Molecular phylogenetics and taxonomy of *Hypocenomyce* sensu lato (Ascomycota: Lecanoromycetes): Extreme polyphyly and morphological/ecological convergence

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Abstract We have addressed phylogenetic relationships and tested hypotheses about five presumed subgroups among 15 species of *Hypocenomyce* s.l. (including *Pycnora*) by use of nuclear (ITS, LSU) and mitochondrial (SSU) ribosomal DNA-regions. Bayesian, likelihood and parsimony phylogenetic analyses, of a dataset with broad Lecanoromycete taxon sampling, mostly support the five presumed subgroups, but two of these were found to be polyphyletic (the *H. friesii*-group and *Pycnora*). The seven supported *Hypocenomyce* s.l. clades belong in different genera, families, orders and even subclasses, and represent a remarkable example of morphological and ecological convergence. Based on our molecular phylogenetic results, we split *Hypocenomyce* into four genera placed in two subclasses: (1) *Carbonicola* gen. nov. (Carbonicolaceae fam. nov., Lecanorales, Lecanoromycetidae; including *C. anthracophila* comb. nov., *C. foveata* comb. nov., and *C. myrmecina* comb. nov.); (2) *Fulgidea* gen. nov. (Umbilicariaceae, Umbilicariales, Umbilicariomycetidae subcl. nov.; including *F. oligospora* comb. nov. and *F. sierrae* comb. nov.); (3) *Hypocenomyce* (Ophioparmaceae, Umbilicariales; including *H. australis*, *H. scalaris*, and *H. tinderryensis*; and (4) *Xylopsora* gen. nov. (Umbilicariaceae; including *X. caradocensis* comb. nov. and *X. friesii* comb. nov.). We split *Pycnora* into two genera: (1) *Pycnora* (Pycnoraceae fam. nov., Candelariales, "Candelariomycetidae"; including *P. praestabilis*, *P. sorophora*, and *P. xanthococca*); and (2) *Toensbergia* gen. nov. (Sporastatiaceae fam. nov., unknown order, Lecanoromycetidae; including *T. leucococca* comb. nov.). We place *Hypocenomyce isidiosa* in *Xylographa* (Trapeliaceae, Baeomycetales, Ostropomycetidae; *X. isidiosa* comb. nov.). We place the family Ophioparmaceae in the Umbilicariales. Our type studies have shown that the epithet "*myrmecina*" should replace "*castaneocinerea*", and lectotypes are chosen for *Lecidea friesii* Ach., *L. scalaris* var. *myrmecina* Ach., *Psora cladonioides* var. *albocervina* Räsänen, and *P. cladonioides* var. *castaneocinerea* Räsänen. *Elixia cretica* is reported as new to North America (from Mexico) and Australia.

Keywords burnt wood; *Hypocenomyce*; lecideoid lichens; molecular phylogenetics; polyphyly; taxonomy

Supplementary Material The Electronic Supplement (Figs. S1 and S2) and the alignment files are available in the Supplementary Data section of the online version of this article (http://www.ingentaconnect.com/content/iapt/tax).

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■ INTRODUCTION

The lichen genus *Hypocenomyce* M. Choisy grows on bark and wood, especially on burnt trunks and stumps in conifer forests (Fig. 1). *Hypocenomyce* sensu lato (s.l.; including *Pycnora* Hafellner) is widely distributed in the Northern Hemisphere and also occurs in Australia. Seventeen species have been assigned to *Hypocenomyce*, of which two have been shown to belong elsewhere (reviewed below). Timdal (1984a) revised the genus and identified four evolutionary groups. More recently described *Hypocenomyce* species have been assigned to one of these groups or to a fifth group. The characters uniting the five groups are mainly morphological and ecological, and Timdal (1984a: 93) hypothesized that the genus was polyphyletic. Table 1 shows the main anatomical and chemical differences between the five species groups based on the data of Timdal (1984a, 2001, 2002) and Elix (2009). Although the *Hypocenomyce xanthococca*-group (Table 1), which does not grow on burnt wood, was raised to the level of genus (as *Pycnora*) by Hafellner in Hafellner & Türk (2001), all four species assigned to that group are included in the present study together with the eleven remaining *Hypocenomyce* species.

Two *Hypocenomyce* (*H. friesii* (Ach.) P. James & Gotth. Schneid. and *H. scalaris* (Ach.) M. Choisy) and two *Pycnora* (*P. sorophora* (Vain.) Hafellner and *P. xanthococca* (Sommerf.) Hafellner) species were included in a molecular phylogenetic study of the Lecanoromycetes by Wedin & al. (2005). Their phylogenetic results corroborated a polyphyletic *Hypocenomyce* s.l.: (1) *Hypocenomyce friesii* was strongly supported as sister to *Umbilicaria* Hoffm.; (2) *H. scalaris* (two accessions) was sister to a clade consisting of *Boreoplaca* Timdal and *Ophioparma* Norman; and, (3) a clade of *P. sorophora* and *P. xanthococca* was either sister to the Acarosporaceae (parsimony) or the Candelariaceae (Bayesian). The *H. scalaris*–*Boreoplaca*–*Ophioparma* group was corroborated in a separate study of Lecanoromycetes phylogeny (Miądlikowska & al., 2006), in which two different collections of *H. scalaris* were included.

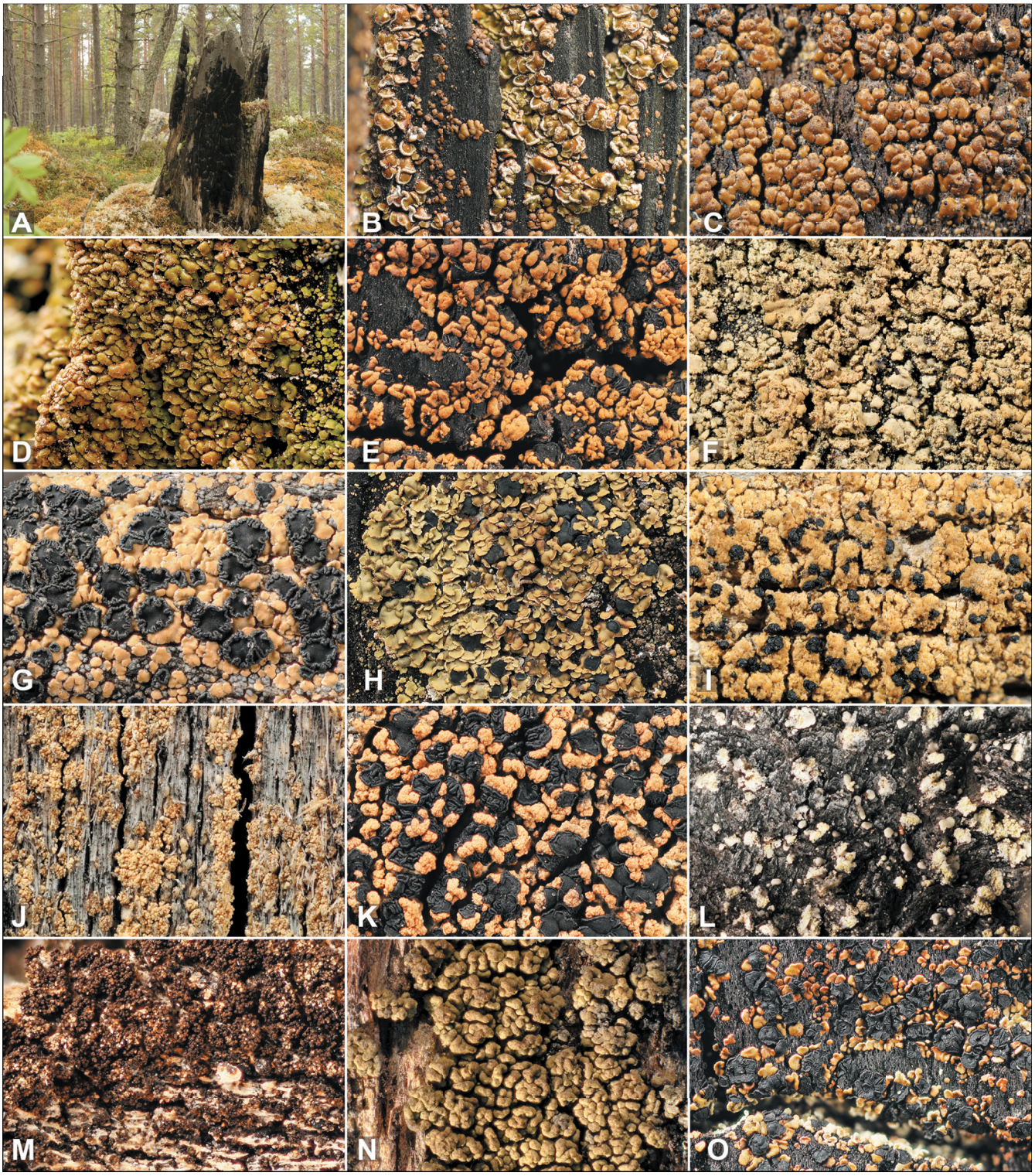


Fig. 1. A, typical habitat, burnt stump in boreal pine forest, Norway; **B,** *Carbonicola anthracophila*, Norway (O L-179442); **C,** *C. foveata*, Australia (O L-50, holotype); **D,** *C. myrmecina*, Norway (O L-179443); **E,** *Fulgidea oligospora*, U.S.A. (O L-767, holotype); **F,** *F. sierrae*, U.S.A. (O L-60059, holotype); **G,** *Hypocenomyce australis*, Australia, *Elix 6153* (CANB); **H,** *H. scalaris*, Sweden (O L-170870); **I,** *Pycnora praestabilis*, Sweden (O L-144278); **J,** *P. sorophora*, Sweden (O L-144312); **K,** *P. xanthococca*, Norway (O L-149736); **L,** *Toensbergia leucococca*, Norway (O L-170828); **M,** *Xylographa isidiosa*, Australia (CANB 737037-1, isotype); **N,** *Xylopsora caradocensis*, Norway (O L-73317); **O,** *X. friesii*, Norway (O L-158541). — Photos: E. Timdal.

Table 1. Morphological and chemical differences between the five *Hypocenomyce* species groups. Black dot means presence of the character, black dot in brackets means that the character is rarely present, and questions mark means unknown.

Species group	*anthracophila*	*friesii*	*oligospora*	*scalaris*	*xanthococca*
Additional species	*castaneocinerea foveata*	*caradocensis isidiosa*	*sierrae*	*australis tinderryensis*	*leucococca praestabilis sorophora*
Apothecia					
brown, convex	●				
black, plane		●	●	●	●
Proper exciple					
entirely conglutinated; hyphae thick-walled, with thread-like lumina; inner part colorless; rim pale brown; not containing crystals	●				
entirely conglutinated, hyphae thin-walled, with ellipsoid lumina; inner part and rim blackish brown; not containing crystals		●	●		●
only partly conglutinated, hyphae thin-walled, with ellipsoid lumina; inner part colorless; rim green; containing crystals (lecanoric acid)				●	
Epihymenium					
brown, N−	●	●	●		
green, N+ violet				●	●
without amorphous substances	●			●	
with amorphous substances, effusion in K brown		●	●		
with amorphous substances, effusion in K violet					●
Paraphyses					
capitate, with an apical brown pigment cap	●				
not capitate, without pigment cap		●	●	●	●
Ascus					
clavate, without cap; tholus with amyloid tube	●				
clavate, without cap; tholus with lateral amyloid zone					●
rhombic, with apical cap; tholus small, deeply amyloid		●	●	?	
immature			(●)	●	
Pycnidum wall					
brown, N−	●	●	●		
green, N+ violet				●	●
Pycnoconinida					
filiform	●			●	
bacilliform		(●)	●	●	(●)
ellipsoid		●			●
subglobose					●
Main secondary compound					
alectorialic acid			●		●
colensoic acid	●				
friesiic and/or confriesiic acid		●			
lecanoric acid				●	
thamnolic acid			●		

Taxonomic history. — *Hypocenomyce* was introduced by Choisy (1951) for the single species *H. scalaris* which had been placed in *Lecidea* Ach. sect. *Psora* (Hoffm.) Schaer. by Zahlbruckner (1925, as *Lecidea ostreata* (Hoffm.) Schaer.) The genus was originally characterized by having a squamulose thallus, lecideine, adnate apothecia and short, straight, cylindrical pycnoconidia. Choisy (1953) later also included *H. rubiformis* (Ach.) M. Choisy in the genus; a species which is now regarded as belonging in *Psora* Hoffm. (as *P. rubiformis* (Ach.) Hook., cf. Timdal, 1984b; Ekman & Blaalid, 2011) and is not discussed further in this paper.

