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Multigene phylogeny and taxonomic revision of *Atheliales s.l.*: reinstatement of three families and one new family, *Lobuliciaceae fam. nov.*

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Abstract

Atheliales (*Agaricomycetes*, *Basidiomycota*) is an order mostly composed of corticioid fungi, containing roughly 100 described species in approximately 20 genera. Members exhibit remarkable ecological diversity, including saprotrophs, ectomycorrhizal symbionts, facultative parasites of plants or lichens, and symbionts of termites. Ectomycorrhizal members are well known because they often form a major part of boreal and temperate fungal communities. However, *Atheliales* is generally understudied, and molecular data are scarce. Furthermore, the order is riddled with many taxonomic problems: some genera are non-monophyletic, and several species have been shown to be more closely related to other orders. We investigated the phylogenetic position of genera that are currently listed in *Atheliales sensu lato* by employing an *Agaricomycetes*-wide dataset with emphasis on *Atheliales* including the type species of genera therein. A phylogenetic analysis based on LSU, 5.8S, *rpb2*, and *tef1* (excluding third codon) returnedretrieved *Atheliales* in subclass *Agaricomycetidae*, as sister to *Lepidostromatales*. In addition, a number of *Atheliales* genera were retrieved in other orders with strong support: *Byssoporia* in *Russulales*, *Digitatispora* in *Agaricales*, *Hypochnella* in *Polyporales*, *Lyoathelia* in *Hymenochaetales*, and *Pteridomyces* in *Trechisporales*. Based on this result, we assembled another dataset focusing on the clade with *Atheliales sensu stricto* and representatives from *Lepidostromatales* and *Boletales* as outgroups, based on LSU, ITS (ITS1–5.8S–ITS2), *rpb2*, and *tef1*. The reconstructed phylogeny of *Atheliales* returned five distinct lineages, which we propose here as families. *Lobulicium*, a monotypic genus with a distinct morphology of seven-lobed basidiospores, was placed as sister to the rest of *Atheliales*. A new family is proposed to accommodate this genus, *Lobuliciaceae fam. nov*. The remaining four lineages can be named following the family-level classification by Jülich (1982), and thus we opted to use the names *Atheliaceae*, *Byssocorticiaceae*, *Pilodermataceae*, and *Tylosporaceae*, albeit with amended circumscriptions.

Keywords

Agaricomycetes, Basidiomycota, corticioid fungi, multi-locus phylogeny, family-level taxonomy

Supplementary Materials

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INTRODUCTION

Atheliales Jülich (1982) is a fungal order in the subclass *Agaricomycetidae,* class *Agaricomycetes*, phylum *Basidiomycota* (Hibbett et al., 2007; Wijayawardene et al., 2020). Unlike most other orders within the extremely diverse *Agaricomycetes*, members of *Atheliales* are generally inconspicuous with relatively simple gross morphology, possessing few diagnostic features. Members of the order are generally corticioid and athelioid, producing effused, crust-like fruiting bodies that are loosely attached to the substrate and with non-differentiated margins (Eriksson et al., 1984, 1981, 1978). *Atheliales* species prefer moist habitats on the forest floor, and they are mostly documented in temperate regions (Dai, 2011; Ezhov et al., 2017; Ginns, 1998; Gorjón and Bernicchia, 2013; Gorjón and Hallenberg, 2013; Ordynets et al., 2017; Rosenthal et al., 2017). The order encompasses approximately 100 species in 20 genera (He et al., 2019; Index Fungorum, 2020; Wijayawardene et al., 2020), mostly composed of described species from Europe. However, new taxa are being added not only from Europe (Duhem, 2013; Kotiranta et al., 2011), but also from Argentina (Gorjon et al., 2012), Chile (Gorjón and Hallenberg, 2013), Bhutan (Dhingra and Singh, 2018), and India (Singh et al., 2010; Prasher, 2015).

Despite their simple gross morphology, members of *Atheliales* exhibit a remarkable diversity of ecological strategies, which include: ectomycorrhizal (*Amphinema*, *Byssocorticium*, *Piloderma* and *Tylospora*; Tedersoo et al., 2010), white rot saprotrophic (*Athelia*, *Athelopsis*, *Fibulomyces*, *Leptosporomyces*; Tedersoo et al., 2014), lichenicolous (*Athelia arachnoidea*; Yurchenko and Olubkov, 2003), and putatively parasitic on termites involving mimicry of termite eggs (*Athelia termitophila*; Maekawa et al., 2020; Matsuura et al., 2000; Yashiro et al., 2011). Sequences obtained from the roots of achlorophyllous orchids *Lecanorchis spp.* and *Erythrorchis altissima* also suggest that members of *Atheliales* are associated with mycoheterothrophy (Ogura-Tsujita et al., 2018; Okayama et al., 2012). Some members are economically important because they cause spoilage of vegetables and fruits in cold storage (Adams and Kropp, 1996; de Vries et al., 2008; Wenneker et al., 2017). Ectomycorrhizal members of *Atheliales* form a major part of many ectomycorrhizal communities (Peter et al., 2008; Rosenthal et al., 2017), and are potentially diverse in the tropics (Tedersoo and Smith, 2013). Despite their importance in ecological studies and recent additions of new taxa, such as *Fibulomyces cystoideus* (Dhingra and Singh, 2018) and *Athelia termitophila* (Maekawa et al., 2020), no molecular phylogenetic study has focused on *Atheliales* thus far.

Most of the core *Atheliales* genera were initially grouped within *Corticiaceae sensu lato* (Donk, 1964). Parmasto (1968) then described the subfamily “Athelioideae” with three subsequent groups: “Atheliae”, “Amylocorticieae”, and “Byssomerulieae”. Jülich (1972) published a monograph of “Atheliae” that contained core *Atheliales* genera such as *Athelia*, *Byssocorticium*, *Fibulomyces*, *Leptosporomyces*, *Piloderma*, and *Tylospora*. Subsequently, in his classification of basidiomycetes, Jülich (1982) introduced a family-level classification of the order *Atheliales* with four families: *Atheliaceae*, *Byssocorticiaceae*, *Pilodermataceae*, and *Tylosporaceae*. With the advent of molecular phylogenetics, *Atheliales* started to be included in large-scale studies (Boidin et al., 1998). In phylogenetic studies focusing on corticioid fungi, Larsson et al. (2004) and Binder et al. (2005) recovered *Atheliales* as a monophyletic group, which was later recognized as an order in the latest comprehensive classification of corticioid fungi (Larsson, 2007) and of the fungal kingdom (Hibbett et al., 2007), placed within the subclass *Agaricomycetidae*. With the limited sampling of *Atheliales* in these studies, Jülich's (1982) subdivision into four families could not be tested and therefore only one family is currently recognized: *Atheliaceae* (He et al., 2019; Wijayawardene et al., 2020).

The relationship between *Atheliales* and *Amylocorticiales*, another order in *Agaricomycetidae* dominated by corticioid species, is still unclear. Based on phylogenomic studies (Li et al., 2020; Nagy et al., 2015), *Atheliales* is closely related with *Amylocorticiales* (Figure 1A). However, large-scale multigene phylogenies inferred from nuclear ribosomal SSU and LSU, 5.8S, *rpb1*, *rpb2*, and *tef1* (Chen et al., 2019; Zhao et al., 2017) showed that *Amylocorticiales* is most closely related to *Agaricales*, while *Atheliales* is closely related to *Lepidostromatales* (Figure 1B), for which no genomes are currently available. Varga et al. (2019) constructed a phylogeny of *Agaricomycetes* based on LSU, *rpb2*, and *tef1* with a phylogenomic backbone constraint on the deep nodes, and *Atheliales* forms a clade with *Amylocorticiales* and *Lepidostromatales* with unresolved relationships (Figure 1C).

Over the years, a number of genera have been described and added to *Atheliales*, based on morphological characters alone (Hjortstam and Ryvarden, 2010, 2004) or combined with molecular phylogenetic evidence (Kotiranta et al., 2011). Sequence-based studies found some of these genera to be polyphyletic, sometimes with members clustering within other orders (Binder et al., 2010; Ertz et al., 2008; Hibbett et al., 2007). Genera of *Atheliales sensu lato* are summarized in Table 1, as well as significant sources indicating their presumed affiliations. Well-annotated molecular data in public databases are scarce for *Atheliales*, and a phylogeny of the order is lacking.

In this study, we present the first comprehensive phylogenetic treatment of the order *Atheliales* with two specific aims. First, we aimed to delimit *Atheliales* by sampling the type species of the genera listed in *Atheliales sensu lato* (Table 1) as well as representatives of various orders within *Agaricomycetes*. Due to the taxonomic breadth of this analysis, we used molecular data from 5.8S and LSU of the nuclear ribosomal DNA as well as the protein coding regions of *rpb2* and *tef1* excluding the third codon position to reconstruct the phylogeny of *Agaricomycetes*. Second, we aimed to delineate phylogenetic lineages within the order. For this aim, we assembled a dataset composed of taxa belonging to *Atheliales sensu stricto*. This dataset was based on the nuclear ribosomal ITS1, 5.8S, ITS2, and LSU, as well as *rpb2* and *tef1* including the third codon position.

MATERIALS AND METHODS

Taxon sampling, fungal isolates, and DNA extraction

We targeted taxa in *Atheliales sensu lato* as summarized in Table 1, with emphasis on the type species of each genus. Specimens were retrieved from the herbarium of Uppsala University Museum of Evolution (UPS), the herbarium of University of Gothenburg (GB), and the Farlow Herbarium at Harvard University (FH), as well as the private collections of B.P. Sulistyo (BPS) and M. Ryberg (MR) (Table 2). Several specimens from GB (Table 2: E. Bendiksen 645 07, E. Bendiksen 523 07, E. Bendiksen 580 07, KHL 13899, E. Bendiksen 573 07, KHL 13496b, V. Spirin 8810a) were extracted using the DNeasy Plant Mini Kit (Qiagen, Stanford, CA), whereas specimens from FH were extracted using the Extract-N-Amp Plant PCR Kit (Sigma-Aldrich, St. Louis, MO) according to Haelewaters et al. (2018), or the E.Z.N.A. HP Fungal DNA Kit (Omega Bio-Tek, Norcross, GA) following the manufacturer's instructions. Specimens from UPS, BPS, and MR, as well as the rest of specimens from GB were extracted using a modified CTAB/chloroform-isoamyl alcohol DNA extraction (Cubero et al., 1999). Approximately 5 × 5 mm hymenium was picked from the substrate and grinded using a micropestle in 500 µl of 2% CTAB extraction buffer (100 mL Tris, 20 mM Na_2EDTA, 1.4 M NaCl, pH 8.0) with 1% β-mercaptoethanol. The resulting mixture was then incubated at 65 ˚C for up to 2 hours. Subsequently, 500 µl of chloroform: isoamyl alcohol (24:1) was added and the mixture was shaken horizontally at low speed for 1 hour before centrifugation at 12,000 rpm for 14 min. Following this, 360 µl of the upper phase was transferred into a new tube and 240 µl of cold isopropanol was added. After the sample precipitated overnight at cold temperature, it was centrifuged and the resulting DNA pellet was washed using wash buffer (76% EtOH, 10 mM ammonium acetate). Finally, the DNA was dissolved in 50 µl TE buffer (10 mM Tris, 1 mM

EDTA, pH 8.0), and its concentration and integrity were determined by means of Qubit Fluorometric Quantitation (Invitrogen, Carlsbad, CA) and gel electrophoresis.

