Re-shaping the family-level classification of *Agaricineae* (*Agaricales*, *Basidiomycota*) using a phylogenomic approach

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Abstract: Genomic-level data have enabled us to infer better resolved phylogenetic estimates and revolutionised our views on fungal relationships. *Agaricineae* is the largest suborder of *Agaricales* and mainly comprises the brown- and dark-spored *Agaricales* with thick-walled and pigmented basidiospores. Our study is the most extensive phylogenomic study of the suborder *Agaricineae* to date including 54 genera and 86 species. For 25 of them, shallow whole genome sequence data were produced in this study from dried fungarium specimens collected between 1997 and 2016. A total of 24 families is recognised including five that are proposed as new: *Agrocybaceae*, *Galerinaceae*, *Hemipholiotaceae*, *Kuehneromycetaceae* and *Phaeocollybiaceae*. In addition, *Battarreaceae* and *Chromocyphellaceae* are accepted at family level based on previous phylogenetic studies, bringing the total number of accepted families in the suborder *Agaricineae* to 26. The families are further grouped into eight informal "superfamilies": Agaricacea, Bolbitiacea, Cortinariacea, Galeropsidacea, Inocybacea, Nidulariacea, Psathyrellacea, and Strophariacea. Several families have been emended based on the current study and recent phylogenetic studies and as a result, a total of 190 genera are listed as accepted in suborder *Agaricineae*.

Key words: Fungariomics, fungi, museomics, new taxa, whole genome sequencing.

Taxonomic novelties: New families: *Agrocybaceae* Locq. ex. Niskanen, Kytöv. & Liimat., *Galerinaceae* Locq. ex. Niskanen, Kytöv. & Liimat., *Hemipholiotaceae* Niskanen, Kytöv. & Liimat., *Kuehneromycetaceae* Niskanen, Kytöv. & Liimat., *Phaeocollybiaceae* Niskanen, Kytöv. & Liimat. **Epitypes (basionym):** *Agaricus destruens* Brond., *Agaricus mutabilis* Schaeff., *Agaricus praecox* Pers., *Agaricus vittiformis* Fr. **Lectotypes (basionym):** *Agaricus destruens* Brond., *Agaricus mutabilis* Schaeff., *Agaricus praecox* Pers., *Agaricus vittiformis* Fr. **Neotypes (basionym):** *Agaricus lugubris* Fr., *Agaricus populneus* Pers.

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INTRODUCTION

Evolutionary trees are powerful tools for prediction, species discovery, monitoring, and conservation. Genomic-level data have enabled us to infer better resolved phylogenetic estimates and revolutionised our views on fungal relationships (e.g., Galindo *et al.* 2021, Li *et al.* 2021). Historical collections of biological specimens provide a vast resource for phylogenetic studies. The latest technology has made it possible to produce whole genome sequence data from a variety of samples, including fungarium specimens ranging from a few to more than 70 years old (Dentinger *et al.* 2015, Bradshaw *et al.* 2022, Liimatainen *et al.* 2022, Varga *et al.* 2025).

Agaricineae is the largest suborder of *Agaricales*, the largest order of mushroom-forming fungi, with more than 11,000 species in 193 genera and at least 15 families (Kalichman *et al.* 2020, He *et al.* 2024), including two of the 10 most species-rich soil fungal genera, *Cortinarius* and *Inocybe* based on the fungal DNA-barcoding of global soil samples by Tedersoo *et al.* (2022). The suborder contains many ecologically important ectomycorrhizal and saprotrophic fungi, some of which are also edible and commercially important, such as *Agaricus*.

The suborder *Agaricineae* has its origin in the late Jurassic or early Cretaceous period, about 150 Myr ago (Varga *et al.* 2019, He *et al.* 2024) when the flowering plants also began to diversify rapidly (Zuntini *et al.* 2024). However, most of the current *Agaricineae* diversity originates from (mid to) late Cretaceous and early Paleogene (100 to 50 Myr ago; Varga *et al.* 2019).

The suborder is mainly composed of the brown- and dark-spored *Agaricales* with thick-walled, pigmented, and multinucleate basidiospores, derived features for the group. The spores could be an adaptation to harsh environmental conditions since they may be more resistant to dehydration and UV radiation than thin-walled and hyaline basidiospores encountered in the other suborders. This may have opened new ecological niches, e.g. permitting the colonization of dung substrates, since the spores are able to survive the passage through the digestive tract of herbivores (Garnica *et al.* 2007). Most species also possess an open-pore hilum that might be important in spore dispersal, and many dark-spored species have a germ pore to facilitate germination.

Agaricineae was shown to be monophyletic by Matheny *et al.* (2006) and Garnica *et al.* (2007) and promulgated as a suborder by Dentinger *et al.* (2015). The most up to date classification of the suborder is presented by Kalichman *et al.* (2020) and He

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et al. (2024). The latest phylogenomic trees including species from this suborder are presented in He *et al.* (2024; 31 genera), Kraisitudomsook *et al.* (2024; 22 genera), Wang *et al.* (2024; 36 genera), Li *et al.* (2025; 36 genera), and Qu *et al.* (2025; 31 genera), but the main focus of these studies is not on the classification within the suborder. In addition, the phylogenetic estimate presented in MycoCosm (2025, Grigoriev *et al.* 2011, 2014) includes species of the suborder sequenced as part of the Joint Genome Institute's (JGI) Fungal programme, but this phylogenetic tree lacks other genomic-level data available in public sequence repositories. Thus, a phylogenomic study focusing specifically on the suborder *Agaricineae* is still lacking and relationships within the suborder are partially unresolved. The aim of this study is to generate a phylogenetic estimate of the suborder *Agaricineae* using genome-wide DNA sequence data and provide a revised classification of the group.

MATERIALS AND METHODS

Molecular sampling

Sampling was designed to cover as many of the major lineages of *Agaricineae* as possible complementing the already existing published genomic data. Vouchers of 25 dried fungarium specimens sampled for genomics work are deposited in the collections of the Royal Botanic Gardens, Kew, United Kingdom (K), University of Helsinki, Finland (H), or Aberystwyth University (ABS) (Supplementary Table S1). The specimens were collected between 1997 and 2016.

DNA extraction, genomic library preparation, WGS and genome assembly, Sanger sequencing

Except for *Dissoderma paradoxum*, DNA was extracted from 2–4 mg of dried ground lamella with the DNeasy Plant Mini kit (Qiagen, Germantown, USA). Extracted DNA was quantified using a Quantus™ fluorometer and the Quantifluor dsDNA system kit (Promega Corporation, Madison, WI, USA). Estimation of the average fragment size of the samples was obtained on a 2100 Bioanalyzer (Agilent Technologies, Santa Clara, CA, USA). The DNA was then fragmented using an M220 Focused-ultrasonicator™ (Covaris, Woburn, MA, USA). Genomic DNA was extracted from *D. paradoxum* at the Natural History Museum of Utah using the enzymatic digestion-glass filtration method (Dentinger *et al.* 2010).

Except for *D. paradoxum*, dual-indexed sequencing libraries were prepared using the NEBNext® Ultra™ II Library Prep kit and the NEBNext® Multiplex Oligos for Illumina® (Dual Index Primer Set 1), according to the manufacturer's protocols (New England BioLabs, Ipswich, MA, USA). The resulting genomic libraries were quantified and qualified as above (i.e. Quantus and Bioanalyzer). For the whole genome sequencing, 24 libraries were pooled and the paired-end sequencing (2 × 150 bp) was performed on an Illumina HiSeq sequencer (Illumina, San Diego, CA, USA) at University of Utah, Salt Lake City, UT, USA with a mean of ~10 M reads per sample. Sequencing library preparation and 2 × 150 paired-end sequencing of *D. paradoxum* was carried out by Rapid Genomics (Gainesville, FL) on an Illumina HiSeq 4000 with a target coverage of ~30×. Reads were trimmed using Trimmomatic v. 0.36 (Bolger *et al*. 2014) with settings: LEADING:20 TRAILING: 20 SLIDINGWINDOW:4:20 MINLEN:36, and assembled with SPAdes v. 3.10.0 (Bankevich *et al.* 2012).

The raw genome libraries of the 25 *Agaricineae* specimens sequenced for the present study are deposited in the European Nucleotide Archive (Study ID PRJNA1209105 and PRJNA1217492). Assemblies and alignments as well as associated data files are available on FigShare (doi: 10.6084/m9.figshare.30763751). In addition, sequences for ITS (21 specimens successfully sequenced) and LSU (18 specimens successfully sequenced) regions were generated from the specimens sampled [GenBank accessions PX870832–PX870852 (ITS), PX869270–PX869287 (LSU); Supplementary Table S1]. Primer pairs ITS1F/ITS4 (White *et al.* 1990, Gardes & Bruns 1993) and LR0R/LR5 (Moncalvo *et al.* 2000) were used to amplify and sequence the loci. The PCR amplification and sequencing followed Liimatainen *et al.* (2014). Alternatively, sequencing was done by commercial companies.

Data mining and data matrix generation

The data matrix consisted of the BUSCO genes mined from the newly produced genomic data and from the publicly available entries, for a total of 86 species of suborder *Agaricineae* and five outgroup species (Supplementary Table S1). Using BUSCO with the "agaricales_odb_10" dataset 3867 highly conserved single copy orthologs were identified for the subsequent phylogenomic analysis. The data matrix was designed to cover as many genera of *Agaricineae* as possible. Because it was compiled before the publication of Kraisitudomsook *et al.* (2024), Wang *et al.* (2024), Li *et al.* (2025), MycoCosm (2025), and Qu *et al.* (2025), this dataset lacks the newly sequenced genera included in those studies/database. However, the 15 missing genera belong to families that are represented by other genera of those families in our analysis. The missing genera are: *Conioexocarpus* and *Chlorophyllum* (*Agaricaceae*), *Bolbitius* and *Conocybe* (*Bolbitiaceae*), *Lycoperdon* (*Lycoperdaceae*), *Nidula*, *Mycocalia*, and *Retiperidiolia* (*Nidulariaceae*), *Ephemerocybe* (*Psathyrellaceae*), *Cystoderma*, *Phaeolepiota*, and *Cystodermella* (*Squamanitaceae*), *Clavogaster* and *Protostropharia* (*Strophariaceae*), and *Phaeosolenia* (*Tubariaceae*).