Schneider (1980) proposed a new generic arrangement for the species placed in *Lecidea* sect. *Psora* sensu Zahlbruckner. He accepted *Hypocenomyce* and added two more squamulose species to it, *H. anthracophila* (Nyl.) P. James & Gotth. Schneid. and *H. friesii*. Three more species were soon added, one transferred from *Toninia* A. Massal. (*H. caradocensis* (Nyl.) P. James & Gotth. Schneid. in Hawksworth & al., 1980) and two crustose species from *Lecidea* sect. *Lecidea* sensu Zahlbruckner (*H. xanthococca* (Sommerf.) P. James & Gotth. Schneid. in Hawksworth & al., 1980, and *H. sorophora* (Vain.) P. James & Poelt in Poelt & Vězda, 1981).

Timdal (1984a) revised *Hypocenomyce* and added four more species to it (*H. australis* Timdal, *H. castaneocinerea* (Räsänen) Timdal, *H. foveata* Timdal, and *H. praestabilis* (Nyl.) Timdal). He recognized four groups of species within the genus, based on anatomical and chemical characters: the *H. anthracophila*-, *H. friesii*-, *H. scalaris*- and *H. xanthococca*-groups (Table 1). The characters uniting the four groups were found to be mainly morphological (thallus) and ecological, and he expressed doubts about the homogeneity of the genus.

Abassi Maaf & Roux (1984) described *H. stoechadiana* Abassi & Cl. Roux, but that species is now placed in *Waynea* Moberg (Roux & Clerc, 1991) and is not treated further here. Santesson (in Moberg, 1986) described *H. leucococca* R. Sant. from sterile material, and its inclusion in *Hypocenomyce* seems to have been based on its general resemblance in morphology, secondary chemistry and ecology with species of the *H. xanthococca*-group. Hafellner (1993) placed *H. anthracophila* and *H. foveata* in the genus *Biatora* Fr., a view that was not supported by Printzen (1995) in his revision of the European species of *Biatora*. As mentioned above, Hafellner (in Hafellner & Türk, 2001) raised the *H. xanthococca*-group to the level of genus, but no new data were presented to support this arrangement and we hence include *Pycnora* in this study. Timdal (2001) described two new species (*Hypocenomyce oligospora* Timdal and *H. sierrae* Timdal) which in morphological (thallus shape) and anatomical (apothecial pigments, proper exciple, ascus type) characters seemed to bridge the *H. friesii*- and *H. scalaris*-groups and also shared the secondary chemistry (alectorialic acid) with the *H. xanthococca*-group. The two species are here regarded as representing a fifth group, the *H. oligospora*-group. Finally, Elix (2006, 2007) described two new species from Australia, *H. isidiosa* Elix and *H. tinderryensis* Elix, which may be placed in the *H. friesii*- and *H. scalaris*-groups, respectively.

Aims. — Our aim with the present study was to test whether the suggested five species groups are supported by DNA sequence data, and to reveal their phylogeny. The molecular phylogenetic study of Wedin & al. (2005) only included two *Hypocenomyce* and two *Pycnora* species, which represent three of the five presumed *Hypocenomyce* s.l. subgroups. In the present study, we included DNA sequences data of all currently recognized species of *Hypocenomyce* (11 spp.) and *Pycnora* (4 spp.), some presumed relatives, and a broad taxon sampling of the entire Lecanoromycetes (the latter sequences obtained from public databases). Based on our molecular phylogenetic results, we propose several taxonomic and nomenclatural changes.

■ MATERIALS AND METHODS

Taxon sampling. — For this molecular phylogenetic and taxonomic study of *Hypocenomyce*, we used herbarium specimens of varying age (up to 45 years old) held at the following herbaria: ASU, CANB, O, and S. The *Hypocenomyce* s.l. specimens studied originated from Australia, Norway, Russia, Sweden and the U.S.A. We have extracted DNA from multiple specimens of all *Hypocenomyce* s.l. species (41 accessions in total) as well as selected species relevant for the phylogenetic placement of *Hypocenomyce* (i.e., *Biatora*: 1, *Catillaria* A. Massal.: 1, *Elixia* Lumbsch: 5, *Ophioparma*: 3, and *Xylographa* (Fr.) Fr.: 3). These numbers include four collections presumed to belong in *Hypocenomyce* (collected and sequenced as *Hypocenomyce* sp.), but, based on the DNA sequences, later identified as *Elixia cretica* T. Sprib. & Lumbsch (*E. cretica*, specimens 1 and 2) and a possibly new species of *Elixia* (*Elixia* sp., specimens 1 and 2). We generated 113 DNA sequences of the nuclear ribosomal internal transcribed spacer region (nrITS: ITS1, 5.8S, ITS2) and large subunit (nrLSU; partial), and the mitochondrial small subunit (mtSSU; partial). Corresponding sequences of additional taxa (covering most relevant Lecanoromycete taxa from family level and above) were obtained from GenBank. We have, mostly during previous studies, examined the morphology and the secondary chemistry of type specimens of all currently accepted species of *Hypocenomyce* s.l. with the exception of *H. scalaris* which has never been typified. Thin-layer chromatography (TLC) was performed in accordance with the methods of Culberson (1972), modified by Menlove (1974) and Culberson & Johnson (1982). See Appendix 1 for voucher information for all DNA extracted specimens.

DNA extraction. — We crushed up to 5 mg of tissue (apothecia, if present) from 54 archived specimens in 2 mL plastic tubes with two tungsten carbide beads in each for 2 × 1.5 min at 23 Hz on a mixer mill (MM301, Retsch GmbH & Co., Haan, Germany). We extracted total DNA from the crushed samples using the E.Z.N.A SP Plant DNA Mini Kit (Omega Bio-tek, Inc., Norcross, Georgia, U.S.A.) according to the manufacturer's manual. We performed additional steps related to the elution for increasing DNA yield (as suggested in the manual), such as eluting twice, using the first eluate also the second time, and

pre-warming to 65°C for 5 min prior to spinning. We deposited all DNA aliquots used in the present study in the DNA tissue collection at The Natural History Museum, Oslo (O).

PCR amplification and DNA sequencing. — We amplified DNA in 25 µL reactions using the AmpliTaq GOLD DNA polymerase buffer II kit (Applied Biosystems, Foster City, California, U.S.A.) containing 0.2 mM of each dNTP, 0.04% bovine serum albumen (BSA), 0.01 mM tetramethylammonium chloride (TMACl), 0.4 µM of each primer, and 2 µL unquantified genomic DNA. We performed all amplifications in a GeneAmp PCR System 9700 (Applied Biosystems) using the following cycling conditions: 95°C for 10 min, 32 (nrITS, nrLSU) or 34 (mtSSU) cycles of 95°C for 30 s, 60°C for 30 s, 72°C for 1 min, followed by 72°C for 10 min and hold forever at 10°C. For DNA extracts that would not amplify using the above described approach, we amplified shorter fragments or used the replicate procedure described in Bendiksby & al. (2011). We designed 10 primers for the present study. All primers, which we used in various combinations and both as PCR and sequencing primers, are listed with references in Table 2. We purified the PCR products using 2 µL 10 times diluted ExoSAP-IT (USB Corporation, Santa Clara, California, U.S.A.) to 8 µL PCR product, incubating at 37°C for 45 min followed by 15 min at 80°C. Prepared amplicons for sequencing contained: 9 µL 0–30× diluted purified PCR product (depending on product strength) and 1 µL of 10 µM primer. Cycle sequencing was outsourced to the ABI laboratory at the Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, where the ABI BigDye Terminator sequencing buffer and v.3.1 Cycle Sequencing kit (Applied Biosystems) are used. Sequences were processed on an ABI 3730 DNA analyser (Applied Biosystems). We assembled and edited the sequences using SEQUENCHER v.4.1.4 (Gene Codes Corporation, Ann Arbor, Michigan, U.S.A.). See Appendix 1 for the GenBank accession numbers of all sequences included in the present study.

Alignment and phylogeny reconstructions. — We aligned the sequences using the "ClustalW/Multiple alignment" option in BioEdit v.7.0.9.0 (Hall, 1999) with subsequent manual adjustments. We analyzed the data using maximum likelihood, maximum parsimony and Bayesian inference phylogenetic methods. In order to check for gene-tree incongruence, we compared preliminary strict consensus trees from parsimony analyses of the three genetic regions. For selecting optimal models of nucleotide substitution for the various markers we used TreeFinder (Jobb & al., 2004). We performed maximum parsimony phylogenetic analyses using TNT (Goloboff & al., 2008) applying the traditional search option with equal character weights, gaps treated as missing (replaced with question marks prior to analysis), 1000 random entry order replicates saving 10 trees per replicate, and tree bisection reconnection (TBR) branch swapping. We performed parsimony jackknifing with 1000 replicates. We also did maximum likelihood bootstrapping (BS) using RAxML v.7.2.6 (Stamatakis, 2006) under the GTRCAT model with 500 replicates. For the BI phylogenetic analyses we used MrBayes v.3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003) with priors set according to the output of TreeFinder. We determined posterior probabilities by running one cold and three heated chains for 12 to 20 million generations in parallel mode (the 134 and 166 accessions datasets, respectively, see below), saving trees every 1000th generation. We performed the analyses twice to check their convergence for the same topology. To test whether the Markov Chain converged, we monitored the average standard deviation of split frequencies (ASDSF), which should fall below 0.01 when comparing two independent runs. We discarded as burn-in the generations prior to the point where the ASDSF fell below 0.01 and summarized the remaining trees

Table 2. List of primers used in the present study with primer sequence and references.

DNA region	Primer name / primer sequence 5′ → 3′ direction	Reference
nrITS	ITS4 / TCCTCCGCTTATTGATATGC (rev)	White & al., 1990
	ITS5 / GGAAGTAAAAGTCGTAACAAGG(fwd)	White & al., 1990
	ITS6 / TAAGTTCAGCGGGTATCCCTA (rev)	This study
	ITS-lichF / TGAATTGCAGAATTCAGTGAAT (fwd)	This study
	ITS-lichR / ATTCACTGAATTCTGCAATTCA (rev)	This study
	ITS-hypF / TCTTTGAACGCACATTGCGCC (fwd)	This study
	ITS-hypR / GGCGCAATGTGCGTTCAAAGA (rev)	This study
nrLSU	LSU-hypF / CGCTGAACTTAAGCATATC (fwd)	This study
	LSU-hypR / CTATCCTGAGGGAAACTTCG (rev)	This study
	LSU-hypR2 / CTTGGTCCGTGTTTCAAGACG (rev)	This study
mtSSU	mitSSU1 / AGCAGTGAGGAATATTGGTC (fwd)	Zoller & al., 1999
	mitSSU3R / ATGTGGCACGTCTATAGCCC (rev)	Zoller & al., 1999
	mtSSU-hypF / AGCATTCCACCTCAAGAGTA (rev)	This study
	mtSSU-hypR / TACTCTTGAGGTGGAATGCT (rev)	This study

Abbreviations: nrITS = nuclear ribosomal internal transcribed spacer; nrLSU = nuclear ribosomal large subunit; mtSSU = mitochondrial ribosomal small subunit; rev = reverse primer; fwd = forward primer.

as a 50% majority-rule consensus tree. We used the Bioportal server, University of Oslo, Norway (http://www.bioportal.uio.no) for the RAxML analyses.

