycetes to assess their taxonomical identities.

MATERIALS AND METHODS

Genes and taxon sampling.—Molecular data were generated for 21 *Lecidea* species (22 taxa), including two putatively undescribed taxa and 22 putative allied taxa, for a total of 44 specimens. This dataset was combined with Miadlikowska et al. (2006) five-gene supermatrix (271 taxa, including three *Lecidea* species) for Lecanoromycetes, resulting in a total of 315-OTUs (SUPPLEMENTAL TABLE I). From the original 274-taxon supermatrix (Miadlikowska et al. 2006) three taxa (*Xanthoparmelia conspersa*, *Amandinea punctata* 1 and *Pseudocyphellaria crocata*) were removed because of the detection of contaminated sequences (necessary corrections were submitted to GB). In addition to the nucSSU, nucLSU, mtSSU, *RPB1* and *RPB2* loci used by Miadlikowska et al. (2006), the 5.8S region of the nuclear ribosomal DNA was added to the 315-OTU supermatrix. A total of 129 unpublished sequences of the entire ITS region were generated. One hundred eight ITS sequences were retrieved from the AFTOL 1 project (Assembling the Fungal Tree of Life; aftol.org), 21 were generated by the first author specifically for this study, 116 sequences were taken from GenBank and 70 sequences were missing. For the remaining five loci, 60 new sequences were generated by the first author: three nucSSU, 20 nucLSU, 25 mtSSU, three *RPB1* and 9 *RPB2*. Every newly added taxon was represented in our 315-OTU supermatrix by sequences of at least two of the six targeted loci. Compared to Miadlikowska et al. (2006), the 315-OTU supermatrix contained four additional families: Catillariaceae, Megalariaceae and Pilocarpaceae (Lecanoromycetidae) and Schaereriaceae (Ostropomycetidae).

For seven of the 21 newly added *Lecidea* species and two of the 22 putatively allied taxa the rDNA ITS region of the photobiont was sequenced. The photobionts were identified by searching for maximal similarity of the ITS sequences in GenBank (blastn, optimized for megablast).

Molecular data.—To obtain fungal sequences apothecia were used for extracting the total DNA with the DNeasy Plant Mini Kit™ (QIAGEN). For the PCR of the mtSSU primer pairs mrSSU1 and mrSSU2R (Zoller et al. 1999) or mrSSU2 and MSU7 (Zoller et al. 1999, Zhou and Stanosz 2001) were used. The amplification was performed in 25 μL volumes employing an initial denaturation at 94 C for 4 min, six cycles at 94 C for 1 min, 62 C decreasing 1 C per cycle for 1 min and 72 C for 1 min 45 s, followed by 34 cycles of 94 C for 30 s, 56 C for 30 s, 72 C for 1 min 45 s increasing 3 s per cycle, and an extension at 72 C for 10 min followed by a 4 C soak. The same protocol was used to amplify the entire internal transcribed spacer (ITS1, 5.8S and ITS2) of the nuclear ribosomal DNA with the primer pair ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). For the nucLSU the primer pairs LR0R and LR5 or LR3R and LR7 (Vilgalys and Hester 1990) were used. The amplification also was performed in 25 μL volumes but with an initial denaturation at 95 C for 3 min, five cycles at 95 C for 1 min, 53° C for 30 s and 72 C for 1 min, followed by 35 cycles at 95 C for 1 min, 50 C for 30 s, 72 C for 1 min and an extension at 72 C for 10 min followed by a 4 C soak. The PCR products were cloned with the TOPO TA Cloning® Kit (Invitrogen, Darmstadt, Germany). About 30 clones for each PCR product were selected, and PCR amplification was performed for all of them with the same primer pairs and protocol as above. Sequencing was performed with the same primers as for PCR amplification, the standard reagents and conditions for the BigDye® Terminator Cycle Sequencing Kit (Applied Biosystems, Darmstadt, Germany) and the standard procedure for an automated capillary sequencer ABI 3730 XL (Applied Biosystems, Darmstadt, Germany). Only one type of the mycobiont sequence was obtained for each cloned PCR product. Protocols and primers for the amplification of the remaining loci (nucSSU, *RPB1* and *RPB2*) and the ITS region for taxa sequenced as part of the AFTOL project can be found elsewhere (Lutzoni et al. 2004, James et al. 2006, Hofstetter et al. 2007).

To obtain photobiont DNA sequences the primer pair AL1800f (Beck pers comm) and ITS4 was used for amplifying and sequencing the ITS region. Amplification was performed in 25 μL volume using either protocol A or protocol B. In protocol A the PCR cycling parameters included an initial denaturation at 95 C for 5 min, 33 cycles at 94 C for 40 s, 51 C for 30 s, and 72 C for 120 s increasing 2 s per cycle, followed by an extension at 72 C for 10 min and a 4 C soak. Protocol B differed from protocol A in the annealing temperature and time (50 C for 40 s) and an extension of 70 C for 120 s increasing 5 s per cycle. Sequencing was performed as described above with the same primers as for PCR amplification. Samples with ambiguous sequences were cloned with the TOPO TA Cloning® Kit (Invitrogen, Darmstadt, Germany) and resequenced with the protocols described above.

Alignments.—Fungal sequences were aligned manually with MacClade 4.07 (Maddison and Maddison 2003) based on the secondary structure model (Kjer 1995) of *Saccharomyces cerevisiae* Meyen *ex* E.C. Hansen (Cannone et al. 2002) for the nucSSU and nucLSU. A summary of alignment lengths and the number of included sites for each dataset is provided (SUPPLEMENTARY TABLE II). The *RPB1* and *RPB2* genes provided the largest number of characters included in the phylogenetic analyses. Although the 5.8S region contained the lowest proportion of ambiguously aligned characters, most of the included characters were constant. Compared to the remaining ribosomal genes, *RPB1* and *RPB2* contained the lowest proportion of sites, which had to be excluded from the analyses (15–24% vs. 72–88%). By removing 106 taxa from the 315-OTU dataset, the proportion of missing data decreased by 13% and the number of included sites increased by 270. The nexus 315-OTU and 209-OTU supermatrices are available on the AFTOL Website and in TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S11062).

Phylogenetic analyses.—To detect topological incongruence among single-gene datasets a reciprocal 70% ML bootstrap support criterion 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 at ≥ 70% as monophyletic with one locus but supported as non-monophyletic by another locus. ML bootstrap trees for each locus were obtained with RAxML 7.0.4 (Stamatakis 2006a) using the same conditions as for the bootstrap analysis on the combined supermatrices described below. No conflict was detected and therefore each single-locus dataset was concatenated.

Maximum likelihood (ML) analyses were performed on the 315-OTU supermatrix using RAxML for 1000 replicates, implementing a GTR model with gamma distribution (GTRGAMMA) and four discrete rate categories for each of the ten data partitions (5.8S, nucSSU, nucLSU, mtSSU, *RPB1* 1st, 2nd, 3rd, and *RPB2* 1st, 2nd, 3rd positions). The ML tree revealed that all newly added taxa, except *Schaereria*, were placed within Lecanoromycetidae. To recover more phylogenetic signal from fast evolving regions we reduced our dataset to 209 OTUs restricted to Lecanoromycetidae (excluding Umbilicariales), using *Sporastatia* to root the tree, which allowed the unambiguous alignment of additional sites that were equivocally aligned because of the broader array of taxa included in the 315-OTU sampling. The second RAxML analysis was performed on this reduced 209-OTU supermatrix using the same conditions and data partitions as the first ML run but implementing a backbone constraint tree during the run. The base for the backbone constraint tree was the 70% majority rule bootstrap consensus tree of Miadlikowska et al. (2006) resulting from the analysis of 111 taxa for which five genes were available for each taxa (full multilocus data matrix). All taxa outside Lecanoromycetidae (a clade supported by ML bootstrap value of 95%) were pruned, and the final backbone constraint tree contained 72 taxa.

Phylogenetic confidence was estimated for each dataset (315-OTU and 209-OTU supermatrices) using RAxML for 1000 replicates, implementing a GTRCAT model (Stamatakis 2006b) for the same 10 data partitions used in the maximum likelihood search. The 72-taxon backbone constraint tree was used for bootstrap analysis on the 213-OTU supermatrix. In addition to ML bootstrap support the latter supermatrix was subjected to a Bayesian analysis with MrBayes 3.1.1 for a second estimate of phylogenetic confidence (Huelsenbeck and Ronquist 2001). To facilitate a good exchange between cold and hot chains the Bayesian analysis was run with 16 independent chains for 25 000 000 generations, sampling every 2000th tree, with the temperature of the hottest chain (lambda) set to 0.067, using a six-parameter model for nucleotide substitution (GTR, Rodríguez et al. 1990) and the Kimura-2-parameter model (Kimura 1980) for the 5.8S, with a gamma distribution approximated with four categories, and a proportion of invariable sites. All model parameters were unlinked. The nucleotide substitution models for Bayesian analysis were selected by applying the hierarchical likelihood ratio test (HLRT, Huelsenbeck and Crandall 1997) with the Akaike information criteria (AIC, Akaike 1973) using Modeltest 3.7 (Posada and Crandall 1998).