PCR amplification, sequencing, and sequence analyses

Six molecular markers were used in this study: nuclear ribosomal regions of ITS1, 5.8S, ITS2, and LSU, as well as the protein coding regions of *rpb2* and *tef1* (Binder et al., 2010; Matheny et al., 2007; Miettinen et al., 2012; Zhao et al., 2017). Amplification of *rpb2* targeted the region between conserved domains 5 and 7 (Liu et al., 1999), whereas for *tef1* the target region was between exons 4 and 8 (Wendland and Kothe, 1997). Primers used for PCR and sequencing of these target regions are listed in Table 3. Modifications to two primers used in previous studies were also done to facilitate amplification and sequencing of *Atheliales* taxa. LB-W-R is a reverse-complement of LB-W (Tedersoo et al., 2008), used to bridge the gap in the sequencing of LSU PCR products. Additionally, EF1-1577Fa was based on EF1-1577F (Rehner and Buckley, 2005) with one nucleotide difference for better priming in *Atheliales*, and this primer was designed using the dataset of Binder et al., (2010).

Cycling conditions for the amplification of ITS began with initial denaturation at 95 ˚C for 3 min, followed by 35-40 cycles of denaturation at 95 ˚C for 15 s, annealing at 55 $^{˚0}$C for 30 s, and extension at 72 ˚C for 1 min, concluded by final extension at 72 ˚C for 10 min. LSU amplification used similar cycling conditions as ITS, but with annealing temperature of 48 ˚C. Cycling conditions for the amplification of *rpb2* and *tef1* were based on the methods of Rehner and Buckley (2005) and Matheny *et al.* (2007). The program started with denaturation at 94 ˚C for 2 min, 8 cycles of denaturation at 94 ˚C for 40 s, annealing at 60 ˚C for 40 s with 1 ˚C decrease/cycle, and extension at 72 ˚C for 1-2 min, followed by 36 cycles of denaturation at 94 ˚C for 45 s, annealing at 53 ˚C for 90 s, and extension at 72 ˚C for 1-2 min, concluded by final extension at 72 ˚C for 10 min. All PCR products were cleaned by means of ExoSAP-IT (Applied Biosystems, Foster City, CA) and sent for sequencing to Macrogen Europe (Amsterdam, the Netherlands). Purification and sequencing of PCR products for samples obtained from FH were outsourced to Genewiz (South Plainfield, NJ). Sequencing reads were assembled, assessed, and edited using CodonCode Aligner (CodonCode Corporation, Centerville, MA) or Sequencher 4.10.1 (Gene Codes Corporation, Ann Arbor, MI). To confirm their identities and filter out contaminations, ITS sequences of all samples were blasted against the UNITE database (Kõljalg *et al.*, 2013; https://unite.ut.ee/).

Dataset assembly and multiple sequence alignment

We constructed two datasets: an *Agaricomycetes*-wide dataset and an *Atheliales sensu stricto* dataset. The *Agaricomycetes* dataset comprised representatives of each order in the class (except *Hysterangiales* and *Geastrales* in the *Phallomycetidae*), with *Dacrymycetes* as outgroup. This *Agaricomycetes* dataset was used to identify the members of *Atheliales sensu stricto* and to ascertain the phylogenetic position of several taxa that had not yet been considered in a phylogenetic context. Based on the result of this dataset's phylogenetic analysis, we then constructed the *Atheliales sensu stricto* dataset, with *Atheliales* as ingroup, and *Lepidostromatales* and *Boletales* as outgroups.

In total, 108 sequences were newly generated during this study: 31 ITS, 32 LSU, 26 *rpb2*, and 19 *tef1* sequences. These were supplemented with 310 sequences downloaded from NCBI GenBank for phylogenetic analyses. The complete list of taxa and GenBank accession numbers can be found in Table 2. For both datasets, taxa without LSU were excluded from subsequent analyses to avoid indistinguishable branches in the tree (Sanderson et al., 2010). The molecular markers for the *Agaricomycetes* dataset were LSU, 5.8S, *rpb2*, and *tef1*. The ITS regions (ITS1 and ITS2) were excluded from the *Agaricomycetes* dataset to avoid erroneous alignment due to the large numbers of indels (Tedersoo et al., 2018). Furthermore, we also excluded the third codon positions of both *rpb2* and *tef1* from the *Agaricomycetes* dataset since this position is prone to saturation under broad taxonomic range (Binder et al., 2010; Matheny et al., 2007). This finding was supported by preliminary analyses, which showed that the exclusion of third codon positions increased overall support values. However, the opposite was true for the *Atheliales* dataset due to its narrower taxonomic breadth; as a result, third codon positions were included in this dataset. All three ITS regions, ITS1, 5.8S, and ITS2, were also included in the *Atheliales* dataset since direct comparison suggested that they contained significant phylogenetic signals as marked by the change in overall support values.

Alignments and overall data management were done in Geneious v.10.2 (Biomatters, Auckland, New Zealand). Sequences were grouped according to their respective region and aligned separately. Full-length ITS1, 5.8S, and ITS2 regions were identified and separated using ITSx (Bengtsson-Palme et al., 2013). Multiple sequence alignments were carried out using MAFFT v7.388 (Katoh et al., 2002; Katoh and Standley, 2013). LSU, *rpb2,* and *tef1* were aligned using the MAFFT E-INS-I algorithm, whereas G-INS-I was used for aligning full-length 5.8S, ITS1, and ITS2 sequences. Afterwards, alignments were improved by realigning several challenging regions, manual adjustments, including trimming the ends of sequences and the removal of introns from *rpb2* and *tef1* alignments.

Phylogenetic analyses

Prior to phylogenetic analyses, the topological congruence among different regions was evaluated using RAxML v8.2.12 (Stamatakis, 2014), with the GTRGAMMA model and 500 rapid bootstrap replicates. Since no well-supported conflict (BS≥75) was found among the topologies of each region, the sequences were concatenated for further analyses. For each dataset, partitioning schemes and substitution models were determined using PartitionFinder2 (PF2) (Kainer and Lanfear, 2015). Phylogenetic trees were estimated based on maximum likelihood (ML) using RAxML v8.2.12 (Stamatakis, 2014) and Bayesian inference (BI) with MrBayes v3.2.7a (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003). All PF2, ML, and BI analyses were done on the CIPRES Science Gateway webserver (Miller et al., 2010).

Input for PF2 was the concatenated alignment with user-defined data blocks for each region as well as each codon position for *rpb2* and *tef1* (only the 1st and 2nd for the *Agaricomycetes* dataset and all three for the *Atheliales* dataset), analyzed using the greedy algorithm (Lanfear et al., 2012) and based on Bayesian information criterion (BIC), with options for models according to those that are available in either RAxML or MrBayes. Consequently, phylogenetic analyses were done following the partitioning scheme and substitution model recommended by PF2 (Table 4).

For RAxML analyses, a phylogenetic tree was inferred through 1000 rapid bootstrap replicates. Since the specification of different models among partitions is not possible with RAxML, GTRGAMMA+I was selected as it fitted most of the partitions. As for MrBayes analyses, the MrBayes block appended to the PF2 output was directly used to define the partitions as well as their respective substitution models, with independent estimation of substitution rate matrix, gamma shape parameter, transition/transversion rate ratio, proportion of invariant sites, and character state frequencies for each partition. Each MrBayes analysis was performed with two separate runs and four chains for each run, for 100,000,000 generations with a stop rule based on max standard deviation of split frequencies below 0.01 and sampling of trees every 1,000 generations. Tracer v1.7 (Rambaut et al., 2018) was used to assess the convergence of parameter values for each run. FigTree v1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/), TreeGraph2 (Stöver and Müller, 2010), and Inkscape (https://inkscape.org/en/) were used to visualize trees and edit the final figures.

RESULTS

Phylogenetic analyses of the *Agaricomycetes* dataset

Alignment statistics for the *Agaricomycetes* dataset are summarized in Table 5. The final concatenated alignment for the *Agaricomycetes* dataset contained 3254 total characters, 2841 of which were variable (87.30%), with mean coverage of 80.22%. Furthermore, based on subsequent RAxML searches the corresponding alignment contained 1997 distinct alignment patterns and a proportion of gaps and completely undetermined characters of 36.30%. Partitioned RAxML analyses resulted in the best scoring tree with a likelihood value of -42267.72. In addition to this, MrBayes analyses, which consisted of two runs, converged into a stable distribution with mean likelihood value of -42251.59 and -42253.66, respectively. There was no significant conflict between the RAxML and MrBayes analyses. The topology shown in Figure 3 is based on the ML tree, with bootstrap (BS) support and posterior probability (PP) values from the BI consensus tree. To facilitate discussion, support values are mentioned in the text as (BS/PP).

The reconstructed phylogeny of *Agaricomycetes* (Figure 3) recovered species that had been classified in *Atheliales s.l.* in the following major groups with strong support (BS≥75/PP≥0.95): *Byssoporia terrestris* in *Russulales* (96/1.00), *Digitatispora marina* in *Agaricales* (98/1.00), *Lyoathelia laxa* in *Hymenochaetales* (87/1.00), and *Pteridomyces galzinii* in *Trechisporales* (100/1.00). Two additional species were retrieved in other orders, receiving weak to moderate BS support but strong PP values: *Hypochnella violacea* in *Polyporales* (60/0.99), and *Leptosporomyces septentrionalis* in *Amylocorticiales* (55/1.00). The order *Lepidostromatales* was inferred as sister group to *Atheliales*, but without strong support in the ML analysis (49/0.96), and *Boletales* as sister to the *Atheliales-Lepidostromatales* clade (34/0.96). *Atheliales* was strongly supported (89/0.99) and contained *Stereopsis vitellina*, in congruence with previous results by Sjökvist et al. (2012).

Phylogenetic analyses of the *Atheliales sensu stricto* dataset

The *Atheliales* dataset consisted of 59 ingroup taxa and 11 outgroup taxa (2 *Lepidostromatales* and 9 *Boletales* taxa). Various alignment statistics for the *Atheliales* dataset are summarized in Table 5. The final concatenated alignment added up to 3713 total characters, 3130 of which were variable (84.30%), with mean coverage level of 71.85%. Based on successive RAxML searches, the alignment consisted of 2036 distinct alignment patterns with the proportion of gaps and completely undetermined characters of 40.53%. Partitioned RAxML analyses of the dataset yielded a final optimized likelihood value of -33904.79, whereas the two MrBayes runs each converged into a stable distribution with mean likelihood of -33449.37 and -33451.04, respectively. Similar to the *Agaricomycetes* dataset, the best tree from RAxML and the consensus tree from MrBayes analyses showed congruent topology without any strongly supported conflict. The reconstructed ML phylogeny of *Atheliales* is shown in Figure 4 with ML BS and Bayesian PP values.

In the resulting *Atheliales* phylogeny (Figure 4), *Lobulicium occultum* was placed as sister to the rest of *Atheliales* taxa, which formed a clade with relatively strong support (72/1.00). Because of its unique and isolated phylogenetic position in combination with a distinct spore morphology and ecology, we propose to place *Lobulicium* in a new family, *Lobuliciaceae*. *Atheliales* was further divided into four major clades with moderate to strong support, proposed to correspond to families *sensu* Jülich (1982): *Atheliaceae* (92/1.00) with *Athelia* and *Fibulomyces*; *Byssocorticiaceae* (55/1.00) with *Athelopsis*, *Byssocorticium*, and *Leptosporomyces*; *Pilodermataceae* (83/1.00) with *Piloderma*, *Tretomyces*, and *Stereopsis vitellina*; and *Tylosporaceae* (89/1.00) with *Amphinema* and *Tylospora*. A number of genera were found to be non-monophyletic, including *Amphinema*, *Athelia*, *Athelopsis*, and *Leptosporomyces*. In addition to this, *Athelopsis subinconspicua* and *Leptosporomyces raunkiaeri* could not be placed with confidence in any of the proposed families. These two taxa formed a maximum supported clade (100/1.00), which was placed sister to *Pilodermataceae* with only high PP support (45/0.99).