■ RESULTS

Sequences and alignments. — DNA sequences of all three genetic regions (nrITS, nrLSU, mtSSU) were successfully generated for most of the specimens extracted for this study, except for a few old and/or poor-quality specimens, from which only the nrITS region (or parts of it) could be amplified and sequenced using the methods described herein. GenBank sequences of the three genetic regions were always based on the same voucher specimen. The highly variable ITS1 of the nrITS region was treated as missing data for accessions for which character homology could not be hypothesized (indicated with † in Appendix 1). Lengths in basepairs (bp) of the aligned DNA-regions were: 650 bp for the nrITS region, 905 bp for the nrLSU region, and 1037 bp for the mtSSU region. The best-fit nucleotide substitution models, as proposed by TreeFinder based on the AICc model selection criterion, were general time reversible with gamma distribution (GTR+G) for the nrLSU and mtSSU regions and J2+G for the nrITS region. As no manual exists for implementing the J2+G model in MrBayes, the GTR+G model was used for all three regions. The concatenated matrix of 2592 bp contained 1186 parsimony-informative characters.

Analyses. — The preliminary parsimony analyses showed congruent gene trees, although resolved to various extents and at different levels (not shown). The nrITS increased resolution of the more recent speciation events, whereas the mtSSU and nrLSU provided resolution of the backbone relationships. The nrLSU was less informative than the mtSSU. We therefore analyzed a concatenated dataset of all three genetic regions (nrITS, nrLSU, mtSSU), 166 accessions, and 2592 bp (hereafter referred to as the 166 accession dataset). In the Bayesian analysis, the ASDSF had fallen to 0.004683 at termination (20 million generations), and the first 5000 trees (25%) were discarded as burn-in. The remaining trees were summarized as a Bayesian 50% majority-rule consensus tree, which is presented in Fig. 2. Since the ITS1 and ITS2 of the nrITS region included several alignment ambiguities, we also performed a Bayesian analysis of a dataset consisting of only the more conserved 5.8S part of the nrITS region in combination with the nrLSU and mtSSU regions. This dataset included 134 accessions (only accessions for which the mtSSU region was available) and 2081 bp (hereafter referred to as the 134 accession dataset). At 12 million generations, the ASDSF had fallen to 0.004653, and the analysis was terminated. We discarded as burn-in the first 3000 trees (50%), and summarized the remaining trees into a 50% majority-rule consensus tree (Electr. Suppl.: Fig. S1). The parsimony strict and jackknife consensus trees with tree statistics for both datasets are provided in the Electr. Suppl.: Fig. S2. The parsimony results were largely consistent with the Bayesian and likelihood results, and the resultant topologies from the 166 vs. the 134 accession datasets were highly similar (Fig. 2; Electr. Suppl.: Figs. S1–S2).

The 15 included species of *Hypocenomyce* s.l. form seven strongly supported groups in our molecular phylogeny (Fig. 2; Electr. Suppl.: Figs. S1–S2). Through nucleotide BLAST searches at NCBI (http://www.ncbi.nlm.nih.gov/), it became clear that the seven groups were far from being each other's closest relatives, and a broad taxonomic sampling had to be included in order to place these groups phylogenetically. The resultant phylogeny shows that the *Hypocenomyce* species belong in different families, orders and even different subclasses (Fig. 2).

The backbone of the phylogeny (the oldest speciation events) received poor support from parsimony jackknifing (Electr. Suppl.: Fig. S2), and the parsimony strict consensus trees were partly incongruent with the Bayesian majority-rule trees (Fig. 2; Electr. Suppl.: Fig. S1). The incongruences (indicated with asterisks on Fig. 2) mainly concerned long-branch taxa in the Ostropomycetidae and the Lecanoromycetidae. The backbone support was generally higher with likelihood bootstrapping (Fig. 2).

See the Discussion for other relevant aspects of our phylogenetic results.

The concatenated alignment of 166 accessions and three genetic regions and the resultant Bayesian phylogenetic tree are provided as supplementary material.

■ DISCUSSION

Although *Hypocenomyce* s.l. (including *Pycnora*) has been extensively studied by anatomical and chemical approaches (e.g., Timdal, 1984a, 2001, 2002; Elix, 2009), the present study is the first comprehensive molecular phylogenetic investigation of the genus. Our aim has been to investigate phylogenetic relationships among the 15 species of *Hypocenomyce* s.l. and to test hypotheses about the presumed groups among them (Table 1).

Our phylogenetic results (Fig. 2), based on three DNA regions of various levels of molecular divergence from two different genomes and with a broad taxonomic sampling, reveal that *Hypocenomyce* s.l. is extremely polyphyletic. Although the backbone of the phylogeny (the oldest speciation events) mostly receives moderate support from likelihood bootstrapping (Fig. 2) and parsimony jackknifing (Electr. Suppl.: Fig. S2), the Bayesian majority-rule consensus topology (Fig. 2) corresponds well with all recently published phylogenetic hypothesis (Wedin & al., 2005; Miądlikowska & al., 2006; Hofstetter & al., 2007; Lumbsch & al., 2007; Ekman & al., 2008; Schoch & al., 2009; Schmull & al., 2011) that have included similar sets of taxa, but without the present extensive sampling of *Hypocenomyce* s.l. The five presumed subgroups (see Introduction and Table 1) are mostly supported by our molecular data, but two species, *H. isidiosa* and *P. leucococca*, form independent groups remotely positioned from any of the other groups (Fig. 2B). The resultant seven subgroups are surprisingly distantly related and clearly belong in different genera, families, orders and even subclasses. Further below, we discuss the *Hypocenomyce* subgroups and their phylogeny, and we

undertake several taxonomic changes that are now supported by multiple sources of evidence. In the following paragraph, "Morphological convergence", we use the new taxonomy proposed (see Nomenclatural novelties for author names).

Morphological convergence. — Traditional classifications are based largely on morphological and ecological aspects of organisms. Since the early 1990s, molecular phylogenetics has revolutionized the field of systematics, in particular in the

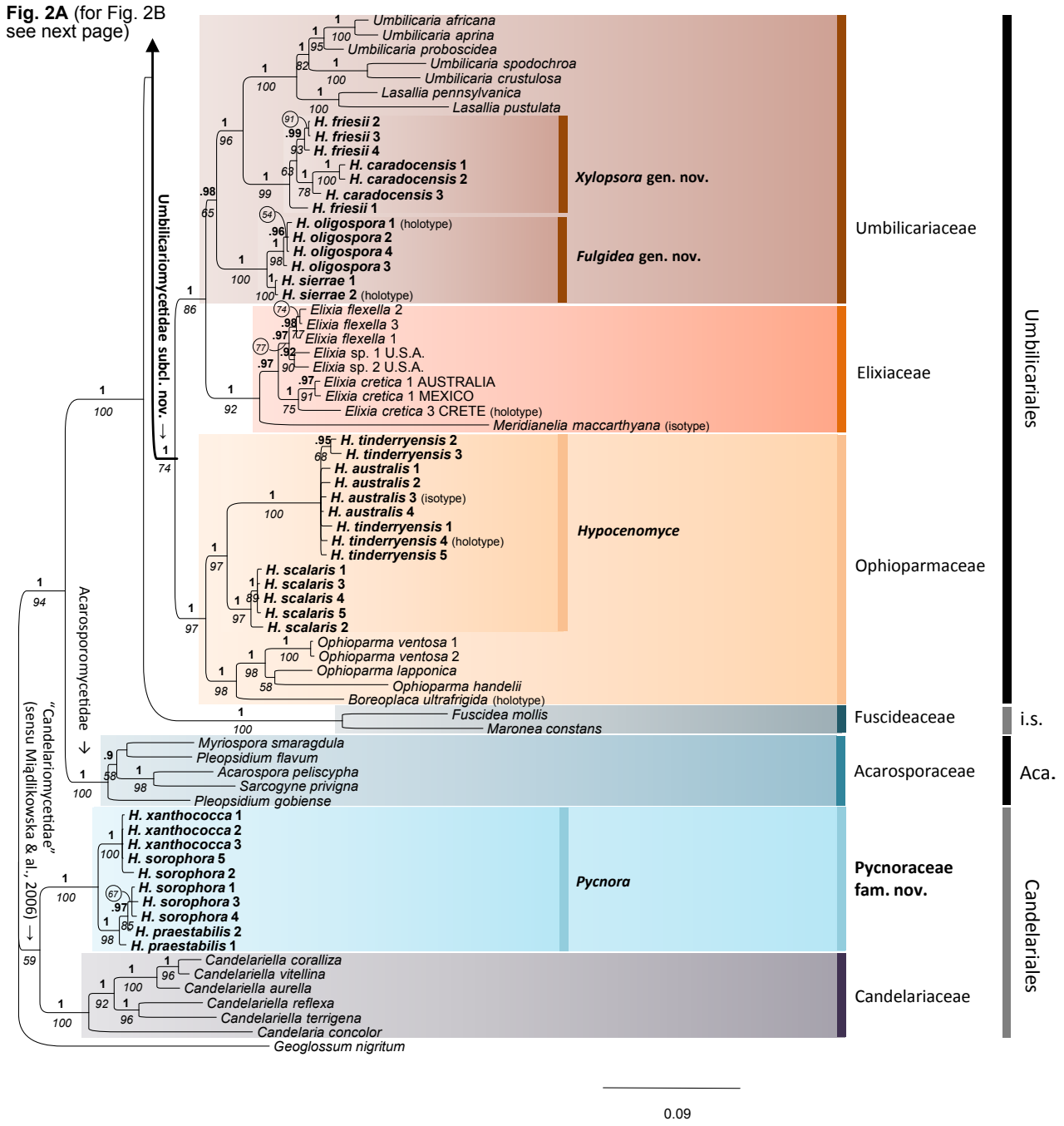
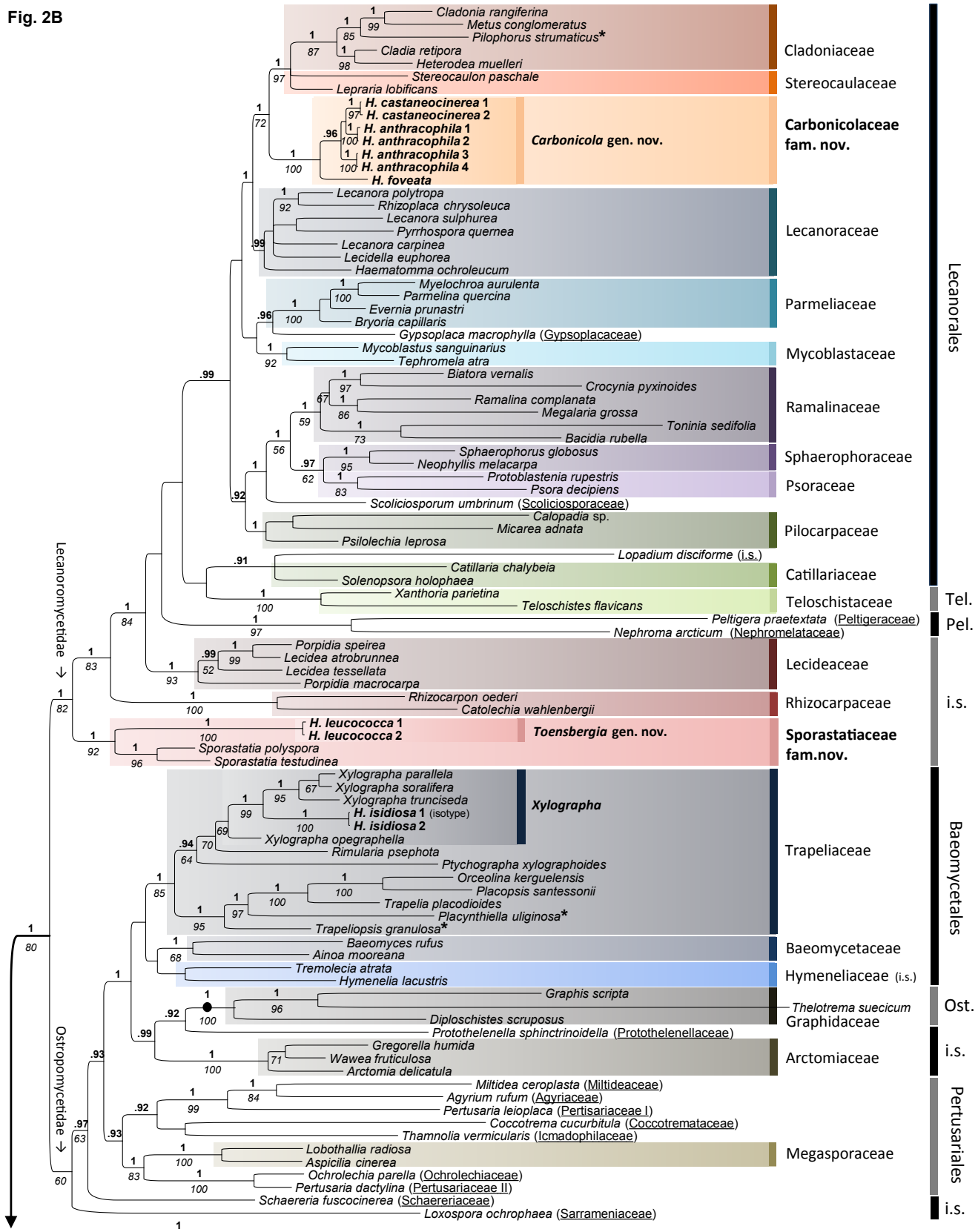