Two independent Bayesian runs were conducted to ensure that stationarity was reached and the runs converged at the same log-likelihood level (verified by eye and with the AWTY [Are we there yet?] option; Wilgenbusch et al. 2004, Nylander et al. 2008). After discarding the burn-in 10 000 trees of each run were pooled to calculate a 50% majority rule consensus tree. Bootstrap proportions ≥ 70%, and posterior probabilities ≥ 0.95, were considered significant.

Microscopic measurements.—For the 22 newly sequenced taxa of *Lecidea* s.l. anatomical characters of the apothecia were investigated by light microscopy on hand-cut sections mounted in water or 10% KOH, stained with 50% HNO_3 or I-Lugol (Merck1.09261) or lactophenol cotton blue (LCB; Merck 1.13741). Microscopic measurements were made at 1000× magnification in water.

Chemical analysis.—Phenolic metabolites of 16 species of *Lecidea* s.l. were analyzed with high performance liquid chromatography (HPLC). Lichen material was air dried, cleaned from substrate under a dissecting microscope (Olympus SZ 30) and transferred into vials. The samples were extracted with methanol for 4 h and the extracts transferred to HPLC vials.

Natural compounds were characterized by HPLC with a Merck-Hitachi Spectra System, a Beckman ODS 250 C 8 column (250 × 4.6 mm), and a spectrometric detector operating at 254 nm at a flow of 1 mL/min. Retention index values (RI) were calculated with benzoic acid and E-1-(9-anthryl)-2-phenylethene as controls (Feige et al. 1993, Elix and Wardlaw 2000). Solvent A was 1% aqueous orthophosphoric acid: methanol (3 : 7). Methanol was used as solvent B. The gradient started with 0% B and was raised to 58% B within 15 min, then to 100% B within a further 15 min, followed by 100% B for 10 min. A photodiode array detector (DAD) was used to identify secondary products by comparing their UV spectra with those of authentic metabolites eluted under identical conditions.

RESULTS

Multilocus phylogenies from this study showed similar relationships within Lecanoromycetes to those reported by Miadlikowska et al. (2006). However, the addition of new taxa lowered support values (ML bootstrap and PP) for several internodes (FIGS. 1, 2), which might be the result, in part, of missing sequences from non-ribosomal genes for some of the newly added taxa. All four subclasses of the Lecanoromycetes, that is Acarosporomycetidae, Candelariomycetidae (Miadlikowska et al. 2006), Lecanoromycetidae (excluding Umbilicariales) and Ostropomycetidae, were recovered as monophyletic and, except for Lecanoromycetidae and Ostropomycetidae, are well supported (FIG. 1). The monophyly of Lecanorales, Peltigerales (as well as its two suborders Peltigerineae and Collematineae) and Teloschistales (and its two suborders Physciineae and Teloschistineae) were confirmed, although Lecanorales and Teloschistales lacked significant support (FIG. 2). In agreement with Miadlikowska et al. (2006), the monophyletic Rhizocarpaceae and Candelariaceae are placed outside currently recognized orders and

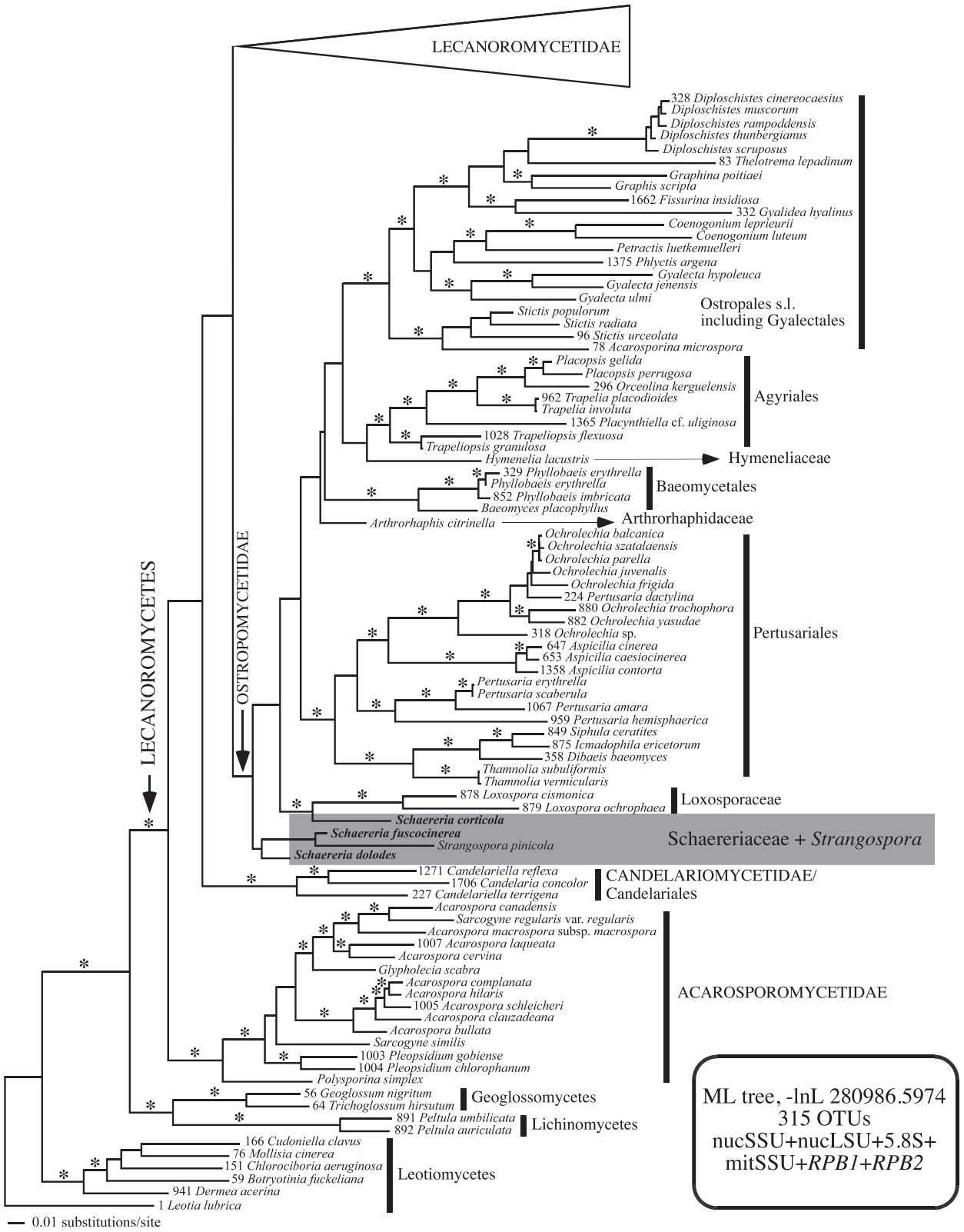


FIG. 1. Lecanoromycetes phylogenetic relationships resulting from the maximum likelihood analysis (RAxML) of a 315-OTU supermatrix containing a combined dataset of nucSSU, nucLSU, 5.8S, mitSSU, *RPB1* and *RPB2* sequences. The top part of the tree, comprising Lecanoromycetidae and Umbilicariales, is represented by a triangle. Ten taxa from Lichinomycetes, Geoglossomycetes and Leotiomycetes were used as outgroup. Stars above internodes indicate ML bootstrap support ≥ 70%. Placement of *Schaereria*, one of the newly added taxa to the five-gene supermatrix of Miadlikowska et al. (2006) as part of this study, is shown in the shaded box.