TAXONOMY

***Atheliales* Jülich (1982) emend.**

Bibliotheca Mycologica 85: 343 (1982)

Type family: Atheliaceae Jülich.

Description: Basidiomata annual, resupinate or spathulate, soft to tough, byssoid, pellicular or membraneous; hymenium smooth; hyphal system monomitic, septa with or without clamps, subicular hyphae sometimes with encrustation, hyphal strands present or absent; cystidia present or absent; basidia clavate to pedunculate, with 2 or 4 sterigmata; basidiospores smooth or verruculose, globose, elliptic, cylindrical, or lobed, thin- to slightly thick-walled, never amyloid or dextrinoid, sometimes cyanophilous. Saprotrophic, ectomycorrhizal, or parasitic on plants and lichens.

Confirmed genera: *Amphinema*, *Athelia*, *Athelopsis*, *Byssocorticium*, *Fibulomyces*, *Leptosporomyces*, *Lobulicium*, *Piloderma*, *Tretomyces*, *Tylospora*.

Remarks: Jülich (1982) included four families in the order: *Atheliaceae*, *Byssocorticiaceae*, *Pilodermataceae*, and *Tylosporaceae*. Here we confirm that all four families should be accepted and that a fifth family, *Lobuliciaceae fam. nov.*, should be added. *Athelopsis subinconspicua* and *Leptosporomyces raunkiaerii* are currently left as *Atheliales incertae sedis*.

Our results showed that *Pteridomyces* (type: *P. galzinii* (Bres.) Jülich) should be placed in *Trechisporales* and *Lyoathelia* (type: *L. laxa* (Burt) Hjortstam & Ryvarden) in *Hymenochaetales* (Figure 3). *Pteridomyces galzinii* differs from *Atheliales* through the presence of sterile hyphal pegs and adnate, slightly ceraceous basidiomata (Gorjon et al., 2012; Jülich, 1979; Nakasone, 2013). *Lyoathelia laxa* has pellicular-membraneous basidiomata like most species in *Atheliales* but differs by having doliform-pedunculate basidia and well-differentiated, capitate cystidia (Hayashi, 1974; Hjortstam and Ryvarden, 2004; Jülich, 1972).

***Atheliaceae* Jülich (1982) emend.**

Type genus: *Athelia* Pers., Traité champ. Comest. (Paris): 57 (1818) **–** Figure 2A.

Description: Basidiomata annual, resupinate, effused, loosely adnate, pellicular, undifferentiated margin; hymenium smooth, sometimes slightly plicate when fresh, light colored; hyphal system monomitic, septa with or without clamps, hyphae thin- to slightly thick-walled, in subiculum loosely arranged, hyphal strands present in some species; cystidia absent; basidia clavate, rarely pedunculate, arranged in clusters, with 2–4 sterigmata; basidiospores thin-walled, hyaline, smooth, subglobose to elliptic or fusoid, neither amyloid, dextrinoid nor cyanophilous. Saprotrophic on various substrates, rarely parasitic on plants or lichens.

Genera: *Athelia*, *Fibulomyces* Jülich.

Remarks: Jülich (1982) included also the genera *Athelopsis*, *Caerulicium*, *Confertobasidium*, *Leptosporomyces,* and *Luellia* in *Atheliaceae*. Here we show that *Athelopsis* and *Leptosporomyces* belong in *Byssocorticiaceae*. *Caerulicium* seems to be closely related to *Byssocorticium* but this can only be confirmed after sequencing of the type species, *C. neomexicanum*. *Confertobasidium* (type: *C. olivaceoalbum*) has its place in *Russulales* (Larsson and Larsson, 2003), and *Luellia* seems to belong in *Trechisporales* (Larsson, 2007).

Athelia and *Fibulomyces* share a pellicular basidioma and basidia arranged in clusters (Eriksson and Ryvarden, 1975, 1973). The decision to keep the two genera separate has been questioned (Eriksson and Ryvarden, 1973). Our analyses show that if the current concept of *Athelia* is to be maintained, then *Fibulomyces* must be reduced to synonomy. If, on the other hand, we want to keep *Fibulomyces* separate, then *Athelia bombacina* and *A. singularis* must be transferred to a new genus. Morphologically, *A. bombacina*, *A singularis,* and *F. mutabilis* are united by their consistently clamped hyphae (Eriksson et al., 1984, 1978; Kunttu et al., 2016). Eriksson and

Ryvarden (1973) stated that *A. bombacina* resembles *F. mutabilis* morphologically and even ecologically. *Athelia singularis*, on the other hand, is morphologically closer to *A. fibulata* (Kunttu et al., 2016), which is phylogenetically further related (Figure 4). More data are needed before taxonomic changes can be made.

A future circumscription of *Athelia* should include more related taxa as well as an effort to delimit the type species, *A. epiphylla* (Figure 2A). Eriksson and Ryvarden (1973) noted that *A. epiphylla* is a complex with a considerable variation in morphology and they admittedly adopted a wide species concept when treating the species for North Europe.

***Byssocorticiaceae* Jülich (1982) emend.**

Type genus: *Byssocorticium* Bondartsev & Singer, Mycologia 36: 69 (1944) **–** Figure 2B.

Description: Basidiomata annual, resupinate, effused, soft, byssoid to membranous, easily detached, margin undifferentiated; hymenium smooth, continuous, white, blue or greenish blue; hyphal system monomitic, septa with or without clamps, hyphae thin-walled or slightly thick-walled, hyphal strands present or absent; cystidia absent; basidia clavate or pedunculate, with four sterigmata; basidiospores smooth, globose, elliptic or cylindrical, thin- or slightly thick-walled, neither amyloid, dextrinoid nor cyanophilous. Saprotrophic or ectomycorrhizal.

Genera: *Athelopsis* Oberw. ex Parmasto, *Byssocorticium*, *Leptosporomyces* Jülich.

Remarks: Jülich (1982) included three genera in this family, beside the type genus also *Byssoporia* and *Hypochnopsis*. However, *Byssoporia* has its place near *Albatrellus* in *Russulales* (Bruns et al., 1998; Larsson, 2007; Smith et al., 2013), and *Hypochnopsis* is a synonym of

Amaurodon and belongs to *Thelephorales* (Kõljalg, 1996). In addition to the type genus, *Byssocorticiaceae* now includes *Athelopsis* and *Leptosporomyces*, both of which are in need of revision as they are non-monophyletic. This has been shown in the present study as well as in previous work (Hodkinson et al., 2014; Larsson, 2007).

Athelopsis was introduced to accommodate four species with an *Athelia*-like basidioma but having pedunculate instead of clavate basidia (Parmasto, 1968). Of these four species, only the type, *Athelopsis glaucina*, remains. Several other species have subsequently been added to the genus but a great majority of them are probably placed elsewhere. In our *Atheliales* analysis, *A. glaucina* was placed as sister to the rest of *Byssocorticiaceae* with moderate ML support (50<BS<75) but strong PP support (Figure 4). However, its placement seems to be unstable and affected by dataset composition, as it clustered with *Athelia* in the *Agaricomycetes* dataset with strong support (Figure 3). More data is needed to ascertain its position within the *Byssocorticiaceae*.

Jülich (1982) introduced *Leptosporomyces* to accommodate species with *Athelia*-like basidiomata but with short-cylindrical instead of clavate basidia. The genus was introduced with five species although subsequent additions have raised the number of species to 15 (He et al., 2019; Index Fungorum, 2020). For most of these, DNA sequences are currently not available. In our analyses, only the type species was retrieved in *Byssocorticiaceae*, whereas *Leptosporomyces raunkiaeri* was placed in a separate clade with *Athelopsis subinconspicua*, both currently ranked as *Atheliales incertae sedis*.

Lobuliciaceae* Sulistyo, K.H. Larss., & M. Ryberg, *fam. nov.

Mycobank no.: MB 835270

Type and single genus: *Lobulicium* K.H. Larss. & Hjortstam, Mycotaxon 14: 69 (1982).

Description: Basidiomata annual, resupinate, thin and soft, easily detached, margin very finely fibrillose; hymenium smooth, porulose, white; hyphal system monomitic, septa with clamps, hyphae thin-walled; cystidia absent; basidia small, clavate, with four sterigmata, basally clamped; basidiospores strongly lobed, neither amyloid, dextrinoid nor cyanophilous. Presumably saprotrophic on coniferous trees.

Remarks: *Lobulicium* is a monotypic genus and contains only *L. occultum*, a saprotrophic species that produces small pellicular fruiting bodies with a soft and loose hymenial construction, typical of most *Atheliales* members. However, it is notable for its peculiar basidiospores (Figure 2C), which are strongly lobed but still bisymmetrical. *Lobulicium occultum* also has a specialized habitat, growing in the cracks formed when trunks of *Abies* or *Picea* are subjected to brown cubic-rot decay by *Fomitopsis pinicola* (Hjortstam and Larsson, 1982; Nordén et al., 1999). This habitat preference is somewhat similar to that of *A. subinconspicua* (Kotiranta and Saarenoksa, 2005). Despite always being associated with brown-rot, *Lobulicium* is very likely not performing brown-rot but rather feeds from organic molecules left by other organisms. This species could be an interesting candidate for genome sequencing, in relation to its nutritional mode.

***Pilodermataceae* Jülich (1982) emend.**

Type genus: *Piloderma* Jülich, Ber. dt. bot. Ges. 81: 415 (1969) – Figure 2E.

Description: Basidiomata annual, resupinate and effused or spathulate, soft, byssoid to membranous, margin undifferentiated; hymenium smooth, continuous or porulose, white, yellowish or olivaceous brown; hyphal system monomitic, septa with or without clamps, hyphal strands present or absent, subicular hyphae often with crystals; cystidia absent; basidia clavate, with 2–4 sterigmata; basidiospores smooth, subglobose to elliptic, slightly thick-walled, neither amyloid nor dextrinoid, slightly cyanophilous. Saprotrophic or ectomycorrhizal.

Genera: *Piloderma*, *Tretomyces*, *Stereopsis vitellina.*

Remarks: Only one genus, *Piloderma,* was mentioned in the original description of this family (Jülich, 1982). *Tretomyces lutescens,* the type species of *Tretomyces*, was described as *Byssocorticium lutescens* in Eriksson and Ryvarden (1973), but shares micro-morphological characters with *Piloderma* (Kotiranta et al., 2011). The major difference in relation to the original circumscription is the inclusion of *Stereopsis vitellina*, which produces stipitate stereoid fruiting bodies and thus deviates from all other species in *Atheliales*. The type species of *Stereopsis* (*S. radicans*) belongs to the order *Stereopsidales*, and is characterized by two-spored basidia and spores that become slightly angular upon drying (Sjökvist et al., 2014, 2012). These features are lacking in *S. vitellina*. In addition, *S. vitellina* becomes brittle upon drying (Eriksson et al., 1984) similar to most other *Atheliales* members, whereas *S. radicans* becomes tough (Reid, 1965).

Piloderma species are completely devoid of clamps whereas *Tretomyces* species have clamps at all septa in hymenium and subhymenium and variably on subicular hyphae. Ecologically, both *Piloderma* and *Tretomyces* are ectomycorrhizal (Aučina et al., 2019; Erland and Söderström, 1990; Kyaschenko et al., 2017; Tedersoo et al., 2010). The nutritional mode of *Stereopsis vitellina* on the other hand, has been reported to be saprotrophic (Maaroufi et al., 2019), preferring very old pine-dominated forests (Kunttu et al., 2018). *Piloderma* was found to be monophyletic in our analyses, although this monophyly lacked strong support in both ML and BI analyses, whereas the *Tretomyces* clade was strongly supported. The interrelationships among the three lineages are still unresolved.