Multiple sequence alignment and phylogenetic analyses

Orthologs were aligned using MAFFT v. 7.397 (Katoh & Standley 2013) with the L-INS-i algorithm and maximum-likelihood gene trees were inferred using IQ-TREE v. 2.0.3 (Minh *et al.* 2020) with automatic model selection in ModelFinder (Kalyaanamoorthy *et al.* 2017) and ultrafast bootstrapping ("BS"; Hoang *et al.* 2018) with 1000 replicates. A summary coalescent species tree was constructed from the gene trees using the weighted ASTRAL-hybrid tool from ASTER* (Zhang & Mirarab 2022). Maximum likelihood branch lengths were estimated on the species tree (the summary coalescent topology) using IQ-TREE, allowing model parameter estimation separately for each gene partition and allowing each partition to have its own evolutionary rate (option -p).

Gene tree performance and discordance

Gene tree performance was estimated using six metrics calculated in SortaDate (average bootstrap support, clocklike branch lengths and tree length) and the "MutualClusteringInfo" function in the R package TreeDist (generalised Robinson-Foulds distance), in addition to data matrix summaries (number of taxa and alignment length). Gene tree discordance was visualised using DiscoVista (Sayyari *et al.* 2018).

Compiling a data table on the current classification of *Agaricineae*

The supplementary table S3 from Kalichman *et al.* (2020) and the classification of *Agaricineae* from He *et al.* (2024) were taken as a basis for the work. These were then complemented and updated based on the results of the current study and other recent studies (Kraisitudomsook *et al.* 2024, Li *et al.* 2024, 2025, Yang *et al.* 2024, 2025, MycoCosm 2025).

RESULTS

WGS and genome assembly

Shallow whole genome sequence data were produced from 25 dried fungarium specimens collected between 1997 and 2016 including 15 genera lacking from the previous phylogenomic studies using single copy loci [He *et al.* (2024), Kraisitudomsook *et al.* (2024), Wang *et al.* (2024), Li *et al.* (2025), Qu *et al.* (2025)]. Total reads per sample ranged from 6.8 M–13.1 M, with a mean of 10.6 M (Supplementary Table S2). Assembly quality as measured by N50 and number of contigs varied greatly, with N50s from 1,688–35,764 (mean = 12,043) and number of contigs from 4,685–93,612 (mean = 28,612) (Supplementary Table S2). Assembly lengths ranged from 34,586,110 (*Mythicomyces corneipes*) to 177,204,304 (*Leratiomyces ceres*). BUSCO completeness was relatively high across all samples, from 81 % (*Cortinarius caperatus*) to 97.88 % (*Phaeomarasmius erinaceus*) (Supplementary Table S2). Statistics and performance of the BUSCO genes extracted from all 91 genomes included in the phylogenomic analysis are provided in the Supplementary Table S2.

Phylogenomic analysis

The data matrix for phylogenomic analysis consisted of 3,867 BUSCO genes mined from the newly produced genomic data as well from the publicly available entries from a total of 86 species of suborder *Agaricineae* and five outgroup species. The phylogenomic tree resulting from the analysis is shown in Fig. 1. ASTER* quartet support values from summary coalescence of individual gene trees are 1 for all nodes, except for the branch after the division of *Bolbitiaceae* for which it is 0.97. Eight deeper clades I–VIII are recognised from the tree. Clades II–VII include 12 lineages corresponding to family names used and accepted in recent taxonomic overviews of *Agaricales* (Kalichman *et al*. 2020, He *et al*. 2024). Within the clade II, an additional lineage is resolved sister to *Crepidotaceae*, *Inocybaceae*, and *Tubariaceae*. This lineage includes *Cyclocybe* and *Hemipholiota*, which were previously placed in *Agaricineae* incertae sedis (*Cyclocybe*; Kalichman *et al*. 2020), *Hymenogastraceae* (*Hemipholiota*; Kalichman *et al*. 2020) or *Tubariaceae* (He *et al*. 2024). Clade VIII comprises five family-level lineages that largely correspond to the most recent review of this clade by Li *et al*. (2025), with the additional recognition of *Podaxaceae* at the family level. Finally, the clade I includes genera previously placed in *Strophariaceae* and *Hymenogastraceae*. A division of this clade into six families is proposed. Justification for this division is presented in the Taxonomy and Discussion parts below. As a summary, 24 families are recognised based on the phylogenetic tree.

Gene performance and discordance

Gene performance was most strongly influenced by the number of taxa present, average bootstrap support, and generalised Robinson-Foulds (gRF) distances to the species tree topology (Supplementary Table S2). Average bootstrap support had the highest positive correlation with the number of taxa present (Pearson's coefficient = 0.74). Average bootstrap support was also moderately correlated with gRF (Pearson's coefficient = 0.57). Alignment length, clock-like branch lengths (root-to-tip variation), and total tree length had no to weak correlations with all metrics, except alignment length was moderately correlated with gRF (Pearson's coefficient = 0.42) and weakly correlated with both average bootstrap support (Pearson's coefficient = 0.26) and clocklike branch lengths (Pearson's coefficient = 0.29).

Discordance analyses revealed low gene tree conflict for most family-level nodes in the phylogenetic tree (Fig. 2). However, five families *Agaricaceae*, *Agrocybaceae*, *Crepidotaceae*, *Squamanitaceae*, and *Nidulariaceae* had less than 50 % of gene trees with bootstrap supports that weakly or strongly supported the monophyly of the group but this did not impact nodal quartet support (Fig. 1).

TAXONOMY

A revised classification of the suborder *Agaricineae*, based on a combination of the current and previously published studies, is presented in Table 1. Twenty-six families are recognised including five that are proposed as new. Of these, 24 families are associated with existing -omics level data and two (*Battarreaceae* and *Chromocyphellaceae*) are based on previous studies which included the traditional markers ITS, LSU, *rpb1, rpb2* and/or *tef1*.

Kalichman *et al.* (2020) pointed out three family names belonging to the suborder *Agaricineae* that were threatened by earlier synonyms: *Cortinariaceae*, *Psathyrellaceae*, and *Tulostomataceae*. In Kalichman *et al.* (2020), the valid publication date for *Cortinariaceae* was indicated as 1983. However, the correct date is 1951, as stated in Wiersema *et al.* (2018). Thus, *Cortinariaceae* is not threatened by *Thaxterogastraceae* or *Gigaspermataceae*, which were described in 1962 and 1982, respectively. *Psathyrellaceae* was protected against the competing earlier synonym *Zerovaemycetaceae* (Stalpers *et al.* 2021, May 2024) and thus *Psathyrellaceae* is now the accepted name for the family. The type species of *Battarreaceae*, *Battarrea phalloides*, is shown to belong to the same clade as the type species of the family *Tulostomataceae*, *Tulostoma brumale* in Gube (2009). As *Battarreaceae* is the older of the two family names, it is therefore used here for the family.

The families are further grouped into informal "superfamilies" (Fig. 1) and are named as (see Discussion for justifications): I Strophariacea (incl. *Strophariaceae*, *Agrocybaceae*, *Galerinaceae*, *Hymenogastraceae*, *Kuehneromycetaceae*, *Phaeocollybiaceae*), II Inocybacea (incl. *Inocybaceae*, *Crepidotaceae*, *Hemipholiotaceae*, *Tubariaceae*), III Cortinariacea (incl. *Cortinariaceae*, *Crassisporiaceae*), IV Galeropsidacea (incl. *Galeropsidaceae*), V Bolbitiacea (incl. *Bolbitiaceae*), VI Psathyrellacea (incl. *Psathyrellaceae*, *Hydnangiaceae*, *Mythicomycetaceae*), VII Nidulariacea (incl. *Nidulariaceae*, *Squamanitaceae*), and VIII Agaricacea (incl. *Agaricaceae*, *Coprinaceae*, *Verrucosporaceae*, *Lycoperdaceae*, *Podaxaceae*, *Battarreaceae*).

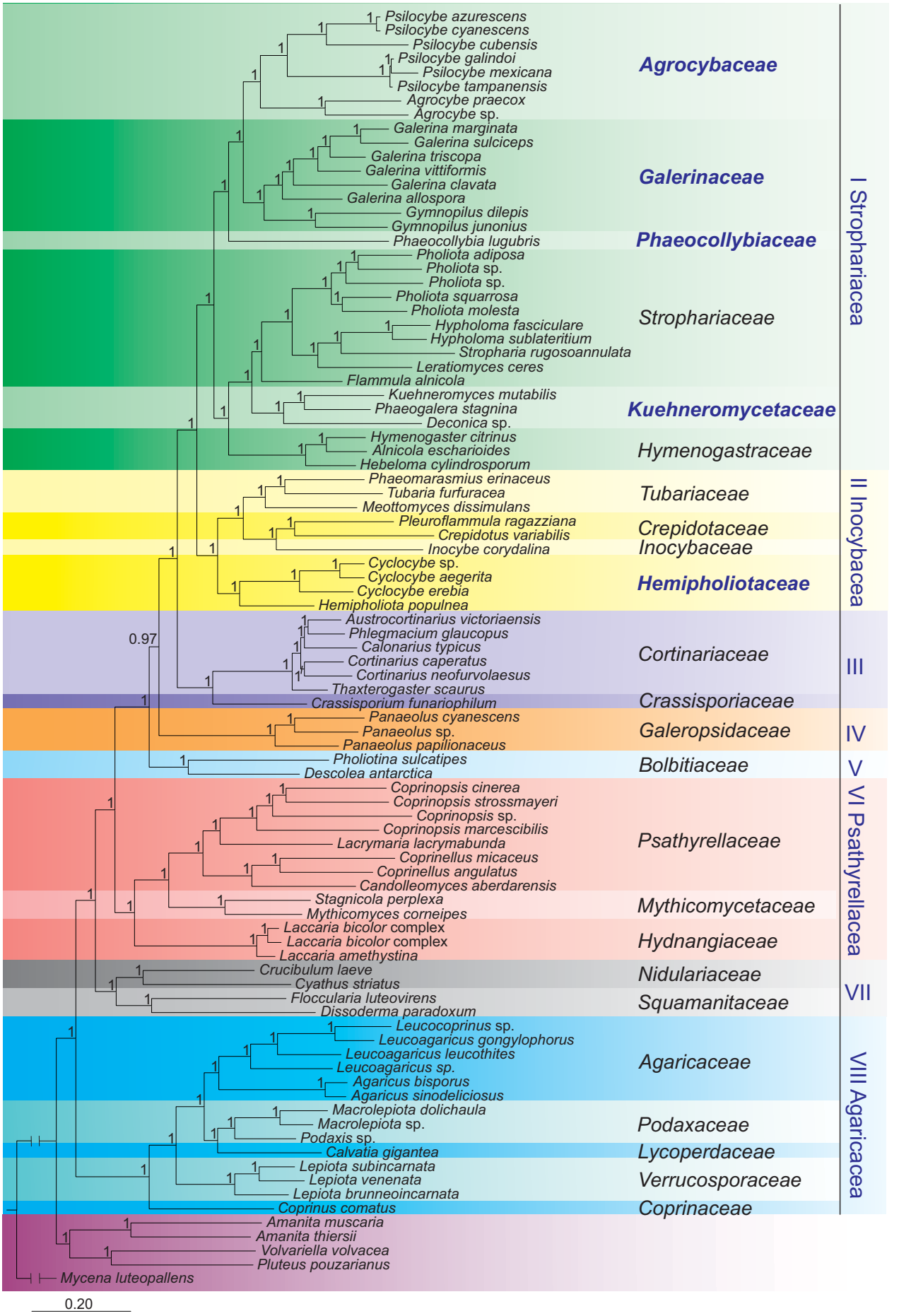

Fig. 1. ASTRAL coalescent-based species tree based on the 3867 single-copy genetic markers. Maximum likelihood branch lengths were estimated on the species tree using IQ-TREE. ASTER* quartet support values from summary coalescence of individual gene trees are 1 for all nodes, except for the branch after the division of *Bolbitiaceae* for which it is 0.97. The newly described families are marked in blue and bold. The roman numerals III, IV, V, VII correspond the "superfamilies" III Cortinariacea, IV Galeropsidacea, V Bolbitiacea and VII Nidulariacea.