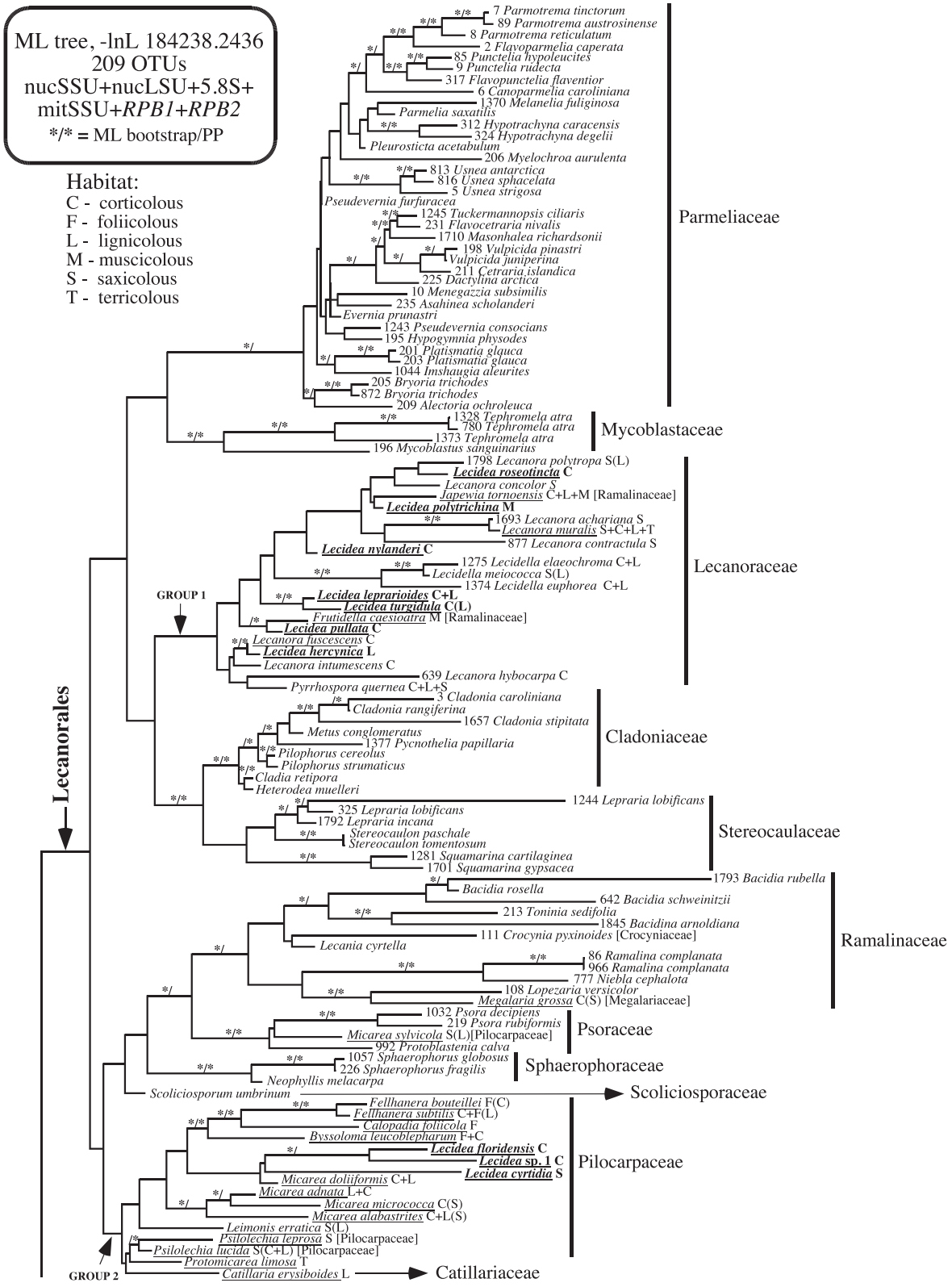
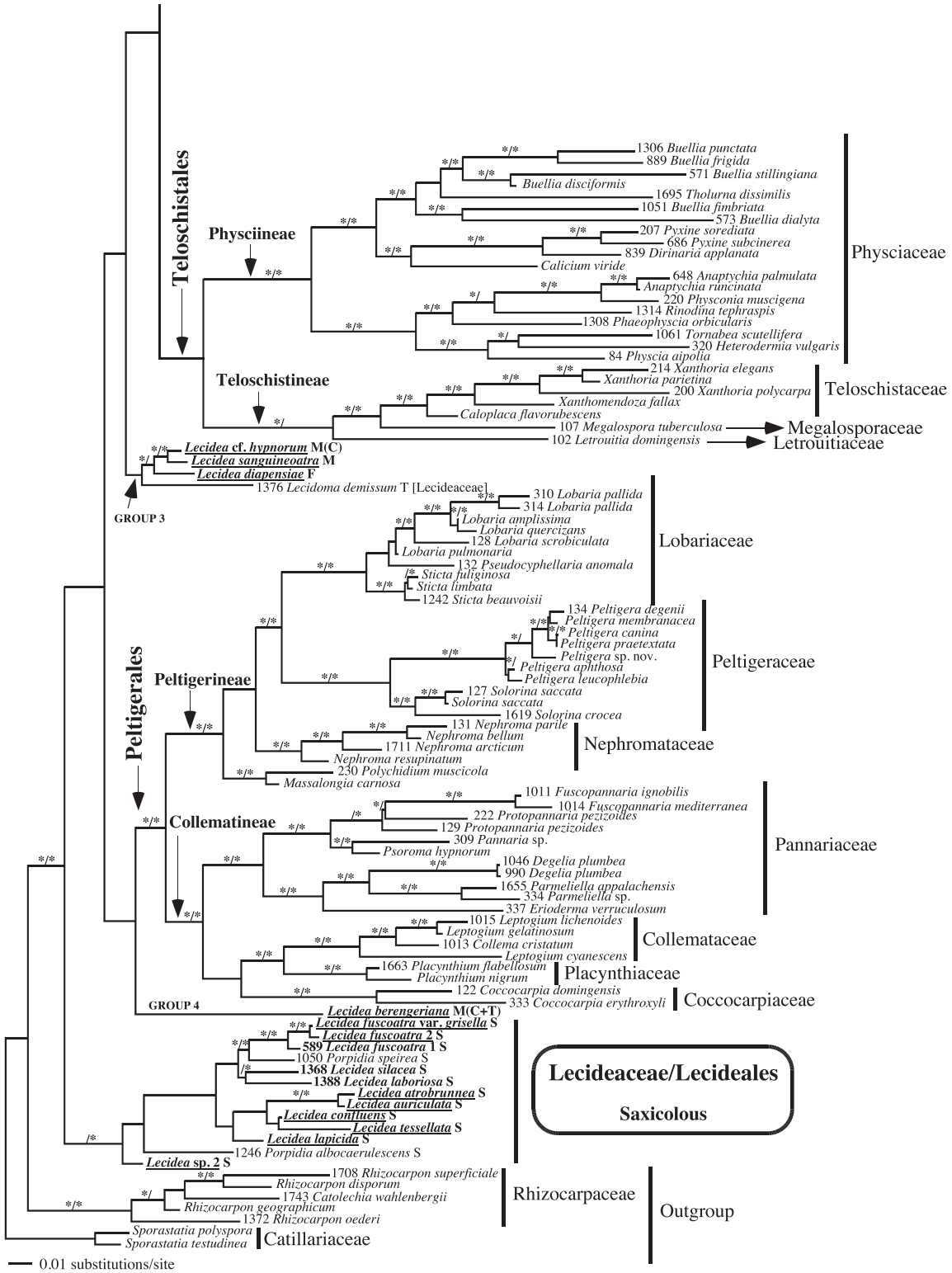


FIG. 2. Phylogenetic relationships among 209-OTUs within Lecanoromycetidae (excluding Umbilicariales) based on a combined dataset of nucSSU, nucLSU, 5.8S, mitSSU, *RPB1* and *RPB2* sequences that resulted from a maximum likelihood analysis. *Sporastatia* and Rhizocarpaceae (i.e. Rhizocarpales sensu Miadlikowska et al. 2006) were used as outgroup. Underlined names indicate taxa added to the five-gene supermatrix (Miadlikowska et al. 2006) as part of this study. All *Lecidea*



←

s.l. species are in boldface. Stars above internodes indicate significant support, ML bootstrap values ≥ 70% before the slash and PP values ≥ 0.95 after the slash. Habitats for *Lecidea* and allied taxa are given after taxon names (see abbreviations in the legend near the top of the figure). Rare substrates are shown in parenthesis. In square brackets are given-family names according to Myconet, Jun 2010, (Lumbsch and Huhndorf 2007) for taxa placed outside expected families.

represent early diverging lineages within Lecanoromycetidae and Lecanoromycetes, respectively. These results support the new order Candelariales Miadl., Lutzoni & Lumbsch (Hibbett et al. 2007) and the proposal by Miadlikowska et al. (2006) to recognize the Rhizocarpaceae at least at the ordinal rank as well.

The newly added taxa, except the three *Schaereria* species, belong to Lecanoromycetidae (FIGS. 1, 2). Two species from the genus *Schaereria* (Schaereriaceae) form a poorly supported clade with *Strangospora* associated with the first divergence during the early evolution of the Ostropomycetidae lineage. *Schaereria corticola* Muhr & Tønsberg is well supported as sister to Loxosporaceae (FIG. 1). All species of *Lecidea* s.s., including the type species, *L. fuscoatra* (L.) Ach., together with *Porpidia*, form a monophyletic group (PP > 95%) outside currently recognized orders in Lecanoromycetidae, supporting its recognition as the order Lecideales Vain. (FIG. 2).

Ten members of *Lecidea* s.l. are phylogenetically placed in Lecanorales: Seven species are nested within the Lecanoraceae (Group 1, FIG. 2), intermixed with *Lecanora* Ach., *Lecidella* Körb., *Pyrrhospora* Körb., *Japewia* Tønsberg and *Frutidella* Kalb (we propose here that the latter two taxa be recognized as members of Lecanoraceae; they are currently classified in Ramalinaceae) and three species form a clade within Pilocarpaceae (monophyly not supported; Group 2, FIG. 2). The remaining three of four species (*L. sanguineoatra* auct., non [Wulfen] Ach., *L.* cf. *hypnorum*, and *L. diapensiae* Th. Fr.) represent a new significantly supported lineage with unsettled placement outside major groups in Lecanoromycetidae (sister to *Lecidoma demissum* [Rutstr.] Gotth. Schneid. & Hertel, but without significant support; Group 3, FIG. 2). A separate, but unsettled, phylogenetic placement in Lecanoromycetidae also was inferred for *Lecidea berengeriana* (A. Massal.) Nyl. (Group 4, FIG. 2).