Tylosporaceae **Jülich (1982) emend.**

Type genus: *Tylospora* Donk, Taxon 9: 220 (1960) – Figure 2D.

Description: Basidiomata annual, resupinate, effused, soft to tough, byssoid to hypochnoid, margin undifferentiated; hymenium smooth, porulose to continuous, white to yellowish or brownish; hyphal system monomitic, septa with clamps, hyphae thin-walled to firm-walled, hyaline to yellowish, subicular hyphae often with encrustation; cystidia present or absent; basidia clavate, with (2–)4 sterigmata, always with a basal clamp; basidiospores elliptic, cylindrical, triangular or lobed, thin-walled to slightly thick-walled, neither amyloid nor dextrinoid, sometimes cyanophilous. Ectomycorrhizal.

Genera: *Amphinema*, *Tylospora*.

Remarks: The family was introduced with only one genus (Jülich, 1982). Whereas our concept of the family corresponds to the /amphinema-tylospora lineage of Tedersoo et al. (2010), the close relationship of *Amphinema* and *Tylospora* is surprising when considering the differences in morphology. Stalpers (1993) suggested that *Tylospora*, with its lobed and ornamented basidiospores, had affinities to *Thelephorales*. *Amphinema* has smooth basidiospores but stands out by having cystidia, contrary to all other *Atheliales*. Eriksson (1958) suggested a relationship with *Hyphodontia*, an idea that prevailed until DNA data became available (Eriksson and

Ryvarden, 1973; Jülich, 1982; Parmasto, 1968). Both genera form ectomycorrhiza with *Picea* (Danielson and Pruden, 1989; Eberhardt et al., 1999; Taylor and Alexander, 1991).

In our phylogenetic analyses, *Amphinema* was not recovered as monophyletic (Figure 4). *Tylospora asterophora* was placed between *Amphinema byssoides* (type) and *A. diadema*, indicating that the latter species should be moved out of *Amphinema*. However, this arrangement was not strongly supported by either BS or PP, and thus more data are needed before any taxonomic changes are made. Additionally, *Tylospora* was also found to be non-monophyletic in Tedersoo and Smith (2013).

<u>Atheliales incertae sedis</u>

Athelopsis subinconspicua (Litsch.) Jülich
Leptosporomyces raunkiaerii (M.P. Christ.) Jülich

Two species included in our analyses did not cluster with any of the recognized families. *Athelopsis subinconspicua* and *Leptosporomyces raunkiaeri* formed a strongly supported clade, which was also inferred in previous studies (Binder et al., 2010; Hodkinson et al., 2014; Liu et al., 2018). This clade seems to be closely related to the *Pilodermataceae* clade but this relationship was only supported by PP (Figure 4). These two species are reported to be saprotrophic (Ambrosio et al., 2014; Kubartová et al., 2012) but are morphologically rather different, which is obvious from their generic placement. It is doubtful that they should be united in the same genus. *Leptosporomyces raunkiaeri* is rather similar to the type of *Leptosporomyces*. It differs primarily by somewhat larger basidiospores and by growing on dead angiosperm leaves whereas *L. galzinii* is above all found on decaying conifer wood. *Athelopsis subinconspicua* has typical pedunculate basidia but is in other respects not so similar to *A. glaucina*, the type species of *Athelopsis*. We believe the classification on genus level should first be disentangled before a clade name on family level is introduced.

DISCUSSION

The class-wide phylogeny (Figure 3) of this study made it possible to circumscribe *Atheliales sensu stricto*. Each order included in this dataset received either strong support from both ML BS (≥75) and Bayesian PP (≥0.95), or moderate support from ML BS (50-74) and strong support by PP. The resulting topology of our four-locus *Agaricomycetes* dataset (Figure 3) lacked support on several deep nodes, although it is largely congruent with previous studies (Binder et al., 2010; Chen et al., 2019; Hodkinson et al., 2014; Liu et al., 2018; Nagy et al., 2015; Sjökvist et al., 2014; Zhao et al., 2017). *Atheliales* was placed within *Agaricomycetidae* (96/1.00), as sister to *Lepidostromatales*, although only with strong support from PP. The *Atheliales*–*Lepidostromatales* clade was placed as sister to *Boletales* with weak ML BS support but strong PP support. Close relationships among *Atheliales*, *Boletales*, and *Lepidostromatales* mirrors results of previous studies using similar sets of genes (Chen et al., 2019; Liu et al., 2018; Zhao et al., 2017). Unlike these studies, however, a sister relationship between *Amylocorticiales* and *Agaricales* was not recovered in our analyses (Figure 3), further highlighting the uncertainty of the placement of this order.

Only two members of *Atheliales* (*Fibulorhizoctonia* sp. — anamorph of *Athelia* sp. — and *Piloderma olivaceum*) and five members of *Amylocorticiales* (*Amylocorticium subincarnatum*, *Anomoloma albolutescens*, *Anomoporia bombycine*, *A. myceliosa*, and *Plicaturopsis crispa*) have their genomes sequenced, while no genomes are available for any representative of *Lepidostromatales* according to JGI's MycoCosm (https://mycocosm.jgi.doe.gov/mycocosm/home, accessed 1 October 2020; Grigoriev et al., 2012). Compared to the number of genomes of *Agaricales* and *Boletales* (147 and 59, respectively), this number is very low. Future phylogenomic studies on the relationships among orders within *Agaricomycetidae* should focus on sampling more taxa from *Amylocorticiales*, *Atheliales*, and *Lepidostromatales* and carefully sort out the signal for different placements of *Amylocorticiales*.

Out of 23 described genera of *Atheliales sensu lato.* (Table 1), 15 were included in our analyses, of which five genera fell outside of *Atheliales* and are phylogenetically placed in other orders (Figure 3, taxa in bold with an asterisk): *Byssoporia* (type: *B. terrestris*), *Digitatispora* (type: *D. marina*), *Hypochnella* (type: *H. violacea*), *Lyoathelia* (type: *L. laxa*), and *Pteridomyces* (type: *P. galzinii*). *Byssoporia terrestris* is placed within *Russulales*, specifically in *Albatrellaceae* according to previous studies (Chen et al., 2016; Chen and Cui, 2014; Larsson, 2007; Smith et al., 2013; Zhou and Dai, 2013), making it the only corticioid taxon in this family. *Digitatispora marina*, a marine species, is placed in the *Agaricales*. Previous studies placed it within *Niaceae*, closely related with other marine genera such as *Calathella*, *Halocyphina*, and *Nia* (Abdel-Wahab et al., 2019; Azevedo et al., 2018). In our results (Figure 3), *Leptosporomyces septentrionalis* clustered with *Amylocorticiales*. This was also shown in previous studies (Binder et al., 2010; Song et al., 2016; Zhou et al., 2016), where it is found to be closely related to other corticioid taxa with smooth hymenium: *Amyloxenasma allantosporum* and *Serpulomyces borealis*. *Hypochnella violacea*, *Lyoathelia laxa*, and *Pteridomyces galzinii* clustered with *Polyporales*, *Hymenochaetales*, and *Trechisporales*, respectively. Blasting the sequences against

UNITE's database indicated that *H. violacea* closely resembles *Australohydnum dregeanum* (*Phanerochaetaceae*), another corticioid taxon with purple fruiting body, whereas *L. laxa* is closely related to *Poriodontia subvinosa* (*Schizoporaceae*). For the aforementioned taxa of *Atheliales sensu lato*, their prior morphological association within *Atheliales sensu lato* largely stemmed from soft and pellicular fruiting bodies with microscopic characteristics that resemble core *Atheliales* taxa such as *Athelia*, *Byssocorticium*, and *Piloderma* (Eriksson and Ryvarden, 1975, 1973; Hjortstam, 1991; Jülich, 1972; Larsen and Zak, 1976). However, several authors have previously also expressed doubts regarding their association with *Atheliales sensu lato* (Eriksson et al., 1984; Gorjon et al., 2012; Hayashi, 1974; Larsson, 2007; Nakasone, 2013). On the other hand, the stipitate-stereoid species *S. vitellina* clustered within the *Atheliales* clade, as was also shown by Sjökvist et al. (2012). The phylogenetic placement of *S. vitellina* within *Pilodermataceae* is strongly supported, but not its relationship with other lineages within the family. This makes it difficult to infer the evolution of fruiting body type and nutritional modes within *Pilodermataceae*.

Athelopsis and *Leptosporomyces* were found to be non-monophyletic, and the monophyly of *Amphinema*, *Athelia*, and *Piloderma* was unsupported. This can probably be attributed to incomplete taxon sampling in combination with low molecular data coverage. Although previous studies have found members of *Athelia*, *Athelopsis*, and *Leptosporomyces* to be phylogenetically affiliated with other orders (Binder et al., 2010; Ertz et al., 2008; Larsson, 2007; Miettinen and Larsson, 2011), this study confirmed that their respective type species belong to *Atheliales*. Notwithstanding, revisions of these genera is necessary especially for *Athelia*, the type genus of the family. Corticioid fungi are particularly prone to misidentification (Binder et al., 2005). To minimize this problem, we used specimens that were identified by known experts of corticioid fungi. In addition, we utilized multiple collections for each species whenever possible. Future studies should build on this work by including type specimens.

Atheliales is a suitable group to study the evolutionary patterns of different nutritional modes because of the remarkable diversity observed within the group (Adams and Kropp, 1996; Matsuura et al., 2000; Stokland and Larsson, 2011; Tedersoo et al., 2010; Wenneker et al., 2017; Yurchenko and Olubkov, 2003). *Atheliaceae* is dominated by saprotrophic taxa, with one lichenicolous species (*Athelia arachnoidea*), while *Byssocorticiaceae*, *Pilodermataceae*, and *Tylosporaceae* are dominated by ectomycorrhizal taxa. Within *Byssocorticiaceae*, the earlier branching taxa (*Athelopsis glaucina*, *Leptosporomyces galzinii*, and *Leptosporomyces* sp.) are saprotrophic, which seemed to be the plesiomorphic state of the family. Although the overall relationships among taxa within *Pilodermataceae* are still lacking in support, this seems to also be the case within the family, as the earliest branching taxon likely is *Stereopsis vitellina,* a non-corticioid and reportedly saprotrophic species (Maaroufi et al., 2019). *Tylosporaceae*, on the other hand, seems to consist of strictly ectomycorrhizal species. However, our sampling only represents a fraction of the true *Atheliales* diversity, thus it is possible that *Tylosporaceae* also contains saprotrophic members. Based on our analyses, the earliest branching taxon in *Atheliales* is *Lobulicium occultum*, a saprotrophic species (Figure 4). It is likely that the plesiomorphic state for nutrition in *Atheliales* is saprotrophic, and that ectomycorrhizal evolved multiple times in different groups. Ectomycorrhizal symbiosis arose several times from saprotrophic ancestors within fungi (Kohler et al., 2015; Tedersoo and Smith, 2013), as well as within smaller groups (Sánchez-García and Matheny, 2017; Sato and Toju, 2019; Veldre et al., 2013). To make conclusive statements on the evolution nutritional modes, more data, better phylogenetic resolution on key nodes, and more comprehensive analyses of ancestral states are needed.

Compared with most other orders within *Agaricomycetidae* except *Amylocorticiales*, *Atheliales* is relatively understudied and undersampled (Rosenthal et al., 2017). It is possible that *Atheliales* contains undiscovered lineages. This gives hope to add taxa in the future that can break up long branches and pinpoint evolutionary relationships that are currently unresolved (e.g., the placement of *A. subinconspicua* and *L. raunkiaeri*, and the relationships among lineages). Additionally, the different placement of *A. glaucina* depending on the composition of the dataset and its relatively long branch, as well as the weakly-supported placement of the *A. subinconspicua*–*L. raunkiaeri* clade suggest that these lineages might be composed of many more taxa.