Descriptions of the newly described families are presented below in order of their appearance in Fig. 1, starting from the top. Four of them belong in "superfamily" I Strophariacea, one in II Inocybacea and one in VIII Agaricacea. For some of them an invalid name already existed. We wanted to keep using those names that people are familiar with. Thus, we here validate the names and provide a modern description of them with the current delimitation of the family.

"Superfamily" I Strophariacea

This "superfamily" contains genera previously classified in families *Hymenogastraceae* and *Strophariaceae*. Several studies have already shown that the previous delimitations of the two families were not monophyletic (e.g. Matheny *et al.* 2015, Moreno *et al.* 2017, He *et al.* 2024) and a stabilised family-level classification for the group has been lacking. We retain the use of both family names and introduce four new families in the "superfamily". See "Discussion: Guiding principles for delimiting families" and "Discussion: Different options for family-level classification" for further information.

Agrocybaceae Locq. ex. Niskanen, Kytöv. & Liimat., ***fam. nov.*** MB 862166.
Synonym: *Agrocybaceae* Locq., *Syn. Gen. Fung*. (Paris): [1]. 1972, nom. inval. (Art. 39.1).

Type genus: *Agrocybe* Fayod, *Ann. Sci. Nat., Bot., Ser.* **7**, 9: 358. 1889.

Type species of the genus: *Agrocybe praecox* (Pers.) Fayod, *Ann. Sci. Nat., Bot., Ser.* **7**, 9: 358 (1889). *Basionym*: *Agaricus praecox* Pers., *Comm. Schaeff. Icon. Pict.*: 89. 1800, nom. sanct. (Fr., *Syst. Mycol*. **1**: 282. 1821). *Lectotype*: The illustration in Schaeffer (1771) *Fung. Bavar. Palat. Nasc.* **3**: tab. CCXVII, figs 1–5 (**lectotype** designated here, MBT 10031114). *Epitype*: **UK**, Worksop, Clumber Park, Lime Tree Avenue, in parkland, near *Tilia* sp., 7 Jun. 2008, *J. Leach*, K-M000158251 (K, **epitype** designated here, MBT 10031115). GenBank No. PX870836 (ITS).

Currently included genera: *Agrocybe* and *Psilocybe*.

Basidiomata small- to medium-sized, mycenoid, crepidotoid, collybioid to tricholomatoid. *Pileus* 2–10 cm, smooth, rarely velvety, usually viscid to slimy, white, yellowish or brown, hygrophanous or not. *Lamellae* adnate to adnexed or emarginate, distant to crowded, at first very pale brown, pale brown to pale grey, sometimes with a purple tint, later ± brown to almost black. *Stipe* cylindrical, in some species clavate, in some species with basal mycelial cords. *Veil* in some species forming a ring on the stipe, in some species abundant, both on pileus and stipe, and in some species very sparse or seemingly absent. *Smell* indistinct or farinaceous. *Spore deposit* brown to black. *Basidiospores* ellipsoid to amygdaloid or ovoid, sometimes rhomboid or hexagonal in face view, thin- to thick-walled, smooth, in many species with a germ pore. *Cheilocystidia* present. *Pleurocystidia* present or absent. *Clamps* present or absent. Blueing species of *Psilocybe* are hallucinogenic.

Ecology: Saprotrophic on soil, in grass or herbaceous litter, among mosses, on wood, including wood chips, and on dung.

Notes: The species of this family are characterised by usually smooth, viscid to slimy pileus and smooth spores that in many species have a distinct germ pore. The species of the sister families *Galerinaceae* and *Phaecollybiaceae* have usually ±verrucose to rugulose spores without a distinct germ pore.

Galerinaceae Locq. ex. Niskanen, Kytöv. & Liimat., ***fam. nov.*** MB 862167.
Synonym: *Galerinaceae* Locq., *Mycol. gén. struct*. (Paris): 147. 1984, nom. inval. (Art. 39.1).

Type genus: *Galerina* Earle, *Bull. New York Bot. Gard*. **5**: 423. 1909.

Type species of the genus: *Galerina vittiformis* (Fr.) Singer, *Trudy Bot. Inst. Akad. Nauk S.S.S.R, Ser. 2, Sporov. Rast.* 6: 472. 1950. *Basionym*: *Agaricus vittiformis* Fr., *Epicr. syst. mycol*.: 207. 1838 [as 'vittaeformis']. *Lectotype*: The illustration [described as *Agaricus* "quinquagesimus sextus"], in Schaeffer (1762) *Fung. Bavar. Palat. Nasc.* **1**: tab. LXIII, figs IV–VI (**lectotype** designated here, MBT 10031117) [as selected in Fries (1838)]. This painting was subsequently labelled as *A. campanulatus* (nom. illegit.) on p. 28 of Schaeffer (1774). *Epitype*: **Finland**, Savonia australis, Lappeenranta, Ihalainen, Mattila, on dryish heath forest dominated by *Pinus sylvestris* on rich, calcareous ground (*Epipactis helleborine*, etc.), 9 Oct. 1999, *U. Nummela-Salo & P. Salo* 6107, H6016931 (H, **epitype** designated here, MBT 10031116). GenBank No. PX870833 (ITS).

Currently included genera: *Galerina* and *Gymnopilus.*

Basidiomata very small- to large-sized, mycenoid to collybioid or tricholomatoid. *Pileus* 0.1–15 cm, conical, bell-shaped, convex to plane, often with an umbo, smooth, scaly or finely rugulose, dry, viscid or glutinous, ochre to red brown, hygrophanous or not. *Lamellae* emarginate, yellow to brown. Stipe 0.2–15 cm long, cylindrical, can be subclavate to bulbous at base, smooth or fibrillose, top can be pruinose, yellow to brown. *Veil* in many species evanescent or absent, in some species forming a ring or membranous patches on the stipe. *Smell* indistinct or farinaceous. *Spore deposit* brown. *Basidiospores* amygdaloid to ellipsoid, rarely subglobose, in most species verrucose or rugulose, in most species dextrinoid. *Cheilocystidia* present. *Pleurocystidia* present or absent. *Clamps* generally present.

Ecology: Saprotrophic, some species can be parasitic, on rotting wood, herb debris, peat, grass turf, humus, and bryophytes.

Notes: Typical for the members of the family *Galerinaceae* are often ± brown basidiomata and usually verrucose spores. The species of the sister family *Agrocybaceae* have smooth spores that in many species have a distinct germ pore and the general coloration of the basidiomata is less saturated yellow brown or red brown. The species of *Phaeocollybiaceae* are easily distinguished by having a long, cartilaginous, rooting stipe, and the species are ectomycorrhizal (Põlme *et al.* 2020).

Phaeocollybiaceae Niskanen, Kytöv. & Liimat., ***fam. nov.*** MB 862168.

Type genus: *Phaeocollybia* R. Heim, *Inocybe*: 70. 1931. Nom. cons., see Art. 14.

Current name of the type species: *Phaeocollybia lugubris* (Fr.) R. Heim, *Inocybe*: 71. 1931. *Basionym*: *Agaricus lugubris* Fr., *Syst.*

Mycol. **1**: 254. 1821, nom. sanct. (Fr., Syst. Mycol. 1: 254. 1821). *Neotype*: **Finland**, Etelä-Häme, Kouvola, Jaala, between Mauonsuo and the road, mesic spruce forest, 13 Aug. 2004, *U. Salo & P. Salo*, H6028452 (H, **neotype** designated here, MBT 10031118). GenBank No. PX869274 (LSU).

Currently included genus: *Phaeocollybia*.

Basidiomata rather small- to large-sized. *Pileus* 1–12(–15) cm, initially acutely conical, later with a papilla or umbo, smooth, viscid to glutinous, orange, red, brown, grey, or sordid green, hygrophanous. *Lamellae* narrowly adnate, adnexed to almost free, narrow, becoming reddish spotted with age, finally brown. *Stipe* 2–20 cm long, tapering in the lower part, deeply rooting, continuing into a pseudorrhiza, solid or fistulose, cartilaginous, smooth to slightly fibrillose, viscid. *Veil* present in primordia. *Smell* distinctive or absent. *Spore deposit* ochre to rusty brown. *Basidiospores* ellipsoid to amygdaloid or citriform, verruculose to almost smooth. *Cheilocystidia* present. *Pleurocystidia* rare. *Clamps* absent, in some species present.

Ecology: Mycorrhizal (Põlme *et al.* 2020), usually occurring in small groups both in coniferous and deciduous forests.

Notes: The members of this family are easily identified already in the field by the long, cartilaginous, rooting stipe. Typical are also smooth, viscid to glutinous pileus and verruculose to almost smooth spores without a germ pore. All species are mycorrhizal. The species of the sister families *Agrocybaceae* and *Galerinaceae* do not have a rooting stipe and are saprotrophic or parasitic. In addition, members *Agrocybaceae* have smooth spores which, in many species, have a germ pore.

Kuehneromycetaceae Niskanen, Kytöv. & Liimat., ***fam. nov.*** MB 862169.

Type genus: *Kuehneromyces* Singer & A.H. Sm., Mycologia 38(5): 504. 1946.