TAXONOMY

Based on morphological, anatomical and chemical similarities, as well as phylogenetic reconstructions (FIG. 2), a new combination from *Lecidea pullata* to *Frutidella pullata* is proposed here:

Frutidella pullata (Norman) Schmull, comb. nov.

Basionym: *Biatora pullata* Norman, Öfvers. Kongl. Vetensk.-Akad. Förh. 27: 803. 1870.

= *Lecidea pullata* (Norman) Th. Fr., Lich. Scand. Rar. Crit. Exsicc. 1:471. 1874.

MycoBank MB561066

DISCUSSION

Ostropomycetidae including Schaereria *and* Strangospora.—The genus *Schaereria*, represented here for the first time with three species (*S. corticola* [corticolous], *S. fuscocinerea* [saxicolous] and *S. dolodes* [corticolous or lignicolous]), is revealed as an early diverging paraphyletic group in Ostropomycetidae but without strong support (FIG. 1). Previous studies included only *S. fuscocinerea* and *S. corticola*, which formed a separate, well supported clade (Wedin et al. 2005, Lumbsch et al. 2007). In this study *S. dolodes*, which was transferred from the genus *Lecidea* to *Schaereria* (Schmull and Spribille 2005), was included in phylogenetic analyses for the first time, revealing the potentially polyphyletic nature of *Schaereria* (however without significant support; FIG. 1).

Non-monophyly of the genus Schaereria.—*Schaereria* encompasses 10 species (Fries 1861, Clauzade and Roux 1985, Hertel and Zürn 1986, Rambold 1989, Tønsberg 1992, Lumbsch 1997, Kantvilas 1999, Fryday and Common 2001, Schmull and Spribille 2005, Spribille et al. 2009) and generally was considered to be well defined morphologically and chemically, although closer relationships among some species in comparison to others have been discussed (*S. corticola* + *S. parasemella*, Lumbsch 1997, Spribille et al. 2009; *S. corticola* + *S. cinereorufa* + *S. fuscocinerea*, Tønsberg 1992; *S. dolodes* + *S. cinereorufa*, Schmull and Spribille 2005; *S. fabispora* + *S. tenebrosa*, Hertel and Zürn 1986; *S. xerophila* + *S. cinereorufa*, Rambold 1989). Hafellner (1984) pointed out that *S. fuscocinerea* (syn. *S. tenebrosa* [Flotow] Hertel & Poelt) and *S. cinereorufa* should be classified in two separate genera because of differences in thallus organization and ascocarp anatomy, and Lumbsch (1997) indicated that *S. parasemella* ''is very similar to *Schaereria* … and it might be useful to place that species in *Hafellnera*.''

Taxonomic placement of the genus Schaereria.—Typus: ''*Schaereria lugubris*'', Falkenstein, *Krempelhuber* (M) (typ. cons.) (= *S. cinereorufa* [Schaer.] Th. Fr. [*Lecidea cinereorufa* Schaer.]). The genus *Schaereria* has been included and excluded from Lecideaceae several times in the past 160 y (Körber 1855; Poelt and Vězda 1977, 1981), and its placement in Lecideaceae has been questioned for a long time (e.g. Choisy 1949, Hafellner 1984, Eriksson and Hawksworth 1985). Our data support the exclusion of *Schaereria* from Lecideaceae but do not provide an alternative placement with high confidence (FIG. 1). The family Schaereriaceae Choisy ex Hafellner was described to accommodate a single genus, *Schaereria* (Hafellner 1984). Morphological similarities between Schaereriaceae and Pezizales were pointed out by Hafellner

TABLE I. Lichen photobionts identified by BLAST queries in GenBank (GB; blastn, optimized for megablast) using the entire internal transcribed spacer (ITS1, 5.8S, and ITS2) of the nuclear ribosomal DNA of algae from selected *Lecidea* s. l. and putatively allied taxa

Mycobiont	Photobiont	Total score[a]	Query coverage [%][a]	Maximum identity [%][a]	GB accession number
Lecanora fuscescens[b]	*Trebouxia jamesii*	1223	98	98	HQ667317
Lecidea hercynica[c]	*T. simplex*[d]	1201	96	99	HQ667316
Lecidea leprarioides	*T. jamesii*	1083	88	99	HQ667315
Lecidea nylanderi	*T. jamesii*	928	93	90	HQ667314
Lecidea polytrichina	*T. jamesii*	1238	98	99	HQ667313
Lecidea pullata	*T. jamesii*	1225	98	99	HQ667312
Lecidea roseotincta[e]	*T. jamesii*	1218	98	99	HQ667311
	T. "roseotinctae"	1131	90	100	HQ667310
Lecidea turgidula	*T. jamesii*	1173	93	100	HQ667309
Schaereria dolodes[e]	*T. jamesii*	1214	98	99	HQ667308
	Chlorella ellipsoidea	414	64	84	HQ667307
	"uncultured Trebouxiophyceae"	327	58	81	HQ667306

[a] Total score, query coverage, and maximum identity are listed for the first best hit obtained from blasting the sequences against GenBank database.

[b] Underlined names represent taxa newly added to the five-gene supermatrix of Miadlikowska et al. (2006) and subjected to phylogenetic analyses.

[c] *Lecidea* species are in boldface.

[d] BLAST query resulted in *Trebouxia jamesii* as the top hits, but the GB accession numbers are identical to those used in Hauck et al. (2007), who identified the photobionts as *T. simplex*.

[e] Specimens in which more than one algal species was detected.

(1984), based on the lack of a tholus in the ascus, globose ascospores and the structure of the hymenium. During the next 19 y the taxonomic position of the genus was discussed controversially, based on morphological characters, ascoma ontogeny and secondary compounds (Eriksson and Hawksworth 1985, Aptroot [in Hawksworth] 1994, Hawksworth 1994, Lunke et al. 1996, Lumbsch 1997, Eriksson et al. 2003). Recent phylogenetic studies revealed an early divergence of Schaereriaceae in Ostropales (Lumbsch et al. 2007) or Ostropales s.l. and in Pertusariales and Agyriales (Wedin et al. 2005). The current Outline of Ascomycota (Lumbsch and Huhndorf 2007) lists the genus in the family Schaereriaceae with incertae sedis status in Ostropomycetidae. This uncertain placement of the genus *Schaereria* is confirmed by our data for *S. fuscocinerea* (with *Strangospora pinicola*) and *S. dolodes*.

Although the placement of *S. dolodes* in Ostropomycetidae lacks significant support, it can be explained by a shared photobiont pattern. BLAST queries showed that, similar to other families in Ostropomycetidae (e.g. Icmadophilaceae, Loxosporaceae, Pertusariaceae; Miadlikowska et al. 2006), *S. dolodes* accommodates several green algal partners. This includes *Trebouxia jamesii* and two algae of uncertain identity, one similar to *Chlorella ellipsoidea* and the second one to an uncultured Trebouxiophyceae (TABLE I).

Relationships of Schaereria *to Loxosporaceae and* Strangospora.—It is difficult to explain the sister relationship of *S. corticola* and *Loxospora* A. Massal. (significant support) because of substantial anatomical and chemical differences between the two genera (Hafellner 1984, Wirth 1995). However, the phylogenetic placement of Loxosporaceae among the first evolutionary split in Ostropomycetidae group is in agreement with previous studies (FIG. 1; e.g. Miadlikowska et al. 2006).

Strangospora pinicola was included in the phylogenetic analyses by Miadlikowska et al. (2006), where it was placed in Lecanorales outside currently delimited families. The genus *Strangospora* is currently recognized as incertae sedis in Lecanorales (Lumbsch and Huhndorf 2007). Our results suggest that *S. pinicola* is part of Ostropomycetidae and is closely related to members of *Schaereria* (*S. fuscocinerea*) but without significant support. *Strangospora pinicola* is a corticolous and lignicolous species and differs considerably in morphological characters (Körber 1865, Duke and Coppins 1992, Hafellner 1995), as well as in its chemistry, from *S. fuscocinerea*. Hafellner (1995) suggested a close affiliation between *Scoliciosporum* and *Strangospora*, because both genera have similar ascomata and *Lecanora*-type asci (Miadlikowska et al. 2006). In this study *Soliciosporum umbrinum* remains unsettled within Lecanorales (FIG. 2).

Lecanoromycetidae including Lecidea *and allied genera.*—With the addition of 22 taxa of *Lecidea* and 22 putatively allied species the inferred phylogeny for the Lecanoromycetidae (FIG. 2) does not confirm the current delimitation of Ramalinaceae, Megalariaceae, Lecanoraceae, Pilocarpaceae and Catillariaceae (Lumbsch and Huhndorf 2007).