Fig. 2. The 50% majority-rule consensus phylogram (**2A** above, **2B** next page) from a Bayesian analysis of a concatenated matrix with 166 accessions and 2592 basepairs from two nuclear (ITS and LSU) and one mitochondrial (SSU) ribosomal DNA region. The Bayesian posterior probability values of at least 0.9 are reported above branches, and maximum likelihood bootstrap values of at least 50% are reported below branches. Asterisks indicate incongruent topology with parsimony results (see Electr. Suppl.: Fig. S2). Multiple accessions of the same species are numbered according to Appendix 1. The *Hypocenomyce* s.l. accessions are in bold. One branch was manually shortened to reduce the size of a broad figure (indicated with a black dot). Names to the right of branches indicate the classification as supported herein. Taxonomic changes undertaken in the present study from genus and above are also in bold face. — Aca., Acarosporales; i.s., incertae sedis; Ost., Ostropales; Pel., Peltigerales; Tel., Teloschistales.

Fig. 2B



for Fig. 2A
see previous page

most taxonomically challenging groups. Fungi (incl. lichenized fungi) represent one such taxonomically challenging group due to few phenotypic characters and a high level of homoplasy. Hence, fungal molecular phylogenies have resulted in numerous novel classifications (e.g., Lutzoni & al., 2004; James & al., 2006; Miądlikowska & al., 2006; Hibbet & al., 2007; Schoch & al., 2009) and revealed numerous instances of convergent evolution (see Rivas Plata & Lumbsch, 2011, and references therein; Rivas Plata & al., 2012).

Our phylogeny shows that the great morphological and ecological similarity between the former *Hypocenomyce* species is the result of convergence in seven clades. Brown, squamulose thalli, often geotropically arranged and with lip-shaped soralia, occur in *Carbonicola*, *Hypocenomyce*, *Fulgidea*, and *Xylopsora.* Ten species in five clades occur on burnt wood (*Carbonicola*, all species; *Fulgidea*, all species; *Hypocenomyce*, all species; *Xylographa isidiosa*; and *Xylopsora friesii*). We have observed that very few crustose lichen species grow on burnt wood in northern Europe. In addition to *Hypocenomyce*, these are mainly *Chaenotheca ferruginea* (Sm.) Mig., *Hertelidea botryosa* (Fr.) Printzen & Kantvilas, *Micarea melaenida* (Nyl.) Hedl., and *Trapeliopsis flexuosa* (Fr.) Coppins & P. James. The presence of four clades containing such ecological specialists in the Umbilicariales (*Elixia*, *Fulgidea*, *Hypocenomyce*, *Xylopsora*) may be explained as a plesiomorphy in this order, in which case the saxicolous genera *Boreoplaca*, *Lasallia* Mérat, and *Umbilicaria* have evolved from ancestors growing on burnt wood. Alternatively, the specialized ecology is a homoplasy and evolved up to four times in the order, or the topology in our Umbilicariales phylogeny does not correctly reflect the evolution of the four clades.

Abundant production of apparently persistently immature asci occurs in *Hypocenomyce* (all three species) and *Fulgidea* (*F. oligospora*), and must be a homoplasy of the two genera. The selective forces behind this character state remain obscure. In *H. scalaris* and *H. tinderryensis* it may be viewed as an incomplete step in reduction of fertility as a response to the species having switched to vegetative dispersal (soredia), but in the two other species (*H. australis*, *F. oligospora*) no vegetative dispersal units are produced and they should rely only on ascospore dispersal. We suggest an ecological study of the effect of heat from forest fire on spore production in those species.

The chemical similarity between *Pycnora* and *Toensbergia* (alectorialic acid) and between *Xylopsora* and *Xylographa isidiosa* (confriesiic/friesiic acids) are clearly homoplasies.

The *Hypocenomyce anthracophila*-group. — There are no previously published sequences or phylogenies of species in this group. In our results (Fig. 2B; Electr. Suppl.: Figs. S1–S2), the three species comprising the *H. anthracophila*-group (*H. anthracophila*, *H. castaneocinerea*, *H. foveata*) form a monophyletic clade within the order Lecanorales. The *H. anthracophila*-group clearly does not belong in any of the lecanoralean families included in the present phylogeny (i.e., Catillariaceae, Cladoniaceae, Gypsoplacaceae, Haematommataceae, Lecanoraceae, Mycoblastaceae, Parmeliaceae, Pilocarpaceae, Psoraceae, Ramalinaceae, Scoliciosporaceae, Sphaerophoraceae, Stereocaulaceae). We do not have sequence data for the remaining currently accepted families of the Lecanorales (Biatorellaceae, Calycidiaceae, Dactylosporaceae, Pachyascaceae). However, judging from anatomical characters, especially the ascus type, the *H. anthracophila*-group does not belong in any of these families. In the Biatorellaceae, the asci are polysporous and have a well-developed, weakly amyloid tholus which lacks an amyloid tube (Hafellner & Casares-Porcel, 1992). In the Pachyascaceae, the asci are surrounded by a thick, amyloid gelatinous wall; a small, weakly amyloid tholus, apparently without any tube structure, may be developed in young asci (Grube, 2002). In the Calycidiaceae the asci are prototunicate and disintegrate early as a part of the formation of a mazaedium (Tibell, 1984). In the Dactylosporaceae the asci lack a tholus and are apically covered by a thick gelatinous sheet; the ascospores are brown and septate (Bellemere & Hafellner, 1982). The sister clade of the *H. anthracophila*-group is the clade consisting of the Cladoniaceae and Stereocaulaceae. As long as these two families are kept separate, a new family is needed for the *H. anthracophila*-group. Hence, we describe a new genus (*Carbonicola* Bendiksby & Timdal) and a new family (Carbonicolaceae) for this clade (see Nomenclatural novelties, below).

Within the clade, *H. foveata* is a sister to *H. anthracophila* and *H. castaneocinerea* (Fig. 2B). *Hypocenomyce anthracophila* seems to be genetically heterogeneous, as indicated by two distinct clades among the four accessions included (Fig. 2B) and should be studied further for a possible phenotypically cryptic species. Molecular approaches to systematics of lichen-forming fungi have revealed a substantial number of unrecognized fungal species hidden within traditional phenotype-based species (Crespo & Lumbsch, 2010; Lumsch & Leavitt, 2011; Leavitt & al., 2012). Note that our type studies have shown that the species epithet "*myrmecina*" should replace "*castaneocinerea*" (see Nomenclatural novelties, below).

The *Hypocenomyce friesii*- and *H. oligospora*-groups. — The only previously published phylogenetic study of species in these groups is that of Wedin & al. (2005), who found *H. friesii* to be sister to three *Umbilicaria* species and more distantly related to *H. scalaris*. Our phylogenetic results support their conclusion: *H. caradocensis* and *H. friesii* form a monophyletic group which is supported as sister to a clade consisting of seven species of *Lasallia* and *Umbilicaria* (Fig. 2A; Electr. Suppl.: Figs. S1–S2). *Hypocenomyce friesii* appears paraphyletic in our phylogeny and should be studied further for a possible phenotypically cryptic species. The morphology of the *H. friesii*-group differs significantly from the saxicolous, umbilicate-foliose lichens of *Umbilicaria* and *Lasallia*. We therefore describe the new genus *Xylopsora* Bendiksby & Timdal for the *H. friesii*-group (see Nomenclatural novelties, below).

Hypocenomyce isidiosa, which is not known with apothecia, was originally thought to be related to *H. friesii* because of its similar secondary chemistry (the rare compounds confriesiic and friesiic acids) and its substrate preference (burnt wood; Elix, 2006). However, our molecular results show that *H. isidiosa* is not closely related to *Xylopsora* but rather nests within *Xylographa* (Trapeliaceae, Baeomycetales, Ostropomycetidae; Fig. 2B). Morphologically, *H. isidiosa* resembles

sorediate species of *Xylographa* in forming an endoxylic thallus with vegetative dispersal units bursting out through cracks in the wood (Fig. 1M). Confriesiic acid occurs in two other genera of the Trapeliaceae, i.e., *Rimularia* Nyl. and *Trapeliopsis* Hertel & Gotth. Schneid. Hence, we propose the new combination *Xylographa isidiosa* (Elix) Bendiksby & Timdal (see TNomenclatural novelties, below).

The *H. oligospora*-group forms a monophyletic group moderately supported as sister to the *Xylopsora*-*Lasallia*-*Umbilicaria*-clade (Fig. 2A; Electr. Suppl.: Figs. S1–S2). But as the *H. oligospora*-group cannot be placed in *Xylopsora* without making it paraphyletic, and lumping *Xylopsora* with *Lasallia* and *Umbilicaria* seems impossible, we describe the new genus *Fulgidea* Bendiksby & Timdal for the *H. oligospora*-group (see Nomenclatural novelties, below).

Moreover, we suggest that *Fulgidea* and *Xylopsora* are included in the Umbilicariaceae. Thus, the concept of the previously exclusively foliose family Umbilicariaceae is extended to include crustose and squamulose genera. We find this not unreasonable as we believe thallus growth form is not a character of great importance at the family level (compare, e.g., the current concept of the Physciaceae, Ramalinaceae and Teloschistaceae; Lumbsch & Huhndorf, 2010). Whether the Elixiaceae (which consists of only three known species) should be accepted as a separate family is here left for future studies. But when *Fulgidea* and *Xylopsora* are included in the Umbilicariaceae, there are hardly any morphological, anatomical, or ecological arguments for accepting the Elixiaceae. Note that two specimens growing on burnt wood and identified as *Hypocenomyce* sp. in our study were identified as *Elixia cretica* (Fig. 2A: *Elixia cretica* 1 and 2) and represent the first report of this species, recently described from Greece (Spribille & Lumbsch, 2010), in North America and Australia. Two additional collections (Fig. 2A: *Elixia* sp., specimen 1 and 2) may represent a new species of *Elixia* (see Appendix 1 for voucher information).

The *Hypocenomyce scalaris*-group. — Our molecular phylogenic results support the monophyly of the *H. scalaris*-group, consisting of *H. australis*, *H. scalaris*, and *H. tinderryensis* (Fig. 2A; Electr. Suppl.: Figs. S1–S2). The separation of *H. tinderryensis* from *H. australis* is, however, not supported and should be studied further. The *H. scalaris*-group is sister to a clade consisting of *Boreoplaca* and *Ophioparma* (Fig. 2A), corroborating previous findings by Wedin & al. (2005) and Miądlikowska & al. (2006; although with a different internal topology). The circumscription of *Hypocenomyce* should hence be restricted to the *H. scalaris*-group (see Nomenclatural novelties, below).