Type species of the genus: *Kuehneromyces mutabilis* (Schaeff.) Singer & A.H. Sm., *Mycologia* **38**(5): 505. 1946. *Basionym*: *Agaricus mutabilis* Schaeff., *Fung. Bavar. Palat. Nasc.* **4**: 6. 1774, nom. sanct. (Fr., *Syst. Mycol.* **1**: 245. 1821). *Lectotype*: Schaeffer, *Fung. Bavar. Palat. Nasc.* **1**: tab. IX, fig. 3. 1762 (**lectotype** designated here, MBT 10031120). *Epitype*: **UK**, East Norfolk, North Walsham, Aylsham, Blickling Hall, on *Fagus sylvatica*, 31 Oct. 2003, *B.M. Spooner*, K-M000118189 (K, **epitype** designated here, MBT 10031119). GenBank No. PX870840 (ITS), PX869278 (LSU).

Currently included genera: *Kuehneromyces*, *Deconica*, and *Phaeogalera*.

Basidiomata rather small to medium-sized, mycenoid, collybioid to crepidotoid. *Pileus* 0.5–6 cm, smooth, slimy, viscid or dry, pale yellow brown to dark brown, hygrophanous. *Lamellae* adnate to adnexed or emarginate, distant to crowded, yellow to brown, in some species black. *Stipe* 1–15 cm long, cylindrical or with a clavate base. *Veil* often forming a more or less distinct ring and/or more or less distinct patches on the stipe. *Smell* indistinct or pleasant. *Spore* deposit brown to black. *Basidiospores* ellipsoid to ovoid, sometimes rhomboid or hexagonal in face view, in some species truncate, smooth, in most species with a germ pore. *Cheilocystidia* present. *Pleurocystidia* absent. *Clamps* present or absent.

Ecology: Saprotrophic on wood, dung, soil, mosses, leaf litter or twigs.

Notes: Typical for the members of the family are rather small to medium-sized basidiomata with often slimy or viscid, hygrophanous pileus, smooth basidiospores with a germ pore in the vast majority of species, presence of cheilocystidia and absence of pleurocystidia. The species of the sister family *Strophariaceae* often have pleurocystidia or chrysocystidia.

"Superfamily" II Inocybacea

Hemipholiotaceae Niskanen, Kytöv. & Liimat., ***fam. nov.*** MB 862170.

Type genus: *Hemipholiota* (Singer) Bon, *Doc. Mycol.* **17**(65): 52. 1986.

Generic type (see more details under the notes): *Pholiota* subgen. *Hemipholiota* Singer, *Sydowia* **15**(1–6): 70. 1962 [1961].

Type species of the genus: *Agaricus destruens* Brond., *Rec. Pl. Crypt. Agenais* **2**: 20. 1829 [1828–1830]. *Lectotype*: Brond., *Rec. Pl. Crypt. Agenais* **2**: tab. 6. 1829 (**lectotype** designated here, MBT 10031122). *Epitype*: **UK**, West Kent, London, Bexley, Footscray Meadows, on *Populus* hybrid, 30 Oct. 2002, *J. Weightman*, K-M000106695 (K, **epitype** designated here, MBT 10031121). GenBank No. PX870846 (ITS).
Synonym: *Hemipholiota populnea* (Pers.) Bon, *Doc. Mycol.* **17**(65): 52. 1986.
Basionym: *Agaricus populneus* Pers., *Mycol. Eur.* **3**: 171. 1828, nom. sanct. (Fr., *Syst. Mycol.*, Index: 36. 1832). *Neotype*: **UK**, West Kent, London, Bexley, Footscray Meadows, on *Populus* hybrid, 30 Oct. 2002, *J. Weightman*, K-M000106695 (K, **neotype** designated here, MBT 10031123).

Currently included genera: *Hemipholiota* and *Cyclocybe*.

Basidiomata medium- to large-sized, tricholomatoid. *Pileus* 2–20 cm, smooth to rugulose or scaly, with more or less remnants of veil on top or scaly, dry or viscid, pale brown, ochre brown to dark brown, more or less hygrophanous. *Lamellae* adnate or emarginate, crowded to medium spaced, at least at first whitish grey or pale brown, in some species becoming darker, ± brown, with age. *Stipe* 3–15 cm long, cylindrical or clavate, white, pale brown. *Veil* forming a ring on the stipe. *Smell* indistinct or aromatic. *Spore deposit* brown. *Basidiospores* smooth, ovoid-amygdaloid, ellipsoid to slightly phaseoliform, thick-walled, in most species with a germ pore. *Cheilocystidia* thin-walled, cylindrical, clavate or lageniform. *Pleurocystidia* absent, or lageniform or utriform. *Clamps* present.

Ecology: Saprotrophic or parasitic on deciduous trees, or saprotrophic on parts of wood buried in soil.

Notes: The members of this family are characterised by medium- to large-sized, tricholomatoid basidiomata with a ring on the stipe. The spores are smooth, thick-walled, amygdaloid to ellipsoid and in most species with a germ pore. All species have cheilocystidia, some

Table 1. Emended classification of suborder *Agaricineae*.

"Superfamily"	Family	Genus	Author(s) of the genus	Type species (current name)	Genus citation/phylogenetic placement
Strophariacea I	*Agrocybaceae*	*Agrocybe*	Fayod	*Agrocybe praecox*	Current study; Mycocosm (2025)
		Psilocybe	(Fr.) P.Kumm.	*Psilocybe semilanceata*	Current study; Bradshaw *et al.* (2024); Mycocosm (2025)
	Chromocyphellaceae	*Chromocyphella*	De Toni & Levi	*Chromocyphella muscicola*	Moreno *et al.* (2017); Tian & Matheny (2020)
	Galerinaceae	*Galerina*	Earle	*Galerina vittiformis*	Current study; Mycocosm (2025)
		Gymnopilus	P.Karst.	*Gymnopilus picreus*	Current study; Mycocosm (2025)
	Hymenogastraceae	*Alnicola*	Kühner	*Alnicola luteolofibrillosa*	Current study; Soop *et al.* (2016)
		Hebeloma	(Fr.) P.Kumm.	*Hebeloma mesophaeum*	Current study; Soop *et al.* (2016)
		Hymenogaster	Vittad.	*Hymenogaster citrinus*	Current study; Soop *et al.* (2016)
		Psathyloma	Soop, J.A.Cooper & Dima	*Psathyloma leucocarpum*	Soop *et al.* (2016)
	Kuehneromycetaceae	*Deconica*	(W.G.Sm.) P.Karst.	*Deconica bullacea*	Current study; Ramírez-Cruz *et al.* (2013)
		Kuehneromyces	Singer & A.H.Sm.	*Kuehneromyces mutabilis*	Current study
		Phaeogalera	Kühner	*Phaeogalera stagnina*	Current study
	Phaeocollybiaceae	*Phaeocollybia*	R.Heim	*Phaeocollybia lugubris*	Current study
	Strophariaceae	*Bogbodia*	Redhead	*Bogbodia uda*	Walther *et al.* (2005)
		Clavogaster	Henn.	*Clavogaster novozelandicus*	Cooper (2012); Mycocosm (2025)
		Flammula	(Fr.) P.Kumm.	*Flammula alnicola*	Current study
		Hypholoma	(Fr.) P.Kumm.	*Hypholoma fasciculare*	Current study; Mycocosm (2025)
		Leratiomyces	Bresinsky & Manfr.Binder ex Bridge, Spooner, Beever & D.C.Park	*Leratiomyces similis*	Current study; Mycocosm (2025)
		Phaeonematoloma	(Singer) Bon	*Phaeonematoloma myosotis*	Moncalvo *et al.* (2002)
		Pholiota	(Fr.) P.Kumm.	*Pholiota squarrosa*	Current study; Mycocosm (2025)
		Protostropharia	Redhead, Moncalvo & Vilgalys	*Protostropharia semiglobata*	Walther *et al.* (2005)
		Pyrrhulomyces	E.J. Tian & Matheny	*Pyrrhulomyces astragalinus*	Tian & Matheny (2020)
		Stropharia	(Fr.) Quél.	*Stropharia aeruginosa*	Current study; Mycocosm (2025)
	Strophariacea incertae sedis	*Synnematomyces*	Kobayasi	*Synnematomyces capitatus*	GenBank (ITS) LC146764.1
		Tympanella	E.Horak	*Tympanella galanthina*	GenBank (ITS) KY827308.1
Inocybacea II	*Crepidotaceae*	*Crepidotus*	(Fr.) Staude	*Crepidotus mollis*	Current study; Mycocosm (2025)
		Neopaxillus	Singer	*Neopaxillus echinospermus*	Watling & Aime (2013)
		Pleuroflammula	Singer	*Pleuroflammula dussii*	Current study; Vizzini *et al.* (2019a)

Table 1. (Continued).