Families Ramalinaceae and Lecanoraceae.—The family Ramalinaceae is well supported under ML in this study and therefore should now encompass Crocyniaceae (represented by *Crocynia pyxinoides* Nyl.; FIG. 2; shown also in Miadlikowska et al. 2006) and Megalariaceae (represented by the newly included *Megalaria grossa* [Pers. ex Nyl.] Hafellner). Two current members of Ramalinaceae (*Japewia tornoensis* [Nyl.] Tønsberg and *Frutidella caesioatra* [Schaer.] Kalb) need to be transferred to the Lecanoraceae. Seven additional taxa from *Lecidea* s.l. are nested within Lecanoraceae but without significant support, except for the sister relationship of *Lecidea leprarioides* with *L. turgidula* and *L. hercynica* with *Lecanora fuscescens,* which are both highly supported, and *Lecidea pullata* with *Frutidella caesioatra*, which are supported by PP (FIG. 2).

Family Pilocarpaceae.—Pilocarpaceae is not monophyletic, which also was found by Andersen and Ekman (2005), but there is no significant support for an alternative delimitation of the family (FIG. 2). The core of Pilocarpaceae (*Fellhanera*, *Calopadia*, *Byssoloma* and *Micarea*) is shown to be monophyletic and closely related to three members of *Lecidea* s.l., however, this sister relationship was without significant support. The newly added species *Micarea sylvicola* (Flot.) Vězda & Wirth (placed in Psoraceae with significant support [FIG. 2, Andersen and Ekman 2005]) is not part of the Pilocarpaceae clade. *Micarea sylvicola* is not associated with ''micareoid'' algae, which are typical for the genus, but contains instead a cholorococcoid photobiont considered by Coppins as the ''second algal type'' (1983). All species with this type of photobiont are placed outside Pilocarpaceae (Andersen and Ekman 2005).

The family Catillariaceae.—The family Catillariaceae was described to accommodate species with dark apothecia, a more or less lecideine excipulum, paraphyses sparingly branched toward the tip and apically swollen with a brown-pigmented cap, and the *Catillaria*-type ascus (Hafellner 1984). *Catillaria erysiboides*, with the *Porpidia*-type ascus and paraphyses without brown caps, probably does not belong to Catillariaceae. The genus *Catillaria* A. Massal. was recognized to be polyphyletic and is in need of taxonomic revision (Hertel et al. 2007). Its close relationship to Psoraceae and Ramalinaceae (including Bacidiaceae) was shown in Andersen and Ekman (2005). Our analysis places *Catillaria erysiboides* into one clade with Pilocarpaceae, but the result is not significantly supported (FIG. 2).

Family Lecideaceae.—The phylogenetic placement of the family Lecideaceae (excluding *Lecidoma demissum*) within Lecanoromycetidae is unsettled (FIG. 2; whereas it was shown to be sister to Peltigerales in Miadlikowska et al. 2006), and therefore Lecideaceae will retain its status as incertae sedis within Lecanoromycetidae (Lumbsch and Huhndorf 2007). In agreement with Peršoh et al. (2004) and Miadlikowska et al. (2006), Lecideaceae is monophyletic (but significantly supported only by PP) and constitutes an independent lineage, for which the name Lecideales Vain. is available at ordinal rank. All members of the genus *Lecidea* s.s. are grouped in Lecideales, whereas the majority of other members of *Lecidea* s.l. fall into various existing families within Lecanorales or represent undetermined lineages within Lecanoromycetidae (FIG. 2).

Lecidea *s.s. (Lecideaceae/Lecideales).*—Ten saxicolous species of *Lecidea*, considered to belong to *Lecidea* s.s. based on morphological characters (Hertel 1995, Hertel and Printzen 2004; FIG. 3A–D), were found to be part of the monophyletic family Lecideaceae (FIG. 2). Although some species, such as *L. atrobrunnea*, *L. fuscoatra* and *L. tessellata*, are phenotypically variable, they all share the same substrate preference (mostly siliceous rock) and general morphological characters (FIG. 3A–D). All species included in this study are crustose, with black apothecia with a persistent margin, pigmented epihymenium, simple ascospores and a *Lecidea*-type ascus (Hertel 1995, Hertel and Printzen 2004). *Lecidea fuscoatra* and *L. fuscoatra* var. *grisella* should be recognized at species rank based on morphological differences of the thallus margin and substrate preferences, according to Aptroot and van Herk (2007). *Lecidea fuscoatra* forms an areolate thallus on a prothallus at early growth stages and occurs preferentially on natural rock, whereas *L. grisella* starts with a continuous thallus and prefers artificial substrata. Because the margins of the specimens included in our phylogenetic analysis were not readily categorized and the substrate preferences for the two taxa are frequently overlapping (Aptroot and van Herk 2007), we consider both specimens as part of *L. fuscoatra* and keep the identification of *L. fuscoatra* var. *grisella* following Hertel (1995).

Except for *L. lapicida* and *L. silacea*, all species from *Lecidea* s.s. included in this study have orcinol *para*-depsides as secondary compounds, sometimes

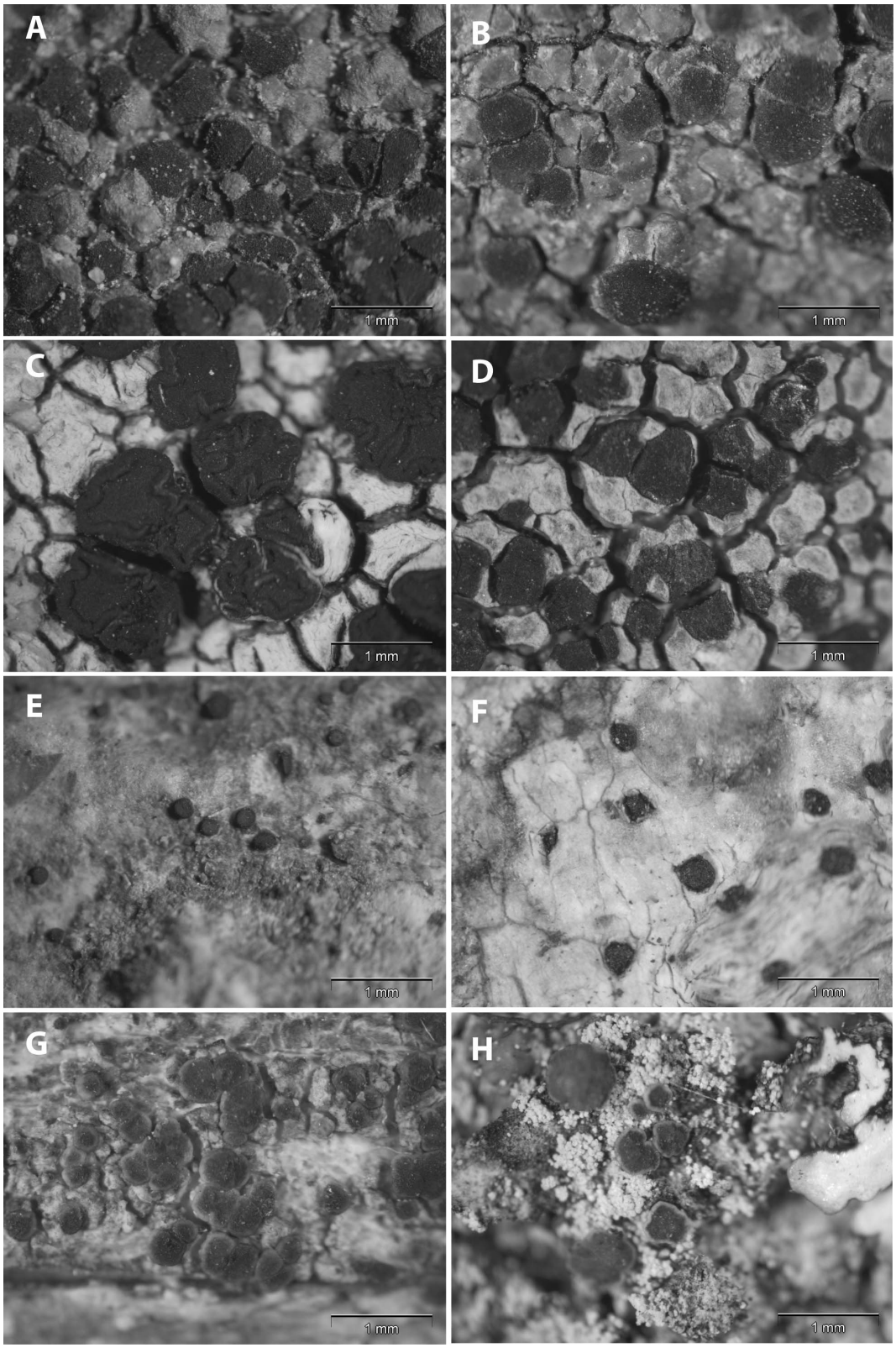


FIG. 3. Habit photographs of *Lecidea* sensu stricto (A–D) and *Lecidea* sensu lato (E–H) species. A. *Lecidea fuscoatra* (*Knudsen 9219*; Hb. FH). B. *L. atrobrunnea* (*Lay 04-0125*; Hb. Lay). C. *L. lapicida* (*Lendemer 11081*; Hb. FH). D. *L. tesselata* (*Lay 01-0360*; Hb. FH). E. *L. cyrtidia* (*Lay 07-0076*; Hb. Lay). F. *L. roseotincta* (*Tønsberg 34577*; Hb. Schmull). G. *L. hercynica* (*Hauck s.n.*, Isotype; Hb. FH). H. *L. nylanderi* (*Spribille 10020*; Hb. Spribille).

with the addition of dibezofurans or depsidones (Hertel 1995, Leuckert and Hertel 2003). Depsidones and dibenzofurans were identified only in *L. lapicida* and *L. silacea*, and in the highly variable *L. atrobrunnea* (Leuckert and Hertel 2003). Besides the orcinol *para*-depside lecanoric acid, *L. fuscoatra* and *L. fuscoatra* var. *grisella* have the orcinol tridepsides hiascic acid and gyrophoric acid (TABLE II).