Our phylogeny further supports a sister-relationship of the *Hypocenomyce*-*Boreoplaca*-*Ophioparma* clade (Ophioparmaceae) with the Umbilicariaceae-Elixiaceae clade (Fig. 2A), partly corroborating the phylogenetic topologies published by Wedin & al. (2005) and Miądlikowska & al. (2006). In Miądlikowska & al. (2006), Fuscideaceae was sister to the Ophioparmaceae (and this group again sister to the Umbilicariaceae), a sister-relationship neither supported nor strongly contradicted by our data (Fig. 2A; Electr. Suppl.: Figs. S1–S2). Miądlikowska & al. (2006) considered the Fuscideaceae-Ophioparmaceae-Umbilicariaceae clade as the Umbilicariales, and noted that the subclass Umbilicariomycetidae should be considered for this group in the future. Regardless, Lumbsch & Huhndorf (2010) and Hodkinson (2012) kept the Umbilicariales among the Lecanoromycetes orders incertae sedis. Lumbsch & Huhndorf (2010) placed the Fuscideaceae and the Ophioparmaceae among the Lecanoromycetidae families incertae sedis, whereas Hodkinson (2012) recognized their inclusion in the Umbilicariales. Our phylogenetic results, with increased taxon sampling, support a clade consisting of the Elixiaceae, Ophioparmaceae and Umbilicariaceae (Fig. 2A; Electr. Suppl.: Figs. S1–S2). We refer to this clade as the Umbilicariales and the Umbilicariomycetidae subcl. nov. in this paper (see Nomenclatural novelties, below). We leave it to future more comprehensive studies to consider the inclusion of the Fuscideaceae in the Umbilicariomycetidae, but would like to point out that our microscopical examination of asci in *Umbilicaria* revealed a type similar to the *Fuscidea*-type, i.e., with amyloid layers lining both the inside and outside of the ascus wall near its apex.

The *Hypocenomyce xanthococca*-group (*Pycnora*). — In Wedin & al. (2005), *Pycnora sorophora* and *P. xanthococca* formed a strongly supported group that was sister to the Acarosporaceae (parsimony) or Candelariaceae (Bayesian). In our phylogeny (Fig. 2A), which includes multiple accessions of all four *Pycnora* species, all, except *P. leucococca*, form a strongly supported clade. The already existing name for the *H. xanthococca*-group, *Pycnora*, hence comprises the three species *P. praestabilis* (Nyl.) Hafellner, *P. sorophora*, and *P. xanthococca* (see Nomenclatural novelties, below).

Our phylogenetic results support a sister-relationship between *Pycnora* and the Candelariaceae (Fig. 2A; Electr. Suppl.: Figs. S1–S2), corroborating the Bayesian results by Wedin & al. (2005). Although only representatives from two Candelariaceae genera have been included here (i.e., *Candelaria* A. Massal. and *Candelariella* Müll. Arg.), Westberg & al. (2007) showed that the family also comprises the two genera *Candelina* Poelt and *Placomaronea* Räsänen. We believe differences in the secondary chemistry (pulvinic acid derivatives vs. dibenzofurans) and in the apothecia (lecanorine and biatorine vs. lecideine) between the Candelariaceae and *Pycnora* justify placing the latter in the new family Pycnoraceae, and we include it in the order Candelariales. This order may be placed in the "Candelariomycetidae" (nom. inval.).

Our results (Fig. 2) support the previously published finding that the Candelariales is distinct from the Lecanorales (Wedin & al., 2005; Miądlikowska & al., 2006; Hofstetter & al., 2007; Lumbsch & al., 2007); a finding that made Lumbsch & Huhndorf (2010) place Candelariales among the Lecanoromycetes orders incertae sedis. The six-gene phylogenetic results by Schoch & al. (2009: fig. 3), however, shed doubts on whether Candelariales at all belong in the Lecanoromycetes. Based on the phylogenetic results by both Miądlikowska & al. (2006) and Schoch & al. (2009), Hodkinson (2012) recognized the "Subclass Candelariomycetidae", but, no formal description has been provided (see Nomenclatural novelties, below). Our

restricted ascomycote taxon sampling does not provide information about the phylogenetic placement of "Candelariomycetidae", but in the six-gene Ascomycota tree by Schoch & al. (2009), Candelariales fell outside all well-supported classes in superclass Leotiomyceta (sensu Eriksson & Winka, 1997).

Pycnora sorophora seems to be a polyphyletic species (Fig. 2A). We hypothesize that this species evolved as a sorediate taxon from both *P. praestabilis* and *P. xanthococca*. This should be investigated further with more accessions and a better geographic coverage of all three species.

The fourth species of the *H. xanthococca*-group, *Pycnora leucococca* (R. Sant.) R. Sant., occurs remotely from the other *Pycnora* species in the phylogeny (Fig. 2B). *Pycnora leucococca* groups with strong support with two accessions of the genus *Sporastatia* A. Massal. (Fig. 2B; Electr. Suppl.: Figs. S1–S2). In Miądlikowska & al. (2006), a clade consisting of Rhizocarpaceae and *Sporastatia* was recovered and supported. This relationship was not recovered here. In the present study, the *P. lecococca–Sporastatia* clade is sister group to Rhizocarpaceae plus all remaining members of subclass Lecanoromycetidae (Fig. 2B; Electr. Suppl.: Figs. S1–S2). It should be noted, however, that regardless of the placement of Rhizocarpaceae, the phylogenetic results support the removal of *Sporastatia* from the Catillariaceae (Lecanorales; Fig. 2B; Electr. Suppl.: Figs. S1–S2; Miądlikowska & al., 2006).

Fruiting bodies are not known in *P. leucococca*, but from a morphological and ecological point of view, it seems impossible to include *P. leucococca* in *Sporastatia*. Hence, we describe a new genus, *Toensbergia* Bendiksby & Timdal, for this species and place it in the new family Sporastatiaceae based on our molecular phylogenetic results (see Nomenclatural novelties, below).

■ NOMENCLATURAL NOVELTIES

"Candelariomycetidae" Miądl. & al. in Mycologia 98: 1091. 2006, nom. inval. (Art. 39.1). See Fig. 2A and Electr. Suppl. Fig. S1 for clade "Candelariomycetidae" as applied to by Miądlikowska & al. (2006).

Candelariales Miądl., Lutzoni & Lumbsch in Mycol. Res. 111: 530. 2007.

Pycnoraceae Bendiksby & Timdal, **fam. nov.** [MB 804835] – Type: *Pycnora* Hafellner.

Diagnostic characters. – The Pycnoraceae is the clade sister to the Candelariaceae and differs in forming lecideine, black apothecia with consistently octosporous asci and consistently simple ascospores, and in the secondary chemistry of dibenzofurans (alectorialic acid). In the Candelariaceae, the apothecia are lecanorine or biatorine, yellow to orange, the asci are often polysporous, the ascospores often septate, and the secondary chemistry consists of pulvinic acid derivatives.

Pycnora Hafellner in Stapfia 76: 157. 2001 – Type: *Pycnora xanthococca* (Sommerf.) Hafellner.

Included species. – *Pycnora praestabilis* (Nyl.) Hafellner, *P. sorophora* (Vain.) Hafellner, *P. xanthococca* (Sommerf.) Hafellner.

Lecanoromycetidae Miądl., Lutzoni & Lumbsch in Mycol. Res. 111: 529. 2007.

Lecanorales Nannf. in Nova Acta Regiae Soc. Sci. Upsal., ser. 4, 8(2): 68. 1932.

Carbonicolaceae Bendiksby & Timdal, **fam. nov.** [MB 804836] – Type: *Carbonicola* Bendiksby & Timdal.

Diagnostic characters. – The Carbonicolaceae is the clade sister to a clade consisting of the Cladoniaceae and Stereocaulaceae. It differs from those families in forming a purely crustose to squamulose, dark brown thallus with a thick, shiny upper cortex, and in having a strong preference for the substrate charred wood and bark. The core genera of the Cladoniaceae and Stereocaulaceae form a fruticose secondary thallus, which is absent in the Carbonicolaceae.

Carbonicola Bendiksby & Timdal, **gen. nov.** [MB 804837] – Type: *Carbonicola anthracophila* (Nyl.) Bendiksby & Timdal.

Diagnostic characters. – Thallus squamulose, adnate or ascending and geotropically oriented, (greenish to) medium to dark brown, shiny, epruinose, without hypothallus. Apothecia brown, convex, weakly marginate when young, soon becoming immarginate, epruinose; exciple composed of conglutinated, thick-walled hyphae with thread-like lumina, colorless in inner part, pale brown in the rim, K–, N–, lacking crystals; epihymenium brown, N–, without amorphous substances; ascus clavate, octosporous, without an apical amyloid cap, with a well-developed, amyloid tholus containing a deeper amyloid tube. Pycnidium wall brown, N–; pycnoconidia filiform. Chemistry: colensoic acid, 4-O-methylphysodic acid and related compounds (in all species), fumarprotocetraric and protocetraric acid (in *C. anthracophila*).

Etymology. – The name refers to its preferred substrate, burnt wood (lat. carbo: charcoal, -cola: dweller).

Notes. – The genus differs from the other genera formerly included in *Hypocenomyce* in having brown, convex, more or less immarginate apothecia; a pale exciple composed of entirely conglutinated hyphae; a brown epihymenium lacking amorphous substances; asci with a deeply amyloid tube; and in the main secondary chemistry consisting of compounds of the colensoic acid complex. *Biatora*, in which Hafellner (1993) placed two *Carbonicola* species, differs mainly in forming a crustose or at most a subsquamulose thallus and in having a conical amyloid zone in the tholus (ascus of *Bacidia*-type, typical of the Ramalinaceae).

Carbonicola anthracophila (Nyl.) Bendiksby & Timdal, **comb. nov.** [MB 804838] ≡ *Lecidea anthracophila* Nyl. in Flora 48: 603. 1865 ≡ *Psora anthracophila* (Nyl.) Arnold in Flora 53: 471. 1870 ≡ *Biatora anthracophila* (Nyl.) Tuck., Syn. N. Amer. Lich. 2: 14. 1888 ≡ *Hypocenomyce*

anthracophila (Nyl.) P. James & Gotth. Schneid. in Biblioth. Lichenol. 13: 81. 1980 ≡ *Biatora anthracophila* (Nyl.) Hafellner in Herzogia 9: 729. 1993 – Lectotype (designated by Timdal, 1984a): Finland, "Evois ad lignium [sic!] carbonatum", 1865, *J.P. Norrlin s.n.* (H-NYL No. 20375 p.p.!)

= *Psora cladonioides* var. *albocervina* Räsänen, Lichenes Fenniae Exsiccati: No. 281. 1936 ≡ *Lecidea cladonioides* var. *albocervina* (Räsänen) Zahlbr., Cat. Lich. Univ. 10: 346. 1939– **Lectotype (designated here):** Finland, Karelia borealis, Pielisjärvi, Louhivaara, ad orientem versus ab lacu Ylinen Pitkäjärvi, ad lignum vetustum carbonatum trunci erecti altique *Pini silvestris* in pineto aprico deserto, July 1936, *M. Laurila s.n.* = Räsänen, Lichenes Fenniae Exsiccati No. 281 (O No. L-894!; isotypes: BM!, S!, UPS No. L-533305!).

= *Lecidea cladonioides* Fr. ex Th. Fr., Lichenogr. Scand.: 417. 1874, nom. illeg. superfl. (nomenclaturally superfluous name for *L. anthracophila* Nyl.; Art. 52.1) ≡ *Psora cladonioides* (Th. Fr.) Elenkin, Fl. Lishaynikov Sredney Rossii [Lichenes Florae Rossiae Mediae] 2: 345. 1907.

– "*Biatora ostreata* var. *cladonioides*" Fr., Summa Veg. Scand.: 111. 1845, nom. nud.