"Superfamily"	Family	Genus	Author(s) of the genus	Type species (current name)	Genus citation/phylogenetic placement
		Simocybe	P.Karst.	*Simocybe centunculus*	Petersen *et al.* (2010)
	Hemipholiotaceae	*Cyclocybe*	Velen.	*Cyclocybe erebia*	Current study; Vizzini *et al.* (2014)
		Hemipholiota	(Singer) Bon	*Hemipholiota populnea*	Current study; Gulden et al. (2008)
	Inocybaceae	*Auritella*	Matheny & Bougher	*Auritella dolichocystis*	Latha *et al.* (2016)
		Inocybe	(Fr.) Fr.	*Inocybe relicina*	Current study; Alvarado *et al.* (2010)
		Inosperma	(Kühner) Matheny & Esteve-Rav.	*Inosperma calamistratum*	Matheny *et al.* (2019); Mycocosm (2025)
		Mallocybe	(Kuyper) Matheny, Vizzini & Esteve-Rav.	*Mallocybe terrigena*	Matheny *et al.* (2019)
		Nothocybe	Matheny & K.P.D.Latha	*Nothocybe distincta*	Matheny *et al.* (2019)
		Pseudosperma	Matheny & Esteve-Rav.	*Pseudosperma sororium*	Matheny *et al.* (2019)
		Tubariomyces	Esteve-Rav. & Matheny	*Tubariomyces inexpectatus*	Alvarado *et al.* (2010)
	Inocybacea incertae sedis most likely	*Episphaeria*	Donk	*Episphaeria fraxinicola*	Petersen *et al.* (2010)
		Hemistropharia	Jacobsson & E.Larss.	*Hemistropharia albocrenulata*	Petersen *et al.* (2010)
		Nanstelocephala	Oberw. & R.H.Petersen	*Nanstelocephala physalacrioides*	Oberwinkler *et al.* (1990)
	Tubariaceae	*Flammulaster*	Earle	*Flammulaster carpophilus*	Vizzini *et al.* (2019a)
		Meottomyces	Vizzini	*Meottomyces dissimulans*	Current study
		Pachylepyrium	Singer	*Pachylepyrium fulvidula*	Matheny *et al.* (2015)
		Phaeomarasmius	Scherff.	*Phaeomarasmius rimulincola*	Current study; Vizzini *et al.* (2019a)
		Phaeosolenia	Speg.	*Phaeosolenia platensis*	Wang *et al.* (2024)
		Pleuromyces	Dima, P.-A.Moreau & V.Papp	*Pleuromyces hungaricus*	Dima *et al.* (2018)
		Tubaria	(W.G.Sm.) Gillet	*Tubaria furfuracea*	Current study
Cortinariacea III	*Cortinariaceae*	*Aureonarius*	Niskanen & Liimat.	*Aureonarius kroegeri*	Liimatainen *et al.* (2022)
		Austrocortinarius	Niskanen & Liimat.	*Austrocortinarius victoriaensis*	Current study; Liimatainen *et al.* (2022)
		Calonarius	Niskanen & Liimat.	*Calonarius typicus*	Current study; Liimatainen *et al.* (2022)
		Cortinarius	(Pers.) Gray	*Cortinarius violaceus*	Current study; Mycocosm (2025)
		Cystinarius	Niskanen & Liimat.	*Cystinarius rubiginosus*	Liimatainen *et al.* (2022)
		Hygronarius	Niskanen & Liimat.	*Hygronarius renidens*	Liimatainen *et al.* (2022)
		Mystinarius	Niskanen & Liimat.	*Mystinarius lustrabilis*	Liimatainen *et al.* (2022)
		Phlegmacium	(Fr.) Wünsche	*Phlegmacium saginum*	Current study; Liimatainen *et al.* (2022); Mycocosm (2025)

Table 1. (Continued).

"Superfamily"	Family	Genus	Author(s) of the genus	Type species (current name)	Genus citation/phylogenetic placement
		Thaxterogaster	Singer	*Thaxterogaster magellanicus*	Current study; Liimatainen *et al.* (2022)
		Volvanarius	Niskanen & Liimat.	*Volvanarius chlorosplendidus*	Liimatainen *et al.* (2022)
	Crassisporiaceae	*Crassisporium*	Matheny, P.-A.Moreau & Vizzini	*Crassisporium funariophilum*	Current study; Vizzini *et al.* (2019a); Mycocosm (2025)
		Romagnesiella	Contu, P.-A.Moreau, Vizzini & A.de Haan	*Romagnesiella clavus*	Vizzini *et al.* (2019b)
Galeropsidacea IV	*Galeropsidaceae*	*Copelandia*	Bres.	*Copelandia cyanescens*	Örstadius *et al.* (2015)
		Panaeolina	Maire	*Panaeolina foenisecii*	Matheny *et al.* (2006)
		Panaeolopsis	Singer	*Panaeolopsis sanmartiniana*	Tóth *et al.* (2013)
		Panaeolus	(Fr.) Quél.	*Panaeolus papilionaceus*	Current study; Tóth *et al.* (2013); Mycocosm (2025)
Bolbitiacea V	*Bolbitiaceae*	*Bolbitius*	Fr.	*Bolbitius titubans*	Tóth *et al.* (2013); Mycocosm (2025)
		Conocybe	Fayod	*Conocybe tenera*	Tóth *et al.* (2013); Mycocosm (2025)
		Descolea	Singer	*Descolea antarctica*	Current study; Tóth *et al.* (2013)
		Galerella	Earle	*Galerella plicatella*	Tóth *et al.* (2013)
		Pholiotina	Fayod	*Pholiotina blattaria*	Current study; Tóth *et al.* (2013)
		Tubariella	E.Horak & Hauskn.	*Tubariella rhizophora*	Tóth *et al.* (2013)
	Bolbitiacea incertae sedis most likely	*Cyttarophyllopsis*	R.Heim	*Cyttarophyllopsis cordispora*	Natarajan (1978)
		Ptychella	Roze & Boud.	*Ptychella ochracea*	Watling (1967)
		Tubariopsis	R.Heim	*Tubariopsis torquipes*	Heim (1931)
		Wielandomyces	Raithelh.	*Wielandomyces robustus*	Raithelhuber (1988)
Psathyrellacea VI	*Hydnangiaceae*	*Hydnangium*	Wallr.	*Hydnangium carneum*	Wilson *et al.* (2017)
		Laccaria	Berk. & Broome	*Laccaria laccata*	Current study; Wilson *et al.* (2017); Mycocosm (2025)
		Podohydnangium	G.W.Beaton, Pegler & T.W.K.Young	*Podohydnangium australe*	Sheedy *et al.* (2016)
	Mythicomycetaceae	*Mythicomyces*	Redhead & A.H.Sm.	*Mythicomyces corneipes*	Current study
		Stagnicola	Redhead & A.H.Sm.	*Stagnicola perplexa*	Current study; Vizzini *et al.* (2019a)
	Psathyrellaceae	*Britzelmayria*	D. Wächt. & A. Melzer	*Britzelmayria supernula*	Wächter & Melzer (2020)
		Candolleomyces	D. Wächt. & A. Melzer	*Candolleomyces candolleanus*	Current study
		Cantonopsathyra	Kun L. Yang, Jia Ying Lin, Zhen C. Liu & Zhu L. Yang	*Cantonopsathyra serendipita*	Yang *et al.* (2025)
		Coprinellus	P.Karst.	*Coprinellus deliquescens*	Current study; Mycocosm (2025)

Table 1. (Continued).

"Superfamily"	Family	Genus	Author(s) of the genus	Type species (current name)	Genus citation/phylogenetic placement
		Coprinopsis	P.Karst.	*Coprinopsis friesii*	Current study; Mycocosm (2025)
		Cystoagaricus	Singer	*Cystoagaricus strobilomyces*	Örstadius *et al.* (2015)
		Homophron	(Britzelm.) Örstadius & E.Larss.	*Homophron spadiceum*	Örstadius *et al.* (2015)
		Jugisporipsathyra	J.Q. Yan, Y.G. Fan & S.N. Wang	*Jugisporipsathyra reticulopilea*	Wang *et al.* (2022)
		Kauffmania	Örstadius & E.Larss.	*Kauffmania larga*	Örstadius *et al.* (2015)
		Lacrymaria	Pat.	*Lacrymaria lacrymabunda*	Current study; Örstadius *et al.* (2015)
		Narcissea	D. Wächt. & A. Melzer	*Narcissea patouillardii*	Wächter & Melzer (2020)
		Olotia	D. Wächt. & A. Melzer	*Olotia codinae*	Wächter & Melzer (2020)
		Parasola	Redhead, Vilgalys & Hopple	*Parasola plicatilis*	Örstadius *et al.* (2015)
		Psathyrella	(Fr.) Quél.	*Psathyrella corrugis*	Örstadius *et al.* (2015)
		Punjabia	D. Wächt. & A. Melzer	*Punjabia pakistanica*	Wächter & Melzer (2020)
		Typhrasa	Örstadius & E.Larss.	*Typhrasa gossypina*	Örstadius *et al.* (2015)
	Psathyrellaceae?	*Gasteroagaricoides*	D.A.Reid	*Gasteroagaricoides ralstoniae*	Reid (1986)
Nidulariacea VII	*Nidulariaceae*	*Crucibulum*	Tul. & C.Tul.	*Crucibulum laeve*	Current study; Kraisitudomsook *et al.* (2024); Mycocosm (2025)
		Cyathus	Haller	*Cyathus striatus*	Current study; Kraisitudomsook *et al.* (2024); Mycocosm (2025)
		Mycocalia	J.T.Palmer	*Mycocalia denudata*	Kraisitudomsook *et al.* (2024); Mycocosm (2025)
		Nidula	V.S.White	*Nidula candida*	Kraisitudomsook *et al.* (2024); Mycocosm (2025)
		Nidularia	Fr.	*Nidularia deformis*	Kraisitudomsook *et al.* (2024); Mycocosm (2025)
		Retiperidiolia	Kraisit., Choeyklin, Boonprat. & M.E. Sm.	*Retiperidiolia reticulata*	Kraisitudomsook *et al.* (2024)
	Squamanitaceae	*Cystoderma*	Fayod	*Cystoderma amianthinum*	Cooper (2018b)
		Cystodermella	Harmaja	*Cystodermella granulosa*	Saar *et al.* (2009)
		Dissoderma	(A.H. Sm. & Singer) Singer	*Dissoderma paradoxum*	Saar *et al.* (2022)
		Floccularia	Pouzar	*Floccularia luteovirens*	Current study; Varga *et al.* (2019)
		Leucopholiota	(Romagn.) O.K.Mill., T.J.Volk & Bessette	*Leucopholiota decorosa*	Varga *et al.* (2019); Saar *et al.* (2022)
		Phaeolepiota	Maire ex Konrad & Maubl.	*Phaeolepiota aurea*	Saar & Peintner (2016)
		Squamanita	Imbach	*Squamanita schreieri*	Current study; Cooper (2018b)

Table 1. (Continued).