Rambold (1989) introduced a subgeneric division of the genus *Lecidea* s.s. based on the combination of growth habitat and anatomical characters. *Lecidea* subg. *Lecidea* includes the type species *L. fuscoatra*, and seven other species and comprises non-alpine, mostly thermophilous species with short conidia and an I+ red to brown hymenium. Species in the *Lecidea* subg. *Rehmiopsis* (Müll.Arg.) Rambold & Pietschmann grow in more or less alpine regions and have relatively long conidia and an I+ blue to blue-brown hymenium. This subgenus includes for example *L. atrobrunnea*, *L. auriculata* and *L. lapicida*. *Lecidea tessellata* belongs to the third subgenus *Cladopycnidium* (H.Magn.) Hertel, Rambold & Pietschmann. Species from the latter subgenus grow in alpine habitats, have an I+ bluish hymenium, cylindrical conidia and thick spore walls. Our results only partially agree with this intrageneric classification mainly because of the lack of phylogenetic support and the nesting of two *Porpidia* species (*P. albocaerulescens* [Wulfen] Hertel & Knoph and *P. speirea* [Ach.] Kremp.) in *Lecidea* (FIG. 2). The non-monophyly of *Lecidea* s.s. was reported earlier by Buschbom and Mueller (2004) and Miadlikowska et al. (2006).

Two *Porpidia* species, which are part of Lecideaceae, share with *Lecidea* s.s. similar habitats, secondary compounds and trebouxioid algae. Orcinol *para*-depsides are found in *P. speirea*, whereas *P. albocaerulescens* contains depsidones (TABLE II). They differ from *Lecidea* s.s. by having halonate spores and a *Porpidia*-type ascus. However, Hertel (1987) originally pointed out that *Porpidia*- and *Lecidea*-type asci are both variable and intermediate stages can be found. A close relationship between *Porpidia* and *Lecidea* was recognized early when Körber described the genus *Porpidia* under the subfamily Lecidinae (1855). Since then *Porpidia* has been the subject of several taxonomic and molecular phylogenetic studies (e.g. Hertel 1975, 1977; Inoue 1984; Knoph 1984; Gowan 1989; Buschbom and Mueller 2004; Fryday 2005; Miadlikowska et al. 2006). *Porpidia* is divided into three infra-generic groups, two of which are represented in our study (*P. albocaerulescens* from the *P. albocaerulescens*-group and *P. speirea* from the *P. speirea*-group), according to Buschbom and Mueller (2004). However, as in our study, except for the sister relationship of *P. speirea* to *L. fuscoatra*, Buschbom and Mueller (2004) were not able to clarify phylogenetic relationships among members of *Lecidea* s.s. and *Porpidia* s.l. with high confidence. So far, the delimitation of both genera and species within each genus is still problematic and should be subjected to a comprehensive phylogenetic study.

Lecidea *s.l.*—All non-saxicolous species of *Lecidea* s.l. are distributed within Lecanoromycetidae, with the majority nested in Lecanorales, more specifically in Lecanoraceae (FIG. 2). This extended delimitation of Lecanoraceae includes taxa inhabiting wood, bark or bryophytes (FIGS. 2, 3F–H; TABLE II). All species have asci with an amyloid tholus structure with a well defined non-amyloid masse axiale, which sometimes is surrounded by a stronger amyloid tube. Ascus types that are found in this clade are the *Lecanora*-type (*Lecanora*, *Lecidea roseotincta* Coppins & Tønsberg, *Pyrrhospora*), *Lecidella*-type (*Lecidella*, *Japewia*), *Bacidia*-type (*Lecidea nylanderi* [Anzi] Th. Fr.), and the *Biatora*-type (*Lecidea polytrichina* Hertel, *L. pullata* [Norman] Th. Fr.; as a reference for ascus types see e.g. Hafellner 1984, Pruvis et al. 1992). For the following species the ascus type showed some variability and was not unambiguously assigned to a certain type; *Frutidella caesioatra* has an ascus type similar to the *Bacidia*-type or, when the amyloid tube is more strongly developed, the *Biatora*-type ascus. *Lecidea turgidula* Fr. and *Lecanora fuscescens* (Sommerf.) Nyl. have an indistinct *Lecanora*- or *Bacidia*-type ascus, whereas *Lecidea hercynica* M. Hauck & Schmull has an indistinct *Lecanora*- or *Micarea*-type ascus. In 1984 Hafellner pointed out the importance of differences in the ascus apical structure for classification purposes at family and genus ranks. He divided the large families Lecideaceae and Lecanoraceae into smaller families based almost solely on differences in ascus structure. However, several molecular studies (e.g. Ekman and Wedin 2000, Buschbom and Mueller 2004, Wedin et al. 2005, Lumbsch et al. 2007) revealed that ascus structure is not a consistent systematic character within families. In addition to the fact that it sometimes is difficult to assign a specific ascus type to particular species due to some variability in the ascus structure, several ascus types such as the *Bacidia*- and *Lecanora*-type evolved more than once and are found in phylogenetically unrelated families (Tibell 1998, Ekman and Wedin 2000, Lumbsch et al. 2001, Wedin et al. 2005, Ekman et al. 2008).

The photobionts in Lecanoraceae are broadly defined as trebouxioid (i.e. in *Japewia*, *Lecanora*, *Pyrrhospora*) or as Trebouxiaceae (*Lecidella*). For *Lecidea* species included in this study, such as *L. nylanderi*, *L. polytrichina*, *L. pullata*, *L. roseotincta* as

well as *L. turgidula*, the primary photobiont is *Trebouxia jamesii* (TABLE I). *Lecidea hercynica* differs from them by having *T. simplex* as a primary photobiont. *Trebouxia simplex* is morphologically very similar to the type culture of *T. jamesii* and therefore was suggested by Friedl (1989) to represent a synonym of the latter. Molecular data do not confirm the affiliation of *T. jamesii* with the *T. simplex* complex but support the importance of pyrenoid size as a diagnostic character for species delimitation in the genus *Trebouxia* (Beck 2002, Hauck et al. 2007). Except for *L. roseotincta*, all *Lecidea* species placed in Lecanorales have no secondary photobiont. *Lecidea roseotincta* has an additional photobiont from the genus *Trebouxia*, similar to the *T. arboricola* and *T. asymmetrica* group based on the similarity of the ITS sequence (Schmull unpubl; TABLE I).This secondary photobiont may represent a new species, *T.* ''*roseotinctae*'', according to our results (TABLE I).

''Group 1'' (in FIG. 2).—The close relationship between *Frutidella caesioatra* and *Lecidea pullata*, significantly supported by PP value, is corroborated by morphological and chemical characters. In both species the epihymenium and the outer parts of the excipulum are pigmented (yellowish brown and greenish blue respectively), the greenish blue pigment reacting red with HNO_3. Sphaerophorin, an uncommon secondary metabolite from the group of the *para*-depsides, can be detected in both species. Additionally an unknown dibenzofuran was identified in *L. pullata* (TABLE II). The paraphyses are branched and anastomosing, apically not or rarely slightly swollen, and the ascospores are simple in both species. A new combination for *F. pullata* (Norman) Schmull is proposed (TAXONOMY).

The genus *Frutidella* originally was described by Kalb (1994) to accommodate a single species, *F. caesioatra*, and was placed in Biatoraceae. Currently *Frutidella* is included in Ramalinaceae (Lumbsch and Huhndorf 2007), a family characterized by fruticose or crustose growth forms, *Bacidia*- or *Biatora*-type asci, (simple to) transversely septate spores and a rare group of orcinol *meta*-depsides (Ekman 2001, Lumbsch et al. 1995). Although *F. caesioatra* has the *Bacidia*- to *Biatora*-type ascus and simple spores, it does not produce the orcinol *meta*-depsides but instead the orcinol *para*-depside sphaerophorin. Based on the phenotypic features and molecular data included in molecular phylogenetic studies (Andersen and Ekman 2005, Ekman et al. 2008), the monotypic *Frutidella* should be considered a member of Lecanoraceae.