The classification proposed here is only a first step in improving the taxonomy of *Atheliales*, and further refinement will be needed as more taxa will continue to be included in phylogenetic analyses. Future systematic studies of *Atheliales* should include genera of *Atheliales s.l.* that were not included in our study (Table 1): *Athelicium*, *Athelocystis*, *Butlerelfia*, *Elaphocephala*, *Hypochniciellum*, *Melzericium*, and *Mycostigma*.

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Figure 1. Comparison of relationships among orders within Agaricomycetidae according to: A) Nagy et al. (2015), B) Chen et al. (2019), Liu et al. (2018), and Zhao et al. (2017), C) Varga et al. (2019).

Figure 2. *Atheliales*. A. *Athelia epiphylla*; section through basidioma and basidiospores. B. *Byssocorticium atrovirens*; section through basidioma and basidiospores. C. *Lobulicium occultum*; basidiospores. D. *Tylospora fibrillosa*; section through basidioma and basidiospores. E. *Piloderma fallax*; basidioma. Scale bar for sections = 20 µm and for basidiospores = 5 µm. Scale bar for photo = 1 cm. Drawings J. Eriksson. Photo K-H Larsson. Drawings reproduced with permission from Fungiflora A/S, Oslo.

Figure 3. Phylogenetic relationships of *Agaricomycetes* based on LSU, 5.8S *rpb2*, and *tef1* excluding the third codon position. Topology and branch lengths originated from RAxML analyses. Color shading indicates different orders. Thickened branches are strongly supported with BS≥75 and PP≥0.95. Branches supported by only either BS or PP have their support values noted above the branches as (BS/PP). Thickened species name denotes the type species of genera within *Atheliales sensu lato*, an asterisk (*) indicates that the corresponding taxon used to belong to *Atheliales sensu lato*, double asterisk (**) indicates that the taxon used to be placed outside of *Atheliales*. Arrow points to the clade corresponding to subclass *Agaricomycetidae*.

Figure 4. Phylogenetic relationships of *Atheliales sensu stricto* based on LSU, 5.8S, ITS1, ITS2, *rpb2*, and *tef1* including the third codon position, with *Lepidostromatales* and *Boletales* as outgroups. Topology and branch lengths originated from RaxML analyses. Within *Atheliales*, colored shading indicates different families, while non-shaded groups are *incertae sedis*. Thickened branches are strongly supported with BS≥75 and PP≥0.95. Branches well-supported by only either BS or PP have their support values noted above the branches as (BS/PP).

Thickened species name denotes the type species of genera within *Atheliales*, while an asterisk (*) indicates the type genus of the family. Symbols before the names indicate the nutritional mode: empty circle (○) for saprotrophic, filled circle (●) for ectomycorrhizal, and diamond (◊) for lichenicolous.

Table 1. Overview of *Atheliales*-associated taxa. Plus (+) indicates that the taxon belongs to *Atheliales*, minus (-) that it does not, and both (+/-) suggests non-monophyly because members exist both inside and outside *Atheliales*. Question mark (?) indicates uncertain placement, while asterisk (*) marks that the name is treated as a synonym. Empty cell means that it was not treated in the study. Numbered columns indicate the source: [1]=(Jülich, 1982), [2]=(Larsson et al., 2004), [3]=(Larsson, 2007), [4]=(Kirk et al., 2008), [5]=(Ertz et al., 2008), [6]=(Hjortstam and Ryvarden, 2010), [7]=(Binder et al., 2010), [8]=(Kotiranta et al., 2011), [9]=(Sjökvist et al., 2012), [10]=(Hodkinson et al., 2014), [11]=(Liu et al., 2018), [12]=(He et al., 2019), [13]=(Index Fungorum, 2020), [14]=*MycoBank* (accessed: February 2020). [1] and [6] were based on morphology, whereas [3], [4], [12], [13], and [14] summarize previous studies. Remaining sources were based on molecular data.

Taxon	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**
Amphinema	-	+	+	+			+	+		+	+	+	+	+
Athelia	+	+	+	+	+		+/-	+	+	+	+	+	+	+
Athelicium			-	+								+	-	-
Athelocystis						+						+	+	+
Athelopsis	+	+	+	+	+		+/-		+	+	+	+	+	+
Butlerelfia				+								+	+	+
Byssocorticium	+	+	+	+	+			+		+	+	+	+	+
Byssoporia	+		-	+						-		-	+	+
Caerulicium	+		+?	+*								+*	+*	+*
Digitatispora				+								-	+	+
Elaphocephala			?	+?								+	+	+

Fibulomyces	+		+/-	+				+		+		+*	+	+
Hypochnella	-		?	+?								+	+	+
Hypochniciellum		-	-	+			-					+	+	+
Hypochnopsis	+		-	-									-	-
Leptosporomyces	+		+	+	+		+/-	+		+	+	+	+	+
Lobulicium			+	+								+	+	+
Luellia	+		-	-								-	-	-
Lyoathelia			+?									+	+	?
Melzericium			?	+								+	+	+
Mycostigma				+?								+	+	+
Piloderma	+	+	+	+	+			+	+	+	+	+	+	+
Pteridomyces			+?	+								+	+	+
Tretomyces								+				+	+	+
Tylospora	+	+	+	+	+					+	+	+	+	+
Stereopsis vitellina									+				-	-

Table 2. Species names, voucher information, GenBank accession numbers and references of taxa included in this study. Taxon in bold denotes type species of genera listed in *Atheliales sensu lato*. Taxon followed by an asterisk (*) indicates that it was placed in *Atheliales sensu lato* but placed elsewhere according to this study, double asterisks (**) indicates the opposite.

Order/Species	**ID**	**Country of origin (ISO code)**	**GenBank accession number**				**Source**
			ITS	**LSU**	***rpb2***	***tef1***	
Agaricales							
Anthracophyllum archeri	AFTOL-973		DQ404387	AY745709	DQ385877	DQ028586	Matheny et al., unpublished
Aphanobasidium pseudotsugae	HHB-822	US	GU187509	GU187567	GU187781	GU187695	(Binder et al., 2010)
Chondrostereum purpureum	AFTOL-441	US	DQ200929	AF518607	AY218477.2	DQ457632	(Hibbett and Binder, 2002; Matheny et al., 2007, 2006; Wang et al., 2004)
Digitatispora marina *	3027C	NO	KM272371	KM272362			(Rämä et al., 2014)
Gymnopilus picreus	ZRL2015011	CN	LT716066	KY418882	KY419027	KY419077	(Zhao et al., 2017)
Henningsomyces candidus	AFTOL-468		AY571043	AF287864	AY218513.2	AY883424	(Bodensteiner et al., 2004; Hibbett et al., 2000; Wang et al., 2004)
Lepiota cristata	ZRL20151133	CN	LT716026	KY418841	KY418992	KY419048	(Zhao et al., 2017)
Lepista irina	AFTOL-815	US	DQ221109	DQ234538	DQ385885.2	DQ028591	(Matheny et al., 2007)

Mythicomyces corneipes	AFTOL-972		DQ404393	AY745707	DQ408110	DQ029197	Matheny et al., unpublished
Amylocorticiales							
Amylocorticiellum molle	KHL 13500	SE		GU187667			(Binder et al., 2010)
Amylocorticiellum subillaqueatum	KHL 8493		AY463431	AY586679			(Larsson et al., 2004)
Amylocorticium cebennense	HHB-2808	US	GU187505	GU187561	GU187770	GU187675	(Binder et al., 2010)
Amylocorticium subsulphureum	HHB-13817	US	GU187506	GU187562	GU187773	GU187680	(Binder et al., 2010)
*Leptosporomyces septentrionalis * 1*	GB-0090937	SE	LR694203	LR694181	LR694276	LR694219	This study
*Leptosporomyces septentrionalis * 2*	JS 16122	NO	GU187497	GU187664			(Binder et al., 2010)
Plicaturopsis crispa	MR00464		LR694209	LR694187	LR694281	LR694225	This study
Atheliales							
Amphinema byssoides 1	EL 11/98	EE	AY463375	AY586626			(Larsson et al., 2004)
Amphinema byssoides 2	M. Ryberg	SE	GQ162810	GQ162810			(Kotiranta et al., 2011)
Amphinema byssoides 3	MR00333		LR694190	LR694167			This study
Amphinema diadema	JS 25999	NO	GQ162811	GQ162811			(Kotiranta et al., 2011)
Amphinema sp.	BS1710028	SE	LR694191	LR694168	LR694266	LR694212	This study
Athelia acrospora	E. Bendiksen 645/07		MT305993	MT305993	*	*	This study
Athelia arachnoidea 1	CBS 418.72	NL	GU187504	GU187557	GU187769	GU187672	(Binder et al., 2010)
Athelia arachnoidea 2	GB0087426	SE	LR694192	LR694169	LR694267	LR694213	This study
Athelia bombacina 1	E. Bendiksen 523/07		MT305994	MT305994	*		This study
Athelia bombacina 2	E. Bendiksen 580/07		MT305995	MT305995	*		This study

Athelia decipiens 1	GB0090493	SE	LR694193	LR694170	LR694268		This study
Athelia decipiens 2	JS 4930	NO	AY463381	AY586632			(Larsson et al., 2004)
Athelia decipiens 3	L-10567	US	GU187537	GU187592	GU187802	GU187739	(Binder et al., 2010)
Athelia epiphylla 1	GB0090655	SE	LR694194	LR694171			This study
Athelia epiphylla 2	KHL 13899		MT305996	MT305996	*		This study
Athelia fibulata	E. Bendiksen 573 07		MT305997	MT305997	*	*	This study
Athelia neuhoffii	GB0087199	SE	LR694195	LR694172	LR694269		This study
Athelia singularis	JS 25630	NO	GQ162813	GQ162813			(Kotiranta et al., 2011)
Athelia sp. 1	BHI-F636	US	MK958813	MK958817	MK983172	MK983174	This study
Athelia sp. 2	BHI-F645	US	MK958814	MK958818	MK983173	MK983175	This study
Athelia sp. 3	HHB-15599	US	GU187502	GU187565	GU187767	GU187678	(Binder et al., 2010)
Athelopsis glaucina 1	GB0058723	SE	LR694196	LR694173			This study
Athelopsis glaucina 2	KHL 11901	SE	GU187495	GU187662			(Binder et al., 2010)
Athelopsis subinconspicua	GB0058732	SE	LR694197	LR694174	LR694270	LR738852	This study
Byssocorticium atrovirens 1	BS1710033	SE	LR694198	LR694175	LR694271	LR694214	This study
Byssocorticium atrovirens 2	GB0078129	SE	LR694199	LR694176	LR694272	LR694215	This study
Byssocorticium caeruleum	RS 09400	FI	GQ162814	GQ162814			(Kotiranta et al., 2011)
Byssocorticium pulchrum 1	GB0078135	SE	LR694200	LR694177	LR694273	LR694216	This study
Byssocorticium pulchrum 2	KHL 11710	FI	AY463388	AY586639			(Larsson et al., 2004)
Fibulomyces mutabilis	HG-B 5753	DE	GQ162817	GQ162817			(Kotiranta et al., 2011)