"Superfamily"	Family	Genus	Author(s) of the genus	Type species (current name)	Genus citation/phylogenetic placement
Agaricacea VIII	*Agaricaceae*	*Agaricus*	L.	*Agaricus campestris*	Current study; Li *et al.* (2025); Mycocosm (2025)
		Asperosporus	Karlsen-Ayala, Gazis & M.E. Sm.	*Asperosporus subterraneus*	Li *et al.* (2025)
		Barcheria	T.Lebel	*Barcheria willisiana*	Lebel & Syme (2012); Li *et al.* (2024)
		Candelolepiota	Kun L. Yang, Jia Ying Lin & Zhu L. Yang	*Candelolepiota sinica*	Yang *et al.* (2024)
		Chlorophyllum	Massee	*Chlorophyllum molybdites*	Gube (2009); Li *et al.* (2024, 2025)
		Clarkeinda	Kuntze	*Clarkeinda trachodes*	Ge & Yang (2017); Li *et al.* (2024)
		Conioexocarpus	R.L. Zhao & J.X. Li	*Conioexocarpus cretaceus*	Li *et al.* (2025)
		Coniolepiota	Vellinga	*Coniolepiota spongodes*	Ge *et al.* (2015); Li *et al.* (2024, 2025)
		Eriocybe	Vellinga	*Eriocybe chionea*	Ge *et al.* (2015); Li *et al.* (2024, 2025)
		Furfuragaricus	R.L. Zhao & J.X. Li	*Furfuragaricus microsporus*	Li *et al.* (2025)
		Heinemannomyces	Watling	*Heinemannomyces splendidissimus*	Ge *et al.* (2015); Li *et al.* (2024)
		Hiatulopsis	Singer & Grinling	*Hiatulopsis amara*	Kooij *et al.* (2024)
		Hymenagaricus	Heinem.	*Hymenagaricus hymenopileus*	Li *et al.* (2024, 2025)
		Leucoagaricus	Locq. ex Singer	*Leucoagaricus rubrotinctus*	Current study; Li *et al.* (2025)
		Leucocoprinus	Pat.	*Leucocoprinus cepistipes*	Current study; Li *et al.* (2025)
		Macropsalliota	Kun L. Yang, Jia Ying Lin & Zhu L. Yang	*Macropsalliota americana*	Yang *et al.* (2024); Li *et al.* (2025)
		Micropsalliota	Höhn.	*Micropsalliota pseudovolvulata*	Parra *et al.* (2016); Li *et al.* (2025)
		Mystagaricus	V. Papp, Radnóti & Dima	*Mystagaricus brunneolilacinus*	Radnóti *et al.* (2025); Li *et al.* (2025)
		Pseudolepiota	Z.W.Ge	*Pseudolepiota zangmui*	Ge & Yang (2017); Li *et al.* (2025)
		Termiticola	E.Horak	*Termiticola rubescens*	Vellinga (2010); Li *et al.* (2024)
		Xanthagaricus	(Heinem.) Little Flower, Hosag. & T.K.Abraham	*Xanthagaricus flavidorufus*	Hosen *et al.* (2017); Li *et al.* (2025)
	Battarreaceae	*Battarrea*	Pers.	*Battarrea phalloides*	Gube (2009); Li *et al.* (2025)
		Battarreoides	T.Herrera	*Battarreoides diguetii*	Gube (2009); Li *et al.* (2025)
		Chlamydopus	Speg.	*Chlamydopus clavatus*	Gube (2009); Li *et al.* (2024)
		Dictyocephalos	Underw. ex V.S.White	*Dictyocephalos attenuatus*	Gube (2009); Li *et al.* (2024)
		Phellorinia	Berk.	*Phellorinia herculeana*	Gube (2009); Li *et al.* (2024)
		Queletia	Fr.	*Queletia mirabilis*	Gube (2009)
		Schizostoma	Ehrenb. ex Lév.	*Schizostoma laceratum*	Gube (2009)

Table 1. (Continued).

"Superfamily"	Family	Genus	Author(s) of the genus	Type species (current name)	Genus citation/phylogenetic placement
		Tulostoma	Pers.	*Tulostoma brumale*	Gube (2009); Li *et al.* (2024, 2025)
	Coprinaceae	*Coprinus*	Pers.	*Coprinus comatus*	Current study; Li *et al.* (2025)
		Montagnea	Fr.	*Montagnea arenaria*	Gube (2009); Li *et al.* (2025)
	Incertae sedis	*Arachniopsis*	Long	*Arachniopsis albicans*	Li *et al.* (2025)
		Chlorolepiota	Sathe & S.D.Deshp.	*Chlorolepiota mahabaleshwarensis*	Atri *et al.* (2014); Li *et al.* (2025)
		Crucispora	E. Horak	*Crucispora naucorioides*	Noordeloos & Vrinda (2007); Li *et al.* (2025)
		Endolepiotula	Singer	*Endolepiotula ruizlealii*	Vellinga (2010); Li *et al.* (2025)
		Janauaria	Singer	*Janauaria amazonica*	Vellinga *et al.* (2011); Li *et al.* (2025)
		Phyllogaster	Pegler	*Phyllogaster pholiotoides*	Beaton *et al.* (1985); Li *et al*. (2025)
		Rugosospora	Heinem.	*Rugosospora ochraceobadia*	Vellinga *et al.* (2011); Li *et al.* (2025)
	Lycoperdaceae	*Abstoma*	G.Cunn.	*Abstoma purpureum*	Gube (2009); Li *et al.* (2024)
		Acutocapillitium	P.Ponce de León	*Acutocapillitium torrendii*	Bates (2004); Li et al. (2024)
		Apioperdon	(Kreisel & D.Krüger) Vizzini	*Apioperdon pyriforme*	Vizzini & Ercole (2017); Li *et al.* (2024)
		Arachnion	Schwein.	*Arachnion album*	Gube (2009); Li *et al.* (2024)
		Bovista	Pers.	*Bovista plumbea*	Li *et al.* (2024)
		Bovistella	Morgan	*Bovistella ohiensis*	Gube (2009); Li *et al.* (2024)
		Bryoperdon	Vizzini	*Bryoperdon acuminatum*	Vizzini & Ercole (2017); Li *et al.* (2024)
		Calbovista	Morse ex M.T.Seidl	*Calbovista subsculpta*	Gube (2009); Li *et al.* (2024)
		Calvatia	Fr.	*Calvatia craniiformis*	Current study; Li *et al.* (2025)
		Calvatiopsis	Hollós	*Calvatiopsis bovistoides*	Bates (2004); Li et al. (2024)
		Disciseda	Czern.	*Disciseda collabescens*	Larsson & Jeppson (2008); Li et al. (2024)
		Fuscospina	R.L. Zhao & J.X. Li	*Fuscospina scabricapillitia*	Li *et al.* (2024)
		Gastropila	Homrich & J.E.Wright	*Gastropila fragilis*	Revriev & Assyov (2012); Li *et al.* (2024)
		Globaria	Quél	*Globaria aestivalis*	Li *et al.* (2024)
		Glyptoderma	R.Heim & Perr.-Bertr.	*Glyptoderma coelatum*	Li *et al.* (2024)
		Holocotylon	Lloyd	*Holocotylon brandegeeanum*	Bates *et al.* (2009); Li *et al.* (2024)
		Japonogaster	Kobayasi	*Japonogaster oohashianus*	Bates (2004); Li *et al.* (2024)
		Leptocaulis	R.L. Zhao & J.X. Li	*Leptocaulis sublongistipes*	Li *et al.* (2024)
		Lycoperdiscus	R.L. Zhao & J.X. Li	*Lycoperdiscus tianzhuensis*	Li *et al.* (2024)

Table 1. (Continued).

"Superfamily"	Family	Genus	Author(s) of the genus	Type species (current name)	Genus citation/phylogenetic placement
		Lycoperdon	Pers.	*Lycoperdon perlatum*	Li *et al.* (2024); Mycocosm (2025)
		Lycoperdopsis	Henn.	*Lycoperdopsis arcyrioides*	Pegler & Young (1994); Li *et al.* (2024)
		Morganella	Zeller	*Morganella fuliginea*	Larsson & Jeppson (2008); Li *et al.* (2024)
		Mycenastrum	Desv.	*Mycenastrum corium*	Gube (2009); Li *et al.* (2024)
		Pseudoperdon	R.L. Zhao & J.X. Li	*Pseudoperdon medogense*	Li *et al.* (2024)
		Sinoperdon	R.L. Zhao & J.X. Li	*Sinoperdon gyirongense*	Li *et al.* (2024)
		Utraria	Quél	*Utraria excipuliformis*	Li *et al.* (2024)
		Vascellum	F.Šmarda	*Vascellum pratense*	Larsson & Jeppson (2008); Li *et al.* (2024)
	Podaxaceae	*Macrolepiota*	Singer	*Macrolepiota procera*	Current study; Li *et al.* (2025); Mycocosm (2025)
		Podaxis	Desv.	*Podaxis senegalensis*	Current study; Li *et al.* (2025)
		Volvolepiota	Singer	*Volvolepiota brunnea*	Li *et al.* (2025)
	Verrucosporaceae	*Chamaemyces*	Battarra ex Earle 1909	*Chamaemyces alphitophyllus* [nom. inval., Art. 35.2 (Melbourne)]	Li *et al.* (2024)
		Cystolepiota	Singer	*Cystolepiota constricta*	Gube (2009); Li *et al.* (2024, 2025)
		Echinoderma	(Locq. ex Bon) Bon	*Echinoderma asperum*	Gube (2009); Li *et al.* (2024, 2025)
		Lepiota	(Pers.) Gray	*Lepiota clypeolaria*	Current study; Li *et al.* (2024, 2025)
		Melanophyllum	Velen.	*Melanophyllum haematospermum*	Gube (2009); Li *et al.* (2024)
		Neosecotium	Singer & A.H.Sm.	*Neosecotium macrosporum*	Lizárraga *et al.* (2012)
		Pulverolepiota	Bon	*Pulverolepiota pulverulenta*	Li *et al.* (2025)
		Smithiomyces	Singer	*Smithiomyces mexicanus*	Justo *et al.* (2015); Li *et al.* (2024, 2025)
		Verrucospora	E.Horak	*Verrucospora verrucispora*	Vellinga (2009); Kooij *et al.* (2024)
Agaricineae incertae sedis		*Cercopemyces*	T.J.Baroni, Kropp & V.S.Evenson	*Cercopemyces crocodilinus*	Baroni *et al.* (2014)
		Fissolimbus	E.Horak	*Fissolimbus fallaciosus*	Horak (1972)
		Phaeopholiota	Locq. & Sarwal	*Phaeopholiota crinipellis*	Sarwal & Locquin (1983)
		Ripartitella	Singer	*Ripartitella brasiliensis*	Zhang *et al.* (2019)