Another representative of familiy Ramalinaceae nested within Lecanoraceae is *Japewia tornoensis*. The genus *Japewia* (Tønsberg 1990) was introduced based on an ascus structure similar to the one found in the family Bacidiaceae (Tønsberg 1990, Eriksson and Hawksworth 1991), which is currently considered conspecific with Ramalinaceae (Ekman 2001). A broader circumscription of Lecanoraceae resulting from phylogenetic analyses (FIG. 2; Arup et al. 2007) suggests that *Japewia* belongs to Lecanoraceae.

Highly supported by our data is the sister relationship between *Lecidea leprarioides* and *L. turgidula* (FIG. 2). *Lecidea leprarioides* originally was described as a variety of *L. turgidula* (*L. turgidula* var. *pulveracea* Th.Fr.) before it was raised to species rank (Tønsberg 1992). *Lecidea leprarioides* differs from *L. turgidula* by having a sorediate thallus (*L. turgidula* being esorediate) and by chemistry (*L. leprarioides* containing pseudoplacodiolic acid and *L. turgidula* containing placodiolic acid; TABLE II).

The sister relationship of *Lecanora fuscescens* and *Lecidea hercynica* within Lecanoraceae is surprising because these species differ morphologically and chemically (e.g. Hawksworth and Dalby 1992, Ryan et al. 2004a, Schmull and Hauck 2005; TABLE II; FIG. 3G). Atranorin and protocetraric acid originally were reported as secondary metabolites of *L. hercynica* (Schmull and Hauck 2005), however, subsequent studies revealed presence of usnic acid and probably argopsin (TABLE II). Pérez-Ortega et al. (2010; Erratum published online 1 Dec 2010) included *L. hercynica* in their study of the *Lecanora varia* group (listed as *Lecanora filamentosa* 1) and established the species within *Lecanora* in the informal ''filamentosa group'' (with significant PP and ML bootstrap support). The authors introduced a new combination, *Lecanora filamentosa* (Stirt.) Elix & Palice, and included *Lecanora ramulicola* (H. Mag.) Printzen & P.F. May in the synonymy. *Lecanora ramulicola* displays high phenotypical plasticity and shares morphological features with *Lecanora hercynica* (Pérez-Ortega and Printzen 2007). However *Lecidea hercynica* was not synonymized in Pérez-Ortega et al. (2010). The potential close relationship between these two species needs to be tested phylogenetically; unfortunately, due to the lack of fresh material, *Lecanora filamentosa* could not be included in this study. The genus *Lecanora* is known to be heterogeneous, and many phylogenetic relationships within and among informal groups recognized within this genus remain unresolved (e.g. Arup and Grube 1998, 2000; Pérez-Ortega et al. 2010; Sliwa et al. unpubl). *Lecanora* is in great need of a comprehensive phylogenetically based taxonomic revision.

''Group 2'' (in FIG. 2).—Members of the unsupported clade containing *Catillaria erysiboides, Protomicarea*

TABLE II. Secondary compounds and substrate preferences for species from *Lecidea* s.l. and closely related taxa selected for this study. Underlined names represent taxa added to the five-gene supermatrix of Miadlikowska et al. (2006) and subjected to phylogenetic analyses as part of this study. *Lecidea* species are in boldface. Lowercase letters in superscript indicate literature references used to complete this table. Rare substrates are in parenthesis

Taxon	Secondary compounds	Substrates
Byssoloma leucoblepharum	none[a]	foliicolous & corticolous[a]
Calopadia foliicola	2,7-dichlorolichexanthone, pannarin[b]	foliicolous[c]
Catillaria erysiboides	none	lignicolous
Fellhanera bouteillei	none[d]	foliicolous (corticolous)[d]
Fellhanera subtilis	none[d]	corticolous & foliicolous (lignicolous)[d]
Frutidella caesioatra	sphaerophorin[e]	muscicolous[e]
Japewia tornoensis	none[f]	corticolous & lignicolous[f]; on terricolous bryophytes & on humus in rock crevices[g,h]
Lecanora achariana	zerorin, usnic acid, unidentified triterpenoids[i]	saxicolous[i]
Lecanora concolor	major compound: usnic acid[k]	saxicolous[j]
Lecanora contractula	major compound: usnic acid[k]; 2,5-dichloro-6-*O*-methylnorlichexanthone, 5-chloro-6-*O*-methylnorlichexanthone, 5-chlorolichexanthone[l]	saxicolous[l]
Lecanora fuscescens	lobaric, fumarprotocetraric & confumarprotocetraric acids[m]	corticolous
Lecanora hybocarpa	atranorin, chloratranorin, roccellic acids[m]	corticolous[m]
Lecanora intumescens	atranorin, chloratranorin, psoromic & 2′-*O*-demethylpsoromic acid, lichexanthone, zeorin[i]	corticolous[i]
Lecanora muralis	atranorin, murolic, psoromic & usnic acids, zeorin; fumarprotocetraric acid[i]	saxicolous; corticolous & lignicolous[i]; terricolous[x]
Lecanora polytropa	rangiformic, usnic, & eulecanoral acids, zeorin[i]	saxicolous (processed wood)[i]
Lecidea atrobrunnea	2′-*O*-methylperlatolic, norsticric, stictic acid[ee]	saxicolous
Lecidea auriculata	confluentic acid[g]	saxicolous
Lecidea berengeriana	none[n]	muscicolous (corticolous or terricolous)
Lecidea confluens	confluentic acid[o]	saxicolous[o]
Lecidea cyrtidia	unknown (all spot test reactions negative)	saxicolous
Lecidea diapensiae	trace of atranorin	foliicolous on *Diapensia lapponica*
Lecidea floridensis	none; unidentified xanthones[n]	corticolous
***Lecidea fuscoatra* 1**	three chemotypes[n]: gyrophoric acid syndrome; gyrophoric acid syndrome & 2′-*O*-methylperlatolic acid; gyrophoric acid syndrome & schizopeltic acid; unknown which chemotype represents the specimen used in this study	saxicolous
***Lecidea fuscoatra* 2**	lecanoric, hiascic & gyrophoric acids	saxicolous
Lecidea fuscoatra* var. *grisella	lecanoric, hiascic & gyrophoric acids	saxicolous
Lecidea hercynica	usnic acid, ?argopsin	lignicolous
Lecidea* cf. *hypnorum	none	muscicolous (corticolous)
Lecidea laboriosa	4-*O*-demethylplanaic acid; planaic acid or none[n]	saxicolous[n]
Lecidea lapicida	stictic & constictic acids[g]	saxicolous
Lecidea leprarioides	pseudoplacodiolic & usnic acids, unknown depsidone	corticolous & lignicolous
Lecidea nylanderi	divaricatic, sphaerophoric, gyrophoric & psoromic acids, atranorin	corticolous
Lecidea polytrichina	atranorin, usnic, 2-*O*-demethylpsoromic, subpsoromic & psoromic acids	muscicolous
Lecidea pullata	sphaerophoric acid (trace of unknown dibenzofurane)	corticolous
Lecidea roseotincta	psoromic acid	corticolous
Lecidea sanguineoatra	none[g]	muscicolous[g]
Lecidea silacea	porphyrillic acid[g]	saxicolous[g]
Lecidea tessellata	confluentic acid[n] (all spot test reactions negative)	saxicolous
Lecidea turgidula	none; placodiolic acid[cc]	corticolous (lignicolous[g])
***Lecidea* sp. 1**	unknown (K + yellowish, C-, KC-, P + yellow)	corticolous
***Lecidea* sp. 2**	unknown (all spot test reactions negative)	saxicolous

TABLE II. Continued

Taxon	Secondary compounds	Substrates
Lecidella elaeochroma	several chemotypes[p]; unknown which chemotype represents the specimen used in this study	corticolous & lignicolous[p]
Lecidella euphorea	2,5,7-trichloro-3-*O*-methylnorlichexanthone, 3-*O*-methylasemone & 3-*O*-methylthiophanic acids, 5,7-dichloro-3-*O*-methylnorlichexanthone, atranorin, isoarthothelin, thiophanic acid[p]	corticolous & lignicolous[p]
Lecidella meiococca	2,5,7-trichloro-3-*O*-methylnorlichexanthone, atranorin, isoarthothelin or thiophanic acid[p]	saxicolous (lignicolous)[p]
Leimonis erratica	none[r]	saxicolous (lignicolous)[r]
Megalaria grossa	none[q]	corticolous (saxicolous)[q]
Micarea adnata	none[s]	lignicolous & corticolous[s]
Micarea alabastrites	gyrophoric, lecanoric & 5-*O*-methylhiascic acids[t]	corticolous, muscicolous, lignicolous (saxicolous)[s]
Micarea doliiformis	usnic acid	corticolous & lignicolous
Micarea micrococca	methoxymicareic acid[u]	corticolous (saxicolous)[u]
Micarea sylvicola	none[v]	saxicolous (lignicolous)[s]
Porpidia albocaerulescens	two chemotypes[x]: stictic & cryptostictic acids; norstictic & connorstictic acids; unknown which chemotype represents the specimen used in this study	saxicolous[x]
Porpidia speirea	confluentic, 2′-*O*-methylmicrophyllinic & 2′-*O*-methylperlatolic acids[y]	saxicolous[y]
Protomicarea limosa	pannarin, hypopannarin, dechloro-pannarin	muscicolous (terricolous)
Psilolechia leprosa	gyrophoric & porphyrillic acids[z]	saxicolous[z]
Psilolechia lucida	rhizocarpic acid[z]	saxicolous (corticolous & lignicolous)[z]
Pyrrhospora quernea	two chemotypes[aa]: unknown which chemotype represents the specimen used in this study	corticolous (lignicolous & saxicolous)[aa,bb]
Schaereria corticola	gyrophoric, lecanoric & 5-*O*-methyhiascic acids[cc]	corticolous[cc]
Schaereria fuscocinerea	gyrophoric acid[x]	saxicolous[x]
Schaereria dolodes	gyrophoric, lichesterinic & protolichesterinic acids	corticolous
Strangospora pinicola	none[dd]	corticolous (lignicolous)[dd]