Carbonicola foveata (Timdal) Bendiksby & Timdal, **comb. nov.** [MB 804840] ≡ *Hypocenomyce foveata* Timdal in Nordic J. Bot. 4: 98. 1984 ≡ *Biatora foveata* (Timdal) Hafellner in Herzogia 9: 729. 1993 – Holotype: Australia, Victoria, Cultivation Creek, Billywing area, Western Grampians, 37°15′S, 142°16′E, August 1981, *H. Krog Au1401* (O No. L-50!).

Carbonicola myrmecina (Ach.) Bendiksby & Timdal, **comb. nov.** [MB 804841] ≡ *Lecidea scalaris* var. *myrmecina* Ach., Methodus: 78. 1803 ≡ *Lecidea myrmecina* (Ach.) Fr. in Kongl. Vetensk. Akad. Handl. 1822: 257. 1822 ≡ *Parmelia ostreata* var. *myrmecina* (Ach.) Torss., Enum. Lich. Byssacearum Scand.: 14. 1843 ≡ *Lecidea ostreata* var. *myrmecina* (Ach.) Nyl., Lich. Scand.: 243. 1861 ≡ *Psora ostreata* var. *myrmecina* (Ach.) Th. Fr. in Nova Acta Regiae Soc. Sci. Upsal., ser. 3, 3: 269. 1861 ≡ *Psora myrmecina* (Ach.) Boistel, Nouv. Fl. Lich. 2: 94. 1902 ≡ *Psora scalaris* var. *myrmecina* (Ach.) Räsänen, Lichenes Fenniae Exsiccati: No. 825. 1943 – **Lectotype (designated here):** [s. loco], "*Parmelia* (*Psoroma*) *myrmecina*, e collect. cel. Acharii accepi" [scrips. G. Wahlenberg], ex herb. G. Wahlenberg (UPS-ACH No. 256!). Probable isolectotypes: [s. loco], ex herb. Agrelius (UPS-ACH No. 251!); "Svecia" (H-ACH No. 312D photo!).

= *Hypocenomyce castaneocinerea* (Räsänen) Timdal in Nordic J. Bot. 4: 97. 1984 ≡ *Psora cladonioides* var. *castaneocinerea* Räsänen, Lichenes Fenniae Exsiccati: No. 282. 1936 ≡ *Lecidea cladonioides* var. *castaneocinerea* (Räsänen) Zahlbr., Cat. Lich. Univ. 10: 346. 1939 – **Lectotype (designated here):** Finland, Karelia borealis, Pielisjärvi, Kitsinvaara, Ylinen Pitkäjärvi, ad truncum erectum carbonatum *Pini silvestris* in silva aprica deserta, July 1936, *M. Laurila s.n.* = Räsänen, Lichenes Fenniae Exsiccati: No. 282 (O No. L-895!; isotypes: BM!, UPS No. L-533306!).

Note. – UPS-ACH 256 contains colensoic acid, 4-O-methylphysodic acid, ± norcolensoic acid and possibly trace of physodic acid (by TLC).

Lecanoromycetidae families incertae sedis

Sporastatiaceae Bendiksby & Timdal, **fam. nov.** [MB 804842] – Type: *Sporastatia* A. Massal.

Diagnostic characters. – Thallus crustose, containing unicellular green algae, lacking cephalodia. Apothecia lecideine, black. Ascus narrowly clavate, polysporous, with a well-developed, deeply amyloid tholus without further amyloid structures. Ascospores hyaline, thin-walled, non-halonate, simple.

Notes. – The family consists of two genera, *Sporastatia* and *Toensbergia*, and the description of the apothecia given above is made from the former as the latter is not known from fertile material. *Sporastatia* is currently placed in the Catillariaceae (Lumbsch & Huhndorf, 2010) because of its *Catillaria*-type ascus, but it differs from that family in its polyspory.

Toensbergia Bendiksby & Timdal, **gen. nov.** [MB 804843] – Type: *Toensbergia leucococca* (R. Sant.) Bendiksby & Timdal.

Diagnostic characters. – Thallus of minute, adnate, crenulate, grayish white areolae, lacking a hypothallus, containing alectorialic acid.

Etymology. – The name honors Dr. Tor Tønsberg (born 1948), Bergen, in appreciation of his important work on sorediate, corticolous lichens.

Notes. – The genus consists of a single, sterile species which was originally placed in *Hypocenomyce*, later in *Pycnora*, apparently due to its morphological, ecological and chemical resemblance with species of the *H. xanthococca*-group.

Toensbergia leucococca (R. Sant.) Bendiksby & Timdal, **comb. nov.** [MB 804845] ≡ *Hypocenomyce leucococca* R. Sant. in Thunbergia 2: 3. 1986 ≡ *Pycnora leucococca* (R. Sant.) R. Sant. in Santesson & al., Lichen-forming Lichenicol. Fungi Fennoscand.: 275. 2004 – Holotype: Sweden, Härjedalen, Tännäs par., ca. 1 km E of Ramundbergets Fjällgård, 63°42′N, 12°25′E, alt. ca. 750 m, on the trunk of a birch in the subalpine birch forest, August 1977, *R. Santesson 27901* = Moberg, Lichenes Selecti Exsiccati Upsaliensis No. 6 (UPS No. L-86993!; isotype: O No. L-328!).

Ostropomycetidae Reeb, Lutzoni & Cl. Roux in Molec. Phylogen. Evol. 32: 1055. 2004.

Baeomycetales Lumbsch, Huhndorf & Lutzoni in Mycol. Res. 111: 529. 2007.

Trapeliaceae Hertel in Vorträge Gesamtgeb. Bot., n.s., 4: 181. 1970 – Type: *Trapelia* M. Choisy.

Xylographa (Fr.) Fr., Fl. Scan.: 344. 1836 ≡ *Stictis* subg. *Xylographa* Fr., Syst. Mycol. 2: 197. 1822 – Type: *Xylographa parallela* (Ach.) Fr.

Xylographa isidiosa (Elix) Bendiksby & Timdal, **comb. nov.** [MB 804846] ≡ *Hypocenomyce isidiosa* Elix in Mycotaxon 94: 219. 2006 – Holotype: Australia, Western Australia, Avon district, Charles Gardner Flora Reserve, central track, 20 km SW of Tammin along old York Road, 31°47′24″ S, 117°28′07″ E, alt. 305 m, on dead, charred wood in *Eucalyptus* woodland with *Casuarina* and *Acacia* in shallow gully, 22 April 2004, *J.A. Elix 31849* (PERTH n.v.; isotype: CANB No. 737037!).

Umbilicariomycetidae Miądl. & al. ex Bendiksby, Hestmark & Timdal, **subcl. nov.** [MB 805269]

Description. – Thallus containing green algae, lacking cephalodia, crustose, squamulose, peltate, or umbilicate-foliose. Apothecia lecideine or lecanorine. Ascus rhombic to clavate, usually covered by an amyloid cap, usually with an amyloid inner layer near the ascus apex (±*Fuscidea*-type) or with a small, amyloid tholus, mono- to octosporous.

Note. – Miądlikowska & al. (2006) published the name as a nomen nudum.

Umbilicariales J.C. Wei & Q.M. Zhou in Mycosystema 26: 44. 2007.

Ophioparmaceae R.W. Rogers & Hafellner in Lichenologist 20: 172. 1988 – Type: *Ophioparma* Norman.

Hypocenomyce M. Choisy in Bull. Mens. Soc. Linn. Lyon 20: 133. 1951 – Type: *H. scalaris* (Ach.) M. Choisy.

Included species. – *Hypocenomyce australis* Timdal, *H. scalaris* (Ach.) M. Choisy, *H. tinderryensis* Elix.

Umbilicariaceae Chevall., Fl. Gen. Env. Paris 1: 640. 1826 – Type: *Umbilicaria* Hoffm.

Fulgidea Bendiksby & Timdal, **gen. nov.** [MB 804847] – Type: *Fulgidea oligospora* (Timdal) Bendiksby & Timdal.

Diagnostic characters. – Thallus squamulose, adnate or ascending and geotropically oriented, grayish green to dark brown, dull to shiny, epruinose, without hypothallus. Apothecia black, plane, persistently marginate, egyrose, epruinose; exciple composed of conglutinated, rather thin-walled hyphae with ellipsoid to shortly cylindrical lumina, inner part and rim blackish brown, the pigment partly dissolving in K with a brown effusion, N−, lacking crystals; epihymenium brown, N−, containing amorphous substances dissolving in K with a brown effusion; ascus narrowly rhombic, with an apical amyloid cap and a small, amyloid tholus containing a non-amyloid central plug. Pycnidium wall brown, N−; pycnoconidia bacilliform, 7–10 × ca. 1 µm. Chemistry: alectorialic and thamnolic acids.

Etymology. – The name refers to its preferred substrate, burnt wood (lat. fulgur: lightning), and to its morphological resemblance to *Lecidea* species.

Notes. – The genus differs from *Hypocenomyce* mainly in the anatomy of the exciple which in *Hypocenomyce* is colorless in the inner part, green in the rim (K−, N+ violet), and composed of only partly conglutinated hyphae which are separated by crystals of lecanoric acid (C+ red). Furthermore, in *Hypocenomyce* the epihymenium and the pycnidium wall are green, N+ violet, and the epihymenium contains lecanoric acid and lacks amorphous substances. The pycnoconidia are generally longer in *Hypocenomyce*, i.e., bacilliform to filiform.

Fulgidea differs from *Pycnora* mainly in the ascus, which in *Pycnora* is broadly clavate, lack an amyloid cap, have a well-developed, amyloid tholus with a parietal deeper amyloid area (fig. 3 in Timdal 1984a). Furthermore, in *Pycnora* the thallus is strictly crustose, the epihymenium is green, N+ violet, containing amorphous substances dissolving in K with a violet effusion, the pycnidium wall is green, N+ violet, and the pycnoconidia shorter (subglobose to shortly bacilliform).

Elixia differs from *Fulgidea* in forming a crustose or endoxylic thallus, star-shaped to lirelloid apothecia, capitate paraphyses with a sharply delimited pigment zone in the top of the apical cell, and in lacking secondary compounds.

See also *Xylopsora*, below.

Fulgidea oligospora (Timdal) Bendiksby & Timdal, **comb. nov.** [MB 804848] ≡ *Hypocenomyce oligospora* Timdal in Mycotaxon 77: 446. 2001 – Holotype: U.S.A., Arizona, Gila Co., Little Diamond Rim above Beaver Valley, 34°20′30″ N, 111°18′30″ W, alt. 1840 m, piñon-juniper woodland, on burned *Juniperus* wood, March 1999, *T.H. Nash 42735a* = Nash, Lichenes Exsiccati Distributed by Arizona State University No. 311 (O No. L-767!).

Fulgidea sierrae (Timdal) Bendiksby & Timdal, **comb. nov.** [MB 804849] ≡ *Hypocenomyce sierrae* Timdal in Mycotaxon 77: 449. 2001 – Holotype: U.S.A., California, Los Angeles Co., San Gabriel Mts, along State Hwy 2, 0.3 mi NE (road) of Newcomb Ranch, 34°20.3′ N, 117°59.6′ W, alt. 1650 m, on trunk of *Libocedrus decurrens*, on lower, partly charred parts, March 1998, *E. Timdal SON1251* (O No. L-60059!).

Xylopsora Bendiksby & Timdal, **gen. nov.** [MB 804850] – Type: *Xylopsora friesii* (Ach.) Bendiksby & Timdal.

Diagnostic characters. – Thallus squamulose, adnate or irregularly bullate, grayish green to dark brown, dull to shiny, epruinose, without hypothallus. Apothecia black, plane, persistently marginate, often gyrose, epruinose; exciple composed of conglutinated, rather thin-walled hyphae with ellipsoid to shortly cylindrical lumina, inner part and rim blackish brown, the pigment partly dissolving in K with a brown effusion, N−, lacking crystals; epihymenium brown, N−, containing amorphous substances dissolving in K with a brown effusion; ascus narrowly rhombic, with an apical amyloid cap and a small, amyloid tholus containing a non-amyloid central plug. Pycnidium wall brown, N−; pycnoconidia narrowly ellipsoid to shortly bacilliform, 2.5–5 × ca. 1 µm. Chemistry: friesiic acid (major; also confriesiic acid as minor or trace, according to Elix, 2006).