Leptosporomyces galzinii	GB0107211	SE	LR694202	LR694180	LR694275	LR694218	This study
Leptosporomyces raunkiaerii	HHB-7628	US	GU187528	GU187588		GU187719	(Binder et al., 2010)
Leptosporomyces sp.	GB0087510	SE	LR694204	LR694182	LR694277	LR694220	This study
Lobulicium occultum	KHL 13496b		*	*			This study
Piloderma bicolor	BS1710030	SE	LR694205	LR694183	LR694278	LR694221	This study
Piloderma byssinum 1	GB0121002	SE	LR694206	LR694184	LR694279		This study
Piloderma byssinum 2	JS 20399	NO	DQ469281	DQ469281			Larsson, unpublished
Piloderma byssinum 3	KHL 8456	SE	AY463453	AY586699			(Larsson et al., 2004)
Piloderma croceum	MR00338		LR694207	LR694185	LR738853	LR694223	This study
Piloderma fallax	S-12		GU187535	GU187591	GU187797	GU187738	(Binder et al., 2010)
Piloderma lanatum 1	JS 22149	NO	DQ469288	DQ469288			Larsson, unpublished
Piloderma lanatum 2	JS 24861	NO	AY463454	AY586700			(Larsson et al., 2004)
Piloderma olivaceum	BS1710031	SE	LR694208	LR694186	LR694280	LR694224	This study
*Stereopsis vitellina ** 1*	F703241	SE	LR694211	LR694189	LR694283		This study
*Stereopsis vitellina ** 2*	Gilsenius	SE	JN649374	JN649374			(Sjökvist et al., 2012)
Tretomyces lutescens	GB0052596	NO	GQ162820	GQ162820			(Kotiranta et al., 2011)
Tretomyces microsporus	GB0090789	FI		GQ162821			(Kotiranta et al., 2011)
Tylospora asterophora	KHL 8566	SE		AY463480			(Larsson et al., 2004)
Auriculariales							
Auricularia sp.	AFTOL-676	US	DQ200918	AY634277	DQ366278	DQ408143	(Matheny et al., 2007)

Boletales							
Coniophora arida	FP-104367	US	GU187510	GU187573	GU187775	GU187684	(Binder et al., 2010)
Coniophora marmorata	MUCL 31667	BE	GU187515	GU187571	GU187780	GU187688	(Binder et al., 2010)
Gomphidius roseus	AFTOL-1780	DE	DQ534570	DQ534669	GU187818	GU187702	(Binder et al., 2010)
Gyrodontium sacchari	MUCL 40589	GF	GU187522	GU187579	GU187764	GU187703	(Binder et al., 2010; Binder and Hibbett, 2006)
Hydnomerulius pinastri	MD312	US	GU187523	GU187580	GU187787	GU187708	(Binder et al., 2010)
Leucogyrophana lichenicola	DAOM 194172	CA	GU187531	GU187583	GU187789	GU187715	(Binder et al., 2010)
Leucogyrophana olivascens	HHB-11134	US	GU187532	GU187587	GU187790	GU187717	(Binder et al., 2010)
Pseudomerulius aureus	FP-103859	US	GU187534	GU187590	GU187799	GU187731	(Binder et al., 2010)
Psudomerulius curtisii	REH8912	AU	GU187533	GU187589	GU187796	GU187725	(Binder et al., 2010)
Cantharellales							
Clavulina sp.	AFTOL-667		DQ202266	AY745694	DQ366286	DQ028589	(Matheny et al., 2007)
Hydnum albomagnum	AFTOL-471	US	DQ218305	AY700199	DQ234553	DQ234568	(Matheny et al., 2007)
Sistotrema confluens	AFTOL-613		DQ267125	AY647214	DQ381837		Nilsson et al., unpublished
Corticiales							
Punctularia strigosozonata	AFTOL-1248		DQ398958	AF518642	DQ381843	DQ408147	Matheny et al., unpublished; (Hibbett and Binder, 2002)
Vuillemenia comedens	AFTOL-1247		DQ398959	AF518666	DQ381844		Matheny et al., unpublished; (Hibbett and Binder, 2002)

Dacrymycetes							
Calocera cornea	AFTOL-438		AY789083	AY701526	AY536286	AY881019	Matheny et al., unpublished
Gloeophyllales							
Gloeophyllum striatum	ARIZ AN027866		HM536092	HM536063	HM640259	HM536111	(Garcia-Sandoval et al., 2011)
Gloeophyllum trabeum	1320	US	HM536094	HM536067	HM536112	HM536113	(Garcia-Sandoval et al., 2011)
Heliocybe sulcata	IBUG 9930	MX	HM536095	HM536069	HM536114	HM536115	(Garcia-Sandoval et al., 2011)
Neolentinus adhaerens	DAOM 214911		HM536096	HM536071	HM536116	HM536117	(Garcia-Sandoval et al., 2011)
Gomphales							
Gautieria otthii	AFTOL-466	US	AF377072	AF393058	AY218486	AY883434	(Bidartondo and Bruns, 2002; Wang et al., 2004)
Hymenochaetales							
Coltricia perennis	AFTOL-447		DQ234559	AF287854	AY218526	AY885147	Matheny and Hibbett, unpublished; (Hibbett et al., 2000; Wang et al., 2004)
Cotylidia sp.	AFTOL-700		AY854079	AY629317	AY883422	AY885148	Wang et al., unpublished; Matheny and Hibbett, unpublished
FomitIporia gabonensis	MUCL 47576	GA	GU461971	GU461990	JQ087972	GU461923	(Amalfi et al., 2012, 2010)
Fomitiporia mediterranea	AFTOL-488		AY854080	AY684157	AY803748	AY885149	Binder et al., unpublished
FomitopIria sonorae	MUCL 47689	US	JQ087893	JQ087920	JQ088006	JQ087947	(Amalfi et al., 2012)
Lyoathelia laxa *****	V. Spirin 8810a		MT305998	MT305998			This study

Resicinium bicolor	AFTOL-810		DQ218310	AF393061	DQ457635	DQ061277	(Binder and Hibbett, 2002; Matheny et al., 2007)
Rickenella fibula	AFTOL-486		DQ241782	AY700195	DQ408115	DQ435794	Matheny et al., unpublished;
Jaapiales							
Jaapia argillacea	CBS 252.74	NL	GU187524	GU187581	GU187788	GU187711	(Binder et al., 2010)
Lepidostromatales							
Lepidostroma vilgalysii	RV-MX16	MX	JN698907	JN698908			(Hodkinson et al., 2012)
Sulzbacheromyces caatingae	Sulzbacher 1479	BR	KC170320	KC170318			(Sulzbacher et al., 2012)
Phallales							
Phallus hadriani	AFTOL-683		DQ404385	AY885165	DQ408114	DQ435792	Matheny et al., unpublished
Polyporales							
Formitopsis pinicola	AFTOL-770		AY854083	AY684164	AY786056	AY885152	Wang et al., unpublished
Ganoderma tsugae	AFTOL-771		DQ206985	AY684163	DQ408116	DQ059048	Wang et al., unpublished; (Matheny et al., 2007)
Grifola frondosa	AFTOL-701		AY854084	AY629318	AY786057	AY885153	Matheny and Hibbett, unpublished
Hypochnella violacea *	GB0090070	SE	LR694201	LR694179	LR694274	LR694217	This study
Phlebia radiata	AFTOL-484		AY854087	AF287885	AY218502	AY885156	Matheny and Hibbett, unpublished; (Hibbett et al., 2000)
Postia rennyi	KEW57		AY218416	AF287876	AY218499		(Hibbett et al., 2000; Wang et al., 2004)

Sparassis crispa	AFTOL-703	CN	DQ250597	AY629321	DQ408122	DQ056289	(Matheny et al., 2007); Matheny and Hibbett, unpublished
Steccherinum tenue	KHL 12316	US	JN710598	JN710598	JN710739	JN710733	(Miettinen et al., 2012)
Trametes vesicolor	ZRL20151477		LT716079	KY418903	KY419041	KY419091	(Zhao et al., 2017)
Russulales							
Bondarzewia montana	AFTOL-452		DQ200923	DQ234539	AY218474.2	DQ059044	(Matheny et al., 2007; Wang et al., 2004)
Byssoporia terrestris * 1	GB0058650	SE		LR694178			This study
Byssoporia terrestris * 2	Hjm 18172	SE	EU118608	EU118608			(Larsson, 2007)
Echinodontium tinctorium	AFTOL-455		AY854088	AF393056	AY218482.2	AY885157	Matheny and Hibbett, unpublished;
Heterobasidion annosum	AFTOL-470		DQ206988	AF287866	AH013701.2	DQ028583	(Hibbett et al., 2000; Matheny et al., 2007); Matheny et al. unpublished;
Lactarius deceptivus	AFTOL-682	US	AY854089	AY631899	AY803749	AY885158	Matheny and Hibbett, unpublished
Lactarius lignyotus	AFTOL-681	US	DQ221107	AY631898	DQ408128	DQ435787	(Matheny et al., 2007); Matheny and Hibbett, unpublished
Sebacinales							
Piriformospora indica	AFTOL-612		DQ411527	AY293202	DQ408131	AJ249911	Nilsson et al., unpublished; (Binder et al., 2005; Bütehorn et al., 2000)
Tremellodendron pallidum	AFTOL-699		DQ411526	AY745701	DQ408132	DQ029196	Matheny and Hibbett, unpublished;
Stereopsidales							

Clavulicium macounii	KHL 15566	SE	KC203500	KC203500	KC203506	KC203520	(Sjökvist et al., 2014)
Stereopsis globosa	KHL 12592	CR	KC203495	KC203495	KC203501	KC203515	(Sjökvist et al., 2014)
Stereopsis radicans	LR45395	BZ	KC203496	KC203496	KC203502	KC203516	(Sjökvist et al., 2014)
Thelephorales							
Boletopsis leucomelanea	AFTOL-1527	US	DQ484064	DQ154112	GU187820	GU187763	(Binder et al., 2010; Matheny et al., 2006)
Hydnellum geogenium	AFTOL-680	US	DQ218304	AY631900	DQ408133	DQ059053	(Matheny et al., 2007)
Trechisporales							
Pteridomyces galzinii *	GB0150230	ES	LR694210	LR694188	LR694282	LR694226	This study
Trechispora alnicola	AFTOL-665	US	DQ411529	AY635768	DQ408135	DQ059052	Matheny and Hibbett, unpublished
Trechispora sp.	AFTOL-678	US	DQ411534	AY647217	DQ408136	DQ059051	Matheny and Hibbett, unpublished

Table 3. Summary of PCR primers used in this study. Asterisk (*) indicates a slight modification from the original primer.