[a]Sérusiaux (1992); [b]Elix and Øvstedal (2009); [c]Lücking (1999); [d]Coppins (1992a); [e]Kalb (1994); [f]Printzen and Tønsberg (2004); [g]Hawksworth and Coppins (1992); [h]Olech (2004); [i]Hawksworth and Dalby (1992); [j]Obermayer and Poelt (1992); [k]Arup and Grube (2000); [l]Elix and Crook (1992); [m]Ryan et al (2004a); [n]Hertel and Printzen (2004); [o]Hertel and Andreev (2003); [p]Knoph and Leuckert (2004); [q]Coppins (1992b); [r]Harris (2009); [s]Coppins (1992c); [t]Tønsberg and Coppins (2000); [u]Fryday and Coppins (2007); [v]Coppins (1983); [x]Brodo et al (2001); [y]Galloway and Coppins (1992); [z]Coppins and Purvis (1992); [aa]Ryan et al (2004b); [bb]Hawksworth (1992); [cc]Tønsberg (1992); [dd]Duke and Coppins (1992); [ee]Leuckert and Hertel (2003)

limosa (Ach.) Hafellner (syn. *Lecidea limosa* Ach.), *Psilolechia leprosa* and *P. lucida* are characterized by a *Porpidia*-type ascus, share ovoid spores, and trebouxioid photobionts (*Trebouxia asymmetrica* or possibly *Chlorella* sp. in the case of *C. erysiboides*; Schmull unpubl), or *Stichococcus* in the case of *Psilolechia* (Brodo et al. 2001) but grow on different substrates (TABLE II). *Lecidea limosa* was transferred to the genus *Protomicarea* by Hafellner (Hafellner and Türk 2001). The genus currently is listed as a questionable taxon within Psoraceae by Lumbsch and Huhndorf (2007), which is confirmed by our data (FIG. 2). *Psilolechia* was included tentatively in Micareaceae (Hafellner 1984) and later transferred to Pilocarpaceae (Eriksson 2005). Its placement in Pilocarpaceae (Micareaceae are included in Pilocarpaceae; FIG. 2; Andersen and Ekman 2005) is confirmed by our data, however, without strong support.

Sister to the core group of Pilocarpaceae (*Byssoloma*, *Calopadia*, *Fellhanera* and *Micarea*) are *Lecidea cyrtidia* Tuck., *L. floridensis* Nyl., and *L.* sp. 1 (without support) with *Micarea doliiformis* (Coppins & P. James) Coppins & Sérus. (FIG. 2; without support; syn. *Lecidea doliiformis* Coppins & P. James; Sérusiaux et al. 2010). *Leimonis erratica* (Körb.) R.C. Harris & Lendemer seems to have diverged early during the evolution of Group 2 (FIG. 2; without support; syn. *Lecidea erratica* Körb. and *Micarea erratica* (Körb.) Hertel, Rambold & Pietschm.; Harris 2009), which also was reported in a phylogenetic study by Andersen and Ekman (2005). The two corticolous species *L. floridensis* and *L.* sp. 1 are significantly supported by

ML bootstrap but share no obvious phenotypical characters. In contrast to *L. floridensis* (e.g. Hertel and Printzen 2004), the apothecia of *L.* sp. 1 have a colorless hypothecium and a well defined red-brown (K+ olivaceous) excipulum whose edges are covered by brown pigment granules that disappears with age. The clavate asci resemble the *Biatora*- or *Bacidia*-type. The phylogenetic placement of these two species as a monophyletic group remains uncertain in our study.

The possible relationship between *Lecidea cyrtidia* and *Leimonis erratica* was discussed by Brodo (1968) and Harris (1997) based on similar habitat preferences and phenotypical appearance (FIG. 3E). However, Brodo (1968) pointed out the differences between these two species in the epithecium and the outer portions of the excipulum. Although Harris (1997) initially proposed the inclusion of *L. cyrtidia* in *Micarea*, he did not do so due to the anatomical differences between the genera. Sérusiaux et al. (2010) suggested broadening the circumscription of the genus *Leimonis* to accommodate additional taxa such as *Micarea assimilata* and *M. doliiformis*; the latter species was transferred from the genus *Lecidea* to *Micarea* based on the close relationship with *M. paratropa*, *M. assimilata* and *Leimonis erratica* (Sérusiaux et al. 2010). Our results do not support the suggested broader circumscription of the genus *Leimonis* (FIG. 2); however, higher phylogenetic confidence and broader taxon sampling is needed to reach a stable classification of the genus *Micarea* and its allied taxa.

"Group 3" (in FIG. 2).—Another phylogenetically unsettled significantly supported clade of *Lecidea* s.l. includes *Lecidea diapensiae*, *L.* cf. *hypnorum* and *L. sanguineoatra*. *Lecidoma demissum* (Lecideaceae) was found to be sister to this well supported monophyletic group, however, this relationship did not receive significant support (FIG. 2). This is contrary to the placement of *Lecidoma* in Lecideaceae/Lecideales together with saxicolous *Lecidea* s.s. reported in Miadlikowska et al. (2006; but supported only by PP). While the above *Lecidea* species grow on plants as epiphytes (TABLE II), *Lecidoma demissum* is found mainly on soil and sporadically on decaying plants (Brodo et al. 2001).

Lecidea cf. *hypnorum* and *L. sanguineoatra* belong to the *Lecidea hypnorum* group, which is in need of a taxonomic revision. Currently some authors treat this group under the genus *Mycobilimbia* s.l. (Wirth 1987, Hafellner 1989, Ekman 2004). *Mycobilimbia* s.l. differs from *Mycobilimbia* s.s. by including taxa with simple spores, the *Porpidia*-type ascus, and often the presence of bluish granules in the hymenium and hypothecium (Ekman 2004). *Lecidea* cf. *hypnorum* and *L. sanguineoatra* differ in their ecology, with *L. sanguineoatra* growing preferentially on bryophytes from acidic substrates and *L.* cf. *hypnorum* on bryophytes (TABLE II) and bark from more basic substrates. *Lecidea hypnorum* is found additionally on plant debris on basic soil (Wirth 1987, Hawksworth and Coppins 1992). *Lecidea sanguineoatra* also can be distinguished from *L. hypnorum* by the lack of bluish granules in the hymenium (Kalb and Hafellner 1992) and narrower ascospores (Hawksworth and Coppins 1992).

"Group 4" (in FIG. 2).—Another member of the *Lecidea hypnorum*-group included in our analyses is *Lecidea berengeriana* (Ekman 2004) with an undetermined placement within Lecanoromycetidae (FIG. 2). This species was included in the genus *Mycobilimbia* (Wirth 1987), currently classified in Lecideaceae (Lumbsch and Hundorf 2007). Morphologically and anatomically *L. berengeriana* is similar to *Mycobilimbia* but differs in having simple ascospores (*Mycobilimbia* has 1–3-septate ascospores) and a *Porpidia*-like type ascus (*Mycobilimbia* is characterized by an apical ascus structure with a relatively short, strongly amyloid, ring- or tube-like structure).

General conclusions.—This phylogenetic study confirms the artificial genus concept of *Lecidea* s.l. used by Zahlbruckner and shows a scattered phylogenetic distribution of its members within Lecanoromycetes. Our phylogeny supports the monophyletic recognition of order Lecideales incorporating saxicolous taxa from *Lecidea* s.s. and members of *Porpidia*. Several non-saxicolous species from *Lecidea* s.l. are placed in various families in order Lecanorales, but some were found outside currently recognized families in this order. Phylogenetic affiliation and systematic placement of a number of taxa remain unsettled mainly due to the lack of significant support in our phylogeny. However, many reconstructed but poorly supported relationships can be explained by phenotypic similarities (morphology, anatomy and chemistry), as well as common habitats and photobiont patterns. To disentangle questionable relationships and clarify taxonomic position of members of *Lecidea* s.l. further phylogenetic and systematic studies should be conducted in a broad context of Lecanoromycetes, especially Lecanoromycetidae, but also independently in smaller groups within this class and subclass. Future studies require better taxon sampling and more complete molecular data, including new loci.

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