Etymology. – The name refers to its preferred substrate, wood (gr. xylos), and its previous inclusion in *Lecidea* sect. *Psora*.

Notes. – The genus is morphologically and anatomically very similar to *Fulgidea*, and differs mainly in two characters: the size of the pycnoconidia (2.5–5 vs. 7–10 µm long) and the secondary chemistry friesiic acid (depsido-depsone) vs. alectorialic acid (benzyl ester) and thamnolic acid (β-orcinol *meta*-depside). *Xylopsora* differs from *Elixia*, *Hypocenomyce*, and *Pycnora* in the same characters as listed under *Fulgidea*, above.

Xylopsora caradocensis (Nyl.) Bendiksby & Timdal, **comb. nov.** [MB 804851] ≡ *Lecidea caradocensis* Leight. ex Nyl. in Actes Soc. Linn. Bordeaux 21: 383. 1857 ≡ *Psora caradocensis* (Leight. ex Nyl.) Mudd, Man. Brit. Lich.: 169. 1861 ≡ *Toninia caradocensis* (Leight. ex Nyl.) J. Lahm in Jahres-Ber. Westfäl. Prov.-Vereins Wiss. 11: 125. 1884 ≡ *Bilimbia caradocensis* (Leight. ex Nyl.) A.L. Sm. in Crombie & Smith, Monogr. Lich. Britain 2: 133. 1911 ≡ *Hypocenomyce caradocensis* (Nyl.) P. James & Gotth. Schneid. in Lichenologist 12: 107. 1980 – Lectotype (designated by Timdal, 1992): U.K., Wales, Shropshire, Caer Caradoc, *W. Leighton s.n.* = Leighton, Lichenes Britannici Exsiccati No. 160 (BM!; isotypes: O No. L-450!; UPS!).

Xylopsora friesii (Ach.) Bendiksby & Timdal, **comb. nov.** [MB 804852] ≡ *Lecidea friesii* Ach. in Liljeblad, Utkast Sv. Fl., ed. 3: 610. 1816 ≡ *Psora friesii* (Ach.) Hellb. in Kongl. Svenska Vetensk. Acad. Handl., nov. ser., 9 (no. 11): 61. 1870 ≡ *Biatora friesii* (Ach.) Tuck., Syn. N. Amer. Lich. 2: 15. 1888 ≡ *Psora ostreata* f. *friesii* (Ach.) Boistel, Nouv. Fl. Lich. 2: 94. 1902 ≡ *Hypocenomyce friesii* (Ach.) P. James & Gotth. Schneid. in Biblioth. Lichenol. 13: 84. 1980 – **Lectotype (designated here):** "*Lecidea friesiana.* Suecia" (H-ACH No. 436A photo!).

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Appendix 1. Taxa and GenBank accession numbers for all samples included in this study; voucher information is given for newly generated sequences. An asterisk after the accession number indicates sequences reported here for the first time.

Taxon, voucher, accession number of nrITS, nrLSU, mtSSU. — Signs/symbols used: – missing data; * newly generated sequence; † only 5.8S and ITS2; ♦ sequences less than 200 bp that are provided below Appendix 1 because GenBank does not accept sequences shorter than 200 bp.

Acarospora peliscypha Th. Fr., DQ374132, –, DQ374108. ***Agyrium rufum*** (Pers.) Fr., –, EF581826, EF581823. ***Ainoa mooreana*** (Carroll) Lumbsch & I. Schmitt, –, AY212828, AY212850. ***Arctomia delicatula*** Th. Fr., –, AY853355, AY853307. ***Aspicilia cinerea*** (L.) Körb., HQ650637†, DQ986779, DQ986890. ***Bacidia rubella*** (Hoffm.) A. Massal., AF282087†, –, AY567723. ***Baeomyces rufus*** (Huds.) Rebent., AF448458†, DQ871008, DQ871016. ***Biatora vernalis*** (L.) Fr., Norway, *J.T. Klepsland JK09-L616* (O L-165159), KF360369*†, KF360446*, KF360418*. ***Boreoplaca ultrafrigida*** Timdal, HM161512, AY853360, AY853312. ***Bryoria capillaris*** (Ach.) Brodo & D. Hawksw., AF058032†, DQ923655, DQ923626. ***Calopadia* sp.,** –, EU601752, EU601739. ***Candelaria concolor*** (Dicks.) Stein, GU929922, DQ986791, DQ986806. ***Candelariella aurella*** (Hoffm.) Zahlbr., EF535162, AY853361, AY853313. ***Candelariella coralliza*** (Nyl.) H. Magn., AF182074, AY853362, AY853314. ***Candelariella reflexa*** (Nyl.) Lettau, EF535190, DQ912331, DQ912272. ***Candelariella terrigena*** Räsänen, HQ650602, DQ986745, –. ***Candelariella vitellina*** (Hoffm.) Müll. Arg., AJ640085, AY853363, AY853315. ***Catillaria chalybeia*** (Borrer) A. Massal., Norway, *R. Haugan 7947* (O L-155291), KF360370*†, KF360447*, –. ***Catolechia wahlenbergii*** (Ach.) Körb., AF250792, DQ986794, DQ986811. ***Cladia retipora*** (Labill.) Nyl., GQ500918†, AY340540, AY340487. ***Cladonia rangiferina*** (L.) F.H. Wigg, EU266113†, AY300832, AY300881. ***Coccotrema cucurbitula*** (Mont.) Müll. Arg., AF329162†, AF274092, AF329161. ***Crocynia pyxinoides*** Nyl., AF517920†, AY584653, AY584615. ***Diploschistes scruposus*** (Schreb.) Norman, HQ650716†, AF279389, AY584692. ***Elixia cretica*** T. Sprib. & Lumbsch **1,** Australia, New South Wales, Tinderry Range, 10 km E of Michelago, *H. Streimann & J.A. Curnow 50968 p.p.* (CANB-9304299 p.p.), KF360371*, KF360448*, –. **2,** Mexico, Chihuahua, along route 16 ca. 20 km W of Basaseachic, *E. Timdal SON78/03* (O L-15969), KF360372*, KF360449*, KF360419*. **3,** –, –, GQ892058. ***Elixia flexella*** (Ach.) Lumbsch **1,** Austria, *J. Halda, S. Palica & J. Steinova 12407* (O L-157191), KF360373*, KF360450*, KF360420*. **2,** –, AY853368, AY853320. **3,** –, AY300837, AY300887. ***Elixia* sp.** T. Sprib. & Lumbsch **1**, U.S.A., Arizona, Gila Co., McFadden Peak, 15 mi S of Young, *T.H. Nash III 11177* (ASU), KF360374*, KF360451*, –. **2,** U.S.A., Arizona, Cochise Co., Chiricahua National Monument, along the Loop Trail, *T.H. Nash III 41750* (ASU), KF360375*, KF360452*, –. ***Evernia prunastri*** (L.) Ach., HQ650611†, AF107562, AF351162. ***Fuscidea mollis*** (Wahlenb.) V. Wirth & Vezda, –, AY853369, AY853321. ***Geoglossum nigritum*** (Fr.) Cooke, DQ491490, AY544650, AY544740. ***Graphis scripta*** (L.) Ach., AF229195†, AY853370, AY853322. ***Gregorella humida*** (Kullh.) Lumbsch, AF429263†, AY853378, –. ***Gypsoplaca macrophylla*** (Zahlbr.) Timdal, –, DQ899298, –. ***Haematomma ochroleucum*** (Neck.) J.R. Laundon, EU075536†, AY756350, AY756367. ***Heterodea muelleri*** (Hampe) Nyl., GQ500906†, AY340545, AY340494. ***Hymenelia lacustris*** (With.) M. Choisy, –, AY853371, AY853323. ***Hypocenomyce anthracophila*** (Nyl.) P. James & Gotth. Schneid. **1,** Norway, *B.P. Løfall & A. Ognedal L10657* (O L-129736), KF360376*, KF360453*, KF360421*. **2,** Norway, *J.T. Klepsland JK08-L282* (O L-158453), KF360377*, KF360454*, KF360422*. **3,** Norway, *E. Timdal 11024* (O L-158536), KF360378*, KF360455*, KF360423*. **4,** Norway, *E. Timdal 11027* (O L-158539), KF360379*, KF360456*, KF360424*. ***Hypocenomyce australis*** Timdal **1,** Australia, *J.A. Elix 19801* (O L-144372), KF360380*†, –, –. **2,** Australia, *H. Krog Au14/2* (O L-144373), ♦*, –, –. **3,** Australia, *W.A. Weber & D. McVean s.n.*, 1967–10–11 (O L-201, isotype), KF360381*†, –, –. **4,** Australia, *G. Thor 6047a* (S), KF360382*, –, –. ***Hypocenomyce caradocensis*** (Nyl.) P. James & Gotth. Schneid. **1,** Norway, *E. Timdal 2410* (O L-32967), KF360383*†, –, –. **2,** Sweden, *G. Westling s.n.*, 1992–04–05 (S-L-53582), KF360384*†, –, –. **3,** Sweden, *G. Odelvik 599* (S-L-29227), KF360385*, –, KF360425*. ***Hypocenomyce castaneocinerea*** (Räsänen) Timdal **1,** Norway, *R. Haugan 9677* (O L-166561), KF360386*, KF360457*, KF360426*. **2,** Norway, *E. Timdal 11028* (O L-158540), KF360387*, KF360458*, KF360427*. ***Hypocenomyce foveata*** Timdal, Australia, *G. Thor 6047b* (S), ♦*, –, –. ***Hypocenomyce friesii*** (Ach.) P. James & Gotth. Schneid. **1,** Norway, *E. Timdal 11029* (O L-158541), KF360388*, KF360459*, KF360428*. **2,** Norway, *A. Breili 3615* (O L-167185), KF360389*, KF360460*, KF360429*. **3,** –, AY853372, AY853324. **4,** Norway, *E. Timdal 1055* (O L-56480), KF360390*†, –, –. ***Hypocenomyce isidiosa*** Elix **1,** Australia, *J.A. Elix 31849* (CANB-737037.1, isotype), KF360391*, KF360461*, KF360430*. **2,** Australia, *J.A. Elix 39837* (O L-171593), KF360392*, KF360462*, KF360431*. ***Hypocenomyce leucococca*** R. Sant. **1,** Norway, *E. Timdal 12232* (O L-170732), KF360393*, KF360463*, KF360432*. **2,** Norway, *E. Timdal 12328* (O L-170828), KF360394*, KF360464*, KF360433*. ***Hypocenomyce oligospora*** Timdal **1,** U.S.A., *T.H. Nash III 42735a* (O L-767, holotype), KF360395*, KF360465*, –. **2,** U.S.A., *S. Rui & E. Timdal US215/01* (O L-59862), KF360396*, KF360466*, KF360434*. **3,** U.S.A., *S. Rui & E. Timdal US272/01* (O L-59992), KF360397*, KF360467*, KF360435*. **4,** Russia, *R. Haugan & E. Timdal YAK04/05* (O L-18713), KF360398*, KF360468*, –. ***Hypocenomyce praestabilis*** (Nyl.) Timdal **1,** U.S.A., *E. Timdal SON70/13* (O L-15871), KF360399*, –, –. **2,** Sweden, *E. Timdal 2860* (O L-144277), KF360400*, KF360469*, –. ***Hypocenomyce scalaris*** (Ach.) M. Choisy **1,** Norway, *E. Timdal 11022* (O L-158534), KF360401*, KF360470*, KF360436*. **2,** DQ782852, DQ782914, DQ912274. **3,** HQ650632, DQ986748, DQ986861. **4,** –, AY853373, AY853325. **5,** –, AY853374, AY853326. ***Hypocenomyce sierrae*** Timdal **1,** U.S.A., *S. Rui & E. Timdal US249/01* (O L-59964), KF360402*, KF360471*, KF360437*. **2,** U.S.A., *E. Timdal SON125/01* (O L-60059, holotype), KF360403*, –, –. ***Hypocenomyce sorophora*** (Vain.) P. James & Poelt **1,** Norway, *M. Bendiksby & J. Klepsland MB-L1* (O L-175410), KF360404*, –, KF360438*. **2,** Norway, *E. Timdal 2643* (O L-60179), KF360405*†, –, –. **3,** Norway, *E. Timdal 3343* (O L-28248), KF360406*, –, KF360439*. **4,** Sweden, *E. Timdal 2908* (O L-144310), ♦*†, –, –. **5,** FJ959357, AY853387, AY853338. ***Hypocenomyce tinderryensis*** Elix **1,**

Appendix 1. Continued.