Primer name	**Target region**	**Dir.**	**Sequence (5'-3')**	**Reference**	**Function**
5.8SR	ITS	F	TCGATGAAGAACGCAGCG	(Vilgalys and Hester, 1990)	Sequencing
ITS1	ITS	F	TCCGTAGGTGAACCTGCGG	(White et al., 1990)	Sequencing
ITS1F	ITS	F	CTTGGTCATTTAGAGGAAGTAA	(Gardes and Bruns, 1993)	PCR and sequencing
ITS2	ITS	R	GCTGCGTTCTTCATCGATGC	(White et al., 1990)	Sequencing
ITS3	ITS	F	GCATCGATGAAGAACGCAGC	(White et al., 1990)	Sequencing
ITS4	ITS	R	TCCTCCGCTTATTGATATGC	(White et al., 1990)	PCR and sequencing
ITS4B1	ITS	R	CAAGRGACTTRTACACGGTCCA	(Tedersoo et al., 2007)	PCR
LR21	ITS/LSU	R	ACTTCAAGCGTTTCCCTTT	(Hopple and Vilgalys, 1999)	PCR and sequencing
LB-W-R	LSU	F	CCGTGAGGGAAAGATGAAAAG	(Tedersoo et al., 2008)*	Sequencing
LR0R	LSU	F	ACCCGCTGAACTTAAGC	(Hopple and Vilgalys, 1999)	PCR and sequencing
LR3	LSU	R	CCGTGTTTCAAGACGGG	(Hopple and Vilgalys, 1999)	Sequencing

LR3R	LSU	F	GTCTTGAAACACGGACC	(Hopple and Vilgalys, 1999)	Sequencing
LR5	LSU	R	TCCTGAGGGAAACTTCG	(Hopple and Vilgalys, 1999)	PCR and sequencing
LR7	LSU	R	TACTACCACCAAGATCT	(Hopple and Vilgalys, 1999)	PCR and sequencing
bRPB2-6F	RPB2	F	TGGGGYATGGTNTGYCCYGC	(Matheny, 2005)	PCR and sequencing
bRPB2-6R2	RPB2	R	GGRCANACCATNCCCCARTG	(Matheny et al., 2007)	PCR and sequencing
bRPB2-7R	RPB2	R	GAYTGRTTRTGRTCRGGGAAVGG	(Matheny, 2005)	PCR and sequencing
bRPB2-7.1R	RPB2	R	CCCATRGCYTGYTTMCCCATDGC	(Matheny, 2005)	PCR and sequencing
fRPB2-5F	RPB2	F	GAYGAYMGWGATCAYTTYGG	(Matheny, 2005)	PCR and sequencing
1567R	TEF1	R	ACHGTRCCRATACCACCRATCTT	(Rehner and Buckley, 2005)	PCR and sequencing
1577Fa	TEF1	F	CARGAYGTBTAYAAGATYGGTGG	(Rehner and Buckley, 2005)*	PCR and sequencing
2218R	TEF1	R	ATGACACCRACRGCRACRGTYTG	(Rehner and Buckley, 2005)	PCR and sequencing
983F	TEF1	F	GCYCCYGGHCAYCGTGAYTTYAT	(Rehner and Buckley, 2005)	PCR and sequencing

Table 4. Partition scheme and substitution models of *Agaricomycetes* dataset and *Atheliales sensu stricto* dataset for RAxML and MrBayes analyses based on PF2.

***Agaricomycetes* dataset**

ML			
Subset	**Regions**	**no. of sites**	**Best Model**
1	5.8S, LSU	1164	GTR+I+G
2	*rpb2* 1st codon	726	GTR+I+G
3	*rpb2* 2nd codon, *tef1* 2nd codon	1045	GTR+I+G
4	*tef1* 1st codon	319	GTR+I+G

MB			
Subset	**Regions**	**no. of sites**	**Best Model**
1	LSU	997	GTR+I+G
2	5.8S	167	K80+G
3	*rpb2* 1st codon	726	GTR+I+G
4	*rpb2* 2nd codon, *tef1* 2nd codon	1045	GTR+I+G
5	*tef1* 1st codon	319	GTR+I+G

***Atheliales sensu stricto* dataset**

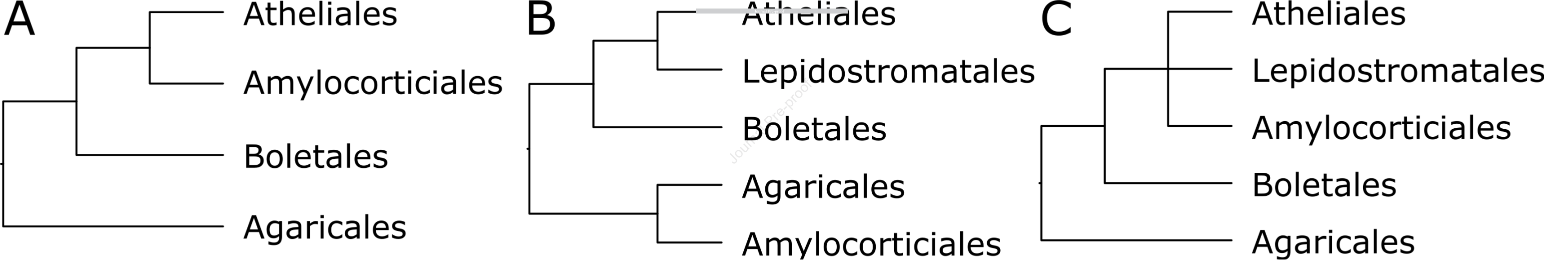
ML			
Subset	**Regions**	**no. of sites**	**Best Model**

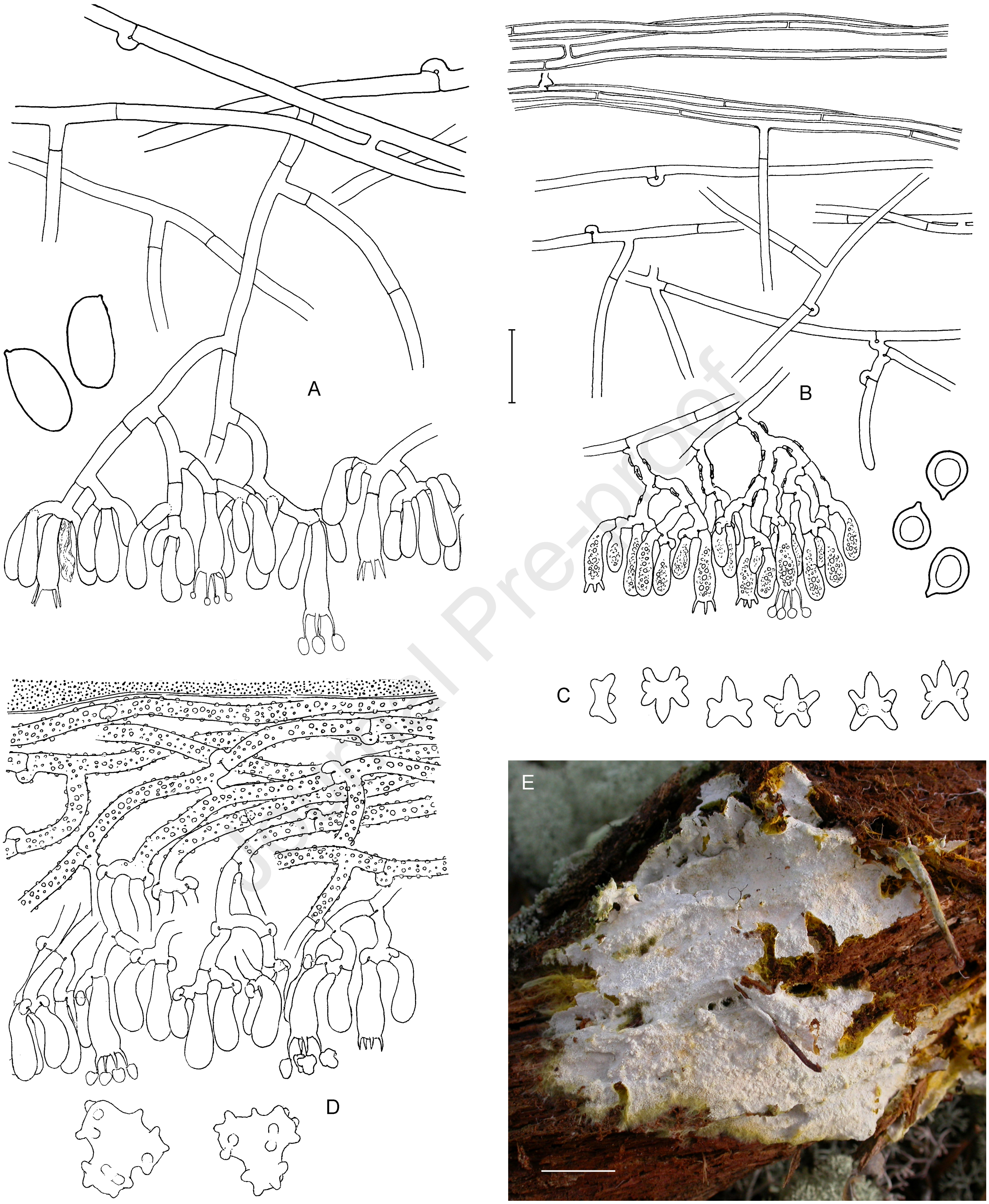
1	*rpb2* 1st codon, LSU	1271	GTR+I+G
2	5.8S, *rpb2* 2nd codon, *tef1* 2nd codon	818	GTR+I+G
3	ITS1, ITS2	660	GTR+I+G
4	*rpb2* 3rd codon	348	GTR+I+G
5	*tef1* 1st codon	308	GTR+I+G
6	*tef1* 3rd codon	308	GTR+G
	MB		
Subset	**Regions**	**no. of sites**	**Best Model**
1	*rpb2* 1st codon, LSU	1271	GTR+I+G
2	5.8S	162	K80+G
3	ITS1, ITS2	660	GTR+I+G
4	*tef1* 2nd codon, *rpb2* 2nd codon	656	GTR+I+G
5	*rpb2* 3rd codon	348	GTR+I+G
6	*tef1* 1st codon	308	HKY+I+G
7	*tef1* 3rd codon	308	GTR+G

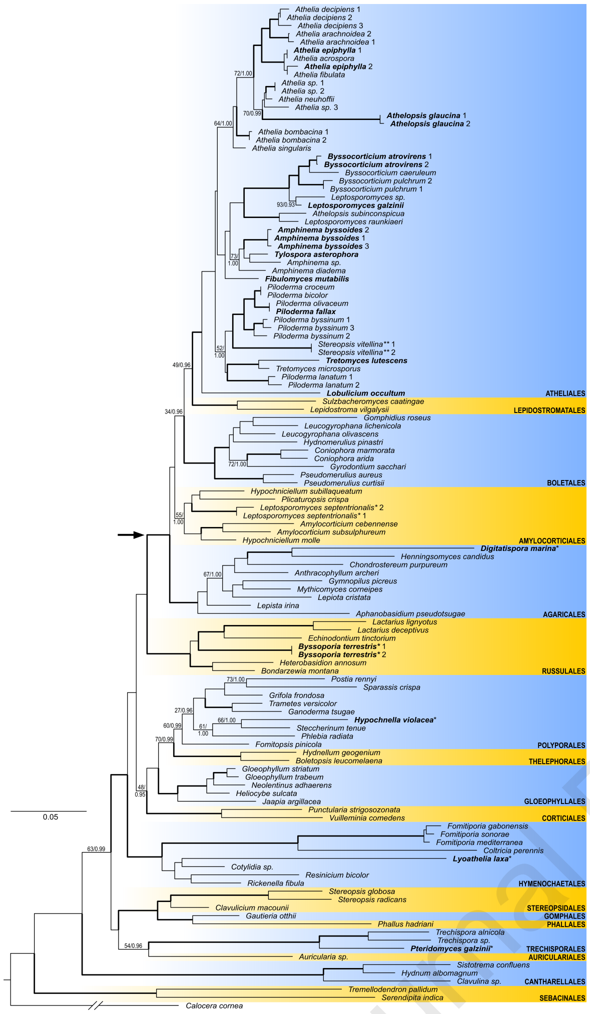
Table 5. Summary of various statistics for the alignment of LSU, 5.8S, *rpb2*, *tef1*, ITS1, ITS2, as well as the final concatenated alignment.