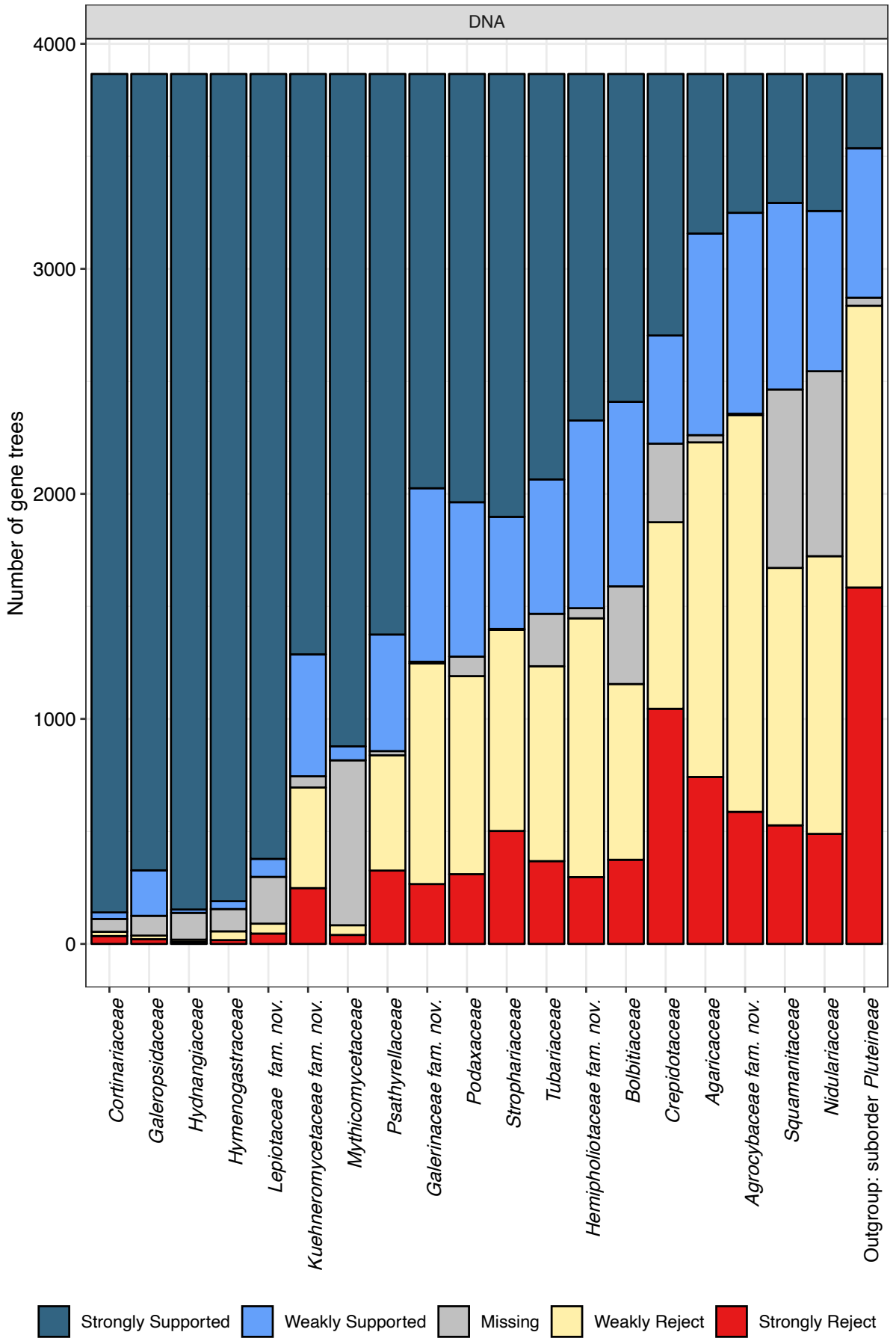

Fig. 2. Gene tree discordance for key clades estimated across 3867 gene trees using DiscoVista. Each bar represents a clade of interest and colored segments reflect the proportion of gene trees in which that clade is strongly supported (dark blue; bootstrap support ≥ 75%), weakly supported (light blue; clade present but bootstrap support < 75%), weakly rejected (yellow; clade absent but compatible with the gene tree after contracting branches with support < 75%), rejected (red; clade incompatible with the gene tree even after contracting low-support branches), or not represented (gray; clade absent from the gene tree due to missing taxa). Gene trees were estimated using IQ-TREE. Bootstrap support thresholds follow DiscoVista defaults (MLBS = 75

also pleurocystidia. Members of the related families *Tubariaceae*, *Crepidotaceae*, and *Inocybaceae* are generally smaller in size and all species of *Crepidotaceae*, *Inocybaceae*, and part of the species of *Tubariaceae* also lack a ring on the stipe. In addition, members of the family *Tubariaceae* do not have pleurocystidia.

The basionym of the genus *Hemipholiota* is *Pholiota* subgen. *Hemipholiota* Singer 1962. When describing the subgenus, Singer (1962) designated *Pholiota destruens* as the type species. Kuyper & Tjallingii-Beukers (1986) considered *Pholiota destruens* and *Pholiota populnea* as synonyms. We agree with Kuyper & Tjallingii-Beukers that these two names are synonyms and thus *populnea* is the correct epithet for the species.

DISCUSSION

Our study represents the most comprehensive phylogenomic analysis of the suborder *Agaricineae* to date including 54 genera and 86 species. In comparison, previous studies have included up to 36 genera: He *et al.* (2024) included 31, Kraisitudomsook *et al*. (2024) 22, Wang *et al.* (2024) 36, Li *et al.* (2025) 36 and Qu *et al*. (2025) 31. Within the eight deep divisions (I–VIII), the family-level topology of our phylogenomic tree (Fig. 1) is largely congruent with those reported in earlier studies with two exceptions. The first is the placement of *Flammula alnicola* within "superfamily" I Strophariacea in He *et al*. (2024), Li *et al*. (2025) and in our study (the species is not present in other studies). In our analysis and the analysis of Li *et al*. (2025), *Flammula* is resolved as sister to *Strophariaceae*, whereas He *et al*. (2024) recovered it as sister to both *Strophariaceae* and *Kuehneromycetaceae*. Our gene tree discordance analysis (Fig. 2) indicates that nearly two-thirds of the gene trees support *Flammula* as sister to *Strophariaceae*. Based on this evidence, we propose that the placement of *Flammula* in *Strophariaceae* currently represents the best-supported hypothesis. The second difference in the family-level topology between the different studies is the placement of *Podaxaceae* within "superfamily" VIII Agaricacea: in three studies (Kraisitudomsook *et al*. 2024, Qu *et al*. 2025, our study) *Podaxaceae* is resolved as a sister to *Lycoperdaceae* and in two studies as a sister to *Agaricaceae* (Wang *et al.* 2024, Li *et al*. 2025). For determining the phylogenetic placement of *Podaxaceae* within *Agaricaceae* s. l. further studies are needed.

The branching order of the eight deep divisions (I–VIII) in our phylogenomic tree is largely consistent with those of the four previous studies (Wang *et al.* 2023, He *et al.* 2024, Kraisitudomsook *et al*. 2024, Li *et al*. 2025, Qu *et al*. 2025). The difference between our and the previous studies is the branching order of III Cortinariacea and IV Galeropsidacea. While all previous studies recover "superfamily" III Cortinariacea branching earlier than "superfamily" IV Galeropsidacea, our results indicate the opposite: IV Galeropsidacea branches before III Cortinariacea. The analysis by Qu *et al*. (2025) suggested that both introgression/hybridization (IH) and incomplete lineage sorting (ILS) may contribute to the conflicting placement of IV Galeropsidacea. All four previous studies used less than half the number of markers analyzed in our study. In addition, four out of five of them did not include V Bolbitiacea (He *et al*. 2024, Kraisitudomsook *et al*. 2024, Li *et al*. 2025 and Qu *et al*. 2025). Increased genetic sampling generally enhances the precision of phylogenetic inference and can help mitigate some of the challenges that incomplete lineage sorting poses. Also, broader taxon sampling can contribute to a better phylogenetic reconstruction. A third factor accounting for the differences between the studies could be the different methods and parameters used for the analysis of data. That said, the influence of IH and ILS still likely accounts for the only non-maximal support value in our phylogenomic tree, namely in the branch IV Galeropsidacea and deep divisions III to I. Qu *et al*. (2025) observed ILS also related to the placement of *Hydnangiaceae* outside VI Psathyrellacea in their phylogenetic tree. However, all the three other phylogenomic studies and also our study place *Hydnangiaceae* as part of VI Psathyrellacea.

Based on our study 26 families are recognised within the suborder *Agaricineae* (see "Guiding principles for delimiting families" and "Different options of family-level classification below"). The family-level classification mainly follows Kalichman *et al.* (2020) and He *et al.* (2024). The sensu stricto view of *Agaricaceae* proposed in Kalichman *et al.* (2020) is accepted here with the addition of *Podaxaceae*. The main changes proposed compared to Kalichman *et al.* (2020) and He *et al.* (2024) are in the "superfamily" I Strophariacea that was already considered as a problematic entity by both studies. Kalichman *et al.* (2020) proposed to treat the entity either as one large family or if retaining the use of the two existing family names, then at least one new family would need to be described; this was also confirmed by the phylogenetic estimate of He *et al.* (2024). Based on the phylogenomic data and morphological characters, we propose the entity to be divided into six families: *Agrocybaceae*, *Galerinaceae*, *Hymenogastraceae*, *Kuehneromycetaceae*, *Phaeocollybiaceae*, and *Strophariaceae*. The "superfamily" also includes a seventh family, *Chromocyphellaceae*, recognised in Kalichman *et al.* (2020), for which there are no genome-level data. The family includes cyphelloid species and its phylogenetic placement within I Strophariacea was found to be ambiguous in previous studies (Moreno *et al*. 2017, Tian & Matheny 2021). Further studies with -omics data are needed to determine its sister families within the "superfamily" I Strophariacea.

We also propose a new family for *Cyclocybe* and *Hemipholiota*. The family-level placement of the genus *Cyclocybe* had remained unresolved in the phylogenetic studies based on traditional genetic markers (Matheny *et al.* 2015). The phylogenomic study of He *et al.* (2024) and Wang *et al.* (2024) showed it to belong in "superfamily" II Inocybacea as a sister lineage of *Inocybe*, *Crepidotus*, and *Tubaria*. Our study is concordant with those studies and shows *Hemipholiota* as a sister genus of *Cyclocybe*. In addition, the family name *Podaxaceae* is taken up for *Podaxis* and *Macrolepiota*.

Finally, several families have been emended compared to the classification presented in Kalichman *et al.* (2020) and He *et al.* (2024) based on the current study and recent phylogenetic studies. A total of 190 genera is listed as accepted in suborder *Agaricineae*.

Eight deep divisions of suborder *Agaricineae* were indicated by our phylogenomic analysis. No official rank between the suborder and family exists and thus the groups are here recognised as informal "superfamilies": I Strophariacea, II Inocybacea, III Cortinariacea, IV Galeropsidacea, V Bolbitiacea, VI Psathyrellacea, VII Nidulariacea, and VIII Agaricacea. The "superfamilies" are created to better communicate the internal relationships and diversity of the group. VIII Agaricacea and I Strophariacea are the two largest "superfamilies" containing six families/77 genera, and six families/29 genera respectively.