Australia, *J.A. Elix 38733* (CANB-790800), KF360407*, –, KF360440*. **2,** Australia, *J.A. Elix 33386* (CANB-9801742.1), KF360408*†, –, –. **3,** Australia, *J.A. Elix 33387* (CANB-676257), KF360409*†, –, –. **4,** Australia, *H. Streimann & J.A. Curnow 50968* (CANB-9304299, holotype), KF360410*, –, –. **5,** Australia, *H. Streimann & J.A. Curnow 35001* (CANB-610213.1), ♦*†, –, –. ***Hypocenomyce xanthococca*** (Sommerf.) P. James & Gotth. Schneid. **1,** Norway, *R. Haugan 8090* (O L-160472), KF360411*, KF360472*, KF360441*. **2,** Norway, *E. Timdal 11646* (O L-163707), KF360412*, KF360473*, KF360442*. **3,** AY853388, AY853388, AY853339. ***Lasallia pennsylvanica*** (Hoffm.) Llano, HM161513, AF356665, AY631278. ***Lasallia pustulata*** (L.) Mérat, HM161456, DQ883690, DQ986889. ***Lecanora carpinea*** (L.) Vain., AF070020†, DQ787363, DQ787364. ***Lecanora polytropa*** (Hoffm.) Rabenh., HQ650643†, DQ986792, DQ986807. ***Lecanora sulphurea*** (Hoffm.) Ach., AF070030†, –, EF105419. ***Lecidea atrobrunnea*** (Lam. & DC.) Schaer., EU259897, AY532993, GU074510. ***Lecidea tessellata*** Flörke, EU263926, AY532998, GU074491. ***Lecidella euphorea*** (Flörke) Hertel, HQ650596†, –, DQ986784. ***Lepraria lobificans*** Nyl., HQ650623, DQ986768, DQ986887. ***Lobothallia radiosa*** (Hoffm.) Hafellner, JF703124†, DQ780306, DQ780274. ***Lopadium disciforme*** (Flot.) Kullh., –, AY756355, AY756373. ***Loxospora ochrophaea*** (Tuck.) R.C. Harris, HQ650641†, DQ986750, DQ986900. ***Maronea constans*** (Nyl.) Hepp, –, AY640956, EF659771. ***Megalaria grossa*** (Nyl.) Hafellner, AF282074†, AY756356, AY762095. ***Meridianelia maccarthyana*** Kantvilas & Lumbsch, –, –, FJ763185. ***Metus conglomeratus*** (F. Wilson) D.J. Galloway & P. James, GQ500912†, AY340555, AY340510. ***Micarea adnata*** Coppins, AY756468†, AY756326, AY567751. ***Miltidea ceroplasta*** (C. Bab.) D.J. Galloway & Hafellner, –, HQ391558, HQ391557. ***Mycoblastus sanguinarius*** (L.) Norman, DQ782842†, DQ912333, DQ912276. ***Myelochroa aurulenta*** (Tuck.) Elix & Hale, –, DQ973025, DQ972972. ***Myriospora smaragdula*** (Wahlenb.) Nägeli, AY853354, AY853354, AY853306. ***Neophyllis melacarpa*** F. Wilson, –, AY340556, AY340511. ***Nephroma arcticum*** (L.) Torss., –, DQ973040, –. ***Ochrolechia parella*** (L.) A. Massal., AF332123†, AF274097, AF329173. ***Ophioparma handelii*** (Zahlbr.) Printzen & Rambold, China, *W. Obermayer 5135* (O L-168529), KF360413*, –, –. ***Ophioparma lapponica*** (Räsänen) Hafellner & R.W. Rogers, Norway, *E. Timdal 12353* (O L-170853), KF360414*, –, KF360443*. ***Ophioparma ventosa*** (L.) Norman **1,** Norway, *R. Haugan 7615* (O L-151477), KF360415*, KF360474*, KF360444*. **2,** AY011013, AY853380, AY853331. ***Orceolina kerguelensis*** (Tuck.) Hertel, AY212814, AY212830, AF381561. ***Parmelina quercina*** (Willd.) Hale, AY611105†, AY607818, AY611164. ***Peltigera praetextata*** (Sommerf.) Zopf, –, AF286813, –. ***Pertusaria dactylina*** (Ach.) Nyl., DQ782843†, DQ782907, DQ912307. ***Pertusaria leioplaca*** DC., AF332125†, AY300852, AY300903. ***Pilophorus strumaticus*** Cromb., AF517931†, AY340560, AY340517. ***Placopsis* sp.** D.L. Galloway, ined., AY212826, AY212845, AY212867. ***Placynthiella uliginosa*** (Schrad.) Coppins & P. James, HQ650633, DQ986774, DQ986877. ***Pleopsidium flavum*** Körb., AY853385, AY853385, AY853336. ***Pleopsidium gobiense*** (H. Magn.) Hafellner, HQ650723, DQ883698, DQ991755. ***Porpidia macrocarpa*** (DC.) Hertel & A.J. Schwab, EU263923, AY532964, GU074512. ***Porpidia speirea*** (Ach.) Kremp., HQ650631, DQ986758, DQ986865. ***Protoblastenia rupestris*** (Scop.) J. Steiner, EF524318†, AY756358, –. ***Protothelenella sphinctrinoidella*** (Nyl.) H. Mayrhofer & Poelt, –, AY607735, AY607747. ***Psilolechia leprosa*** Coppins & Purvis, AY756496†, AY756333, AY567730. ***Psora decipiens*** (Hedw.) Hoffm., HQ650619†, DQ986760, –. ***Ptychographa xylographoides*** Nyl., –, –, AY212872. ***Pyrrhospora quernea*** (Dicks.) Körb., AF517930†, AY300858, AY567712. ***Ramalina complanata*** (Sw.) Ach., –, DQ973038, DQ972986. ***Rhizocarpon oederi*** (Weber) Körb., AF483612, DQ986804, DQ986788. ***Rhizoplaca chrysoleuca*** (Sm.) Zopf, AF159940†, DQ787353, DQ787354. ***Rimularia psephota*** (Tuck.) Hertel & Rambold, –, DQ871012, DQ871019. ***Sarcogyne privigna*** (Ach.) A. Massal., DQ374145, AY853392, DQ374124. ***Schaereria fuscocinerea*** (Nyl.) Clauzade & Cl. Roux, AF274090†, AY300860, AY300910. ***Scoliciosporum umbrinum*** (Ach.) Arnold, AY541277†, AY300861, AY300911. ***Solenopsora holophaea*** (Mont.) Samp., AM292708†, –, –. ***Sphaerophorus globosus*** (L.) DC., HQ650622†, DQ986767, DQ986866. ***Sporastatia polyspora*** (Nyl.) Grummann, –, AY640968, AY584724. ***Sporastatia testudinea*** (Ach.) A. Massal., –, AY640969, AY584725. ***Stereocaulon paschale*** (L.) Hoffm., HQ650690†, AY340568, AY584726. ***Teloschistes flavicans*** (Sw.) Norman, –, EU680955, –. ***Tephromela atra*** (Huds.) Hafellner, HQ650608†, DQ986766, DQ986879. ***Thamnolia vermicularis*** (Sw.) Schaer., EU714437†, –, AY853345. ***Thelotrema suecicum*** (H. Magn.) P. James, AJ508684†, AY300867, AY300917. ***Toninia sedifolia*** (Scop.) Timdal, HQ650689†, DQ973039, DQ972987. ***Trapelia placodioides*** Coppins & P. James, AF274081, AF274103, AF431962. ***Trapeliopsis granulosa*** (Hoffm.) Lumbsch, AF353569, AF274119, AF381567. ***Tremolecia atrata*** (Ach.) Hertel, –, AY853397, AY853397. ***Umbilicaria africana*** (Jatta) Krog & Swinscow, HM161482, HM161545, HM161572. ***Umbilicaria aprina*** Ach., HM161483, HM161514, HM161573. ***Umbilicaria crustulosa*** (Ach.) Lamy, HM161496, HM161590, HM161612. ***Umbilicaria proboscidea*** (L.) Schrad., FR799305, AY300870, AY300920. ***Umbilicaria spodochroa*** Hoffm., HM161481, DQ986773, DQ986815. ***Wawea fruticulosa*** Henssen & Kantvilas, –, DQ007347, DQ871023. ***Xanthoria parietina*** (L.) Beltr., –, AF356687, –. ***Xylographa opegraphella*** Rothr., Norway, *E. Timdal 12066* (O L-170568), –, KF360475*, –. ***Xylographa parallela*** (Ach. : Fr.) Fr., Norway, *E. Timdal 10892* (O L-152948), KF360416*, KF360476*, KF360445*. ***Xylographa trunciseda*** (Th. Fr.) Redinger, Norway, *R. Haugan ål2804c2* (O L-131751), KF360417*, KF360477*, –. ***Xylographa soralifera*** Holien & Tønsberg, –, AY212849, AY212878.

♦ Sequences shorter than 200 bp:

***Hypocenomyce australis* 2,** Australia, *H. Krog Au14/2* (O L-144373), ITS1 and 5.8S ribosomal RNA gene, partial
AGGCCGAACCTCCCACCCTTTGTGTACCTTACCTTTGTTGCTTTGGCGGGCCCGTGGGGATCACCCACCGTCGGCTCCGGTTGACGCGTGCC
CGCCAGA

Hypocenomyce foveata, Australia, *G. Thor 6047b* (S), 5.8S ribosomal RNA gene and ITS2, partial sequences:
CTTTGAACGCACATTGCGCCCCTTGGTATTCCGGGGGGCATGCCTGTTCGAGCGTCATTGCAACCCTCAAGCGCAGCTTGGTGTTGGGCCTC
CGCCCCCCTGGGCGTGCCCGAAAAGCAGTGGCGGTCCGGGATGACTCCAAGCGAAGTAGAATTTTTCCGCTTCCGGAGTTCGCCCCGTGGC
CCGCCAGACAACCAC

***Hypocenomyce sorophora* 4,** Sweden, *E. Timdal 2908* (O L-144310), 5.8S ribosomal RNA gene and ITS2, partial sequences:
ACGCACATTGCGCCCCTTGGTATTCCGAGGGGCATGCCTGTTCGAGCGTCATTACACCACTCAAGCTCAGCTTGGTATTGGGCCTTCACCCCT
CGCGGGTGTGCCTAAAAATCAGTGGCGGTGCCGCCTGGCTTCAAGCGTAGTAATTATTTCTCGCTCTGGAAGTCCGGGTGCGTTGCCTGCCAT
CAACCCCC

***Hypocenomyce tinderryensis* 5,** Australia, *H. Streimann & J.A. Curnow 35001* (CANB-610213.1), 5.8S ribosomal RNA gene and ITS2, partial sequences:
GCACATTGCGCCCCTCGGTATTCCKAGGGGCATGCSTGTTCGAGCGTCATTACACCCCTCAAGCCCTGCTTGGTCTTGGGCCTCGTCCCCCGG
GACGTGCCCGAAAGTCAGTGGNGGCCCGGTCCGACTTCAAGCGTAGTAAATACATCATTCCGCTTTGGAAGCCTCTGGGCCGGTC