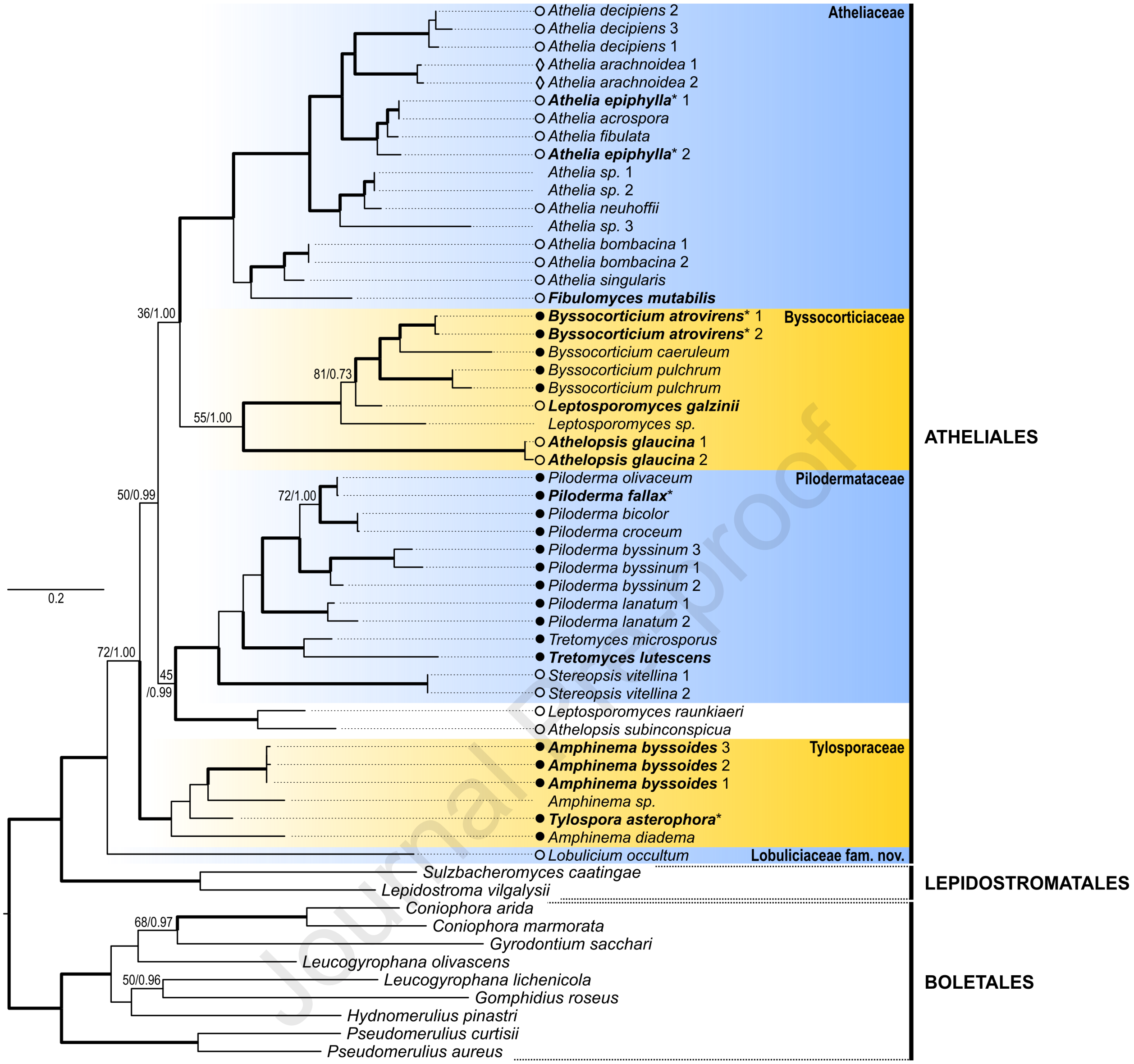
	LSU	**58S**	***rpb2***	***tef1***	**ITS1**	**ITS2**	**concatenated**
***Agaricomycetes* dataset**							
sequence lengths before excluding characters	-	-	387-2231	465-1126	-	-	-
sequence lengths in final alignment	526-916	84-162	224-1420	266-638	-	-	685-3046
final alignment length	997	167	1452	638	-	-	3254
number of sequences	123	116	93	84	-	-	123
mean coverage in final alignment	97.97%	97.83%	51.06%	61.85%	-	-	80.22%
pairwise identity in final alignment	87.30%	95.00%	87.10%	63.50%	-	-	74.10%
variable sites in final alignment	65.60%	56.90%	59.40%	36.50%	-	-	87.30%
***Atheliales sensu stricto* dataset**							
sequence length before excluding characters	-	-	395-	467-	-	-	-

			1118	1093			
sequence length in final alignment	530-899	84-160	346-1044	396-924	168-267	180-285	689-3481
final alignment length	923	162	1044	924	311	349	3713
number of sequences	59	56	34	31	44	46	59
mean coverage in final alignment	96.72%	91.81%	46.66%	47.35%	74.37%	77.53%	71.85%
pairwise identity in final alignment	91.10%	97.20%	78.10%	86.40%	54.00%	56.60%	74.50%
variable sites in final alignment	44.30%	32.70%	52.60%	37.70%	91.60%	94.80%	84.30%


A
Atheliales
Amylocorticiales
Boletales
Agaricales
B
Atheliales
Lepidostromatales
Boletales
Agaricales
Amylocorticiales
C
Atheliales
Lepidostromatales
Amylocorticiales
Boletales
Agaricales


A
B
C
D
E


Athelia decipiens 1
Athelia decipiens 2
Athelia decipiens 3
Athelia arachnoidea 2
Athelia arachnoidea 1
Athelia epiphylla 1
Athelia acrospora
Athelia epiphylla 2
Athelia fibulata
72/1.00
Athelia sp. 1
Athelia sp. 2
Athelia neuhoffii
Athelia sp. 3
70/0.99
Athelopsis glaucina 1
Athelopsis glaucina 2
64/1.00
Athelia bombacina 1
Athelia bombacina 2
Athelia singularis
Byssocorticium atrovirens 1
Byssocorticium atrovirens 2
Byssocorticium caeruleum
Byssocorticium pulchrum 2
Byssocorticium pulchrum 1
Leptosporomyces sp.
93/0.93
Leptosporomyces galzinii
Athelopsis subinconspicua
Leptosporomyces raunkiaeri
Amphinema byssoides 2
Amphinema byssoides 1
Amphinema byssoides 3
Tylospora asterophora
73/ 1.00
Amphinema sp.
Amphinema diadema
Fibulomyces mutabilis
Piloderma croceum
Piloderma bicolor
Piloderma olivaceum
Piloderma fallax
Piloderma byssinum 1
Piloderma byssinum 3
Piloderma byssinum 2
Stereopsis vitellina** 1
Stereopsis vitellina** 2
52/ 1.00
Tretomyces lutescens
Tretomyces microsporus
Piloderma lanatum 1
Piloderma lanatum 2
49/0.96
Lobulicium occultum
ATHELIALES
Sulzbacheromyces caatingae
Lepidostroma vilgalysii
34/0.96
LEPIDOSTROMATALES
Gomphidius roseus
Leucogyrophana lichenicola
Leucogyrophana olivascens
Hydnomerulius pinastri
Coniophora marmorata
Coniophora arida
72/1.00
Gyrodontium sacchari
Pseudomerulius aureus
Pseudomerulius curtisii
BOLETALES
Hypochniciellum subillaqueatum
Plicaturopsis crispa
Leptosporomyces septentrionalis* 2
Leptosporomyces septentrionalis* 1
55/ 1.00
Amylocorticium cebennense
Amylocorticium subsulphureum
Hypochniciellum molle
AMYLOCORTICIALES
Digitatispora marina*
Henningsomyces candidus
Chondrostereum purpureum
Anthracophyllum archeri
67/1.00
Gymnopilus picreus
Mythicomyces corneipes
Lepiota cristata
Lepista irina
Aphanobasidium pseudotsugae
AGARICALES
Lactarius lignyotus
Lactarius deceptivus
Echinodontium tinctorium
Byssoporia terrestris* 1
Byssoporia terrestris* 2
Heterobasidion annosum
Bondarzewia montana
RUSSULALES
73/1.00
Postia rennyi
Sparassis crispa
Grifola frondosa
Trametes versicolor
Ganoderma tsugae
27/0.96
66/1.00
Hypochnella violacea*
Steccherinum tenue
61/ 1.00
Phlebia radiata
60/0.99
70/0.99
Fomitopsis pinicola
POLYPORALES
Hydnellum geogenium
Boletopsis leucomelaena
THELEPHORALES
Gloeophyllum striatum
Gloeophyllum trabeum
Neolentinus adhaerens
Heliocybe sulcata
48/ 0.95
Jaapia argillacea
GLOEOPHYLLALES
0.05
Punctularia strigosozonata
Vuilleminia comedens
CORTICIALES
Fomitiporia gabonensis
Fomitiporia sonorae
Fomitiporia mediterranea
63/0.99
Coltricia perennis
Lyoathelia laxa*
Cotylidia sp.
Resinicium bicolor
Rickenella fibula
HYMENOCHAETALES
Stereopsis globosa
Stereopsis radicans
Clavulicium macounii
STEREOPSIDALES
Gautieria otthii
GOMPHALES
Phallus hadriani
PHALLALES
Trechispora alnicola
Trechispora sp.
54/0.96
Pteridomyces galzinii*
TRECHISPORALES
Auricularia sp.
AURICULARIALES
Sistotrema confluens
Hydnum albomagnum
Clavulina sp.
CANTHARELLALES
Tremellodendron pallidum
Serendipita indica
SEBACINALES
Calocera cornea


Atheliaceae
○ Athelia decipiens 2
○ Athelia decipiens 3
○ Athelia decipiens 1
◊ Athelia arachnoidea 1
◊ Athelia arachnoidea 2
○ **Athelia epiphylla*** 1
○ Athelia acrospora
○ Athelia fibulata
○ **Athelia epiphylla*** 2
Athelia sp. 1
Athelia sp. 2
○ Athelia neuhoffii
Athelia sp. 3
○ Athelia bombacina 1
○ Athelia bombacina 2
○ Athelia singularis
○ **Fibulomyces mutabilis**
36/1.00
Byssocorticiaceae
● **Byssocorticium atrovirens*** 1
● **Byssocorticium atrovirens*** 2
● Byssocorticium caeruleum
81/0.73
● Byssocorticium pulchrum
● Byssocorticium pulchrum
○ **Leptosporomyces galzinii**
55/1.00
Leptosporomyces sp.
○ **Athelopsis glaucina** 1
○ **Athelopsis glaucina** 2
ATHELIALES
Pilodermataceae
● Piloderma olivaceum
72/1.00
● **Piloderma fallax***
50/0.99
● Piloderma bicolor
● Piloderma croceum
● Piloderma byssinum 3
● Piloderma byssinum 1
● Piloderma byssinum 2
0.2
● Piloderma lanatum 1
● Piloderma lanatum 2
● Tretomyces microsporus
72/1.00
● **Tretomyces lutescens**
45
/0.99
○ Stereopsis vitellina 1
○ Stereopsis vitellina 2
○ Leptosporomyces raunkiaeri
○ Athelopsis subinconspicua
Tylosporaceae
● **Amphinema byssoides** 3
● **Amphinema byssoides** 2
● **Amphinema byssoides** 1
Amphinema sp.
● **Tylospora asterophora***
● Amphinema diadema
○ Lobulicium occultum
Lobuliciaceae fam. nov.
Sulzbacheromyces caatingae
LEPIDOSTROMATALES
Lepidostroma vilgalysii
Coniophora arida
68/0.97
Coniophora marmorata
Gyrodontium sacchari
Leucogyrophana olivascens
50/0.96
Leucogyrophana lichenicola
BOLETALES
Gomphidius roseus
Hydnomerulius pinastri
Pseudomerulius curtisii
Pseudomerulius aureus

- Sequences from nrLSU, nrITS, *rpb2* and *tef1* regions were generated across *Atheliales s.l.*
- Taxon sampling focused on the type species of genera within *Atheliales s.l.*
- Maximum Likelihood and Bayesian analyses were conducted on two datasets to delimit the order and identify lineages therein.
- Five families are recognized in *Atheliales*, of which one is newly described.
- Some genera of *Atheliales s.l.* is placed in other orders.