Guiding principles for delimiting families

There are five guiding principles that we considered when trying to find an optimal family-level classification. These are tools for thinking about what to consider when trying to make a subjective decision about where to draw the limits of a family. None of them clearly

points to a single solution and, when applying them in practice, a single principle may be satisfied but the outcome may conflict with one or more of the other principles. Thus, the final decision depends on how the guiding principles are weighted in each case, considering the pros and cons of the outcome.

The first principle is commonly accepted for modern classification: a monophyletic group with strong support in phylogenetic analyses. In our case, based on the first category, we have all the options between only one family to having all genera in their own families since we obtained a well resolved phylogenetic tree with a probability value of 1 for all, except one (0.97) node (Fig.1). In practice, however, neither of these extreme options would be ideal, since one of the main purposes of taxonomic ranks is that a given rank should, whenever possible, contain some information about the grouping that is contained in neither the rank above nor the rank below.

Extending this idea, our second principle was to try to avoid monotypic families wherever possible. However, because of past evolution and extinction, it is clear that extant diversity is not evenly distributed. Therefore, there can be lineages that are worth recognizing at the family-level, even if they only include one genus. Also, the current intrafamilial knowledge and classification are not necessarily the final word.

The third principle was to aim for a classification with as few changes as possible. The fourth principle was to have approximately concordant limits for each family in the suborder so that the different traits show roughly equal amounts of variation within each family.

Finally, the fifth principle was to have groups with a unique combination of character states. These have traditionally mainly been morphological but can also be e.g. ecological, including nutritional mode. However, due to convergent evolution, having groups that can also be recognised based on morphology has become more challenging when the true relationships of taxa have been inferred based on DNA-data. The monophyletic groups presumably have shared evolutionary traits, but many of them can be characters that we have not yet observed, for example biochemical or enzymatic traits.

Different options for family-level classification

No matter how well we formulate our principles for delimiting families, we do not start our classification from scratch. There is always a history of what has been done in the past to consider. In the phylogenetic tree we produced, we recognised eight deep divisions (marked with Roman numerals in Fig. 1), which were further subdivided into progressively smaller groups, eventually leading to single genera. As a first step in our consideration of family-level classification, we used the third principle, which aims to present a classification with as few changes as possible. Six of the eight deep divisions contained more than one family name, and only divisions IV and V contained a single family, *Galeropsidaceae* and *Bolbitiaceae* respectively. Therefore, we concluded that deep divisions I–VIII did not reflect the current consensus of the family level in the suborder *Agaricineae* and thus we rejected the idea of labelling the deep divisions as families.

However, we wanted to provide a tool to communicate these deep divisions. In fungi and plants, there is no official rank between suborder and family (Turland *et al.* 2025). Thus, the options were to use an unofficial name for the divisions, or to consider elevating the current suborder *Agaricineae* to the order level so that the suborder-level names could be used for the divisions. Nomenclaturally, elevating the suborder to order level would be relatively easy, since many suborders of *Agaricales* already have valid order-level names, e.g. *Tricholomatales* Kühner, *Pluteales* Kühner, and *Fistulinales* Jülich. However, this would require a broader consideration of the classification of *Agaricales* which is beyond the scope of this study. Therefore, we decided to use informal names. We considered using clade names (e.g., /strophariacea) or "-oids" names (e.g., stropharioids) for the eight deep divisions, but we rejected these options because they give no indication of rank and are thus suboptimal for communication. Furthermore, "-oids" names do not always imply monophyly, as they can refer to non-monophyletic groups of species that share an, e.g. stropharioid appearance. In the end, we decided to introduce informal "superfamily" names for the clades to facilitate communication of the higher relationships within the suborder.

We then started to look at each "superfamily" separately to make the final decision on the families. In five "superfamilies", the current nine families already cover all genera, and they do not overlap with one another (Fig. 1, Table 1) and were therefore also accepted here: III Cortinariacea (incl. *Cortinariaceae*, *Crassisporiaceae*), IV Galeropsidacea (incl. *Galeropsidaceae*), V Bolbitiacea (incl. *Bolbitiaceae*), VI Psathyrellacea (incl. *Psathyrellaceae*, *Hydnangiaceae*, *Mythicomycetaceae*), and VII Nidulariacea (incl. *Nidulariaceae*, *Squamanitaceae*).

The "superfamily" I Strophariacea includes the two currently used family names *Hymenogastraceae* and *Strophariaceae*. Without any nomenclatural novelties, it would be treated as one family *Hymenogastraceae*, since the younger family *Strophariaceae* is nested within the clade and includes 25 genera. These 25 genera are not a homogeneous group, e.g. morphologically, and thus we also explored other options that did not retain all these genera in a single family.

We first examined the clade including *Strophariaceae* and *Hymenogastraceae*. These are morphologically distinct, non-monotypic entities that were already recognised as sensu stricto groups within *Hymenogastraceae* s. lato in Kalichman *et al.* (2020). Thus, their preservation as two separate families seemed the best solution. It also follows our principle five to have groups with a unique combination of character states, as well as principle four to have the limits of the families somewhat in concordance with others in the suborder, since in the "superfamilies" II–VII, the existing 12 families are rather small, compact units. When making this decision we also abandoned the option of *Hymenogastraceae* sensu lato.

Then, we further considered the branch leading to *Strophariaceae*. The upper part contains genera where most species have pleurocystidia or chrysocystidia, except *Flammula*, whereas the *Phaeogalera/Kuehneromyces/Deconica* clade includes species lacking pleurocystidia/chrysocystidia. Our options here would be to have: i) one family *Strophariaceae*, ii) two families, viz. *Strophariaceae* and *Kuehneromycetaceae*, and iii) three families, viz. *Strophariaceae*, *Flammulaceae* and *Kuehneromycetaceae*. If only considering morphology, option iii) could be chosen but if considering the existing names, option i) could be chosen. We chose option ii) because we wanted to recognise the morphological differences at family level, whilst avoiding the creation of a monotypic family.

The clade above the *Hymenogastraceae*/*Kuehneromycetaceae*/*Strophariaceae* group contains members that have previously been considered either to be in the family *Hymenogastraceae* or *Strophariaceae*. Here our options were to i) keep the groups as one family, ii) have two families: *Phaeocollybiaceae*, with the remainder forming another family, iii) have three families: *Phaeocollybiaceae*, *Agrocybaceae*, and *Galerinaceae*, or iv) split the group even further

into monotypic entities. Keeping all as one family would lead into an entity with significant variation, especially since the *Agrocybe*/*Psilocybe* clade stands out as being morphologically different. In order to have that clade separate, then the least disruptive option would be option iii), having three families, viz. *Phaeocollybiaceae*, *Agrocybaceae,* and *Galerinaceae*. We chose this third option.

Next, we considered the "superfamily" II Inocybacea that includes a monophyletic group consisting of *Hemipholiota* and *Cyclocybe* that fell outside the current classification. Based on the phylogenetic tree, our options were to: i) have one family *Crepidotaceae* (including *Crepidotaceae*, *Inocybaceae*, *Tubariaceae*, and /*Hemipholiota* & *Cyclocybe*), ii) keep the current families and describe one new family, or iii) keep the current families and describe two new families. Using the second principle to avoid monotypic families and the third principle to aim for a classification with as few changes as possible, we choose option ii).

Lastly, we examined the "superfamily" VIII Agaricacea that includes 77 genera. Kalichman *et al.* (2020) presented two options for the group based on earlier studies i) having all genera in one family *Agaricaceae* s. lat. or ii) having five families within the clade, viz. *Agaricaceae*, *Coprinaceae*, *Lepiotaceae* (correct name *Verrucosporaceae*), *Lycoperdaceae*, and *Tulostomataceae* (correct name *Battarreaceae*). During the past two years three larger studies on this group have been published by Kooij *et al.* (2024), Li *et al.* (2024), and Li *et al.* (2025). Of these, Kooij *et al.* (2024) kept *Agaricaceae* as one family and treated the internal units as tribes. Li *et al.* (2024) recognised seven families including those proposed by Kalichman *et al*. (2020), as well as *Mycenastraceae* Zeller and *Phelloriniaceae* Doweld. Li *et al.* (2025) recognised the same five families as Kalichman *et al.* (2020) and treated the monotypic *Mycenastraceae* as a synonym of *Lycoperdaceae,* and the *Phelloriniaceae* as a synonym of *Battarreaceae,* since these two are sister lineages and both include gasteroid species. When examining "superfamily" VIII in the context of the whole suborder and considering its diversity as well as the number of internal groups that have already been identified within it at family level, we decided to follow the five-family classification proposed in Kalichman *et al.* (2020) and in Li *et al.* (2025). We also propose for the time being to recognise *Podaxaceae* (including subfamilies *Macrolepioideae* and *Podaxioideae*) as its own family until its relationships within the "superfamily" have been fully resolved.

In the pre-DNA era, classification relied primarily on morphological characters, with groups regarded as natural based on their apparent morphological coherence. Nowadays, when we incorporate the latest knowledge about the relationships inferred from DNA data into our classification, compromises often need to be made. For macrofungi, groupings that make sense morphologically are preferable, but it is often tricky to achieve a balance between having smaller groups which are easily recognised morphologically, as opposed to larger groups, which are morphologically more diverse and challenging. When making these decisions it is important to consider name stability and how the size of any new groupings relates to those currently in use. Our proposed classification is a compromise of the five principles we presented initially, but we believe it is the best and most useful one for the group in question.

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DATA AVAILABILITY

The raw genome libraries of the 25 *Agaricineae* specimens sequenced for the present study are deposited in the European Nucleotide Archive (Study ID PRJNA1209105 and PRJNA1217492). Assemblies and alignments as well as associated data files are available on FigShare (doi: 10.6084/m9.figshare.30763751). The newly generated ITS and LSU regions are deposited with NCBI GenBank [accessions PX870832–PX870852 (ITS), PX869270–PX869287 (LSU)].

DECLARATION ON CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

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Supplementary Material: https://studiesinmycology.org/

Table S1. Specimens used for the phylogenomic analysis (rows 7 –105). Sequence data produced in this study marked in bold. *) *Inocybe corydalina* genome available at https://www.biorxiv.org/highwire/filestream/114780/field highwire adjunct files/6/374199-7.zip. Rows 108–135: Metadata (voucher number, fungarium, collection year, collection location) and GenBank numbers of the ITS and LSU regions of the specimens sequenced by us.

Table S2. Sequencing and assembly statistics for the 25 specimens sequenced in this study, as well as statistics and performance of the BUSCO genes extracted from the 91 genomes included in the phylogenomic analysis.